Superfamily Membracoidea (Homoptera: Auchenorrhyncha).
II. Cladistic analysis and conclusions

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Abstract. Homologies among traditional morphological characters in the Membracoidea (*sensu lato*) are reassessed and the phylogenetic relationships among higher membracoid taxa are explored, incorporating new morphological evidence from nymphs and adults. Weighted and unweighted parsimony analyses of a matrix of sixty-three characters and thirty-nine OTUs representing the families Aetalionidae, Cicadellidae, Melizoderidae and Membracidae, and an outgroup (superfamily Cercopoidea) yielded various topologies that were largely congruent but presented alternative hypotheses of relationships among the Membracidae. These analyses indicate that the superfamily consists of the following clades: Cicadellidae + (Melizoderidae + (Aetalionidae + Membracidae)). The family Membracidae, traditionally characterized by the presence of a posterior pronotal process, apparently gave rise to *Nicomia* Stål and other genera that lack this process.

Introduction

The phylogenetic relationships among the Membracoidea have been the subject of much discussion (Emel'yanov, 1987; Evans, 1946a, b, 1947, 1948, 1958, 1975b, 1977; Hamilton, 1983; Haupt, 1929; Ross, 1957; Wagner, 1951), but have mainly focused on the family Cicadellidae. Few workers have attempted to estimate phylogenetic relationships among higher taxa of non-cicadellid Membracoidea (Haupt, 1929; Strümpel, 1972), and until now, no quantitative cladistic analyses of the membracoid family-group taxa have been published.

Many aspects of Evans' (1946b, 1947, 1948, 1977) classification of the higher taxa of Membracoidea (as Jassoidea or Cicadelloidea), in which the Cicadellidae and the remaining Membracoidea are treated as sister groups, remain widely accepted (Nielson, 1985; Oman *et al.*, 1990). More recently, Hamilton (1983) suggested that the family Cicadellidae is paraphyletic, having given rise to the Membracidae and Aetalionidae. Both Evans and Hamilton underestimated the extent of morphological variation among the non-cicadellid Membracoidea.

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Our observations on the non-cicadellid Membracoidea (Deitz, 1975; Dietrich, 1989; and unpublished) complement the observations of other authors to form a substantial body of phylogenetically relevant information. Here we present the results of our endeavours to determine the relationships among the non-cicadellid family-groups of Membracoidea.

Phylogenetic context

Outgroups

Earlier attempts to estimate the phylogeny of the Auchenorrhyncha (reviewed by Kramer, 1950, and Evans, 1963) produced no consensus. More recently, Hamilton (1981, 1983) using cladistic criteria, treated either the superfamily Cercopoidea or the extinct family Jascopidae Hamilton, 1971, as the sister group of the Membracoidea.

Hamilton's (1983) assertion that the Jascopidae represent a sister group of the Membracoidea requires that (1) the Jascopidae share at least one synapomorphy with Membracoidea, and (2) the taxa included in Jascopidae share at least one synapomorphy not present in Membracoidea. To date, only the first criterion is clearly documented (Hamilton, 1971a, 1990, 1992). The jascopid species *Jascopus notabilis* Hamilton and *Homopterulum*

jelli Hamilton share putative synapomorphies with Cicadellidae: front and middle tibiae with setal rows, tarsal pectens narrow, hind tarsomere I with double row of plantar setae. These taxa also apparently differ from most Cicadellidae in having conical hind coxae and in lacking macrosetal rows on the hind tibiae, but these features are apparent plesiomorphies shared with Cercopoidea and other Auchenorrhyncha. Hamilton (1971a, 1992) listed no unique apomorphies shared by *Jascopus* Hamilton and *Homopterulum* Handlirsch, and evidence uniting these genera with other taxa placed in Jascopidae is weak. With the exception of *Paracarsonus aphrodoides* Hamilton, other taxa placed in the Jascopidae (Hamilton, 1990, 1992) either have the hind legs poorly preserved or are represented by unassociated wings. Forms with preserved forewings have veins M and Cu fused for a short distance preapically, a putative synapomorphy; but the only species for which both forewings and hind legs are sufficiently preserved (*P.aphrodoides*) differs from *Jascopus* and *Homopterulum* in lacking macrosetae on the pro- and mesothoracic tibiae and plantar setae on hind tarsomere I. Thus, although taxa placed in the Jascopidae differ somewhat from modern Cicadellidae and Cercopidae, evidence supporting the monophyly of the Jascopidae and their status as a sister group of Membracoidea is tenuous (see Shcherbakov, 1992, for further discussion of the status of Jascopidae).

Hamilton's (1981) treatment of the Cercopoidea and Membracoidea as sister groups seems reasonable. Apparent synapomorphies on the head (absence of a medial ocellus), thorax (pronotum extending to scutellum (except Cicadellidae)), wing (venation reduced) and abdomen (male with subgenital plate) unite these two superfamilies and distinguish them from the Cicadoidea and Fulgoroidea.

Unique apomorphies shared by most known Cercopoidea include: exposed areas of the integument (including wings) pubescent, forewing with subcostal ridge, meron of mesothoracic coxa large and acutely produced posterad, nymphs produce 'spittle'. Therefore the Cercopoidea apparently represent a monophyletic sister group of the Membracoidea and are an appropriate outgroup for our phylogenetic analysis.

Monophyly of the Membracoidea

The following synapomorphies unite the Membracoidea: tentorium incomplete (Evans, 1963); metathoracic coxae enlarged, transverse (Hamilton, 1992); and (with few exceptions) metathoracic tibia with rows of cucullate setae.

Further support for the monophyly of the Membracoidea is found in the previously unstudied internal structure of the mesonotum. In the Membracoidea, the scutellar suture is associated with a pair of rod-shaped lateral apodemes, the ends of which are attached to points along the suture (Figs 5–9, sa). The points of attachment of the scutellar apodemes are often indicated externally by the presence of pits. In those Membracidae having the scutellum com-

pletely concealed by the pronotum, these pits are enlarged, shifted toward each other, and separated by an oblique external ridge (Fig. 10), and thus resemble those of Cicadoidea. The pits of cicadas, however, are not connected by an apodeme and are therefore not homologous. The presence of scutellar apodemes and their associated external pits is a feature unique to the Membracoidea.

In the Cercopoidea, the scutellar suture is associated with an internal ridge and a pair of elongate lateral fenestrae that are probably points of muscle attachment (Fig. 4, f). The lateral fenestrae of the cercopoid scutellar suture occupy roughly the same position as the scutellar apodemes of Membracoidea and may be similar to the evolutionary precursors of the membracoid scutellar apodemes.

Cladistics

Characters

We used thirty-seven binary and twenty-six multistate characters in our phylogenetic analyses. Morphological terminology, unless otherwise noted, follows Kramer (1950) for thoracic sclerites, Deitz (1975) for wing venation and other gross adult features, Dietrich (1989) for features of the integumental fine-structure, and Quisenberry *et al.* (1978) and Kitching & Filshie (1974) for features of the nymphs. We arranged multistate characters in hypothesized transformation series, but treated some as unordered for some analyses (see below).

Head

1. Dorsal projections: 0, absent; 1, small, narrow (Fig. 1); 2, short, broad (Deitz, 1975: fig. 40A); 3, large, conical (Fig. 2).

2. Beak apex: 0, reaching or surpassing metathoracic coxae; 3, not reaching metathoracic coxae.

Pronotum

3. Posterior margin: 0, extending to or beyond scutellar suture; 3, not reaching scutellar suture. The scutum is entirely concealed by the pronotum in the Cercopoidea and most non-cicadellid Membracoidea. In the Cicadellidae, the posterior portion of the scutum and the scutellar suture are exposed.

4. Posterior process: 0, absent; 2, extenting over, but not concealing scutellum; 3, concealing scutellum.

5. Posterolateral projections: 0, absent; 3, present.

6. Suprahumeral horns: 0, absent; 2, polymorphic; 3, well developed.

7. Ventral postocular carina: 0, absent; 3, present (Fig. 3, vpc).

8. Dorsal postocular carina: 0, absent; 2, polymorphic; 3, present (Fig. 3, dpc).

9. Distance from eye to wing base: 0, less than half eye width; 1, slightly more than half eye width; 2, subequal to eye width; 3, much greater than eye width.

