

Phylogeny of Psephenidae (Coleoptera: Byrrhoidea) based on larval, pupal and adult characters

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Abstract. We conducted the first comprehensive phylogenetic analysis of Psephenidae, based on 143 morphological characters of adults, larvae and pupae and coded for 34 taxa, representing three outgroups and 31 psephenid genera, including four undescribed ones. A strict consensus tree calculated (439 steps, consistency index = 0.45, retention index = 0.75) from the two most-parsimonious cladograms indicated that the monophyly of the family and subfamilies is supported, with the exception of Eubriinae, which is paraphyletic when including *Afroebria*. Here a new subfamily, Afroebriinae (**subfam.n.**), is formally established for *Afroebria*. The analysis also indicated that the ‘streamlined’ larva is a derived adaptive radiation. Here, suprageneric taxonomy and the evolution of some significant characters are discussed. Keys are provided to the subfamilies and genera of Psephenidae considering larvae, adults and pupae.

Introduction

Psephenidae, the ‘water penny’ beetles, are characterized by the peculiar larval body shape (Figs 4–7). The phylogeny of this family has been difficult to understand because of two past problems. One was taxonomic confusion, caused especially by Pic (1916, 1918, 1923, 1934, 1938, 1944). Although he assigned all eubriine species to *Macroebria*, *Drupeus*, *Grammeubria*, and *Ectopria*, *Drupeus* belongs to a genus of Ptilodactylidae (Satô, 1983), and *Grammeubria* has been synonymized with *Ectopria* (Satô, 1985). The second problem is a lack of association of adults and immature stages. Identification of the Psephenidae is mostly based on adult stages, but larvae are more easily available, as they are long-lived and common in streams. If associated with adults, larval characters would contribute significantly to phylogenetic studies. Unfortunately, few species have had larval–adult associations, especially for those from the Oriental Region. For example, the subfamily Eubrianacinae, comprising some 40 species, had been regarded as monogeneric, with larvae only of *Eubrianax edwardsii* (LeConte) described (Blackwelder, 1930). After a re-examination of

type specimens and the association of adults and immature stages by rearing, five new genera were proposed for Oriental taxa and a well-resolved phylogenetic tree was obtained for genera within the family (Lee *et al.*, 1999a, b, c, 2000a, b, 2001, 2003a) by using larval, pupal and adult characters. Thus, it seems promising to conduct a phylogenetic study of the whole family by combining characters of adults and immature stages.

Pic’s problems have been solved by revisionary studies (Appendix 1) (Jäch & Lee, 1994; Lee & Yang, 1995, 1996; Lee *et al.*, 1998). In addition, successful associations of immature stages with adults by rearing have been made for *Homoeogenus* (Lee & Yang, 1993), *Schinostethus* (Lee *et al.*, 1993), *Nipponeubria* (Lee & Satô, 1996), *Macroebria* (Lee *et al.*, 1997), *Granuleubria* (Lee & Yang, 1999), *Mubrianax* (Lee *et al.*, 1999b), *Jinbrianax* (Lee *et al.*, 1999c), *Odontanax* (Lee *et al.*, 2000a), *Jaechanax* (Lee *et al.*, 2000b), *Afrobrianax* (Lee *et al.*, 2003a), and *Microebria* (Lee & Yang, 2002) allowing the inclusion of larval, pupal and adult characters in phylogenetic studies. So far, only Costa *et al.* (1999) has discussed the phylogenetic position of Psephenidae, based on one synapomorphy, flattened larvae, can support the monophyly of the family. This claim is questionable, because their phylogenetic analysis did not include some genera of Elmidae that share this same state (e.g. Fig. 4B, C).

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The suprageneric taxonomy of Psephenidae has been confused, mainly because of dissimilarity between adults of subfamilies and incorrect association of immature stages and adults. Members of Eubrianacinae had been placed in the family Dascillidae, until Blackwelder (1930) described the larva of *Eubrianax edwardsii* (LeConte) and assigned it to Psephenidae. *Psephenoides immsi*, the first member of Psephenoidinae, was described by Gahan (1914). It was placed in Psephenidae, partly on account of the similar habits of the adults and the great similarity of the larvae of Psephenidae and *Psephenus*. Champion (1920, 1924) transferred the genus to Scirtidae (= Helodidae) because adults of *Psephenoids* are more similar to members of Scirtidae than those of *Psephenus*. Böving (1926, 1929) and Böving & Craighead (1931) transferred *Psephenoides* to Dryopidae because of the similarity of the larvae of *Psephenoides* and *Helichus* (Dryopidae) in that both had anal gills in contrast to ventral gills in *Psephenus*. At that time, larvae of some eubriines had been identified erroneously as *Helichus* by Kellicott (1883). This confusion still existed when Hinton (1939) proposed that Psephenidae should contain three subfamilies: Psepheninae, Psephenoidinae and Eubrianacinae, based on the comparative anatomy of the larvae, pupae and adults. The first true larva for Eubriinae was recognized when Bertrand (1939) correctly described the life history of *Eubria palustris* Germar. Hinton (1955, 1966) formally included Eubriinae in Psephenidae when discussing the respiratory adaptations of the larvae and pupae. This assignment has been followed by Lawrence & Newton (1995), but other researchers have disagreed. For example, Bertrand (1972) treated Eubrianacinae as a subfamily of the Dascillidae, and raised Psephenoidinae and Eubriinae up to the family level – Psephenoididae and Eubriidae. Eubriidae was also adopted by some other researchers, e.g. Brigham (1981).

Crowson (1960) was the first to discuss the phylogenetic position of the Psephenidae. Psephenidae was attributed to the superfamily Dryopoidea (= Byrrhoidea), which was split into two main lineages. Psephenidae, Heteroceridae, Dryopidae, Limnichidae and Elmidae were one lineage united by the synapomorphy of five or six lateral ocelli in larvae. *Eulichas* (Eulichadidae), Ptilodactylidae, Chelonariidae and Eurypogonidae represented a second lineage united by the synapomorphy of a single lateral ocellus. Later, Crowson (1978) thought that Psephenidae should be grouped with Elmidae, Lutrochidae, Heteroceridae and Limnichidae, due to the presence of the specialized hydrofuge pubescence that enables the adults to move freely into water. The reduced and nonfunctional adult mouthparts and the strongly onisciform larvae were considered autapomorphic for Psephenidae. Lawrence (1987) used 25 taxa and 112 characters (87 from adults, 25 from larvae) to conduct a phylogenetic analysis of the Elateriformia. He recognized four superfamilies, of which Psephenidae, Cneoglossidae, Chelonariidae, Ptilodactylidae, Eulichadidae and Callirhipidae constituted Psephenoidea. Beutel (1995) used 28 taxa and 27 larval characters to conduct the phylogenetic analysis of Elateriformia. The monophyly of *Araeopidius*

(Ptilodactylidae: Araeopidinae), Cladotominae (Ptilodactylidae), Chelonariidae, Psephenidae, Dryopidae, Lutrochidae and Elmidae was suggested by the presence of a ventrally hinged operculum of segment IX. The presence of plumose setae on the mouthparts was regarded as a possible synapomorphy of Chelonariidae, Psephenidae, Lutrochidae and Elmidae. The presence of three retractable anal gill-tufts was considered as a significant synapomorphy of the latter three families. The monophyly of Psephenidae and Elmidae was supported by the flexible, pilose mandibular appendage. Costa *et al.*'s (1999) phylogenetic analysis of Byrrhoidea using 32 taxa and 72 characters (43 from adults, 28 from larvae, one from pupae) is consistent with Lawrence's (1987) analysis. Sister-group relationships between Cneoglossidae and Psephenidae were supported by one adult character, the presence of paired glandular openings on abdominal tergites.

Hinton (1966) discussed phylogenetic relationships between subfamilies of Psephenidae based on the respiratory systems of the immature stages, arguing that Psepheninae had the most primitive respiratory systems of all subfamilies. However, his discussion focused on the autapomorphic respiratory system of each subfamily, which provided no information on the relationships between subfamilies. Thus, when he drew the phylogeny of Psephenidae (Hinton, 1966: fig. 16), the cladogram united all subfamilies. Although all subfamilies were represented in Costa *et al.*'s (1999) phylogenetic analysis of Byrrhoidea, subfamily relationships within Psephenidae were not discussed.

In this study, we tested monophyly of the family Psephenidae and its subfamilies and clarified the relationships between subfamilies based on adult and immature stages, using most of the known genera.

Materials and methods

Terminology

The terminology for hind wing venation is based on Kukulová-Peck & Lawrence (1993, 2004). Terms for larval structure follow Lee *et al.* (2001) for Eubrianacinae and Lee *et al.* (2003c) for Psepheninae. However, there are autapomorphic arrays of marginal fringes within Psephenidae. Especially in some eubriine genera, the marginal fringes are highly developed: there are four layers of setae on the outward margin of larvae. These setae are named based on their position. For example, the setae of the most outward layer are called first dorsal setae (= D1), the setae of the following layers are called second dorsal setae (D2) (e.g. Fig. 9J) and third dorsal setae (D3) (e.g. Fig. 9K). The most inner layer of setae (fourth dorsal setae) can be clearly observed in ventral view. Thus, this layer of setae is called ventral setae (VS) (Fig. 9K). Several pairs of long hair-like setae appear in larvae of some genera of Eubriinae, especially in *Ectopria*. The terminology of setae on the dorsum is based on this genus (Fig. 4J).

Selection of taxa

Psephenidae currently comprise 31 genera and approximately 263 species. We have examined adults of 28 genera and approximately 200 species. Excluded from the analysis are *Bertrandia* Pic (Psepheninae), *Falsodrupeus* Pic (Eubriinae), and *Sinopsephenoides* Yang (Psephenoidinae), which are unknown as larvae and unavailable as adults. Immature stages of species available for the study are listed in Appendix 2. Larvae of three undescribed genera were added to the data matrix for the phylogenetic analysis. Elmidae and Cneoglossidae were chosen as outgroups because they are sister groups to Psephenidae, as proposed by Beutel (1995) and Costa *et al.* (1999), respectively. Within Elmidae, *Elmis* and *Phanocerus* were chosen as they represent both subfamilies (Elminae and Larainae) and their larvae are flattened, which can provide more information about character polarities. Because the purpose of the study was not to expose the sister-group relationships of Psephenidae, but to root cladograms, few outgroups were selected: Cneoglossidae was designated to the root of the tree based on Beutel's (1995) phylogenetic analysis of the Elateriformia. Character states shown on the data matrix (Appendix 3) are not hypothetical groundplans, but are from real species.

Character coding and phylogenetic analysis

In total, 143 morphological characters were used (Appendix 3), of which 50 were from adults, 70 from larvae and 23 from pupae. We found seven ontogenetic characters in the Psephenidae, of which five were included in the analysis. Two were excluded because of insufficient material. All characters were analysed under equal weights and treated as nonadditive.

The parsimony analysis was implemented in NONA (Goloboff, 1993), run within WINCLADA (Nixon, 2000). The most-parsimonious trees were discovered by using the search commands 'rs 0' and 'mult 50'. A strict consensus tree was calculated from the most-parsimonious trees. Bremer support (Bremer, 1994) was calculated using NONA, and the search was set to a Bremer support of 5, with a buffer of 4000 trees.

Characters

1. *Male antennae*: (0) filiform (Fig. 1A); (1) moniliform (Fig. 1B); (2) serrate (Fig. 1C); (3) pectinate (Fig. 1D); (4) flabellate (Fig. 1E) [consistency index (CI) = 0.50, retention index (RI) = 0.63].

Moniliform antennae in males are found in some genera within Psepheninae (*Psephenus*, *Psephenops*, genus D) and Eubriinae (*Sclerocyphon*, *Tychepephus*). Serrate antennae in males are present in some members of Eubriinae (*Ectopria*, *Nipponeubria*, *Microeubria*, *Eubria* and most species of *Macroeubria* and *Dicranopselaphus*). Pectinate antennae

appear in the *Macroeubria pectinata* species group and American members of *Dicranopselaphus*. This type of antenna is also found in most members of Psephenidae, including Psephenoidinae, Eubrianacinae (except *Eubrianax serratus*), some genera within Eubriinae (*Afroeubria*, *Granuleubria*, *Homoeogenus*, *Schinostethus* s.str.). Flabellate antennae, defined as having extremely short antennomeres 3–10, which have long appendages, occur in *Schinostethus* subgenus *Sundodrupeus*, and *Acneus* within Eubriinae. Filiform antennae appear only in *Mataeopsephus* and *Pheneps* (both in Psepheninae). In general, the pectinate antenna is uniform, with rami originating from the apices of antennomeres 5–10 except in Eubrianacinae. Lee *et al.* (2001) coded another state for *Odontanax*, *Jaechanax*, *Eubrianax pellucidus*, *E. amamiensis* and *E. manakikikuse*, whose antennae have rami originating from the middle or bases of antennomeres 5–7. However, we excluded this state due to a lack of information (because it is polymorphic in *Odontanax* and *Eubrianax*, it cannot provide phylogenetic information).

2. *Male antennae*: (0) without cup-shaped sensillae; (1) with cup-shaped sensillae (Fig. 2A) (CI = 0.50, RI = 0.87).

Cup-shaped sensillae occur in most genera of Eubriinae, except *Sclerocyphon*, *Tychepephus*, *Afroeubria* and *Granuleubria*.

3. *Male antennae*: (0) without paddle-shaped sensillae; (1) with paddle-shaped sensillae (Fig. 2B) (CI = 0.33, RI = 0).

Paddle-shaped sensillae occur in some genera of Eubriinae, including *Afroeubria*, *Granuleubria* and *Nipponeubria*.

4. *Female antennae*: (0) without appendages; (1) with short appendages (Fig. 1G) (CI = 0.50, RI = 0).

Female antennae with short appendages only occur in two genera of Psephenoidinae: *Afropsephenoides* and *Xylopsephenoides*.

5. *Distance between eyes in males*: (0) equal to or greater than the diameter of each compound eye (Fig. 2C); (1) smaller than the diameter of each compound eye (Fig. 2D) (CI = 0.25, RI = 0.40).

The eyes of males in some genera of Eubriinae (*Granuleubria* and *Ectopria*) and Psephenoidinae (*Neopsephenoides*, *Afropsephenoides*, *Xylopsephenoides*) are larger than in females, which are attributed to state 1. It is polymorphic in *Dicranopselaphus*.

6. *Antennal socket*: (0) very weakly convex or flat; (1) strongly convex (CI = 0.50, RI = 0.50).

The strongly convex antennal socket occurs in most genera within Psephenoidinae, except *Psephenoides*.

7. *Clypeus*: (0) smooth (Fig. 2C); (1) raised (Fig. 2D) (CI = 1.00, RI = 1.00).

The raised clypeus occurs in most Psephenidae, except Psepheninae.

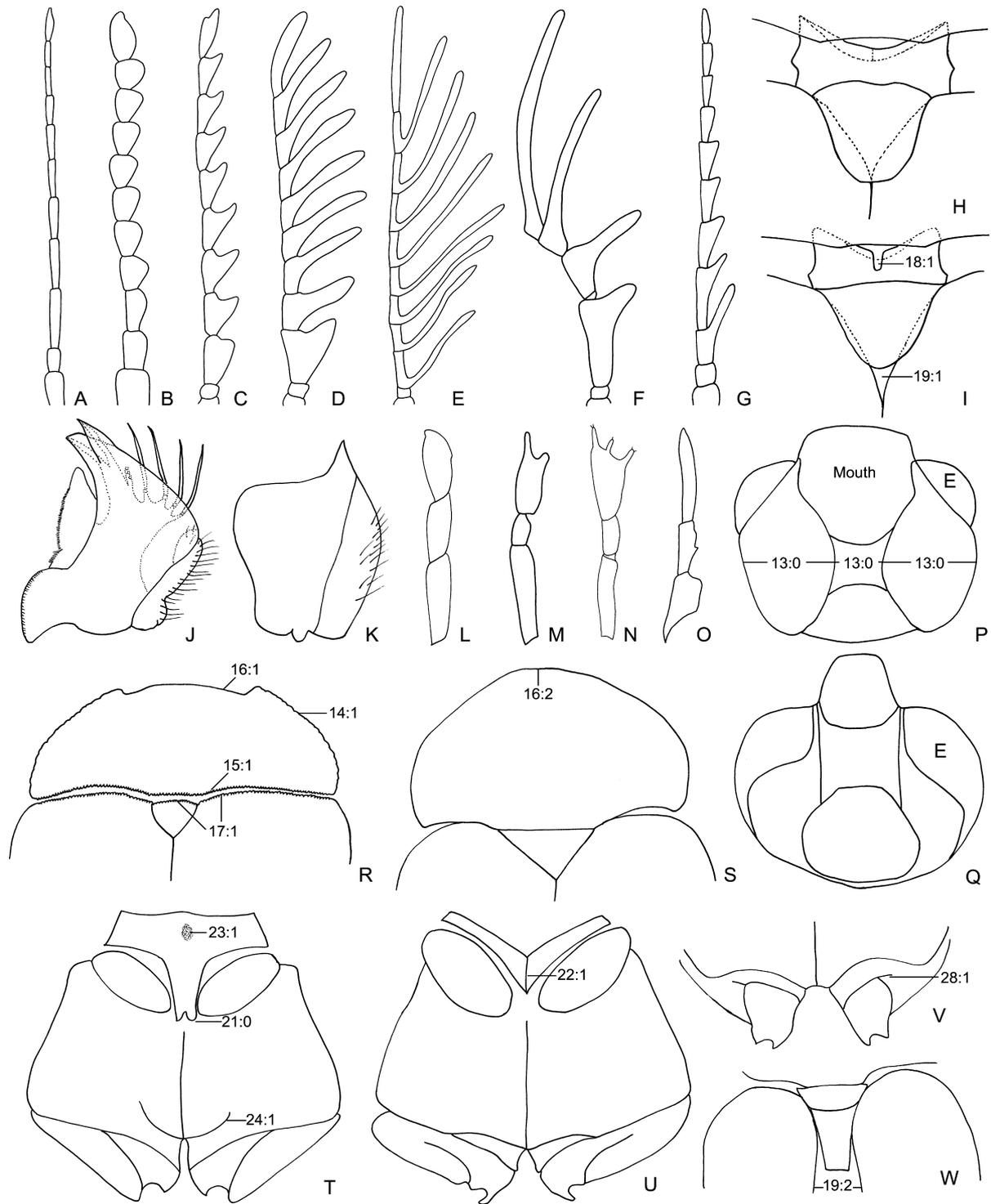


Fig. 1. Adult features used in the phylogenetic analysis. A–G, Antenna; H, I, elytra folding and scutellum; J, K, mandible, dorsal view; L–O, maxillary palpus; P, Q, head, ventral view; R, S, pronotum, scutellum and base of elytra; T, U, mesoventrite and metaventrite; V, base of metaventrite and metacoxae; W, wing folding. A, *Mataeopsephus taiwanicus*; B, *Psephenus herricki*; C, *Macroebria lewisi*; D, *Macroebria pectinata*; E, *Jaechanax illiesi*; F, *Schinostethus (Sundodrupeus) albosulcus*; G, *Xyloapsephenoides gihongi*; H, *Psephenoides subopacus*; I, *Xyloapsephenoides gihongi*; J, *Phanocerus clavicornis*; K, *Sclerocephon minimus*; L, *Mataeopsephus japonicus*; M, *Granuleubria satoi*; N, *Eubria palustris*; O, *Afroebria monodi*; P, *Phanocerus clavicornis*; Q, *Ectopria nervosa*; R, *Sclerocephon minimus*; S, *Afrobianax ferdyi*; T, *Ectopria nervosa*; U, *Psephenoides subopacus*; V, *Neopsephenoides nanus*. E = compound eye.

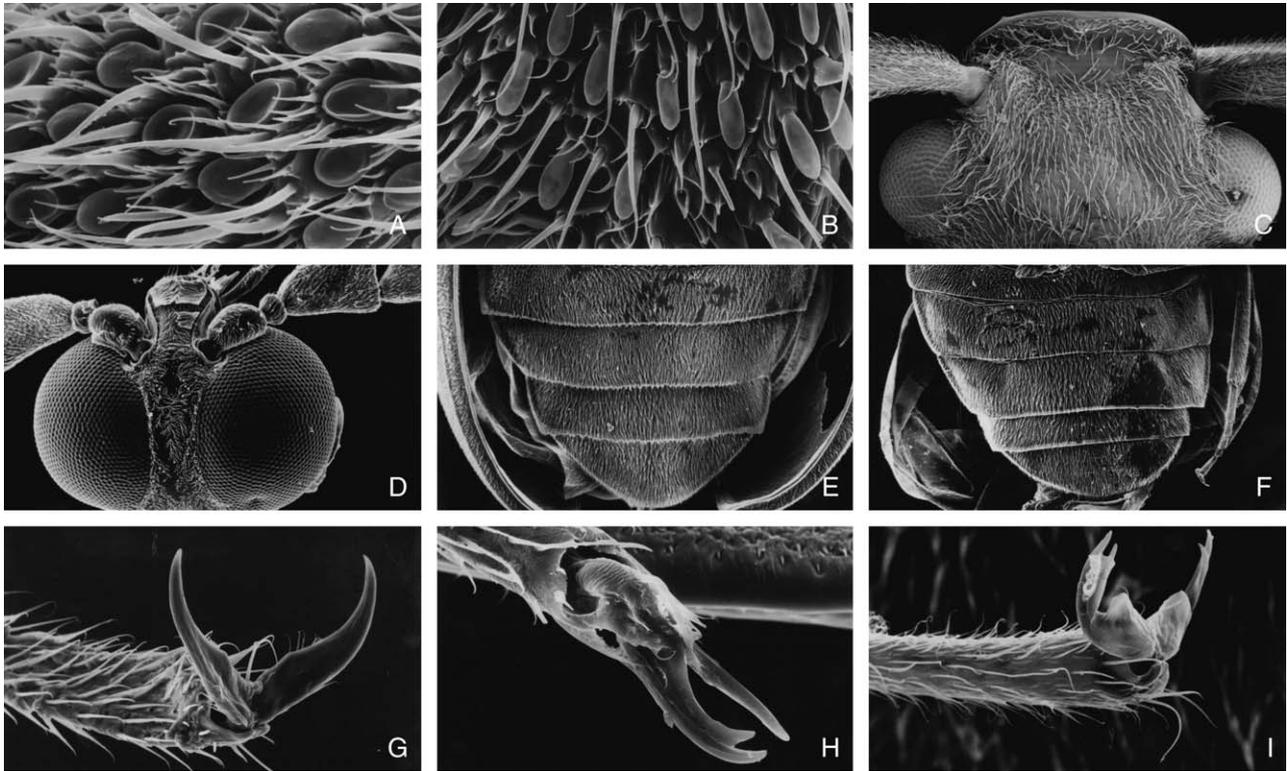


Fig. 2. Adult features used in the phylogenetic analysis. A, B, Sensilla on antenna; C, D, head; E, F, abdominal ventrites; G–I, tarsal claws. A, *Ectopria hsui*; B, *Granuleubria fontana*; C, *Mataeopsephus japonicus*; D, *Macroebria luei*; E, *Ectopria hsui*; F, *Macroebria luei*; G, *Nipponeubria yoshitomi*, male; H, *Eubria palustris*, male; I, *Ectopria hsui*, male.

