A phylogenetic analysis of higher-level gall wasp relationships (Hymenoptera: Cynipidae)

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Abstract. We present the most comprehensive analysis of higher-level relationships in gall wasps conducted thus far. The analysis was based on detailed study of the skeletal morphology of adults, resulting in 164 phylogenetically informative characters, complemented with a few biological characters. Thirty-seven cynipid species from thirty-one genera, including four genera of the apparently monophyletic Cynipini and almost all of the genera in the other tribes, were examined. The outgroup included exemplar species from three successively more distant cynipoid families: Figitidae (the sister group of the Cynipidae), Liopteridae and Ibaliidae. There was considerable homoplasy in the data, but many groupings in the shortest tree were nonetheless well supported, as indicated by bootstrap proportions and decay indices. Partitioning of the data suggested that the high level of homoplasy is characteristic of the Cynipidae and not the result of the amount of available phylogenetically conservative characters being exhausted. The analysis supported the monophyly of the Cynipini (oak gall wasps) which, together with the Rhoditini (the rose gall wasps), Eschatocerini and Pediaspidini formed a larger monophyletic group of gall inducers restricted to woody representatives of the eudicot subclass Rosidae. The inquilines (Synergini) were indicated to be monophyletic, whereas the Aylacini, primarily herb gall inducers, appeared as a paraphyletic assemblage of basal cynipid groups. The shortest tree suggests that the Cynipidae can be divided into three major lineages: one including the inquilines, the Aylacini genera associated with Rosaceae, and *Liposthenes*; one consisting entirely of Aylacini genera, among them *Aulacidea*, *Isocolus* and *Neaylax*; and one comprising the woody rosid gallers (the oak and rose gall wasps and allies), the *Phanacis-Timaspis* complex and the Aylacini genera associated with Papaveraceae.

Introduction

As currently understood, the family Cynipidae is entirely restricted to the phytophagous gall-inducing or gall-associated cynipoids, for which the vernacular name gall wasps is particularly apt. Gall wasps are small insects (2–8 mm long) that form spectacular galls on various plants. About 1360 species are currently known (Table 1), but Nordlander (1984) estimated the actual number to be between 3000 and 6000. Gall wasps mainly occur in the temperate areas of the Northern

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Hemisphere. A few species extend into the Northern Hemisphere tropics, but then probably only at high altitudes (Askew, 1984). The species *Adleria imitator* (Cameron) and *Andricus guatemalensis* (Cameron) have been recorded from Guatemala, and *Adleria championi* (Cameron) from both Guatemala and Panama (Dalla Torre & Kieffer, 1910). Four genera are endemic to the temperate parts of the Southern Hemisphere: *Rhoophilus* Mayr and an undescribed genus in South Africa (Mayr, 1881; personal observation), and *Eschatocerus* Mayr and *Paraulax* Kieffer in South America (Mayr, 1881; Kieffer, 1904; Diaz, 1980; personal observation). Other cynipids occurring in the Southern Hemisphere (Diaz, 1980; Naumann, 1991; personal observation) are obviously recent introductions as their host plants do not occur naturally in these areas. There are no cynipids indigenous to Australia.

Table 1. Overview of cynipid tribes. The Aylacini are paraphyletic (Ronquist, 1994), indicated here by quotation marks.

Tribe	Genera	Species	Host
'Aylacini'	21	156	Asteraceae, Rosaceae, Lamiaceae, Papaveraceae, Apiaceae, Valerianaceae, Brassicaceae
Cynipini	44	974	Fagaceae (mostly *Quercus*)
Eschatocerini	1	3	*Acacia, Prosopis* (Fabaceae)
Pediaspidini[1]	2	2	*Acer* (Aceraceae)
Rhoditini[2]	2	63	*Rosa* (Rosaceae)
Synergini	7	170	Inquilines in galls induced by *Diastrophus, Diplolepis* and Cynipini

[1]Including the genus *Himalocynips* Yoshimoto.
[2]Including the genus *Liebelia* Kieffer.
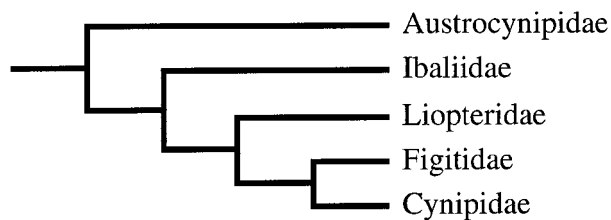
Fig. 1. Higher-level relationships of the Cynipoidea according to the analysis of Ronquist (1995b).

The gall wasps belong to the parasitic wasp superfamily Cynipoidea and apparently evolved from ancestors parasitizing endophytic insect larvae (Ronquist, 1995b). Higher-level relationships in the Cynipoidea have been analysed by Ronquist (1995b: Fig. 1). The sister group of the Cynipidae is the Figitidae (*s.l.*), a diverse family consisting of species parasitic on Neuroptera, Hymenoptera and Diptera larvae in various microhabitats. Austrocynipidae, Ibaliidae and Liopteridae, the other lineages in the Cynipoidea, are less speciose; the members are parasitoids of woodboring or coneboring insect larvae belonging to the orders Coleoptera, Hymenoptera and Lepidoptera.

The Cynipidae almost certainly form a monophyletic group, although the only known unique synapomorphy for members is the phytophagous habit, and even in this case there is some uncertainty because of missing biological data for a few figitids reared from galls (Ronquist, 1994). Ronquist (1995b) listed two additional morphological synapomorphies for cynipids, the open marginal cell and the lack of a lateral pronotal carina, but both characters show secondary reversals within the Cynipidae and parallel occurrences in the Figitidae. The present analysis adds six more morphological synapomorphies for cynipids that, despite some homoplasy, strengthen the hypothesis of monophyly.

Several subfamilies were previously recognized in the Cynipidae, but recent work has shown that only one subfamily, the Cynipinae, properly belongs there (Ronquist, 1995b). The Cynipinae are currently separated into six tribes (Table 1; Nieves-Aldrey, 1994; Ronquist, 1994, 1995b), partly based on morphology and partly on biology. The Synergini are inquilines which cannot induce galls on their own but develop inside the galls of other cynipids. They evolved from gall-inducing ancestors and the inquiline larva has apparently maintained the phytophagous habit (Ronquist, 1994, and references cited

therein). Members of the five remaining tribes are gall inducers. Two tribes are speciose: the Aylacini, mainly including herb gallers, and the Cynipini, the oak gall wasps. The three other tribes contain only one or two genera each (Table 1).

A species which has been difficult to place is *Himalocynips vigintilis*. It was originally placed in a monotypic subfamily of the Figitidae (Yoshimoto, 1970; Quinlan, 1979), but the subfamily was later moved to the Cynipidae (Nordlander, 1982; Ritchie, 1984, 1993; Kovalev, 1994) and Fergusson (1990, 1995) raised it to separate family status. None of these classifications were well supported by critical phylogenetic analyses. Ronquist (1995b) recently placed *H. vigintilis* in the cynipid tribe Pediaspidini, and we are able to confirm this placement in the present study.

No complete revision of the Cynipidae has been accomplished since Dalla Torre & Kieffer's (1910) monograph and Weld's (1952) generic revision primarily based on type species of genera. Many of the genera recognized by Weld are likely to be paraphyletic or even polyphyletic. However, Nieves-Aldrey (1994) recently revised the west-European genera of Aylacini, about three-quarters of the world genera and one third of the world species in the tribe, and managed to split many of the heterogeneous genera into apparently natural groups. Most of the obviously problematic genera that now remain belong to the Cynipini, with some notable exceptions such as the Aylacini genera *Aulacidea* and *Aylax*.

There are only two previous studies of higher-level relationships in the Cynipidae. Kinsey (1920) studied inter- and intrageneric variation for three morphological and four biological characteristics of gall wasps (excluding inquilines) and arrived at a phylogenetic hypothesis based on intuitive evaluation of the results (Fig. 2a). He considered the oak gall wasps, Cynipini, to be monophyletic and closely related to the rose gall wasps, Rhoditini. Cynipini and Rhoditini, in his opinion, together formed an apomorphic offshoot from a paraphyletic Aylacini. Ronquist (1994) recently presented a parsimony analysis of higher-level cynipid relationships based on 108 skeletal characters of adults coded for twelve exemplar species (Fig. 2b). The results of this analysis are in line with those of Kinsey (1920) concerning the origin of the Cynipini and Rhoditini from the Aylacini, but there is considerable disagreement on relationships among Aylacini genera; note, e.g. the different positions of *Diastrophus* and *Phanacis* (Fig. 2). Ronquist's (1994) analysis also included inquilines (Synergini),
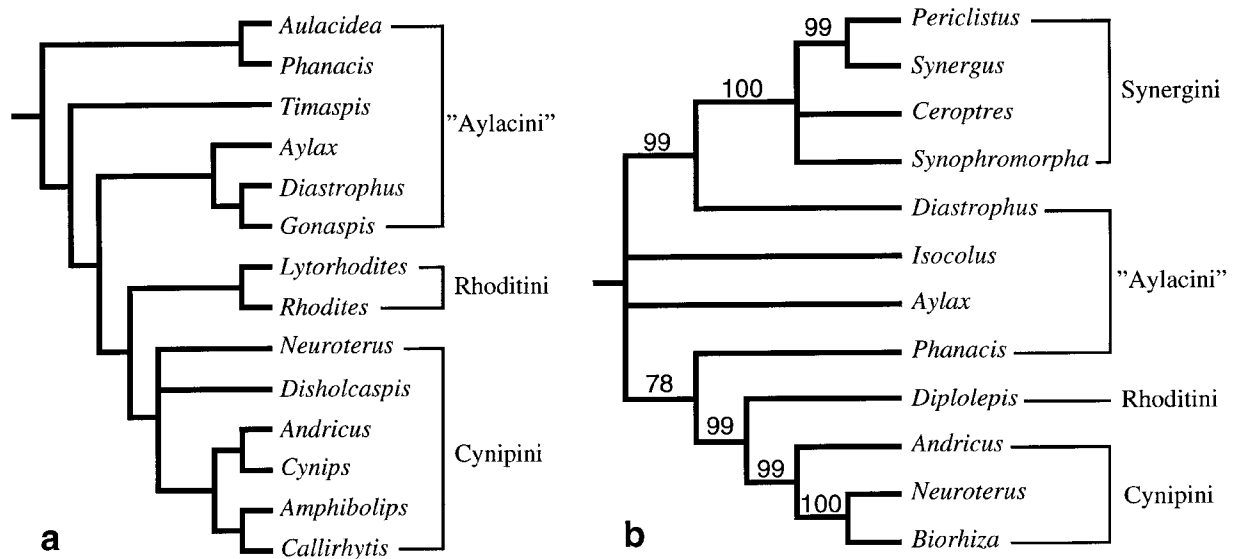
Fig. 2. Proposed hypotheses of higher-level relationships in the Cynipidae. Current classification of the Cynipidae indicated to the right of each hypothesis. a, Analysis of Kinsey (1920) based on intuitive evaluation of variation in three morphological and four biological characters. *Rhodites* and *Lytorhodites* are now considered synonyms of *Diplolepis*. b, Parsimony analysis of Ronquist (1994) based on 108 skeletal characters of adults coded for twelve exemplar species. The numbers on the branches are bootstrap proportions. *Phanacis* refers to a species currently included in *Timaspis* (*T. phoenixopodos*; cf. Nieves Aldrey, 1994).

and indicated that they form a monophyletic group which had a separate origin from gall inducers in the Aylacini.

In this paper we present the most comprehensive phylogenetic analysis of higher-level relationships in the Cynipidae conducted thus far, basically being an expansion of the study of Ronquist (1994). The analysis was primarily based on the skeletal morphology of adults, as this is the only significant source of data readily available for many of the problematic taxa. Like Ronquist (1994), we selected a limited number of representative species and studied their morphology in detail, rather than study a few characters in a comprehensive sample of species. Simulations indicate that the former strategy is more efficient in inferring higher-level relationships, provided that the exemplars are chosen correctly (see below and Ronquist, unpublished observations). The sample in the current analysis included representatives from almost all genera in all tribes of the Cynipidae except the Cynipini. The Cynipini are speciose and diverse, but share some critical, apparently apomorphic, features, including a narrow pronotum, a prominent hypopygial spine, alternation of generations and an association with Fagaceae. They were considered a natural group by Kinsey (1920) and this was supported by Ronquist (1994). Therefore, we consider it likely that Cynipini form a monophyletic entity, and only included four exemplars in our analysis. In contrast, we sampled the problematic tribe Aylacini rather comprehensively. The present analysis also included a wider selection of outgroup taxa (from the Figitidae, Liopteridae and Ibaliidae) than the single species from the distantly related Ibaliidae (cf. Fig. 1) studied by Ronquist (1994). The results of the analysis will serve as the basis for a study

of phylogenetic patterns in the evolution of gall wasps (Ronquist & Liljeblad, unpublished observations).

Materials and methods

Terminology

Terms for skeletal features follow Ronquist & Nordlander (1989) and Ronquist (1995a). Surface-sculpture terminology is from Harris (1979), except that 'glabrous' and 'glabrate' are used to describe surface texture, regardless of the presence or absence of pubescence.

Selection of exemplars

An optimal sample of exemplars for studies of higher-level relationships should maximize the diversity in the sample and minimize the effect of long branch attraction by inclusion of archaic species (Yeates, 1995; Ronquist, unpublished observations). To maximize diversity, we selected representatives from all cynipid tribes and from many different genera, particularly in the heterogeneous tribe Aylacini, where we managed to obtain material of all currently recognized genera except *Parapanteliella* and *Zerovia*. For large and structurally diverse genera, such as *Aulacidea* and *Phanacis*, we included several exemplars. To find archaic representatives of larger groups, we used 'indicator' characters. Thus, we included *Plagiotrochus* as one of the Cynipini exemplars because, unlike most other

Table 2. Ingroup (Cynipidae) and outgroup (Figitidae, Liopteridae and Ibaliidae) taxa studied. Explanation of abbreviations: SM = specimens studied with stereo microscopy only, without preparation; CM = specimens dissected, studied with stereo and compound microscopy; SEM = specimens dissected, studied with stereo, compound and scanning electron microscopy; FR/JL = authors' collection; BMNH = The Natural History Museum, London; CNCI = Canadian National Collection of Insects, Ottawa; MNCN = Museo Nacional de Ciencias Naturales, Madrid; NHMV = Naturhistorisches Museum, Vienna; ZMLU = Museum of Zoology, University of Lund; ZMAS = Zoological Museum, Academy of Sciences, St. Petersburg.