Mesothoracic sclerites

10. Parapsidal clefts: 0, absent; 3, present (Figs 4, 5, 9, pc). The mesoscutum of Membracoidea bears two pairs of sutures, the parapsidal and parascutal sutures (Fig. 5, pps,
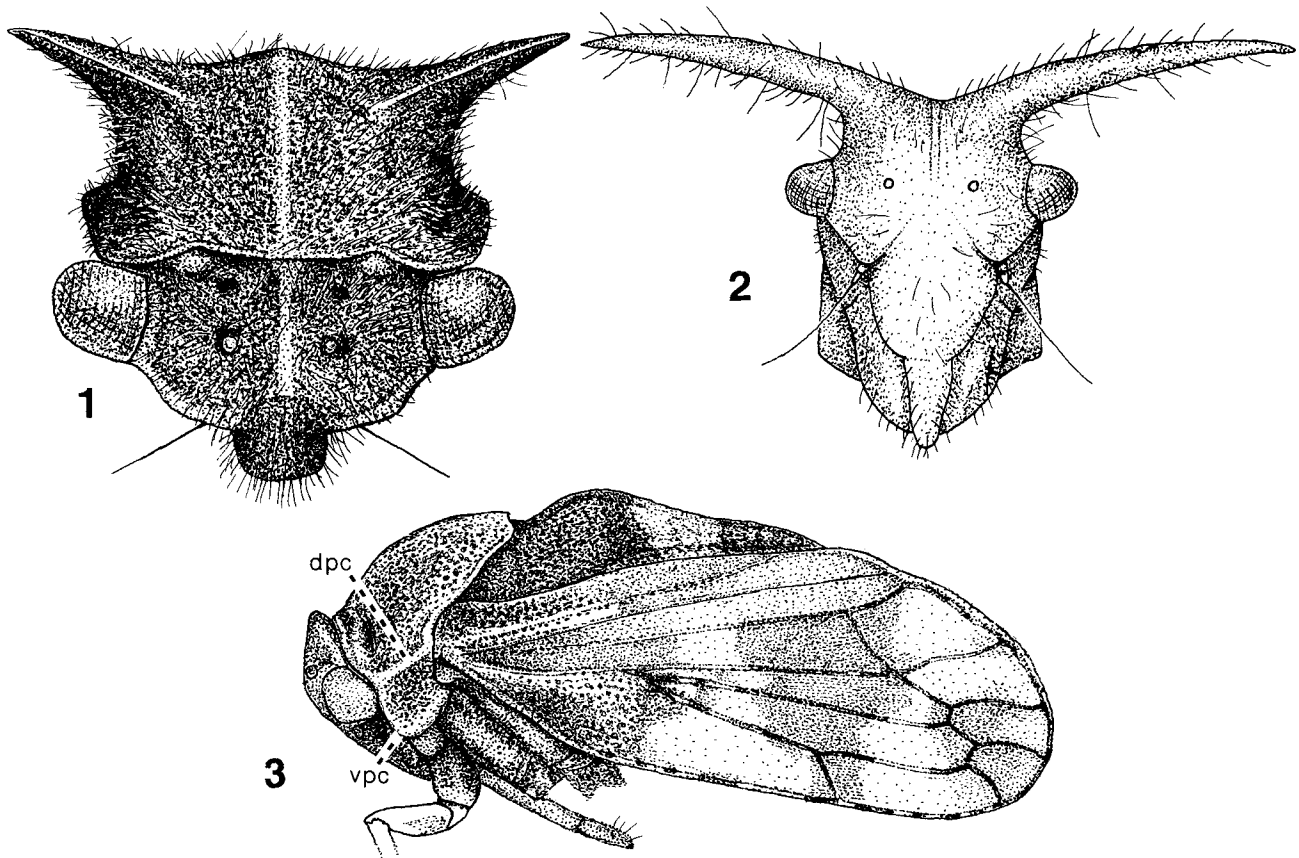
Figs 1–3. 1, *Tolania opponens* Walker, head and pronotum, anterior view; 2, *Mina aliena* Walker, head, anterior view; 3, *Tropidaspis* sp., habitus, lateral view. dpc, dorsal postocular keel; vpc, ventral postocular keel.

pss; Hamilton, 1983). In the Cicadellidae (Fig. 5) and the genera *Melizoderes* Blanchard (Fig. 9) and *Llanquihuea* Linnavuori & DeLong, the parapsidal sutures form membranous clefts. Such clefts are also present in the Cercopoidea (Fig. 4, pc), which have the parascutal sutures weak or absent. The parapsidal sutures of Membracidae (Fig. 10) and Aetalionidae (Figs 6, 7) are indistinct and do not form clefts.

11. Scutellum, posterior margin: 0, acuminate (Figs 4–9); 1, emarginate; 2, acuminate with posteromedial depression; 3, rounded. Not easily comparable to those having an exposed scutellum, taxa having the scutellum reduced and completely concealed by the pronotum were coded as indefinite.

12. Scutellar keel: 0, absent; 1, weak, not elongate (Fig. 15); 2, elongate, not projecting dorsally (Figs 3, 8, sk); 3, elongate and strongly produced dorsally.

13. Mesepisternum: 0, not keeled; 3, strongly keeled (Fig. 11, k). This feature is apparently unique to the Ulopinae and one fossil membracoid.

14. Anepisternum and katepisternum: 0, separated by suture (Figs 11, 12); 3, not separated by suture (Figs 13–16). The mesepisternum of Cicadoidea, Cercopoidea and Cicadellidae is divided into two sclerites, the anepisternum and katepisternum (Figs 11, 12) (Kramer, 1950;

Ross, 1957). In the non-cicadellid Membracoidea (Fig. 13, es; Figs 14–16), the mesepisternum is a single sclerite.

15. Dorsal mesepisternal hook: 0, absent; 3, present (Figs 14–16). In the Membracidae and Biturritiinae, the apex of the anterodorsal arm of the mesepisternum bears a digitate process (Figs 14–16, eh) called the episternal hook (McAtee & Malloch, 1928). Although this process appears to arise on the mesepimeron in some genera (*Tropidaspis* Stål, *Llanquihuea*), we found, upon examination of KOH-cleared specimens, that the process is invariably mesepisternal in origin. The mesepisternal processes of the cicadellid subfamilies Ulopinae (Fig. 11, vsep, k) and Ledrinae (Fig. 12) seem too dissimilar in structure and position to be considered homologous.

Forewing

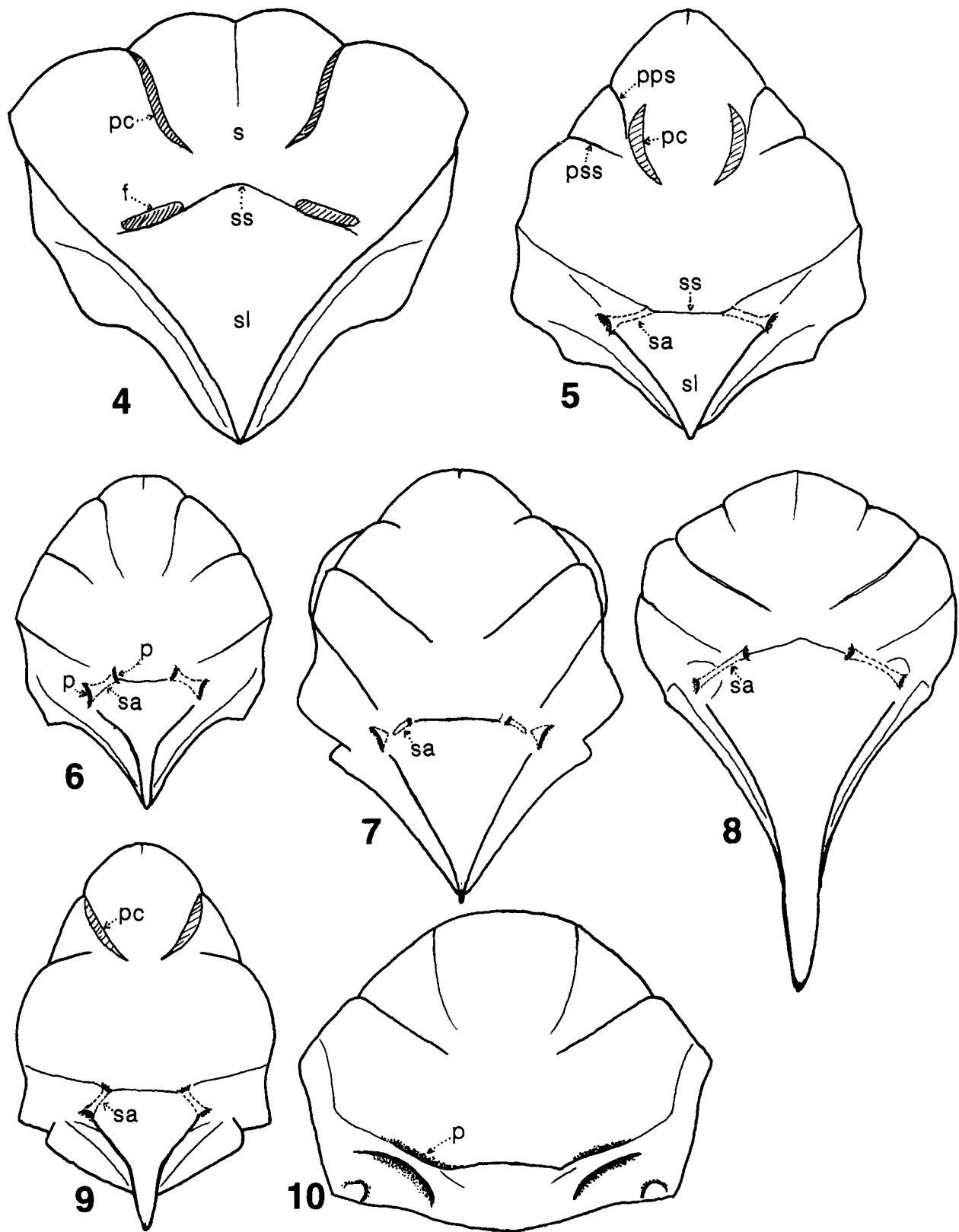16. Clavus: 0, acuminate (Fig. 3); 3, oblique apically.

