Redescription of *Acanthaegilips* Ashmead, 1897, with characterization of the Anacharitinae and Aspiceratinae (Hymenoptera: Cynipoidea: Figitidae)

PALMIRA ROS-FARRÉ*

Universitat de Barcelona, Facultat de Biologia, Departament Biologia Animal, Avda Diagonal 645, ES-08028 Barcelona, Spain

FREDRIK RONQUIST

Department of Zoology, Uppsala University, Villavägen 9, SE-752 36 Uppsala, Sweden

JULI PUJADE-VILLAR

Universitat de Barcelona, Facultat de Biologia, Departament Biologia Animal, Avda Diagonal 645, ES-08028 Barcelona, Spain

We redescribe the South American genus *Acanthaegilips* Ashmead, 1897 and discuss its phylogenetic position within the Figitidae (*sensu lato*). The genus was originally placed in the Anacharitinae but shows affinities with both the Anacharitinae and the Aspiceratinae in the characters used currently to separate figitid subfamilies. In a recent revision of the higher-level classification of cynipoids, *Acanthaegilips* was separated from the remainder of the Anacharitinae and placed in a monotypic higher-level taxon. We analyse the morphological differences between the Anacharitinae and Aspiceratinae and their bearing on the monophyly of the two subfamilies and the placement of *Acanthaegilips*. We conclude that, after removal of *Seitneria* and *Paraegilips* from the Anacharitinae, both subfamilies are well defined monophyletic groups and that *Acanthaegilips* belongs to the Anacharitinae, within which it forms a monophyletic group together with the South American genera *Calofigites* Kieffer, 1909 and *Solenofigites* Diaz, 1979.

© 2000 The Linnean Society of London

ADDITIONAL KEY WORDS:—phylogeny – cynipoids – figitids.

CONTENTS

* Corresponding author. E-mail: pujade@porthos.bio.ub.es

INTRODUCTION

The figitid genus *Acanthaegilips* was proposed by Ashmead (1897) for a single species, *A. brasiliensis* Ashmead, 1897, described in the same paper from a single female specimen collected in Brazil. Weld (1921) provided a more complete characterization of the female holotype of *A. brasiliensis* and Díaz (1983) described the male and recorded additional female specimens from Argentina. Examination of the holotype of *A. brasiliensis* and additional material of the genus by the first author revealed several inaccuracies in Weld's and Díaz' descriptions. These errors are corrected in the present paper, and a comprehensive description of the genus is provided.

The position of the genus *Acanthaegilips* is currently debated. Traditionally, the genus has been placed in the Anacharitinae, one of three subfamilies of the Figitidae (the others being Aspiceratinae and Figitinae) (Ashmead, 1903; Weld, 1952). However, in most keys to figitid subfamilies, *Acanthaegilips* specimens do not run easily to the Anacharitinae. In particular, the genus shares several key features with the Aspiceratinae, such as an open marginal cell, a long scutellar spine, a slightly saddle-shaped third abdominal tergum, and a longitudinal carina on the metatibia. Nordlander (1982) raised the Anacharitinae to family status without adding information on characters separating anacharitids from other figitids. Kovalev (1996) recently removed *Acanthaegilips* from the Anacharitidae and placed it in a separate monotypic family, the Acanthaegilipidae.

The argument over the position of the genus *Acanthaegilips* is part of a larger debate concerning the classification of the figitid complex of the Cynipoidea. At one extreme are Rasnitsyn (1980, 1988) and Ronquist (1995b), who recognize a single family, the Figitidae *sensu lato*, with six subfamilies: the Figitinae, Anacharitinae, Aspiceratinae, Charipinae, Eucoilinae, and Pycnostigmatinae. Ronquist (1995b) provided some evidence that the Figitidae *sensu lato* are monophyletic, and suggested that all subfamilies except the obviously heterogeneous Figitinae may be monophyletic. Other authors split the complex into several families, the most extreme variant being represented by Kovalev (1994, 1995, 1996). In addition to the genus *Acanthaegilips*, Kovalev treated the Figitinae genera *Thrasorus* Weld, 1944 and *Emargo* Weld, 1969, as well as the subfamilies Anacharitinae (excluding *Acanthaegilips*), Eucoilinae, Pycnostigmatinae, and Charipinae as separate families.

Here we present a preliminary analysis of the phylogenetic position of *Acanthaegilips* and the status of the Aspiceratinae and Anacharitinae based on characters employed in recent or widely used keys to figitid subfamilies (Weld, 1952; Fergusson, 1986, 1995; Gauld & Bolton, 1988; Ritchie, 1993) and some characters described here for the first time. We also comment on the position of two genera that have been placed previously in the Anacharitinae: *Seitneria* and *Paraegilips*. In reporting on

character distributions, we provisionally follow the higher-level figitid classification of Ronquist (1995b).

MATERIAL AND METHODS

The material of *Acanthaegilips* is listed below. We studied the holotype and additional material of different undescribed morphospecies of the genus; SEM pictures of *Acanthaegilips* were obtained at low voltages (200–800 V) without coating; the pattern of vertical lines on the images is due to the use of such low voltages. Most of the other SEM figures are from gold-coated specimens. Line drawings were made from SEM photographs.

For the character analysis, we studied material of *Anacharis* Dalman,1823, *Xyalaspis* Hartig, 1843, *Aegilips* Walker, 1835, *Acanthaegilips*, *Calofigites*, *Solenofigites*, and *Petricynips* Belizin, 1961 (Anacharitinae); *Seitneria* Tavares, 1928 and *Paraegilips* Kieffer, 1910 (previously placed in the Anacharitinae); and *Balna* Cameron, 1883, *Paraspicera* Kieffer, 1907, *Prosaspicera* Kieffer, 1907, *Aspicera* Dahlbom 1842, *Omalaspis* Giraud, 1860, *Callaspidia* Dahlbom, 1842, and *Anacharoides* Cameron, 1904 (Aspiceratinae). This set includes all genera currently or recently placed in the Anacharitinae or Aspiceratinae except *Acothyreus* Ashmead, 1887 and *Proanacharis* (Anacharitinae), of which we did not have access to specimens. Nevertheless, *Proanacharis* could be included in the analysis based on information in Kovalev (1996).

To polarize characters we studied material of *Figites*, *Neralsia*, *Melanips* and *Myrtopsen* in the Figitinae and *Phaenoglyphis* in the Charipinae. These figitid genera were chosen to represent taxa that are similar to the Aspiceratinae (*Figites* and *Neralsia*) or to the Anacharitinae (*Melanips* and *Phaenoglyphis*), or taxa that seem to be archaic figitids (*Myrtopsen*) (Ronquist, 1995b). Anacharitinae and Aspiceratinae may not form a monophyletic group excluding all five of these genera; thus, the studied Figitinae and Charipinae are mainly useful for polarizing character states within each of the subfamilies. For true outgroups, we studied *Diastrophus*, *Aulacidea* and *Aylax*, morphologically archaic representatives of each of the three major lineages of the Cynipidae, the sister group of figitids (Ronquist, 1995b; Liljeblad & Ronquist, 1998). We also used published information on character states in more remote cynipoid lineages (the macrocynipoid families Austrocynipidae, Liopteridae, and Ibaliidae; see Riek, 1971; Ronquist & Nordlander, 1989; Ronquist, 1995a, 1995b). Several additional papers were consulted for character states in some Aspiceratinae and Anacharitinae (Weld, 1952; Evenhuis & Barbotin, 1977; Quinlan, 1979; Diaz, 1979a,b; Nieves-Aldrey & Fontal-Cazalla, 1997).

The following abbreviations and terms are used for measurements: POL—distance between the lateral ocelli; OOL—distance between one lateral ocellus and the compound eye; LOL—distance between lateral and central ocelli; transfacial line—shortest distance between compound eyes. Remaining terms for skeletal structures and abbreviations follow Richards (1977), Ronquist and Nordlander (1989), and Ronquist (1995a).

Phylogenetic analyses were performed using PAUP 3.1.1 (Swofford, 1993).

REDESCRIPTION OF *ACANTHAEGILIPS*

Examined material. Holotype of *A. brasiliensis.*—1♀ Cat. n° 23645 NMNH Collected in April at Chapada (Brazil), Ashmead collection (det. Ashmead), antenna mounted.
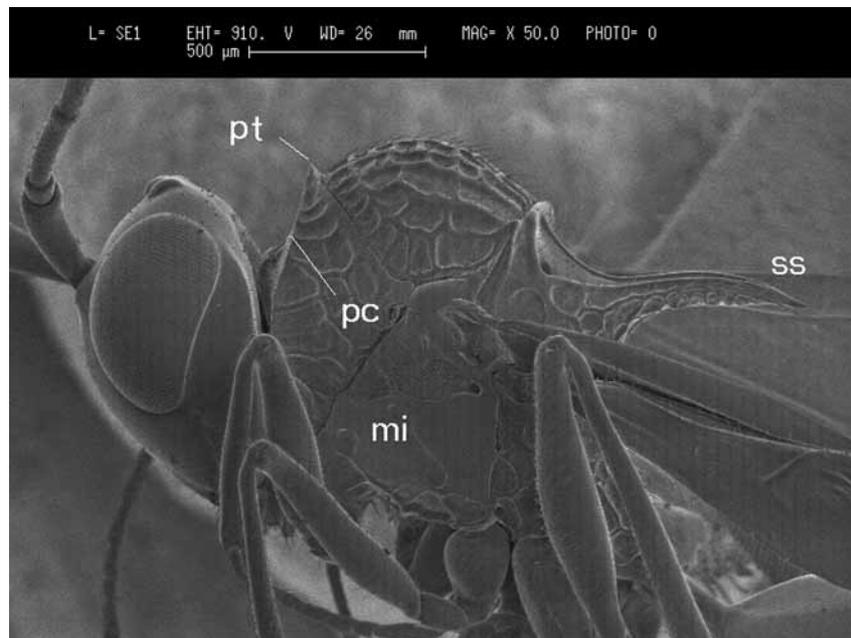
Figure 1. Head and mesosoma, lateral view of *Acanthaegilips* sp. Abbreviations: pt=pronotal tooth; pc=pronotal crest; mi=mesopleural impression; ss=scutellar spine (char. 10, state 2).

