

Water striders from the Paleogene of Denmark with a review of the fossil record and evolution of semiaquatic bugs (Hemiptera, Gerromorpha)

By NILS MØLLER ANDERSEN



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Water striders from the Paleogene of Denmark with a review of the fossil record and evolution of semiaquatic bugs (Hemiptera, Gerromorpha)

By NILS MØLLER ANDERSEN



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Abstract

Water striders and other semiaquatic bugs (Hemiptera-Heteroptera, Gerromorpha) comprises about 1,600 extant species classified in eight families. So far, about 30 fossil species belonging to six families have been described or recorded, spanning more than 120 million years of geological history. Most fossils are of Cenozoic age but a few indisputable Mesozoic fossils have been recognised. The Fur and Ølst Formations of northern Denmark (Paleocene-Eocene transition, 55-54 Ma) contain an unusually rich fauna of insects, including seven species classified in four genera and three families of Gerromorpha. The following taxa are described here: *Palaeogerris* gen. nov., *P. furensis*, *grandis*, and *mikkelseni* spp. nov. (Gerridae), *Eocenometra longicornis* sp. nov., *Palaeometra* gen. nov., *P. madseni* sp. nov. (Hydrometridae), *Daniavelia* gen. nov., *D. morsensis* sp. nov. (Macroveliidae). Furthermore, *Electrovelia* gen. nov., *E. baltica* sp. nov. (Veliidae) is described from Baltic amber, Denmark. The fossil record of Gerromorpha is reviewed, with redescriptions, descriptive notes, etc. of all fossil taxa known from the literature. In addition, *Limnoporus wilsoni* sp. nov. (Gerridae) is described from the Middle Eocene of British Columbia, Canada, and the following new combinations proposed: *Telmatrechus defunctus* (Handlirsch, 1910) comb. nov. and *Aquarius lunpolaensis* (Lin, 1981) comb. nov. Reinterpretations are presented for a number of other fossils: *Metrobates aeternalis* (Scudder) and *Halobates bagonensis* Lin are cast nymphal skins (exuviae) of contemporaneous gerrine water striders; *Palaeovelvia spinosa* Scudder from the Upper Eocene of Colorado, U.S.A. and *Engynabis tenuis* Bode from the Lower Jurassic of Mecklenburg, Germany, are incorrectly classified in the Gerromorpha. Although the fossil record is immensely imperfect, available fossil taxa can in most cases be placed in phylogenies (cladograms) together with their extant relatives. Cladograms calibrated against the fossil record yield phylogenetic trees which can be used to estimate minimum divergence time of extant clades. The oldest members of the Gerromorpha are of Lower Cretaceous (Aptian) age, but the infraorder probably evolved in the Lower Mesozoic. Gerromorphan life on the water surface (pleustonic zone) probably evolved before the beginning of the Paleogene and the marine environment was colonised before Middle Eocene time. The geographical distribution of fossil water striders provides in some cases information which contradict biogeographical hypotheses based on the distribution of extant taxa alone.

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Introduction

Water striders and other semiaquatic bugs (Hemiptera-Heteroptera, infraorder Gerromorpha) include about 1,600 species most of which occupy an adaptive zone defined by water surfaces (the pleustonic zone). Most species occur in freshwater, but several lineages have colonised marine habitats. These insects have conspicuous adaptations for life on the surface film of water, especially with respect to locomotion, feeding, reproductive behaviour, and life history (Andersen 1982b). Their two-dimensional habitat makes water striders ideal subjects for ecological and behavioural studies and many northern temperate species have been extensively used as model organisms in such studies (for a recent review of the literature, see Spence & Andersen 1994).

Evolutionary biology has the evolutionary history or phylogeny of organisms as its general framework of reference. Understanding evolution requires the concerted efforts of neontological systematics and palaeontology (studies of fossils). It is through systematics that biologists delimit and identify species and establish how they are related, grouping them into appropriate higher taxa. And it is through the fossil record that biologists establish the times of appearance and disappearance of species and higher taxa. The study of fossils provides the most direct evidence of how evolution has proceeded through geological time.

Phylogenies of extant semiaquatic bugs are now available for a reasonably large number of higher taxa, mainly based on comparative morphological characters (e.g. Andersen 1982b, 1989b, 1990, 1991b, 1993b, 1995c; Andersen & Spence 1992) and, more recently, also on allozymes and DNA-sequences (Sperling & Spence 1990; Sperling *et al.* 1997). As is the case with most groups of insects, however, the fossil re-

cord of semiaquatic bugs is immensely imperfect. Yet, recent findings of fossil water striders have provided useful insights into the evolutionary history of this group (Andersen 1982a; Andersen & Poinar 1992, 1998; Andersen *et al.* 1993, 1994).

The present work was prompted by the discovery of an unusually rich and diverse fauna of semiaquatic bugs in sediments of the Paleogene Fur and Ølst Formations of Denmark (Fig. 1). So far, this extinct fauna comprises seven species classified in four genera and three families of the infraorder Gerromorpha. The new genera and species are described and illustrated in detail below. In addition, this work presents the first comprehensive, critical review of the fossil record of semiaquatic bugs, spanning more than 120 million years of geological history. All fossil taxa are discussed in a phylogenetic perspective, with evaluation of their contribution to understanding the adaptive evolution and historical biogeography of semiaquatic bugs. For the benefit of readers not familiar with the principles and methods of modern systematic biology, elementary introductions are offered to phylogenetic reconstruction (cladistics), ecological phylogenetics, and cladistic biogeography.

The fossil record of Gerromorpha

The first fossil semiaquatic bugs were recorded by Germar & Berendt (1856) from Baltic amber (Eocene/Oligocene). Reviews including fossil Gerromorpha can be found in Handlirsch (1906-1908), Bachofen-Echt (1949), Keilbach (1982), Andersen (1982b), Spahr (1988), Carpenter (1992), and Nel & Paicheler (1993). The maps (Figs 2-3) show the localities from which fossil gerromorphans have been recov-

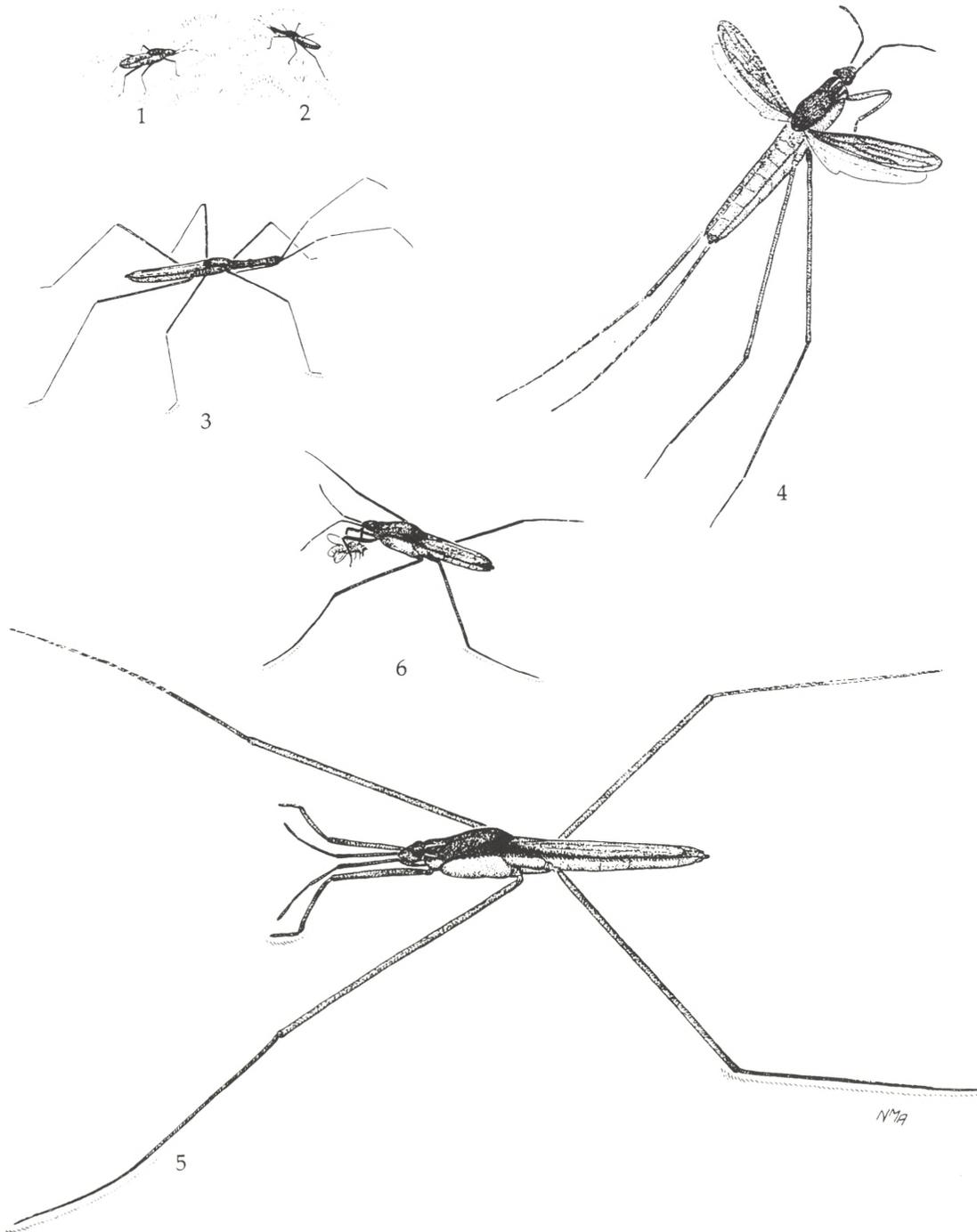


Fig. 1. Paleogene water striders, Fur and Ølst Formations, Denmark. Reconstructions (drawn to same scale, x 1.5). 1, *Daniavelia morsensis* gen. et sp. nov.; 2, *Palaeometra madseni* gen. et sp. nov.; 3, *Eocenometra danica* Andersen; 4, *Palaeogerris furensis* gen. et sp. nov. (female); 5, *Palaeogerris grandis* gen. et sp. nov. (male); 6, *Palaeogerris mikkelseni* gen. et sp. nov.

ered, including a few other localities mentioned in this work. Localities with subfossil (Pleistocene) gerrormorphans are not included. A list of all localities with geological horizon and other relevant information including references is given below with the same numbering as used on the maps (Figs 2-3).

Mesozoic localities

1. Mecklenburg, Germany. Lower Jurassic (Toarcian) (Popov & Wootton 1977).
2. Koonwarra fossil bed (Korumburra Group), Victoria, Australia. Lower Cretaceous (Aptian). Lacustrine (Jell & Duncan 1986).
3. Santana Formation, Araripe Plateau, northeastern Brazil. Lower Cretaceous (Aptian). Lacustrine (Grimaldi & Maisey 1990).

Cenozoic localities

4. Fur and Ølst Formations, Denmark. Paleocene-Eocene transition. Marine (Larsson 1975; Pedersen & Surlyk 1983; Heilmann-Clausen, 1995; Heilmann-Clausen *et al.* 1985; Willmann 1990a; see also below).
5. Havighorst near Hamburg, Germany. Lower Eocene. Marine (Illies 1941).
6. British Columbia, Canada. Middle Eocene. Lacustrine. (Wilson 1977, 1978a, 1996).
7. Green River Formation, Wyoming, U.S.A. Middle Eocene. Lacustrine (Scudder 1890; Wilson 1978a).
8. Bolca, Northern Italy. Middle Eocene. Marine (Andersen *et al.* 1994).
9. Messel, Darmstadt, Germany. Middle Eocene. Lacustrine (Lutz 1990, 1991).
10. Florissant, Colorado, U.S.A. Lower Oligocene (Upper Eocene according to M.V.H. Wilson, in. litt.). Lacustrine (Scudder 1890; Wilson 1978a).
11. Baltic amber, Denmark, northern Germany, etc. Eocene/Oligocene (secondary in

Pleistocene deposits). Terrestrial (Larsson 1978; Schlee 1990; Poinar 1992).

12. Bitterfeldt amber, Germany. Eocene/Oligocene (secondary in Miocene deposits). Terrestrial (Poinar 1992).
13. Kleinkemps at Mulhouse, Rhein Valley, France. Lower Oligocene (Nel & Paicheler 1993).
14. Rott-am-Siebengebirge, Germany. Middle Oligocene (Statz 1950; Nel & Paicheler 1993).
15. Gypse d'Aix, Aix-en-Provence, France. Upper Oligocene (Nel & Paicheler 1993).
16. Dominican amber, Dominican Republic, Hispaniola. Oligocene/Miocene. Terrestrial (Schlee 1990; Poinar 1992; Grimaldi 1996).
17. Mexican (Chiapas) amber, Mexico. Oligocene/Miocene. Terrestrial (Hurd *et al.* 1962; Poinar 1992; Grimaldi 1996).
18. Karagan Formation, northern Caucasus, Russia. Miocene. (Y. Popov, personal communication).
19. Lunpola Basin, Tibet, China. Miocene. Lacustrine (Lin 1981).

The ash-bearing Fur and Ølst Formations

Geology and biostratigraphy

The Fur Formation (Pedersen & Surlyk 1983) is composed of a about 60 m thick unit of highly porous diatomite, so called mo-clay, which mainly consists of diatomaceous shells and a small clay content. At certain levels, the diatomite is cemented with calcium carbonate, forming large calcareous concretions, so-called "cementstones" (Fig. 4, A-E). The formation is further characterised by having about 180 conspicuous, black layers of volcanic ash. Paleogene ash-layers are found in several other Danish formations and all over the North Sea Basin (Heilmann-Clausen 1995). Estimates of the duration of the sedimentation and formation of the volcanic ash-layers range from 1 to 3 Ma.

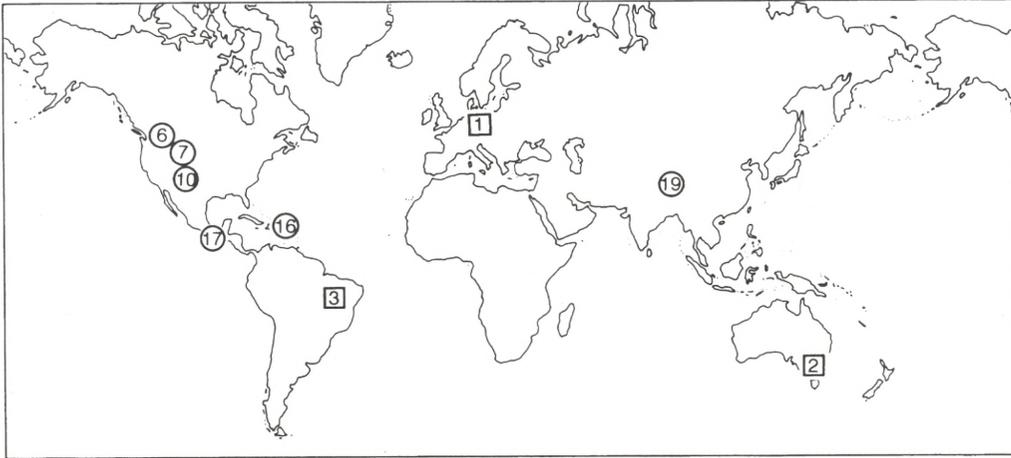


Fig. 2. World map with fossil localities for semiaquatic bugs (Heteroptera, Gerromorpha). Further explanation in text.

