TITLE A PHYLOGENETIC STUDY OF THE CYNIPOIDEA (HYMENOPTERA).

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A PHYLOGENETIC STUDY OF THE CYNIPOIDEA (HYMENOPTERA).

by

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ABSTRACT

A phylogenetic study of the Cynipoidea (Hymenoptera).

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The current classification of the Cynipoidea was subjected to compatibility analysis on the basis of the characters then employed and shown to have a very poor resolution. A comprehensive morphological investigation of 31 exemplar species was undertaken and 234 characters were found, a 450% increase over the established classification. These characters were analysed and the compatibility clique contained 135 apomorphies, 68 of which were synapomorphies. This is an increase of 600% and 300% respectively over the established data, this is a tremendous improvement in the data-base leading to a great improvement in resolution.

In addition, the principal morphological character-suites were analysed independently. This technique was used to locate the weaknesses in earlier classifications and, by this method, the distortion caused by the allometric bias to wing-data was recognized.

Many extralimital cynipoids were examined and a new tribe was discovered. Other forms of cladistic analysis, Parsimony and O'Nolan weighting, were undertaken and the results considered. After detailed analysis, a phylogeny of the Cynipoidea was reconstructed.

The evolutionary biology of the Cynipoidea provided particularly strong support for the phylogenetic reconstruction. Concepts of host defence, host range, gall complexity, gall position, host switching, reproductive cycles, biogeographical distribution, plate tectonics, palaeobotany, palaeoclimatology, the origin of hyper-parasitism and the adaptive characters associated with xylophagous hosts were all considered. All the available fossil cynipoids were examined and the evolutionary history, holophyly, and relationships of the Cynipoidea with other Hymenoptera were all discussed.

Finally the phylogenetic reconstruction was used to provide the first reasoned classification for the superfamily.

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I am particularly keen to thank my supervisors, Dr, G. Underwood and Dr I Gauld, it would be very hard to find better. Dr Underwood kindly provided "state of the art" compatibility programs, and Dr Gauld's extensive knowledge was a great asset.

Most of all, I thank my family for their support. Perhaps when my daughter can read this, she will understand why I could not always come out to play.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: INTRODUCTION AND METHODS

INTRODUCTION

The current classification of the Cynipoidea has been criticized as being, "far from definitive as nearly all authors repeatedly admit... we desperately need a thorough review of the family level classification of the Cynipoidea based on morphology" (Menke, 1989). Riek (1971) complained that "most families and subfamilies are defined more on their biologies than on distinctive morphological attributes". He further commented that the lack of characters for the families was a particular problem. Ritchie (1988) observed that "the families, and later, the subfamilies and tribes, have been expanded without real appraisal over the last 150 years." Thus the current classification of the Cynipoidea is unsubstantiated, and overdue for a complete review.

Objectives

The aims of this investigation are to provide the first detailed study of the phylogenetic relationships of the families, subfamilies and tribes of the Cynipoidea; to relate cynipoid biology to the phylogeny and to propose the first reasoned reclassification of the superfamily.

The thesis consists of the following six principal elements.

1 An analysis of the existing classification.
2 A comprehensive survey of cynipoid morphology.
3 Cladistic analysis of the morphological data; reconstruction of the phylogeny and an evaluation of why previous classifications were unsuccessful.
4 A discussion of the evolutionary biology of the Cynipoidea.
5 A commentary on cynipoid holophyly and the relationships of the Cynipoidea to other Hymenoptera.
6 Construction of a new classification of the Cynipoidea.

Cladistics and the Cynipoidea

Modern cladistic techniques can be employed to uncover "many unexpected patterns" (Kluge, 1983) and because of this they were used in this study. From a purely pragmatic stance, any methodology that provides a new view, not necessarily tied to previous classifications, will, either directly or in response to it, stimulate discussion and a better understanding of the phylogeny.

Very little has been published about phylogenetic relationships within the Cynipoidea. There has been no cladistic analysis of the whole superfamily, and until very recently there were no cladistic studies even of small groups. However, Ritchie (1984) has recently investigated the phylogeny of North American Synergini (Cynipidae). His work on the tribal structure of the family Cynipidae has enabled me, while still including the Cynipidae, to concentrate on the parasitoid Cynipoidea - the area where the greatest confusion exists.

The Cynipoidea is remarkably suitable for studies relating evolutionary biology to taxonomy because the various cynipoid lifeways are thought to be restricted within taxonomic groupings. Such investigations are widely considered to be of major importance (Clutton-Brock & Harvey, 1984; Gould & Lewontin, 1979; Ridley, 1983; Tinbergen, 1963).

The "microhymenoptera"

The Cynipoidea, Chalcidoidea and Proctotrupoidea *sensu lato* are derived, generally small, Apocrita that exhibit many parallelisms. Therefore, increased knowledge of one superfamily can assist the study of the others. It is time for one of these superfamilies to be comprehensively investigated, and the size of the Cynipoidea makes it the obvious choice. Phylogenetic investigations of the Chalcidoidea (Gibson, 1985; 1986) are hampered by the large size of this superfamily, and the Proctotrupoidea is not a single holophyletic group.

THE STUDY GROUP: CYNIPOIDEA

The cynipoids are mostly small (5mm or less) or very small parasitoids. They are robust insects, frequently brown or black in colour. The antennae are usually 13 segmented in females, the pronotum reaches back to the tegulae and the gaster is laterally compressed. The characteristic forewing venation is moderately reduced (Fig. 151) compared to that of most Ichneumonidae. The marginal cell is distinctively triangular (Fig. 114). There is usually no pterostigma, the costal vein is absent, and the discal cell is incomplete.

The superfamily consists of about 3500 species but there are many more species, especially Eucoilidae, awaiting description (Nordlander, 1984). The best known Cynipoidea are probably the gall-formers. However, most Cynipoidea are parasitoids of Symphyta, Coleoptera, Neuroptera or Diptera larvae and hyperparasitoids of Homoptera.

MATERIAL

Most of the Cynipoidea that have been examined are from the extensive collection in the Natural History Museum. A large number of additional specimens have been borrowed from collections housed in the major Natural History Institutions of the world (see Acknowledgements).

Collection of material

During the course of this study Cynipoidea were collected using techniques described by Fergusson (1986) and Noyes (1982), including malaise trapping (Townes, 1972), sweep netting, use of pitfall and yellow-pan traps and leaf-litter sampling. The specimens were mounted, on one side, onto pinned card triangles using a water soluble glue.

Rearing Cynipoidea.

Several species were reared in order to acquire

larvae, and fresh adults. Galls were collected and the cynipids reared under ambient conditions or in a controlled environment room (16 hour day, 18 degrees Celsius).

Larvae of the parasitoid species were much more difficult to obtain, but some larvae were obtained from cultures of Diptera in Holland. Older material, including the original slides made by Haviland (1921a; 1921b) were also studied.

Attempts were made to rear eucoilids on decaying banana and on rotten meat but with little success; *Alysia manducator* (Braconidae) was the only parasitoid reared.

SELECTION OF OPERATIONAL TAXA

It is not feasible with the computer facilities available to perform a detailed cladistic analysis on a large number of taxa. Therefore some form of selection is required before the higher classification of the Cynipoidea can be studied. The last broad-range study of the Cynipoidea (Weld, 1952) lists eleven subfamilies and since then three more subfamilies have been described. These 14 subfamilies provide a basis for the selection of exemplar species.

The International Code of Zoological Nomenclature defines a name of the family-group in terms of a type-genus (Article 63) and the type-genus name is born by a type-species (Article 67a). So the type-species of the type-genus of each of the 14 subfamilies were taken as exemplar species (see Rohwer & Fagen, 1917; 1919). Extra genera (represented, whenever possible, by the type-species) were selected in order to represent diversity and areas of current taxonomic difficulty. Altogether 31 exemplar species were chosen (Table 1). This selection took place after an examination of over 150 nominal genera.

Taxon No.	Species	Current subfamily (see Chapter 3)
1	*Ibalia leucospoides* Hochenwarth	IBALIINAE
2	*Oberthuerella lenticularis* Saussure	OBERTHUERELLINAE
3	*Tessmanella expansa* Quinlan	..
4	*Liopteron compressum* Perty	LIOPTERINAE
5	*Plastibalia violaceipennis* Kieffer	..
6	*Pseudibalia fasciatipennis* Kieffer	..
7	*Mesocynips insignis* Cameron	MESOCYNIPINAE
8	*Paramblynotus punctulatus* Cameron	..
9	*Kiefferiella rugosa* Ashmead	..
10	*Aspicera scutellata* Villers	ASPICERINAE
11	*Callaspidia defonscolombei* Dahlbom	..
12	*Omalaspis carinata* Kieffer	..
13	*Anacharis eucharioides* Dalman	ANACHARITINAE
14	*Aegilips nitidula* Dalman	..
15	*Xyalaspis laevigatus* Hartig	..
16	*Figites scutellaris* Rossi	FIGITINAE
17	*Melanips opacus* Hartig	..
18	*Lonchidia maculipennis* Dahlbom	..
19	*Neralsia rufipes* Cameron	..
20	*Eucoila crassinerva* Westwood	EUCOILINAE
21	*Kleidotoma psiloides* Westwood	..
22	*Rhoptromeris heptoma* Hartig	..
23	*Dilyta subclavata* Förster	CHARIPINAE
24	*Apocharips xanthocephala* Thomson	..
25	*Phaenoglyphis xanthochroa* Förster	ALLOXYSTINAE
26	*Alloxysta macrophadna* Hartig	..
27	*Pycnostigmus rostratus* Cameron	PYCNOSTIGMATINAE
28	*Aulacidea hieracii* Bouché	CYNIPINAE
29	*Cynips quercusfolii* Linnaeus	..
30	*Austrocynips mirabilis* Riek	AUSTROCYNIPINAE
31	*Himalocynips vigintilis* Yoshimoto	HIMALOCYNIPINAE

Table 1. The 31 cynipoids selected as representative taxa.

METHODS

Terminology

The morphological terms used in this thesis are taken from Eady (1968), Fergusson (1985, 1986; 1988), Harris (1979), Nordlander (1982), Richards (1977), Ronquist & Nordlander (1989) and Snodgrass (1935).

Wing vein and cell terminology (Comstock, 1918; Eady, 1974; Rohwer & Gahan, 1916 & Ross, 1936), is illustrated in figure 102. Veins can be present, present only as pigment, or "spectral" i.e. only visible in reflected light (Mason, 1986). Here the normal convention of not including spectral venation has been followed.

The Snodgrass (1941) terminology for male genitalia is widely used for the smaller parasitica and is adopted here, rather than the older Peck (1937) terminology.

Cladistic terminology is explained in chapter 2.

Microscopy

A Leitz T.S. stereo and a Leitz Dialux phase contrast microscope were used for optical microscopy. Scanning Electron Microscope photographs were taken on International Scientific Instruments 60A, Cambridge 180 and Hitachi 2500 machines. Specimens were gold coated on a Polaron E500 coating unit and a Polaron E100 Series II cool sputter coater.

Computation & computers

Principal components analysis is an ordination technique that reduces the dimensionality of hyperspace by calculation of orthogonal eigenvectors. Thus, with a reasonably well structured data-set, a valid summary of variation can be projected in three dimensions. This technique, which is explained in Sneath & Sokal (1973), was used to analyse antennal measurements. The cynipoid data was analysed on a PDP 11/24 minicomputer via the system program PIP and the multivariate analysis facility of MINITAB.

The application of the cladistics programs used in this study is best explained in conjunction with cladistic theory (see chapter 2). The LEQU suite of programs and the O'NOLAN weighting program (see Appendix 1) are written in BASIC. A BBC model B microcomputer with 6502 co-processor was used for this analysis. The parsimony program HENNIG86 was run on a Sanyo MBC-16 Plus 2 microcomputer.

The partition of continuous variables was investigated using the STEP programs. Continuous variables could be divided into intervals each containing one recorded value, but that would quickly overwhelm the analysis. The STEP programs provide a way of chosing a few from the many possible partitions of the continuous data. STEPONE analyses continuous numerical variables, and ranks

the discrete steps in the data. The scores are replaced by their rank numbers, matching scores get matching rank numbers. The lowest score is counted as step zero, the remaining scores are numbered in rank order as steps 1, 2, etc. STEPTWO uses Fisher's 2 X 2 exact probability to assign a probability to each of the possible partitions. The distribution of the data is viewed in the light of the null hypothesis - that there is no difference in the distribution of the data. Thus the most significant partition can be deduced. The program assigns each probability to a significance level on a simple scale representing significance at 5, 1, .33, .1 .033, .01, .0033, .001, .00033 and .0001 percentage levels. The output from STEPTWO consists of a matrix of the rank values for two variables. The matrix cells containing the significance scale values. [For further details see, Underwood and Stimson (*in press*).] The output was converted into a three dimensional map of the probability scale contours. [A graph drawing program (Harding, 1982) was modified and used for this purpose]. These plots (Figs 17-20) represent the rank value of one variable v that of another v the significance scale number. When two continuous variables are correlated there is a diagonal group of higher significance levels around which other pairs of probabilities form contours. The STEP suite was run, in BASIC, on the BBC computer.

Dissections

Both dry (very brittle) and freshly collected specimens were softened in warm 10% Potassium hydroxide and dissected in distilled water. Dissections were secured in wax, or on adhesive tape and tissue was removed using a needle tip covered in adhesive, the adhesive was applied by scraping the needle over Cellulose acetate tape (Gibson, 1985). Specimens and dissections were cleaned, in Tepol, in a small tube placed in an ultrasonic cleaner. Thoracic musculature was investigated in specimens dried with a Tousimis Research Corporation Samdri-780A critical-point drier.

CHAPTER 2: CLADISTIC THEORY

PHYLOGENETIC RECONSTRUCTION

Orthodox classification (e.g. Mayr, 1963; 1969; Simpson, 1961; 1975) is based on intuitive judgements founded on systematic experience. The results can be excellent but are subjective, and invalid in terms of Popperian logic (Popper, 1959).

Phenetics (Sokal & Sneath, 1963; Sneath & Sokal, 1973) led to the development of numerical techniques, but no account was taken of evolutionary polarity, and the groups were not always uniquely defined (Pratt, 1972; Nelson & Platnik, 1981). Phenetics has now been displaced by cladistics.

Hennig (1950; 1965; 1966; 1969; 1981) produced the first operational method (CLADISTICS) for reconstructing phylogenies. He postulated that common ancestry is defined by shared, derived, homologous character-states (SYNAPOMORPHIES), but not by shared primitive character-states (SYMPLESIOMORPHIES), nor by independently derived and thus non-homologous character-states. Organisms are grouped together (CLADES) on the basis of features that they all possess, and that other organisms do not. Patterns of synapomorphies - CLADOGRAMS are distinguished from representations of evolutionary history - TREES, and from trees that incorporate biological, ecological and similar data - SCENARIOS (Eldredge, 1979; Eldredge & Cracraft, 1980; Eldredge & Tattersall, 1975; Harper & Platnick, 1978; Patterson, 1980; 1982; Platnick, 1977; Tattersall & Eldredge, 1977).

An important advantage of cladistics is that it lends itself to modern computational methods (Farris et.al., 1970; Kluge & Farris, 1969).

Homoplasy

Ideally each character helps to establish the phylogeny, but with real data HOMOPLASY (similarity not due to common descent) will create incompatibilities between characters. Homoplasy is a significant restriction

on analysis, and is caused by evolutionary parallelism, convergence or character-state reversal. CONVERGENCE is similarity caused by independent acquisition of an attribute by two or more unrelated lineages whose (remote) common ancestor did not have the character. PARALLELISM is independent development (not as a direct result of common ancestry) of a character-state by related organisms due to similar selective pressures (Cantino, 1985). REVERSALS are back mutations (double apomorphies), they may arise by the failure of genetic suppression of a character (Hecht & Edwards, 1977).

Holophyly

Hennig (1966) defined a MONOPHYLETIC taxon as a group of species derived from a common ancestor. Due to an ambiguity the term HOLOPHYLETIC is now used to include an ancestral taxon and all of its descendants (Ashlock, 1971. c.f. Farris, 1974). A PARAPHYLETIC group consists of the ancestor plus some, but not all, of the ancestor's descendants, and a POLYPHYLETIC assemblage is an artificial aggregation based on shared non-homologous characters. Thus holophyly, paraphyly and polyphyly are characterized by synapomorphies, synapomorphies / symplesiomorphies and convergence respectively (Fig. 1).

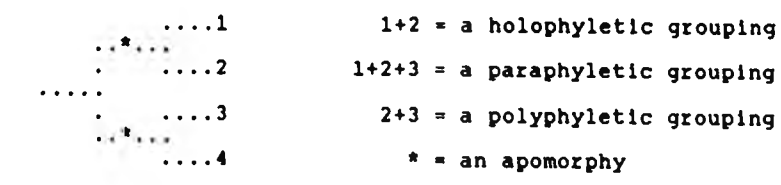

Figure 1. Holophyly, paraphyly & polyphyly.

CLADISTIC ANALYSIS

Modern science is founded on Occam's Razor (that the best explanation is the one that accommodates all the relevant facts with the fewest explanatory assumptions). However, no method that is consistent with this principle has yet been developed to deal with homoplasy. Instead,

the two approaches of making changes to account for all the data, or making no assumptions and accounting for as many facts as possible, have been developed independently. PARSIMONY analysis seeks the answer with the smallest number of character transformations. COMPATABILITY analysis seeks the answer with the largest number of compatible characters (Felsenstein, 1973; 1978a; 1978b; 1979). As the frequency of homoplasy increases so the two methods give increasingly different results (Gauld, 1983). Both methods are NP-complete i.e. they are computations that lack an efficient algorithm (Day, 1983; Day & Sankoff, 1988; Felsenstein, 1982). This means that the results are only locally optimal and cannot be considered completely reliable (hence the need for the supporting evidence e.g. biology).

Parsimony

Apart from doctrinal criticisms by Felsenstein (1981), Friday (1982), Panchen (1982) and Pratt (1972); there are specific criticisms of the parsimony method.

1 Because transformations are minimized, a set of "poor" characters can be chosen instead of a slightly smaller set of "good" characters (Gauld, 1985).
2 Different (equally parsimonious) trees can be found depending on the sequence of data entry (Gauld, 1985).
3 It is not possible to predict the minimum tree length for a data set (Felsenstein, 1982). With as few as twenty taxa it is impracticable to register the vast number of trees in order to select the most parsimonious. Thus it can only be assumed that the result is *the* shortest tree.
4 Parsimony methods estimate minimum transformation, but there is no reason to assume that evolution is by *minimum* modification (Darwin, 1859; Underwood, 1982; Gauld & Underwood, 1986).
5 Parsimony sometimes results in a plethora of minimum length trees with vastly different topologies (Sharkey; 1989).

Compatibility

LeQuesne (1969) following the work of Wilson (1965), showed that the consideration together of independent two-state characters could indicate the possibility of their non-unique derivation. Thus if all 4 possible combinations of a pair of two-state (plesiomorphic 0 to 1 apomorphic) characters occur (0,0; 0,1; 1,0 and 1,1) then there is an incompatibility (Fig. 2). This is a NON-POLAR INCOMPATIBILITY and reversing the 0 and 1 scores does not dispel it. [The states 0,1; 1,0; and 1,1 occuring together in the same lineage, without the 0,0 score, cause a POLAR-INCOMPATIBILITY which can be dissipated by reversing the polarity of either or both the characters.]

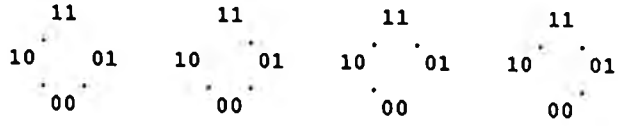

Figure 2. The four homoplasies of four paired characters.

By comparing each character against every other it is then possible to calculate the ratio of the actual number of non-polar incompatibilities found, to the total number of non-polar incompatibilities expected (on a null hypothesis of random distribution of character-states) for each character. LeQuesne (1972, 1974, 1979) defined this ratio (expressed as a percentage) as the COEFFICIENT OF CHARACTER STATE RANDOMNESS; a coefficient of 100% would suggest a random distribution. In the production of a totally compatible data-set (CLIQUE) the LeQuesne ratio is used to locate the most incompatible character. This character is deleted from the data and the new set re-analysed. Repeating this "BOIL-DOWN" will eventually leave a clique, which is used to construct the cladogram (Estabrook et.al. 1976a; 1976b; 1977; 1978; 1979; Meacham, 1981).

Compatibility analysis has two significant failings. The clique may be too small to provide sufficent resolution of the taxa (Farris, 1983). Secondly, two or

more equally large cliques may be produced with no great evidence to predict which is the better (Kluge, 1976). The first failing can be reduced by the application of LeQuesne's procedure to subsets of the data. Characters eliminated from the clique may still be compatible within a subset and can provide valuable secondary evidence (Strauch, 1984). In response to the second criticism, Estabrook & Anderson (1978) developed a technique of "core" analysis - the core defines a dendrogram that is supported by all the known cliques.

CHOICE OF ANALYTICAL METHODS

According to Felsenstein (1982) it is the rate of evolution in the group, which determines which method should be used. If rates of evolution are uniformly high, then neither method is applicable. If the rate is low and uniform then unweighted parsimony is indicated and if low but unevenly scattered then compatibility is indicated. Unfortunately Felsenstein does not explain what "low" or "high" are, and what sort of scatter is "uneven". Also it is not known in advance what the rate of evolution might be in the Cynipoidea. If the rate of evolution is proportional to the level of homoplasy then the rate is very high in at least some parasitic Hymenoptera (e.g. Gauld, 1985 found a LeQuesne coefficient of 83% in the Ichneumonidae).

There is a strong suspicion that cynipoid homoplasy is not evenly distributed and that this is why the past classifications have been unsuccessful - because they were biased towards certain "poor" character-suites. An advantage of compatibility methods is that they provide the opportunity to see the actual pattern of incompatibilities. "Poor" characters are identified and thus at least some homoplasy may be understood. Such an understanding is vital before a better classification can be produced.

The Cynipoidea, like other derived Hymenoptera, exhibit many loss-characters and these are a major source of homoplasy. It could be argued that these characters

should be deleted before analysis but that would be invalid data dredging (Selvin & Stuart, 1966).

It is concluded that compatibility is the most appropriate technique for this study of the Cynipoidea. However, in order to be thorough, a parsimony analysis was also conducted.

COMPUTER PROGRAMS

Compatibility programs

Underwood (1982; Gauld and Underwood, 1986) developed the LEQU programs (see Appendix 1). The characters of the study taxa are awarded binary scores and these scores are converted by the CONVERT program into a form that can be read by the other programs. The program LEQUA prints out a matrix of scores for taxa versus characters. The second program (LEQUB) computes the Lequesne ratio (see above) for each character. The polar and non-polar incompatabilities are tabulated and an overall LeQuesne coefficient is computed. The characters are then listed in order of their ratios. A "boil-down" facility enables the compatible clique to be ascertained (see above). The program LEQUC tabulates a matrix of taxa versus characters and the frequency of incompatibilities is used to award "MARKS" (demerits). A "mark" is awarded each time one taxon is uniquely responsible for an incompatibility between a given character pair. The output from the program consists of a character / taxon matrix but, in place of the original score, each cell contains the number of times that a particular score was marked (e.g. Table 12). Against each taxon the LEQUC program prints the number of "marks" accumulated. The taxa or characters most frequently marked will be the most discordant; a high mark for any character / taxon combination indicates the likelihood of homoplasy with respect to the other taxa (see Guise et.al., 1982).

Character weighting

O'Nolan (1985; Moody & O'Nolan, 1987) developed LeQuesne compatibility into a weighting scheme in order to discover the best supported or least contradicted cladogram. Detection of an incompatibility does not indicate which of the characters is homoplasious. However, if one of two such characters has a lower overall compatibility (tested against all the other characters) it is more likely to be the homoplastic character.

Dr G. Underwood has developed O'Nolan's algorithm (Table 2) into a BASIC program (O'NOLAN). The program (see appendix 1) provides weights for the characters and indicates both the surviving characters and those characters that were rejected as having lowest weight on an iteration.

1 Eliminate unvarying and singleton characters.
2 Assign a weight of one to all characters.
3 Construct a character compatibility matrix.
4 Count the compatibilities for each character.
5 Construct a new array. For each character A make a pairwise compatibility test using the matrix (above).
  a) If A is compatible with character B then add B's compatibility total to the total for A.
  b) If A and B are incompatible then subtract B's total multiplied by the weight for B, from A. [This produces a more conservative weighting by reducing the weight penalty for incompatibility].
6 Divide each row sum by the square of (n-1). [This scales the row sum between +1 and -1.]
7 If this is the first pass then no characters are elliminated. [This is reduces the influence of poor characters, which have an initial weight of 1.]
8 Eliminate the character(s) of equal lowest weight.
9 Stop if remaining characters have a weight of one or if only two characters remain, otherwise go to three.

Table 2. The O'Nolan algorithm.

The parsimony program

HENNIG86 is the most recently available parsimony program. It is subject to copyright so details of the code are unknown. With the large cynipoid data-set only limited tree construction options are available. Extended branch-swapping was applied to the trees found, all but

the shortest trees were rejected and the remainder were used to construct a Nelson consensus tree (Farris, 1969; 1970; 1977; 1979).

CHARACTER SCORING

A transformation series can have only one ancestral condition but there may be more than one apomorphic state (Hecht & Edwards, 1976; 1977). The scoring of multistate characters for compatibility analysis is in additive binary form i.e. the binary components of a multistate variable bear the same character number but are distinguished by figures after a decimal point (e.g. Table 8). Branching patterns can be included in this method of scoring. Variable "V" scores will be interpreted as both 0 and 1, and missing scores "-" are not used in character comparison.

Ghiselin (1984) analysed nonsubstantive characters, e.g. distribution, but as distribution is not directly inheritable it is not a valid character (O'Nolan, 1985). In the present study the morphological characters are subjected to cladistic analysis and the results are then compared with the available nonsubstantive characters.

ASSIGNMENT OF EVOLUTIONARY POLARITY

The decision about which character-states are derived (apomorphic) depends on the evolutionary direction or POLARITY of the phenocline (Nelson,1973; 1978). Several CRITERIA have been used to assign polarity (Solbrig, 1970) and they are discussed below.

In-group analysis of character-state distribution

The most frequently occurring character-state in the group is taken to be primitive. This "commonality principle" infers that shared states are ancestral and not parallelisms (Crisci, 1980; Crowson, 1970; Estabrook et. al., 1977; Melville, 1962; 1963). This criterion is rejected because the frequency of a character-state depends on the evolutionary history of the lineage

(Stevens, 1980) subsequent to the origin of the state.

Out-group analysis of character-state distribution

Out-group analysis requires a knowledge of the relationship between the taxon being examined, its sister-group, and at least one taxon that is more primitive (the latter two being the out-groups). A character-state that occurs in the in-group and the basal group is primitive. A character-state that occurs only in the out-groups is primitive and the state in the in-group is derived.

There are two sources of error that can affect this criterion. The first is homoplasy, but this should be detected during subsequent cladistic analysis. The second is that an incorrect out-group may be selected (Throckmorton, 1967). Colless (1967, 1969) asked how a comparison can be made with a *closely* related group when the phylogeny is unknown. However, the requirement for a *close* relationship is a practical one (more characters in common). So a provisional phylogeny is acceptable for out-group analysis, providing continued efforts are undertaken to assure holophyly, that the in-group is not the basal group, and that the out-groups are correct (Bremer & Wanntorp, 1978; Hull, 1967; Jong, 1980; Schlee, 1969; Wagner, 1961; 1969; 1973; Walker, 1976).

Palaeontology

The temporal sequence of fossils was regarded as central to the concept of phylogeny (Lam, 1959). However, for polarity determination, fossils should be interpreted only after they have been assigned to Recent holophyletic groups (Cracraft, 1974; 1979; Crisci & Stuessy, 1980; Hull, 1980; Patterson, 1977; 1981; Platnick, 1980; Schaffer et.al., 1972). Further it is impossible to study the entire structure (holomorphology) of a fossil organism. Too few fossil Cynipoidea are available for this criterion to be appropriate here.

Karyology

Genetic structure has been used to establish polarity

(Gibby, 1981; Jones, 1977; Turner, 1984). However, little is known about cynipoid karyology and so this criterion is inappropriate at present.

Other Criteria

Complexity, specialization, function, ontogeny, vestigial organs, teratology, correlation, character sequences and trends are now known to be invalid as direct determinants of polarity (Alberch, 1980; Bishop, 1982; Cronquist, 1968; Lande, 1978; Marx & Rabb, 1970; 1972; Platnick, 1979; Sporne, 1976; 1977; Stern, 1978; Thorne, 1976).

Summary

Out-group analysis forms the only acceptable method for assigning evolutionary polarity (Arnold, 1981; Colless, 1967; Jong & Burtt, 1975; Lundburg, 1972; Ross, 1974; Watrous & Wheeler, 1981; Wiley, 1981) to cynipoid character-states.

CHAPTER 3: ANALYSIS OF THE ESTABLISHED CLASSIFICATION

If the classification of the Cynipoidea is to be improved, it is important to understand what is wrong with the current classification. Poor resolution is most likely to be caused by a dearth of characters and particularly too few apomorphies and synapomorphies (poor character definition can be included here) or high levels of homoplasy reducing the information value of characters. In order to establish the extent of these two factors, the existing classification was subjected to cladistic analysis.

ESTABLISHMENT OF OUT-GROUPS FOR POLARITY DETERMINATION

Phylogeny of the Hymenoptera

The Hymenoptera is divided into the Symphyta, which contains the most primitive species, and the Apocrita. The latter is generally considered to be a holophyletic group (Rasnitsyn, 1968; 1969; 1980), but its phylogeny is incompletely resolved. Königsmann (1978) investigated the apocritan lineages and found eleven holophyletic groups (Fig. 3). He also provided an alternative postulate of

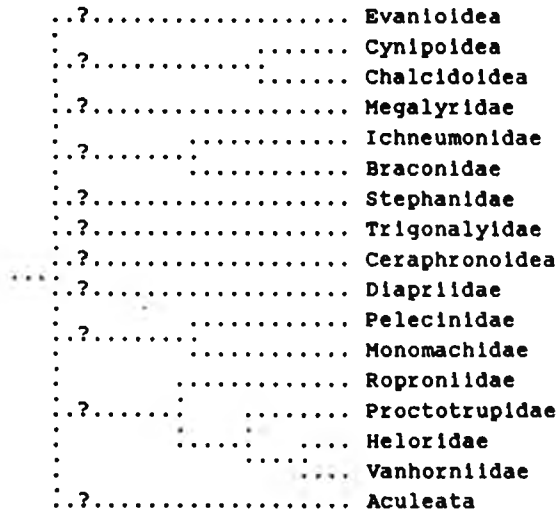

Figure 3. Königsmann's 1978 arrangement of the Apocrita.

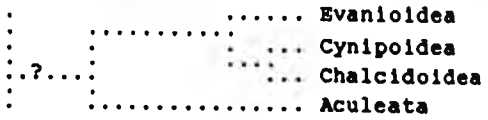

Figure 4. Königsmann's alternative arrangement.

which taxa are related to the Cynipoidea (Fig. 4). In both arrangements the Chalcidoidea is the sister-group of the Cynipoidea. The features that link the Evanoidea and Aculeata to the Cynipoidea and Chalcidoidea have been shown to be symplesiomorphies (Gibson, 1985; 1986; Richards, 1977; Mason, *in. litt.*) and thus Königsmann's second arrangement is not accepted.

Rasnitsyn (1969) provided a different phylogeny of the Apocrita (Fig. 5), which he changed (Rasnitsyn, 1980) to include only four groups: Stephanomorpha, Evaniomorpha, Ichneumonomorpha and Vespomorpha; the "microhymenoptera" (Cynipoidea, Chalcidoidea and Proctotrupoidea) being placed with the Ichneumonoidea in the Ichneumonomorpha. Recently, Rasnitsyn (1988) has produced yet another arrangement (Fig. 6); here the Cynipoidea is contained within the infraorder Proctotrupomorpha. The Cynipoidea is shown as the sister-group of the Diapriidae but the

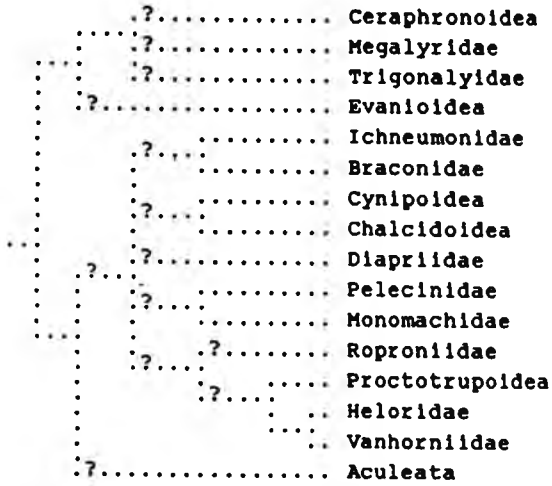

Figure 5. Apocritan phylogeny (Rasnitsyn, 1969).

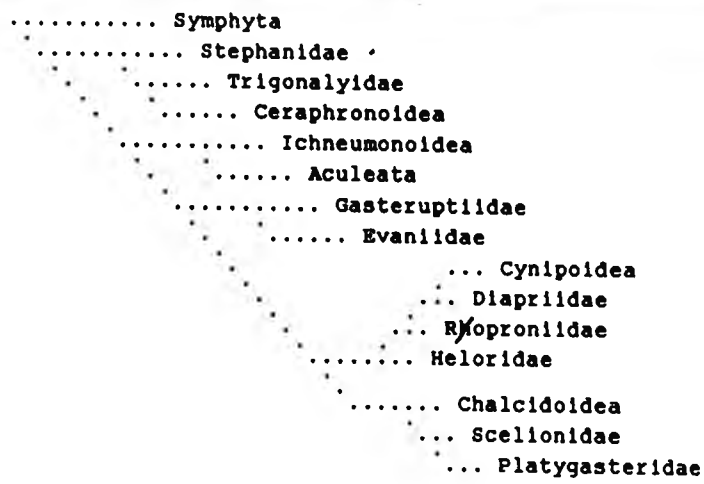

Figure 6. Rasnitsyn's 1988 arrangement of the Hymenoptera.

characters linking these two groups are loss-features likely to be parallelisms.

Out-groups of the Cynipoidea

The above examples show that it is not possible, at present, to provide anything like a definitive phylogeny of the Apocrita. However, a wide investigation of the likely taxa indicates that the sister-group of the Cynipoidea is probably to be found amongst the Chalcidoidea or proctotrupoid groups.

Polarity determination requires knowledge of the basal out-group and, for the Cynipoidea, this must be sought amongst the less derived Apocrita. Several of the "primitive superfamilies" are rare, specialized, or of a very uncertain position, and therefore the Ichneumonoidea appear to be the most appropriate basal out-group. However, if, during polarity assessment, there was any doubt about the evolutionary direction of a phenocline, then several groups were investigated and, in order to be assured of knowing the plesiomorphic state, these studies always included examination of Symphyta.

Polarity decisions

There has been no previous attempt to establish the

polarity of a comprehensive range of cynipoid character--states. Therefore, a large number of cynipoid and out--group specimens (over 35,000) were examined so that the assessments should be well founded. The inevitably repetitious explanations of the polarity decisions have not been provided in the text because the compatibility programs do not require evolutionary direction for clique formation. A confident assessment of polarity for some, but not necessarily all, characters is sufficient to produce a rooted tree.

THE TAXONOMIC HISTORY OF THE CYNIPOIDEA

Linnaeus (1758) placed the cynipoids in a single genus (*Cynips*) and in 1805 Latreille elevated them into a family, but it was not until 1899 that their current status, as a superfamily, was recognised by Ashmead (Table

Families	Subfamilies	Tribes
Figitidae	Figitinae	-
	Onychiinae 1	-
	Anacharinae	-
	Liopterinae	-
	Eucoilinae	-
	Xystinae 2	Xystini
		Loboscelidiini 3
Cynipidae	Cynipinae	
		Cynipini
		Rhoditini
		Pedaspidini 4
		Aulacini
		Eschatocerini 4
	Synerginae	-
	Ibaliinae	-

Table 3. Ashmead's 1903 classification (1 = Aspicerinae, 2 = Alloxystinae, 3 - Chrysidoidea, 4 = aberrant genera).

Families	Subfamilies	Tribes
Ibaliidae	-	-
Liopteridae	-	-
Cynipidae	Cynipinae	Cynipini
		Charipini
	Eucoilinae	-
	Figitinae	Figitini
		Anacharitini
		Aspicerini

Table 4. The classification from Hedicke, 1942.

Families	Subfamilies	Tribes
Ibaliidae	Ibaliinae	-
Liopteridae	Liopterinae	-
	Oberthuerellinae	-
	Mesocynipinae	-
Figitidae	Figitinae	-
	Aspicerinae	-
	Anacharitinae	-
Cynipidae	Cynipinae	-
	Pycnostigmatinae	-
	Charipinae	-
	Eucoilidae	-

Table 5. The classification from Weld, 1952.

Families	Subfamilies	Tribes
Ibaliidae	-	-
Liopteridae	Liopterinae	-
	Oberthuerellinae	-
	Mesocynipinae	-
Figitidae	Figitinae	-
	Aspicerinae	-
	Anacharitinae	-
	Himalocynipinae	-
Eucoilidae	-	-
Cynipidae	Cynipinae	-
	Alloxystinae	-
	Austrocynipinae	-
	Pycnostigmatinae	-

Table 6. The classification from Quinlan, 1979.

Families	Subfamilies	Tribes
Ibaliidae	-	-
Eucoilidae	-	-
Aspiceratidae	-	-
Cynipidae	-	-
Anacharitidae	-	-
Figitidae	-	-
Charipidae	-	-
Alloxystidae	-	-

Table 7. Classification from Evenhuis, 1982.

3). Most subsequent authors (e.g. Hedicke, 1942) included the Eucoilinae and the Figitinae in the family Cynipidae (Table 4), but later (Tables 5 & 6) these were accepted as distinct families. The tendency of taxonomists to upgrade higher taxa is shown in a recent classification (Table 7), where all the suprageneric taxa are treated as families.

Representative classification

The most detailed of the modern studies is that of

Weld (1952), but it does not include the Himalocynipinae and Austrocynipinae which were not described until 1970/1. However, these subfamilies are considered in the work of Quinlan (1979). Therefore the classifications of both Weld and Quinlan will be used to represent the "current classification". The family / subfamily keys of these two authors were broken down into their consitituent character-states, which were then analysed.

The family / subfamily keys of both Weld (1952) and Quinlan (1979) contain monochotomies, many badly defined characters and several repetitions. With the exception of the latter, all the characters are listed below. The original wording has been maintained, therefore the terminology is inconsistent with the remainder of this thesis. Comments and polarity assessments are given within brackets - []. Scores: 0 = plesiomorphic state, 1 = apomorphic state.

CHARACTER-STATES FROM WELD, 1952

1.1, 1.2 Species larger than 2mm. [0,0]. / Large heavy-bodied forms [1,0]. / Under 2mm long. [0,1].

2 Scutellum without spine [0]. / Scutellum ending in a spine(s) [1].

3 - [Scutellum sculptured (0)]. / Scutellum smooth [1].

4 Scutellum without a "cup" [0]. / Characteristic raised "cup" present on disc [1].

5.1, 5.2 Body usually sculptured [0,0]. / Thorax without sculpture [0,1]. / Thorax dull [rough] sculptured [1,0].

6 Radial cell closed [0]. / - [open (1)].

7 Radial cell less than nine times as long as broad [0]. / Radial cell at least nine times as long as broad (internal measurements) [1].

8 Areolet present [0]. / Areolet absent [1].

9 Areolet directly under first cubital cell [0]. / Areolet under centre of radial cell [1].

10 Venation normal [0]. / Radial cell suggesting a stigma [1].

11 - [winged (0)]. / Fully winged, with rudimentary wings

or wingless [Reduced wings (1)].

12 Hind femur unarmed [0]. / Hind femur with a tooth on the underside [1].

13 Tarsal claws simple or toothed [toothed (0)]. / - [bifid (1)].

14 First segment of hind tarsus less than twice as long as segments 2-5 united [0]. / First segment of hind tarsus twice as long as segments 2-5 united [1].

15 Petiole sulcate [0]. / Petiole smooth [1].

16 Petiole inconspicuous or sessile not or scarcely longer than medially broad [0]. / Petiole at least as long as medially broad [1].

17 Petiole attached normally [0]. / Petiole attached tangentially [1]. [It was considered that only the Liopterinae showed this feature but a careful examination has shown that this is also present in the Oberthuerellinae.]

18 - [not wedge-shaped (0)]. / Body, when seen from above, distinctly wedge-shaped [1].

19 - [not blade-like (0)]. / Abdomen of female elongated, knife-like [1].

20 Tergite two not liguliform [0]. / Tergite two liguliform [actually saddle-shaped (1)].

21 Largest [gastral] segment [of female], in side view, tergite two or three (or the two fused with, or without, a visible suture). Never more than one short tergite in front of the large tergite [0]. / Largest [gastral] segment [of female], in side view, tergite four, five or six. With two three or four short tergites behind the petiole and preceeding the big tergite [1].

22 Tergite two [of female] longer than tergite three [0]. / Tergite two [of female] shorter than tergite three [1].

23 Abdomen with tergites two and three not fused [0]. / Tergites two and three fused [1].

ANALYSIS OF WELD DATA

All available specimens of the exemplar species (Table 1) were compared against the Weld characters and species scores were awarded (see Appendix 2). The data was processed through the LEQU programs (Tables 8-13) and fifty four non-polar incompatibilities were found, compared with 102 expected on the null hypothesis (of random distribution), an overall LeQuesne coefficient of 53% (Table 9). There were no polar-incompatibilities, and this strongly suggests that the assigned polarities are correct (or all wrong !). Characters 7, 9, 11, 14, 18 and 19 were completely compatible because they were all plesiomorphic (11, 18) or only scored a single apomorphy (7, 9, 14 and 19). The remaining characters all showed at least one incompatibility.

	1	1	2	3	4	5	5	6	7	8	9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2
	.	.				.	.																	
	1	2				1	2																	
23	-	X	-	X	-	-	X	X	-	-	-	X	-	-	-	-	-	X	-	-	-	-	-	-
22	X	X	X	X	-	X	X	X	-	X	-	-	-	-	X	-	X	X	-	-	-	-	X	
21	-	-	X	-	-	-	-	-	-	X	-	-	-	-	-	-	X	X	-	-	-	-		
20	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
17	-	-	X	-	-	-	-	-	-	X	-	-	-	-	X	-	-	-						
16	X	-	X	-	-	X	-	-	-	X	-	-	-	-	X	-	X							
15	X	X	-	-	-	X	-	X	-	X	-	-	-	-	-	-								
14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-								
13	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-									
12	-	-	-	-	-	-	-	-	-	X	-	-	-	-										
11	-	-	-	-	-	-	-	-	-	-	-	-	-											
10	-	-	-	-	-	X	-	X	-	-	-													
9	-	-	-	-	-	-	-	-	-	-	-													
8	X	-	X	-	-	X	-	X	-															
7	-	-	-	-	-	-	-	-																
6	-	X	X	X	X	X	X																	
5.2	-	-	-	-	-	-																		
5.1	-	-	X	-	-																			
4	-	X	-	-																				
3	-	-	-																					
2	X	-																						
1.2	-																							

Table 8. Incompatibilities (X) between Weld characters.

Char	Incompatibilities obs	exp	ratio	pol	Char	Incompatibilities obs	exp	ratio	pol
1.1	5	13.17	0.38	- 0	1.2	5	11.25	0.44	- 0
2	10	12.15	0.82	- 0	3	3	9.98	0.30	- 0
4	2	8.27	0.24	- 0	5.1	7	14.58	0.48	- 0
5.2	3	9.09	0.33	- 0	6	11	15.47	0.71	- 0
7	0	0.00	0.00	- 0	8	10	8.27	1.21	- 0
9	0	0.00	0.00	- 0	10	3	5.58	0.54	- 0
11	0	0.00	0.00	- 0	12	1	5.58	0.18	- 0
13	4	5.58	0.72	- 0	14	0	0.00	0.00	- 0
15	9	12.91	0.70	- 0	16	8	13.54	0.59	- 0
17	3	11.20	0.27	- 0	18	0	0.00	0.00	- 0
19	0	0.00	0.00	- 0	20	1	8.27	0.12	- 0
21	5	14.07	0.36	- 0	22	12	15.14	0.79	- 0
23	6	11.20	0.54	- 0					

Table 9. LeQuesne ratios for the Weld data. [Char = character number, obs = number of observed incompatibilities, exp = number of incompatibilities expected if distribution random, ratio = obs/ex, pol = number of polar incompatibilities].

7	9	11	14	18	19	20	12	4
17	3	5.2	21	1.1	1.2	5.1	23	10
16	15	6	13	22	2	8		

Table 10. Weld characters ranked in order of their ratios.

Incompatibilities observed	expected	ratio	character deleted
54	102.65	0.53	8
44	94.38	0.47	2
35	82.72	0.42	22
25	69.28	0.36	15
18	58.71	0.31	10
15	54.48	0.28	6
9	43.26	0.21	13
7	39.67	0.18	23
4	32.76	0.12	16
1	25.16	0.04	4
0	21.07	0.00	

Table 11. Boil-down of the Weld characters.

The boil-down facility of the LEQUB program was used to find a compatible clique (Table 11) for the data. Homoplasy was eliminated by the deletion of ten characters. The resultant cladogram (Fig. 8) was compiled from the clique apomorphies (Table 13). The cladogram is unrooted and taxa 13-16, 18-20, 27-29 and 31 are unresolved (see Table 1 for taxon numbers). The 1.2 (small

size) clade does not correspond to any previously recognized taxon, it contains the Charipidae (Charipinae + Alloxystinae) and most of the Eucoilidae. However, *Eucoila* is a large eucoilid and has been excluded. The Eucoilidae is traditionally defined by the presence of a scutellar "cup", but this character (4) is incompatible with character 1.2 and was the last character deleted (Fig. 7 shows the alternative tree with character 4 retaind).

The 5.1 clade includes the Ibaliidae, Liopteridae, Aspicerinae and *Melanips*; this is a novel concept, the Aspicerinae and *Melanips* are normally associated with the Figitidae. Characters 1.1 and 21 unite the Ibaliidae with the Liopteridae, and within this clade *Ibalia* has three autapomorphies. The Liopteridae is divided into its traditional subfamilies but only the Oberthuerellinae is holophyletic.

		Characters																			
										1	1	1	1	1	1	2	2	2	2
		1	1	2	3	4	5	5	6	8	0	2	3	5	6	7	0	1	2	3
		.	.				.	.												
		1	2				1	2												
Taxa	(N)																			
1	(4)	1	-	-	-	-	1	-	-	1	-	-	-	4	-	-	-	1	-	-
2	(5)	-	-	1	-	-	-	-	-	5	-	1	-	-	1	1	-	-	1	-
3	(1)	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-
5	(4)	-	-	1	-	-	-	-	-	-	-	-	4	-	1	1	-	-	1	-
7	(4)	-	-	1	-	-	-	-	-	-	-	-	4	-	1	1	-	-	1	-
10	(1)	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
13	(1)	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
15	(1)	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
20	(1)	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	(1)	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
23	(3)	-	-	-	1	-	-	1	-	-	-	-	-	1	-	-	-	-	-	3
24	(4)	-	1	-	1	-	-	1	-	-	-	-	-	1	-	-	-	-	4	-
25	(2)	-	-	-	1	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-
27	(3)	-	-	-	-	-	1	-	1	-	3	-	-	-	-	-	-	-	-	1
29	(4)	1	-	-	-	-	1	-	1	4	-	-	-	-	-	-	-	1	-	-
30	(3)	-	-	-	-	-	1	-	1	-	3	-	-	-	-	-	-	-	-	1

Table 12. LEQUC marks for the Weld data.
(Column N gives the mark component for each taxon.)

```
          ..... 5.1 clade
          .
          ..... Taxa 13-16,18,19,27-29 & 31
        ...
          ...4..... Eucoilidae
          .
          ..3..5,2.. Charipidae
```

Figure 7. Weld data: tree with character 4 retained.

Characters

Taxa	5.1	1.1	21	17	12	7	14	19	20	9	1.2	3	5.2	11	18
1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0
2	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
3	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
4	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
5	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
6	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
7	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
8	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
9	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
10	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
11	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
12	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
17	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
30	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
24	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
25	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
26	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 13. Data-matrix of the Weld clique; order rearranged.

Next, the subsets of the Weld data were reanalysed. Characters eliminated from the clique, but still compatible within the subset, can be used to provide further resolution of the subset (Strauch, 1984). Because subset analysis uses an incomplete sample, it is possible for polarities to be incompatible within the subset while compatible for the clique. Only one of the Weld characters, character 8, caused such a polarity change.

The analysis of the 5.1 subset found 18 incompatibilities, against 36.18 expected, a ratio of 0.5 (Table 14). Characters 8, 2, 13 and 22 were sequentially

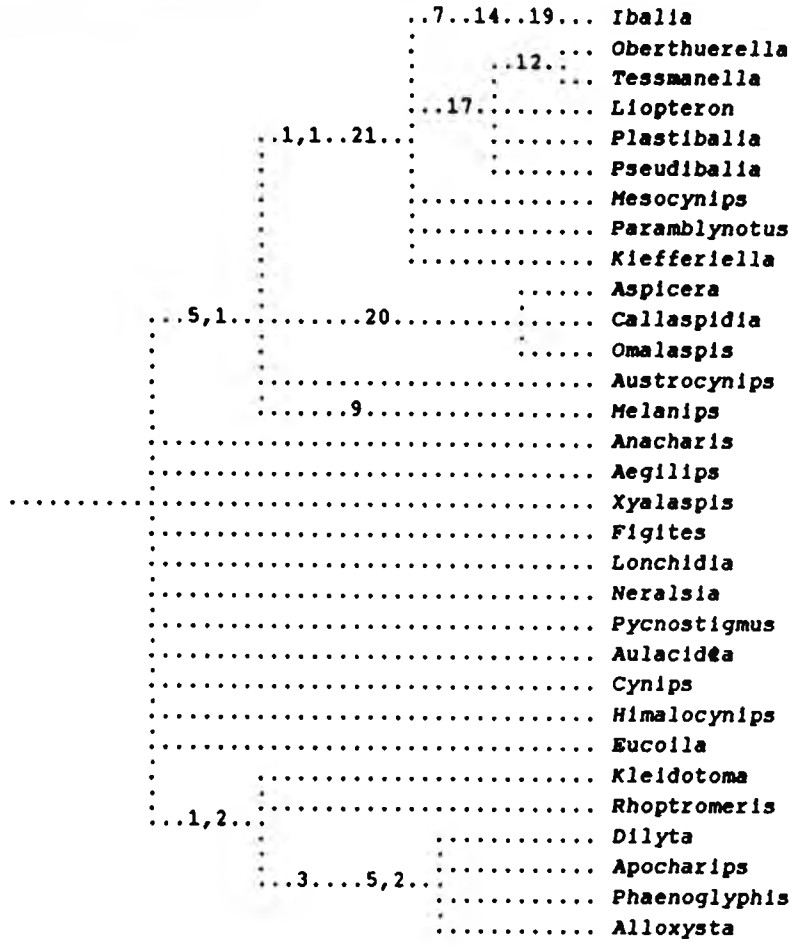

Figure 8. Cladogram from the Weld data.

Char	Incompatibilities				Char	Incompatibilities			
	obs	exp	ratio	pol		obs	exp	ratio	pol
1.1	2	7.74	0.26	- 1	2	8	7.16	1.12	- 0
6	2	7.16	0.28	- 0	8	5	4.27	1.17	- 2
12	1	4.27	0.23	- 0	13	4	4.27	0.94	- 0
16	3	7.74	0.39	- 0	17	3	7.74	0.39	- 0
20	1	6.16	0.16	- 0	21	2	7.74	0.26	- 1
22	5	8.08	0.62	- 0					

Table 14. Analysis of the Weld 5.1 subset
(see table 9 for legends).

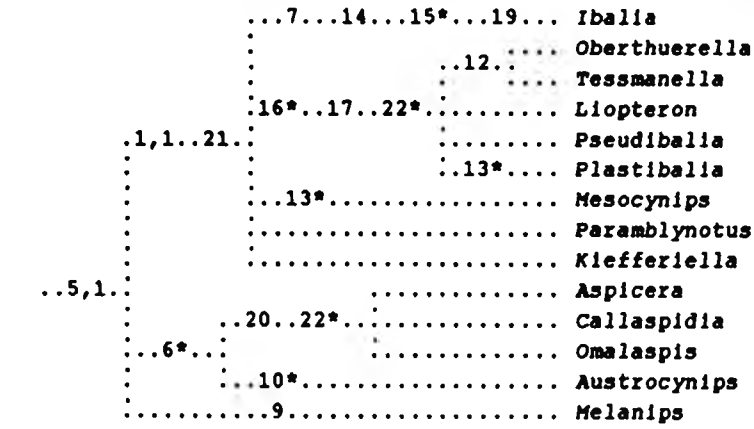

Figure 9. The Weld 5.1 subset (* = additional character).

Char	Incompatibilities				Char	Incompatibilities			
	obs	exp	ratio	pol		obs	exp	ratio	pol
1.2	5	7.38	0.68	- 0	2	3	3.69	0.81	- 0
3	3	6.32	0.47	- 0	4	2	5.38	0.37	- 0
5.2	3	6.32	0.47	- 0	6	7	7.67	0.91	- 1
8	0	0.00	0.00	- 1	15	5	7.38	0.68	- 0
16	2	5.38	0.37	- 0	22	5	6.32	0.79	- 0
23	5	6.72	0.72	- 0					

Table 15. Weld data: analysis of the taxa outside the 5.1 subset (See table 9 for legends).

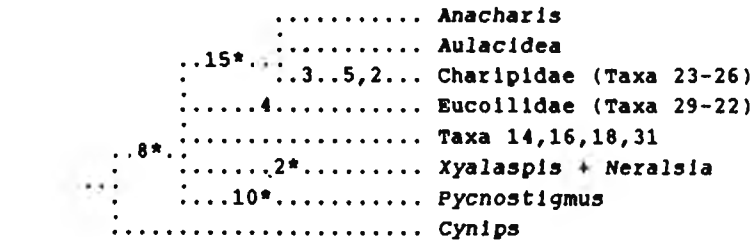

Figure 10. Simplified tree for the taxa outside the Weld 5.1 subset (* = additional character).

deleted in the boil-down and the resultant tree is shown in figure 9.

The remainder of the clique was investigated (Table 15), 20 incompatibilities were found against 31.40 expected, that is a ratio of 0.64. Characters 6, 22, 23, 16 and 1.2 were deleted in the boil-down. The tree was compiled (Fig. 10) and it shows character 8 linking all the subset taxa except *Cynips*, thus the two genera of Cynipidae are separated. *Eucoila* is now associated with the other Eucoilidae, so perhaps this genus underwent a reversal with regard to character 1.2. Character 15, as well as isolating *Anacharis* from the other anacharitines, delimits an assemblage of morphologically dissimilar taxa.

CHARACTER-STATES FROM QUINLAN, 1979

1 Head broader than thorax when viewed dorsally [0]. / Head narrower than thorax, oblong in dorsal view [1].

2 - [Clypeus normal (0)]. / Clypeus projecting forward and upward away from the labium [1].

3 Antenna of male with modified segment, when present, always the third [0]. / Male with the fourth, sometimes the third to fith antennal segment(s) modified [1].

4 Antenna of male 14-segmented [0]. / Male unknown [other than 14 segments (1)].

5.1, 5.2, 5.3 Antenna of female 13-segmented [0,0,0]. / Antenna of female 12-segmented [1,0,0]. / Antenna of female 14 to 19-segmented [0,1,0]. / Antenna of female 20-segmented [0,1,1].

6 Pronotum if raised dorsally into an indistinct anterior plate then without a posterior margin [0]. / Pronotum produced frontodorsally into an anterior plate with a strong posterior margin [1].

7 Pronotum not sharply angled anteriorly, [0]. / Pronotum generally sharply angled anteriorly, forming a lateral carina [1].

8 Scutellum without a spine [0]. / Scutellum with a distinct spine [or spines] at apex [1].

9 Scutellum without a "cup" [0]. / Scutellum with a "cup" on dorsal surface [1].

10 Scutellum without three longitudinal carinae [0]. / Scutellum with one or more [three] longitudinal carinae [1].

11.1, 11.2 Sculpture present on the vertex, mesonotum, scutellum, mesopleuron or gaster [0,0]. / Vertex, mesonotum, scutellum, mesopleuron and gaster smooth and shiny [0,1]. / Thorax [strongly] sculptured [1,0].

12 Radial cell closed [0]. / Radial cell open on front margin (R1 and Rs2 not reaching margin of wing) [1].

13 Forewing without a pterostigma [0]. / Radial cell of forewing with a distinct pterostigma [1].

14 Radial cell normal [0]. / Radial cell much reduced, its veins thick and heavy [1].

15 Radial cell less than nine times as long as broad [0]. / Radial cell at least nine times as long as broad [1].

16 Alate, without apterous forms [0]. / Winged, brachypterous or apterous [1].

17 Cubitalis divided externally before point of emission of 2rm (i.e. areolet present though often obsolete) [0]. / Cubitalis (Rs+M) divided externally at the point of emission of 2rm (i.e. areolet vestigial) [1].

18 Cubitalis (Rs+M), when visible, arising from a point nearer the middle of basalis (Rs and M) than to the junction of basalis with median (Cu1) [0]. / Cubitalis, when visible, arising from a point at or close to junction of basalis with median (Cu1) [1].

19 Cubitus (M) almost reaching apex of forewing, nervellus (Cu and Cu-a) and post nervellus (M-Cu) indicated [0]. / Cubitus vestigial, nervellus and post nervellus absent [1].

20 Mid tibia with two distinct spurs [0]. / Mid tibia often with only one spur [1].

21.1, 21.2 Hind tibia with two distinct spurs [0,0]. / Hind tibia with one spur [1,1] or more often with two very unequal spurs [1,0].

22 Hind tibia not longitudinally ridged or furrowed externally or posteriorly, at most with a longitudinal

carina or groove internally [0]. / Hind tibia, in most genera, longitudinally ridged or furrowed on outer margin or posteriorly [1].

23 First segment [proximal] of hind tarsus not as long as segments 2-5 combined [0]. / First segment of hind tarsus as long as segments 2-5 combined [1].

24 Hind femur without a tooth [0]. / Hind femur with a distinct ventral tooth [1].

25 Mid and hind coxae elongated [0]. / Mid and hind coxae almost round, and strongly swollen [1].

26 First gastral segment [petiole] attached normally [0]. / First gastral segment attached tangentially [1].

27.1, 27.2 [In dorsal view] First gastral segment [petiole] as long as broad [0,0]. / Segment 1 of gaster twice as long as wide [1,0]. / Segment 1 of gaster forming a [small] ring or collar, never longer than wide [0,1].

28 Petiole sulcate [0]. / Petiole smooth [1].

29 Gaster rarely with pubescence at base of tergite two [0]. / Gaster with pubescent ring at base of tergite two [1].

30 - [not fused (0)]. / Segments two and three of gaster completely fused, without visible suture [1].

31 Tergite two of gaster not liguliform [0]. / Tergite two of gaster liguliform [1].

32.1, 32.2 Tergite two of gaster (when viewed laterally) longer, along dorsal curvature, than tergite three [0,0]. / Tergite two of gaster shorter than tergite three [1,0]. / Tergite two at least half as long as the remaining visible segments (when viewed laterally) [i.e. T2 approximatly = T3-T8] [0,1]. [0,0 if T2 fused with T3.]

33 Both sexes with gaster laterally compressed [0]. / Male with the gaster [almost] cylindrical [1].

34 - [not wedge shaped (0)]. / Gaster wedge shaped [1].

35 Largest segment of gaster the second or third or formed by these two segments fused together. With only one small segment preceding the largest [0]. / Largest

segment of the gaster (in lateral view) the fourth, fifth (except if which has 2-4 fused), or sixth. With two to four small segments preceding the largest segment [1].

ANALYSIS OF QUINLAN DATA

The Quinlan matrix (Appendix 2) was analysed using the LEQU programs, 187 non-polar incompatibilities were found, compared with 280.58 expected on the null hypothesis, this gives a LeQuesne coefficient of 67% (Tables 16 - 19). As with the Weld data, no polar incompatibilities were encountered. The boil-down deleted nineteen characters leaving a clique of twenty two characters, the resultant cladogram is shown in figure 11. The last incompatibilities were between characters 18 versus 5.2 and 18 versus 29 thus the deletion of character 18 seems reasonable. An alternative tree with character 18 retained is shown in figure 12.

The Quinlan cladogram is similar to that from the Weld data. The "large" cynipoids (taxa 1-9 & 31) are arranged in the same way, but here they are not linked with *Melanips* or the Aspicerinae. The Charipidae and Eucoilidae are again associated, but now *Eucoila* is united with the other two eucoilid genera. *Melanips*, *Lonchidia* (Figitidae) and *Aulacidea* (Cynipidae) are also associated with the Eucoilidae and Charipidae, together forming the 29 clade. Therefore the two gall-forming genera, *Cynips* and *Aulacidea*, are separated.

Next, the Quinlan subsets were investigated. The 11.1 clade was analysed (Table 20), 27 incompatibilities were found compaired with 37.23 expected, a ratio of 0.73. The boil-down procedure deleted characters 17, 21.1, 22 and 27.2. The resultant cladogram is shown in figure 13. Characters 17, 21.1 and 27.2 cause show polar incompatibilities within this subset, but only character 27.2 contributes to the subset clique. However, reversing the polarity of this character would just move *Paramblynotus* even further from the rest of the Mesocynipinae. So the original assessment seems more

	3	4	5	6	7	8	9	10	11	11	12	17	18	19	20	21	22	23	26	27	28	29	32	32	33
			.						.	.										.			.	.	
			2						1	2						1				1			1	2	
35	-	X	-	-	-	X	-	-	-	-	-	X	-	X	X	X	X	X	-	-	X	X	X	-	X	-	X
33	-	-	-	-	-	X	-	-	X	-	-	X	X	X	-	X	-	-	-	X	X	-	X	-	X	X	
32.2	X	X	X	-	X	X	-	-	-	X	X	X	X	X	-	X	-	-	-	-	-	X	X	X	-		
32.1	-	-	-	-	X	X	-	-	X	X	X	X	X	X	X	X	X	X	-	-	X	X	X	X			
31		-	-	-	-	-	X	-	-	-	-	-	-	-	-	X	X	-	-	-	-	X	-	-			
30		X	X	X	-	X	-	-	-	-	X	X	-	-	-	X	X	-	-	-	-	-	-	X	X		
29		-	X	-	-	X	-	-	-	-	-	X	-	X	X	X	-	-	-	-	-	-	X	X			
28		X	X	-	-	X	-	-	-	X	-	X	X	X	X	-	-	X	X	-	-	X	X				
27.2		-	-	-	-	X	X	-	X	X	-	X	X	X	X	-	X	X	-	-	-	-					
27.1		-	-	-	-	-	X	-	-	X	-	-	-	X	X	-	-	X	-	X	X						
26			-	-	-	-	X	-	-	-	-	-	X	-	X	-	X	X	-	-							
24			-	-	-	-	-	-	-	-	-	-	x	-	-	-	x	-	-								
23			-	X	-	-	-	X	-	-	X	-	X	X	X	X	X	X									
22			-	X	-	-	-	X	-	X	X	-	X	X	X	X	X	X									
21.1			-	X	X	-	X	X	-	X	X	-	X	X	X	X	-										
20			-	X	-	-	-	-	-	X	X	X	X	X	X												
19			-	X	X	-	X	X	-	-	X	-	X	-	X												
18			-	X	X	-	X	X	-	-	-	-	X	-													
17			-	X	X	-	X	X	-	-	X	-	X														
12			X	X	X	X	X	X	X	-	X	X															
11.2			X	-	-	-	X	-	-	-	-																
11.1			-	X	-	-	X	X	-	-																	
10				-	-	-	-	X	-																		
9			X	-	-	-	-	-																			
7			-	X	X	-																					
6			X	-	-																						
4			X																								

Table 16. Incompatibilities (X) between Quinlan characters

Char	Incompatibilities				Char	Incompatibilities			
	Obs	Exp	Ratio	Pol		Obs	Exp	Ratio	Pol
3	8	9.41	0.85	- 0	4	16	21.84	0.73	- 0
5.2	8	13.51	0.59	- 0	6	2	13.75	0.15	- 0
7	15	24.72	0.61	- 0	8	17	20.31	0.84	- 0
9	2	13.75	0.15	- 0	10	4	13.75	0.29	- 0
11.1	15	23.34	0.64	- 0	11.2	7	15.84	0.44	- 0
12	22	25.69	0.86	- 0	17	18	13.75	1.31	- 0
18	17	25.16	0.68	- 0	19	20	25.47	0.79	- 0
20	13	13.75	0.95	- 0	21.1	21	21.58	0.97	- 0
22	18	16.64	1.08	- 0	23	13	13.75	0.95	- 0
24	3	9.23	0.32	- 0	26	7	18.71	0.37	- 0
27.1	11	17.79	0.62	- 0	27.2	16	24.26	0.66	- 0
28	18	21.58	0.83	- 0	29	11	24.19	0.45	- 0
30	10	18.71	0.53	- 0	31	4	13.75	0.29	- 0
32.1	18	24.21	0.74	- 0	32.2	15	20.51	0.73	- 0
33	12	18.71	0.64	- 0	35	13	23.48	0.55	- 0

Table 17. Quinlan data incompatibilities.
(see Table 9 for legends.)

Incompatibilities Observed	Expected	Ratio	character deleted
187	280.58	0.67	17
169	266.83	0.63	22
152	250.54	0.61	21.1
133	230.16	0.58	3
125	221.57	0.56	20
114	209.17	0.55	28
99	190.58	0.52	8
85	173.81	0.49	19
70	154.17	0.45	12
56	135.38	0.41	32.1
46	118.93	0.39	32.2
38	105.04	0.36	27.1
32	94.66	0.34	4
25	82.23	0.30	7
18	68.97	0.26	27.2
12	56.43	0.21	23
9	50.56	0.18	33
5	42.91	0.12	30
2	35.86	0.06	18
0	26.92		

Table 18. Quinlan data: incompatibility ratios as characters are deleted during LEQUB boil-down.

Characters

Taxa	N	3	4	5	6	7	8	9	10	11	12	15	18	19	21	22	23	24	25	26	27	28	29	30	31	32	33	35
1	(23)	-	3	-	-	-	-	-	2	1	1	5	1	1	@	1	6	4	-	-	-	-	6	1	-	-	1	-	-	2
2	(13)	-	1	-	-	-	2	-	-	-	-	7	-	-	4	-	-	3	3	2	1	-	-	-	-	1	-	2	-
3	(3)	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	3	-	1	-	-	-	-	-	-	-	-	-
4	(2)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	1	-	-	-	-	-	-	-	-
6	(4)	-	-	-	-	-	-	-	1	-	-	1	4	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
7	(1)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
10	(3)	-	-	-	-	-	3	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-
11	(5)	-	-	-	-	-	-	-	2	-	-	-	-	-	3	1	-	-	-	2	-	-	2	-	-	-	-	-	-
12	(2)	-	-	-	-	-	-	-	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-
13	(8)	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	1	6	1	3	-	-	1	-	1	1	
15	(2)	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	
18	(1)	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
19	(8)	-	1	-	-	-	1	-	-	1	-	1	1	-	6	-	-	-	-	-	-	-	-	-	1	-	-	-	
21	(2)	-	-	-	1	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	
22	(8)	8	1	-	1	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
23	(5)	-	1	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	1	-
24	(3)	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	1	-	5	-	-	-	-
25	(1)	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	3	-	-
26	(8)	8	1	-	1	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27	(6)	-	-	4	-	-	-	-	-	-	1	-	-	1	-	1	-	-	-	-	-	-	1	-	1	-	-	1	-
28	(1)	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	3	-	-	1	-
29	(9)	-	1	2	-	1	-	-	-	1	-	1	6	1	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-
30	(2)	-	-	-	-	1	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	1
31	(2)	-	-	2	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 19. The number of LEQUC marks for each taxon. Column N gives the mark component for each taxon (@ = 11).

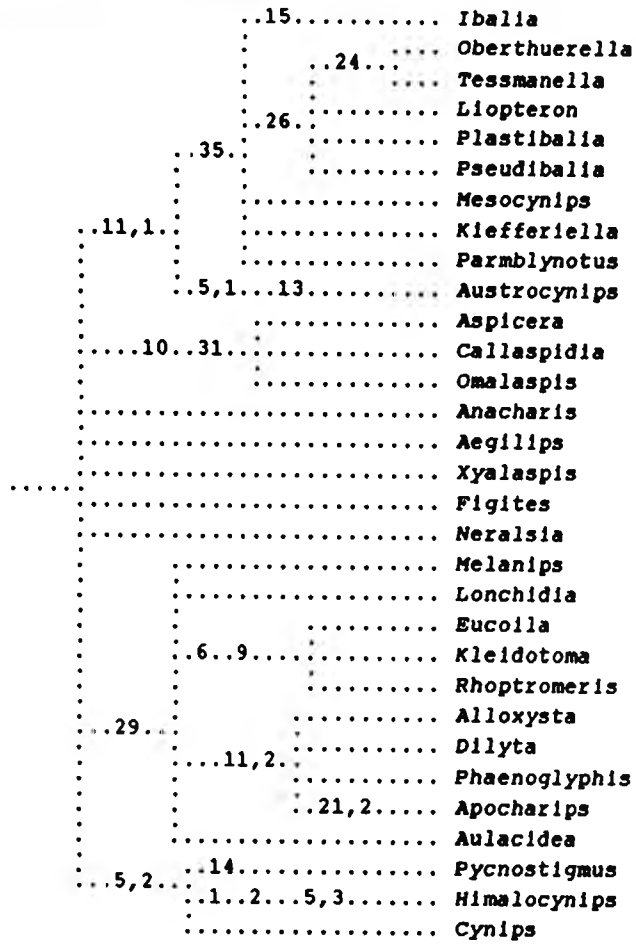

Figure 11. Cladogram from the Quinlan data.

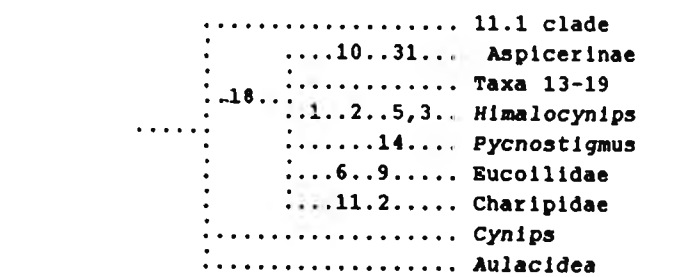

Figure 12. Alternative tree, including character 18.

Char	Incompatibilities				Char	Incompatibilities			
	Obs	Exp	Ratio	Pol		Obs	Exp	Ratio	Pol
4	3	5.17	0.58	- 0	8	3	6.90	0.43	- 0
17	10	4.99	2.00	- 2	21.1	9	7.77	1.16	- 2
22	7	4.99	1.40	- 0	23	3	4.99	0.60	- 0
24	3	4.99	0.60	- 0	26	3	8.02	0.37	- 0
27.1	4	6.85	0.58	- 0	27.2	3	6.80	0.44	- 2
32.1	3	8.02	0.37	- 0	33	3	4.99	0.60	- 0

Table 20. Analysis of the Quinlan 11.1 subset
(See Table 9 for legends).

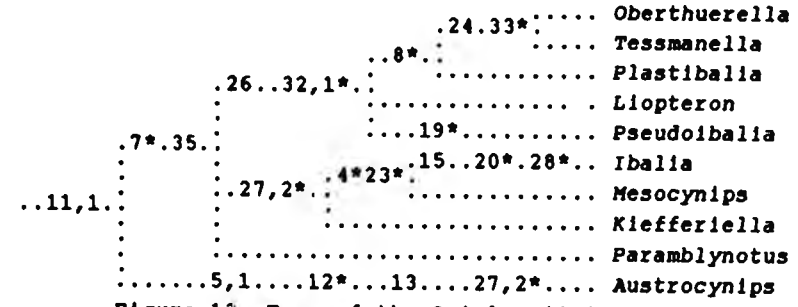

Figure 13. Tree of the Quinlan 11.1 subset
(* = extra character).

Char.	Incompatibilities				Char.	Incompatibilities			
	Obs	Exp	Ratio	Pol		Obs	Exp	Ratio	Pol
3	8	5.80	1.38	- 0	4	2	8.13	0.25	- 2
6	2	8.13	0.25	- 0	7	2	5.80	0.78	- 2
9	2	8.13	0.25	- 0	11.2	5	9.20	0.54	- 0
12	10	9.20	1.09	- 1	18	0	0.00	0.00	- 4
19	4	5.80	0.69	- 0	20	2	5.80	0.34	- 0
27.2	3	5.80	0.52	- 1	28	5	9.52	0.52	- 1
30	6	9.20	0.65	- 0	32.1	5	5.33	0.94	- 0
32.2	4	7.67	0.52	- 1					

Table 21. Analysis of the Quinlan data: 29 subset
(See Table 9 for ledgends).

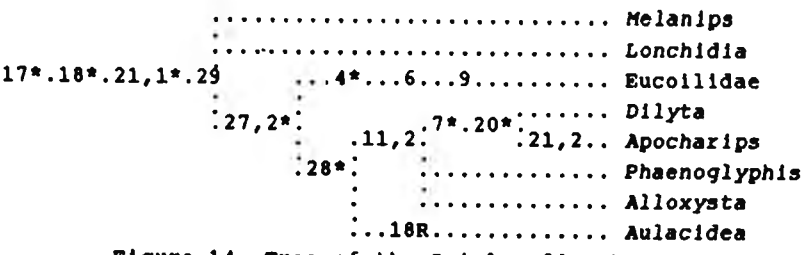

Figure 14. Tree of the Quinlan 29 subset.
(R = possible reversal, * = additional character).

Char	Incompatibilities				Char	Incompatibilities			
	Obs	Exp	Ratio	Pol		Obs	Exp	Ratio	Pol
C01.1	15	28.04	0.53	- 0	C01.2	11	24.19	0.45	- 0
C02	21	25.09	0.84	- 0	C03	8	20.57	0.39	- 0
C04	3	17.01	0.18	- 0	C05.1	19	30.70	0.62	- 0
C05.2	8	19.68	0.41	- 0	C06	26	31.58	0.82	- 0
C08	21	17.01	1.23	- 0	C10	7	10.90	0.64	- 0
C12	3	11.41	0.26	- 0	C13	10	11.41	0.88	- 0
C15	22	26.42	0.83	- 0	C16	14	27.90	0.50	- 0
C17	8	23.13	0.35	- 0	C20	4	17.01	0.24	- 0
C21	15	28.94	0.52	- 0	C22	23	30.98	0.74	- 0
C23	13	23.13	0.56	- 0	C26	9	11.56	0.78	- 0
C27	19	26.65	0.71	- 0	C28.2	9	16.76	0.54	- 0
C29	3	17.01	0.18	- 0	C30	18	30.43	0.59	- 0
C31	4	17.01	0.24	- 0	C34	21	30.96	0.68	- 0
C35	24	31.32	0.77	- 0	C36	17	17.01	1.00	- 0
C37.1	26	26.64	0.98	- 0	C38	20	20.57	0.97	- 0
C39	16	17.01	0.94	- 0	C41.1	14	22.20	0.63	- 0
C41.2	19	30.05	0.63	- 0	C42	13	29.78	0.44	- 0
C43.1	23	30.00	0.77	- 0	C43.2	18	25.57	0.70	- 0
C44	14	23.13	0.61	- 0					

Table 22. Analysis of the combined data.
(See table 9 for legends.)

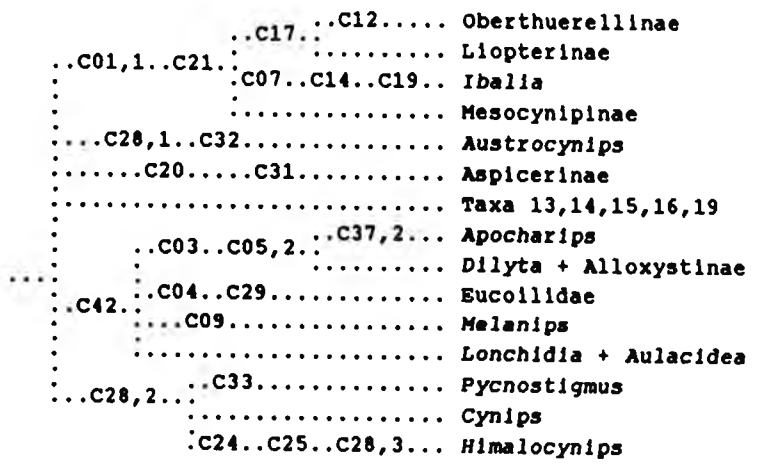

Figure 15. Summary tree of combined data clique.

likely (Fig. 13).

Analysis of the 29 subset, found 30 incompatibilities against the 51.76 expected on the null hypothesis, a ratio of 0.58 (Table 21). The boil-down deleted characters 3, 12, 32.1, 19, 30, and 32.2. The resulting tree (Fig. 14)

shows the Eucoilidae, Charipidae and *Aulacidea* linked together by character 27.2 (petiole short). However, this character is also shared by eleven of the other exemplar taxa and therefore it is of limited value in reconstructing the phylogeny. Character 18 was only included after the program changed the polarity of the *Aulacidea* score, this change is not congruent outside the subset.

ANALYSIS OF COMBINED DATA

Finally the Weld and Quinlan data were combined and analysed as a composite set of 51 characters (see Appendix 2). Fourteen characters occur in both the matrices of Weld and Quinlan (Table 23). The Weld characters were numbered as before but plus C00 (i.e. 1.1 becomes C01.1). The Quinlan characters, minus the 14 repetitions, were renumbered as follows: 1=C24; 2=C25; 3=C26; 4=C27; 5.1, 5.2, 5.3=C28.1, C28.2, C28.3; 6=C29; 7=C30; 10=C31; 13=C32; 14=C33; 18=C34; 19=C35; 20=C36; 21.1, 21.2=C37.1, C37.2; 22=C38; 23=C39; 25=C40; 27.1, 27.2=C41.1, C41.2; 29=C42; 32.1, 32.2=C43.1, C43.2; 33=C44.

W	Q	W	Q	W	Q	W	Q	W	Q
2	8	4	9	5	11	6	12	7	15
8	17	11	16	12	24	15	28	17	26
18	34	20	31	21	35	23	30		

Table 23. Weld (W) and Quinlan (Q) character equivalence.

Analysis of the combined data (table 22) showed 269 incompatibilities against 424.47 expected, a ratio of 0.63. Again no polar incompatibilities were encountered. The clique was established by sequential deletion of characters C08, C37.1, C36, C38, C13, C26, C15, C02, C35, C06, C43.1, C22, C43.2, C10, C27, C41.1, C30, C39, C41.2, C23, C44, C16, C34, C01.2 and C05.1. The resultant cladogram is summarized in figure 15. The last character deleted was C05.1 (thorax dull) and this is incompatible with character C42 (gaster with an anterior ring of hairs). If C42 is rejected in favour of C05.1 then *Melanips* is placed with the large cynipoids, as shown in the Weld cladogram. *Melanips* has little morphological

similarity with these taxa, it is more like the genus *Lonchidia*. Character C05.1 is, probably, badly defined - certainly the dull thorax of *Melanips* although unusual for the Figitidae is not quite as rough as that found in the other genera that are apomorphic for this character.

The subset analysis of the combined data provided an almost identical result to that of the Quinlan data and so it is not reproduced here.

Summary

This study of the characters used in the current classification shows that the superfamily is divided into five units (Fig. 16).

1 The large cynipoids (taxa 1-9), which may, or may not, include *Austrocynips*. Within this group *Ibalia* has many autapomorphies, the Oberthuerellinae is holophyletic, but the Liopterinae and Mesocynipinae are paraphyletic.
2 The Aspicerinae, which is holophyletic.
3 The Eucoilidae, Charipidae (both holophyletic groups), *Melanips* and *Lonchidia* (Figitidae), and *Aulacidea* (Cynipidae). The Figitidae appears to be a paraphyletic assemblage.
4 The gall-causer *Cynips*, plus *Pycnostigmus* and *Himalocynips*. The Quinlan data places *Aulacidea* and *Cynips* in separate lineages, this would indicate that cynipoid gall-causing has a multiple origin.
5 The unresolved remainder of the taxa.

The characters given by Weld provided a very limited resolution of the Cynipoidea. The Quinlan characters give a slightly enhanced resolution but even with the benefit of the extra (homoplasious) characters derived from subset analysis, the resolution is still poor. The analysis of all the data makes it abundantly clear that there are not enough "good" characters present to establish the phylogeny of the Cynipoidea.

It is also apparent that the level of homoplasy in the Cynipoidea is not particularly high. The Weld data

has a LeQuesne coefficient of 53%, and 60% of the characters survived the boil-down to contribute to the clique. The Quinlan data has a coefficient of 67%, and 54% of the characters formed the clique, and the percentages for the combined data are 63% and 51% respectively. The level of homoplasy, at approximately 60%, is relatively favourable, especially when compared with some other hymenopterous data, for example an analysis (Gauld, 1985) of the Ophioninae (Ichneumonidae) had a coefficient of 86% and clique containing only 10% of the characters.

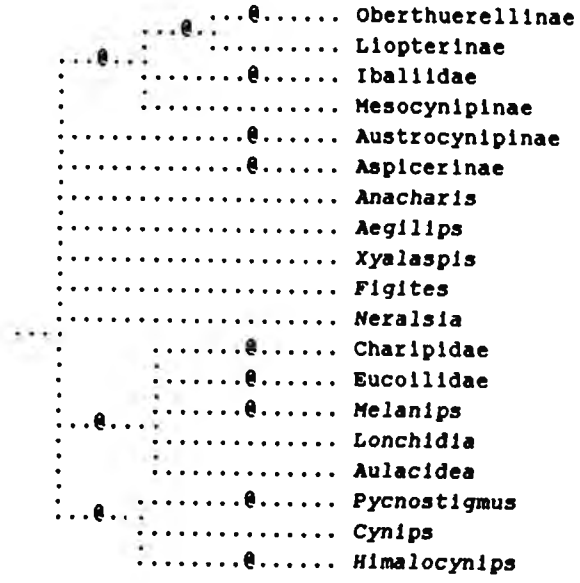

Figure 16. Final summary tree of the combined data. (@ = at least one apomorphy / synapomorphy.)

Conclusion

The above analyses confirm that the inadequacy of the currently recognized structure of the Cynipoidea is caused by poor resolution, - more apomorphies and synapomorphies are required. Therefore an extensive search of cynipoid morphology is needed to provide a significant increase in the number of useful characters.

CHAPTER 4: SURVEY OF CYNIPOID MORPHOLOGY

This chapter contains the results of an extensive investigation into the morphology of the Cynipoidea. All the features that appeared to have potential value for phylogenetic analysis of the higher taxa were characterized. A total of 234 apomorphic states were found, and many of these were newly discovered or reassessed.

Where the characters are of common occurrence in the parasitoid Hymenoptera (e.g. some leg features) they are not commented upon, but the majority of the features are discussed at some length.

THE HEAD

The cynipoid head is broad, tapers downwards, and commonly has a short clypeus. The epistomal suture is fine and the anterior tentorial pits are small. The frontal orbits (the lateral face, near the eyes) are not differentiated from the face and the malar space is often marked by a line of fine sculpture, the malar (or subocular) sulcus. The antennal toruli are between the eyes (not near the clypeus, as in some Proctotrupoidea) and, in some taxa, antennal scrobes occur on the frons. The vertex is short and the ocelli are well separated from the compound eyes. The lower face may bear a central swelling or vertical ridge. Facial pubescence varies in both length and direction but provides useful characters only at lower taxonomic levels.

The foramen magnum is flanked by very small posterior tentorial pits and in some taxa a ridge, the postoccipital suture, extends above the foramen and links the posterior tentorial pits. The occipital carina is normally incomplete, but the vertex is distinguishable from the occiput by a change in surface curvature. The genal carina is well developed and separates the postgena (the area outside the postoccipital suture) from the gena (the area between the genal carina and the eye). The genal carina

meets the hypostomal carina at the base of the mandible.

The biting surface of the mandibles is weakly differentiated into a distal "incisor" and a proximal "molar" part. The basal cardo of the maxilla is folded inside the head and attaches, distally, to a large flat stipes, both are loosely articulated (Fig. 28). The galea is large and the lacinea is highly membranous, lightly coloured and pubescent. The visible labium consists mostly of the prementum, a large median plate which closes the oral cavity from below (Fig. 27). The mentum is reduced in cynipoids and the submentum folded within the proboscidial cavity. The glossa and paraglossa consist of membanous folds of almost colourless tissue and the two components are not clearly distinguishable. In many cynipoid taxa, sensory hairs on the labial palp rest against the palpiger of the prementum (Fig. 26) and presumably provide positional information. Similar hairs occur on the maxillary palps but as the proximal segment appears to be rigidly joined to the stipes, at least in some taxa, the sensory hairs are on the next segment. Frequently a stout sensory spine (Fig. 25) is visible on the apices of the labial and maxillary palps.

Head measurements

The number and ease of measurement of most head parameters make the cynipoid head a good subject for morphometrics. In addition to the search for useful characters, it was felt that certain head parameters could be a better measure of size than say body length (gastral segments can telesope).

The agamic and sexual forms of *Cynips* were found to show significant size differences, so separate values for both forms have been included in the measurements listed below.

Toruli

The inter-toruli distance (TTL) and the eye to toruli distance (OTL) are standard taxonomic indices used

by Hymenopterists. The measurements of TTL and OTL simply reflected the size differences between the exemplar taxa. For example the large cynipoids of the Liopteridae had measurements approximately twice those of the small Charipidae. The ratio of TTL to OTL was calculated for each species, but the results form a continuous series and no separation was available for character formulation (Table 24).

	TTL/ OTL		TTL/ OTL		TTL/ OTL
Ibalia	0.7	*Oberthuerella*	0.5	*Tessmanella*	1.1
Liopteron	0.5	*Plastibalia*	0.6	*Pseudibalia*	0.9
Mesocynips	0.5	*Paramblynotus*	1.2	*Kiefferiella*	1.3
Aspicera	0.8	*Callaspidia*	1.1	*Omalaspis*	0.9
Anacharis	1.1	*Aegilips*	1.0	*Xyalaspis*	0.7
Figites	0.5	*Melanips*	0.7	*Lonchidia*	0.7
Neralsia	0.6	*Eucoila*	0.8	*Kleidotoma*	0.8
Rhoptromeris	0.7	*Dilyta*	0.5	*Apocharips*	1.1
Phaenoglyphis	0.8	*Alloxysta*	0.8	*Pycnostigmus*	1.4
Aulacidea	0.3	*Cynips* sexual	0.8	*Cynips* agamic	1.2
Austrocynips	0.9	*Himalocynips*	0.4		

Table 24. TTL / OTL ratios (n=<6).

Ocelli

The standard ocelli measurements are OOL (ocular to posterior ocellar line) and POL (post ocellar line - distance between the two posterior ocelli), to these was added the distance between the anterior and posterior ocellus (APL). As with the torular ratios, these measurements were found to show allometric (Gould, 1966) variations. The ratios of OOL to POL, OOL to APL and POL to APL were calculated (Table 25). The OOL / POL and POL / ALP ratios produced almost continuous series. The ratio of OOL to APL was only usable as a character at the highest value which separates *Mesocynips* from all other taxa.

Measurements related to eye length

The allometric bias found in the above head measurements can be reduced by dividing by a size related parameter. The obvious parameter, head length, was not

				RATIOS		
	OOL	POL	APL	OOL/ POL	OOL/ APL	POL/ APL
Ibalia	410	256	154	1.60	2.67	1.67
Oberthuerella	563	307	128	1.83	4.40	2.40
Tessmanella	333	326	96	1.02	3.47	3.40
Liopteron	333	410	154	0.81	2.17	2.67
Plastibalia	512	333	109	1.54	4.71	3.06
Pseudibalia	307	461	141	0.67	2.18	3.27
Mesocynips	422	205	58	2.06	7.33	3.55
Paramblynotus	230	224	77	1.03	3.00	2.92
Kiefferiella	160	224	102	0.71	1.56	2.19
Aspicera	154	333	128	0.46	1.20	2.60
Callaspidia	115	275	115	0.42	1.00	2.39
Omalaspis	102	243	122	0.42	0.84	2.00
Anacharis	109	179	64	0.61	1.70	2.80
Aegilips	115	154	58	0.75	2.00	2.67
Xyalaspis	128	166	70	0.77	1.82	2.36
Figites	154	192	96	0.80	1.60	2.00
Melanips	128	224	83	0.57	1.54	2.69
Lonchidia	77	115	58	0.67	1.33	2.00
Neralsia	96	179	77	0.54	1.25	2.33
Eucoila	109	205	102	0.53	1.06	2.00
Kleidotoma	115	96	58	1.20	2.00	1.67
Rhoptromeris	96	102	51	0.94	1.88	2.00
Dilyta	70	96	70	0.73	1.00	1.36
Apocharips	58	102	51	0.56	1.13	2.00
Phaenoglyphis	90	109	51	0.82	1.75	2.13
Alloxysta	90	102	45	0.88	2.00	2.29
Pycnostigmus	141	256	128	0.55	1.10	2.00
Aulacidea	154	154	77	1.00	2.00	2.00
Cynips sexual	90	224	64	0.40	1.40	3.50
Cynips agamic	173	237	109	0.73	1.59	2.18
Austrocynips	147	192	51	0.77	2.88	3.75
Himalocynips	269	154	58	1.75	4.67	2.66

Table 25. Ocelli measurements (units - 0.001mm). Ratios and measurements calculated from graticule units, n = < 6.

used because certain taxa have the genae disproportionally developed (e.g. *Lonchidia*). Also the curvature of the head can make equivalent measurements of head length difficult. In cynipoids, eye length is a superior measure of size because it is a relatively stable and accurately measurable character. Eye length and several other head parameters, that are easily associated with eye length were analysed together (Table 26). The head was viewed from the side and the eye length, eye breadth, gena length plus the height of the antennal insertion (above the ventral limit of the eye) were measured.

The eye-associated measurements were subjected to

	eye l	eye b	antenna up eye	gena l	RATIOS eye l/b	antenna /eye l	gena /eye l
Ibalia	1229	819	493	512	1.50	0.40	0.42
Oberthuerella	1126	922	384	973	1.22	0.34	0.86
Tessmanella	845	742	256	717	1.14	0.30	0.85
Liopteron	973	691	294	1280	1.41	0.30	1.32
Plastibalia	1178	947	307	691	1.24	0.26	0.59
Pseudibalia	1075	870	461	666	1.24	0.43	0.62
Mesocynips	794	640	512	768	1.24	0.65	0.97
Paramblynotus	717	563	282	512	1.27	0.39	0.71
Kiefferiella	499	339	192	358	1.47	0.39	0.72
Aspicera	666	512	205	269	1.30	0.31	0.40
Callaspidia	589	371	192	269	1.59	0.33	0.46
Omalaspis	512	384	160	224	1.33	0.31	0.44
Anacharis	371	282	128	288	1.32	0.35	0.78
Aegilips	384	301	179	250	1.28	0.47	0.65
Xyalaspis	397	307	96	275	1.29	0.24	0.69
Figites	358	243	141	224	1.47	0.39	0.63
Melanips	461	320	224	128	1.44	0.49	0.28
Lonchidia	198	128	51	243	1.55	0.26	1.23
Neralsia	384	275	160	109	1.40	0.42	0.28
Eucoila	531	307	288	160	1.73	0.54	0.30
Kleidotoma	179	128	90	102	1.40	0.50	0.57
Rhoptromeris	192	134	160	154	1.43	0.83	0.80
Dilyta	243	141	96	90	1.73	0.40	0.37
Apocharips	256	160	90	115	1.60	0.35	0.45
Phaenoglyphis	198	134	102	77	1.48	0.52	0.39
Alloxysta	205	147	64	122	1.39	0.31	0.59
Pycnostigmus	422	339	192	294	1.25	0.46	0.70
Aulacidea	358	186	128	243	1.93	0.36	0.68
Cynips sexual	416	224	256	115	1.86	0.62	0.28
Cynips agamic	499	275	256	128	1.81	0.51	0.26
Austrocynips	435	275	192	192	1.58	0.44	0.44
Himalocynips	474	346	205	352	1.37	0.43	0.74

Table 26. Eye related measurements. l = length, b = breadth. Units - 0.001mm. (Ratios and measurements calculated from graticule units). n = <6.

computer analysis using the program STEP (see methods section) and the probability contours mapped at levels of significance of 5%, 1%, 0.33%, 0.1%, 0.03%, 0.01%, 0.0033%, 0.001%, 0.00033% and 0.0001% using a three dimensional plotting program adapted from Harding (1982).

