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A fully web-illustrated morphological phylogenetic study of relationships among oak gall wasps and their closest relatives (Hymenoptera: Cynipidae)

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Abstract

Large morphological phylogenetics analyses are often poorly documented because of the constraints of traditional print journals, making it difficult to critically evaluate the data and build on it in future studies. We use modern information technology to overcome this problem in a comprehensive analysis of higher relationships among oak gall wasps and their closest relatives. Our morphological characters are documented by more than 2,000 images deposited in the open web image database Morphbank (http://www.morphbank.net), allowing one-click access from character and character state descriptions to the raw data.

The oak gall wasps (Cynipidae: Cynipini) form one of the largest specialized radiations of galling insects with almost 1,000 described species attacking oaks or oak relatives. According to previous morphological studies, the Cynipini form a monophyletic clade, the Woody Rosid Gallers (WRG), together with three small cynipid tribes (Diplolepidini, Eschatocerini, and Pediaspidini). The WRG all attack woody representatives of the rosid clade of eudicots. Little was previously known about higher WRG relationships. We studied 54 exemplar taxa of WRG, including representatives from 34 of the 41 valid genera of oak gall wasps, and two outgroups. The study resulted in 308 characters, 283 from morphology and 25 from biology and distribution; most of these are original to the present paper.

Parsimony analyses supported the monophyly of three major WRG lineages: Diplolepidini + Eschatocerini, Pediaspidini + *Paraulax*, and Cynipini. The poorly known South American genus *Paraulax*, developing in galls on *Nothofagus*, is moved from Cynipini to Pediaspidini to reflect these results. The single Japanese species described in *Paraulax* by Shinji (types lost) is transferred to *Ceroptres* as *C. quereicola* (Shinji 1938) **comb. nov**. Two major lineages of oak gallers were recognized in most analyses: (1) the *Neuroterus*-group (*Neuroterus*, *Pseudoneuroterus*, the previously recognized genus *Trichagalma*, *Plagiotrochus*, possibly also Palearctic *Dryocosmus* and *Aphelonyx*+*Disholcaspis*); and (2)

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the *Cynips*-group (*Cynips*, *Belonocnema*, *Atrusca*, *Acraspis*, *Philonix*, *Biorhiza* and *Trigonaspis*). The large and problematic genus *Andricus* was paraphyletic in some analyses and monophyletic in others, with *Disholcaspis spectabilis* being the sister to other Cynipini in the former case and European *Callirhytis* in the latter.

Our results suggest that WRG are conservative in their host plant preferences but there is no evidence for parallel insect-plant cladogenesis. Distributional patterns suggest a possible origin for the oak gall wasps in the Nearctic but the picture is otherwise complicated. Both heterogeny, the cyclical alternation of sexual and parthenogenetic generations, and heteroecy, the use of different sections of *Quercus* as host for the two generations, appear to have evolved twice within the WRG.

Key words: Morphbank, Cynipini, Diplolepidini, Pediaspidini, Eschatocerini, taxonomy, phylogeny, host plant, distribution

Introduction

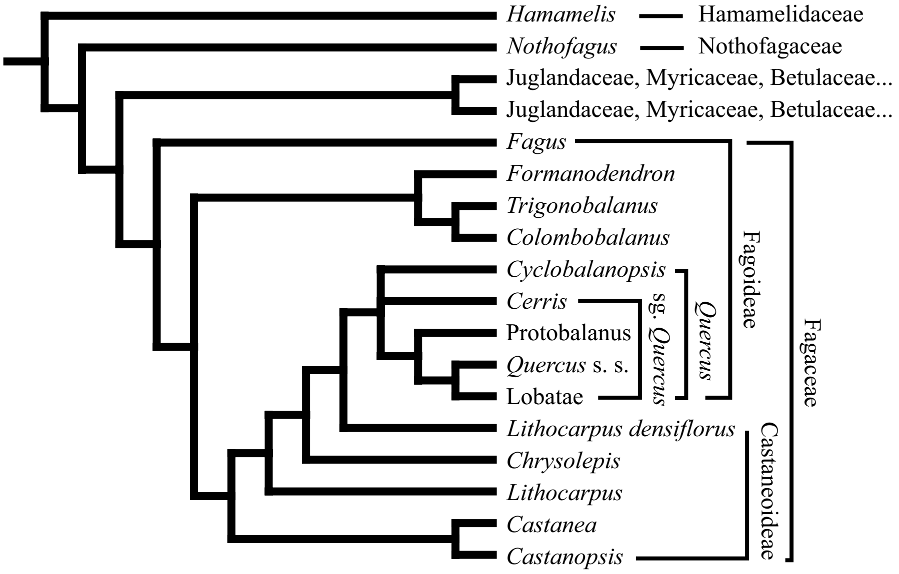
Despite rapid progress in the development of molecular techniques, morphological phylogenetics continues to play an important role in evolutionary studies. Surprisingly often, morphological characters can contribute significant phylogenetic signal even when combined with Tmuch larger sets of molecular characters (for an example involving gall wasps, see Nylander *et al.* 2004). Even when this is not the case, there is a growing interest in mapping comparative morphological data onto phylogenies to better understand the morphological adaptations characterizing different clades, and to provide morphological characters for identification purposes and for the placement of taxa that are difficult to sequence. Dating phylogenies using fossils is also becoming increasingly important, and it ultimately depends on an accurate understanding of how morphology can be used to place fossils.

Unfortunately, large morphological phylogenetics analyses are typically poorly documented because of the constraints of traditional print journals. This makes it difficult to critically evaluate the data and build on it in future studies, effectively slowing progress in this field. Modern information technology can be used to overcome this problem, as we show here in a comprehensive, largely morphology-based analysis of gall wasp relationships (Hymenoptera: Cynipidae). Our morphological characters are documented by more than 2,000 images deposited in the open web image database Morphbank (http://www.morphbank.net), which provides long-term archiving of, and stable URL links to, high-resolution biological images and collections of such images. Each character in our dataset is hyperlinked to the relevant set of images, allowing one-click access to information that is very close to the raw data on which our observations are based.

The gall wasps (Hymenoptera: Cynipidae) have long since drawn attention for their spectacular galls, especially those on oaks and roses, which even have common English names like the marble gall of *Andricus kollari* (Hartig) and the bedeguar gall of *Diplolepis rosae* (Linnaeus). These two species both belong to the woody rosid gallers (WRG), a lineage of gall wasps first established based on morphological evidence (Liljeblad & Ronquist 1998; Ronquist 1999). The WRG, the higher phylogeny of which forms the main focus of this paper, all make galls on woody plants of the eudicot subclass Rosidae. The WRG include the cynipid tribes Diplolepidini, Eschatocerini, Pediaspidini and Cynipini but exclude a few other cynipid species with a similar habit, namely the species of *Diastrophus* galling *Rubus* bushes, which belong to the otherwise herb galling tribe Aylacini. The WRG also exclude the phytophagous cynipid inquilines (gall guests) belonging to the tribe Synergini, most members of which inhabit galls induced by WRG.

As currently construed, the Cynipidae comprise only one extant subfamily divided into the six tribes mentioned above. Of the two tribes outside the WRG, the Aylacini and Synergini have around 170 species each. This leaves roughly 1,000 described species in the WRG tribes. In Diplolepidini, there are 55 species in two genera, *Diplolepis* and *Liebelia*, all inducing galls on roses. The three species of *Eschatocerus*, the single genus in the tribe Eschatocerini, are found on *Acacia* and *Prosopis* (Fabaceae). There are only two Pediaspidini species, of which the sycamore (maple) gall wasp, *Pediaspis aceris* (Gmelin), has its host in Sapindaceae (which now includes Aceraceae: Angiosperm Phylogeny Group 2003). The host of the other, *Himalocynips vigintilis* Yoshimoto, is unknown.

In the remaining WRG tribe, Cynipini (oak gall wasps), we find the vast majority of cynipid species, about 70%, or around 900 of the family's around 1,300 valid species. With only a few notable exceptions, they occur exclusively on oaks from *Quercus* subgenus *Quercus*. Two species are known from the other, strictly Southeast Asian, oak subgenus *Cyclobalanopsis.* In 1940 and 1941 Shinji described *Andricus shirokashi* and *A. shirokashicola* respectively, from leaf galls on the evergreen *Quercus (Cyclobalanopsis) myrsinaefolia* in Japan, although he mistakenly spelled it *Cyclonopsis* (Shinji 1940, 1941). Other species with hosts outside of the genus *Quercus*, but still among its closest relatives in the Fagaceae, (Tree 1) are *Andricus mendocinensis* Weld on tan bark oak (*Lithocarpus densiflorus*), *Dryocosmus kuriphilus* Yasumatsu on chestnuts (*Castanea*), and *Dryocosmus castanopsidis* (Beutenmueller) and an undescribed species from a single-chambered leaf gall (Weld 1952, 1957) on chinquapins (*Chrysolepis chrysophylla* and *C. sempervirens*, both formerly in *Castanopsis*). The tribe Cynipini also includes the poorly known and peculiar genus *Paraulax* from South America. Although there was no host record for the type *P. perplexa* Kieffer, several undescribed species have since been reared from galls on southern beech (Nothofagaceae: *Nothofagus*; Pujade-Villar *et al.* 2001; De Santis *et al.* 1993; Liljeblad unpublished; Nieves-Aldrey unpublished). In 1938, Shinji described a second species, *P. quereicola* from Japan, but unfortunately the types are lost. However, the host plant was not *Nothofagus*, but *Quercus*, and judging from the description the insect is an inquiline (see below). The tribal affinity of *Paraulax* has always been problematic, all the more so since the location of the types of *P. perplexa* are unknown, but because of the former taxonomic inclusion of *Nothofagus* in Fagaceae it has tentatively been placed in the Cynipini (Ronquist 1999).



TREE 1. Summary of relationships between "higher" Hamamelididae, including genera of Fagaceae (modified from Manos & Steele, 1997; Manos *et al.*, 2001).

The WRG are small insects (2-9 mm), with the Cynipini harboring the largest species. Their generally compressed habitus and black-brown-reddish coloration are typical for cynipids, but they can usually be recognized by a medially narrow pronotum and an enlarged third abdominal tergum. Furthermore, it is only in the WRG we find densely pubescent cynipids, and cynipids with reduced or absent wings are extremely rare outside of this group. Gall wasps occur almost exclusively in the temperate regions of the northern hemisphere, with the majority of the species of WRG being described from the Nearctic region (Table 1). This may be at least partly explained by the distribution of the host plants, as the diversity of oaks is greatest in the Nearctic (Manos *et al.* 1999).

TABLE 1. Overview of geographic distribution of species in the WRG tribes.

Geographic region	Diplolepidini	Eschatocerini	Pediaspidini	Cynipini[1]
Palearctic	23	0	2	270
Nearctic	32	0	0	653
Neotropic[2]	0	3	1[3]	0[3]

[1]Not counting the Japanese *Ceroptres quereicola*, here transferred from *Paraulax*. [2]Central America here regarded as Nearctic because of the distribution of *Quercus* extending from the north down to the southernmost Neotropic. [3]Not including *Pediaspis* and some species of Cynipini, which are introduced to South America (Pujade-Villar & Diaz, 2001); for information about Cynipini species in northern South America, see Fergusson (1995), Nieves-Aldrey (2005), and Pujade-Villar and Hanson (2006).

The WRG, in particular the oak gall wasps (Cynipini), are well known for peculiarities in their life history, including heterogeny (cyclical alternation between sexual and parthenogenetic generations) and heteroecy (alternation between host plants). Heterogeny (or heterogony) is solely known from *Pediaspis aceris* and the oak gall wasps in the tribe Cynipini. Of the latter, the life cycle is only known for about 100 of the 925 species (Pujade-Villar *et al.* 2001; Melika et al. 2001; Pujade-Villar *et al*. 2003; Folliot et al. 2004; Folliot & Pujade-Villar 2006; Abe 2006; Pujade-Villar *et al*. 2007) but many of the species with poorly known life histories are likely to have a cyclical life-history (Stone *et al*. 2008). This is particularly obvious for the species known only from a parthenogenetic generation with reduced wings; they most likely have an alternating, fully winged migratory sexual generation. Generally there is a sexual generation in spring and a parthenogenetic in fall, with galls differing both in kind and location, and in the case of heteroecy even host plant (Stone *et al.* 2002). This contributes to the problematic taxonomy of the oak gall wasps, since part of the current classification and identification is based on host plant choice and gall characteristics. The two generations are often morphologically strikingly different and have sometimes been described as different species, occasionally even placed in separate genera (Pujade-Villar *et al.* 2001).

Almost all WRG are highly host specific, being confined to one or a complex of closely related host species. The exception is some European species of *Andricus* and *Callirhytis*, and involves heteroecy. In the case of *Andricus* the bisexual generation has its host in section *Cerris* sensu Camus and the parthenogenetic generation in *Quercus* s.s., while for *Callirhytis* it is the other way around. Each generation is, however, still host specific. The subgenus *Quercus* is divided into four sections (Tree 1; Manos *et al.* 1999; Manos *et al.* 2001) and gall wasps are known from all of them. The majority is found on the Holarctic white oaks (section *Quercus* sensu stricto), with fewer numbers on the Nearctic red oaks (Lobatae), golden cup or intermediate oaks (Protobalanus) and the Palearctic section *Cerris* sensu Camus (including the *Ilex*-group).

The taxonomy of the smaller WRG tribes is relatively unproblematic but this is not the case for the Cynipini. Of the 58 genera in the family (not counting *incertae sedis*: *Poncyia* which may be an inquiline, or *Australofigites*, which probably is a synonym to an introduced Aylacini), 24 currently reside in this tribe (Table 2). In a comprehensive revision of the tribe, Melika and Abrahamson (2002) recently synonymized several Cynipini genera. After this paper appeared, *Pseudoneuroterus* has been reestablished as a valid genus and *Repentinia* has been moved there (Pujade-Villar *et al*. 2004); *Fioriella* was synonymized with *Plagiotrochus* (Melika *et al*. 2001); *Liodora* was synonymized with *Andricus* (Pujade-Villar 2003); *Trichagalma* has been synonymized with *Neuroterus* (Abe 2006); and *Chilaspis* has been synonymized with *Dryocosmus* (Ács *et al.* 2007). *Paraulax* is transferred in this paper to Pediaspidini (see below).

TABLE 2. All genera of WRG with some distributional and host plant data. Names synonymized after Weld (1952) indicated as separate entries. Data taken from Liljeblad (in prep.) current as of Apr 24, 2008.

Genus	Species	Distribution	Host
Diplolepis Geoffroy	46	HA	*Rosa*
Liebelia Kieffer	9	PA	*Rosa*
Eschatocerus Mayr	3	NT	*Acacia, Prosopis*
Pediaspis Tischbein	1	WPA	*Acer*
Himalocynips Yoshimoto	1	EPA	?
Paraulax Kieffer	1[1]	NT	*Nothofagus*
Acraspis Mayr	32	NA	Q
= *Paracraspis* Weld	*3*	WNA	P
Amphibolips Reinhard	40	NA	L
Andricus Hartig	409	HA	Li, Cy, C, L, P, Q
= *Dros* Kinsey	*11*	WNA	Q
= *Erythres* Kinsey	*2*	WNA	L
= *Liodora* Förster	*6*	HA	Q
= *Parandricus* Kieffer	*1*	EPA	?
= *Trichoteras* Ashmead	*8*	WNA	P, Q
Aphelonyx Mayr	5	PA	C
Atrusca Kinsey	63	NA	Q
Bassettia Ashmead	8	NA	L, Q
Belonocnema Mayr	2	NA	Q
Biorhiza Westwood	9[2]	PA	Q
= *Sphaeroteras* Ashmead	23[3], *9*	NA	(L), Q
Callirhytis Förster	37	HA	C, L, P, Q
Cynips Linnaeus	39	PA	Q
= *Antron* Kinsey	26[4], *33*	WNA	Q
= *Besbicus* Kinsey	*8*	WNA	Q
Disholcaspis Dalla Torre & Kieffer	52	NA	Q
Dryocosmus Giraud	28	HA	Ca, Ch, C, L, P, (Q)
= *Chilaspis* Mayr	*3*	WPA	C
Eumayria Ashmead	6	NA	L, (Q)
= *Trisoleniella* Rohwer & Fagan	*4*	ENA	L, (Q)
Eumayriella Melika & Abrahamson	2	ENA	L
Heteroecus Kinsey	12	WNA	P
Holocynips Kieffer	4	NA	L, P, Q
Loxaulus Mayr	14	NA	L, P, Q
Neuroterus Hartig	92[5]	HA	C, Q
= *Neoneuroterus* Monzen	*5*	EPA	C, Q
= *Trichagalma* Mayr	*1*	EPA	C
Odontocynips Kieffer	1	ENA	Q
Philonix Fitch	7	ENA	Q

......*continued*

TABLE 2 (continued)

Genus	Species	Distribution	Host
Phylloteras Ashmead	9	ENA	Q
= *Euxystoteras* Lyon, Xystoteras	*1*	WNA	Q
= *Xystoteras* Ashmead	*3*	ENA	Q
Plagiotrochus Mayr	17	PA	C
= *Fioriella* Kieffer	*1*	PA	C
Pseudoneuroterus Kinsey	1	PA	C
= *Repentinia* Maisuradze	*1*	PA	C
Trigonaspis Hartig	21	PA	Q
= *Belizinella* Kovalev	*2*	EPA	Q
= *Ussuraspis* Kovalev	*1*	EPA	Q
= *Xanthoteras* Ashmead	*24*	NA	Q
Zopheroteras Ashmead	5	ENA	L, Q

HA = Holarctic, PA = Palearctic, NA = Nearctic, NT = Neotropic, E = Eastern, W = Western, Ca = *Castanea*, Ch = *Chrysolepis*, Li = *Lithocarpus*, Cy = *Quercus* subgenus *Cyclobalanopsis*, C = section *Cerris*, L = section *Lobatae*, P = section *Protobalanus*, Q = section *Quercus* s.s. Letters in brackets represent a single occurrence. Number of species in genera before their recent synonymization shown in italics.

[1] Not including the Japanese *Ceroptres quereicola*, here transferred from *Paraulax*.

[2] Not including a species described from Australia, which probably is introduced.

[3] Not transferred from *Sphaeroteras* by Melika and Abrahamson (2002).

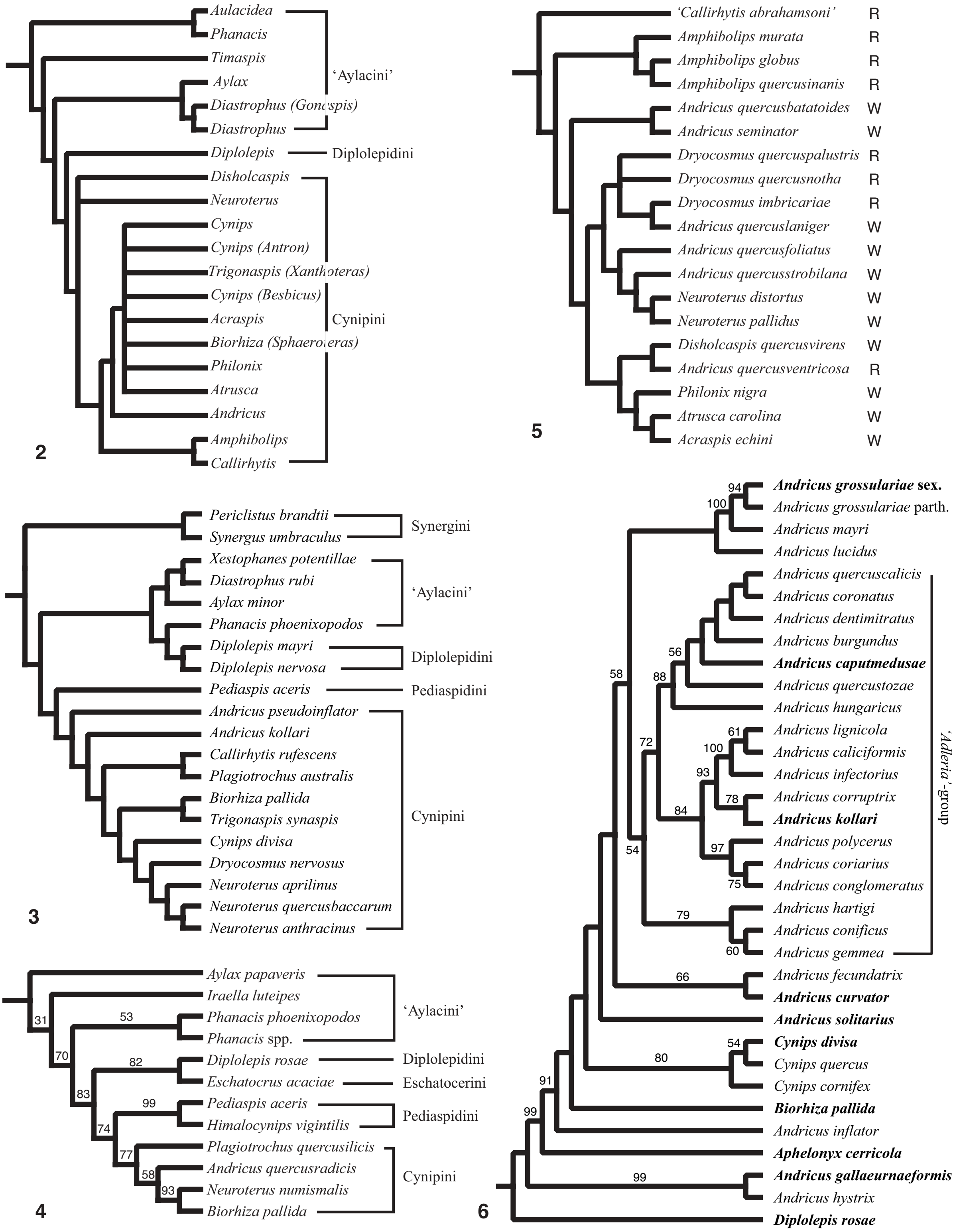
[4] Not yet examined and therefore not transferred to *Cynips* although *Antron* as a genus was synonymized with *Cynips* by Melika and Abrahamson (2002).

[5] Not including a species described from Australia, which probably is introduced.

The taxonomy and systematics of the Cynipini have long been chaotic, especially for the large genus *Andricus* but also for the North American genera *Callirhytis* and *Dryocosmus*. There are few recognized larger groupings except for Kinsey's broadly circumscribed genus *Cynips*. However, the subgenera of Kinsey's *Cynips* have since been raised to genus-status (Weld 1952), synonymized (Melika & Abrahamson 2002), as well as had their species being moved around, so if one attempts to reconstruct this group now, it would contain *Cynips* (including the former *Besbicus* and *Antron*), *Acraspis, Philonix, Atrusca*, the part of *Biorhiza* formerly placed in *Sphaeroteras* and possibly those species of *Trigonaspis* formerly placed in *Xanthoteras*. Kinsey himself knew of no single character without homoplasy to characterize his *Cynips*, but based this genus upon "…a striking, even if not invariable, correlation of insect structures, gall characters, host relationships, life histories, and distributional data…" (Kinsey 1930: p. 62).

Species identification is often based solely on gall characteristics in combination with host plant, and use of morphology is especially difficult for males (Weld 1952). In some genera, however, the parthenogenetic females are more difficult to separate than the sexual forms. The reliance on the gall is potentially problematic, since the galls induced by different gallwasp species can be structurally very similar. Much of the taxonomic confusion also stems from the use of too few and problematic characters: *e.g.* the metatarsal claw, the hypopygial spine and the notauli. There are, however, exceptions. For instance, the genus *Neuroterus* is seemingly well defined by a fusion of the mesoscutum and the scutellum, *Callirhytis* by transverse sculpture of the mesoscutum, *Belonocnema* by an extension of the apex of the fore tibia, and Kinsey's *Cynips*-group by a distinct modification of the hypopygial spine.

Until recent years, the only phylogenetic hypothesis for the WRG was due to Kinsey (1920; Tree 2). He based it on perceived evolutionary trends in three morphological and four biological characters. Although he believed *Neuroterus* to be a relatively primitive genus, and closely related to *Bassettia* and *Plagiotrochus*, he



TREES 2–6. Previous phylogenetic hypotheses involving the Cynipini. Numbers on branches are bootstrap proportions. Bootstrap frequencies below 50% are not shown: **2**. Kinsey (1920) intuitively evaluated three morphological and four biological characters. Note that he treated *Phanacis* and *Timaspis* as separate genera. **3**. Pujade-Villar and Arnedo (1997) used a morphology-based parsimony analysis to map the character evolution of male genitalia. Outgroup not shown. **4**. Parsimony analysis based on morphology (Liljeblad & Ronquist, 1998), taxa outside of *Aylax* removed. **5**. Parsimony analysis of cytochrome oxidase I by Drown and Brown (1998). R = host plant among the red oaks (section Lobatae), W = host plant among the white oaks (section *Quercus* s.s.). *Callirhytis abrahamsoni,* so named in this paper, is a *nomen nudum*. **6**. Parsimony analysis based on cytochrome *b* by Stone and Cook (1998). Taxa in common with present analysis are in bold face. Neither *Andricus burgundus*, nor *A. gemmea* were included in *'Adleria'*, but the former is known from the sexual generation only. Note that the sequence for *Andricus gallaeurnaeformis* in Tree 6 has since been shown to be for an inquiline rather than a gall inducer; the same may apply to the sequence for *A. hystrix* (see text).

still recognized specialization in, *e.g.*, the reduced mesosomal sculpture (Kinsey 1923). He suggested a sister-group relationship between *Amphibolips* and *Callirhytis* as well as putting *Andricus* close to his *Cynips*. Since Ronquist's (1994) morphologically based family analysis, focused on investigating the origin of inquilinism but suggesting monophyly of the Cynipini and a close relationship between the Cynipini and Diplolepidini, things have changed drastically. Pujade-Villar and Arnedo (1997) built upon that analysis to produce a phylogenetic tree on which they tracked the character evolution of male genitalia (Tree 3). They did not, however, present any support for the respective groupings, making it difficult to evaluate their results. Next, Liljeblad and Ronquist (1998) sampled a wider range of gall wasps to include representatives from all tribes (Tree 4, numbers on branches are bootstrap proportions). Their morphology-based parsimony analysis suggested all tribes but Aylacini to be monophyletic. They also proposed monophyly of the WRG clade, unambiguously supported in their analysis by seven character changes, most of which, unfortunately, are relatively difficult to examine in traditionally mounted specimens. The Diplolepidini were supported as monophyletic based on characters such as the horizontal furrow of the lower mesopleuron, while the dorsal impression of the scutellum is one of many characters defining the Pediaspidini. The oak gall wasps turned out somewhat less strongly supported than the other tribes, but the sample only included four species from this diverse group.

Several molecular phylogenies of WRG taxa have also been published. Drown and Brown (1998) used cytochrome oxidase I sequences from a sample of exclusively Eastern Nearctic oak gall wasps and found two most parsimonious trees for these data (Tree 5). Several genera turned out para- or even polyphyletic, but they did not present any support values and no other WRG, or even cynipoid, taxa were included to test the monophyly of the Cynipini. Largely, the analysis showed the need for a thorough revision of the group. *Callirhytis abrahamsoni*, so named in this paper, had not yet been described and is a *nomen nudum*. Stone and Cook (1998; see also Cook *et al*. 2002), on the other hand, sampled only European taxa to produce a cytochrome *b* based phylogeny (Tree 6, numbers on branches are bootstrap proportions, the ten taxa in common with the present analysis are shown in bold face). Eighteen species of *Andricus* were included, as their aim was to trace the evolution of gall characteristics in this genus. They also included a fair number of other European oak gall wasps as well as *Diplolepis rosae* as outgroup. The results show *Andricus* to be polyphyletic because of some outliers, but the results for these are all in doubt. The sequence for *A. gallaeurnaeformis* was later shown to be for a *Synergus* species (G. Stone, pers. comm.) and it seems likely that the same holds true for *A. hystrix*. Furthermore, the position of *A. inflator* turned out to be uncertain in a subsequent Bayesian analysis including additional data from the nuclear gene long wavelength rhodopsin (Cook *et al*. 2002). Thus, their results are possibly consistent with a monophyletic *Andricus* but, as neither the type *A. quercusradicis* (Fabricius), nor any non-European species, was included in the analysis, the taxonomic limits of the genus remain unclear.

Later, Rokas *et al*. (2003; tree not shown here) expanded upon this analysis, again focusing upon European taxa. The type species was still left out but they did, however, add four Japanese and one North American species: the Japanese *A. symbioticus* Kovalev grouped with the European *A. inflator* Hartig outside of a large group of all other *Andricus*, including the basally positioned *Andricus mukaigawae* (Matsumura in Mukaigawa) and *A. kashiwasphilus* Abe from Japan; while the Nearctic *Disholcaspis spectabilis* (Kinsey) grouped with *Biorhiza* + *Trigonaspis*. The tribe Diplolepidini has also received attention with an analysis using both cytochrome *b* and 12S genes (Plantard *et al.* 1998; tree not shown here). The one representative of *Liebelia*, the Japanese *L. fukudae* (Shinji), always fell outside of the *Diplolepis* clade, supporting the distinctness of these genera.

A number of fossil species have been placed among the WRG. Ronquist recently (1999) considered most of these although he did not mention *Antronoides schorni* Waggoner & Poteet 1996, known only from a mid-Miocene (~15 Mya) gall on *Quercus hannibali*. The key fossil, however, is the considerably older *Kinseycynips succinea* (Kinsey 1919), presumably of Eocene age, or about 45 Mya. Ronquist (1999) suggested that it belongs to the *Synergus*-*Saphonecrus* complex of inquilines, and as the modern hosts of these are found among the oak gall wasps, it sets a minimum age of the Cynipini at around 45 My (Ronquist 1999; Ronquist

& Liljeblad 2001). This fits reasonably well the finding that the major lineages of oaks should have been present about 40 million years ago (Manos *et al.* 1999). Liu *et al*. (2007) instead argue that *K. succinea* is closely related to the Rosacae gallers in the Aylacini (*Diastrophus* and *Xestophanes*), in which case its age would not be immediately relevant for the dating of the Cynipini. Nevertheless, they agree on an Eocene age for the Cynipini based on the age of the host oaks, among other things.

The present paper is the first attempt at a cladistic analysis through careful morphological examination of an extensive sample of WRG. We aimed to bring some stability into the taxonomy and classification, and to lay the ground for further work in this group. In particular we were interested in finding some larger groupings within the Cynipini, testing groupings suggested by earlier workers as well as placing the genus *Paraulax* and investigating the limits of the genus *Andricus*.

We also wanted to address a series of evolutionary questions. In particular, we wanted to use the resulting trees to trace the history of the host plant associations, the biogeography of the group and the evolution of different gall characteristics. We were also interested in the number of origins of heterogeny and whether specific characters were typical of, and associated with the origin of, the two alternating generations. Several of these trends have been discussed in the literature but they have never been quantified within the context of a comprehensive phylogenetic analysis. For instance, the parthenogenetic generation seems often to be larger than the sexual one (*e.g.* Liljeblad & Ronquist 1998), even though the relationship is reversed in *Trigonaspis* (Nieves-Aldrey 1990, 2001; Pujade-Villar *et al.* 2001). Females of the parthenogenetic generation generally appear more apotypic than the sexual generation. Different species of *Cynips* are morphologically almost indistinguishable with regard to the sexual generation, and the same applies to some European *Andricus* with a heteroecic life cycle (Eady & Quinlan 1963; Wiebes-Rijks 1976; Nieves-Aldrey 2001; Pujade-Villar *et al*. 2001; Folliot *et al*. 2004; Melika 2006). In the case of the closely related *A. kollari* and *A. hispanicus* (Hartig) though, the galls of the parthenogenetic generations are virtually identical, and the two closely related species have to be separated on the basis of the alternate generation (Pujade-Villar 1992; Pujade-Villar *et al*. 2001; Pujade-Villar *et al*. 2003; Folliot *et al*. 2004). The genus *Adleria* was erected as a substitute name by Rohwer and Fagan (1917) for a group of species known only from parthenogenetic females and characterized by, among other things, large size and extensive pubescence. Benson (1953) confirmed that this genus' type species, *A. kollari*, has a sexual generation typical of *Andricus*, and the analysis by Stone and Cook (1998) shows that this group is nested within other European *Andricus* (cf. Tree 6).

Materials and methods

Terminology

Morphological terms except surface-sculpture follow Richards (1977), Gibson (1985: mesoscutal lobes), 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. Three new skeletal terms are here introduced and defined: The **subaxillular strip** is the shining posterior continuation of the subaxillular bar lateroventrally on the scutellum (Figs. 5c, 5d: char. 148). The **petiolar hump** is a more or less pronounced projection of the petiole. It is located ventrally of the articular bulb and adjacent to, or sometimes fused with, the 3rd sternum (Figs. 12b–d: char. 245). The **dorsal groove** of the aedeagus is the basal continuation of the apical incision of the same. It is sometimes clearly expanding basally (Pujade-Villar & Arnedo 1997: char. 276 indicated by 3a in their fig. 2). The term **lateral flaps** of the female 7th abdominal sternum (the hypopygium) was defined by Ronquist (1995a), and refers to the paired, often rounded, parts attaching laterally to the hypopygial spine as indicated in figs. 10–11: char. 260. Kinsey (1930) used the term lateral lobes for the same feature, but we prefer flaps as it seems more descriptive. The flaps are separate from the actual spine, although the spine itself may have lateral lobe-like extensions (Fig. 13b: char. 258). This separation is often marked by a distinct incision (Fig. 10: char. 259).

Selection of exemplar taxa

We tried to sample all tribes of the WRG with respect to both morphological and biological diversity, but also keeping the taxonomic problems in mind. As far as available material permitted we included cynipids from all major geographical regions, all host plant genera, except *Chrysolepis* and *Lithocarpus* (material unavailable to us), and representing as many cynipid genera as possible (Table 3). *Diplolepis triforma* Shorthouse & Ritchie was chosen because it seems to be a more plesiomorphic representative of this genus than *D. rosae* (Plantard *et al.* 1998), and because it provided a test of the monophyly of the genus. The specimens of the undescribed species of *Paraulax*, which we examined, were caught in malaise traps in *Nothofagus* forests in Chile. Choice of taxa from the smaller and six monotypic genera was unproblematic, and from most other genera we tried to get, when possible, the type species (Tables 2 & 3).

TABLE 3. Taxa in analysis.