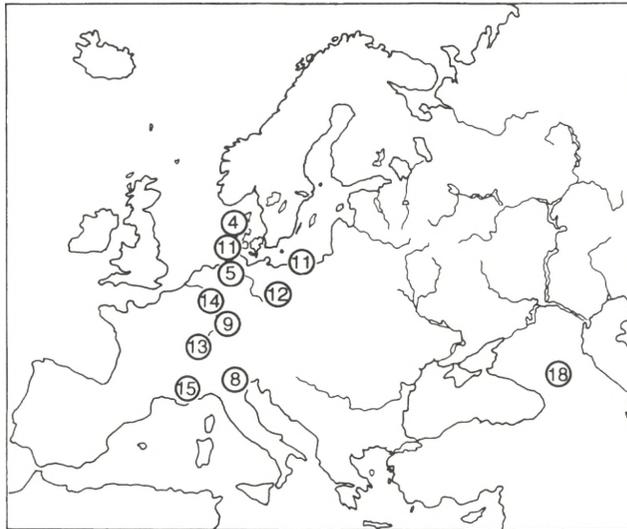


Fig. 3. Map of Europe with fossil localities for semiaquatic bugs (Heteroptera, Gerromorpha). Further explanation in text.

Sediments belonging to the Fur Formation are exposed in several localities in northwestern part of Denmark, in particular on the islands Fur and Mors in the western Limfjord area of Jutland (see map, Fig. 5). Most localities are situated on the north coast of Fur and Mors, but since the mo-clay have been exploit-

ed commercially, the formation is also exposed in pits (e.g. at Skarrebage and Ejerslev, Mors).

The ash-layers of the Fur Formation have been associated with volcanic activity during the Lower Paleogene period (60-54 Ma ago), where Greenland and Europe drifted apart. The thickness of the ash-layers decreases to-

wards southeast, which means that the active volcanoes probably were situated Northwest of Jutland, approximately at the present location of the Faroe Islands. The ash-layers are numbered according to their relative age, from -39 (the oldest layer) to +140 (the youngest layer). Certain ash-layers are so characteristic that they quite easily can be traced from locality to locality. The most complete series of ash-layers is found on the north coast of Fur, at Knuden and Stolleklint (Fig. 5), but most insect fossils from these localities are associated with the ash layers from No. -28 to -24 (in laminated cementstone of the "B" horizon) or below No. -33 (in laminated clay, more or less silicified). Most of the fossil water striders have been found at Stolleklint, usually in loose blocks on the shore washed out from the cliffs by the sea. Other fossil-rich locations are associated with the cementstone horizons containing the ash layers below No. -13 or above No. -11 (the "C" horizon) and from No. +25 to No. +30 (the "E" horizon). Fossil water striders are known from these horizons at Skarrehage and Ejerslev, Mors (Fig. 5).

The ash-layer series of the Fur Formation also occur in the correlated Ølst Formation (Heilmann-Clausen *et al.* 1985). The oldest sediments of this formation is a more or less silicified, laminated clay which is exposed below the Fur Formation at Stolleklint, intergrading with the latter at ash-layer No. -33. It is now recognised that many insect fossils previously associated with the lowermost ash-layers of the Fur Formation in reality belong to the Ølst Formation (Heilmann-Clausen 1995 and personal communication).

The biostratigraphy of Danish Upper Paleocene-Middle Eocene sediments is mainly based on dinoflagellates, since calcareous microfossils usually are absent. The dinoflagellate biostratigraphy as summarised by Heilmann-Clausen (1985, 1995) integrates previous zonations covering the Upper Paleocene and lowermost

Eocene. The oldest ash-layers in the top of the Holmehus Formation occur on Fur and Mors and belong to the dinoflagellate Zone 5. This zone correlates with the calcareous nannofossil NP9 Zone, suggesting that the oldest ash-layers in Denmark are of Upper Paleocene age (about 55 Ma). Sediments belonging to the Fur and Ølst Formations were deposited during the Paleocene-Eocene transition, but the exact position of the boundary between these two epochs remains to be settled (Heilmann-Clausen, personal communication).

Palaeoenvironment and biodiversity

The sediments of the Fur Formation were deposited on the bottom of an epicontinental sea covering all of Denmark in early Paleogene time (Fig. 6). Based on the composition of the fish fauna, Bonde (1966, 1974) suggested that the formation was deposited at some distance from the coast, at depths of 50-500 m. The regular lamination of the diatomite indicates that the sediment was deposited without being disturbed by wave action and also suggests that bottom-dwelling, burrowing marine animals were rare (Pedersen 1981).

There are numerous remains of plants (leaves, rhizomes, pieces and trunks of wood) in the Fur Formation, including conifers, bamboo, *Ginkgo*, and *Salvinia* (Larsson 1975; Bonde 1987). Some pieces of wood have partly enclosed pieces of resin preserved as amber. The plant material bears evidence of having undergone considerable transport, probably washed out by rivers and streams from a coastal woodland area. According to Bonde (1974) and Larsson (1975), this land area was located at about the same position as the southwestern coast of modern Scandinavia.

The fauna of the Fur Formation comprises birds, turtles, about 50 species of fishes, and an abundance of insects (Bonde 1966, 1973, 1974, 1987; Larsson 1975; Nielsen 1959, 1963; Hoch 1975; Willmann 1990a; Andersen & Andersen

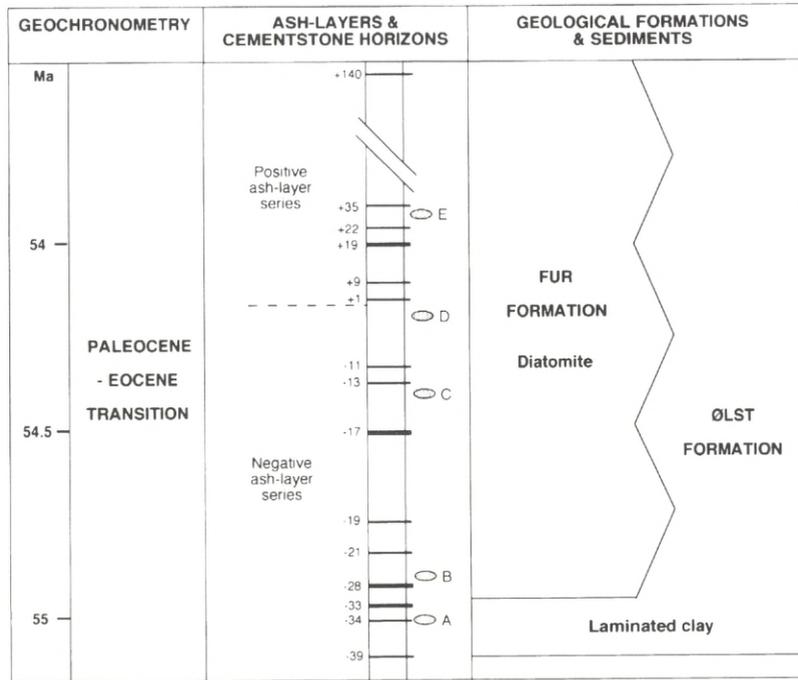


Fig. 4. Fur and Ølst Formations, northern Jutland, Denmark. Geochronometry, idealized profile with ash-layers (numbered from -39 to +140) and principal cementstone horizons (A-E), and boundaries of formations. Further explanation in text (redrawn from Heilmann-Clausen 1995).

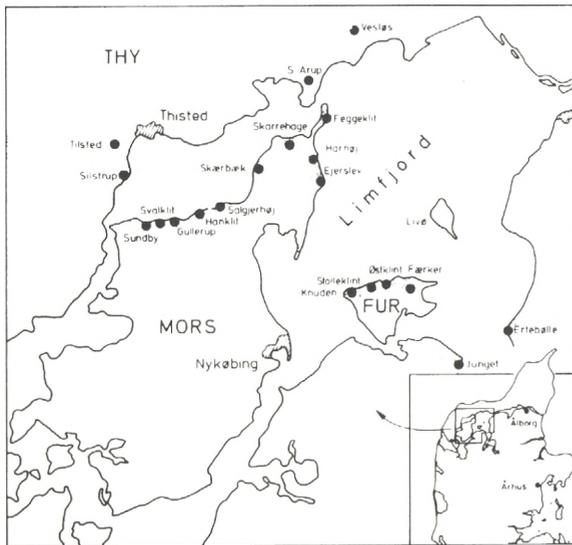


Fig. 5. Fur and Ølst Formations, fossil localities (after Willmann 1990).

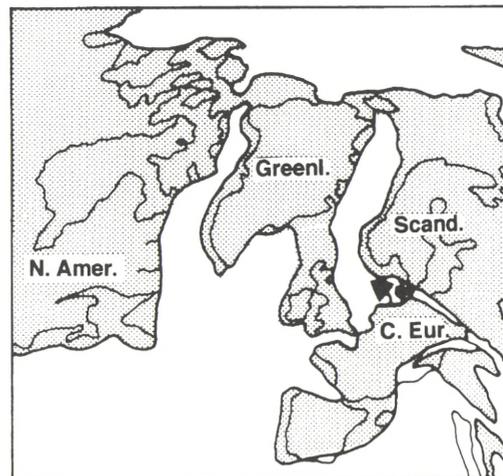


Fig. 6. Palaeogeography of Europe and the North Atlantic area in Late Paleocene time (60 Ma) (redrawn from Smith *et al.* 1994).

1996; Rust & Ansoerge 1996; Rust, in press). Henriksen (1922, 1929) described the first insects from the formation belonging to the orders Odonata, Orthoptera, Neuroptera, Hemiptera (including Heteroptera), and Diptera. Other species were described by Zeuner (1936), Heie (1967, 1970), Willmann (1977), Andersen (1982a), and Schlüter (1982). During recent years, the accumulation of material has been intensified and an estimated 20,000 insect fossils are presently known from private and public collections. The largest insect groups are the Diptera (both nematocerans and Brachycera), Hemiptera-Auchenorrhyncha, Heteroptera, and Trichoptera. The Fur and Ølst Formations now appear to be some of the richest and most diverse insect-bearing Paleogene deposits in Europe, only exceeded by Baltic amber (Eocene/Oligocene). The scientific processing of this material has just been initiated with works on Odonata (Madsen & Nel 1997), Dermaptera (Willmann 1990b), Hemiptera-Aphidoidea (Heie 1993), Neuroptera (Willmann & Brooks 1991; Willmann 1993), Diptera-Tipulomorpha (Freiwaldt 1990, 1991), Ptychopteridae (Freiwaldt & Willmann 1992), Dixiidae (Ansoerge 1992), Hymenoptera-Parasitica (Rust 1990), and Formicidae (Rust & Andersen, in press). Preliminary studies by Stig Andersen, Jes Rust, and the author, have revealed representatives of many other insect groups, including the oldest known fossil but-

terfly (Lepidoptera-Hesperiidae; R. de Jong, unpublished) and species of Psychopsidae (Neuroptera), a family at present only known from South Africa, Southeast Asia, and Australia.

So far, only winged adult insects have been recorded from the Fur Formation. The wingless "giant" ants are queens which have shed their wings after the completion of their nuptial flight (Andersen & Andersen 1996; Rust & Andersen, in press). The chironomid larvae described by Kohring (1994) is in reality an incompletely preserved heteropteran (Rust, in press). Larsson (1975) therefore suggested that the insects of the Fur Formation were carried out to sea by the wind and not by water currents as the plant material (see above). Investigations of recent faunas have shown that flying insects belonging to many orders are transported far out over the sea by air currents (Bowden & Johnson 1976). Insects that fall upon the water surface are usually eaten by surface-feeding fish and birds and have little chance of being deposited on the sea bottom. Exceptional conditions, however, may have prevailed at certain periods, during which many insects could sink to the bottom of the sea without being eaten by benthic fishes. Contemporaneous mass mortality of fish (Bonde 1966) has been explained by periodic anoxic conditions and/or excessive bloom of pelagic dinoflagellates, in modern tropical seas known as "red tide" (Larsson 1975).

Material and methods

The fossils examined in the present work were gathered from a number of sources. Fossil insects from the Fur and Ølst Formations are deposited in the Geological Museum, University of Copenhagen, Fur Museum, Fur, and in Møllermuseet, Skarrehage, Mors, and have been examined by me. The collections of the first two mentioned institutions were also examined by the late S. G. Larsson in connection with his survey of the insect fauna of the mo-clay (Larsson 1975). There are smaller collections of insects from the Fur Formation in the Natural History Museum, London, U.K., and in the Palaeontological Institute, University of Uppsala, Sweden. To my knowledge, there are no fossil water striders in the London museum. Yuri Popov, Palaeontological Institute, Russian Academy of Science, Moscow, Russia, has kindly provided me with photographs of mo-clay fossils from the latter institution (Figs 93-96).

By far the most important material of fossil insects from the Fur and Ølst Formations have been accumulated during the past 5-7 years by private collectors, in particular Henrik and Rebekka Madsen, Nykøbing Mors, and Bent Søb Mikkelsen, the former leader of the collections and exhibitions of Møllermuseet, Skarrehage, Mors. Valuable material have also been collected by Erwin Rettig, Nykøbing Mors, and Søren Kristensen, Veksø.

In 1990, the Danish Parliament passed a bill declaring "earth-found natural history objects of unique scientific and public value" for national property. Such objects shall be handed over to an appropriate institution by the finder who will then receive a proper compensation. An object falling within this law has been give the popular name "Danekræ" (derived from the ancient concept of "Danefæ" which concerns earth-found objects of national, historical value). During the

past 5-6 years, my research associate Stig Andersen and I have evaluated about one hundred potential "Danekræ" insects and many of the specimens used to complete this work have come to my knowledge in this way.

Another important source of fossil water striders is amber. The Zoological Museum, University of Copenhagen, houses one of the largest collections of Baltic amber with insect inclusions (Larsson 1978; Poinar 1992), including three specimens of semiaquatic bugs. Through the courtesy of George O. Poinar, Jr., Oregon State University, Corvallis, U.S.A., I have been able to examine some extremely well-preserved water striders found in Dominican amber (Figs 118-119, 120-123).

Other fossil gerromorphans (specimens and/or photographs) have kindly been provided by Rolf Mathewes, Simon Fraser University, Canada (Figs 113-114), Alessandro Minelli, University of Padua, Italy (Fig. 106), André Nel, Muséum National d'Histoire Naturelle, Paris, France, Yuri Popov, Palaeontological Institute, Russian Academy of Science, Moscow, Russia (Figs 96, 97-99), and Mark V. H. Wilson, University of Alberta, Edmonton, Canada (Figs 111-112). Finally, an extensive literature search have been conducted to complete the review of the fossil record of semiaquatic bugs.