17. Apical limbus (appendix): 0, narrow (Fig. 3); 3, broad.

18. Crossvein r: 0, present (Deitz & Dietrich, 1993: fig. 11); 3, absent.

19. Crossvein r-m₁: 0, present; 3, absent.

20. Crossvein m-cu₁ (*sensu* Evans, 1946a): 0, absent; 3, present.

21. Crossvein m-cu₂ (*sensu* Evans, 1946a): 0, present, 3, absent. Deitz (1975) did not number the forewing

Figs 4–10. Mesonotum and scutellum, dorsal view: 4, *Aphrophora* sp.; 5, *Coloborrhis corticina* Germar; 6, *Darthula hardwickii* Gray; 7, *Aetalion reticulatum* (L.); 8, *Tropidaspis* sp.; 9, *Melizoderes* sp.; 10, *Telamona* sp. (Membracidae). f, fenestra; p, pit; pc, parapsidal cleft; pps, parapsidal suture; pss, parascutal suture; s, scutum; sa, scutellar apodeme (internal); sl, scutellum; ss, scutellar suture.
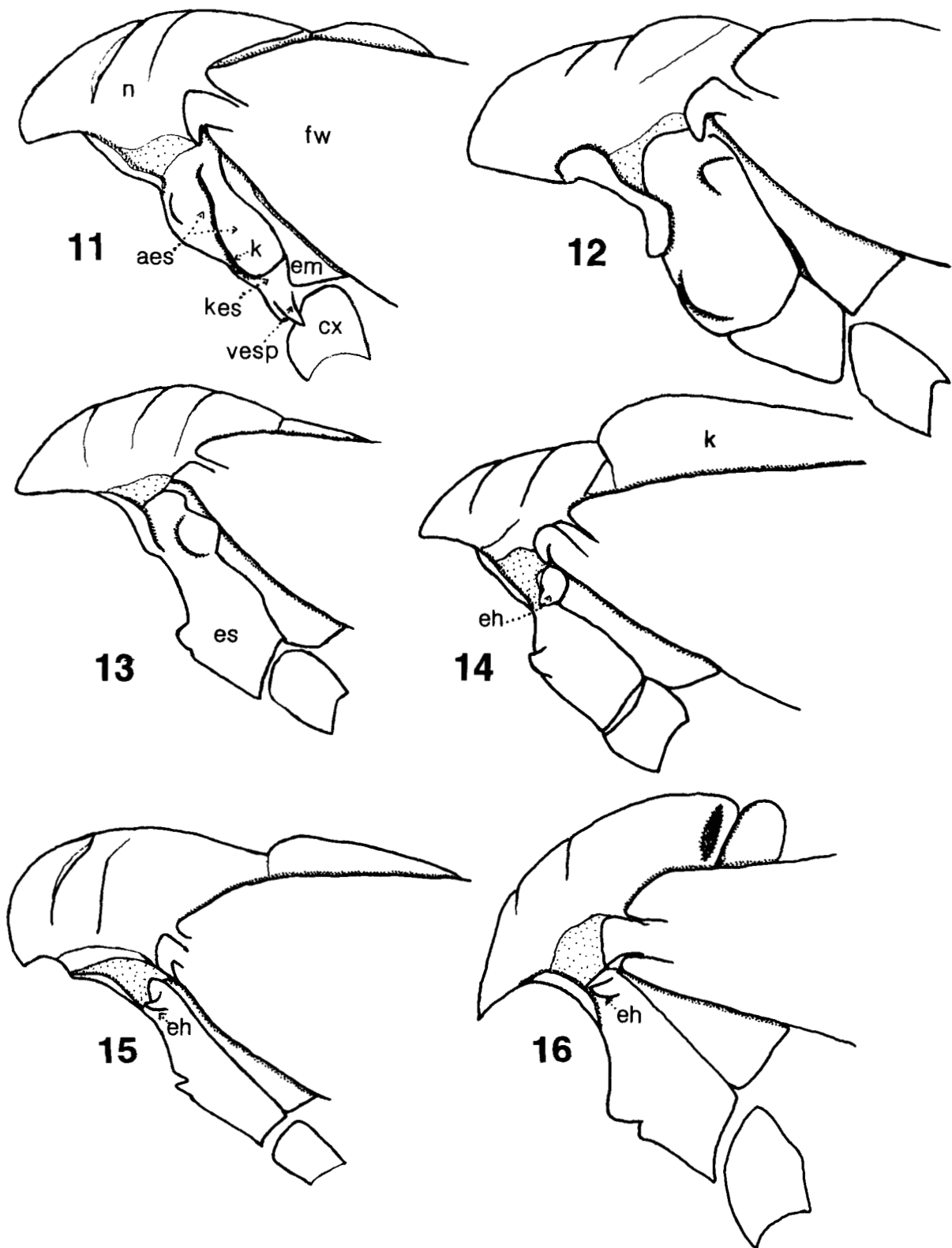
Figs 11–16. Mesothorax, in part, lateral view: 11, *Coloborrhis corticina*; 12, *Ledra aurita* (L.); 13, *Aetalion reticulatum*; 14, *Tropidaspis* sp.; 15, *Melizoderes* sp.; 16, *Telamona* sp. aes, anepisternum; cx, coxa; eh, episternal hook; em, epimeron; es, episternum; fw, forewing; kes, katepisternum; n, notum; k, scutellar keel; vesp, ventral episternal process.

crossveins of Membracidae, which usually have two or fewer m-cu crossveins. Situated towards the wing apex, these crossveins probably correspond to m-cu$_2$ and m-cu$_3$ of Evans (1946a). Among the Membracidae, three m-cu crossveins occur consistently only in the subfamily Oxyrhachinae and a few Old World genera of Centrotinae.

22. Second anal vein: 0, present; 3, absent.

23. R and M fused basally: 0, no; 3, yes (Deitz & Dietrich, 1993: fig. 11).

24. M and Cu fused basally: 0, no; 3, yes (*op. cit.*: fig. 22).

25. Number of branches of R reaching marginal vein: 0, 2 or 3; 1, 4; 2, 5; 3, more than 5.

26. Vein M: 0, 2-branched (Fig. 3); 2, 3-branched

(Evans, 1948: fig. 4b); 3, with more than 3 branches (Evans, 1946b: figs 1f, g).

27. Crossvein m-cu$_2$: 0, distad of fork of vein M (Deitz, 1975: fig. 1); 3, basad of fork of vein M (Deitz, 1975: fig. 38A–F). This character is ambiguous in those Membradidae having the venation reticulate or with M 3-branched.

Hindwing

28. Marginal vein: 0, well developed; 3, weak or absent (Deitz & Dietrich, 1993: fig. 23).

29. Veins R and M: 0, not fused, with crossvein (*op. cit.*: fig. 12); 1, not fused, without crossvein; 2, partially fused (Deitz, 1975: fig. 13J); 3, entirely fused.

