

**Evolution of the semi-aquatic bugs  
(Hemiptera: Heteroptera: Gerromorpha)  
with a re-interpretation of the fossil record**

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**Abstract.** The fossil history of semi-aquatic bugs (Gerromorpha) is reviewed in light of the many important recent records and new developments in our understanding of the phylogeny of the group. Based on the age of its sister group, the Panheteroptera, the Gerromorpha probably extends back into the Triassic, even though the oldest fossil forms assigned to the group are dubious. The recent discovery of *Cretogerris albianus* Perrichot, Nel & Neraudeau, 2005 from the Lower Cretaceous shows that all families were present in the Mesozoic, and phylogenetic and biogeographic evidence suggest that most – perhaps all – extant subfamilies were also present at that time. By comparison, the fossil record of the families Hydrometridae and Gerridae is far richer than that of any other family, which allows a more detailed interpretation of the phylogenetic relationships among extinct and extant taxa of these two groups.

**Keywords.** Heteroptera, Gerromorpha, water striders, phylogeny, amber, Mo clay, historical biogeography, ecological phylogenetics, phylogeography

### Introduction

The heteropteran infraorder Gerromorpha (ŠTYS & KERZHNER 1975), or semi-aquatic bugs, has been considered a distinct group since the time of DUFOUR (1833), who named the group ‘Amphibicorisae’, thus referring to their ability to walk on the surface of water, as distinct from the aquatic bugs, ‘Hydrocorisae’, and the terrestrial bugs, ‘Geocorisae’. ANDERSEN (1982) convincingly demonstrated that Gerromorpha was a monophyletic group, and could be diagnosed based on the presence of three pairs of cephalic trichobothria, quadriangular mandibular levers, pretarsi with one dorsal and one ventral arolium, and female genital tract with a gynatrial complex. He recognized eight gerromorphan families: Mesoveliidae,

Hebridae, Paraphrynoveliidae, Macroveliidae, Hydrometridae, Hermatobatidae, Veliidae and Gerridae, and diagnosed relationships within and among these families on the basis of a manual optimisation of 'ground plan characters' (the character states inferred as ancestral to the respective families and subfamilies). Shortly before his untimely passing in 2004 he provided a morphological data matrix for representatives of all extant families and subfamilies (ANDERSEN & WEIR 2004), hereby providing a testable hypothesis of all higher levels of gerromorphan relationships. Meanwhile, several attempts had been made to include DNA sequence data in phylogenetic reconstructions. MURAJI & TACHIKAWA (2000) published a study of five gerromorphan families and six subfamilies based on data from two ribosomal genes (16SrRNA and 28SrRNA), and DAMGAARD et al. (2005) expanded this taxon sample with one additional family and several subfamilies, and performed simultaneous analyses of a data set comprising both molecular and morphological characters. Recently, DAMGAARD (in press) performed simultaneous analyses of an expanded molecular data set (COI+II, 16SrRNA and 28SrRNA) and a morphological data set for a complete sample of families, and with representatives of most subfamilies. This study resulted in completely new relationships within Gerromorpha, especially by rejecting the subfamily 'Cylindrostethinae' (Gerridae), the family 'Veliidae', and the two superfamilies 'Hydrometroidea' and 'Gerroidea' *sensu* ANDERSEN (1982) (the latter two taxa comprising Paraphrynoveliidae + Macroveliidae + Hydrometridae and Hermatobatidae + Veliidae + Gerridae respectively) as paraphyletic assemblages, and by recognising Halobatinae + Ptilomerinae as sister group to all other Gerridae. While relationships among extant families and subfamilies of Gerromorpha have been revisited repeatedly in recent years, those among extinct and extant taxa have not been addressed since ANDERSEN (1998) reviewed the fossil evidence more than ten years ago. Since then many new fossils have been described, but all have been evaluated according to the traditional view of gerromorphan phylogeny. This study is an attempt to incorporate the fossil evidence of Gerromorpha into the new phylogenetic relationships in order to date and diagnose nodes, and to point out directions for future research on the evolution of the group.

### Fossil Gerromorpha

While the Nepomorpha (aquatic bugs) has a very extensive fossil record dating back into the Triassic (POPOV 1971), the Gerromorpha has by comparison left much fewer fossils (GRIMALDI & ENGEL 2005: Fig. 8.62). Those fossils that are available range from beautiful amber inclusions with lots of details preserved (e.g. ANDERSEN & POINAR 1992) to rock impressions of various qualities (e.g. ANDERSEN 1998, WAPPLER & ANDERSEN 2004). According to GRIMALDI & ENGEL (2005), the oldest fossil gerromorphan bug is *Karanabis kiritschenkoii* Bekker-Migdisova, 1962 from the Upper Jurassic (152 million Ma) of Kazakhstan, which was initially assigned to Nabidae (BEKKER-MIGDISOVA 1962), but transferred to Gerridae by POPOV (1968) and later to Mesoveliidae by POPOV & BECHLY (2007: 325). Another fossil, *Engynabis tenuis* Bode, 1953 from the Lower Jurassic, Posidonia Shales of northern Germany (BODE 1953) was considered as 'closely related to *Karanabis*' by POPOV & WOOTTON (1977: 350), and as 'undoubtedly a member of Mesoveliidae' by POPOV & BECHLY (2007). ANDERSEN (1998: 93) however, hesitated to accept such taxonomic assignments. According to DOLLING (2000), ANDERSEN (1998) overlooked Brodie's mention (BRODIE 1845), without description, of '*Hydrometra*' and '*Velia*(?)'

from the Jurassic of Britain and stated that 'if genuine, Brodie's fossils would be both the earliest recognition of fossil Gerromorpha in print and the oldest known representatives of the group'. BRODIE (1845: 121) mentions several specimens coming from the 'Wealden' and which 'appear from their proportions to be those of species of *Velia* and *Hydrometra*, but their veins were not sufficiently clear to be figured with precision'. Brodie's use of the term 'Wealden' was much broader than the definition of the term today, and it is very likely that he was referring to the Purbeck Beds of Dorset (S. W. Heads, pers. comm.). Nevertheless, both the Purbeck and Wealden groups of southern England are now considered to be Early Cretaceous in age and not Jurassic as previously thought (MILNER & BATTEN 2002).