The following abbreviations for repositories of types and other fossils are used in the text:

- ERC Erwin Rettig collection, Nykøbing Mors, Denmark.
- FM Fur Museum, Fur, Denmark.
- GMUC Geological Museum, University of Copenhagen, Denmark.
- GOPC Georg O. Poinar, Jr. collection, University of Oregon, Corvallis, U.S.A.
- HRMC Henrik and Rebekka Madsen collection, Nykøbing Mors, Denmark.

MM	Molermuseet, Skarrehage, Mors, Denmark.
PIM	Palaeontological Institute, Russian Academy of Science, Moscow, Russia.
PIU	Palaeontological Institute, Uppsala University, Sweden.
ROM	Royal Ontario Museum, Ottawa, Canada.
SKC	Søren Kristensen collection, Veksø, Denmark.
ZMUC	Zoological Museum, University of Copenhagen, Denmark

Essentially two kinds of fossil material have been available for study:

- (1) Compression fossils in sediments of various derivation.
- (2) Inclusions in fossil resin (amber).

All of the insects from the Fur and Ølst Formations are preserved as compression fossils, either in the silicified, laminated clay of the Ølst Formation or in the calcareous cementstones of the Fur Formation. The best preserved specimens are usually found in the more fine-grained clay. Fortunately, both parts and counterparts have been available for the fossils examined here (except as noted) and the importance of keeping these parts together in collections should be emphasised. In many specimens, details like hairs, spines, and microtrichia are well preserved. Wings and some bodies usually show patterns of original pigmentation. While being studied, specimens were covered by distilled water, which has the effect of rendering transparent the thin layers of rock covering many of the fossils. Many specimens cannot be detected without first being wetted.

Amber inclusions were examined either directly, in some cases after the piece of amber had been polished to bring the inclusion closer to its surfaces, or by submerging the piece in distilled water or vegetable oil. All observations during the present work were made with a Leitz stereomicroscope and a Volpi fiberoptic lig-

ht source. Drawings were made with the aid of an ocular grid net and squared paper.

Documentation of the overall structure and morphological details of a fossil specimen is provided using the following ways of presentation (apart from descriptions):

- (1) Unretouched photographs of the fossil *in situ* (Figs 93-123).
- (2) Line-drawings of the fossil *in situ* (e.g. Figs 10, 17, and 23) and of morphological details with interpretations of structures (e.g. Figs 11-15).
- (3) More or less detailed reconstructions of fossil species also using information about the morphology of extant relatives (e.g. Figs 7-8).

All measurements are in millimeters. Except when noted, measurements are the greatest length of body (as measured from the tip of head to the end of abdomen), body parts, appendages, or their segments. The age of the fossils are given as geological period and as million years before present, abbreviated Ma. The following abbreviations of figure lettering apply to all text-figures (except when noted):

1A,	first anal vein
ab,	abdomen
ac,	anteclypeus
ag,	acetabular groove
an,	antenna
bu,	buccula
cl,	clypeus
cn,	connexivum
co,	connexival spine
ct,	cephalic trichobothrium
cx,	coxa
cx2,	middle coxa
Cu,	cubitus
ev,	evaporative structure on metacetabulum
fe,	femur
fe1, fe2, fe3,	front, middle, and hind femur
fw,	forewing
gr,	grasping comb of front tibia
gx,	gonocoxa (segment 8)

he, head
 hw, hind wing
 la3, la4, labial segments 3 and 4
 lp, lateral process on proctiger
 M, media
 m, membranous area
 mn, mesonotum
 ms, mesosternum
 mt, metanotum/metasternum
 oc, eye
 pa, paramere
 pn, pronotum
 po, postnotal suture
 pr, proctiger
 py, pygophore (segment 9)

r-m, cross-vein
 ro, rostrum
 Sc, subcosta
 sp, metathoracic spiracle
 sc, evaporative scent channel
 so, metasternal scent orifice
 s2-7, abdominal sternites 2-7
 s8, abdominal segment 8
 ta, tarsus
 ta1, ta2, ta3, front, middle, and hind tarsus
 th, thorax
 ti, tibia
 ti1, ti2, ti3, front, middle, and hind tibia
 tr, trochanter
 t1-7, abdominal tergites 1-7.

Water striders from the Paleogene of Denmark

Family **GERRIDAE** Leach

Water striders, pondskaters

Subfamily **Gerrinae** Leach

Genus *Palaeogerris* gen. nov.

Type species: *Palaeogerris furensis* sp. nov.; by present designation.

Diagnosis and description

Large water striders, length 14.2-31.5 mm, with long and slender legs, in particular middle and hind legs. Ground colour chiefly dark brownish or black. Pronotum usually dark with median pale stripe anteriorly.

Head (Figs 7-8, he) extended in front of eyes. Eyes (Fig. 21, oc) large and globose. Antenna (Figs 7-8, an) longer than half of body length; first antennal segment more than 1.3x head length; second and third segment together subequal to or longer than first segment (at least in *P. furensis* and *P. mikkelsenii* spp. nov.). Rostrum (Figs 8 and 21, ro) relatively long and slender, apex surpassing prosternum.

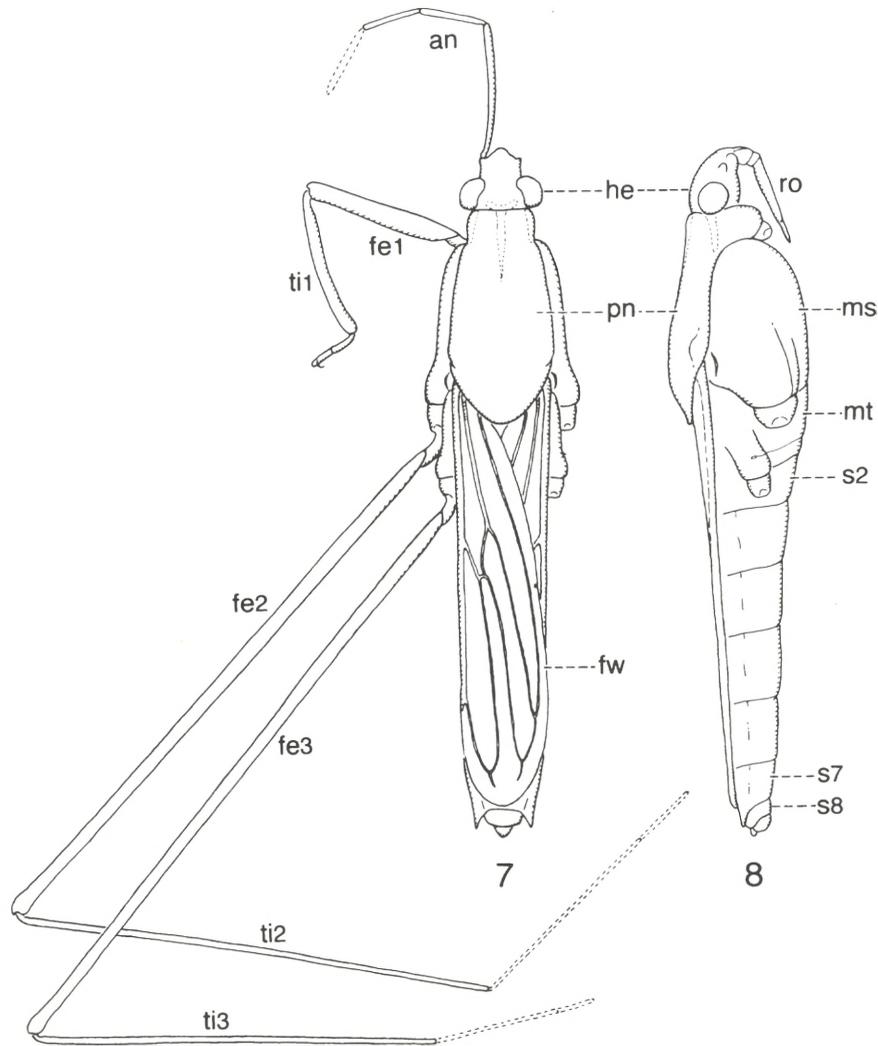
Thorax. Pronotum (Figs 7-8, pn) of macropterous (long-winged) form more than 2x as long as wide across humeri; pronotal lobe behind humeri broadly rounded (Figs 10 and 12, pn). Mesothorax (Fig. 8, ms) moderately prolonged, distance between pro- and mesoacetabulum less than 2.5x the distance between meso- and metacetabula. Metathoracic spiracle situated less than its own length from wing bases (*P. furensis* sp. nov.; Fig. 12, sp). Metasternum (Fig. 8, mt) longer than 0.4x mesoster-

num. Area of metasternum surrounding scent orifice modified, tuberculate (= omphalium of Matsuda 1960); scent orifice circular (*P. furensis* sp. nov.; Fig. 13, so); evaporative scent channels (sc) present, leading laterally from scent orifice to metacetabula.

Legs. Front femur (Fig. 7, fe1) slender, less than twice as thick as middle femur; apex of front tibia rounded on inner margin. Middle femur (fe2) subequal to or shorter than body length; middle tibia more than 0.7x length of middle femur; middle tarsus almost 0.5x length of middle tibia. Hind femur (fe3) subequal to or longer than middle femur; hind tibia more than 0.5x hind femur.

Wings. Forewings (Fig. 7, fw) when folded over the back, not reaching abdominal end; forewing venation resembling that of most extant Gerrinae, with three basal veins (Fig. 16; terminology after Andersen 1982b): the fused subcosta and radius (Sc + R), the fused media and cubitus (M + Cu), and the first anal vein (1A). Radius and Media connected by oblique crossvein (r-m) after first branching of M + Cu. Branching of M located close to anterior crossvein (r-m). Veins connected in distal part of wing and there forming two closed cells.

Abdomen distinctly longer than meso- and metathorax; abdominal segments 2-6 (Fig. 8, s2) subequal in length, segment 7 (s7) slightly shorter; posterior corners of abdominal seg-



Figs 7-8. *Palaeogerris furensis* gen. et sp. nov. (reconstructions). 7, macropterous male, dorsal view; antennae and legs of right side omitted. 8, macropterous male, lateral view; antennae and legs omitted.

ment 7 laterally produced, forming a pair of relatively short connexival spines (Figs 14-15, co), which barely reach the apex of the genital segments. Posterior margin of sternum 7 (Fig. 14, s7) broadly concave but simple in both sexes.

Genital segments of both male and female relatively small, without conspicuous modifications (Figs 14-15, 20, 22). Segment 8 (s8) of

male subcylindrical, pygophore (= segment 9) almost completely withdrawn into segment 8 (Fig. 20, py); proctiger (Figs 14 and 20, pr) situated on top of segment 9, protruding behind segment 8. Segment 8 of female very short, barely visible behind segment 7; proctiger triangular, protruding behind segment 8 (Fig. 15, pr).

Distribution and geological horizon

Western Limfjord area, northern Denmark (see map, Fig. 5). Ølst and Fur Formations, Paleocene-Eocene transition, 55-54 Ma (Fig. 4). Possibly also present in sediments at Havighorst near Hamburg, northern Germany (Fig. 5), of about the same geological age (Illies 1941).

Remarks

Species of *Palaeogerris* gen. nov. are superficially quite similar to living water striders belonging to the subfamily Gerrinae. With body lengths between 14.2 mm and 31.5 mm, the species of this extinct genus are larger than most living water striders. The pregenital abdomen is terminated by a pair of short, but distinct spinous processes (= connexival spines), structures which are shared with some genera of the subfamilies Gerrinae and *Cylindrostethinae* (Matsuda 1960). The location of the metathoracic spiracle (close to the wing bases) affiliates the fossil genus with the gerrine genera *Aquarius*, *Limnoporos*, *Gerris*, and *Gigantometra*.

Palaeogerris is distinguished from the cosmopolitan genus *Aquarius* Schellenberg (Andersen 1990) by the relatively longer antennae, especially longer second and third antennal segments. The Holarctic genus *Limnoporos* Latreille (Andersen & Spence 1992) shares the antennal structure of *Palaeogerris* and both genera also have hind femora which are longer than middle femora (Table 1), although more distinctly so in the former genus. However, the six living species of *Limnoporos* all have a pronotal lobe which is paler than anterior pronotum. Most species belonging to the genus *Gerris* have angular instead of spinous connexival corners and the first antennal segment is relatively shorter than in *Palaeogerris* spp. nov.

The monotypic genus *Gigantometra* Hungerford & Matsuda includes the largest living gerrid, *G. gigas* (China) from Vietnam and Hainan, China (body length 32-36 mm). The me-

sothorax of this giant water strider is relatively short, only about twice as long as metathorax, and the abdomen relatively long. As the only gerrine genus, *Gigantometra* has distinct evaporative scent channels on metathorax (see Matsuda 1960: fig. 173). If this structure occurs in all species of *Palaeogerris* (only observed in one specimen of *P. furensis* sp. nov.; see below), it further adds to the similarity between *Palaeogerris* and *Gigantometra*. It is true, however, that evaporative scent channels and connexival spines also are present in the genus *Cylindrostethus* Mayr (*Cylindrostethinae*), but other characters separate this genus from *Palaeogerris*, viz., shorter antennae (segments 2 and 3 together much shorter than segment 1), short and stout rostrum, and relatively longer mesothorax.

Based upon the comparisons above, it might be justified to place the palaeogene gerrid species from the Ølst and Fur Formations in the extant genus *Gigantometra*. However, none of the fossil specimens identified as males have the extraordinary long middle and hind legs characterising the male *G. gigas* (China) (see Andersen 1982b: fig. 424). I therefore prefer to erect a new genus for the fossil species.

Decisions on species separation

More than 50 specimens of gerrids from the Ølst and Fur Formations have been examined and measured. Only 12 of these are so completely preserved that estimates of body length (from anterior margin of head to apex of abdomen) could be obtained. The range of variation is 14.2-31.5 mm (Mean= 22.7, S.D.= 5.41, C.V.= 23.9). The pronotum (dorsal part of first segment of thorax including its posterior, shield-like extension or lobe) is the body part which is most constantly well preserved and measurable. A total of 31 measurements of pronotum length was obtained. The frequency distribution of these measurements is shown in a diagram (Fig. 9). The range of variation is 4.0-9.0 mm (Mean= 6.0, S.D.= 1.24, C.V.= 20.7)

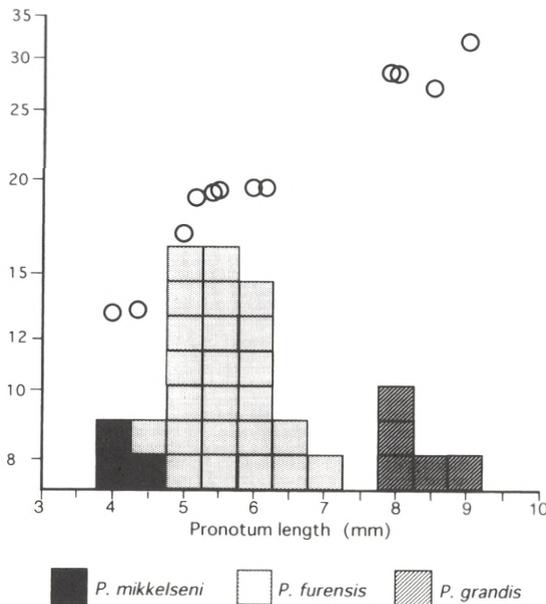


Fig. 9. *Palaeogerris* spp. Distribution of pronotum lengths (histogram; each box represents one specimen) and body length (left ordinate, logarithmic scale) of most complete specimens plotted against pronotum length (abscissa).

which is a much higher variability than observed in four large, extant species of water striders (Table 1). Assuming that the variability of the fossil species is comparable to that of extant species, I conclude that the samples of fossil water striders most likely contain more than one species.

