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Higher-level phylogeny of Hydrophilinae (Coleoptera: Hydrophilidae) based on larval, pupal and adult characters

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Abstract. A phylogenetic analysis, at a tribal and subtribal level, of the subfamily Hydrophilinae was conducted. The analysis was based on twenty-nine taxa (twenty-three genera) and 148 characters (fifty-eight from immature stages and bionomics, and ninety from adults). According to the present study, Hydrophilinae is monophyletic, and except for the tribe Hydrophilini which appears as polyphyletic (it includes the subtribes Hydrophilina, Hydrobiina, and Acidocerina), the remaining tribes are monophyletic. The tribes Berosini and Chaetarthriini form the basal clade of Hydrophilinae. One unexpected result is the relationship between the subtribe Hydrobiina and the tribe Sperchopsini, which form a well-supported clade. The final tree has the following structure: (((((Sperchopsini Hydrobiina) (Anacaenini Laccobiini)) Acidocerina) Hydrophilina) (Berosini Chaetarthriini)). The results partially disagree with the phylogeny presented by Hansen, in 1991, which was based mostly on adult characters. Several evolutionary trends are briefly discussed: the types of egg case, the morphology of the clypeolabrum, mouthparts, legs, and breathing adaptations in larvae.

Introduction

Hydrophiloidea is a diverse superfamily of staphyliniform beetles (Lawrence & Newton, 1995; Hansen, 1997) and, according to most authors, constitutes a well-defined monophyletic group (Hansen, 1991, 1995, 1997; Archangelsky, 1998). The superfamily includes over 2800 species and comprises six families (Table 1). The families Helophoridae, Epimetopidae, Georissidae, Hydrochidae and Spercheidae have been given a subfamily rank by other authors (Lawrence & Newton, 1982, 1995; Newton & Thayer, 1992; Van Tassell, 2000), but this does not challenge the monophyly of the group. These first five families are less diverse, and they are not subdivided into subfamilies or tribes. Hydrophilidae (s.str.), on the other hand, comprises over 2300 species (Hansen, 1999) and has been subdivided into four subfamilies (Table 1). Of these, Hydrophilinae and Sphaeridiinae are the most diverse and include several tribes.

Adults and larvae of Hydrophilidae (s.str.) are fairly common, their size ranging from about 1.5 to over 50 mm in some genera (e.g. *Hydrophilus* Geoffroy and *Dibolocelus* Bedel). They can be found in most freshwater environments, as well as terrestrial habitats (especially the Sphaeridiinae). Whereas adults are mostly scavengers, larvae are mostly predatory (Balduf, 1935; Böving & Henriksen, 1938; Miller, 1963; Archangelsky, 1997). The subfamily Hydrophilinae includes species which inhabit both aquatic and semi-aquatic habitats, and has almost sixty genera (Hansen, 1999). These beetles can be found in most freshwater environments, and also in some unusual habitats, such as phytotelmata, hot springs, temporary pools and brackish waters. Hydrophilinae include close to 1600 species (Hansen, 1999) subdivided into six tribes (Table 2). The tribe Hydrophilini is furthermore subdivided into three subtribes (Hansen, 1991, 1995).

The most recent phylogenetic analysis including tribes, and other suprageneric groups, of Hydrophilidae was carried out by Hansen (1991), based mostly on adult characters. Larval, pupal and bionomical characters have been important in establishing the phylogenetic relationships at a family and subfamily level within Hydrophiloidea (Beutel, 1994, 1999; Archangelsky, 1998; Hansen, 2000). As new

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Table 1. Classification of Hydrophiloidea (Hansen, 1991, 1995).

Family	Subfamily
Helophoridae	
Epimetopidae	
Georissidae	
Hydrochidae	
Spercheidae	
Hydrophilidae	Horelophinae Horelophopsinae Hydrophilinae Sphaeridiinae

information on the immature stages and biology of hydrophilids has become available in the last few years (Beutel, 1994, 1999; Archangelsky, 1997, 1999a, b, c, 2000, 2001, 2002a, b), I believe it is important to combine this with what is already known from adults and to perform a new and more complete analysis. This paper presents a phylogenetic analysis of the subfamily Hydrophilinae, at a tribal and subtribal level, including new characters from the preimaginal stages, and also characters from their biology. These characters have been combined with Hansen's (1991) adult characters. The results of this analysis are contrasted with the phylogenetic hypothesis derived from Hansen's (1991, 1995) analysis. Several evolutionary scenarios involving the modification of some larval characters are discussed.

Materials and methods

For this analysis, immature stages of twenty-nine species, belonging to twenty-three genera of Hydrophiloidea, were studied (see Appendix 1). When possible, more than one genus of each tribe and subtribe was included. For some diverse genera (e.g. *Berosus* Leach, *Tropisternus* Solier, *Enochrus* Thomson), more than one species was included in the analysis. Larvae and pupae of additional species were studied to corroborate the consistency of the characters and their states, or their diversity, within different genera (Appendix 1). Several outgroups were included, Helophoridae (*Helophorus* Fabr.), Spercheidae (*Spercheus* Kugelann) and five genera of the sister subfamily Sphaeridiinae (*Phaenonotum* Sharp, *Dactylosternum* Wollaston, *Cercyon* Leach, *Oosternum* Sharp, and *Sphaeridium* Fabr.). Descriptions from the literature of other larvae were consulted (Böving & Henriksen, 1938; Moulins, 1959; Spangler, 1962, 1979, 1986; Bertrand, 1972; Angus, 1992). The correspondence between terminal groups obtained by Hansen (1991) and the larvae included in this study is shown in Table 3.

Most larvae and pupae were reared in the laboratory from eggs laid by adults in order to assure correct species association. Collecting and rearing techniques are discussed in detail in Archangelsky (1997). The larvae and pupae were fixed in boiling water and stored in 75% alcohol. Lactic acid was used to clear the specimens; after clearing they were rinsed with distilled water, dissected and mounted on slides using Hoyer's as the mounting medium.

Bionomical information was mostly from personal observations (Archangelsky & Durand, 1992a, b; Archangelsky, 1994, 1997, 1999a, b, c, 2000, 2001, 2002a, b, c; Fernández *et al.*, 2000), additional data were obtained from the literature (Richmond, 1920; Wilson, 1923a, b; Balduf, 1935; Böving & Henriksen, 1938; Spangler, 1961, 1962; Angus, 1992; Wilson, 2000).

Table 2. Suprageneric classification of Hydrophilinae (*sensu* Hansen, 1991), with the number of genera and species for each group, modified from Hansen (1999).

Tribe	Subtribe	Number of genera and species
Sperchopsini		Five genera; twenty-two species
Berosini		Five genera; 344 species
Chaetarthriini		Five genera; seventy-seven species
Anacaenini		Nine genera; 202 species
Laccobiini		Nine genera; 296 species
Hydrophilini	Acidocerina	Fifteen genera; 426 species
	Hydrobiina	Five genera; seventeen species
	Hydrophilina	Six[a] genera; 191 species

[a] *Dibolocelus*, considered by Hansen as a subgenus of *Hydrophilus*, is kept in this study as a separate genus, following the position of most American workers.

Table 3. Correspondence between terminal groups obtained by Hansen (1991) and genera (larvae) included in this study. Those with unknown larvae were not included in the study.

Adults (Hansen, 1991)	Larvae
Helophoridae	*Helophorus*
Spercheidae	*Spercheus* spp.
Sperchopsini	*Sperchopsis*
	Ametor
Berosini	*Berosus* spp.
	Hemiosus
	Derallus
Chaetarthriini	*Chaetarthria*
Notohydrus	Unknown
Anacaena group	*Paracymus* spp.
Pelthydrus	Unknown
Laccobius	*Laccobius*
Oocyclus group	*Oocyclus*
Acidocerus group	*Helochares*
	Enochrus spp.
Hydrobiina	*Hydrobius*
	Hydramara
Hydrophilina	*Tropisternus* spp.
	Dibolocelus
	Hydrophilus
Coelostoma group	*Phaenonotum*
	Dactylosternum
Megasternini	*Cercyon*
	Oosternum
Sphaeridiini	*Sphaeridium*

Of the 148 characters used, fifty-eight are derived from the biology and morphology of the preimaginal stages, the remaining are adult characters: eighty-nine from Hansen's (1991) work and one (size of adults) from the present study. Adult characters from Hansen (1991) are listed in Appendix 2; characters from the preimaginal stages and biology of Hydrophilidae are discussed below.

Most characters (142) are qualitative; six continuous or quantitative characters were coded using the gap-weighting method (Thiele, 1993). Continuous characters were subdivided into twenty states (A–T) and considered ordered. Five continuous characters were coded for larvae; for constancy they were based on third instar larvae alone (those larvae for which only first instars are known were coded with a '?'). The resulting matrix, twenty-nine taxa × 148 characters (Appendix 3) was analysed using PAUP*b10 (Macintosh version; Swofford, 2002). Different analyses were performed: (1) 142 characters (continuous characters not included) without any kind of weighting (abbreviated 142NW); (2) 148 characters weighted differentially (continuous characters with weights = 1, qualitative characters weighted in a way as to make them equal to the quantitative characters based on the number of steps (nineteen in continuous characters), e.g. characters with one step weight = 19, with two steps weight = 9, and so on) (abbreviated 148DW); (3) 148 characters, all qualitative characters with equal weight (continuous characters = 1 and all qualitative = 19) (abbreviated 148EW). Weighting was performed to maintain parity in the number of steps (Kitching *et al.*, 1998); in conventional analyses, binary characters, for example, have a range of 0–1 (one step) whereas the quantitative characters in the present study have a range of 0–19 (nineteen steps).

In all cases the search was heuristic due to the number of taxa (twenty-nine); the optimality criterion used was maximum parsimony; the starting tree was obtained by stepwise addition; the addition sequence was random, and the branch-swapping algorithm used was tree bisection-reconnection; the number of replicates in each search was 1000; ACCTRAN was used for character optimization. To measure the support of the clades, jackknife analyses were performed on each of the three analyses: 142NW, 148DW and 148EW, 200 replicates were performed in each case.

Description of bionomical, larval and pupal characters

Bionomical characters

1. Larvae terrestrial (0); larvae aquatic or semi-aquatic (1).

The major habitats utilized by hydrophiloids are: riparian, aquatic and terrestrial. This is the best way to summarize their environmental preferences, but it should be kept in mind that any of these habitats can be subdivided into many different microhabitats. For example, terrestrial species can be found in dung, rotting mushrooms, carrion, flowers, ant nests, etc.; aquatic species can be found in lotic or lentic environments, phytotelmata, caves, saline or hypersaline waters, etc. Hydrophiloids seem to come from a riparian environment, as Helophoridae, a basal group, inhabit such places (Hansen, 1995, 1997; Archangelsky, 1999c). Spercheidae are aquatic, the same as most Hydrophilinae. Within Sphaeridiinae we find the greatest diversity of habitats. They are mostly terrestrial but in some cases secondarily aquatic, living on floating vegetation or in phytotelmata (e.g. *Phaenonotum*). Consistency index (CI) = 0.50; retention index (RI) = 0.75 (CI and RI values refer to the 148DW analysis).

2. Egg cases laid on substrate (0); floating freely (1); carried by female (2).

Most hydrophiloids build silk egg cases, usually on some kind of substratum (sand, rocks, aquatic plants, soil, dung, etc.). In a few genera the females carry the cases underneath the abdomen (*Spercheus* and some Hydrophilinae such as *Helochares* Mulsant). In some hydrophiline genera the cases float freely on the water's surface (*Dibolocelus*, *Hydrophilus*). CI = 0.67; RI = 0.67.

3. Larval development (including prepupal stage) long, over 30 days, usually over 35 days (0); short, under 30 days, usually 25 days or less (1).

In general larval development in hydrophiloids is quite fast (most species range from 1 to 2 months). Developmental time is associated with the kind of habitat each species inhabits; Sphaeridiinae such as *Oosternum* and *Cercyon*, whose larvae develop in temporary habitats such as dung or rotting plant/animal tissues, have developmental times from egg to pupa of 10 days or less (Hafez, 1939a, b; Archangelsky, 1997, 1999c). On the other hand, Hydrophilinae usually live in more stable aquatic habitats; this is reflected in longer periods of development from egg to pupa, usually over a month. One special case within Hydrophilinae are species such as *Tropisternus lateralis* and *Tropisternus flavescens*, which are colonizers and have short developmental times in short-lived pools. CI = 0.50; RI = 0.80.

Characters from the head capsule and mouthparts

4. Head prognathous (0); subprognathous (1); hyperprognathous (2).

Within hydrophiloids, the mouthparts can be found in three different positions (Beutel, 1999). Helophoridae have a prognathous head. In Spercheidae the mouthparts are slightly inclined downwards; this position is called subprognathous. In Hydrophilidae (s.str.), the mouthparts are typically hyperprognathous (inclined upwards). CI = 1.00; RI = 1.00.

5. Gula absent (0); present (1).

Most hydrophiloids lack a well-developed gula; all that remains visible is the gular suture (Archangelsky, 1998; Beutel, 1999). A well-developed gula is present in *Spercheus* and *Hydrochus* (this last genus was not included in the analysis). CI = 1.00; RI = 1.00.

6. Frontal sutures converging towards base of head capsule (0); not converging (1).

The frontal sutures have different shapes: V-shaped, bell-shaped, lyriform, subparallel (Archangelsky, 1997), but can be grouped into two groups, those in which the sutures converge towards the base of the head (e.g. *Helophorus*, *Enochrus*; Fig. 1A, C), and those in which the sutures remain widely separated at the base of the head (*Paracymus* Thomson, *Berosus*, most Sphaeridiinae; Fig. 1B). CI = 0.25; RI = 0.73.

7. Coronal suture absent (0); present (1).

In some Hydrophilidae the frontal sutures converge into a short coronal suture before reaching the occipital margin (e.g. *Sperchopsis* LeConte, *Tropisternus*; Fig. 1C). In *Helophorus*, *Spercheus*, many Sphaeridiinae, and some Hydrophilinae such as the Berosini, the frontal sutures may or may not converge, but they never fuse into a coronal suture (Fig. 1A, B). CI = 0.50; RI = 0.90.

8. Nasale symmetrical (0); asymmetrical (1).

The clypeolabrum (= labroclypeus) is composed of the median nasale and the lateral lobes of the epistome. The nasale is usually a median projection with one or more teeth (e.g. *Helophorus*, *Enochrus*, *Paracymus*; Fig. 1D–H). The shape of the nasale is characteristic for each genus, and can be symmetrical (e.g. *Helophorus*, *Chaetarthria* Stephens, *Derallus* Sharp; Fig. 1D) or asymmetrical (e.g. *Helochares*, *Enochrus*; Fig. 1E, G, H). In *Spercheus* the nasale is not developed. CI = 0.50; RI = 0.71.

9. Nasale with teeth (0); smooth, lacking teeth (1).

The nasale is generally formed by one or more projections or teeth (it can also be serrated as in *Enochrus*, *Helochares*, or *Paracymus*; Fig. 1E, G), but in some genera there are no projections and this area of the clypeolabrum is smooth or even concave (e.g. *Hydrophilus*, many Sphaeridiinae; Fig. 1F). CI = 0.67; RI = 0.75.

10. Lateral lobes of epistome symmetrical (0); slightly asymmetrical (1); strongly asymmetrical: left lobe with strong spines pointing mediad and projecting further than nasale (2).

As in the nasale, the lateral lobes of the epistome can have different shapes, and can be symmetrical (e.g. *Helophorus*, *Phaenonotum*, *Sperchopsis*, *Tropisternus*; Fig. 1D, E) or asymmetrical (e.g. *Enochrus*, *Oocyclus* Sharp). The level of asymmetry varies between genera; some have a slight asymmetry (many Sphaeridiinae, among Hydrophilinae *Paracymus* and *Enochrus*; Fig. 1G) represented by a slight difference in the shape. Those genera with a strong asymmetry (*Berosus*, *Hemiosus* Sharp, *Laccobius* Erichson and *Oocyclus*; Fig. 1H) have a strong difference in the shape, as well as a marked difference in the chaetotaxy of both lobes, with the left lobe strongly developed, covering the base of the left mandible, and with a row of strong spines projecting mediad, meanwhile the right lobe is usually poorly developed and usually lacks setae. CI = 0.33; RI = 0.67.

11. Both epistomal lobes with 3 or more stout setae projecting mediad (0); only left lobe with setae (1); with 2 setae or less (2).