Label data: Chapada, April; Coll Ashmead. Acanthaegilips brasiliensis ♀, Type.
Additional material. ARGENTINA: 1♂, Horca Molle nr. Tucuman 18-X-1968, leg. C.W. & L.B. O'Brien (CAS). BOLIVIA: 1♀, 19/20-XII-1955 Chulumani, 1700 m, Yungas, L. E. Pena (CNC). BRAZIL: 1♀, 12-X-87 Fazenda Jacutinga, Dias col. (UFSCar). COSTA RICA: 1♂, IX/X-1989 Guanac Estac. Mengo, S. W. Volcan Cacao 1100 m. (INB); 1♀, X/XII-1990 San Jose de Moravia, 1600 m, Paul Hanson. (INB); 1♀, III-95 San Jose de Moravia, 1600 m, Paul Hanson (INB); 1♀, VIII/IX-1995 Alagüela Est. Biol. San Ramón, 900 m, P. Hanson (INB); 1♀, VI/VIII-1993 Cartago Dulce Nombre, Vivero Linda Vista, 1300 m, P. Hanson (INB); 1♀, 16-XI-1994 Heredia Est. Biol. La Selva, 100 m, P Hanson (INB). 2♀♀, 14-VI-1985 San Antonio de Escazu, 1300 m, W. Ebehard (NMNH). ECUADOR: 4♂♂ and 2♀♀, 17-II-1983 Napo bellow papallacta 3000 m, L.M. Masner (CNC). GUA-TEMALA: 1♀, July-80 Antigua, 1500–1600 m. Krauss (NMNH). HONDURAS: 1♂, 17-II-1918 Tegucigalpa, F. J. Dyer nº 35396 (NMNH). JAMAICA: 1♀, XII-967 Kingston, NLH Kraus (NMNH). MEXICO: 1♂ and 1♀, 8-VI-1969 Yerba Buena, N. Bochil (CNC). PERU: 1♂, July-1964 Machu-Pichu, B. Malkin (MZUSP). VENEZUELA: 1♀, 18-VIII/3-IX-1992 Aragua, Rancho Grande N.P., L. Masner (CNC); 1♂, 30-IV-1081 Merida Mucui nr. Tavay, 2300 m, Masner & Marh (NMNH).

Coloration. Predominantly dark. Head entirely black. Antenne with articles yellow to dark; scape sometimes black basally. Scutum and mesopleural triangle reddish brown to black; mesopleuron, scutellar spine, propodeum and metasoma brown to almost black. Legs light yellowish brown to dark brown.
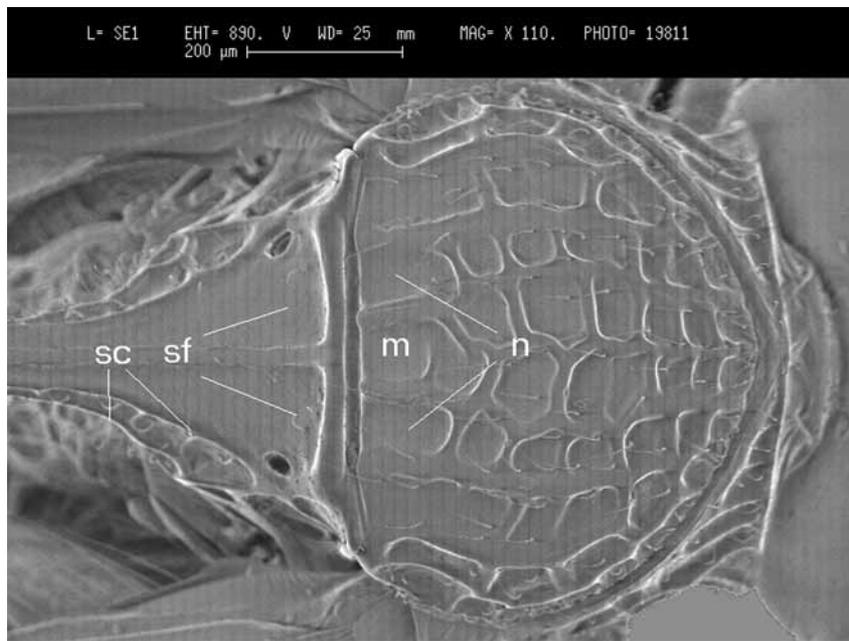
Figure 2. Mesosoma, dorsal view of *Acanthaegilips* sp. Abbreviations: n = notauli; m = medial furrow; sc = scutellar carinae; sf = scutellar fobeae (char. 9, state 1).
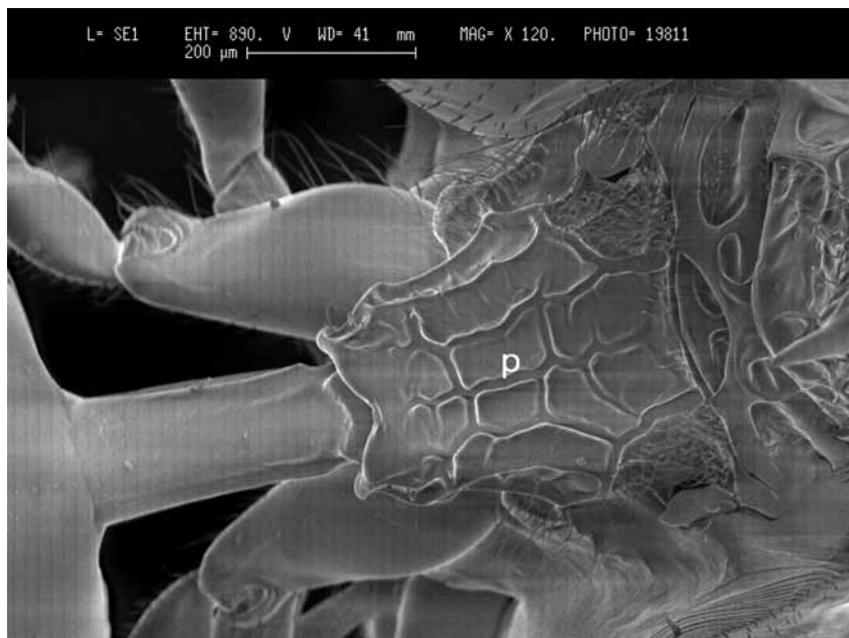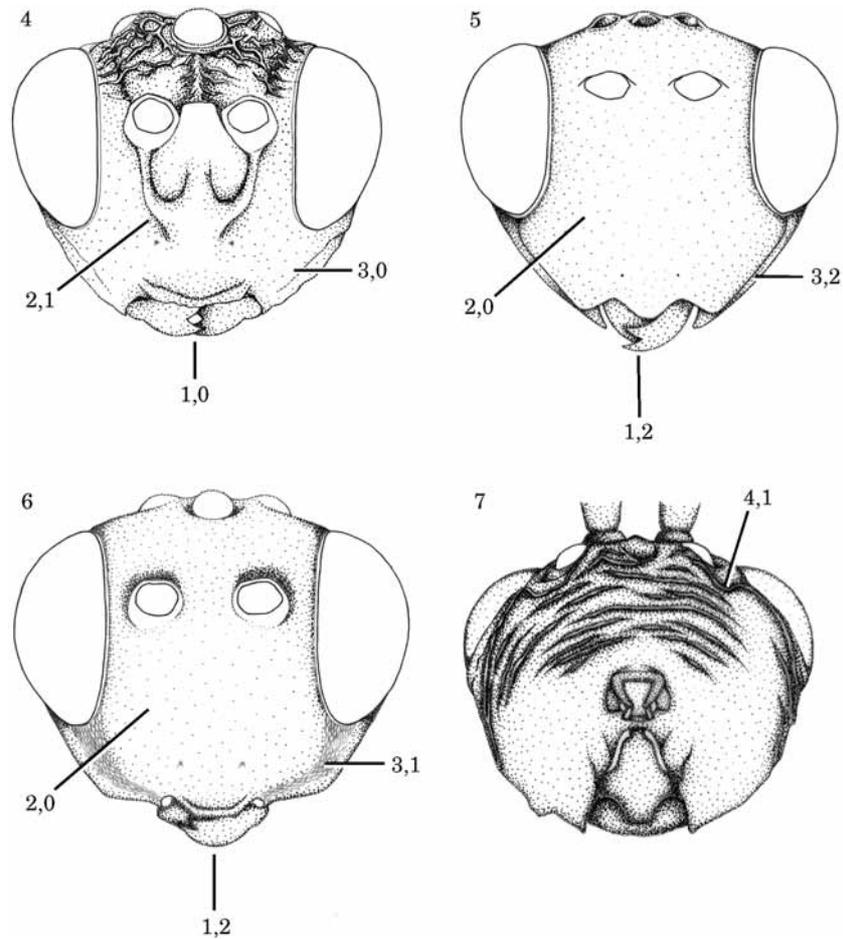

Figure 3. Propodeum (p) and petiole of *Acanthaegilips* sp.