Higher taxon	Species	Material	Preparation	Depository
Cynipidae				
Synergini	*Synergus crassicornis* Curtis	6♀/3♂	SEM	FR/JL
	Periclistus brandtii (Ratzeburg)	6♀/3♂	SEM	FR/JL
	Ceroptres clavicornis Hartig	6♀	SEM	FR/JL
	Synophromorpha rubi Weld	6♀/3♂	SEM	FR/JL
'Aylacini'	*Xestophanes potentillae* (Retzius)	6♀/3♂	SEM	FR/JL
	Diastrophus turgidus Bassett	6♀/3♂	SEM	FR/JL
	Gonaspis potentillae (Bassett)	6♀/3♂	SEM	FR/JL
	Liposthenes glechomae (Linnaeus)	6♀/1♂	SEM	FR/JL
	Aulacidea kerneri (Wachtl)	2♀	SM	MNCN
	Cecconia valerianellae (Thomson)	4♀	SM	MZLU
	Antistrophus pisum Ashmead	4♀	CM	FR/JL
	Rhodus oriundus Quinlan	3♀/2♂	SM	BMNH
	Hedickiana levantina (Hedicke)	2♀/2♂	SM	BMNH
	Neaylax salviae (Giraud)	2♀	CM	FR/JL
	Isocolus rogenhoferi Wachtl	6♀/3♂	SEM	FR/JL
	Aulacidea tragopogonis (Thomson)	6♀	SEM	FR/JL
	Aulacidea phlomica Belizin	1♀	SM	ZMAS
	Aulacidea verticillica Belizin	1♀	SM	ZMAS
	Vetustia investigata Belizin	1♀	SM	ZMAS
	Panteliella fedtschenkoi (Rübsaamen)	2♀/1♂	SM[1]	ZMAS/NHMV
	Barbotinia oraniensis (Barbotin)	6♀/3♂	SEM	FR/JL
	Aylax papaveris (Perris)	6♀/3♂	SEM	FR/JL
	Iraella luteipes (Thomson)	2♀	CM	FR/JL
	Timaspis phoenixopodos Mayr	6♀/3♂	SEM	FR/JL
	Phanacis hypochoeridis (Kieffer)	6♀	SEM	FR/JL
	Phanacis centaureae Förster	6♀	SEM	FR/JL
	Phanacis phlomidis Belizin	1♀	SM	ZMAS
	Asiocynips lugubris Kovalev	1♀	SM	ZMAS
	Asiocynips pannucea Kovalev	1♀	SM	ZMAS
Eschatocerini	*Eschatocerus acaciae* Mayr	6♀/3♂	SEM	FR/JL
Rhoditini	*Diplolepis rosae* (Linnaeus)	6♀/1♂ [2]	SEM	FR/JL
Pediaspidini	*Himalocynips vigintilis* (Yoshimoto)	2♀	SM	CNCI
	Pediaspis aceris (Gmelin)	6♀/3♂	SEM	FR/JL
Cynipini	*Plagiotrochus fusifex* (Ratzeburg)	6♀/3♂	SEM	FR/JL
	Andricus quercusradicis (Fabricius)	6♀/6♀̄/3♂	SEM	FR/JL
	Neuroterus numismalis (Fourcroy)	6♀̄	SEM	FR/JL
	Biorhiza pallida (Olivier)	6♀/3♂	SEM	FR/JL
Figitidae	*Euceroptres montanus* Weld	6♀/3♂	CM	FR/JL
	Undescribed genus[3]	1♀/1♂	SM	FR/JL
Liopteridae	*Paramblynotus zonatus* Weld	3♀/1♂	CM	FR/JL
Ibaliidae	*Ibalia rufipes* Cresson	6♀/3♂	SEM	FR/JL

[1]Male (from ZMAS) studied only with stereo microscopy without preparation, females (from NHMV) in old poor-quality whole-body preparations on microscope slides allowing examination of some characters with compound microscopy.
[2]Male of *Diplolepis* belonging to *D. centifoliae* (Hartig).
[3]Referring to *Aulacidea nigripes* Barbotin (cf. Ronquist, 1994).

oak gall wasps, the members gall evergreen, apparently archaic oaks (Wanntorp, 1983), and *Synophromorpha* as one representative of the Synergini because it resembles some Aylacini gall inducers. All in all, the analysis comprised thirty-seven cynipid species from thirty-one genera (Table 2).

We used representative species from the Figitidae, Liopteridae and Ibaliidae as outgroups. In the Figitidae, we studied two species of figitoid inquilines, a group of apparently archaic, cynipidlike figitids associated with galls (Ronquist, 1994, 1995b). We avoided including more derived figitids because

they are likely to have lost many of the ground-plan characters of the Figitidae. In the Liopteridae and Ibaliidae, our choice of exemplars was mainly determined by the availability of suitable material for dissection.

Study techniques

Most specimens were killed and preserved in 70% ethanol; dried specimens were transferred to 70% ethanol at least one week before preparation. Head, mesosoma, metasoma, antennae, legs and wings were separated from each other and cleaned overnight in concentrated NH_3 diluted with an equal volume of water. After cleaning, the body parts were transferred to absolute ethanol through a series of ethanol dilutions and then to acetone, before being air-dried and mounted in different angles to make all surfaces visible. Specimens for stereo microscopy were glued on cardboard; specimens for scanning electron microscopy (SEM) were mounted on stubs by means of carbon tape and coated with gold prior to examination. Mouth parts, genitalia and hind tarsi were macerated in 10% KOH after dissection and mounted in Euparal on microscope slides. Micrographs were taken from these and from SEM specimens for convenient comparison of species. Drawings were made from micrographs or with a tracing device fitted to a stereo microscope.

External skeletal structures were studied on the female head, antennae, mouthparts, mesosoma, wings, legs, metasoma and genitalia and on the male antennae, metasoma and genitalia. Some additional internal skeletal structures of the female head and metasoma and the male metasoma were studied by dissection under a stereo microscope. Most species were studied using all techniques described above but, due to lack of material, eighteen species could not be studied using SEM and thirteen of these could not be dissected (Table 2). In the case of *Panteliella*, we only had access to one male specimen mounted on a piece of cardboard and two old, poor-quality preparations of females on microscope slides.

Character coding

Many of the characters in the present study are from Ronquist (1994) and a few from Ronquist (1995b), but all characters and character states were re-examined for this study. Seventy-eight character definitions were taken directly from Ronquist (1994) and eight from Ronquist (1995b). Twenty-three characters were modified from Ronquist (1994) and an additional fifty-seven are entirely new, as noted in the character list (Appendix 1). Qualitative differences were coded for analysis, but only when potentially informative about phylogenetic relationships, i.e. autapomorphies were not included. Morphometric measurements were only used as an aid in describing character states. Unless suitable material was lacking, characters were coded after studying at least two specimens of each species. In a few instances the state differed among the specimens examined, in which case more specimens were studied and the species coded for the state present in the

vast majority of specimens. This 'majority coding' compares favourably with alternative schemes of coding polymorphisms (Wiens, 1995). Members of both Cynipini and Pediaspidini have alternating sexual and parthenogenetic generations with more or less distinct morphological differences between the females of different generations. Except for *Neuroterus numismalis* (only agamic females) and *Andricus quercusradicis* (both generations), only sexual females were used because they appear generally to retain more plesiomorphic character states than parthenogenetic females. When the states of the sexual and agamic females of *A. quercusradicis* differed, the species was coded as being polymorphic. Male specimens were not available for all species (Table 2). For *Diplolepis*, female data were taken from *D. rosae* and male data from *D. centifoliae*. Some missing data on male flagellomere numbers (character 47) were taken from literature as noted in the character list (Appendix 1). For a few characters, the state observed in the outgroup exemplars differed from that indicated to be ancestral for the Ibaliidae or the Liopteridae in the comprehensive phylogenetic analyses of those families by Ronquist (1995a, 1995b). To increase the precision of the analysis, the outgroups were, in these cases, coded for the hypothesized ancestral state of the higher-level taxon they represented, rather than for the observed state in the exemplar, as noted in the character list (Appendix 1). Multistate characters were coded as ordered if the states appeared to form a natural sequence (morphocline), otherwise they were left unordered. The character matrix (cf. Table 3, Appendix 1) is available from F.R.'s homepage (www.systbot.uu.se/staff/f_ronquist.html).

Phylogenetic analysis

Heuristic parsimony analyses were carried out using PAUP version 3.1.1 (Swofford, 1993) and the resulting trees were examined with MACCLADE version 3.05 (Maddison & Maddison, 1992). Hennig86 version 1.5 (Farris, 1988) and NONA version 1.1 (Goloboff, 1993) were used to check the results obtained with PAUP. Bootstrap values were computed using PAUP and decay indices using PAUP in combination with AUTODECAY version 3.0 (Eriksson & Wikström, 1995). Polymorphisms were treated as such in calculation of tree lengths (terminal steps included).

Results and discussion

Phylogenetic analysis

The morphological study resulted in a set of 166 characters with a sum of minimum possible lengths of 239 and a sum of maximum possible lengths of 1690 (cf. Appendix 1, Table 3). Heuristic search of this data set with PAUP (options in all searches unless otherwise stated: simple stepwise addition with reference taxon *Synergus*, tree bisection-reconnection swapping, collapse zero-length branches enabled, steepest descent not in effect) produced one minimum-length tree (Figs 3, 4), and a more exhaustive heuristic search (1000

replicates of random stepwise addition) failed to produce any additional trees of equal length or shorter. The tree had a length of 821, an ensemble consistency index (CI) of 0.29 and an ensemble retention index (RI) of 0.60. The tree was consistent with the relationships among outgroups indicated by the analysis of Ronquist (1995b; cf. Fig. 1), and was rooted accordingly. A listing of unambiguous character state changes on the branches of the shortest tree is given in Appendix 2. Running the data set in Hennig86 (m*;bb* and tr;bb*) and in NONA (mswap*2 on the shortest tree from PAUP) resulted in the same minimum-length tree as in the original analysis. Successive weighting (in PAUP) according to the character consistency indices or retention indices did not change the tree topology, but two small changes occurred when using the character rescaled consistency index: *Aulacidea kerneri* and *Diastrophus turgidus* were each placed one internode closer to the root compared with the unweighted tree. This slightly different tree had a length of 825 after reweighting all characters back to one.

Bootstrap proportions (Fig. 3) were calculated from 1000 replications of the analysis. Decay indices (Fig. 3) were calculated for each internode separately by constrained heuristic searches (five replicates of random stepwise addition).

The mean number of changes among alternative character optimizations was obtained for each branch in the tree using MACCLADE (Fig. 5). Note that the lengths of the terminal branches represent minimum estimates, because autapomorphies were not included in the analysis. Furthermore, branch lengths may be underestimated in some parts of the tree, particularly in the *Isocolus-Neaylax* group, because some terminals had a large proportion of unknown states.

To examine the influence of taxa with many entries unknown in the character matrix, we excluded the thirteen taxa that we could only study with stereo microscopy without preparation (marked SM in Table 2) from the analysis, which was otherwise run as before. This pruning of the matrix resulted in a reduction from 11.1% to 1.5% cells with missing data. The pruned matrix had a sum of minimum possible lengths of 232 and a sum of maximum possible lengths of 1323. The analysis resulted in one minimum-length tree of length 669 steps (Fig. 6), a CI of 0.35 and a RI of 0.60. The topology was completely congruent with the original tree. The bootstrap proportions were generally higher than in the original analysis, but five clades still occurred in less than 50% of the bootstrap replications (Fig. 6).

Homoplasy and the reliability of the results

There is considerable homoplasy in the cynipid data. The CI for the full analysis (0.29) is well below that expected for data sets with forty-one taxa according to the polynomial regression analysis of Sanderson & Donoghue (1989) on empirical data (expected value 0.36), although it is comparable with the levels observed in another study of the relationship between CI and the number of taxa in real data sets (Archie, 1989; see also Klassen *et al.*, 1991). The large number of missing entries in the complete analysis (Fig. 3) could have inadvertently increased the CI value; on the other hand, the

number of characters is large compared to most other studies of the same size, which could have decreased the value (Klassen *et al.*, 1991). The restricted analysis (Fig. 6), which had very few missing entries, had a CI of 0.35 for twenty-eight taxa; this is even further away from the expected value of 0.45 in the polynomial regression of Sanderson & Donoghue (1989) but still within the range of values reported by Archie (1989).

Despite the high level of homoplasy, it is obvious that the data exhibit a distinct hierarchical structure. Both the full and the restricted analysis have CI values significantly above those expected from randomized or permuted data sets (Archie, 1989; Klassen *et al.*, 1991). The high bootstrap proportions for many groupings also show that there is a clear phylogenetic signal, although the power of the signal is very unequally distributed among groups. Unfortunately, many of the basal branchings in the family are poorly supported (Figs 3, 6).

To further examine the nature of the homoplasy in the dataset, we partitioned the characters into those that were adopted with or without changes from earlier studies (old characters) and those that were original to the current analysis (new characters). The two biological characters were omitted from these comparisons. There was only a marginal difference in the ensemble consistency and retention indices on the shortest tree between the new and old characters (CI = 0.26 and 0.30; RI = 0.56 and 0.61, respectively). The mean character consistency index was lower for the new characters (0.37 compared to 0.46; *t*-test, $P = 0.053$), but the difference was only marginally significant. Furthermore, the frequency of characters perfectly congruent with the shortest tree was not significantly lower in the new character set (11%) than in the old set (19%; $\chi^2 = 1.86$, $P = 0.17$). These results suggest that the present study was successful in adding characters that were as phylogenetically informative as those described in previous studies, indicating that the high level of homoplasy observed in the Cynipidae is characteristic of the taxon, and not a consequence of the inclusion of characters of dubious value in our study. Among the old characters, the modified ones were significantly more incongruent with the shortest tree than the unmodified ones (*t*-test on character consistency index, $P = 0.005$). Thus, the difficulties encountered in coding some of the old characters for new taxa were associated with these characters being poor indicators of phylogenetic relationship.