8. *Clypeus*: (0) normal (Fig. 2D); (1) apically lengthened (Fig. 2C) (CI = 0.50, RI = 0).

The apomorphic state appears in *Mataeopsephus* and genus D. The clypeus is apically lengthened and recurved.

9. *Frontoclypeal suture*: (0) present; (1) absent (CI = 1.00, RI = 1.00).

The frontoclypeal suture is absent in all members of Psephenidae, except *Mataeopsephus esakii*.

10. *Mandible*: (0) well developed (Fig. 1J); (1) reduced (Fig. 1K) (CI = 1.00, RI = 1.00).

The mandibles lacking the mola and prostheca are weakly sclerotized and smaller in Psephenidae. Crowson (1978) supposed that adults of Psephenidae are short-lived based on the reduced mandibles. Reduced mandibles are also found in Cneoglossidae (Costa *et al.*, 1999).

11. *Labrum*: (0) partly exposed; (1) concealed under clypeus (CI = 0.25, RI = 0.57).

In Psephenoidinae and some genera of Eubriinae (*Afroebria*, *Eubria*, *Macroebria* and *Dicranopselaphus*), the labrum is concealed under the clypeus.

12. *Apices of maxillary and labial palpi*: (0) truncate or rounded (Fig. 1L); (1) bifurcate (Fig. 1M); (2) apically

tapering (Fig. 1N); (3) with several processes (Fig. 1O) (CI = 0.75, RI = 0.75).

The truncate or rounded apices of maxillary and labial palpi occur in Eubrianae and Psepheninae, and some genera of Eubriinae (*Ectopria*, *Homoeogenus*, *Nipponeubria* and *Acneus*), and some species of *Cneoglossa*, *Macroebria* and *Dicranopselaphus*. The bifurcate apices of palpi occur in *Afroebria*, *Psephenoides* and *Afropsephenoides*, and some species of *Cneoglossa*, *Macroebria*, *Dicranopselaphus* and *Neopsephenoides*. The pointed apices occur in *Afroebria*, *Xylopsephenoides* and some species of *Neopsephenoides*. The apices with several processes only occur in *Eubria*.

13. *Gula and postgena in ventral view*: (0) gula relatively narrower than postgena (Fig. 1P); (1) gula as wide as postgena (Fig. 1Q) (CI = 1.00, RI = 1.00).

The narrow gula and wide postgena occur in outgroups and Psepheninae. The wide gula and narrow postgena occur in other subfamilies of Psephenidae.

14. *Lateral margins of pronotum*: (0) serrate (Fig. 1R); (1) smooth (Fig. 1S) (CI = 0.50, RI = 0).

The serrate lateral margins of the pronotum occur in *Elmis*, some species of *Sclerocyphon*, and *Tycheapsephus*.

15. *Basal rim of pronotum*: (0) smooth (Fig. 1S); (1) crenulate (Fig. 1R) (CI = 0.50, RI = 0.90).

The crenulate basal rim of the pronotum occurs in most Eubriinae, except *Afroebria* and *Eubria*. The basal rims of the pronota of *Mataeopsephus chinensis* and *M. dentatus* are also crenulate.

16. *Apical margin of pronotum*: (0) moderately emarginated (Fig. 1R); (1) straight; (2) arcuate (Fig. 1S) (CI = 0.50, RI = 0.75).

The concave apical margin of the pronotum is present in *Elmis* (Elmidae), *Sclerocyphon* and *Tychepsephus* (both in Eubriinae). When the apical margin of the pronotum is rounded, the entire head is concealed by the pronotum. The rounded pronotum occurs in *Psephenoides*, *Afropsephenoides* and Eubrianacinae.

17. *Basal rims of scutellum and elytra*: (0) smooth (Fig. 1S); (1) crenulate (Fig. 1R) (CI = 0.33, RI = 0.77).

The state distribution is consistent with that of character 15, except *Microebria* (Eubriinae), which have smooth basal rims of the scutellum and elytra but a crenulate rim of the pronotum. In addition, *Mataeopsephus chinensis* and *M. dentatus* have the same features as *Microebria*.

18. *Scutellum*: (0) without notches at basal margin (Fig. 1H); (1) with a notch at basal margin (Fig. 1I) (CI = 1.00, RI = 1.00).

The basal margin of the scutellum with a notch appears in *Neopsephenoides* and *Xylopsephenoides*.

19. *Connection of both elytra in males*: (0) immediately behind scutellum (Fig. 1H); (1) between metanotal grooves (Fig. 1I); (2) without connection (Fig. 1W) (CI = 1.00, RI = 1.00).

The connection of both elytra folding between metanotal grooves in males appears in *Neopsephenoides* and *Xylopsephenoides*.

20. *Proventrite*: (0) smooth; (1) a pair of longitudinal ridges near prosternal process (CI = 0.33, RI = 0).

A pair of longitudinal ridges near the prosternal process is present in *Acneus* and *Nipponeubria*.

21. *Apex of mesoventrite*: (0) truncate or emarginate (Fig. 1T); (1) tapering (Fig. 1U) (CI = 0.33, RI = 0.33).

The pointed apex of the mesoventrite occurs in *Cneoglossa*, *Afroebria*, *Psephenoides* and *Afropsephenoides*.

22. *Median longitudinal sulcus on mesoventrite*: (0) absent (Fig. 1T); (1) present (Fig. 1U) (CI = 0.12, RI = 0.46).

A median longitudinal sulcus on the mesoventrite appears in *Elmis*, *Sclerocyphon*, *Tychepsephus*, *Acneus*, *Schinostethus*, *Microebria*, *Psephenoides*, *Afropsephenoides*, *Jinbrianax*, *Mubrianax*, *Psepheninae* and some species of *Dicranopselaphus*.

23. *Connection between prosternal process and mesoventral cavity*: (0) present (Fig. 1T); (1) absent (Fig. 1U) (CI = 0.50, RI = 0.90).

The reduced prosternal process associated with the absence of the mesosternal cavity is found Eubrianacinae, Psephenoidinae and *Afroebria* (Eubriinae).

24. *Transverse suture of metaventricle*: (0) well developed (Fig. 1U, V); (1) vestigial (Fig. 1T); (2) reduced (CI = 0.50, RI = 0.84).

The transverse suture of the metaventricle is vestigial in Psepheninae and Eubriinae, except *Sclerocyphon* and *Tychepsephus*, and reduced completely in Cneoglossidae.

25. *Abdomen*: (0) five ventrites in both sexes; (1) seven ventrites in males, six ventrites in females (CI = 1.00, RI = 1.00).

Males with seven abdominal ventrites and females with six abdominal ventrites characterize Psepheninae.

26. *Apical margins of abdominal ventrites II–IV*: (0) smooth (Fig. 2E); (1) serrate (Fig. 2F) (CI = 0.33, RI = 0.33).

Serrate apical margins of abdominal ventrites II–IV appear in some genera of Eubriinae (*Sclerocyphon*, *Granuleubria*, *Ectopria* and *Eubria*).

27. *Metacoxal suture*: (0) present (Fig. 1T, U); (1) absent (Fig. 1V) (CI = 1.00, RI = 1.00).

The metacoxal suture is absent in *Neopsephenoides* and *Xylopsephenoides*.

28. *Femur*: (0) without groove; (1) with groove for reception of tibia (CI = 0.25, RI = 0.72).

Femora with grooves for the reception of tibiae appear in *Phanocerus*, Eubriinae and Psepheninae (except *Psephenops*).

29. *Groove on femur*: (0) both ridges at same height (Fig. 3E); (1) both ridges at different heights (Fig. 3F) (CI = 0.33, RI = 0.33).

The external ridge is higher than internal one in some genera of Eubriinae (*Eubria*, *Schinostethus*, *Macroebria* and *Microebria*).

30. *Apical spurs of tibiae*: (0) present; (1) absent (CI = 1.00, RI = 1.00).

Apical spurs of the tibiae are absent in Psephenoidinae.

31. *Formula of apical spurs of tibia in males*: (0) 2-2-2; (1) 2-1-1 (CI = 1.00, RI = 1.00).

The reduced number of apical spurs appears in Eubrianacinae, except *Jinbrianax*. It is inapplicable to Psephenoidinae, as apical spurs are completely absent.

32. *Apical spurs on tibiae in males*: (0) both the same size; (1) one smaller on middle and hind tibiae (CI = 0.50, RI = 0.50).

Different sizes of apical spurs on the tibiae appear in males of most genera within Psepheninae (*Pheneps*, *Psephenops* and genus D).

33. *Formula of apical spurs of tibiae in females*: (0) 2-2-2; (1) 2-2-1; (2) 2-1-1 (CI = 1.00, RI = 1.00).

This character transformation is new to Lee *et al.* (2003a). Only one spur on each hind tibia appears in *Odontanax* and *Jaechanax*. One spur on each middle and hind tibia appears in *Afrobrianax* and *Eubrianax*.

34. *Ventral teeth of tibiae*: (0) absent (Fig. 3F); (1) present (Fig. 3E) (CI = 0.25, RI = 0).

Ventral teeth on tibiae appear in most genera of Psepheninae (*Mataeopsephus*, *Psephenus* and genus D).

35. *Tarsomeres I and II*: (0) slender (Fig. 3A); (1) dilated on front and middle legs in males (Fig. 3B–D) (CI = 0.50, RI = 0.50).

Dilated tarsomeres I and II on front and middle legs appear in *Pheneps*, *Psephenops* and genus D.

36. *Ventral laminar expansions on tarsomeres I and II in males*: (0) absent (Fig. 3A, B); (1) present (Fig. 3C, D) (CI = 1.00, RI = 1.00).

Ventral lobes on tarsomeres I and II in males appear in *Psephenops* and genus D.

37. *Claws*: (0) without angular bases (Fig. 2G, H); (1) with angular bases (Fig. 2I) (CI = 0.14, RI = 0.33).

The hardened and expanded bases of tarsi appear in some genera of Eubriinae, including *Granuleubria*, *Ectopria*, *Homoeogenus*, *Acneus*, *Schinostethus*, *Macroebria* and *Dicranopselaphus*, as well as *Mubrianax* and *Afrobrianax* within Eubrianacinae.

38. *Anterior claw in males*: (0) simple (Fig. 2G); (1) one tooth at apex (Fig. 2H, I); (2) one tooth at middle (CI = 0.20, RI = 0.33).

One bifurcate claw of both claws in males appears in *Granuleubria*, *Ectopria*, *Homoeogenus*, *Acneus*, *Eubria*, *Schinostethus*, *Macroebria*, *Dicranopselaphus*, *Neopsephenoides* and *Afropsephenoides*. Those of *Homoeogenus* are diverse. There is a small tooth on each claw or no teeth at both claws (*H. elongatum*). Thus, *Homoeogenus* can not be coded for characters 38 and 39.

39. *Posterior claws (males)*: (0) simple (Fig. 2G, H); (1) one tooth at apex of claw (Fig. 2I); (2) one tooth at middle of claw (CI = 0.20, RI = 0.50).

The state distribution is consistent with the preceding character, except for *Acneus* and *Eubria*, which have one bifurcate claw and one simple claw.

40. *Claws (females)*: (0) simple; (1) bifurcate near apex (CI = 0.50, RI = 0.50).

The bifurcate claws in females occur in most genera of Psephenoidinae, except *Psephenoides*.

41. *Pulvilli on tarsal claws*: (0) absent; (1) present (CI = 0.50, RI = 0).

The apomorphic condition appears in *Eubrianax* and *Jaechanax* (both in Eubrianacinae). Costa *et al.* (1999; character 24) implied that the apomorphic conditions also appeared in Psephenoidinae. Actually, none of the species of this subfamily has pulvilli.

42. *Aedeagus*: (0) fibula absent (Fig. 3K, N–P); (1) fibula present, V-shaped (Fig. 3L); (2) fibula with two apical processes (Fig. 3M) (CI = 0.28, RI = 0.58).

The V-shaped fibula appears in *Sclerocyphon*, *Tychepephus*, *Afroebria*, *Granuleubria*, *Ectopria* and some species of *Macroebria*. The apically bifurcate fibula occurs in *Nippoebria*, *Acneus*, *Eubria* and some species of *Macroebria*.

43. *One pair of slender auxiliary sclerites articulated with penis*: (0) absent; (1) present (Fig. 3N) (CI = 0.50, RI = 0).

The auxiliary sclerites appear in *Psephenoides* and *Neopsephenoides*.

44. *Apices of parameres*: (0) rounded; (1) recurved, hook-like (Fig. 3O) (CI = 0.50, RI = 0.50).

The recurved and hook-like apices of parameres appear in some genera of Eubrianacinae (*Mubrianax*, *Afrobrianax* and *Eubrianax*).

45. *Apices of parameres*: (0) exposed; (1) covered by a rounded sclerite (Fig. 3O) (CI = 1.00, RI = 1.00).

The state distribution is the same as with the preceding character, except in *Mubrianax*, whose parameres have hook-like apices not covered by a rounded sclerite.

46. *Mesal margin of each paramere*: (0) smooth; (1) with one process (Fig. 3P) (CI = 0.50, RI = 0).

The presence of a process on the mesal margin of each paramere occurs in *Jinbrianax* and *Odontanax*.

47. *Basal piece*: (0) asymmetric; (1) symmetric (Fig. 3K) (CI = 1.00, RI = 1.00).

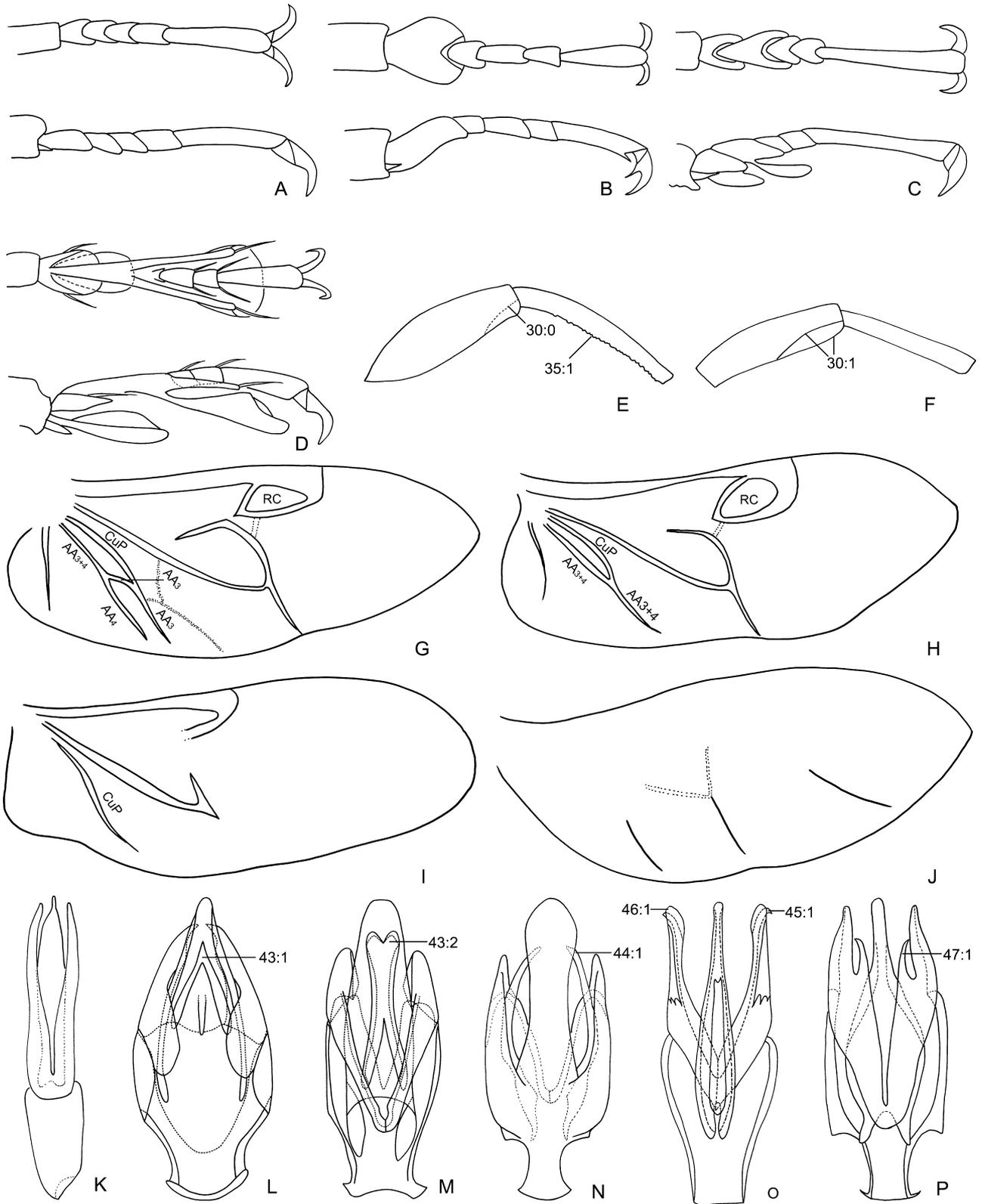
The pleisomorphic condition only appears in Elmidae. The asymmetric aedeagus is shared with the elmid–dryopid line (Crowson, 1978), including Elmidae, Dryopidae, Lutrochidae, Limnichidae and Heteroceridae.

48. *CuP of hind wing*: (0) ending with AA veins (Fig. 3G, H); (1) intact (Fig. 3I); (2) veins absent (Fig. 3J) (CI = 0.66, RI = 0.75).

The presence of only vein CuP occurs in *Mataeopsephus* and *Pheneps*. All veins are reduced in Psephenoidinae. Such an autapomorphy in Psephenoidinae is applied to characters 48–50.

49. *AA₃₊₄ of hind wing*: (0) forked (Fig. 3G); (1) not forked (Fig. 3H); (2) veins reduced (Fig. 3I, J) (CI = 0.33, RI = 0.71).

The forked vein AA₃₊₄ occurs in all outgroups, *Sclerocyphon*, *Tychepephus*, *Schinostethus*, *Eubrianacinae* and some



species of *Psephenus*. The unforked vein AA_{3+4} occurs in the remaining eubriines and some species of *Psephenus*. The vein is reduced in *Mataeopsephus*, *Pheneps* and Psephenoidinae.

50. *Radial cell of hind wing*: (0) open (Fig. 3I); (1) closed (Fig. 3G, H); (2) veins absent (Fig. 3J) (CI = 0.66, RI = 0.80).

The open radial cell occurs in *Phanocerus*, *Elmis* and *Jinbrianax*.

Larva

51. *Antennae*: (0) short, antennomere I smaller than antennomere II; (1) moderately long, antennomere I subequal or longer than antennomere II (CI = 0.25, RI = 0.80).

Costa *et al.* (1999) coded larval antennae into two discrete states: moderately long and very short. They are not objectively coded because of insufficient comparisons. Costa *et al.* (1999) supposed that only Eubriinae had very short antennae. If short antennae indicate the relatively smaller first antennomere, their assumption is incorrect because several exceptions exist (*Sclerocyphon*, *Tycheapsephus*, genus B and *Granuleubria* have relatively longer antennae). According to this definition, Psephenoidinae and *Cneoglossa* also have the relatively smaller first antennomere.

52. *Number of segments in maxillary palpi*: (0) four-segmented; (1) three-segmented; (2) two-segmented (CI = 0.66, RI = 0.93).

Three-segmented maxillary palpi occur in most genera in Eubriinae, except *Sclerocyphon* and *Tycheapsephus*, and genus A.

53. *Number of segments in labial palpi*: (0) three-segmented; (1) two-segmented; (2) one-segmented (CI = 0.66, RI = 0.93).

The state distribution is the same as with the preceding character.

54. *Mandible*: (0) with four apical teeth (1) without apical teeth (CI = 0.28, RI = 0.44).

Unlike the outgroups, ingroups whose mandibles have four apical teeth are somehow correlated with a xylophagous or saprophytophagous lifestyle. For example, *Macroebria* (Eubriinae), *Xylopsephenoides* (Psephenoidinae), *Mubrianax* and *Jaechanax* (Eubrianacinae) are xylophagous; *Homoeogenus* are saprophytophagous.