Head. Almost glabrous, nitid. In frontal view of triangular shape (Fig. 5); mandibles small and broadly overlapping. In dorsal view, head distinctly broader than mesosoma. Gena not inflated. Occipital carina absent or present extending along the

Figures 4–7. Figs 4–6. Head in frontal view. 4. *Callaspidia*. 5. *Acanthaegilips*. 6. *Xyalaspis*. Fig. 7. Head in posterior view of *Callaspidia*.

lateral margins of the head but absent dorsally. Compound eye protruding laterally. Lower face (between antennal foramina and clypeus) distinctly convex, upper face almost flat. Malar space long, about 0.5 to 0.9 times the height of the compound eye; malar furrow narrow, conspicuous and deep, slightly curved, extending from median part of the base of the mandible to ventral margin of eye (Fig. 5). Clypeus distinctly projecting ventrally; projecting part with rounded, strongly convergent sides and ventral emargination. Epistomal furrow and clypeopleurostomal lines generaly distinct, clypeus delimited by a change of curvature in these specimens. Transfacial line between 2 and $3\times$ the width and between 1.17 and $1.50\times$ the height of a compound eye. Antennal foramina large, separated from each other by a distance between 0.7 and $2.0\times$ the distance between the foramen and the compound eye. Antennal rim very narrow. Ocelli subequal in size; OOL distance long, about $2.0–2.6\times$ the maximum diameter of the lateral ocellus; POL/OOL: 0.70–1.14; OOL/LOL: 2.75–4.

Antenna. Female. Antenna with 13 articles; length of F1 1.25–1.60 × the length of F2; flagellomeres cylindrical; sometimes the first ones increase slightly in width towards apex. Scape and pedicel nitid, covered with sparse pubescence, flagellomeres coriarious and covered with dense or sparse, short pubescence. Placodeal sensilla start on F1, F2 or F3. *Male.* Antenna with 14 articles; length of F1 1.1–1.5 × the length of F2; flagellomeres cylindrical, not expanded in width towards apex. F1 not modified. F2–F4 or F3–F5 slightly expanded dorsolaterally with a longitudinal ridge on the raised part. Scape and pedicel nitid, flagellomeres coriarious and densely covered with short pubescence. Placodeal sensilla start on F1.

Mesosoma. Pronotum (Fig. 1) broad medially, median width about 0.22–0.50 × the lateral width. Lateral pronotal carinae distinct, continuous with each other medially, forming a distinct anterior pronotal plate, the margin of which sometimes projects above the pronotal surface dorsomedially to form a thin, slightly raised transverse pronotal crest (Fig. 1). Anterior pronotal plate nude; submedian depressions small or very big. Remaining part of pronotum areolate, with sparse white pubescence. Mesoscutum strongly convex in lateral view (Fig. 1), 1.1–1.7 × wider than long in dorsal view. Mesoscutum areolate; median mesoscutal impression distinct, lenght variable; notauli distinctly impressed but short (Fig. 2); pubescence sparse, consisting of long and white hairs, sometimes with a conspicuous line of hairs on the anterolateral margins of the scutum. Mesopleuron smooth, glabrous and nude, provided with a median oblique, shallow impression from the anterior part of the ventral margin of the mesopleural triangle towards, but not reaching, the ventral margin of the mesopleuron (Fig. 1); the impression sometimes subdivided by carinae into large cells in the ventral part, sometimes without sculpture. Mesopleural triangle distinctly impressed, pubescent. Scutellum large, in dorsal view 1.0–1.4 × the length of the scutum, posteriorly forming a long, posterodorsally directed, narrow spine (Fig. 1). Scutellar foveae large and shallow, glabrous and usually nude, separated by a distinct median carina (Fig. 2); posteriorly with no distinct margin. Scutellum areolate-rugose, sparsely pubescent with long, white hairs. Scutellum distinctly projecting over metanotum posteriorly. Dorsellum narrowed medially, with two large depressions submedially. Propodeum narrowing posteriorly to form a tube, at the end of which the metasoma is inserted. Propodeum arealote (Fig. 3), densely pubescent anterolaterally and dorsolaterally, sparsely pubescent dorsally and posteriorly. Calyptra istinct.

Legs. Metatibia with a distinct longitudinal carina on the posterior surface and with relatively short spurs, the inner one somewhat larger than the width of the tibia.

Wings. Wing membrane hyaline, pubescent. Marginal cell open or closed in both sexes, 2.7–3.4 × longer than wide; vein 2r curved to not curved; vein R1 visible but short, sometimes reaching the wing margin; areolet absent, vein Rs + M absent; marginal pubescence of the wing starting from vein R1 and conspicuous down to the posterior margin of the wing.

Metasoma. Petiole about 2–3 times as long as wide (Fig. 3); the body of the petiole distinctly set off from the anterior articular bulb laterally and ventrally but not dorsally; body of petiole sometimes longitudinally carinate. Third abdominal tergum glabrous, posterolateral margin slightly concave (Fig. 21); dorsally almost one third the length of the fourth tergum, which covers the rest of the metasoma.

POSITION OF *PARAEGILIPS* AND *SEITNERIA*

In his monograph on the Cynipoidea, Weld (1952) listed two genera as possibly belonging to the Anacharitinae: *Paraegilips* and *Seitneria*. FR examined material of both genera.

Paraegilips was synonymized with *Paramblynotus* (Liopteridae: Mayrellinae) by Hedicke (in Hedicke & Kerrich, 1940) but Weld (1952) insisted that it was a valid genus and was not able to decide whether it belonged to the Liopteridae or the Figitidae: Anacharitinae. FR examined specimens of *P. reticulata* Kieffer, 1910 the type species of *Paraegilips*, including the holotype female. The species is a typical liopterid except that it is smaller than most species in the family. It shares all of the 12 synapomorphies of liopterids listed by Ronquist (1995b). Ronquist's (1995b) cladistic analysis of liopterid relationships supports Hedicke's original synonymization of *Paraegilips* with *Paramblynotus*.

Specimens of *Seitneria* have been reared repeatedly from anthomyid flies in *Larix* cones. On the basis of its biology, Weld (1952) considered the genus to belong to the Figitidae: Figitinae, possibly as a synonym of *Figites*, but he also listed the genus under Figitidae: Anacharitinae where it was originally placed by Tavares (1928). FR studied reared material of *Seitneria* from Austria and is confident that the genus does not belong to the Anacharitinae. *Seitneria* is most similar to *Melanips*, *Sarothrus* and *Amphitectus* in the Figitidae: Figitinae, in which subfamily it should be placed. *Seitneria* differs from *Figites* in many characters and should not be synonymized with this genus.

CHARACTERS SEPARATING ANACHARITINAE AND ASPICERATINAE

Unless otherwise noted, the Anacharitinae includes *Acanthaegilips* but not *Petricynips* in the following descriptions of character state distributions. References are to the papers in which the characters were mentioned in the description of the subfamilies or in the keys separating them. The distribution of character states is summarized in Table 1.

(1) Shape of head in anterior view (*new character*). All Anacharitinae have a triangular head (state 2; Fig. 5). The ventral half of the head capsule is expanded in size and narrowed ventrally, with the lower face being high and the malar space long. The mandibles are small and broadly overlapping. *Aegilips* differs in having the head more squarish, but the mandibles are small and broadly overlapping, the lower face is high, the malar space long, and the sides of the head straight and convergent rather than rounded, indicating that the squarish form in *Aegilips* is secondarily derived from a distinctly triangular head. Other examined figitids and cynipids, as well as macrocynipoids, have a broader, squarish head and larger mandibles that do not overlap as extensively (state 0; Fig. 4), and this is apparently the plesiomorphic state for the Figitidae. *Petricynips* and *Proanacharis* are intermediate both in the shape of the head and in the size of the mandibles (state 1), and may represent an intermediate stage in a transformation series from a squarish to a distinctly triangular head.

(2) Facial impression (*mew character*). The lower face is distinctly impressed beneath the antennae in all aspiceratines (state 1; Fig. 4). The impression is marked laterally

TABLE 1. Character matrix. Symbols used for polymorphisms/uncertainties: p = 0, 1 polymorphism; q = 2/3 uncertainty. Morphological analysis suggest that characters 1, 3, 6, 9, 12, 16, 17, and 19 should be treated as additive (ordered)

Taxon	Character				
	1	6	11	16	21
Hyp. antecesor	00000	1?000	00000	1100?	0?
Petricynips	1000?	11000	00???	1?000	??
Proanacharis	10001	00100	??100	2q001	0?
Anacharis	20101	00100	10100	22001	01
Aegilips	20101	00100	10100	23001	11
Xyalaspis	20101	00003	10100	23001	11
Acanthaegilips	20201	00012	101p0	23111	11
Solenofigites	2020?	00100	1?110	23101	11
Calofigites	20201	00100	10110	23101	11
Paraspicera	01010	41011	01111	10121	00
Aspicera	01010	41011	01111	10121	00
Prosaspicera	01010	41011	02111	10121	00
Balna	01010	41023	0?111	10122	00
Omalaspis	01010	41020	01111	10122	00
Callaspidia	01010	41020	02111	00122	00
Anacharoides	01010	41020	02111	00122	00
Myrtopsen	00100	11000	00100	01??0	0?
Phaenoglyphis	00100	10000	00000	11000	03
Melanips	00000	21000	00000	11100	00
Figites	00000	30000	00001	11101	02
Neralsia	00011	30001	00011	1p1p1	02

by distinct carinae. This character is unique to aspiceratines among the examined figitids, cynipids, and macrocynipoids, which lack a distinct facial impression (state 0; Figs 5, 6).