Size

The resultant probability plots were all very noisy. The plots against eye length (i.e. overall size) all show an approximately oval distribution at a significance of 0.33% or better (Figs 17-19). Of course this was expected,

bigger taxa tend to have larger head measurements. However, in most plots, imposed on the general size trend is a bimodality (Figs 17, 18) which only becomes evident at the higher levels of probability. These two nodes separate the "smaller" and "larger" cynipoids from the remaining taxa. The smaller cynipoids are *Lonchidia*, the Charipidae, *Aulacidea*, *Figites*. Also included are the Eucoilidae with the exception of *Eucoila* which correlates with the analysis of the Weld data, that showed *Eucoila* to be unusually large for a eucoilid. The "larger" taxa are *Ibalia* and the Liopteridae, although *Kiefferiella* is clearly small for a liopterid. The Aspicerinae (which are large compared to other Figitidae), *Himalocynips* and *Pycnostigmus* could also be included in the large taxa but this is less likely (different contour). These results correspond with the results of principal component analysis of antennal segment dimensions.

The size adjusted view (Fig. 18) of the position of antennal insertion (the distance, in lateral view, from the lower eye margin to the toruli) uncovers some allometric displacements, for example the insertions of *Ibalia*, *Pseudibalia*, *Paramblynotus*, *Liopteron*, *Plastibalia* and the Oberthuerellinae are "lower" than is indicated by direct measurement. Similarly the antennal insertions of *Rhoptromeris*, *Melanips*, *Pycnostigmus*, *Phaenoglyphis* and *Kleidotoma* are "higher" than is apparent.

Gena length

The plots of eye length versus gena length (Fig. 19) and antennal insertion versus gena length (Fig. 20) do not show the small / large bimodality, instead these plots are approximately conical and separate only the larger cynipoids. This shows that although the large taxa have long genae, the small taxa do not have especially short genae.

Ratios

The plots of ratios were mostly not significant and none were of any value for characterization or for phylogenetic reconstruction.

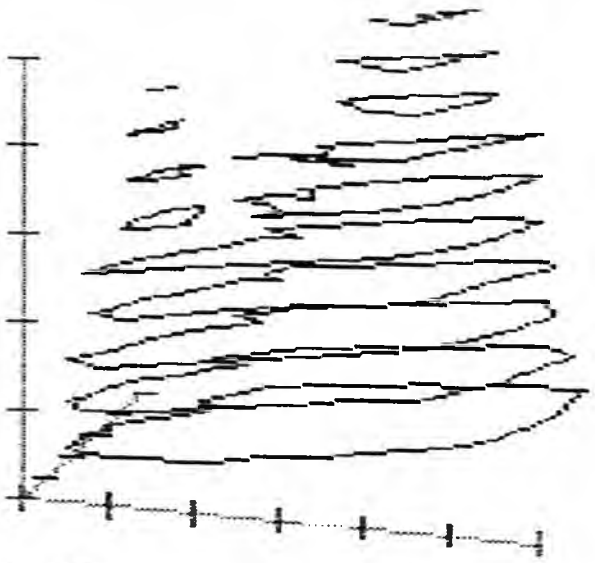

Figure 17. STEP probability plot for eye length v breadth. (x axis = steps in eye length, y axis = steps in eye breadth, z axis = significance level.)

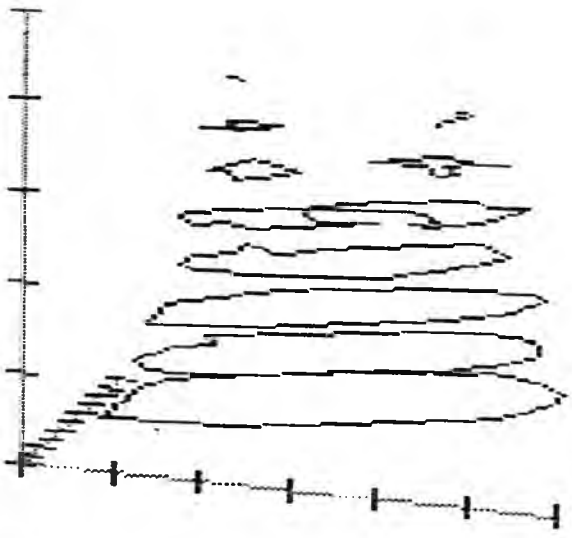

Figure 18. STEP probability plot for eye length v hight of antennal insertion. (x axis = steps in eye length, y axis = steps in hight of antennal insertion, z axis = significance level.)

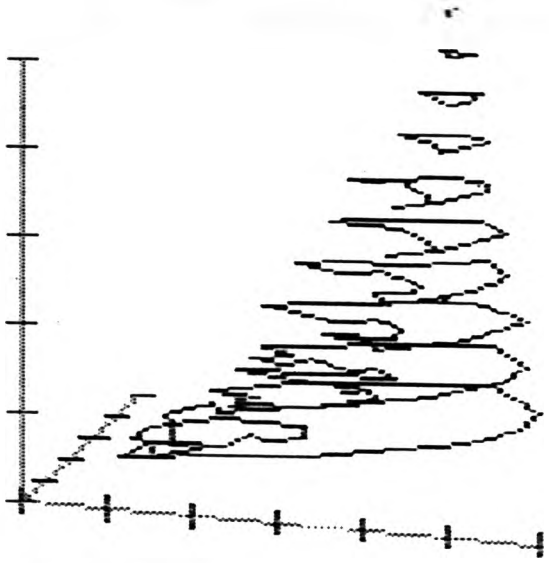

Figure 19. STEP probability plot for eye length v gena length. (x axis = steps in eye length, y axis = steps in genal length, z axis = significance level.)

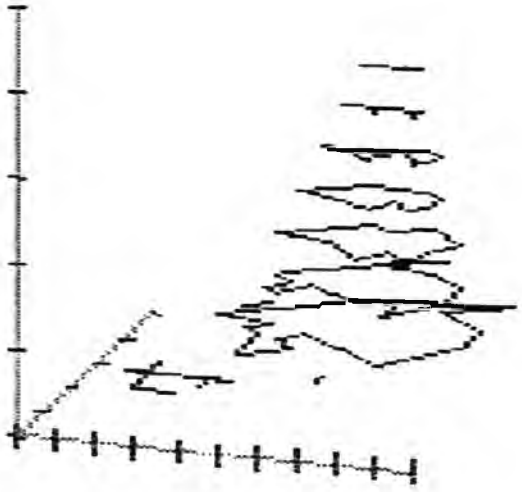

Figure 20. STEP probability plot for hight of antennal insertion v gena length. (x axis = steps in hight of antennal insertion, y axis = steps in genal length, z axis = significance level.)

Although the merit of measuring head length has been questioned, an attempt was made to compare head length (clypeus to top of vertex) against head width (outer margins of eyes, across the vertex). However, the measurements of head length and breadth and their ratio were of little value for characterization. The ratios (table 27) showed an almost normal distribution of the taxa about a value of 0.8. No pattern was evident except that some smaller taxa (*Lonchidia*, Eucoilidae & Charipidae) tend to have a higher than average ratio.

The value of head measurements

In general the head measurements (and probably most other cynipoid parameters) are strongly influenced by the size of the species. There are three approximate size ranges - the large taxa (*Ibalia* and most Liopteridae) with eye lengths over 0.7mm, the small taxa (Charipidae and most Eucoilidae) with eye lengths under 0.25mm, and a large section of medium sized taxa. These ranges do not correspond with known (or feasible new) higher categories and it is clear that morphometrics is a poor source of characters.

Ibalia	0.80	*Oberthuerella*	0.67	*Tessmanella*	0.73
Liopteron	0.93	*Plastibalia*	0.77	*Pseudibalia*	0.63
Mesocynips	0.85	*Paramblynotus*	0.83	*Kiefferiella*	0.81
Aspicera	0.80	*Callaspidia*	0.77	*Omalaspis*	0.86
Anacharis	0.76	*Aegilips*	0.84	*Xyalaspis*	0.70
Figites	0.73	*Melanips*	0.58	*Lonchidia*	1.01
Neralsia	0.86	*Eucoila*	0.97	*Kleidotoma*	1.12
Rhoptromeris	0.98	*Dilyta*	0.89	*Apocharips*	1.01
Phaenoglyphis	0.76	*Alloxysta*	0.91	*Pycnostigmus*	0.74
Aulacidea	0.87	*Cynips* sexual	0.80	*Cynips* agamic	0.69
Austrocynips	0.70	*Himalocynips*	0.68		

Table 27. Ratios of head length to breadth n=<6.

Other features of the head

Mandibles

Cynipoids feed as larvae rather than as adults and it is presumed (Richards, 1977) that the mandibles have

remained stout to aid adult emergence.

The mandible of the gall-inducing Cynipidae has a well defined lower tooth but the upper tooth is incompletely subdivided (Fig. 97). In the parasitoid taxa the upper region tends to be more clearly bifid (Fig. 23). In the Liopteridae and *Ibalia* (Fig. 22) the mandibles are large, strong and rather blunt. The upper section being chisel-like. The remaining Cynipoidea have cutting / piercing type mandibles (Fig. 23).

Two specialized forms of sharp mandible have been developed; the Anacharitinae have sharp teeth positioned at a characteristic angle (Fig. 24) and in *Pycnostigmus* (Fig. 98) the lower tooth is a large scythe-shaped blade.

The hypostomal region

A study of the back of the cynipoid head has revealed an important and hitherto unsuspected suite of characters. The characters of the hypostomal / postgenal region are complicated by reversals in the direction of formation or destruction, of "bridges" between the foramen magnum and the proboscidial fossa (Fig. 99). Rasnitsyn (1975, 1980) has studied these features in the Ichneumonomorpha and his work has facilitated interpretation of the characters and establishment of their polarities within the Cynipoidea.

The foramen magnum and the proboscidial fossa (oral cavity) of the higher Hymenoptera were primitively separated by postgenae that close along the vertical medial line (Rasnitsyn 1980). Apart from some Symphyta, in most other Hymenoptera the hypostomes are either "open" (Figs 29-32) and the back of the head capsule is closed by a secondary tentorial plate, or the hypostomes are closed (Figs 41-48). In the least derived Ichneumonidae (e.g. *Rhyssa*, Xoridini and *Ephialtes*) a "primitive" bridge persists (Fig. 29). In more derived taxa subsequent modifications to the labiomaxillary complex (often by elongation of the cardo) has caused an elongation of the proboscidial fossa, this is combined with a posterior widening so that the closed bridge is forced apart. In between the diverging hypostomal crests a triangular

plate, the lower tentorial bridge, emerges to the surface and fills the opening (Figs 34, 36, 38) (Rasnitsyn, 1980; Tobias & Potapova, 1982).

The next phase in the evolution of the hymenopterous hypostoma is the beginning of a movement in the reverse direction, the lower tentorial bridge is secondarily reduced (Figs 41-43) as a result of a decrease in size of the labiomaxillary complex and a corresponding shortening of the oral opening (Rasnitsyn 1980). As the proboscidial fossa "retreats" the space is filled by the hypostomes, rather than postgenae and a second or derived hypostomal bridge formed. [The postgenae are the lower lateral areas under the occiput and behind the genae.]

Morphological states of the cynipoid hypostomal region.

A study of the hypostomal region has revealed the presence of three or perhaps four separate morphological lineages which together show a consecutive sequence of hypostomal development in the Cynipoidea.

Cynipidae: open hypostomes. The least derived hypostomal morphology occurs in the genera near *Aulacidea*, in these genera the first hypostomal bridge has only just been lost. In *Aulacidea* (Fig. 34) and *Phanacis* (Fig. 33) the hypostomal carinae are parallel in the central region and only diverge dorsally. The hypostomes are separated by a narrow region of lower tentorial bridge this region extends dorsally to form a large triangular area between the divergent hypostomes, the foramen and the posterior tentorial pits. In *Isocolus* the hypostomal region is shorter and the lower tentorial bridge has increased in size.

In more derived genera (e.g. *Aylax*) the lower tentorial bridge expands but the hypostomal crests remain relatively close together ventrally. However, the lower bridge eventually forces apart the hypostomal crests so that only the lower bridge separates the foramen magnum from the proboscidial fossa (*Neuroterus*, *Andricus* and *Callirhytis* - Figs 35-37).

In *Himalocynips* the hypostomes are broadly separated,

and this state may represent a separate lineage.

Ibalidae & Liopteridae: hypostomes in a cavity. Subsequent stages of hypostomal development involve a reduction of the lower tentorial bridge, closure of the hypostomes and the formation of a hypostomal bridge. In the Ibalidae and Liopteridae the hypostomal region is set in a deep cavity (Figs 38, 39). The hypostomal crests have started to close again (*Ibalia* Fig. 38). In *Mesocynips insignis* hypostomal closure has not progressed very far, but in *Oberthuerella* the crests have considerably expanded, virtually coming together, and the lower tentorial bridge has retreated towards the foramen.

Liopteron compressum and some species of *Mesocynips* have a short length of hypostomal bridge. Other species (*Plastibalia*, *Paramblynotus* (Fig. 39) show a longer line of hypostomal fusion but the lower tentorial bridge is still present, although reduced (Fig. 40).

Other cynipoids: hypostomes completely fused. In these taxa the hypostomes are not set within a cavity. In the Figitidae and *Pycnostigmus*, the suture line (of hypostomal fusion) is short (Fig. 42). The carinae from the posterior tentorial pits to the hypostomal carinae are strongly curved in the Anacharitinae (Fig. 41), *Aspicera*, *Callaspidia* and *Neralsia*. However, in *Anacharoides*, *Paraspicera* and *Melanips* these carinae are absent or have moved away from the suture and are more or less vertical under the posterior tentorial pits. [It is possible to further subdivide these heads but the morpological differences are subtle.]

In the next stage the length of the hypostomal region has increased and thus the suture line is long. This state is found in the Charipidae (Fig. 46) and Synergini (Fig. 45). The hypostomal morphology of the Synergini (Cynipidae) is remarkably advanced compared to that of all other Cynipidae.

Finally, in the Eucoilidae, the suture is lost and thus the area has effectively become a postgenal bridge (Figs 47, 48).

Similar hypostomal developments have evolved independently, and to varying extents, in the

Ichneumonoidea (Rasnitsyn, 1980), Cynipoidea, Chalcidoidea and Proctotrupoidea (Figs 31, 44, 49). However, the hypostomal development of the Cynipoidea spans a very "wide" evolutionary range. The primitive gall-wasps have a head morphology not far removed from that found in the less derived Ichneumonidae (e.g. *Rhyssa*). The subsequent stages of reduction of the lower tentorial bridge and a closing of the hypostomes are frequent amongst the microhymenoptera. Closed hypostomes, like that of the Figitidae are also found in the Diapriidae (Fig. 49) and Scelionidae (Fig. 44) (Mineo & Villa, 1982). Total loss of the suture only occurs in the most advanced Parasitica e.g. Eucoilidae and some Diapriidae (Snodgrass, 1928; 1960 reports the existence of a postgenal bridge in the Vespomorpha).

Palp formula

The palp formula is a two digit expression of the number of maxillary and labial palp segments. The Hymenoptera generally have a formula of 6/4 (Richards, 1977). However, this is reduced in more derived taxa and in the Cynipoidea the plesiomorphic formula is 5/3. Dissection reveals that a small, easily overlooked, basal segment is present on the maxillary palp in most Cynipoidea. (See also Ritchie & Shorthouse, 1987). The labial palp is supported on a palpiger (from the prementum) and the maxillary palp on a palpifer (from the stipes) and these non-palp structures can look like palp segments (Fig. 26). Eight of the study taxa show a reduction of palp segments.

List of head character-states

1 Galea normal [0]. / Galea strongly expanded and projecting downwards [1].

2.1, 2.2, 2.3 The Eucoilidae, Charipidae and Pycnostigmus all show an apomorphic reduction of palp segments (see Table 28). [This feature could be coded as two characters but that would not give due consideration to the four palp combinations (5/3, 4/2, 4/3 & 5/2)

	Palps Maxillary	Labial.	Code
Most taxa	5	3	0,0,0
Eucoilidae	4	2	0,1,1
Charipidae	4	3	0,1,0
Pycnostigmus	5	2	1,0,0

Table 28. Palp scoring.

represented in the Cynipoidea. It is unlikely that the 4/2 combination was derived from the 5/2 combination because the palps of *Pycnostigmus* are long and appear to result from segment fusion whereas the other taxa have very small palp segments indicating segment loss.

3 Clypeus simple [0]. / Clypeus with a low, central depression and a marginal notch (Fig. 21) [1]. [The notch is weak in *Kiefferiella* and the depression occupies most of the clypeus in *Pseudibalia*].

4 Clypeus not projecting outwards [0]. / Clypeus projecting upwards and away from the exposed unsclerotized area and the labium beneath [1].

5 Face without distinctive radiating striae. [0]. / Lower face strongly striate, the striae forming two conspicuous fan-like radiations [1].

6 Face without ridge often with a general hump over this area [0]. / Face with a weak central ridge [1].

7 Face without a vertical line of striations [0]. / Face with a strip of vertical striations which has a small clear patch on either side [1].

8 Face without grooves or at most with a central ridge [0]. / Central facial region with two vertical grooves, separated by a central keel, running from the anterior tentorial pits to the toruli [1].

9.1, 9.2 The malar sulcus (subocular sulcus) is usually marked by a narrow band of coriaceous sculpture [0,0]. / Malar sculpture lost [1,0]. / Sulcus represented by a fine band of longitudinal striae [0,1].

10 Eye glabrous or with short hairs between the facets [0]. Eye pubescence long [1].

11 Frontal carina absent [0]. / Frontal carina present from the antennae to near the median ocellus [1].

12 Frons without distinct scrobes [0]. / Frons with scrobes (Fig. 21) [1].

13 OOL/APL ratio less than 5.5 [0]. / OOL/APL ratio over 7.0 [1].

14 In most taxa the the occipital carina is only present as a dorsolateral extension of the genal carina in the region of the facial orbit [0]. / Occipital carina almost complete, reaching close to the posterior ocelli [1].

15.1, 15.2, 15.3 Sculpture of occiput alutaceous [0,0,0]. / With vertical striae on the occiput [1,0,0]. / With transverse or curved striations on the occiput [0,1,0]. / Occiput smooth [0,0,1].

16.1, 16.2 Face with light sculpture (alutaceous, granulate, sparsely punctate, weakly rugose or striate) [0,0]. / Face coarsely sculptured (coarsly striate deeply punctate or rugose (Figs 21, 22) [1,0]. / Face mostly smooth [0,1].

17 Head wider than the thorax [0]. / Head narrower than the thorax. [1].

18 Mandibles with one simple lower tooth and a subdivided upper tooth [0]. / At least one mandible with three teeth [1].

19 Mandibles not chisel-like [0]. / Mandibles blunt and chisel-like (Fig. 22) [1].

20 Mandibles not of the piercing- cutting type [0]. / Mandibles of the piercing-cutting type (Fig. 23) [1].

21 Mandibles not especially sharp [0]. / With sharp cutting mandibles [1].

22 Lower tooth of normal proportions [0]./ Scythe-like lower tooth to mandible [1].

23 Lower two teeth not spine like [0]. / Lower two teeth spine-like [1].

24.1 24.2 24.3 Head flat with lower tentorial bridge ventrally narrow (Fig. 33) [0,0,0]. / Head with hypostomes set in a cavity (Fig. 39) [1,0,0]. / Head with lower tentorial bridge ventrally wide [0,1,0]. / Head flat with hypostomal bridge present (Fig. 41) [0,0,1].

Fig. 21. *Paramblynotus* X40. Face.

Fig. 22. *Ibalia* X380. Ventral view of head.

Fig. 23. *Eucoila* X170. Mandibles.

Fig. 24. *Anacharis* X300. Mandible.

Fig. 25. *Cynips* X1070. Sensory projection on the apex of the labial palp.

Fig. 26. *Xyalaspis* X1030. Sensory hairs on the base of the labial palp.

Fig. 27. *Ceroptres* X350. Mouthparts in posterior view.

Fig. 28. Dissected mouthparts of an anacharitine X200.

Fig. 29. *Ephialtes* X170 (Ichneumonidae). Rear of head, foramen magnum and lower tentorial bridge.

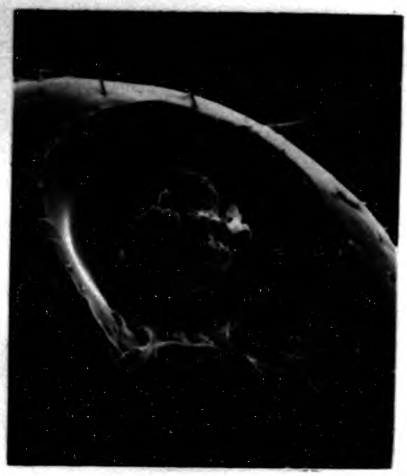

Fig. 30. *Paramesius* X250 (Proctotrupoidea). Rear of head, "open" hypostomes, and mouthparts (below).

Fig. 31. *Codrus* X130 (Proctotrupoidea). Rear of head &, just visible, the lower tentorial bridge.

Fig. 32. *Codrus* X250 & X1250. Enlargements of Fig. 31. Lower tentorial bridge.

Fig. 33. *Phanacis* X300. Rear of head and narrow lower tentorial bridge.

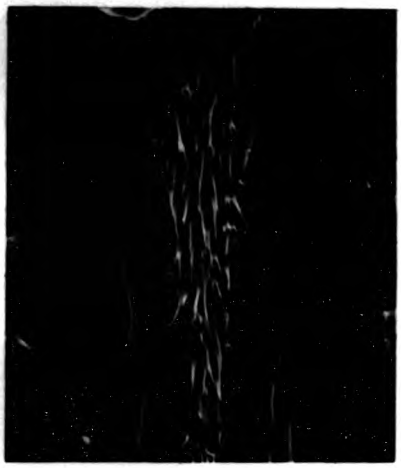

Fig. 34. *Aulacidea* X1500. Lower tentorial bridge between the narrowly separated hypostomes.

Fig. 35. *Andricus* X400. Lower tentorial bridge and hypostomal crests.

Fig. 36. *Andricus* X1000. Hypostomal carinae and crests (Fig. 83 enlarged).

Fig. 37. *Cynips* X250. Hypostomal crests.

Fig. 38. *Ibalia* X130. Hypostomes in a cavity.

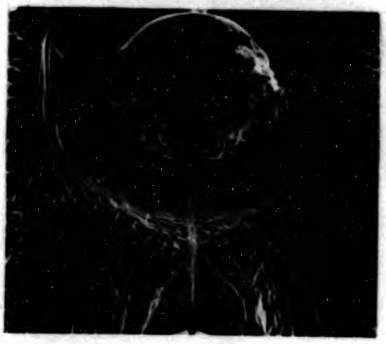

Fig. 39. *Paramblynotus* X110. Hypostomes and lower bridge in a cavity.

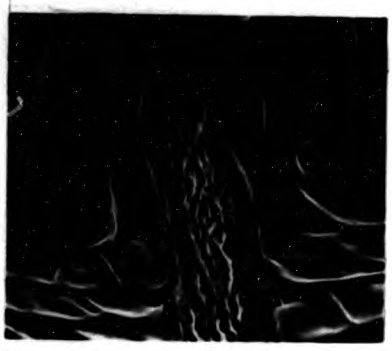

Fig. 40. *Paramblynotus* X700. Fig. 39. magnified showing lower bridge.

Fig. 41. *Xyalaspis* X130. Rear of head. Hypostomal bridge and suture short.

Fig. 42. *Melanips* X130. Rear of head. Hypostomal bridge and suture short.

Fig. 43. *Anacharoides* X80 & X400. Head with a short hypostomal bridge.

Fig. 44. *Telenomus* (Proctotrupoidea) X350. Head with long hypostomal bridge and suture.

Fig. 45. *Synergus* X150. Inquiline with a long figitid-like hypostomal bridge and suture.

Fig. 46. *Phaenoglyphis* X350. Head with the hypostomal bridge and suture long.

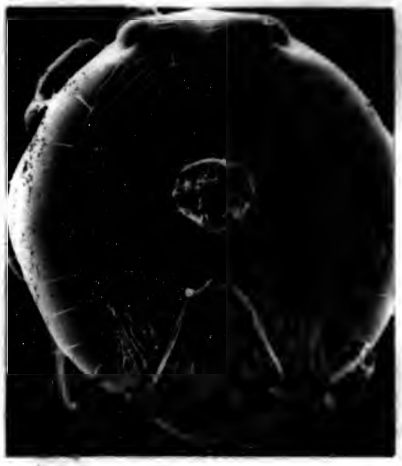

Fig. 47. *Kleidotoma* X250. Rear of head. Fusion of the hypostomes complete and suture lost.

Fig. 48. *Rhoptromeris* X350. Rear of head. Fusion of the hypostomes complete and suture lost.

Fig. 49. *Trichopria* X400 (Proctotrupoidea). Rear of head.

Fig. 50. *Kleidotoma* X2200. Antennal sensilla.

Fig. 51. *Kleidotoma* X800. Antennal sensilla.

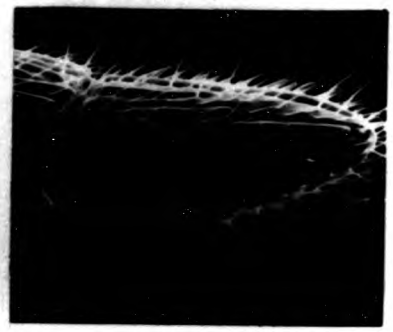

Fig. 52. *Cynips* X400. Antennal sensilla.

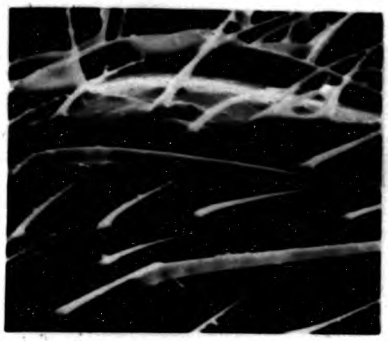

Fig. 53. *Trichopria* X1700 (Proctotrupoidea). Raised type of antennal sensilla.

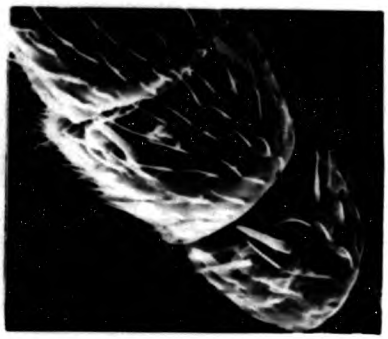

Fig. 54. *Inostemma* X920 (Proctotrupoidea). Raised type of antennal sensilla.

Fig. 55. *Lytarmes* X1000. (Ichneumonoidea). Antennal sensilla. [Photo: P. Eggleton.]

Fig. 56. *Melanips* X1770. Freeze fracture to show "floor" (arrows) to antennal sensilla.

Fig. 57. *Callaspidia* X1220. Closely packed antennal sensilla.

Fig. 58. *Callaspidia* X1770. Gland (arrow) on modified third segment of male antenna.

25 Concave hypostomes with normal crests [0]. / Concave hypostomes with crests strongly expanded [1].

26.1 26.2 26.3 Hypostomal fusion incomplete [0,0,0]. / Hypostomal fusion complete but short (Fig. 41) [1,0,0]. / Hypostomal fusion complete and long. (Fig. 46) [1,1,0]. Suture lost (Figs 47, 48) [1,1,1].

27 If with a short hypostomal bridge then without carinae or with approximately straight carinae (Fig. 42) [0]. / The short hypostomal bridge of the Anacharitinae has strongly curved hypostomal carinae (Fig. 41) [1].

ANTENNAE

Antennal measurements

The relative lengths and breadths of various antennal segments have been used as characters for classifying the Cynipoidea (e.g. Quinlan, 1978). As these measurements are likely to be biased by allometry it was felt that detailed analysis was required to establish if these features could be used as valid discriminants.

The dimensions of the antennal segments were measured for a female and male (where available) of each of the 31 exemplar species of Cynipoidea (see Appendix 2). Because of the variation in total numbers of antennal segments between both species and sexes, it was difficult to provide a standardized data-set, for further analysis. The only non-biased system was to take data on the first ten segments, thus avoiding the exaggeration found in the terminal segments (i.e. the apical 13th. and 14th. segments of one species, which would have to be related to ordinary mid-flagella segments in a species with, say, 20-segmented antennae).

Analysis of segment length

The segment lengths (see Appendix 2) obviously bear a relationship to species size, the largest segments generally occurring in the "big cynipoids" (i.e Ibaliidae

and Liopteridae). The rest of the species show no clear pattern so a Principal Components analysis was performed.

The Principal Components matrix shows a high percentage correlation in segment lengths (Tables 29 & 30), even the lowest correlation, pedicel to segment ten, was over 80%. Thus segment length is most likely to be an allometric character, the length of each flagellar segment being related to that of each other.

Principal components analysis accounted for 94.5% of the total variation in the first dimension, and the first three dimensions accounted for 98.8% of the variation. The variates contribute approximately equally in determining axis 1 (-0.3 or -0.4) only the pedicel at -0.08 has a noticeably lower contribution (Table 31). On the second axis, variate 2 and 6 have a small contribution and variate 3 has the highest, followed by the outer flagellar segments. The scape has the major influence on the third axis. Thus for the first 95% of the variation no variate stands out as a strong determinant which could be a useful character. The impact of the third antennal segment on

	Antennal Segment									
	1	2	3	4	5	6	7	8	9	10
Mean	0.24	0.11	0.27	0.28	0.27	0.26	0.24	0.24	0.22	0.21
Minimum	0.08	0.04	0.06	0.04	0.04	0.03	0.03	0.03	0.04	0.04
Maximum	0.74	0.27	0.91	1.04	1.02	0.93	0.80	0.72	0.69	0.67
S. D.	0.16	0.05	0.16	0.22	0.20	0.19	0.18	0.16	0.15	0.14
S. E.	0.02	0.01	0.02	0.03	0.03	0.03	0.02	0.02	0.02	0.02

Table 29. Summary data of antennal lengths (S = standard, D = deviation, E = error).

	Antennal segment									
	1	2	3	4	5	6	7	8	9	10
Segment										
1	1.00									
2	0.90	1.00								
3	0.86	0.83	1.00							
4	0.89	0.86	0.93	1.00						
5	0.89	0.88	0.93	0.99	1.00					
6	0.88	0.86	0.92	0.99	0.99	1.00				
7	0.88	0.87	0.90	0.98	0.98	0.99	1.00			
8	0.87	0.85	0.88	0.96	0.97	0.98	0.99	1.00		
9	0.85	0.82	0.83	0.93	0.93	0.95	0.97	0.99	1.00	
10	0.84	0.81	0.81	0.91	0.91	0.94	0.96	0.98	0.99	1.00

Table 30. Correlation matrix of segment lengths.

Segment	Axis 1	Axis 2	Axis 3
1	-0.29	0.39	0.84
2	-0.08	0.08	0.13
3	-0.29	0.55	-0.24
4	-0.41	0.15	-0.23
5	-0.39	0.13	-0.23
6	-0.37	-0.03	-0.19
7	-0.34	-0.16	-0.06
8	-0.31	-0.28	0.01
9	-0.28	-0.43	0.15
10	-0.26	-0.46	0.19

Table 31. Principal Component axes of segment lengths.

axis 2 and the scape on axis 3 indicates that a plot of these two segments could be of some value (see below).

The plot of Principal Components axes 1 v 2 (Fig. 59) shows most of the Cynipoidea fitting tightly into one large unresolved cluster. Six of the larger cynipoids (*Pseudibalia*, *Oberthuerella*, *Tessmanella*, *Plastibalia*, *Liopteron*, and *Ibalia*, which has seven maximum scores) are outside the cluster but the Mesocynipinae, which are relatively large cynipoids, are clustered with the smaller cynipoids. Therefore this feature appears to be of little use as a discriminant. As the length data appeared to be biased by allometry, ratios of lengths to breadths were investigated to see if they provided a more useful statistic.

Ratios of length to breadth

A principal components analysis was run on the ratios of the first ten antennal segments of each sex for all available species (Tables 32-34). No logarithmic transformations were made. The correlation matrix for ratios provided a more interesting result than the matrix for lengths alone. Although the flagellar segments are highly correlated, there is a very low correlation (sometimes a slight negative correlation) between size of scape or size of pedicel and that of any of the flagellar segments. This indicates that scape or pedicel ratio, when compared with a flagellar ratio, may be a useful character (see below). The scape had little correlation with the pedicel (24%). The flagellum showed a steady relationship, most segments being 95% correlated with the following

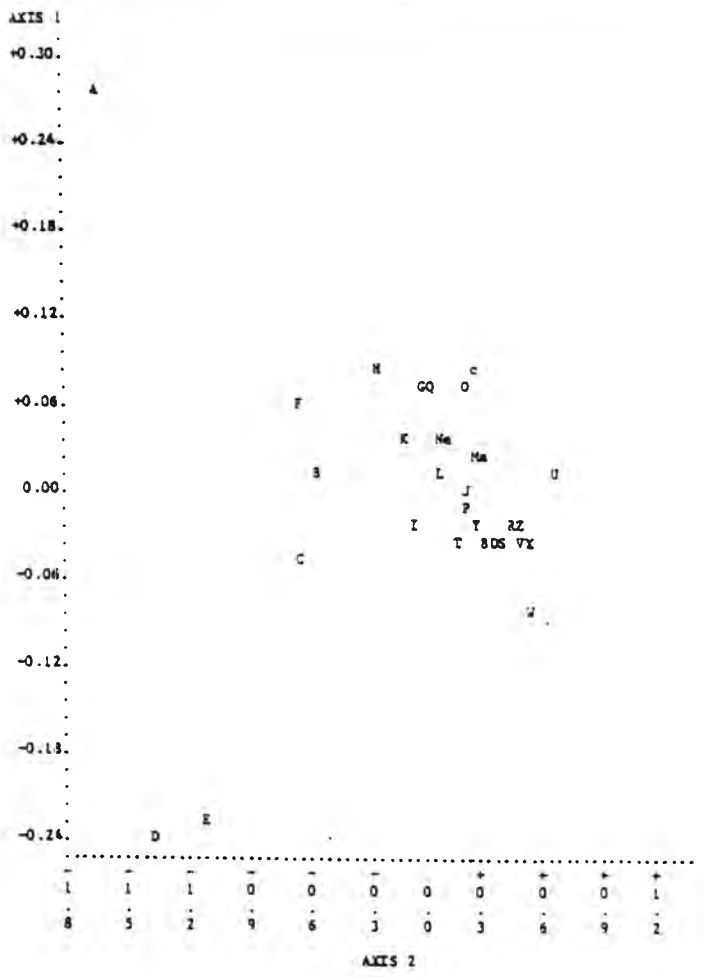

Figure 59. Plot of Principal Components axis 1 v axis 2, for antennal segment lengths. (Females only, for clarity.)

[A = *Ibalia*, B = *Oberthuerella*, C = *Tessmanella*, D = *Liopteron*, E = *Plastibalia*, F = *Pseudibalia*, G = *Mesocynips*, H = *Paramblynotus*, I = *Kiefferiella*, J = *Aspicera*, K = *Callaspidia*, L= *Omalaspis*, M = *Anacharis*, N = *Aegilips*, O = *Xyalaspis*, P = *Figites*, Q = *Melanips*, R = *Lonchidia*, S = *Neralsia*, T = *Eucoila*, U = *Kleidotoma*, V = *Rhoptromeris*, W = *Dilyta*, X = *Apocharips*, Y = *Phaenoglyphis*, Z = *Alloxysta*, a = *Pycnostigmus*, b = *Aulacidea*, c = *Cynips*, d = *Austrocynips* & e = *Himalocynips*.]

	Antennal Segments									
	1	2	3	4	5	6	7	8	9	10
Mean	1.97	1.20	3.08	2.95	2.70	2.64	2.45	2.40	2.24	2.21
Minimum	0.9	0.7	1.4	1.1	1.3	1.1	1.1	1.1	1.0	1.0
Maximum	2.9	2.0	5.7	5.4	5.6	5.3	4.6	4.6	4.3	4.7
S. D	0.46	0.32	0.96	0.98	0.89	0.86	0.78	0.76	0.73	0.75
S. E	0.06	0.04	0.13	0.13	0.12	0.11	0.10	0.10	0.10	0.10

Table 32. Data for antennal ratios
(S = standard D = deviation E = error).

	Segments									
Segments	1	2	3	4	5	6	7	8	9	10
1	1.00									
2	0.24	1.00								
3	0.14	0.27	1.00							
4	0.12	-0.07	0.69	1.00						
5	0.13	-0.06	0.64	0.94	1.00					
6	0.12	-0.02	0.57	0.88	0.94	1.00				
7	0.14	0.04	0.49	0.79	0.86	0.94	1.00			
8	0.10	0.11	0.44	0.66	0.70	0.82	0.90	1.00		
9	0.08	0.12	0.39	0.56	0.59	0.74	0.85	0.95	1.00	
10	0.13	0.13	0.32	0.48	0.51	0.65	0.77	0.91	0.95	1.00

Table 33 Correlation matrix for antennal ratios.

Segment	Axis 1	Axis 2	Axis 3
1	-0.03	0.02	0.10
2	-0.09	0.00	0.30
3	-0.30	0.60	0.70
4	-0.40	0.30	-0.30
5	-0.40	0.20	-0.30
6	-0.40	-0.00	-0.30
7	-0.40	-0.20	-0.10
8	-0.30	-0.30	0.10
9	-0.30	-0.40	0.20
10	-0.30	-0.50	0.30

Table 34. Principal Components axes for antennal ratios.

segment and 85% with the one following that. This decreased with distance so that the third was only 32% correlated with the tenth segment. Thus it seems unlikely that flagellar characters are of widespread value for cynipoid phylogenetics.

In the first axis of the ratio data the scape and pedicel have low scores and little correlation with the rest of the variates which all have very similar scores.

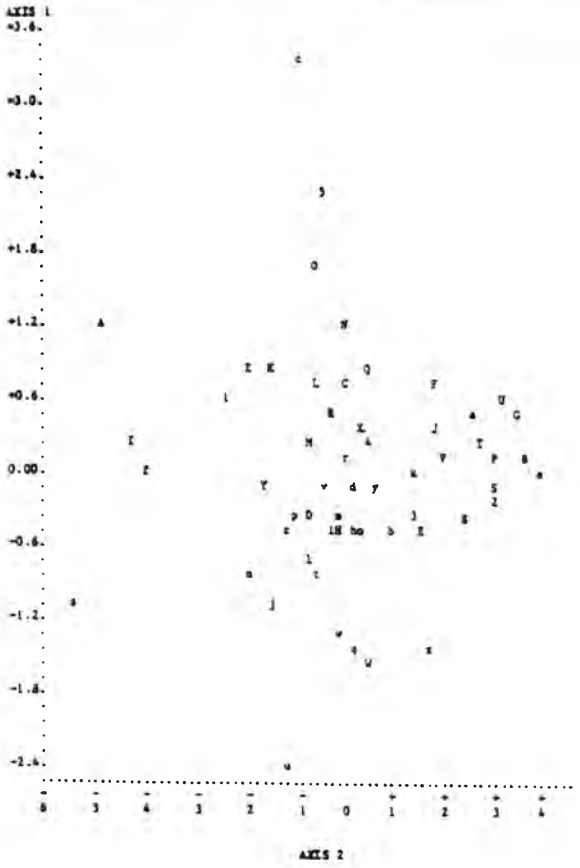

Figure 60. Plot of Principal Components axis 1 v axis 2 for antennal ratio data.

[Females: A = *Ibalia*, B = *Oberthuerella*, C = *Tessmanella*, D = *Liopteron*, E = *Plastibalia*, F = *Pseudibalia*, G = *Mesocynips*, H = *Paramblynotus*, I = *Kiefferiella*, J = *Aspicera*, K = *Callaspidia*, L = *Omalaspis*, M = *Anacharis*, N = *Aegilips*, O = *Xyalaspis*, P = *Figites*, Q = *Melanips*, R = *Lonchidia*, S = *Neralsia*, T = *Eucoila*, U = *Kleidotoma*, V = *Rhoptromeris*, W = *Dilyta*, X = *Apocharips*, Y = *Phaenoglyphis*, Z = *Alloxysta*, a = *Pycnostigmus*, b = *Aulacidea*, c = *Cynips*, d = *Austrocynips* & e = *Himalocynips*. Males: f = *Ibalia*, g = *Oberthuerella*, h = *Liopteron*, i = *Mesocynips*, j = *Paramblynotus*, k = *Aspicera*, l = *Callaspidia*, m = *Omalaspis*, n = *Anacharis*, o = *Aegilips*, p = *Xyalaspis*, q = *Figites*, r = *Melanips*, s = *Lonchidia*, t = *Neralsia*, u = *Eucoila*, v = *Kleidotoma*, w = *Rhoptromeris*, x = *Dilyta*, y = *Apocharips*, z = *Phaenoglyphis*, 1 = *Alloxysta*, 2 = *Pycnostigmus*, 3 = *Aulacidea*, 4 = *Cynips* & 5 = *Cynips* agamic female.

The second orthogonal axis, shows the greatest variation between the third and tenth antennal segments. The scape, pedicel and the sixth antennal segment have little impact. The third axis has the greatest difference between the third and fourth to sixth segments.

Principal Components analysis accounted for 71.02% of the variation in the first dimension and 92.32% in the first three dimensions. The axis plots provide no useful discrimination. Most of the species are grouped in one cluster (Fig. 60) and those outside show no obvious relationship.

Segment 3 v segment 10

The analysis of lengths and ratios indicates that segments three to ten are highly correlated and that the least correlated segments and the best source of characters should be ratios of the first versus the third segment. A graph of these ratios (Fig. 61) shows most cynipoids clustered together without any clear delimitation. However, there is a noticeable gap between scape ratios of 1.3 and 1.7. A few taxa with scape ratios of 0.9 to 1.3 fall below this: *Austrocynips* female (A) *Aspicera* male (B) *Aulacidea* male (C) *Liopteron* male (D) and female (E) *Callaspidia* male (F) and female (G) *Cynips* agamic (H) and sexual female (I). This assemblage cuts across all sensible concepts of cynipoid phylogeny. [The other sexes of these taxa (J-P) are not similarly associated - Fig. 61] The lower group can be subdivided into two sections (segment three ratio less than 3 or more than 4) but again, this is of little phylogenetic significance.

Thus the analysis of the antennal dimensions has shown that even the feature most likely to be of value (ratio of scape to ratio of third segment) is of no use for establishing cynipoid phylogeny.

Total antenna length

It is generally assumed (e.g. Richards, 1977) that the antenna of male parasitica is slightly longer than that of the female - having both a greater length and more

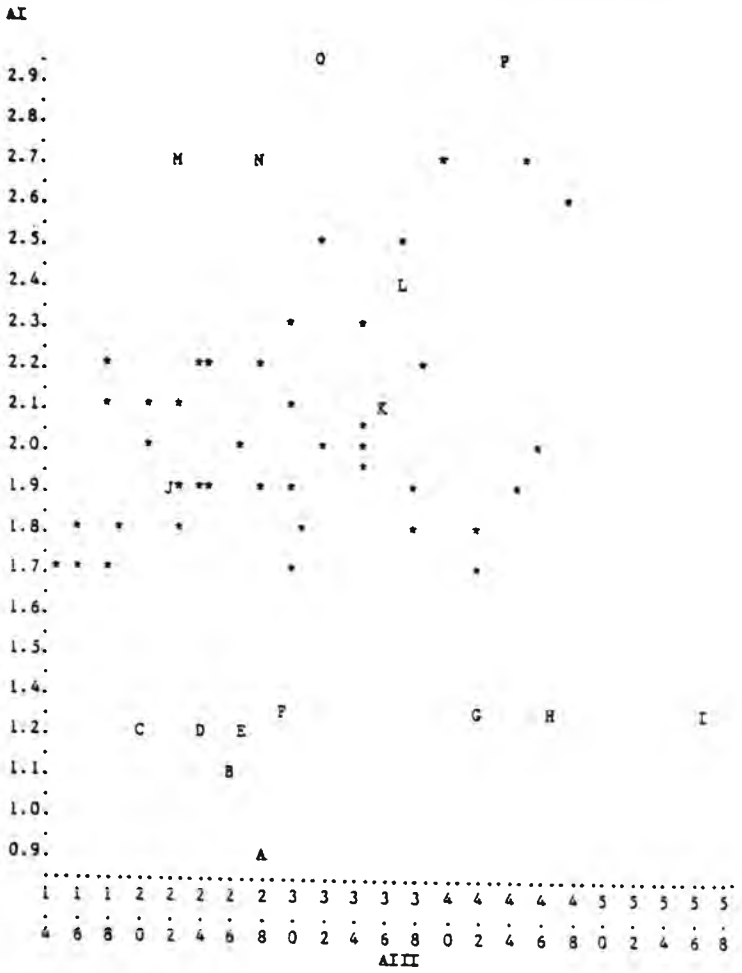

Figure 61. Plot of length / breadth for the scape versus the third antennal segment. (Based on graticule units.)

[A = *Austrocynips* female, B = *Aspicera* male, C = *Aulacidea* male, D = *Liopteron* male, E = *Liopteron* female, F = *Callaspidia* male, G = *Callaspidia* female, H = *Cynips* agamic female, I = *Cynips* sexual female, J = *Aulacidea* female, K = *Cynips* male, L = *Ibalia* male, M = *Pseudibalia* female, N = *Aspicera* female, O = *Melanips* female, P = *Ibalia* female. * = other taxa and sexes.]

segments. The measurements of the Cynipoidea generally support this statement, but the measured specimens of *Ibalia leucospoides*, *Liopteron compressum*, and *Phaenoglyphis xanthochroa* had antennae that were longest in the female. No evolutionary significance attaches to this grouping of diverse taxa.

Antennal sensilla

Although the Cynipoidea have most of the main types of antennal sensilla that are found in other parasitic Hymenoptera, one type, - placoid sensilla (or multiporous plate sensilla), are abundant and have been used as taxonomic characters but were generally called rhinaria (e.g. Quinlan, 1979). Placoid sensilla are considered (Schmidt & Kuhbandner 1983) to be derived from basiconic hair sensilla. Each placoid is a non-socketed elongate plate, which is slightly raised or domed from the antennal surface, but only separated from the surface by a fine groove (Figs 50-52). [According to Gibson (1986) the sensilla of *Pseudeucoila* lack this groove but my scanning electron microscope photographs show fine grooves in all the *Pseudeucoila* species that were available for study. However, in several antenna preparations the gold coating covered this fine groove so it is possible that the exception observed by Gibson was an artefact.] The longitudinal axis of the sensillum is always parallel to that of the antenna and the cynipoid placoids do not project beyond the apex of the segments (Fig. 52) to the extent found in the Chalcidoidea and some Proctotrupoidea (Fig. 54).

In the larger cynipoids (e.g. *Ibalia*) an approximately central pore is visible through the cuticle of the placoid sensilla (Börner, 1919; Chrystal, 1930). Subjecting the antennae to ultrasonic vibration renders the pores visible in both the Cynipoidea and Ichneumonidae.

Trichoid sensilla are ~~the next most~~ also as abundant type of antennal sensilla in cynipoids, they are hair-like, have a thick non-porous cuticular wall and are slightly inclined in the same direction as the antenna. Short pegs in pits

(sensilla coeloconica) occur, often near the distal margin, on the more apical segments in several taxa (e.g. *Cynips*, Fig. 52). Smooth sensilla have been found in the Ibaliidae, Cynipidae, Charipidae and Eucoilidae. Fluted basiconic sensilla (Norton & Vinson, 1974a) also occur in the Cynipoidea.

Placoids as an indicator of relationships

The types and distribution of cynipoid sensilla are similar to those of many Ichneumonoidea; in both groups trichoid and placoid sensilla are common, and smooth basiconic or coeloconic sensilla often occur singly on each distal segment. However, cynipoids have a remarkably high density of placoid sensilla, the entire surface of the segment is often covered (Fig. 57) and it is obvious that the cynipoids have specialized in the use of this type of sensillum.

The Cynipoidea (Fig. 50), like the Ichneumonoidea (Fig. 55), have each placoid sensillum surrounded by a groove (and ridge) (Barlin & Vinson 1981). The placoid sensilla are integrated into the surface of the antenna and have no part free above the surface. This is a plesiomorphic feature that the Cynipoids share with the less derived parasitic Hymenoptera, e.g. Ichneumonoidea (Schmidt & Kuhbandner, 1983). However, the sensilla of the Cynipoidea (Fig. 51) are higher and more domed than those of the Ichneumonoidea (Fig. 55).

Placoid sensilla are present in the Chalcidoidea s.l. (except Mymarommatidae - Gibson, 1986) and in the small Proctotrupoidea (Diapariidae, Platygasteridae and Scelionidae). In these groups the sensilla are of a more derived type in which the distal end of each sensillum is free and not connected to the antennal surface (Barlin & Vinson, 1981) (Figs 53, 54).

In chalcidoids the placoid sensilla show a difference between the sexes; two forms of sensillum occur on the flagellum of females but only type one occurs in males. The type one sensillum is broader than type two and is attached to the antennal cuticle for almost its entire length, the tip being the only region that is free. The

type two sensillum is attached for half to two thirds of its length (Barlin, Vinson, & Piper 1981). In the Ichneumonoidea the placoid sensilla are reported (Borden, Chong & Rose, 1978) to have no significant sexual dimorphism (although numbers differ) and Gibson (1986) suggests using the presence / absence of sexual dimorphism as a character to distinguish the Chalcidoidea from the Ichneumonoidea. However, at least one ichneumonoid, *Cardiochiles nigriceps* (Braconidae) is reported to show sexual dimorphism (Norton & Vinson, 1974b). So it seems unwise to make much of this character until a greater number of species has been studied. No great morphological differences were found between the sensilla of males and females in the Cynipoidea. The differences that do exist are of little taxonomic value, for example Chrystal (1930) found that females of *Ibalia* have slightly more sensilla than males.

The sensilla of the Ichneumonoidea have an internal "floor" (Richardson et al 1972). In chalcidoids there is no "floor" to the sensilla ~~(Borden, Rose & Charney 1978)~~ and the many neurotubules run longitudinally in a central channel (with transverse ridges) that lies between two pendant lamellae. Studies of carefully fragmented cynipoid antennae indicate that a ichneumonid type "floor" is present (Fig. 56).

Sensilla function

It is generally assumed that all the sensilla mentioned above are involved in chemoreception (Barlin, Vinson, & Piper, 1981; Schneider & Steinbrecht, 1968). Placoid sensilla may also be involved in host finding through perception of infrared radiation (Borden, Rose & Charney, 1978; Richerson & Borden, 1972). The Liopteridae and Ibaliidae could perhaps oviposit at "hotspots" detected on the surface of tree bark over subcortical beetle larvae.

"Sex segment"

The third, or sometimes the fourth or fifth, antennal segment of the male cynipoid frequently has an elongate

cavity. This modified segment is used in precopulation antennation, which is an isolating mechanism of courtship behaviour (Alam, 1969; 1970; Gordh & DeBach, 1978). Olfaction is likely to play an important role in this process. Scanning electron microscope studies of this segment showed the pores and an evaporative surface of a large gland. The gland occurs (Fig. 58) in both parasitic and cecidogenic cynipoids, and it is probably present in most species. It is here postulated that this gland releases a courtship pheromone. Similar large dermal glands have been found on the male "sex segment" of *Melittobia australica* (Chalcidoidea) (Dahms, 1984) and in *Trissolcus basalis*, (Proctotrupoidea) (Bin & Vinson, 1986).

The anellus and geniculation

The distinctive geniculate antennae and anellus, or ring segment(s) found in Chalcidoidea and some Proctotrupoidea s.l. do not occur in the Cynipoidea.

Antennal number

In the Cynipoidea the number of antennal segments varies from 12 (reported by Weld, 1952 in a specimen of *Pycnostigmus*) to 20 (Table 35). However, the range is relatively limited and 13:14 (females : males) is very frequent and this combination was treated by Königsmann (1978) as the groundplan number and as a possible synapomorphy for the Cynipoidea. Königsmann (1978) was concerned that the greatest variation in antennal segment numbers was in the possibly "primitive" Cynipinae but several subfamilies have figures other than 13:14, thus the variability in numbers of segments could easily be secondary.

The number of antennal segments is also interesting with regard to other parasitic Hymenoptera (Table 36). The Stephanidae and Ichneumonoidea generally have high numbers of antennal segments (this is probably an apomorphic feature in each group). Other parasitica (Cynipoidea, Evanoidea, Gasteruptionidae, Pelecinidae, Megalyridae,

	female	:	male
Ibaliidae	13	:	15
Oberthuerelinae	13	:	14
Liopterinae	13	:	14
Mesocynipinae	13	:	14-15
Aspicerinae	13	:	14
Anacharitinae	13	:	14
Figitinae	13	:	14
Eucoilidae	13-14	:	13-16
Charipidae	13	:	14
Pycnostigmatinae	12-19	:	15
Cynipidae	13-14	:	14-15
Austrocynipinae	15	:	-
Himalocynipinae	20	:	-

Table 35. The numbers of antennal segments in the families and subfamilies of the Cynipoidea (exceptions are likely).

Chalcidoidea	4 to 26
Mymaridae	7 to 13
Mymarommatidae	9 to 13
Scelionidae *	6 to 14
Platygasteridae	7 to 10
Ceraphronoidea	10 to 11
Proctotrupidae	13
Vanhorniidae	13
Evaniidae	13
Cynipoidea	10 to 20
Gasteruptiidae	13 to 14
Pelecinidae	14
Ropronidae	14
Megalyridae	14
Diapriidae	12 to 15
Monomachidae	14 to 15
Austroniidae	14 to 15
Heloridae	16
Trigonalyidae	14 to 32
Stephanidae	30 to 40
Ichneumonoidea	8 to 92+

Table 36. The numbers of antennal segments in various parasitic Hymenoptera. (After Gibson, 1986.) (* the groundplan number is 14 - Masner,1970).

Monomachidae and many Proctotrupoidea) have a medium number of about 12 to 15. The smallest parasitica (some Proctotrupoidea and Chalcidoidea) have an antennal number in single figures and this is likely to be a derived state. It seems probable that the groundplan number for the Parasitica as a whole is between 10 and 16 segments. Thus like other antennal characters, antennal segment

number indicates that the Cynipoidea are not as derived as the Chalcidoidea and most Proctotrupoidea.

List of antennal character-states

28.1, 28.2, 28.3, 28.4 Antenna of female 13-segmented [0,0,0,0]. / Antenna 14-segmented [1,0,0,0]. / Antenna 15-segmented [1,1,0,0]. / Antenna 19-segmented [1,1,1,0]. / Antenna 20-segmented [1,1,1,1]. [These variations must be treated, at least initally, as a series, but experience suggests that they are probably all independent lineages.]

29.1, 29.2 Antenna of male 14-segmented [0,0]. / Antenna of male 15-segmented [1,0]. / Antenna of male 24-segmented [1,1].

30.1, 30.2 Number of segments by which antenna of male exceeds that of female: 1 [0,0]; / 2 [1,0] / or 5 [1,1].

31.1, 31.2, 31.3, 31.4 Male with the third antennal segment, to some degree, emarginate (sometimes only slightly) [0,0,0,0]. / Male without modified segment [1,0,0,0]. Emargination on segments 2+3 [0,1,0,0]; / 3+4 emarginate [0,0,1,0] / segments 4+5 emarginate [0,0,0,1].

32.1, 32.2, 32.3, 32.4 The cynipoid antenna is often filiform but, as in the Chalcidoidea, the terminal segments of the female may be differentiated (swollen) to form a clava or club. Club absent [0,0,0,0]. / Club 3-segmented [1,0,0,0]. / Club 6-segmented [1,1,0,0]. / Club 7-segmented [1,1,1,0]. / Club 8-segmented [1,1,1,1].

33 The third antennal segment is usually longer than the fourth [0]. / Third antennal segment shorter than the fourth [1]. [In doubtful cases the measurment of the female was chosen.]

34 The antennal segments of almost all Cynipoidea are fully articulated [0]. / Two taxa have the last two segments partially fused in the females. The division between the two segments is apparently incomplete or not functional [1]. [Scanning electron microscopy of

this character indicates that the segments are not physically amalgamated. However, under light microscopy the apparent fusion is a stable character.]

35 Antenna normal [0]. / Antenna slightly flattened [1].

36 Antennal segments of females densely covered with placoid sensilla (0). / In a few females an increased area of cuticle is visible between a slightly reduced number of sensilla [1].

37 Antennal segments, of males, densely covered with placoid sensilla [0]. / Antennae of males with a slightly reduced number of sensilla [1].

38.1, 38.2, 38.3, 38.4, 38.5, 38.6 Antenna of females with many sensilla from segment 3 onwards [0,0,0,0,0,0]; / 4 onwards [1,0,0,0,0,0]; / 5 onwards [1,1,0,0,0,0]; / 6 onwards [1,1,1,0,0,0]; / 7 onwards [1,1,1,1,0,0]; / 8 onwards [1,1,1,1,1,0]; / 11 onwards [1,1,1,1,1,1].

39.1, 39.2, 39.3 Males with placoid sensilla from segment 3 onwards [0,0,0]; / 4 onwards [1,0,0]; / 5 onwards [1,1,0]; / 6 onwards [1,1,1].

40 Antennal segment four of male not swollen [0]./ Segment four swollen [1].

41 Antennal segment three of male not swollen [0]. / Segment three swollen [1].

42 Antennae with normal sculpture [0]. / Antenna densely punctate [1].

43 Antennae with long placoid sensilla [0] / Placoid sensilla very short [1].

THORAX

The apocritan thorax consists of the pro- meso- and metathorax, which together form the "true" thorax, and the first abdominal segment, the propodeum.

Prothorax

In lateral view the cynipoid pronotum is triangular (Fig. 66), closely joined to the mesepisternum and the posterior corner reaches to the tegula (not so in the Chalcidoidea).

Between the pronotum and the mesopleuron there is a pubescent slit (Figs 72, 73), presumably the opening of a gland. The epomia, netrion and skaphion, occuring in some Proctotrupoidea (Masner, 1979), are absent from the studied cynipoids. The pronotum does not extend round to the mid-ventral line and thus is not fused ventrally (as in Gasteruptiidae and some Proctotrupidae). The point of invagination of the occlusor muscle apodeme, (Gibson, 1985) visible near the posterolateral edge of the pronotum in many chalcids (Gibson, 1985), is not clearly indicated in the Cynipoidea.

Pronotal plate

The cynipoid pronotum is modified anteriorly to form a complex structure that in its most derived condition forms a raised pronotal plate (Fig. 65). The groundplan state for this structure is the presence of a frontal bar, caulis, submedian depressions and lateral depressions (c.f. Fig. 68). This is the condition found in the gall-wasps (Fig. 75). Primitively the anterior edge of the pronotal plate, the lobe carina, fades out dorsally (although it is well-developed in *Biorhiza pallida*). All remaining cynipoids also have a pair of lateral carinae (Figs 64, 66, 67). (In *Austrocynips* the lateral carinae are indistinct but their position is marked by a ridge or hump on the sides of the pronotum.) Initially the lateral carinae do not meet dorsally. In the Liopteridae and Ibaliidae and the posterior pronotal margin has a median dorsal expansion or "tooth" (Figs 70-72, 74). [In *Oberthuerella* the lateral carinae are incomplete and the frontal bar is indistinct, but the tooth is virtually absent]. In more derived states the lateral carinae unite dorsally (Fig. 62). The next stage involves the lateral carinae dividing (low down near the lateral depression) into a dorsal and two ventrolateral sections (Fig. 63). The ventrolateral sections are then reduced (Fig. 64) or lost. In the Charipidae the dorsal section is reduced to a trace (Fig. 67), but in other cynipoids this section is well developed and unites with an expanded plate lobe carina, to form a dorsal pronotal plate (Fig. 69). In the

most derived states this plate is partially (Fig. 68) and then fully raised off the pronotum (Fig. 65) to form a very distinctive structure.

A similar, but less complex, structure occurs in the Belytidae and Platygasteridae (Proctotrupoidea), and other forms of pronotal plate occur elsewhere in the Hymenoptera (e.g. Pelecinidae).

Intersegmentalia and the mesothoracic spiracle

The basalare and prepectus are the only intersegmental sclerites between the pro- and mesothoracic segments in the Apocrita. The basalare is present in all macropterous forms but an independent prepectus is found only in the Chalcidoidea, Roproniidae Austroniidae, Stephanidae and Monomachidae (Gibson, 1985; Rasnitsyn, 1980). In other Apocrita, including the Cynipoidea, the prepectus is reduced and fused to the pronotum.

In the Cynipodea, Proctotrupoidea, Evanioidea and Trigonalyoidea the mesothoracic spiracle lies below the lateral edge of the pronotum and is surrounded by a remnant of the prepectus - the posterior pronotal inflection (Gibson, 1985). The inflection forms a groove with the outer edge of the pronotum into which fits the anterior edge of the mesepisternum. The Ichneumonoidea and Chalcidoidea show other, independent, conditions of the spiracle / prepectus (Gibson. 1985).

The mesothoracic spiracle has a thick peritreme (Fig. 70) and the occlusor muscle is twisted around the thin-walled secondary atrium (Tonapi,1958). The pronotal lobe, at the posterolateral corner of the pronotum, is only weakly enlarged and incompletely conceals the spiracle.

Mesothorax

The mesothorax (Figs 71-85) contains the dorsoventral and longitudinal indirect flight muscles (Figs 89-92) and therefore is the largest thoracic segment. Contraction of the indirect flight muscles causes the mesoscutum to flex relative to the posterodorsal scutellar / axillar complex

at the transscutal articulation (Figs 71, 75-77). This enables flight by moving, in turn, the anterior and posterior notal wing processes, the axillary sclerites, and finally the wing (Pringle, 1957; Matsuda 1970; Webber 1925). The transscutal articulation is commonly lost in apterous species (Reid, 1941). Some alate Proctotrupoidea and Cynipoidea and many Ichneumonoidea have an incomplete transscutal articulation, but in the Cynipoidea at least a remnant is usually visible at the extreme lateral edge of the mesoscutum. Loss of this articulation in the Apocrita is secondary (Gibson, 1985) and has occurred in several lineages.

The mesoscutum is large and anteriorly curved. The notauli (Figs 75-78, 130) are external indications of internal phragmata (endoskeletal ridges) and mark the line of separation between the dorsolongitudinal (median origin) and dorsoventral indirect flight muscles (lateral origin) (Michener, 1944; Wong, 1963). Percurrent notauli occur in many Cynipoidea but frequently they are absent or only indicated posteriorly.

A percurrent median mesoscutal line occurs in cynipoids but more typically it is present only towards the posterior of the mesoscutum. Dissections show that even when the median line is as deep as the notauli (e.g. *Ibalia*) it is not invaginated into a phragma and thus is not a true median mesoscutal sulcus (Rasnitsyn, 1980). The cynipoid mesoscutum also shows traces of secondary lines. Anterio-admedian lines [misinterpreted as notauli by Ritchie and Peters, 1981] are usually weakly indicated, also traces of parapsidal lines are present (Fig. 78) in all but the smallest and smoothest cynipoids (Figs 85, 86).

Large axillae are likely to have arisen primarily as a consequence of their role as an attachment site for the second phragmal flexor and the mesotrochanteral depressor muscles (Gibson, 1985). Most parasitica have secondarily lost elements of the axillar muscles and thus the axillae are typically small and widely separated. Therefore the relatively well defined axillae of the Cynipoidea (Fig. 84) must be either a primitive or more probably a

secondarily derived feature. The cynipoid axillae are expanded dorsolaterally in the form of the lateral bars (Figs 85, 86), which connect with the scutellum (lateral extensions of the axillae occur in some Ichneumonoidea, Proctotrupinae and Diapriidae). The axillae are partially separated from the scutellum by the scutoscutellar sulcus. In many parasitica this is a transverse groove but in the Cynipoidea it consists mostly of two deep scutellar foveae and, on each side, a lateral groove which continues under the lateral axillary bar. Only a thin area of cuticle, the fenestra (Fig. 87), separates the fovea from the lateral scutellar area. In taxa with a broad axillar bar e.g. *Pycnostigmus*, the fenestra is in a distinct tunnel under the bar. In some taxa, e.g. *Neuroterus*, the scutoscutellar sulcus may be lost and the lateral bars absent. Strong scutellar foveae are a groundplan character for the Cynipoidea, only rarely are they absent; in other apocrita with lateral bars there is often a single central fovea. Cynipoid foveae (Figs 78, 84, 130) are usually small but in most Aspicerinae and some Figitidae (e.g. *Neralsia*) they can be up to half the length of the scutellum. The cynipoid scutellum is strongly raised above the metanotum (Figs 82, 86), this condition has been considered a synapomorphy for the superfamily (Königsmann, 1978), but other parasitica, especially the Chalcidoidea, have a similar scutellum. The scutellum of the Eucoilidae bears a characteristic raised plate (or "cup") (Figs 84-87). The scutellum lacks a frenum (found in Chalcidoidea).

The mesopleuron consists mostly of a large mesepisternum (Figs 71-76, 79-83). The mesopleuron is posteriorly rotated so that the small mesepimeron lies horizontally above the mesepisternum. The upper edge of the mesepimeron bears a line of sensory hairs that probably provide information on wing position (Fig. 96). The anterior plate of the mesepisternum consists of a large depressed triangular area (Fig. 82), delineated ventrally by the ventral margin of the anterior oblique sulcus. The episternal scrobe is distinct and the subalar pit is concealed but deep (Fig. 80). In certain small taxa (e.g. *Kleidotoma* and *Rhoptromeris*) the anterior plate is

not depressed, the subalar pit and episternal scrobe are not visible and the epimeron is hardly distinguishable from the mesepisternum (Fig. 85). The posterodorsal corner of the mesopleuron is produced into a weak lobe which conceals most of the second thoracic spiracle. A "speculum" is present in *Ibalia* (Fig. 71); because it lies below the scrobal sulcus it is not homologous with the speculum in other groups which lies above the scrobal sulcus.

Metathorax

The small metathorax (Figs 74, 79-83) bears the hindwings. Laterally it is poorly differentiated from the propodeum. The metanotum is a short, transverse sclerite. The metathoracic spiracle is concealed behind the posterodorsal margin of the mesepimeron. In the larger Hymenoptera (Symphyta, Ichneumonoidea, Evanioidea and most aculeates) this spiracle is open, but in the microhymenoptera it is frequently nonfunctional. However, in at least one large cynipoid, *Ibalia*, it is apparently functional; also a trace of this spiracular system may persist in Aulacid¢a.

Propodeum

The first abdominal segment, the propodeum (Figs 74, 85) is generally convex and, in dorsal view, divided by carinae into areas. The propodeum, as well as other regions of the functional thorax, have conspicuous fields of sensory hairs (Achterberg, 1977). The propodeal spiracles are conspicuous; they have a raised anterior lip which lies over the opening and reduces it to an elongate slit. The walls of the atrium are thin. The closing mechanism consists of a valve that lies between two large levers, which arise from the anterior propodeal wall (Tonapi, 1958).

Thoracic myology

Cynipoid thoracic musculature (Figs 89-95, 100, 101) is similar to that of other small Hymenoptera (Daly, 1963; Gibson, 1985). Considerable size variation was found, the

largest cynipoids (e.g. *Ibalia*) have stout muscles, especially the flight muscles (Fig. 89), and each muscle consists of many fibrils. The muscles of small species, especially the Alloxystinae, were often quite fine and more spindle-shaped. This variation probably reflects the lifeways and in particular the differing powers of flight of these two groups. *Ibalia* is a relatively strong flyer, whereas the Alloxystinae are less active, being mostly windborne like their aphid hosts (Yoshimoto & Gressitt, 1965).

Mesotrochanteral depressor and the second-phragmal flexor.

Gibson (1985) studied the distribution of the two muscles thought to be most valuable for phylogenetic analysis of the parasitoid Hymenoptera - the mesotrochanteral depressor and the second-phragmal flexor. The position of these two muscles in the Cynipoidea has been investigated and Gibson's character-states are confirmed as applying to a wide range of cynipoid species.

The mesotrochanteral depressor is a mesothoracic muscle (Figs 93-95) that inserts into the basomedial edge of the mesotrochanter; contraction rotates the apex of the trochanter. The mesotrochanteral depressor may consist of two elements, the mesotergal-trochanteral depressor and a much smaller muscle the mesofurcal-trochanteral depressor. The latter muscle is absent from the Chalcidoidea, and many other parasitica lack the mesotergal-trochanteral depressor. In both the Ichneumonoidea and Cynipoidea the mesofurcal-trochanteral depressor is conical or fan-shaped (Figs 94, 95). The Pelecinidae, Proctotrupidae, Vanhorniidae and Evaniidae have a mesofurcal-trochanteral depressor which has a pleural component (mesopleural-trochanteral depressor) and in the Scelionidae only the pleural branch is retained (Gibson, 1985). Reduction of the mesotrochanteral depressor to similar states in the Cynipoidea and Ichneumonoidea is a parallelism and not a reliable indicator of a close evolutionary relationship.

The Second-phragmal flexor is an oblique lateral

muscle (Figs 90-92) from the axilla to a lateral process of the second phragma. According to Daly (1963) the Cynipoidea are the only parasitoid Hymenoptera to have this muscle but Gibson (1985) also found it in the Ceraphronoidea, Diapriidae, Monomachidae and Vanhorniidae. Presence of the second-phragmal flexor in these taxa is regarded as a symplesiomorphy.

List of thoracic character-states

44 Lateral pronotal carinae absent [0]. / Lateral pronotal carinae present (Fig. 66) [1].

45 Pronotal tooth absent [0]. / Pronotal tooth present (Fig. 70) [1]. [As mentioned above, *Oberthuerella* is difficult to score for this feature, it will be awarded a variable "V" score thus invoking a scoring option of the LEQU program which will iterate for both 0 and 1.]

46 Lateral pronotal carinae curved [0]. / Lateral pronotal carinae straight and converging [1].

47 Caulis of pronotal plate curved (Fig. 68) [0]. [In the Anacharitinae the frontal bar caulis and frontal lobe are faint.] / Frontal bar of pronotum very thin so that the caulis is pointed [1].

48 Pronotum without a ridge-like hump, either with a carina, no matter how small, or with an evenly curved lateral pronotal surface [0]. / Lateral surface of pronotum with a ridge-like hump [1].

49 Carinae present laterally but not joined dorsally [0]. / The lateral carinae unite dorsally to form a semicircular plate (Figs 62-63) [1].

50 Without a lateral disjunction (Fig. 62) [0]. / With a separation of the dorsolateral part of the carina from the most ventral section (Fig. 64) [1].

51.1 51.2 Plate not raised off the surface of the pronotum [0,0]. / Pronotal plate partially raised (Fig. 63) [1,0]. / Plate completely raised, the pronotum is markedly produced frontodorsally into a raised anterior plate with a strong posterior margin (Fig. 65) [1,1].

52 Without a precoxal tooth [0]. / With a frontolateral pronotal tooth next to the fore coxa [1].

53.1, 53.2 Light mesoscutal and scutellar sculpture (Alutaceous - punctate - granulate - rugulose - strigulose) present [0,0] (Figs 75, 76). / Loss of the sculpture so that the dorsal surface, including the scutellum, is smooth and shiny is apomorphic (Figs 81, 82, 85, 160) [1,0]. / The acquisition of heavy (rugose - foveolate - striate) sculpture (Figs 70-72, 74) is also apomorphic [0,1]. [In *Anacharis*, the scutellum is almost smooth but there is a little fine sculpture present, so it has been scored 0,0. The Aspicerinae have strong sculpture (e.g. Figs 77, 148) but this just falls within the definitions of rugulose to strigulose and thus they are scored 0,0.]

54 Mesoscutal ridges absent (Fig. 81) [0]. / Strong, transverse, mesoscutal ridges present (Fig. 71) [1]. [In *Paramblynotus* the ridges are distorted by strong foveolate sculpture (Fig. 74).]

55 Notauli percurrent (Fig. 77) [0]./ Notauli reduced or lost (Figs 81, 82, 85) [1]. [In *Austrocynips* the notauli are obscured by strong sculpture.]

56 Percurrent median mesoscutal line (sometimes partially obscured by sculpture e.g. *Liopteron* - Figs 77, 130) [0]. / Median mesoscutal line reduced or lost [1].

57 Mesoscutal line simple [0]. / With a characteristic inverted "Y" pattern to the mesoscutal line [1] (Fig. 77).

58 Most cynipoids either have no mesoscutal flanges or have these flanges on the side of the mesoscutum [0]. / Posterolateral corners of the mesoscutum ending in a distinct flange which is preceded by a depression.

59 Axillar flange absent [0]. / With a horizontal flange on the axilla [1]. [This flange is not homologous with character 58].

60 Axillae present, even if occasionally lacking the distinctive dorsal bar (some Charipidae - Fig. 82) [0]. / Axillae virtually absent dorsally [1].

61.1, 61.2 The junction of the axillary bar with the scutellum is not normally visible, or, in those cynipoids with an especially flat and broad axillar

bridge, a trace of the junction may be seen [0,0]. / Axillary bar - scutellum junction evident and the axillary bar transverse [1,0]. / Axillar junction clear and the bar vertical (Figs 84-86) [0,1].

62.1, 62.2, 62.3, 62.4 Scutellum without spine(s) (Fig. 82) [0,0,0,0]. / Scutellum with a simple spine (Fig. 78) [1,0,0,0]. / Scutellum with a "spine" that is a continuation of the whole scutellum [0,1,0,0]. / With (in various degrees) a small projection on each side of the scutellum [0,0,1,0]. / With a central spine in addition to the lateral scutellar projections [0,0,1,1].

63 Posterior scutellar ridge absent [0]. / With a transverse ridge across the rear edge of the scutellum. It is interrupted centrally by a large emargination [1].

64 Scutellum not apically downcurved [0]. / Scutellum roundly declivous posteriorly [1].

65 Scutellum smooth, or with small weak carinae, or weak marginal flanges, or with a curved marginal flange (especially posteriorly), or with a short central ridge [0]. / With three large and distinctive scutellar carinae, one median and two lateral (Fig. 77, 78). The carinae are long straight and percurrent [1]. [The carinae of *Neralsia* are similar to those of the derived state but are not complete.]

66 Scutellar plate absent [0]. / The scutellum with a unique plate (="cup"), a raised circular or longitudinally oval area that frequently has a central depression (Figs 84-87) [1].

67 Scutellar foveae present (Fig. 130) [0]. / Scutellar foveae very faint and shallow or absent (Figs 81, 82) [1].

68 Foveae approximately round [0]. / Foveae of a distinctive, transverse, almost trianguar shape [1].

69 The central area between the scutellar foveae raised and, at most, moderately sculptured [0]. / Central area striate, either deeply depressed betweeen the striae or the striae are weaker and the area depressed so it almost forms a third fovea [1].

70 Scutellar foveae separate [0]. / Foveae virtually fused into one deep fovea [1].

71 Scutellum without a posterior depression [0]. / Posterior region of the scutellum with a shallow, approximately triangular, depression (Fig. 158) [1].

72 Anterior scutellar flange present above the transscutal articulation and on the mesoscutum [0]. / This flange present on the anterior corner of the scutellum [1].

73.1, 73.2, 73.3 Mesepisternal suture absent, or obscured by sculpture (Figs 81, 82) [0,0,0]. / With a transverse suture or a line of foveae on the ventral region of the mesepisternum (Figs 83, 85) [1,0,0]. / In two taxa the suture is high on the mesepisternum [1,1,0] and in two others the suture is wide (Fig. 74) [1,0,1].

74 Speculum-like area absent [0]. / The mesepisternum of a few large cynipoids has a distinct area (Fig. 71), reminiscent of the speculum found in ichneumonids [1].

75 Upper mesepisternal structures distinct [0]. / In some small species the subalar pit and the epistomal scrobe are indistinct and the epimeron is little differentiated from the mesepisternum (Fig. 85) [1].

76 The metathoracic spiracle is nonfunctional in most Cynipoidea [0]. / The largest cynipoid appears to have a functional spiracle [1].

77 Where the anteroventral region of the mesepisternum joins the metapleuron there is an inconspicuous depression [0]. / This depression forming a distinct pubescent cavity (Fig. 88) [1].

78.1, 78.2, 78.3 Junction between the metapleuron and the mesepisternum with a vertical metapleural trough which is constricted centrally, (Figs 79, 80, 83); or with a reduced trace of this structure [0,0,0]. / Region of metapleural trough obscured by rough multidirected sculpture - rugose to foveolate; without a clear trough, horizontal groove, or constriction (Fig. 72) [1,0,0]. / Metapleuron with upper part of trough and central constriction plus a strong horozontal groove (Fig. 71) [0,1,0]. / Metapleuron with a trough, which has a constriction and a sinuate lower margin

Fig. 62. *Anacharis* X150. Anterior of thorax, head removed, to show the pronotal plate.

Fig. 63. *Aspicera* X170. Anterior of thorax, head removed, to show the pronotal plate.

Fig. 64. *Melanipa* X110. Anterior of thorax, head removed, to show the pronotal plate.

Fig. 65. *Trybliographa* X220. Anterior of thorax, head removed, to show the raised pronotal plate.

Fig. 66. *Xyalaspis* X120. Anterior of the thorax, head removed. Lateral view of the pronotal plate.

Fig. 67. *Alloxysta* X220. Anterodorsal view of the pronotum, and frontal bar; head removed.

Fig. 68. *Figites* X150. Dorsal view of frontal bar and caulis (between the submedian depressions).

Fig. 69. *Meralsia* X220. Lateral view of pronotum. Submedian depression and frontal bar.

Fig. 70. *Ibalia* X80.
Lateral view of pronotum.

Fig. 71. *Ibalia* X25.
Lateral view of thorax.

Fig. 72. *Liopteron* X40.
Lateral view of thorax.

Fig. 73. *Liopteron* X70.
Mesepisternum. Slit-shaped opening of gland (arrow) and transverse suture.

Fig. 74. *Paramblynotus* X50. Lateral view of thorax.

Fig. 75. *Aulacidea* X120.
Lateral view of thorax.

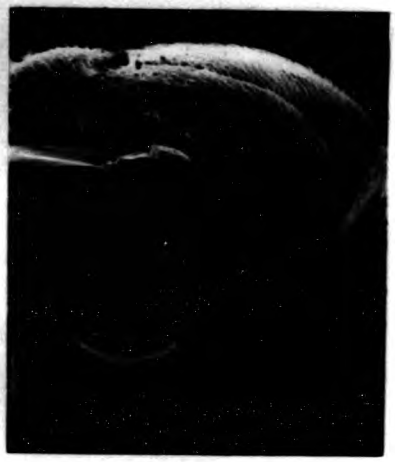

Fig. 76. *Melanips* X70.
Lateral view of thorax.

Fig. 77. *Callaspidia* X80.
Mesoscutum.

Fig. 78. *Aspicera* X50.
Dorsal view of thorax.

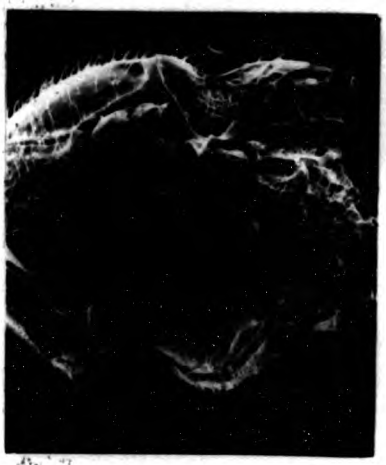

Fig. 79. *Aegilips* X80.
Lateral view of thorax.

Fig. 80. *Figites* X70.
Lateral view of thorax.

Fig. 81. Apocharips X150. Lateral view of thorax.

Fig. 82. Alloxysta X130. Lateral view of thorax.

Fig. 83. *Phaenoglyphis* X130. Lateral view of thorax; mesepisternal suture.

Fig. 84. *Trybliographa* X103. Dorsal view of axillae, scutellar foveae and the scutellar plate.

Fig. 85. *Kleidotoma* **X170. Posterolateral view of scutellum.**

Fig. 86. *Kleidotoma* **X300. Posterolateral view of scutellum.**

Fig. 87. *Eucoila* **X110. Lateral view of scutellum. Fenestra (arrow) under axillary bar.**

Fig. 88. *Kleidotoma* **X350. Pubescent cavity at the base of the metapleuron.**

Fig. 89. *Ibalia* X40. Dorsal view of thoracic flight muscles; mesonotum removed.

Fig. 90. A charipid X150. Lateral view of the thoracic musculature; side of thorax removed.

Fig. 91. *Cynips* X80. Lateral view of thoracic musculature. See Fig. 100.

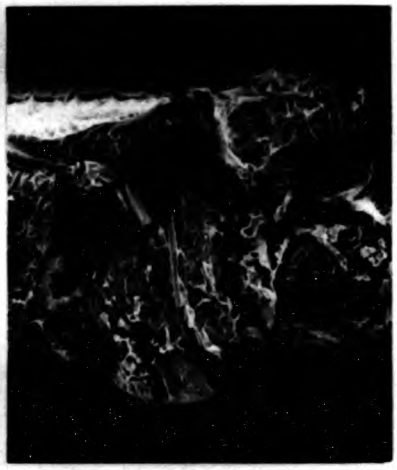

Fig. 92. *Ibalia* X35. Lateral view of thoracic musculature.

Fig. 93. Biorhiza X100. Mesotrochanteral muscle complex. See Fig. 101.

Fig. 94. Biorhiza X300. Mesotrochanteral muscle complex. Enlagement of Fig. 93.

Fig. 95. Ibalia X40. View from centre into rear of thorax (longitudinal flight muscles removed).

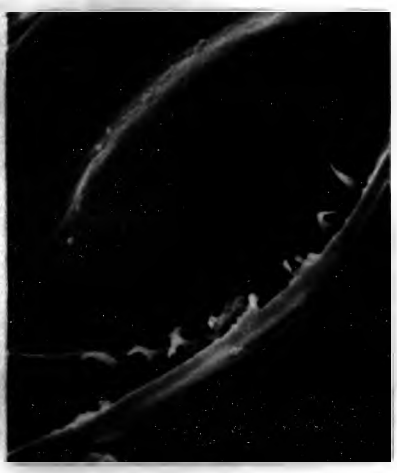

Fig. 96. Alloxysta X2000. Sensory hairs, on upper edge of mesepimeron, that touch the wing (above).

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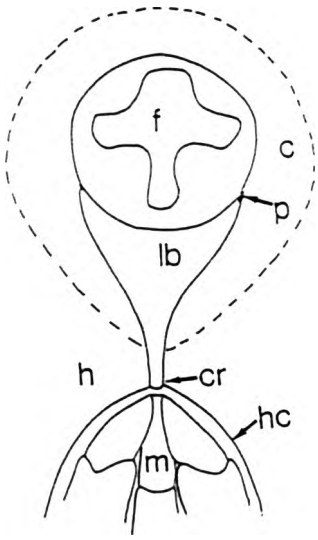

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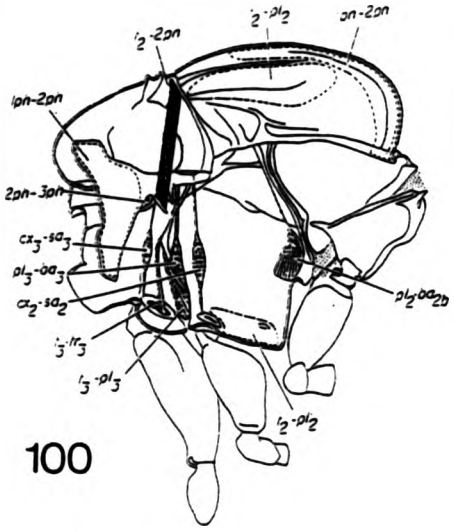
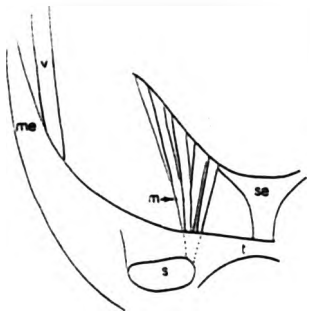
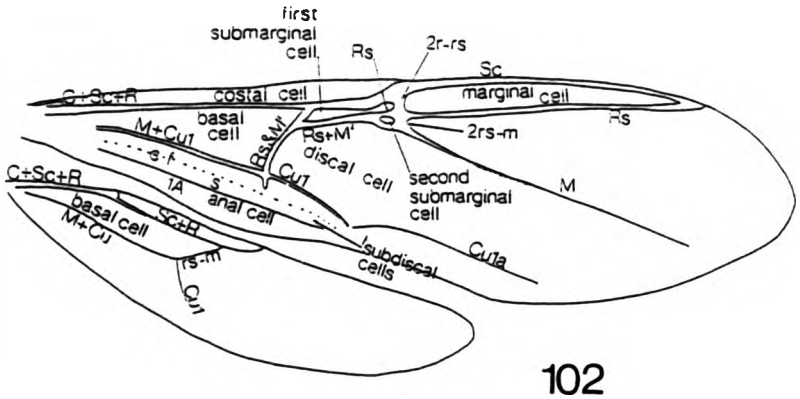
Figures 97-99. 97, right mandible of *Cynips*. 98, right mandible of *Pycnostigmus*. 99, hypostomal region of *Ibalia* (c.f. Fig. 38). Mouthparts (m) in the proboscidial fossa; hypostomal carina (hc); left hypostome (h); hypostomal crest (cr); lower tentorial bridge (lb); posterior tentorial pit (p); foramen magnum; back of head around the foramen set in a cavity (c).







Figures 100-102. 100, thoracic muscles of *Andricus*; second phragmal flexor (t2-2ph) shown in black. Vertical flight muscle t2-p12 removed. (After Daly, 1963). 101, *Biorhiza* - lower section of mesothorax showing mesotrochanteral depressor muscle (m). See Figs 93-94 (me = mesepisternum, s = socket of mid leg, se = septum, t = trochantinal lobe, v = vertical muscles. 102, cynipoid wing terminology (1 = basal vein, 2 = cubital vein, cf = claval furrow, s = subbasal cell) (discal cell = discoidal cell).

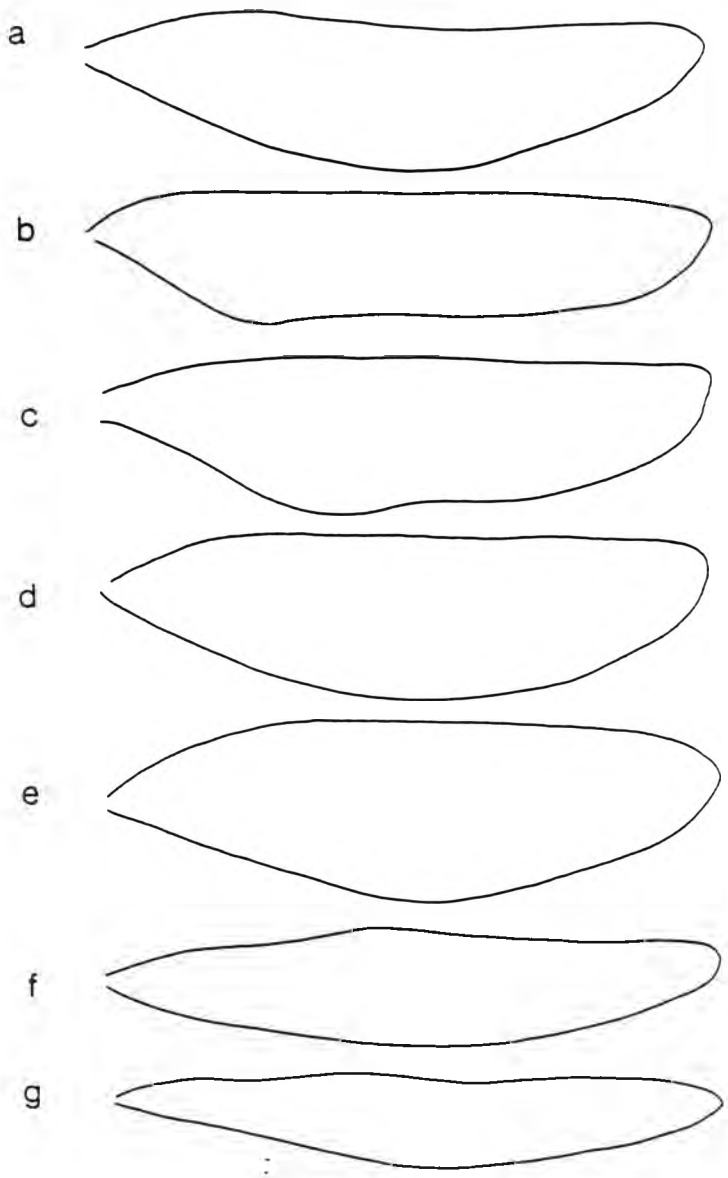
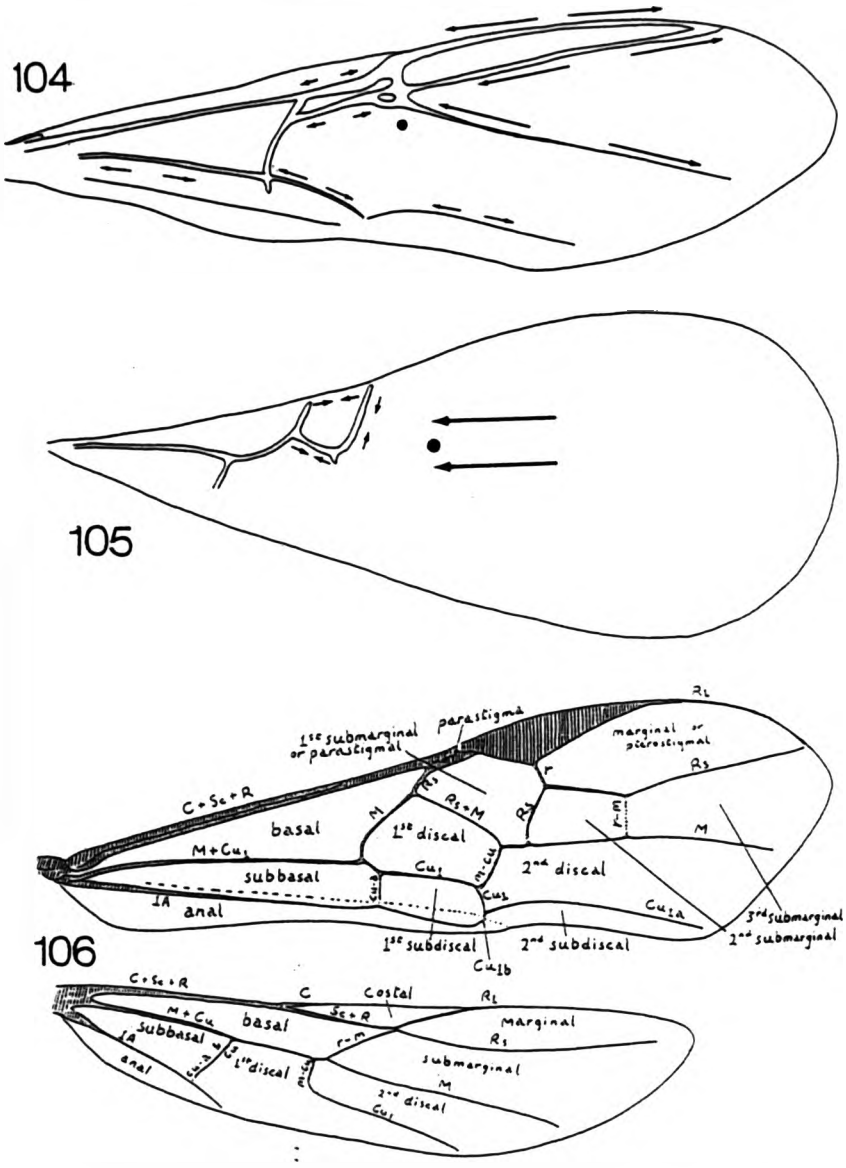
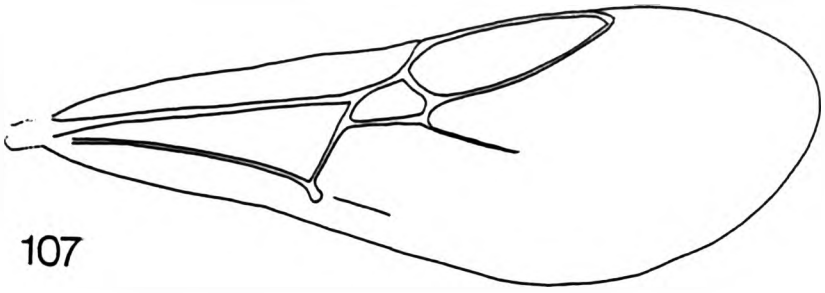


Figure 103. Allometry in hindwings.
Hindwing of *Ibalia* (a), *Tessmanella* (b), *Liopteron* (c), *Cynips* (d), *Figites* (e), *Lonchidia* (f) and *Rhoptromeris* (g), drawn to the same length.