To examine whether or not the phylogenetically conservative characters (good characters; character retention index above 0.60) in the new set were mainly informative about groupings among taxa that had not been included in previous studies, we partitioned the branches in the shortest tree from the current analysis into those that would remain after removal of the new taxa, i.e. the taxa not included in the analyses by Ronquist (1994, 1995b) (old branches) and those that would disappear (new branches). The observed frequencies of changes in good characters came close to those expected, based on the number of old and new branches in the tree. Thus, the good characters added in this study were equally informative about groupings among new and among old taxa. This suggests that, even without the addition of taxa, our study has not exhausted the possibilities of discovering new, phylogenetically informative characters in the external skeletal morphology of adult cynipids.
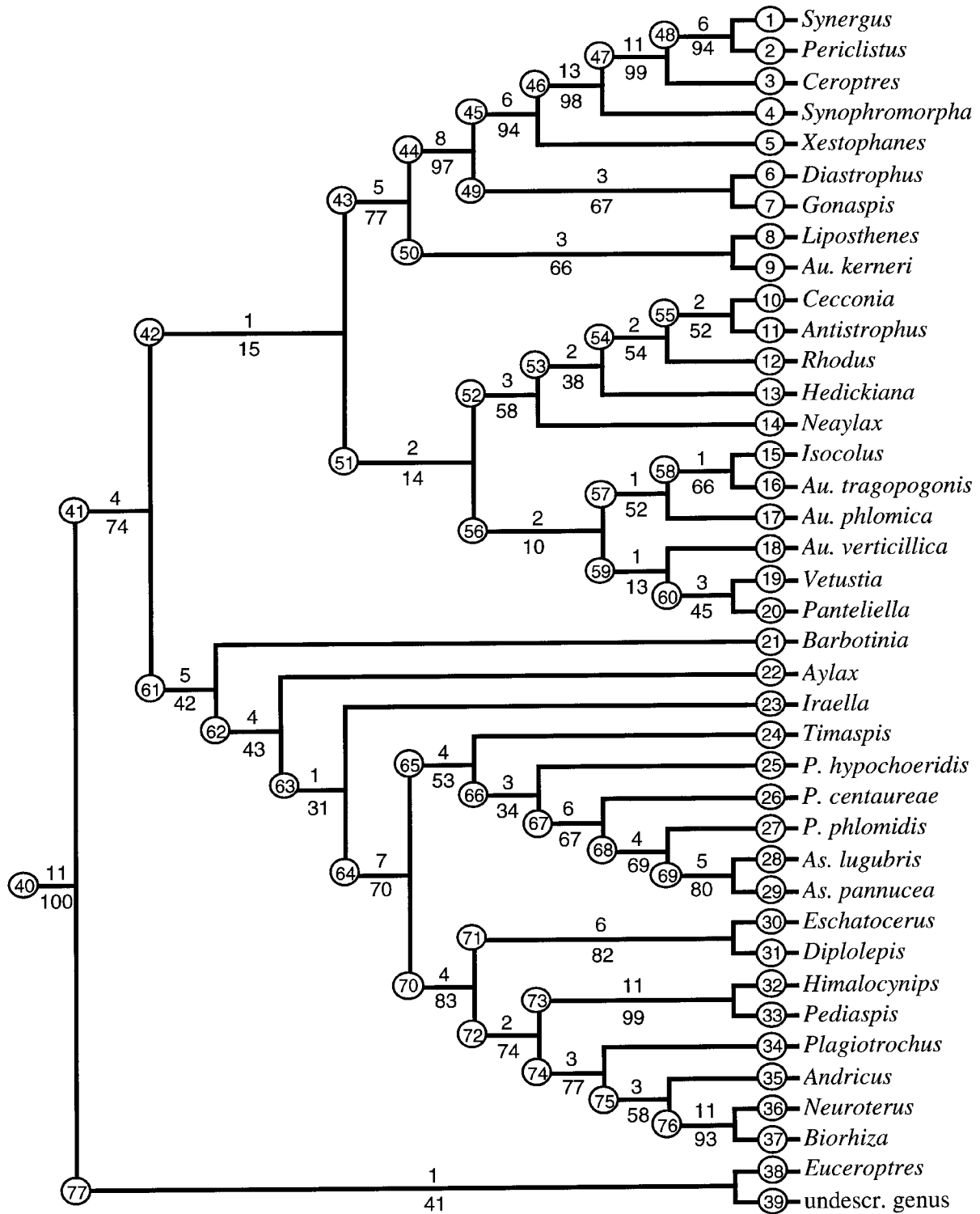
Fig. 3. The shortest tree resulting from heuristic analysis of the complete data set (all taxa included). Tree length 821 steps, CI = 0.29, RI = 0.60. Above each branch is the number of steps needed to break up that particular group (decay index); under each branch is the percentage of 1000 bootstrap replications of the analysis in which that particular branch appeared in the shortest tree (bootstrap proportion). The two most basal outgroups, *Ibalia* (Ibaliidae) and *Paramblynotus* (Liopteridae), are not shown (see instead Fig. 1). Abbreviations: *As* = *Asiocynips*; *Au* = *Aulacidea*; *P* = *Phanacis*.
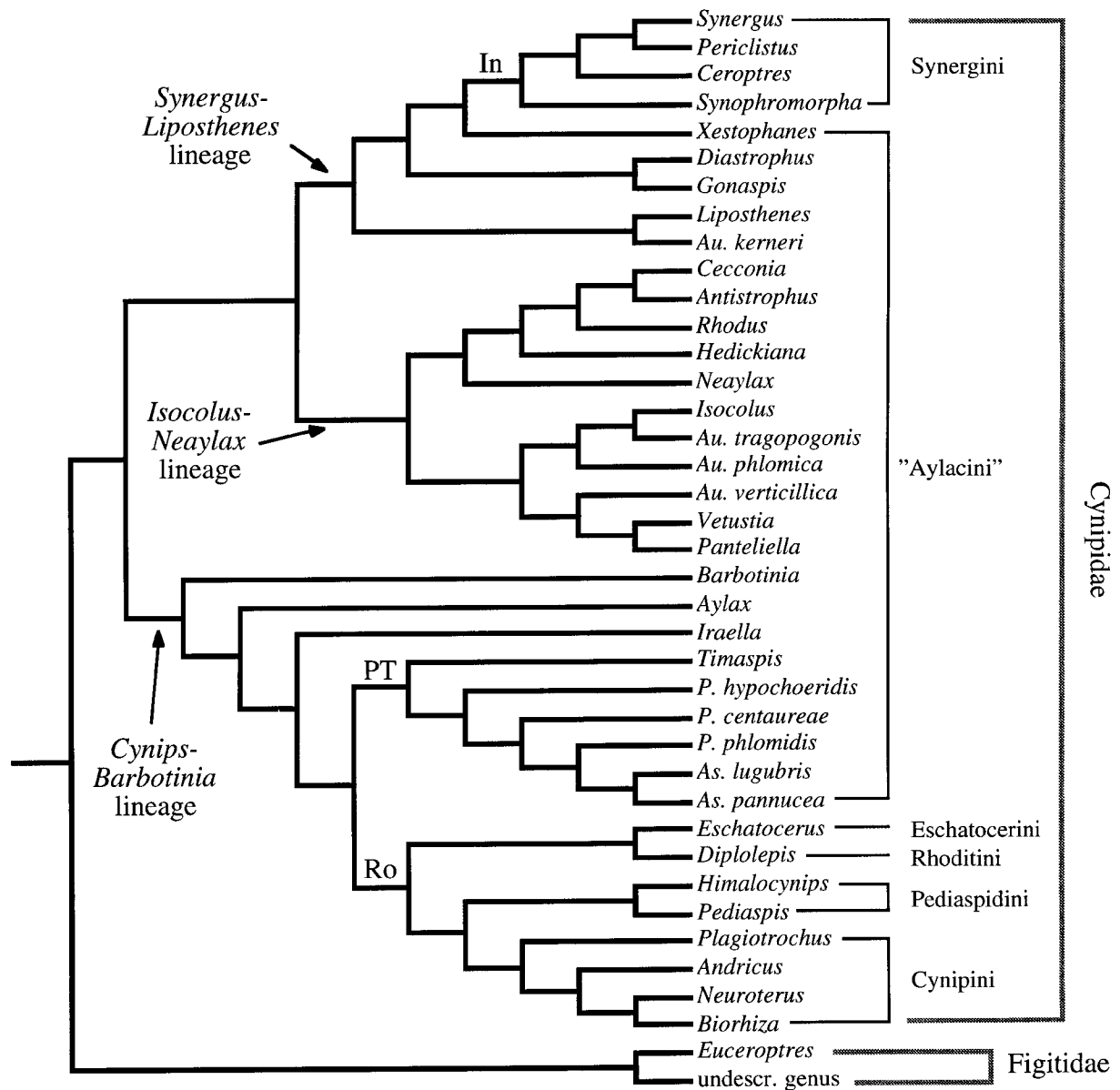
Fig. 4. Comparison of the groupings suggested by the shortest tree (names on branches) and the current higher-level classification of the Cynipidae (indicated to the right). Abbreviations of clades: In = Inquilines; PT = *Phanacis-Timaspis* complex; Ro = woody rosid gallers.

The difficulty of resolving basal cynipid relationships (Figs 3, 6) and the short branch lengths basally in the cynipid tree (Fig. 5; notice that the branch lengths in the *Neaylax-Isocolus* lineage are artificially short because many representatives were coded for only some characters, and that terminal branches are likewise short because of the exclusion of autapomorphies) indicate rapid early radiation of gall wasps, possibly initiated by the transition to a new adaptive zone. An alternative interpretation is that the rate of morphological character evolution has been accelerated in some terminal groups. In either case, basal cynipid relationships will undoubtedly prove difficult to resolve correctly regardless of the type of data used.

The high level of homoplasy in skeletal characters of the Cynipidae makes it difficult to find good morphological key characters for reliable identification of higher cynipid groupings. It also means that large sets of skeletal characters need to be studied before the phylogenetic position of many cynipid species and higher taxa can be determined with confidence.

Cynipid monophyly

Although gall wasps have never been seriously challenged as a natural group, there is a paucity of morphological evidence
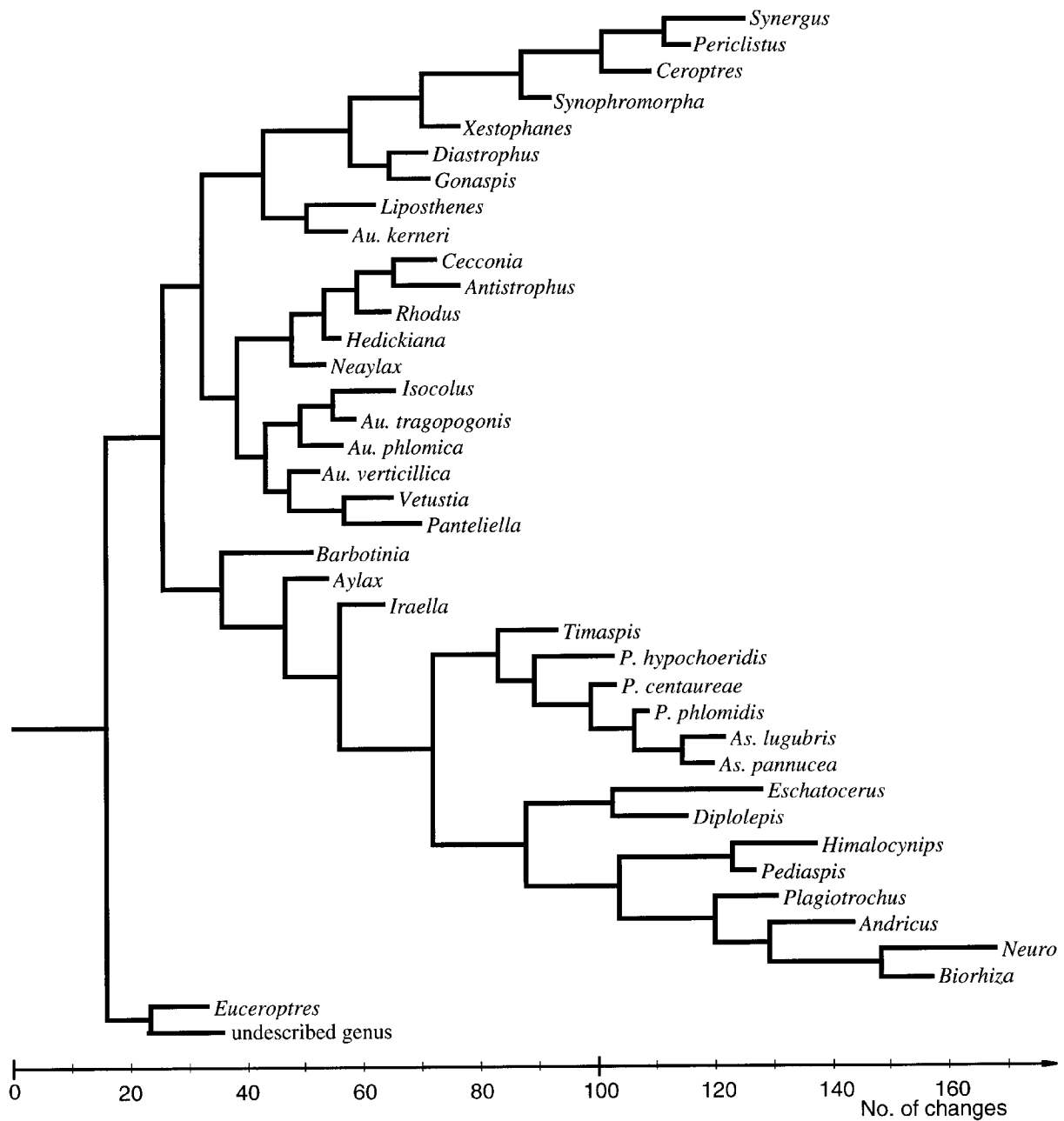
Fig. 5. Phylogram showing branch lengths, measured as the mean number of changes among alternative character reconstructions, in the shortest tree from heuristic analysis of the complete data set. Note that the lengths of the terminal branches are minimum estimates as autapomorphies were not included in the analysis. Abbreviations and inclusion of outgroup taxa as in Fig. 3.

to support their monophyly. Characters currently used to distinguish gall wasps from other cynipoids are obviously present in the plesiomorphic state in cynipids, such as the size and structure of the metasomal terga, the presence of sculpture on the mesosoma and the absence of a scutellar plate (Weld, 1952; Eady & Quinlan, 1963; Quinlan, 1979; Ritchie, 1993). The only possible exception is the hypopygial spine character discussed by Riek (1971), but Ronquist (1995b) examined

this structure and could not find any consistent qualitative differences between cynipids and other cynipoids.

The matter is further complicated by some cynipid-like figitid genera and species associated with galls that have previously been included in the Cynipidae (Ronquist, 1994, 1995b). It is notable that, although two of these figitids were included in the present analysis, the Cynipidae still appeared as a monophyletic group in the shortest tree. The bootstrap
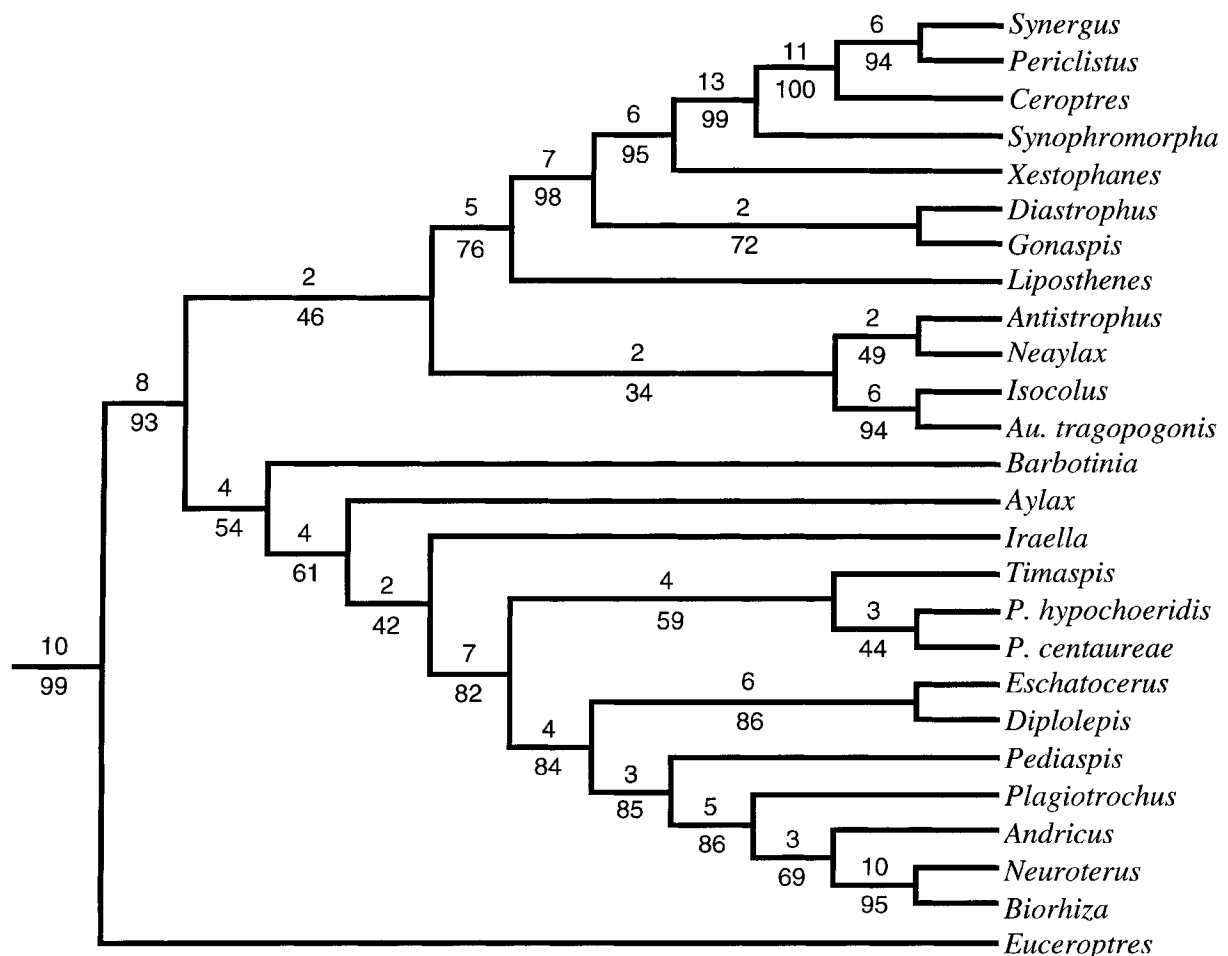
Fig. 6. The shortest tree resulting from heuristic analysis of the pruned data set, only including taxa that could be coded for all morphological characters. Tree length 669 steps, CI = 0.35, RI = 0.60. Support values, abbreviations and inclusion of outgroup taxa as in Fig. 2.

proportion and decay index show relatively low support for cynipid monophyly in the complete analysis (Fig. 3). However, we did not have sufficient material of the undescribed figitid genus for dissections and SEM studies. Therefore, there was a large proportion of missing data for this taxon, possibly resulting in less information to contradict its placement in the Cynipidae. When the undescribed genus was removed from the analysis, the support for cynipid monophyly, as indicated by the bootstrap proportion and decay index, increased significantly (Fig. 6).

Ronquist (1995b) listed two possible autapomorphies of the Cynipidae: the lack of a lateral pronotal carina and the open marginal cell. The present study confirms the first autapomorphy (internode 41, character 60; Appendix 2) but casts doubt on the latter (character 132) because of considerable homoplasy. However, a transition from a completely to an incompletely closed marginal cell in the most recent common ancestor of the Cynipidae is still among the optimal reconstructions for this character.

Six new autapomorphies of the Cynipidae are added by the current analysis (internode 41; Appendix 2): the pronotal

area being completely absent or hidden by the mesoscutum (character 57); the shining strip of the scutellum being extended dorsally (character 83); the dorsellum being conspicuously narrowed medially (character 102); the second abscissa of R_1 being directed obliquely laterad instead of anterad (character 131); the first abscissa of R_1 being angled in relation to R + Sc (character 137); and the marginal cell being relatively wide and short, with the last abscissa of Rs being long and 2r short (character 130). Although there is homoplasy in all of these characters [except the absence of the pronotal area (character 57), but parallelisms occur in this character also when studying figitids not included in the present analysis], taken together they provide fairly strong morphological evidence for cynipid monophyly. Again, these results show the necessity of considering several morphological characters in combination in order to correctly identify a cynipid.