(3) Malar line or furrow (*new character*). All Anacharitinae except *Petricynips* and *Proanacharis* have a line or ± narrow field from the mandibular base toward the ventral margin of the compound eye slightly impressed and marked by coriarious sculpture (*Anacharis*, *Aegilips*, *Xyalaspis*; state 1, Fig. 6) or distinctly impressed as a narrow and polished furrow (*Solenofigites*, *Acanthaegilips*, *Calofigites*; state 2; Fig. 5). In *Solenofigites* and *Calofigites*, the furrow runs posterior to the compound eye and continues toward the occiput rather than ending at the compound eye as in other anacharitines; in *Acanthaegilips*, the furrow may run directly to the eye or divide close to the ventral margin of the eye into one branch running posterior to the eye and one to the ventral margin of the eye. A coriarious malar line or band is also present in *Phaenoglyphis* and *Myrtopsen*, and this is interpreted here as being homologous to state 1. The other examined figitids, cynipids and macrocynipoids lack a distinct malar line or band (state 0; Fig. 4), although the region between the eye and the mandible is often broadly coriarious, as in *Figites*, *Neralsia*, and *Melanips*. The character may be interpreted as a transformation series in which absence of the malar line is plesiomorphic, the coriarious line (state 1) is intermediate, and the distinct furrow (state 2) derived. The alternative interpretation that the intermediate state (1) is plesiomorphic and both terminal states represent apomorphic conditions is also possible.

(4) Shape of occipital carina and posterior part of head (Weld, 1952; Ritchie, 1993). Aspiceratines have the occipital carina and surrounding part of the cranium conspicuously raised and the entire posterior surface of the head flat or slightly concave with transverse ridges (state 1; Fig. 7). This character is unique to aspiceratines and *Neralsia*; other cynipoids do not have the entire occiput flat and concave with horizontal ridges, and the occipital carina is usually less pronounced (state 0).

(5) Modification of male F1 (Weld, 1952; Fergusson, 1986). Modification of the male F1 in cynipoids may involve presence of a ridge and/or changes in the shape of the flagellomere. The modifications improve the function of F1 as a smearing organ applying pheromones from a male antennal gland onto the female antenna during courtship (Ronquist & Nordlander, 1989; Isidoro *et al.*, 1996). The male F1 is modified (state 0) in basal cynipids, most figitids, and some macrocynipoids, and this appears to be the plesiomorphic condition in the Figitidae. All anacharitines have a simple F1 (state 1) but some of the more distal flagellomeres are sometimes modified instead, being swollen and/or bearing ridges as in *Acanthaegilips*. Charipinae tend to have F2 or more distal flagellomeres modified in addition to F1 and 'advanced' charipinae (*Alloxysta*, *Dilyta*, *Apocharips*) often have F1 unmodified. The simple F1 may be a synapomorphy of the Anacharitinae but the character is fairly homoplastic within the Figitidae.

(6) Anterior pronotal plate (Weld, 1952; Fergusson, 1995). All Anacharitinae except *Petricynips* have a completely defined, vertical anterior pronotal plate (state 0; Fig. 9). The plate is delimited by the lateral pronotal carinae, which are continuous from the ventral pronotal margin on one side across the dorsum to the ventral margin on the other side. It is rounded dorsally, not incised, and its margin projects above the narrow posterior part of the pronotum and forms a transverse, disc-like pronotal crest. Laterally, the sides of the plate are vertical. In the plesiomorphic state (state 1)—present in ibaliids, austrocynipids, and most figitids—the lateral pronotal carinae do not meet medially and do not run to the ventral pronotal margin leaving the anterior pronotal plate incompletely defined. This is the state in the examined Figitinae, Charipinae and in *Petricynips*. States 0 and 2–4 apparently represent separate lines of evolution from this ancestral state.

Primitively, the pronotum is not raised ventrally. In *Melanips*, however, the ventral pronotal margin is distinctly albeit only slightly raised (state 2; Fig. 8). In *Neralsia* and *Figites* the ventral margin is more prominently raised dorsally towards the ventral margin of the lateral pronotal carina, which projects anteroventrally (state 3; Fig. 10). Between these dorsal and ventral cuticular projections there is a deep longitudinal furrow. The Aspiceratinae have an anterior pronotal plate which is apparently derived from the state in *Neralsia* and *Figites* by closure of the gap between the ventral and dorsal projections (state 4; Fig. 11). In aspiceratines there is usually a marked discontinuity in the pronotal plate in the position of the furrow in *Neralsia* and *Figites*, and the furrow is usually evident both anterior and posterior to the lateral margin of the plate. The lateral margin of the aspiceratine plate projects forwards in the middle, forming a distinct V-shape, similar to the shape of the lateral pronotal carina and ventral projection in *Figites* and *Neralsia*. The lateral pronotal carinae are continuous medially in aspiceratines, as in anacharitines, but the dorsal margin is distinctly incised and not raised above the rest of the pronotum. Furthermore, the surface of the aspiceratine plate is oblique and not vertical as in anacharitines. We conclude that the aspiceratine plate (state 4) is derived from a
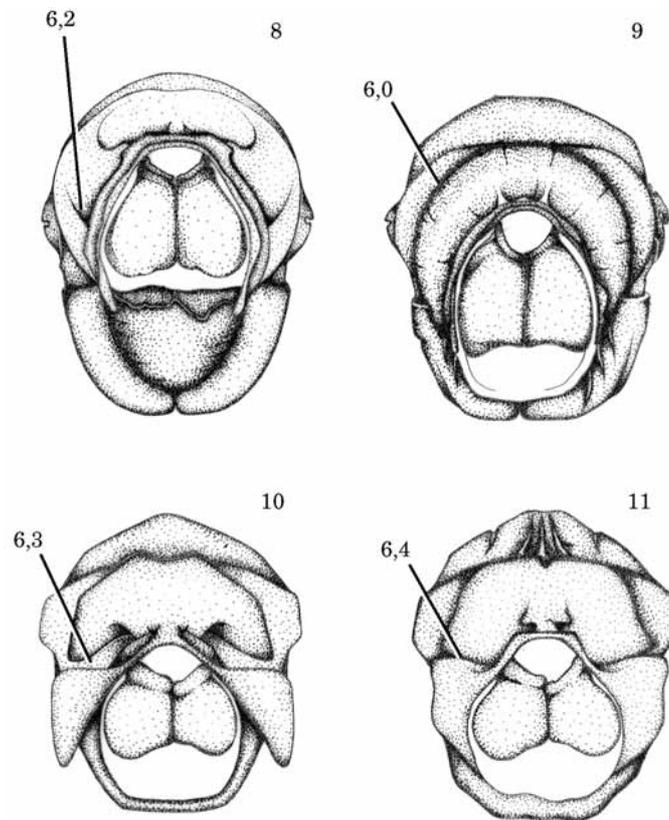
Figures 8–11. Pronotal plate. 8. *Melanips*. 9. *Xyalaspis*. 10. *Neralsia*. 11. *Callaspidia*.

state similar to that in *Neralsia* and *Figites* (state 3), which in turn evolved from a less modified condition as in *Melanips* (state 2), and that this and the anacharitine plate (state 0) are independently derived from the primitive condition (state 1).

(7) Sculpture of mesoscutum (Fergusson, 1986; Weld, 1952). The mesoscutum is shiny (state 0) in all anacharitines except *Petricynips* (apparently only partly shiny in *Proanacharis*) and dull in all aspiceratines (state 1). The polarity of this character is difficult to determine. Most figitids have a shiny mesoscutum, but some apparently archaic figitids, such as *Melanips*, some 'figitoid inquilines' (Figitinae), and *Hemicrisis* (Charipinae) have the mesoscutum dull. Cynipids have dull sculpture but more distant cynipoids (macrocynipoids) have the mesoscutum shiny except for the presence of coarse transverse sculpture. The dull mesoscutal sculpture in *Myrtopsen*, *Melanips*, *Hemicrisis* and *Petricynips* suggests that the shiny mesoscutum may be a synapomorphy of anacharitines excluding *Petricynips*. The status of the dull sculpture in aspiceratines is uncertain; it may be inferred to be a synapomorphy or a plesiomorphy depending on relationships within the Figitinae.

