Evolutionary Relationships of the Discoglossoid Frogs-
Osteological Evidence

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ABSTRACT

B.T. Clarke. Evolutionary Relationships of the Discoglossoid Frogs - Osteological Evidence.

The discoglossoid Frogs (Discoglossidae and Leiopelmatidae) are generally considered to be the most primitive of the living frogs. Previous authors have grouped them on the basis of common possession of a limited number of primitive features of little phylogenetic significance, leaving the question of intra-discoglossoid relationships uncertain.

The present study is a re-examination of the supraspecific relationships in the superfamily using computer-aided cladistic analyses of a large set of osteological data - specifically 95 characters (153 binary characters) in 21 modern discoglossoid taxa. Where possible, characters are assigned a polarity, principally using urodeles as the outgroup. Evolutionary relationships are inferred from the congruence of cladograms generated from compatibility and parsimony analyses of the data set.

In an introductory section, modern approaches to systematic analysis and classification are reviewed and a justification for the chosen method is provided. The concepts of natural taxa and natural classifications are discussed, criteria for hypothesizing character polarities and accounts of compatibility and parsimony analysis methods are given.

A remarkable degree of congruence between the cladograms produced from a Le Quesne compatibility analysis and a Wagner parsimony analysis is evident. Results suggest:-

(a) The leiopelmatid genera _Ascaphus_ and _Leiopelma_ are a sister pair but are probably only weakly related.

(b) The modern Discoglossidae is a monophyletic group in which _Alytes_ is sister to _Bombina_ + _Barbourula_ + _Discoglossus_.

(c) _Discoglossus_ is sister to _Bombina_ + _Barbourula_.

(d) _Bombina_ and _Barbourula_ are a sister pair.

(e) All the discoglossoid genera are monophyletic.

(f) _Bombina_ comprises two species groups: small (_B. bombina_ - _B. variegata_ - _B. orientalis_) and large species (_B. maxima_ and _B. microdeladigitora_).

Comparisons are made with previous work and an overview hypothesis of the historical zoogeography of the discoglossoid frogs is presented.

CONTENTS

A. Introduction

1. INTRODUCTION

The modern discoglossoid frogs comprise two currently recognised families (Frost, 1985): the Discoglossidae Gunther 1858 and the Leiopelmatidae Mivart 1869, families which, since their inception, have almost universally been considered to include the most primitive of the living frogs. [Although Roček (1981) has put forward a classification for frogs in which the families Pipidae, Palaeobatrachidae (extinct: known only from fossils), Rhinophrynidae and the pelobatid genus *Pelobates* are assigned to the order Archaeosalientia and placed the remainder of the Anura (= all other frogs including the discoglossoids) and the proanuran fossil *Triadobatrachus* in a second order, the Neosalientia]. The higher level classification of the Anura is still a matter of some debate, yet most authorities recognise the Discoglossidae + Leiopelmatidae as a separate group at superfamily level - as the Discoglossoidae Gunther 1858 - e.g. Duellman (1975), Laurent (1979) and Dubois (1983, 1984).

Sokol (1977) went one step further in recognising the discoglossoids as a separate group than did Duellman (1975) et. al. cited above. He divided the modern Anura into two suborders - the Discoglossoidei (= Discoglossoidea) and the Ranoidei (= all other frogs). He distinguished the two on the basis of separate trigeminal and facial nerve ganglia and, as a "subsidiary character", the presence of free ribs (discoglossoid group) versus a fused condition of the two nerve ganglia into a single prootic ganglion, and free ribs lacking (at any stage of development *fide* Sokol). However, it should be noted that separate nerve ganglia and free ribs are conditions found in most fish (except some sharks) and in other vertebrates in general (Sokol 1977: 505; Lynch 1973: 114-115) and are therefore shared primitive features and consequently not (necessarily) indicative of close phylogenetic relationship.

The practice of grouping the two discoglossoid families into a single superfamily is, I would suggest, attributable to the fact that between 1865 and 1923 all the known discoglossoid species were included in a single family, the Discoglossidae (Boulenger 1897: 124; Stejneger 1899: 899). It is also clear that, since Cope (1865) first used the presence of free ribs to characterize the Discoglossidae, this feature has had considerable and unwarranted influence on all subsequent higher level classifications of the Anura. As noted above, common possession of "free" ribs (see character 57, this work) is a shared primitive condition and may not necessarily indicate close phylogenetic relationship (but may if the free ribs show special detailed resemblance not found in other groups). The grouping of the Discoglossidae withthe Leiopelmatidae into a superfamilial category is usually justified on the basis of a limited number of shared primitive characters (e.g. Boulenger 1897: 123 and more particularly Duellman 1975: 5) of which only one - the common possession of free ribs - is confined to adults of these two families. In fact, as far as I am aware, the only (questionable) evidence for the monophyly of the superfamily Discoglossoidae is that they share a derived type tadpole - Orton (1953) Type III, which Starrett (1968 and 1973) interestingly dubbed "lemmanuran" from the Greek lemma "an assumption or something taken for granted", because, while it had long been assumed that the discoglossoids were the most primitive of frogs, they share a type of tadpole which Starrett (1973) and later Sokol (1975) regarded as clearly derived. Even here the data is not clearcut for _Leiopelma_ (Leiopelmatidae) have either direct intracapsular development or a non-swimming, non-feeding larva that hatches with a tail, leading Savage (1973) to leave _Leiopelma_ placed in a category "suborder uncertain".

It seems clear that, even given Roček's 1981 classification of the Anura + Proanura, the discoglossoid group _is_ the most primitive of the modern frogs. Consequently the discoglossoid frogs are of particular interest in any serious consideration of the phylogeny of the Anura. While the monophyly of the discoglossoid frogs has yet to be satisfactorily established, they are provisionally recognized as a suitably and sufficiently closely related group for the present investigation into their phylogeny.

The position adopted is essentially the same as that expressed by Duellman/Trueb (1986: 468); that it is convenient to use for "the purposes of discussion, generally accepted suprafamilial categories..." with the "clear understanding that such categories are not necessarily monophyletic..." (see Section 4.2 on Cladistic analysis: Monophyly). The use here of 'discoglossoid' as a descriptor for the Discoglossoidae + Leiopelmatidae is one such convenient suprafamilial category and thus follows the usage of this term as specifically established in Duellman/Trueb (1986: 468).

Distribution

The modern discoglossoid frogs have a remarkably disjunct distribution. The discoglossids are a fairly small, predominantly European-based family which consists of four genera - Alytes and Discoglossus are found in western Europe and North Africa, with one species of Discoglossus in Israel; Bombina with a disjunct distribution - most of continental Europe (excluding the Iberian peninsula) and western Russia, China, Korea, eastern Siberia and Vietnam, and Barbourula from Borneo and two Philippine islands (Busuanga and Palawan). The leiopelmatids comprise two genera: Ascaphus, found in northwestern N. America including southwestern Canada (British Columbia), and Leiopelma from New Zealand. Distribution data are taken primarily from Clarke (and others) in Frost (1985) and Arnold and Burton (1978). Disjunct distributions are a characteristic of relictual faunas (Cox, Healey and Moore, 1973: 13-15); either evolutionary relicts or climatic relicts. While it is more likely that the present-day discoglossoids represent the remnants of an originally more widespread group (McCulloch 1919, Estes 1969, Estes and Reig 1973, Savage 1973, and Duellman/Trueb 1986) it is interesting to note that the majority of discoglossoid species are found in areas with temperate climatic conditions. Barbourula is an apparent exception (see below), although data on the microhabitat of members of this genus have yet to be presented.

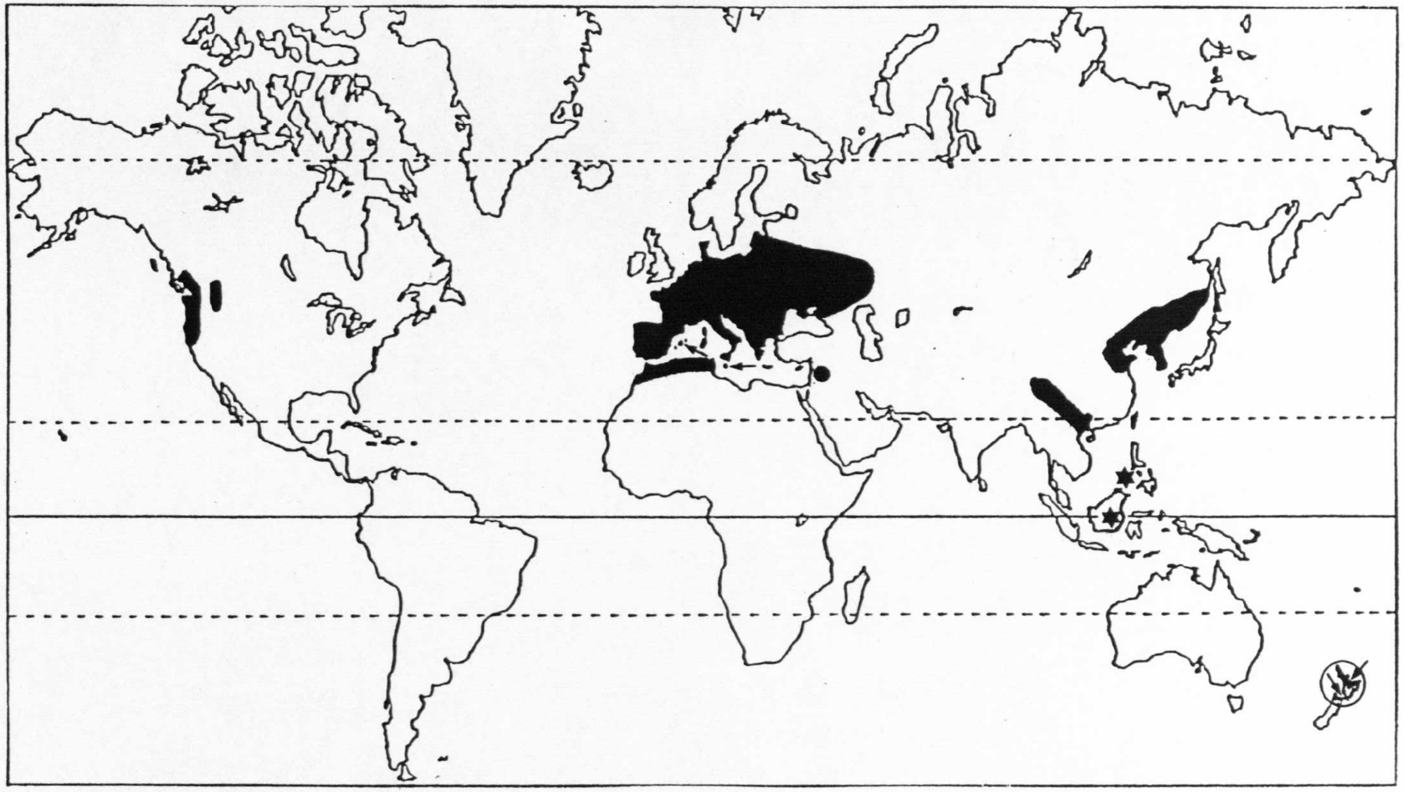


Fig. 1. Distribution of discoglossoid frogs (see text for details).

Historical background and content

While the origin of the name Discoglossidae is attributed to Gunther 1858 the first recognizably modern usage of the family name - to include *Alytes*, *Bombina*, *Discoglossus* and *Leiopelma* - was that of Cope (1865). Mivart (1869) used the name Liopelmatina as a family-group name for *Leiopelma hochstetteri* Fitzinger 1861, an action which was largely ignored by his contemporaries. Boulenger (1897) followed Cope's 1865 scheme which, as noted previously, was generally adopted until 1923. (Although Lataste 1879 had used Alytidae Fitzinger 1843 for *Alytes* Wagler 1830 on the basis of the shape of the pupil - vertical - and the unique breeding behaviour of members of this genus). In 1923 Fejervary erected the family Ascaphidae to accommodate *Ascaphus truei* Stejneger on the basis of the presence of the Nobelian cartilages in the "tail" (= male copulatory organ) and the presence of a caudaliopuboischiotibialis muscle previously only recorded in urodeles (fide Fejervary 1923). Yet curiously Fejervary omitted any mention of the relationship of *Leiopelma* in his discussion and emended classification (ibid: 181). Noble (1922) commented on the primitive nature of *Ascaphus* (it was from this Fejervary had obtained the reference to the caudeliopuboischiotibialis muscle). In 1924, Noble established the Leiopelmidae (= Leiopelmatidae) to accommodate both *Leiopelma* and *Ascaphus* (Noble 1924). Some authors, principally Savage (1973: 409), have been influenced primarily by the broadly disjunct distribution of *Ascaphus* and *Leiopelma* and also the direct development/non-comparable larval form of *Leiopelma*, and have recognized two separate families - Ascaphidae and Leiopelmatidae respectively - for these two genera. Most, however, have followed the move by Fawcett and Smith (1971: 51) to use the name Leiopelmatidae, an emended form of the family-group name Liopelmatina Mivart 1869 accepted by the International Commission on Zoological Nomenclature Opinion 1071 (1977), to include both *Ascaphus* and *Leiopelma*.

(a) Discoglossidae

The genus *Alytes* Wagler 1830 - the wellknown Midwife toads - comprises three species: *A. cisternasii* Boscá 1870, *A. muletensis* Sanchiz and Adrover 1979 [1977] and *A. obstetricans* (Laurenti 1768) - type species. *A. obstetricans* includes two subspecies in addition to the nominate form: *A. o. boscai* Lataste 1879 and *A. o. maurus* Pasteur and Bons 1962. As noted under Distribution above, the genus is confined to western Europe amd N. Africa. *A. cisternasii* is found in Portugal and W. and central Spain; *A. muletensis* in northern Majorca - originally described as a fossil and placed in a separate genus *Baleaphryne* Sanchiz and Adrover, 1979; *A. o. obstetricans* in Western Europe (Holland, Belgium, Luxemburg, France, Germany and Switzerland); *A. o. boscai* in Portugal and Spain - *A. o. obstetricans* may cross the Pyrenees into northern Spain - the status of Cantabrian *A. obstetricans* remains uncertain; *A. o. maurus* is found in Morocco. *Alytes* are small to moderate size frogs; adults approximately 30 to 55 mm snout-vent length (Boulenger 1897; Arnold and Burton, 1978, Mayol et al. 1984 and pers. obs.). The egg-carrying habit of male Midwife toads is well known, less well known is the variation in egg clutch size: 7 - 12 in *A. muletensis*, 35-95 in *A. obstetricans*, 42-119 in *A. cisternasii* (Alcover et al. 1984), and the habit of some males in taking on a second, perhaps even a third clutch of eggs. *A. cisternasii* and *A. obstetricans* are burrowers; some *A. obstetricans* are found in deep rock piles (especially *A. o. maurus*); *A. muletensis* is found only in certain deep gorges in northern Majorca - they are relatively long-limbed *Alytes* and have long fingers - they are particularly adept climbers (and crevice-dwellers, hence the reduced egg clutch) and are capable of hanging on to vertical surfaces in one position for protracted periods of time, at least two hours probably considerably longer, (pers. obs.). Adaptations to burrowing in *A. cisternasii* led Lataste (1879) to erect the genus *Ammoryctis* - a move dismissed by Boulenger (1897: 162). *A. muletensis* was originally described from fossil remains upon which basis a new genus *Baleaphryne* was established; a thorough examination (Hemmer and Alcover 1984; Maxson and Szymura 1984) suggests this species should be assigned to the genus *Alytes*, although some authors e.g. Hemmer (1984) have proposed retaining *Baleaphryne* as a subgenus of *Alytes.*

Barbourula Taylor and Noble 1924 includes only two species: *B. busuangensis* Taylor and Noble 1924 - the type species from Busuange and Palawan Islands, Philippines and *B. kalimantanensis* Iskandar 1978 known only from a single specimen from West Kalimantan, Borneo. *Barbourula* species are amongst the largest of the discoglossoids: Myers (1943) gave the largest adult he examined as 88 mm snout-vent length; Iskandar (1978) gave the SVL of the male holotype of *B. kalimantanensis* as 68.0 mm. Both species are highly aquatic (Taylor and Noble 1924, Myers 1943, Iskandar 1978) and have completely webbed fingers and toes and a free nasolacrimal papilla beneath the eye (also found in the highly aquatic pipids,genus *Xenopus*). *B. kalimantensis* shows extreme flattening of the head and body; probably both it and *B. busuangensis* take refuge under submerged boulders. Duellman and Salthe(1973: 232-235)note a clutch size of ca. 80 eggs with an individual ovum diameter of 5-6 mm. Despite Lynch's (1973: 168)contradictory statements, "(26) larvae aquatic, *Barbourula* in stage II ... (27) ... (larvae of *Barbourula* not known)", the life history of *Barbourula* remains unknown - larval stage, direct development, parental care (?).

The genus *Bombina* Oken 1816 - the Fire - and Yellow-Bellied Toads - comprises some six species (see note below): *Bombina bombina* (Linnaeus 1761) type species, *B. variegata* (Linnaeus 1758), *B. orientalis* (Boulenger 1890), *B. maxima* (Boulenger 1905), *B. microdeladigitora* Liu, Hu and Yang 1960 and *B. fortinuptialis* Tian and Wu 1981. For *B. variegata* Mertens and Wermuth (1960) recognize three subspecies in addition to the nominate form: *B. v. kolombatovici* (Bedriaga 1890), Dalmatian coastal region, Yugoslavia; *B. v. scabra* Kuster 1843, S. Balkans - Albania, Bulgaria, Macedonia, Rumania and *B. v. pachypus* (Bonaparte 1838), S. of Po Basin, Italy and Sicily. Nascetti, Vanni, Bullini and Lanza (1982) have suggested on immunological grounds that *B. v. pachypus* should be considered a full species. As noted under Distribution above, the genus has a disjunct distribution. *B. bombina* is found principally in Eastern Europe, as far south at N. Yugoslavia and Bulgaria and east into western USSR, also southern Sweden, Denmark, Western Germany and Turkey (it has been re-introduced into Sweden where natural population are probably extinct, and is rare in Denmark - six small populations-J. B. Rasmussen, E. Wederkinch pers. comn.). *B. variegata* is found in most of west, central and southern continental Europe but not in the north nor in the Iberian Peninsula, its easterly limit is in the Carpathian Mountains in the USSR. The remaining species are found in the East: *B. orientalis* in the Soviet Far East (eastern Siberia), northeastern China and Korea; *B. maxima* in Yunnan and Sichuan Provinces, China and N. Vietnam; *B. microdeladigitora* in Yunnan and Hubei Provinces, China and *B. fortinuptialis* in Guangxi Province, China. The two European species, *B. bombina* and *B. variegata* have long been known to produce natural hybrids in regions where their distribution overlaps (Boulenger 1897: 141). As far as is known all species of *Bombina* are aquatic (but may also be found on land usually near small bodies of water especially ponds and small lakes), and all lay their eggs singly or in small groups, one female producing in the region of 80 - 100 eggs (each approximately 3 mm in diameter: Boulenger 1897; Salthe and Duellman 1973), followed by a normal aquatic larval stage. Tian and Hu (1985) placed the larger eastern species in a separate genus *Glandula*, leaving *B. bombina*, *B. variegata* and *B. orientalis* in the nominate subgenus *Bombina*. The name *Glandula* is preoccupied by *Glandula* Stimpson 1852; Dubois (1986) consequently proposed *Grobina* as a replacement name. *Grobina* species rival *Barbourula* in size, up to 80 + mm. All *Bombina* have brightly coloured bellies although the underside may be almost completely black in some European *Bombina* (Boulenger 1897: Pl. VI, and Arnold and Burton 1978).

Discoglossus Otth 1827, as presently conceived - Lanza, Nascetti, Capula and Bullini, 1984 and Clarke and Lanza (in prep.) - comprises five species: *D. pictus* Otth 1837, type species; *D. sardus* Tschudi 1837; *D. galganoi* Capula, Nascetti, Lanza, Bullini and Crespo 1985; *D. montalentii* Lanza, Nascetti, Capula and Bullini 1984 and *D. nigriventer* Mendelssohn and Steinitz 1943. Lanza et al. (1984) suggested *D. scovazzi* Camerano 1878 is a subspecies of *D. pictus*, and Lanza in Clarke and Lanza (in prep.) suggests that *D. jeanneae* Busack 1986 is a subspecies of *D. galganoi*. In broad terms, *Discoglossus* species may be thought of as having an almost circum-Mediterranean distribution. *D. pictus* is found in Sicily, Malta and the eastern Pyrenees (with *D. p. scovazzi* in N. Africa - Tunisia, Algeria and Morocco); *D. sardus* in Sardinia, Corsica, Giglio, Montecristo, and Argentario (Tuscany); *D. galganoi* north of the Guadelquivir River basin in Spain with *D. g. jeanneae* to the south of this area in Spain (Busack 1986); *D. montalentii* from Corsica sympatrically with *D. sardus* in the area around Evisa, and *D. nigriventer* from Israel, Lake Huleh region - possibly extinct - ? in adjacent parts of Syria. (Honegger 1980-81: 142). *Discoglossus* are apparently always found either in, or around water, either still or running, usually in the shallow regions in ponds or streams; they are able to tolerate brackish water. Between 300 and 1000 small eggs are produced, each approximately 2 mm in diameter (Boulenger 1897; Salthe and Duellman 1973). *Discoglossus* are also among the larger of the discoglossoid species and may exceed 70 mm SVL.

(b) *Leiopelmatidae*

The genus *Ascaphus* Stejneger 1899 contains only one species *A. truei* Stejneger 1899 (type species by monotypy) - the so-called Tailed Frog, the "tail", found only in the male, actually being a copulatory organ. Mittleman and Myers (1949) differentiated and described two subspecies -

A. t. californicus and *A. t. montanus* - in addition to the nominate form. Myers (1952) questioned the validity of these subspecies and Metter (1964, 1967 and 1968) after examination of larger samples frommore sites within the range concluded that there is no reason to justify recognition of spearate subspecies. As Ritland (1955: 279) has commented, few frogs are more highly specialized for life in such a unique habitat. *Ascaphus* live in and around the mountain streams in two large, separated areas of northwestern North America and extreme southwestern Canada. The main part of the range is the mountains from northern California north to Bute Inlet, British Colombia; the second part of its range includes the mountains of southeastern Washington, northeastern Oregon, Idaho and western Montana extending north just into British Colombia (Metter, 1968, Green and Campbell 1984). They are usually found under stones or rocks by fast flowing streams or in nearby pools or rivulets where the water is very cold - rarely more than 4 or 5°C even on warm days (van Denburgh 1912; Gaige 1920, Green and Campbell 1984). *Ascaphus* are small to moderate size frogs: 30 - 50 mm SVL. The male uses the tail for insemination ; mating takes place in the autumn, the female stores the sperm in her oriduct, and thus practices internal fertilization. The eggs, some 35 to 50, each approximately 5 mm in diameter are laid in a twisted string forming a circular mass, usually attached to the underside of a submerged stone (Gaige ibid., Salthe and Duellman 1973). The tadpoles are highly adapted to life in cold, fast flowing streams; in such temperatures development is slow and take 3 years to transform, reproductive maturity is not attained until the frogs are seven to nine years old; estimated maximum life span 15-20 years (Daugherty and Sheldon 1982).

Leiopelma Fitzinger 1861 includes only three extant species: *L. archeyi* Turbott 1942, *L. hamiltoni* McCulloch 1919 and *L. hochstetteri* Fitzinger 1861, the type species. All three are found in New Zealand - its only (living) native anurans (amphibians). *L. archeyi* and *L. hochstetteri* are

are both found on North Island where they are sympatric on the Coromandel Peninsula; *L. archeyi* is confined to the Cape Colville Range on the Coromandel Peninsula whereas *L. hochstetteri* is also found on the Rangitoto Range and also found from Warkworth in the north, south and east to Te Araroa (Stephenson and Stephenson 1957) and on Great Barrier Island. *L. hamiltoni* is found only on Maud Island and Stephens Island (where the total population is restricted to a rock pile known as "Frog Bank"), in the Cook Strait. While there are discontinuities in the ranges of each of the three species, none of the isolated populations have been regarded as sifficiently different to warrant recognition as separate subspecies. (The *L. archeyi* on Mt. Moehau may be smaller than are other *L. archeyi*; *L. hamiltoni* on Stephens Island tend to be paler than those on Maud Island; the *L. hochstetteri* on Great Barrier Island are not obviously different from other *L. hochstetteri*; - Bell 1982). *L. hochstetteri* is the only one of the three species which is usually found close to water, under flat stones or fallen vegetation, along seepage areas by the abnks of streams; *L. archeyi* may be found near stream banks or in marshy areas but is generally found under stone or rotting logs or moss-covered mountain ridges, areas which are usually shrouded in mist or cloud and consequently have a humid atmosphere; *L. hamiltoni* take cover in the rock pile of Frog Bank on Stephens Island and need an atmosphere where the rocks are moss-covered to thrive, typically the bank is misty and humid. On Maud Island *L. hamiltoni* is found amongst dead leaves and other decaying vegetation (Robb, 1986). There is clearly a strong correlation between habitat and mode of reproduction in the three species. Bell (1985) described their breeding behaviour and development in some detail. *L. hochstetteri* females lay 10-22 large eggs, some 5-6 mm in diameter and males may be found near, but not in close association, with the eggs, which are laid in seepage areas. *L. archeyi* and *L. hamiltoni* lay their eggs in moist or fairly dry sites under cover on the forest floor - 1-13 eggs, 4-5 mm in diameter in *L. archeyi*; 2-19 eggs, 5-6 mm in diameter in *L. hamiltoni*. Eggs hatch at a fairly early stage in *L. hochstetteri*, and the larvae is more adapted to an aquatic existence, they are able swimmers and are not associated with the male. In *L. archeyi* and *L. hamiltoni* the males exhibit a form of parental care: the larvae are less adapted to an aquatic life and are less able swimmers and climb onto the back of the male where they remain until metamorphosis is complete (Bell ibid.: 274, Fig. 4). *Leiopelma* are moderate size frogs, 30-36 mm SVL in *L. archeyi*, up to just under 50 mm SVL in *L. hochstetteri* and *L. hamiltoni*.

2. AIMS AND OBJECTIVES

The principal aims of the investigation are to identify natural supraspecific groups within the discoglossoid frogs and to infer the evolutionary relationships betwen such groups using comparative morphological criteria.

This study follows Gaudin (1969) in adopting, as a working s assumption, the principle that a detailed analysis of the skeletal morphology of a group should be valuable in elucidating the evolutionary relationships of the taxa within that group. The general approach adopted is to examine the skeletons of modern discoglossoid frogs in detail - literally from the tip of the snout (nasals) to the tips of the toes (terminal phalanges) - in order to obtain a large data set for phylogenetic analysis. The rationale behind this is that experience suggests, that in the case of relatively primitive taxa, there are relatively few shared derived characters available to provide an unequivocal hypothesis of phylogenetic relationship. Consequently, a large data set is more likely (than a smaller data set) to increase the possibility of finding these characters which allow a full/complete resolution of relationships. It is also a subsidiary aim of this work to survey discoglossoid skeletons for new characters; not only for (potentially) uniquely derived characters indicating close phylogenetic relationship, but also for characters which are likely to be informative about the mode of life of the taxa concerned. That is to say, while in a phylogenetic analysis like this, it is characters which provide evidence of evolutionary relationship which are of primary importance, independently derived functionally-related characters are also of interest - they are not 'lost' or 'non -' characters. In addition, it is only possible to differentiate between characters which indicate phylogenetic relationship from characters which are derived independently post-analysis.

This work is intended to be, as far as is possible, a "fresh" look at discoglossoid frogs, the main aim being, as suggested above, to obtain a full resolution of the relationships within the discoglossoid group. Drawings depicting osteological features are included where necessary, to supplement and clarify character state descriptions.

This investigation is concerned with discoglossoid frog relationships at the following levels:-

a) Intra - and intergeneric relationships within the Discoglossidae;

b) Intrageneric relationships in the genus Leiopelma (Note: Ascaphus is monotypic).

c) Relationships between Ascaphus, Leiopelma and the supraspecific groupings within the Discoglossidae (as currently understood).

Specifically, the objectives of this study are (using osteological data) :

1. To test the homogeneity (monophyly) of the Discoglossidae, i.e. to ascertain whether the currently recognised genera in this family constitute a natural assemblage.

2. To test the monophyly of the individual discoglossoid genera (the species comprising the respective currently recognised genera) to see if they constitute natural assemblages. While there is little reason to question the monophyly of the individual discoglossoid genera. There is still a need to establish the sister - group (cladistic) relationships at the species level.

3. To assess the relative phylogenetic proximity of the extant members of the two currently recognised discoglossoid families - with special reference to the relationships of Ascaphus and Leiopelma.

4. To infer primitive and derived character states ('plesiomorph' and 'apomorph' states respectively, of Hennig 1965, 1966) for the characters examined.

5. To infer morphological transformation series for these character states and suggest the 'polarity' or direction(s) of character state change within these series (using criteria given in Section 4.4 Character polarity).

6. To infer a phylogeny for the supraspecific groups recognised in the discoglossoid group.

7. To provide a definition for each of the generic or supraspecific groups recognised based only on uniquely derived characters ('unique' in the context of the Discoglossoidea Gunther 1858).

Testing the monophyly of the Discoglossoidea is not an objective of this study; this would require a full survey of the remainder of the Anura and is beyond the scope of the present study. Consequently, the Discoglossoidea can either be seen as a provisionally monophyletic group, or merely a defined assemblage of primitive frogs whose intra-relationships are under investigation. Then in 3. above the questions being addressed are - is Ascaphus more closely related to Leiopelma, or is one or the other more closely related to the other discoglossoid frogs?

3. Systematics : background

3.1 Modern approaches to systematic analysis and classification.

Mayr (1969: 55) commented that it is difficult to define classification without introducing circularity into the definition or "including terms that bias the definition in favour of a particular philosophy of classification". He suggested the following "tentative definition":- "Zoological classification is the ordering of animals into groups on the basis of their similarity and relationship (in the broadest, not necessarily biological meaning of the latter word)". Mayr (loc. cit.) noted that the two terms "similarity" and "relationship" used in his definition "are the reason for controversies that have raged for hundreds of years". The interpretation of these two terms depends on one's attitude/response to the proposition that the 'correct' reconstruction of the evolutionary history (phylogeny) of a group is an unattainable goal*, that is to say whether or not it is possible to reconstruct the evolutionary history of a group - since one can never <u>know</u> when that goal has been achieved (*see also Section4.5 Numerical cladistic analysis).

Simpson (1961: 7) defined systematics as "the scientific study of the kinds and diversity of organisms and of any and all relationships among them".

There are three main modern approaches to systematic analysis and classification, each differing in its interpretation of the term 'relationship' and in its response to the premise that knowledge of the phylogeny of a group is an unattainable goal (key references in brackets):-

1. <u>Phenetics</u> (Sokal and Sneath 1963: Sneath and Sokal 1973).
2. <u>Evolutionary Systematics</u> (Simpson 1961 and Mayr 1969; <u>"Simpsonian" Systematics</u> of Charig 1982).
3. <u>Cladistics</u>, presently indivisible into two schools:-
    a). <u>"Hennigian" cladistics</u> or <u>Phylogenetic Systematics</u> (Hennig 1965, 1966 and Wiley 1981).

b). <u>"Transformed" cladistics</u> (Platnick 1980, Patterson 1980 and Nelson and Platnick 1981; <u>"Natural Order Systematics"</u> of Charig 1982). There is, in addition to the 'key' works cited above, an extensive literature on each of the three main approaches to systematic analysis. Consequently this section will include only a brief resumé on each approach.

<u>Phenetics</u>

The development of phenetics was a response to a feeling of dissatisfaction with taxonomic procedures at the time (late 1950's to early 1960's). Sokal and Sneath published their "Principles of Numerical Taxonomy" in 1963 and remarked (p.9) that "Contemporary taxonomy, while progressive in the establishment and revision of taxa, is decidedly conservative in its practices and philosophy. Published systematic work at the generic level and above is little different from that at the turn of the century". Sokal and Sneath's 1963 book was a landmark publication in the philosophy of systematics as well as a description of a new method of systematic analysis. They admired "The New Systematics" (Ed. J. Huxley, 1940) and associated literature, saying that it was progress at the species and infraspecies levels but it was apparent that there was (up to 1963 at least) "little increase in our understanding of the nature and evolution of higher categories". (Sokal and Sneath 1963: 5). Their "Principles of Numerical Taxonomy" was intended to be a "New Systematics" for the higher categories. They saw the main faults of taxonomy as a consequence of attempting to fulfil too many functions and so performing none of these functions well. Taxonomy, they said (p.6), attempted "(1) to classify, (2) to name, (3) to indicate degree of resemblance (affinity), and (4) to show relationship by descent - all at the same time". Sokal and Sneath (loc. cit.) also noted "an important logical fallacy" in contemporary taxonomic procedure, namely the use of a self re-inforcing circular argument to establish categories, which on repetition gave the semblance of a method with "objective and definable reality". The circular reasoning arose from the fact that new characters were being prejudiced on the basis of their agreement with the existing systematic arrangement or classification, which was merely based on a different character set. (It is interesting to note that evolutionary systematists see this as a positive feature of their method (Mayr 1969: 208) - cf. section on 'Evolutionary Systematics' below). Sokal and Sneath went on to comment (p.7) that the Taxonomists' "sound knowledge is usually restricted to an estimate of resemblance of a number of organisms without any knowledge of phylogeny andhence common origin of their characters" and that "Once it is looked at critically, it becomes evident how much of Taxonomic procedure is circular reasoning and extrapolation".

Modern phenetic taxonomy (see Sneath 1971 and Sneath and Sokal 1973) insists on the strict separation of phenetic from phylogenetic considerations in taxonomy. To a pheneticist consideration of the proposition that phylogeny is an unattainable goal leads to the conclusion that it may not be used as a basis for classification. Grouping and ranking of taxa is by some stated measure of overall similarity or difference or some measure of relationship between pairs or sets of operational taxonomic units (OTU'S). Characters are classically given equal weight although some of the more modern numerical taxonomic techniques (computer programs) include a scheme for weighting characters. The information content of a phenetic classification is related to the number of characters used in its construction (within limits, i.e. subject to the Law of Diminishing Returns).

Evolutionary Systematics

Mayr (1969: 198), like Sokal and Sneath before him, noted that there had been considerable progress in taxonomy at the species level but less at higher taxonomic levels. While Sokal and Sneath had hoped that their 'Principles of Numerical Taxonomy' would be a 'New Systematics' for higher categories, Mayr commented "We are still waiting for a new systematics of macrotaxonomy, even though recent work represents significant forays into this terra incognita". Mayr went on to say that there was a need for a greater interest in taxonomic method and that he considered that the new interest in methodology "aroused by Hennig, Cain, Michner, Simpson, and the numerical pheneticists....." would produce "as much of an advance on the level of macrotaxonomy as the new systematics did on the species level".

The evolutionary taxonomist may accept that knowledge of the phylogeny of a group is an unattainable goal yet considers it worthwhile to attempt to reconstruct the evolutionary history of a group. 'Relationship' for an evolutionary biologist means "inferred genetic similarity" (Mayr ibid: 200). Most accept the importance of using shared derived characters ('synapomorphies' of the Hennigian cladist) in determining branching patterns in the evolutionary history of a group, in other words a cladistic analysis, but will not accept the direct translation of this into a cladistic classification (e.g. Mayr 1969, 1974 and Charig 1982). This is because evolutionary systematics attempt to include divergence as well as branching sequence (cladistic) data in their classifications. The aim is to give a more complete representation of the evolutionary history of a group. (See also Section 3.3 on Clades, grades, evolutionary processes and the problems of phylogenetic reconstruction in relatively primitive groups). The "important logical fallacy" in contemporary taxonomic procedure mentioned by Sokal and Sneath (1963: 6) is usually taken to be a positive feature of evolutionary systematics. As Mayr (1969: 208) said "When a new set of characters is utilized, it will have one of three possible effects on the existing classification. The new characters either confirm the traditional classification (this being what usually happens), or lead to a clear improvement of the classification, or introduce ambiguity and contradiction which can be resolved by the application of additional new characters".

This is in stark contrast to the phenetic viewpoint (cf. section on 'Phenetics' above) which regards this as an example of undesirable circularity and symptomatic of the subjective nature of evolutionary systematics. In fact as Ridley (1986) has pointed out there has been some confusion of circular reasoning with the procedure of successive approximation (Hull 1967) or 'reciprocal illumination' (Hennig 1966). The process of using new characters to test an existing classification is <u>not</u> an example of circular reasoning "but a normal scientific sequence of an initial crude hypothesis, a test, a hypothetical extrapolation, a further test, and so on. It is a process of theory-building" (Ridley 1986: 27).

Hennigian cladistics (Phylogenetic Systematics)

The basic principles of cladistics were set out by Hennig in his 1950 book 'Grundzuge einer Theorie der Phylogenetischen Systematik', which made little impact on taxonomy in the English-speaking areas of the world, until 1966 when a revised version 'Phylogenetic Systematics' was published. The preface of the 1966 translation noted that not only had the work been extensively revised but much of it had been completely rewritten, and that it was from the revised, rewritten manuscript that the 1966 book was prepared. The clearest, most straightforward exposition of Hennig's principles of cladistic systematics was given by Hennig himself in his rarely quoted, almost overlooked 1965 paper (Hennig 1965: 97-116). The literature on cladistic theory, including criticisms, critiques and re-interpretations, is now immense; some of Hennig's work has been translated (e.g. Hennig 1960 translated as Hennig 1966b by P. Wygodzinsky); some important work has still to be translated. In the latter category Hennig (1969) 'Die Stammegeseschichte der Inseckten' considered by Patterson (1982) as probably one of Hennig's most important contributions, the impact of which is still to be felt in Entomology, and which will also be significant to the conduct of phylogeny reconstruction in other groups of organisms.

Hennigian cladists, like evolutionary systematists accept that phylogeny is unknowable, that one can never know if one has managed to reconstruct the actual branching sequence component of the evolutionary history of a group. Nonetheless, like evolutionary systematists, they consider that "testable hypotheses of phylogeny.... can be generated through appropriate handling of data on living organisms" (Kavanaugh 1978: 141). 'Relationship' to a Hennigian cladist means genealogical relationship. Hennig defined relationship using branching pattern, he saw the branching diagrams or 'cladograms' produced by the application of his method as evolutionary trees. Grouping of taxa is based on strict monophyly (see section on Cladistic analysis), that is, on recency of common ancestry. Ranking of taxa is therefore dependant on age rather than on phenetic similarity. The resulting classification is a direct translation of the cladogram, the information content of such a classification is "proportional to the degree to which it reflects phylogeny". (Kavanaugh 1978: 141).

Transformed cladistics (Natural Order Systematics)

Criticism of the evolutionary component of Hennigian cladistics led to a questioning of the need for an evolutionary interpretation of Hennig's method. Platnick (1980), in what may be regarded as the founding paper on transformed cladistics-"Philosophy and the transformation of cladistics"-drew attention to a paper presented by David Hull at the 1977 meeting of the Society of Systematic Zoology (later published as Hull 1979), in which Hull distinguished early views of cladistics as a means of reconstructing phylogeny (i.e. Hennigian cladistics) from later more general views of cladistics "as a means of discerning natural order in any system that involves some sort of descent with modification" (Platnick 1980: 537). This latter view of cladistics has developed into transformed cladistics or as Charig (1982: 368) prefers to call it 'natural order systematics'. As Patterson (1980: 239) succinctly put it "...it has been realized that more and more of the evolutionary framework is inessential..." (to a 'successful' 'cladistic' analysis) and that "the transformation is away from dependence on evolutionary theory".

Transformed cladists do not directly concern themselves with the proposition that phylogeny is an unattainable goal - the possibility or otherwise of reconstructing the evolutionary history of a group - because as Patterson (1980: 239) said "cladistics, as I have tried to show, is not necessarily about evolution..... It is about a simpler and more basic matter, the pattern in nature...." This pattern, the pattern of character distribution is, according to the transformed cladistic viewpoint, basic to an understanding of the process of evolution. Platnick (1980: 546) commented "we are hardly likely to achieve any understanding of the evolutionary process until we have achieved an understanding of the patterns produced by that process, and that even today we have hardly begun to understand the patterns". Grouping and ranking of taxa is by maximal character congruence or parsimony, the characters producing nested sets of organisms in a hierarchical arrangement. Classification consists of naming the nested sets of organisms (=taxa) and ranking them according to their position in the hierarchy.

Dawkins (1986; Chapter 10 "The one true tree of life", especially p. 279 - 284) provides brief criticism of transformed cladistics. Ridley (1986) gives a reasoned critique of the school in his book on "Evolution and Classification - The reformation of cladism".

3.2 Natural taxa and natural classifications

One of the most consistent trends in modern taxonomy has been the search for 'natural' groups. Advocates of each of the respective modern approaches to systematic analysis and classification claim that their method is to be preferred because it in some way identifies 'natural' taxa or groups which may therefore be used to construct the most 'natural' classifications. To a taxonomist there are two kinds of naturalness, which are not necessarily mutually exclusive: naturalness due to high information content and naturalness due to phylogenetic (genealogical) relationship. Phenetic, and to some extent transformed cladistic classifications, rely on some measure of high information content as a criterion of naturalness, whereas evolutionary systematics and Hennigian cladistics rely on phylogenetic relationship for their naturalness. Wiley (1981: 71) identified phenetic naturalness and phylogenetic naturalness; on the grounds of essential similarity of method, I would suggest that one may group transformed cladistic with phenetic naturalness.

According to Wiley (loc. cit.) a taxon exhibits phenetic naturalness if it is composed of members that resemble each other more than any nongroup member, i.e. if all the members are (phenetically) more similar to each other than anything outside the group. Pheneticists, like Sokal and Sneath (1963) and McNeil (1980, 1982), have followed the concept of naturalness as advanced by Gilmour (1937, 1940, 1951, 1961). Gilmour suggested that a natural classification would contain taxa that would explain the distribution of as many characters as possible. Hence Gilmour's dictum:- "a system of classification is the more natural the more propositions there are that can be made regarding its constituent classes". It should be noted that Gilmour's concept of naturalness may also be applied to phylogenetic classifications. The high information content estimate of naturalness is equally applicable to transformed cladistic classifications; indeed this school of systematics is actively seeking 'natural' classifications - as indicated by its alternative name 'natural order of systematics'. Character selection is followed by the arrangement of the organisms under consideration into nested hierarchical sets, where one particular arrangement is preferred over any other on the basis of maximal character congruence and parsimony.

Wiley (1981: 71 et seq.) was more concerned with phylogenetic naturalness. He considered that a taxon exhibits phylogenetic naturalness if its members share a common ancestor which is not ancestral to any other group, that is if they are thought to be phylogenetically related. Wiley went on to define 'the natural taxon' and consider its properties and those of a natural higher taxon. For Wiley a natural taxon is one which "exists in nature independant of man's ability to perceive it", in other words a natural taxon possesses objective reality. Wiley said that his definition carried specific connotations, these are:-

" 1. Natural taxa exist whether or not there are any systematists around to perceive or name them."

" 2. Because they exist in nature, natural taxa must be discovered, they cannot be invented. "

" 3. Natural taxa originate according to natural processes and thus must be consistent with these natural processes."

" 4. When we propose natural taxa, that is, when we hypothesize that a particular grouping is natural, we invoke all of the connotations implied in 1-3".

Wiley (1978, 1981) differentiated between species and natural higher taxa. For Wiley, species are individuals in the sense that they are restricted in space and time. They also possess cohesion and continuity - they participate in evolutionary processes and are historically connected, i.e. members of a species share a common origin in some previous population. In contrast, Wiley considered natural higher taxa to be historical groups: "species are units of evolution, and higher taxa containing more than one species are not units of evolution.... rather, natural supraspecific taxa are units of history" (Wiley, 1981: 75). He explained that natural supraspecific taxa are restricted in space and time but do not participate in natural (evolutionary) processes although they are composed of units (species) which do participate in such processes. Wiley's assertions that the species is the unit of evolution cannot be allowed to pass without comment. Since the publication of 'The New Systematics' in 1940 there has been a great deal of debate on the unit of evolution. The debate is really concerned with the level at which selection operates. It is easy to see that selection operates below the species level and that in most cases, the species is <u>not</u> the unit of evolution. One may reasonably put forward and defend the idea that the species <u>per se</u> is, and behaves like, a 'higher' taxon. Alternative candidates for the unit of evolution include the deme, the individual and the gene. The deme - a term originally proposed by Gilmour and McGregor (1939), later refined by Simpson (1953) and Mayr (1969) - is a local population of a species, a community of potentially interbreeding individuals at a given locality (Mayr 1969: 401). In situations where a species distribution is restricted to a single locality, the deme will be equivalent to the species. The concept of the individual as the unit of evolution has been attributed to Darwin (1859). Hamilton (1964a and b) put forward the idea that an individual organism behaves in such a way that it benefits its own inclusive fitness, in other words organisms attempt to "maximize the survival of copies of the genes inside them" (Dawkins 1982: 55). Inclusive fitness is a measure of the reproductive success of an organism. Dawkins (1976, 1982) elaborated and popularized Hamilton's ideas but came to the conclusion that the gene should be thought of as the unit of selection, although he does not deny the importance of the individual (Dawkins 1982: 6 and 251). He commented "If individual organisms can be assumed to work for the aggregate benefit of all their genes, it doesn't matter whether we think in terms of genes working to ensure their survival, or of individuals working to maximize their inclusive fitness" (ibid. : 188). I suggest that the gene should be thought of as the unit of selection and the individual the unit of evolution, since selection may act on the frequency of individual genes within a gene pool but evolution is concerned with the interaction of the phenotype of an organism and its environment.

Just as the nature of a classification depends upon its purpose, so consideration of the level at which selection or evolution operates depends upon the purpose at hand. When one is concerned with higher taxonomic relationships it is usually more appropriate to consider organisms at the species level. (Nonetheless, it should be remembered that in other situations(at other taxonomic levels) different groups will be more appropriate - at low taxonomic levels the deme may be more significant). Most attempts at phylogenetic reconstruction, however, are concerned primarily with interspecific relationships and thereafter with relationships at increasingly higher taxonomic levels. The present study is no exception. It is an attempt to determine the phylogenetic (evolutionary) relationships within each of the supraspecific discoglossid taxa, between these supraspecific groups, and finally to ascertain the relationship between the discoglossid taxa and the remaining discoglossoid genera, *Ascaphus* and *Leiopelma*. Nonetheless it should be borne in mind that this study is one which deals with the evolutionary relationships of living organisms and not merely with the patterns of their character state distributions (see section33on Clades, grades, evolutionary processes and the problems of phylogenetic reconstruction in relatively primitive groups). It is therefore important to remember that although results are expressed in terms of species, the actual evolving units are the demes comprising these species, the individuals themselves and their genes (gene pools).

3.3 Clades, grades, evolutionary processes and the problems of phylogenetic reconstruction in relatively primitive groups.

Sir Julian Huxley, one of the most able and perceptive writers on evolutionary topics identified three main types of evolutionary processes - anagenesis, cladogenesis and stasigenesis (Huxley 1959). Anagenesis produces biological improvement e.g. adaptation to a particular differentiation of function, or some other kind of increase in efficiency. Cladogenesis gives rise to diversification, the production of splitting within "a single stock or group at any level" and results in the divergence of the separated forms so produced. Stasigenesis is probably the most overlooked of the three evolutionary processes and results in persistence - the maintenance of a form or group of any size against the effects of varying conditions (selection pressures).

Huxley pointed out that the interaction of these processes produces forms or groups which undergo some form of biological improvement, become successful, spread and split up into new forms which may maintain their "new form of organisation" under differing environmental conditions. Thus new groups appear "each characterized by a definite step forward in evolution, and each therefore recognizable as a distinct grade of organisation". The point is that several of these groups may advance in the same direction and "reach the same improved state, simultaneously or successively". We would now say these groups have developed in parallel (or convergently depending upon our estimation of the recency of their common ancestry). These groups may be recognized as a grade - "a group of animals similar in level of organization; a level of anagenetic advance" (Mayr 1969) in contradistinction to a clade - "a delimitable monophyletic unit" (Huxley 1957). The use of more general, that is, widely distributed character states will greatly increase the chances of producing a grade-level classification which will not include phylogenetically closer forms which have not yet reached the same improved state or have diverged in a different direction.

Such a classification will consist of paraphyletic or even polyphyletic groups. I would agree with Huxley (1959) that "Such groups are of evolutionary interest...." but would agree more readily with his contention that using "A double system of categories," (of clades and grades) "expressing anagenetic level and cladogenetic divergence, would be more adequate for setting out the evolutionary facts".

One of the main problems with current attempts with the systematic analysis of relatively primitive groups is the persistent use of characters with a more general distribution, i.e. grade-level or primitive characters. All the use of these characters does is testify to the primitive status of the taxa in question and allow us to rank them with respect to their level of organization. In order to obtain information on the genealogy of a group - the number and sequence of phyletic splits in its evolutionary history - we need to use characters with a more limited distribution, and not just those with a limited distribution but ones which we can reasonably/confidently hypothesize to be uniquely derived, that is, to have evolved only once in the history of the group, without subsequent reversal (to a pseudoprimitive state). This is the uniquely derived character concept of Le Quesne (1969, 1972, 1979, 1982). In this way information on the results of the process of cladogenesis is obtained in the form of synapomorphies which allow us to hypothesize monophyletic (holophyletic) groups and their sister group relationships.

There are three main problems associated with attempting to infer the phylogeny of relatively primitive groups: (i) finding, as Arnold (1981) put it, "Enough derived features, with appropriate distributions".
(ii) distinguishing minority primitive from minority derived states
(iii) selection of an appropriate outgroup or outgroups for making outgroup comparisons.

(i) <u>Finding enough derived features, with appropriate distributions</u>

To paraphrase Arnold (1981: 5) a cladistic analysis can only give a complete resolution of a phylogeny if there are enough synapomorphies and if these are distributed such that all sister group pairs are defined. To this end the minimal requirement is a single well-founded synapomorphy for each sister group pair - as Hecht and Edwards (1977: 13) pointed out, criticizing Heyer (1975), Marx and Rabb (1970) and Kluge and Farris (1969) for the practice of using "great numbers of characters..." to "override the few mistaken parallelisms" - "They all failed to realize that, in the recognition of branching points in a phylogeny, only one reliable character is necessary to indicate lineage". Hecht and Edwards (loc. cit.) actually went so far as to say "We feel that it is better to use fewer well-interpreted morphoclines than to allow obfuscation by mere quantity". They suggested the use of character weighting to resolve character conflicts. In the present study a different view is taken - our knowledge of characters is rarely such that so high a level of confidence can be accorded to any one character. Consequently large numbers of characters are used, not merely in the hope that this will outweigh character conflicts due to parallelism (homoplasy), but in order to find a large set of compatible characters - a clique of uniquely derived characters - from which a robust phylogenetic dendrogram may be inferred.

There is an implicit general view that the chances of finding enough derived features with appropriate distributions to permit a reasonable phylogenetic reconstruction are low in the case of relatively more primitive groups. The idea is that most features will be primitive (plesiomorphic); there will be a few to many autapomorphies - uniquely derived features found only in a single lineage i.e. derived characters arising after a phyletic split - and that the few remaining characters in the data set will be synapomorphies providing (at best) equivocal evidence of the group's cladistic relationships. I would suggest this view is ill-founded for two reasons:-

(i) It is based on 'overview' analyses of the whole of the Anura e.g.

Duellman 1975, Sokol 1977 and Laurent 1979 which have over-emphasized the primitive attributes of the relatively primitive families and have produced grade level classifications of the Anura by employing the use of more primitive - less primitive characters instead of using synapomorphies as a basis for classification.

(ii) As Underwood (1982: 253) commented there is an "unsupported assumption that evolution proceeds from generalized to specialized...." (In general this may be so, yet this does not allow for situation where changes in the reverse direction, specialized to generalized, may well, and it seems do, occur). The point is this leads to an expectation, and often an a priori interpretation that primitive groups have primitive features and more derived groups have more derived features e.g. Canatella, 1985. This may be true, but it tends to produce a defeatist attitude in respect of the chances of finding enough derived features with appropriate distributions for a"successful" cladistic analysis of a relatively primitive group. A successful cladistic analysis is one which permits complete resolution of the sister group relationships of the study group. The aim of the present study is to use a large data set taken from one organ system, the skeleton, with the expectation that this should increase the number of synapomorphic characters available for a cladistic analysis.

(ii) Distinguishing minority primitive from minority derived states.

One of the tasks in the cladistic analysis of any group is to identify and place (in the context of a dendrogram) the most primitive member of the group being studied. This is a problem in the analysis of any group - in the case of the analysis of a relatively primitive group it is always likely to be a particular difficulty. The reason for this is related to the objection to using distribution of states within the ingroup ("commonality principle" of Schaeffer, Hecht and Eldredge 1972) as a criterion for inferring character state polarity.

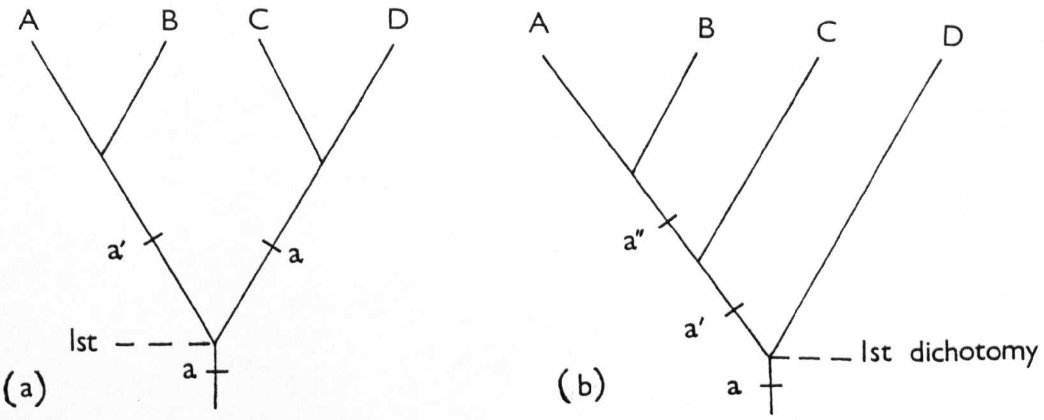


Fig. 2

In the case of a symmetrical cladogram, (a) above, a character transformation above the first dichotomy, from a to a', will result in 50% of the taxa (A and B) having the derived state a', while the remaining 50% (C and D) retain the primitive state a (providing there are no subsequent transformations to confuse the situation - e.g. a 'reversal' to a pseudoprimitive state a). In this case the commonality principle will not be applicable since there is no common state.

In the case of an asymmetrical cladogram, (b) above, a character transformation above the first dichotomy, from a to a' will, with the same proviso given above, result in 75% of the taxa (A, B and C) having the derived state a' while 25%, i.e. D, retains the primitive state a. In this situation use of the commonality principle (briefly common state primitive) will result in an incorrect interpretation; a' as primitive instead of derived. Underwood (1982: 251 - 252) referred to this kind of error and commented that use of distribution of states within the ingroup is inadmissible since systematic errors "can only lead to distortion of our analysis".

Minority distribution states in a relatively primitive group present a special kind of difficulty. They are potentially of the kind cited in the case of the asymmetrical cladogram. If two character states have the distribution state A - taxa A, B, C and state B - taxon D, and the character state polarity has to be inferred, then clearly there are two possibilities:-

a) state A is primitive; state B is derived. A, B and C retain the primitive condition, D has the derived character state. No cladistic information, i.e. no information on sister group relationship is imparted; the only phylogenetic (evolutionary) information to be gained is that D has diverged from the primitive condition in respect of this character. Following Huxley (1959) this change may be interpreted as likely to be anagenetic, that is, some form of biological improvement.

b) state A is derived; state B is primitive. A, B and C, on the basis of this character alone i.e with no evidence to the contrary, may be a monophyletic (holophyletic) group; D retains the primitive condition. Following Huxley (ibid.) the transformation to the derived condition may be interpreted as possible evidence of cladogenesis, the phyletic splitting off and diversification of A, B and C with respect to D. This may also be considered to be an anagenetic change if some form of biological improvement has resulted from the character state transformation. No information on sister group relationship has been imparted but if a further transformation occurs such that A and B share a state not found in C - e.g. a" in Fig. 2 (b) then: A and B are a sister pair, (share a"), and ABC are a group (pass through or possess state a' in the transformation series a a' a"). If state a is unique to ABCD then the group is completely resolved as shown in Fig. 2 (b). From this it may be seen that the only way of placing the most primitive taxon in a cladogram, in this case taxon D, is on the basis of two items of information - that the study group is holophyletic (ABCD), and that the taxa (ABC) above the 1st dichotomy/the basal taxon (D) are also a holophyletic group. The most primitive group taxon can only be placed on the basis of situational logic - no single piece of information can provide the evidence for its placement in a cladogram.

It will be noted that in(a) and(b) above the direction of change has been assumed. Polarity inferences should only be based on reasonably reliable indicators of character polarity. Clearly, from the above, the distribution of states within the ingroup is of no use since it is positively misleading in the case of minority derived states. Outgroup comparison is the preferred criterion for inferring character polarity yet even this may mislead (see Fig.3 below).

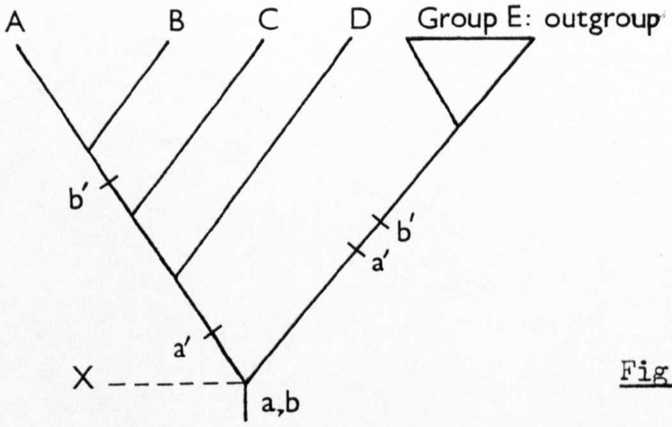


Fig. 3

Assuming Group E actually is the outgroup, i.e. the primitive sister group to ABCD it may still include characters which could provide erroneous polarity inferences. If state a′ in Group E appears to be the same as state a′ in ABCD but has arisen independently in the lineage leading to group E, i.e. it was not present in the common ancestor X, then it would be a parallelism, and an erroneous indicator of polarity. It would not, however, mislead since it does not provide evidence for an incorrect alternative cladogram. If character b′ is independently derived in the line leading to AB and in the outgroup, then outgroup comparison would mislead since it would suggest that b' is the primitive state and not a derived state as it actually is in Fig. 3 . However, Ridley (1986: 164) in listing outgroup comparison as one of three criteria for distinguishing "ancestral from derived character states" observed "All of them are practical and useful, none is perfect." I suggest, therefore, that where appropriate behavioural, developmental and functional criteria and evidence of ecological and/or morphological specialization are also valid indicators of character polarity, and may provide conflicting or corroborative evidence with respect to outgroup information. Conflicts can only be resolved on the grounds of biological plausibility or *post hoc* when the phylogenetic dendrogram has been constructed on the basis of the total data set.

(iii) Selection of an appropriate outgroup(s) for making outgroup Comparisons

Underwood (1982: 249) required that "The members of the outgroup must bear sufficient resemblance to the ingroup to allow detailed comparison" and suggested that the "choice of the outgroup depends upon the characters" - that is, he advocated not just using one outgroup for all character comparisons but varying the outgroup as appropriate in each character comparison. Nonetheless it is usually appropriate to select one outgroup in particular for the majority of the character comparisons, since this outgroup will bear more detailed aggregate similarity to the ingroup than to any other group/more primitive group. He also mentions the supposition that "the ingroup arose from an ancestor phylogenetically closer to members of the outgroup than to non-members". In respect of the analysis of the phylogenetic relationships of a relatively primitive group it may often be the case that the outgroup is phylogenetically *more distant* than other, more derived, members of the same lineage as the ingroup.

The problem with attempting a phylogenetic analysis of a relatively primitive group, especially an analysis of a basal group like the discoglossoid frogs, is the lack of a closely related outgroup. In the present study the Urodela (tailed amphibians, the newts and salamanders) are taken to be the most appropriate outgroup.

4. Systematics : methods

4.1 Systematic Analysis: justification of method employed.

There are now three main approaches to the systematic analysis of a group of organisms; phenetics, cladistics and transformed cladistics. McNeill (1982: 338) pointed out the similarities between cladistic and phenetic analysis: both are made possible by evolution but neither method provides evolutionary trees as such nor do they, by themselves, permit phylogenetic reconstruction. It should be noted that McNeill was specifically referring to the concept of cladistics which we would now call 'transformed cladistics'. McNeill (loc. cit.) drew parallels between Patterson's (1980) comments about this form of cladistics not necessarily being about evolution but about the pattern in nature, and his own account of phenetics as being dependant upon evolution for its success but making "no attempt to reflect evolution" and seeking "to describe the distribution among organisms of as many of their character states as possible" (McNeill 1980). Nonetheless the dependency of both transformed cladistics and phenetics on evolution cannot be denied. The hierarchical pattern in nature which the transformed cladists attempt to discern is a product of the evolutionary process. The existence of a classificatory hierarchy was used by Darwin as one of his main arguments for natural selection (Darwin 1859: 340). Platnick, in his key paper on the transformation of cladistics acknowledged the importance of evolution in his comment "We are hardly likely to achieve any understanding of the evolutionary process until we have achieved an understanding of the patterns produced by that process...." Platnick (1980: 546).
In their 1980 papers Patterson and Platnick do not deny the existence of the evolutionary process, they merely suggest that it is not an essential part of a systematic analysis. In fact one could take a different view; one could say that in these two papers Patterson and

Platnick did not deny the existence of the evolutionary process - they actually assumed it. The pheneticists have similarly acknowledged the underlying importance of evolution:- "The theoretical principle of descent, with modification - phylogenetics - is clearly responsible for the existence and structure of a natural system of classification; we may even agree with Tschulok (1922) that the natural system can be considered as proof of the theory of evolution."

Given the underlying importance of evolution to classification it seems logically unsatisfactory to exclude all consideration of it from our classificatory schemes. Even the phenetic taxonomists, while insisting on the exclusion of phylogenetic considerations at the data analysis stage, acknowledge that once a (phenetic) classification has been established "biologists will inevitably attempt to arrive at phylogenetic deductions from the evidence at hand" (Sokal and Sneath 1963: 216). In other words, for most biologists, the temptation to provide an evolutionary explanation for the pattern of character state distribution observed in any given taxonomic group proves too strong. The reason for this clearly stated in Sokal and Sneath (1963: 20) "With the publication of Origin of Species ....the reason for the existence of natural systematic categories became apparent: their members were related because of descent from a common ancestor ! A taxon was now interpreted as a monophyletic array of related forms." One may of course carry out a purely phenetic analysis of character state distributions, rank taxa according to their percentage similarity or some other measure of phenetic similarity and then make phylogenetic inferences from the dendrogram or classification thus constructed. However, the main problem with most forms of phenetic analysis is that results are strongly influenced by the clustering technique used. Similarly one can attempt to choose between the sets of possible evolutionary trees which can be derived from the more general cladogram (s) constructed as a summary/summaries of the pattern of character distribution following the transformed cladistic methodology. Yet the "preferred" cladogram using this method is usually chosen on the basis of maximal congruence of shared characters or parsimony, when the shortest length tree in terms of the minimum number of transformation steps required to account for the distribution of the characters is preferred over trees requiring a greater number of steps. There are often many cladograms to choose from and consequently even more trees. In addition the assumption that evolution itself is parsimonious is almost certainly dubious; parsimony is a useful working hypothesis yet it may have little relevance in the matter of attempting to reconstruct the evolutionary history of a group. The method employed in the present study is that of evolutionary or Hennigian cladistics; the reasons for using this as the preferred method of data analysis are given below.

The express aim of this study is to investigate the phylogenetic relationships of the discoglossid and leiopelmatid frogs (see Objectives). Using similar reasoning to that of Gauld (1985: 63), I suggest that an investigation into the phylogenetic relationships of a group logically entails the use of phylogenetic methods of data analysis. In the case of phenetic and transformed cladistic analyses where an evolutionary component if 'read in' after the data analysis stage, the analytical phase is merely dissected out into two parts - an initial analysis (pre-evolutionary input) and a secondary analysis (the input of an evolutionary perspective) which is really a re-analysis of data to provide a new dendrogram or classification of hypothesized phylogenetic relationships. This may be seen as:-

Initial Analysis:

(Phenetic). Data set + analysis = Phenetic dendrogram (or classification)

(Transformed cladistic).

Data set + analysis = Cladogram(s) (or classification(s)).

<u>Secondary Analysis</u>:

Phenetic dendrogram + evolutionary perspective = Estimate of phylogenetic relationships as evolutionary tree or classification. *

Cladogram + evolutionary perspective = Estimate of phylogenetic relationships as evolutionary tree or classification. *

In the case of a <u>phylogenetic analysis</u> this becomes:-

Data set + analysis involving complete or partial polarity inference = Estimate of phylogenetic relationships as evolutionary tree or classification. *

<u>Fig. 4.</u>

Note: * This is not meant to indicate that the methods are equivalent nor that they will necessarily produce the same result.

The present study seeks to obtain not only information on the number and sequence of phyletic splits within the study group comprising the modern discoglossoid frogs, but also some estimate of the divergence since those splits occurred - an assessment of the relative phylogenetic proximity of the species comprising the modern discoglossoid group. It is also a dual aim to obtain an insight into the mode of life of the individual species on the basis of their osteology, hence data on adaptive characters, parallels and convergences, are also of interest. Evolutionary systematists and Hennigian cladists are now in general agreement on the validity of using synapomorphies as evidence of common ancestry (e.g. especially Mayr 1974, also Wiley 1981 and Charig 1982). Their disagreement is over the issue of classification. This study is an attempt at a cladistic analysis of osteological features. It is taken as self evident that it is not possible <u>a priori</u> to distinguish/infer characters providing evidence for sister group relationship (synapomorphies) from those derived in parallel or as convergences (homoplasies). Consequently all the osteological data derived from a detailed examination of the study sample are included in the analysis as being of potential cladistic significance and of general interest for the reasons given at the top of this paragraph. The primary method of analysis is, for the same reasons, essentially a cladistic analysis specifically a compatibility analysis based upon the Le Quesne compatibility test. A computer program devised by Dr. G. Underwood and developed by Gauld and Underwood (1986) is used. This method accepts but does not require assignment of polarity to character states and can also accept mixed data sets of polar and non-polar data. A second method, that of Wagner tree analysis was also included for comparison.

4.2 Cladistic Analysis

The type of cladistic analysis used in this study is essentially cladistic analysis in its simplest form; the kind of analysis which is common ground for Hennigian cladists and evolutionary systematists like Mayr (1969, 1974) and, in part, Wiley (1981). Mayr (1969: 211-212) noted that cladistic methods have two main aims - to determine the number and the sequence of phyletic splits within a lineage. Huxley (1957: 455) defined a clade as a "delimitable monophyletic unit". Cladistic analysis is thus an attempt at phylogenetic reconstruction by the recognition of such monophyletic groups and then a search for their sister groups. A sister group is a species or species group arising from the stem species of a monophyletic group "by one and the same splitting process" (Hennig 1966: 139). Thus a species and its sister species share a common ancestor which is not shared with any other species - the common ancestor may be a third, different, species or it may be the same species as one of the two sister (or perhaps more appropriately "daughter") species when speciation has resulted from isolation of the ancestral species in part of its range. A nested hierarchy is produced by considering successively more inclusive groups of sister species. (If A and B are sister species then a more inclusive group would include C, the sister species of the group A + B, and a still more inclusive group would include species D, sister to A + B + C and so on...). In this way the genealogy of a group may be built up as rested hierarchical sets of monophyletic groups at increasingly higher taxonomic levels. For evolutionary systematists and Hennigian cladists evidence of sister group relationship (and hence monophyly) is provided by synapomorphy, that is by possession of common features (or characters) which are not found in any other group. This last is a very important point, for as Groombridge (unpublished PhD thesis, 1980) succinctly pointed out "All synapomorphies are shared derived...(character)...states, but the converse is not true". Groombridge went on to cite "Hennig's stipulation" that to constitute a synapomorphy an apomorphic (i.e.derived) state has to "belong to one and the same transformation series" (Hennig 1966: 89); that is they must be homologous. Groombridge also suggested that the more general term 'shared derived' remains useful for character states "whose status as synapomorphies or parallelisms is unclear at a given stage of analysis". From all the foregoing discussion it is evident that the two concepts monophyly and homology are the central, and most important factors in phylogenetic reconstruction and are in need of clear, unambiguous definition and further discussion. Both have been the subject of many heated debates, some of which have been merely exercises in semantics, arising from the quite unnecessary and rather confusing practice of the proponents of the respective systematic schools of thought, of redefining these terms to suit their own purposes and viewpoints. I do not propose to include a discussion on these controversies, only to provide definitions for these terms which are appropriate to phylogenetic analysis/reconstruction in general, and consequently to this study in particular, and to give reasons for preferring these definitions over some of the others currently in use.

Monophyly

This study follows Ashlock's (1984) definitions for monophyletic, paraphyletic and polyphyletic groups. Ashlock (ibid) reviewed his own (1971) work and that of others on the meaning and importance of monophyly. Ashlock noted the need for the continuity of the traditional concept of monophyly, which he sought to preserve by retaining Haeckel's distinction of single versus multiple origin for, respectively, monophyletic and paraphyletic groups (Haeckel 1874). Hennig (1966: 73) characteristically tried to provide a more rigorous definition for monophyly; for Hennig a monophyletic group is "a group of species descended from a single ("stem") species, and which includes all species descended from this stem species".

Ashlock noted that this "narrow concept" of monophyletic groups is substantially different from the traditional concept and that "actual application of Hennig's definition to systematics would produce "gross changes in classification". According to Ashlock (1984) Hennig coined the term paraphyletic for "groups derived from a single stem species but not containing all descendants of that ancestor". I have to say that I could not find this definition explicitly stated in Hennig (1966). Hennig (ibid. 146-147) did however note that groups could be distinguished on the basis of the nature of their morphological similarity: in monophyletic group the similarity is based on synapomorphy, in paraphyletic groups it is based on symplesiomorphy (shared primitive character states) and in polyphyletic groups similarity is due to convergence. The point is, while one may draw Ashlock's conclusion concerning paraphyletic groups from Hennig's text it was not so stated by Hennig himself - it is a property of paraphyletic groups. Nonetheless Ashlock has provided probably the clearest definitions of the terms monophyletic, paraphyletic and polyphyletic, while at the same time retaining a continuity of meaning with the traditional concept of monophyly. For Ashlock (1984: 40) a monophyletic group is "one whose most recent common ancestor is a member of that group". He distinguished two kinds of monophyletic group; holophyletic (a term he had coined, Ashlock, 1971) and paraphyletic - "A monophyletic group may be either holophyletic (containing all descendants of the most recent common ancestor of that group; monophyly sensu Hennig) or paraphyletic (not containing all descendants of the most recent common ancestor of the group)". A polyphyletic group, in contrast, is "one whose most recent common ancestor is not a member of that group". Note that Hennig (1966: 73) did not specifically include the common ancestor (stem species); Ashlock has clarified the situation. He also noted that the common ancestor may be inferred and that his definitions are not based the use of actual characters, although evidence for relationship and group membership has to come from an analysis of characters.

The following should be borne in mind:-

i) The above definitions are theoretical definitions. Just as we can never actually know if we have correctly reconstructed the course of evolutionary history for a group, we cannot know if a group is holophyletic. Our aim is to include all known members of a monophyletic lineage - we cannot include all the fossil forms (for many/most will be unknown to us) nor can we include modern species which have yet to be described. In the case of the present study only living species of discoglossoids are included. Yet we can speak of monophyletic groups sensu Hennig: Hennig himself noted that when he said that his monophyletic groups not only had "all species....included in it actually descended from a single stem species", but also required that "no species derived from this stem species..." be "allocated outside the group in question. Naturally..." he did not mean "that the birds, for example, cannot be called a monophyletic group if the fossil species are disregarded in a presentation of the system. They are not classified outside the group "Aves," but are simply disregarded for a special reason" (Hennig 1966: 73).

ii) From i) above it is clear that the concept of holophyly sensu Ashlock (monophyly sensu Hennig) is of practical use, and it is equally clear that there is a difference between paraphyletic groups in theory and holophyletic and paraphyletic groups in actual fact (in practice). It is highly likely that most of our hypothesized holophyletic groups in phylogenetic reconstructions are, in fact, paraphyletic groups sensu Ashlock. But, it should be noted that there is a difference between aiming for holophyletic groups (and probably getting paraphyletic ones) and deliberately admitting paraphyletic groups into our classifications (worse, into our cladistic analyses). Other definitions of monophyly, paraphyly and polyphyly have been advanced, notably by Nelson (1971), Farris (1974) and Platnick (1976). Ashlock (1984) provided a critique of these definitions which either cloud or otherwise confuse the issues. Nelson (1971) defined monophyletic groups as "complete sister group systems" and effectively subdivided Hennig's concept of paraphyly into two parts:- a sister group system incomplete through the ommission of one species or monophyletic species - group (Nelson's paraphyly) and one incomplete ommissiom of two such species or groups (to which Nelson misapplied Haeckel's term polyphyly). Farris (1974) reworded Ashlock's principles given in the latter's 1971 and 1972 papers, while Platnick (1976) asked if monophyletic groups were possible, unnecessarily requiring that ancestors of ancestors be included to form a monophyletic group. The clear trend toward transformed cladistics is evident in the writings of these three authors which can therefore be disregarded in an investigation expressly concerned with phylogenetic reconstruction/inference.

Homology

"Classifications are only as good as the homologies of the characters on which they are based". (Sokal and Sneath 1963: 23).

Sokal and Sneath were recognising and drawing attention to the fact that "good" classifications, in their terms ones with a high information content, are based on characters which may confidently be considered to be strictly comparable. That Sokal and Sneath use "good" character homology as the basis of a "good" classifications should not seem as surprising as perhaps it initially appears: for originally the concept of homology did not carry any evolutionary connotation. The term "homologue" was coined by Owen (1848) for the purpose of making valid anatomical comparisons and for interpreting anatomical data. Owen defined a homologue as "the same organ in different animals under every variety of form and function" and 'special homology' (now simply referred to as homology) as "the correspondency of a part or organ determined by its relative position and connections, with a part or organ in a different animal". Owen's purpose was to distinguish structures that were essentially the same in different animals and which could therefore reasonably be compared with one another, from those which were not the same and for which comparisons would be meaningless. He used the existing term "analogue" for this second class of character which he defined as "a part or organ in one animal which has the same function as a part or organ in a different animal". For Darwin the existence of homology was further evidence for the theory of evolution. Since the "Origin of Species" (Darwin 1859) the significance of homologous features has been recognised: homologues are structures derived from descent from a common ancestor; analogues are structures having the same function but are derived from very different ancestors. The 'problem of homology' is in fact two problems: (i) defining homology without invoking circularity and (ii) distinguishing convergent and parallel from 'true' homologies (structures inherited from a common ancestor).

(i) Defining homology without invoking circularity

The circularity arises when a phylogenetic definition of homology is attempted. For example, Wiley (1981: 21) says "A character of two or more taxa is homologous if this character is found in the common ancestor of these taxa....". The circularity is clear; what defines a homology? The presence of the homologous feature in the common ancestor; how does one define the common ancestor? - by the presence of the homologous feature. This circularity(which, if admitted, produces a 'closed-system' method of phylogenetic reconstruction) is not only logically undesirable, but it can lead to mistaken phylogenetic hypotheses because it does not preclude convergent similarities - similarity in structure derived from different ancestry, or parallel similarities - the independant acquisition of similar characters in closely related phylogenetic lineages. To paraphrase and repeat Groombridge's (1980) dictum all synapomorphies are shared derived characters, but not all shared derived characters are synapomorphies. How can we know that the characters we are using for phylogenetic reconstruction are synapomorphies, that is, how can we be sure we are obeying Hennig's stipulation that the derived states we are using "belong to one and the same transformation series"? The answer is of course that in absolute terms we cannot know, but we can attempt to minimise the occurrence of convergence and parallelism (homoplasy) in our character sets. This is achieved by adopting the concept of operational homology as advanced by Sneath and Sokal (1973: 79) who said that two characters are operationally homologous if they are "very much alike in general and in particular". The problem is, just how similar is this? Underwood (1982: 246) was a little more specific: "Two features are operationally homologous if they admit of detailed comparison at a descriptive level".

(ii) Distinguishing convergent and parallel similarities from 'true' homologies (structures inherited from a common ancestor).

Underwood (1982: 254) and Cain (1982: 2) noted that character similarity due to parallelism or convergence may be recognised (detected) from discordance of characters using a Le Quesne Test. Le Quesne's test is based on his uniquely derived character concept (for details see section 4.5 on Numerical cladistic analysis - Compatibility analysis).

4.3 Characters, character states and transformation series.

This attempt to infer phylogeny of the discoglossoid frogs follows certain principles of cladistic analysis sensu Hennig (1965, 1966) and Mayr (1969, 1974). The importance of identifying and using synapomorphies as evidence of monophyly and sister group relationship has already been discussed in the previous section. The previous section also noted that to constitute a synapomorphy the derived character state must belong to "one and the same transformation series". Consequently, the present section is concerned with characters, character states and transformation series and their relevance to phylogenetic reconstruction.

The term "character" has been defined in different ways, with different purposes in mind (as is the case with many taxonomic terms). In the present context Mayr's (1969) definition is appropriate:- "A taxonomic character is any attribute of a member of a taxon by which it differs or may differ from a member of a different taxon". Sneath and Sokal (1973: 71) specifically objected to Mayr's definition pointing out that characters are thereby restricted to differences between members of the taxa but the taxa concerned cannot be recognised without their characters being known in the first place. Sneath and Sokal preferred the alternative definition of a character as a "feature which varies from one kind of organism to another" (Michner and Sokal 1957). This definition is not appropriate to a phylogenetic study because it does not exclude those features by which individuals of a single population may differ from one another (e.g. differences between the sexes) and are not, therefore, taxonomic characters. In addition the Michner-Sokal definition is subject to the same kind of objection that Sneath and Sokal level at Mayr; for how does one recognise different kinds of organism in the first place other than by their characters? Mayr's (1969) definition is acceptable for the purpose of utilizing characters for phylogenetic analysis, for we may either test the homogeneity of the individual taxa by investigating intra- and interpopulational character variation before attempting a phylogenetic reconstruction at say, species level or, accept our taxa as given (i.e. monophyletic) and use their characters to estimate their degree of phylogenetic relationship. (A practice which is often adopted in studies concerned with higher level relationships). Hecht and Edwards (1977) usefully pointed out that, in the case of phylogenetic inference above the species level, a character can be defined as "a set of limited homologous features that are distributed among two or more taxa". It should be noted that for the purposes of this study some definitions are too restrictive, e.g. Nelson and Platnick (1981: 301) - "A character is a theory, a theory that two attributes which appear different in some way are nonetheless the same (homologous)". If this definition is applied then only synapomorphies are considered to be characters. We certainly want to identify (and use) synapomorphies for the purpose of phylogenetic reconstruction but, as stated in the section on 'Systematic Analysis' the aim of this study is not only to obtain information on the number and sequence of phyletic splits within the discoglossoid frogs (which application of the Nelson-Platnick definition* would give), but also some estimate of the divergence since the splits occurred (which * it would not give) and an insight into the mode of life of individual discoglossoid species (which * it may or may not give).

Mayr (1969: 126-142) listed and discussed five categories of taxonomic characters: Morphological (including embryological and karyological), Physiological (including biochemical and immunological), Ecological (including parasites and symbionts), Ethological and Geographical. Hecht and Edwards (1977: 5) noted that only intrinsic data should be used in phylogenetic reconstruction/inference; in other words, only data derived from the genotype and/or from the phenotype since in practice it is usually more convenient to collect phenotypic data. Phenotypic data are acceptable since they are primarily determined by the interaction of the genotype and the environment. Extrinsic data e.g. geographical distribution should not be used, for while they may partly be determined by an organism's phenotype they are also dependant upon factors that have nothing to do with the organism's genetic (genealogical) history. In the present analysis only osteological data are used.

For the purpose of phylogenetic analysis the unit of comparison is the character state; a character state is an expression or condition e.g. the character 'condition of the clavicles' may have the states 'clavicles straight' and 'clavicles curved' of a character exhibited by an organism. (Although Mayr 1969: 122 has pointed out that using his definition the term 'taxonomic character' is the same as the 'character state' of other workers, and that their distinction between character and character state is unnecessary and confusing. Since 1969 however the use of the term 'character state' has become widely accepted and is therefore used throughout this thesis. Where more than two states are recognised the character states are arranged in a series called a "transformation series" (Hennig 1966: 89 et seq.) or more specifically a "morphological transformation series" or a "morphocline" (Maslin 1952). The character states in a transformation series are usually arranged in order of phenetic similarity; most similar states adjacent in the series. Underwood (1982) called this the formal or logical approach, commenting that in this approach "treats each state as a pattern and seeks to place it next to that other pattern which it most closely resembles, such that the aggregated differences between adjacent pairs are at a minimum; it aims for phenetic parsimony". Underwood also suggested that certain biological criteria might also be used in order states in a transformation series: his biological approach "views each state at the phenotypic expression of a genotype" and consequently seeks to order states with the most similar genotypes - " it aims for genetic parsimony".

Underwood points out that this approach involves a certain amount of interpretation but is admissible in that it does not presuppose any evolutionary relationship in the group being analysed. (In fact it should be noted that, at this stage, no evolutionary implications whatsoever have been made: transformation series order on the basis of formal (logical) or biological criteria are series of similarity states. An evolutionary component is added only when a decision on character polarity has been made (- see next section on "Polarity"). Underwood (loc. cit.) cites several ways of inferring similarity of genotype, ranking in decreasing genetic proximity pairs of states found in two sides of a bilaterally symmetrical individual, two individuals in the same population and two individuals from different populations of the same species. He also mentions that a knowledge of development may be of some assistance in helping to "confirm or suggest a particular transformation series". Once a transformation series has been assembled the next step is to root it, that is decide which of the states is primitive (see next section). In practice these two processes are normally (but need not necessarily be) carried out at one and the same time.

4.4 Character polarity

In a phylogenetic analysis the next stage - inferring the polarity of the steps in a transformation series - is critical; it is the stage where the evolutionary component is 'read in'. Thus far the analysis has effectively been a phenetic analysis with little or nothing to give a pheneticist cause for objection. The data used in this investigation into discoglossoid relationship comprise only those features intrinsic to the organisms being studied. This is a requirement which is common to both phenetic and phylogenetic systematics - "It is undesirable to use attributes that are not a reflection of the inherent nature of the organisms themselves" (Sneath and Sokal 1973: 103) and "...only intrinsic data should be used in phylogenetic reconstruction" (Hecht and Edwards 1977: 5). The concept of character homology used in the present study is that of operational homology which is, I would suggest, equivalent to Arnold's 'provisional homology' (Arnold 1981: 6): operational homology relies on "detailed comparison at a descriptive level" (Underwood 1982: 246) whereas provisional homology is based upon "similarity in location structure and ontogeny" (Arnold loc. cit.). Provisional homology, like operational homology, makes no phylogenetic assumptions but both may be held to have phylogenetic implications. In cladistic and evolutionary systematics the implication is that taxa which share homologous features, i.e. synapomorphies, are members of the same monophyletic group. It should, however, be remembered that this is an optional viewpoint, not a necessary logical sequence of the concept of either operational homology or provisional homology. In this way the interpretation of monophyly from these two forms of homology should, I suggest, be regarded as the "evolutionary option". However, the change produced by establishing/inferring the polarity of the transformation series is such that the data sets are no longer the same - a polar data set is one possible subset of which may be derived desirable from the non-polar data set - a particular perspective has been added, when the only meaningful interpretation of the data is an evolutionary one.

Using Hecht and Edwards' definition of a character as a set of limited homologous features distributed amongst two or more characters, and assuming the correct application of the principle of operational homology for all characters in all taxa in the study group, i.e. the features (character states) seen in the individual taxa are sufficiently similar such that they may be regarded as different expressions of the same character amongst these taxa, then it is deemed reasonable fide Hecht and Edwards (1977) to make the following assumptions:-

i) the character states observed are homologous and share a common ancestral condition and,

ii) in every morphoclinal/morphological transformation series there is always a single ancestral or primitive condition but there may be one or more derived states.

It is the purpose of character polarity determination/inference to identify the ancestral or primitive condition in a transformation series and thereby hypothesize the direction of evolutionary change. Kluge and Farris (1969) used the term 'polarity' for the direction of change in a morphological transformation series. The direction of change may be unidirectional or multidirectional - Marx and Rabb (1972) list different types of possible evolutionary character paths.

I do not propose to provide a critical review of the possible character polarity indicators since there is already an extensive literature on the subject including Hennig (1966), Marx and Rabb (1972), Sneath and Sokal (1973), Kluge (1976), Crisci and Stuessy (1980), Arnold (1981), Watrous and Wheeler (1981), Bishop (1982), Farris (1982), Underwood (1982) and Maddison, Donaghue and Maddison (1984). This account follows Underwood (1982) for the following reasons: most authors give a list of criteria for character polarity with comments on their application but Underwood gives a critical review of the most commonly used in phylogenetic analyses (with special reference to the criteria of Marx and Rabb, 1972) dividing them into three categories, logical, biological and rejected criteria; he gives a clear exposition of the application of outgroup comparison and an equally clear argument for not using the distribution of states within the ingroup (the " commonality principle of character state distribution" of Schaeffer, Hecht and Eldredge, 1972) which considers the character state with the widest distribution among the taxa to be the most primitive. These last two features of Underwood's review of polarity are of particular relevance to the analysis of a primitive group like the discoglossoid frogs (see Section 3.3 on Clades,grades, evolutionary processes and the problems of phylogenetic reconstruction in relatively primitive groups).

The opening paragraph to this section mentions that this stage in a phylogenetic analysis is critical - in fact I would agree with Kavanaugh (1978b:436) who said that determination of polarity "is the critical phase of cladistic analysis... hypotheses generated from these analyses are valid only to the extent that hypotheses on polarity and sequence of individual characters are accurate (i.e. reflect evolutionary history of the characters". As Kavanaugh (loc. cit.) pointed out if it were possible to "know (with certainty)" the polarity of the transformation series, then reconstruction of phylogenetic relationships would be relatively simple. Unfortunately such certainty is not possible, and we are therefore obliged to make use of carefully reasoned criteria for inferring the polarity of a transformation series and test these hypotheses of polarity by subjecting them to logically independant tests (like compatibility analysis - see Section 4.6). Because the accuracy of hypotheses on polarity and sequence of character states in a transformation series are of prime importance in phylogeny reconstruction, I will include examples of polarity criteria as advanced by Marx and Rabb (1972), Kavanaugh (1978b) and Arnold (1981) and give a brief resume of Underwood (1982: 249-254) on outgroup comparison, functional and developmental criteria for polarity inference and rejected criteria.

Marx and Rabb (1972) listed ten criteria for assigning polarity to character state changes these were: (1) Uniqueness (2) Relative abundance (3) Correlation of derived states (4) Morphological specialization (5) Ecological specialization (6) Geographic restriction (7) Closely related taxa (8) Correlation of applied criteria (9) Genetic structure and (10) Fossil record. These criteria have been quite widely criticized (e.g. Arnold 1981, Bishop 1982, Underwood 1982). In fairness to Marx and Rabb it should be noted that they assumed the phylogeny of the group to be at least partially known; consequently the application of their criteria is seen as a means of extending this knowledge to the interpretation of the direction of evolutionary change in the transformation series, and also provides a way of assessing levels of confidence in such interpretations.

Kavanaugh (1978) gave five criteria for polarity inference, in order of "overall usefulness" these were (1) Ex-group comparisons (= outgroup comparison) (2) Character correlations (3) Group trends (4) Correlation with adaptative significance and (5) In-group comparisons. Of these five the use of group trends is particularly questionable since it expressly admits use of parallel and convergent characters (homoplasies). Kavanaugh commented that Ball (1975) noted that within groups, certain characters appear to follow the same evolutionary development (i.e. transformation) in many independent lineages. Kavanaugh cited the example of members of Nebria species (Coleoptera) which inhabit high montane habitats tend "without regard to their phylogenetic relationships" to have reduced hindwings, shortened elytra, shortened metasterna and lengthened appendages. Even if such characters are counted as a single character, the use of this character is still open to question since it may be regarded as an ecological specialization (see below - Underwood

1982 - rejected criteria).

Arnold (1981) in his paper on estimating phylogenies at low taxonomic levels lists twelve indicators for determining character polarity in a transformation series. These are: (1) Distribution of states in outgroups (2) Frequency and distribution of states within the studied group (3) Non-coinciding minority states (4) Correlation with states of other characters (5) Ontogenetic clues (6) Complexity (7) Functional clues (8) Hierarchical structure of character state distribution (9) Fossil evidence (10) Biogeographical indicators (11) Ecological specialization and (12) Adaptations of general use. It should be remembered that Arnold is particularly concerned with estimating phylogenies at low taxonomic levels and is therefore concerned with relatively derived groups, whereas the present study is concerned with phylogeny reconstruction in relatively primitive groups. Arnold also requires that "The group to be analysed... must be holophyletic" - in the case of relatively primitive groups this is often not known initially but is one of the goals the analysis seeks to attain. Some of Arnold's criteria require brief explanation. His criterion 3 'Non-coinciding minority states' (which may be regarded as a special case of Marx and Rabb's criterion 3 'Correlation of derived states') uses the frequency and distribution of rare states to provide clues to polarity. If the rare states of different characters are distributed such that they are found in small, non-overlapping species groups, then using the limited range of possible structures ("topologies") for branching phylogenies he suggests that "the majority are derived features defining holophyletic groups and that not more than one group is being indicated by primitive features" (i.e. only one error is made). It is not possible to identify the primitive state on the basis of character state frequency, evidence from another source is needed. Of his criterion 6, Complexity, Arnold comments that it is often argued that a more complex state is more likely to be derived compared with primitive states, but points out that "there are many instances where simplifications of complex features by fusion, reduction or loss seems to have occurred", and that using increasing complexity as an indicator of polarity "will often mislead". Use of complexity as a polarity indicator is open to the same objection as using morphological specialization (see below: Underwood rejected criteria). For criterion 12, Adaptations of general use, Arnold quotes Van Valen (1978) saying adaptations of general use are likely to be lost and "are therefore presumably liable to be derived states". As Arnold goes on to point out, defining adaptations of general use can be a problem "since even widespread structures of obvious utility in most situations may occasionally be lost," and cites the instance of presence of lungs in most vertebrates and lung loss in plethodontid salamanders.

From the above it is evident that there is an abundance of criteria for inferring the polarity of a transformation series. Some are the same criteria expressed in different terms (e.g. Kavanaugh's "ex-group comparisons" for outgroup comparisons), or maybe redefined in a special or restricted sense for use in particular situations (Kavanaugh's use of "Group trends" in a group like Nebria with a large number of closely related species) or for application to certain kinds of problems (Arnold's use of "Non-coinciding minority states" for the analysis of "known" holophyletic groups at low taxonomic levels). In the case of the analysis of a primitive group - where one of the tasks of the anlaysis is, if possible, to establish the monophyly of the group (or a subset of the group), or at least to make an assessment of the relative phylogenetic proximity of monophyletic (holophyletic) taxa within the initial study group - use of Underwood's (1982) criteria, for inferring polarity of the steps in a transformation series, is appropriate.

Underwood (1982: 249-251) considers only three criteria to be admissable for the purpose of polarity inference - outgroup comparison, functional and developmental criteria. He specifically rejects the

Erratum: p. 57. Repetition of text on p. 56: delete text on p. 57, line 1 "for inferring ..." to line 19 (para. 2, line 4) "... of states".

distribution of states for inferring the polarity of a transformation series. Some are the same criteria expressed in different terms (e.g. Kavanaugh's "Ex-group comparisons" for outgroup comparisons), or may be redefined in a special or restricted sense for use in particular situations (Kavanaugh's use of "Group trends" in a group like Nebria with a large number of closely related species) or for application to certain kinds of problems (Arnold's use of "Non-coinciding minority states" for the analysis of 'known' holophyletic groups at low taxonomic levels). In the case of the analysis of a primitive group - where one of the tasks of the analysis is, if possible, to establish the monophyly of the group (or a subst of the group), or at least to make an assessment of the relative phylogenetic proximity of monophyletic (holophyletic) taxa within the initial study group, use of Underwood's (1982) criteria, for inferring polarity of the steps in a transformation series, is appropriate.

Underwood (1982: 249 - 251) considers only three criteria as admissable indicators of polarity - outgroup comparison, functional and developmental criteria. He specifically rejects the use of distribution of states within the ingroup because it is subject to systematic error see Section 3.3 ; association with states of other characters (= multiple use of the other charcters); morphological specialization ("unsupported assumption that evolution proceeds from generalized to specialized"); ecological specialization (data includes extrinsic element); geographical restriction (extrinsic data); genetic structure ("rarely available"... "not clear how it could be used") and fossil record (a priori assumptions about evolutionary progression"). The use of outgroup comparison relies upon the assumption that detailed resemblance between members of the ingroup and the outgroup is due to community of ancestry (Darwin's 'propinquity of descent' - "something more is included in our classification, than mere resemblance... and that propinquity of descent, - the only known cause of the similarity of organic beings, - is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications", Charles Darwin 'The Origin of Species' 1859: 399). That is to say, if the ingroup and outgroup share a more (special) detailed similarity to one another than either does with any other group, then this similarity may be attributed to a closer phylogentic relationship - we may "therefore suppose that the ingroup arose from an ancestor phylogenetically closer to members of the outgroup than to non-members" (Underwood 1982: 250). The outgroup comparison criterion sensu Underwood requires that members of the outgroup must bear sufficient resemblance to the ingroup to allow detailed comparison; supposes that if a state is common in the outgroup it is likely to be primitive for the ingroup and suggests that the choice of the outgroup depends upon the character. Underwood (ibid) also provides interpretations of character polarity using outgroup comparison in given situations and includes notes on possible instances where the interpretation could mislead.

Table 1. Application of outgroup criterion for character polarity

	Outgroup	Ingroup	Interpretation
(a)	one state	one matching	matching ingroup state primitive[1]
(b)	several states	one matching	matching ingroup state primitive[1]
(c)	several states	none matching - but one more than others.	similar state primitive for ingroup[2]
(d)	several states - one in a clear majority[3]	two or more matching	majority matching ingroup state primitive
(e)	one or more states	no matching state[4]	no polarity inference may be made[5]

NOTES: [1] If the outgroup is sister to part of the ingroup (ingroup paraphyletic) then the test might mislead, for the matching state could be derived for the outgroup + part of ingroup or be independently derived in the outgroup and in part of the ingroup; in both cases the remainder of the ingroup would have or at least include the primitive state.

[2] Note[1] still applies and the chance of error is greater because of the increased phenetic gap between the outgroup and the more similar ingroup state - "we may more likely misjudge a measure of similarity than misjudge a match" (Underwood, loc. cit.).

[3] If there is no clear majority then either (i) no polarity inference can be made or (ii) if applicable, other criteria may be used to decide between the matching state.

[4] The phenetic gap is such that there is no ingroup: outgroup pair of states obviously closer than any other pair.

[5] Polarity may be inferred post-analysis from a polar dendrogram, when this kind of character may add further resolution i.e. more definition or structure to such a dendrogram.

Functional evidence may help in situations where given "a non-polar transformation series, we may conclude that, in respect of a particular step, change in one direction is functionally more plausible than in the other" (Underwood ibid.: 251). Clearly the confidence with which this criterion can be used will vary with each situation, i.e. with the evidence at hand.

Developmental (ontogenetic) evidence may provide some clues to polarity. Information on the course of development of either an ingroup or an outgroup member may provide both evidence for "assembly of the transformation series" (and) "may suggest a sequence of evolutionary change". This criterion is based on the assumption that "evolution has proceeded by incremental extension of the developmental process concerned" (Underwood loc. cit.). There are two main problems with using ontogenetic clues: arrest of the development process could give rise to the production of a pseudoprimitive state (Underwood) and the fact that developing animals, like adults, must function as individuals, hence parallel adaptations are just as likely to occur as they are in adults (Bishop 1982: 205). Bishop further suggests that "The study of ontogeny is better seen as a particular branch of the study of the functional morphology of living organisms." Nonetheless, in the absence of (clear) outgroup indications of polarity, ontogenetic clues may be of some help. Again, as in the case of functional evidence, the confidence with which this criterion can be used will vary with the quality of the evidence to hand.

Underwood's rejected criteria (see above) include three - distribution of states within the ingroup, morphological specialization and ecological specialization - which ought not to be totally rejected. While I agree with the general points he makes, I would suggest that under certain circumstances these criteria may be of value. Distribution of states within the ingroup is the least satisfactory of the three but may be used to provide an hypothesized polarity to a transformation series in the absence of evidence from any of the admissible criteria (which here includes morphological and ecological specializations. This hypothesized polarity can be tested against more confidently polarized character states using the compatibility analysis program which is based upon Le Quesne's uniquely derived character concept (Le Quesne 1969, 1972, 1979, 1982). Morphological and ecological specialization may be permissible, I would suggest, in situations where such specializations exhibit detailed similarity and especially when there is correlation with some behavioural specialization - these are a special category of adaptation - of limited distribution, detailed similarity, possibly also of behavioural significance. For example, in the Midwife Toads, genus <u>Alytes</u>, two wrist bones (radiale and ulnare + intermedium) are longer than wide rather than as wide as long or wider than long, as in other discoglossoid frogs - a morphological specialization, and they use their hands in a particular way for digging burrows and probably also for clearing earth out of rock crevices (behavioural and ecological specializations). In this case the character state wrist bones longer than wide can be confidently scored as derived on the basis of outgroup comparison (other discoglossoids have wrist bones as wide as, or wider than long) and on the basis of morphological, ecological and behavioural specializations. For the purpose of this study in particular (and any morphological study in general) I rank the criteria for polarity inference in order of preference: outgroup comparison; (jointly) behavioural, developmental, ecological specialization, functional, morphological specialization; distribution of states within the ingroup (at least, with the stipulation that it be used only in the absence of any other evidence and when it can be tested against more confidently inferred characters, e.g. using a Le Quesne test - i.e. it is only admitted as an alternative to a totally arbitrary selection of the primitive state - in this way one can find out how 'good' or how 'poor' a criterion it proves in a given situation.

4.5 Numerical cladistic analysis.

Modern numerical methods of data analysis in taxonomy originated with the publication of two papers by Sneath (1957a on bacterial classification; 1957b on computers in taxonomy), and two by Michener and Sokal on bees (Michener and Sokal 1957; Sokal and Michener 1958). While the development of numerical taxonomy by Sokal and Sneath was concerned with divorcing phylogenetic speculation from the processes of systematics and classification, and attempted to aim for repeatability and objectivity in the methods used, it is clear that the lasting benefit to taxonomy has been in the utilization of relatively larger data sets and the introduction of computers and computer-aided analytical techniques (algorithms and computer programs) to process such data sets. Historically, this concern with utilizing large quantities of data, and the need for suitable methods for handling large data sets, may be attributed to the research interests of the early numerical taxonomists - bacteriology (Sneath) and entomology (Michener and Sokal) - fields in which large numbers of taxa and large quantities of data per taxa are commonly encountered.

The use of numerical methods in cladistic analysis not only permit the use of large data sets, they also provide a means of handling and discriminating between the large numbers of possible dichotomous cladograms encountered in the analysis of even relatively small numbers of taxa. Cladograms can be generated 'by hand', that is, by inspection of the total data set in much the same way as for key construction - for sets of character states which divide the data set into successively smaller dichotomies. In some cases, this approach has proved quite successful, in that it has led to cladograms having a 'good fit', not only with the data at hand, but also with cladograms derived from alternative character sets. There is, however, a steep rise in the numbers of possible alternative cladograms. While computer-aided data-handling techniques are useful the impossibility of examining <u>all</u> possible alternative cladograms soon becomes evident. For 3 taxa there are 3 possible dichotomous cladograms; for 4 taxa there are 15; 10 taxa - 282, 137, 824 (Patterson 1980: 237) and for 20 taxa, Dawkins (1986: 273) calculated the number of possible trees to be 8, 200, 794, 532, 637, 891, 559, 375 (and, as Dawkins noted, 8, 200, 794, 532, 637, 891, 559, 374 of these have one thing in common - ("all of them are wrong"). Problems of this order are beyond the capabilities of even the most modern computers. Dawkins (loc. cit.) commented "It has been calculated that the fastest of today's computers would take 10,000 million years, approximately the age of the universe, to discover the most parsimomious tree for a mere 20 animals. And taxonomists often want to construct trees of more than 20 animals". (The present study is concerned with 21 taxa).

Gauld (1985) writing on advantages and disadvantages of the parsimony method noted, citing Felsenstein (1982) and Day (1983), "that it is not possible to predict, from any given data set, the actual minimum tree length". As Gauld (ibid.: 65-66) says "This means that, for large data sets, in practice one is guessing that the minimum length tree obtained is the shortest possible". Of his own data set, Gauld commented that his study showed that for highly homoplastic data, "a number of equally short, quite different cladograms may be obtained" and that "It appears to be merely an act of faith that a slightly shorter and yet totally different arrangement does not exist.." (his italics). As Gauld rightly says, this is "a rather disconcerting observation if one accepts the principle of parsimony as paramount in phylogenetic reconstruction". Gauld, in large part, overcomes these difficulties by utilizing both compatibility and parsimony methods (see under Sections 4.6 to 4.7) to construct a preferred cladogram. The same general principle, involving congruence between cladograms derived from a compatibility method (LEQU. BAS, a computer program written by Dr. G.L. Underwood, and developed by Gauld and Underwood 1986), and a parsimony method (the Wagner parsimony program from Felsenstein's PHYLIP package - package for inferring phylogenies) to arrive at, if possible, a completely resolved consensus cladogram, was also adopted in the present study.

Compiling a matrix.

The programs employed in this work require that all data is coded in binary form in a data matrix.

Prior to matrix construction:-

(i) A number of characters are recognized in respect of which the animals/taxa vary.

(ii) The individual characters are ordered into discrete states as either two - or multi-state characters.

(iii) The character states are then arranged into non-polar transformation series on the basis of detailed morphological similarity of adjacent states, such that any given state is adjacent, or between the state or states which it most resembles.

(iv) In each transformation series, where possible, one state is postulated to be the most primitive, and a polarity is thereby assigned to the series. Note: not a necessary step i.e. not required by the programs used. This is primarily done on the basis of outgroup comparison, but functional and/or developmental clues may also be of some help (see Section 4.4 on Character polarity). For some characters, evidence from outgroup comparison may not be available - the outgroup state might not bear sufficiently detailed resemblance to permit comparison or the structure is neomorphic in the ingroup; that is, it is a new structure which has arisen within the ingroup or in some unknown/unspecified form which is ancestral to the ingroup. If, additionally, there is neither functional nor developmental evidence to suggest possible polarity then the character may be left without a polarity being assigned. In the present study, in non-polar transformation series, the state found in the majority of taxa is coded as state 0. Both

O/C

the LEQU. BAS compatibility program and the PHYLIP Wagner parsimony program can accept non-polar data.

(v) States are converted into binary coding; in the case of two state characters this is very simple - the primitive state is coded as 0, the derived state as 1. For multistate characters, states are converted to binary using the additive binary coding system of Farris, Kluge and Eckardt (1970) - see next section:

Additive binary coding.

This is basically a system which converts multistate characters into an expanded series of two state characters which, taken together, include all the information contained in the original morphological transformation series. Note that the original transformation series can be polar (with direction of evolutionary change implied) or non-polar (no direction implied).

Taking the simplest case of a three-state character (C) with states 0, 1 and 2, then this may be coded into <u>two</u> binary characters: C(a) and C(b).

For a non-polar character (no direction of change implied):

		(a)	(b)
	0 ——	1 ——	2
C(a)	0	1	1
C(b)	0	0	1

Fig. 5.

The character state scoring becomes a set of identities - a taxon with state 0 becomes C(a):0; C(b) : 0; with state 1 C(a): 1; C(b): 0; with state 2 C(a): 1; C(b): 1. These identities, taken together merely serve to distinguish taxa with states 0, 1 and 2 respectively (see also note below). If a polarity is inferred, then the binary score is made with respect to the position of the primitive state relative to the character transformations (Figs. 6, 7).

State 0 primitive; state 1 derived; state 2 derived from state 1:

		(a)		(b)	
	0	⟶	1	⟶	2
C (a)	0		1		1
C (b)	0		0		1

Fig. 6.