30. Base of M$_{3+4}$: 0, well developed; 3, weakened basad of crossvein m-cu (Deitz & Dietrich, 1993: fig. 12).
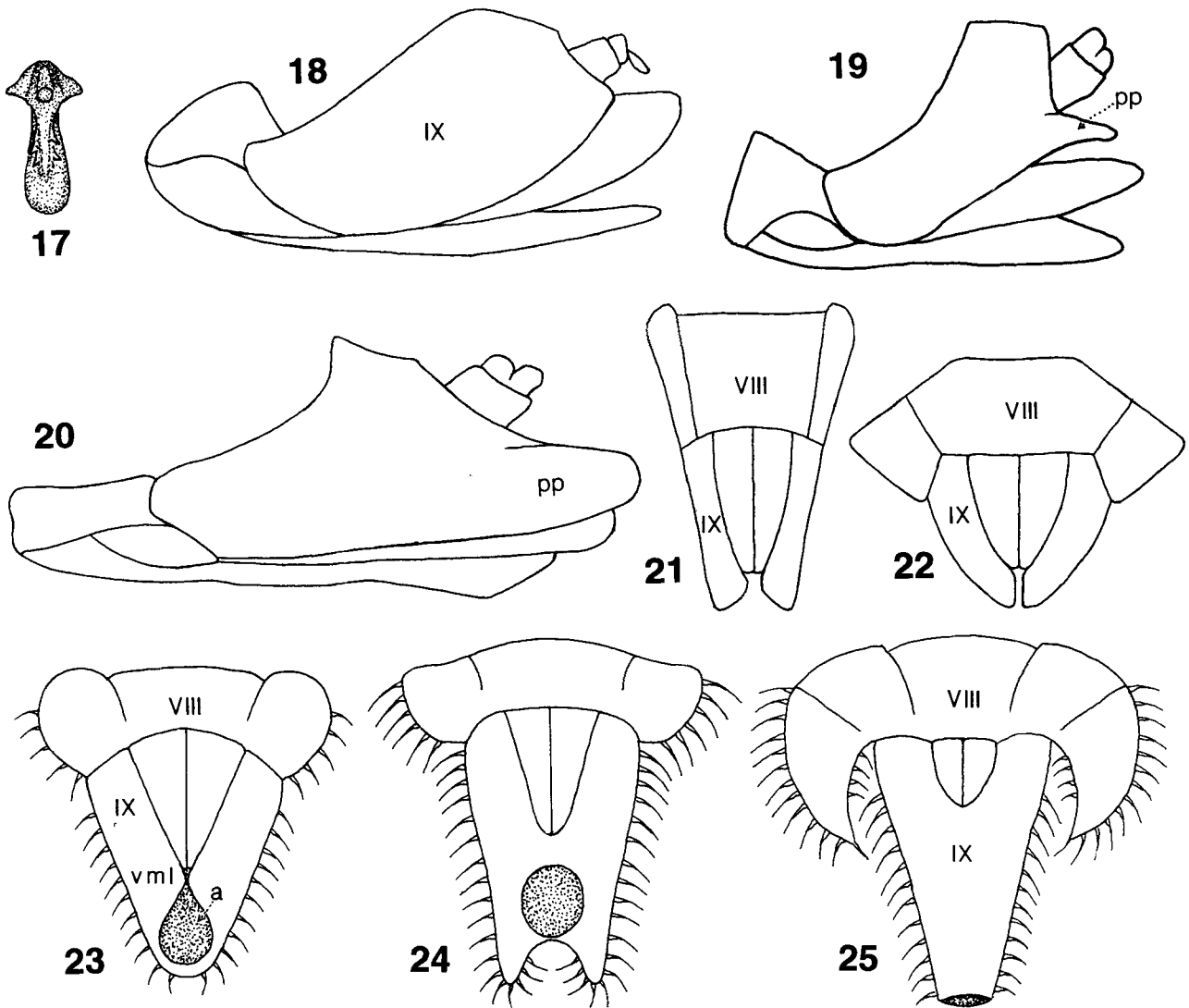
Figs 17–25. 17, *Nicomia* sp., aedeagus, ventral view. 18–20, female terminalia, lateral view: 18, *Coloborrhis corticina*; 19, *Gerridius* sp.; 20, *Aetalion reticulatum*. 21–25, Nymph (fourth or fifth instar), abdominal apex, ventral view: 21, *Draeculacephala* sp. (Cicadellidae); 22, *A. reticulatum*; 23, *Melizoderes* sp.; 24, *Llanquihuea pilosa* Linnavuori & DeLong; 25, *Microcentrus caryae* (Fitch). a, anal opening; pp, pygofer process; vml, ventomesal lobe.

Legs

31. Prothoracic trochanter: 0, not fused to femur; 3, immovably fused to femur (suture may be visible).

32. Mesothoracic tibia cucullate setae: 0, absent; 2, 1 row; 3, 2 rows.

33. Metathoracic femur, ventral row of cucullate setae: 0, absent; 3, present (Deitz, 1985: fig. 4).

34. Metathoracic femur, dorsal row of cucullate setae: 0, absent; 3, present (Deitz, 1975: fig. 39B).

35. Metathoracic tibia, enlarged setal rows: 0, absent; 1, row II only; 2, rows II and III (or only row III — most *Aetalion* Latreille); 3, three rows present (or only rows 1

Figs 26–28. SEMs 26–27, Hindwing apex, ventral surface: 26, *Membracis foliata* (L.); 27, *Microcentrus caryae*; 28, *M.caryae*, abdominal tergum integument.

and II — most Membracinae; Deitz, 1975: fig. 2). By our interpretation, Cercopoidea lack setal rows on the metathoracic tibia. Alternatively, the preapical spines with subtending setae found in Cercopoidea might be regarded as homologous to setal row II of Membracoidea.

36. Metathoracic tibia, setal row IV: 0, absent; 2, poorly delimited, setae minute; 3, distinct, setae long.

37. Metathoracic tarsomere I, apical cucullate seta(e): 0, absent; 3, distinct.

Male terminalia

38. Pygofer, posteroapical lobe (Deitz & Dietrich, 1993: fig. 14) or tooth (Deitz, 1975: fig. 41B): 0, absent; 3, present.

39. Subgenital plate, lobes: 0, not fused medially; 2, fused basally (Deitz, 1985: fig. 6); 3, fused to apical quarter of plate (Linnavuori & DeLong, 1978: fig. 65).

40. Sternum IX: 0, not fused to pygofer; 3, fused to pygofer (separate sclerite not distinguishable).

41. Sternum IX and subgenital plate: 0, not fused; 1, partially fused; 2, fused, but distinguishable; 3, fused, indistinguishable. The cercopoid subgenital plate is usually indistinguishably fused to sternum IX. Thus, based on the outgroup criterion, the articulated subgenital plates found in many membracoids may be derived from the fused subgenital plates similar to those found in the Cercopoidea. Yet Evans (1975a) provided evidence that the subgenital plate of Membracoidea and Cercopoidea was derived from the gonocoxites and gonostyli of abdominal segment IX of the primitive pterygote insect. Therefore, it remains unclear whether the fused condition was derived from the unfused condition or vice versa.

42. Lateral plate: 0, absent; 2, partially free (Deitz, 1975: fig. 41D); 3, entirely free (Deitz, 1985: fig. 42). We did not consider the posterior lobe of the pygofer of male Aetalionidae to be homologous to the lateral plate of Membracidae. Unlike the Membracidae, the pygofers of both male and female Aetalionidae have posterior lobes (character 45).

43. Aedeagal shape (lateral view): 0, U-shaped, short (Deitz, 1975: fig. 3C); 3, L-shaped, elongate (Ramos, 1957: fig. 15e). Because we were unable to determine their homologies, aedeagi that are neither U- nor L-shaped were coded as indefinite.

44. Aedeagus, broad triangular lateroapical processes: 0, absent; 3, present (Fig. 17).

Female terminalia

45. Pygofer, posterior lobe: 0, absent (Fig. 18); 3, present (Figs 19, 20).

46. Second valvulae, width: 0, abruptly broadened preapically (Deitz, 1985: fig. 11); 3, narrow throughout (*op. cit.*: fig. 43).
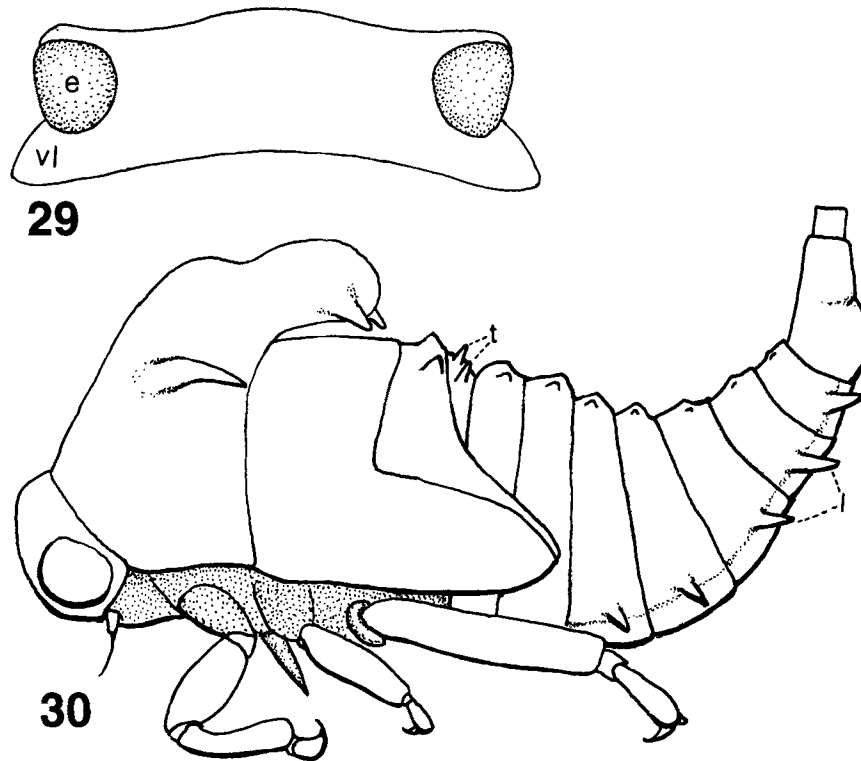
47. Second valvulae, dorsal serrations: 0, absent; 3, present.