The earliest fossil gerromorphan bug accepted by ANDERSEN (1998) was *Duncanovelia extensa* Jell & Duncan, 1986 from the Lower Cretaceous (120 Ma) Koonwarra Lagerstätte of Victoria, Australia, which was assigned to Mesoveliidae by the authors (JELL & DUNCAN 1986). Two incomplete fossils assigned to 'Veliidae sp.' from the same deposit were likewise accepted with some reservations by ANDERSEN (1998: 88-89) as the oldest fossils of the Veliidae-Gerridae clade. *Cretaceometra brasiliensis* Nel & Popov, 2000 and *Incertametra santanensis* Perez Goodwyn, 2002 (both Hydrometridae) were described from quarries in the Nova Olinda Member laminated limestone in the Araripe Basin of northeastern Brazil. These and other authors assigned all fossils from the site to the 'Santana Formation', thus causing considerable confusion as to the composition of the respective assemblages and their relative ages. Today it is well established that the deposition of the older (Aptian) Crato Formation (110 Ma) and the younger (?Albian) Santana Formation are discontinuous and separated by a thick series of evaporates, now called the Ipubi Formation and a stratigraphic disconformity (MARTILL 1993, MARTILL et al. 2007: 27). Fossil from the Crato Formation were named 'limonite (iron oxide) mummies' by NEL & POPOV (2000: 2316) apparently due to their three dimensional structure, which differs technically from two-dimensional compression fossils. It is nearly always the cuticle that is preserved, with the soft tissues rotted away and the void space left behind filled with calcite. Specimens recovered from the weathered, creamy buff-coloured limestone are preserved as reddish-brown replacements of the initial iron sulphide (pyrite) preservations with goethite (one of the main mineral components of limonite). Fossils from the blue-grey unweathered levels of the Nova Olinda Member are preserved as a mixture of organic material and extremely fine-grained iron sulphide (pyrite or perhaps mackinawite or greigite). This oxidises *in situ*, and results in a specimen that is essentially replaced by goethite. In both cases goethite is the major component of the fossils, and the term 'limonite mummies' is therefore appropriate for this type of fossils (S. W. Heads and D. Martill, pers. comm.).

The remaining Mesozoic fossils are a few, but excellently preserved, amber inclusions from Lower-Mid Cretaceous, including *Carinometra burmensis* Andersen & Grimaldi, 2001 (Hydrometridae) from Burmese amber (Myanmar) (100 Ma), *Cretogerris albianus* Perrichot, Nel & Neraudeau, 2005 (Gerridae) from Archingeay amber (France) (100 Ma), and a complete but immature specimen from the same deposit assigned to Gerromorpha, but without further affinities (PERRICHOT et al. 2005).

Compared to the Mesozoic, many more fossils have been recorded from the Cenozoic (Tertiary). Some of the earliest fossils from this period are a specimen of Gerrinae from the Palaeocene of Menat (France) (A. Nel, pers. comm.), and Mo clay impressions from the

Palaeocene-Eocene transition (55-54 Ma) of Denmark and Germany (ANDERSEN 1998). These sites have yielded fossils of several families, including *Daniovelia morsensis* Andersen, 1998 (Macroveliidae); *Eocenometra danica* Andersen, 1982b, *E. longicornis* Andersen, 1998, and *Palaeometra madseni* Andersen, 1998 (Hydrometridae); and *Palaeogerris furensis* Andersen, 1998, *P. grandis* Andersen, 1998, and *P. mikkelsenii* Andersen, 1998 (Gerridae). From the Lower/Middle Eocene (52-47 Ma) are several compression fossils from western North America, including *Limnopus wilsoni* Andersen, 1998, *Telmatrechus stali* (Scudder, 1879) and *T. defunctus* (Handlirsch, 1910) from British Columbia, Canada, and *T. parallelus* Scudder, 1890 from Wyoming, USA. *Halobates ruffoi* Andersen, Farma, Minelli & Piccoli, 1994 (Gerridae) was described from the Middle/Upper Eocene boundary deposits (45 Ma) of Monte Bolca near Verona, northern Italy. Several fossils have been described from the Upper Eocene (40 Ma) Florissant Formation of Colorado, USA, including *Metrobates aeternalis* Scudder, 1890, which was interpreted as an exuvium of a gerrine water strider by ANDERSEN (1998: 70); *Gerris protobates* Cockerell, 1927, which ANDERSEN (1998: 70-71) found to be too incomplete to be included in *Gerris* Fabricius, 1794; and *Steinovelina nigra* Scudder, 1890, which ANDERSEN (1998: 77-78) accepted as a member of Veliidae. The Eocene-Oligocene (40-35 Ma) Baltic amber contains several inclusions, including *Electrovelia baltica* Andersen, 1998 (redescribed by ANDERSEN (2000)) and *Balticovelina weitschati* Andersen, 2000 (both Veliidae); *Hydrometra groehni* Andersen, 2003; *Limnaxis succini* Germar & Berendt, 1856; *L. hoffeinsi* Popov, 1996 and *Metrocephala anderseni* Popov, 1996 (redescribed by ANDERSEN (2000)) (all Hydrometridae); *Electrogerris kotashevichi* Andersen, 2000; *Succineogerris larssoni* Andersen, 2000; and *Gerris* sp. (all Gerridae). Contemporary with Baltic amber are compression fossils from Eckfeld and Messel, Germany of *Lutetiabates eckenfeldensis* Wappler & Andersen, 2004, *Cylindrobates messelensis* Wappler & Andersen, 2004 and a *Gerris* nymph (all Gerridae) (WAPPLER & ANDERSEN 2004). From the Upper Oligocene of France (22.5 Ma) is *Protobacillometra oligocenica* Nel & Paicheler, 1993 (Hydrometridae) and a Gerridae (A. Nel, pers. comm.), and from the Czech Republic are three fossil Gerridae (PROKOP & NEL 2007). From Mid Miocene Dominican amber (20-17 Mya) is a rich fossil record including *Electrobates spinipes* Andersen & Poinar, 1992 and *Brachymetroides atra* Andersen, 2001 (both Gerridae); and *Halovelina electrodominica* Andersen & Poinar, 1998, *Microvelia polhemi* Andersen, 1999, *M. electra* Andersen, 2001, and *M. grimaldii* Andersen, 2001 (all Veliidae). The exact age of these deposits has been confused with unsubstantiated claims of Eocene age, but is now known to be of Miocene origin (GRIMALDI 1994, ITURRALDE-VINENT & MCPHEE 1996, GRIMALDI & ENGEL 2005). Mexican amber is contemporary with Dominican amber, but so far only *Stenohebrus glaesarius* Polhemus, 1995 (Hebridae) has been described from this material. Also from the Miocene (24-5 Mya) is *Aquarius lunpolaensis* (Lin, 1981) and *Halobates bagonensis* Lin, 1981 from the Lunpola Basin, Baingoin Country, Xizang (Tibet), China. ANDERSEN (1998: 72) however, stated that the latter probably was exuvium of the former. Finally, a contemporary specimen assigned to *Aquarius* (?) sp. from the Karagan Formation in Northern Caucasus, Russia was mentioned by ANDERSEN (1998: 61), but the fossil was too incomplete for a taxonomic assignment.