Species	Material	Preparation	Source
Outgroup (Aylacini)			
Aylax papaveris (Perris)	7f/5m	SEM/LM/CM	LR
Phanacis phoenixopodos Mayr	7f/5m	SEM/LM/CM	LR
Diplolepidini			
Diplolepis rosae (Linnaeus)	7f/1m	SEM/LM/CM, cyt *b*	LR
Diplolepis triforma Shorthouse & Ritchie	7f/5m	SEM	JS
Liebelia magna Vyrzhikovskaja	7f/5m	SEM/LM/CM	SIZ
Eschatocerini			
Eschatocerus acaciae Mayr	7f/5m	SEM/LM/CM	LR
Pediaspidini			
Pediaspis aceris (Gmelin)	7f/5m/3p	SEM/LM/CM	LR/PV
Himalocynips vigintilis Yoshimoto	2p	–	CNCI
Cynipini			
Paraulax sp.	3f/1m	SEM	LR
Acraspis erinacei (Beutenmueller)	9f/3m/9p	SEM/LM/CM	AMNH
Amphibolips gainesi Bassett	6p	SEM/LM/CM	AMNH
Andricus caputmedusae (Hartig)	*/7p	SEM, cyt *b*	LR
Andricus curvator Hartig	7f/*	SEM, cyt *b*	LR/AR
Andricus [Liodora] cylindratus (Kinsey)	7p	SEM/LM/CM	AMNH
Andricus gallaeurnaeformis (Fonscolombe)	3f/4m/3p	SEM/LM, cyt *b*	PV
Andricus grossulariae Giraud	7f/3m/*	SEM/LM/CM, cyt *b*	PV
Andricus [Erythres] hastatus (Kinsey)	7p	SEM/LM/CM	AMNH
Andricus kingi Bassett	*/7p	SEM/LM/CM	AMNH
Andricus kollari (Hartig)	3f/4m/3p	SEM/LM, cyt *b*	PV
Andricus [Dros] perlentus (Kinsey)	7p	SEM/LM/CM	AMNH
Andricus quercusflocci (Walsh)	7p	SEM/LM/CM	AMNH
Andricus quercusfoliata (Ashmead)	7p	SEM/LM/CM	AMNH
Andricus quercusradicis (Fabricius)	7f/7p	SEM/LM/CM	LR
Andricus quercusramuli (Linnaeus)	3f/4m/*	SEM/LM, cyt *b*	PV

...... *continued*

TABLE 3 (continued)

Species	Material	Preparation	Source
Andricus [Callirhytis] serricornis (Kinsey)	7f/4m/*	SEM/LM/CM	AMNH
Andricus sieboldi (Hartig)	4f/2m/7p	SEM/LM/CM	RF
Andricus solitarius (Fonscolombe)	5f/*	SEM/LM/CM, cyt *b*	NA
Aphelonyx cerricola (Giraud)	6p	SEM/LM/CM, cyt *b*	LR/AR
Atrusca emergens (Kinsey)	7p	SEM/LM/CM	AMNH
Belonocnema treatae Mayr	6f/2m/*	SEM/LM/CM	AMNH
Biorhiza [Sphaeroteras] mellea Ashmead	7p	SEM/LM/CM	AMNH
Biorhiza pallida (Olivier)	7f/5m/7p	SEM/LM/CM, cyt *b*	LR/AMNH
Callirhytis erythrocephala (Giraud)[1]	*/7p	SEM	PV
Callirhytis glandium (Giraud)	6f/5m/5p	SEM/LM/CM, cyt *b*	NA
Cynips [Besbicus] conspicua Kinsey	7p	SEM/LM/CM	AMNH
Cynips divisa Hartig	2f/4m/7p	SEM/LM/CM, cyt *b*	LR
Cynips [Antron] douglasi (Ashmead)	*/7p	SEM/LM/CM	AMNH
Disholcaspis quercusglobulus (Fitch)	7p	SEM/LM/CM	AMNH
Disholcaspis [Andricus] spectabilis (Kinsey)	6p	SEM/LM/CM, cyt *b*	AMNH
Dryocosmus kuriphilus Yasumatsu	7p	SEM/LM/CM, cyt *b*	YA
Dryocosmus [Chilaspis] nitidus (Giraud)	3f/5m/4p	SEM/LM/CM, cyt *b*	LR/AR
Eumayria floridana Ashmead	5f/4m	SEM/LM/CM	AMNH
Heteroecus pacificus (Ashmead)	*/7p	SEM/LM/CM	AMNH
Loxaulus quercusmammula (Bassett)	2f/2m	SEM	AMNH
Neuroterus numismalis (Fourcroy)	4f/7p	SEM/LM/CM	LR
Neuroterus [Trichagalma] serratus (Ashmead)	*/7p	SEM/LM/CM, cyt *b*	YA
Odontocynips nebulosa Kieffer	7p	SEM/LM/CM	AMNH
Philonix gigas Weld	7p	SEM/LM/CM	AMNH
Plagiotrochus australis (Mayr)	7f/5m/7p	SEM/LM/CM	PV/NA
Plagiotrochus cardiguensis (Tavares)	7f/2m	SEM/LM/CM	PV
Plagiotrochus quercusilicis (Fabricius)	7f/5m/*	SEM/LM/CM, cyt *b*	LR
Pseudoneuroterus macropterus (Hartig)	7p	SEM/LM/CM, cyt *b*	LR
Trigonaspis [Belizinella] gibbera (Kovalev)	5p	SEM/LM/CM	ZMAS
Trigonaspis megaptera (Panzer)	7f/5m/*	SEM/LM/CM	AMNH
Trigonaspis mendesi Tavares	6p	SEM/LM/CM	LR
Trigonaspis [Xanthoteras] quercusforticornis (Walsh)	7p	SEM/LM/CM	AMNH

Underlining indicates that a species is the type of the corresponding genus. Previous generic placement of the species is shown in square brackets if the placement was changed recently. Explanation of abbreviations: f = sexual female, m = male, p = parthenogenetic female. * = alternate generation is known, but could not be included. Abbreviation of preparation techniques: SEM=Scanning electron microscope preparations, LM = Light microscope preparations, CM = Compound microscope preparations. cyt *b* = cytochrome *b* gene sequence. Abbreviation of sources: LR = Johan Liljeblad and Fredrik Ronquist's collection, JS = J. Shorthouse' collection, SIZ = Schmalhausen Institute of Zoology, Kiev, PV = J. Pujade-Villar's collection, AMNH = American Museum of Natural History, New York, CNCI = Canadian National Collection of Insects, Ottawa, ZMAS = Zoological Museum, Academy of Sciences, S:t Petersburg, AR=A. Rokas' collection, YA = Y. Abe's collection, NA = J.-L. Nieves-Aldrey's collection, RF = R. Folliot's collection.

[1] Probably the alternate generation of the type species *C. hartigi* Förster (Nieves Aldrey, 1992).

From the more problematic genera *Andricus* and *Callirhytis* we included a fair sample from the Palearctic. We were, however, only able to get a smaller sample from the Nearctic, especially of *Callirhytis*; the only American species we managed to include, *C. serricornis* Kinsey, was transferred to *Andricus* (Melika & Abrahamson 2002) after we had selected and made preparations of all taxa. For *Andricus*, we tried to match the taxa in the analysis of Stone and Cook (1998) to allow joint analysis of morphological and molecular data, except that we added the type species of the genus, *A. quercusradicis*. The Nearctic representatives of *Andricus* were chosen to represent both western and eastern regions as well as host plants from different sections of subgenus *Quercus*. We only included a few representatives from the large Holarctic genus *Neuroterus* because some characters suggest this to be a monophyletic genus and we decided to leave a detailed analysis of this lineage to the future (Pujade-Villar *et al*. 2004). Since the coding was finished, eleven species have been transferred as the result of revisionary work (Melika & Abrahamson 2002; Ács *et al*. 2007). These species' previous generic belongings are shown within square brackets in Table 3.

Choice of outgroup taxa was based on the family level analysis by Liljeblad and Ronquist (1998; Tree 3). The chosen exemplars added up to a total of 56 taxa, including the outgroups *Aylax papaveris* (Perris) and *Phanacis phoenixopodos* (Mayr) (previously known as *Timaspis phoenixopodos* but we follow Melika (2006) here in treating *Timaspis* as a synonym of *Phanacis*), as well as 54 taxa representing 27 [35] of the 32 [46] currently recognized genera of WRG. Of the missing genera, we were simply not able to get enough material of *Bassettia*, *Eumayriella* and *Holocynips*, while we judged *Phylloteras* and *Zopheroteras* to be sufficiently close to other included taxa to safely leave them out without endangering the generality of the results.

Pediaspis aceris and many of the Cynipini are known from two alternating generations, and for a total of twelve taxa we managed to include both generations. For the genus *Trigonaspis* we included the sexual generation of *T. megaptera* (Panzer) but the parthenogenetic generation of *T. mendesi* Tavares. They were, however, not constrained to be each other's sister taxa in the present analysis. Seven-teen species were represented by the sexual generation only, while for another twenty-six we only studied the parthenogenetic generation. Males were possible to include in twenty-six cases. In total, fourteen taxa (marked with an asterisk in Table 3) were represented here by a single generation even though an alternating generation is known or strongly suspected (Pujade-Villar *et al.* 2001).

Study techniques

Whenever possible, specimens were killed and stored in 70-80% EtOH prior to preparation, but a large number of the American taxa were obtained as dry specimens from the American Museum of Natural History. These were transferred to 70% EtOH at least a month before preparation. Specimens were dissected into parts under stereomicroscope and cleaned in 20% NH_3 overnight. When appropriate, mouthparts and ovipositor were instead macerated in 10% KOH overnight. After cleaning, the parts were first washed in water, then in a series of increasingly concentrated EtOH solutions finishing in absolute EtOH, and finally transferred to acetone. Parts thus air-dried quickly before being either mounted on stubs for scanning electron microscopy (SEM) using carbon tape, or glued on pieces of cardboard for stereo microscopy. Wings, mouthparts and ovipositor were mounted in Euparal on microscope slides for light microscopy (LM). From these preparations, we took high-resolution digital images in the same standardized views as Fontal-Cazalla *et al*. (2002), ending up with a total of 1801 SEM and 227 LM images. We printed all major views (totaling 942 printouts) to make simultaneous comparison between many taxa practically feasible, leaving a few views for on-screen examination only. Images were in most cases complemented with preparations for stereomicroscopy, which were used for three-dimensional interpretation and for double-checking. Drawings were made, using a graphics tablet, from the digital images.

Character coding

As noted in Appendix 1, the morphological features coded in this analysis represent a mix of characters original to this study and characters taken from earlier analyses (Ronquist 1994, 1995b; Pujade-Villar & Arnedo 1997; Liljeblad & Ronquist 1998), in the latter case typically with modifications to fit the current context.

The character descriptions reflect what we perceive as qualitative differences between the studied taxa. Specific morphometric measurements mentioned in a character description are intended to facilitate the understanding of the character and do not indicate that the character itself is fundamentally quantitative. No autapomorphies were coded, as they are not informative about relationships in parsimony analyses.

When sexual and parthenogenetic generations of the same taxon had different states for a character, the taxon was coded as being polymorphic in the original matrix (TreeBASE Matrix 15062). In a separate matrix, however, we kept each generation as a separate terminal taxon (TreeBASE Matrix 15063). This allowed us to keep the original generation-specific observations and also permitted phylogenetic analyses with each generation treated as a separate taxon. Outside of the Cynipini, taxa with only a sexual generation (including *Paraulax*) were coded for parthenogenetic-female-only characters based on the sexual female, as a best estimate of the ancestral states for the parthenogenetic generation females of the Cynipini. For three of the 29 species represented by a sexual generation, no males were available (Table 3). For these, and a few other taxa, some missing data were taken from the literature as noted in the character descriptions (Appendix 1).

Information for coding of biological and distributional characters was mainly extracted from Dalla Torre & Kieffer (1910) and Houard (1908, 1909, 1933, 1940) but taking into account the many additions and corrections published since then.

Character analysis

Multistate morphological characters were treated as ordered when the states appeared to form a natural sequence, as indicated in the character list (Appendix 1).

We used three characters based on geographical distribution (chars. 286–288). The three major geographical regions (char. 286) were treated as distinct states and ordered according to their proximity and reconstructed historical relations, putting the Nearctic in-between the Palearctic and Neotropic. The other distributional characters, representing finer divisions of the Nearctic and Palearctic, were treated as unordered. Some authors argue against the use of biogeography in phylogeny reconstruction on the grounds that geographical distribution is not heritable (*e.g.* Grandcolas *et al.* 2001) but continental-scale distribution patterns are obviously phylogenetically conservative in gall wasps. This is perhaps because they are so host-plant specific and because the adults do not fly very well, but recent work has shown that gall wasps can expand their ranges with surprising speed given favorable conditions and suitable hosts (Rokas *et al*. 2003; Challis *et al*. 2007; van der Ham *et al*. 2007). A few cases of recent invasions are also well documented in Europe, like that of *A. kollari* (Schönrogge *et al*. 2000; Stone *et al*. 2001; Walker *et al*. 2002). Even in the worst case of frequent dispersal, the distributional characters should add only random noise to the analysis.

The host plant taxa of the WRG were coded in three characters (chars. 290–292). The character states were ordered to represent host plant relationships (Manos & Steele 1997; Manos *et al.* 1999; Manos *et al.* 2001; Angiosperm Phylogeny Group 2003). As an example, characters 291 and 292 have their states ordered to reflect the phylogenetic relationships among sections within subgenus *Quercus* (Tree 1): (*Cerris* sensu Camus, (Protobalanus, (*Quercus* s.s., Lobatae))) is represented as the undirected transformation series *Cerris*–Protobalanus–*Quercus* s.s.–Lobatae. This coding method is a simple approximation of the additive binary coding of the pruned host tree, the type of coding used in Brooks Parsimony Analysis. There is no known coding scheme that maintains entirely accurate representation of the host phylogeny in a set of ordered and unordered parsimony characters, unless one is willing to use unorthodox (non-metric), slow cost matrices. Thus, some type of approximation like the one used here is preferable to reduce the computational complexity of a large analysis (Ronquist, 2003).

Availability of data

All the 2,028 micrographs used to code morphological characters in the current study were deposited in Morphbank (http://www.morphbank.net). Each morphological character description (Appendix 1) includes a clickable hyperlink to a permanent collection of relevant images in Morphbank. The collections represent different subsets of the images used for the study. Most of our characters can be coded solely from these images but examination of real specimens is sometimes required and always recommended for better appreciation of the variation within and among the studied taxa. The character matrices (the Combined Matrix, cf. Appendix 1, Table 5, and the Separate Matrix) and the shortest trees are available in Nexus format from TreeBASE (Matrix 15062 and 15063, respectively; http://treebase.org/).

Phylogenetic analysis

Heuristic analyses were mainly carried out using PAUP* 4.0b8/b8a (Swofford 2001) with some minor additional analyses with b10 (Swofford 2002) and the resulting trees were examined in MacClade 3.08a (Maddison & Maddison 1992). In PAUP* we used the following settings unless otherwise noted: Implied weights using Goloboff fit criterion K=2, Emulate PeeWee (to avoid excessive precision, which may cause hill-climbing algorithms to stop at sub-optimal trees; Goloboff 1997; Ronquist *et al.* 1999); Heuristic search with swap on best tree only when multiple starting trees exist, and TBR swapping. In calculation of tree length, taxa coded with multiple states were interpreted as polymorphic (terminal steps included) in the original matrix where alternating generations were kept together (the Combined Matrix), but treated as uncertain (terminal steps excluded) in the matrix where generations were kept apart (the Separate Matrix). Bootstrap analyses were carried out with Simple addition sequence. Bootstrap frequencies below 50% were not considered.

For phylogenetic analysis we preferred using implied weights parsimony to un-weighted standard parsimony. The former often produces more resolved trees, which agree better with intuitive notions of relationships (Fontal-Cazalla *et al.* 2002). For morphological datasets in particular, implied weights can help separate signal from the unavoidable noise due to difficulties in identifying discrete character states and in coding characters from poorly preserved specimens. We tested the performance of implied weights by *a priori* identifying 42 “uncertain” characters (*viz*. 4, 6–9, 16, 17, 26, 31, 33, 36, 41, 43, 48, 53–56, 58, 65, 94, 99, 108, 109, 116, 133, 135, 138, 147, 148, 153, 169, 171, 177, 181, 197, 202, 207, 211, 254, 256, 257), which were particularly difficult to code, and then comparing results from analyses with and without these characters.

We assessed alternative groupings by using the Topological Constraints option in PAUP*. The decrease in G-fit resulting from enforcing topological constraints was evaluated by comparing with the decrease in G-fit observed for clades with known bootstrap support values.

Total evidence analysis

Graham Stone kindly provided us with an aligned matrix of 433 base pair cytochrome *b* fragments, sequenced for a paper on evolution of gall structures in European *Andricus* (Cook *et al.* 1998; Stone & Cook 1998). The matrix contained a total of forty taxa though only twelve were shared with the present study. Two of the sequences did not appear in any of their published papers, *viz. Dryocosmus nitidus* AJ131069 and *Pseudoneuroterus macropterus* AJ131070. Cytochrome *b* sequences were retrieved from GenBank for an additional six species coinciding with exemplars in the present analysis: *Andricus quercusramuli* AF481706, *Dryocosmus kuriphilus* DQ286803, *Callirhytis glandium* AF539590, *Plagiotrochus quercusilicis* AF395138, *Neuroterus serratus* AF539579 and *Disholcaspis spectabilis* AF539577 (marked cyt *b* in Table 3). This final molecular data set was first analyzed with all forty-six taxa included (both un-weighted and using implied weights), and the resulting trees pruned to the eighteen shared taxa in order to simplify comparisons with the morphology-based results. The total-evidence analysis, based on morphology and molecules, was restricted to the eighteen shared taxa. Simply combining all taxa in the two datasets resulted in a matrix with excessive amounts of missing data, causing serious problems with wild-card taxa floating around in the tree.

Results and discussion

Morphological characters and informatics

The morphological study resulted in the coding of 283 characters for 56 taxa (Appendix 1, Table 5), that is, a character matrix with almost 16,000 observations of morphological features. Until recently it would not have been possible to document more than a few of these observations in carefully selected illustrations because of the constraints of traditional print journals. However, the combination of high-resolution digital imaging techniques, open web repositories of biological images like Morphbank (http://www.morphbank.net), and online taxonomy journals like Zootaxa, now make it possible to hyperlink morphological phylogenetics papers to large sets of voucher images documenting the character coding. In this paper, we chose a very simple approach. We first deposited the 2,028 images we used for the morphological coding in Morphbank. Then we created a number of permanent subcollections of these images in Morphbank. Finally, we linked each character description (Appendix 1) to one or more of these collections using stable URL links provided by the Morphbank repository. Although simple, this approach allows other workers easy and rapid access to the images from which we coded particular characters, so that they can efficiently evaluate our character coding. The Morphbank platform also provides other workers with the ability to copy our image collections, add images to them, and then use the new image collections in extending our character matrix.

More sophisticated ways of storing and working with morphological phylogenetics observations in web databases will undoubtedly be developed in the near future. For instance, instead of archiving just the images it would be advantageous to store character descriptions, character state descriptions, and character state observations as well. With a sophisticated data model, it should be possible to then allow future workers to add new characters by modifying the definition of previously entered characters and character states, while mapping many of the observations of the old character states into the new states. Ultimately, the development of informatics tools will revolutionize the publication of morphological phylogenetics papers, such that long appendices with character descriptions and character matrices can be replaced entirely by relevant links to online databases. This should give an important boost to the productivity of all comparative morphologists.

The 2,028 Morphbank image vouchers referenced in the present study are not only important in documenting the morphological data in our character matrix. They also represent, among other things, a virtual reference collection of reliably determined WRG species, a source of information for coding morphological features in phylogenetic analyses at lower or higher taxonomic levels than the one studied here, and an image resource for illustration of the variation in key characters used in the identification of WRG groups.

Phylogeny

In total, our analysis comprised 308 characters, of which 283 come from morphology, 4 from biology, 4 from host plant choice, 3 from distribution and 14 from gall characteristics (Appendix 1). Comparisons with earlier analyses (Ronquist 1994, 1995b; Liljeblad & Ronquist 1998) show that a substantial 169 morphological characters are completely new for the present analysis, suggesting that skeletal structures will continue to be a source of new phylogenetic information in future analyses of gall-wasp relationships. The comparisons further reveal that, of the characters taken from previous analyses, only 47 are identical while 67 are significantly modified. Furthermore, 57 previous characters (not counting the characters in the superfamily analysis by Ronquist 1995b) are excluded from the present analysis, mainly because of being uninformative (29) or because the present variation makes it too difficult to distinguish qualitatively distinct states (26) (as noted in Appendix 1).

Four-hundred and seventy-nine of the 17,248 cells, or 2.8%, lacked data, while another 1,288, or 7.5%, were coded as inapplicable. Of these last instances, most were due to twenty characters that applied to parthenogenetic females only and nine characters for sexual females only. For the morphological characters there were 246 out of 3,096 possible instances, or 7.9%, in which the states differed between the two alternating generations.

Main analyses. Analysis of the Separate Matrix (alternating generations kept as separate taxa; cf. Appendix 1, Table 5) resulted in all pairs of alternating generations except those of *Pediaspis aceris* coming out as sister groups. For *P. aceris,* the parthenogenetic generation clustered together with *Himalocynips vigintilis,* indicating that the two known female specimens of this latter species represents the parthenogenetic generation of a species with heterogeny. Many parthenogenetic females are larger than the alternating sexual generation and so the relatively large size, almost 5 mm, of the *H. vigintilis* females corroborates this. Body size was, however, not included as a character in the current analysis because the variation was more or less continuous and did not allow coding into discrete states.

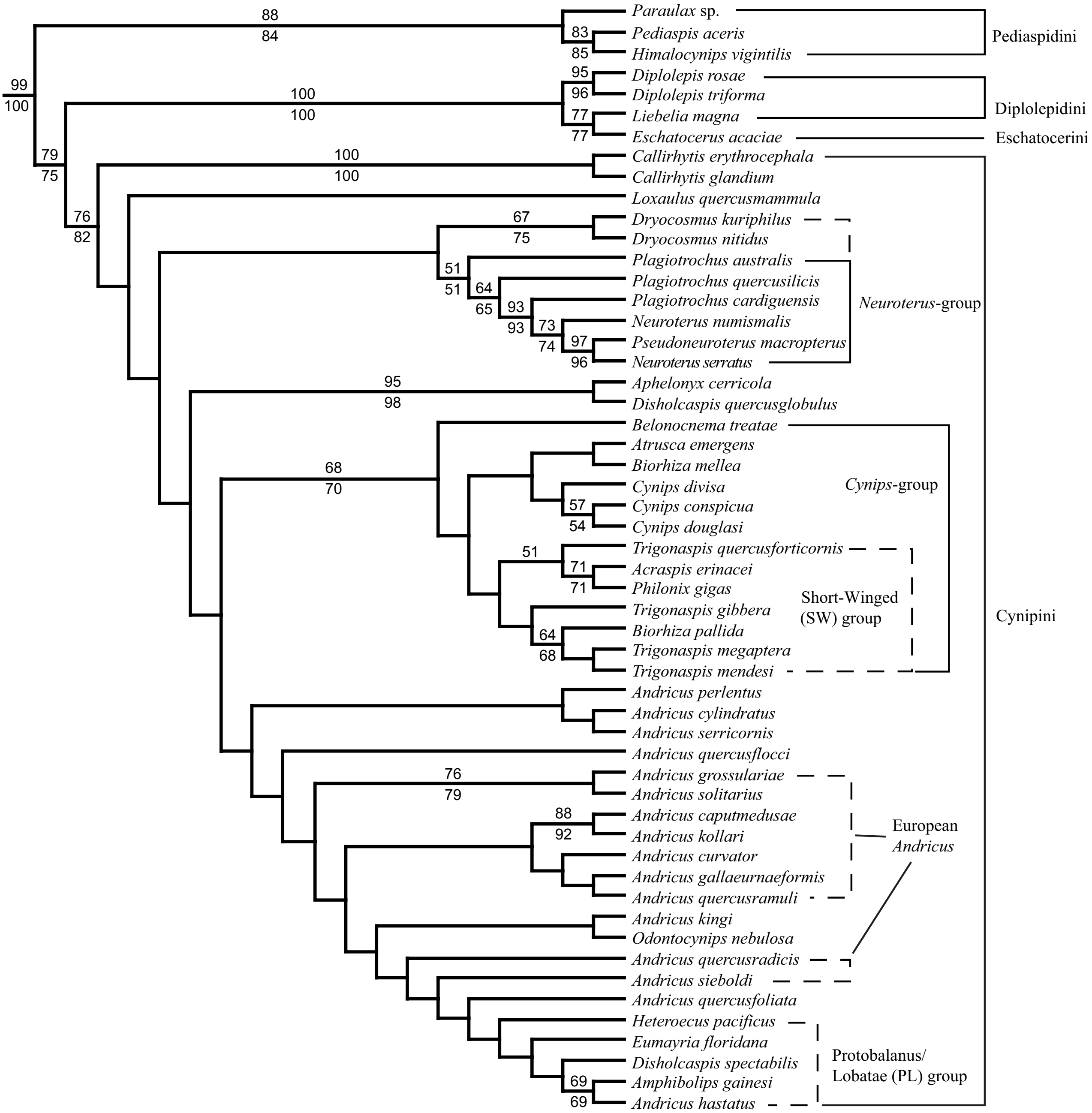
Running 100 random addition sequences on the Combined Matrix (alternating generations lumped) resulted in one island with one best tree of Goloboff fit -1140.6 (corresponding to an un-weighted length of 3161), consistency index (CI) = 0.25, retention index (RI) = 0.47 (Tree 7; bootstrap values above 50 %, based on 5,000 replicates, above each branch). The tree from the Separate Matrix was slightly different but no conflicting branches were supported with bootstrap proportions above 50% (Tree 7; 1,000 replicates, bootstrap values above 50 % below each branch).

As expected, *Phanacis phoenixopodos* comes out as the sister of the ingroup lineage, but in contrast to the analysis of Liljeblad and Ronquist (1998), the Pediaspidini clustering with *Paraulax* come next, leaving the Diplolepidini + Eschatocerini as the sister group of a monophyletic Cynipini. The Diplolepidini are paraphyletic with *Diplolepis* being the sister group to *Liebelia* + *Eschatocerus*. In the oak gall wasps, there are two larger lineages with some support. We call the first of these the *Neuroterus* group; it consists of *Plagiotrochus, Neuroterus, Pseudoneuroterus* and the previously recognized genus *Trichagalma*). The genus *Dryocosmus* may be the sister lineage to this group but its position is still relatively uncertain and it seems advisable to leave it outside the *Neuroterus* group for now. The second large lineage will be referred to as the *Cynips* group. It contains *Belonocnema, Acraspis, Philonix, Biorhiza, Trigonaspis, Atrusca* and *Cynips*. Within this group, there is a clade with reduced wings consisting of one subgroup of Palearctic apterous taxa (*Biorhiza pallida*, *Trigonaspis gibbera*, *T. megaptera* and *T. mendesi*) and another subgroup of brachypterous Nearctic taxa (*Acraspis, Philonix* and *Trigonaspis quercusforticornis*). Together they will be referred to as the Short-Winged group (SW group; Tree 7).

The remaining well-supported groups of oak gall wasps are only pairs of taxa, of which the *Aphelonyx/ Disholcaspis* clade seems to belong somewhere between the *Neuroterus* and *Cynips* groups. The *Aphelonyx/ Disholcaspis* clade itself is fairly strongly supported despite the fact that there are obvious differences between these genera in host plant preferences, gall structure, and general life history.

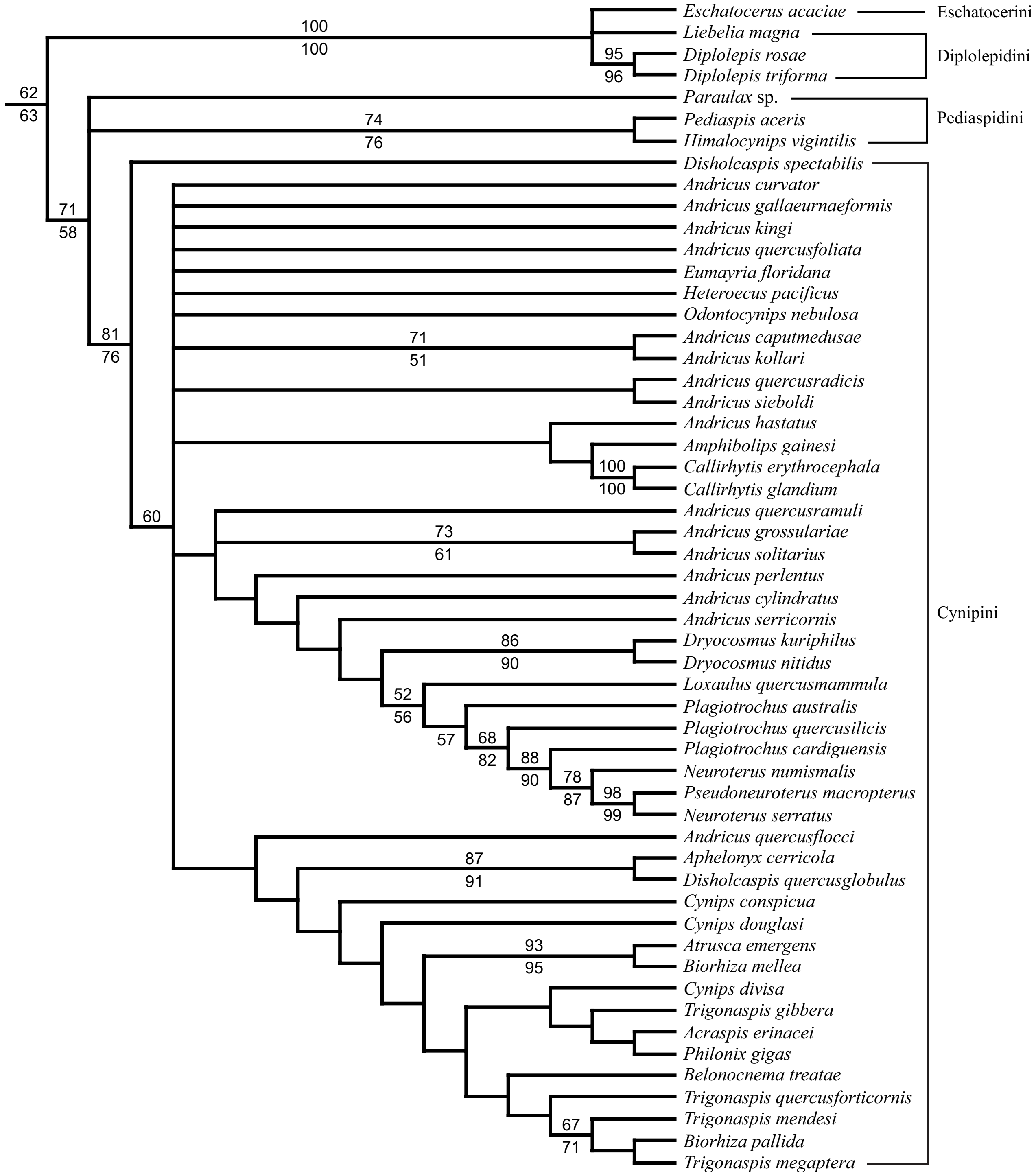
There is no convincing support for a single monophyletic *Andricus* group. The genus forms part of a monophyletic clade that also includes *Odontocynips* as well as a deeply nested terminal subgroup, which we will refer to as the Protobalanus/Lobatae-group (PL group; Tree 7) based on their host plant preferences (even though there are other taxa that also gall these sections of the subgenus *Quercus*). The PL group includes the apotypic *Eumayria*, *Heteroecus*, *Amphibolips* and *Andricus* (former *Erythres*) *hastatus*. *Loxaulus* was found outside of all the above-mentioned genera, with the European *Callirhytis* sitting unsupported at the base of the Cynipini.

Unweighted analysis. Running the Combined Matrix using un-weighted parsimony (100 random addition sequences) resulted in seven shortest trees of length 3100 (cf. 3161 for the best trees under implied weights), consistency index (CI) = 0.25, retention index (RI) = 0.48 (Tree 8). The CI of 0.25 is clearly lower than that expected from the polynomial regression analysis of empirical data by Sanderson and Donoghue (1989; expected value 0.34) or Klassen *et al.* (1991; expected value 0.30). They are, however, seemingly higher than levels observed in another study of real data sets if one extrapolates to 56 taxa (Archie, 1989: his fig. 3). The level of homoplasy is also well above that for randomized or permutated data sets (Archie 1989; Klassen *et al.* 1991). Together with the high bootstrap support for some of the branches in both the weighted and un-weighted analysis (Trees 7, 8) the data set is shown to exhibit clear phylogenetic signal.



TREE 7. The shortest tree, found when running the Combined Matrix under implied weights, K = 2. Goloboff fit = -1139.0 (L = 3178), CI = 0.25, RI = 0.47. Numbers above branches are bootstrap proportions (5000 replicates). Numbers below branches are bootstrap proportions (1000 replicates) when running the Separate Matrix, but constraining species to remain monophyletic. Bootstrap frequencies below 50% are not shown.

The unweighted analysis has somewhat different groupings than the implied-weights analysis, the major difference being that the Pediaspidini + *Paraulax* occur as the sister group to the Cynipini; this sister-group relationship appeared in 71% of the 1000 bootstrap replicates (support values found at branches in Tree 8). The consensus tree still contains the *Cynips* and *Neuroterus* groups. *Andricus,* however, is scattered in the tree, with some species basal of the two former groups while others appear in a basal Cynipini grade. In this tree, *Disholcaspis spectabilis* forms the sister group to all other Cynipini. The apotypic genera of the PL group that were deeply nested within *Andricus* in the weighted analysis emerge closer to the base of this grade in the unweighted analysis. Here, we also find the European *Callirhytis* clustering with *Amphibolips* and *Andricus hastatus,* while *Loxaulus* now shows affinities to the *Neuroterus*-group. The resolved parts of the unweighted tree do not support intuitive notions as well as the weighted analyses. For instance, the expected monophyletic groups of *Cynips* and European *Trigonaspis/Biorhiza* are both missing. Thus, we agree with the view of Fontal-Cazalla *et al.* (2002), *viz.* that results under implied weights tend to agree better with intuitive notions of relationships. We interpret this to mean that analyses under implied weights make more efficient use of the data in difficult analyses. In the following only implied-weights analyses are considered unless otherwise noted.



TREE 8. Strict consensus of the seven shortest trees discovered when running the Combined Matrix using un-weighted parsimony. L = 3104, CI = 0.25, RI = 0.48. Numbers above branches are bootstrap proportions (1000 replicates). Numbers below branches are bootstrap proportions (1000 replicates) when running the Separate Matrix. Bootstrap frequencies below 50% are not shown.