In Fig. 6 , state 0 is primitive relative to both transformation (a) and (b) and is given the score C(a): 0; C(b): 0. State 1 is derived with respect to transformation (a) but primitive relative to transformation (b); its score is C(a): 1; C(b): 0. State 2 is derived with respect to both transformations and its score is therefore C(a): 1; C(b): 1.

State 0 primitive; states 1 and 2 independently derived from state 0.

		(a)		(b)	
	1	⟵	0	⟶	2
C(a)	1		0		0
C(b)	0		0		1

Fig. 7.

In Fig. 7 , state 0 is primitive to both transformations and is scored as before. Similarly, state 1 is derived with respect to transformation (a) and primitive relative to transformation (b) and is therefore also scored as before. But, state 2 is here <u>primitive</u> relative to transformation (b). Thus when state 2 is independently derived from state 0 its score becomes C(a): 0; C(b): 1 which serves to distinguish it in binary from C(a): 1; C(b): 1 where state 2 is derived from state 1.

Transformation series with four or more states are coded in the same way - the number of binary characters is always one less than the number of character states.

The convention, established by Underwood (1982: 259), of numbering binary states of multistate characters as decimals is adopted in the present study. Thus 48.1 and 48.2 are the two binary characters comprising character 48. The number before the decimal point indicates the character number; the number after , the character state. (for a summary of characters, character states and their binary coding, and their polarity patterns see Section D 'Characters and character states: a synopsis and Table 2 respectively).

Matrices.

The binary data are now entered in a data matrix. The matrix contains all the primary data needed for numerical analysis of the study group. Sneath and Sokal (1973: 114) describe a conventional data matrix, Fig. 8 below, as being in the form of an n x t matrix, in which n variables (arranged in n rows) are recorded for t taxa (in t columns). Each entry Xij in the matrix is the score of taxon j for character i.

$$\begin{array}{lll}
\underline{\text{Characters}} & & \underline{\text{Taxa}} \\
 & 1 & 2 \ldots\ldots\ldots\ldots t \\
1 & X11 & X12 \ldots\ldots\ldots X1t \\
2 & X21 & X22 \ldots\ldots\ldots X2t \\
\vdots & \vdots & \vdots \qquad\qquad \vdots \\
n & Xn1 & Xn2 \ldots\ldots\ldots Xnt
\end{array}$$

Fig. 8. Conventional data matrix, after Sneath and Sokal (1973).

For most numerical cladistic studies the matrix is arranged such that the taxa are in t rows and the binary characters are in n columns (see Fig. 9).

$$\begin{array}{lll}
\underline{\text{Taxa}} & & \underline{\text{Characters}} \\
 & 1 & 2 \ldots\ldots\ldots\ldots n \\
1 & X11 & X12 \ldots\ldots\ldots X1n \\
2 & X21 & X22 \ldots\ldots\ldots X2n \\
\vdots & \vdots & \vdots \qquad\qquad \vdots \\
t & Xt1 & Xt2 \ldots\ldots\ldots Xtn
\end{array}$$

Fig. 9. Data matrix assembled for use in most numerical cladistic analysis programs.

4.6 Compatibility methods

(a) Principles

The aim of compatibility methods is to identify a set of characters which are likely to be uniquely transformed (derived) and use these characters to construct possible unrooted or, preferably, rooted trees (in which case they provide a means of making plausible phylogenetic inferences about the group of organisms under consideration). A rooted tree can only be produced if the polarities of these characters are known, if the polarities are not known then an unrooted tree or network is produced (Le Quesne 1982). In practice, of course, it is not possible to know the polarity of any given character with certainty and therefore one can only produce unrooted networks or hypothesized rooted trees. There are two main schools of compatibility analysis: the Estabrook school and the Le Quesne school. The difference between the two is that the Estabrook school requires that a polarity be hypothesized for each and every character employed in the analysis (Estabrook, Strauch and Fiala 1977; Meacham and Estabrook 1985); the Le Quesne school does not make such a stipulation, their method accepts both polar and non-polar characters (Gauld and Underwood 1986). The latter method thereby permits the use of a wider range of characters and is the method employed in this study. In the present study, the zero state is arbitrarily assigned when coding non-polar characters (in cases where there is a clear majority, the majority state is designated as 0). If the character is multi-state, a system of additive binary coding is used (Section 4.5) so that morphologically similar states are adjacent (as for characters with hypothesized polarities - see under individual character descriptions, Section C).

Le Quesne (1969) pointed out that a character which has evolved only in one direction on a single occasion in the history of a group would give an unambiguous indication of the phylogeny of that group. Such characters he termed 'uniquely derived'. He noted that, when making pair-wise comparisons of characters coded in binary form i.e. as 'two-state' characters, normally coded 0 and 1, if all four combinations - 00, 10, 01, 11 - of the states of the two characters are found, then it is a necessary logical consequence that either one or other of the two characters is not uniquely derived or that neither is. Pairs of characters 'pass' the test if they do not show all four combinations. Estabrook, Johnson and McMorris (1976) designated pairs of characters that pass the test as 'compatible'(their usage being restricted to the special case where the 00 combination occurs - it is also used in a broader sense; to include characters passing the Le Quesne test). It is important to note that if only three or less of the four possible combinations are found it does not necessarily prove that both characters in a pair-wise comparison are uniquely derived characters; only that they may be. For example, one of the two characters may have transformed from the 01 state (for example) on more than one occasion while the second character remained in the same state on each occasion, when only three of the four combinations would be found. Alternatively, all four combinations may have evolved in the history of a group but are no longer found if one has died out (lineage has become extinct) or not all four occur in the available study material. Le Quesne (1982: 268) also noted that an incompatibility in a pair-wise character comparison does not indicate which of the characters is, or is not, uniquely derived.

The object of the Le Quesne test is to produce a set of compatible characters by (i) making pair-wise comparison of every character with every other character (but not with the states of the same multistate character, which cannot logically fail the Le Quesne test - see below for further details), and (ii) deleting the character with the largest number of observed incompatibilities, recounting the incompatibilities of the remaining characters deleting the character with the most incompatibilities, and repeating the process until no compatibilities remain in the character set. The compatible character set produced by these means has been termed a 'clique' by Estabrook, Strauch and Fiala (1977). There may be more than one way of deleting the characters to arrive at a clique: when comparing every character with every other character it may happen that a particular character pair is responsible for producing a non-polar incompatibility. Either character may be deleted to produce alternative character cliques.

The Le Quesne test includes two forms of incompatibility: unconditional (non-polar) and conditional (polar). If the states are coded 0 and 1, then two characters are unconditionally incompatible if all four character state combinations are present (see p. 69). This form of incompatibility is non-polar; it does not matter which combination represents the primitive condition, it is not possible to link the four combinations in a phylogenetic sense without invoking homoplasy - forward parallel (= independent) derivation or reversal of at least one or other of the characters, see below . This type of incompatibility cannot be removed by reversing the 0 and 1 scores.

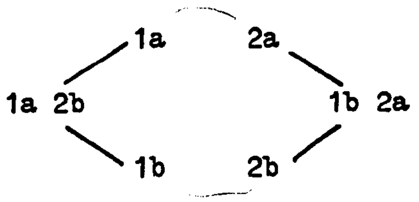


Fig. 10. Unconditional or non-polar incompatibility.

If all four combinations are present then there are always at least two ways of transforming both character states, i.e. of accounting for the presence of all four combinations. This is true whatever the starting point (whichever combination is taken as the primitive condition).

If 0 is the inferred primitive and 1 the inferred derived state, and no more than the three combinations 01, 10 and 11 occur, then the two characters are polar incompatible. Lacking the 00 combination they can only be linked at the expense of two convergent derivations of the 11 combination. This type of incompatibility is 'conditional' - it is dependant upon the polar coding of the states; the incompatibility can be removed by reversing the 0 and 1 scores of one or both of the characters (Fig. 11).

Fig. 11. To demonstrate removal of incompatibility by reversal of character state coding.

Original combination:	01	10	11	gives 01 → 11 ← 10
Reverse 1st only :	11	00	01	gives 00 → 01 → 11
Reverse 2nd only :	00	11	10	gives 00 → 10 → 11
Reverse both :	10	01	00	gives 10 ← 00 → 01

Singleton characters - ones in which the 0 or 1 score is found only in one taxon - cannot logically fail the Le Quesne test. Derived (apomorphic) singleton characters or non-polar characters with a single '1' score can give, at most, only three of the four combinations: either 01, 00, 10 or 00, 01, 11; which cannot therefore be polar incompatible since they are linked via a 00 combination. Primitive (plesiomorphic) singletons or non-polar characters with a single '0' score, however, while not being able to fail the Le Quesne test may show polar incompatibility - when comparison with another character gives the 01, 11, 10 combination.

A non-polar compatible character set may be obtained by applying some specified criterion for the elimination of those characters with high incompatibility counts. Le Quesne (1969, 1972, 1982) has given a number of methods for character elimination, these include:-

i) Using the Le Quesne matrix, simply by drawing vertical and horizontal lines. The remaining incompatibilities are recounted and the process is repeated until no incompatibilities remain. (The original Le Quesne procedure).

ii) Alternatively, the character with the smallest number incompatibilities is accepted as uniquely derived and those characters incompatible with it are eliminated. Again, the process is repeated until no incompatibilities remain.

iii) Le Quesne (1972) gave a formula for the probability of finding all four character combinations for a pair of characters based on the null hypothesis of random distribution of character states amongst the taxa being examined. The number of incompatibilities actually observed in the data set divided by the sum of the calculated expected incompatibilities gives a ratio which Le Quesne called the 'coefficient of character-state randomness'. If calculated for each character (with respect to all the other characters) the coefficient gives an indication of the likelihood of a character being uniquely derived: the closer the ratio is to 0 the more likely it is to be uniquely derived (derived singleton characters always score 0).

iv) Le Quesne (1972) also gave a 'normal deviate method' which can be applied to single characters and groups of completely correlated characters. It shows if the deviation from random is statistically significant. The character with the largest positive normal deviate value is accepted as uniquely derived and the characters incompatible with it are eliminated. The process is repeated until no incompatibilities remain.

One of the problems with compatibility analysis is that it may (especially in the absence of a limiting criterion) give a very large number of possible compatible sets (cliques). Choice of the 'best' set is difficult in such cases. Estabrook, Strauch and Fiala (1977) put forward the 'biggest-is-best' concept - suggesting acceptance of the clique with the largest number of characters. Le Quesne (1982: 270) suggested that such large sets are likely to include parallelisms based on function.

Once obtained, a compatible set may be used - together with other characters which permit further resolution at the cost of a minimal/limited number of homoplasies (parallelisms and reversals) - to derive as fully a resolved dendrogram as the data permits. The following section gives further information on the means by which such a resolution may be achieved, with specific reference to a particular compatibility analysis program.

(b) Le Quesne compatibility and the LEQU. BAS program.

A computer programe, LEQU. BAS. written by Dr. G.L. Underwood and developed in Gauld and Underwood (1986), incorporate much of Le Quesne's work (1969, 1972, 1979 and 1982) and is used in the present study. Both Le Quesne's method and the program require that the characters are coded as two-state or binary characters (0, 1) in a matrix. Multistate characters may be used - they are reduced to binary form by the method of additive binary coding (as noted above p.65). Briefly, the LESQ. BAS program operates as follows:-

1) The primary data matrix is written in with the computer in wordprocessing mode. The data matrix has data in columns (characters) and rows (taxon numbers). Multistate characters are broken down into series of binary characters which are numbered as incremental figures after a decimal point behind the main character number, e.g. character 5 is broken down into three binary characters; 5.1 5.2 and 5.3 (a numbering convertion established by Underwood 1982). Variable characters are denoted by a 'V'; missing data by a '-'. Variable scores are treated as both a 0 and a 1 entry - both scores are checked for incompatibility. In the case of missing data the pairwise character comparison is not made - the program 'skips' that particular comparison.

2) The main LEQU. BAS program includes a procedure for discovering character pair incompatibilities in the binary coded data set. Every character is compared pair-wise with every other character to see if the four combinations occur in the taxa concerned (but does not compare the binary components of a multistate character, which cannot logically fail the Le Quesne test). A Le Quesne test matrix is produced and may be printed out, where non-polar incompatibilities are printed as an 'X'; absences of the 00 combination, = polar incompatibilities in the case of characters for which a polarity has been postulated, as a ':'.

3) The number of non-polar compatibilities and the number of polar

incompatibilities are totalled for each character. As Le Quesne (1969: 202) points out, it is not possible to say that any particular character cannot be a uniquely derived chacacter but characters with high numbers of incompatibilities are least likely to be uniquely derived.

4) The printout from LEQU. BAS thus includes for each character: a total of the observed incompatibilities, their expected incompatibilities calculated with respect to the null hypothesis of random distribution of character states and the coefficient of character-state randomness - also known as randomness ratios, or observed/expected (O/E) values. Grand totals for the whole data set are also given for each of these categories and the characters are ranked in ascending order of O/E value (see Table 4).

As Gauld and Underwood note, the coefficient of character state randomness gives a measure of the degree of order of the distribution of the states of a character in relation to the rest of the character set. Similarly, the O/E value for the data set gives a measure of the order within the data set. A coefficient approaching or exceeding 1.0 suggests that the states of that character (or of the data set) approximate a random distribution.

5) The next stage is the application of one of the criteria for the elimination of characters with high non-polar incompatibility counts in order to arrive at a (non-polar) compatible character set or clique. The LEQ. BAS program uses method (iii) - the 'coefficient of character-state randomness' outlined above (p. 72).

6) Also derived from Le Quesne's 1972 paper is the LEQU. BAS 'boil-down' procedure - the system of character elimination used by Gauld and Underwood (1986) to arrive at a non-polar compatible set. This is achieved by serial deletion of the character with the worst O/E score and re-running the Le Quesne test for the remaining characters until no incompatibilities remain, leaving a totally compatible data set (which may however include characters which are polar incompatible - see Results). This is one set

of compatible characters. In order to obtain the maximum set and/or some indication of possible alternative sets, usually the last six to eight characters to be deleted are restored (but see Results - I. Compatibility analysis). The number to be restored is determined by the intervals in the O/E ratios. Either the number of incompatibilities or a sudden reduction in the O/E ratio usually marks the set to be restored; if the O/E values were to go : 0.6, 0.55, 0.4, 0.38, 0.15, 0.14, 0.09*, 0.05*, 0.03*, 0.01*, 0 (*which are printed out as 9E-2, 5E-2, etc.), then one would restore the characters up to, and including, the 0.15 level. The Le Quesne test is re-run but now the compatibility matrix is examined each time for possible alternative character deletions thus giving alternative sets of compatible character sets.

The LEQU. BAS also incorporates a 'marking' procedure based on the 'labelling' procedure of Guise, Peacock and Gleaves (1982). This procedure counts the number of occasions on which a taxon is uniquely responsible for a pair of characters failing the non-polar Le Quesne incompatibility test and the number of occasions each character is involved. The results are printed as a table (Table 11). The figure in brackets next to the taxon is the total number of marks the taxon has received. Frequently marked taxa have the most discordant (least well-ordered) character sets. High mark scores for a taxon for any given character suggests parallelism for that character score - that the taxon will not fit on the dendogram without multiple homoplasies; in other words, that taxon may be responsible for most or all of the Le Quesne test failures for that character.

4.7 Parsimony methods.

In their efforts to infer evolutionary trees, most systematists have adopted, often somewhat uncritically, the principle of minimum evolution. This principle can be construed in a number of ways; commonly as the search for a minimum length tree. This is usually justified on the grounds of parsimony - the preference for hypotheses requiring the fewest, i.e. the least number, of character state changes - in fact, as Sneath and Sokal (1973: 321) note, it is not easy to justify minimum length evolutionary trees in any other way. Felsenstein (1982: 387) notes the unsatisfactory practice of accepting a minimum length tree as a basis for phylogenetic inference, by drawing attention to a remark made by Sneath at a meeting: "why are we so obsessed with finding an absolutely minimal tree when there may be others of nearly minimal length? Should having one more evolutionary step rule out a phylogeny?". Parsimony is invoked for one reason, and one reason only - it is a useful methodological principle. The point is very neatly put by Friday (1982), who said that parsimony is "an inevitable component of scientific method..." and that its use in the inference of patterns of phylogenetic relationship "reflects the intuitive appeal to simplicity...." which "underlies our approach to the construction of hypotheses". Friday (loc. cit.) also observes that advocates of parsimony methods do not usually make the claim that evolution actually is simple. Panchen (1982: 317) specifically makes the point that we know that the course of evolution is <u>not</u> parsimonious, citing the work of Romero-Herrera et al., (1978: 61ff) on the molecular evolution of myoglobin.

The position adopted in the present study, regarding parsimony and the use of parsimony methods, is essentially that of Gauld (1985) and also Felsenstein (1982). <u>In summary</u>: Parsimony is a useful methodological principle. There is, however, no reason to expect the course of evolution to have been parsimonious; indeed, there is good reason to suggest that it is not. The use of a parsimony method provides a second, logically soundly-based, method for making a phylogenetic analysis of a fairly large data set. The aim is to produce a cladogram (s) for comparison with a cladogram (s) derived from compatibility analysis, and so arrive at a preferred, consensus cladogram.

The program used in the present study is the Wagner parsimony method from PHYLIP (package for inferring phylogenies), written by Dr. J. Felsenstein, Department of Genetics, University of Washington. PHYLIP offers four routines for analysing discrete state data: (i) Camin-Sokal parsimony, (ii) Dollo parsimony, (iii) Wagner parsimony and (iv) MIX - a mixed method which allows (i), (ii) or (iii) to be specified by individual characters. Fortuitously, for technical reasons, at the time the parsimony analysis was undertaken only the Wagner option was available. Fortuitous, because neither the Camin-Sokal nor the Dollo Parsimony methods (and therefore not the MIX method either) give as short a tree as the Wagner method because they place restrictions on the 'tree-growing' process (Felsenstein 1982, Gauld 1985). The Camin-Sokal method does not permit reversal from 1 ⟶ 0; the Dollo parsimony does not allow forward parallel development of characters. It is not, in view of comments given above, the case that a shorter tree is in some way more desirable than longer trees generated by the Camin-Sokal, Dollo and MIX methods. The objection is that there is no reason to assume <u>either</u> parallel development is more likely than character state reversal (Camin-Sokal parsimony), <u>or</u> that reversals are more likely than parallelisms (Dollo parsimony). There is simply no basis upon which either assumption may be made. The Wagner method regards both as improbable (rather than equally likely) and so minimizes the number of character state changes. The way in which the Wagner method minimizes the character state changes in a network or tree is described, in principle, below.

In trees and networks taxa are linked such that the distance between them is directly proportional to the number of character state differences between them. The distance indicates the character state changes needed to 'change from' one taxon to another. Parsimony methods (in this case the Wagner method) seek to minimize the overall length of the tree. Sneath and Sokal (1973: 324) refer to 'minimally connected graphs or trees'; they use the terminology of graph theory where such structures are referred to as 'Steiner minimal trees'. The distance between taxa operational taxonomic units - OTU's or 'points' in graph theory) may be minimized by postulating common ancestors (hypothetical taxonomic units - HTU's or 'nodes'= 'Steiner points').

The simplest case is the construction of a Wagner <u>network</u>. A simplified example, based on Sneath and Sokal (1973: 330-332), is given in Fig. 12 and is described briefly below. An algorithm for constructing Wagner networks was originally given by Farris (1970). For any given data matrix, in this case one comprising 3 taxa and 7 characters, the distances between the component taxa are calculated. These distances are the number of character state differences between pairs of taxa and are referred to as 'Manhatten' or 'city blocks' distances in the literature (e.g. Sokal and Sneath, ibid., 125-126). These distances are entered in a 'Manhatten distance matrix'. The pair of taxa <u>a</u> and <u>b</u> with the greatest Manhatten distance d, (a, b) is identified. Thus the first internode may be drawn (Step 1, Fig. 12). The distance between all the remaining taxa j and the internode (a, b) is calculated using the formula given under Step 2 (Fig. 12). The taxon with the greatest distance is then joined on at the interval INT (a, b) = HTV at node in (Step 3). In the example given, C is joined on to internode a, b at u.

The construction of a 'rooted' Wagner tree is different in that one taxon is selected as ancestor. There are a number of convertions/ methods for selecting the ancestral taxon - one can hypothesize an all-states 0 taxon, or use a character profile where the character state vector ? is a configuration common to all the taxa in the study group, or else, if good evidence is available, nominate the character profile of either one of the study taxa or an outgroup taxon as ancestor. The taxon with the fewest additional derived characters is connected to the ancestor. Tree construction then proceeds as with the network except that the order in which taxa are added to the tree is-taxa with minimum additional derived characters first - taxa with the highest number of additional derived characters last. As Sneath and Sokal (ibid. : 333) put it "it is readily apparent that the number of evolutionary steps between an ancestral HTU j and a descendant OTU k on a cladogram is nothing but the Manhatten distance between these nodes over all characters".

Felsenstein's PHYLIP Wagner Network Parsimony Method program carries out the unrooted parsimony method first introduced by Eck and Dayhoff (1966), and independently by Kluge and Farris (1969). The program is a variant of the Camin-Sokal parsimony method which allows changes in both directions along the character state tree, 0 → 1 and 1 → 0, does not assume that we know the ancestral state, and minimizes the total number of changes. Felsenstein listed six, implicit assumptions in his program:-

1. The characters are evolving independently.
2. Different lineages are evolving independently.
3. The ancestral state is not known (but see below).
4. Over the evolutionary times which are relevant for the particular group, changes 0 → 1 or 1 → 0 are a priori improbable, i.e. by taking character state change to be an improbable event it is evoked as little as possible in the tree-building process, thereby minimizing the total number of changes.
5. Retention of polymorphism for both states is far less probable than are changes of state.
6. Inequality of lengths of segments of the tree is not so extreme that two changes of state along a long segment are more probable than one change along a short segment.

The program, as given above, produces a Wagner network or unrooted tree (ancestor not specified), but in the present study the option, for rooting the tree by running the program with an additional, hypothetical, all-states zero ancestor (i.e. a plesiomorphic ancestor) - mentioned above, was adopted. As Gauld (1985: 65) pointed out, use of any other kind of outgroup taxon is liable to introduce more incidences of homoplasy (parallelisms - forward and reverse).

One particular general point about Wagner trees is that the order in which taxa are incorporated into the tree during the tree-building process can make a difference to the topology of the trees produced. Two usual methods of dealing with this are: (i) to add the taxon with the highest number of zero scores, then the taxon with the second highest and so on, to the taxon with the least zero scores. (ii) to compare the trees produced as a result of several different taxon-order incorporations and choose the tree with the minimum length.

The first of the two methods seems logical but may not necessarily produce a shorter tree than a tree produced by the second method. In the present study two taxon order incorporations were tried. Taxa were numbered somewhat arbitrarily, 1-21 - in alphabetical order with respect to the initial letter of the genera name and with respect to the species name within the genus; thus _Alytes_ species preceed _Ascaphus_ etc. and _A. cisternasii_ (taxon 1) preceeds _Alytes muletensis_ (taxon 2), but _A. o. obstetricans_ (taxon 3) preceeds _A. o. boscai_ (taxon 4) - nominate forms come first. The two orders of incorporation were:-

1. In numerical order 1 first, 2 second and so on to number 21.
2. With respect to the LEQU. BAS marking procedure scores - least marked taxon first, most heavily marked taxon last. Since high mark scores are associated with unique responsibility for higher levels of homoplasy then introducing the taxa in order of increasing mark scores might be expected to produce a shorter tree than 1. above.

The shorter tree is to be preferred on the grounds of parsimony. However, should either of the two trees be congruent with/more similar to the tree produced by compatibility methods then this tree would be favoured since the two trees are generated by different methods - even if the congruent parsimony analysis tree is the longer of the parsimony trees. (For further details see Parsimony Analysis section).

Fig. 12 To construct a Wagner Network.

Given data matrix.

Characters	1	2	3	4	5	6	7
Taxa							
A	0	0	0	1	0	0	0
B	0	1	0	0	1	1	1
C	0	0	1	1	1	1	1

Manhatten distance matrix.

	A	B	C
A	-		
B	5	-	
C	4	3	-

Step 1

Take d, (A, B) = 5

This gives the first internode : A 5 B

Step 2.

Calculate distance for all OTU's j to the HTU uj representing the interval INT (a, b) for the given j using the formula:-

$$d, (j, \mathrm{INT}\ (a, b)) = \tfrac{1}{2} \left[d, (a, j) + d, (a, b) \right]$$

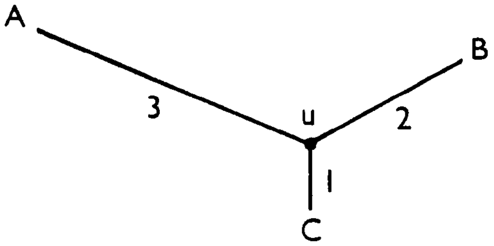
in this example

$$d, (C, \mathrm{INT}\ (a, b)) = \tfrac{1}{2} (4 + 3 - 5) = 1$$

Step 3.

The HTU u is constructed between taxa A, B and C. u is a vector, its character states are given by the median states of the taxa. For character 1 the states are 0, 0, 0 - the median is therefore 0; for ch. 2, 0, 1, 0 so the median is 0; for ch. 4 1, 0, 1 so the median is 1, and so on. Thus the character state vector for HTU u is

$$\left[0, 0, 0, 1, 1, 1, 1\right]$$



Note: This example shows the simplest case of tree-building - for three taxa where it is not possible to get character incompatibility. If, when dealing with four (or more) taxa there are character incompatibilities then the calculated distances will become distorted (i.e. the distances between pairs of taxa on the network will not be the same as the distances given in the Manhatten distance matrix).

B. MATERIALS AND METHODS.

Osteological data were obtained from a total of 220 specimens representing 21 of the 22 presently recognized taxa (see Introduction). This study is based primarily upon the detailed study of 64 skeletal preparations - alizarin preparations; some stained for bone only, others double stained for cartilage and bone, and wet and dry skeletons. In addition, x-radiographs of a further 136 specimens were prepared or otherwise made available, thus supplementing the data obtained from skeletal preparations with some additional data from larger samples and from rare specimens - notably *Barbourula kalimantanensis*, known only from the type specimen, and *Discoglossus nigriventer*, now possibly extinct - data otherwise unavailable because of the destructive nature of skeletal preparation.

For a full listing of material examined see Appendix I.

Characters

"We care not how trifling a character may be - let it be the mere inflection of the angle of the jaw, the manner in which an insect's wing is folded, whether the skin may be covered by hair or feathers - if it prevail throughout many and different species, especially those having very different habits of life, it assumes high value; for we can account for its presence in so many forms with such different habits, only by its inheritance from a common parent. We may err in this respect in regard to single points of structure, but when several characters, let them be ever so trifling, occur together throughout a large group of beings having very different habits, we may feel almost sure, on the theory of descent, that these characters have been inherited from a common ancestor. And we know that such correlated or aggregated characters have especial value in classification. "

Charles Darwin (1859) "The Origin of Species" (p.408-409).

Erratum: Character 1, pp. 85-86. Delete text from p. 85, line 17 "the maxilla - Sato 1934..." to p. 86, line 4 "... between *Discoglossus* and *Barbourula* detailed above".

Character 1. Nasal capsules - lateral displacement. (Fig. 31).

Trueb (1973: 87) noted that in ascaphids (meaning *Ascaphus* and *Leiopelma*), *Bombina* and the salamanders the nasal capsules tend to be depressed and laterally displaced compared with other anurans and commented "presumably this is a primitive trait". I disagree with Trueb's interpretation of the condition of the nasal capsules in *Bombina*. Trueb is citing two separate features: depression and displacement. In *Bombina* the nasals may be depressed (most noticeable in *B. bombina*, *B. orientalis*, less so in *B. maxima* and *B. microdeladigitora*) but they are not or only slightly laterally displaced - certainly not as widely separated as in *Ascaphus*, *Leiopelma* and the salamanders (urodeles). Estimating the degree of depression of the nasal capsules tends to be rather subjective, whereas the state or lateral displacement may be confirmed by reference to the width of the septum nasii. In species with laterally displaced nasal capsules the septum nasii is broad and the medial margins (inner walls) of the nasal capsules are clearly widely separated - particularly evident in *Ascaphus*. In the maxilla - Sato 1934 a, b and c on *Hynobius* spp. and *Pachypalaminus boulengeri*. In some urodeles the lacrimal bone separates the nasal and maxilla e.g. in *Batrachuperus sinensis* (Carroll and Holmes 1980, fig. 4B). It is also of interest that state 0 seems to be the common condition in the majority of Anura (Trueb 1973, Duellman and Trueb 1986 and BM dry and alizarin skeleton collections) but is probably quite a labile character.

State 0 is considered primitive : i) because the states seen in *Barbourula* and *Discoglossus* are evidently 'special', of limited distribution, possibly even unique to these genera and are therefore considered derived conditions. ii) because contact between the nasal and maxilla in urodeles is between the anterolateral margin of the nasal and the dorsal margin of the maxilla; the posterolateral margin of the nasal (the site of the maxillary process of the nasal in the Anura) is separated from the maxilla by a distinct gap. The differences between Discoglossus and Barbourula detailed above species with little or no lateral displacement the septum nasi is narrow and the inner walls of the nasal capsules are almost abutting. I therefore restrict this character to the degree of displacement of the nasal capsules (compared with other anurans), and on this basis re-ally Bombina with the other discoglossids.

Two states of this character are recognized:-

State 0. Nasal capsules laterally displaced; septum nasi broad.

State 1. Nasal capsules not, or only slightly displaced; septum nasi narrow.

On the basis of outgroup comparison with the urodeles, especially with reference to the Hynobiidae, also Francis (1934: 22-24, citing Bremer in Stadtmuller 1924, and Francis' pl. I, figs. 1 and 2), I agree with Trueb's suggestion that lateral displacement is the primitive condition.

The direction of change is therefore: 0 ⟶ 1.

Character 2. Nasals - medial contact. (Fig. 32).

The nasals are paired dermal bones overlying and protecting the olfactory region of the skull. They vary widely in size and shape in the Anura and may cover part or even all of the nasal capsules. This character reflects nasal size, which is not included in the data set because of difficulties in coding/differentiating between character states. While there is an actual correlation within the study group between laterally displaced nasal capsules and widely separated nasals this is not a necessary logical correlation; members of the outgroup - urodeles, especially hynobiid salamanders and salamandrids - have laterally displaced nasal capsules and nasals in medial contact or only slightly separated.

Three states are recognized:-

State 0. Nasals in medial contact or only narrowly separated.

State 1. Nasals widely separated.

State 2. Nasals fused medially, for at least part of their length.

State 0 includes the condition where the nasals are narrowly separated anteriorly and we are diverging posteriorly (Alytes species with the exception of A. cisternasii). State 0 includes all the Discoglossidae with the exception of Bombina maxima which shows state 2, interpreted as a special condition of state 0. State 1 includes only Ascaphus and Leiopelma. Outgroup comparison, with special reference to hynobiids (diagrams given in Sato 1934 a, b and c) and salamandrids (Francis 1934: 28) suggests medial contact/narrow separation in primitive. In the case of this character the outgroup could be expanded to include the temnospondylous labyrinthodonts which also have nasals in medial contact. The temnospondylous labyrinthodonts are important because there has been general agreement that they include the possible common ancestor of anurans + urodeles (Duellman and Trueb 1986: 437). With state 0 primitive and state 2 considered to be a special case of state 0, the direction of change is postulated as:-

$$2 \leftarrow 0 \rightarrow 1$$

Character 3. Nasal - maxilla contact. (Fig. 33).

This character is concerned with the relationship between the maxillary process of the nasal and preorbital process of the maxilla (terminology of Trueb 1973: 75 and 78 respectively). In the study group the maxillary process of the nasal is absent in *Leiopelma*, weakly developed to absent in *Alytes*, *Ascaphus*, *Bombina bombina*, *B. variegata* and *B. orientalis* and moderate to well developed in *B. maxima*, *B. microdeladigitora*, *Barbourula* and *Discoglossus*. In the moderate to well developed category there are three clearly different conditions. In *B. maxima* and *B. microdeladigitora* the maxillary process of the nasal is slightly separated from the maxilla (and in this it is similar to other species of *Bombina*, *Alytes*, *Ascaphus* and *Leiopelma*), yet exhibit a very special condition, being only slightly separated from the elongate medially curving anterior ramus of the pterygoid. In *Barbourula* and *Discoglossus* there is contact between the maxillary and preorbital processes but it is "achieved" in different ways. In *Discoglossus* the distal end of the maxillary process abuts the pars facialis of the maxilla and the preorbital process of the maxilla passes ventrally to the maxillary process. In *Barbourula* the distal end of the maxillary process does not abut the pars facialis of the maxilla but the anterior margin of the maxillary process abuts along the length of the posterior margin of the preorbital process of the maxilla.

Three states are recognized:-

State 0. Nasal and maxilla not in contact.

State 1. Nasal and maxilla in contact; Maxillary process of the nasal overlying the preorbital process of maxilla.

State 2. Nasal and maxilla in contact; anterior margin of the maxillary process of nasal abutting along the length of the posterior margin of the preorbital process of maxilla.

Outgroup comparison using hynobiids and *Salamandra* (Francis 1934 - see character 2) suggests contact to be primitive but the nature of the contact differs from that in the discoglossids *Barbourula* and *Discoglossus* (there is no maxillary process to the nasal in these urodeles - the lateral margin of the nasal contacts the dorsal margin of part of suggest that states 1 and 2 are independently derived from state 0.

The direction of change is therefore:-

$$2 \longleftarrow 0 \longrightarrow 1$$

Character 4. Nasals - maxillary process. (Figs. 34 and 35).

The development of the maxillary process of the nasal is variable; there may be no sign of any evident process (a state which I would term 'absent'), the process may be weakly to moderately developed or it may be elongate appearing as a distinct, well developed process. Extension of the maxillary process, especially where there is articulation with the maxilla (as in Barbourula and Discoglossus), increases the level of protection given to the olfactory region.

Three states are recognized:-

State 0. Nasals, maxillary process absent.

State 1. Nasals, maxillary process present, weakly to moderately developed.

State 2. Nasals, maxillary process present as a long, distinct and well developed process.

The development of the maxillary process in the various discoglossoid taxa has been described under Character 3 (above). Outgroup comparison (urodeles, with special reference to hynobiids and salamandrids and also using temnospondylous labyrinthodonts as part of an extended outgroup) suggests state 0 is primitive. I further suggest that the presence of a maxillary process is a neomorph for the Anura but may well be subject to a high level of homoplasy in the Anura as a whole. The parsimonious assumption is that, with state 0 primitive, the maxillary process will transform from a weak/moderate to a long, distinct, well developed process.

The direction of change is therefore taken to be:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 5. Sphenethmoid ossification: presence and development. (Fig. 36).

The sphenethmoid is an endochondral bone located medially, posterior to the nasal capsules. According to Trueb (1973: 87) it is invariably present as a housing around the anterior end of the brain. Trueb (loc.cit.) also commented that the precise limits of the sphenethmoid, as with other neurocranial bones, are "extremely difficult to define because all these elements are formed in a continuous system of cartilage surrounding the central nervous system". The sphenethmoid probably has a dual function: protection of the forebrain and provision of support to anterior region of the skull and neurocranium, when it may provide points of articulation with the nasals, frontoparietals, cultriform process of the parasphenoid and palatines if present (all discoglossoid frogs lack free palatines see Character 33). The sphenethmoid may or may not be ossified.

The present character is concerned with sphenethmoid ossification, structure and appearance in dorsal view. Four states are recognized:-

State 0. Sphenethmoid ossified; a compact deep tubular structure.

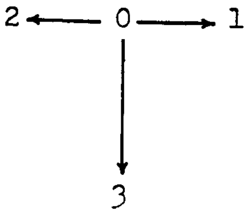
State 1. Sphenethmoid ossified; a compact shallow structure.

State 2. Sphenethmoid ossification present as two ill-defined lateral patches.

State 3. Sphenethmoid ossification variable within species at adult stage; usually not ossified, if ossified ossification may extend to olfactory canal and nasal septum.

State 0 includes *Barbourula* and all species of *Bombina*; the sphenethmoid is well ossified, long in dorsal view, even longer ventrally and relatively narrow producing a characteristic 'tubular' appearance. State 1 is found in *Alytes* and *Discoglossus*; the sphenethmoid is well ossified, short although still longer ventrally and wide in relation to its anterior - posterior length. (A. muletensis has the least well developed, most lightly built sphenethmoid in this group; Clarke 1984 provides figures and a comparison of sphenethmoid structure in Alytes spp.). State 2 is confined, within the study group, to Ascaphus. Occasionally, some Ascaphus show signs of separate ethmoid ossification (s) anterior to the frontoparietals, between the nasals (Altig 1969: 61 and Fig. 1). State 3 is only found, within the study group, in Leiopelma. Stephenson, E.M. (1951: 277-278) pointed out that there is a differential rate of development in the sphenethmoid bone (heterochrony) in Leiopelma, and later noted (Stephenson 1960: 476) that "it is rare to find any trace of a sphenethmoid ossification in L. archeyi, except in occasional large and relatively old specimens...." also that development of a bony sphenethmoid is "associated with advancing age in L. hamiltoni". Stephenson (ibid: 477) considered that the condition of the sphenethmoid in L. hochstetteri is approximately the same as in L. hamiltoni but thought that it probably ossifies at a faster rate. Study material of these three species showed one L. archeyi to have a well ossified sphenethmoid, and no sign of ossification in L. hamiltoni and hochstetteri (3 specimens). Stephenson's explanation that the ossification develops with increasing size and advancing age is probably correct for all three species of Leiopelma (Stephenson 1951: 278 gives further details).

Outgroup comparisons, with hynobiid salamanders (Sato 1934 a - c, Carroll and Holmes, 1980), also ambystomatids and salamandrid urodeles (Carroll and Holmes, 1980), suggest state 0 to be the primitive condition. State 1 may be interpreted as a less developed form of state 0. Trueb (1973: 88) commented that ontogenetically, all sphenethmoids pass through a "paired" stage and so Ascaphus/state 2 has 'failed' to develop beyond this stage. State 3 is a special case as described by Stephenson (1951, 1960). I consider the simplest (most parsimonious) interpretation of the data is to suggest states 1, 2 and 3 to be independently derived from state 0 :-



Character 6. Frontoparietals - lateral margins and neurocranial shape. (Fig. 37).

This character is concerned with the supraorbital shape (outline) of the frontoparietals and neurocranium. The lateral margins of the frontoparietals from the dorsolateral borders of the supraorbital neurocranium. The shape of these margins and the shape of the neurocranium in this region probably reflect many features/characters of the underlying brain itself, especially the forebrain and midbrain. Since there are three distinct neurocranial patterns within the study group and because of the neurocranial - brain correlation and interaction, then the shape of lateral margins of the frontoparietals might be expected to be a particularly informative and significant character.

Three states are recognized:-

State 0. Frontoparietals, supraorbital lateral margins straight.

State 1. Frontoparietals, supraorbital lateral margins slightly biconvex.

State 2. Frontoparietals, supraorbital lateral margins divergent.

State 0 includes all discoglossoids with the exception of *Bombina bombina*, *B. variegata*, *B. orientalis* and *Barbourula*. State 1 includes the three aforementioned species of *Bombina* and state 2 includes only *Barbourula*. (for further details of state 2 and the neurocranial condition of *Barbourula* see character 7).

Outgroup comparison, using hynobiid and ambystomatid salamanders, suggests state 0 to be the primitive condition. (Note: in these urodeles the frontals and parietals are separate yet the shape of the lateral margins of their neurocrania and the individual frontals and parietals are still obvious - straight sided). States 1 and 2 are considered independently derived from state 0.

The direction of change is therefore:-

$$2 \longleftarrow 0 \longrightarrow 1$$

Character 7. Neurocranial/skull width proportions.

Within the study group, Barbourula busuangensis and B. kalimantanensis are the only species to have a very narrow, tubular neurocranium (Duellman/Trueb 1986: 314, Fig. 13 - 17 A & B; Clarke 1987: 881-2, Figs. 1 & 2). All other discoglossoid species examined have moderately wide neurocrania - approximately a quarter to one-fifth the width of the skull. (Neurocranial measurement taken at the midpoint between the anterior and posterior corners of the orbits; the skull width measurement is the maximum skull width).

Two states are recognized:

State 0. Neurocranium moderately wide, ca. 1/5 (0.2) maximum width of the skull or wider.

State 1. Neurocranium narrow, ca. 1/10 (0.1) maximum width of skull.

Outgroup comparison (urodeles especially hynobiids, salamandrids - Salamandra and Triturus) and ontogenetic evidence (juvenile and subadult Barbourula have wider neurocrania than adults) suggest state 0 to be primitive. The direction of change is therefore:

$$0 \longrightarrow 1$$

This is seen as a very significant character in biological terms since the shape of the neurocranium must necessarily influence/correlate with the shape and disposition of the brain, especially the fore - and midbrain areas (which include the olfactory areas, the cerebral hemispheres, the hypothalamus - an important control centre in the autonomic nervous system, the optic lobes and penduncular portion of the midbrain which controls "mass movements of the body and limbs" Duellman/Trueb 1986: 392).

Frontoparietals.

Trueb (1973) noted that variation in the frontoparietals may include their fusion with one another (and possibly with surrounding elements like the nasals, sphenethmoid, exoccipital and prootic) and the extent to which they are marginally ossified. Minimally, the frontoparietals are present as narrow, longitudinal strips of bone overlying the dorsolateral margins of the neurocranium producing extensive anterior-posterior exposure of the frontoparietal fontanelle (e.g. in some hylids like Hyla arborea, Pseudacris clarkii, centrolenids, microhylids and myobatrachids). Maximally, the anterior margins of the frontoparietals articulate with the posterior margins of the nasals; the medial margins articulate with one another such that there is no dorsal exposure of either the posterior end of the sphenethmoid or frontoparietal fontanelle. Posteriorly and laterally, the frontoparietals may produce shelves which roof over the lateral region of the prootic, articulating with the dorsomedial margin of the squamosal (e.g. in Ceratophrys calcarata, see Lynch, 1971: 47, Fig. 20 A, and other ceratophryine leptodactylids). Other forms of maximal-type frontoparietal development may be seen in brachycephalids and hemiphractine and other casque headed hylids like Trachycephalus and Triprion. Trueb went on to comment that between these extremes "nearly every intermediate degree of frontoparietal ossification is represented in anurans" and also remarked (1973: 74) "... I would like to point out that the extent of ossification of the frontoparietal is one of the most reliable indices to the overall ossification of the cranium. A small, poorly developed frontoparietal is normally indicative of minimal ossification throughout the entire cranium, whereas if the frontoparietal is well developed, one can anticipate a corresponding degree of ossification elsewhere in the cranium". It should be noted that this remark refers to the level of the the cranial ossification, but not (necessarily) to that of the postcranial ossification. Trueb also noted that a frontoparietal fontanelle - a dorsal opening in the roof of the chondrocranium "is invariably present" and that "complete medial articulation of the frontoparietal obscures the fontanelle, which lies ventral to the bones".

Notwithstanding the foregoing, the marginal development of the frontoparietals, particularly of the medial margins, often (and this is certainly the case in the discoglossoid frogs) exhibits a discrete form or pattern in supraspecific or generic groups, and within these groups the differences seen are differences of degree - 'variation on a theme' (i.e. variation within a pattern/type). Clearly, in cases where there is dorsal exposure of the frontoparietal fontanelle the shape of the fontanelle and of the medial margins of the frontoparietal are necessarily logically correlated. To avoid duplication the fontanelle/marginal development of frontoparietal can be considered to be one character/character complex (Character 8). The other frontoparietal characters included in this study are: relationship of the frontoparietals with the foramen magnum 'Character 9) and the presence/absence of frontoparietal - otoccipital ridges (Character 10).

Character 8. Frontoparietals: degree of development and dorsal exposure of the fontanelle. (Fig. 38).

In the discoglossoid frogs the marginal development of the frontoparietals varies from weak (Bombina bombina, B. variegata, Alytes muletensis, A. (o). maurus, A. o. obstetricans, A. o. boscai, Ascaphus and Leiopelma) to moderate (Alytes cisternasii, Bombina maxima, B. microdeladigitora, B. orientalis, Discoglossus galganoi, D. pictus, D. sardus and some older/larger specimens of species given above), to well developed (D. montalentii, D. nigriventer and Barbourula spp.). Trueb's (1973: 74) general observation that there is a correlation between the development ("extent of ossification") of the frontoparietals and the overall ossification of the cranium is here confirmed in the case of the discoglossoid frogs. In those species having well developed frontoparietals, i.e. in Discoglossus montalentii, D. nigriventer and the two Barbourula species, the frontoparietal fontanelle is roofed over. In the remaining species where the fontanelle is dorsally exposed there may be one continuous fontanelle or a tendancy toward separation into anterior and posterior fontanelles (which may therefore be thought of as frontal and parietal portions of the fontanelle). In Alytes and Leiopelma this separation is indicated by a medially directed spur of bone on each frontoparietal which, as Boulenger (1897: 166) commented in the case of Alytes obstetricans, "gives the fontanelle the shape of the sole of a shoe". In A. cisternasii the separation into anterior ('frontal') and posterior ('parietal') fontanelles is complete in some specimens but not in others - in the extreme condition "the anterior fontanelle is large and kite-shaped, the posterior very small, a mere foramen between the fronto-parietals" (Boulenger 1897: 177 and Fig. 66); the 'normal' conditions in Alytes muletensis, A. obstetricans and A. cisternasii are shown in Clarke (1984: Figs. 1A and 2). It is evident that Alytes species share a distinct frontoparietal pattern - individual taxa exhibiting different degrees of development of this pattern - see general comments on frontoparietals preceeding this character.

The variation in degree of marginal development and the shape of the medial margins of the frontoparietals - which are intimately related to the shape and dorsal exposure of the frontoparietal fontanelle(s) - together give rise to five discrete types or patterns of frontoparietals/ frontoparietal fontanelles. Thus five states are recognized:

State 0. Frontoparietals, medial margins well separated and parallel; one continuous anterior-posterior fontanelle.

State 1. Frontoparietals, posteromedial margins approaching or in medial contact but not fused, leaving one anterior or anterior/posterior fontanelle.

State 2. Frontoparietals, medial margins fused posteriorly diverging anteriorly; no dorsally exposed fontanelle.

State 3. Frontoparietals, medial margins separated for most of their length (may be in contact posteriorly); with medially directed spurs of bone, fontanelle has "sole-of-shoe" shape - anterior and posterior portions (='doubling').

State 4. As per state 3, posterior fontanelle smaller; medially directed spurs of bone in contact or slightly separated. Effectively two fontanelles - anterior and posterior are kite-shaped or posterior reduced to a small foramen.

State 0 is found in Ascaphus; State 1 in Bombina and Discoglossus except D. montalentii and D. nigriventer ; State 2 in Barbourula, D. montalentii and D. nigriventer; State 3 in Alytes (except A. cisternasii and in Leiopelma and State 4 in A. cisternasii.

Outgroup comparison: Urodeles (all but esp. hynobiids, ambystomatids and salamandrids - Carroll and Holmes 1980, Dowling and Duellman 1974-78, Francis 1934) and Gymnophiona (Dowling and Duellman loc. cit., Taylor 1969). In urodeles (and gymnophiones) the frontals and parietals are separate bones and there is no dorsal exposure or the fontanelle. I do not regard the outgroup as being of sufficiently detailed similarity to allow the direct selection of one of the five described states as the primitive state. In Barbourula State 2 the anterior ends of the frontoparietals are diverging; in the outgroup they are parallel to the midline. If one allows for fusion of the frontals and parietals (see Trueb 1973: 71) and reduction of medial margins or separation of the frontoparietals then the state most closely resembling the outgroup state is State 0 - seen in Ascaphus (Underwood 1982: 250, criterion C). State 4 is considered to be a special form of State 3. With State 0 primitive and linking other states on the grounds of morphological similarity (aggregated differences between adjacent pairs at a minimum - criterion of Underwood ibid. : 247), the direction of change is:-

$$2 \longleftarrow 1 \longleftarrow 0 \longrightarrow 3 \longrightarrow 4$$

Character 9. Frontoparietals and the foramen magnum. (Fig. 39).

This character relates to the size, in particular the length and the anterior-posterior placement/position, of the frontoparietals. The foramen magnum is used as a reference point. In skulls where the posterior margins of the frontoparietals reach the foramen magnum they form a roof over the dorsal margin of the foramen magnum, bridging the otoccipitals; possibly effecting dome strengthening of the skull in this region. Two states sre recognized:

State 0. Posterior margins of frontoparietals in contact with, or slightly separated from the dorsal margin of the foramen magnum.

State 1. Posterior margins of frontoparietals clearly separated from the dorsal margin of the foramen magnum.

The urodeles have the posterior margins of the parietals in contact with, or only slightly separated from the foramen magnum especially in the Hynobiidae, although some urodeles e.g. the plethodontid salamanders may show the separated condition (Carroll and Holmes 1980). Using hynobiid salamanders as outgroup the direction of change is:-

$$0 \longrightarrow 1$$

Character 10. Frontoparietal - otoccipital ridges. (Fig.40).

Barbourula busuangensis has very high, confluent bony ridges extending from the posterolateral borders of the frontoparietals onto the medial part of the otoccipital. *Discoglossus galganoi*, *D. nigriventer* and *D. pictus* have low ridges in the same region. *Bombina maxima* and *B. microdeladigitora* have horizontal posteriorly directed flanges of bone in the same region.

Four states are recognized:

State 0. Frontoparietal-otoccipital ridges absent - no trace.

State 1. Frontoparietal-otoccipital ridges elevated into a low crest.

State 2. Frontoparietal-otoccipital ridges well developed, dorsally directed prominent crests. (Fig. 40 a and b).

State 3. Frontoparietal-otoccipital ridges present but poorly developed, horizontal and posteriorly directed.

Outgroup comparison with urodeles (Carroll and Holmes 1980; Francis 1934, BM skeletal collection - hynobiids, ambystomatids and salamandrids) indicates state 0 to be primitive. The direction of change is hypothesized to be:

$$3 \longleftarrow 0 \longrightarrow 1 \longrightarrow 2$$

Character 11. Otoccipital pattern. (Fig. 41).

The otoccipitals are the combined prootic and exoccipital bones which are fused in most (adult) modern Anura; together they form the neurocranium posterior to the sphenethmoid. The prootic portion is the more anterior part comprising the auditory capsules and the area anterior to the auditory capsules. The exoccipital portion is the posterior part of the neurocranium and includes the occipital condyles and the bony areas around the foramen magnum (Trueb 1973: 88). Note that Trueb in Duellman/Trueb 1986 treats the prootic and exoccipital separately but comments, p. 313, that in most anurans the ossified parts of the prootic are united medially and are indistinguishably fused with the exoccipitals posteriorly "to form one massive element" housing the posterior areas of the brain and the otic organs (inner ear), and says "this element has been referred to as the otoccipital by some authors". I suggest that the degree of development of the otoccipitals (note: usually referred to in the plural) provides a second, possibly more reliable, index for assessing the overall ossification of the skull; see comments on frontoparietals above.

The present character is concerned with the configuration of the otoccipitals, in particular their shape as defined by the anterior, lateral and posterior margins, seen in dorsal view.

Three states are recognized:

State 0. Otoccipitals tapering medially to laterally; anterior and posterior margins strongly convergent, - narrow, trapezoidal shape.

State 1. Otoccipitals narrow, truncate bar-like; anterior and posterior margins slightly convergent.

State 2. Otoccipitals bar-like; anterior and posterior margins almost parallel.

State 0 is confined to *Ascaphus* and *Leiopelma*; *Alytes cisternasii*, *Barbourula busuangensis* and *Kalimantanensis* show State 2; all remaining species in the study group are State 1. The equivalent structure in Urodeles is the occipito-petrosal (Stadtmüller) *fide* Francis 1934: 26 and Plate I, which appears, in hynobiids, ambystomatids and salamandrids, to be closest to State 0. Carroll and Holmes (1980) use otic-occipital for fused prootic, opisthotic and exoccipital; opisthotic-exoccipital and opisthotic-prootic for fusion of opisthotic with exoccipital and opisthotic with prootic respectively, and note that in *Batrachuperus* and *Hynobius* the otic capsule, the area equivalent to the part of the otoccipital under consideration, is composed of two separate ossifications - the prootic and fused exoccipital and opisthotic. Carroll and Holmes further note that in ambystomatids and salamandrids the otic is ossified as a unit as an otic-occipital (fused prootic, opisthotic and exoccipital) - p. 12, 14 and their Figs. 6 and 8. Whatever the designation of these bones comparison with the otic/otoccipital region in the discoglossoids suggest state 0 to be the closest equivalent condition.

The direction of change by arranging the states in order of similarity is:

$$0 \longrightarrow 1 \longrightarrow 2$$

where State 2 is seen as a more derived form of State 1.

Character 12. Otoccipitals - lateral margin. (Figs. 42 and 43).

The lateral development of the otoccipitals, as determined by the position of the lateral margin of an otoccipital relative to the outer margin of the orbital fossa and the medial margin of the pterygoid fossa, provides an indication of the width of the skull at the level of the otic capsules. To develop the analogy given in Duellman/Trueb (1986: 313), if the braincase of anurans is thought of as an inverted T-shaped box then this character is a reflection of the (maximum) width of the neurocranium taken across the arms of the 'T' (Fig. 42).

Four states are recognized:

State 0. Otoccipitals narrow, not reaching the outer margin of the orbital fossa or the medial margin of the pterygoid fossa.

State 1. Otoccipitals moderately wide, reaching or extending slightly beyond the outer margin of the orbital fossa but not reaching the medial margin of the pterygoid fossa.

State 2. Otoccipitals wide, extending beyond the outer margin of the orbital fossa and reaching the pterygoid fossa.

State 3. Otoccipitals very wide, extending beyond the outer margin of the orbital and the medial margin of the pterygoid fossa.

Only Discoglossus galganoi and D. pictus show State 1; only Alytes cisternasii has State 2 and Barbourula busuangensis and B. Kalimantanensis show State 3. The remainder of the study group are State 0 for this character. Urodeles, partly by extrapolation of pterygoid toward the maxilla to complete a notional orbital fossa, and notional extension of the quadrate and maxilla to give a hypothetical pterygoid fossa, and partly by comparison with the position of the lateral margin of the otic-occipital region with the outer margin of the 'open' orbital fossa are judged to be State 0. Hence State 0 is considered to be the primitive condition for the discoglossoids.

The direction of change is therefore:

$$0 \longrightarrow 1 \longrightarrow 2 \longrightarrow 3$$

Remarks: It might initially be considered that there is an element of repetition involved between this and the previous character, yet this character partitions off *D. galganoi* and *D. pictus* from other *Discoglossus* species and *Alytes cisternasii* from *Barbourula* species (*A. cisternasii* shares State 2, character 11 with *Barbourula*). In addition there is no reason to assume a logical correlation of State 0, character 11 with State 0 of character 12; the trapezoidal shape of the otoccipitals need not, *a priori*, necessarily be narrow - they could equally well be wide and trapezoidal.

Squamosals. (Fig. 44).

The squamosals are paired dermal bones which invest the quadrates (palatoquadrate cartilages) laterally and articulate ventrally with the quadrate dorsal and adjacent to the pars glenoidalis of the quadratojugal (terminology of Bolkay 1919) and dorsally with the crista parotica of the auditory capsule. The crista parotica invests the lateral margin of the otoccipital forming a cartilaginous pad between the squamosal and the otoccipital. In most anurans the squamosals are triradiate comprising an anterior or zygomatic ramus, a posterior (otic) ramus (which may or may not bear a medially-directed flange of bone known as the otic plate) and a squamosal shaft. There is considerable variation in the development of the squamosal and its rami. I agree with Trueb's (1973: 86) observation that the squamosals are invariably present in the Anura - I know of no case where they are actually absent yet taken individually, each of the rami may be considerably reduced if not actually absent. As Trueb in Duellman/Trueb (1986: 318) points out among hypo-ossified anurans like Notaden (Myobatrachidae) the squamosal may be reduced to a sliver of bone applied laterally to the quadrate. In other species either the otic or the zygomatic rami may be very poorly developed, almost vestigial. In Schmaderma carens (Bufonidae) only the dorsal portion of the squamosal shaft is ossified and is unusually short - no longer than either the otic or zygomatic rami. In other African bufonid species the ossified portion of the squamosal shaft is an even more poorly developed vestigial structure. In hyperossified anurans the otic ramus may articulate with a posterolaterally expanded frontoparietal to form a temporal arcade, as in Ceratophrys (Leptodactylidae) species (Lynch, 1971: 108) . In some species e.g. Pyxicephalus (Ranidae) the zygomatic may form a suture with the maxilla.

Francis (1934: 29-30) described the squamosals of Salamandra as "paired splint-like bones lying on the dorsal side of the quadrates, to which they become very closely fixed" and noted that while there is "a distinct tendency for the bone to be 'T'-shaped it is not so definite as in the Frog". In fact in the urodeles any tendency toward 'T'-arm formation is ill-defined. (Francis 1934, Plate 1, and Figs. 2, 4-6, 8 - **Tylototriton:** Salamandridae more developed than usual but different from the anuran pattern, and also Figs. 9-11 in Carroll and Holmes, 1980). Following Francis' comment, and with regard to the form of the squamosal commonly found in the urodeles, I suggest that the anuran otic plate should be regarded as a neomorph, there being apparently no equivalent structure in urodeles. It is possible that the otic and zygomatic rami, in the form in which they are seen in the Anura, might also be regarded as neomorphs, although it is convenient to regard them as derived from the urodele type.

Character 13. Squamosal - otic plate. (Figs. 44b and 45).

Within the discoglossoid frogs there is considerable variation in the development of the otic plate. In *Alytes cisternasii*, *Bombina bombina*, *B. orientalis* and *B. variegata* the otic plate is absent or present as a minute medially directed of bone (see Character 14 on the condition of the otic ramus in these three species of *Bombina*); it is either absent or present as a *very* poorly developed/differentiated sliver of bone along the medial margin of the otic ramus in *Alytes O. obstetricans*, *A. o. bascai*, *A. O. maurus* *A. muletensis*, and *Ascaphus*. In *Leiopelma* the otic plate is present but is rather weakly developed and poorly differentiated from the otic ramus; it may have a jagged medial outline and is closely applied to the crista parotica/weakly or unossified otoccipital (opisthotic) area. *Discoglossus*, *Barbourula* *(B. busuangensis)*, *Bombina maxima* and *B. microdeladigitora* have a well-defined, moderately well developed otic plates which overlie all or part of the dorsal surface of the crista parotica, and may also overlie part of the lateral margin of the otoccipital.

Three states are recognized:

State 0. Squamosal - otic plate present absent or present as a very poorly developed differentiated sliver of bone.

State 1. Squamosal - otic plate present, but weakly developed and poorly differentiated from the otic ramus, overlying and closely applied to the crista parotica.

State 2. Squamosal - otic plate a moderately well developed, well defined structure, overlying the dorsal surface of the crista parotica.

Following the comments made by Francis (1934) and others given above, in the introduction to this group of squamosal characters, I regard the otic plate as a neomorphic structure in the Anura. I also consider State 1 to be a special condition (autopomorphy) for *Leiopelma*; consequently the direction of change for this character is:-

$$2 \longleftarrow 0 \longrightarrow 1$$

Character 14. Squamosal - otic ramus. (Figs. 44c and 46).

The otic ramus provides (with the otic plate if present) a point of articulation between the squamosal and the lateral margin of the crista parotica, against which the jaws are simultaneously braced and suspended. It should also be noted that the posterior medial portion of the zygomatic ramus and, to a lesser extent, the extreme dorsomedial surface of the squamosal shaft articulate with the crista parotica and thereby share the same function as the otic ramus.

In *Bombina bombina* and *B. variegata* the otic ramus is either absent or present as a very small spur of bone extending medially from the posterior dorsal margin of the squamosal shaft (*contra* Trueb 1973: 87 who stated that in the Anura the "otic ramus, is always present"). Alternatively these small spurs of bone (usually one side only in *B. bombina* and *B. variegata* but present on both left and right squamosals in *B. orientalis*) may be interpreted as otic plate - but this interpretation would give otic plate present - otic ramus absent. *Alytes cisternasii* has a slightly more distinct yet very poorly developed otic ramus, separated/demarcated from the zygomatic ramus by a dorsal notch. Taken simply, the *A. cisternasii* condition is coded as the same state as seen in the three above-mentioned *Bombina* species. Alternatively, the *A. cisternasii* condition may be considered a special form of the short, distinct otic ramus seen in *Leiopelma* and the other *Alytes*, and the *B. bombina* - *B. variegata* - *B. orientalis* type otic ramus be assigned to a separate state. This alternative coding is not used since it might be argued that such an interpretation introduces a circularity into the analysis by being influenced by the fact that the absent/small spur condition is found in *Bombina* while the very poorly developed, almost absent condition in *A. cisternasii* is different *because* it is found in an *Alytes*. Similarly it is also circular reasoning to assume/consider the *A. cisternasii* condition to be a special form of the state found in other *Alytes* species.

In both cases the reasoning may be considered to be influenced by the current systematic assignment of the taxa concerned - such reasoning is circular because one of the main aims of this study is to test this assignment (the monophyly of the discoglossoid genera) - to assume it is self-defeating; it begs the question. Hence the alternative coding is not considered valid. Should it be correct the *A. cisternasii* condition will emerge post analysis as a parallel state with respect to the condition seen in the three *Bombina* species.

The remaining species in the study group, *Barbourula* (*B. busuangensis*), *Discoglossus* spp, *Bombina maxima* and *B. microdeladigitora*, exhibit a third condition (the second, described above, being found in *Leiopelma* and *Alytes* with the exception of *A. cisternasii*), in which the otic ramus is difficult to distinguish from, i.e. is continuous with, the otic plate and curves over the dorsal surface of the crista parotica. Thus, the three states are:-

State 0. Squamosal - otic ramus a short, distinct process

State 1. Squamosal - otic ramus absent, or present as a small spur of bone.

State 2. Squamosal - otic ramus; difficult to distinguish from, possibly continuous with, otic plate - curves medially over dorsal surface of crista parotica.

Although one might consider the otic ramus as seen in the Anura to be a neomorph (see introductory comments on Squamosals) it is evident that state 0 bears the closest morphological similarity to the condition of the otic process of the squamosal seen in the urodeles (Salamandrids, hynobiids and ambystomatids - BM specimens, Francis 1934 and Carroll and Holmes, 1980) and other squamosal features. States 1 amd 2 are considered to be independently derived from State 0.

The direction of change is therefore:

$$2 \longleftarrow 0 \longrightarrow 1$$

Character 15. Squamosal - zygomatic ramus. (Figs. 44d and 47).

In the Anura the zygomatic ramus of the squamosal may be absent or developed as a knob-like process, it may be a short to moderate process tapering to a point distally or it may be long and curve distally and ventrally toward the postorbital region of the maxilla. In some species a moderately long or long zygomatic ramus may articulate with an ascending postorbital facial process on the maxilla (see character 16). Trueb (1973: 87) commented that every conceivable degree if intermediate development of the zygomatic ramus occurs among anurans and that development is often positively correlated with skull size and level of ossification.

There is a great deal of variation in the zygomatic rami of discoglossoid frogs encompassing most of the variation described above. A zygomatic ramus is always present but poorly developed, as a short tapering process, in some Alytes species; in A. cisternasii the zygomatic ramus is a tiny round-ended, knob-like process Three basic types of zygomatic ramus in the discoglossoid group:-

(1) Simple short to moderate in length. This pattern is seen in Alytes (except A. cisternasii), Ascaphus, Bombina, Discoglossus and Leiopelma. Alytes species belonging to this group have a short ramus which tapers to a point distally reminiscent of the shape of an arrow head. Bombina has three forms of zygomatic ramus; short, slender, tapering and dorsally directed distally (B. bombina, B. variegata); short to moderate, simple, not tapering but slightly dorsally directed (B. orientalis); moderate, not tapering, distal end truncate/rounded and slightly dorsally directed (B. maxima, B. microdeladigitora). Discoglossus; short, approaching 'arrow-head' shape of an Alytes in D. sardus; longer, slender, tapering to a point in D. montalentii; short-moderate, pointed or truncate in other Discoglossus species. Yet they are not readily divisible into more detailed states; subdivision is risky in terms of imposing preconceived ideas onto states e.g. assuming all Bombina states are more similar to one another than to

any other zygomatic ramus type. It is also not particularly useful or practical in the context of an analysis into supraspecific relationships, to recognise a large number of states which are only slightly different one from another, especially when it would be difficult to confidently hypothesize the direction of polarity between such states. Consequently these species are grouped under the single state, zygomatic ramus simple, short to moderate.

(2) Long, curving distally toward the post-/suborbital maxilla - *Barbourula busuangensis* and *B. kalimantanensis* (seen in x-radiographs).

(3) A very small round-ended knob-like process - *A. cisternasii*.

State 0. Squamosal - zygomatic ramus simple, short to moderate in length.

State 1. Squamosal - zygomatic ramus long, curving distally toward post-/suborbital maxilla

State 2. Squamosal - zygomatic ramus a very small round-ended knob-like process

Outgroup comparison with urodeles (see introduction to this section on squamosal characters) suggests state 0 to be the most similar and therefore the most primitive, of the three states - not state 2 because although very short like the urodele condition, this type is round-ended whereas there is almost always some indication of a distally pointed end in the urodele zygomatic ramus. States 1 and 2 are considered to be, most likely, independently derived from state 0. The direction of change is therefore:-

$$2 \longleftarrow 0 \longrightarrow 1$$

Character 16. Squamosal - zygomatic ramus/maxilla articulation. (Fig. 48).

As mentioned under character 15 (above) in some anurans the zygomatic ramus may articulate with an ascending facial process on the maxilla. Articulation between these two processes may be effected in any one of three ways:

(1) A short zygomatic articulating with a well developed facial process (as in Discoglossus sardus). The facial process may be deep, plate-like structure.

(2) A moderate zygomatic articulating with a moderately well developed facial process (most other Discoglossus species except D. montalentii).

(3) A long well developed and usually plate-like zygomatic articulating with a long, low plate-like facial process. A condition not found within the study group but seen in Ceratophrys species (Leptodactylidae) and in Pyxicephalus adspersus (Ranidae).

In species with a zygomatic/maxilla articulation, the skull may be heavily ossified and the lateral surfaces of the zygomatic ramus and ascending postorbital process of the maxilla may be heavily exostosed (an heavy deposition of dermal bone usually producing a sculptured, reticulate bone surface) - as in species cited under (3) above.

Articulation of the zygomatic ramus with the maxilla almost certainly strengthens and braces the upper jaw (maxilla) against the neurocranium via the crista parotica; it is probably associated with durophagy - the ingestion of hard items of food (H. Martens in litt. noted that molluscs form 21.1% of the diet in Pyrenean Discoglossus pictus).

Two states are recognised:-

State 0. Squamosal - zygomatic ramus not articulating with maxilla.

State 1. Squamosal - zygomatic ramus articulates with ascending facial process of maxilla.

State 1 is seen in all Discoglossus species except D. montalentii

(Clarke and Lanza, in prep.) In *D. montalentii* and the other discoglossoid species in the study group there is no sutural contact between the zygomatic ramus and the maxilla, although there is, as in other species lacking the articulation, probably always a ligament passing from the tip of the zygomatic to the maxilla.

Urodeles (fide Figs in Francis 1934, Dowling and Duellman 1974-1978 and Carroll and Holmes, 1980) do not develop the articulation, also in species with the articulation it is present only in adults, not in juveniles. Therefore outgroup comparison and development (ontogeny) suggest state 1 is derived.

The polarity of this character is therefore:

0 → 1

Character 17. Squamosal - 'medial' ramus. (Fig. 49).

The presence of a further ramus on the squamosal of *Barbourula busuangensis* was noted by me during the course of this work and is reported in Clarke (1987) The medial ramus has its origin close to that of the zygomatic ramus and, extends medially and postorbitally. investing the anterior lateral margin of the otoccipital (prootic - opisthotic region) as a moderately well developed, rounded process extending ventrally along approximately the dorsal half to one-third of the inner (medial) surface of the squamosal shaft. *Bombina* shows a distinct but less developed expansion on the dorsal half to one-third of the squamosal shaft *but* this is not a separate ramus - more a flange of bone, and it is more ventral in position than the medial ramus in *Barbourula busuangensis*. The *Bombina* condition is most fully developed in *B. maxima* and *B. microdeladigitora*. Other discoglossoids either lack a flange or, at most, have a deep, weakly developed rib of bone along the squamosal shaft.

Three states are recognized:-

State 0. Squamosal - medial ramus absent or at most a poorly developed rib of bone along the squamosal shaft. (Fig. 49a).

State 1. Squamosal - medial ramus absent but a ventromedial expansion present on dorsal half to one-third of squamosal shaft. (Fig. 49b).

State 2. Squamosal - medial ramus present. (Figs. 49 c and d).

Outgroup comparison (urodeles) suggests 0 is primitive; the simplest, most parsimonious interpretation of the character states gives the direction of change as:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 18. Squamosal shaft. (Figs. 44e and 50).

The squamosal shaft is generally overlooked as a source of taxonomic characters by most workers; Trueb (1973) omitted to mention the structure only noting that the squamosals are "basically... triradiate" and that the "greatest variation" occurs in the zygomatic and otic rami. However, as noted under the general comments, there is some variation in bufonid species, and it is suggested here that the form of the squamosal shaft is likely to be of some significance since they invest part of the palatoquadrate cartilage and both are important parts of the suspensorium which function to "brace and suspend the jaws against the neurocranium". (Trueb 1973: 84).

In the discoglossoid frogs three basic types of squamosal shaft are recognized:

State 0. Squamosal shaft triangular, blade-like, no, or only slight, posterolateral curvature (longitudinal axis tends to be vertical).

State 1. Squamosal shaft intermediate between state 0 and state 2: not much wider ventrally than dorsally, with a slight posterolateral curve.

State 2. Squamosal shaft slender, broadest at mid-point, slightly posteriorly directed - with a posterolateral 'sigmoid' ('S') curve.

Ascaphus, Barbourula, Bombina and Leiopelma all show state 0. State 1 is seen only in Discoglossus and state 2 only in Alytes spp.

Ascaphus shows the closest approximation to the urodele squamosal shaft which is usually broad, blade-like and with its longitudinal axis vertically orientated. Ascaphus and Bombina are most like the urodeles in that the shaft is either a weak triangular or straight-sided blade-like shape; Barbourula and Leiopelma are more triangular i.e. broader at the base (ventrally), narrower at the junction with the otic and zygomatic rami.

If state 0 is primitive then the simplest interpretation of the direction of change is clearly:

0 → 1 → 2

Character 19. Quadratojugal. (Fig. 51).

The quadratojugal is a small dermal bone found in most anurans at the posterolatural margin of the skull and comprises two parts:- the proximal pars glenoidalis and a distal pars jugularis (terminology of Bolkay 1919) respectively articulating with, and linking, the quadrate and the posterior end of the maxilla, thereby completing the maxillary arch. The quadratojugal is, according to Trueb (1973: 79), "highly variable in its occurrence and is frequently lost or reduced in smaller frogs or those in which ossification is reduced". Carroll and Holmes (1980: 7-8) comment that among salamanders there is only rarely an independent quadratojugal and always a gap between quadrate and maxilla, even in Tylototriton, which has a heavily ossified skull (their Fig. 8C). They note that the quadratojugal ossifies late in ontogeny and suggest that its general absence in urodeles may be attributed to paedomorphosis. Given its general absence in urodeles, especially the primitive urodeles, it is possible that either the anuran quadratojugal is a neomorph, or the ability to produce a quadratojugal is retained in the Anura and that its scattered distribution in the group is attributable to its late ossification in some species and paedomorphosis in others.

Three states are recognized in the discoglossoids:-

State 0. Quadratojugal absent.

State 1. Quadratojugal present - up to 80% of the pterygoid fossa length.

State 2. Quadratojugal present - 80 to 100% of the pterygoid fossa length.

State 0 is seen only in Ascaphus and Leiopelma in which the quadratojugal is replaced by a ligament. State 1 is found in Alytes and Discoglossus, most having a quadratojugal approximately two-thirds the length of the pterygoid fossa (subject to some variation in Alytes - ca. 40-50% in A. cisternasii, 50% in A. o. obstetricans and 60-80% (rare:

one specimen only) in *A. o. boscai*, but sample sizes may be small - n = 4-5). State 2 is found in *Barbourula* and *Bombina* - usually 100%

It is interesting to note that using the level of ossification of the otoccipitals as an index for assessing overall ossification of the skull, *Ascaphus* and *Leiopelma* would be considered the most poorly ossified members of the group and they lack quadratojugals - which is in line with the Carroll and Holmes paedomorphosis theory given above. Application of Trueb's (1973: 74) 'frontoparietal ossification index' (see general comments on frontoparietals) would enlarge the group to include some *Alytes* species, inappropriately, ones with moderately long quadratojugals, while those with well developed frontoparietals, like *A. cisternasii* may have shorter quadratojugals.

Three factors indicate state 0 (quadratojugal absent) to be primitive:- (i) absence in most salamanders, (ii) considering the anuran quadratojugal to be a neomorph, and (iii) late ossification in ontogeny, when absence may be attributed to paedomorphosis.

The simplest interpretation of the direction of change is:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Maxillae (Fig. 30).

The maxillae are paired dermal bones, they are the main elements comprising the maxillary arch. In discoglossoid frogs each maxilla consists of a tooth bearing pars dentalis, an orally directed pars palatina or lingual ledge which may or may not bear a pterygoidal process (see character 22), and a pars facialis which may or may not bear a preorbital process or facial spine.

Trueb (1973: 78) noted that the maxilla may have as many as five points of articulation - with the pars dentalis and pars palatina at the lateral edge of the premaxilla; the preorbital process of maxilla with the maxillary process of the nasal (see character 3) - if they are both present; posterolaterally with the anterior ramus of the pterygoid (where a maxillary pterygoidal process may be present); there may sometimes be a distinct ascending postorbital process to the maxilla, if well developed it may articulate with the zygomatic ramus of the squamosal (see character 16), and finally the posterior end of the maxilla may articulate with the pars jugalis of the quadratojugal (see character 19).

In general, the maxilla is important in prey capture (aided by the maxillary teeth (invariably present in discoglossoid frogs) and may, with the nasals, be important in providing protection to the nasal capsules - if the preorbital pars facialis is well developed. Development of articulations with adjoining bones will serve to strengthen the skull in general and the maxilla in particular.

Character 20. Maxilla - anterior end of the pars palatina. (Fig. 52).

Anteriorly, the maxilla articulates with the pars dentalis (tooth bearing portion) and the pars palatina or lingual ledge of the premaxilla. The shape of the pars palatina of the maxilla may be useful in assessing relationships at low (generic/supraspecific) levels - see Clarke (1981).

In discoglossoid frogs, three states are recognized:-

State 0. Maxilla - anterior end of pars palatina narrow, straight or convex.

State 1. Maxilla - anterior end of pars palatina staggered, transverse or indented (slightly concave).

State 2. Maxilla - anterior end of pars palatina a deep V-shaped (concave) cleft.

State 0 is found in *Alytes* and *Discoglossus*; state 1 in *Ascaphus*, *Barbourula* and *Bombina* and state 2 is confined to *Leiopelma*. Outgroup comparison, using hynobiids and ambystomatids (BM dry skeleton collection, Carroll and Holmes 1980), suggests state 0 to be the primitive condition. Similarity of states, with state 2 as a special more extreme version of state 1, suggests increasing concavity of the anterior margin of the pars palatina. The direction of change is therefore hypothesized to be:-

0 → 1 → 2

Character 21. Maxilla: longitudinal groove at the base of the tooth row.

In *Barbourula busuangensis*, *Bombina orientalis*, and in *Discoglossus* spp. the lateral margin of the pars palatina bears a longitudinal groove at the junction with the pars dentalis (base of the tooth row) . The groove is deepest in *Barbourula busuangensis* which has a very narrow pars palatina or lingual ledge to the maxilla (condition in *Barbourula kalimantanensis* not known - indeterminable in x-radiographs of only known specimen). *Leiopelma* species have a weak indication of a groove but this extends from, and is clearly associated with, the deep V-shaped cleft at the anterior margin which passes posteriorly along the medial margin of the pars palatina; *not* at the base of the tooth row and is therefore considered not be homologous to the tooth row base groove. Other species in the discoglossoid study groove lack any form of groove - having a smooth surfaced horizontal pars palatina (oral surface). Two states are recognized:-

State 0. Maxilla - no longitudinal groove at base of the tooth row (*lateral* margin of pars palatina, oral surface usually horizontal; if present the groove runs anteriorly - posteriorly, adjacent to the medial margin of the pars palatina.

State 1. Maxilla - longitudinal groove present at the base of the tooth row.

Using urodeles as outgroup, in particular hynobiids and ambystomatids (BM specimens), suggests state 0 to be primitive. The direction of change is therefore:

$$0 \longrightarrow 1$$

Character 22. Maxilla - pterygoidal process. (Fig. 53).

Lynch (1971: 40 and 41, Fig. 12) noted that in most leptodactylid frog genera there is an expansion of the posterior (posteromedial) end of the maxillary palatal shelf (= pars palatina of maxilla). He named this the pterygoidal process and noted that when present it either abuts or overlaps i.e. passes ventrally (orally) to the anterior ramus of the pterygoid. In some heavily ossified anurans, usually those which are at least at the exostosis level of the exostosis - casquing - co-ossification sequence mentioned by Trueb (1973: 80) there is a broad suture between the pterygoidal process of the maxilla and the anterior ramus of the pterygoid, e.g. in Caudiverbera caudiverbera (in Lynch 1971: 41, Fig. 12C and 114 - 116, including Fig. 78) and Pyxicephalus adspersus (Clarke 1981: 297) there is a broad suture between the pterygoidal process of the maxilla and the anterior ramus of the pterygoid. This condition is not present in any of the taxa in the discoglossoid study group (nor, for that matter, is exostosis, casquing or co-ossification) where the pterygoidal process is either absent, very poorly developed, usually as an asymmetrical variant to absent, or present and well developed. Two states are recognized:-

State 0. Maxilla - pterygoidal process absent or present as a very small process (not or barely overlapping the anterior ramus of the pterygoid).

State 1. Maxilla - pterygoidal process present, well developed (overlapping i.e. passing ventrally to the anterior ramus of the pterygoid).

Most discoglossoid frogs show state 0, state 1 is seen only in Barbourula, Bombina microdeladigitora andDiscoglossus. In urodeles the maxilla does not usually extend as far posteriorly as in anurans; there is either no expansion at the posteromedial margin of the maxilla or, at most, possibly a very slight expansion in some Hynobius species, e.g.

BM wet (spirit preserved) skeletons of H. nebulosus and H. tsuensis.

The direction of change is therefore:

0 ⟶ 1

Character 23. Maxilla - tooth counts.

Gaudin (1974) used number of premaxillary teeth as a character in a phenetic analysis of the Holarctic Tree Frogs (Hyla, Acris, Pseudacris and Limnaeodus. He noted that "two distinct conditions" were present in his study group: less than 10 teeth per premaxilla versus more than 10. In the present analysis the number of teeth on the maxilla are also considered.

Maxillary tooth counts in my discoglossoid study group varied from 25 to 55 teeth per maxilla. Low teeth counts were noted in Alytes cisternasii (26 - 28 teeth per premaxilla), some A. o. boscai (25/28: left/right side, although others were much higher 38/33, while 34/34 seemed a more normal count) and Bombina variegata (25-28). High counts include Barbourula busuangensis (juveniles and subadults but not adults: 55/55, 49/47, Discoglossus pictus (47/47) and Leiopelma hamiltoni (51/53). There are some interesting trends:-

(1) In some species of discoglossoids (and possibly also in most anurans) the number of maxillary teeth appears to increase with age/size within a species. In L. hochstetteri a juvenile had a count of 30/33 while adults showed counts of 41/43 and 46/46.

(2) Barbourula busuagensis not only shows a decrease in the number of teeth with age/size: 55/55 in a juvenile/subadult to 49/47 and 38/35 in medium and larger specimens but it also appears to reduce the number in a quantum step (see under Prēmaxilla: tooth count for remarks).

Notwithstanding the ontogenetic reduction in maxillary tooth counts in B. busuangensis, i.e. considering only the counts in adults two groups are evident with respect to teeth number hence two states are recognized:

State 0. Less than 40 teeth per maxilla.

State 1. More than 40 teeth per maxilla.

Outgroup comparison produces conflict in deciding the direction of change - hynobiids Hynobius nebulosus and H. tsuensis have counts of 24 and 27 teeth and ambystomatids Ambystoma maculatum and A. opacum have counts of 45 and 48/49 teeth per maxilla respectively. One may either adopt the view point that hynobiids are relatively more primitive and therefore state 0 would be the primitive state or else not assign polarity to this character: in this analysis no polarity is assigned.

Remarks:

Given the ontogenetic shifts in this character and the possibility **that** there is also a heterochronic correlation - adult Leiopelma archeyi has the count seen in juveniles of other species of Leiopelma, this should be considered a highly labile character. For comments on heterochrony in Leiopelma see Stephenson, E.M. (1960) and Trueb (1973: 68).

Character 24. Maxilla - development of pars facialis and preorbital process. (Fig. 54).

The maxilla bears a dorsally directed preorbital flange or pars facialis which may or may not bear a preorbital process at its posterior margin, immediately in front of the anterior margin of the orbit. When fully developed, the pars facialis is a deep plate-like process and the preorbital process is present and usually moderately to well developed. When minimally developed, the pars facialis is a shallow process and the preorbital process is either distinct but minute or absent.

In the discoglossoid frogs two states are recognized:-

State 0. Maxilla - pars facialis poorly to moderately developed; preorbital process absent or weakly developed.

State 1. Maxilla - pars facialis and preorbital process moderately well to well developed.

Urodeles, especially hynobiids and cryptobranchids, show state 0 - they have a poor moderately well developed pars facialis but lack a distinct preorbital process (Sato 1934 a, b, c, Carroll and Holmes 1980, Dowling and Duellman 1974 - 1978 and BM specimens).

The direction of change is therefore:

$$0 \longrightarrow 1$$

Premaxillae. (Figs. 30b and 55).

The premaxilla are paired, dermal bones which complete the maxillary arch anteriorly. Each discoglossoid premaxilla comprises three parts: ventrally, a tooth-bearing pars dentalis (with teeth directed ventrally or ventrally and orally); posteriorly, a pars palatina or lingual ledge bearing a medial palatine process, the pars palatina may also bear a lateral process which is directed toward the maxilla. The area between the palatine process and the lateral margin may be shallowly or deeply concave (if a lateral process is present) or straight lateral to the palatine process (lateral process absent); dorsally the premaxilla bears an alary process.

Like the maxilla, the premaxilla is important in prey capture (assisted by the teeth) and also provides support and protection to the anterior areas of the nasal capsules.

Character 25. Premaxilla - pars palatina. (Fig. 56).

The pars palatina or lingual ledge of the premaxilla may be shallow or deep anteriorly/posteriorly. This character provides an indication of the overall (aggregate) development of the whole premaxilla in general and of the pars palatina in particular. The character is concerned with depth of the mid-region of the palatal ledge, a condition which is not influenced by, or correlated with, the development of the palatine or its lateral processes, nor is it necessarily related to the degree of concavity of the posterior margin of the palatal ledge.

Two states are recognized:-

State 0. Premaxilla - pars palatina, mid-region shallow. (Fig. 56 a-c).

State 1. Premaxilla - pars palatina, mid-region deep. (Fig. 56 d-f).

State 0 is found in Alytes, Ascaphus and Discoglossus; state 1 in Barbourula, Bombina and Leiopelma.

In hynobiid salamanders, in cryptobranchids (Cryptobranchus allegheniensis), and ambystomatids the pars palatina is shallow; state 0 is therefore considered primitive for discoglossoid frogs and the direction of change is:-

$$0 \longrightarrow 1$$

Character 26. Premaxilla - palatine process. (Fig. 57).

Three discrete forms of palatine process on the premaxilla are here recognized in discoglossoid frogs:-

(1) in which there is no distinct but the medial end of the pars palatina is (posteriorly) dilated - this is termed the 'spatulate' type. (Fig. 57 a-b).

(2) where a distinct usually pointed palatine process is present. (Fig. 57 d-e).

(3) an intermediate type, between the spatulate and pointed forms. (Fig. 57 c).

Thus the three states are:-

State 0. Premaxilla - no distinct palatine process: spatulate type.

State 1. Premaxilla - intermediate condition.

State 2. Premaxilla - a distinct palatine process present.

State 1 is seen in Alytes muletensis, Bombina orientalis and B. variegata, and Discoglossus sardus, State 2 in Alytes (except A. muletensis) and Discoglossus (except D. sardus). All the remaining taxa in the study group are state 0.

Outgroup comparison suggest state 0 is primitive: Cryptobranchus have slightly dilated palatine processes rather like a reduced spatulate type, hynobiids (Hynobius and Onychodactylus) have straight edged abutting medial ends to their partes palatinae. Thus state 0 is the most similar to the outgroup condition.

The direction of change is:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 27. Premaxilla - lateral process. (Fig. 58).

In Ascaphus, Bombina and Leiopelma the posterolateral margin (lateral process) of the pars palatina is a well-developed, elongate process. The function of a long lateral process is unknown; the posterolateral margin of the premaxilla (aboral side) articulates with, or is slightly separated from and closely follows, the anterior medial margin of the maxilla (oral side) - see Fig.52c and Carroll and Holmes 1980: 7 Fig. 3A for palatal view of an Ascaphus skull. This 'long form' of the lateral process of the premaxilla is not found in other discoglossoids in the study group. (Bombina fortinuptialis, if it is similar to B. maxima and B. microdeladigitora, may be expected to have a moderately long lateral process). Urodeles, notably hynobiids, cryptobranchids, ambystomatids and most salamandrids, also lack an elongate (projecting) lateral process. Carroll and Holmes (1980: 13) Fig. 8A - ventral view following Wiedersheim 1877, shows Salamandra atra to have an elongate process on the premaxilla, but this process is posteriorly rather than posterolaterally directed and for the most part abuts an enlarged vomerine plate and part of the anterior end of the maxilla, instead of being in prolonged contact/slight separation with only the anterior medial margin of the maxilla.

I therefore suggest that the condition in Salamandra atra is not homologous with that found in Ascaphus, Bombina and Leiopelma, and further suggest that the absence of an elongate process in most urodeles indicates absence to be the primitive condition in discoglossoid frogs. Therefore, two states are recognized:-

State 0. Premaxilla - lateral process absent or poorly developed, not projecting.

State 1. Premaxilla - lateral process present, a distinct, projecting process.

and the direction of change is:

$$0 \longrightarrow 1$$

Character 28. Premaxilla - alary process. (Fig. 59).

The alary process of the premaxilla is a dorsally projecting process. Within the Anura, the alary processes vary greatly in their degree of development. While they may be very short, I know of no case in which they are completely absent. Trueb (1973: 76) notes that they may be long - up to five times the height of the pars dentalis. Tihen (1958: 9) points out that in hynobiids the alary processes of the premaxillae (which he called "nasal processes") are short and well separated from each other. In most adult ambystomatids, except Rhyacosiredon, the processes are closely approximated medially (Tihen also excluded Rhyacotriton - i.e. R. olympicus which is now considered as the single representative of the subfamily Rhyacotritoninae in the Dicamptodontidae). Other urodeles exhibit a great deal of elaboration of the alary process (Wake, D.B., 1966 7 et seq. and his Fig. 2. "Trends in premaxillary evolution").

All discoglossoids have separate alary processes. This character relates to the degree of separation and the direction of the alary processes - Ascaphus is alone in having widely separated alary processes which are laterally directed and inclined from their bases; all other discoglossoids examined are moderately separated and dorsally directed with, at most, a slight lateral inflection of the dorsal end. The condition in Ascaphus is apparently unique, and the state found in other discoglossoids resembles that seen in hynobiid salamanders. Consequently, two states are recognized in discoglossoid frogs:

State 0. Premaxilla - alary process dorsally directed from its base. (Fig. 59 a and b).

State 1. Premaxilla - alary process laterally directed from its base. (Fig. 59 c and d).

and the direction of change is:

$$0 \longrightarrow 1$$

Character 29. Premaxilla - tooth counts.

As mentioned under Character 23 (Maxilla - tooth counts) Gaudin (1974) made use of tooth counts in his phenetic analysis of Holarctic Tree Frogs. He noticed "two distinct conditions" in his study group: frogs with less than 10 teeth per premaxilla versus those with more than 10.

Premaxillary tooth counts in the discoglossoid study group varied from 6 to 22 teeth per premaxilla. Low teeth counts were noted in Alytes 7 - 12, rarely 13, (lowest counts in A. cisternasii 7 - 8 per premaxilla; 9 - 12 in A. o. obstetricans, A. o. boscai sometimes up to 13 in A. muletensis and A. o. maurus) and Barbourula busuangensis which has 6 per premaxilla but 14 in juveniles (see comments below). Some Bombina variegata have 13 - 14 teeth per premaxilla while others have 17 - 18, in the study sample (size n = 7) counts of 15 and 16 were not recorded. In D. pictus counts varied from 13 - 16 teeth. All the remaining discoglossoid species in the study group have more than 13 teeth per premaxilla, up to a maximum of 20 - 22 in Ascaphus and 20 in Leiopelma hochstetteri. On the figures available to me I tentatively divide the discoglossoids into two groups, one averaging about 10 the other averaging about 15 teeth, which, for the purpose of assigning individual taxa, I have characterised as those with less than 14 teeth per premaxilla and those with 14 or more. (Yet I would still retain the idea that for most anurans 10 - 12/premaxilla may be more significant).

Thus two states are recognized:-

State 0. Premaxillary tooth count of 14 or more teeth per premaxilla.

State 1. Premaxillary tooth count of less than 14 teeth per premaxilla.

Outgroup comparison, using urodeles, gives no clear indication of character polarity - within the Hynobiidae Hynobius nebulosus have 12/12

? 13 (left/right premaxillae), H. stejnegeri 12/12, H. tsuensis 14/13, Batrachuperus pinchonii 11/11 and Onychodactylus japonicus 20/20; ambystomatids e.g. Ambystoma tigrinum 20/20; plethodontids (Plethodon glutinosus 12/12 and salamandrids Cynops pyrrhogaster 11/11, Triturus cristatus 12/12, T. vulgaris 15/15. Consequently this character is left without an inferred polarity.

Remarks:

It is interesting to note the occurrence of an abrupt change in the number of teeth on the premaxilla of subadult Barbourula busuangensis - juvenile and half grown specimens usually have ca 14 teeth per premaxilla; subadult and adults 6 very robust teeth. The change is apparently effected by losing alternate teeth, when one large adult tooth takes up the space previously occupied by two juvenile teeth. It seems likely, although there is no supporting evidence, that this may be correlated with a dietary shift.

Vomers (Figs. 30b and 60).

The vomers ('prevomers' of some authors) are subject to a great deal of variation within the Anura. They may be present and well developed, reduced or even absent; they may be fused with one another medially or with a reduced palatine to form a compound vomerpalatine. The vomers are usually sufficiently variable and elaborate structures such that they provide a number of discrete characters for the purpose of phylogenetic analysis. I have given a simple terminology for the different regions of the vomer (as a 'prevomer') in Clarke 1984: 47 - 48 and Fig. 4 - Fig. 60 in the present work. Each vomer consists of a broad antero-medial plate-like portion, a circumchoanal portion and a dentigerous process. The resemblance between the anuran and urodele vomer is such that the terminology cited above may also be used to describe the equivalent regions in the urodele vomer. (Although urodele vomers are usually larger and the tooth row may be very long and have an anterior-posterior orientation in some salamanders, but not in hynobiids and ambystomatids which exhibit the transverse condition found in most Anura. Consequently, for the purpose of character polarity determinations, comparisons are made with the conditions seen in the vomers of hynobiid and, if appropriate, ambystomatid salamanders.

Character 30. Vomer - plate-like portion. (Figs. 60a and 61).

In the hynobiids and ambystomatids the plate-like portion of the vomer is very large, whereas in most discoglossoids the plate-like portion is moderately to well developed (e.g. as in *Alytes* and *Discoglossus*). In *Ascaphus* the vomers are poorly developed and this is particularly evident in the plate-like portion which is very small, almost vestigial structure.

Two states are recognized:-

State 0. Vomer - plate-like portion moderately to well developed.

State 1. Vomer - plate-like portion very small.

On the basis of outgroup comparison with the hynobiids and ambystomatids, state 0 is seen to be the more primitive condition in the discoglossoids and the direction of change is therefore:-

$$0 \longrightarrow 1$$

Remarks:

Trueb in Duellman/Trueb (1986: 317) noted that the vomers (when present) form part of the palate and floor of the nasal capsules. It may be that the development of the plate-like portion of the vomer is correlated with the development of the vomerine teeth and their role in prey capture and restraint. Large and/or active prey may be restrained in the buccal cavity by the vomerine, as well as the premaxillary and maxillary teeth. The pressure transmitted upward toward the nasal capsules would be spread and reduced by the large surface area of a well-developed, bony, plate-like process, simultaneously reducing the likelihood of damage to the olfactory areas. The reduction in size of the plate-like portion in *Ascaphus* may therefore be diet related; data given in Bury (1970: 170-171) suggest that soft bodied invertebrates form a major part of the diet in *Ascaphus*, especially in juveniles which ingest large numbers of Collembola, coleopteran larvae, dipteran larvae and adults and amphipods. Probably more significant is the poor overall level of ossification of the skull in Ascaphus and the late appearance of the vomer in this species (at stage 46 - the last recognized larval stage of Gosner 1960) according to Altig (1969: 60) who specifically noted that in comparison with Leiopelma and the discoglossid frogs "... the vomers are smaller and less complex", ibid : 62).

Character 31. Vomer - circumchoanal process. (Figs. 60b and 62).

The circumchoanal process is absent in Ascaphus, present in all other discoglossoid species in the study group and present, even if weakly developed, in most hynobiids and ambystomatids (Tihen 1958, Carroll and Holmes 1980). The absence of a circumchoanal process in Ascaphus may also be correlated with diet and/or low overall level of ossification of the skull and late appearance of the vomer as detailed under Remarks: Character 30, and consequently may be logically correlated with that character. However, since the circumchoanal process may, in some other species of discoglossids e.g. in A. cisternasii, and A. obstetricans, be distinct from the plate-like process, I am treating the circumchoanal process as a separate character. (In Stumpffia psologlossa, a microhylid frog from Madagascar, the vomer is present only as a circumchoanal process see Trueb 1973: 83, Fig. 2-5d - further evidence for considering the different regions of the vomer separately).

Two states are recognized:-

State 0. Vomer - circumchoanal process present.

State 1. Vomer - circumchoanal process absent.

Presence of a circumchoanal process in most hynobiids and ambystomatids suggests state 0 is primitive and the direction of change to be:-

$$0 \longrightarrow 1$$

Character 32. Vomer - dentigerous process. (Figs. 60c and 63).

Trueb (1973: 82) considered differences in the overall size of the vomerine bones and the orientation of their dentigerous ridges to be "minor prevomerine...(i.e. vomerine) ... variation" and commented that the orientation of the ridges is "a useful diagnostic character at the species and genus level". Character 32 is concerned with the type of dentigerous ridge (its size and the arrangement of the teeth - in a row or as a tooth patch) and the disposition of the ridge relative to the internal nares or choanae.

Four states are recognized in the discoglossoid study group:-

State 0. Vomerine teeth in a narrow linear series on a medially situated contiguous process; posterior or only slightly posterior to the choanae.

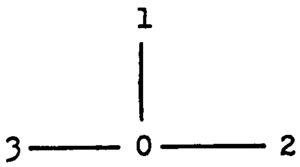
State 1. Vomerine teeth in a very narrow linear series on a distinct, separate, posteriorly directed process; posterior to the choanae.

State 2. Vomerine teeth in an oval patch between the choanae.

State 3. Vomerine teeth in a broad, slightly arched linear series, (well) posterior to the choanae.

The distribution of the character states in the study group is as follows: state 0 *Alytes*, *Leiopelma archeyi* and *L. hamiltoni*; state 2 *Ascaphus*; state 3 *Discoglossus*; state 1 - remainder of study group.

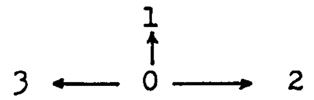
Morphological similarity of states suggests the following non-polar transformation series (morphocline):-



that is, states 1, 2 and 3 linked via state 0.

Outgroup comparison using hynobiid salamanders (*Hynobius* spp.)

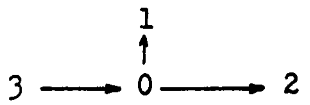
suggests state 0 is the primitive state and the polarity of this character to be:-



Polarity A.

Cryptobranchid salamanders have a large number of vomerine teeth but they are found in a different position on the vomer (along the anterior margin of the plate-like portion, e.g. as in *Cryptobranchus alleghenlensis*; Carroll and Holmes 1980: 10 Fig. 3). Consequently this condition does not admit detailed comparison at a descriptive level - it is therefore not considered operationally homologous with any state in the discoglossoid group (criterion of Underwood, 1982: 246), and may not be used for outgroup comparison.

Ambystomatid salamanders have a broad linear tooth row posterior to the choanae, in some species the row may be arched. Superficially therefore state 3 might be considered to be primitive and the polarity of character 32:-



Polarity B.

Yet on detailed examination the teeth in ambystomatids (e.g. in *Ambystoma maculatum*) are not all grouped together on an odontoid as in anurans - there is a break in the tooth row, a diasteme, and laterally some of the teeth are found on the postchoanal part of the circumchoanal portion.

Therefore the condition found in *Hynobius* is the only one bearing a sufficiently detailed resemblance to an ingroup state, and so state 0 is considered primitive and polarity A (above) is the hypothesized polarity for this character.

Character 33. Vomeropalatine - presence/absence. (Figs. 60d and 64).

A free (i.e. separate) palatine is lacking in discoglossoid frogs. It is Linda Trueb's contention (pers. comm.) that the palatine is a neomorph in the Anura and is not, therefore, homologous with the palatine in other vertebrates. Maree (1945: 52) considered "a poorly developed palatine" to be present and synosteotically fused to the vomer in Alytes obstetricans. I agree with Maree's interpretation: in my material a vomeropalatine is present in all Alytes species. The very small palatine part of this compound structure is dorsal to the vomerine odontoid process - as Maree (loc. cit.) says "the vomer is applied to the ventral side of the poorly developed palatine". The vomeropalatine in palatal view, is seen as a process extending laterally from the region dorsal to the odontoid/dentigerous process and is obscured by the latter process. The development of the vomerine component of the vomeropalatine is subject to a great deal of variation. The vomeropalatine is usually a small process in most Alytes, but it may, exceptionally, be quite well developed in some A. o. boscai (as in BM 1973. 1725). Maree (loc. cit.) also says that a vomeropalatine is present in Leiopelma, quoting Wagner 1934. The situation in Leiopelma, however, is different from that in Alytes. There is no equivalent dorsal and lateral process in the region dorsal to the odontoid/dentigerous process as in Alytes. In Leiopelma the palatine, if truly present, is indistinguishably fused to the postchoanal portion of the circumchoanal process, thereby forming an elongate postchoanal ramus. The (?) palatine component of the Leiopelma 'vomeropalatine' is no more than a small rib of bone on the posteromedial corner of the postchoanal ramus of the vomer (see Fig. 64). If the two structures described above, in Alytes and Leiopelma, both include 'palatine' bone then these palatine bones have attached to different parts of the vomer and the resulting vomeropalatines are not operationally homologous. For the reasons given above only Alytes are considered to have a true vomeropalatine; Leiopelma have an elongate postchoanal process/postchoanal vomeropalatine - all other discoglossoids lack a vomeropalatine.

Two states are recognized:-

State 0. Vomeropalatine absent.

State 1. Vomeropalatine present.

According to Carroll and Holmes (1980: 8) the palatine appears during development in most salamander groups but is lost in most adults except sirenids, the axolotl and other neotenic forms. Its presence in the Anura may therefore be an instance of a feature which is a genetically retained yet suppressed in some taxa, notably most discoglossoids, rather than the presence of a neomorphic structure as Trueb suggests. I put this forward as an alternative explanation - in either case I suggest state 1 is derived for the discoglossoids.

The direction of change is therefore:-

$$0 \longrightarrow 1$$

Character 34. Vomer - postchoanal ramus. (Fig. 65).

There are three discrete forms or conditions of the postchoanal ramus in the discoglossoid frogs; the following three states are recognized:-

State 0. Vomer - postchoanal ramus absent (circumchoanal process absent). (Fig. 65 a).

State 1. Vomer - postchoanal ramus short - moderate, plate-like. (Figs. 65 b and c).

State 2. Vomer - postchoanal ramus a slender, elongate rod-like process. (Figs. 65 d and e).

State 0 is found only in Ascaphus; state 2 only in Leiopelma - all other discoglossoids examined exhibit state 1. I consider state 0 to be the primitive condition because:-

1) hynobiid salamanders either lack or have a very feeble indication of a postchoanal ramus. (The tooth-bearing process in the postchoanal area in Ambystoma spp. may be an extension of the dentigerous process and therefore not operationally homologous with the postchoanal ramus of the discoglossoid frogs).

2) I am also greatly influenced by the close phenetic similarity between the vomers of Ascaphus truei and the fossil Notobatrachus degiustoi from the late Jurassic of Argentina. The only real differences between the two are the slightly better overall development of the vomer in the latter species and the fact that it apparently possessed a postchoanal ramus (Estes and Reig 1973: 20 and their Fig. 1 - 5). As Trueb (1973: 81-82) and Lynch (1973: 148) indicate, the anuran vomers and their processes are subject to a great deal of variation-even loss. The gain or loss of a postchoanal process to give the transition from the Notobatrachus to the Ascaphus condition (or vice versa) could easily occur.

Hence state 0, being closest to the hynobiid and Notobatrachus conditions, is considered primitive. The polarity of this character is therefore taken to be:

$$0 \longrightarrow 1 \longrightarrow 2$$

Where 0 embraces the conditions in *Ascaphus*, *Notobatrachus* (a moderate tapering, but neither plate-like nor slender rod-like, process) and hynobiid salamanders.

As noted under character 33 the postchoanal condition seen in *Leiopelma* (state 2 of this character 34) may be a combination of palatine + postchoanal ramus, where the palatine is indistinguishably fused, or it may simply be an elongate postchoanal ramus with a posteromedial rib of bone. The latter interpretation is adopted in this study/analysis.

Parasphenoid. (Fig. 30b).

The parasphenoid is a dermal bone which invests the neurocranium ventrally, bridging and strengthening the ventral neurocranium from the exoccipital region posteriorly to the sphenethmoid anteriorly. The parasphenoid is a triradiate bone which resembles an inverted letter 'T' in shape. The anterior portion, the body of the 'T', is termed the cultriform process and the arms of the 'T' the parasphenoid alae. Variation in the discoglossoid parasphenoid bone includes differences in the shape of the cultriform process; in the anterior-posterior depth of the alae; the presence/absence of a longitudinal keel on the cultriform process and of a transverse keel on the ala, and the degree of overlap of the medial ramus of the pterygoid and corresponding parasphenoid ala in the anterior-posterior plane. I therefore consider that there is more variation in the parasphenoid than Trueb (1973: 80) suggests - "Variation in the parasphenoid is slight....".

Character 35. Parasphenoid - cultriform process (overall shape). (Fig. 66).

Three distinct conditions were found in the discoglossoid study group:-

State 0. Parasphenoid cultriform process - straight sided or slightly to moderately biconvex.

State 1. Parasphenoid cultriform process - widest at junction with alae, tapering gradually to a point anteriorly.

State 2. Parasphenoid cultriform process - distal $\frac{1}{3}$ - $\frac{1}{2}$ only tapering to a point.

State 1 is found only in Alytes muletensis (see Clarke 1984: 46, Fig. 1B); State 2 in Barbourula busuangensis, Leiopelma hamiltoni and L. hochstetteri but not in L. archeyi (= state 0); state 0 is found in the remainder of the study group. Outgroup comparisons (hynobiid and ambystomatid salamanders) suggest state 0 is primitive. States 1 and 2 are considered special forms of state 0; the direction of change is therefore:-

$$2 \longleftarrow 0 \longrightarrow 1$$

Character 36. Parasphenoid alae - anterior/posterior depth. (Fig. 67).

In *Ascaphus* and *Leiopelma* the parasphenoid ala are narrow medially to laterally, but are deep anteriorly - posteriorly. The alae of *Barbourula busuangensis*, *Bombina maxima*, *B. microdelegitora* and most *Discoglossus* species (condition not known in *D. nigriventer*) are moderately deep, showing a tendency to be shallow medially and flared laterally. The remaining species in the study group have alae which are shallow anteriorly-posteriorly. Three states are therefore recognized:-

State 0. Parasphenoid alae uniformly deep. (Fig. 67a).