Fine structure

48. Brochosomes (excretory granules, visible only at high magnification; Smith & Littau, 1960): 0, absent; 3, present (Dietrich, 1989: fig. 1). Dietrich's (1989) report of brochosomes in *Aetalion*, based on a contaminated specimen, was erroneous.
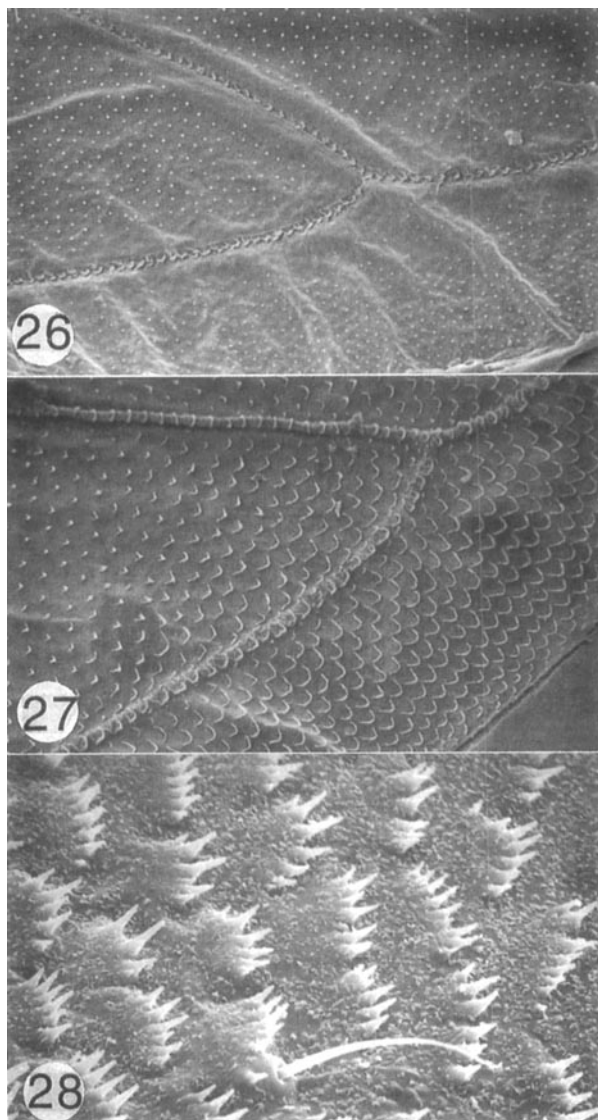
Figs 29–30. 29, *Lycoderes* sp., fifth instar nymph, head, anterior view; 30, *Heteronotus* sp., fifth instar nymph, dorsolateral view. e, eye; 1, lamellae; vl, ventrolateral lobe; t, tubercles.

49. Forewing membrane, macrotrichia: 0, absent; 3, present.

50. Hindwing membrane, vestiture: 0, glabrous; 1, microtrichia or granules (Fig. 26); 2, sparse, weakly arcuate chaetoids; 3, dense, semicircular chaetoids (Fig. 27). Shcherbakov (1981, 1982) referred to minute hairlike and arcuate structures on the wings collectively as chaetoids. Here, we use 'microtrichia' for the hairlike structures (Fig. 26) following general usage, and refer only to the arcuate structures as 'chaetoids' (Fig. 27).

51. Abdominal tergum, inornate pits (with marginal setae): 0, absent; 2, polymorphic; 3, always present (Dietrich, 1989: fig. 17).

52. Abdominal tergum, acanthae: 0, simple (Dietrich, 1989: fig. 23); 2, dentate (*op. cit.*: fig. 26); 3, divided (microtrichia; *op. cit.*: fig. 24).

53. Microscopic waxy exudates: 0, absent; 3, present (Fig. 28).

54. Thoracic pleuron, white wax: 0, absent; 2, polymorphic; 3, always present.

Nymph

55. Chalazae: 0, absent; 2, short, hairlike; 3, long, with enlarged bases (Quisenberry *et al.*, 1978: fig. 12).

56. Head, venter: 0, produced; 3, excavated (Fig. 29).

57. Vertex, ventrolateral lobes: 0, absent; 2, digitate; 3, foliaceous (Fig. 29, vl).

58. Dorsal paired protuberances: 0, absent; 2, short, without multiple chalazae (Fig. 30); 3, long, with multiple chalazae (Quisenberry *et al.*, 1978: fig. 12).

59. Forewing pad: 0, not emarginate; 3, emarginate (*op. cit.*: fig. 18).

60. Abdominal lamellae: 0, absent; 2, short, digitate; 3, long, depressed (Fig. 30, 1).

61. Tergum IX, ventromesal lobes: 0, absent (Fig. 21); 2, contiguous (Fig. 23, vml); 3, fused (Figs 24, 25).

62. Tergum I, tubercles: 0, absent; 2, short, broad; 3, digitate (Fig. 30, t).

63. Anal opening: 0, on posterior or dorsal surface of abdominal apex; 3, entirely on ventral surface of abdominal apex (Figs 23, 24).

Data matrix

Our data (Table 2) consisted of the coded character states of the above characters based on adult and nymphal morphology of thirty-nine Operational Taxonomic Units (OTUs) (Table 2). The OTUs (Table 1) represented all genera of the Aetalionidae and Melizoderidae, two unplaced membracoid genera, and an outgroup, the Cercopoidea. We also included representatives of four undescribed genera, including a fossil genus from Oligo-Miocene Dominican amber, that have character state combinations absent in other Membracoidea; formal descriptions will be presented elsewhere.

Because we were most interested in the relationships among the non-cicadellid Membracoidea, we included only a few representatives of the family Cicadellidae. We

Table 1. Material examined. An asterisk (*) denotes collections containing immature specimens.

OTU: taxon represented: material examined (repositories[1]).