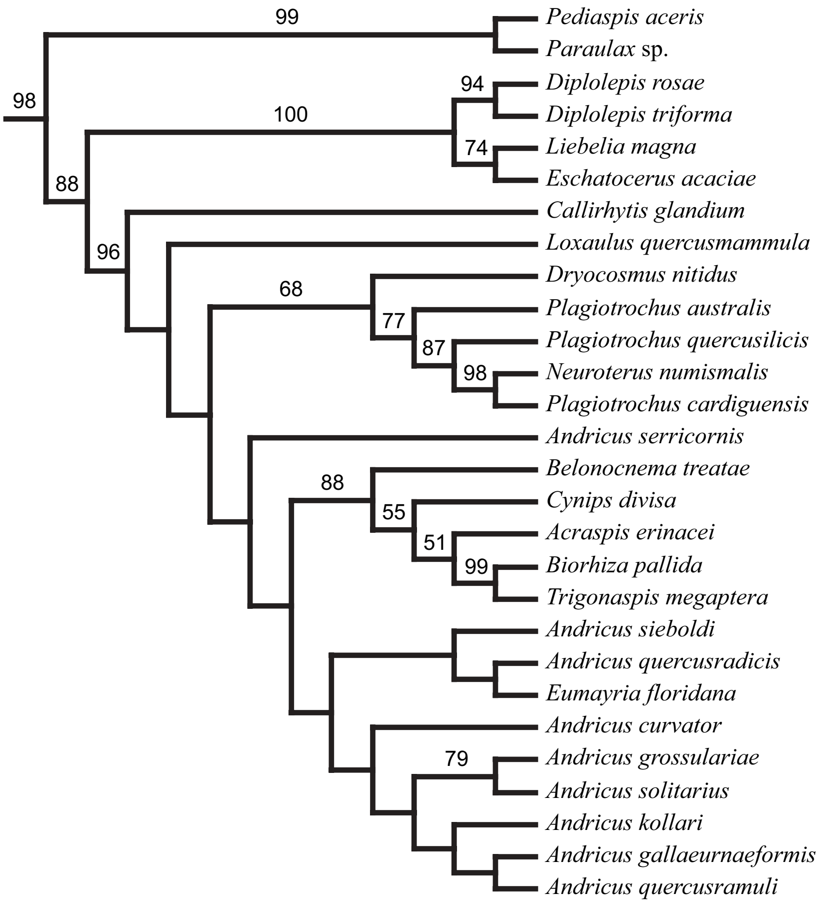
Excluding "poor" characters. Running weighted or unweighted analyses without the 42 "poor" characters gave results similar to those presented above for the complete matrix (100 random addition sequences). Bootstrap support values were overall slightly lower, with no branches in the analysis of the pruned matrix conflicting with the corresponding analysis of the complete matrix. This suggests that the removed characters generally support the same groupings as the other characters and that it is better to weight them differentially than to remove them completely. Removal of the uncertain characters did not result in noticeably better congruence between unweighted and implied weights analyses.

Excluding taxa with a missing generation. To further assess the stability of the results we analyzed the Separate Matrix while omitting taxa represented by only one generation in Cynipini and Pediaspidini. No constraints were used to force species to be monophyletic, but all alternating generations of the same species came out together with at least 94% bootstrap support (1,000 replicates).

Analyzing sexual and parthenogenetic generations separately. A potential problem in the analysis is that sexual generation taxa are compared with parthenogenetic generation ones, while it is possible that some characters have evolved independently in the two generations, maybe through gene duplication (see Stone and Cook (1998) and Cook *et al*. (2002) for examples of independent evolution involving host plant preferences, gall morphology, and gall location). To investigate this we ran two analyses of the Separate Matrix, each including *Aylax*, *Phanacis* and one of the generations of the WRG. No groupings supported in a bootstrap (> 50 %) were in conflict between either of these analyses and previous analyses (sexual generations only, Tree 9; parthenogenetic generations only, Tree 10). There were, however, some additional groupings supported as well as differences in general topology. With sexual generations only *Dryocosmus nitidus* grouped with the *Neuroterus*-group, while *Callirhytis glandium* was the sister group to the rest of the Cynipini (Tree 9). The general topology reminded of the implied-weights result (Tree 7), while with parthenogenetic generations only (Tree 10) it showed more affinity to the shortest trees from the un-weighted analysis (Tree 8).

Convergence in the Short-Winged group. It could be argued that the Short-Winged group is supported by a number of convergently evolved, partly dependent characters, all associated with wing reduction and therefore unjustly inflating support. If this is the case, removal of those characters should reveal any suppressed phylogenetic signal, which should then change the topology of the tree. If, on the contrary, the group were natural, there should be no conflicting signal and we would only see a loss of resolution upon removal of the characters associated with wing loss (Ronquist 1994). When the relevant characters in our case (23, 79, 130, 210 and 215; both matrices) are removed, the Short-Winged group becomes paraphyletic but still belongs to a monophyletic *Cynips* group, indicating that the SW-group is indeed natural. Furthermore, of the potential apomorphies supporting the SW group, the straight part of the inner margins of the compound eyes ventrally diverging (23:0) as well as the presence of longitudinal carinae in the transverse impression anteriorly on the pronotum (79:1) both seem to have little to do with wing reduction. It should be noted, however, that apterous or brachypterous species appear to have evolved several times independently in the Cynipini outside of the SW-group, e.g., in the genera *Andricus* and *Eumayriella*. Even within or closely related to the *Cynips*-group, the genera *Zopheroteras* and *Phylloteras* may have become short-winged independently of the SW-group.

Monophyly of previously proposed higher groups. The use of constraint trees, to test some groupings that have been suggested or discussed in the literature, gives some credibility to the monophyly of a European group of *Andricus* (Table 4). All other considered groups, if forced to be monophyletic in our analysis, decreased the G-fit more than the decrease seen when the *Cynips* group or the *Neuroterus* group, both supported by bootstrap values around 70%, were forced to be non-monophyletic: A group including all species of the genus *Andricus* would also have to contain the taxa in the PL group to be natural. Kinsey's notion of *Cynips* (*Cynips*, *Atrusca* and all Nearctic taxa of the SW group) seems improbable, regardless of whether the former *Xanthoteras* (here represented by *Trigonaspis quercusforticornis*) is included or not. Or, in other words, you cannot exclude only the Palearctic taxa from the SW group.



TREE 9. The shortest tree using implied weights for running the Separate Matrix pruned to contain only sexual generation taxa. Bootstrap frequencies from 1000 replicates shown at branches. Bootstrap frequencies below 50% are not shown.

TABLE 4. Comparison of unconstrained implied-weights analysis with analyses using different kinds of constraint trees (Combined Matrix). In each analysis, 100 random addition sequences were tried followed by TBR swapping.

Analysis	**G-fit**[1]
Unconstrained	-1140.6
Cynips-group (68% bootstrap) non-monophyletic	-1139.1
Cynipini (76% bootstrap) non-monophyletic	-1136.2
Pediaspidini (88% bootstrap) non-monophyletic	-1135.9
Kinsey’s *Cynips* with *‘Xanthoteras’* monophyletic	-1136.7
Kinsey’s *Cynips* without *‘Xanthoteras’* monophyletic	-1135.4
Andricus monophyletic	-1130.3
European *Andricus* monophyletic	-1139.7

[1] G-fit = Goloboff fit, K = 2.

In contrast to what Kinsey (1920) believed (Tree 2), *Neuroterus* seems to be an apomorphic genus, nested within the Cynipini. *Callirhytis*, on the contrary, might be one of the more basal genera although there also is some support for Kinsey’s view that it is closely related to *Amphibolips*.

TREE 10. The shortest tree using implied weights for running the Separate Matrix pruned to contain *Aylax* and *Phanacis*, but otherwise only parthenogenetic generation taxa. Bootstrap frequencies from 1000 replicates shown at branches. Bootstrap frequencies below 50% are not shown.

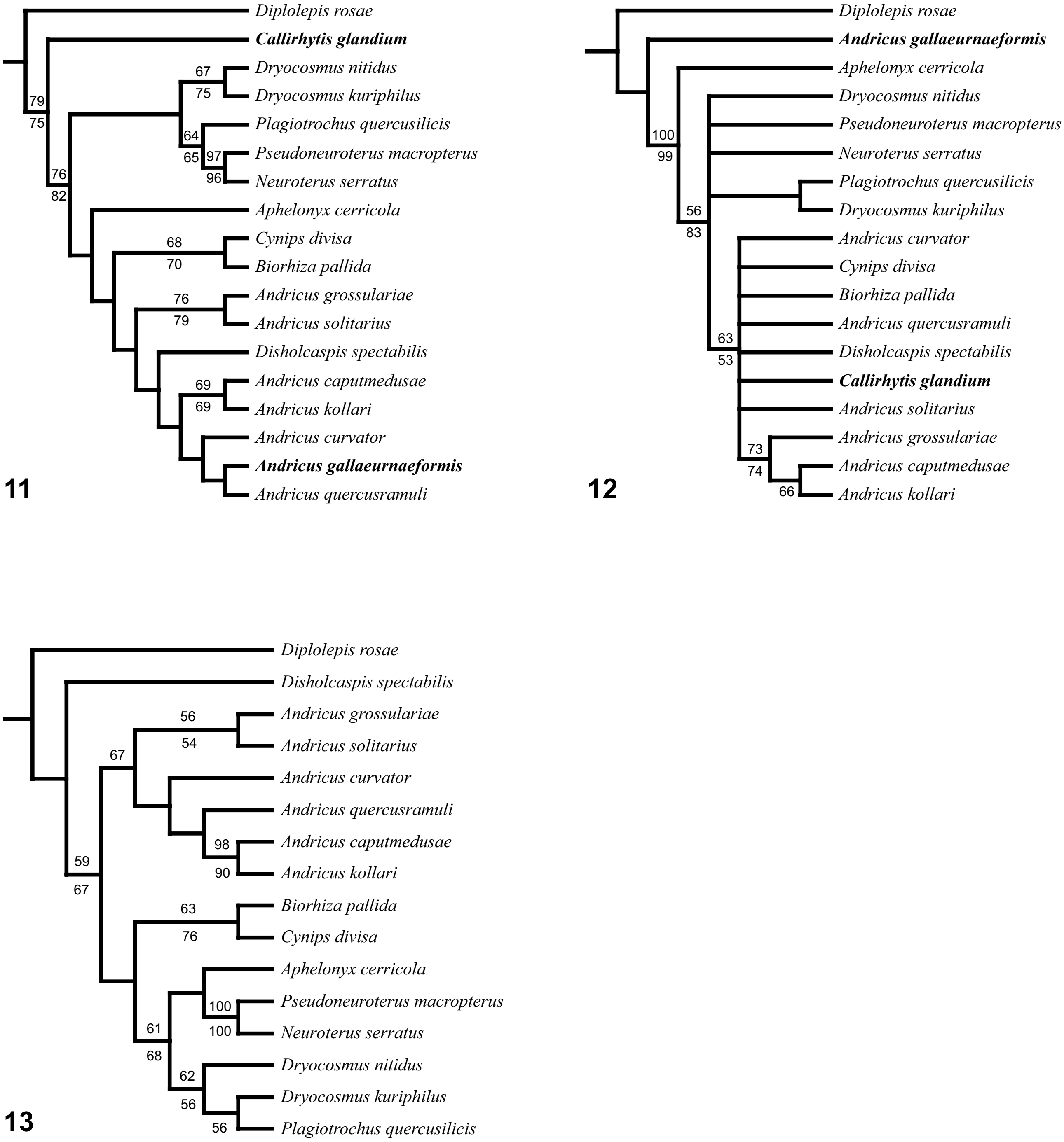
The present results differ from that of the family analysis of Liljeblad and Ronquist (1998; Tree 4) in the relative position of Diplolepidini and Pediaspidini as well as the placement of *Plagiotrochus quercusilicis*. This could be explained by the re-evaluation or exclusion of a fair number of the characters supporting the topology of the family level analysis, or it could be attributed to taxon sampling. To investigate the latter we pruned the Combined Matrix to contain only taxa shared between the two matrices. Analysis resulted in 83% bootstrap support for the Pediaspidini as the sister group to the Cynipini, while the clade *P. quercusilicis* +

Neuroterus numismalis was retained with 84% support. *Biorhiza pallida* grouped with the last two in 86% of replicates, while the Cynipini were supported at a 97% level. The switch in the sister group of the Cynipini from Diplolepidini to Pediaspidini, with about 80% bootstrap support in both cases, reveals considerable sensitivity of the previous result to taxon sampling. Trees 7 and 8 indicate that the inclusion of taxa like *Paraulax, Callirhytis* and *Disholcaspis spectabilis* might be crucial in this respect. A closer inspection reveals that some of the family-analysis characters supporting the basal position of *P. quercusilicis* were excluded in the present analysis due to too much morphological variation, while others were rendered uninformative with the inclusion of the parthenogenetic generation of *Biorhiza pallida*. Others still were redefined and/or re-evaluated, leaving only a few unchanged. With the inclusion of several new characters and taxa, the current analysis seems to have alleviated several shortcomings of the previous analysis, which apparently resulted in a seemingly basal position of *Plagiotrochus*. This conclusion agrees well with the close phylogenetic relationship between *Neuroterus* and *Plagiotrochus* suggested by Pujade-Villar *et al.* (1998) and Bellido & Pujade-Villar (2001).

The results of Drown and Brown (1998; Tree 5) agree with ours in several respects. They also find a *Cynips* group and near it a *Disholcaspis* species, probably similar to *D. quercusglobulus*. The undescribed *Callirhytis abrahamsoni* (nomen nudum) in Drown and Brown is probably closely related to the European species of this genus, and its basal position in the Cynipini in their analysis therefore agrees well with our results (Tree 7). If the position of *Andricus quercusventricosa* (Bassett) in their analysis is correct, this species is probably misplaced in *Andricus* as well as in *Callirhytis*, where it was placed at the time of the analysis. The most dramatic difference between our analysis and theirs lies in the position of *Neuroterus*, a relatively basal lineage in ours but deeply nested within a clade of *Andricus* and *Dryocosmus* in theirs. Unfortunately, the lack of clade support estimates in Drown and Brown make it impossible to evaluate how robust their results are. They also used four extremely distant outgroups, which could have affected the rooting of their Cynipini tree.

Combined analysis of morphology and published cytochrome B sequences. Tree 11 and 12 show the shortest trees from the morphology and the published cytochrome B sequence data sets, respectively, pruned to the eighteen taxa in common. At a first glance there is considerable conflict between the fully resolved trees, but at closer inspection this mainly stems from the placement of three taxa, *Andricus gallaeurnaeformis*, *Callirhytis glandium* and *Aphelonyx cerricola*. If we ignore these, however, there is common support for a *Neuroterus* group and a group consisting of *Andricus* and *Cynips*-like taxa.

We performed the joint analysis without *Andricus gallaeurnaeformis* and *Callirhytis glandium* because of the severe conflict between the data sets with respect to their placement. The former sequence appears to be from an inquiline and not from the gall inducer (see above); in the latter case, the cause of the conflict remains uncertain. Of the original characters, 355 were informative of relationships between the sixteen remaining taxa. Two hundred and forty of these were from the present study, while 115 originated from cytochrome *b*. The shortest tree (Tree 13; bootstrap values above 50 % based on 1,000 replicates indicated) had a G-fit of -2124.0, or un-weighted parsimony length of 1534 (CI = 0.45, RI = 0.41). There was no conflict between the supported groups in this tree and those supported in an unweighted parsimony analysis. Surprisingly, the shortest tree suggests a sister-group relationship between the *Neuroterus*- and *Cynips*-groups and a basal position for *Disholcaspis spectabilis* although this is not supported in either of the separate analyses. There is also support for a clade with all species of *Andricus* although we must bear in mind that they are all European. The findings should also be taken with caution, as many of the support values are relatively low and the taxon sample is poor (cf. the dramatic taxon sampling effect on the most likely sister group of the Cynipini). There is also potential doubt as to the usefulness of *Diplolepis rosae* for rooting purposes, as this is a highly derived taxon.



TREES 11–13. **11**. The shortest tree pruned to taxa in common with the cytochrome *b* data set (bootstrap frequencies as in fig. 3). **12**. Strict consensus of un-weighted parsimony (bootstrap proportions out of 1000 replicates above branches) and implied weights parsimony (bootstrap proportions out of 1000 replicates below branches) of the cytochrome *b* data set. **13**. The shortest tree found with either un-weighted (bootstrap proportions out of 1000 replicates above branches) or implied weights (bootstrap proportions out of 1000 replicates below branches) parsimony, when combining morphological and cytochrome *b* data, pruning the resulting matrix to taxa in common. Bootstrap frequencies below 50% are not shown.

Morphology

The Cynipini are unambiguously supported by the following 24 characters (with secondary reversals or modifications within the tribe in many cases): large inferior flat area of clypeus (6:0), facial strigae reaching or almost reaching eye margin (10:3), occiput more or less sharply separated into dorsal and ventral area (24:1/2), sculpture differing in these two occipital areas (26:1), a short lateral carina dorsad occipital foramen

(30:1), laterally directed carinae along hypostomal ridge (43:1), sparse pubescence in basal region of anterior surface of mandible (51:1), transverse carinae across submarginal pronotal impression (90:1), very sparse pubescence of lateral pronotal surface (98:1), anterior margin of foveae curved, gradually bending posteriorly laterad (138:1), axillar carina dorsally convex in lateral view (146:0), mesopleural triangle sparsely pubescent (156:1), no pubescence in dorsal part of median propodeal area (192:2), toothed metatarsal claw (212:1), medium length marginal cell of wing (219:1), shape of 2r clearly angled medially in parthenogenetic females (221:1), 7tg distinctly expanded ventrolaterally (239:1), presence of a petiolar hump (245:1), coarse and well defined sculpture on surface of petiole around articular bulb (250:2), an abrupt transition between dorsal flange and lateral part of annulus (252:1), dorsal groove of aedeagus narrow or absent (276:1), basidorsal margin of parameral plates distinctly incised medially (280:0), heterogeny present (285:1), host plant within *Quercus* (290:7).

All but three of these characters display some degree of homoplasy. One of the exceptions is the petiolar hump (245) while the other two come from the male genitalia (276 and 280), characters that either could not be coded for taxa with males missing or were inapplicable to taxa solely represented by a parthenogenetic generation. The ventrolateral expansion of 7tg seems to be a relatively reliable diagnostic character, as well as the host belonging to Fagaceae (excluding Nothofagaceae) if the inquilines are ruled out.

In analogy with Liljeblad and Ronquist (1998) we wanted to compare the completely new morphological characters with the old ones, whether original or modified. There were only slight differences in the ensemble consistency and retention indices between analyses including or excluding the new characters (CI=0.24 and 0.25; RI=0.48 and 0.47, respectively). The mean character consistency index was also similar (0.35 compared to 0.33) as was the frequency of characters perfectly congruent with the shortest tree (9% compared to 12%). Thus, the present analysis added a substantial number of new characters of the same quality as the old ones, suggesting that further morphological study can produce even more phylogenetically useful characters in the Cynipini.

Heterogeny

A general problem in morphological phylogenetics is how to code different morphs (semaphoronts), like males and females or sexual and parthenogenetic generations in organisms with alternating generations (heterogeny). The problem is particularly serious when many taxa can only be coded for one of the morphs because of a lack of material or because all morphs are not universally expressed. Comparing a character of one morph with that of another might involve a comparison of two things that are not homologous. A particular character might be shared across morphs in one part of a phylogeny but in another part it might have been duplicated and evolve independently in different morphs. If this character is coded as just one character we potentially lose information in the second part of the tree. However, if we make two characters out of it, we essentially duplicate the information for the first part of the tree. So, even if we knew *a priori* which characters were duplicated and where, how would we be able to code this information? In the present study, we coded some characters as applicable to one morph only, avoiding the problem of duplication, but potentially losing information if in fact no duplication had occurred and an alternate morph was available for coding. We found little difference between coding the alternating generations combined or separate, and from this we conclude that the fourteen alternating generations that we failed to include (cf. taxa marked with asterisks in table 3) probably wouldn’t influence the results much had they been included. Hence, we base our main conclusions on the Combined Matrix. Nevertheless, for future exploration of alternative analytical strategies, we make available the observations for each separate generation in the Separate Matrix.

Tree 7 suggests that heterogeny has evolved at least twice, once in *Pediaspis* (or possibly in the ancestor of it and *Himalocynips*) and once in the Cynipini. The knowledge of alternating generations is still largely incomplete, especially in the Nearctic (Pujade-Villar *et al*. 2001), and additional data could indicate that heterogeny arose several times within the Cynipini even if it seems improbable. There are a few well-documented cases, like *Dryocosmus kuriphilus* and *Andricus targionii*, where the sexual generation is not expressed (Abe 1986, 1994), but this is apparently due to secondary loss. Facultative or partial parthenogenesis apparently occurs in several species, including *Andricus quadrilineatus* (Folliot 1964) and *Plagiotrochus suberi* (Zuparko 1996; Garbin *et al*. 2008).

Plantard and Solignac (1998) and Plantard *et al.* (1999) investigated the influence of the endosymbiotic bacteria *Wolbachia* on the reproduction of several species of herb-galling cynipids. They concluded that *Wolbachia* seems to induce thelytoky, but that the Cynipidae have been infected through several infection events. This led them to conclude that this was not relevant as a character for phylogeny reconstruction. However, at a closer look there seems to be a non-random distribution of *Wolbachia*. Apart from *Liposthenes glechomae*, all infected taxa in Aylacini belong to the *Phanacis/Timaspis*-clade. *Wolbachia* is now also known from the Cynipini and the Synergini (Rokas *et al*. 2001; Rokas *et al*. 2002), but neither the Pediaspidini nor the Eschatocerini have been sampled. Thus, *Wolbachia* infection seems to be largely restricted to two clades, the inquilines and *Phanacis/Timaspis* + the WRG (cf. tree 4). The mere presence of *Wolbachia* in the Cynipini and its close relatives suggests the possibility that these bacteria might be involved in the origin of heterogeny but it is unclear how. Detailed studies suggest that *Wolbachia* is not associated with secondary loss of sex in oak gall wasps (Abe & Miura 2002).

When comparing the two alternating generations to see if either is more morphologically derived than the other, we used two different approaches. First, we ran an unconstrained analysis of the Separate Matrix comparing the generation pairs species by species; secondly, we constrained the respective generations to two different clades comparing them node by node. In the second case we used either *Pediaspis aceris*, the Diplolepidini or none of these, to root the generation groups in a simultaneous constrained analysis. Regardless of the approach used, there was no significant trend towards either kind of generation having gained more apomorphies than the other. There were, however, a couple of more characters defining an ancestral parthenogenetic female than an ancestral sexual one. The actual characters varied somewhat depending upon which of the three outgroups was used, but this was the only indication of the parthenogenetic generation being generally more apotypic than the sexual one. It must be borne in mind that no effort was made to code autapomorphies, and that our results do not preclude a significant trend towards either generation being more apotypic at a lower taxonomic level.

It is interesting that the apotypic nature of the parthenogenetic generation is supported by gall characteristics. The gall of the ancestral parthenogenetic generation of Cynipini (the one in which the larva of the parthenogenetic generation develops after oviposition of a sexual-generation female) was probably more complex than the sexual generation gall, something that is generally true also for extant cynipids. The average size of a species was excluded from the present analysis due to more or less continuous variation, making coding into discrete states too difficult. If we look at the relative size of the two generations, however, the pattern is more easily interpreted. The sexual generation is generally smaller, and if the size difference had been mapped onto the current tree, a distrinctly smaller sexual generation would have been the favored ancestral state. In *Neuroterus*, however, this difference has more or less disappeared, while the relationship between the generations is reversed in *Trigonaspis*. Many other exceptions are known in species not included in the current study, so the conclusion about ancestral size differences between generations remains tentative.

Taxonomy

The placement of *Eschatocerus acaciae* as the sister group to *Liebelia magna* renders the Diplolepidini paraphyletic, but the group as a whole is still strongly supported. However, due to contradictory results from preliminary molecular analyses (Nylander *et al.* in ms.), we consider it premature to synonymize Eschatocerini with Diplolepidini**.** The former placement of the genus *Paraulax* in Cynipini is incorrect, and because of the support for its sister group relationship to *Pediaspis* + *Himalocynips*, we here transfer it to the Pediaspidini. *Paraulax quereicola* was not reared from *Nothofagus*, but *Quercus*, and in the description the females are said to oviposit in already swollen terminal branches, suggesting that the insect is an inquiline and not a gall-inducer. This observation in combination with the 12-segmented female antenna, the closed margin of the marginal cell, and the small adult size, 1.4 mm, strongly suggest that this species belongs to the genus *Ceroptres*, to which it is here transferred as *Ceroptres quereicola* (Shinji 1938) **comb. nov**.

The combination *Ceroptres quereicola* appeared first in 2002 in a manuscript, included as part of J. Liljeblad's PhD dissertation, with a disclaimer stating that any nomenclatural acts should not be regarded as validly published according to the International Code of Zoological Nomenclature. Thus, this is the first valid publication of the new combination. Abe, Melika and Stone (2007) recently suggested that the species be treated as unplaced to higher taxon and eventually discarded from cynipid taxonomy but, given the evidence cited above, we prefer to place the species in *Ceroptres* and then leave it to future revisions of Japanese *Ceroptres* to determine whether the name should be used or discarded as a *nomen oblitum*.

The genera *Callirhytis* and *Andricus* have traditionally been separated more or less solely by the absence or presence of toothed claws. The problem is of course not as easily solved as that, and even this single character has been confused (Weld 1952). Both generations of the genotype of *Andricus*, and most other *Andricus* species, have toothed claws, while the situation is not as clear in *Callirhytis*. The European genotype species *C. hartigi* has simple claws (Pujade-Villar *et al*. 2007). It was previously reported that the suspected parthenogenetic generation of *C. hartigi*, *C. erythrocephala*, displays simple or weakly toothed claws (Nieves Aldrey 1992) but it now appears that this may have been due to the mixing of the parthenogenetic form of two different species (Pujade-Villar *et al*. 2007).

Among other species placed in *Callirhytis*, we find both representatives with simple and weakly toothed claws, and this character is obviously not good for diagnosis of *Callirhytis*. Weld (1952) considered four groups of *Callirhytis*, and although these were to some extent unnatural he believed it should be possible to found new genera from these four groups. JL managed to examine some American representatives of *Callirhytis* (*C. lapillula* Weld and *C. fructuosa* Weld) and found them to be closely related to the European taxa. This group would represent *Callirhytis* s. s., characterized by a transversely rugose mesoscutum as diagnosed by Melika and Abrahamson (2002). In addition to the transversely rugose mesoscutum, all of these species also induce galls on acorns, which is typical for the asexual generation of the Western Palearctic *Callirhytis*. Other species that were formerly placed in *Callirhytis*, like *Andricus serricornis* as well as *A. quercusbatatoides* (Ashmead) and *A. seminator* (Harris) from the analysis by Drown and Brown (1998), seem correctly transferred to *Andricus* (cf. Trees 5 and 7). The European *Andricus sulcatus* (Förster), which is the type of *Liodora*, also appears more closely related to European *Andricus* than to American former *Liodora* species like *Andricus cylindratus* (Pujade-Villar 2003).

Andricus continues to be a problematic and heterogeneous genus. Even if the European species would constitute a monophyletic group, which seems improbable considering the total evidence analysis, we are stuck with a paraphyletic (Tree 7) or even polyphyletic (Tree 8) assemblage of American species. The group might become monophyletic if we include in *Andricus* the whole PL group. This latter strategy seems unfortunate, as we would lose the information stored in the genus-group names of the PL group, not to mention adding to the almost 400 species already present in *Andricus*.

The apparent close affinity of *Andricus hastatus* (formerly in *Erythres*) with *Amphibolips* (Tree 7) suggests a possible synonymization of *Erythres* with *Amphibolips* rather than *Andricus*. However, in terms of gall structure, there are few obvious similarities between *A. hastatus*, or other species formerly placed in *Erythres*, and *Amphibolips*. Given this and that the support values for this clade in the current analysis are low and the taxon sampling incomplete, any definite phylogenetic conclusions will have to await more detailed studies.

In the *Cynips* group, our results indicate that the recent synonymization of *Belizinella* and *Xanthoteras* with *Trigonaspis*, and *Sphaeroteras* with *Biorhiza*, were unfortunate in that they rendered both *Trigonaspis* and *Biorhiza* nonmonophyletic (Tree 7). The former genus *Sphaeroteras*, represented in our analysis by *Biorhiza mellea*, does not appear to be closely related at all to core *Biorhiza*, represented by *B. pallida*. Furthermore, inclusion of *Trigonaspis quercusforticornis* (formerly in *Xanthoteras*) and *T. gibbera* (formerly in *Belizinella*) in *Trigonaspis* appears to create problems with the recognition of core *Biorhiza*, and maybe also *Philonix* and *Acraspis*, as separate genera since they tend to fall within this expanded circumscription of *Trigonaspis*. However, because of the relatively poor taxon sampling in our analysis, and the lack of convincing support values for the clades within the *Cynips* group, we refrain from proposing formal taxonomic changes here.

Relationships of taxa not included in the analysis

For a more complete picture of the phylogeny of the WRG, we tried to assess the phylogenetic affinities of the genera not included in the analysis. For some of these taxa, we had access to specimens that could be examined under the stereo microscope even though we did not have enough material to include them in the proper analysis. For others, only literature data were available as indicated below.

According to Ács et al. (2007), *Dryocosmus kuriphilus*, the only representative of *Dryocosmus* included in our analysis, is congeneric with the European type species. If our results are correct, then, this means that the genus *Dryocosmus* belongs to the *Neuroterus* group. The position of Nearctic *Dryocosmus* species remains uncertain, however; some of them differ considerably from the type species of the genus and may not be closely related.

Judging from descriptions, both *Bassettia* and *Eumayriella*, not included in our analysis, seem closely related to *Loxaulus* and maybe *Callirhytis*, rather than *Eumayria*, as has been speculated before (Melika & Abrahamson 1997; Melika & Abrahamson 2002). *Holocynips*, inducing galls on red oaks, shows affinity to the PL group, but also to the former *Trichoteras* (synonymized with *Andricus* by Melika & Abrahamson 2002). The latter genus may prove related to *Andricus kingi* and a resurrected and expanded *Dros* (including *Andricus* species related to *A. serricornis*, as well as the American former *Liodora*). As already mentioned, *Phylloteras* and *Zopheroteras*, both American genera with reduced wings, seem closely related to the other taxa with reduced wings included in the analysis, occupying a position immediately basal of the *Cynips*-group. This would, however, lend support for the SW group being paraphyletic rather than monophyletic.

For the following taxa the types are apparently lost, but we include them to make the listing complete. We agree with Melika & Abrahamson (2002) that both *Parandricus* and *Neoneuroterus* show affinities with *Andricus*. The subgenus *Latuspina* of *Neuroterus* would seem not to belong to *Neuroterus*, but its relationships are uncertain, while *Australofigites poeta* Girault may belong to the Aylacini. *Poncyia ferruginea* Kieffer, finally, is suggested not to be a gall inducer at all but an inquiline (Weld 1952, unpublished manuscript).

Geographical origin

We included the biological and distributional characters in the phylogenetic analysis. Some workers argue that circularity arises if one discusses the evolution of these character systems on the resulting tree. For the benefit of those workers, we performed an analysis with all biological and distributional characters excluded. No branches conflicting with tree 7 were retained in more than 50% of bootstrap replicates. Thus, we proceed with our discussion based on tree 7, knowing that our results would have been very similar even if these characters had been excluded from the phylogenetic analysis.

While the family of gall wasps probably originated from somewhere in the Mediterranean region (Ronquist & Liljeblad 2001) the situation is more complex for the WRG. The genus *Diplolepis* seems to have its origin in the Nearctic (Plantard *et al.* 1998), but because the sister group contains the Palearctic *Liebelia* and the Neotropic *Eschatocerus*, the origin of the Diplolepidini remains uncertain. The situation for the Pediaspidini is also intriguing with the basal Neotropic *Paraulax*, the western Palearctic *Pediaspis* and the eastern Palearctic *Himalocynips*. Adding to the puzzle, there is an undescribed cynipid reared from galls on *Scolopia mundii* (Flacourtiaceae) in South Africa, which, after examination of JL, seems to have a phylogenetic position intermediate between the Diplolepidini and Pediaspidini.

The low support for the relationship between these tribes, as well as the basal branchings within the Cynipini, makes it even more difficult to infer the area of origin for the Cynipini. Our results could be consistent with an American, a European, or a widespread ancestor of the extant Cynipini. Even an Eastern Palearctic ancestor could be possible, given that the gall wasp fauna of this region is so poorly studied that basal lineages originating there may easily have been overlooked (Abe et al. 2007). Recent evidence also indicates that at least one major clade (the *Plagiotrochus* - *Neuroterus* clade; Tree 7) may have originated in the southeastern Palearctic (Bellido *et al*. 2000; Bellido & Pujade-Villar 2001).

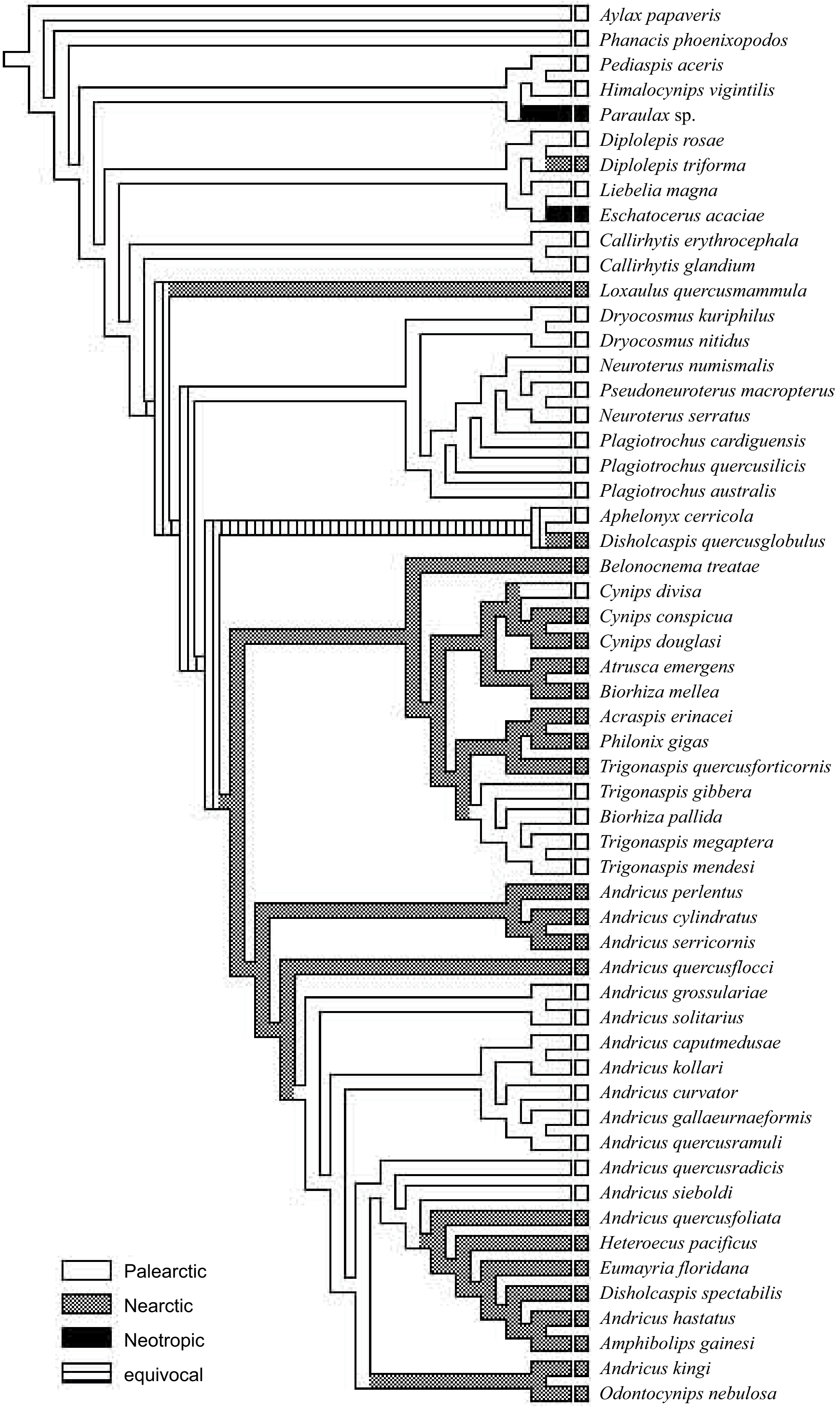
With phylogenetic uncertainties and biogeographic complexities in mind, we nevertheless carried out a simple optimization of geographic distribution (char. 286) using Wagner parsimony (Tree 14). From this reconstruction, it is obvious that there has been a large number of vicariance events or dispersals involving the Nearctic and Palearctic. The number would be even greater if we considered genera and species not included in the present analysis. With the exception of *Dryocosmus kuriphilus*, the Holarctic *Neuroterus* is the only genus in the *Neuroterus* group that is not restricted to making galls on oaks of the Palearctic section *Cerris*. As *Neuroterus* currently contains 91 species, this suggests colonization of and relatively rapid radiation in the Nearctic from a Palearctic origin. The *Cynips*-group appears to have originated in the Nearctic, with later dispersals to the Palearctic of the genus *Cynips* itself as well as the ancestor to the group of apterous taxa (the SW group).