55. *Body form*: (0) cylindrical (Fig. 4A); (1) elongate and flattened (e.g. Figs 4B, E, H, J, 5H, I); (2) broadly oval and flattened (e.g. Figs 4D, F, G, 5D, E) (CI = 0.25, RI = 0.60).

Costa *et al.* (1999) assumed that the flattened body shape is autapomorphic for Psephenidae. However, some members of both subfamilies within Elmidae are also flattened and a division into three states is required to distinguish representatives of Psephenidae from others. The broadly oval and flattened body form occurs in Psepheninae, most genera of Psephenoidinae (except *Xylopsephenoides*) and Eubrianacinae (except *Mubrianax* and *Jaechanax*), and some genera of Eubriinae (*Tycheapsephus*, *Afroebria*, *Schinostethus* and *Dicranopselaphus*). This character is polymorphic in *Sclerocyphon* (Eubriinae).

56. *Medial suture*: (0) well developed, reaching abdominal segment VII (Figs 4D–G, 6); (1) abbreviated on segment VII–IX (CI = 0.25, RI = 0.75).

The medial suture is reduced on abdominal tergites VII–IX in *Cneoglossa*, *Phanocerus*, Eubrianacinae and most genera of Eubriinae (except *Sclerocyphon*, *Tycheapsephus* and *Afroebria*).

57. *Cuticular beads on dorsal surface*: (0) present; (1) reduced (CI = 0.12, RI = 0.41).

Cuticular beads on the dorsal surface are reduced in some genera of Eubriinae (including *Homoeogenus*, *Acneus*, *Schinostethus*, *Macroebria*, *Microebria*, and *Dicranopselaphus*, genera A and C) and most psephenoidines (except *Xylopsephenoides*).

58. *Apical margins of prothorax*: (0) emarginate or truncate, head exposed (Fig. 4A–C); (1) anteriorly produced, head concealed (Figs 4D–L, 5–7) (CI = 1.00, RI = 1.00).

The anteriorly produced prothorax characterizes the family Psephenidae.

59. *D1 (hair-like) setae on outward margins of thoracic and abdominal paratergites I–VII segments*: (0) absent; (1) present (CI = 0.25, RI = 0.70).

Macroebria and *Microebria* have one layer of dorsal setae on paratergites. Those of *Macroebria* should be regarded as D2, and those of *Microebria* as D1 when homologizing those of genus C. The D1 setae are present in eubrianacines, eubriines (except *Macroebria* and *Dicranopselaphus*), and two genera of Psephenoidinae (*Afropsephenoides* and *Xylopsephenoides*). This character is polymorphic in *Sclerocyphon* (Eubriinae), *Psephenoides* (Psephenoidinae) and *Mataeopsephus* (Psepheninae).

60. *D1 hair-like setae on lateral margin of abdominal paratergites VIII*: (0) absent; (1) present (CI = 0.25, RI = 0.66).

Fig. 3. Adult features used in the phylogenetic analysis. A–D, Tarsus, dorsal (upper) and lateral (lower) views; E, F, femur and tibia; G–J, hind wing; K–P, aedeagus. A, *Psephenus herricki*; B, *Pheneps cursitatus*; C, *Psephenops* sp.; D, genus D; E, *Psephenus herricki*; F, *Schinostethus (Sundodrupheus) notatithorax*; G, *Sclerocyphon minimus*; H, *Ectopria nervosa*; I, *Elmis aenea*; J, *Psephenoides subopacus*; K, *Phanocerus clavicornis*; L, *Ectopria chikuni*; M, *Macroebria diffusa*; N, *Psephenoides subopacus*; O, *Eubrianax insularis*; P, *Odontanax dohertyi*.

This character is inapplicable to Cneoglossidae, Psephenoidinae and Psepheninae without abdominal paratergites VIII. The state distribution is consistent with character 59, except for some genera of Eubriinae (*Nipponeubria*, *Acneus*, *Eubria*, *Schinostethus*, genus B), whose D1 setae appear on the outward margins of thoracic and abdominal paratergites I–VII, but are reduced on lateral margins of abdominal paratergites VIII.

61. *D1 hair-like setae on outward margin of abdominal tergite IX*: (0) absent; (1) all over lateral and apical margin (Figs 10E, F, 11A); (2) only present on lateral margins (Figs 10C, 11B–D) (CI = 0.28, RI = 0.61).

The state distribution is consistent with that of character 59, except that *Ectopria*, *Nipponeubria*, *Acneus* and *Schinostethus* have D1 setae confined to lateral margins of abdominal tergite IX, and *Afroebria*, *Microebria*, genera B and C lack D1 setae on abdominal tergite IX.

62. *D1 setae on abdominal paratergites I–VII*: (0) all over outer margins of paratergites (Fig. 8F); (1) confined to areas near apices of paratergites (Fig. 9A, B, E, F, H, J, L, P); (2) reduced into one pair (Fig. 9T–V) (CI = 0.50, RI = 0.80).

This character is inapplicable to *Cneoglossa*, *Phanocerus*, *Elmis*, *Dicranopselaphus* and Psepheninae due to the lack of D1 setae. D1 setae are restricted to near the apex (most eubriines, including *Afroebria*, *Granuleubria*, *Ectopria*, *Homoeogenus*, *Nipponeubria*, *Acneus*, *Eubria*, *Schinostethus* and genus B), or even reduced to one pair on the outer margin of each paratergite (*Microebria* and genus C).

63. *D2 setae*: (0) without basal pieces (e.g. Fig. 8A, C, H, I, O, Q); (1) with basal pieces (CI = 0.25, RI = 0.62).

The D2 setae with basal pieces occur in *Macroebria*, genera A and C, and Eubrianacinae.

64. *Basal pieces of marginal peg setae*: (0) without lateral teeth (Figs 8L, 9N, V); (1) with lateral teeth on one side; (2) with lateral teeth on both sides (Fig. 8E) (CI = 1.00, RI = 1.00).

This character is inapplicable to those taxa without basal pieces, which are coded as zero in the preceding character. Teeth on one side of the basal piece occur only in *Jinbrianax*. Teeth on both sides of the basal piece occur in the remaining genera of Eubrianacinae.

65. *D2 setae on apical margins of abdominal paratergites VIII*: (0) present; (1) absent (CI = 0.50, RI = 0.66).

This character is inapplicable for those taxa without abdominal paratergite VIII, as in character 60. D2 setae (on apical margins of abdominal paratergites VIII) are absent in *Afroebria*, *Schinostethus*, *Microebria*, *Dicranopselaphus*, and genus C.

66. *D2 setae on outward margin of prothorax*: (0) ramose; (1) hair-like (CI = 0.20, RI = 0.33).

This character is inapplicable to *Microebria* due to the lack of D2 setae and Cneoglossidae due to the absence of setae on the outer margin of the prothorax. Ramose D2 setae on the outward margin of the prothorax occur in *Elmis* and *Granuleubria*, *Ectopria*, *Homoeogenus*, *Nipponeubria*, *Acneus* and *Dicranopselaphus*.

67. *Hair-like D2 setae on outward margin of prothorax*: (0) basal halves sclerotized; (1) without sclerotization (CI = 0.25, RI = 0.70).

This character is inapplicable to those taxa with ramose D2 setae, as mentioned in the preceding character. Unsclerotized D2 setae on the outward margin of the pronotum occur in *Phanocerus*, *Eubria*, *Schinostethus*, *Macroebria*, genera A, B and C, Eubrianacinae and most Psephenoidinae (except *Xylophenoides*).

68. *D2 setae on outward margins of all paratergites except for prothorax, abdominal paratergites VIII and tergite IX*: (0) ramose (Figs 8Q, 9A, B, E, G, I, J, L, S); (1) hair-like (Figs 8A, C, E, H, I, L, O, 9N, Q, V) (CI = 0.33, RI = 0.75).

The state distribution is consistent with that of character 66, except in *Eubria* and genus B (both in Eubriinae). In both genera, D2 setae are hair-like and unsclerotized on the prothorax, but they are ramose on other segments. D2 setae of *Phanocerus* and *Schinostethus* should be coded as state 1, although the D2 setae are covered with dense hairs.

69. *Hair-like D2 setae on lateral margins of all paratergites except for prothorax, abdominal paratergites VIII and tergite IX*: (0) basal halves sclerotized (Fig. 8A, C, H, I); (1) without sclerotization (Figs 8E, L, O, 9N, Q, V) (CI = 0.25, RI = 0.70).

The state distribution is consistent with that of character 67, except that it is inapplicable to *Eubria* and genus B due to the ramose D2.

70. *Distribution of D2 setae on outward margins of paratergites*: (0) overlapping with D1 setae; (1) separated from D1 setae (Fig. 9A, B, E, J) (CI = 0.66, RI = 0.66).

This character is inapplicable to those genera with only one layer of both D1 and D2 setae, including Elmidae, *Macroebria*, *Microebria* and *Dicranopselaphus*. The separation between D2 and D1 setae on pleurites occurs in some genera within Eubriinae, including *Granuleubria*, *Ectopria*, *Homoeogenus* and *Eubria*.

71. *D2 setae on lateral margins of abdominal tergite IX*: (0) ramose (Figs 10A, B, E, 11B–D); (1) simple (Fig. 10C, D, F); (2) absent (CI = 0.28, RI = 0.44).

The state distribution is consistent with character 68, except that *Granuleubria* has ramose D2 setae on paratergites and flattened D2 setae on the lateral margins of abdominal tergite IX, and *Afroebria* has hair-like D2 setae on paratergites and ramose D2 setae on lateral margins of abdominal tergite IX. Although D2 setae of *Elmis* look like hairs, they are apically bifurcate.

72. *D2 setae on apical margin of abdominal tergite IX*: (0) ramose (Figs 10A, 11B); (1) simple (Fig. 10B, C, F); (2) absent (CI = 0.28, RI = 0.37).

The state distribution is consistent with the preceding character, except that *Ectopria* have flattened D2 setae; *Homoeogenus*, *Nipponeubria*, *Eubria*, *Schinostethus*, *Macroebria* and *Microeuria* have no D2 setae.

73. *Simple D2 setae on apical margin of abdominal tergite IX*: (0) shorter than those on paratergites (Fig. 10F); (1) as long as those on paratergites (CI = 0.33, RI = 0.66).

This character is inapplicable to those genera without D2 setae or with ramose D2 setae (cf. character 72). The shorter simple D2 setae occur in *Phanocerus*, *Granuleubria*, *Ectopria* and Psephenoidinae.

74. *D2 setae on anterior margins of all paratergites*: (0) present on entire margin (e.g. Fig. 9A, B); (1) present from basal one-third or middle (Fig. 9E, G, I, N, Q, V) (CI = 0.25, RI = 0.40).

The plesiomorphic condition occurs in Elmidae, *Granuleubria*, *Ectopria*, *Eubria* and genus A.

75. *D3 (flattened) setae on anterior margins of paratergites except for abdominal paratergites VIII and tergite IX*: (0) absent; (1) present (Fig. 9D, F, H, K, Q) (CI = 1.00, RI = 1.00).

D3 setae occur in most genera of Eubriinae, except *Sclerocyphon*, *Tychepsephus*, *Afroebria*, *Granuleubria*, *Ectopria* and genus A.

76. *D3 setae*: (0) small (Fig. 9F, H, K); (1) well developed (Fig. 9D, Q) (CI = 0.50, RI = 0.66).

This character is inapplicable to those taxa having no D3 setae, which have the plesiomorphic condition of the preceding character. The well-developed D3 setae may be correlated with more slender paratergites, which occur in *Homoeogenus*, *Schinostethus*, *Macroebria*, *Microebria*, *Dicranopselaphus* and genus C.

77. *D3 (flattened) setae on lateral margin of abdominal tergite IX*: (0) absent; (1) present (CI = 0.50, RI = 0.85).

The state distribution is consistent with that of character 75, except that *Homoeogenus* and *Dicranopselaphus* lack D3 setae on abdominal tergite IX.

78. *VS on outer margin of all paratergites*: (0) present; (1) absent (CI = 0.50, RI = 0).

VS are absent in *Cneoglossa* and genus C. They are polymorphic in *Homoeogenus*. Characters 79–81 are inapplicable to those taxa having no VS.

79. *VS on outer margins of thoracic paratergites*: (0) lanceolate; (1) ramose; (2) hair-like setae (CI = 0.25, RI = 0.53).

Lanceolate processes are located on the outer margins of paratergites ventrally in psephenoidines; additionally, some

hair-like setae appear (Fig. 8D). Thus, the VS of Psephenoides are hair-like and lanceolate. Most eubrianacines have lanceolate VS (Fig. 8E, F). However, VS in early-instar *Jinbrianax* are widened and with a number of longitudinal veins (Fig. 8G). They are apically ramose in the late-instar larvae. This should be coded as states 0 and 1 simultaneously.

80. *VS on anterior margins of abdominal paratergites I–VIII*: (0) lanceolate (Figs 8J, 9C, R, T, U); (1) apically ramose (Figs 8B, N, Q, 9K, M, S); (2) hair-like setae (Figs 8H, 9O) (CI = 0.28, RI = 0.61).

The state distribution is consistent with the preceding character, except for *Eubria* and genus A. Both genera have hair-like VS on the thoracic paratergites (Fig. 8M) and apically ramose VS on the abdominal paratergites (Fig. 8N). VS of *Phanocerus* (Elmidae) are ring-like (Fig. 8P). This should be coded as state 2 because they can be the curved hair-like setae.

81. *VS*: (0) one row (Figs 8B, J, M, N, P, Q, 9K, R–U); (1) two rows (Figs 8D, 9C, M, O) (CI = 0.25, RI = 0.76).

Two rows of VS occur in *Granuleubria*, *Ectopria*, *Macroebria*, genus B, Eubrianacinae, Psephenoidinae and some species of *Schinostethus*. Those on eubrianacines have one row on the outer margins of the paratergites (Fig. 8F, G), and the other on apices of basal pieces (Fig. 8E).

82. *Setae on posterior margins of all but last two abdominal paratergites (SPP)*: (0) similar to D2 setae (Fig. 8I, L, Q); (1) different from D2 setae, wide and flattened (Fig. 8A, E, H, O); (2) different from D2 setae, elongate and flattened (Fig. 8D); (3) absent (CI = 0.60, RI = 0.86).

SPP of *Elmis*, *Sclerocyphon*, *Tychepsephus* and genus A are similar to D2 setae, although they are a little different in shape. SPP of Eubrianacinae, Psepheninae, *Phanocerus* and *Afroebria* differ from D2 setae by the wide and flattened shape. The remaining genera of Eubriinae have long, flattened SPP. The SPP of *Psephenoides*, *Neopsephenoides* and *Afropsephenoides* are elongate, but they also look like the widened and flattened setae due to bearing numerous branches (Fig. 8C) and thus should be coded as states 1 and 2. The SPP of *Xyloapsephenoides* are similar to those of other psephenoidines, but without branches (Fig. 8D). They should be coded as state 2. *Cneoglossa* lacks SPP.

83. *Mid-dorsal pronotal plate*: (0) absent; (1) incomplete (Fig. 7E, F); (2) well developed (Fig. 7C) (CI = 1.00, RI = 1.00).

The mid-dorsal pronotal plate is located along the medial suture, halfway between the outward margin of the pronotum. The incomplete condition has only the anterior half of the mid-dorsal pronotal plate visible. This condition occurs in *Eubrianax pellucidus*, *E. amamiensis*, *Jaechanax* and *Mubrianax*. In the latter two genera, the plate is connected with the pericellar sulci. The mid-dorsal pronotal plate appears in *Afrobrianax* and some species of *Eubrianax* (cf. Lee *et al.*, 2001: character 10).

84. *Dividing sulci at posterior plates on pronotum*: (0) absent; (1) present (Fig. 7D–F) (CI = 1.00, RI = 1.00).

This character applies only to Psepheninae and Eubrianacinae, which have posterior plates on the pronotum. The dividing sulci occur in *Odontanax*, *Jaechanax* and *Mubrianax*. It is polymorphic for *Jinbrianax* and *Eubrianax* (cf. Lee *et al.*, 2001: character 12).

85. *Periocular sulci*: (0) absent; (1) present, not connected with anterior half of mid-dorsal pronotal plate (Fig. 7A, B); (2) present, connected with anterior half of mid-dorsal pronotal plate (Fig. 7E, F) (CI = 1.00, RI = 1.00).

The periocular sulci are separated from the mid-dorsal pronotal plate in *Jinbrianax* and some species of *Eubrianax*. The combination of the periocular sulci and the anterior half of the pronotal plate occurs in *Jaechanax* and *Mubrianax*.

86. *Posterior plates on thoracic tergites*: (0) absent; (1) present, not segmented on meso- and metathorax (Fig. 6A, B); (2) present, segmented on meso- and metathorax (Fig. 7) (CI = 1.00, RI = 1.00).

The posterior plates on thoracic tergites appear in Eubrianacinae and Psepheninae (Figs 6B, 7A). Division of the posterior plates occurs in Eubrianacinae.

87. *Posterior plates on abdominal tergites I–III*: (0) absent; (1) present (Fig. 7F) (CI = 1.00, RI = 1.00).

The posterior plates on abdominal tergites I–III appear in *Odontanax*, *Jaechanax*, *Mubrianax* and some species of *Eubrianax* (Fig. 7B, D–F).

88. *Posterior plates on abdominal paratergites I–V*: (0) absent; (1) present (Fig. 7E) (CI = 0.50, RI = 0).

The state distribution is consistent with the preceding character, except for *Jaechanax*, whose posterior plates occur only on abdominal tergites I–III (Fig. 7B, D, E).

89. *Costal lines*: (0) absent; (1) present (Figs 6A, 7D) (CI = 0.50, RI = 0.88).

Costal lines occur in Eubrianacinae (except *Jinbrianax*) and Psepheninae (Figs 6A, B, 7B–F).

90. *Tergopleural sutures*: (0) absent; (1) present, including prothorax but excluding abdominal tergite VIII; discontinuous between segments (Fig. 6B); (2) present, excluding pronotum but including abdominal tergites VIII; continuous between segments (Fig. 7C) (CI = 1.00, RI = 1.00).

Tergopleural sutures occur in Psepheninae and Eubrianacinae. They appear between the prothorax and abdominal tergites VII in Psepheninae (Fig. 6A, B), but are discontinuous between segments. In Eubrianacinae, they appear continuous between the mesothorax and abdominal tergites VIII (Fig. 7).

91. *Sulci 1 on pronotum*: (0) absent; (1) present (Figs 4G, 5D, G, 6B, 7A) (CI = 0.20, RI = 0.50).

Sulci 1 were first found in *Jinbrianax* (Eubrianacinae), which Lee *et al.* (1999c) termed as 'midpronotal longitudinal sulci'. However, these sulci have been found in Psepheninae and some members of Eubriinae (*Afroebria*, *Schinostethus* and genus B), especially for Psepheninae, in which a similar structure is also present at meso- and metanota.

92. *Sulci 2 on meso- and metanota*: (0) absent; (1) present (Fig. 6B) (CI = 1.00, RI = 1.00).

An additional pair of sulci (sulci 2) appears on the meso- and metanota in Psepheninae (Fig. 6A, B).

93. *Functional spiracles on abdominal segments I–VII*: (0) present (Fig. 4A, B); (1) absent (CI = 1.00, RI = 1.00).

The absence of functional spiracles on abdominal segments I–VII characterizes Psephenidae.

94. *Functional spiracles on abdominal segment VIII of earlier-instar larvae*: (0) absent; (1) present (Figs 4G, 6B, 7B) (CI = 0.33, RI = 0.71).

Functional spiracles on young larvae appear in most psephenids, except *Sclerocyphon*, *Tychepephus* and Psephenoidinae. Lee & Yang (2002) assumed the spiracles of *Microebria* on the eighth abdominal segment to be reduced due to a lack of spiracular brushes. However, this hypothesis is incorrect, as connecting trachea and apices of pleurites can be observed.

95. *Functional spiracles on abdominal segment VIII of last-instar larvae*: (0) present; (1) absent (CI = 1.00, RI = 1.00).

This is an ontogenetic character of the preceding character. The state distribution is consistent with the preceding character, except Elmidae, *Sclerocyphon*, *Tychepephus* (both in Eubriinae). Larvae of these taxa have functional spiracles only in the last instar. Other eubriines, Psepheninae and Eubrianacinae have functional spiracles throughout the entire larval stage. Larvae of Psephenoidinae have lost spiracles throughout the entire larval stage.

96. *Position of functional spiracles on abdominal segment VIII*: (0) inside tergites (Fig. 4B); (1) near base of paratergites (Fig. 4F, H, 7B); (2) at apices of paratergites (Fig. 4I) (CI = 0.60, RI = 0.90).

Although the spiracles of Eubrianacinae are inside the segment, they are near the bases of paratergites. Spiracles are located at the apices of abdominal paratergites VIII in Psepheninae: the paratergites are so short that the position of spiracles is the same as those at the bases of paratergites (such as *Sclerocyphon*, *Tychepephus* and genus A). Thus, this character is coded as polymorphic (states 1 and 2) for Psepheninae. Spiracles of most eubriines (except *Sclerocyphon*, *Tychepephus* and genus A) are located on the apices of paratergites VIII.

97. *Position of functional spiracles on abdominal segment VIII*: (0) inside segment (Fig. 4B); (1) at margin of segment (Fig. 4F) (CI = 0.50, RI = 0.87).