Phylogenetic relationships among gall wasps

The current analysis gives considerable support for the monophyly of the inquilines (Synergini; Figs 3, 4). The

monophyly of the oak gall wasps (Cynipini) is also reasonably well supported. Together with the Eschatocerini, Rhoditini and Pediaspidini, the Cynipini form a monophyletic group of gall inducers restricted to woody rosids (woody representatives of the large monophyletic eudicot subclass Asteridae); this grouping appeared in 83% of the bootstrap replications of the analysis (Fig. 3). Among the woody rosid gallers there is evidence for sister group relationships between the Rhoditini and Eschatocerini, and between the Cynipini and Pediaspidini.

Although low bootstrap and decay values indicate that many of the basal cynipid branchings are difficult to resolve correctly (Fig. 3), it is obvious that the Aylacini are a paraphyletic group. The shortest tree suggests that the genera in this tribe fall into three major cynipid lineages (Fig. 4). In the first lineage (the *Cynips-Barbotinia* lineage), *Timaspis, Phanacis* and *Asiocynips* form a monophyletic group. These genera consist of small cynipids that induce more or less inconspicuous stem galls on hosts in the Asteraceae and, occasionally, Lamiaceae and Apiaceae (*P. phlomidis* and *P. eryngii*). The *Phanacis-Timaspis* complex (PT) appears to be the sister group of the woody rosid gallers (Ro), whereas the Aylacini genera associated with hosts in the Papaveraceae (*Iraella, Aylax* and *Barbotinia*) form basal branches in this lineage (Fig. 4).

In the second lineage (the *Synergus-Liposthenes* lineage; Fig. 4), the inquilines (In) group together with the Aylacini genera associated with rosaceous hosts, the small genus *Xestophanes* being strongly supported as the sister group of the inquilines (Fig. 3). This clade is nested within a larger group, including some gall inducers on Lamiaceae (*Liposthenes* and *A. kerneri*). The third lineage (the *Isocolus-Neaylax* lineage; Fig. 4) consists entirely of Aylacini genera, mainly gall inducers on Asteraceae and Lamiaceae such as *Isocolus* and *Neaylax*. The relationships among the three major lineages and within the *Isocolus-Neaylax* clade are poorly supported by the data, possibly in part due to *Panteliella fedtschenkoi* showing several apparent convergences with *Iraella* and the *Phanacis-Timaspis* complex.

At the generic level it is obvious that the genus *Aulacidea* is polyphyletic, as might have been suspected, and that the small genus *Asiocynips* nests within the more speciose *Phanacis*.

The current analysis leaves no doubt about the sister group relationship between *Himalocynips* and *Pediaspis* (both genera are monotypic), justifying the inclusion of *Himalocynips* in the Pediaspidini proposed by Ronquist (1995b). *Himalocynips* is only known from the two type specimens collected at 1800 m altitude on Mount Godavari in central Nepal, and there are no data on the biology (Yoshimoto, 1970). However, several species of *Acer*, the host plant genus of *Pediaspis*, occur at this height in central Nepal (Hara, 1966; Polunin & Stainton, 1984). *Himalocynips* might well have alternating generations like *Pediaspis* and the oak gall wasps. The type specimens of *Himalocynips* are unusually large cynipid females, in that respect being similar to the parthenogenetic females of *Pediaspis*.

The results of this study agree well with those of Ronquist (1994). His anlysis of relationships among twelve of the cynipid species included in the present study resulted in five minimum-length trees, one of which is exactly congruent with the shortest tree from the current analysis. Of course, many of the characters in the present analysis correspond to those of Ronquist (1994). Nevertheless, the study presented here is independent in that all characters and character codings were re-examined. Only seventy-eight of the 166 characters (47%) in the present analysis were taken directly from Ronquist (1994), representing only 14% of the cells in the data matrix.

It is somewhat difficult to evaluate the results of this study against the hypothesis proposed by Kinsey (1920). Kinsey's work primarily rests on intuitive evaluation of seven morphological and biological characters, but he made an extensive survey of cynipid species. In this respect, Kinsey's study represents a different approach to the study of higher-level relationships than the one taken here. Nonetheless, his phylogeny (Fig. 2a) agrees in several respects with the hypothesis presented in this paper: the Cynipini are monophyletic and closely related to the rose gall wasps (Rhoditini), and *Gonaspis* is the sister group of *Diastrophus*. However, other relationships indicated by Kinsey (1920) among Aylacini genera conflict with our study.

The results of this analysis and that of Ronquist (1994) point out several problems in the classification of the Cynipidae, including the paraphyletic nature of Aylacini, *Aulacidea* and *Phanacis*. However, we consider formal changes to the higher-level classification of the Cynipidae to be premature at this point, partly because of the relatively low support for some of the early branchings in the family, and partly because of the restricted sample of Aylacini species that have been studied thus far.

Relationships of genera and species not included in the analysis

In an exemplar study such as this, the potential impact of species not included in the analysis is an important concern. The oak gall wasps are the only major group to be sparingly represented in our analysis (four genera). The group is speciose and structurally diverse, but it has long been considered natural (Ashmead, 1903a,b; Kinsey, 1920; Weld, 1952; Askew, 1984; Ritchie, 1984; Roskam, 1992) and both the results of this analysis and that of Ronquist (1994) support Cynipini monophyly. All Cynipini species are associated with *Quercus* or closely related genera in the Fagaceae, a unique feature among the gall-inducing species. There is no known unique morphological autapomorphy, but all Cynipini have a pronotum which is short medially (Weld, 1952), a derived gall wasp character state only occurring in the Rhoditini + Eschatocerini outside the Cynipini.

Three of the genera in the Synergini were not included in this analysis or that of Ronquist (1994), namely *Rhoophilus*, *Synophrus* and *Saphonecrus*. However, Ronquist (1994) examined representatives of these genera and reached the conclusion that they are all closely related to *Synergus*. Three of the genera in the Synergini are speciose, *Periclistus*, *Synergus* and *Ceroptres*, but only *Ceroptres* appears obviously heterogeneous. The *Ceroptres* species that we studied is one of two European species of the genus (Pujade i Villar &

Nieves-Aldrey, 1993); these species are quite distinct from other inquilines. The North American species resemble other inquilines more closely, and a few of them show apparently apomorphic similarities with *Synergus* in the structure of the petiolar annulus (Ritchie, 1984). Thus, it is possible that inclusion of North American representatives of *Ceroptres* might affect the conclusions reached here on inquiline relationships.

In the Rhoditini, we did not include any representative of the poorly known genus *Liebelia* in the analysis. However, one of us (F.R.) later had the opportunity to examine specimens of five of the nine species in the genus, *L. magna* Vyrzhikovskaja, *L. fukudae* (Shinji), *L. sibirica* Belizin, *L. popovi* Vyrzhikovskaja and *L. dzhungarica* Vyrzhikovskaja (cf. Vyrzhikovskaja, 1963). All these had a crenulate furrow across the mesopleuron, an apparent autapomorphy of the Rhoditini (Eady & Quinlan, 1963; Nieves-Aldrey, 1994; personal observation).

Many of the currently recognized genera in the other cynipid tribes are monotypic or consist of a small number of apparently closely related species, and we are confident that the inclusion of additional species from these genera would have little impact on the conclusions reached here. The few more speciose genera will be discussed below.

The genus *Isocolus* is large but appears homogeneous and distinct from other cynipids, with most species galling *Centaurea* (Dyakonchuk, 1982; Zerova *et al.*, 1988). *Aulacidea* is probably paraphyletic relative to *Isocolus*, even if the species associated with Lamiaceae (*A. kerneri*, *A. verticillica* and *A. phlomica*) are removed.

The genus *Aylax* was previously a 'waste-basket' for Aylacini species that did not fit elsewhere (e.g. Dalla Torre & Kieffer, 1910). Nieves-Aldrey (1994) restricted *Aylax* to a few apparently closely related species galling plants in the Papaveraceae, but did not suggest alternative positions for some of the species that were then placed in the genus. Because most of these species gall Asteraceae, and *Aylax* was previously distinguished from *Aulacidea* mainly on the open marginal cell, which is a plesiomorphic character state for the Cynipidae, it seems likely that, with a few exceptions, these species will prove to belong to the *Aulacidea-Isocolus* group of gall inducers associated with Asteraceae (Fig. 3).

The genus *Diastrophus* includes many species galling *Rubus* and *Potentilla*, and one species galling *Fragaria*. Because the monotypic *Gonaspis* is separated from *Diastrophus* only on the apomorphic shape of the scutellum (Weld, 1952), one might suspect that *Gonaspis*, inducing galls on *Potentilla*, represents a recent offshoot of a paraphyletic *Diastrophus* which was originally associated with *Rubus*. However, as *Xestophanes* is also associated with *Potentilla*, the results of the present analysis (cf. Fig. 3) actually indicate that *Potentilla* is the ancestral host of *Diastrophus*, in which case *Gonaspis* may well be the sister group of a monophyletic *Diastrophus*.

The speciose genera *Phanacis* and *Timaspis* were synonymized by Eady & Quinlan (1963), but Nieves-Aldrey (1994) re-established them as separate genera. This complex is distinct from other cynipids in several features, including their small size and elongate metasoma. It is obvious from the results of the present study that *Asiocynips* belongs here.

Although the support for the monophyly of the *Phanacis-Timaspis* complex is surprisingly weak (Figs 3 and 6), we consider it unlikely that any of the species in *Phanacis* or *Timaspis* would place among the woody rosid gallers or basal to *Aylax* in the *Cynips-Barbotinia* lineage (Fig. 4).

After the present analysis was completed, one of us (J.L.) had the opportunity to examine dried and mounted specimens of the two Aylacini genera not included in the analysis. The characters that could be coded for these genera indicate that *Zerovia* belongs to the *Phanacis-Timaspis* complex and that *Parapanteliella* is close to *Panteliella*, perhaps being its sister group.

Evolutionary implications

The results of the present analysis have far-reaching implications concerning the evolution of the gall wasp-host plant association and other aspects of gall wasp evolution. These macroevolutionary patterns will be discussed in detail elsewhere (Ronquist & Liljeblad, unpublished observations).

Acknowledgements

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Appendix 1. Characters used for phylogenetic analysis.

The following abbreviations have been used in the character descriptions (*x* refers to an integer): F*x* = flagellomere *x*; *x*tg = abdominal tergum *x*; *x*st = abdominal sternum *x*. References to characters and figures in Ronquist (1994) are preceded by an R, references to Ronquist (1995b) by a Q. Transformation series hypotheses are given for multistate characters. Following each character, the character consistency index and retention index on the shortest tree (Fig. 2) are given.

Head, anterior view, female

1. [Modified from R1] *Shape of ventral part of clypeus*: (a) rounded, broadly projecting over mandibles (Fig. R8); (b) not projecting from cranial margin or slightly and narrowly projecting medially (Fig. R7). (CI = 0.20, RI = 0.67)
2. *Shape of projecting ventral clypeal margin*: (a) straight or rounded (not illustrated); (b) with a median incision (Fig. R8). (CI = 0.29, RI = 0.29)
3. [= R2] (CI = 1.00, RI = 1.00)
4. *Direction of clypeo-pleurostomal lines*: (a) ventrally diverging (Fig. R8); (b) ventrally converging (Fig. R7a). (CI = 0.33, RI = 0.67)
5. [= R3] (CI = 0.17, RI = 0.38)
6. *Relative distance between anterior tentorial pits*: (a) long, pits closer to ventral clypeal margin than to each other (Fig. R8); (b) short, pits closer to each other than to ventral clypeal margin (Fig. R7a). (CI = 0.33, RI = 0.50)
7. [Modified from R4 & R5] *Facial strigae radiating from clypeus*: (a) laterally reaching or almost reaching compound eye (Fig. R7); (b) laterally reaching past 0.7 distance to compound eye (not ill.); (c) distinct but not reaching past 0.6 distance to compound eye (Fig. 7a); (d) entirely absent or only a few strigae indicated close to clypeus (Fig. R8). Ordered abcd. (CI = 0.14, RI = 0.54)
8. [= R6] (CI = 0.50, RI = 0.50)
9. *Raised vertical carina from ventral margin of antennal socket* (not illustrated): (a) absent; (b) present, at least close to antennal socket. (CI = 0.33, RI = 0.60)
10. [= R12] (CI = 0.33, RI = 0.50)
11. [= R7] (CI = 0.67, RI = 0.93)
12. [Modified from R9] *Size of antennal socket*: (a) small, ratio of max. width of head to max. width of antennal socket excluding antennal rim > 9.0 (Fig. R7); (b) large, ratio < 8.5 (Fig. R8). (CI = 0.33, RI = 0.50)
13. [= R10] (CI = 0.50, RI = 0.80)
14. *Transition between dorsomesal margin of eye and surface of face* (not illustrated): (a) smooth, surface of face slightly raised just before meeting margin of eye; (b) smooth, face not raised; (c) abrupt, distinct angle between face and eye. (CI = 0.22, RI = 0.65)
15. [Modified from R13] *Sculpture on vertex dorsad compound eye* (not illustrated): (a) regular and non-parallel (polygonal); (b) more or less erased; (c) punctate. Unordered. (CI = 0.40, RI = 0.50)
16. [Modified from R13] *Regular sculpture on vertex dorsad compound eye* (not illustrated): (a) concave (alveolate-reticulate); (b) flat (coriarious); (c) convex (acinose-colliculate). Ordered abc. (CI = 0.17, RI = 0.54)

Head, posterior view, female

17. [Modified from R16] *Median hairy strip of gula*: (a) broad, at least in upper half (not illustrated); (b) narrow throughout (Fig. R9); (c) reduced or absent (Fig. R10). Unordered. (CI = 0.33, RI = 0.64)
18. [= R17] (CI = 1.00, RI = 1.00)
19. [Modified from R15] *Position of gular ridges*: (a) united well before reaching hypostomata (Fig. R9); (b) free, but meeting at hypostomata (not illustrated); (c) free, well separated at hypostomata (Fig. R10). Ordered abc. (CI = 0.17, RI = 0.33)
20. *Appearance of gular sulci* (not illustrated): (a) distinctly marked; (b) indistinct; (c) absent, at most barely indicated. Ordered abc. (CI = 0.18, RI = 0.53)
21. *Distinctness of gular ridges* (not illustrated): (a) distinctly raised; (b) reduced, not ridge-like. (CI = 0.50, RI = 0.50)
22. [= R14] (CI = 0.50, RI = 0.80)
23. *Position of posterior tentorial pits*: (a) high, dorsal margin of pits positioned higher than ventral postoccipital rim of occipital foramen (Fig. R9); (b) low, dorsal margin of pits positioned lower (not illustrated). (CI = 1.00, RI = 1.00)
24. *Shape of posterior tentorial pits*: (a) more or less rounded (Fig. R7b); (b) slitlike (Fig. R10). (CI = 0.20, RI = 0.67)
25. [= R18] (CI = 0.25, RI = 0.75)
26. *Ridge from hypostomata close to ventral margin of cranium reaching laterad*: (a) absent; (b) present (Fig. R9). (CI = 0.33, RI = 0.33)
27. [= Q5] (CI = 1.00, RI = 1.00)
28. *Shape of occiput medially*: (a) flat or only slightly impressed close to postocciput (Fig. 7c); (b) distinctly impressed close to occiput, impression separated by a sharp edge from rest of occiput (Fig. 7d); (c) broadly impressed, rising gradually towards vertex (Fig. 7e). Unordered. (CI = 0.33, RI = 0.33)
29. *Sculpture on occiput* (not illustrated): (a) transversely wrinkled; (b) not wrinkled. (CI = 0.12, RI = 0.56)
30. *Shape of odontoidea*: (a) narrow and more or less pointed laterally, abruptly broadened close to mesal margin (Fig. 7b); (b) broader and more rounded laterally, gradually broadened towards mesal margin (Figs R9 and R10). (CI = 0.25, RI = 0.73)

Mandibles, female

31. [= R19] (CI = 0.50, RI = 0.86)
32. [= R20] (CI = 0.67, RI = 0.67)
33. [= R21] (CI = 0.25, RI = 0.62)
34. [= R22] (CI = 0.50, RI = 0.86)
35. [= R23] (CI = 0.50, RI = 0.50)