Host plant association

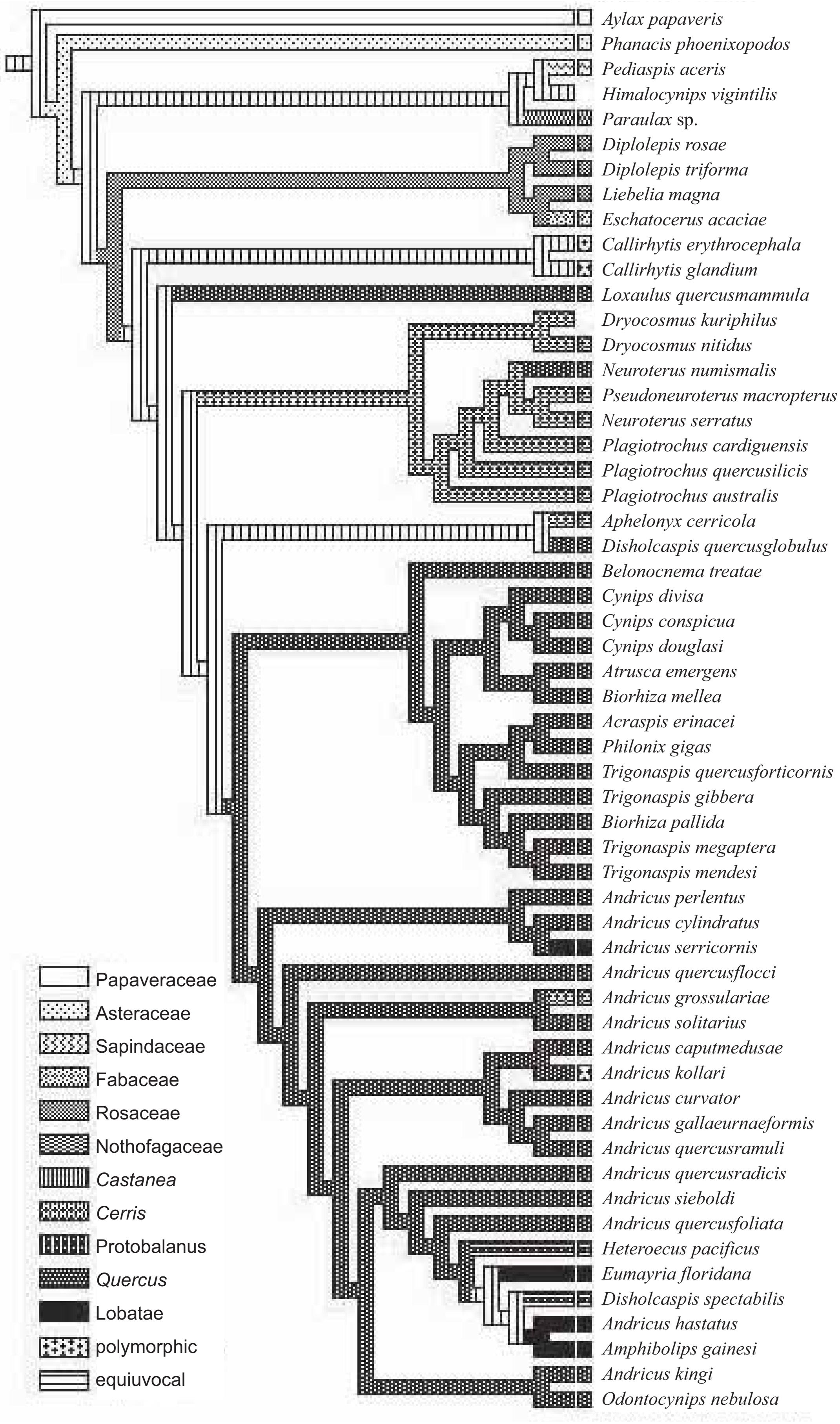
The Cynipini are naturally heavily dependent upon the evolution of their oak hosts. The major oak lineages were present at middle latitudes in the Tertiary about 40 Mya, with a split between the red and the white oaks no later than the Oligocene (40–24 Mya) because of the postulated use of a trans-Atlantic land bridge in the colonization of the Old World by white oaks (Manos *et al.* 1999). Ronquist and Liljeblad (2001) concluded from their family-level analysis that there was no evidence for parallel cladogenesis between gall wasps and their host plants. However, there is definitely potential for parallel speciation between the oak gall wasp subclade and their oak hosts. First, the Cynipini are present on all four sections of the subgenus *Quercus*, as well as on the subgenus *Cyclobalanopsis* and a few other closely related genera of the Fagaceae, as one would expect if there had been parallel speciation between oak gall wasps and oaks. Second, although there is some disagreement on the interpretation of the fossil record of cynipids (Ronquist 1999; Liu *et al*. 2007), it is at least compatible with an Eocene age for the Cynipini, suggesting that the oaks and wasps could have radiated concomitantly.

The phylogenetic uncertainty of tree 7 makes rigorous tests of cospeciation difficult. However, if the optimal tree is accepted at face value and the host plants mapped onto it, the pattern is impossible to differentiate from one produced solely by duplication and switching events. We therefore optimized host plant group onto tree 7 using Wagner optimization (Tree 15). The traced character was a combination of characters 290–292, where the states were ordered in a grade reflecting the phylogenetic relationships of the host plants, which in turn is likely to reflect the probability of host-plant shifts. The three cases of heteroecy were coded as section *Cerris*/*Quercus*-polymorphism.

Although many cynipid taxa were missing from the analysis (see Table 2), the oak gall wasps clearly show a considerable degree of conservatism in their choice of host plant even at the level of *Quercus* section. Most taxa occur on *Quercus* s.s., with only a few switches to other sections, the most obvious example being the PL-group. The *Neuroterus*-group (including *Dryocosmus*) has switched to section *Cerris*, with a reversal back to *Quercus* s.s. within the genus *Neuroterus* itself. Some workers consider this reversal in host plant preferences so unlikely that they question the monophyly of *Neuroterus*. Our results provide fairly strong evidence against a diphyletic *Neuroterus* in that the *Quercus* s.s. galler *N. numismalis* is firmly embedded within the clade of *Cerris* gallers (Tree 7; Tree 15).



TREE 14. Mapping of distribution into main geographical areas (character 286) onto the shortest tree.



TREE 15. Mapping of host plant groups (combination of characters 290-292) onto the shortest tree.

Dryocosmus kuriphilus has apparently shifted to *Castanea* from section *Cerris*, the host of the European *Dryocosmus*. If the cynipids on *Chrysolepis, Lithocarpus* and subgenus *Cyclobalanopsis* were added to the phylogeny, there could potentially be four more such shifts from the subgenus *Quercus* to related hosts. Although less likely, it is also possible that all these species, none of which could be included in the current study, fall outside of the clade to which the true oak gallers belong.

Due to the difficulties of resolving the basal relationships within the Cynipini, it is impossible to provide a definitive reconstruction of the original host for the oak gall wasps at this point in time. One possibility, based on Tree 7 and the facts that the American *Callirhytis* are mainly found on oaks in section Lobatae, while three species in *Loxaulus* have their hosts in section Protobalanus, is that there was a basal split in the Cynipini reflecting the split between these two host plant lineages. Another possibility is that the original host of the Cynipini belonged to the oak section *Cerris,* supported by the use of this section by both basal *Neuroterus* group members as well as several other potentially basal Cynipini lineages (Bellido & Pujade-Villar 2001), or that there was a basal split in the oak gall wasps between *Cerris* gallers (the *Dryocosmus* and *Neuroterus* lineage) and gallers of the sections Protobalanus, Lobatae, and *Quercus* s.s. (remaining Cynipini; Abe *et al*. 2007; Ács *et al*. 2007). However, either of these scenarios would exclude the possibility of a Cynipini origin in the Nearctic.

Heteroecy

Heteroecy apparently have evolved at least twice in the Cynipidae. In the ancestor of some European species of *Andricus* the sexual generation switched to section *Cerris* with the parthenogenetic generation remaining on section *Quercus*, while the opposite seems to have happened in the European *Callirhytis*. Cook *et al*. (2002) came to the conclusion that this transition for *Andricus* to section *Cerris* involves just a single irreversible event. This is not supported here, but neither Tree 7 nor Tree 13 gives very strong support against it, especially considering the poor sample of taxa relevant to the testing of this hypothesis.

Conclusions

One of the most important contributions of the current study is the freely available Morphbank set of more than 2,000 images documenting the 283 morphological characters used in the analysis. By linking each of our characters to the relevant set of images in Morphbank, we have facilitated for other workers to critically evaluate our coding, and to build on our data in future analyses. Hopefully, this approach will become standard in future morphological phylogenetics studies. Beyond the image vouchering of the raw data, our study has improved the understanding of the higher phylogeny and evolution of the WRG and represents an important step towards a more stable classification of the oak gall wasps. Nevertheless, many important questions remain, for instance concerning the basal Cynipini branchings. Our results clearly indicate that a more extensive sample of American *Callirhytis*, *Dryocosmus* and *Andricus* is crucial in resolving this question. More robust estimates of the early Cynipini radiation could also result from increased accuracy in the inference of ancestral Cynipini states through inclusion of more non-Cynipini WRG, such as undescribed South American species found in *Nothofagus* galls (Nieves-Aldrey *et al*. in prep.) or the recently discovered (van Noort pers. comm.) and also undescribed South African species making galls on the rosid bush *Scolopia mundii* (Eckl. & Zeyh.) Warb. (Salicaceae, formerly Flacourtiaceae). This could prove all the more important since molecular data show the currently included exemplars from the Pediaspidini, Diplolepidini and Eschatocerini to be highly derived and therefore poorly suited for the rooting of the oak gall wasp radiation.

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JL organized the work, gathered most of the material, did preparations of 51 species, prepared all images of these and additional images of four species, identified, described and coded most characters, performed all analyses, wrote most of the paper and made all illustrations. FR contributed in the planning of the paper, provided some material, participated in the coding and description of many characters, and wrote sections of the final version of the paper. JLNA contributed material and coded a major part of the biological characters. FFC helped in developing the image database approach. PRF helped with the phylogenetic belonging of the genus *Paraulax*. DG developed the permanent collection functionality in Morphbank. JPV contributed material, prepared and imaged four species as well as helped with identifying potentially informative characters and character states.

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Appendix 1. Characters used for phylogenetic analysis

Explanation of abbreviations 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 illustrations in earlier analyses: L = Liljeblad & Ronquist (1998), P = Pujade-Villar and Arnedo (1997), Q = Ronquist (1995b), R = Ronquist (1994). In these earlier analyses, character states are translated as a = 0, b = 1, etc. Transformation series hypotheses are given for multistate characters. Consistency index (CI), retention index (RI) and Goloboff fit (G-fit) on the Preferred Tree are stated for each character.

Head, anterior view, female

1. [= L1] Shape of ventral part of clypeus[1]: (0) rounded, broadly projecting over mandibles (Fig. R8); (1) not projecting from cranial margin or slightly and narrowly projecting medially (Fig. R7). (CI = 0.50, RI = 0.00, G-fit = 0.75)
2. [= L2] Shape of projecting ventral clypeal margin[1]: (0) straight or rounded (not illustrated); (1) with a median incision (Fig. R8). (CI = 0.27, RI = 0.27, G-fit = 0.18)
3. [= R2/L3] Clypeo-pleurostomal lines[1]: (0) present, at least visible by different sculpture (Fig. R8); (1) absent (Fig. R7). (CI = 0.33, RI = 0.33, G-fit = 0.60)
4. Lateral border of clypeus at ventral margin of head[1]: (0) distinct angle marking clypeal border (Fig. 1a); (1) no distinct angle, smooth transition between clypeal margin and rest of ventral margin (Fig. 1b). (CI = 0.25, RI = 0.65, G-fit = 0.30)
5. [modified from L4 and L6] Shape of non-projecting part of clypeus[1]: (0) broadly trapezoidal or rectangular, distance between anterior tentorial pits larger than distance to ventral margin (Fig. R8); (1) square, distance between anterior tentorial pits about the same as distance to ventral margin (Figs. R7, L7a). (CI = 0.20, RI = 0.20, G-fit = 0.43)
6. Lateral inferior flat area of clypeus[1]: (0) large (Fig. 1a); (1) small or absent (Fig. 1b). (CI = 0.11, RI = 0.53, G-fit = 0.27)
7. Area of clypeus just below tentorial pits[1] (not illustrated): (0) smooth and glabrate, nude; (1) sculptured and pubescent. (CI = 0.13, RI = 0.44, G-fit = 0.18)
8. Shape of lower border of smooth and glabrate area just below tentorial pits[1]: (0) with two sublateral projections, sometimes connected by a carina (Fig. 3a); (1) without such sublateral projections (not illustrated). (CI = 0.14, RI = 0.33, G-fit = 0.33)
9. Carina just dorsolaterad tentorial pits, directed ventrally[1]: (0) absent (not illustrated); (1) present (Fig. 3b). (CI = 0.29, RI = 0.43, G-fit = 0.16)
10. [modified from L7] Facial strigae radiating from lateral clypeus[1]: (0) absent (Fig. R8); (1) present, but only close to clypeus (not illustrated); (2) present, reaching about half ways to eye margin (Fig. L7a); (3) present, reaching or almost reaching eye margin (Fig. R7). Ordered 0123. (CI = 0.11, RI = 0.38, G-fit = 0.08)
11. Distinctness of facial strigae[1] (not illustrated): (0) regular and strong; (1) irregular and weak. (CI = 0.25, RI = 0.40, G-fit = 0.30)
12. [modified from R6/L8] Subocular impression[1] (= malar sulcus): (0) absent (Fig. R7); (1) present, only indicated by different sculpture (not illustrated); (2) present, clearly marked by a furrow (Fig. R8). Ordered 012. (CI = 0.15, RI = 0.55, G-fit = 0.14)
13. Vertical carinae ventrolaterally on gena (not illustrated): (0) absent; (1) present, irregular; (2) present, regular. Ordered 012. (CI = 0.40, RI = 0.00, G-fit = 0.50)
14. [modified from L9] Vertical carinae between antennal sockets and anterior tentorial pits[1] (not illustrated): (0) absent; (1) present. (CI = 0.33, RI = 0.20, G-fit = 0.38)
15. Distance between antennal sockets, compared to diameter of sockets including rim[1]: (0) short, shorter than diameter (Figs. R8, L7a); (1) long, as least as long as diameter (not illustrated). (CI = 0.20, RI = 0.33, G-fit = 0.43)
16. Distance between mesal margin of compound eye and lateral margin of antennal sockets[1]: (0) shorter than diameter of antennal sockets including rim (Fig. R7); (1) subequal to diameter of sockets (Figs. R8, 1a, 1b); (2) a little longer than diameter of sockets (Fig. L7a); (3) much longer than diameter of sockets (not illustrated). Ordered 0123. (CI = 0.21, RI = 0.21, G-fit = 0.12)

17. Carinae connecting antennal sockets[1]: (0) absent (not illustrated); (1) present (Fig. 1a). (CI = 0.22, RI = 0.42, G-fit = 0.27)
18. Shape of surface of face in area around antennal sockets[1] (not illustrated): (0) more or less flat, sockets directed more anteriorly; (1) ledge-like, sockets directed slightly obliquely dorsad. (CI = 0.25, RI = 0.40, G-fit = 0.50)
19. [modified from R12/L10] Shape of area between antennal sockets and ocelli[1]: (0) slight longitudinal depression (not illustrated); (1) evenly flat (Fig. R7); (2) smooth bulge (not illustrated); (3) distinct elevation, often longitudinally ridgelike (Fig. R8). Ordered 0123. (CI = 0.21, RI = 0.27, G-fit = 0.12)
20. [modified from L15] Coriarious or finely colliculate sculpture between antennal sockets and ocelli[1] (not illustrated): (0) present; (1) absent. (CI = 0.33, RI = 0.60, G-fit = 0.60)
21. [modified from L15] Carinate sculpture between antennal sockets and ocelli[1] (not illustrated): (0) absent; (1) present. (CI = 0.20, RI = 0.20, G-fit = 0.43)
22. [modified from R10/L13] Orbits[1]: (0) not impressed, continuing smoothly into rest of facial surface (Fig. R7); (1) distinctly and narrowly impressed (Fig. R8); (2) weakly and broadly impressed (not illustrated). Ordered 012. (CI = 0.40, RI = 0.50, G-fit = 0.50)
23. Direction of straight part of inner margins of compound eyes[1]: (0) ventrally diverging (Fig. R8); (1) more or less parallel (Figs. 1a, 1b); (2) ventrally converging (not illustrated). Ordered 012. (CI = 0.19, RI = 0.44, G-fit = 0.18)

Head, posterior view, female

24. [modified from L28] Shape of occiput medially[2]: (0) evenly rounded (Fig. L7c); (1) sharply rounded, diffusely separating occiput into an inner and outer area (not illustrated); (2) occiput impressed, sharp dorsal edge clearly separating occiput into an inner and outer area (L7e). Ordered 012. (CI = 0.09, RI = 0.38, G-fit = 0.13)
25. Occiput immediately dorsad occipital foramen[2] (not illustrated): (0) shallowly impressed; (1) more or less deeply impressed. (CI = 0.12, RI = 0.53, G-fit = 0.30)
26. Superficial sculpture of dorsal and ventral areas of occiput[2] (not illustrated): (0) with similar sculpture; (1) with different sculpture, typically sculptured dorsally and smooth ventrally. (CI = 0.20, RI = 0.58, G-fit = 0.25)
27. [modified from L29] Sculpture on occiput[2]: (0) more or less smooth (Fig. 1d); (1) transverse carinae (not illustrated); (2) transversely wrinkled costulae (Fig. 1c). Ordered 012. (CI = 0.30, RI = 0.52, G-fit = 0.12)
28. Pubescence of occiput[2] (not illustrated): (0) absent only dorsally of occipital foramen; (1) glabrous area extending laterally, but not ventrally; (2) glabrous area extending laterally and ventrally. Ordered 012. (CI = 0.25, RI = 0.38, G-fit = 0.14)
29. Distance between dorsal cranial margin and occipital foramen[2]: (0) short, clearly shorter than height of occipital foramen including postoccipital rim (Fig. 1d); (1) long, about as long as height of foramen or longer (Fig. L7c). (CI = 0.41, RI = 0.50, G-fit = 0.16)
30. Lateral carina dorsad occipital foramen[2]: (0) absent or very weak (Fig. 1d); (1) short, ventrally not continuing further than posterior tentorial pits (Fig. L7b); (2) long, ventrally continuing past posterior tentorial pits (Fig. 1c). Ordered 012. (CI = 0.37, RI = 0.33, G-fit = 0.15)
31. [= L30] Shape of odontoidea[2]: (0) narrow and more or less pointed laterally, abruptly broadened close to mesal margin (Fig. L7b); (1) broader and more rounded laterally, gradually broadened towards mesal margin (Figs. R9, R10). (CI = 0.29, RI = 0.43, G-fit = 0.16)
32. [modified from L23] Position of posterior tentorial pits[2]: (0) high, ventral margin of pit higher than ventral margin of rim of occipital foramen (Fig. L7b; (1) intermediate, ventral margin of pit around same level as ventral margin of rim of occipital foramen (Fig. 4); (2) low, ventral margin of pit lower than ventral margin of rim of occipital foramen (Fig. L7e). Ordered 012. (CI = 0.32, RI = 0.38, G-fit = 0.13)
33. [modified from L24] Shape of posterior tentorial pits at cranial surface[2]: (0) narrow, slit-like (Fig. 1d); (1) more broadly rounded, sometimes irregularly so (Fig. 1c). (CI = 0.29, RI = 0.54, G-fit = 0.19)
34. Shape of posterior tentorial pits dorsally[2]: (0) gradually narrowing, continuing into a furrow (Fig. 1d); (1) abruptly terminated, not continuing into a furrow (Fig. 1c). (CI = 0.27, RI = 0.42, G-fit = 0.18)
35. Shape of ventral border of posterior tentorial pits[2]: (0) narrowly rounded (Fig. 1d); (1) broad and straight (Fig. 1c). (CI = 0.09, RI = 0.54, G-fit = 0.23)

36. Shape of lateral border of posterior tentorial pits[2] (not illustrated): (0) diffuse, posterior surface of head more or less gradually continuing into pits; (1) distinct, posterior surface of head not continuous with pits. (CI = 0.80, RI = 0.67, G-fit = 0.43)
37. [= L19] Position of gular sulci and gular ridges[2]: (0) united well before reaching hypostoma (Fig. R9); (1) free, but meeting at hypostoma (not illustrated); (2) free, well separated at hypostoma (Fig. R10). Ordered 012. (CI = 0.29, RI = 0.25, G-fit = 0.14)
38. [modified from L20] Appearance of gular sulci[2] (not illustrated): (0) strong and complete, marked by strong carinae; (1) weak and complete, marked by weaker sculpture; (2) weak and incomplete, only marked in ventral region; (3) absent, not marked by different sculpture. Ordered 0123. (CI = 0.21, RI = 0.28, G-fit = 0.09)
39. [= L21] Distinctness of gular ridges[2] (not illustrated): (0) distinctly raised; (1) reduced, not ridge-like. (CI = 0.17, RI = 0.29, G-fit = 0.38)
40. [modified from L17] Median membranous strip of gula[3] (not illustrated): (0) covered with at least some hairlike structures; (1) hairlike structures absent. (CI = 1.00, RI = 1.00, G-fit = 1.00)
41. [modified from R14/L22] Distance between occipital and oral foramina[2]: (0) short, much shorter than height of occipital foramen including postoccipital rim (Fig. R10); (1) medium, subequal to height of occipital foramen including postoccipital rim (Fig. 1d); (2) long, longer than height of occipital foramen including postoccipital rim (Fig. R9). Ordered 012. (CI = 0.40, RI = 0.57, G-fit = 0.27)
42. Posterodorsal margin of oral foramen[2]: (0) distinctly margined medially, hypostomal ridges almost meeting (Fig. 1d); (1) less distinctly margined medially, hypostomal ridges interrupted by some distance, but still forming a rounded arch (not illustrated); (2) not margined medially, hypostomal ridges well separated and not forming a rounded arch (Fig. 1c). Ordered 012. (CI = 0.19, RI = 0.21, G-fit = 0.09)
43. Carinae directed laterally along hypostomal ridge[2] (not illustrated): (0) absent; (1) present. (CI = 0.24, RI = 0.32, G-fit = 0.16)
44. [= R17/L18] Shape of ventral part of hypostoma[2]: (0) not or only slightly projecting from cranial margin, only slightly raised (Fig. R10); (1) distinctly projecting from cranial margin, distinctly raised (Fig. R9). (CI = 1.00, RI = 1.00, G-fit = 1.00)

Mandibles, female

45. [= R19/L31] Number of teeth with corresponding internal rods on right mandible: (0) three (Fig. R11); (1) two (Fig. R12). (CI = 1.00, RI = 1.00, G-fit = 1.00)
46. [= R20/L32] Basal swelling on anterior side of mandible[4]: (0) small or indistinct (Fig. R12); (1) large, conspicuous (Fig. R11). (CI = 0.30, RI = 0.30, G-fit = 0.25)
47. [= R21/L33] Size of oval window on posterior surface of mandible: (0) large (Fig. R13); (1) small or almost absent (Fig. R14). [Typing errors corrected from L33]. (CI = 0.12, RI = 0.12, G-fit = 0.30)
48. [= R23/L35] Posterior region of ventral surface of mandible[5]: (0) horizontal, set off from posterior surface of mandible by a distinct carina (Fig. R13); (1) oblique, gradually continued in posterior surface of mandible (Fig. R14). (CI = 0.11, RI = 0.27, G-fit = 0.27)
49. Length of ventralmost tooth of right mandible[4]: (0) long, apex reaching at least as far as other teeth (Figs. R11, R12); (1) short, shorter than other teeth (not illustrated). (CI = 0.33, RI = 0.00, G-fit = 0.60)
50. Shape of dorsal margin of mandible[5]: (0) straight or slightly convex (Fig. R11); (1) concave (Fig. R12). (CI = 0.29, RI = 0.54, G-fit = 0.33)
51. Pubescence in basal region of anterior surface of mandible[4] (not illustrated): (0) present and abundant; (1) present but sparse; (2) absent or almost so. Ordered 012. (CI = 0.23, RI = 0.38, G-fit = 0.11)

Labiomaxillary complex, female

52. [= L38] Shape of cardo[2]: (0) bent distally some distance from apex, large part visible in posterior view of head (Fig. R9); (1) bent distally close to apex, only small part visible posteriorly (not illustrated); (2) straight, not bent distally, not or almost not visible posteriorly (Fig. R10). Ordered 012. (CI = 0.25, RI = 0.25, G-fit = 0.18)
53. Dorsal surface of cardo in posterior view[2]: (0) almost horizontal, the cardines together forming a flat area (Fig. 1f);

(1) oblique, cardines forming a rounded or angled arch (Fig. 1e). (CI = 0.24, RI = 0.20, G-fit = 0.13)

54. Shape of cardo[2]: (0) narrow, cardo laterally not reaching outer margin of stipes (not illustrated); (1) broad, cardo laterally reaching outer margin of stipes (Figs. 1e, 1f). (CI = 0.09, RI = 0.17, G-fit = 0.23)
55. Transition between posterior surfaces of cardo and stipes laterally, in posterior view[2]: (0) marked by a distinct incision (Fig. 1f); (1) invisible, not marked by an incision (Fig. 1e). (CI = 0.20, RI = 0.00, G-fit = 0.43)
56. [= R24/L37] Longitudinal mesal carina on posterior surface of stipes[2]: (0) present (Fig. R9); (1) absent (Fig. R10). (CI = 0.20, RI = 0.38, G-fit = 0.25)
57. Relative length of stipes compared to prementum[2]: (0) long, stipes at least reaching base of labial palps (Figs. 1e, 1f); (1) short, stipes not reaching base of labial palps (not illustrated). (CI = 0.08, RI = 0.27, G-fit = 0.21)
58. Lateral margin of stipes[2]: (0) straight, more o less parallel to mesal margin, posterior surface of stipes rectangular (Figs. 1e, 1f); (1) clearly curved outwards, posterior surface of stipes oval (not illustrated). (CI = 0.06, RI = 0.38, G-fit = 0.16)
59. Shape of prementum[2]: (0) rectangular, lateral margins subparallel (Fig. 1f); (1) distally broadening, lateral margins diverging ventrally (Fig. 1e). (CI = 0.27, RI = 0.52, G-fit = 0.18)
60. Shape of prementum distally[2]: (0) rounded, not elongate (Fig. 1e); (1) pointed and elongate (Fig. 1f). (CI = 0.12, RI = 0.36, G-fit = 0.30)
61. Longitudinal median crest of prementum[2]: (0) absent (Fig. 1e); (1) present but indistinct or incomplete (not illustrated); (2) present, distinct and narrow (Fig. 1f). Ordered 012. (CI = 0.10, RI = 0.44, G-fit = 0.14)
62. Shape of postmentum in posterior view[2]: (0) more or less square (Fig. 1f); (1) longitudinally elongate (Fig. 1e). (CI = 0.21, RI = 0.42, G-fit = 0.19)
63. [= R26/L39] Shape of apical peg of last segment of maxillary[6] and labial palps: (0) long and narrow, situated subapically (Figs. R15, R17); (1) short and broad, situated apically (Figs. R16, R18). (CI = 0.20, RI = 0.78, G-fit = 0.43)
64. [= R28/L40] Articulation between fourth and fifth segments of maxillary palps[7]: (0) normal, free articulation (Fig. R15); (1) fifth segment rigidly inserted into fourth (Fig. R16); (2) fifth and fourth segment fused (not illustrated). Ordered 012. (CI = 0.13, RI = 0.24, G-fit = 0.19)
65. [modified from R31/L42] Length of first segment of maxillary palp[7]: (0) short, not longer than broad (Fig. R16); (1) long, somewhat longer than broad (Fig. R15). (CI = 0.09, RI = 0.09, G-fit = 0.23)
66. [= R32/L43] Number of segments of labial palps[8]: (0) three normal segments (Figs. R17, R18); (1) three segments, second strongly reduced in size (not illustrated); (2) two segments (not illustrated). Ordered 012. (CI = 0.35, RI = 0.50, G-fit = 0.17)
67. Shape of last segment of labial palp[8]: (0) long and about as broad as other segments (not illustrated); (1) only somewhat broader than other segments, often broadest in mid-part (Fig. R18); (2) drop-shaped, much wider than other segments and clearly broadest in apical part (not illustrated). Ordered 012. (CI = 0.22, RI = 0.18, G-fit = 0.16)

Antennae, female

68. [modified from R34/L45] Number of completely separated flagellomeres[9] (not illustrated): (0) 10; (1) 11; (2) 12; (3) 13; (4) 14; (5) 15 or more. Ordered 012345. (CI = 0.47, RI = 0.10, G-fit = 0.10). [*Andricus curvator* parth. gen., *A. quercusramuli* parth. gen., *A. serricornis* parth. gen., *Callirhytis hartigi*, *Philonix fulvicollis* and *Trigonaspis megaptera* parth. gen. are coded from literature data.]
69. [modified from R35/L46] Length of F1[9] (not illustrated): (0) short, about as long as F2; (1) long, clearly longer than F2. (CI = 0.08, RI = 0.15, G-fit = 0.21)
70. [modified from L50] Shape of basal flagellomeres[9] (not illustrated): (0) compact and thick, F1 almost as thick as pedicel and shorter than six times width at narrowest part; (1) thin and elongate, F1 much thinner than pedicel and at least six times longer than width at narrowest part. (CI = 0.11, RI = 0.50, G-fit = 0.27)
71. Shape of flagellum[9] (not illustrated): (0) not broadening apically; (1) broadening apically only in basal part; (2) broadening apically further than only basal part. Ordered 012. (CI = 0.12, RI = 0.42, G-fit = 0.18)

Antennae, male

72. [modified from L47] Number of flagellomeres[10] (not illustrated): (0) 11; (1) 12; (2) 13; (3) 14; (4) 15. Ordered 01234. (CI = 0.33, RI = 0.20, G-fit = 0.27). [*Diplolepis triforma*, *Andricus curvator*, *A. kingi*, *A. sieboldi*, *Callirhytis erythrocephala*, *Cynips douglasi*, *Neuroterus numismalis* and *Philonix fulvicollis* are coded from literature data.]
73. [modified from L48] Shape of F1[11]: (0) cylindrical, at most with a slight modification basally (Fig. R20); (1) sligthly flattened laterally (not illustrated); (2) distinctly excavated (Fig. R19). Ordered 012. (CI = 0.33, RI = 0.57, G-fit = 0.30)
74. [modified from L48] Pubescence of F1[11] (not illustrated): (0) more or less evenly covering the article; (1) leaving a bare area laterally. (CI = 0.33, RI = 0.50, G-fit = 0.60)
75. [modified from R39/L49] Longitudinal ridge along modification of F1[11]: (0) absent (Figs. R20, L7f); (1) present (Fig. R19). (CI = 0.25, RI = 0.73, G-fit = 0.50)

Pronotum, female

76. Pronotal proportions in lateral view[13]: (0) elongate, ratio of horizontal length to shortest distance between posteroventral corner and dorsal margin > 1.35 (Fig. 3b); (1) intermediate, ratio between 0.80 - 1.25 (Fig. 3a); (2) short and compact, ratio < 0.75 (Fig. R26). Ordered 012. (CI = 0.80, RI = 0.75, G-fit = 0.50)
77. Outline of dorsal pronotal margin in anterior view[12]: (0) concave or straight (Figs. 2a, 2b); (1) slightly elevated medially (Fig. 2c). (CI = 0.67, RI = 0.67, G-fit = 0.60)
78. [= R40/L54] Admedian depressions of pronotum[12]: (0) separated medially (Fig. R29); (1) united medially, forming a transverse impression anteriorly on the pronotum (Fig. R30). (CI = 1.00, RI = 1.00, G-fit = 1.00)
79. Longitudinal carinae in transverse impression anteriorly on pronotum[12] (in parthenogenetic female): (0) absent (Figs. 2a, 2c); (1) present (Fig. 2b). (CI = 0.25, RI = 0.50, G-fit = 0.50)
80. [= L55] Shape of admedian depressions[12]: (0) round (Fig. L8b); (1) oval (Fig. R29); (2) linear (Fig. R25 and L9a). Ordered 012. (CI = 1.00, RI = 1.00, G-fit = 1.00)
81. [modified from L51] Length of pronotum medially[12] (= shortest distance between dorsal and anterior margins): (0) long, ratio of length to width of pronotum (measured near mesopleural spiracle) > 0.133 (Fig. 2a); (1) short, ratio < 0.115, usually ratio < 0.105 (Fig. 2c). Inapplicable to forms with reduced wings. (CI = 1.00, RI = 1.00, G-fit = 1.00)
82. Posterolateral tooth-like section of anterior part of pronotal plate[12]: (0) present (Figs. 2a, 2b); (1) absent (Fig. 2c). (CI = 0.33, RI = 0.75, G-fit = 0.60)
83. [modified from R43/L59] Dorsal part of pronotal plate[12]: (0) distinctly set off, with anterolateral corners, ventral and lateral margins marked (Fig. 2b); (1) less distinctly set off, ventral margin distinct, anterolateral corners weakly marked at most, and lateral margin lacking (Fig. 2a); (2) not set off, also ventral margin diffuse (not illustrated). Ordered 012. (CI = 0.33, RI = 0.47, G-fit = 0.23)
84. [modified from R41/L56] Shape of pronotal plate in profile, above impression/pits[13]: (0) almost flat or even somewhat concave (Figs. R26, 3a); (1) sligthly convex (Fig. R27); (2) rounded, distinctly convex (Figs. L8c, 3b). Ordered 012. (CI = 0.18, RI = 0.53, G-fit = 0.17)
85. Median impression of pronotal plate, dorsad transverse impression[12]: (0) absent (Figs. 2a, 2b); (1) present (Fig. 2c). (CI = 1.00, RI = 1.00, G-fit = 1.00)
86. Ventral margin of pronotum, laterad pronotal plate[13]: (0) without a submarginal expansion (Figs. 2a, 2c); (1) with a narrow, separate submarginal expansion running close to margin (Fig. 2b); (2) with a broad, separate submarginal expansion distant from margin (not illustrated). Ordered 012. (CI = 0.40, RI = 0.46, G-fit = 0.27)
87. [= L66, wording changed] Shape of submarginal pronotal impression anteriorly[13]: (0) narrow and more or less distinct (Figs. R25-27, 3); (1) broad and shallow (Fig. L8b). (CI = 0.67, RI = 0.50, G-fit = 0.60)
88. Shape of submarginal pronotal impression posteriorly[13]: (0) not expanded, of about same width throughout (Fig. 3a); (1) slightly expanded, gradually widening posteriorly (Fig. 3b); (2) distinctly expanded and shallow posteriorly, continuing in a flange-like portion of the pronotum (not illustrated). Ordered 012. (CI = 0.23, RI = 0.47, G-fit = 0.13)