CER: Cercopoidea: *Aphrophora* sp., *Clastoptera* sp., *Tomaspis* sp. (all USNM*). AET: *Aetalion* Latreille: *A.reticulatum* (L.) (USNM), *Aetalion* spp. (MNHN, NCSU*). ANT: *Antillotolania* Ramos: *A.doramariae* Ramos (JARC, NCSU [holotype ♂)]. BIT: *Biturritia* Goding: *B.capreolus* (Germar) (UFPB), *B.cristata* (Stål) (USNM), *Biturritia* sp(p). (MNHN, NCSU*). BOC: *Bocydium* Latreille (Stegaspidini): *Bocydium* spp. (NCSU*, USNM). COL: *Coloborrhis* Germar (Ulopinae): *C.corticina* Germar (NCSU, USNM). CTD: Centrodontinae: *Centrodontus atlas* (Goding), *Multareoides* sp. (both NCSU, USNM*). CTN: *Centronodus* Funkhouser (Centronodinae): *Centronodus* spp. (NCSU, USNM). DAR: *Darthula* Kirkaldy: *D.hardwickii* (Gray) (USNM), *Darthula* sp. (NCSU). DEI: *Deiroderes* Ramos: *D.inermis* Ramos (BMNH, JARC, NCSU [holotype ♀]), *Deiroderes* spp. (JARC, USNM). END: *Endoiastus* Fowler: *E.caviceps* Fowler (JARC, USNM), *Endoiastus* sp. (NCSU). EUR: Eurymelinae: *Eurymeloides pulchra* (Signoret) (NCSU*), *Ipo* sp. (USNM). EUW: *Euwalkeria* Goding: *E.latipes* (Walker) (BMNH [holotype ♀]). FOS: Oligo-Miocene amber fossil, gen. & sp.n. (♀♀ and nymph, USNM). GER: *Gerridius* Fowler: *G.scutellatus* Fowler (UFPB, USNM), *Gerridius* sp. (JARC, MNHN, NCSU*). HET: Heteronotinae: *Dysyncritus* sp. (NCSU), *Heteronotus* sp. (NCSU*), *Nassunia* sp. (NCSU*), *Rhexia* sp. (NCSU). HOL: *Holdgatiella* Evans: *H.chepuensis* Evans (BMNH [holotype ♂], JARC, JWEC, NCSU). HYL: Hylicinae: *Hylica paradoxa* Stål (NCSU), *Hatigoria* sp. (NCSU), *Sudra* sp. (USNM). LED: Ledrinae: *Ledra aurita* (L.) (NCSU*), *Ledra auditura* Walker (NCSU), *Petalocephala* spp. (NCSU, USNM), *Xerophloea major* Baker (NCSU). LLA: *Llanquihuea* Linnavuori & DeLong: *L.pilosa* Linnavuori & DeLong (JARC, MNNC, NCSU, USNM*). LOP: *Lophyraspis* Stål: *L.muscaria* (F.) (USNM, ZMUC [type material]), *L.scutellata* (F.) (UFPB), *Lophyraspis* sp. (BMNH). MCC: Microcentrini (Stegaspidinae): *Microcentrus* spp. (NCSU*, USNM*). MEL: *Melizoderes* Spinola: *M.carinata* Blanchard (USNM), *M.osborni* (Funkhouser) (JARC), *M.variegata* (Funkhouser) (OSUC, USNM), *Melizoderes* spp. (BMNH*, JARC, MNNC, NCSU*). MEM: Membracinae: *Calloconophora caliginosa* (Walker) (NCSU*), *Eunusa* sp. (NCSU*), *Membracis foliata* (L.) (NCSU), *Paragargara* sp. (NCSU). MIN: *Mina* Walker: *M.aliena* Walker (BMNH [holotype ♀], JARC, USNM), *Mina* sp. (ABFC, AMNH). MOO: *Moonia* Distant (Ulopinae): *Moonia* spp. (NCSU, USNM). NGA: new genus A: 1 sp.n. (NCSU, UFPB, USNM), 1 sp.n. (SHMC). NGB: new genus B: 1 sp.n. (1♀, USNM). NGC: new genus C: 1 sp.n. (1♂, USNM). NIC: *Nicomia* Stål: *N.cicadoides* (Walker) (BMNH), *N.lemniscata* Stål (NMRS [type material]), *Nicomia* spp. (BMNH, MNHN, UFPB, USNM). OXY: Oxyrhachinae: *Oxyrhachis taranda* (F.) (NCSU*). PCN: *Paracentronodus* Sakakibara (Centronodinae): *Paracentronodus* spp. (NCSU, USNM). PRO: Procyrtini (Darninae): *Procyrta pectoralis* (F.) (NCSU, USNM), *Procyrta* sp. (NCSU*). SCY: *Scytodepsa* Stål: *S.exigua* (F.) (USNM), *Scytodepsa* spp. (MNHN, NCSU*). STE: Stegaspidini in part (Stegaspidinae): *Lycoderes* spp. (NCSU*), *Flexocentrus* sp. (NCSU). STI: *Stictodepsa* Stål: *S.neotropicalis* Kirkaldy (BMNH, ZMUC [type material of *Cicada fuscata* (F.)]). TOL: *Tolania* Stål: *T.semipellucida* (Stål) (USNM), *T.opponens* (Walker) (USNM), *T.fraterna* Stål (USNM [as *T.obtusa* Fowler]), *Tolania* spp. (JARC, JWEC, MNHM, NCSU, USNM). TRO: *Tropidaspis* Stål: *T.carinata* (F.) (USNM), *Tropidaspis* spp. (ABFC, JARC, MNHM, NCSU*).

[1] Repositories: ABFC, A. Forsyth collection, c/o Queens University, Kingston, Ontario, Canada; AMNH, American Museum of Natural History, New York, New York; BMNH, The Natural History Museum, London; JARC, J. A. Ramos Collection, c/o University of Puerto Rico, Mayagüez; JWEC, J W. Evans Collection, c/o Australian Museum, Sydney; MNHN, Muséum National d'Histoire Naturelle, Paris; MNNC, Museo Nacional de Historia Natural, Santiago, Chile; NCSU, North Carolina State University, Raleigh; NHRS, Naturhistoriska Riksmuseet, Stockholm, Sweden; OSUC, Ohio State University, Columbus, Ohio; SHMC, S. H. McKamey Collection, c/o University of Connecticut, Storrs; UFPB, Universidade Federal do Paraná, Curitiba, Brazil; USNM, National Museum of Natural History, Washington; ZMUC, Zoologisk Museum, Copenhagen, Denmark.

also included only a few representatives of the 'higher Membracidae' − those having an apically oblique clavus. Both groups are supported by synapomorphies (see Results and Discussion).

We assigned intermediate states to OTUs that were polymorphic for characters 6, 8, 51 and 54. For other instances of polymorphism we used the character state that occurred in most of the representative taxa examined. Outgroup states were coded as indefinite for characters that lacked homologues, or varied considerably, among the Cercopoidea.

To give binary and ordered multistate characters equal weight, we assigned states to each character ranging from 0 to 3; binary characters had states 0 and 3, and the intermediate states of multistate characters were assigned values of 1 and 2 for four-state characters and 2 for three-state characters. Thus, a change from the least to most derived state in an ordered multistate character added the same length as a change in a binary character. Transformation series seemed dubious in characters 1 and 29, so we treated then as unordered initially and, for some analyses,

gave them weights = 3 (thus, any transformation in one of these characters would add length equivalent to a transformation in a binary character).

Parsimony analysis

We searched for maximally parsimonious trees using Hennig86 (ver. 1.5, Farris, 1988) and used PAUP (ver. 3.0, Swofford, 1990) to check results and output apomorphy lists. The implicit enumeration algorithm of Hennig86 proved too time consuming, so we used the heuristic branch breaking routine (command sequence 'mh; bb*;'), which searches for as many equally parsimonious tress as will fit in memory, but is not guaranteed to find maximally parsimonious tree(s). To increase our chances of finding as many maximally parsimonious clado-grams as possible, we repeated each analysis several times using different orderings of the OTUs. We also rearranged topologies manually (using the 'xx' facility of Hennig86).

To find the topologies supported by the most consistent

Table 2. Data matrix for cladistic analyses of the Membracoidea. Missing values are indicated by question marks. OTU abbreviations are defined in Table 1.

OTU	Character 1–10	11–20	21–30	31–40	41–50	51–60	
CER	0000000313	0000000030	300?000000	0000003003	30000??031	0200000000	000
AET	0000003030	0103000303	0030330013	3000203330	2000333002	0230000000	000
ANT	3000023010	2003300003	0003103023	0000323000	3030????03	0??0??????	???
BIT	3030000010	0303300030	3030000003˙	3033303330	1200333003	0303200000	000
BOC	0002030020	2003300030	3003003003	0000223000	3300003003	0233333033	330
CEN	0002030210	1003333000	0003000003	0000323300	3300003001	3303333233	330
COL	2030000013	0030000003	0030300000	0000330303	0000?33?01	00?0??????	???
CTD	0003020010	?003300??0	?0??33?023	0000333300	3300033001	2303333200	330
CTN	0002030310	1003300033	000333?003	0003323330	2200030001	0230??????	???
DAR	0000003030	0103000?03	0030330013	3000000330	00?0333002	0230000000	000
DEI	1000020010	2003300030	3003003003	0000323300	3330033?33	0??0??????	???
END	3000000030	0103300330	3003000303	0000323???	????033033	30?0??????	???
EUR	0330000013	0000000033	0030300000	0000330000	0000000301	0300000000	000
EUW	000202031?	100?300003	000333?000	?000020????	????033?01	03?0??????	???
FOS	100000303?	013?000033	3030330013	?0002?0???	????3???01	0??0230000	2??
GER	3030000310	0303300030	3030000003	3033323330	1200330003	0303200000	000
HET	0303030210	?003333030	3303000003	0000323300	3300030001	0300332203	330
HOL	1000020300	0003300030	000322?003	0033303300	3230003?03	03?0??????	???
HYL	0330003233	0000003033	0030000000	0000330?03	0000???32	3300??????	???
LED	0330020233	0000000003	0030330000	0000330003	0000003003	0200233002	000
LLA	0000003303	0103300000	0030000003	0200323330	3000003033	0200332002	323
LOP	3030003010	0203300030	3030000003	3033323330	3200333?03	03?0??????	???
MCC	2002330010	1003300000	0003003003	0003303300	1300003033	0333333233	330
MEL	0000000003	0103300030	0030000003	0000323030	3000003?33	0200332000	223
MEM	0003023210	?003333000	0303000003	0000320000	3300030001	2202302302	330
MIN	3030000010	0303300030	3030000003	3033303???	????333?03	0??0??????	???
MOO	0030003013	0030000033	0030000000	0000330000	0000033300	0300??????	???
NGA	2000023310	1003300003	000333?003	0003323300	2333003?01	02?0??????	???
NGB	100303030?	??03300000	000333?033	000022????	????003?31	02?0??????	???
NGC	1000300010	2003300030	300312?003	0230323300	3230????01	02?0??????	???
NIC	0000300000	3003330000	300012?003	0003223300	2333003001	3300??????	??0
OXY	0003030030	1003333003	0003000003	0000300?00	3300033?01	30?3333033	330
PCN	0002030310	1003300030	000333?003	0303323???	?200030?01	0??0??????	???
PRO	0303020310	?003333330	0003000003	0003323000	3300030001	0300333233	330
SCY	0000000030	0103300330	3003000303	0000323320	2300033033	3030000000	330
STE	0002000020	1003300030	3003003003	0000103330	3000003003	0330333033	330
STI	3000000030	0103300030	3003000303	0000220???	????003?33	30?0??????	???
TOL	1000333000	2003300030	300312?003	0303323300	0230003?01	03?0??????	???
TRO	3000003330	0203300030	3030000013	3003303030	30?0333003	0330200000	000

characters, we applied successive approximations character weighting (Hennig86 command 'xs w;' Farris, 1969, 1988; Carpenter, 1988).