Living species of water striders exhibit sexual size dimorphism (Andersen 1994, 1996a). The female is usually slightly larger than the male (the female/male size ratio about 1.1), but the size difference varies allometrically (slope of regression line for male size over female size less than 1.0), which means that males approach or reach the size of females as the overall length of the species increases. Assuming that the fossil species exhibit the same characteristics of sexual size dimorphism as extant species, the females should generally be larger than the males except when the body length of the species sur-

pass 20 mm (Table 1). Among the 24 fossil specimens for which the sex could be determined, the males have pronotal lengths varying between 4.7 and 9.0 mm, females between 4.0 and 8.5 mm. This also indicates that we are dealing with more than one species.

Given the more or less incomplete state of preservation of the fossil specimens, the decision on how many species there should be recognised and how to separate these from each other must necessarily be rather arbitrary. I have used the following criteria to identify the species of *Palaeogerris* of the Fur and Ølst Formations:

(1) Differences in overall size, in particular gaps in the distribution of size measurements (e.g. body length and length of pronotum). There are significant gaps in the measurements of pronotal length (Fig. 9), dividing the specimens into three groups which corresponds to the three species recognised (Table 2).

(2) Presence of diagnostic, structural characters in the most completely preserved specimens.

(3) Geological age as indicated by the position of the specimen in relation to the series of ash-layers of the Ølst and Fur Formations. The oldest specimens are found in sediments with ash-layers from the negative series at the localities Ejerslev and Skarrehege on Mors, and in particular Stolleklint on Fur. Younger species associated with ash-layers from the positive series at Ejerslev and Sundby on Mors.

By applying these criteria, three species of *Palaeogerris* can be separated by the following characters (see also Table 2):

P. grandis sp. nov. is a very large species (length 27.0–31.5 mm) with pronotum longer than 7.0 mm. Pronotum dark with a median and two sublateral pale stripes anteriorly. First antennal segment 0.8x pronotal length. Front femur slightly longer than pronotum, slender, not thicker than middle femur. Middle femur 0.7x (female) to 0.9x (male) as long as body

length, hind femur distinctly longer than middle femur. Found at Ejerslev, Mors, and Stolleklint, Fur (negative ash-layer series).

P. furensis sp. nov. is intermediate in size (length 19.0-23.0 mm) with pronotum measuring 4.7-6.9 mm. Colour of pronotum similar to that of *P. grandis* sp. nov. First antennal segment about 0.7x pronotal length and distinctly longer than second segment. Front femur not longer than pronotum and distinctly thicker than middle femur. Middle femur 0.7x (female) to 0.9x (male) as long as body length, hind femur slightly longer than middle femur. Most frequently found at Stolleklint, Fur (negative ash-layer series), less common at Ejerslev and Sundby, Mors (positive ash-layer series).

P. mikkelsenii sp. nov. is distinctly smaller than the two other species (length 14.2-16.6 mm) with pronotum measuring 4.0-4.4 mm. Pronotum uniformly dark, lacking the pale stripes anteriorly. First antennal segment less than 0.7x pronotal length and only slightly longer than second segment. Front femur about as long as pronotum, slender, not as thick as middle femur. Middle femur 0.7x as long as body length, hind femur slightly longer than middle femur. Only known from Ejerslev, Mors (both negative and positive ash-layer series).

***Palaeogerris furensis* sp. nov.**
(Figs 10-16, 93-99)

Material examined

Holotype

Macropterous male (Figs 10, 93-94); whole specimen in lateral aspect with abdomen in distorted position, obscured by overlying brownish material not belonging to specimen; antennae and most leg segments preserved; wing venation distinct. Locality data: Skarrethage Møllergrav, Mors; date unknown, Bent Søren Mikkelsen leg. Part and counterpart unmarked. Geological data: cementstone, ash-layer unknown. Holotype deposited in MM.

Paratypes

No. 1. Macropterous female (Fig. 95); complete specimen in dorsal aspect; head (incomplete), thorax, abdomen, wings, and parts of middle and hind legs preserved. Locality data: Fur, date and collector unknown. Part and counterpart marked "220" (also containing the holotype of *Palaeogerris grandis* sp. nov.). Geological data: cementstone, ash-layer unknown. Paratype deposited in FM.

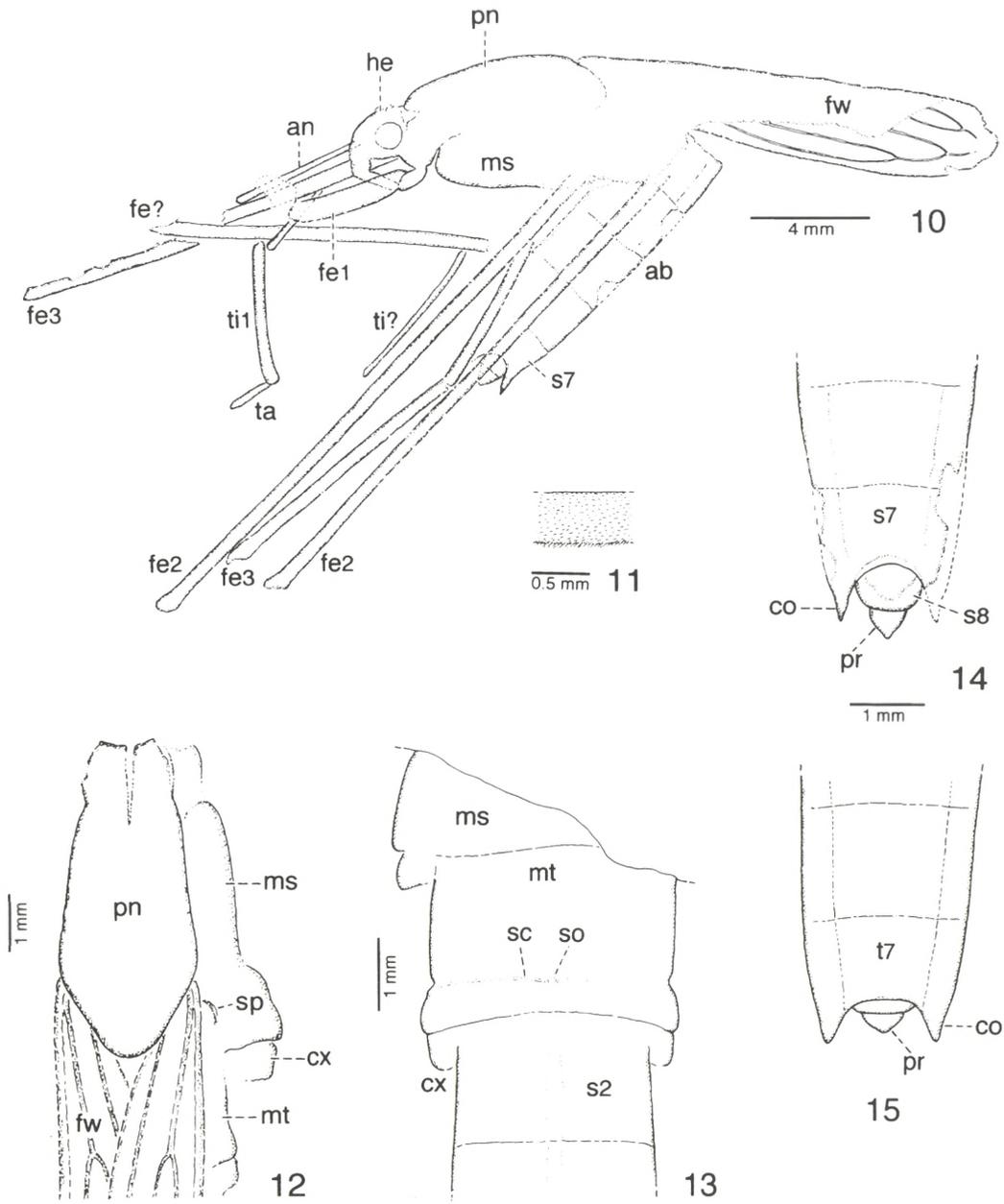
No. 2. Macropterous specimen, probably female (Figs 97-99); almost complete, head and thorax in lateral aspect, abdomen partly in dorsal aspect; antennae and legs almost complete. Locality data: locality, date, and collector unknown. Part and counterpart marked "I 157". Geological data: cementstone, ash-layer unknown. Paratype deposited in PIU.

No. 3. Macropterous female; complete specimen in dorsal aspect with parts of antennae and legs preserved. Locality data: Stolleklint, Fur, 8.xii.1991, Henrik Madsen leg. Part and counterpart marked "16-2835". Geological data: striped cementstone, ash-layer No. -25. Note: Two other, poorly preserved specimens are present in the same part and counterpart. Paratype deposited in HRMC.

No. 4. Macropterous male; pronotum and abdomen in oblique dorsal aspect; wings distinct. Locality data: Stolleklint, Fur, 29.xii.1991, Henrik Madsen leg. Part and counterpart marked "16-2891". Geological data: laminated clay, ash-layer No. -31 or lower. Paratype deposited in GMUC.

No. 5. Macropterous female; thorax and abdomen in dorsal aspect. Locality data: Stolleklint, Fur, 23.vii.1992, Henrik Madsen leg. Part and counterpart marked "16-3562". Geological data: laminated clay, ash-layer No. -31 or lower. Paratype deposited in GMUC.

No. 6. Macropterous specimen, sex unknown; complete specimen in dorso-lateral aspect, most of antennae and legs preserved. Locality data: Ejerslev, Mors, date unknown, Bent



Figs 10-15. *Palaeogerris furensis* gen. et sp. nov. 10, macropterous male holotype, oblique lateral view. 11, chaetotaxy of hind femur. 12, thorax of paratype No. 24, dorsal view. 13, thorax of paratype No. 9, ventral view. 14, abdominal end of male paratype No. 9, ventral view. 15, abdominal end of female paratype No. 5, dorsal view.

Søe Mikkelsen. Part unmarked (no counterpart). Geological data: cementstone, ash-layer unknown. Paratype deposited in GMUC.

No. 7. Macropterous specimen, probably male; thorax and abdomen in dorsal aspect. Locality data: Stolleklint, Fur, date unknown, Henrik Madsen leg. Part marked "16-4707" (no counterpart). Geological data: laminated clay, probably negative ash-layer series. Paratype deposited in HRMC.

No. 8. Incomplete specimen, probably macropterous male (in same plate as paratype No. 7); thorax and incomplete abdomen in oblique dorsal aspect, wings indistinct. Locality data: Stolleklint, Fur, date unknown, Henrik Madsen leg. Part and counterpart marked "16-4707". Geological data: laminated clay, probably negative ash-layer series. Paratype deposited in HRMC.

No. 9. Macropterous male; thorax (incomplete) and abdomen in ventral aspect, counterpart with indistinct wings. Locality data: Stolleklint, Fur, date unknown, Henrik Madsen leg. Part and counterpart marked "16-4730". Geological data: laminated clay, probably negative ash-layer series. Paratype deposited in HRMC.

No. 10. Macropterous specimen, probably male; thorax and abdomen in ventral aspect. Locality data: Manhøj, Fur, date unknown, Henrik Madsen leg. Part and counterpart marked "23-2645". Geological data: cementstone, ash-layer Nos. -28 to -24. Paratype deposited in HRMC.

No. 11. Macropterous specimen, sex unknown; pronotum and incomplete abdomen in dorsal aspect. Locality data: Stolleklint, Fur, 6.iv.1992, Henrik Madsen leg. Part and counterpart marked "16-3151". Geological data: striped cementstone, ash-layer No. -25. Paratype deposited in HRMC.

No. 12. Macropterous specimen, sex unknown; pronotum and abdomen in dorsal aspect, loose femur. Locality data: Skarrehage

Molergrav, Mors, 16.v.1992, Henrik Madsen leg. Part and counterpart marked "11-3250". Geological data: shale, ash-layer Nos. -11 to -13. Paratype deposited in HRMC.

No. 13. Macropterous specimen, sex unknown; head (incomplete), thorax, and abdomen (incomplete) in dorsal aspect. Locality data: Ejerslev Molergrav, Mors, 19.x.1991, Henrik Madsen leg. Part and counterpart marked "14M-2643". Geological data: shale, ash-layer Nos. -11 to -13. Paratype deposited in HRMC.

No. 14. Macropterous specimen, probably male; thorax in oblique dorsal aspect, abdomen in dorsal aspect, wings indistinct. Locality data: Stolleklint, Fur, date unknown, Henrik Madsen leg. Part and counterpart marked "16-4547". Horizon, laminated clay, probably negative ash-layer series. Paratype deposited in HRMC.

No. 15. Macropterous specimen, probably male; thorax, abdomen, and wings in dorsal aspect. Locality data: Stolleklint, Fur, 1994, Henrik Madsen leg. Part and counterpart marked "16-B2052". Geological data: laminated clay, ash-layer No. -33. Paratype deposited in HRMC.

No. 16. Isolated forewing from specimen of unknown sex (Fig. 96). Locality data: locality, date, and collector unknown. Part marked "I 140". Geological data: cementstone, ash-layer unknown. Paratype deposited in PIU.

No. 17. Macropterous specimen, probably male; thorax and abdomen in oblique dorsal aspect, two middle femora, one detached. Locality data: Sundby, Mors, 1995, Henrik Madsen leg. Part and counterpart marked "5-B2741". Geological data: cementstone, ash-layer Nos. +25 to +30. Paratype deposited in HRMC.

No. 18. Incomplete macropterous male; thorax and abdomen in dorsal aspect. Locality data: Stolleklint, Fur, date unknown, Bent Søe Mikkelsen leg. Part marked "I 514" (no coun-

Table 1. Comparisons between size measurements and variation in *Palaeogerris* spp. and large extant species of water striders (Gerridae). C.V. = coefficient of variation; N = number of specimens; S.D. = standard deviation. All measurements in mm.