Figures 104-106. 104, lengthened longitudinal veins of large cynipoids e.g. Ibalia. 105, proximal position and short veins of small cynipoids e.g. Apocharips. Dot = position of the centroid (After Danforth, 1983). 106, Braconidae wings, and nomenclature (After Eady, 1974).



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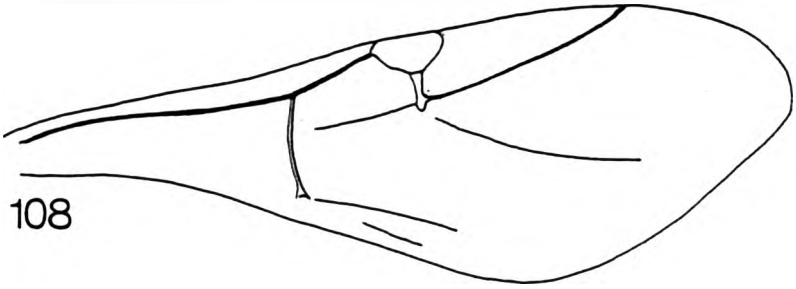

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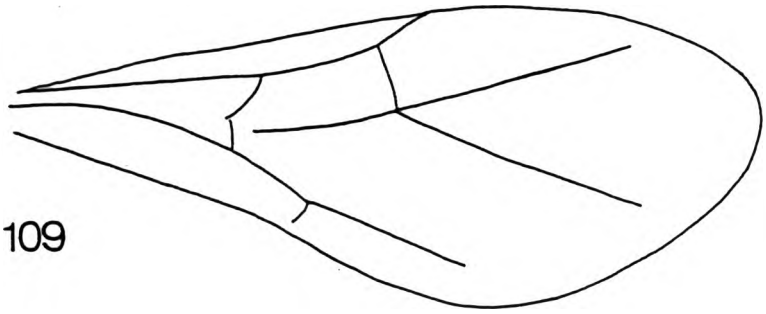

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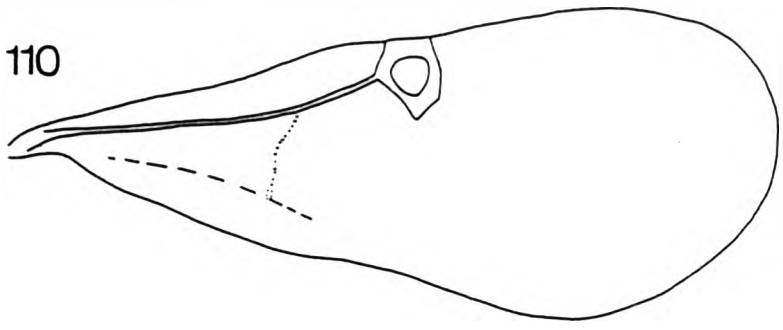
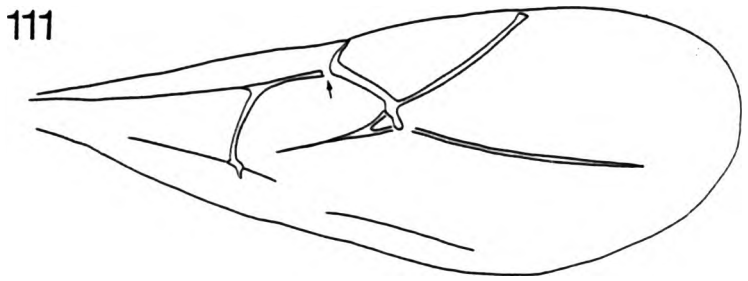
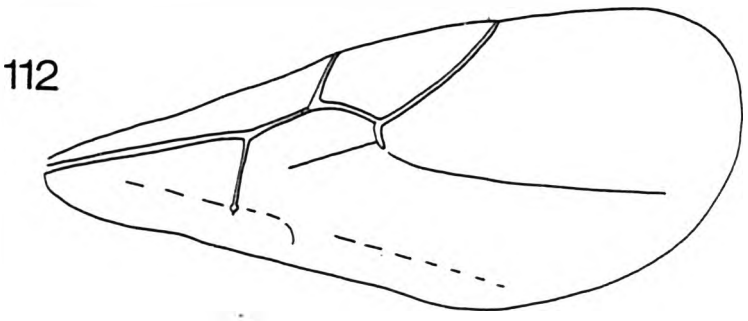
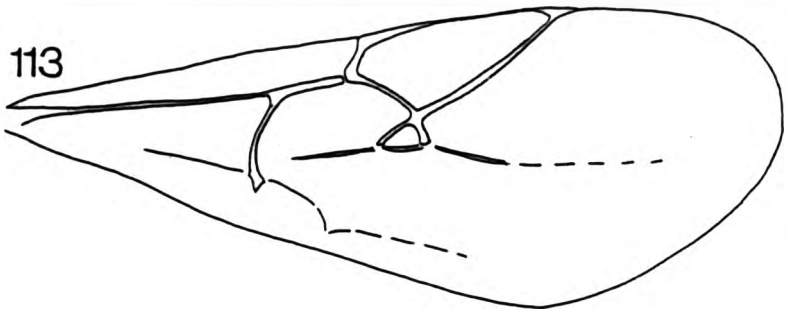
Figures 107-109. 107, forewing of *Liopteron*. 108, forewing of *Austrocynips*. 109, forewing of *Himalocynips*.

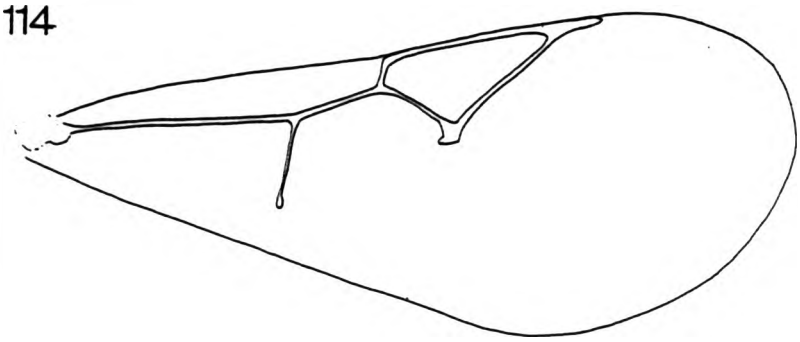


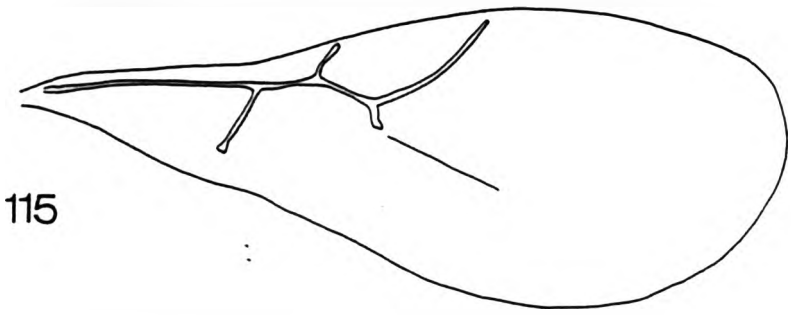




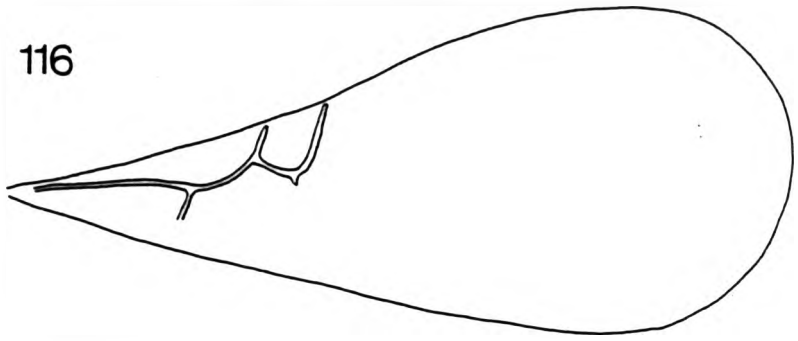
Figures 110-112. 110, forewing of *Pycnostigmus*. 111, forewing of Callaspidia (fenestra marked by an arrow). 112, forewing of Aulacidea.

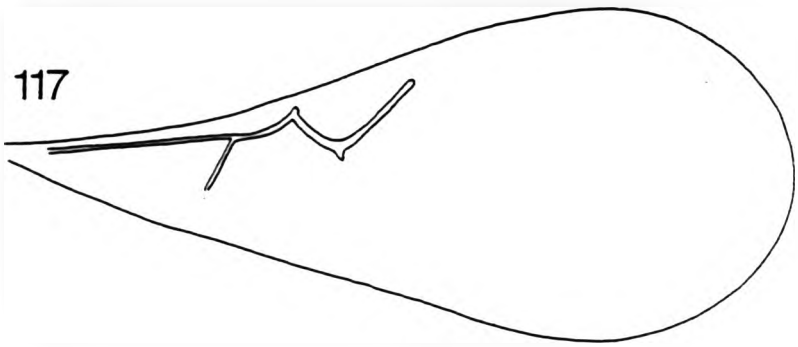


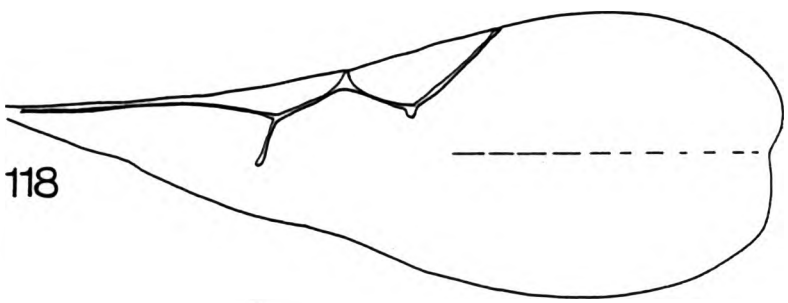




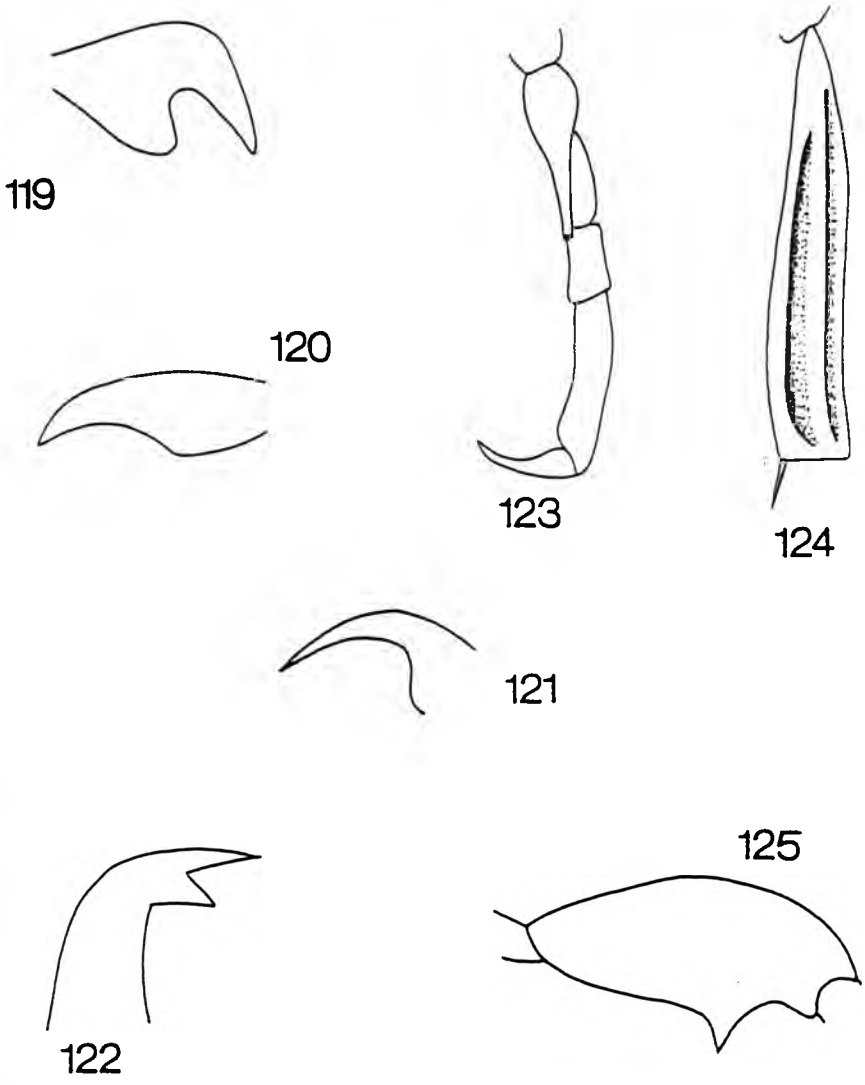
Figures 113-115. 113, forewing of *Melanips*. 114, forewing of *Xylaspis*. 115, forewing of *Alloxysta*.



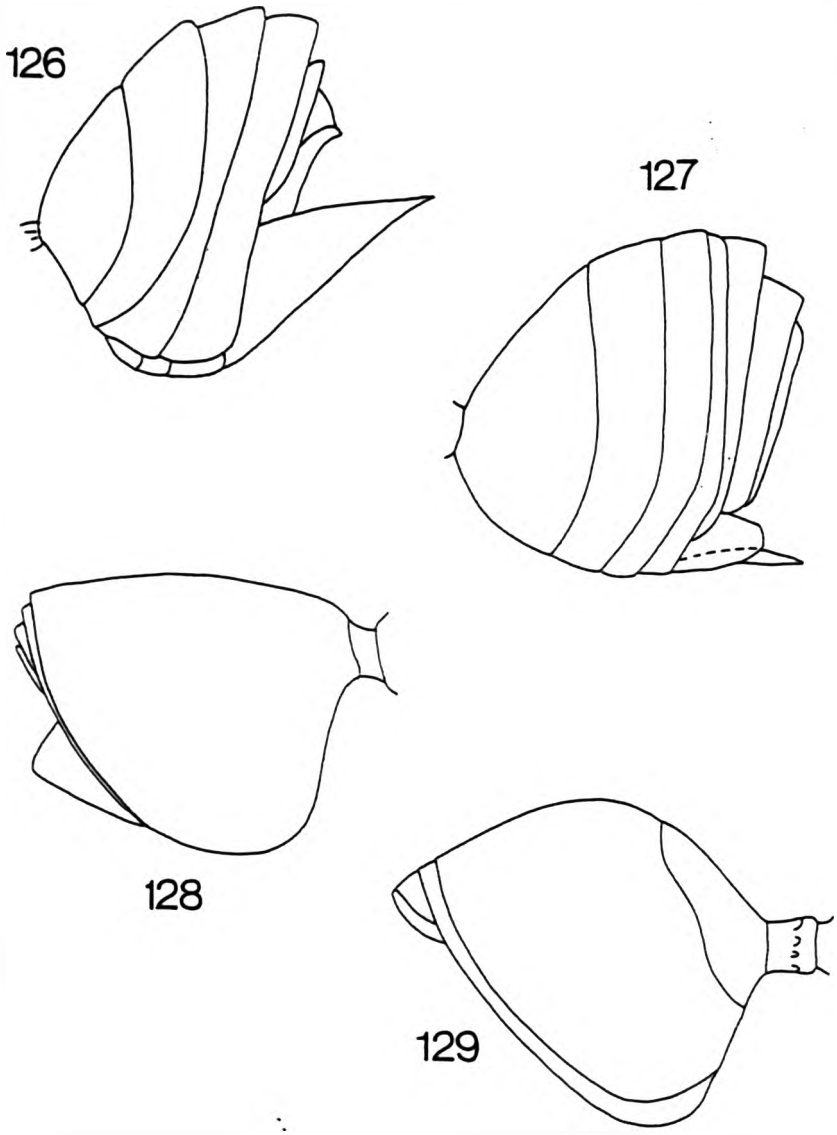




Figures 116-118. 116, forewing of *Apocharips*. 117, forewing of *Dilyta*. 118, forewing of *Kleidotoma*.



Figures 119-125. 119, claw of *Diastrophus*. 120, claw of *Liposthenus*. 121, claw of *Kiefferiella*. 122, claw of *Mesocynips*. 123, hind tarsus of *Ibalia*. 124, hind tibia of *Callaspidia*. 125, hind femur of *Oberthuerella*.



Figures 126-129. 126, lateral view of *Diplolepis* gaster. 127, lateral view of *Neuroterus* gaster. 128, lateral view of *Synergus* gaster. 129, lateral view of *Aspicera* gaster.

[0,0,1] [Further subdivision of this character is possible but difficult to characterize. *Austrocynips* has a shallow groove. In *Himalocynips* the lower half fades out in a distinctive manner. In *Liopteron* the groove is effectively absent but part of the posterior margin persists. A similar reduction occurs in the Eucoilidae. The Charipidae show a reduction series culminating in the retention of little more than the central constriction.]

79.1 79.2 Opening of propodeal spiracle partially covered by a flap [0,0]. / The form of the flap giving the opening a "figure-of-eight" shape [1,0]. / Flap small and the opening wide and round [0,1].

WINGS

The evolution of the apocritan wing is, to a large extent, a series of vein reduction trends. The most primitive and also the most complete wing venation is found amongst the Symphyta. In the Ichneumonoidea (Fig. 106) the venation is still extensive, but in the microhymenoptera the veins are much reduced. In the Chalcidoidea and many derived Proctotrupoidea the fore wing venation is reduced to a single vein complex (based on the submarginal, marginal, stigmal and postmarginal veins) near the costal margin, but in many microhymenoptera some or all of these veins are lost (e.g. Platygasteridae). In general terms the cynipoid venation occupies a position between the venation of the Braconidae and that of most microhymenoptera. The venation and in particular the hind wing venation is more similar to that of certain Proctotrupoidea than to that of the Chalcidoidea.

When the most complete cynipoid venation (Fig. 102) is compared to a generalized ichneumonoid venation e.g. *Bracon* (Braconidae) (Fig. 106) it is easy to see how the cynipoid venation has evolved. Cynipoids have lost the pterostigma, and the apex of the marginal cell has moved

round to the leading edge of the wing so that the cell becomes triangular. The m-cu cross veins have been lost so that there are no closed discal cells, the subcosta (Sc), and virtually all of the costa (C) is lost and the costal field is very wide. The maximum number of closed cells (*Ibalia*) is six: basal, marginal, first and second submarginal, subbasal and subdiscal. The last two cells are open where the claval furrow passes through the cu cross veins. The second submarginal cell is very small. It should not be called an "areolet" (Königsmann, 1978) as this is likely to be confused with the well-established and different use of this term in the Ichneumonidae. The hind wing has only one closed (basal) cell.

In slightly less well veined cynipoids (e.g. Cynipidae, larger Liopteridae and *Himalocynips*) the second submarginal cell is lost. Next the anal veins and the cu cross veins have been lost, and to a lesser extent there is a loss of veins in the basal region. On the hind wing, the basal cell is lost and the venation is reduced to one longitudinal vein (C+ Sc+R). In the smallest taxa the outer region of the wing loses all venation. *Pycnostigmus* shows a greater reduction of venation than any other cynipoid - veins 2r-rs, 2rs-m, Rs&M and Rs all being lost.

Hamuli

Hamuli, on the leading edge of the hind wing, engage in a fold on the posterior margin of the fore wing and hold the wings together. Cynipoid hamuli are long, close together and there are no costal hamuli. All examined taxa had three hamuli although five have been reported (Königsmann, 1978). A reduced number of hamuli, often three, is common in the microhymenoptera. Unlike many Hymenoptera (Gauld & Bolton, 1988), large body size does not appear to cause an increase in the number of hamuli in the Cynipoidea.

Convex veins

Wing veins are generally alternately convex and concave (Comstock, 1918). However, the Hymenoptera have

lost virtually all concave venation so that in the Apocrita the longitudinal veins are exclusively convex (Mason, 1986). However, in the Cynipoidea the trace venation of the hindwing has become secondarily concave (Mason, 1986), a peculiarity of this group, although it is possible that vein M+Cu is partially concave in some Diapriidae (e.g. *Aclista*).

Pterostigma

The Cynipoidea have lost the pterostigma but two subfamilies, Himalocynipinae and Pycnostigmatinae, have a "pseudopterostigma" (Figs 108, 110, 149, 159). This structure consists of a small cell surrounded by very thick sclerotized veins and therfore is is not directly homologous with the pterostigma of other Apocrita (Danforth, 1983; Fergusson, 1986; Königsmann, 1978; Weld, 1952). Nor is this structure homologous with the parastigma of the Chalcidoidea - formed by the broadened junction of the submarginal and marginal veins.

In *Pycnostigmus* the R veins are very thick and the central circular area is only moderately pigmented and smooth. *Pycnostigmus* has lost many wing veins and it is most likely that the pseudopterostigma helps to strengthen the leading edge of the wing. The pseudopterostigma of *Austrocynips* is very different to that of *Pycnostigmus* because the R veins are not so broad and distinct although they are visible. Also the surface of the sclerotized cell is granulate.

Wing pubescence

The wings of small cynipoids (e.g. Charipidae and Eucoilidae) often have a dense fringe of long hairs which increase the aerodynamically effective wing area. Also they have elongate leading edge setae which presumably assist in the generation of turbulence in a thick boundary layer (c.f. Danforth 1983). Many of the larger cynipoids (e.g. Liopteridae) have no wing fringe or only a short fringe of hairs.

Some taxa have conspicuous hairs on Sc+R+Rs these hairs are longest in small taxa, the exemplar

Rhoptromeris, *Phaenoglyphis*, *Apocharips*, *Dilyta*, *Figites*, *Neralsia* and *Alloxysta* all have five of these long hairs. *Kiefferiella*, a small liopterid, also has very long hairs, but all other Liopterids and other taxa have vein hairs of the same length or shorter than other wing hairs.

Flexion & fold lines

The wings of virtually all but the smallest Hymenoptera have fine flexion lines, which are primarily aerodynamic in function, and wing fold lines (Danforth & Michner, 1988; Wootton, 1979). Insect wings are aerofoils subject to passive deformation by the airstream and the extent of this deformation is partially controlled and limited by the architecture of the wing. This deformation is helped and localized by the flexion lines which permit areas of wing to hinge against each other thus allowing an alternation of camber at different stages of beat-cycle.

In most cynipoids the outer part of the wing is not supported by veins and thus the radial flexion system (a derivative of the median flexion line) found in the Ichneumonoidea is indistinct or absent. However, there may be a fenestra (= bulla) present (Fig. 111) where Sc separates from Rs (e.g. *Callaspidia*). This corresponds to the characteristic radial flexion fenestra, just proximal to the pterostigma, in other Hymenoptera. The claval furrow is present, just anterior and parallel to the line of vein 1A, in all Cynipoidea studied. It originates at the wing base but there is no clear notch (preaxillary excision) in the distal wing membrane. Flexion lines also occur in the hind wings of many Hymenoptera but only a faint trace of this flexion system is present in the Cynipoidea.

The reduction of these lines in the Cynipoidea means that the great bulk of the forewing and all of the hindwing conists of remigium. Thus wing flexion and indeed cynipoid flight is unlikely to be identical to that of larger Hymenoptera and is more likely to be similar to that of other microhymenoptera, e.g. Chalcidoidea, that have also lost much wing structure (see below).

Insect wings may undergo longitudinal plication along

fold lines (e.g. the jugal fold). Also the fold lines may secondarily contribute in flight (and the flexion lines may help in folding at rest). In the examined Cynipoidea, fold lines were only seen in *Kleidotoma*. This genus has a semi-longitudinal fold line which runs from a notch in the wing margin to the hind margin of the wing, so the distal part of the wing can flex down when the wings overlap above the gaster.

Allometry and wing shape

In general the hymenopterous wing becomes more elongate and narrow with increasing size (Danforth, 1983) (Fig. 104). In the Cynipoidea this has been found to be true of all but the smallest species where the trend is reversed (Danforth did not study very small Hymenoptera). This is the same bimodal allometry that was detected in the cynipoid head measurements. Wing shape allometry is particularly well evidenced by the hindwing (Fig. 103). In *Ibalia* and the largest Liopteridae (e.g. Oberthuerellinae) the wings are elongate and narrow, but with decreasing size (e.g. *Liopteron*) down to the smallest liopterids the wing becomes shorter and broader and the apex becomes round. Medium sized cynipoids (*Himalocynips*, *Austrocynips*, Figitidae, Pycnostigmatinae and Cynipidae) all have broad wings and the smallest cynipoids - Charipidae, *Lonchidia*, Eucoilidae (minus *Eucoila*) have very thin hind wings.

Allometry and venation

The longitudinal veins, especially the distal elements, become less elongate as the body size decreases (Danforth, 1983). The basal portion of the cynipoid forewing is not so affected, and responds approximately isometrically to size differences. The hindwing venation does not show clear allometric changes because it is limited to the basal region and, except for vein Sc+R+Rs is only present in the largest taxa.

Large cynipoids (*Ibalia* many Liopteridae, *Himalocynips* and *Austrocynips*) tend to retain wing veins (e.g. Cu1 & Cu1a) and cells (e.g. submarginal & subdiscal

cells) (Figs 104, 107) which are lost or reduced in smaller taxa. For example vein M is present and reaches to the wing margin in the Oberthuerellinae, *Ibalia*, *Mesocynips*, *Plastibalia Paramblynotus*, *Himalocynips* (Fig. 109), and Cynipidae, but in smaller taxa it is reduced and finally lost. Similarly Rs is particularly long in *Ibalia*, *Liopteron*, *Oberthuerella* and *Plastibalia*. It is much shorter in the smaller Liopteridae (*Kiefferiella* & *Paramblynotus*) and many Figitidae, and it is very short in the Charipidae and most Eucoilidae (see Table 37).

Ibalia	3.3	Oberthuerella	2.1	Tessmanella	1.5
Liopteron	3.1	Plastibalia	2.4	Pseudibalia	1.6
Mesocynips	1.7	Paramblynotus	0.7	Kiefferella	0.6
Aspicera	0.6	Callaspidia	0.8	Omalaspis	0.5
Anacharis	0.4	Aegilips	0.5	Xyalaspis	0.5
Figites	0.5	Melanips	0.7	Lonchidia	0.3
Neralsia	0.4	Eucoila	0.6	Kleidotoma	0.2
Rhoptromeris	0.3	Dilyta	0.1	Apocharips	0.2
Phaenoglyphis	0.3	Alloxysta	0.4	Pycnostigmus	0.0
Aulacidea	0.6	Cynips sexual	1.1	Cynips agamic	1.6
Austrocynips	1.0	Himalocynips	1.7		

Table 37. Exemplar lengths of Rs (in mm) of study taxa.

The basal part of vein C+Sc+R+Rs is very long in the large taxa (*Ibalia* and most Liopteridae) it is not so long in mid range cynipoids (e.g. *Omalaspis* and *Xylaspis*) but in the smallest taxa where the rotation (see below) of Rs+M is greatest, vein Sc+R+Rs becomes proportionally a little longer again.

Danforth (1983) showed that cross veins are positively allometric with decreasing body size, this is true of all but the smallest cynipoids. For example the costal field, above vein C+Sc+R+Rs, is thin in large taxa (e.g. *Ibalia*, *Oberthuerella*, *Tessmanella*, *Pseudibalia*, and *Plastibalia*); and broader in the small examples of the "large taxa" (e.g. *Kiefferiella*) and in the medium sized taxa (e.g. *Xylaspis*, *Melanips* and *Cynips*). However, the field is long and thin again in very small cynipoids (*Apocharips*, *Dilyta*, *Lonchidia* & *Phaenoglyphis*).

An important consequence of wing vein allometry is that the cells and veins become withdrawn from the wing

apex with decreasing body size. In the smallest Cynipoidea the venation is restricted to the upper inner quarter of the wing and the majority of the membrane is unsupported (Fig. 105).

Rotation

A suite of venation changes is associated with an angular rotation of Rs+M about the base of the marginal cell, and this rotation increases as wing size decreases. In *Ibalia* the first and second submarginal cells are complete but in medium sized cynipoids (e.g. Cynipinae) Rs+M is detached from Rs&M and has moved down to a position pointing near the middle of Rs&M (Figs 109, 112), and the submarginal cells are lost. In still smaller species (Figitidae, Charipidae, and Eucoilidae) Rs+M points to the base of Rs&M and becomes faint (Figs 111, 113-115).

Associated with this rotation is a change in the angle of 2r-rs to Rs. Vein 2r-rs is almost vertical in the large liopterids, it is angled in the medium sized cynipoids and in some small Eucoilidae and Charipidae it is closer to the horizontal than to the vertical. Vein 2rs-m moves in a similar fashion, moving outwards from a vertical position under 2r-rs (in *Ibalia*) to a position under the marginal cell, and then, in the smallest taxa, becomes strongly angled to the vertical. Where vein M is not lost, it tends to become more curved (e.g. Eucoilidae and Charipidae) as the central venation is rotated.

As rotation increases Sc becomes obliquely angled away from the horizontal Sc+R+Rs (Figs 116, 117), becoming nearer the vertical in smaller taxa. Also Sc angles upwards from the point of junction with M&Rs in the most "rotated" taxa.

As the base of the marginal cell rotates, both Rs and the marginal cell must become shorter; this explains why the apex of the cell has moved round the wing margin to form the characteristic triangular marginal cell of the Cynipoidea. In the largest taxon (*Ibalia*) the cell is exceptionally long (nine times longer than broad) but as Rs shortens the marginal cell becomes smaller so that in

the Charipidae the marginal cell is about as broad as long. In two very small taxa (*Apocharips* and *Lonchidia*) the cell is so small that the basal angles are 90 degrees (Fig. 116). Finally Rs becomes curved and moves further along the wing edge towards the base. In the highly specialized venation of *Pycnostigmus* Rs is absent.

Flight & Morphology

Encarsia formosa (Chalcidoidea) is the only microhymenopteron that has had its flight well-studied and it has been shown (Weis-Fogh, 1973) to have aerodynamic parameters that are not compatible with the aerodynamics of most other insects. In particular it has a low Reynolds number which means that drag would tend to be greater than lift and therefore normal flight would be energy-expensive. It is clear that such small insects use a flight mechanism which involves wing movements quite different from those of the forward flapping flight of larger insects (see Ellington, 1975). The method employed by *Encarsia* has been named the clap-and-fling mechanism. The wings clap together at the upper extreme of their motion then suddenly split apart along their leading edges. The wings then twist and separate completely, each carrying with it a vortex providing lift in excess of body weight.

The small cynipoidea (and other microhymenoptera) show three morphological features that would help exploit this clap-fling mechanism. The initial angular movement of flinging open the wings requires a relatively stong leading edge to the wing and in the smaller Cynipoidea the veins are concentrated in this area. Secondly the outer region of the wings tend to become unencumbered with veins, this allows passive flexion. Thus the smallest Cynipoidea (Charipidae and Eucoilidae) have a remarkably limited venation to the upper proximal quarter. [The moment of inertia of a wing about its base depends on the distribution of mass along the wing. Withdrawal of venation from the wing apex moves the centroid outside the veined area and decreases the wing aspect ratio (Danforth, 1983) (Figs 104, 105)].

Lastly the pterostigma is associated with determining

wing pitch and controlling flutter in the standard model of wing motion (Norberg, 1972). These functions are controlled by the fore margin veins in the microhymenopteran clap-fling system and all cynipoids (except *Himalocynips* and *Pycnostigmus*) have lost the pterostigma / pseudopterostigma.

Summary

The cynipoid wings show a sequence of vein losses that represents part of an evolutionary trend towards reduced size in most taxa. Further it is likely that many of the characteristic wing features of the smaller Cynipoidea have developed in response to the adoption of a clap-fling flight mechanism. The wing characters show a high degree of homoplasy and a strong allometric bias.

List of wing character-states

80 Hindwing with an enclosed basal cell [0]. / Basal cell absent [1].

81.1 81.2 Hindwing with M+Cu present [0,0]. / A trace of M+Cu present [1,0] . / M+Cu lost from hindwing [1,1].

82.1 82.2 Hindwing with rs-m present [0,0]. / Only a trace of rs-m present [1,0]. / Hindwing with rs-m lost [1,1].

83 Hindwing with a slight stub of vein C present [0]. / Vein C lost [1].

84 Hindwing with vein M indicated [0]. / M absent [1].

85 Hindwing with vein R indicated [0]. / R absent [1].

86 Hindwing with a very faint trace of Rs [0]. / Rs absent [1].

87 Vein C absent [0]. / Trace of vein C present at base of forewing [1]. [Vein loss is normally considered to be apomorphic, but in the outgroups vein C is closely associated with with Sc+R (Fig. 106), thus the isolated presence of this vein in *Ibalia* is an apomorphic feature.]

88 Vein M+Cu1 almost complete to wing base (basal cell closed) or at least well indicated [0]. / M+Cu1 lost or very poorly indicated, often just a fine trace of

pigment [1].

89 Path of vein 1A indicated by a trace of pigmentation which is well indicated and almost complete to the wing base [0]. / 1A weakly indicated or lost [1].

90.1 90.2 When present, vein 1cu-a is limited by the claval furrow to being only a stub [0,0]. / Vein 1cu-a only indicated [1,0]. / Vein 1cu-a absent [1,1].

91 Vein cu1b present or indicated [0]. / Vein cu1b absent [1].

92 Vein Cu1 present [0]. / Cu1 weakly indicated or absent [1].

93 Vein Cu1a present and long, extending almost to wing edge [0]. / Cu1a only faintly indicated or absent [1].

94 Subbasal cell indicated, almost complete (it is not complete because of the claval furrow) [0]. / Subbasal cell open or absent [1].

95 First subdiscal cell present but not complete, or only indicated [0]. / First subdiscal cell absent [1].

96.1 96.2 Vein M present and reaching near to wing margin [0,0]. / Vein M indicated [1,0]. / Vein M absent or very weakly indicated [1,1].

97.1 97.2 Vein Rs present and reaching margin [0,0]. / Rs present but not reaching margin [0,1]. / Rs absent [1,0].

98 Rs mostly straight, or absent [0]. / Rs curved [1].

99 Marginal cell without Rs parallel to Sc [0]. / Vein Rs parallel to vein Sc and the basal angles of the marginal cell approximately 90 degrees [1].

100.1 100.2 Without a triangular marginal cell [0,0]. / The distinctive triangular marginal cell (Fig. 118) found in the Cynipoidea is regarded as a synapomorphy for the superfamily [1,0]. / *Pycnostignus* has a highly modified venation and has lost the marginal cell, this exception is considered a higher derived state [1,1].

101 Marginal cell much less than nine times as long as broad [0]. / The marginal cell exceptionally long (nine times as long as broad) (Fig. 102) [1].

102 Marginal cell longer than 1.4mm [0]. / Marginal cell very short, under 1.4 mm long and almost as wide as

high [1] (Fig. 116).

103 Marginal cell closed by Sc. [0]. / Sc reduced so that the marginal cell is open, part open, or absent [1].

104 Pterostigma (Fig. 106) present [0]. / Pterostigma absent [1].

105.1 105.2 Pseudopterostigma absent [0,0]. / Pseudopterostigma present (Figs 149, 159). This is not homologous with the pterostigma and is regarded as an apomorphic feature. R veins very thick and the central area smooth [1,0]. R veins not so broad and the surface granulate [0,1].

106 Stub of vein R absent [0]. / Stub of (the second abcissa of) vein R present [1].

107 Vein 2rs-m present [0]. / Vein 2rs-m absent [1].

108 Vein 2r-rs present [0]. / Vein 2r-rs absent [1].

109.1, 109.2, 109.3, 109.4 Angle of vein 2rs-m. Vein 2rs-m angled from the vertical and under the marginal cell [0,0,0,0]. / 2rs-m absent [1,0,0,0]. / 2rs-m vertical and under the marginal cell [0,1,0,0]./ 2rs-m vertical and under 2r-rs [0,1,1,0]. / 2rs-m almost horizontal, strongly angled from vertical [0,0,0,1].

110 Rs+M clearly present [0]. / Rs+M absent or incompletely indicated [1].

111.1 111.2 111.3 Rs+M (cubitalis) complete and joined with Rs&M (first submarginal cell closed) near top of basalis (Fig. 107) [0,0,0]. / Rs+M incomplete and not fully distinct, pointing to the top of the basalis [1,0,0]. / The internal end of Rs+M pointing at the middle of Rs&M (basalis) (Fig. 112) [1,1,0]. / Rs+M pointing at the junction of the basalis with the median (Cu1) (Fig. 111) [1,1,1].

112.1 112.2 Minute second submarginal cell present [0,0]. / Second submarginal cell indicated [1,0]. / Second submarginal cell lost [1,1]. [A careful examination has shown that it is the small part of M that is lost not Rs.]

113.1 113.2 Vein Rs&M complete with terminal "knob" [0,0]. / Vein Rs&M long but without terminal "knob" [1,0]. / Vein Rs&M absent, and only indicated by pigment [0,1].

114 Veins covering most of the wing area (Fig. 109) [0] /

Veins restricted to internal upper diagonal (Figs 116, 117) [1].

115 Apex of wing regularly curved [0]. / Apex of wing incised (Fig. 118) [1].

116 The Hymenoptera normally have hairs on both sides of the wing membrane [0]. Occasionally these hairs are almost or completely lost eg *Trichosteresis glabra* (Ceraphronoidea). A few cynipoids have reduced pubescence, either no hairs or just a few hair bases or hairs limited to the basal region. [1].

117.1 117.2 Wings clear [0,0]. / Wing with colour around certain veins (e.g. 2rs-m) [1,0]. / Wing fumate [1,1] [Possibly a camouflage feature of these large taxa].

LEGS

The cynipoid leg is similar to that of other apocritans and the characters present are mostly generic or specific discriminants.

Tibial spurs

Hymenopterous tibiae have distal articulated spurs and the plesiomorphic spur formula is 2,2,2 but, together with many apocrita, most cynipoids have a formula of 1,2,2. The first spur, together with the first tarsal segment, is modified to form an antennal cleaner - the strigil.

Tarsi

The Cynipoidea have five-segmented tarsi, this is a symplesiomorphic number, shared with other parasitica (e.g. the Ichneumonoidea). In more derived microhymenoptera the tarsus is reduced, for example to 4, 3 or even 2 segments in some chalcidoids.

Trochantellus

The trochantellus is a section divided off from the proximal end of the femur (Fig. 131). A trochantellus is distinct, at least on the hind leg, in most Ichneumonoidea and Trigonalyoidea and it is often present in the

Chalcidoidea. Most Proctotrupoidea have presumably lost the trochantellus but it is retained in *Helorus*.

In *Ibalia* and *Cynips* the trochantellus is a distinct, possibly free, segment on all three legs. In some genera of Liopteridae (*Oberthuerella*, *Tessmanella*, *Liopteron*, *Plastibalia* and *Pseudibalia*) the segment is distinct on at least one leg. However, in other taxa it is indistinctly separated and partially fused to the femur. Ultimately it is completely fused and lost, although its position is often traceable from the shape of the femur. The partially fused trochantellus was considered to be a possible groundplan synapomorphy for the Cynipoidea by Königsmann (1978). However, the trend of trochantellus loss occurs as a parallelism in at least three independent lines of the parasitica.

Claws

The structure of the cynipoid claw (Weld character 113) has been reappraised and, under high magnification, a variety of claw structures has become apparent.

All Cynipidae examined, including inquiline genera, have a large basal lobe to the claw; in *Aulacidea*, *Phanacis*, *Aylax*, *Isocolus* and *Liposthenus* (Fig. 120) the lobe is simple but in all other examined genera the lobe is dentate (Fig. 119). The polarity of this character is difficult to assess. The basal lobe found in the Cynipoidea is similar to that found in many other Hymenoptera. Thus it is considered that a basal lobe is primitive in the Cynipoidea. However, the polarity assessment may have to be reviewed after analysis.

The Anacharitinae have a long spine which projects at 90 degrees from the base of the claw. This structure may help these parasitoids of Neuroptera gain a firm hold on the hosts cocoon.

Certain Liopteridae (*Liopteron*, *Plastibalia*, *Pseudibalia* & *Mesocynips*) have bifid claws (Fig. 122), and in the Oberthuerellinae the second tooth is a small flap of cuticle. The second tooth is not present (Fig. 121) in the smallest Liopteridae (*Kiefferiella* & *Paramblynotus*) and thus is likely to be a size-related feature. In the

smallest cynipoids (Eucoilidae and Charipidae) the claws are very small and weakly curved, and the arolium is more obvious than the claws. Although the Eucoilidae live in messy habitats (e.g. dung) the Charipidae do not, so claw reduction is more likely to be an allometric effect than a feature associated with microhabitat.

List of leg character-states

118 The hind femora are normally without teeth [0]. / Hind femora with a tooth (Fig. 125) [1].

119 Trochantellus present on foreleg [0]. / Trochantellus lost [1].

120 Trochantellus present on midleg [0]. / Trochantellus lost [1].

121 Trochantellus present on hindleg [0]. / Trochantellus lost [1].

122 The ground-plan tibial spur formula for the Cynipoidea is 1,2,2. [0]. / Thus a reduction to a single spur on the middle tibia is an apomorphic feature [1]. / The scoring this character in the very small Charipidae is very difficult as the tibial hairs are of a similar length to spurs. They have been scored as double spur (this interpretation is different from that of the Quinlan scoring of character 220).

123 Longitudinal furrow and ridge present on the outer or posterior surface of the hind tibia (Fig. 124) [1]. / Traces of this character occur in other Cynipoidea but not to the same extent [0].

124 Teeth of strigil blunt [0]. / Teeth of strigil fine and sharp [1].

125 Hind leg without a spur on first tarsal segment [0]. / Hind leg with a blunt spur on distal end of the first tarsal segment [1].

126.1 126.2 Hind leg without a spur [0,0]. / Short blunt spur on distal end of the second tarsal segment [1,0]. / Long blunt spur on distal end of second segment (Fig. 123) [1,1].

127 The first segment of the hind tarsus normally conforms to the apocritan pattern [0]. / First segment of hind tarsus long, approximately twice as long as segments

2-5 combined [1].

128 Fifth tarsal segment not long, and never much longer than segments 3 plus 4 [0]. / Fifth tarsal segment longer than the second third and fourth together [1].

129 Claws with a large basal lobe [0]. / Claws fine and without a basal lobe [1].

130 Claws without a spine [0]. / Claws with a basal spine [1].

131.1 13[illegible].2 Without bifid claws [0,0]. / Claws bifid [1,0]. / Claws bifid but the second "tooth" is a flange of ~~chitin~~ cuticle [1,1].

GASTER

In all apocritans the first abdominal segment (the propodeum) is incorporated into the thorax, therefore the "apparent abdomen" (= gaster) consists of the second and following abdominal segments. Thus, for example, the second abdominal segment is the petiole and the third is the second gastral segment.

PETIOLE

An investigation of many Cynipoidea showed that there are, at least, fourteen different types of petiole. However, these types do not form a simple transformation series and it is clear that homoplasy is present.

The petiole can be short (Fig. 134), simple, lightly sculptured (smooth to granulate) and with a narrow ventral keel (Eucoilidae - Fig. 135) or with a small dorsal lip (Fig. 134) (a recurved part of the distal end of the petiole) (Charipidae, Himalocynipinae and all Cynipidae except the Synergini). The petioles of many species have strong canaliculate sculpture and an anterior flange (Figs 136, 137). This flange may be developed into a complete collar (Oberthuerellinae, some Mesocynipinae and most aspicerines - Fig. 136), but in many cynipoids the two components of the petiole (the first gastral tergite and

sternite) combine, in different ways, to produce a range of incomplete collars. These include a collar with dorsal and ventral elements separated by a lateral indentation (Fig. 137) (*Figites, Neralsia* and the Synergini); the collar present only dorsally (Fig. 133) (*Callaspidia, Melanips*); the collar present dorsally and laterally (*Lonchidia*); the collar present ventrally and laterally but not dorsally (Anacharitinae except *Anacharis*). Where taxa with these types of petiole also have a long petiole then the collar and sculpture tend to be reduced (*Anacharis*, Liopterinae). The petiole of many Liopteridae is attached to the gaster at a characteristic angle (Fig. 132).

Other structures may contribute to the apparent petiole. For example in *Pycnostigmus* the petiole is short but the posterior of the propodeum is markedly extended. In *Austrocynips* the petiole is dominated by a strong, laterally divided, flange which is actually derived from the second gastral segment.

The fourteen forms of petiole were re-assessed in order to produce a list of petiole characters. Characters 132 and 133 were not combined into one series because the morphological evidence indicates that these characters represent separate developments. The apomorphic state of character 137 is similar to, but morphologically distinct from, that of character 136.

Petiole sculpture (138) proved to be most difficult to characterize. Two of the exemplar taxa (*Ibalia* and *Anacharis*) have smooth petioles that, although different, are difficult to differentiate with reference only to this feature. However, the sculpture of the condyle (of the petiole / gaster articulation) is distinctive in *Ibalia*.

List of petiole character-states

132.1, 132.2, 132.3 Collar absent (Fig. 135) [0,0,0]. /
Collar only present dorsally (Fig. 133) [0,0,1]. /
Collar present dorsally and laterally [0,1,1]. /
Collar complete (Fig. 136) [1,1,1].

133 Collar absent or present dorsally [0]. / Canaliculate

collar present ventrally and laterally but missing dorsally [1].

134 If present then side of collar not notched [0]. / Side of collar with a small notch (Fig. 137) [1].

135 Condyle, of articulation with the thorax, exposed [0]. / Condyle sunk within the collar [1].

136 Distal end of petiole without a ventral keel [0]. / Underside of distal end of petiole with a narrow central keel (Fig. 135) [1].

137 Petiole without a ventral hump [0]. / Underside of petiole with a narrow hump that forms the under part of a strong but non-continuous collar [1].

138.1, 138.2, 138.3 Petiole weakly sculptured (granulate) [0,0,0]. / Petiole strongly canaliculate [1,0,0]. / Petiole smooth, with sparse punctation on underside of condyle (Fergusson, 1985) [0,1,0]. / Petiole smooth, with dense punctation on underside of condyle [0,0,1].

139 Without a dorsal lip above distal end of petiole [0]. / Small dorsal lip present above distal end of petiole [1].

140 No flange present second gastral segment [0]. / Strong flange present on second gastral tergite and sternite [1].

141 Petiole not meeting an extended propodeum [0]. / Short petiole with two ventral indentations meeting an extended propodeum [1].

142.1, 142.2 Petiole short, not obviously longer than hind coxa [0,0] / Petiole long, clearly longer than hind coxa and with at least part of a collar present [0,1]. / Petiole long but without a collar [1,0].

143 Underside of condyle and lower plate of anterior articulation normal [0]. / Underside of condyle incised so that the underlying muscle is visible; lower plate enlarged [1].

144 Petiole attached normally [0]. / Petiole attached tangentially to dorsal curvature of gaster (Fig. 132) (Hedicke & Kerrich, 1940) [1].

REMAINING GASTRAL SEGMENTS

Tergites

In the Cynipoidea the sides of the tergites are strongly compressed and there are no laterotergites. Gastral segments two to eight are unspecialized and the hind edge of each tergite overlaps the front margin of the following tergite (Figs 126-129). In a few genera gastral segments two, three (e.g. *Dilyta*) and sometimes four (e.g. *Pycnostigmus*) may fuse to form a syntergite (Fig. 149). In at least some Eucoilidae the syntergite composition is related to sex, females having three and males two fused segments. Dissection and clearing often reveal the lines of fusion between the constituent segments. [In all the cases examined the syntergite contains the missing segments. Although an obvious conclusion this has previously only been assumed to be true.] Normally the syntergite is the largest segment but according to Weld (1952) the small anterior tergite of *Xenocynips* (Oberthuerellinae) is supposed to be the syntergite rather than the larger following segment. This genus was not available for dissection, and the exception remains open to question.

Sternites

Except in certain Anacharitinae, the terminal tergite and sternite are not directly apposed. The sternites are sclerotized, and are often folded along the midline, especially the terminal sternite, the hypopygium (Börner, 1919).

Spiracles

The plesiomorphic apocritan gaster (e.g. most Ichneumonidae) has spiracles on abdominal segments two to eight. The gaster of the Cynipoidea, Chalcidoidea, Mymaridae, Mymarommatidae, Evanioidea, Gasteruptidae, Pelecinidae (females; none in males), Rhopronidae, Megalyridae, Diapriidae, Monomachidae, Austronidae, Heloridae and Stephanidae have only one functional spiracle which is on abdominal segment eight (Gibson,

1986). The Vanhornidae, Scelionidae and Platygasteridae lack gastral spiracles (Nauman and Masner, 1985; Richards, 1977; Tonapi, 1958).

List of remaining gastral character-states

145 Gaster not compressed [0]. / A marked lateral compression of the gaster [1] is a characteristic of the Cynipoidea.

146 Gaster not blade-like [0]. / Gaster so strongly compressed, laterally, that it is almost flat and blade-like (Fig. 150) [1].

147 Without a ruff of hair on the second gastral tergite [0]. / With a ruff of hair on the second gastral tergite (Fig. 135) [1]. This ruff may be complete or consist of two tufts, but the extent of the hair and the number of tufts varies considerably.

148 The less derived Apocrita have abdominal tergite ten (gastral tergite 9) present [0]./ The cynipoid gaster consists of abdominal segments two to eight, the ninth (gastral 8) forms part of the genitalia and the tenth abdominal segment is lost (fused with the ninth abdominal segment) [1].

149.1, 149.2, 149.2 The proportions of the distal gastral tergites, in females, are affected by ovipositor shape. In lateral view, the largest gastral segment is the third, the fourth, or a syntergite of the anterior segments [0,0,0]. / In the apomorphic states gastral tergites four to six, of females, are expanded (in lateral view). [Scoring: - gastral tergite five the longest = 1,0,0; tergite six the longest = 1,1,0; tergite seven the longest = 1,1,1].

150 More than one gastral segment with spiracles [0]. / Only gastral segment seven (abdominal eight) with spiracles [1].

151 The size of the first two post-petiolar tergites is not so dependant on ovipositor characters as are the latter tergites. Second gastral segment the largest [0]. / Third gastral tergite longer (dorsally) than the second [1]. Where the the two tergites are fused

into a syntergite then the "-" score is applied.

152.1, 152.2 Tergites not fused [0]. / Syntergite, in the female, consisting of gastral segments two and three [1,0]. / Syntergite, in female, consisting of gastral segments two, three and four [1,1].

153 Anterior tergites not significantly smaller than the following tergites [0]. / Certain taxa have the two anterior tergites of the gaster much smaller than the other tergites [1].

154 Hypopygium not produced [0]. / Hypopygium produced into a narrow, and sometimes long, ventral spine [1].

155 The second gastral tergite (third abdominal) is normally a simple, curved plate [0]. / Second tergite saddle-shaped (Fig. 129) (Often inappropriately called liguliform) [1].

156 Nearly all male Cynipoidea have some slight sculpture and often some pubescence near the apex of the gaster [0]. / With a very slight upturning of the last tergite [1].

FEMALE GENITALIA

The section of this thesis which describes the cynipoid ovipositor and its functioning, has already been published (Fergusson, 1988) and therefore will not be repeated here. A copy of the paper is bound with this thesis.

Gastral shape and genitalia structure

One aspect that does need to be emphasized is the way that genitalia shape effects the proportions of the gastral segments (Fig. 154). In past classifications (e.g. Weld, 1952; Quinlan, 1979) considerable taxonomic weight has been given to the length and shape of female gastral tergites. It is now known (Fergusson, 1988) that these features all relate to genitalia structure and in particular to the three basic types of cynipoid genitalia.

Curved genitalia. In this plesiomorphic condition the gonapophyses are short and gonocoxite 9 is slightly curved (Fig. 144). This structure produces little or no distortion of the distal gastral segments and so the anterior tergites remain the largest. The Anacharitinae and Aspicerinae often have a very short "stabbing" ovipositor in which gonocoxite and tergite 9 are reflexed upwards to reduce the length of the genitalia (Fig. 146). In these species the last tergite and sternite tend to be apposed.

Elbowed genitalia. In many Eucoilidae and Figitidae the ovipositor is elongate, this is achieved by "elbowing" gonocoxite and tergite 9 (Fig. 145). In these species the frontoventral region of the gaster is expanded and, in lateral view, the dorsal margin of the gaster tends to be straight.

Looped ovipositor. The Ibaliidae and Liopteridae have a greatly expanded ovipositor which is accommodated within the gaster by being looped in a complete turn around the ovipositor base (Fig. 147). In these species the distal segments are expanded to accommodate the genitalia (Figs 152, 153).

List of female genitalia character-states

In the study of the cynipoid female genitalia (Fergusson, 1988) 16 new morphological characters were found, of these 14 characters were likely to be useful for establishing the phylogeny. The two characters involving the numbers of sensory spines on the horn and articulation of gonocoxite 9 were too variable to be of any value for further analysis. (Taxon 31 was not available for disection so it could not be fully scored.)

157 Gonapophyses not looped around the base [0]. / Ovipositor completely looped around the ovipositor--base (Fig. 147) [1].

158 Ovipositor not sharply elbowed [0]. / Ovipositor sharply angled or "elbowed" (Fig. 145) [1].

159 Remnant of tergite ten present [0]. / Tergite 10 totally lost (Figs 142, 143) [1].

160 Gonostylus approximately level [0]. / Gonostylus folded and downcurved [1].

161 Tergite 9 approximately level inside the gaster [0]. / Tergite 9 folded upward (dorsally) in the middle [1].

162 Cerci present [0]. / Cerci absent [1].

163 Bulbous articulation present [0]. / Bulbous articulation absent [1].

164 Bridge present [0]. / Bridge absent [1].

165 Gonapophysis 9 without cavity [0]. / Gonapophysis 9 with a cavity (c.f. Rogers, 1972) [1].

166 Gonapophysis 9 with teeth [0]. / Gonapophysis 9 without exposed serrations [1].

167 Gonapophysis 8 without teeth or with curved teeth [0]. / Apex of gonapophysis 8 with teeth, - one large tooth and often with a second more distal smaller tooth [1].

168 Gonostylus not separated from gonocoxite 9 by an indentation. [0]. / "Gonostylus" indicated by an indentation in gonocoxite 9 [1]. [Outgroup comparison shows that the presence of a distinct gonostylus, if it occurred in the Cynipoidea, would be primitive. The evidence indicates that the gonostylus is absent from the Cynipoidea but that a few taxa have developed a fold in gonocoxite nine.]

169 Apex of "gonostylus" rounded or slightly pointed, without membrane or notch [0]. / Apex of "gonostylus" with a notch covered by a pubescent membrane [1].

170 "Gonostylus" long and narrow [0]. / "Gonostylus" almost globular, apically [1].

Character	most Apocrita	Cynipoidea
166 gonapophysis 9	toothed	toothed to smooth
167 gonapophysis 8	smooth	smooth to toothed

Table 38. Polarity trends in the cynipoid ovipositor

The polarity of character 166 is opposite to that of character 167, thus the two halves of the ovipositor have evolved in opposing directions. Although this appears to

be odd it is consistent with what is known of hymenopterous ovipositors. In sawflies both gonapophyses are normally toothed, but in the Apocrita gonapophysis 9 normally has teeth while gonapophysis 8 is often smooth (Richards, 1977). The trends in the Cynipoidea are summarized in Table 38). Character 166 shows the general reduction trend common to many cynipoid features, while character 167 is a specialization.

FEMALE ACCESSORY GLANDS

Associated with the ovipositor are accessory glands which provide a lubricant for the passage of the egg along the lumen of the ovipositor (Robertson, 1968), and venoms that modify the ovipositional substrate (Sychevskaya, 1966). The accessory glands (Fig. 156) were found to be similar in all the Cynipoidea, and little different from those of the Chalcidoidea (Copland, 1976; Copland & King, 1971; 1972a; 1972b; 1972c; Copland, King & Hill, 1973; King & Copland, 1969; King & Ratcliffe, 1969).

In the Cynipoidea the ovaries form two hemispheres, one on each side of the gaster, but when teased out they are elongate and, especially in the larger species, pear-shaped. The generally stout oviducts fuse to form a slightly swollen common oviduct, closely connected to this is a small spermatheca and two pairs of collateral glands. The first pair of glands are long, coiled and blind ended tubes. The second (distal) pair of collateral glands are large sack-like spheres; internally each gland has a thick wall and a large central lumen. Near the top of the ovipositor are the ducts of two further glands; the proximal alkaline gland (or Dufour's gland) is inconspicuous, and the distal acid gland is tube-like with a large and obvious reservoir. The Charipidae also have a small accessory gland at the end of the acid gland reservoir and near to the oviduct.

A comparative study of the venom apparatus of the Braconidae by Edson & Vinson (1979) showed that the more advanced taxa had a thinner walled reservoir with fewer

muscles and the gland was reduced to only two filaments. This trend of simplification, especially to just one filament, has been continued in many of the microhymenoptera (Robertson, 1968).

The acid gland, and especially its reservoir, are much larger in the gall-causers than in the parasitoid Cynipoidea. There appears to be a positive correlation between gall complexity and the size of the reservoir. It is therefore speculated that in the Cynipidae the secretions of the acid gland are used in the galling process. Copland *et al* (1973) reported a similar enlarged acid gland and reservoir in gall-causing Chalcidoidea. The inquiline cynipidae also have a large reservoir.

The parasitoid *Figites* has been shown (James, 1928) to possess a potent secretion which is injected, at oviposition, into the host to render it quiescent. The entomophagous cynipoids are all endoparasitoids and so venoms are also used to combat the hosts immune defence system. For example the venom from the acid gland of female eucoilids contains lamellolysin which disrupts the hosts encapsulation system (see biology chapter) (Boulêtreau & Wajnberg, 1986; Rizki & Rizki, 1984; Streams & Greenberg, 1969; Walker, 1959; Weideli, 1967).

MALE GENITALIA

The general similarity and parallel reduction of features, both within the Cynipoidea and in the microhymenoptera, mean that the male genitalia are of very limited value for elucidating cynipoid phylogeny above the genus level.

The male repoductive organs are similar to those of most Hymenoptera and consist of paired testes, seminal vesicles and vas deferens. The latter join in a common ejaculatory duct, which opens into the aedeagus.

Cynipoid males (Figs 138-141) have slender, and rather short, parameres and a simple aedeagus. The digiti are small, slightly curved and armed with several teeth. The volsellae are partially fused with the parameres, and

the cuspal lobes are reduced or lost. The basal ring is present and has a gonocondyle. The ninth abdominal tergite and sternite are greatly reduced and are closely associated with the genital capsule.

Cuspis

Königsmann (1978) considered that the lack of a cuspis in both the Cynipoidea and Chalcidoidea indicated a sister-group relationship. However, this is a parallel reduction that also occurs in many Proctotrupoidea and some Braconidae (Gibson, 1986).

The presence of a cuspis has been reported for *Ibalia* (Ronquist & Nordlander, 1989) and *Synergus* spp. (Schulz, 1961). [The latter case was used by Vasey, 1975 to infer that the parasitoid cynipoids evolved from inquilines like *Synergus*]. This structure occurs in a wide range of cynipoids but, even after scanning electron microscopy, I remain unsure whether it is a remnant of the cuspis or perhaps a fold of the digitus / volsella. These delicate structures are not easy to differentiate and low power microscopy can be deceptive.

Tergite nine

The ninth abdominal tergite is very small and mostly membranous, only the two ventrolateral apices are chitinized and exposed beyond the eighth tergite. In most species a few hairs are present on these chitinized regions and thus, superficially, they look like cerci and it is likely that they perform a similar sensory function. However, only in the Cynipidae are the sensory regions raised from the remainder of tergite nine and thus appear to be true cerci.

Ninth sternite

Sternite nine is very small, lightly chitinized and entirely concealed by the preceding sternite. The main ~~chitinised~~ reflected element is a slender median apodeme that links the distal part of the sternite to the muscles of the basal ring.

Although a possible autapomorphy for the Cynipoidea

the reduction of sternite nine is likely to occur, as a parallelism, in some of the smaller Proctotrupoidea. In fact, a limited survey soon located a similar apodeme in *Aneurhynchus* (Diapriidae) and in *Piestopleura* (Platygasteridae). No doubt many other examples exist. Presumably the final stage in reduction would, be direct attachment of the basal muscles to sternite eight and the total loss of sternite nine, and this stage may also occur in some small Proctotrupoidea. There have been few extensive studies of chalcidoid male genitalia but the survey by Domenichini (1953) shows an external ninth sternite in a very wide range of taxa. Further, Dr Z. Boucek, who has a vast knowledge of the Chalcidoidea, has not seen this apodeme in any chalcidoid (*pers. comm.*) Therefore with regard to this single character the Chalcidoidea appear to be the least derived of the microhymenoptera.

Basal ring

The basal ring provides a further difference between the Cynipoidea and the Chalcidoidea. This structure is present in the less derived Hymenoptera, the Cynipoidea and most of the small Proctotrupoidea (Scelionidae - Rasnitsyn, 1980; Nixon, 1936: Diapriidae - Nixon, 1957; Snodgrass, 1941). However, the Chalcidoidea (including mymarids and mymarommatids) lack a complete basal ring (Gibson 1986); although a few males have a groove across the ventral surface of the phalobase which is likely to be a remnant of a basal ring (Snodgrass, 1941). Gibson (1986) noted the absence of a ring from the genitalia of *Atanycolus* (Braconidae) and *Aphanogmus* (Ceraphronidae), but my dissections and the work of Dessart (1963) show that the great majority of *Aphanogmus* species have a small basal ring. Nevertheless it is very likely that separate and independant loss of the basal ring has occurred more than once in the microhymenoptera.

Fusion of the volsellae and parameres.

According to Snodgrass (1941) some cynipoids (e.g. *Figites* and *Diplolepis*) have parameres that are entirely

confluent with the volsellae. Although, there is a strong tendency towards fusion, none of the examined taxa (under high magnification) exhibit total fusion. This trend is also found in the Diapriidae and Scelionidae (Proctotrupoidea) where a progressive union takes place between the aedeagus and the volsellae which is eventually accompanied by an elimination of the parameres. This converts the phallus into a single two-segmented shaft, composed of the basal ring and the united aedeago-volsellar shaft (Snodgrass, 1941).

Spines on the digitus

The digitus bears an apical row of short stout spines. Up to fourteen spines were seen in the Cynipoidea, the greatest number were in large taxa e.g. *Ibalia*, but usually only three to six spines are developed. The number of teeth can vary within a species, and even bilaterally (Wiebs-Rijks 1979). No useful characterization could be defined for this feature.

KARYOLOGY

Chromosome characters have been used in insect taxonomy (Fittakau et al. 1976; Petitpierre, 1981; Yoon et al. 1972) with some success. However, studies of the Hymenoptera have been limited to only a few species, and have concentrated on the determination of chromosome number. The Symphyta have a haploid number (n) of 6 to 26. The parasitica are more restricted, the available evidence shows that 10 is the groundplan number and this is found in the Ichneumonidae (Crozier, 1975) Scelionidae and Cynipoidea (Dodds, 1938). In the Chalcidoidea n = 5 (Hung, 1982), this suggests that the Chalcidoidea are the more derived of the microhymenoptera.

Dodds (1938) reported that cynipoid chromosomes had no characteristic morphological features and that their size gradation made them difficult to study. Certainly my attempts at preparation and interpretation were disappointing and indicated a haploid number between 8 and 11, a more precise figure could not be obtained.

IMMATURE STAGES

It was not possible to examine the immature stages of more than a few cynipoids and therefore this section is largely based on published information (much of it collated here for the first time).

THE EGG

The cynipod egg (Fig. 155) is an elongate oval, sometimes slightly curved (Shorthouse, 1973) or centrally constricted (James, 1928). The egg has a pedicel which is very slightly clavate at the apex (Jenni, 1951). As development proceeds the pedicel gradually degenerates and the egg increases in volume and becomes spherical. The eggs are small, generally 0.1-0.4mm long (excluding pedicel) by 0.02-0.2mm wide (James, 1928). However, the Charipinae have particularly small eggs, being as little as 0.01mm long by 0.006mm wide (Haviland, 1921a).

The Cynipidae have relatively yolky eggs and these could be lecithal and nourished by the female. However, parasitoid cynipoids (also some Braconidae and Platygasteridae) have very small alecithal eggs (Haviland, 1921a; 1921b) with little yolk (Iwata, 1958). Much of the egg nourishment is derived from the host (Oglobin, 1913) and this reduces the cost of infant mortality (Price, 1974).

The eggs are clear or white with a thin smooth chorion (Schröder, 1967). The trophic membrane is visible (Haviland, 1921a), but the abandoned trophamnion does not break up during the larval stages so it is considered not to aid larval nutrition (Chrystal, 1930).

Pedicel (= peduncle or stalk)

Pedicellate eggs are common in the parasitic Hymenoptera (Iwata, 1950) but the Cynipoidea appear to be unusual in having only this type of egg. Pedicellate eggs occur in the Ichneumonidae e.g. *Rhyssa* and *Ephialtes* but

in these genera the egg goes into the ovipositor pedicel first (Chrystal, 1930). In contrast the cynipoid pedicel is at the anterior pole and the eggs lie in the ovary with the pedicel pointing away from the oviduct (Sychevskaya, 1974). The micropyle is at the tip of the pedicel (Wishart & Monteith, 1954).

The pedicel of the gall-wasps, is very long, three to seven times the length of the egg body (Frühauf, 1924; Marsden-Jones, 1953); in *Ibalia*, it is up to four times the body length (Chrystal, 1930), but in most of the remaining taxa the pedicel is little longer than the egg body (Clausen, 1940). Although, in *Kleidotoma japonica* (Huzimatu, 1940) it is only half the body length, and in *Aegilips* the pedicel is almost absent (Lipkow, 1969).

Pedicel function

As the egg passes down the ovipositor it stretches and the contents are compressed and temporarily diverted into the pedicel, so that the egg "flows down itself". Thus the pedicel enables an egg that is much (up to ten times) broader than the ovipositor lumen to be oviposited (Frühauf, 1924). Once the egg is laid the process is reversed and the egg returns to its original shape. In many Cynipidae this second stage may be used to assist in egg entry; only part of the egg is inserted into the plant tissue and the contents then flow into the inserted portion (Shorthouse, 1973).

As the pedicel is closer to the surface, where the Oxygen tension is higher, than the rest of the egg, the pedicel may also have a respiratory function (Adler, 1881). Cameron (1890) suggested that the pedicel is longest in those gall-wasps that deposit their eggs most deeply; however, Haviland (1921a) thought this to be unlikely.

Egg numbers

All the Cynipidae that were dissected had over one hundred eggs, and up to 1000 eggs have been counted (Beijerinck, 1877; Schröder, 1967; Yasumatsu & Taketani,

1967). Clearly the gall-wasps have a very high reproductive potential. The parasitoid families have a much smaller number of eggs, generally between 20 and 200. Although Sychovskaya (1974) reported 360 in one eucoilid and *Ibalia* has about 600 eggs (Chrystal, 1930),

LARVAL INSTARS

Metamorphic Cynipids

Gallwasp larvae, because they live within a gall, have little need for highly developed sense organs, legs or a coloured integument. They develop through a series of essentially similar larval instars. The gall-wasp larva is a short and stout grub (Bouche, 1834), it is broadly rounded at both ends, more or less C-shaped, and the integument is smooth and devoid of setae. The head is followed by thirteen body segments (Evans 1965) although these are not easily discernible and sometimes only twelve are reported (Shorthouse, 1973). There are an estimated five larval instars (Evans, 1965; Shorthouse, 1973) and the fully grown larva has inconspicuous open spiracles on segments two to ten (Askew, 1984) or two to eleven (Evans, 1965).

In the first instar the mandibles are only just discernible, but in later stages they become conspicuous, strongly sclerotized and tridentate (Evans, 1965) or quadridentate (Askew, 1984). The larva feeds and grows but only defaecates just prior to pupation, thus avoiding unnecessary contamination of the larval cell. The larva does not make a partial exit from the gall, or accumulate frass in the gall as do some other gallicolous larvae (e.g. some Symphyta).

First larval instar of the hypermetamorphic cynipoids.

In the parasitoid taxa the successive instars are frequently dissimilar to the preceding instar. In particular, the first larval instar is different from subsequent forms. The first instar is probably the most

vulnerable larval stage, so it is understandable that it should be the most adaptive. This dramatic change in larval type is known as hypermetamorphosis.

Eucoilidae

The primary larva of the Eucoilidae (Fig. 157e) is of a unique eucoilidiform type which has a pair of long (depending on species) processes on the ventral region of each of the three thoracic segments. The larva also has a long tapering cauda, often as long as the body, which is curved ventrally and terminates in a sharp point. The segment immediately preceding the cauda bears a prominent fleshy projection on the median ventral line. The integument of the posterior abdominal segments and the cauda bears numerous setae, there are also a few setae on the thoracic processes (Molchanova, 1930). The mouth is nearly oval and is borne on a large rounded proboscis (Keilin & Baume-Pluvinel, 1913). Slender mandibles are present inside the proboscis (not seen by James, 1928), and in the middle of the oral cavity there is a small beak-like sclerite which can be moved up and down by means of a large muscle (Huzimatu, 1940). The structure of the mouth indicates that feeding is entirely haemophagous. It is difficult to discern the exact number of abdominal segments; James (1928) and Molchanova (1930) counted seven but presumed that the caudal appendage includes another two; Keilin & Baume-Pluvinel (1913) and Huzimatu (1940) found twelve segments behind the head. The anus opens dorsally at the base of the cauda, it is large, round and has a ring of long inwardly pointing chitinous spines that gives it the appearance of a spiracle.

On hatching the larva remains partially enclosed in the serous membrane, but the head and cauda are free. Later it disengages itself and straightens out.

Figitidae

The larva of *Figites anthomyiarum* is similar to the eucoilidiform type (Fig. 157c) and consists of a head plus twelve body segments (James, 1928). It has three pairs of short thoracic processes, the prothoracic appendages being

very short and only as long as wide. The cauda is short and at its base there is a ventral process. The mouth, like that in the eucoilidiform type, is adapted for haemophagy, it is borne on a proboscis and is surrounded by a number of papillae. A minute sclerite is discernible inside the oral region. The anus is not of the enlarged type found in the Eucoilidae or Charipidae.

Charipidae

Haviland (1921a; 1921b) described the larvae of several alloxystines. The first instar is remarkable in that it is armoured with dark segmental plates of chitin (Fig. 157b). The larva has a long cauda, but no thoracic appendages. The mouth is produced into a proboscis, within which lie two simple mandibles. The round anus is large and conspicuous, it is surrounded by a chitinous ring and bands of chitin radiate from the periphery to the centre.

Ibaliidae

The larva of *Ibalia* is polypodeiform, each of the twelve body segments bearing a pair of long fleshy processes ("pseudopodia") (Fig. 157a). The body is elongate (0.6 - 2.0mm by 0.1 - 0.3mm, Spradbery, 1970) and the segments taper rapidly from the fifth onwards, the larva ends in a prominent cauda (Chrystal, 1930). The labral region forms a broad arch over the mouth cavity and extends over the conspicuous scythe-like mandibles. The salivary glands are prominent. The large sac-like mesenteron occupies most of the body and the proctodaeum has a large lumen. The anus is dorsal but has no conspicuous ring round it. The two malpighian tubules are short and narrow and the nerve cord is visible almost to the cauda (Chrystal, 1930).

Respiration: larval processes and the rectum

Early cynipoid instars are apneustic and respiration is cutaneous. It is possible that the cauda (a feature present in the first instars of all parasitoid cynipoids), the thoracic processes (found in Eucoilidae and Figitidae)

and the "pseudopodia" of *Ibalia*, all assist in cutaneous respiration by increasing the surface area of the larva.

Proctodaeal respiration has been postulated for some braconids (Thorpe, 1932) and it is possible that rectal respiration occurs in many parasitoid cynipoids. In particular alloxystines are likely to respire rectally because their ~~chitinous~~ cuticle must hinder cutaneous respiration. In the first instars of all the parasitoid cynipoids the rectal lumen is large and yet the proctodaeum is not connected to the mesenteron. Also in alloxystines and eucoilids the anus is enlarged and described as "spiracle-like". Further, the anus and the rectal lumen diminish in size as the tracheal system develops and the alimentary tract unites. The large proctodaeum (together with the malphigian tubules) of the parasitic cynipoids may, additionally be a secretory area, producing chemicals important for control of the endoenvironment. For example *Pimpla* and *Itoplectis* (Ichneumonidae) larvae have a large rectum and produce a secretion from the malpighian tubules which has antibiotic properties (Führer & Willers, 1986). The maintenance of asepsis is important because digestion of the host will liberate the bacteria from the host's alimentary tract.

James (1928), Kopelman & Chabora (1984) and Sychevskaya (1974) postulated that both the cauda and the thoracic processes assist the larva to escape from the egg membrane and possibly help during fighting between different species. Movement of the processes was observed (James, 1928) but did not result in locomotion, so a locomotary function has not been established.

Later larval instars of the hypermetamorphic cynipoids

Cynipoid second instars show some of the diversity found in the first instars, but subsequent stages difffer little betweeen taxa. In mature larvae the cauda and the ventral processes are lost and the anus moves to a terminal position. During the later stages the proctodaeum is reduced, haemophagy and rectal respiration cease and a

tracheal system develops.

Figitidae - Anacharitinae

The second instar of *Aegilips*, has a head, followed by thirteen body segments and a short stubby cauda (Lipkow, 1969). The body is without projections and the mandibles are dagger-like. Handlirsch (1886) and Miller & Lambdin (1985) have described the fifth instar of *Anacharis* (Fig. 157h). This larva is unusual because it has a pair of fleshy pointed projections, set with hairs, on the dorsal surface of segments two to nine (one to nine, in Miller & Lambdin, 1985), segments ten to twelve either have very small projections or are unarmed. [The presence of dorsal projections in *Anacharis* but not in *Aegilips*, (Fig. 157i) a very similar genus, is probably usable as a generic level character.] The larva is 3mm long, the anterior end is reflexed dorsally, and on the side of each thoracic segment there is a large rounded tubercle. The mandibles are strong and triangular, with a long apical tooth and two shorter basal teeth. In both genera the spiracles are located near the anterior edge of body segments two to ten.

Figitidae - Figitinae

The second instar is polypodeiform (Fig. 157d), there are a pair of ventral processes (decreasing posteriorly) on each of the first ten body segments (James, 1928). A cauda is present and held almost at right angles to the rest of the body and the integument is smooth and devoid of hairs or setae. The larva has eleven (James, 1928), or more likely twelve body segments, as in the final instar. There is a chitinous endoskeleton inside the head and the mouth is suctorial. About the mouth are a pair of long sensory papillae and the head has a conspicuous ventral sensory organ consisting of a chitinous projection surmounted with a transparent tip. In following instars the pseudopodia and cauda shorten and disappear. A tracheal system develops which consists of two lateral trunks each of which gives off dorsal and ventral segmental branches. Pairs of spiracles are present on

segments two to ten.

Eucoilidae

Because of the similarity of the later, hymenopteriform, larval stages. The exact number of eucoilid instars is uncertain, but in most cases is likely to be five (James, 1928; Molchanova, 1930; Sychevskaya, 1974; Huzimatu, 1940). Some authors (Wishart & Monteith, 1954; Nappi and Streams, 1970) noted only four and from their descriptions it appears that these authors have missed an instar near to the third instar.

The second instar may be polypodeiform (Fig. 157f), the first ten body segments having a pair of ventral processes, but in other eucoilids the second instar lacks abdominal processes. The cauda is reduced compared with the previous eucoiliform stage. The anus is small, transversely oval, and not furnished with spines. James (1928) counted eleven body segments but other authors found ten (Eskafi & Legner, 1974 a&b), twelve or thirteen (Wishart & Monteith, 1954).

The rounded proboscis and beak-like sclerite of the first instar are lost. The mouth is still suctorial, the maxillae and labium being fused (Huzimatu, 1940). The head segment now contains a conspicuous endoskeleton. James (1928) did not see the mandibles, but other authors (Huzimatu, 1940) found distinct mandibles. According to Eskafi & Legner (1974a; 1974b) the mandibles are rod-like and capable of a coordinated back and forth movement that assists in the suctorial function of the mouth.

In the remaining stages tail reduction continues and the larva becomes sac-like and hymenopteriform (Fig. 157g). Size (0.9 to 4.4mm by 0.9 to 2.8.mm) depends on the size of the host (Sychevskaya, 1974). The mandibles are adapted to feeding on hard tissues and the mesenteron now occupies almost the entire body cavity. The fifth (mature) stage larva is large 2.5 - 5mm, by 1.0-2.0mm. The tracheal system is now extensive and there are pairs of spiracles on the second and third thoracic segments and on each of the first seven adbominal segments (Wishart & Monteith, 1954).

Charipidae

The second instar resembles the first except that the chitinous plates are absent, and the thoracic segments now have a pair of ventral processes. The mouthparts are less produced and furnished with two large, simple mandibles. Below the mouth is a pair of ventrolateral lobes, surmounted by conspicuous sensory papillae. The salivary glands are two straight tubes which lie on either side of the mesenteron. The two Malpighian tubules are very short. The large proctodaeum communicates with the exterior via a wide anus.

In the third and later stages the larva increases in size, the tail becomes reduced and the thoracic processes disappear. As the cauda is reduced the anus becomes terminal, and proportionally smaller. The mandibles become conspicuous. The proctodaeum includes a typhlosole-like outgrowth into the lumen.

The tracheal system consists of two main lateral trunks which are united by an anterior and a posterior commissure. Dorsal and ventral lateral branches are given off in each segment. There are six pairs of open spiracles. The first is between segments one and two and the remainder on segments three, four, five, seven and nine. Rarely there may be an additional pair on on segment eight (Haviland, 1921a).

Ibaliidae

The "pseudopodia" of the first instar have now completely disappeared. The body is more cylindrical, although arched dorsally, and the cuticle is traversed by minute furrows. The mandibles are still large. The third instar is hymenopteriform, and measures approximately 4 - 6mm by 0.7-1.4mm (Chrystal, 1930). The cauda is now small and the mandibles are straight. There are spiracles on the second and third thoracic segments and the anal opening is transverse and terminal.

The final instar does not feed; it measures approximately 10 mm by 4mm. The head and the last segment are both retracted within the rest of the body.

Longitudinal pleural folds are very marked on abdominal segments one to six. There are ten pairs of well-developed pleural swellings on body segments two to eleven. These swellings are oval and thickly beset with minute spines (Chrystal, 1930). There are ten pairs of spiracles (on thoracic segments two and three and abdominal segments one to eight), the last spiracle is vestigial and the spiracles on the first abdominal segment much reduced (Spradbery, 1970). *Ibalia* is the only cynipoid larva known to to have spiracular valves (Spradbery, 1970). As it is considerably larger than other larvae studied, this and also the presence of vestigial tenth spiracle on abdominal segment 8 could be allometric features.

James / Berlese theory

James (1928) compared cynipoid larval types to certain putative developmental phases which in other insects are passed through in the egg (Berlese, 1913). These stages are protopod (appendages on thorax), polypod (appendages on thorax and abdomen) and oligopod (thoracic appendages retained but abdominal appendages resorbed [thus showing homoplasy with the protopod stage]). James opined that protopod first instars would be followed by polypod second instars. However, Huzimatu (1940) and Eskafi & Legner (1974a; 1974b) have shown that this is not necessarily true in the Eucoilidae. Further the larvae of the Alloxystinae do not conform to this simplistic theory.

Summary

The number of instars reported in the literature is often only an estimate but most cynipoids appear to have five, although the Ibaliidae and Charipidae have four. Many cynipoids have 12 body segments. However, in most cynipoids, the number of body segments needs confirmation; many authors have admitted difficulty in ascertaining a figure. Most Cynipoidea have nine spiracles (although ten have been recorded in the Cynipidae - Evans, 1965). The Charipidae have six, rarely seven, spiracles and therfore show the most derived condition. A similar reduction

occurs in other microhymenoptera (Parker & Thompson, 1925; Stehr, 1987). The second instars of hypermetamorphic cynipoids are all caudate. The Figitidae and Eucoilidae have a weakly polypodeiform second instar, but some taxa go straight to the hymenopteriform stage. The Charipidae have a modified form of this type with only thoracic processes and the chitinous armour of the first instar has been lost. The Ibaliidae is unique in having a polypodeiform first instar, all other parasitoid Cynipoidea have evolved a specialised first instar and deferred the (reduced) polypodeiform type to the second instar.

In cynipoids strong scythe-like mandibles only occur in *Ibalia*. In other Hymenoptera the mandibulate larval type occurs in both endoparasites and ectoparasites. It is a common larval type in the Ichneumonoidea and Proctotrupoidea and frequently occurs where early instars fight other parasitoids.

PUPAL STAGE

There may be a short prepupal resting stage (Eskafi & Legner, 1974a&b; Matejko & Sullivan, 1980; Shorthouse, 1973).

Although a cocoon, even if slight, is of general occurence in the Hymenoptera, the Cynipoidea and most Chalcidoidea do not have one and the pupae are exarate (Schröder, 1967). In the parasitoid forms pupation is inside the host's cocoon (Anacharitinae), puparium (Eucoilidae, and most Figitidae), aphid mummy (Charipidae) or in the tunnel of the host (Ibaliidae). Gall-wasps, in their sheltered environment have no need of a cocoon. In *Andricus quercuscalicis* (Cynipidae) there is a cocoon-like structure present, but this appears to be of plant origin and may represent a detached sclerenchyma layer.

The pupal stage can last a few days in summer generations but in overwintering generations diapause occurs in the mature larva or pupal state (Haviland,

1920a) and then it may take up to 300 days, in some Eucoilidae (Sychevskaya, 1974).

Finally the cynipoid becomes hardened and darkened and then eats its way out of the host or gall (Connold, 1901).

As the information, given above, on the immature stages is based on isolated examples mostly taken from the literature, it would be inappropriate to subject the data to LeQuesne analysis.

Conclusion

It was shown (Chapter 3) that the existing classification of the Cynipoidea is based on too few characters. In chapter 4 an extensive study of cynipoid morphology has produced 234 characters (including multistates); this is a 450% increase in the number of characters over that of the established classification. It is believed that this character bank will be sufficiently comprehensive, both in number and range of characters, to provide the basis for an increased resolution of cynipoid phylogeny.

In the next chapter this morphological data will be scored and analysed.

Fig. 130. *Andricus* X60. mesoscutum & scutellum.

Fig. 131. *Sarothrus* X260. Trochantellus.

Fig. 132. *Liopteron* X60. Lateral view of petiole.

Fig. 133. *Melanips* X193. Petiole, semiventral view.

Fig. 134. *Alloxysta* X450. Petiole, lateral view.

Fig. 135. *Trybliographa* X150. Petiole, lateral view.

Fig. 136. *Aspicera* X125.
Petiole (frontoventral).

Fig. 137. *Figites* X246.
Petiole (frontoventral).

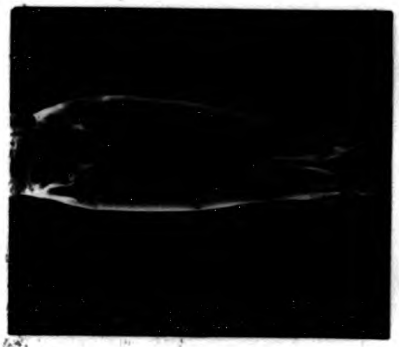


Fig. 138. *Ibalia* X69.
Male genitalia.

Fig. 139. *Anacharis* X225.
Apex of male genitalia.

Fig. 140. *Ibalia* X193.
Digiti of male genitalia.

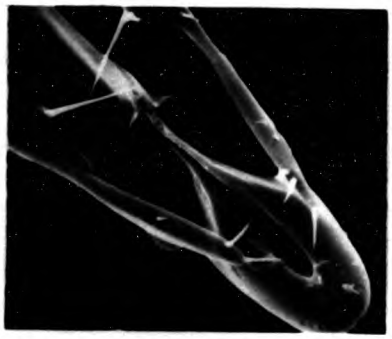


Fig. 141. *Figites* X700.
Apex of male genitalia.

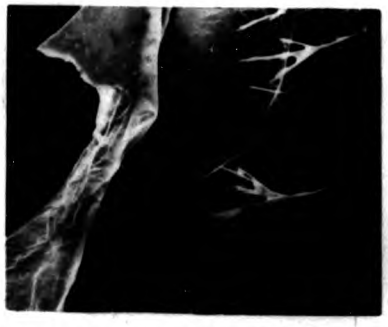


Fig. 142. *Biorhiza* X250. Tergite 9.

Fig. 143. *Isocolus* X200. Tergite 9.

Fig. 144. *Lonchidia* X170. Female genitalia.

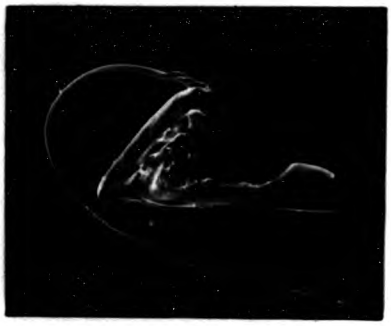


Fig. 145. *Figites* X44. Female genitalia.

Fig. 146. *Paraspicera* X120. Female genitalia.

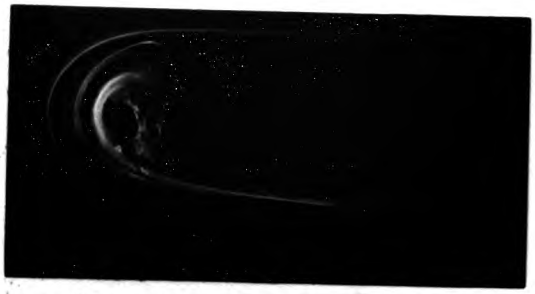


Fig. 147. *Ibalia* X15. Female genitalia.

Fig. 148. *Aspicera* X14.

Fig. 149. *Pycnostigmus* X11.

Fig. 150. *Ibalia* X7.

Fig. 151. *Diastrophus* X14.

Fig. 152. *Ibalia* (X6) antennating bark near the oviposition hole of its siricid host (Photo: Spradbery).

Fig. 153. *Ibalia* (X6), hypopygium lowered, ovipositing into a siricid larva in the tree (Photo: Spradbery).

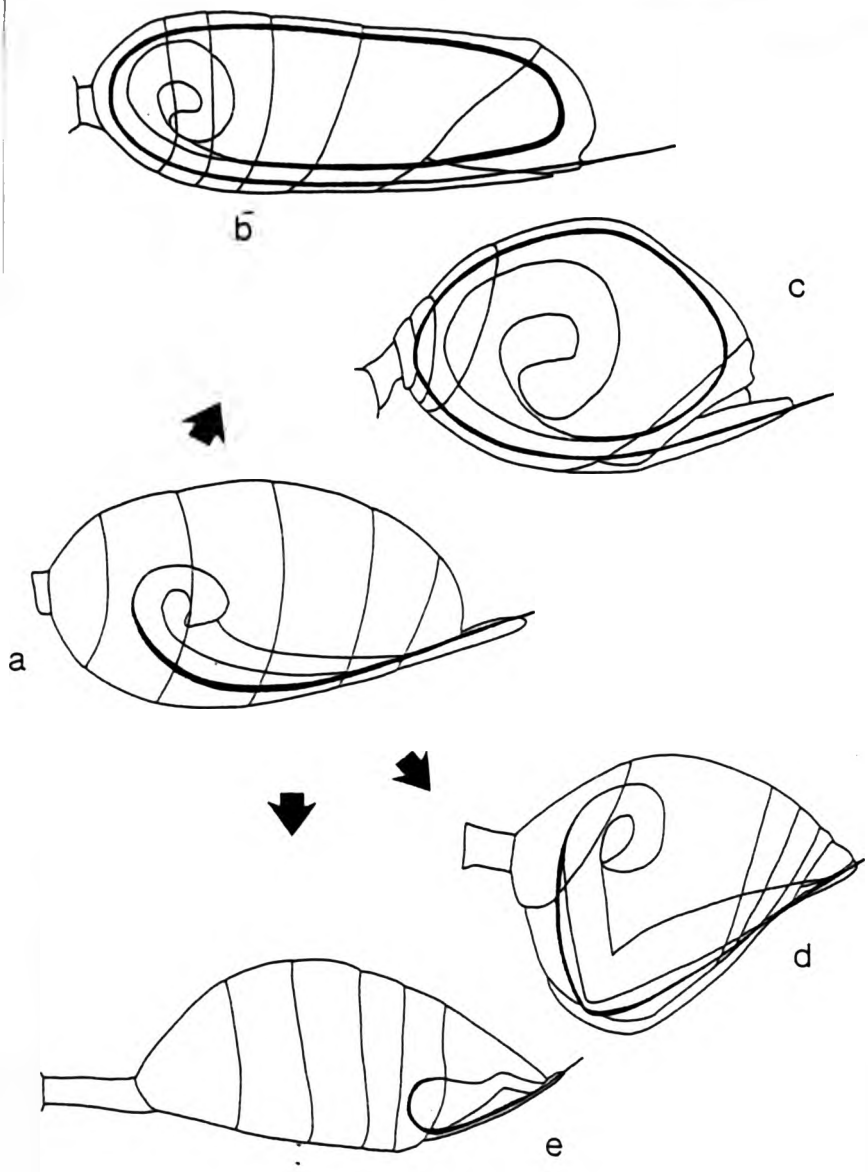
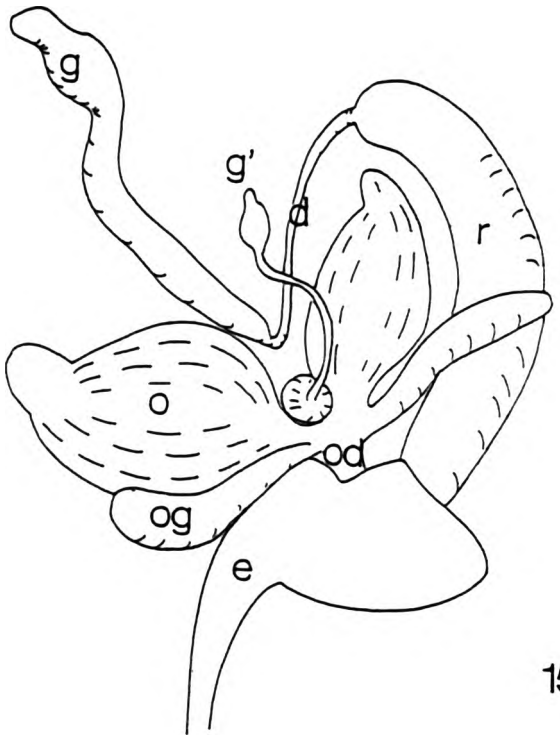


Figure 154. Ovipositor types and gastral shape. Groundplan, curved type (a) and three specializations - the looped ovipositor of *Ibalia* (b) and Liopteridae (e.g. *Oberthuerella*- c); elbowed type (e.g. *Figites* - d) and the short stabbing ovipositor (e.g. *Anacharis* - e).

155



156

Figures 155-156. 155, egg of *Ibalia*. 156, accessory glands of the female genitalia (Eucoilidae). Acid gland (g) duct (d) and reservoir (r); alkaline gland (g'); ovary (o); common oviduct (od); collateral or oviducal gland (og); and the base of the external genitalia (e). [After Rizki & Rizki (1984) and dissections.]