The number of epistomal setae is also characteristic for different genera. Genera such as *Helophorus*, *Phaenonotum*, the hydrophilines *Chaetarthria*, *Hydrobius* Leach, *Hydramara* Knisch and *Sperchopsis* have three or more strong setae projecting mediad (Fig. 1D). Other genera have two or less setae (e.g. *Paracymus*, *Enochrus*; Fig. 1E, F), or have setae only on the left lobe (e.g. *Berosus*, *Laccobius*; Fig. 1H). CI = 0.33; RI = 0.64.

12. Left epistomal lobe without pubescence (0); with a patch of dense pubescence (1).

In some Sphaeridiinae the left epistomal lobe has a shallow notch with a dense patch of pubescence which usually corresponds with the hypopharingeal lobe (e.g. *Cercyon*, *Sphaeridium*). This pubescence is absent in other Sphaeridiinae (e.g. *Phaenonotum*, *Dactylosternum*) and all known Hydrophilinae. CI = 1.00; RI = 1.00.

13. Antennae with 2 sensory appendages (0); with one sensorium (may be reduced) (1).

The number of sensory appendages carried by the second antennal segment can be two (in the helophorid lineage; Fig. 2B) or one (Fig. 2A, E). Sometimes this appendage can be reduced to a small oval plate in genera such as *Tropisternus*, *Hydrophilus*, etc. (Fig. 2C, D). CI = 1.00; RI = 0.

14. First antennal segment bare (0); with a strong distal inner seta or spine projecting forwards (1); with numerous inner and outer setae (2).

In most Hydrophilinae the first antennal segment (scape) lacks setae, but in Berosini there is a stout distal inner seta on this segment (*Derallus* has a strong spine in this same position, which is considered to be homologous of the seta) (Fig. 2E, F). Members of the subtribe Hydrophilina have numerous inner and outer setae on the first antennal segment (Fig. 2D). CI = 1.00; RI = 1.00.

15. Ratio: length third antennal segment/length antennal sensorium (A–T).

The length of the sensory appendage of the second antennal segment is quite variable, but it is usually distinctive in most genera. For example, the Hydrophilina have a very short sensory appendage (Fig. 2D), whereas other genera, such as the Berosini, have a longer appendage (Fig. 2F). The best way to express this measure is as a ratio between the third antennal segment and the sensory appendage. The states have been coded using Thiele's (1993) gap-weighting method, subdivided into twenty (states A–T). Ordered. CI = 0.53; RI = 0.62.

16. Mandibles symmetrical (0); slightly asymmetrical (equal number of teeth) (1); strongly asymmetrical (different number of teeth) (2).

The shape of the mandibles is quite variable among different genera of hydrophiloids (Archangelsky, 1997). Many genera have symmetrical mandibles (e.g. *Helophorus*, *Paracymus*). Other genera have asymmetrical mandibles, and the asymmetry may involve both the shape and the number of inner teeth; these asymmetries are directional. For example *Berosus*, *Enochrus* and *Laccobius* have mandibles which differ in the shape and number of teeth (Fig. 3B). Other genera, such as *Helochares*, some *Enochrus*, have a similar number of teeth in both mandibles, but the shape of the teeth in each mandible is slightly different (Fig. 3A). CI = 0.25; RI = 0.60.

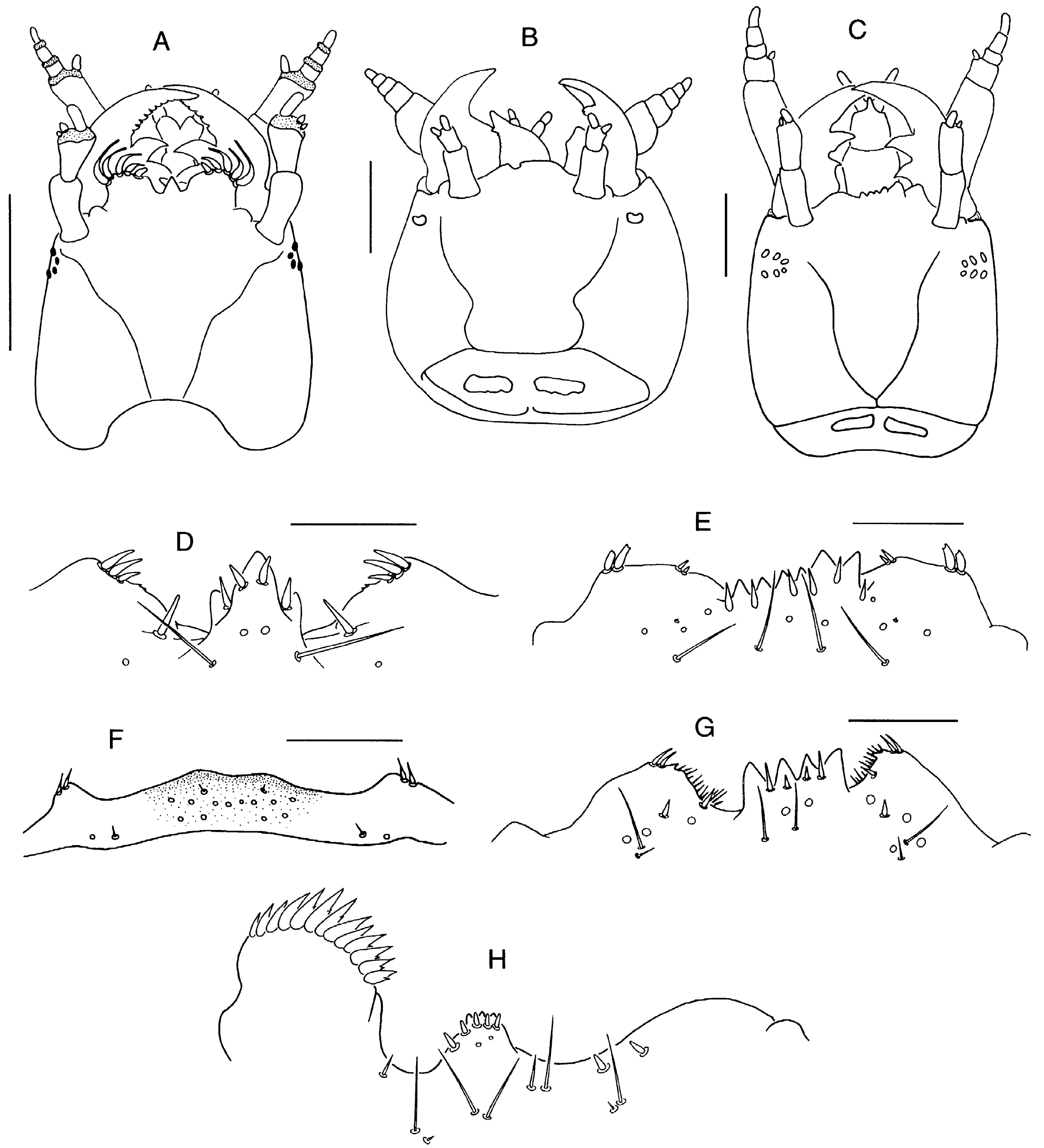

Fig. 1. A, *Helophorus orientalis*, head, dorsal view; B, *Cercyon praetextatus*, head, dorsal view; C, *Enochrus* (*Hugoscottia*) *tremolerasi*, head, dorsal view; D, *Phaenonotum exstriatum*, clypeolabrum, dorsal view; E, *Helochares maculicollis*, clypeolabrum, dorsal view; F, *Dibolocelus ovatus*, clypeolabrum, dorsal view; G, *Paracymus subcupreus*, clypeolabrum, dorsal view; H, *Berosus auriceps*, clypeolabrum, dorsal view. Scales = 0.2 mm (A–C); 0.05 mm (D, G); 0.1 mm (E); 1 mm (F).

17. Number of inner teeth on left mandible: none (0); one (1); 2 (2); 3 (3); *Berosus*-type (4).

The number of inner teeth on the mandibles (retinacula) varies from none to three; this number is usually constant for each genus or subgenus (Fig. 3A, C, E). *Berosus*, *Hemiosus*, *Laccobius* and *Oocyclus* have a special type of left mandible where the number of teeth is difficult to establish as they have projections which may carry several points and

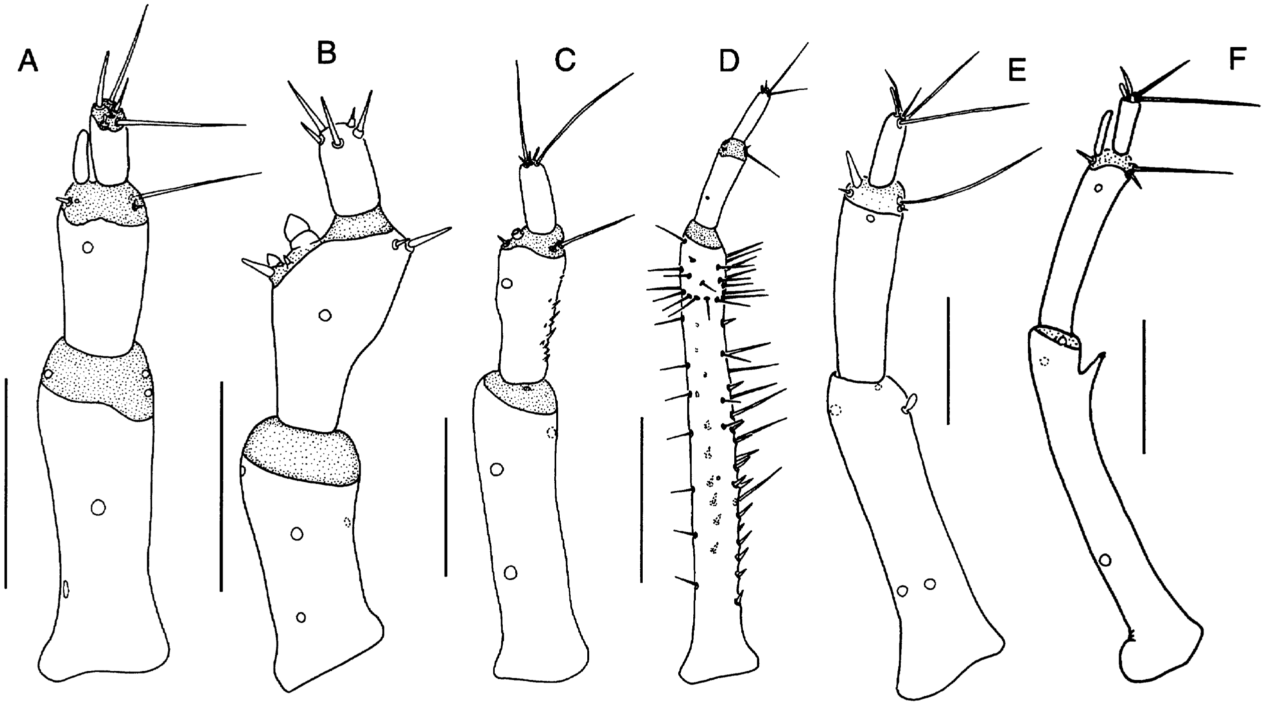

Fig. 2. A, *Dactylosternum* sp., antenna, dorsal view; B, *Helophorus orientalis*, antenna, dorsal view; C, *Hydrobius melaenus*, antenna, dorsal view; D, *Tropisternus noa*; E, *Hemiosus bruchi*, antenna, dorsal view; F, *Derallus angustus*, antenna, dorsal view. Scales = 0.1 mm (A, B, E, F); 0.2 mm (C); 0.5 mm (D).

others which bear short spines (Archangelsky, 1997, 1999a, 2002b, c); these structures are difficult to homologize with regular inner teeth (they can be modified retinacula or secondarily evolved structures), so this special type of mandible has been coded as a different state and is referred to as '*Berosus*-type' (Fig. 3B). CI = 0.40; RI = 0.65.

18. Number of inner teeth on right mandible: none (0); one (1); 2 (2); 3 (3).

As above, the number of inner teeth (retinacula) is usually constant for each genus or subgenus (Fig. 3A, D). In this case, the right mandibles of Berosini and Laccobiini are not modified, as are the left mandibles, and the number of inner teeth can be established readily (Fig. 3B). CI = 0.27; RI = 0.47.

19. Mandible simple at apex (0); bifid at apex (1).

In most Hydrophiloidea the mandibles have a simple apex. The only known exception is found in Spercheidae, which have mandibles with a bifid apex (Fig. 3F). CI = 1.00; RI = 1.00.

20. Stipes without inner cuticular spines (0); with spines only at base (1); with spines along most of inner margin (2).

The stipes always carries some setae on the inner and outer margins. In addition to those setae there can be other structures such as cuticular spines (Moulins, 1959; Archangelsky, 1997). In some genera the stipes is smooth (e.g. *Enochrus*, *Berosus*; Fig. 4A), but in other genera there may be cuticular spines at the base of the stipes (e.g. *Tropisternus*, *Hydramara*, *Sperchopsis*; Fig. 4B) or along most of the inner margin (e.g. *Chaetarthria*, *Paracymus*, *Laccobius*; Fig. 4C, F). CI = 0.29; RI = 0.58.

21. Stipes without pubescence (0); with a more or less developed pubescence (1).

Some genera, especially those which live in terrestrial habitats, tend to have pubescent mouthparts in order to aid the absorption of preorally liquefied food (Quennedey, 1965; Archangelsky, 1999c). This pubescence can be found in the stipes of many Sphaeridiinae (e.g. *Sphaeridium*, *Cercyon*; Fig. 4D) (Böving & Henriksen, 1938). CI = 1.00; RI = 1.00.

22. Stipes with an inner row of 5 setae (0); with 9 or more setae (1).

This character is constant for most genera, although some variation may occur within Sphaeridiinae; for example, the number of setae in *Phaenonotum* can vary between eleven and fourteen, and in *Dactylosternum* between twelve and nineteen (Fig. 4D). In Hydrophilinae, the number is usually five (Fig. 4A, C, F); exceptions are: *Hydrophilus* (a primary row of five setae and a secondary row of about ten to twelve inner setae), *Hydramara* (with six to seven setae; Fig. 4B) and *Chaetarthria* (with four or five setae). In *Spercheus,* this character does not apply as they have a well-developed lacinia on the inner margin of the stipes. CI = 1.00; RI = 1.00.

23. Distal inner apex of stipes without a stout spine (0); ending in a stout spine projecting forwards (1).

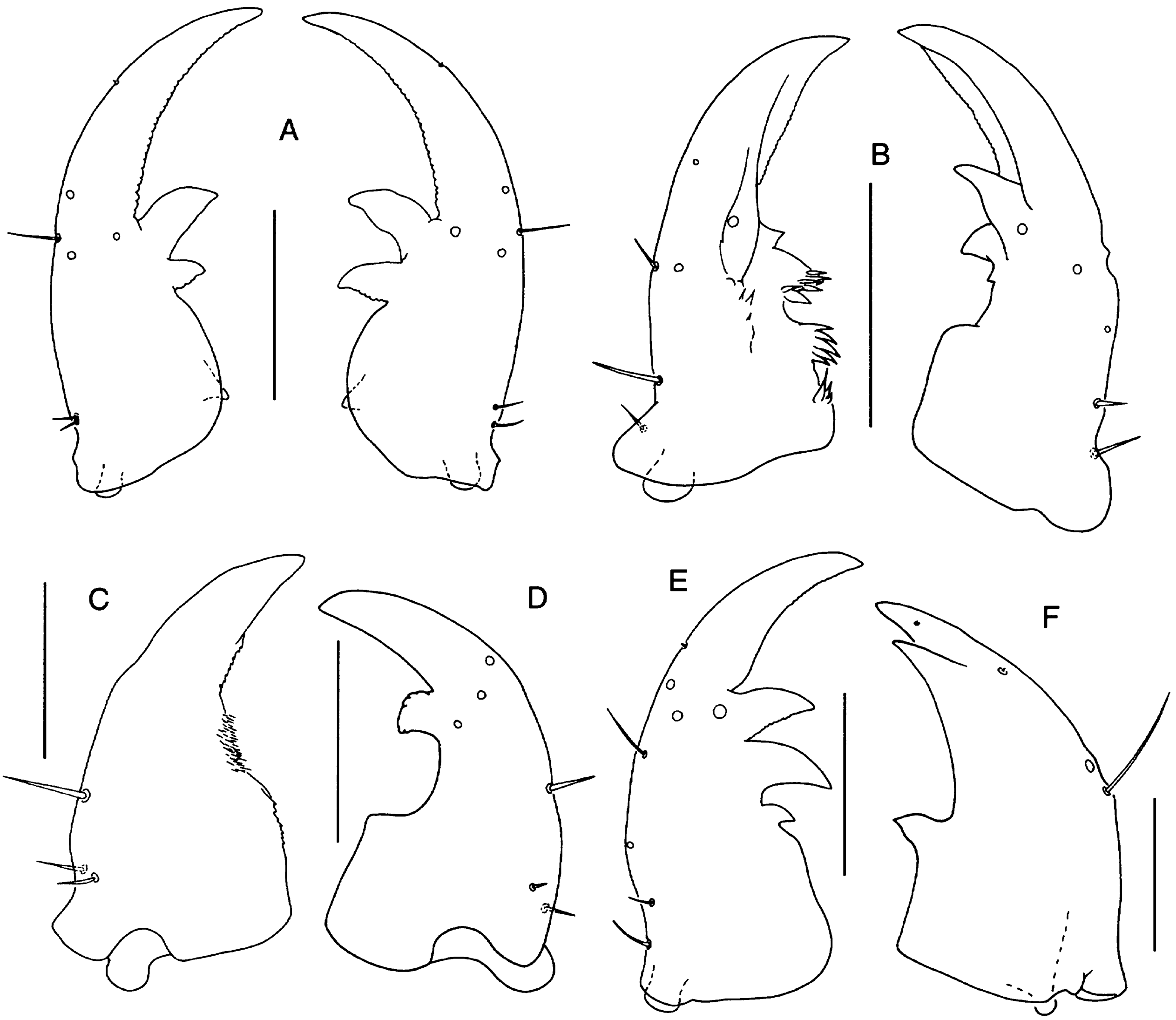

Fig. 3. A, *Helochares maculicollis*, mandibles, dorsal view; B, *Laccobius minutoides*, mandibles, dorsal view; C, *Sphaeridium scarabaeoides*, left mandible, dorsal view; D, *Oosternum costatum*, right mandible, dorsal view; E, *Paracymus subcupreus*, left mandible, dorsal view; F, *Spercheus halophilus*, right mandible, dorsal view. Scales = 0.2 mm (A); 0.1 mm (B–F).