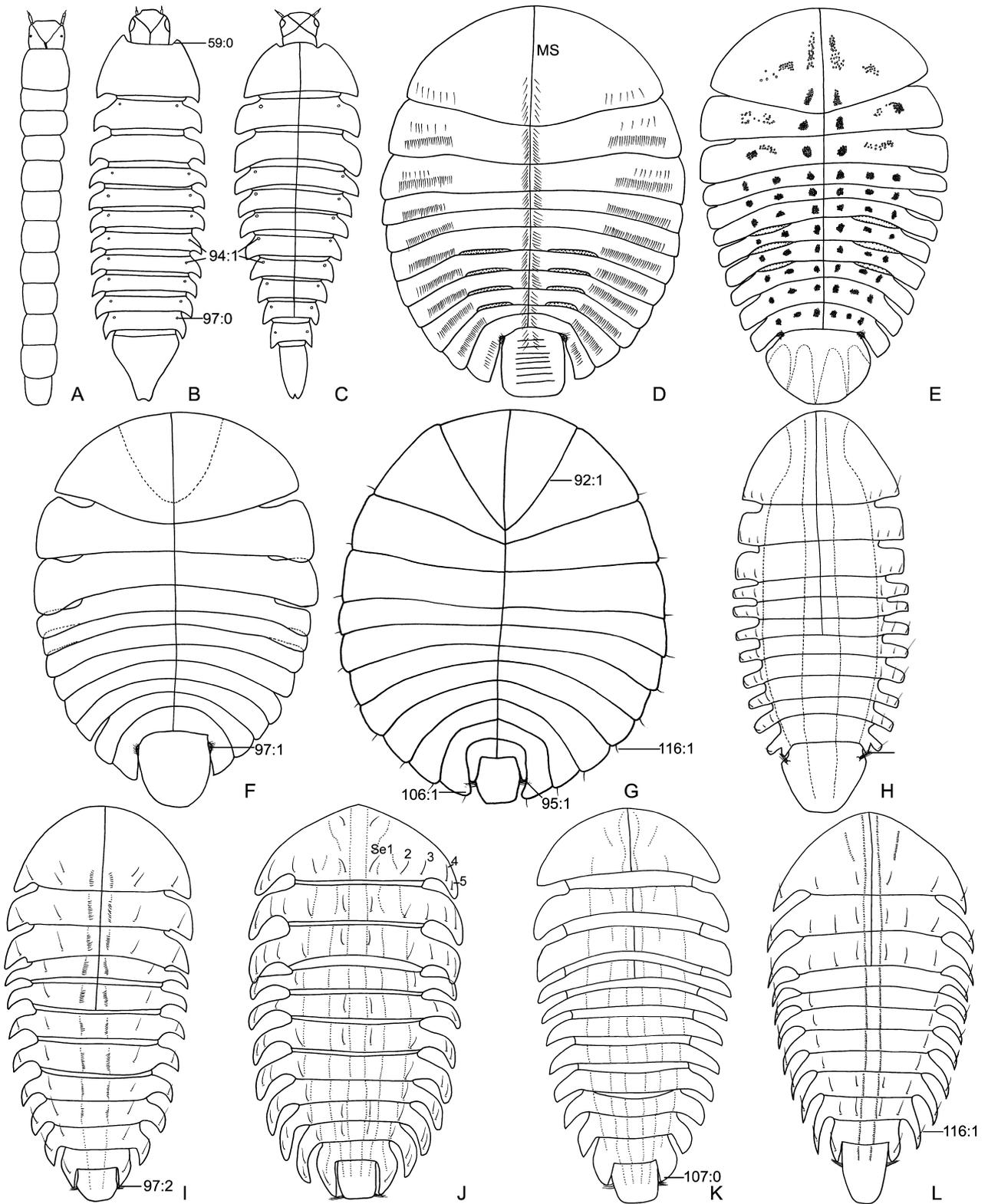


Fig. 4. Larval habitus, dorsal view. A, *Cneoglossa edsoni* [redrawn after Costa *et al.* (1999)]; B, *Phanocerus clavicornis*; C, *Elmis aenea*; D, *Sclerocyphon* type A; E, *Sclerocyphon striatus*; F, *Tychepephus felix*; G, *Afroebria sebastiani*; H, genus A; I, *Granuleubria* sp.; J, *Ectopria leechi*; K, *Ectopria nervosa*; L, *Homoeogenus laurae*. Se = setae; MS = medial suture.

Characters 96 and 97 are inapplicable to Psephenoidinae, as they have no spiracles. Spiracles on abdominal segment VIII in Eubriinae and Psepheninae are located at the margins.

98. *Spiracular brush of earlier-instar larvae*: (0) absent; (1) present (CI = 0.20, RI = 0.73).

Spiracular brushes in earlier-instar larvae are present in Psepheninae, most eubriines (except *Sclerocyphon*, *Tychecephus*, *Microeubria* and genus C) and *Jinbrianax*.

99. *Spiracular brush of last-instar larvae*: (0) absent; (1) present (CI = 0.25, RI = 0.76).

This is an ontogenetic character consistent with the preceding character with the exception of *Sclerocyphon* and *Tychecephus*. Spiracles in mature larvae of *Sclerocyphon* and *Tychecephus* are associated with the presence of spiracular brushes.

100. *Distribution of spiracular brush setae*: (0) all along the lateral margin of abdominal tergite IX; (1) a cluster of setae (Fig. 16A) (CI = 1.00, RI = 1.00).

Spiracular brushes are arranged as one row along the lateral margin in Psepheninae.

101. *Functional spiracles on mesothorax*: (0) present (Figs 6B, 7B); (1) absent (CI = 0.50, RI = 0.91).

Functional spiracles on the mesothorax are absent in Eubriinae and Psephenoidinae.

102. *Anal gills*: (0) present; (1) absent (CI = 0.33, RI = 0.81).

Anal gills are absent in Psepheninae and Eubrianacinae, which have abdominal gills instead.

103. *Anal gills*: (0) with three gill-tufts; (1) with two gill-tufts (CI = 0.50, RI = 0.50).

The two-tufted anal gills occur in *Sclerocyphon*, *Tychecephus* and genus A.

104. *Abdominal gills*: (0) absent; (1) pectinate; (2) fan-like (CI = 1.00, RI = 1.00).

Abdominal gills occur in Psepheninae and Eubrianacinae. In Psepheninae, they are pectinate and located between abdominal segments I and VII (or II and VII or III and VII). However, they are fan-like and always located between abdominal segments III and VII in Eubrianacinae.

105. *Abdominal paratergites VII*: (0) normal; (1) lengthened, reaching anterolateral angles of abdominal segment IX (Figs 4G, 6A); (2) lengthened, reaching apex of abdominal segment IX (Fig. 6C) (CI = 0.66, RI = 0.87).

The shortened abdominal paratergites VIII and lengthened abdominal paratergites VII that reach anterolateral angles of abdominal segment IX occur in *Afroebria* and Psepheninae. Abdominal segments IX in Psephenoidinae are apically tapering and surrounded by the lengthened abdominal segments VII.

106. *Abdominal paratergites VIII*: (0) same size as abdominal paratergites VII (Fig. 4K); (1) shorter than abdominal paratergites VII (Fig. 5G); (2) longer than abdominal paratergites VII (Fig. 5H) (CI = 0.28, RI = 0.66).

Shorter or absent abdominal paratergites VIII occur in Psephenoidinae, Psepheninae and most eubriines (except *Sclerocyphon*, *Tychecephus*, *Eubria*, genus A, *Granuleubria*, *Ectopria* and *Macroeubria*). Longer abdominal paratergites VIII only occur in *Microeubria*.

107. *Apex of abdominal segment IX of earlier-instar larvae*: (0) with notch; (1) smooth (CI = 0.50, RI = 0.87).

The bifurcate abdominal segment IX of earlier-instar larvae occurs in Elmidae and some eubriines (*Nipponeubria*, *Schinostethus*, *Macroeubria*, *Microeubria*, *Dicranopselaphus* and genera B and C).

108. *Apex of abdominal segments IX of last-instar larvae*: (0) with notch (Fig. 5B, C); (1) smooth (Fig. 5A) (CI = 0.50, RI = 0.88).

This is an ontogenetic character consistent with the preceding character, with the one exception of *Acneus*. Younger larvae of *Acneus* have the rounded apical margin of the last abdominal segment, which look like those of *Eubria*. However, mature larvae have a notch at the middle of the outward margin of the last abdominal segment (Fig. 5B). This difference between young and old stages of larvae caused Brown's (1976) misidentification: young larvae were identified as *Dicranopselaphus* and mature ones as *Acneus*. The true identity of the larva of *Dicranopselaphus* was revealed when Barr & Spangler (1994) established the synonymy of *Alabameubria* Brown (1980) with *Dicranopselaphus*.

109. *Orientation of setae on apex of last abdominal segment in young larvae*: (0) all orientated in same direction (1) setae on two sides orientated in different directions (CI = 0.50, RI = 0.90).

110. *Orientation of setae on apex of last abdominal segment in mature larvae*: (0) all orientated in same direction (1) setae on two sides orientated in different directions (CI = 0.50, RI = 0.91).

The state distributions of characters 109 and 110 correspond with characters 107 and 108, except in Psepheninae. Although larvae of Psepheninae have rounded outward margins of the last abdominal segments throughout the entire larval stage, setae at both sides of the outer margin orientate in different directions (Fig. 16D).

111. *Setae on posterior margin of thoracic and abdominal tergites*: (0) ramose; (1) hair-like; (2) absent (CI = 0.33, RI = 0.55).

The absence of setae on the posterior margins of thoracic and abdominal tergites occurs in Eubrianacinae, Psephenoidinae, Psepheninae and some eubriines (*Sclerocyphon*, *Afroebria*, *Microeubria* and genera A, B and C). The hair-like setae occur in *Tychecephus* and *Granuleubria*.

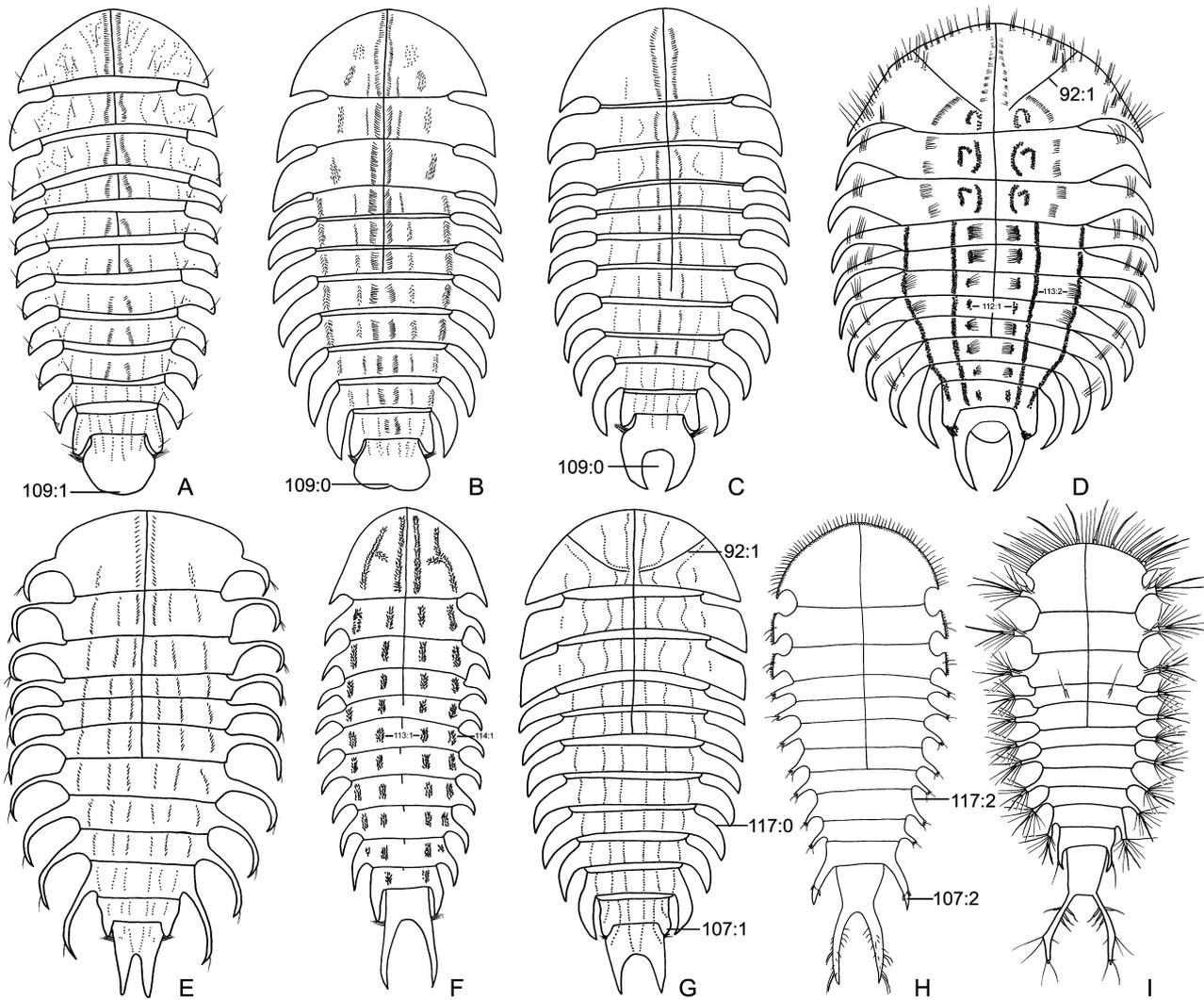


Fig. 5. Larval habitus, dorsal view. A, *Eubria palustris*; B, *Acneus* sp.; C, *Nipponeubria yoshitomi*; D, *Schinostethus (Sundodrupeus) albosulcus*; E, *Dicranopselaphus variegatus*; F, *Macroebria luei*; G, genus B; H, *Microebria* sp.; I, genus C.

112. One pair of longitudinal rows of setae or sensillae near medial suture: (0) absent; (1) present (Fig. 5D, F) (CI = 0.50, RI = 0.92).

The paired longitudinal rows of setae or sensillae near the medial suture occur in most eubriines (except *Tychepephus*). It is polymorphic in *Afroebria*.

113. Pairs of longitudinal rows of setae or sensillae on abdominal tergites: (0) absent; (1) one paired row (Fig. 5F); (2) two paired rows (Fig. 5D) (CI = 0.50, RI = 0.77).

Longitudinal rows of setae or sensillae on abdominal tergites occur in eubriines. One pair of rows appears in *Macroebria*, *Microebria* and genera A and C. Two pairs of rows appear in *Ectopria*, *Nipponeubria*, *Acneus*, *Eubria*, *Dicranopselaphus* and genus B. This character is polymorphic in *Sclerocyphon*, *Afroebria* and *Schinostethus*.

114. Pairs of longitudinal rows of setae or sensillae on abdominal tergites: (0) in the form of sensillae or hair-like setae; (1) granules or setae derived from granules; (2) ramose setae; (3) deciduous, membranous and hollow setae (CI = 0.50, RI = 0.40).

This is inapplicable to those genera without longitudinal rows of setae or sensillae on the abdominal tergites. Sensillae or hair-like setae occur in *Sclerocyphon*, *Afroebria*, *Homoeogenus* and *Schinostethus*. Granules occur in *Granuleubria*, *Ectopria*, *Nipponeubria*, *Acneus*, *Eubria*, *Dicranopselaphus* and genus B. Ramose setae occur in *Macroebria*. Membranous, hollow setae occur in *Microebria* and in genera A and C.

115. Setae V on anterior margin of paratergites: (0) absent; (1) present (Figs 4G, L, 6D) (CI = 0.16, RI = 0.68).

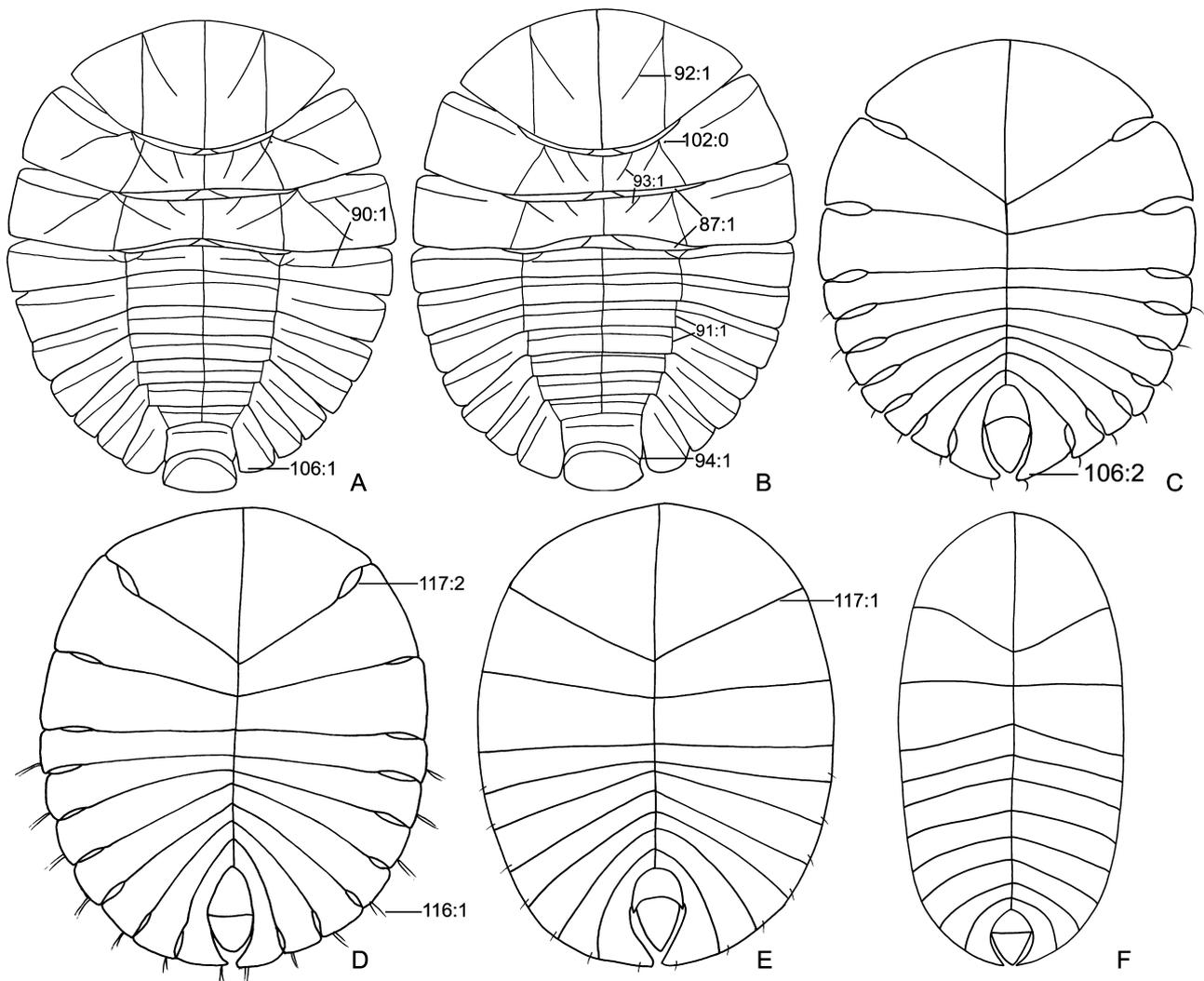


Fig. 6. Larval habitus, dorsal view. A, *Mataeopsephus esakii*; B, *Psephenus herricki*; C, *Afroapsephenoides ruthae*; D, *Psephenoides subopacus*; E, *Neopsephenoides nanus*; F, *Xyloapsephenoides gihongi*.

Setae V occur in *Elmis*, *Afroebria*, *Granuleubria*, *Ectopria*, *Homoeogenus*, *Eubria*, *Dicranopselaphus*, genus A, psephenoidines (except *Afroapsephenoides*) and eubrianacines.

116. *Anterior margins of paratergites*: (0) curved (Fig. 5G); (1) straight (Fig. 6E); (2) emarginate (Figs 5H, 6D) (CI = 0.50, RI = 0.85).

Straight anterior margins of paratergites occur in *Sclerocyphon*, *Tycheapsephus*, *Afroebria*, genus A, *Neopsephenoides*, eubrianacines and psephenines. Emarginate anterior margins of paratergites occur in *Microebria*, genus C and the remaining genera of Psephenoidinae. Although the paratergites of *Xyloapsephenoides* are very short, the emarginate anterior margins of paratergites can still be observed.

117. *Proventrite*: (0) medially segmented; (1) intact; (2) laterally segmented (CI = 1.00, RI = 1.00).

The intact proventrite occurs in *Sclerocyphon*, *Tycheapsephus*, *Afroebria*, psephenoides, eubrianacines and psephenoidines. The lateral division of the proventrite occurs in the remaining genera of Eubriinae.

118. *Operculum*: (0) laterally open; (1) laterally closed, fused with auxiliary sclerites and tergite IX (CI = 0.50, RI = 0.88).

A laterally open operculum connects with abdominal ventrite IX only basally and can move upward 90°. It occurs in elmids, *Sclerocyphon*, *Tycheapsephus*, genus A and psephenines. The laterally closed operculum connects with the abdominal ventrite basally and laterally. It can move upward only 30° at most.