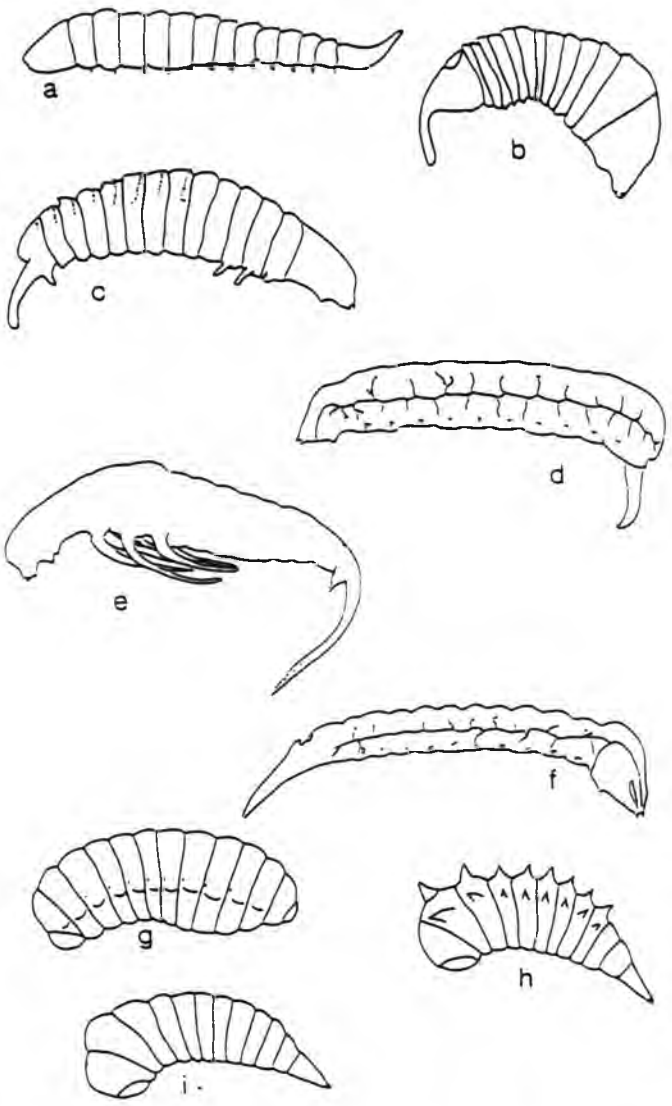
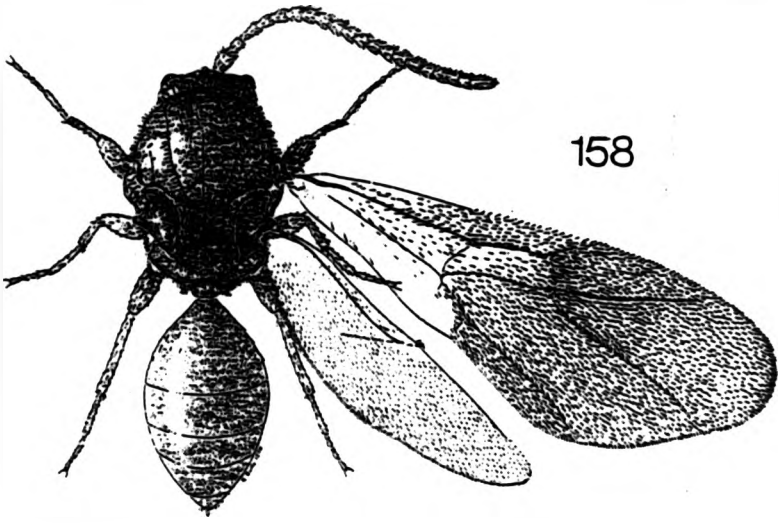
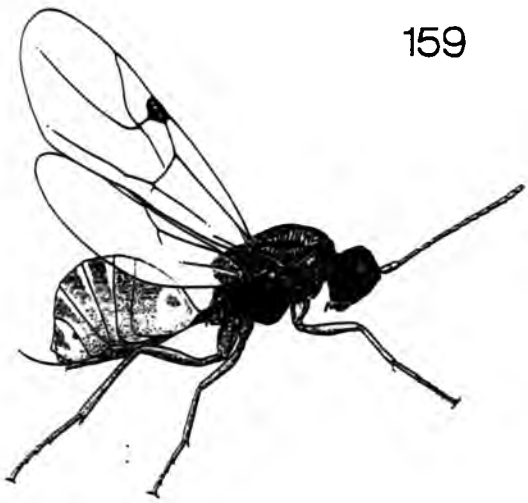


Figure 157. Cynipoid larvae. *Ibalia* first instar (a); *Phaenoglyphis* first instar (b); *Figites* first (c) and second (d) instars; *Trybliographa* first instar (e); *Kleidotoma* second instar (f); *Cothonaspis* late instar (g); *Anacharis* (h) and *Aegilips* (i) late instars [After: Chrystal, 1930; Haviland, 1921a; James, 1928; Molchanova, 1930 & Lipkow, 1969].





Figures 158-159. 158, *Himalocynips* [After Yoshimoto, 1970]. 159, *Austrocynips* [After Riek, 1971].

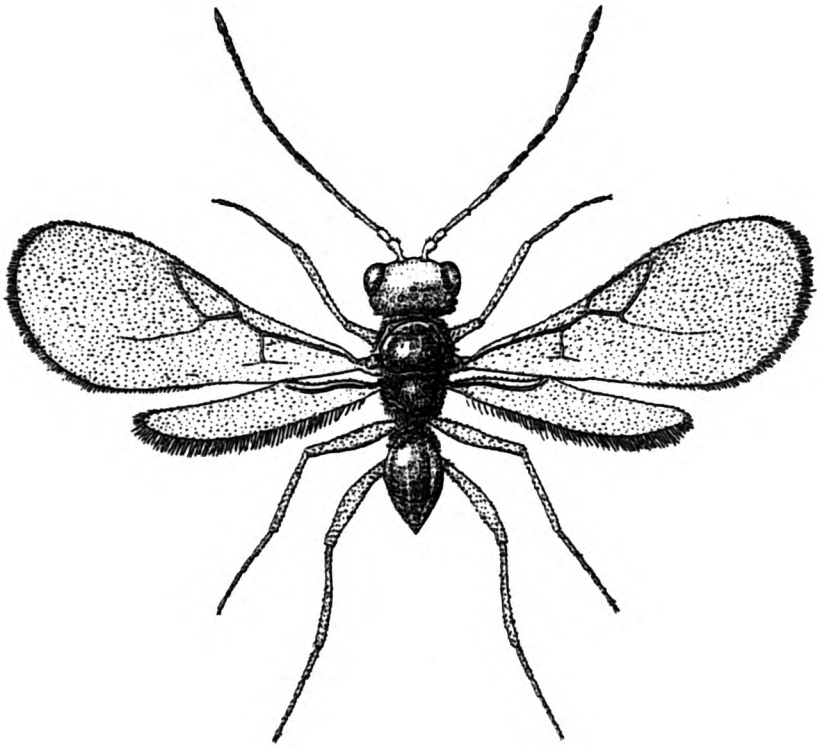


Figure 160. Alloxysta in dorsal view [Fergusson, 1986].

CHAPTER 5: PHYLOGENY OF THE CYNIPOIDEA

CLADISTIC ANALYSIS OF CYNIPOID MORPHOLOGY

The 31 exemplar taxa (see Table 1) were compared against the morphological character-states listed in Chapter 4, and scores (0, 1, - or V) were awarded. The resultant master matrix (Appendix 2) consists of 234 binary characters (including multistates) and therefore 7254 (234 X 31) cells. It is believed that this matrix is one of the largest, on any group of the parasitic Hymenoptera, ever to have been subjected to cladistic analysis. A LeQuesne compatibility analysis was completed which took over three days of continuous computer time to run the boildown to a compatible clique. The initial matrix of incompatiblities and the LeQesne ratios of character-state randomness are shown in Appendix 2. The analysis found a total of 4022 incompatibilities compared

1	2.1	4	5	7	8	13	14	5.1
22	24.2	28.4	29.2	30.2	31.2	31.4	38.6	39.3
40	41	42	43	46	47	48	52	59
60	61.1	62.2	63	68	70	71	72	76
78.2	79.1	79.2	80	87	97.1	100.1	100.2	101
104	105.1	105.2	106	108	109.1	109.3	111.1	113.1
113.2	115	122	125	126.2	127	137	138.2	138.3
40	141	142.1	143	145	146	148	150	169
170	23	27	130	133	163	164	134	78.3
75	109.4	39.2	25	69	118	131.2	62.4	73.2
66	77	61.2	124	136	51.2	2.3	9.2	26.3
34	98	102	114	53.1	64	65	57	155
73.3	31.3	144	153	62.3	159	128	18	44
129	51.1	165	142.2	2.2	26.2	111.3	24.3	6
19	156	26.1	24.1	149.1	111.2	55	83	157
168	58	131.1	117.2	49	160	161	99	16.2
152.2	50	3	78.1	167	117.1	54	35	53.2
15.2	20	91	92	21	90.1	74	109.2	147
37	152.1	89	11	45	162	90.2	149.2	96.2
86	88	139	85	32.3	16.1	81.2	158	32.1
62.1	84	96.1	38.4	154	94	56	166	95
93	67	10	112.1	12	82.2	116	103	135
31.1	32.2	132.1	32.4	126.1	15.3	138.1	28.1	17
110	132.2	151	119	28.2	73.1	112.2	132.3	38.3
9.1	82.1	36	149.3	30.1	38.5	120	29.1	28.3
38.2	33	39.1	81.1	121	123	38.1	97.2	107

Table 39. Initial ranking of characters according to LeQuesne ratio. (The first 81 characters show no incompatibilities.)

Incompatibilities found	expected	ratio	character deleted	Incompatibilities found	expected	ratio	character deleted
4022	7735.04	0.52	107	3955	7687.45	0.51	97.2
3907	7645.08	0.51	38.1	3830	7574.65	0.51	123
3741	7486.62	0.5	121	3614	7357.07	0.49	81.1
3550	7289.10	0.49	38.2	3430	7159.12	0.48	33
3310	7027.82	0.47	39.1	3230	6939.88	0.47	120
3116	6810.44	0.46	29.1	3022	6702.5	0.45	30.1
2935	6602.02	0.44	38.5	2867	6522.51	0.44	36
2761	6398.03	0.43	28.3	2729	6359.54	0.43	9.1
2628	6235.78	0.42	38.3	2533	6118.31	0.41	149.3
2499	6075.83	0.41	73.1	2404	5955.28	0.40	112.2
2343	5878.09	0.40	151	2262	5774.43	0.39	132.3
2171	5657.3	0.38	119	2083	5542.03	0.38	132.2
1998	5428.66	0.37	82.1	1956	5372.79	0.36	138.1
1879	5268.14	0.36	132.1	1810	5173.02	0.35	135
1730	5062.37	0.34	32.2	1665	4971.06	0.33	31.1
1591	4867.4	0.33	32.4	1551	4811.65	0.32	28.2
1513	4758.36	0.32	15.3	1446	4663.85	0.31	110
1389	4580.88	0.30	17	1345	4515.13	0.30	103
1275	4409.67	0.29	28.1	1233	4345.57	0.28	82.2
1167	4242.07	0.28	166	1118	4161.92	0.27	56
1062	4066.49	0.26	126.1	1042	4032.37	0.26	38.4
994	3949.08	0.25	67	945	3862.34	0.24	116
911	3801.04	0.24	62.1	893	3767.89	0.24	95
850	3688.15	0.23	93	815	3621.12	0.23	96.1
772	3536.25	0.22	32.3	739	3470.21	0.21	12
706	3404.42	0.21	10	679	3347.91	0.2	112.1
664	3316.14	0.2	32.1	627	3236.72	0.19	94
596	3167.91	0.19	81.2	560	3085.22	0.18	86
529	3012.68	0.18	84	502	2946.37	0.17	90.2
468	2861.53	0.16	85	447	2808.72	0.16	37
423	2748.78	0.15	96.2	392	2666.10	0.15	16.1
364	2591.09	0.14	99	354	2563.50	0.14	88
327	2488.95	0.13	158	304	2423.30	0.13	45
281	2351.52	0.12	15.2	266	2303.90	0.12	154
259	2281.33	0.11	147	237	2210.39	0.11	139
220	2149.36	0.10	109.2	210	2112.39	0.10	74
200	2075.52	0.10	11	182	2006.34	0.09	149.2
169	1957.25	0.09	152.1	156	1908.41	0.08	162
143	1854.42	0.08	89	130	1795.59	0.07	21
116	1727.97	0.07	152.2	108	1687.30	0.06	92
96	1623.56	0.06	91	84	1560.82	0.05	142.2
77	1522.58	0.05	161	70	1483.95	0.05	160
63	1445.76	0.04	90.1	53	1391.26	0.04	55
45	1345.73	0.03	35	39	1310.06	0.03	16.2
31	1252.66	0.02	83	26	1209.62	0.02	26.2
21	1165.58	0.02	2.2	16	1121.42	0.01	64
14	1103.70	0.01	73.3	12	1086.08	0.01	31.3
10	1067.82	0.01	20	6	1017.77	0.01	111.2
4	974.73	0.00	117.1	2	929.13	0.00	49
0	881.96	0.00					

Table 40. The character-state deletions, made by the LEQU program, which lead to the formation of the clique.

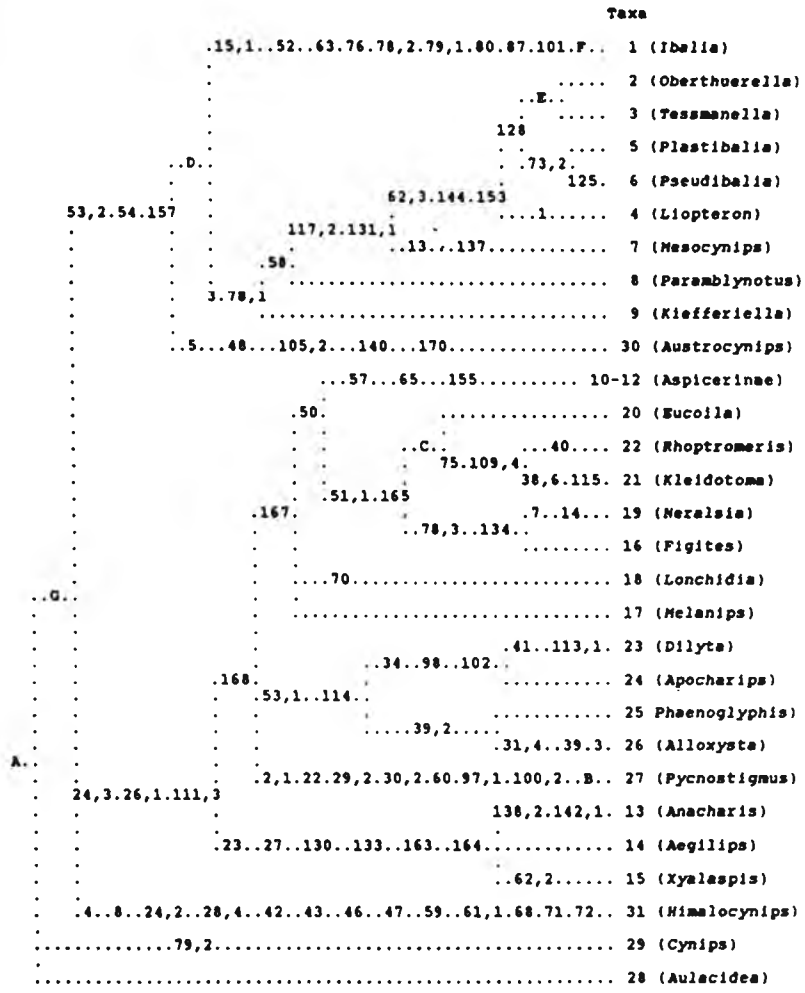


Figure 161. Clique cladogram of the morphological characters for the exemplar cynipoid taxa. [Note: multistates are normally shown with a decimal point but for clarity this has been replaced by a comma in the trees. Code: A =100.1 104 145 148 150; B = 105.1 108 109.1 113.2 141 169; C = 2.3 9.2 26.3 51.2 61.2 66 77 124 136; D = 6 19 24.1 149.1 156; E = 25 62.4 69 118 131.2; F = 109.3 111.1 122 126.2 127 138.3 143 146 & G = 18 44 129 159]

with the 7735.04 expected on the null hypothesis. This represents an overall LeQuesne coefficient of 52%, which is a "good" figure indicating a moderately well-ordered data-set. However, this value for the coefficient also shows the presence of a considerable amount of homoplasy - a common state of affairs in the parasitoid Hymenoptera. Analyses of other apocritan groups e.g. Ichneumonidae have produced much higher randomness ratios e.g. 70% (Eggleton, 1989) to over 80% (Gauld, 1985).

Initially the LEQU program ranked the characters in the order shown in Table 39. The stepwise deletion of the worst character, the "boil-down", led to the removal of 99 binary characters (Table 40) to give a clique of 135 binary characters (almost 60%).

The resultant clique cladogram was plotted (Fig. 161). The program indicated that two of the clique characters (80 & 111.1) should have their polarities reversed. Both of these wing venation characters were only plesiomorphic in *Ibalia* and their reversal to become autapomorphies for this genus seems feasible. The cladogram is rooted with five characters (31.2 and 106 are ostensible symplesiomorphies) - triangular marginal cell (100.1), true pterostigma absent (104), lateral compression of gaster (145), number of tergites, i.e. tergite 10 lost, (148) and gastral spiracles limited to tergite 8 (150). These five features are all classic characters of the superfamily. All these synapomorphies are discussed in the section on cynipoid holophyly.

LAST TEN CHARACTERS DELETED

An investigation of the last few characters deleted during the compatibility analysis can give an insight into the more likely of the alternative trees. The position of the analysis at ten deletions before clique establishment is shown in figure 162. The first deletion to be reconsidered is that of character 83. This character was rejected because it is incompatible with five characters (3, 58, 78.1, 117.2, & 131.1) and it also shows polar

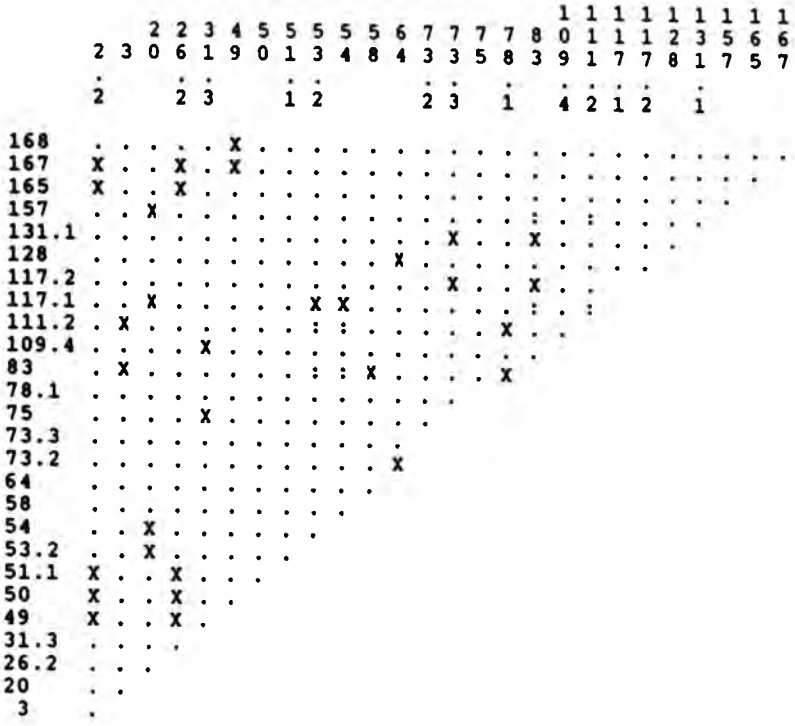


Figure 162. The last 39 character incompatibilities.

incompatibilities with characters 53.2, 54, 117.1 and 157. Character 83 links all the taxa except 1-6, if the polarity was reversed then *Ibalia* (taxon 1) would be linked to the Oberthuerellinae (taxa 2 & 3) and Liopterinae (taxa 4-6) but not to the Mesocynipinae. Such an arrangement would be unacceptable, *Ibalia* is a most distinct genus with many unique features. Both the polarity reversal and parallelisms need to be postulated in order to accommodate this character into the clique.

The next character deleted was 26.2, this is incompatible with characters 49, 50, 51.1, 165 and 167. The same incompatibilities are shared by character 2.2, the subsequent deletion. Both 26.2 and 2.2 link the Charipidae with the Eucoilidae but oppose the close link with the genera near *Figites* (Fig. 163). These two characters are morphological features (palp reduction and

hypostomal stucture) that cannot be dismissed, so it is most likely that these are parallelisms, and in particular character 2.2 is probably a feature of small cynipoids.

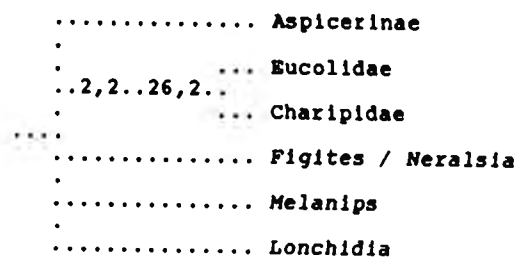


Figure 163. Tree with character 2.2 and 26.2 included.

Character 64 (scutellar curvature) was deleted next. This feature links *Liopteron* with *Plastibalia* and is opposed by two apparently "good" characters 73.2 (anterior scutellar flange) and 128 (length of last tarsal segment) (Fig. 164), so it is possible that character 64 could show reversals in *Pseudibalia* and the Oberthuerellinae. Both *Plastibalia* and *Liopteron* were highly marked by the LEQUC program (see Appendix 2) for character 64 - scoring 11 marks. A reversal could also be postulated for *Liopteron* with respect to character 128 (Fig. 165). However, character 73.2 does not occur in *Liopteron* and a reversal

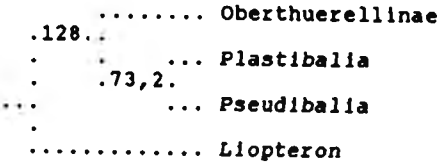


Figure 164. Part of the clique cladogram (simplified).

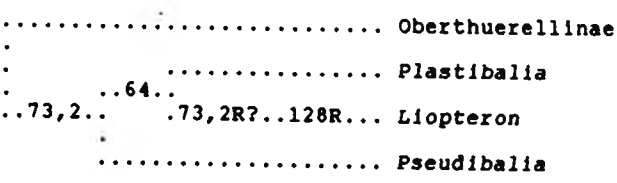


Figure 165. Alternative arrangement including character 64

seems unlikely, thus the Liopteridae must remain paraphyletic.

The incompatibilities still remaining are shown in figure 166. Character 73.3 (wide mesepisternal suture) was deleted because it is incompatible with 117.2 & 131.1. It links *Pseudibalia* and *Mesocynips* and this is probably a parallelism. A direct link between these two genera is rejected as unlikely because the total morphology of *Pseudibalia* has much more in common with *Plastibalia* than it has with *Mesocynips*. Both *Mesocynips* and *Pseudibalia* were highly marked by LEQUC for character 73.3 - each scoring 12 marks.

```
                                                1 1 1 1 1 1 1
      2 3 4 5 5 7 7 7 0 1 1 1 3 5 6
  3 0 1 9 3 4 3 5 8 9 1 7 7 1 7 7
      .   .   .   .   .   .   .   .
      3   2   3   1 4 2 1 2 1

168   . . . X . . . . . . . . . . . .
167   . . . X . . . . . . . . . . . .
157   . X . . . . . . . . : . . . .
131.1 . . . . . . X . . . . . . .
117.2 . . . . . . X . . . . . .
117.1 . X . . X X . . . . :
111.2 X . . . : : . . X .
109.4 . . X . . . . . .
 78.1 . . . . . . . .
 75   . . X . . . .
 73.3 . . . . . .
 54   . X . . .
 53.2 . X . .
 49   . . .
 31.3 . .
 20   .
```

Figure 166. Incompatibilities after character 64 deleted.

The next character deleted was 31.3 (position of emargination on male antenna) this is a highly homoplasious character amongst the Cynipoidea and is of little value above the generic level.

Character 20 was removed because of its incompatibity with characters 53.2, 54, 117.1 and 157. *Austrocynips*, however, has piercing-cutting mandibles and this is inconsistent with its position in a group adapted for a wood associated biology. The alternative position of

Austrocynips (near to *Himalocynips*) will be considered later.

Character 111.2 (loss of second submarginal cell) is shared by taxa 9-31 and is an allometric feature, in no sensible classification would *Kiefferiella* be linked with the figitids. However, if the large cynipoids are secondarily large then this could be an apomorphy for all of the Ibaliidae / Liopteridae except *Kiefferiella*. The character is rejected.

The penultimate character deleted was 117.1. This wing colour feature is not supported by a study of extralimital taxa, and it was highly scored (33 marks) by the LEQUC program. This character is easily rejected.

The final character deleted was 49, it is incompatible with characters 168 and 167. Character 49 was only lightly marked by the LEQUC program and both 167 and 168 had worse scores (see Appendix 2). Character 49 (complete lateral carinae) links taxa 10-16 + 19-22. As mentioned above it is hard to support the exclusion of the Anacharitinae from the 168 clade (Fig. 167). It seems most likely that the anacharitines have secondarily lost the gonostylus (character 168) in the same way as they lost the bridge (164) and bulbous articulation (163). The incompatibility between characters 49 and 167 (teeth on gonapophysis 8) is a more complex problem. Here also a secondary loss in the Anacharitinae is likely. It is also

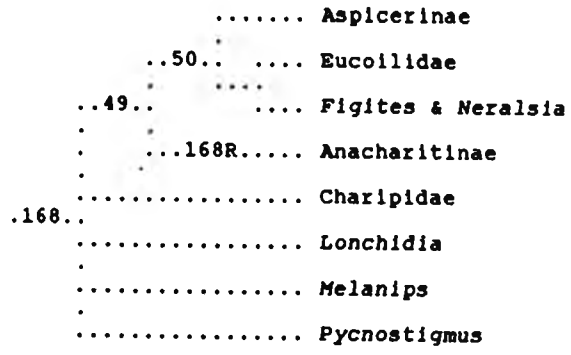


Figure 167. Tree with 168 reversed for the Anacharitinae.

possible that these ovipositor teeth have been secondarily lost by the Charipidae and *Pycnostigmus* (taxon 27), perhaps such teeth are not required in order to puncture the soft cuticle of their hosts. So *Pycnostigmus* and the Charipidae could be outside or inside the 167 grouping (Fig. 168). [See the study of extralimital taxa for a further consideration of this problem.]

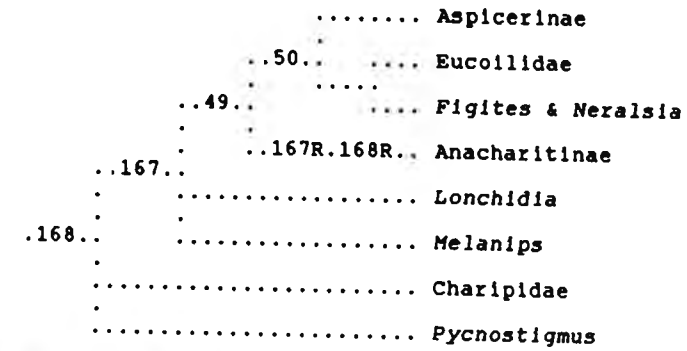


Figure 168. Possible amendments to the cynipoid tree. A study of the last 10 deletions indicates that characters 167 and 168 could show reversals in the Anacharitinae.

To summarize; nine of the last ten deletions are accepted, but the last deletion is not. There is good morphological evidence that the Anacharitinae show a secondary reduction of the female genitalia and therefore this reduction is also likely to include reversals of characters 167 and 168 (Fig. 168).

THE CLIQUE CLADOGRAM

The cladogram divides the Cynipoidea into taxa 28, 29 (the Cynipidae) and the remaining taxa, this latter unit is subdivided into the ibaliid group, the figitid group and the Himalocynipinae. These groupings are discussed below.

The Cynipidae

The clique cladogram places the Cynipidae as the least derived of all the Cynipoidea and, partly because of their primitive nature, no morphological autapomorphy exists for them. They are the paraphyletic sister-group of all other Cynipoidea.

The remaining cynipoids

The remaining cynipoids are united by four synapomorphies. Character 18 (mandibles with three teeth) is a particularly poor character, and one which does not stand up well against a study of extralimital taxa (i.e. cynipoids outside the 31 exemplar taxa). For example some species of *Melanips*, (i.e. *M. microcera*) can have mandibles quite like those of the Cynipidae. Character 129 (claw with basal lobe) would appear to be a similarly poor character that is unlikely to survive detailed examination of a large number of extralimital taxa. Character 44 (lateral ridges on the pronotum) is present in taxa 1-27, 30 & 31 and absent from the exemplar Cynipidae (both gall-wasps), but this feature is present in the inquiline Cynipidae. The distribution of this character causes one to wonder if these ridges could have been present in the ancestor, lost in the Cynipidae (as an apomorphy), and regained in the inquilines as a apomorphic reversal! Character 159 (remnant of tergite 10 lost - Figs 142, 143) appears to be a good character, but the apomorphic state is a loss-condition, so parallel losses are quite feasible. A second possibility is that character 159 underwent a reversion to the primitive state in the gallwasps, thus with the polarity reversed this character would become an autapomorphy for the Cynipidae.

Thus the primary node of the clique cladogram is rather dubious and in need of further consideration (see improvements section, below).

The ibaliid group

The clique cladogram shows that the ibaliid group is holophyletic and well defined by three characters - 53.2

(heavy sculpture), 54 (transverse mesoscutal ridges) and 157 (looped ovipositor). These features form part of a fundamental suite of adaptive characters (see Chapter 6). Size is also a factor here, because the majority of this lineage are large and strong (well muscled - Fig. 89) cynipoids.

Austrocynips has previously (Quinlan, 1979) been placed in the Cynipidae and indeed it has a generalized "primitive" morphology like that of *Himalocynips*. However *Austrocynips* has the looped ovipositor and strong sculpture of the ibaliid group. *Austrocynips* is characterized by several autapomorphies - facial striae (5), pronotal hump (48), pseudopterostigma (105.2), flange on the petiole (140), and gonostylus almost globular (170). The possession of a pseudopterostigma is a most interesting feature, the cladogram position of *Austrocynips* shows that this structure could be a primitive feature. However, it is unlike the linear pterostigma found in the oldest fossil cynipoid (see section on fossils) so it is likely to be a secondary feature analogous (and not homologous) to the secondary pseudopterostigma of *Pycnostigmus*. There is no doubt that *Austrocynips* is a very specialized (and extremly rare) relict genus having little in common with other genera in the ibaliid group. As the cladogram shows, its morphology is perhaps closest to that of *Ibalia*.

The remaining taxa are grouped together by five characters - 6 (central ridge on face), 19 (blunt mandibles), 24.1 (hypostoma in a cavity), 149.1 (expansion of gastral segments) and 156 (uplifting of the last tergite).

Ibalia is characterized by the following unique features. Characters 15.1 (occiput with striae), 52 (precoxal tooth present), 63 (scutellar ridge), 122 (single mid-tibial spur), 126,2 (spur present on the second tarsal segment) and 127 (long hind basitarsus) form a suite of related adaptations (see later). Characters 146 (blade like gaster), 143 (petiole condyle incised) and probably 138.3 (petiole smooth) relate to oviposition.

Characters 76 (open metathoracic spiracle) and 79.1 (shape of the flap to the propodeal spiracle) and wing characters 80, 87, 101, 109.3 and 111.1 are all allometric features relating to the large size of this insect.

The remaining taxa constitute the Liopteridae, and are defined by two characters - a notched clypeus (character 3) and an obscured metapleural trough (78.1). The latter is not a strong morphological feature and the former is only slightly better. Also at least one extralimital liopterid (*Paramblynotus yangambicola*) is very *Ibalia*-like so this "family" construction looks weak. Within the 3 / 78.1 clade, the smaller taxa are separated plesiomorphically; *Kiefferiella* is removed first, and the remaining taxa are defined by character 58 (mesoscutal flanges). *Paramblynotus* (Mesocynipinae) is plesiomorphic to the Oberthuerellinae plus Liopterinae plus *Mesocynips*, which are grouped together by characters 117.2 (wing with colour around veins) and 131,1 (claws bifid). Although 117.2 is a weak feature, character 131.1 appears to be sound. *Mesocynips* is removed from the remaining taxa by two specializations - characters 13 (OOL/APL ratio) and 137 (hump on petiole). Thus the cladogram does not support the "Mesocynipinae" as a subfamily.

The Liopterinae is linked with the Oberthuerellinae by characters 62.3 (scutellar spines) 144 (tangential petiole) and 153 (small anterior tergites). These all seem particularly "good" characters and this node is considered to be well founded.

Liopteron has normal tarsomeres and so is excluded from the 128 clade, within which the other two liopterine genera (*Plastibalia* and *Pseudibalia*) are linked by character 73.2 (mesepisternal suture high).

The Oberthuerellinae is exceptionally well-characterized by five characters - 25 (condyles expanded), 62.4 (scutellar spines), 69 (striations between the scutellar foveae), 118 (tooth on hind femur), 131.2 (claws bifid).

The clique cladogram supports only one subfamily of

the established liopterid classification, the Oberthuerellinae. The Liopterinae and Mesocynipinae are paraphyletic assemblages. As the older classifications were not based on autapomorphies it is not surprising that they have failed to be supported by analysis.

Himalocynips

Himalocynips is intermediate in size between the ibaliid and figitid taxa and like *Austrocynips* it is a rare, very specialized (Yoshimoto, 1970) and yet primitive taxon. *Himalocynips* was heavily marked by the LEQUC program (see Apendix 2). This genus has 13 unique features and the anatomical distribution of these autapomorphies is rather interesting. Two are facial characters (4 & 8), one is hypostomal (24.2), three are antennal characters (28.4, 42, 43), two pronotal characters (46 & 47) and five are scutellar / axillar characters (59, 61.1, 68, 71, 72). The bias to, and the function of the thoracic modifications are a puzzle that is unlikely to be solved until the biology of this species is known.

The figitid group

The remaining taxa consist of the smaller parasitoids. This group is probably the most phylogeneticaly interesting and the centre of most controversy as to exact relationships. The reconstruction postulated in the clique cladogram is largely new and, in my opinion, reasonable (improvements will be suggested below).

The figitid taxa are defined by three characters - 24.3 26.1 & 111.3. The latter (position of Rs & M) is an established wing venation character that, although very difficult to use, remains as a feature of major importance. Fortunately it is now supported by two new hypostomal characters (24.3 and 26.1).

Within the figitid group the Anacharitinae is holophyletic and, in the initial cladogram (Fig. 161) the sister-group of the remaining taxa. This is a totally new

arrangement. The holophyly of the Anacharitinae is demonstrated by six characters. The lower two mandibular teeth are spine-like (23), and the claws have a fine basal spine (130). The ovipositor of the Anacharitinae is secondarily reduced - (bulbous articulation and bridge absent; characters 163, 164) and the petiole is specialized - character 133. The function of character 27 (hypostomal carina curved) is not understood. Additional petiole characters (138,2 142,1) that may be associated with oviposition are found in *Anacharis*.

The remaining taxa are united by character 168 (gonostylus indicated) but it seems likely (see above) that the secondary reduction of the anacharitine genitalia could also include secondary loss of the gonostylus (Fig. 168).

Pycnostigmus is very specialized having 13 autapomorphies: 2.1 (palp formula), 22 (scythe-like lower mandibles), 29.2 (number of segments in antenna of male), 30.2 (number of segments by which antenna of male exceeds that of female), 60 (reduced axillae), 141 (short petiole with two indentations), 169 (gonostylus with notch) plus six characters that relate to the very reduced and specialized venation (97.1, 100.2, 105.1, 108, 109.1, 113.2).

The residual taxa are divided into two lineages; the Charipidae, and the remaining Figitidae plus the Eucoilidae. The Charipidae is a holophyletic group defined by the traditional feature - their smooth thorax (53.1), and a new character (114 - the extent of the wing covered by veins). Both these characters reflect the very small size of these species, and therefore this group still lacks a nonallometric autapomorphy, other than its hyperparasitic lifeway.

The cladogram supports the two subfamilies of the Charipidae. Character 39.2 (extent of antennal sensilla), which "defines" the Alloxystinae, is a poor character and is unlikely to apply to all alloxystine species. The Charipinae is supported by three characters - 34 (fusion of terminal segments), 98 (curvature of Rs) and 102 (small

marginal cell). The last two are size related characters are not especially significant. Character 34 is the traditional delimiting feature for this subfamily, it appears to be a good character. The validity of these two subfamilies is open to question, and they will be discussed further (below).

The 167 (gonostylus 8 with teeth) group has *Lonchidia* and *Melanips* as primitive genera. [The Anacharitinae could also be included here (Fig. 168) - see above.] The remaining taxa are united by character 50 (pronotal disjunction). Within the 50 clade the Aspicerinae form a well-defined holophyletic group (57 - shape of mesonotal line, 65 - scutellar carinae & 155 - shape of second gastral tergite).

The 51.1 group unites the Eucoilidae with the genera near *Figites*. It has already been noted (Fergusson, 1986) that the genera near *Figites* are well removed from other Figitinae genera near *Melanips*. This 51.1 grouping is remarkable because it means that the Figitidae, as currently defined, can no longer be supported as a holophyletic group. The most derived Figitidae are now the sister-group of the Eucoilidae. The characters that define the 51.1 clade (51.1 - pronotal plate part raised & 165 - gonostylus with cavity) appear to be particularly strong morphological characters. The genera near *Figites* are defined by 78.3 (metapleural trough) and 134 (petiole with notch).

The Eucoilidae is strongly supported by nine characters - 2.3 (palp formula), 9.2 (malar sulcus), 26.3 (hypostomal fusion), 51.2 (pronotal plate raised), 61.2 (axillar / scutellum junction), 66 (tear-shaped plate), 77 (ventral cavity of metapleuron), 124 (fine teeth to the strigil) and 136 (underside of petiole). This is the best defined of all the groups within the superfamily. Two of the eucoilid genera are united by size-related characters (75 and 109.4) which exclude the larger genus *Eucoila*.

SUBSET ANALYSIS

An analysis of the subsets of the clique cladogram was undertaken in an attempt to enhance the phylogenetic reconstruction (as was done with the Weld and Quinlan data - see chapter 3). There are two major subsets to the clique cladogram the 53.2 clade and the 24.3 clade, both were analysed.

The 53.2 clade

This clade includes taxa 1 to 9 and taxon 30. Analysis of this subset found 884 incompatibilities against 1191.35 expected on the null hypothesis; a LeQuesne coefficient of 74%. The boil-down deleted 41 characters in the order shown in Table 41. The resultant tree was constructed (Fig. 169) but the analysis of the

45	149.3	38.2	30.1	29.1	123	126.1
81.1	112.2	110	121	112.1	85	96.1
149.2	132.3	132.2	135	132.1	94	82.2
120	73.1	95	84	109.2	74	9.1
78.1	3	93	82.1	58	36	131.1
117.2	142.2	89	90.1	111.2	64	

Table 41. Deleted characters in 53.2 clade.

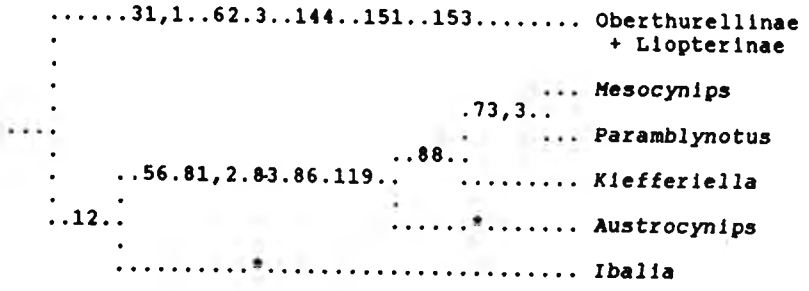


Figure 169. Subset analysis tree for the 53.2 clade.
* = many autapomorphies & polarity changes.

53.2 subset was of little value. The 62.3 clade, consisting of taxa 2-6 was supported in the same format as in the clique cladogram. The remaining taxa - Mescynipinae + *Ibalia* + *Austrocynips* are in a new configuration defined only by character 12 (presence of scrobes). Scrobes help to protect the antennae from damage during emergence from the host's tunnel in the tree. This is an adaptive feature that could have arisen independently in these taxa, or could have been secondarily lost in the 62.3 clade.

The Mesocynipinae are linked to *Austrocynips* by characters 56, 81.2, 83, 86 and 119. These are allometric reduction states relating to the small size of the mesocynipines compared to the larger Liopteridae and *Ibalia*. *Austrocynips* shares these characters because it is of a similar size and has a relatively simple morphology (even though it is a very specialized taxon).

In summary, the 62.3 subgroup is sound, but the Mesocynipinae are weakly resolved and their placement is easily upset by extraneous factors. A further investigation of the Mesocynipinae is required (see extralimital taxa).

The 24.3 clade

Analysis of the figitid subset produced very little additional information. Several extant groupings were further supported by additional characters. The *Neralsia* / *Figites* grouping was supported by character 17, the Aspicerinae by characters 21 and 56, the Anacharitinae by character 164, the Charipinae by 139, and the 51.1 clade by character 166. One difference was that character 132.1 links *Aspicera* with *Omalaspis*; this is because the third aspicerine genus (*Callaspidia*) lacks the complete petiolar collar of the other two taxa. However, this character was rejected in the full analysis because the *Aspicera*-type of petiole also occurs in some Liopteridae. Therefore the subset analysis of the master data-set provided very little additional information. This is interpreted as a sign of the robustness of the large master matrix.

LOSS CHARACTERS

As well as the presence of unique structures, hypothesised apomorphic character-states can also be reductions, fusions or losses. These latter types of character are generally considered (Hecht, 1976) to be the least reliable of all transformations, because it cannot be determined whether common absence is the result of single or multiple loss.

Most groups of Parasitica exhibit parallel trends of diminutions leading to reduction or loss of sculpture, wing venation and other structures. The cynipoid data-set includes many loss characters and now that a cladogram has been produced it is instructive to assess how much reliance has been placed on these loss characters.

The clique cladogram was redrawn with all the loss characters removed. The reconstruction is very robust and the resultant tree (Fig. 170) is little changed from the cladogram. Only one subfamily, the Alloxystinae is no longer supported.

POSSIBLE IMPROVEMENTS TO THE TREE

Many of the master matrix characters were reinvestigated to see if some of the homoplasy could be explained and the resolution improved. In most cases this involved the postulation of multiple parallelisms. However, in a few cases the required assumptions were more limited and therefore could be considered here.

Character 12 (presence of scrobes) links taxa 1,7,8, & 9. The functional nature of this feature, mentioned in the subset analysis, would make it probable that this was an early acquisition of the "wood-associated" taxa which was lost in the more derived examples.

Character 16.1 (head sculpture) links taxa 1-6, 8, 9, 30 & 31. It is quite reasonable to assume an apomorphic loss in taxon 7 (*Mesocynips*). This would then point to *Himalocynips* being in the ibaliid group. As stated

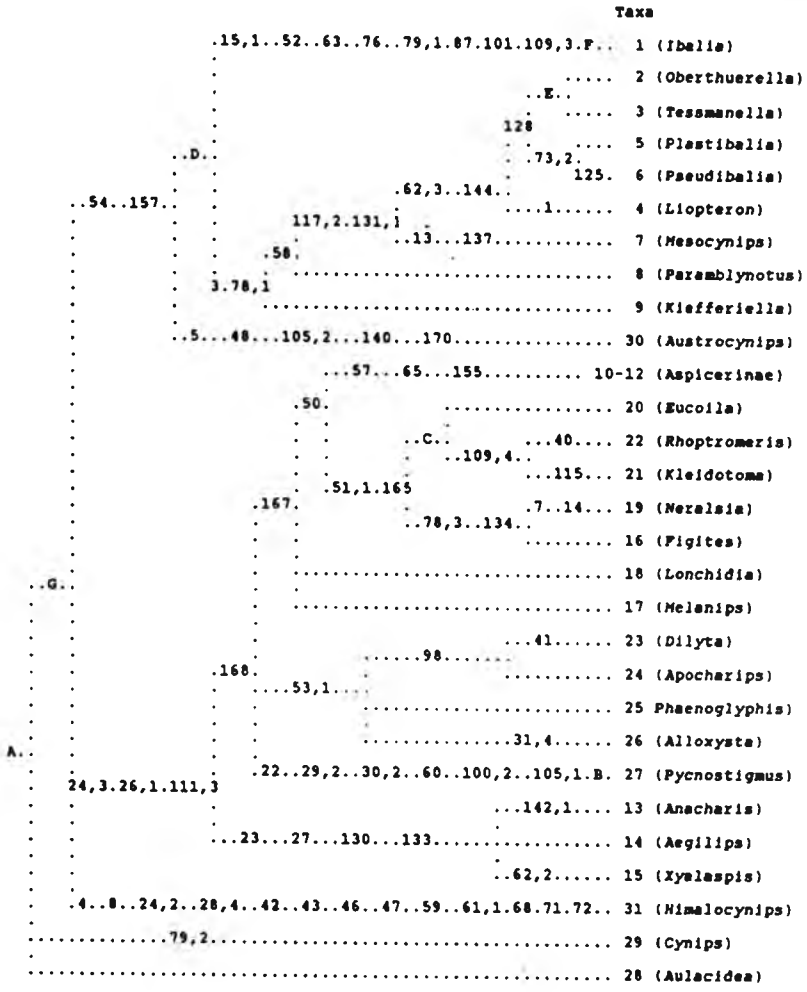


Figure 170. Tree without reduction characters.
[A = 100.1 145; B = 108 109.1 113.2 141 169; C = 61.2 66 77 124 136; D = 6 19 24.1 149.1 156; E = 25 62.4 69 118 131.2; F = 111.1 126.2 127 138.3 143 146 & G = 18 44 129.]

elsewhere there is a case for this, but on present evidence it cannot be accepted.

Character 20 (piercing mandibles) did not survive analysis and that may have been due to an incorrect polarity determination. If reversed, character 20 would be apomorphic for taxa 1-9 and the Cynipidae. This would reflect a two-fold origin of blunt mandibles developed, in both lineages, for chewing an exit from plant tissue.

Character 35 (flattened antennae) was apomorphic for taxa 4-7. A secondary loss of this feature can be postulated for the Oberthuerellinae, then this character would further support the 117.2 clade.

Character 45 (pronotal crest present) the weak state of this character in *Oberthuerella* (scored as V) is most likely to be a secondary reduction.

Character 49 will be considered in the section on extralimital taxa.

Character 58 could be used to separate *Kiefferiella* from its close relative *Paramblynotus*. However, extra material of *Kiefferiella* borrowed from American institutions included a second, and undescribed, species which bridges the gap between this genus and *Paramblynotus*. Therefore the two genera will be synonymized, the name *Kiefferiella* having priority. A careful re-examination of character 58 (mesoscutal flanges) has revealed that *Kiefferiella rugosa* does have a trace of this flange and so this score must be revised.

Characters 117.2 and 131.1 divide the Mesocynipini into two sections. These characters were re-examined to see if this division was valid. Character 117.2 (wing colour) is a poor feature which, although prevalent in the Liopteridae, occurs sporadically across the Cynipoidea. Amongst the mesocynipines it occurs in species of *Mesocynips* *Paraibalia*, *Dallatorrella* and *Kiefferiella* (= *Paramblynotus*). Unlike wing colour, claw structure (131.1) appears to be a useful character that separates *Kiefferiella*, *Paraibalia*, and *Paraegilips* which have simple claws, from a second group of mesocynipines (*Dallatorrella* and *Mesocynips*) which have bifid claws.

Characters 160 and 161 (gonostylus and tergite 9 folded) link *Aspicera*, but not other aspicerines, with the anacharitines. It is postulated (see chapter 4) that these genital modifications relate to oviposition over very short distances. In the anacharitines this means oviposition into neuropterous larvae. If *Aspicera* is the least derived taxon within the 50 clade then this same short stabbing action may have been transferred to the initial parasitism of dipterous larvae.

Characters 157 to 170 were not recorded for *Himalocynips* because only two specimens of this genus are known. As complete dissection of the genitalia was not acceptable, "-" scores were used in the analysis. However, the phylogenetic reconstruction of the Cynipoidea has established the great importance of these features. So a careful but limited investigation of the female genitalia of the paratype was undertaken. The ovipositor is not looped (character 157) or elbowed (158). The gonostylus (160) and the ninth tergite (161) are not downcurved. Gonapophysis 9 is without a cavity (165) and has apical teeth (166). The apex of gonapophysis 8 is without teeth (167), the gonostylus is not indicated (168) and there is no apical notch (169) or swelling (170). All these scores are plesiomorphic. The scores for characters 163 and 164 are not known and further dissection was not risked, but these scores are probably also plesiomorphic. The only apomorphic scores are for characters 159 and 162. Like all non-Cynipidae the small remnant of tergite ten is not present (159). The cerci are well-developed (162), this character also occurs in several other cynipoids and was deleted during analysis. The above scores confirm that *Himalocynips* belongs in the position indicated by the compatibility analysis.

Size

The modification of gastral segments in many taxa means that body length is only a crude measurement of size. (c.f. head measurements in Chapter 4). However, it was thought worthwhile to measure the overall body length

of a small sample of the study taxa (Table 42). As the males of several taxa are not known, this sex was not measured.

Size could be used as a character (Weld, 1952) to divide the cynipoids into the small (Charipidae and Eucoilidae), medium and large (Ibaliidae and Liopteridae) taxa. However, the regions of of separation are muddled by exceptions. For example "large" could be over 6mm, but there is a *Synergus* (Cynipidae) over 7mm long (Shorthouse & Ritchie (1987).

As a character, size is unworkable; this is unfortunate because the underlying size trends are pervasive, even if not expressable as characters.

Ibalia	14.0	*Oberthuerella*	10.6	*Tessmanella*	8.2
Liopteron	9.6	*Plastibalia*	11.6	*Pseudibalia*	9.0
Mesocynips	8.5	*Paramblynotus*	6.5	*Kiefferiella*	4.5
Aspicera	3.0	*Callaspidia*	4.1	*Omalaspis*	3.2
Anacharis	3.5	*Aegilips*	2.8	*Xylaspis*	2.7
Figites	2.2	*Melanips*	3.8	*Lonchidia*	2.0
Neralsia	3.0	*Eucoila*	3.9	*Kleidotoma*	1.4
Rhoptromeris	1.6	*Dilyta*	1.2	*Apocharips*	1.4
Phanoglyphis	1.3	*Alloxysta*	1.3	*Pycnostigmus*	3.2
Aulacidia	2.2	*Cynips*	2.3	*Austrocynips*	4.0
Himalocynips	5.5				

Table 42. Lengths, in mm, of female cynipoids (n = < 4).

O'NOLAN CHARACTER WEIGHTING ANALYSIS

The master data matrix was subjected to the O'Nolan character weighting program. The matrix was so large that the O'Nolan program took four days to complete. The assigned weights are shown in Table 43. The resultant cladogram is identical to that of the LEQU analysis. The last seven characters, just outside the clique, are listed in table 44; the same characters, in a slightly different sequence were the last seven deletions in the LEQU analysis. The O'NOLAN results strongly support the results of the LEQU analysis and this independent support increases the confidence that can be placed in the phylogenetic reconstruction.

char.	weight	char.	weight	char.	weight	char.	weight
2.2	0.86	2.3	1.00	3	1.00	6	1.00
9.1	0.06	9.2	1.00	10	0.70	11	0.68
12	0.51	15.2	0.70	15.3	0.22	16.1	0.44
16.2	0.67	17	0.51	18	1.00	19	1.00
20	0.89	21	0.60	23	1.00	24.1	1.00
24.3	1.00	25	1.00	26.1	0.10	26.2	0.86
26.3	1.00	27	1.00	28.1	0.54	28.2	0.76
28.3	0.88	29.1	0.14	30.1	0.20	31.1	0.19
31.3	0.94	32.1	0.40	32.2	0.21	32.3	0.41
32.4	0.41	33	0.02	34	1.00	35	0.80
36	0.02	37	0.54	38.1	0.30	38.2	0.05
38.3	0.06	38.4	0.30	38.5	0.26	39.1	0.22
39.2	1.00	44	1.00	45	0.55	49	0.94
50	1.00	51.1	1.00	51.2	1.00	53.1	1.00
53.2	1.00	54	1.00	55	0.76	56	0.27
57	1.00	58	1.00	61.2	1.00	62.1	0.77
62.3	1.00	62.4	1.00	64	0.94	65	1.00
66	1.00	67	0.31	69	1.00	73.1	0.06
73.2	1.00	73.3	0.94	74	0.74	75	1.00
77	1.00	78.1	1.00	78.3	1.00	81.1	0.38
81.2	0.38	82.1	0.49	82.2	0.18	83	0.86
84	0.43	85	0.59	86	0.48	88	0.46
89	0.61	90.1	0.66	90.2	0.39	91	0.64
92	0.64	93	0.46	94	0.39	95	0.35
96.1	0.35	96.2	0.40	97.2	0.57	98	1.00
99	0.79	102	1.00	103	0.13	107	0.31
109.2	0.74	109.4	1.00	110	0.29	111.2	0.94
111.3	1.00	112.1	0.67	112.2	0.33	114	1.00
116	0.53	117.1	0.94	117.2	1.00	118	1.00
119	0.10	120	0.01	121	0.36	123	0.21
124	1.00	126.1	0.64	128	1.00	129	1.00
130	1.00	131.1	1.00	131.2	1.00	132.1	0.22
132.2	0.12	132.3	0.06	133	1.00	134	1.00
135	0.16	136	1.00	138.1	0.16	139	0.71
142.2	0.83	144	1.00	147	0.59	149.1	1.00
149.2	0.73	149.3	0.82	151	0.20	152.1	0.65
152.2	0.80	153	1.00	154	0.84	155	1.00
156	1.00	157	1.00	158	0.56	159	1.00
160	0.84	161	0.84	162	0.74	163	1.00
164	1.00	165	1.00	166	0.36	167	1.00
168	1.00						

Table 43. O'Nolan weights for the master matrix. Initial all-plesiomorphic scores and initial singleton apomorphies are omitted, for brevity. (char = character number.)

	LEQU ANALYSIS	O'NOLAN ANALYSIS	
deletion	character	character	weight
7	64	20	0.89
6	73.3	64	0.94
5	31.3	73.3	0.94
4	20	31.3	0.94
3	111.2	111.2	0.94
2	117.1	117.1	0.94
1	49	49	0.94

Table 44. The last 7 LEQU & O'Nolan character deletions.

PARSIMONY ANALYSIS

Apart from compatibility, the main cladistic methodology is parsimony analysis. In this technique trees are produced by making a minimum (most parsimonious) number of enforced changes to the scores. In order to provide a robust phylogenetic reconstruction the cynipoid data was also analysed using a parsimony program - HENNIG86 (Version 1.5 - J.S. Farris 1988). This is, at the moment, the most recently available parsimony program that attempts to calculate the shortest tree.

The master compatibility matrix was recoded to fit the data entry parameters of the HENNIG86 program (Table 45). This program cannot cope with complex multistate characters involving more than one lineage, so these were re-scored, either as separate characters or as simple transformation series - e.g. state 1 - state 2 - state 3 being scored 1, 2 or 3. Variable scores are not accepted by this program, they were recorded as unscored i.e. "-".

With large data-sets, like the cynipoid matrix, only certain tree construction options are feasible. The option selected for this analysis applied extended branch-swapping to the trees found, all but the shortest trees were rejected. This option produced four trees which differed in the arrangement of only two clades. Two sequences of the mesocynipine genera (Figs 171, 172) were generated and the aspicerines also generated two different answers (Figs 173, 174).

The four trees were used to construct a Nelson consensus tree (Figs 175, 176). The program made 484 enforced character-state changes. The consensus tree shows considerable similarity with the compatibility clique cladogram (considering that the two data sets are not identical). The robustness of the compatibility method is demonstrated by the areas where the reconstructions differ, because all of these areas represent problems that had already been considered following the compatibility analysis.

1 = H001	2.1 = H002	2.2 = H003	2.3 = -
3 = H004	4 = H005	5 = H006	6 = H007
7 = H008	8 = H009	9.1 = H010	9.2 = H011
10 = H012	11 = H013	12 = H014	13 = H015
14 = H016	15.1 = H017	15.2 = H018	15.3 = H019
16.1 = H020	16.2 = H021	17 = H022	18 = H023
19 = H024	20 = H025	21 = H026	22 = H027
23 = H028	24.1 = H029	24.2 = -	24.3 = H030
25 = H031	26.1 = H032	26.2 = -	26.3 = -
27 = H033	28.1 = H034	28.2 = -	28.3 = -
28.4 = -	29.1 = H035	29.2 = -	30.1 = H036
30.2 = -	31.1 = H037	31.2 = H038	31.3 = H039
31.4 = H040	32.1 = H041	32.2 = -	32.3 = -
32.4 = -	33 = H042	34 = H043	35 = H044
36 = H045	37 = H046	38.1 = H047	38.2 = -
38.3 = -	38.4 = -	38.5 = -	38.6 = -
39.1 = H048	39.2 = -	39.3 = -	40 = H049
41 = H050	42 = H051	43 = H052	44 = H053
45 = H054	46 = H055	47 = H056	48 = H057
49 = H058	50 = H059	51.1 = H060	51.2 = -
52 = H061	53.1 = H062	53.2 = H063	54 = H064
55 = H065	56 = H066	57 = H067	58 = H068
59 = H069	60 = H070	61.1 = H071	61.2 = H072
62.1 = H073	62.2 = H074	62.3 = H075	62.4 = -
63 = H076	64 = H077	65 = H078	66 = H079
67 = H080	68 = H081	69 = H082	70 = H083
71 = H084	72 = H085	73.1 = H086	73.2 = H087
73.3 = H088	74 = H089	75 = H090	76 = H091
77 = H092	78.1 = H093	78.2 = H094	78.3 = H095
79.1 = H096	79.2 = H097	80 = H098	81.1 = H099
81.2 = -	82.1 = H100	82.2 = -	83 = H101
84 = H102	85 = H103	86 = H104	87 = H105
88 = H106	89 = H107	90.1 = H108	90.2 = -
91 = H109	92 = H110	93 = H111	94 = H112
95 = H113	96.1 = H114	96.2 = -	97.1 = H115
97.2 = H116	98 = H117	99 = H118	100.1 = H119
100.2 = -	101 = H120	102 = H121	103 = H122
104 = H123	105.1 = H124	105.2 = H125	106 = H126
107 = H127	108 = H128	109.1 = H129	109.2 = H130
109.3 = -	109.4 = H131	110 = H132	111.1 = H133
111.2 = -	111.3 = -	112.1 = H134	112.2 = -
113.1 = H135	113.2 = H136	114 = H137	115 = H138
116 = H139	117.1 = H140	117.2 = -	118 = H141
119 = H142	120 = H143	121 = H144	122 = H145
123 = H146	124 = H147	125 = H148	126.1 = H149
126.2 = -	127 = H150	128 = H151	129 = H152
130 = H153	131.1 = H154	131.2 = -	132.1 = H155
132.2 = -	132.3 = -	133 = H156	134 = H157
135 = H158	136 = H159	137 = H160	138.1 = H161
138.2 = H162	138.3 = H163	139 = H164	140 = H165
141 = H166	142.1 = H167	142.2 = H168	143 = H169
144 = H170	145 = H171	146 = H172	147 = H173
148 = H174	149.1 = H175	149.2 = -	149.3 = -
150 = H176	151 = H177	152.1 = H178	152.2 = -
153 = H179	154 = H180	155 = H181	156 = H182
157 = H183	158 = H184	159 = H185	160 = H186
161 = H187	162 = H188	163 = H189	164 = H190
165 = H191	166 = H192	167 = H193	168 = H194
169 = H195	170 = H196		

Table 45. Master / Hennig character equivalence.

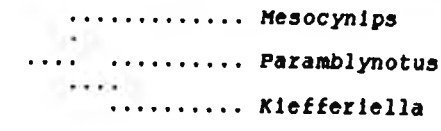


Figure 171. First arrangement of the Mesocynipinae.

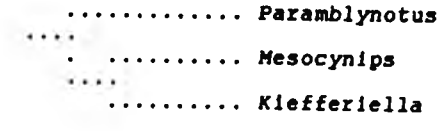


Figure 172. Second arrangement of the Mesocynipinae.

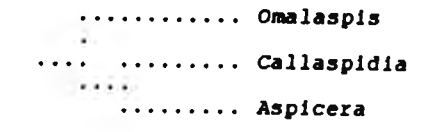


Figure 173. First arrangement of the Aspicerinae.

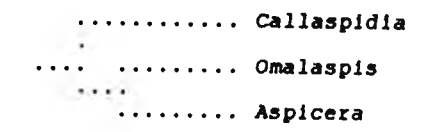


Figure 174. Second arrangement of the Aspicerinae.

COMPARISON OF THE PARSIMONY AND COMPATIBILITY TREES

First node

The first dichotomy of the compatibility cladogram (Fig. 161) was between the Cynipidae and the parasitoid groups. However, the synapomorphies used to define the parasitoid grouping were subsequently shown to be weak. The parsimony tree (Fig. 176) has a different first node, here the Ibaliidae/Liopteridae are divided from the remaining Cynipoidea. However, there are no synapomorphies for taxa 10-31, unless considerable character-state changes are postulated. For example,the closest characters are H25 and H108 both of these would require two character-state changes. Neither of these characters

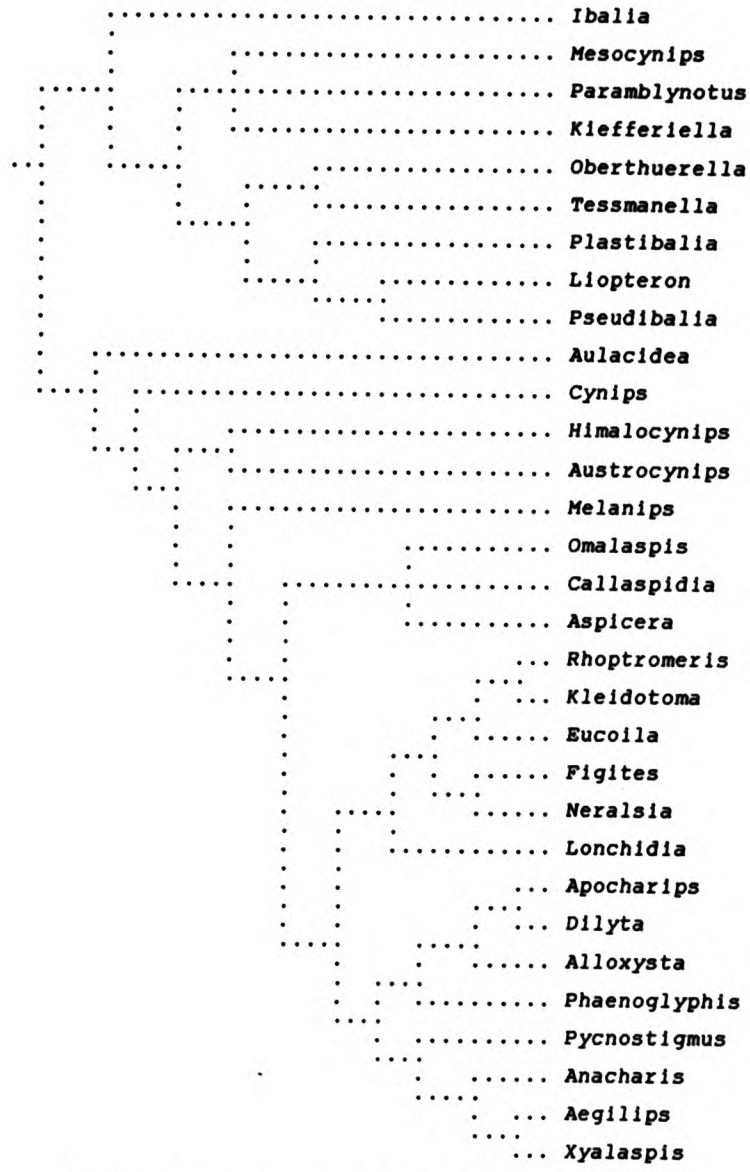


Figure 175. Consensus tree of parsimony analysis.

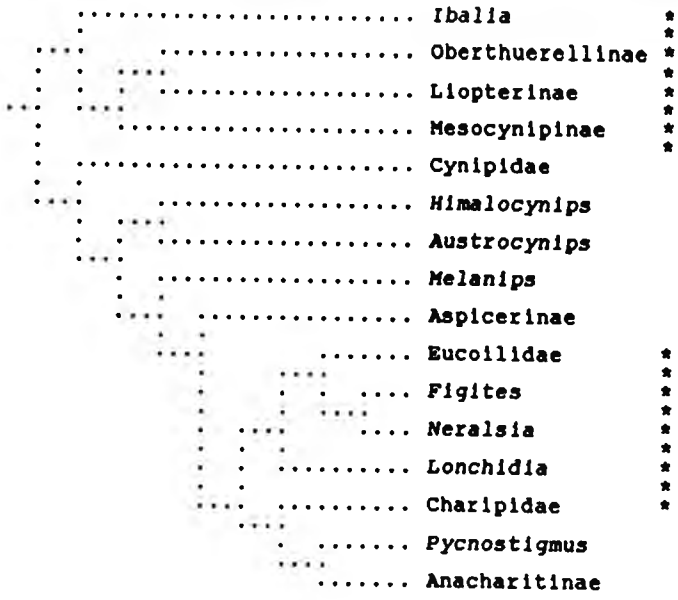


Figure 176. Summary of the parsimony tree.
(* = section that corresponds with the compatibility tree)

(mandible shape; reduction of vein cu-a) is a sufficiently strong feature for such an important node.

As both the parsimony and compatibility trees lack a robust first node, this basal division will be discussed further (below).

The ibaliid group

The parsimony arrangement of the Ibaliidae + Liopteridae is almost the same as that of the compatibility cladogram. The only difference is that *Liopteron* is here included with the other Liopterinae. The parsimony program has assumed a secondary loss of character H151 (128 - length of last tarsal segment) and H87 (73.2 - mesepisternal suture). These changes were considered in the discussion of the last characters deleted to form the compatibility clique. A secondary loss of character 128 was considered possible but that of 73.2 was unlikely.

Himalocynipinae / Austrocynipinae

The difficulties associated with these two taxa have already been identified during the compatibility analysis. The Austrocynipinae has many features of the ibaliid group (e.g. coiled ovipositor, strong sculpture). However, these characters are associated with a particular biology and could have been acquired secondarily by *Austrocynips* in response to host switching. *Himalocynips* does not, quite, have the rough sculpture nor the looped ovipositor of the ibaliid group. Similarly a host switch by *Himalocynips* could have caused the loss of these features. However, there is no synapomorphy for just these two taxa, in fact they have many differences and it is not reasonable to place them together. Their characters must be accepted at face value, thus *Himalocynips* forms an independent lineage, outside both the ibaliid and figitid groups. The parsimony position of *Austrocynips* cannot be accepted, this genus is best placed as shown in the compatibility tree.

The figitid group

The HENNIG86 tree is least satisfactory in its arrangement of the figitid lineage. In parts, it is a poor representation of the morphological similarities. For example, although it is true that *Melanips* has some less derived features and shows a resemblance to the Cynipidae, yet it is placed too far away from *Lonchidia*, a genus with which it is similar. The position of the Aspicerinae as the sister-group of the remaining taxa would be more viable if *Pycnostigmus* (and probably the Charipidae) were excluded. Linking the Charipidae, *Pycnostigmus* and the Anacharitinae together in a clade has no advantages and there is no synapomorphy to justify this grouping.

Phaenoglyphis

Within the Charipidae, the primitive nature of *Phaenoglyphis* is perhaps better represented here, than in the compatibility cladogram. The parsimony analysis does not support the Alloxystinae as a subfamily, while the

Charipinae is supported.

Eucoilidae

The Eucoilidae and the figitine genera *Figites* and *Neralsia* have the same arrangement in both parsimony and compatibility trees.

Comment

Generally the parsimony tree seems rather unsympathetic, forcing dichotomies where a less structured approach is more consistent with the morphology. Some character-state changes are postulated which seem most unlikely. For example the "clean" arrangement of the Liopteridae does not reflect the morphological realities. Therefore the parsimony answer is, in the main, rejected in favour of the compatibility tree. However, this is not necessarily a rejection of parsimony. The cynipoid matrix was much too large to get optimal results from the parsimony program, and a very limited operational option had to be selected. Further by the appropriate application of iterative weighting it would, presumably have been possible to remove the more unacceptable of the forced character-state changes made by the program.

THE PRIMARY DIVISION OF THE CYNIPOIDEA

The parsimony and compatibility analyses provide very different versions of the first node of the tree. Although, in both, it is evident that there are four basal groups (the ibaliid lineage, the figitid lineage the Cynipidae and *Himalocynips*). There are just three *likely* arrangements (Fig. 177) of these basal groups (other arrangements are not supported by analysis).

Arrangement A is supported by the compatibility cladogram. There was no synapomorphy for the Cynipidae. The four characters (18, 44, 129 and 159) that define the parasitoid group have already been discussed. The first two are poor features, the third occurs in extralimital Cynipidae and character 159 (Figs 142 & 143) could, if the

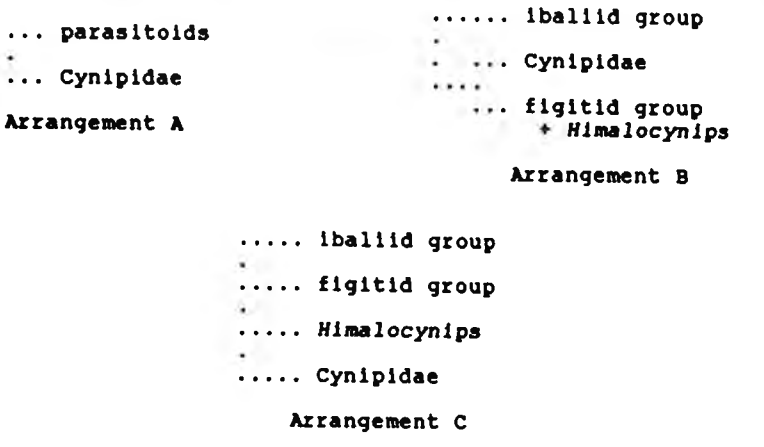


Figure. 177. The main cynipoid lineages: alternatives.

polarity was reversed, be an apomorphy for the Cynipidae. [It was speculated (Fergusson, 1988) that this feature was a remnant of tergite 10, but it could be a unique depression to house the cerci in the phytophagous lineage.] The main attraction of arrangement A is the clear division between phytophagous and entomophagous taxa.

Arrangement B is supported by the parsimony analysis, but not by the morphological evidence. Although, the evidence from fossils (see later), size and biogeography all indicate that the Ibaliidae are a distinct lineage, this does not necessarily imply that the remaining taxa had a common origin.

Arrangement C is the most acceptable configuration. It is consistent with the early origin of the Ibaliidae, the single and early origin of phytophagy, and the reinterpreted compatibility tree. This arrangement can be criticised for not being a dichotomy. But after considerable analysis, it is now evident that the Cynipoidea consist of four major units that show no obvious interrelationships. [The polarity of character 159 is reversed.] Although this is a pragmatic solution it is consistent with the available evidence and has the advantage of being stable.

Himalocynips: can it be "merged" with another lineage?

As one of the four main cynipoid lineages consists of a single species, perhaps it can be incorporated into one of the other three groups.

Several features, and also the parsimony tree, indicate that there could be a link between *Himalocynips* and *Austrocynips*. So could *Himalocynips* be "fitted" into the ibaliid lineage? The relevant characters (16.1, 19, 24.1, 45, 53.2, 54, 78.1, 117.1, 149.1 and 156) were re-evaluated, but only in one case was a change reasonable. Rough head sculpture (16.1) is present in all these taxa except *Mesocynips*. Thus a secondary loss could be postulated for this exception, and indeed this score was marked 22 times by the master LEQUC analysis. This change would mean that rough head sculpture, not an especially good character, would be the sole feature defining a ibaliid / *Himalocynips* group. Although this reversal is likely, the occurrence of this feature in both *Himalocynips* and the ibaliid lineage could so easily be a parallelism.

There is very little support for the placement of this genus in the Cynipidae.

The possibility of placing *Himalocynips* in the figitid group was also explored, but there are few potential synapomorphies. Characters 20, 24.3, 26.1 and 111.3 were reinvestigated but a reversal of 20 is unlikely and reversals of 24.3 or 26.1 are very unlikely. When character 111.3 (position of Rs&M) was re-examined (see section on fossils) it was found that *Himalocynips* has a unique venation feature - a small gap in the basalis (Rs+M).

It is concluded that *Himalocynips* must stand isolated from other cynipoids. It probably was derived from ancestors of the ibaliid lineage but so long and so many specializations ago that the morphological links have been lost.

Conclusion

It can only be concluded that the cynipoidea consists

of four main lineages - the ibaliid group, the figitid group, *Himalocynips* and the Cynipidae.

EXTRALIMITAL TAXA

The detailed analysis of the Cynipoidea was, of necessity, confined to a limited number of representative taxa. In this section of the thesis many of the remaining cynipoid genera are discussed in the light of the analysis. The generic content for each of the higher categories is taken from Weld (1952), the last revision to give such information for all the Cynipoidea.

Cynipidae

Of all the Cynipoidea only the Cynipidae have had their phylogeny investigated. Kinsey (1920) provided a tribal structure for the gall causers based on morphological, biological and gall characters. More recently Ritchie (1984) has improved on this structure and has included the inquilines. The work of Ritchie has not been duplicated in this thesis, rather his results have been used (with permission) as support for the phylogenetic study of the superfamily. In view of the existence of these works it was considered that two Cynipidae were sufficent representation of the family amongst the 31 exemplar species. However, most cynipid genera were examined to see if Ritchie's phylogeny was supported.

Aulacideini

Kinsey (1920) placed the primitive gall-wasps (e.g. *Aulacidea, Aylax, Phanacis, Isocolus*) in a tribe, the "Aulacini". This is an incorrect formation of the family group name, and actually applies to another (non-cynipoid) group of the Hymenoptera (*Aulacus*: Aulacidae). The correct family group name from *Aulacidea* is Aulacideini. Askew (1984) used the tribal name Aylaxini but this changes the nomentypical genus to *Aylax* and this is not necessary.

[Kovalev (1982) raised the tribe to a subfamily, mistakenly spelled Aylacinae, but such a status cannot be justified.]

I have examined all the available Aulacideini genera and, like other authors (Kinsey, 1920; Ritchie, 1984) can find no synapomorphy for this assemblage. Ritchie (1984) has shown that *Diastrophus* (which has strongly lobate claws) is the sister-group of the inquiline taxa, so the Aulacideini is a paraphyletic aggregation at the stem of the cynipoid lineage (Fig. 178).

Kinsey (1920) placed *Pediaspis* in a tribe Pediaspidini but other workers (e.g. Weld, 1952) have placed this genus in the Aulacideini and there is no reason, at present, to change this latter interpretation.

Synergini

Most authors (e.g. Burks, 1979; Eady & Quinlan, 1963; Quinlan, 1979; Ritchie & Shorthouse, 1987) have recognized the holophyly of the inquilines, placing them either in a subfamily or a tribe - Synergini. Ritchie (1984) has supported this group as, at most, a tribe. The holophyly of the inquilines is demonstrated by their possession of a long hypostomal bridge. This is a very derived condition compared to that of most other Cynipidae and is similar to that of the Figitidae. Further, lateral pronotal carinae are present in the Synergini, (again, like the Figitidae) but absent from the pronota of *Cynips* and *Aulacidea*. Finally the Synergini have the visible gaster consisting of one large tergite, although this last character also occurs elswhere in the superfamily (e.g. Eucoilidae).

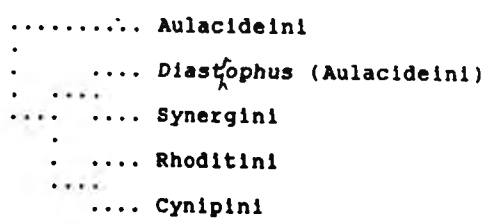


Figure 178. Phylogeny of the Cynipidae (Ritchie, 1984).

Rhoditini & Cynipini

Kinsey (1920) showed that the derived gall-inducers were composed of two tribes, the Rhoditini and their sister-group the Cynipini. Both Weld (1952) and Eady & Quinlan (1963) showed that the synapomorphy for these two tribes was their short (in dorsal view) pronotum which is less than 1/7 of its lateral length. The Rhoditini consists of *Diplolepis* (= *Rhodites*) and the autapomorphy for this tribe is its peculiar ploghblade-shaped hypopygium. The synapomorphy (Ritchie, 1984) for the Cynipini being the developed hypopygidial spine (which has distinct ventral hairs). This feature also occurs in *Himalocynips* and *Pycnostigmus* but without the hairs.

Kinsey (1920) elevated the genus *Eschatocerus* to a tribe (Eschatocerini) but this is not required as this genus is similar to *Diplolepis*, having the same type of hypopygium (Weld, 1952) (c.f. Figs 126, 127).

Ibaliidae

Weld (1952) listed two genera of Ibaliidae, *Ibalia*, (see analysis), and *Protoibalia*, (considered below, in the section on fossils). Kerrich (1973) placed *Myrmoibalia* with *Ibalia* but it was already a synonym of *Heteribalia*, a mesocynipine. Recently, Ronquist & Nordlander (1989) have moved *Heteribalia* to the Ibaliini. Unfortunately the types are not available and the placement cannot be confirmed. Specimens under the name *Myrmoibalia* in the Natural History Museum collection are probably species of *Ibalia*, but one may possibly be of a second genus quite similar to *Ibalia*.

Oberthuerellinae

Oberthuerella and *Tessmanella* were analysed. The third genus, *Xenocynips*, is a typical oberthuerelline and has the characteristic spine on the hind femur (118), although the claws are simple (c.f. 131.2). There is only one small tergite before the large gastral tergite (see note on this genus in Chapter 4).

Liopterinae

The three known genera were all analysed.

Mesocynipinae

Weld listed seven genera - *Mesocynips*, *Kiefferiella*, *Paramblynotus*, *Dallatorrella*, *Paraibalia*, *Heteraibalia* and *Paraegilips*. The first three were analysed. No specimens of *Heteribalia* could be obtained.

Dallatorrella exhibited apomorphic scores for characters 3, 6, 19, 24.1, 53.2, 54, 58, 78.1 (only just), 117.2, 131.1, 149.1, 156 and 157. It is plesiomorphic for the 62.3 clade and therefore it is placed next to *Mesocynips* in the tree. It does not share character 13 but has a similar, although less well-developed, petiole (character 137). Kieffer (1911) elevated *Dallatorrella* to subfamily status but this was unnecessary as the Mesocynipinae had already been designated (c.f. Weld, 1952: 161).

Paraegilips has similar scores up to the 117.2 clade, it is apomorphic for this, poor, character but plesiomorphic for the important bifid claw character (131.1). Therefore like *Dallatorrella*, this genus should be placed next to *Kiefferiella* (= *Paramblynotus*).

Paraibalia has very similar scores although character 156 is weak and the clypeus has more of a depression than a notch (3). This genus is plesiomorphic for both 117.2 and 131.1, and also belongs near *Kiefferiella*. *Paraibalia* has a peg-like projection on the hind basitarsus, that distinguishes it from all neighbouring genera.

E--------ini

The new genus *E*--------- (see Appendix 3) is apomorphic for characters 18, 44, 53.2, 54, 129 and 157; that places it within the wood-associated group. It does not have the *Austrocynips* characters (5, 48, 105.2, 140 & 170). Of the characters that unite taxa 2-9 with *Ibalia*, the new genus is apomorphic for 19, 24.1, 149.1 and 156 (trace); but not character 6 (face with central ridge). *E*--------- is plesiomorphic for the *Ibalia* characters and the liopterid characters (3 and 78.1). Although the

clypeus (character 3) is depressed rather than being notched, this is a similar modification. This genus forms a unique lineage and must be placed between *Ibalia* and taxa 2-9, as a new tribe - the E--------ini.

Pycnostigmatini

This tribe contains a second genus, *Tylosema*, but unfortunately type-material cannot be found. The type-material was examined by Weld (1952) and he showed that the two genera are quite close, differing in petiole structure and notauli.

Examination of further material, to that analysed, of *Pycnostigmus* has shown that the female has a ventral spine on the hypopygium similar to that of the Cynipidae. Thus the score for character 154 must be amended, but as this was not a clique character the change does not alter the cladogram.

Charipidae

Weld (1952) lists nine genera, five have been synonymized (see Fergusson, 1986) and three, plus a recently described genus (*Apocharips*), have been analysed (Chapter 4). [*Adelixysta*, recently described by Kierych (1988), will shortly be synonymized with *Alloxysta* (Menke & Evenhuis, *in prep.*).] That only leaves *Lytoxysta*. This rare genus is unlike all other charipids because it has weak alutaceous sculpture; also the vein area is not particularly reduced. *Lytoxysta* occupies an intermediate position between the Charipidae and the Figitidae. It does not fit into either subfamily of the Charipidae and thus it makes these subfamilies less tenable. *Lytoxysta* lacks the triangular depression under the epimeron on the mesopleuron but this may also be absent in some Eucoilidae and is probably a size-related feature

Aspicerinae

The following aspicerine genera are listed by Weld - *Paraspicera, Balna, Prosaspicera, Anacharoides*, plus the three taxa analysed (*Aspicera, Omalaspis* and *Callaspidia*). *Prosaspicera* and *Balna* correspond with all the cladogram

characters for the Aspicerinae, except that the genitalia characters 167 and 168 could not be examined. *Balna* has a remarkable spine in the centre of the mesonotum. *Paraspicera* posesses the above characters but the hypostomal bridge is very short - this indicates a primitive position amongst the Aspicerinae and confirms the less derived status of the group with respect to most other Figitidae. *Anacharoides* has the aspicerine characters but it also has two interesting features: the scutellum has a distinctive round apical cavity and the pronotal plate (character 50) is only present ventrally, the dorsal part above where the disjunction would be is missing.

Anacharitine

Weld (1952) listed 10 anacharitine genera, three (*Anacharis*, *Aegilips* and *Xylaspis*) have been analysed, one (*Prosynaspis*) is a synonym of *Aegilips*. *Acanthaegilips* is consistent with the Anacharitine characters although the genitalia were not dissected (for characters 163 and 164) and no claws were present (for character 130). The remaining 5 genera were not available for study.

Figitinae

Weld (1952) lists the following genera of Figitinae - *Pegacynips*, *Hormorus*, *Lonchidia*, *Figites*, *Neralsia*, *Melanips*, *Xyalophora*, *Anolytus*, *Paraschiza*, *Sarothrus*, *Thrasorus*, *Trischiza*, *Zygosis*, *Australofigites* and *Thoreauella*. The first two were not available for study; the next four have been analysed, and *Anolytus* is now a synonym of *Melanips* (Fergusson, 1986). A study of the remaining taxa led to the reappraisal of characters 49 (complete carinae) and 50 (disjunction in the lateral carina of the pronotal plate).

The Anacharitinae have a complete lateral carina from the base of the pronotum on one side, over the dorsal region to the base on the other side. The Aspicerinae have a discontinuity or disjunction in the lateral carina (character 50). In *Aspicera* (Fig. 63) this is a step or

lip, in *Callaspidia* and *Omalaspis* (also aspicerines) the lateral carina is raised at this point and there is a cavity under the step. The Charipidae have the ventral portion of the lateral carina present but the dorsal portion is very weak, although still indicated (especially in the less derived examples, e.g *Phaenoglyphis*). *Pycnostigmus* only has the ventral portion of the lateral carina present. The morphology of all these taxa makes it likely that this reduction of the dorsal element occurred after the carina split into two (character 50). *Neralsia*, *Figites* and the Eucoilidae all have a well-developed dorsal element. The genera near *Melanips* have a partial development of the dorsal portion of the carina, although it is almost lost in one of them (*Lonchidia*). Thus characters 49, 50 and 51 form part of the same transformation series. First the carina is "complete" (character 49) - found only in the Anacharitinae. This stage was followed by a division of the carina in all other Figitidae (but now obvious only in the Aspicerinae) which in turn was followed either by a reduction of the dorsal portion of the carina (Charipidae & *Pycnostigmus*) or a development of this section into a partially (51.1) or fully (51.2) raised plate (in *Figites* and the Eucoilidae). This sequence confirms that the Anacharitinae are the least derived Figitidae (Fig. 179).

The re-evaluation of characters 49 and 50, prompted

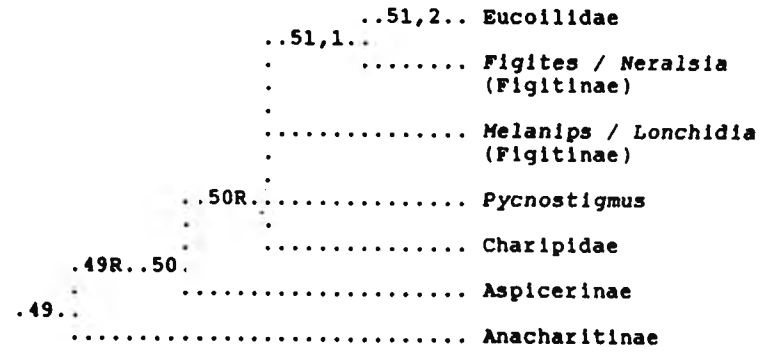


Figure 179. Improved version of the Figitidae tree.
[R = feature lost in a a higher character-state.

by study of the extralimital material, provides a marked improvement in the tree, especially with regard to the incompatibility of character 49 with characters 167 and 168. In the discussion of the last character deletions, it was shown that reversals of 167 and 168 were likely for the anacharitines and that 167 could also have reversed in the Charipinae. (Thus implying that the ancestor of the Figitidae had characters 167 and 168). Now that these four characters have been investigated more fully, they and the reversals postulated for them together provide a tree (Fig. 180) that fits the specimens much better than previous postulates.

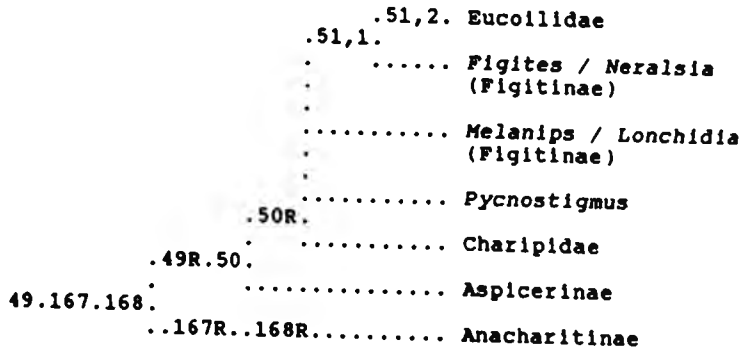


Figure 180. Final re-evaluation of the figitid lineage
R = feature not evident in a higher character state

The extralimital taxa did not precisely conform to character 51.1 (plate partially raised off the surface) for example *Trischiza* is midway between the positions of *Melanips* (no undercut or raised lateral portion of the plate) and *Neralsia* (plate round and distinct laterally, and slightly raised dorsally). Probably a better way of dividing the genera of the Figitinae is on the presence / absence of gastral hair tufts; this feature (character 147) also occurs in the Charipidae and Eucoilidae and therefore was outside the clique but in the Figitinae it appears to be a useful character. *Melanips*, *Lonchidia*, *Sarothrus*, *Pegocynips* and *Paraschiza* have hair tufts.

Figites, *Neralsia*, *Xylophora*, *Trischiza*, *Zygosis* and *Hormorus* are without tufts.

The available extralimital taxa were examined (except for genitalia characters 165, 167 & 168 which require dissection) to see how they relate to the study taxa. *Zygosis*, *Trischiza* and *Xylophora* fit into the tree near *Figites*, although in *Xylophora* characters 78.3 and 134 are poorly defined. *Sarothrus* is apomorphic for character 78.3 but character 134 is not well-defined. *Paraschiza* has a petiole similar to that of *Melanips* but the metapleural furrow is more like that of *Figites*. This renders untenable any idea of the genera near *Melanips* being an independent group / tribe.

It is evident that after the Figitinae had evolved a derived element of this group developed into what is, at present, called the Eucoilidae. In this context *Paraschiza cupressana* is interesting because its scutellum is smooth with a sculptured and slightly raised margin. This could represent the very first stage of the development of the eucoilid-type scutellar plate (see Eucoilidae below).

Australian taxa

Several slightly unusual genera have been described, as Figitidae, from Australia.

Thoreauella

Thoreauella was described (Girault, 1930) in a privately printed, but valid, publication (see Gordh et al, 1979).

The only specimen, the type of *T. amatrix*, is in poor condition. It is very small, under 1mm long, and therefore has features in common with other small cynipoids. The thorax is smooth (c.f. Charipidae) but the hypostomal bridge is complete, like that of the Eucoilidae. The wing is bifid and similar to that of the eucoilid genus *Kleidotoma*. However, the venat'on is like that of the Charipinae, being restricted to the upper

inner quarter. The marginal cell is small, almost parallel-sided and like that of the Charipidae, but it is also reminiscent of *Pycnostigmus*. The presence of the "pseudopterostigma" of *Pycnostigmus* rather detracts from the underlying similarity of this genus to the Charipinae, but the similarity of *Thoreauella* to both these taxa makes the link obvious.

Other features: antennna 12-segmented; thorax long and ending in a round cavity; percurrent notauli; metapleural trough and sulcus similar to that of *Lonchidia* (Figitidae); propodeum and second gastral segment with dense pubescence; genitalia obscured. The maxillary palps appear to be three-segmented and the labial palps appear to be only two-segmented. If these values are correct then the reduction of palp segments goes beyond that in *Pycnostigmus*, the Eucoilidae and the Charipidae.

This genus has unique features that places it in a separate lineage within the Figitidae - a new tribe, Thoreauellini - unfortunately known only from one glue encrusted specimen. Further evaluation of this tribe must be postponed until more material is available.

Thrasorus

Weld (1944) described *Thrasorus* from a species (*T. pilosus*) which he considered to be close to *Sarothrus* (Figitidae). Riek (1970, 1971) transferred *Thrasorus* to the Cynipidae, without any explanation. Many specimens of this genus (including several undescribed species) are present in Australian collections, they undoubtedly belong in the Cynipidae because they have the indented area (character 159) on the ninth tergite. The host records show that this genus is an inquiline (Synergini) in galls of the Brachyscelidiphaginae (Chalcidoidea) on Acacia and Eucalyptus. Like other Synergini the pronotum is well-developed, but in this genus the carina and the pronotal plate are especially well-developed and form a plate which, although not raised, is very similar to that of the Eucoilidae (51.2). This homoplasy is yet another example of the derived morphology of the Synergini in comparison to other Cynipidae, and their parallelism with

the Figitidae.

As in other inquilines, characters 18 and 129 are plesiomorphic, the hypopygidial spine is present and gastral tergites two and three are fused.

Australofigites

Girault (1932) described this genus and likened it to *Amblynotus* (= *Melanips*). The head of the type is missing, the rest of the specimen is embedded in glue and is very difficult to identify. It could be either a figitid near *Melanips*, or a gall-wasp. Several undescribed species were examined, from the collections of the Natural History Museum and various Australian museums, that appear to be close to *Melanips*, and have figitid wing venation (character 111.3). These specimens all illustrate the symplesiomorphic similarities between *Melanips* and the Cynipidae (in this case Cynipidae near *Thrasorus*). Both groups often have medium-sized species with distinctive granulate sculpture, and the general shape of the head and thorax similar. These similarities are not surprising considering the less derived position of *Melanips* with regard to the derived Figitidae and Eucoilidae. Riek (1970) raised *Australofigites* to a tribe but a subdivision of the Synergini for the Australian inquilines is not justified by known morphological characters.

Eucoilidae

The genera of the Eucoilidae are too numerous to investigate here, beyond those already analysed. However, the group has no obvious subdivisions.

The genus *Emargo* was described as a figitid (Weld, 1960) but Quinlan (1988) placed it in the Eucoilidae. This reassesment is supported by the cladogram characters except that the ventral cavity of the metapleuron is virtually absent. The "typical" tear-drop shaped plate of the Eucoilidae is only just discernible in *Emargo* and this genus shows the close relationship between the Eucoilidae and Figitidae.

The tear-drop shaped plate is also very reduced in

certain species of *Nordlanderia*, especially an undescribed species from Tonga.

FOSSIL CYNIPOIDEA

Fossil Cynipoidea are particularly scarce (Carpenter, 1937), only fourteen species have been recognized from just five localities. There are several other references to fossil cynipoids but they are too vague to be ascribed to this superfamily with any assurance, e.g. *Cynips succinea* described by Presl (1822), (Kinsey, 1919; 1937; Menge, 1856).

List of cynipoid fossils

Andricus vectensis Cockerell, 1921. Oligocene Marls. Isle of Wight, England [Examined].

Archaeocynips villosa Rasnitsyn & Kovalev, 1988. Cretaceous sediments. Buryataskaya, U.S.S.R.

Archaeocynips major Rasnitsyn & Kovalev, 1988. Cretaceous sediments. Chitinskaya, U.S.S.R.

Aulacidea ampliforma Kinsey,1919. Miocene. Florissant, Colorado, U.S.A. [Examined].

Aulacidea progenitrix Kinsey, 1919. Miocene. Florissant, Colorado, U.S.A. [Examined].

Aulacidea succinea Kinsey, 1919. Oligocene, Baltic amber. West Germany.

Dahurocynips dahurica Rasnitsyn & Kovalev, 1988. Cretaceous sediments. Chitinskaya, U.S.S.R.

Figites planus Statz, 1939. Oligocene, Baltic amber. Rott, West Germany .

Figites rotundalis Statz, 1939. Oligocene, Baltic amber. Rott, West Germany .

Figites solus Brues, 1910. Miocene. Florissant, Colorado, U.S.A. [Examined].

Figites spiniger Statz, 1939. Oligocene, Baltic amber. Rott, West Germany.

Protimaspis costalis Kinsey, 1937. Cretaceous amber. Cedar Lake, Manitoba, Canada [Examined].

Protoibalia connexiva Brues, 1910. Miocene. Florissant, Colorado, U.S.A. [Examined].

Diplolepis (=Rhodites) vectus Cockerell, 1921. Oligocene Marls. Isle of Wight, England [Examined]. Comb. nov.