(8) Circumscutellar carina (*new character*). All anacharitines except *Xyalaspis* and *Acanthaegilips* have a circumscutellar carina, which is particularly distinct posteriorly, where the scutellum is often slightly produced (state 1; Fig. 15). The carina has apparently been lost in *Xyalaspis* and *Acanthaegilips* due to the secondary development
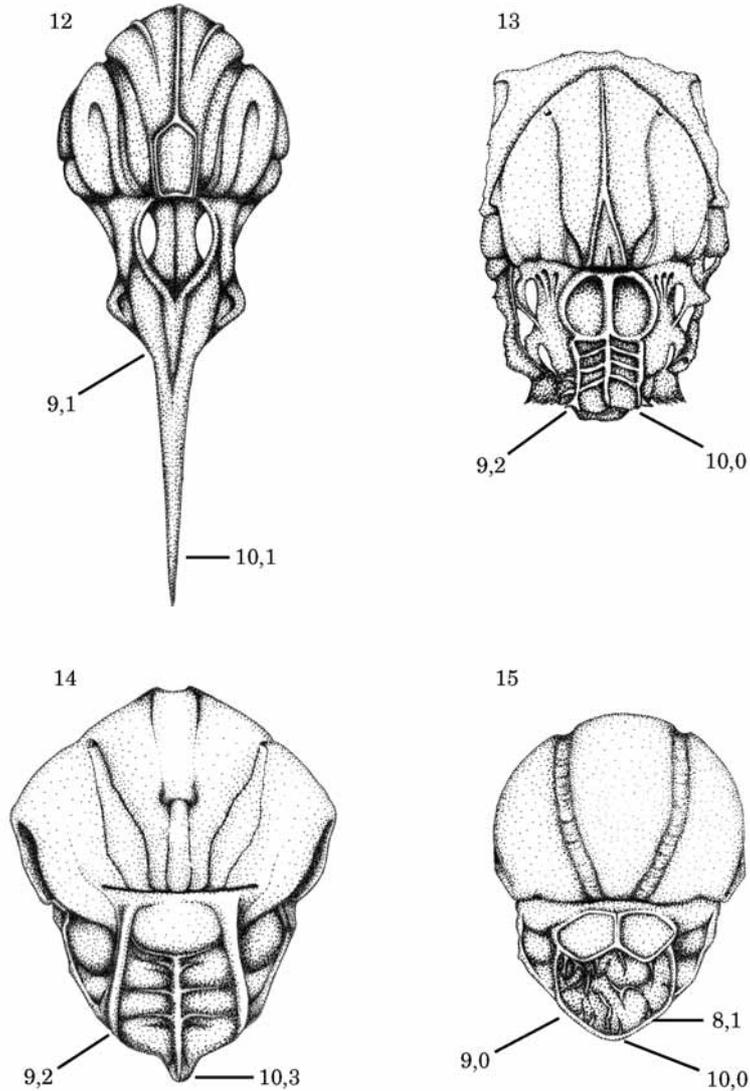
Figures 12–15. Scutellum. 12. *Prosaspicera*. 13 *Callaspidia*. 14. *Balna*. 15. *Anacharis*.

of scutellar spines (see below) but traces of the carina are still visible laterally in both genera. The distinct, evenly curved circumscutellar carina is unique to anacharitines. It is not present in *Petricynips*. Other cynipoids either lack a scutellar margin less distinctly marked, in the latter case either by a change in the curvature of the scutellum or by an irregular marginal carina.

(9) Longitudinal scutellar carinae (Fergusson, 1986, 1995). *Balna*, *Anacharoides*, *Callaspidia* and *Omalaspis* (Aspiceratinae) have three conspicuous, longitudinal carinae on the scutellum, the median of which is a continuation of the carina separating the scutellar foveae (state 2; Figs 13, 14). In other aspiceratines, the two lateral carinae are absent or replaced by several smaller, parallel carinae (state 1; Fig. 12).

In *Prosaspicera* the median logitudinal carina is sometimes not the continuation of the carina separating the scutellar foveae but the union of two lateral carinae from the posterior margins of the foveae. In *Acanthaegilips* (Fig. 2), the scutellar spine has a median and several lateral carinae reminiscent of the condition in aspiceratines such as *Aspicera*. Similar strong carinae are completely lacking in other examined figitids, cynipids and primitively in macrocynipoid families (state 0; Fig. 15). Thus, the median scutellar carina may be a synapomorphy of aspiceratines, but the presence in *Acanthaegilips* must be explained by parallel gain if *Acanthaegilips* is an anacharitine. The two strong lateral scutellar carinae (state 2) were probably derived within the Aspiceratinae, as indicated by the presence of multiple weak lateral carinae in *Neralsia*, similar to the weak lateral carinae characteristic of state 1.

(10) Scutellar spine (Ritchie, 1993). The scutellar spine is present in all aspiceratines except *Anacharoides*, *Callaspidia*, and *Omalaspis*. It is also present in *Neralsia* (Figitinae), *Xyalaspis*, and *Acanthaegilips* (Anacharitinae). The spine is pointed and directed posterodorsally in *Acanthaegilips* (state 2; Fig. 1), blunt and thick and directed posteriorly in *Xyalaspis*, and *Balna* (state 3; Fig. 14), and pointed, usually slender, and directed posteriorly in the other taxa (state 1; Fig. 12). The spine is absent (state 0; Figs 13, 15) in other examined figitids and cynipids and primitively in more basal cynipoids, suggesting that absence is the primitive state for figitids. Some eucoilines, e.g. *Odontoeucoela*, have a scutellar spine blunt this is obviously secondarily derived within the Eucoilinae. If *Neralsia* is closely related to aspiceratines, presence of the spine may be plesiomorphic for the Aspiceratinae, with reduction (represented by *Balna*) and then secondary loss in *Anacharoides*, *Callaspidia*, and *Omalaspis*. The differences in structure suggest that the spines in *Acanthaegilips* and *Xyalaspis* were independently derived from each other and from the spines of *Neralsia* and aspiceratines. Thus, scutellar spines appear to have evolved repeatedly in figitids.

(11) Lateral propodeal carina (Ritchie, 1993). Anacharitines except *Petricynips* have the lateral propodeal carina weak or absent throughout most of its length, although it may remain as a small process dorsally (state 1). The lateral propodeal carina is distinct (state 0) in all other examined figitids and cynipids, as well as primitively in more basal cynipoids.

(12) Longitudinal ridge or furrow on the posterior surface of the metatibia (Weld, 1952; Fergusson 1986, 1995; Ritchie, 1993). Some aspiceratines, such as *Callaspidia* species, have two conspicuous longitudinal carinae on the posterior surface of the metatibia (state 2). Other aspiceratines have a single carina, apparently corresponding to the inner one of the carinae in *Callaspidia*, and no furrow (state 1). The same carina is present, but much less pronounced, in all other figitids examined (state 0), and this is likely to be the plesiomorphic state for the Figitidae (Ronquist, 1995b; Liljeblad & Ronquist, in press) even though the carina is absent in cynipids and most macrocynipoids.

(13) Forewing areolet (Fergusson, 1986). The areolet is absent (state 1; Fig. 16) in anacharitines and aspiceratines. It is present, although partly defined by spectral or nebulous veins, (state 0; Fig. 17) in all Figitinae and Cynipidae examined except *Myrtopsen*. The areolet is absent in macrocynipoids (except in *Ibalia* and *Oberthuerella*; cf. Ronquist, 1995a,b). It appears likely that the areolet was primitively present in figitids and then lost several times independently.
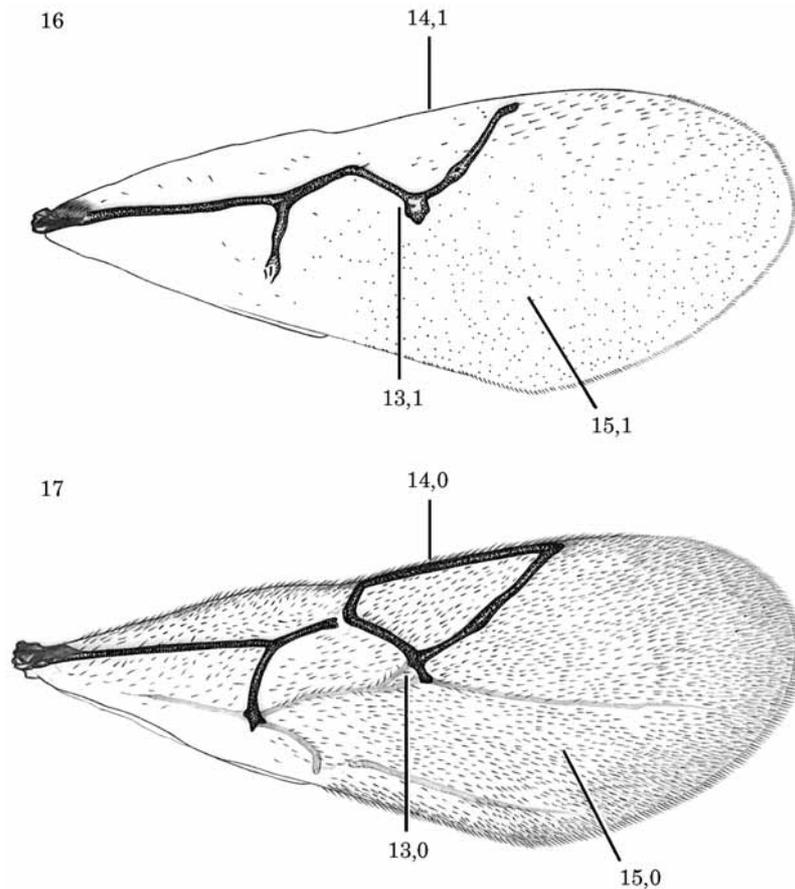
Figures 16, 17. Forewing. 16. *Callaspidia*. 17. *Melanips*.