119. *Operculum*: (0) near apex of abdominal ventrite (Fig. 10A); (1) near base, with pseudosegment connected

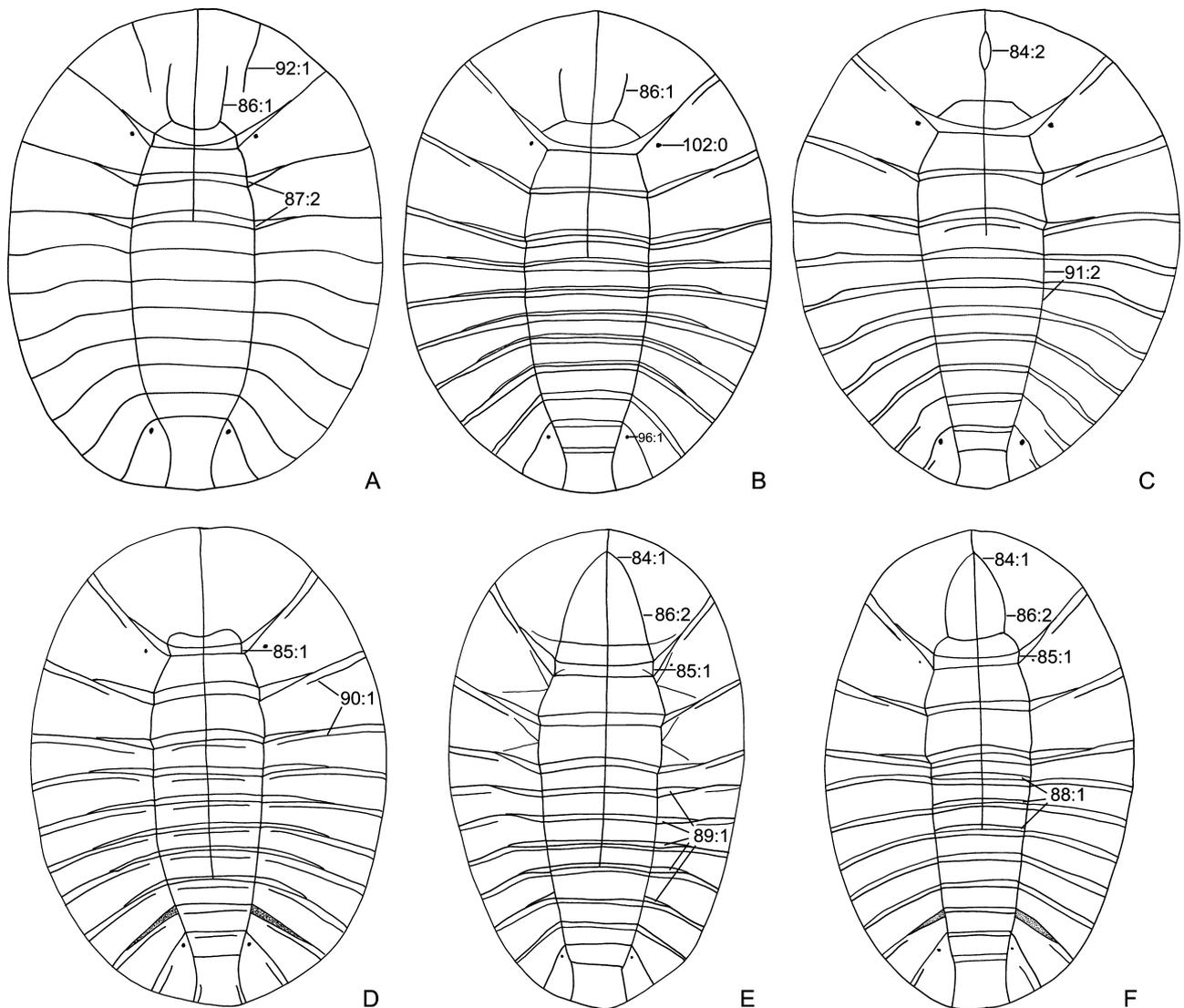


Fig. 7. Larval habitus, dorsal view. A, *Jinbrianax jaechi*; B, *Eubrianax manakikikuse*; C, *Afrobrianax ferdyi*; D, *Odontanax dohertyi*; E, *Mubrianax robustior*; F, *Jaechanax dentatus*.

with base of abdominal ventrite IX (Fig. 10C); (2) connected with base of abdominal ventrite (Fig. 10E) (CI = 0.50, RI = 0.83).

Costa *et al.* (1999: character 60) thought that only Eubriinae have opercula, and supposed that the operculum functions to cover the anal gills. Actually, such a structure exists in all members of Psephenidae. Even if the anal gills are reduced and ventral gills appear in Eubrianacinae and Psepheninae, the opercula do not disappear, but become very small. The opercula of Psephenoidinae extend into the entire ventrite (Hinton, 1955). The operculum derives from abdominal ventrite IX (Böving, 1929) and why Costa *et al.* (1999; characters 60 and 61) called it abdominal segment X is puzzling. The transverse plate separating the operculum from the base of the abdominal ventrite in Eubrianacinae,

Sclerocyphon, *Tychepephus*, genus A, *Ectopria* and *Granuleubria* (all in Eubriinae) was thought to be the original abdominal segment IX by Costa *et al.* (1999). It should be called a 'pseudosegment' to avoid confusion (see Fig. 10C).

120. *Number of paired auxiliary sclerites along sides of ninth abdominal sternite:* (0) zero (Fig. 10A); (1) one (Fig. 10B); (2) two (Figs 10C, 11A); (3) three (Figs 10D–F, 11B–D) (CI = 0.75, RI = 0.94).

This character is polymorphic in *Sclerocyphon* (states 2 and 3). A single pair of auxiliary sclerites occurs in *Afroebria*, psephenoidines and eubrianacines. Two pairs of auxiliary sclerites appear in *Eubria* and genus A. Three pairs of auxiliary sclerites occur in the remaining genera of Eubriinae.

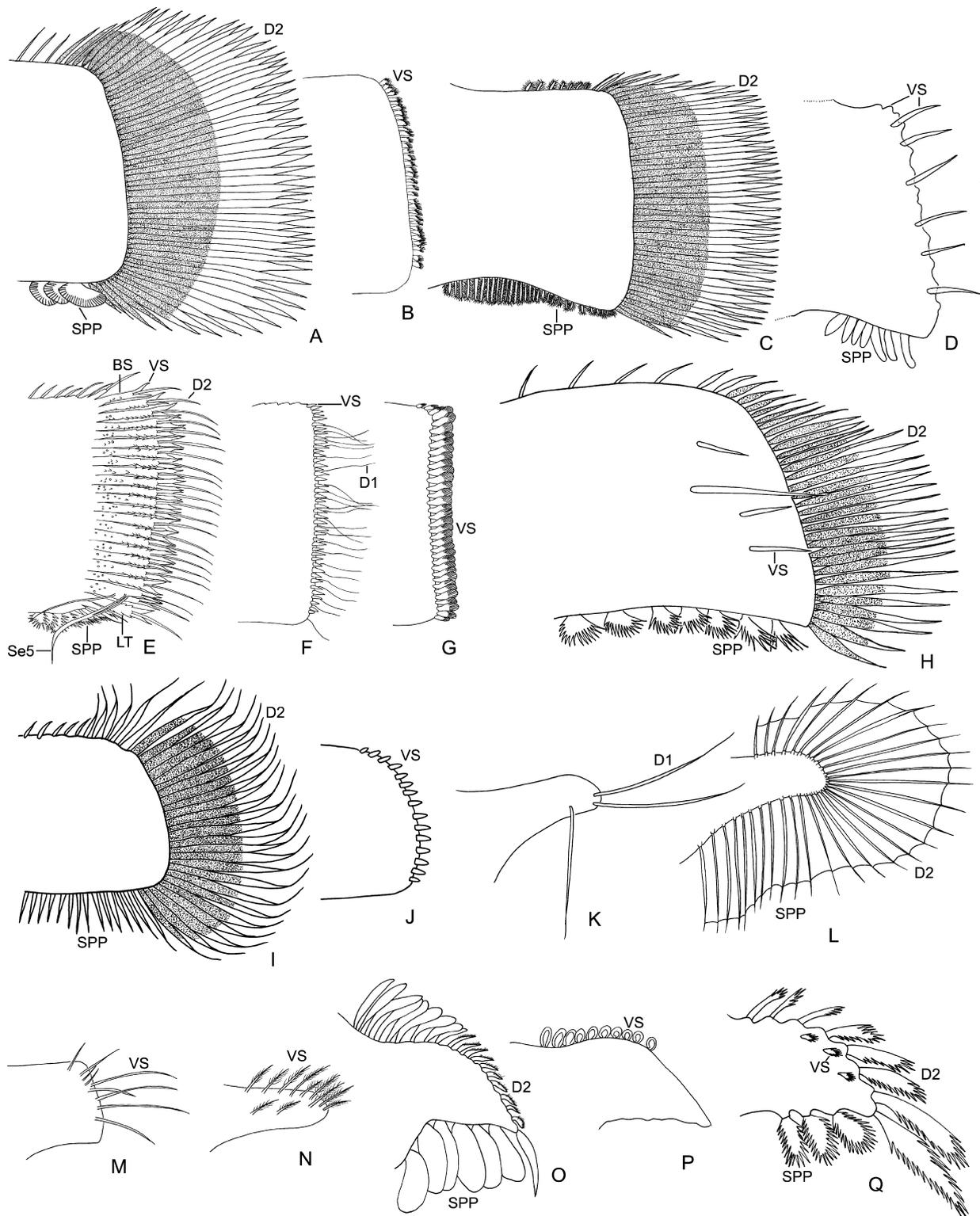


Fig. 8. Chaetotaxy on abdominal paratergite I (except for M, metathoracic paratergite). A, B, *Mataeopsephus esakii*; C, *Psephenoides subopacus*; D, *Xyloapsephenoides gihongi*; E, F, *Afrobrianax ferdyi*; G, earlier-instar larva of *Jinbrianax jaechi*; H, *Afroebria sebastiani*; I, J, *Tycheapsephus felix*; K–N, genus A; O, P, *Phanocerus clavicornis*; Q, *Elmis aenea*. BS = basal pieces; D1 = first dorsal setae; D2 = second dorsal setae; LT = lateral teeth; Se5 = seta 5; SPP = setae on posterior margins of paratergites; VS = ventral setae.

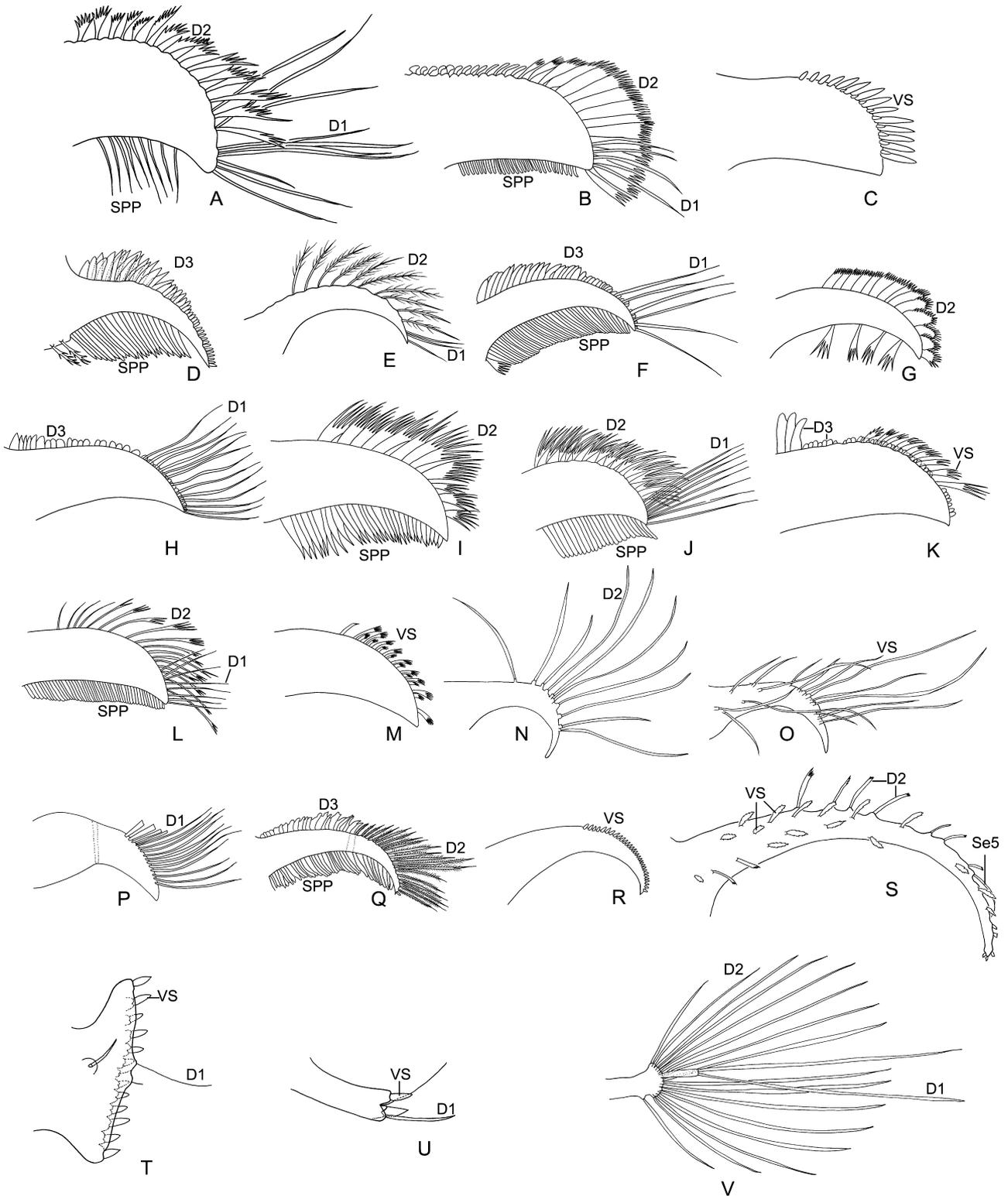


Fig. 9. Chaetotaxy on abdominal paratergite I (except for P and T, metathoracic paratergite). A, *Granuleubria* sp.; B, C, *Ectoptria nervosa*; D, E, *Homoeogenus laurae*; F, G, *Nipponneubria yoshitomi*; H, I, *Aeneus* sp.; J, K, *Eubria palustris*; L, M, genus B; N, O, *Macroebria luei*; P–R, *Schinostethus (Sundodrupeus) albosulcus*; S, *Dicranopselaphus variegates*; T, U, *Microebria* sp.; V, genus C. D1 = first dorsal setae; D2 = second dorsal setae; D3 = third dorsal setae; Se5 = seta 5; SPP = setae on posterior margins of paratergites; VS = ventral setae.

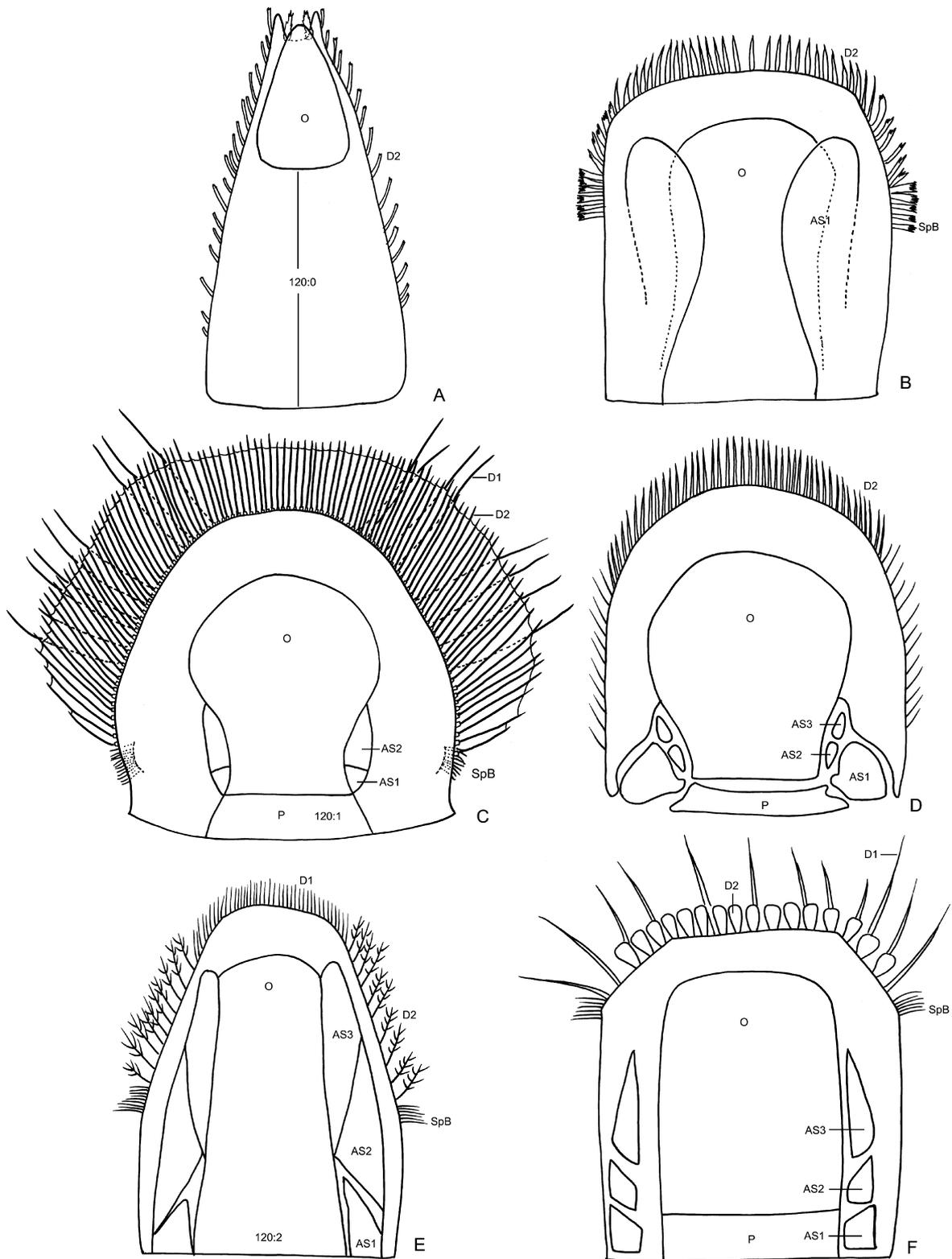


Fig. 10. Chaetotaxy on abdominal ventrite IX. A, *Elmis aenea*; B, *Afroebria sebastiani*; C, genus A; D, *Tychepsephus felix*; E, *Homoeogenus laurae*; F, *Granuleubria* sp. AS1 = first auxiliary sclerite; AS2 = second auxiliary sclerite; AS3 = third auxiliary sclerite; D1 = first dorsal setae; D2 = second dorsal setae; O = operculum; P = pseudosegment; SpB = spiracular brush.

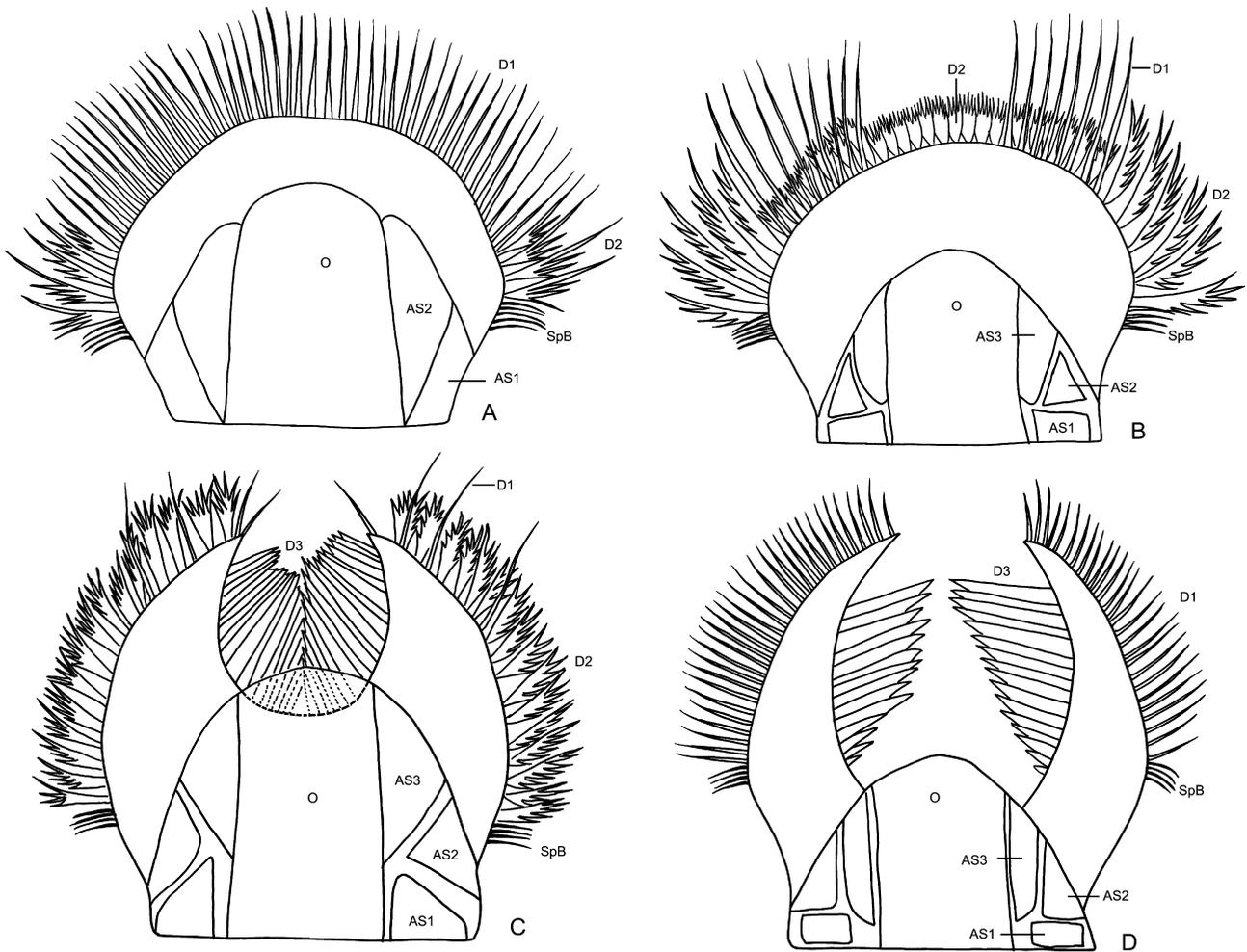


Fig. 11. Chaetotaxy on abdominal ventrite IX. A, *Eubria palustris*; B, *Aeneus* sp.; C, *Niponeubria yoshitomii*; D, *Schinostethus* (s.str.) *satoi*. AS1 = first auxiliary sclerite; AS2 = second auxiliary sclerite; AS3 = third auxiliary sclerite; D1 = first dorsal setae; D2 = second dorsal setae; O = operculum; SpB = spiracular brush.