State 1. Parasphenoid alae shallow medially, flaring (deeper) laterally (Fig. 67b).

State 2. Parasphenoid alae uniformly shallow or nearly so (- may be slightly posteriorly directed, Fig. 67c).

State 0 most closely resembles the condition in hynobiid salamanders (see e.g. Carroll and Holmes 1980: 9, Fig. 4) and is therefore considered to be the primitive state.

The direction of change is:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 37. Parasphenoid - cultriform process, keel present/absent. (Fig. 68).

Trueb (1973: 80) notes that true teeth are not found on the (anuran) parasphenoid but that the posterior part of the cultriform process may bear a smooth medial keel. Of the discoglossoids examined only Barbourula busuangensis has a smooth longitudinal (median) keel which is more fully developed (i.e. deeper) anteriorly and extends to the distal end or tip of the cultriform process. Two states are therefore present:-

State 0. Parasphenoid, cultriform process - lacking a medial keel.

State 1. Parasphenoid, cultriform process - medial keel present.

In hynobiid and ambystomatid salamanders the cultriform process is smooth, consequently state 0 is considered to be the primitive condition in discoglossoids and the direction of change is:

$$0 \longrightarrow 1$$

Trueb (1973: 80-81) commenting on the various forms of dermal ornamentation on the cultriform process (including keels) said "The utility of these structures is questionable; it is possible that they function with the prevomerine...(i.e. vomerine)... teeth to control prey in the oral cavity".

Character 38. Parasphenoid ala - transverse (median) keel. (Fig. 69).

A transverse (or median) keel is present on the parasphenoid ala in Alytes cisternasii, Barbourula busuangensis, Bombina maxima and B. microdeladigitora and most, if not all, Discoglossus species (condition in D. nigriventer not known). The presence of a keel on the ala provides an increased area for the muscle attachment in this region. Therefore the presence of a keel and its significance is dependent upon the reasón for having a more heavily developed muscle and/or an increased area for muscle attachment across the ala. The form and development of the keel (when present) is subject to some variation - in Alytes cisternasii and in Discoglossus species the keel has a more developed anterior leading edge; in Barbourula the anterior and posterior keels are confluent. Whereas in keel-bearing Bombina species the posterior keel is the more developed. However, the sample sizes for this character were small and the character is therefore concerned only with two conditions:

State 0. Parasphenoid ala - transverse (median) keel absent.

State 1. Parasphenoid ala - transverse (median) keel present.

A transverse keel may easily be produced by increased ossification and its presence might be expected to be, and often is, sporadic in the Anura and in hynobiid salamanders (absent in Hynobius species yet present in Onychodactylus japonicus). Absence is therefore taken to be primitive. The direction of change is therefore:

$$0 \longrightarrow 1$$

Character 39. Parasphenoid ala/medial ramus of pterygoid- lateral/ medial overlap (respectively) in the anterior - posterior plane. (Fig. 70).

The medial ramus of the pterygoid may or may not overlap the anterior border of the parasphenoid ala in the anterior-posterior plane. This character is concerned with any such overlap should it occur and, if it does occur, the extent of the overlap.

Three states of this character are recognized in the discoglossoids:-

State 0. Parasphenoid ala/medial ramus of pterygoid slightly to moderately overlapping; medial ramus overlapping 1/6 - ⅓ lateral width of the anterior border of the ala in the anterior-posterior plane (Fig.70a).

State 1. Parasphenoid ala/medial ramus of pterygoid not overlapping or, at most, tips of ala and ramus in alignment, in the anterior-posterior plane (Fig.70b).

State 2. Parasphenoid ala/medial ramus of pterygoid strongly overlapping, medial ramus overlapping more than 2/3 lateral width of the anterior border in the anterior-posterior plane (Fig.70c).

State 0 is found in *Bombina maxima*, *B. microdeladigitora*, *Discoglossus* and *Leiopelma*; state 1 in *Alytes*, *Ascaphus* and the remaining *Bombina* species; state 2 is confined to *Barbourula* (*B. busuangensis and B. kalimantanensis*).

Outgroup comparison with hynobiid and ambystomatid salamanders suggests slight overlap (= state 0) to be primitive. The polarity of character 39 is therefore:-

$$2 \longleftarrow 0 \longrightarrow 1$$

Pterygoid. (Figs. 30 and 71).

The pterygoids are paired dermal bones each is basically triradiate, comprising an anterior, a medial and a posterior ramus. The anterior ramus is longest; it articulates with the maxilla dorsal to the pars palatina and invests the cartilaginous pterygoid process (= processus pterygoideus figured in Maree, 1945: 54, Fig. 8 - which is part of the chondrocranium and should not be confused with the bony pterygoidal process of the maxilla; terminology of Lynch 1971: 40). The medial ramus articulates with the ventral part of the prootic/otoccipital anterior to the parasphenoid ala, usually investing a cartilaginous pad-like pseudobasal process. The posterior ramus invests the medial surface of the quadrate cartilage. The pterygoid, via these points of contact serves to brace the posterior maxillary arch; the maxilla and quadratojugal and the squamosal (squamosal shaft), against the posterior neurocranium.

In discoglossoid frogs the pterygoid may be further differentiated, when orbital and ventral flanges may be present (see characters 41 and 42 respectively). The present study is also concerned with variation in the development of the anterior ramus of the pterygoid (character 40).

Character 40. Pterygoid - anterior ramus. (Fig. 71).

Three discrete configurations of the anterior ramus of the pterygoid are seen in the discoglossoid frogs:-

State 0. Pterygoid - anterior ramus short to moderate, with little or no anterior curvature, anterior end pointed. (Type A).

State 1. Pterygoid - anterior ramus short, no anterior curvature, anterior end truncate (Type B).

State 2. Pterygoid - anterior ramus long, anterior end curving medially and terminally rounded to slightly pointed. (Type C).

The state 0 condition is found in *Alytes*, *Ascaphus*, *Discoglossus montalentii* and *Leiopelma*; state 1 in *Barbourula busuangensis*, *B. kalimantanensis* and *Discoglossus* species with the exception of *D. montalentii*; state 2 is confined to *Bombina* species.

Comparisons with hynobiid and ambystomatid salamanders suggest state 0, i.e. Type A, to be the primitive condition; the direction of change is therefore:

2 ← 0 → 1

Character 41. Pterygoid - orbital flange. (Fig. 72).

Bombina microdeladigitora is apparently unique amongst the discoglossoid frogs in having a medially (orally) directed orbital flange on the pterygoid, extending from the anterior to the medial ramus. It is not known if an orbital flange is also present in B. fortinuptialis which, according to the original description, is related to B. microdeladigitora (comment in Frost 1985: 107).

Two states are recognized:-

State 0. Pterygoid - orbital flange lacking.

State 1. Pterygoid - orbital flange present; very well developed. (Fig. 72).

I am not aware of the presence of an orbital flange on the pterygoid of any other species of anuran. An orbital flange is, to the best of my knowledge also lacking in the urodele outgroup (hynobiid and ambystomatid salamanders). I therefore regard state 1 as a possibly uniquely derived state (autapomorphy) for Bombina microdeladigitora.

The direction of change is therefore:-

$$0 \longrightarrow 1$$

Character 42. Pterygoid - ventral flange. (Fig. 73).

Trueb (1973: 84) noted: "In one discoglossid - Barbourula (Fig. 2 6b) - and three leptodactylid species - Cycloramphus, Hydrolaetare and Zachaenus - the pterygoid bears a peculiar ventral flange. Lynch (1969) suggested that in the leptodactylids this flange may be a specialization for muscle attachment as an adaptation for burrowing". Trueb's reference to Barbourula specifically refers to B. busuangensis; a similarly well developed ventral flange, extending from the anterior to the posterior pterygoid ramus, is also found in B. kalimantanensis and in Discoglossus nigriventer) easily seen in radiographs of both species). A less well developed flange is seen in other Discoglossus species. All the remaining discoglossoid species examined lack a ventral flange.

Consequently, three states are recognized:-

State 0. Pterygoid - ventral flange absent.

State 1. Pterygoid - ventral flange present, moderate.

State 2. Pterygoid - ventral flange present; deep and well developed.

I follow Trueb (ibid: 82) in regarding the pterygoids of modern anurans to be different in appearance, function and position from the pterygoids of primitive amphibians. Essentially the pterygoids of primitive amphibians are palatal bones, whereas the anuran pterygoids are part of the cranial suspensory mechanism. In the Anura, the pterygoid serves to brace the maxilla and squamosal/quadrato jugal against the posterior neurocranium. The urodele pterygoid represents an intermediate condition between those of the primitive amphibian and the modern anuran. In hynobiid and ambystomatid salamanders an anteriorly placed flange may be present but this is different in appearance and position from, and therefore not valid for the purpose of comparison with the more posteriorly placed flange of the anurans (a neomorphic condition). I therefore regard state 0 to be the primitive condition for the discoglossoid frogs and the direction of change to be:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 43. Columella - presence/absence. (Fig. 30a).

Important note: this character is recorded with respect to the gross morphological appearance. At the gross morphology level only two states are recognizable - present and absent. Using serial sections Wever (1985) has demonstrated that the columella may be present but minute in some discoglossoid species (see Remarks below). Consequently the two states recorded for this character are:-

State 0. Columella present, well developed.

State 1. Columella absent at a gross morphological
level (or present but minute - only visible
in serial section preparations).

Using this coding, a well developed columella is found in Alytes, Barbourula and Discoglossus; Ascaphus, Bombina and Leiopelma apparently lack a columella (but see Remarks).

Lynch (1973: 148)noted that the columellae are one of the most frequently lost of the skull bones, and that such loss "occurs sporadically among the genera and families of frogs". While the form of the columella ('stapes' of Carroll and Holmes 1980) may differ in the anurans and urodeles - rod-shaped in the former and short-stemmed with a very large foot-plate in the latter - the presence of a columella/stapes is common to most anurans and to primitive urodeles (hynobiids and ambystomatids) and is therefore considered the primitive state in discoglossoids. Further Estes and Reig (1973: 54) confirm Hecht's (1963) observation that "a columella (plectrum)" was present in Notobatrachus degiustoi from the late Jurassic of Argentina. Estes and Reig (loc. cit.) took the view that the presence of middle ear elements in Notobatrachus and the Jurassic discoglossid Eodiscoglossus "makes it clear that no evidence supports the view of N.G. Stephenson (1951) that the absence of a middle ear is primitive for ascaphids".

The polarity for character 43 is therefore:-

$$0 \longrightarrow 1$$

REMARKS

Wever (1985) in his detailed and comprehensive investigations into the amphibian ear found that Ascaphus truei and Leiopelma hochstetteri (the other two species of Leiopelma were not available to him) genuinely lack a columella, as does Bombina bombina, while B. orientalis and B. variegata have a vestigial cartilaginous columella. Auditory sensitivity tests show responses to low frequency sounds in all the above-mentioned species denoting poor response to aerial sounds but a greater sensitivity to sounds conducted through water and the substrate. Wever (ibid.) also pointed out that in Ascaphus and L. hochstetteri the amphibian papilla is simpler than in advanced frogs in that although the anterior division of the papilla is present, the long posterior division and sensing membrane are lacking. Wever regards this as support for the view that the two species are "closely related and are properly included in a separate family". However, these structures are also lacking in urodeles (Wever, ibid.: 304) and therefore their absences in Ascaphus and L. hochstetteri are here interpreted as shared primitive conditions - which would not constitute evidence for close phylogenetic relationship but would provide further indication of the relatively primitive grade-level status of these taxa.

Character 44. Squamosal - mandibular sesamoid. (Fig. 70c)

Barbourula busuangensis may be unique in the Anura in having a sesamoid bone at the angle of the jaw between the base of the squamosal shaft and the mandible (reported for the first time in Clarke 1987: 882-883, and loc. cit. Figs 1 and 2 and designated 'squamosal - mandibular sesamoid'). Briefly, this element is usually cartilage (especially in juvenile and subadult frogs) but may be ossified in large adult specimens - as in FMNH 50999. These sesamoids are hemicylindrical in shape (i.e. semicircular in cross-section) and articulate by means of a ligament passing dorsally across the inner posterior/ventral surface of the squamosal shaft and the anterior-lateral edge of the posterior ramus of the pterygoid, and ventrally with the posterior end of Meckel's cartilage on the mandible. This sesamoid consequently spans the space between the medial side of the calcified quadrate and the mandible. It is not known if Barbourula kalimantanensis also possess a squamosal-mandibular sesamoid.

Nussbaum (1982: 312) noted that heterotopic bones and cartilages are rare in amphibians - only a "few and scattered reports of sesasmoid elements in frogs" and later (p. 316-317) commented that the "assumptions that sesamoid bones serve a common function is reasonable. These elements usually occur at stress points in tendons, often where a narrow tendon transmits the force of a powerful muscle across a joint". He also noted that calcification of a sesamoid may strengthen the tendon or ligament concerned, maintain its shape under stress and increase the mechanical advantage of the force translation. Haines (1969: 107, 111-112) also ascribed to the view sesamoids protect tendons and ligaments from pressure and/or increase the effect of leverage.

Two states are recognized:-

State 0. Squamosal - mandibular sesamoid absent.

State 1. Squamosal - mandibular sesamoid present.

State 0 is considered to be primitive: urodeles lack such a sesamoid and the presence of a squamosal-mandibular sesamoid is clearly functionally related and it is therefore biologically more plausible to regard it as a derived condition. (Nussbaum 1982: 316-317) quoted Hildebrand 1974: 190 who said "These sesamoid bones are of more functional than evolutionary significance").

The direction of change is therefore postulated to be:-

$$0 \longrightarrow 1$$

Character 45. Mandible - coronoid process. (Fig. 74).

The coronoid is important as a site for the insertion of the *adductor mandibulae posterior articularis* and *lateralis* muscles (Starrett 1968). Four discrete coronoid conditions are found in discoglossoid frogs:-

State 0. Mandible - coronoid process with smooth, convex, or slightly triangular outline (i.e. lacking a notch); dorsally or slightly orally directed. (Figs. 74a-b).

State 1. Mandible - coronoid process with smooth, convex outline but has either a weak notch or a vertical margin posteriorly; slightly orally directed. (Fig. 74c).

State 2. Mandible - coronoid process with smooth, convex outline interrupted by a deep notch producing a backward-sloping posterior margin; moderately orally directed. (Fig. 74d).

State 3. Mandible - coronoid process a distinctive three-sided to smoothly convex 'lug' of bone; strongly orally directed. (Fig. 74e).

State 0 is found in *Ascaphus*, *Discoglossus* and *Leiopelma*, state 1 in *Alytes* species excepting *A. cisternasii*; state 2 is confined to *A. cisternasii*; state 3 is found in *Barbourula* and *Bombina*. Outgroup comparison with hynobiid and ambystomatid salamanders suggests state 0 is the primitive condition. Morphological similarity suggests states 1 and 3 are close to, but independently derived from state 0 and that state 2 is a more derived form (a special case) of state 1. The direction of change is therefore hypothesized to be:-

$$3 \longleftarrow 0 \longrightarrow 1 \longrightarrow 2$$

Character 46. Mandible - Mentomeckelian bones.

Trueb (1973: 89) noted that in anurans the anterior end of Meckel's cartilage is "usually ossified to produce a symphysial bone..." and that this bone may be "synosteotically united with the dentary".

In the discoglossoid frogs two states are recognized:-

State 0. Mandible - Mentomeckelians; two separate bones, each fused on its outer margin to dentary.

State 1. Mandible - Mentomeckelians; indistinguishably fused to dentary (dentary appears to have an expanded anterior end).

State 1 is found only in Barbourula (B. busuangensis and B. kalimantanensis and Discoglossus galganoi and D. pictus; all other discoglossoids examined have the state 0 condition. In urodeles there is a prominent posterior mental process at the median symphysis (Francis, 1934: 32-3). This gives the dentary the appearance of having an expanded anterior end - which is different to that of discoglossoids exhibiting state 1. I consider it likely that the urodele condition may not be sufficiently similar in detail (operationally homologous) to admit comparison with state 1 (above). I further suggest that morphologically, states 0 and 1 are more similar to one another than either is to the urodele condition - that state 1 is a special case of state 0, and that with respect to development it is more plausible to suggest that the direction of change is:-

$$0 \longrightarrow 1$$

Occipital condyles. (Fig 30).

Lynch (1971: 52-55 and Figs. 26-28) described, illustrated and discussed, the form and arrangement of the occipital condyles and cervical cotyles which comprise the articulation between the skull and vertebral column. He noted that Gallardo (1965) had regarded the degree of separation of the occipital condyles to be "of considerable importance in discerning intrafamilial relationships of the Leptodactylidae" and considered that this character is "also reflected in the positions of the atlantal cotyles". Lynch commented that the condyles could be confluent, presenting a continuous articular surface, 'closely juxtaposed' (= slightly separated medially) or widely separated. He considered the distinction between the two latter conditions may be size-related, and that it can be difficult, in practice, to determine if the condyles are narrowly separated or confluent - a problem which may often, though not always, as Lynch implies, be resolved by reference to the cotylar arrangement on the cervical vertebra. (see Character 52 - Cervical cotyles). Lynch (1971: 53-54) provided definitions for the three cervical cotylar arrangements which he designated Types I, II and III. Use of these Lynch Types permits a more precise description of the position and size of the respective articular surfaces and their medial separation and is therefore considered under Character 52. There are, in addition, two further attributes of the occipital condyles not considered in Lynch (1971) which are independent of the Lynch Types and are also, I suggest, of functional significance. These are:-

(i). the orientation of the major axes of the occipital condyles (Character 47) and

(ii) the position of the occipital condyles relative to the foramen magnum (Character 48).

Note: The Lynch Types are concerned with medial separation of the articular surfaces, whereas (i) is concerned with their inclination and

(ii) with their dorsoventral position. It does not matter if one refers specifically to the occipital condyles or to the cervical cotyles for, as Gallardo (1965) implied, the state in one reflects the state in other. The only advantage in using one rather than the other is to facilitate description.

Character 47. Occipital condyles - orientation of major axes. (Fig. 75).

The occipital condyles are usually either elliptical or pear-shaped but may be almost circular in some species (e.g. Bombina bombina). Taking the elliptical shape as the standard this character is concerned with the orientation of the major axes of the condyles with respect to one another. (Pear-shaped and near-circular condyles are special forms of ellipse - pear-shaped condyles are like elliptical condyles but are narrower medially, and near-circular condyles are analogous to circles versus ellipses in mathematics - they are a special case of elliptical condyle in which the two foci of the ellipse are almost co-incident, i.e. they approach a single point which, if co-incident, would then be the centre of a circular condyle.

Three clearly recognizable, discrete states are recognized:-

State 0. Occipital condyles with major axes horizontal, i.e. linear.

State 1. Occipital condyles with major axes at a shallow obtuse angle.

State 2. Occipital condyles with major axes at a steep obtuse angle.

State 0 is found in Alytes and Ascaphus; state 1 is confined to Leiopelma and state 2 is found in the remainder of the study group. In hynobiid and ambystomatid salamanders the condyles are pear-shaped and have horizontal major axes.

The direction of change is therefore:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 48. Occipital condyles - position relative to the foramen magnum. (Fig. 76).

In discoglossoid frogs (and probably all anurans), the occipital condyles occupy one of three positions: (i) most of the condyle beneath, i.e. ventral to the foramen magnum; (ii) condyle ventrally and laterally sited - at the bottom left and right 'corners' of the foramen magnum, or (iii) in a more dorsal position where the ventral margins of the occipital condyles are dorsal to the ventral margin of the foramen magnum. This character is independent with respect to character 47 - there is usually a space between the foramen magnum which allows the condyles to be inclined at either a shallow or a more steep acute angle - see Data matrix.

Thus three states are recognized:-

State 0. Occipital condyles ventral to the foramen magnum.

State 1. Occipital condyles at the ventrolateral margins of the foramen magnum.

State 2. Occipital condyles on the (lower) lateral margins of the foraman magnum.

State 0 is found in Alytes, Ascaphus and Leiopelma, state 2 is confined to Bombina bombina - all other discoglossoids examined have the 'ventrolateral' state 1 condition.

The occipital condyles of hynobiid salamanders do not admit detailed comparison with those of discoglossoid frogs (for details see section on Cervical cotyles and Character 52), whereas those of the cryptobranchid and ambystomatid salamanders more closely resemble the discoglossoid type, and may be assigned to state 0 as described above. State 0 is therefore considered primitive for the discoglossoids and the direction of change is:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Hyoid. (Figs. 77-79).

The anuran hyoid is basically a bilaterally symmetrical, cartilaginous, plate-like structure which may bear some or all of the following processes (anteriorly to posteriorly): paired hyale (also known as ceratohyals or anterior cornua), which are separated by a hyoglossal sinus and extend from the anterior margin of the plate and serve to anchor the hyoid on either side to the otic capsules; anterolateral alary processes; posterolateral processes and posteromedial processes (= thyrohyals). In discoglossoid frogs, the hyoid plate may bear up to five kinds of endochondral ossification: i) a U- or V-shaped splint bone which may or may not be joined medially ii) a medial parahyoid ossification iii) paired, round, laterally placed patches of bone and iv) long, thin, stalk-like proximal thyrohyal bones; i) - iii) above are situated on the body of the hyoid plate, v) a fifth type of bone may be found along the margin of the hyoglossal sinus. The thyrohyal ossifications extend from the posterior margin of the central plate posteriorly and comprise most, or all, of the posteromedial processes.

Characters 49 - 51 are concerned with the presence/absence of anterior processes on the hyale, of alary processes and the ossification on the central hyoid plate respectively.

Trewavas (1933) is still the standard reference on the anuran hyoid. The other major / original references figuring discoglossoid hyoids are:-

Alytes: Boulenger (1897), Ridewood (1898) and Maree (1945); Ascaphus: Van Denburgh (1912); Barbourula: Clarke (1987); Bombina: Boulenger (1897) and Slabbert (1945); Discoglossus: Lataste (1879), Boulenger (1897) and Van Zyl (1950); Leiopelma: Stephenson, E.M., (1951) and Trueb (1973).

Character 49. Hyoid - anterior processes on hyale. (Fig. 77).

Stephenson, E.M., (1951: 274 and Fig. 15) drew attention to the presence of a medially-directed anterior process on the hyale in *Leiopelma hochstetteri* and the absence of this process in *L. archeyi*. In addition, Stephenson noted the presence of distinct alary processes and relatively narrow ceratohyals ('hyale' of Trewavas 1933) in *L. hochstetteri* - structures which are respectively absent and relatively wide in *L. archeyi*. Stephenson therefore concluded, and was able to confirm, by reference to the original material, that Trewavas's 1933 Fig. 4 depicted the hyoid of a *L. archeyi* (described as a distinct species by Turbott in 1942). Trueb in Duellman/Trueb 1986 has clearly reproduced the original Trewavas figure and so Trueb's Fig. 13-21 A is incorrectly given as *L. hochstetteri* instead of *L. archeyi*. (Duellman/Trueb are apparently unaware of the E.M. Stephenson 1951 reference which is missing from their bibliography - an error perpetuated from Trueb 1973: 90, Fig. 2-70).

The anterior process on the hyale/ceratohyal is present in *Ascaphus* and *L. hochstetteri*, variable in *L. hamiltoni* and absent in *L. archeyi* and all discoglossoid species, for this feature (data not available for *Barbourula kalimantanensis* and *Discoglossus nigriventer*).

Two states of this character are recognized:

State 0. Hyoid - anterior processes on hyale lacking.

State 1. Hyoid - anterior processes on hyale present.

The anuran hyoid is structurally quite different from the urodele hyoid apparatus and therefore does not admit detailed comparison. Consequently no direction of change is postulated for these two character states; state 0 is arbitrarily assigned to the majority condition.

0 ——————— 1

Character 50. Hyoid - alary processes. (Fig. 78).

The main body of the hyoid plate may bear anterolateral to lateral alary processes, if present and well developed they may be large, wing-like processes in some species. Alary processes are absent in *Ascaphus*, *Leiopelma archeyi* and *L. hamiltoni*; present as a distinct but not very large process in *L. hochstetteri*, moderate to large in *Bombina* and large and wing-like in *Alytes*, *Barbourula* and *Discoglossus*.

Two states of this character are recognized:-

State 0. Hyoid - alary processes present.

State 1. Hyoid - alary processes absent.

As in the case of Character 49 outgroup comparison is not possible because of the structural differences between anuran and urodele hyoids. State 0 is arbitrarily assigned to the majority condition.

0 ——— 1

Character 51. Hyoid - parahyoid ossifications. (Fig. 79).

The section introducing the hyoid characters mentions that in discoglossoid frogs the hyoid plate may bear up to four kinds of endochondral ossification. These four forms of ossification are treated as a single character because:

(i) The combinations of presence/absence of the ossified areas suggest a logical progression or sequence for linking the character states described below; this may be of some use in postulating the direction of evolutionary change.

(ii) In view of (i) above, treating each area or type of ossification as a separate character with states present/absent would unduly bias (weight) the data set with respect to hyoid ossification.

Figs. 79a-g illustrate representatives of the six discrete patterns of parahyoid ossification.

Thus, six states are recognized:-

State 0 Medial ossification only present - may or may not have slight anterolateral projections. (Figs. 79a and b)

State 1 Medial ossification only present - a 'V'-shaped splint bone, junction of arms of the 'V' may be quite pronounced. (Fig. 79c)

State 2 Small medial ossification usually present, plus a pair of discrete flat, circular or triradiate lateral patches of ossification. (Fig. 79d)

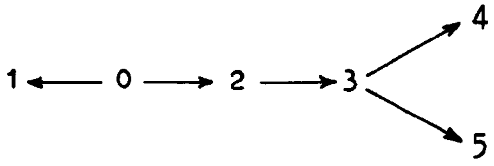
State 3 Medial ossification absent; paired, large circular, lateral patches only present. (Fig. 79e)

State 4 Medial ossification absent; a pair of keeled splint bones, arranged in a 'V', slightly separated or in contact but not joined at their bases. (Fig. 79f)

State 5 Medial ossification absent; an anterior ossification present along the margin of the hyglossal sinus plus paired, circular, lateral patches of ossification. (Fig.79g)

It is important to note that the splint bones of states 1 and 4 are quite different in detail. In state 1 the splint bone is simple, not keeled, and the arms of the 'V' are joined at the base, whereas in state 4 the two bones corresponding to the arms of the 'V' in state 1 are raised or keeled, when there may be a rib of bone around the keeled area, giving each bone a very narrow elliptical shape. In addition, the splint bones of state 4 are separate, although they may be in posterior contact.

Polarity of character 51. As mentioned in the introduction to the hyoid characters, outgroup comparison may not be used to infer hyoid character polarities because urodele and anuran hyoids do not bear sufficient detailed similarity comparison. For characters 49 and 50 it was not possible to decide if it is more possible to lose a cartilaginous process or grow one as an extension of the central plate. In the case of the present character however, I consider it is biologically more plausible to suggest that the primitive anuran hyoid plate lacked endochondral ossifications and that developmentally, the first such ossification would be likely to be the weak medial ossification of the type described as state 0 above. From this condition, and with respect to the detailed morphological appearance of each of the remaining four states, I suggest the most likely direction of change is:-



Note that as a result of this interpretation: the 'splint' bones of states 1 and 4 are not considered homologous; the splint bones of state 1 represent a neomorphic structure; the 'splint' bones of state 4 *are* considered homologues of the circular, lateral patches of ossification of states 2, 3 and 5, of which state 2 represents a neomorphic condition; The bone along the margin of the hyoglossal sinus in state 5 is also a neomorph and is *not* homologous with the 'splint' bones of states 1 and 4.

State 0 is found in *Ascaphus* and *Leiopelma*; state 1 in *Alytes*; state 2 in *Bombina bombina*, *B. orientalis* and *B. variegata*; state 3 in *Bombina maxima* and *B. microdeladigitora*; state 4 in *Discoglossus* and state 5 in *Barbourula busuangensis*.

Character 52. Cervical cotylar arrangement. (Fig. 80).

Lynch (1971: 55 and Fig. 28) described and designated three kinds of cervical cotylar arrangement:

Type I	Cervical cotyles widely spaced.
Type II	Cervical cotyles narrowly separated, two discrete articular surfaces.
Type III	Cervical cotyles confluent representing a single articular surface.

Trueb (1973: 100 and 101 - Table 2-2) stated that ascaphids have a Type III arrangement but now agrees (in litt.) that her material should be assigned to Type II.Of the species in the present study group only Bombina bombina is considered to have Type I cotyles, whereas those of B. microdeladigitora closely approach/are functionally Type III - the confluent condition. The remaining species have Type II cotyles but may be separated into two groups;those lacking a shallow - moderate medial notch, separating the cotyles (Ascaphus, Alytes, Bombina maxima, Discoglossus sardus and Leiopelma), and those having such a notch (Barbourula busuangensis and B. kalimantanensis, Bombina orientalis, B. variegata, and all the Discoglossus species except D. sardus). Gradations between the Types may make determination of the cotylar arrangement difficult in the discoglossoids and in other groups, yet the arrangement may be clear and taxonomically useful in some cases. Variation, as well as possible differences in one's conception of the Type states, may also account for reported differences in Type assignment in some 'difficult' cases. For example, Sanchiz (1984: 69) reported Type III cotyles in Alytes muletensis, while I (Clarke 1984: 48 and this work) have recorded Type II in this species (but in different specimens).

Four states are recognized in discoglossoid frogs:-

State 0. Type II cotyles; moderately separated, no medial notch.

State 1. Type II cotyles, moderately separated by a shallow-moderate medial notch.

State 2. Type I cotyles; widely separated by an anteriorly/ posteriorly shallow notch.

State 3. Type II/functional type III cotyles; median groove present.

It should be noted that there are difficulties in using the urodeles as outgroup - certainly for determining the polarity of Lynch's states or Types. In urodeles, specifically in the hynobiids, ambystomatids and in *Salamandra*, there are *three* or *four* articular surfaces on the cervical vertebra instead of the *two* in anurans: two cup-like cotyles are present as in anurans but between these the urodeles have an anteriorly directed process with possibly one, or more usually two, ventral articular facets. The three/four articular surfaces are quasi-continuous - present as articular surfaces that are continuous or nearly so, i.e. functionally continuous. If one compares only the *cotyles* of urodeles with the cotyles of the discoglossoids there are conflicting indications of polarity: - hynobiids approach a Type I condition, cryptobranchids are Type III and ambystomatids Type II. I am inclined to suggest, on functional grounds that Type II is primitive since Type III is generally found in large or heavy-skulled species with restricted head movement (cryptobranchid salamanders, ceratophryine frogs fide Lynch 1971) and Type I is associated with small lightly ossified species (e.g. hynobiid salamanders, microhylid, hylid and centrolenid frogs) and apparently allows a greater degree of dorso-ventral head movement .

The direction of change is postulated to be:-

$$3 \longleftarrow 0 \longrightarrow 1 \longrightarrow 2$$

Character 53. Presacral vertebrae. (Fig. 81).

The Anura are unique amongst the vertebrates in having a greatly reduced vertebral count - a maximum of nine and a minimum of five presacrals have been recorded in modern anurans. Nine presacrals are known only in Vieraella herbstii * (early Jurassic, Argentina), Notobatrachus degiustoi * (late Jurassic, Argentina; * = counts given in Estes and Reig 1973) Ascaphus and Leiopelma. Discoglossid frogs, as far as it is known (data not available for Bombina fortinuptialis), almost invariably have eight presacral vertebrae. Boulenger (1897: 39) once recorded a count of nine presacrals - "eleven segments.... including the sacral vertebra and the urostyle" in a Bombina variegata, but this was a rare variant of the normal count of eight.

Two states are therefore recognized:-

State 0. Nine presacral vertebrae.

State 1. Eight presacral vertebrae.

The direction of change in this character is evident: all other vertebrates have more than 9 presacral vertebrae, hynobiid and ambystomatid salamanders have approximately 16-22 presacrals and the reconstruction of the proanuran Triadobatrachus massinoti in Estes and Reig 1973: 40, Figure 1-13, shows the presence of 14 presacrals.

The direction of change is clearly:-

$$0 \longrightarrow 1$$

Remarks:-

Any change, in this case we are concerned with reduction, in vertebral counts will normally involve single, whole vertebrae (in occasional aberrant individuals a half vertebrae - transverse process plus part of the centrum - may be gained or lost on one side). Consequently it is likely that common possession of a reduced count, e.g. eight against nine or seven against eight, will be a grade-level step which may occur independently in the same or different lineages. The incidence of homoplasy (parallelisms and convergences) *may* be high. On the other hand, it is likely that lineages with a reduced count will inherit the reduced number - there are (aside from aberrant specimens), to the best of my knowledge, no data to suggest that the count will uniformly revert to a higher presacral number *within a lineage* once the count has reduced.

Character 54. Vertebral column - vertebral centra type.

Nicholls (1916) identified four kinds of vertebral centrum which he termed opisthocoelous, procoelous and diplasiocoelous. Noble (1931) noted a fifth condition, the amphicoelous centrum. As Mookerjee (1930, 1931), Mookerjee and Das (1939) and Griffiths (1963) have shown, the configuration of the vertebral centra is determined by the intervertebral cartilages (see Summary below).

Griffiths (ibid) utilized developmental evidence to propose another classification of anuran vertebral centra. He recognized three types which he called ectochordal, stegochordal and holochordal, and noted that the stegochordal type could be produced by two different developmental pathways although the stegochordal centra thus produced are indistinguishable in the adult anurans. Griffiths (ibid.,: 259-260) noted that anuran vertebral centra and intervertebral bodies develop as, respectively, thin and thick cylindrical segments along the length of an unbroken fibro-cartilaginous perichordal tube surrounding the notochord. If the perichordal sheath is converted first into cartilage and then into bone the centrum becomes an ossified cylinder enclosing a persistent notochord (ectochordal type - Leiopelmatidae: Ascaphus and Leiopelma, also Rhinophrynidae: Rhinophrynus). In the holochordal type the developmental process goes one step further; not only is the perichordal sheath converted to cartilage and then to bone, the notochord is also completely replaced by bone giving a solid cylindrical centrum (some pelobatids, some 'advanced' frogs). The stegochordal condition, in which the centra are transverse, flattened and rather cylindrical, may be produced in two ways, either : (i) the perichordal sheath is converted to cartilage but subsequent ossification is limited to the dorsal part of the cylinder; the lateral and ventral walls of the perichordal sheath and the notochord atrophy, or (ii) chondrification and ossification are again limited to the dorsal part of the perichordal cylinder, but the remainder stays fibrous and subsequently atrophies along with the notochord. The two types of stegochordal centrum are here referred to as respectively stegochordal A and stegochordal B. Stegochordal A is found in pipids and some pelobatids; stegochordal B is confined to the Discoglossidae (fide Griffiths).

Trueb (1973: 103-104 included Griffiths' observations in a redefinition of Nicholls' (1916) and Noble's (1931) terminologies (see Summary below).

	Centra		Intervertebral cartilages
	Type	Nature	
Amphicoelous	Ectochordal	Sl. biconcave or flat terminally.	Contiguous between successive presacrals.
Anomocoelous	Stegochordal	"	Free, subdivided anteriorly and posteriorly. Subsequently ossifies, remains free.
Opisthocoelous	Ectochordal	Convex anteriorly.	Subdivided anteriorly, ossifies and fuses to posteriorly adjacent centrum.
or	Stegochordal	Concave posteriorly.	
Procoelous	Holochordal	Concave anteriorly; convex posteriorly.	Subdivided posteriorly, ossifies and fuses to anteriorly adjacent centrum.
Diplasiocoelous	Holochordal	1st seven presacrals as per procoelous; eigth biconcave.	Presacrals 1 - 7 as per procoelous condition, 8 to sacrum - opisthocoelous type.

Summary of Vertebral column types (after Trueb 1973).

Only two states are found in discoglossoid frogs:

State 0. Amphicoelous/ectochordal.

State 1. Opisthocoelous/stegochordal.

State 0 is confined to Ascaphus and Leiopelma; state 1 to Alytes Barbourula, Bombina and Discoglossus. State 0 is considered (with some reservations) to be the primitive condition, following Moffatt (1974 a) who cited presence of uninterrupted notochord in labryinthodonts. Moffatt (1974b) however, drew attention to the uncertainties regarding homologies of amphibian vertebrae with those of other vertebrates. Moffatt (1974 a: 161) noted that while the term amphicoelous has been used to describe the vertebrae of Ascaphus and Leiopelma, the accuracy of this terminology has been questioned by E.M. Stephenson (1952, 1960) and by Ritland (1955) on the grounds of structural differences compared with notochordal amphicoelous vertebrae of some other vertebrates. Indeed, it should be noted that in hynobiids and cryptobranchids the centrum is hollow allowing for the passage of notochord, but is also spool shaped. There is a notable constriction in the middle of each centrum where the notochordal cells are converted into cartilage - the intravertebral cartilage (Mookerjee 1930: 440 on Triturus: Salamandridae). I therefore regard the vertebral centra of urodeles as too different to permit ready comparison. Moffatt (1974 a:142, 161) also noted differences in internal morphology between Ascaphus and Leiopelma.

The amphicoelous condition is as developmentally the simplest type with least change from the condition which is common to Griffiths three types of centra. The polarity of this character is therefore tentatively given as:

$$0 \longrightarrow 1$$

Character 55. Presacral vertebrae - shape of centra (dorsal view). (Fig. 82).

This character specifically concerns the shape of the presacral centra in dorsal view. Two distinct conditions are found in discoglossoid frogs:

State 0. Vertebral centra elongate, tubular with, at most, a weak hour glass shape.

State 1. Vertebral centra short, squat hour glass shape (each centrum narrowest at midlength).

Only three discoglossoids have the state 0 condition - Bombina bombina, B. orientalis and B. variegata, all the remaining taxa in the study group show State 1. Urodele vertebrae are more similar to state 0 than to the state 1 condition, consequently outgroup comparison suggests the direction of change to be:

$$0 \longrightarrow 1$$

Remarks:

The elongate vertebral centra condition may be correlated with an elongate body shape, if so then the polarity of this character might have to be reversed. Further information on the vertebrae of higher anura is urgently needed. In this instance, data on the shape of the centra in long, narrow-bodied anurans especially in some centrolenids, hylids and hyperoliids e.g. Afrixalus would be of particular interest. In the relatively long-bodied pelodytids, Pelodytes caucasicus and P. punctatus, the centra are state 1 (pers. obs.) so it may be that the polarity of this character should be inverted. Nonetheless, for the reasons given in the section on "Clades, grades, evolutionary processes and the problems of phylogenetic reconstruction in relatively primitive groups", I have tentatively assigned polarity on the basis of comparison with a relatively more primitive outgroup. Clearly, correlation of a character state with an evident, specific function for that state would override outgroup comparison as a polarity indicator.

Character 56. Ribs - numbers of pairs present.

The presence of (vestigial) ribs in adult discoglossoid frogs is taken to be an indication of the 'primitive' status of the group. Trueb (1973: 105-106) provides a reasonably concise resume of current opinion. She notes that ribs are: present in only three anuran families, Ascaphidae (includes Leiopelma), Discoglossidae and Pipidae; free in aschaphids and discoglossids but "indistinguishably fused to the transverse processes in adult pipids", and that normally there are three pairs of ribs present articulating with the transverse processes of the second, third and fourth presacral vertebrae. Although Trueb qualifies the last comment with "normally", she did not give details of other configurations of rib counts and most other authors appear to assume three pairs of ribs are present e.g. In fact, the number of ribs present is subject to interspecific (between individual species)or sometimes supraspecific (between groups of species) variation in discoglossoid frogs, even if one does not distinguish between free and ankylosed ribs (see Character 56).

Four states are recognized:-

State 0. Two or more usually three pairs of ribs present; there are usually signs of fused ribs on the 5th and possibly even the 6th presacral vertebrae. (If only two pairs present, 2nd presacral lacks ribs).

State 1. Three pairs of ribs only; on the 2nd, 3rd and 4th presacrals.

State 2. Two pairs of ribs; usually on the 3rd and 4th but alternatively may be on the 2nd and 3rd presacrals.

State 3. One pair of ribs; on the 3rd presacral vertebrae.

State 0 is confined to Ascaphus truei; state 3 to Alytes cisternasii. State 2 is found in Alytes muletensis (Clarke 1984: 48), A. (o). maurus and in Leiopelma. All other discoglossoids examined are State 1.

Using all other (non-anuran) vertebrates as outgroup, but with special reference to urodeles, Triadobatrachus (ribs on all presacrals including fide Estes and Reig 1973: 39 and 40, Fig. 1-13) and Notobatrachus (ibid: 24, Fig. 1-9 showing four pairs also p. 21 "ribs always present on vertebrae 2-5 and occasionally on 6", it is clear that the trend is toward reduction in rib number. The primitive status of the discoglossoids and their intermediary position between urodeles, Triadobatrachus and "higher frogs" is further indicated by the complete absence of ribs in the last-named group, in which it is seen as the culmination of a trend towards reduction and loss. The reported presence of ribs in subadult, but absence in adult, pipids and palaeobatrachids (Lynch 1973: 168) is also seen as part of this trend. Consequently state 0 is considered primitive; the simplest interpretation of the direction of change of the four discoglossoid states is:

$$0 \longrightarrow 1 \longrightarrow 2 \longrightarrow 3$$

Character 57. Ribs - free, ankylosed or fused. (Figs. 83a, b ahd c respectively).

The presence of free ribs has been widely regarded as diagnostic for discoglossoid frogs, e.g. Inger 1967, Kluge and Farris 1969, Lynch 1973, Duellman 1975, Dowling and Duellman 1974-1978 and Sokol 1977. Lynch (1973: 144-145) noted that this character has been subdivided into two character states : (a) ribs free in adults and subadults or free in subadults only, and (b) ribs not free at any stage of development of the individual. Unless and until ontogenetic series of all the known species have been examined (b) above will remain unknown; to record (b) for any anuran family would be recording data which are supposed to be true but not verified in fact - i.e. in the absence of actual observations. (To claim (b) is correct for any family group goes beyond extrapolation from selected sample taxa). In addition, the observation that all discoglossoids have free ribs, is not correct, as already borne out in the literature by Lynch's (1973: 167) note "(8) ribs free in subadults and adults, although generally ankylosed to transverse processes in Bombina". The situation in discoglossoids is far more complex than is generally suggested (stated to be "freely articulating" by Trueb 1973: 106) - the vestigial ribs in anurans may be free, ankylosed (weakly fused with a clear boundary between rib and transverse process) or fused, when the boundary between the rib and transverse process is not clear. In the fused condition, the rib is clearly present because it is either inclined at angle to the transverse process and tapers from the dilated bony junction with the transverse process or there is a thickening in the bone, at the junction. Thus the fused condition of the discoglossoids is quite distinct from the indistinguishably fused condition seen in pipids where the rib plus transverse process look like a wide transverse process (Trueb 1973: 106 and Lynch 1073: 145 Fig. 3-2, showing condition in Pipa pipa).

Three states are recognized:

State 0. All ribs present are free ribs.

State 1. Some ribs are free, some are ankylosed or fused.

State 2. All ribs present are fused.

State 0 is found in Barbourula busuangensis, B. kalimantanensis, Bombina maxima and B. variegata and in Discoglossus; state 1 in Alytes (except A. cisternasii) and state 2 in the remaining taxa in the study group.

As Trueb (loc. cit.) says "The occurrence of ribs is obviously primitive. The fused condition of the ribs of pipids represents an advancement over the freely articulating ribs of the ascaphids and discoglossids". Urodeles do have freely articulating ribs which are therefore considered primitive. The trend toward rib reduction and loss has already been commented upon under Character 56; this character is concerned with a different aspect of reduction - fusion with the transverse processes.

The direction of change is clear:

$$0 \longrightarrow 1 \longrightarrow 2$$

Notes:

(1) One juvenile Ascaphus truei (CAS 113963) and one juvenile Leiopelma hochstetteri (CAS 156253) examined were found to have free ribs - adults of these species were found to have the fused condition. Thus the polarity is consilient with these ontogenetic data.

(2) Ritland (1955: 134-135) suggests much variation is possible in Ascaphus truei from free to fused. In view of the occurrence of errors of observation in the literature I have decided to code characters with reference only to study material available to me. I nonetheless recognize that Ritland was able to examine far larger samples of A. truei, and that this character may be subject to a great deal of variation in A. truei in particular and discoglossoids in general.

Character 58. Uncinate processes. (Fig. 84).

Uncinate processes are short, terminally truncate or sharply pointed postero-dorsally directed processes on the ribs of some discoglossoid species. Ritland (1955: 135) commented, "It is not rare to find an uncinate process absent or in a slightly different position in any of the ascaphids or discoglossids". Ritland notes that the rib and uncinate process provide the origin for the group of muscles that insert into the suprascapula or scapula from behind (verified in study group material bearing uncinate processes). According to Ritland these muscles are responsible for posterior movements of the dorsal part of the pectoral girdle.

Uncinate processes are usually found on the ribs of the 3rd presacral vertebrae but may also be found on the 3rd and 4th in *Ascaphus truei* and *Leiopelma hamiltoni* and on the 2nd and 3rd in *Discoglossus sardus*. Out of five *Alytes (o) maurus* alizarin preparations examined only one had a definite process on the rib on the left side of the 3rd presacral but an indistinct process on the right rib. A similarly indistinct uncinate process was found on a *Bombina bombina*.

Two states are recognized:-

State 0. Uncinate processes present.

State 1. Uncinate processes absent.

With the exception of the variant condition in one specimen of *Alytes (o) maurus* mentioned above, *Alytes* species are the only discoglossoids to lack uncinate processes. Urodele ribs do not admit detailed comparison at the descriptive level, therefore no polarity is postulated for this character.

State 0 is arbitrarily assigned to the majority condition.

Character 59. 2nd presacral - transverse processes/ribs distally rounded or flared. (Fig. 85).

This character is concerned with the nature of the distal (lateral) margins of the ribs or transverse processes on the 2nd presacral vertebrae and the area they present for muscle insertion (see comments under Character 58).

Three states of this character are recognized:

State 0. Area for muscle insertion simple, rounded (distalend of rib or of transverse process if rib absent).

State 1. Area for muscle insertion flared posteriorly only ("prong-like" rib).

State 2. Area for muscle insertion flared anteriorly and posteriorly (fully developed flared rib).

State 0 is found in *Alytes cisternasii*, *A. muletensis*, *Ascaphus* and *Leiopelma*; State 1 in *Alytes o. obstetricans*, *A. o. boscai* and *Discoglossus* species except *D. pictus*; state 2 is found in *Barbourula busuangensis*, *B. kalimantanensis* and in *Bombina*. *Alytes (o.) maurus* shows variation between states 0 and 1 - simple rounded or posteriorly flared; *D. pictus* a weak anterior expansion coded as variation between states 1 and 2.

Urodeles do not have flared lateral margins to the ribs on the 2nd presacral - they are closest to state 0. Consequently state 0 is considered primitive and the simplest interpretation of the direction of change is:

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 60. Neural arches - imbricate/non-imbricate. (Fig. 86).

Lynch (1973: 146) noted that Griffiths (1963) and Tihen (1965) regarded imbricate neural arches (where the spinal canal is completely roofed over by bone) to be primitive with respect to the non-imbricate condition (spinal canal exposed). In the imbricate condition the posterior margin of one vertebra overlies the anterior margin of the vertebra immediately posterior to it - thus the posterior margin of the 1st presacral overlies the anterior margin of the 2nd, the posterior margin of the 2nd overlies the anterior margin of the 3rd and so on (like tiles on a roof). Lynch commented "In large measure this character reflects degree of ossification, but is not entirely dependant on that factor" saying that it is possible, as in Notaden (Myobatrachidae), to have extensive bone reduction but still have imbricate neural arches. I am in agreement with Lynch's and Tihen's general comments - that the shift from the imbricate to the non-imbricate condition is not a quantum jump but a gradual one, which makes character coding rather difficult - however, the character is worth retaining since it reflects an underlying evolutionary trend and will therefore help provide an indication of relationships rather than "enhance the distinctions between groups". (Note the similarity with Kavanaugh's 1978b "group trends" concept see Section 4.4 on Character polarity). These "trend characters" are potentially very useful, provided, as in this case, the trend is more clear-cut than usual and it is possible to confidently assign taxa to one of the following three states:-

State 0. Neural arches imbricate.

State 1. Neural arches weakly imbricate or imbricate on 1st presacral, weakly imbricate on 2nd and 3rd and progressively less imbricate on presacrals 4–8.

State 2. Neural arches non-imbricate.

Barbourula busuangensis has the most strongly imbricate neural arches; *Bombina* and *Discoglossus* (except *D. sardus*) are also imbricate and are therefore state 0. *Alytes cisternasii* is imbricate on 1st to 3rd presacral, less so on 4–8; *A. o. obstetricans* and *A. o. boscai* are imbricate on the 1st presacral, less so on 2–8 and *A. muletensis* and *A. (o.) maurus* are weakly imbricate on the 1st and progressively less imbricate on presacrals 2–8. *D. sardus* vertebrae are all weakly imbricate. *Alytes* and *D. sardus* are therefore assigned to state 1. *Ascaphus* and *Leiopelma* have non-imbricate presacral vertebrae: state 2.

Urodeles (hynobiids, ambystomatids and *Salamandra* – Francis 1934) show state 0, thus outgroup comparison confirms Lynch's and Tihen's comments for the Anura as a whole.

The simplest interpretation for the direction of change of this character is:–

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 61. Neural arches - posterior margins flared and upturned or simple. (Fig. 87).

The posterior margins of the neural arches in *Barbourula busuangensis* are very noticeable in that they are flared medially to laterally and postero-dorsally directed (upturned) - Clarke 1987: 886). A similar condition is found in *Bombina bombina*, *B. maxima* and *B. microdeladigitora*. In *Alytes*, *Ascaphus* and *Leiopelma* the posterior margins of the neural arches are neither flared nor upturned and therefore designated as 'simple'. An intermediary condition - slightly flared, slightly upturned is seen in *Bombina orientalis*, *B. variegata* and in *Discoglossus*. Thus, three states are recognized:-

State 0. Neural arches - posterior margins simple.

State 1. Neural arches - posterior margins slightly flared, upturned.

State 2. Neural arches - posterior strongly flared, upturned.

In the urodeles there is also some variation in this character - the hynobiids have simple to slightly flared, upturned posterior margins to the neural arches, more derived urodeles e.g. the salamandrids (*Salamandra*, *Triturus*) have slightly flared posterior margins. I suggest that this is also a 'trend character' as described above under character 60. On the basis of reference to the hynobiids for outgroup comparison and, more importantly, on the grounds that it is developmentally more plausible to proceed from state 0 and pass to state 2 via state 1 (juvenile/subadult *B. busuangensis* e.g. dry skeleton CAS-SU 6015 is closer to the state 1 condition). The direction of change is hypothesized to be:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 62. Neural spines. (Fig. 87).

The neural arches, in addition to having posterior margins which may be imbricate or non-imbricate, flared and upturned or simple, may (or may not) also bear neural spines on the anterior presacral vertebrae. A neural spine, if present, is seen as a dorso-median keel which projects posteriorly (to a variable extent) beyond the posterior margin of the neural arch. There is an anterior-posterior gradient in this character; the neural spine on the first presacral is usually the most fully developed, on the second less well developed and so on - the spine on the last presacral is either the least well developed or may even be absent. (The posterior margins of the 7th and 8th presacrals are *invaginated* in *Barbourula busuangensis*). This character is therefore concerned only with the neural spines on presacrals 1 - 4 . Trueb (1973: 104) considers that there **may** be a correlation between imbricate and neural arches and well developed neural spines and makes a set of assumptions:- "the presence and development of neural spines *seems* to be associated with size and degree of ossification of the species; terrestrial taxa *seem* to have better-developed spines than do aquatic or arboreal species. Thus, *one is led to assume*... a *trend towards* elaboration of neural spines in frogs whose locomotory activity or size *demands more*... muscle development... more surface area for muscle insertion" (my italics). As usual Trueb's observations are empirically based and represent reasonable generalisations yet there is no *necessary logical correlation* between presence and development of spines and size and degree of ossification or the presence of imbricate neural arches. That this is so is seen, for example, in the heavily built *Bombina maxima* and *B. microdeladigitora* which have imbricate neural arches but only moderately developed neural spines while *Barbourula busuangensis* of similar size have imbricate neural arches and strongly developed neural spines. Similarly, *Bombina bombina* has imbricate neural arches but no or only the weakest indication of neural spines.

Discoglossoid frogs exhibit three neural spine states:-

State 0. Neural spines absent or only weakly developed. (Fig. 87a).

State 1. Neural spines moderately developed. (Fig. 87b).

State 2. Neural spines strongly developed. (Fig. 87c).

State 0 is found in *Alytes*, *Ascaphus*, *Bombina bombina*, *B. orientalis*, *B. variegata* and *Leiopelma*; state 1 in *Bombina maxima*, *B. microdeladigitora* and *Discoglossus*. State 2 is confined to *Barbourula* (state in *B. kalimantanensis* not known). Hynobiid salamanders lack neural spines[*], therefore state 0 is considered primitive and the direction of change for this character is considered to be:-

$$0 \longrightarrow 1 \longrightarrow 2$$

[*] Ambystomatid salamanders have neural spines; *Salamandra* lacks them - the presence of neural spines must therefore be regarded as a somewhat labile character state.

Character 63. Posterior presacral vertebrae: transverse processes - orientation. (Fig. 88).

This character is concerned with the orientation of the transverse processes on the last three presacral vertebrae immediately anterior to the sacral vertebra - on the 7th, 8th and 9th presacrals in Ascaphus and Leiopelma and on the 6th, 7th and 8th in Alytes, Barbourula, Bombina and Discoglossus. Three discrete orientation patterns are recognized:-

State 0. Transverse processes on the last three presacrals perpendicular to the longitudinal axis of the vertebral column or slightly posteriorly directed.

State 1. Transverse processes on the last two presacrals weakly anteriorly directed; on the preceeding vertebra, transverse processes usually perpendicular, or only very weakly anteriorly directed.

State 2. Transverse processes on the last two presacrals strongly anteriorly directed; on the preceeding vertebra, the transverse processes may be perpendicular or slightly anteriorly directed.

In states 1 and 2 there is a gradient: the transverse processes on the last presacral vertebra are more strongly anteriorly directed than those on the penultimate presacral, which in turn are more anteriorly directed than those on the antepenultimate presacral. Thus, the antepenultimate have the weakest, and the last presacral the most strongly, anteriorly directed transverse processes, while the penultimate presacral vertebra is intermediate between the two.

State 0 is found in Ascaphus, Leiopelma archeyi and L. hamiltoni; State 1 in Alytes, Discoglossus and Leiopelma hochstetteri and State 2 in Barbourula (B. busuangensis and B. kalimantanensis) and Bombina. All the transverse processes in urodeles, particularly the last three, are very short and slightly posteriorly directed. State 0 is therefore closest to the outgroup condition and is considered the primitive state. With state 0 primitive and noting the morphological trend in states 1 and 2, the direction of change is considered to be:

$$0 \longrightarrow 1 \longrightarrow 2$$

Note: It is possible that derived states of this character may be correlated with derived states of character 66: Dilation of sacral diapophyses, yet it is not clear that there necessarily need be a correlation between the two characters. There is no obvious reason why (short) perpendicular transverse processes might not be paired with broadly dilated sacral diapophyses - although there might be a functional requirement (involving the dorsal musculature) which precludes such a character state combination. In the present state of knowledge characters 63 and 66 are treated separately.

Character 64. Posterior presacral vertebrae: transverse processes. (Fig. 88).

In urodeles, especially in hynobiid salamanders, the transverse processes on the posterior presacral vertebrae (specifically, those on the 3-4 presacrals immediately anterior to the sacral vertebra) are even shorter (in terms of their proximal to distal length) than those on preceding 3-4 vertebrae. Amongst the discoglossoid frogs a similar antero-posterior gradient is observed in *Ascaphus* and *Leiopelma*, while in *Alytes*, *Barbourula*, *Bombina* and *Discoglossus* the transverse processes on the posterior presacrals tend to be relatively longer in comparison (i) with those of the preceding presacrals or (ii) with the sacral diapophyses.

Thus, two states are recognized:-

State 0. Transverse processes on the last two presacrals poorly developed, shorter than on preceding vertebra.

State 1. Transverse processes on the last two presacrals usually well developed, as long or longer than on preceding vertebra.

and the direction of change is considered to be:

$$0 \longrightarrow 1$$

Notes: The transverse processes on the last (8th) presacral may be wider than on the 7th in *Bombina maxima*. In *B. bombina* the transverse processes on the 8th are poorly developed, needle-like processes sharply inclined anteriorly but are nonetheless, proximally to distally, as long as the transverse processes on the 7th and are accordingly assigned to state 1 rather than state 0.

Character 65. Posterior presacral vertebrae: transverse processes - marginal flanges. (Fig. 88).

In *Barbourula busuangensis* each of the transverse processes on the 6th, 7th and 8th presacrals bears a posterior marginal flange (referred to as a "marginal extension" in Clarke, 1987: 887). There is also a morphological gradient in this character - the marginal flanges on the transverse processes of the 8th are more fully developed than those on the 7th, which, in turn, are more developed than those on the 6th. The rather blurred radiograph of the holotype (and to date the only known specimen) of *Barbourula kalimantanensis*, kindly supplied by Dr.D.T. Iskander, Museum Zoologicum Bogoriense, also shows the presence of medial flanges on the same transverse processes. Examination of the transverse processes on the posterior presacral vertebrae of the other discoglossoid taxa showed:- (1) marginal flanges are absent in *Alytes*, *Ascaphus* and *Leiopelma*. (2) flanges present but usually weakly developed in *Bombina* and *Discoglossus* - again, the flanges are more fully developed on the 7th and 8th, not necessarily 6 7 8; the flange on the 7th may be equally as well or more developed on the 7th in *Discoglossus* species. Two states of this character are recognized:-

State 0. Posterior marginal flanges on transverse processes of posterior presacral vertebrae - absent.

State 1. Posterior marginal flanges on transverse processes of posterior presacral vertebrae - present.

Urodeles have short well defined transverse processes on the posterior presacral vertebrae but lack marginal flanges, consequently state 0 is considered primitive and the direction of change is:-

$$0 \longrightarrow 1$$

Remarks: It is possible that there might be a correlation between this and

Character 63 if both are related to the development of the dorsal muscles in this region used for locomotion. This has not been demonstrated and so characters 63 and 65 are treated separately.

Character 66. Dilation of the sacral diapophyses. (Fig. 89).

Trueb (1973: 106) commented that the sacral diapophyses represent modified transverse processes. Most authors (e.g. Trueb ibid., Lynch 1973 and Duellman/Trueb 1986) recognize the existence of three conditions: broadly dilated, moderately dilated and "round" or cylindrical. Trueb (loc.cit.) maintains that the sacral diapophyses are "broadly expanded in some Primitive families...." and cites her own Table 2-2, p. 101 which records the sacral diapophyses as "Expanded" in Ascaphidae and Discoglossidae. Lynch (1973: 144) went further: "Broadly dilated sacral diapophyses characterize the four archaic families, the three transitional families, and only a few advanced families....." and specifically listed " (8) sacral diapophyses broadly dilated" as one of his "38 characteristics" for Ascaphidae (p.166) and Discoglossidae (p. 167). I find Lynch, and to a lesser degree, Trueb (it depends on her interpretation of 'expanded'), to be in error. In fact the sacral diapophyses of Ascaphus are usually only slightly dilated or 'bar-like', although Ritland (1955: 138 - 139, Fig. 5) has noted that the expansion of the diapophyses increases with age. He also noted that even in mature Ascaphus there is variation in expansion which is not sex-related. Ritland's Fig. 5 shows that even individuals with relatively well dilated sacral diapophyses would, in the context of the Anura, be considered only slightly expanded. Exceptionally e.g. Ritland's Fig. 5.B they may approach a moderately dilated condition. I find Leiopelma to possess a similar condition to Ascaphus, except that in Leiopelma the sacral diapophyses are only very slightly dilated and may have clubbed ends. In Alytes and Discoglossus the sacral diapophyses are moderately dilated, while in Barbourula and Bombina they are broadly dilated. These latter two conditions are herein designated 'hatchet-shaped' and 'butterfly-wing type' respectively, since these terms more graphically and accurately give an idea of the degree of dilation present. (I consider there to be four states of this character within the Anura as a whole - the three described above, plus the cylindrical condition which is only seen in some advanced frogs, notably the ranids).

Thus in discoglossoids three states of this character are recognized:-

State 0. Sacral diapophyses 'bar-like', clubbed or slightly expanded. (Fig. 89a).

State 1. Sacral diapophyses moderately dilated ('hatchet-shaped'). (Figs. 89b and c).

State 2. Sacral diapophyses broadly dilated ('butterfly-wing type'). (Fig. 89d).

In urodeles, the transverse processes of the sacral vertebrae (= diapophyses of the anurans) are clubbed, each having two heads which articulate with a Y-shaped rib. While they do not correspond in detail with the form of the sacral diapophysis in the Anura, they are sufficiently similar to suggest that the slightly dilated or clubbed form seen in Ascaphus and Leiopelma may be thought of as closest to the urodele type. Stephenson (1952: 605) noted that in L. hochstetteri the diapophysis "is relatively unspecialized". In addition, Trueb's comment - that the sacral diapophyses represent modified transverse processes (cited above) - is clearly evident in the case of the urodeles. Francis (1934: 20) noted of the sacral vertebra "The vertebra itself conforms to the general pattern of the trunk vertebrae... but it is slightly larger and its transverse processes and ribs are very stout and long". Therefore state 0 is considered primitive and the simplest interpretation of the direction of change is an increase in the dilation of the diapophyses:

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 67. Sacral centrum: divided or entire. (Fig. 90).

I independently noted the presence of a divided sacral centrum in Leiopelma and later discovered that Stephenson, E.M., (1952) was the first to comment on this feature. This reference was picked up by Ritland 1955 (who also commented on the sacrum of Leiopelma) but curiously was overlooked by Lynch (1973) and Trueb (1973) - both of whom were aware of Ritland's work. Stephenson (ibid.: 604-605) commented that the sacral vertebra of L. hochstetteri "is extremely peculiar, if not unique" in that it comprises "two separate bony halves joined dorsally and ventrally by cartilage" also that it is "narrow antero-posteriorly compared with the other vertebrae". I agree with Stephenson's description for L. hochstetteri and would also add that the same type of sacral centrum is found in L. archeyi and L. hamiltoni (confirming Stephenson, E.M. 1960: 479-480, Fig. 3), and with Ritland (1955: 138) that the sacrum is therefore flexible, but the significance of this, if any, is not known. Separation is clearly a form of arrested development (paedomorphosis) - a juvenile L. hochstetteri CAS 156253 examined, shows lack of dorsal fusion of all presacral vertebrae as well as separation of the sacral. Alytes, Ascaphus, Barbourula, Bombina and Discoglossus have sacral centra which are fused (complete) dorsally and ventrally. Thus, two states are recognized:

State 0. Sacral centrum entire.

State 1. Sacral centrum divided.

Urodeles have entire sacral centra. Therefore state 0 is considered primitive on the basis of outgroup comparison and developmental evidence.

The direction of change is therefore:-

$$0 \longrightarrow 1$$

Character 68. Sacrum - position of the prezygapophyses. (Fig. 91).

The prezygapophyses of the sacral vertebrae articulate with the postzygapophyses of the last presacral vertebrae. The prezygapophyses are paired and, in discoglossoid frogs, may occupy one of the two positions relative to the anterior margin of the sacral diapophyses:-

State 0. Sacral prezygapophysis - anterior to the anteromedial margin of the sacral diapophysis.

State 1. Sacral prezygapophysis - posterior to the anteromedial margin of the sacral diapophysis or at least -

The distinction is, that in state 0 the prezygapophysis is not on, but in front of, the anteromedial margin of the sacral diapophysis - it is an anteriorly projecting process, whereas in state 1 the prezygapophysis is actually on the dorsal surface of the sacral diapophysis - just behind the anteromedial margin.

In urodeles, the prezygapophysis is anteriorly placed relative to the sacral diapophyses (transverse processes) - suggesting state 0 to be the primitive condition in the discoglossoid group. In fact, the prezygapophysis is even more anteriorly placed than in state 0. In respect of the placement of their prezygapophyses (i) the sacral vertebra resembles the presacral (trunk) vertebrae in urodeles and (ii) the presacral vertebrae resemble those of urodeles. Trueb's (1973: 106) comment that the sacrum is .... "somewhat modified" from the presacral form - "Like the latter, the sacrum bears a pair of prezygapophyses...." suggests the prezygapophyses of the sacral and presacral vertebrae are serially homologous, as in urodeles. Consequently, by outgroup comparison and serial homology, state 0 is considered primitive and the direction of change is:-

$$0 \longrightarrow 1$$

Character 69. Sacrococcygeal articulation.

In the discoglossoid study group there are three forms of sacrococcygeal articulation/junction: (i) contiguous cartilage (ii) monocondylar and (iii) bicondylar. *Ascaphus* and *Leiopelma* are the only discoglossoids to have contiguous cartilage between the sacrum and coccyx, there are therefore *no articular surfaces* between these two elements - the sacral centrum and the coccyx present flat surfaces to the connecting cartilage. Ritland (1955:128) neatly summarized the situation in *Ascaphus* by reference to Nobles' observation that a single condyle is present - "no such condyle exists, for the cartilage is exactly the same as that between successive vertebrae". The articulation is monocondylar in *Barbourula* and *Bombina*; bicondylar in *Alytes* and *Discoglossus*. Since they lack articular surfaces *Ascaphus* and *Leiopelma* are not comparable with other discoglossoids and are scored as 'not logically applicable' for this character. Thus only two states are recognized:-

State 0. Sacrococcygeal articulation monocondylar.

State 1. Sacrococcygeal articulation bicondylar.

In urodeles the sacro-postsacral articulation is the same as that found in the preceding trunk vertebrae (described in Francis 1934: 18) and does not admit detailed comparison with the anuran sacrococcygeal articulation - the intervertebral cartilage remains and the posterior surface of the sacral centrum and the anterior surface of the first postsacral centrum are deeply concave. No anuran sacrococcygeal condition resembles this condition. In the absence of a comparable outgroup condition a polarity is not assigned to this character.

Notes.

(i) The condition in *Ascaphus* and *Leiopelma* may be regarded as paedomorphic - persistent notochord, persistent cartilage - and therefore derived. Trueb (1973: 106) gives this interpretation for the contiguous cartilage condition of the sacrococcygeal articulation in sooglossids yet a priori interprets the same condition as primitive in ascaphids.

(2) I disagree with Trueb's interpretation (loc. cit.) that a bicondylar articulation is widespread amongst 'primitive' families other than ascaphids. Such an interpretation is clearly the result of sampling error - discoglossids as noted above are monocondylar or bicondylar not bicondylar as recorded in Table 2-2 in Trueb (1973). Of the remaining primitive families pipids are fused and rhinophrynids (1 extant species) are bicondylar. Thus no one condition predominates in the primitive frog families.

(3) I further disagree with Trueb's conclusion that the monocondylar condition is a modification of, i.e. derived from, either "the ascaphid or bicondylar plan". Serial homology of the sacral with the presacral centra would suggest the monocondylar condition is more likely to be primitive - a reasonable hypothesis, I believe, based on the interpretation that the sacral is a specialized form of presacral vertebrae (an interpretation which is substantiated by outgroup comparison with urodele trunk and sacral vertebrae).

(4) This character is not further, or alternatively, coded as sacrococcygeal articulation present or absent since the absence condition (no articular facets) still does not resemble the primitive urodele condition (see above). So, again, no polarity inference is possible - based on outgroup comparison.

The Ilium, ischium and other pelvic elements.

The ilia are paired endochondral bones which comprise the major part of the pelvic girdle, which also includes the ischia (paired: endochondral) bone and pubes (paired: cartilaginous and calcified). The ilia articulate; one with the other posteriorly and medially; with the paired ischia posteriorly and the pubes ventrally. Each of the three components - ilium, ischium and pubis - contribute to an acetacular fossa which accommodates the head of the femur on that side (left acetabular fossa - left femur; right acetabular fossa - right femur) in a ball-and-socket joint. The ilia provide the link between the hindlimbs and the vertebral column - anteriorly they articulate with the outer, ventral surfaces of the sacral diapophyses, posteriorly with the femora as described above. Thus the pelvic girdle, (the ilium in particular), plays an important part in locomotion (discussed at length in Emerson 1979). Consequently, it is not surprising that it is the ilium which subject to a great deal of variation/modification, seen as changes in length and shape and also variation in ,the presence/absence of processes and protruberances. Most of this variation corresponds with differences in muscle origins and insertions associated with changes in the locomotory habit. Longer ilia are associated with improved swimming ability or jumping ability compared with those forms having shorter ilia. Short ilia are more characteristic of terrestrial and especially fossorial forms which tend to walk or progress in short hops rather than jump (Whiting 1961; Trueb 1973; Emerson 1979; Duellman/Trueb 1986 and pers. obs.).

This analysis is concerned chiefly with the ilium, its configuration, the placement of the dorsal acetabular expansion and the presence/absence of an iliac synchondrosis. Lynch (1971) provides a useful terminology for the ilial processes and protruberances. The development and orientation of the ischium is also considered, as is the form of the epipubis and the presence of postpubic or Nobelian bones). The pubis either remains cartilaginous throughout life or may califý and is subject to little variation in discoglossoid frogs.

Character 70. Ilium - configuration. (Fig. 92).

The major variation in the configuration of the ilium, aside from the differences in the length of the ilial shaft, is in the presence or absence of a dorsal ilial crest and the disposition of the dorsal protruberance and the dorsal prominence (terminology of Lynch 1971: 61). These areas provide important sites for the origin and insertion of many of the thigh muscles. Lynch (ibid) recognized two main forms of ilial configuration; one, in which the dorsal protruberance is well developed and situated on an equally well developed dorsal prominence, and which has a dorsal ilial crest (his 'leptodactyline type'); and the second, with a very weak dorsal protruberance, a weak to moderate spike-like dorsal prominence and no dorsal ilial crest (Lynch's 'ceratophryine type'; see also Clarke 1981: 310). In discoglossoid frogs a third type is also found: dorsal protruberances very poorly developed, no evident dorsal prominence, no dorsal ilial crest. Trueb (1973: 107-108) underestimated the variation present in primitive frogs: "Primitive anurans have a plain shaft that tends to be cylindrical in cross section...Among advanced frogs the ilial shaft may bear crests or ridges".

Three states are recognized:-

State 0. Ilium - dorsal protruberance very weak, dorsal prominence absent; no dorsal ilial crest. (Fig. 92a).

State 1. Ilium - dorsal protruberance very weak, dorsal prominence weak to moderate (but present as an evident 'bump' which is not, or only poorly differentiated from the dorsal protruberance); no dorsal ilial crest - weak ceratophryine type. (Fig. 92b).

State 2. Ilium - dorsal protruberance moderate to well defined and situated on a large dorsal prominence; dorsal ilial crest present - leptodactyline type. (Figs. 92c,c').

State 0 is found in Ascaphus and Leiopelma; state 1 in Alytes, *Barbourula busuangensis* and *Bombina*; state 2 is confined to *Discoglossus*. Urodeles (especially hynobiid and ambystomatid salamanders) have a relatively undifferentiated ilium. The state most closely resembling the urodele condition is state 0. With state 0 primitive there is an evident morphological cline - the direction of change is considered to be:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 71. Ilium - dorsal acetabular expansion. (Fig. 93).

This character is concerned with the position of the apex of the dorsal margin of the dorsal acetabular expansion (modification of terminology of Lynch 1971) relative to the dorsal limit of the ischium. In the discoglossoid study group two clearly distinct types are found:

State 0. Ilium - dorsal acetabular expansion *anteriorly* placed; does not extend to the dorsal limit of the ischium (Type A).

State 1. Ilium - dorsal acetabular expansion *posteriorly* placed; extends to the dorsal limit of the ischium (Type P).

In state 0 (Type A) the dorsal portion of the ischium extends above the level of the apex of the dorsal acetabular expansion; in state 1 (Type P) the dorsal limit of the ischium is level with the apex of the dorsal acetabular expansion. State 0 is found in *Ascaphus*, *Barbourula busuangensis*, *Bombina* and *Leiopelma*; state 1 in *Alytes* and *Discoglossus*.

In urodeles the ilia are small and relatively less differentiated than in the Anura. In addition, the configuration of the ischia in urodeles is different (for a description see under Character 73). The differences between the urodele and anura ilia are such that they do not permit outgroup comparison - the morphology of the ilium and the relationship between the ilium and ischium are too dissimilar. Thus no polarity is postulated for this character.

Character 72. Ilium - iliac synchondrosis.

In all discoglossoids examined there is no anterior expansion of the ventral preacetabular zone i.e. no distinct ventral acebular zone (terminology of Lynch 1971) but there may be a ventral acetabular expansion (ibid.: Fig.36). Trueb (1973: 108) commented "it seems that an expanded preacetubular zone is advanced" meaning that this condition is found in groups which have on other grounds been considered to be advanced (have large numbers of apparently derived characters) - which is not the same as having independent, i.e. outgroup, information indicating that the expanded condition is derived.

The only apparent difference in the ventral pre-actular zones of the taxa in the study group is in the junction of the ilia in this region i.e. the presence of an iliac synchondrosis seen in Barbourula. Estes (1964: 57) compared a right ilium (UC 55705) and a left ilium (UC 55704) taken from the late Cretaceous Lance Formation, Eastern Wyoming, U.S.A. with a Barbourula busuangensis ilium and labelled the Wyoming fossil material "cf. Barbourula". Estes commented: "Identification with this recent genus of such fragmentary material as is discussed here would certainly be suspect were it not for the unique structure of the ilium in the Recent form, in which the two ilia meet in a prominent medially directed midline synchondrosis, as in the fossil". Estes went on to note that examination of members of "all groups of frogs" provided no parallel with this condition and considered with the close morphological similarity with other preserved (fossil) ilia "suggests reference to this genus or one closely related". Estes and Reig (1973: 35 - 36) noted that "cf. Barbourula from the late Cretaceous Lance Formation of Wyoming is with great probability referable to the Palaeobatrachidae", and also that pipids "also have the unusual iliac synchondrosis".

Two states of this character are recognized:

State 0. Ilium - medial synchondrosis absent.

State 1. Ilium - medial synchondrosis present.

The medial synchondrosis is also present in the second *Barbourula* species, *B. kalimantanensis* - evident from radiographs prepared by Dr. D.T. Iskandar - and is therefore confined within the discoglossoids to *Barbourula*.

The synchondrosis is not seen in hynobiid and ambystomatid salamanders. The direction of change is therefore suggested to be:-

0 ⟶ 1

Character 73. Ischium - development and orientation. (Fig. 94, also 92a).

The ischia are paired endochondral bones comprising the posteriormost part of the pelvic girdle. They may be elliptical or semicircular and serve two main functions: (i) to maintain the integrity of the pelvic girdle by providing the major area of articulation between the two halves of the girdle - the two ischia are in medial articulation, each ischium also articulates with its own ilium (anterodorsally) and pubis (antero-ventrally) (ii) to provide an important surface for the insertion of many of the thigh muscles. The ischium is therefore of great significance, serving many aspects of the locomotory function.

Two discrete forms of ischium are seen in discoglossoid frogs:-

State 0. Ischium - relatively small, elliptical approaching semicircular in shape, major axis perpendicularly or slightly anteriorly inclined; no posterior-dorsal expansion.

State 1. Ischium - relatively large, more or less elliptical in shape, major axis inclined posteriorly; with postero-dorsal expansion.

State 0 is found in Alytes, Ascaphus, Discoglossus and Leiopelma; state 1 in Barbourula busuangensis and Bombina. This character does not admit detailed comparison with the urodele condition since the urodele ischium is a ventrally positioned plate-like structure. Consequently, a direction of change is not postulated for this character.

Character 74. Epipubis (Fig. 95).

The presence of an epipubis in anurans has been reported for *Ascaphus*, *Leiopelma*, *Xenopus* and *Pseudhymenochirus* (de Villiers 1934; Ritland 1955; Trueb 1973; Duellman/Trueb 1986). Ritland (ibid.: 154) aptly describes the epipubis in *Ascaphus* as 'shield-shaped' and quotes Stephenson (1952) saying that in *Leiopelma* the structure generally ossifies, but notes that in *Ascaphus* only calcification has been observed. The ontogenetic change, from cartilaginous epipubis in a juvenile *L. hochstetteri* to an ossified epipubis in an adult of the same species, is particularly striking in two specimens examined - CAS 156253 (juvenile); CAS 156252 (adult) - which had been cleared and differentially (double) stained to show cartilage and bone. The presence of a small, narrow epipubis - an elongate, inverted heart - to inverted Y-shaped cartilaginous or weakly calcified structure - in *Alytes* and *Discoglossus* is, apparently previously unreported; *Bombina* and *Barbourula* lack any sign of an epipubis (pers.obs: condition in *Barbourula kalimantanensis* not known). In *Alytes* the epipubis may be perforated by a small, round foramen).

Thus three states are recognized:

State 0. Epipubis a small, inverted 'Y' - or heart-shaped, elongate cartilage or calcified cartilage. (Fig.95a).

State 1. Epipubis a broad, shield-shape cartilage, usually calcified or ossified in adults. (Figs. 95b and c).

State 2 Epipubis absent.

Ritland (1955: 154) noted that it is generally accepted that the ypsiloid cartilage of urodeles is homologous with the epipubis of the Anura (Hoffman 1930) although this had been questioned by Green (1931) on embrological grounds (see also van Dijk 1955 for comment). The suggestion that the ypsiloid cartilage is derived from the linea alba of the ventral musculature in urodeles, was made by Whipple (1906), and has also been suggested as the origin for the epipubis in *Ascaphus*, *Leiopelma* and *Xenopus* by de Villiers (1934). While the ypsiloid cartilage is Y-shaped and the epipubis is an *inverted* Y-shape in state 0 above, the state 0 condition bears closest resemblance to the urodele structure. (The medial margin between the arms of the Y of the ypsiloid cartilage is very well defined, almost semicircular in specimens of *Hynobius tsuensis* and *Salamandra salamandra* examined in the BM collection. It may be that the arms of the Y might have been united in some ancestral form between urodeles and anurans and that the circular foramen seen in some *Alytes* is a product of this unification. The ypsiloid cartilage has been implicated in the hydrostatic function on the lungs, and in defaecation and parturition in urodeles because of its ability to compress the posterior abdomen. The ypsiloid cartilage of urodeles and epipubis of anurans are here considered to be provisionally homologous (close correspondence of muscle attachment to cartilage fide Ritland 1955: 154; is merely site of attachment for *rectus abdominis* muscles in both cases Ritland 1955b and pers. obs.).

Therefore, state 0 is considered to be the primitive condition and the direction of change is:-

$$2 \longleftarrow 0 \longrightarrow 1$$

Character 75. Postpubic or Nobelian bones.

Ascaphus (A. truei) is unique amongst the Anura in that the male possesses a copulatory organ - the so-called "tail" - giving A. truei its popular name of 'Tailed Frog', for details of the breeding behaviour see Noble & Putnam (1931). Within this organ are paired rod-like structures which are proximally united, but separate distally (de Villiers 1934. Figs. 6-8). De Villiers (ibid) noted that the postpubic or Nobelian bones are "almost certainly capable of considerable motion" and that the histology and staining properties of these bones are "very peculiar". De Villiers used a haemalum - Bismark brown stain; where bone normally takes up haemalum and appears a blue-purple colour, the Nobelian bones do not take up haemalum at all. He therefore concluded that the Nobelian bones may be sesamoids. Van Dijk (1955) provided an even more detailed analysis of the "tail" of Ascaphus, including a graphical reconstruction of the organ based on serial sections.

Two states of this character are recognized:-

State 0. Nobelian/postpubic bones absent.

State 1. Nobelian/postpubic bones present.

Urodeles do not possess a copulatory organ (the phallodaeum of caecilians is quite a different structure to the tail of Ascaphus). I therefore regard the tail and, more specifically, the Nobelian bones as neomorphic structures, which are therefore derived. The direction of change is therefore:-

$$0 \longrightarrow 1$$

Pectoral girdle. (Characters 76 - 89). (Figs. 96 - 109).

The pectoral girdle may be divided into two areas: the ventral and the lateral elements. Ventrally, the girdle may include (anteriorly to posteriorly): an omosternum - absent in most discoglossoid species; paired clavicles which invest the procoracoid cartilages; paired, overlapping epicoracoid cartilages which link the clavicles/procoracoid cartilages with paired coracoids laterally and a sternum (xiphisternum) posteriorly. The sternum may bear a pair of presternal pieces, or 'Sternalblattchen' of de Villiers (1922), between the coracoids on the ventral side of the sternum (see character 88 for discussion). Laterally there are, proximally to distally, paired scapulae, and paired suprascapulae; each suprascapula bears a dermal bone, the cleithrum, which invests the anterior margin and the dorsal and/or ventral margin of the suprascapula to a variable extent. Inscriptional ribs (see Character 89) are present only in Leiopelma and may be associated with the sternum.

The pectoral girdle has always been regarded as a source of significant characters in anuran systematics. Cope (1864, 1865) distinguished between arciferal and firmisternal anurans: the former having free overlapping epicoracoid cartilages; the latter having fused epicoracoids, for the higher-level classification of the Anura - a division utilized by Boulenger (1882) and which remained unchallenged until Noble (1922, 1926) drew attention to the existence of an intermediate, arcifero-firmisternal condition. All discoglossoid frogs have arciferal pectoral girdles. Other authors have drawn attention to other attributes of the pectoral girdle; some, e.g. Kluge and Farris's (1969) and Trueb (1973), have been particularly concerned with the clavicle-scapula ratio, in the belief that the scapula is small relative to the clavicle in primitive anurans. This belief is mistaken - Leiopelma have relatively long scapulae - and poorly based because of the practical difficulties involved in measuring lengths of strongly curved clavicles (see Section C on Excluded characters).

The pectoral girdle characters, like other characters used in the present study, are concerned with the attributes of individual bones and/or their relationships with one another, and with surrounding or adjacent bones (particularly if such relationships are likely to be of some clear, functional significance). A large number of differences are evident in the pectoral girdles of discoglossoid species - this study consequently includes quite a high number of pectoral girdle characters (14).

Character 76. Omosternum. (Fig. 96).

The omosternum is one of the ventral components of the pectoral girdle. It lies anterior to, and posteriorly articulates with the epicoracoids/medial ends of the clavicles. In discoglossoid frogs the omosternum, if present, remains cartilaginous throughout life, although exceptionally it may become calcified. An omosternum was recorded in Bombina orientalis and in Discoglossus but not in any other discoglossoids. Thus two states are recognized:-

State 0. Omosternum absent/? very poorly developed. *

State 1. Omosternum present, cartilaginous.

*In some cases, it may be very difficult to be certain that there is no omosternum present since the epicoracoid cartilages may extend antermedially in this region. Any fragmentation of the epicoracoids occurring during dissection or alizarin preparation or appearing as a staining artefact on the anteromedial margin of the epicoracoids, might give rise to doubts on the presence/absence of a very small omosternum. In taxa exhibiting state 1 the omosternum is unquestionably present and well developed.

Lynch (1973: 146), without discussion or justification, codes presence of 'prezonal elements' (= omosterna) as primitive. Trueb (1973: 95) provides a more detailed consideration of the distribution of omosterna amongst anurans in general and discoglossoids in particular. Trueb (loc. cit.) comments " The status of the omosternum in terms of its primitive or derived nature is a moot question" and notes its absence in three primitive families - ascaphids, pipids and rhinophrynids and that an omosternum is present in two of the four discoglossoid genera - Bombina and Discoglossus. Unless there is intraspecific variation in Bombina, Trueb's statement that an omosternum is present in Bombina would suggest that she had only B. orientalis available for study, for as mentioned above, this is the only species of Bombina found to have an omosternum. I agree with Trueb's suggestion/implication that absence is primitive; presence derived -

"The distribution of omosterna among modern anurans seems to suggest that the element was absent among primitive arciferous groups...", and also her suggestion that presence/absence is likely to be an extremely labile character. More important to the present study urodeles lack an omosternum which I therefore regard as a neomorph in the Anura. The direction of change is therefore considered to be:-

0 → 1

Character 77. Clavicles - straight or curved. (Fig. 97).

In discoglossoid frogs the clavicles are always present and are either straight and perpendicular to the midline of the body, slightly anteromedially curved, strongly arched or curved and anteromedially directed. In the 'straight' condition there may be a slight 'bump' or inflexion approximately halfway along the clavicle. This bump is usually more evident along the anterior margin, although it may signal a slightly bent clavicle. This 'straight-type' clavicle is very clearly figured in Ritland (1955: 146, Fig. 6A; Ascaphus) and in Estes and Reig (1973: 1-7; showing the condition in Leiopelma hamiltoni and in the late Jurassic ribbed frog Notobatrachus degiustoi). These three species may be arranged in a sequence: L. hamiltoni - Ascaphus - N. degiustoi, in which L. hamiltoni has the straightest anterior margin; N. degiustoi has the greatest inflexion in the anterior margin. It is interesting to note that in the Estes and Reig (ibid.: 16, Fig. 1-3) restoration of the skeleton of the early Jurassic ribbed frog Vieraella herbstii, the clavicle, originally broken and present as two fragments, was interpretated as "Clavicles apparently curved" (p. 13). Yet the lateral margin is not reconstructed as bifid as in Notobatrachus and Leiopelma. I therefore regard the Estes-Reig interpretation of the Vieraella clavicle as open to question, as they themselves recognized (p. 17), "Even if we are in error about the curvature of the clavicles....". I tentatively suggest that the Vieraella condition may be seen as straight-with-an-inflexion if the lower fragment is considered to be worn and is inverted or turned medially to laterally in the Fig. 1-3 (p.16) restoration. This would result in a Leipelma - Notobatrachus i.e. straight-type clavicle, and would indicate, albeit weakly, that early frogs may have had straight clavicles. Clearly, however, the suggestion is weakly based.

The strongly arched condition is more common than the straight, inflected condition described above - Trueb (1973: 97) remarked "In the majority of arciferal frogs, the clavicles tend to be gently to strongly arched and separated medially...."

Thus, two clavicle states are recognized:-

State 0. Clavicles - straight, nearly perpendicular to the midline or slightly anteromedially directed.

State 1. Clavicles - strongly curved (arched) and anteromedially directed.

In the context of the study group, (i.e. leaving aside interpretation of fossil *Vieraella* and *Notobatrachus*), state 0 is confined to *Ascaphus* and *Leiopelma*; all other discoglossoids examined exhibit state 1.

Urodeles lack clavicles (Francis 1934); the anuran clavicle is therefore considered a neomorph and consequently no polarity is inferred for this character.

Character 78. Scapula - uncleft or bicapitate. (Fig. 98).

The scapula is an endochondral bone which occupies a central and important position in the anuran pectoral girdle. It articulates, not only with the clavicle, coracoid and suprascapula but also with the humerus, via the glenoid fossa. The scapula and the coracoid probably receive and absorb most of the impact forces directed through the forelimbs during the landing and walking phases of locomotion. The scapula therefore deserves more attention than it has received to date - Trueb (1973: 91) noted that Proctor's (1921) paper on their taxonomic significance has been "largely overlooked". Trueb (ibid.: 98) and Estes and Reig (1973: 21, 54) noted that the scapula bears two proximal heads - the pars acromialis (anteriorly) and the pars glenoidalis (posteriorly) - and distinguished between scapula which are proximally uncleft and those which are proximally cleft or bicapitate. Estes and Reig (1973: 17) noted that Vieraella had a "probable Leiopelma-like scapula" and showed it - as bicapitate in their restoration Figure 1-3, even though the proximal end was not discernible/present in their material; i.e. in the absence of any evidence. Notobatrachus, originally believed to be uncleft by Reig (1957) was found, on the basis of better preserved specimens, to be "clearly separated by a deep cleft" i.e. bicapitate (Estes and Reig ibid: 54).

Within the discoglossoid study group only Ascaphus shows the uncleft condition, all other discoglossoid taxa have proximally bicapitate scapulae. Thus Trueb's comment that "The scapulae of primitive anurans (e.g. leiopelmatids, discoglossids, and pipids)....tend to be....proximally uncleft or unicapitate" (Trueb in Duellman/Trueb 1986) is misleading. Alytes cisternasii has a closed cleft or foramen in place of the open cleft, the bony partes acromialis and glenoidalis are in contact but are still distinct proximal heads to the scapula - their boundaries evidenced by a groove. In Bombina maxima the bicapitate scapula may be closed to a foramen *by cartilage*, but the bony heads of the pars acromialis and pars glenoidalis *are separate*. This latter state is not the same as that in *A. cisternasii*, since this character is based on the separation of the bony portions of the proximal heads of the scapulae.

Three states are recognized:-

State 0. Scapula - uncleft. (Fig. 98a).

State 1. Scapula - bicapitate. (Figs. 98b and c).

State 2. Scapula - bicapitate but with evidence of a closed bony groove or terminal foramen. (Fig. 98d).

The urodeles (except the sirenids) have a combined scapulocoracoid in sirenids the coracoid persists (Goin and Goin 1971). The urodele conditions do not admit detailed comparison so no polarity is assigned to this character. The states ordered in respect of their morphological similarity are:

0 ——— 1 ——— 2

Remarks:

This could be an important character within the Anura since pipids also have the uncleft condition.

(i) If uncleft is derived - the character would provide a possible synapomorphy for *Ascaphus* + Pipidae.

(ii) If bicapitate is derived - the character would provide a possible synapomorphy for discoglossoids + all other Anura except *Ascaphus* and Pipidae.

Character 79. Scapula - relative development and position of proximal heads. (Fig. 99).

In character 78, it was noted that there are two proximal heads to the scapula - the anterior pars acromialis (pa) and the posterior pars glenoidalis (pg), and that these may be separated by a deep cleft in some species. The present character concerns the relative development of the two heads. In most discoglossoids the pa and pg are approximately equally developed. There are however two minority conditions. In *Bombina*, the pg is relatively much reduced, almost vestigial and the pa is small in comparison with most other species. In *Leiopelma*, the pg is not only smaller than the pa, it is a short process because it arises from approximately half way along the posterior margin of the scapula. This latter condition is not coded as a separate state because it is evident that the position of the pa on the scapula and its proximity to the glenoid fossa are necessarily correlated with a short pg - i.e. these two features are logical consequences of one another.

Three states are recognized:-

State 0. Scapula - pars acromialis and pars glenoidalis equally well developed; proximal. (Figs. 99a and b).

State 1. Scapula - pars glenoidalis much smaller than pars acromialis; proximal. (Fig. 99c).

State 2. Scapula - pars gelnoidalis shorter than pars acromialis; pars acromialis proximal - pars glenoidalis on posterior margin of scapula. (Fig. 99d).

While, for the reasons cited under character 78, a polarity cannot be assigned to this character, it seems reasonable to suggest on the basis of the morphology of the character states:-

(a) that states 1 and 2 be regarded as equidistant from state 0 but in opposite directions.

(b) that states 1 and 2 are clearly special, derived states - this only leaves state 0. Since states 1 and 2 may be derived from a state 0 condition it does not seem unreasonable to infer, that in view of its morphological simplicity of state 0 represent the median condition between states 1 and 2 :

2 ——— 0 ——— 1

Character 80. Scapula - overall shape (ventral view). (Fig. 100).

In most anurans the overall shape of the scapula (in ventral view) is roughly rectangular. This is an over-simplification but is useful for the purpose of making character comparisons and possibly also for considering the scapula from a functional/mechanical point of view. In fact, the outline shape of the scapula is quite complex. In most discoglossoid frogs, the proximal margin may be uncleft or bicapitate (as described in character 78, above); the partes acromialis and glenoidalis may both be situated on the proximal margin or the pars glenoidalis may be more on the posterior margin (character 79); the anterior margin is weakly concave while the posterior margin is more markedly concave, the distal margin is straight. In Bombina, however, the scapula assumes a more overall triradiate shape - this is because the posterior margin is very narrow, proximally to distally, and is only shallowly or moderately concave. In Bombina bombina and B. variegata the anterior margin is deeply cleft; in other discoglossoid species the anterior margin is shallowly concave appearing 'filled in' (thinner bone) across the anterior concavity.

Three states are therefore recognized:-

State 0. Scapula approximately rectangular; no cleft on anterior margin. (Fig. 100a).

State 1 Scapula approximately triradiate; no cleft on anterior margin. (Figs. 100b and c).

State 2. Scapula approximately triradiate; with a distinctly cleft anterior margin. (Fig. 100d).

State 1 is found in Bombina maxima, B. microdeladigitora and B. orientalis; state 2 is confined to Bombina bombina and B. variegata while all other discoglossids examined show state 0.

As mentioned previously, under character 78, the urodele scapula/scapulocoracoid is too dissimilar to allow detailed comparison, and therefore no polarity is inferred for this character. Morphological similarity of discoglossoid states suggests the following non-polar, transformation series:

0 ——— 1 ——— 2

Character 81. Scapula - posterior margin. (Fig. 101).

In urodeles (see Francis 1934: 37 and pl. IV, Figs. 20, 21) and in the majority of the study group the deepest point of the concavity on the posterior margin of the scapula (as scapula or scapulocoracoid in most urodeles) is closer to the proximal than to the distal margin - concavity biased toward the glenoid fossa. In Bombina the deepest point of the concavity is situated at the midpoint along the posterior margin.

Thus two states are recognized:-

State 0. Scapula - concavity on the posterior margin biased toward the glenoid fossa (Type gf.)

State 1. Scapula - concavity on the posterior margin central - symmetrical about the midpoint along the posterior margin. (Type c.)

State 1 is confined to Bombina; all other discoglossoid species show state 0. Outgroup comparison with urodeles suggests state 0 is primitive.

The direction of change is therefore:-

$$0 \longrightarrow 1$$

The functional implications of possession of a narrow scapula with a Type c posterior margin are not known.

Character 82. Contributions to the glenoid fossa - pars acromialis of scapula. (Fig. 102).

In Alytes cisternasii both proximal heads on the scapula - the pars acromialis and pars glenoidalis - contribute articular surfaces to the glenoid fossa. In all other members of the study group examined only the pars glenoidalis contributes to the fossa. Thus in A. cisternasii the pectoral girdle contributes (up to) four articular surfaces to the glenoid fossa - the distal end of the coracoid, clavicle (?), pars acromialis and pars glenoidalis of the scapula. In other discoglossoids the pectoral girdle contributes only two or three articular surfaces - the distal end of the coracoid, clavicle (?) and pars glenoidalis of the scapula. In all cases it is difficult, in practice, to discern the relationship between the distal end of the clavicle and the glenoid fossa, because the procoracoid cartilage is quite thick in this region. In Leiopelma at least, the clavicle does not make any contribution to the fossa.

This feature of A. cisternasii is almost certainly an adaptation to burrowing (see also character 86, Coracoids - orientation). In A. cisternasii the glenoid fossa is deeper than in other discoglossoid species, accommodating far more of the proximal head of the humerus.

Thus two states are recognized:-

State 0. Pars acromialis of scapula does not contribute an articular surface to the glenoid fossa. (Fig. 102a).

State 1. Pars acromialis of scapula contributes an articular surface to the glenoid fossa. (Figs. 102b,b').

As previously stated, the urodele condition does not admit detailed comparison, and therefore, unless one regards the functional correlation of burrowing with state 1, (morphological specialization signifying a derived state)then, a polarity may not be hypothesized for this character. Underwood (1982: 253) regards morphological specialization as inadmissible for the purpose of polarity inference (see Character polarity).

Character 83: Cleithrum - uncleft or bifurcate. (Fig. 103).

The cleithrum is a dermal bone investing the anterior margin of the suprascapula. Trueb (1973: 99) considers that it is principally found on the ventral surface of the suprascapula but may also extend around the anterior margin of the suprascapula to invest a small anterior portion of the dorsal surface (but this is incorrect: see character 84). Trueb (loc. cit.) also mentions that in most anurans, though not the ascaphids, the cleithrum is distally bifurcate into anterior and posterior rami (see Fig. 103c). In ascaphids the cleithrum is poorly developed and lacks a posterior ramus (uncleft). In Ascaphus the cleithrum shows a greater level of development than in Leiopelma, but both clearly show the uncleft condition.

Three states are recognized:-

State 0. Cleithrum uncleft, a thin rib of bone along the anterior margin (leading edge) of the suprascapula.

State 1. Cleithrum uncleft, moderately deep anteriorly - posteriorly.

State 2. Cleithrum bifurcate.

State 0 is found in Leiopelma; state 1 in Ascaphus - all other discoglossoid species show the state 2 condition. It is interesting to note that Estes and Reig (1973) record the uncleft condition in Vieraella and Notobatrachus and that both are state 1, as here defined; although of the two, Vieraella more closely approaches state 0.

Urodeles have a cartilaginous suprascapula but lack a cleithrum and therefore the anuran cleithrum is a neomorph. It seems more plausible to suggest that the development of the cleithrum starts as an ossification along the leading edge (only) of the suprascapula, and that the ossification increases posteriorly ultimately giving rise to the state 2 condition. (This evolutionary/morphological trend reaches a state of maximal development in the heavily ossified, but dwarf, *Brachycephalus ephippuim* (Brachycephalidae) - where the ossification of the suprascapula invades the entire suprascapula; the cleithrum = the ossified suprascapula see Duellman/Trueb 1986: 347, Fig. 13-36 A).

The direction of change is therefore postulated to be:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 84. Cleithrum: presence/absence on ventral surface of suprascapula. (Fig. 104).

Trueb's (1973: 99) description of the cleithrum is in error (a mistake perpetuated in Duellman/Trueb 1986: 346) - the cleithrum principally invests the dorsal not the ventral surface of the suprascapula and may also extend around the anterior margin onto the anterior part of the ventral, not the dorsal surface. However, Trueb is correct with her descriptions in parentheses; the principal surface is the lateral surface and the lesser surface is the medial surface. It seems likely that the transposition in terminology may have arisen as a result of 'flattening out' the pectoral girdle for diagrammatic purposes, when the cleithrum and suprascapula are 'flipped over'. It is interesting to note that a confusion of dorsal and ventral surfaces also occurs in Estes and Reig, (1973: 22 Fig. 1-7).

Two states of this character are recognized:-

State 0. Cleithrum absent or present as only a slight 'lip' on ventral surface of suprascapula.

State 1. Cleithrum clearly investing ventral surface of suprascapula.

State 0 is confined to *Leiopelma*.

Using the same reasoning as for character 83, I suggest state 0 is primitive - because the cleithrum is a neomorphic structure and it is simpler and more plausible to consider the less elaborated condition as primitive (closer to absent condition) and the more elaborated condition derived.

The direction of change is therefore:

$$0 \longrightarrow 1$$

Character 85. Coracoids - medial expansion. (Fig. 105).

There are three distinct levels of medial expansion of the coracoid in discoglossoid frogs:-

State 0. Coracoid with a very broadly expanded medial end.

State 1. Coracoid with a moderately expanded medial end.

State 2. Coracoid with a slightly/barely expanded medial end.

State 0 is confined (within the study group) to Leiopelma; the medial expansion is broadest in L. hamiltoni and L. archeyi, slightly less developed in L. hochstetteri. The medial dilation is so broad in Leiopelma that the anterior margin of the coracoid appears deep and notch-like. State 2 is found in Alytes muletensis, Bombina bombina and B. variegata. All the remaining discoglossoid species examined show the state 1 condition (which is also the most widespread condition in the Anura).

This character is of particular interest because comparison may be made with the condition in urodeles and Notobatrachus. The medial margin of the scapulocoracoid (the coracoid portion) is broadly dilated. However, it is difficult to be confident about homologies when dealing with a compound bone like the scapulocoracoid. However, taken in conjunction with the condition depicted in the Estes and Reig (1973: 22, Fig. 1-7, lower) reconstruction of the shoulder girdle of Notobatrachus, in which the medial expansion of the coracoid far exceeds even that seen in Leiopelma, it seems reasonable to suggest that the dilated condition may be primitive. I consider the interpretation of the condition of the coracoid of Vieraella, made by Estes and Reig (ibid.: 13-17, Figs. 1-1 to 1-3) may be in error. Vieraella is only known from the type specimen (part) and its counterpart. From Estes and Reig's Figs. 1-1 and 1-2 it appears that only part of one coracoid is present, and this appears to be angled into the matrix. Nonetheless, the medial portion of the coracoid, as seen in their Figure 1-2 of the counterpart, should also, I suggest, be interpreted as very broadly dilated and referable to state 0.

I therefore tentatively suggest that state 0 is the primitive condition and the direction of change is:-

$$0 \longrightarrow 1 \longrightarrow 2$$

Character 86. Coracoids - orientation. (Fig. 106).

In most discoglossoid species (and in most anurans) the long axis of the coracoid is straight and the coracoid is either perpendicular to the midline or slightly-moderately posteromedially directed. In *Alytes cisternasii* however, the long axis is bent into a sigmoid curve or 'step-down' (‾_) profile. It is particularly noticeable that the medial ends of the clavicle and coracoids are, as a result of this curvature and of the forwardly directed clavicles, highly divergent. It is likely that the form of the coracoids in *A. cisternasii* may be attributed to the highly developed fossorial habit in this species and may be part of a functional complex of burrowing-related features.

Two states are recognized:-

State 0. Coracoids - long axes straight; perpendicular to midline of body, or slightly to moderately posteromedially directed.

State 1. Coracoids - long axes in a sigmoid ('step-down') curve; strongly posteromedially directed.

Urodele scapulocoracoids do not admit detailed comparison and may not therefore be used for the purpose of outgroup comparison. While it may be tempting to suggest that the functional correlation with burrowing suggests state 1 is the derived condition, I must agree in principle with Underwood (1982: 253), that morphological specialization is not admissible as a criterion for determining derived states. In this case it may be, as Hillenius (1976) postulated, that burrowing is primitive for the Anura; in which case the *A. cisternasii* condition would be interpreted as primitive. I suspect, however, that it is more likely that the 'head-forwards' type of burrowing seen in *A. cisternasii* is a specialization and is therefore derived.

In the absence of convincing (pre-analysis) evidence, no polarity is given.

Character 87. Sternum. (Fig. 107).

Trueb (1973: 97) stated that "The discoglossid sternum is unique; it is produced into posterolaterally divergent horns....", but was apparently unaware that this condition is also found in Leiopelma (reported in de Vos 1938, Stephenson, E.M. 1952 and Ritland 1955; the last-named was actually cited in Trueb's 1973 references). Trueb, in Duellman/Trueb 1986, noted the presence of the discoglossid-type sternum in Leiopelma when she commented that, according to de Vos 1938, the inscriptional ribs found in Leiopelma (see Character 89), "may be serially homologous with the posterior horns of the sternum....".

Of the discoglossoid species examined all, except Ascaphus, have a sternum with posterolaterally divergent horns which are usually cartilaginous but may become ossified or calcified in part at least.
Stephenson (1952: 608) noted that in L. hochstetteri the horns, which she referred to as styles, "may become fairly heavily calcified....but always retain an uncalcified medial connection between each other". Stephenson also drew attention to de Vos' (1938) paper which had shown that the cartilage of the medial, anteriorly projecting portion of the sternum comprises both dorsal and ventral elements, the former embedded in the sternohyoideus muscle, the latter lying "below" (i.e. dorsal to) "the epicoracoids at their posterior border". I can confirm, on the basis of the material I have examined, Stephenson's 1952 and 1960 comments on the nature, and extent of calcification, of the sternum in Leiopelma species, also de Vos' (1938) remarks on the detailed anatomy of the anterior, central, cartilaginous portion of the sternum. In fact, the detailed description of this part of the sternum made by de Vos, may also be applied to the sternum in all the discoglossoid taxa examined and to the sternum in urodeles (see Francis 1934, Pl.IV, Fig. 22). This means that the sternum in all these groups may be considered homologous, and that the urodeles may be referred to, for the purpose of outgroup comparison.

In *Ascaphus* the sternum is rather variable in shape. It may be rather globular in outline, with pointed anterior and posterior ends, producing a shape like a child's toy top or it may approach the 'discoglossid-type' sternum in having extended or produced lateral margins (see Fig. 107a). Ritland (1955) provides a very good semidiagrammatic representation of the sternum in *Ascaphus* in his Fig. 6 A and C, p. 146.

Thus, two states are recognized:-

State 0. Sternum 'top-shaped' or flattened 'top-shape' with weak to moderate lateral processes (Fig. 107a).

State 1. Sternum with long posterolaterally divergent horns. (Fig. 107b).