In most genera the distal inner apex of the stipes has a straight or blunt margin (Fig. 4A, C), but in some Sphaeridiinae (*Phaenonotum exstriatum*) and in the Sperchopsini and Hydrobiina, the apex ends in a stout and sharp cuticular spine (Fig. 4B). CI = 0.50; RI = 0.75.

24. Lacinia absent (0); present (1).

There is a well-developed lacinia in Spercheidae (Fig. 4E), the remaining hydrophiloids lack a lacinia. An exception is seen in Hydrochidae (not included in this analysis), which have a small, reduced structure on the inner margin of the stipes which can be interpreted as a reduced lacinia. CI = 1.00; RI = 1.00.

25. Maxilla with appendage of palpal segment 1 sclerotized (0); unsclerotized (1).

The first palpal segment of the maxilla carries a small inner appendage. This appendage is well sclerotized in most Hydrophiloidea (Fig. 4A–C), but in some Anacaenini and Sphaeridiinae this appendage is unsclerotized (Fig. 4F). CI = 0.50; RI = 0.75.

26. First palpal segment of maxilla completely sclerotized (0); incompletely sclerotized (1).

The first palpal segment of the maxilla is usually well sclerotized, forming a ring (Fig. 4A, D). In several genera this first segment is incompletely sclerotized, especially on the dorsal surface (e.g. *Hydrobius*, *Hydramara*, *Laccobius*; Fig. 4B, C, F). CI = 0.33; RI = 0.71.

27. Ratio: length stipes/length palpal segment 1 (A–T).

The relative lengths of several maxillary structures vary among different genera. These differences help to group and separate taxa, and have been coded as ratios. The ratio between the length of the stipes and the first palpal

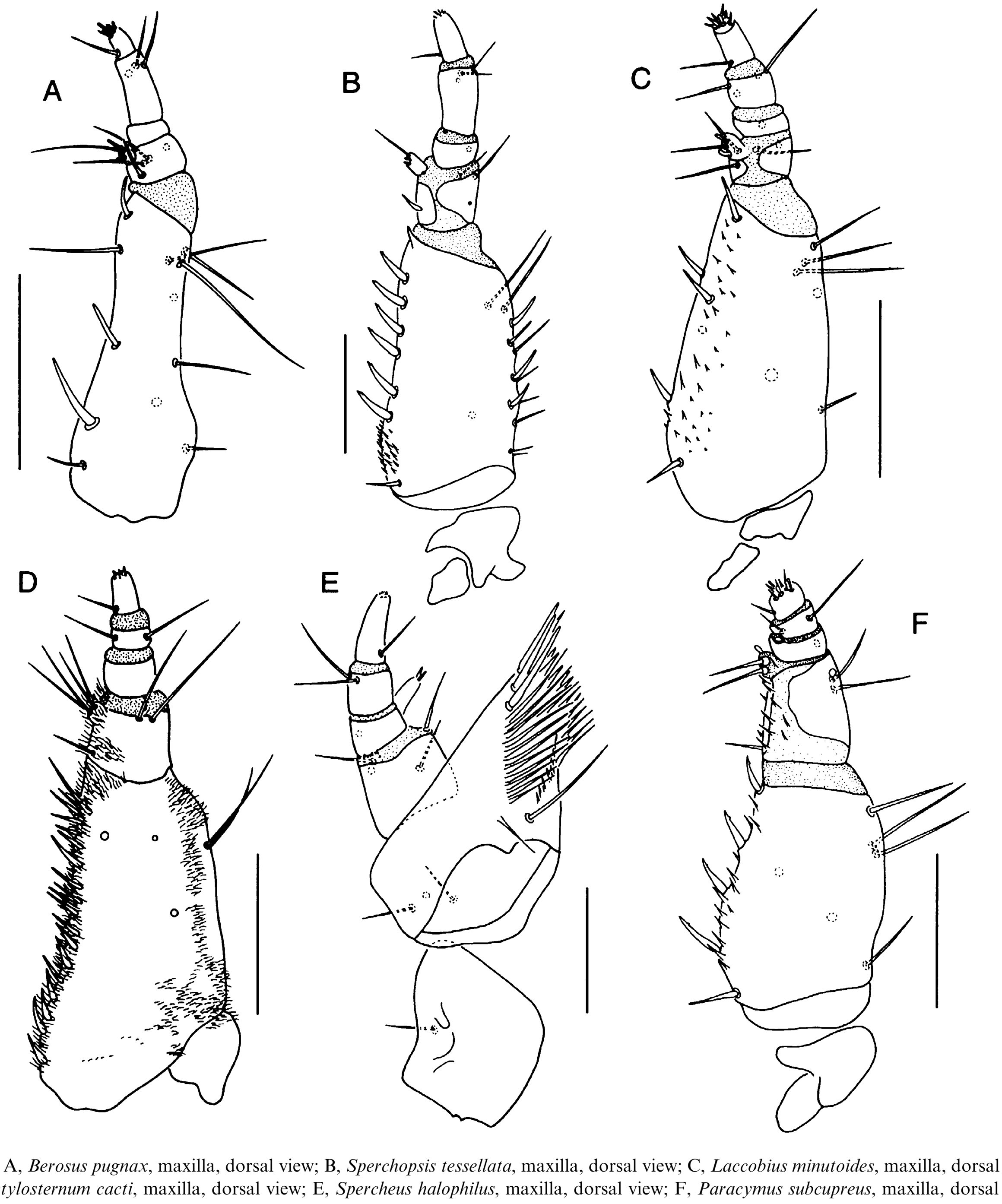

Fig. 4. A, *Berosus pugnax*, maxilla, dorsal view; B, *Sperchopsis tessellata*, maxilla, dorsal view; C, *Laccobius minutoides*, maxilla, dorsal view; D, *Dactylosternum cacti*, maxilla, dorsal view; E, *Spercheus halophilus*, maxilla, dorsal view; F, *Paracymus subcupreus*, maxilla, dorsal view. Scales = 0.2 mm (A, B, D); 0.1 mm (C, E, F).

segment is characteristic for most genera. For example, in Berosini this ratio has a very high value (Fig. 4A), whereas in other genera such as *Paracymus*, *Helophorus* and *Spercheus*, this ratio has a very low value (Fig. 4F). The states have been coded using Thiele's gap method, subdivided into twenty (states A–T). Ordered. CI = 0.31; RI = 0.53.

28. Ratio: length maxillary palp/length palpal segment 3 (A–T).

The relative length of the third palpal segment varies among different genera and tribes. For example, in Berosini this ratio is rather low (Fig. 4A), whereas in genera such as *Paracymus* and *Chaetarthria* this ratio is high (Fig. 4F). In

Hydrophilini this ratio is variable but has an intermediate value. Ordered. CI = 0.30; RI = 0.59.

29. Ratio: length maxillary palpal segment 1/length maxillary palpal segment 3 (A–T).

Within Hydrophilinae the ratio between the length of the first and third palpal segments is characteristic. For example, in Anacaenini (also in *Helophorus*) this ratio yields a high value (Fig. 4F), whereas in the Berosini this value is very low (Fig. 4A). Ordered. CI = 0.34; RI = 0.56.

30. Ratio: length maxillary palpal segment 1/length appendage (A–T).

This ratio is also useful. For example, in Hydrophilina and Anacaenini this sensorium is very small, and the ratio therefore has very high values; on the other hand, in Acidocerina, Berosini and *Chaetarthria* the appendage is longer when compared with the length of the first palpal segment. Ordered. CI = 0.33; RI = 0.64.

31. Ligula absent (0); present (1); reduced (2).

The ligula is a middle projection of the labium. It can be present, reduced or absent. It is absent in *Helophorus* (and the other genera of the helophorid lineage; Fig. 5A). It is secondarily reduced in many Sphaeridiinae (Megasternini, some Coelostomatini), and in Laccobiini and *Berosus* (Fig. 5D, E) (Archangelsky, 1998, 1999a); for this reason this character has been coded as ordered. In all the other groups it is a well-developed, variously shaped projection (Fig. 5C, F). Ordered. CI = 0.40; RI = 0.57.

32. Hypopharyngeal lobe absent (0); present (1).

Many of the higher Sphaeridiinae have a well-developed, asymmetrical, hypopharyngeal lobe on the left side of the labium, in the dorsal position (Fig. 5D). This structure resembles a hairy tongue, and probably aids in the absorption of preorally digested prey in these terrestrial Sphaeridiinae (Archangelsky, 1999c). This lobe is absent in all known Hydrophilinae (Fig. 5C, E, F). CI = 1.00; RI = 1.00.

33. Dorsal surface of mentum without cuticular spines (0); with spines (1).

The dorsal surface of the mentum can be smooth or may have cuticular spines covering, in many cases, a subtriangular or subrectangular area on the basal half (Fig. 5C, F). The mentum is smooth in many sphaeridiines, especially those found in terrestrial environments, in benthic hydrophilines such as *Berosus* and *Hemiosus*, and also in *Laccobius*. CI = 0.33; RI = 0.75.

34. Mentum less than 2× wider than prementum (0); more than 2× wider than prementum (1).

In most genera the prementum and the mentum are almost similar in width (Fig. 5A, C), but in *Derallus* and genera of the subtribe Hydrophilina the mentum is much wider than the prementum (twice or more; Fig. 5F). CI = 0.50; RI = 0.75.

35. Mentum without distal crown of long and stout setae (0); with distal crown of 3 or more pairs of long and stout setae (1).

Some hydrophilid larvae have a distal crown of long and stout setae on the mentum (e.g. *Paracymus*, *Sperchopsis*, *Hydramara*; Fig. 5C), which is missing in other Hydrophilinae and all other known hydrophiloid larvae (Fig. 5A, D) (Archangelsky, 1997). CI = 0.50; RI = 0.80.

36. Prementum without ‘comb’ of lateral spines (0); with comb of lateral spines (1).

In *Spercheus* the prementum has a lateral comb of long and strong cuticular spines, this comb is lacking in all other hydrophiloids (Fig. 5B). This structure seems to be associated with the feeding habits of *Spercheus* larvae, which may feed on detritus and drifting organic remains (Archangelsky, 2001). CI = 1.00; RI = 1.00.

37. Prementum sclerotized, forming a ring (0); mostly membranous, sclerotized ventrally (1).

Most Hydrophiloids have a well-sclerotized prementum (Fig. 5A, C, E), forming a variously shaped ring; in many higher Sphaeridiinae (e.g. *Cercyon*, *Oosternum*) the prementum is poorly sclerotized and appears as a small, sometimes subdivided, narrow plate (Fig. 5D). CI = 1.00; RI = 1.00.

38. Labial palps without cuticular spines (0); with spines on the membrane joining segments (1); with spines on the segments and membrane (2).

The labial palps in hydrophilids can be bare, lacking cuticular spines (e.g. *Berosus*, *Laccobius*, *Tropisternus*; Fig. 5E, F) or they can have small cuticular spines, either on the membrane connecting the segments (e.g. *Helophorus*, *Hemiosus*; Fig. 5A) or on both the segments and the membrane (e.g. *Paracymus*, *Helochares*, *Enochrus*; Fig. 5C). These spines are always pointing forwards, and probably help to manipulate the prey. CI = 0.29; RI = 0.58.

39. Cervical sclerites absent (0); present (1).

The cervical sclerites are two small plates located close to the occipital margin on the dorsal side of the neck (Fig. 1B, C). The shape of these plates is usually suboval or subquadrangular, and in some cases they may be very small and difficult to see. In many genera these plates are absent (e.g. *Helophorus*, *Spercheus*, and most *Berosus*; Fig. 1A). CI = 0.50; RI = 0.80.

40. Number of stemmata: 6 (0); 5 (1); fused, in one or 2 groups (2).

Previous studies have established that the ancestral number of stemmata is six pairs (Fig. 1C) (Hansen, 1991; Archangelsky, 1998), as found in Helophoridae and most Hydrophilidae (Archangelsky, 1998). Reductions occur in Spercheidae (five pairs in all known larvae) and in many Sphaeridiinae, where fusions of these stemmata into one or two groups can be seen (Fig. 1B). In *Chaetarthria* the stemmata are partially fused in one group, but the individual stemmata are evident so they are coded with the presumably ancestral state (0). CI = 0.67; RI = 0.75.