89. Dorsal margin of submarginal pronotal impression[13]: (0) indistinct, not marked (Fig. 3b); (1) marked by a carina or ledge (Fig. 3a). (CI = 0.50, RI = 0.50, G-fit = 0.75)
90. Transverse carinae across submarginal pronotal impression[13]: (0) absent (Fig. 3a); (1) present (Fig. 3b). (CI = 0.33, RI = 0.67, G-fit = 0.38)
91. Horizontal submarginal costula posteroventrally on lateral surface of pronotum raised above remaining sculpture[13] (not illustrated): (0) absent; (1) present. (CI = 0.22, RI = 0.63, G-fit = 0.27)
92. [modified from L63] Dorsolateral part of pronotum[13]: (0) not inflected dorsad (Figs. L8a, L8b); (1) slightly inflected dorsad (Fig. L8c); (2) conspicuously inflected dorsad (Fig. 2b). Ordered 012. (CI = 0.19, RI = 0.54, G-fit = 0.14)
93. Shape of lateral pronotal surface[13]: (0) nearly flat, vertical (Fig. L8b); (1) slightly bulging (Fig. 2b); (2) conspicuously bulging forming a large projection medially (not illustrated). Ordered 012. (CI = 0.67, RI = 0.89, G-fit = 0.75)
94. [modified from R44/L60] Lateral pronotal carina[13]: (0) absent (Figs. R26, R27); (1) present as a weakly indicated carina (Fig. R25); (2) present as a conspicuous, sharp crest. Unordered. (CI = 0.36, RI = 0.22, G-fit = 0.25)
95. [modified from L61] Carinate sculpture on lateral pronotal surface[13] (not illustrated): (0) absent; (1) present only posteriorly; (2) present both posteriorly and medially. Ordered 012. (CI = 0.38, RI = 0.23, G-fit = 0.18)
96. Type of carination on lateral pronotal surface[13]: (0) weaker, more dense, usually curved and carinulate (Fig. R27); (1) stronger, more sparse, straight and costulate (not illustrated). (CI = 0.50, RI = 0.33, G-fit = 0.50)
97. [modified from L62] Superficial sculpture on central part of lateral pronotal surface, disregarding hair punctures[13] (not illustrated): (0) present; (1) absent. (CI = 0.14, RI = 0.67, G-fit = 0.33)
98. Pubescence of lateral pronotal surface, excluding subventral impression[13] (not illustrated): (0) dense, at least dorsally; (1) very sparse or absent. (CI = 0.17, RI = 0.50, G-fit = 0.38)
99. Carina along pronotal margin anterior to mesopleural spiracle[13] (not illustrated): (0) absent; (1) present. (CI = 0.33, RI = 0.60, G-fit = 0.60)
100. Shape of spiracular incision of pronotum[13]: (0) distinct, usually deep (Fig. 3); (1) shallow and indistinct (not illustrated); (2) absent, cuticle forming a projection entirely covering spiracle laterally (not illustrated). Unordered. (CI = 1.00, RI = 1.00, G-fit = 0.75)

Propectus (propleuron and prosternum), female

101. [modified from R48/L67] Position of profurcal pit[14]: (0) at or anterior to middle of furcasternum (Fig. R23); (1) posterior to middle of furcasternum (Fig. R24). (CI = 0.18, RI = 0.47, G-fit = 0.23)
102. [= R49/L68] Shape of profurcal pit[14]: (0) rounded, small (Fig. R23); (1) transverse, large (Fig. R24). (CI = 0.18, RI = 0.65, G-fit = 0.23)

Mesoscutum, female

103. [modified from L69] Transition between anterior part of mesoscutum and pronotum in lateral view[13]: (0) even, pronotum more or less continuous with mesoscutum (Fig. 3b); (1) angled, distinct change in slope at transition between pronotum and mesoscutum (Fig. 3a). (CI = 0.50, RI = 0.80, G-fit = 0.75)
104. [= L73] Relation between anterolateral mesoscutal margin and dorsal pronotal margin[15]: (0) mesoscutal margin not projecting over pronotum (Fig. R26); (1) mesoscutal margin projecting over pronotum (Fig. R27). (CI = 0.20, RI = 0.50, G-fit = 0.43)
105. General shape of mesoscutum[15]: (0) compressed, mesoscutum about as wide as, or wider than, long (Fig. L9a); (1) elongate, mesoscutum longer than wide (Fig. 4). (CI = 0.29, RI = 0.29, G-fit = 0.13)
106. [modified from L70] Shape of median mesoscutal lobe (between notauli) anteriorly[15]: (0) not projecting beyond arch indicated by lateral mesoscutal lobes (outside notauli), (Fig. 4); (1) projecting beyond arch indicated by lateral flaps (Figs. L9b, L9c). (CI = 0.23, RI = 0.33, G-fit = 0.20)
107. [= R50/L72] Impression mesad parascutal carina[15]: (0) anteriorly ending just in front of tegula (Fig. R29); (1) anteriorly continuing to anterior end of notaulus (Fig. R30). (CI = 0.33, RI = 0.00, G-fit = 0.38)
108. Shape of parascutal carina around anterior end of notaulus[15]: (0) absent or not raised (Fig. 2c); (1) raised (Fig. 2b).

(CI = 0.10, RI = 0.55, G-fit = 0.25)

109. Submarginal, mesally directed carinae along parascutal carina[15]: (0) absent (not illustrated); (1) present (Figs. 2b, 2c). (CI = 0.12, RI = 0.29, G-fit = 0.16)

110. [modified from R53/L76] Sculpture of mesoscutum[15] (not illustrated): (0) absent, at most some superficial sculpture present; (1) present, covering major part of mesoscutum. (CI = 0.50, RI = 0.67, G-fit = 0.75)

111. [modified from R52/L75] Superficial sculpture of mesoscutum[15] (not illustrated): (0) more or less distinct; (1) reduced, often partially absent; (2) completely absent. Ordered 012. (CI = 0.20, RI = 0.58, G-fit = 0.14)

112. Irregularly reticulate sculpture between anteroadmedian signa[15] (not illustrated): (0) absent; (1) present. (CI = 0.20, RI = 0.50, G-fit = 0.43)

113. Distribution of mesoscutal pubescence[15] (not illustrated): (0) evenly distributed; (1) concentrated along notauli and in median region; (2) present along notauli only. Ordered 012. (CI = 0.31, RI = 0.51, G-fit = 0.10)

114. [modified from R54/L77] Density of pubescence along notaulus in posterior half of mesoscutum[15] (not illustrated): (0) dense; (1) sparse; (2) absent. Ordered 012. (CI = 0.29, RI = 0.50, G-fit = 0.17)

115. Pubescence of anterior part of mesoscutum[15] (in parthenogenetic female), (not illustrated): (0) normal, as dense as pubescence of posterior part; (1) dense, distinctly denser than pubescence of posterior part. (CI = 0.50, RI = 0.50, G-fit = 0.75)

116. Length of pubescence of mesoscutum[15] (not illustrated): (0) short; (1) intermediate; (2) long. Ordered 012. (CI = 0.15, RI = 0.62, G-fit = 0.21)

117. Width of anteroadmedian signa[15]: (0) narrow (Fig. 4b); (1) broad (not illustrated). (CI = 0.50, RI = 0.75, G-fit = 0.75)

118. Prominence of anteroadmedian signa[15]: (0) marked by raised sculpture (Fig. 4b); (1) marked only by different but not raised sculpture (not illustrated); (2) not marked (Fig. 4a). Ordered 012. (CI = 0.32, RI = 0.54, G-fit = 0.13)

119. [= L84] Notauli[15]: (0) percurrent and distinct (Figs. R29, R30); (1) percurrent or almost percurrent, but anterior half indistinct (Fig. L9b); (2) present posteriorly, but absent in anterior half (Fig. L9a); (3) entirely absent (Fig. 4a). Ordered 0123. (CI = 0.22, RI = 0.46, G-fit = 0.13)

120. Width of notauli[15]: (0) posteriorly wide, distinctly wider than in middle (Fig. 4b); (1) uniformly narrow throughout (Fig. L9b). (CI = 0.14, RI = 0.43, G-fit = 0.19)

121. Sculpture of notauli[15]: (0) absent (Fig. L9c); (1) consisting of irregular transverse carinae (Fig. 4b). (CI = 0.08, RI = 0.14, G-fit = 0.20)

122. Shape of posterior part of mesoscutum between lateral margins of notauli[15]: (0) subrectangular, lateral margins well separated at posterior margin (Fig. 4b); (1) more triangular, lateral margins close to each other at posterior margin (Fig. 4a). (CI = 0.23, RI = 0.33, G-fit = 0.20)

123. Shape of posterior mesoscutal margin[15]: (0) evenly rounded or straight (Fig. 4b); (1) sinuous, middle part slightly curved anteriorly (not illustrated); (2) incised, middle part strongly curved anteriorly (Fig. 4a). Ordered 012. (CI = 0.33, RI = 0.73, G-fit = 0.30)

124. [= L85] Median mesoscutal impression[15]: (0) present, extending some distance from posterior margin mesoscutum (Fig. L9c); (1) present only as a slight impression at posterior margin of mesoscutum (Fig. R30); (2) absent (Fig. L9a and L9b). Ordered 012. (CI = 0.16, RI = 0.48, G-fit = 0.15)

125. Posterior surface of mesoscutum[15]: (0) more or less flat (Fig. 4b); (1) with a distinct submarginal depression laterally (Fig. 4a). (CI = 1.00, RI = 1.00, G-fit = 1.00)

126. Relation between mesoscutum and scutellum (transscutal articulation)[15]: (0) separated by a distinct transscutal fissure throughout but closely abutting laterally (Figs. L9b, L9c, 5b); (1) fused, fissure absent medially (Fig. 4a). (CI = 1.00, RI = 1.00, G-fit = 1.00)

Mesoscutellum, female

127. General outline of scutellum in lateral view[13]: (0) rectangular, dorsal and ventral margins subparallel, posterior margin of scutellum more or less vertical (Fig. R27); (1) triangular, dorsal margin sloping posteriorly (Figs. 5c, 5d). (CI = 0.22, RI = 0.30, G-fit = 0.15)

128. Dorsal surface of scutellum[15]: (0) not margined posteriorly and posterolaterally (Fig. 5c); (1) with a distinct margin

posteriorly and posterolaterally (Fig. 5d). (CI = 0.10, RI = 0.36, G-fit = 0.25)

129. Shape of scutellum posteroventrally in lateral view[13]: (0) not dropping, ventral margin more or less straight (Fig. 5c). (1) dropping, ventral margin sloping downwards posteriorly (Fig. 5d). (CI = 0.25, RI = 0.25, G-fit = 0.50)
130. Extension of scutellum posteriorly[13]: (0) short, at most extending slightly past dorsellum (Fig. 5c); (1) long, extending well past dorsellum (Fig. 5d). (CI = 0.23, RI = 0.62, G-fit = 0.20)
131. Dorsoposterior margin of scutellum[15]: (0) incised (Fig. 5a); (1) rounded (Fig. 5b); (2) with a distinct process. Ordered 012. (CI = 1.00, RI = 1.00, G-fit = 1.00)
132. Ventroposterior margin of scutellum[16] (not illustrated): (0) rounded; (1) drawn out to a point. (CI = 0.33, RI = 0.50, G-fit = 0.60)
133. Reticulate sculpture on lateral surface of scutellum[13] (not illustrated): (0) scabrous to areolate-rugose; (1) alveolate to areolate-rugulose; (2) coriarious (3) absent. Ordered 0123. (CI = 0.18, RI = 0.48, G-fit = 0.18)
134. Rugulose-rugose sculpture of scutellum dorsally[15]: (0) present throughout (Fig. 5a); (1) present marginally, but erased medially (not illustrated); (2) absent (Fig. 4a). Ordered 012. (CI = 0.28, RI = 0.55, G-fit = 0.16)
135. Superficial sculpture of scutellum mediodorsally[15] (not illustrated): (0) coriarious; (1) colliculate; (2) absent. Unordered. (CI = 0.15, RI = 0.23, G-fit = 0.14)
136. [= L88] Round, distinctly margined posteromedian scutellar impression[15]: (0) absent (Fig. L9a); (1) present (Fig. L9c). (CI = 1.00, RI = 1.00, G-fit = 1.00)
137. [= L86] Scutellar foveae[15]: (0) present, at least as transverse furrows (Figs. L9a, L9b); (1) strongly reduced or absent (Fig. L9c). (CI = 0.17, RI = 0.44, G-fit = 0.38)
138. Shape of anterior margin of foveae[15]: (0) more or less straight (Fig. 5b); (1) curved, gradually bending posteriorly laterad (Fig. 5a). (CI = 0.56, RI = 0.78, G-fit = 0.27)
139. Shape of mesal margins of foveae[15]: (0) diverging posteriorly (Fig. 5b); (1) subparallel, not diverging posteriorly (Fig. 5a). (CI = 0.20, RI = 0.14, G-fit = 0.18)
140. Width of foveal septum[15]: (0) broad, 1/4 or more of length of fovea (Fig. 5b); (1) narrow, 1/5 or less of length of fovea (Fig. 5a); (2) absent. Ordered 012. (CI = 0.30, RI = 0.12, G-fit = 0.27)
141. Posterior margin of fovea[15]: (0) closed (Fig. 5b); (1) open, no clear border to rest of scutellum (Fig. 5a). (CI = 0.13, RI = 0.32, G-fit = 0.18)
142. Sculpture in scutellar foveae[15] (not illustrated): (0) smooth; (1) with longitudinal, sometimes irregular carinae; (2) with transverse carinae. Unordered. (CI = 0.25, RI = 0.50, G-fit = 0.23)
143. Pubescence of foveae[15] (not illustrated): (0) present; (1) absent. (CI = 1.00, RI = 0/0, G-fit = 0.60). Uninformative unless coded separately for the generations of *Andricus quercusradicis* and *A. sieboldi*.
144. [= R55/L78] Lateral bar[15]: (0) present (Figs. R26, R27); (1) absent (Fig. 4a). (CI = 0.25, RI = 0.67, G-fit = 0.50)
145. [= L81] Axillar carina separating lateral axillar area from dorsal axillar area[13]: (0) more or less distinct (Figs. R26, R27); (1) indistinct or absent (Fig. L8c). (CI = 0.50, RI = 0.80, G-fit = 0.75)
146. Shape of axillar carina dorsally in lateral view[13]: (0) convex (Fig. 5d); (1) straight (Fig. 5c). (CI = 0.22, RI = 0.53, G-fit = 0.27)
147. [= R57/L82, wording changed] Shape of subaxillular bar[13]: (0) broad, vertical, evenly continuing posteriorly in subaxillular strip (Fig. R26); (1) narrow, horizontal, rapidly expanding posteriorly in subaxillular strip (Fig. R27). (CI = 0.50, RI = 0.80, G-fit = 0.50)
148. Dorsal margin of subaxillular strip[13]: (0) more or less straight (Fig. 5d); (1) with an abrupt bend around mid-part (Fig. 5c). (CI = 0.21, RI = 0.42, G-fit = 0.19)
149. [modified from L83] Narrow, anteriorly directed, posterodorsal projection of subaxillular strip[13]: (0) long, almost closing axillula dorsally (Fig. 5c); (1) short (Fig. 5d); (2) absent (Figs. L8b, L8c). Ordered 012. (CI = 0.11, RI = 0.45, G-fit = 0.16)
150. Posterodorsal extension of body of subaxillular strip[13]: (0) absent (Fig. 5c); (1) present (Fig. 5d). (CI = 0.11, RI = 0.33, G-fit = 0.27)
151. [modified from R56/L79 and L80] Dorsal margin of axillula[13]: (0) distinct, axillula deeply impressed and closed by a sharp ledge (Fig. L8b); (1) less distinct, axillula only shallowly impressed and closed by a less prominent ledge (Figs. 5c, 5d); (2) absent, axillula dorsally continuing smoothly into rest of scutellum (Fig. 4a). Ordered 012. (CI =

0.50, RI = 0.78, G-fit = 0.60)

152. Pubescence of axillula[13] (not illustrated): (0) dense; (1) sparse; (2) absent. Ordered 012. (CI = 0.15, RI = 0.15, G-fit = 0.21)

Mesopectus (mesopleuron and mesosternum), female

153. Dorsal border of mesopleural triangle[13]: (0) diffuse (Fig. 6b); (1) distinct (Fig. 6a). (CI = 0.20, RI = 0.76, G-fit = 0.43)
154. [modified from L94] Ventral border of mesopleural triangle[13]: (0) absent or only indicated by a change in curvature of the mesopleural surface (Fig. L8c); (1) marked anteriorly and posteriorly, but diffuse medially (Fig. L8b); (2) marked throughout by a distinct carina or ledge (Fig. L8a). Ordered 012. (CI = 0.30, RI = 0.45, G-fit = 0.12)
155. [modified from L96] Sculpture of mesopleural triangle[13] (not illustrated): (0) smooth or at most with a few irregular carinae; (1) entirely irregularly carinate. (CI = 0.20, RI = 0.43, G-fit = 0.43)
156. Pubescence of mesupleural triangle[13] (not illustrated): (0) dense; (1) sparse; (2) absent. Ordered 012. (CI = 0.30, RI = 0.50, G-fit = 0.27)
157. Furrow extending posteroventrad from subalar pit[13]: (0) absent (Fig. 6a); (1) present, but short (Figs. R27, L8c); (2) present, long (Fig. 6b). Ordered 012. (CI = 0.50, RI = 0.44, G-fit = 0.27)
158. Pubescence of mesopleuron[13] (not illustrated): (0) sparse, distinctly more sparse than that of the posterior part of the mesoscutum; (1) denser, about as dense as that of the posterior part of the mesoscutum. (CI = 0.44, RI = 0.38, G-fit = 0.27)
159. Horizontal furrow in lower part of mesopleuron[13]: (0) absent (Fig. 6b); (1) present (Fig. 6a). (CI = 0.33, RI = 0.60, G-fit = 0.60)
160. [modified from L91 and L93] Sculpture in median lower part of mesopleuron[13]: (0) glabrous (Fig. 6a); (1) striate (Figs. R26, 6b); (2) reticulate/crenulate (not illustrated). Unordered. (CI = 0.35, RI = 0.52, G-fit = 0.17)
161. Kind of striation in median lower part of mesopleuron[13] (as in char. 160:1): (0) irregularly striate (Fig. 6b); (1) regularly striate (Fig. R26). (CI = 0.33, RI = 0.60, G-fit = 0.60)
162. Kind of reticulation in median lower part of mesopleuron[13] (as in char. 160:2), (not illustrated): (0) weak, reticulate; (1) coarse, crenulate. (CI = 0.33, RI = 0.33, G-fit = 0.60)
163. Homogeneity of sculpture in lower part of mesopleuron[13]: (0) median sculpture different (Fig. 6b); (1) sculpture same in whole region (Fig. R26). (CI = 0.29, RI = 0.44, G-fit = 0.33)
164. Ventral depression of mesopleuron, anterior to mesocoxal foramen[13] (not illustrated): (0) absent; (1) present, as if allowing for mid-coxa to move forward. (CI = 1.00, RI = 1.00, G-fit = 1.00)
165. [modified from R60/L98] Prominence of acetabular carina submedially[14]: (0) well developed (Fig. R23); (1) reduced (Fig. R24). (CI = 0.20, RI = 0.60, G-fit = 0.43)
166. [modified from R62/L99] Mesodiscrimen posterior to acetabular carina[14]: (0) marked by a distinct carina (Fig. R23); (1) distinctly marked by different sculpture or a furrow (not illustrated); (2) at most very slightly marked externally by different sculpture (not illustrated). Ordered 012. (CI = 0.33, RI = 0.60, G-fit = 0.43)
167. Small submedian carinae orthogonally to mesodiscrimen[14]: (0) absent (Fig. 7b); (1) present, irregular and diffuse (not illustrated); (2) present, more regular and distinct (Fig. 7a). Ordered 012. (CI = 0.28, RI = 0.44, G-fit = 0.16)
168. Position of mesofurcal pit[14]: (0) situated posterior to centers of mesocoxal foramina (Fig. 7a); (1) situated around centers of mesocoxal foramina (Fig. 7b). (CI = 0.12, RI = 0.39, G-fit = 0.17)
169. Shape of mesal part of mesocoxal rim[14]: (0) continuing more straight posteriorly towards mesosternal margin, rim not expanding posteriorly (Fig. 7a); (1) continuing obliquely posteriorly towards mesosternal margin, rim expanding posteriorly (Fig. 7b). (CI = 0.13, RI = 0.46, G-fit = 0.18)
170. Lateral position of mesocoxal foramen relative to metacoxal foramen[14]: (0) lateral margin of mesocoxal foramen positioned around center of metacoxal foramen or more medially (Fig. 7b); (1) lateral margin of mesocoxal foramen positioned clearly laterad center of metacoxal foramen (Fig. 7a). Inapplicable to brachypterous and apterous forms. (CI = 0.21, RI = 0.42, G-fit = 0.19)
171. Shape of posterior margin of mesosternum[14]: (0) straight (Fig. R24)); (1) with a rounded incision (Fig. 7a); (2) with an angled incision (Fig. 7b). Ordered 012. (CI = 0.13, RI = 0.24, G-fit = 0.19)

Metanotum, female

172. [= R65/L102] Shape of metascutellum[16]: (0) subrectangular (Fig. R22); (1) distinctly constricted medially (Fig. R21). (CI = 1.00, RI = 1.00, G-fit = 1.00)
173. [modified from R66/L103] Shape and sculpture of bar ventral to metanotal trough[16]: (0) broad and smooth throughout (Fig. 8a); (1) only posteriorly broad and more irregularly sculptured (not illustrated); (2) narrow and often irregularly sculptured (Fig. 8b). Ordered 012. (CI = 0.19, RI = 0.48, G-fit = 0.18)
174. Pubescence of metanotal trough[16] (not illustrated): (0) present in most of foveae and relatively abundant; (1) only present in part of trough and often scarce; (2) absent or only represented by some anterodorsal hairs. Ordered 012. (CI = 0.22, RI = 0.65, G-fit = 0.16)
175. Sculpture of metanotal trough[16]: (0) absent (Fig. 8a); (1) present, at least as some vertical carinae ventrally (Fig. 8b). (CI = 0.20, RI = 0.27, G-fit = 0.25)

Metapectal-propodeal complex

176. Metepimeron[13]: (0) distinctly impressed, metepimeron marked by a distinct ledge posteriorly (Fig. 6a); (1) shallowly or not impressed, metepimeron not marked by a distinct ledge posteriorly (Fig. 6b). (CI = 0.25, RI = 0.52, G-fit = 0.17)
177. Propodeal carina along posterior metepimeral margin[13]: (0) absent or very diffuse (Fig. 6a); (1) present (Fig. 6b). (CI = 0.08, RI = 0.52, G-fit = 0.20)
178. Anterior propodeal projection between metepimeron and metepisternum[13]: (0) narrow (Fig. 6a); (1) broad (Fig. 6b). (CI = 0.20, RI = 0.56, G-fit = 0.43)
179. Posterolateral propodeal process, between metacoxal foramen and propodeal spiracle[16] (not illustrated): (0) absent; (1) small and indistinct; (2) long and distinct. Ordered 012. (CI = 0.12, RI = 0.30, G-fit = 0.18)
180. Calyptra[13]: (0) large, covering most of spiracular opening in lateral view (Fig. 6a); (1) smaller, spiracular opening visible in lateral view (not illustrated); (2) absent, at most a slight remnant present (Fig. 6b). Ordered 012. (CI = 0.23, RI = 0.56, G-fit = 0.21)
181. Sculpture on calyptra[13] (not illustrated): (0) irregularly carinulate; (1) smooth, at most with one or two carinae. (CI = 0.33, RI = 0.60, G-fit = 0.21)
182. [modified from R69/L110] Shape of nucha[13]: (0) distinctly set off from propodeum, nucha directed posteriorly so nucha and propodeum are at a distinct angle to each other dorsally (Fig. 6a); (1) not distinctly set off from propodeum, nucha directed more ventrally so nucha and propodeum are more or less continuous dorsally (Fig. 6b). (CI = 0.22, RI = 0.67, G-fit = 0.27)
183. [= L111] Posterodorsal edge of nucha, in lateral view[13]: (0) rounded (Figs. R26, R28); (1) angled (Fig. R27). (CI = 0.10, RI = 0.50, G-fit = 0.25)
184. Carina along dorsal propodeal margin, connecting lateral propodeal carinae[16]: (0) absent (Fig. 8a); (1) present (Fig. 8b). (CI = 0.22, RI = 0.53, G-fit = 0.27)
185. [modified from L108] Lateral propodeal carina[16]: (0) complete (Fig. 8a); (1) reduced, especially in ventral half (not illustrated); (2) absent (Fig. 8b). Ordered 012. (CI = 0.50, RI = 0.83, G-fit = 0.60)
186. Extent of lateral propodeal carina dorsally[16]: (0) reaching above dorsal propodeal margin (not illustrated); (1) ending at level of margin (Fig. 8a); (2) ending well before margin (not illustrated). Ordered 012. (CI = 0.31, RI = 0.31, G-fit = 0.18)
187. General direction of dorsal half of lateral propodeal carina[16]: (0) slightly converging ventrad (not illustrated); (1) more o less vertical, carinae parallel (Fig. 8a); (2) slightly diverging ventrad; (3) strongly diverging ventrad (Fig. 8b). Ordered 0123. (CI = 0.36, RI = 0.82, G-fit = 0.27)
188. Shape of lateral propodeal carina[16]: (0) more or less straight or slightly but evenly curved, not subdivided (Fig. 8a); (1) subdivided into two distinct parts running in different directions (Fig. 8b); (2) subdivided into three distinct parts running in different directions (not illustrated). Ordered 012. (CI = 0.17, RI = 0.52, G-fit = 0.23)
189. [modified from L109] Width of lateral propodeal carina in dorsal part[16]: (0) broad, often much broader than ventralmost part, surface partly distinctly flattened (Fig. 8a); (1) narrow or of medium width, often more or less of

same width as ventral part, surface not or very slightly flattened (not illustrated). (CI = 0.22, RI = 0.53, G-fit = 0.27)

190. Relationship between dorsal and ventral parts of lateral propodeal carina[16]: (0) dorsal (first or first and second) part longer than ventral (last) part (Fig. 8a); (1) dorsal part of equal length to ventral part (Fig. 8b). (CI = 0.22, RI = 0.53, G-fit = 0.27)

191. Pubescence on dorsal part of lateral propodeal carina[16]: (0) present (Fig. 8a); (1) absent (not illustrated). (CI = 0.22, RI = 0.67, G-fit = 0.27)

192. Pubescence in dorsal part of median propodeal area[16]: (0) abundant (Fig. 8a); (1) reduced (not illustrated); (2) absent (Fig. 8b). Ordered 012. (CI = 0.38, RI = 0.52, G-fit = 0.18)

193. Median propodeal carina[16]: (0) absent (Fig. 8b); (1) vaguely indicated (not illustrated); (2) distinctly present but not necessarily percurrent (Fig. 8a). Ordered 012. (CI = 0.13, RI = 0.32, G-fit = 0.19)

194. Sculpture of median propodeal area[16] (not illustrated): (0) smooth; (1) with some carinae radiating from nucha; (2) areolate-rugose. Ordered 012. (CI = 0.22, RI = 0.31, G-fit = 0.12)

195. [modified from R70/L112] Relation between anterior margin of metasternum and rim of metacoxal foramina[14]: (0) anterior margin and rim not contiguous, rim closest to metasternal margin directly anterior to center of foramen (Fig. 7b); (1) anterior margin and rim contiguous, rim closest to metasternal margin more mesally (Fig. 7a). (CI = 0.20, RI = 0.64, G-fit = 0.25)

196. [= R71] Shape of posterolateral process of rim surrounding metacoxal foramen[14]: (0) pointed, glabrous, on same level as remaining part of rim, not set off (Fig. R23); (1) obtuse, sculptured and pubescent, distinctly set off from remaining part of rim (Fig. R24). (CI = 1.00, RI = 1.00, G-fit = 1.00)

197. Sculpture on surface of metasternum anterior to metafurcal pit[14] (not illustrated): (0) smooth, at most with some superficial sculpture; (1) irregularly carinate. (CI = 0.14, RI = 0.25, G-fit = 0.33)

198. [modified from R73/L114] Position of metafurcal pit[14]: (0) situated anterior to centers of metacoxal foramina (Fig. R24); (1) situated around centers of metacoxal foramina (Fig. 7); (2) situated posterior to centers of metacoxal foramina (not illustrated). Ordered 012. (CI = 0.50, RI = 0.33, G-fit = 0.23)

199. Shape of metafurcal pit[14]: (0) round (Fig. 7b); (1) transversely elongate (Fig. 7a). (CI = 0.30, RI = 0.70, G-fit = 0.25)

200. Connection between metacoxal and petiolar foramina[14]: (0) foramina not connected by any differentiated sculpture (not illustrated); (1) rim of metacoxal foramen connected to petiolar foramen by an elevated, more or less flat strip (Figs. R23, 7b); (2) rim of metacoxal foramen connected via one or more carinae (Fig. 7a). Unordered. (CI = 0.40, RI = 0.87, G-fit = 0.50)

201. [modified from L115 and L116] Position of petiolar foramen[14]: (0) posterior, ventral margin of nucha posterior to hind margins of metacoxal foramina (Fig. 7b); (1) median, ventral margin approximately at posterior margins of metacoxal foramina (Fig. 7a); (2) anterior, ventral margin anterior to posterior margins of metacoxal foramina (not illustrated). Ordered 012. (CI = 0.33, RI = 0.69, G-fit = 0.19)

202. Shape of petiolar foramen[14]: (0) narrower ventrally than dorsally (Fig. 7b); (1) oval, more or less longitudinally symmetric (Fig. R24); (2) narrower dorsally (Fig. 7a). Ordered 012. (CI = 0.14, RI = 0.60, G-fit = 0.20)

Legs, female

203. [= R75/L117] Carina from posteroventral corner of procoxa towards basal area[17]: (0) absent (Fig. R36); (1) present (Fig. R35). (CI = 0.07, RI = 0.33, G-fit = 0.18)

204. [= R77/L119] Shape and position of annular girdle of procoxa[17]: (0) posteriorly only just touching peripheral margin of basal area (Fig. R35); (1) posteriorly following peripheral margin of basal area for some distance (Fig. R36). (CI = 0.12, RI = 0.56, G-fit = 0.30)

205. Peripheral margin of basal area of procoxa[17]: (0) set off and more or less complete (Figs. R35, R36); (1) set off anteriorly but posteromesally fused to procoxa (Fig. 9a); (2) very diffuse or absent (not illustrated). Ordered 012. (CI = 0.21, RI = 0.45, G-fit = 0.20)

206. Length of protibia[17] (not illustrated): (0) long, longer than length of protarsus; (1) short, not longer than protarsus. (CI = 0.11, RI = 0.11, G-fit = 0.27)

207. [= R79/L120] Shape of anterior surface of mesocoxa[18]: (0) strongly protruding, peak close to base of coxa (Fig. R33); (1) less strongly protruding, peak farther from base of coxa (Fig. R34). (CI = 0.17, RI = 0.41, G-fit = 0.21)
208. [= R80/L121] Shape of annular girdle of mesocoxa[18]: (0) distinctly set off from rest of coxa (Fig. R31); (1) posteriorly continuous with posterior surface of coxa (Fig. R32). (CI = 0.33, RI = 0.33, G-fit = 0.60)
209. [modified from L122] Posterolateral extension on mesocoxa[18]: (0) not conspicuous and ridgelike (Figs. R33, R34); (1) conspicuous and ridgelike (Fig. 9b). (CI = 0.08, RI = 0.37, G-fit = 0.20)
210. [modified from L123] Shape of mesofemur[18]: (0) broad, mesofemur shorter than 3.5 times its widest part (not illustrated); (1) intermediate, mesofemur longer than 3.5 times its widest part, but not uniformly wide (Fig. R31); (2) thin, almost same width throughout (Fig. R32). Ordered 012. (CI = 0.10, RI = 0.29, G-fit = 0.15)
211. [= L126] Pubescence on lateral surface of metacoxa[19] (not illustrated): (0) restricted to two lateral bands, no hairs in the middle; (1) less distinct and regular bands, some hairs in the middle; (2) not arranged into bands, more evenly pubescent. Ordered 012. (CI = 0.18, RI = 0.50, G-fit = 0.25)
212. [= R82/L124] Shape of metatarsal claw[20]: (0) apex slightly bent, base not expanded (Fig. R40); (1) apex strongly bent, base expanded to a lobe or tooth (Figs. R39, 12d, 13a, 13b). (CI = 0.09, RI = 0.47, G-fit = 0.23)
213. Shape of lobe or tooth of metatarsal claw[20]: (0) weak, incision between apex of claw and tooth rounded (Fig. 12d); (1) pronounced but blunt, incision rounded or weakly angled (Figs. R39, 13a); (2) pronounced and pointed, incision usually sharply angled (Fig. 13b). Ordered 012. (CI = 0.19, RI = 0.23, G-fit = 0.14)
214. Pubescence of metatarsal claw[20]: (0) dense, evenly covering the claw (not illustrated); (1) more sparse, at least apically (Figs. 9c–e). (CI = 0.17, RI = 0.29, G-fit = 0.38)