Urodeles e.g. *Salamandra* (Francis loc. cit., above) have an 'arrow-head' shaped sternum, which is closer to the *Ascaphus* than to the 'discoglossid-type' condition. The *Salamandra* condition was also noted in dissections of the following hynobiid species: *H. kimurae* (one from BM series 1916.2.3. 11-13), *H. nebulosus* (1907. 12. 10. 43), *H. tsuensis* (two from 1911. 2. 24. 6-8) and *Onychodactylus japonicus* (86. 6. 30. 46).

The direction of change is therefore considered to be:-

0 → 1

Character 88. Presternal pieces or 'Sternalblattchen/epicoracoid processes. (Fig. 108).

De Villiers (1922) reported the presence of 'Sternalblattchen' or presternal pieces in Bombina which are found between the coracoids on the ventral surface on the sternum. These structures are very difficult to observe even in single and double stained and cleared (alizarin/alizarin and alcian blue) preparations. The presternal pieces are very thin pieces of cartilage and their position and relationships are mentioned in this account with some reservations, simply because they are so difficult to see. Probably the only way to be sure of their position, form and relationships is by graphical reconstruction of serial sections of this region. Bombina undoubtedly have sternalblattchen - in Alytes, Barbourula and Discoglossus it is difficult to tell, in dissections and cleared and stained preparations, if they are absent or fused into one broader anterior section of the sternum, and it is a matter of interpretation whether or not this area is regarded as Sternalblattchen. Ascaphus and Leiopelma appear to lack Sternalblattchen. However, there does seem to be a related character which is apparently correlated with the presence and development of Sternalblattchen; again, only graphical reconstruction of this region of the pectoral girdle, using serial sections, would be needed before it is possible to be sure if any such correlation exists. This character is therefore concerned with the development of the medial margins of the epicoracoid cartilages adjacent, and posterior to the medial ends of the coracoids. In the discoglossoids, three conditions are found:-

State 0. Epicoracoid cartilage not extending posteriorly beyond coracoid (Fig. 108a).

State 1. Epicoracoid cartilage extending posteriorly beyond coracoid but not produced into an elongate process. (Fig. 108b).

State 2. Epicoracoid cartilage extending posteriorly beyond coracoid and produced into a laterally directed, elongate process (Fig. 108c).

State 0 is found in *Ascaphus* and *Leiopelma* which lack Sternalblattchen; state 1 is found in *Alytes*, *Barbourula* and *Discoglossus montalentii* which show the absent/?fused Sternalblattchen condition described above; and state 2 is found in *Bombina* (Sternalblattchen clearly present) and the remaining *Discoglossus* species (Sternalblattchen absent/? fused).

Urodeles do not admit comparison in this character and therefore no direction of change is hypothesized. Morphological similarity of states suggests the following non-polar transformation series:-

0 ——— 1 ——— 2

Character 89. Inscriptional ribs. (Fig. 109).

Stephenson, E.M., (1952: 608-609) provided a concise account of the literature on the inscriptional ribs of Leiopelma. Leiopelma are the only anurans known to possess inscriptional ribs, originally described as "abdominal ribs" by Noble (1931). Noble described them as "large cartilages of much the same form as the abdominal ribs of the lizards, appearing in the myosepta of the M. rectus abdominis of Leiopelma". He considered them to be dermal in origin, and that they have neither an ontogenetic nor a phylogenetic relationship with true ribs. In a study based on serial sections de Vos (1938) reconstructed the inscriptional ribs of an adult Leiopelma. De Vos concluded that these ribs were not dermal elements but cartilage bones similar to the ventral parts of true ribs in lizards, and therefore different from abdominal ribs found in Sphenodon, crocodiles, Archaeopteryx and fossil reptiles, which "do not pass through a cartilaginous stage but ossify directly....". Inscriptional ribs form a continuous series with the cartilaginous horns of the sternum, with which they may be serially homologous, and may become calcified or ossified in older specimens. Stephenson, E.M., (loc. cit.) noted that Noble had realized that the inscriptional ribs "are better developed in Leiopelma than in any urodele in which they occur".

Thus two states are recorded in discoglossoid frogs:-

State 0. Inscriptional ribs absent.

State 1. Inscriptional ribs present.

From the above it seems equally plausible that inscriptional ribs arose independently in Leiopelma as much as they are likely to have been inherited from an inscriptional rib-bearing urodele-like condition. Consequently no polarity is inferred for this character.

Character 90. Humerus - development of the humeral condyle.

In the Anura the humerus articulates with the compound radioulna collection; pers. obs.) the humeral condyle (capitata eminentia of some authors) is large, well developed and fits into a deep socket at the proximal head of the radioulna. In *Ascaphus* and *Leiopelma* the humeral condyle is small and in *Leiopelma* remains cartilaginous; in *Alytes*, *Barbourula*., *Bombina* and *Discoglossus* the condyle is large. Size is judged with respect to the maximum width of the distal end of the humerus - i.e. width of condyle width of distal humerus x 100%.

Two discrete states are recognized:-

State 0 Humeral condyle small, < 60% distal width of humerus.

State 1 Humeral condyle large, > 66% distal width of humerus.

In urodeles, the humerus bears two, separate humeral condyles - the radial and ulnar condyles (Francis 1934: 41); the former is also known as the *capitata eminentia* and, of the two, is clearly homologous in relative size, shape and position with the anuran humeral condyle or capitata eminentia. In hynobiid and ambystomatid urodeles this condyle is small - usually 55% or less of the distal width of the humerus.

Therefore, by outgroup comparison the direction of change is considered to be:

$$0 \longrightarrow 1$$

Character 91. Radioulna. (Fig. 110).

The distal end of the radioulna is fused in all anurans, but in most shows clear indications of separate radial and ulnar portions - the line of fusion is marked by a deep groove on the dorsal and ventral surfaces. The radial and ulnar portions diverge distally and articulate, respectively, with the radiale and ulnare + intermedium of the wrist. This character distinguishes two groups (i) in which the radial head is terminally distinctly separated from, and usually longer than, the ulnar head (ii) where the radial and ulnar head are terminally confluent. Thus two states are recognized:-

State 0. Radial and ulnar heads of radioulna
separate, not confluent terminally.

State 1. Radial and ulnar heads of radioulna not
separate; confluent terminally.

State 0 is found only in Ascaphus and Leiopelma, state 1 is found in all remaining discoglossoid taxa examined.

In urodeles (special reference to hynobiids) the radius and ulna are completely separate bones. Thus there is no matching ingroup state, but state 0 more closely resembles the outgroup state and is therefore considered relatively more primitive. The direction of change is therefore:

$$0 \longrightarrow 1$$

Note: The proximal end of the compound radioulna possesses a groove (state 0 type), indicating an affinity with the separated condition of the urodeles. Taxa having the state 1 condition also have a fused proximal end to the radioulna. I suggest these additional features provide corroboration for the polarity of character 91, given above (see Fig. 110).

Character 92. Wrist bones - radiale, ulnare + intermedium. (Fig. 111).

A great deal has been, and still remains to be written on mesopodial elements in amphibians (e.g. Howes and Ridewood 1888: Francis 1934; Trueb 1973; Andersen 1978 and Duellman/Trueb 1986). As far as the present study is concerned one mesopodial character is of particular interest. The radiale and ulnare + intermedium show a special condition which is unique in the context of the discoglossoid frogs: the radiale and the ulnare + intermedium are rather long bones - they are proximally to distally longer than they are wide. In other discoglossoids, these bones are usually wider than long (especially the radiale) or else as wide as they are long (sometimes; ulnare + intermedium, rarely the radiale).

Alytes species, except perhaps A. muletensis and A. (o.) maurus, are 'head-first' burrowers and make very efficient use of their hands in digging in soft-fairly firm earth and/or sand. The digging motion in A. cisternasii and A. o. obstetricans is a medial to lateral pushing motion, away from the head and body, with the wrist and especially the palm turning increasingly upward and outward on the power (out) stroke (pers obs.). At the end of the outstroke the wrist has changed from the horizontal almost to the vertical plane, at which point the concave outer margin of the radiale almost 'locks' with the concave inner margin of the ulnare + intermedium, thus producing a functionally single unit (seen by manipulating alizarin preparations). This is important, for it is at this time that the hand, and these bones in particular, are subjected to the greatest pressure - for at the end of the outstroke the hand is pushing the most substrate. In side view the hand has a 'step-down' profile and is capable of much flexion and rotation. Alytes are often found in burrows which they probably dig; these burrows are almost perfectly circular in cross-section and the earth/sand walls are packed down - a movement which would also exert much pressure on the hand (if, indeed, the hand is used by Alytes for this purpose). The condition seen in Alytes is considered to be correlated with a specialized, burrowing function (although its presence in *A. muletensis* and *A. (o.) maurus* requires further discussion) and is therefore tentatively considered derived.

Thus two states are recognized:-

State 0. Radiale (and ulnare + intermedium) wider than long or, at most, as wide as long.

State 1. Radiale (and ulnare + intermedium) longer than wide.

The direction of change of this character is considered to be:

$$0 \longrightarrow 1$$

Character 93. Hand: configuration of 1st and 4th fingers. (Fig. 112).

The phalangeal formula is normal, i.e. 2-2-3-3, in all discoglossoids, but the first finger is rather slender and rather short, and the elements of the fourth finger and the fourth metacarpal are relatively short and squat in *Alytes cisternasii*, *A. o. obstetricans* and *A. o. boscai*, *compared* with those of other discoglossoid species. There is a difference of degree in these three forms: *A. cisternasii* shows the most extreme condition (1st finger thin and spike-like); *A. o. boscai* the least extreme, most closely resembling other discoglossoid species. Again, the reduction in finger length *may* be correlated with the burrowing habit of these three species.

Two states are recognized:-

State 0. First and fourth fingers 'normal' (not slender, short and short, squat and compact, respectively). (Fig. 112a).

State 1. First and fourth fingers slender, short and short, squat and compact, respectively. (Fig. 112b; also 112c).

For the same reasons given in the previous character state 0 is considered primitive, the direction of change is:-

$$0 \longrightarrow 1$$

Character 94. Relative lengths of metatarsals. (Fig. 113).

In alizarin and x-radiographs as well as dry skeleton preparations, it was noticeable that some species have long phalanges and relatively short metatarsals, whilst other species have short phalanges and relatively long metatarsals.

Thus two states are recognized:-

State 0. Short metatarsals; relatively long phalanges.

State 1. Long metatarsals: relatively short phalanges.

State 1 is only found in *Alytes cisternasii*, *Bombina variegata* and *B. maxima*; all other discoglossoid species have the state 0 condition.

While *A. cisternasii* is a burrower, other burrowing species lack the same condition. *B. variegata* may dive to "conceal itself in holes or under stones or bury in the mud when disturbed" (Boulenger 1897: 148), but is not notably as much of a burrowing species as *A. o. obstetricans* - which shows state 0.

Urodele feet are not sufficiently similar to permit detailed comparison, so no polarity is assigned to this character.

Character 95. Terminal phalanges - fingers and toes. (Fig. 114).

Lynch (1971) said that the nature of the terminal phalanges had been one of the major character complexes in the classification of leptodactylid frogs. He considered the only acceptable technique for determining the state of terminal phalanges to be alizarin preparation, since dissection may easily damage delicate toe tips especially fine lateral processes. Clarke (1981) found that this character may be of some help in identifying lower level supraspecific groups. One source of problems with this character can be the large number of states recognized and the resulting difficulty in linking those states.

In the present study, three states are recognized:-

State 0. Terminal phalanges - simple; pointed, rounded or slightly truncate.

State 1. Terminal phalanges - some slightly spatulate on fingers, otherwise simple, rounded especially on most toes.

State 2. Terminal phalanges - some mushroom shaped, others simple rounded.

In the study group development of the terminal phalanges of the fingers and toes is the same unless stated otherwise. State 1 is found only in *Alytes muletensis*, *A. o. boscai*, *A. (o.) maurus* and *Discoglossus montalentii*. In *A. muletensis* and *D. montalentii* the fingers are noticeably more spatulate than the toes. State 2 is confined to *Leiopelma hamiltoni*. All other discoglossoids examined are state 0.

Urodele terminal phalanges are simple, rounded, consequently state 0 is considered primitive, and by morphological similarity of states the direction of change is considered to be:

$$2 \longleftarrow 0 \longrightarrow 1$$

Excluded characters.

There are three characters/character groups which have been mentioned in the literature purporting to be of significance in respect of either discoglossid or discoglossoid relationships, but which on critical examination do not bear close scrutiny. The three characters are (i) clavicle-scapula ratio (Trueb 1973 and Estes and Reig 1973) (ii) fossa cubitus ventralis (distal end of humerus) and (iii) tubercles and muscle insertions in the region of the dorsal protruberance/dorsal prominence ofthe ilium, (ii) and (iii) - Estes and Sanchiz (1982). The reasons for excluding these characters from mthe present analysis are given briefly below.

(i) Clavicle - scapula ratio

Trueb (1973: 92, Table 2-1) records clavicle to scapula ratios of "greater than three" for Ascaphidae (Ascaphus) and Discoglossidae, but omitted to mention how the measurements were taken. On enquiry Trueb in. litt. (3rd March 1986) commented "I have no idea how I measured the clavicle : scapula ratio". From my own investigations I find it impossible to arrive at such a disproportionate ratio in discoglossoids. Estes and Reig (1973) give a ratio of 1.5 - 1.7 for Notobatrachus deguistoi based on the "maximum length of clavicle and anterior length of scapula". While their figure is more acceptable in terms of order of magnitude, their criteria are not as straightforward or as easily applicable as might initially appear. What is the 'maximum' length of a curved clavicle - the straight line distance between its ends (which will be strongly affected by the degree of curvature i.e. how arched the clavicles are) or the midline length (a curved measurement in arched clavicles - how is this to be taken in practice)? The anterior length of the scapula is also open to interpretation, particularly the medial (proximal) point from which the measurement is mto be taken.

I regard this character as invalid being too imprecisely defined and of questionable utility in any case, particularly in a group like the discoglossoids which show a good deal of variation in scapula shape and curvature of the clavicle.

(ii) Fossa cubitus ventralis (distal end of humerus).

The fossa cubitus ventralis is a cresentic depression/groove abutting the proximal margin of the humeral condyle (eminentia capitata). Estes and Sanchiz (1982: 14, Table 1) indicate that the fossa is "present but not well defined laterally" in Bombina and Barbourula a condition shared in common with Scotiophryne, but not shared with other discoglossids (condition not specified). It is not entirely clear whether Estes and Sanchiz are suggesting that the fossa is absent in other discoglossids or that it is present and is well defined laterally (their ' - ' designation indicates "various classes of dissimilarity amongst taxa involved"). In all discoglossoid material examined in the course of the present study (in which the character is available), a fossa is present even if weakly indicated. The fossa is usually open laterally although the margin may be defined on one side e.g. in Barbourula (B. busuangensis FMNH 50999). I cannot support Estes' and Sanchiz' observations, and in any case regard scoring of this character as given, i.e. : the lateral definition of the fossa, as open to question (condition too variable and usually not sufficiently evident to permit partition into states). Since all the discoglossoids examined have a fossa this character was of no taxonomic use in the present context and was excluded from the present analysis.

(iii) Tubercles and muscle insertions in the region of the dorsal protruberance of the ilium.

Reference to dry skeleton and alizarin preparations of modern species leads me to suggest that the subtle features relating to the dorsal tubercle of the ilium (= dorsal protruberance of Lynch 1971) and adjacent muscle insertions mentioned in the Estes and Sanchiz (1982) paper, are not sufficiently distinct to enable reliable scoring of character states. (An opinion shared with other reviewers of this paper: Drs. E. Crespo, O. Sokal and Z. Spinar as well as myself - Estes and Sanchiz 1982 : 19;

Acknowledgements - "we are grateful for their suggestions although they do not necessarily accept all of our conclusions". I therefore reject the use of these characters, preferring to use Lynch's (1971) designation of ceratophryine and leptodactyline ilial types to summarize difference in the region of the dorsal protruberance of the ilia (Character 70, this work).

D. Characters and character states: a synopsis.

In order to facilitate interpretation of the character state matrix (Table 3), a brief listing of the characters and character states used in this study is included. For each multistate character the additive binary coding of the component states is given, indicating the form of the transformation series. In the case of characters for which a polarity is postulated this also indicates the hypothesized direction of evolutionary change. Characters for which no polarity is postulated are prefixed with a minus sign.

In all other cases 0 indicates the primitive (plesiomorph) condition.

1.	Nasal capsules			1
		0. Widely displaced		0
		1. Little or no lateral displacement.		1
2.	Nasals - medial contact/separation		2.1	2.2
		0. Contact - narrow separation.	0	0
		1. Widely separated	1	0
		2. Fused	0	1
3.	Nasal - maxilla contact		3.1	3.2
		0. None	0	0
		1. Nasal overlying maxilla	1	0
		2. Nasal abutting maxilla	0	1
4.	Nasals - maxillary process		4.1	4.2
		0. Absent	0	0
		1. Present, weak-moderate	1	0
		2. Present, long process	1	1

5.	Sphenethmoid ossification	5.1	5.2	5.3
	0. Tubular	0	0	0
	1. Shallow	1	0	0
	2. Two patches	0	1	0
	3. Variable	0	0	1

6.	Frontoparietals - lateral margins and neurocranial shape	6.1	6.2
	0. Straight	0	0
	1. Biconvex	1	0
	2. Divergent (biconcave)	0	1

7.	Neurocranial width: max. width skull	7
	0. > 0.2	0
	1. ca. 0.1	1

8.	Frontoparietal fontanelles.	8.1	8.2	8.3	8.4
	0. One continuous; ant.-post.	0	0	0	0
	1. One anterior/principally ant.	1	0	0	0
	2. No exposed fontanelle	1	1	0	0
	3. One ant.-post.; some medial separation	0	0	1	0
	4. One or two; similar to 3-much increased separation	0	0	1	1

9.	Frontoparietals: foramen magnum	9
	0. Contact/slight separation	0
	1. Well separated	1

10.	Frontoparietals - otocciptal ridges	10.1	10.2	10.3
	0. Absent	0	0	0
	1. Low dorsal crest	1	0	0
	2. High dorsal crest	1	1	0
	3. Horizontal/posterior ridge	0	0	1

11.	Octoccipitalpattern	11.1	11.2
	0. Narrow, trapezoidal	0	0
	1. Truncate bar-like	1	0
	2. Bar-like	1	1

12.	Otoccipitals, lateral extent/width	12.1	12.2	12.3
	0. Narrow	0	0	0
	1. Moderately wide	1	0	0
	2. Wide	1	1	0
	3. Very wide	1	1	1

13.	Squamosal: otic plate	13.1	13.2
	0. Absent or poorly developed	0	0
	1. Present, poorly differentiated from otic ramus.	1	0
	2. Present, mod, well developed, well defined	0	1

14.	Squamosal: otic ramus	14.1	14.2
	0. Short, distinct process	0	0
	1. Absent or present as small spur of bone	1	0
	2. Present, contigous with otic plate	0	1

15.	Squamosal: zygomatic ramus.	15.1	15.2
	0. Short to moderate	0	0
	1. Long, curving toward maxilla	1	0
	2. Knob-like process	0	1
16.	Squamosal (zygomatic r.) - maxilla articulation	16	
	0. No articulation	0	
	1. Articulation present	1	
17.	Squamosal: medial ramus	17.1	17.2
	0. Absent rib of bone along squamosal shaft	0	0
	1. Absent, but ventromedial expansion present.	1	0
	2. Present	1	1
18.	Squamosal shaft	18.1	18.2
	0. Triangular not or slightly curved	0	0
	1. Intermediate	1	0
	2. Slender, broadest medially, with 'S' curve shape	1	1
19.	Quadratojugal	19.1	19.2
	0. Absent	0	0
	1. Present, 80% pterygoid fossa length (p.f.l.)	1	0
	2. Present, 80-100% p.f.l.	1	1
20.	Maxilla - anterior end	20.1	20.2
	0. Straight or convex	0	0
	1. Staggered; transverse or indented - slightly concave	1	0
	2. Deep 'V' (concave cleft)	1	1

21.	Maxilla - longitudinal groove, base of tooth row	21	
	0. Absent	0	
	1. Present	1	
22.	Maxilla - pterygoidal process	22	
	0. Absent or vestige (v. small process)	0	
	1. Present, well developed	1	
-23.	Maxilla - tooth count	-23	
	0. 40 per maxilla	0	
	1. 40 per maxilla	1	
24.	Maxilla - development of pars facialis: preorbital process	24	
	0. Poor-moderate: absent-weak	0	
	1. Both moderate - well developed	1	
25.	Premaxilla - pars palatina	25	
	0. Shallow	0	
	1. Deep	1	
26.	Premaxilla - palatine process	26.1	26.2
	0. Spatulate	0	0
	1. Intermediate	1	0
	2. Elongate, often pointed	1	1
27.	Premaxilla - lateral process	27	
	0. Absent or poorly developed	0	
	1. Present, elongate (projecting) process	1	

28.	Premaxilla - alary process	28		
	0. Dorsally directed	0		
	1. Laterally directed	1		
-29.	Premaxilla - tooth count	-29		
	0. 14 or more per premaxilla	0		
	1. Less than 14 per premaxilla	1		
30.	Vomer - plate-like portion	30		
	0. Moderately to well developed	0		
	1. Very small	1		
31.	Vomer - circumchoanal process	31		
	0. Present	0		
	1. Absent	1		
31.	Vomer - dentigerous process	32.1	32.2	32.3
	0. Narrow linear series, on contiguous process, posterior to choanae.	0	0	0
	1. Narrow linear series, separate process, posterior to choanae	1	0	0
	2. Teeth in oval patch, between choanae	0	1	0
	3. Broad linear series, well posterior to choanae	0	0	1
33.	Vomeropalatine	33		
	0. Absent	0		
	1. Present	1		

34.	Vomer - postchoanal ramus	34.1	34.2
	0. Absent	0	0
	1. Present, short-moderate; plate-like	1	0
	2. Present, slender, elongate, rod-like	1	1
35.	Parasphenoid	35.1	35.2
	0. Straight sided or biconvex	0	0
	1. Tapering from alae	1	0
	2. Distal $\frac{1}{3}$ to $\frac{1}{2}$ tapering to a point	0	1
36.	Parasphenoid alae - ant./post. depth	36.1	36.2
	0. Uniformly deep	0	0
	1. Deeper laterally	1	0
	2. Uniformly shallow	1	1
37.	Parasphenoid - keel on cultriform process	37	
	0. Absent	0	
	1. Present	1	
38.	Parasphenoid - keel on ala	38	
	0. Absent	0	
	1. Present	1	
39.	Parasphenoid ala/medial ramus of pterygoid: overlap	39.1	39.2
	0. Slight-moderate	0	0
	1. Not overlapping	1	0
	2. Strongly overlapping	0	1

40.	Pterygoid - anterior ramus.	40.1	40.2	
	0. Short-moderate, not curved, anterior end pointed.	0	0	
	1. Short, not curved, anterior end truncate	1	0	
	2. Long, curved, anterior end rounded - pointed	0	1	
41.	Pterygoid - orbital flange	41		
	0. Absent	0		
	1. Present	1		
42.	Pterygoid - ventral flange	42.1	42.2	
	0. Absent	0	0	
	1. Present, moderate	1	0	
	2. Present, deep	1	1	
43.	Columella	43		
	0. Present	0		
	1. Absent (at gross level)	1		
44.	Squamosal - mandibular sesamoid	44		
	0. Absent	0		
	1. Present	1		
45.	Mandible - coronoid process	45.1	45.2	45.3
	0. Lacking notch; dorsally to slightly orally directed.	0	0	0
	1. Weak notch or vertical margin; sl. orally directed.	1	0	0
	2. Deep notch; moderately orally directed	1	1	0

45.	Continued					
	3. Three sided lug of bone; strongly orally directed.	0	0	1		
46.	Mentomeckelian bones	46				
	0. Fused on outer margin to dentary	0				
	1. Indistinguishably fused to dentary.	1				
47.	Occipital condyles - orientation of major axes.	47.1	47.2			
	0. Horizontal	0	0			
	1. Shallow obtuse angle	1	0			
	2. Steep obtuse angle	1	1			
48.	Occipital condyles - position relative to foramen magnum	48.1	48.2			
	0. Ventral	0	0			
	1. At ventrolateral margins	1	0			
	2. (Lower) lateral margins	1	1			
-49.	Hyoid - anterior processes	-49				
	0. Absent	0				
	1. Present: medially directed	1				
-50.	Hyoid - alary processes	-50				
	0. Present	0				
	1. Absent	1				
51.	Hyoid - parahyoid ossifications	51.1	51.2	51.3	51.4	51.5
	0. Medial ossification only - with/without small anterolateral projections	0	0	0	0	0

51.	Continued					
	1. Medial ossification only - 'V'-shaped splint bone (joined at base)	1	0	0	0	0
	2. Medial plus paired, lateral ossifications	0	1	0	0	0
	3. Medial absent; paired lateral ossifications only	0	1	1	0	0
	4. Medial absent; paired splint bones (not joined at base)	0	1	1	1	0
	5. Medial absent; anterior hyoglossal present, paired lateral present.	0	1	1	0	1
52.	Cervical cotylar arrangement	52.1	52.2	52.3		
	0. Type II; no medial notch	0	0	0		
	1. Type II; shallow medial notch	1	0	0		
	2. Type I; shallow medial notch	1	1	0		
	3. Type II/functional Type III; medial groove	0	0	1		
53.	Presacral vertebrae (number)	53				
	0. Nine	0				
	1. Eight	1				
54.	Vertebral column - vertebral centra type	54				
	0. Amphicoelous/ectochordal	0				
	1. Opisthocoelous/stegochordal	1				

55.	Presacral vertebrae (shape of centra)		55		
	0.	Elongate, tubular	0		
	1.	Short, squat, hourglass shape	1		
56.	Ribs (no. of pairs)		56.1	56.2	56.3
	0.	At least 2 or 3 pairs; usually also fused onto 5th (poss. also on 6th) presacrals	0	0	0
	1.	3 pairs; on 2nd, 3rd and 4th	1	0	0
	2.	2 pairs; on 3rd and 4th (or 2nd and 3rd)	1	1	0
	3.	1 pair; on 3rd	1	1	1
57.	Ribs - free, ankylosed or fused		57.1	57.2	
	0.	All free	0	0	
	1.	Some free; some ankylosed or fused	1	0	
	2.	All fused	1	1	
-58.	Uncinate processes		-58		
	0.	Present	0		
	1.	Absent	1		
59.	2nd presacral - transverse processes or ribs distally rounded or flared		59.1	59.2	
	0.	Simple, rounded	0	0	
	1.	Flared posteriorly	1	1	
	2.	Flared anteriorly and posteriorly	1	1	

60.	Neural arches (imbricate/non-imbricate.	60.1	60.2
0.	Imbricate	0	0
1.	Weakly imbricate or imbricate on 1st, progressively less imbricate on 2nd - 8th	1	0
2.	Non-imbricate	1	1

61.	Neural arches - posterior margins	61.1	61.2
0.	Simple	0	0
1.	Slightly flared/upturned	1	0
2.	Strongly flared/upturned	1	1

62.	Neural spines	62.1	62.2
0.	Absent - weakly developed	0	0
1.	Moderately developed	1	0
2.	Strongly developed	1	1

63.	Posterior presacral vertebrae: orientation of transverse processes (relative to longitudinal axis of vertebral column) antepennultimate = apen.	63.1	63.2
0.	Last 3: perpendiculars - sl. post. directed	0	0
1.	Last 2 sl. ant. directed (apen - perpendicular)	1	0
2.	Last 2 strongly ant. directed, (apen-perpendicular or sl. ant.directed)	1	1

64.	Posterior presacral vertebrae: transverse processes - length	64

64.	Continued		
	0. Short	0	
	1. Long	1	
65.	Posterior presacral vertebrae: transverse processes - marginal flanges	65	
	0. Absent	0	
	1. Present	1	
66.	Sacral diapophyses	66.1	66.2
	0. Bar-like, clubbed or slightly dilated	0	0
	1. Moderately dilated	1	0
	2. Broadly dilated	1	1
67.	Sacral centra	67	
	0. Entire	0	
	1. Divided	1	
68.	Sacral prezygapophyes	68	
	0. Anterior	0	
	1. Posterior	1	
-69.	Sacrococcygeal articulation	-69	
	0. Monoconylar	0	
	1. Bicondylar	1	
70.	Ilium: configuration	70.1	70.2
	0. Simple, relatively poorly differentiated	0	0
	1. Weak ceratophryine type	1	0
	2. Leptodactyline type	1	1
-71.	Ilium - dorsal acetabular expansion	-71	
	0. Not extending to dorsal limit of ischium (Type A)	0	

-71.	Continued		
	1. Extending to dorsal limit of ischium (Type P)	1	
72.	Ilium - medial synchondrosis	72	
	0. Absent	0	
	1. Present	1	
-73.	Ischium - development and orientation	-73	
	0. Small, major axis perpendicular or slightly anteriorly inclined	0	
	1. Relatively large, major axis posteriorly inclined	1	
74.	Epipubis:	74.1	74.2
	0. Present: inverted Y - or heart-shaped cartilage - calcified cartilage	0	0
	1. Present: Shield-shaped cartilage (calcified - ossified in adults)	1	0
	2. Absent	0	0
75.	Postpubic or Nobelian bones	75	
	0. Absent	0	
	1. Present	1	
76.	Omosternum	76	
	0. Absent/very poorly developed	0	

76.	Continued		
	1. Present (cartilaginous)	1	
-77.	Clavicles	-77	
	0. Straight - perpendicular to the midline	0	
	1. Strongly curved - antero-medially directed	1	
-78.	Sacpula	-78.1	-78.2
	0. Uncleft	0	0
	1. Bicapitate (open cleft)	1	0
	2. Bicapitate (with closed groove and terminal foramen)	1	1
-79.	Scapula - proximal heads	-79.1	-79.2
	0. Equally developed	0	0
	1. Pars acromialis smaller than pars glenoidalis	1	0
	2. Pars gelnoidalis smaller than pars acromialis	0	1
-80.	Scapula - overall shape (ventral view)	-80.1	-80.2
	0. Rectangular, no cleft on anterior margin	0	0
	1. Triradiate; no cleft on anterior margin	1	0
	2. Approx. triradiate; distinctly cleft anterior margin	1	1
81.	Scapula - posterior margin	81	
	0. Asymmetric - Type gf.	0	
	1. Symmetrical - Type c	1	

–82.	Scapula: glenoid fossa	–82	
	0. Pars acromialis does not present an articular surface to fossa	0	
	1. Pars acromialis does present articular surface	1	
83.	Cleithrum - uncleft or bifurcate	83.1	83.2
	0. Uncleft - thin rib of bone	0	0
	1. Uncleft - moderately deep	1	0
	2. Bifurcate	1	1
84.	Cleithrum - presence/absence on ventral suprascapula	84	
	0. Absent/present as slight 'lip'	0	
	1. Present - clearly investing ventral surface	1	
85.	Coracoids - medial expansion	85.1	85.2
	0. Very broadly expanded/dilated	0	0
	1. Moderately expanded/dilated	1	0
	2. Slightly - barely expanded/dilated	1	1
–86.	Coracoids - orientation	–86	
	0. Long axes perpendicular to midline	0	
	1. Long axes in sigmoid curves - 'step-down' type	1	

87.	Sternum	87	
	0. 'Top-shaped' to flattened 'top-shape'	0	
	1. With posterolaterally divergent horns	1	
-88.	Epicoracoid cartilages	-88.1	-88.2
	0. Not extending posteriorly beyond coracoids	0	0
	1. Extending beyond coracoids but not produced into elongate processes	1	0
	2. Extending beyond coracoids, laterally directed elongate processes	1	1
-89.	Inscriptional ribs	-89	
	0. Absent	0	
	1. Present	1	
90.	Humerus - humeral condyle development	90	
	0. Small, < 60% distal width of humerus	0	
	1. Large, > 66% distal width of humerus	1	
91.	Radioulna - radial and ulnar heads	91	
	0. Separate	0	
	1. Confluent	1	
92.	Wrist bones - radiale, ulnare + intermedium	92	
	0. Wider than long or as wide as long	0	

92.	Continued			
	1.	Longer than wide	1	
93.	Hand - 1st and 4th fingers		93	
	0.	Normal	0	
	1.	1st short, slender; 4th short, squat	1	
-94.	Relative lengths of metatarsals		-94	
	0.	Short metatarsals: long phalanges	0	
	1.	Long metarsals: short phalanges	1	
95.	Terminal phalanges - fingers and toes		95.1	95.2
	0.	Simple; fingers and toes	0	0
	1.	Spatulate (fingers); simple (toes)	1	0
	2.	Some mushroom-shaped, some simple (fingers and toes)	0	1

Table 2. Polarity patterns

A. $0 \longrightarrow 1$ $= 0 - 1$ for non-polar characters

Characters with Type A pattern:

1, 7, 9, 16, 21, 22, -23, 24, 25, 27, 28, -29, 30, 31,33, 37, 38, 41, 43, 44, 46, -49, -50, 53, 54, 55, -58, 64, 65, 67, 68, -69, -71, 72, -73, 75, 76, -77, 81, -82, 84, -86, 87, -89, 90, 91, 92, 93, -94,

B. $0 \longrightarrow 1 \longrightarrow 2.$ $= 0 - 1 - 2$ for non-polar characters

Characters with Type B pattern:

4, 11, 17, 18, 19, 20, 26, 34, 36, 42, 47, 48, 57, 59, 60, 61, 62, 63, 66, 70, -78, -80, 83, 85, -88.

C. $0 \longrightarrow 1 \longrightarrow 2 \longrightarrow 3$

Characters with Type C pattern:

12, 56.

D. $2 \longleftarrow 0 \longrightarrow 1$ $= 2 - 0 - 1$ for non-polar characters

Characters with Type D pattern:

2, 3, 6, 13, 14, 15, 35, 39, 40, 74, -79, 95.

E. $3 \longleftarrow 0 \longrightarrow 1 \longrightarrow 2$

Characters with Type E pattern:

10, 45, 52.

F. $4 \longleftarrow 3 \longleftarrow 0 \longrightarrow 1 \longrightarrow 2$

Character with Type F pattern:

8.

G. $$\begin{tikzcd} & & & & 4 \\ 1 & 0 \arrow[l] \arrow[r] & 2 \arrow[r] & 3 \arrow[ur] \arrow[dr] & \\ & & & & 5 \end{tikzcd}$$

Character with Type G pattern:

51.

H. $$\begin{tikzcd} 2 & 0 \arrow[l] \arrow[r] \arrow[d] & 1 \\ & 3 & \end{tikzcd}$$

Characters with Type H pattern:

5, 32.

Table 3. Data matrix (combined cranial and postcranial).

COMBINED DATA SET

Taxon Nos.	1	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	5.3	6.1	6.2	7	8.1	8.2	8.3	8.4	9	10.1	10.2	10.3	11.1	11.2
1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1
2	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
3	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
4	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
5	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
6	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
7	1	0	0	0	1	1	1	0	0	0	0	1	1	1	1	0	0	0	1	1	0	1	1
8	1	0	0	0	1	1	1	0	0	0	0	1	1	1	1	0	0	-	-	-	-	1	1
9	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0
10	1	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0
11	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0
12	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0
13	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0
14	1	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0
15	1	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
16	1	0	0	1	0	1	1	1	0	0	0	-	0	1	1	0	0	-	1	0	0	1	0
17	1	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0
18	1	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
19	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
20	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
21	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0

	12.1	12.2	12.3	13.1	13.2	14.1	14.2	15.1	15.2	16	17.1	17.2	18.1	18.2	19.1	19.2	20.1	20.2	21	22	-23	24	25
1	1	1	0	0	0	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
7	1	1	1	0	1	0	1	1	0	0	1	1	0	0	1	1	1	0	1	1	V	1	1
8	1	1	1	-	-	-	-	1	0	0	-	-	-	-	1	1	1	0	-	1	-	-	1
9	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1
10	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1
11	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1	1	0	0	1	0	0	1
12	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	1	0	0	0	1
13	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1
14	1	0	0	0	1	0	1	0	0	1	0	0	1	0	1	0	0	0	1	1	1	1	0
15	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	-	1	0
16	-	-	-	0	1	0	1	0	0	1	-	-	1	0	1	0	0	0	1	1	-	1	0
17	1	0	0	0	1	0	1	0	0	1	0	0	1	0	1	0	0	0	1	1	1	1	0
18	0	0	0	0	1	0	1	0	0	1	0	0	1	0	1	0	0	0	1	1	1	1	0
19	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1
20	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1
21	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1

	26.1	26.2	27	28	-29	30	31	32.1	32.2	32.3	33	34.1	34.2	35.1	35.2	36.1	36.2	37	38	39.1	39.2	40.1	40.2
1	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	1	1	0	0	0
2	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0
3	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0
4	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0
5	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0
6	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
7	0	0	0	0	V	0	0	1	0	0	0	1	0	0	1	1	0	1	1	0	1	1	0
8	0	0	0	-	-	-	-	1	0	0	-	-	-	-	-	-	-	-	-	0	1	1	0
9	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1
10	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1
11	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1
12	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1
13	1	0	1	0	V	0	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1
14	1	1	0	0	V	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0
15	1	1	0	0	-	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0	0
16	1	1	0	-	-	0	0	0	0	1	0	1	0	0	0	-	-	0	-	0	0	1	0
17	1	1	0	0	V	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0
18	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0
19	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
20	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0
21	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0

	41	42.1	42.2	43	44	45.1	45.2	45.3	46	47.1	47.2	48.1	48.2	-49	-50	51.1	51.2	51.3	51.4	51.5	52.1	52.2	52.3
1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
6	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
7	0	1	1	0	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	1	0	0
8	0	1	1	0	-	0	0	1	1	1	1	1	0	-	-	-	-	-	-	-	1	0	0
9	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	0	0	1	1	0
10	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0
11	1	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1
12	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0
13	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0
14	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0	0
15	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0
16	0	1	1	0	0	0	0	0	0	1	1	1	0	-	-	0	1	1	1	0	1	0	0
17	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0	0
18	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0
19	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
20	0	0	0	1	0	1	0	0	0	1	0	0	0	V	1	0	0	0	0	0	0	0	0
21	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0

	53	54	55	56.1	56.2	56.3	57.1	57.2	-58	59.1	59.2	60.1	60.2	61.1	61.2	62.1	62.2	63.1	63.2	64	65	66.1	66.2
1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0
2	1	1	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0
3	1	1	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	1	0
4	1	1	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	1	0
5	1	1	1	1	1	0	1	0	1	V	0	1	0	0	0	0	0	1	0	1	0	1	0
6	0	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
7	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1
8	1	1	1	1	0	0	0	0	-	1	1	-	-	-	-	-	-	1	1	1	1	1	1
9	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	0	1	1	1	1	1	1
10	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1	1	0	1	1	1	1	1	1
11	1	1	1	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	1
12	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	0	0	1	1	1	1	1	1
13	1	1	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1	1	1	1	1
14	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1	0
15	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1	0
16	1	1	1	1	0	0	0	0	-	1	0	0	0	1	0	1	0	1	0	1	1	1	0
17	1	1	1	1	0	0	0	0	0	1	V	0	0	1	0	1	0	1	0	1	1	1	0
18	1	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0
19	0	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
20	0	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
21	0	0	1	1	1	0	1	V	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0

	67	68	-69	70.1	70.2	-71	72	-73	74.1	74.2	75	76	-77	-78.1	-78.2	-79.1	-79.2	-80.1	-80.2	81	-82	83.1	83.2
1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1
2	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1
3	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1
4	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1
5	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1
6	0	0	-	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0
7	0	1	0	1	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1
8	0	1	0	-	-	-	1	-	-	-	0	-	1	-	-	-	-	-	-	-	-	-	-
9	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1	0	1	1	1	0	1	1
10	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1	0	1	0	1	0	1	1
11	0	0	0	1	0	0	-	1	0	1	0	0	1	1	0	1	0	1	0	1	0	1	1
12	0	0	0	1	0	0	0	1	0	1	0	1	1	1	0	1	0	1	0	1	0	1	1
13	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1	0	1	1	1	0	1	1
14	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1
15	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1
16	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	-	-	-	-
17	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1
18	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1
19	1	0	-	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
20	1	0	-	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
21	1	1	-	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0

	84	85.1	85.2	-86	87	-88.1	-88.2	-89	90	91	92	93	-94	95.1	95.2
1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	0
2	1	1	1	0	1	1	0	0	1	1	1	0	0	1	0
3	1	1	0	0	1	1	0	0	1	1	1	1	0	0	0
4	1	1	0	0	1	1	0	0	1	1	1	1	0	1	0
5	1	1	0	0	1	1	0	0	1	1	1	0	0	1	0
6	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
7	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0
8	-	1	0	0	1	-	-	0	1	0	0	0	0	-	-
9	1	1	1	0	1	1	1	0	1	0	0	0	0	0	0
10	1	1	0	0	1	1	1	0	1	0	0	0	1	0	0
11	1	1	0	0	1	1	1	0	1	0	0	0	1	0	0
12	1	1	0	0	1	1	1	0	1	0	0	0	0	0	0
13	1	1	1	0	1	1	1	0	1	V	0	0	1	0	0
14	1	1	0	0	1	1	1	0	1	0	0	0	0	0	0
15	1	1	0	0	1	1	1	0	1	0	0	0	0	1	0
16	-	1	0	0	1	-	-	0	1	0	0	0	0	0	0
17	1	1	0	0	1	1	1	0	1	0	0	0	0	0	0
18	1	1	0	0	1	1	1	0	1	0	0	0	0	0	0
19	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
20	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1
21	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0

E. Phylogenetic Analysis

I. Compatibility Analysis

Using the Le Quesne test program, LEQU. BAS, the primary data matrix (Table 3) for 21 discoglossoid taxa was analysed.

Of the 153 binary characters used in the analysis, 30 were singletons, i.e. characters for which only one of the 21 taxa possessed a 0 or a 1 score. Of the thirty characters, twenty six were single derived or 1 states (this includes three characters for which no polarity was assigned) viz., 2.2, 5.2, 8,4, 15.2, 28, 30, 31, 32.2, 35.1, 41, 45.2, 48.2 52.2, 52.3 56.3, 75, -78.2, -82, -86 and also a second group: 10.2, 17.2, 37, 44, 51.5, 62.2 and 95.2. The first group are shown in Table 4 as 0 - - 0; the second group as either 2 0.96 2.08 0 (all except character 95.2) or as 1 0.27 3.73 0 (ch. 95.2). The reason for the appearance of non-zero numerical values for the observed and expected figures in the second group is that they clash with variable scores for the same taxon. In the second group, characters 10.2 to 62.2 all include single derived scores for taxon 7 which clash with variable (v) scores in respect of characters -23 and -29; hence 2 observed incompatibilities compared with 0.96 expected (calculated value) giving an O/E ratio of 2.08. In the case of ch. 95.2 the single derived score is for taxon 20 which clashes only with a single variable score for character -49, giving one observed incompatibility, 0.27 expected and an O/E ratio of 3.73. The distribution of the derived singleton and non-polarized 1 scores is as follows:-

Taxon 1 (7 singleton '1' scores): 8.4, 15.2, 45.2, 56.3, -78.2, -82 and -86.

Taxon 2 (1): 35.1

Taxon 6 (6): 5.2, 28, 30, 31, 32.2 and 75.

Taxon 7 (6): 10.2, 17.2, 37, 44, 51.5 and 62.2.

Taxon 9 (2): 48.2 and 52.2.

Taxon 10 (1) : 2.2

Taxon 11 (2) : 41 and 52.3. and Taxon 20 (1) : 95.2

These singleton characters thus include uniquely derived states for the taxa listed above, indicating evolutionary change which they, and they alone, have undergone (at least in the context of the discoglossoid frogs - it remains to be seen, of course, if any of these features are also found in any of the remaining 4000 + species in the Anura). It is interesting to note that the remaining thirteen of the twenty-one discoglossoid taxa examinedlack, in respect of the present data set, uniquely derived defining character states (autapomorphies) while this survey was able to show as many as six in taxon 6 and taxon 7. The non-polar '1' scores in taxon 1 are included in the list above merely for the sake of convenience. It may be possible, with the benefit of post-analysis hindsight, to infer the polarity of these characters, that is, if the single 1 scores represent uniquely derived states or if their original polarity should be 'reversed' making them primitive singleton states.

The remaining four of the thirty singleton characters were single primitive or 0 states (this includes one character for which no polarity was assigned), these were: 34.1, 56.1, -78.1 and 87. They are easily found in Table 4 as 0 - - 18. Primitive singletons will always show up in the form 0 - - n (where n is a whole number) when they show polar incompatibility with other character. The non-polar character -78.1 also appears in this form for, in this respect, the program treats the character as if it were assigned polarity. All four characters show the 0 state in respect of taxon 6. Primitive singleton states are important since they help in rooting the tree in that they provide an indication of the most primitive taxon in the study group. It does not necessarily indicate that this taxon comes off at the base of the tree <u>on its own</u>; it may share sufficient derived characters with another taxon/other taxa to come off

Table 4.

```
LeQuesne's coefficient of character state randomness = ratio x 100%

             COMBINED DATA SET

Incompatibilities: observed  expected  ratio - polar

1       : 12   83.54  0.14 - 7      2.1    : 12   83.54  0.14 - 9
2.2     : 0    -      -    - 0      3.1    : 12   91.6   0.13 - 0
3.2     : 2    27.62  7E-2 - 0      4.1    : 9    69.02  0.13 - 19
4.2     : 42   107.52 0.39 - 0      5.1    : 44   109.25 0.4  - 0
5.2     : 0    -      -    - 0      5.3    : 9    69.01  0.13 - 0
6.1     : 10   70.32  0.14 - 0      6.2    : 2    27.94  7E-2 - 0
7       : 2    28.01  7E-2 - 0      8.1    : 28   107.43 0.26 - 4
8.2     : 36   73     0.49 - 0      8.3    : 49   105.66 0.46 - 4
8.4     : 0    -      -    - 0      9      : 53   102.45 0.52 - 23
10.1    : 32   79.47  0.4  - 0      10.2   : 2    0.96   2.08 - 0
10.3    : 4    45.21  9E-2 - 0      11.1   : 12   83.06  0.14 - 7
11.2    : 62   60.35  1.03 - 0      12.1   : 66   89.14  0.74 - 0
12.2    : 61   60.25  1.01 - 0      12.3   : 2    27.54  7E-2 - 0
13.1    : 9    66.83  0.13 - 0      13.2   : 42   102    0.41 - 0
14.1    : 57   80.76  0.71 - 1      14.2   : 42   101.87 0.41 - 0
15.1    : 2    28.01  7E-2 - 0      15.2   : 0    -      -    - 0
16      : 10   82.26  0.12 - 0      17.1   : 36   96.15  0.37 - 1
17.2    : 2    0.96   2.08 - 0      18.1   : 44   104.1  0.42 - 0
18.2    : 12   89.35  0.13 - 0      19.1   : 12   82.72  0.15 - 7
19.2    : 37   101.91 0.36 - 1      20.1   : 44   109.25 0.4  - 24
20.2    : 9    69.01  0.13 - 0      21     : 51   99.82  0.51 - 0
22      : 43   105.69 0.41 - 0      -23    : 100  103.28 0.97 - 0
24      : 69   104.47 0.66 - 4      25     : 66   109.92 0.6  - 5
26.1    : 61   107.7  0.57 - 1      26.2   : 54   106.05 0.51 - 0
27      : 48   109.31 0.44 - 23     28     : 0    -      -    - 0
-29     : 90   111.93 0.8  - 0      30     : 0    -      -    - 0
31      : 0    -      -    - 0      32.1   : 75   105.46 0.71 - 1
32.2    : 0    -      -    - 0      32.3   : 12   91.04  0.13 - 0
33      : 12   90.32  0.13 - 0      34.1   : 0    -      -    - 18
34.2    : 9    67.59  0.13 - 0      35.1   : 0    -      -    - 0
35.2    : 76   67.84  1.12 - 0      36.1   : 12   79.81  0.15 - 7
36.2    : 50   101.63 0.49 - 1      37     : 2    0.96   2.08 - 0
38      : 60   102.51 0.59 - 0      39.1   : 68   108.85 0.62 - 6
39.2    : 2    27.49  7E-2 - 0      40.1   : 34   95.22  0.36 - 0
40.2    : 22   92.72  0.24 - 1      41     : 0    -      -    - 0
42.1    : 30   101.04 0.3  - 0      42.2   : 29   53.66  0.54 - 0
43      : 48   109.31 0.44 - 23     44     : 2    0.96   2.08 - 0
45.1    : 59   99.1   0.6  - 0      45.2   : 0    -      -    - 0
45.3    : 37   101.8  0.36 - 1      46     : 33   78.77  0.42 - 0
47.1    : 44   99     0.44 - 9      47.2   : 28   108.34 0.26 - 4
48.1    : 28   109.32 0.26 - 4      48.2   : 0    -      -    - 0
-49     : 26   69.01  0.38 - 4      -50    : 21   67.46  0.31 - 4
51.1    : 12   87.61  0.14 - 0      51.2   : 28   101.7  0.28 - 4
51.3    : 42   99.87  0.42 - 0      51.4   : 12   86.14  0.14 - 0
51.5    : 2    0.96   2.08 - 0      52.1   : 59   108.32 0.54 - 1
52.2    : 0    -      -    - 0      52.3   : 0    -      -    - 0
53      : 12   83.54  0.14 - 7      54     : 12   83.54  0.14 - 7
55      : 10   70.58  0.14 - 53     56.1   : 0    -      -    - 18
56.2    : 56   99.88  0.56 - 4      56.3   : 0    -      -    - 0
57.1    : 56   107.32 0.52 - 30     57.2   : 100  108.22 0.92 - 5
-58     : 12   90.2   0.13 - 0      59.1   : 38   102.36 0.37 - 4
59.2    : 49   104.7  0.47 - 2      60.1   : 45   104.16 0.43 - 30
60.2    : 12   79.86  0.15 - 9      61.1   : 28   103.71 0.27 - 4
61.2    : 41   80.73  0.51 - 0      62.1   : 42   102.76 0.41 - 0
62.2    : 2    0.96   2.08 - 0      63.1   : 21   68.96  0.3  - 11
63.2    : 37   102.04 0.36 - 1      64     : 12   83.54  0.14 - 7
65      : 28   109.32 0.26 - 4      66.1   : 12   82.72  0.15 - 7
66.2    : 37   101.91 0.36 - 1      67     : 9    69.79  0.13 - 0
68      : 72   60.71  1.19 - 0      -69    : 31   81.23  0.38 - 9
70.1    : 12   80.05  0.15 - 7      70.2   : 12   88.14  0.14 - 0
-71     : 44   105.06 0.42 - 0      72     : 2    28.31  7E-2 - 0
-73     : 37   96.39  0.38 - 1      74.1   : 12   79.98  0.15 - 9
74.2    : 37   95.6   0.39 - 1      75     : 0    -      -    - 0
76      : 50   95.32  0.52 - 0      -77    : 12   83.54  0.14 - 7
-78.1   : 0    -      -    - 18     -78.2  : 0    -      -    - 0
-79.1   : 22   89.77  0.25 - 1      -79.2  : 9    67     0.13 - 0
-80.1   : 22   89.97  0.24 - 1      -80.2  : 7    45.62  0.15 - 0
81      : 22   90.24  0.24 - 1      -82    : 0    -      -    - 0
83.1    : 9    67.06  0.13 - 19     83.2   : 12   80.18  0.15 - 7
84      : 9    67.58  0.13 - 19     85.1   : 9    69.41  0.13 - 19
85.2    : 52   70.2   0.74 - 0      -86    : 0    -      -    - 0
87      : 0    -      -    - 18     -88.1  : 12   79.8   0.15 - 7
-88.2   : 49   102.77 0.48 - 1      -89    : 9    69.79  0.13 - 0
90      : 12   83.54  0.14 - 7      91     : 51   99.61  0.51 - 0
92      : 12   93.59  0.13 - 0      93     : 10   70.33  0.14 - 0
-94     : 66   84.36  0.78 - 0      95.1   : 42   81.32  0.52 - 0
95.2    : 1    0.27   3.73 - 0

Grand total - 1953   5263.32   0.37
```

Table 4, continued. Ranking ratios in ascending order of O/E values.

```
Ranking ratios
2.2       5.2       8.4       15.2      28        30        31        32.2      34.1      35.1
41        45.2      48.2      52.2      52.3      56.1      56.3      75        -78.1     -78.2
-82       -86       87        72        7         15.1      6.2       3.2       12.3      39.2
10.3      16        92        -89       67        85.1      4.1       5.3       20.2      3.1
32.3      33        -58       34.2      84        83.1      18.2      -79.2     13.1      70.2
51.1      51.4      55        93        6.1       1         2.1       53        54        64
-77       90        11.1      66.1      19.1      83.2      70.1      74.1      60.2      36.1
-88.1     -80.2     40.2      81        -80.1     -79.1     65        48.1      47.2      8.1
61.1      51.2      42.1      63.1      -50       40.1      63.2      19.2      66.2      45.3
59.1      17.1      -49       -69       -73       74.2      4.2       10.1      5.1       20.1
22        62.1      13.2      14.2      -71       46        51.3      18.1      60.1      27
43        47.1      8.3       59.2      -88.2     36.2      8.2       61.2      26.2      21
91        95.1      9         57.1      76        42.2      52.1      56.2      26.1      38
45.1      25        39.1      24        14.1      32.1      12.1      85.2      -94       -29
57.2      -23       12.2      11.2      35.2      68        10.2      17.2      37        44
51.5      62.2      95.2
```

at the base of the tree with this/these other taxa, in which case the derived and non-polar '1' scores of characters 34.1, 56.1, -78.1 and 87 would be derived in parallel in the taxon/taxa in question and the remaining taxa in the study group (see below).

Because they have no further contribution to make to the rest of the analysis, the singleton characters were subsequently deleted to save machine running time.

A Le Quesne test run on the primary data matrix gave a grand total of 1953 observed incompatibilities (instances of characters failing the Le Quesne test) against 5263.32 (calculated value) expected on the null hypothesis of random distribution of character states, giving an O/E ratio of 0.37 (Table 4) - which indicates a well-structured data set with a low level of homoplasy (parallelism and reversal). On running the LEQU. BAS boil-down procedure a non-polar compatible set of 67 characters was obtained - a large clique of characters. Successive elimination of characters with the highest O/E score, in the boil-down phase of analysis, produced a steady, gradual reduction in the O/E ratios in the progressively smaller data sets - a further indication of a well-ordered data set. The feature of particular interest is the sharp drop to 0 in the observed incompatibilities with the last character deletion. Deletion of character 5.1 removed six incompatibilities - with characters 8.1, 47.2, 48.1, 51.2, 61.1 and 65 to give a compatible data set (Table 5). This would normally suggest only one likely cladogram based on a single maximum clique of characters and no realistic, alternative structure; for the alternative would be to retain character 5.1 and delete the six characters, listed above, with which it is incompatible (which would be contrary to the principle of parsimony).

(a) Construction of the cladogram based on an appraisal of the total data set following a LEQU. BAS compatibility analysis.

Table 6 shows a set of characters which are a compatible set with respect to the Le Quesne test but are not necessarily polar compatible

Table 5.

```
BOILDOWN: COMBINED DATA SET

Grand total -  1868      5196.57   0.36  Ch. deleted :  35.2
Grand total -  1792      5129      0.35  Ch. deleted :  11.2
Grand total -  1732      5069.3    0.34  Ch. deleted :  12.2
Grand total -  1673      5010.13   0.33  Ch. deleted : -23
Grand total -  1583      4912.45   0.32  Ch. deleted :  57.2
Grand total -  1488      4808.42   0.31  Ch. deleted : -94
Grand total -  1425      4727.7    0.3   Ch. deleted : -85.2
Grand total -  1375      4660.98   0.3   Ch. deleted : -29
Grand total -  1299      4559.08   0.28  Ch. deleted :  12.1
Grand total -  1239      4475.77   0.28  Ch. deleted :  32.1
Grand total -  1173      4378.8    0.27  Ch. deleted :  14.1
Grand total -  1124      4304.83   0.26  Ch. deleted :  24
Grand total -  1061      4210.16   0.25  Ch. deleted :  39.1
Grand total -  1000      4112.93   0.24  Ch. deleted :  25
Grand total -   945      4015.71   0.24  Ch. deleted :  38
Grand total -   896      3925.94   0.23  Ch. deleted :  95.1
Grand total -   858      3855.33   0.22  Ch. deleted :  45.1
Grand total -   814      3770.49   0.22  Ch. deleted :  26.1
Grand total -   768      3679.22   0.21  Ch. deleted :  76
Grand total -   729      3599.16   0.2   Ch. deleted :  91
Grand total -   691      3516.68   0.2   Ch. deleted :  42.2
Grand total -   671      3473.25   0.19  Ch. deleted :  36.2
Grand total -   634      3390.19   0.19  Ch. deleted :  56.2
Grand total -   599      3309.91   0.18  Ch. deleted :  52.1
Grand total -   561      3223.67   0.17  Ch. deleted :  8.2
Grand total -   537      3166.67   0.17  Ch. deleted :  21
Grand total -   504      3088.87   0.16  Ch. deleted :  57.1
Grand total -   470      3005.51   0.16  Ch. deleted :   9
Grand total -   439      2927.09   0.15  Ch. deleted :  26.2
Grand total -   407      2846.65   0.14  Ch. deleted :  47.1
Grand total -   380      2773.77   0.14  Ch. deleted : -88.2
Grand total -   353      2698.22   0.13  Ch. deleted :  46
Grand total -   334      2642.42   0.13  Ch. deleted :  8.3
Grand total -   308      2566.47   0.12  Ch. deleted :  10.1
Grand total -   289      2511.23   0.12  Ch. deleted :  61.2
Grand total -   272      2456.09   0.11  Ch. deleted :  51.3
Grand total -   252      2388.3    0.11  Ch. deleted :  22
Grand total -   231      2316.53   0.1   Ch. deleted :  13.2
Grand total -   211      2248.59   9E-2  Ch. deleted :  62.1
Grand total -   191      2180.9    9E-2  Ch. deleted :  14.2
Grand total -   171      2114.2    8E-2  Ch. deleted :  40.1
Grand total -   153      2054.09   7E-2  Ch. deleted : -49
Grand total -   140      2010.9    7E-2  Ch. deleted :  4.2
Grand total -   120      1943.67   6E-2  Ch. deleted : -50
Grand total -   109      1903.22   6E-2  Ch. deleted :  63.1
Grand total -    98      1862.88   5E-2  Ch. deleted :  27
Grand total -    82      1796.7    5E-2  Ch. deleted :  43
Grand total -    66      1731.52   4E-2  Ch. deleted :  42.1
Grand total -    52      1672.38   3E-2  Ch. deleted :  59.1
Grand total -    42      1614.35   3E-2  Ch. deleted :  60.1
Grand total -    33      1556.16   2E-2  Ch. deleted :  59.2
Grand total -    24      1497.57   2E-2  Ch. deleted :  18.1
Grand total -    18      1441.43   1E-2  Ch. deleted : -71
Grand total -    12      1385.32   1E-2  Ch. deleted :  20.1
Grand total -     6      1327.38   0     Ch. deleted :  5.1
Grand total -     0      1270.43   0
```

Table 6.

```
LeQuesne's coefficient of character state randomness = ratio x 100%

        COMBINED DATA SET

Incompatibilities: observed  expected  ratio - polar

1      : 0   80.26  0    - 1    2.1    : 0   80.26  0    - 4
3.1    : 0   90.1   0    - 0    3.2    : 0   25.14  0    - 0
4.1    : 0   66.12  0    - 4    5.3    : 0   66.12  0    - 0
6.1    : 0   67.14  0    - 0    6.2    : 0   25.84  0    - 0
7      : 0   25.9   0    - 0    8.1    : 0   112.44 0    - 2
10.3   : 0   43.28  0    - 0    11.1   : 0   80.26  0    - 1
12.3   : 0   26.38  0    - 0    13.1   : 0   63.1   0    - 0
15.1   : 0   25.9   0    - 0    16     : 0   79.88  0    - 0
17.1   : 0   95.9   0    - 1    18.2   : 0   87.86  0    - 0
19.1   : 0   78.62  0    - 1    19.2   : 0   101.98 0    - 1
20.2   : 0   66.12  0    - 0    32.3   : 0   90.86  0    - 0
33     : 0   87.86  0    - 0    34.2   : 0   63.1   0    - 0
36.1   : 0   77.46  0    - 1    39.2   : 0   25.9   0    - 0
40.2   : 0   92.38  0    - 1    45.3   : 0   103.62 0    - 1
47.2   : 0   112.44 0    - 2    48.1   : 0   112.44 0    - 2
51.1   : 0   84.32  0    - 0    51.2   : 0   101.72 0    - 2
51.4   : 0   82.9   0    - 0    53     : 0   80.26  0    - 1
54     : 0   80.26  0    - 1    55     : 0   67.66  0    - 34
-58    : 0   88.88  0    - 0    60.2   : 0   76.42  0    - 4
61.1   : 0   105.56 0    - 2    63.2   : 0   103.62 0    - 1
64     : 0   80.26  0    - 1    65     : 0   112.44 0    - 2
66.1   : 0   78.62  0    - 1    66.2   : 0   101.98 0    - 1
67     : 0   66.12  0    - 0    -69    : 0   65.52  0    - 6
70.1   : 0   74.98  0    - 1    70.2   : 0   85.02  0    - 0
72     : 0   26.3   0    - 0    -73    : 0   95     0    - 1
74.1   : 0   74.84  0    - 4    74.2   : 0   93.42  0    - 1
-77    : 0   80.26  0    - 1    -79.1  : 0   86.68  0    - 1
-79.2  : 0   61.92  0    - 0    -80.1  : 0   87.06  0    - 1
-80.2  : 0   42.48  0    - 0    81     : 0   88.88  0    - 1
83.1   : 0   63.02  0    - 4    83.2   : 0   76.4   0    - 1
84     : 0   64.08  0    - 4    85.1   : 0   66.12  0    - 4
-88.1  : 0   77.46  0    - 1    -89    : 0   66.12  0    - 0
90     : 0   80.26  0    - 1    92     : 0   92.5   0    - 0
93     : 0   67.66  0    - 0

Grand total - 0   1270.43   0
```

with one another. In order to construct a cladogram it is necessary to resolve the problem of the conflicting character polarities.

Table 7 provides a breakdown of the distribution of the derived scores and, for the sake of convenience only, the 1 scores of those characters for which a polarity was not assigned. Then, since this study is particularly concerned with phylogenetic inference and character polarity if, with the benefit of post-analysis hindsight, it is possible to infer the polarity of these characters, these 1 scores will represent either primitive or derived states. If derived, then the 1 score will represent the derived state in the usual way; if primitive, then taxa with the 1 score should be redesignated as 0 when the complement of these taxa (the remainder of the study group for which the character has been recorded) will show the derived 1 score).

Table 7 . To show the distribution of the derived and non-polar '1' scores of the characters amongst the taxa in the maximum clique of 67 characters, plus 4 singleton 0 characters (Group D).

Group	Taxa	Characters
A.	1-5, 7-18	1, 11.1, 19.1, 36.1 53, 54, 64, 66.1, 70.1, -77, 83.2, -88.1, 90.
B.	6, 19-21	2.1, 60.2, 74.1.
C.	1-18	4.1, 83.1, 84, 85.1.
D.	1-5, 7-21	34.1, 56.1, -78.1, 87.
E.	1-5	18.2, 33 , 51.1, -58, 92.
F.	1, 3, 4	93.
G.	7-18	8.1, 47.2, 48.1, 51.2, 61.1, 65.
H.	7-13	17.1, 19.2, 45.3, 63.2, 66.2,-73, 74.2.
I.	7, 8[a]	3.2, 6.2, 7, 12.3, 15.1, 39.2, 72.
J.	9-13	40.2, -79.1, -80.1, 81.
K.	9,12, 13	6.1, (55) *
L.	9, 13	-80.2.
M.	10, 11	10.3
N.	14-18	3.1, 32.3, 51.4, 70.2.
O.	14, 16-18	16.
P.	19-21	5.3, 13.1, 20.2, 34.2, 67, -79.2, -89.
Q.	1-5, 14-18	-69.[b]

a, b, - See text for details.

* - Character polarity reversed - ch. 55 has 34 polar incompatibilities (see Table 6) in respect of the non-polar compatible data set; reversing its polarity removes most of the polar incompatibilities in this set.

Table 7 shows the following:-

1. The taxa in Group A form the most robust assemblage being supported by 11 polar characters (characters for which a polarity has confidently been assigned).

2. Group B taxa are the complement of those in Group A, i.e. together they comprise the total study group (A + B = (1-5, 7-8) + (6, 19-21) = 1-21).

3. Similarly, Group P is the complement of Group C and,

4. Taxon 6 is the complement of Group D.

5. Groups E. to O are all subsets of Group A and hence are polar compatible with it; similarly Group P is a subset of Groups B and D,

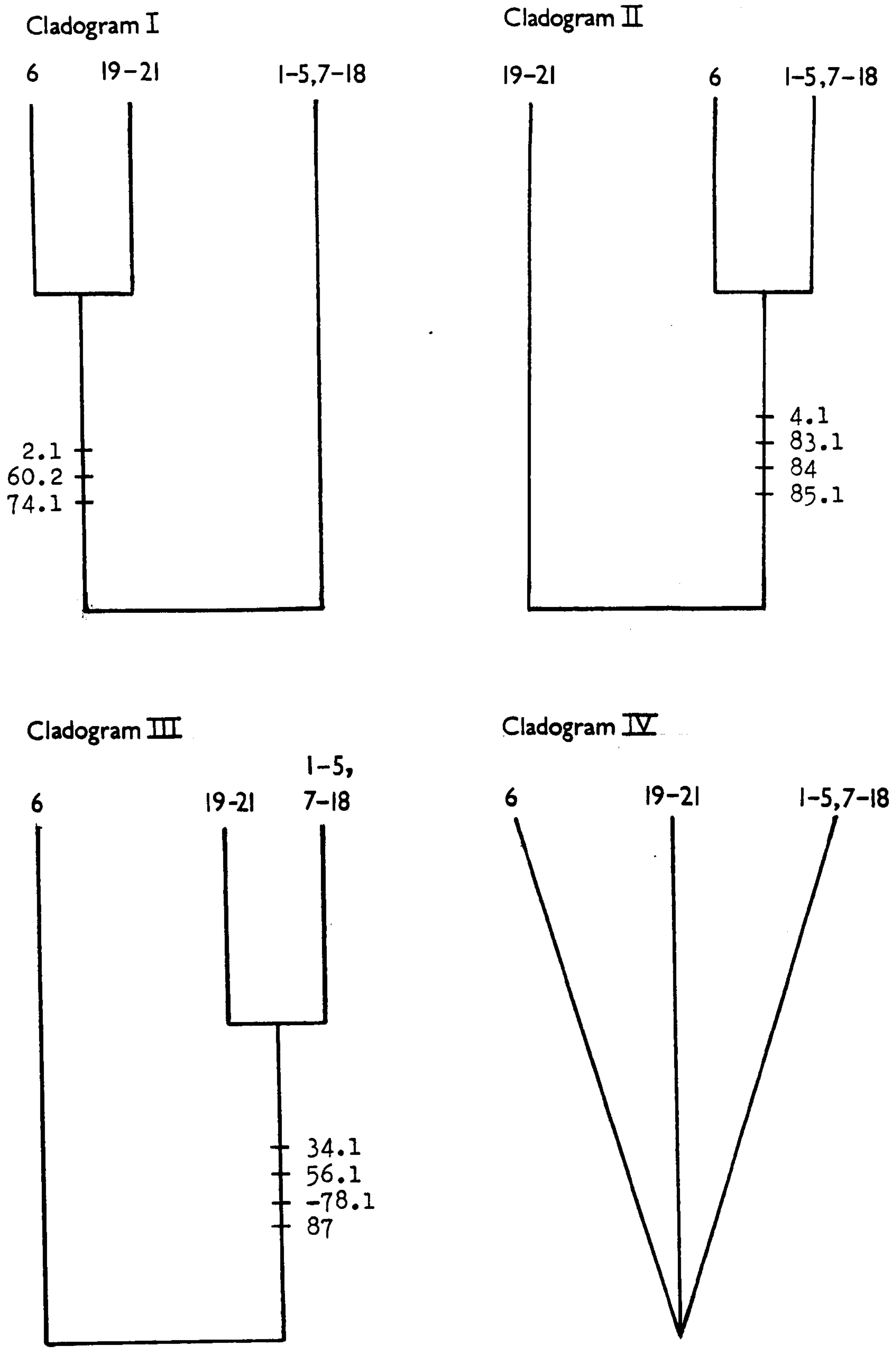
6. Groups E to O and Q include (i) groups which are subsets of one another, e.g. Group L (9, 13) is a subset of Group K (9, 12, 13) which is itself a subset of Group J (9-13); (ii) groups which are partial complements of one another, i.e. together comprise a larger subset of the total study group, e.g.'s Group K (9, 12, 13) is a partial complement of Group M (10, 11) - together they comprise Group J (9-13), similarly Groups I (7, 8) + J (9-13),= Group H (7-13), and also partialcomplementary sets: Groups I (7, 8) + J (9-13) + N (14-18) = Group G (7-18).

Group A is polar compatible with either Group B <u>or</u> Group C <u>or</u> Group D but these groups are not compatible with one another. Consequently, if A and B provide the major structure/principal dichotomy in the cladogram for discoglossoid frogs, then the polarities of the character states defining Groups C and D (both) would have to be reversed to obtain a polar compatible data set (for ch. -78.1 the 1 score would then indicate the primitive state). If A and C provide the major structure, then the polarities of the character states of B and D would need to be reversed; if A and D then it would be the states of B and C that would have to be reversed to obtain a polar compatible data set. Reversal of the states of the characters listed for Groups B, C and D provides apomorphies for their respective complements. Thus reversal of the polarities of Group B characters would produce further derived characters defining Group A; reversal of the polarities of Group C characters would provide further apomorphies for Group P and reversal of Group D character polarities would give more apomorphies for taxon 6.

Group A is not only the best supported group in terms of having the largest clique of derived character states to define it, it is also supported by the derived states of the characters of Groups E - O and Q. Since all of these latter groups are subsets of Group A (see Table 7 and 6. above) their characters are also polar compatible with those of Group A. These data strongly suggest that Group A is a monophyletic group comprising a nested hierarchy of polar compatible subsets of subordinate taxa, albeit not a completely resolved hierarchy (see Table 7). Group A is therefore taken to be an essential part of the cladogram for discoglossoid frogs.

It should be noted that Groups E - O and Q do not provide evidence for resolving the question of the major structure of the cladogram, since these groups only contribute to the (partial) resolution of Group A and A is common to the three possible alternative cladograms mentioned above. The major structure is given either by Groups A, B or A, C or A, D and may be resolved in terms of the relationships of three taxon groupings - Group A, Group P and taxon 6 i.e. (1-5, 7-18) (19-21) (6). The cladogram given by Groups A, B is therefore resolved into ((6) (19-21) (1-5, 7-18); note: Group A (1-15, 7-18) is placed on the right hand side because it is the most derived taxon, having 11 apomorphies. The cladogram given by A, C is (19-21) ((6) (1-5, 7-18)) and that given by A, D is (6) ((19-21) (1-5, 7-18)). (Fig 13).

Since Group A is common to all three schemes it need not be considered further (at present; further resolution within Group A is considered later on; p.311-). Resolution of the main structure of the cladogram for discoglossoid frogs may, therefore, be considered in terms of a choice between accepting either Group B or Group C or Group D as a best estimate of discoglossoid relationships. The alternatives are, therefore:



Cladogram I

Cladogram II

Cladogram III

Cladogram IV

Fig. 13.

Taxon Nos.	GROUP B CLADOGRAM I			GROUP C CLADOGRAM II				GROUP D CLADOGRAM III			
	Character Nos.										
	2.1	60.2	74.1	4.1	83.1	84	85.1	34.1	56.1	-78.1	87
1	0	0	0	1	1	1	1	1	1	1	1
2	0	0	0	1	1	1	1	1	1	1	1
3	0	0	0	1	1	1	1	1	1	1	1
4	0	0	0	1	1	1	1	1	1	1	1
5	0	0	0	1	1	1	1	1	1	1	1
6	1	1	1	1	1	1	1	0	0	0	0
7	0	0	0	1	1	1	1	1	1	1	1
8	0	-	-	1	-	-	1	-	1	-	1
9	0	0	0	1	1	1	1	1	1	1	1
10	0	0	0	1	1	1	1	1	1	1	1
11	0	0	0	1	1	1	1	1	1	1	1
12	0	0	0	1	1	1	1	1	1	1	1
13	0	0	0	1	1	1	1	1	1	1	1
14	0	0	0	1	1	1	1	1	1	1	1
15	0	0	0	1	1	1	1	1	1	1	1
16	0	0	0	1	-	-	1	1	1	1	1
17	0	0	0	1	1	1	1	1	1	1	1
18	0	0	0	1	1	1	1	1	1	1	1
19	1	1	1	0	0	0	0	1	1	1	1
20	1	1	1	0	0	0	0	1	1	1	1
21	1	1	1	0	0	0	0	1	1	1	1

Table 8. Characters supporting Cladograms I, II and III respectively.

1. The polarities of the characters defining Group B taxa (6, 19-21) remain unchanged and those of Group C and D characters are reversed - requires 7 or 8* reversals (* if the 1 state of -78.1 represents the derived condition).

2. Polarities of Group C (= taxa 1-18) characters remain unchanged; those of B and D are reversed - requires 6 or 7* reversals.

3. Polarities of Group D (= taxa 1-5, 7-21) characters remain unchanged; those of B and C are reversed - requires 7 reversals.

4. A fourth possibility exists - that the polarity of the characters defining all three groups B, C and D be reversed. This would require the reversal of 10 or 11* characters.

Option 4 is rejected since it would require the highest number of character state reversals to produce the least ordered cladogram - an unresolved trichotomy: (6) (19-21) (1-5, 7-18). Adopting option 4 would be contrary to the methodological principle of parsimony and to Hennig's principle of adopting dichotomous branching in cladograms; options 1-3 require only 6-8 character state reversals and all produce dichotomously branching trees.

With the choice of schemes requiring 6 or 7 reversals there is no clear reason to prefer the scheme requiring only 6 reversals except on the grounds of parsimony, but as Sneath noted should having only one more evolutionary step rule out a prospective phylogeny? (See Section 4.7 - Parsimony methods). At this stage in the analysis it is necessary to:-

a). Make an assessment of the biological significance of the characters supporting the alternative cladograms, and review the plausibility of homoplasy (character state reversal; likelihood of independent derivation of apomorphic state) or erroneous assignment of polarity in these characters.

b.) Search for any additional qualified support from other characters subject to minimal/low levels of homoplasy.

Comment: This analysis is somewhat unusual in that the structure of the terminal branches of the cladogram is evident at this stage, whereas the 'coarser' structure is as yet unresolved. This information can be used to assess the incidence of homoplasy in the qualified support for each of the groups B, C and D. E.g., using the principle of parsimony, a character having the same distribution as one of these groups and also having the derived state in taxa 1-5 minimally shows only one parallel transformation - in the stem to 1-5 - rather than five independent transformations because these 5 taxa are recognised as a group on the basis of Group E characters. Similarly if the derived state had been found in each of the Group G taxa, 7-18, other than in Group E. taxa, the interpretation would be a single transformation instead of anything up to 12 independent transformations of the derived state! Thus, in this analysis, resolution of the terminal taxa preceeds, and can be helpful in, the resolution of the basal dichotomies/major structure of the cladogram. As a generalization this may be expected to be the case in the phylogenetic analysis of any primitive group which has well-defined terminal taxa. In such cases resolution of the tree proceeds from the top of the tree downwards instead of the other way around as is usual in the phylogenetic analysis of more 'advanced' (relatively more derived) groups.

Group B (6, 19 - 21)

Group B apomorphies suggest taxa (6) and (19-21) are a sister pair. They are compatible with derived states of Group A characters and together these provide support for cladogram I (Fig. 13) in which the sister pair (6) (19-21) are primitive with respect to 1-5 plus 7-18 (the remainder of the study group. The three relevant character transformations defining Group B are:-

2.1: medial separation of the nasals. Trueb (1973: 75) considered the extent of ossification of the nasal to be "an especially labile character" in the Anura - smaller frogs or arboreal anurans tend to have smaller nasals.

Medial contact and extent of ossification are logically correlated: a high level of ossification with medial contact; a low level of ossification with medial separation. In the Anura, the apomorph condition is by no means unique to taxa 6 and 19–21 of the present analysis; e.g. the African ranine frogs, Tomopterna, Rana, Hylarana, Strongylopus and the more advanced genera Ptychadena, Lanzarana and Hildebrandtia, share the apomorphic state of this feature (Clarke 1981: 289) – presumably the result of parallel derivation. It may therefore be the case that this character has phylogenetic value at a local, but not a global level in the Anura. Structurally, having large, well ossified nasals in medial contact affords a higher degree of protection to the delicate nasal capsules, it is therefore not surprising that the apomorphic state has probably arisen independently in different evolutionary lineages within the Anura. Nonetheless, in view of Trueb's comments this character should be treated with some caution; reversal of its polarity is certainly a possibility.

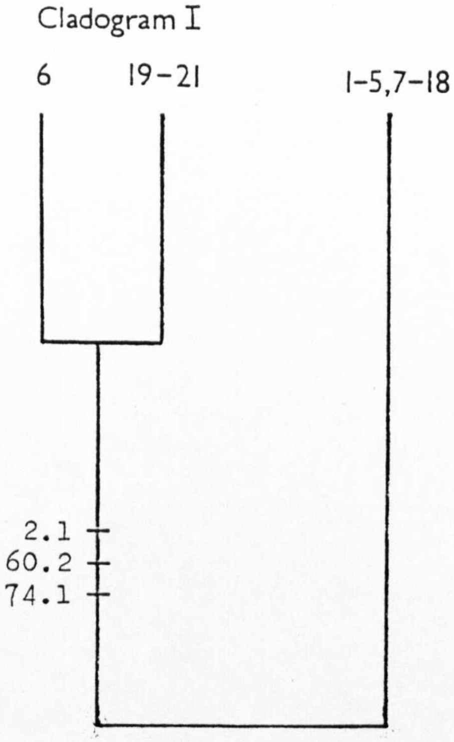
60.2 : neural arches non-imbricate. While the neural arches may not seem to be a source of phylogenetically significant characters – the non-imbricate condition may be seen as one end of a morphological cline : neural arches imbricate — weakly imbricate — non-imbricate, and it is likely that the change from one state to another may be a gradual rather than a quantum change (fide Lynch 1973 "this character reflects degree of ossification....") – there may also be a definite phylogenetic component to character 60,2. Lynch (ibid.) goes on to complete the above quotation by saying that the character is not entirely dependent on the degree of ossification. Trueb (1973: 104) notes that non-imbricate neural arches are found in "small, poorly ossified, or primitive members of some families" and that ascaphids (= 6, 19–21), rhinodermatids, centrolenids and pseudids are "uniformly characterized" by non-imbricate arches. Thus, as in the case of 2.1 (above), the apomorphic state of ch. 60.2 has probably arisen independently in different evolutionary lineages in the Anura. Nonetheless, while this character may well be of phylogenetic value at a local level in the Anura, its presence in a morphological cline in which states may form a continium, subject to gradual change, also suggests that in some instances a local reversal of the polarity of the states of character 60.2 may obtain. Having non-imbricate neural arches may lighten the skeleton and/or provide increased flexibility to the vertebral column.

74.1: Epipubis - large, inverted heart-shaped. The polarity of this character is dependent upon the homology of the epipubis with the ypsiloid cartilage of salamanders. The slender epipubis is certainly very similar to the elongate ypsiloid cartilage, lacking only the anterior bifurcating arms of the Y-shaped ypsiloid cartilage. The homology of these structures is here accepted - certainly as a functional homology and most likely as morphological homology indicative of phylogenetic relationship - as evidence of the primative (grade) level of the anurans possessing an epipubis. It is further suggested that the close, detailed morphological similarity of the apomorphic state in 6, 19, 20, 21, and the differences between the form of the epipubis in these taxa (heart-shaped) and the epipubis of *Pseudhymenochirus* (stalked and roundly dilated anteriorly) and *Xenopus* (diamond shaped) are sufficient evidence to suggest that the character is of phylogenetic value at at least a local level in the primitive Anura. Reversal is therefore considered relatively unlikely.

Qualified support for cladogram I. (Fig. 14).

Nine characters offer qualified support for cladogram I; seven shows the apomorphic state in other taxa in addition to (6, 19-21); two show partial corroboration for (6, 19-21). A tenth, character 55, nominally offers support, being apomorphic for all taxa except 9, 12,and 13. However, as already mentioned above (p.286) character 55 should, almost certainly, have its polarity reversed to become an apomorphy for taxa 9, 12 and 13. Consequently, it does not provide support for cladogram I. The seven showing apomorphic states in other taxa are:-

9: Frontoparietal - separation from the foramen magnum; apomorphic



	2.1	60.2	74.1	9	20.1	27	43	57.1	57.2	60.1	-49	-50
1	0	0	0	0	0	0	0	1	1	1	0	0
2	0	0	0	0	0	0	0	1	0	1	0	0
3	0	0	0	0	0	0	0	1	0	1	0	0
4	0	0	0	0	0	0	0	1	0	1	0	0
5	0	0	0	0	0	0	0	1	0	1	0	0
6	1	1	1	1	1	1	1	1	1	1	1	1
7	0	0	0	0	1	0	0	0	0	0	0	0
8	0	-	-	-	1	0	0	0	0	-	-	-
9	0	0	0	1	1	1	1	1	1	0	0	0
10	0	0	0	0	1	1	1	0	0	0	0	0
11	0	0	0	1	1	1	1	1	1	0	0	0
12	0	0	0	1	1	1	1	1	1	0	0	0
13	0	0	0	1	1	1	1	0	0	0	0	0
14	0	0	0	0	1	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	-	0	0	0	0	0	0	-	-
17	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	1	0	0
19	1	1	1	1	1	1	1	1	1	1	0	1
20	1	1	1	1	1	1	1	1	1	1	V	1
21	1	1	1	1	1	1	1	1	V	1	1	0

<u>Fig. 14.</u> Qualified support for cladogram I (obtained by inspection of Table 3). Characters 2.1, 60.2 and 74.1 included for comparison.

condition also found in taxa 9, 11, 12 and 13. Table E shows 9-13 and 9, 12 and 13 are recognised as Groups (J and K respectively) on the basis of uniquely derived apomorphic states. Thus a minimum of two additional transformations (homoplasies) are required for inclusion of this state on cladogram I (taxon 10 shows the plesiomorphic state for ch. 9), where either ch. 9 is derived for (9-13) and undergoes reversal to 0 for taxon 10 or it is independently derived for (9, 12 and 13) and (11).

20.1: Anterior end of maxilla - 'staggered' (plan view); apomorphic state also found in (7-13): Group H.

27: Premaxilla - lateral processes: elongate; apomorphic state also found in (9-13):

Group J.

43: Columella - absent (at gross level); apomorphic state also found in (9-13):

Group J. Lynch (1973: 148) notes that the columella are "frequently lost" in the Anura.

57.1: Ribs, some free: some ankylosed or fused; apomorphic state also found in (1-5): Group E, 9, 11 and 12 - requires a minimum of four transformations - one for Group E (1-5); three for 9, 11, 12 (independent derivation), or derived for (9-13): Group J with reversals for 10 and 13, or derived for 11 (independently) and derived for (9, 12, 13): Group K, with a reversal for 13.

57.2: Ribs - all fused; apomorphic states also found in 9, 11 and 12 - requires a minimum of three additional transformations as outlined under 57.1 above. Notes: (i) a case could be made for amalgamating characters 57.1 and 57.2, (ii) taxon 21 has a variable score for 57.2, (iii) taxon 1 derived.

60.1: Neural arches - weakly imbricate; apomorphic states also found in (1-5): Group E and taxon 18, requiring only two additional transformations.

The two characters showing partial corroboration are:-

-49: Hyoid: a medially directed anterior process: 1 (postulated apomorphic) scores confined to 6 and 21, variable score on 20 - is partial corroboration with (6, 19-21) if the plesiomorphic score on 19 is taken to be a character state reversal (one additional transformation).

-50: Hyoid - alary process: absent; 1 (apomorphic) scores confined to 6, 19 and 20 - is partial corroboration if the 0 or 'plesiomorphic' score on 21 is a character state reversal (one additional transformation required).

There is little to offer in the way of detailed critical comment on these nine characters. They provide a high level of support with the proviso that homoplasy due to changes in the level of ossification may occur. This is, however, possible for most, if not all, osteogical characters.

Group C (1 - 18)

Group C apomorphies suggest taxa (6) and (1-5, 7-18) are a sister pair. Group C is Group A plus taxon 6 so derived states of Group A characters are, naturally, compatible with those of Group C; together they provide support for cladogram II (Fig. 13) where (19-21) is primitive to the sister-pair (6) and (1-5, 7-18). The four relevant character transformations defining Group C are:-

4.1: Nasals - presence of weak/moderate maxillary process. As noted above p.292, under 2.1, the extent of ossification of the nasal is a variable character. Just as the level of ossification plays a part in the presence/absence of medial contact between the nasals, so it also affects, in part, the presence and development of a maxillary process on the posterolateral corner of the nasal. Nonetheless it is only a factor influencing the development of a maxillary process; there is no direct correlation between level of ossification and the presence or development of a maxillary process. If there were a direct correlation, then the coding of characters 2.1 and 4.1 would be the same; as it is taxa (6) (19-21) share the apomorph condition of 2.1 (medial separation of the nasals) but (6) and (1-5, 7-18) have the apomorphic condition of 4.1. There are a number of difficulties associated with character 4.1 :-

(i) distinguishing between the 0 and 1 state: between absence and presence of a weakly developed process - especially in the case of taxa 1-5 and 9, 12 and 13.

(ii) Outgroup comparison provides a slightly unusual coding for the binary characters of ch. 4 - especially for 4.1. Using hynobiid urodeles suggests a maxillary process is a neomorphic structure in the urodeles, however, if a more recent common ancestor for the discoglossoids had a maxillary process then the polarity of 4.1 would have to be reversed.

(iii) Reference to Trueb (1973: 73, Fig. 2-2) and Duellman/Trueb (1986: Fig.13-17,18 suggests that multiple loss/acquisition of a maxillary process is highly likely in the Anura.

Consequently, in character 4, binary characters 4.1, 4.2 perhaps ought to be recoded as a single binary state: maxillary process absent/poorly or moderately developed (0) versus a long, well developed process (1), thereby removing ch. 4.1 from the analysis, or the polarity of 4.1 should be reversed (as mentioned above). 4.1 is therefore a suspect character.

83.1 Cleithrum - uncleft, moderately deep.

84. Cleithrum - present, investing ventral surface of suprascapula.

These two characters are subject to the same reservation: using urodeles for outgroup comparison suggests the anura cleithrum is a neomorphic structure. The same difficulty applies to both of these characters as it does to 4.1 - (ii) above. If a more recent common ancestor for the discoglossoids is found and has the apomorph condition for 83.1 and 84, then the polarity of these characters should be reversed. In addition, if the changes in level of ossification of the cleithrum in the Anura are gradual rather than quantum changes then these characters should be treated with caution.

85.1 Coracoid with moderately dilated medial margin. The polarity of characters 85.1 and 85.2 were made tentatively and with respect to the condition of the coracoid in Notobatrachus (as reported by Estes and Reig,

1973) and in Vieraella (as re-interpreted in the present work), and with reference to the compound scapulocoracoid of the urodeles (salamanders). Broad dilation - to the extent seen in Leiopelma and Notobatrachus (and envisaged in Vieraella) is very unusual; possibly confined only to these two/three genera in the Anura. There is, therefore, a strong possibility that the coding for character 85.1 should be reversed.

Qualified support for cladogram II. (Fig. 15).

Qualified support for cladogram II i.e. (6) with (1-5, 7-18) would take the form of an apomorphic score for taxon 6 with a majority of apomorphic scores in (1-5, 7-18), and the plesiomorphic condition in all, or the majority, of (19-21). Only one character gives any qualified support for cladogram II.

39.1: Parasphenoid ala/medial ramus of pterygoid - not overlapping. Here the apomorphic condition is found in (6) (1-5) (9, 12, 13); the plesomorphic condition in (19-21), (10,11) (7-8) (15-18). The possible interpretations for the transformations of this character include:

(i) independent derivation in (6) (1-5) and (9, 12 and 13) i.e. three forward transformations - this would not provide support for cladogram II, i.e. 1-18 as a group.

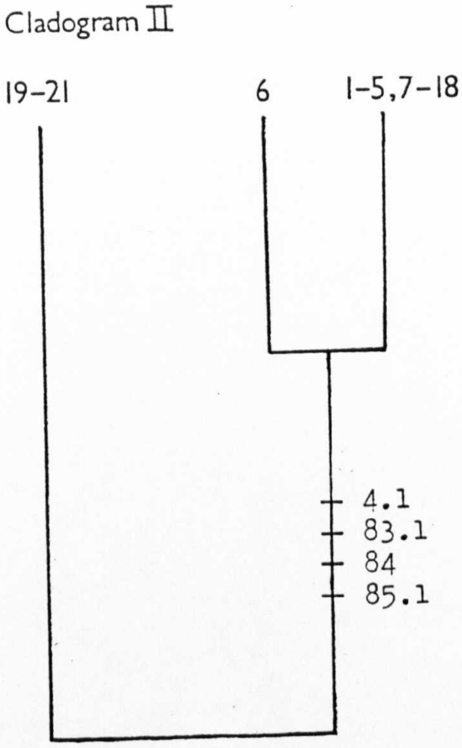
(ii) apomorphic state for (1-18) with reversals in (10, 11): Group M, Table E (7, 8): Group I and (14-18).

(iii) apomorphic state for (1-18) with reversal for (7-18): Group G, Table E, and a further change - a return to an apomorphic (or pseudo - apomorphic) state for (9, 12 and 13) Group K.

(ii) above would provide support for cladogram II at the cost of 3 additional transformations.

(iii) above would also provide support for cladogram II at the cost of only two additional transformations.

It should be noted that the degree of overlap of the parasphenoid ala and the medial ramus of the pterygoid is subject to a high level of



	4.1	83.1	84	85.1	39.1
1	1	1	1	1	1
2	1	1	1	1	1
3	1	1	1	1	1
4	1	1	1	1	1
5	1	1	1	1	1
6	1	1	1	1	1
7	1	1	1	1	0
8	1	-	-	1	0
9	1	1	1	1	1
10	1	1	1	1	0
11	1	1	1	1	0
12	1	1	1	1	1
13	1	1	1	1	1
14	1	1	1	1	0
15	1	1	1	1	0
16	1	-	-	1	0
17	1	1	1	1	0
18	1	1	1	1	0
19	0	0	0	0	0
20	0	0	0	0	0
21	0	0	0	0	0

Fig. 15. Qualified support for cladogram II. Characters 4.1 - 85.1 included for comparison.

homoplasy (see Clarke 1981: 302, Grandison 1981: 206). Independent derivation of the apomorphic condition, as described in (i) above, is a strong possibility.

Group D (1-5, 7-21)

Group D apomorphies suggest taxa (19-21) and (1-5, 7-18) are a sister pair. Group D is Group A plus Group P (19-21), so Group A apomorphies are, naturally, compatible with those of Group D; together they provide support for cladogram III (Fig. 13) where taxon 6 is primitive to the sister-pair (19-21) and (1-5, 7-18).

The four relevant character transformations defining Group D are:-

34.1: Vomer - postchoanal ramus present, short-moderate, plate-like. While outgroup comparison strongly suggests the polarity to this character is correct, Trueb (1973) and Lynch (1973) have noted that in the Anura vomerine bones are subject to variation and even loss. Thus character 34.1 may be subject to homoplasy. It is therefore possible that the apomorphic condition may have arisen independently in the taxa comprising 1-5, 7-21; minimally requiring only two independent transformations - once in the lineage leading to (19-21): Group P (Table E) and once in the lineage leading to (1-5, 7-18): Group A. Because the character is known to be subject to loss (reversal to plesiomorphic condition) in the Anura, reversal of the polarity of this character remains a possibility when the single 0 state would become an autapomorphy for taxon 6.

56.1: Reduction in total number of ribs. This is one character for which there can be no real doubt that the polarity assigned is other than correct (the outgroup is all the other vertebrates). Also, regaining 'lost' characters is contrary to Dollo's Rule that once a character has been lost it cannot be regained. It should be noted, however, that the stepwise loss of rib remnants on the transverse processes produces grade-level groupings which may not necessarily indicate close phylogenetic relationship of taxa sharing the same apomorphic condition. There is also no a priori way of telling if these groups containing taxa at the same grade level (in respect of the character concerned) may or may not be phylogenetically closely related.

-78.1: Scapula bicapitate.

The polarity of this character is certainly in question. Urodeles have a compound scapulocoracoid which is too dissimilar to admit a meaningful comparison. Trueb (1973: 98) implies that a small, uncleft scapula is primitive with respect to a larger, bicapitate one but this implication is based on circular reasoning - the small uncleft condition is primitive because it is found in primitive frogs ("pipids and ascaphids") - circular because Trueb's aim was to make an assessment of evolutionary trends in the anuran skeletal system (ibid: 117). The bicapitate condition is not a special condition confined to (19-21) and (1-5, 7-18) - it is found in all anurans except *Ascaphus* and the Pipidae (*fide* Trueb 1973: 92, and this work).

It would seem that, from a developmental point of view it is equally plausible that the bicapitate condition may be produced by the differentiation of anterior and posterior of an uncleft scapula as it is for the uncleft condition to be produced by the loss of such areas. Consequently, in the absence of any firm evidence to indicate the primitive condition, this character is of little help in the inference of anuran phylogenetic relationships, although its polarity may be inferred with respect to other, more confidently polarized characters when it may be used as corroborative evidence.

87: Sternum - with long divergent cartilaginous horns.

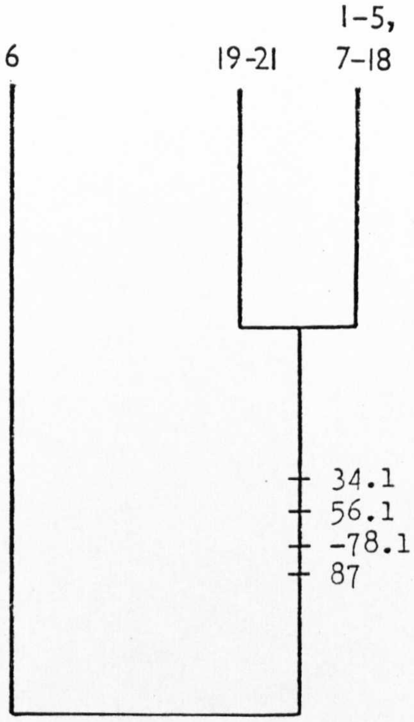
This seems to be a very significant character. Trueb (1973) and Duellman/Trueb (1986) noted that, within the Anura, a sternum with postero-laterally divergent horns is unique to *Leiopelma* and the discoglossoid frogs - a statement based on only a small sample of discoglossoid taxa. This investigation specifically demonstrates: (i) that this type of sternum is present in *all* the discoglossoid taxa examined except taxon 6 (i.e. in all discoglossoid species except *Ascaphus truei*; condition in *Bombina fortinuptialis* not known), and (ii) that, by outgroup comparison, the minority condition (found only in taxon 6 of the present analysis) is the plesiomorphic condition; taxa 1-5, 7-18 consequently share the apomorphic state. Sharing such an apparently, clearly unique character state would normally be regarded as *prima facie* evidence of close relationship. However, while there seems to be little doubt concerning the polarity of this character, de Vos' comment that the inscriptional found in *Leiopelma* may be serially homologous with the posterior horns of the sternum (de Vos 1938) is of special significance. If characters 87 (Sternum) and 89 (Inscriptional ribs) were considered as a single character, the significance of the postulated serial homology becomes apparent. 19-21 have a divergent sternum + inscriptional ribs; 1-5, 7-18 have a divergent sternum but no inscriptional ribs. *If* the divergent sternum *is* serially homologous with the inscriptional ribs, i.e. it is no more than an anterior pair of inscriptional ribs which have become associated with the pectoral girdle, *then* the loss of the posterior pairs of ribs comes into the same category as character 56 - loss of ribs on presacral vertebrae - a grade level character. Under this interpretation 19-21 would be primitive with respect to 1-5, 7-18. As noted under 56.1 above, such grade-level groupings do not necessarily indicate close phylogenetic relationship of taxa at the same grade level - taxa in different lineages may independently attain the same grade. (In this case, by independent loss of inscriptional ribs, leaving a divergent sternum).

Qualified support for cladogram III (Fig. 16).

The better forms of qualified support for cladogram III would include characters giving support with a minimal/low level of homoplasy; such characters would have:

a) preferably, 1 scores for 19, 20 and 21 and *most* of 1-5, 7-18. (Clearly, this type of support is graded: a

Cladogram III



	34.1	56.1	-78.1	87	8.3	24	25	47.1	63.1	-23	56.2	68
1	1	1	1	1	1	0	0	0	1	0	1	0
2	1	1	1	1	1	0	0	0	1	0	1	0
3	1	1	1	1	1	0	0	0	1	0	0	0
4	1	1	1	1	1	0	0	0	1	0	0	0
5	1	1	1	1	1	0	0	0	1	0	1	0
6	0	0	0	0	0	0	0	0	0	0	0	0
7	1	1	1	1	0	1	1	1	1	V	0	1
8	-	1	-	1	0	-	1	1	1	-	0	1
9	1	1	1	1	0	0	1	1	1	0	0	0
10	1	1	1	1	0	0	1	1	1	0	0	0
11	1	1	1	1	0	0	1	1	1	0	0	0
12	1	1	1	1	0	0	1	1	1	0	0	0
13	1	1	1	1	0	0	1	1	1	0	0	0
14	1	1	1	1	0	1	0	1	1	1	0	0
15	1	1	1	1	0	1	0	1	1	-	0	0
16	1	1	1	1	0	1	0	1	1	-	0	0
17	1	1	1	1	0	1	0	1	1	1	0	0
18	1	1	1	1	0	1	0	1	1	1	0	0
19	1	1	1	1	1	1	1	1	0	0	1	0
20	1	1	1	1	1	1	1	1	0	1	1	0
21	1	1	1	1	1	1	1	1	1	1	1	1

Fig. 16. Qualified support for cladogram III. Characters 34.1 - 87 included for comparison.

single zero score in 1-5, 7-18 is better support than two zeros which is better than three, and so on. Unless, of course, the zero scores are 'organized' such that they define one of the subgroups of Group A - see b) below);

b) 1 scores for 19-21 and the members of at least one of the discoglossid groups/subgroup given in Table 7 (see Comment p.307);

c) 1 scores for 1 or more of 19-21 and all of 1-5, 7-18, here taxon 6 would have a zero score in all cases. Other forms of support are considered on their merits; see below, but as in c) above, these are more likely to be instances of independent derivation rather than support.

Four characters provide an acceptable level of support for cladogram III: 8.3, 24, 25 and 47.1; only 47.1 approaches type a) support, the other three are type b). Character 63.1 provides type c) support (above).

8.3: Frontoparietal fontanella - trend towards separation into anterior and posterior fontanellas.

The apomorphic state is also found in taxa 1-5. Given Trueb's (1973: 74) comment that extent of ossification of the frontoparietals is an indication of the overall ossification of the skull, the condition of the fontanelles may well be subject to homoplasy (forward parallel and reverse evolutionary change). It may also be noted that the form of the fontanelles in 1-5 and 19-21 are somewhat different in detail. In 1-5 the 'separation' may be attributed to the development of a medially directed spur of bone at approximately the mid-point along the inner margin of each frontoparietal. Whereas, in 19-21 the form of the fontanelle is similar to that in taxon 6 anteriorly, i.e. the inner margins of the frontoparietals and fairly straight, almost parallel, but posteriorly they are biconcave - giving a biconvex appearance to the posterior part of the fontanelle; i.e. there is no medial spur of bone, no midpoint 'waist' to the fontanelle. It is therefore suggested that these differences in detail may be sufficient to suggest the conditions in 1-5 and 19-21 be reconsidered and assigned to separate binary characters.

24: Maxilla - development of pars facialis and preorbital processes. The derived state of this character is found in 7 and 14-18 (Group N) in addition to 19-21. Inclusion of this character in the cladogram suggested by taxon groupings in Table 7 would require two additional steps - one for taxon 7 or Group I (7 and 8 - state in 8 not known) and one for Group N (14-18). However, it may again be the case that differences in morphological detail suggest that the condition in 19-21 is not the same as that/those in 7 and 14-18. Comparison with character 3 highlights the differences. In 19-21 the pars facialis of maxilla is a particularly deep plate-like process and the preorbital process is moderately developed (ch. 24) yet there is no contact with the nasal (ch. 3). In 7 and 14-18 the pars facialis is not so deep but the preorbital process is well developed and there is contact with the nasal, which either overlies the preorbital process of the maxilla (14-18) or abuts the same process (7).

Thus, as in the case of 8.3, not only is apomorph condition probably not support for cladogram III; it may be that it ought to be broken up into separate characters. With the benefit of post-analysis hindsight at this stage, one might suggest a clearer, more accurate interpretation of relationships would emerge if characters 3 and 24 were considered in combination and used to derive a new set of binary characters.

25: Premaxilla - pars palatina deep: apomorphic condition also found in Groups I and J = Group H, thus only a single additional (homoplasic) transformation is required to include this character on cladogram III. Little is known of the significance of this character but it is probably correlated with diet and overall ossification. Thus frogs that have heavily ossified skulls and/or take larger prey items than usual will probably have a deep pars palatina - character possibly subject to homoplasy.

47.1: Occipital condyles - with major axes inclined; apomorphic state also found in Group G, thus only one additional transformation required. Again little is known of the functional significance of this character but likely to be subject to homoplasy.

63.1: Posterior presacral vertebrae - last two anteriorly directed; only taxon 21 out of 19-21 shares the apomorph condition but does so with all of 1-5, 7-18. It may therefore be an instance of independent derivation in taxon 21. This character only constitutes support for cladogram III if the 0 states in 19 and 20 are character state reversals (since 19-21 are a group, Group P, based on 5 clear apomorphic states plus 1 for two other characters to which no polarity was assigned, viz., -79.2 and -89.

Other characters

Three other characters show derived conditions in one or more of 19-21 and 1-5, 7-18 (Group P and Group A taxa respectively); these are characters -23, 56.2 and 68.

-23: Maxilla - tooth counts. Shows a 1 score for 20 and 21, a variable score for taxon 7, 1 scores for 14, 17 and 18 with missing data scores for 8, 15 and 16. It seems equally plausible that these are cases of independent derivation of a putative apomorphic state as it is of evidence of support for cladogram III. No polarity was assigned to this character; it was included to see if the partitioning of taxa with either more than or less than 40 teeth per maxilla was significant in terms of compatibility with other characters. Present evidence suggests it is very difficult to assign a polarity to this character and that it is almost certainly subject to a high level of homoplasy.

56.2: Reduction to less than three pairs of free ribs. The occurrence of apomorphic states of this character for taxa 1, 2 and 5 in addition to 19-21 may be regarded as support for cladogram III. However, the same comments apply as for ch. 56.1 - while the polarity of this character is not in dispute, the step-wise loss of rib remnants produces grade level grouping which are not necessarily closely related. Independent loss, including further loss, of rib remnants is likely. In Group E (1-5) there has been a progressive reduction in the number of ribs present from three to two pairs to one pair. The suggestion these reductions are more than just grade-level groupings requires corroboration from other characters (in fact the suggestion is contradicted by character 93 which gives 1, 3 and 4 as a group rather than 1, 2 and 5).

68: Sacrum - posterior placement of prezygapophses. A single instance of the apomorphic state in 19-21 - in taxon 21 and apomorphic state scores for 7 and 8 are almost certainly a case of independent derivation. The function significance of a change to a more posteriorly placed prezyapophysis is not known.

(i) An asssment of the four possible cladograms depicting relationships of taxa (6), (19-21) and (1-5, 7-18). (Fig. 13).

Of the four possible cladograms two are discounted - cladograms II and IV. Cladogram II is discounted because it is based on weak characters - ch. 4.1 should either be combined with 4.2, when the presently postulated apomorphic state would become a plesiomorphic state and thereby removed from the analysis or otherwise have its polarity reversed on other grounds; characters 83.1 and 84 are particularly susceptible to changes in the overall level of ossification and are therefore weak characters, otherwise they and ch. 85.1 are likely candidates for polarity reversal. Cladogram IV is discounted on the ground of parsimony with respect to the present data (Table E) it would require the reversal of 10 characters, (11 if 1 scores for ch. -78.1 represents the apomorphic state), whereas cladograms I and III require reversals in 7 (8) and 7 characters respectively.