Characters from the thorax and abdomen

41. Larvae holopneustic (0); metapneustic (1); apneustic (2).

Helophoridae have nine pairs of functional biforous spiracles (one mesothoracic pair and eight abdominal pairs) (Fig. 6A). The hydrophilid lineage has a different condition in which the only pair of functional spiracles is the one on segment VIII (the thoracic and first seven pairs of abdom-

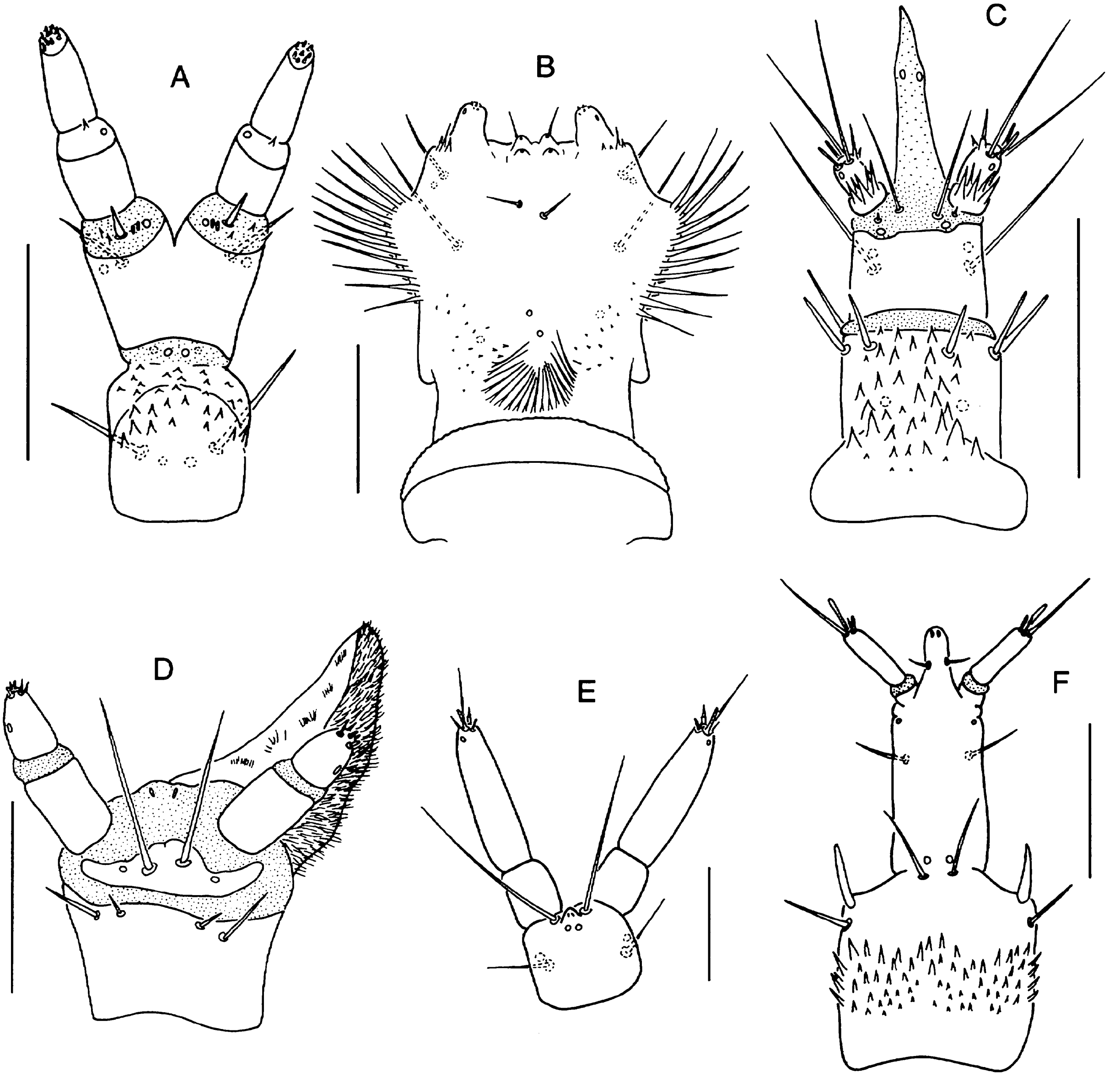

Fig. 5. A, *Helophorus orientalis*, labium, dorsal view; B, *Spercheus halophilus*, labium, dorsal view; C, *Paracymus rufocinctus*, labium, dorsal view; D, *Oosternum costatum*, labium, ventral view; E, *Berosus auriceps*, labium, dorsal view; F, *Derallus angustus*, labium, dorsal view. Scales = 0.1 mm (A–C, F); 0.05 mm (D, E).

inal spiracles are reduced). The eighth abdominal pair is enclosed within the spiracular atrium (Fig. 6E), is enlarged and annular instead of biforous. An autapomorphic condition is found in *Berosus*, where functional spiracles are absent (*Berosus* species have abdominal gills; Fig. 6D). CI = 1.00; RI = 1.00.

42. Spiracular atrium absent (0); present (1); reduced (2).

In the helophorid lineage (Hansen, 1997) the abdomen has segments I–IX well developed and a small tenth segment, usually in the ventral position. In the hydrophilid lineage, segments IX–X become more reduced, and segments VIII–IX form a spiracular atrium or 'breathing pocket' which harbours the eighth pair of spiracles (Fig. 6E). In this case segment VIII forms the dorsal part of the pocket, whereas segment IX becomes somewhat trilobed and forms the ventral part, as found in most Hydrophilidae. The spiracular atrium is absent in the genus *Berosus* and functionally replaced by gills (typically on segments I–VII, although this can vary) and the reduction of segments IX–X is more pronounced (Fig. 6D). A genus related to *Berosus*, *Hemiosus*, has an intermediate stage, with a reduced spiracular atrium and no gills (Fig. 6F). CI = 0.67; RI = 0.67.

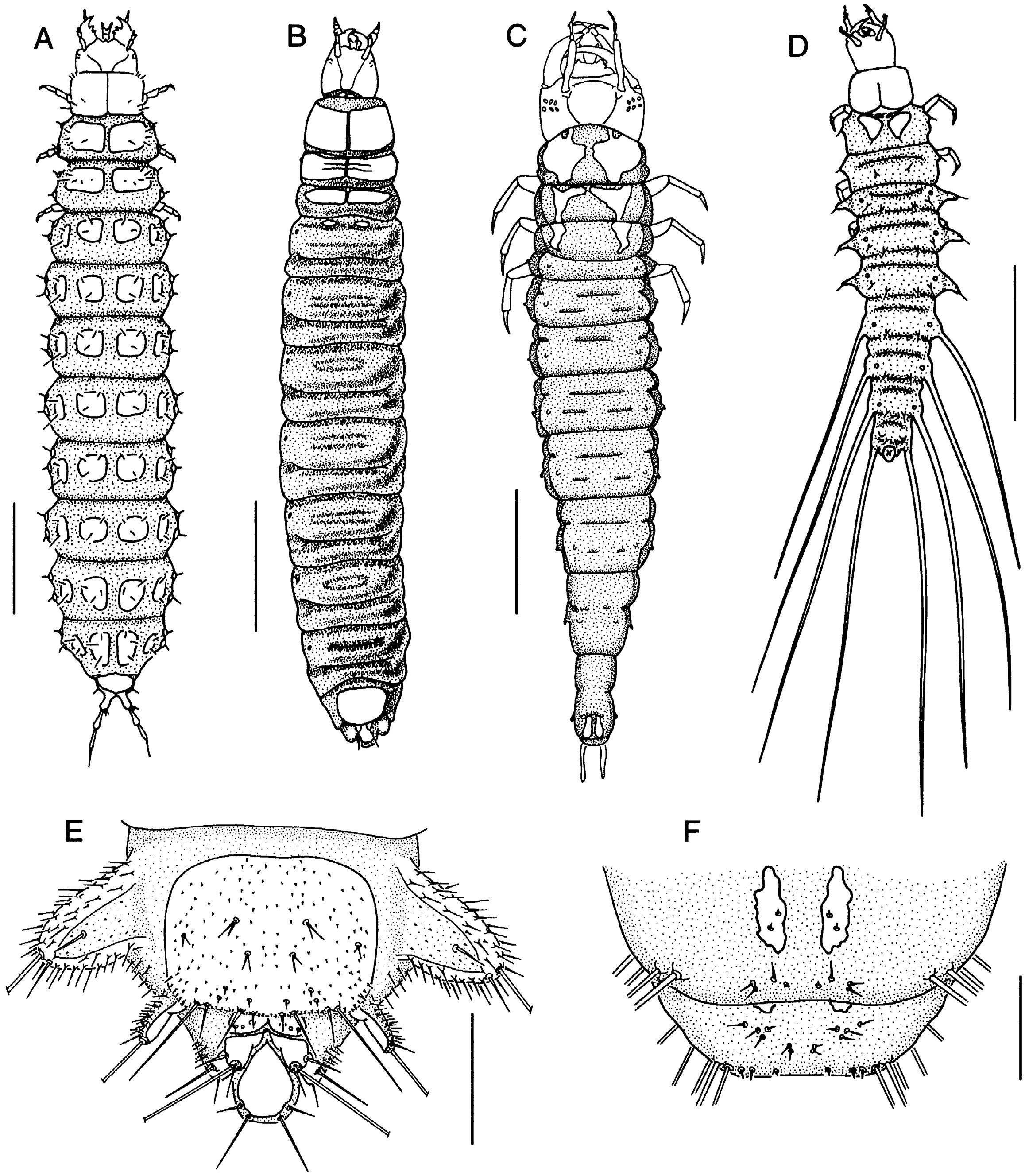

Fig. 6. A, *Helophorus orientalis*, habitus, dorsal view; B, *Dactylosternum cacti*, habitus, dorsal view; C, *Hydrophilus triangularis* habitus, dorsal view; D, *Berosus pugnax*, habitus, dorsal view; E, *Paracymus rufocinctus*, spiracular atrium, dorsal view; F, *Hemiosus bruchi*, spiracular atrium, dorsal view. Scales = 2 mm (A, B, D); 10 mm (C); 0.2 mm (E, F).

43. Legs visible in dorsal view (0); not visible in dorsal view (1).

The size of the legs is usually correlated with the habitat or levels of larval activity. Those species which live in terrestrial habitats, such as dung or rotting plant material, are not very active and usually have short legs (often reduced) which are not visible in dorsal view even when the legs are normal (five-segmented) (Fig. 6B). Species which are active have longer legs, which are seen easily in dorsal view. CI = 0.25; RI = 0.57.

44. Legs normal, 5-segmented (0); reduced, with 3 segments or less (1).

Leg reductions have occurred at least three times among Hydrophiloidea (Archangelsky, 1999c). The most common condition is a five-segmented leg (Fig. 7A): coxa, trochanter, femur, tibiotarsus and pretarsus (tibia and tarsungulus for some authors). Reductions occur in Georissidae (not included in this study; three-segmented legs), one genus of Hydrophilinae: *Chaetarthria* (three-segmented legs; Fig. 7C) and in the two terminal tribes of Sphaeridiinae: Megasternini and Sphaeridiini. CI = 0.50; RI = 0.50.

45. Claw normal, pointed (0); rodlike (1); reduced or fused to last segment of leg (2).

Two modifications involve the claws: *Sphaeridium* has a five-segmented leg but a rodlike claw (Fig. 7B); in *Chaetarthria* and *Cercyon* the claw is lost or fused to another leg segment (Fig. 7D). CI = 0.67; RI = 0.50.

46. Pleural areas (leg articulation) sclerotized (0); membranous (1).

The pleural areas usually carry a small pleurite which bears the leg articulation; this is present in all known Hydrophilinae genera (including those with reduced legs such as *Chaetarthria*). In some Sphaeridiinae with reduced legs the pleurite is membranous. CI = 1.00; RI = 1.00.

47. Femur and tibiotarsus with fringe of swimming hairs (0); without swimming hairs (1).

Most Hydrophilidae have only a few setae on the femur and tibiotarsus (Fig. 7A). Species with swimming abilities (e.g. *Tropisternus*, *Hydrophilus*) have a fringe of long and slender setae on the inner margin of the femur and tibiotarsus. CI = 1.00; RI = 1.00.

48. Tergites present on all thoracic segments (0); absent in the meso- and/or metathorax segment (1).

The pronotum is usually well developed in all hydrophiloid larvae. On the other hand, the meso- and metathoracic tergites are less developed, and in many cases they can be reduced or completely lost (e.g. *Hemiosus*, *Berosus*; Fig. 6D). CI = 0.50; RI = 0.80.

49. Prosternum completely divided (0); incompletely divided (1); entire (2); reduced (absent) (3).

The prosternal plate of hydrophiloid larvae can be entire or completely divided by a sagittal line; an intermediate stage is partially divided, and the sagittal line is restricted to the basal third or half of the plate. In a few cases the prosternal plate is reduced and absent (e.g. *Spercheus* and *Chaetarthria*). CI = 0.33; RI = 0.57.

50. Tergites present on abdominal segments I–VIII (may be reduced to an extremely small plate in some segments) (0); present only on abdominal segments I and VIII (1); present only on segment VIII (2).

The sclerotization of the abdominal segments in hydrophiloids is reduced. The most complete condition is that found in *Helophorus*, in which all the abdominal segments carry several small tergal plates (Fig. 6A). In some hydrophiline genera (e.g. *Chaetarthria*, *Hydramara*, *Hydrobius*, *Paracymus*, etc.), small plates are found on segments I–VIII; these plates can be large or, in some cases, they are reduced to very small sclerotized spots. Other genera carry small tergites only on segments I and VIII (e.g. *Tropisternus*, some Sphaeridiinae; Fig. 6B). The strongest reduction is found in some genera where the only tergal plates are those of abdominal segment VIII (some sphaeridiines, *Hemiosus*, *Berosus*, *Hydrophilus*; Fig. 6C, D). CI = 0.29; RI = 0.71.

51. Abdomen with 10 segments well developed (0); with segments VIII–X modified (1).

Helophorus has ten abdominal segments well developed (Fig. 6A). In *Spercheus*, Hydrochidae (not included in the study), and all the Hydrophilidae (*sensu stricto*) the last three abdominal segments are modified (Fig. 6B–D). CI = 1.00; RI = 0.

52. When spiracular atrium present, plate of segment VIII entire (0); divided (1).

The tergal plate of abdominal segment VIII is generally entire in those species with a well-developed spiracular atrium (Fig. 6B, E). Only in a few cases is this plate subdivided (e.g. the sphaeridiine *Phaenonotum exstriatum* and the hydrophiline genera *Hemiosus* and *Chaetarthria*; Fig. 6F). CI = 0.40; RI = 0.40.

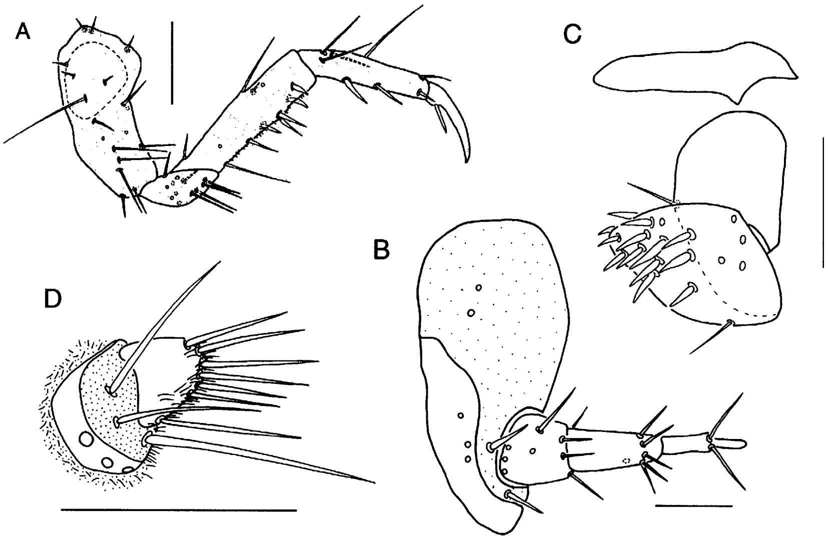

Fig. 7. A, *Berosus corrini*, mesothoracic leg; B, *Sphaeridium scarabaeoides*, prothoracic leg; C, *Chaetarthria bruchi*, prothoracic leg; D, *Cercyon praetextatus*, prothoracic leg. Scales = 0.2 mm (A); 0.05 mm (B, C, D).

53. Urogomphi 3-segmented (0); one-segmented (1); absent (2).

This reduction follows the acquisition of semi-aquatic and aquatic ways of life. Helophoridae (Fig. 6A), with mostly terrestrial and very active larvae, have three-segmented urogomphi. The remaining families show a reduction in the number of segments and the size of the urogomphi (Fig. 6E). This reduction also occurs in the clade including Epimetopidae and Georissidae (not included in this study). One autapomorphic condition is found in *Berosus* and *Hemiosus*, with completely reduced urogomphi (Fig. 6D, F). CI = 1.00; RI = 1.00.

Pupal characters

54. Number of cephalic styli: none (0); one pair (1); 2 pairs (2).

In pupae, the number of cephalic (supraorbital) styli can be two pairs (Fig. 8C), one pair (Fig. 8B), or none at all (Fig. 8A). The only known hydrophiloid, not included in this analysis, with three pairs is *Georissus* Latreille (Hansen, 2000), all others have two pairs or less. This number is usually constant for each genus, but at least in *Berosus* may vary among different species. CI = 0.40; RI = 0.50.

55. Number of pronotal styli: 7 pairs (0); 10 pairs (1); 11 pairs (2); 12 pairs (3); 13 pairs (4).

The number of pronotal styli is variable, but usually constant within the different genera. The number of pairs can be seven, ten, eleven, twelve and thirteen (Fig. 9A–F). In some species (e.g. *Phaenonotum exstriatum*) the number varies between ten and thirteen pairs, but as eleven pairs is the most common number, that one has been used in the matrix. CI = 0.57; RI = 0.40.

56. Number of styli on abdominal segment I: one pair (0); 2 pairs (1); 3 pairs (2); 6 pairs (3).

The first abdominal segment usually has a different number of styli than the remaining abdominal segments. This number ranges between one and six pairs. The most common number seems to be two pairs (Fig. 9A, F), but six pairs occur in *Dactylosternum* (Fig. 9E) and three pairs in some Hydrophilinae (e.g. some *Berosus* and *Paracymus*, and some Acidocerina). Only one pair is found in *Berosus corrini*. CI = 0.60; RI = 0.50.

57. Number of styli on abdominal segments II–VII: 2 pairs (0); 3 pairs (1); 4 pairs (2); 7 pairs (3).

The number of abdominal styli on segments II–VII is usually two, three, or four pairs (Fig. 9A–D, F). The sphaeridiine *Dactylosternum* is the only genus known with more than four pairs of styli (Archangelsky, 1994); in *Dactylosternum cacti* (Fig. 9E) seven pairs are present. CI = 0.60; RI = 0.60.