Pupa

121. *Dorsum of pupa*: (0) soft; (1) sclerotized; (2) soft except sclerotization of last three abdominal tergites; (3) soft except sclerotization of outer margin of abdominal paratergites VII (CI = 0.75, RI = 0.87).

The sclerotization of the pupa is associated with the lack of other protective devices (such as hardened larval exuviae) or concealment under other substrates. Pupae of eubriines and psephenoidines are dorsally sclerotized because they are exposed. Pupae of *Jinbrianax*, *Mubrianax*, *Afrobrianax* and *Eubrianax* have sclerotized abdominal tergites VII–IX because they are exposed from larval exuviae. By contrast, those of *Jaechanax* and *Odontanax* have a sclerotized outward margin of abdominal segment VII.

122. *Functional spiracles on abdominal segment I*: (0) present (Fig. 12A); (1) reduced (CI = 0.50, RI = 0.66).

Spiracles on abdominal segment I appear in Elmidae and Psepheninae.

123. *Functional spiracles on abdominal segments II–VI*: (0) present (Fig. 12A, B, D); (1) reduced or absent (Fig. 12C) (CI = 1.00, RI = 1.00).

The absence of spiracles on abdominal segments II–VI characterizes Eubrianacinae.

124. *Spiracles on each paratergite*: (0) single (Fig. 11A, B); (1) subdivided into numerous small openings (Fig. 12C, D) (CI = 0.50, RI = 0.88).

Numerous fine spiracular openings occur in psephenoidines and eubrianacines.

125. *Spiracular gills*: (0) absent; (1) present (Fig. 12D) (CI = 1.00, RI = 1.00).

Each spiracular opening develops into the spiracular gills in psephenoides.

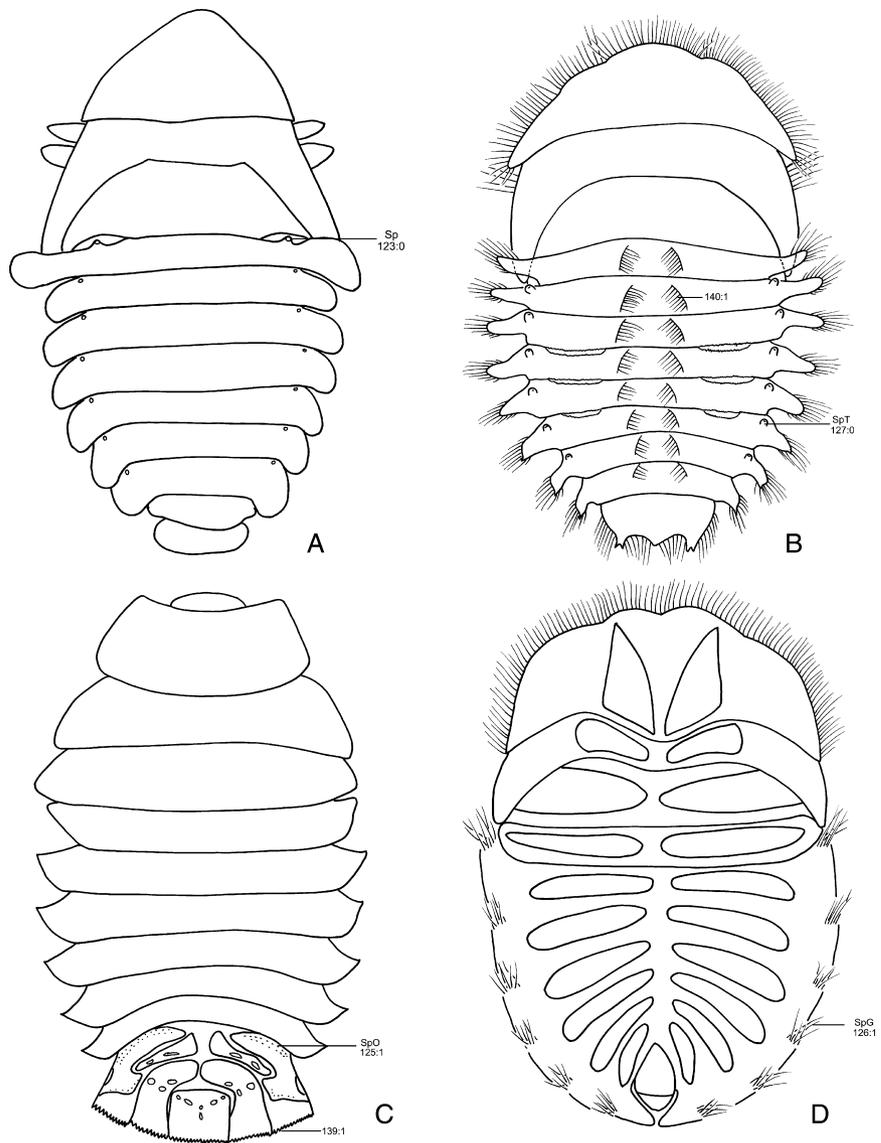


Fig. 12. Pupal habitus, dorsal view. A, *Psephenus* sp.; B, *Sclerocyphon* sp.; C, *Eubrianax* sp.; D, *Psephenoides* sp. Sp = spiracle; SpG = spiracular gills; SpO = spiracular openings; SpT = spiracular tubercle.

126. *Spiracular tubercles*: (0) very short (Fig. 12B); (1) moderately long, as long as paratergites; (2) very long, much longer than paratergites; (3) absent (CI = 0.60, RI = 0.84).

Moderately long spiracular tubercles occur in *Granuleubria*, *Ectopria*, *Homoeogenus*, *Eubria*, *Macroebria* and psephenoidines. Long spiracular tubercles occur in *Schinostethus* and *Microebria*. Spiracular tubercles are absent in eubrianacines.

127. *Pronotum*: (0) normal; (1) expanding outward (CI = 0.50, RI = 0.90).

An expanding pronotum that covers the head occurs in eubriines and psephenoidines.

128. *Abdominal paratergites I*: (0) normal; (1) reduced or absent, mesothoracic paratergite connected with abdominal paratergite II (Fig. 12D) (CI = 1.00, RI = 1.00).

The absence of abdominal paratergite I characterizes Psephenoidinae.

129. *Paratergites II–VI*: (0) separated; (1) tightly connected (Fig. 12D) (CI = 0.66, RI = 0.66).

Pupae of *Afroebria* and psephenoidines (except *Afropsephenoides*; Fig. 13A) have abdominal paratergites II–VI tightly connected.

130. *Setae of outer margins of abdominal paratergites II–VI*: (0) hair-like; (1) absent; (2) stout (CI = 0.50, RI = 0.83).

Setae on outward margins of abdominal paratergites II–VI are absent in *Afroebria*, *Microebria*, eubrianacines and psephenines. Setae of psephenoidines become sclerotized and stout.

131. *Abdominal ventrite VI*: (0) without adherent device; (1) with adherent device (CI = 1.00, RI = 1.00).

Pupae of eubrianacines have an adherent device on abdominal ventrite VI.

132. *Adherent material on outer margins of abdominal segments II–VI*: (0) none (Fig. 13A); (1) on basal halves of outer margins (Fig. 13B); (2) on entire outer margins (Fig. 13C) (CI = 0.66, RI = 0).

Pupae of most psephenoidines (except *Afropsephenoides*) can secrete adherent material on the outer margins of abdominal segments II–VI. Adherent material occurs all over the outward margins in *Neopsephenoides* and *Psephenoides*, but only on the basal halves in *Xylopsephenoides*.

133. *Paratergites VII–IX*: (0) separated; (1) tightly connected (Fig. 12C, D) (CI = 1.00, RI = 1.00).

Tightly connected abdominal paratergites VII–IX occur in *Afroebria*, psephenoidines and eubrianacines.

134. *Abdominal paratergites VII*: (0) similar in size to abdominal paratergites VI; (1) lengthened, surrounding abdominal IX (Fig. 12D) (CI = 1.00, RI = 1.00).

Lengthened seventh abdominal paratergites characterize Psephenoidinae.

135. *Apical margin of abdominal segment IX*: (0) with posterolateral processes (Fig. 12B); (1) truncated (Fig. 11C); (2) rounded (Fig. 12A, D) (CI = 0.50, RI = 0.83).

A truncated apical margin of the ninth abdominal segment appears in *Afroebria*, *Homoeogenus* and eubrianacines. A round one occurs in psephenoidines and psephenines.

136. *Aedeagus*: (0) concealed under abdominal tergite IX (Fig. 13E); (1) exposed (Fig. 13D) (CI = 0.50, RI = 0).

The aedeagus is exposed in *Afropsephenoides* and *Xylopsephenoides*.

137. *Setae on outer margins of last three abdominal segments*: (0) long; (1) absent; (2) stout (CI = 0.40, RI = 0.75).

The state distribution is consistent with character 130, except that *Jinbrianax* has long setae only on the outer margin of the last three abdominal segments.

138. *Outer margins of abdominal segments VII–IX*: (0) intact; (1) subdivided into slender processes (Fig. 12C) (CI = 0.33, RI = 0).

Division of the outward margins of the posterior three abdominal segments occurs in *Mubrianax* and *Eubrianax*.

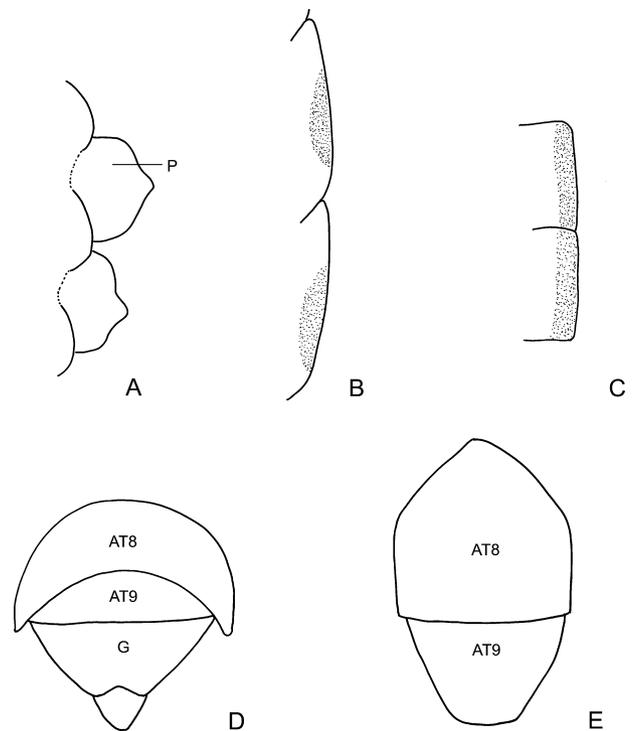


Fig. 13. Lateral margins of abdomen of pupae (A–C) and abdominal tergites VIII and IX (D, E). A, *Afropsephenoides* sp.; B, *Xylopsephenoides* sp.; C, *Psephenoides* sp.; D, *Afropsephenoides* sp.; E, *Psephenoides* sp. P = paratergite; AT8 = abdominal tergite VIII; AT9 = abdominal tergite IX; G = genitalia.

139. *Pair of longitudinal rows of long setae near medial suture*: (0) absent; (1) present (Fig. 12B) (CI = 0.50, RI = 0.88).

A pair of longitudinal rows of long setae near the medial suture occurs in most eubrianacines (except *Afroebria*).

140. *Outer margins of spiracles on abdominal segment VII*: (0) without openings (Fig. 14A); (1) with a row of openings (Fig. 14B–D) (CI = 0.50, RI = 0.80).

Most eubrianacines (except *Jinbrianax*) have one row of spiracular openings on the outward margins of abdominal segment VII.

141. *Distribution of openings of spiracles on abdominal segment VII*: (0) confined to vermiculations and surrounding spiracle (Fig. 14A); (1) reduced except those on outward margins of spiracles (Fig. 14C, D); (2) random (Fig. 14B); (3) scattered (Fig. 14E) (CI = 1.00, RI = 1.00).

This character is only applied to Eubrianacinae whose pupae have numerous fine openings on the spiracles of abdominal segment VII. They are confined to vermiculations in *Jinbrianax*, or to the outward margins in *Odontanax* and *Jaechanax*, or distributed randomly in *Mubrianax*, or sparsely distributed in *Afrobrianax* and *Eubrianax*.

142. *Outer margin of each spiracle*: (0) without processes; (1) with one process (Fig. 14D) (CI = 0.50, RI = 0.50).

One small process on the outward margin of each spiracle occurs in *Mubrianax*, *Afrobrianax* and *Eubrianax* (Fig. 14B, D, E).

143. *Pupation under or above water*: (0) above water; (1) underwater (CI = 1.00, RI = 1.00).

Only pupae of psephenoidines can pupate under water.

Results

The phylogenetic analysis yielded two most-parsimonious trees. The strict consensus tree calculated from both trees has 439 steps, CI = 45, RI = 75. Psephenidae and all of its subfamilies are monophyletic, with the exception of Eubriinae. The inclusion of *Afroebria* causes Eubriinae to be paraphyletic (Fig. 15). Although only unambiguous character state changes are shown on the tree, some evolutionary scenarios are proposed for those characters with ambiguous state changes.

Discussion

Monophyly of Psephenidae

Costa *et al.* (1999) concluded that two larval characters support the monophyly of Psephenidae, of which one is larvae having the 'flattened' body form. However, this may not be correct, because several Elmidae have 'flattened' larvae, as in most eubriine genera, but these genera were not included in their phylogenetic analysis. On the basis of the current phylogenetic analysis (Fig. 15) with the use of unambiguous transformation, the monophyly of Psephenidae is supported by eight apomorphies. Some of these characters may be associated with larvae living in fast-running water. In one way, the 'flattened' larvae are transformed further into the 'streamlined' ones. Those characters include the anterior expanded apical margin of the prothorax that conceals the head (58: 1) and the widened body. Such a body shape may promote their survival in fast-running waters because they can move across smooth surfaces easily (Smith & Dartnall, 1980; McShaffrey & McCafferty, 1987). Thus, water pennies can exploit food sources on the surfaces of rocks exposed to high-energy flows. In addition, the monophyly of Psephenidae is supported by the specialized mandibles that have no apical teeth (54: 1) and enable specialized feeding on diatoms and algae growing on the smooth surfaces of stones.

Changes in morphology reflect the use of a diversity of substrates and habitats. The recurrence of elongate larvae (55: 1) appears once in Eubrianacinae, Psephenoidinae and Eubriinae. The transformation of the body in Eubrianacinae (*Mubrianax* + *Jaechanax*) and Psephenoidinae (*Xylopsphenoides*) appears to be a parallelism associated with similar substrates – slender twigs. Another change is the recurrence of

the thickened and apically toothed mandibles (54: 0) associated with xylophagy. In addition, there are a number of homoplastic characters for both Eubriinae and Elmidae. Not only does the elongate body recur in larvae of Eubriinae (55: 1), but also the curved and loosely connected paratergites (116: 0).

Parallel evolution occurs in those taxa that can pupate on smooth surfaces of stones. Psepheninae and Eubrianacinae adopt a similar strategy – pupating within the hardened larval terga. In the respiratory system, pupae of Psepheninae maintain the pleisomorphic state – spiracles appear at abdominal segments I–VII (122: 0, 123: 0). By contrast, those of Eubrianacinae have spiracles confined to abdominal tergum VII (122: 1, 123: 1). Either the last three abdominal tergites are sclerotized and replace the larval ones (Fig. 12C) or the spiracles are sclerotized and project from the crevice between abdominal paratergites VI and VII of larval skins. An adherent device has developed on abdominal ventrite VI in Eubrianacinae (131: 1). Pupae of *Afroebria* and Psephenoidinae are not covered by the larval skin, but their dorsal surface is sclerotized. There is no crevice left between the lateral margins of pupae and substrate. Such pupae resemble larvae, including in Eubrianacinae (133: 1). Paratergites of pupae in *Afroebria* expand and connect tightly (129: 1), presumably so that the pupa can attach to stones easily. However, in Psephenoidinae, the paratergites of the pupae are reduced, but their lateral margins secrete sticky material (132). A reduction of abdominal paratergite I (128: 1) in Psephenoidinae is correlated with the absence of spiracles on the first abdominal segment of all psephenids, except Psepheninae.

The monophyly of Psephenidae indicates that there are some significant evolutionary events in the respiratory systems of larvae. The respiratory system of larval Elmidae (outgroup) is very uniform, with anal gills (composed of three gill-tufts), and in mature larvae, functional spiracles on the mesothorax and abdominal segments I–VIII (Spangler & Santiago-Fragoso, 1992) suggesting the uptake of atmospheric oxygen when they crawl out of the water for pupation.

Two evolutionary events appear in Psephenidae: the presence of spiracles extends throughout all instars (94: 1) and spiracles on abdominal segments I–VII are reduced (93: 1). The former change may promote larval survival in more fluctuating environments, because they can utilize atmospheric oxygen during any stage. An exception is Psephenoidinae, whose larvae have no spiracles in any instar (95: 1); the absence of spiracles may be associated with underwater pupation (143: 1). The second event has the functional spiracles of the eighth abdominal segment moved to the margin, with the exception of Eubrianacinae (97). Associated with this change is the development of spiracular brushes, which are present on abdominal segment IX opposite the spiracles on abdominal segment VIII. Spiracular brushes, composed of a cluster of stout setae (Fig. 16A), were reported in Eubriinae, perhaps functioning to clean the spiracles (Hinton, 1955). Spiracular brushes also occur in Psepheninae, in which they are arranged as a row of flattened ramose setae along the complete lateral margin

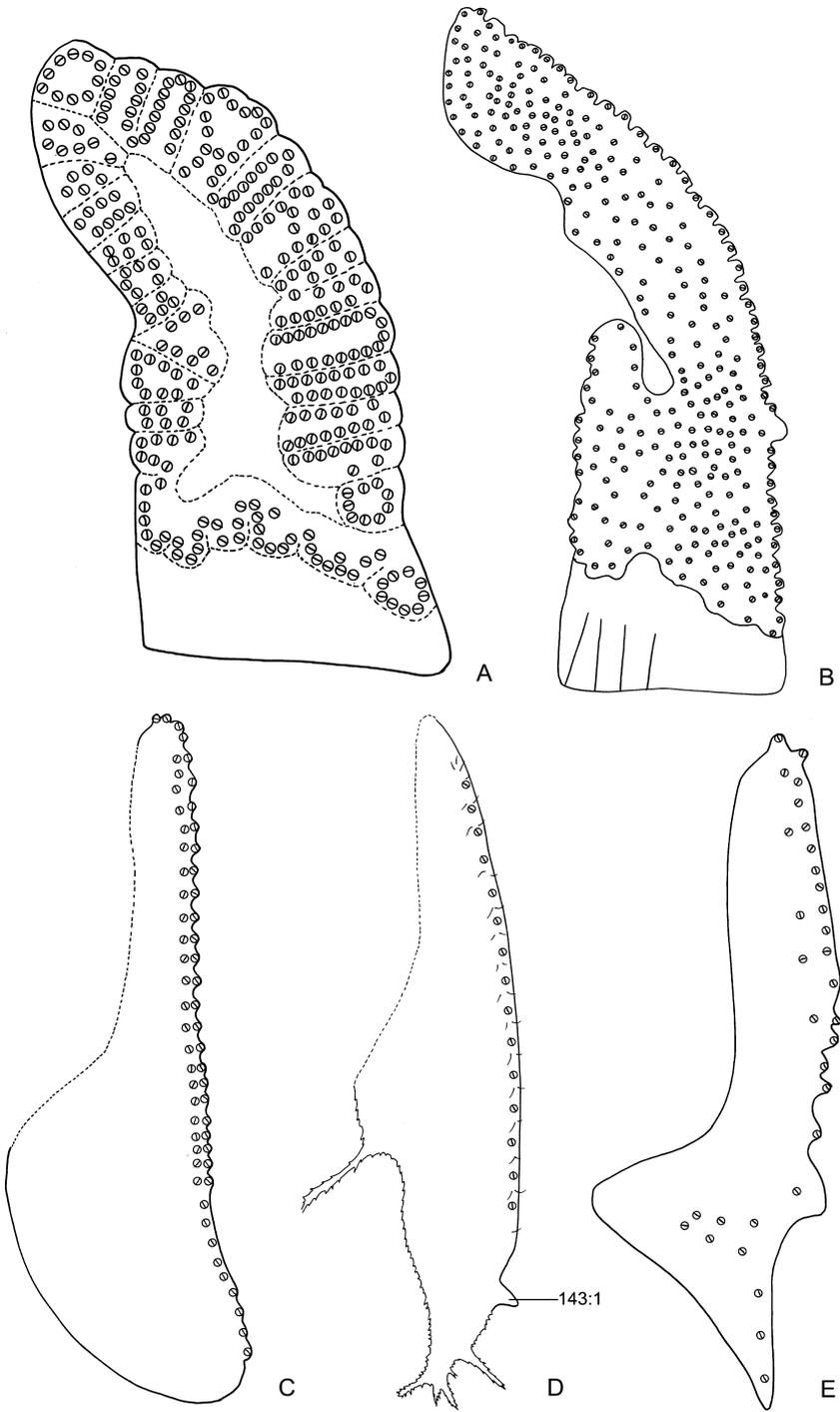


Fig. 14. Pupal spiracles. A, *Jinbrianax jaechi*; B, *Mubrianax robustior*; C, *Odontanax dohertyi*; D, *Jaechanax dentatus*; E, *Eubrianax serratus*.