Thus the two competing cladograms worthy of serious consideration are I and III. Of these two, cladogram I is preferred. While, in both cases, much of the support includes instances of independent derivation, i.e. shared derived characters providing evidence at a lower, more local level, the evidence for cladogram I is (slightly) more convincing. The real conflict, the particularly interesting conflict, is centred on two characters in particular; ch. 74.1 for cladogram I versus ch. 87 for cladogram III. I consider cladogram I to be more likely - character 74.1 (possession of a large, inverted heart-shaped epipubis) is convincing because it represents a special/modified condition of a retained primitive feature which is of limited distribution; one which firmly places a limited number of primitive anurans together - a particularly informative feature. I also accept, but with some reservation, the explanation as given for character 87 as a grade level character. These two characters are particularly informative concerning the nature of the evolutionary relationships of (6) (19-21) (1-5, 7-18) - see Characters. Nonetheless, while preferring cladogram I the evidence for cladogram III is such that it should not be completely discounted, but borne in mind for future comparisons with other, non-osteological data.

(ii) Restoration of deleted characters to give further resolution of relationships.

The characters listed in Table 7 are compatible save for those defining Groups B, C and D - discussed above and Group Q. Group Q - taxa 1-5, 14-18 are defined by character -69, which contradicts six characters for Group G (7-18). Had character -69 been assigned a polarity and the 1 scores denoted the apomorphic state then it would be considered polar incompatible with the six characters defining Group G. Character -69 has entered the boildown data set because it is Le Quesne compatible with the other characters in the set (and because there are missing data scores for 6, 19-21, see below). If the 'polarity' of -69 were reversed it would be 'polar' compatible with Group G.(- for further discussion see below).

The next step in the construction of the 'best estimate' cladogram based on character compatibility is the restoration of the characters deleted in reverse order of 'boil-down'. Thus the characters with the least number of incompatibilities are restored first. These characters may be included

Table 9.

```
            COMPAT. SET +4

        5.1   18.1  47.2  51.2  65
           8.1   20.1  48.1  61.1

-71      -  X  -  -  X  X  X  X  X

65       X  -  X  X  -  -  -  -

61.1     X  -  X  X  -  -  -

51.2     X  -  X  X  -  -

48.1     X  -  X  X  -

47.2     X  -  X  X

20.1     -  X  -

18.1     -  X

8.1      X
```

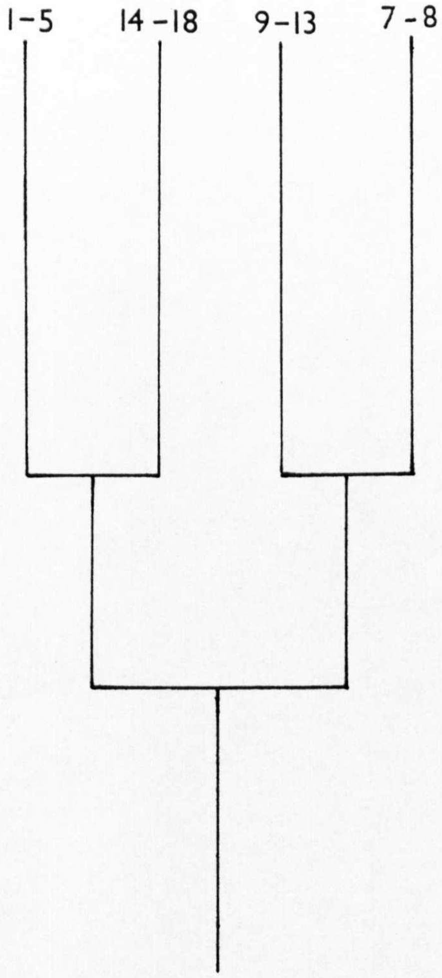
```
LeQuesne's coefficient of character state randomness = ratio x 100%

          COMPAT. SET +4

Incompatibilities: observed  expected  ratio - polar

5.1    : 6   9      0.67 - 0     8.1    : 4   9      0.44 - 0
18.1   : 6   9      0.67 - 0     20.1   : 6   9      0.67 - 0
47.2   : 4   9      0.44 - 0     48.1   : 4   9      0.44 - 0
51.2   : 4   9      0.44 - 0     61.1   : 4   9      0.44 - 0
65     : 4   9      0.44 - 0     -71    : 6   9      0.67 - 0

Grand total - 24    44.99    0.53

Ranking ratios
51.2   61.1   65    8.1    47.2   48.1   18.1   -71    5.1    20.1
```

on a cladogram based on the boildown compatible character set by allowing a minimal level of homoplasies (forward parallels and reversals).

Of the last four characters to be deleted; 5.1, -71 and 18.1 share in common 1 scores (apomorphic states in case of 5.1 and 18.1) for taxa 1-5, 14-18; 20.1 provides another (possible) apomorphic state if its polarity is reversed. Like character -69 they contradict six characters for Group G (7-18) - see Table 9. Ch. -69 entered the compatible set whereas ch. -71 was excluded because -69 has missing data scores (in this case character not logically applicable) for 6, 19-21; -71 has 0 scores for these taxa. If the 0/1 scores were inverted then -69 would become a character defining Group H (7-13); -71 however, would still be ('polar') incompatible with the other Groups in that it does not define any Group listed in Table 7. Thus there are five possible apomorphic characters (-69, 5.1, 20.1, -71 and 18.1) which support a cladogram including a Group Q taxa arrangement - (1-5, 14-18), and which are in conflict with six characters (8.1, 47.2, 48.1, 51.2, 6.1 and 65) supporting a cladogram including a Group G arrangement (7-18). Table 9 shows the character conflict clearly; the conflict may be removed either by deletion of 5.1, 20.1, -71 and 18.1 each of which have six incompatibilities (-69 would also have the same six incompatibilities) or by deletion of 8.1, 47.2, 48.1, 51.2, 61.1 and 65) each having four incompatibilities. As above, the preferred cladogram is arrived at by reference to the biological significance and plausibility of the characters concerned, probability of character state reversal and likelihood of homoplasy, and the availability of qualified support from other characters.

Group Q (1-5, 14-18) (Fig. 17).

The character state transformations suggesting a cladogram including this grouping are: 5.1, 18.1, -69, -71 and, (potentially) 20.1.



	5.1	18.1	-69	-71	20.1	26.1	25	26.2
1	1	1	1	1	0	1	0	1
2	1	1	1	1	0	1	0	0
3	1	1	1	1	0	1	0	1
4	1	1	1	1	0	1	0	1
5	1	1	1	1	0	1	0	1
6	0	0	–	0	1	0	0	0
7	0	0	0	0	1	0	1	0
8	0	–	0	–	1	0	1	0
9	0	0	0	0	1	0	1	0
10	0	0	0	0	1	0	1	0
11	0	0	0	0	1	0	1	0
12	0	0	0	0	1	1	1	0
13	0	0	0	0	1	1	1	0
14	1	1	1	1	0	1	0	1
15	1	1	1	1	0	1	0	1
16	1	1	1	1	0	1	0	1
17	1	1	1	1	0	1	0	1
18	1	1	1	1	0	1	0	0
19	0	0	–	0	1	0	1	0
20	0	0	–	0	1	0	1	0
21	0	0	–	0	1	0	1	0

Fig. 17. Support for a cladogram having 1-5, 14-18 as a group - Group Q.

5.1: Sphenethmoid ossification - deep, tubular to shallow, compact, structure.

Trueb's (1973: 88) suggestion that all sphenethmoids pass through a paired stage would give a different developmental transformation sequence for the states of character 5 viz., 3←2→1→0. However, the outgroup evidence is more convincing for the direction of change as given under the description of ch. 5. Trueb (loc. cit.) also noted that reduction of sphenethmoid ossification in small frogs is a "neotenous adaptation to reduce the weight of the skull at the expense of protection for the brain". It therefore seems reasonable to suggest that independent derivation of the apomorphic state is likely.

18.1: Squamosal shaft-reduction in width, increase in posterolateral curvature.

The effect of this transformation is also to lighten the skull and it may therefore be expected to change with 5.1 above. The change in these two characters could be the consequence of a single factor - reduction in ossification. This character is clearly subject to variation associated with different mechanical constraints which may be imposed on the suspensory system of the jaws against the neurocranium. The possibility of homoplasy, in this case particularly of parallel or convergent development of the same/very similar apomorphic state may be quite high.

-69: Sacrococcygeal articulation. No polarity was assigned to the states of this character. This character is subject to a great deal of variation throughout the Anura: Grandison (1981) reported monocondylar, bicondylar and fused states for the sacrococcygeal articulation in the African Bufonidae - in one case, all three states were found in a single species! At best this character may have some phylogenetic significance at a local level at low taxonomic levels in some cases; in other cases the variation will be due to homoplasy.

-71: Ilium - change in position of articulation with the ischium. No direction of change is postulated for this change - the possible changes are: (i) the posterior migration of the dorsal point of articulation between the ilium and ischium or (ii) the anterior migration of the same articulation. While this is a convenient character for partitioning and grouping members of the study group significance of the change in position of the articulation between these two bone is, as yet, unknown. It must therefore be borne in mind that this character may be subject to homoplasy.

<u>20.1: Maxilla - anterior end of pars palatina straight or convex</u>. This character only provides support for a cladogram with a Group Q grouping i.e. (1-5) sister to (14-18) <u>if</u> its hypothesized polarity is reversed. Although the states described under character 20 are by no means unique to the discoglossoid frogs and may only be of use at lower taxonomic levels. There is no good reason for reversing the polarity of ch. 20.1 - especially when the outgroup information provides such a clear indication that 0 is the plesiomorphic state.

Only one character provides a reasonable level of support for Group Q; ch. 26.1.

<u>26.1: Premaxilla - palatine process (intermediate condition)</u>. The apomorphic state of this character represents a change toward the presence of a distinct palatine process. In four taxa - 2, 12, 13 and 18 - the condition is not clear; it appears to be intermediate between a spatulate and a pointed palatine process. Assignment of the initial character states is somewhat subjective - a good reason to reconsider character state partitioning or removal of the character from the data set. The present character, as coded, is likely to be subject to homoplasy probably multiple forward parallel change.

Only two other characters may be considered in terms of support - characters 25 and 26.2.

25: Premaxilla - change in depth of pars palatina. For this character to provide support its polarity would have to be reversed (direction of change deep to shallow instead of shallow to deep), when the state in taxon 6 would become an independent derivation. Outgroup comparison (pars palatina shallow) suggests the polarity presently assigned polarity is correct.

26.2: Premaxilla - distinct pointed palatine process present. The 0 (plesiomorphic) states in taxon 2 and taxon 18 demonstrate that this character is subject to homoplasy.

Group G (7-18) (Fig. 18).

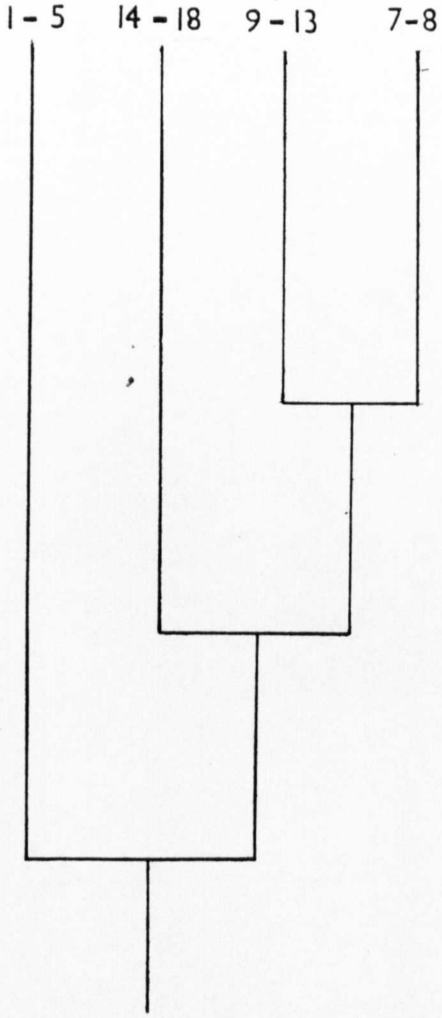
Group G characters suggest taxa (7-8), (9-13) and (14-18) are a derived grouping; together Group A and Group G characters suggest 1-5, 7-18 is a derived group, in which 1-5 are primitive sister group to 7-18. Six character state transformations suggest a cladogram including Group G, these are 8.1, 47.2, 48.2, 61.1, 65 and, possibly also 51.2.

8.1: Frontoparietal fontanella - change from one continuous fontanelle to a (progressively) reduced fontanelle.

The change is in the reduction of the fontanelle, only taxa (1-5), (6) and(19-21) show an open, anterior/posterior fontanelle. In the Anura, there is, as Trueb (1973) commented, a correlation between the extent of ossification of the frontoparietals and the overall ossification of the skull; hence the possibility of homoplasy due to changes in the level of ossification of the skull. Nonetheless in the discoglossoid frogs taxa 1-21 the pattern of detailed resemblances of the frontoparietals/fontanelles suggest there are distinct changes starting from a taxon 6 type fontanelle. It is suggested that character 8 (8.1 - 8.4) is an important character and its binary characters provide clear, distinct and probably uniquely derived states, at least in the context of the discoglossoid frogs.

47.2: Occipital condyles - shallow to a steep obtuse angle.

48.1: Occipital condyles - migrating from ventral to ventrolateral



	8.1	47.2	48.1	61.1	65	51.2	4.2	13.2	14.2	38	51.3	62.1	47.
1	0	0	0	0	0	0	0	0	0	1	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0
7	1	1	1	1	1	1	1	1	1	1	1	1	1
8	1	1	1	-	1	-	1	-	-	-	-	-	1
9	1	1	1	1	1	1	0	0	0	0	0	0	1
10	1	1	1	1	1	1	1	1	1	1	1	1	1
11	1	1	1	1	1	1	1	1	1	1	1	1	1
12	1	1	1	1	1	1	0	0	0	0	0	0	1
13	1	1	1	1	1	1	0	0	0	0	0	0	1
14	1	1	1	1	1	1	1	1	1	1	1	1	1
15	1	1	1	1	1	1	1	1	1	1	1	1	1
16	1	1	1	1	1	1	1	1	1	-	1	1	1
17	1	1	1	1	1	1	1	1	1	1	1	1	1
18	1	1	1	1	1	1	1	1	1	1	1	1	1
19	0	0	0	0	0	0	0	0	0	0	0	0	1
20	0	0	0	0	0	0	0	0	0	0	0	0	1
21	0	0	0	0	0	0	0	0	0	0	0	0	1

<u>Fig. 18.</u> Support for a cladogram having 7-18 as a group - Group G.

margins, foramen magnum.

These characters are considered together because it might be thought that they are logically related - that a change of orientation of the condyle from shallow to steep would be correlated with a change in condyle position from the ventral to the ventrolateral margins of the foramen magnum. There may be a correlation in some cases, but it is not a necessary logical correlation. Taxa 1-5 have occipital condyles with horizontal axes and ventrally positioned relative to the foramen magnum; Taxa 19-21 have occipital condyles with shallowly inclined axes while being ventral to the foramen magnum. The possibility of a correlation in other taxa means that it is still possible to consider these two characters to be related, they may also be subject to homoplasy, particularly if there is a functional significance in the orientation and/or placement of the condyles.

61.1: Neural arches - upturned, flared. The apomorphic state of this character is quite distinct; the significance of the character is, however, not known. It is therefore difficult to make any assessment of the likelihood of homoplasy in this character except that the apomorphic state is also found in salamandrids.

65: Posterior presacral vertebrae bearing marginal flanges. The apomorphic state (marginal flanges present) is also found in Aubria (Ranidae), Pipa and Xenopus (Pipidae) all of which are moderate to large, fully or highly apuatic frogs. There may therefore be a correlation between size and/or more likely aquatic habit, the marginal flanges allowing for a greater area of muscle insertion for muscles of transverse processes and/or sacrum, allowing increased rigidity of the skeleton in the sacral region preventing loss of propulsive power from legs during swimming. Nonetheless, the character is still probably phylogenetically significant at a low taxonomic level.

51.2: Hyoid - parahyoid ossifications (separate/paired lateral ossifications present).

In large part the assignment of taxa 14–18 is a matter of interpretation. If the parahyoid ossifications in these taxa are interpreted as separate paired lateral ossifications, more especially if they are interpreted as a reduced form of the round form of lateral ossification seen in (7–13), then (14–18) belong to Group 6 (7–18). The evidence that they are is somewhat slim – the diverging lateral ossifications bear longitudinal medial ridges surrounded by a narrow flange/rib of bone. Alternatively, they are very like the lateral ossifications seen in taxa 1–5 which are different only in lacking the longitudinal ridge and its circummarginal flange. The succession of character states given in the description of ch. 51, suggests the direction of change is as suggested, particularly in view of the relationships of the medial ossification. The states of ch. 51 are sufficiently discrete that homoplasy is unlikely within the binary states. This character only fails as an apomorphy for Group G if taxa 14–18 should be assigned to State 1.

Support for a cladogram with Group G (7–18) would include seven further characters involving a limited level of homoplasy. These characters are:

4.2 Nasals with a well developed maxilla process.

13.2 Squamosal – otic plate well defined, moderately developed.

14.2 Squamosal – otic ramus indistinguishable from/continuous with otic plate – curving medially over crista parotica.

38. Presence of transverse (medial) keel on parasphenoid ala.

51.3 Loss of medial ossification on the hyoid plate.

62.1 Neural spines present – moderately to strongly developed (i.e. <u>not</u> absent or weakly developed).

47.1 Occipital condyles with major axes non-colinear (i.e. inclined at an obtuse angle).

The first six (4.2 to 62.1) of these seven characters provide a synapomorphies for Group G <u>if</u> the occurrence of 0 states of these characters in taxa 9, 12 and 13, are taken to be instances of reversal to a (pseudo-) primitive state. In all except ch. 51.3 this may be attributed to arrested development in these characters - paedomorphosis when these 0 state would be re-interpreted as secondarily derived features. In the case of ch. 51.3 the retention of a medial ossification on the hyoid plate may be seen either as a retained primitive or a secondarily derived feature. The seventh character (47.1) - is subject to homoplasy in the form of a forward parallelism with taxa 19-21.

An assessment of the sister group relationships of taxa 14-18.

On the basis of the available data taxa 14-18 could be sister either to 1-5 (Group E; to give Group Q above) or to 7-13 (Group H; to give Group G above). A sister group relationship with taxa 1-5 is considered less likely since the data suggesting such a relationship is relatively poor and is weakly supported. Sister group relationship of 14-18 with 7-13 is considered more likely; not only is the data suggesting such a relationship is more convincing but it also receives more support from other characters. Moreover, even the nature of the homoplasy is accounted for, for six of the seven supporting characters - 're-appearance' of the 0 state in taxa 9, 12 and 13 due to paedomorphosis (see previous paragraph). It is therefore suggested that taxa 14-18 (Group N) are sister to 7-13 (Group H).

(b) Compatibility analysis - the preferred cladogram (for Group designations refer to Table 7).

At this stage the taxa show a high level of resolution into groups. There are two major groups (6, 19-21) and (1-5, 7-18) corresponding, respectively, to Groups B and A of Table 7. Group B is further resolved into sister groups taxon 6 (characters 5.2, 28, 30, 31, 32.2 and 75) and Group P (taxa 19-21). Group A is resolved primarily into two sister groups - Group E (taxa 1-5) and Group G (taxa 7-18). Character 93 suggests taxa 1, 3 and 4 are a derived group, Group F, within Group E. Taxa 7-13 are sister to 14-18 (Groups H and N respectively). Group H is further resolved as follows (7, 8; Group I) sister to (9–13; Group J) and J is resolved into:

(i) taxon 9 sister to 13 (Group L); (ii) 9, 12 and 13 are a Group (K) in which taxon 12 is primitive with respect to 9, 13; and (iii) taxa 10 and 11 (Group M) sister to 9, 12 and 13 (Group K). Within Group N (14–18), taxon 15 is primitive to 14, 16–18 (Group O). Using in bracket notation this gives:–

((6) (19–21)) ((2, 5 (1, 3, 4)) ((15 (14, 16–18)) (((10, 11) (12 (9, 13))) (7, 8))). – see also Fig. 19.

Further resolution of the relationships between the discoglossoid taxa may be obtained by reference to the characters deleted in reverse order of 'boildown', this time with respect to the structure already discerned. Thus the character with the least number of incompatibilities with respect to the compatible set defining the bracketed arrangement/cladogram in Fig. 19 is examined first, and so on. In most cases the character incompatibility may be resolved by invoking simple forward parallel occurrence of a character i.e. independent derivation in two or more lineages e.g. character 5.1 independently derived in Groups E (taxa 1–5) and N (14–18); character 43 independently derived in Groups B (6, 19–21) and J (9–13) and character 10.1 in taxa 7, 14, 16 and 17. The first two characters add no further resolution to the cladogram in Fig. 19 but the third, ch. 10.1, does, it suggests 14, 16 and 17 are a derived group within Group O (14, 16–18), in turn a derived group within Group N (14–18) – this extra resolution of 14, 16 and 17 is gained at the 'cost' of a single parallel transformation in taxon 7. This process gives a cladogram with as much resolution as the data set will allow (see Fig. 24 and Discussion). Reference to the bracketed series above/Fig. 19 shows there are three Groups needing resolution by reference to characters showing limited homoplasy: (19–21); ((2, 5 (1, 3, 4)); ((15 (14, 16–18)).

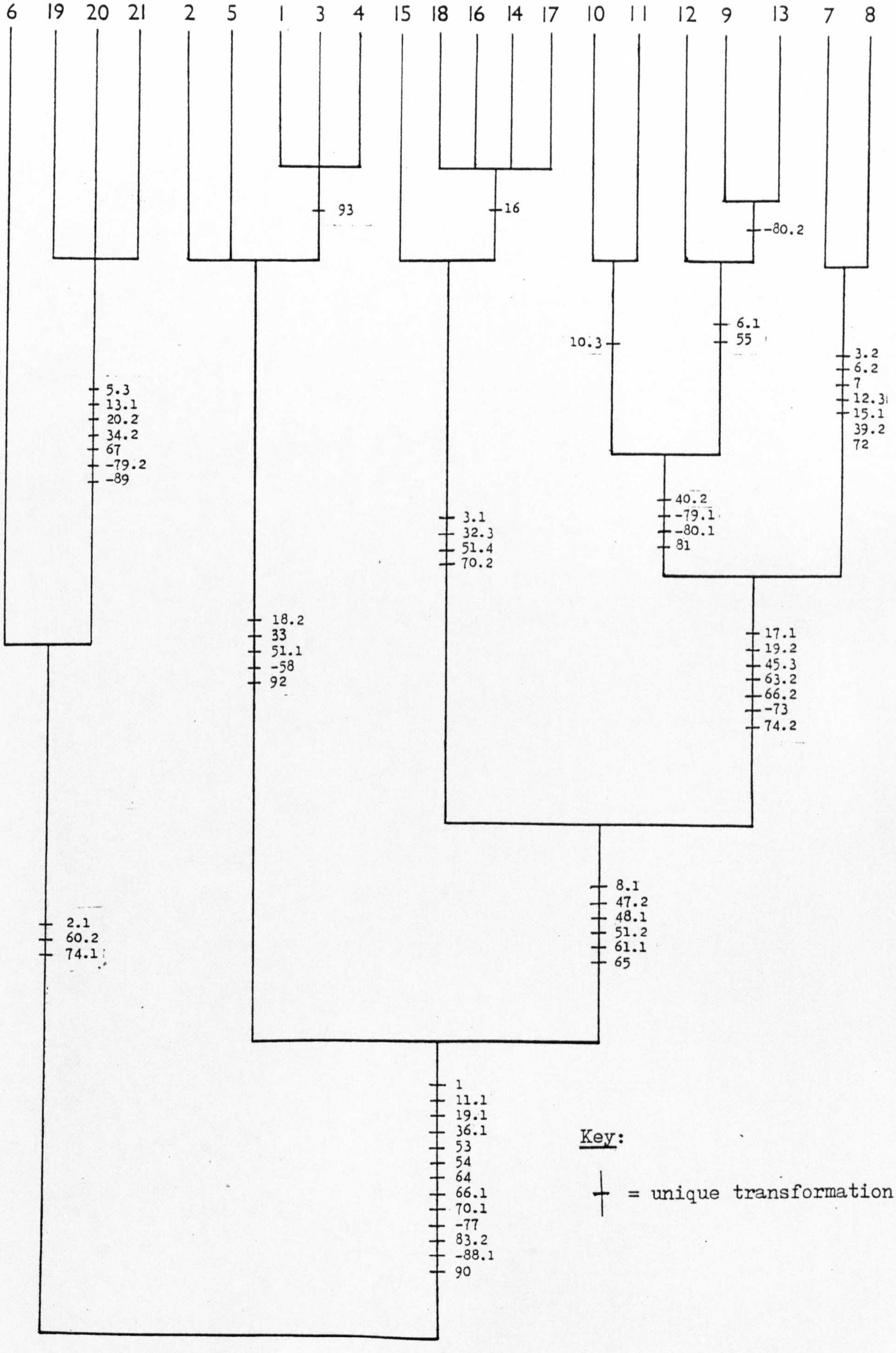

6
19
20
21
2
5
1
3
4
15
18
16
14
17
10
11
12
9
13
7
8
93
16
-80.2
10.3
6.1
55
3.2
6.2
7
12.3
15.1
39.2
72
5.3
13.1
20.2
34.2
67
-79.2
-89
40.2
-79.1
-80.1
81
3.1
32.3
51.4
70.2
18.2
33
51.1
-58
92
17.1
19.2
45.3
63.2
66.2
-73
74.2
8.1
47.2
48.1
51.2
61.1
65
2.1
60.2
74.1
1
11.1
19.1
36.1
53
54
64
66.1
70.1
-77
83.2
-88.1
90
Key:
= unique transformation

Fig. 19.

(19–21) (Fig. 20).

Four characters help provide a resolution of the relationships within 19–21 these are: (in reverse order of boildown deletion) –50, –49, –23 and 35.2. Thus three of these characters were not confidently assigned a polarity and the fourth was the first character to be deleted in boildown. The four characters and their distributions amongst the study group taxa are as follows:–

–50: Absence of alary processes on hyoid plate. Alary processes absent in 6, 19 and 20; present though small in 21, and moderate or large in all other discoglossoid taxa examined. It seems more plausible to suggest this is a loss character in which case it may only be given low weight. If it *is* a loss character it would have been independently lost in 6 and (19, 20) – it could have been independently lost in all three taxa. If the acquisition of an alary process is postulated, independent acquisition must have occurred in taxon 21 if the integrity of (19–21) is to be maintained, whichever the polarity this is clearly a poor character.

–49: Absence of anterior processes on hyale. The distribution of this character is as for ch. 50, only its occurrence in taxon 20 is variable.* The comments given above under ch. 50 also apply to this character.

–23: Maxillary tooth count – greater than 40. Tooth counts of 40 + teeth per maxilla recorded for taxa 7, 14, 17 and 18, 20 and 21. This is clearly a highly labile character – see account for ch. 23. More importantly the low tooth count for taxon 19 is also found in juveniles of taxon 21 – a further example of heterochrony or arrest of development in this taxon (see Trueb 1973: 68). Thus the condition in taxon 19 may be interpreted as secondarily derived with respect to that in 20 and 21, when this character becomes, at best, a grade level character.

35.2: Parasphenoid – anterior ⅓ – ½ of cultriform process tapering abruptly to a point. This condition is found in taxon 7 in addition to 20 and 21. The significance of this feature is not known.

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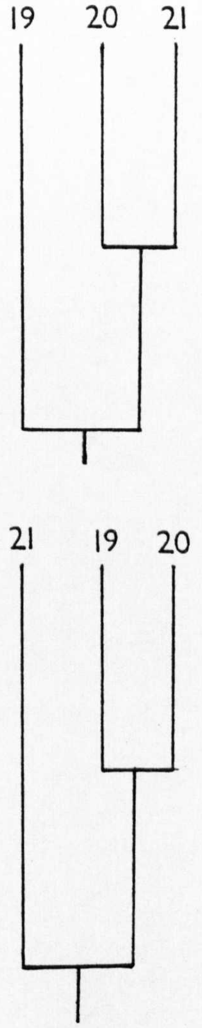
* In terms of presence/absence of processes on the hyoid – but the coding is different; so the character state distribution is different.



	-50,	-49,	-23,	35.2
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0	0	0
5	0	0	0	0
6	1	1	0	0
7	0	0	V	1
8	-	-	-	-
9	0	0	0	0
10	0	0	0	0
11	0	0	0	0
12	0	0	0	0
13	0	0	0	0
14	0	0	1	0
15	0	0	-	0
16	-	-	-	0
17	0	0	1	0
18	0	0	1	0
19	1	0	0	0
20	1	V	1	1
21	0	1	1	1

Fig. 20. Alternative resolutions of taxa 19, 20 and 21.

Note: ch. 57.2 ribs fused - a variable score was recorded for taxon 21 on the basis of presence of some free ribs in a juvenile/subadult of this species; possibly a 1 score would have been more correct. This character therefore has nothing to contribute to the resolution of 19-21.

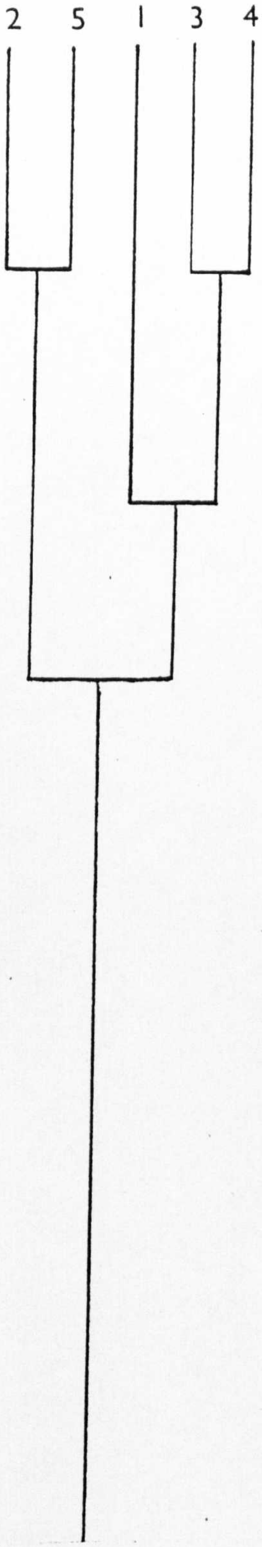
In view of the above comments, I would suggest that evidence for a sister group relationship between taxa 19 and 20 is poor and for taxa 20 and 21 it is a little better. Thus 19-21 may be resolved into 21 (19, 20) or 19 (20, 21), or alternatively left as an unresolved trichotomy. Further data (including non-osteological data) are needed for a satisfactory resolution of the within-group relationships of 19-21.

(2,5 (1,3,4)). (Fig. 21).

Five characters provide information on the relationships of the taxa within Group E (1-5), these are: 93 (a member of the fully compatible character set) and, in reverse order of boildown deletion, 59.1, 26.2, 56.2 and 95.1 - all characters for which a polarity had been assigned. The five characters and their distributions amongst the study group taxa are as follows:-

93: Hand - reduction in length of 1st and 4th fingers. This character is confined to taxa 1, 3 and 4 and is therefore a uniquely derived character for these three taxa and primary evidence of close relationship. Although this character is clearly an adaptation to burrowing with the forelimbs the nature of the adaptation - reduction of both 1st and 4th fingers, where the 1st is slender and spike-like and the 4th short and stubby - and the method of digging (described under character 92) may be unique within the Anura to these three taxa. Other 'head-first' burrowing frogs e.g. Hemisus (Hemisidae) and Myobatrachus (Myobatrachidae) have only 4th finger reduced or all fingers stubby and reduced (Passmore and Carruthers 1979; Barker and Grigg 1977, and BM specimens). This character is consequently considered to be of great phylogenetic significance.

59.1: Distal expansion of transverse processes/ribs on 2nd presacral. The apomorphic condition is found in taxa 3 and 4 and 7-18; taxon 5 exhibits variation in presence/absence of this feature. Consequently,



	93	59.1	26.2	56.2	95.1
1	1	0	1	1	0
2	0	0	0	1	1
3	1	1	1	0	0
4	1	1	1	0	1
5	0	V	1	1	1
6	0	0	0	0	0
7	0	1	0	0	0
8	0	1	0	0	-
9	0	1	0	0	0
10	0	1	0	0	0
11	0	1	0	0	0
12	0	1	0	0	0
13	0	1	0	0	0
14	0	1	1	0	0
15	0	1	1	0	1
16	0	1	1	0	0
17	0	1	1	0	0
18	0	1	0	0	0
19	0	0	0	1	0
20	0	0	0	1	0
21	0	0	0	1	0

Fig. 21. Further resolution of taxa 1-5.

given the major structure of the cladogram shown in Fig. 19, the presence of the apomorph state in 3, 4 (and some members of taxon 5) may be interpreted either as independent derivation or the presence of the plesiomorph state in 1, 2 and (5) as reversal to a pseudoprimitive state (secondary derivation). In either case this character suggests partitioning of 1-5 into two groups-1, 2: 3, 4 with 5 intermediate in respect of this character.

26.2: Premaxilla with a distinct palatine process. The original description of character 26 gives three character states: no distinct process (spatulate type); distinct process (pointed type) and an intermediate condition. Given the structure of the cladogram in Fig. 19, I suggest that partition of this character into two states is more plausible - taxon 5 would be reassigned with 1-4 and taxon 18 with 14-17 to become additional apomorphies for the already well defined taxon groups E (1-5) and N (14-18). The status of this character would be unchanged in respect of taxa 12 and 13.

I therefore suggest this character provides no further resolution to the infragroup relationships of 1-5.

56.2: Reduction in number of pairs of ribs to one or two pairs. Reduction in rib number is step-wise - 3 pairs to 2 pairs to 1 pair and consequently gives rise to grade-level groups - the character may therefore be subject to homoplasy. The apomorph state of 56.2 is found in taxa 19-21 in addition to 1, 2 and 5. Its occurrence in 19-21 is almost certainly independent derivation; the possibility of independent derivation of this character in any/all of 1, 2 and 5 is at least as likely as this character providing evidence of close phylogenetic relationship.

95.1: Development of expansions on terminal phalanges. The apomorph state of this character is found in taxa 2, 4, 5 and 15. It is highly likely that the presence of expansions on terminal phalanges are correlated with the climbing habitat in frogs (e.g. in hylid, rhacophorid and hyperoliid frogs; Gaudin 1974; Liem 1970, Schiøtz 1975 and Drewes 1984). As with the previous character the likelihood of homoplasy is high, as shown by the presence of the apomorph state in taxon 15; independent derivation as possible as inheritance from a recent common ancestor. Taxon 2 and taxon 5 are known to be crevice dwellers in gorges and rock piles.

On the basis of the distribution of apomorph states of characters 93, 59.1 and 95.1, taxa 1–5 are resolved into the following groups:-

(2, 5) (1 (3, 4))

See also Fig. 24.

((15 (14, 16–18)). (Fig. 22).

Nine characters provide information on the relationships of the taxa within Group N (14–18), these are: 16 (a member of the fully compatible character set) and, in reverse order of boildown deletion, 40.1, 10.1, 46, 26.2, 8.2, 52.1, 12.1 and -29, the only character of the nine not assigned a polarity. Of these nine characters, seven are compatible with respect to 14–18 but were deleted during boildown because of homoplasy in the remainder of the study group. The seven characters and their distributions in the study group are listed in Table 10 below:

Character	Distribution: (i) within 14–18	(ii) in 1–13, 19–21.
16	14, 16, 17, 18	-
40.1	14, 16, 17, 18	7,8
10.1	14, 16, 17,	7
46	14, 17,	7,8
52.1	14, 15, 16, 17	7,8,9,12,13
12.1	14, 17	7,8
-29	14 (v) 17 (v)	1-5,7(v), 13(v)

Characters

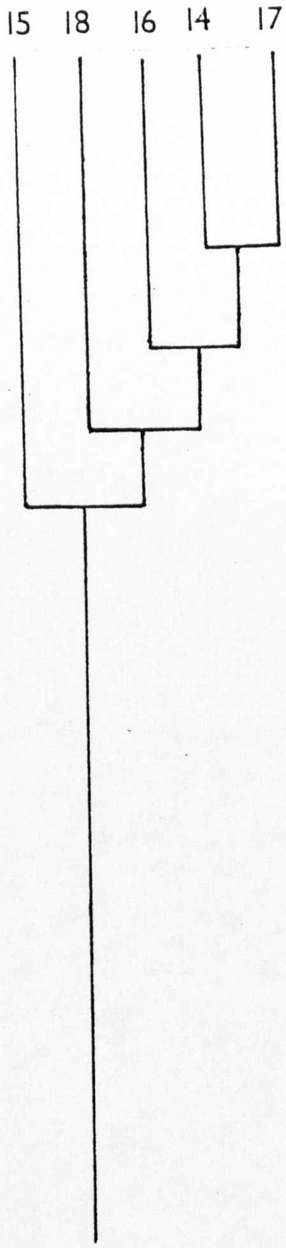
16. Zygomatic ramus of squamosal and maxilla in articular contact.

40.1 Anterior ramus of pterygoid short, truncate distally.

10.1 Frontoparietal - otoccipital ridges present.

46. Mentomeckelian bone indistinguishably fused to dentary.

52.1 Cervical cotyles separated by a shallow-moderate notch.



	16	40.1	10.1	46	52.1	12.1	-29	26.2	8.2
1	0	0	0	0	0	1	1	1	0
2	0	0	0	0	0	0	1	0	0
3	0	0	0	0	0	0	1	1	0
4	0	0	0	0	0	0	1	1	0
5	0	0	0	0	0	0	1	1	0
6	0	0	0	0	0	0	0	0	0
7	0	1	1	1	1	1	V	0	1
8	0	1	-	1	1	1	-	0	1
9	0	0	0	0	1	0	0	0	0
10	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0
12	0	0	0	0	1	0	0	0	0
13	0	0	0	0	1	0	V	0	0
14	1	1	1	1	1	1	V	1	0
15	0	0	0	0	1	0	-	1	1
16	1	1	1	0	1	-	-	1	1
17	1	1	1	1	1	1	V	1	0
18	1	1	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0

Fig. 22. Further resolution of taxa 14-18.

12.1 Otoccipitals wide, reaching or extending beyond outer margin of orbital fossa.

-29. Premaxillary teeth 14 or < 14.

Table 10 . Distribution of informative characters relevant to resolution of taxa 14-18.

The remaining two characters 26.2 and 8.2 are not compatible with the groupings shown in Table 10.

26.2: Premaxilla - with a distinct palatine process. See p.326 above. By analogous reasoning this character provides no further resolution to the infragroup relationships of 14-18.

8.2: Frontoparietals - fusion of medial margins; no dorsally exposed fontanelle.

The apomorph state of this character is found in taxa 15, 16, 7 and 8. Given the main structure of the cladogram in Fig. 19 the structure suggests this character is independently derived in 7 and 8 and in 15 and 16. The condition is different in detail in 7, 8; 15 and 16 show more of a tendency toward the 7,8 condition.

On the basis of the distribution of apomorph states of characters 16, 40.1, 10.1, 46, 52.1 and 12.1 taxa 14-18 are resolved into the following groups:-

(15 (18 (16 (14,17)))).

See also Fig. 24.

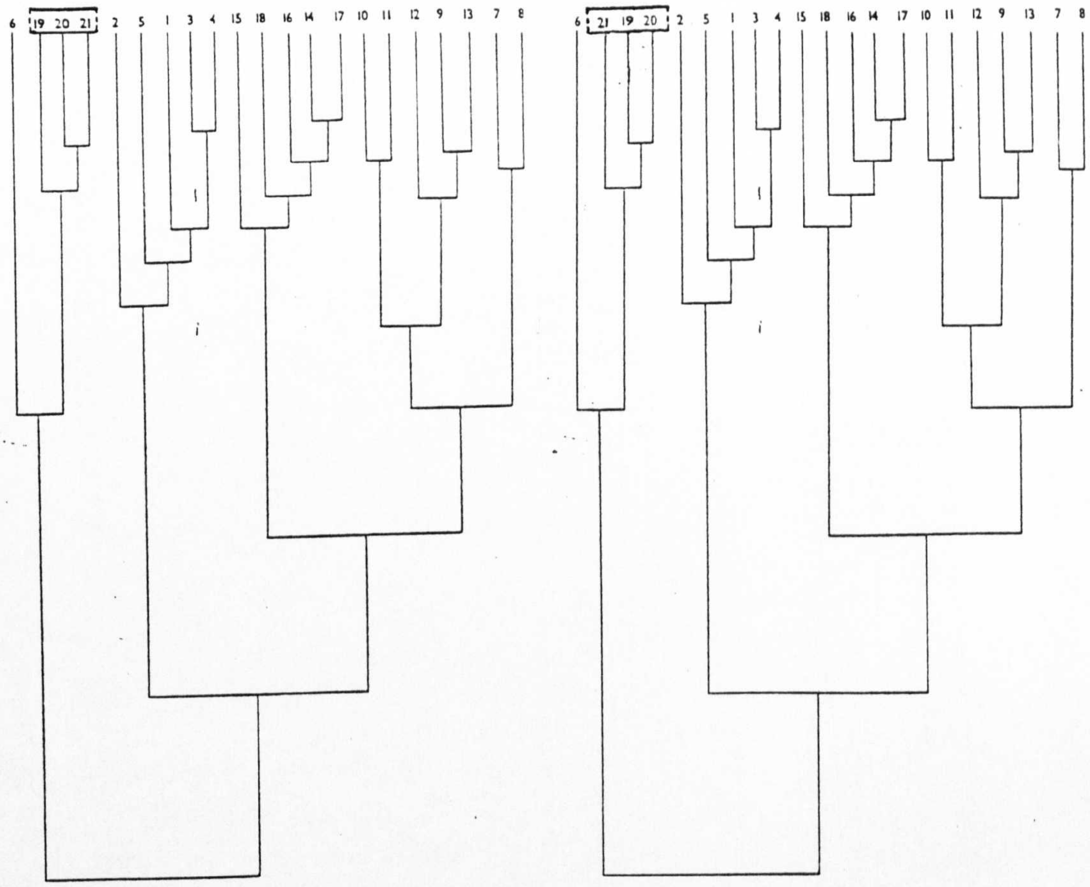
The present LEQU. BAS compatibility analysis therefore provides the following alternative resolutions for the discoglossoid frogs examined:-

A (6) (19 (20,21)) ((2,5) (1 (3,4))) ((15 (18 (16 (14,17))))
(((10,11) (12 (9,13))) (7,8)))).

B (6) (21 (19,20)) ((2,5) (1 (3,4))) ((15 (18 (16 (14,17))))
(((10,11) (12 (9,13))) (7,8)))).

19, 20 and 21 could be considered an unresolved trichotomy but this would not constitute a resolution of relationships which is the whole purpose of the present study. Note that the only difference between alternatives A and B is in the arrangement of taxa 19, 20 and 21. See Fig. 23 for cladograms depicting A and B above. Fig. 24 shows a cladogram for alternative A with the character transformations for the total data set. The equivalent figure for alternative B would only differ in respect of the characters concerning the alternative arrangement of taxa 19-21 - see Fig. 20.

Note: A copy of the printout for the marking procedure is included here for completeness and because it is referred to in the next section - E. Parsimony Analysis. It is of interest to compare the marking scores with the cladogram in Fig. 24 in view of the comments given on p. 75 (Section 4.6 Compatibility Methods). No further comment is made here since the cladogram has been reasonably unequivocally resolved - reference to the marking scores adds little to the present analysis.



Cladogram A.

Cladogram B.

Fig. 23.

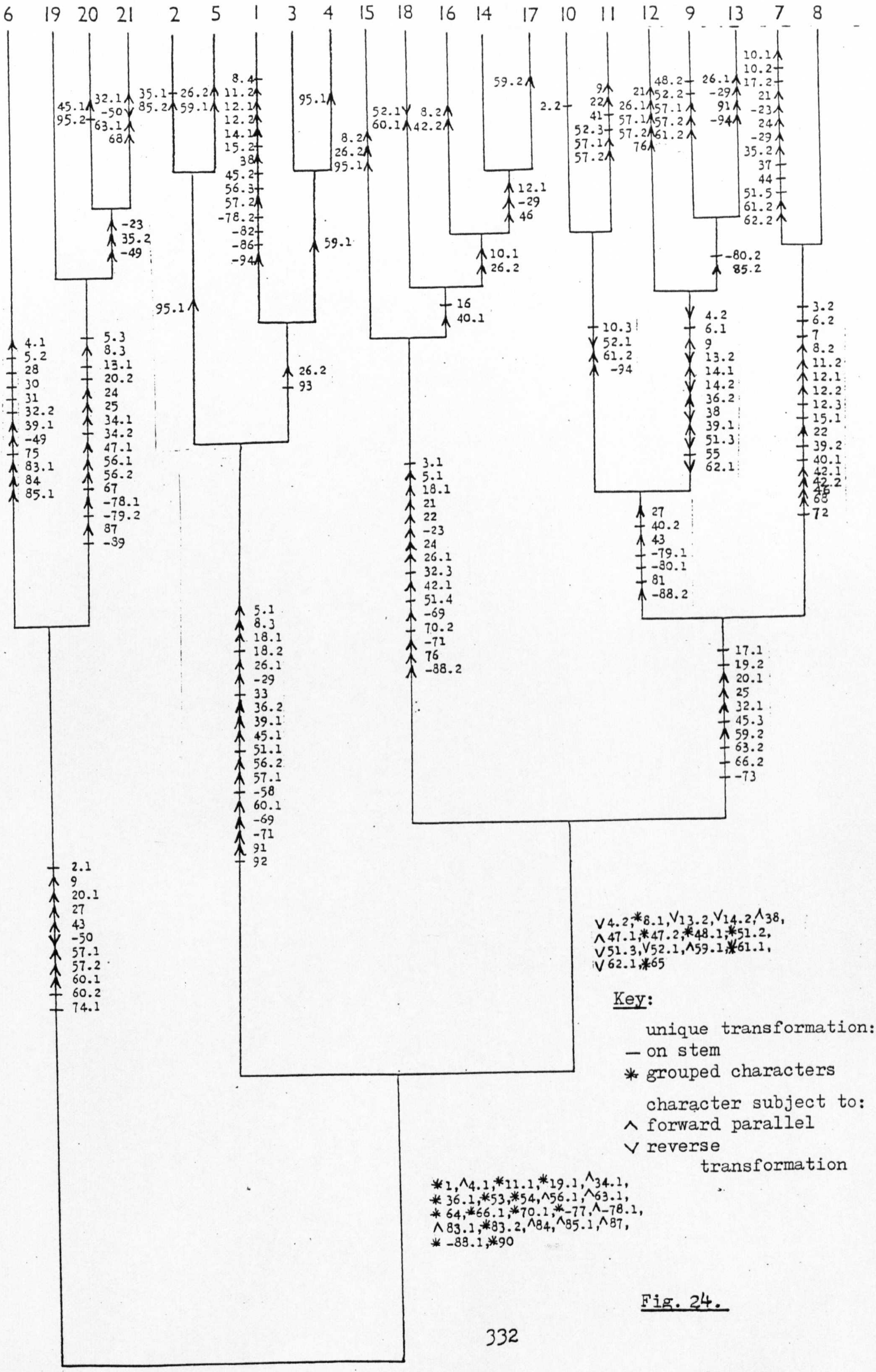

6
19
20
21
2
5
1
3
4
15
18
16
14
17
10
11
12
9
13
7
8
V4.2,*8.1,V13.2,V14.2,^38,
^47.1,*47.2,*48.1,*51.2,
V51.3,V52.1,^59.1,*61.1,
V62.1,*65
Key:
unique transformation:
— on stem
* grouped characters
character subject to:
^ forward parallel
V reverse
transformation
*1,^4.1,*11.1,*19.1,^34.1,
*36.1,*53,*54,^56.1,^63.1,
*64,*66.1,*70.1,*-77,^-78.1,
^83.1,*83.2,^84,^85.1,^87,
*-88.1,*90

Fig. 24.

Table 11.

Species and characters 'marked'

MARKING PROCEDURE

Taxon Nos	1	2.1	3.1	3.2	4.1	4.2	5.1	5.3	6.1	6.2	7	8.1	8.2	8.3	9	10.1	10.2
1 (279)	--	--	--	--	--	3	5	--	--	--	--	6	2	6	2	2	--
2 (51)	--	--	--	--	--	--	1	--	1	--	--	1	--	1	1	--	--
4 (1)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
5 (1)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6 (168)	6	6	--	--	3	--	1	3	--	--	--	--	--	21	2	--	--
7 (311)	1	1	1	2	1	2	1	1	--	2	2	1	13	1	2	29	2
9 (23)	--	--	--	--	--	1	--	--	2	--	--	--	--	--	--	--	--
10 (8)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	5	--	--
11 (32)	--	--	--	--	--	3	--	--	--	--	--	--	--	--	8	--	--
12 (62)	--	--	--	--	--	2	1	--	3	--	--	--	--	--	2	--	--
13 (75)	--	--	--	--	--	1	1	--	5	--	--	1	--	1	3	--	--
15 (47)	--	--	2	--	--	1	--	--	--	--	--	1	7	1	--	1	--
16 (28)	--	--	1	--	--	--	1	--	--	--	--	--	1	--	--	--	--
17 (12)	--	--	1	--	--	--	1	--	--	--	--	--	--	--	--	--	--
18 (34)	--	--	3	--	--	1	--	--	--	--	--	--	--	--	--	1	--
19 (22)	--	--	--	--	2	--	--	2	--	--	--	--	--	--	--	--	--
20 (53)	1	1	--	--	1	--	1	1	--	--	--	--	--	--	1	--	--
21 (161)	3	3	--	--	5	1	--	5	--	--	--	2	1	2	1	1	--

	10.3	11.1	11.2	12.1	12.2	12.3	13.1	13.2	14.1	14.2	15.1	16	17.1	17.2	18.1	18.2	19.1
1	--	--	60	36	59	--	--	3	47	3	--	--	4	--	5	7	--
2	--	--	--	--	--	--	--	--	1	--	--	--	1	--	1	2	--
4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6	--	6	--	--	--	--	3	--	--	--	--	--	--	--	1	--	6
7	--	1	25	7	25	2	2	5	2	5	2	1	15	2	9	2	1
9	--	--	--	--	--	--	--	1	2	1	--	--	--	--	--	--	--
10	4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
11	4	--	--	--	--	--	--	3	--	3	--	--	--	--	--	--	--
12	--	--	--	--	--	--	--	2	2	2	--	--	1	--	1	--	--
13	--	--	--	--	--	--	--	1	2	1	--	--	1	--	1	--	--
15	--	--	--	1	1	--	--	1	--	1	--	--	1	--	--	1	--
16	--	--	1	--	--	--	--	--	--	--	--	2	--	--	1	--	--
17	--	--	--	--	--	--	--	--	--	--	--	1	--	--	1	--	--
18	--	--	--	2	--	--	--	1	--	1	--	5	--	--	--	--	--
19	--	--	--	--	--	--	2	--	--	--	--	--	--	--	--	--	--
20	--	1	--	--	--	--	1	--	--	--	--	--	--	--	1	--	1
21	--	3	1	1	1	--	5	1	--	1	--	--	1	--	--	--	3

	19.2	20.1	20.2	21	22	23	24	25	26.1	26.2	27	29	32.1	32.3	33	34.2	35.2
1	4	5	--	3	3	--	3	4	2	5	3	1	4	--	7	--	2
2	1	1	--	--	--	--	--	1	--	6	1	--	1	--	2	--	--
4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6	--	1	3	--	--	1	19	23	2	--	2	1	--	--	--	3	1
7	5	1	1	7	2	32	11	1	3	1	5	21	1	1	2	2	70
9	--	--	--	--	--	--	--	--	6	--	--	--	--	--	--	--	--
10	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--
11	--	--	--	1	13	--	1	--	--	--	1	--	--	--	--	--	--
12	1	1	--	22	2	1	2	1	--	--	2	--	1	--	--	--	--
13	1	1	--	--	--	--	--	1	1	--	2	11	1	--	--	--	--
15	--	--	--	1	1	--	1	--	--	--	--	--	--	2	1	--	--
16	1	1	--	--	--	--	--	1	1	1	--	--	1	1	--	--	1
17	--	1	--	--	--	--	--	1	--	1	--	--	1	1	--	--	--
18	--	--	--	2	1	--	--	--	--	5	--	--	--	3	--	--	--
19	--	--	2	--	--	11	--	--	--	--	--	--	--	--	--	2	11
20	--	1	1	--	--	3	1	1	1	--	1	1	1	--	--	1	4
21	1	--	5	1	1	--	--	--	--	--	1	--	39	--	--	5	--

	36.1	36.2	37	38	39.1	39.2	40.1	40.2	42.1	42.2	43	44	45.1	45.3	46	47.1	47.2
1	--	4	--	21	4	--	3	2	3	1	3	--	6	4	2	6	6
2	--	--	--	--	--	--	--	1	--	--	1	--	1	1	--	1	1
4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6	6	1	--	--	19	--	--	--	--	--	2	--	1	--	--	32	--
7	2	2	2	2	--	2	12	1	10	11	5	2	--	5	12	--	1
9	--	2	--	1	1	--	--	--	--	--	--	--	--	--	--	--	--
10	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--
11	--	--	--	1	--	--	--	1	--	--	1	--	--	--	--	--	--
12	--	2	--	2	2	--	--	2	1	--	2	--	--	1	--	--	--
13	--	1	--	2	1	--	--	2	--	--	2	--	1	1	--	1	1
15	--	1	--	1	1	--	5	--	1	--	--	--	1	--	--	1	1
16	--	--	--	--	--	--	--	--	--	27	--	--	--	1	1	--	--
17	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
18	--	--	--	--	--	--	3	--	2	--	--	--	--	--	--	--	--
19	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
20	1	1	--	--	1	--	--	--	--	--	1	--	47	--	--	1	--
21	3	--	--	1	--	--	1	--	1	1	1	--	--	1	1	--	2

	48.1	49	50	51.1	51.2	51.3	51.4	51.5	52.1	53	54	55	56.2	57.1	57.2	58	59.1
1	6	--	--	7	6	3	--	--	4	--	--	--	7	3	20	7	7
2	1	--	--	2	1	--	--	--	1	--	--	1	1	--	--	2	1
4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	1
6	--	19	17	--	--	--	--	--	--	6	6	--	20	--	--	--	2
7	1	1	--	2	4	5	5	2	2	1	1	--	1	2	--	2	1
9	--	--	--	--	--	1	--	--	--	--	--	2	--	1	2	--	--
10	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--
11	--	--	--	--	--	3	--	--	--	--	--	--	--	7	7	--	--
12	--	--	--	--	--	2	--	--	--	--	--	3	--	2	2	--	--
13	1	--	--	--	1	1	--	--	2	--	--	5	--	15	4	--	--
15	1	--	--	1	1	1	2	--	1	--	--	--	--	1	--	1	--
16	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--
17	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--
18	--	--	--	--	--	1	3	--	9	--	--	--	--	1	--	--	--
19	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
20	--	2	3	--	--	--	--	--	--	1	1	--	--	--	--	--	--
21	2	5	12	--	2	1	--	--	1	3	3	--	2	1	29	--	2

	59.2	60.1	60.2	61.1	61.2	62.1	62.2	63.1	63.2	64	65	66.1	66.2	67	68	69	70.1
1	4	5	--	6	2	3	--	--	4	--	6	--	4	--	2	5	--
2	1	1	--	1	--	--	--	--	1	--	1	--	1	--	--	1	--
4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6	--	--	6	--	--	--	--	17	--	6	--	6	--	3	--	--	6
7	2	5	2	4	22	5	2	--	5	1	1	1	5	1	29	4	2
9	--	--	--	--	13	1	--	--	--	--	--	--	--	--	--	--	--
10	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
11	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	--	--
12	--	--	--	--	--	2	--	--	1	--	--	--	1	--	--	1	--
13	1	1	--	1	1	1	--	--	1	--	1	--	1	--	--	1	--
15	--	1	--	1	--	1	--	--	--	--	1	--	--	--	--	--	--
16	1	--	--	--	1	--	--	--	1	--	--	--	1	--	1	1	--
17	12	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
18	--	17	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--
19	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--
20	--	--	1	--	--	--	--	3	--	1	--	1	--	1	--	--	1
21	2	2	3	2	1	1	--	12	1	3	2	3	1	5	70	--	3

	70.2	71	72	73	74.1	74.2	76	77	79.1	79.2	80.1	80.2	81	83.1	83.2	84	85.1
1	--	5	--	4	--	4	--	--	2	--	2	--	2	--	--	--	--
2	--	1	--	1	--	1	--	--	1	--	1	--	1	--	--	--	--
4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6	--	1	--	--	6	--	--	6	--	3	--	--	--	3	6	3	3
7	5	9	2	16	2	16	6	1	1	2	1	--	1	2	2	2	1
9	--	--	--	--	--	--	--	--	--	--	--	5	--	--	--	--	--
10	--	--	--	--	--	--	--	--	1	--	1	--	1	--	--	--	--
11	--	--	--	--	--	--	--	--	1	--	1	--	1	--	--	--	--
12	--	1	--	1	--	1	38	--	2	--	2	--	2	--	--	--	--
13	--	1	--	1	--	1	--	--	2	--	2	7	2	--	--	--	--
15	2	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--
16	1	1	--	1	--	1	1	--	--	--	--	--	--	--	--	--	--
17	1	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
18	3	--	--	--	--	--	2	--	--	--	--	--	--	--	--	--	--
19	--	--	--	--	--	--	--	--	--	2	--	--	--	2	--	2	2
20	--	1	--	--	1	--	--	1	--	1	--	--	--	1	1	1	1
21	--	--	--	1	3	1	--	3	--	5	--	--	--	5	3	5	5

	85.2	88.1	88.2	89	90	91	92	93	94	95.1	95.2
1	--	--	2	--	--	5	7	9	44	--	--
2	45	--	1	--	--	--	2	--	--	2	--
4	--	--	--	--	--	--	--	1	--	1	--
5	--	--	--	--	--	--	--	--	--	--	--
6	--	6	--	3	6	1	--	--	--	--	--
7	--	2	25	1	1	--	--	--	--	--	--
9	3	--	--	--	--	--	--	--	1	--	--
10	--	--	--	--	--	--	--	--	--	--	--
11	--	--	--	--	--	--	--	--	1	--	--
12	2	--	--	--	--	--	--	--	--	--	--
13	2	--	1	--	--	39	--	--	6	--	--
15	--	--	2	--	--	1	1	--	--	37	--
16	--	--	--	--	--	--	--	--	--	--	--
17	--	--	--	--	--	--	--	--	--	--	--
18	--	--	1	--	--	--	--	--	--	--	--
19	--	--	--	2	--	--	--	--	--	--	--
20	--	1	--	1	1	1	--	--	--	--	1
21	--	3	--	5	3	--	--	--	--	--	--

Unmarked taxa: 3 8 14

II. Parsimony Analysis.

The theory underlying Wagner Parsimony Analysis using Felsenstein's PHYLIP package is given in Section 4.7. The data matrix has to be modified for Wagner analysis (compare Tables 3 and 12); variable scores are recorded as 'P' for polymorphic; missing data is denoted by '?'; the matrix is not listed in columns and rows with decimal notation signifying character state number but data is given as a string of 153 states - 0's, 1's, P's or ?'s. Table 13 gives the equivalent character numbers in the in the parsimony analysis and binary character numbering systems. The problem of different order of data entry producing different tree topologies is addressed by performing two separate analyses: (i) the first, entering data in ascending order of taxon number - the all-states 0 ancestor first, followed by taxon 1, then taxon 2, taxon 3 and so on to taxon 21, (ii) the second, entering data with respect to results of the LEQU. BAS marking procedure. Taxa with no marks being entered first, the remaining taxa in ascending order of marks gained; the one with the least number of marks (lowest scores for unique responsibility for incompatibility) first and the most heavily marked taxon being entered last. Since the most heavily marked taxa will be the ones with the most discordant character sets. Thus the order of incorporation in the tree-building process this time is: all-states 0 ancestor first, then 3, 8, 14, 4, 5, 10, 17, 19, 9, 16, 11, 18, 15, 2, 20, 12, 13, 21, 6, 1 and 7. (Table 11).

Using these criteria for incorporation of taxa in the tree-building process, the two analyses produced two, almost identical trees, both requiring 250 transformation steps. The computer printout gives the structure of the tree, the number of steps required and a matrix showing the number of steps in each character (see Figs. 25 and 27).

From the data in these printouts a full cladogram may be drawn, giving the character state transformations (with the aid of Table 13 Parsimony analysis - character numbering system) - see Fig. 26 drawn from the first analysis - (i) above; from printout data in Fig. 25. In some cases, the combination of character state distribution obtained from the original data matrix, Table 3, the number of steps in each character and the topology of the cladogram allow only one interpretation for the position of the character transformation on the cladogram. Hence character 97 = 56.2 can only be accommodated in the tree given in Fig. 26 by locating the 3 transformations allotted to this character (same Fig.) as follows: one on common stem to taxa 19-21, one on the stem to 1-5 with a reverse transformation for taxa 3 and 4 (see Fig. 26). In other cases the data admit alternative placements of the character transformations in Fig. 26. E.g. character 99 = 57.1 shows derived score for taxa 6, 19-21, 1-5, 9, 11 and 12. Fig. 25 shows 5 transformations allotted to this character. There are at least 3 ways of accommodating this character on the cladogram:-

A. One transformation on the common stem to 6, 19-21; one transformation on the stem to 1-5, and independent transformations in taxa 9, 11 and 12 (see Fig. 26).

B. As per A above, but one transformation on the common stem to 9-13 with reversals in taxa 10 and 13.

C. Also a possibility, one transformation on a common stem to all taxa 1-21, a reversal on the common stem to 9-18 and transformations for 9-13 as described in A or B above.

I consider C to be least likely given ontogenetic evidence for taxa 6 and 21 (see under character 57.1) and there to be no firm basis for choosing between A and B. It should be noted that, in this and other cases where alternative placement of character transformations are possible on the cladogram, it makes no difference to the topology - which is fixed in respect of the total number of steps required (250) and the number of steps given for each character.

To return to the two, almost identical, trees produced by different orders of taxon incorporation. The differences between the two trees are, indeed, minor. The trees in Figs. 25 and 27 are identical except for the arrangement of taxon 1-5, for, starting from the Ancestor we have:

(6 (19 (20, 21))) and ((15 (18 (16 (14,17)))) ((7,8) ((10,11) (12 (9, 13))))).

common to both. The arrangement of 1-5 however is as follows:-

Regime (i) entering data in numerical order of taxa number

(2 (5 (1 (3,4)))) Fig. 25 (and 26)

Regime (ii) data entered in ascending order of marks (LEQU. BAS marking procedure).

(3 (4 (1 (2,5)))). Fig. 27 (and 28)

As mentioned above, both trees are the same length - 250 steps. It is the difference in distribution of the steps amongst the characters which is different - and then only within taxa 1-5. It is interesting to note the influence of the order of incorporation of taxa. In Regime (ii) 1-5 are entered in the following order 3 (first), 4, 5, 2 and 2 (last) which has the effect of link 3 closest to the Ancestor followed by 4 then 1 rather than 2, 5 and 1 under Regime (i). Only four characters are affected:- character 48 (= 26.2), 97 (= 56.2), 150 (= 93) and 152 (= 95.1).

Under Regime (i) ch. 26.2 requires 3 steps; 56.2, 3 steps; 93, 1 step and 95.1, 4 steps. Under Regime (ii) the number of steps becomes 26.2 (4); 56.2 (2); 93 (2) and 95.1 (3). The questions which need answering are which interpretation, in terms of number of steps for each character is the more plausible, and, in particular, is ch. 93 likely to be uniquely derived or not? (see Fig. 29)

<u>Character 26.2</u>

Derived scores in taxa 1, 3, 4, 5, 14, 15, 16 and 17. Given that the resolution of taxa 14-18 is common to both and takes the form that it does, 2 steps are required in placing transformation; either parallel transformation in taxon 15 and on the stem to (16 (14,17)) or transformation on the stem to 14-18 with a reversal in taxon 18. This leaves a single transformation of this character for the group (5 (1 (3,4))) under Regime (i) or, necessarily, a transformation on the stem to 1-5 with a reversal on taxon 2, under Regime (ii).

A single transformation of this character, Regime (i), is in accord with the original polarity designation for this character; a reversal, Regime (ii), argues against the original polarity. The possibility of character reversal is however indicated in one of the interpretations for character transformation in 14-18 (above).

Character 56.2

The apomorphic condition is found in 19, 20, 21, 1, 2 and 5. Only 1 step is needed for 19-21, this leaves 2 steps under Regime (i) - which must be one transformation on the common stem to 1-5 and a reversal on the stem to taxa 3 and 4; one step under Regime (ii) on the common stem to (1 (2,5)). This character provides convincing evidence for the arrangement under Regime (ii), for the reversal required in the Regime (i) arrangement of taxa necessitates the re-appearance of a loss character - a pair of ribs (a change from two pairs of ribs to three pairs) - which is contrary to Dollo's Rule that a character once lost, cannot be regained. The only other possibility being the suppression of a 'gene' 'for' the third pair of ribs, the suppression being absent in the taxa which apparently underwent character reversal to regain the 'lost' ribs.

Character 93.

Under Regime (i) this character is uniquely derived - on the stem leading to (1 (3,4)); under Regime (ii) 2 steps are allocated when it is necessarily transformed on the common stem to 1-5 and undergoes a reversal on the stem to (2,5). Reference to the original character description suggests a very plausible explanation. The configuration of the hand especially the reduction of the 1st and 4th fingers suggests a special condition in taxa 1, 3 and 4 - probably associated with burrowing, but the condition of the hand/fingers in 2 and 5 may either be considered a reversal to a more 'normal' state or, more likely a secondarily derived condition. On reconsideration the fingers in these taxa are probably specialized for rock climbing. Both interpretations are acceptable, the one under Regime (ii) is favoured since it is more informative.

Character 95.1

The apomorphic condition of this character is found in taxa 2, 4, 5 and 15. Under Regime (i) the apomorphic state is independently derived in each of the four taxa; under Regime (ii) it is independently derived in taxon 15 and derived on the stem leading to (4(1(2,5))) with a reversal required for taxon 1. (Alternatively, it may be transformed on the stem to 1-5 and undergo independent reversals in 1 and 3 in both Regimes 1 and 2).

Character 95.1 is clearly a poor character in phylogenetic terms.

Using Wagner Parsimony the discoglossoid taxa are resolved as follows:-

(6 (19 (20, 21). ((3 (4 (1 (2,5)))) ((15 (18 (16 (14,17))))
((7,8) ((10,11) (12 (9,13)))))). ... (Fig. 28).

It is particularly interesting to note that a detailed review of the characters generating two different cladograms from two different taxa-order incorporations favours the scheme in which taxa are incorporated in order of marking score from the LEQU.BAS program.

Table 12.

```
 ******************************** [305,004] OUTPUT    .    ;1

   Wagner parsimony algorithm version 2.0

   22 species, 153  characters

   Character-state data:

   Ancestor      00000 00000 00000 00000 00000 00000 00000 00000 00000 00000
                  00000 00000 00000 00000 00000 00000 00000 00000 00000 00000
                  00000 00000 00000 00000 00000 00000 00000 00000 00000 00000
                  000
    1            10000 10100 00000 11000 01111 00010 01000 11100 00000 01100
                  10000 01100 01101 10000 00001 10000 00001 00000 00111 11111
                  10010 00001 01010 00110 10000 00111 00000 11111 01110 01111
                  100
    2            10000 10100 00000 10000 01000 00000 00000 11100 00000 01000
                  10000 01101 01100 10000 00001 00000 00001 00000 00111 11010
                  10010 00001 01010 00110 10000 00110 00000 01111 10110 01110
                  010
    3            10000 10100 00000 10000 01000 00000 00000 11100 00000 01100
                  10000 01100 01100 10000 00001 00000 00001 00000 00111 10010
                  11010 00001 01010 00110 10000 00110 00000 01111 00110 01111
                  000
    4            10000 10100 00000 10000 01000 00000 00000 11100 00000 01100
                  10000 01100 01100 10000 00001 00000 00001 00000 00111 10010
                  11010 00001 01010 00110 10000 00110 00000 01111 00110 01111
                  010
    5            10000 10100 00000 10000 01000 00000 00000 11100 00000 01100
                  10000 01100 01100 10000 00001 00000 00001 00000 00111 11010
                  1P010 00001 01010 00110 10000 00110 00000 01111 00110 01110
                  010
    6            01000 10010 00000 00100 00000 00000 00000 00001 00000 00011
                  01101 00000 00000 10000 00100 00000 00110 00000 00001 00011
                  00011 00000 00000 00?00 00010 10000 00000 01011 00000 00000
                  000
    7            10001 11000 01111 00011 01111 10101 10011 00111 011P1 10000
                  P0010 00100 11011 01100 11010 01111 10000 11011 00111 10000
                  01100 11111 11111 01010 01101 00110 00000 01111 00110 01000
                  000
    8            10001 11000 01111 00??? ?1111 1???? 100?? ??111 0?1?? 1000?
                  ???10 0???? ????? 01100 110?0 01111 10??? ????1 00111 10000
                  ?11?? ????1 11111 010?? ?1??? 0?1?? ????? ????1 001?? 01000
                  0??
    9            10000 10000 10010 00100 01000 00010 00010 00111 00000 10010
                  00010 00100 01100 10010 00100 01011 11000 10001 10110 10011
                  01100 11001 11111 00010 00101 00110 10111 01111 10111 01000
                  000
   10            10100 11000 00010 00000 11000 00101 00010 00111 00000 10010
                  00010 00100 01001 00010 00100 01011 10000 11000 00111 10000
                  01100 11101 11111 00010 00101 00110 10101 01111 00111 01000
                  100
   11            10000 11000 00010 00100 11000 00101 00010 00111 00100 10010
                  00010 00100 01001 00011 00100 01011 10000 11000 01111 10011
                  01100 11101 11111 00010 0?101 00110 10101 01111 00111 01000
                  100
   12            10000 10000 10010 00100 01000 00010 00010 00111 01000 11010
                  00010 00100 01100 10010 00100 01011 10000 10001 00110 10011
                  01100 10001 11111 00010 00101 01110 10101 01111 00111 01000
                  000
   13            10000 10000 10010 00100 01000 00010 00010 00111 00000 11010
                  P0010 00100 01100 10010 00100 01011 10000 10001 00110 10000
                  01100 10001 11111 00010 00101 00110 10111 01111 10111 01P00
                  100
   14            10010 11100 00010 00010 01010 00101 00100 10100 01111 01100
                  P0000 10100 01001 00100 10000 00111 10000 11101 00111 10000
                  01000 10101 01110 00111 10000 01110 00000 01111 00111 01000
                  000
   15            10010 11100 00011 00000 01000 00101 00000 10100 011?1 01100
                  ?0000 10100 01001 00000 10000 00011 10000 11101 00111 10000
                  01000 10101 01110 00111 10000 01110 00000 01111 00111 01000
                  010
```

```
16          10010 11100 0?011 00?10 010?? ?0101 001?? 10100 011?1 0110?
             ?0000 10100 0??0? 00100 11000 00011 10??0 11101 00111 10000
             ?1000 10101 01110 00111 10000 01110 0000? ????1 001?? 01000
             000
17          10010 11100 00010 00010 01010 00101 00100 10100 01111 01100
             P0000 10100 01001 00100 10000 00111 10000 11101 00111 10000
             01P00 10101 01110 00111 10000 01110 00000 01111 00111 01000
             000
18          10010 11100 00010 00000 01000 00101 00100 10100 01111 01000
             00000 10100 01001 00100 10000 00011 10000 11100 00111 10000
             01010 10101 01110 00111 10000 01110 00000 01111 00111 01000
             000
19          01000 00001 00000 10100 00000 01000 00000 00001 10001 10010
             00000 00110 00000 00000 00100 00010 00010 00000 00001 11011
             00011 00000 00000 10?00 00010 00010 01000 00000 00100 10000
             000
20          01000 00001 00000 10100 00000 01000 00000 00001 10011 10010
             00000 00110 10000 00000 00101 00010 00P10 00000 00001 11011
             00011 00000 00000 10?00 00010 00010 01000 00000 00100 10000
             001
21          01000 00001 00000 10100 00000 01000 00000 00001 10011 10010
             00010 00110 10000 00000 00100 00010 00100 00000 00001 1101P
             00011 00001 00000 11?00 00010 00010 01000 00000 00100 10000
             000
```

Table 13, Parsimony analysis - character numbering system.

Abbreviations:

Parsimony analysis character number = PACN

Binary character number = BCN

PACN	BCN	PACN	BCN	PACN	BCN
1	1	26	12.3	51	-29
2	2.1	27	13.1	52	30
3	2.2	28	13.2	53	31
4	3.1	29	14.1	54	32.1
5	3.2	30	14.2	55	32.2
6	4.1	31	15.1	56	32.3
7	4.2	32	15.2	57	33
8	5.1	33	16	58	34.1
9	5.2	34	17.1	59	34.2
10	5.3	35	17.2	60	35.1
11	6.1	36	18.1	61	35.2
12	6.2	37	18.2	62	36.1
13	7	38	19.1	63	36.2
14	8.1	39	19.2	64	37
15	8.2	40	20.1	65	38
16	8.3	41	20.2	66	39.1
17	8.4	42	21	67	39.2
18	9	43	22	68	40.1
19	10.1	44	-23	69	40.2
20	10.2	45	24	70	41
21	10.3	46	25	71	42.1
22	11.1	47	26.1	72	42.2
23	11.2	48	26.2	73	43
24	12.1	49	27	74	44
25	12.2	50	38	75	45.1

PACN	BCN	PACN	BCN	PACN	BCN
76	45.2	106	61.1	136	-82
77	45.3	107	61.2	137	83.1
78	46	108	62.1	138	83.2
79	47.1	109	62.2	139	84
80	47.2	110	63.1	140	85.1
81	48.1	111	63.2	141	85.2
82	48.2	112	64	142	-86
83	-49	113	65	143	87
84	-50	114	66.1	144	-88.1
85	51.1	115	66.2	145	-88.2
86	51.2	116	67	146	-89
87	51.3	117	68	147	90
88	51.4	118	-69	148	91
89	51.5	119	70.1	149	92
90	52.1	120	70.2	150	93
91	52.2	121	-71	151	-94
92	52.3	122	72	152	95.1
93	53	123	-73	153	95.2
94	54	124	74.1		
95	55	125	74.2		
96	56.1	126	75		
97	56.2	127	76		
98	56.3	128	-77		
99	57.1	129	-78.1		
100	57.2	130	-78.2		
101	-58	131	-79.1		
102	59.1	132	-79.2		
103	59.2	133	-80.1		
104	60.1	134	-80.2		
105	60.2	135	81		

```
4
!
!  5
!  !
!  !  2
!  !  !
!  !  !  Ancestor
!  !  !  !
!  !  !  !  6
!  !  !  !  !
!  !  !  !  !  19
!  !  !  !  !  !
!  !  !  !  !  !  20
!  !  !  !  !  !  !
!  !  !  *--*--*--*--21
!  !  !  !
!  !  !  !              17
!  !  !  !              !
!  !  !  !              *--14
!  !  !  !              !
!  !  !  !              *-----16
!  !  !  !              !
!  !  !  !              *--------18
!  !  !  !              !
!  !  !  !              *-----------15
!  !  !  !              !
!  !  !  !              !              7
!  !  !  !              !              !
!  !  !  !              !              *-- 8
!  !  !  !              !              !
!  !  !  !              !              !     12
!  !  !  !              !              !     !
!  !  !  !              !              !     !  9
!  !  !  !              !              !     !  !
!  !  !  !              !              !     *--*--13
!  !  !  !              !              !     !
!  !  !  !              !              !     !        10
!  !  !  !              !              !     !        !
!  *--*--*--------------*--------------*-----*--------*--11
!  !
!  *------------------------------------------------------ 1
!  !
L--*--------------------------------------------------------- 3

   remember, this is an unrooted tree!

requires a total of     250.000

steps in each character:
          0    1    2    3    4    5    6    7    8    9
     *--------------------------------------------------
   0!          1    1    1    1    1    2    2    2    1
  10!     1    1    1    1    1    3    2    1    3    2
  20!     1    1    1    2    3    2    1    1    2    2
  30!     2    1    1    1    1    1    2    1    1    1
  40!     2    1    3    3    3    3    2    4    3    2
  50!     1    5    1    1    2    1    1    1    2    1
  60!     1    2    1    2    1    3    3    1    2    1
  70!     1    2    2    2    1    2    1    1    2    2
  80!     1    1    1    3    2    1    1    2    1    1
  90!     3    1    1    1    1    2    2    3    1    5
 100!     6    1    3    2    3    1    1    3    2    1
 110!     2    1    1    1    1    1    1    2    2    1
 120!     1    2    1    1    1    1    1    2    1    2
 130!     1    1    1    1    1    1    1    2    1    2
 140!     2    2    1    2    1    2    1    1    2    1
 150!     1    3    4    1
```

Fig. 25.

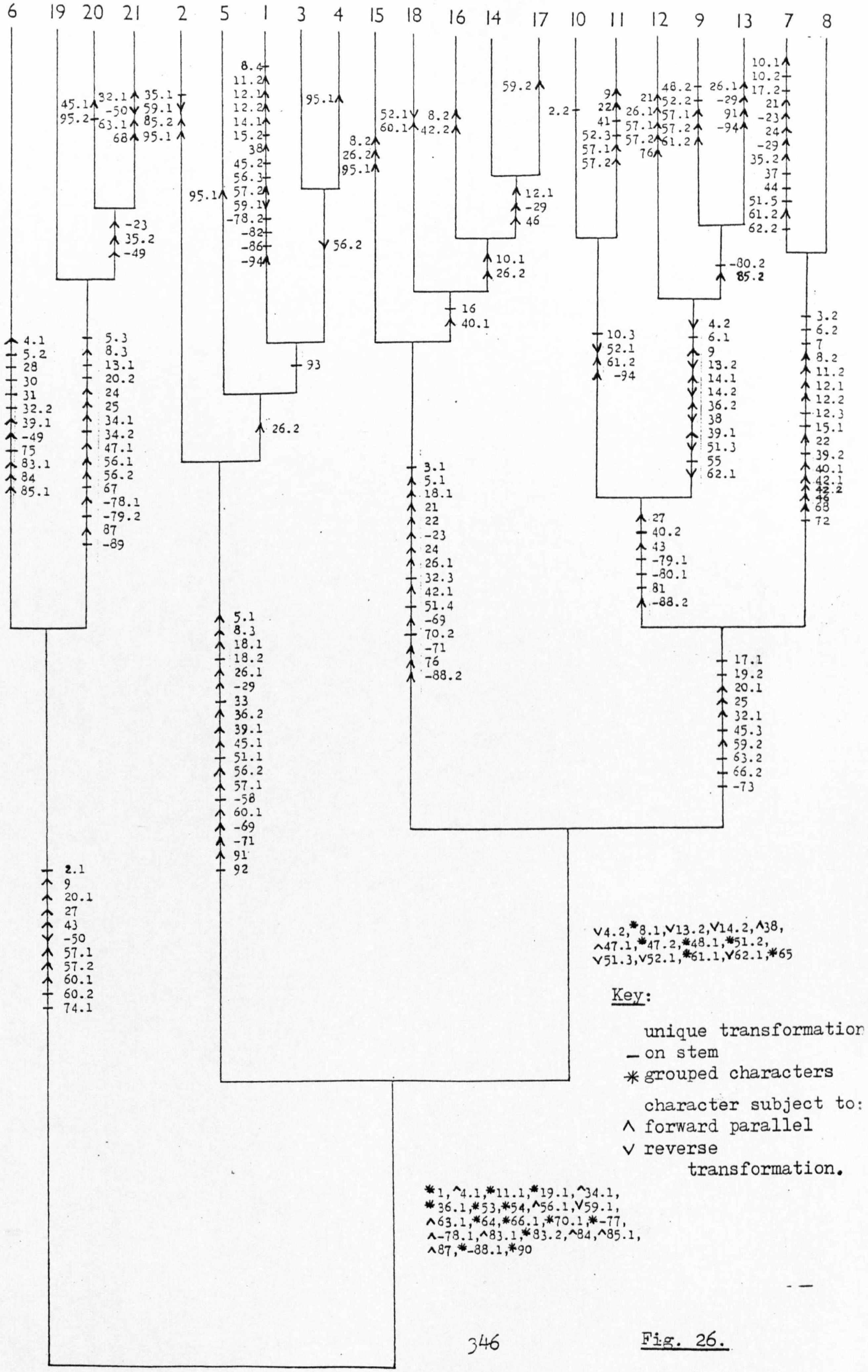

6
19
20
21
2
5
1
3
4
15
18
16
14
17
10
11
12
9
13
7
8
45.1
95.2
32.1
-50
63.1
68
35.1
59.1
85.2
95.1
-23
35.2
-49
8.4
11.2
12.1
12.2
14.1
15.2
38
45.2
56.3
57.2
59.1
-78.2
-82
-86
-94
95.1
56.2
95.1
93
26.2
8.2
26.2
95.1
52.1
60.1
8.2
42.2
59.2
12.1
-29
46
10.1
26.2
16
40.1
2.2
9
22
41
52.3
57.1
57.2
21
26.1
57.1
57.2
76
48.2
52.2
57.1
57.2
61.2
26.1
-29
91
-94
10.1
10.2
17.2
21
-23
24
-29
35.2
37
44
51.5
61.2
62.2
-80.2
85.2
10.3
52.1
61.2
-94
4.2
6.1
9
13.2
14.1
14.2
36.2
38
39.1
51.3
55
62.1
3.2
6.2
7
8.2
11.2
12.1
12.2
12.3
15.1
22
39.2
40.1
42.1
42.2
46
68
72
4.1
5.2
28
30
31
32.2
39.1
-49
75
83.1
84
85.1
5.3
8.3
13.1
20.2
24
25
34.1
34.2
47.1
56.1
56.2
67
-78.1
-79.2
87
-89
27
40.2
43
-79.1
-80.1
81
-88.2
3.1
5.1
18.1
21
22
-23
24
26.1
32.3
42.1
51.4
-69
70.2
-71
76
-88.2
5.1
8.3
18.1
18.2
26.1
-29
33
36.2
39.1
45.1
51.1
56.2
57.1
-58
60.1
-69
-71
91
92
17.1
19.2
20.1
25
32.1
45.3
59.2
63.2
66.2
-73
2.1
9
20.1
27
43
-50
57.1
57.2
60.1
60.2
74.1
∨4.2,✱8.1,∨13.2,∨14.2,^38,
^47.1,✱47.2,✱48.1,✱51.2,
∨51.3,∨52.1,✱61.1,∨62.1,✱65
Key:
unique transformation
— on stem
✱ grouped characters
character subject to:
∧ forward parallel
∨ reverse
transformation.
✱1,^4.1,✱11.1,✱19.1,^34.1,
✱36.1,✱53,✱54,^56.1,∨59.1,
^63.1,✱64,✱66.1,✱70.1,✱-77,
^-78.1,^83.1,✱83.2,^84,^85.1,
^87,✱-88.1,✱90

Fig. 26.

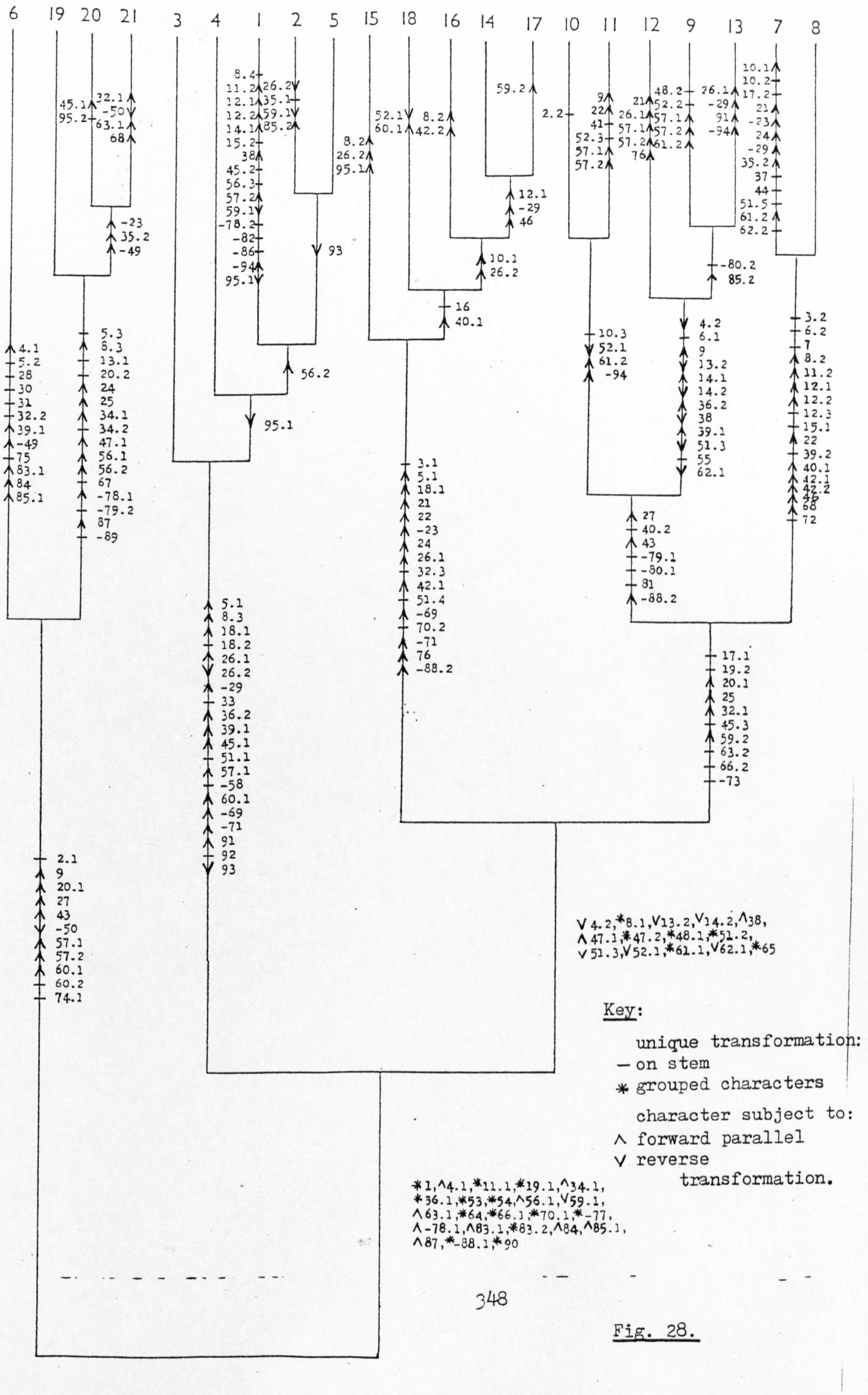
```
 2
!
!    1
!  !
!  !  21
!  !  !
!  !  *--20
!  !  !
!  !  *-----19
!  !  !
!  !  *-------- 6
!  !  !
!  !  *----------- Ancestor
!  !  !
!  !  !              11
!  !  !              !
!  !  !              *--10
!  !  !              !
!  !  !              !     12
!  !  !              !     !
!  !  !              !     !   9
!  !  !              !     !  !
!  !  !              *-----*--*--13
!  !  !              !
!  !  !              !               7
!  !  !              !              !
!  !  !              *--------------*-- 8
!  !  !              !
!  !  !              !                    15
!  !  !              !                    !
!  !  !              !                    !  16
!  !  !              !                    !  !
!  !  !              !                    !  !  14
!  !  !              !                    !  !  !
!  !  !              !                    !  *--*--17
!  !  !              !                    !  !
!  !  *--------------*--------------------*--*--------18
!  !  !
!  !  *-------------------------------------------------- 3
!  !  !
!  *--*----------------------------------------------------- 4
!  !
L--*----------------------------------------------------------- 5

remember, this is an unrooted tree!

requires a total of    250.000

steps in each character:
         0   1   2   3   4   5   6   7   8   9
     *----------------------------------------
    0!       1   1   1   1   1   2   2   2   1
   10!   1   1   1   1   1   3   2   1   3   2
   20!   1   1   1   2   3   2   1   1   2   2
   30!   2   1   1   1   1   1   2   1   1   1
   40!   2   1   3   3   3   3   2   4   4   2
   50!   1   5   1   1   2   1   1   1   2   1
   60!   1   2   1   2   1   3   3   1   2   1
   70!   1   2   2   2   1   2   1   1   2   2
   80!   1   1   1   3   2   1   1   2   1   1
   90!   3   1   1   1   1   2   2   2   1   5
  100!   6   1   3   2   3   1   1   3   2   1
  110!   2   1   1   1   1   1   1   2   2   1
  120!   1   2   1   1   1   1   1   2   1   2
  130!   1   1   1   1   1   1   1   2   1   2
  140!   2   2   1   2   1   2   1   1   2   1
  150!   2   3   3   1
```

Fig. 27.

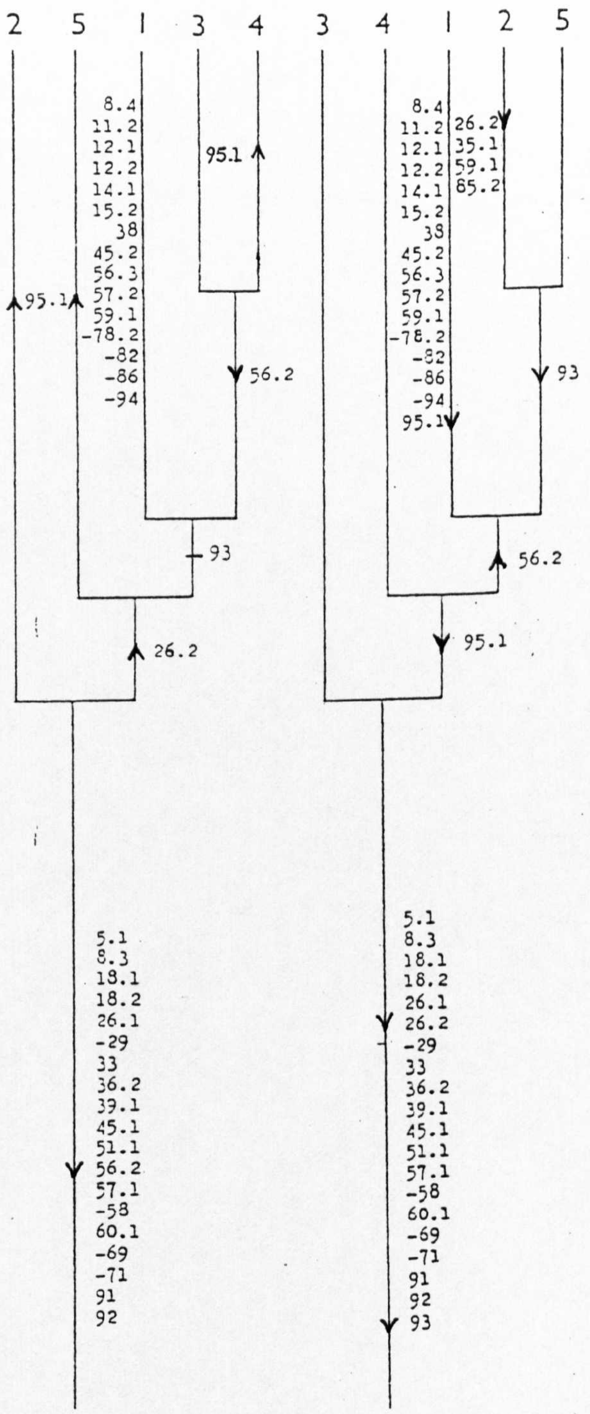


Key:

unique transformation:
— on stem
* grouped characters

character subject to:
∧ forward parallel
∨ reverse
transformation.

Fig. 28.



	26.2	56.2	93	95.1
1	1	1	1	0
2	0	1	0	1
3	1	0	1	0
4	1	0	1	1
5	1	1	0	1
6	0	0	0	0
7	0	0	0	0
8	0	0	0	-
9	0	0	0	0
10	0	0	0	0
11	0	0	0	0
12	0	0	0	0
13	0	0	0	0
14	1	0	0	0
15	1	0	0	1
16	1	0	0	0
17	1	0	0	0
18	0	0	0	0
19	0	1	0	0
20	0	1	0	0
21	0	1	0	0

<u>Key</u>:

— unique transformation

character subject to:
∧ forward parallel } transformation.
∨ reverse

Fig. 29.

CONCLUSIONS

The first and most striking conclusion - evident even before translating taxa numbers back into names - is that the two methods of data analysis; the LEQU. BAS compatibility analysis and the PHYLIP Wagner parsimony analysis of 153 binary characters for the 21 discoglossoid taxa examined, yield *almost identical trees*. The likelihood of such close agreement occurring purely by chance is truly negligible. In the case of the alternative resolutions in the compatibility analysis, the *only* difference between Resolutions A and B is in the arrangement of taxa 19, 20 and 21: A gives 21 (19, 20) whereas B gives 19 (20, 21). Under parsimony analysis, changing the order in which taxa are incorporated into the tree during the tree-building process gives 19 (20, 21) in both cases, but two different arrangements for taxa 1-5, viz., (2(5(1(3,4)))) and (3(4(1 (2,5)))). For taxa 1-5 compatibility analysis gives: ((2,5) (1(3,4))). The structure of the remainder of the tree *is* identical under the two methods.

Translating taxa numbers back into scientific names (Appendix I : Table 14) it soon becomes apparent that the currently recognised genera are valid (monophyletic): 6 = *Ascaphus*; 19-21 = *Leiopelma*; 14-18 = *Discoglossus*; 9-13 = *Bombina* and 7-8 = *Barbourula*. The following conclusions are also drawn (numbering is with reference to the specific objectives of this investigation listed in Section 2 Aims and Objectives):-

1. The family Discoglossidae is a monophyletic group and therefore constitutes a phylogenetically natural group (sensu Wiley, 1981).

2. Similarly, each of the discoglossoid genera, listed above are monophyletic and so each is a phylogenetically natural group.

3. *Ascaphus* and *Leiopelma* are a sister pair i.e. they are more closely related to one another than either is to any of the discoglossid genera, in that they share some uniquely derived characters in common. It therefore seems more appropriate to continue to recognise a single family, the

Leiopelmatidae, to accommodate the two genera. Nonetheless, the relationship between the Leiopelmatidae and Discoglossidae - the question of the monophyly of the Discoglossoidea - remains open (see p. 15 Aims and Objectives).

Within the Discoglossidae two main divisions are noted - (a) the genus Alytes on the one hand, which is sister to (b) a well-defined suprageneric group comprising Bombina - Barbourula - Discoglossus on the other, in which Discoglossus is sister to a subordinate group comprising Bombina + Barbourula. Barbourula is a well characterized genus distinct from Bombina. Bombina may be subdivided into two groups: large Bombina (B. maxima and B. microdeladigitora - B. fortinuptialis,not examined, is probably referable to this group) and small Bombina (B. bombina, B. variegata and B. orientalis). Use of Dubois' subgenus Grobina Dubois 1986 is appropriate since the genus Bombina is a well-supported monophyletic group.

There is little reason to change the classification of the discoglossoid frogs at these levels since these results are consistent with the present classification. However, it would be appropriate to subdivide the family Discoglossidae into 2 subfamilies: the Alytinae Fitzinger 1843 (Alytes only) and the Discoglossinae Gunther 1858 (1845) (Bombina, Barbourula, Discoglossus). The Discoglossinae may be further divided into the tribes Bombinatorini (Bombina + Barbourula) and Discoglossini (Discoglossus only) Gunther 1858 (1845); following application of names after Dubois (1987). These additions are appropriate because each group is well-defined by large numbers of derived characters. Similarly, I suggest the Leiopelmatidae should be subdivided into two subfamilies the Ascaphinae (for Ascaphus) and the Leiopelmatinae (for Leiopelma,but see also Discussion). In this way the relationship between Ascaphus and Leiopelma is acknowledged - closer to one another than to any of the discoglossids, yet their distinctiveness (and geographical separation) is also acknowledged by the recognition of the two subfamilies.

Species-level (within-genus) relationships.

The most robust portion of the tree in respect of relationships within genera is the Discoglossinae (Bombina, Barbourula and Discoglossus) - compatibility and parsimony analysis yielding identical trees. In Bombina B. maxima (10) is sister to B. microdeladigitora (11) and B. orientalis (12) is primitive, and more closely related, to the two European Bombina B. bombina (9) and B. variegata (13) which are a sister pair. Barbourula kalimantenensis (8), in respect of this analysis, lacks any derived characters to define it, but this is probably because the character set for this species included a large amount of missing data. Where data were available B. kalimantanensis showed the same character state as B. businangensis (7) - except for the ones marked on the stem to taxon 7 on cladogram p.346- these are either unique to B. busuangensis or not known for B. kalimantanensis. I consider B. kalimantanensis to be the sister species of B. busuangensis not its ancestor (which is the alternative conclusion - taxon 8 lacking any derived characters of its own, see Discussion). In Discoglossus, D. montalentii (15) emerges as the most primitive species (as evidenced by its lacking the articulation between the zygomatic ramus of the squamosal and the maxilla, and in possessing a pointed anterior ramus to its pterygoid, whereas all other Discoglossus have the articulation and a truncate anterior ramus to the pterygoid respectively). The arrangement, in order from the most primitive to the most derived taxon in Discoglossus is therefore D. montalentii (15) - D. sardus (18) - D. nigriventer (16) - with D. galganoi (14) either sister to, or conspecific with, D. pictus (17). In respect of the characters examined for this analysis taxa 14 and 17 were identical except for a variable score for ch. 59.2 in taxon 17; the difference between the distal end of the ribs on the 2nd presacral vertebra being flared posteriorly only or anteriorly and posteriorly is, most likely, attributable to intraspecific variation anyway. (see Discussion for further comment on the status of D. galganoi/D. pictus).

In the case of *Alytes* three possible resolutions of their relationships are suggested on the basis of the present osteological data:-

1. In order, primitive to derived: *A. muletensis* (2) - *A. o. maurus* (5) - *A. cisternasii* (1) - with *A. o. obstetricans* (3) and *A. o. boscai* (4) as a sister pair.
2. In order primitive to derived: *A. o. obstetricans* (3) - *A. o. boscai* (4)- *A. cisternasii* (1)- with *A. muletensis* (2) sister to *A. o. maurus* (5).
3. Two groups: *A. muletensis* (2) sister to *A. o. maurus* (5) and *A. cisternasii* (1) primitive to the sister pair *A. o. obstetricans* (3) and *A. o. boscai* (4).

While an examination of the characters seemed to favour scheme 2 (Section E/II Parsimony Analysis) it is clear that scheme 1 (derived from a parsimony analysis) and scheme 3 (from compatibility analysis) are essentially very similar. In fact, there is insufficient evidence for a realistic appraisal of the interspecific relationships of members of the genus *Alytes*. Relationships remain equivocal but two possible groups are likely - *A. muletensis* and *A. o. maurus*; *A. cisternasii*, *A. o. obstetricans* and *A. o. boscai*. Further data is needed to help resolve the relationships of this genus (see Discussion).

The available data suggest two alternative possibilities regarding the relationships of *Leiopelma* spp. Either *L. archeyi* (19) primitive to the sister pair *L. hamiltoni* (20) and *L. hochstetteri* (21) or, *L. hochstetteri* (21) primitive to *L. archeyi* (19) and *L. hamiltoni* (20) - (see Discussion).

The genus *Ascaphus* is monotypic and includes only *A. truei* (6).

DISCUSSION

Interpreting the evolutionary history of a group from a cladogram derived from an analysis of the morphological features of members of the group is a hazardous business. Cladograms are two-dimensional whereas the evolution of a group of organisms, considered as the changes that occur during their history, is multidimensional. Evolutionary change may be considered at gene, individual or populational levels (Section 3.2). The evolutionary relationships of a group are an historical, and therefore a coarse-level, overview of the fine-level changes that have occurred in the lineages leading to the modern species of which the study-group specimens are a representative sample. Furthermore, the hypothesis and discussion of the evolutionary relationships of the discoglossoid frogs outlined here is based on an analysis of a single system - the skeleton (thereby providing only a partial view of the total evolutionary picture). Nonetheless, while for some parts of the cladogram evidence of relationship remains weak, for others a very clear pattern of relationships emerges; although all, of course, are hypotheses of relationship which may be tested against other cladograms derived from different data.

This discussion is concerned with:- (a) an evolutionary interpretation of the sister group relationships in the discoglossoid frogs suggested by the cladograms in the present study, (b) comparisons with other cladograms or comment on relationships in previous work with special attention to results obtained from the relatively recent application of immunological methods and (c) a brief overview comment on the historical zoogeography of the discoglossoid frogs.

(a) An evolutionary interpretation of the present work.

The modern Discoglossidae are a monophyletic group in the sense that they share a large set of apomorphic characters which are not found in either *Ascaphus* or *Leiopelma*. In the absence of knowledge of the distribution of some of these characters in the remainder of the Anura it would be more accurate to describe the Discoglossidae as a provisionally monophyletic group (although in a sense the description of any group can only ever be regarded as comprising a series of provisional apomorphies - a hypothesis which is open to testing). As mentioned in the Conclusions section, each of the currently recognized modern discoglossid genera is a clearly distinct, monophyletic group. In this Discussion section I will provide evidence to support the opinion that each genus comprises a group(s) of relatively recent species/subspecies which are members of an ancient lineage. Thus the individual discoglossid genera may be thought of as relict groups which are only distantly related to one another. In each case the genus consists of a crown group of closely related recent species (see below: immunological data). The most robust (well-supported part of the cladogram with respect to supraspecific sister-group relationships is the part concerning Bombina and Barbourula. Bombina, as noted in the Conclusions, is divisible into two groups: large Bombina (subgenus Grobina Dubois 1986) and smaller Bombina, and Bombina (s.l) is sister to Barbourula. Unfortunately this is where the more confidently hypothesized discoglossid relationships end. While the monophyly of the Discoglossidae is clear and the relationship of Bombina and Barbourula (= Bombinatorini) is well supported, the relationships of Alytes and Discoglossus are less certain. The data presented in the present study seem to provide slightly more support for a Bombina - Barbourula - Discoglossus grouping than for two groups: Alytes with Discoglossus; Bombina with Barbourula. However, it is evident that further data are required to provide a firmer indication of relationships. On the basis of current evidence it seems likely that the relationships of Alytes and Discoglossus are likely to remain equivocal; I would however suggest that while there are some discordant potential synapomorphies for Alytes and Discoglossus, these may prove to be characters derived in parallel rather than uniquely derived characters. I therefore suggest, after an examination of the supporting data, the balance of the evidence is in favour of grouping Discoglossus with Bombina and Barbourula.

In the Leiopelmatidae Ascaphus and Leiopelma are only very weakly related to one another. The shared derived characters indicating this relationship probably look more convincing than is actually the case - the picture of relationships that emerges is probably of one that is 'cleared up by extinctions' where many fossil taxa at successively more inclusive sister group levels between Ascaphus and Leiopelma have become extinct, leaving those characters which would have been indicative of such sister group relationships as evidence of Ascaphus - Leiopelma as a sister pair. This principle of extinctions apparently 'cleaning up' the overall picture of relationships - also applies to the discoglossid genera. In fact it may not only provide an unrealistically clear pattern of relationships, it may also confuse, as in the case of Discoglossus, producing set of conflicting characters providing equivocal support for different theories of relationship. The important point regarding Ascaphus and Leiopelma is that they are more closely related to one another than either is to the Discoglossidae.

The species-level relationships within the discoglossid genera and in Leiopelma are, in general, as given under Conclusions. Further discussion on species relationships is included below when other data providing further insight on such relationships is reviewed.

(b) Comparison with previous work.

Boulenger (1897: 124), as ever, made one of the most perceptive comments on the relationships of three of the discoglossoid genera (Alytes, Bombina and Discoglossus), when he said "The relationships of the three genera cannot be well expressed in a linear arrangement". Discoglossus he regarded as "unquestionably the most generalized" and Bombina and Alytes "almost equally related to it, the latter being, on the whole more affine to Discoglossus...". He paid particular attention to osteological characters in reaching this view. On the same page he commented that he considered *Leiopelma*, then known only from *L. hochstetteri*, to be "closely allied" to *Alytes*.