Results and Discussion

Our preferred estimate of cladistic relationships among the Membracoidea (Fig. 31; apomorphy list, Table 3) was: (1) one of ten equally parsimonious tress found when characters 1 and 29 were unordered with weights of 1 or 3; and (2) the most parsimonious tree found when all characters were ordered with weights = 1. This tree had length = 683, consistency index (ci) = 27, and retention index (ri) = 63 when all characters had weight = 1 and characters 1 and

29 were unordered. Other topologies found were less parsimonious than Fig. 31 for one or more of the alternative weighting/ordering schemes. Nonetheless, these alternative trees varied only within component 72.

Four iterations of successive weighting using the original most parsimonious tree, with all characters weighted equally and 1 and 29 unordered, as the initial estimate, produced a stable solution of one tree. This tree differed from the preferred topology only within component 72, but was twenty-five steps longer based on the original character weights and orderings. We therefore rejected the tree produced by successive weighting because it was substantially less parsimonious than the original tree (Fig. 31) for the overall data.

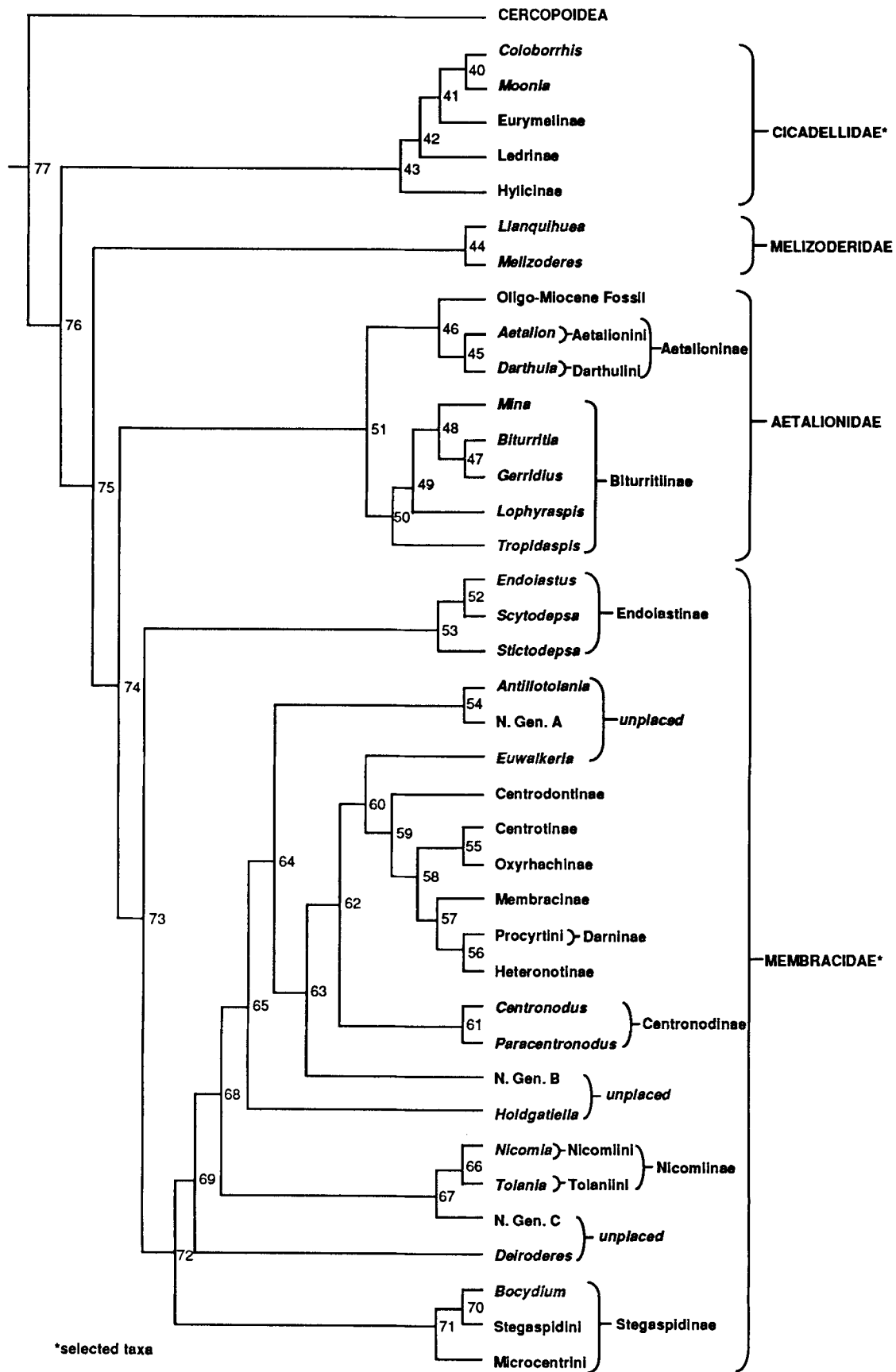When we treated all characters as unordered and of

Fig. 31. Hypothesized cladistic relationships among the Membracoidea.

Table 3. List of apomorphies for phylogeny estimate of Membracoidea (Fig. 31), based on accelerated transformation (ACCTRAN) character state optimization (other equally parsimonious optimizations are possible). Characters are listed with states in parentheses. Non-homoplastic changes are indicated by an asterisk (*). Abbreviations for terminal taxa are explained in Table 1.

Node	Subtending apomorphies	Node	Subtending apomorphies
76	9(3), 23(3), 35(3), 36(2), 50(2), 55(2)	CER	8(3), 21(3)
75	8(0), 12(1), 14(3)*, 15(3), 30(3), 38(3), 39(3), 40(0), 50(3), 61(2), 62(2)	COL	1(2), 19(0), 38(3), 40(3), 52(0)
		MOO	7(3), 25(0), 50(0)
74	10(0)*, 21(3), 53(3)	EUR	47(0)
73	23(0), 24(3), 39(2), 42(3), 61(3), 62(3)*	LED	6(2), 19(0), 26(3), 50(3), 52(2), 55(2), 56(3), 57(3), 60(2)
72	6(2), 9(1), 11(1), 12(0), 27(3), 39(0), 52(3), 55(3), 56(3), 57(3), 58(2), 60(3)	HYL	7(3), 17(3), 50(2), 51(3)
71	4(2), 6(3), 36(0), 54(3), 59(3)	LLA	7(3), 8(3), 19(0), 32(2), 60(2), 61(3)
70	9(2), 35(2), 49(0), 58(0)	MEL	38(0)
69	1(1), 11(2), 43(3), 53(0)	FOS	1(1), 13(3), 50(1), 56(3), 61(2)
68	25(1), 26(2), 42(2), 49(0), 50(1)	AET	37(3)
67	5(3), 6(0), 32(2)	DAR	35(0), 41(0)
66	9(0), 34(3), 41(2)	MIN	
65	8(3), 11(1), 21(0), 25(2)	BIT	
64	19(0), 25(3), 26(3), 52(2)	GER	8(3), 36(2), 47(0)
63	4(2), 6(3), 27(0), 43(0)	LOP	36(2)
62	1(0), 46(3)	TRO	8(3), 38(0)
61	19(3), 34(3), 39(3), 41(2), 47(0), 53(3)	END	
60	6(2), 42(3), 52(3)	SCY	1(0)
59	4(3), 8(2), 51(2), 54(3)	STI	35(2), 37(0)
58	16(3), 17(3), 25(0), 26(0)	ANT	1(3), 8(0), 11(2), 25(1), 26(0), 29(2), 38(0), 42(0), 50(3)
57	22(3), 38(0), 47(0), 54(2), 57(2)		
56	2(3), 19(3), 51(0), 54(0)	NGA	34(3), 41(2), 42(3), 44(3)
55	6(3), 51(3), 59(3)	EUW	20(3), 30(0), 35(2), 36(0)
54	1(2), 7(3), 20(3)	CTD	8(0), 29(2), 36(3), 60(0)
53	1(3), 28(3)*, 41(2), 51(3), 52(0), 55(0)	CEN	4(2), 46(0)
52	18(3), 46(3)	OXY	8(0), 9(3), 20(3), 36(0), 37(0), 52(0), 58(0)
51	7(3), 29(1), 31(3)*, 36(0), 45(3)*, 46(3), 49(0), 61(0), 62(0)	MEM	7(3), 37(0), 52(2), 56(0), 58(3), 60(2)
		PRO	8(3), 18(3), 22(0), 34(3), 57(3), 59(3)
50	1(3), 12(2), 34(3), 52(3)	HET	6(3), 21(30), 38(3)
49	3(3), 9(1), 29(0), 33(3), 42(2), 53(0)	CTN	20(3)
48	7(0), 12(3)*, 41(1)	PCN	32(3)
47	54(3)	NGB	4(3), 9(0), 29(3), 35(2), 49(3)
46	15(0), 20(3), 25(3), 26(3), 35(2), 37(0), 41(2), 50(2)	HOL	9(0), 11(0), 33(3), 34(3), 36(0), 50(3)
45	18(3), 19(0), 21(0), 55(0)	NIC	1(0), 11(3)*, 16(3), 19(0), 24(0), 32(0), 35(2), 42(3), 44(3), 51(3)
44	9(0), 55(3), 56(3), 57(2), 63(3)*		
43	2(3), 3(3), 20(3), 36(3), 37(0), 41(0), 52(3)	TOL	6(3), 7(3), 32(3), 41(0)
42	25(3), 49(0)	NGC	33(3), 52(2)
41	8(0), 9(1), 40(0), 48(3)*, 50(1), 55(0)	DEI	46(3)
40	2(0), 13(3), 46(3)	BOC	11(2), 36(2), 38(0), 52(2)
		STE	35(1), 39(3), 42(0), 54(0)
		MCC	1(2), 5(3), 19(0), 21(0), 34(3), 41(1)