Table 1 provides a checklist of all fossils that have been convincingly assigned to families and subfamilies of Gerromorpha.

Table 1. Fossil Gerromorpha assigned to families and subfamilies.

Taxon / reference	Type	Locality	Age
<b>Hebrididae: Hebrinae</b>			
<i>Stenhebrus glaesarius</i> Polhemus, 1995	Amber inclusion	Mexico, Chiapas	Mid Miocene (20–17 Ma)
<b>Hydrometrididae: Heterocephalinae</b>			
<i>Carinometra burmesensis</i> Andersen & Grimaldi, 2001	Amber inclusion	Myanmar (Burma)	Mid Cretaceous (100–90 Ma)
<b>Hydrometrididae: Hydrometrinae</b>			
<i>Cretacoemetra brasiliensis</i> Nel & Popov, 2000	Limonite mummy	Brazil, Crato Formation	Lower Cretaceous (110 Ma)
<i>Incertametra santanensis</i> Perez Goodwyn, 2000	Limonite mummy	Brazil, Crato Formation	Lower Cretaceous (110 Ma)
<i>Eocenometra danica</i> Andersen, 1982	Compression fossil	Denmark, Fur Formation	Palaeocene-Eocene (55–54 Ma)
<i>Eocenometra longicornis</i> Andersen, 1998	Compression fossil	Denmark, Fur Formation	Palaeocene-Eocene (55–54 Ma)
<i>Palaeometra madseni</i> Andersen, 1998	Compression fossil	Denmark, Fur Formation	Palaeocene-Eocene (55–54 Ma)
<i>Hydrometra groehmi</i> Andersen, 1993	Amber inclusion	Baltic Sea, Germany	Eocene-Oligocene (40–35 Ma)
<i>Limnachus succini</i> Germar & Berendt, 1856	Amber inclusion	Baltic Sea, Germany	Eocene-Oligocene (40–35 Ma)
<i>Limnachus hoffeinsi</i> Popov, 1996	Amber inclusion	Baltic Sea, Germany	Eocene-Oligocene (40–35 Ma)
<i>Metrocephala anderseni</i> Popov, 1996	Amber inclusion	Baltic Sea, Germany	Eocene-Oligocene (40–35 Ma)
<i>Protobacillometra oligocenica</i> Nel & Patcheler, 1993	Amber inclusion	France, Aix-de-Provence	Upper Oligocene (22.5 Ma)
<b>Veliidae: Microvelinae</b>			
<i>Microvelia electra</i> Andersen, 2001	Amber inclusion	Dominican Republic	Mid Miocene (20–17 Ma)
<i>Microvelia grimaldii</i> Andersen, 2001	Amber inclusion	Dominican Republic	Mid Miocene (20–17 Ma)
<i>Microvelia polhemi</i> Andersen, 1999	Amber inclusion	Dominican Republic	Mid Miocene (20–17 Ma)
<b>Veliidae: Halovelinae</b>			
<i>Halovelia electrodominica</i> Andersen & Poinar, 1998	Amber inclusion	Dominican Republic	Mid Miocene (20–17 Ma)
<b>Veliidae: Veliinae</b>			
<i>Balticovelia weitschati</i> Andersen, 2000	Amber inclusion	Baltic Sea, exact locality unknown	Eocene-Oligocene (40–35 Ma)
<i>Electrovelia baltica</i> Andersen, 1998	Amber inclusion	Baltic Sea, Denmark	Eocene-Oligocene (40–35 Ma)
<b>Veliidae: incertae sedis</b>			
<i>Steinovelia nigra</i> Scudder, 1890	Compression fossil	USA, Colorado, Florissant Formation	Upper Eocene (40 Ma)
<b>Gerridae: Halobatinae</b>			
<i>Halobates ruffoi</i> Andersen, Furma, Minelli & Piccoli, 1994	Compression fossil	Italy, Verona, Monte Bolca	Middle-Upper Eocene (45 Ma)
<b>Gerridae: Charmatometrinae</b>			
<i>Brachymetroides atra</i> Andersen, 2000	Amber inclusion	Dominican Republic	Mid Miocene (20–17 Ma)
<b>Gerridae: Gerrinae</b>			
<i>Palaeogerris furensis</i> Andersen, 1998	Compression fossil	Denmark, Fur Formation	Palaeocene-Eocene (55–54 Ma)
<i>Palaeogerris grandis</i> Andersen, 1998	Compression fossil	Denmark, Fur Formation	Palaeocene-Eocene (55–54 Ma)
<i>Palaeogerris mikkelsenii</i> Andersen, 1998	Compression fossil	Denmark, Fur Formation	Palaeocene-Eocene (55–54 Ma)

Table 1 (continued from previous page)