Noble (1922) was convinced of the primitive status of *Ascaphus*. In 1924 he assigned both *Ascaphus* and *Leiopelma* to a new family which he called the Liopelmidae (= Leiopelmatidae). Fejervary had reached a similar opinion, at least in respect of *Ascaphus* for which he had created the family Ascaphidae. In 1931 Noble placed *Ascaphus* and *Leiopelma* in a separate suborder Amphicoela, identified as the most primitive - at the base of the anuran phylogenetic tree (Noble 1931: 485). Noble's work exerted a considerable influence on future analyses and discussion on anuran phylogeny. In 1924, in the original description of *Barbourula*, Taylor and Noble commented that Barbourula (*B. busuangensis*) is "strikingly different" from other members of the Discoglossidae" ... but more closely allied to the eastern Asiatic forms than to any of the others" (i.e. to *Bombina maxima* and *B. orientalis*). Myers (1943: 150) agreed with Taylor and Noble saying that superficial observation seemed to confirm their opinion but nonetheless noted that *Barbourula* lacks the "gay belly marbling of *Bombina* ... and it is very different in many other ways". Thus even as early as 1931 an apparently accurate picture of discoglossoid relationships was available (albeit largely based on shared primitive characters): *Ascaphus* and *Leiopelma* grouped together in Leiopelmatidae; *Leiopelma* "closely allied" to *Alytes*, and the Discoglossidae with *Alytes* and *Discoglossus* "more closely affine" fide Boulenger (1897) and *Barbourula* "more closely allied" to (eastern) *Bombina* fide Taylor and Noble (1924). Extend the time-frame forward to 1954 and we have Inger (1954: 209) commenting that the Taylor/Noble suggestion concerning the relationships of *Bombina* - *Barbourula* are based as much upon geographical considerations as on anatomical evidence. Based on two characters - the condition of the sacrococcygeal articulation (moncondylar/bicondylar) and the presence/absence of an adductor longus muscle in the thigh - Inger concluded that Barbourula is "intermediate between Bombina and Discoglossus": - Bombina(monocondylar a.1. muscle absent) - Barbourula (monocondylar: a.1. present) - Discoglossus (bicondylar: a.1. present). Inger followed Noble (1922, 1924) in interpreting the Bombina condition as primitive.

Therefore, by 1924 an hypothesis of the intergeneric relationships of the discoglossoid frogs is available which is much the same as one of the possible phylogenies considered during the analysis phase of this investigation. By 1954 a scheme is available which mirrors the phylogeny suggested by the present study, in that Inger's scheme has Barbourula intermediate between Bombina and Discoglossus, whereas the present scheme has Bombina and Barbourula as a sister pair with Discoglossus as sister-group to the Bombina-Barbourula pair. What progress, if any, has therefore been made? The main point about the earlier comments on discoglossoid relationship is that they are poorly founded, the descriptions of relationship - "the most generalised", "almost equally related", "on the whole more affine", "(more) closely allied" and "intermediate between,..." are indicative of opinions based on phenetic similarity or limited sets of characters whose polarity is often guessed at, with a low level of confidence. In addition, the present investigation has involved the examination of more modern discoglossid taxa than any previous investigation (this includes the work of Sanchiz, primarily unpublished although some indication of the scope of his work was given in an abstract - 1985 and in Sanchiz 1984; also the work of Cannatella 1985). The present study therefore has been able to provide, for the first time, a phylogenetic analysis of almost all the currently described discoglossoid taxa thereby providing a firmer basis for an assessment of their phylogenetic relationships than has previously been possible. The more recent work on discoglossoid relationships unfortunately seems, in each case, to include some serious logical flaws. Briefly, Wassersug (1980) in his study on internal oral features of anuran tadpoles suggested that a case could be made for "grouping *Ascaphus* closely with the discoglossids", further suggesting on the basis of the microanatomy of the food traps a "morphological sequence...." (in a section on evolutionary trends in the Discoglossidae) "going from *Ascaphus* to *Bombina* to *Alytes* and *Discoglossus*". The use of tadpoles to derive phylogenies is still contentious. While they must clearly share the same genotype as the adult it may well be a different part of the genotype which is expressed in the larval features; it is well known that phylogenies derived from larval morphology differ from those derived from the morphology of the adult stage. Larvae are effectively feeding machines; most if their efforts are concerned with feeding and increasing their size, an analysis of their morphology is more likely to reflect adaptations to feeding and their ecological niche than the evolutionary history of the group. Sanchiz (1985) referred to a larval/adult intermediate or sintetotype as a hypothetical ancestor for determining character polarities - being an abstract he did not explain this system fully. His discoglossid phylogeny grouped *Alytes* with *Discoglossus* and *Bombina* with *Barbourula*. His system seems to be flawed for similar reasons to the Wassersug (1980) study. Cannatella kindly provided a xerox of his thesis, Cannatella (1985), as yet unpublished as a formal paper. Sadly, with respect to the discoglossoid part of his work it is seriously logically flawed. He maintains evolutionary direction of character states in his thesis are determined by outgroup comparison. He says that this was done at two levels: "at the first level, salamanders are the appropriate outgroup for anurans" (a view with which I entirely agree, this being the approach in the present thesis); he then goes on to point out the difficulties in comparing some features but instead of leaving such characters as non-polar, as in the present work, he uses them to justify the use of *Ascaphus* and *Leiopelma* as a pseudo-outgroup, primarily on the basis of four characters. He then used these four characters - two of which place *Ascaphus* primitive to *Leiopelma* and 'other frogs' (root of facial nerve passing through anterior acoustic foramen into the auditory capsule while still fused to auditory nerve/nerves entering auditory capsule in *Leiopelma* + others; jaw suspension with true basal articulation/pseudobasal articulation in *Leiopelma* + others), and two grade-characters which he misinterpreted as synapomorphies (nine presacral vertebrae in *Ascaphus* and *Leiopelma* / eight in other frogs; tail-wagging muscles present in *Ascaphus* and *Leiopelma* / absent in other frogs) - to justify the use of *Ascaphus* and *Leiopelma* as "outgroups to make decisions about polarities within the primitive frogs". When states differ in these two genera *Ascaphus* was *a priori* regarded as having the primitive state. I can do no better than Cannatella in describing the consequences of such an action:- "I realize that such an approach precludes the discovery of autapomorphies for *Ascaphus* because any state in this species will be considered as *prima facie* primitive. Also, it will be difficult to identify synapomorphies of *Ascaphus* and *Leiopelma* if any exist". (Cannatella had only nine discoglossoid taxa available for study *Ascaphus truei*, *Leiopelma*, *hochstetteri*, *Alytes obstetricans*, *Barbourula busuangensis*, the three smaller *Bombina* species plus *B. maxima* and *Discoglossus pictus*). He has *Ascaphus* primitive to *Leiopelma* and the same arrangement of the discoglossid genera as Sanchiz; *Alytes* with *Discoglossus* ("poorly supported" p. 265, and "no autopomorphies for *Alytes*" p. 266, and *Bombina* with *Barbourula*, but no resolution (a polychotomy) for *Bombina* species - his Fig. 49. The most alarming result of Cannatella's work is his suggestion that the Discoglossidae is paraphyletic based on three apparent synapomorphies:- loss of an epipubis muscle which is later "regained" in the Pipidae; development of the bicondylar condition of the sacrococcygeal articulation and the appearance of an episternum. All three as Cannatella says are subject to homoplasy; the first is a loss character and the remaining two are notoriously subject to homoplasy in the remainder of the Anura (see Lynch 1973 and Trueb 1973, also pers. obs.).

I will now compare the scheme obtained in the present study with the results obtained from the relatively recent application of immunological methods.

One of the first attempts at using an immunological evidence for obtaining an assessment of the relationship of the discoglossid frogs was that of Lanza, Cei andCrespo (1975) and again in (1976). Using Libby's photronreflectrometric technique Lanza et al concluded that Discoglossus pictus and D. sardus should be regarded as separate species rather than subspecies; that Discoglossus should be placed, on its own, in the Doscoglossidae and that Alytes and Bombina should be placed in a separate family which they called the Bombinidae. This result is not only different from the present study it is also at variance with the work of Sanchiz and of Cannatella. Libby's technique is a quantitative measurement of a precipitin reaction, which Maxson and Szymura (1984) regarded as more a qualitative study of the serum proteins. Maxson and Szymura (ibid.) pointed out the advantages of using their method - microcomplement fixation (MC'F) of a single homologous protein - namely, it provides a quantitative estimate of amino acid sequence differences between the albumins studied, thus allowing the sequence divergence of the single protein in the species being studied to be compared rather than making an aggregate averaging of general similarities of some unspecified mixture of serum protein as in the case of the Lanza et al. study. The MC'F technique permits estimation of divergence (separation) time between genera and species (Maxson and Szymura 1979). Data are given in immunological distance units (IDU'S). In the case of albumin it has been estimated that 1 IDU is approximately equivalent to 1 amino acid difference between the albumins compared (Maxson and Wilson 1974) and that 10 such differences accumulate every 5.5 million years (Wilson et al. 1977) - the so-called "albumin clock". Maxson and Szymura (1984) concluded that their data did not support the Lanza et al (1975, 1976) scheme, instead their evidence suggests that Bombina and Discoglossus shared a common lineage after the Alytes lineage had become independent. They found that the albumin differentiation between the three genera is "substantial" - corresponding to a Cretaceous divergence time, (ca 85-92 million years b.p. and a divergence of late Cretaceous 69-75 m.y.b.p. for Bombina and Discoglossus), and concluded that it is not possible to "determine unequivocally a closer relationship between any two of the three lineages". Nonetheless, it is of particular interest to note that the Maxson - Szymura scheme of relationships Bombina with Discoglossus on a common lineage with Alytes primitive is in accord with the phylogeny put forward in this osteological study. (Neither Lanza et al, 1975, 1976 nor Maxson and Szymura 1984, had Barbourula available for their work).

The MC'F tests of Maxson and Szymura (1979, 1984) yielded particularly interesting results with respect to the intrageneric relationships of Alytes, Bombina and Discoglossus. Maxson and Szymura show that the distances within Bombina and Discoglossus vary from 0 to 21 and in Alytes 0 to 27, indicating speciation in the Miocene and Pliocene (and m.y.b.p. respectively). For A. cisternasii the IDU value is 27 with respect to A. obstetricans which indicates a divergence time of approximately 16 million years; for A. muletensis the figure is 12 or approximately 7 million years before present; for A. obstetricans from different areas of Europe-Spain, France, Germany the value is zero suggesting no divergence between A. o. obstetricans and A. o. boscai. In the case of Moroccan Rif Mountains Alytes (A.o. maurus), the value is only 3 - a divergence of 1.8 million years - which is of the same order as Bombina variegata from B. bombina; yet Maxson and Szymura (1984) suggest such a difference is an indication of conspecific populations, while the same authors (1979) suggest that the same value (3) for the two Bombina is equivalent to a divergence time of 1 million years and is similar to the differentiation reported for two closely related N. American Cricket frogs genus Acris. They (1979) give a distance of 15-20 IDU for B. orientalis against B. bombina equivalent to a separation of 11 million years. In their 1984 paper they give a distance of 16 IDU *B. maxima* - *B. bombina* similarly giving a separation of ca 11 million years and suggest, on electrophonetic evidence that *B. orientalis* and *B. maxima* are as different from one another as each is from *B. bomina*. *Discoglossus 'pictus'* from Spain (= *D. galganoi*) and *D. sardus* from Sardinia are 9 IDU apart, equivalent to a separation of some 5 million years. *D. 'pictus'* from Spain and N. Africa average 16.5 IDUS - a separation of some 9-10 million years; Maxson and Szymura therefore conclude (confirm) they are not conspecific. Thus the divergence times, based on the MC'F immunological data, provide support for the congruent schemes of relationship derived from the compatibility and parsimony analysis of the present osteological data.obtained from *Bombina* but do not help decide between the schemes obtained for *Alytes*, being at variance with all three suggested schemes (see Conclusions). In *Bombina*, the osteological data suggests *B. maxima* is more different from *B. orientalis* than *B. orientalis* is from *B. bombina*. In *Alytes*, the osteological data suggests a closer relationship for *A. cisternasii* and *A. obstetricans*, and a relatively more distant relationship for *A. obstetricans* and *A. muletensis*. Clearly, the support for the cladograms derived from osteology are weak in the case of relationships within *Alytes*; further data are required to satisfactorily resolve this problem. In the case of *Discoglossus* too few taxa were examined in the immunological, as compared with the current osteological investigation, to give a meaningful comparison of the two.

Reciprocal crosses are needed in order to derive a phylogeny; one-way crosses permit only an estimate of divergence times (Cadle 1988). Thus the Maxson and Szymura (1984) comments on the relationship of *Alytes* - *Bombina* - *Discoglossus* are more informative than their remarks on divergence between species within each of the three genera. I therefore regard the Maxson - Szymura immunological findings as corroborative support for the scheme of discoglossid relationships put forward in the present study and contra the findings of Sanchiz (1985) and Cannatella (1985). Unfortunately, thus far there has been no immunological study on Ascaphus - Leiopelma - discoglossid relationships nor even Ascaphus - Leiopelma relationships. Although the species within Leiopelma have been compared with one another (Maxson and Szymura ibid.,: 246; Daugherty, Maxson and Bell 1982). The immunological evidence supports the scheme where L. hochstetteri is primitive to the sister pair L. archeyi - L. hamiltoni - a scheme further corroborated by data on Leiopelma breeding behaviour - see Introduction.

However, Maxson and Daugherty (1980), in an immunological study primarily designed to investigate the relationships of the Mexican Burrowing Toad, Rhinophrynus dorsalis (the sole representative of a monotypic family Rhinophrynidae), did obtain an indication of the divergence time between Ascaphus and the discoglossids. They made MC'F tests using antisera to Rhinophrynus and reciprocal tests were also performed using antisera to Ascaphus and Bombina and concluded:- "using albumin as a molecular clock... and assuming approximately equal rates of albumin evolution in all salientians, we estimate the lineage leading to pipids, pelobatids, and discoglossids have shared a common ancestor with the lineage leading to Ascaphus and Rhinophrynus no more recently than 110 million years ago" and that Rhinophrynus and Ascaphus may have shared a common lineage for a longer period diverging from one another "at least some 94 million years ago".

c). An overview of the historical zoogeography of the discoglossoid frogs.

The comments in this section are confined to general observations; the species level hypothesizing of works like Arntzen (1978) being beyond the scope of this study.

The discoglossoid frogs as a group are, beyond any reasonable doubt, an ancient group. They probably had their origins at least some 120 million years ago (following Maxson and Daugherty 1980), possibly a good deal earlier. The present distribution of the discoglossoids together with the immunological data puts their origin on the supercontinent Pangea. The leiopelmatids clearly owe their origins to this dating and placement. *Vieraella* and *Notobatrachus* (early and late Jurassic of Argentina, 190–140 million years before present) fide Estes and Reig (1973) reconstructions show particular similarities osteologically to the leiopelmatids. Goin and Goin's (1972) hypothesis of a southern, possibly Antartic origin for frogs appears a reasonable and particularly interesting hypothesis. From the dates suggested from MC'F analysis it also seems reasonable to suggest that the split of discoglossids from a presumably leiopelmatid-like ancestor coincided with the break-up of Pangea into Laurasia and Gondwanaland. By present distribution and the hypothesis of Maxson and Daugherty (1980) that *Ascaphus* and *Rhinophrynus* may have shared a common lineage after a split from the lineages leading to the discoglossids and other frogs the following hypotheses are suggested:-

1) That leiopelmatids had a southern origin and extended northwards into what is now N. America - *Ascaphus* being a relict of this distribution.

2) That the discoglossids are primarily a Laurasian group with a northerly origin.

3) That the fossil discoglossoid *Scotiophryne* Estes 1969 is of particular importance vis-a-vis the relationships of leiopelmatids to doscoglossids.

4) That the present genera are all relatively modern species ('crown' groups atop ancient lineages) and that it is mistaken to regard any extant species as a 'living fossil'.

The discoglossid genera are the descendants of relict lineages and are only distantly related to one another; *Bombina* and *Barbourula* being the most closely related. The living species of discoglossids are all probably quite close to their centres of origin:- *Alytes* with a Franco - Iberian origin; *Discoglossus* possibly a North African - Iberian origin or possibly slightly more easterly given the primitive status of the Corsican D. montalentii; Bombina and Barbourula with a Chinese origin. Savage's (1973) description of the discoglossids having, at one time, a circumpolar distribution and Barbourula being a hanging relict seems reasonable. Similarly, his comment that the distribution of the discoglossids parallels "so closely that of the deciduous forest derivatives of the Arcto-Tertiary geoflora and the salamandrids that a common historical association seems certain"; although it might be more prudent to substitute likely perhaps rather than "certain". I would also like to suggest that discoglossoid species may be climatic relicts - they all seem to prefer/be adapted to temperate climates, Barbourula may be an exception, but even it is aquatic, found in fast-flowing waters and may, more likely, turn out to be more abundant in colder waters at higher altitudes within its range. I strongly suggest that the low temperature preference/dependancy of discoglossoid species may be a governing factor in their present scattered distribution.

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J. *Figures.*

All scale lines indicate 5 mm. unless otherwise indicated.

30. Skull of *Alytes muletensis* to show positions of cranial bones: a. dorsal and b. ventral views.

31. Nasal capsules (in black): a. laterally displaced - *Ascaphus truei* and b. not displaced - *Bombina bombina*. Scale lines = 2 mm.

32. Nasals - medial contact: a. contact/slight separation, top to bottom - *Alytes muletensis*, *A. obstetricans* and *A. cisternasii*, b. widely separated - *Ascaphus truei*, and c. partial medial fusion - *Bombina maxima*.

33. Nasal - maxilla contact: a. no contact - *Alytes o. boscai*, b. contact, nasal overlying - *Discoglossus galganoi*, and c. contact, nasal abutting - *Barbourula busuangensis*.

34. Nasals - terminology. Scale lines = 1 mm.

35. Nasals - maxillary process: a. absent - *Leiopelma archeyi*, b. present, weak to moderately developed - *Alytes obstetricans*, and c. present, well developed - *Bombina maxima*.

36. Sphenethmoid ossification: a. deep tubular type - *Bombina maxima*, b. compact shallow type - *Alytes o. boscai*, c. two lateral patches - *Ascaphus truei* and d. variable, extending anteriorly to nasal septum - *Leiopelma archeyi*.

37. Frontoparietals - lateral margins: a. straight - *Bombina maxima*, b. biconvex - *Bombina orientalis* and c. divergent - *Barbourula busuangensis*.

38. Frontoparietal fontanelles - exposure: a. one continuous - *Ascaphus truei*, b,c. one anterior/anterior-posterior, narrowing posteriorly - *Bombina bombina* (b) and *Discoglossus sardus* (c), d. no dorsal exposure - *Barbourula busuangensis*, e,f. 'sole-of-shoe' type (doubling) - *Leiopelma archeyi* (e) and *Alytes obstetricans* (f), g. extreme doubling - second (parietal) fontanelle - *Alytes cisternasii*.

39. Frontoparietals - foramen magnum: a. contact/slight separation - *Discoglossus sardus*, and b. clearly separated - *Ascaphus truei*.

40. Frontoparietals - otoccipital ridges (or): state 2 *Barbourula busuangensis*.

41. Otoccipital pattern: a. convergent margins - *Leiopelma archeyi*, b. truncate, bar-like - *Bombina bombina*, c,d. bar-like - *Barbourula busuangensis* (c) and *Alytes cisternasii* (d).

42. Anuran braincase an inverted 'T' -shaped box - *Alytes cisternasii*.

43. Otoccipitals - lateral margins: a. narrow - *Bombina bombina*, b. moderately wide - *Discoglossus galganoi*, c. wide - *Alytes cisternasii* and d. very wide - *Barbourula busuangensis*. (See character 12, p. 106 for character state descriptions).

44. Squamosal bone - terminology: a. T-shaped squamosal - position, b. otic plate (op), c. otic ramus (or), d. zygomatic ramus (zr) and e. squamosal shaft (sqs).

45. Squamosal - otic plate: a. absent/present as small sliver of bone - *Bombina variegata*, b. present, closely applied to crista parotica - *Leiopelma hochstetteri*, and c. moderately developed, well defined - *Bombina maxima*.

46. Squamosal - otic ramus: a. short - *Alytes obstetricans*,b,c.absent/very small spur of bone - *Alytes cisternasii* (b) and *Bombina bombina* (c), d,e. present, difficult to distinguish from otic plate - d and e *Barbourula busuangensis*. Scale lines = 1 mm, Figs. 46 and 47.

47. Squamosal - zygomatic ramus: a,b. short - *Alytes obstetricans* (a) to moderate - *Bombina bombina* (b), c. long, curving distally - *Barbourula busuangensis*, and d. very small, knob-like process - *Alytes cisternasii*.

48. Squamosal (z.r.)-maxilla articulation: a. not articulating - *Discoglossus montalentii* and b. articulating - *Discoglossus sardus*. Scale lines = 2 mm.

49. Squamosal - 'medial' ramus: a. absent - at most a rib on squamosal shaft - *Alytes obstetricans*, b. absent, but with ventromedial expansion on upper shaft - *Bombina bombina* and c. medial ramus present - *Barbourula busuangensis* - d. as per c. but viewed from anterodorsal aspect. Scale lines = 1 mm.

50. Squamosal shaft. a. triangular type - *Leiopelma hamiltoni*, b. intermediate type - *Discoglossus sardus* and c. slender, sigmoid type - *Alytes obstetricans*.

51. Quadratojugal: a. absent (replaced by a ligament) - Ascaphus truei, b. up to 80% of pterygoid fossa length - Alytes o. boscai and c. 80 - 100% of pterygoid fossa length - Bombina bombina.

52. Maxilla - anterior end of pars palatina: a,b. narrow straight type - Discoglossus galganoi (a), convex type - Alytes obstetricans, c. staggered, indented type - Ascaphus truei and d. concave type (V-shaped cleft) - Leiopelma hamiltoni.

53. Maxilla - pterygoidal process: a. absent or a very small process - Bombina orientalis and b. present, well developed - Discoglossus sardus.

54. Maxilla - development of pars facialis and preorbital process (pfa and pop respectively): a,b. pfa poorly to moderately developed, pop absent/weakly developed - Alytes o. boscai (a) and Bombina variegata (b), and c. pfa and pop both moderately well to well developed - Leiopelma archeyi.

55. Premaxilla - terminology: pp = palatine process, mr = mid-region of pars palatina and lp = lateral process. Note: in Figs. 55-59 scale lines = 1 mmm.

56. Premaxilla - pars palatina: a-c. mid-region shallow - a = Ascaphus truei, b = Alytes obstetricans and c = Discoglossus galganoi and d-f. mid-region deep - d = Leiopelma hamiltoni, e = Bombina orientalis and f = Bombina maxima.

57. Premaxilla - palatine process: a,b. spatulate type - a = Leiopelma hamiltoni and b = Bombina maxima, c. intermediate condition - Bombina orientalis and d,e. distinct, pointed type - d = Alytes obstetricans and e = Discoglossus galganoi.

58. Premaxilla - lateral process: a. absent/poorly developed - Alytes obstetricans and b. present as distinct, projecting process - Ascaphus truei.

59. Premaxilla - alary process: a-b. process dorsally directed from its base - Alytes obstetricans and c-d. process laterally directed from base - Ascaphus truei.

60. Vomers - terminology: a. p-lp = plate-like portion. b. c-cp = circumchoanal process. c. dp = dentigerous process and d. v-p = vomeropalatine. All Alytes muletensis. Note: in Figs. 60-65 scale lines = 1 mm.

61. Vomer - plate-like portion: a. moderately to well developed - Alytes

muletensis and b. very small - *Ascaphus truei*.

62. Vomer - circumchoanal process: a. present - *Alytes muletensis* and b. absent - *Ascaphus truei*.

63. Vomer - dentigerous process (teeth - arrangement and position relative to choanae): a. narrow linear series, posterior/ slightly posterior - *Alytes muletensis*, b. very narrow linear series on separate process, posterior - *Bombina orientalis*, c. oval patch, between choanae - *Ascaphus truei* and d. broad, slightly arched linear series, well posterior - *Discoglossus galganoi*.

64. Vomeropalatine: a. absent - *Bombina orientalis* and b. present - *Alytes muletensis*. Note: In *Leiopelma* there is a rib of bone along the posterior margin of the postchoanal portion of the circumchoanal process; the extent of the rib is variable - c. *Leiopelma hamiltoni* and d. *Leiopelma hochstetteri*

65. Vomer - postchoanal process: a. absent - *Ascaphus truei*, b,c. short - moderate, plate-like, b = *Bombina orientalis* and c = *Discoglossus galganoi*, d,e. slender, elongate rod-like process, d = *Leiopelma hochstetteri* and e = *Leiopelma hamiltoni*.

66. Parasphenoid - cultriform process*(shape): a. biconvex - *Alytes o. boscai* (otherwise straight-sided but not tapering as in b.), b. tapering - *Alytes muletensis* and c. distal ½-⅓ tapering - *Leiopelma hochstetteri*. (*cp).

67. Parasphenoid ala (pa) depth: a. uniformly deep medially to laterally - *Leiopelma hochstetteri*, b. shallow medially flaring deeper laterally - *Barbourula busuangensis* and c. uniformly shallow or nearly so - *Alytes o. boscai*.

68. Parasphenoid - cultriform process (medial keel, mk): a. absent - *Alytes o. boscai* and b. present - *Barbourula busuangensis*. Note: in Figs. 66-69 scale= 2mm.

69. Parasphenoid ala - transverse (median) keel (t(m)k): a. absent - *Alytes o. boscai* and b. present - *Barbourula busuangensis*.

70. Parasphenoid ala/medial ramus of pterygoid - overlap in anteriro/posterior plane: a. slight to moderate - *Discoglossus sardus*, b. no overlap - *Bombina orientalis* and c. strong overlap - *Barbourula busuangensis*.

71. Pterygoid - anterior ramus (arp): a. short, little/no curvature, pointed -

Alytes cisternasii, b and d. short, no curvature, truncate - Discoglossus sardus (d. is a dorsal view to show anterior end of arp, obscured in ventral view by the pterygoid process of maxilla) and c. long, curved, rounded/slightly pointed - Bombina orientalis.

72. Pterygoid - orbital flange: character 41 state 1 - present a. dorsal, b. ventral views - Bombina microdeladigitora.

73. Pterygoid - ventral flange: Note: a,b and c are from medio-lateral (oral) view and a', b' and c' are from ventral view.a,a'ventral flange absent - Leiopelma hochstetteri, a' - Bombina orientalis, b,b'- flange present - Discoglossus galganoi and c,c'- flange present, deep, well developed - Barbourula busuangensis. Note: a-c scale = 1 mm; a'-c' scale = 5 mm.

74. Mandible - coronoid process: a,b. smooth or slightly triangular, dorsally or sl. orally directed - a = Ascaphus truei, b = Leiopelma hochstetteri, c. smooth, convex with notch, sl. orally directed - Alytes obstetricans, d. as c. but with deep notch, moderately orally directed - Alytes cisternasii, e. distinctive 3-sided 'lug' of bone, strongly orally directed - Bombina orientalis. Scale = 1 mm.

75. Occipital condyles - orientation: a. linear - Alytes obstetricans, b. shallow obtuse - Leiopelma archeyi and c. steep obtuse - Discoglossus galganoi. Scale = 1 mm.

76. Occipital condyles - position: a. ventral - Alytes obstetricans, b. ventrolateral - Discoglossus galganoi and c. lower lateral - Bombina bombina. Scale = 1 mm.

77. Hyoid - anterior processes on hyale: a,b. absent - a = Leiopelma archeyi and b = Discoglossus montalentii , c,d. present - c = Leiopelma hochstetteri and d = Ascaphus truei. Note: Scale on hyoid figs = 1 mm unless stated otherwise.

78. Hyoid - alary processes (alp): a-c. present - a = Leiopelma hochstetteri, b = Bombina bombina , c = Discoglossus montalentii, d-e. absent - d = Leiopelma archeyi and e = Ascaphus truei.

79. Hyoid - parahyoid ossifications: a-b. medial only - a = Ascaphus truei and b = Leiopelma hochstetteri, c. medial only, V-shaped splint bone - Alytes

obstetricans, d. small medial plus pair large laterial ossifications - *Bombina bombina* , e. medial absent, pair large laterals only - *Bombina microdeladigirora*, f. medial absent. pair of keeled splint bones - *Discoglossus montalentii*, g. medial absent, pair of laterals plus anterior hyoglossal - *Barbourula busuangensis*. *Note*: Scale e and g = 2 mm, others 1 mm.

80. Cervical cotyles: a. Type II, no notch - *Discoglossus sardus*, b-c. Type II moderately separatedby notch - b = *Discoglossus galganoi* and c = *Barbourula busuangensis*, d. Type I - *Bombina bombina* and e. Type II/III, median groove - e = ventral, e' = dorsal view *Bombina microdeladigitora*. Scale = 1 mm.

81. Presacral vertebrae: a. nine - *Leiopelma hamiltoni* and b. eight - *Alytes o. boscai*.

82. Presacral vertebrae - centra (shape): a. elongate, tubular - *Bombina bombina* (6th) and b. short hour-glass shape - *Alytes o. boscai*. Scale = 1 mm.

83. Ribs - terminology: a. free (separated fom transverse process by pad of cartilage), b. ankylosed, c. fused.

84. Uncinate processes (up): terminology

85. 2nd presacral- distal end of transverse process/rib: a. simple, rounded - *Alytes muletensis*, b. prong-like rib - *Discoglossus sardus* and c. flared rib - *Barbourula busuangensis*. Scale = 1 mm.

86. Neural arches: a. imbricate - *Discoglossus galganoi*, b,c. weakly imbricate on presacrals 1-3, less so on 4-8 - b = *Alytes o. boscai* and c = *Discoglossus sardus*, d. non-imbricate - *Leiopelma hamiltoni*.

87. Ch. 61 - Neural arches, posterior margins: a. simple (m) - *Alytes o. boscai*, b. slightly flared (m') - *Discoglossus galganoi*, and c. strongly flared (fm) - *Barbourula busuangensis*.

Ch. 62 - Neural spines: a. absent/weak, b. moderate, and c. strongly developed - taxa as for ch. 61 above.

88. Posterior presacral vertebrae: transverse processes

Ch. 63 - orientation - a. perpendicular/sl. posteriorly directed - *Leiopelma hamiltoni*, b,c. last two weakly anteriorly directed - b = *Alytes o. boscai*, c = Discoglossus galganoi and d. last two strongly anteriorly directed - Barbourula busuangensis.

Ch. 64 - proximal to distal length - a. last two shorter than on preceding vertebrae and b,c,d. longer than on preceding vertebrae - taxa as for ch. 63.

Ch. 65 - marginal flanges (mf) - a,b. absent, c,d. present - taxa as fot ch. 63.

89. Dilation of sacral diapophyses: a. bar-like, clubbed - Leiopelma hamiltoni, b,c. 'hatchet-shaped' - b = Alytes o. boscai and c = Discoglossus galganoi and d. 'butterfly-wing type' - Barbourula busuangensis.

90. Sacral centrum: a-b. entire - Alytes o. boscai and c-d.divided - Leiopelma hamiltoni.

91. Sacrum - prezygapophyses: a. anterior - Discoglossus sardus and b. posterior - Barbourula busuangensis.

92. Ilium - configuration a. state 0 type - Leiopelma hochstetteri, b. state 1, weak ceratophryine, tvpe - Barbourula busuangensis and c. state 2, leptodactyline type, note ilial crest extending fom arrow posteriorly, - Discoglossus galganoi (c' second, mcre juvenile specimen; crest more distinct).

93. Ilium - dorsal acetabular expansion: a Type A - Barbourula busuangensis, b. Type P - Alytes cisternasii. Note: for Figs 92-94 scale line = 10 mm.

94. Ischium - development and orientation: a. small, round-elliptical, no posterodorsal expansion - Discoglossus galganoi and b. large, elliptical, with posterodorsal expansion - Barbourula busuangensis.

95. Epipubis: a. inverted Y-shape - Discoglossus galganoi, b,c. broad, shield-shaped cartilage - b. Ascaphus truei and c = Leiopelma hochstetteri. Scale = 1mm.

96. Omosternum: a. absent/? poorly developed - Alytes o. boscai and b. present (o) - Discoglossus sardus.

97. Clavicles. a. state 0 straight - Leiopelma hochstetteri and b. state 0 slightly anteromedially directed - Ascaphus truei, c. state 1 - strongly arched (anteromedially directed) - Bombina variegata.

98. Scapula - uncleft or bicapitate: a. uncleft - Ascaphus truei, b,c. bicapitate b = Leiopelma hochstetteri and c = Alytes o. boscai, d. Bicapitate with closed groove and foramen - Alytes cisternasii. Scale = 1 mm.

99. Scapula - development, position of proximal heads: pa = pars acromialis, pg = pars glenoidalis. a,b. equal; proximal a = Ascaphus truei and b = Alytes o. boscai, c. pg. smaller; proximal - Bombina variegata and d. pg. shorter; pa proximal, pg on posterior margin - Leiopelma hochstetteri. Scale = 1 mm.

100. Scapula - overall shape: a. rectangular - Alytes o. boscai, b,c. triradiate, no cleft on anterior margin - b = Bombina orientalis and c = Bombina maxima, d. triradiate, with cleft anterior margin (arrowed) - Bombina bombina.

101. Scapula - posterior margin: a. Type gf - Alytes o. boscai, b. Type c - Bombina orientalis.

102. Contributions to the glenoid fossa: a. pars acromialis (pa) does not contribute articular surface to glenoid fossa - Alytes o. boscai, b. pa contibutes artcular surface - Alytes cisternasii (b' as b with articular surface blocked in),

103. Cleithrum - uncleft/bifurcate: a.uncleft, shallow - Leiopelma hochstetteri, b. uncleft, deep - Ascaphus truei and c. bifurcate (arrowed) - Alytes o. boscai.

104. Cleithrum on ventral surface of suprascapula: a. absent/present as slight 'lip' - Leiopelma hochstetteri, b. clearly investing ventral surface - Alytes o. boscai. Note: in Figs 103 and 104 scale = 1 mm.

105. Coracoids - medial expansion: a. broad medial expansion - Leiopelma hochstetteri, b. moderately expanded - Alytes o. boscai and c. medial end barely expanded - Bombina variegata.

106. Coracoids (cor) - orientation: a. long axes straight - Alytes o. boscai, b. long axes in 'step-down' configuration - Alytes cisternasii.

107. Sternum: a. top-shaped - Ascaphus truei, b. with long, divergent horns - Discoglossus sardus.

108. Presternal pieces (epc = epicoracoid cartilages; cor = coracoid; 'st' = sternalblattchen): a. epicoracoid not extending beyond coracoid - Ascaphus truei, b. extending beyond coracoid but not produced - Alytes o. boscai and c. extending beyond coracoid as an elongate process - Bombina variegata.

109. Inscriptional ribs: a,b. absent - a = Alytes o. boscai, b = Discoglossus sardus, c. present - Leiopelma hochstetteri.

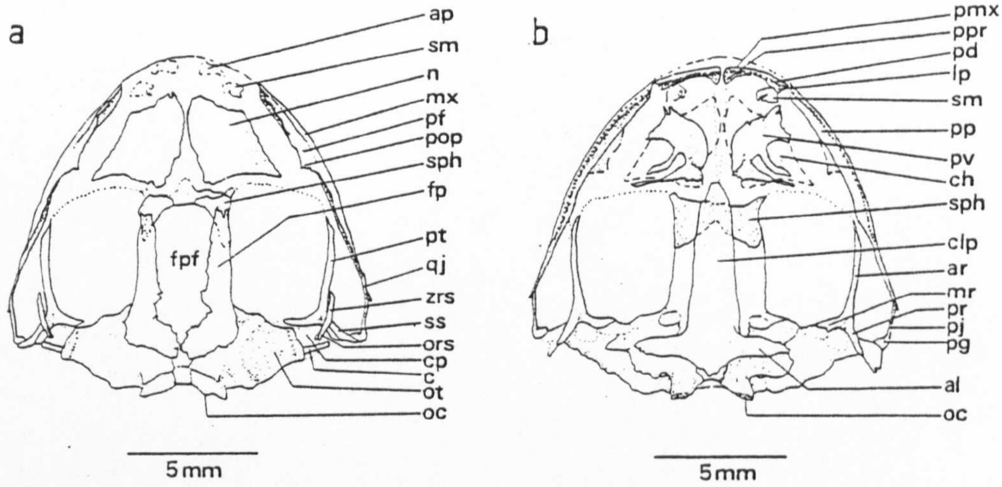
110. Radioulna - radial and ulnar heads; proximal groove: a. heads not confluent; groove present - Leiopelma hochstetteri, b. heads confluent; groove absent (fused condition) - Discoglossus sardus.

111. Wrist bones - radiale (on left), ulnare+intermedium (on right): a. wrist bones wider than long or as wide as long - Discoglossus sardus,b,c.wrist bones longer than wide - b = Alytes obstetricans boscai and c = Alytes cisternasii. Scale line = 1 mmm.

112. Hand - configuration of 1st and 4th fingers: a. normal - Discoglossus sardus and b. 1st slender; 4th short, squat and compact - Alytes o. boscai; c. as per b, but a more extreme condition - Alytes cisternasii. Scale lines= 1 mm.

113. Relative lengths of metatarsals: a. short metatarsals - long phalanges - Bombina bombina, b. long metatarsals - short phalanges - Bombina variegata. c. as per b. but showing a more extreme condition on 5th toe - Alytes cisternasii.

114. Terminal phalanges - terminology: a. simple, b and c spatulate (c more so), d. mushroom-shaped. Scale lines = 1 mm.



Skull of (gravid female, S-V.L. 37.8mm, ALCOVER collection number 81090207). A. Dorsal view. B. Ventral view. *Abbreviations.– al* ala, *ap* alary process of premaxilla, *ar* anterior ramus of pterygoid, *c.* columella, *ch* choana (position of), *clp* cultriform process of parasphenoid, *cp* crista parotica, *fp* frontoparietal, *fpf* frontoparietal fontanelle, *lp* lateral process of pars palatina of premaxilla, *mr* medial ramus of pterygoid, *mx* maxilla, *n* nasal, *oc* occipital condyle, *ors* otic ramus of squamosal, *ot* otoccipital, *pd* pars dentalis of premaxilla, *pf* pars facialis of maxilla, *pg* pars glenoidalis of quadratojugal, *pmx* premaxilla, *pop* preorbital process of maxilla, *pp* pars palatina of maxilla, *ppr* palatine process of premaxilla, *pt* pterygoid, *pv* prevomer, *qj* quadratojugal, *sm* septomaxilla, *sph* sphnethmoid, *ss* squamosal shaft, *zrs* zygomatic ramus of squamosal.

Fig. 30

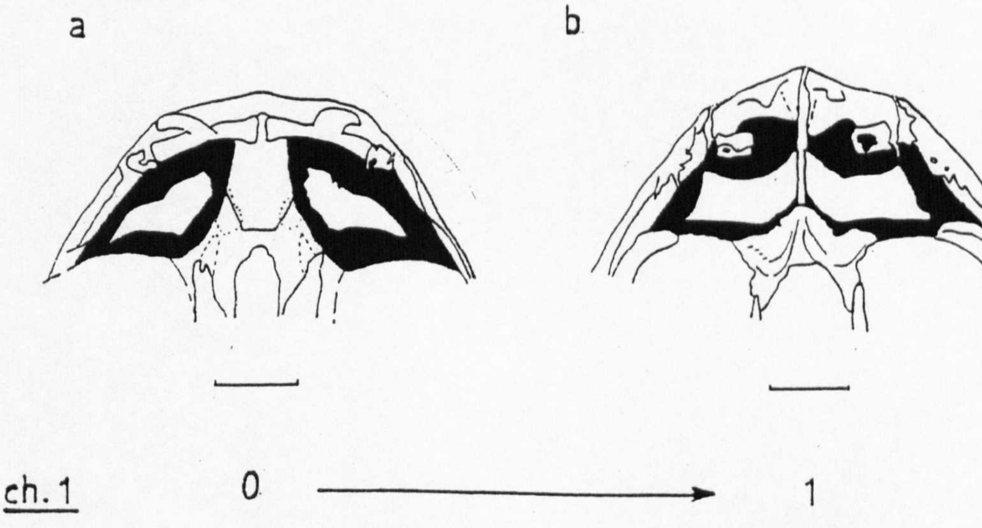


Fig. 31

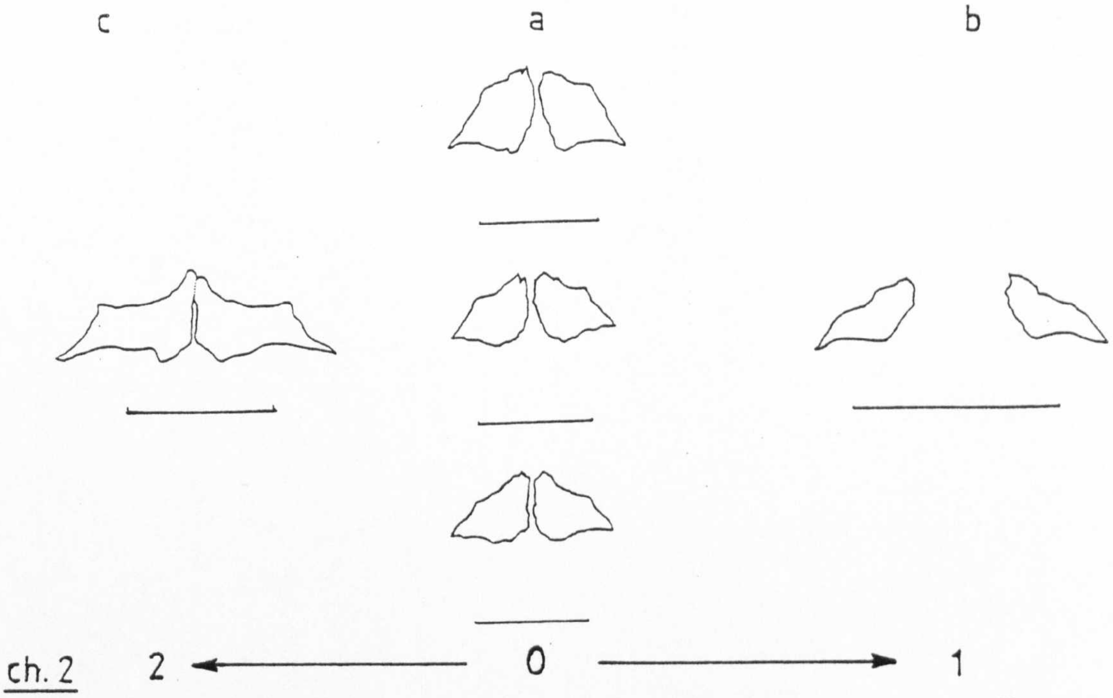


Fig. 32

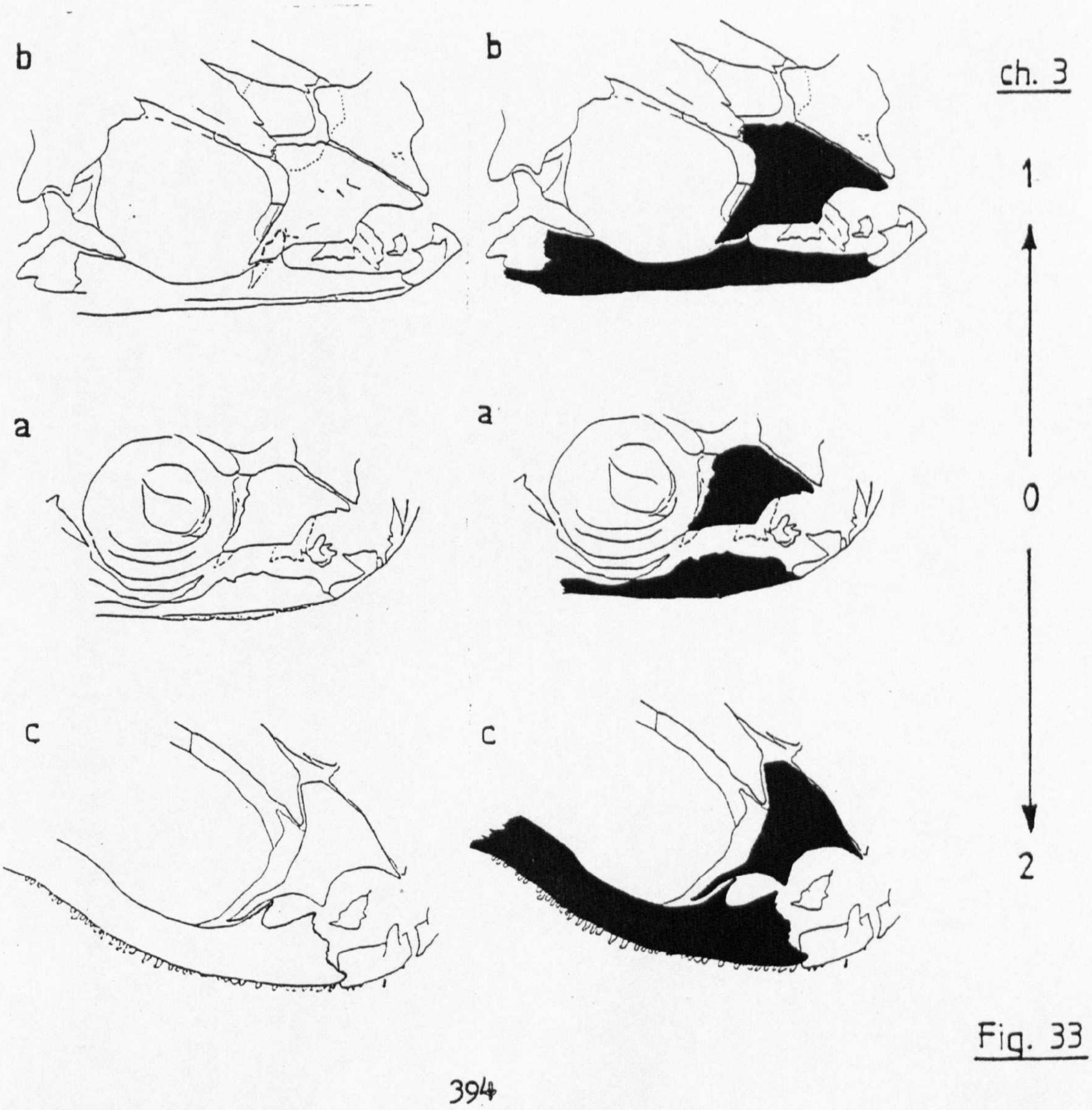
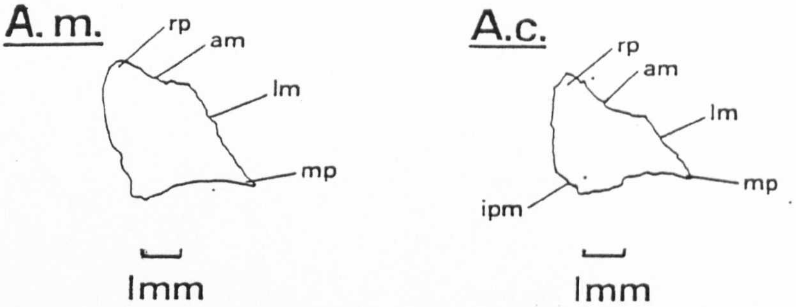


Fig. 33



Right nasals of **A.** *muletensis* and *A. cisternasii*. *Abbreviations.– am* anterior margin, *ipm* inner, posteromedial margin, *lm* lateral margin, *mp* maxillary process, *rp* rostral process.

Fig. 34

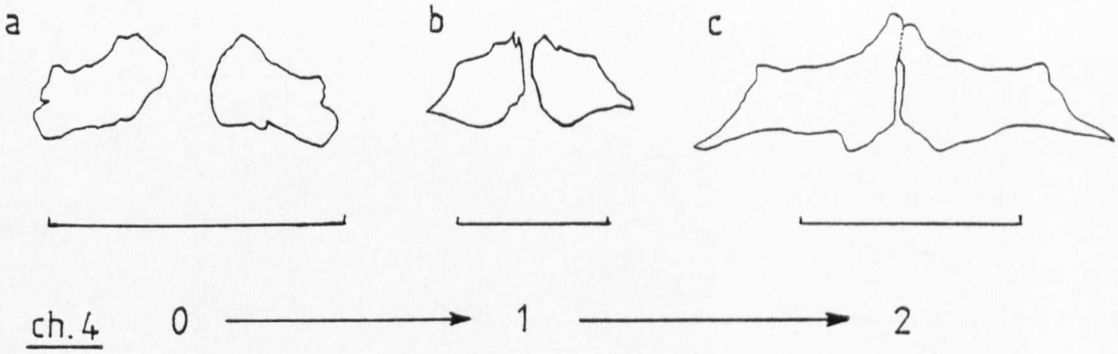


Fig. 35

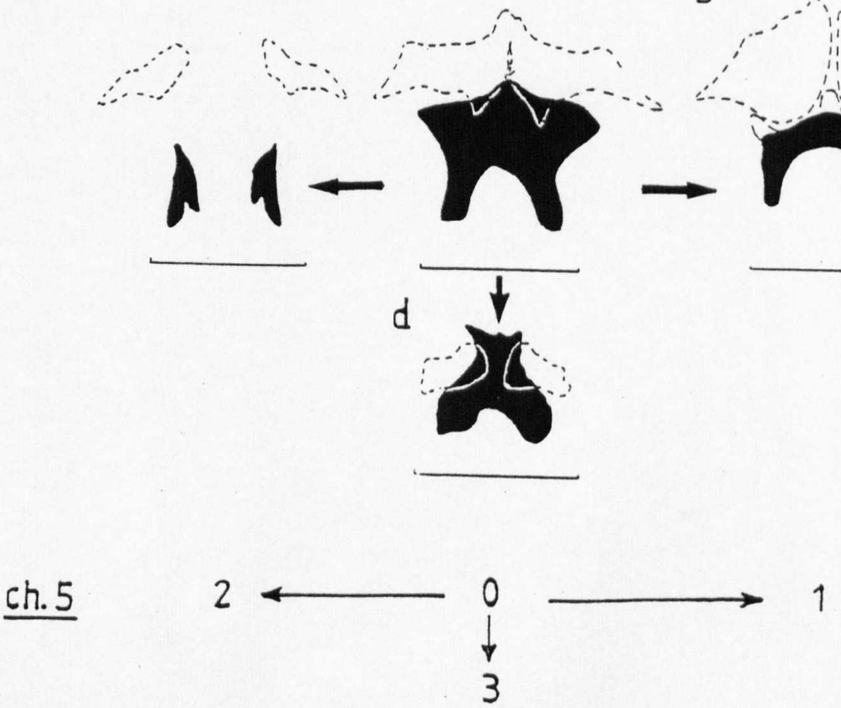


Fig. 36

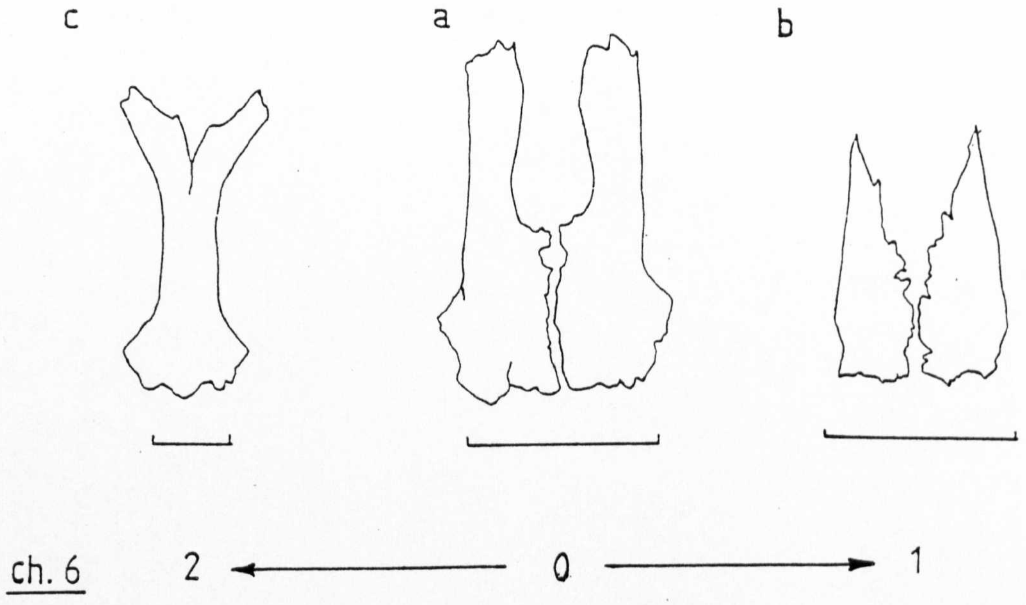


Fig. 37

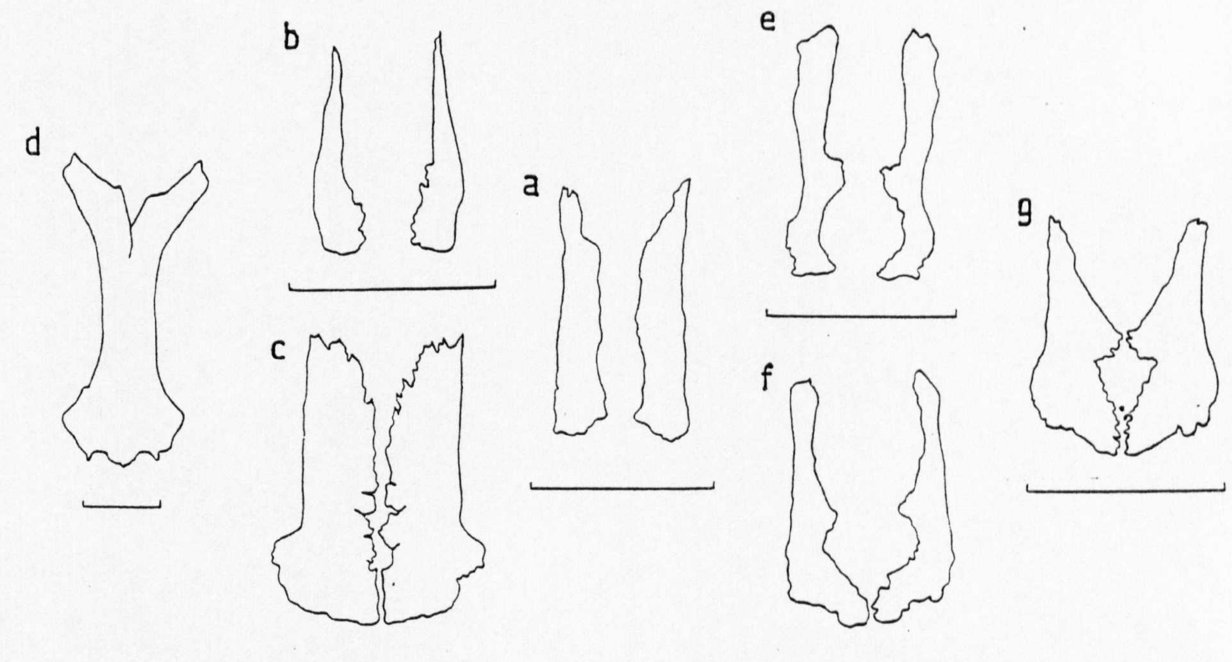
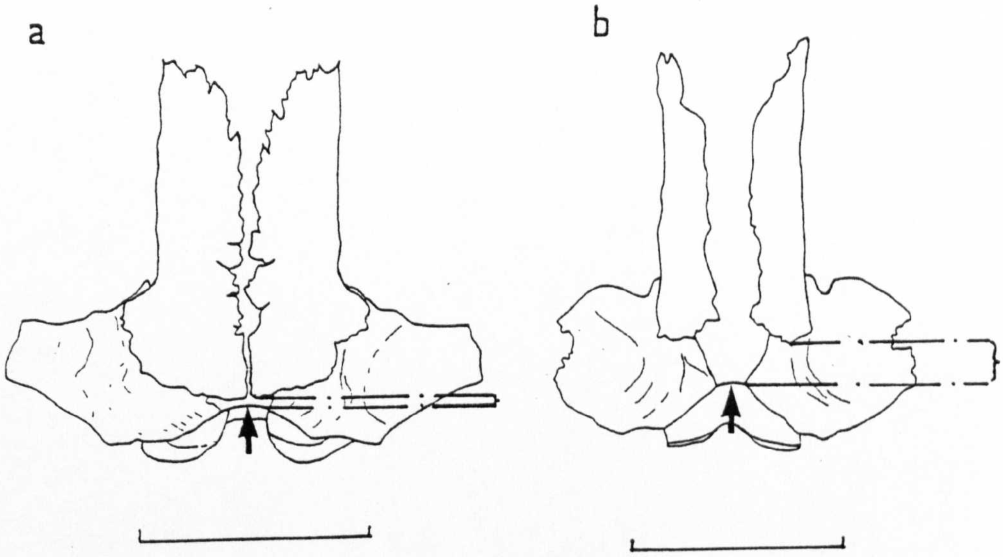
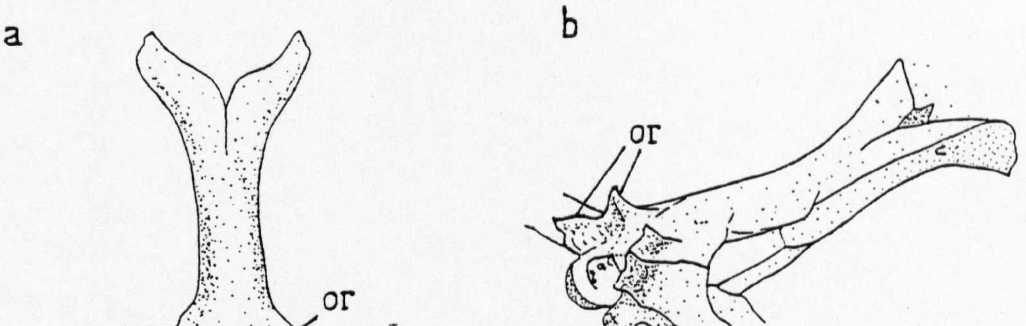


Fig. 38



ch. 9 0 → 1

Fig. 39



ch. 10, st. 2

Fig. 40

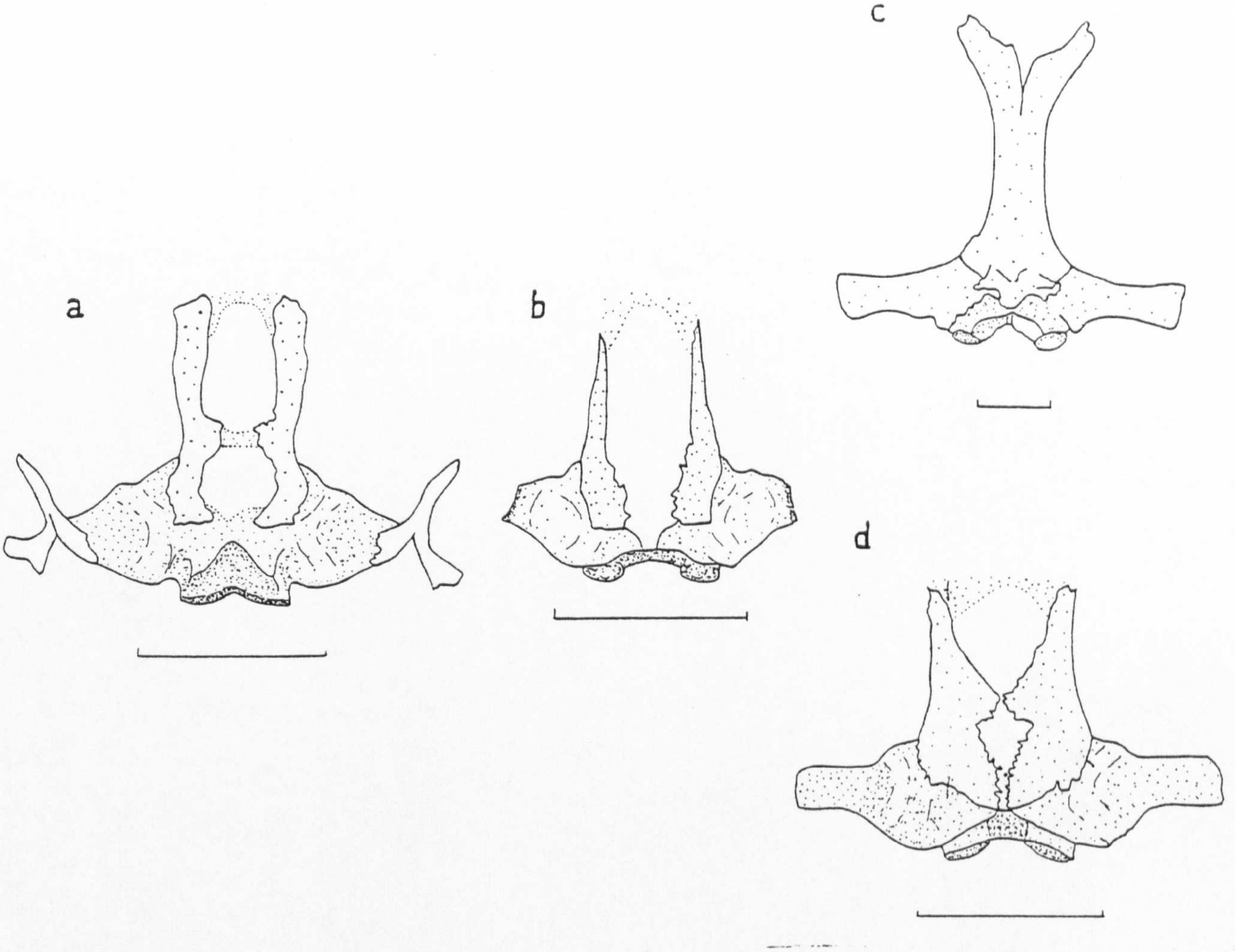


Fig. 41

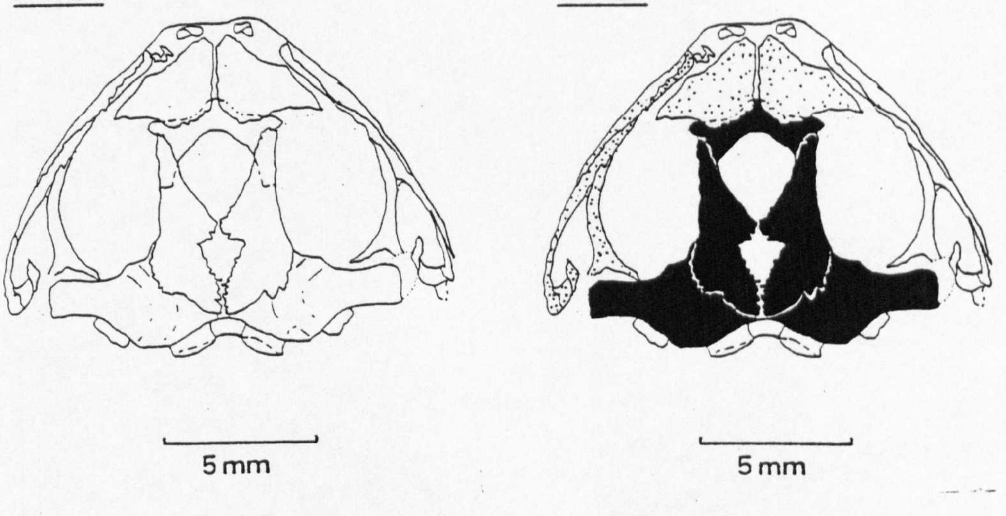


Fig. 42

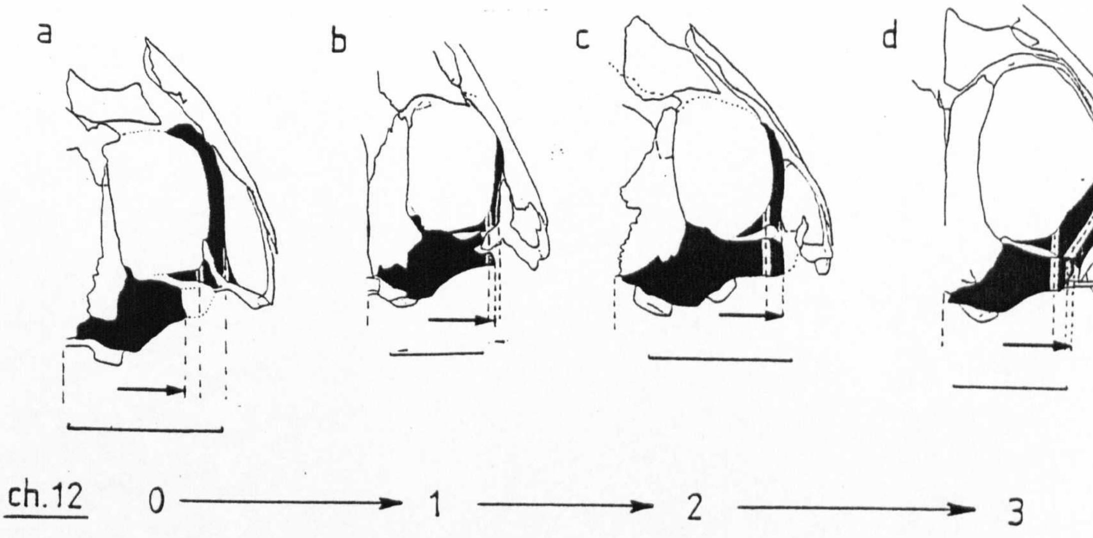


Fig. 43

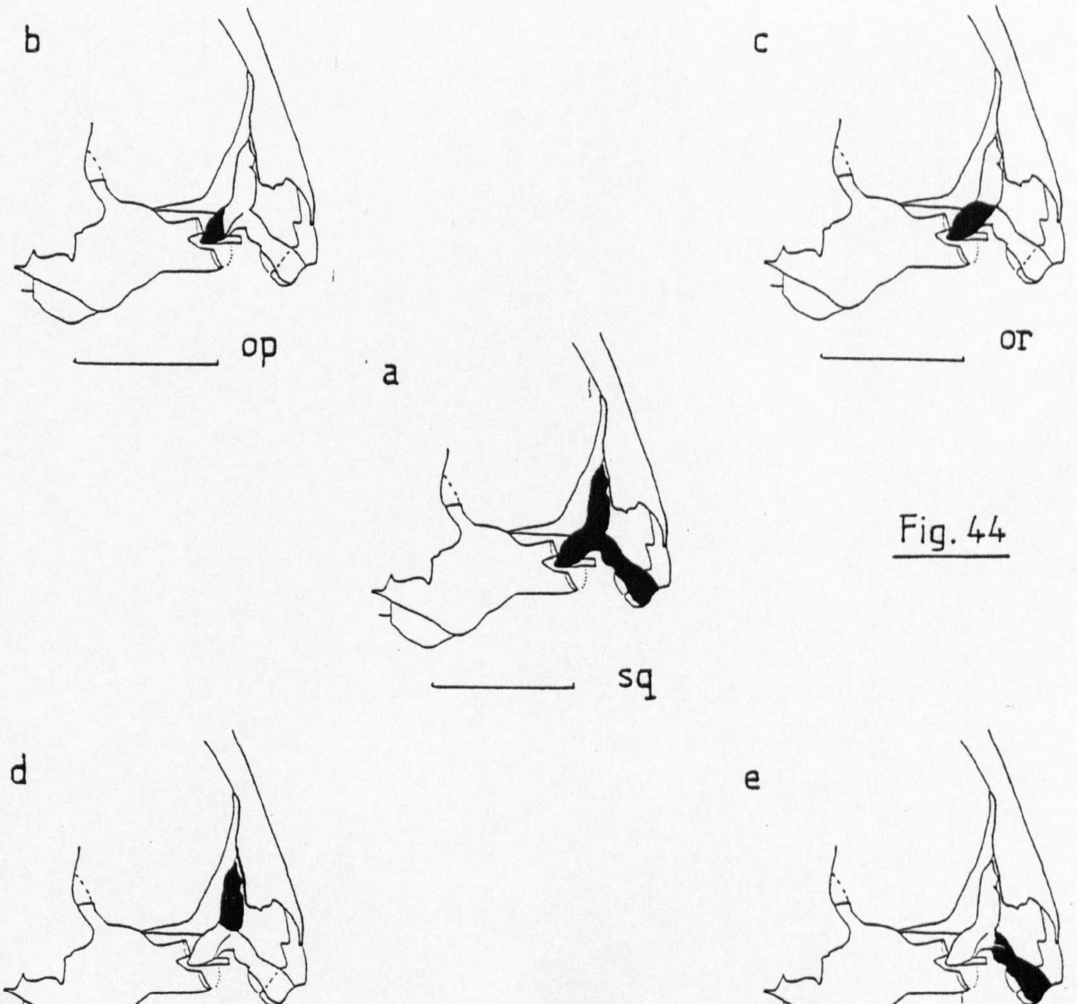


Fig. 44

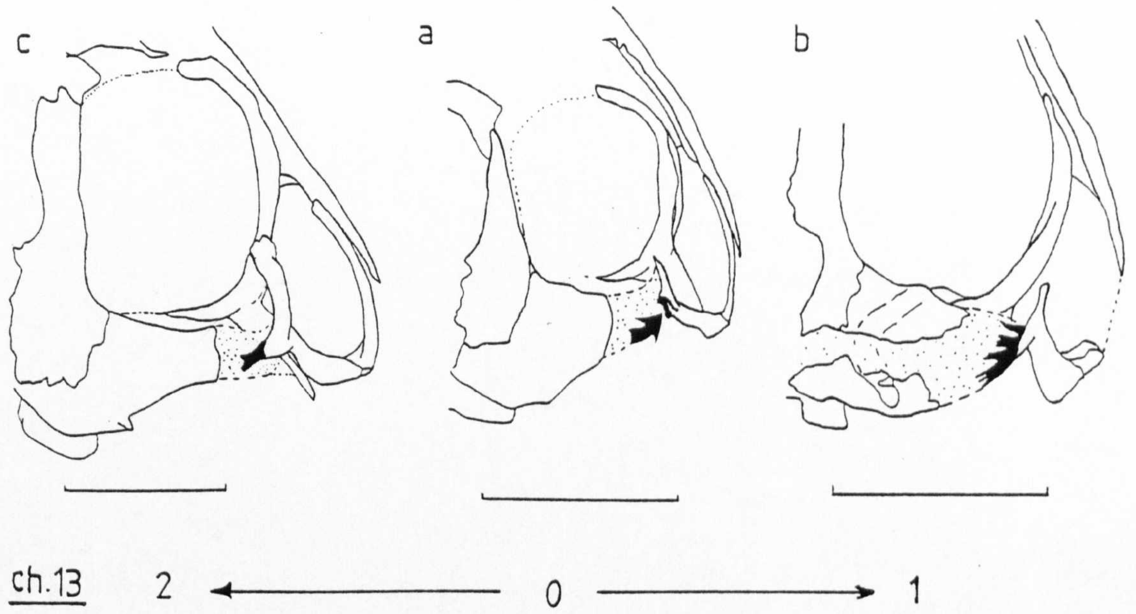


Fig. 45

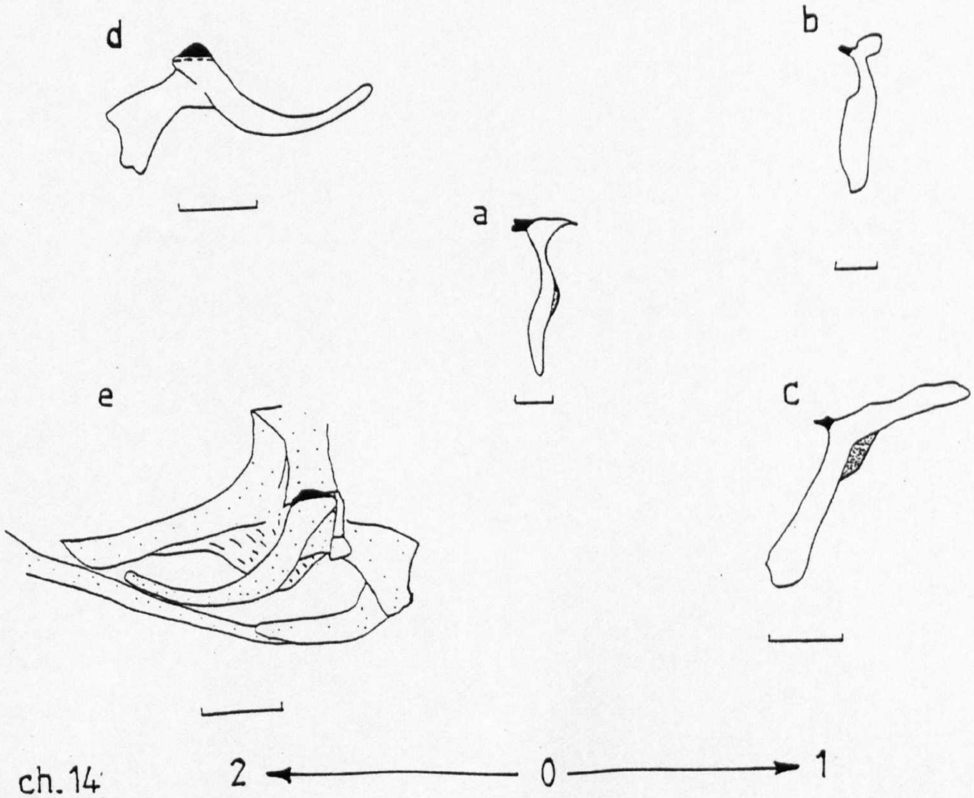
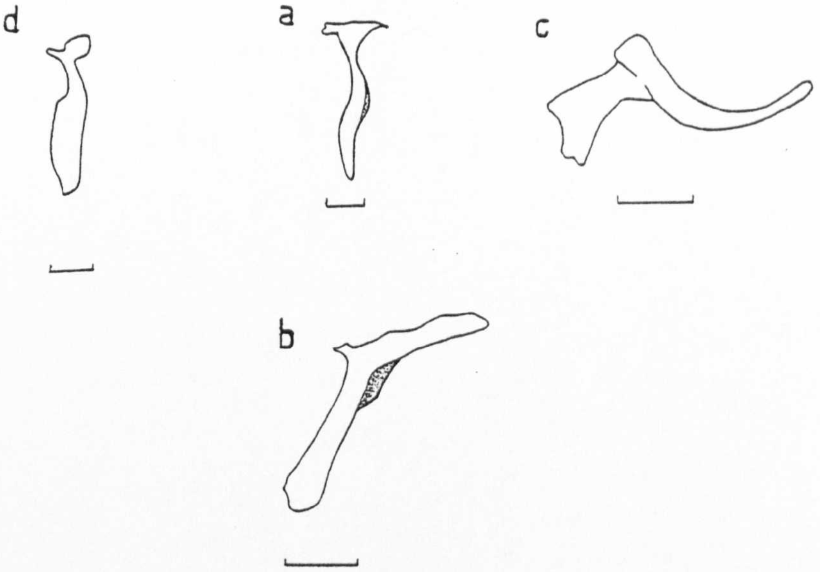
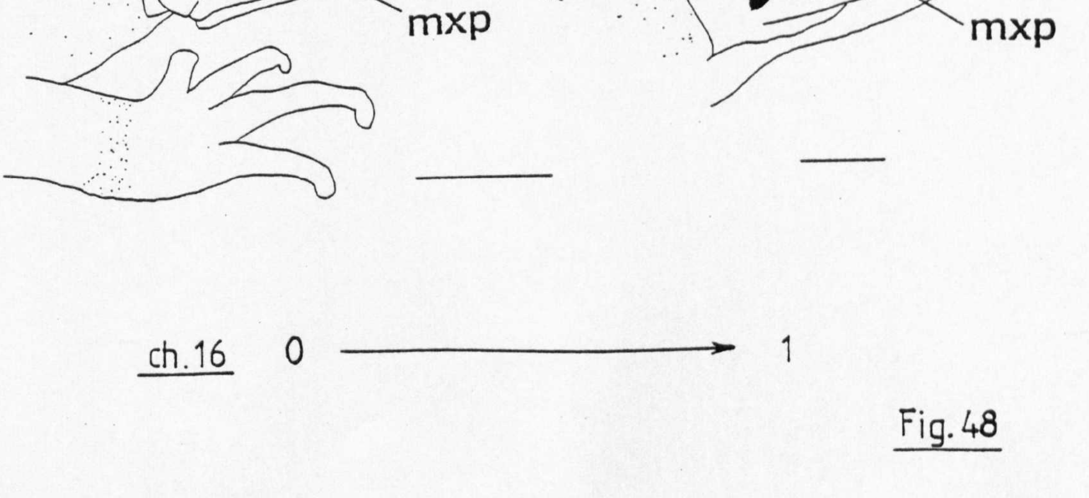


Fig. 46



ch.15 2 ← 0 → 1

Fig. 47



ch.16 0 → 1

Fig. 48

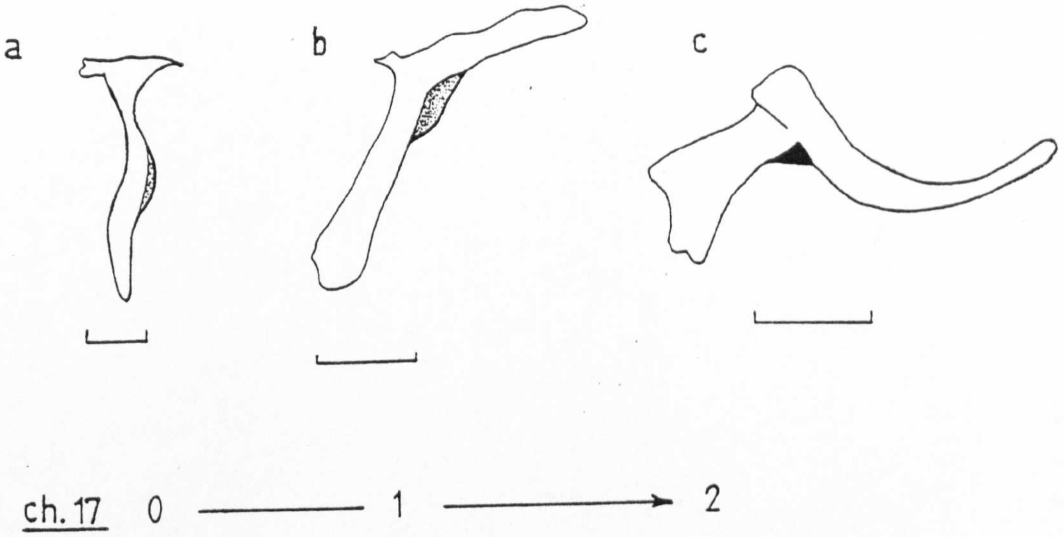
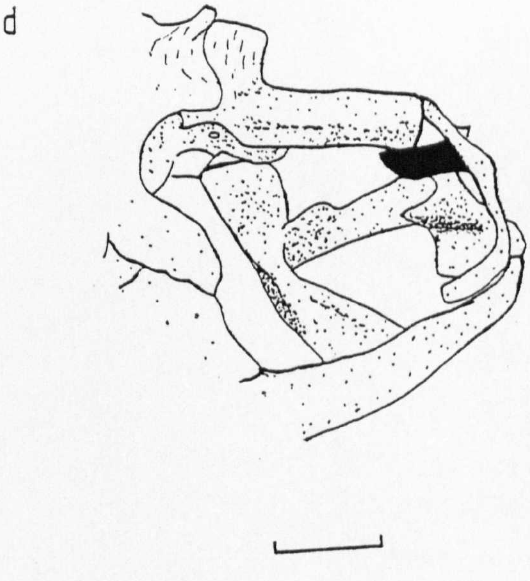


Fig. 49



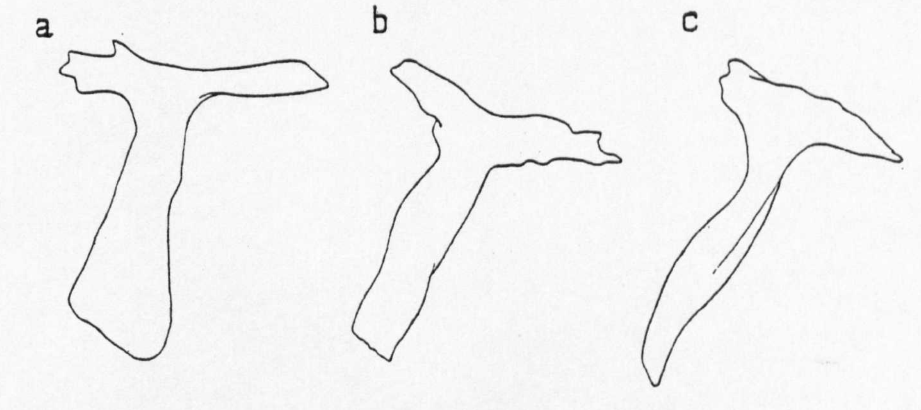


Fig. 50

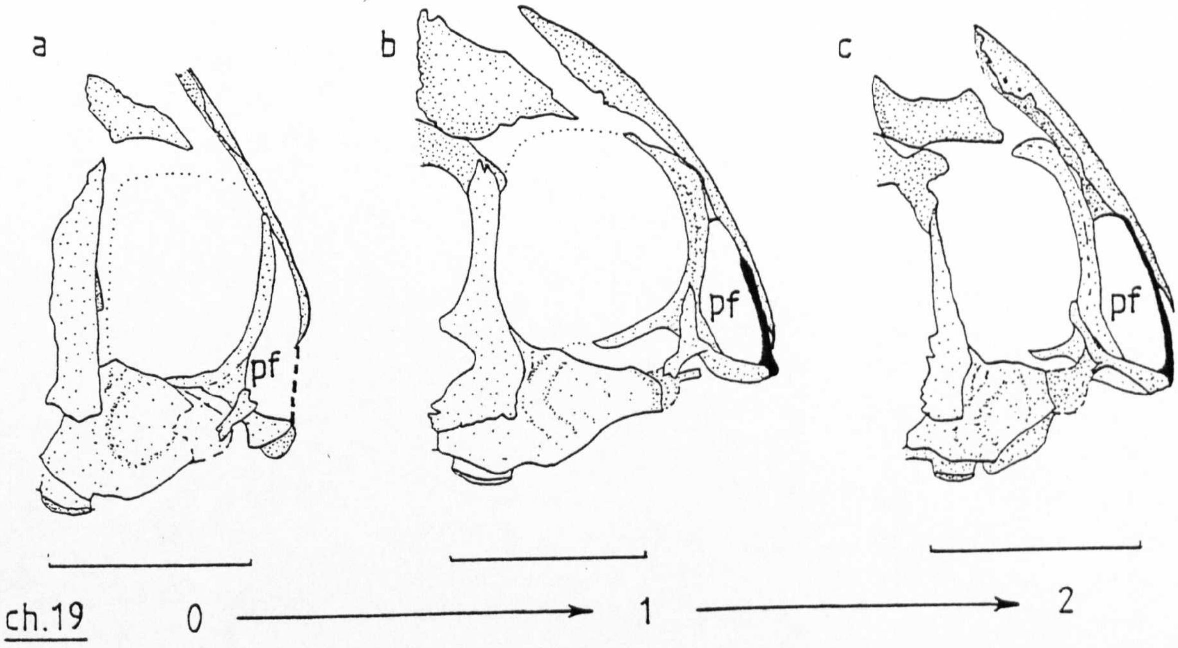


Fig. 51

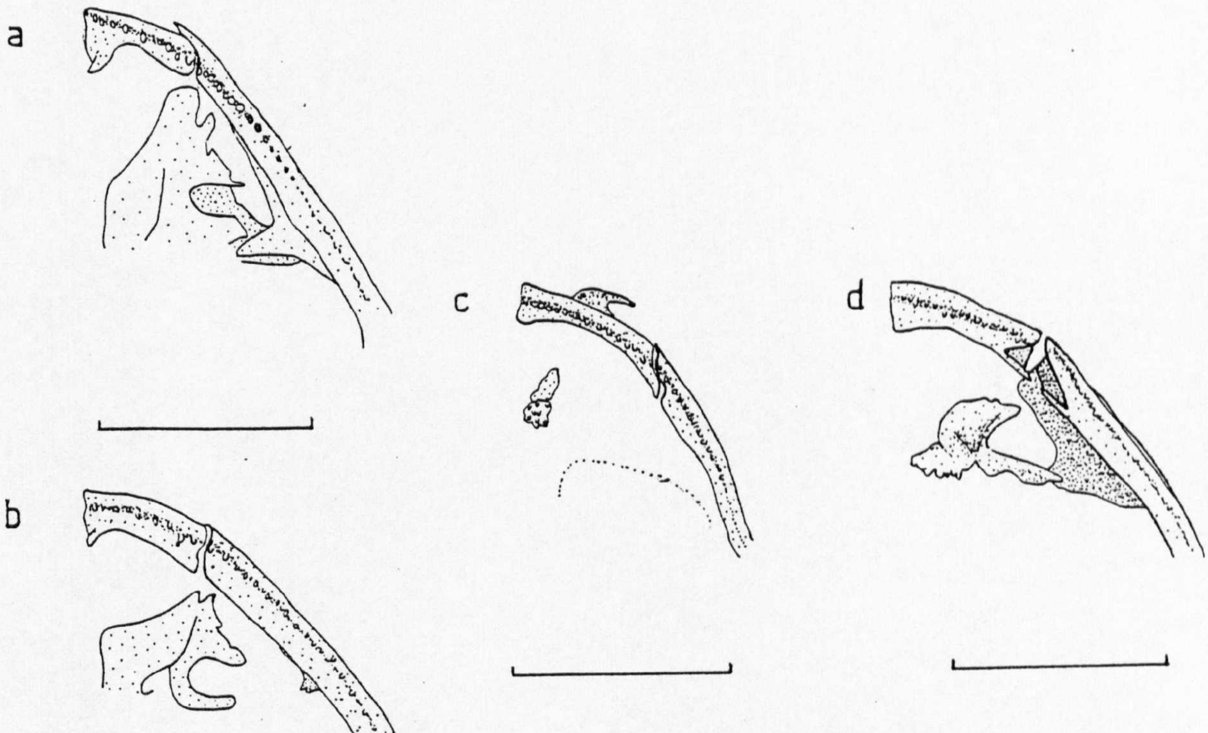
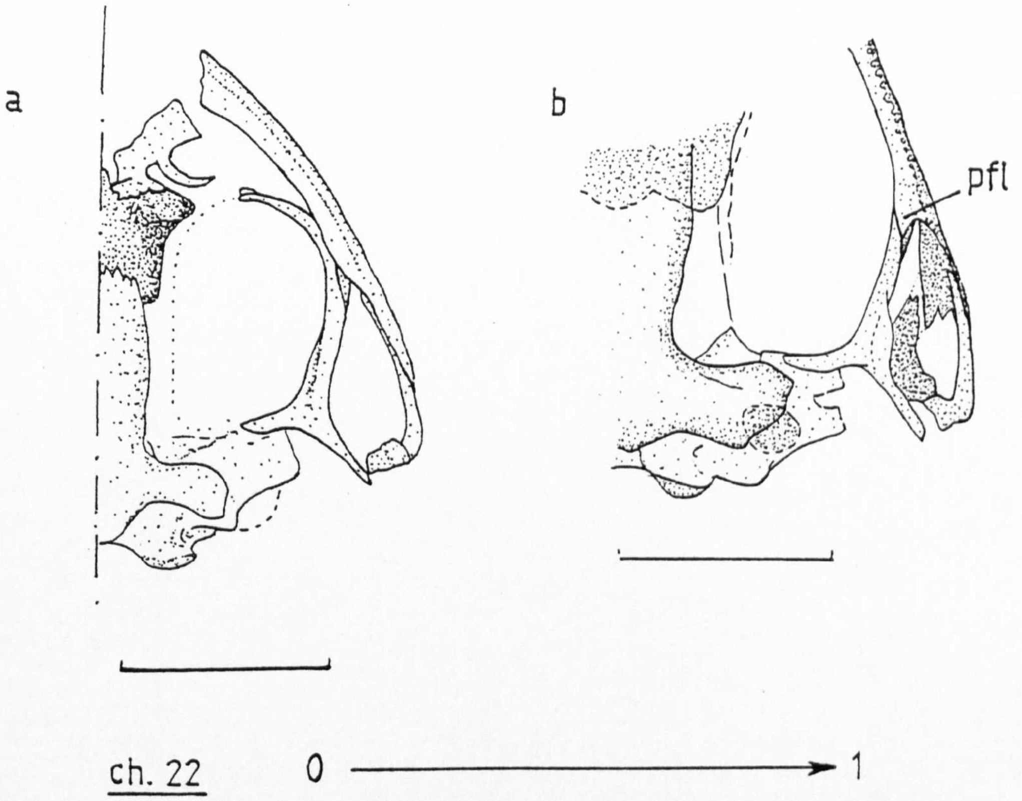


Fig. 52



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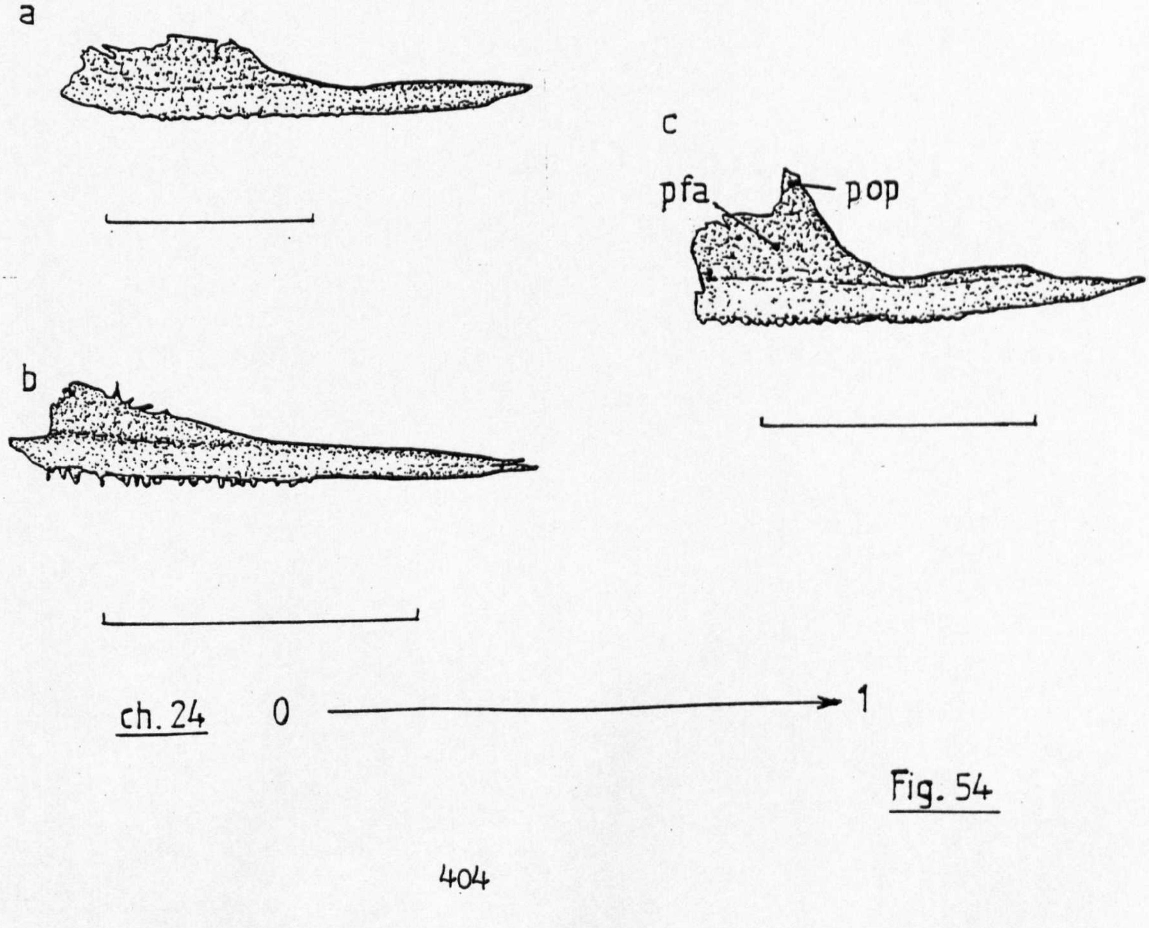


Fig. 54

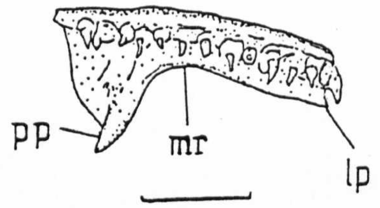


Fig. 55

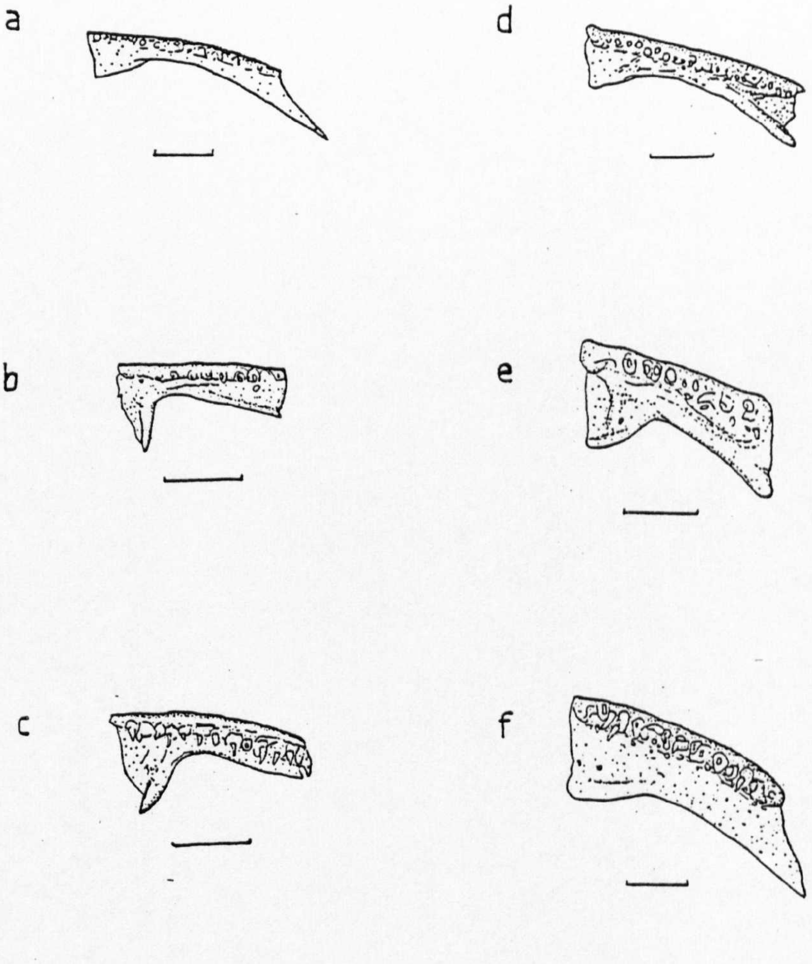


Fig. 56

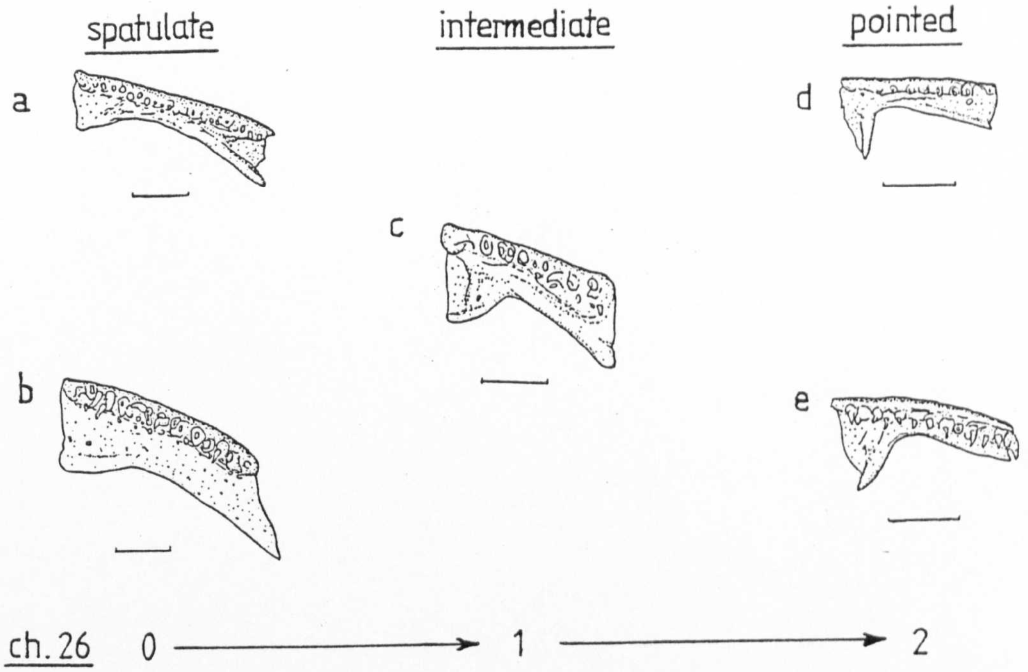


Fig. 57

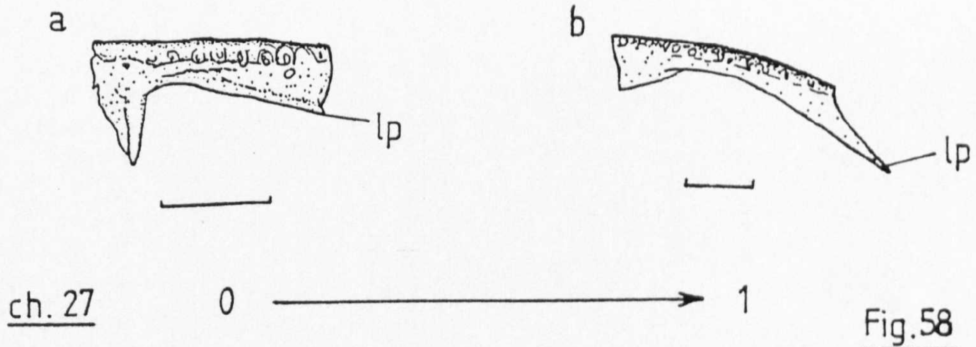


Fig.58

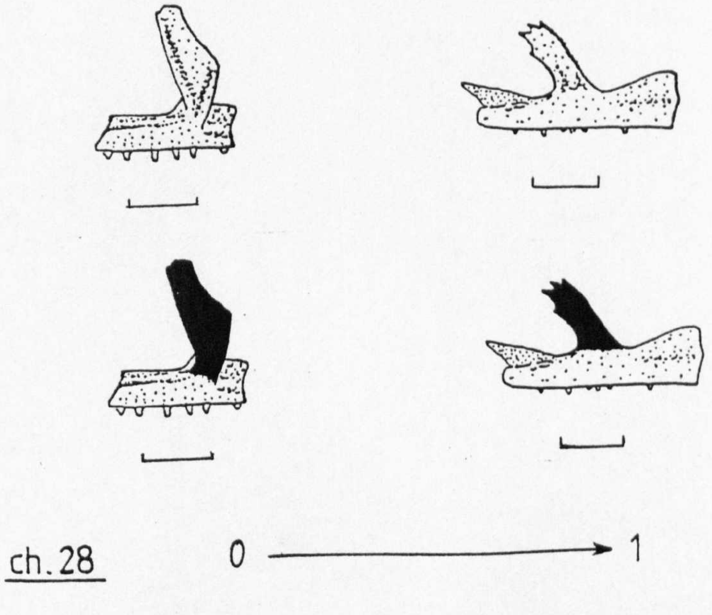


Fig. 59

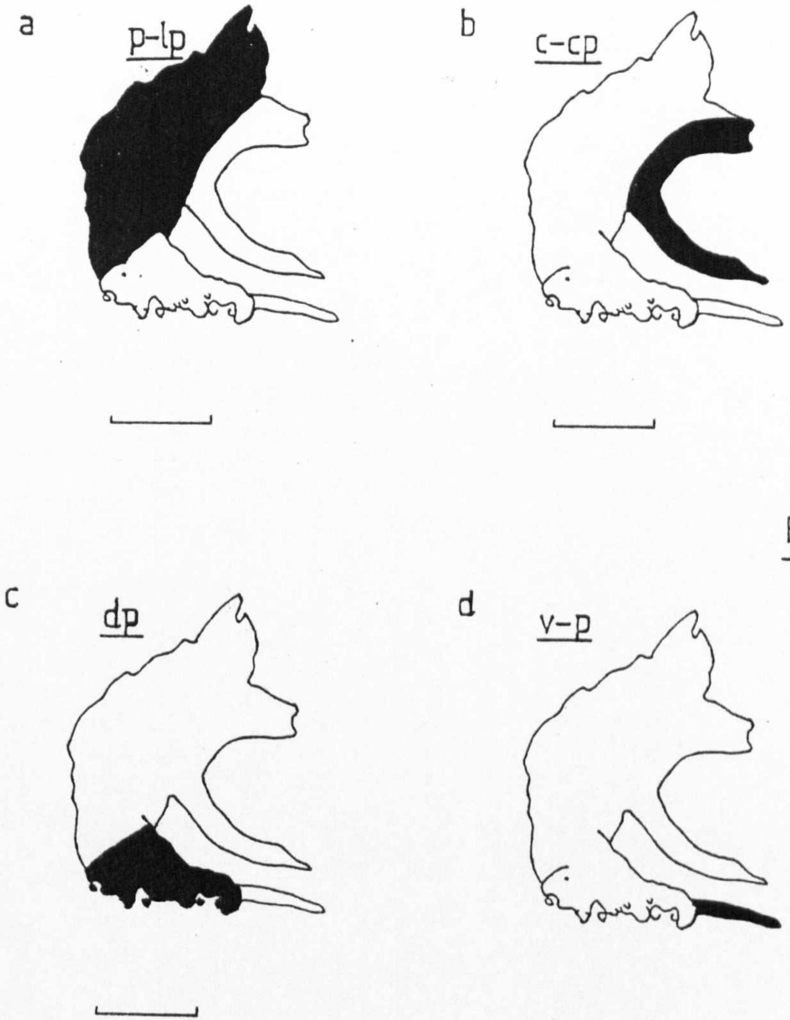


Fig. 60

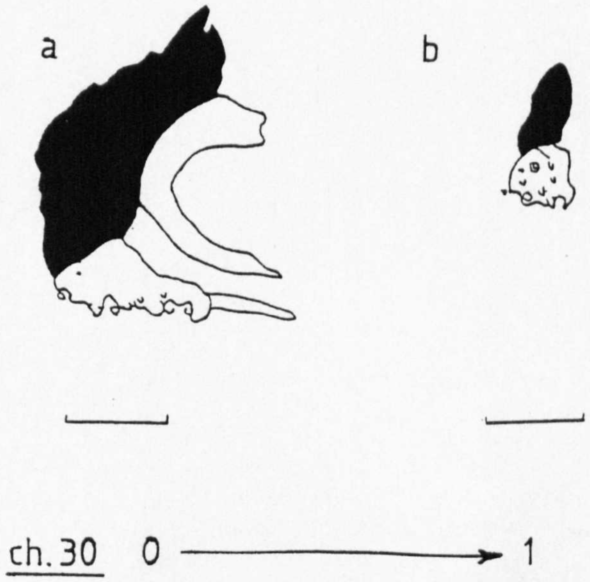


Fig. 61

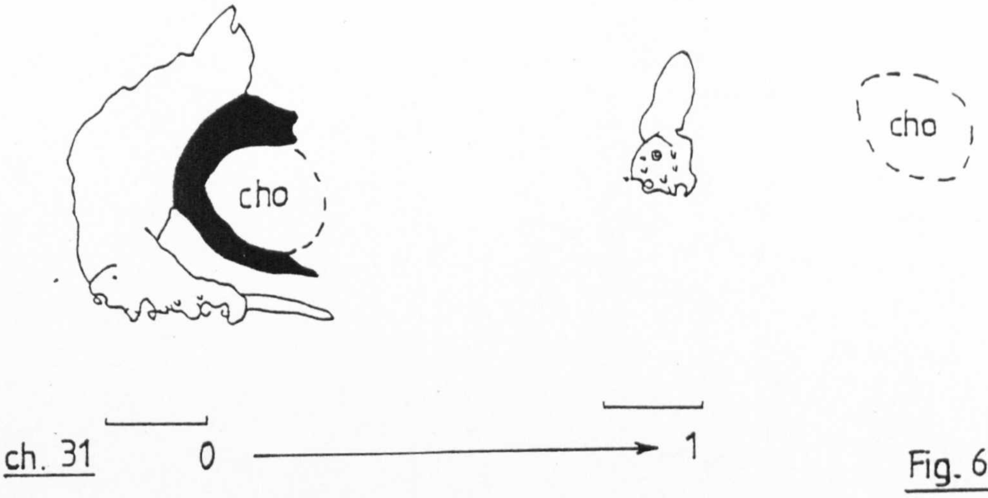
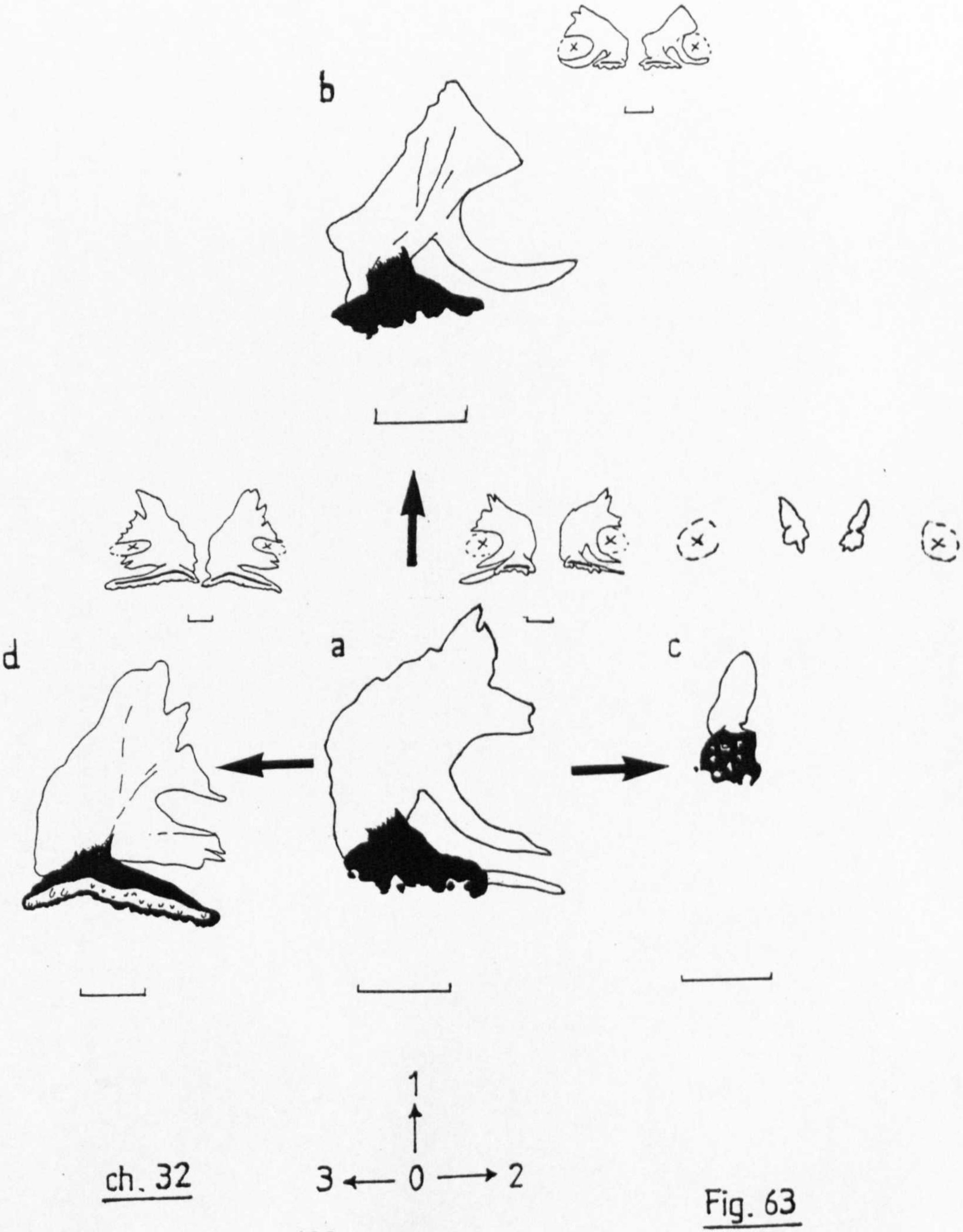