weight = 1, Hennig86 found eighteen trees of length 298, ci 32, and ri 62. These trees (which had lengths of 689–692 based on the original character weights and orderings) again differed from Fig. 31 only in the relationships within component 72.

Several components remained unchanged among our results. The included Cicadellidae (component 43) consistently formed a monophyletic group and always represented a sister clade to the remaining Membracoidea. The Cicadellidae are united in having the mesonotum exposed posteriorly (character 3), a feature that was apparently derived independently within the Biturritiinae. This result differs from that of Hamilton (1983), who suggested that

the Aetalionidae and Membracidae were derived from within the Cicadellidae. Additional data are needed to elucidate relationships among the Cicadellidae and to test our hypothesis of monophyly for this family.

Those Membracidae having the clavus of the forewing oblique and the pronotum at least partially concealing the scutellum also consistently formed a monophyletic group (component 58). Results of analyses of these 'higher' membracid taxa will be presented elsewhere.

Nymphs of the family Melizoderidae, component 44 (Fig. 31), have the anal opening completely concealed by tergum IX dorsally, a unique synapomorphy. This family consistently formed a sister group of the remaining non-

cicadellid Membracoidea. Both genera of Melizoderidae have tergum IX of the nymph ensheathing segment X (Figs 23, 24), an apparently unique derivation shared with all Membracidae for which nymphs are known. Yet the Melizoderidae have parapsidal clefts on the mesonotum, a feature also present in Cicadellidae and Cercopoidea (Figs 4, 5), but absent in other Membracoidea (Figs 6–8, 10). The Melizoderidae resemble the Aetalionidae (component 51) in having a keeled scutellum, but lack other derived aetalionid features (such as fused prothoracic femora and trochanters). Thus, the Melizoderidae represent a distinct lineage, intermediate between Cicadellidae and Membracidae, but independent of Aetalionidae.

Component 51, the family Aetalionidae, was invariant among the maximally parsimonious topologies obtained. The monophyly of this component is supported by the fusion of the prothoracic trochanter and femur and by the presence of posterior processes on the female pygofer (Figs 19, 20), both unique derivations. The biturritiine genera of component 50 are united in having the head strongly produced dorsally and the scutellum enlarged. *Aetalion* and *Darthula*, component 45, are united with the Oligo-Miocene fossil in having reticulate forewing venation and two or fewer rows of cucullate setae on the hind tibia.

Component 73, the family Membracidae, is supported by the following synapomorphies: forewing veins M and Cu fused basally; male pygofer with lateral plate; nymphal abdominal tergum I with pair of tubercles (Fig. 30). The Endoiastinae, component 53, have the marginal vein of the hindwing reduced or absent, a unique synapomorphy. This group consistently formed a sister clade to component 72, which included the remaining membracids in various arrangements.

Certain taxa within component 72 consistently grouped together: component 67: Nicomiinae; component 61: Centronodinae; component 58: subfamilies Centrotinae, Oxyrhachinae, Membracinae, Heteronotinae, and tribe Procyrtini. However, the relationships among these three clades and other members of component 72 varied considerably among the cladograms obtained. According to Fig. 31, the membracid subfamily Stegaspidinae is monophyletic, but on some topologies this group was paraphyletic, giving rise to various other membracid groups. Much of this instability may be attributable to the lack of data on immatures or males for several taxa.

Despite their occurrence as distinct lineages on the cladogram (Fig. 31), *Antillotolania* and *Deiroderes* share an apomorphy with the Stegaspidinae: crossvein m-cu$_2$ connects to vein M basad of its fork (character 27). Genera arising between nodes 69 and 58 (not inclusive) may also share this feature, but because they either have reticulate venation or have vein M 3-branched, we were unable to interpret their venational homologies.

The topologies obtained from unweighted data imply that the posterior process of the membracid pronotum arose twice, once in the Stegaspidinae (component 71) and once in component 63. However, morphological evidence suggests that the posterior pronotal process arose once and was lost in various lineages. In the Centrotinae and

Stegaspidinae, this process usually rests in a groove or emargination in the scutellum. The genera *Tolania*, *Deiroderes*, *Antillotolania*, *Euwalkeria*, and new genera A and C, all of which lack posterior pronotal processes, nonetheless have the scutellum similarly grooved or emarginate. This suggests that the ancestors of these genera had posteriorly produced pronota. The posterior pronotal process was apparently also lost in two centrotine genera (Deitz, 1985). Among the Membracidae, only the subfamily Endoiastinae arose prior to the initial derivation of the posterior pronotal process.

Conclusions

Phylogeny

Based on our analyses, the sister group relationships among families of Membracoidea are: Cicadellidae + (Melizoderidae + (Aetalionidae + Membracidae)). Representatives of the family Cicadellidae formed a monophyletic group, but the 'Aetalionidae', 'Biturritiidae', 'Membracidae' and 'Nicomiidae' (of authors, except Evans' 1948 concept of Nicomiidae) are para- or polyphyletic. Moreover, our analyses support: (1) formal recognition of a new membracoid family (Melizoderidae) and a new membracid subfamily (Endoiastinae) for genera previously placed in Biturritiinae; (2) placement of *Nicomia* in the Membracidae (Evans, 1946b), rather than in the Aetalionidae (Haupt, 1929) or in a separate family 'Nicomiidae' (Evans, 1948); (3) placement of *Microcentrus* Stål and related genera in the membracid subfamily Stegaspidinae (Deitz, 1975) rather than Aetalionidae (Hamilton, 1971b) − features listed by Hamilton (1971b) as unique to Aetalionidae and *Microcentrus* (e.g. elongate beak, lateral pronotal carina) are found in many other membracoids and are thus apparently plesiomorphic; and (4) recognition of Centrodontinae and Centronodinae as separate subfamilies rather than tribes of the subfamilies Membracinae and Stegaspidinae, respectively (Deitz, 1975).

Biogeography

The predominantly Neotropical distribution of the non-cicadellid Membracoidea (Fig. 31, component 75) suggests that this lineage originated in the New World. The most plesiomorphic group, family Melizoderidae, is known only from Chile and Argentina. Among the Aetalionidae, the subfamily Biturritiinae is exclusively Neotropical; but the disjunct Neotropical (Aetalionini) and Oriental (Darthulini) distribution of the subfamily Aetalioninae, and the presence of fossils in Oligo-Miocene Dominican amber, imply that the family was once much more widespread and may have originated prior to the Tertiary.

The cosmopolitan distribution of the subfamily Centrotinae also suggests a pre-Tertiary origin for the family Membracidae (Wood, 1993). However, because the most plesiomorphic membracid subfamilies (Endoiastinae,

Stegaspidinae, Nicomiinae and Centronodinae) are restricted to the New World, either these subfamilies had a restricted distribution in tropical Gondwanaland (Wood, 1993), or the Membracidae did not arise until after the Tertiary isolation of South America. Under the latter scenario, the Centrotinae would have arisen in the New World and reached the Old World subsequently through dispersal. This hypothesis might be tested by assessing the cladistic relationships among New and Old World Centrotinae. Clearly, the Membracidae of the Eastern and Western Hemispheres diversified in isolation (Wood, 1993), for the two regions have one subfamily, one tribe, and, at most, one endemic genus in common (Deitz, 1975).

Acknowledgments

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