Oligocene / Miocene cynipoids

The fossils that are attributable to the Cynipoidea are mostly Cynipidae, and the less derived gall-wasps (e.g. *Aulacidea*) are particularly well-represented. The Oligocene and Miocene cynipids, especially *Andricus vectensis* and *Diplolepis vectus* are very similar to modern species.

Statz (1939) described three species which he tentatively placed in the genus *Figites* (Figitidae). Unfortunately I have not been able to examine these specimens, the descriptions are not sufficient to enable these species to be placed into a genus, nor perhaps even a family, with any degree of confidence. *Figites* was used in a similar, liberal sense when Brues (1910) described *F. solus*, and this specimen could be either a cynipid or a figitid species.

All these Oligocene / Miocene fossils are cynipids or possible figitids. However, Brues (1910) described a Miocene ibaliid - *Protoibalia connexiva*. I have carefully examined this fossil and I believe that it is a cynipid. True, the mesocutum bears transverse sculpture and both the side of the pronotum and the scutellum are reticulate, but this form of sculpture is within the range of variation of the Cynipidae. For example, *Callirhytis* has mesoscutal striations of a very similar nature, and various species of *Synergus* are strongly sculptured. Crucially, the ovipositor of *Protibalia*, although distorted, is clearly not of the looped *Ibalia* type.

Cretaceous cynipoids

Until very recently the earliest known cynipoid was *Protimaspis costalis* (Kinsey, 1937), a well-preserved specimen in Cretaceous amber. This insect has several interesting features. The antennae are at least 14-segmented and probably 15-segmented. If the latter is

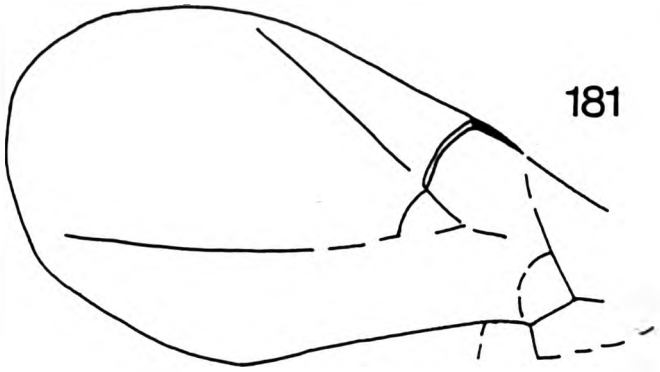
the case, then it supports the contention that the usual cynipoid number is a reduction. The antennae are well supplied with distinct multiporous plate sensilla. Vein Rs+M points to the middle of Rs&M (character 111.2) (see below). The wing venation is not very reduced - vein M reaches to the edge of the wing and veins Cu1, Cu1a and Cu1b are present. The genitalia appear to be unremarkable and the hypopygium does not reach to the end of the gaster. Apart from being rather hairy this is, as might be expected, a rather unspecialized species. Kinsey showed that it belongs to the group of genera near Aulacidea, and is therefore near to the base of the Cynipidae. However, it is not particularly different from the Oligocene and Miocene fossils.

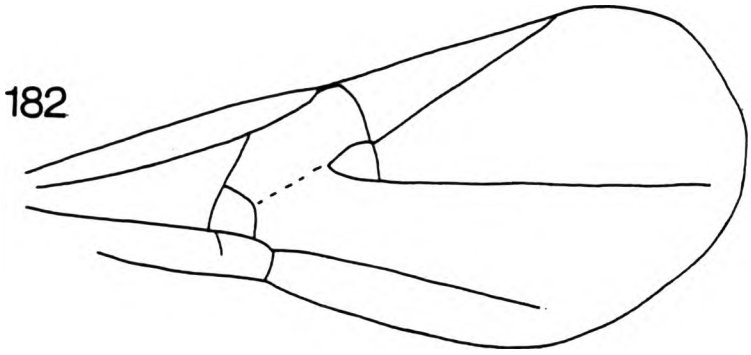
In 1973, Zerichin & Sukaceva reported further (unnamed) Cynipoidea from Cretaceous amber, in Northern Siberia. Recently, Rasnitsyn & Kovalev (1988) described three more Cretaceous cynipoids (*Archaeocynips villosa*, *A. major* & *Dahurocynips dahurica*). These fossils are from early to middle Necomian sediments of the Transbaikalia. Rasnitsyn & Kovalev have placed these Necomian cynipoids in a new family, the Archaeocynipidae [not made available for study]. This family has three important features. Vein m-cu is present in the forewing and therefore the first discal cell is complete (Figs 181-183). There is a slight remnant of a linear pterostigma. Finally the gaster does not appear to be especially compressed from the side. Thus the wing venation of this family is very different from that of extant Cynipoidea. Otherwise the family is representative of the Cynipoidea and has the typical marginal cell. The thorax of *Archaeocynips* shows similarities with that of *Protolbalia*.

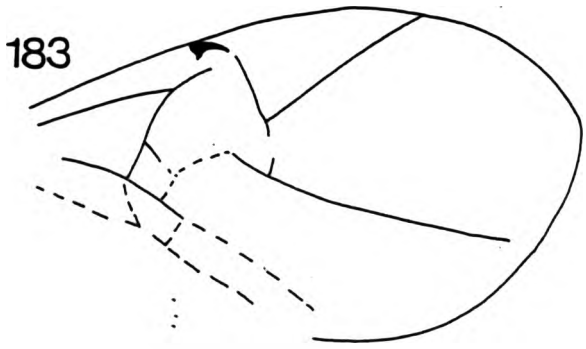
What does the oldest fossil tell us about cynipoids?

Pterostigma

The small linear pterostigma of the Archaeocynipidae shows that the cynipoids must have lost their pterostigma by gradual reduction. Thus it is now clear that the pseudopterostigma of *Pycnostigmus* is a derived structure.







Figures 181-183. 181, forewing of *Archaeocynips*. 182 & 183 forewings of *Dahurocynips* [After Rasnitsyn & Kovalev, 1988].

The status of the pseudopterostigma in *Austrocynips* is still not absolutely certain but it is also likely to be a derived feature and is clearly dissimilar to the pterostigma of *Archaeocynips*.

Wing venation

The wing venation of *Archaeocynips* is like that of the other Cretaceous fossil, *Protimaspis costalis*, and some living cynipoids that have a distinct anal venation. The assigned polarities and character transformations given in the section on wing venation (Chapter 4) are largely confirmed by comparison with the venation of the Archaeocynipidae. The loss of veins Cu1, Cu1a and Cu1b, the shortening of vein M, and the rotation of RS+M etc are all shown to be derived features.

Character 111.3 (position of Rs+M) is one of the traditional characters that has been used to recognize the Figitidae. This character survived the compatibility analysis and remains an important discriminant. It is a particularly difficult character to use but it is only after the discovery of the Archaeocynipidae that the significance of this character has been proven. In *Archaeocynips* there is present a remnant of the discal cell and it is to the upper outer corner of this cell that Rs+M points. With the loss of the discal cell in all remaining Cynipoidea vein Rs+M was left free. This central and primitive position is shown in the Cynipidae. The Figitidae have a more derived position where Rs+M has moved downwards and points to the base of the basalis. The Ibaliidae/Liopteridae group are demonstrably an independent lineage with Rs+M high and joined to Rs&M so that the first submarginal cell is closed, at least in the less derived (or large) representatives. The fourth cynipoid lineage - *Himalocynips* also has a unique configuration with a small gap in vein Rs&M (Fig. 109).

Cynipoid phylogeny

Rasnitsyn & Kovalev considered the Archaeocynipidae as the probable ancestral group for all the Cynipoidea.

However, I feel that the ibaliid/liopterid lineage should be excluded from this scenario. The Archaeocynipidae are small (4mm or less) and morphologically much closer to the cynipid and figitid lineages. It is not possible to say whether only the Cynipidae, or the figitid group or both together, evolved from an ancestor of this type.

The age of the Cynipoidea

The Archaeocynipidae are from Early to Middle Necomian strata. This would place the origin of the Cynipoidea in the Berriasian (135mya). The ibaliid group are unlikely to have originated much earlier than this because the Apocrita evolved in the Middle to Upper Jurassic (Rasnitsyn, 1980).

Although the basic divisions of the Cynipoidea probably arose in the Necomian, the more derived Cynipoidea must have evolved much later, perhaps in the Upper Cretaceous. Even in such a limited fossil record it is significant that there are no Charipidae or Eucoilidae present. However, these families and the majority of extant groups are likely to have become established by the late Tertiary.

Fossil galls

The oldest known insect caused galls are from the upper Cretaceous (Hickey & Doyle, 1977; Larew, 1986; Möhn, 1960;). Pre-Quarternary cynipid galls are very rare and those that are recorded are of doubtful identity. Brues (1910) described the gall of *Andricus myricae* but it is a *Cecidomyia* gall (Kinsey, 1919). Scudder (1886) mentions Cynipidae galls found at Florissant but Kinsey (1919) found that they are not cynipoid galls. An examination of all the fossil galls in the Palaeontology Department of the Natural History Museum and in a collection of material on loan from American Universities and Museums was conducted, but no cynipoid galls were found. Definite evidence of fossil cynipoid galls does not occur until Recent (0-2 mya) times. Larew (1986) recorded

Callirhytis acorn galls inside the mouth of a Sabre-tooth cat in the tar pits of California. Even more modern are the galls preserved by carbonization at Herculaneum when Vesuvius erupted in A.D. 79 and destroyed a commercial store of galls (Larew, 1987).

RELATIVE VALUE OF THE CHARACTER-SUITES

In past classifications great emphasis was placed on a few character-suites e.g. wing venation and gastral segmentation. However, the results of the compatibility analysis indicate that these are probably not the best character-suites.

The large data-set assembled for this thesis was used to assess the relative merits of the cynipoid character-suites. The data was subdivided into obvious suites and each unit analysed separately (Tables 46-47).

Character-suite	Incompatibilities found	expected	ratio	polar
head	69	226.51	0.30	0
antenna	126	135.38	0.93	0
thorax	50	205.50	0.24	0
legs	20	30.68	0.65	0
wings	224	413.71	0.54	14
petiole	11	35.31	0.31	0
gaster	7	29.82	0.23	0
ovipositor	16	42.93	0.37	0

Table 46. Results of the analysis of cynipoid character-suites. [LeQuesne coefficient = ratio X100]

	SUITE CLIQUE No. of chars	% in clique	MASTER CLIQUE No. in clique	% of clique	MASTER CLIQUE Synapomorphies No.	%
head	37	64.9	24	17.6	13	20.6
antennae	34	38.2	13	9.6	2	3.2
thorax	47	78.8	37	27.2	20	31.8
legs	16	68.8	11	8.1	7	11.1
wings	53	43.4	23	16.9	6	9.5
petiole	18	61.1	11	8.1	4	6.4
gaster	15	53.3	8	5.9	4	6.4
ovipositor	14	64.3	9	6.6	7	11.1

Table 47. Comparison of character-suite apomorphies.

Head

The 37 head features included many new characters and had a good (low) LeQuesne coefficient. Twenty four characters contributed to the master clique. That was second only to the contribution provided by the thoracic data. Twenty per cent of the head apomorphies were synapomorphies, so again this was an important character--suite that provided much information. The head-data cladogram (Fig. 184) is similar to the master clique cladogram, although *Austrocynips* is placed near *Himalocynips* (a position discussed and rejected). The only oddity is the placement of the Eucoilidae as the sister-group of the Charipidae, but this is caused by parallelisms in these derived groups.

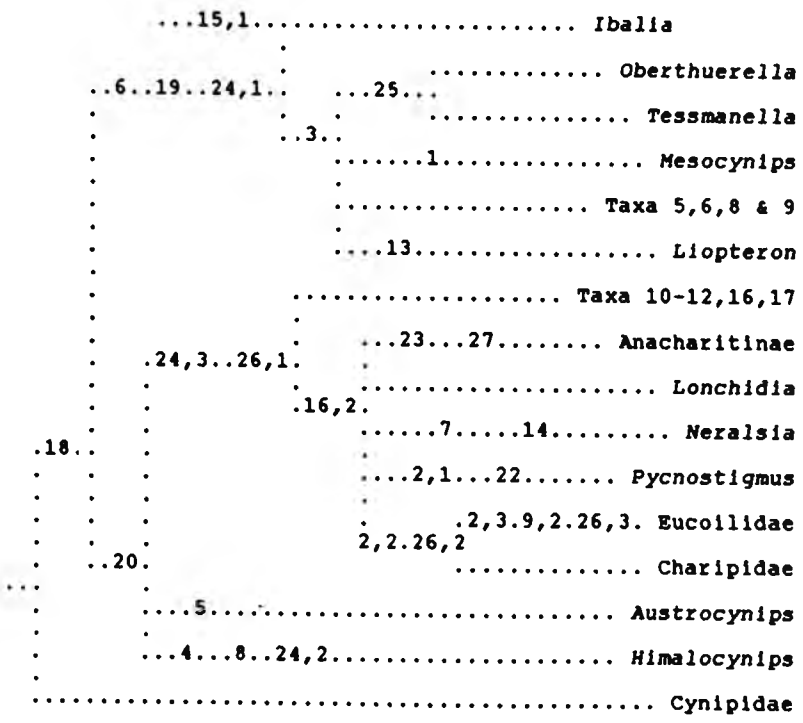


Figure 184. Clique cladogram for the head data.

Antennae

The antennal data was highly homoplasious and had the highest LeQuesne coefficient. Only 38% of the antennal characters got through to the antennal clique, and only two characters were synapomorphies in the master clique. Many of the antennal characters were of a rather speculative nature e.g. position of placoid sensilla; or the number of segments in the club (32.1). [There was a need to investigate such characters even though they were suspected to be very plastic features.] For example, the antennal cladogram (Fig. 185) shows a disparate assemblage of taxa (2-6, 13-15, 24, 27, 30 and 31) linked by the presence of an emarginate segment (character 31.1).

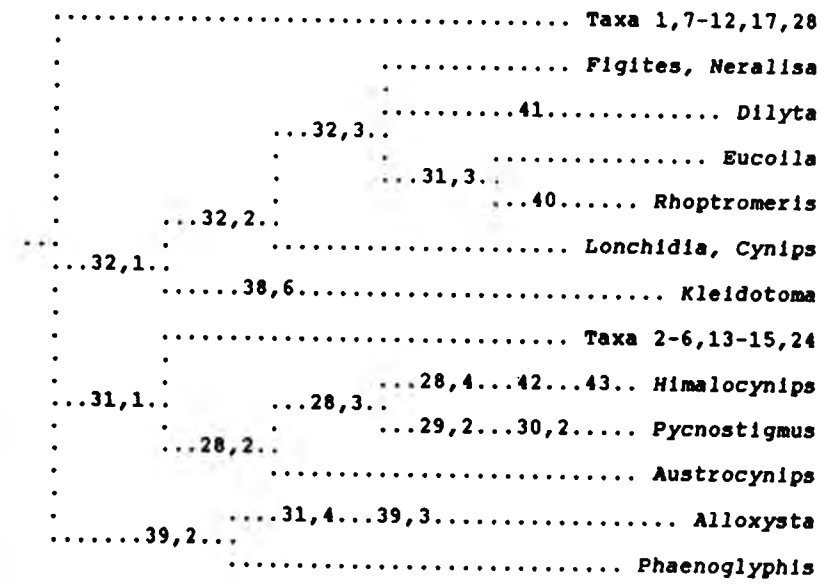


Figure 185. Clique cladogram for the antenna data.

Thorax

The thoracic data had the greatest number of characters (47) for almost the lowest LeQuesne coefficient (24%). Only the wings provide more characters, but their coefficient was poor (54%). The thoracic data made the

greatest contribution to the master clique, providing 37 characters, which is 10% more than any other suite. Twenty of these apomorphies were synapomorphies, so the thoracic data provides almost one third of the cardinal characters of the master clique. The thoracic cladogram is similar to, but slightly less resolved than, the master clique cladogram (Fig. 186).

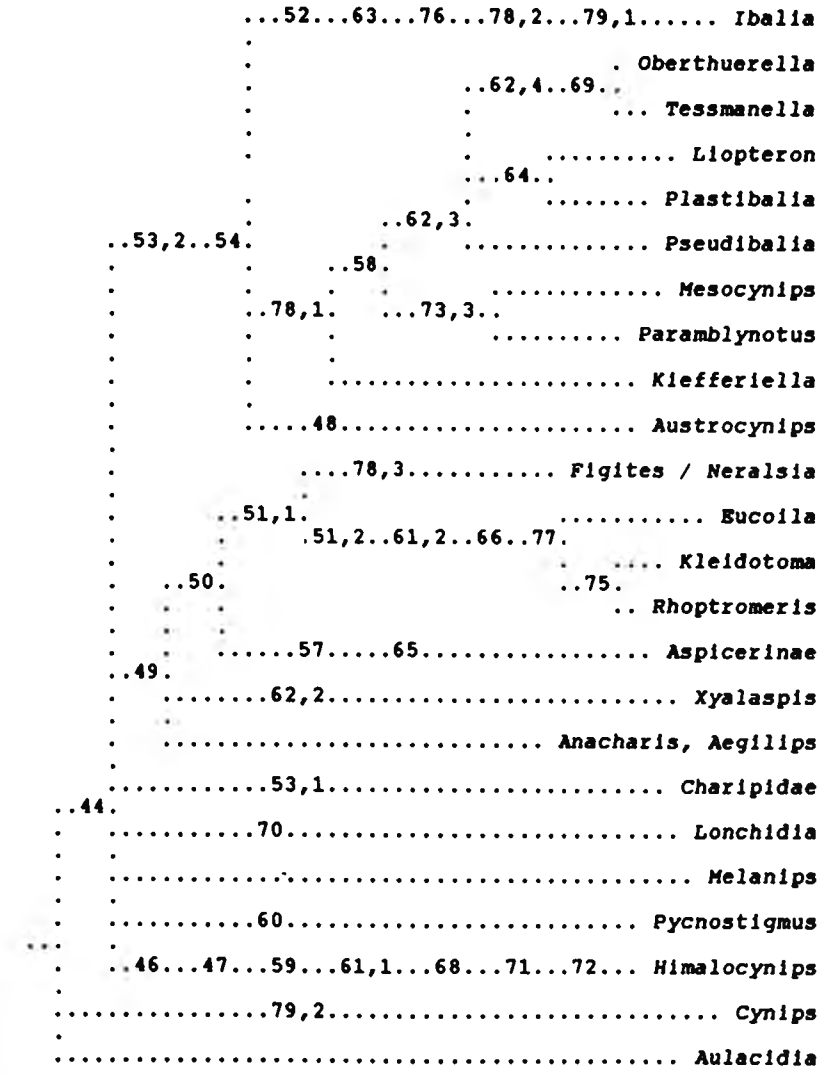


Figure 186. Clique cladogram for the thorax data.

Legs

There were only 16 leg characters but these were highly incompatible, having a LeQuesne coefficient of 65%. Leg characters formed only 8% of the master clique but 11% of the clique synapomorphies. Leg characters are important discriminants of the Ibalidae / Liopteridae lineage (see next chapter for reason). Apart from these taxa the leg cladogram provides very limited resolution of the Cynipoidea (Fig. 187). Character 120 (loss of mid trochantellus), forms a spurious group containing a wide range of taxa.

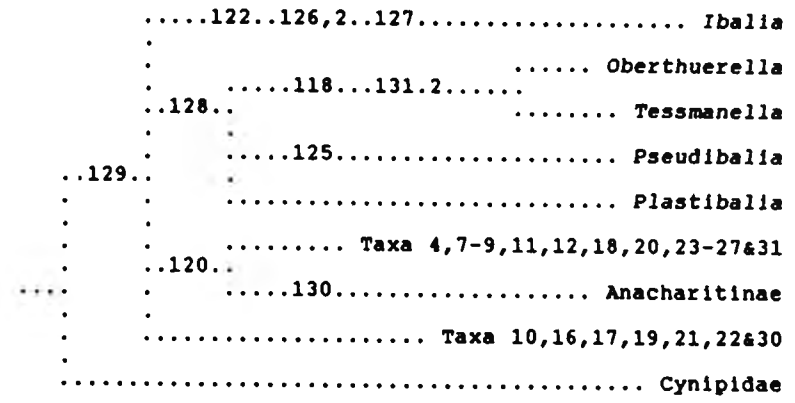


Figure 187. Clique cladogram for the leg data.

Wings

The wing data was particularly poor, and were badly affected by allometric factors. It was the only suite to show polar incompatibilities, no less than 14 of them, and these were caused by the large taxa. The 53 characters had a LeQuesne coefficent of 54%. Less than half of these characters survived analysis to contribute to the master clique and only 6 were synapomorphies.

The wing data cladogram is particulary poor, many taxa are "taken off" plesiomorphically (Fig. 188). Allometric characters progressively isolate the largest down to the smallest cynipoids and this cladogram bears no relation to the master cladogram.

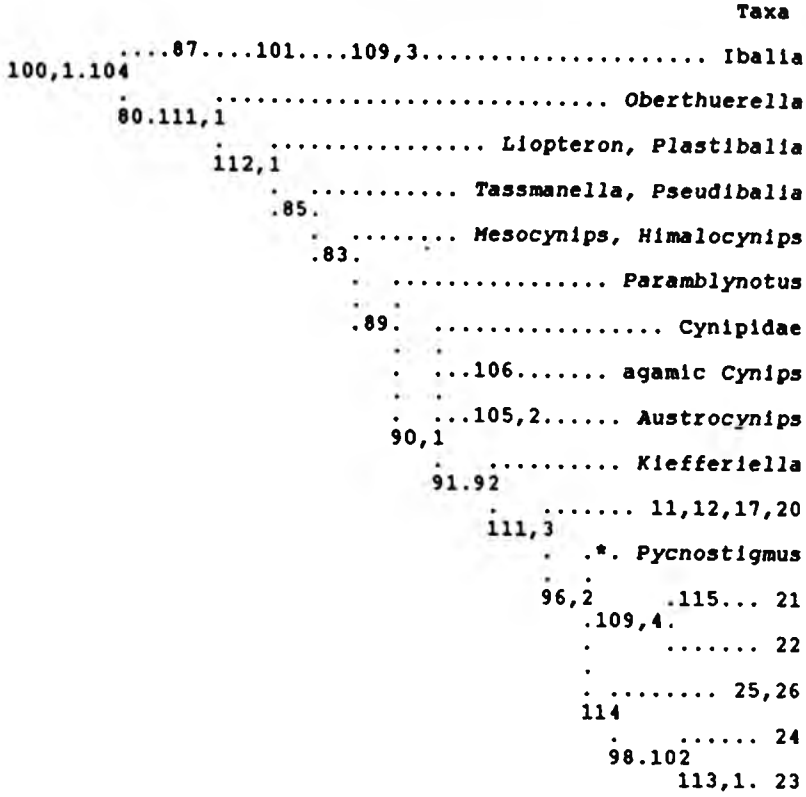


Figure 188. Clique cladogram for the wing data.
* = 97.1, 100.2, 105.1, 108, 109.1 & 113.2

Petiole

The petiole is here treated separately from the remaining gastral characters (see below) because they appear to be influenced by different evolutionary trends.

The 18 petiole characters had a good (low) LeQuesne coefficient (31%) and provided 11 (8%) of the master clique apomorphies, but only four of these were synapomorphies. The petiole suite cladogram is very poor (Fig. 189). It is likely that many of the characteristic petiole types represent reduction states and thus parallelism is widespread. For example, character 139 links the Charipidae, Cynipidae and *Himalocynips*;

similarly many taxa are linked by character 138.1 (petiole with rough sculpture).

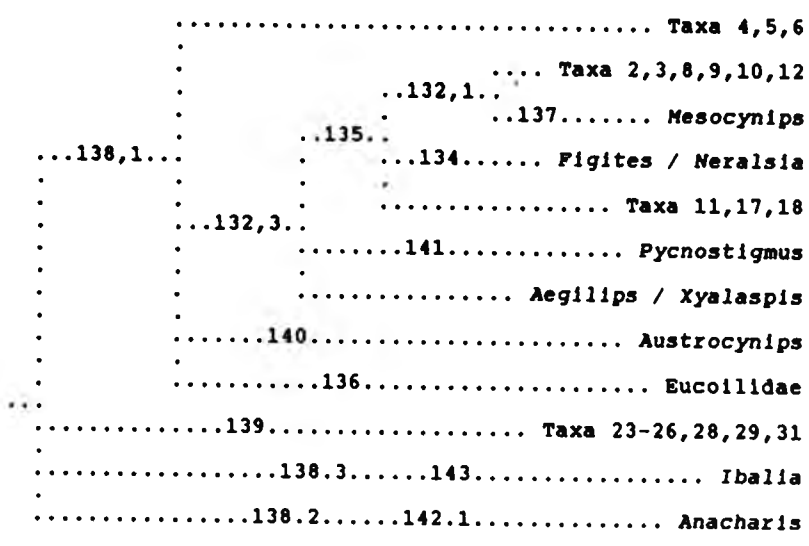


Figure 189. Clique cladogram for the petiole data.

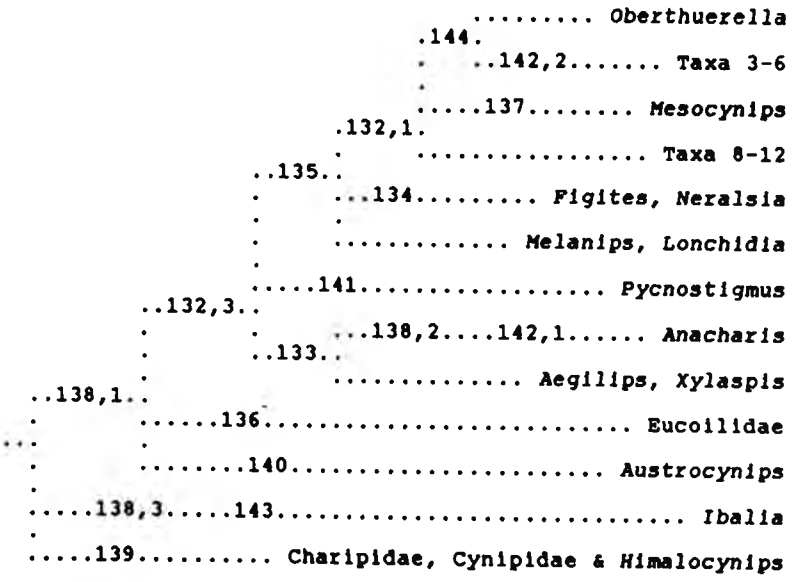


Figure 190. Revised petiole tree after sculpture reduction in elongated petioles was taken into consideration.

Several of the taxa with long petioles show a reduction of collar structure and petiole sculpture compared with related taxa. These secondary reductions in long petioles is particularly shown by *Anacharis*, *Liopteron*, *Plastibalia*, *Pseudibalia* and to a lesser extent *Callaspidia*. However the revised tree, with these scores reversed (characters 132.1, 132.2, 132.3, 135 & 138.1) is still not congruent (Fig. 190) with the master cladogram.

Gaster

The gastral data had a good LeQuesne coefficient (23%). However, it made the lowest contribution to the master clique, providing only 8 apomorphies and of these only half were synapomorphies. The gastral cladogram (Fig. 191) gives a very poor resolution of the taxa. It creates two spurious groups, *Himalocynips* is linked to *Cynips*, and the fusion of gastral tergites links the Eucoilidae with *Pycnostigmus* and *Dilyta*, these are clearly parallel states.

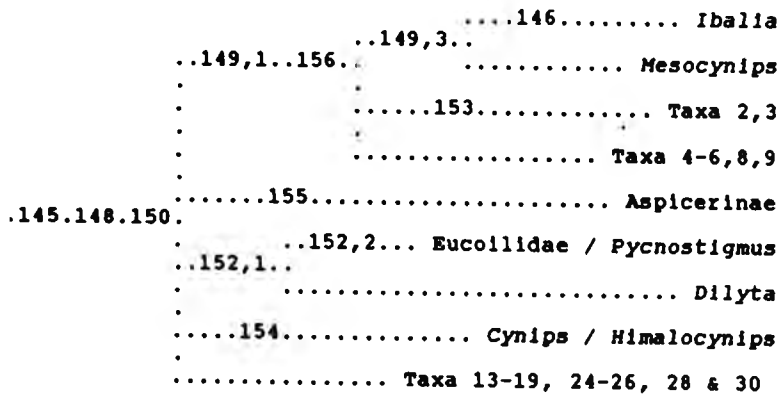


Figure 191. Clique cladogram for the gastral data.

Female genitalia

The ovipositor data had a good (low) LeQuesne coefficient, the 14 characters provided the master clique with 9 apomorphies and no less than 7 synapomorphies. Thus this data gives a high proportion (11%) of the of cardinal

characters of the master clique. The ovipositor synapomorphies are of major importance, as they link large groups of taxa. The influence of the ovipositor data far outweighs the size of its data-set. Apart from its diminished resolution, the ovipositor cladogram (Fig. 192) was congruent with the master clique.

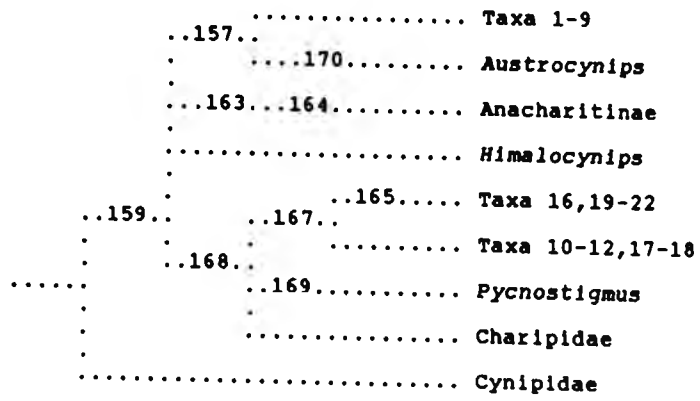


Figure 192. Clique cladogram for the ovipositor data.

Evaluation of suites: "good" suites / "poor suites"

The separate analysis of the character-suites shows that the head, thoracic, leg and ovipositor data were very important sources of synapomorphies. However, the petiole and gastral characters were not particularly valuable and the antennal data is highly homoplasious. The wing data is extremely misleading and heavily biased by allometric factors. Weld included size as a character, but this feature is part of many characters, especially the wing data, and is not easy to analyse independently.

WHAT WAS WRONG WITH THE OLD CLASSIFICATION ?

It is necessary to find out why the previous classification was so poor. So that any newly proposed classification does not suffer from the same faults.

Size of data-set

It has already been shown (Chapter 3) that the established classification was founded on too few characters to provide adequate resolution. The Weld, Quinlan and combined classifications consisted of only 25, 41 and 51 characters respectively. Analysis of these three data-sets produced cliques of only 15, 22 and 23 characters and only 9, 11 and 12 of these were synapomorphies (the characters vital for establishing phylogeny).

Character-suite balance

Table 48 shows the proportions of the character-suites used by Weld and Quinlan. Weld did not use head or ovipositor characters and yet, in the master data, these are the second and third most important character-suites for providing clique synapomorphies. Weld unfortunately chose two thirds of his characters from poor character-suites. In particular, wing venation and gastral characters were heavily used (half of all his characters). The Quinlan data relies slightly less on gastral and wing characters but many antennal characters were used and again almost two thirds of the characters are from poor character-suites.

It is now evident that the previous attempts at classification were poor because firstly there were too few characters to provide resolution and secondly the morphological distribution of the characters was not well balanced, too much emphasis being placed on gastral and wing characters. These two suites have a low percentage of synapomorphies and high degrees of incompatibility. Wing characters are particularly poor because some are strongly distorted by allometry. It was most unfortunate that Weld and Quinlan made little use of the more productive character-suites (head, thorax) and none of the singularly important ovipositor characters.

	WELD DATA		QUINLAN DATA		COMBINED		MASTER DATA	
	char. states	% of total	char. states	% of total	char. states	% of total	char. states	% of total
GOOD SUITES								
head	0	0	2	5	2	4	37	16
thorax	5	20	7	17	8	15	47	20
legs	3	12	7	17	9	17	16	7
ovipositor	0	0	0	0	0	0	14	6
% Good		32		39		36		49
POOR SUITES								
antenna	0	0	5	12	5	10	34	14
wings	6	24	8	20	10	20	53	23
petiole	3	12	4	9	5	10	18	8
gaster	6	24	8	20	10	20	15	6
size	2	8	0	0	2	4	0	0
% Poor		68		61		64		51

Table 48. Character-suites used in cynipoid classification

CONCLUSIONS

For this thesis 234 characters were investigated, an increase of 450% over the established classification. Analysis of these characters yielded 135 clique apomorphies, 68 of which were synapomorphies. This is a 600% increase in the number of apomorphies and a 300% increase in the number of synapomorphies, leading to an enormous improvement in resolution over previous studies. The characters are as extensive and as well balanced (amongst the character-suites) a representation of cynipoid morphology as is currently feasible.

Final postulate of cynipoid phylogeny

The Cynipoidea has been extensively analysed using cladistic techniques. The resultant postulate of the cynipoid phylogeny is shown in the following four trees (Figs 193-196).

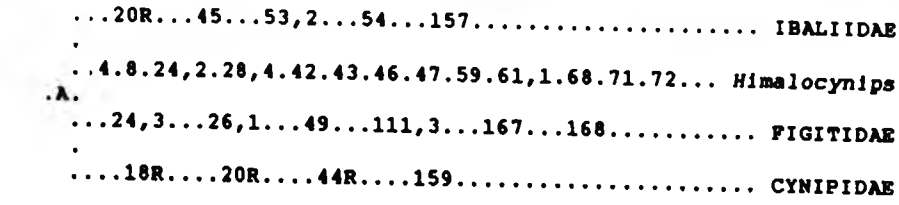


Figure 193. Cynipoid phylogeny: the four lineages.
[A = 18,20,44,100.1,104,145,148,150. R = reversal.]
[Polarity of 159 now reversed.]

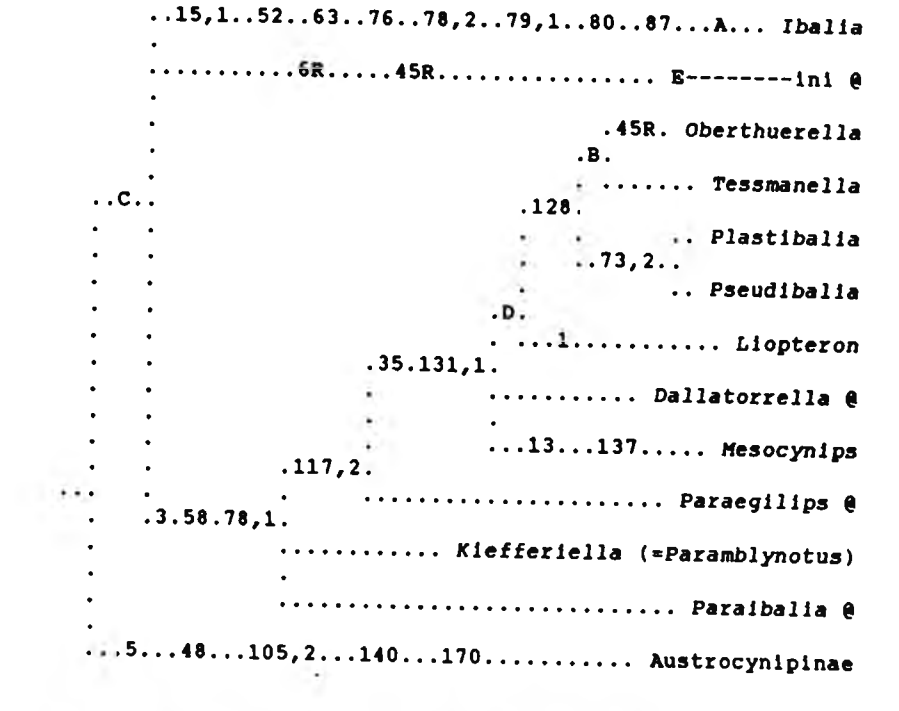


Figure 194. Phylogeny of the ibaliid lineage
[A = 101 109.3 122 126.2 127 138.3 143 146; B = 25 35R
62.4 69 118 131.2; C = 6 19 24.1 45 149.1 156; D = 12R
62.3 144 153. P = parallelism; R = reversal;
@ = extralimital taxa.]

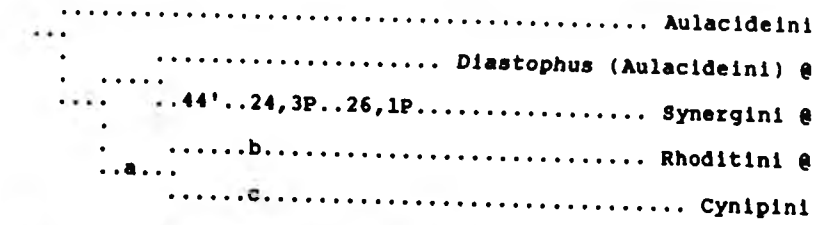


Figure 195. Phylogeny of the Cynipidae
[a = pronotum short dorsally, 1/7th. of its lateral length; b = hypopygium ploughblade-shaped; c = hypopygium spine-like; ' = character regained, @ = extralimital taxa.]

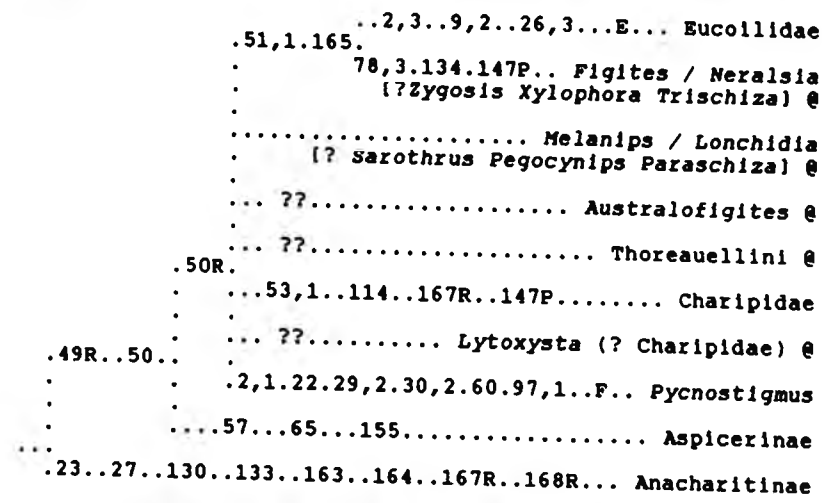


Figure 196. Phylogeny of the figitid lineage
E = 51.2 61.2 66 77 124 136 147P; F = 100.2 105.1 108 109.1 113.2 141 169. P = parallelism; R = reversal; ?? = lineage requiring more study; @ = extralimital taxa.]

The next stage in this study will be to investigate the biology of the Cynipoidea in terms of the reconstructed phylogeny. If the result is a coherent and believable sequence of evolutionary biology, then the phylogeny established in this chapter will be a reasonable approximation to the evolution of the Cynipoidea.

CHAPTER 6: DISCUSSION OF EVOLUTIONARY BIOLOGY

INTRODUCTION

Origin of the Cynipoidea

The earliest known fossil apocritans are from the Jurassic and the evidence from fossils indicates that cynipoids originated in the Berriasian (135mya) at the start of the Cretaceous (Rasnitsyn & Kovalev, 1988) (Table 50). The derived morphology and biology of the Cynipoidea means that the origin of the modern Cynipoidea probably occurred after the very first "flush" of apocritan radiation. If the cynipoids were a very early group of the Apocrita then the ibaliid lineage would be expected to consist of idiobiont ectoparasitoids (see below), like many other hymenopterous parasitoids of wood-borers. On the other hand, the cynipoids are by no means a late group (such as Apidae) and they probably originated along with other derived microhymenopterans in a second or subsequent wave of apocritan evolution.

The ancestral cynipoid is most likely to have been a "medium" sized apocritan (say 3-6mm long) [the Archaeocynipidae are approximately 3-4mm long] with a parasitoid biology perhaps similar to that of the ancestors of other microhymenoptera.

Parasitoidism

Hymenopterous parasitoidism is likely to have arisen when endophytic hymenopteran larvae consumed other endophytic larvae that they happened to encounter (Bradley, 1958; Handlirsch, 1907; Königsmann, 1977; 1978; Lanham, 1951; Raznitsyn, 1980; Telenga, 1969). Co-development by the adult female of host / prey location behaviour, and deliberate oviposition, through the plant material, near to the new source of larval food, led to a form of parasitoidism not far removed from the least specialized lifeway of modern Hymenoptera - ectoparasitic idiobiosis (Askew & Shaw, 1986).

Many potential hosts have an exposed feeding stage followed by a quiescent concealment period before pupation. Another parasitoid strategy - koinobiosis (Askew & Shaw, 1986) takes maximum advantage of this situation. Koinobionts oviposit onto or into their hosts when they are easily located, and larval development is delayed thus gaining the selective advantage of concealment within the host's pupation retreat. Ectoparasitic koinobiosis is restricted to a few groups (attachment of the egg to the host needs to be especially secure). However, endoparasitic koinobiosis is a very common lifeway which has evolved independently in several lineages of the more derived Parasitica. As far as is known all the parasitoid Cynipoidea are koinobiont endoparasitoids.

Cynipoid koinobiont endoparasitoidism

The cynipoid slowly develops inside its host, which continues to be mobile and capable of feeding. Later, when the host is ready to pupate (some Hymenoptera can control host pupation - Shaw, 1981; Varley & Butler, 1933), the cynipoid develops rapidly to a late instar, eats its way out, consumes most of the host remains (and thus kills the host), and then pupates within the host's cocoon or puparium. Most parasitoid cynipoids attack early larval instars of their hosts so often being early in the parasitoid succession on any given host.

Host range

The endoparasitoid must live in a physiologically demanding environment. Mechanisms must be developed to overcome or avoid the host's immunodefence system without seriously interfering with the host's metabolism. Defence suppression mechanisms are often specific, thus koinobiont endoparasitoids tend to be limited to a narrow host range. However, the parasitoid Cynipoidea have a surprisingly limited range of hosts (Table 49); only the Hymenoptera, Coleoptera, Neuroptera and Diptera are attacked. Other superfamilies of the Hymenoptera (e.g. Ichneumonoidea & Chalcidoidea) have a much broader host range. Moreover in

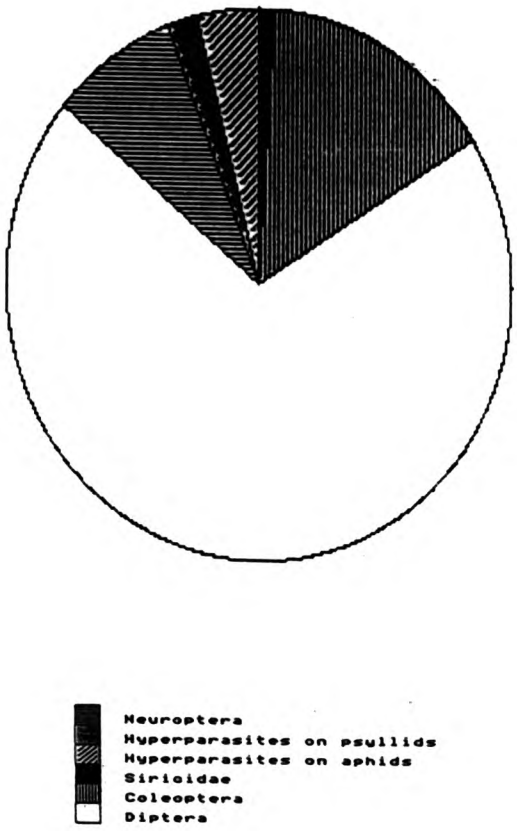


Figure 197. The host preferences of the parasitoid cynipoids. Over 70% being parasitoids of Diptera.

the Cynipoidea about 70% of all the parasitoid genera attack Diptera (Fig. 197) a remarkable specialization that has not been emphasised in the past. The Cynipoidea (in common with other Parasitica) that attack Diptera appear to have moved into an "evolutionary sink" and have little prospect of moving onto other host groups (Gauld, 1988).

Taxa	Host
Cynipidae	phytophagy: cecidogenic or inquilines
Ibaliidae	Siricidae larvae deep in pine trees
Liopteridae	Siricidae larvae in deciduous trees
	Coleoptera larvae in deciduous trees
Austrocynips	?? on *Araucaria* seeds
Anacharitinae	Neuroptera: Hemerobiidae
Alloxystinae	Hyperparasitoids of Homoptera, Aphidoidea via hymenopterous primaries
Charipinae	Hyperparasitoids of Homoptera, Psylloidea via hymenopterous primaries
Aspicerinae	Diptera, Cyclorrhapha (Syrphidae)
Figitinae	Diptera, Cyclorrhapha (many families)
Eucoilidae	Diptera, Cyclorrhapha (many families)

Table 49. Summary of cynipoid biology.

It appears that endoparasitoidism of distantly related (and therefore chemically dissimilar) hosts is difficult (Brues, 1921). There are no cynipoid primary parasitoids of the Apterygota, Exopterygota or of the non-insect Arthropods (e.g. spiders). It is not clear why the cynipoids, unlike some other groups (e.g. Chalcidoidea and Ichneumonoidea) have been unable to overcome these difficulties. The delayed larval development of koinobiosis means that there are no (or few) cynipoid egg (one species of *Ibalia* may be an exception) or pupal parasitoids (situations where rapid development can be an advantage).

The four cynipoid lineages

The original cynipoid lineage is likely to have developed koinobiont endoparasitoidism before subdividing into the four basic lineages (see last chapter). The

biology of *Himalocynips* is not known but each of the remaining three lineages has a distinctive biology. The ibaliid lineage are parasitoids of xylophagous hosts and are secondarily large. The Cynipidae are phytophagous and have remained medium-sized. The figitid lineage developed a lifeway closest to the original biology, they exploited smaller hosts, became secondarily small and eventually specialized mostly on Diptera. These three lineages are discussed below.

		million years ago
CAENOZOIC		
QUATERNARY		2-0
PLIOCENE.....		6-2
MIOCENE .		25-6
OLIGOCENE .	TERTIARY	40-25
EOCENE .		60-40
PALAEOCENE...		65-60
MESOZOIC		
UPPER CRETACEOUS		95-65
MAASTRICHTIAN ...		
CAMPANIAN .		
SANTONIAN .SENONIAN		
CONIACIAN ...		
TURONIAN		
CENOMANIAN		
LOWER CRETACEOUS		135-95
ALBIAN		
APTIAN		
BARREMIAN		
HAUTERIVIAN .		
VALANGINIAN .NEOCOMIAN		
BERRIASIAN		
UPPER JURASSIC		155-135
TITHONIAN		
KIMMERIDGIAN		
OXFORDIAN		
MIDDLE JURASSIC		175-155
CALLOVIAN		
BATHONIAN		
BAJOCIAN		
LOWER JURASSIC		200-175
TOARCIAN		
PLENSBACHIAN		
SINMURIAN		
HETTANGIAN		
TRIASSIC		240-200
PALAEOZOIC		600-240

Table 50. Geological stages of the upper Mesozoic (After Howarth, 1981).

The four main lineages must have developed early in cynipoid evolution because development of the complex host and host-plant interactions of modern cynipoids must have taken a considerable time (Askew, 1984). However, the fossils indicate that the Cynipoidea had gained its current configuration by the mid to late Tertiary.

PHYTOPHAGY: THE CYNIPIDAE

The Cynipidae are distinguished from all other cynipoids by being phytophagous. Evidence that this habit has arisen only once and that the family is holophyletic is provided by the unique depressed area on tergite nine (character 159, polarity reversed).

It is widely accepted that the Cynipidae are derived from (parasitoid) apocritan ancestors (Königsmann, 1978; Telenga, 1969). The postulated Neocomian origin for the Cynipoidea confirms that the cynipoids evolved from ancestral apocritans after the evolution of entomophagy in the Jurassic. Therefore the phytophagy of the Cynipidae is most likely to be secondary. So why did one cynipoid family revert to phytophagy? Firstly it must be said that adoption of the phytophagous habit is perhaps not such a large change as might be imagined. Certainly the Chalcidoidea have adopted this lifeway separately in several distinct lineages. Both the Cynipoidea and Chalcidoidea are small insects, and that is likely to be an advantage when developing in galls, especially complex galls. Also, the well-developed apocritan ovipositor has retained its suitability as a penetrator of plant tissue. However, the cynipoid reversion to phytophagy is most easily explained in terms of exploitation of the massive radiation of the angiosperms. Major shifts onto flowering plants occurred in many animal groups during the Lower Cretaceous. Indeed, from the Mid-Cretaceous almost all terrestrial animal life has been largely dependent on angiosperms as primary producers. Soon after the Barremian the angiosperms became established and rapidly

differentiated (Couper 1958; Friis et al., 1986). Modern cynipid host-plants were soon available for galling. For example Rosidae were present in the Albian and Fagaceae in the Turonian (Friis et al., 1987). It is possible that the Cynipidae were initially parasitoids of endophytic insects, perhaps stem-miners (Quinlan, 1986) but there is now no remnant of such a stage.

Malyshev's "seed-eaters" theory

Although Malyshev (1968) accepted that the Cynipidae are secondarily phytophagous, he felt that they (and other Apocrita) were derived from "seed-eaters". He equated the meristematic site of gall formation with plant embryonic tissue, and the nutritive area of the gall with the seed nutritive supply. He felt that the gall chamber was similar to the confines of the seed and that both the Cynipoidea and the seed-eaters show the same "imprint".

This theory of simplistic generalizations is based on analogy and the characters used to support it are symplesiomorphic (Königsmann, 1978), this theory is widely rebutted (Tobias, 1967, 1981). The kataplasmic galls of primitive cynipids do not have a defined nutritive area. A key element in Malyshev's argument is that a great majority of cynipidae are cecidogenic on generative organs (equivalent to seeds). This is simply not true of the less derived gall-wasps which are overwhelmingly stem-galling species (Kinsey, 1920). I see no reason to accept a seed-eating origin for cynipid phytophagy.

Climate and the expansion of the Cynipidae

After an origin in the Lower Cretaceous, the Cynipidae continued to develop its cecidogenic biology during the Upper Cretaceous and the fossil evidence indicates that this process was complete by the early Tertiary.

The climate during the Upper Cretaceous was relatively stable and this was perhaps the warmest interval during Phanerozoic time (Upchurch & Wolfe, 1987).

The latitudinal temperature gradient was low (Parrish 1987) and due to the abundant precipitation, humid multistratal non-seasonal forests occupied palaeolatitudes 32 degrees North to 32 degrees South (Creber & Chaloner, 1985). From the early Cenomanian the higher palaeolatitudes (45 degrees N and 45 degrees S) of Laurasia were populated by seasonal broad-leaf forest (Reid & Chandler, 1933; Dilcher, 1973; Parrish, 1987). Later the climatic gradation from pole to equator became less isothermal and there was a considerable replacement of the subtropical forests by modern high density deciduous forests (Upchurch & Wolfe, 1987). It was these North Laurasian forests that nurtured the Cynipidae and the expansion of these strongly seasonal forests provided ideal conditions for the success and radiation of the higher Cynipidae (especially the Cynipini) which could incorporate plant seasonality into their complex life-cycles.

Cynipoid cecidogenesis

Cecidogenesis can be caused, as in the Symphyta, by venoms injected at oviposition (Leach, 1987; McCalla et al., 1962; Meyer, 1957; 1987; Maresquelle, 1983). However, Cynipidae galls are initiated by secretions from the immature wasp. Cynipid eggs produce lytic enzymes (Bronner, 1973; 1977) that convert the underlying plant cells into a highly vacuolated concave pad of cells. At eclosion the larva moves into this cavity and within a few days is enclosed by plant tissue. Apart from the numerous digestive enzymes, the saliva of cynipid larvae contains auxins, amino acids and amides which promote gall growth (Rohfritsch & Shorthouse, 1982). In fact Molliand (1917) was able to induce gall formation by injecting a homologate of *Aulax papaveris* larvae into the host plant (*Papaver*). If the cynipid larva dies then gall formation stops (Shorthouse 1986).

Galls

There has been much speculation (see below) as to the

possible evolutionary advantage of developing the cecidogenic habit. The main theories involve supposed refuge / defence, microhabitat or nutritional advantages for the cynipoid.

Mani (1964) argued that galling has advantages for the plant - as an encapsulation response by the plant against the herbivore. However, galls diminish host plant fitness (Abrahamson, & McCrea, 1986; Craige et al., 1986; Weis, & Kapelinski, 1984; Schröder, 1967; Whitham, 1980). Further, if galling is a plant defence then its distribution would be correlated with plant phylogeny, as is the distribution of alkaloids and mustard oils. Price, Waring & Fernandes, (1986) have shown however, that the distribution of cecidogenesis is a function of cecidozoan, not hostplant phylogeny.

REFUGE / DEFENCE. One possible advantage of cecidogenesis is as a refuge or defence against parasites (Niblett 1940). However, the contents of galls have such a concentrated nutritive value that attempted parasitism, inquilinism or predation is almost inevitable (Mani, 1964; Shorthouse, 1973; Shorthouse et al., 1986). Evidence for the defence value of galls is not strong (Price & Pschorn-Walcher, 1988). For example, increase in gall size can reduce parasitoid attack (Weiss Abrahamson, & McCrea, 1985), but so can reduction in size (Price, Waring, & Fernandes, 1986). Similarly the high concentrations of tannic acid in some galls (over 50% in *Cynips tinctoria* - Marsden-Jones, 1953) could have a possible defensive function, but it is now thought that tannin content may not necessarily have the deterrent effect that was generally supposed (Bernays, 1981). Both Askew (1961) and Cornell (1983) explain gall diversity in terms of defence against the diversity of parasitoids. However, Price et al. (1986) showed that cecidozoans without parasites (e.g. some eriophyid mites and aphids) had similar levels of diversity. The defence factor clearly has some relevance because some galls develop nectaries (c.f. Bequaert, 1924)

that attract ants which, in turn, reduce gall parasitism by approximately 25% (Washburn, 1984). However, nectaries, and gall diversity are features of derived galls and would have little bearing on the evolution of the first cynipoid galls.

MICROHABITAT. The argument in favour of galls providing microhabitat advantages like shelter (c.f. Felt, 1940) is not strong. For example plant tissue closely parallels ambient temperature (Baust et al., 1979; Uhler, 1951) so the gall provides little thermal insulation, although it is possible that hygrothermal stress is reduced within the gall.

NUTRITION. It seems most likely that the early cynipoids developed cecidogenesis to provide the nutritional advantages of increased plant protein and mineral concentrations and reduced levels of phenols that occur in their galls (Price, Waring, & Fernandes, 1986; Shannon, & Brewer, 1980; Wangberg, 1978; Gandar, 1979; Shorthouse 1986). It may be supposed that cynipoid cecidogenesis originated when salivary secretions caused a swelling to appear at the feeding site. The greater the amount of the excrescence the greater the tendency to feed on it (Cockerell, 1890) and the greater the tendency to develop the growth promoters found in modern gall-wasps. Accompanying this habit would be the evolution of oviposition and other behavioural developments to locate the potential gall site.

1 Gall structure	- from simple to complex.
2 Reproduction	- from simple to complex.
3 Gall site	- from stem galls to bud galls.
4 Host-plant range	- from general to specific.

Table 51. Biological trends within the Cynipidae

Biological trends within the Cynipidae

The Cynipidae have four distinctive biological features each with an evident evolutionary trend (Table 51).

1. Gall structure

The morphological variety of complex cynipoid galls is specific to the cynipid species and not determined by the plant taxon. Some gall polymorphism does occur in cynipids, but this is correlated with insect activity, e.g. parasitism or secondary site for oviposition (Shorthouse & Ritchie, 1984).

The galls of the genera near *Aulacidea* are simple or kataplasmic galls (Kuster, 1911) with no tissue differentiation, the homogeneous gall parenchyma being little changed from the original plant meristematic tissue. Larval cells are not distinct and there is little hypertrophy. This tribe is less derived than other gall-wasps.

The galls of the Rhoditini (Blair, 1944) and to a greater extent, those of the Cynipini have evolved from kataplasmic galls (Wells, 1921), into complex, prosoplasmic galls, with a definite size, external form and internal structure (especially noticeable in unilocular galls). In these galls the plant cells lining the larval chamber differentiate to become a nutritive layer, the sole larval food, which is rich in acid phosphatases, soluble sugars and amino-soluble products (Bronner, 1977). The surrounding parenchymatous cells accumulate starch reserves which increase in concentration outwards, and there is a lipid gradient in the reverse direction (Shorthouse 1986). A vascular layer, which connects the gall to the vascular bundles of the host plant, develops between the nutritive layer and a supportive, lignified, sclerenchyma layer (Fourcroy & Braun 1967). A cortical layer of enlarged parenchyma cells contains tannins and large vacuoles which store water

(Maresquelle & Meyer, 1965). The cortex has an outer epidermis, the gall wall, which is derived from the epidermis of the host plant. It is a protective layer, often pigmented with anthocyanins, and may be rough, hairy, or have nectaries (Rohfritsch & Shorthouse, 1982). Winter galls harden as they age, thus increasing the protection against predation and parasitism (Askew, 1961). In some cases gall abscission may occur (Cosens, 1912; Hough, 1953), the wasp overwintering in the protection of the leaflitter.

The Synergini are (believed to be) incapable of gall formation, they inhabit and are dependant on the galls of other cynipids (and rarely those of the Chalcidoidea or Diptera). A few inquilines may slightly modify the external shape of the gall (Askew, 1961). Others cause more definite changes, for example *Cynips mirabilis* has a smooth spherical gall but *Synergus pacificus* converts it into a knobbly sphere (Meyer 1987). Parasites may have a similar effect (Shorthouse & Ritchie, 1984) e.g. the gall of *Diastrophus rubi* is given a ribbed appearance by *Eurytoma rosae* (Chalcidoidea).

Some *Synergus* species construct subsidiary chambers inside the host gall, making the galls plurilocular, and do not come into contact with the gall-causer (Sternlicht, 1968). Other species (e.g. *Periclistus*) develop so rapidly that they obliterate the host's chamber and may kill the gall-causer (Askew, 1971; Shorthouse 1973) and sometimes the host is eaten by the inquiline (Askew, 1984).

2. Reproduction and life cycles

Like most other Hymenoptera, some Cynipoidea have haploid males which develop by arrhenotokous parthenogenesis from unfertilized eggs and diploid females which develop from fertilized eggs. However, in the Cynipidae development of diploid females from unfertilized eggs (thelytokous parthenogenesis) is also prevalent (Askew, 1984). The Aulacideini and Rhoditini are surpassed in reproductive specialisation by the complex heterogony

found in the Cynipini.

I bisexual species

In *Diastrophus rubi*, *Aulacidea hieracii*, *Aylax minor*, *Xestophanes potentillae* and *X. brevitarsis* (all Aulacideini) both females and males occur although males are less common. Mated females produce females from fertilized eggs and males from unfertilzed eggs. These species are normally univoltine, the larvae overwinter in the gall and adults emerge in early summer.

II unisexual species

In *Phanacis hypochoeridis*, *P. lampsanae*, *Aulacidea pilosellae* and *A. substerminalis* (all Aulacideini) males are absent or very rare (<5%). Females normally produce only females, by thelytokous parthenogenesis. These species are also univoltine. Although a few Rhoditini may be bisexual most species are unisexual; males occur, but are rare. The species are univoltine and not heterogonous (Shorthouse & Ritchie, 1984).

III heterogonous species

Only one species of the Aulacideini is known to have this advanced reproductive mechanism. *Pedaiaspis aceris* has two alternating generations on *Acer*, an agamic generation on the roots and a sexual generation on leaves (Meyer 1987). Heterogony is particularly associated with the Cynipini. The female-only agamic generation lays unfertilized eggs in plant tissue, galls containing the sexual generation form and these develop quickly, usually in spring or early summer. Males and females emerge from these galls and mate. The fertilized female oviposits into the host-plant, and galls of the agamic generation develop slowly, overwintering and the agamic females emerge in the following spring (although exceptions occur). The life cycle may be from one to several years. The galls of the two generations are usually very dissimilar and on different locations on the host-plant. The most derived cynipini have highly complex heterogony, involving

different types of females in one generation. These systems are very far from being fully understood.

Presumably this form of life cycle increases reproductive potential (Askew, 1984) at the expense of some reduction in genetic variability. Early galls may have a low parasitoid load (Askew, 1984) and the autumnal galls are mostly more substantial, so the diversity may reduce mortality. However, the potential doubling of parasite opportunity must reduce some of the advantage.

The Synergini contain bisexual, but with both univoltine and bivoltine, species. In bivoltine species the two generations show morphological differences (Wiebes-Rijks, 1979) and do not necessarily attack the two generations of the same bivoltine host. *Synergus* species (or populations in polyphagous species) adapt to the optimum host seasonality, this may involve a one or two year diapause in the ultimate larval instar (Evans 1965).

3 Gall position

Each gall-wasp is specific in the position of its gall on the plant. Closely related cynipids often show resource partitioning and niche differences in the form of widely divergent gall structures and locations (Cornell, 1983).

Over half of the Aulacideini form galls in plant stems, about 25% of the species gall fruits or flowers, 15% are on leaves and 10% on roots. About one third of the Rhoditini are stem-gallers, the remainder have advanced to leaf-galling. Very few Cynipini gall stems, approximately 40% form galls on buds, 25% are on fruits or flowers, and 25% are on leaves.

Plant stems are likely to have been the primitive gall site. Galling soft stems must have been a relatively simple beginning for prosoplasmic gallers. The shift to ovipositing into undifferentiated tissue, like leaflets still within the bud, coincides with optimum host cell plasticity (Shorthouse, 1973; 1982; 1986) and must be an advantage for the formation of complex galls.

4 Host-plant range

The genera near *Aulacidea* represent about 15% of gall-wasp species, they gall a wide range of about 40 different plants and this accounts for approximately 90% of cynipid host-plant diversity. This assemblage includes the very few cynipid species that gall more than one plant genus (Kinsey, 1920). *Diastrophus* species gall Rosaceous genera (*Fragaria*, *Potentilla*, and *Rubus*), as do the Rhoditini (*Rosa* plus one species on *Rubus*). The restricted host-plant range of *Diastrophus* (Fig. 198) was one of the reasons why Kinsey (1920) described this genus as "incipiently specialized". Ritchie (1984) has confirmed this and showed that this genus is the sister-group of the Synergini.

The inquilines are usually host-plant specific but they often have broad host-gall ranges. Most species (*Synergus*, *Ceroptres*, *Saphonecrus* and *Euceroptres*) occur in galls on *Quercus*. *Periclistus* species are inquilines of the Rhoditini in Rose galls and *Synophromorpha rubi* and *S. terricola* are in *Diastrophus* galls on *Rubus*.

The Cynipini represent about 80% (Askew 1984; Kinsey, 1920; Felt, 1940) of the gall-wasps and they almost all gall *Quercus* (plus two genera on allied Fagaceae) species. The reason for this extreme specialization is not understood, *Quercus* belongs to a small family and has a limited distribution. However, oaks must have optimal host plant characteristics for complex galls. One such characteristic may be slow growth, which means that fresh plant tissue is available for galling, by the several generations, over most of the year (Malyshev, 1968). Also woody shrubs and trees may provide a good substrate for overwintering. Whatever the advantages of oaks, it is not apparent why other plants are so little used as hosts by the Cynipidae, especially when they are exploited by other gall-inducers e.g. Diptera (Darlington, 1968).

The available evidence indicates that the primitive Cynipidae galled a range of plants, especially those with

soft but robust stems (Fig. 198). *Diastrophous*, the Rhoditini and some inquilines have rosaceous host-plants, and in particular *Rubus* appears to be a likely ancestral host plant for all these taxa (Ritchie, 1984). Later the Cynipini dramatically radiated as gall-causers on *Quercus*.

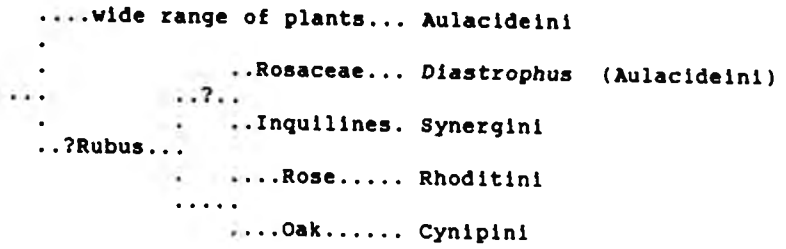


Figure. 198. Cynipidae: host-plants and phylogeny (After Ritchie, 1984).

Inquilines

Although Askew (1984) felt that the Synergini was a mixed assemblage, there is now good morphological evidence of their holophyly (see Chapters 4 & 5). The Synergini show several very derived states compared to other cynipids and show similarities with the Figitidae.

In general, inquilines are frequently related to their host species (Emery's rule - c.f. Wilson, 1971). For example, inquiline ants are closely related to their slave species (Gauld & Bolton, 1988). Therefore it is reasonable to ask (Shorthouse, 1975, 1980) if the Synergini are primitive gall-wasps, only just entering the cecidozoic lifeway, or derived cynipids that once were cecidogenic. The structure of the back of the head and the pronotum provide the answer, the Synergini are firmly placed in a derived position. It is therefore presumed that the inquilines are likely to have originated from a gall-inducing ancestor.

Origin of inquilinism

It can be speculated that a lack of oviposition sites or temporal urgency in relation to lateness of the season and development time, may have led to gall induction in the tissue of other galls. This could have been followed by an obligate inquilism and development of specificity. This theory is supported by the fact that the ability to induce cell proliferation is retained in many species e.g. *Periclistus pirata* (Shorthouse, 1980). A parallel situation occurs amongst inquiline Bees, where *Psithyrus* species take over the nests of *Bombus* species. Both Richards (1927) and Wheeler (1919) showed that the immediate cause of inquilinism in Bees was the urgency of oviposition.

Askew (1971) has suggested that inquilinism is a stage on the path from phytophagy to entomophagy. Although this is probably true, the Synergini are nevertheless not directly related to the parasitoid cynipoids.

Cynipidae larvae

The reversion to phytophagy has affected the larval stages of the Cynipidae. Unlike that of other cynipoids the cynipid larva is not markedly caudate, also it does not undergo hypermetamorphosis. The mandibles are relatively blunt - for feeding on plant tissue. Unlike gall-inducing sawflies and parasitoid cynipoids there is no external larval phase in the Cynipidae.

Larval development within the gall cavity has led to the cynipids having a characteristic "chunky" shape that is not seen in other Cynipoidea.

PARASITOIDISM OF HOSTS WITHIN TREES: THE IBALIID LINEAGE

Siricinae (Symphyta) hosts in Pine trees

The first Hymenoptera, the Symphyta, developed (in the Triassic) on the ancient Palaeozoic plant communities (Rasnitsyn, 1969,1980). A large element of this flora was

the Coniferopsida, and of these the Pinaceae began a major radiation so that the distribution of Conifers was probably pan-global by the Lower Cretaceous (Miller, 1976; 1977). Some of the sawflies (e.g. Siricidae: Siricinae) exploited this radiation. The parasitoid Hymenoptera originated in the Jurassic (Rasnitsyn, 1980) and, in time, some of these (e.g. *Rhyssa* & *Ibalia*) became parasitioids of the Siricinae in Pines. Brues (1921) noted that the host defence reaction increases with taxonomic distance, and thus parasitoidism of another hymenopteran may be relatively "easy" to establish.

In the Cynipoidea, parasitoidism of Siricinae in Pine trees led to the development of the ibaliid/liopterid lineage and the specialized suite of characters associated with xylophagous hosts (see below). One of the important aspects of this biology was the development of host location using the semiochemicals associated with the host and the host habitat. In the case of *Ibalia* the female antennates (Fig. 152) the tree bark (Spradbery, 1970) and locates the host by the odour of acetaldehyde (Madden, 1968) emanating from a fungal symbiont (e.g. *Amylostereum* spp.) of the host (Spradbery, 1973; 1974). The *Ibalia* female responds to this cue by inserting its ovipositor into the host's oviposition shaft and probing for the host (Fig. 153). The egg is placed in the haemocoel usually of an early stage larva.

Parasitoidism by *Ibalia* affects the feeding behaviour of the siricine larva, in the first year the tunnel is only half the normal length and it tends to turn toward the surface (a feature normally only shown at the end of the larval development) (Clausen, 1940).

The *Ibalia* larva develops inside the host, the third instar emerges from the host, completes feeding externally and moults to a long, non-feeding, fourth instar. The life cycle is long, and can be 3 years (Flanders, 1962), finally the adult *Ibalia* must chew its way out of the tree. Males emerge first and congregate near emerging females (Chrystal, 1930).

The two European species of *Ibalia* demonstrate complementary usage of the host resource. In August to October, *I. leucospoides* oviposits into early host instars, before they migrate too far from the oviposition shaft. However, in May to June of the following year, the less common, *I. drewseni*, oviposits into overwintering host larvae, of up to the third instar, even when these have tunnelled some millimeters from the oviposition shaft (Spradbery 1970). The two species respond to the odours of different developmental stages of the fungal symbiont (Madden, 1968). The emergence of *I. drewseni* coincides with that of *Rhyssa persuasoria* (Ichneumonidae) an ectoparasitoid of siricid larvae, and it is possible that *drewseni* behaves as a facultative cleptoparasitoid, utilising the drill shafts of *R. persuasoria* to gain access to host.

Ousting of the Pines

During the Barremian to Aptian (Table 50) the angiosperms became established and then dramaticaly increased in both diversity and abundance (Axelrod, 1959). Within a relatively short time (Aptian to Turonian) the angiosperms started to out-compete the gymnosperms. During the upper Cretaceous and early Tertiary the gymnosperms, ferns, horsetails and lycopods were replaced by an Angiosperm-dominated vegetation (Friis et al., 1987). At this time there were widespread extinctions (k-t boundary extinctions) in many groups that had once dominated the vegetation. These extinctions were then followed by an expansion of modern plant types.

Palynological evidence shows that Angiosperm radiation began at low palaeolatitudes (Brenner, 1976; Huges, 1976) and spread polewards (Axelrod, 1959). The range of the Pinaceae was reduced to mostly northern and high altitude habitats (Flenley, 1979; Upchurch & Wolfe, 1987). The Siricinae, and their parasitoids, e.g. *Ibalia*, have remained specialized (Benson 1942) on this reduced flora up to the present. Thus *Ibalia* is a relict genus with a basically alpine-boreal distribution.

Siricidae hosts in deciduous trees

While the Siricinae with their Pinaceae host-plants survived the angiosperm expansion, other Sawflies (e.g. Siricidae: Tremicinae & Xiphidriidae) underwent a host-plant shift to exploit the new arborescent Angiosperm fauna. Similarly, some of the parasitoid cynipoids responded, presumably to the same pressure, by host-switching from Sawflies in Pines to Sawflies in Angiosperm trees.

Although most species of *Ibalia* are associated with Siricinae in pines there are a few on deciduous trees. For example *Ibalia maculipennis* from the eastern U.S.A is a parasitoid of *Tremex* (Siricidae: Tremicinae) (Weld, 1952). It is likely that a cynipid with this second type of biology gave rise to the Liopteridae. Indeed one of the least derived liopterids, *Heteribalia divergens*, has also been bred from *Tremex* (Maa, 1949). Another similarity between *Ibalia* and the less derived Liopteridae is shown by *Kiefferiella* (= *Paramblynotus*) *yangambicola* comb. nov. This species has a gaster similar to that of *Ibalia*, and therefore may have a similar deep-oviposition type of biology. Once established, the Liopteridae became the main group of cynipoids exploiting hosts in deciduous trees.

Coleoptera in deciduous trees

The siricid fauna of deciduous trees formed a rather limited resource when compared to the greatly expanding numbers of xylophagous Coleoptera that were exploiting the radiation of arborescent angiosperms during the Lower Cretaceous. So it was almost inevitable that a second host-switch, from Symphyta to coleopterous larvae, occurred soon after the first move. The early Liopteridae were already adapted for deep-wood parasitoidism so this new shift to coleopterous hosts, some of which occur near to the surface, would have been a relatively simple change. A significant aspect of this host-switch would have been the retention of host-location by use of fungal cues.

Unfortunately there are few published host records

for the Liopteridae. *Kiefferiella* (= *Paramblynotus*) *zonatus* comb. nov. is a parasitoid of *Oncideres* sp. (Cerambycidae) (Diaz, 1973) and *Kiefferiella* sp. was recorded (Weld, 1952) from a *Acmaeodera* (Bruprestid) tunnel. To these, can be added a new record - *Oberthuerella crassicornis* from Kilimanjaro (Tanzania), on a dry stump of *Chlorophora excelsa* infested with *Trachyostus schausussi* (Coleoptera, Platypodidae).

As far as is known the Liopteridae exploit dry (sound or rotting) timber but it is possible that some have moved onto hosts in moist rotting timber, which have a different suite of fungal cues. It is also possible that some liopterids have gone on to attack Coleoptera in other habitats because the gaster of *Liopteron abdominale* is very similar to the gaster of those Proctotrupidae that parasitize beetle larvae in the soil and in fungi.

Parasitoidism inside the tree - stasis

The ibaliid / liopterid taxa develop in a relatively stable environment and the uniformity of conditions inside the tree are likely to be conducive to species conservation. Indeed there are many xylophagous examples of relatively primitive host groups and parasitoids which have persisted as relicts of a once larger fauna (Brues, 1921; 1927). The frequency of this lifeway encourages the speculation that xylophagous Coleoptera are relatively "easy" hosts with weak immune defences. However, although wood-boring / -probing is a relatively primitive lifeway, it is a specialization, involving morphological adaptations, and thus is not the ancestral lifeway of the Apocrita.

Austrocynips

Like *Ibalia*, *Austrocynips* is a Pine relict species, it was probably more widespread in the Southern Hemisphere but now it is only known from one Australian locality. The details of its biology are not known, but it occurs on the Hoop Pine (*Araucaria cunninghami*). It may be (Riek, 1971)

associated with the cones, if so that would be a specialization. That might explain why it has a long ovipositor (for ovipositing into seeds inside cones) but not the characters associated with the biology of the Ibaliidae/Liopteridae.

Himalocynips

Although *Himalocynips* has some morphological similarities with the large cynipoids, especially *Austrocynips*, it does not have a looped ovipositor. Nothing is known of its biology other than that it was found at 6000ft. Its rarity (only two known specimens) may indicate that it is a relict species. It is a relatively large cynipid so it could perhaps be associated with Pine or broadleaf trees (ancient forests of both types are present in the Himalayan region).

CHARACTERS ASSOCIATED WITH XYLOPHAGOUS HOSTS.

Many of the characters of the 53.2 group form an adaptive character-suite which is associated with the biology of this group. The Ibaliidae, Liopteridae and possibly *Austrocynips* all parasitize symphytan or coleopterous hosts which live within the wood of trees (some may be subcortical). There are two separate problems associated with this habitat - reaching the host in order to oviposit, and secondly emergence of the adults from the tree.

The most obvious morphological adaptation for reaching to the host is a long and strong ovipositor, and all the 53.2 taxa have this feature. As the cynipoid ovipositor is internal, the confines of the gaster neccesitates coiling the long ovipositor (Fergusson, 1988) within the gaster (character 157). Following from this there are associated changes to the proportions of the gastral segments (character 705). Other characters that assist deep oviposition are the possession of a long

petiole (142) and, in some Liopteridae, a tangential attachment of the petiole to the rest of the gaster (144), both of these characters increase gastral mobility.

Getting an egg onto the host is not so difficult, especially if, like *Ibalia*, the host's oviposition tunnel is used. The great problem of exploiting this habitat is escape! The cynipoid must chew and squeeze its way out, and to do that an array of adaptive characters has been developed. Firstly it needs strong, massive rather than sharp, mandibles (19). These mandibles need a strong mandibular axis and that involves having the hypostomal crests well separated (25) and set in a depression (24.1). Also the mouthparts and clypeus tend to be modified (1 & 3). Wriggling out of the escape tunnel is aided by spurs and ridges on the legs (118, 122, 123, 125, 126.1 & 126.2), possibly by bifid claws (131.1 & 131.2) and by having elongated tarsal segments (127, 128). Coarse sculpture on the head (16.1) and thorax (53.2) including distinctive transverse ridges (54), and scutellar spines (in some liopterids) (62.3, 62.4) probably all help to gain purchase on the inside of the tunnel. The head can have a facial and a frontal carina (6, 11); and scrobes (12) protect the antennae. The cynipoids exploiting this habitat tend to be large and this size factor is reflected in allometric characters, such as features of the wing venation. The thorax is often slightly flattened and the propodeum elongated.

Character congruence amongst the Parasitica

Parasitism of hosts in the deep-wood habitat is a relatively primitive lifeway of the parasitic Hymenoptera and it occurs in many of the less derived lineages. In each of these groups a very similar character-suite has evolved independently. This is a remarkable example of adaptive character congruence. Similar characters occur in the Pelecinidae, Monmachidae, Vanhorniidae, some Chalcidoidea (e.g. *Leptofoenus*), Stephanidae, Aulacidae, Megalyridae, Ichneumonidae (e.g. *Rhyssa*) and Braconidae (Doryctinae) - Table 52. These taxa tend to have rough

sculpture, a long propodeum, a flattened thorax, strong claws, elongated legs, a large head with strong mandibles, and powerful mandibular muscles.

	PELECINUS	MONOMACUS	VANHORNIA	LEPTOFOENUS	STEPHANIDAE	AULACIDAE	MEGALYRIDAE	RHYSSA	DORYCTINAE
MANDIBULAR MODIFICATIONS									
Strong mandibles	+	+	+	+	+	+	+	+	-
Modified mouthparts / clypeus	-	-	-	-	+	+	+	+	-
Hypostoma in cavity	+	+	+	+	+	+	+	+	+
Wide hypostoma	+	+	+	+	+	+	+	+	+
HEAD SCULPTURE									
Head sculpture rough	+	t	-	+	+	+	+	-	-
Median facial carina or hump	+	+	+	-	+	+	+	-	t
Frontal carina or hump	t	-	-	-	+	-	-	-	+
Scrobes	t	-	-	+	-	-	+	-	+
THORACIC SCULPTURE									
Pronotal tooth, hump or ridge/s	+	+	-	+	+	-	-	+	+
Rough sculpture	-	-	-	+	-	+	+	+	+
Transverse mesoscutal ridges	-	-	-	+	-	+	-	+	+
LEGS									
At least one spur, peg or spine	+	-	-	+	+	+	+	-	+
With strongly thickened region	+	+	-	-	-	-	-	-	-
Tarsi, or all of leg, elongated	+	+	+	+	+	+	+	+	+
Strong claws	+	+	+	+	+	+	+	+	+
SIZE & SHAPE									
Large head	+	+	+	+	+	+	+	+	-
Long neck	-	+	t	+	+	+	-	-	+
Propodeum long	+	+	+	+	+	+	+	+	+
Thorax dorsally flattened	+	t	t	+	+	t	t	+	+
OVIPOSITOR/GASTER LENGTH									
Petiole long	-	+	-	+	+	-	-	-	+
Gaster long	+	+	+	+	+	-	-	+	+
Ovipositor long	-	-	+	+	+	+	+	+	+
Ovipositor toothed	+	-	-	+	+	t	+	+	+
Petiole attachment very mobile	+	+	-	+	+	-	-	-	-

Table 52. The congruence of adaptive characters associated with hosts deep in wood. [T = trace, weak or +/-.]

The modifications take slightly different forms in each group. Deep penetration is achieved in the cynipoids by a long ovipositor which is coiled inside the gaster. In

Vanhornia the ovipositor is long and external, but it is carried in a ventral groove (Mason, 1983). The Ichneumonidae have a long trailing ovipositor and the terminal gastral segments can pivot. In *Pelecinus* (Mason, 1984) and *Monomachus* the ovipositor is short but it is at the apex of a remarkably long gaster. These two genera may oviposit into soft or rotting wood, which would allow them to thrust the gaster into the substrate.

In nearly all cases the gaster is very flexible, this is achieved either by a complex hinge between gaster and propodeum, or by a long gaster or petiole. The dorsal flattening of the thorax is often an adaptation for moving under horizontally layered substrates, and occurs in various habitats e.g. within grass stems (Fergusson, 1983), and in this character-suite it may assist movement under bark or in the host's tunnels.

There is most variety in the rough sculpture characters, as might be expected with a more "plastic" type of feature. The most remarkable example being the ring of spines around the median ocellus in the Stephanidae. The remaining characters are rather variable, e.g. the clypeal modification, and these may relate more to host-specific activities.

The doryctines are marginal examples of this character-suite, many are parasites of beetles in softer (rotting) wood and do not show the modifications for hard healthy wood but some taxa are clearly modified for this latter habitat and the example chosen here was *Curtisella*.

The chalcidoid genus *Leptofoenus* is a classic example of the dangers of this type of adaptive character-suite, because it was these very characters that caused it to be mistakenly placed in the Aulacidae until LaSalle & Stage (1985) recognized its correct position.

BIOGEOGRAPHY

In terms of their distribution the Cynipoidea divide into two units - the Cynipidae + figitid taxa which are Laurasian, and the ibaliid lineage which are mostly

Gondwanan.

Laurasian cynipids

The Cynipidae and the figitid lineage have essentially the same, Holarctic distribution. About two thirds of all cynipoid genera occur in the Holarctic; 25% in the Palaearctic, 25% in the Nearctic and the remaining 16% (approximately) are common to both regions (percentages based on Weld, 1952). This strong bias suggests a Laurasian origin for these taxa [even after making allowance for the limited number of collections from the tropics].

The superfamily is reasonably well represented in the Neotropical region (17% of all genera) but poorly represented from the rest of the world. The Ethiopian, Indo-Oriental, Polynesian-Australasian regions each having only 5% (approximately) of the genera. In particular, the gall-wasps are poorly represented in the tropics, although other cecidogenic insects (e.g. Thrips, Scale-insects and Gall-midges) are present. (Gagné, 1984).

Endemism is not very marked in these cynipoids. The Pycnostigmatinae are restricted to Africa and there are some interesting genera from the Australian region (see extralimital taxa). However, in general there are no obvious large-scale distributional patterns.

From the origin of the cynipoids in the early Neocomian (see Chapter 5) until the Upper Cretaceous, North America and Europe remained in tectonic contact (Pitman et al., 1974). The exchange of species would have been hindered only by shallow seaways, and even these may have been crossed by land bridges (e.g. the Faeroes bridge) (Parrish, 1987; Vail et al. 1977). Therefore these cynipoids are likely to have become dispersed in the North before the Coniacian when Greenland + Scandinavia moved away from Canada (Schuchert, 1955).

From this primary distribution in Laurasia a restricted number of cynipid and figitid genera then spread to the rest of the world. In particular the Eucoilidae have radiated in the tropics.

Distribution linked to that of Pine trees.

Unlike the Cynipoidea mentioned above the groups of the ibaliid lineage have major distributional pattens that correlate with their phylogeny. The distributions of the Ibaliini and *Austrocynips* have already been mentioned in connection with the Pine-associated evolutionary biology of these taxa. *Ibalia* is basically a boreal genus which has a similar distribution to that of Pine trees. *Ibalia* now occurs in Australasia, where it was introduced to control Sawflies (Taylor, 1965).

Vicariance and dispersal of the Liopteridae.

Hennigian principles can be applied to biogeography, and area cladograms constructed by superimposing areas of endemism onto morphological cladograms (Humphries & Parenti, 1986; Nelson 1978; Nelson and Platnick, 1981). The area cladogram for the Liopteridae (Fig. 199) shows a perplexing alternation of Old and New World taxa. Apart from the Oberthuerellinae the subfamilies of the established classification are not supported.

In order to improve the resolution of the biogeographical cladogram, the locality data of a large number of Liopteridae was examined. This data shows that the Oberthuerellinae is known only from the Ethiopian region. The "Liopterinae" is from the Neotropical (*Plastibalia* & *Liopteron*) and Sonoran (*Pseudibalia*) regions. The "Mesocynipinae" occurs in the Sonoran, Neotropical, Oriental (*Kiefferiella* and *Mesocynips*),

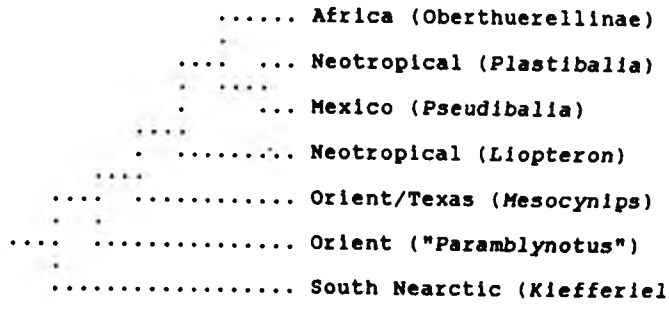


Figure 199. Area cladogram for the ibaliid lineage.

Ethiopian, Australasian (*Dallatorrella*) and just into the East Palaearctic region (*Heteribalia*). Distribution maps of the three "subfamilies" illustrate the difficulty (Figs 200, 201): the Oberthuerellinae and the "Liopterinae" each have a distinct range but the "Mesocynipinae" are pantropical and overlap the other two distributions.

It will be shown below that this distribution pattern, when considered in the light of plate tectonics and the separation of Gondwana, can be used to explain why parts of the liopterid classification are paraphyletic.

Postulate of liopterid distribution

The expansion of the angiosperms, during the Upper Cretaceous led to the development of extensive Angiosperm forests between palaeolatitudes 32 degrees North and 32 degrees South (Creber & Chaloner, 1985). The Liopteridae responded to this major floristic change by switching from hosts in gymnosperms to exploit hosts in the southern part of these new, high density, Angiosperm forests (see sections of this chapter on climate and the Cynipidae, and parasitoids within trees). Evidence from the cladogram and distribution records leads me to the speculation that *Kiefferiella*, was the first modern liopterid. It probably originated in the forests of the Borneo-Australasian-Antarctic plate and then expanded westwards from the "Orient" across southern latitudes. However, very few, if any, "mesocynipines" reached Africa from this plate because of the south-western arm of the Tethys Sea which was expanding between Africa and Antarctica in the Hauterivian (Howarth, 1981) (Fig. 202). Between the Hauterivian and the Cenomanian, *Kiefferiella* and other "mesocynipines" expanded northwards in the Neotropical forests. It is likely that the "mesocynipines" that reached Africa did so from the Neotropical plate before its separation from Africa in the Cenomanian. Eventually the "mesocynipines" reached the Sonoran region, their northern limit in the West; they similarly expanded northwards in the East and reached Japan and mainland China.

Figure 200. Distribution of the Mesocynipinae.

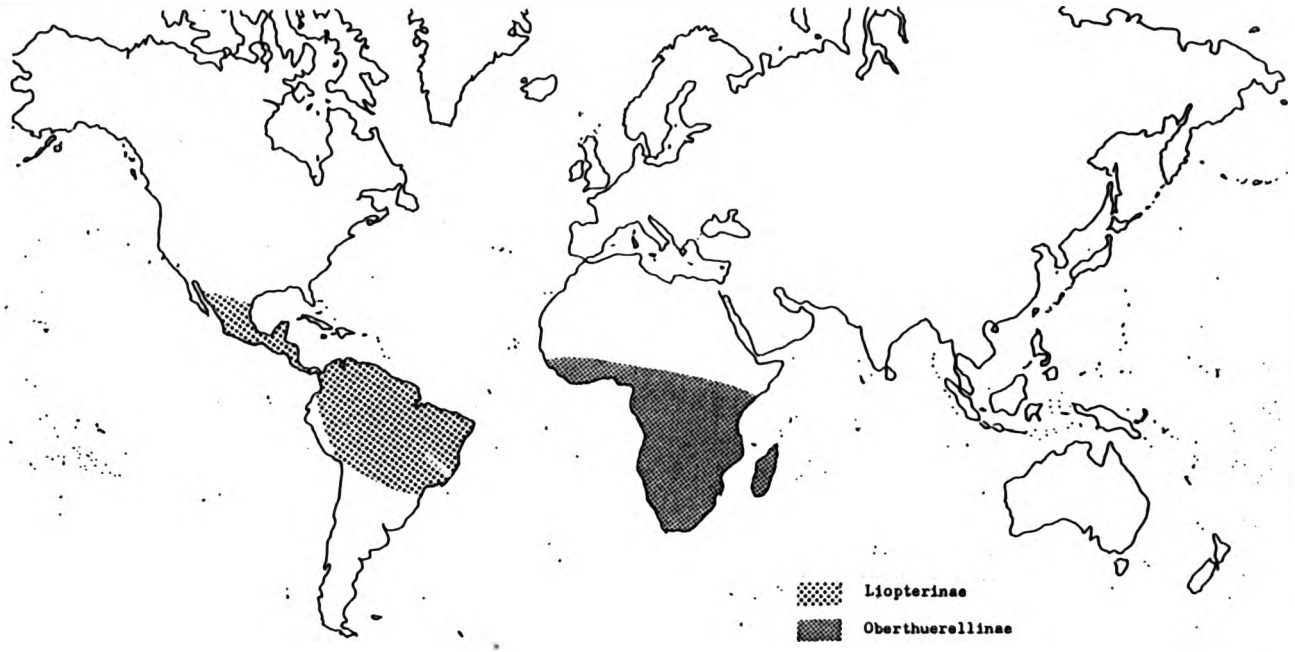


Figure 201. Distribution of the Liopterinae and Oberthuerellinae.

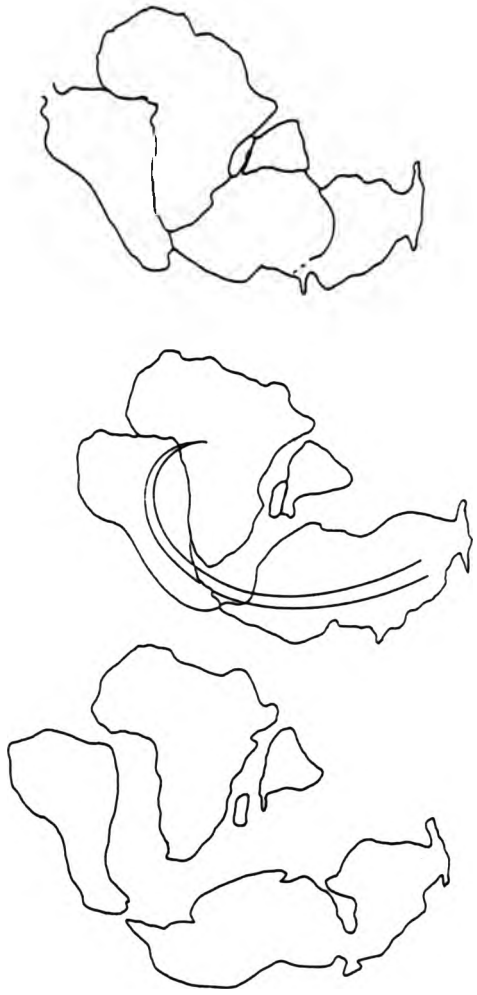


Figure 202. Palaeogeography and liopterid radiation. Approximate positions of southern continental plates (land + epicontinental sea) in the Triassic (top), Hauterivian (middle) and Senonian (bottom); before, just after, and well after, the primary radiation (main direction shown by the arrow) of the Liopteridae (Maps after Howarth, 1981).

At or about the Aptian - Albian, one element of the Neotropical "mesocynipine" lineage formed a separate group, which became the "Liopterinae". Distribution records indicate that this occurred in the North or North East of the Neotropical region. The reason for this event is not known but it may have involved a host-related specialization.

At this time (Aptian-Albian) South America and Africa were still joined in the North, but the rift-faulted division between them was open at the southern end and the sea reached as far North as Angola (Maack, 1969). A more derived element of the new North East Neotropical "liopterine" lineage, originated and crossed into Africa before this continent finally separated from the Neotropical plate in the Cenomanian (Reyment & Taitt, 1972; Reyre, 1966). Because of its taxonomic isolation this last, oberthuerelline, lineage did not interact with the very few "mesocynipine" species that had also crossed to Africa. Once established in Africa the Oberthuerellinae specialized and rapidly developed many autapomorphies.

In the Neotropical region, the "liopterine" lineage was not sufficiently isolated (taxonomically or geographically) from the "mesocynipine" lineage to avoid interaction, and this accounts for the paraphyly of the "Liopteridae" and "Mesocynipinae".

During the Senonian - Tertiary, sea-floor spreading and continental drift led to further breakup of Pangea (Fig. 202). Sea levels were relatively high (Savin, 1977) and the biogeographical distribution of the Liopteridae was almost in its modern configuration.

The Borneo-Australasian-Antarctic plate finally separated into its constituent parts and the eastern "mesocynipines" "rode" on the Borneo plate into the Orient and, presumably by island hopping, reached Japan and mainland China. Eventually, global climatic cooling led to a reduction of the tropical forests which left the Liopteridae isolated as relict species with their present distribution pattern.

The Palaearctic nature of the Indian fauna is a

result of the separation of the Indian plate (Moullade & Nairn, 1978) before the origin of the Cynipoids. Only when it collided with the Palaearctic, in the Tertiary, was it colonised by cynipoids. Similarly the presence of the Oberthuerellinae in Madagascar must have been a recent event, perhaps aided by man, because the Malagasy plate was isolated (Moullade & Nairn, 1978) before the origin of the cynipoids.