Fig. 62



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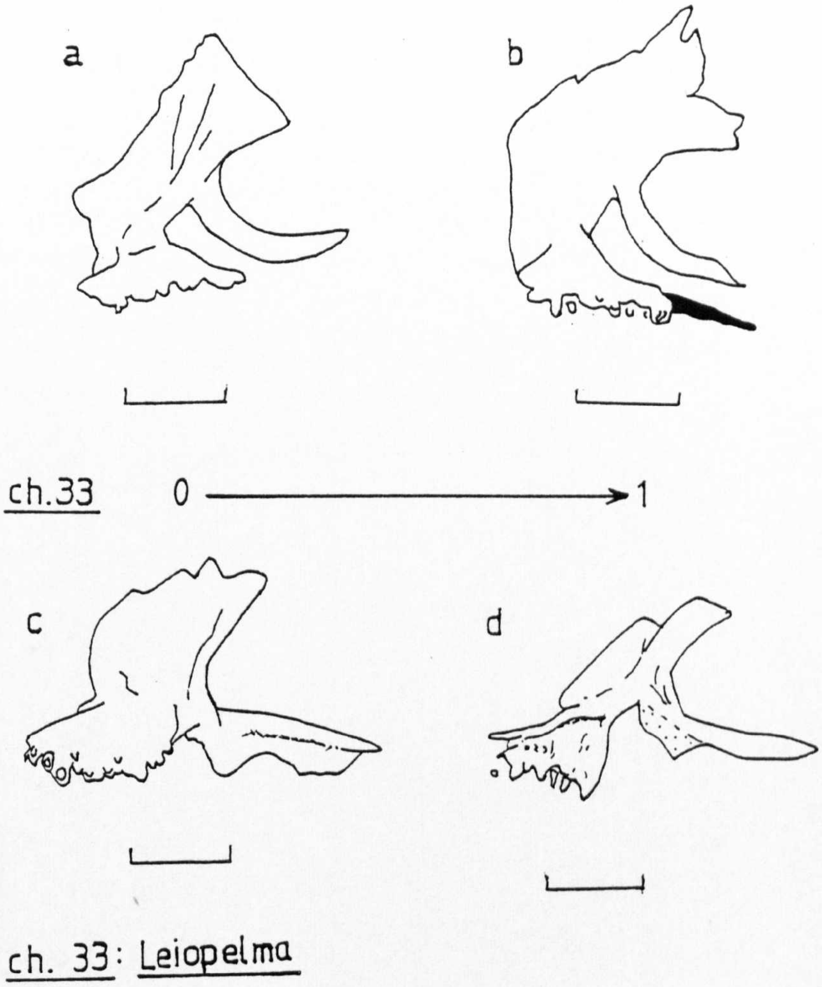


Fig. 64

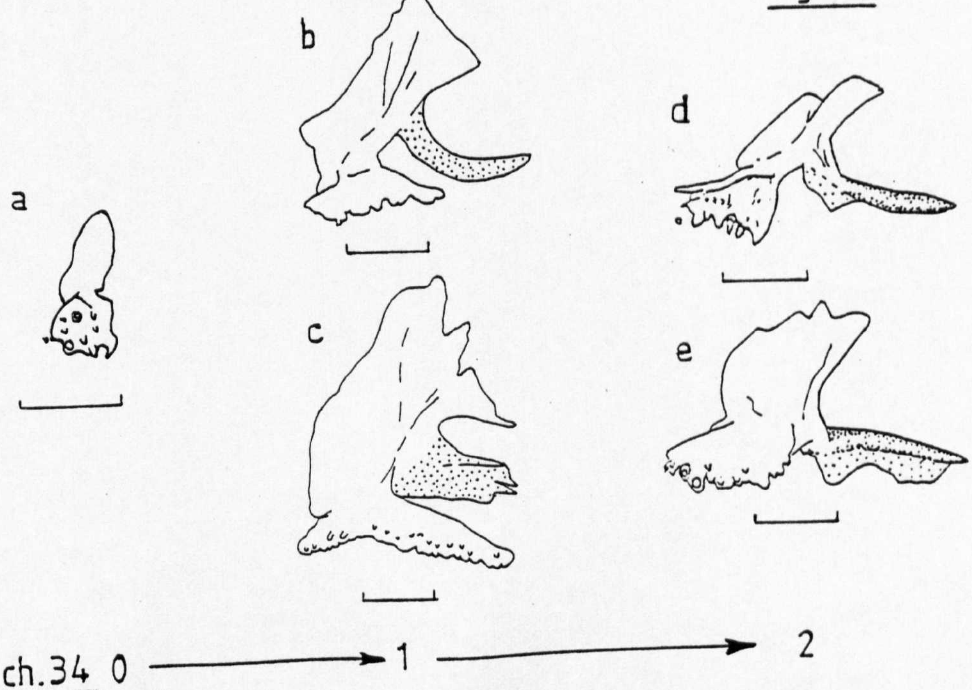


Fig. 65

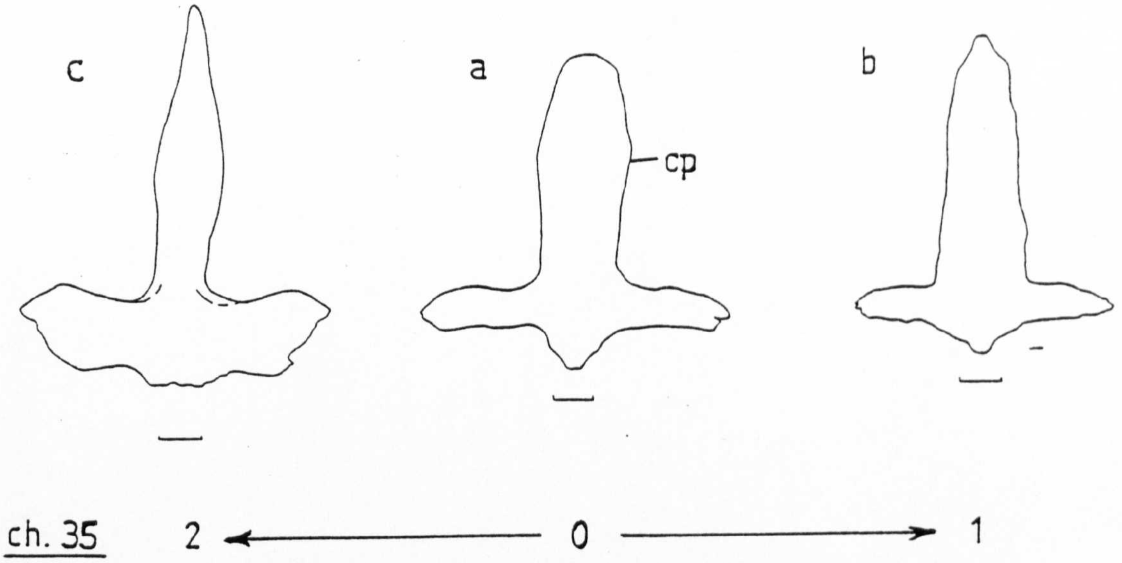


Fig. 66

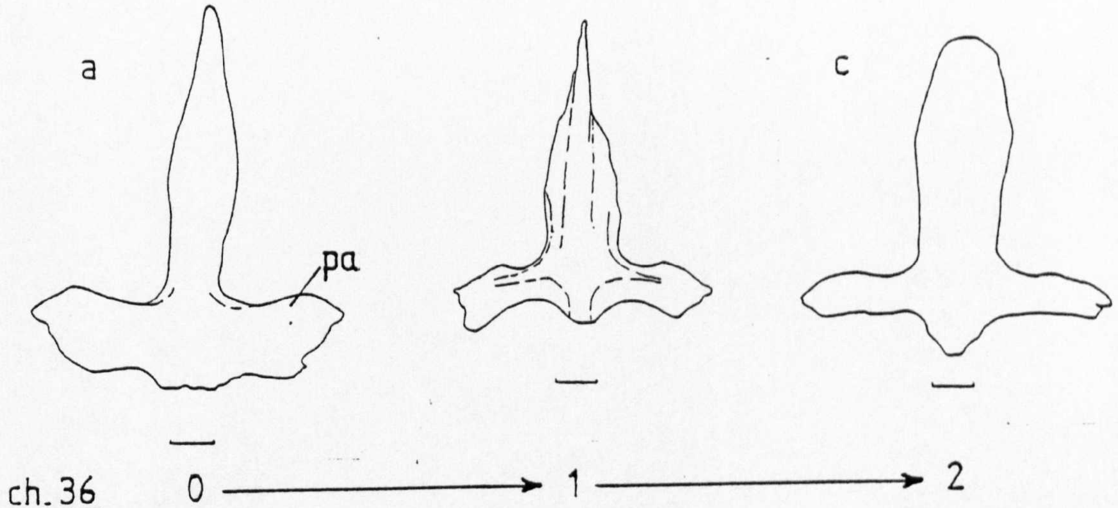


Fig. 67

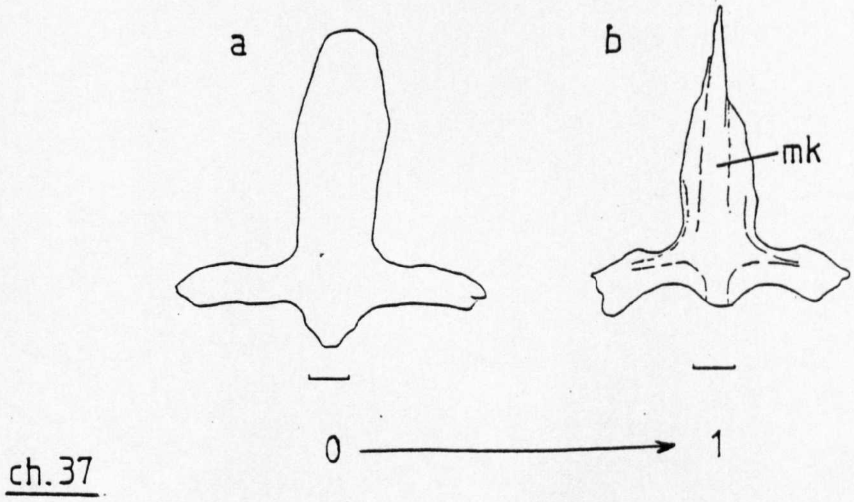
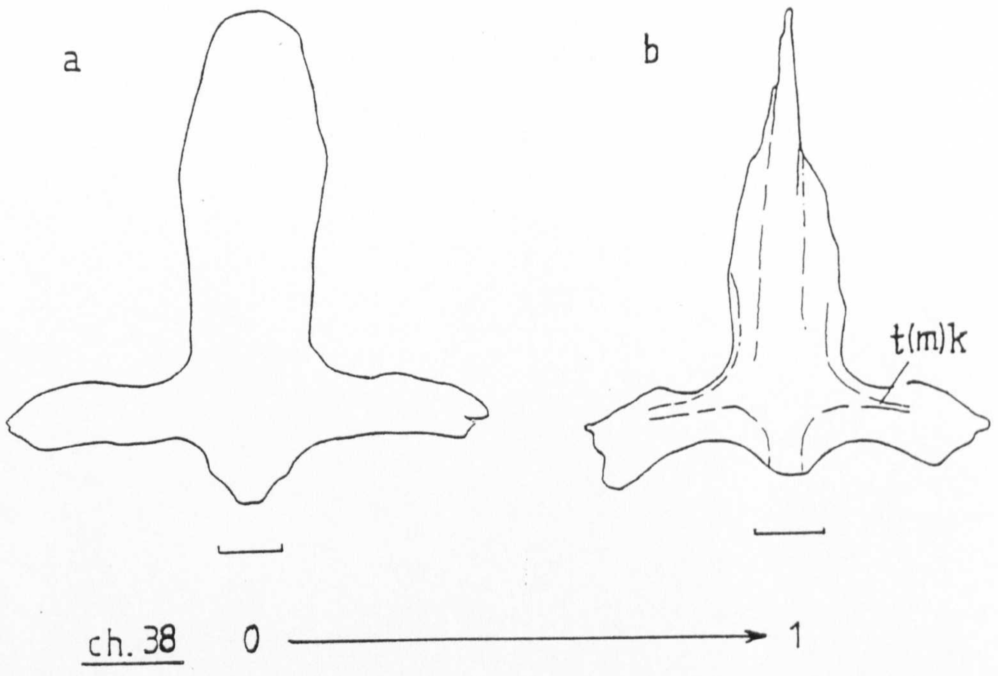


Fig. 68



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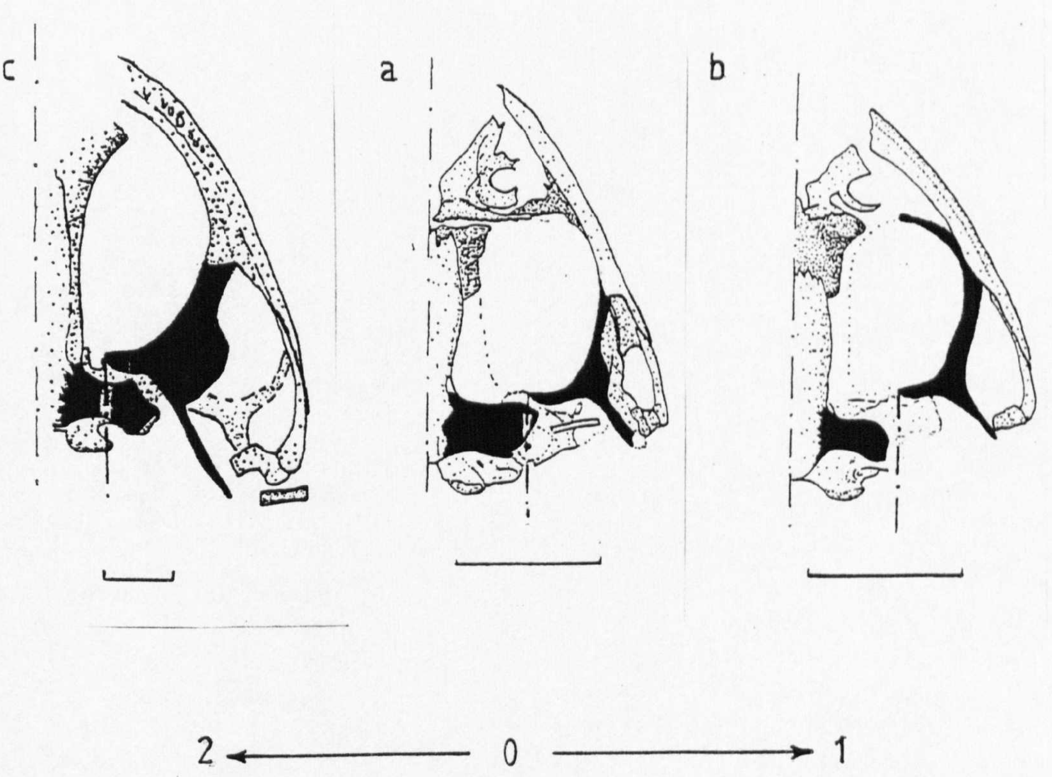

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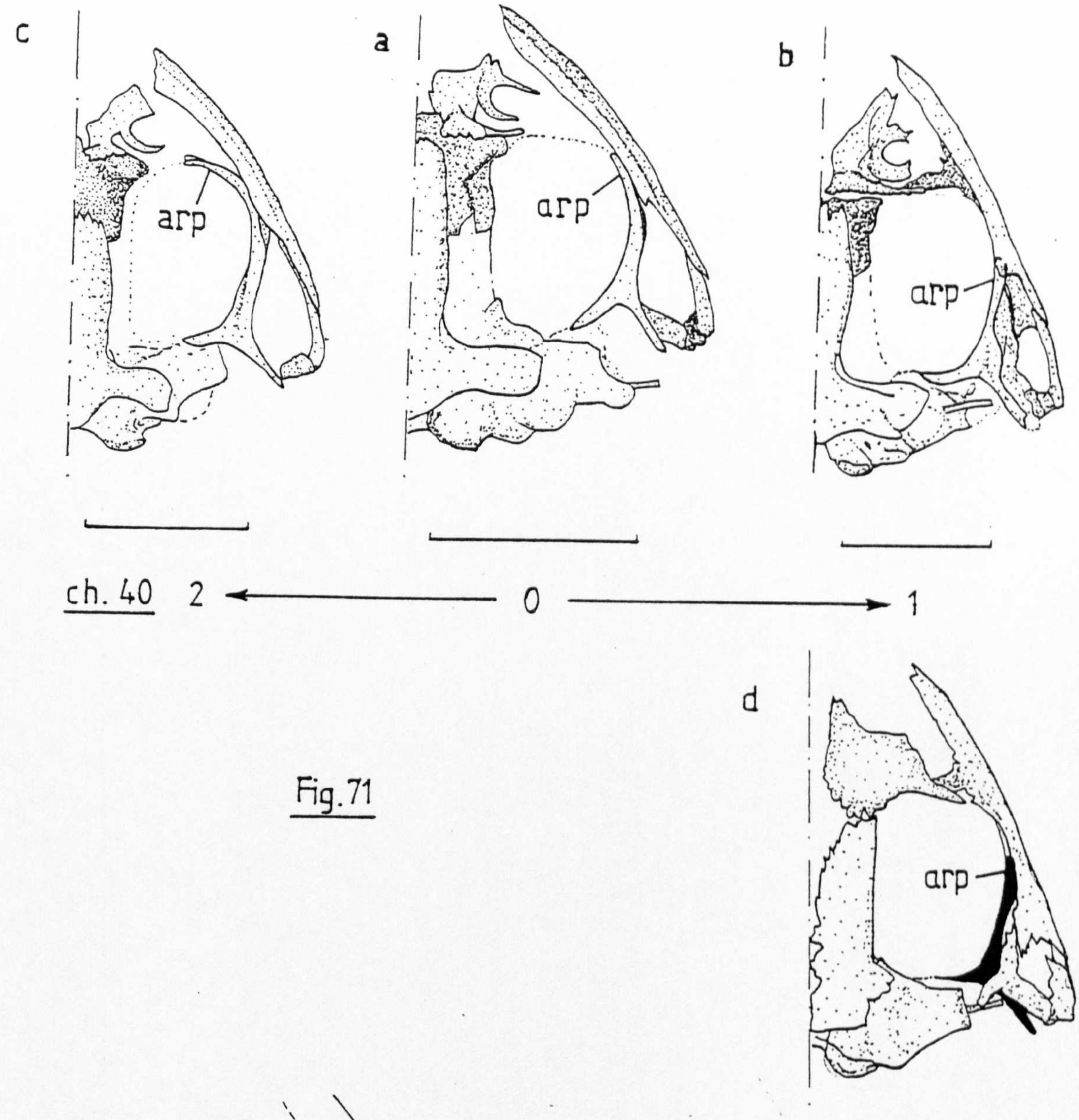

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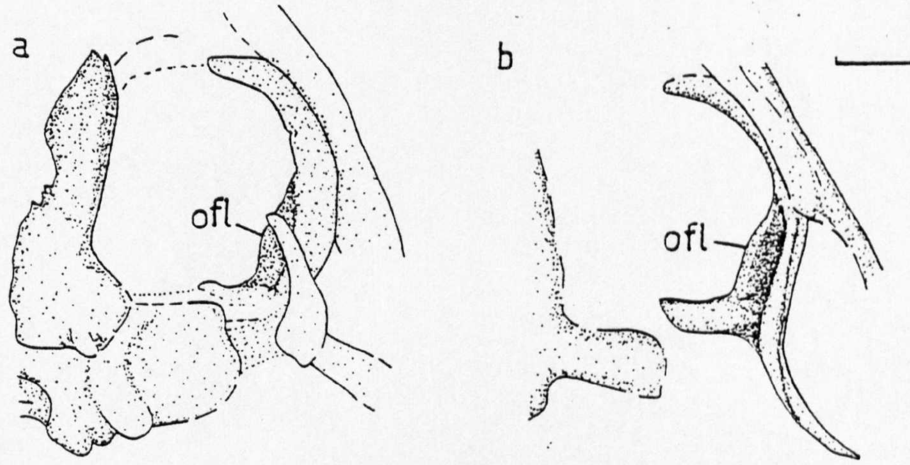


ch. 41: state 1

Fig. 72

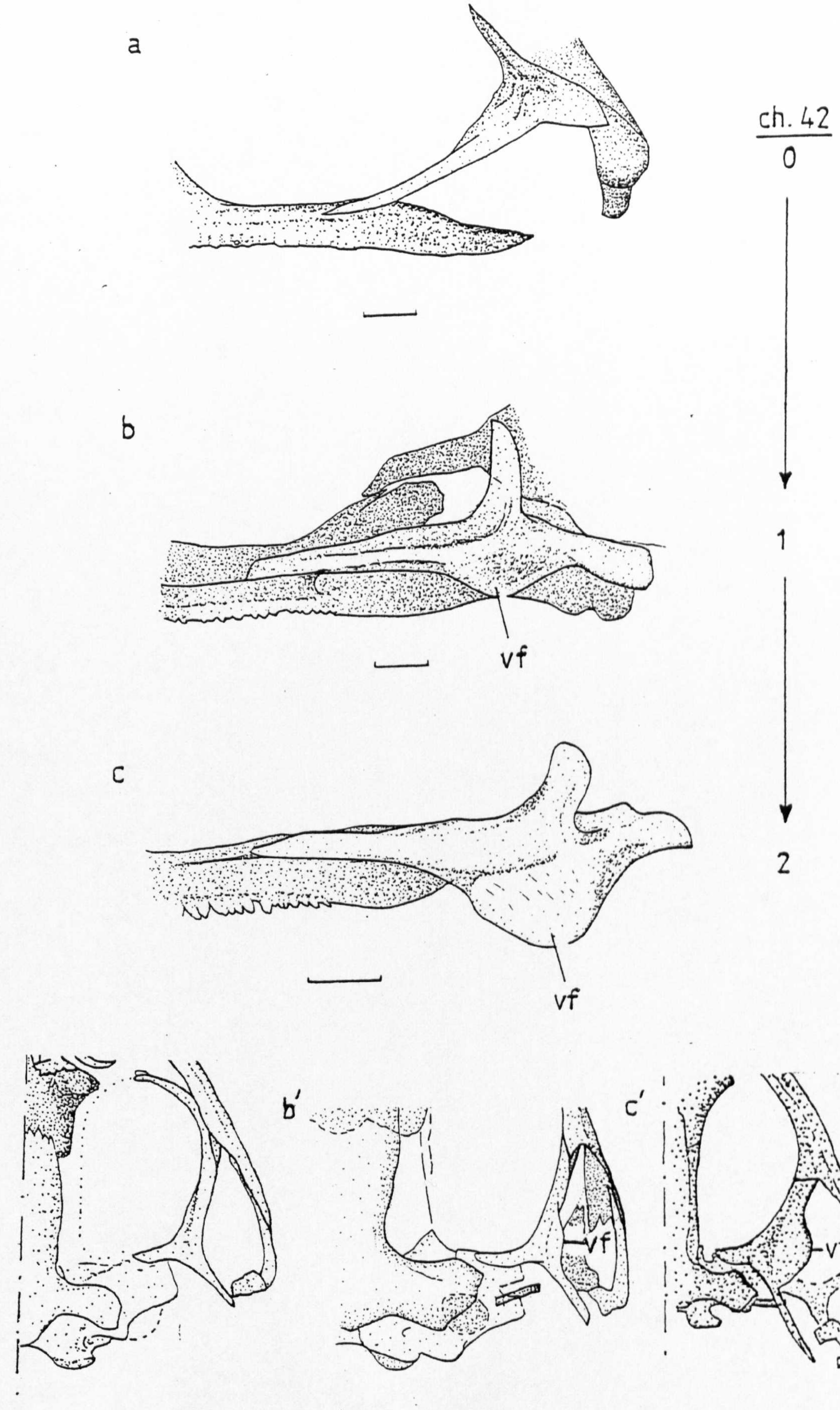


Fig. 73

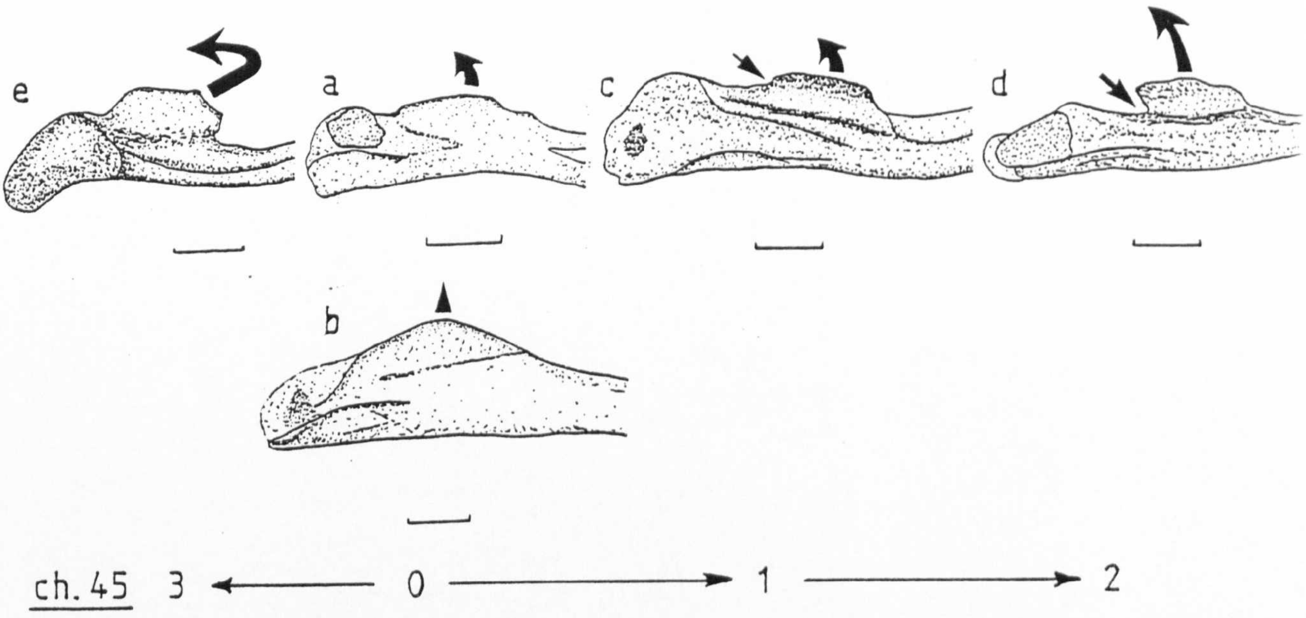


Fig. 74

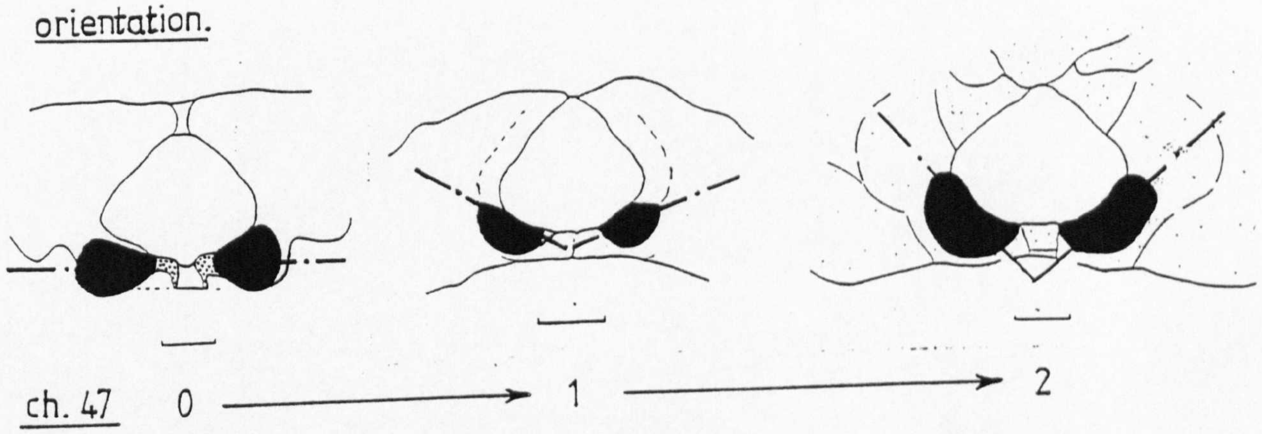


Fig. 75

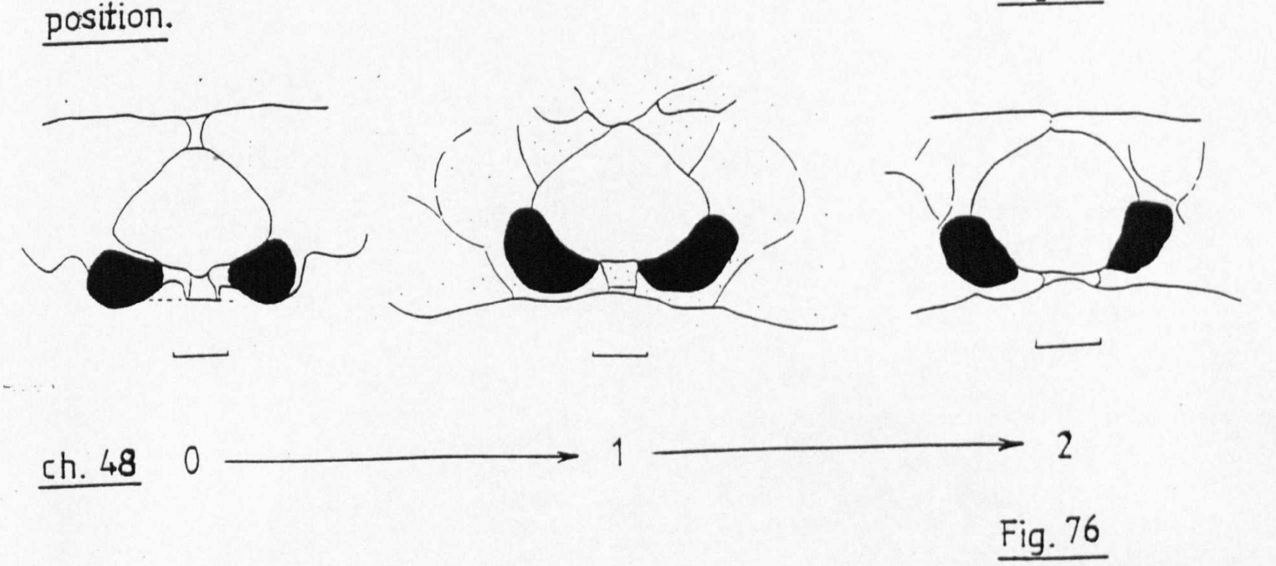
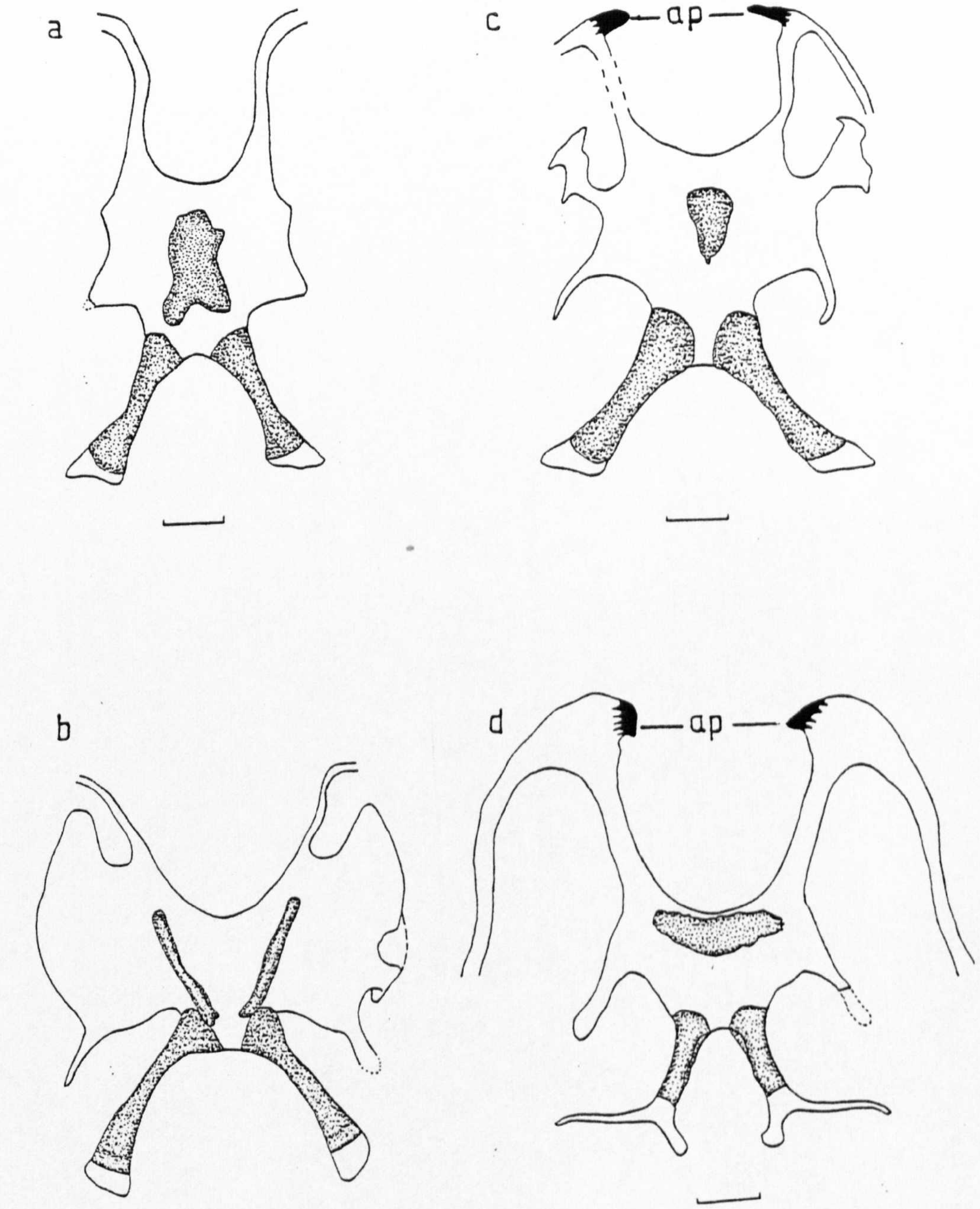


Fig. 76



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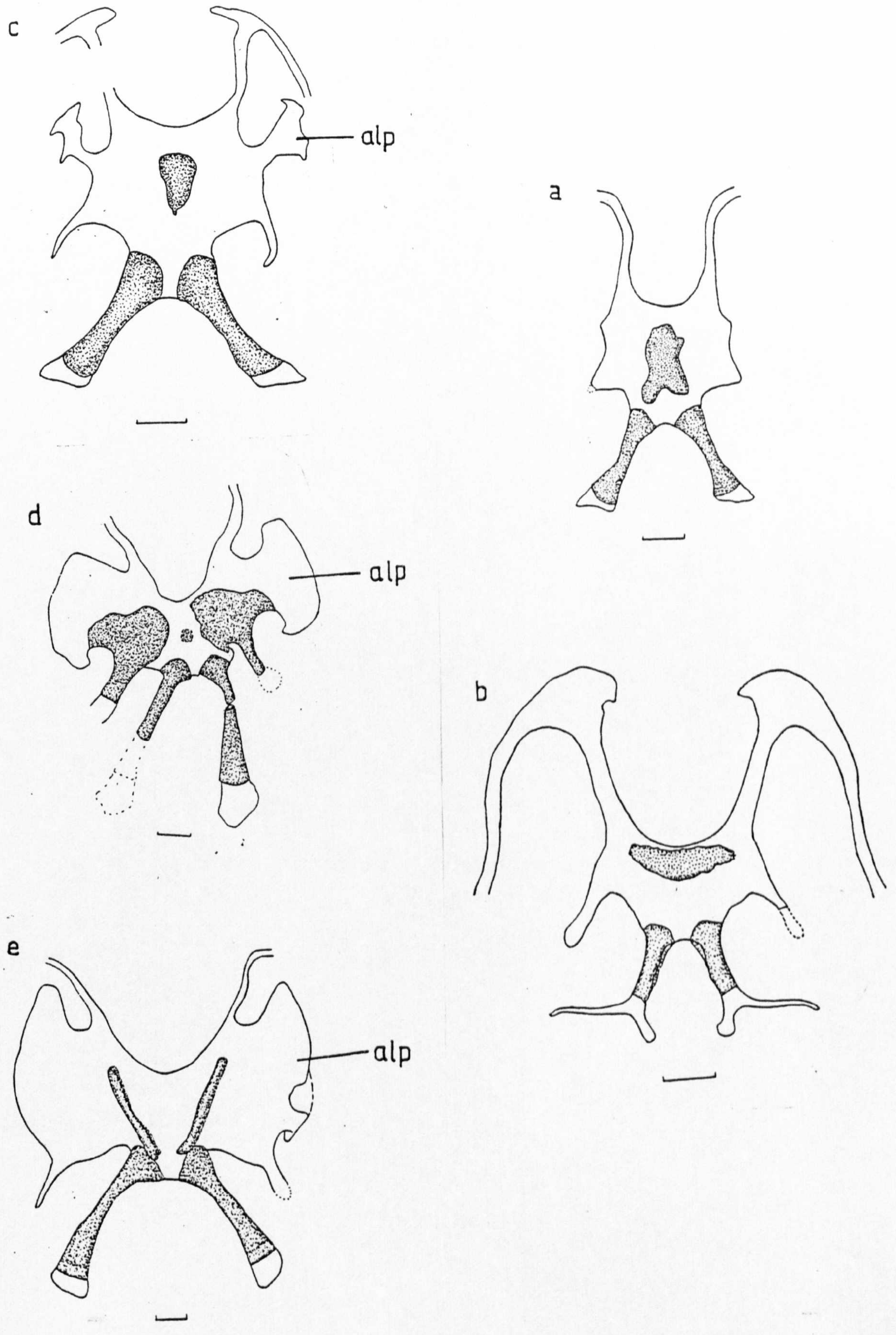


Fig.78

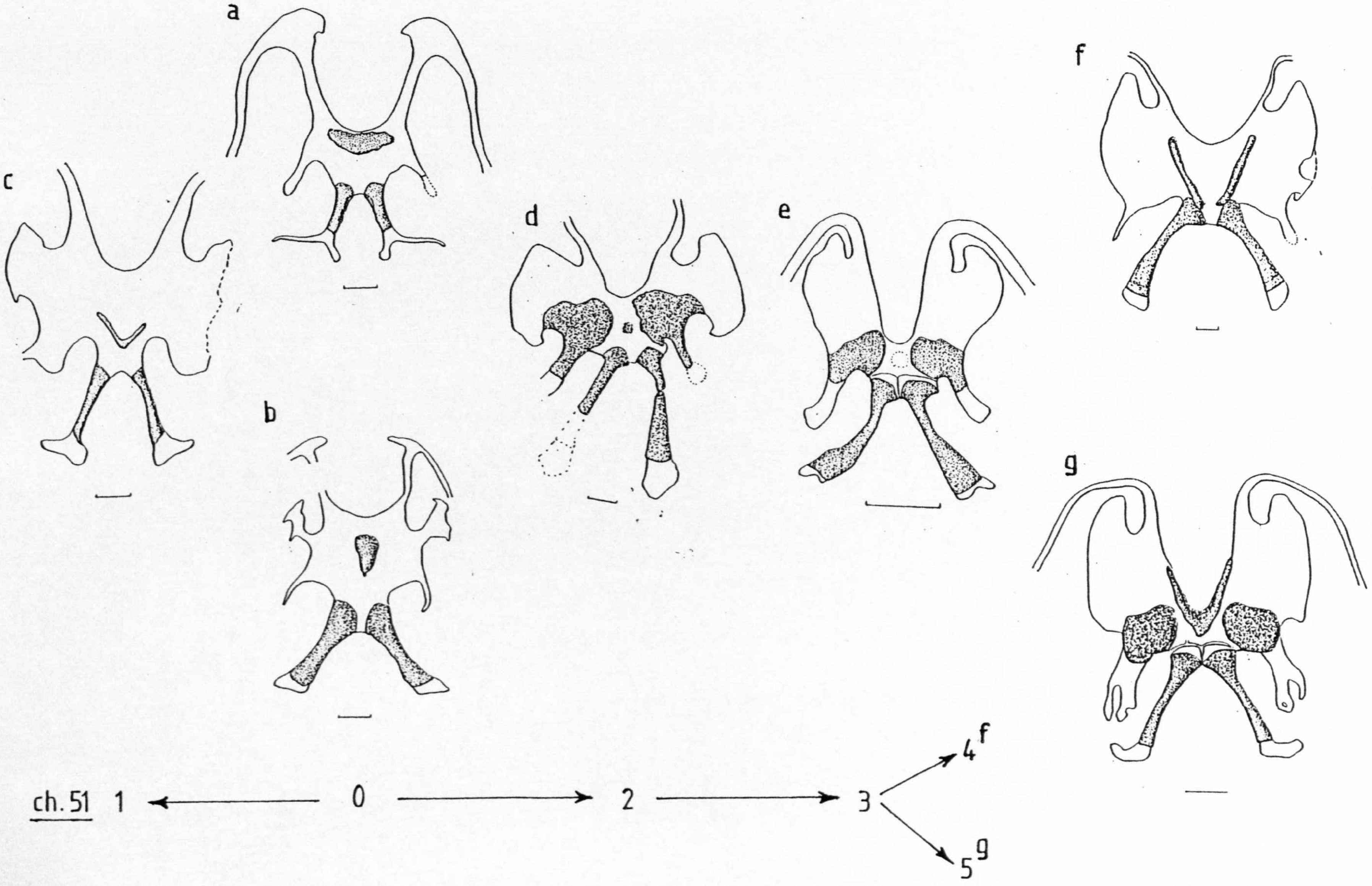


Fig. 79

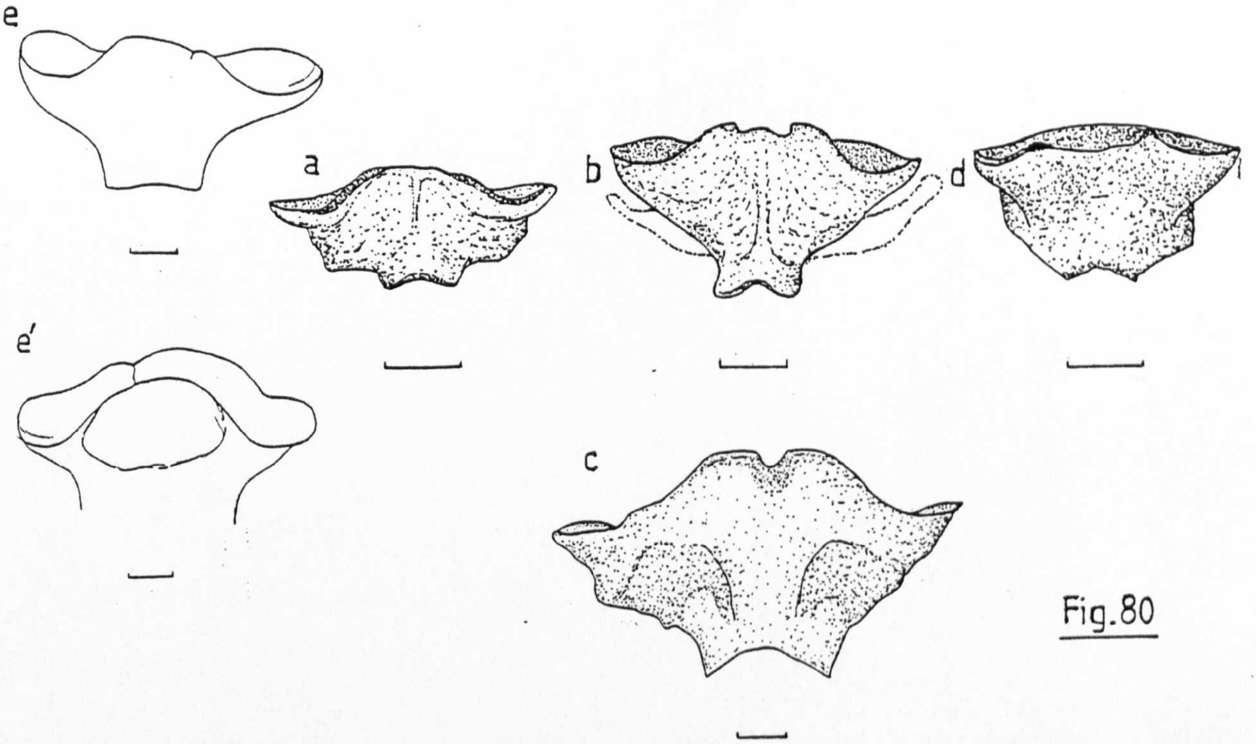
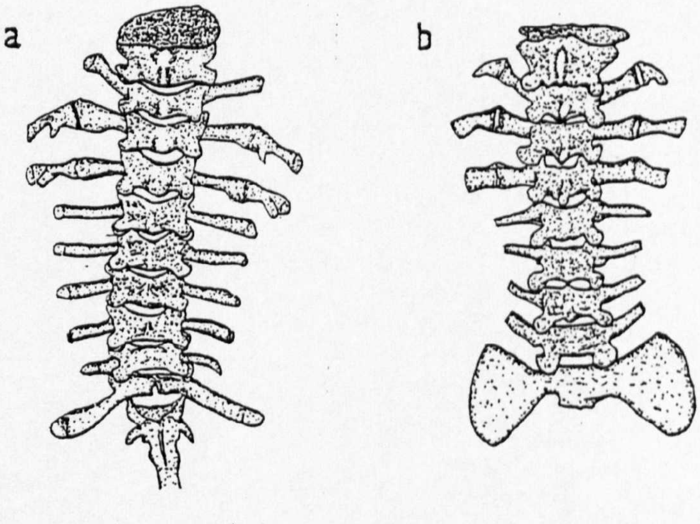


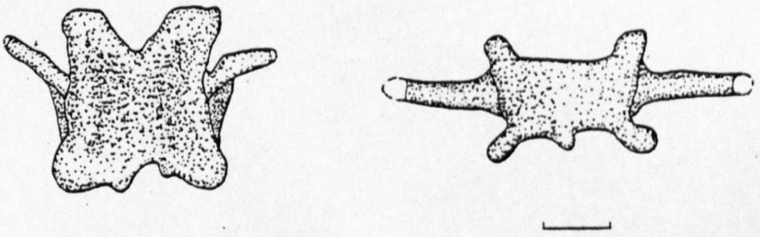
Fig.80

ch. 52 3 ← 0 → 1 → 2



ch. 53 0 → 1

Fig.81



ch. 55 0 → 1

Fig.82

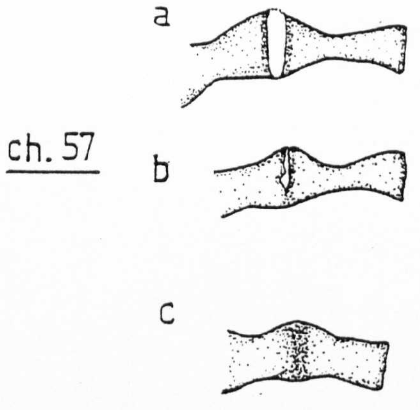


Fig. 83

Fig. 84

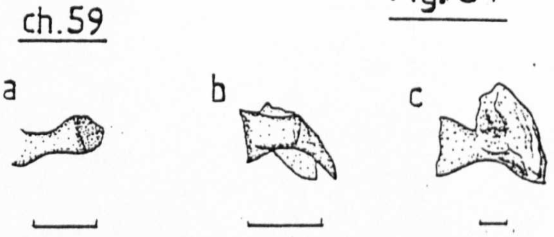


Fig. 85

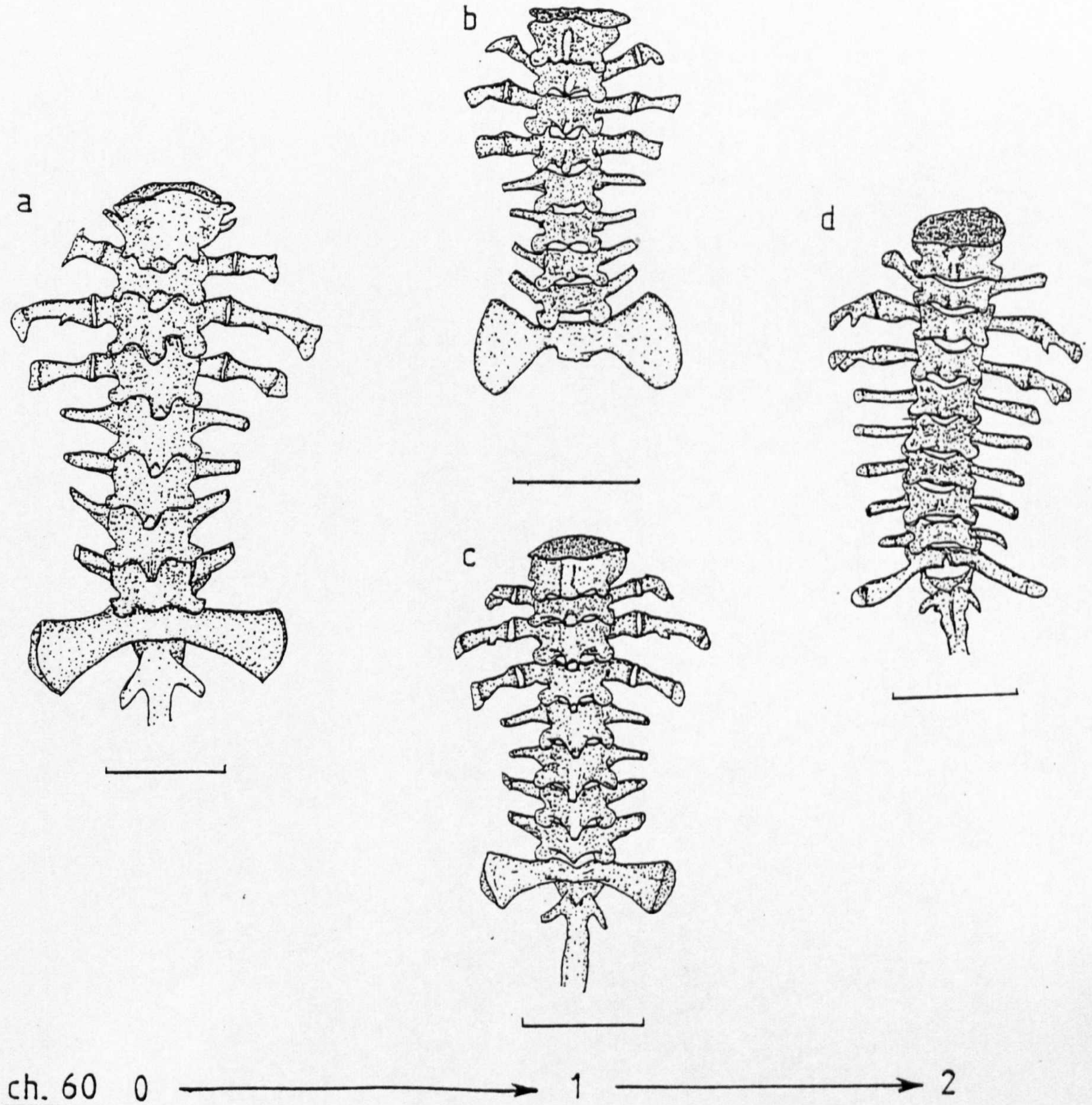


Fig.86

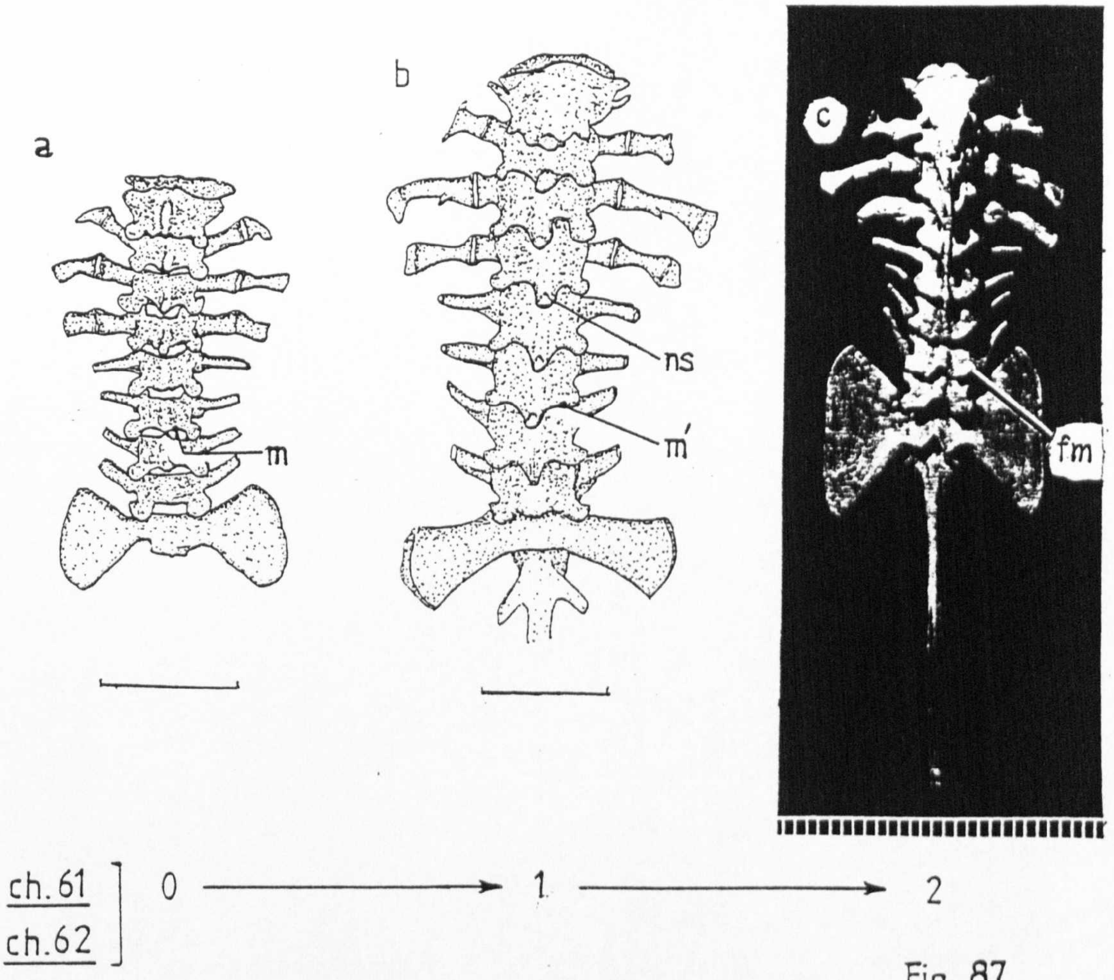


Fig. 87

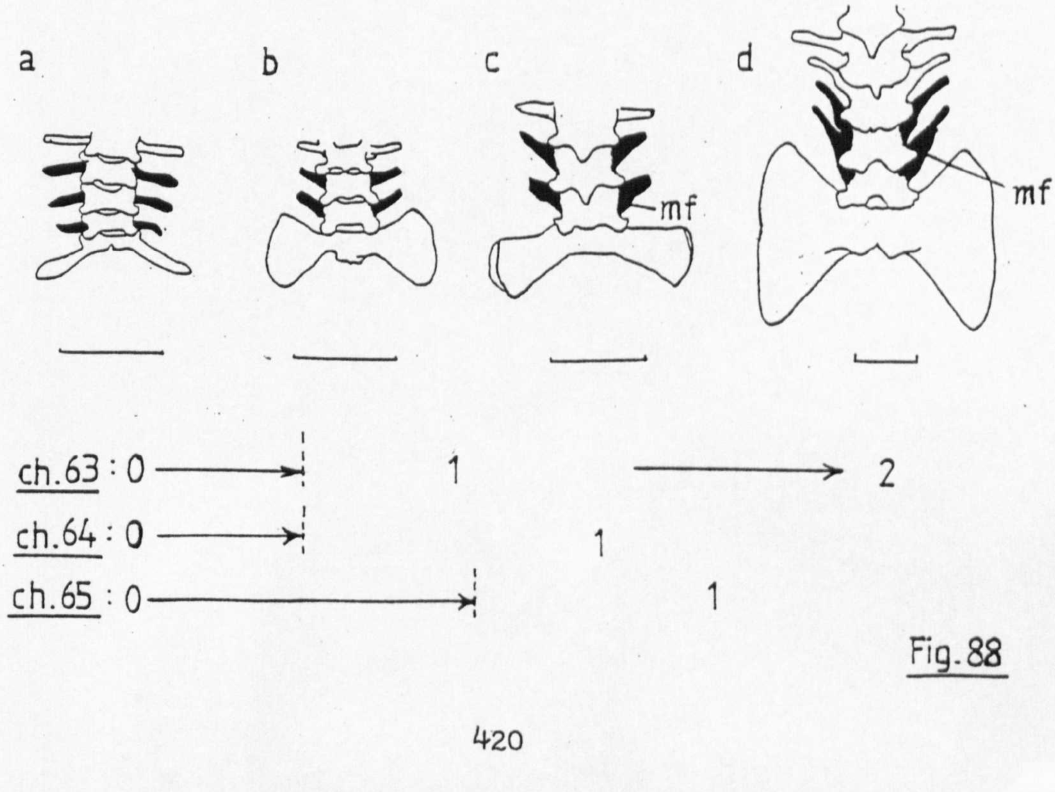


Fig. 88

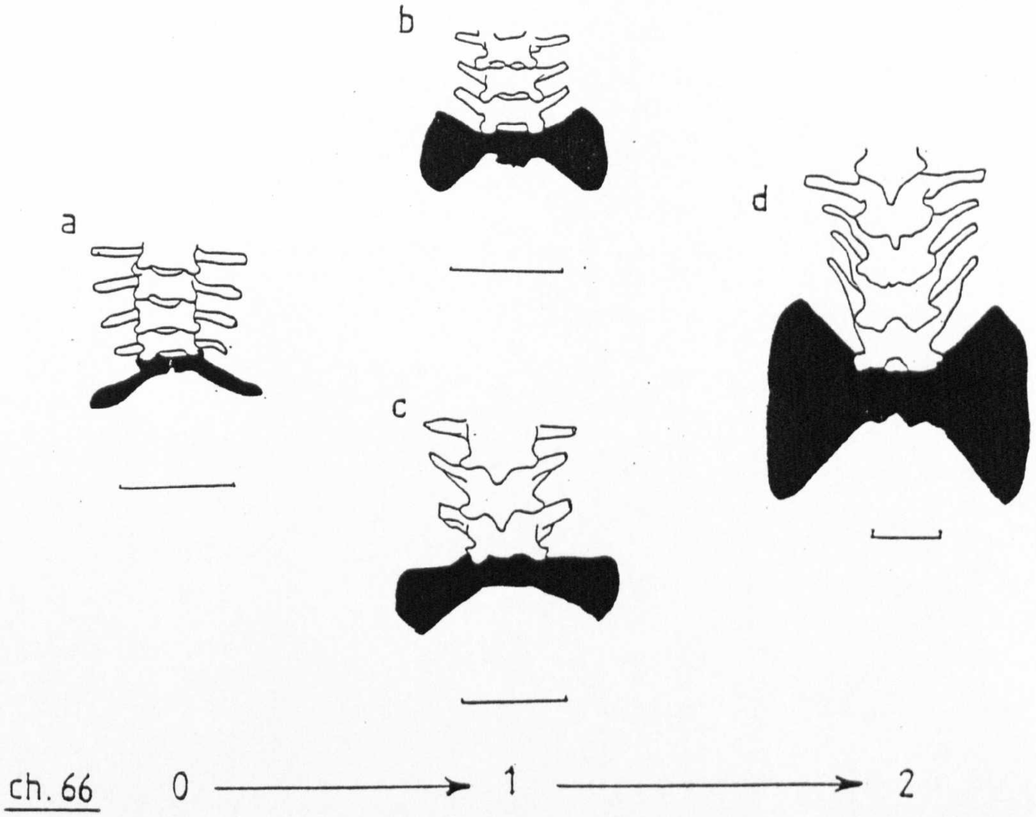


Fig. 89

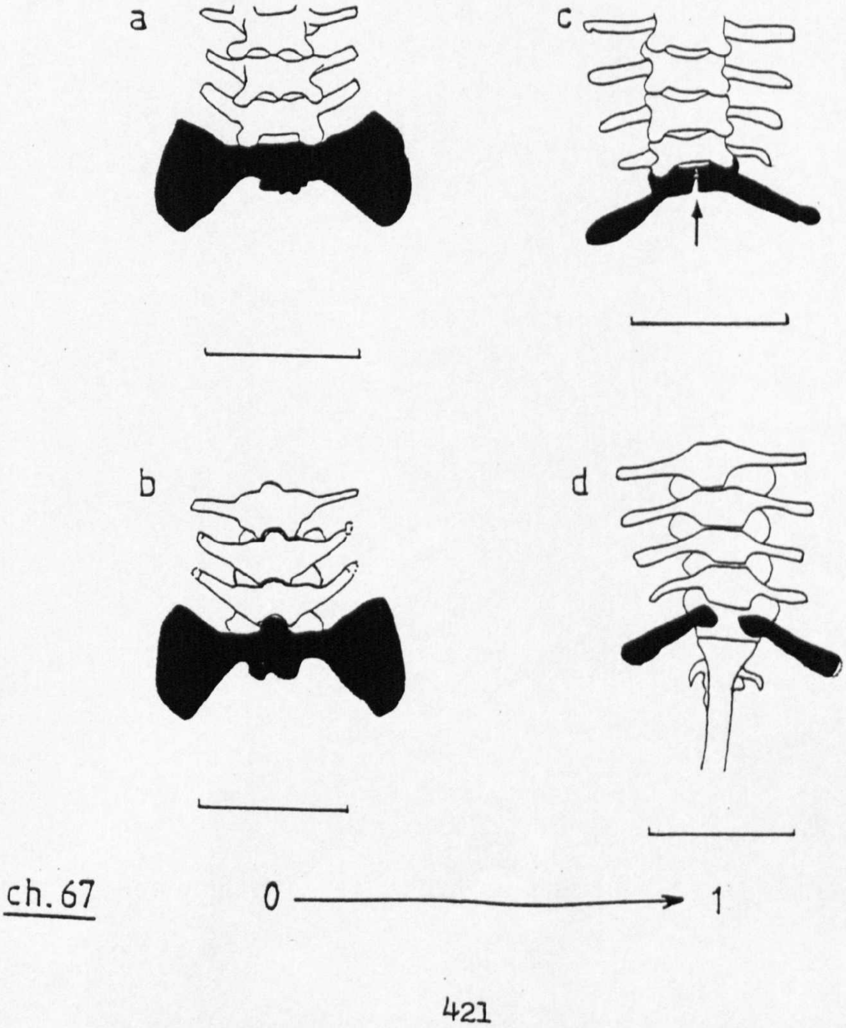


Fig. 90

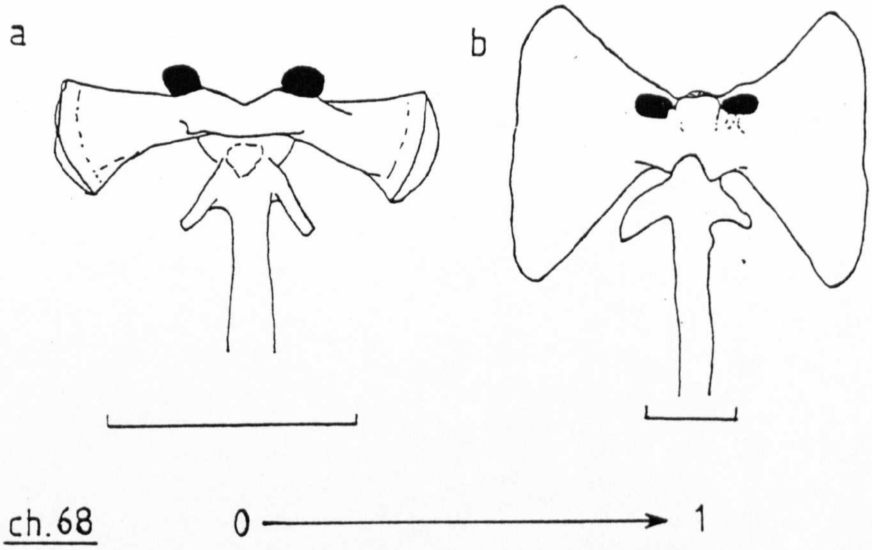


Fig. 91

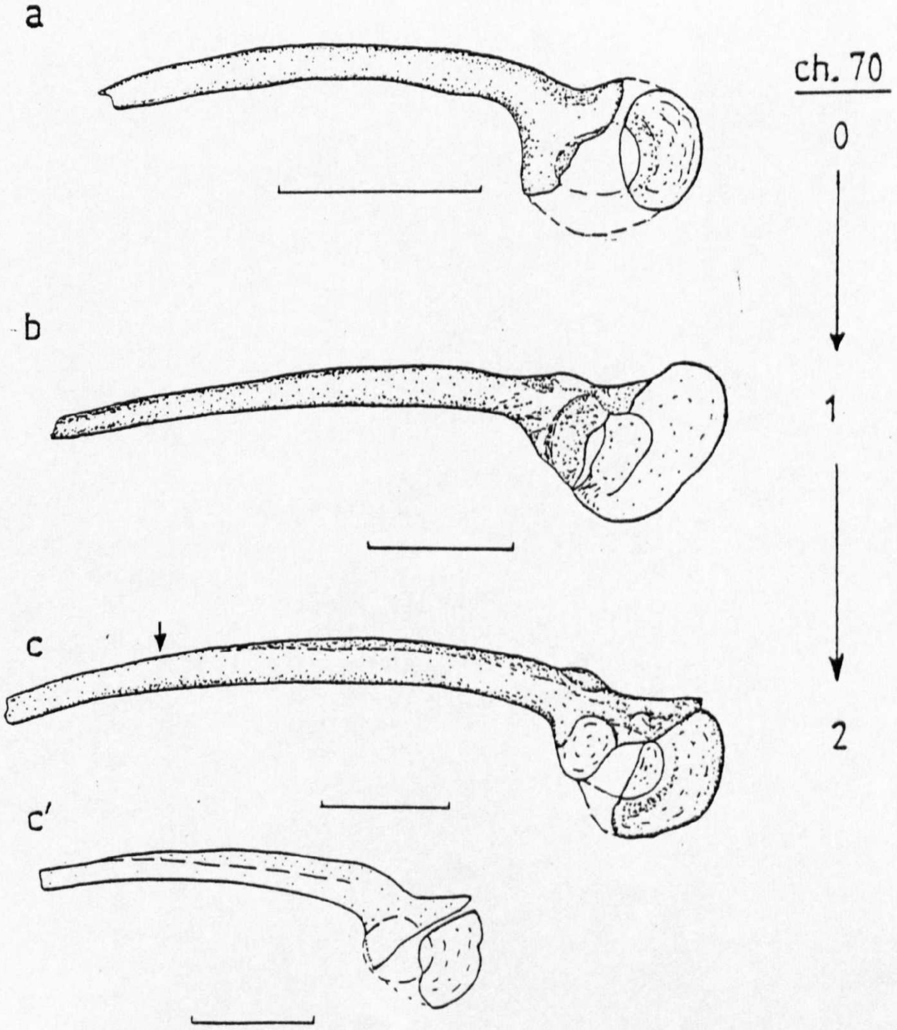


Fig. 92

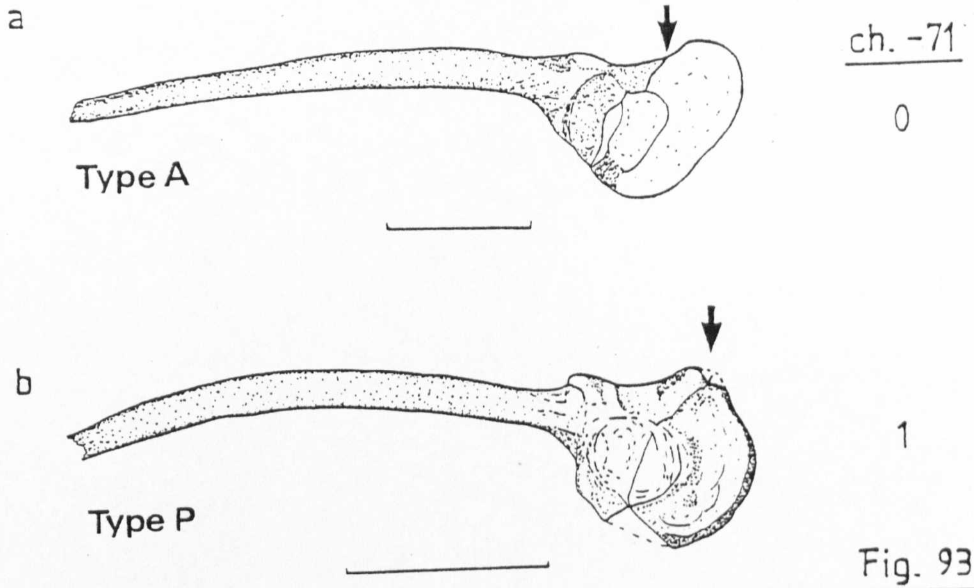


Fig. 93

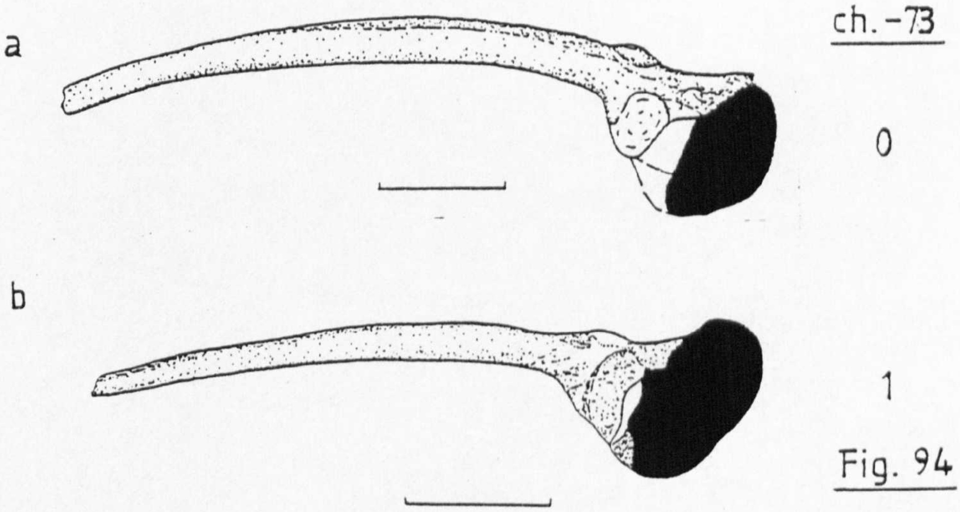


Fig. 94

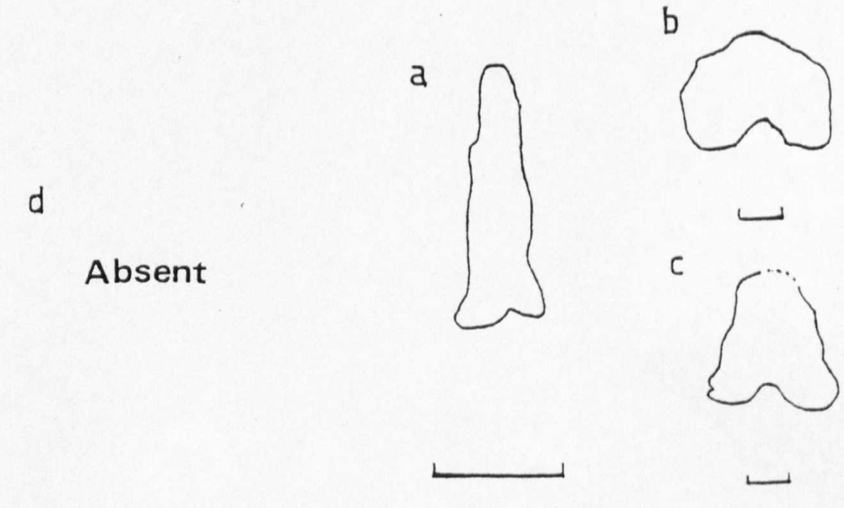


Fig. 95

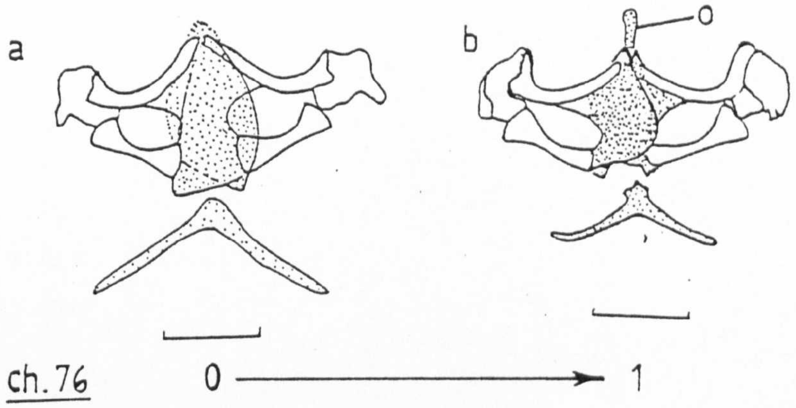


Fig. 96

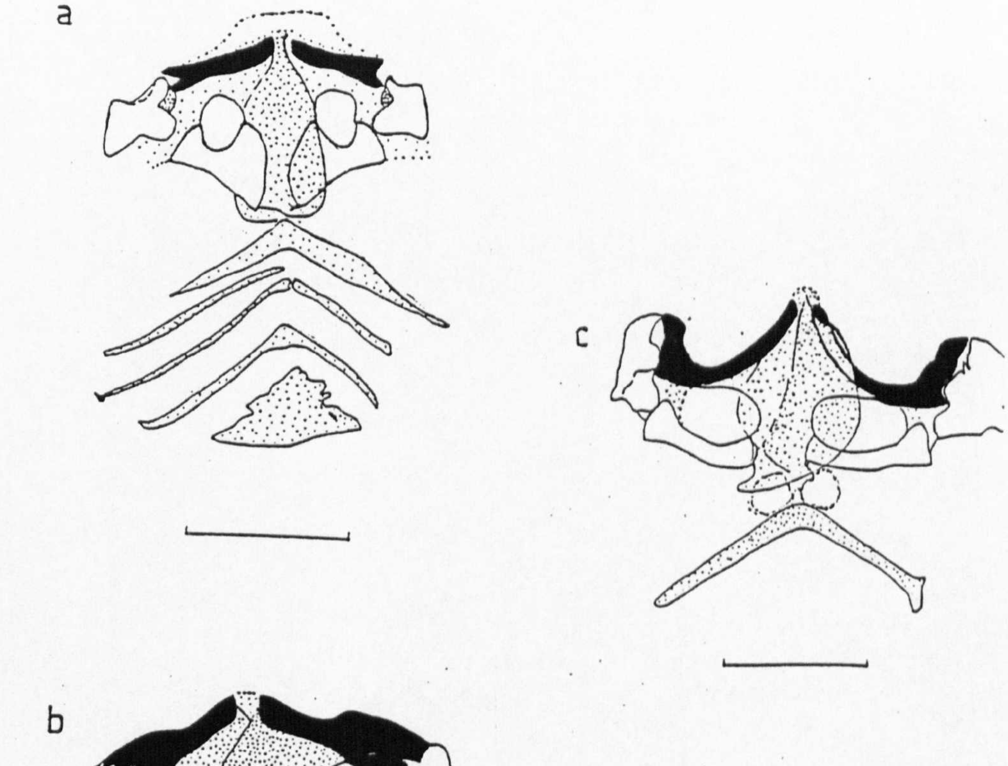


Fig. 97

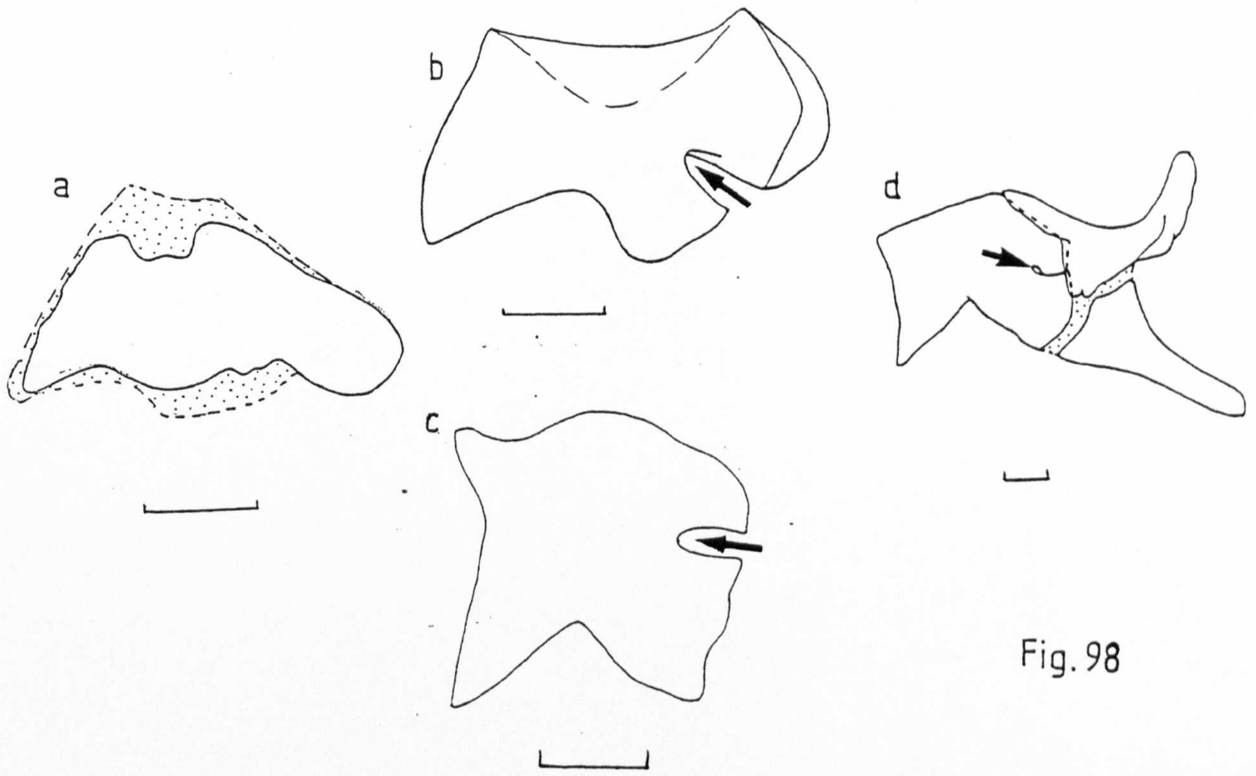
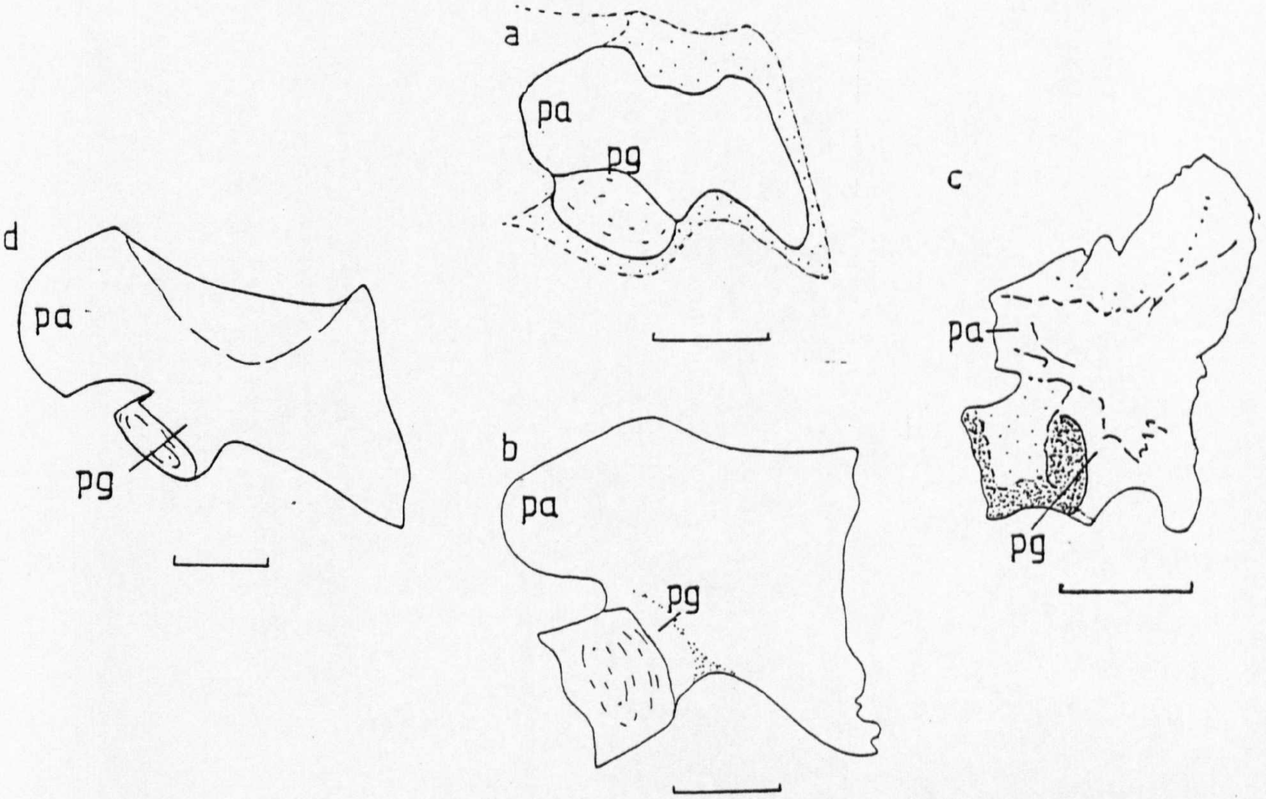


Fig. 98

ch.-78 0 1 2



ch.-79 2 0 1

Fig. 99

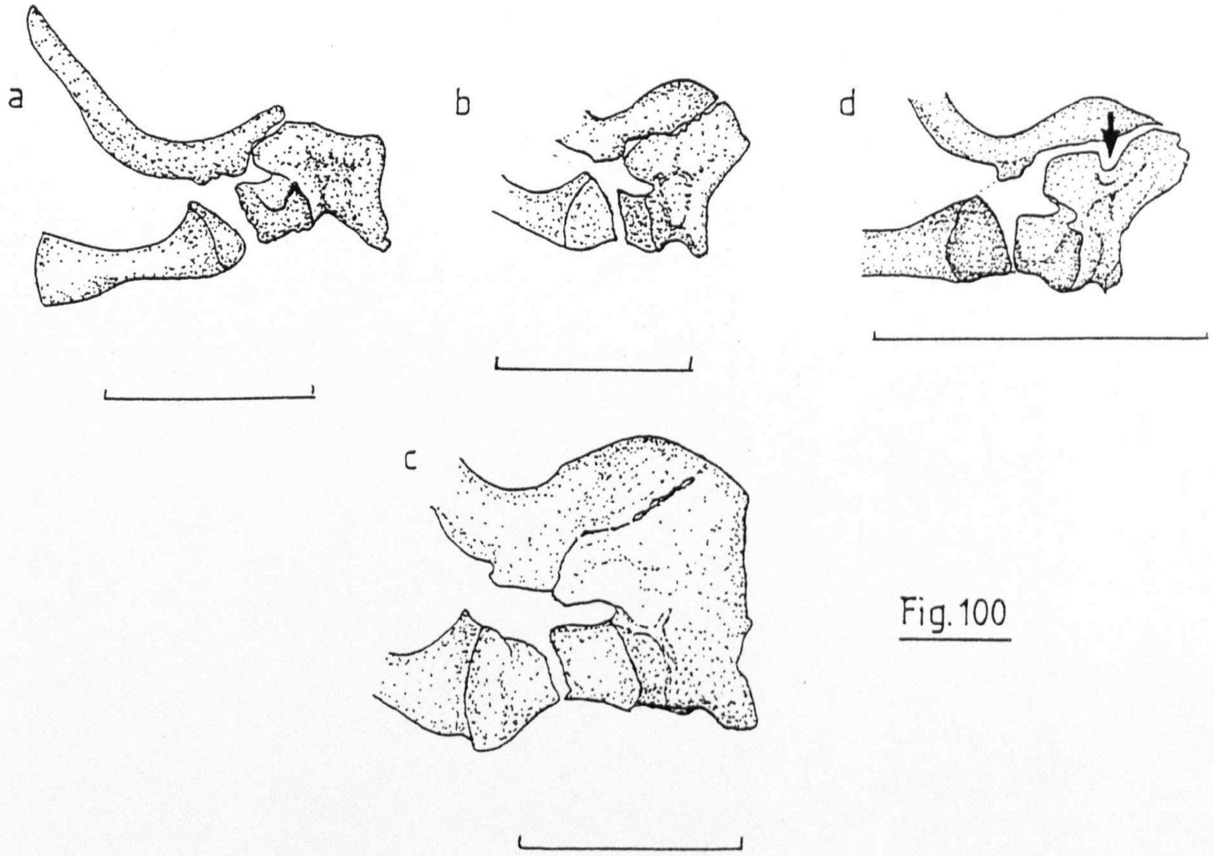
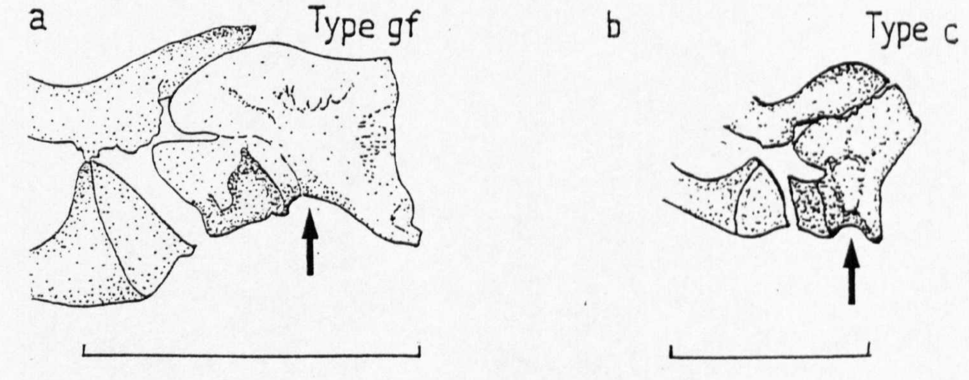


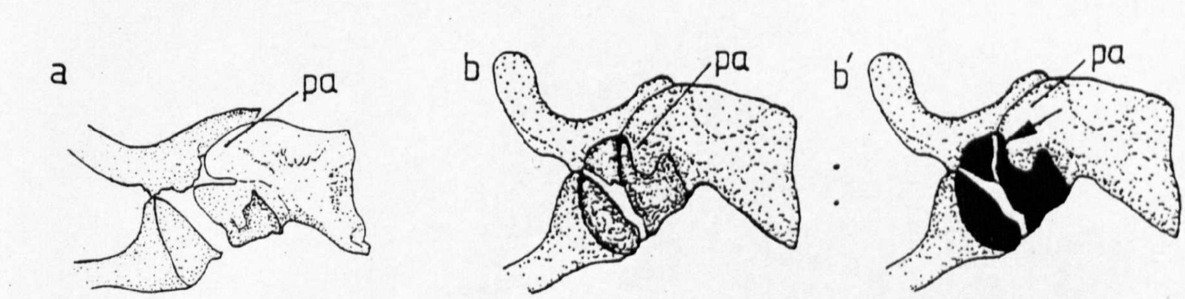
Fig. 100

ch.-80 0 1 2



ch.81 0 ⟶ 1

Fig.101



ch.-82 0 1

Fig. 102

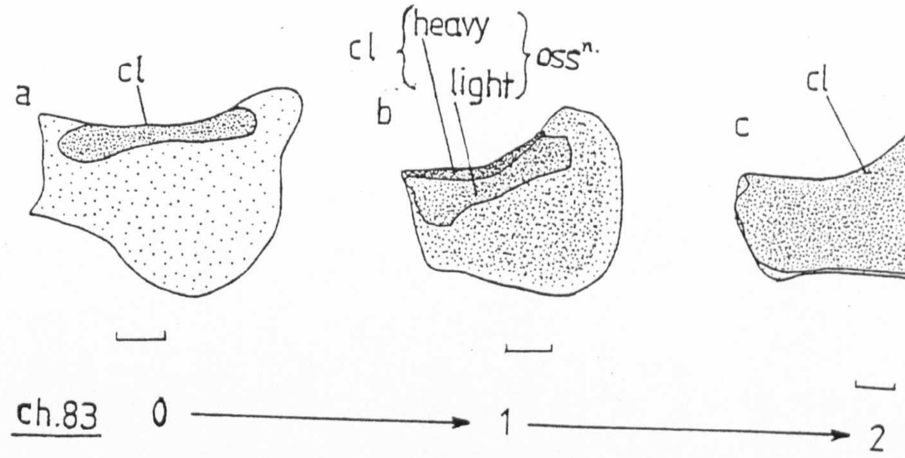


Fig.103

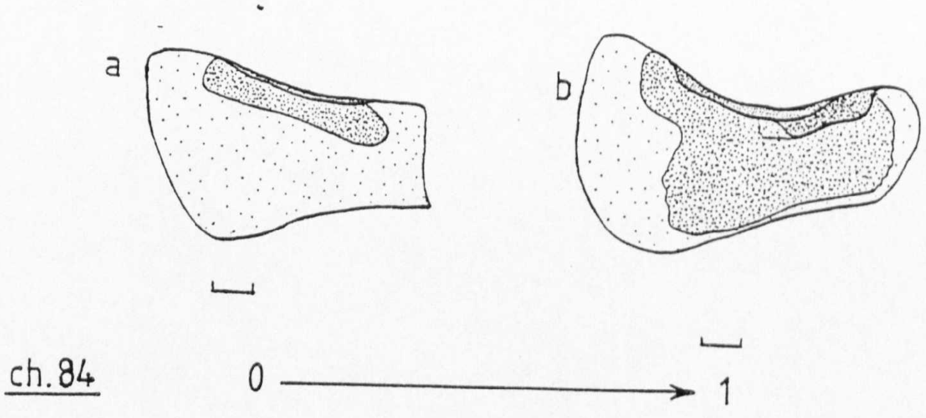


Fig.104

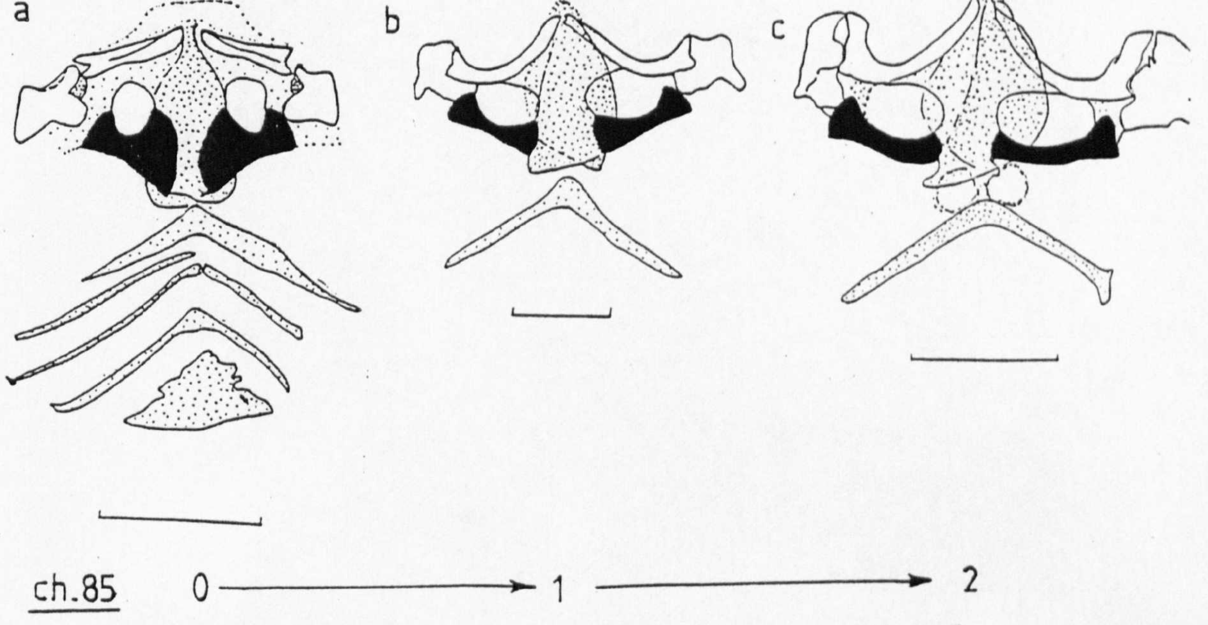


Fig.105

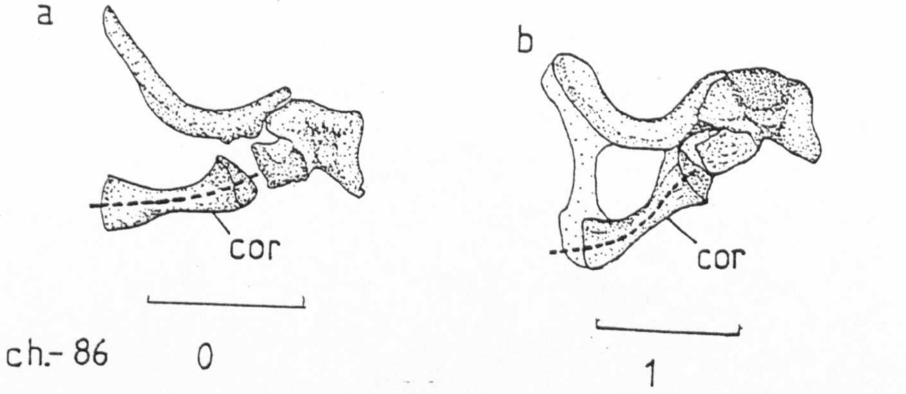


Fig. 106

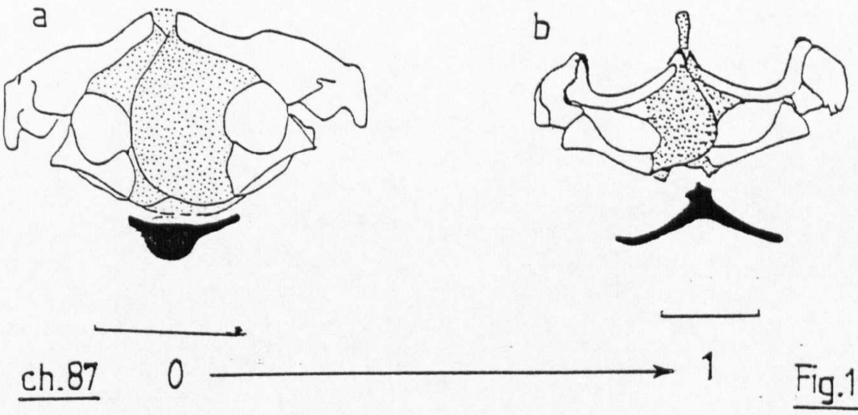


Fig.107

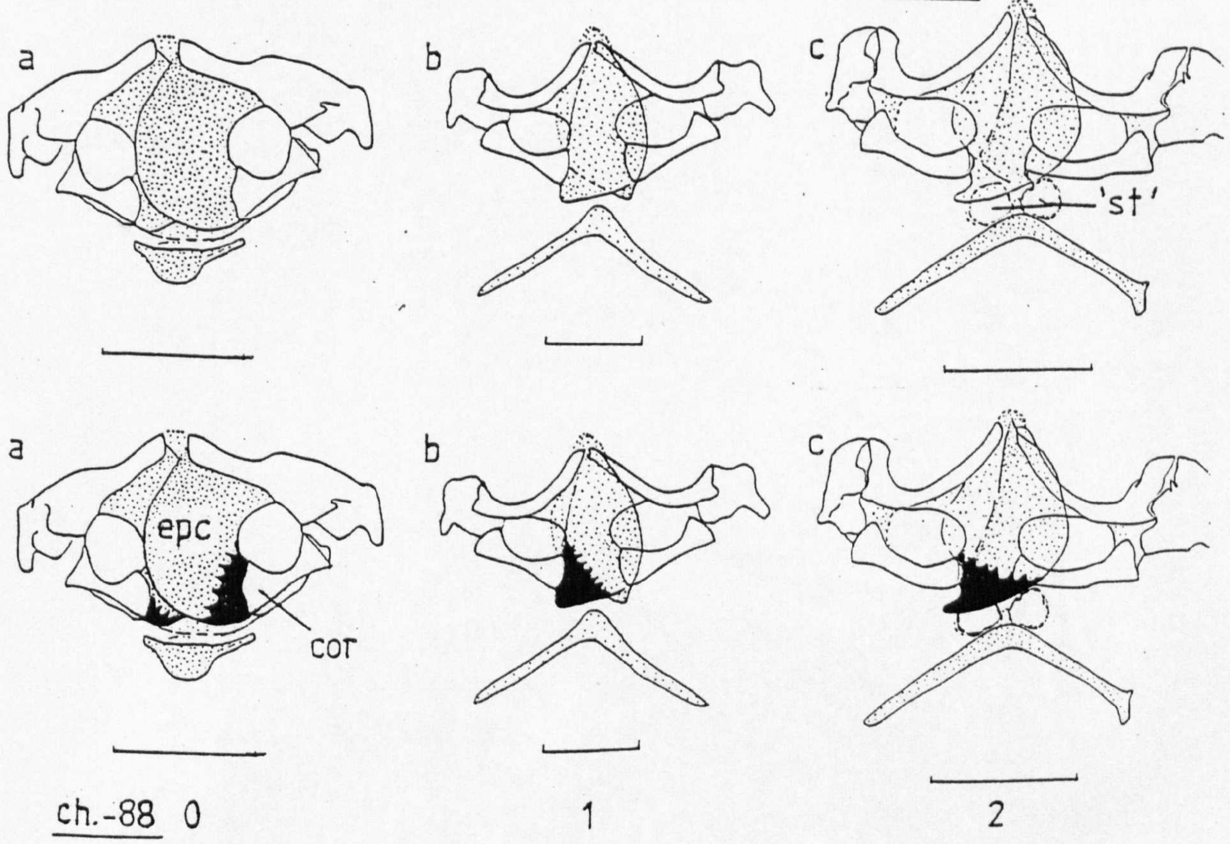


Fig.108

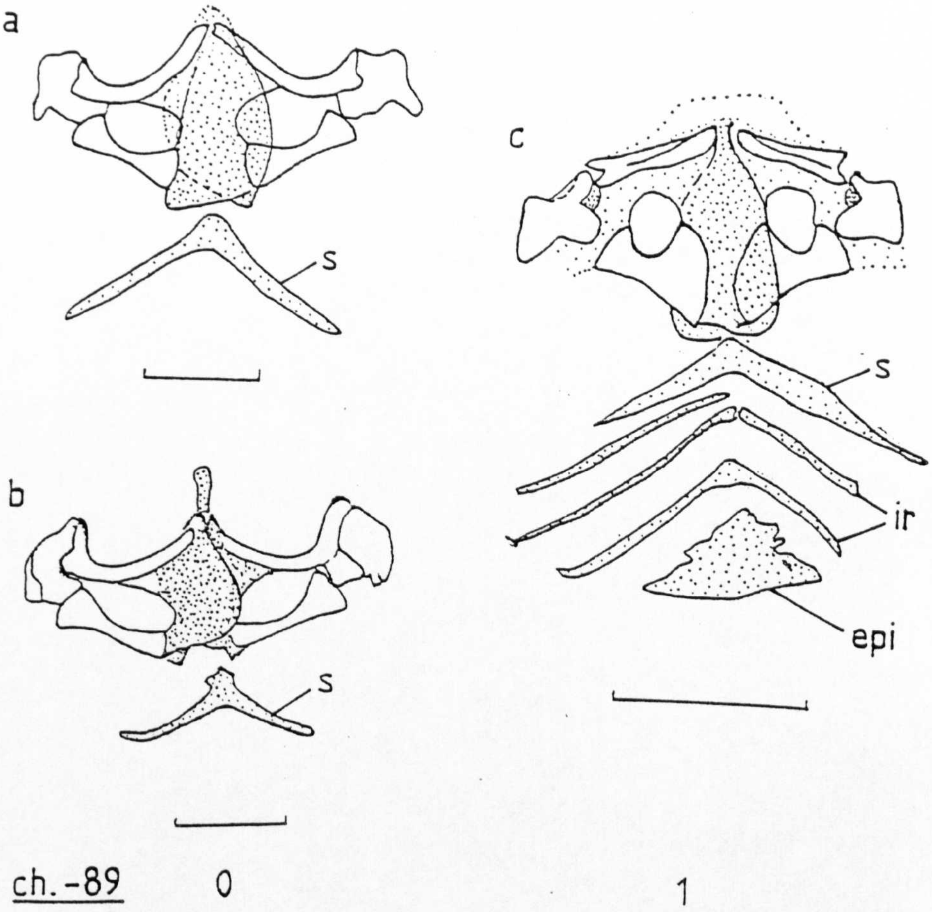


Fig.109

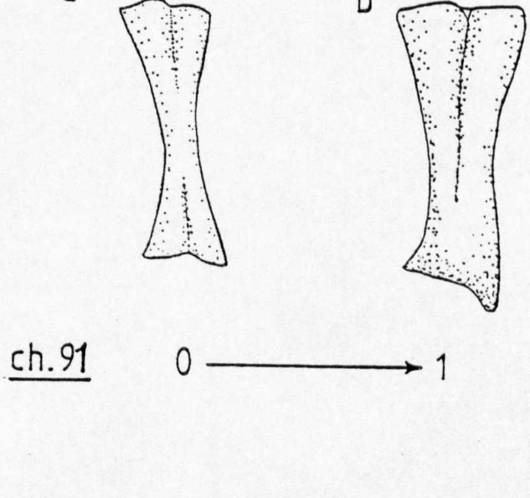


Fig.110

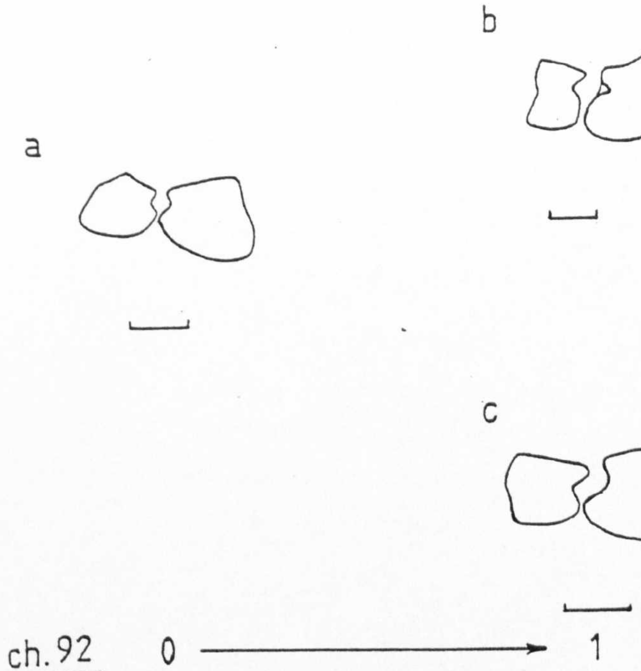


Fig.111

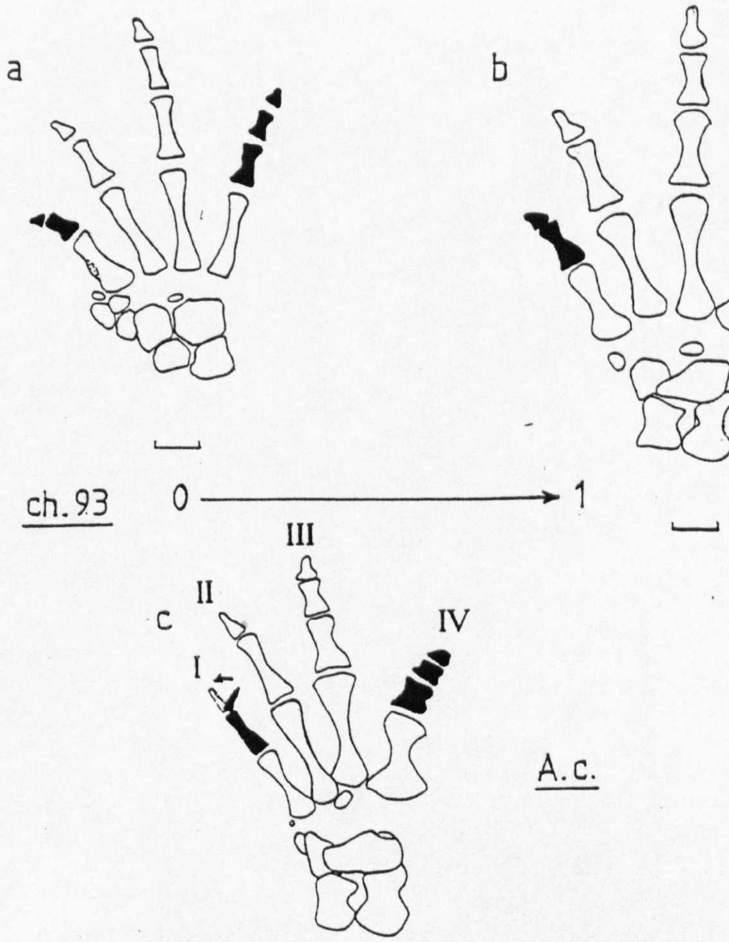


Fig.112

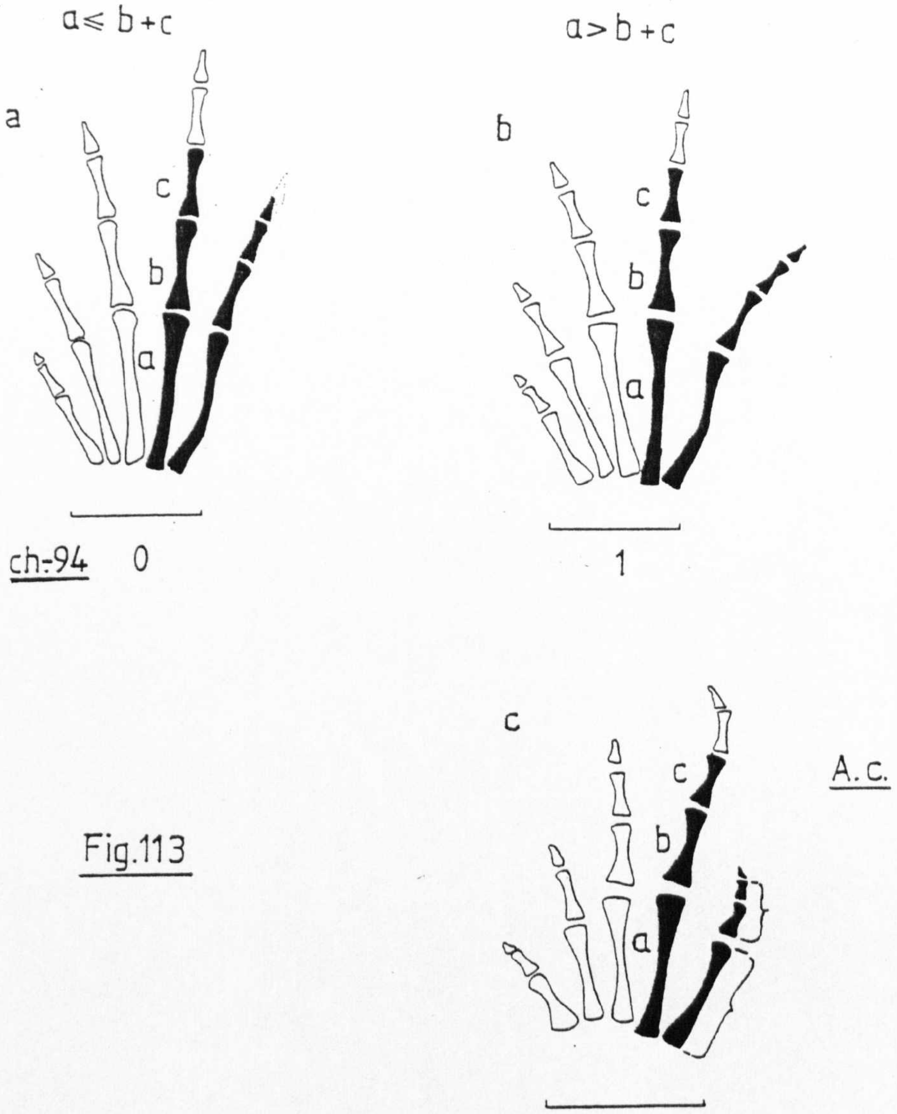


Fig.113

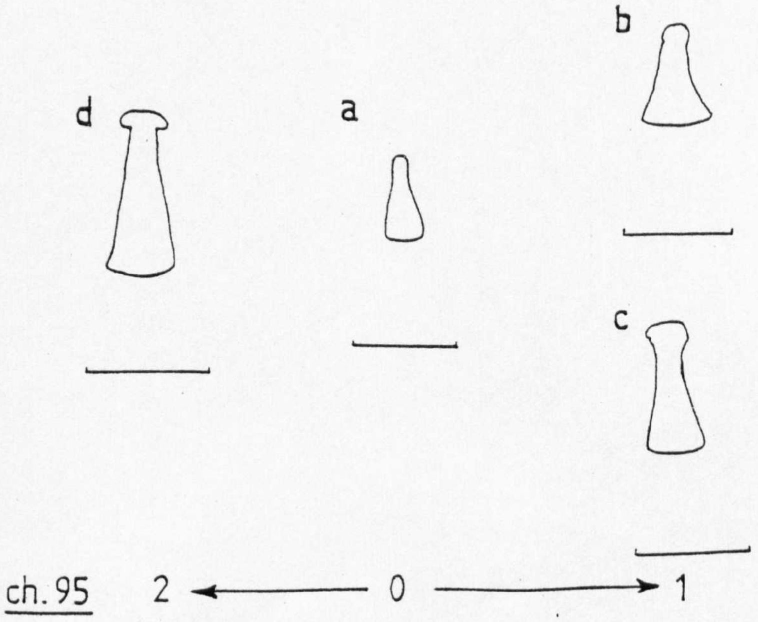


Fig.114

Appendix I. Material examined.