(Fig. 16B). Such an array of spiracular brushes may imply an evolutionary trend of abdominal paratergite VIII. Spiracles might have been moving towards the base of abdominal segment IX from the apex by shortening abdominal paratergites VIII. To live in fast-running water, spiracles are parallel to the body and the spiracular brushes become smaller and flattened. The discovery of a spiracular brush in

Psepheninae extends this character to the whole family – the spiracular brush (98: 1, 99: 1) becomes synapomorphic for all Psephenidae. However, the phylogenetic position of Eubrianacinae then becomes a bit puzzling, because their spiracles are inside abdominal segment VII (97: 0), as in Elmidae. However, this character state is probably a reversal in the Eubrianacinae. Supporting evidence exists in the most

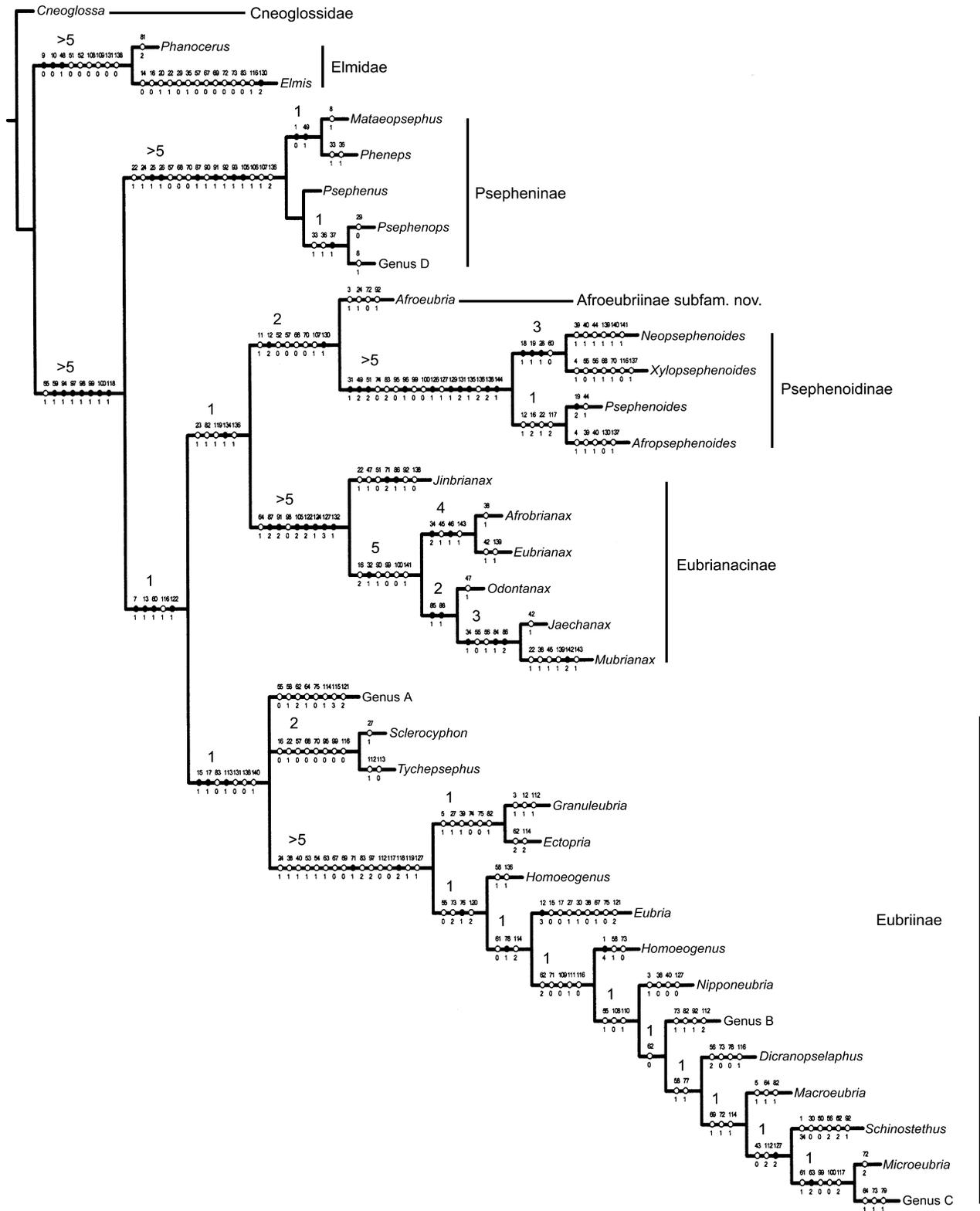


Fig. 15. Strict consensus of two most-parsimonious trees based on the full dataset (439 steps, consistency index = 0.45, retention index = 0.75). Only unambiguous changes are shown on the cladogram. Nonhomoplastic apomorphies are indicated by black circles, whereas homoplastic apomorphies are indicated by white circles. The numbers above the clades are Bremer support values (maximum Bremer support value = 5).

ancestral clade within Eubrianacinae – *Jinbrianax*. Larval *Jinbrianax* retain the spiracular brush on abdominal segment IX (Fig. 16C), implying that the ancestors of *Jinbrianax* (which are equal to Eubrianacinae) have larval spiracles that are located at the posterior margin of abdominal segment VIII and the base of paratergites, and the spiracular brushes on abdominal segment IX are responsible for cleaning. Spiracular brushes are reduced in other eubrianacine genera (98: 0, 99: 0).

Position of *Psepheninae*

Although the sister-group relationship between *Psepheninae* and the remaining taxa of *Psephenidae* is weakly supported (Fig. 15), this position reveals trends in some important characters. An evolutionary trend may exist involving the bifurcate apex of abdominal segment IX in Elmidae being transformed into the smooth apex of basal *psephenids* (107, 108). Only *Psepheninae* have ontogenetic characters to support the hypothesis that the emarginate apex of abdominal segment IX is ancestral: the pharate larva has an emarginate apex and the setae at the posterior margin of the abdominal segment are orientated in two directions and separated at the middle during the whole larval stage.

Thus, *Psepheninae* seems unlikely to be a descendant of those that have convex or straight apices, i.e. all other subfamilies except some advanced eubrianacine genera.

The operculum is a cover for the anal gills near the apex of abdominal ventrite IX, as in the Elmidae. Two evolutionary trends involving the operculum in *Psephenidae* are indicated (Fig. 17): the operculum may move anteriorly to the base of abdominal segment IX; the restriction of the opening of the operculum by fusion laterally with auxiliary sclerites. The operculum approaches the base of abdominal ventrite IX, which either connects with the base (Fig. 17B, C, G) or forms a ‘pseudosegment’ between the operculum and the base of abdominal segment IX (Fig. 17D–F). Auxiliary sclerites arise along side the operculum. These are either reduced to a single slender sclerite laterally connected with the operculum and abdominal tergum IX (Fig. 17C, E) or the apical pair of auxiliary sclerites expands posteriorly and fuses with the operculum and tergum IX (Fig. 17F, G). This fusion limits movement of the operculum, which then cannot rotate up to 90°.

Parallelism between *Psepheninae* and *Eubrianacinae*

Psepheninae were presumed to be close to *Eubrianacinae*, based on the immature stages (Hinton, 1955, 1966). For

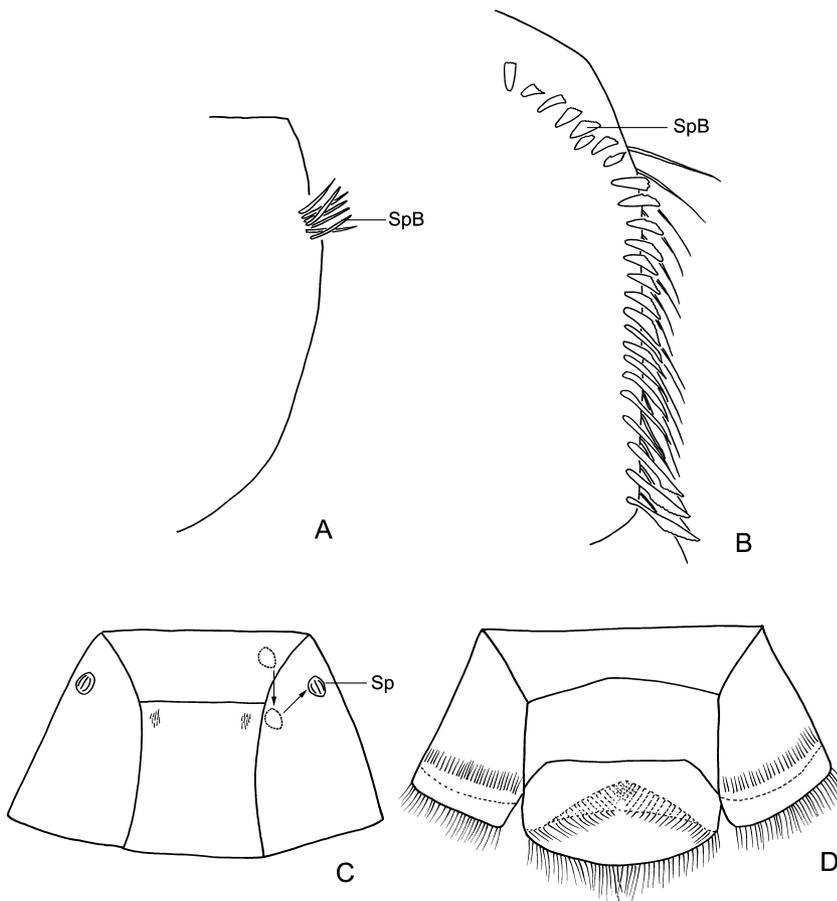


Fig. 16. Lateral margin of abdominal tergite IX (A, B) and abdominal tergites VIII–IX (C) or VII–IX (D). A, *Tycheapsephus felix*; B, *Psephenus herricki*; C, *Jinbrianax jaechi*, margin peg setae are omitted, arrows indicate evolutionary scenarios of the positions of the spiracles; D, *Psephenus herricki*, spiracular brushes are omitted, the shaped lines indicate the pharate larva.

example, larvae of both subfamilies have ventral gills, tergopleural sutures, posterior plates, an amphipneustic respiratory system, costal lines, and they use the hardened larval exuvium for covering the pupa. However, differences in structure and composition have indicated that most of those characters are homoplastic (Hinton, 1955; Lee *et al.*, 2001). The phylogenetic analysis supports this hypothesis.

Eubrianacinae have similar pupal protection as Psepheninae in that they use the hardened larval terga to cover the pupae. However, the larval exuviae are so hard that some morphological modification of the cuticle must appear to promote its flexibility. Some additional sulci are present. For example, tergopleural sulci are found on all but the last two abdominal terga in the Psepheninae (90: 1), but in Eubrianacinae they are absent on the pronotum and present on abdominal tergum VIII (90: 2). In addition, some supplementary sclerites, e.g. posterior plates on the thoracic terga, are found in Psepheninae (86: 1) and Eubrianacinae (86: 2). The oblong larvae of *Mubrianax* and *Jaechanax* have additional apomorphies compared with others within Eubrianacinae. They include additional sulci, such as that which divides the posterior plate on the pronotum (84: 1), and the periocellar sulci (85: 2). Additional posterior plates appear on abdominal terga I–III (87: 1). This seems to imply that the oblong body needs more sulci for flexibility.

In another view, the pharate pupa is possibly homologous in Psepheninae and Eubrianacinae. The entire pupa of *Jaechanax* and *Odontanax* is covered by the larval exuvia. Fine spiracular openings, which are confined to the outward margin of the pupal paratergite VII, project from crevices between larval paratergites VI and VII. Hinton (1966) found that the spiracles on abdominal segment VII of *Mataeopsephus* are enlarged. Does it imply that the ancestor of pupae in Eubrianacinae is derived from a taxon like *Mataeopsephus*? This idea is not supported by two facts. First, pupae of

all members of Eubrianacinae have widened paratergites on the last three abdominal terga resembling those of the larvae (133: 1) (Fig. 12C), including the unexposed pupae of *Jaechanax* and *Odontanax*, which become softened and hide under the larval exuviae. However, no psephenine pupae have the last three abdominal terga resembling larval terga. Second, the unexposed pupae have spiracular openings confined to the outer margins of abdominal paratergite VII because only the outer margins of abdominal paratergite VII project from under the hardened larval exuviae and contact air. The exposed pupae whose last three abdominal terga of the larval exuviae are shed and replaced by those of pupae have the whole surface of the last three pupal terga contacting the air. Thus, additional spiracular openings can appear inside abdominal tergite VII for breathing more air and those openings on the outer margins are not necessarily reduced. However, the exposed pupae of the most primitive clade, *Jinbrianax*, have spiracular openings inside abdominal tergite VII, but not on the outer margins. This implies that Eubrianacinae ancestrally have spiracular openings inside of abdominal tergite VII. Ancestors of Eubrianacinae probably did not come from a taxon like *Mataeopsephus*.

Parallel evolution also happens in the respiratory systems of larvae living in fast-running water. Comparing streams, ponds and creeks, there is relatively higher dissolved oxygen in fast-running water. One trend involves changes in the primitive respiratory system (which includes three tufts of anal gills, hidden between the ninth abdominal ventrite and tergum). Three gill-tufts are reduced to two in *Sclerocyphon*, *Tycheapsephus*, genus A (Eubriinae), and *Neopsephenoides* and *Xylopsephenoides* (both in Psephenoidinae). A second trend involves the lateral shape of larvae. According to hydrodynamics, an oblique slope along the anterior margin of the long, flattened and straight paratergite can increase

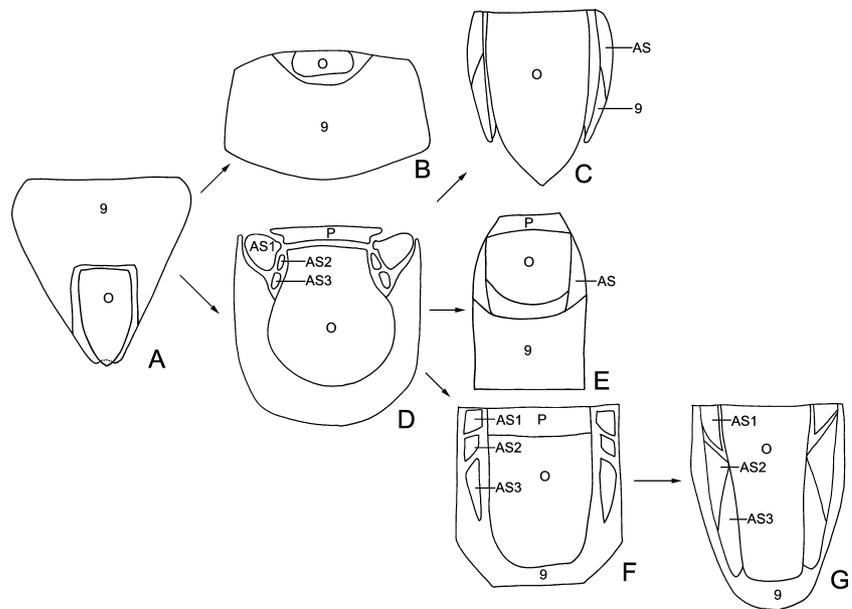


Fig. 17. Putative evolutionary trend of abdominal ventrites IX. A, *Phanocerus* (Elmidae) (118: 0, 119: 0, 120: 0); B, *Mataeopsephus* (Psepheninae) (118: 0, 119: 2, 120: 0); C, *Psephenoides* (Psephenoidinae) (118: 1, 119: 2, 120: 1); D, *Sclerocyphon* (Eubriinae) (118: 0, 119: 1, 120: 3); E, *Mubrianax* (Eubrianacinae) (118: 1, 119: 1, 120: 2); F, *Ectopria* (Eubriinae) (118: 1, 119: 1, 120: 3); G, *Homoeogenus* (Eubriinae) (118: 1, 119: 2, 120: 3). 9 = abdominal ventrite IX; O = operculum; P = pseudosegment; AS = auxiliary sclerite.

the attachment power, thus helping to avoid being washed off the substrate. The costal lines that are present in Eubrianacinae and Psepheninae help to form a peak in the oblique slope (89: 1). The species of *Psephenoides* (Psephenoidinae) have similar structures.

Evolution of the marginal peg setae in Eubrianacinae

An intriguing question concerns the origin of the delicate, autapomorphic marginal peg setae of Eubrianacinae. A marginal peg seta is composed of two discrete parts (Fig. 18B). The basal piece is cylindrical, with teeth on the sides and one pair of lanceolate setae on the base and apex. The apical piece is either filamentous or paddle-like. Are the hair-like setae with darkened basal halves (Fig. 18A) (D2, as in Psepheninae, Psephenoidinae, *Afroebria*, *Sclerocyphon* and *Tychepsephus*) directly transformed into the marginal setae of Eubrianacinae (Fig. 18B)? That is, did the basal, darkened half of the hair-like seta (D2) develop into the basal piece of marginal peg seta, and the apical one into the apical piece? If so, it is difficult to explain two unique phenomena in the Eubrianacinae. One marginal peg seta near the posterolateral angles of the paratergites has two apices, and one long hair-like seta is located at the base of two apices (Fig. 18B). The other phenomenon is that in the primitive clade, *Jinbrianax*, the marginal peg seta at the posterolateral angle of each paratergite has a row of branches on the outer side. One explanation is that only the apical pieces of the marginal peg setae are attributed to the hair-like setae (D2); and the basal pieces grew from the base. When basal pieces grow, they push the cuticle of paratergites towards the margin. One hair-like seta (seta 5) near the posterolateral angle of each paratergite has been pushed into the margin, finally connecting with marginal pegs. This seta (115: 1) is also found in *Afroebria*, some members of Psephenoidinae and Eubriinae. As the basal pieces continue growing, the marginal peg seta at the posterolateral angle of each paratergite adds branches. Thus, we propose a hypothesis of evolution of the typical marginal peg setae (Fig. 19): the primitive marginal peg setae have one row of D2 setae and two rows of VS, as in *Granuleubria*, *Ectopria* and genus B within Eubriinae (Fig. 19A) (81: 1). One of two rows of VS is located at the apices of the basal pieces of the marginal peg setae when the basal pieces grow (Fig. 19B). Then, one of the sides of the basal pieces has setae developed into teeth (Fig. 19C) (64: 1, as in *Jinbrianax*). Finally, the other side of the basal pieces also has setae developing into teeth (Fig. 19D) (64: 2, as in other members of Eubrianacinae). An additional ontogenetic character supports the basal pieces of the marginal peg setae being derived from the D2 setae. Pharate larvae of Eubrianacinae have reversed apical pieces of marginal peg setae, but basal ones are normal. This phenomenon also happens to the D2 setae of those of Psepheninae, implying that only the apical pieces are derived from the hair-like setae (D2).

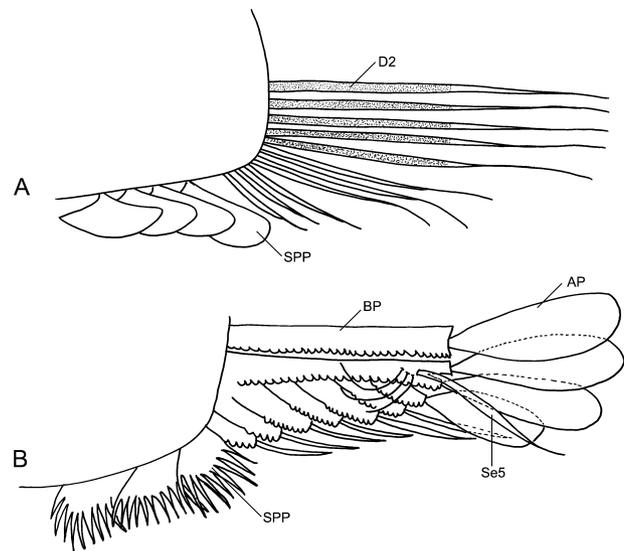


Fig. 18. Posterolateral angle of paratergite. A, *Mataeopsephus* (Psepheninae); B, *Jinbrianax* (Eubrianacinae). AP = apical piece; BP = basal piece; D2 = second dorsal setae; Se5 = seta 5; SPP = setae at posterior margin of paratergite.

Monophyly of subfamilies

The phylogenetic analysis and Bremer support indices indicate that all subfamilies are monophyletic and well supported, with the exception of Eubriinae, which is paraphyletic due to the inclusion of *Afroebria*. This genus, originally placed in Eubriinae, is now hypothesized to be the sister group of Psephenoidinae. Thus, *Afroebria* should either be raised to be a discrete subfamily or transferred into Psephenoidinae in order to maintain the monophyly of all subfamilies. A number of apomorphic characters for Psephenoidinae may be related to the underwater pupation, which is unique for aquatic beetles. If *Afroebria* is transferred into Psephenoidinae, these synapomorphies will be replaced by much fewer, indicating the monophyly of *Afroebria* + Psephenoidinae s.str. Because the support of the monophyly of the subfamilies (except Eubriinae) is very strong, adding more taxa in the future could only cause the phylogenetic position of *Afroebria* to become more variable and perhaps necessitate a transfer of its origin to the base of other subfamilies. Because all other subfamilies will not change their contexts, even if *Afroebria* is transferred to any of the subfamilies, establishing a discrete subfamily for *Afroebria* will not affect the monophyly of other subfamilies.