PARASITOIDISM OUTSIDE THE TREE: THE FIGITID LINEAGE

Origin of the figitid biology

The third major cynipoid group, the figitid lineage, consists of species (parasitoids of larvae) with relatively vulnerable larval stages. Although some species of the figitid lineage parasitize hosts within plant tissue, many parasitize more exposed hosts and tend to develop quite rapidly (for koinobionts), being bi or trivoltine (Roberts, 1935).

When host preferences are plotted on the figitid phylogenetic tree, it is clear that figitid biology originated on the predator complex associated with aphids. The aphid-associated cynipoids exhibit three distinct biologies - parasitoidism of aphidophagous Neuroptera, parasitoidism of aphidophagous Diptera and hyperparasitoidism of aphids. Hyperparasitoidism is a derived lifeway (see below), so which host group came first, Diptera or Neuroptera? Gauld (1988) has shown that it is most unusual for hymenopterous parasitoids of Diptera to make any significant host-shift to other groups. The considerable adaptations required to overcome the dipterous immune system (see below) once attained, tend to limit the parasitoid to this host group. Parasitoidism of Diptera is obviously a major evolutionary step, in comparison the Neuroptera appear to be less "difficult" hosts. In fact the Neuroptera have much to recommend them as the early hosts of the figitid lineage: they are not too small (parasitoidism of the smallest hosts is a derived feature in the Cynipoidea), they are an ancient insect group but, like the Cynipoidea, they

exploited the faunal changes associated with Angiosperm radiation. The Neuroptera do not appear to have effective chemical defences, and they have a vulnerable inactive cocoon stage.

Therefore it seems very likely that the ancestral figitid was a parasitoid of Neuroptera and that this biology has persisted up to the present in the Anacharitinae.

Neuroptera frequently occur in the crevices of shrubs and trees (Lipkow, 1969). or even under bark (Psychopsidae). Thus the three main cynipoid lineages all show, at least initally, a distinct plant association.

Of the three major cynipoid groups, the figitid lineage has a biology (exophytic parasitoidism) closest to that of most apocritans and therefore, it is speculated, closest to that of the Cynipoid ancestor. If the cynipoid ancestor was a parasitoid of Neuroptera then parasitoidism of hosts within their cocoon could have led the cynipoidea to the development of endoparasitoidism and then koinobiosis. Also parasitoidism of Neuroptera had already been achieved elsewhere in the Apocrita - for example the Heloridae (Proctotrupoidea s.s.) (Fergusson & Smith, 1974), one of the earliest (Jurassic) apocritan families (Rasnitsyn, 1980).

Anacharitinae: parasitoids of Neuroptera

Anacharitines are solitary endoparasitoids of Hemerobiidae (Neuroptera) larvae (Cave & Miller, 1987; Handlirsch, 1886; Miller & Lambdin, 1985). During oviposition the parasitoid curves its gaster downwards, between the legs, and inserts the ovipositor into the centre of the hemerobiid's dorsum. This oviposition technique accounts for the distinctive petiole of the Anacharitinae (character 133) and the tendency for the petiole to be long (142.1). It may also be the reason for the reduction of the female genitalia (characters 163 & 164). The characteristic mandibular tooth (character 23) and the spine on the claw (130) are probably modifications for cutting open and holding the host's cocoon during

emergence.

Oviposition is into late second and third instar larvae, a later host stage than that exploited by most primary parasitoid cynipoids and this may be an indication of a biology less derived than that of other figitid taxa. The host larva is allowed to spin its cocoon before it is killed. The last larval instar of the anacharitine emerges from its host and in a short external phase [probably common to all parasitoid cynipoids] eats the remains. The mature anacharitine larva pushes its gaster through cocoon to excrete the meconium, withdraws its gaster back inside the host's cocoon and then pupates (Selhime & Kanavel, 1986). There may be a facultative larval diapause, induced by short daylength, and hibernation is as a late larva or prepupa within the host's cocoon.

Pycnostigmatini

Pycnostigmus has a very specialized and distinctive morphology, but unfortunately its biology is unknown. Weld (1952) commented on the similar fusion of gastral tergites in *Pycnostigmus* and the inquilines (Synergini). However, this also occurs in the Charipinae and Eucoilidae and it does not imply an inquiline lifeway.

Aspicerinae & *Melanips*: parasitoidism of the Syrphidae

The next stage in the evolutionary biology of the Figitid group was the lateral shift, from the anacharitine lifeway of parasitising aphidophagous Neuroptera to the aspicerine / *Melanips opacus* lifeway of parasitising aphidophagous Diptera (Syrphidae).

The aspicerines and *Melanips opacus* oviposit into the head (central ganglion) of syrphids (Rotheray, 1979; 1981) thus ovoiding early exposure to the hosts haemocyte immune system (see below). This type of oviposition may also disrupt central nervous control of the host's physiology. The similar lifeways of *Melanips* and the Aspicerines is reflected in their very similar short ovipositors.

Syrphids are relatively large hosts and thus the Aspicerinae (Fig. 148) and *Melanips opacus* are larger than

many of the more derived figitids that parasitize smaller Diptera.

Figitinae & Eucoilidae: parasitoids of Diptera

Species of *Melanips* are not restricted to the Syrphidae, the Chamaemyiidae (Schizophora) are also parasitized. This genus illustrates how the Figitinae have expanded from initial parasitoidism of the Syrphidae to attack a wider range of dipterous hosts (Cyclorrhapha - Aschiza and Schizophora) (Eskafi & Legner, 1974a; 1974b; Carton et al., 1986; Nappi & Streams, 1970; Schreiber & Campbell, 1986).

The analysis (Chapter 5) linked the genera near *Figites* to the Eucoilidae, this relationship is also shown by the biologies of these groups. The genera near *Figites* are frequently parasitoids of flies in carrion and dung, often sharing the same hosts with eucoilids. For example the horn fly, *Haematobia irritans*, is parasitized by *Trischiza* sp. (Figitini) and by several eucoilid genera - *Eucoila*, *Kleidotoma*, *Rhoptromeris* and *Cothonaspis*.

Both figitine and eucoilid larvae develop in the haemocoel of the host larva, later they complete their development inside the host's puparium. The mouthparts of early instars are haematophagous but later instars develop chewing mandibles. The primary instars of the Eucoilidae, and to a lesser extent the Figitini, have long thoracic processes; it is supposed that these processes are an adaptation to conditions within the haemocoel (See Chapter 4).

During the summer the life cycle is short e.g. 60 days in *Figites* (James, 1928), in the overwintering generation diapause is as a mature larva, prepupa or pupa, inside the host puparium (Kopelman & Chabora 1984; Sychevskaya, 1974).

The cynipoids are a very important element in the natural control of many economically important Diptera. Parasitoidism is often very effective, with up to 40% of the available hosts killed; and exceptionally parasitoidism may approach 80% (Sychevskaya, 1974). The Cynipoidea have pursued their dipterous hosts into many

different habitats. They are parasitoids of coprophagous, saprophagous, fungivorous and carrion flies; also flies living on sap, yeasts, fruit (many drosophilid species), and on endophytic flies (including leafminers). It appears that any environment that can support a fly can also support its parasitoid. For example *Kleidotoma japonica* is a parasitoid of *Scatella calida* the immature stages of which occur in a very hostile environment - hot acidic springs (Huzimatu, 1940).

Dipterous defences

The eggs of these derived cynipoids are placed in the haemocoel, either free floating or attached to the intestine, malpighian tubules or fat body. The shift to dipterous hosts involved overcoming their elaborate immune reactive haemocyte system (Nappi, & Carton, 1986).

Dipterous haemolymph contains spherical phagocytic cells (plasmatocytes) that can differentiate into flat lamellocyte cells (Carton et al., 1986). When a foreign protein, e.g. a cynipoid egg, is detected there is a precocious production of lamellocytes and these adhere to the parasite to form a compact laminated cellular capsule (Carton, & Boulêtreau, 1985). Crystal cells, another type of haemocyte, then lyse and release phenol oxidases that melanize the capsule (Nappi, & Carton, 1986). The melanized capsule isolates, asphyxiates and starves the parasitoid (Carton, et al 1983; 1986; 1987).

Successful development in the dipterous haemocoel depends upon the parasitoid's ability to avoid encapsulation. The eggs of some Parasitica have a specialized surface that does not arouse a response, or fine projections that inhibit encapsulation (Salt, 1968; 1980). Other parasitoids actively interfere with the immune reaction. This may be by injecting a symbiotic virus, from the genital glands, which affects the host (Edson et. al., 1981). However, many Apocrita have evolved sophisticated venoms which can overcome host defences (Van Veen, 1981).

Although little studied, the development of these

venoms must have played a crucial part in the evolution of the parasitic Cynipoidea. The venom secreted by the acid gland of female eucoilids contains lamellolysin (Boulêtreau & Wajnberg, 1986; Rizki & Rizki, 1984; Streams & Greenberg, 1969; Walker,1959; Weideli, 1967). This substance, when injected into the host's haemocoel, affects the host's lamellocytes which become distorted and die, but most importantly it causes the lamellocytes to lose their adhesivness and this makes effective encapsulation difficult (Nappi & Carton,1986). Only host lamellocytes are affected, other haemocytes and the host's ability to heal wounds and phagocytose bacteria is not affected (Rizki,& Rizki, 1984).

In the cynipoids that oviposit into the host's central ganglion a venom is used to temporarily paralyse the host and thus facilitate accurate placement of the egg (Rotheray, 1981).

Even if a fly larva manages to encapsulate the cynipoid, the adult fly will tend to have a reduced weight, size, and fecundity when compared to the average unparasitized fly (Carton & David, 1983). This reduced fitness slows down the dissemination amongst the fly population of any genes providing resistance against the parasitoid, and this favours parasitoid virulence.

Charipidae: hyperparasitoids

Hyperparasitoidism is a highly evolved lifeway which only occurs in Hymenoptera, Diptera and Coleoptera (Sullivan, 1987). Although hyperparasitoidism has evolved several times in the Hymenoptera it is relatively uncommon amongst the less derived Parasitica. For example, hyperparasitoidism is limited to a few subfamilies of Ichneumonoidea (chiefly Pimplinae, Phygadeuontinae and Mesochorinae). However, in the microhymenoptera it is a more frequent strategy. Amongst the Proctotrupoidea (s.l.) it occurs in a few isolated genera e.g. *Ismarus* (Chambers, 1955) and *Dendrocerus* (Fergusson, 1980). In the Cynipoidea hyperparasitoidism is limited to the Charipidae. However, in the Chalcidoidea approximately half the families have some hyperparasitoid species (Sullivan, 1987).

The host of hymenopterous hyperparasitoids is usually another hymenopteran itself parasitising a phytophagous host. Hymenopterous hyperparasitoids are more likely to be parasitic on other Hymenoptera because their physiological similarity (Brues, 1921) makes it easier to overcome the primary parasitoid's defence mechanisms.

Origin of charipid hyperparasitoidism

Hyperparasitoidism generally originates from one of three associations, a host, primary parasitoid, or predator association (Pseudohyperparasitoids, that attack the primary parasitoid only after it has killed the host, may be exceptions) (Gauld & Bolton, 1988; Sullivan, 1987). In the case of the Charipidae, there are no obvious host or primary parasitoid associations but, there are predator associations; the Aspicerinae, *Melanips* and the Anacharitinae all have aphidophagous hosts. So it is likely that the Charipidae evolved by host-switching from ancestors that were primary parasitoids on aphidophagous hosts.

The two subgroups of the Charipidae (Alloxystinae and Charipinae) have slightly different host preferences.

Alloxystinae: hyperparasitoids on aphids

The Alloxystinae lay a single egg (Haviland, 1921a; 1921b) into the haemocoel of a late larval instar, usually the third or fourth (Matejko & Sullivan, 1980; Sullivan, 1972), of the primary parasitoid (often Braconidae; Aphidiinae). [Oviposition into late instar larvae is unusual in the Cynipoidea.] The primary parasitoid is in the haemocoel of the host aphid (Aphididae). [This cynipoid lifeway differs from that of some other hyperparasitoids e.g. *Dendrocerus* (Ceraphronidae) and *Asaphes* (Chalcidoidea) which insert their eggs only after the primary parasite has spun its cocoon, also these examples are ectoparasitoids.] The first instar larva has a strongly chitinised cuticle, presumably for protection against attack from other larvae. The primary parasitoid kills the aphid, the skin of the aphid then becomes parchment-like and is known as a "mummy". The primary host

lines the mummy with silk and pupates, only then is it killed by the cynipoid. The cynipoid larva eventually emerges and completes its feeding externally, but within the aphid mummy (not observed by Gutierrez & Van Den Bosch). This ectoparasitic phase only lasts for about 12 hours. The adult emerges by biting an irregular hole in the aphid skin (Spencer, 1926; Gutierrez & Van Den Bosch, 1970a; 1970b; Gutierrez, 1970a; 1970b).

Charipinae: hyperparasitoids on psyllids

Until recently it was believed that the Charipinae were primary parasitoids (Fergusson, 1986; Quinlan & Evenhuis, 1980) but Herard (1986) showed that *Dilyta subclavata* is a hyperparasitoid of *Psylla pyri* (Psylloidea) via *Prionomitus mitratus* (Chalcidoidea, Encyrtidae). Rathman and Brunner (1988) and Rathman and Paulson (In Menke & Evenhuis, *in press*) have recently shown that *Dilyta rathmani* is a hyperparasitoid, via *Trechnites* sp. (Encyrtidae), on a pear psyllid (*Cacopsylla pyricola*) and additionally on *Cacopsylla alba* nymphs on Willow (*Salix exigua*). The details of charipine biology have yet to be elucidated.

The shift from the ancestral, aphid, host (see above) to psyllids means that the Charipinae are the more derived of the two subfamilies.

Dispersal of the alloxystines

Aphids are mostly distributed by winds. The evolutionary advantage for the Alloxystinae to be dispersed along the same thermals as their hosts has been a contributory factor in the close size and weight correlation between the two groups. Therefore there is a close congruence in the aerial distribution (both number and altitude at any given flight time) of aphids and aphid parasitoids (Glick, 1939; Yoshimoto & Gressitt, 1964).

Host searching and the figitid lineage

The cynipoids that are parasitoids of aphidophagous Syrphidae and those that are hyperparasitoids of aphids respond not to the odours of their hosts, but to cues

emanating from the aphid colonies (Hagen, 1986). These cynipoids are not normally restricted to the odour of any one aphid species, and this is an advantage as few of the hosts are specific to only one aphid (Rotheray, 1979; 1981).

Many figitids and eucoilids parasitize Diptera that frequent carrion or dung, and the adult females of these cynipoids are attracted to the odour of such habitats (James, 1928; Sychevskaya, 1974). Eucoilids are often highly specific in their response to the olfactory cues from different microhabitats. For example *Leptopilina clavipes* is attracted only to decaying fungi, *Cothonaspis rapae* and *Kleidotoma dolichocera* to decaying plants and *L. bouardi* and *Pseudeucoila bochei* to decaying fruit. All these species are attracted only to a certain stage of decay, which is synchronised with the succession period of their particular dipterous hosts (James, 1928; Vet, 1984).

Once in the host habitat the host must be located. This is achieved by vibrotaxis, antennation, and by probing with the ovipositor (Vet 1984; Vinson, 1976). Alloxystines, anacharitines and *Melanips* normally antennate their hosts (Gutierrez, 1970a; 1970b; Rotheray, 1979, 1981). However, many figitids and eucoilids tend to probe the substrate with the ovipositor, presumably because of its messy nature - dung, fermenting fruit etc (Lenteren, 1972, Sychevskaya, 1974).

The final stage before oviposition is host acceptance and this is achieved by probing into the host with the ovipositor. Chemoreceptors present at the tip of the ovipositor (Fergusson, 1988), enable the cynipoid to recognize an acceptable host and distinguish parasitized (usually avoided - c.f. Fulton, 1933) from unparasitized hosts (Lenteren, 1972; 1976; Singh & Srivastava 1988). Probed larvae are not necessarily parasitized (Gutierrez, 1970a; 1970b).

Summary of cynipoid evolutionary biology

The biological evidence strongly correlates with the results of the cladistic analysis (Chapter 5), and these

both support the following reconstruction of cynipoid evolutionary biology (Fig. 203).

The ancestral cynipoid probably had a generalized apocritan type biology. Endoparasitism and koinobiosis were developed and then the Cynipoidea divided into three main lineages with different lifeways (the biology of the fourth lineage is unknown). This division occurred very early in cynipoid evolution.

The Ibaliid lineage developed parasitoidism of hymenopterous larvae in Pine trees. With the expansion of the angiosperms the lineage shifted (in Gonwanaland) to parasitoidism of hymenopterous and then coleopterous larvae boring in wood of deciduous trees. This lineage consists of relatively few, relict, species, they are specialized but not very derived.

Another lineage, the gall-wasps, exploited the expansion of the angiosperms by developing a phytophagous lifeway; they specialized in cecidogenesis. The first gall-wasps had simple life-cycles and made simple stem-galls probably on Rosaceae or perhaps Compositae. The derived species developed heterogony and highly structured galls on Oak. *Diastrophus* and the Rhoditini appear to occupy intermediate stages. The Synergini originated from a relatively early lineage, underwent considerable specialization and developed inquilinism.

The smaller cynipoids probably continued, for some time, a lifeway similar to that of the ancestral cynipoid. [This may have involved following neuropterous hosts in a switch from ancient plant types to the angiosperms.] This line eventually developed into the modern figitid lineage. The first hosts of this lineage were aphidophagous Neuroptera, later a more derived group became parasitoids of aphidophagous Diptera (Syrphidae). The association with aphid predators led to the development of a specialized group of hyperparasitoids, first of aphids and then of psyllids.

The move into dipterous hosts, that have sophisticated host defences, was first achieved by oviposition into the cerebral ganglion. Once the cynipoids had developed the appropriate venom chemistry (e.g.

lamellolysin), the remaining Figitinae and Eucoilidae went on to become major parasitoids of a wide range of dipterous hosts.

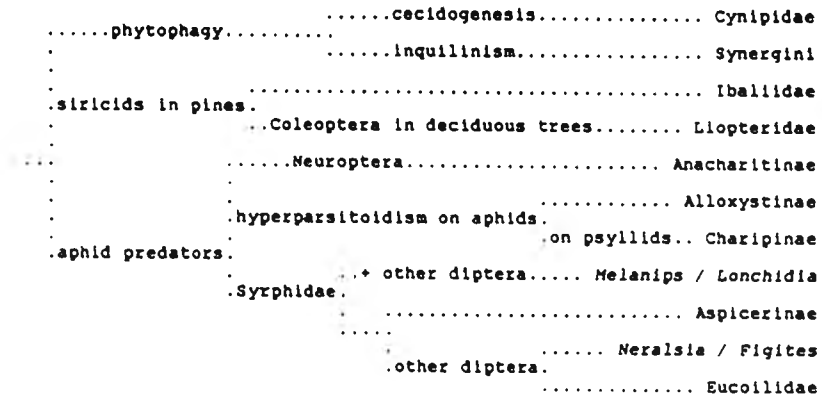


Figure 203. Host preferences and the evolutionary biology of the Cynipoidea.

CHAPTER 7: CONCLUSIONS

THE RELATIONSHIPS OF THE CYNIPOIDEA WITH OTHER APOCRITA

It was shown in chapter 3 that the phylogeny of the Apocrita is not established with any exactitude. However, the investigation of cynipoid morphology and biology has shown that the Cynipoidea share many similarities with the more derived parasitoid superfamilies.

The Cynipoidea have occasionally been linked with less derived parasitoids, e.g. Ichneumonoidea (Dalla Torre & Kieffer, 1910; Rasnitsyn, 1980), but the quoted similarities are symplesiomorphies or parallelisms and thus do not imply a close relationship. For example the comparatively complete venation of the Ibaliidae and the horizontal type of placoid plate sensillae found in all Cynipoidea are plesiomorphic features that are also present in the Ichneumonoidea. In general the Ichneumonoidea are amongst the more primitive Apocrita (Richards, 1977) and they are currently placed near the bifurcation of the aculeate and the parasitoid lineages (Gauld & Bolton, 1988).

Similarly the Evanioidea and the microhymenopteran superfamilies have a parallel reduction in the number of abdominal spiracles to a pair on segments 1 and 8. Mason (in litt.) has shown that the Evanioidea form a holophyletic group with a unique type of petiole. Thus there is no direct relationship between the Evanioidea and the Cynipoidea.

Microhymenoptera

The Chalcidoidea, Cynipoidea and the derived proctotrupoid families are morphologically similar. They share many parallelisms, especially reduction-states: reduced venation, reduction in the number of abdominal spiracles and loss of the cocoon. In particular the loss of the pterostigma probably occurred several times in the microhymenoptera. All three groups have a low number (two to three, seldom five) of hamuli which are concentrated on

a narrow area of the hind wing (Rasnitsyn, 1969). However, this feature is related to wing length, flight-range and thus to body size (Richards, 1949).

Chalcidoidea s.l.

The Cynipoidea and Chalcidoidea share a general similarity and both superfamilies have repesentatives that are secondarily phytophagous (Malyshev, 1968). The wing venation is similar (Bradley, 1958) although generally more reduced in the Chalcidoidea. Farish (1972), from studies of their grooming behaviour, concludes that the two superfamilies are related, but this requires further study before its validity can be assessed.

Both the Chalcidoidea and Cynipoidea have a low number of antennal segments, ~~with a possible~~ commonly ~~ground-plan number of~~ 13. However, a number of this magnitude ~~would be primitive for~~ many Parasitica (the very large numbers found in the Ichneumonoidea and the low numbers found in the Scelionidae and Chalcidoidea being derived).

Similarities of the female genitalia (Königsmann, 1978; Domenichini, 1953) may be parallel adaptations associated with comparable lifeways. In both superfamilies the male genitalia lack a cuspis (although, there may be an indication of a cuspis-like process in some cynipoids see chapter 4) but, unlike the Cynipoidea, the Chalcidoidea have lost the basal ring (Snodgrass, 1941).

Although the Cynipoidea and Chalcidoidea share many parallelisms, there are no reliable synapomorphic states shared by both superfamilies that are not also possessed by the Proctotrupoidea (Gibson, 1985; 1986). Further there are some significant differences between the Cynipoidea and Chalcidoidea. The chalcidoids have placoid sensilla that are raised above the surface of the antennae, the chalcidoid pronotum does not reach to the tegulae (in some Chalcidoidea, Eucharitinae and Perilampidae, the posterolateral angle of the pronotum appears to extend to the tegula but only because the prepectus is secondarily fused to the pronotum); the chalcidoid hindwing venation is not similar to that of the Cynipoidea (Figs 205, 206).

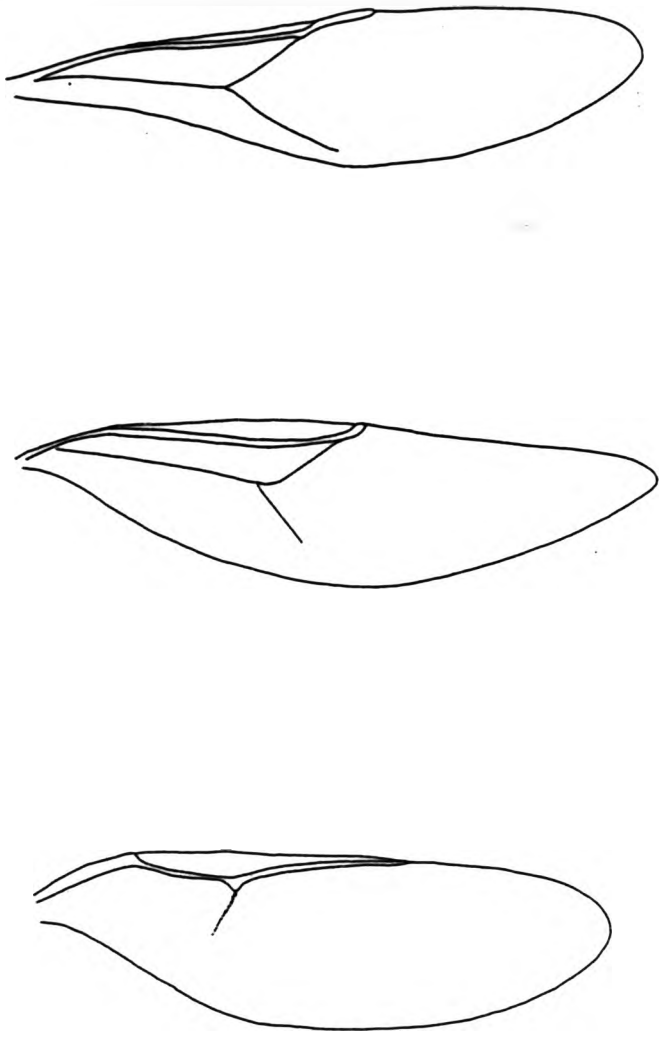
In particular the Chalcidoidea have a unique type of prepectus (Gibson, 1985; 1986).

Proctotrupoidea s.l.

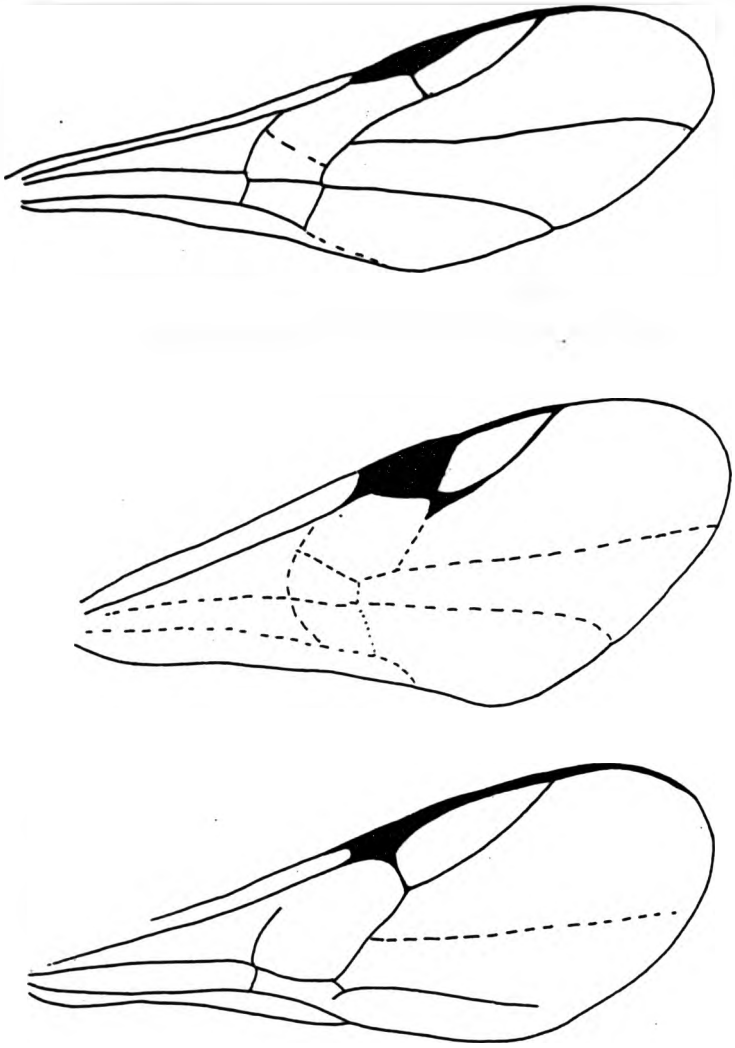
All small Parasitica that were not Chalcidoidea or Cynipoidea have traditionally been placed in the Proctotrupoidea s.l., and it is evident that this "superfamily" is polyphyletic (Masner, 1956). The Cynipoidea is similar to the Proctotrupoidea in that the pronotum reaches to the tegulae and the prepectus is concealed but fused to the posterolateral edge of the pronotum forming a groove with the outer edge of the pronotum (Gibson 1985, 1986). The hind wings of the Diapriidae have have a similar venation to the Cynipoidea, in that there are usually four veins (Figs 204, 205): R, M+Cu, rs-m and Cu, the last three form a Y-shape with M+Cu forming the stem. (The venation of less derived proctotrupoid families is similar.) There are further similarities in the structure of the petiole (Mason, *in litt.*). It is not clear how many of these similarities are parallelisms, and how many are genuine indicators of some relationship.

The origin of the Cynipoidea has been clarified by the recent discovery of the Archaeocynipidae, fossil cynipoids, from very early Cretaceous strata. These fossils indicate that the ancestor of the Cynipoidea may have been similar to certain of the less derived families of the Proctotrupoidea. The small and linear pterostigma of *Archaeocynips* is similar to that of *Austroserphus* and *Acanthoserphus* (Proctotrupoidea s.s.) (Figs 207, 209) and shows that the cynipoids must have lost their pterostigma by gradual reduction. The closed discal cell of the Archaeocynipidae is particularly reminiscent of the venation of the proctotrupoid families - Proctotrupidae, Heloridae, Roproniidae, and Vanhorniidae (Figs 207-212). Thus it is suggested here that the Cynipoidea plus at least some of the less derived proctotrupoid families had a common ancestor.

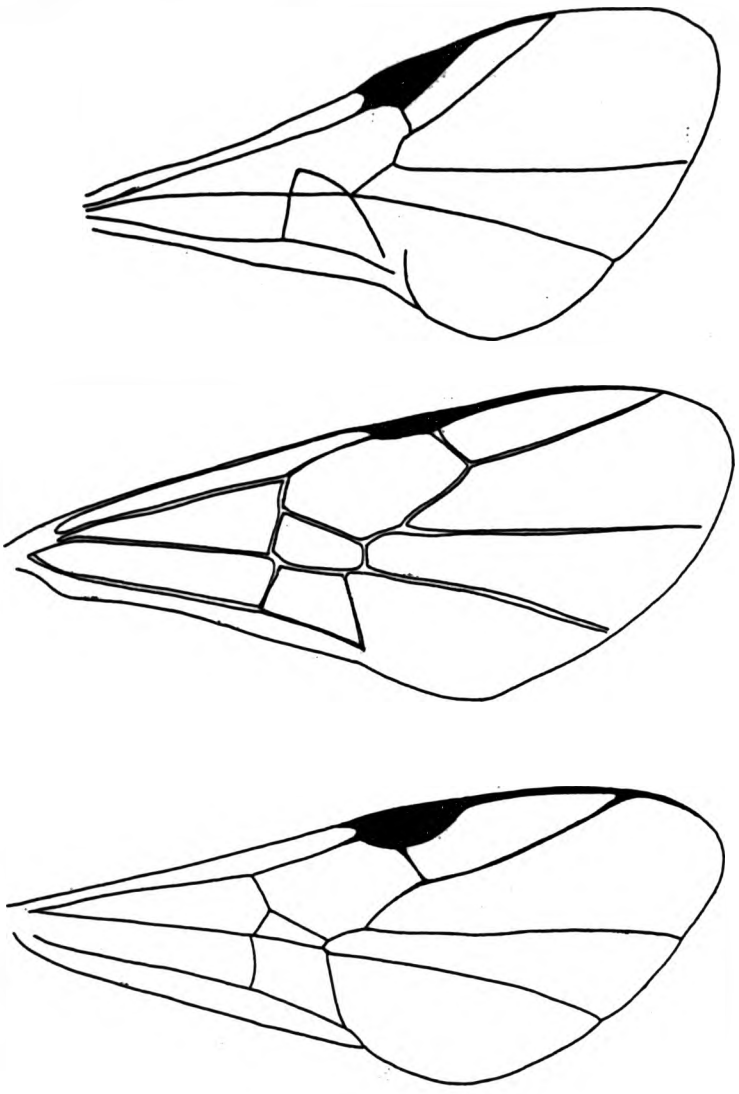
It is possible that all the microhymenoptera had a common ancestor. However, the morphology of the



Figures 204-206. 204, hindwing of *Pantoclis* (Proctotrupoidea s.l.). 205, hindwing of *Ibalia* (Cynipoidea). 206, hindwing of *Pteromalus* (Chalcidoidea).



Figures 207-209. 207, forewing of Austroserphus. 208, forewing of *Heloriserphus*. 209, forewing of *Acanthoserphus*.



Figures 210-212. 210, forewing of Helorus. 211, forewing of Ropronia. 212, forewing of Vanhornia

Chalcidoidea, especially the type of prepectus and the small chromosome number, indicates that this superfamily has not shared a *recent* ancestor with the Cynipoidea plus Proctotrupoidea.

The microhymenoptera have evolved separately, yet in parallel, for a considerable time and they have adopted similar solutions to the problems inherent in size reduction, biology etc. This homoplasy makes it unlikely that the relationships of the microhymenopteran superfamilies will be fully resolved at least until the problems of the proctotrupoid classification are resolved.

THE HOLOPHYLY OF THE CYNIPOIDEA

The morphological evidence indicates that the Cynipoidea is likely to be a single Holophyletic group. However, because the Cynipoidea have developed in parallel with other groups of microhymenoptera, there are very few unique cynipoid features. The clique cladogram has seven "rooting" characters (31.2, 100.1, 104, 106, 145 148 and 150) although characters 31.2 and 106 are symplesiomorphies.

Characters 148 and 150 are reduction states shared by many other microhymenoptera. The cynipoid gaster (148) consists of abdominal segments two to eight, tergite nine being part of the genitalia. Although a small tenth tergite occurs in the less derived Apocrita (e.g. some Ichneumonidae and Proctotrupidae), in the Cynipoidea, Chalcidoidea and the derived Proctotrupoidea this tergite is fused with tergite nine. Similarly the plesiomorphic apocritan gaster has spiracles on the second to eighth abdominal tergites but the Chalcidoidea, Cynipoidea and many derived Proctotrupoidea have a single spiracle on tergite eight (150). The Platygasteridae (Proctotrupoidea) exhibit the most extreme reduction, they have no gastral spiracles.

Character 145 (lateral compression) applies particularly to the gaster, but also to the thorax. This

character can be weak, and is perhaps least obvious in the Anacharitinae (and the Archaeocynipidae). This feature is not particularly common in other apocritans and, in them, is often related to their need to oviposit in crevice living hosts.

The remaining characters (100.1 and 104) are wing venation features. The distinctive triangular marginal cell (101.1) is present in all cynipoids except *Pycnostigmus*, the phylogenetic reconstruction shows that this genus is a highly derived cynipoid, and thus its reduced venation must be accepted as a specialization. Loss of the pterostigma (104) is a feature shared by the Cynipoidea, the derived Proctotrupoidea and the Chalcidoidea. Two cynipoids that are not closely related, *Austrocynips* and *Pycnostigmus*, have a pseudopterostigma, but these structures are not homologous with the linear pterostigma of the earliest known fossil cynipoid so in both genera the pseudopterostigma is likely to be a secondary structure.

Several other features have been suggested (Königsmann, 1978; Richards, 1977) as delimiters of the Cynipoidea: pygostyles absent; antennal number 13 (female) / 14 (male); pronotum reaching to the tegulae; lack of enclosed hindwing cells. These features, however, are ground-plan characters which are not unique to the Cynipoidea, and except for the pronotum character show exceptions within the Cynipoidea.

The wing venation of the Cynipoidea is particularly interesting because it marks a stage in vein reduction between that of the less derived Parasitica and that of the most derived microhymenoptera. The distinctive nature of the cynipoid venation is caused by a suite of characters associated with the angular rotation of Rs+M about the base of the marginal cell and also movement of the marginal cell upwards and inwards (see section on venation). The totality of these characteristics is most easily visualized in the distinctive shape of the cynipoid marginal cell. A few other Apocrita, especially certain less derived Proctotrupoidea (e.g. Figs 207-212) have similar marginal cells and these may represent a stage

prior to that found in the Cynipoidea.

To quote Königsmann (1978) "the monophyly of the Cynipoidea is very probable, although the constituent characters are not very striking". The lateral compression and the triangular marginal cell are the most significant features of the Cynipoidea.

A NEW CLASSIFICATION OF THE CYNIPOIDEA

The overview of past classifications given in Chapter 3 highlighted the general trend to upgrade all taxa without adequate justification. This was shown in its most extreme form in the Evenhuis (1982) classification, where virtually all recognisable groupings were called families. The phylogenetic reconstruction (Chapter 5 provides a very different and more conservative structure for the superfamily. The Cynipoidea is divided into four lineages which, given the presumed holophyly of the Cynipoidea, are interpreted as families - Cynipidae, Ibaliidae, Himalocynipidae and Figitidae. The Himalocynipidae is upgraded (after deliberation) from its current subfamily status, the Cynipidae is unchanged but the Ibaliidae and Figitidae have very different constructions from their previous usages. This new family-level structure is robustly supported by morphological, palaeontological, biogeographic and biological evidence (Table 53).

The families, subfamilies and tribes of the Cynipoidea are discussed below and a key to these taxa is provided in Appendix 4. A summary of all the changes to the classification is given in Table 54 and scenarios showing the phylogeny and biology of the cynipoid families are provided (Figs 215-218) at the end of this thesis.

Cynipidae

The Cynipidae is distinguished from all other cynipoids by being phytophagous. Except in the Synergini, there are no lateral carinae on the pronotum and the hypostomes are not fused. The development, in the female,

of a hypopygial spine is cited by Ritchie (1984) as a synapomorphy for the family. This feature is poorly developed in some of the less derived Cynipidae. However it also occurs in *Himalocynips* and *Pycnostigmus*. In contrast, the depressed area (Fig. 142) on tergite nine (character 159) is unique to the Cynipidae. Unlike the larvae of the other cynipoid families, the cynipid larva is neither hypermetamorphic nor markedly caudate.

The cynipids are subdivided into four tribes - Aulacideini, Synergini, Rhoditini and Cynipini, but the Aulacideini is a paraphyletic assemblage. Although the Rhoditini and the Cynipini could be linked together as a subfamily, the remaining taxa would be paraphyletic and could not be justified as a second subfamily. Thus in the following classification all the tribes are included in a single subfamily - Cynipinae.

Aulacideini

The species of this tribe form simple galls, often stem-galls, on a wide range of host plants. They have a simple life-cycle and an unspecialized morphology. The pronotum is long, and the gaster and hypopygium are simple.

Synergini

Species of the Synergini have a distinctive biology, inquilinism, and are morphologically derived. In particular the structure of the hypostomes (Fig. 45) and pronotum is similar to that of the Figitidae (homoplasy). The gaster usually appears to consit of a single tergite (tergite 2 fused with tergite 3) and the maxillary palps are reduced to four segments. The Synergini is a very specialized tribe and this has, in the past, made them difficult to place, but it has now been shown (character 159) that they are indubitably members of the Cynipidae.

Rhoditini

This tribe is represented in the Holarctic region by

Diplolepis, which has a specialized plough-blade like hypopygium (Fig. 126). The species mostly make stem or leaf-galls on Rosaceae. *Eschatocerus*, from Acacia galls in the Neotropical region, has a similar hypopygium.

Cynipini

The Cynipini contains the most derived gall-formers, they usually make complex galls on Oak and have complex heterogonous life cycles. Like the Rhoditini they have (in dorsal view) a very short pronotum (median length less than 1/7 of lateral height). The hypopygium is modified into a long spine (Fig. 127) which has ventral hairs.

Ibaliidae

This family consists of the Austrocynipinae plus two previous families, the "Ibaliidae" and "Liopteridae". The Ibaliidae now contains all the large cynipoids (4.5 - 30mm) that are parasitoids of xylophagous larvae. The very long ovipositor of these cynipoids is coiled in a loop within the gaster (Figs 154b, 154c). Adult emergence is helped by the presence of strong mandibles and coarse sculpture on the head and thorax. The Ibaliidae tend to have distinct biogeographical distribution patterns.

Austrocynipinae

This subfamily consists of a single aberrant species (Fig. 159) which has a pseudopterostigma on the forewing; fan-like facial striae; 15-segmented antennae; a pronotal hump; a distinctive petiolar flange and an almost globular gonostylus. This is the only species with a coiled ovipositor not to have a distinct expansion of the distal gastral segments. The male is unknown.

Ibaliinae

The Ibaliinae have the hypostomal region set in a cavity (Fig. 39). The face has a weak central ridge (except *E*---------) and there is a normally a dorsal tooth on the pronotum (Fig. 70). The posterior gastral tergites are expanded to accommodate the long coiled ovipositor,

and the last tergite has a slighty upturned end.

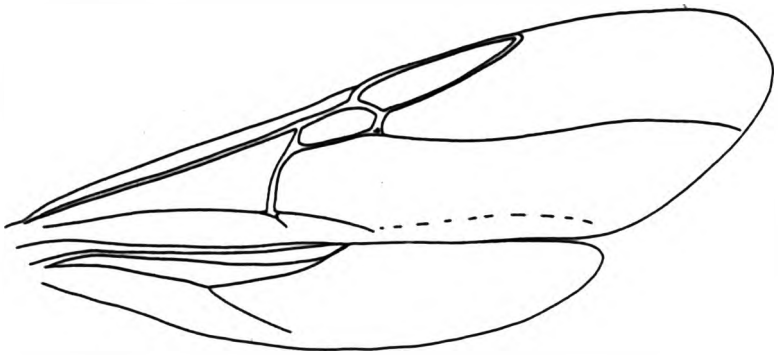
Ibaliini

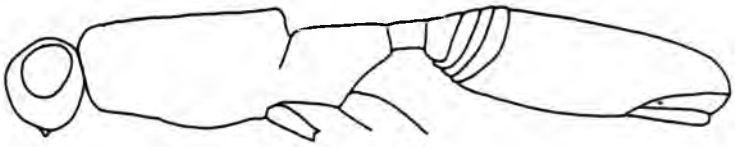
The Ibaliini is represented by a single genus *Ibalia* (Fig. 150) (although there may be further genera, see Chapter 5). It is defined by many autapomorphies. It has an occipital suture with vertical striae; a frontolateral precoxal tooth on the pronotum, and the rear of the scutellum has a transverse ridge which is interrupted centrally by a large emargination. The metanotal spiracle appears to be functional and the propodeal spiracle has a figure-of-eight shaped opening. The upper part of the metapleural trough is present and has a strong horizontal groove (Fig. 71). Wing venation: the hindwing has a closed basal cell; in the forewing there is a trace of vein C, a long marginal cell (9 times as long as broad), vein 2rs-m is vertical and under vein 2r-rs, and the cubitus (Rs+M) is complete and joined with Rs & M (Fig. 102). The midleg has only a single tibial spur, the hindleg has a long blunt projection on the second tarsal segment (Fig. 123) and the hind basitarsus is very long (about twice as long as tarsal segments 2-5 combined). The petiole is smooth and the gaster is laterally compressed and blade-like (Fig. 150).

Ibalia is the only member of the Ibaliidae to have had its larvae studied. The larval instars have large sharp mandibles, the first instar is polypodeform (Fig. 157) and late instars are the only cynipoid larvae reported to have spiracles with valves.

E-------ini New Tribe

This new tribe is described in Appendix 3, it has several distinctive characteristics (Figs 213, 214): antennae 14-segmented; thorax long and thin, in side view about three times longer than high. The propodeum is very long and separated from the metanotum by a deep incision. The seventh gastral tergite is greatly elongate and forms most of the gaster. The placement of this genus in a position between the Ibaliini and Liopterini tends to





Figures 213-214. 213, wings of *E*---------- *c*----------. 214, lateral outline of *E. c*---------- showing propodeal cleft and gastral tergites.

confirm that the separation of these two taxa into families was an excessive division.

Liopterini

These insects all have a notch or depression in the centre of the clypeal margin, although this can be weak (e.g. *Kiefferiella*). The metapleural trough is obscured by sculpture and the posterolateral corners of the mesonotum end in a flange. A number of species have scutellar spines and modifications to the legs (e.g. Fig 125) which aid egress from the trees in which their hosts live. The petiole is often long and tangentially attached to the gaster (Fig. 132).

The Liopterini is not easily subdivided, the old subfamilies ("Oberthuerellinae", "Mesocynipinae" and the "Liopterinae") could be recognised as subtribes but only the "Oberthuerellina" would be holophyletic, the "Liopterina" and "Mesocynipina", or a fusion of the two, would be paraphyletic assemblages. The only reasonable alternative is to treat them as generic groups and to recognise the strength of the morphological and biogeographic isolation of the genera near *Oberthuerella*. The latter is the best solution, especially as subtribes have not previously been employed in the Cynipoidea and are not needed elsewhere in this classification.

Himalocynipidae New family

The phylogenetic reconstruction shows that *Himalocynips vigintilis* constitutes an independent lineage of the Cynipoidea. *Himalocynips* is a very distinctive insect (Fig. 158) with many unique features. The clypeus projects upwards and away from the labrum. The face has two vertical grooves separated by a keel, which extends from the anterior tentorial pits to the toruli. The hypostomes have the lower tentorial bridge exposed and wide. The antennae have 20 segments, and these are densely punctate, and have very short placoid sensilla. The pronotal plate has straight lateral carinae, a thin frontal bar and a pointed caulis. The axillar flange is horizontal, the junction between the axillae and the

scutellum is evident, the axillar bar is transverse, and the scutellar foveae are transverse and almost triangular. The anterior corner of the scutellum bears a flange (this is on the mesoscutum in other cynipoids). The posterior region of the scutellum has a distinctive, approximately triangular, depression.

It is possible that this genus was derived from ancestors of the Ibaliidae but so long and so many specializations ago that the morphological links have been lost. Creation of a family for a single species is not something that should be done casually. However, the alternatives have been examined and rejected (see Chapter 5).

Figitidae

The Figitidae have a distinctive venation with vein Rs+M pointing at the junction of the basalis with the median (Fig. 111). The back of the head is flat, the hypostomal bridge is present and hypostomal fusion is complete (Figs 41-43, 46-48). The pronotum has at least a trace of lateral carinae and a gonostylus is present (except in the Anacharitinae).

This arrangement is the most controversial of the proposed changes because it merges the three previous families of small non-phytophagous cynipoids ("Figitidae", "Eucoilidae" and "Charipidae") into one new family.

The "Charipidae" cannot be justified as a family purely on its hyperparasitoid lifeway. Indeed in many other Hymenoptera (e.g. the Megaspilidae), hyperparasites and parasites occur together in the same taxonomic group, or even in the same species in some chalcids. The distinctive features of the hyperparasitoid cynipoids are functions of their small size, and family level status cannot be justified on these features alone. In fact the extralimital genus *Lytoxysta* makes it difficult to sustain even a tribal rank for these cynipoids.

The "Eucoilidae" represent the apex of cynipoid evolution; this group has dramatically radiated - to the point where it accounts for the majority of cynipoid

species. The group is very well-defined with many "strong" characters. Indeed, this is the main problem of the figitid classification. Compared to its relatives the "Eucoilidae" is almost overdistinct (Quinlan, 1979) and thus appears to justify a higher status than it truly deserves. The reconstruction shows that the "Eucoilidae" cannot be more than a tribe. This explains why the classification of the small parasitoids was so poor - one very successful tribe has dominated the other less numerous "also rans" of the Figitidae.

Anacharitinae

The Anacharitinae have spine-like lower teeth to the mandibles (Fig. 24) and the claws have a fine basal spine. The hypostomal carinae are curved. The petiole has elements of the collar present ventrally and laterally but not dorsally. Although, examples (e.g. *Anacharis*) with long petioles tend to lose the collar. Finally the ovipositor has lost both the bridge and the bulbus articulation.

Aspicerinae

The aspicerines are easily recognized by their scutellum, which has three long carinae, one median and two lateral (Fig. 78). The mesoscutal line is distinctive and in the form of an inverted Y (Fig. 77). The hind tibia usually has a longitudinal ridge or furrow on the outer or posterior surface (Fig. 124). The petiole is short and the second gastral tergite is saddle-shaped (Fig. 129). Aspicerines are slightly larger than most other Figitidae as they are parasitoids of relatively large dipterous hosts (Syrphidae).

Figitinae

This subfamily is not strongly defined, it is based on a single character reversal (character 50 - see chapter 5). Either there is a dorsal pronotal plate or the lateral carinae of the pronotum are reduced (e.g. Charipini - Fig. 67). It is the many reduction states of the Charipini that make this part of the classification particularly

difficult to improve.

Pycnostigmatini

This tribe is very well characterized, especially by its specialized venation. It has a pseudopterostigma; vein Rs is short; the marginal cell is absent, as are veins M, 2rs-m and Rs&M (Figs 110, 149). The antennae have 12 to 19 segments in the female and 15 segments in the male. The labial palps have only 2 segments, the lower mandibular tooth is scythe-like (Fig. 98), the axillae are reduced, the gonostylus has a notch and the short petiole has two ventral notches. The hosts of this tribe are unknown.

Charipini

These species are all small (1-2mm) and the tribe is defined by size-related characters, vein area reduced to the upper inner quarter (Figs 116, 117) and lack of thoracic sculpture (Figs 81, 82). Neither feature is particularly "strong", and one genus (*Lytoxysta*) has some thoracic sculpture. Also some Eucoilini may approach the Charipini in both these features. The genera near *Alloxysta* are hyperparasitoids of aphids and those near *Dilyta* are hyperparasitoids of psyllids, in both groups the primary hosts are other Hymenoptera. These two generic groups are not well distinguished. *Alloxysta* + *Phaenoglyphis* share character 39.2 (placoid sensilla from segment 5 onwards) which is a very poor character. *Dilyta* + *Apocharips* share two allometric features (98 & 102) and have the terminal antennal segments partially fused, a character of doubtful value. Other characters have been used as delimiters (e.g. mandibular shape, tergal proportions, presence of a frontoclypeal sulcus, open / closed marginal cell) but they all fail to some extent. Menke and Evenhuis (*in prep.*) recently considered this problem but found no real support for a subdivison.

Only the genera near *Alloxysta* have had their larvae described, the first instars are heavily chitinized and have a stigma-like anus.

Figitini

The Figitini are paraphyletic. The genera near *Figites* form the sister-group of the Eucoilini. This group of genera have a metapleural trough with a constriction and a sinuate lower margin. There is a ruff of hairs on the second gastral segment (e.g. Fig. 135), also the side of the petiole has a small notch (Fig. 137). Along with the Eucoilini these genera have a strongly developed pronotal plate and a cavity in gonostylus 9. The remaining Figitini (genera near *Melanips*) lack the ring of pubescence but are without a synapomorphy.

The first instar larva of the Figitini is similar to the eucoilidiform type of larva and is probably the precursor of this larval type.

Eucoilini

The Eucoilini is extremely well-defined with no less than nine synapomorphies. The palp segments are reduced to four maxillary and two labial segments, the malar sulcus is present as a fine band of longitudinal striae. The hypostomal fusion is complete and the suture is lost. The pronotal plate is raised frontodorsally and has a strong posterior margin. The junction of the axillae with the scutellum is distinct and the axillary bar is vertical. A pubescent anteroventral cavity is present on the metapleuron (Fig. 88), the legs have a strigil with fine sharp teeth and the petiole has a ventral keel. The most characteristic feature being the raised tear-drop shaped plate on the scutellum (Figs 84-87). The Eucoilini have a characteristic type of first instar larva, named after this group, the eucoilidiform larva (Fig. 157e).

CONCLUDING REMARKS .

Present and past classifications

Past classifications of the Cynipoidea have been criticized (Menke, 1989; Ritchie, 1988) for their dearth of characters and for representing biology rather than morphology. In this investigation the extensive

morphological survey has remedied the first point. The second criticism was answered by investigating the biology only after the morphological characters had been analysed and a phylogeny reconstructed. In fact the new classification is very well-supported by biological, distributional, fossil and other evidence.

The comment (Ritchie, 1988) that there are genera that appear to be intermediate between two or more "subfamilies" has now been shown to be true. Where possible this has been resolved but the generic groups of the Liopterini and the tribes Figitini and Aulacideini remain paraphyletic. Paraphyletic assemblages are almost inevitable in complex, highly homoplasious, groups like the Parasitica. But such assemblages can still be useful as long as it is remembered that they are not uniquely defined by apomorphies (Gauld & Mound, 1982).

The high level of homoplasy that is prevalent in the parasitic Hymenoptera has not prevented the production of a robust reconstruction. Also the establishment of polarity proved to be relatively straightforward. So it is claimed that the analysis and reconstruction represent a success. One aspect of this study, the status of the Eucoilini, has particularly highlighted the advantages of a reasoned phylogenetic classification. This approach has enabled the, very understandable, overgrading of what is now known to be only a tribe (Eucoilini), even if a very well-defined tribe, to be recognized.

Future improvements

It is not suggested that the reconstruction presented in this investigation (Figs 215-218) is the *one and only* correct answer, of course new characters will be discovered and more exceptions to existing features will be found. Although a representative selection of taxa have been analysed and a wide range of extra taxa have been examined, it was not possible extensively to investigate all the taxa. Therefore the study of other taxa will give rise to corrections and improvements. However, this first cladistic reconstruction of cynipoid phylogeny provides a strong and reasoned foundation for future work. Hopefully

the existence of this thesis will now make posible more compartmentalized (smaller but more detailed) research, and that should help future workers.

Hopefully further fossil evidence will be discovered that will improve the knowledge of the first node of the tree. The discovery of an early Cretaceous Ibaliid would tell us much about the position of the ancestors of the Cynipoidea, in relation to other Hymenoptera and, the relationships of the four cynipoid families.

More research is need into some of the rare extralimital taxa, especially the Australian genera. The

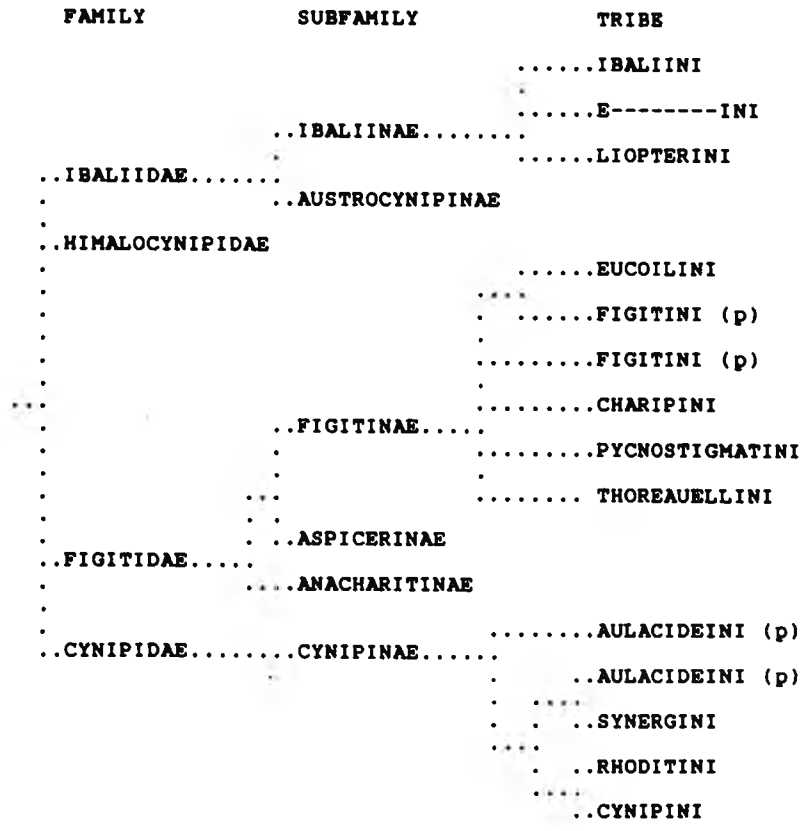


Table 53. A new classification for the Cynipoidea. (p = paraphyletic.)

validity of the Charipini and especially the "awkward" genus *Lytoxysta* would benefit from an autapomorphy that could inspire some confidence.

Finally, the biology of three very specialized genera (*Himalocynips*, *Austrocynips* and *Pycnostigmus*) is unknown and information on these would help improve our understanding of the Cynipoidea.

NEW compared with the OLD classification

IBALIIDAE	Ibaliidae, Liopteridae & Austrocynipinae
IBALIINAE	= Ibaliidae + Liopteridae
IBALIINI	no change
E--------INI	new tribe, genus and species
LIOPTERINI	downgraded from a family
AUSTROCYNIPINAE	no change, but moved from the Cynipidae
HIMALOCYNIPIDAE	upgraded from a subfamily of Figitidae
FIGITIDAE	= Figitidae + Charipidae + Eucoilidae
FIGITINAE	= Figitinae + Charipidae + Eucoilidae
EUCOILINI	downgraded from a family
FIGITINI	no change
CHARIPINI	downgraded from a family
PYCNOSTIGMATINI	down & moved from subfamily of Cynipidae
Australofigites	downgraded from a tribe
THOREAUELLINI	upgraded from a genus
ASPICERINAE	no change
ANACHARITINAE	no change
CYNIPIDAE	no change
AULACIDEINI	no change
SYNERGINI	no change
RHODITINI	no change
CYNIPINI	no change

Table 54. Changes to the cynipoid classification. (Also *Paramblynotus* is synonymized under *Kiefferiella*).

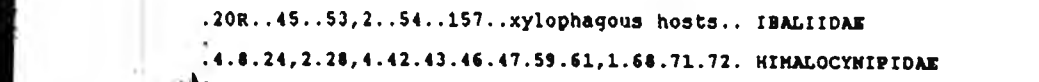


Figure 215. Scenario of the four families of the Cynipoidea. [R = reversal. Polarity of 159 reversed.]

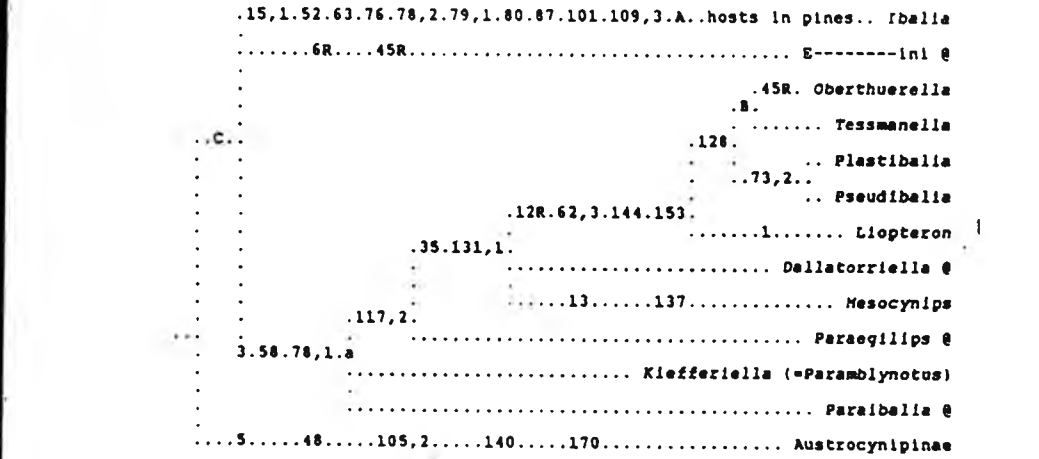


Figure 216. Scenario of the Ibalidae.

[A = 122 126.2 127 138.3 143 146; B = 25 35R 62.4 69 118 131.2; C = 6 19 24.1 45 149.1 156. P = parallelism; R = reversal; a = hosts in deciduous trees; @ = extralimital taxa, with apomorphies not included in analysis.]

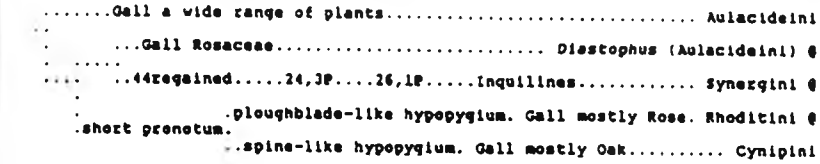


Figure 217. Scenario of the Cynipidae.
[@ = extralimital taxa. P = Parallelism.]

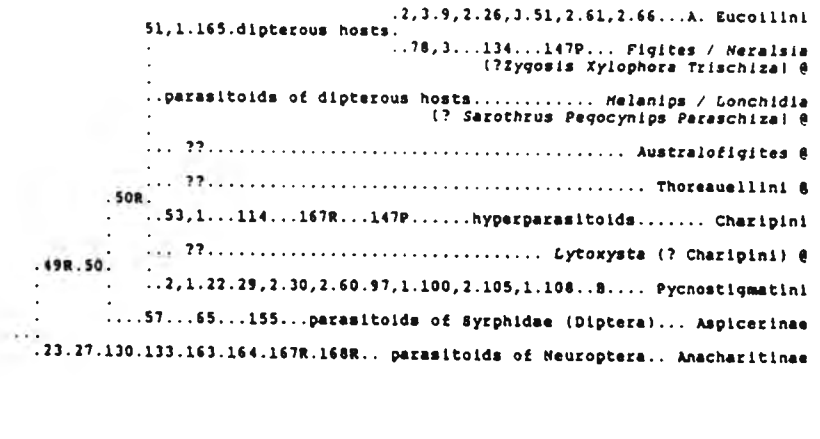


Figure 218. Scenario of the Figitidae.

A = 77 124 136 147P; B =109.1 113.2 141 169. P = parallelism; R = reversal; ?? = lineage requiring more study; @ = extralimital taxa, with apomorphies not included in analysis.]

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APPENDIX 1: COMPUTER PROGRAMS

The computer programs used in this thesis (see chapters 1 & 2) are listed below. The three dimensional plotting program used for the probability constructs of head allometry was adapted from L3-CO3D (Harding, 1982), this program and also the parsimony program HENNIG86 are subject to copyright and are therefore not listed below.

1. The data conversion program CONVERT.

```
100 REM *EXEC Input filename
120 CLOSE#0
130 INPUT"Enter output filename ";F$
140 A=OPENOUT F$
150 READ M,N
160 PRINT#A,M,N
170 FOR X=0 TO M
180 FOR Y=0 TO N
190 READ B
200 PRINT#A,B
210 NEXT
220 NEXT
230 CLOSE#0
240 END
```

2. The first main program, LEQUA.

```
 10 REM LEQUA Prints binary coded data
 20 CLOSE#0
 30 INPUT"Enter input filename ";F$;" Enter date ";D$
 40 CH=OPENIN F$
 50 INPUT#CH,M%,N%
 60 T%=M%-1: P%=N%
 70 DIM Q%(T%,N%),C%(T%),D(1,N%)
 80 FOR Y%=0 TO N%
 90 INPUT#CH,D(0,Y%):D(1,Y%)=Y%
100 NEXT
110 FOR X%=0 TO M%-1
120 C%(X%)=X%
130 FOR Y%=0 TO N%
140 INPUT#CH,Q%(X%,Y%)
150 NEXT
160 NEXT
170 PRINT"P = Print data"
180 PRINT"I = Invert scores of specified character"
190 PRINT"E = End run"
200 I$="Y":PRINT'': INPUT "Enter P,I or E";H$
210 IF H$="E" THEN 1010
220 IF H$="P" THEN 250
230 IF H$="I" THEN 840
240 REM Data printout
250 INPUT "Enter title";T$
260 INPUT"Characters Unchanged or Rearranged - U OR
```

```
   R";E$
270 IF E$="U" OR E$="u" THEN 370
280 INPUT"How many characters ";P%
290 PRINT"Enter nos., singly"
300 FOR Z%=1 TO P%
310 INPUT D(1,Z%)
320 FOR Y%=1 TO N%
330 IF ABS(ABS(D(0,Y%))-D(1,Z%))>1E-4 THEN 350
340 D(1,Z%)=Y%: Y%=1000
350 NEXT
360 NEXT
370 INPUT "Taxa Unchanged or Rearranged - U OR R";U$
380 IF U$="U" OR U$="u" THEN 480
390 INPUT "How many taxa ";T%
400 PRINT"Enter taxon nos., singly"
410 FOR Z%=0 TO T%-1
420 INPUT C%(Z%)
430 FOR X%=0 TO M%
440 IF C%(Z%)<>Q%(X%,0) THEN 460
450 C%(Z%)=X%: X%=1000
460 NEXT
470 NEXT:T%=T%-1
480 INPUT;"Scereen or Printer - S or P";S$
490 IF S$<>"P" THEN 510
500 VDU2
510 PRINT'TAB(20);T$,D$''' "Taxon"'"Nos.",,"Character
   Nos."
520 FOR Z%=1 TO N% STEP 23
530 R%=-1:PRINT;TAB(8);
540 FOR Y%=Z% TO Z%+22 STEP 2
550 R%=R%+1
560 IF Y%>P% THEN 580
570 PRINT;TAB(8+6*R%);D(0,D(1,Y%));
580 IF Y%>P% THEN Y%=1000
590 NEXT
600 R%=-1:PRINT'TAB(10);
610 FOR Y%=Z%+1 TO Z%+22 STEP 2
620 R%=R%+1
630 IF Y%>P% THEN 650
640 PRINT;TAB(11+6*R%);D(0,D(1,Y%));
650 IF Y%>P% THEN Y%=1000
660 NEXT
670 PRINT''
680 FOR X%=0 TO T%
690 PRINT;Q%(C%(X%),0);TAB(8);
700 FOR Y%=Z% TO Z%+22
710 IF Y%>P% THEN 770
720 IF Q%(C%(X%),D(1,Y%))<2 THEN 760
730 IF Q%(C%(X%),D(1,Y%))>3 THEN 750
740 PRINT;"V  ";: GOTO 780
750 PRINT;"-  ";: GOTO 780
760 PRINT;Q%(C%(X%),D(1,Y%));"  ";
770 IF Y%>P% THEN Y%=1000
780 NEXT
790 PRINT': NEXT X%
800 PRINT'''': NEXT Z%
810 VDU3
820 GOTO 200
```

```
 830 REM Inversion of scores
 840 INPUT "Invert the scores of how many characters
     ";V%
 850 PRINT"Enter character nos., singly"
 860 FOR Z%=1 TO V%
 870 INPUT W
 880 FOR Y%=1 TO N%
 890 IF ABS(D(0,Y%))=ABS(W) THEN 910
 900 GOTO 920
 910 W=Y%: Y%=1000
 920 NEXT
 930 FOR X%=0 TO M%-1
 940 IF Q%(X%,W)>1 THEN 980
 950 IF Q%(X%,W)=0 THEN 970
 960 Q%(X%,W)=0: GOTO 980
 970 Q%(X%,W)=1
 980 NEXT
 990 NEXT
1000 GOTO 200
1010 END
```

3. The compatability program LEQUB.

```
  10 REM LEQUB computes LeQuesne matrix, randomness
     ratios and boil-down
  20 CLOSE#0:READ G$
  30 DATA Incompatibilities: observed  expected  ratio
     - polar
  40 INPUT"Enter input filename ";F$;"Enter title
     ";T$;"Enter date ";DATE$
  50 CH=OPENIN F$
  60 INPUT#CH,M%,N%
  70 M%=M%-1
  80 DIM Q%(M%,N%),C(M%,3),D(4,N%)
  90 FOR Y%=0 TO N%: D(4,Y%)=.1: INPUT#CH,D(0,Y%):
     NEXT
 100 FOR X%=0 TO M%
 110 C(X%,0)=X%
 120 FOR Y%=0 TO N%
 130 INPUT#CH,Q%(X%,Y%)
 140 NEXT
 150 NEXT
 160 A$="N": C$="N": E$="N": N2=N%: R%=0:
 170 PRINT"I = Invert scores of specified character"
 180 PRINT"O = One LeQu run"
 190 PRINT"B = 'Boil down' data"
 200 PRINT"D = Delete all characters"
 210 PRINT"R = Restore all characters"
 220 PRINT"E = End run"
 230 I$="Y":INPUT'"Enter I,O,B,D,R or E";H$
 240 IF H$="D" THEN 280
 250 IF H$="R" THEN 270
 260 GOTO 290
 270 FOR Y%=1 TO N%: D(4,Y%) = ABS(D(4,Y%)): NEXT:
     GOTO 230
 280 FOR Y%=1 TO N%: D(4,Y%)= -ABS(D(4,Y%)): NEXT:
     GOTO 230
```

```
290 IF H$="E" THEN 2480
300 IF H$="I" THEN 370
310 INPUT "Data Unchanged or Altered - U or A";D$
320 IF D$="A" THEN 2180
330 IF H$="O" THEN 540
340 A$="N": B$="N": I$="N"
350 IF H$="B" THEN 590
360 REM Inversion of scores
370 INPUT"Invert the scores of how many characters
    ";L3
380 PRINT" Enter the character nos., singly"
390 FOR Z%=1 TO L3
400 INPUT C4
410 FOR Y%=1 TO N%
420 IF ABS(D(0,Y%))=ABS(C4) THEN 440
430 GOTO 450
440 C4=Y%: GOTO 460
450 NEXT
460 FOR X%=0 TO M%
470 IF Q%(X%,C4)>1 THEN 510
480 IF Q%(X%,C4)=0 THEN 500
490 Q%(X%,C4)=0: GOTO 510
500 Q%(X%,C4)=1
510 NEXT
520 NEXT Z%
530 GOTO 230
540 INPUT;"Title changed - Y or N";U$
550 IF U$="N" THEN 570
560 INPUT;"Enter new title";T$
570 INPUT "LeQuesne matrix - Y or N";A$
580 INPUT "Ratios - Y or N";I$
590 INPUT "Screen or printer - S or P";S$
600 IFS$<>"P"THEN620
610 VDU2
620 IF A$="N" THEN 640
630 R=0:K=0
640 FORX%=0 TOM%: C(X%,1)=0: NEXT
650 C3%=0
660 FOR Y%=1 TO N%
670 IF D(4,Y%)<0 THEN 710
680 D(4,Y%)=.1
690 C3%=C3%+1
700 D(3,C3%)=Y%
710 NEXT
720 FOR W=1 TO C3% STEP 23
730 IF A$="N" THEN 880
740 PRINT'TAB(10);T$;"    ";DATE$'
745 PRINT"Taxa analysed: ";: FOR X=0 TO M%: IF
    Q%(X,0)>0 THEN PRINT;Q%(X,0);" ";
746 NEXT: PRINT'
750 N1=-1: PRINT;TAB(7);
760 FOR Y%=W TO W+22 STEP 2
770 N1=N1+2
780 IF Y%>C3% THEN 810
790 PRINT;D(0,D(3,Y%));TAB(10+3*N1);
800 NEXT
810 PRINT';TAB(10);: N1=1
820 FOR Y%=W+1 TO W+22 STEP 2
```

```
 830 N1=N1+2
 840 IF Y%>C3%-1 THEN 870
 850 PRINT;D(0,D(3,Y%));TAB(7+3*N1);
 860 NEXT
 870 PRINT'
 880 FOR Z%=C3% TO W+1 STEP -1
 890 Z1%=D(3,Z%)
 900 IF A$="N" THEN 920
 910 PRINT;D(0,Z1%);TAB(7);
 920 W1=W+22
 930 FOR Y%=W TO W1
 940 IF Y%>C3% THEN 1620
 950 IF Y%>Z%-1 THEN 1610
 960 Y1%=D(3,Y%)
 970 IF INT(D(0,Y1%))-INT(D(0,Z1%))=0 THEN 1620
 980 A%=0: B%=0: C%=0: D%=0: E%=0: F%=0: G%=0
 990 FOR X%=0 TO M%
1000 IFQ%(X%,0)<0 THEN 1230
1010 Q1=(Q%(X%,Y1%)+Q%(X%,Z1%))
1020 IFQ1>6 THEN 1230
1030 IFQ1=0 THEN 1140
1040 IFQ1=2 THEN 1170
1050 IFQ1>2 THEN 1080
1060 IFINT(Q%(X%,Z1%))=0 THEN 1160
1070 GOTO 1150
1080 IF Q1>3 THEN 1110
1090 IF INT(Q%(X%,Z1%))=0 THEN 1180
1100 GOTO 1200
1110 IF INT(Q%(X%,Z1%))=1 THEN 1190
1120 IF INT(Q%(X%,Y1%))=1 THEN 1210
1130 GOTO 1220
1140 A%=A%+1: A1%=X%: GOTO 1230
1150 B%=B%+1: B1%=X%: GOTO 1230
1160 C%=C%+1: C1%=X%: GOTO 1230
1170 D%=D%+1: D1%=X%: GOTO 1230
1180 A%=A%+1: A1%=X%: C%=C%+1: C1%=X%: GOTO 1230
1190 B%=B%+1: B1%=X%: D%=D%+1: D1%=X%: GOTO 1230
1200 A%=A%+1: A1%=X%: B%=B%+1: B1%=X%: GOTO 1230
1210 C%=C%+1: C1%=X%: D%=D%+1: D1%=X%: GOTO 1230
1220 A%=A%+1: A1%=X%: B%=B%+1: B1%=X%: C%=C%+1:
     C1%=X%: D%=D%+1: D1%=X%
1230 NEXT
1240 IF B%=0 THEN 1320
1250 IF C%=0 THEN 1320
1260 IF D%=0 THEN 1320
1270 IF A%=0 THEN 1290
1280 GOTO 1340
1290 D(4,Z1%)=D(4,Z1%)+1: D(4,Y1%)=D(4,Y1%)+1
1300 IF A$="N" THEN 1370
1310 PRINT;":  ";: GOTO 1370
1320 IF A$="N" THEN 1370
1330 PRINT;"-  ";: GOTO 1370
1340 IF A$="N" THEN 1360
1350 PRINT;"X  ";
1360 D(1,Y1%)=D(1,Y1%)+1: D(1,Z1%)=D(1,Z1%)+1: R%=R%+1
1370 IF A%<D% THEN 1390
1380 K1=-1: GOTO 1400
1390 K1=1
```

```
1400 IF B%<C% THEN 1420
1410 K1=K1-2: GOTO 1430
1420 K1=K1+2
1430 IF K1=-3 THEN 1490
1440 IF K1=-1 THEN 1480
1450 IF K1=1 THEN 1470
1460 E%=A%+B%: F%=A%+C%: G%=B%+D%: GOTO 1500
1470 E%=B%+D%: F%=A%+B%: G%=C%+D%: GOTO 1500
1480 E%=A%+C%: F%=A%+B%: G%=C%+D%: GOTO 1500
1490 E%=C%+D%: F%=A%+C%: G%=B%+D%
1500 I=1: J=1: H%=A%+B%+C%+D%
1510 IF E%<2 THEN 1620
1520 FOR X%=0 TO E%-1
1530 I=I*(F%-X%)/(H%-X%)
1540 J=J*(G%-X%)/(H%-X%)
1550 NEXT
1560 P=1-I-J
1570 IF P<1E-8 THEN 1620
1580 D(2,Z1%)=D(2,Z1%)+P
1590 D(2,Y1%)=D(2,Y1%)+P: K=K+P
1600 GOTO 1620
1610 W1=W1-1
1620 NEXT Y%: IF A$="N" THEN 1640
1630 PRINT'
1640 NEXT Z%: IF A$="N" THEN 1660
1650 PRINT''
1660 NEXT W
1670 IF I$="N" THEN 1700
1680 PRINT'"LeQuesne's coefficient of character state
     randomness = ratio x 100%"
1685 PRINT"Taxa analysed: ";:FOR X=0 TO M%:IF
     Q%(X,0)>0 THEN PRINT;Q%(X,0);" ";
1686 NEXT: PRINT'
1690 PRINT'TAB(10);T$;"    ";DATE$''G$': Z%=0
1700 FOR Y%=1 TO N%
1710 IFD(1,Y%)=0 THEN D(3,Y%)=0: IF D(4,Y%)<0 THEN
     1880
1720 IF I$="N" THEN 1750
1730 PRINT;TAB(Z%*32);D(0,Y%);TAB(6+Z%*32)": ";
1740 PRINT;D(1,Y%);TAB(12+Z%*32);
1750 IF D(2,Y%)>.01 THEN 1790
1760 IF I$="N" THEN 1780
1770 PRINT;"-       -";: GOTO 1840
1780 IF D(1,Y%)=0 THEN 1830
1790 D(3,Y%)=D(1,Y%)/D(2,Y%)
1800 D(2,Y%)=(INT(D(2,Y%)*100+.5))/100
1810 IF I$="N" THEN 1880
1820 PRINT;D(2,Y%);TAB(19+Z%*32);INT(D(3,Y%)*100
     +.5)/100;
1830 IF I$="N" THEN 1850
1840 PRINT;TAB(23+Z%*32);" - ";INT(D(4,Y%));
1850 IF Z%=0 THEN 1870
1860 Z%=0: PRINT: GOTO 1880
1870 Z%=1: PRINT;TAB(32);
1880 NEXT
1890 IFI$="N"THEN1910
1900 PRINT
1910 PRINT'"Grand total - ";
```

```
1920 PRINT;R%;"   ";(INT(K*100+.5))/100;"   ";(INT(R%
     /K*100+.5))/100;
1930 IF R%>0 THEN 1950
1940 VDU3: PRINT: GOTO 230
1950 A2=0: IF H$="B" THEN 1970
1960 PRINT''"Ranking ratios"
1970 C2=1E6
1980 FOR Y%=1 TO N%: IF D(3,Y%)<0 THEN 2030
1990 IF D(4,Y%)<0 THEN 2030
2000 IF D(3,Y%)<C2 THEN 2020
2010 GOTO 2030
2020 C2=D(3,Y%): Y1%=Y%
2030 NEXT
2040 IF C2=1E6 THEN 2090
2050 IF H$="B" THEN 2080
2060 A2=A2+1: PRINT;D(0,Y1%);TAB(A2*7);: D(3,Y1%)=-1:
     IF A2<10 THEN 1970
2070 A2=0: PRINT: GOTO 1970
2080 D(3,Y1%)=-1: GOTO 1970
2090 IF H$="B" THEN 2110
2100 PRINT: GOTO 2130
2110 D(4,Y1%)=-D(4,Y1%): N2=N2-1
2120 PRINT;"   Ch. deleted : ";D(0,Y1%)
2130 K=0: R%=0
2140 FOR Y%=1 TO N%: D(2,Y%)=0: D(1,Y%)=0: NEXT
2150 IF H$="B" THEN 630
2160 VDU3
2170 GOTO 230
2180 C3%=0: INPUT "Delete or restore characters, taxa
     or both (1st C then T) - C, T or B ";C$
2190 IF C$="T" THEN 2220
2200 N1=N%: GOTO 2230
2210 C$="T"
2220 N1=M%
2230 INPUT"How many ";F
2240 A$="N": PRINT"Enter singly"
2250 FOR Z%=1 TO F
2260 INPUT G
2270 FOR Y%=1 TO N1
2280 IF C$="T" THEN 2350
2290 IF ABS(D(0,Y%))=G THEN 2310
2300 GOTO 2380
2310 IF D(4,Y%)>0 THEN 2330
2320 N2=N2+1: GOTO 2340
2330 N2=N2-1
2340 D(4,Y%)=-D(4,Y%): GOTO 2390
2350 IF ABS(Q%(Y%,0))=G THEN 2370
2360 GOTO 2380
2370 Q%(Y%,0)=-Q%(Y%,0): GOTO 2390
2380 NEXT
2390 NEXT Z%
2400 IF C$="B" THEN 2210
2410 FOR Y%=1 TO N%
2420 IF D(4,Y%)<0 THEN 2450
2430 C3%=C3%+1
2440 D(3,C3%)=Y%
2450 NEXT
2460 IF H$="B" THEN 340
```

```
2470 GOTO 540
2480 END
```

4. The compatability program LEQUC.

```
  10 REM LEQUC LeQuesne test program computes marks
  20 CLOSE#0
  30 INPUT"Enter input filename ";F$;"Enter title
     ";T$;"Enter date ";DATE$
  35 INPUT;"Screen or Printer: S or P ";S$
  36 IF S$ = "P" THEN VDU3
  40 CH=OPENIN F$
  50 INPUT #CH,M%,N%
  60 DIM Q(M%,N%),E%(M%),D%(3,N%)
  70 FOR Y%=0 TO N%
  80 D%(0,Y%)=1
  90 D%(2,Y%)=Y%
 100 NEXT
 110 FOR X%=0 TO M%
 120 FOR Y%=0 TO N%
 130 INPUT#CH,Q(X%,Y%)
 140 NEXT Y%
 150 NEXT
 160 INPUT "Data Unchanged, Altered or End run - U, A
     or E ";D$
 170 IF D$="A" THEN 1280
 180 IF D$="E" THEN 1600
 190 FOR X%=1 TO M%:E%(X%)=0:NEXT
 200 J%=0
 210 FOR Y%=1 TO N%
 220 D%(3,Y%)=0
 230 IF D%(0,Y%)<0 THEN 260
 240 J%=J%+1
 250 D%(2,J%)=Y%
 260 NEXT
 270 FOR Z%=J% TO 1 STEP -1
 280 Z1%=D%(2,Z%)
 290 FOR Y%=1 TO J%
 310 IF Y%>Z%-1 THEN 750
 320 Y1%=D%(2,Y%)
 330 IF INT(Q(0,Y1%))-INT(Q(0,Z1%))=0 THEN 750 ELSE
     A%=0: B%=0: C%=0: D%=0
 350 FOR X%=1 TO M%
 360 IF Q(X%,0)<0 THEN 590 ELSE Q1%=INT(Q(X%,Y1%)+
     Q(X%,Z1%))
 380 IF Q1%>6 THEN 590
 390 IF Q1%=0 THEN 500
 400 IF Q1%=2 THEN 530
 410 IF Q1%>2 THEN 440
 420 IF INT(Q(X%,Z1%))=0 THEN 520 ELSE 510
 440 IF Q1%>3 THEN 470
 450 IF INT(Q(X%,Z1%))=0 THEN 540 ELSE GOTO 560
 470 IF INT(Q(X%,Z1%))=1 THEN 550
 480 IF INT(Q(X%,Y1%))=1 THEN 570 ELSE 580
 490 GOTO 580
 500 A%=A%+1: A1%=X%: GOTO 590
 510 B%=B%+1: B1%=X%: GOTO 590
```

```
 520 C%=C%+1: C1%=X%: GOTO 590
 530 D%=D%+1: D1%=X%: GOTO 590
 540 A%=A%+1: A1%=X%: C%=C%+1: C1%=X%: GOTO 590
 550 B%=B%+1: B1%=X%: D%=D%+1: D1%=X%: GOTO 590
 560 A%=A%+1: A1%=X%: B%=B%+1: B1%=X%: GOTO 590
 570 C%=C%+1: C1%=X%: D%=D%+1: D1%=X%: GOTO 590
 580 A%=A%+1: A1%=X%: B%=B%+1: B1%=X%: C%=C%+1:
     C1%=X%: D%=D%+1: D1%=X%
 590 NEXT
 600 X1%=0: IF A%*B%*C%*C%*D%=0 THEN 750
 640 IF A%>1 THEN 660 ELSE X1%=A1%: PROCMARK
 660 IF B%>1 THEN 680 IF B1%=X1% THEN 750 ELSE
     X1%=B1%: PROCMARK
 680 IF C%>1 THEN 700 IF C1%=X1% THEN 750 ELSE
     X1%=C1%: PROCMARK
 700 IF D%>1 THEN 750 IF D1%=X1% THEN 750 ELSE
     X1%=D1%: PROCMARK
 750 NEXT
 760 NEXT
 765 INPUT;"Screen or printer: S or P "; S$
 766 IF S$<>"P" THEN 780
 770 VDU2
 780 PRINT'"Species and characters 'marked'"
 790 PRINT: PRINT;TAB(20);T$;"   ";DATE$: PRINT:
     PRINT;"Taxon": PRINT;"Nos"
 800 C%=0
 810 FOR Y%=1 TO N%:IF D%(3,Y%)=0 THEN 830
 820 C%=C%+1: D%(1,C%)=Y%
 830 NEXT
 840 FOR W=1 TO C% STEP 17
 850 N1=-1: PRINT;TAB(14);
 860 FOR Y%=W TO W+16 STEP 2
 870 IF Y%>C% THEN 900
 880 N1=N1+2: PRINT;ABS(Q(0,D%(1,Y%)));TAB(18+4*N1);
 890 NEXT
 900 PRINT: PRINT;TAB(18);: N1=1
 910 FOR Y%=W+1 TO W+16 STEP 2
 920 IF Y%>C% THEN 950
 930 N1=N1+2: PRINT;ABS(Q(0,D%(1,Y%)));TAB(14+4*N1);
 940 NEXT
 950 PRINT'
 960 FOR X%=1 TO M%
 970 IF E%(X%)=0 THEN 1120
 980 V=Q(X%,0): GOSUB 1550
 990 IF W>1 THEN 1010
1000 PRINT;" (";E%(X%);")";
1010 PRINT;TAB(14);: N1=1
1020 FOR Y%=W TO W+16
1030 IF Y%>C% THEN 1090
1040 I=Q(X%,D%(1,Y%)) -INT(Q(X%,D%(1,Y%))) +1E-5
1050 IF I<.0001 THEN 1070
1060 PRINT;INT(I*100);TAB(14+4*N1);: GOTO 1100
1070 PRINT;"--  ";
1080 GOTO 1100
1090 PRINT: Y%=1000
1100 N1=N1+1: NEXT Y%
1110 PRINT
1120 NEXT X%
```

```
1130 PRINT'': NEXT W
1140 PRINT;"Unmarked taxa: ";
1150 FOR X%=1 TO M%
1160 IF E%(X%)>0 THEN 1190
1170 IF Q(X%,0)<0 THEN 1190
1180 PRINT;Q(X%,0);" ";
1190 NEXT: PRINT
1200 Z%=0: PRINT'
1210 VDU3
1220 FOR X%=1 TO M%
1230 FOR Y%=1 TO N%
1240 Q(X%,Y%)=INT(Q(X%,Y%))
1250 NEXT
1260 NEXT
1270 GOTO 160
1280 H=0
1290 INPUT;"Delete or restore characters, taxa or both
     (1st C then T) - C, T or B ";C$
1300 IF C$="T" THEN 1330
1310 N1=N%: GOTO 1340
1320 C$="T"
1330 N1=M%
1340 INPUT "How many";F
1350 A$="N": PRINT "Enter singly"
1360 FOR Z%=1 TO F
1370 INPUT G
1380 FOR Y%=1 TO N1
1390 IF C$="T" THEN 1430
1400 IF ABS(Q(0,Y%))=G THEN 1420
1410 GOTO 1460
1420 D%(0,Y%)=-D%(0,Y%): GOTO 1470
1430 IF ABS(Q(Y%,0))=G THEN 1450
1440 GOTO 1460
1450 Q(Y%,0)=-Q(Y%,0): GOTO 1470
1460 NEXT Y%
1470 NEXT Z%
1480 IF C$="B" THEN 1320
1490 FOR Y%=1 TO N%
1500 IF D%(0,Y%)<0 THEN 1530
1510 H=H+1
1520 D%(2,H)=Y%
1530 NEXT Y%
1540 GOTO 190
1550 IF V<10 THEN 1590
1560 IF V<100 THEN 1580
1570 PRINT;V;: RETURN
1580 PRINT;" ";V;: RETURN
1590 PRINT;"  ";V;: RETURN
1600 CLOSE#0: END
1610 DEFPROCMARK
1620 Q(X1%,Y1%)=Q(X1%,Y1%)+.01: Q(X1%,Z1%)=Q(X1%,Z1%)+
     .01:E%(X1%)=E%(X1%)+1:D%(3,Y1%)=1: D%(3,Z%)=1
1630 ENDPROC
```

5. The character weighting program O'NOLAN"

```
5 REM O'NOLAN
```

```
 10 REM O'NOMOD computes O'Nolan weights from
    compatibility matrix,
 11 REM avoiding same variable  comparisons in
    multistate characters
 20 CLOSE#0
 30 INPUT"Enter input filename  ";F$;"Enter title
    ";T$;"Enter date  ";DATE$
 40 CH = OPENIN F$
 50 INPUT#CH,M%,N%
 60 DIM Q%(M%+1,N%),C%(N%*(N%-1)/2),B%(N%),D(2,N %):
    P% = M%+1
 70 REM   FOR Z% = 1 TO N%*(N%-1)/2: C%(Z%) = -2:
    NEXT
 80 FOR Y% = 0 TO N%: INPUT#CH,D(0,Y%): D(2,Y%) = 1:
    NEXT
100 FOR X% = 1 TO M%
110 FOR Y% = 0 TO N%
120 INPUT#CH,Q%(X%,Y%)
130 NEXT: NEXT
140 PRINT"R = Run"
150 PRINT"T = Delete or restore Taxa"
160 PRINT"E = End run"
170 VDU3: INPUT'"Enter R, T or E";H$
180 IF H$ = "E" THEN 1150
190 IF H$ ="T" THEN GOSUB 1170
200 FOR Y% = 1 TO N%
220 O% = 0: I% = 0
230 FOR X% = 1 TO M%
235 IF Q%(X%,0)<0 THEN 270
240 IF Q%(X%,Y%) = 7 THEN 270
250 IF Q%(X%,Y%) = 0 THEN O% = O%+1: GOTO 270
260 IF Q%(X%,Y%) = 1 THEN I% = I%+1 ELSE O% = O%+1:
    I% = I%+1
270 NEXT
280 IF O%<2 OR I%<2 THEN D(0,Y%) = -D(0,Y%): D(1,Y%)
    = -11
290 NEXT
300 INPUT;"Title changed - Y or N";U$
310 IF U$ = "N" THEN 330
320 INPUT;"Enter new title";T$
330 INPUT;"Screen or Printer - S or P";S$
340 IF S$ = "P" THEN VDU2
355 PRINT;"Program O'NOMOD    Datafile:";F$
360 PRINT'TAB(10);T$;"   ";DATE$'
380 PRINT"Taxa analysed "
390 FOR X% =1 TO M%: IF Q%(X%,0)>0 THEN
    PRINT;Q%(X%,0); " ";
400 NEXT: PRINT'
410 PRINT;TAB(8);"Ch.nos.";TAB(18);"Weights";TAB(40);
    "Ch.nos.";TAB(50);"Weights"
420 FOR Z% = 1 TO N%
430 IF D(0,Z%)<0 THEN 720
440 FOR Y% = Z%+1 TO N%
450 IF Y%>N% THEN 710
460 IF D(0,Y%)<0 THEN 710
463 IF INT(D(0,Y%))-INT(D(0,Z%)) = 0 THEN 710 470 A%
    = 0: B% = 0: C% = 0: D% = 0
480 FOR X% = 1 TO M%
```

```
490 IF Q%(X%,0)<0 THEN 670 ELSE Q1% = (Q%(X%,Y%)+
    Q%(X%,Z%))+1
500 IF Q1%>4 THEN 550
510 ON Q1% GOTO 580, 520, 610, 540
520 IF Q%(X%,Z%) = 0 THEN 600 ELSE 590
530 IF Q1%>3 THEN 560
540 IF Q%(X%,Z%) = 0 THEN 620 ELSE 640
550 IF Q1%>7 THEN 670
560 IF Q%(X%,Z%) = 1 THEN 630
570 IF Q%(X%,Y%) = 1 THEN 650 ELSE 660
580 A% = A%+1: GOTO 670
590 B% = B%+1: GOTO 670
600 C% = C%+1: GOTO 670
610 D% = D%+1: GOTO 670
620 A% = A%+1: C% = C%+1: GOTO 670
630 B% = B%+1: D% = D%+1: GOTO 670
640 A% = A%+1: B% = B%+1: GOTO 670
650 C% = C%+1: D% = D%+1: GOTO 670
660 A% = A%+1: B% = B%+1: C% = C%+1: D% = D%+1
670 NEXT
680 IF A%*B%*C%*D%>0 THEN 690 ELSE 700
690 C%(Y%*(Y%-3)/2+Z%+1) = 0: GOTO 710
700 C%(Y%*(Y%-3)/2+Z%+1) = 1: Q%(0,Y%) = Q%(0,Y%)+1:
    Q%(0,Z%) = Q%(0,Z%)+1
710 NEXT
720 NEXT
722 FOR Y% = 1 TO N%
723 IF D(0,Y%)<0 THEN 729
724 FOR Z% = 1 TO N%
725 IF D(0,Z%)<0 OR INT(D(0,Y%))-INT(D(0,Z%)) = 0
    THEN 728
727 Q%(P%,Y%) = Q%(P%,Y%)+1
728 NEXT
729 NEXT
730 FOR Z% = 1 TO N%
740 IF D(0,Z%)<1 THEN 890
750 D(1,Z%) = 0: F% = 0
760 FOR Y% = 1 TO N%
770 IF D(0,Y%)<1 THEN 870
775 IF Y% = Z% THEN 870
780 IF INT(ABS(D(0,Y%)))-INT(ABS(D(0,Z%))) = 0 THEN
    870
790 F% = F%+Q%(P%,Y%)
800 IF Y%>Z% THEN 810 ELSE C% = Z%*(Z%-3)/2+Y%+1:
    GOTO 830
810 C% = Y%*(Y%-3)/2+Z%+1
830 IF C%(C%) = 0 THEN 850
840 D(1,Z%) = D(1,Z%)+Q%(0,Y%): GOTO 870
850 IF D(2,Y%)<0 THEN D(2,Y%) = (D(2,Y%)+1)/2
860 D(1,Z%) = D(1,Z%)-Q%(0,Y%)*D(2,Y%)
870 NEXT
880 D(1,Z%) = D(1,Z%)/F%
890 NEXT
900 G = 100
910 FOR Y% = 1 TO N%
920 IF D(0,Y%)<1 THEN 940
930 IF D(1,Y%)<G THEN G = D(1,Y%)
940 NEXT: VDU3
```

```
 950 IF G<1 THEN 980
 960 IF S$ = "P" THEN VDU2
 980 PROCPrint
1000 FOR Y% = 1 TO N%
1010 IF D(0,Y%)<1 THEN 1050
1020 IF D(1,Y%) = G THEN 1030 ELSE 1040
1030 D(0,Y%) = -ABS(D(0,Y%)): GOTO 1050
1040 D(2,Y%) = D(1,Y%): D(1,Y%) = 0: Q%(0,Y%) = 0
1050 NEXT
1060 FOR Z% = 1 TO N%
1070 IF D(0,Z%)<1 THEN 1130
1080 FOR Y% = Z%+1 TO N%
1090 IF Y%>N% THEN 1120
1100 IF D(0,Y%)<1 THEN 1120
1110 IF C%(Y%*(Y%-3)/2+Z%+1) = 1 THEN Q%(0,Y%) = Q%(0,
     Y%)+1:Q%(0,Z%) = Q%(0,Z%)+1
1120 NEXT
1130 NEXT
1140 IF G<1 THEN FOR Y% = 1 TO N%: Q%(P%,Y%) = 0:
     NEXT: GOTO 722
1145 FOR Y% = 0 TO N%: D(0,Y%) = ABS(D(0,Y%)): D(1,Y%)
     =1: D(2,Y%) = 1: NEXT:GOTO 170
1150 VDU3: CLOSE#0: END
1170 INPUT"Delete or restore how many taxa ";F%
1180 PRINT"Enter singly"
1190 FOR Z% = 1 TO F%
1200 INPUTH
1210 FOR X% = 1 TO M%
1220 IF ABS(Q%(X%,0)) = H THEN Q%(X%,0) = -Q%(X%,0)
1230 NEXT:NEXT
1250 RETURN
1680 DEFPROCPrint
1690 Z% = 0
1700 FOR Y% = 1 TO N%: B%(Y%) = 0
1730 PRINT;TAB(10+Z%*32);ABS(D(0,Y%));TAB(16+Z%*32)":
     ";
1740 IF D(1,Y%)<-10 THEN PRINT;"-";: GOTO 1850
1750 PRINT;INT((D(1,Y%)*100)+.5)/100;
1850 IF Z% = 0 THEN 1870
1860 Z% = 0: PRINT: GOTO 1880
1870 Z% = 1: PRINT;TAB(42);
1880 NEXT
1950 A2 = 0
1960 PRINT''"Ranking weights"
1970 C2 = -10
1980 FOR Y% = 1 TO N%: IF D(1,Y%)<-10 THEN 2030
1990 IF B%(Y%)<0 THEN 2030
2000 IF D(1,Y%)< = C2 THEN 2030
2020 C2 = D(1,Y%): Y1% = Y%
2030 NEXT
2040 IF C2 = -10 THEN 2100
2060 A2 = A2+1: PRINT;D(0,Y1%);TAB(A2*7);: B%(Y1%)=-1:
     IF A2<10 THEN 1970
2070 A2 = 0: PRINT: GOTO 1970
2100 PRINT: ENDPROC
```