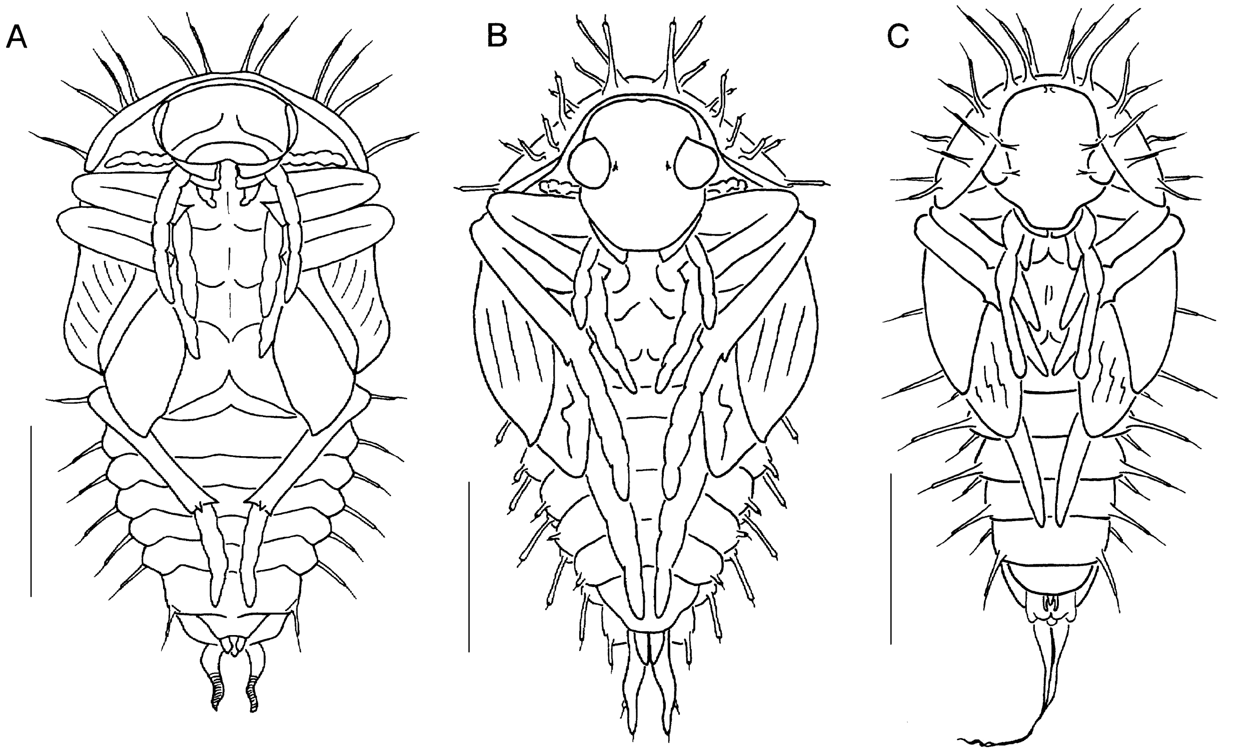

Fig. 8. A, *Sperchopsis tessellata*, pupa, ventral view; B, *Hydramara argentina*, pupa, ventral view; C, *Enochrus* (*Methydrus*) *vulgaris*, pupa, ventral view. Scales = 2 mm (A, B); 1 mm (C).

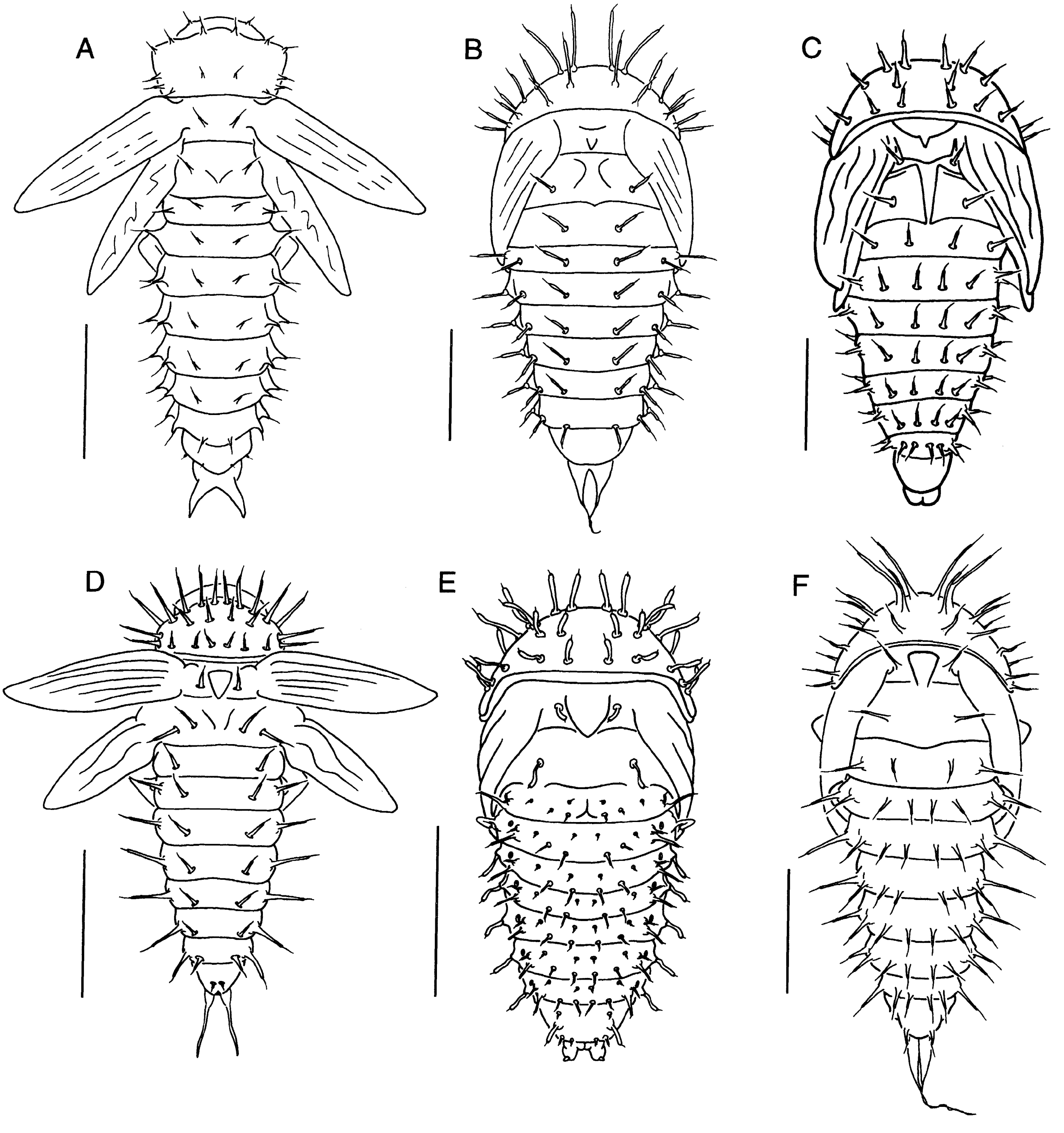

Fig. 9. A, *Helophorus orientalis*, pupa, dorsal view; B, *Cercyon praetextatus*, pupa, dorsal view; C, *Phaenonotum exstriatum*, pupa, dorsal view; D, *Berosus hoplites*, pupa, dorsal view; E, *Dactylosternum cacti*, pupa, dorsal view; F, *Enochrus* (*Methydrus*) *vulgaris*, pupa, dorsal view. Scales = 1 mm (A–C, F); 2 mm (D, E).

58. Number of styli on abdominal segment VIII: none (0); one pair (1); 2 pairs (2); 3 pairs (3).

The eighth abdominal segment of pupae may lack styli, or may have one, two or three pairs. Most Hydrophilinae have one pair, except for some *Berosus* species and *Sperchopsis*, with two pairs. Most known Sphaeridiinae lack styli (except *Dactylosternum*); *Helophorus* has two pairs of minute styli. CI = 0.60; RI = 0.67.

Results of the analysis

The 142NW analysis produced two equally parsimonious trees of 395 steps (CI = 0.46; CI excluding uninformative characters = 0.45; RI = 0.73; rescaled consistency index (RC) = 0.34). The only difference between the two cladograms is the relationship between *Helochares* and the two species of *Enochrus* (Acidocerina), but this does not conflict with tribal relationships. The 148DW analysis resulted in only one tree of 6280 steps (CI = 0.46; CI excluding uninformative characters = 0.45; RI = 0.74; RC = 0.34). The third analysis, 148EW, also resulted in one tree of 7819 steps (CI = 0.45; CI excluding uninformative characters = 0.45; RI = 0.73; RC = 0.33). All three analyses resulted in similar tribal relationships (Fig. 10).

An additional analysis, weighting all 148 characters by nineteen (and also with all 148 characters unweighted) was performed, because not everyone agrees with a priori differential weighting of characters. These analyses produced six equally parsimonious cladograms, very similar among themselves (CI = 0.43; CI excluding uninformative characters = 0.43; RI = 0.70; RC = 0.30); the consensus is shown in Fig. 11. These results are not convincing for the following reasons: Sphaeridiinae is placed within Hydrophilinae; Anacaenini is basal to the remaining Hydrophilinae + Sphaeridiinae; Laccobiini appears as the sister group of Berosini; and *Chaetarthria* appears as the sister group of the subfamily Sphaeridiinae. These unexpected results are influenced by the added weight of nineteen to the quantitative characters. This additional analysis, weighting all characters by nineteen (Fig. 11), was not considered for this discussion due to the reasons mentioned above.

Considering the jackknife values, some of the clades show good support (Fig. 12), whereas others do not hold up as well. Below each of the hydrophiline clades is discussed and the autapomorphies characterizing each clade are listed (synapomorphies considered within the subfamily Hydrophilinae). Sphaeridiinae is strongly supported and, without doubt, monophyletic (jackknife values of 100% in all analyses); this suggests that several characters shared between some Hydrophilinae and some Sphaeridiinae are probably convergent. Finally, the discussion is restricted to the preimaginal characters, which are the core of this study (adult characters are only listed as numbers).

Clade 1 (Sperchopsini)

Character 38.1, labial palps with spines on membrane (shared with *Hemiosus*, probably a convergence); character 58.2, pupa with two pairs of styli on abdominal segment VIII (shared with one species of *Berosus*, *B. hoplites*, probably a convergence too, as pupal chaetotaxy in the genus *Berosus* is quite variable; Archangelsky, 1997). Adult characters supporting this clade are: 76 and 82 (both shared with Sphaeridiinae), and 106, an unambiguous apomorphy.

Clade 2 (Hydrobiina)

Character 15, ratio of length of third antennal segment/length of sensorium; character 54.1, pupa with one pair of cephalic styli (shared with *Dibolocelus* and *Hydrophilus*, probably a convergence as Hydrophilina shows strong support, jackknife values of 98–100). Two adult characters support this clade: 100 (shared with *Hemiosus*) and 148, size of the adults, not used by Hansen (1991) (shared with *Tropisternus*).

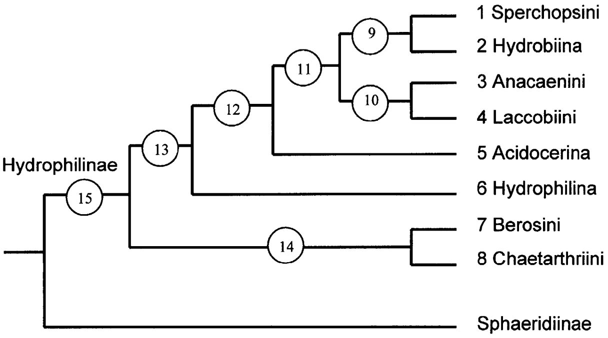

Fig. 10. Cladogram depicting the tribal and subtribal relationships within Hydrophilinae, based on the analyses of 148 characters (all noncontinuous characters weighted by nineteen and also differentially weighted) and from the analysis of 142 characters (continuous characters removed). The numbers refer to the clades discussed in the text.

Clade 3 (Anacaenini)

Character 25.1, maxilla with appendage of first palpal segment unsclerotized (shared with some derived Sphaeridiinae, probably due to convergency); character 43.1, legs not visible in dorsal view (shared with *Hemiosus* and *Chaetarthria*). The continuous characters supporting Anacaenini are 27, ratio of length of stipes/length of palpal segment 1; 28, ratio of length of maxillary palp/length of palpal segment 3; 29, ratio of length of maxillary palpal segment 1/length of maxillary palpal segment 3; 30, ratio of length of maxillary palpal segment 1/length of appendage. These continuous characters are characteristic as the relative proportions among the maxillary segments in this group are quite distinctive. The stipes is relatively short, and the palp is relatively long; at the same time the first palpal segment is very long when compared with the stipes, to the whole palp, and to the sensorium (this can also be seen in other genera of Anacaenini not included in this analysis, such as *Notionotus* and *Crenitis*). No good adult characters support this clade.

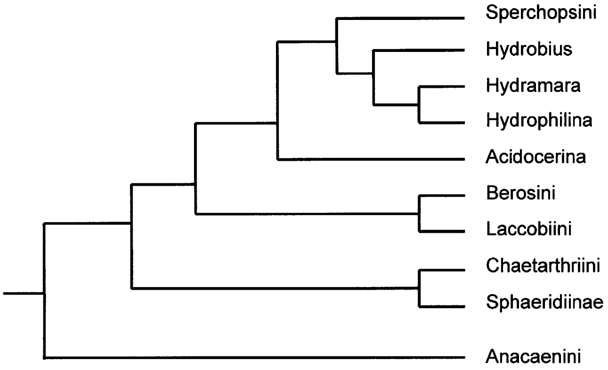

Fig. 11. Cladogram depicting the tribal and subtribal relationships within Hydrophilinae, based on the analyses of 148 characters (all characters weighted by nineteen and also unweighted).

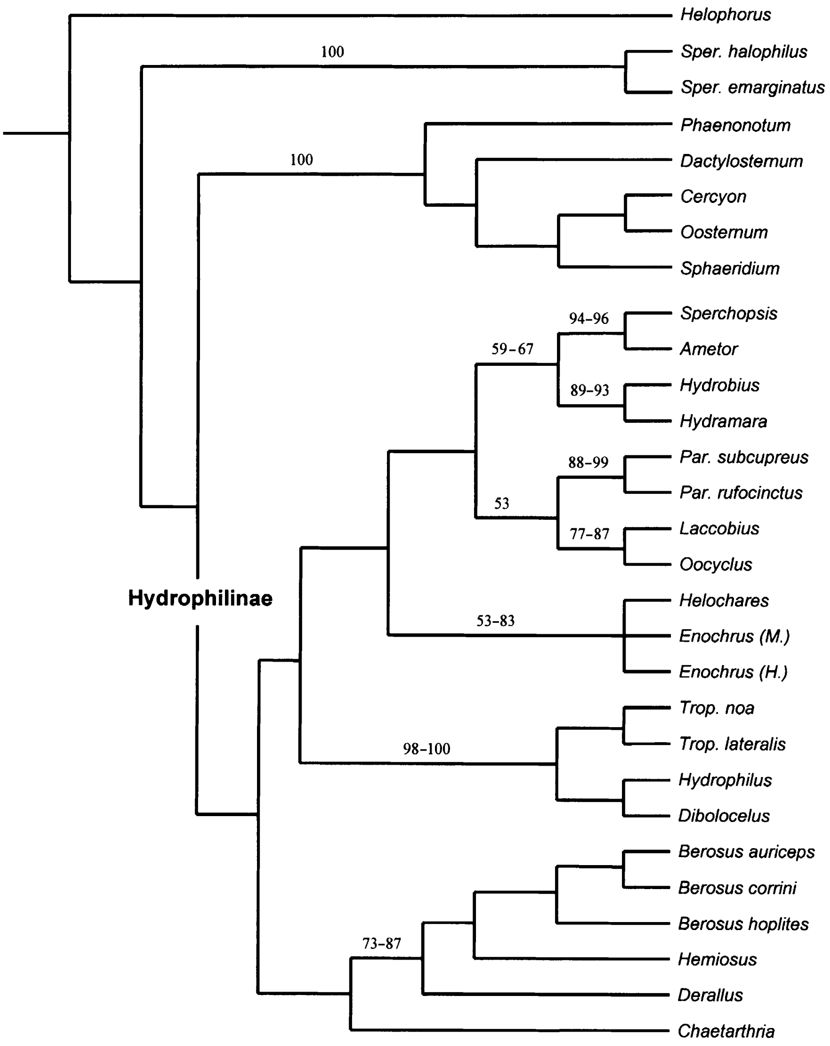

Fig. 12. Strict consensus of the three analyses (142NW, 148DW, and 148EW) showing the relationships of all the taxa included in the study. The upper numbers on branches represent the range of jackknife values.