Species	N	Body length Mean (Range)	S.D.	C.V.	Pronotum length Mean (Range)	S.D.	C.V.
<i>Palaeogerris</i> spp. nov. all	*	22.7 (14.2-31.5)	5.41	23.9	6.0 (4.0-9.0)	1.24	20.7
<i>Aquarius paludum</i> males	10	13.6 (12.6-14.6)	0.66	4.9	4.9 (4.6-5.2)	0.24	5.0
females	10	15.3 (14.2-15.8)	0.55	3.6	5.3 (4.9-5.5)	0.19	3.5
all	20	14.4 (12.6-15.8)	1.03	7.1	5.1 (4.6-5.5)	0.29	5.8
<i>Aquarius elongatus</i> males	5	23.4 (20.6-26.0)	1.95	8.4	7.9 (7.1-8.6)	0.54	6.9
females	3	23.8 (22.3-25.0)	1.37	5.7	8.0 (7.6-8.3)	0.36	4.5
all	8	23.5 (20.6-26.0)	1.66	7.0	7.9 (7.1-8.6)	0.46	5.8
<i>Limnopus notabilis</i> males	12	18.1 (16.6-19.2)	0.93	5.2	5.9 (5.4-6.4)	0.39	6.6
females	10	18.4 (16.6-19.6)	0.85	4.6	5.7 (5.2-6.2)	0.26	4.6
all	22	18.2 (16.6-19.6)	0.88	4.8	5.8 (5.2-6.4)	0.35	5.9
<i>Gigantometra gigas</i> males	5	34.3 (32.0-36.0)	1.51	4.4	10.5 (10.0-10.9)	0.36	3.4
females	2	33.4 (31.8-35.0)	2.26	6.8	9.7 (9.3-10.0)	0.49	5.1
all	7	34.1 (31.8-36.0)	1.60	4.7	10.3 (9.3-10.9)	0.56	5.5
Species	N	Middle femur length Mean (Range)	S.D.	C.V.	Hind femur length Mean (Range)	S.D.	C.V.
<i>Palaeogerris</i> spp. nov. all	*	18.1 (9.7-30.0)	6.37	35.2	18.7 (10.6-34.7)	7.32	39.2
<i>Aquarius paludum</i> males	10	11.0 (10.3-12.0)	0.52	4.8	11.6 (10.5-12.6)	0.63	5.4
females	10	11.8 (10.7-12.4)	0.62	5.2	12.1 (11.1-12.8)	0.69	5.7
all	20	11.4 (10.3-12.4)	0.68	6.0	11.9 (10.5-12.8)	0.68	5.8
<i>Aquarius elongatus</i> males	5	29.9 (23.2-37.0)	5.15	17.2	23.2 (19.8-26.8)	2.63	11.3
females	3	22.1 (20.3-23.5)	1.64	7.4	20.4 (19.4-21.0)	0.87	4.3
all	8	27.0 (20.3-37.0)	5.67	21.0	22.2 (19.4-26.8)	2.51	11.3
<i>Limnopus notabilis</i> males	12	12.6 (11.1-14.0)	1.06	8.4	15.3 (13.6-17.0)	1.45	9.5
females	10	11.1 (9.7-11.9)	0.64	5.8	13.1 (11.0-14.2)	0.97	7.4
all	22	11.9 (9.7-14.0)	2.14	9.5	14.3 (11.0-17.0)	1.60	11.2
<i>Gigantometra gigas</i> males	5	47.1 (42.0-52.0)	3.84	8.1	42.9 (42.0-52.0)	3.22	6.8
females	2	31.5 (29.9-33.0)	2.19	7.0	30.9 (28.8-33.0)	2.97	9.6
all	7	42.7 (29.9-52.0)	8.32	19.5	42.9 (28.8-52.0)	8.68	20.2

* For *Palaeogerris* spp., N = 12 (total length and middle femur length), N = 31 (pronotum length), N = 8 (hind femur length).

terpart). Geological data: laminated clay, probably negative ash-layer series. Paratype deposited in MM.

No. 19. Incomplete specimen, probably macropterous female; thorax and abdomen in oblique dorsal aspect. Locality data: Ejerslev Møllergrav, Mors; date unknown, Bent Søren Mikkelsen leg. Part and counterpart marked "I 515". Geological data: cementstone, ash-layer unknown. Paratype deposited in MM.

No. 20. Macropterous specimen, probably female; head, thorax, and abdomen in lateral aspect, parts of legs preserved. Locality data: Stolleklint, Fur, date unknown, Søren Kristensen leg. Part marked "9573". Geological data: laminated clay, probably negative ash-layer series. Paratype deposited in SKC.

No. 21. Incomplete specimen, probably female; incomplete abdomen in dorsal aspect. Locality data: Stolleklint, Fur, 9.ii.1992, Henrik Madsen leg. Part and counterpart marked "16-3056". Geological data: laminated clay, ash-layer No. -31 or lower. Paratype deposited in HRMC.

No. 22. Incomplete macropterous specimen, sex unknown; abdomen and forewing (incomplete). Locality data: Stolleklint, Fur, 23.vii.1992, Henrik Madsen leg. Part and counterpart marked "16-3561". Geological data: laminated clay, ash-layer No. -31 or lower. Paratype deposited in HRMC.

No. 23. Isolated pronotum from specimen of unknown sex. Locality data: Stolleklint, Fur, date unknown, Henrik Madsen leg. Part and counterpart marked "16-4560". Geological data: laminated clay, probably negative ash-layer series. Paratype deposited in HRMC.

No. 24. Macropterous specimen, sex unknown; thorax in oblique dorsal aspect, abdomen (incomplete) in dorsal aspect, wings distinct. Locality data: Stolleklint, Fur, date unknown, Henrik Madsen leg. Part and counterpart marked "16-4617". Geological data: laminated clay, probably negative ash-layer series. Paratype deposited in HRMC.

No. 25. Macropterous specimen, probably male; thorax and abdomen in oblique lateral aspect. Locality data: Stolleklint, Fur; date unknown, Henrik Madsen leg. Part marked "16-4709" (no counterpart). Geological data: laminated clay, probably negative ash-layer series. Paratype deposited in HRMC.

Description

Holotype. Macropterous male embedded in dorsolateral position (Figs 10, 93-94); abdomen detached from body, rotated about 90° to dorsoventral position; basal antennal segments, front legs, and femora of middle and hind legs preserved but partly obscured by pale brownish colouration of stone; distal parts of forewing venation distinct. Cuticular remains dark brown to black. Pronotum dark without indication of pale stripes. Possible remains (legs) of another specimen below head and anterior thorax (Fig. 10, fe?).

Body elongate, length 21.7 mm (from tip of head to apex of forewing) or 23.5 mm (including abdomen). *Head* relatively short (2.4 mm), about one third of the pronotal length. First antennal segment 4.8 mm (Fig. 10, a1), or twice the head length. Rostrum indistinct, slender. *Thorax.* Pronotum (Fig. 10, pn) including posterior lobe about 6.4 mm long. Structure of meso- and metathorax not observable. *Legs.* Front femur (Fig. 10, fe1) 5.4 mm and stout, about 0.9 mm wide; tibia (ti1) 5.1 mm, slightly curved and widened towards apex; tarsus (ta) 1.4 mm. Middle femur (fe2) 19.8 mm or slightly shorter than body, greatest width 0.6 mm. Middle tibia and tarsus missing. Hind femur (fe3) about 20 mm or about as long as middle femur; greatest width 0.5 mm; tibia and tarsus missing. Middle and hind femora with dense pilosity of slender hairs (Fig. 11), but without spinous hairs (as in *P. grandis* sp. nov.). Front and middle femora with fringe of short, slender hairs along ventral margin. *Wings* folded over the back, distal part of wing venation

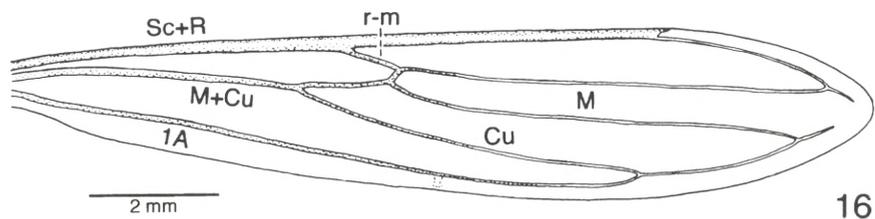


Fig. 16. *Palaeogerris furensis* gen. et sp. nov.; right fore wing of paratype No. 16.

distinct (Fig. 10, fw). *Abdomen* (Fig. 10, ab) detached from body, measuring about 11.5 mm (from third segment and backward); lengths of terga 3-7: 2.2, 2.3, 2.2, 2.2, and 1.7 mm; connexival spines (Fig. 14, co), slender and pointed, about 0.6 mm long. Genital segments relatively small; proctiger triangular (Fig. 14, pr).

Paratype No. 1. Macropterous female embedded in dorsal view (Fig. 95). Head incomplete (antennae missing); thorax, abdomen, wings and parts of middle and hind legs preserved. Measurements: length 20 mm, greatest width (across mesoacetabula) 4.5 mm; head 2.5 mm; pronotum 5.5 mm, with median and lateral pale stripes on anterior lobe; distance between pro- and mesoacetabula 4.9 mm, between meso- and metacetabula 2 mm; middle femur about 13 mm or distinctly shorter than body; hind femur 13.5 mm. Wing venation indistinct. Abdominal end with relatively short, triangular connexival spines; genital segments small, proctiger triangular.

Paratype No. 2. Probably a macropterous female with head and thorax in lateral view, abdomen partly in dorsal view (Figs 97-99); antennae and legs almost complete. Measurements: length 22.5 mm; head about 2 mm; antennal segments 1-2: 4.5 and 2.3 mm; pronotum about 6 mm; distance between pro- and mesoacetabula 5 mm, between meso- and metacetabula 2 mm; front femur 5.5 mm, distinctly thicker than middle femur; front tibia 4.8 mm; middle femur 16.8 mm or distinctly shorter than body, middle tibia 12 mm or more; hind

femur 17.3 mm, hind tibia 10.5 mm or more. Abdominal end indistinct.

Paratype No. 3. Macropterous female embedded in dorsal view. Head, thorax, abdomen, and parts of antennae and legs preserved. Measurements: length 19.2 mm; first antennal segment 3.4 mm, second segment 2.8 mm; middle femur 13.4 mm.

Paratype No. 4. Macropterous male with thorax, wings, and abdomen in oblique dorsal view. Pronotum dark with anterior median and submarginal pale stripes. Forewing venation distinct (as in Figs 16 and 94). Measurements: thorax width about 4.3 mm; pronotum length 6.2 mm; distance between pro- and mesoacetabulum 6.2 mm; length of abdomen 13.3 mm; connexival spines about 1.0 mm, slender.

Paratype No. 5. Macropterous female with thorax and abdomen in dorsal view. Measurements: length of thorax + abdomen 17.9 mm; width of thorax 4.3 mm; distance between pro- and mesoacetabulum 4.6 mm; distance between meso- and metacetabulum 2.7 mm; abdominal tergites 4-5 measure 1.9 mm, tergite 6 measures 1.6 mm, and tergite 7 measures 1.2 mm; length of connexival spines 0.6 mm (Fig. 15, co).

Paratype No. 6. Macropterous specimen of unknown sex preserved in dorso-lateral view. Measurements: body length 22.5 mm; length of head 2 mm; length of pronotum 6.2 mm; distance between pro- and mesoacetabulum 5 mm; between meso- and metacetabulum 2 mm; lengths of antennal segments 1-3: 4.5, 2.3,

and about 2 mm; length of front femur 5.5 mm; front tibia 4.8 mm; length of middle femur 16.8 mm and middle tibia about 12 mm; length of hind femur 17.2 mm and hind tibia about 10.5 mm.

Paratypes Nos. 7-25. More or less incompletely preserved specimens. Pronotum large, sides slightly diverging posteriorly to humeral angles (*Paratype No. 24*, Fig. 12, pn); hind margin of pronotal lobe broadly rounded; colouration chiefly dark, anterior lobe with a broad, pale median stripe fading toward middle of pronotal lobe; anterior pronotum usually with a pair of pale, sublateral stripes. Mesothorax distinctly widened across mesoacetabula; metathoracic spiracle situated close to bases of wings (Fig. 12, sp). Forewings dark brownish; venation distinct in some specimens and especially in isolated wings (*Paratype No. 16*, Figs 16 and 96); length of forewing 13.0-14.9 mm. Ventral structure of thorax usually indistinct except for sutures between meso- and metasternum. One specimen (*Paratype No. 9*), however, has a mid-ventral, circular structure on metasternum (Fig. 13, so) which probably marks the position of the scent orifice and superficial, evaporative scent channels (sc) leading laterally from the scent orifice to the metacetabula. Abdomen relatively long, segments 2-5 subequal in length, segments 6 and 7 slightly shorter. Abdominal end of male (*Paratype No. 9*, Fig. 14) with relatively short, slender and pointed connexival which do not extend beyond apex of genital segments. Connexival spines of female triangular, pointed, reaching apex of genital segments (Fig. 15).

Measurements of paratypes nos. 7-25 (including range of variation): head length 1.9 mm; antennal segments 1-3: 3.0, 2.4, and 2.4 mm, length of thorax + abdomen 15.7-22.7 mm; greatest width of thorax (across mesoacetabula) 4.2-5.4 mm; length of pronotum 5.1-6.5 mm; distance between pro- and mesoacetabulum 4.3-6.2 mm; between meso- and met-

acetabulum 2.4-3.5 mm; mesosternum 5.6 mm; metasternum 2.7 mm; length of leg segments: front femur 5.0-5.5 mm, front tibia 4.4 mm, middle femur 15.5 mm; length of forewing 14.5-17.8; length of abdominal tergites 4-7: 1.9, 1.9, 1.6, and 1.2 mm (male); 1.6, 1.7, 1.2, and 1.1 mm (female); length of ventral abdomen 10.1-13.6 mm; length of abdominal sternites 2-7: 1.8, 2.0, 1.8, 1.8, 1.5, 1.1 mm (male); length of connexival spines 0.6-0.7 (male) and 0.6 mm (female); length of genital segments 0.8-1.1 mm (male) and 0.6-0.7 mm (female).

Geological horizon

Ølst and Fur Formations (ash-layer series Nos. -33 to +30). Paleocene-Eocene transition, 55-54 Ma.

Distribution

Most frequently found at Stolleklint, Fur, less common at Ejerslev and Sundby, Mors, northern Jutland, Denmark (see map, Fig. 5).

Remarks

Palaeogerris furensis sp. nov. is a distinctly smaller species than *P. grandis* sp. nov. (Table 1), with body length between 19.0 and 23.0 mm and length of pronotum between 4.7 and 6.9 mm (minimum values recorded for *P. grandis* are 27.0 mm and 7.8 mm, respectively). The first antennal segment is 1.5-1.7 times as long as second segment. The front femur is distinctly thicker than middle femur. The middle femur is 0.7-0.8 times as long as the body length, shortest in the female. The hind femur is slightly longer than the middle femur. The colour pattern of pronotum is similar in *P. furensis* and *P. grandis* spp. nov., dark with anterior median and submarginal pale stripes.

Palaeogerris grandis sp. nov.

(Figs 17-22, 100-103)

Material examined

Holotype. Macropterous male (Figs 100-101); complete specimen in lateral view, including parts of antennae and most of leg segments. Locality data: Fur, date and collector unknown. Part marked "220A" and counterpart marked "220B". Geological data: cementstone, ash-layer unknown. Holotype deposited in FM. The specimen is embedded in a large block of cementstone together with a specimen of *Palaeogerris furensis* sp. nov. (Fig. 93), numerous plant leaves as well as twigs and branches of trees, and scales of fish. This block is on permanent display in the exhibitions of Fur Museum.