6. STEPONE - a program to step code continuous variable data.

```
 10 REM STEPONE
 20 CLOSE# 0: @% = 10
 30 INPUT "Enter input filename ";E$
 40 F = OPENIN E$
 50 INPUT "Enter date "; D$
 60 INPUT "Enter title "; T$
 70 INPUT#F,M%,N%
 80 DIM A%(M%,N%),C(M%,N%)
 90 FOR X% = 0 TO M%
100 FOR Y% = 0 TO N%
110 INPUT# F,C(X%,Y%)
120 IF C(X%,Y%)>-1 THEN A%(X%,Y%) = M%+1 ELSE
    A%(X%,Y%) = -1
130 NEXT
140 NEXT
150 FOR Y% = 1 TO N%
160 PRINT;Y%;" ";
170 GRADE% = 0
180 REPEAT
190 B = 1E6
200 FOR X% = 1 TO M%
210 IF A%(X%,Y%) < GRADE% OR C(X%,Y%) <0 OR C(X%,Y%)>
    = B THEN 230
220 B = C(X%,Y%)
230 NEXT
240 R% = 0
250 FOR Z% = 1 TO M%
260 IF A%(Z%,Y%)>M% THEN R% = R%+1
270 IF C(Z%,Y%)<>B THEN 290
280 A%(Z%,Y%) = GRADE%
290 NEXT
300 GRADE% = GRADE%+1
310 UNTIL R% = 0
320 NEXT:PRINT
322 INPUT;"Screen or Printer - S or P";S$
324 IF S$<>"P" THEN 330
325 VDU2
330 PRINT;TAB(18); "Step coding of continuous
    variables"
335 PRINT;TAB(17); "St=Step no.  Raw=Raw score of
    variable"'
340 PRINT; TAB(10); T$; TAB(40); E$;"  ";D$
350 PRINT; "Sample"; TAB(30); "Variable nos."
360 PRINT;"nos."
370 FOR W% = 1 TO N% STEP 7
380 Z% = W%-1: W7% = W%+6: Y% = 0: PRINT; TAB(7);
390 REPEAT
400 Z% = Z%+1: Y% = Y%+1
410 PRINT;C(0,Z%); TAB(7+10*Y%);
420 UNTIL Z% = W7% OR Z% = N%
430 Y% = 0: Z%=W%-1: PRINT;TAB(3);
440 REPEAT
450 Y% = Y%+1: Z% = Z%+1
460 PRINT;"  St Raw  ";
470 UNTIL Y% =7 OR Z% = N%
```

```
480 PRINT'
490 FOR X% = 1 TO M%
500 PRINT;C(X%,0);:Z% = W%-1: Y% = 0
510 REPEAT
520 Z% = Z%+1:Y% = Y%+1: D% = 10*(Y%-1)
530 PRINT; TAB(5+D%); A%(X%,Z%); TAB(8+D%); C(X%,Z%);
540 UNTIL Z% = W7% OR Z% = N%
560 PRINT
570 NEXT
580 PRINT''
590 NEXT W%
595 VDU3
600 CLOSE# 0:END
```

7. STEPTWO - probability matrix program for step coded variables.

```
 10 REM STEPTWO
 11 REM For characters 1 to N against N to x,
 20 CLOSE#0
 30 DIM PR(9): FOR X% = 0 TO 8: READ PR(X%): NEXT
 40 DATA .01,.0033,.001,.00033,.0001,.000033,.00001,
    .0000033,.000001
 50 INPUT "Date";D$: INPUT "Title";T$: INPUT "Enter
    input filename ";F$
 60 B = OPENIN F$
 70 INPUT#B,M%,N%
 80 DIM A(M%,N%),C(M%),I%(M%,1),J%(N%),E(24),G%(3)
    ,F(3)
 90 FOR X% = 0 TO M%
100 FOR Y% = 0 TO N%
110 INPUT#B,A(X%,Y%)
120 NEXT
130 NEXT
140 E(24) = N%+1: TSTEP% = 0
150 FOR Y% = 1 TO N%
160 FOR X% = 1 TO M%
170 C(X%) = A(X%,Y%): A(X%,Y%) = M%+1
180 NEXT
190 GRADE% = 1
200 REPEAT
210 B = 1E6
220 FOR X% = 1 TO M%
230 IF A(X%,Y%)<GRADE% OR C(X%)> = B OR C(X%)<0 THEN
    250
240 B = C(X%)
250 NEXT
260 R% = 0
270 FOR X% = 1 TO M%
280 IF A(X%,Y%)>M% THEN R% = R%+1
290 IF C(X%)<0 THEN A(X%,Y%) = -4
300 IF C(X%)<>B THEN 320
310 A(X%,Y%) = GRADE%
320 NEXT
330 GRADE% = GRADE%+1
340 UNTIL R% = 0
350 J%(Y%)  = GRADE%-3: TSTEP% = TSTEP%+J%(Y%)
```

```
360 PRINT;J%(Y%);": ";TSTEP%;" ";
370 NEXT Y%
374 INPUT'"Screen or Printer - S or P";S$
376 IF S$<>"P" THEN 390
380 VDU2
390 PRINT''TAB(10);T$;TAB(55);F$;TAB(65);D$''
    "Fisher's exact probability"
400 PRINT;TAB(11);"Number:- 1   2   3    4    5    6
    7       8     9      *"
410 PRINT;"Significant at % :- 5   1  .33  .1   .033
    .01  .0033  .001  .00033  .0001"'
420 L% = 1: O% = TSTEP%-J%(N%): PROCSet: WB% = 0
430 Y% = 1: K% = 1
440 F% = 0
450 FOR WA% = L% TO J%(Y%)
460 F% = F%+1: K% = K%+1
470 E(F%) = A(0,Y%)+WA%/100
480 IF F% = 23 THEN 530
490 IF K% = O% THEN 520
500 NEXT
510 Y% = Y%+1:L% = 1: GOTO 450
520 E(F%+1) = N%+1
530 @% = &00020205: D% = -1
540 PRINT
550 FOR Z% = 1 TO F% STEP 3
560 D% = D%+1: PRINT; TAB(7+9*D%); E(Z%);
570 NEXT
580 D% = -1: PRINT
590 FOR Z% = 2 TO F% STEP 3
600 D% = D%+1: PRINT; TAB(10+9*D%); E(Z%);
610 NEXT
620 D% = -1: PRINT
630 FOR Z% = 3 TO F% STEP 3
640 D% = D%+1: PRINT; TAB(13+9*D%); E(Z%);
650 NEXT
660 PRINT'
670 Y1% = N%
680 FOR X% = 1 TO M%:I%(X%,0) = 0: NEXT: W1% = 1
690 FOR Z% = J%(Y1%) TO 1 STEP -1
700 PRINT;A(0,Y1%)+Z%/100;TAB(7);
710 FOR X% = 1 TO M%
720 IF A(X%,Y1%)>Z% THEN I%(X%,0) = 1
730 NEXT
740 W% =1: E1% = INT(E(1))
750 IF WB% = 0 THEN 790
760 FOR X% = 1 TO M%
770 IF A(X%,E1%)< = WB% THEN I%(X%,1) = 0
780 NEXT: W1% = WB%+1
790 REPEAT
800 X% = 0
810 REPEAT: X% = X%+1
814 IF A(X%,E1%)>-1 THEN 820
816 I%(X%,1) = -4: GOTO 830
820 IF A(X%,E1%) = W1% THEN I%(X%,1) = 0
830 UNTIL X% = M%
840 A% = 0: B% = 0: C% = 0: D% = 0
850 X% = 0
860 REPEAT: X% = X%+1
```

```
 870 Q% = I%(X%,0)+I%(X%,1)
 880 IF Q%<0 THEN 930
 890 IF Q% = 0 THEN A% = A%+1
 900 IF Q% = 2 THEN D% = D%+1
 910 IF Q%<>1 THEN 930
 920 IF I%(X%,0) = 0 THEN C% = C%+1 ELSE B% = B%+1
 930 UNTIL X% = M%
 940 G%(0) = A%:G%(1) = B%: G%(3) =  C%: G%(2) = D%
 950 ASS% = A%*D%-B%*C%
 960 IF ASS%<0 THEN ASS$  = "-" ELSE ASS$ =" "
 970 PROCrelabel: TP = 0
 980 I% = -1
 990 REPEAT: n = 0: ap = 1
1000 I% = I%+1
1010 PROCprob(I%+1,a+b)
1020 PROCprob(d-a+I%+1,c+d)
1030 PROCprob(a+c-I%+1,a+c)
1040 PROCprob(a+b-I%+1,b+d)
1050 TP = TP+ap
1060 UNTIL I% = a
1070 IF TP>.05 THEN 1140
1080 S% = -1
1090 REPEAT
1100 S% = S%+1
1110 UNTIL TP>PR(S%) OR S% = 9
1120 IF S%<9 THEN PRINT; ASS$; STR$(S%+1);" "; ELSE
     PRINT; ASS$;"* ";
1130 GOTO 1150
1140 PRINT;" . ";
1150 W% = W%+1: W1% = W1%+1
1160 IF E(W%)<E1%+1.01 THEN 1180
1170 E1% = INT(E(W%)): W1% = 1: PROCSet
1180 UNTIL W% = F%+1 OR INT(E(W%)) = A(0,Y1%)
1190 W1% = 1: PRINT': NEXT Z%
1200 Y1% = Y1%-1
1210 IF Y1% = INT(E(1)) THEN 1230
1220 GOTO 680
1230 PRINT'':IF K% = O% THEN 1270
1240 PRINT:  IF WA%<J%(Y%) THEN 1260
1250 Y% = Y%+1: WB% = 0: GOTO 440
1260 L% = WA%+1: WB% = WA%: GOTO 440
1270 VDU3
1280 END
1290 DEF PROCrelabel
1300 min = 0: F(min) = G%(0)
1310 IF G%(1)<F(0) THEN min = 1: F(0) = G%(1)
1320 IF G%(2)<F(0) THEN min = 2: F(0) = G%(2)
1330 IF G%(3)<F(0) THEN min = 3: F(0) = G%(3)
1340 F(1) = G%((1+min)MOD4)
1350 F(2) = G%((2+min)MOD4)
1360 F(3) = G%((3+min)MOD4)
1370 a = F(0): b = F(1): d = F(2): c = F(3)
1380 ENDPROC
1390 DEF PROCprob(x,y)
1400 IF x>y GOTO 1450
1410 J% = x-1
1420 REPEAT: J% = J%+1
1430 n = n+1: ap = ap*J%/n
```

```
1440 UNTIL J% = y
1450 ENDPROC
1460 DEF PROCSet
1470 X% = 1
1480 REPEAT: I%(X%,1) = 1: X% = X%+1
1490 UNTIL X% = M%
1500 ENDPROC
```

APPENDIX 2: DATA MATRICES & NUMERICAL DATA

MATRIX OF THE WELD DATA
(See Chapter 3)

Characters

Taxa	1.1	1.2	2	3	4	5.1	5.2	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0
2	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1
3	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	1	1
4	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1
5	1	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	1
6	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1
7	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0
8	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
9	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
10	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1
11	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1
12	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1
13	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
15	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
16	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
17	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
19	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
20	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
21	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
22	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
23	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
24	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0
25	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
26	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1
28	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Taxa	23	24	25	26	27	28	29	30	31
1	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	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	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0
15	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
18	0	0	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
22	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0

MATRIX OF THE QUINLAN DATA
(See Chapter 3)

Characters

Taxa	1	2	3	4	5.1	5.2	5.3	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0
2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0
4	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0
5	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0
6	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
7	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
8	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
9	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
10	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	1	1	1	0	1	0
11	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	0	0
12	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	1	0
13	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0
14	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0
15	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0
16	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0
19	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0
20	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0
21	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	0	1	0
22	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0
23	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	0
24	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0
26	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	1	0
27	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
29	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
30	0	0	-	-	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0
31	1	1	-	-	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0

Taxa	24	25	26	27	28	29	30	31
1	1	1	0	1	1	1	1	1
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
4	1	0	1	0	0	0	0	0
5	0	0	0	0	0	0	0	0
6	1	0	1	0	0	0	0	0
7	0	0	0	0	0	0	0	1
8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0
10	1	0	0	0	0	0	0	0
11	1	0	0	0	0	0	0	0
12	1	0	0	0	0	0	0	0
13	1	0	0	0	0	0	0	0
14	1	0	0	0	0	0	0	0
15	1	0	0	0	0	0	0	0
16	1	0	0	0	0	0	0	0
17	1	0	0	0	0	0	0	0
18	1	0	0	0	0	0	0	0
19	1	0	0	0	0	0	0	0
20	1	0	0	0	0	0	0	0
21	1	0	0	0	0	0	0	0
22	1	0	0	0	0	0	0	0
23	1	0	0	0	0	0	0	0
24	1	0	0	0	0	0	0	0
25	1	1	0	0	0	0	0	0
26	1	0	1	0	0	0	0	0
27	1	0	0	1	0	0	0	0
28	1	0	0	0	1	0	0	0
29	0	0	0	0	0	1	0	0
30	1	0	0	0	0	0	1	0
31	1	0	0	0	0	0	0	1

[- = a missing score, e.g. a character of the male when only the female is known.]

Quinlan matrix continued

Characters

Taxa	24	25	26	27.1	27.2	28	29	30	31	32.1	32.2	33	34	35
1	0	0	0	0	1	1	0	0	0	0	0	0	0	1
2	1	0	1	0	0	0	0	0	0	1	0	1	0	1
3	1	0	1	1	0	0	0	0	0	1	0	1	0	1
4	0	0	1	1	0	0	0	0	0	1	0	0	0	1
5	0	0	1	1	0	0	0	0	0	1	0	0	0	1
6	0	0	1	1	0	0	0	0	0	1	0	0	0	1
7	0	0	0	0	1	0	0	0	0	0	0	0	0	1
8	0	0	0	0	0	0	0	0	0	0	0	0	0	1
9	0	0	0	0	1	0	0	0	0	0	0	0	0	1
10	0	0	0	0	1	0	0	0	1	1	0	0	0	0
11	0	0	0	0	0	0	0	0	1	1	0	0	0	0
12	0	0	0	0	1	0	0	0	1	1	0	0	0	0
13	0	0	0	1	0	1	0	0	0	0	0	1	0	0
14	0	0	0	0	0	0	0	0	0	0	1	1	0	0
15	0	0	0	0	0	0	0	0	0	0	1	1	0	0
16	0	0	0	0	1	0	0	0	0	1	0	0	0	0
17	0	0	0	0	0	0	0	1	0	0	0	0	0	0
18	0	0	0	0	0	0	1	0	0	1	0	0	0	0
19	0	0	0	0	1	0	0	0	0	1	0	0	0	0
20	0	0	0	0	1	0	1	1	0	0	0	0	0	0
21	0	0	0	0	1	0	1	1	0	0	0	0	0	0
22	0	0	0	0	1	0	1	1	0	0	0	0	0	0
23	0	0	0	0	1	1	1	1	0	0	0	0	0	0
24	0	0	0	0	1	1	1	0	0	1	0	0	0	0
25	0	0	0	0	1	1	1	0	0	0	1	0	0	0
26	0	0	0	0	1	1	1	0	0	0	1	0	0	0
27	0	0	0	0	1	0	0	1	0	0	0	0	0	0
28	0	0	0	0	1	1	1	0	0	0	1	0	0	0
29	0	0	0	0	1	0	0	0	0	0	1	0	0	0
30	0	0	0	0	1	0	0	0	0	0	0	0	0	0
31	0	0	0	0	1	0	0	0	0	0	1	0	0	0

COMPOSITE MATRIX OF THE WELD AND QUINLAN DATA
(See Chapter 3)

Characters

Taxa	C01.1	C01.2	C02	C03	C04	C05.1	C05.2	C06	C07	C08	C09	C10	C11	C12	C13	C14	C15	C16	C17	C18	C19	C20	C21	C22	C23	C24
1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0
2	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	0	0
3	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	1	1	0	0
4	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0
5	1	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	1	0	0
6	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0
7	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
8	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
9	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
10	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
11	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
12	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
13	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
15	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
17	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
19	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
20	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
21	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
22	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
23	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0
24	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
25	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
26	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
28	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Composite matrix continued

Characters

Taxa	C25	C26	C27	C28.1	C28.2	C28.3	C29	C30	C31	C32	C33	C34	C35	C36	C37.1	C37.2	C38	C39	C40	C41.1	C41.2	C42	C43.1	C43.2	C44
1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0
2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1
4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0
5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0
6	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0
7	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
8	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
10	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	1	0	0	0	1	0	1	0	0
11	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0
12	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0
13	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	1
14	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	1
15	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	1
16	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0
19	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	0	1	0
20	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0
21	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0
22	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0
23	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0
24	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	1	1	1	0
25	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	1
26	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	1
27	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1
29	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
30	0	-	-	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
31	1	-	-	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0

MEASUREMENTS OF ANTENNAL SEGMENTS
(See Chapter 4)

(L = length in mm, B = breadth in mm) (R = ratio of L/B.)
(Principal components analysis based on graticule units)

	Segment number										
	1	2	3	4	5	6	7	8	9	10	11
	12	13	14								
Ibalia leucospoides											
					Female						
L	0.74	0.27	0.91	1.04	1.02	0.93	0.80	0.67	0.50	0.43	0.34
	0.30	0.48									
B	0.26	0.22	0.21	0.19	0.18	0.18	0.18	0.18	0.18	0.18	0.18
	0.18	0.19									
R	2.9	1.2	4.3	5.5	5.7	5.2	4.4	3.7	2.8	2.4	1.9
	1.7	2.5									
					Male						
L	0.54	0.21	0.66	0.81	0.74	0.70	0.64	0.62	0.56	0.53	0.48
	0.50	0.48	0.43	0.42							
B	0.22	0.18	0.18	0.16	0.16	0.16	0.16	0.18	0.18	0.16	0.16
	0.15	0.15	0.18	0.13							
R	2.5	1.2	3.7	5.1	4.6	4.4	4.0	3.4	3.1	3.3	3.0
	3.3	3.2	2.4	3.2							
Oberthuerella lenticularis											
					Female						
L	0.54	0.22	0.40	0.53	0.48	0.40	0.42	0.37	0.35	0.35	0.43
	0.37	0.74									
B	0.32	0.29	0.29	0.32	0.32	0.34	0.34	0.34	0.35	0.35	0.34
	0.35	0.32									
R	1.7	0.8	1.4	1.7	1.5	1.2	1.2	1.1	1.0	1.0	1.3
	1.1	2.3									
					Male						
L	0.48	0.19	0.40	0.58	0.58	0.56	0.53	0.53	0.53	0.53	0.53
	0.48	0.43	0.60								
B	0.29	0.25	0.26	0.24	0.24	0.27	0.30	0.30	0.29	0.29	0.30
	0.30	0.30	0.25								
R	1.7	0.8	1.6	2.4	2.4	2.1	1.8	1.8	1.8	1.8	1.8
	1.6	1.4	2.4								
Tessmanella expansa (male unknown)											
					Female						
L	0.42	0.13	0.38	0.64	0.56	0.48	0.43	0.40	0.40	0.36	0.35
	0.32	0.58									
B	0.22	0.16	0.13	0.16	0.18	0.18	0.19	0.18	0.19	0.20	0.19
	0.20	0.21									
R	1.9	0.8	3.0	4.0	3.1	2.7	2.3	2.2	2.1	1.8	1.8
	1.6	2.8									
Liopteron compressum											
					Female						
L	0.56	0.21	0.59	0.82	0.77	0.78	0.75	0.72	0.69	0.67	0.61
	0.51	1.10									
B	0.46	0.24	0.22	0.22	0.26	0.24	0.26	0.26	0.27	0.27	0.27
	0.26	0.26									
R	1.2	0.9	2.7	3.7	3.0	3.3	2.9	2.8	2.6	2.5	2.3

2.0 4.2

Male

L 0.[illegible] 0.19 0.53 0.67 0.62 0.61 0.58 0.57 0.54 0.54 0.50
0 0.53 0.70
B 0.23 0.24 0.22 0.22 0.22 0.22 0.22 0.22 0.24 0.24 0.24
0.24 0.22 0.21
R 1.2 0.8 2.4 3.1 2.8 2.8 2.6 2.6 2.3 2.3 2.1
2.2 2.4 3.3

Plastibalia violaceipennis (Only first 10 segments seen. Male unknown)

Female

L 0.58 0.18 0.42 0.77 0.70 0.69 0.67 0.62 0.61 0.56
B 0.30 0.26 0.26 0.30 0.32 0.32 0.32 0.32 0.34 0.32
R 1.9 0.7 1.6 2.6 2.2 2.2 2.1 1.9 1.8 1.8

Pseudibalia fasciatipennis (male unknown)

Female

L 0.61 0.17 0.45 0.56 0.51 0.48 0.40 0.38 0.37 0.34 0.32
0.29 0.53
B 0.22 0.18 0.19 0.20 0.21 0.22 0.24 0.25 0.26 0.27 0.27
0.26 0.26
R 2.8 0.9 2.4 2.8 2.4 2.2 1.7 1.5 1.4 1.3 1.2
1.1 2.0

Mesocynips insignis

Female

L 0.40 0.14 0.30 0.27 0.22 0.21 0.19 0.19 0.19 0.19 0.19
0.18 0.43
B 0.19 0.14 0.14 0.16 0.18 0.18 0.18 0.18 0.18 0.18 0.19
0.19 0.18
R 2.1 1.0 2.1 1.7 1.2 1.2 1.1 1.1 1.1 1.1 1.0
1.0 2.4

Male

L 0.66 0.16 0.51 0.49 0.46 0.47 0.46 0.48 0.45 0.45 0.43
0.42 0.42 0.40 0.43
B 0.22 0.16 0.16 0.16 0.18 0.18 0.18 0.18 0.17 0.16 0.16
0.16 0.15 0.14 0.14
R 3.0 1.0 3.2 3.1 2.6 2.6 2.6 2.7 2.7 2.8 2.7
2.6 2.8 2.9 3.1

Paramblynotus punctulatus

Female

L 0.34 0.14 0.40 0.40 0.37 0.35 0.30 0.27 0.24 0.23 0.23
0.19 0.24
B 0.18 0.13 0.14 0.13 0.14 0.11 0.11 0.10 0.10 0.10 0.10
0.10 0.10
R 1.9 1.1 2.9 3.1 2.6 3.2 2.7 2.7 2.4 2.3 2.3
1.9 2.4

Male

L 0.29 0.11 0.35 0.35 0.34 0.37 0.32 0.32 0.29 0.29 0.27
0.29 0.22 0.29
B 0.16 0.12 0.11 0.11 0.11 0.11 0.10 0.10 0.09 0.10 0.09
0.09 0.09 0.08
R 1.8 0.9 3.2 3.2 3.1 3.4 3.2 3.2 3.2 2.9 3.0
3.2 2.4 3.6

Kiefferiella rugosa (male unknown)

Female

L	0.21	0.10	0.22	0.35	0.34	0.32	0.29	0.24	0.19	0.18	0.19
	0.18	0.26									
B	0.11	0.10	0.06	0.07	0.07	0.06	0.06	0.06	0.06	0.07	0.08
	0.08	0.08									
R	1.9	1.0	3.7	5.0	4.9	5.3	4.8	4.0	3.2	2.6	2.4
	2.3	3.3									

Aspicera scutellata

Female

L	0.26	0.08	0.18	0.18	0.16	0.18	0.16	0.14	0.14	0.14	0.13
	0.13	0.26									
B	0.10	0.08	0.06	0.07	0.08	0.08	0.08	0.10	0.09	0.08	0.08
	0.09	0.08									
R	2.6	1.0	3.0	2.6	2.0	2.3	2.0	1.4	1.6	1.8	1.6
	1.4	3.3									

Male

L	0.13	0.08	0.22	0.18	0.19	0.18	0.19	0.18	0.17	0.16	0.16
	0.16	0.14	0.22								
B	0.11	0.10	0.09	0.09	0.08	0.08	0.10	0.10	0.09	0.09	0.09
	0.09	0.08	0.08								
R	1.2	0.8	2.4	2.0	2.4	2.3	1.9	1.8	1.9	1.8	1.8
	1.8	1.8	2.8								

Callaspidia defonscolombei

Female

L	0.19	0.08	0.40	0.35	0.34	0.32	0.29	0.27	0.24	0.22	0.19
	0.19	0.42									
B	0.14	0.11	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.11	0.11
	0.10	0.10									
R	1.4	0.7	4.0	3.5	3.4	3.2	2.9	2.7	2.4	2.0	1.7
	1.9	4.2									

Male

L	0.16	0.08	0.32	0.32	0.32	0.32	0.30	0.29	0.26	0.26	0.24
	0.26	0.24	0.34								
B	0.13	0.11	0.11	0.10	0.11	0.11	0.10	0.10	0.10	0.10	0.09
	0.08	0.08	0.08								
R	1.2	0.7	2.9	3.2	2.9	2.9	3.0	2.9	2.6	2.6	2.4
	3.3	3.0	4.3								

Omalaspis carinata

Female

L	0.19	0.10	0.26	0.24	0.22	0.22	0.19	0.18	0.17	0.17	0.16
	0.18	0.34									
B	0.10	0.08	0.08	0.06	0.06	0.06	0.08	0.08	0.08	0.08	0.08
	0.08	0.08									
R	1.9	1.3	3.3	4.0	3.7	3.7	2.4	2.3	2.1	2.1	2.0
	2.3	4.3									

Male

L	0.16	0.06	0.22	0.22	0.19	0.21	0.21	0.19	0.18	0.18	0.16
	0.14	0.13	0.24								
B	0.09	0.08	0.10	0.06	0.07	0.07	0.07	0.08	0.08	0.08	0.08
	0.08	0.06	0.06								
R	1.8	0.8	2.2	3.7	2.7	3.0	3.0	2.4	2.3	2.3	2.0
	1.8	2.2	4.0								

Anacharis eucharioides

Female

L	0.17	0.09	0.21	0.19	0.16	0.15	0.15	0.14	0.13	0.12	0.13
	0.11	0.27									
B	0.07	0.06	0.06	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.06
	0.06	0.06									
R	2.4	1.5	3.5	3.8	3.2	3.0	3.0	2.8	2.6	2.0	2.2
	1.8	4.5									

Male

L	0.21	0.09	0.23	0.23	0.21	0.21	0.20	0.20	0.19	0.19	0.19
	0.19	0.16	0.22								
B	0.10	0.09	0.06	0.06	0.07	0.07	0.06	0.06	0.06	0.06	0.06
	0.06	0.06	0.06								
R	2.1	1.0	3.8	3.8	3.0	3.0	3.3	3.3	3.2	3.2	3.2
	3.2	2.7	3.7								

Aegilips nitidula

Female

L	0.24	0.10	0.26	0.23	0.21	0.21	0.18	0.17	0.16	0.16	0.14
	0.14	0.21									
B	0.09	0.08	0.06	0.07	0.06	0.08	0.08	0.08	0.09	0.08	0.08
	0.08	0.08									
R	2.7	1.3	4.3	3.3	3.5	2.6	2.3	2.1	1.8	2.0	1.8
	1.8	2.6									

Male

L	0.19	0.10	0.24	0.21	0.22	0.21	0.19	0.21	0.18	0.18	0.18
	0.18	0.16	0.22								
B	0.11	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.07	0.07
	0.06	0.06	0.06								
R	1.7	1.3	3.0	2.6	2.8	2.6	2.4	2.6	2.3	2.6	2.6
	3.0	2.7	3.7								

Xyalaspis laevigatus

Female

L	0.26	0.10	0.29	0.24	0.21	0.19	0.16	0.16	0.16	0.14	0.13
	0.13	0.19									
B	0.10	0.08	0.06	0.06	0.06	0.07	0.07	0.07	0.08	0.08	0.08
	0.08	0.08									
R	2.6	1.3	4.8	4.0	3.5	2.7	2.3	2.3	2.0	1.8	1.6
	1.6	2.4									

Male

L	0.24	0.11	0.26	0.27	0.26	0.24	0.24	0.22	0.21	0.21	0.19
	0.19	0.19	0.24								
B	0.10	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.07	0.07
	0.07	0.06	0.06								
R	2.4	1.4	3.3	3.4	3.3	3.0	3.0	2.8	2.6	3.0	2.7
	2.7	3.2	4.0								

Figites scutellaris

Female

L	0.24	0.12	0.19	0.14	0.15	0.16	0.16	0.16	0.14	0.16	0.16
	0.16	0.23									
B	0.11	0.10	0.08	0.10	0.10	0.11	0.11	0.11	0.11	0.11	0.11
	0.11	0.11									
R	2.2	1.2	2.4	1.4	1.5	1.5	1.5	1.5	1.3	1.5	1.5
	1.5	2.1									

Male

L	0.21	0.10	0.24	0.22	0.24	0.24	0.23	0.24	0.22	0.24	0.24
	0.24	0.23	0.32								

B 0.11 0.09 0.10 0.10 0.10 0.10 0.10 0.08 0.08 0.08 0.08
0.08 0.08 0.08
R 1.9 1.1 2.4 2.2 2.4 2.4 2.3 3.0 2.8 3.0 3.0
3.0 2.9 4.0

Melanips opacus

Female

L 0.24 0.11 0.37 0.27 0.22 0.24 0.22 0.21 0.19 0.18 0.18
0.18 0.32
B 0.13 0.10 0.10 0.10 0.10 0.10 0.10 0.11 0.10 0.10 0.10
0.10 0.10
R 1.9 1.1 3.7 2.7 2.2 2.4 2.2 1.9 1.9 1.8 1.8
1.8 3.2

Male

L 0.29 0.08 0.46 0.29 0.29 0.26 0.22 0.22 0.22 0.24 0.21
0.22 0.18 0.30
B 0.13 0.08 0.13 0.10 0.10 0.10 0.10 0.10 0.10 0.10 0.10
0.09 0.08 0.08
R 2.2 1.0 3.5 2.9 2.9 2.6 2.2 2.2 2.2 2.4 2.1
2.4 2.3 3.8

Lonchidia maculipennis

Female

L 0.11 0.09 0.15 0.11 0.10 0.09 0.10 0.12 0.11 0.11 0.12
0.13 0.26
B 0.06 0.05 0.04 0.04 0.03 0.04 0.03 0.05 0.05 0.06 0.06
0.06 0.08
R 1.8 1.8 3.8 2.8 3.3 2.5 3.3 2.4 2.2 1.8 2.0
2.2 3.3

Male

L 0.14 0.08 0.29 0.27 0.24 0.26 0.24 0.26 0.24 0.22 0.19
0.19 0.19 0.27
B 0.06 0.06 0.06 0.06 0.06 0.06 0.06 0.06 0.06 0.05 0.05
0.05 0.05 0.05
R 2.3 1.3 4.8 5.0 4.0 4.3 4.0 4.3 4.0 4.4 3.8
3.8 3.8 5.4

Neralsia rufipes

Female

L 0.16 0.09 0.11 0.13 0.12 0.14 0.14 0.14 0.11 0.11 0.11
0.11 0.22
B 0.10 0.08 0.06 0.08 0.08 0.09 0.10 0.10 0.10 0.09 0.09
0.10 0.10
R 1.6 1.1 1.8 1.6 1.5 1.6 1.4 1.4 1.1 1.2 1.2
1.1 2.2

Male

L 0.21 0.10 0.22 0.29 0.29 0.29 0.26 0.27 0.21 0.23 0.22
0.21 0.19 0.27
B 0.10 0.10 0.08 0.10 0.10 0.10 0.10 0.08 0.08 0.08 0.08
0.08 0.08 0.07
R 2.1 1.0 2.8 2.9 2.9 2.9 2.6 3.4 2.6 2.9 2.8
2.6 2.4 3.9

Eucoila crassinerva

Female

L 0.21 0.13 0.19 0.16 0.14 0.18 0.18 0.18 0.16 0.18 0.16
0.18 0.24
B 0.11 0.10 0.08 0.09 0.10 0.11 0.13 0.13 0.13 0.13 0.13
0.13 0.13

R 1.9 1.3 2.4 1.8 1.4 1.6 1.4 1.4 1.2 1.4 1.2
1.4 1.9

Male

L 0.24 0.13 0.29 0.35 0.35 0.37 0.37 0.37 0.40 0.38 0.40
0.35 0.35 0.35 0.38
B 0.13 0.13 0.13 0.13 0.13 0.13 0.11 0.11 0.10 0.10 0.09
0.09 0.08 0.08 0.08
R 1.9 1.0 2.2 2.7 2.7 2.9 3.4 3.4 4.0 3.8 4.4
3.9 4.4 4.4 4.8

Klidotoma psiloides

Female

L 0.10 0.06 0.08 0.04 0.04 0.03 0.03 0.03 0.04 0.04 0.08
0.08 0.10
B 0.04 0.04 0.03 0.03 0.03 0.03 0.03 0.03 0.03 0.04 0.05
0.05 0.05
R 2.5 1.5 2.7 1.3 1.3 1.0 1.0 1.0 1.3 1.0 1.6
1.8 2.0

Male

L 0.09 0.06 0.18 0.10 0.10 0.10 0.10 0.10 0.11 0.11 0.11
0.11 0.10 0.10 0.10
B 0.05 0.05 0.04 0.04 0.04 0.04 0.04 0.04 0.04 0.04 0.04
0.04 0.03 0.03 0.03
R 1.8 1.2 4.5 2.5 2.5 2.5 2.5 2.5 2.8 2.8 2.8
2.8 3.3 3.3 3.3

Rhoptromeris heptoma

Female

L 0.10 0.05 0.08 0.08 0.06 0.06 0.07 0.08 0.08 0.08 0.08
0.08 0.10
B 0.04 0.04 0.03 0.03 0.03 0.03 0.04 0.05 0.04 0.04 0.04
0.04 0.04
R 2.5 1.3 2.7 2.7 2.0 2.0 1.8 1.6 2.0 2.0 2.0
1.7 2.2

Male

L 0.09 0.04 0.10 0.18 0.11 0.12 0.12 0.13 0.12 0.12 0.12
0.12 0.12 0.12 0.13
B 0.05 0.04 0.05 0.06 0.04 0.04 0.04 0.04 0.04 0.04 0.04
0.04 0.04 0.04 0.04
R 1.8 0.8 2.0 3.0 2.8 3.0 3.0 3.0 3.0 3.0 3.0
3.0 3.0 3.0 3.3

Dilyta subclavata

Female

L 0.08 0.07 0.06 0.04 0.04 0.05 0.07 0.10 0.10 0.10 0.10
0.09 0.10
B 0.04 0.04 0.03 0.02 0.02 0.02 0.03 0.03 0.03 0.04 0.04
0.05 0.05
R 2.0 1.8 2.0 2.0 2.0 2.5 2.3 3.3 3.3 2.5 2.5
1.8 2.0

Male

L 0.08 0.07 0.07 0.04 0.05 0.08 0.08 0.09 0.10 0.10 0.08
0.09 0.08 0.09
B 0.04 0.04 0.03 0.03 0.03 0.04 0.04 0.04 0.04 0.04 0.04
0.04 0.04 0.04
R 2.0 1.8 2.3 1.3 1.7 2.0 2.0 2.3 2.5 2.5 2.0
2.3 2.0 2.3

Apocharips xanthocephala

Female

L 0.09 0.07 0.09 0.07 0.06 0.07 0.07 0.09 0.08 0.08 0.08
0.08 0.10
B 0.04 0.04 0.03 0.03 0.03 0.03 0.03 0.03 0.04 0.04 0.05
0.05 0.05
R 2.3 1.8 3.0 2.3 2.0 2.3 2.3 3.0 2.0 2.0 1.6
1.6 2.0

Male

L 0.08 0.07 0.11 0.08 0.09 0.10 0.10 0.10 0.10 0.10 0.10
0.10 0.09 0.10
B 0.04 0.04 0.03 0.04 0.04 0.04 0.04 0.04 0.04 0.04 0.04
0.04 0.04 0.04
R 2.0 1.8 3.7 2.0 2.3 2.5 2.5 2.5 2.5 2.5 2.5
2.5 2.3 2.5

Phaenoglyphis xanthochroa

Female

L 0.12 0.10 0.18 0.15 0.15 0.15 0.14 0.14 0.13 0.15 0.13
0.13 0.20
B 0.06 0.05 0.04 0.04 0.05 0.05 0.04 0.05 0.04 0.04 0.04
0.04 0.04
R 2.0 2.0 4.5 3.8 3.0 3.0 3.5 2.8 3.3 3.8 3.3
3.3 5.0

Male

L 0.11 0.08 0.16 0.11 0.12 0.13 0.12 0.13 0.12 0.12 0.12
0.12 0.11 0.13
B 0.06 0.05 0.04 0.03 0.05 0.05 0.05 0.04 0.04 0.04 0.04
0.04 0.04 0.04
R 1.8 1.6 4.0 3.7 2.4 2.6 2.4 3.3 3.0 3.0 3.0
3.0 2.8 3.3

Alloxysta macrophadna

Female

L 0.10 0.07 0.13 0.13 0.11 0.11 0.10 0.10 0.11 0.10 0.10
0.09 0.12
B 0.05 0.05 0.03 0.03 0.03 0.03 0.04 0.04 0.04 0.04 0.04
0.04 0.04
R 2.0 1.4 4.3 4.3 3.7 3.7 2.5 2.5 2.8 2.5 2.5
2.3 3.0

Male

L 0.13 0.09 0.13 0.14 0.13 0.12 0.11 0.11 0.10 0.10 0.10
0.10 0.08 0.10
B 0.06 0.04 0.03 0.03 0.03 0.04 0.04 0.04 0.04 0.04 0.04
0.04 0.04 0.04
R 2.2 2.3 4.3 4.7 3.9 3.0 2.8 2.8 2.5 2.5 2.5
2.5 2.0 2.5

Pycnostigmus rostratus

Female

L 0.19 0.10 0.20 0.15 0.18 0.11 0.13 0.13 0.13 0.11 0.12
0.11 0.12 0.11 0.11 0.11 0.10 0.10 0.18
B 0.10 0.09 0.08 0.08 0.08 0.08 0.08 0.09 0.09 0.08 0.09
0.09 0.09 0.08 0.09 0.09 0.09 0.08 0.09
R 1.9 1.1 2.5 1.9 2.3 1.4 1.6 1.4 1.4 1.4 1.3
1.2 1.3 1.4 1.2 1.2 1.1 1.3 2.0

Male

L 0.18 0.11 0.15 0.13 0.13 0.12 0.13 0.13 0.11 0.12 0.12
0.12 0.11 0.11 0.11 0.11 0.10 0.10 0.10 0.10 0.10 0.10

0.10 0.15
B 0.08 0.08 0.08 0.08 0.09 0.08 0.08 0.08 0.08 0.09 0.08
0.08 0.08 0.08 0.08 0.08 0.08 0.08 0.08 0.08 0.08 0.08
0.08 0.08
R 2.2 1.4 1.8 1.6 1.5 1.5 1.5 1.5 1.4 1.4 1.5
1.5 1.4 1.5 1.4 1.4 1.2 1.2 1.2 1.3 1.3 1.3
1.3 2.0

Aulacidea hieracii

Female

L 0.13 0.09 0.12 0.15 0.15 0.15 0.13 0.13 0.12 0.12 0.11
0.10 0.21
B 0.07 0.06 0.05 0.06 0.06 0.06 0.06 0.06 0.06 0.06 0.06
0.06 0.05
R 1.9 1.5 2.4 2.5 2.5 2.5 2.2 2.2 2.0 2.0 1.8
1.7 4.2

Male

L 0.11 0.10 0.13 0.16 0.16 0.15 0.14 0.13 0.11 0.12 0.10
0.10 0.10 0.15
B 0.10 0.08 0.06 0.07 0.07 0.07 0.06 0.07 0.06 0.06 0.06
0.06 0.06 0.06
R 1.1 1.3 2.2 2.3 2.3 2.1 2.3 1.9 1.8 2.0 1.7
1.7 1.7 2.5

Cynips quercusfolii

Female

L 0.13 0.11 0.25 0.23 0.19 0.16 0.13 0.11 0.10 0.09 0.09
0.07 0.08 0.12
B 0.10 0.09 0.04 0.05 0.06 0.06 0.06 0.07 0.07 0.08 0.08
0.08 0.08 0.07
R 1.3 1.2 6.3 4.6 3.2 2.7 2.2 1.6 1.4 1.1 1.1
0.9 1.0 1.7

Male

L 0.17 0.10 0.28 0.21 0.20 0.21 0.16 0.18 0.17 0.16 0.14
0.16 0.15 0.13 0.15
B 0.08 0.10 0.08 0.09 0.08 0.08 0.08 0.08 0.08 0.08 0.08
0.08 0.07 0.07 0.06
R 2.1 1.0 3.5 2.3 2.5 2.6 2.0 2.3 2.1 2.0 1.8
2.0 2.1 1.9 2.5

Agamic

L 0.16 0.10 0.35 0.32 0.27 0.23 0.18 0.16 0.12 0.11 0.11
0.10 0.20
B 0.12 0.10 0.08 0.08 0.08 0.08 0.09 0.09 0.08 0.08 0.08
0.09 0.08
R 1.3 1.0 4.4 4.0 3.4 2.9 2.0 1.8 1.5 1.4 1.3
1.1 2.5

Austrocynips mirabilis (male unknown)

Female

L 0.13 0.09 0.14 0.15 0.15 0.15 0.12 0.13 0.14 0.13 0.13
0.13 0.13 0.13 0.10
B 0.15 0.07 0.05 0.05 0.05 0.05 0.05 0.06 0.06 0.06 0.06
0.06 0.06 0.06 0.06
R 0.9 1.3 2.8 3.0 3.0 3.0 2.4 2.2 2.3 2.2 2.2
2.2 2.2 2.2 1.7

Himalocynips vigintilis (male unknown)

Female

L 0.30 0.16 0.26 0.16 0.19 0.17 0.21 0.18 0.16 0.16 0.15

```
  0.14 0.16 0.16 0.16 0.14 0.15 0.13 0.13 0.28
B 0.15 0.14 0.14 0.14 0.14 0.16 0.18 0.17 0.16 0.14 0.16
  0.14 0.16 0.15 0.16 0.15 0.16 0.16 0.14 0.14
R 2.0  1.1  1.9  1.1  1.4  1.1  1.2  1.1  1.0  1.1  0.9
  1.0  1.0  1.1  1.0  0.9  0.9  0.8  0.9  2.0
```

THE CYNIPOID DATA MATRIX
AND THE OUTPUT FROM THE COMPATIBILITY PROGRAMS
(See Chapter 5)

Master matrix of scores for the morphological characters and thirty one exemplar taxa.

[0 = plesiomorphic state 1 = apomorphic state]
[V = variable score - = missing score]

Characters

	1	2	2	2	3	4	5	6	7	8	9	9	10	11	12	13	14	15	15	15	16	16	17	18	19
		.	.	.							.	.							.	.	.	.			
		1	2	3							1	2							1	2	3	1	2		
Taxa																									
1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1
2	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1
3	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1
4	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1
5	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1
6	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1
7	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1
8	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1
9	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1
10	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0
11	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
16	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0
17	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
18	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0
19	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	1	1	0
20	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
21	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
22	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
23	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0
24	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0
25	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0
26	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0
27	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
28	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
30	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	1	0
31	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0

	19	20	21
Taxa			
1	0	1	1
2	0	1	1
3	0	1	1
4	0	1	1
5	0	1	1
6	0	1	1
7	0	1	1
8	0	1	1
9	0	1	1
10	0	1	0
11	0	1	0
12	0	1	0
13	1	1	1
14	0	1	1
15	0	1	1
16	0	1	1
17	0	1	1
18	0	1	1
19	1	1	1
20	0	1	1
21	0	1	1
22	0	1	1
23	0	1	1
24	0	1	1
25	0	1	1
26	0	1	1
27	0	1	1
28	0	0	0
29	0	0	0
30	0	1	1
31	0	1	0

Matrix continued

Characters

Taxa	0223	0224.1	0224.2	0224.3	0225	0226.1	0226.2	0226.3	0227	0228.1	0228.2	0228.3	0228.4	0229.1	0229.2	0230.1	0230.2	0231.1	0231.2	0231.3	0231.4	0232.1	0232.2	0232.3	0232.4	0233
1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1
2	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
3	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
6	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
7	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
8	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
9	0	0	1	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	0	0	0	0	1
10	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
11	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
14	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
15	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
16	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
17	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
19	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
20	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	0	1	1	1	1	0
21	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0
22	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	0	1	1	1	0	1
23	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
24	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
25	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
27	1	0	0	0	1	0	1	0	0	0	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
29	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0
30	0	0	0	0	0	0	0	0	0	0	1	1	0	0	-	-	-	-	-	-	-	0	0	0	0	1
31	0	0	0	1	0	0	0	0	0	0	1	1	1	1	-	-	-	-	-	-	-	0	0	0	0	0

Matrix continued

Characters

Taxa	034	035	036	037	038.1	038.2	038.3	038.4	038.5	038.6	039.1	039.2	039.3	040	041	042	043	044	045	046	047	048	049	050	051.1	051.2	052
1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	V	0	0	0	0	0	0	0	0
3	0	0	0	-	1	0	0	0	0	0	-	-	-	0	0	0	0	1	1	0	0	0	0	0	0	0	0
4	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
5	0	1	0	-	1	0	0	0	0	0	-	-	-	0	0	0	0	1	1	0	0	0	0	0	0	0	0
6	0	1	0	-	1	0	0	0	0	0	-	-	-	0	0	0	0	1	1	0	0	0	0	0	0	0	0
7	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
9	0	0	1	-	1	0	0	0	0	0	-	-	-	0	0	0	0	1	1	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0
11	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0
12	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0
13	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
14	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
15	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
16	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0
17	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
18	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
19	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0
20	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0
21	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0
22	0	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0
23	1	0	1	1	1	1	1	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
24	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
25	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
26	0	0	1	1	1	1	1	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
27	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
28	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	1	-	1	1	1	1	1	0	-	-	-	0	0	0	0	1	0	0	0	1	0	0	0	0	0
31	0	0	1	-	1	1	1	0	0	0	-	-	-	0	0	1	1	1	0	1	1	0	0	0	0	0	0

Matrix continued

Characters

Taxa	053.1	053.2	054	055	056	057	058	059	060	061.1	061.2	062.1	062.2	062.3	062.4	063	064	065	066	067	068	069	070	071	072	073.1	073.2
1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
2	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0
3	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0
4	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
5	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1
6	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
7	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
8	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
9	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
10	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0
11	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0
12	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0
13	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
14	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
19	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
21	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
22	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
23	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
24	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
25	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
26	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
27	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
31	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	

Matrix continued

Characters

Taxa	073.3	074	075	076	077	078.1	078.2	078.3	079.1	079.2	080	081.1	081.2	082.1	082.2	083	084	085	086	087	088	089	090.1	090.2	091	092	093
1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
3	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1
4	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
5	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
6	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1
7	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1
8	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	1
9	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
10	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1
11	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	0	1	1	1
12	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
13	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1
14	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1
15	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1
16	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
17	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	1	1	1	0	1	1	1
18	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
19	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
20	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
21	0	0	1	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
22	0	0	1	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
23	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
24	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
25	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
26	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
27	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
28	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0
29	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	1	1	0	0	1	1	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	0	0	1	1	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0

Matrix continued

Characters

Taxa	09	09	09	09	09	09	09	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
	4	5	6	6	7	7	8	9	0	0	1	2	3	4	5	5	6	7	8	9	9	9	0	1	1	1	1
			.1	.2	.1	.2			.1	.2					.1	.2				.1	.2	.3	.4		.1	.2	.3
1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0
2	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0
3	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0
4	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
5	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0
6	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
7	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
8	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
9	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0
10	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
11	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
12	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
13	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
14	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
15	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
16	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
17	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
18	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
19	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
20	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
21	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1
22	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1
23	1	1	1	1	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
24	1	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
25	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
26	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
27	1	1	1	1	1	0	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	0	0	1	1	1	1
28	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0
29	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0
30	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0
31	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0

Matrix continued

Characters

Taxa	1 1 2 . 1	1 2 . 2	1 3 1 .	1 3 2 .	1 4	1 5	1 6	1 7 . 1	1 7 . 2	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6 . 1	2 6 . 2	2 7	2 8	2 9	3 0	3 1 . 1	3 1 . 2	3 2 . 1	3 2 . 2
1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	0	1	0	0	0	0	0
2	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1
3	1	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	1
4	1	1	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0
5	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0
6	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0
7	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1
8	1	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1
9	1	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1
10	1	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1
11	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1
12	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1
13	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
14	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
15	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
16	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1
17	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
18	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1
19	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1
20	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0
21	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
22	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
23	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
24	1	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
25	1	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
26	1	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
27	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
28	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
31	1	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Matrix continued

Characters

Taxa	132.3	133	134	135	136	137	138.1	138.2	138.3	139	140	141	142.1	142.2	143	144	145	146	147	148	149.1	149.2	149.3	150	151	152.1	152.2
1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	1	1	1	1	1	1	0	0
2	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	1	1	0	0
3	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	1	1	0	1	1	0	0
4	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	1	1	0	0
5	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	1	1	0	0
6	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	1	1	0	0
7	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0
8	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0
9	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0
10	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0
11	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0
12	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0
13	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0
14	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0
15	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0
16	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0
17	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0
18	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0
19	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0
20	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	-	1	1
21	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	-	1	1
22	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	-	1	1
23	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	-	1	0
24	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0
25	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0
26	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0
27	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	-	1	1
28	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0
29	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0
30	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0
31	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0

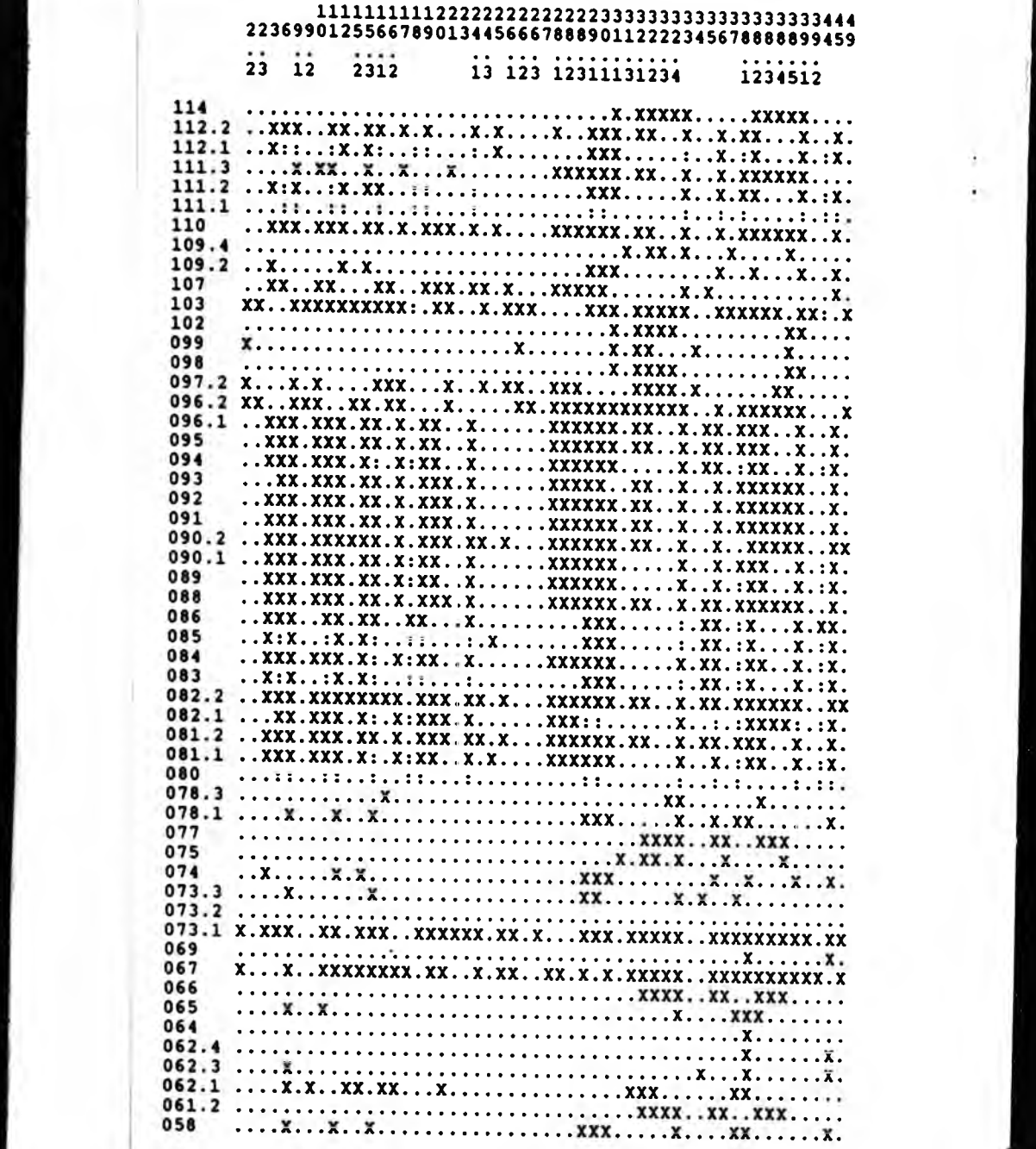
Matrix continued

Characters

Taxa	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170
1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
2	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
3	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
4	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
5	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
6	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
7	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
8	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0
9	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
10	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0
11	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
12	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
13	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
14	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
15	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
16	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	0
17	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
18	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0
19	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	0
20	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	0
21	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	0
22	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	0
23	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
24	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
25	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
26	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
27	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0
28	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
29	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1
31	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Matrix of incompatibilities (X) between characters
(: = polar incompatibility. See Chapter 5.)

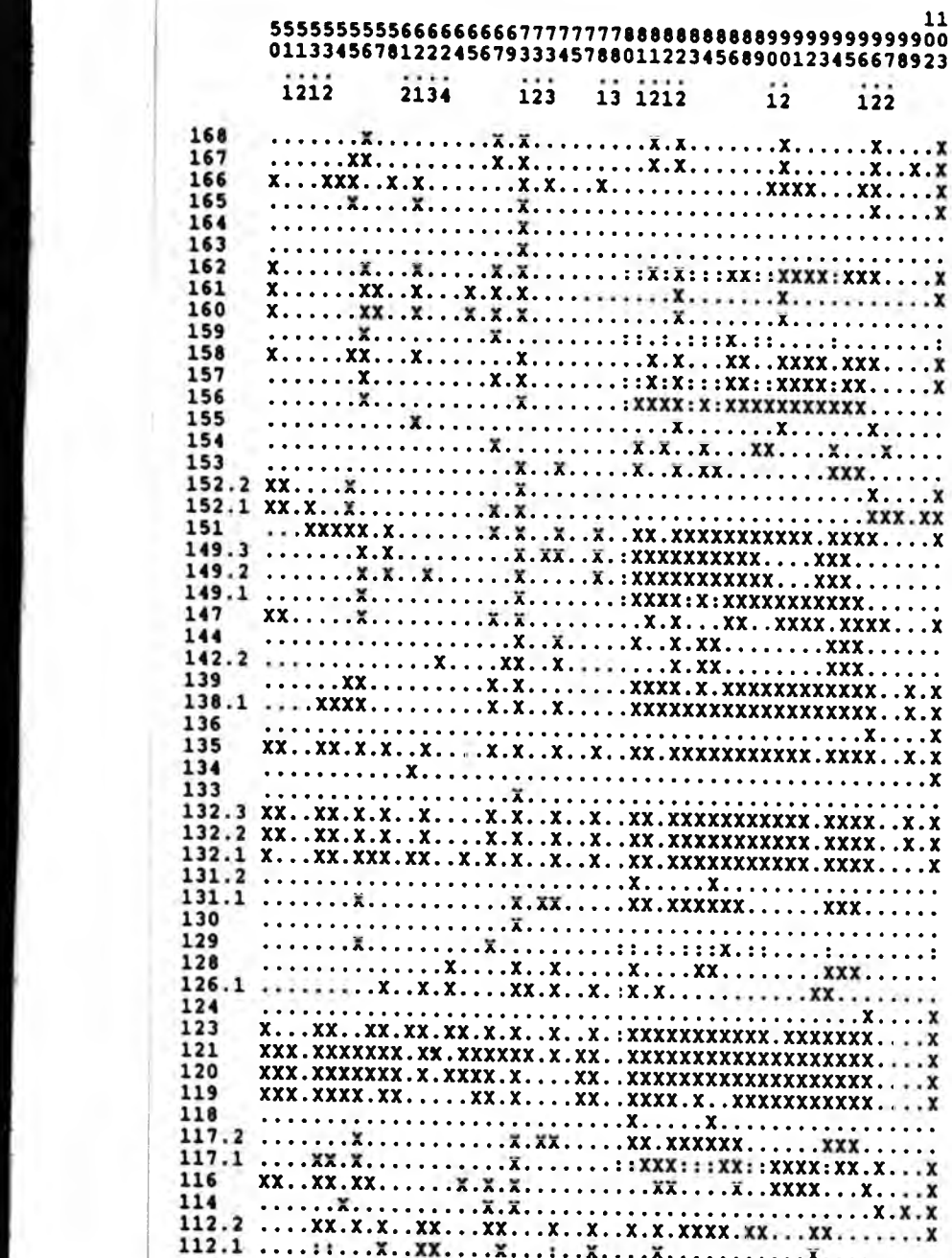
```
                        characters
          1111111111222222222222223333333333333333333444
      2236990125566789013445666788890112222345678888899459
      ..  ..   ....      .. ... ...........     .......
      23  12   2312      13 123 12311131234     1234512
chars
168   ....X..X.XX.XX...X.......XX.XXX.XX..X..X.XXXXXX...X
167   X...X.XX.XX.XX...X.....X.....XX..XXXXX..XXXXXXX....X
166   X.XXX.XXX..XXX.XXX.XX.XX.....XX..XXXXX..XXXXXXX...XX
165   X.....X.....XX.........X.....XX...XXXX..XX..XXX.....
164   .........XX.............................X..XX.......
163   .........XX.............................X..XX.......
162   ....X..X.X...X..XX..X.X...X..X...XX..X....XXX..X...X
161   ....X....XX.X....X.............X.....X..X.XXX.......
160   ....X....XX.X....X.............X.....X..X.XXX.......
159   ....X........X.............X..X...XX..X....X....X....
158   X...X.....X.XXX.XX..X.XX..XX.XXX.XXXXX..XX.XXXXX.X.X
157   ....X.....X.....XX........XX.XXX.....X..X.XXXXXX.....
156   ....X...X.XX.................XXX.....X..X.XX...X.....
155   ....X..X.............................X....XXX.......
154   ......X...XX..X.X..........XX....XX.....X.XXX....X..
153   ....X.....................................X...X......X.
152.2 X.....X.............X..XXX..X.XXXXX..XX.XXXX....X
152.1 X...X.X.............X..XXXXXX.XXXXXX.XX.XXXXX...X
151   X.XXX.XX.XXXXX.XXX.XX.XX.......X.XX..X.XXXXXXXX...XX
149.3 ..X.X.....XX.........................X.XX......X....
149.2 ..X.X...X.XX.................XXX.....X.XX.XX...X..X.
149.1 ....X...X.XX.................XXX.....X..X.XX...X....
147   ....X.....X.X.X.XX..X.X......XXX.XXXXX..X..XXXXX.X.X
144   ....X.....................................X...X......X.
142.2 ....X.............X.................X...X........
139   X...X.X...XXXX:.XX..X.XX..XXXX.X.XXXXX..XXXXXXXX.:..
138.1 X..XX.XXXXXXXX.XXXXXX.XX.XXXXXXX.XXXXX..XXXXXXX...XX
136   ..................................XXXX..XX..XXX.....
135   ..XXX.XXXXXXXX.XXX.XX.X.....XXX.XXXXX.XXXXXXXX...XX
134   ...........X.......................XX......X.......
133   .........XX.................................X..XX.....
132.3 ..XXX.XXXXXXXX.XXXXXX.X..XXXXXXX.XXXXX.XXXXXXXX...XX
132.2 ..XXX.XXXXXXXX.XXX.XX.X...XXXXXX.XXXXX.XXXXXXXX...XX
132.1 ..XXX..XXXXX...XX..XX.X.....XXX.....X.XX.XXX.....XX
131.2 ...........................................X......X.
131.1 ....X...X..X.................XXX.....X.....X......X.
130   .........XX.................................X..XX.....
129   ....X........X...........X..X...XX..X....X....X.....
128   ....X.....................................X...X......X.
126.1 ..X.X...X.X..:.............XXX.......XX...........
124   ..................................XXXX..XX..XXX.....
123   ..XXX..XXXXX...XX..XX.X......XXX.....X.XX.XX...X..XX
121   XXXXXXXXXXXXX.XXX.XXXXXX.XXXXXXXXX.X.XXXXXXXX..XX
120   XXXXXXXXXXXXX.XXX.XX.XXX.XX.XXXXXXXX.XXXXXXXX..XX
119   XXXXXX.XX.XXXX.XXX.XX.XXX.XX.XXXXXXX.X.XXXXXXXX..XX
118   ...........................................X......X.
117.2 ....X...X..X.................XXX.....X.....X......X.
117.1 ....X.XXX.XX.X..X.........XXXXX.....X..X.XXX..X....
116   ....X.XXXXXXX...X..X.X...XX.....XXXXX..X.XXXX....X
```

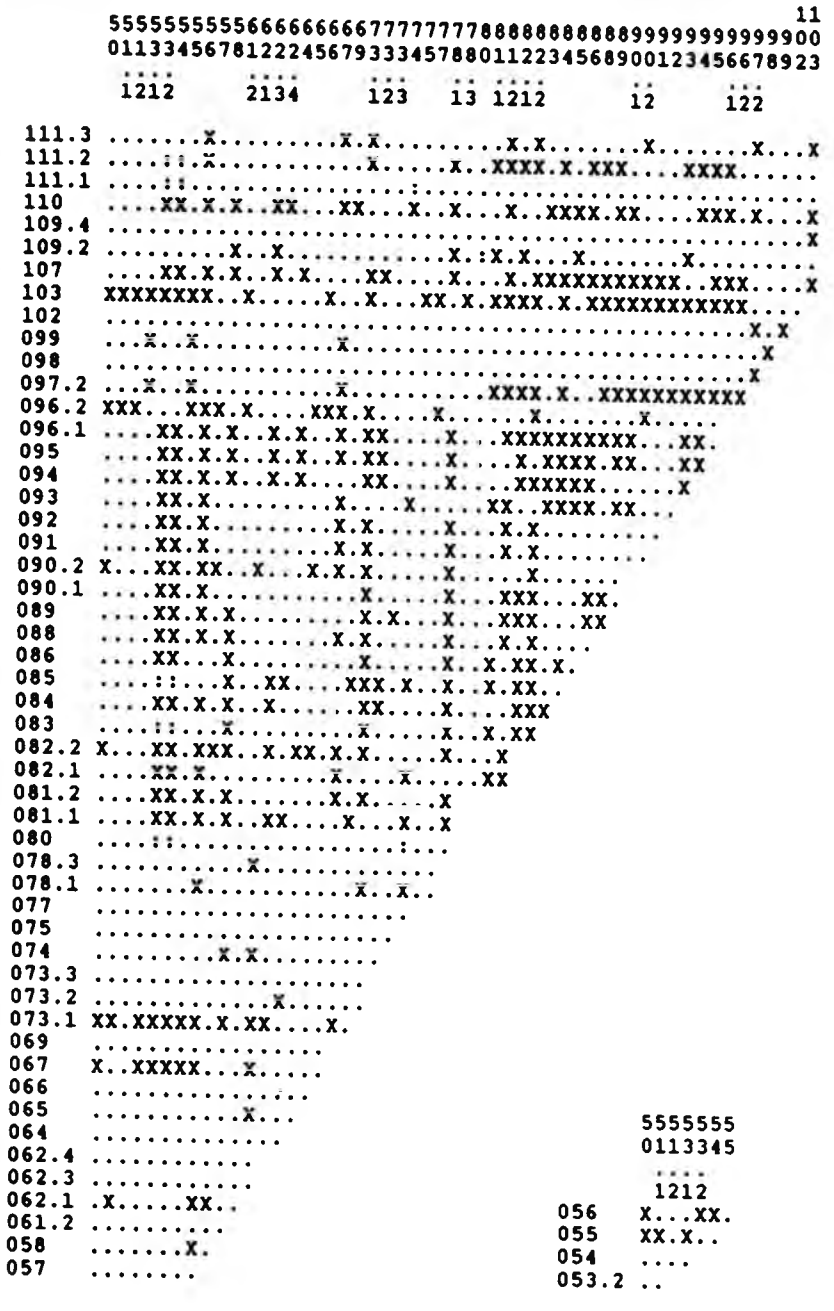


Page 393

```
          1111111111222222222222222333333333333333333333444
      223699012556678901344566678889011222234567888889945 9
      ..  ..   ....      .. ... ...........     ........
      23  12   2312      13 123 12311131234     1234512

057   ....x..x.............................x....xxx.......
056   ..xxx..xxxxx..xxx..xx.x......xxx.....x.xx.xxx..x.xxx
055   ....x.........................xxx.xxxxx..xx..xxxxx..x
054   ....x.....xx....xx........xx.xxx.....x..x.xxxxxx....
053.2 ....x.....xx....xx........xx.xxx.....x..x.xxxxxx....
053.1 ..............................x.xxxxx.....xxxxx....
051.2 ...................................xxxx..xx..xxx....
051.1 x.....x.....xx.........x.....xx...xxxx..xx..xxx....
050   x...x.xx.xx.xx...x.....x.....xx..xxxxx..xxxxxxx...
049   x...x.xx..x.xx...x.....x.....xxx.xxxxx..xxxxxxx..
045   ..x.x...x.xx.........x.......xxx.....x..x.xx...x.
044   ....x........x............x..x...xx..x....x....x.
039.2 ...........................................x.....xxx..
039.1 x..x...xx.xxx.xxxx.xx.xx.....xx..xxxxxx.xx.xxxx.
038.5 xx..xx.xx..xx.......x.xxx.xx.xx..xxxxxx..x
038.4 xx..xx.xx..xx.......x.xxx.xx.xxxxxxxxx...x
038.3 xx..xxxxxxxxxx...xx.x.xxxxxxxxxxxxxxxx..xx
038.2 x.xxx.xxxxxxxx.xxxxxxxx.xxxxxxx.xx..x.xxx
038.1 ..xxx..xxxxx.xxxx..xx.x...x..x...xx..x....
037   xx..xx.................xx....xxxxxxxxx...
036   xxxxxxxxx.xxxx.xxxxxx.xxxxxxxxxxxxxxxx..
035   ........x..x.................xxx.....x.
034   ..............................x.xxxx.
033   xxxxxxxxxxxxxxxxx.xx.xxx.xx.xxxxxxx.
032.4 xx..xxx.....xx.........xx....xx.x
032.3 xx..xxx.....xx.........xx....xx.
032.2 xx..xxx...x.xxx.xx..x.xxx.x..xx.
032.1 x...x.x...x.xxx.xx..x.xx..x..xx.
031.1 x.xxx.xx.xxxx..xxx.xx.xx..x..xx
030.1 x.xxx.xxx.xxx..xxx.xx.xx..x...
029.1 x.xxx.xxx.xxxxxxxx.xx.xx.....
028.3 ...........xxx...x..x.x...
028.2 ....x.xxx..xxx...x..x.x...
028.1 ....x.xxx.xxxxx.xx..x.x...
027   .........xx.............
026.2 ....x.................
026.1 ....x.xx..x..x...x....
024.3 ....x.xx..x..x...x..
024.1 ....x...x.xx......
023   .........xx.......
021   ....x.xxxxxx.x...
020   ....x..xx.xx.x..
019   ....x...x.xx...
018   ....x........x
017   ......x...xxx
016.2 ....x.x..xx
016.1 ..xxx.xxx.x
015.3 ...xx..xx
015.2 ....x..x.
012   ..xxx...
011   ....x..
009.1 x.xx
```


1212
2134
123
13 1212
12
122



```
      11111111111111111111111111111111111111111111111111111
      00111111111111122222233333333334444455555556666
      79011122467789013689011222358924799122567801 26
       . .....  ..     .   .....  . .  .. ..
       2 12312  12     1   12123  1 2  12 12

168   X........X...XXXX.....XXX.XXX..X..X.....XXXXX
167   .........X...XXXX.....XXX.X....X..XXX...XXXXX
166   ....XX...XX..XXX.......XXX.X....XXXXXX.XXX...
165   .........X...XXX........XX.X....X...XX.......
164   ........................X..X..............
163   ........................X..X..............
162   ..X::X:X.X...XXXX.....XXX.XXX..X..X.....XXX
161   .........X....X.X......XXX.XX......X..X....
160   .........X....X.X......XXX.XX......X..X...
159   ...:.:.........................:..X........X
158   X.X..X.X.X...XXX...X....XX.XXX..X..XX....
157   X.X::.:X.X...XXXX......XXX.XX......X....
156   X.X::.:X.....XXXX......XXX.XX......X...
155   .........X....XXX......X..............
154   .......X..X..XXX...X.................
153   XXX...XX......XXXX.....XXX.X......X..
152.2 X............XXX........XX......X....
152.1 X.......X....XXX........XX..XX..X...
151   .XX.XXXXXXXX.XXXXX...X.XXX.XXX..XXX
149.3 .XX:..XX...X.XXXXX...X.XXX.XX...
149.2 ..X:..:X...X.XXXXXX..X.XXX.XX.XX
149.1 X.X::.:X.....XXXX......XXX.XX...
147   ..X..X.X.....XXX...X....XX.XXX..
144   XXX...XX......XXXX.....XXX.X...
142.2 XX..........X.XXXXX...XXXX.X..
139   ..X..X.X..X..XXX...:.........
138.1 .XX.XXXX..X..XXXXX..X.....X.
136   ............XXX...........
135   .XX.XXXX.XXX.XXXX.X..X..X..
134   ........................
133   ........................X
132.3 XXX.XXXX.XXX.XXXX.X.XX.
132.2 XXX.XXXX.XXX.XXXX.X..X.
132.1 .XX.XXXX.XXX.XXXX.X..X:
131.2 ..X...XX.......X....
131.1 XXX...XX.....XXXXX..
130   ..................
129   ...:.:............
128   XXX...XX.......X.X
126.1 XXX:..XX...X...XX
124   ............XXX.
123   .XX:XXXX.XXX.XXX                          111
121   XXX.XX...XXXXXX                           001
120   X.X.XX....XX.X                            790
119   X.X.XX...XXX.                              .
118   ..X...XX....                               2
117.2 XXX...XX..                        111.3 X..
117.1 X.X::X..                          111.2 X.X
116   ..X..X.                           111.1 .:.
114   .....                             110   .X
112.2 .X..X                             109.4 .
112.1 .:...                             109.2 .
```

Compatibility analysis data for the cynipoid characters (char). Polar (pol) observed (obs) and expected (exp) incompatibilities, and the ratio of observed to expected.

	Incompatibilities					Incompatibilities			
char	obs	exp	ratio	pol	char	obs	exp	ratio	pol
1	00	000.00	0.00	0	2.1	00	000.00	0.00	0
2.2	37	115.02	0.32	0	2.3	14	71.85	0.19	0
3	49	120.53	0.41	0	4	00	000.00	0.00	0
5	00	000.00	0.00	0	6	44	125.17	0.35	6
7	00	000.00	0.00	0	8	00	000.00	0.00	0
9.1	113	136.59	0.83	3	9.2	14	71.62	0.20	0
10	60	86.76	0.69	0	11	66	131.64	0.50	6
12	71	98.95	0.72	2	13	0	000.00	0.00	0
14	00	000.00	0.00	0	15.1	00	000.00	0.00	0
15.2	38	88.13	0.43	0	15.3	93	120.60	0.77	0
16.1	75	126.98	0.59	9	16.2	53	134.89	0.39	0
17	68	86.88	0.78	0	18	15	48.97	0.31	14
19	44	125.17	0.35	6	20	58	131.85	0.44	0
21	63	137.28	0.46	0	22	00	000.00	0.00	0
23	8	73.17	0.11	0	24.1	44	124.17	0.35	6
24.2	00	000.00	0.00	0	24.3	47	134.37	0.35	0
25	9	48.31	0.19	0	26.1	47	133.63	0.35	0
26.2	37	114.04	0.32	0	26.3	14	71.09	0.20	0
27	8	73.17	0.11	0	28.1	66	85.09	0.78	0
28.2	54	67.21	0.80	0	28.3	38	42.08	0.90	0
28.4	00	000.00	0.00	0	29.1	103	114.80	0.90	3
29.2	00	000.00	0.00	0	30.1	95	107.87	0.88	3
30.2	00	000.00	0.00	0	31.1	94	126.85	0.74	0
31.2	00	000.00	0.00	0	31.3	12	47.86	0.25	0
31.4	00	000.00	0.00	0	32.1	73	118.91	0.61	0
32.2	86	113.49	0.76	0	32.3	57	97.79	0.58	0
32.4	54	70.84	0.76	0	33	126	136.75	0.92	6
34	10	48.45	0.21	0	35	37	88.12	0.42	0
36	115	135.62	0.85	3	37	50	100.84	0.50	0
38.1	77	70.79	1.09	11	38.2	123	133.68	0.92	0
38.3	105	128.23	0.82	0	38.4	73	112.22	0.65	0
38.5	75	84.99	0.88	0	38.6	00	000.00	0.00	0
39.1	85	92.18	0.92	3	39.2	8	44.64	0.18	0
39.3	00	000.00	0.00	0	40	00	000.00	0.00	0
41	00	000.00	0.00	0	42	00	000.00	0.00	0
43	00	000.00	0.00	0	44	15	48.97	0.31	14
45	65	126.55	0.51	2	46	00	000.00	0.00	0
47	00	000.00	0.00	0	48	00	000.00	0.00	0
49	51	132.18	0.39	0	50	49	121.27	0.40	0
51.1	31	99.34	0.31	0	51.2	14	71.97	0.19	0
52	00	000.00	0.00	0	53.1	19	87.91	0.22	0
53.2	54	127.82	0.42	6	54	54	128.62	0.42	6
55	39	108.44	0.36	0	56	85	129.11	0.66	0
57	17	73.17	0.23	0	58	43	115.25	0.37	0
59	00	000.00	0.00	0	60	00	000.00	0.00	0
61.1	00	000.00	0.00	0	61.2	14	72.39	0.19	0
62.1	30	48.56	0.62	0	62.2	00	000.00	0.00	0
62.3	27	98.74	0.27	0	62.4	9	47.90	0.19	0
63	00	000.00	0.00	0	64	11	48.10	0.23	0
65	17	73.17	0.23	0	66	14	72.39	0.19	0
67	83	121.07	0.69	0	68	00	000.00	0.00	0

char	Incompatibilities obs	exp	ratio	pol	char	Incompatibilities obs	exp	ratio	pol
69	9	48.31	0.19	0	70	00	000.00	0.00	0
71	00	000.00	0.00	0	72	00	000.00	0.00	0
73.1	110	135.84	0.81	0	73.2	9	47.46	0.19	0
73.3	12	48.33	0.25	0	74	35	72.87	0.48	3
75	7	48.45	0.14	0	76	00	000.00	0.00	0
77	14	72.39	0.19	0	78.1	49	120.14	0.41	0
78.2	00	000.00	0.00	0	78.3	6	48.57	0.12	0
79.1	00	000.00	0.00	0	79.2	00	000.00	0.00	0
80	00	000.00	0.00	31	81.1	67	69.66	0.96	9
81.2	77	127.93	0.60	0	82.1	56	67.23	0.83	12
82.2	98	135.91	0.72	0	83	39	108.22	0.36	18
84	68	107.29	0.63	9	85	51	88.62	0.58	18
86	62	115.25	0.54	2	87	00	000.00	0.00	0
88	70	128.33	0.55	0	89	60	120.07	0.50	8
90.1	58	123.80	0.47	7	90.2	73	136.28	0.54	0
91	61	133.79	0.46	0	92	61	133.79	0.46	0
93	67	98.02	0.68	0	94	70	107.29	0.65	9
95	78	114.51	0.68	0	96.1	80	123.99	0.65	0
96.2	73	135.87	0.54	0	97.1	00	000.00	0.00	0
97.2	48	42.49	1.13	0	98	10	48.45	0.21	0
99	19	48.97	0.39	0	100.1	00	000.00	0.00	0
100.2	00	000.00	0.00	0	101	00	000.00	0.00	0
102	10	48.45	0.21	0	103	100	136.80	0.73	4
104	00	000.00	0.00	0	105.1	00	000.00	0.00	0
105.2	00	000.00	0.00	0	106	00	000.00	0.00	0
107	67	47.58	1.41	0	108	00	000.00	0.00	0
109.1	00	000.00	0.00	0	109.2	35	72.69	0.48	3
109.3	00	000.00	0.00	0	109.4	7	48.27	0.15	0
110	84	107.29	0.78	0	111.1	00	000.00	0.00	31
111.2	43	119.89	0.36	15	111.3	47	134.37	0.35	0
112.1	34	48.94	0.69	22	112.2	72	88.69	0.81	0
113.1	00	000.00	0.00	0	113.2	00	000.00	0.00	0
114	19	88.72	0.21	0	115	00	000.00	0.00	0
116	64	88.12	0.73	0	117.1	53	127.40	0.42	11
117.2	41	107.30	0.38	0	118	9	48.31	0.19	0
119	107	134.12	0.80	0	120	122	136.83	0.89	0
121	130	132.04	0.98	0	122	00	000.00	0.00	0
123	90	88.84	1.01	2	124	14	72.39	0.19	0
125	00	000.00	0.00	0	126.1	37	48.10	0.77	2
126.2	00	000.00	0.00	0	127	00	000.00	0.00	0
128	26	87.33	0.30	0	129	15	48.97	0.31	14
130	8	73.17	0.11	0	131.1	41	107.90	0.38	0
131.2	9	47.99	0.19	0	132.1	86	113.34	0.76	0
132.2	105	132.28	0.79	0	132.3	110	135.38	0.81	0
133	8	73.17	0.11	0	134	6	48.97	0.12	0
135	99	134.26	0.74	0	136	14	72.39	0.19	0
137.0	00	000.00	0.00	0	138.1	97	125.23	0.77	0
138.2	00	000.00	0.00	0	138.3	00	000.00	0.00	0
139	66	114.89	0.57	4	140	00	000.00	0.00	0
141	00	000.00	0.00	0	142.1	00	000.00	0.00	0
142.2	28	87.25	0.32	0	143	00	000.00	0.00	0
144	27	99.30	0.27	0	145	00	000.00	0.00	0
146	00	000.00	0.00	0	147	64	129.34	0.49	0
148	00	000.00	0.00	0	149.1	44	123.90	0.36	6
149.2	53	98.90	0.54	3	149.3	42	48.26	0.87	2

char	Incompatibilities obs	exp	ratio	pol	char	Incompatibilities obs	exp	ratio	pol
150	00	000.00	0.00	0	151	94	118.25	0.79	0
152.1	49	98.72	0.50	0	152.2	35	87.42	0.40	0
153	27	99.30	0.27	0	154	28	43.01	0.65	0
155	17	73.17	0.23	0	156	44	125.17	0.35	6
157	46	126.82	0.36	12	158	69	114.23	0.60	0
159	14	48.53	0.29	14	160	34	87.98	0.39	0
161	34	87.98	0.39	0	162	56	107.71	0.52	12
163	8	72.49	0.11	0	164	8	72.49	0.11	0
165	31	98.73	0.31	0	166	71	107.51	0.66	0
167	53	127.55	0.42	0	168	50	134.56	0.37	0
169	00	000.00	0.00	0	170	00	000.00	0.00	0

Grand total of incompatibilities

Observed	expected	LeQuesne ratio	polar
4022	7735.04	0.52	398

Marks matrix from the program LEQUC.
(Unmarked characters omitted.)
(See Chapter 5.)

Characters

Taxa	N	2	2	3	6	9	9	1 0	1 1	1 2	1 5	1 5	1 6	1 6	1 7	1 8	1 9	2 0
		.	.			.	.					.	.	.				
		2	3			1	2				2	3	1	2				
1	(345)	.	.	10	5	4	.	.	2	18	.	29	5	.	.	.	5	1
2	(157)	.	.	5	.	.	.	.	.	1	.	2	.	.	.	.	.	.
3	(60)	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
4	(51)	.	.	1	.	1	.	.	.	.	.	1	.	.	.	.	.	.
5	(128)	.	.	2	1	1	.	1	1	1	.	1	1	1	.	.	1	1
6	(20)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7	(147)	.	.	5	2	4	.	.	.	6	.	1	22	.	.	.	2	.
8	(80)	.	.	2	2	2	.	.	2	4	.	1	3	.	.	.	2	1
9	(63)	.	.	6	4	.	.	.	1	3	.	.	3	.	.	.	4	3
10	(131)	.	.	.	.	3	.	1	1	.	5	2	.	3	1	.	.	1
11	(24)	.	.	.	.	.	.	.	12	.	2	.	.	.	.	.	.	.
12	(25)	.	.	.	.	3	.	.	.	.	2	2	.	.	.	.	.	.
13	(64)	.	.	.	.	.	.	.	.	.	21	8	.	2	.	.	.	.
14	(8)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
16	(32)	1	.	.	.	.	.	2	.	.	.	.	.	6	2	.	.	.
17	(13)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18	(32)	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
19	(44)	.	.	.	.	1	.	2	.	.	1	1	.	5	3	.	.	.
20	(107)	2	8	.	.	.	8	.	.	.	.	.	.	1	.	.	.	.
21	(67)	.	4	.	.	1	4	.	.	.	.	.	.	.	.	.	.	.
22	(60)	.	2	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.
23	(130)	1	.	.	.	4	.	1	.	.	.	.	1	1	1	.	.	.
24	(65)	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
25	(30)	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
26	(11)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27	(188)	2	.	1	1	.	.	12	1	.	.	.	3	4	2	.	1	1
28	(122)	.	.	.	1	5	.	.	1	.	.	1	1	.	4	15	1	2
29	(185)	.	.	.	.	6	.	2	.	.	.	5	1	.	20	15	.	6
30	(164)	.	.	.	1	2	.	1	7	18	.	.	6	2	.	.	1	4
31	(297)	1	.	.	5	3	.	31	8	1	.	1	10	2	15	1	5	9

[N = total marks recorded for that taxon. Only taxon 15 was unmarked.]

Marks matrix from the program LEQUC - continued.

Characters

Taxa	21	23	24.1	24.3	25	26.1	26.2	26.3	27	28.1	28.2	28.3	29	30	31	31	32	32
1	.	.	5	.	1	.	.	.	.	1	1	.	15	24	9	.	.	.
2	.	.	.	.	9	.	.	.	.	.	.	.	2	2	4	.	.	.
3	.	.	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.
4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
5	1	.	1	1	.	1	.	.	.	1	1	1	2	2	1	.	.	.
6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7	.	.	2	.	.	.	.	.	.	.	.	.	9	9	3	.	.	.
8	1	.	2	1	.	1	.	.	.	.	.	.	2	2	.	.	1	.
9	.	.	4	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.
10	5	.	.	1	.	1	.	.	.	.	.	.	.	.	2	.	1	1
11	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.
12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	1	7	.	.	.	.	.	.	7	.	.	.	.	.	2	.	.	.
14	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
16	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
17	2	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.
18	.	.	.	.	.	.	2	.	.	.	.	.	.	.	1	.	1	1
19	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
20	.	.	.	.	.	.	2	8	.	.	.	.	1	1	.	12	.	.
21	.	.	.	.	.	.	.	4	.	.	.	.	1	1	.	2	.	13
22	.	.	.	.	.	.	.	2	.	.	.	.	1	1	.	12	.	2
23	1	.	.	1	.	1	1	.	.	1	1	1	1	1	3	.	7	7
24	.	.	.	.	.	.	3	.	.	.	.	.	.	.	14	.	4	4
25	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27	2	.	1	4	.	4	2	.	.	21	25	38	3	4	7	.	2	.
28	2	.	1	2	.	2	.	.	.	4	.	.	5	.	.	.	4	4
29	2	.	.	2	.	2	.	.	.	13	1	1	9	1	1	.	28	28
30	15	.	1	4	.	4	.	.	.	10	16	.	.	.	.	.	1	.
31	4	.	5	3	.	3	1	.	.	8	16	38	.	.	.	.	3	3

Marks matrix from the program LEQUC - continued.

Characters

Taxa	32.3	32.4	33	34	35	36	37	38	38	38	38	38	39	39	44	45	49	50
1	.	.	1	.	2	14	.	.	3	1	.	.	31	.	.	7	.	.
2	.	.	.	.	.	2	.	.	11	.	.	.	4	.	.	21	.	.
3	.	.	.	.	1	.	.	.	5	.	.	.	.	.	.	.	.	.
4	.	.	.	.	2	.	.	.	4	.	.	.	.	.	.	.	.	.
5	.	.	1	.	3	1	.	.	1	.	.	.	.	.	.	1	.	.
6	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
7	.	.	20	.	24	1	.	1	.	.	.	.	1	.	.	2	.	.
8	.	.	1	.	1	.	.	26	1	.	.	.	.	.	.	2	1	1
9	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	5	.	.
10	1	.	6	.	.	.	.	23	2	.	.	.	.	.	.	.	1	3
11	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2
12	.	.	.	.	.	.	.	.	6	8	.	.	.	.	.	.	.	.
13	.	.	.	.	.	6	.	.	6	.	.	.	.	.	.	.	1	1
14	.	.	.	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.
16	1	15	3	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18	.	.	.	1	.	.	5	.	.	.	3	5	.	.	.	.	.	.
19	1	2	4	.	.	.	.	1	1	2	.	.	.	.	.	.	.	.
20	1	16	1	.	.	13	1	.	.	12	11	.	.	.	.	.	.	.
21	13	.	2	.	.	.	4	.	.	.	1	23	.	.	.	.	1	1
22	4	1	14	.	.	1	25	.	.	1	2	2	.	.	.	.	1	1
23	19	23	.	10	.	1	1	.	.	.	2	11	9	.	.	.	2	2
24	3	3	.	10	.	.	1	.	.	.	1	4	5	.	.	.	.	.
25	.	.	1	.	.	.	3	.	6	4	4	.	1	8	.	.	.	.
26	.	.	3	.	.	.	.	.	1	1	1	.	.	8	.	.	.	.
27	.	.	1	.	1	2	.	.	5	2	.	.	.	.	.	1	1	1
28	.	.	4	.	.	1	.	4	.	.	.	.	7	.	15	.	.	.
29	.	.	6	.	.	1	.	28	4	1	.	.	5	.	15	.	.	.
30	.	.	3	.	.	1	.	.	1	5	24	27	.	.	.	1	1	1
31	1	1	5	1	.	4	.	1	2	11	1	1	.	.	1	.	.	.

Marks matrix from the program LEQUC - continued.

Characters

Taxa	51.1	51.2	51.3	51.4	51.5	51.6	51.7	51.8	61.2	62.1	62.2	62.3	62.4	64.1	65.1	66.1	67.1	69.1
1	.	.	.	3	3	.	6	.	8	.	.	5	1	1	.	.	.	1
2	.	.	.	.	.	.	.	.	5	.	.	5	9	.	.	.	.	9
3	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	.	8
4	.	.	.	.	.	.	.	.	1	.	.	3	.	11	.	.	.	.
5	.	.	.	1	1	.	1	.	2	.	.	3	.	11	.	.	.	.
6	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.
7	.	.	.	2	2	.	4	.	5	.	.	1	.	.	.	.	.	.
8	.	.	.	2	2	.	.	.	3	.	.	.	.	.	.	.	1	.
9	.	.	.	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.
10	1	.	.	.	.	.	6	8	.	.	30	.	.	.	8	.	3	.
11	.	.	.	.	.	.	.	4	.	.	.	.	.	.	4	.	.	.
12	.	.	.	.	.	.	2	5	.	.	.	.	.	.	5	.	.	.
13	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.
14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
16	1	.	.	.	.	1	.	.	.	.	2	.	.	.	.	.	.	.
17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.
19	1	.	.	.	.	.	1	1	.	.	30	.	.	.	1	.	1	.
20	2	8	.	.	.	4	.	.	.	8	.	.	.	.	.	8	.	.
21	3	4	.	.	.	.	.	.	.	4	.	.	.	.	.	4	.	.
22	1	2	.	.	.	.	.	.	.	2	.	.	.	.	.	2	.	.
23	2	.	7	.	.	1	.	.	.	.	.	.	.	.	.	.	4	.
24	.	.	4	.	.	3	.	.	.	.	.	.	.	.	.	.	2	.
25	.	.	7	.	.	3	.	.	.	.	.	.	.	.	.	.	3	.
26	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	1	.
27	1	.	.	1	1	2	1	.	1	.	.	1	.	1	.	.	.	.
28	.	.	.	1	1	.	7	.	.	.	.	.	.	.	.	.	4	.
29	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	12	.
30	.	.	.	11	11	.	.	.	.	.	.	.	.	.	.	.	7	.
31	.	.	1	8	8	1	3	.	.	.	.	.	.	.	.	.	2	.

Marks matrix from the program LEQUC - continued.