Taxon / reference	Type	Locality	Age
<b>Gerridae: Gerrinae (continued)</b>			
<i>Linnoporus wilsoni</i> Andersen, 1998	Compression fossil	Canada, British Columbia, Driftwood Creek	Lower-Middle Eocene (52-47 Ma)
<i>Telmatrechus defunctus</i> (Handlirsch, 1910)	Compression fossil	Canada, British Columbia, Quilichena	Lower-Middle Eocene (52-47 Ma)
<i>Telmatrechus stali</i> (Scudder, 1879)	Compression fossil	Canada, British Columbia, Similkameen River	Lower-Middle Eocene (52-47 Ma)
<i>Telmatrechus paratellus</i> (Scudder, 1890)	Compression fossil	USA, Wyoming, Green River Formation	Lower-Middle Eocene (52-47 Ma)
<i>Electrogerris kotaschewichi</i> Andersen, 2000	Amber inclusion	Baltic Sea, Kaliningrad (Russia)	Eocene-Oligocene (40-35 Ma)
<i>Aquarius lupoalaensis</i> (Lin, 1981)	Compression fossil	China, Xizang (Tibet), Lunpola Basin	Miocene (25-5 Ma)
<b>Gerridae: Electrobatinae</b>			
<i>Electrobates spinipes</i> Andersen & Poinar, 1992	Amber inclusion	Dominican Republic	Mid Miocene (20- 17 Ma)
<b>Gerridae: incertae sedis</b>			
<i>Cretogerris albianus</i> Perrichot, Nel & Neraudeau, 2005	Amber inclusion	France, Archingeay-Les Nouillers	Lower Cretaceous (100 Ma)
<i>Lutettabates eckfeldensis</i> Wappler & Andersen, 2004	Compression fossil	Germany, Eckfeld Maar	Mid Eocene (49 Ma)
<i>Cylindrobates messelensis</i> Wappler & Andersen, 2004	Compression fossil	Germany, Grube Messel	Mid Eocene (44 Ma)

## Discussion

### Phylogeny of Gerromorpha

Living on a water surface enforces some strong ecological, physiological and behavioural constraints (ANDERSEN 1982, SPENCE & ANDERSEN 1994). The comparison of the fossil *Limnoporus wilsoni* with extant congeners was used by to infer a 'structural stasis' in the group because the general habitus of fossil and extant specimens was practically inseparable ANDERSEN et al. (1993: Fig. 2). On the other hand, the adaptive shifts in habitats, for which gerromorphan bugs are so renowned, have ensured a rapid evolution of characters associated with locomotion, mating, feeding, and anti-predation strategies (ANDERSEN 1982, SPENCE & ANDERSEN 1994). The many constraints associated with life history adaptations in Gerromorpha have lead to numerous autapomorphies and convergences in morphological characters, which have complicated the interpretation of these traits in a phylogenetic context. The waterstriders have long been preferred organisms for comparisons of morphological and molecular characters in simultaneous analyses in order to make a reciprocal illumination of the molecular and morphological evidence. Most studies have addressed the three principal Holarctic water strider genera: *Limnoporus* Stål, 1868, *Aquarius* Schellenberg, 1800 and *Gerris* Fabricius, 1794 (DAMGAARD & COGNATO 2003, 2005), but also sea skaters (*Halobates* Eschscholtz, 1822) have been studied (DAMGAARD et al. 2000). Along with these investigations of more shallow relationships, a few studies have addressed relationships among families and subfamilies by including DNA sequence data (MURAJI & TACHIKAWA 2000, DAMGAARD et al. 2005). So far, DAMGAARD (in press) has presented the most inclusive study in terms of taxon and character sampling. A few subfamilies, such as Madeoveliinae (Mesoveliidae), Hyrcaninae (Hebridae), Heterocleptinae and Limnobatodinae (both in Hydrometridae) still await inclusion, and will be very important for understanding the basal divergences of the infraorder.

Figure 1 shows recognized gerromorphan fossils optimized onto the most parsimonious tree resulting from a simultaneous parsimony analysis of molecular and morphological characters by DAMGAARD (in press). The fossil gerrid subfamily Electrobatinae and *Cretogerris albianus*, which has not been assigned to any subfamily, are placed unresolved at the base of the Gerridae, and the two extant hydrometrid subfamilies, Heterocleptinae and Limnobatodinae, are placed according to ANDERSEN (1982).

### Evolutionary history of Gerromorpha

Gerromorpha is sister group to the Panheteroptera, including Nepomorpha, Leptopodomorpha, Cimicomorpha and Pentatomomorpha (SCHUH & SLATER 1995), and since members of Nepomorpha are found back into the late Triassic, the Gerromorpha must be of at least the same age. Considering the rich fossil record of Mesozoic Nepomorpha, the scarcity of Mesozoic Gerromorpha inhabiting the same environments, is an enigma (GRIMALDI & ENGEL 2005), and so far, none of the better-known localities for Cretaceous amber (e.g. Siberia, Lebanon, New Jersey, Spain and Canada) have produced any gerromorphans (ANDERSEN & GRIMALDI 2001). The amber fossils often reveal a number of morphological characters, which are extremely important for elucidating their precise phylogenetic relationships, while compression fossils often are more difficult to interpret. Notable exceptions are members of