Forewing, female

215. Wingedness (in parthenogenetic female), (not illustrated): (0) wings fully developed; (1) brachypterous; (2) apterous. Ordered 012. (CI = 1.00, RI = 1.00, G-fit = 1.00)
216. [modified from L132] Extent of R$_1$[21]: (0) very long, continuing along wing margin until reaching Rs (Fig. L10); (1) long, continuing somewhat along wing margin but not reaching Rs (not illustrated); (2) intermediate, ending at wing margin (Fig. R38); (3) short, ending somewhat before wing margin (not illustrated); (4) absent beyond junction with 2r (not illustrated). Ordered 01234. (CI = 0.25, RI = 0.42, G-fit = 0.13)
217. [modified from L131] Direction of R$_1$ laterad 2r[21]: (0) more anteriorly directed, angle between R$_1$ and anterior wing margin approximately 60° (Fig. L10a); (1) more apically directed, angle approximately 45° or less (Fig. R38). (CI = 0.17, RI = 0.38, G-fit = 0.38)
218. [modified from Q46/L135] Position of Rs+M, particularly the basal end[21]: (0) anteriorly situated, around middle of basalis (Fig. L10b); (1) posteriorly situated, clearly posterior to middle of basalis (Fig. L10a). (CI = 0.25, RI = 0.33, G-fit = 0.30)
219. Length of marginal cell[21]: (0) short, ratio of length of cell measured along Rs apically of 2r to widest part of cell measured perpendicularly to Rs < 2.5 (Fig. L10); (1) medium, ratio between 2.5 and 3.5 (Fig. R38); (2) long, ratio > 3.5 (not illustrated). Ordered 012. (CI = 0.15, RI = 0.43, G-fit = 0.14)
220. Shape of Rs apically[21]: (0) simple, ending without curving off or widening (Figs. R37, R38); (1) modified, curving off parallel to wing margin and/or distinctly widened (not illustrated). (CI = 0.25, RI = 0.87, G-fit = 0.50). [*Philonix fulvicollis* coded from literature data.]
221. [modified from L129] Shape of 2r[21] (in parthenogenetic female): (0) almost straight or slightly bent (Fig. R37); (1) clearly angled medially, projecting apically (Fig. R38). (CI = 0.12, RI = 0.42, G-fit = 0.30)
222. [modified from L130] Length of 2r[21]: (0) long, ratio between 2r and Rs+Sc > 0.55 (Fig. L10); (1) short, ratio < 0.50 (Fig. R38). (CI = 0.20, RI = 0.43, G-fit = 0.43)
223. Clearly defined spots in apical part of wing[21] (not illustrated): (0) absent; (1) present. (CI = 0.33, RI = 0.00, G-fit = 0.60)
224. [modified from Q45/L133] Areolet[21]: (0) large and distinct (Fig. L10); (1) absent, or very small and poorly defined (not illustrated). (CI = 0.25, RI = 0.25, G-fit = 0.50)

Metasoma, female

225. Shape of metasoma in lateral view[22]: (0) elongate, metasoma extending more ventrad than dorsad petiole (Figs. 10a, 11); (1) short and high, metasoma extending more dorsad than ventrad petiole (Fig. 10b). (CI = 0.25, RI = 0.57, G-fit = 0.50)

226. Shape of metasoma dorsally in cross section (not illustrated): (0) rounded, both 3tg and 4tg without median fold; (1) sharp, at least 4tg posteriorly with a median fold. (CI = 0.20, RI = 0.47, G-fit = 0.25)

227. Lateral outline of metasoma in dorsal view (not illustrated): (0) narrowly elliptical, if somewhat broader then broadest at middle; (1) broadly dropshaped, broadest in anterior part. (CI = 0.14, RI = 0.25, G-fit = 0.33)

228. Sclerotization of metasoma[22]: (0) normal sclerotization, at most slight deformation of sclerites in dried specimens (Fig. 11); (1) weak sclerotization, obvious deformation in dried specimens (Fig. 10). (CI = 0.33, RI = 0.50, G-fit = 0.38)

229. [modified from R87/L140] Length of 3tg[22]: (0) short, ratio of median length of 3tg to 4tg less than 2.0 (Fig. L11a); (1) medium, ratio between 2.0 and 4.0 (Figs. 10, 11); (2) long, ratio more than 4.0 (Fig. R42). Ordered 012. (CI = 0.25, RI = 0.48, G-fit = 0.18)

230. [= R88/L141] Shape of anterior margin of 3tg[22]: (0) straight, not upcurved (Fig. R41); (1) upcurved (Fig. R42). (CI = 0.20, RI = 0.00, G-fit = 0.43)

231. Shape of 3tg laterally[22]: (0) long, anteroventrally embracing petiole (Figs. 10a, 11); (1) short, anteroventrally not embracing petiole (Fig. 10b). (CI = 0.43, RI = 0.50, G-fit = 0.33)

232. [modified from L142] Shape of posterior margin of 3tg in lateral view[22]: (0) vertical, rounded (Figs. 10, 11); (1) oblique, more or less straight or sinuous (not illustrated). (CI = 0.20, RI = 0.69, G-fit = 0.43)

233. [modified from R89/L143] Pubescence of 3tg anterodorsal to spiracular remnant[22] (in parthenogenetic female): (0) present (Fig. 10a); (1) absent (Figs. 10b, 11). (CI = 0.14, RI = 0.62, G-fit = 0.33)

234. Pubescence of 3tg ventral to spiracular remnant[22] (in parthenogenetic female): (0) absent (Figs. 10b, 11); (1) present (Fig. 10a). (CI = 0.17, RI = 0.76, G-fit = 0.38)

235. Relation between anterior and ventral pubescence on 3tg[22] (in parthenogenetic female): (0) continuous, no clear distinction between an anterodorsal and a lateral area (Fig. 10a); (1) interrupted, forming separate dorsal and lateral areas (Fig. R42). (CI = 0.33, RI = 0.71, G-fit = 0.60)

236. Pubescence of mid/posterior area of 3tg[22] (in parthenogenetic female): (0) absent (Fig. 11); (1) at least a few hairs in a transverse row (Fig. 10). (CI = 0.09, RI = 0.47, G-fit = 0.23)

237. Pubescence of 4tg[22] (in parthenogenetic female): (0) completely absent (Figs. 10b, 11); (1) present, fairly dense and covering a large part of the sclerite (Fig. 10a). (CI = 0.20, RI = 0.20, G-fit = 0.43)

238. [modified from R91/L145] Posterior margin of 3tg-5tg (not illustrated): (0) straight, occasionally with a minute, sharp incision medially; (1) broadly incised medially. (CI = 0.33, RI = 0.50, G-fit = 0.60)

239. Shape of 7tg[22]: (0) about equally broad throughout (Figs. 10b, 11); (1) distinctly expanded ventrolaterally (Fig. 10a). (CI = 0.20, RI = 0.60, G-fit = 0.43)

Petiole and third sternum, female

240. Width of petiole[23]: (0) narrow, maximum distance between lateral margins of petiole less than three times width of articular bulb (Figs. 12a–c); (1) broad, maximum distance between lateral margins of petiole at least three times width of articular bulb (Fig. 12d). (CI = 0.10, RI = 0.50, G-fit = 0.25)

241. Length of ventral part of petiole[23]: (0) short, maximum longitudinal distance from ventral margin of articular bulb to ventral margin of petiole shorter than width of articular bulb anteriorly (Figs. 12a, 12c); (1) long, distance longer than width of bulb (Figs. 12b, 12d). (CI = 0.30, RI = 0.36, G-fit = 0.25)

242. Direction of posterolateral margins of petiole[23]: (0) more or less parallel (not illustrated); (1) slightly diverging ventrally (Figs. 12a, 12b); (2) strongly diverging ventrally (Figs. 12c, 12d). Ordered 012. (CI = 0.19, RI = 0.29, G-fit = 0.14)

243. Ventral margin of petiole in lateral view[23]: (0) distinctly angled, anterior part horizontal (Fig. 10); (1) very weakly angled, anterior part oblique (Fig. 11). (CI = 1.00, RI = 1.00, G-fit = 1.00)

244. Anterior margin of 3st submedially[23]: (0) present, distinct border to petiole (Figs. 12a, 12c); (1) diffuse, border partially indistinct (Fig. 12d); (2) absent, border missing (Fig. 12b). Ordered 012. (CI = 0.09, RI = 0.23, G-fit =

0.13)

245. Petiolar hump[23]: (0) absent (Fig. 12a); (1) present (Figs. 12b–d). (CI = 1.00, RI = 1.00, G-fit = 1.00)
246. Relation between petiolar hump and 3st[23]: (0) hump distinctly separated from 3st (Fig. 12b); (1) hump continuous with anterior margin of 3st (Figs. 12c, 12d). (CI = 0.25, RI = 0.36, G-fit = 0.21)
247. Shape of anterior margin of 3st disregarding median extension[23]: (0) v-shaped (Fig. 12); (1) u-shaped or more or less straight (not illustrated). (CI = 1.00, RI = 1.00, G-fit = 1.00)
248. Shape of petiolar hump[23] (in parthenogenetic female): (0) smoothly rounded and only slightly projecting (Fig 12b and 12d); (1) abruptly and conspicuously projecting (Fig. 12c). (CI = 0.50, RI = 0.83, G-fit = 0.75)
249. Surface lateroventrally of articular bulb compared to adjacent surface of 3st[23]: (0) deeply impressed (not illustrated); (1) shallowly impressed (Figs. 12a, 12c, 12d); (2) neither impressed nor elevated (Fig. 12b); (3) elevated (not illustrated). Ordered 0123. (CI = 0.28, RI = 0.13, G-fit = 0.17)
250. Sculpture on surface of petiole around articular bulb[23] (not illustrated): (0) absent; (1) fine or diffuse; (2) more coarse and well defined. Ordered 012. (CI = 0.16, RI = 0.53, G-fit = 0.15)
251. Petiolar annulus[23]: (0) present, with dorsal flange that is at least medially broad (Figs. 12a, 12c, 12d); (1) present, with narrow dorsal flange (not illustrated); (2) present as a narrow ring but dorsal flange absent (Fig. 12b); (3) completely absent (not illustrated). Ordered 0123. (CI = 0.33, RI = 0.47, G-fit = 0.25)
252. Transition between dorsal flange and lateral part of annulus[23]: (0) smooth, lateral extent of flange diffuse (Fig. 12d); (1) abrupt, lateral extent of flange distinct (Figs. 12a, 12c). (CI = 0.23, RI = 0.33, G-fit = 0.20)
253. Small group of hairs close to annulus, posterolaterally to articular bulb[23] (not illustrated): (0) present; (1) absent. (CI = 0.50, RI = 0.33, G-fit = 0.50)
254. Internal margins of anterodorsal swelling of articular bulb[23]: (0) well separated, dorsal parts diverging ventrally (Fig. 12a); (1) more close, dorsal margins parallel or converging ventrally (Fig. 12c); (2) very close, margins meeting or almost meeting (Fig. 12d). Ordered 012. (CI = 0.25, RI = 0.59, G-fit = 0.23)

Hypopygium

255. [modified from R97/L152] Length of projecting part of hypopygial spine[24] (beyond attachment of lateral flap): (0) short, shorter than basal height of spine (Fig. 11); (1) intermediate, length 2-4 times basal height (Fig. 10b); (2) long, length more than five times basal height (at least in parthenogenetic females), (Fig. 10a). Ordered 012. (CI = 0.17, RI = 0.60, G-fit = 0.23)
256. Apical part of hypopygial spine[24]: (0) with deep median incision separating a pair of lateral lips (Fig. 13b); (1) without incision, lips absent (Fig. 13a). (CI = 0.33, RI = 0.60, G-fit = 0.38)
257. Shape of hypopygial spine ventrally[24]: (0) without median mark or with median furrow extending from apical incision (Fig. 13a); (1) with median crest from apical incision (Fig. 13b). (CI = 0.33, RI = 0.82, G-fit = 0.60)
258. Lateral part of hypopygial spine[24] (of parthenogenetic female): (0) not widened (Fig. 13a); (1) widened throughout, but without a distinct lobe (not illustrated); (2) widened, forming a large, rounded subapical lobe (not illustrated); (3) widened, forming a triangular lobe (not illustrated); (4) widened, forming a conspicuous triangular lobe (Fig. 13b). Ordered 01234. (CI = 0.36, RI = 0.65, G-fit = 0.30)
259. Lateral flap and spine[24]: (0) clearly separated, usually by distinct incision (Fig. 10); (1) confluent or almost so (Fig. 11). (CI = 1.00, RI = 1.00, G-fit = 1.00)
260. Shape of lateral flap[24]: (0) rounded, dorsal margin convex (Fig. 10); (1) drawn out posteriorly, dorsal margin concave (Fig. 11). (CI = 0.50, RI = 0.50, G-fit = 0.75)
261. Length of apical pubescence of hypopygial spine[24]: (0) short, projecting less than width of spine (excluding lateral sclerotised parts), (Fig. 13a); (1) long, projecting far more than width of spine (Fig. 13b). (CI = 0.43, RI = 0.71, G-fit = 0.33)
262. Lateral extent of hypopygial pubescence, excluding apical part[24]: (0) hairs restricted to one or two submedian row(s), close to midventral line (Fig. 13b); (1) pubescence more irregular, extending further laterally (Fig. 13a). (CI = 0.50, RI = 0.75, G-fit = 0.75)
263. Distribution of pubescence of hypopygial spine[24]: (0) more or less even (Fig. 13a); (1) forming a dense lateral tuft subapically (Fig. 13b). (CI = 0.25, RI = 0.73, G-fit = 0.50)

264. Structure of pubescence of hypopygial spine[24]: (0) subapical and apical hairs of about the same length, tip of subapical hairs far removed from tip of apical hairs (Fig. 13a); (1) subapical hairs longer, posterior tips of subapical and apical hairs forming a hair tuft with common posterior border (Fig. 13b). (CI = 1.00, RI = 1.00, G-fit = 1.00)

265. [= R100/L156] Position of cercus[25]: (0) relatively close to apex of 9tg (Fig. R45); (1) well removed from apex of 9tg (Fig. R46). (CI = 0.14, RI = 0.74, G-fit = 0.33)

Ovipositor

266. [= R99/L155] Shape of dorsal margin of 9tg[26]: (0) straight or very slightly curved dorsally for the attachment of the transverse muscle t_{ix} - t_{ix} (Fig. R45); (1) distinctly curved dorsally to form a lobe for the attachment of t_{ix} - t_{ix} (Fig. R46). (CI = 0.50, RI = 0.80, G-fit = 0.75)

267. [= R103/L158] Shape of third valvula[26]: (0) distinctly broadened apically (Fig. R46); (1) not broadened apically (Fig. R45). (CI = 0.11, RI = 0.27, G-fit = 0.27)

268. [modified from L159] Length of terebra[26]: (0) extremely long, articulation between second valvifer and second valvula situated far posterior to dorsalmost part of second valvifer, basal part of dorsal margin of 9tg more or less horizontal (not illustrated); (1) long, position of articulation posterior to dorsalmost part of second valvifer, basal part of dorsal margin of 9tg oblique (Fig. R46); (2) intermediate, position around dorsalmost part of second valvifer, basal part of dorsal margin of 9tg vertical (Fig. R45); (3) short, position anterior to dorsalmost part of second valvifer, basal part of dorsal margin of 9tg oblique (not illustrated); (4) extremely short, position far anterior to dorsalmost part of second valvifer, whole dorsal margin of 9tg more or less straight and almost horizontal (Fig. L11b). Ordered 01234. (CI = 0.30, RI = 0.21, G-fit = 0.08)

Metasoma, male

269. Dorsal flange of petiole[27]: (0) present (Fig. 13c); (1) absent (Fig. 13d). (CI = 0.33, RI = 0.75, G-fit = 0.60)

270. Relation between 3tg and petiole[27]: (0) abutting, no membranous area visible (Fig. 13c); (1) connected by an exposed membranous area (Fig. 13d). (CI = 0.33, RI = 0.75, G-fit = 0.60)

Phallus

271. Shape of aedeagus in lateral view[29]: (0) more or less straight (Figs. P9, 13e); (1) apex bending ventrad in region around digitus (Figs. P10, P11, 13f). (CI = 1.00, RI = 1.00, G-fit = 1.00)

272. Shape of apex of aedeagus in lateral view[29]: (0) relatively abruptly terminated without narrowing (Figs. P10, P11, 13e); (1) gradually narrowing to apex (Figs. P9, 13f). (CI = 0.20, RI = 0.56, G-fit = 0.43)

273. [= R106/L162/P1] Shape of apical part of aedeagus[30]: (0) only slightly expanded subapically (Figs. R49, P1, P2); (1) distinctly and abruptly expanded subapically (Figs. R50, P3, P4). (CI = 1.00, RI = 1.00, G-fit = 1.00)

274. [= P9] Setaceous area at internal margin of subapical expansion of aedeagus[30]: (0) absent (Fig. P14); (1) present (Fig. P13). (CI = 1.00, RI = 1.00, G-fit = 1.00)

275. [modified from P3] Depth of apical incision of aedeagus in dorsal view[28]: (0) long, longer than half width of aedeagus (Fig. P2); (1) short, length intermediate (Fig. P4); (2) very short, at most one tenth of width of aedeagus (not illustrated). Ordered 012. (CI = 0.67, RI = 0.90, G-fit = 0.75)

276. Dorsal groove of aedeagus, continuing into apical incision[28]: (0) broad, often expanding basally (Fig. P2); (1) narrow or absent (Figs. P1, P3, P4, P6). (CI = 1.00, RI = 1.00, G-fit = 1.00)

277. [modified from P11] Hairs on volsellar plate[30]: (0) absent (not illustrated); (1) short (Fig. P7); (2) long (Fig. P8). Ordered 012. (CI = 0.50, RI = 0.71, G-fit = 0.60)

278. [modified from P7] Shape of paramere[29]: (0) outer surface convex, apex straight (Fig. P10); (1) outer surface flattened, apex slightly bent mesad (Fig. P12); (2) outer surface flattened, apex strongly bent mesad, parameres overlapping (not illustrated). Ordered 012. (CI = 1.00, RI = 1.00, G-fit = 0.75)

279. [modified from R107/L163/P6] Length of paramere[29]: (0) long, reaching clearly beyond digitus (Fig. P10); (1) short, at most reaching just beyond digitus (Figs. P9, P12). (CI = 0.25, RI = 0.50, G-fit = 0.50)

280. [= R108/L164/P2] Shape of basidorsal margin of parameral plates[28]: (0) distinctly incised medially (Figs. R50, P4);

(1) not or only weakly incised medially (Figs. R49, P2). (CI = 1.00, RI = 1.00, G-fit = 1.00)

281. [modified from P4] Shape of apical incision on dorsal side of parameral plate[28]: (0) rounded (Fig. P1); (1) sharp, with fold not continuing far basally (Fig. P3); (2) sharp, with fold continuing far basally (not illustrated). Ordered 012. (CI = 0.18, RI = 0.18, G-fit = 0.25)
282. Extent of incision separating parameres dorsally[28]: (0) not reaching half total length of plate including parameres (not illustrated); (1) reaching slightly past half plate length (Figs. P3, P4); (2) reaching far past half plate length (Fig. P2). Ordered 012. (CI = 0.18, RI = 0.31, G-fit = 0.25)
283. [modified from P10] Shape of apical margin of basal ring in ventral view[30]: (0) incised (Fig. P5); (1) straight (Figs. P7, P8); (2) pointed (not illustrated). Ordered 012. (CI = 0.67, RI = 0.67, G-fit = 0.75)

Biology and distribution

284. [modified from L165] Sexual generation: (0) present; (1) absent. (CI = 0.33, RI = 0.00, G-fit = 0.60). [*Philonix fulvicollis* is suggested to represent the sexual generation of *P. gigas* according to literature.]
285. Heterogeny [modified from L165]: (0) absent; (1) present. (CI = 0.25, RI = 0.62, G-fit = 0.50)
286. Geographical distribution: (0) Palearctic; (1) Nearctic (2) Neotropic. Ordered 012. (CI = 0.15, RI = 0.56, G-fit = 0.21)
287. Palearctic distribution: (0) Western Palearctic; (1) Eastern Palearctic. (CI = 0.20, RI = 0.00, G-fit = 0.43)
288. Nearctic distribution: (0) Southern Nearctic; (1) Western Nearctic; (2) Eastern Nearctic. Unordered. (CI = 0.25, RI = 0.25, G-fit = 0.33)
289. Host plant growth form: (0) herbaceous; (1) woody. (CI = 1.00, RI = 1.00, G-fit = 1.00)
290. [modified from L166] Host plant group: (0) Papaveraceae; (1) Asteraceae; (2) Sapindaceae; (3) Fabaceae; (4) Rosaceae; (5) Nothofagaceae; (6) *Castanea*; (7) *Quercus*. Ordered 01234567. (CI = 0.58, RI = 0.82, G-fit = 0.38)
291. Host plant section within *Quercus* subgenus *Quercus* (in sexual generation): (0) *Cerris* sensu Camus; (1) Protobalanus; (2) *Quercus* s.s; (3) Lobatae. Ordered 0123. (CI = 0.27, RI = 0.43, G-fit = 0.27)
292. Host plant section within *Quercus* subgenus *Quercus* (in parthenogenetic generation): (0) *Cerris* sensu Camus; (1) Protobalanus; (2) *Quercus* s.s; (3) Lobatae. Ordered 0123. (CI = 0.30, RI = 0.61, G-fit = 0.30)
293. Gall complexity (in sexual generation): (0) small elliptical chamber only, at most a slight swelling of surrounding plant tissue; (1) a clearly defined outer gall not very different from structure of surrounding plant tissue; (2) a clearly defined outer gall differing in structure from surrounding plant tissue, often with tertiary outgrowths. Ordered 012. (CI = 0.12, RI = 0.25, G-fit = 0.17)
294. Gall complexity (in parthenogenetic generation): (0) small elliptical chamber only, at most a slight modification of surrounding plant tissue; (1) a clearly defined outer gall not very different from structure of surrounding plant tissue; (2) a clearly defined outer gall differing in structure from surrounding plant tissue, often with tertiary outgrowths. Ordered 012. (CI = 0.12, RI = 0.12, G-fit = 0.18)
295. Differentiation of inner and outer gall (in sexual generation): (0) no differentiated inner gall; (1) inner gall present, larval chamber presenting a differentiated wall, separated from surrounding tissue from outer gall by an air space and/or being easily detachable from it. (CI = 0.50, RI = 0.00, G-fit = 0.75)
296. Differentiation of inner and outer gall (in parthenogenetic generation): (0) no differentiated inner gall; (1) inner gall present, larval chamber presenting a differentiated wall, separated from surrounding tissue from outer gall by an air space and/or being easily detachable from it. (CI = 0.20, RI = 0.20, G-fit = 0.43)
297. Gall regularity (in sexual generation): (0) irregular, even if showing some basic pattern in shape; (1) regular, constant shape but often of different sizes. (CI = 0.12, RI = 0.30, G-fit = 0.30)
298. Gall regularity (in parthenogenetic generation): (0) irregular, even if showing some basic pattern in shape; (1) regular, constant shape but often of different sizes. (CI = 0.10, RI = 0.50, G-fit = 0.25)
299. Gall separation (in sexual generation): (0) single-chambered, usually separate galls; (1) clustered, single-chambered or occasionally double-chambered, closely abutting galls; (2) multi-chambered galls with inseparable larval chambers. Ordered 012. (CI = 0.17, RI = 0.44, G-fit = 0.16)
300. Gall separation (in parthenogenetic generation): (0) single-chambered, usually separate galls; (1) clustered, single-chambered or occasionally double-chambered, closely abutting galls; (2) multi-chambered galls with inseparable larval chambers. Ordered 012. (CI = 0.12, RI = 0.12, G-fit = 0.12)

301. Gall attachment (in sexual generation): (0) gall fused with plant and not detachable without damaging rest of plant; (1) relatively rigidly attached but detachable without damaging plant much; (2) attached via a small point and easily detachable or falling off by itself at maturity. Ordered 012. (CI = 0.15, RI = 0.48, G-fit = 0.21)

302. Gall attachment (in parthenogenetic generation): (0) gall fused with plant and not detachable without damaging rest of plant; (1) relatively rigidly attached but detachable without damaging plant much; (2) attached via a small point and easily detachable or falling off by itself at maturity. Ordered 012. (CI = 0.32, RI = 0.24, G-fit = 0.15)

303. Gall position (in sexual generation): (0) fruit; (1) catkin/inflorescence; (2) bud; (3) leaf, petiole; (4) stem, twig or runner; (5) root or underground stem. Unordered. (CI = 0.50, RI = 0.52, G-fit = 0.17)

304. Gall position (in parthenogenetic generation): (0) fruit; (1) catkin/inflorescence; (2) bud; (3) leaf, petiole; (4) stem, twig or runner; (5) root or underground stem. Unordered. (CI = 0.27, RI = 0.24, G-fit = 0.14)

305. Hardiness and texture of outer gall (in sexual generation): (0) soft and juicy, galls quickly desiccating and disappearing after maturation and emergence of insects; (1) moderately hard and spongy, galls can stay some time on host plant; (2) hard and tough, often staying on host plant and keeping its shape for a long time after emergence of insects. Ordered 012. (CI = 0.25, RI = 0.33, G-fit = 0.33)

306. Hardiness and texture of outer gall (in parthenogenetic generation): (0) soft and juicy, galls quickly desiccating and disappearing after maturation and emergence of insects; (1) moderately hard and spongy, galls can stay some time on host plant; (2) hard and tough, often staying on host plant and keeping its shape for a long time after emergence of insects. Ordered 012. (CI = 0.15, RI = 0.21, G-fit = 0.21)

307. Emergence of adults (in sexual generation): (0) spring; (1) summer; (2) fall; (3) winter. Ordered 0123. (CI = 0.43, RI = 0.38, G-fit = 0.20)

308. Emergence of adults (in parthenogenetic generation): (0) spring; (1) summer; (2) fall; (3) winter. Ordered 0123. (CI = 0.68, RI = 0.23, G-fit = 0.10)

Omitted characters from Liljeblad & Ronquist (1998) and Pujade-Villar & Arnedo (1997).

L12. Size of antennal sockets: Not independent of characters 15 and 16.

R93=L147: Not investigated due to necessary dissections not made.

Variation makes it difficult to distinguish qualitatively distinct states: R3=L5, R7=L11, L14, L16, R18=L25, R22=L34, L36, L41, L50, L52, L64, L65=R46, L95, L97-98, R64=L101, L104, R72=L113, L134, L137-9, R92=L146, R96=L151, R98=L153, L154, P5.

No informative variation: L26, Q5=L27, R33=L44, L53=Q14, L57=Q20, L58, L71, L74, L87, L89-90, L92, R63=L100, R68=L105, L106-7, R76=L118, R83=L125, L127, Q51=L128, Q44=L136, R90=L144, R94=L148, R95=L149, L150, R101=L157, R104=L160, R105=L161, P8.

Footnotes

[1] http://www.morphbank.net/?id=77655
[2] http://www.morphbank.net/?id=77656
[3] http://www.morphbank.net/?id=77657
[4] http://www.morphbank.net/?id=77658
[5] http://www.morphbank.net/?id=77659
[6] http://www.morphbank.net/?id=77660
[7] http://www.morphbank.net/?id=77661
[8] http://www.morphbank.net/?id=77662
[9] http://www.morphbank.net/?id=77663
[10] http://www.morphbank.net/?id=77664
[11] http://www.morphbank.net/?id=77665
[12] http://www.morphbank.net/?id=77666
[13] http://www.morphbank.net/?id=77667
[14] http://www.morphbank.net/?id=77668
[15] http://www.morphbank.net/?id=77669
[16] http://www.morphbank.net/?id=77670
[17] http://www.morphbank.net/?id=77671
[18] http://www.morphbank.net/?id=77672
[19] http://www.morphbank.net/?id=77673
[20] http://www.morphbank.net/?id=77674
[21] http://www.morphbank.net/?id=77675
[22] http://www.morphbank.net/?id=77676
[23] http://www.morphbank.net/?id=77677
[24] http://www.morphbank.net/?id=77678
[25] http://www.morphbank.net/?id=77679
[26] http://www.morphbank.net/?id=77680
[27] http://www.morphbank.net/?id=77681
[28] http://www.morphbank.net/?id=77682
[29] http://www.morphbank.net/?id=77683
[30] http://www.morphbank.net/?id=77684

TABLE 5. Observed character states (for charcters 1–50), coding alternating generations of a species as a single taxon (the Combined Matrix).

		10	20	30	40	50	
Aylax papaveris	**1**	0100011102	0000010000	0010000100	0100001000	1000010000	**1**
Phanacis phoenixopodos	**2**	0000010112	1000020000	0000000110	0100001000	1010010000	**2**
Diplolepis rosae	**3**	0001010101	1000030110	0110100100	0100000a00	1000110100	**3**
D. triforma	**4**	0001010101	1000030110	0110100110	000000100	1000?1?100	**4**
Liebelia magna	**5**	0100011100	1100031110	0110100110	1010000011	1000110101	**5**
Eschatocerus acaciae	**6**	0100011100	110001-13?	0111100210	?100000201	1-00111-00	**6**
Pediaspis aceris	**7**	0000010101	1010010011	0101100211	0111111010	020011010b	**7**
Himalocynips vigintilis	**8**	0000011002	100001-121	1112?0?2?2	?2111120??	?200?1??00	**8**
Paraulax sp.	**9**	1-1-011103	0020000011	0110100210	0100120?0	0000?1??0?	**9**
Acraspis erinacei	**10**	000100b1b2	1100010120	01011bc1b0	b1000bb200	10b0?10001	**10**
Amphibolips gainesi	**11**	0100001003	0001011110	1112112002	1111101100	0200?10001	**11**
Andricus caputmedusae	**12**	0101000112	1000021120	0112112001	1111101110	1000?0?001	**12**
A. curvator	**13**	0100001102	1000011120	0110111100	1110102110	1100?0?001	**13**
A. cylindratus	**14**	0001011003	1100011110	0222000211	0100001100	1100?1?011	**14**
A. gallaeurnaeformis	**15**	01010001b3	1000011120	0111111dbb	121110d1?0	1100?1?001	**15**
A. grossulariae	**16**	0101000103	1000011120	1110110111	0110001300	1000?11101	**16**
A. hastatus	**17**	0100101103	0200021120	0110110111	0111100200	1010?10001	**17**
A. kingi	**18**	0101000113	1200011110	0110111011	0210102000	1210?1?001	**18**
A. kollari	**19**	0b01000112	10000d1120	01121110bd	b2110011?0	1b00?00001	**19**
A. perlentus	**20**	0001000000	1000000111	0100100111	020000?300	1000?1?001	**20**
A. quercusflocci	**21**	0001000113	1000011110	0112111112	0100001200	1100?1?001	**21**
A. quercusfoliata	**22**	1-1-111113	0000010120	0110111110	0010001110	1010?01000	**22**
A. quercusradicis	**23**	0b0b001112	1000011120	0111101101	1d11100b00	10101b1000	**23**
A. quercusramuli	**24**	0101000102	1000021120	0220100211	1100002?0	1010?0?011	**24**
A. serricornis	**25**	0101000000	1100011120	0222110111	1210001300	1200?0?000	**25**
A. sieboldi	**26**	0b00000102	1000021120	01d110cbbb	bb1100bd10	0010?b?011	**26**
A. solitarius	**27**	0101000003	1000011120	1110111112	1111001000	1000?1?101	**27**
Aphelonyx cerricola	**28**	0101011113	0001011120	1110011101	1200000100	1010?10001	**28**
Atrusca emergens	**29**	0101011100	1200011120	0102010101	1211002000	1210?10101	**29**
Belonocnema treatae	**30**	0001000100	1200031120	0111110101	1200101100	1010?1?001	**30**
Biorhiza mellea	**31**	0101000100	1100011120	0111000101	0201012100	1200?11001	**31**
B. pallida	**32**	0101000010	1200011130	0102112bb1	1111101000	0db0101101	**32**
Callirhytis erythrocephala	**33**	0110001103	0201031110	1102?11112	1110012?0	1011???000	**33**
C. glandium	**34**	0110001103	0201031li0	011211b11c	1bbb001200	d011?11000	**34**
Cynips conspicua	**35**	0101011113	1100111120	0101012101	1200100100	1000?10001	**35**
C. douglasi	**36**	0101001100	1200121120	0111012001	1200101100	1000?10001	**36**
C. divisa	**37**	01010001b2	1d00111130	01110121b0	bd10101000	12b0?10101	**37**
Disholcaspis quercusglobulus	**38**	0101010103	1000011120	0102011101	0100001000	1110?10001	**38**
D. spectabilis	**39**	0001011113	0010021130	0100100011	0011102110	0200?1??01	**39**
Dryocosmus kuriphilus	**40**	0000100113	0101011121	0121000210	0110000100	1010??0001	**40**
D. nitidus	**41**	010000011a	b10b0d1121	0121100210	0111101200	1d10?1?001	**41**
Eumayria floridana	**42**	0101001103	0000011110	0100101110	1011100200	0010?1?000	**42**
Heteroecus pacificus	**43**	0100001100	1000011100	0110100002	011110?a10	0200110001	**43**
Loxaulus quercusmammula	**44**	0100000103	1200020110	011???211	?d0?00?3?0	bb10?1?001	**44**
Neuroterus numismalis	**45**	00010000b0	120011b120	0212010211	12bb0bb000	2200100101	**45**
N. serratus	**46**	0101001112	1000121020	?111012001	1200001000	2100?10101	**46**
Odontocynips nebulosa	**47**	0101000113	1010011130	0101111001	0111101000	0000?10001	**47**
Philonix gigas	**48**	0101000112	1100110130	0101011001	1200102000	1200??001	**48**
Plagiotrochus australis	**49**	0000100113	1001011130	0121111211	01bb0b0100	2010?11001	**49**
P. cardiguensis	**50**	0001110112	1000021100	0221010211	1100000200	2000?1?001	**50**
P. quercusilicis	**51**	0000110113	1000011120	0221011211	1200001?0	2000100001	**51**
Pseudoneuroterus macropterus	**52**	0101001110	1100011120	0111110011	1200001000	2100?00001	**52**
Trigonaspis gibbera	**53**	0101001002	1200110120	0101112001	0210101000	1210?1?001	**53**
T. megaptera	**54**	0101001110	1200011130	0102112101	1211001100	0000?01001	**54**
T. mendesi	**55**	0101000000	1200020120	0102112101	1210101 1?0	1010??101	**55**
T. quercusforticornis	**56**	0101000110	1200031020	0100112001	1211101000	1000?1?001	**56**
		10	**20**	**30**	**40**	**50**	

Explanation of symbols: monomorphic states 0-9; polymorphic states a = 2/3, b = 0/1, c = 0/2, d = 1/2, e = 0/2/3, f = 2/4, g = 0/3, h = 3/4, i = 1/3, j = 1/4, k = 4/5. Characters are unordered unless otherwise noted in the character descriptions in Appendix 1.

TABLE 5 (Continued). Observed character states (for charcters 121–190).