(14) Marginal cell (Weld, 1952). The marginal cell is open (state 1; Fig. 16) on the front margin in Aspiceratinae, *Neralsia*, *Solenofigites*, and *Calofigites* (Anacharitinae); in *Acanthaegilips* it can be open or closed in both sexes. It is closed (state 0; Fig. 17) by a tubular or nebulous vein in the other examined figitids, as well as in macrocynipoids, and this is likely to be the plesiomorphic state for figitids even though cynipids have the cell open in the groundplan (Ronquist, 1995b). An open marginal cell could be a synapomorphy of Aspiceratinae+*Neralsia* and the open cell in a subset of the Anacharitinae is apparently independently derived.

(15) Pubescence of wing (Weld, 1952). Aspiceratinae, *Neralsia* and *Figites*, have the pubescence of the wing membrane and the marginal cilia considerably reduced in number and sometimes in size (state 1; Fig. 16). *Omalaspis* and *Prosaspicera* have the pubescence reduced in number but not in size, whereas *Callaspidia* and *Aspicera* have it reduced both in number and size. The reduction in wing pubescence in these taxa is usually associated with a reduction in the sclerotization of the wing veins (Ritchie, 1993). The other examined cynipoids all have normal wing pubescence (state 0; Fig. 17). However, reductions do occur secondarily in some groups that
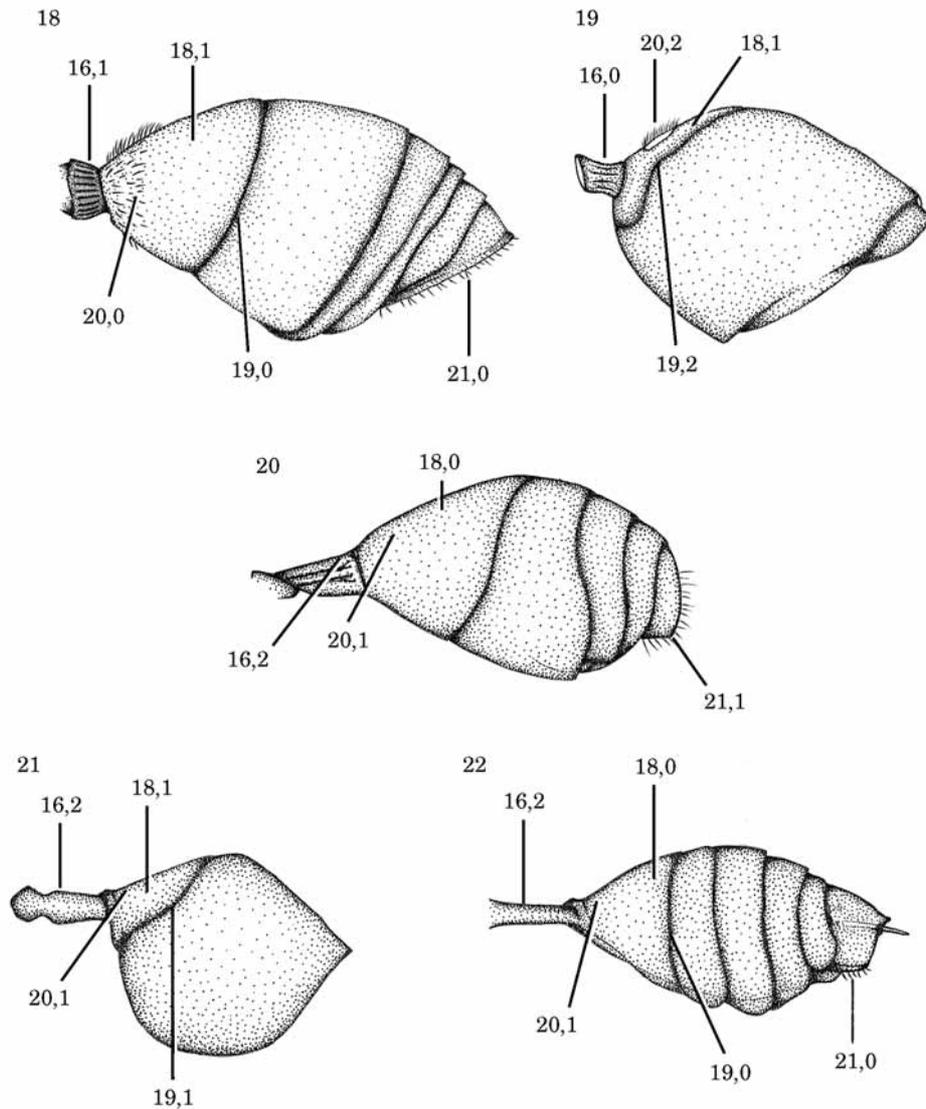
Figures 18–22. Metasoma in lateral view. 18. *Melanips*. 19. *Callaspidia*. 20. *Xyalaspis*. 21. *Acanthaegilips*. 22. *Anacharis*.

were not examined here, e.g. *Eucoila* (Figitidae: Eucoilinae) and some *Isocolus* (Cynipidae: Aylacini).

(16) Length of petiole (Weld, 1952; Fergusson, 1986, 1995; Ritchie, 1993). Anacharitines except *Petricynips*, have a long petiole (longer than broad). The petiole is also long in *Callaspidia* and *Anacharoides*, but short in all other figitids and cynipids examined (state 1; Fig. 18), as well as primitively in macrocynipoids.

In cynipoids the petiole usually consists of an anterior articular bulb which is connected through a short, narrow neck to a wide but rather short posterior annulus (Ronquist, 1995b). The annulus primitively consists of a tergal part, which projects

anteriorly to cover the neck, and a separate, smaller sternal part. When the petiole is elongated, as in *Callaspidia* and *Anacharoides*, the elongation is usually achieved through expansion of the annulus, and the anterior margin of the annulus still projects dorsally to cover the short neck at the anterior end of the petiole (state 0; Fig. 19). Dissections of *Anacharis*, *Calofigites* and *Xyalaspis* by FR suggest that the long petiole of anacharitines (state 2; Figs 20–22) is derived from the petiolar neck and not from the annulus, since a small tergal flange representing the annulus can be seen at the extreme posterior end of the long petiole of *Anacharis* when the third abdominal tergum is removed. This flange is apparently absent in other anacharitines. The neck derivation of the anacharitine petiole is further supported by the fact that the body of the petiole is not separated from the neck in *Anacharis*, and only weakly separated laterally and ventrally in other anacharitines. The annulus is almost always distinctly separated from the neck, particularly dorsally where it projects to cover the neck. In *Calofigites* and *Solenofigites* the petiole has secondarily become shorter, but the petiolar body is still composed of the neck and not the annulus, as shown by detailed similarity in petiolar structure between these taxa and genera such as *Acathaegilips* and *Aegilips*. Thus, we consider it likely that the usually long petiole of anacharitines (state 2) and the long petiole of some aspiceratines (state 0) were each independently derived from a primitive, short petiole (state 1).

(17) Annulus (*new character*). There seem to be two different transformation series in the evolution of the annulus in the Figitidae. Pritimively, the annulus is separated into distinct tergal and sternal parts (state 1; cf. Ronquist, 1995b); the sternal part is often small. Starting from this state, one transformation series ends with the tergal and sternal parts being somewhat enlarged and fused to each other forming a continuous ring as in aspiceratines (state 0). The other transformation series involves no enlargement but loss of the sternal part, as seen in *Anacharis* (state 2), and then loss of the tergal part as well (state 3; found in all anacharitines except *Anacharis*). In *Petricynips*, the tergal part of the annulus is considerably enlarged, but we have not been able to establish the condition of the sternal part and the connection between the sternal and tergal parts from the single known specimen. States 0 and 2–3 apparently represent separate lines of evolution from this ancestral state.

(18) Size of third abdominal tergum (Weld, 1952; Fergusson, 1986). We restrict this character to females, since there is some size variation between the sexes, the tergum usually being larger in males. The female third tergum is longer than the fourth (state 0; Figs 20, 22) in *Petricynips*, *Proanacharis*, *Anacharis*, *Xyalaspis*, and *Aegilips* but not in *Calofigites*, *Solenofigites*, and *Acanthaegilips*. The third tergum is shorter than the fourth (state 1; Figs 18, 19, 21) in most figitids, including all aspiceratines. *Melanips* is somewhat intermediate in that the third tergum is about as long as the fourth but we consider it here as belonging to state 1. The third tergum is distinctly larger than the fourth in *Phaenoglyphis* (Charipinae) and many 'figitoid inquilines' (it is fused to the fourth tergum in *Myrtopsen*, and we were not able to determine its relative size in this genus), as well as in the examined Cynipidae and primitively in more basal cynipoids. Therefore, it appears likely that the tergum was initially large in figitids, and then reduced in size several times independently. Hence, a small third tergum may be a synapomorphy of *Calofigites*, *Solenofigites*, and *Acanthaegilips* within the Anacharitinae, but a large tergum is unlikely to be a synapomorphy defining the Anacharitinae.

(19) Shape of the third abdominal tergum (Weld, 1952; Fergusson, 1986, 1995; Ritchie, 1993). All aspiceratines have a distinctly saddle-shaped third abdominal tergum (state 2; Fig. 19). The posterior margin of the same tergum is rounded in all cynipids, most figitids, and primitively in macrocynipoids (state 0; Figs 18, 22), and this must be the plesiomorphic condition for the Figitidae. In some *Neralsia* (Figitinae) and in *Acanthaegilips* (Anacharitinae) the posterolateral margin of the third abdominal tergum is slightly but distinctly concave (state 1; Fig. 21). A similar state occurs in some species of *Xyalaspis* (Anacharitinae). The conspicuously saddle-shaped third tergum is likely to be a synapomorphy of the Aspiceratinae. *Neralsia* and *Acanthaegilips* may represent intermediate stages in a transformation series leading to the aspiceratine state, or independent gains of a slightly saddle-shaped tergum.