Abbreviations.

C&S = cleared and alizarined stained (bone only).
C&2S = cleared and double stained (bone and cartilage).
DS = dry skeleton.
WS = wet skeleton.
Numbers in brackets indicate numbers of specimens examined; first number indicates number of skeletal preparations, the second the total number of specimens examined (skeletal preparations + radiographed specimens).

1. *Alytes cisternasii.* (3; 11).
BM 1920.1.20.664 SPAIN: Badajos. (DS complete skeleton; skull only figured in Boulenger, G.A. 1897: 177, Fig 66).
BM 1980.251 PORTUGAL: Alentejo Valley; Moura. (C&2S).
BM 1982.35 SPAIN: Provincia del Caceres. (C&S).
Plus radiographs of a further 8 specimens:-
BM 98.3.30.47 PORTUGAL: Mertola.
BM 86.12.29.74-76 SPAIN: Merida.
BM 1906.1.10.5-6 SPAIN: Madrid.
BM 1920.1.20.614 SPAIN: Merida.
BM 1970.397 S. PORTUGAL: Algarve; Sierra de Monchique, Nave.

2. *Alytes muletensis.* (5; 13).
BM 1985.343 BALEARIC ISLANDS: Mallorca; Serra de Tramuntana. (C&S: Skull only, previously JAA 81090207).
BM 1985.344 -same data as BM 1985.343- (Skull C&2S; postcranial skeleton C&S: JAA 81090203).
BM 1985.345 -same data as BM 1985.343- (Skull C&S: JAA 81090507).
OM 1985.348 -same data as BM 1985.343- (Skull C&S .JAA 81090509).
BM 1985.355 -same data as BM 1985.343- (Skull C&S).
The above 5 plus another 8 (unregistered, same data) radiographed.

3. *Alytes obstetricans.* (7; 24).
BM 1920.1.20.662 FRANCE: near Paris. (DS).
BM 1928.1.20.117 FRANCE: Paris. (Skull C&S; postcranial skeleton C&2S).
BM 1983.914 SWITZERLAND: Canton Berne; Oppligen, about 10 km. N. of Thoune. (C&S).
BM 1920.1.20.803. BASSES PYRENEES.
BM 1920.1.20.2462. FRANCE: near Paris.
ZMA 7593/1-2.
Plus radiographs of a further 17 specimens:-
BM 85.9.2.51 FRANCE: Jura Mountains.
BM 87.8.25.37 LUXEMBURG: Mondorf.
BM 92.4.18.48 FRANCE: Paris.
BM 97.5.28.23-24 BELGIUM: near Liege.
BM 1910.9.12.9 FRANCE: Brittany; Finistere, Roscoff.
BM 1913.8.30.19 FRANCE: Brittany; near St. Malo.
BM 1983.659-668 S. BELGIUM: Romedenne, 12.5 km E. of Philippeville; 50 10´N 4 42´E.

4. *Alytes obstetricans boscai.* (4; 14).
BM 1908.5.29.12A&B SPAIN: La Granja. (C&S: -12A Skull only).
*BM 1972.1726 N.W. SPAIN: Lago Ercina near Covadonga. (C&S).
BM 1972.1537 PORTUGAL: Vila Real district; Vidago. (C&S).
Plus radiographs of a further 10 specimens:-
*BM 1972. 1725, 1727-33 N.W. SPAIN: Lago Ercina near Covadonga.

BM 1972.1537, 1541 PORTUGAL: Vila Real district; Vidago.
N.B. specimens marked with an * are tentatively assigned to *A. o. boscai* but the subspecific assignment of many of the Iberian populations remains uncertain.

5. *Alytes (o.) maurus.* (5; 6).
ZMA 7597 (5 specimens). MOROCCO: Rif Mountains; Tleta-Ketama. (C&S).
In addition, the following specimen was radiographed:-
MNHNP 5960 HOLOTYPE. MOROCCO: Massif du Talass n'Tane (Rif).

6. *Ascaphus truei.* (6; 12).
BM 1960.1.5.82 No locality. (C&S).
BM 1980.1058 OREGON: Jackson County; Bybee Creek. (C&S: skull only).
CAS 113961-64 OREGON: Benton County; top of Mary's Peak. (C&S).
Plus radiographs of a further 6 specimens:-
BM 1953.1.5.93 OREGON: Lane County; Oak Ridge. (X).
BM 1980.1058-1062 OREGON: Jackson County; Byebee Creek. (X).

7. *Barbourula busuangensis.* (4; 60).

BM 1982.409 PHILIPPINE ISLANDS: Busuanga Island; Singai (skull C&S, postcranial skeleton DS).
CAS-SU 6015 - same data as BM 1982.409. (DS).
CAS 21250. PHILIPPINE ISLANDS: Palawan Island. (C&2S).
FMNH 50999 PHILIPPINE ISLANDS: Busuanga. (DS).
Plus radiographs of a further 56 specimens:-
*MCZ 14004 HOLOTYPE
BM 1977.1202-03
*BM 1980.410
*BM 1982.410
CAS 100453-55
CAS 157355
*CAS-SU 6004, 6006
*CAS-SU 6013-14, 6017
*CAS-SU 6024, 6043
CAS-SU 21220-22
CAS-SU 21225-30
CAS-SU 21332-33, 21336-38
CAS-SU 21240-46
CAS-SU 21253-54
*FMNH 40482
*FMNH 50997-98
*FMNH 51000-01
*FMNH 51003-05
*FMNH 51011, 51011
*FMNH 51013
*FMNH 51020-24
*FMNH 123477

* From Busuanga Id., allothers from Palawan Id.

8. *Barbourula kalimantanensis.* (0; 1).
Radiographs of the holotype and only known specimen were made available - registration no. MZB Amph. 2330. INDONESIA (BORNEO): West Kalimantan; Nanga Sayan (0 44'S 111 40'E).

9. *Bombina bombina.* (2; 4).
BM RR1937.7.29.31 GERMANY: Berlin. (WS).
BM 1973.2187 CZECHOSLOVAKIA: Moravia; Dist. Sumperk, Moravicany.

(C&S).
In addition limited dissections of two "no data" specimens were also made - BM 1982.30-31.

10. Bombina maxima. (7; 11).
BM 1906.5.29.15 CHINA: Yunnan Province; Tong Chuan Fu. (C&S).
BM 1906.5.29.32 CHINA: Yunnan Province; Tong Chuan Fu. (WS).
UF 51246 "China". (DS).
UF 54133-35 No data. (DS).
UF 55486 No data. (DS).
Plus radiographs of a further 4 specimens:-
BM 1906.10.30.16-19. CHINA: Yunnan Province; Tong Chuan Fu.

11. Bombina microdeladigitora. (1; 5).
BM 1985.1491 CHINA: Southern Yunnan; Jingdong, Modao River. (WS).
Plus radiographs of a further 4 specimens:-
BM 1985. 1487-90 CHINA: Southern Yunnan; Jingdong, Modao River.

12. Bombina orientalis. (4; 9).
BM 1907.12.10.40 KOREA: Ai-san, 30 mls. W. of Chefoo. (C&S).
BM 1907.12.10.42 KOREA: Ai-san, 30 mls. W. of Chefoo. (W.S).
UF 41038 "N. Korea." (DS).
UF 42781 No data. (DS).
Plus radiographs of a further 5 specimens:-
BM 1907.2.12.4 N. CHINA: Tsingtan.
BM 1907.12.10.36-39 KOREA: Ai-san, 30 mls. W. of Chefoo.

13. Bombina variegata. (3; 4).
BM 1970.1325, 1331 YUGOSLAVIA: Hercegovina; between Kluc and Zagredici, near Gacho. (C&S).
BM 1983.918 SWITZERLAND: Canton Fribourg; Lac de la Gruyere. (C&S).
An additional specimen was radiographed:-
BM 1970.1333 YUGOSLAVIA: Hercegovina; between Kluc and Zagredici, near Gacho.

14. Discoglossus galganoi. (1; 7).
BM 1951.1.6.15 PORTUGAL: Porto. (C&S).
Plus radiographs of a further 6 specimens:-
BM 87.3.29.25-26 PORTUGAL: Coimbra.
BM 1920.1.20.635A-C SPAIN: Coracolbra.
BM 1951.1.6.13 PORTUGAL: Porto.

15. Discoglossus montalentii. (1; 3).
BM 1985.341 CORSICA: near Vizzavone; Agnone stream, 1100m. a.s.l. (WS).
Plus radiographs of a further three specimens:-
BM 1985.340-342 -same data.
Limited dissections of 1985.340 and 342 also carried out.

16. Discoglossus nigriventer. (0;2).
Radiographs only of:-
HUJ 236 HOLOTYPE. ISRAEL: Eastern shore of Lake Huleh.
plus second specimen - adult. HUJ 544. ISRAEL: Lake Huleh.

17. Discoglossus pictus. (2; 6).
MF 14665, 14670 SICILY: Provincia Palermo; Madonie, Castelbuono. (WS).
Plus radiographs of a further four specimens:-
MF 13433-34 SICILY: near Palermo.

MF 14811 and 14814 SICILY: Catania.

18. Discoglossus sardus. (2; 7).
BM 1920.1.20.1647 CORSICA. (DS).
BM 1951.1.5.92 FRANCE: Ile de Port Cros, near Hyeres. (C&S).
Plus radiographs of a further 5 specimens:-
BM 1931.8.7.13-14 FRANCE: Ile de Port Cros, Iles d'Hyeres.
BM 1951.1.5.93-95 FRANCE: Ile de Port Cros.

19. Leiopelma archeyi. (1; 8).
BM 1980.949 NEW ZEALAND: Coromandel. (C&S).
Plus radiographs of a further 7 specimens:-
BM 1976.1771-1772 NEW ZEALAND: Coromandel Peninsula.
5 unregistered specimens, NEW ZEALAND: Coromandel Peninsula.

20. Leiopelma hamiltoni. (1; 5).
NMNZ AM 106 NEW ZEALAND: Maud Island. (C&S).
Plus radiographs of a further 4 specimens:-
BM 1922.5.23.1 NEW ZEALAND: Stephens Island.
NMNZ AM 103-105 NEW ZEALAND: Maud Island.

21. Leiopelma hochstetteri. (5; 8).
BM 1971.1042 NEW ZEALAND: no other data. (C&S).
CAS 156252-53 NEW ZEALAND: Coromandel Range; W side Tapu-Coroglen Saddle, 435 m. (C&2S).
FMNH 51641-42 NEW ZEALAND: Huia Dam, W. of Auckland. (DS).
BM 1971.1042 and a further 3 specimens were radiographed:-
BM 1971.1043 NEW ZEALAND: no other data.
and two unregistered specimens:
A. NEW ZEALAND: Eastern Cape.
B. NEW ZEALAND: Warkworth; Dome Valley.

Appendix II . Uniquely derived characters defining generic and supra-generic discoglossoid taxa.

Leiopelmatidae.

(2.1) widely separated nasals, (60.2) neural arches non-imbricate, (74.1) epipubis a broad, shield-shaped cartilage; usually calcified or ossified in adults.

Ascaphus.

(5.2) sphenethmoid ossification - two ill-defined lateral patches, (28) alary processes of premaxillae laterally directed from their bases, (30) plate-like portion of vomer very small, (31) circumchoanal process of vomer absent, (32.2) vomerine teeth in an oval patch between the choanae, (75) Nobelian/postpubic bones present.

Leiopelma.

(5.3) sphenethmoid usually remains unossified (variable), if ossified may extend anteriorly to nasal septum, (13.1) squamosal - otic plate present but weakly developed and poorly differentiate from otic ramus, closely applied to crista parotica/otoccipital, (20.2) maxilla with a deep, V-shaped cleft to the anterior end of the pars palatina, (34.2) postchoanal ramus of vomer a slender rod-like process, (67) sacral centrum divided, plus two non-polar characters which may also be uniquely derived defining characters - (-79.2) scapula, pars glenoidalis shorter than pars acromialis and on posterior margin of scapula, (-89) inscriptional ribs present.

Discoglossidae.

(1) nasal capsules abutting or only slightly laterally displaced, (11.1) otoccipitals with anterior and posterior margins parallel or only slightly convergent, (19.1) quadratojugal present, at least 40-50% of pterygoid fossa length, (36.1) parasphenoid alae either uniformly shallow or shallow medially, flaring laterally, (53) eight presacral vertebrae, (54) vertebral centra opisthocoelous/stegochordal, (64) proximal-distal length of transverse processes on the last (posterior) two presacral vertebrae as long or longer than on those immediately anterior, (66.1) sacral diapophyses moderately or

broadly dilated, (70.1) ilium with a dorsal prominence. (83.2) cleithrum bifurcate, (90) humeral condyle large, greater than 66% distal width of the humerus, plus two non-polar characters - (-77) clavicles strongly arched (anteromedially directed), (-88.1) epicoracoid cartilages extending psteriorly beyond the coracoids.

Alytes.

(18.2) squamosal shaft slender, broadest at mid-point, slightly posteriorly directed and with a sigmoid curve, (33) vomeropalatine present, (51.1) paired medio-lateral ossifications present on hyoid plate, either as V-shaped splint bone or separate ossifications, (92) wrist bones, radiale and ulnare + intermedium longer than wide, plus one non-polar character - (-58) uncinate processes absent.

Bombina + Barbourula + Discoglossus ('Discoglossinae')

(8.1) frontoparitals, posteromedial margins convergent, in medial contact or fused, (47.2) occipital condyles with major axes at a shallow or steep obtuse angle, (48.1) occipital condyles at the ventolateral or lower lateral margins of the foramen magnum, (51.2) hyoid plate with separate medio-lateral ossifications, (61.1) neural arches with upturned, flared posterior margins, (65) transverse processes of posterior presacral vertebrae with posterior marginal flanges.

Discoglossus.

(3.1) maxillary process of nasal overlying preorbital process of maxilla, (32.3) vomerine teeth in a broad, slightly arched linear series, well posterior to the choanae, (51.4) hyoid plate with a pair of keeled splint bones in a 'V'-shape, slightly separated or in contact but not joined at their bases, (70.2) ilium with a leptodactyline type configuration - dorsal protruberance moderate to well defined, situated on a large dorsal prominence.

Bombina + Barbourula.

(17.1) squamosal with a ventromedial expansion or a medial ramus, (19.2) quadratojugal 80-100% of pterygoid fossa length, (45.3) mandible with distinctive three-sided or smoothly convex coronoid process, strongly orally directed, (63.2) transverse processes on last two (7th and 8th) presacral vertebrae strongly anteriorly directed, (66.2) sacral diapophyses broadly dilated, (74.2) epipubis absent, <u>plus</u> one non-polar character - (-73) ischium relatively large, approximately elliptical in shape, major axis inclined posteriorlu, with postero-dorsal expansion.

<u>Bombina.</u>

(40.2) pterygoid with a long anterior ramus, anterior end curving medially, (81) scapula with concavity on the posterior margin symmetrical about its mid-point (central type), <u>plus</u> two non-polar characters - (-79.1) scapula, pars glenoidalis smaller than pars acromialis and proximal, (-80.1) scapula triradiate.

<u>Barbourula.</u>

(3.2) anterior margin of maxillary process of nasal abutting posterior margin of preorbital process of maxilla, (6.2) frontoparietals, supraorbital lateral margins divergent, (7) neurocranium narrow, approx. 0.1x maximum width of skull, (12.3) otoccipitals very wide, extending beyond outer margin of orbital and medial margin of the pterygoid fossa, (15.1) squamosal - zygomatic ramus long, curving distally toward maxilla, (39.2) medial ramus of pterygoid overlapping more than 2/3 lateral width of the anterior border of the parasphenoid ala (anterior-posterior plane), (72) ilium - medial synchondrosis present.

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HISTÒRIA BIOLÒGICA DEL FERRERET

(LIFE HISTORY OF THE MALLORCAN MIDWIFE TOAD)

SEPARATA

CIUTAT DE MALLORCA
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1984

3. General skeletal morphology

by B. T. CLARKE

RESUM.- Per primera vegada es presenta una descripció detallada de l'esquelet de *Baleaphryne muletensis* basada en material modern. Presentam una comparació de l'osteologia de *B. muletensis* amb la de les espècies de *Alytes*. *B. muletensis* resulta una espècie que té estretes semblances morfològiques (fenètiques) amb els membres del grup *A. obstetricans*, i entre ells s'assembla més estretament a *A. o. boscai*. Se suggereix que *Baleaphryne muletensis* és no més divergent morfològicament de *A. obstetricans* que el que ho és *A. cisternasii*. Llavors es conclou que basant-se en l'evidència osteològica presentada, *B. muletensis* es pot acomodar fàcilment en el gènere *Alytes*, i no hi ha justificació per assignar el calàpet llevador de Mallorca (ferreret) a un gènere diferent.

SUMMARY.- A detailed description of the skeleton of *Baleaphryne muletensis,* based on modern material is presented for the first time. A comparison of the osteology of *B. muletensis* with close morphological (phenetic) resemblance to members of the *A. obstetricans* group, most closely resembling *A. o. boscai*. It is suggested that *Baleaphryne muletensis* is no more morphologically divergent from *A. obstetricans* than is *A. cisternasii*. It is therefore concluded that on the basis of the osteological evidence presented *B. muletensis* may easily be accommodated in the genus *Alytes,* and that there is no justification for assigning the Mallorcan Midwife toad to a separate genus.

The description of the osteology of *Baleaphryne muletensis* which follows is based solely on recent material collected by Dr. J. A. Alcover. The methods, criteria and terminology used are the same as in CLARKE (1982, 1983). Present evidence suggests that *B. muletensis* more closely resembles members of the genus *Alytes* (the Midwife toads), in particular *A. obstetricans*, than any other group of anurans (MAYOL *et al*, 1980; MAYOL and ALCOVER, 1981; ALCOVER, MOYÀ-SOLÀ and PONS-MOYÀ, 1981 and personal observations). Consequently a comparison of the osteology of *B. muletensis* with that of *Alytes cisternasii, A. o. obstetricans* and *A. o. boscai* is given. The Moroccan *A.* (*o.*) *maurus*, a taxon of doubtful status, was excluded from the present study because of scarcity of material.

Baleaphryne muletensis

Cranial features

The nasals are large and well developed, longer than wide, not in medial contact being slightly separated anteriorly and diverging posteriorly. The anterior margin is narrow and only faintly concave; the lateral margin is long, much longer than the anterior margin. The rostral process is poorly defined; the maxillary process is moderately well defined but not produced into an elongate process, and is well separated from the preorbital process of the maxilla.

The sphenethmoid is short in the anterior / posterior plane and is almost completely exposed in dorsal view; anteriorly the sphenethmoid and nasals are well separated, posteriorly the frontoparietals overlap the posterolateral corners of the sphenethmoid.

The frontoparietals are poorly developed, and a large frontoparietal fontanelle is present. At approximately two-thirds way along from the anterior margin the medial margin of each frontoparietal has a weak media-

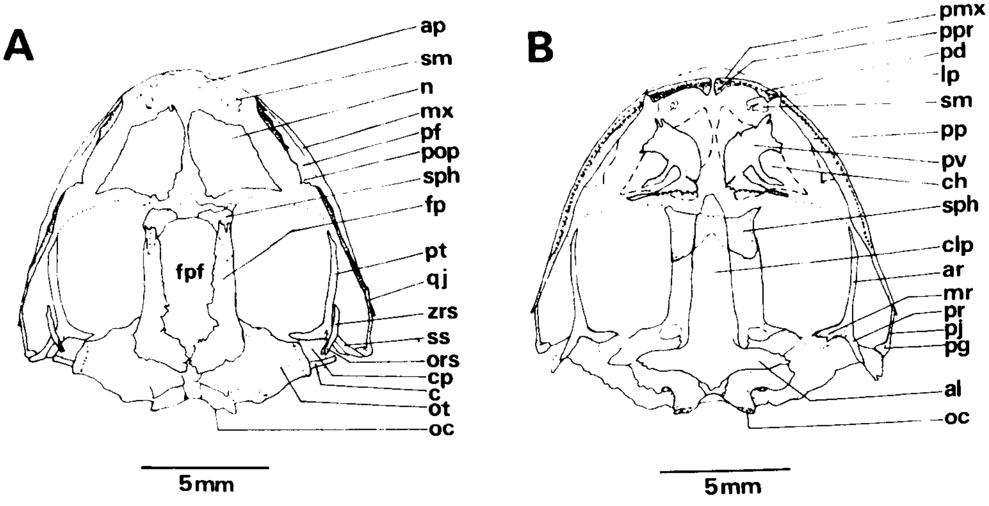

Fig. 1. Skull of *Baleaphryne muletensis* (gravid female, S-V.L. 37.8mm, Alcover collection number 81090207). A. Dorsal view. B. Ventral view. *Abbreviations.*- *al* ala, *ap* alary process of premaxilla, *ar* anterior ramus of pterygoid, *c.* columella, *ch* choana (position of), *clp* cultriform process of parasphenoid, *cp* crista parotica, *fp* frontoparietal, *fpf* frontoparietal fontanelle, *lp* lateral process of pars palatina of premaxilla, *mr* medial ramus of pterygoid, *mx* maxilla, *n* nasal, *oc* occipital condyle, *ors* otic ramus of squamosal, *ot* otoccipital, *pd* pars dentalis of premaxilla, *pf* pars facialis of maxilla, *pg* pars glenoidalis of quadratojugal, *pmx* premaxilla, *pop* preorbital process of maxilla, *pp* pars palatina of maxilla, *ppr* palatine process of premaxilla, *pt* pterygoid, *pv* prevomer, *qj* quadratojugal, *sm* septomaxilla, *sph* sphnethmoid, *ss* squamosal shaft, *zrs* zygomatic ramus of squamosal.

lly directed spur of bone producing a 'double' fontanelle shape where the larger anterior fontanelle can scarcely be distinguished from a smaller posterior one. The overall fontanelle shape is similar to that in *Alytes obstetricans*, described by BOULENGER (1897:166) as "the shape of the sole of a shoe". In *Baleaphryne muletensis* the lateral margins of the anterior fontanelle are straight and diverge slightly. There is no carotid canal; the carotid artery passes over the posterior lateral surface of the frontoparietal.

The otoccipitals are narrow medially to laterally; the lateral margin is well separated from the level of the medial margin of the pterygoid fossa and does not even extend as far laterally as the junction of the medial and posterior pterygoid rami.

The crista parotica is almost completely exposed in dorsal view.

The otic plate of the squamosal is vestigial in the sample examined, it is possible that it may be absent in other individuals. The otic ramus is as long as, or slightly shorter than the zygomatic. The zygomatic ramus is fairly short, slightly less than one-third the height of the ventral ramus or squamosal shaft; the zygomatic ramus tapers anteriorly to a point, giving a modified 'arrow-head' shape in lateral view. The squamosal shaft is narrow and rather slender dorsally and only slightly broader (more dilated) ventrally, and invests most of the lateral surface of the palatoquadrate.

The quadratojugal is long and slender extending anteriorly for approximately two-thirds of the length of the pterygoid fossa. The anterior end of the quadratojugal, or pars jugalis (p.j.) to use the terminology of BOLKAY (1919), has a ventral notch; anterior to the notch the abruptly tapering one-third to one-half of the pars jugalis curves medially slightly to overlap the dorsal margin of the posterior end of the maxilla.

The preorbital pars facialis of the maxilla is moderately well developed, the shape of its dorsal margin is poorly defined but appears slightly concave. A preorbital process is evident but poorly developed. The postorbital pars facialis tapers abruptly, from vestigial anteriorly to absent posteriorly. The anterior end of the pars palatina is straight and very narrow; the pars palatina is narrow, horizontal and lacks a pterygoidal process (terminology of LYNCH, 1971:40).

The alary processes of the premaxilla are expanded dorsally and diverge laterally, each has a distinct concave dorsal margin. The pars palatina on each premaxila is shallow anteriorly to posteriorly, a palatine process is vestigial and does not project laterally beyond the pars dentalis.

Each premover consists of a broad anterior and medial plate-like portion, a circumchoanal region and a dentigerous process. The medial margins of the plate-like portion are long and almost parallel to the midline; the plate-like portions as a whole do not diverge anteriorly. The choana is large, and the well developed anterior and posterior choanal processes are widely separated. The tooth rows are moderately wide and separated by a space approximately equal to the width of one tooth row.

There are no free palatine bones in *Baleaphryne muletensis*, but a short to moderately well developed spur of bone is present extending laterally from, and fused medially to, the dorsal surface or the dentigerous process on either prevomer. These small bony processes are here designated 'vomeropalatines' in accordance with the interpretation of similar structures in *Alytes obstetricans* by MAREE (1945).

The lateral margins of the cultriform process of the parasphenoid are straight but diverge posteriorly; the cultriform process is therefore narrow anteriorly becvoming progressively wider posteriorly and does not narrow anterior to the junction with the alae. The width of the alate portions is equal to the length of the cultriform process. The alae are not expanded laterally; there is no overlapí of the parasphenoid ala with the medial ramus of the pterygoid in the anterior / posterior plane, the ala and ramus are widely separated.

The medial and posterior rami of the pterygoid are shor, much shorter than the anterior ramus, which is approximately 2 1/2 times longer. The anterior ramus is almost straight or only very slightly curved; the distal end does not curve medially.

A columella is present. The occipital condyles are shallow and narrowly separated, Type II sensu LYNCH (1971).

Postcranial skeleton

B. muletensis has an arciferal pectoral girdle with broadly overlapping epicoracoid cartilages. The omosternum is absent possiby present as a vestige of cartilage. The clavicles are curved, anteromedially directed and each has a deep posterior groove giving and inverted U-shape in cross-section. The coracoids are flattened and spatulate medially and are conical laterally. The scapula is bicapitate laterally along the margin articulating with the clavicle and coracoid, and has a deep cleft between the pars acromialis and pars glenoidalis (terminology of TRUEB, 1973). A characteristic discoglossid type sternum is present, with posterolaterally divergent cartilaginous horns.

The vertebral column in opisthocoelous and has 8 presacral vertebrae. The first or cervical vertebra has shallow, narrowly separated cotyles corresponding with the occipital condyles. Free ribs are clearly present on the 3rd and 4th presacral vertebrae but not on the 2nd (data based on an x-ray of a single well ossified adult, showing the left rib on the 4th presacral to be ankylosed onto the transverse process, and a second, cleared and stained specimen).

The sacral diapophyses are moderately dilated, and the sacrococcygeal articulation bicondylar. The coccyx (urostyle) has a pair of poorly developed transverse processes which are very short, almost triangular and laterally directed. The ilia are simple, the ilial shaft is almost cylindrical and lacks a dorsal ilial crest or ridge (see ALCOVER, MOYÀ–SOLÀ and PONS MOYÀ, 1981 for a summary of the ilial features of *Baleaphryne muletensis,* the fossil *Baleaphryne*, and SANCHIZ, below; following chapter).

The limb bones, humerus and radioulna in the forelimb; femur, tibiofibula, tibiale and fibulare[1] in the hindlimb are long and slender. In x-rays of the most fully ossified adult specimen available for study, a gravid female[2], only four carpal elements are evident in the hand (i.e. four *ossified* elements), and no tarsal elements are discernible in the foot. The proximal pair of carpal elements are the radiale and the combined ulnare + intermedium, the large oval bone distal to the radiale and ulnare + intermedium is probably distal carpal 4, and the very small bone situated medially to distal carpal 4 *might* be a small ossified area within centrale 2. Determination and naming of carpal bones is difficult, and is compounded when few bones are ossified. Examination of a cleared and stained halfgrown *B. muletensis*[3] showed the following carpal elements to be present (proximally to distally): ulnare + intermedium, radiale, distal carpal 4, centrale 2, prepollex, centrale 1 and distal carpals 1-3[4]. Only the first three of these are ossified in the halfgrown specimen, the remainder being cartilaginous elements. In the foot the following tarsal elements were found in the cleared and stained specimen: centrale, distal tarsals 1-3 and a prehallux[4] (a single strap-like element); all of these are cartilaginous.

The phalanges of the fingers and toes are long (fingers especially), this is most noticeable on the 3rd finger and 4th toe (longest respectively). The tips of the terminal phalanges of the fingers and toes are slightly dilated and spatulate. The phalangeal formula is normal; 2-2-3-3 (fingers) and 2-2-3-4-3 (toes).

Comparison with *Alytes* species

Comparison of the skeletons of *Baleaphryne muletensis* and *Alytes* species suggests that members of this group may be arranged in order of increasing levels of robustness and ossification, from least to most heavily ossified: *B. muletensis – A. o. boscai – A. o. obstetricans – A. cisternasii.*

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[1] The last two are often referred to as the astagalus and calcaneum respectively.

[2] ALCOVER collection number 81090207.

[3] ALCOVER collection number 81090203.

[4] Terminology and nomenclature by comparison with text and Figure 2-12 in TRUEB (1973), which follows RITLAND (1955).

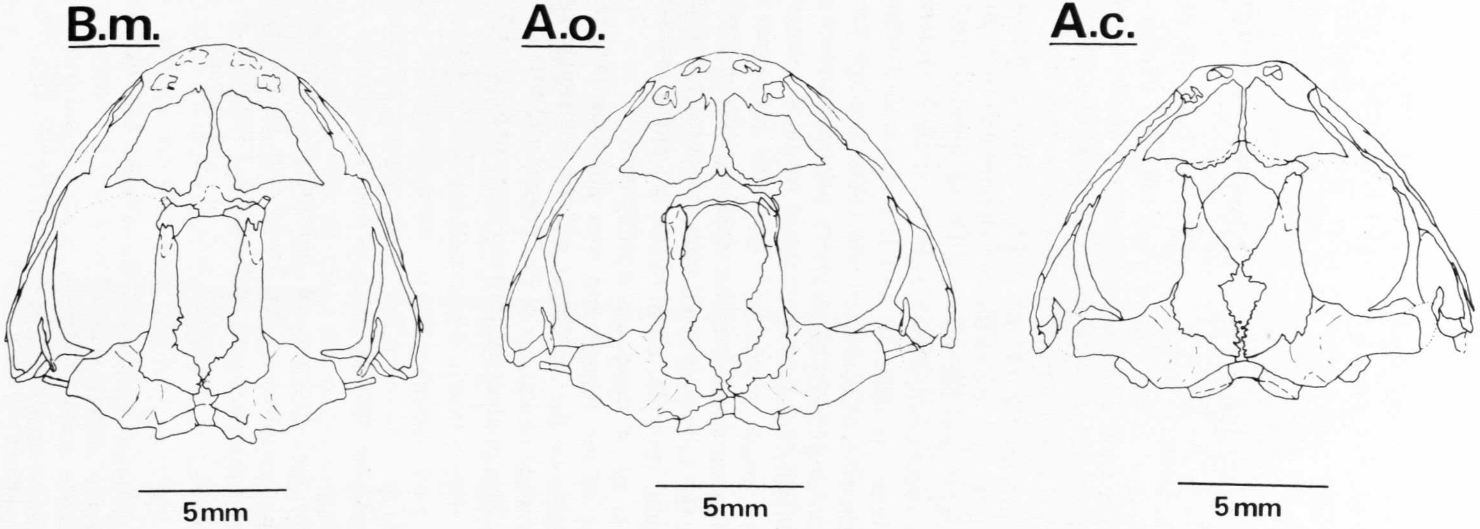

Fig. 2. Dorsal views of the skulls of *B. muletensis* (gravid ♀, ALCOVER collection number 81090207), *A. obstetricans* (♂, BM 1972.1726) and *A. cisternasii* (♂, BM 1982.35).

X-rays of the (sub-?) adult female holotype of A. *(o.) maurus* suggest that it is approximately as heavily ossified as *A. o. boscai.* These increasing levels of ossification follow a step-wise sequence from one species to the next, where the skeletons of individual species in the chain may be likened to the body form ('morphotype') designations used by the physical anthropologist. Hence *B. muletensis* may be thought of as the ectomorph of the group, the *A. obstetricans* group the mesomorphs and *A. cisternassi* the endomorph. This pattern is repeated in most of the features used above to describe *B. muletensis, B. muletensis* having the most lightly built, slender bones in the group and *A. cisternasii* the most robust and heavily ossified. This observation does not imply direction of evolutionary change, it merely indicates a purely morphological set of differences. Similarly, in the comparative accounts which follow, phases like "increase in the level of ossification" and "greater degree of development" are used to describe differences in the above series, where *B. muletensis* may be thought of as the reference taxon.

CRANIAL FEATURES

NASALS. There is an increase in the level of ossification, width, development of the rostral process and anterior margin and a corresponding decrease in the separation of the nasals in the series. *B. muletensis* – *A. cisternasii* mentioned above. Thus in *B. muletensis* the nasals are poorly ossified, longer than wide, the anterior margin is relatively narrow and only slightly concave and the rostral process is poorly defined; in addition the nasals are slightly separated for approximately the anterior 25% of the medial length, after which they diverge posteriorly. In the *A. obstetricans* group (*obstetricans* and *boscai*) the nasals are more fully ossified, as wide as long, the anterior margin is moderately wide and concave and the rostral process is poorly defined; anteriorly the nasals are slightly separated for approximately 50% of their medial length, becoming increasingly more

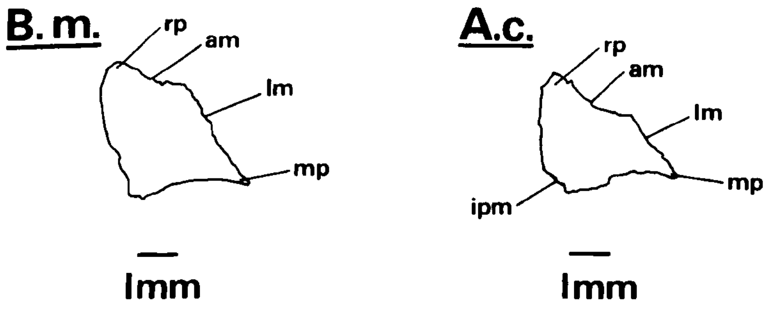

Fig. 3. Right nasals of *B. muletensis* and *A. cisternasii. Abbreviations.– am* anterior margin, *ipm* inner, posteromedial margin, *lm* lateral margin, *mp* maxillary process, *rp* rostral process.

divergent posteriorly. In *A. cisternasii* the nasals are the most heavily ossified in the group, they are wider than long, the anterior margin is very wide and shallowly concave and the rostral process is well defined; the medial margins of the nasals are almost parallel to the midline and only very slightly separated, diverging abruptly for the *posterior* 25% of their medial length (this part of the nasal may be interpreted as an inner, posteromedial margin).

The maxillary processes are moderately well developed and well separated from the maxilla in *all* species.

SPHENETHMOID. Variation in the group is expressed as an increase in the level of development and degree of dorsal exposure. *B. muletensis* has the least exposed and most exposed; *A. cisternasii* the most developed and least exposed sphenethmoid. In all species the sphenethmoid is overlain posterolaterally by the frontoparietals. In *B. muletensis* the sphenethmoid is well separated from the nasals, by a very short to short gap (*boscai*) or barely separated, when the nasal follows the anterolateral curvature of, or is in point overlap over, the anterolateral margin of the sphenethmoid (*obstetricans*). The sphenethmoid is moderately deep in the anterior / posterior plane in both *A. o. obstetricans* and *A. o. boscai*. In *A. cisternasii* the anterior margin of the spehnethmoid is overlain by the posterior borders of the nasals, and is the deepest, most fully developed sphenethmoid in the group.

FRONTOPARIETALS. The frontoparietals of members of the *B. muletensis – A. cisternasii* series exhibit a step-wise increase in their level of ossification, and more noticeably, in the development of the medial margin. The frontoparietals vary from poorly ossified (*B. muletensis*), poor to moderately well ossified (*A. o. boscai* and *A. o. obstetricans*) to the most heavily ossified in the series (*A. cisternasii*). The presence of a medially directed spur of bone, at approximately two-thirds way along from the anterior end of the medial margin, is a constant feature of the frontoparietals of members of the *B. muletensis – Alytes* species group. In *B. muletensis* these posteromedial spurs are poorly developed producing a slight constriction in the fontanelle – a faint "double" fontanelle as described above (see Fig. 2). In the *A. obstetricans* group the spurs are more fully developed producing a more distinct "double" fontanelle, in "the shape of the sole of a shoe" (BOULENGER, 1897, see also Fig. 2 above). The constriction in the fontanelle is more pronounced in *obstetricans* than in *boscai*. The constriction in the fontanelle is more pronounced in *obstetricans* than in *boscai*. In *A. cisternasii* the spurs are in medial contact, or are only slightly separated, producing distinct anterior and posterior fontanelles, both of which may be "kite-shaped" (see Fig. 2), or in its extreme condition the posterior fontanelle may be "very small, a mere foramen between the frontoparietals" (BOULENGER, 1897: 177).

The carotid canal is absent in *all* members of the *B. muletensis* – *Alytes* species group; the carotid artery passes over the posterolateral surface of the frontoparietal.

OTOCCIPITALS. The otoccipitals of *B. muletensis* more closely resemble those of the *Alytes obstetricans* group in general outline shape and in medial-lateral width (not reaching the level of the lateral margin of the orbital fossa); *A. cisternasii* exhibits an extreme form within the series, having a bar-shaped outline and being wider (extending beyond the lateral margin of the orbital fossa to the level of the medial margin of the pterygoid fossa, see Fig. 2).

CRISTA PAROTICA. The crista parotica is well developed and almost completely exposed in dorsal view in all species in the group. Even in *A. o. boscai* where the otic plate may be vestigial or poorly developed, the crista parotica is still almost completely exposed.

SQUAMOSALS. *Otic plate.* Vestigial in *B. muletensis, A. o. boscai* (some), *A. o. obstetricans* and *A. cisternasii;* usually a thin rib of bone along the medial margin of the otic ramus which may extend anteriorly along the zygomatic ramus. Some *A. o. boscai* show a greater degree of development of the otic plate than others, but the otic plate nonetheless remains a poorly developed process. *Otic ramus.* Usually about as well developed as the zygomatic ramus. Most fully developed in *A. o. obstetricans* and *A. o. boscai; B. muletensis* has the most slender otic and zygomatic rami and *A. cisternasii* the most reduced, with a vestigial, knob-like otic ramus. *Zygomatic ramus.* Modified arrow head shaped type in all species in the group, and pointed in nearly all; in *A. cisternasii* the zygomatic ramus is usually reduced, knob-like and blunt distally. *Squamosal shaft.* An increase in dilation of the ventral portion of the squamosal shaft is evident in the series *B. muletensis*– *A. cisternasii.* In *B. muletensis* the squamosal shaft is slender with little or no apparent dilation in any view; in the– *A. obstetricans* group the shaft is dilated in (antero-) lateral view, but apparently not dilated from the posterolateral view; in *A. cisternasii* the shaft is narrow dorsally, ventral to the junction with the otic and zygomatic rami, becoming progressively more dilated ventrally in both anterolateral and lateral (posterolateral) views.

QUADRATOJUGAL. The length of the quadratojugal (pars jugalis plus pars glenoidalis, terminology of BOLKAY, 1919), compared with that of the pterygoid fossa, the dorso-ventral depth of the pars jugalis and the nature of the quadratojugal – maxilla contact are variable within the series. The quadratojugal is relatively longer in *B. muletensis* and *A. o. boscai,* two-thirds or one-half to two-thirds the length of the pterygoid fossa respectively; but only one-third or at most one-half the length of the pterygoid fossa in *A. o. obstetricans* and *A. cisternasii.* The pars jugalis is slender in *B. muletensis,* and deepest (posteriorly) in *A. cisternasii.* The quadratojugal is usually in contact with the medial surface of the maxilla, but is in dorsal to dorsomedial contact in some *A. o. obstetricans*. The ventral notch in the pars jugalis, apparently a constant feature in *B. muletensis* is variably present in *Alytes* species.

Maxilla. *Pars facialis including preorbital process*. The pars facialis is relatively shallow in *B. muletensis*, moderately deep to deep in the *Alytes obstetricans* group and a deep plate-like process in *A. cisternasii*. A distinct preorbital process is present in *B. muletensis* and *A. o. boscai*, and is weakly indicated in *A. o. obstetricans*. *A. cisternasii* lacks an obvious preorbital process; i. e. the process is more fully developed in the less heavily ossified members of the group. *Anterior end of pars palatina*. Straight in all species in the group except *A. cisternasii* (slightly convex). *Pterygoidal process*. Absent in *B. muletensis* but present as a weak or vestigial processes in all *Alytes* species.

Premaxilla. *Alary process*. Some *A. o. boscai* have a fairly distinct concave dorsal margin to the alary process similar to that in *B. muletensis*, the others, *A. o. obstetricans*, *A. o. boscai* (some) and *A. cisternasii*, have an indistinct or convex dorsal margin. *Pars palatina*. Shallow in nearly all members of the *B. muletensis – Alytes* species group; *A. cisternasii* has a slightly deeper pars palatina. *Palatine process*. Present, well developed and pointed in all except *B. muletensis* which has a blunt, poorly developed palatine process (the process may also be slightly blunt in *A. cisternasii*). *Lateral process*. In *A. o. obstetricans* the lateral process is a distinct, pointed process which does not extend, or extends only slightly, beyond the lateral edge of the pars dentalis; in other members of the group the process is vestigial or may even be absent, and similarly does not extend beyond the pars dentalis. In *B. muletensis* the lateral process lies mesad to the lateral limit of the pars dentalis (see Fig. 1B).

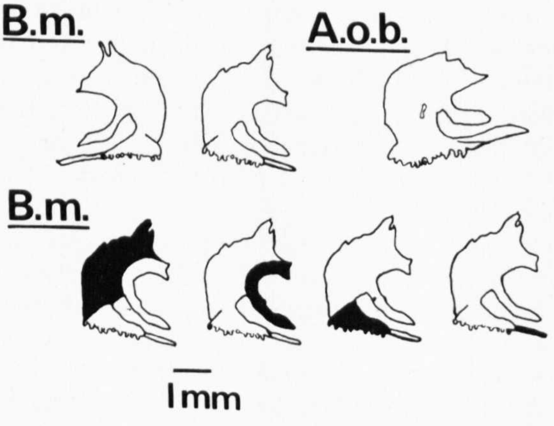

Fig. 4. Top left: *B. muletensis* right and left prevomers. Top right: *A. o. boscai* left prevomer. Bottom row: *B. muletensis* left prevomer shaded to show from left to right: plate portion, circumchoanal region, dentigeroud process and the vemeropalatine.

PREVOMER. All species in the group have prevomers like those in *B. muletensis,* but vary in the size and degree of development of the different processes. The prevomers are largest and most fully developed in the *A. obstetricans* group, which also have the widest and hence the least separated tooth rows.

PALATINES. All species in the group lack free palatine bones, but possess vomeropalatines, which vary inter- and intraspecifically (to a lesser degree), from well developed to almost absent. There may even be some slight variation in the degree of development within a single individual.

PARASPHENOID. *Cultriform process.* Only *B. muletensis* has a distinctly tapering cultriform process (narrow anteriorly; wider posteriorly); *Alytes* species have almost straight to slightly biconvex cultriform processes which are narrow anterior to the parasphenoid alae. *Ala / medial ramus of pterygoid overlap.* No overlap in the anterior / posterior plane, widely separated in all species; only *A. o. boscai* approaches a condition of "point" overlap.

PTERYGOID. *Anterior ramus.* Variable in the group with no obvious trends. The anterior ramus is straight, i.e. not curved distally toward the midline in *B. muletensis* and *A. o. obstetricans,* and not or slightly curved in Spanish *A. o. boscai,* slightly curved in *A. cisternasii* and strongly curved distally in Portuguese *A. o. boscai.* The variation in *A. o. boscai* may be populational, clinal or merely due to small sample size, and requires further investigation using larger samples. *Medial ramus.* Short in all species; see above under Parasphenoid. *Posterior ramus.* The posterior is the deepest of the three rami dorso-ventrally, and is most fully developed in *A. cisternasii.*

COLUMELLA. Present and well developed in all species.

OCCIPITAL CONDYLES. Lynch Type II, narrow to moderately separated in all species. The individual condyles are relatively narrower in *A. cisternasii* than in any other member or the group.

MANDIBLE. The coronoid process has a smooth outline in almost all species; in *A. cisternasii* the process is pointed posteriorly and has a backward sloping posterior margin. Some *A. o. obstetricans* have a coronoid process which *A. cisternasii* condition.

POSTCRANIAL SKELETON.

PECTORAL GIRDLE. An arciferal pectoral girdle with broadly overlapping epicoracoid cartilages; omosternum apparently absent or ? approaches the present as minute vestige of tissue and a characteristic discoglossid sternum with diverging posterolateral cartilaginous processes are common to all species in the group. All species have anteromedially curved or "arched" clavicles (terminology or TRUEB, 1973:97), which have an inverted U shape in crosssection laterally. The degree of curvature is greatest, and the clavicles are more robust and dorsoventrally flattened in *A. cisternasii* than in any other member or the group. The coracoids are typically flattened and spatulate medially, and conical laterally. *B. muletensis* has the most slender coracoids (slightly dilated medially, and weakly conical laterally) in the *B. muletensis* – *A. cisternasii* series; *A. cisternasii* the most robust, being fairly broadly dilated medially and distinctly conical laterally. The scapula has a deep, open cleft between the pars acromialis and pars glenoidalis in all species in the group except *A. cisternasii* which has the end of the cleft closed, reducing the gap between the pars acromialis and pars glenoidalis to a foramen-like space.

VERTEBRAL COLUMN. Opisthocoelous, normally with 8 presacral vertebrae (occasional anomalies have been recorded e.g. BOULENGER, 1897: 39), shallow, narrowly separated cervical cotyles and bicondylar sacrococcygeal articulation are common to all species in the group. The nature of the ribs is variable in the group, *B. muletensis* has free ribs on the 3rd an 4th presacral vertebrae, but lacks ribs on the 2nd presacral (the most adult specimen available had left rib on the 4th presacral ankylosed onto the transverse process, a common occurrence in the Discoglossidae). Members of the *A. obstetricans* group usually have free ribs on the 2nd, 3rd and 4th presacrals, which may or may not be ankylosed; a few individuals lack ribs on the 2nd. *A. cisternasii* has ribs which are apparently fused onto transverse processes on the 2nd, ankylosed or fused onto the 3rd, and absent on the 4th presacrals; on the 2nd and 3rd most have signs of fusion – an irregular anterior and/or posterior border. *Sacral diapophyses*. Moderately dilated in *B. muletensis, A. o. boscai* and some *A. o. obstetricans* (variable, larger specimens seem to have more dilated diapophyses); the greatest degree of dilation is exhibited by *A. cisternasii*, some *A. o. obstetricans* approach the *A. cisternasii* condition. *Coccyx (urostyle)*. A single pair of transverse processes are present on the coccyx in all members of the group, and are usually well developed and curved posterolaterally in *Alytes* species, although some individuals may have the transverse processes reduced on one or both sides. The processes are apparently uniformly reduced in *B. muletensis*.

ILIUM. Lacking a dorsal crest in all species in the group.

FORE– and HINDLIMBS. In the series *B. muletensis* – *A. cisternasii* there is a distinct, progressive decrease in length and increase in robustness of the limb bones (humerus, radioulna, femur, tibiofibula, tibiale and fibulare); *B. muletensis* having the longest and most slender, *A. cisternasii* the shortest and most robust.

CARPAL ELEMENTS. The total number of carpal elements is constant in the *B. muletensis* – *Alytes* species group, all species possessing (proximally to distally): a combined ulnare + intermedium, radiale, distal carpal 4, centrale 2, prepollex, centrale 1 and distal carpals 1-3. There is some evidence of an increase in the number of carpal elements which have undergone ossification in the *B. muletensis* – *A. cisternasii* series. In *B. muletensis* there is, apparently, a maximum of four ossified elements; the combined ulnare + intermedium, radiale, distal carpal 4 and centrale 2. The *Alytes obstetricans* group additionally have ossified distal carpal 3 and centrale 1. *A. cisternasii* has nearly all carpal elements ossified with the exception of distal carpals 1 and 2.

TARSAL ELEMENTS. *B. muletensis* and the *A. obstetricans* group have the same tarsal element conformation: centrale, distal tarsals 1-3 and a single, strap-like element to the prehallux. *A. cisternasii* has a slightly different arrangement: centrale, an enlarged distal tarsal 3, and possibly distal tarsals 1 and 2, or only two distal tarsals i.e. an enlarged tarsal 3 (or 2+3) and distal tarsal 1 (or 2?), and *two* elements to the prehallux. The tarsal elements are cartilaginous in all species.

FINGERS AND TOES. The phalangeal formula is normal in all species (see above under *B. muletensis* description). The differences in the fingers (in particular) and toes of members of the *B. muletensis* – *A. cisternasii* series is consistent with the variation seen in the limb bones. *B. muletensis* has the longest phalanges, and consequently the longest fingers (especially) and toes, and has slightly spatulate terminal phalanges. The *A. obstetricans* group exhibit an intermediate condition with less obviously spatulate terminal phalanges, and *A. cisternasii* has the shortest, stubbiest fingers with little or no sign of dilation of the terminal phalanges. In addition, *A. cisternasii* has a noticeably short first finger with slender phalanges and a short fourth finger with broad stubby phalanges, the terminal phalanx being cone-like and very broad at the base.

Conclusions and discussion.

On the evidence presented in this section on general skeletal morphology *Baleaphryne muletensis* emerges as a species with close phenetic resemblance to the *Alytes obstetricans* group. Of the members of this group it is apparent that it most closely resembles the Iberian *A. o. boscai.* Overall, members of the *B. muletensis* – *Alytes* species group may be arranged in a series from the most slender, lightly built to the most robust, by which criterion the species order is *B. muletensis* – *A. o. boscai* – *A. o. obstetricans* – *A. cisternasii.* Alternatively, using *A. o. obstetricans* the type species of the genus *Alytes* as reference taxon, the order may equally well be given as *B. muletensis* – *A. o. boscai* – *A. o. obstetricans* – *A. cisternasii.* The characters as presented in the present account fit either order. Thus, using purely morphological (phenetic) evidence with no evolutionary implications, it is suggested that *B. muletensis* is no more divergent morphologically from *A. obstetricans* in one direction than *A. cisternasii* is in the opposite direction. The conclusion is therefore, that on evidence from general skeletal morphology *B. muletensis* may easily be accommodated in the genus *Alytes*, and that there is no justification for referring the Mallorcan Midwife toad to a separate genus.

This section of the chapter has not attempted to formally break up characters into character states and infer polarity of character state change (i.e. determine direction of evolutionary change), because of problems in polarity determination and outgroup selection in the analysis of discoglossoid frog relationships; this is the subject of a larger, more broadly based study currently in progress.

Acknowledgements.

My thanks to Dr. R. ESTES, San Diego State University, California for informing me of the existence ol live *Baleaphryne muletensis* on Mallorca, and to Dr. J. A. ALCOVER, Universitat Central de Barcelona for inviting me to contribute to this book and for providing specimens. I am also grateful to Miss A. G. C. GRANDISON and Dr. E. N. ARNOLD, BM (NH), London for reading and constructively criticising the manuscript and for general advice; to Dr. G. L. UNDERWOOD, City of London Polytechnic for supervising the broader based study on the relationships of discoglossoid frogs currently in progress, and to Dr. M. A. LINLEY, London and Dr. VALENTIN PEREZ MELLADO, Universidad de Salamanca for providing specimens of *A. cisternasii;* and to Dr. A. DUBOIS, Museum National d'Histoire Naturelle, Paris, for the loan of the holotype of *A.*(*o*). *maurus*.

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Material examined.

(C&S = cleared and alizarin stained to show bone; C&2S = cleared and double stained to show cartilage and bone; DS = dry skeleton).

B. muletensis

ALCOVER collection numbers 81090203 (♂, skull C&2S; postcranial skeleton C&S); 81090207 (gravid ♀, skull C&S); 81090507 (sub-adult ♂, skull C&S); 81090509 (half-grown, skull C&S); plus one with no number (juvenile, skull C&S).
The above 5 and another 8 specimens were x-rayed.

A. cisternasii

BM 1920.1.20.664 (♀, DS, skull figured in BOULENGER, 1879: 177, Fig. 66); BM 1980.251 (♀, skull + postcranial skeleton C&2S); BM 1982.35 (♂, skull C&S).
A futher 11 specimens were x-rayed.

A. o. obstetricans

BM 1920.1.20.662 (♀, DS), BM 1920.1.20.2462 (♂, DS); BM 1928.12.20.117 (gravid ♀ skull C&S).
A further 17 specimens were x-rayed.
BM 1972.1726 (♂, skull + postcranial skeleton) and a further 6 specimens were x-rayed; these all came from Lago Erina, nr. Covadonga, N.W. Spain and are probably referable to *A. o. obstetricans*, but resemble *A. o. boscai* in some features.

A. o. boscai.

BM 1908.5.29.12A (♂, skull C&S); BM 1908.5.29.12B (♂, skull + postcranial skeleton C&S); BM 1920.1.20.663 (DS); BM 1920.1.20.796 (DS); BM 1972. 1537 (♀, skull + postcranial skeleton C&S).
A further 15 specimens were x-rayed.

A. o. maurus

MNHNP 5960 Holotype female was x-rayed.

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A description of the skeletal morphology of *Barbourula* (Anura: Discoglossidae), with comments on its relationships

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This paper, the second in a series on the skeletal morphology of the discoglossid frogs, provides a detailed description of the skeleton of *Barbourula busuangensis* for the first time. The presence of a medial ramus in the squamosal and a sesamoid in the ligament passing from the squamosal shaft to the posterior end of the angular bone of the mandible are noted. Both the medial ramus of squamosal and squamosal-mandibular sesamoid are previously unreported in the Anura, and may be unique to *Barbourula*. Additional information on the second known species in the genus, *Barbourula kalimantanensis*, is also presented. An historical review of past opinions and a tentative current assessment of the relationships of the genus are given (pending a computer-aided cladistic analysis of the Discoglossidae). The concept of an osteogram is introduced.

KEYWORDS: *Barbourula*, *Bombina*, Borneo, Discoglossidae, osteogram, osteology, Philippines, relationships.

Introduction

This is the second in a series of papers on the osteology and phylogenetic relationships of the 'archaic' frog family Discoglossidae. The primary aim of this series of papers is to provide a set of standardized osteological descriptions or 'osteograms' for each of the four discoglossid genera. The origin and concept of an osteogram is an adaptation of the ethologists' term 'ethogram': 'a behavioral inventory'... a 'precise catalogue of all the behaviour patterns of an animal' (Eibel-Eibelsfeldt, 1970: 10). An osteogram is an osteological inventory, a 'complete' description or precise catalogue of the general skeletal morphology of a species or other low-level monophyletic group; genus or superspecies complex.

The first paper in the series (Clarke, 1984) gave a detailed description of the general skeletal morphology of the Mallorcan Midwife Toad *Alytes* (*Baleaphryne*) *muletensis*, and included data on the other *Alytes* species. This, together with a paper on the skeleton of the Moroccan Midwife Toad *A.* (*o.*) *maurus* (B. T. Clarke, in preparation), will provide the data set for the genus *Alytes*. The present paper will be the osteogram for *Barbourula*, to be followed by equivalent accounts on *Bombina* spp. and *Discoglossus* spp. The completed series will provide: (*a*) the basis for a phylogenetic analysis of the Discoglossidae and the other rib-bearing frogs, Ascaphidae and Leiopelmatidae (=suborder Discoglossoidei of Sokol, 1977) and (*b*) a firmer foundation for future studies on the higher frog families comprising the second anuran suborder, Ranoidei Sokol, 1977, that is, will be the basis for a more informed assessment of the phylogeny of the Anura.

Barbourula was described by Taylor and Noble (1924) from a single specimen collected by E. H. Taylor from Busuanga Island in the Philippines. The genus currently comprises two species: *Barbourula busuangensis* Taylor and Noble, 1924, Busuanga Island and Palawan Island, Philippines, type-species by monotypy; *Barbourula kalimantanensis* Iskandar, 1978. West Kalimantan, Indonesia (= Borneo).

Barbourula is the least known of the discoglossid genera and hitherto only a few osteological features have been described. The original description included sufficient osteological characters to justify inclusion of *Barbourula* in the Discoglossidae: 'no omosternum; sternum with two diverging cartilaginous processes; eight opisthocoelous presacral vertebrae; sacral vertebra strongly dilated; coccyx with a single condyle; terminal phalanges simple', yet omitted to mention the presence of ribs on transverse processes of presacral vertebrae 2–4. Trueb (1973) mentioned the ventral flange on the pterygoid (p. 84) and the plain cylindrical ilial shaft (pp. 107–108) and figured the posterior ventral view of the skull (fig. 2–6 b) and the pelvic girdle (fig. 2–11 b). Iskandar (1978) also included sufficient osteological data for the purpose of placing his *B. kalimantanensis* in the Discoglossidae: 'three pairs of ribs, expanded sacral diapophyses, short transverse processes at the anterior end of the coccyx, broadly overlapping epicoracoids and long cartilaginous projections from the sternum'.

The present account extends the current state of knowledge of the osteology of *Barbourula* to the level of an osteogram for *B. busuangensis* and additional data on the skeleton of *B. kalimantanensis*.

Abbreviations used

BMNH	British Museum (Natural History)	FMNH	Field Museum of Natural History, Chicago
CAS	California Academy of Sciences	MCZ	Museum of Comparative Zoology, Harvard University
CAS–SU	California Academy of Sciences, Stanford University	MZB	Museum Zoologicum Bogoriense

CS = cleared and alizarin stained (to stain for bone only).
C&2S = cleared and double stained (to stain for bone and cartilage).
DS = dry skeleton.

Materials and methods

Osteological data were obtained from alizarin preparations (single-stained preparations for bone and double-stained preparations for cartilage and bone), dry skeletons and radiographs of larger samples including type-material. Unless designated CS, C&2S or DS all material was radiographed.

Barbourula busuangensis

MCZ 14004 (HOLOTYPE). BMNH 1977. 1202–1203; BMNH 1980.410; BMNH 1982.409 (skull CS; post-cranial skeleton DS); BMNH 1982.410. CAS 100453–55; CAS 157355. CAS–SU 6004; CAS–SU 6006; CAS–SU 6013–14; CAS–SU 6015 (DS); CAS–SU 6017; CAS–SU 6024; CAS–SU 6043; CAS–SU 21220–22; CAS–SU 21225–30; CAS–SU 21232–33; CAS–SU 21236–38; CAS–SU 21240–46; CAS–SU 21250 (C&2S); CAS–SU 21253–54. FMNH 40482; FMNH 50997–98; FMNH 50999 (DS); FMNH 51000–01; FMNH 51003–05; FMNH 51011; FMNH 51013; FMNH 51020–24; FMNH 123477.

Cranial features. The nasals are large to massive, plate-like, in medial contact or only very slightly separated, sloping forward in front of the anterior margin of the sphenethmoid. Some adult specimens have a low but distinct transverse ridge in this region. The anterior margin of the nasal is wide and fairly deeply concave; the lateral margin is long and concave with a slightly projecting process at the junction with the anterior margin. The rostral process is present, well developed, the maxillary process is long and slender, its anterior margin in broad contact with the posterior border of the preorbital process of the maxilla. The posterior borders of the nasals abut or interdigitate with the anterior margins of the frontoparietals. The nasal capsules are large, well developed and not laterally displaced.

Septomaxillae large, well developed, situated well forward; each extending from the lateral margin of the naris to a region dorso-lateral to the alary process of the premaxilla.

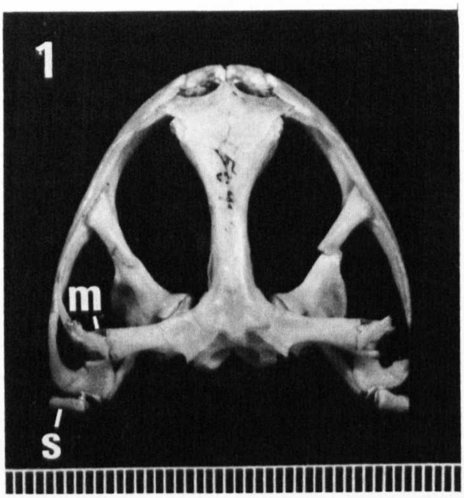
The sphenethmoid is very well developed, being long and quite broad anteriorly, but has minimal dorsal exposure in three separate places—medially at the junction of the medial borders of the nasals and frontoparietals and laterally, on either side at the anterior medial corners of the orbits. Ventrally the sphenethmoid is fully developed, extending anteriorly beyond the prevomerine odontophores and the choanae. The sphenethmoid narrows posteriorly, tapering for the anterior 60% of the length of the cultriform process of the parasphenoid.

The frontoparietals are long and narrow, giving a cylindrical/tubular neurocranium. The frontoparietals are fused for most of their length but are progressively more separated and divergent anteriorly, over the sphenethmoid region. Posteriorly each frontoparietal bears an elevated laterally spike-like process, which in the largest skull available for study (FMNH 50999) is continuous with an elevated ridge on the otoccipital. This elevated frontoparietal/otoccipital ridge corresponds to the dilatio tectiformis + torus termina supraorbitale of Bolkay (1919). There is no frontoparietal fontanelle (or, following Trueb, 1973: 74 who maintains that a fontanelle is always present; no dorsal exposure of the fontanelle, which is roofed over by the frontoparietals).

The otoccipitals are broad medially to laterally, short anteriorly–posteriorly; consequently in larger (adult) specimens the otoccipitals have a bar-like appearance, and are only very slightly expanded laterally. In smaller (juvenile to subadult) specimens the otoccipitals taper, being deeper medially and shallower laterally. The lateral margin reaches, or extends slightly beyond, the lateral margin of the orbital fossa in smaller subadult specimens but extends well beyond it in adults (to beyond the medial margin of the pterygoid fossa)—an indication of broadening of the skull with increasing maturity.

The crista parotica is a moderately wide lateral extension of the otoccipital, slightly to moderately exposed in dorsal view.

The otic plate of the squamosal is vestigial to absent in subadult, and poorly developed in adult specimens. The otic ramus is short, more an otic process passing ventrally to the crista parotica, not extending posteriorly for the entire length of the crista parotica. The otic ramus is much shorter than the zygomatic. The zygomatic ramus is very long, longer than the height of the squamosal shaft, and curves anteroventrally toward, but does not articulate with, the post-orbital pars facialis of the maxilla. The distal end of the zygomatic ramus is bluntly rounded to truncate in lateral view and may be slightly dorsally directed. The squamosal shaft is short, squat and robust, the blade-like shaft curving laterally outward. The shaft is narrow dorsally



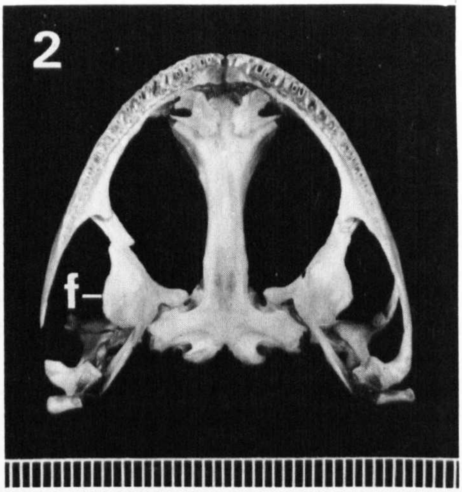


FIG. 1. *Barbourula busuangensis*, FMNH 50999: dorsal view of skull, m = medial ramus of squamosal, s = sesamoid; Fig. 2. *B. busuangensis*, FMNH 50999 ventral view of skull, f = ventral flange of pterygoid. For other features see text. *N.b.* Right zygomatic ramus of squamosal broken, missing; left and right anterior pterygoid rami fractured; right quadratojugal broken, missing and vomerine teeth missing. Scale line divisions = 1 mm.

becoming broadly dilated ventrally where it articulates at four points: medially, with the posterior ramus of the pterygoid; posteriorly, with a sesamoid or heterotopic bone (see below); ventrally, with the calcified quadrate and laterally with the pars glenoidalis of the quadratojugal (terminology of Bolkay, 1919). There is a further process on the squamosal, extending from the dorsal part of the inner (medial) surface of the squamosal shaft, at the junction of the shaft with the zygomatic ramus. This medial process is broad, well developed and articulates with the antero-ventral portion of the crista parotica and extends medially beneath the antero-ventral surface of the otoccipital. As far as I am aware this process is unique to *Barbourula* in the context of the Anura, although other frogs may have a broad flange of bone along the medial (inner) margin of the squamosal shaft; for the sake of simplicity I am calling it the 'medial ramus of the squamosal'.

At the angle of the jaw between the base of the squamosal shaft and the mandible there is a sesamoid element, which is usually cartilage (especially in juvenile and subadult frogs), but may be ossified in large adult specimens. In the larger of the two dry skeletons available for study, these sesamoids are hemicylindrical in shape (semicircular in cross-section) and 4·6 × 2·1 × 1·1 (left) and 4·5 × 2·0 × 1·4 (right; length × width × depth, measurements in mm). They articulate by means of ligament, passing dorsally across the inner posterior almost ventral surface of the squamosal shaft and the posterior-most lateral edge of the posterior ramus of the pterygoid; and ventrally with the posterior end of Meckel's cartilage on the mandible. This sesamoid therefore spans the space at the medial side of the calcified quadrate to the mandible, probably protecting the articulation at the angle of the jaw (see also *Discussion*, below). I will refer to it as the squamosal-mandibular sesamoid hereafter.

Discussion of sesamoid function: Haines (1969: 107 and 111–112) suggests that sesamoids may protect tendons and ligaments from pressure and/or increase the effect of leverage. Ray (1959) noted the presence of a sesamoid bone, the os transiliens in the jaw musculature of the tortoise *Gopherus polyphemus*. The presence of sesamoids in such situations in *Barbourula* and *Gopherus* is in accord with Haines' interpretation.

The quadrate cartilage is calcified in larger specimens.

The quadratojugal, in particular the pars jugalis (terminology of Bolkay, 1919, = p.j.) is very long, extending anteriorly for the entire length of the pterygoid fossa. The pars jugalis is shallow, that is not expanded proximally adjacent to the pars glenoidalis (Bolkay, 1919); slightly expanded, blade-like at the point of articulation with the posterior tip of the maxilla, becoming more slender and tapering to a point anteriorly (distally). The distal half of the pars jugalis of the quadratojugal passes medially to, and articulates with, the dorso-medial surface of the posterior post-orbital pars facialis of the maxilla.

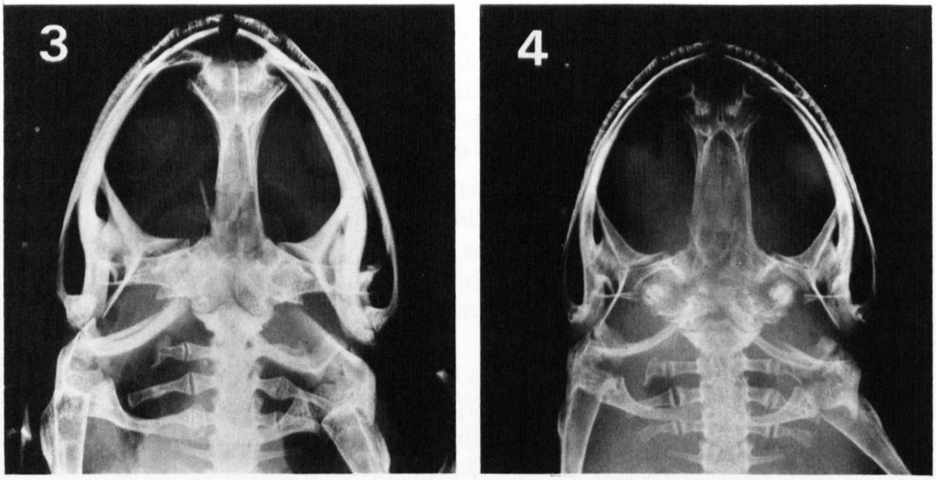
The maxilla has a deep pre-orbital pars facialis anteriorly, with a deep posteriorly directed U-shaped notch in its dorsal margin. A pre-orbital process is present, well developed and abuts or is only slightly separated from the maxillary process of the nasal; the pre-orbital process is medially directed and passes anteriorly alongside or slightly ventral to the maxillary process of the nasal. The post-orbital pars facialis is slightly concave beneath the orbit; the maxilla is deeper, more expanded post-orbitally and terminates posteriorly in a ventrally directed pointed tip. Ventrally the post-orbital pars facialis bears a labial flange which covers the outer margin of the last few posterior maxillary teeth. The anterior end of the pars palatina is straight. The pars palatina itself is very narrow, not horizontal as is usual in most anurans, but concave ventrally, having a moderately deep to deep longitudinal groove at the base of the tooth row. Posteriorly the pars palatina has a pterygoidal process (terminology of Lynch, 1971: 40) which overlaps the distal end of the anterior ramus of the pterygoid.

The premaxillae have poorly developed alary processes, they are short, narrow and almost vertical/perpendicular. The pars palatina on each premaxilla is deep medially, having a spatulate palatine process and is shallow laterally, the lateral (maxillary) process is poorly developed and projects only slightly beyond the pars dentalis. The shallower lateral portion of the pars palatina of the premaxilla has a transverse groove beneath the tooth row which is continuous with that found on the maxilla.

The vomers are moderately well developed but not like the massive plate-like structures found in *Alytes* and *Discoglossus*, but more like the vomers found in *Bombina* spp. (particularly *Bombina maxima*). Each vomer has a moderately wide anterior and medial portion which is confluent with the circumchoanal region, and a narrow well-differentiated dentigerous process. The medial margin of the antero-medial or 'plate' portion of the vomer diverges anteriorly and laterally from the midline. The choana is small and oval, and the moderately developed anterior and posterior choanal process of the vomer are not particularly widely separated (compared with other discoglossoid species). The tooth rows are narrow and separated by a space approximately equal to the width of half of one tooth row. (Terminology follows that of Clarke, 1984: 47 and fig. 4).

There are no free palatine bones in *Barbourula busuangensis*, nor is there *any* indication of a palatine remnant in the form of a vomeropalatine.

The lateral margins of the cultriform process of the parasphenoid are straight/parallel-sided immediately anterior to their junction with the parasphenoid alae, but taper to a point anteriorly. The distal third of the cultriform process bears a pronounced but smooth median keel (terminology of Trueb, 1973: 80). The width of the alate portions is approximately equal to, or slightly greater than, the length of the cultriform process. The alae are slightly to moderately expanded laterally and are



FIGS 3 & 4. Radiographs of *Barbourula busuangensis*: (*a*) BMNH 1980.410 (Busuanga, ad.); and Fig. 4. BMNH 1977.1203 (Palawan, juv.). *N.b.* (*a*) The narrow neuocranium characteristic of an adult, also visible is the V-shaped and circular ossifications of the hyoid plate (in the posterior orbital region, see also Fig. 3). In Fig. 4 the broader juvenile-type neurocranium is evident. Also the cotylar surfaces are narrowly separated in 1980.410 (*a*) and more widely separated in 1977.1203 (*b*). Separation is usually greater in Palawan specimens but age/increasing ossification also affect separation, viz., wider separation in juveniles; narrower separation in adults.

weakly postero-laterally directed (='slight posterolateral orientation' condition of Trueb, 1973: 80). There is considerable overlap of the parasphenoid ala by the medial ramus of the pterygoid in the anterior/posterior plane; the prootic has a well-developed process covered by a broad pad of cartilage by which it articulates with the anterior ramus of the pterygoid (see Trueb, 1973: 85, fig. 2–6 b). The extent of the medial overlap apparently increases age/size: approx. 50% lateral overlap of alae by the medial ramus of pterygoid in CAS 21250; 66% in CAS–SU 6015 and 72–83% in FMNH 50999.

The medial ramus of the pterygoid is shortest; the anterior and posterior rami are of approximately equal length. The anterior ramus is short, straight (not curved as in *Bombina*) and distally abuts the inner surface of the pars facialis of the maxilla dorsal to the pterygoidal process. There is an extremely well developed ventral flange on the pterygoid at the junction of the anterior and posterior rami (mentioned and figured in Trueb, 1973: 84 and 85; fig. 2–6 b).

A well-developed columella is present.

The otoccipital condyles are narrowly separated (Type II of Lynch, 1971:54).

The coronoid process on the mandible is a smooth convex dorso-medially directed flange; the symphysial bone is fused to the dentary (='synosteotically united with the dentary' Trueb, 1973: 89).

Hyoid apparatus. (See Fig. 5; terminology follows Trewavas, 1933: 408.) The hyoid apparatus is large; the hyale is well developed; the alary process is deeply dilated; the posterior-lateral process on the hyoid plate is divided and/or perforated posteriorly, and most of the postero-medial process—the anterior (proximal) part—is ossified, the remaining (posterior) portion is cartilaginous and dilated. The hyoid plate itself is broad but shallow anteriorly–posteriorly, and bears a pair of large round endochondral ossifications and a U- to V-shaped ossification along the antero-medial margin of the hyoid plate adjacent to the hyoglossal sinus.

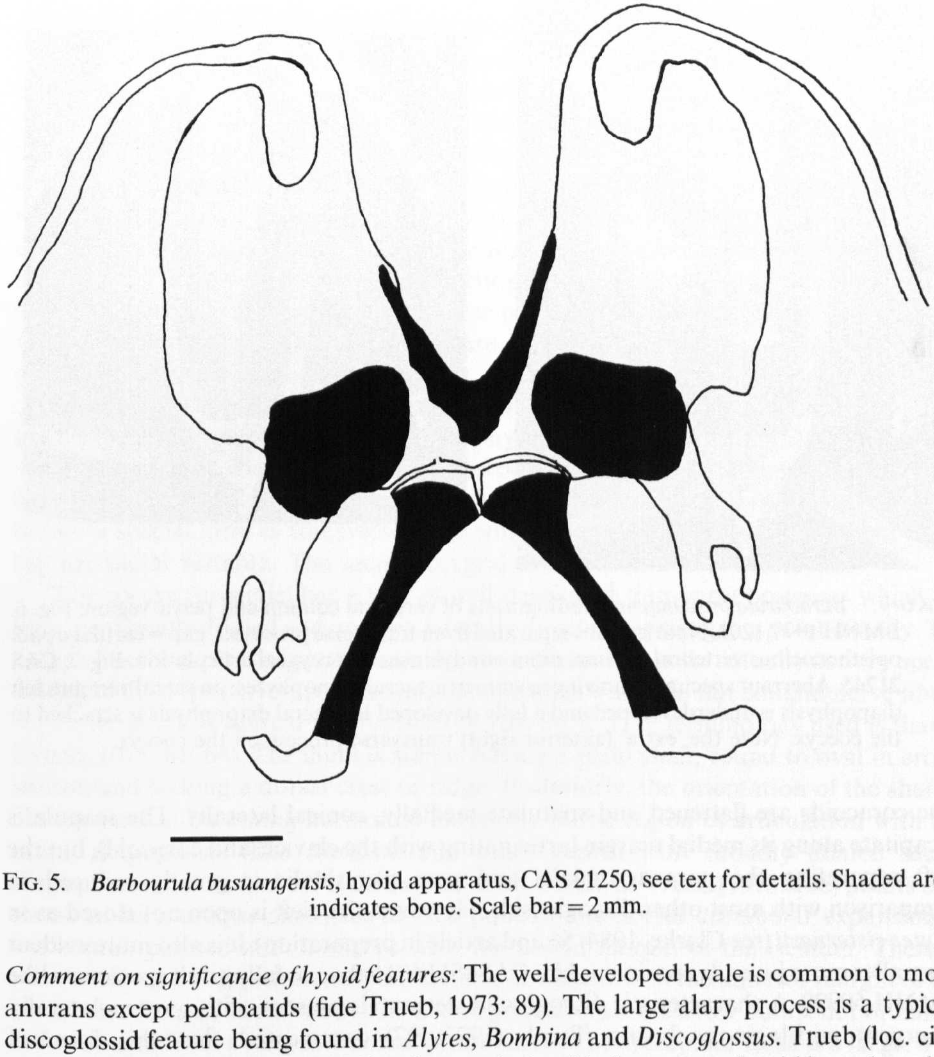
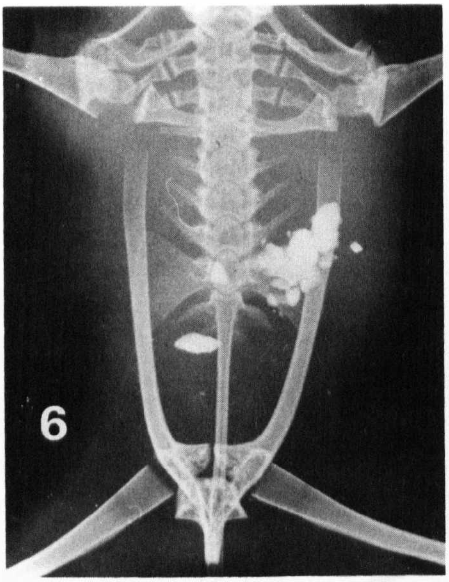


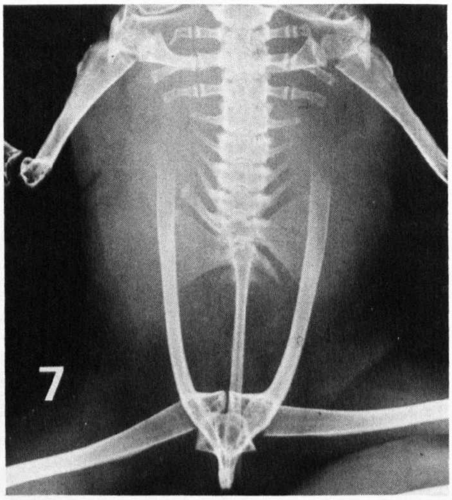
FIG. 5. ***Barbourula busuangensis***, hyoid apparatus, CAS 21250, see text for details. Shaded area indicates bone. Scale bar = 2 mm.

Comment on significance of hyoid features: The well-developed hyale is common to most anurans except pelobatids (fide Trueb, 1973: 89). The large alary process is a typical discoglossid feature being found in *Alytes*, *Bombina* and *Discoglossus*. Trueb (loc. cit.) interprets the round areas of ossification on the hyoid plate as parahyoid bone (see also her fig. 2–7 c showing the hyoid in *Bombina variegata*). However, she also figures *Leiopelma hochstetteri* (fig. 2–7 a) and designated the single central area of ossification in this species as parahyoid bone. Some *Bombina variegata* have the central bone *and* the paired lateral bones (personal observation; Trewavas, 1933: 415–416 and Fig. 6). The U-shaped ossification at the margin of the hyoglossal sinus is reminiscent of the V-shaped ossification or 'splint' bones found more posteriorly *in the body of the hyoid plate* in *Alytes* and *Discoglossus* (see Boulenger, 1897: 133, fig. 51: 167, fig. 62).

A more detailed survey on the hyoid and its ossifications, particularly in the more primitive frog families, may be of considerable phylogenetic significance.

*Post-cranial features. **Barbourula busuangensis*** has an arciferal pectoral girdle with broadly overlapping epicoracoid cartilages. A vestigial omosternum is apparently present—a very small structure, appearing as a small flat rectangular area of blue stain in the cleared and double-stained CAS 21250 preparation barely discernible in spirit specimens. The clavicles are curved, antero-medially directed and each has a shallow groove along the posterior margin for approximately two-thirds of its lateral width.





FIGS 6–7. *Barbourula busuangensis*, radiographs of vertebral column and pelvic region: Fig. 6. BMNH 1977.1202. Note free ribs separated from transverse processes, gap = cartilage pad; opisthocoelous vertebral column; monocondylar sacrococcygeal articulation. Fig. 7. CAS 21245. Aberrant specimen showing asymmetric sacral diapophyses: on sacral vertebra left diapophysis is underdeveloped and a fully developed left sacral diapophysis is attached to the coccyx. Note the 'extra' (anterior right) transverse process on the coccyx.

The coracoids are flattened and spatulate medially, conical laterally. The scapula is bicapitate along its medial margin (articulating with the clavicle and coracoid), but the cleft separating the pars acromialis and pars glenoidalis is greatly reduced in comparison with most other discoglossids. However, the cleft is open not closed as in *Alytes cisternasii* (see Clarke, 1984: 56 and article in preparation); it is also more evident in smaller more juvenile specimens like CAS–SU 6015 than in fully adult specimens like FMNH 50999. A characteristic discoglossid sternum is present, with postero-laterally divergent cartilaginous horns. Trueb (1973: 97) commented that this form of sternum is 'unique' to discoglossids; it is in fact found in *Leiopelma* as well as the discoglossids but not in *Ascaphus* (B. T. Clarke, in preparation, see also Stephenson, 1952: 612).

The vertebral column is opisthocoelous (stegachordal in the sense of Griffiths (1963: 259–260) and has eight pre-sacral vertebrae. The first pre-sacral or cervical vertebra has large moderately deep cotyles which are narrowly separated by a distinct ventral notch which correspond with the Type II occipital condyles (but see note under Figs 3, 4). Free ribs are present on the 2nd, 3rd and 4th pre-sacral vertebrae; these ribs are separated from their corresponding transverse processes by narrow cartilaginous pads. The distal cartilaginous caps on the ends of the ribs have a particularly distinctive shape; they are calcified/ossified and expanded into moderately elongate processes. The ribs on the 3rd pre-sacral bear postero-dorsally directed uncinate processes (small pointed spike-like bony processes; terminology of Ritland, 1955: 135 and Figs 1 and 4). The neural arches are strongly imbricate and pre-sacral vertebrae 4–8 have dorsally directed flared posterior margins. Neural spines are presented on vertebrae 1–5, the degree of development of these spines decreases posteriorly; the 1st pre-sacral most developed, with the longest and broadest neural spine to the 5th which has the shortest narrowest neural spine, a needle-like process. The neural spines bear median keels, the 6th pre-sacral has a vestigial spine with little or no sign of a median keel. The transverse processes on the 6th, 7th and 8th pre-sacrals are inclined—anteriorly directed at an acute angle from the longitudinal axis of the vertebral column—and there is marginal extension of the posterior borders of the same three transverse processes. (There is a morphological 'cline' here, where the transverse processes on the 8th have the greatest degree of marginal extension and are the most acutely directed transverse processes, through to those on the 6th which have little posterior marginal extension and are only slightly anteriorly directed. The transverse processes on the 5th vertebra have only a vestigial postero-medial extension and are almost perpendicular to the longitudinal axis of the vertebral column.)

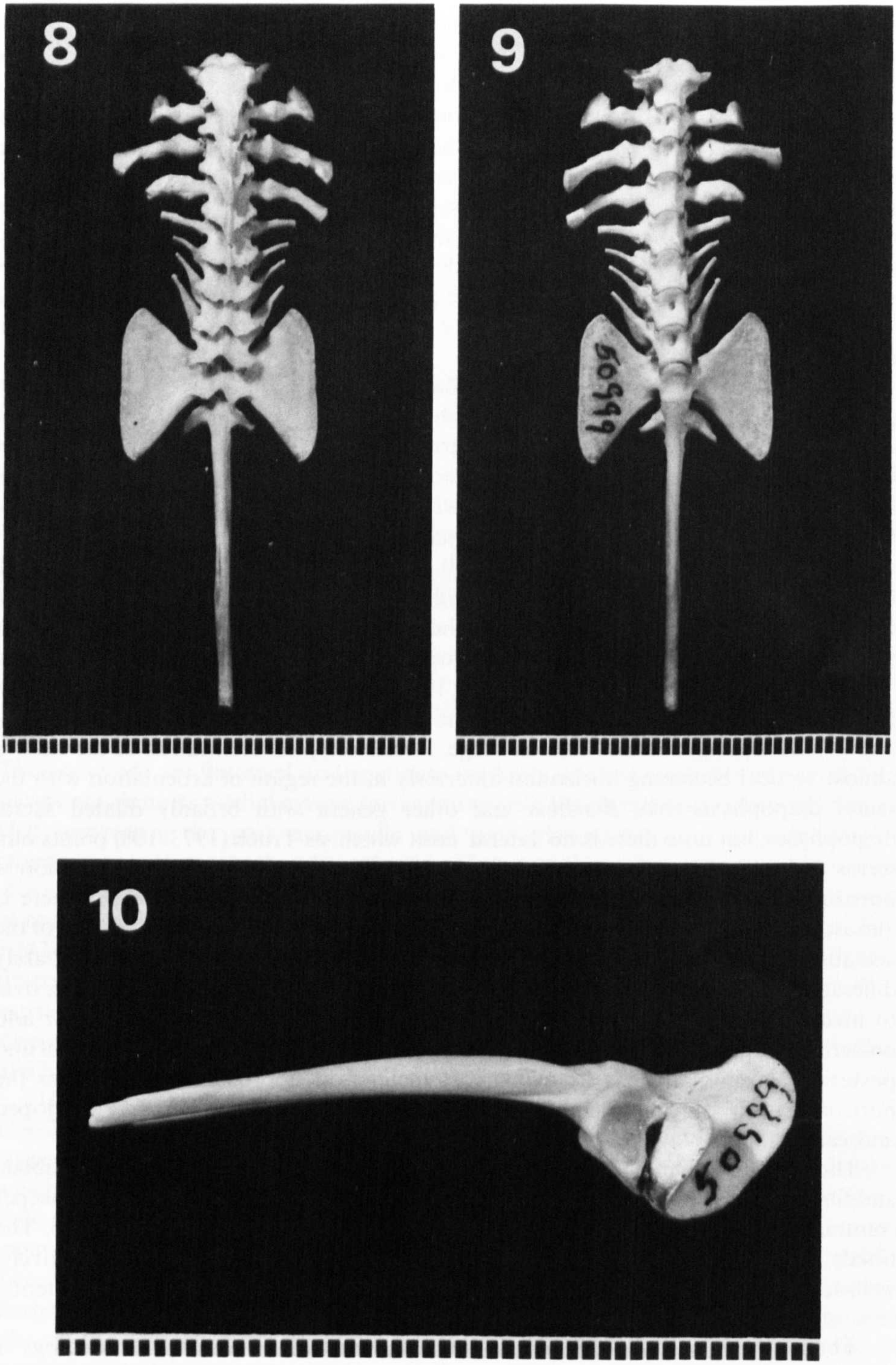
The sacral diapophyses are broadly dilated ('butterfly-wing' type, B. T. Clarke, in preparation) and bear a pair of prezygapophyses antero-medially on the dorsal surface, adjacent to the anterior margin. The postero-medial margin of the sacral diapophyses has a median notch situated between two posteriorly directed V-shaped spurs of bone—a special form of transverse ridge which resembles the posterior margin of the 8th pre-sacral vertebra. The sacrococcygeal articulation is monocondylar.

The coccyx (urostyle) has a pair of well-developed transverse processes which are long, proximally dilated and postero-laterally directed, tapering to a point distally. The coccyx has three pairs of nerve foramina, the anterior two pairs actually convey nerves while the third (posterior) pair are minute openings which do not contain nerve fibres.

Pelvic girdle. (Figure d in Trueb, 1973: 109. fig. 2 11 b; terminology used is that of Lynch, 1971: 61–64). The ilium is simple having a plain shaft, round to oval in cross-section and lacking a dorsal crest or ridge. Posteriorly, the orientation of the shaft is almost vertical becoming horizontal anteriorly in the region of articulation with the sacral diapophysis (like *Bombina* and other genera with broadly dilated sacral diapophyses; but note there is no 'lateral' crest which, as Trueb (1973: 108) points out, seems to be a unique character for the pipids). The dorsal acetabular expansion is horizontal, pointed and confluent with the dorsal margin of the ischium. There is almost no ventral acetabular expansion; it is confluent with the anterior margin of the acetabular fossa in lateral view. The dorsal protruberance is a low bump, not or barely differentiated from a long low dorsal prominence. The acetabular fossa is a large, oval to inverted rounded triangle in shape, with well-developed projecting anterior and posterior margins. The ischium is large, expanded and oval with projecting dorsal and posterior margins and has its major axis inclined at approximately 45° from the horizontal, it is barely separated from the ilium ventrally; the pubis is poorly developed and cartilaginous.

The limb bones, humerus and radioulna in the forelimb; femur, tibiofibula, tibiale and fibulare in the hindlimb are short to moderately long and fairly stout. The deeper (ventral) groove between the radial and ulnar heads of the radioulna is broad. The tibiale and fibulare (= astragalus and calcaneum of some authors) have, respectively, well-developed laterally and medially directed margins, which are consequently separated by a relatively small fossa.

The following carpal elements are present (proximally to distally; terminology of Trueb, 1973: 110–111): ulnare + intermedium, radiale, distal carpal 4, centrale 2, centrale 1, the prepollex complex and the distal carpals, slightly more proximal is what appears to be a combined distal carpal 2 + 3 and centrale is a small, oval distal carpal 1. The prepollex is rather unusual; there is a 'chain' of prepollical elements, the proximal



FIGS 8–10. *Barbourula busuangensis*, FMNH 50999: Fig. 8. Vertebral column, sacral region and coccyx (urostyle) in dorsal view; Fig. 9. Same, in ventral view; Fig. 10. Pelvic girdle: ilium, ischium and pubis. See text for details. Scale line divisions = 1 mm.

(first) is the largest, then the second and third are approximately equal in size and the fourth is about half the size of the second or third. Anteriorly and ventrally to the distal three of these four elements are a group of 10–12 ?cartilaginous elements (which pick up alcian blue stain), of which the proximal three to four are small and the remaining seven to nine are minute. Some or all these elements may be artifacts of staining or represent a fragmentation of prepollical elements or vestiges of a primitive condition of a high number of prepollical elements. (Based on CAS 21250 C&2S, only.)

In the foot the following tarsal elements were found: centrale, distal tarsals 1–3 and a prehallux. The prehallux, like the prepollex, consists of a large number of cartilaginous elements; four main elements, proximally to distally; first largest, second almost equal in size, third rectangular and equal to half the second, fourth with three distal articular facets and 12 other small cartilage (alcian blue stained) elements, some of which are two to three times as wide as long and may represent fusions of two to three minor elements.

The phalanges of the fingers and toes are short. *Barbourula* is unusual, possibly unique, among the Anura in having the 3rd finger on the hand barely longer than the 2nd, and the 4th toe barely longer than the 3rd. The phalangeal formula is normal; 2–2–3–3 (fingers) and 2–2–3–4–3 (toes) but the basal phalanx on the 2nd finger (two phalanges) is *longer* than than that on the 3rd finger (three phalanges), hence the 3rd finger is only slightly longer than the 2nd. Similarly, the basal and antepenultimate phalanges in the 3rd toe are *longer* than those in the 4th, so the 4th is only slightly longer than the 3rd (having four phalanges to the 3rd's three).

The terminal phalanges are simple, knobbed or slightly bilobed.

Barbourula kalimantanensis

HOLOTYPE. MZB Amph. 2330.

Described from a single specimen by Iskandar (1978), *B. kalimantanensis* is clearly distinct from *B. busuangensis*. Most immeditely noticeable are the flattened head and more fully webbed hands and feet of *B. kalimantanensis*. The following additional data are based on radiographs of the holotype.

Cranial features. Essentially similar to *B. busuangensis*, although it is apparent from the radiographs that the neurocranium is very narrow, much narrower than in *B. busuangensis*. The skull appears relatively shorter (the neurocranium looks shorter and the orbital fossae are more rounded). The anterior ramus of the pterygoid is longer, the articulation with the maxilla is further forward in the orbital fossa. A well-developed pterygoidal flange is present at the junction of the anterior and posterior rami; the medial ramus is at a more obtuse angle to the otoccipital and to the midline. The zygomatic ramus of the squamosal is long and of the same type as in *B. busuangensis*. There is no sign of an ossified squamosal-mandibular sesamoid (?cartilaginous or absent). The coronoid process on the mandible is well-developed and horizontally (orally) directed as in *B. busuangensis*; the symphysial bone appears to be fused to the dentary. The occipital condyles are narrowly separated, Lynch Type II.

Post-cranial features. The vertebral column is opisthocoelous, stegachordal, and has eight pre-sacral vertebrae. The first pre-sacral (cervical) vertebra has large moderately deep cotyles which are narrowly separated by a distinct notch (suggesting the specimen is subadult or adult). The transverse process on vertebrae 2–4 bear distinct ribs, the junctions between the two are well-defined as in *B. busuangensis*. The transverse processes on pre-sacral vertebrae 7 and 8 are strongly anteriorly inclined, slightly less so on the 6th—as per *B. busuangensis*. A characteristic discoglossid-type sternum is present. The sacrococcygeal articulation is monocondylar. The sacral diapophyses are broadly dilated ('butterfly-wing' type). There is a single pair of transverse processes on the coccyx.

The pelvic girdle and fingers and toes are essentially very similar to the *B. busuangensis* pattern.

***Barbourula*: relationships**

Historical review

The suggestion that *Barbourula* is more closely related to *Bombina* than to any other discoglossid dates from the original description of the genus, in which Taylor and Noble (1924: 1) noted that *Barbourula* (*B. busuangensis*) is 'strikingly different from the described members of this group, but more closely allied to the two eastern Asiatic forms than to any of the others' (= *Bombina maxima* and *B. orientalis*).

Myers (1943: 150) agreed with Taylor and Noble. 'Superficial examination seems to confirm Taylor and Noble's suggestion that the closest known relative of *Barbourula* is *Bombina* of the Eurasian mainland', but nevertheless noted that '*Barbourula* shows no sign of the gay belly marbling of *Bombina*... and it is very different in many other ways'.

Inger (1954: 209) introduced a note of doubt to these opinions, that are as much based on geographical considerations as on anatomical evidence; 'The present study indicates that *Barbourula* is intermediate between *Bombina* and *Discoglossus*'. Inger based this opinion on the condition of the sacrococcygeal articulation (monocondylar in *Barbourula* and *Bombina*; bicondylar in *Discoglossus*) and the presence/absence of an adductor longus muscle in the thigh (present in *Barbourula* and *Discoglossus*; absent in *Bombina*). Inger followed Noble (1922, 1924) in interpreting the *Bombina* condition—monocondylar articulation/adductor longus muscle absent—as primitive. Inger further stated: 'Other characters of indeterminate phylogenetic significance show resemblances to *Bombina* in some instances and to *Discoglossus* in others'.

Sanchiz (1985: 104), using a comparative osteological approach, firmly placed *Barbourula* back in association with *Bombina*.

Current assessment: discussion

The present paper is a detailed account of the osteology of *Barbourula*, particularly *B. busuangensis*, the second in a series of such accounts which will form the basis of an assessment of the phylogenetic relationships of the discoglossoid frogs. It is therefore premature to speculate on the outcome of these investigations. Difficulties of the kind mentioned by Inger (1954: 209, 210), 'characters of indeterminate significance... showing... resemblances to *Bombina* in some instances and to *Discoglossus* in others', and, 'Finally there remain several specializations of *Barbourula* that have no apparent bearing on the relationship to the other living discoglossids', are something of an obstacle to the inference of the phylogenetic relationships of *Barbourula*. Nonetheless, data obtained so far strongly suggest that *Barbourula* and *Bombina* are phenetically closer to each other than either is to any other discoglossoid genus. It remains to be seen if this is also true of their phylogenetic relationship, but it does seem likely that, in this case, there is a concordance between phenetic and phylogenetic relationship.

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