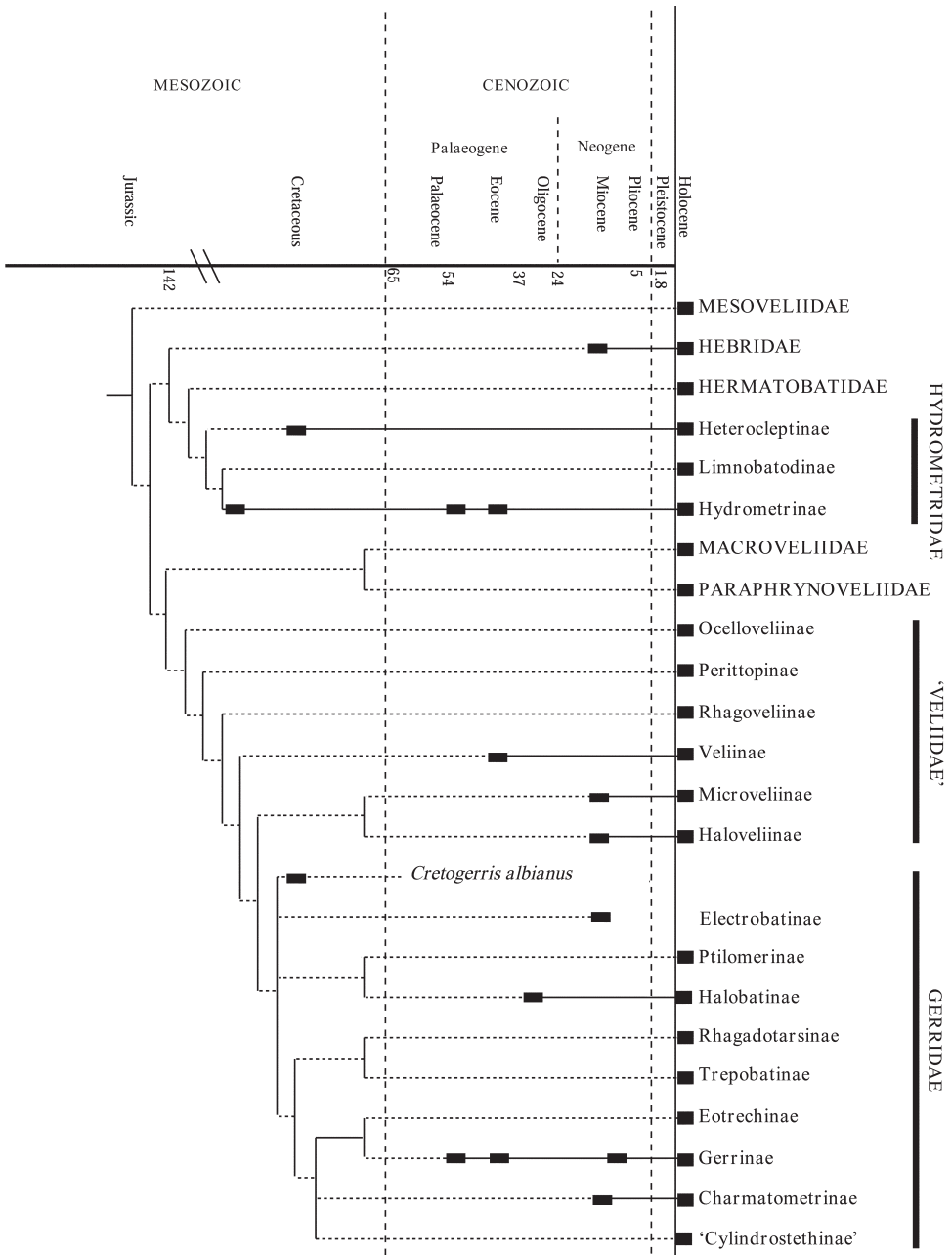


Fig. 1. Phylogenetic tree for the families of Gerromorpha and subfamilies of Hydrometridae, Veliidae and Gerridae summarized from DAMGAARD (in press). Temporal distribution of fossils indicated by heavy branches; unbroken branches denote range extensions inferred from fossils; broken branches denote range extension inferred from sister group relationships.



Hydrometridae and Gerridae, which have unique structural features (long, slender mid- and hindlegs in Gerridae; threadlike appendages and an extremely elongated head in most members of Hydrometridae), and are therefore easier to assign to families, as compared to other families with more generalized morphologies.

Despite the scarcity of fossil Gerromorpha, any specimen that can be assigned to a certain taxon provides an opportunity for dating clades, and a unique insight into the diversity of the past. *Halovelina electrodominica* from Dominican amber was described on the basis of a male riding the back of a female (ANDERSEN & POINAR 1998), presumably as an example of prolonged mate guarding, which is common in extant males of *Halovelina* Bergroth, 1893 (ANDERSEN 1982). Even though the anterior part of the male was missing, the fossil was well enough preserved for scoring 37 of the 46 morphological characters used in a cladistic analysis of *Halovelina* (ANDERSEN 1989), and a phylogenetic analyses showed that the fossil was sister group to all extant congeners. Since all extant *Halovelina* are restricted to the Indian and West Pacific Oceans, the discovery of *H. electrodominica* in the Caribbean provides important information about the historical biogeography of the group, showing that it was much more widely distributed in the past. While the present Caribbean still has a rich fauna of gerromorphan bugs (ANDERSEN 1982: 379), the European fauna is by comparison quite poor (AUKEMA & RIEGER 1995). The rich record of compression fossils and Baltic amber inclusions from central and northern Europe shows that even this region had a much more diverse fauna in the early Cenozoic, but that most of the fauna became extinct most likely during the Pleistocene glaciations. That the glaciations also had a strong impact on the extant European fauna has been revealed in several phylogeographic studies (largely summarized in DAMGAARD 2008).

### Re-interpretation of the fossil record

Although the fossil record is notoriously incomplete, and many of the diagnostic characters are not directly accessible from fossils, other diagnostic characters are and can be taken as evidence for the sister group relationship of fossil and extant taxa. As our knowledge of informative and diagnostic characters from extant taxa accumulates, fossils should be scored for these characters, so that they eventually can be directly included in phylogenetic analyses, as done by ANDERSEN & POINAR (1998). The following re-evaluation of the fossil record of Gerromorpha is based on comparisons of information from the literature with the current hypothesis of gerromorphan phylogenetic relationships, and the characters found to diagnose clades from DAMGAARD (in press).

Mesoveliidae was assigned as sister group to all other Gerromorpha by ANDERSEN (1982), and this position has been conformed by DAMGAARD (in press), even though the taxon sample was restricted to a few species of the cosmopolitan genus *Mesovelia* Mulsant & Rey, 1852 in the quite diverse subfamily Mesoveliinae. Mesoveliidae is foremost diagnosed on characters in the male and female genitalia (presence of an ejaculatory bulb and pump in the male genital tract; long, laciniate ovipositor to embed eggs in substrate) and embryos (lack of embryonic egg-burster), all of which are impossible to see in fossils. *Duncanovelia extensa* Jell & Duncan, 1986 was assigned to Mesoveliidae on the basis of an overall interpretation of the fossil, and ANDERSEN (1998: Fig. 76) accepted this interpretation and provided a reconstruction based on

the original photograph. He admitted however, that the general habitus of the fossil resembles several families of terrestrial Heteroptera, including Nabidae, Miridae, Lygaeidae and Alydidae. There is no doubt that the Mesoveliidae is an old group, but until a more inclusive phylogeny of the family is available whereupon external morphological characters can be evaluated, the assignment of fossils to this family (POPOV & BECHLY 2007) is not followed.