Labiomaxillary complex, female

36. *Shape of prementum and stipes*: (a) short (Fig. R10); (b) elongate (Fig. 7b). (CI = 0.25, RI = 0.25)
37. [= R24] (CI = 1.00, RI = 1.00)
38. [Modified from R25] *Shape of cardo*: (a) bent distally some distance from apex, large part visible in posterior view of head. (Fig. R9); (b) bent distally close to apex, only small part visible posteriorly (not illustrated); (c) straight, not bent distally, not or almost not visible posteriorly (Fig. R10). Ordered abc. (CI = 0.22, RI = 0.65)
39. [= R26] (CI = 1.00, RI = 1.00)
40. [= R28] (CI = 0.50, RI = 0.33)
41. [Modified from R30] *Length of second segment of maxillary palp*: (a) short, ratio of length of second segment to length of third to fifth segment combined < 0.50 (Fig. 15); (b) long, ratio > 0.54 (Fig. 16). (CI = 0.50, RI = 0.50)
42. [= R31] (CI = 1.00, RI = 1.00)
43. [= R32] (CI = 0.56, RI = 0.56)
44. [= R33] (CI = 1.00, RI = 1.00)

Female antenna

45. [= R34] (CI = 0.24, RI = 0.41)
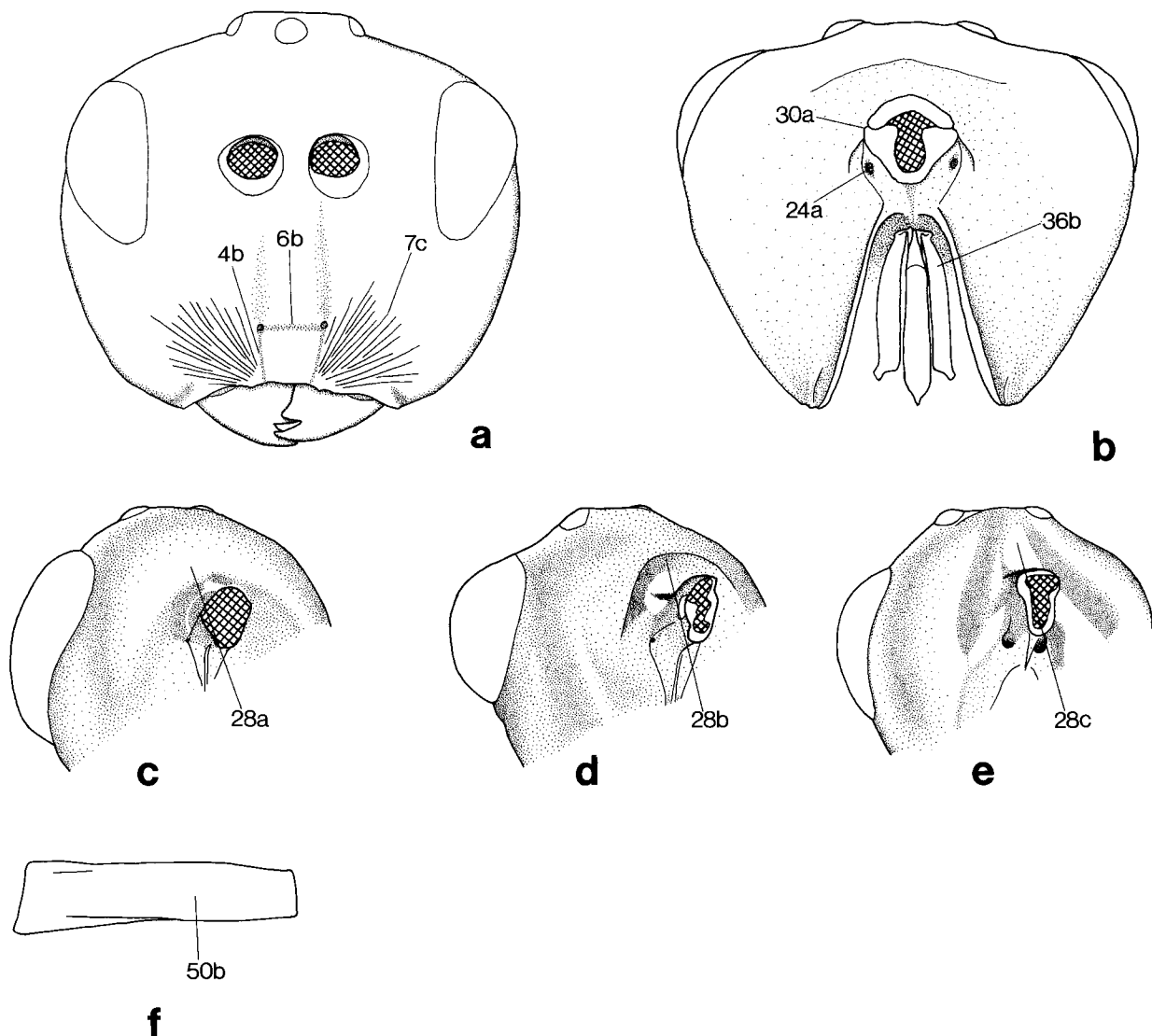
Fig. 7. Characters of the head and the antenna. a, Head, anterior view, female, *Antistrophus pisum*; b, head, posterior view, female, *Barbotinia oraniensis*; c–e, dorsal part of head, posterolateral view, females; c, *Periclistus brandtii*; d, *Liposthenes glechomae*; e, *Neuroterus numismalis*, part. gen.; f, first flagellomere of left antenna, dorsal view, male, *Pediaspis aceris*, sex. gen.

46. [= R35] (CI = 0.14, RI = 0.62)

Male antenna

47. [Modified from R36] (a) 13 or more; (b) 12; (c) 11. Ordered abc. (CI = 0.42, RI = 0.42). Data for *Ceroptres, Aulacidea kerneri, Cecconia, Antistrophus, Neaylax, Aulacidea tragopogonis, Iraella, Phanacis hypochoeridis, Phanacis centaureae* and *Neuroterus* taken from literature (Dalla Torre & Kieffer, 1910; Nieves Aldrey, 1988, 1994). *Paramblynotus* has 12, but in the groundplan of Liopteridae it is uncertain whether it is 12 or 13 (Ronquist, 1995a). As a representative of the Liopteridae, *Paramblynotus* was therefore coded as being polymorphic for this character

48. [Modified from R38] *Modified part of F1*: (a) present, clearly set off as a separate flattened or bare surface (Fig. R19); (b) absent or at most indicated basally (Fig. 7f). (CI = 0.29, RI = 0.29). *Ibalia* has F1 modified, but it is uncertain whether or not this

belongs to the ground plan of the Ibaliidae (Ronquist, 1995b). As a representative of the Ibaliidae, *Ibalia* was therefore coded as being polymorphic. *Paramblynotus* has F1 modified, but F1 is not modified in the ground plan of the Liopteridae (Ronquist, 1995a). As a representative of the Liopteridae, *Paramblynotus* was therefore coded as having F1 unmodified.

49. [= R39] (CI = 0.33, RI = 0.71)

50. *Shape of F1*: (a) short, ratio of length of F1 to width of F2 < 3.5 (Fig. R19); (b) long, ratio > 4.2 (Fig. 7f). (CI = 0.25, RI = 0.50)

Pronotum, female

51. [Modified from R42] *Shape of pronotum*: (a) long medially, ratio of median distance between dorsal and ventral margins to shortest lateral distance between anterior margin and anteroventral corner of mesopleural triangle ⩾ 0.43 (Fig. R26); (b) intermediate, ratio 0.35–0.34 (Fig. 8b); (c) short, ratio 0.29–0.22

(Fig. R25); (d) very short, ratio $\leqslant 0.17$ (Fig. R27). Ordered abcd. (CI = 0.21, RI = 0.63)

52. *Shape of anteroventral margin of pronotum in anterodorsal view*: (a) evenly rounded (Fig. R29); (b) with a median incision (Fig. R30). (CI = 0.14, RI = 0.57)

53. [= Q14] (CI = 1.00, RI = 1.00)

54. [= R40] (CI = 0.33, RI = 0.60)

55. *Shape of admedian depressions*: (a) round (Fig. 8b); (b) oval (Fig. R29); (c) linear (Fig. 9a, R25). Ordered abc. (CI = 0.40, RI = 0.77)

56. [= R41] (CI = 0.25, RI = 0.40)

57. [= Q20] (CI = 1.00, RI = 1.00)

58. *Sculpture on pronotal plate*: (a) at least partly glabrous-glabrate and shining; (b) coriarious and dull. (CI = 0.33, RI = 0.67)

59. [= R43] (CI = 0.29, RI = 0.71)

60. [= R44] (CI = 0.33, RI = 0.60)

61. [Modified from R45] *Ridges on lateral surface of pronotum*: (a) lacking (Fig. R26); (b) some irregular, horizontal costulae posteriorly in lower half (Figs R25, R27); (c) many regular, radiating costulae dorsally and posteriorly (not illustrated). Unordered. (CI = 0.17, RI = 0.41)

62. *Surface sculpture on lateral surface of pronotum (excluding ridges)*: (a) at least superficially sculptured; (b) largely glabrous. (CI = 0.50, RI = 0.50)

63. [Modified from R51] *Shape of laterodorsal surface of pronotum*: (a) more or less vertical (Fig. R26); (b) broad strip along dorsal margin distinctly inflected (Fig. R27); (c) gradually curved inwards dorsally, particularly subposteriorly (Fig. 8a). Unordered. (CI = 0.67, RI = 0.80)

64. *Shape of ventral corner of spiracular incision of pronotum*: (a) pointed (Fig. 8a); (b) rounded (Fig. R25). (CI = 0.12, RI = 0.46)

65. [= R46] (CI = 0.50, RI = 0.91)

66. *Shape of subventral impression of pronotum*: (a) narrow and more or less distinct (Figs R25–R27); (b) broad and shallow (Fig. 8b). (CI =1.00, RI = 1.00)

Prosternum, female

67. [= R48] (CI = 1.00, RI = 1.00)

68. [= R49] (CI = 0.50, RI = 0.67)

Mesonotum, female

69. *Lateral profile of anterior part of mesoscutum*: (a) not recurved, anteriormost part same as anteroventral margin (Figs R26, R27); (b) recurved, anteriormost part dorsad anteroventral margin (not illustrated). (CI = 1.00, RI = 1.00)

70. *Shape of anterior mesoscutal margin in dorsal view*: (a) angled laterally, narrowly rounded medially (Fig. R29); (b) angled laterally, broadly rounded medially (Fig. R30); (c) angled laterally, truncate medially (Fig. 9b); (d) evenly rounded throughout (Fig. 9a). Unordered. (CI = 0.43, RI = 0.69)

71. *Incision in anterior margin of mesoscutum at anterior end of anteroadmedian signum*: (a) absent or indistinct (Fig. R28); (b) present, distinct (Fig. R29). (CI = 0.50, RI = 0.80)

72. [= R50] (CI = 0.50, RI = 0.80)

73. [Modified from R51] *Relation between anterolateral mesoscutal margin and dorsal pronotal margin*: (a) mesoscutal margin not projecting over pronotum (Fig. R26); (b) mesoscutal margin projecting over pronotum (Fig. R27). (CI = 0.50, RI = 0.83)

74. *Shape of mesoscutum midlaterally, in cross section*: (a) slightly rounded (Figs R26, R27); (b) distinctly rounded; (c) conspicuously rounded (Fig. 8a). (CI = 0.33, RI = 0.60)

75. [= R52] (CI = 0.30, RI = 0.67)

76. [= R53] (CI = 0.20, RI = 0.20)

77. [= R54] (CI = 0.025, RI = 0.55)

78. [= R55] (CI = 0.33, RI = 0.75)

79. [= R56] (CI = 0.12, RI = 0.53). *Aylax* and *Timaspis* were erroneously coded as having a in Ronquist (1994).

80. *Shape of posterior part of axillular surface: (a) shallowly impressed* (Fig. R26); (b) deeply impressed (Fig. 8a). (CI = 0.25, RI = 0.67)

81. Axillar carina separating lateral axillar area from dorsal axillar area: (a) more or less distinct (Fig. 26, R27); (b) indistinct or absent (Fig. 8c). (CI = 0.11, RI = 0.20)

82. [= R57] (CI = 1.00, RI = 1.00)

83. *Posterodorsal part of shining strip*: (a) without a dorsal projection (not illustrated); (b) with a dorsal projection (Figs R26 and R27). (CI = 0.25, RI = 0.57)

84. *Notauli*: (a) percurrent and distinct (Figs R29, R30); (b) percurrent or almost percurrent, but anterior half indistinct (Fig. 9b); (c) present posteriorly, but absent in anterior half (Fig. 9a); (d) entirely absent (not illustrated). Ordered abc. (CI = 0.16, RI = 0.52)

85. *Median mesoscutal impression*: (a) present, extending some distance from posterior margin of mesoscutum (Fig. 9c); (b) present only as a slight impression at posterior margin of mesoscutum (Fig. R30); (c) absent (not illustrated). Ordered abc. (CI = 0.13, RI = 0.32)

86. *Scutellar foveae*: (a) present, at least as transverse furrows (Fig. 9a); (b) strongly reduced or absent (not illustrated). (CI = 0.50, RI = 0.50)

87. *Sculpture in scutellar foveae*: (a) glabrous to glabrate, except occasionally for some rugosity, without distinct microsculpture; (b) finely coriarious. (CI = 0.50, RI = 0.80)

88. *Round, distinctly margined posteromedian scutellar impression*: (a) absent (Fig. 9a); (b) present (Fig. 9c). (CI = 1.00, RI = 1.00)

Mesopectus (mesopleuron and mesosternum), female

89. [= Q32] (CI = 1.00, RI = 1.00)

90. *Shape of lateral part of mesopectus*: (a) long and low, ratio of maximum height to maximum width $\leqslant 1.12$ (not illustrated); (b) intermediate, ratio 1.30–1.51 (Figs R26, R27); (c) short and high, ratio $\geqslant 1.60$ (Fig. 8c). Ordered abc. (CI = 0.27, RI = 0.33)

91. [= R58] (CI = 0.33, RI = 0.65)

92. *Direction of regular costulae-strigae on speculum*: (a) horizontal or directed obliquely upwards posteriorly (Fig. R26); (b) directed obliquely downwards posteriorly. (CI = 1.00, RI = 1.00)

93. *Sculpture anteriorly on mesopleuron, below mesopleural triangle*: (a) without regular sculpture (Fig. R27); (b) covered with regular, closely set striae, occasionally these striae only indicated (Fig. R26); (c) covered with regular, reticulate sculpture (not illustrated). Unordered. (CI = 0.20, RI = 0.62)

94. *Line marking ventral border of mesopleural triangle*: (a) clearly set off (Figs R26, R27); (b) diffuse, no clear border (Fig. 8c). (CI = 0.25, RI = 0.77). *Paramblynotus* has a distinct ventral border of the mesopleural triangle, but this is not plesiomorphic for the Liopteridae (Ronquist, 1995a). As a representative of the Liopteridae, *Paramblynotus* was therefore coded as lacking the distinct ventral border of the mesopleural triangle.