Paratypes

No. 1. Macropterous male; head, thorax, and abdomen in lateral view, one incomplete middle femur. Locality data: Stolleklint, Fur, date unknown, Henrik Madsen leg. Part and counterpart marked "16-4635". Geological data: cementstone, ash-layer probably No. -31 or lower. Paratype deposited in HRMC.

No. 2. Incomplete specimen, probably male; thorax and abdomen in lateral view, basal parts of legs. Locality data: Ejerslev Molergrav, Mors, 24.xi.1991, Henrik Madsen leg. Part and counterpart marked "14M-2766". Geological data: cementstone, ash-layer above or below Nos. -11 to -13. Paratype deposited in GMUC.

No. 3. Macropterous female (Fig. 102); whole specimen in lateral view, including most of middle and hind legs. Locality data: Ertebølle, 1954, collector unknown. Part and counterpart marked "1954-401". Geological data: cementstone, ash-layer unknown. Paratype deposited in GMUC.

No. 4. Macropterous male (Fig. 103); head (incomplete), thorax, and abdomen in lateral view, one complete middle femur. Locality data: Stolleklint, Fur, date unknown, Søren Kristensen leg. Part marked "9528A", counterpart marked "9528B". Geological data: cementstone, ash-layer unknown. Paratype deposited in SKC.

No. 5. Incomplete specimen, sex unknown; part of thorax and whole abdomen except apex in dorsal view. Locality data: Skibsted Strand, Mors, date unknown, Bent Søe Mikkelsen leg. Part and counterpart marked "I 516". Geological data: cementstone, ash-layer unknown. Paratype deposited in MM.

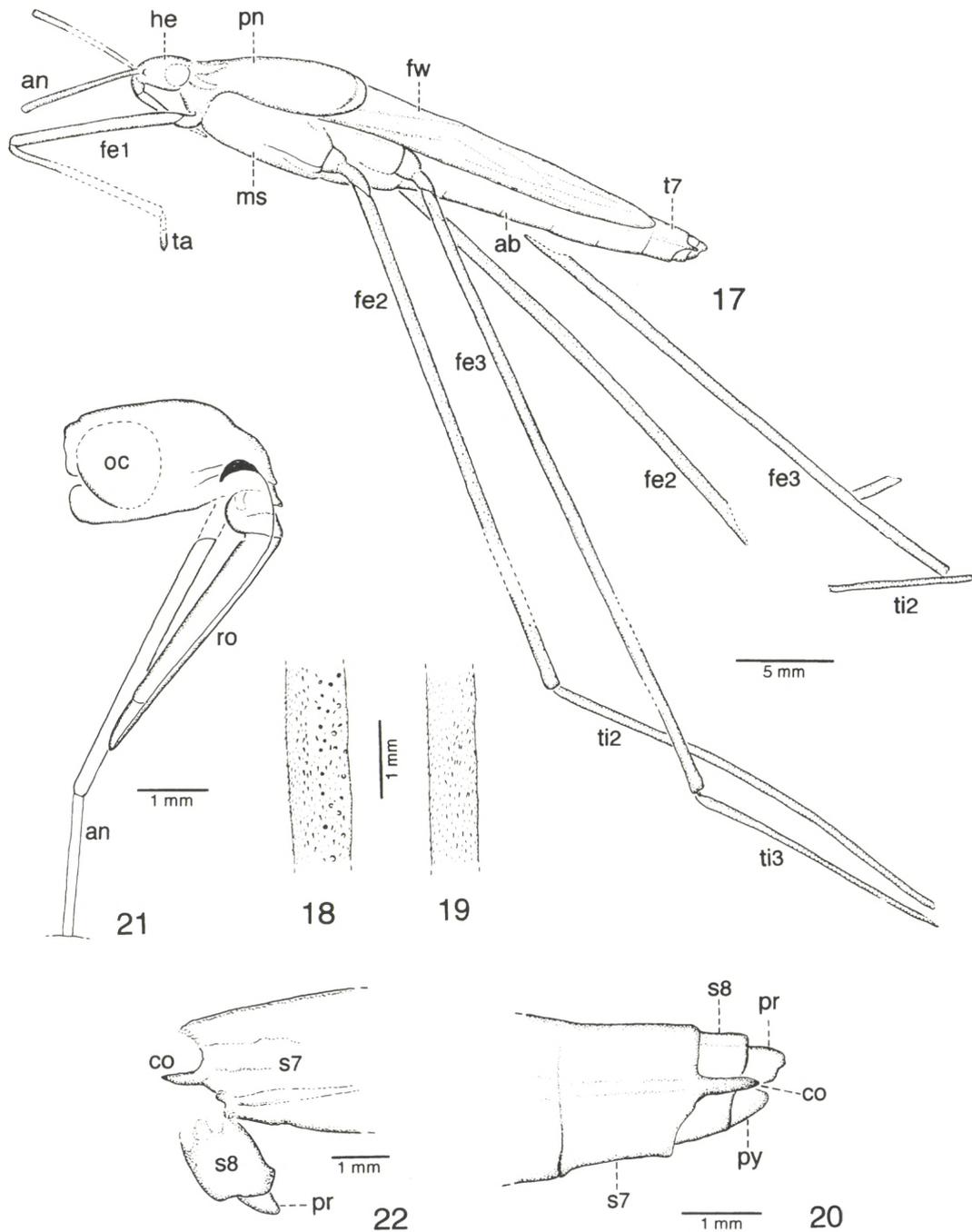
No. 6. Incomplete specimen, sex unknown; head, thorax, and part of abdomen in lateral view, rostrum, parts of antenna, middle and hind femora. Locality data: Svalklit, Mors, 1995, Erwin Rettig leg. Part marked "SV 95" (no counterpart). Geological data: cementstone, ash-layer unknown. Paratype deposited in ERC.

No. 7. Isolated forewing from specimen of unknown sex. Locality data: Stolleklint, Fur, 1993, Henrik Madsen leg. Part and counterpart marked "16-A2111". Geological data: laminated clay, ash-layer No. -33. Paratype deposited in HRMC.

Description

Holotype. Macropterous male preserved in dorso-lateral position (Figs 17, 100-101), showing pronotum and wings in oblique dorsal view, and head, rest of thorax, and abdomen in lateral view. Most of the legs and the basal antennal segments present. Cuticular remains dark brown to black. Pronotum dark with indication of pale, median and lateral stripes on anterior pronotum.

Body elongate, length (from tip of head to abdominal end) 31.5 mm. *Head* (Fig. 17, he) relatively short (3.0 mm), about one third of the pronotal length. First antennal segment (an) 6.5 mm, or slightly more than 2x head length. Rostrum (Fig. 21, ro) with its apex reaching anterior part of mesosternum; segments 3 and 4 together about 5 mm. *Thorax.* Pronotum (Fig. 17, pn) including posterior lobe about 9 mm long; hind margin of pronotal lobe broadly rounded. Mesothorax (ms) relatively short, distance between pro- and mesoa-



Figs 17-22. *Palaeogerris grandis* gen. et sp. nov. 17, macropterous male holotype, lateral view. 18, chaetotaxy of middle femur. 19, chaetotaxy of hind femur. 20, abdominal end of male holotype. 21, head of paratype No. 6, lateral view. 22, abdominal end of male paratype No. 4, lateral view.

Table 2. Comparison between *Palaeogerris grandis*, *P. furensis*, and *P. mikkelsenii* spp. nov. based upon selected dimensions of body and appendages. All measurements in mm.

	<i>P. grandis</i>	<i>P. furensis</i>	<i>P. mikkelsenii</i>
Body length	27.0 - 31.5	19.0 - 23.0	14.2 - 16.6
Head length	2.8 - 3.4	2.0 - 2.4	1.9
Pronotum length	7.8 - 9.0	4.7 - 6.9	4.0 - 4.4
Abdomen length	15.6 - 20.0	11.1 - 13.6	8.0 - 9.7
Antennal segment 1	7.1	3.4 - 4.8	2.5 - 3.0
Antennal segment 2	?	2.3 - 2.8	2.0 - 2.4
Front femur	9.5	4.5 - 5.5	4.1 - 4.5
Middle femur	18.5 - 28.5	13.0 - 19.8	9.7 - 12.0
Hind femur	21.0 - 34.7	13.5 - 20.2	10.6 - 14.9

cetabula 6.5 mm, or one fifth of body length. Distance between meso- and metacetabula 4.0 mm. *Legs*. Front femur (Fig. 17, fe1) 9.5 mm and slender throughout, only about 0.5 mm wide. Front tibia and tarsus (ta) incomplete. Middle femur (fe2) 28.5 mm, or almost as long as body, relatively stout, 0.7 mm wide. Middle tibia (ti2) 24.0 mm long and 0.5 mm wide. Middle tarsus missing. Hind femur (fe3) 34.7 mm or distinctly longer than middle femur; greatest width 0.7 mm. Hind tibia 15 mm but probably incomplete. Hind tarsus missing. Chaetotaxy of middle and hind legs distinct (Figs 18-19); there are three kinds of hairs: (1) numerous small, slender hairs which form a dense pile on the entire surface; (2) scattered, larger hairs, chiefly on ventral surface; and (3) scattered spinous hairs on the ventral parts of middle femur and basal tibia, some of these have been torn off, only leaving traces of their circular sockets. *Wings* folded over the back of abdomen, with apices of forewings (Fig. 17, fw) reaching hind margin of tergum 6; wing venation indistinct. *Abdomen* (Fig. 17, ab) relatively long, measuring about 19.5 mm from hind margin of pronotum to abdominal end. Intersegmental sutures between sterna fairly distinct; lengths of sterna 3-7: 2.8, 2.9, 2.8, 2.4, and 1.6 mm; lateral sutures between terga and sterna visible on segment 6 and 7 (Fig. 20, s7);

each postero-lateral corner of tergum 7 (Fig. 17, t7) produced into a slender connexival spine (Fig. 20, co), 0.8 mm long. *Male genital segments* (Fig. 20) relatively small, protruding from pregenital abdomen with less than length of tergum 7; segment 8 (s8) subcylindrical, ventral length slightly less than dorsal length; pygophore (py) withdrawn into segment 8 with its apex barely visible; proctiger (pr) small, blunt.

Paratype No. 1. Macropterous male preserved in dorsolateral view. Head, thorax, and abdomen well preserved; one incomplete middle femur present. Measurements: length 29.2 mm; head 3.4 mm; pronotum 8.0 mm; and abdomen 17.8 mm. Incomplete middle femur 15.3 mm, stout (0.6 mm wide), and with spinous hairs (as in Fig. 18). Connexival spines slender, relatively short (0.7 mm).

Paratype No. 2. Probably a macropterous male embedded in lateral position. Head missing; thorax, abdomen, and basal parts of legs preserved. Measurements: thorax + abdomen 23.4 mm; pronotum 7.8 mm; middle femur about 30 mm; fourth and fifth abdominal sterna 2.4 mm and 2.5 mm, respectively.

Paratype No. 3. Macropterous female embedded in a lateral position (Fig. 102). Head incomplete (antennae missing); thorax, abdomen, and basal segments of middle and hind

legs preserved. Measurements: length about 27 mm; head about 2.8 mm; pronotum 8.5 mm; distance between pro- and mesoacetabula 7.5 mm, between meso- and metacetabula 3.2 mm. Middle and hind femora both distinctly shorter than body length (18.5 and 21 mm, respectively). Abdomen stouter than in male; connexival spines short, triangular; genital segments small, slightly protruding from pregenital abdomen.

Paratype No. 4. Macropterous male embedded in a lateral position (Fig. 103). Head incomplete (antennae missing); thorax, abdomen, and one middle femur completely preserved; other legs incomplete or missing. Measurements: body length about 29 mm; pronotum 7.9 mm; middle femur 23.3 mm. Connexival spines (Fig. 22, co) slender and pointed, 0.65 mm long. Genital segments (s8 and pr) small, partly detached from abdominal end.

Paratype No. 5. Specimen with thorax and abdomen partly preserved in a dorso-ventral position. Sex indeterminable. Measurements: thorax + abdomen >18.6 mm; abdomen about 16.1 mm; abdominal tergites 4-6 measure 1.9 mm, tergite 7 measures 1.6 mm.

Paratype No. 6. Specimen embedded in a lateral position. Head (Fig. 22; detached from thorax) and thorax complete, abdomen partly preserved; antennae, middle and hind femora incomplete. Sex indeterminable. Measurements: head 3.0 mm; first antennal segment 4.6 mm; rostrum (segment 3+4) 4.0 mm; pronotum 7.5 mm; middle femur length >17.2 mm, width 0.6 mm.

Paratype No. 7. Isolated forewing. Colour pale brownish, length 17.8 mm. Venation distinct, as in *P. furensis* (Figs 16 and 94).

Geological horizon

Ølst and Fur Formations (ash-layer series No. -33 to -11). Paleocene-Eocene transition, 55-54 Ma.

Distribution

Found at various localities in the western Limfjord area, northern Jutland, Denmark (see map, Fig. 5).

Remarks

Palaeogerris grandis sp. nov. is above all distinguished by its large body size, 27-31.5 mm, which is matched by only one living species of Gerridae, *Gigantometra gigas* (China), which has a body length of 32-36 mm (Table 1 and Fig. 46). The male front femur is slender, about as wide as hind femur. The relative lengths of middle and hind femora are conspicuously different in the two sexes. In the male (Figs 17, 100-101), the middle femur is almost as long as the body length, the hind femur distinctly longer. In the female (Fig. 100), the middle and hind femora are both distinctly shorter than the body length. The ventral surface of the male middle femur is armed with scattered spinous hairs (Fig. 18). The segments of the male abdomen are about equal in length except for the last pregenital segment which is distinctly shorter; the connexival spines are slender and pointed, but relatively short, not reaching the apex of the genital segments (Figs 20 and 22).

Palaeogerris mikkelsenii sp. nov.

(Figs 23, 104-105)

Material examined

Holotype

Macropterous specimen, probably a female (Figs 104-105); almost complete specimen in oblique dorsal view, antennae and legs well preserved. Locality data: Ejerslev, Mors, date unknown, Bent Søe Mikkelsen leg. Part and counterpart unmarked. Geological data: cementstone, negative ash-layer series [No. -13?]. Holotype deposited in GMUC.