Characters

Taxa	73.1	73.2	73.3	74	75	77	78.1	83	81.1	81.2	82.1	82.2	83	84	85	86	88	89
1	3	1	1	27	.	.	10	.	10	3	26	2	17	7	20	6	2	2
2	.	.	.	3	.	.	5	.	27	.	2	.	1	.	10	.	.	.
3	1	.	.	6	.	.	.	.	7	.	.	.	.	.	7	.	.	.
4	.	1	.	.	.	.	1	.	.	1	.	12	2	3	4	2	1	.
5	3	9	.	1	.	.	2	.	1	1	1	2	2	3	3	1	1	1
6	.	9	.	.	.	.	.	.	.	.	.	.	1	8	1	.	.	.
7	1	.	12	1	.	.	5	.	1	5	1	1	4	1	1	4	5	4
8	.	.	12	.	.	.	2	.	.	.	.	.	.	.	.	.	.	4
9	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.
10	2	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.
11	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.
12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
16	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.
17	.	.	.	.	.	.	.	.	.	9	.	.	.	.	.	.	1	.
18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
19	1	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.
20	1	.	.	.	1	8	.	.	.	.	.	.	.	.	.	.	.	.
21	1	.	.	.	7	4	.	.	.	.	.	.	.	.	.	.	.	.
22	.	.	.	.	7	2	.	.	.	.	.	.	.	.	.	.	.	.
23	.	.	.	.	.	.	.	.	1	1	1	1	.	1	.	.	1	1
24	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
25	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
26	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27	2	1	.	.	.	.	1	.	1	2	2	4	1	2	1	1	4	2
28	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	23	2	1
29	1	.	.	.	.	.	.	.	1	4	1	3	.	1	.	5	3	1
30	.	.	.	.	.	.	.	.	1	4	15	3	.	1	.	.	5	1
31	.	.	.	1	.	.	.	.	33	6	15	3	3	25	1	3	4	20

Marks matrix from the program LEQUC - continued.

	Characters																
	9	9	9	9	9	9	9	9	9	9	9	9	1	1	1	1	1	1
	0	0	1	2	3	4	5	6	6	7	8	9	0	0	0	0	0	1
	.	.						.	.	.						.	.	
	1	2						1	2	2						2	4	
Taxa																		
1	2	.	.	.	18	8	4	1	.	.	.	.	.	2	1	27	.	4
2	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	3	.	20
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	7
4	.	.	.	.	.	2	3	3	.	.	.	.	.	.	1	.	.	.
5	1	1	1	1	1	11	5	3	1	.	.	.	.	1	67	1	.	1
6	.	.	.	.	.	2	2	2	.	.	.	.	.	.	1	.	.	.
7	1	.	.	.	1	1	1	.	.	.	.	.	.	.	.	1	.	1
8	2	1	1	1	.	.	.	1	.	.	.	.	.	1	.	.	.	.
9	8	19	15	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.
10	.	4	1	1	.	.	.	1	10	.	.	.	.	2	.	.	.	.
11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
12	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
16	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.
17	.	.	1	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.
18	.	.	.	.	.	.	.	.	.	.	1	19	1	.	.	.	.	.
19	.	1	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
20	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	1	.
21	.	.	.	.	.	.	.	.	.	.	.	.	.	11	.	.	7	.
22	.	.	.	.	.	.	.	.	1	.	.	.	.	3	.	.	7	.
23	1	1	1	1	1	1	1	1	1	48	10	3	10	1	.	.	.	1
24	.	.	.	.	.	.	.	.	.	3	10	19	10	.	.	.	.	.
25	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.
26	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
27	2	4	4	4	3	1	2	2	4	1	.	.	.	1	67	.	.	3
28	1	1	2	2	3	.	2	2	.	.	.	.	.	1	.	.	.	2
29	1	2	2	2	4	1	4	3	.	1	.	.	.	.	.	.	.	3
30	1	2	4	4	8	1	3	3	3	.	.	.	.	4	.	.	.	7
31	19	3	3	3	6	25	8	6	3	48	1	.	1	6	1	1	.	6

Marks matrix from the program LEQUC - continued.

Characters

Taxa	1 1 1 2	1 1 1 3	1 1 2 1	1 1 2 2	1 1 4	1 1 6	1 1 7 . 1	1 1 7 . 2	1 1 8	1 1 9	1 2 0	1 2 1	1 2 3	1 2 4	1 2 6 . 1	1 2 8	1 2 9	1 3 0
1	8	.	33	7	.	.	2	7	1	1	1	2	21	.	37	4	.	.
2	1	.	34	24	.	.	.	5	9	.	.	6	1	.	1	7	.	.
3	.	.	5	7	.	.	.	.	8	.	.	7	.	.	.	.	.	.
4	.	.	.	.	.	.	.	1	.	1	9	.	15	.	1	2	.	.
5	1	1	1	1	.	.	1	2	.	1	2	3	2	.	37	4	.	.
6	.	.	.	.	.	.	.	.	.	.	.	3	.	.	1	3	.	.
7	2	.	1	1	.	.	1	15	.	4	1	1	1	.	1	.	.	.
8	3	1	.	.	.	.	2	1	.	.	1	.	.	.	.	.	.	.
9	3	1	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.
10	.	1	.	.	.	15	.	.	.	.	6	.	8	.	.	.	.	.
11	.	1	.	.	.	.	.	.	.	.	.	4	1	.	.	.	.	.
12	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
16	.	.	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.
17	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
19	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.
20	.	.	.	.	.	.	.	.	.	10	12	11	.	8	.	.	.	.
21	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.
22	.	.	.	.	.	.	.	.	.	3	2	3	.	2	.	.	.	.
23	.	1	.	.	7	.	1	.	.	.	.	.	.	.	.	.	.	.
24	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.
25	.	.	.	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.
26	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
27	1	4	.	.	.	.	2	1	.	1	1	3	.	.	1	1	.	.
28	1	2	.	2	.	.	1	.	.	.	.	.	.	.	.	.	15	.
29	.	2	.	11	.	.	1	.	.	3	1	3	.	.	.	.	15	.
30	.	4	.	.	.	32	5	.	.	2	1	1	.	.	.	.	.	.
31	.	3	.	2	1	.	14	.	.	10	7	8	.	.	.	.	1	.

Marks matrix from the program LEQUC - continued.

Characters

Taxa	1 3 1 . 1	1 3 1 . 2	1 3 2 . 1	1 3 2 . 2	1 3 2 . 3	1 3 3	1 3 4	1 3 5	1 3 6	1 3 8 . 1	1 3 9	1 4 2 . 2	1 4 4	1 4 7	1 4 9 . 1	1 4 9 . 2	1 4 9 . 3	1 5 1
1	7	1	5	5	5	.	.	5	.	22	1	1	5	1	5	15	42	7
2	5	9	6	5	5	.	.	5	.	3	.	6	5	.	.	2	1	4
3	.	8	1	1	1	.	.	1	.	.	.	15	.	.	.	1	.	.
4	1	.	.	.	.	.	.	.	.	.	.	5	3	.	.	.	.	.
5	2	.	.	1	1	.	.	.	.	1	.	3	3	.	1	1	1	1
6	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.
7	15	.	4	2	2	.	.	4	.	1	.	1	1	.	2	4	42	3
8	1	.	1	.	.	.	.	.	.	.	.	.	.	.	2	3	1	1
9	.	.	1	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.
10	.	.	6	2	.	.	1	2	.	.	.	.	.	.	.	.	.	3
11	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
12	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	.	.	.	1	9	7	.	1	.	10	.	.	.	.	.	.	.	1
14	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
16	.	.	.	1	1	.	6	1	.	.	.	.	.	1	.	.	.	.
17	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	1
18	.	.	.	5	4	.	.	4	.	1	1	.	.	1	.	.	.	1
19	.	.	1	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.
20	.	.	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.	.
21	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.
22	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
23	.	.	.	.	.	.	.	.	.	4	4	.	.	1	.	.	.	.
24	.	.	.	1	1	.	.	1	.	2	3	.	.	1	.	.	.	7
25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
27	1	.	.	7	6	.	.	1	.	1	1	1	1	2	1	.	.	.
28	.	.	.	.	.	.	.	.	.	1	3	.	.	20	1	.	.	1
29	.	.	1	1	1	.	.	1	.	1	2	.	.	4	.	.	.	2
30	.	.	.	1	1	.	.	1	.	2	.	.	.	2	1	.	.	2
31	.	.	.	2	2	.	.	.	.	3	11	.	.	1	5	1	.	1

Marks matrix from the program LEQUC - continued.

Characters

Taxa	152.1	152.2	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168
1	.	.	5	.	.	5	3	.	.	.	.	.	.	.	.	.	.	.
2	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5	1	1	3	.	.	1	1	1	.	.	.	.	.	.	.	.	.	1
6	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7	.	.	1	.	.	2	1	.	.	.	.	.	.	.	.	1	.	.
8	.	.	.	.	.	2	2	1	.	.	.	1	.	.	.	40	1	1
9	.	.	.	.	.	4	3	.	.	.	.	.	.	.	.	.	.	.
10	.	.	.	.	8	.	.	1	.	26	26	5	.	.	1	1	3	3
11	.	.	.	.	4	.	.	.	.	.	.	1	.	.	.	.	1	1
12	.	.	.	.	5	.	.	.	.	.	.	3	.	.	.	.	.	.
13	.	.	.	.	.	.	.	.	.	2	2	1	7	7	.	.	1	1
14	.	.	.	.	.	.	.	.	.	1	1	.	1	1	.	.	.	.
16	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
17	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	2	1
18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
19	.	.	.	.	1	.	.	1	.	1	1	1	.	.	1	1	.	.
20	1	3	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.
21	.	1	.	.	.	.	.	1	.	.	.	.	.	.	3	1	.	.
22	1	2	.	.	.	.	.	1	.	.	.	.	.	.	1	1	.	.
23	14	.	.	1	.	.	.	3	.	.	.	.	.	.	2	2	2	.
24	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27	14	21	1	1	.	1	2	4	.	.	.	.	.	.	2	2	2	3
28	.	.	.	3	.	1	1	30	14	.	.	3	.	.	.	.	.	2
29	.	.	.	28	.	.	.	5	14	.	.	5	.	.	1	1	1	3
30	.	.	.	.	.	1	10	1	.	.	.	.	.	.	.	.	1	4
31	2	1	.	28	.	5	.	.	.	.	.	.	.	.	.	.	.	.

HENNIG CHARACTER MATRIX

Scores for the morphological characters and exemplar taxa reworked for the Hennig parsimony program (See Chapter 5).

[0 = plesiomorphic state; 1,2 etc = apomorphic states; - = missing score]

Characters

Taxa	H 0 0 1	H 0 0 2	H 0 0 3	H 0 0 4	H 0 0 5	H 0 0 6	H 0 0 7	H 0 0 8	H 0 0 9	H 0 1 0	H 0 1 1	H 0 1 2	H 0 1 3	H 0 1 4	H 0 1 5	H 0 1 6	H 0 1 7	H 0 1 8	H 0 1 9	H 0 2 0	H 0 2 1	H 0 2 2	H 0 2 3	H 0 2 4	H 0 2 5	H 0 2 6	H 0 2 7
1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	0
2	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0
3	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0
4	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0
5	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0
6	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0
7	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0	0	0
8	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0
9	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0
10	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0
11	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0	
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0	
16	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	
17	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	
18	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0	
19	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	1	1	0	1	1	0
20	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0
21	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0
22	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0
23	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0
24	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0
25	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0
26	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0
27	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	1	1
28	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
30	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	1	0	1	1	0
31	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0

Hennig matrix continued

Characters

Taxa	H028	H029	H030	H031	H032	H033	H034	H035	H036	H037	H038	H039	H040	H041	H042	H043	H044	H045	H046	H047	H048	H049	H050	H051	H052	H053	H054
1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	1	1
2	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	1	-
3	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	-	1	-	0	0	0	0	1	1
4	0	1	0	0	0	0	0	0	0	1	0	0	0	.0	1	0	1	0	0	2	0	0	0	0	0	1	1
5	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	-	1	-	0	0	0	0	1	1
6	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	-	1	-	0	0	0	0	1	1
7	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1
8	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
9	0	1	0	0	0	0	0	-	-	-	-	-	-	0	1	0	0	1	-	1	-	0	0	0	0	1	1
10	0	0	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
11	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
12	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0
13	1	0	2	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
14	1	0	2	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	1	0
15	1	0	2	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0
16	0	0	2	0	1	0	0	0	0	0	0	0	0	4	0	0	0	0	0	3	0	0	0	0	0	1	0
17	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
18	0	0	2	0	1	0	0	0	0	0	0	0	0	2	0	0	0	1	1	5	0	0	0	0	0	1	0
19	0	0	2	0	1	0	0	0	0	0	0	0	0	3	1	0	0	0	0	2	0	0	0	0	0	1	0
20	0	0	2	0	3	0	0	1	1	0	0	1	0	4	0	0	0	0	0	2	0	0	0	0	0	1	0
21	0	0	2	0	3	0	0	1	1	0	0	0	0	1	0	0	0	1	0	6	0	0	0	0	0	1	0
22	0	0	2	0	3	0	0	1	1	0	0	1	0	3	1	0	0	1	1	4	0	1	0	0	0	1	0
23	0	0	2	0	2	0	0	0	0	0	0	0	0	4	0	1	0	1	1	5	1	0	1	0	0	1	0
24	0	0	2	0	2	0	0	0	0	1	0	0	0	0	0	1	0	1	1	4	0	0	0	0	0	1	0
25	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	1	0
26	0	0	2	0	2	0	0	0	0	0	0	0	1	0	1	0	0	1	1	4	3	0	0	0	0	1	0
27	0	0	2	0	1	0	3	2	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0
29	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	2	-	-	-	-	-	-	0	1	0	0	1	-	5	-	0	0	0	0	1	0
31	0	0	1	0	0	0	4	-	-	-	-	-	-	0	0	0	0	1	-	3	-	0	0	1	1	1	0

Hennig matrix continued

Characters

Taxa	H055	H056	H057	H058	H059	H060	H061	H062	H063	H064	H065	H066	H067	H068	H069	H070	H071	H072	H073	H074	H075	H076	H077	H078	H079	H080	H081
1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0
5	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0
6	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0
11	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0
12	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0
13	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
16	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
20	0	0	0	1	1	2	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
21	0	0	0	1	1	2	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
22	0	0	0	1	1	2	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
23	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
24	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
25	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
27	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
30	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
31	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1

Hennig matrix continued

Characters

Taxa	H 0 8 2	H 0 8 3	H 0 8 4	H 0 8 5	H 0 8 6	H 0 8 7	H 0 8 8	H 0 8 9	H 0 9 0	H 0 9 1	H 0 9 2	H 0 9 3	H 0 9 4	H 0 9 5	H 0 9 6	H 0 9 7	H 0 9 8	H 0 9 9	H 1 0 0	H 1 0 1	H 1 0 2	H 1 0 3	H 1 0 4	H 1 0 5	H 1 0 6	H 1 0 7	H 1 0 8
1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0
2	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
3	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0
4	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0
5	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
6	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0
7	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	2	2	1	1	1	1	0	1	0	0
8	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	2	2	1	1	1	1	0	1	1	0
9	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
10	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	1
11	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	1	1	0	1	1	1
12	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
13	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	1	1	0	1	1	2
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	1	1	0	1	1	2
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	1	1	0	1	1	2
16	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	2	1	1	1	1	0	1	1	2
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1
18	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
19	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	2	1	1	1	1	0	1	1	2
20	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
21	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
22	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
25	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	1	0	1	1	2
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	1
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	1
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	1	1	1	0	0	1	1
31	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0

Hennig matrix continued

Characters

Taxa	H 1 0 9	H 1 1 0	H 1 1 1	H 1 1 2	H 1 1 3	H 1 1 4	H 1 1 5	H 1 1 6	H 1 1 7	H 1 1 8	H 1 1 9	H 1 2 0	H 1 2 1	H 1 2 2	H 1 2 3	H 1 2 4	H 1 2 5	H 1 2 6	H 1 2 7	H 1 2 8	H 1 2 9	H 1 3 0	H 1 3 1	H 1 3 2	H 1 3 3	H 1 3 4	H 1 3 5
1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	2	0	0	0	0	0
2	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0
3	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	2	0
4	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	2	0
5	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	2	0
6	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	2	0
7	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	2	0
8	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	2	0
9	1	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	2	2	0
10	1	1	1	1	1	2	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	3	2	0
11	1	1	1	1	1	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	3	2	0
12	1	1	1	1	1	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	3	2	0
13	1	1	1	1	1	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	3	2	0
14	1	1	1	1	1	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	3	2	0
15	1	1	1	1	1	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	3	2	0
16	1	1	1	1	1	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	3	2	0
17	1	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	3	2	0
18	1	1	1	1	1	2	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	3	2	0
19	1	1	1	1	1	2	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	3	2	0
20	1	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	3	2	0
21	1	1	1	1	1	2	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	3	2	0
22	1	1	1	1	1	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	3	2	0
23	1	1	1	1	1	2	0	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1	3	2	1
24	1	1	1	1	1	2	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	1	3	2	0
25	1	1	1	1	1	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	3	2	0
26	1	1	1	1	1	2	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	3	2	0
27	1	1	1	1	1	2	1	0	0	0	2	0	0	1	1	1	0	0	1	1	1	0	0	1	3	2	0
28	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	2	1	0
29	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	2	1	0
30	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	2	2	0
31	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	2	2	0

Hennig matrix continued

Characters

Taxa	H136	H137	H138	H139	H140	H141	H142	H143	H144	H145	H146	H147	H148	H149	H150	H151	H152	H153	H154	H155	H156	H157	H158	H159	H160	H161	H162
1	0	0	0	0	1	0	0	0	0	1	1	0	0	2	1	0	1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	1	1	0	2	3	0	0	1	0	0	1	0
3	0	0	0	0	2	1	0	0	1	0	0	0	0	0	0	1	1	0	2	3	0	0	1	0	0	1	0
4	0	0	0	0	2	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
5	0	0	0	0	2	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	0
6	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0
7	0	0	0	0	2	0	1	1	1	0	0	0	0	0	0	0	1	0	1	3	0	0	1	0	1	1	0
8	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	3	0	0	1	0	0	1	0
9	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	3	0	0	1	0	0	1	0
10	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	3	0	0	1	0	0	1	0
11	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	2	0	0	1	0	0	1	0
12	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	3	0	0	1	0	0	1	0
13	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1
14	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0
15	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0
16	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	2	0	1	1	0	0	1	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0
18	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	2	0	0	1	0	0	1	0
19	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	2	0	1	1	0	0	1	0
20	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
21	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
22	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
23	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
24	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
25	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
26	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
27	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	1	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
31	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Hennig matrix continued

Characters

Taxa	H 1 6 3	H 1 6 4	H 1 6 5	H 1 6 6	H 1 6 7	H 1 6 8	H 1 6 9	H 1 7 0	H 1 7 1	H 1 7 2	H 1 7 3	H 1 7 4	H 1 7 5	H 1 7 6	H 1 7 7	H 1 7 8	H 1 7 9	H 1 8 0	H 1 8 1	H 1 8 2	H 1 8 3	H 1 8 4	H 1 8 5	H 1 8 6	H 1 8 7	H 1 8 8	H 1 8 9
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3	0	0	0	0	0	1	0	1	1	1	0	0	1	2	1	1	0	1	0	0	1	1	0	1	0	0	1	0
4	0	0	0	0	0	1	0	1	1	1	0	0	1	1	1	1	0	1	0	0	1	1	0	1	0	0	1	0
5	0	0	0	0	0	1	0	1	1	1	0	0	1	1	1	1	0	1	0	0	1	1	0	1	0	0	1	0
6	0	0	0	0	0	1	0	1	1	1	0	0	1	1	1	1	0	1	0	0	1	1	0	1	0	0	1	0
7	0	0	0	0	0	0	0	0	0	1	0	0	1	3	1	0	0	0	0	0	1	1	0	1	0	0	1	0
8	0	0	0	0	0	0	0	0	0	1	0	0	1	2	1	0	0	0	0	0	1	1	0	1	0	0	1	0
9	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	0	1	0	0	1	0
10	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	0	0	1	1	1	0	0
11	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0
12	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0
13	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1
14	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1
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16	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	1	0
17	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
18	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0
19	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	1	0
20	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	-	2	0	0	0	0	0	1	1	0	0	1	0
21	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	-	2	0	0	0	0	0	1	1	0	0	1	0
22	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	-	2	0	0	0	0	0	1	1	0	0	1	0
23	0	1	0	0	0	0	0	0	1	0	1	1	0	1	-	1	0	0	0	0	0	0	1	0	0	1	0	0
24	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0
25	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
26	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
27	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	-	2	0	0	0	0	0	1	1	0	0	1	0
28	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
29	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
30	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0
31	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	-	-	-	-	-	-	-

Hennig matrix continued

Characters

Taxa	H 1 9 0	H 1 9 1	H 1 9 2	H 1 9 3	H 1 9 4	H 1 9 5	H 1 9 6
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0
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9	0	0	0	0	0	0	0
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11	0	0	0	1	1	0	0
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13	1	0	0	0	0	0	0
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16	0	1	1	1	1	0	0
17	0	0	0	1	1	0	0
18	0	0	0	1	1	0	0
19	0	1	1	1	1	0	0
20	0	1	1	1	1	0	0
21	0	1	1	1	1	0	0
22	0	1	1	1	1	0	0
23	0	0	0	0	1	0	0
24	0	0	0	0	1	0	0
25	0	0	0	0	1	0	0
26	0	0	0	0	1	0	0
27	0	0	0	0	1	1	0
28	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0
30	0	0	0	0	0	0	1
31	-	-	-	-	-	-	-

APPENDIX 3: DESCRIPTION OF A NEW TRIBE, GENUS AND SPECIES

During the course of this investigation a new species has been discovered which constitutes a new tribe of the Cynipoidea. This tribe will be formally described in a widely circulated journal rather than in this thesis, and therefore the new tribe, genus and species are NOT NAMED below. [Only the initial letters are used as these are not valid names (article 11h of the International Code of Zoological Nomenclature).]

E--------ini Tribe n.

This tribe consists of a single genus and species.

E--------- Gen. n.

Description

Antennae 14 segmented; thorax transversely striate; scutellum without a spine; propodeum long, separated from metanotum by a deep incision (Fig. 214). Without a central tooth on hind femur. Marginal cell long, six times longer than broad; cubital vein fused to the top region of the basalis. Gaster strongly compressed laterally, but not blade-like; longer than head plus thorax. Petiole longer than broad; not attached tangentially; with a collar. The longest gastral tergite is the seventh; the last tergite (the eighth gastral = ninth abdominal) has a small and flat pubescent area at the apex. Ovipositor coiled within gaster; with strong apical teeth. Type species *E.* c---------.

E. c--------- sp. n.

Species description

Antennae with short dense pubescence; third antennal segment slightly shorter than the second and much less than the fourth; the seventh antennal segment longer than the fifth. Mandibles with two stout blunt teeth; with long pubescence. Face strongly rugose. Small keel present

between antennal toruli; scrobes present.

Thorax long and thin, in side view about three times longer than high. Propleuron with a depression just above the anterior coxa. Mesoscutum strongly transversely striate; notauli absent. Scutellum transversely striate and foveae deep; with lateral carinae slightly protruding. Mesepisternum punctate; metapleuron elongate and with a deep depression to accommodate the coxa of the mid leg. Propodeum very long; with two longitudinal carinae and many transverse carinae; deeply rugose laterally; with a ventral depression above each hind coxa. Claws simple; first segment of hind tarsus about 60% of the rest of the tarsus.

Marginal cell long, thin and closed; vein M reaching to the wing margin; submarginal cell closed and narrow. Hindwing with three hamuli and a costal cell (Fig. 213).

Dorsally and laterally the petiole has a distinct, sulcate collar (with anterior flange) but this is absent ventrally, although the first gastral sternite is sulcate. Gaster with tergite two short and tergites three to five very short (Fig. 214). Gastral tergite six greatly lengthened, forming most of gaster. Gaster laterally compressed, but not blade-like; covered (especially posteriorly) with long white pubescence. In side view the gaster is approximately 3.4 times longer than high.

Head, thorax and gaster black, legs mostly orange, tibiae orange-brown. Wings brown with a clear patch at the base of the hindwing.

Long and slender; length (excluding antennae) 8.5 to 11mm.

Material examined

HOLOTYPE female. Papua New Guinea, Bulolo. 18. 1. 1978. H. Roberts. Stony logging area. On *Xanthophyllum*.

PARATYPES: 6 females, same data as holotype.

Etymology

This very elegant cynipoid, is named after my wife and daughter.

Remarks

This species has long and thin body, and ventral depressions in the thorax allow the legs to be folded tight against the body. The hind coxa can only be partially accommodated in the last depression so the remainder must fit under the petiole which is lengthened. Thus it is most likely that *E*--------- has a wood-associated biology like that of other large cynipoids. Perhaps it is a parasitoid of coleopterous larvae that bore into the rather tough wood of *Xanthophylum* (= *Brakenridgea*).

Affinities

E--------- *C*--------- is clearly a member of the group (Ibaliidae) of large timber-associated (wood-probing) Cynipoidea that have coiled ovipositors, transverse sculpture and relatively complete venation. *E*--------- does not belong to the Ibaliini as the marginal cell is not long enough and gaster is not blade-like. The venation is similar to that of the Liopterini but *E*--------- does not correspond to any of the subgroups of that tribe. It is not closely related to *Oberthuerella* as it lacks a femoral spur and scutal spine. The petiole is not attached tangentially so *E*--------- is not related to *Liopteron*. *E*--------- is perhaps closest to the *Mesocynips* group but the petiole is too long for the genus to fall within the traditional concept of this group. The structure of the petiole is similar to that of *Mesocynips* in that the collar is absent ventrally, but *E*--------- does not have the ventral hump which is present in *Mesocynips*. Other genera near *Mesocynips* e.g. *Pseudibalia* have a complete collar.

This new genus clearly belongs to a new tribe, the E--------ini, which is positioned between the Ibaliini and the Liopterini. The most significant tribal features being elongation of the body and the deep incision between the metanotum and propodeum.

APPENDIX 4: KEY TO THE SUPRAGENERIC TAXA OF THE CYNIPOIDEA.

1 Ninth gastral tergite with depressed area on posterior margin (Figs 142, 143). Phytophagous species. . . . . .CYNIPIDAE. . . 2
- Ninth gastral tergite without depressed area. Parasitoid species. 5

2 Pronotum long, in dorsal view median dorsal length greater than 15% of its lateral length. 3
- Pronotum short, in dorsal view median dorsal length less than 15% of its greatest lateral length. 4

3 Third gastral tergite expanded (often 2 + 3 fused), almost reaching to apex of gaster (Fig. 128); maxillary palps 4 segmented. Inquilines. . . . . .SYNERGINI
- Third gastral tergite not expanded, not fused with the second tergite and not reaching to apex of gaster; maxillary palps 5 segmented. Gall-wasps on a wide range of plants. . . . . .AULACIDEINI

4 Hypopygium broad, shaped like a plough blade (Fig. 126). Gall-makers mostly on Rose. . . . . RHODITINI
- Hypopygium spine-like (Fig. 127). Gallmakers on Oak . . . . . .CYNIPINI

5 Mesonotum with rough sculpture (rugose, foveolate or striate), and with strong transverse ridges (Fig. 71). Ovipositor looped in a complete circle within the gaster (Figs 147, 154). Parasites of Siricidae or Coleoptera larvae in trees. Large insects, 5-30mm, usually over 10mm. . . . . IBALIIDAE. . 6
- Mesonotum with light sculpture (alutaceous, punctate, granulate, rugulose, strigulose or smooth), without strong transverse ridges (Figs 76, 82) Ovipositor not forming a complete loop (except in *Sarothrus*). Parasites of Diptera, Neuroptera or hyperparasites of Homoptera via hymenopterous primaries. Not associated

with trees. Small insects, 1-6mm, usually under 4mm 9

6 "Pterostigma" present (Fig. 159); lower face with two conspicuous fan-shaped areas of striations; hypostomal region not set in a cavity; gastral tergites 5-7 not expanded; petiole with a strong anterior flange consisting of both first tergite and first sternite; gonostylus almost globular; apex of gaster not upturned; lateral surface of pronotum with a ridge-like hump. On Araucaria (Cupressaceae) Rare, endemic to Australia . . . . . AUSTROCYNIPINAE

- Pterostigma absent (Fig. 150); lower face not strongly striate (Fig. 21); hypostomal region of head set within in a cavity (Figs 38, 39); gastral tergites 5 to 7 elongate; petiole without a strong anterior flange including a sternal element; gonostylus elongate (Fig. 147); apex of gaster slightly upturned; pronotum without a lateral hump. On Pinaceae or Deciduous trees. World wide. . . . . IBALIINAE . . 7

7 Marginal cell very long (Fig. 102), nine times as long as broad; gaster laterally compressed, blade-like (Fig. 150); petiole short and smooth, with dense punctation on underside of the frontal articulation, which is incised. Trace of vein C present at base of forewing; posterior margin of scutellum with transverse ridge, which is interrupted centrally by a large emargination. Clypeus without a central notch or depression. Mid tibia with a single spur. . . . . .IBALIINI

- Marginal cell much shorter (Fig. 107), at most six times as long as broad; gaster not strongly compressed laterally, not (one exception) blade-like; petiole often long; caniculate or at least sculptured; without dense punctation on underside of frontal articulation, which is not incised. Vein C absent; scutellum without transverse ridge. Clypeus with a central notch or depression. Tibiae with two spurs. 8

8 Propodeum greatly elongate and separated from metanotum

by deep cleft (Fig. 214). Mesonotal trough not obscured by rough sculpture and with a strong horizontal groove. . . . . E--------INI

- Propodeum not particularly elongate and not separated from metanotum by a deep cleft. Mesoscutal trough obscured by rough sculpture but without a strong horizontal groove. . . . . LIOPTERINI

9 Vein Rs+M visible and pointing to middle of basalis; (Fig. 109) hypostomes not fused and lower tentorial bridge visible; clypeus projecting upwards away from labium; face with two vertical grooves separated by central keel; lateral propodeal carinae straight and converging, caulis pointed; scutellar foveae transverse, almost triangular; scutellum with an approximately triangular posterior depression (Fig. 158). Nepal. Rare . . . . . HIMALOCYNIPIDAE

- Vein Rs+M not visible or pointing to junction of basalis with median (Fig. 111); hypostomal bridge present (Fig. 42), lower tentorial bridge not visible; clypeus normal, not projecting upwards; face without vertical grooves; propodeal carinae curved, caulis not pointed; scutellar foveae approximately round; posterior of scutellum without triangular depression. . . . . FIGITIDAE. . 10

10 "Pterostigma" present (Fig. 149), veins Rs, 2r-rs, 2r-sm, Rs&M and marginal cell all absent (Fig. 110). With 5-segmented maxillary palps but only 2-segmented labial palps. Antenna with 24 segments in male. . . . . PYCNOSTIGMATINI

- Without a pterostigma, veins Rs, 2r-rs, 2r-sm, Rs&M and marginal cell present at least as a trace. If with only 2-segmented labial palps then with 4-segmented maxillary palps. Antennae of male with 16 or less segments. 11

11 Pronotal carina complete (Fig. 62), from the ventral region on one side - across the dorsum to the ventral region on other side. Postgenal carina curved; bulbous

articulation and bridge absent; claws with fine basal spine; petiole with a collar ventrally and laterally but not dorsally. Parasites of Neuroptera . . . . . ANACHARITINAE

- Pronotal carinae indistinct (Fig. 67) or with a small lateral gap (Fig. 63), or present only as a developed dorsal plate (Fig. 65). Postgenal carina not markedly curved; bulbous articulation and bridge present; claws without a fine basal spine; petiole otherwise. Parasites of Diptera or Hyperparasites of Homoptera..12

12 Pronotal carinae indistinct (Fig. 67); mesonotum and scutelllum smooth and shiny (Figs 81, 82) (except *Lytoxysta*); vein area restricted to upper inner quarter of wing (Figs 116, 117). Larvae strongly chitinized. Hyperparasites of Homoptera via hymenopterous primary parasites. . . . . .CHARIPINI

- Pronotal carinae distinct (Figs 63, 65); mesonotum and scutelllum never completely smooth (Fig. 76); vein area not restricted to upper inner quarter of wing (Fig. 113). Larvae not strongly chitinized. Parasitoids of Diptera 13

13 Second gastral tergite saddle-shaped (Fig. 129); median mesoscutal line in the form of an inverted Y (Fig. 77). Ventral part of lateral pronotal carina separated from dorsal part by only a small gap (Fig. 63), dorsal part of pronotum not forming a pronotal plate. Scutellum with three strong carinae (Fig. 78); gonapophysis 9 without a cavity. . . . . ASPICERINAE

- Second gastral tegite not saddle-shaped; median mesoscutal line simple or absent. Dorsal part of lateral pronotal carina well separated from ventral part and forming, at least in part, a dorsal plate (Fig. 65). Scutellum without three strong carinae (Figs 82, 85); gonapophysis 9 with subapical cavity covered with a flap of chitin. 14

14 Scutellum without a tear-drop shaped plate (Fig. 80); suture line of hypostomal fusion present and long (Fig.

46); metapleuron without anteroventral cavity; maxillary palps 5-segmented labial palps 3-segmented; no junction visible between axillar bar and scutellum (Fig. 80); underside of petiole without narrow keel . . . . . .FIGITINI

- Scutellum with tear-drop shaped plate (Fig. 87); suture line of hypostomal fusion lost (Figs 47, 48); pubescent anteroventral cavity present on metapleuron (Figs 85, 88); maxillary palps 4-segmented labial palps 2-segmented; junction visible between axillar bar and scutellum (Fig. 86); Underside of petiole with a narrow keel. . . . . EUCOILINI

[N.B. The single specimen of the Thoreauellini is in such poor condition that it was not practicable to include this tribe in the key. See Chapter 5 for details of the features that are visible.]

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A comparative study of the structures of phylogenetic importance of female genitalia of the Cynipoidea (Hymenoptera)

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ABSTRACT. The structure of the female genitalia of the Cynipoidea is described, compared with that of other Hymenoptera and its method of operation discussed. The comparative morphology and the major evolutionary trends within the superfamily are discussed. Cynipoidea have two extraordinary modifications of the female genitalia: the ninth tergite is very long, narrow and centrally bisected so that it apparently forms an extra pair of ovipositor 'sheaths'; and the ovipositor is so elongate in some families that, in order to accommodate it within the gaster, it forms a complete loop.

Introduction

The Hymenoptera is the only order of holometabolous insects that has retained a primitive lepismatid form of ovipositor (Scudder, 1961; Chapman, 1969). In the most primitive hymenopterans, xyeloid sawflies (Rasnitsyn, 1980), the ovipositor is used by the female to place her egg precisely within or adjacent to a highly nutritious food source. For example, *Xyela* species oviposit amongst the microspores in the developing male sporophyll of gymnosperms. The possession of this form of ovipositor has been of major importance in the evolution and radiation of the order (Gauld & Bolton, 1988). In many symphytans the ovipositor is not only used to place an egg accurately, it serves a second function. This is the introduction of a 'venom', a secretion from one of the glands associated with the ovipositor, into the larval food source; this venom in some way modifies the substrate making it more suitable for larval development. For example, substances injected by some nematine sawflies initiate gall formation (McCalla *et al.*, 1962), whilst siricoids inject a venom which promulgates growth of a symbiotic fungus upon which the development of the siricid larva depends (Spradbery, 1973). Amongst the Apocrita, which generally use an animal larval food source, the ovipositor is of major importance. In various evolutionary lineages it has been modified in diverse ways. It may be used to obtain access to concealed hosts which are injected with a paralysing venom and then oviposited upon (e.g. as in the ichneumonid *Rhyssa*), to inject a host modifying venom (e.g. Fitton *et al.*, 1988), or to place an egg internally in a host in a position where it may escape encapsulation by host haemocytes (e.g. Salt, 1968; Van Veen, 1981). There are striking differences in the form and function of the ovipositor complex between different apocritan evolutionary lineages. However, these differences are little studied, thus have not been employed in attempts to resolve the phylogeny of the order.

The Cynipoidea is a large superfamily of Apocrita that contains worldwide about 4000 species. The group is perhaps best known because of the 'gall-wasps', the Cynipidae, which are phytophagous and cause galls on various angiosperms. Approximately 75% of

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European Cynipidae gall *Quercus* species (Askew, 1984). A few genera (e.g. *Synergus*) are inquilines in the galls of other cynipoid species. Also currently included in this family are two poorly known monogeneric subfamilies, the Austrocynipinae from Australia, and the Pycnostigmatinae from Africa.

The remaining families consist of koinobiont endoparasitoids (Askew & Shaw, 1986) of the immature stages of other insects. These families are much less well known than the 'gall-wasps', but they comprise the majority of the Cynipoidea. The Ibaliidae are large (at least 10 mm long) and are rare internal parasites of siricid wood wasp larvae (Hymenoptera: Symphyta: Siricidae) in timber (*Abies*, *Picea*, *Pinus* and *Larix*). The Liopteridae are also large (at least 7 mm long) and in general habitus are similar to the Ibaliidae. There are few host records for this very rare family which is probably associated with hosts living in trees (Diaz, 1973).

The other families contain much smaller species (often 2–4 mm long). The Figitidae consists of four subfamilies. The Figitinae are parasites of Diptera, often in carrion or dung. The Aspicerinae are mostly parasites of larvae or puparia of Syrphidae (Diptera). The Anacharitinae parasitize Hemerobiidae (Neuroptera) whilst the host of the Himalocynipinae (only one species from Nepal) is not known. The Eucoilidae are endoparasites of Diptera, they are figitid-like but have a characteristic 'cup' on the scutellum. Finally, the two subfamilies of Charipidae are very small (often 1–2 mm) and smooth. The Charipinae are parasites of Psylloidea and the Alloxystinae are hyperparasites of aphids via Aphidiinae (Hymenoptera: Braconidae) and Aphelinidae (Hymenoptera: Chalcidoidea).

These families, which show considerable biological diversity, are grouped together because they all have a laterally compressed gaster, and distinctive venation, with a triangular radial cell.

The families of the Cynipoidea are poorly defined and the limits of the various supragenetic taxa are interpreted differently by different authors. In most classifications (e.g. Weld, 1952; Quinlan, 1979) considerable taxonomic weight has been given to easily visible features of the female gaster such as shape, lengths of tergites, etc. These features all relate (as will be shown below) to the ovipositor complex. However, although a few papers describe the form of the genitalia of single, or a few related species (Chrystal, 1930; Wishart & Monteith, 1954; Frühauf, 1924), no study has investigated the comparative functional morphology in a wide range of species in the superfamily. This paper reports the investigation of a wide range of morphological variety within the superfamily; the method of operation of the cynipoid ovipositor is elucidated; and outgroup comparison is used to establish which forms are primitive. The evolutionary implications of the morphological variation are discussed.

Methods and Materials

Specimens were dissected initially with microscissors and pins and then with micropins mounted in matchsticks. Both dry and freshly collected specimens were softened in warm 10% potassium hydroxide and dissected in distilled water; however, dry specimens remained very brittle. For electron microscopy specimens were mounted on double-sided cellulose acetate tape. A fine micropin was then used to scrape up a small amount of glue from the tape and this was used to remove fibres (see Gibson, 1985). The genitalia were cleaned in Teepol in a durham tube which was placed in an ultrasonic cleaner. However, due to the fragility of the specimens, adequate cleaning was difficult. Specimens for optical microscopy were mounted on slides. Other specimens were gold coated with a sputter coater and examined either with an International Scientific Instruments 60A or a Cambridge 180 scanning electron microscope.

The species examined are listed in Appendix 1.

Terminology

Accounts of the general morphology of the hymenopterous ovipositor are given by King (1962), Scudder (1961), Smith (1969) and Snodgrass (1935). Unfortunately there is no consistency in their terminology – synonymic names are listed in Table 1. The latest terminology, that of Smith (1969, 1970), has been adopted here (although there is some doubt as to the exact embryonic origin of 'Gonocoxite 8').

TABLE 1. Synonymies of terminology used to describe the Hymenopterous ovipositor system

Snodgrass, 1935	Scudder, 1961	King, 1962	Smith, 1969
First valvifer	Gonangulum	Fulcral plate	Gonocoxite 8
Second valvifer	Second gonocoxa	Inner plate	Gonocoxite 9
First valvula	First gonapophysis	Stylet	Gonapophysis 8
Second valvula	Second gonapophysis	Stylet sheath	Gonapophysis 9
Third valvula	Gonoplac	Inner plate	Gonostylus
Ninth tergite	Ninth tergite	Outer plate	Ninth tergite

Review of the general morphology of the hymenopterous ovipositor

The plesiomorphic apocritan ovipositor system (for example that of many Ichneumonidae) consists of five basic elements (see Table 1; Fig. 1) which have been derived from the appendages of the eighth and ninth abdominal segments (Smith, 1969). These are both spatially and functionally associated intimately with tergite 9 which is generally fused with the reduced tenth tergite (Richards, 1977) (to form a so-called syntergite) and which posteriorly bears paired cerci (=pygostyles *sensu* Richards, 1977). Primitively the ovipositor has no system for retraction into the abdomen and when the ovipositor is long it pro-

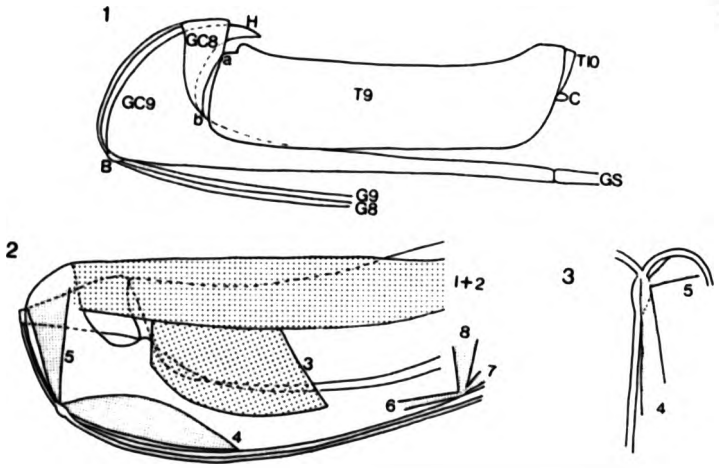


FIG. 1. Schematic diagram of apocritan ovipositor (based on *Venturia*: Ichneumonidae). B=bulbous articulation, GC9=gonocoxite 9, GC8=gonocoxite 8, GS=gonostylus, G9=gonapophysis 9, G8=gonapophysis 8, H=horn of gonocoxite 9, T9=tergite 9, T10=tergite 10, a=articulation of tergite 9 with gonocoxite 9, b=articulation of gonocoxite 8 with gonocoxite 9.

FIG. 2. Schematic diagram of the musculature of the cynipoid ovipositor. 1+2=upper+lower gonapophysis 8 protractors, 3=gonapophysis 8 retractor, 4=gonapophysis 9 depressor, 5=gonapophysis 9 levator; 6, 7 and 8 are respectively the anterior, posterior and superior gonastylus muscles.

FIG. 3. Dorsal view of the bulbous articulation to show orientation of the gonapophysis 9 depressor (4) and levator (5) muscles.

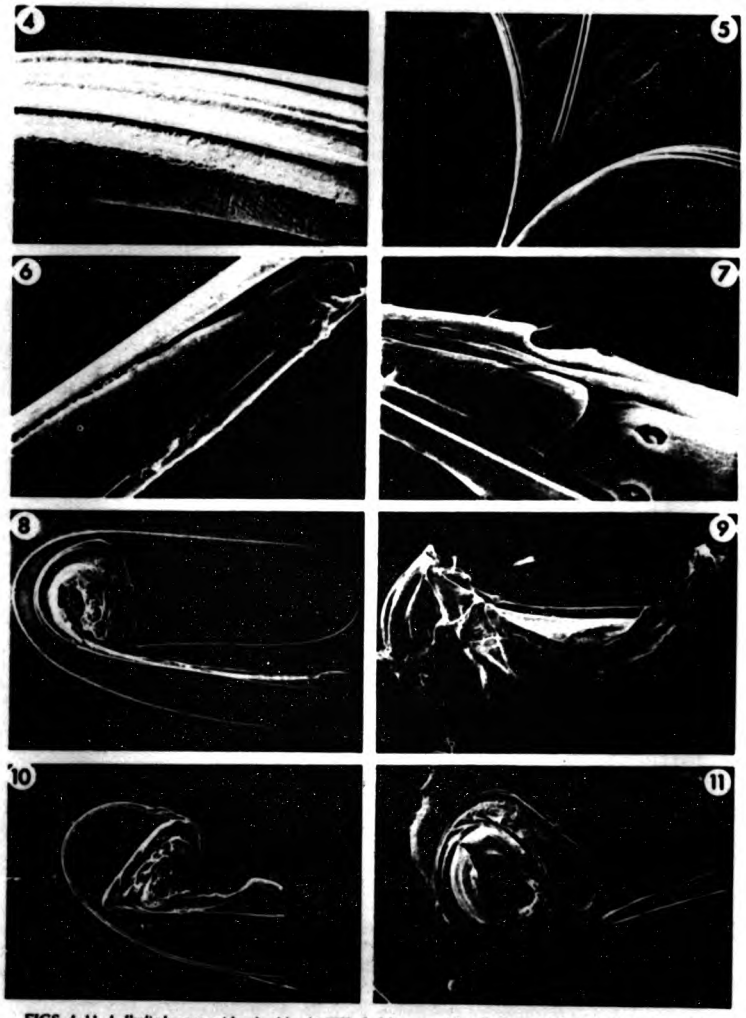
jects beyong the apex of the abdomen and is protected, at rest, by a sheath (Austin, 1983). GONOCOXITE 8 in a small, flat and almost triangular rocking plate (Figs. 9, 12) anteriorly it is fused to the base of gonapophysis 8 (Snodgrass, 1935). Its distal edge has two well-developed articulations (Figs. 27, 28), the upper with tergite 9 and the lower with gonocoxite 9 (Smith, 1969). Anteriorly the two sides of the genitalia curve into each other. GONOCOXITE 9 is large and elongate, centrally it is expanded to accommodate the muscles that are attached here and run to tergite 9 and to the bulbous articulation (Fig. 2) (Smith, 1969). Posteriorly gonocoxite 9 extends (Figs. 35) into the GONOSTYLUS (Scudder, 1961). Internally the two gonastyli are concave, they project backwards and form the sheath about the ovipositor but are deflected during oviposition (Chapman, 1969). The base of GONAPOPHYSIS 9 is attached to gonocoxite 9 at the BULBOUS ARTICULATION – this is a large ball and socket joint (Figs. 26, 28) which allows the shaft of gonapophysis 9 to pivot downwards and permits some degree of rotation (Copland & King, 1972). A dorsal ramus of gonapophysis 9 extends with gonapophysis 8 up to gonocoxite 8. GONAPOPHYSIS 8 meets with gonapophysis 9 immediately after the bulbus articulation at a complex structure, the BRIDGE (Fig. 29), at which the ninth gonapophyses are fused (Fulton, 1933). The anterior ramus of gonapophysis 8 lies in a shallow groove in the edge of gonocoxite 9 (Copland & King, 1972). There is a row of basiconic sensillae (Fig. 22) on gonapophysis 9 near the groove, these almost certainly monitor the degree of extension of gonapophysis 8 (Copland & King, 1972). The movement of gonocoxite 8 relative to gonocoxite 9 is monitored by an area of sensory pegs sited on gonocoxite 9 just below the articulation (Fig. 23). These spines are known from the Chalcidoidea (Copland & King, 1971, 1972) and are here recorded from the Cynipoidea, Braconidae and Proctotrupoidea, so it is likely that most if not all Apocrita have them.

The OVIPOSITOR is a hollow tube consisting of three parts (Fig. 5), the fused ninth gonapophyses (dorsal) and the two eighth gonapophyses (ventral) (Chapman, 1969). The components are crescent shaped in cross section and enclose the egg canal (Snodgrass, 1935). The parts can slide back and forth against one another without disengaging because of a 'tongue and groove' mechanism known as the olistheter (Smith, 1969). This mechanism consists of a pair of longitudinal ridges (termed rhachies) on the ninth gonapophyses (Fig. 4) which link with two grooves (aulax) one on each of the eighth gonapophyses (Fig. 5) (Smith, 1969). As the ovipositor system is comprised of separate sliding parts it may thus accommodate a degree of flexion and in some species even flex in use (Copland & King, 1972). Posteriorly orientated spines (the pectines) are located along the inside of the ovipositor valves, when the gonapophyses move back and forth these cause the egg to move along the ovipositor and into the host (Austin & Browning, 1981). The egg is often large [20 times the width of the ovipositor in the cynipid *Diplolepis rosae* (Bronner, 1985)] but the gonapophyses do not separate as the egg passes down the ovipositor. The egg membrane is distorted hydraulically and the cytoplasm flows within the membrane during passage down the ovipositor tube, it goes down stalk last (Fulton, 1933).

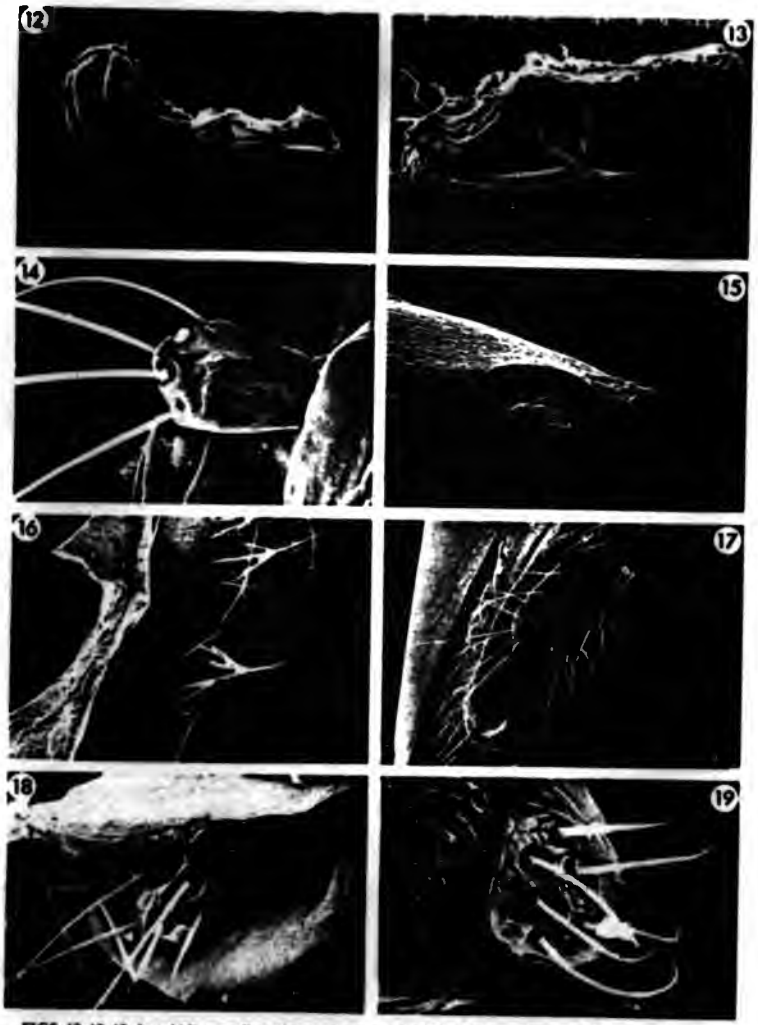
The ovipositor is moved by two opposing sets of muscles (Figs. 2, 3), a protractor (often massive) that extends from the anterodorsal end of gonocoxite 9 to the anterodorsal region of tergite 9 and a retractor set extending from the posteriordorsal apodeme on gonocoxite 9 to an internal ridge on the inside of tergite 9 (Snodgrass, 1935) Contraction of the protractor muscle moves tergite 9 forwards and downwards exerting pressure on gonocoxite 8 via the tergal/gonocoxite 8 articulation. Gonocoxite 8 pivots downwards about its articulation with gonocoxite 9 so that the anterior end is depressed and gonapophysis 8 slides along gonapophysis 9 until its apex projects beyond gonapophysis 9 (Smith, 1969). Contraction of the retractor muscle reverses this process, but since the apical teeth on gonapophysis 8 prevent its retraction, the net result is usually that gonapophysis 9 moves along gonapophysis 8 (Snodgrass, 1935).

General structure of the cynipoid ovipositor

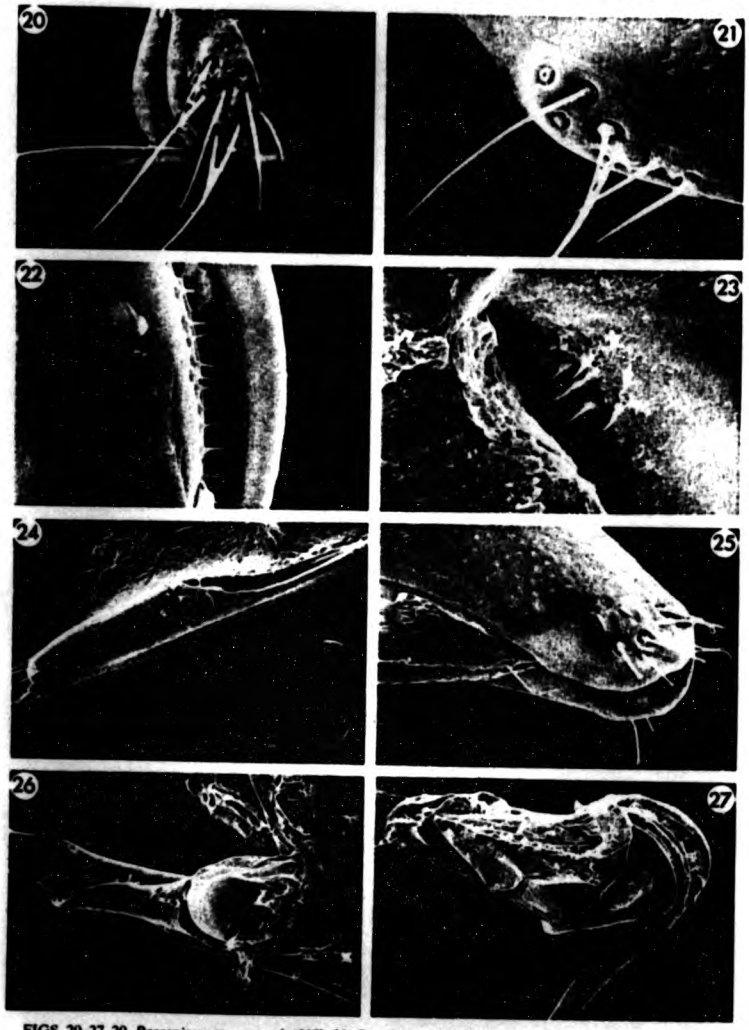
The above review shows that the general structure and function of the hymenopterous ovipositor is reasonably well understood. However, much of the detail is still to be resolved. The remainder of this paper shows, for the first time, the detailed structure of the cynipoid ovipositor characters and how these characters vary between different taxonomic groups.



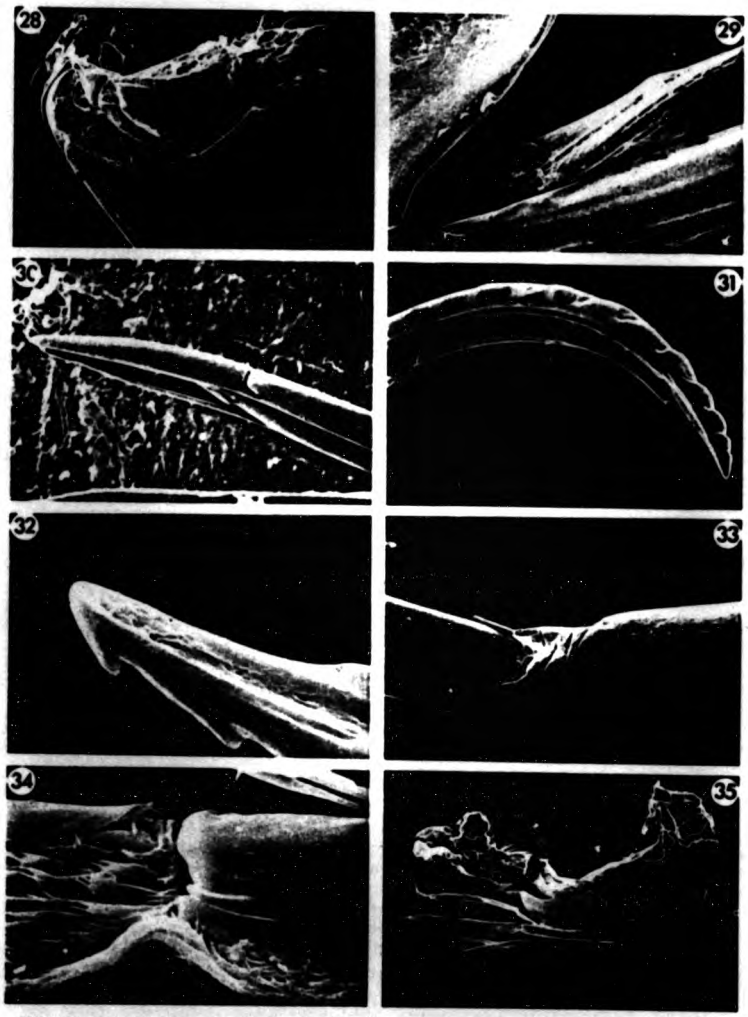
FIGS. 4–11. 4, *Ibalia leucospoides* rhachies (×600); 5, *I.leucospoides* olistheter (×140); 6, *Biorhiza pallida* ovipositor pores (×786); 7, *Melanips opacus* ovipositor teeth and sensillae (×2200); 8, *I.leucospoides* looped ovipositor (×9); 9, *Cynips quercusfolii* curved genitalia (×97); 10, *Figites anthomyiarum* elbowed ovipositor (×30); 11, *I.leucospoides* horn of gonocoxite 9 (×15).



FIGS. 12–19. 12, *Lonchidia maculipennis* curved genitalia (×153); 13, *Parapicrta* sp. fold in genitalia (95); 14, Cercus of a torymid (Chalcidoidea: Torymidae) (×1190); 15, *Isocolus rogenhoferi* tergite 10 and cercus (×190); 16, *Biorhiza pallida* cercus, tergite 9 and 10 (×220); 17, *Synergus* sp. tergite 9, 10 and cerci (×280); 18, *Aspicera scutellata* cercus (×930); 19, *Callaspidia defonscolombei* cercus (×870).



FIGS. 20–27. 20, *Paraspicera* sp. cercus (×660); 21, *Sarothrus areolatus* cercus (×730); 22, *Melanips opacus* sensory spines on horn (×870); 23, *Ibalia leucospoides* sensory spines near articulation (×550); 24, *I. leucospoides* tergite 9 (×80); 25, *Trybliographa rapae* sensory hairs on tergite 9 (×480); 26, *I. leucospoides* internal view of bulbous articulation (×80); 27, *Anacharis eucharioides* (×140).



FIGS. 28–35. 28, *C.defonscolombei* genitalia (×54); 29, *I.leucospoides* bridge (×90); 30, *Trybliographa rapae* apex of gonapophysis 8 (above) and gonapophysis 9 (below) (×350); 31, *Biorhiza pallida* apical teeth on gonapophysis 9 (×460); 32, *Melanips opacus* apex of gonapophysis 9 (×3100); 33, *Aulacidea hieracii* gonostylus fold (×480); 34, *Phaenoglyphis xanthochroa* gonastylus fold (×2200); 35, *P.xanthochroa* to show gonostylus (×140).

The cynipoid ovipositor is a thin structure [a small diameter is thought to lessen damage to the host (Austin & Browning, 1981)]. This delicate structure requires a degree of protection, so at rest it is invaginated within the gaster and methods of protraction and retraction have been developed. The base of the ovipositor tends to be in an anterior position. Tergite 9 is deeply bisected (from the anterior towards the posterior) (Fig. 24), the dorsal surface is limited to the distal extremity where it is retained to maintain the fulcrum between tergite 9 and tergite 8. The remainder of tergite 9 is retracted and less sclerotized; it is so long and thin and the dorsal separation so extended that, in most families, it looks like an extra pair of ovipositor 'sheaths' (Figs. 8, 24, 25, 28). Tergite 10 is fused with tergite 9. However, tergite 8 is always sclerotized and the system is not as delicate and membranous as that found in the advanced Proctotrupoidea, e.g. Diapriidae or Scelionidae. Gonocoxite 9 is elongate and almost vertical, it is the main element of the cynipoid ovipositor system and is expanded and curved upwards into a 'horn' (Figs. 9, 11, 12, 28), and moved anteriorly in order to accommodate an increase in the length of the ovipositor.

The apex of the ovipositor bears pores (Fig. 6), setae and sensory structures that are probably used to determine the suitability of the substrate for oviposition (Vinson, 1976). King & Fordy (1976) noticed peg-like structures and depressions with a central dome in the Cynipinae, van Lenteren (1972) found them in the eucoilid *Pseudeucoila*, and I have found these to be present in many other cynipoids (see e.g. Fig. 7, *Melanips opacus*). The terminal teeth protect these sense organs as the gonapophyses enter the host, and the structures probably flatten into their depressions to avoid damage on the return stroke. The dome-and-peg organs may have been evolved from articulating spines that have lost all but the base (King & Fordy, 1970).

In general terms the ovipositor of Cynipoidea is most like that of the Chalcidoidea (the two superfamilies were considered probable sister-groups by Königman, 1978). The ovipositor systems in both superfamilies have a similar curving of gonocoxite 9 into an anterior horn, and one chalcidoid family, the Eurytomidae, has gonocoxite 9 strongly curved dorsally, for example in *Eurytoma tibialis* it is curved through 160° and in *Sycophila* is curved through 230° (Copland & King, 1972). Many cynipoids have a strongly curved ovipositor and some (e.g. *Ibalia*, gonocoxite 9 curved through 270°, Fig. 11) have the gonapophyses forming a complete loop (Fig. 8) around the base of the sclerites. In both the Eurytomidae and the 'looped' cynipoids the gaster has become laterally compressed. One of the few proctotrupoids with lateral flattening is *Synopeas* (Platygastridae). I found that the ovipositor system of this genus curves round ventrally to become inverted. Thus the principle of coiling of the ovipositor is similar to that found in the Cynipoidea and Chalcidoidea but the coiling in *Synopeas* is in the opposite direction so that gonocoxite 8 is ventral to gonocoxite 9 instead of dorsal.

Another mechanism for accommodating a long, internal ovipositor occurs in the Proctotrupoidea. Most species of *Inostemma* (Platygastridae) and several scelionid genera (e.g. *Odontacolus*) extend a loop of the ovipositor into a horn-like protrusion from the first gastral segment. In *Inostemma* this horn can reach forwards beyond the head. In these species the gaster is often dorsoventrally flattened.

Musculature and function

The female genital musculature of the Cynipoidea consists of five main muscles (Figs. 2, 3). Muscle 1 [the upper protractor of gonopophysis 8] is attached along the upper ridge of tergite 9 and runs to the upper horn region of gonocoxite 9. Muscle 2 [lower protractor of gonapophysis 8] is a large muscle running from the main surface of tergite 9 to the central horn region of gonocoxite 9. The upper and lower protractors are difficult to distinguish in many Cynipoidea. Muscle 3 [gonapophysis 8 retractor] is a large muscle that runs from a ridge on gonocoxite 9 to the diagonal ridge on tergite 9. Muscle 4 [gonapophysis 9 depressor] attaches to the apex of the bulbous articulation and runs to the lower part of gonocoxite 9. Muscle 5 [gonapophysis 9 levator] runs from the anterior part of the bulbous articulation to the edge of the horn of gonocoxite 9. There is a small group of secondary muscles nearer the tip of the gaster (Fig. 3). Muscle 6 [anterior muscle of gonostylus], muscle 7 [posterior muscle of gonostylus] and muscle 8 [superior muscle of gonostylus] link the gonostylus to tergite 9 above, and give mobility to the gonostylus.

In *Neralsia* (Cynipoidea: Figitidae) the lower

fibres of muscle 2 form a muscular bundle which attach to gonocoxite 9 near the articulation of gonocoxite 8. This bundle is not a ligament of the whole muscle. In the Chalcidoidea [except Agaonidae and some Epichrysomallinae (Copland *et al.*, 1973)] a strong ligament, part of muscle 2, connects tergite 9 to the same point on gonocoxite 9. This ligament is not present in the Cynipoidae. Muscles 1 and 2 are discrete in chalcidoids but in the Cynipoidea they tend to form a broad band of fibres attaching down the horn from the apex to the mid horn region.

At the commencement of oviposition the female cynipoid lowers the gaster towards the substrate with the tip of the ovipositor slightly exposed. An upward movement of the anterior end of the hypopygium causes the external part of the hypopygium to pivot downwards (to the substrate) which together with an upward movement of the terminal tergites depresses the ovipositor and raises gonocoxite 9. The angular moment applied to the base of tergite 9 is limited by the distal edge of tergite 8. Gonapophysis 9 is depressed by the muscle (muscle 4) that reaches from the bulbous articulation to the mid-horn region of gonocoxite 9, and is opposed by a levator muscle (muscle 5) extends from the bulbous articulation to gonocoxite 9. These two muscles also act as a brace for gonapophysis 9. The first thrust of the tip of the ovipositor into the host is caused by a downward deflection of the abdomen, but movement of gonapophysis 8 on gonapophysis 9, produced by protractor (muscle 1 plus muscle 2) and retractor (muscle 3) muscles, produces further penetration. Contraction and relaxation of the muscles between tergite 9 and gonocoxite 9 control the rotational movement of gonocoxite 8 (the only muscle directly attached to gonocoxite 8 runs to tergite 8 and probably functions as a brace) about its pivot (the articulation with gonocoxite 9). This in turn moves gonapophysis 8 relative to gonapophysis 9. Thus gonocoxite 8 rocks on the stationary gonocoxite 9. Tergite 9 is virtually bisected into a pair of plates that are free to move independently of each other and as the rest of the system is bilateral, asynchronous movements of the two sides are used to push gonapophysis 8 deeper into the wound. The tip of gonapophysis 9 usually has 'teeth' (Figs. 31, 32) which not only cut but also help to maintain it in the wound, these teeth are small and do not prevent disengagement. Retraction of the ovipositor is achieved by reversing the procedure described above, and the genitalia and gastral segments are rotated back to the normal position.

Character states in cynipoid female genitalia

Before any phylogenetic assessment can be made it is essential to make a detailed examination of the character states of the cynipoid female genitalia.

Genitalia shape and position in gaster

To obtain access to the prospective host the cynipoid needs to penetrate the structure or substance within which the host resides. The morphological diversity of ovipositor systems reflects the diversity of substrata which have to be penetrated. There are three basic types of cynipoid ovipositor system which reflect the habits of the adult: type A is used to penetrate shallow plant tissue or animal tissue; type B, less accessible animal tissue; and type C, wood (or deep plant tissue).

Type A, curved genitalia. In this type the gonapophyses tend to be short and gonocoxite 9 is often only slightly curved (Figs. 9, 12, 28, 35). Even in the taxa with the longest ovipositors it can be accommodated by increasing the curvature of gonocoxite 9 rather than looping the ovipositor or moving the base forwards in the gaster as in type C (see below).

The mechanism of oviposition, in terms of gonocoxal movement, is illustrated by *Diplolepis* (Cynipidae). The gonocoxites are positioned near the apex of the gaster (in contrast to the anterior position in Ibaliidae, Liopteridae and Austrocynipinae) and they are angled upwards distally (e.g. Fig. 9). During oviposition the genitalia base is rotated downwards over 100° so that the gonapophyses emerge ventrally from near the centre of the gaster. The sternites telescope backwards on oviposition to allow the vertical thrust to be made.

The curved (type A) genitalia is the plesiomorphic condition of this character, and is similar to the genitalia of many parasitic Hymenoptera. Type A genitalia are found in the gall-wasps (Cynipidae) and in the parasitic cynipoids (Charipidae and most Figitidae) that oviposit directly into host insect tissue (or at most through a cocoon or aphid mummy). The

Cynipidae are the only family of the Cynipoidea not to deposit the egg in animal tissue, so oviposition is both through and into plant tissue. The eggs are deposited at or near the surface (most galls of Cynipidae are surface structures), so there is little requirement for a long ovipositor. Compared with the smaller parasitic Cynipoidea the Cynipidae are generally well muscled, this is presumably because they must penetrate relatively tough plant tissue rather than animal tissue. Like the Cynipidae the type A parasitic cynipoids have a short curved ovipositor which they use to stab at hosts that are at, or very near, the surface of the substrate. For example, the Anacharitinae parasitize exposed Neuroptera cocoons. The very small parasitic cynipoids of the Charipidae (Fig. 35) have the capsule in an apical position. In this family it is likely that the tergal muscles are capable of moving the capsule back and forth to some degree. This form of movement is found in some of the smaller Proctotrupoidea (s.l.) (e.g. Scelionidae, Diapriidae), and probably is only feasible in species with small capsules. As the capsule is apical, only a short movement is required for this mechanism to aid oviposition. The genera of the Anacharitinae and some Aspicerinae have a relatively small genital capsule that is also apical in position but in these taxa the ovipositor folds upwards in the middle so that when the ovipositor is exposed the proximal part of the capsule is aligned more vertically than horizontally (Fig. 13).

Type B, elbowed genitalia. The Eucoilidae, some Figitidae (e.g. *Figites*, *Neralsia*) and one cynipid (*Aulacidia hieracii*) have elbowed genitalia (Fig. 10). The gonocoxites are sharply curved, in some species almost to the proportions found in looped genitalia (see below) but the ovipositor does not have a complete loop. In the species with the longest ovipositors the shaft is expanded away from the elbow region so that it extends forwards to the petiole (the genital capsule occupies a posterior position). This type of genitalia provides a moderate increase in ovipositor length, without the need for looping, so that a medium depth of ovipositor penetration can be achieved.

Type C, looped ovipositor. The ovipositor is very long, the extra length is accommodated by moving the ovipositor base to the anterior region of the gaster, by the ninth gonocoxite being curved anteriorly (up to 270°) and by gonapophyses being coiled one complete turn around the basal gonocoxites (Figs. 8, 11). The curving of gonocoxite 9 and the looping of the ovipositor is a remarkable adaptation to keeping the extra length of the ovipositor contained within the gaster. This specialization is considered to be independent of the elbowed ovipositor (see Discussion).

Although the ovipositor is very long for a small hymenopteran, it is not long by the standards of the parasitic Hymenoptera as a whole, especially as the more primitive parasitica can have the ovipositor greatly extended externally. Townes (1975) surveyed the length of exposed ovipositors in the Apocrita. He found that the parasitic Hymenoptera seldom have an ovipositor longer than 1.3 times the length of the head plus body. He found that a few species had larger ovipositors, the longest were in the Braconidae – between 2.7 times and 7.7 times the total body length (see Achterberg, 1986). In the Cynipoidea the longest is the looped ovipositor of *Ibalia* (Ibaliidae), specimens were dissected, unwound and measured. The maximum exposable part of the *Ibalia* ovipositor is 1.5 times the length of the head plus body. If the total length of the ovipositor is measured then the ratio is 2 times. Thus the ovipositor of *Ibalia* is not excessively long, but is much longer than the gaster.

Oviposition in those Cynipoidea with a looped ovipositor requires that it be uncoiled in order to use the maximum shaft length. This is achieved by the intertergal muscles contracting and telescoping the tergites which tighten the loose coil of the ovipositor thus causing the ovipositor to protrude from the gaster. The inward telescoping of the tergites has a secondary effect in that it causes the gastral volume to be decreased and thus the hydrostatic pressure is increased, which assists ovipositor protrusion. This method of telescoping the gastral tergites is a fundamentally different mechanism to that found in many other parasitica, e.g. Ichneumonidae, where the gaster is extended during oviposition. In *Ibalia* the pointed tip of the hypopygium just enters the oviposition hole (made by the host's parent) and it guides the uncoiling ovipositor down the open boring.

Where the ovipositor is looped the central tergites (T4, T5 and T6) must be wide and able to telescope within one another so that the maximum available length of shaft can be uncoiled

during oviposition. This is most efficiently effected if the central tergites are the largest gastral tergites (in lateral view). In the Cynipoidea which do not have a looped ovipositor tergite 2 or 3 is the longest. Where the ovipositor is long its outer coil follows and indeed determines the contours of the gaster, also the greatest degree of lateral compression of the gaster occurs in the species with the most coiled ovipositors, so that in the most extreme example, *Ibalia*, the gaster is very flat, blade-like with sharp dorsal and ventral ridges.

The looped (type C) ovipositor is found in the Ibaliidae, Liopteridae, Austrocynipinae and one species of Figitidae. The long ovipositor enables parasitism of hosts living further from the surface than can be reached by most Cynipoidea ovipositors. In the Ibalidae and probably in the Liopteridae and Austrocynipinae the ovipositor penetrates through wood or deep plant tissue which may involve either drilling, or probing down pre-existing borings. The eventual object of oviposition is animal tissue, i.e. wood-dwelling larvae.

Sarothrus areolatus is the only species of Figitidae found to have a looped ovipositor like that of *Ibalia*. It also has, to a lesser extent, a similar lateral compression of the gaster and an expanded fourth gastral segment (although it retains the typical Figitinae gastral pattern with the second segment the largest). The hosts of *S areolatus* are anthomyid Diptera. The host larvae are found deep near the developing seed in lettuce flowers in the autumn, and they pupate in the soil. Presumably the extra long ovipositor of the parasite is needed to penetrate between the flowers or into the soil.

Tergite 10 and cerci

The cerci (=Pygostyles) are a pair of short articulating appendages which project from the apex of the gaster, they carry a tuft of sensory hairs, and are present in most parasitic Hymenoptera. In the more primitive taxa cerci occur on the tenth abdominal tergite but when tergite 10 is reduced or lost (many Chalcidoidea, e.g. *Torymus* (Fig. 14) and Proctotrupoidea) then the cerci are present on the ninth tergite. In the Cynipoidea the ninth tergite is mostly internal, and it was considered (Königsmann, 1978) that both tergite 10 and the cerci were lost. For most families this is true, but the Cynipidae retain a small area (Fig. 15) of tergite 10 [primitive] and the Cynipidae and certain Figitidae possess cerci or remnants of them (Figs. 15–21) [the plesiomorphic condition].

It is impossible to prove the exact origin of the depressed area of tergite that carries the cerci in Cynipidae. However, the fact that in some of the more primitive gall-wasps (e.g. *Isocolus*, Fig. 15) it is clearly a discrete piece of cuticle, strongly suggests that this area represents the last stage in the loss of tergite 10, where the lateral remnant of tergite 10 that bears the cerci has fused to the ventral margin of tergite 9 (any dorsal element of tergite 10 being lost earlier in this family). The depressed area is most unlikely to be an advanced feature (i.e. secondarily acquired) because the family Cynipidae shows a clear reduction sequence for both the area itself and the cerci from the most primitive to the most advanced taxa.

The cercus of Cynipidae is a raised ridge-like structure sited in a depressed area at the ventral margin, and near to the apex of tergite 9 (Figs. 15–17). The cerci in other Hymenoptera are upright cylindrical structures attached at the base (Fig. 14) but in the Cynipidae the cylinder lies along the tergite and is partially fused with it. The genera of the Cynipidae can be arranged in a series with respect to degree of cercus reduction and fusion with the tergite. This series corresponds with the phylogeny of Cynipidae genera, as established by Kinsey (1920). In the most primitive Cynipidae (e.g. *Isocolus*, Fig. 15) the cercus is still slightly raised at the apex but it becomes progressively more fused (*Phanacis*) and less distinct until it becomes a longitudinal ridge on the tergite (*Aylax* and *Aulacidea*) and the ridge progressively decreases in size (*Xestophanes*) until in the most advanced gall-formers it is virtually absent and the sensory hairs emerge directly from the tergite (*Cynips*, *Biorhiza*, Fig. 16). In *Diastrophus* the cerci are slightly more disc-like than cylindrical but this is a derived genus in other respects (Kinsey, 1920). Kinsey did not include the inquilfne genus *Synergus* in his study, but it has relatively well developed ridge-like cerci (Fig. 17) which indicates that it is not derived from the advanced gall-wasps (e.g. *Cynips*, *Andricus*).

Apart from the Cynipidae none of the other Cynipoidea examined have a remnant of tergite 10 present, but the taxa of two subfamilies of Figitidae, the Aspicerinae and Figitinae, have

cerci present on tergite 9. In *Aspicera* (Fig. 18) the cercus is vertical on the tergite, unlike the almost horizontal aspect of the cerci of the Cynipidae. The most developed cerci in the Figitidae were found in *Paraspicera* (Fig. 20) here they form a ridge raised from the tergite anteriorly but fused with the tergite along the posterior edge. The cercus has seven long sensory hairs. In *Aspicera* the cercus lies along the tergite and in *Prosaspicera* it is fused with the tergite. In *Callaspidia* (Fig. 19) the structure is slightly more dome shaped than a ridge. In the Figitinae a few genera related to *Melanips* show the last traces of cerci. In *Melanips* there is an irregular ridge with seven sensory hairs. If this is viewed obliquely and ventrally it is slightly raised off the tergite. In *Sarothrus* (Fig. 21) the seven hairs are mounted on a very slightly raised area and in *Lonchidia* (Fig. 12) the five remaining hairs emerge directly from the tergite. Several taxa of Liopteridae have sensory hairs with large basal depressions at the apex of tergite 9 and taxa from other families (e.g. *Trybliographa*, Eucoilidae; Fig. 25) also have long hairs on tergite 9, these hairs must represent the position of lost cerci.

Basiconic sensilla at gonocoxite 9 articulation

There is a small plate of sensory spines near the point of articulation of gonocoxite 8 with gonocoxite 9 (Fig. 23). These sensilla enable the cynipoid to locate the eighth gonocoxite relative to gonocoxite 9 and hence establish the position of its ovipositor. In the families of small parasitoids the ground-plan number of these sensilla is approximately 5 (examples: *Aspicera scutellata* 6, *Callaspidia defonscolombei* 6, *Anacharis eucharioides* 5, *Aegilips nitidula* 5, *Xyalaspis petiolata* 6, *Figites scutellaris* 5, *Melanips opacus* 8, *Neralsia rufipes* 5, *Phaenoglyphis xanthochroa* 5, *Pycnostigmus rostratus* 5). There are fewer sensilla in the smaller species such as those of the Eucoilidae (3 sensilla in *Eucoila crassinerva*, *Kleidotoma psiloides*, *Rhoptromeris heptoma* and 2 in *Trybliographa rapae*) and only 2 or less sensilla in the very small taxa, e.g. *Lonchidia maculipennis*, *Alloxysta macrophadna* and *Dilyta subclavata* (1 spine). The larger taxa, i.e. those with looped ovipositors, have more sensilla [a derived state] (*Oberthuerella lenticularis* 20, *Ibalia leucospoides* 26, *Mesocynips insignis* 19) but the equally large *Liopteron compressum* and *Paramblynotus punctulatus* (simple gonapophysis 9) have respectively only 7 and 5 sensilla. Thus the number of sensilla in this group appears not to be simply related to size, presumably the need for accuracy is also a significant factor affecting numbers of spines. The Cynipidae have a large number for their size, 14 in *Trigonaspis megaptera* and *Biorhiza pallida*, 17 in *Cynips quercusfolii* but only 5 in *Aulacidea hieracii*.

Marginal sensilla of gonocoxite 9

A series of basiconic sensilla occur along the anterior margin of the horn of gonocoxite 9 (Fig. 22), it is surmised that they monitor the movement of gonapophysis 8. The number of sensilla is approximately constant in any one species. The large cynipoids with looped ovipositors have the greatest number of sensilla, 30–59. Most gall-causers have 17–23 but *Biorhiza pallida* has the relatively high number of 35. The remainder of the parasitic species have between 10 and 22 with the exception of the very small

TABLE 2. The number of marginal sensilla found on gonocoxite 9 in selected species of Cynipoidea.

Ibalia leucospoides	50–52	*Oberthuerella lenticularis*	59
Liopteron compressum	48	*Mesocynips insignis*	54
Paramblynotus punctulatus	30	*Aspicera scutellata*	16
Callaspidia defonscolombei	22	*Anacharis eucharioides*	14
Aegilips nitidula	10	*Xyalaspis petiolata*	10
Figites scutellaris	20	*Neralsia rufipes*	17
Eucoila crassinerva	22	*Trybliographa rapae*	19
Kleidotoma psiloides	11	*Rhoptromeris heptoma*	11
Phaenoglyphis xanthochroa	9	*Pycnostigmus rostratus*	25
Aulacidea hieracii	18	*Cynips quercusfolii*	23
Trigonaspis megaptera	17	*Andricus ostreus*	21

species such as *Lonchidia maculipennis* and *Alloxysta macrophadna* with 6 and 5 respectively. Therefore the ground-plan number for most of the Cynipoidea is probably about 20. This number is reduced in the derived parasitic taxa, e.g. Charipidae and *Lonchidia*, and increased in the larger cynipoids, also derived. Examples of the number found in other Cynipoidea are given in Table 2.

Shape of tergite 9

Apart from a small exposed distal region the ninth tergite is internal in the Cynipoidea. The ninth tergite is virtually separated into two lateral components but these are united where the distal extremity of the tergite is exposed (Fig. 24). Each lateral element forms a long strap like structure, linking the articulation of gonocoxite 8 with the apex of the gaster. Tergite 9 is loosely attached distally to tergite 8, and a degree of flexion is possible. In the large [derived] Cynipoidea (Ibaliidae and Liopteridae) the ninth tergite is long and very thin (Fig. 24), the middle part having a lessened structural importance [agaonid chalcids have a similar membranous centre to tergite 9 (Copland & King, 1972)]. In other cynipoids the ninth tergite is shorter and broader (Figs. 9, 12, 13), the plesiomorphic condition.

Beyond the articulation with gonocoxite 8 and gonocoxite 9 there is a broad central region which has an internal flange running diagonally down from the upper articulation. This is the site of attachment for muscle 2, this ridge is very clear in strongly muscled species such as *Biorhiza pallida* but it is also present, although reduced, in species like *Ibalia* with long thin genitalia.

The distal section is not so broad, and it simply links the muscular section to the apex where the two lateral elements fuse. In the Anacharitinae the last section of tergite 9 is clearly downcurved [derived], the gonostylus is also downcurved because the genital capsule is sited close against the apical curvature of the gaster.

Ritchie & Peters (1981) have suggested that the tergites of *Diplolepis rosae* differ from the typical hymenopterous pattern. However, this is not so; the authors have evidently misinterpreted the gastral segmentation of this species. They overlooked the small sternites and so concluded that the hypopygium is composed of sternites 3–7 rather than the usual 5–7; they missed the spiracle on tergite 8, and confused part of tergite 9 with gonocoxite 9. Also they have erroneously subdivided abdominal tergite 9 at the point where it is folded, misinterpreting the distal part as an extra tergite – abdominal 10 (gastral 9). There is no tenth tergite in most cynipoids, and where one does occur in the microhymenoptera it is small and reduced.

Bulbous articulation and bridge

The bulbous articulation is a complex 'ball and socket' joint connecting gonapophysis 9 with gonocoxite 9 (Figs. 26, 28). It also provides processes for muscle attachment for muscles 4 and 5. It is a paired structure consisting of a lateral socket in each ninth gonocoxite which articulates with the basal rami of gonapophysis 9. The bulbous articulation is present [the plesiomorphic state] in all Cynipoidea except the Anacharitinae (Fig. 27), where the absence of this joint affects the whole structure of the ovipositor base. The two ninth gonocoxites unite basally and articulate laterally with a point on the inside of gonocoxite 9. This articulation is a simple hinge. The united part of gonocoxite 9 is raised as a fold of tissue. This fold forms the muscle attachment for the bulbous articulation. An analogous, although larger, structure, the 'spur', occurs in the Mymaridae (King & Copland, 1969), which is the only family of Chalcidoidea not having a bulbous articulation. As there is no bulb the ovipositor shaft is not so firmly held as it is in other cynipoids during oviposition. The bulbous articulation of some Aspicerinae (e.g. *Paraspicera*) is twisted to one side.

Just before the point where gonapophysis 9 joins with gonocoxite 9 at the bulbous articulation, gonapophysis 8 must disengage from gonocoxite 9 and continue on to gonocoxite 8. This point was termed the Bridge by Fulton (1933). In the Chalcidoidea this is a laminated structure composed of discrete vertical plates, but in the Cynipoidea laminations are not visible. The bridge is present (Fig. 29) [the plesiomorphic state] in all cynipoids except the Anacharitinae.

Apex of gonapophysis 8

In the Ibaliidae the eighth gonapophysis ends in a simple blade, in the Liopteridae the termina-

tion is simple, pointed (except *Paramblynotus* in which it is blunt) and the teeth have been lost. In most Cynipidae gonapophysis 8 is simple and rather blunt (Fig. 9), but in *Aulacidea hieracii* there are three widely separated short teeth. In *Pycnostigmus*, the Anacharitinae and the Charipidae gonapophysis 8 is simple and without teeth, although in *Dilyta subclavata* the apex is rather like a scimitar in shape. In the Eucoilidae, Aspicerinae and Figitinae there are teeth present (Figs. 7, 20, 30) [derived], usually there is a small apical tooth followed by a very large tooth. These teeth are not morphologically homologous with those of *Aulacidea*.

Apex of gonapophysis 9

In most cynipoids the apex of the ninth gonapophysis is armed with ridges (Fig. 32) [the plesiomorphic state]. The wood-drilling genera have stong teeth, for example *Mesocynips* (which probably bores into wood to attack Cerambycidae, see Diaz, 1973) has 8 strong and 2 weaker teeth, but *Ibalia* which exploits prebored holes has only 12 weak ridges present. Spradbery (1970) found that the breadth of the ovipositor was much less (approximately one third) than the width of the oviposition hole made by the host (*Sirex*) so in *Ibalia* the teeth on gonapophysis 9 are presumably used to cut through any debris in the tunnel. In *Paramblynotus punctulatus* (Liopteridae) gonapophysis 9 is blunt, rounded and untoothed, this presumably reflects the biology of *Paramblynotus*, which is more likely to be a woodprober than a wood-driller. *Liopteron compressum* has 11 teeth and *Oberthuerella lenticularis* has 14, the first 5 being large and sharp.

The gall-causers have strong teeth (Fig. 31), in order to penetrate woody plant tissue (generally oak). *Aulacidea hieracii* has 3 sharp teeth and *Cynips quercusolii* has 7 large teeth plus further ridges.

Most of the remaining parasitic cynipoids have small teeth on gonapophysis 9 (Fig. 32). The Aspicerinae (e.g. *Aspicera* and *Callaspidia*) have six equally spaced sharp teeth. The Anacharitinae have a similar number of more irregular teeth and the Charipidae have two or more very small teeth. However, the figitine genera *Figites* and *Neralsia* and all the Eucoilidae examined do not have exposed serrations on gonapophysis 9 (Fig. 30). In these taxa the gonapophysis is tapered to a sharp point that must be used for thrusting rather than for cutting. Just before the apex of the gonapophysis there is a deep cavity which is almost covered by a flap of chitin projecting from the proximal margin (Fig. 30). This cavity can be seen, through the thin flap of chitin, with transmitted light microscopy.

Junction of gonocoxite 9 with the gonostylus

Gonocoxite 9 of the Chalcidoidea and certain Proctotrupoidea s.l. is often divided by an articulation, the distal region forming the gonostylus, although this division is absent in the Eurytomidae and Mymaridae (Copland & King, 1972). No articulation exists in the Cynipoidea, and usually the division is not clearly indicated [the plesiomorphic state] but when visible it is an indentation (Figs. 33, 34). In the taxa with looped ovipositors (Ibaliidae, Liopteridae and Austrocynipinae) there is a continuous transition from gonocoxite 9 to the gonostylus, and in the Cynipidae a very slight bend is present (Fig. 33), in other families there is a some degree of indentation so that the gonostylus is indicated. This indentation is most marked in the Charipidae e.g. *Phaenoglyphis* (Figs. 34, 35). In most Figitidae the gonostylus is long and there is a distinct line across gonocoxite 9 (although it is barely visible in *Figites*). The indentation is poorly defined in the Eucoilidae.

In the Anacharitinae the gonostylus is angled downwards at this point (Fig. 13), and it is broad. In *Aspicera* (Aspicerinae) a ventral incision marks the short, distinct and downcurved gonostylus. In these taxa the genitalia are apical and so positioned that the proximal part is more vertical than horizontal when the ovipositor is exposed (Fig. 13). Compression, by the intertergal muscles, folds the middle of the capsule upwards and then decreases the angle subtended by gonocoxite 9 to the gonostylus until the ovipositor is exserted.

Shape of the gonostylus

In *Pycnostigmus* (Pycnostigmatinae) the apex of the gonostylus has a notch which is covered by a pubescent membrane [derived]. All other Cynipoidea examined have a simple, curved or slightly pointed apex to the gonostlus.

Austrocynips mirabilis (Austrocynipinae) has a unique, approximately globular, gonostylus. The gonostylus of all other taxa examined is long, thin and almost parallel sided.

Discussion

The structure of the ovipositor complex is only the first of several morphological systems that are being investigated as part of a phylogenetic study of the Cynipoidea. It would be premature to derive a phylogeny from the results of this investigation of a single system, but nonetheless this work has provided some surprising evidence about possible relationships within the superfamily.

The Ibaliidae and Liopteridae have genitalia modified in a remarkably similar manner. Both have the ovipositor looped and have a large number of sensillae on the horn of gonocoxite 9. *Austrocynips mirabilis*, the only representative of the Austrocynipinae (presently included as a subfamily in the Cynipidae), also exhibits these apomorphic features. All also have similar cuticular sculpture, suggesting that the Ibalidae + Liopteridae + Austrocynipinae may comprise a holophyletic group. There are no genitalic apomorphies shared by only the Austrocynipinae and other Cynipidae, so the placement of *Austrocynips mirabilis* within the Cynipidae is highly questionable.

Only one other looped ovipositor has been found in the Cynipoidea (in *Sarothrus areolatus*). In many other characters this species is typical of the Figitidae, so the looped ovipositor of this species is considered a separate specialization (convergence).

Initially I considered that the looped ovipositor could be derived from the elbowed ovipositor. However, the absence of a gonostylus fold in both the Cynipidae and the looped forms strongly suggests that this is not a simple transformation series and that the elbowed and looped forms are both independently derived from the curved type.

The Anacharitinae lack a bulbous articulation and bridge. These autapomorphies strongly support the holophyly of the subfamily.

Two distinct sets of genitalic specializations have been found in the Figitinae. Some genera near *Melanips* have both cerci on tergite 9 and teeth on gonapophysis 9 like the Aspicerinae, while genera near *Figites* have elbowed ovipositors and a covered orifice in gonapophysis 9 which suggests they are related to the Eucoilidae. I have not been able to find a single apomorphy supporting the holophyly of the Figitidae; the evidence available suggests this is an unnatural group.

The Charipidae show a reduction in 9 most other — acters so that it is not yet possible to assign them a position in the phylogeny with any degree of confidence, other than placing them among the small parasitic Cynipoidea with a distinct gonostylus.

The parasitic forms have lost all trace of tergite 10. This implies that the phytophagous family Cynipidae, which retains a remnant of tergite 10, is the most primitive of the Cynipoidea.

The presence, in *Aulacidea*, of tergite 10 and teeth on gonapophysis 9 shows that this genus is not closely related to the Eucoilidae, so the development of an elbowed ovipositor in both these taxa must be functional parallelism.

The evidence from the ovipositor characters divides the Cynipoidea into four major groups: the Cynipidae (which are primitive); the looped ovipositor group (Ibaliidae, Liopteridae and Austrocynipinae); the Anacharitinae; and the remaining parasitic taxa (which require further resolution).

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Appendix 1

List of cynipoid species examined

IBALIIDAE
Ibulia leucospoides Hochenwarth

LIOPTERIDAE
Oberthuerella lenticularis Saussure
Liopteron compressum Perty
Mesocynips insignis Cameron
Paramblynotus punctulatus Cameron

FIGITIDAE
Figitinae
Sarothrus areolatus Hartig
Lonchidia maculipennis Dahlbom
Melanips opacus Hartig
Figites anthomyiarum Bouché
Figites scutellaris Rossi
Neralsia rufipes Cameron
Aspicerinae
Aspicera scutellata Villers
Paraspicera sp.
Prosaspicera sp.
Callaspidia defonscolombei Dahlbom
Anacharitinae
Anacharis eucharioides Dalman
Aegilips nitidula Dalman
Xyalaspis petiolata Kieffer

EUCOILIDAE
Pseudeucoila sp.
Eucoila crassinerva Westwood
Trybliographa rapae Westwood
Kleidotoma psiloides Westwood
Rhoptromeris heptoma Hartig

CHARIPIDAE
Alloxysta macrophadna Hartig
Phaenogyphis xanthochroa Förster
Dilyta subclavata Förster

CYNIPIDAE
Pycnostigmatinae
Pycnostigmus rostratus Cameron
Austrocynipinae
Austrocynips mirabilis Riek
Cynipinae
Isocolus rogenhoferi Wachtl
Diplolepis rosae Linnaeus
Phanancis sp.
Aylax sp.
Aulacidea hieracii Bouché
Xestophanes sp.
Biorhiza pallida Olivier
Diastrophus rosae Linnaeus
Andricus ostreus Hartig
Cynips quercusfolii Linnaeus
Trigonaspis megaptera Panzer
Synergus sp.

TITLE A PHYLOGENETIC STUDY OF THE CYNIPOIDEA (HYMENOPTERA).

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