95. *Posterior subalar pit*: (a) large, deep (Fig. 8b); (b) small, shallow (Fig. 8c). (CI = 0.20, RI = 0.00)

96. *Sculpture on lower half of mesopleural triangle*: (a) smooth or irregular (Fig. R27); (b) strigate (Fig. R26). (CI = 0.50, RI = 0.33)

97. *Ventral surface of mesopectus*: (a) only slightly bulging ventrad medially (Figs R26, R27); (b) prominently bulging ventrad medially (Fig. 8b,c). (CI = 0.50, RI = 0.50)

98. [= R60] (CI = 0.29, RI = 0.54)

99. [= R62] (CI = 1.00, RI = 1.00)
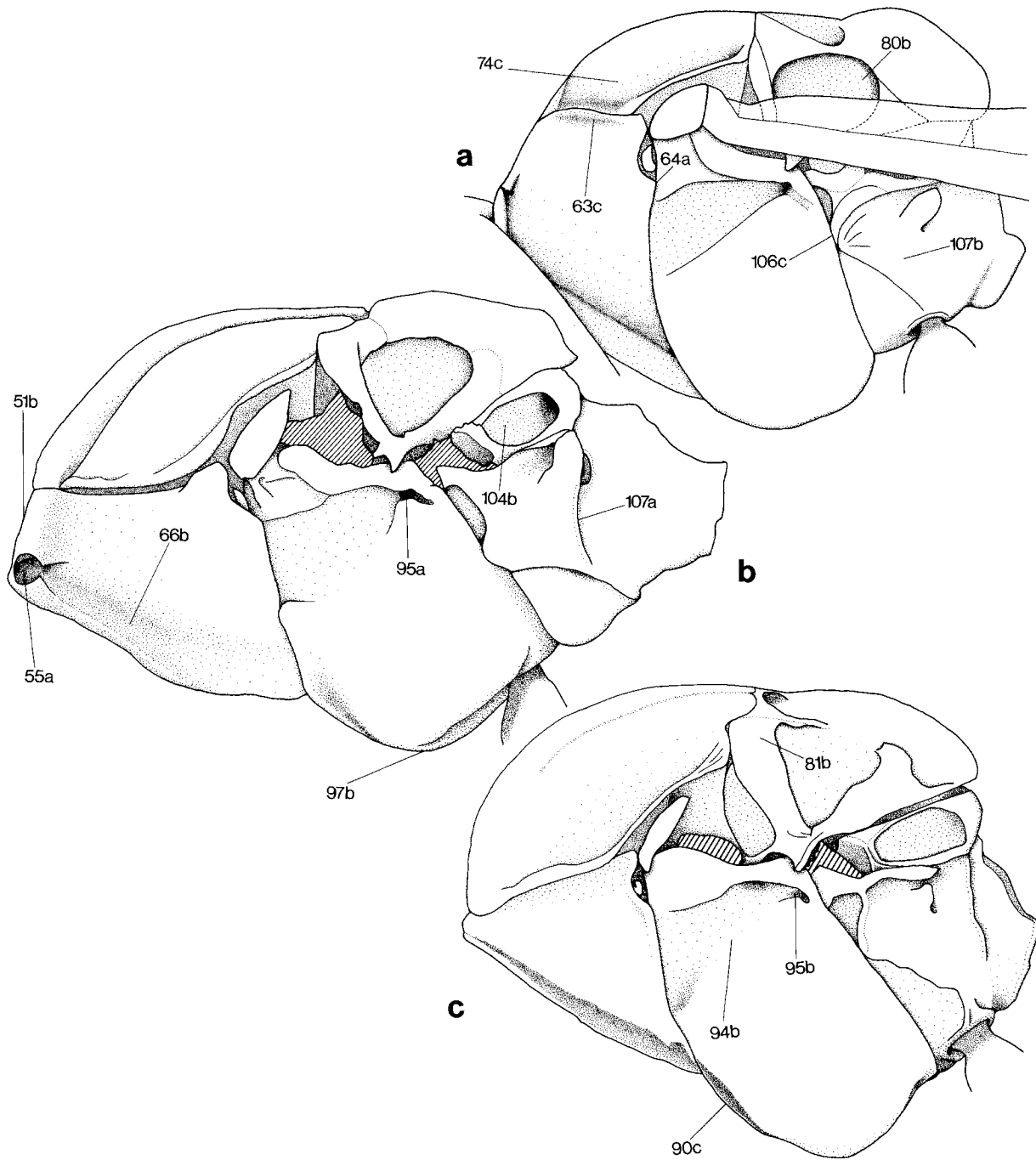
Fig. 8. Mesosoma, lateral view, females. a, *Cecconia valerianellae*; b, *Pediaspis aceris*, sex. gen.; c, *Plagiotrochus fusifex*, sex. gen.

100. [= R63] (CI = 1.00, RI = 1.00)
101. [= R64] (CI = 0.33, RI = 0.71)

Metanotum, female

102. [= R65] (CI = 0.33, RI = 0.83)
103. [= R66] (CI = 0.25, RI = 0.25). *Andricus* was erroneously coded as having a in Ronquist (1994).
104. [Modified from R67] *Shape of metanotal trough*: (a) narrow,

apically rounded (Fig. R27); (b) broad, apically truncate (Fig. 8b). (CI = 0.20, RI = 0.56)

Metapectal-propodeal complex, female

105. [= R68] (CI = 0.20, RI = 0.69)
106. *Distance between metepimeron and metepisternum*: (a) short, distinctly shorter than width of metepimeron (Fig. R26); (b) intermediate, about as long as width of metepimeron (not
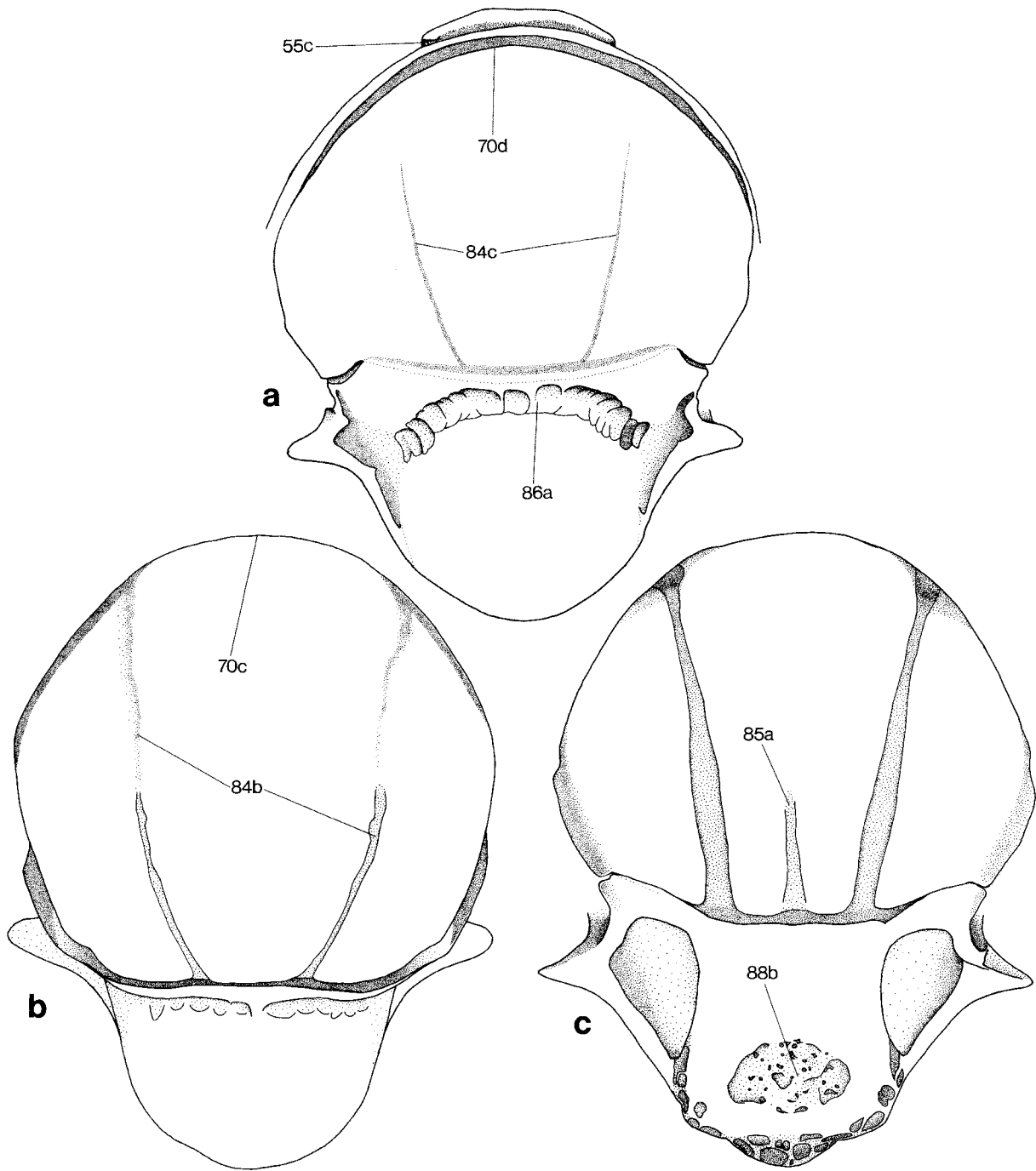
Fig. 9. Mesosoma, dorsal view, females: a, *Phanacis centaureae*; b, *Diplolepis rosae*; c, *Pediaspis aceris*, sex. gen.

illustrated); (c) long, much longer than width of metepimeron (Fig. 8a). Ordered abc. (CI = 0.50, RI = 0.83)

107. *Carina from ventral margin of calyptra to metapleural sulcus*: (a) present (Fig. 8b); (b) absent (Fig. 8a). (CI = 0.20, RI = 0.50)

108. *Lateral propodeal carina* (not illustrated): (a) present; (b) absent. (CI = 0.50, RI = 0.75)

109. *Shape of lateral propodeal carina (not illustrated)*: (a) narrow,

not flattened above; (b) broad, flattened above. (CI = 0.17, RI = 0.50)

110. [= R69] (CI = 0.25, RI = 0.25)

111. *Posterodorsal edge of nucha, in lateral view*: (a) rounded (Figs R26 and R28); (b) angled (Fig. R27). (CI = 0.33, RI = 0.71)

112. [= R70] (CI = 0.33, RI = 0.75)

113. [= R72] (CI = 1.00, RI = 1.00)

114. [= R73] (CI = 0.50, RI = 0.83)

115. *Triangle formed by petiolar and metacoxal foramina*: (a) narrow, ratio of distance between centres of metacoxal foramina to longitudinal distance between anterior margin of metacoxal foramen and anterior margin of petiolar foramen < 2.6 (Fig. R23); (b) broad, ratio > 3.0 (Fig. R24). (CI = 0.25, RI = 0.62)
116. [Modified from R74] *Position of petiolar foramen*: (a) anteriorly situated, ratio of distance between anterior margin of metasubpleuron and anterior margin of petiolar foramen to length of petiolar foramen, in ventral view < 1.8; (b) posteriorly situated, ratio > 2.0. (CI = 0.50, RI = 0.80)

Legs, female

117. [= R75] (CI = 0.33, RI = 0.50)
118. [= R76] (CI = 0.20, RI = 0.00)
119. [= R77] (CI = 1.00, RI = 1.00)
120. [= R79] (CI = 0.33, RI = 0.60)
121. [= R80] (CI = 1.00, RI = 1.00)
122. *Hump laterobasally on mesocoxa* (not illustrated): (a) absent; (b) present. (CI = 1.00, RI = 1.00)
123. [Modified from R78] *Shape of mesofemur*: (a) approximately same width throughout, only slightly widened subbasally (Fig. R32); (b) distinctly and abruptly widened subbasally (Fig. R31). (CI = 0.25, RI = 0.75)
124. [= R82] (CI = 0.25, RI = 0.73)
125. [= R83] (CI = 1.00, RI = 1.00)
126. [Modified from R81] *Pubescence on lateral surface of metacoxa* (not illustrated): (a) restricted to two distinct lateral bands, no hairs in the middle; (b) less distinct and less regular bands, some hairs in the middle; (c) not arranged into bands, more evenly pubescent. Ordered abc. (CI = 0.29, RI = 0.72)
127. *Vertical strigae on lateral surface of metacoxa* (not illustrated): (a) absent; (b) present. (CI = 0.25, RI = 0.00)
128. [= Q51] *Longitudinal carina on posterior surface of metatibia* (not illustrated): (a) absent; (b) present. *Ibalia* has a carina, but the carina is absent in the ground plan of the Ibaliidae (Ronquist, 1995b). (CI = 0.33, RI = 0.33)

Forewing, female

129. [Modified from R84] *Shape of 2r*: (a) simple or with a slight process or bend medially (Fig. R37); (b) with a prominent vein stump medially projecting anterolaterally (Fig. R38). (CI = 0.67, RI = 0.00)
130. [Modified from R85] *Length of 2r*: (a) long, ratio of length of 2r to length of R1 + Sc ⩾ 0.73 (Fig. 10b); (b) intermediate, ratio 0.47–0.65 (Fig. 10a); (c) short, ratio^2 0.44 (Fig. R38). Ordered abc. (CI = 0.38, RI = 0.69)
131. *Direction of R1 laterad 2r*: (a) directed anteriorly, more or less perpendicular to anterior wing margin (Fig. 10a); (b) directed more obliquely laterally (Fig. 10b). (CI = 0.20, RI = 0.64)
132. [Modified from R86] *Extent of R1*: (a) tubular along the entire anterior margin of marginal cell (Fig. R37); (b) tubular only along basal part of anterior margin of marginal cell (not illustrated); (c) ending at or close to anterior margin, not continuing laterally (Fig. R38); (d) ending distinctly before reaching anterior margin (not illustrated). Ordered abcd (CI = 0.19, RI = 0.55)
133. [= Q45] (CI = 0.17, RI = 0.44). *Ibalia* has an areolet, but this is absent in the ground plan of the Ibaliidae (Ronquist, 1995b). As a representative of the Ibaliidae, *Ibalia* was therefore coded as lacking the areolet.
134. *Length of basalis*: (a) short, ratio of R1 + Sc to basalis > 1.1 (Fig. 10a); (b) long, ratio < 1.1 (Fig. 10b). (CI = 0.12, RI = 0.59)
135. [= Q46] (CI = 0.25, RI = 0.50)
136. [= Q44] (CI = 0.50, RI = 0.50)

137. *Angle between R + Sc and R1 + Sc*: (a) no change in direction, R + Sc smoothly continuing in R1 + Sc (Fig. 10b); (b) distinct change in direction, R + Sc angled in relation to R1 + Sc (Fig. 10a). (CI = 0.20, RI = 0.56)
138. *Shape of M at junction with 2r-m*: (a) distinctly angled (not illustrated); (b) straight (Fig. 10a). (CI = 0.12, RI = 0.50)
139. *Hair-fringe along apical margin of wing* (not illustrated): (a) present; (b) very short or absent. (CI = 0.17, RI = 0.29)

Metasoma, female

140. [= R87] (CI = 0.20, RI = 0.65)
141. [= R88] (CI = 0.20, RI = 0.64)
142. [Modified from Q57] *Shape of posterior margin of 3tg in lateral view*: (a) more or less vertical (Figs R41, R42); (b) distinctly oblique (Fig. 11a). (CI = 0.17, RI = 0.58) The posterior margin of 3tg is oblique in *Paramblynotus*, but vertical in the ground plan of the Liopteridae (Ronquist, 1995a,b). As a representative of the Liopteridae, *Paramblynotus* was therefore coded as having state a of this character.
143. [= R89] (CI = 0.22, RI = 0.22)
144. [= R90] (CI = 0.50, RI = 0.67)
145. [= R91] (CI = 0.25, RI = 0.50)
146. [= R92] (CI = 0.11, RI = 0.47)
147. [= R93] (CI = 0.33, RI = 0.50)
148. [= R94] (CI = 0.36, RI = 0.073)
149. [= R95] (CI = 1.00, RI = 1.00)
150. *Irregularly plicate to flabellate protuberance midventrally, close to posterior margin of petiole* (not illustrated): (a) absent; (b) present. (CI = 0.50, RI = 0.00)
151. [= R96] (CI = 0.33, RI = 0.75)
152. [= R97] (CI = 1.00, RI = 1.00)
153. [= R98] (CI = 0.50, RI = 0.80)
154. *Shape of ventral margin of metasoma in lateral view*: (a) oblique, more or less evenly rounded (not illustrated); (b) distinctly angled, anteriorly vertical, posteriorly horizontal (Fig. 11a). (CI = 0.17, RI = 0.62)

Ovipositor

155. [= R99] (CI = 0.14, RI = 0.46)
156. [= R100] (CI = 0.50, RI = 0.50)
157. [= R101] (CI = 0.25, RI = 0.57)
158. [= R103] (CI = 0.12, RI = 0.30)
159. [Modified from R102] *Length of terebra*: (a) long, articulation between second valvifer and second valvulae situated posterior to dorsalmost part of second valvifer (Fig. R46); (b) intermediate, position around dorsalmost part of second valvifer (Fig. R45); (c) short, position of articulation well anterior to dorsalmost part of second valvifer (Fig. 11b). Ordered abc. (CI = 0.12, RI = 0.30)
160. [= R104] (CI = 0.25, RI = 0.33)

Metasoma, male

161. [= R105] (CI = 1.00, RI = 1.00)

Phallus

162. [= R106] (CI = 0.50, RI = 0.67)
163. [= R107] (CI = 0.17, RI = 0.29)
164. [= R108] (CI = 0.33, RI = 0.60)