Paratypes

No. 1. Incomplete macropterous specimen,

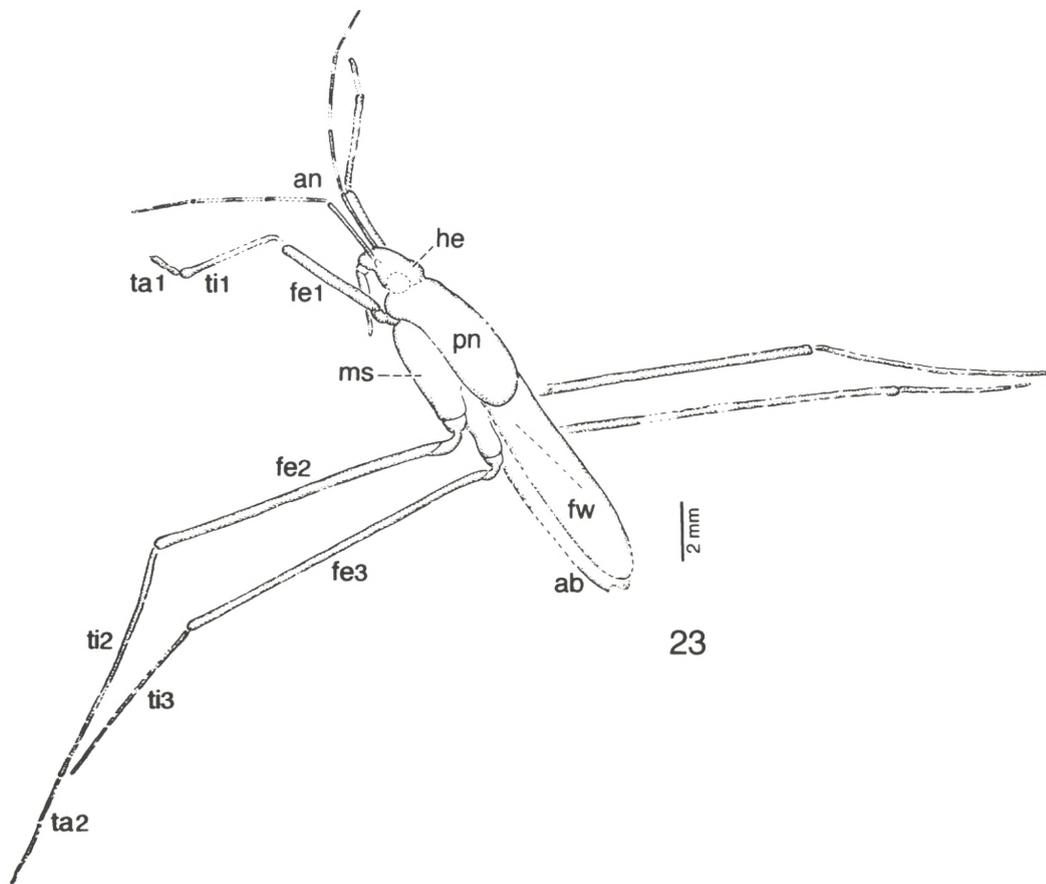


Fig. 23. *Palaeogerris mikkelseni* gen. et sp. nov.; macropterous holotype.

sex unknown. Locality data: Ejerslev, Mors, date unknown, Bent Søren Mikkelsen leg. Part and counterpart marked "I 298". Geological data: cementstone, ash-layer No. +28. Paratype deposited in MM.

No. 2. Macropterous specimen, probably male; head, thorax, and abdomen in oblique dorsal view, parts of antenna, legs, and wings. Locality data: Ejerslev Molergrav, Mors, date unknown, Bent Søren Mikkelsen leg. Part marked "I 513" (no counterpart). Geological data: cementstone, ash-layer unknown. Paratype deposited in MM.

Description

Holotype. Macropterous specimen, probably female, embedded in oblique dorsal position (Figs 23, 104-105); Head, thorax, antenna, and legs well preserved; forewing and abdomen indistinct. Cuticular remains dark brown. Pronotum dark without indication of pale stripes.

Body elongate (Fig. 23), length 14.2 mm, thorax width 3.1 mm. *Head* (Fig. 23, he) 1.9 mm long or about 0.4x pronotal length; large compound eye visible on right side. Lengths of antennal segments 1-4: 2.5, 2.0, 2.7, 1.9 (incom-

plete?); first segment about 1.3x head length, much less than second and third segments together; distal three segments very slender. Rostrum slender, about 3 mm long, its apex reaching anterior part of mesosternum. *Thorax*. Pronotum (Fig. 23, pn) about 4.4 mm long; hind margin of pronotal lobe broadly rounded. Distance between pro- and mesoacetabula 3.5 mm, between meso- and metacetabula 1.8 mm. *Legs*. Front femur (Fig. 23, fe1) 4.1 mm long and about 0.5 mm wide; tibia (ti1) 3.4 mm, slightly widened towards apex; tarsus (ta1) 1.2 mm. Middle femur (fe2) 9.7 mm or distinctly shorter than body, greatest width 0.5 mm wide; tibia (ti2) 8.1 mm; tarsus (ta2) 4.3 mm and very slender. Hind femur (fe3) 10.6 mm or slightly longer than middle femur; greatest width 0.4 mm; tibia (ti3) incomplete but at least 6.5 mm; hind tarsus missing. Chaetotaxy of middle and hind legs quite similar to that of *Palaeogerris furensis* sp. nov. (Fig. 11). *Wings* (Fig. 23, fw) folded over the back of abdomen, wing venation indistinct. *Abdomen* (Fig. 23, ab) about 8 mm (as measured from hind margin of pronotum to abdominal end); segmentation indistinct. Structure of abdominal end and genital segments obscure.

Paratype No. 1. Thorax and wings of a macropterous specimen impressed in a dorso-ventral position, sex indeterminable. Measurements: thorax + wings 10.9 mm; pronotum 4 mm; distance between pro- and mesoacetabula 3.4 mm; between meso- and metacetabula 1.6 mm.

Paratype No. 2. Almost complete macropterous specimen, probably a male; head, thorax, wings, and abdomen in oblique dorsal view; parts of antenna and legs preserved. Colour brownish with some darker parts. Measurements: body length about 16.6 mm; head 1.9 mm; pronotum 4.4 mm; abdomen 9.7 mm; antennal segments 1-3: about 3, 2.4, and about 2.4 mm; front femur about 4.5 mm (width 0.35 mm); front tibia >3.4 mm; middle femur about 12 mm; middle tibia >6.5 mm; hind femur about 14.9 mm.

Geological horizon

Fur Formation (ash-layer series No. -11 to 28). Paleocene-Eocene transition, 55-54 Ma.

Distribution

Only known from Ejerslev, Mors, northern Jutland, Denmark (see map, Fig. 5).

Remarks

Palaeogerris mikkelseni sp. nov. can be separated from the two other species of *Palaeogerris* by being distinctly smaller (Table 1), the body length being 14.2-16.6 mm and the pronotum length 4.0-4.4 mm. (the corresponding minimum values recorded for *P. furensis* sp. nov. are 19.0 mm and 5.1 mm, respectively). Pronotum appears uniformly dark, without pale longitudinal stripes anteriorly. The antennal segments are very slender, first segment only 1.3 times as long as both length of head and second antennal segment. Front femur slender, about as thick as middle femur. In *P. furensis* sp. nov., the first antennal segment is about twice as long as both length of head length and second antennal segment. Front femur distinctly thicker than middle femur. Even allowing for allometric relations, these differences are deemed significant enough to justify a separate specific status of the smaller *Palaeogerris mikkelseni* sp. nov.

Palaeogerris sp. – Paleocene/Eocene, Havighorst, Germany

Material examined

A weak imprint of an isolated forewing in a plate of hardened, laminated clay from Havighorst, northern Germany, date and year unknown; deposited in PIM. Several remains of other insects (mostly wings) in the same plate.

Descriptive notes

The length of the forewing, 13.2 mm, as well as its venation compares favourably with that de-

scribed above for *Palaeogerris furensis* sp. nov. (Figs 16 and 93).

Distribution and geological horizon

Havighorst near Hamburg, northern Germany (see map, Fig. 3). The sediments contain fossil fishes, bird-feathers, and numerous insects (Illies 1941). Volcanic ash-layers have been found in this sediment which can be referred to the same series as the uppermost ash-layers of the Fur Formation which determine their age to the Paleocene-Eocene transition, 55-54 Ma (Heilmann-Clausen 1995).

Remarks

This fossil specimen was presented to me by Yuri Popov, Palaeontological Institute, Academy of Sciences, Moscow. According to Willmann (1990a), fossils from Havighorst deposited in institutions in Hamburg were lost during the 2nd World War.

Genus *Gerris* Fabricius

Gerris Fabricius, 1794: 188.

Limnotrechus Stål, 1868: 397.

Ures Distant, 1911.

Type species:

Gerris: *Cimex lacustris* Linnaeus, 1758; subsequent designation (Latreille, 1810).

Limnotrechus: *Cimex lacustris* Linnaeus, 1758; subsequent designation (Kirkaldy 1906).

Ures: *Ures custos* Distant, 1911 (nymph); designation by monotypy.

Diagnosis

Medium sized water striders, length usually less than 11 mm. Body elongate but usually more robust than in *Limnoporus* or *Palaeogerris* gen. nov. Antennae distinctly shorter than half the body length; first segment less than 1.3x head length; second and third segments together

longer than first segment; fourth segment shorter than third. Adults usually macropterous (long-winged) or brachypterous (short-winged), rarely apterous (wingless). Pronotal lobe usually uniformly dark; median yellowish stripe of anterior pronotum not extending onto pronotal lobe. Metasternal scent orifice transverse ovate, sometimes situated on a tubercle; metathorax without lateral evaporative grooves. Front femora usually pale with dark bands, relatively robust, especially in the male. Hind femora usually shorter than middle femora. Posterior corners of abdominal connexiva angular, rarely produced into spines (females only). Nymphs variable in colour, but never dark with longitudinal pale stripes.

Distribution and habitats

Chiefly Holarctic. The majority of the 42 described, extant species are distributed in Eurasia and North America. A few species occur in Africa (Andersen 1993b).

Species of *Gerris* are almost exclusively confined to stagnant (lentic) freshwater like pools, ponds, and smaller lakes. Some species inhabit temporary pools bodies and these are usually long-winged or wing dimorphic, eventually with seasonal differences in morph frequency (Andersen 1973). The ecology and behaviour has been extensively studied in a number of northern temperate *Gerris* species (for a review, see Spence & Andersen 1994).

Remarks

Pond skaters belonging to *Gerris* are most easily recognised by their moderately sized and rather robust body, moderately thickened front femora, angular connexival spines, and by their relatively short antennae (second and third segments together longer than first segment). A number of fossil gerrids have been assigned to this genus (see below), none of these matching the diagnostic characters of the genus. I classify with some reservation the following

juvenile specimens in the genus *Gerris*. So far, only nymphs are available for study. I therefore decline to give them a specific name.

Gerris sp. – Baltic amber
(Figs 24, 116-117)

Hydrometra (nymph). Germar & Berendt, 1856:
19, plate 2, fig. 7.

Halobates (nymph). Germar & Berendt, 1856:
19, plate 2, fig. 8.

Gerroidea (nymph). Larsson, 1978: 119, plate
8, fig. A.

Material examined

Specimen No. 1 (Fig. 116), almost complete specimen (nymph) embedded in piece of Baltic amber (dimensions in mm: 14 x 10 x 4), Denmark, 28.iii.1968, A.K. Andersen; deposited in ZMUC.

Specimen No. 2, almost complete specimen (nymph) embedded in piece of Baltic amber (dimensions in mm: 6 x 5 x 1), Denmark, 28.iii.1968, A.K. Andersen; deposited in ZMUC.

Descriptive notes

Specimen No. 1 (Figs 24, 116-117) is probably a fourth instar nymph. Length (abdomen extended) 4.65 mm; greatest width (across mesothorax) 2.05 mm. Head length 0.60 mm, width (across eyes) 1.23 mm. Lengths of antennal segments 1-4: 0.63, 0.45, 0.58, and 1.00 mm; first antennal segment slender and slightly curved. Pronotum length 0.53 mm, width 1.08 mm. Mesonotum length 1.60 mm. No wing pads. Lengths of leg segments (femur, tibia, tarsus): front leg: 1.08, 1.15, and 0.48 mm; middle leg: 3.15, 2.78, and 1.70 mm; hind leg: 2.78, 1.43, and 0.73 mm. Front and middle femora of equal width, hind femora distinctly thinner. Ventral side of abdomen abraded.

Specimen No. 2 is probably a third instar nymph. Length (abdomen contracted) 1.98

mm; greatest width (across mesothorax) 1.25 mm. Head length 0.63 mm, width (across eyes) 0.98 mm. Lengths of antennal segments 1-4: 0.25, 0.23, 0.25, and 0.30 (?) mm. Pronotum length 0.35 mm. Mesonotum length 0.65 mm. Without wing pads. Lengths of leg segments (femur, tibia, tarsus): front leg: 0.75, 0.80, and 0.25 (?) mm; middle femur 1.58 mm and hind femur 1.45 mm, both femora thickened; tibiae and tarsi abraded.

Geological horizon

Baltic amber. Eocene/Oligocene, 40-35 Ma.

Distribution and palaeoecology

Denmark (see map, Fig. 3). Accounts of the palaeoenvironment of Baltic amber insects are given by Larsson (1978) and Poinar (1992).

Remarks

I believe that specimen No. 1 is a fourth instar nymph for the following reasons: pronotum is shorter than the head and there are no wing-pads (Figs 24 and 115). Specimen No. 2 is poorly preserved, but may be a third instar nymph. The swollen leg segments of this specimen are judged to be caused by taphonomic processes. Based on comparison with descriptions of all nymphal instars of western Palearctic *Aquarius*, *Gerris*, and *Limnoporus* (Vepsäläinen & Krajewski 1986; Zimmermann 1987), I classify these gerrids as belonging to the genus *Gerris s.lat.* based on the following characters: first antennal segment distinctly shorter than second and third segments together; fourth segment longer than first segment; middle femur longer than hind femur; middle tibia shorter than middle femur.