Hebridae is another very old and basal family in Gerromorpha, and is either sister group to all families, except Mesoveliidae (ANDERSEN 1982), or sister group to Hydrometridae + Hermatobatidae (DAMGAARD, in press). Like in Mesoveliidae, the taxon sample of Hebridae is very poor and restricted to two species of the cosmopolitan genus *Hebrus* Curtis, 1833 in the family Hebrinae. Hebridae is diagnosed on several strong apomorphic characters (bucculae elevated posteriorly to form a pair of ventral plates; fourth labial segment being about half as long as third labial segment; two-segmented middle and hind tarsi (basal segment composed of primitive second and third segment); genital segments inserted ventrally and slightly before apex of pregenital abdomen). Only a single fossil species, *Stenohebrus glaesarius* from Mexican amber, has so far been assigned to the family (POLHEMUS 1995). ANDERSEN (1998: 85) included the fossil in the subfamily Hebrinae on the basis of the fourth antennal segment having a 'false joint', and the paired, ventral carinae of the thoracic venter being parallel throughout.

ANDERSEN (1982) erected a superfamily, 'Hydrometroidea', to include members of the relatively large family Hydrometridae plus the two small families Paraphrynoveliidae and Macroveliidae on the basis of the ventral lobes protruding in from, and hiding, the basal labial segment(s), and the metepisternum having an anteriorly directed process, and stated (p. 258) that 'the discovery of the primitive hydrometrid genus *Veliometra* [Andersen, 1977] bridged the phenetic gap between the Macroveliidae and Hydrometridae'. He furthermore diagnosed the sister group relationship between Macroveliidae and Hydrometridae on basis of the eyes being distinctly removed from the front margin of the prothorax, the dorsal position of the metathoracic spiracle, and the paired longitudinal ridges also reaching abdominal tergum 4. Only recently have molecular data been available for Paraphrynoveliidae and Macroveliidae, and the reconstructed phylogeny show that the two families are strongly supported sister groups, perhaps to a degree that suggests their synonymy, which is further emphasized by the apparent absence of diagnostic characters for Paraphrynoveliidae (DAMGAARD, in press).

Macroveliidae is diagnosed on the presence of paired, longitudinal ridges of the basal abdominal tergites, but also characters found convergent in Hydrometridae are important for diagnosing the family (see below). ANDERSEN (1998: 47-49) assigned *Daniavelia morsensis* from the Danish Mo clay deposits to Macroveliidae, but admitted that 'this decision is based on rather weak evidence and since the diagnostic features for the macroveliids [...] cannot be observed in fossils, the classification is provisional'. Like the case with *Duncanovelia extensa*, the assignment of *Daniavelia morsensis* to an extant family seems premature and is therefore not followed.

Hydrometridae is diagnosed on many characters, of which the most important are the elongate postocular part of the head; the unique insertion of tubercles of the posterior pair of cephalic trichobothria; and the fourth antennal segment with an apical invagination with sensorial structures. ANDERSEN (1982) subdivided Hydrometridae into three subfamilies,

Heterocleptinae, Limnobatodinae and Hydrometrinae, of which the latter two are sister taxa. The subfamily Heterocleptinae has retained many of the plesiomorphic gerromorphan characters, including presence of ocelli and abdominal scent glands, and the presence of ocelli was used to assign *Carinometra burmensis* to this subfamily (ANDERSEN & GRIMALDI 2001). ANDERSEN (1998: 44-46) initially assigned *Palaeometra madseni* to the subfamily Limnobatodinae on account of its relatively short head and broad abdomen, but with inclusion of more and better preserved material, ANDERSEN & GRIMALDI (2001: 389) included *Palaeometra* in Hydrometrinae, to which all other fossil taxa (*Cretaceometra brasiliensis*, *Eocenometra danica*, *E. longicornis*, *Hydrometra groehni*, *Incertametra santanensis*, *Limnaxis succini*, *L. hoffeinci*, *Metrocephala anderseni*, *Protobacillometra oligocenica*) are also assigned. In the description of *Incertametra santanensis*, PEREZ GOODWYN (2002) interpreted a pair of small, round structures at the lateral head margins, just in front of the eyes as 'ocelli', but this interpretation was rejected by ANDERSEN (2003) because ocelli are always found behind the eyes in extant and extinct Hydrometridae. Recently, POPOV & BECHLY (2007: 328) suggested that 'most probably *Cretaceometra* and *Incertametra* are congeneric, the few small differences simply reflecting natural variation'.

While DAMGAARD (in press) found that Macroveliidae + Paraphrynoveliidae was sister group to Veliidae + Gerridae, the Hydrometridae was assigned as sister group to the Hermatobatidae, which previously had been associated with Veliidae + Gerridae in the superfamily 'Gerroidea' (ANDERSEN 1982). The sister group relationship between Hydrometridae and Hermatobatidae is moderately supported, but nevertheless diagnosed by two characters: eggs deposited upright and mesothorax distinctly prolonged (DAMGAARD, in press). The relationships of 'Hydrometroidea' and 'Gerroidea' need to be revisited with inclusion of DNA sequence data from extant members of especially the subfamily Heterocleptinae before any higher-level taxonomic conclusions can be drawn.

The two remaining families, Veliidae and Gerridae, comprise the vast majority of semi-aquatic bugs, and each family is subdivided into several subfamilies (ANDERSEN 1982). ANDERSEN (1982: Table 12) diagnosed the sister group relationship of Veliidae + Gerridae on several apomorphic characters, including body surface with thorn-like structures; salivary pump inflected from behind; pretarsus inserted preapically on tarsus of all legs; parempodia asymmetrically developed or both reduced; metasternum with long evaporative grooves ending with a hair tuft on metepisternum; and absence of abdominal scent glands. ANDERSEN (1982: Table 12) diagnosed the Veliidae on the egg having several micropyles; head deflected in front of eyes; and male front tibia with a grasping comb; while Gerridae was diagnosed on the frontal egg burster; absence of ocelli; four pairs of cephalic trichobothria; mesothorax prolonged, coxal axes of middle and hind legs horizontal; and tarsi with two segments, basal segment comprising the fused primitive first and second segment. The new relationships of the subfamilies of Veliidae and Gerridae found by DAMGAARD (in press) have necessitated a completely new organisation of the diagnostic characters, especially due to the paraphyly of Veliidae, and in the assignment of Ptilomerinae + Halobatinae as sister group to all other Gerridae. The subfamilies Ocelloveliinae, Perittopinae and Rhagoveliinae are successive sister groups to the clade comprising the family Gerridae and the two veliid subfamilies Microveliinae + Haloveliinae, but since no fossils have been assigned to any of these basal veliid