Biological characters

165. *Life history*: (a) non-alternating generations; (b) alternating sexual and agamic generations. (CI = 1.00, RI = 1.00)
166. *Host plant family*: (a) Asteraceae; (b) Papaveraceae; (c) Rosaceae; (d) Lamiaceae; (e) Valerianaceae; (f) Fagaceae; (g) Fabaceae; (h) Aceraceae. Unordered. (CI = 0.50, RI = 0.63)
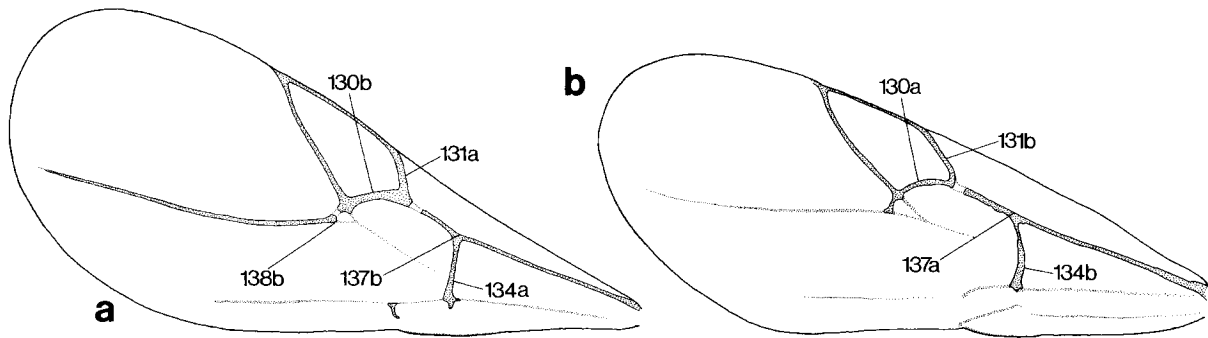
Fig. 10. Left fore wing, dorsal view, females. a, *Aulacidea phlomica*; b, *Synergus crassicornis*.
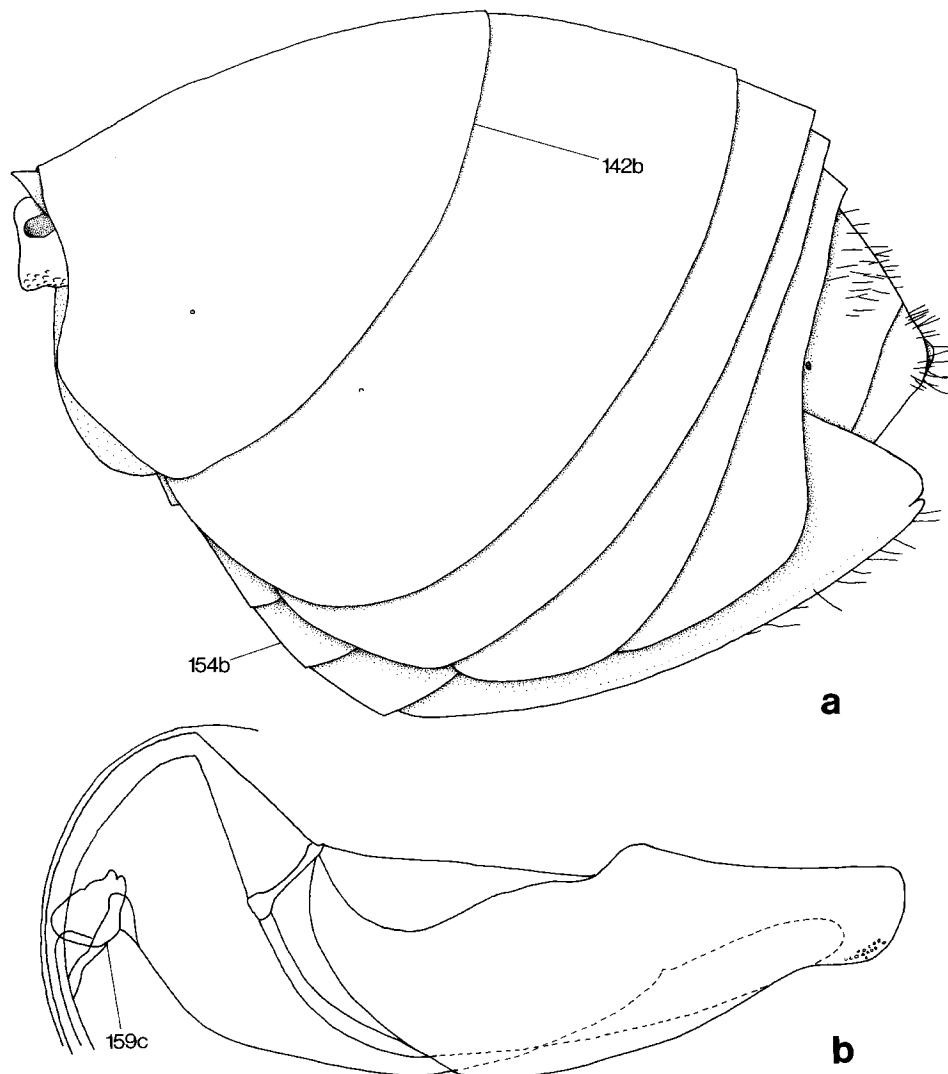

Fig. 11. Characters of the female metasoma and ovipositor. a, Metasoma, lateral view, *Gonaspis potentillae*; b, ovipositor, lateral view, *Diastrophus turgidus*.

Table 3. Observed character states. Explanation of symbols: a–h = monomorphic states; p = a/b polymorphism; q = a/c polymorphism; s = b/c polymorphism; – = character not applicable; ? = state unknown. The multistate characters 7, 10, 16, 19, 38, 40, 43, 45, 47, 51, 55, 59, 74, 75, 77, 84, 85, 90, 98, 106, 126, 130, 132, 140, 148 and 159 were ordered in alphabetic sequence in the analyses, whereas the multistate characters 14, 15, 17, 28, 61, 63, 70, 91, 93, 160 and 166 were unordered.

		Character								
Taxon		1	6	11	16	21	26	31	36	41	
Synergus	1	b–b–b	aaaaa	aaaca	cbbac	ababb	ababb	abaaa	aaaaa	ababc	1
Periclistus	2	b–b–b	aaaaa	aaaca	cbbac	ababb	bbabb	abaaa	aaaaa	ababa	2
Ceroptres	3	b–b–b	aaaba	aaaca	cbaac	ababb	bbaba	abaaa	aaaaa	abbba	3
Synophromorpha	4	b–b–a	aaaba	aaacb	–baab	abaab	bbbbb	abaaa	aaaaa	ababa	4
Xestophanes	5	b–b–a	aaaba	aaabb	–ba–b	baaab	abbab	abaaa	aaaaa	ababb	5
Diastrophus	6	abb–b	ababa	aaacb	–ba–c	baaab	abbab	abaaa	aabaa	aaaab	6
Gonaspis	7	b–b–b	aaaba	aaabb	–ba–c	baaab	abbab	abaaa	aabaa	aaaac	7
Liposthenes	8	abaaa	adaaa	ababa	ccaca	aaaaa	abbab	bbaaa	aabaa	baaab	8
Au. kerneri	9	aaaab	acaaa	aaaba	b????	?????	?????	?????	?????	????b	9
Cecconia	10	b–aba	baaaa	aaaba	a????	?????	???b?	?????	?????	????b	10
Antistrophus	11	b–aba	bcaaa	a?aba	ababa	aaabb	abbaa	abaaa	aabac	aaaab	11
Rhodus	12	b–aba	aaaaa	aaaaa	a????	?????	???a?	?????	????a	????b	12
Hedickiana	13	b–aba	baaaa	aaaaa	a????	?a??b	abab?	?????	b???a	????a	13
Neaylax	14	b–aba	baaaa	aaaaa	abaaa	aaabb	abaaa	abaaa	baaaa	aaaaa	14
Isocolus	15	abaaa	abaaa	aaaba	abaab	aaabb	bbaaa	abaaa	aaaaa	aaaab	15
Au. tragopogonis	16	aaaaa	aaaaa	aaaba	abaac	aaabb	abaaa	abaaa	aaaaa	aaaab	16
Au. phlomica	17	aaaaa	aaaaa	aaaba	a????	?????	?????	?b???	?????	????a	17
Au. verticillica	18	aaaaa	aaaaa	aaaba	a????	?????	???a?	?????	?????	????a	18
Vetustia	19	aaaaa	abaaa	aaaba	b????	?????	??aa?	?b???	?????	????b	19
Panteliella	20	aaaaa	adaaa	baaca	a??b?	aaa??	??a??	aba?a	a????	????c	20
Barbotinia	21	b–aba	baaaa	a?aba	aaaca	aaaaa	abbaa	abaaa	bacaa	aaaac	21
Aylax	22	abaaa	acaaa	baaba	bbaba	aaaba	ababa	abbaa	bacaa	aaaac	22
Iraella	23	abaaa	adaaa	baaba	ababb	aaaba	ababa	abbaa	bacaa	aaaac	23
Timaspis	24	aaaaa	acaaa	baaca	baabb	aaaba	ababa	ababa	aaaaa	aaaac	24
P. hypochoeridis	25	aaabb	aaaaa	baaba	bbabb	aaabb	ababa	ababa	aaaaa	aabac	25
P. centaureae	26	aaaaa	acaaa	baaca	aaaac	ababb	ababa	abbba	aaaaa	aaaab	26
P. phlomidis	27	aaaaa	acaaa	baaca	a????	?????	??ab?	?b???	a????	????b	27
A. lugubris	28	aaaaa	abaaa	baaca	c????	?????	??aa?	?b???	a????	????c	28
A. pannucea	29	aaaaa	aaaaa	baaca	a?aaa	aba?b	?b???	?b???	aa?a?	????b	29
Eschatocerus	30	aaaab	adba-	babca	acaac	aaaba	abab–	bba?b	ab–a–	—cab	30
Diplolepis	31	aaaaa	adaaa	babca	ccaac	aaaaa	ababb	bbbba	abcaa	aacac	31
Himalocynips	32	aaaaa	adaac	bbacb	–cac?	???aa	ab???	?b???	a?c??	?aaad	32
Pediaspis	33	aaaaa	acaba	bbacb	–caba	aaaaa	abbbb	bbbba	abcba	aaqac	33
Plagiotrochus	34	aaaaa	aaaab	babca	bcaab	aaaaa	abcab	babba	abcba	aabac	34
Andricus	35	apaaa	acaab	pabca	ccaab	aaaab	abcab	bpbaa	abbba	aapas	35
Neuroterus	36	aaaab	adbac	bbbca	ccaca	aabaa	abcbb	babbb	abcbc	bacad	36
Biorhiza	37	abaaa	adbac	bbbca	ccaca	aabaa	abcab	babbb	abcbb	bacac	37
Euceroptres	38	abaaa	aaaaa	aaaac	–baaa	aaaab	abaaa	abaaa	aaaaa	aaaac	38
undescr. genus[1]	39	b–aaa	aaaaa	aaaba	a????	?????	?????	?b???	?????	????b	39
Paramblynotus	40	abaaa	aaaac	aaaaa	abaaa	aaaaa	aaabb	abaaa	aabaa	aaaab	40
Ibalia	41	aaaaa	aaaaa	aaaac	–aaaa	aaaaa	aaa??	aaaaa	aaaaa	aaaab	41

[1]Referring to *Aulacidea nigripes* Barbotin (cf. Ronquist, 1994).

Appendix 2. List of unambiguous character changes.

Unambiguous character state changes on the branches of the shortest tree from the heuristic analysis of the complete data set (Fig. 3). The branch numbers (in bold type) correspond to those in Fig. 3; each is followed by a list of character numbers and unambiguously reconstructed state changes.

1: 26 b→a, 45 a→c, 46 a→b, 50 a→b, 51 a/b→c, 59 a→b, 60 b→a, 76 b→a, 79 b→a, 118 b→a, 143 b→a, 159 b→a

2: 109 b→a, 138 a→b

3: 30 b→a, 43 a→b, 107 a→b, 144 b→a, 151 a→b

4: 79 b→a, 138 a→b, 159 b→a

5: 62 a→b, 64 a→b, 84 b→c, 103 a→b

6: 7 a→b, 14 b→c, 73 a→b, 80 a→b, 102 b→a

7: 45 b→c, 85 b→a, 98 b→c, 128 a→b, 148 c→a.

8: 7 c→d, 12 a→b, 61 a→c, 70 a→b, 103 a→b, 118 b→a, 127 a→b, 140 b→c

9: 2 b→a, 5 a→b, 46 a→b, 47 b→a, 120 a→b, 160 a→b

10: 29 a→b, 51 a→b, 85 b→c, 139 b→a, 143 a→b

Table 3, continued.

	Character												
	46	51	56	61	66	71	76	81	86	91	96	101	
1	baabb	cabab	ababa	baaaa	aaaab	baaac	aaaaa	aabbb	aaaba	cabaa	aacbb	abaab	1
2	ababa	aabab	abaab	baaaa	aaaab	baaac	baaba	aabbb	aaabb	cabaa	aacbb	abaab	2
3	aa???	babab	abaab	aaaaa	aaaaa	baaac	baaba	aabbb	aaaba	aaaaa	aacaa	abaab	3
4	ababa	aabaa	abaab	aaaaa	aaaaa	baaaa	bcaaa	aabbb	aaabb	aaaaa	aacaa	abaab	4
5	ababa	aabaa	abaab	ababa	aaaaa	baaaa	bcaba	aabcb	aaabb	aaaaa	aabaa	bbbab	5
6	bbaba	aabaa	abaab	caaaa	aaaaa	aabba	bcabb	aabab	aaabb	aaaaa	aabaa	baaaa	6
7	bbaba	aabaa	abaab	caaaa	aaaaa	aaaba	bcaba	aabaa	aaabb	aaaaa	aacaa	bbaaa	7
8	abbaa	aabaa	abaab	caaaa	aaaab	aaaab	bcabb	aabab	aaabb	cabaa	aabaa	bbbaa	8
9	ba???	a?b aa	abaab	aaaaa	a??aa	aaaab	aaaaa	bbabb	aaabb	cabaa	aa???	?baaa	9
10	ab??a	bbbab	abbbb	aacaa	a??aa	aaacc	baabb	aabcc	ababb	cabaa	aa???	?baa	10
11	ab???	aabab	bbbbb	aacba	aaaaa	aaacc	baabb	babcb	ababb	bacaa	aabaa	bbaaa	11
12	abaaa	a?bab	abbbb	aaaaa	a??aa	aaabc	baabb	babcb	ababb	cabaa	aa???	?baaa	12
13	abaaa	abbab	abbbb	aaaaa	a??aa	aaabc	baabb	aabcb	ababb	babaa	aa???	bbaaa	13
14	ap???	abbaa	abbbb	aaaaa	aaaaa	aaaac	baabb	aabac	ababb	sabaa	aabaa	bbbaa	14
15	abbaa	abbab	ababb	aaaaa	aaaaa	aaaac	aaaaa	baaac	aaabb	cabaa	aabaa	abaaa	15
16	ab???	abbab	ababb	aaaaa	aaaaa	aaaac	baaaa	aaaaa	aaabb	cabaa	aabaa	abaaa	16
17	a????	abbab	ababb	baaaa	a??aa	aaaa?	baaba	b?at?	aaabb	cabaa	aa???	a???b	17
18	a????	a?bab	ababb	baaa?	a??aa	aaaac	bbaba	aabcb	aaabb	cbbaa	aa???	a???a	18
19	a????	abbab	abbbb	baaa?	a??aa	aaabc	bbaba	ba?bb	aaabb	cbbaa	ba???	bbabb	19
20	aa???	b?bab	ababb	baca?	a??aa	aaabc	baaba	babca	aaabs	cbbaa	ba???	bb?ab	20
21	aabaa	cbbab	ababb	baaba	aaaaa	aaaac	baaba	aabaa	aaabb	baaaa	aabaa	bbaaa	21
22	aabaa	cbbab	ababb	aaaaa	aaaad	aaaac	baaba	babaa	aaabb	aabaa	aabaa	bbaaa	22
23	ap???	cbbab	ababb	aaabb	aaaaa	aaaac	baaaa	babba	ababc	bacaa	aabaa	bbbaa	23
24	bbaab	cabac	abaca	baabb	aaaad	aaaac	babba	aabbb	aaabc	baabb	aaaaa	bbbba	24
25	ab???	abbac	abacb	aaaab	aaaad	aaabc	babba	aabcb	aaabc	bacba	aaaaa	bbabb	25
26	bb???	abbac	abacb	aaabb	aaaad	aaaac	babaa	aabcc	aaabc	bacbb	aaaaa	bbaab	26
27	b????	a?bac	abacb	aaab?	a??ad	aaabc	babaa	?abdc	aaabc	bacbb	aa???	?baab	27
28	b????	bbbac	abacb	baab?	a??ad	aaaac	babaa	?abdb	aaabc	baaba	aa???	?baab	28
29	b????	a?bac	ab?cb	baaba	a??ad	aaaac	aab?a	aa?dc	aaabb	bacba	aa???	?baab	29
30	bcbab	dbb—	bbbcb	aaabb	abbbc	a–aac	b–baa	b—dc	b–abc	bacbb	a–aaa	ba—a	30
31	bbaab	dabb–	bbacb	baabb	abbbc	abaac	babaa	baabc	aaabb	aaaba	aaaaa	baaba	31
32	b????	abbaa	bbaab	bbaab	b??ab	babaa	bbabb	abbaa	b-bbb	aaaba	abba?	baaba	32
33	babab	bbbaa	?babb	ababb	bbaab	abbaa	bbabb	abbaa	b-bbb	aaaba	abbaa	babba	33
34	aaaab	dabb–	abacb	aabbb	abaaa	abbab	bcaaa	bbbbb	aaabc	paaba	abbaa	babba	34
35	baaaa	dbbb–	bbabb	babab	abaaa	abbas	bpaaa	abbac	aaabb	aaaaa	pabaa	bapaa	35
36	ba???	dabb–	abacb	babab	abbab	abbaa	bcbaa	abadc	aaabc	aaabb	aaaaa	babba	36
37	baaba	dbbb–	bbabb	babbb	abbab	abbaa	bcaaa	abbab	aaabb	aaaaa	babaa	babba	37
38	aaaba	abbab	aaaba	aaa?a	aaaaa	aaaac	aaaba	aaaaa	aaaba	aaaaa	aabaa	baaaa	38
39	bbbaa	abbbb	aaaba	baaa?	–??aa	aaaac	baaba	aaacb	aaabb	caaaa	aa?a?	?aaba	39
40	apbaa	aaaab	aaa-a	aaaaa	aaaaa	aaaaa	aaaaa	a—aa	aaaaa	aaaba	aacaa	baa–b	40
41	aapab	aaaab	–aaba	aaaa–	aaaaa	aaaaa	abaaa	a–aaa	aaaaa	aabba	baaaa	–aaaa	41