	51 60	70	80	90	100	110	120	
1	0200-00000	0000000200	0200010001	0000010200	10100-0010	000100000	0000010100	**1**
2	0001000010	0000000210	0110010002	0010000001	0011200010	000101100	000100011?	**2**
3	0201-10111	0100021310	010101010-	1120000110	0020200010	1110011010	000010111	**3**
4	0111010111	0101121210	010101010-	1120000010	0021200010	1110111010	000000101	**4**
5	0010010011	0100021410	030100010-	1122000001	0221200010	1111011010	2021010111	**5**
6	020--11011	0-02?20100	0010000-0-	1122000000	0020000100	1110110000	00-200023-	**6**
7	011100000?	001000bf10	22110b0000	0000001100	0000001000	1b01b11000	2011020d00	**7**
8	0?????????	????00510	1----10000	0000001100	000000100c	??01000000	2021020100	**8**
9	1101100000	1110?02000	2221010000	0000000100	1002001000	000111b000	1021020200	**9**
10	b1b0011101	00101d1211	221101010-	1001000c00	b210c01010	1101b01110	d0d1120201	**10**
11	1211-00001	2110002110	2----1011-	1001000200	0021200010	0001101011	?100000021	**11**
12	0100000111	0110001210	2----1010-	1002000100	1210000001	1001001000	0000010001	**12**
13	1110010110	0110001210	22---201--	1002010100	1110200010	1001011110	1021-10100	**13**
14	220--11101	0110121100	2----1010-	1002000200	0210101110	1101101000	2021010201	**14**
15	b200-101b1	0110011310	231012010-	1001000100	1010c00010	b101101000	1021010200	**15**
16	121--10101	0110001110	21211101--	1002010100	1111200010	0000001110	0110-10100	**16**
17	0211-10000	0110?02210	2----1010-	1002000100	0020200010	1001001001	0100000010	**17**
18	1111011011	0010102d11	22d--1010-	1002000200	1210101010	1001011000	0000020001	**18**
19	1db0010101	01100b1110	2121?1010-	10020c0200	1d1bc00001	1001101000	00c0010b00	**19**
20	0200-11001	2010001300	2----1010-	1002000200	1110101010	1101101100	2022010201	**20**
21	121--10101	0110101201	2----1010-	1002000100	1210201012	1101001010	0011000100	**21**
22	1111010101	0110101110	2----1010-	1002020100	1110200010	0001000000	0000020010	**22**
23	0111110010	01100b1d10	222111010-	1001010100	1110200010	0001001000	00bb010001	**23**
24	1201-10011	0112021d10	22101201--	1011000200	1110200010	1101101100	1021-10100	**24**
25	2111010001	2112021210	2????101--	1001000200	0110201110	1101001010	1021--1210	**25**
26	b111111101	0110001110	221111010-	1001010100	1010200010	0001b01000	00cb010001	**26**
27	120--10001	0110021110	2----1010-	1002010200	1011200010	1101011110	0121010100	**27**
28	0101010111	0000102201	2----1010-	1002000101	0210200010	1111001000	0100010011	**28**
29	1111011101	0111002210	1----1010-	1002000200	0210201010	1101111000	2000020000	**29**
30	2111100101	1011001110	22211101--	1002000200	0210201010	1001001100	2021-20201	**30**
31	0211-11101	0100001211	0----1010-	1002000200	0110201010	1101101010	1000010001	**31**
32	1d110110b1	2b110bd210	122111011-	100d00b200	021b100010	11010b1110	d0211202c0	**32**
33	2111000001	2000001a10	13---1010-	1000000001	0010210110	0000101011	0102000011	**33**
34	21b10b0001	2000001210	231101010-	10b100000b	0010210110	00001010b1	0101000021	**34**
35	1211010111	0110102211	2----1010-	1002000100	0210200010	1101001100	1000020001	**35**
36	1111010011	2100001211	22---1010-	1001000200	0010201010	1001001100	0000020000	**36**
37	b2b00101b1	2110001d11	222111b10-	1002000200	0110c01010	11010b1110	20d1020c01	**37**
38	0110010111	00?0002101	1----1110-	1002000201	0210200010	0111001000	0100010021	**38**
39	0111010110	00?0001200	1----1010-	1001000000	1021000010	0001011000	0000010100	**39**
40	0111011011	2000001210	1----1010-	1002000001	0211211110	1101111110	2021010200	**40**
41	1210-10111	2000001d00	122111010-	1012000101	0210001110	1001011110	2021010200	**41**
42	0101010110	0110001210	24210101--	1001020100	1021200010	0001001000	0011-00100	**42**
43	1101001010	0110000211	22---1010-	1002020100	1010200010	0000100000	0110010110	**43**
44	1111000000	0100101101	22211101--	1122000001	1210100110	0001011000	0021-10021	**44**
45	2101101011	1b12022a11	22???1111-	11d2000d10	0b102b0110	1101b01000	102d02123-	**45**
46	0101011111	1000022211	1----1110-	1102100001	0110200010	1001001000	101002123-	**46**
47	0101001100	0110100311	2----1010-	1001000200	0210100010	1001011000	0000020000	**47**
48	0101011001	1111002d11	11---1011-	1001000200	0210201010	1101001000	1001120201	**48**
49	0111010000	0100001210	22210b010-	1001000001	1110210010	0001b01110	0021010b0b	**49**
50	2101001111	1002-11201	22211101--	1112000001	0110200110	1101101100	1021-2113-	**50**
51	2101000111	0000-11200	22211101--	1012000001	0110200110	0001001110	0021-10111	**51**
52	2110010011	1000101201	2----0110-	1102100101	0110200010	0001101010	101002123-	**52**
53	1101010001	1011002210	2----1011-	-002010200	0210201010	1101101110	202102020?	**53**
54	2111010001	2111101110	12211101--	1002000200	0111200010	1101111110	2022-20200	**54**
55	2111010001	2011?01110	2----1011-	-011001200	0210100010	1101101100	10220202 3-	**55**
56	2110010101	2111002210	1----1011-	1001000100	0210201010	1101001110	2021020100	**56**
	51 60	70	80	90	100	110	120	

TABLE 5 (Continued). Observed character states (for charcters 121–190).

	121 130	140	150	160	170	180	190	
1	0000000000	1000200001	0000010000	1002001001	1-10000010	1100000000	000000100-	**1**
2	0000001000	1001100000	0011010100	1000101101	0-10101101	2121100000	010000101-	**2**
3	1102001000	10110000?1	1111110020	210010d012	-100101111	0002110-00	11012-----	**3**
4	1100001000	10110000?0	1111110020	200010d012	-100101101	0002010-00	11002-----	**4**
5	0001001000	1011201--0	0111110020	2000102112	-100110101	1022110-01	01002-----	**5**
6	-001000000	1022101---	--1111-020	220002d102	-010110101	00-2010-02	---02-----	**6**
7	0000001000	1001211---	--1-01b021	0011000110	---0000101	00100b0000	00100000b0	**7**
8	1000000000	100?210000	0?10001000	0011001110	---0000??1	?000?01000	b010??0000	**8**
9	0002000000	1001001---	--1-010021	1012000110	---0000111	1000010000	1100010010	**9**
10	0012000001	2101200102	1010001021	201b001100	---000b110	10200b1002	111002311-	**10**
11	1?00000001	0000200111	1210000120	1012001102	-110002110	1010011100	1001003111	**11**
12	0001000001	1011000001	0010001110	1011001100	---0000000	2010000000	0000012111	**12**
13	0101000101	1000200011	0010001111	1012001100	---0000010	1010000000	0000002101	**13**
14	0012001000	1012100001	1010001010	1002011100	---0000010	1021011000	1111003111	**14**
15	000200b000	1000200001	0010001010	111200110b	1-00000100	1011000000	000b0b2111	**15**
16	1100000001	1000200001	0210001020	1011001001	1-00001101	1010010020	0100001001	**16**
17	0000000001	0000200101	0010000120	1011001101	1-10000110	1010000110	0001001110	**17**
18	0010000001	1011000011	1010001110	1012000000	---0000010	1010011000	0010002100	**18**
19	100100b001	1000200011	0010001b10	101d001b0b	1-10000b0b	2010b00000	000000d111	**19**
20	0011001000	1032200001	0010001010	1011001100	---0000101	1011010000	1100002211	**20**
21	0111000001	1000200111	0010001120	1012001101	1-10001010	1011011010	110000201-	**21**
22	0002000000	1000200000	0010001110	1012001001	1-00000110	1010001010	0000011001	**22**
23	0001000000	1000200b00	10b0001b10	1012001b01	1-b000011b	101b001000	0000002101	**23**
24	0001001001	1000000001	0010001010	1011000100	---0000101	1021000000	100000201-	**24**
25	0111000001	1011100011	1110001020	1100011101	0-00100000	1021001011	1010002211	**25**
26	0b01000001	1001100b0b	1cb0001111	101d001b0b	1-000011b0	10bb000010	0000002101	**26**
27	1100001001	1100200001	0010001010	1012001101	1-00001001	1011000000	0110002100	**27**
28	1011001111	1010200111	0110011120	1010002100	---1010000	2020010002	1110023111	**28**
29	0112000001	1000000101	1010011011	1011001100	---0001010	2022011020	1101013111	**29**
30	1001001111	1001000111	1010001011	1011001100	---0001111	1011001011	1001003211	**30**
31	0111000101	1000000111	0010001011	1011001100	---0001010	2010011020	1111013111	**31**
32	1b0d00000b	100c200bb0	0110011021	1012001100	---0001011	10201b000b	bb1000321b	**32**
33	1000000000	1000200100	0110000120	1001111101	1-10001110	2011101000	?000001000	**33**
34	?000000000	1000200111	1110000120	1001111101	0-0000b110	2011101000	10000b1000	**34**
35	0011000001	1011200101	0010011120	1011001100	---0001100	1010001000	0011013110	**35**
36	0011000001	1011000111	1110011020	1011001100	---0000010	2010011000	1111013110	**36**
37	01b1000001	1001b001b1	10100b1011	101d001100	---000b010	1010001010	01110b3111	**37**
38	0011000001	1010200111	0110011120	1010001100	---1000110	1012010001	11100231-1	**38**
39	0000000100	0000200101	0210001000	1011001000	---0120110	1000011100	b100011000	**39**
40	1001001100	1001100101	0110001120	1211011100	---0002100	2022111011	1111003111	**40**
41	001100b10b	100d200b01	b110001020	1111011100	---0000000	1022011011	1111003101	**41**
42	0000000000	1000000000	1010001000	1112001101	1-10000101	2010000010	0000001000	**42**
43	0000000000	1000200011	1210001011	1012001001	1-10000110	1010000010	0000001000	**43**
44	0101001100	1011100101	1111000020	1101121102	-000001001	1022100001	110001101-	**44**
45	-122110101	1022201---	-011001-20	21010b2101	0-00110101	1022011102	-1-0123111	**45**
46	--22111111	1011201---	-1111?1120	2000002100	---0120000	2022110012	-1-12-31-1	**46**
47	0000000001	1000200101	0010001120	1012000001	1-00000110	2010011110	0010001000	**47**
48	0012000000	2110200101	1010011020	2012001100	---000100-	0020001001	1111003110	**48**
49	1000001100	1011100101	1110001110	100d121102	-100002001	1022011110	11-0003111	**49**
50	-112111011	1022101---	-011001020	120002210d	0000110001	1022011102	-1-0103111	**50**
51	0110001100	1012100101	0010001120	1200021102	-000011100	1022011111	-1-0003111	**51**
52	--22111111	1022101---	-1111?1100	2000002101	0-00120010	1022110102	-1-02-31-1	**52**
53	1012001000	11012011--	--1001-020	1011001100	---000101-	1020001111	1111003111	**53**
54	0102000101	1001200111	0010001011	1012001100	---0001011	0010101000	0100003211	**54**
55	-002001000	10322011--	--1-00----	--02001100	---000101-	10-2-11001	1100003210	**55**
56	1111001100	2101000111	1010001021	1012001100	---000011-	1021101000	1101013211	**56**
	121 130	**140**	**150**	**160**	**170**	**180**	**190**	

TABLE 5 (Continued). Observed character states (for charcters 191–260).

	191	200	210	220	230	240	250 260	
1	**0000000101**	**1010001001**	**10-0010000**	**0000000010**	**0000-00000**	**01000-0-10**	**0000000000**	1
2	0201001002	1110001001	10-0010101	0000000011	0000-10000	02000-0-22	0000000000	2
3	-002011002	1110000112	00-0020000	1000010011	1010-00000	02000-0-11	0010010011	3
4	-012011002	2000100112	00-0020100	00?0010011	0010-00000	01000-0-11	0110010011	4
5	-002011002	2101200102	00-0020000	0101010011	0010-00000	01100-1-31	0000010011	5
6	-20001001-	220-200-01	10-104??20	0001110110	1010-00100	0-100-1-30	3?10010010	6
7	0000010110	0010100111	10-0001110	1100000011	0000-00000	0d000-0-00	00b0000000	7
8	0002010?00	01?0?10?12	20-1011120	0101000011	1010-0000?	??00??????	????1?0000	8
9	0000010200	0000000101	1101001100	0001000010	0000-0001?	??00??????	????100000	9
10	0d0cb10d12	b001101101	2111121021	-1--010011	b101100111	0102110022	0012111200	10
11	0102011101	0111001111	2121031020	1100000020	0001000011	0201110110	0010200000	11
12	0100110101	0000011111	1121021020	1100010011	0001011011	0200100010	0011200000	12
13	1200110101	0010001101	1111021?10	?000010021	00????010	0100100?02	0011200?00	13
14	1200110111	1100101100	1111021020	1100010011	0000-00011	0201110122	0010200000	14
15	1200110101	1010001101	1121021010	1100000021	0001010010	0100100010	0012100000	15
16	1200110101	0010001100	1121031020	?100010021	00????010	1102110?10	0111200?00	16
17	0200110201	0000011110	10-1031010	1100001021	0101111010	0100110111	011?200000	17
18	1110110101	0000001101	1121021020	1100010011	1001010000	0001110000	0111200000	18
19	0200110101	0000011110	11d10a1?20	1100011021	0001011010	01021b0010	bb11200000	19
20	1200110111	1000001101	1121021021	1100010021	0100-00010	0001110012	0011200000	20
21	1200110111	0000001110	1121031010	1100010021	0101000011	0201110012	001d100000	21
22	0100110101	0010000110	1121031010	1100010021	0000-00010	0200110112	0111200000	22
23	bc10110101	0010001101	11d1031010	1100000011	b001010010	b0001100b0	0b11200000	23
24	1200110101	1000011110	1111021020	?100010011	00????010	01021b0?10	1012200?00	24
25	1200110101	11??01??1	1??1031021	-100011021	01-----010	1100110-12	0112100-00	25
26	0d00110201	0010001101	11010310d0	11?0010021	0001010010	0b001101bd	0011200000	26
27	1200110101	0000001100	1121021020	0100010021	0000--0010	0201100012	001?200000	27
28	0210110102	2101101111	20-1011121	1100010111	0001011011	1201110012	0011200000	28
29	1200010102	1110110101	1121030001	1110011021	0100-00111	0201110012	0012201100	29
30	1200010112	1011101111	2101031001	-100010021	01-----011	0200100-12	0012100-00	30
31	0200010112	2000000111	10-1031001	1100111021	0100-00011	1201110012	0012101200	31
32	0202010db2	b00100b110	2101230011	11000b01d1	0001100010	0000100002	101?111100	32
33	1200111202	0010001101	11010?????	????011011	0010-10010	0101100002	0111100000	33
34	12101101b1	0110001101	1121031010	1100010011	0010-00010	0101100012	0111100000	34
35	0210110112	0110001110	2111031011	1110011011	0101111011	0200110012	0011101400	35
36	0200110112	0111000100	2111031011	1100011021	0101100011	0200110012	0011101300	36
37	0200010d12	b000001101	21110a1021	1100010121	0101110011	b201100012	0111101300	37
38	0202110102	1101111110	2121031011	1100011011	0001010011	1202110022	0011100000	38
39	0020010102	0010000110	1120000010	0100000001	0010-00010	0000100110	0011110100	39
40	1220011112	1101001101	10-1011121	0100000011	0010-10011	0200110012	0111110000	40
41	122d111112	1101111100	10-1011b21	0100110b11	0010-10011	0100110012	1011100000	41
42	0200110201	0010010110	10-1-30010	-100000021	00????010	0000110-01	0111101-00	42
43	0000110101	0000001101	10-0021020	1100010021	0001000010	0000110101	0011200000	43
44	1222010112	1211001101	2101-21011	-00000001?	00-----010	0100110-12	0110100-00	44
45	1200110d12	2201101101	2121031021	0101110110	1010-10000	1102100021	2-121b0000	45
46	-200110112	2201201102	20-1021121	1110110101	1010-10011	0-00110010	3-12000000	46
47	0100010101	0010000111	10-1021010	1100000011	0001101010	1100110011	0101200000	47
48	0200010112	1000100100	21211----1	----010011	0111-10110	0100110012	0011101400	48
49	1221111112	1201b01001	1101021121	11000000d1	0010-10010	1101100012	0112100000	49
50	1221110112	2201201101	20-1-11021	-100110101	10-----010	1101100-12	3112100-00	50
51	1220110112	1201101002	10-1-11011	0100100101	10-----010	1100100-12	0112100-00	51
52	-200110112	220-201102	10-1021121	110011011?	1010-10001	1-02110020	3-12000000	52
53	0212010112	1101010100	21012-----	----010021	0101100011	0200110012	1011111200	53
54	0202010102	1000000101	1121231011	1100010011	00-----010	1100100-12	001?111-00	54
55	1202010212	0010001100	11112-----	----010011	0011-00010	0100110002	0012111100	55
56	0202110112	00???00?00	21211-----	----010021	0111-00111	0200110012	0011100000	56
	191	200	210	220	230	240	250 260	

TABLE 5 (Continued). Observed character states (for charcters 261–308).

```
   261     270        280        290        300      308
   .        .          .          .          .        .
 1 0000001200 0000001111 01?0000-00 --0-0-0-2- 0-0-1-0-  1
 2 0000001400 0000001101 2210000-01 --0-0-0-2- 0-4-1-0-  2
 3 0100000200 ?????????? ???0000-14 --2-0-0-2- 1-e-2-0-  3
 4 0100000200 1010002001 111001-214 --0-0-0-2- 1-4-2-0-  4
 5 0100000100 1010001001 00?0001-14 --2-0-0-2- 1-4-2-0-  5
 6 0100000410 1010000001 001002--13 --2-0-0-2- 1-4-2-1?  6
 7 1000010300 0100001111 0210100-12 --11000012 1135011g  7
 8 10000????? ?????????? ????01-?? ?????????? ????????  8
 9 00000???00 ?????????? ???002--15 --2-0-1?0? 2?4?1-1?  9
10 b011110h11 1110112110 11?011-217 3312-01102 2223-10a 10
11 00001102-- ---------- ---?11-217 -1-2-0-1-0 -2-0-1?? 11
12 00001102-- ---------- ---?100-17 -3-2-1-0-1 -1-0-2-g 12
13 00001102?? ?????????? ??-0100-17 33111-0110 02320-bg 13
14 00001101-- ---------- ---?11-017 -3-2-?-1-b -2-301-g 14
15 00001???00 1110012d10 1220100-17 3302-00100 0233-11g 15
16 0000110300 1110012110 12?0100-17 0-11-01102 2210-2b3 16
17 00001101-- ---------- ---?11-017 -1-1-0-0-0 -2-2-1-3 17
18 0000111??? ?????????? ???011-117 3322-00100 1233-1?0 18
19 0000110300 1110012210 1120100-17 0302-01100 2224-201 19
20 00001112-- ---------- ---?11-017 -3-2-0-1-0 -2-3-1-0 20
21 00001102-- ---------- ---?11-217 -3-2-0-1-1 -2-3-1-0 21
22 00001102-- ---------- ---111-217 -3-2-1-0-0 -2-2-1?c 22
23 0000110300 1110??2110 ???0100-17 3312010022 014522d0 23
24 0000110300 1110012210 2220100-17 3321-01110 1212-11g 24
25 0000111400 1110012110 221011-117 1102-01110 2213-103 25
26 00001103?? 1010012110 02?0100-17 3302-00100 ?135-210 26
27 00001113?? ?????????? ???0100-17 3312-01100 2212-102 27
28 00001102-- ---------- ---1100-17 -0-2-1-0-1 -1-4-2-a 28
29 10110103-- ---------- ---?11-017 -3-2-0-1-0 -2-3-1-3 29
30 1011010300 1110112110 11?011-217 3322000100 2253112? 30
31 10110104-- ---------- ---?11-217 -3-2-0-1-0 -2-3-1-g 31
32 1011010311 1010111110 1110100-17 3322000021 22251213 32
33 00000?10-- ---------- ---0100-17 3002-0-021 0c40-210 33
34 0000011g00 1010011100 22?0100-17 3002-0-0b1 0c40-210 34
35 10111103-- ---------- ---?11-117 -3-2-0-1-1 -2-h-1-a 35
36 10110104-- ---------- ---011-117 3322001100 2223110a 36
37 b011010311 1110112110 22?0100-17 3312-01100 22a3-202 37
38 00001113-- ---------- ---?11-217 -3-2-1-1-1 -1-2-2-2 38
39 00100103-- ---------- ---?11-117 -2-0-0-0-2 -0-4-2-g 39
40 10000113-- ---------- ---1101-16 ---1-0-0-0 -0-a-0-0 40
41 1000011211 11?1112100 21?0100-17 0022-01011 1213-1bg 41
42 0000110200 1110012110 0000?1-217 1-1-0-0-2- 1-5-2-0- 42
43 00001112?? ?????????? ???011-117 2212000000 2234111g 43
44 0000110301 1110011100 22?0?1-217 3-1-0-0-2- 0-4-1-1? 44
45 0000110j?? ?????????? ???0100-17 3312-00100 1233-110 45
46 1100110??? ?????????? ???0101-17 00?2???000 ?214???? 46
47 00001103-- ---------- ---?11-217 -3-1-0-0-2 -0-5-2-3 47
48 10110103-- ---------- ---011-217 3302-0?100 ?223-103 48
49 0000110311 1011212110 1200100-17 00101-0000 00341-03 49
50 0000110311 1111212110 11?0100-17 0-10--0-00 1113--0g 50
51 0000110311 1111212110 11?0100-17 0010000022 00340203 51
52 00001100-- ---------- ---?100-17 -0-0-0-0-2 -0-4-2-3 52
53 10110104-- ---------- ---?101-17 -3-2-0-1-0 -2-3-1-2 53
54 0011010411 1010112110 1210100-17 3322001100 22k30112 54
55 10010103-- ---------- ---0100-17 -322-0-100 22k3-1-a 55
56 10011103-- ---------- ---?11-217 ?3?1-1?0?1 ?2?4-1?a 56
   261     270        280        290        300       308
```

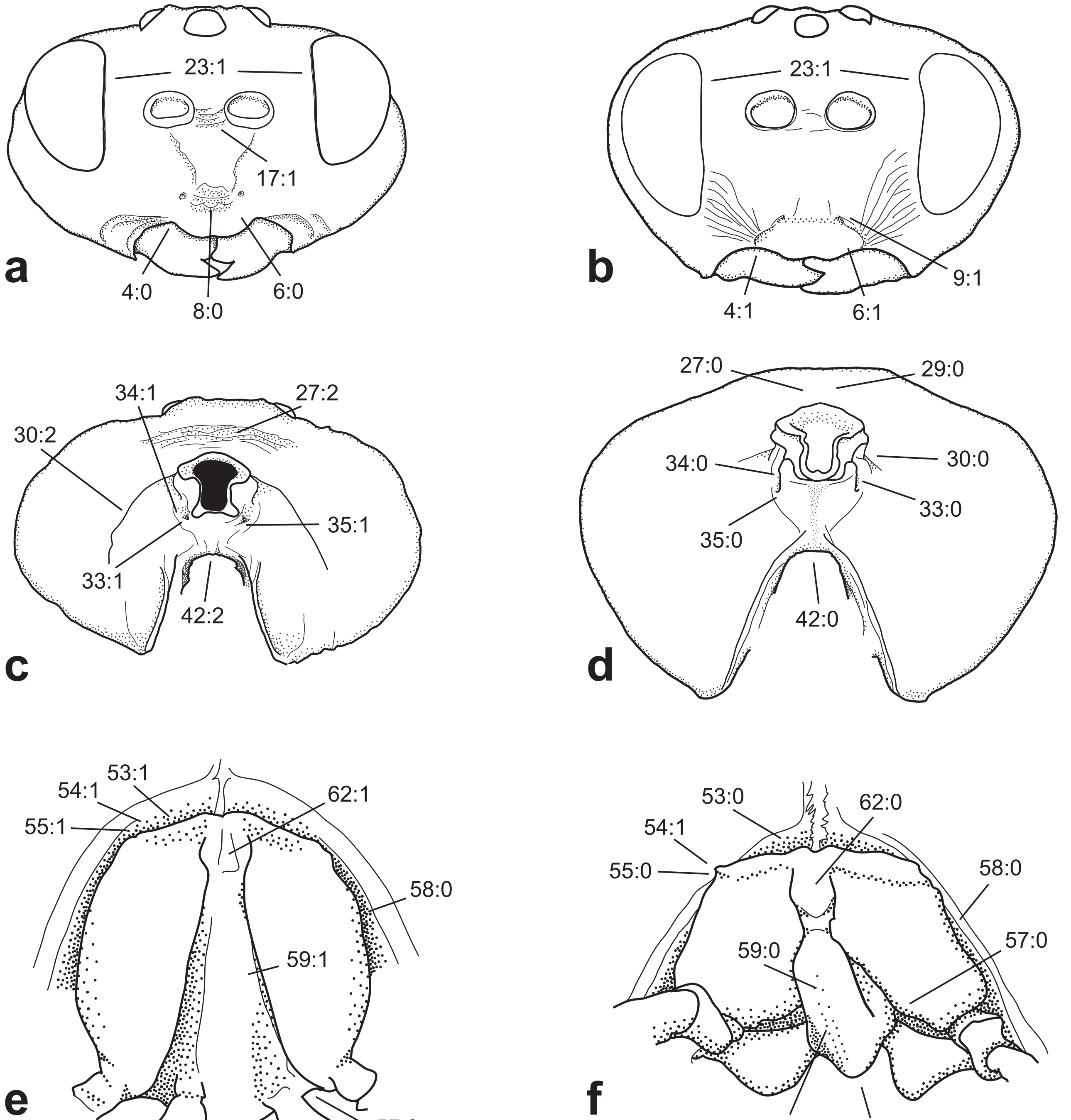

FIGURE 1. Head, anterior view: a *Amphibolips gainesi*, b *Aphelonyx cerricola*. Head, posterior view (excl. mouthparts): c *Amphibolips gainesi*, d *Aylax papaveris*. Mouthparts, posterior view: e *Andricus quercusradicis* sex. gen., f *Callirhytis glandium* sex. gen.

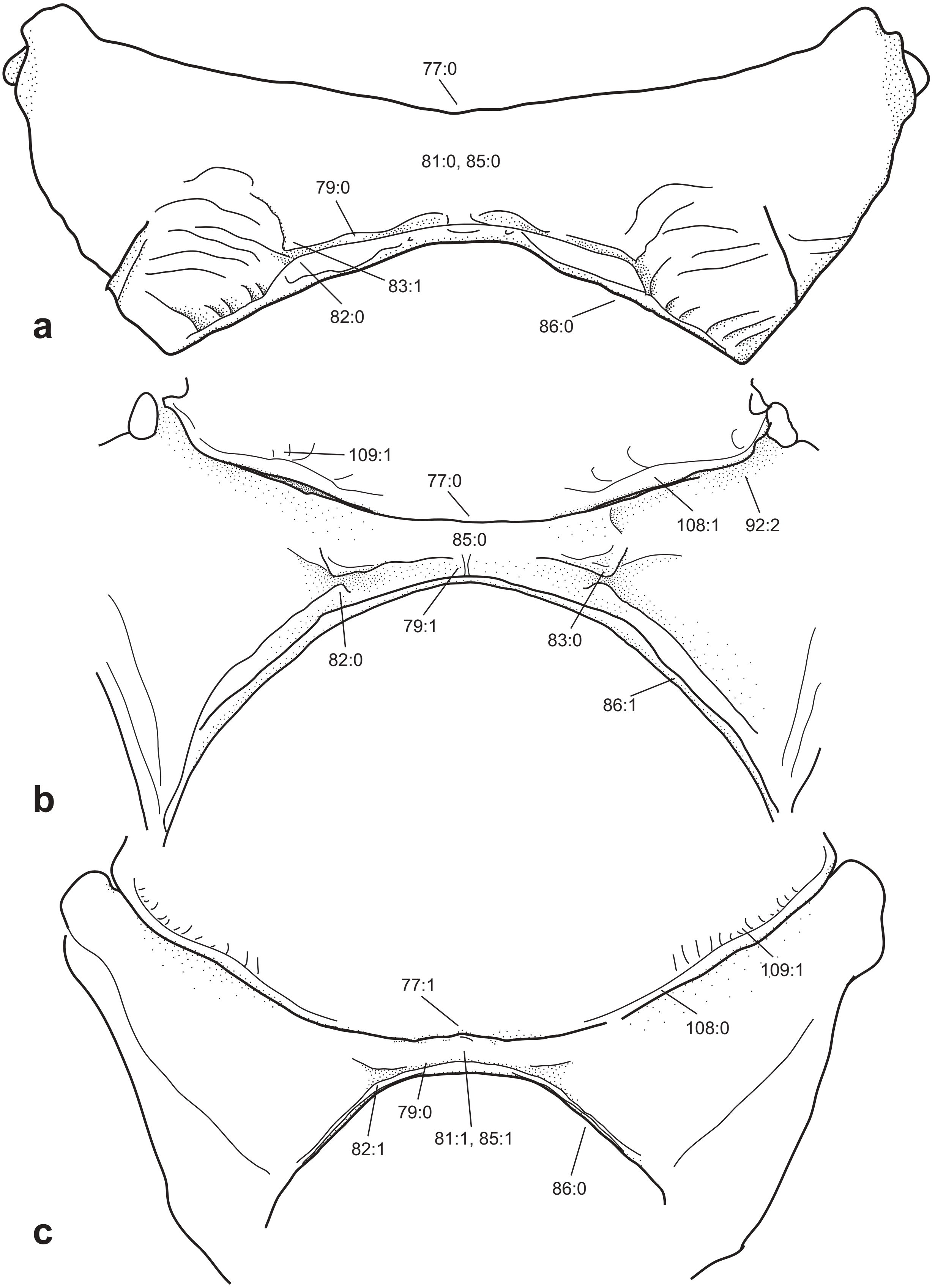

FIGURE 2. Pronotum, anterior view: a *Phanacis phoenixopodos*, b *Trigonaspis gibbera*, c *Trichagalma serratae*.

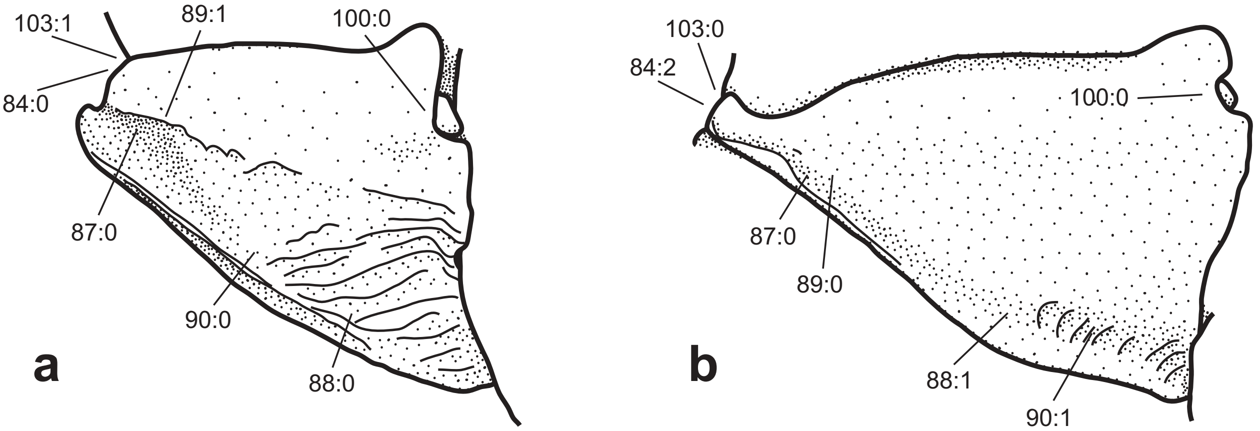

FIGURE 3. Pronotum, lateral view: a *Diplolepis triforma*, b *Pseudoneuroterus macropterus*.

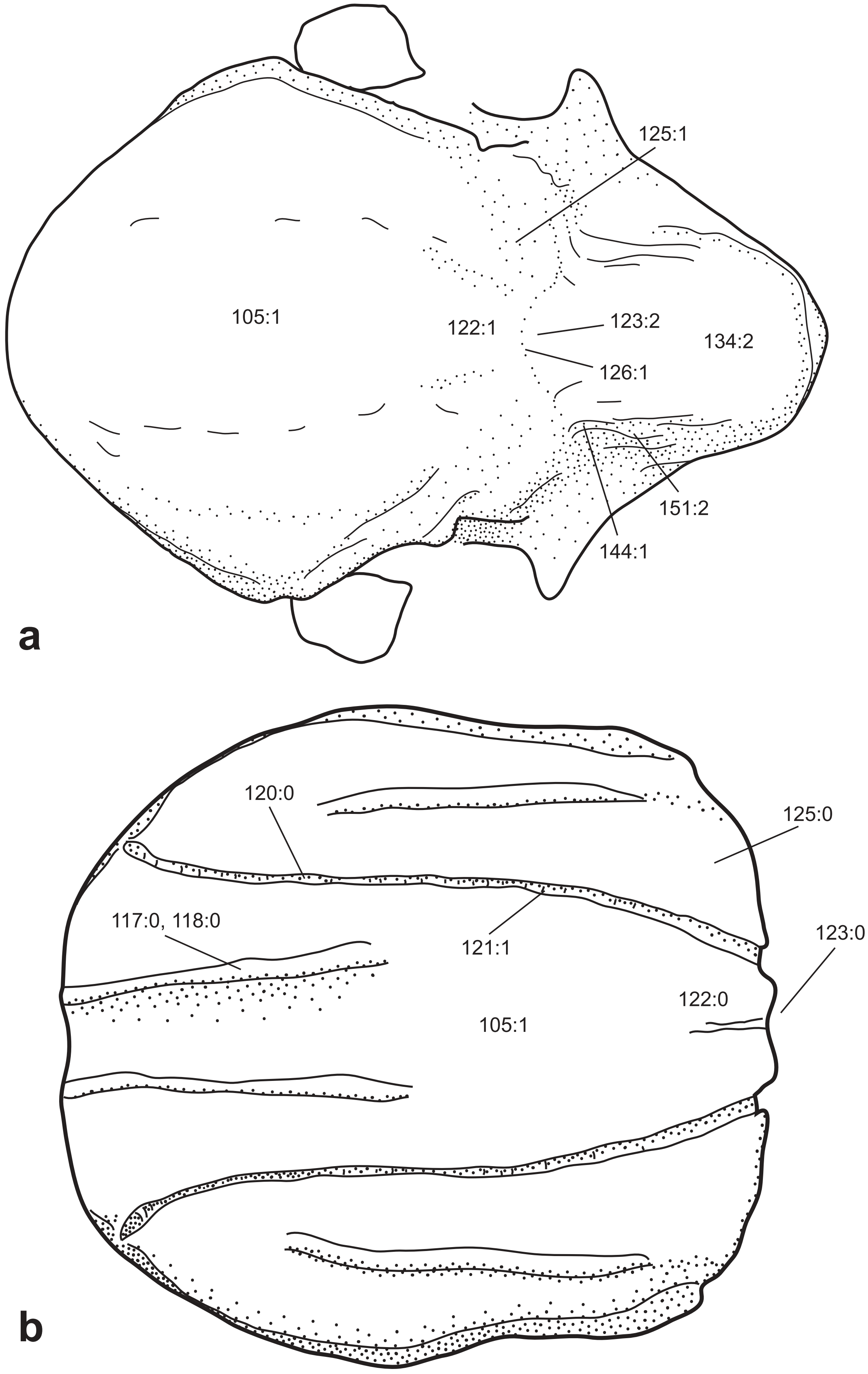

FIGURE 4. Mesoscutum, dorsal view: a *Neuroterus numismalis* sex. gen., b *Andricus kollari* parth. gen.