The monophyly of the Psepheninae is supported by 15 apomorphies: adults with the presence of the median longitudinal sulcus on mesoventrite (22: 1), vestigial meta-ventral transverse suture (24: 1) and seven visible ventrites in males and six in females (25: 1); in larvae (Fig. 6A, B) medial suture well developed, reaching abdominal tergum VII (56: 0), sclerotized bases of D2 setae (67: 0; 69: 0), dorsum having

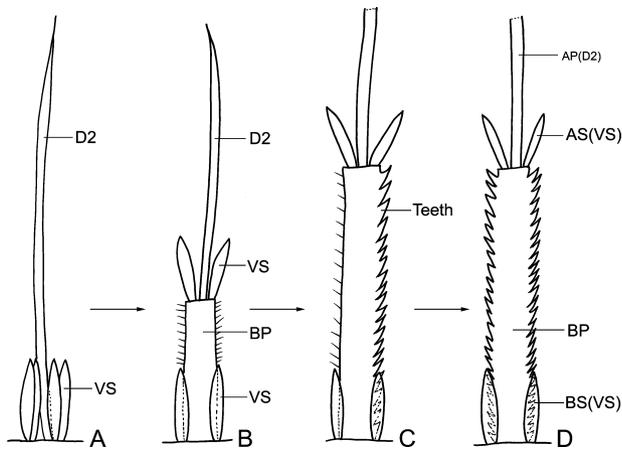


Fig. 19. Putative evolutionary trend of marginal peg setae. A, Two pairs of ventral setae (VS) and one second dorsal seta (D2); B, a growing basal piece (BP) from the base of D2, one pair of VS located at the apex of the BP; C, *Jinbrianax*, hairs at one side of the BP developed into teeth; D, other eubrianacines, hairs at the other side of the basal setae (BS) developed into teeth. AP = apical piece; AS = apical setae.

intact posterior plates on each thoracic tergum (86: 1), costal lines (89: 1), presence of tergopleural suture from pronotum to abdominal segment VII (90: 1), sulci 1 present on pronotum (91: 1), sulci 1 and 2 present on meso- and metanota (92: 1), anal gills replaced by pectinate ventral gills (104: 1), abdominal paratergites VII lengthened and reaching apex of abdominal segment IX (105: 1), abdominal paratergites VIII much shorter than those of paratergites VII (106: 1), and the apical margin of abdominal segment IX rounded (135: 1).

The monophyly of the Psephenoidinae is supported by 16 apomorphies: adults lacking apical spurs on tibiae (30: 1), and with reduced wing veins (48: 2, 50: 2); larvae (Fig. 6C–F) with short simple D2 on the apical margin of abdominal tergite IX (73: 0), lack of functional spiracles on abdominal segment VIII (94: 0, 95: 1) and spiracular brushes in all instars (98: 0, 99: 0); pupae (Fig. 12D) with spiracles replaced by numerous small spiracular gills (125: 1), moderately long spiracular tubercles (126: 1), reduced abdominal paratergites I (128: 1), stout setae on outer margins of abdominal paratergites (130: 2, 137: 1), lengthened abdominal paratergites VII surrounding tergite IX (134: 1), rounded apical margin of abdominal tergite IX (135: 2) and underwater pupation (143: 1).

The monophyly of the Eubrianacinae is supported by nine apomorphies: larvae having basal pieces of D2 setae on paratergites (63: 1), segmented posterior plates on thoracic terga (86: 2), tergopleural sutures on meso- and metathora and abdominal segments I–VIII (90: 2), spiracles inside abdominal paratergites VIII (97: 0) and reduced anal gills replaced by ventrolateral fan-like gills (104: 2); pupae with sclerotization of the last three abdominal tergites (121: 2), flat spiracles (126: 3), abdominal ventrite VI with special

adherent organ (131: 1) and without functional spiracles on abdominal segments II–VI (123: 1).

The monophyly of the Eubriinae is supported by seven apomorphies: crenulation on basal margins of pronotum, elytra and scutellum in adults (absent in *Eubria* and *Microeubria*) (15: 1, 17: 1); larvae with elongate setae on posterior margins of paratergites (82: 1), two-tufted anal gills (103: 1), one pair of longitudinal rows of setae or sensillae near medial suture (112: 1); pupae with hair-like setae on outer margins of abdominal paratergites II–VI (130: 0), with long setae on outer margins of abdominal segments VII–IX (137: 0), one pair of longitudinal rows of long setae near medial line (139: 1).

Adults vs. immature stages

When data derived from adults and immature stages were analysed separately, three undetermined genera (genera A, B and C) were removed from the former analysis because of no information on adults. Adult data comprise 50 characters (1–50), which are 35% of the full dataset. Analysis of adult data yielded 33 most-parsimonious cladograms. The strict consensus (Fig. 20A) calculated from these cladograms is very different and much less resolved than that based on the full dataset. By contrast, analysis of immature stage data yielded 20 most-parsimonious cladograms whose strict consensus (Fig. 20B) is similar to that from the complete dataset. Obviously the immature data provide much more information on phylogeny, supporting Hinton's (1955, 1966) decision to study the taxonomy of Psephenidae based only on larvae and pupae. In addition, it may reflect the life history and strategy of psephenids – the immature stages are long-lived and subject to more selection pressure from living in various habitats, whereas adults, which are responsible only for reproduction, are short-lived and subject to less selection pressure. This life history is similar to that of mayflies, an order in which McCafferty & Wang (2000) also used immature stages to construct phylogenetic systematics of the higher ranks. Psephenids are a good example to emphasize the importance of immature stages, as Emden (1957) indicated.

Conclusion

Psephenidae is a well-defined monophyletic group. Most morphological characters supporting the monophyly of water penny beetles are associated with larvae living in fast-running water. The diversification of various subfamilies results in a number of apomorphies for each subfamily. However, very few morphological characters provide information for relationships between subfamilies. This study shows that immature stages provide more valuable phylogenetic information than adults. Moreover, the complete dataset yields the best phylogenetic results. Although convergencies and parallelisms occur among various taxonomic

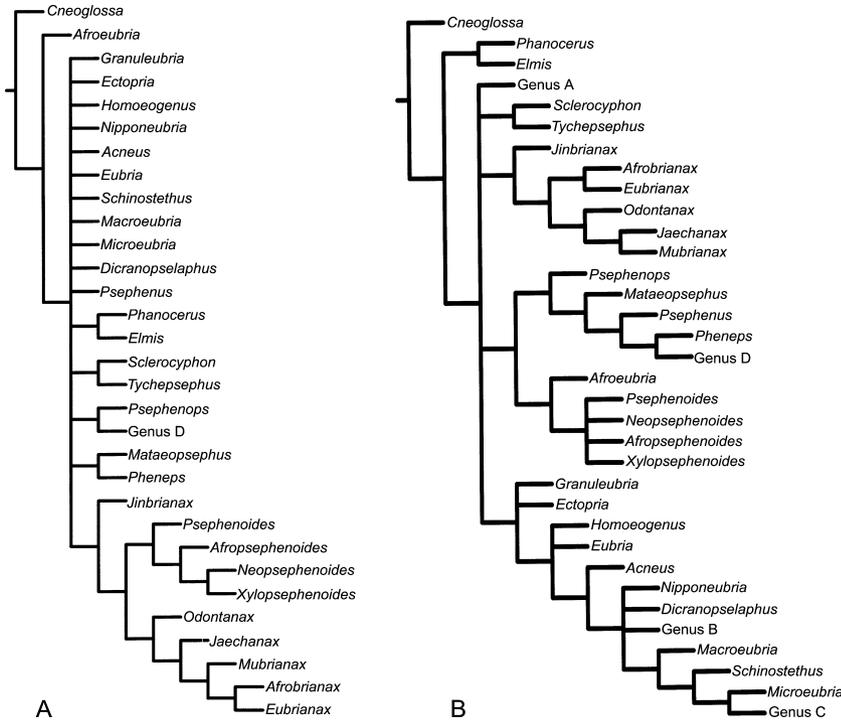


Fig. 20. Strict consensus cladograms. A, Based on adult characters; B, based on immature stage characters.

groups and stages, they seldom affect the phylogenetic analysis because they can be treated as different character states due to morphological differentiation. This morphological differentiation can be detected if sufficient materials are examined. This study indicates that a combined larval and adult dataset, and sufficient materials, are necessary for phylogenetic research.

Systematic account

Afroebriinae, **subfam.n.**

Type genus. *Afroebria* Villiers, 1961.

Larval diagnosis (Fig. 4G). This subfamily is close to *Tychepsephus* and *Sclerocyphon*, sharing wide, rectangular and connected paratergites, anal gills, the presence of spiracles on abdominal segment VIII and spiracular brushes composed of clusters of setae; but differing by the three-segmented maxillary palpi and the two-segmented labial palpi, the shorter antennomere 1, the prominent sulcus 1 on the prothorax, the shortened abdominal paratergite VIII with spiracles on apices, ramose setae on posterior margins of the paratergites (Fig. 8H) and anal gills with three gill-tufts.

Pupal diagnosis. Most similar to Psephenoidinae, pupating above the water on the smooth surfaces of stones; pupae naked; differs by the lack of spiracular gills and the lack of long hair-like setae at the outer margin of the prothorax,

and by the presence of well-developed abdominal paratergites II–VII.

Adult diagnosis. *Afroebria* and *Tychepsephus* are distinguished from all other psephenids by the punctate pronotum and elytra caused by pubescence. *Afroebria* may be distinguished from eubriines by the combination of the following characters: apically tapering terminal segments of maxillary and labial palpi (Fig. 10), acute mesosternal process and smooth basal margins of the elytra, scutellum and pronotum.

Ecology. Like *Sclerocyphon* and *Tychepsephus*, larval *Afroebria* may be found on the underside of stones in clean streams. Pupae were also found on the underside of stones but above the water.

Biodiversity. The monotypic subfamily contains three species, which have been revised by Lee *et al.* (2003b).

Key to larvae of the subfamilies of Psephenidae

- 1. Anal gills; without spiracles on mesothorax 2
- 1'. Abdominal gills; with spiracles on mesothorax 4
- 2. Seventh abdominal paratergites elongate, reaching apex of ninth abdominal segment; eighth abdominal paratergites reduced; mature larvae without spiracles on eighth abdominal segment..... Psephenoidinae
- 2'. Seventh abdominal paratergite normal, not reaching apex of ninth abdominal segment; eighth abdominal paratergite short or normal; mature larvae with spiracles on eighth abdominal segment 3

3. Comb-like setae margined on anterior margins of paratergites Afroebriinae **subfam.n.**
- 3'. Without comb-like setae margined on anterior margins of paratergites Eubriinae
4. Eighth abdominal paratergites normal, spiracles inside eighth abdominal paratergites; marginal peg setae composed of two discrete parts: apical and basal pieces Eubrianacinae
- 4'. Eighth abdominal paratergites shortened, spiracles on apices of eighth abdominal paratergites; marginal setae sclerotized in basal halves Psepheninae

Key to pupae of the subfamilies of Psephenidae

1. Larval terga covering pupae 2
- 1'. Pupae exposed 3
2. Paired spiracles on abdominal segments I–VII; last three abdominal segments normal..... Psepheninae
- 2'. Spiracles on abdominal segments I–VI reduced; openings of spiracles subdividing into numerous tiny holes; last three abdominal paratergites tightly connected, resembling those of larvae..... Eubrianacinae
3. Pupation on underside of stones nearby or in streams; paratergites wide and tightly connected, without visible crevices 4
- 3'. Pupation on cryptic sites, such as wood holes nearby streams; paratergites slender and apically tapering Eubriinae
4. Pupation taking place under water; spiracular gills well developed Psephenoidinae
- 4'. Pupation taking place above water; spiracular gills reduced Afroebriinae **subfam.n.**

Key to adults of the subfamilies of Psephenidae

1. Seven visible abdominal ventrites in males; six visible abdominal ventrites in females Psepheninae
- 1'. Five visible abdominal ventrites in both sexes 2
2. Body flattened; anterior margin of pronotum rounded, concealing head 3
- 2'. Body dorsally convex; anterior margin of pronotum truncate or emarginate; head exposed 4
3. Elytra soft, without punctures Psephenoidinae
- 3'. Elytra sclerotized, with dense punctures Eubrianacinae
4. Apex of mesosternal process acute, posterior and lateral margins of terminal segments of maxillary and labial palpi with sensilla Afroebriinae **subfam.n.**
- 4'. Apex of mesosternal process truncate or emarginate; only lateral margins of terminal segments of maxillary and labial palpi with sensilla. Eubriinae

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Appendix 1. Updated classification of Pic's species belonging to Eubriinae.

Pic's species	Valid name
<i>Drupeus atriceps</i> Pic, 1916	<i>Granuleubria atriceps</i> (Pic)
<i>Drupeus marginatus</i> Pic, 1944	<i>Granuleubria marginata</i> (Pic)
<i>Drupeus notatithorax</i> Pic, 1923	<i>Schinostethus notatithorax</i> (Pic)
<i>Drupeus indicus</i> Pic, 1916	<i>Schinostethus nigricornis</i> Waterhouse, 1880
<i>Drupeus obscurus</i> Pic, 1923	<i>Homoeogenus obscurus</i> (Pic)
<i>Drupeus pruinus</i> Pic, 1923	<i>Schinostethus opacus</i> (Waterhouse, 1880)
<i>Drupeus pruinus</i> Pic, 1944	<i>Schinostethus pruinus</i> (Pic)
<i>Grammeubria atra</i> Pic, 1938	<i>Dicranopselaphus emmanueli</i> (Pic, 1918)
<i>Grammeubria diversipes</i> Pic, 1923	<i>Schinostethus nigricornis</i> Waterhouse, 1880
<i>Grammeubria emmanueli</i> Pic, 1918	<i>Dicranopselaphus emmanueli</i> (Pic)
<i>Grammeubria javana</i> Pic, 1916	<i>Dicranopselaphus javanus</i> (Pic)
<i>Grammeubria rufa</i> Pic, 1916	<i>Dicranopselaphus rufus</i> (Pic)
<i>Grammeubria testaceicornis</i> Pic, 1923	<i>Dicranopselaphus testaceicornis</i> (Pic)
<i>Ectopria multimaculata</i> Pic, 1934	<i>Dicranopselaphus multimaculatus</i> (Pic)
<i>Ectopria multinotata</i> Pic, 1924	<i>Scleroocyphon maculatus</i> Blackburn, 1892

Appendix 2. Taxa and localities of immature stages examined in the analysis.

Scientific name	Locality
Psephenidae	
Eubriinae	
<i>Aeneus</i> sp.	U.S.A.
<i>Afroebria sebastiani</i> Lee, 2003	South Africa
<i>Dicranopselaphus variegatus</i> Horn, 1880	U.S.A.
<i>D. imparis</i> Lee, Yang & Satô, 2000	Laos
<i>Ectopria leechi</i> Brigham, 1980	U.S.A.
<i>E. nervosa</i> (Melsheimer, 1845)	U.S.A.
<i>E. lobata</i> Lee, Yang & Satô, 1998	China
<i>Eubria palustris</i> (Germar, 1818)	Austria
<i>Granuleubria fontana</i> Lee & Yang, 1999	Vietnam
<i>Granuleubria</i> sp.	India
<i>Homoeogenus laurae</i> Lee & Yang, 1993	Taiwan
<i>Homoeogenus</i> sp.	Vietnam
<i>Macroebria lewisi</i> Nakane, 1952	Japan
<i>M. luei</i> Lee, Yang & Satô, 1997	Taiwan
<i>M. okinawana</i> Lee, Yang & Satô, 1997	Japan
<i>M. taiwana</i> Lee, Yang & Satô, 1997	Taiwan
<i>Microebria</i> sp. 1	Laos
<i>Microebria</i> sp. 2	Malaysia
<i>Nipponeubria yoshitomi</i> Lee & Satô, 1996	Japan
<i>Schinostethus albosulcus</i> Lee, Jäch & Yang, 1998	Laos
<i>S. brevicornis</i> Lee, Jäch & Yang, 1998	Malaysia
<i>S. brevis</i> (Lewis, 1895)	Japan
<i>S. notatithorax</i> (Pic, 1923)	Thailand
<i>S. priscus</i> Lee, Jäch & Yang, 1998	Malaysia
<i>S. satoi</i> Lee, Yang & Brown, 1993	Taiwan
<i>Sclerocyphon striatus</i> Lea, 1895	Australia
<i>S. minimus</i> Davis, 1986	Australia
<i>S. type A (sensu Davis, 1986)</i>	Australia
<i>Tychepephus felix</i> Waterhouse, 1876	Chile
Genus A sp.	Costa Rico
Genus B sp.	South Africa
Genus C sp.	Malaysia
Eubrianacinae	
<i>Afrobrianax ferdysi</i> Lee, Philips & Yang, 2003	South Africa
<i>Eubrianax amamiensis</i> Satô, 1965	Japan
<i>E. edwardsii</i> (LeConte, 1874)	U.S.A.
<i>E. ihai</i> Chûjô & Satô, 1970	Japan
<i>E. loochooensis</i> Nakane, 1852	Japan
<i>E. manakikikuse</i> Satô, 1964	Taiwan
<i>E. niger</i> Lee & Yang, 1990	Taiwan
<i>E. pellucidus</i> Lewis, 1895	Japan
<i>E. secretus</i> (Lee, Satô & Yang, 1999)	Taiwan
<i>E. serratus</i> Lee, Yang & Satô, 2001	Taiwan
<i>E. tarokoensis</i> Lee & Yang, 1990	Taiwan
<i>E. meridianus</i> Lee, Satô & Yang, 1999	Taiwan
<i>Mubrianax robustior</i> (Pic, 1928)	Malaysia
<i>Jaechanax dentatus</i> Lee, Satô & Yang, 2000	Indonesia
<i>Jaechanax</i> sp. A	Philippines
<i>Jimbrianax jaechi</i> Lee, Satô & Yang, 1999	Malaysia
<i>Odontanax dohertyi</i> (Pic, 1915)	Malaysia
Psepheninae	
<i>Mataeopsephus chinensis</i> (Nakane, 1964)	China
<i>M. esakii</i> Nakane, 1964	Taiwan
<i>M. japonicus</i> (Matsumura, 1916)	Japan
<i>M. maculatus</i> Nomura, 1957	Japan

Appendix 2. Continued.

Scientific name	Locality
<i>M. nitidipennis</i> Waterhouse, 1876	China
<i>M. quadribanchiae</i> Lee, Jäch & Satô, 2003	Taiwan
<i>M. sichuanensis</i> Lee, Jäch & Satô, 2003	China
<i>M. taiwanicus</i> Lee <i>et al.</i> , 1990	Taiwan
<i>M. vietnamensis</i> Lee, Jäch & Satô, 2003	Vietnam
<i>Psephenus falli</i> Casey, 1893	U.S.A.
<i>P. herricki</i> (De Kay, 1844)	U.S.A.
<i>Pheneps cursitatus</i> Spangler, 1987	Venezuela
<i>Psephenops</i> sp.	Belize
Genus D sp.	Belize
Psephenoidinae	
<i>Psephenoides subopacus</i> (Pic, 1954)	Taiwan
<i>Neopsephenoides</i> sp. 1	Philippines
<i>Neopsephenoides</i> sp. 2	Indonesia
<i>Afropsephenoides ruthae</i> Jeng <i>et al.</i> , 2006	South Africa
<i>Xylopsephenoides</i> sp.	Malaysia
Elmidae	
Larainae	
<i>Phanocerus clavicornis</i> Sharp, 1882	Costa Rico
Elminae	
<i>Elmis aenea</i> (Müller, 1806)	Austria

Appendix 3. Character matrix for the phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	5									
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0										
<i>Cneoglossa</i>	2	0	0	0	0	0	0	1	1	0	A	0	1	0	1	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1						
<i>Phanocerus</i>	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>Elmis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>Sclerocyphon</i>	1	0	0	0	0	1	0	1	1	0	0	1	A	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Tychecephus</i>	1	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Afroebria</i>	3	0	1	0	0	1	0	1	1	1	2	1	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Granuleubria</i>	3	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Ectopria</i>	2	1	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Homoeogenus</i>	3	1	0	0	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Nipponeubria</i>	2	1	1	0	0	1	0	1	1	?	0	1	1	1	1	0	0	1	0	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1			
<i>Acneus</i>	4	1	0	0	0	1	0	1	1	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
<i>Eubria</i>	2	1	0	0	0	1	0	1	1	3	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1		
<i>Schinostethus</i>	E	1	0	0	0	1	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
<i>Macroebria</i>	D	1	0	0	1	0	1	0	1	1	A	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
<i>Microebria</i>	2	1	0	0	0	1	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
<i>Dicranopselaphus</i>	D	1	0	A	0	1	0	1	1	1	A	1	1	1	1	0	0	0	A	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
<i>Psephenoides</i>	3	0	0	0	0	1	0	1	1	1	1	1	0	2	0	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	
<i>Neopsephenoides</i>	3	0	0	0	1	1	0	1	1	C	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	
<i>Afropsephenoides</i>	3	0	0	1	1	1	0	1	1	1	1	1	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	
<i>Xylophsephenoides</i>	3	0	0	1	1	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	
<i>Jinbrianax</i>	3	0	0	0	0	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Odontanax</i>	3	0	0	0	0	1	0	1	1	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Jaechanax</i>	3	0	0	0	0	1	0	1	1	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Mubrianax</i>	3	0	0	0	0	1	0	1	1	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Afrobrianax</i>	3	0	0	0	0	1	0	1	1	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eubrianax</i>	D	0	0	0	0	1	0	1	1	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mataeopsephus</i>	0	0	0	0	0	0	1	A	1	0	0	0	1	A	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Psephenus</i>	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1
<i>Pheneps</i>	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Psephenops</i>	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Genus D	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Genus A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Genus B	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Genus C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