(20) Pubescence of the third abdominal tergum (Fergusson, 1986). Most figitids have distinct, dense pubescence laterally on the third tergum (state 0; Fig. 18), and this state may be primitive for the family although it only occurs in some Cynipidae among other cynipoids. Anacharitines except *Petricynips* lack pubescence on the third abdominal tergum (state 1; Figs 20–22) as do aspiceratines. However, among the latter, there is a small median dorsal patch of hairs situated in a depression (state 2; Fig. 19) in *Balna*, *Callaspida*, *Omalaspis*, and *Anacharoides*. *Figites* and *Neralsia* (Figitinae) lack dense pubescence laterally, but dense hair patches occur in *Phaenoglyphis* (Charipinae) and *Melanips* (Figitinae). We conclude that absence of pubescence is a likely synapomorphy for Anacharitinae excluding *Petricynips*. Absence of pubescence is likely to be plesiomorphic for the Aspiceratinae, with secondary gain of a median patch in *Callaspidia*, *Omalaspis*, and *Anacharoides*.

(21) Shape of terebra and hypopygium (new character). Anacharitine females, except *Anacharis* and *Proanacharis*, have a ventral hypopygial margin which is straight (state 1; Fig. 20) and not curved upwards as usual in figitids and other cynipoids (state 0; Figs 18, 22). The modified hypopygium also lacks the well-defined, submedian, internal ridges that are present in other cynipoids. Dissections of female *Anacharis*, *Acanthaegilips*, and *Xyalaspis* by FR indicate that the deviant hypopygium is associated with modifications in the structure of the terebra. All cynipoids have the terebra curved upwards towards the apex except the anacharitines with modified hypopygium, which have the terebra curved downwards. The modified terebra and hypopygium is a unique synapomorphy for anacharitines excluding *Anacharis* and *Proanacharis* and is likely to be related to altered oviposition behaviour.

(22) Hosts (Weld, 1952). All aspiceratines are parasitoids of aphid-feeding syrphid and chamaemyiid larvae (state 0), whereas anacharitines are parasitoids of aphid-feeding lacewing larvae (Neuroptera: Chrysopidae and Hemerobiidae; state 1). Both states may be derived, but may also form intermediate stages in a more complex transformation series involving other figitid hosts. *Neralsia* and *Figites* attack various cyclorrhaphous Diptera, usually in dung or carrion (state 2), *Melanips* has the same hosts as aspiceratines and *Phaenoglyphis* is parasitic on Aphidiinae (Hymenoptera: Braconidae) larvae in aphids (state 3).

(23) Body shape. According to Weld (1952) and Ritchie (1993) the body is wedge-shaped when viewed from above, i.e. the head is distinctly broader than the mesosoma, in all Anacharitinae but not in other cynipoids. We measured this character in *Phaenoglyphis*, *Melanips*, *Neralsia*, *Figites*, *Callaspidia*, *Paraspicera*, *Prosaspicera*, *Omalaspis*, *Acanthaegilips*, *Xyalaspis* and *Anacharis*; in all of them, the width of the head
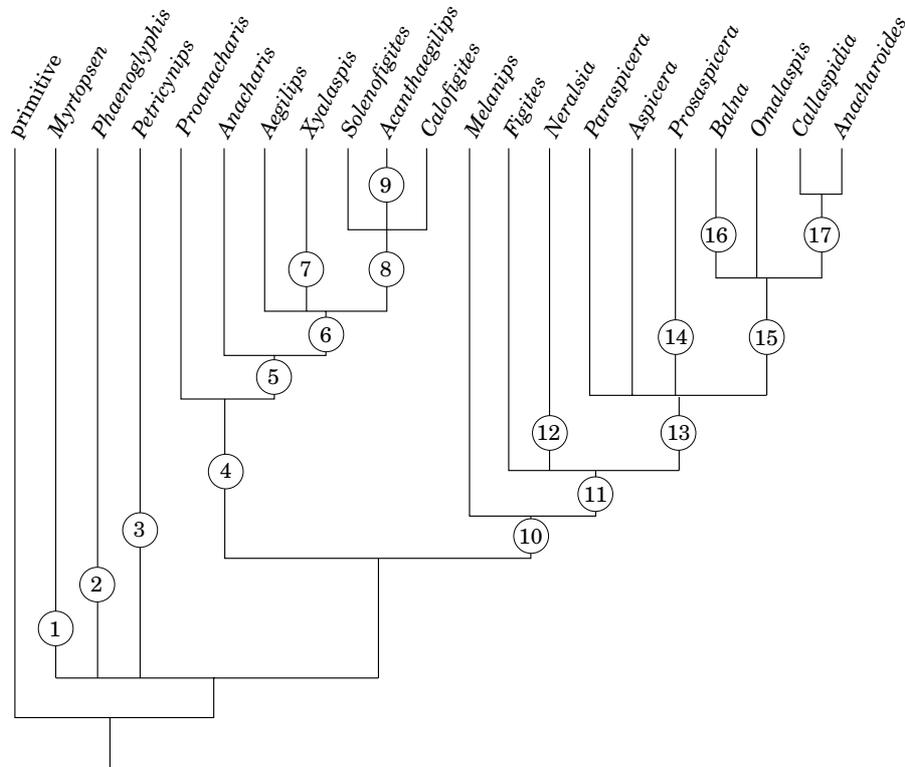
Figure 23. Phylogenetic hypothesis (assuming 'hard polytomies') for the Aspiceratinae and Anacharitinae and some related figitids (see Appendix).

was between 1.0 and 1.3 times the width of the metasoma, and the ratio was not consistently larger in anacharitines. Thus, this character cannot be used to separate anacharitines from other figitids.

(24) Claws with basal seta (Fergusson, 1995). Fergusson used this character to define the Anacharitinae. We found a basal seta in anacharitines, but similar setae were also present in other Figitinae. Detailed studies with scanning electron microscopy are needed to demonstrate that the structure in the Anacharitinae is unique in the Figitidae.

PHYLOGENETIC CONCLUSIONS AND DISCUSSION

We summarize our findings in a phylogenetic hypothesis for the Aspiceratinae, Anacharitinae, and some other figitid groups (Fig. 23). This is also the strict consensus tree of the 477 most parsimonious trees (length 57 with polymorphisms treated as uncertainty, consistency index 0.67, retention index 0.90) resulting when the character matrix (Table 1) is run through the branch-and-bound algorithm of PAUP with characters 1, 3, 6, 9, 12, 16, 17, and 19 ordered, as suggested above, and with the hypothetical ancestor included as an outgroup to root the tree.

The Anacharitinae excluding *Petricynips* (Anacharitinae *sensu stricto*) form a strongly supported monophyletic group on the basis of the unique pronotal plate (char. 6), the circumscutellar carina (char. 8), the neck-derived elongation of the petiole (16), and the reduction of the lateral propodeal carina (char. 11, unknown in *Proanacharis*). Possible additional support for the monophyly of this group is provided by the biology (parasitism of Neuroptera larvae; char. 22), the absence of pubescence on the third abdominal tergum (char. 20), the unmodified male F1 (char. 5), and the absence of the areolet (char. 13).

Petricynips cannot be confidently placed in the Anacharitinae. Unfortunately, the genus is only known from a single, defect female specimen, *P. micuisis* Belizin, 1961, lacking the wings and parts of the legs, and the biology is unknown. The specimen shares many features, presumably plesiomorphies, with *Melanips* in the subfamily Figitinae. The only apparent apomorphies suggesting that *Petricynips* might be placed in the Anacharitinae are the somewhat triangular shape of the head in frontal view and the rather small mandibles (char. 1). Until the relationships of *Petricynips* can be clarified, we prefer to retain the genus in the Anacharitinae.

Within the Anacharitinae *sensu stricto*, all genera except *Proanacharis* appear to form a monophyletic group based on the distinctly triangular head (char. 1). This grouping is also supported by the entirely shining mesoscutum (only partly shining in *Proanacharis*) and possibly also by the presence of a coriarious malar line (3). Of the remaining genera, all but *Anacharis* have a modified terebra and hypopygium (21), lack the tergal flange of the annulus (17) and have a secondary separation of the neck-derived elongation of the petiole from the articular bulb. This anacharitine core contains a well-defined monophyletic group of genera, viz., *Acanthaegilips*, *Solenofigites*, and *Calofigites*, having a distinct malar furrow (and not a coriarious line; char. 3), and a third tergum which is reduced in size (18). These genera are entirely restricted to South America (Argentina, Chile, Brazil, Peru), whereas the other anacharitine genera have a world-wide distribution (*Proanacharis* and *Petricynips* restricted to the Palaearctic).

The monophyly of the Aspiceratinae is supported by the facial impression (char. 2), the unique pronotal plate created by closure of the gap between the raised ventral pronotal margin and the lateral pronotal carina across the submarginal pronotal furrow (6), and the distinctly saddle-shaped third tergum (19), among other characters. A number of characters seem to support the monophyly of a somewhat larger group, including part or all of *Neralsia*: fusion of the tergal and sternal parts of the annulus (17), and the head concave posteriorly with pronounced occipital carina and horizontal ridges on the occiput (4). However, other characters not considered here suggest a close relationship between *Figites* and *Neralsia* (and some other figitines) to the exclusion of aspiceratines. These characters include long setae on the compound eyes, striate third tergum, and moniliform female antennae.