Clade 4 (Laccobiini)

Character 10.2, left epistomal lobe strongly asymmetrical, with strong spines/setae pointing mediad and projecting further than nasale; character 11.1, only left lobe with setae; character 16.2, mandibles strongly asymmetrical; character 17.4, left mandible of *Berosus*-type; character 31.2, ligula reduced (all four characters shared with *Berosus* and *Hemiosus*, probably a convergence). Two continuous characters also support this clade: character 27, ratio of length of stipes/length of palpal segment 1; character 30, ratio of length of maxillary palpal segment 1/length of appendage; both reflect the relative length of the stipes and the short first palpal segment. These quantitative characters have only been coded for *Laccobius*, as third instar larvae of *Oocyclus* were not available for this study, so they should be considered with care. Three adult characters support this clade: 116 (shared with *Hydrophilus* and *Dibolocelus*), 131 (shared with Berosini), and 132, an unambiguous apomorphy.

Clade 5 (Acidocerina)

Character 49.1, prosternum incompletely subdivided (shared with *Hemiosus*, probably a convergence); character 56.1, pupa with two pairs of styli on abdominal segment I (shared with one species of *Paracymus* and one of *Berosus*, both probable convergences); character 57.2, pupa with four pairs of styli on abdominal segments II–VII (shared with one species of *Paracymus*, *P. subcupreus*, seems also to be convergent). Two additional quantitative characters supporting the clade are character 27, ratio of length of stipes/length of palpal segment 1, and character 30, ratio of length of maxillary palpal segment 1/length of appendage. No good adult characters support this clade.

Clade 6 (Hydrophilina)

One of the best-supported clades, as eight larval and pupal characters support it. Character 14.2, first antennal segment with numerous inner and outer setae, is an unambiguous apomorphy; character 34.1, mentum two times wider, or more, than prementum (shared with *Derallus*, probably a convergence); character 47.0, femur and tibiotarsus with a fringe of long swimming hairs, also an unambiguous apomorphy; character 49.2, prosternum entire (shared with *Derallus* and *Sperchopsis*, both probably convergences); character 55.2, pupa with eleven pairs of styli on pronotum, is an unambiguous apomorphy (except for *Dibolocelus* which has twelve pairs). Quantitative characters supporting this clade are character 15, ratio of length of third antennal segment/length of sensorium (characteristic of this clade due to the very short antennal sensorium); character 27, ratio of length of stipes/length of palpal segment 1; character 30, ratio of length of maxillary palpal segment 1/length of appendage (characteristic because of the short maxillary appendage and the relatively long first palpal segment). Adult characters which support this clade are: 106 (shared with some Sphaeridiinae), 133, 134, 138, the three are unambiguous apomorphies, and 148 (shared between *Tropisternus* and *Hydramara*, probably convergent).

Clade 7 (Berosini)

Character 14.1, first antennal segment with a strong distal inner seta/spine projecting forwards, is an unambiguous apomorphy of the group; continuous characters 28, ratio of length of maxillary palp/length of palpal segment 3, and 29, ratio of length of maxillary palpal segment 1/length of maxillary palpal segment 3, are both characteristic of this clade, as berosines have a long third maxillary segment, whereas the remaining segments are rather short. Adult characters supporting this clade are: 99 (shared with some Sphaeridiinae and *Oocyclus*, probably convergences), 125 (shared with *Tropisternus*), 131 (shared with Laccobiini), and 135, an unambiguous apomorphy.

Clade 8 (Chaetarthriini)

Character 43.1, legs not visible in dorsal view (shared with *Hemiosus* and *Paracymus*, but unique among Hydrophilinae because of leg reduction); character 44.1, leg reduced, with three segments, an unambiguous apomorphy; character 45.2, claw reduced or fused to last segment of leg, an unambiguous apomorphy within the subfamily; character 49.3, prosternum reduced or absent, also an unambiguous apomorphy within the subfamily. Three quantitative characters also support this clade, but they should be considered with care, as only *Chaetarthria* here represents Chaetarthriini; character 28, ratio of length of maxillary palp/length of palpal segment 3, rather high, similar to those of *Paracymus* (and some Sphaeridiinae) due to the short palpal segment 3; character 29, ratio of length of maxillary palpal segment 1/length of maxillary palpal segment 3, is characteristic due to the very short third palpal segment; character 30, ratio of length of maxillary palpal segment 1/length of appendage, is the lowest due to the relatively long appendage. Adult characters which support this clade are: 74 (shared with *Oocyclus*), 87 (shared with some Sphaeridiinae), 89 (shared with some Sphaeridiinae too), 111 (shared with *Ametor* Semenov), 148 (shared with the smaller Anacaenini), 93 and 147, both unambiguous apomorphies.

Clade 9 (Sperchopsini, Hydrobiina)

Character 28, ratio of length of maxillary palp/length of palpal segment 3, is low for the clade because of the rather long third palpal segment (only Berosini has lower values); character 23.1, distal inner apex of stipes ending in a stout spine projecting forwards, is an apomorphy within the subfamily (shared with the sphaeridiine genus *Phaenonotum*). Only one adult character supports this clade: 64 (shared with *Helochares*).

Clade 10 (Anacaenini, Laccobiini)

Character 20.2, stipes with inner spines on most of inner margin (shared with Chaetarthriini, but it is probably a convergence). Three adult characters support this clade: 114, an unambiguous apomorphy, 118 (shared with *Dibolocelus* and *Hydrophilus*, probably a convergence), and 123 (shared with *Sphaeridium*).

Clade 11 (Sperchopsini, Hydrobiina, Anacaenini, Laccobiini)

Character 26.1, first palpal segment of maxilla incompletely sclerotized, is an unambiguous apomorphy within the subfamily (shared with one genus of Sphaeridiinae, *Sphaeridium*; the only exception in the clade is *Paracymus rufocinctus*); character 35.1, mentum with distal crown of setae, is also an unambiguous apomorphy (lost in Laccobiini); character 50.0, abdominal segments I–VIII with tergites (shared with *Chaetarthria*, possibly a convergence). The only adult character supporting this clade is 90, shared with *Derallus* and *Chaetarthria*.

Clade 12 (Sperchopsini, Hydrobiina, Anacaenini, Laccobiini, Acidocerina)

Character 8.1, nasale asymmetrical (shared with *Berosus* and *Hemiosus*, probably a convergence). One adult character supports this clade, 102, an unambiguous apomorphy.

Clade 13 (Sperchopsini, Hydrobiina, Anacaenini, Laccobiini, Acidocerina, Hydrophilina)

Larval character 7.1, coronal sulcus present, supports this clade (it is lost in Laccobiini and Acidocerina). Other larval characters (16, 17 and 18) are quite variable and weak for this clade. Five adult characters support the clade: 61 (except for *Tropisternus*), 91 (except for *Laccobius*), 92 (an unambiguous apomorphy for the subfamily, but shared with some Sphaeridiinae), 103 (except for *Laccobius*), and 136 (except for *Paracymus*).

Clade 14 (Berosini, Chaetarthriini)

Character 6.1, frontal sutures not converging towards base of head capsule (shared with *Paracymus* and *Laccobius*, probably convergent). Several adult characters support this clade: 91 (shared with *Laccobius*), 92 (an unambiguous synapomorphy for the subfamily), 102 (shared with Hydrophilina), 103 (shared with *Laccobius*), 136 (shared with *Paracymus*), 137 (shared with *Laccobius*), 145 (an unambiguous synapomorphy).

Clade 15 (Hydrophilinae)

The only preimaginal character which supports this clade is 58.1, pupa with one pair of styli on segment VIII, the only exceptions are *Sperchopsis*, *Ametor*, and *Berosus hoplites*. Several adult characters support the monophyly of Hydrophilinae: 79, 84, 86 and 108 (apomorphic within Hydrophilidae, but shared with Helophoridae and Spercheidae), 116 (except for Laccobiini, *Hydrophilus* and *Dibolocelus*), 127 (apomorphic, shared with Helophoridae), 146 (except for *Derallus* and *Oocyclus*), and 143 (an apomorphy, except for *Laccobius*).

Discussion

The only recent study addressing the relationships among the tribes of Hydrophilinae using cladistic techniques is the excellent, comprehensive revision of Hydrophiloidea by Hansen (1991). Within Hydrophilinae Hansen (1991, 1995) recognized six tribes, one of them (Hydrophilini) subdivided into three subtribes (Table 2). Hansen's hypotheses of relationships were implemented in a novel classification (Hansen, 1991, 1995, 1999). Hansen's results derived from an analysis of 176 characters, mostly from adults. Nine equally parsimonious trees of 534 steps (Fig. 13) were obtained, but applying a more relaxed parsimony a tree with 538 steps was favoured to represent the relationships among subgroups of Hydrophiloidea (Fig. 14). The 538 step cladogram accommodated the tribe Rygmodini as the basal group of Sphaeridiinae and the genus *Pelthydrus* d'Orchymont within Laccobiini. Since then, Hansen's classification and phylogenetic hypothesis have been applied in most recent revisionary studies of Hydrophiloidea (Archangelsky, 1997; Hansen, 1999; Hebauer & Klausnitzer, 2000; Van Tassell, 2000; Oliva *et al.*, 2002; Archangelsky *et al.*, in press).

Earlier attempts to classify the subfamilies and tribes of Hydrophiloidea are discussed in detail by Hansen (1991, 1995) and because they were not based on cladistic methods their analysis is beyond the scope of this paper. However, some of them agree partially with the results presented here (Mulsant, 1844; d'Orchymont, 1916, 1919a, b; 1942) and will be mentioned later in the discussion.

The findings of this analysis show some important differences to Hansen's (1991) results, but at the same time several agreements can be observed. Similarities include the monophyly of most tribes and subtribes recognized by Hansen (except for Hydrophilini which appears here as polyphyletic) and the monophyly of the clade formed by the tribes Berosini and Chaetarthriini. Nothing can be said concerning the position of *Pelthydrus* as the larvae of this genus remain unknown. At the same time, the position of Rygmodini (included within Sphaeridiinae) is irrelevant to the purpose of this study.

The most important difference is the polyphyly of Hydrophilini. Hansen (1991) proposed a monophyletic Hydrophilini composed of the subtribes Acidocerina, Hydrobiina and Hydrophilina (in Hansen's analysis, Acidocerina was not monophyletic because *Dieroxenus* Spangler, included within Acidocerina, was basal to the *Acidocerus* group; Fig. 14). Hansen (1991) also hypothesized Hydrophilina and Hydrobiina as sister groups, with Acidocerina basal to them (Fig. 14); the present study suggests that Hydrobiina are the sister group of Sperchopsini (Fig. 10) (in Hansen's analysis, Sperchopsini was the basal tribe of Hydrophilinae). Another important difference relates to the relationship of the tribes Laccobiini and Anacaenini, which are sister groups in the present analysis. In Hansen (1991) Laccobiini (= Oocyclini) was the sister group of Hydrophilini, and Anacaenini was basal to this clade (Fig. 14).

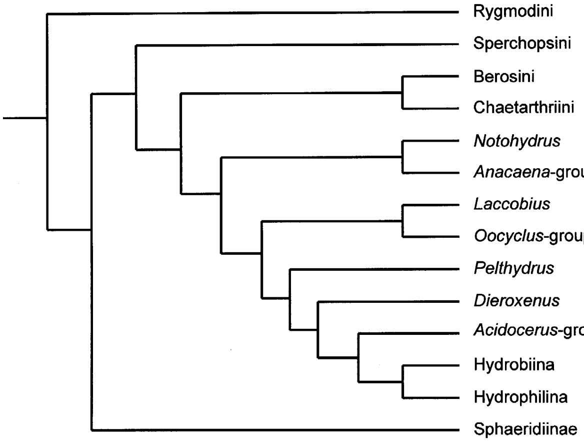

Fig. 13. Cladogram depicting the relationships among subgroups of Hydrophilinae proposed by Hansen (1991) (534 step cladogram).

As mentioned previously, the results of this analysis agree partially with some older classifications. Mulsant (1844) proposed the 'branch' Hydrobiaries composed of Hydrobiates (*Hydrobius*, *Laccobius*) and Philhydrates (*Enochrus*, *Helochares*) for the French fauna. Several years later, d'Orchymont (1916, 1919a, b, 1942) proposed the tribe Hydrobiini (composed of the subtribes Hydrobiae and Helocharae). Crowson (1955) also recognized the subfamily Hydrobiinae composed of the same genera as those of d'Orchymont (1916, 1919a, b), but included the Rygmodini. d'Orchymont's (1942) concept of Hydrobiinae was used later by most authors. For example, Smetana (1988), in his revision of the family Hydrophilidae for Canada and Alaska, considered the subfamily Hydrobiinae, formed by the tribes Hydrobiini (*Laccobius*, *Hydrobius*, *Sperchopsis*, *Paracymus*, *Crenitis* and *Anacaena*) and Helocharini (*Enochrus*, *Cymbiodyta* and *Helocombus*). Both classifications, by d'Orchymont and Smetana, leave the Hydrophilina (*sensu* Hansen) as a separate tribe (d'Orchymont = Hydrophilini) or subfamily (Smetana = Hydrophilinae).

Discussing in detail the evolutionary changes or trends within Hydrophilinae larvae would represent a whole paper in itself, some of the most important ones can be discussed.

Most Hydrophiloidea usually build egg cases on the substratum (rocks, aquatic vegetation, dung, etc.). In larger Hydrophilina, such as *Dibolocelus* and *Hydrophilus* (and also in other genera, not included in this analysis, such as *Hydrochara* Berthold), females construct floating egg cases; even though no phylogeny of this group is available, this trait probably originated only once. A very different situation is observed in females of the genus *Helochares*, which carry the egg cases underneath the abdomen (this is also true for the genus *Helobata* Bergroth, another Acidocerina, not included in the analysis). This behaviour is also present in Spercheidae and Epimetopidae, but these are probably behavioural convergences, as in Epimetopidae and Spercheidae the egg cases are kept in place by the hind femora, whereas in *Helochares* and *Helobata* the egg cases are attached to the hind femora by strands of silk (Archangelsky, 1997).

Within Hydrophilinae (and Hydrophiloidea) the only known larvae which have swimming adaptations are those of Hydrophilina. All known larvae within Hydrophilina have legs which bear a fringe of swimming hairs on the inner margin of both the femur and the tibiotarsus; this trait probably originated only once in the hypothetical ancestor of the subtribe. Furthermore, adults of this group are also among the best swimmers within the subfamily (other good swimmers as adults are the Berosini and members of the genus *Laccobius*). Other modifications in leg morphology, within Hydrophilinae, are seen in the genus *Chaetarthria*. Larvae of *Chaetarthria* have three-segmented legs, with the claw reduced (Böving & Henriksen, 1938; Archangelsky, 2002c), this probably correlates with their riparian habits as both larvae and adults live in small holes or tunnels found in fine sand at the margins of bodies of water. Within Chaetarthriini this trait seems to be unique for *Chaetarthria* as the larvae of *Guyanobius* Spangler, and *Amphiops* Erichson (two other Chaetarthriini) have five-segmented legs (Spangler, 1986; Watts, 2002). Similar leg reductions (convergences) are seen in the riparian *Georissus* (Archangelsky, 1997; Hansen, 2000) and in terrestrial Sphaeridiinae (Archangelsky, 1997, 1999c) which live in

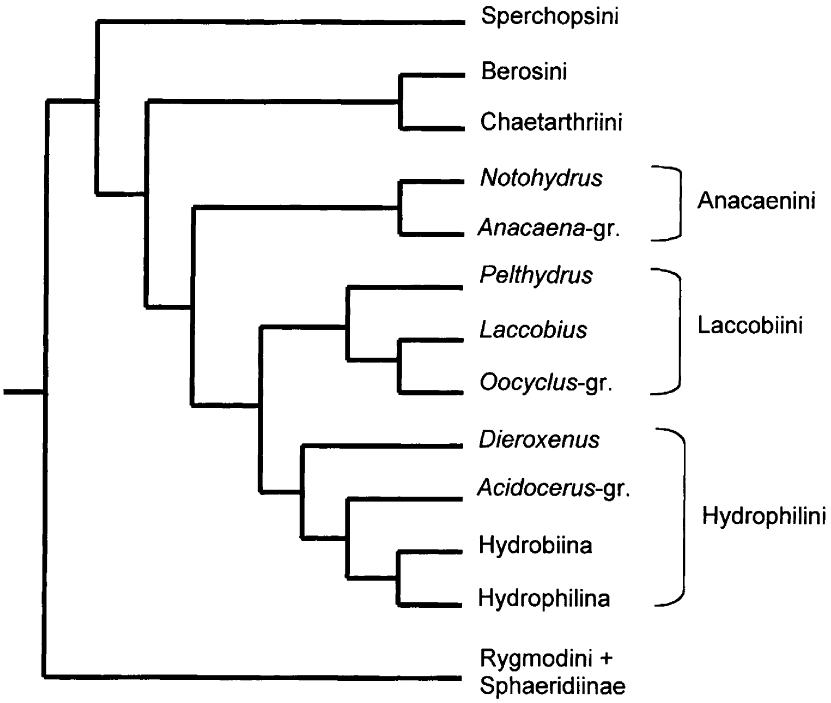

Fig. 14. Cladogram depicting the relationships among subgroups of Hydrophilinae proposed by Hansen (1991, 1995) (based on the 538 step cladogram).

dung or decaying plant material (e.g. *Cercyon* and *Oosternum*).