lineages, they will not be addressed further here. Some excellently preserved fossils from Baltic Amber (*Balticovelia weitschati*, *Electrovelia baltica*) were assigned to the subfamily Veliinae by ANDERSEN (2000), but since this subfamily is poorly defined (DAMGAARD, in press), the assignment of these fossils will have to await a reinvestigation of the phylogeny of Veliidae. The sister group relationship between Gerridae and Haloveliinae + Microveliinae is diagnosed on the presence of a female fecundation pump; and the middle and hind tarsi composed of primitive first and second segments. The sister group relationship between Haloveliinae and Microveliinae is diagnosed on the presence of a dorsal sclerite of salivary pump, and on the structure of the female fecundation pump, but while Microveliinae is strongly diagnosed on the one-segmented fore tarsi, the Haloveliinae can not be diagnosed on any apomorphic characters at present. Excellent fossils from Dominican amber have been assigned to the two groups (ANDERSEN & POINAR 1998; ANDERSEN 1999, 2001), all of which strongly resemble extant taxa, thus suggesting that both subfamilies are of a considerably older age.

Gerridae is diagnosed on many characters, but none are without convergences, or to be found in all included taxa. Until very recently the oldest fossil members of the Gerridae were from the Palaeocene of France (A. NEL, pers. comm.) and the Palaeocene/Eocene deposits in Denmark (ANDERSEN 1998), but with the discovery of *Creto Gerris albianus*, the fossil history of Gerridae has been pushed back into the Early Cretaceous. One of the most characteristic features of the specimen is the presence of three pairs of cephalic trichobothria (PERRICHOT et al. 2005). Most members of the Gerridae have four pairs of cephalic trichobothria, and ANDERSEN (1982: Table 11) assumed that this was the ancestral state in Gerridae, and that the common ancestor of the two subfamilies, Halobatinae and Ptilomerinae, had lost the fourth pair of cephalic trichobothria, thus returning to the ancestral state of Gerromorpha. With the new phylogenetic reconstruction it is evident that the presence of three pairs of cephalic trichobothria is a plesiomorphic condition in Gerridae, and that the fourth pair has evolved only once in the common ancestor of all subfamilies, except for Halobatinae + Ptilomerinae. While no fossil Ptilomerinae are known, *Halobates ruffoi* was convincingly assigned to Halobatinae by ANDERSEN et al. (1994), giving a minimum age for this subfamily, and showing that the marine lifestyle in seaskaters was already present at that time. PERRICHOT et al. (2005: 797) stated that *Creto Gerris* 'is unlikely to be closely related to the Halobatinae, although its general habitus is very similar to that of some extant species of this subfamily, e.g. *Halobates* and *Eurymetra*'. *Electrobates spinipes* from Dominican amber also has only three pairs of cephalic trichobothria, and was assigned to its own family, Electrobatinae, by ANDERSEN & POINAR (1992). Whether *Creto Gerris* belongs to Electrobatinae, or should be assigned as sister group to one of the basal lineages in Gerridae still needs to be examined. For now, the three gerrid lineages showing the plesiomorphic condition in number of cephalic trichobothria are placed unresolved at the base of Gerridae. *Brachymetroides atra*, has been assigned to the subfamily Charmatometrinae. This subfamily is diagnosed on the distinct lateral intersegmental suture between the meso- and metathorax, which is a character reversal also found in the Rhagadotarsinae + Trepobatinae clade. The remaining fossil Gerridae are either without affinities to extant or extinct subfamilies, such as *Cylindrobates messelensis* and *Lutetiabates eckfeldensis* from the Middle Eocene of Germany (WAPPLER & ANDERSEN 2004), or with affinities to Gerrinae. A considerable number of fossils have been assigned to

Gerrinae, even though this subfamily is poorly diagnosed (DAMGAARD, in press). ANDERSEN (1975) erected two tribes, Tachygerrini for two Neotropical genera, *Tachygerris* Drake, 1957 and *Eurygerris* Hungerford & Matsuda, 1958, and Gerrini for all other members of Gerrinae, and diagnosed the latter on the reduction of pretarsal arolia in the adult form. *Electrogerris kotashevichi* has retained the pretarsal arolia and has also a hair tuft at the metasternal scent orifice strikingly similar to that of *Eurygerris*, and therefore ANDERSEN (2000) assigned the fossil to Tachygerrini. No other group of water striders have been discussed as intensively as the clade comprising the three principal Holarctic genera *Limnoporus*, *Aquarius* and *Gerris* (summarized in DAMGAARD 2006). DAMGAARD & COGNATO (2003, 2005) found that *Aquarius* was not monophyletic since *Aquarius chilensis* (Berg, 1881) was placed unresolved at the root of the tree along with the outgroup species, *Gigantometra gigas* (China, 1925), while the North American *remigis*-group was found to be sister group to *Gerris*. *Aquarius chilensis* is unique among Gerrini in having retained the pretarsal aroliae (ANDERSEN 1990), but whether this is a plesiomorphic condition or due to convergent evolution will have to await a phylogenetic analysis of the Gerrinae. Members of the *remigis*-group can be separated from all other members of the clade on basis of their uniquely modified male genitalia (dorsal plate of vesica being prolonged beyond apex of dorsal sclerite) (DAMGAARD & CHRISTIANSEN 2007) and from congeners on their relatively shorter first antennal segment (subequal to 2+3 in *remigis*-group; longer than 2+3 in other *Aquarius*) (DAMGAARD & COGNATO 2005). While many species groups of the clade have trans-Beringian relationships (DAMGAARD & COGNATO 2005), members of the *remigis*-group are confined to the Nearctic Region. The fossil genus *Telmatrechus* Scudder, 1890 with three described species from North America has the same relative length of the antennal segments as members of the *remigis*-group, and the reconstruction by ANDERSEN (1998: Fig. 55) shows great similarities with members of this group, suggesting they may be congeners.