Melanips may belong to the same lineage as *Figites*, *Neralsia* and the Aspiceratinae. This grouping is supported by the projecting ventral pronotal margin (char. 6) but also by the association with dipteran hosts (char. 22) and the reduction in the size of the third tergum (char. 18). This grouping probably includes also the remaining diptera-parasitic figitids, i.e. the Eucoilinae, the Pycnostigmatinae (biology unknown, but obviously closely related to the Eucoilinae) and all Figitinae excluding the gall-associated 'figitoid inquilines'.

Within the Aspiceratinae, it seems likely that *Balna*, *Omalaspis*, *Callaspidia*, and *Anacharoides* form a monophyletic group based on the presence of a median patch

of pubescence on the third tergum (char. 20), distinct lateral scutellar carina (char. 9), and loss or reduction (*Balna*) of the scutellar spine (char. 10). Furthermore, *Callaspidia* and *Anacharoides* are united by having an elongated petiole (char. 16) and a marginal cell which is open basally as well as anteriorly.

Although *Acanthaegilips* shares some characters with aspiceratines, it is obvious that these are superficial similarities, and that the genus truly belongs to the Anacharitinae. In addition, it appears likely that *Acanthaegilips* is deeply nested within the Anacharitinae (Fig. 23). Thus, *Acanthaegilips* cannot be separated from other anacharitines and placed in a monotypic family as suggested by Kovalev (1996) without far-reaching consequences for the classification of figitids in general, and anacharitines in particular.

It is beyond the scope of the current paper to discuss other aspects of Kovalev's (1994, 1995, 1996) extensive revision of the higher-level classification of figitids. However, we suspect that recognition of small families such as the Thrasoridae and Emarginidae will eventually require the creation of more 'figitoid' families than most hymenopterists would like to see. An important step towards a more stable classification of the figitid complex would be an explicit and comprehensive cladistic analysis of higher-level relationships within this important group of parasitic cynipoids.

REFERENCES

Ashmead WH. 1897. Description of some new genera in the family Cynipidae. *Psyche* **8:** 67–69.
Ashmead WH. 1903. Classification of the gall wasp and the parasitic cynipoids, or the superfamily Cynipoidea, I. *Psyche* **10:** 7–13.
Díaz NB. 1979a. Himenópteros neotropicales parasitoides de Neurópteros I cinipoideos (Hymenoptera). *Revista de la Sociedad Entomológica Argentina* **38** (1–4): 21–28.
Díaz NB. 1979b. Sobre algunas especies del género *Prosaspicera* Kieffer, 1907 (Hymenoptera, Cynipoidea). *Revista de la Sociedad Entomológica Argentina* **38** (1–4): 97–104.
Díaz NB. 1983. El género *Acanthaegilips* Ashmead, 1897 en la República Argentina (Hymenoptera, Cynipoidea). *Neotropica* **29** (81): 45–49.
Evenhuis HH, Barbotin F. 1977. Studies on Cynipidae Alloxystinae 6. *Phaenoglyphis villosa* (Hartig) and *Alloxysta arcuata* (Kieffer). *Entomologische Berichten* **37:** 184–190.

Fergusson NDM. 1986. British species of the parasitic cynipid wasp genus *Aegilips* (Hymenoptera: Cynipoidea, Anacharitinae). *Journal of Natural History* **19** (4): 811–818.

Fergusson NDM. 1995. The Cynipoid families: Introduction and Figitidae. In: Hanson PE, Gauld ID, eds. *The Hymenoptera of Costa Rica*. Oxford: Oxford University Press, 147–165.

Gauld I, Bolton B. 1988. *The Hymenoptera*. Oxford: Oxford University Press.

Hedicke H, Kierrich GJ. 1940. A revision of the family Liopteridae (Hymenoptera, Cynipoidea). *Transactions of the Royal Entomological Society of London* **90:** 177–225.

Isidoro N, Bin F, Colazza S, Vinson SB. 1996. Morphology of antennal gustatory sensilla and glands in some parasitoid Hymenoptera with hypothesis on their role in sex and host recognition. *Journal of Hymenoptera Research* **5:** 206–239.

Kovalev OV. 1994. Paleontological history, phylogeny and the system of Brachycleistrogastromorphs and Cynipomorphs (Hymenoptera, Brachycleistogastromorphs infraorder n., Cynipomorphs infraorder n.) with description of new fossil and recent families, subfamilies and genera *Entomologicheskoe Obozrenie* **73:** 385–426. [In Russian].

Kovalev OV. 1995. Paleontological history, phylogeny and the system of Brachycleistrogastromorpha, Infraorder N., and Cynipomorpha Infraorder N. (Hymenoptera) with descriptions of new fossil and recent families, subfamilies, and genera. *Entomological Review* **74:** 105–147.

Kovalev OV. 1996. A new family, new subfamily and genus and remplacement names in cyinipoids (Hymenoptera, Cynipoidea). *Entomologicheskoe Obozrenie* **75:** 408–416.

Liljeblad J, Ronquist F. 1998. A phylogenetic analysis of higher-level gall wasp relationships (Hymenoptera: Cynipidae). *Systematic Entomology* (in press).

Nieves-Aldrey JL, Fontal-Cazalla F. 1997. Inventario de himenópteros parasitoides (Cynipoidea y Chalcidoidea, Hymenoptera, Insecta) de la isla de Coiba (Panamá). In: Flora y fauna del parque Nacional de Coiba (Panamá). Madrid: AECI, 375–397.

Nordlander G. 1982. Identities and relationships of the previously confused genera *Odeonteucoila*, *Coneucoela* and *Trichoplasta* (Hymenoptera, Cynipoidea: Eucolidae). *Entomologica Scandinavica* **13:** 269–292.

Quinlan J. 1979. A revisionary classification of the Cynipoidea (Hymenoptera) of the Ethiopian zoogeographical region. Bulletin of the British Museum (Natural History), *Entomology Series* **39:** 85–133.

Rasnitsyn AP. 1980. Origin and evolution of Hymenoptera. *Trudi Paleontologicheskogo Instituta Akademiya Nauk SSSR* **123:** 1–196.

Rasnitsyn AP. 1988. An outline of evolution of the hymenopterous insects (order Vespida). *Oriental Insects* **22: 115–145.**

Richards OW. 1977. *Hymenoptera. Introuction and key to families. 2nd ed.* Handbooks for the Identification of British Insects. No. 6.

Riek EF. 1971. A new subfamily of Cynipidoid wasps (Hymenoptera: Cynipoidea) from Australia. In: *Entomological Essays to Commemorate the Retirement of Professor K. Yasumatsu.* Hokuryukan Publ. Co. Tokyo, 107–112.

Ritchie AJ. 1993. Cynipoidea. In: Goulet H, Huber JT, eds. *Hymenoptera of the world: An identification guide to families.* Ottawa: Agriculture Canada, 521–536.

Ronquist F. 1995a. Phylogeny and early evolution of the Cynipoidea (Hymenoptra). *Systemattic Entomology* **20:** 309–335.

Ronquist F. 1995b. Phylogeny and classification of the Liopteridae, an archaic group of cynipoid wasps (Hymenoptera). *Entomologica Scandinavica Supplements* **46:** 1–74.

Ronquist F, Nordlander G. 1989. Skeletal morphology of an archaic cynipoid, *Ibalia rufipes* (Hymenoptera: Ibaliidae). *Entomologica Scandinavica Supplements* **33:** 1–40.

Swofford DL. 1993. *PAUP. Phylogenetic analysis using parsimony, Version 3.1.1.* Smithsonian Institution, Washington.

Tavares J da S. 1928. Descripção de una espècie e de um género novo. *Broteria serie zoologica* **25** (1): 5–10.

Weld LH. 1952. Notes on certain genera of Parasitic Cynipidae proposed by Ashmead with descriptions of genotypes. *Proceedings of the United States National Museum* **59:** 433–451.

Weld LH. 1952. *Cynipoidea (Hym.)* 1905–1950. Privately printed, Ann Arbor.

APPENDIX

List of character changes mapped on the tree using the 'hard polytomies' option in MacClade (see Fig. 23).

1: *3* 0→1, *13* 0→1, *16* 1→0
2: *3* 0→1
3: *1* 0→1
4: *1* 0→1, *5* 0→1, *6* 1→0, *8* 0→1, *13* 0→1, *16* 1→2, *17* 1→2
5: *1* 1→2, *3* 0→1
6: *17* 2→3, *21* 0 →1
7: *8* 0→1, *10* 0→3
8: *3* 1→2, *14* 0→1, *18* 0→14
9: *8* 1→0, *9* 0→1, *10* 0→2, *19* 0→1
10: *6* 1→2, *18* 0→1
11: *6* 2→3, *15* 0→1
12: *5* 0→1
13: *2* 0→1, *6* 3→4, *9* 0→1, *12* 0→1, *13* 0→1, *17* 1→0, *19* 0→2
14: *12* 1→2
15: *9* 1→2, *10* 1→0, *20* 1→2
16: *10* 0→3
17: *12* 1→2, *16* 1→0