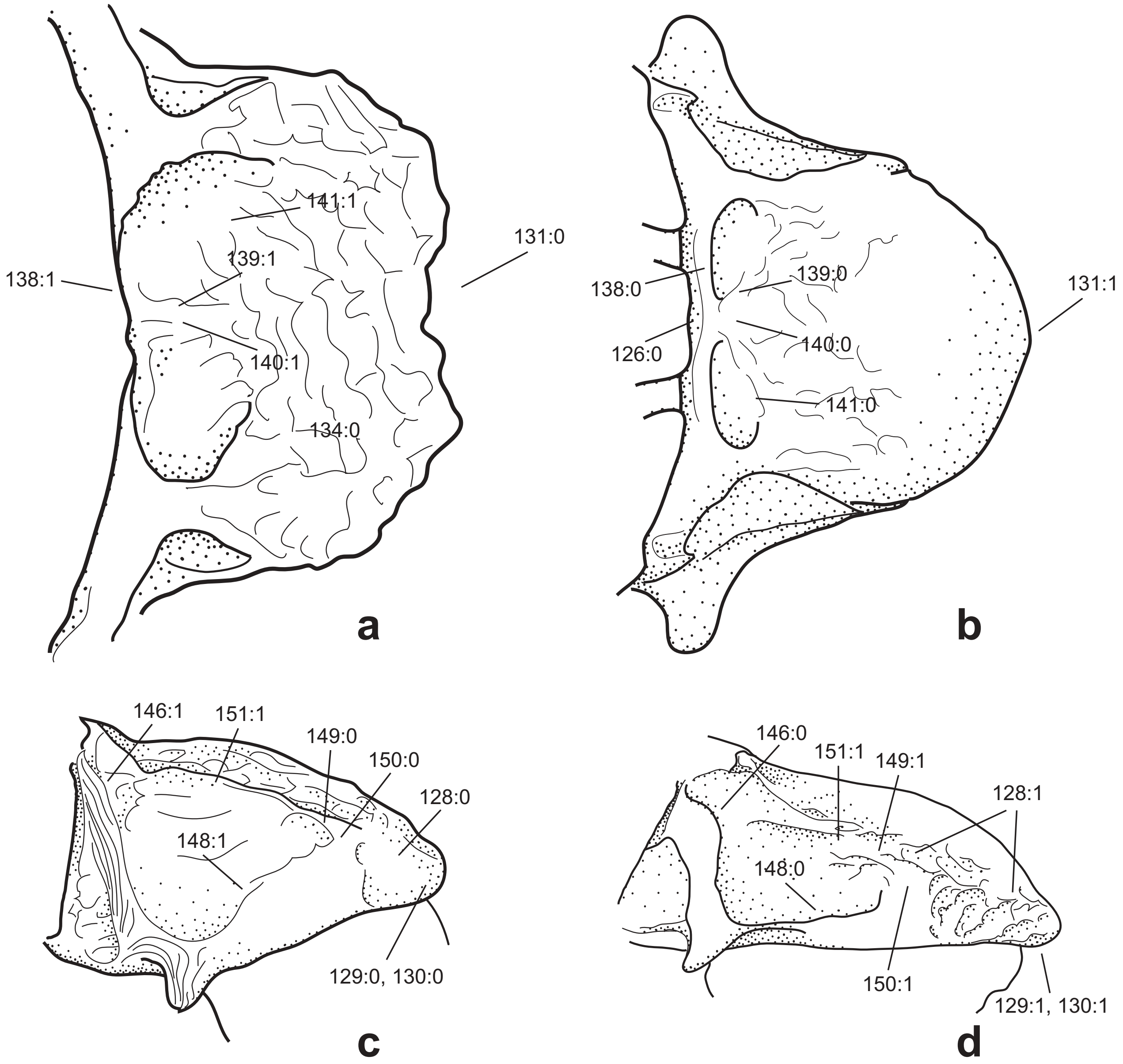

FIGURE 5. Mesoscutellum, dorsal view: a *Amphibolips gainesi*, b *Andricus quercusfoliata*. Scutellum, lateral view: c *Phanacis phoenixopodos*, d *Belonocnema treatae.*

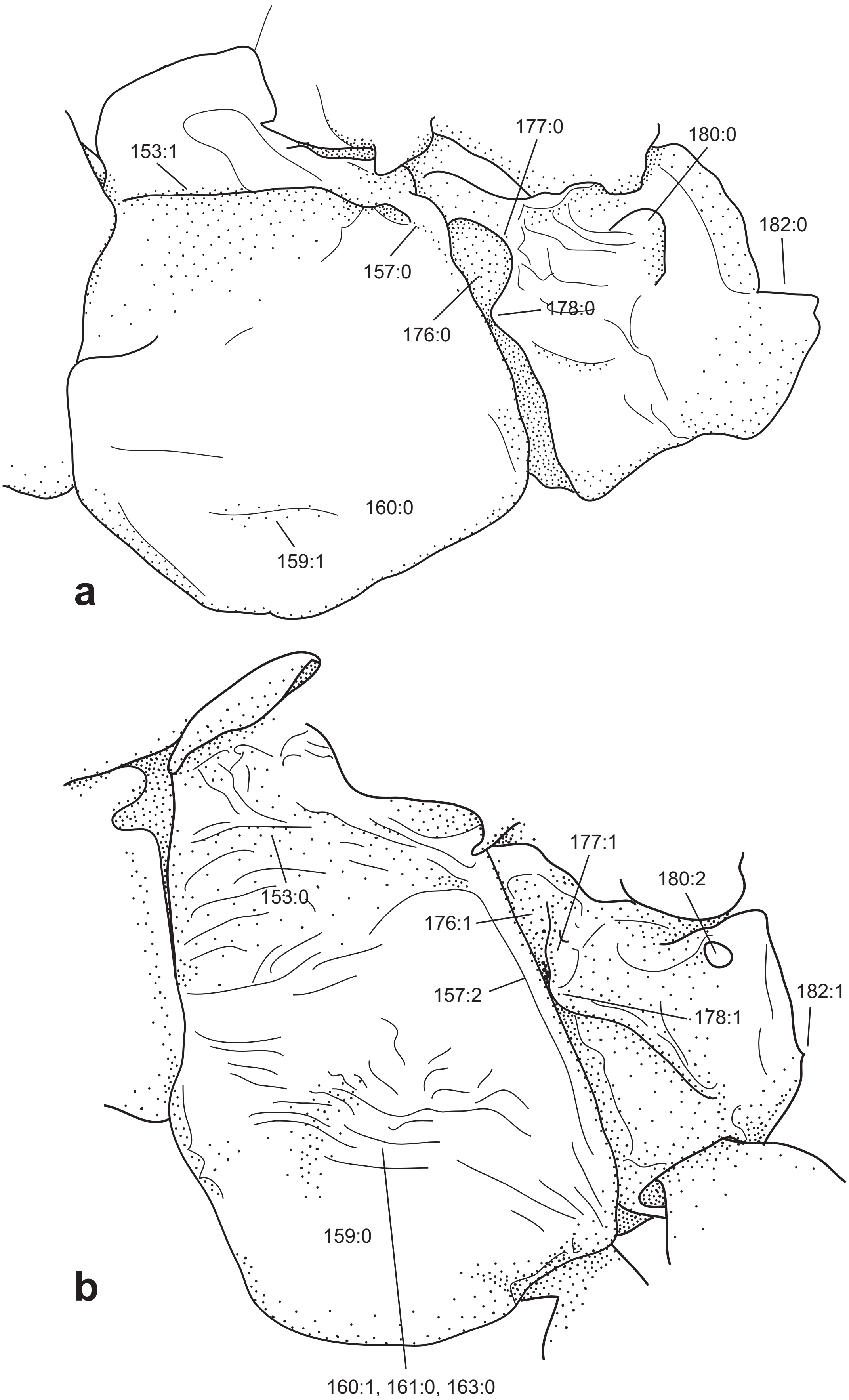

FIGURE 6. Mesopleuron, lateral view: a *Pediaspis aceris* parth. gen., b *Neuroterus numismalis* parth. gen.

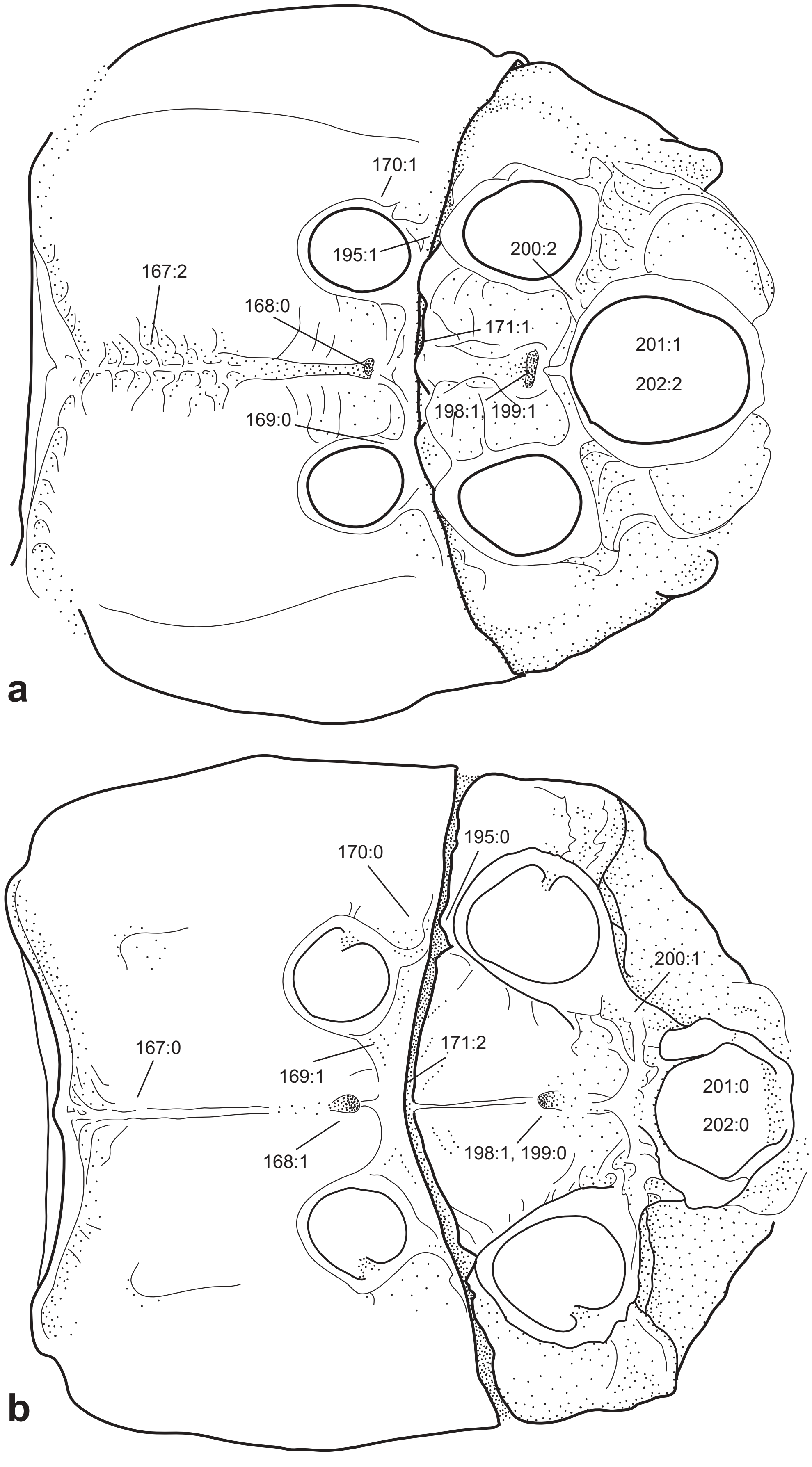

FIGURE 7. Mesosoma, ventral view: a *Plagiotrochus australis* parth. gen., b *Odontocynips nebulosa*.

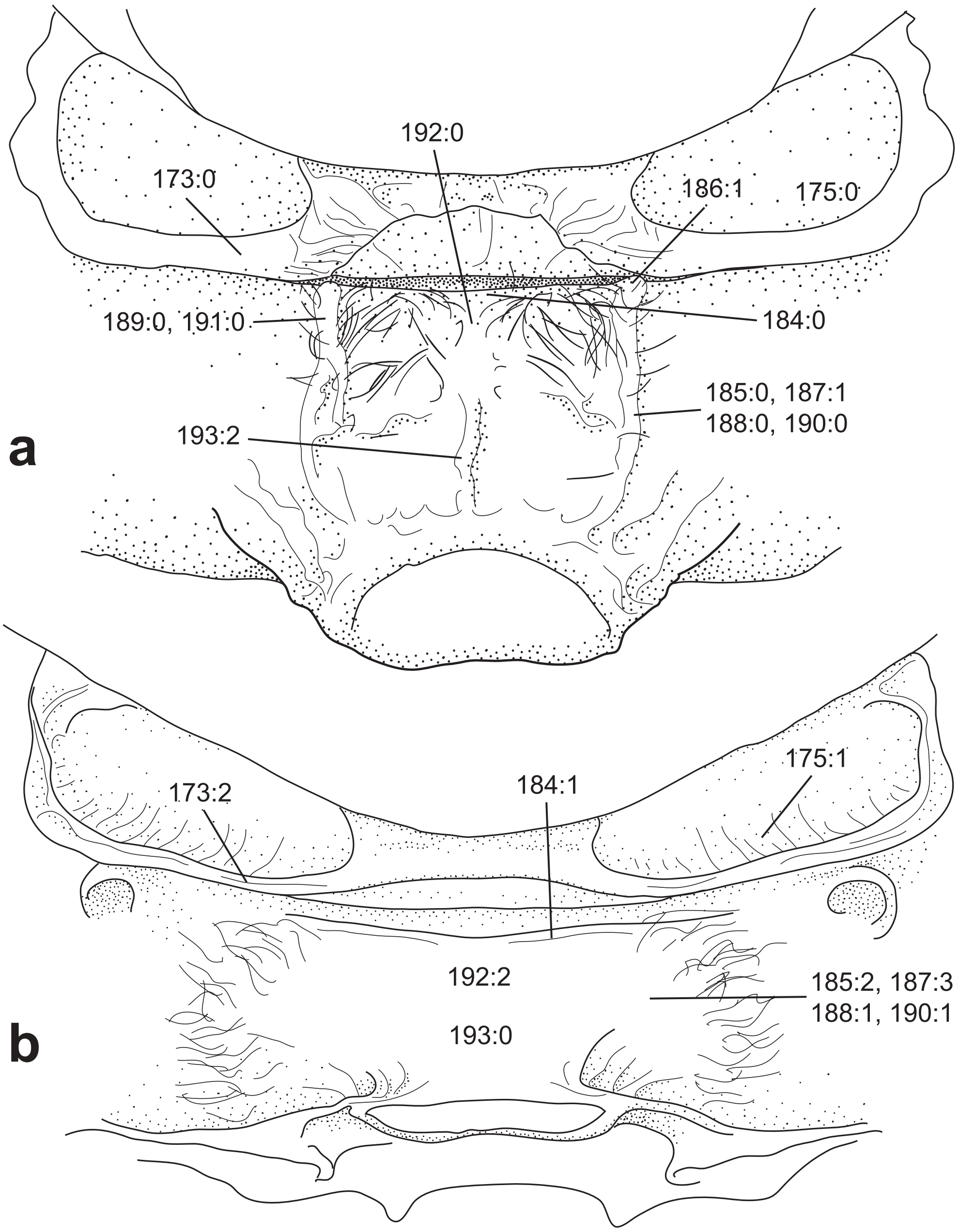

FIGURE 8. Mesosoma, posterior view: a *Disholcaspis spectabilis*, b *Trichagalma serratae*.

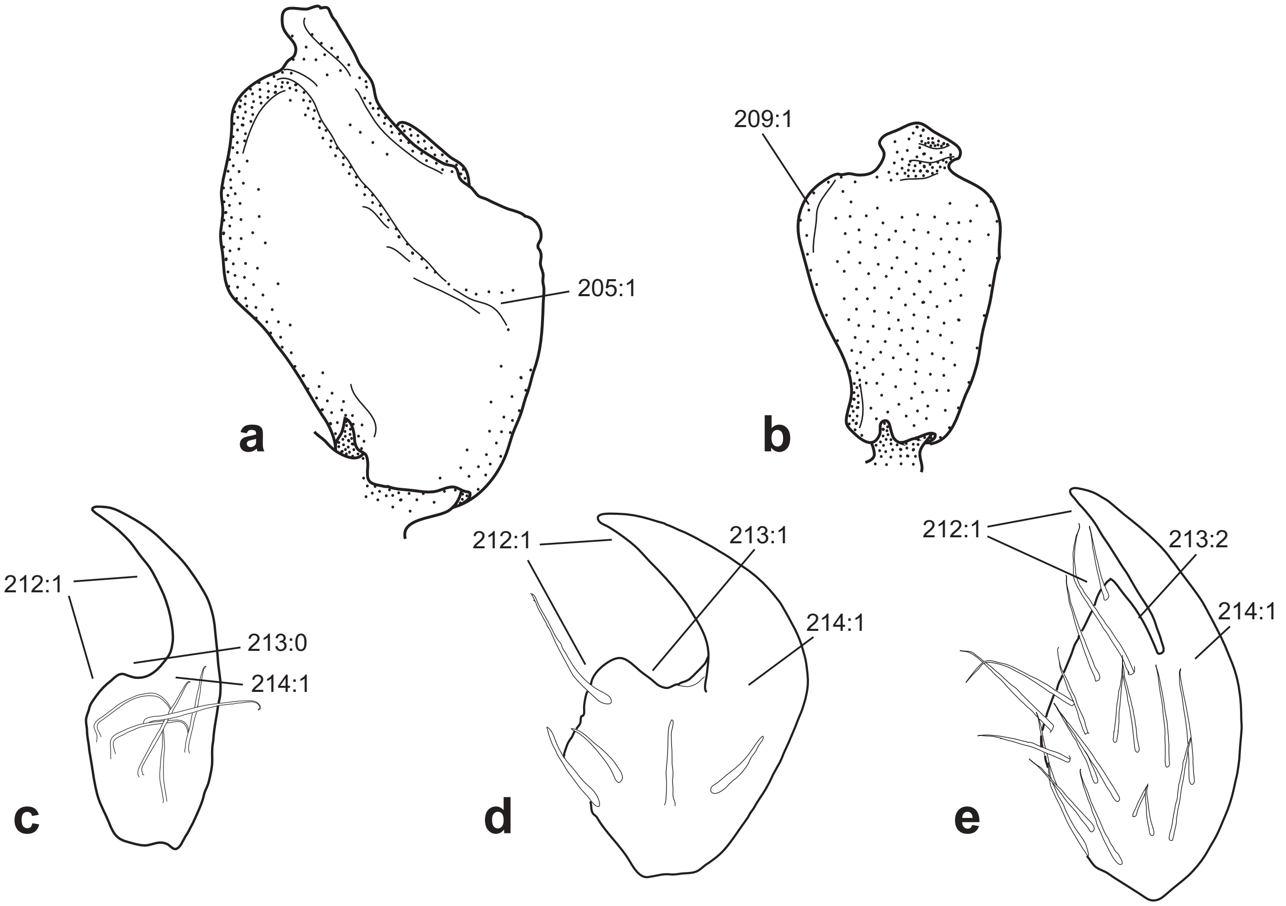

FIGURE 9. a: Procoxa: *Disholcaspis quercusglobulus*. b: Mesocoxa: *Odontocynips nebulosa*. Claws: c *Biorhiza pallida* sex. gen., d *Andricus quercusramuli*, e *Andricus kollari* parth. gen.

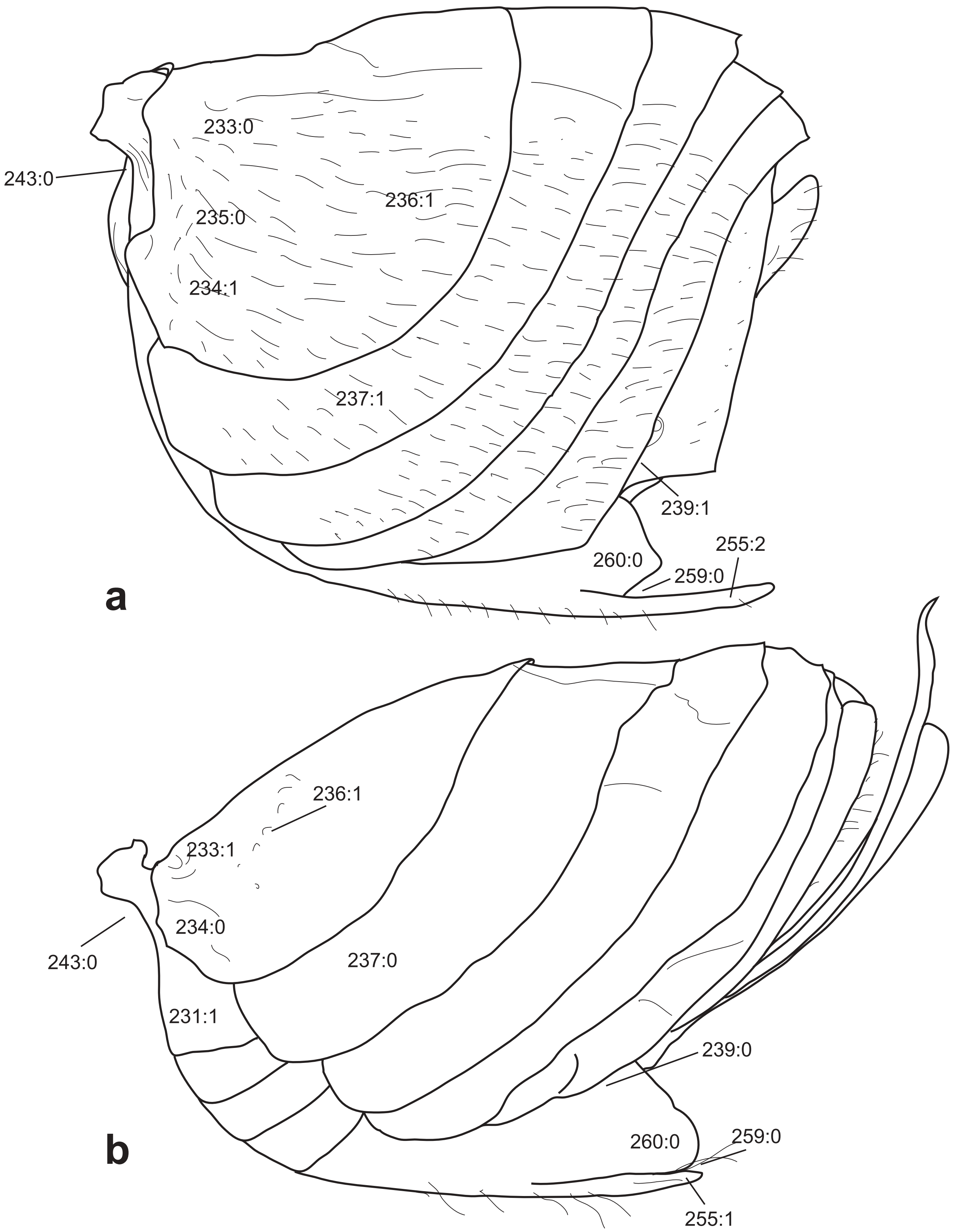

FIGURE 10. Metasoma, female, lateral view: a *Aphelonyx cerricola*, b *Pseudoneuroterus macropterus*.

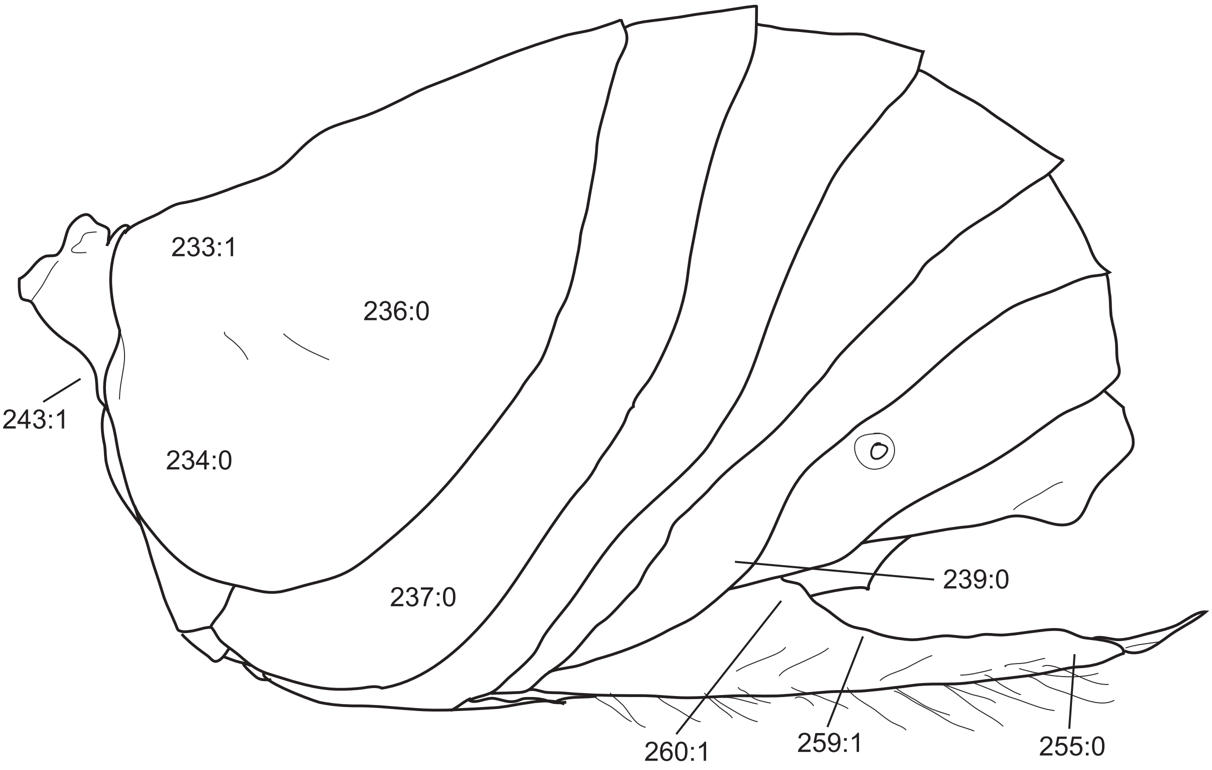

FIGURE 11. Metasoma, female, lateral view, *Liebelia magna*.

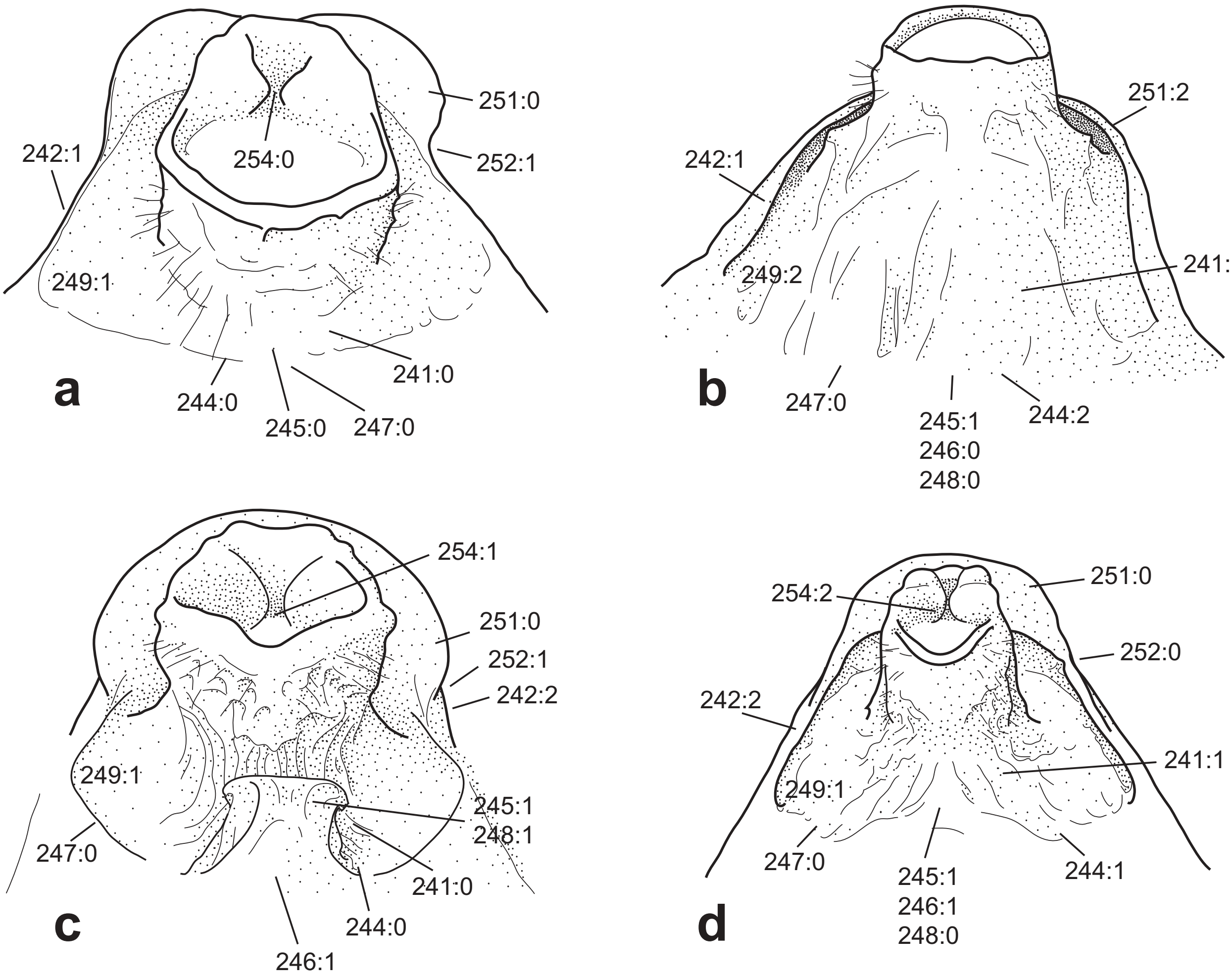

FIGURE 12. Petiole: a *Diplolepis triforma*, b *Neuroterus numismalis* parth. gen., c *Andricus quercusfoliata*, d *Biorhiza mellea*.

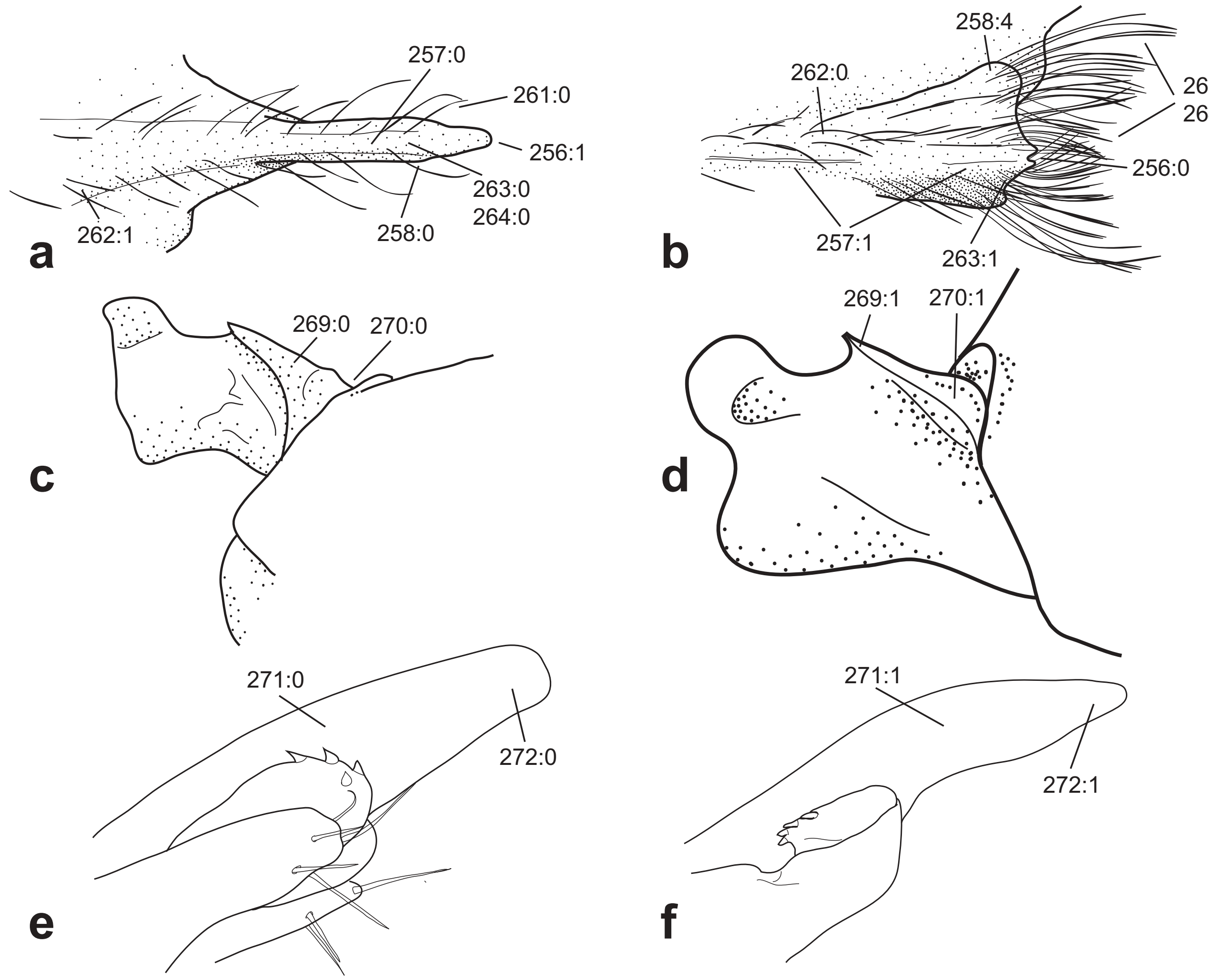

FIGURE 13. Hypopygium: a *Liebelia magna*, b *Cynips conspicua*. Metasoma, male, lateral view: c *Cynips*.