The remaining species of *Aquarius* were assigned to the *najas*-, *paludum*- and *conformis*-groups by ANDERSEN (1990), and the monophyly of these groups have been confirmed in simultaneous analyses of morphological and molecular data (DAMGAARD & COGNATO 2003, 2005). The *najas*-group is today represented by three species in the western part of the Palaearctic Region (DAMGAARD 2005). The fossil *A. lunpolaensis* (Lin, 1981) has strong similarities with the *najas*-group, not only in general appearance, but also in details such as hypogastry to accommodate the ripening eggs (ANDERSEN 1998), and documents that the *najas*-group had a much wider distribution in the Miocene. The *conformis*-group shows a disjunct biogeographical relationship between East Asia and eastern USA, which probably results from a more continuous distribution of the group before habitat fragmentation and isolation of populations following orogeny and climatic changes began on the northern Hemisphere in the late Miocene (DAMGAARD & COGNATO 2005). The *paludum*-group shows a disjunct distribution with species in the Palaearctic, Oriental, Afrotropical and Australian Regions, as well as island endemics on Timor and in the Philippines, and DAMGAARD & ZETTEL (2003) found that the phylogeny of the group was completely congruent with the sequence of break up events of the southern super continent Gondwana, suggesting that the present distribution results from vicariance events beginning in the Mesozoic. This was, however, contradicted by the relative small genetic divergence among the species. The fossil material of *Palaelogerris* Andersen, 1998 includes

some strikingly large specimens (27-31.5 mm body length), which are matched by only one living species of Gerridae, *Gigantometra gigas* (China, 1925) (32-36 mm) (ANDERSEN 1998). As the only gerrine genus, *Gigantometra* Hungerford & Matsuda, 1958 has distinct evaporative scent channels on the metathorax, which has also been observed in *Palaeogerris furensis*. *Palaeogerris* has the metathoracic spiracle close to the wing bases, which affiliates the fossil genus with *Gigantometra*, *Limnopus*, *Aquarius* and *Gerris*, and ANDERSEN (1998: 18) even considered synonymizing extinct and extant taxa, but decided to leave them unresolved at the basis of the clade because *Palaeogerris* does not have the extraordinary long middle and hind legs characteristic of male *Gigantometra gigas*. ANDERSEN (1995) presented a phylogenetic hypothesis based on parsimony analyses of 67 morphological characters scored for all gerrine genera. This data set should be analysed together with a suite of molecular data sets in order to evaluate the diagnostic character combinations for the whole subfamily Gerrinae as well as all included tribes, genera, subgenera and species groups.

### Dating the nodes

Fossil gerromorphans assigned to extant clades provide a unique opportunity to date nodes on the phylogenetic tree and to look for congruent patterns in the evolution of other life forms. Even with the relatively poor fossil record of Gerromorpha, the combination of the fossil evidence with a relatively robust phylogeny provides important insight into the former diversity and the impact of geological and climatic events. Currently, fossils representing most extant families have been described covering more than 100 million years of evolutionary history, but the presence of fossil Nepomorpha in deposits from the Upper Triassic and Lower Jurassic suggest the presence of contemporary Gerromorpha, and the recent discovery of *Creto-gerris albianus* indicates that all families were present in the Lower Cretaceous. The Hydrometridae, which probably has the best fossil record of any gerromorphan family, has representatives of the most derived subfamily, Hydrometrinae, from the Crato Formation, thus showing that all three extant subfamilies were present in the Lower Cretaceous. Since the 'Veliidae' is paraphyletic with regards to Gerridae, all the lineages which ANDERSEN (1982) considered subfamilies must also have been present in the lower Cretaceous. The Microveliinae + Haloveliinae comprise a well supported monophyletic group, and the records of derived members of both subfamilies from Dominican amber suggest that even this clade may also be of Mesozoic origin. The presence of gerrine water striders in the Paleogene Mo clay deposits of northern Europe suggest a considerable age for all subfamilies of Gerridae, but a Mesozoic origin of Gerrinae can so far only be indirectly inferred by the disjunct biogeographical distribution of the *Aquarius paludum*-group. There are no convincing fossils of Mesoveliidae and Hermatobatidae and only a single fossil of Hebridae, but since all three families are basal in Gerromorpha they must be of considerable age. Another issue speaking for an old age of Mesoveliidae is the disjunct amphi-Atlantic distribution of the Madeoveliinae and the presence of endemic genera of Mesoveliinae on isolated islands, such as Hawaii, Galapagos, and New Zealand (ANDERSEN 1982). Another strong amphi-Atlantic sister group relationship is found between Macroveliidae and Paraphrynoveliidae suggesting that the common ancestor of the two families predates the opening of the Atlantic Ocean in the late Cretaceous.

The three marine water strider genera *Halovelina* (Veliidae), *Halobates* (Gerridae) and *Hermatobates* Carpenter, 1892 (Hermatobatidae) provide a particularly interesting case for studies of the ecological phylogenetics and historical biogeography of Gerromorpha because these are the only water striders with a distribution comprising both the western and eastern parts of the Pacific Ocean and/or the Caribbean. One species of *Hermatobates* (*H. breddini* Herring, 1965) occurs in the Caribbean, while the remaining species all have an Indo-Pacific distribution. The sea skaters, *Halobates*, have one endemic species (*H. robustus* Barber, 1925) in the Galapagos Islands, while four open ocean species occur along the Pacific coast of Middle and South America (*H. sericeus* Eschscholtz, 1822, *H. sobrinus* White, 1883, *H. micans* Eschscholtz, 1822 and *H. splendens* Witlaczil, 1886), or along the Caribbean and Atlantic coasts of these areas (*H. micans*). JACZEWSKI (1972) hypothesized that the pantropical *Halobates micans* dispersed from the Indo-Pacific to the Atlantic Ocean through the Tethys Sea, and the discovery of *Halobates ruffoi* from northern Italy shows that sea skaters were present in that area. The current phylogeny of *Halobates* shows that the open-ocean species are among the more derived members of the genus, and that their life style probably originated twice from more coastal species (DAMGAARD et al. 2000). In a phylogeographic study of open ocean sea skaters, ANDERSEN et al. (2000) furthermore found that the Atlantic population most likely descended from the Pacific before the closure of the Isthmus of Panama around three million years ago. According to ANDERSEN & POINAR (1998), the situation in *Halovelina* is considerably different from *Halobates* because *Halovelina electrodominica* was present in the Caribbean in the Oligocene-Miocene, and because this species was found to be sister group to all extant congeners. Even though an impressive number of morphological characters were available from the fossil, these are still to be tested against a more robust phylogeny of extant members in order to find out what characters are plesiomorphic and what are derived. Finally, the phylogenetic relationships of the approximately ten extant species of *Hermatobates* should be worked out in order to look for congruent biogeographical patterns with both *Halobates* and *Halovelina*.

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