In this analysis, the only tribe known to show a reduction of the respiratory system is Berosini. Two genera of this tribe show reductions: *Hemiosus* has the spiracular atrium reduced (Archangelsky, 2000, 2002c) and can probably breath through the cuticle, whereas *Berosus* breathes via long abdominal tracheal gills. Another genus in which a reduction of the respiratory system has been reported is the larva of *Hybogralius* d'Orchymont (not included in the analysis, belonging to the subtribe Hydrobiina). *Hybogralius* also has a reduced spiracular atrium (Watts, 2002). In the genus *Berosus*, breathing through tracheal gills is associated with the reduction (absence) of the urogomphi; larvae of this genus have abdominal segments IX and X extremely reduced, and segment VIII is small compared with that of other Hydrophilinae.

Reductions of the sensorium on the second antennal segment can be seen in two clades. The first is the clade formed by Hydrobiina (*Hydrobius* and *Hydramara*) and Sperchopsini (*Sperchopsis* and *Ametor* Semenov). In these two groups the sensorium is reduced to at least one third of the length of the third antennal segment. The other clade which shows reduction of the sensorium is Hydrophilina, with a pronounced reduction in which the sensorium appears as a flat plate on the outer side of the second segment. The only other hydrophiloid genus showing such an extreme reduction is *Spercheus*, but this is very probably a convergence.

Based on known larval stages, another two modifications of the antennae have unique origins. The first is the inner seta or spine which is characteristic of the tribe Berosini. In *Derallus*, and also *Allocotocerus* Kraatz and *Regimbartia* Zaitzev, there is a large subapical projection on the inner margin of the first antennal segment (Bertrand, 1972; Archangelsky, 1997; Watts, 2002). In the same position in *Hemiosus* and *Berosus* there is a strong seta. The second modification is seen in larvae of Hydrophilina which, at least in second and third instar larvae, show numerous setae on both the inner and outer margins of the first antennomere. In most of the other known Hydrophilinae the first segment of the antenna is bare.

Directional asymmetries originated independently a few times within Hydrophilinae. These asymmetries involve the shape of both the clypeolabrum and the mandibles. The ancestral condition for the subfamily is a symmetrical set of mandibles and a symmetrical clypeolabrum. Within Berosini there is a change in the symmetry of both structures in the genera *Hemiosus* and *Berosus*. These genera have a strongly asymmetrical clypeolabrum and mandibles. The left mandible is strongly modified and has several characteristic structures on the inner margin: in most cases there is a distal tooth or projection which carries a set of stout spines, below this we find a multiple-pointed projection and a small triangular tooth which has a rough margin. Finally there may be a sharp spine pointing forwards. Associated with this modification of the left mandible is the very distinctive shape of the clypeolabrum, in which the left lobe is strongly projected forwards and covers the basal third of the mandible. The berosine genus *Derallus* and the sister tribe of Berosini, Chaetarthriini, have symmetrical mandibles and clypeolabrum. Modifications of the left mandible and clypeolabrum similar to those in *Berosus* and *Hemiosus* occur in larvae of the tribe Laccobiini; these modifications originated independently in this clade, and they are probably related to feeding mechanisms (but this still needs to be studied in detail). At this point it is interesting to mention that the larva of *Hybogralius* (included in the subtribe Hydrobiina), recently described by Watts (2002), has a clypeolabrum and mandibles similar to those of Laccobiini and the Berosini *Hemiosus* and *Berosus*. As Watts (2002) pointed out, larvae of *Hybogralius* have little in common with other known Hydrobiina larvae, and larval characters seem to place this genus closer to Laccobiini or Berosini.

The appearance of modifications in mandible symmetry for the remaining groups is difficult to track based on only a part of the genera which form each tribe or subtribe, but asymmetries occur in some Hydrophilina and in Acidocerina; all known Anacaenini, Hydrobiina (except for *Hybogralius*) and Sperchopsini larvae have symmetrical mandibles. Asymmetries of the clypeolabrum on the other hand seem to appear once in the clade including Acidocerina, Anacaenini, Hydrobiina, Sperchopsini, and also Laccobiini (previously discussed). In all these groups the asymmetries are not very strong (with the exception of Laccobiini) and usually relate to the size of the teeth of the nasale, which are more developed on the right side than on the left.

One important novelty in the morphology of the maxilla is the origin of a distal inner spine in the stipes of the clade formed by Sperchopsini and Hydrobiina. In the sperchopsine genus *Anticura* Spangler, this structure is not as sharply pointed as in the larvae of the other genera (Spangler, 1979; Archangelsky, 1997). A similar spine can be observed in the genus *Phaenonotum* (Sphaeridiinae), but it is almost without doubt a convergence.

Two modifications involving the labium can be mentioned. In Hydrophilina the mentum is two times, or more, wider than the prementum. This is also seen in the berosine genera *Derallus* (Spangler, 1966; Archangelsky & Durand, 1992b; Archangelsky, 1997), *Allocotocerus* and *Regimbartia* (Watts, 2002). Both origins of this feature seem to be independent. The other trend is the reduction of the ligula in the genera *Berosus* and *Hemiosus* (Berosini) and in *Laccobius* and *Oocyclus* (Laccobiini); the reduction seems to have occurred independently in both tribes, as all other Hydrophilinae show a well-developed ligula. Similar reductions originated independently in some terminal Sphaeridiinae (e.g. *Cercyon*, *Oosternum*, etc.).

Conclusion

Several conclusions can be drawn (Figs 10, 12). Hydrophilinae and Sphaeridiinae are monophyletic, in agreement with

Hansen (1991, 1995). Hydrophilini, recognized by Hansen (1991, 1995) as a monophyletic group, appears to be polyphyletic. Most other tribes and subtribes defined by Hansen are monophyletic, although they seem to be related in a different way (except for Berosini and Chaetarthriini). Hydrobiina (*sensu* Hansen, 1991) appears as the sister group of Sperchopsini; Anacaenini and Laccobiini appear as sister groups. Acidocerina (*sensu* Hansen, 1991) is the sister group of the clade ((Sperchopsini + Hydrobiina) (Laccobiini + Anacaenini)), and Hydrophilina is basal to that previous clade (Fig. 10). Berosini and Chaetarthriini are sister groups and fall basal to the remaining Hydrophilinae. Sperchopsini, which was the basal clade of Hydrophilinae in Hansen (1991), has a terminal position in this study. As this was a partial analysis, no changes in the current classification (and nomenclature) are proposed. However, this analysis serves to call our attention to the importance of other sources of information (larval and pupal characters in this case), and how much research is still needed to resolve the tribal relationships within this family. More genera and species (and more characters) will be included in a future analysis; this depends on an improvement in our knowledge of the preimaginal stages and the bionomics of these beetles. In the last few years a strong interest in the study of the immature stages of hydrophiloids has been developing, so I hope that it will not be long before new taxa are described and added to the present study.

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Appendix 1. Genera and species examined for this study. Species marked with an asterisk were included in the analysis. Third instar larvae were studied for most species (unless noted as L1 or L2, first and second instars, respectively). Pupae are unknown for *Spercheus*, *Oocyclus* and *Chaetarthria*.

Helophoridae	**Helophorus orientalis* Motschulsky
Spercheidae	**Spercheus emarginatus* (Schaller)
	**Spercheus halophilus* Archangelsky
Hydrophilidae	
Hydrophilinae	
Sperchopsini	**Sperchopsis tessellata* (Ziegler)
	**Ametor scabrosus* (Horn)
Berosini	**Berosus corrini* Wooldridge
	**Berosus hoplites* Sharp
	Berosus pugnax LeConte
	Berosus aulus d'Orchymont
	**Berosus auriceps* Boheman
	Berosus toxacanthus Oliva
	Berosus coptogonus Jensen-Haarup
	Berosus cornicinus Knisch
	**Hemiosus bruchi* Knisch
	Hemiosus multimaculatus (Jensen-Haarup)
	**Derallus angustus* Sharp
	Derallus paranensis
Chaetarthriini	*Chaetarthria* sp.
	**Chaetarthria bruchi* Balfour-Browne
Anacaenini	**Paracymus subcupreus* (Say)
	**Paracymus rufocinctus* Bruch
	Notionotus liparus Spangler (L1)
Laccobiini	**Laccobius minutoides* d'Orchymont
	**Oocyclus* sp. (L1)
Hydrophilini	
Acidocerina	**Helochares maculicollis* Mulsant
	Enochrus (Methydrus) vulgaris (Steinheil)
	**Enochrus (M.) lampros* Knisch
	Enochrus (M.) ochraceus (Melsheimer)
	**Enochrus (Hugoscottia) tremolerasi* (Knisch)
Hydrobiina	**Hydrobius melaenus* (Germar)
	**Hydramara argentina* (Knisch)
Hydrophilina	**Hydrophilus triangularis* Say
	**Dibolocelus ovatus* (Gemminger & Harold)
	**Tropisternus lateralis* (Fabricius)
	**Tropisternus noa* Fernández & Bachmann
Sphaeridiinae	
Coelostomatini	**Phaenonotum exstriatum* (Say)
	**Dactylosternum cacti* (LeConte)
Megasternini	**Cercyon praetextatus* (Say)
	**Oosternum costatum* (LeConte)
Sphaeridiini	**Sphaeridium scarabaeoides* (Linnaeus) (L2)

Appendix 2

Adult characters, taken from Hansen (1991). The numbers in quote marks refer to the original numbers used by Hansen.

59. '1' Labrum widest at base, not narrowed posteriorly (0); widest anterior to base, narrowed posteriorly (1).
60. '2' Lateral margins of labrum without or with only sparse setae (0); with dense setae (1).
61. '3' Anterior margin of labrum at most with sparse setae (0); with a fringe of dense setae (1).
62. '4' Labrum not retracted under clypeus (0); to a great extent retracted under clypeus, entirely (or almost) concealed by clypeus (1).
63. '5' Lateral margins of labrum without spines or spinelike setae (but often with fine hairlike setae) (0); with a series of stout spines or spinelike setae (rather than fine hairlike setae) (1).
64. '10' Anterior margin of clypeus truncate or slightly convex (0); anterior margin concave, the anterior corners distinctly protruding (1).
65. '11' Clypeus at most with only a few (coarse) setiferous punctures (0); on each side with an anterolateral group of setiferous punctures ('systematic punctures') (1).
66. '12' Clypeus demarcated from frons by a transverse groove (0); at most demarcated by a fine transverse suture (1).
67. '14' Frons without (or with only a few) coarse setiferous punctures (0); on each side with a group of coarse setiferous punctures ('systematic punctures') near inner margin of eyes (1).
68. '15' Anterior margin of eyes not emarginated (by frons) (0); emarginated by the lateral portions of frons (1).
69. '16' Eyes demarcated from temporae by a ridge (0); not demarcated by a ridge (1).
70. '17' Head abruptly narrowed immediately behind eyes (0); not abruptly narrowed immediately behind eyes (1).
71. '18' Head not very strongly deflexed (0); head very strongly deflexed towards ventral face (1).
72. '19' Lateral margins of mentum without fringe of long setae (at most with short sparse setae) (0); with a fringe of rather long setae (1).
73. '22' Lateral margins of mentum converging anteriorly (0); not converging anteriorly (1).
74. '23' Gula well developed, only moderately narrowed anteriorly (0); gula forming a transverse triangle posteriorly, the gular sutures rather closely aggregated and parallel anteriorly, or even fused to a single median suture (1); gula absent, or appearing only as a very narrow transverse sclerite at the rear of the head (2).
75. '24' Ventral face of head without transverse ridge on each side near eyes (0); with a short distinct transverse ridge on each side arising from posteromedian corner of eye (1).
76. '26' Apex of mandibles with at least 2 teeth (0); apex simple (1).
77. '27' Anterior and lateral margin of mandible form an obtuse angle (0); form a right angle (1).
78. '29' Galea flattened forming a wide plate (0); galea almost circular in cross-section (1).
79. '30' Galea much shorter than first and second segments of maxillary palpus, not forming a long, weakly sclerotized lobe (0); galea forming a long, weakly sclerotized lobe, at least as long as first and second segments of palpi, or longer (1).
80. '31' Galea with many setae in apical portion (0); with only a few apical setae (1).

81. '32' Setae of galea arranged in well-defined rows (0); setae not arranged in rows, irregularly distributed (1).
82. '33' Setae of galea curved apically towards middle (0); setae at most weakly curved and not in one particular direction (1).
83. '34' Segment 2 of maxillary palpus less than two-thirds as wide as third segment (0); at least two-thirds as wide as third segment.
84. '36' Paraglossae (excluding setae) short, not reaching longer than to midlength of second segment of labial palpi (0); paraglossae longer, reaching at least to basis of third segment of labial palpi (1).
85. '37' Second segment of labial palpi without a row of setae on inner face (at most with 1–3 setae) (0); with a row (or longitudinal group) of setae on inner face (1).
86. '38' Second segment of labial palpi without subapical wreathlike tuft of setae (0); with a subapical wreathlike tuft of setae (1).
87. '39' Apical segment of labial palpi at least as wide as penultimate (0); distinctly narrower (1).
88. '40' Apical segment of labial palpi wider than penultimate (0); not distinctly wider (1).
89. '41' Apical segment of labial palpi with outer face more convex than inner face (0); almost symmetrical (1).
90. '44' Antennae at least two-thirds as long as width of head (0); distinctly shorter (1).
91. '45' Antennal scape no longer than pedicel and intermediate segments combined (0); scape longer (1).
92. '46' Antennal pedicel not narrowed distally (0); conical, narrowed distally (1).
93. '47' Antennal pedicel not wider than scape (0); distinctly wider (1).
94. '48' Antennae with at least 3 intermediate segments (0); with less than 3 intermediate segments (1).
95. '51' Antennal segments distal to cupule forming a loosely segmented club (0); forming a more or less compact club (1).
96. '52' Lateral margins of pronotum not forming a continuous curve with elytra (0); forming a continuous curve with elytra (1).
97. '53' Pronotal surface uneven (0); surface even (1).
98. '54' Pronotum on each side without (or with only a few indistinct) coarser setiferous punctures (0); on each side with a (often ellipsoid) group of coarser setiferous punctures ('systematic punctures') (1).
99. '57' Accessory ridge below posterior pronotal margin narrow, less than two-thirds as wide as pronotum at posterior margin (0); ridge wide, at least two-thirds as wide as pronotum at posterior margin (1).
100. '58' Accessory ridge below posterior pronotal margin not produced laterally into dentiform process (0); ridge produced laterally into small bluntly dentiform process (1).
101. '59' Accessory ridge below posterior pronotal margin not distinctly continued laterally as an oblique-transverse fold (or such is only detectable in less than medial half) (0); continued as a distinct ridge or fold for at least halfway towards posterior pronotal corners (often almost reaching these) (1).
102. '60' Prosternum well developed, its shortest length anterior to procoxae at least one-tenth width (0); very short, shortest length less than one-tenth width (1).
103. '64' Procoxal cavities continued as a short slit anterolaterally, slit less than half as wide as coxal cavity (0); continued anterolaterally in a longer slit, slit at least half as wide as coxal cavity (1).
104. '65' Procoxal cavities not closed posteriorly by an extension of the 'inner wall' of the coxal cavities (0); procoxal cavities narrowly closed posteriorly by an extension of the 'inner wall' of the cavities (1).
105. '66' Hypomeron with anterior grooves for reception of antennal club (grooves not extending over prosternum) (0); hypomeron without antennal grooves (except that prosternal antennal grooves may sometimes extend some distance across the hypomeron) (1).
106. '68' Mesosternum rather evenly convex, without raised carina or process (0); medially (at least posteriorly) raised to a dentiform process (1); raised to a well-defined plate ('mesosternal tablet') (2).
107. '70' Mesosternum widened posteriorly in straight or slightly curved (concave) lines (0); mesosternum almost parallel sided anteriorly (or only weakly widened behind), then abruptly widened posteriorly, i.e. lateral margins abruptly curved (1).
108. '71' Mesosternum distinctly demarcated from mesepisterna by fine sutures (0); fused with mesepisterna, not demarcated by fine sutures (except sometimes for indistinct vestiges of sutures) (1).
109. '74' Dorsal part of laterosternite 3 without obliquely ribbed area (0); with a well-defined, more or less large, obliquely ribbed area in posterior half (1).
110. '85' Anterior femora rounded in cross-section, i.e. without (or only distally with) ventral ridge delimiting a tibial groove on inner face of femur (0); with a ventral longitudinal ridge delimiting a tibial groove on inner face of femora in more than distal half (1).
111. '86' Anterior femora without (or only distally with) dorsal ridge delimiting a tibial groove on inner face of femur (0); femora with a dorsal ridge (in addition to ventral ridge) delimiting a tibial groove on inner face of femora in more than distal half (1).
112. '87' Anterior tibiae only slightly flattened, less than half as wide as high (0); more strongly flattened, at least half as wide as high (1).
113. '88' Anterior tibiae with the 2 series of spines nearest outer face well separated, not more closely aggregated than the others (0); the 2 series of spines on outer face of anterior tibiae closely aggregated (or even confluent), more closely aggregated than one of them is to the other series of spines (1).
114. '89' Anterior tibiae with the dorsal, sublateral series of spines not composed of very long thin spines (0); composed of long thin spines which are as long as (minimum) width of tarsus (1).
115. '91' Middle coxae globular or almost so, not more than one-third as wide as long (0); more transverse, more than one-third as wide as long (1).