11: 7 a→c, 52 b→a, 56 a→b, 64 a→b, 91 c→b, 93 b→c, 154 b→a

12: 6 b→a, 111 a→b, 127 a→b, 134 a→b

13: 29 a→b, 91 c→b

14: 55 b→a, 85 b→c, 103 a→b, 148 b→a

15: 2 a→b, 7 a→b, 26 a→b, 76 b→a, 85 b→c, 118 b→a, 127 a→b, 132 b→c, 137 b→a

16: 20 b→c, 85 b→a

17: 105 a→b, 124 a→b, 132 b→a, 160 a→b

18: 106 b→c, 135 b→a

19: 16 a→b, 58 a→b, 104 a→b, 127 a→b, 130 b→a, 132 b→a, 134 a→b

20: 7 b→d, 11 a→b, 14 b→c, 45 b→c, 51 a→b, 63 a→c, 85 b→a, 130 b→c, 132 b→c, 133 a→b, 142 b→a

21: 1 a→b, 4 a→b, 6 a→b, 17 b→a, 19 b→c, 28 a→b, 61 a→b, 107 a→b, 109 a→b, 145 a→b, 148 b→c, 155 a→b, 160 a→b

22: 70 a→d, 93 a→b, 120 a→b

23: 7 c→d, 87 a→b, 93 a→c, 126 b→c

24: 52 b→a, 60 b→a, 61 a→b, 110 a→b, 135 b→a, 158 a→b

25: 4 a→b, 5 a→b, 7 c→a, 14 c→b, 43 a→b, 46 b→a, 74 a→b, 153 a→b, 159 c→a, 160 a→c

26: 20 b→c, 111 a→b

27: 74 a→b

28: 16 a→c, 45 b→c, 51 a→b, 85 c→b, 93 c→a, 140 b→c

29: 7 b→a, 76 b→a, 90 c→b, 134 b→a

30: 5 a→b, 8 a→b, 16 b→a, 33 b→a, 35 a→b, 45 c→b, 47 b→c, 58 a→b, 84 b→d, 86 a→b, 93 a→c, 95 a→b, 107 a→b, 112 a→b,

Table 3, continued.

	Character													
	106	111	116	121	126	131	136	141	146	151	156	161		
1	aaaba	abbba	bbaaa	aabbb	aaaaa	baabb	baaaa	aaabb	bbcba	aaaba	abbab	baaaa	f	1
2	aaaaa	abbba	bbbaa	aabbb	aaaaa	baabb	babaa	aabbb	bbcba	aaaba	abbbb	baaaa	c	2
3	ababa	ababa	bbbaa	aabbb	aaaaa	baabb	bbaaa	aabab	bbcba	baabb	aabbb	????a	f	3
4	aaaba	abaaa	bbbaa	aabbb	aaaab	bcaab	bbbaa	aabbb	bbcba	aaaba	abbab	baaaa	c	4
5	aaaba	aaaaa	bbbaa	aabbb	aaaaa	bbaab	bbaaa	aaaba	abcba	aaaab	aabca	aabaa	c	5
6	aaaaa	aaaaa	abbaa	aabbb	aaaab	bcaab	bbaab	aaaaa	abcaa	aaaab	aabca	aabaa	c	6
7	aaaaa	aaaaa	bbbaa	aabbb	aabab	bcaab	bbaab	abaaa	aba-a	aaaab	aabca	aabaa	c	7
8	aaaaa	aaaaa	abaaa	aabaa	abaab	bcbab	bb–ac	abbaa	abcaa	aaaaa	aabca	aaaaa	d	8
9	aaaaa	a????	??b?b	?abaa	aaaab	bcbab	bb–ab	abbaa	a???a	?aaa?	aab?b	????a	d	9
10	bbaaa	a????	??b?a	aabaa	aaaab	bcbaa	bb–ac	abba?	a?c?a	?aab?	aa??a	????a	e	10
11	cbaaa	aaaaa	abbaa	aabaa	aaaab	bcbaa	bb–bc	abaaa	bbcaa	aaaaa	aabca	????a	a	11
12	caaaa	b????	??b?a	aabaa	abaab	bcbba	bb–bc	abaaa	a?caa	?aab?	aab?a	????a	d	12
13	baaaa	a????	??b?a	aabaa	aaaab	bcaab	bbabc	abaaa	b??aa	?aab?	aa??a	????a	d	13
14	baaaa	aaaaa	abbaa	aabaa	aaaab	bcaab	bbaab	abaaa	bba-a	aaaba	aabba	????a	d	14
15	baaba	aaaaa	abaaa	aabaa	abaab	acaab	babbb	aaaaa	bbbaa	aaaba	abbaa	aaaba	a	15
16	baaba	aaaaa	abbaa	aabaa	aaaab	abaab	bbbaa	aabaa	bbbaa	aaaba	abbaa	????a	a	16
17	baaba	a????	?bb?a	?abba	aaaab	aaaab	bbbbb	abbaa	a?s??	?aab?	abb?b	????a	d	17
18	caa?a	a????	?bb?a	?aba?	aaaab	bbaaa	bbbab	abaaa	a????	?aab?	aa??a	????a	d	18
19	baaba	a????	??b?a	?aba?	abaaa	baab?	bbbac	abaaa	b?s??	?aaa?	aab?a	????a	d	19
20	baa??	???aa	????a	?aba?	aaaac	bcbab	bb–ac	aaaa?	b????	?aaab	aabca	????a	d	20
21	ababa	aaaaa	abbaa	aabaa	aaaab	bbabb	bbbab	aaaab	abcab	aaaab	aaabb	aabba	b	21
22	aaaaa	aaaab	abbab	aabaa	baaab	bcabb	bbbac	aabaa	aba–b	aaaaa	aabba	aabba	b	22
23	aaaaa	aaaab	abbaa	aaaaa	caaab	bcabb	bbbab	aabaa	aba–a	aaaaa	aaaca	????a	b	23
24	aaaab	aaaab	abbaa	aabaa	baaaa	ababa	bbaac	baaaa	abaa	baaaa	aabca	aaaba	a	24
25	aaaaa	aaaab	abbaa	aabaa	baaaa	bbabb	bbbac	baaaa	abaaa	aabaa	aaaac	aa??a	a	25
26	aaaaa	baaab	abbaa	aabaa	baaaa	ababb	bbaab	baaaa	aba–a	aaaab	aaaca	????a	a	26
27	aab–a	a????	??b?a	?aa??	?a?aa	aaab?	bbbab	baaaa	a????	?aaa?	a?b?b	????a	d	27
28	aab–a	a????	??b?a	?aaa?	baaap	aaab?	babbc	aaaaa	b????	?aaa?	abb?b	????a	?	28
29	aab–a	a????	??b?a	?aaa?	baaaa	aaaa?	babbb	aaaaa	b????	?aaa?	abb?a	????a	?	29
30	abb–b	–baab	aab–a	–aaaa	baaab	bdb—	ab–bc	aaaab	–ba–a	ba-aa	?abca	ababa	g	30
31	aab–b	baaab	abbaa	baaaa	aabbb	ababb	bbaac	baaaa	aba–a	baaaa	aaaba	????a	c	31
32	aaaaa	ba??a	a?baa	?baaa	caaab	bcba–	bb–ab	baaaa	–?a–a	?aba?	aa??a	?????	?	32
33	aaaaa	baaaa	abbaa	bbaaa	baaab	bcaab	bbaac	baaaa	aba-a	babab	aaaca	aabbb	h	33
34	abaab	bbabb	a?bab	baaaa	baaac	bcaab	bbaac	baaaa	aaa–a	ba–ab	babca	abbab	f	34
35	ababa	bbaba	abbab	baaba	baapc	bcabb	bbbac	bapab	bba–a	bbbbb	baaba	abbab	f	35
36	abaab	–babb	aabbb	baaba	caaac	bcaab	baaac	aaaaa	aaa–b	bbbab	baaaa	????b	f	36
37	abaaa	bbaba	aabbb	baaba	caabc	bcaab	bbaac	baaaa	aaa–a	bbbbb	aaaca	abaab	f	37
38	aaaaa	aaaaa	abbaa	aabba	aabaa	aaaba	baaac	bbaaa	bbbaa	aaaaa	aaaca	aaaaa	f	38
39	aaaaa	aa???	??a?a	aaba?	aabaa	aaaba	baaac	bbaaa	b???–	?aa??	aab?b	????a	b	39
40	–aaba	aaaaa	–abaa	aabaa	aaaaa	abbbb	aa–ab	aaaaa	aacaa	aaaaa	aabaa	a???a	–	40
41	aaaaa	a-a—	–aaaa	aaaaa	caa—	–abab	aaaab	aaaaa	aaa–a	aaaaa	??aaa	aaaaa	–	41

117 b→a, 132 c→d, 133 a→b, 136 b→a, 139 a→b, 141 b→a, 145 a→b, 158 a→b

31: 16 b→c, 52 b→a, 61 a→b, 126 b→a, 128 a→b, 129 a→b, 131 b→a, 132 c→b, 159 c→b

32: 7 c→d, 10 a/b→c, 19 b→c, 45 c→d, 51 b→a, 59 b→a, 61 a→b, 64 b→a, 71 a→b, 72 b→a, 126 b→c, 133 a→b, 140 c→b

33: 9 a→b

34: 7 c→a, 46 b→a, 52 b→a, 56 b→a, 110 a→b, 158 a→b

35: 25 a→b, 34 b→a, 38 c→b, 104 b→a, 109 a→b, 134 a→b, 138 a→b, 145 a→b, 146 a→b

36: 5 a→b, 29 a→b, 40 b→c, 45 c→d, 52 b→a, 56 b→a, 78 a→b, 83 b→a, 84 a/b→d, 95 a→b, 98 b→a, 110 a→b, 137 b→a, 141 b→a, 159 b/c→a

37: 2 a→b, 96 a→b, 129 a→b, 156 b→a

38: 15 a→c, 45 b→c, 48 b→a, 49 a→b, 124 a→b, 166 b→f

39: 1 a→b, 46 a→b, 47 a→b, 54 b→a, 61 a→b, 84 a→c, 85 a→b, 104 a→b, 118 b→a, 160 a→b

40: 27 a→b, 52 a→b, 53 a→b, 75 a→b, 79 a→b, 89 a→b, 94 b→a, 117 a→b, 133 b→a, 136 a→b, 147 a→b, 159 a→b/c

41: 57 a→b, 60 a→b, 83 a→b, 102 a→b, 130 a→b, 131 a→b, 137 a→b

42: 47 a→b, 85 a→b, 134 b→a, 166 b→d

43: 16 a→b/c, 28 a→b, 30 a→b, 52 b→a, 55 b→a, 59 b→a, 75 c→b, 77 a→b/c, 148 b→c

44: 3 a→b, 9 a→b, 15 a→b, 20 a→b, 48 b→a, 49 a→b, 75 b→a, 124 a→b, 125 a→b, 166 d→c

45: 42 a→b, 44 a→b, 71 a→b, 84 a→b, 105 a→b, 109 a→b, 140 b→a, 144 a→b, 149 a→b

46: 14 b→c, 22 a→b, 26 a→b, 29 a→b, 45 b→a, 98 b→c, 101 b→a,

112 a→b, 143 a→b, 145 a→b, 146 a→b, 154 a→b, 159 c→b, 160 a→b, 161 a→b

47: 5 a→b, 15 b→a, 20 b→c, 24 a→b, 28 b→a, 55 a→b, 75 a→c, 77 c→a, 114 a→b, 132 b/c→a, 134 a→b

48: 9 b→a, 18 a→b, 61 a→b, 70 a→b, 91 a→c, 93 a→b, 99 a→b, 100 a→b, 113 a→b, 137 b→a

49: 5 a→b, 20 b→c, 46 a→b, 61 a→c, 74 a→b

50: 7 a→c, 80 a→b, 133 a→b, 143 a→b

51: 24 a→b, 106 a→b, 154 a→b

52: 1 a→b, 4 a→b, 6 a→b, 14 b→a, 58 a→b, 80 a→b, 87 a→b

53: 74 a→b, 84 a→c, 139 a→b, 140 b→c

54: 133 a→b, 135 b→a

55: 14 a→b, 63 a→c, 74 b→c, 107 a→b

56: 109 a→b, 138 a→b

57: 83 b→a, 131 b→a, 157 a→b

58: 79 b→a, 142 b→a, 166 d→a

59: 84 a→b/c, 92 a→b

60: 7 a→b, 74 a→b, 96 a→b, 105 a→b, 140 b→c, 154 b→a

61: 36 a→b, 38 a/b→c, 45 b→c, 51 a→c, 138 a→b

62: 7 a→c, 11 a→b, 24 a→b, 29 a→b, 33 a→b, 115 a→b, 126 a→b, 148 b→a

63: 20 a→b, 65 a→b, 84 a→b

64: 2 b→a, 14 b→c, 34 a→b, 36 b→a, 46 a→b, 85 a→b, 94 a→b, 104 a→b, 141a→b

65: 38 c→a, 55 b→c, 70 a→d, 130 b→a, 132 c→b

66: 25 a→b, 51 c→a, 84 b→c, 93 a→c, 105 a→b

67: 16 b→a, 19 b→a, 22 a→b, 45 c→b, 85 b→c, 104 b→a, 140 c→b

68: 84 c→d, 108 a→b, 123 b→a, 132 b→a, 158 a→b

69: 7 c→b, 61 a→b, 137 b→a, 139 a→b, 141 b→a, 146 a→b

70: 30 a→b, 31 a→b, 37 a→b, 56 a→b, 67 a→b, 72 a→b, 102 b→a, 111 a→b, 121 a→b

71: 7 c→d, 20 b→c, 43 a/b→c, 68 a→b, 69 a→b, 70 a→c, 85 b→c, 108 a→b, 110 a→b

72: 39 a→b, 73 a→b, 75 c→b, 77 a→b, 82 a→b, 134 b→a, 153 a→b, 155 a→b, 165 a→b

73: 12 a→b, 15 a→b, 51 c/d→b, 62 a→b, 66 a→b, 70 a→b, 75 b→a, 80 a→b, 85 b→a, 86 a→b, 88 a→b, 122 a→b

74: 29 b→a, 32 →a, 63 a→b, 107 a→b, 112 a→b, 114 a→b, 120 a→b, 130 b→c, 156 a→b, 164 b→a

75: 16 b→c, 50 b→a, 61 a→b, 124 a→b, 152 a→b

76: 7 c→d, 8 a→b, 10 b→c, 12 a→b, 19 a/b→c, 20 b→a, 23 a→b, 35 a→b, 40 a→b, 41 a→b, 43 b→c, 68 a→b, 70 a→b, 75 b→a, 117 b→a, 119 a→b, 126 b→c

77: 128 a→b, 135 b→a, 140 b→c, 141 a→b, 146 a→b