116. ‘92’ Middle femora without hydrofuge pubescence (0); with more or less distributed hydrofuge pubescence basally (1).
117. ‘97’ Posterior femora at least 3× as long as wide (0); less than 3× as long as wide (1).
118. ‘99’ Posterior femora without hydrofuge pubescence (0); with more or less distributed hydrofuge pubescence basally (1).
119. ‘100’ Basal margin of posterior femur completely contacting the trochanter, i.e. without projecting angle (0); with anterobasal angle freely projecting, not contacting the trochanter (1).
120. ‘101’ Middle and posterior femora rounded in cross-section, i.e. without (or only distally with) ventral ridge delimiting a tibial groove on inner face of femur (0); with a ventral longitudinal ridge delimiting a tibial groove on inner face of femora in more than distal half (1).
121. ‘102’ Middle and posterior femora without (or only distally with) dorsal ridge delimiting a tibial groove on inner face of femur (0); femora with a dorsal ridge (in addition to ventral ridge) delimiting a tibial groove on inner face of femora in more than distal half (1).
122. ‘103’ Middle and posterior tibiae only slightly flattened, less than half as wide as high (0); more flattened, at least half as wide as high (1).
123. ‘104’ Spines on outer face of middle and posterior tibiae not very strong, less than half as long as width of tibiae (0); lateral spines long and stout, at least half as long as width of tibiae (and usually much stronger than ventral spines) (1).
124. ‘105’ Outer face of middle and posterior tibiae not crenulate-serrate (0); outer face of tibiae with 2 longitudinal (parallel) series of small and dense, acute tubercles, thus appearing crenulate-serrate (1).
125. ‘106’ Posterior tibiae without swimming hairs (0); with an outer (dorsal) fringe of long swimming hairs (1).
126. ‘107’ The longest apical spur of middle and posterior tibiae distinctly longer than width of tarsus (0); not longer than width of tarsus (1).
127. ‘109’ Second segment of middle and posterior tarsi (in forms with 5-segmented tarsi) longer than first (0); second segment not longer than first (1).
128. ‘111’ With scutellary stria (at least detectable when elytron examined from below) (0); without any trace of scutellary stria, not even as a vestige when elytron examined from below (1).
129. ‘112’ Elytra without (or with only a few indistinct) coarse setiferous punctures (0); with distinct longitudinal series of coarse setiferous punctures (‘systematic punctures’) in third, fifth and seventh interstice (or, in species with nonstriate elytra, at the homologous position) (1).
130. ‘114’ Pseudepipleuron horizontal or only very slightly oblique (0); distinctly, often very strongly oblique, or almost vertically hanging down in anterior third or more (1).
131. ‘115’ Pseudepipleuron not markedly wider anteriorly than opposite metacoxae, i.e. almost parallel sided (0); widened anteriorly, and here at least twice as wide as opposite metacoxae (1).
132. ‘116’ Epipleuron at least as wide as pseudepipleuron in anterior quarter (0); markedly narrower than pseudepipleuron anteriorly (1).
133. ‘117’ Hindwing at least half as long as elytron (0); less than half as long as elytron (1).
134. ‘118’ Hindwing costa less than half as long as apical portion of wing (i.e. the portion distal to radius) (0); at least half as long as apical portion (1).
135. ‘120’ Widest part of hindwing lies proximal to (or at) M-Cu loop (or apex of pigmented part of Cu, in forms without M-Cu loop) (0); widest part distal to M-Cu loop (1).
136. ‘121’ Hindwing radius detectable proximal to r-m crossvein, and distinctly bifurcate proximally (0); radius distinct proximal to r-m crossvein, but not bifurcate proximally (1); not distinct proximal to r-m crossvein (2).
137. ‘126’ Hindwing with wedge cell distinctly more than half as long as basal cell (0); not more than half as long as basal cell (1).
138. ‘129’ Hindwing with jugal lobe demarcated from the remainder of the wing by a distinct excision at posterior wing margin (0); jugal lobe not demarcated from the remainder of the wing by an excision at posterior wing margin (1).
139. ‘131’ Male, second and third segments of anterior tarsi not dilated (0); second and third segments of anterior tarsi distinctly (sometimes strongly) dilated (1).
140. ‘132’ Male, claws of anterior tarsi simple (as in female) (0); stronger, and more curved, with larger basal tooth than in female (1).
141. ‘134’ Aedeagus with quite (or almost) symmetrical basal piece, not terminating in a hook (0); with asymmetrical basal piece, terminating in an asymmetrical twisted hook (1).
142. ‘159’ Head and pronotum with granulate sculpture (0); not granulate (1).
143. ‘168’ Apical segment of labial palpi without a subapical seta on outer face (although sometimes with differently arranged setae) (0); apical segment of labial palpi with one (or a couple of very closely aggregated), long or rather long, subapical seta on outer face, otherwise without (or with few and more inconspicuous) setae (1).
144. ‘169’ Labrum well sclerotized and well pigmented (0); labrum rather pale (normally paler than clypeus), and rather weakly sclerotized (1).
145. ‘170’ Body without power of rolling up (0); body with more or less well-developed power of rolling up (1).
146. ‘174’ Lateral (glabrous) portion of hypomeron defined from the remainder (pubescent) portion by a sharp ridge (0); lateral portions well defined, but not demarcated by a ridge (1); lateral portions not defined (2).
147. ‘176’ Abdominal ventrites completely (or over most of the surface) with strong microsculpture and fine, dense (hydrofuge) pubescence (0); ventrites without strong microsculpture and dense (hydrofuge) pubescence (1).
148. Size of the adult (A–T). States coded using Thiele’s gap method, subdivided into twenty states (A–T). Ordered.

Appendix 3. Data matrix used for the analysis (29 × 146). Inapplicable characters are coded as '–'.

	1	1111111112	2222222223	3333333334	4444444445
Taxa	1234567890	1234567890	1234567890	1234567890	1234567890
Helophorus orientalis	0000000000	0000B02202	000000AOQE	0010000100	0000001000
Spercheus halophilus	1201100--0	2010T01110	0-0100BLIB	1010010001	1100001132
Spercheus emarginatus	1201100--0	2010K01110	0-0100AGFB	1010010001	1100001132
Phaenonotum exstriatum	1012000100	0010A02201	111000LMHB	1010000112	1100001001
Dactylosternum cacti	0012000101	2010B22200	110000GPLD	2100000110	1110001011
Cercyon praetextatus	0012010111	2110A20100	110010HPK-	2100001012	1111211022
Oosternum costatum	0012010111	2110A20100	110010ELI-	2100001012	1111211022
Sphaer. scarabaeoides	0012010101	2110B10000	110011DHFT	1100000012	1110111021
Sperchopsis tessellata	1002001100	0010B03301	001001GCCD	1010100110	1100001020
Ametor scabrosus	1?02001100	0010B03301	001001ICBC	1010100110	1100001000
Berosus auriceps	1002010102	1011A24300	000000MBBD	2000000000	2000001102
Berosus hoplites	1002010102	1011B24100	000000OBBD	2000000000	2000001102
Berosus corrini	1002010102	1011A24200	000000TAAC	2000000000	2000001102
Hemiosus bruchi	1002010102	1011B24300	000000SAAB	1000000110	1210001112
Derallus angustus	1002010000	2011A02200	000000KABC	1011000010	1100001021
Chaetarthria bruchi	10?2010000	0010A02202	00000?MMGA	1010000010	1111201030
Paracymus subcupreus	1002010101	2010A03302	000011DRRP	1010100210	1110001000
Paracymus rufocinctus	1002010101	2010A02202	000010CTTL	1010100210	1110001000
Laccobius minutoides	1002010102	1010A24202	000001OECB	2000000010	1100001000
Oocyclus sp.	10?2000102	1010?24302	000001????	2010000210	1100001000
Helochares maculicollis	1202001100	2010A12201	000000ODBC	1010000210	1100001011
Enochrus (M.) lampros	1002001101	2010A21200	000000NECB	1010000210	1100001011
Enochr. (H.) tremolerasi	1002001101	2010B12200	000000JFDB	1010000210	1100001011
Hydrobius melaenus	1002001100	0010C03301	001001ICBD	1010100210	1100001000
Hydramara argentina	1002001100	0010G03301	001001HCCC	1010100210	1100001000
Tropisternus noa	1002001000	2012G13301	000000HEEQ	1011000010	1100000021
Tropisternus lateralis	1012001000	2012G13301	000000HDDN	1011000010	1100000021
Hydrophilus triangularis	1102001010	2012G11100	000000GFEK	1011000010	1100000022
Dibolocelus ovatus	1102001010	2012F20100	000000GFDL	1011000010	1100000022

	5555555556	6666666667	7777777778	8888888889	9999999990
Taxa	1234567890	1234567890	1234567890	1234567890	1234567890
Helophorus orientalis	0-02011200	0010000000	0001010000	0000000000	0100000011
Spercheus halophilus	101?????00	1101010000	0010001101	0100000101	1011000001
Spercheus emarginatus	101?????00	1101010000	0010001101	0100000101	1011000001
Phaenonotum exstriatum	1112212011	1100010111	0111110010	0001011110	1000011010
Dactylosternum cacti	1012433311	1100010111	0111110010	0001011110	1000011010
Cercyon praetextatus	1012111011	0100010011	0000110010	1111011110	1100111010
Oosternum costatum	1012111011	0100010011	0000110010	1111011110	1100111010
Sphaer. scarabaeoides	1012311011	1000010111	0110110010	1111011110	1101111000
Sperchopsis tessellata	1010311210	0001010011	0010010000	1100100101	0100011000
Ametor scabrosus	1012111210	0001010011	0010010000	1100100101	0100011000
Berosus auriceps	1-22310110	1000011011	1010001000	1000000100	1001011010
Berosus hoplites	1-22321210	1000011011	1010001000	1000000100	1001011010
Berosus corrini	1-20300110	1000011011	1010001000	1000000100	1001011010
Hemiosus bruchi	1122311110	1000011011	1010001000	1000000100	1001001011
Derallus angustus	1012311110	1000011011	1010001000	1000000001	1001011010
Chaetarthria bruchi	111?????10	1000010011	101100?000	0000001111	1011011000
Paracymus subcupreus	1012322110	0000010011	0010000000	1000000101	0101011000
Paracymus rufocinctus	1012311110	0000010011	0010000000	1000000101	0101011000
Laccobius minutoides	1012311110	0000011011	0010001000	0000000101	1101011000
Oocyclus sp.	101?????10	0000011011	0011001000	0000100101	0101011110
Helochares maculicollis	1012322110	0001110011	0010000000	0000000100	0100011100
Enochrus (M.) lampros	1012322110	0000010011	0010000000	0000000100	0100011100
Enochr. (H.) tremolerasi	1012322110	0000010011	0010000000	0000000100	0100011000

Appendix 3. Continued.

	5555555556	6666666667	7777777778	8888888889	9999999990
Taxa	1234567890	1234567890	1234567890	1234567890	1234567890
Hydrobius melaenus	1011311110	0001111011	0010001000	0000100101	0100011101
Hydramara argentina	1011311110	0001111011	0010001000	0000100101	0100011101
Tropisternus noa	1010211111	1000111011	0010000000	0000100100	0100011100
Tropisternus lateralis	1010211111	1000111011	0010000000	0000100100	0100011100
Hydrophilus triangularis	1011211110	0000111011	0010000000	0000100100	0100011100
Dibolocelus ovatus	1011311110	0000111011	0010000000	0000100100	0100011100

	1111111111	1111111111	1111111111	1111111111	11111111
	0000000001	1111111112	2222222223	3333333334	44444444
Taxa	1234567890	1234567890	1234567890	1234567890	12345678
Helophorus orientalis	1000000000	0000000000	0000000100	0010100000	0100000B
Spercheus halophilus	0100100000	0000010100	0001011100	0011021100	0000000B
Spercheus emarginatus	0100100000	0000010100	0001011100	0011021100	0000000D
Phaenonotum exstriatum	110012?101	1110101011	1100001101	0000110000	0001010B
Dactylosternum cacti	110012?101	1110101011	1100001101	0000110000	0001010C
Cercyon praetextatus	110112?101	1010101011	1100001100	000012??00	1001010A
Oosternum costatum	110112?101	1110101011	1100001100	00001???00	1001010A
Sphaer. scarabaeoides	010111?101	1110101011	1110001101	000002?001	1000010D
Sperchopsis tessellata	0010100000	0010110111	1000000001	00?0000000	0010010D
Ametor scabrosus	0010100001	1010110111	1000000011	00?0000000	0010010C
Berosus auriceps	0100110010	0010110110	1000100010	1000111010	0010110D
Berosus hoplites	0100110010	0010110110	1000100010	1000111010	0010110E
Berosus corrini	0100110010	0010110110	1000100010	1000111010	0010110C
Hemiosus bruchi	0100110010	0010110110	1000100010	1000111000	0010110B
Derallus angustus	1100110011	0010111111	1000100101	1000111000	0010110B
Chaetarthria bruchi	0100110001	1010110111	1000000001	00??011000	001011–A
Paracymus subcupreus	1010111001	0011111011	1010000001	0000010000	0010010A
Paracymus rufocinctus	1010111001	0011111011	1010000001	0000010000	0010010B
Laccobius minutoides	0000110011	0111101010	0010000001	1100001010	0000011B
Oocyclus sp.	1010110011	0011101011	1110000101	1100000000	0010010B
Helochares maculicollis	1010111000	0010111111	1000000011	0000000001	0010010C
Enochrus (M.) lampros	1010111001	0010111111	1000000011	0000000001	0010010B
Enochr. (H.) tremolerasi	1010111001	0010111111	1000000011	0000000001	0010010B
Hydrobius melaenus	1010111001	0010111111	1000000011	0000000000	0010010E
Hydramara argentina	1010111011	0010111111	1000000011	0000000000	0010010F
Tropisternus noa	0110121001	0110110111	1000100011	0011000100	0010010G
Tropisternus lateralis	0110121001	0110110111	1000100011	0011000100	0010010F
Hydrophilus triangularis	0110121001	0010100011	1000000011	0011000101	0010011S
Dibolocelus ovatus	0110121001	0010100011	1000000011	0011000101	0010010T