Specimen No. 1 compares most favourably with fourth instar nymphs of *Gerris* (*Gerriselloides*) *asper* (Fieber) or *G. (G.) lateralis* Schummel. These pondskaters are wing dimorphic, with macropterous and micropterous (short-winged) adult morphs. The fourth and fifth instar nymphs of the latter morph have distinctly

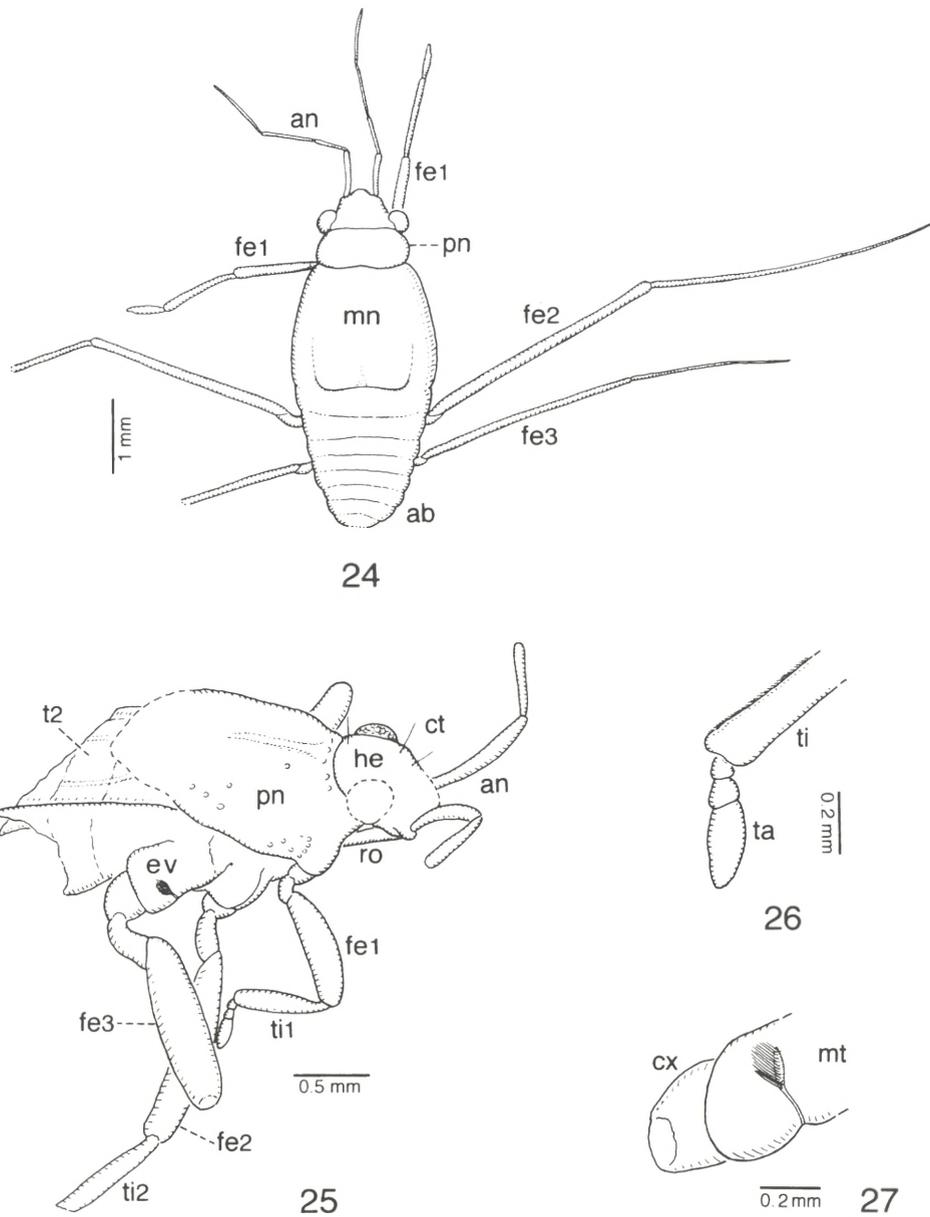


Fig. 24. *Gerris* sp. nymph, dorsal view. Figs 25-27. *Electrovelia baltica* gen. et sp. nov. 25, Holotype, oblique lateral view; abdomen, two distal antennal segments, and tibiae and tarsi of middle and hind legs missing. 26, apex of fore tibia and fore tarsus. 27, metacymbium and hind coxa with evaporative structure of metathoracic scent apparatus.

reduced wing-pads like the specimens from Baltic amber. If specimen No. 1 is a fourth

nymphal instar, then the adult body length of the species can be estimated as 10-12 mm.

Family VELIIDAE Brullé

Water crickets, riffle bugs

Subfamily Veliinae Brullé

Genus *Electrovelia* gen. nov.

Type species: *Electrovelia baltica* sp. nov.; by present designation.

Diagnosis and description

Small water striders, length about 5 mm. Colouration predominantly dark brownish.

Head (Fig. 25, he) moderately deflected in front of eyes. Three pairs of cephalic trichothria (ct); one pair inserted close to pronotal margin, the other two pairs inserted anterior to the eye margins. Eyes large, globular; ocelli absent. Antennae probably four-segmented, first segment stout, slightly longer than head. Rostrum (ro) relatively long and slender, reaching mesosternum.

Thorax. Pronotal lobe (Fig. 25, pn) large, pentagonal, covering meso- and metanotum. Meso- and metapleura relatively short; acetabula (composed of supracoxal lobes) prominent, inserted laterally on body. Meso- and metasternum relatively large. Metasternal scent channel curved forward and leading laterally to scent evaporatoria on metacetabula (Figs 25 and 27, ev), each provided with a tuft of hairs. Only apterous adult form known.

Legs. Front femora (Fig. 25, fe1) rather stout; tibia (ti1) broad, without grasping comb (female only?); tarsi (Fig. 26, ta) with three segments, basal two segments very short; claws not visible but judging from the shape of the last tarsal segment probably inserted preapically on the latter. Middle femora (Fig. 25, fe2)

about as thick as, but distinctly longer than front femora. Hind femora (fe3) as long as middle femora but slightly more incrassate.

Abdomen incomplete. Basal abdominal mediotergites (Fig. 25, t2) with a median pair of longitudinal ridges or carinae. Structure of posterior abdomen including genital segments, unknown.

Distribution and geological horizon

Baltic amber, Denmark (see map, Fig. 3). Eocene/Oligocene, 40-35 Ma.

Remarks

The deflected head, presence of metasternal scent channels and evaporatoria, relatively stout middle and hind femora, and apparently preapical claws, unequivocally place this genus in the family Veliidae (Andersen 1982b). The three-segmented front tarsi, relatively long and slender rostrum, and large pronotal lobe (even in the apterous form), justify the placement of *Electrovelia* in the subfamily Veliinae. The type species, *E. baltica*, is relatively small (estimated body length about 5 mm) compared to most veliines. On account of the presence of longitudinal ridges or carinae on the basal mediotergites of abdomen, the fossil species is seemingly more close to the New World genus *Paravelia* (and related genera) than to the widespread Palearctic genus *Velia* Latreille. The incomplete state of the material, however, does not permit an evaluation of its closer relationships.

Electrovelia baltica sp. nov.

(Figs 25-27, 115)

*Material examined**Holotype*

Incomplete specimen (Fig. 115), embedded in piece of Baltic amber (dimensions in mm: 13 x 13 x 4), Denmark, 22.xi.1961, C.V. Henningsen leg. Holotype deposited in ZMUC.

Description

Holotype. Apterous adult specimen, probably a female (Figs 25 and 115); head, thorax, basal segments of abdomen, and most of the appendages preserved. General colour dark brownish, but most of insect covered with greyish debris.

Head (Fig. 25, he) relatively short and broad, length 0.53 mm, width across eyes 0.75 mm; anterior part of head distinctly deflected. Eyes globular, 0.18 mm wide. Only basal two antennal segments (an) preserved; length of segments 1-2: 0.73 and 0.58 mm; first segment rather stout, curved. Rostrum (ro) long and slender, segments 3+4 measuring 0.95 mm, apex reaching mesosternum. *Thorax.* Pronotum (Fig. 25, pn) with large pentagonal lobe covering meso- and metanotum, length 1.43 mm, greatest width 1.20 mm; antero-lateral corners prominent. Pronotal lobe with a low median longitudinal ridge in anterior part and

some scattered punctures along anterior and lateral margins. Metacubicular scent evaporatoria large (Figs 25 and 27, ev), with a tuft of long hairs. *Legs.* Front femora (Fig. 25, fe1) relatively stout, 1.05 mm long, 0.25 mm wide; front tibia (ti1) 0.95 mm, straight and relatively broad, without tibial grasping comb; front tarsus 0.45, with three segments (Fig. 26, ta) measuring 0.08, 0.13, and 0.25 mm, respectively; claws not visible. Middle legs incomplete; trochanter 0.38 mm, femur (Fig. 25, fe2) 1.50 mm long and 0.28 mm wide; tibia (ti2, broken) more than 0.4 mm. Hind legs incomplete; trochanter 0.40 mm, femur (fe3) 1.45 mm long and 0.33 mm wide, without ventral spines or teeth. *Abdomen* broken off behind segments 2-3; basal two mediotergites (Fig. 25, t2) with a median pair of longitudinal ridges or carinae.

Geological horizon

Baltic amber, Eocene/Oligocene, 40-35 Ma.

Distribution and palaeoecology

Denmark (see map, Fig. 3). The Palaeoenvironment of Baltic amber insects is thoroughly discussed by Larsson (1978) and Poinar (1992).

Remarks

See under generic heading (above).

Family **HYDROMETRIDAE** Billberg

Marsh treaders, water measurers

Subfamily **Hydrometrinae** Billberg

Genus *Eocenometra* Andersen

Eocenometra Andersen, 1982a: 91-92. – Andersen, 1982b: 250; Carpenter, 1992: 263; Nél & Paicheller, 1993: 81.

Type species: *Eocenometra danica* Andersen, 1982; by original designation and monotypy.

Diagnosis and description

Relatively large water measurers, length 13.2-15.8 mm, with very elongate head and body, and long and slender, almost thread-like antennae and legs. Ground colour chiefly dark brownish or black.

Head (Figs 28-29, he) very slender, longer than thorax (as measured from anterior margin of prothorax to point of insertion of hind legs), but shorter than twice length of pronotum; head in lateral view (Fig. 29) swollen in basal and apical fourths. Antennae very long (Fig. 28, an), at least three times as long as head; first antennal segment thicker than other segments, 0.6-1.1x head length; second segment inserted apically on first segment, but much shorter and more slender than the latter (Fig. 31); third (and possibly also fourth) segment very long, thread-like. Rostrum (Fig. 29, ro) long and slender, subequal to or slightly longer than head length.

Thorax prolonged; pronotum (Figs 28-29, pn) almost two-third of thorax length (measured as above), slightly arched above in lateral view. Points of insertion of legs on thorax almost equally spaced apart longitudinally.

Legs slender and very long (Fig. 28), hind leg about 1.6 times body length; front femur (fe1) distinctly shorter than middle femur (fe2), latter slightly shorter than hind femur (fe3), tibia (ti1, ti2, ti3) of each leg longer than femur; tarsi short and very slender with small, apical claws (Fig. 34).

Wings rather long and narrow, forewing with two distinct longitudinal veins (Fig. 28, fw).

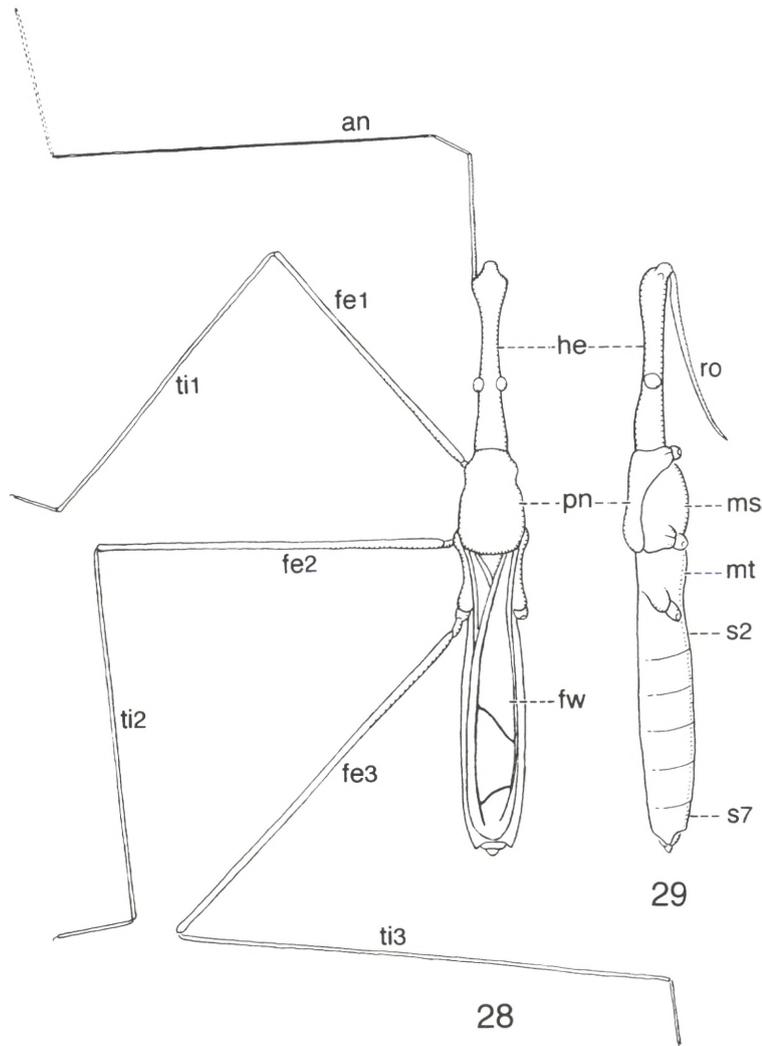
Abdomen (as measured from the point of insertion of hind leg to abdominal end) about two-third of combined length of thorax and abdomen. Lateral hind corner of connexivum slightly produced (Fig. 35). Genital segments of female (s8, pr) small but distinct.

Distribution and geological horizon

Western Limfjord area, northern Denmark (Fig. 5). Ølst and Fur Formations. Paleocene-Eocene transition, 55-54 Ma (Fig. 4).

Remarks

Andersen (1982a) classified *Eocenometra* in the family Hydrometridae which, above all, is characterised by the prolonged state of the head capsule. The phylogeny of the seven extant genera of Hydrometridae was discussed by Andersen (1977a, 1982b) and a cladogram of relationships presented. Species belonging to the subfamily Hydrometrinae have extremely prolonged head, slender body, and very long, almost thread-like antennae and legs. These characters are also shared by *Eocenometra*. Although it is impossible to tell whether the fossil species had other of the autapomor-



Figs 28-29. *Eocenometra danica* Andersen (reconstructions). 28, macropterous female, dorsal view; antenna and legs of right side omitted. 29, macropterous female, lateral view; antennae and legs omitted.

phies of the Hydrometrinae, e.g. absence of metathoracic scent apparatus, Andersen (1982a: 94) classified *Eocenometra* in this subfamily. Its relationships with the four extant hydrometrine genera are more uncertain. The head is not as long relative to the body as in *Dolichocephalometra* Hungerford, *Chaetometra* Hungerford, *Bacillometra* Esaki (Figs 38 and

39), and some species of *Hydrometra* Latreille. The structure of the thorax is more like that of the first three mentioned genera, i.e., the metathorax is not prolonged as in *Hydrometra* (Figs 38 and 40). The first antennal segment of *Eocenometra* is much longer than the second, while it is subequal to or distinctly shorter than the second segment in the four hydrometrine

genera. The antennal structure of *Eocenometra* was judged as plesiomorphic since it is shared with the non-hydrometrine genera, *Veliometra* Andersen, *Heterocleptes* Villiers, and *Limnobates* Hussey. Based upon this evidence, Andersen (1982a) placed *Eocenometra* as sister group of the four extant genera of the Hydrometriinae.

***Eocenometra danica* Andersen**
(Figs 30-35, 107)

Eocenometra danica Andersen, 1982a: 92-93, figs. 1-8. – Andersen, 1982b: 250-251, Plate 15C; Carpenter, 1992: 263; Nél & Paicheller, 1993: 81.

Material examined

Holotype

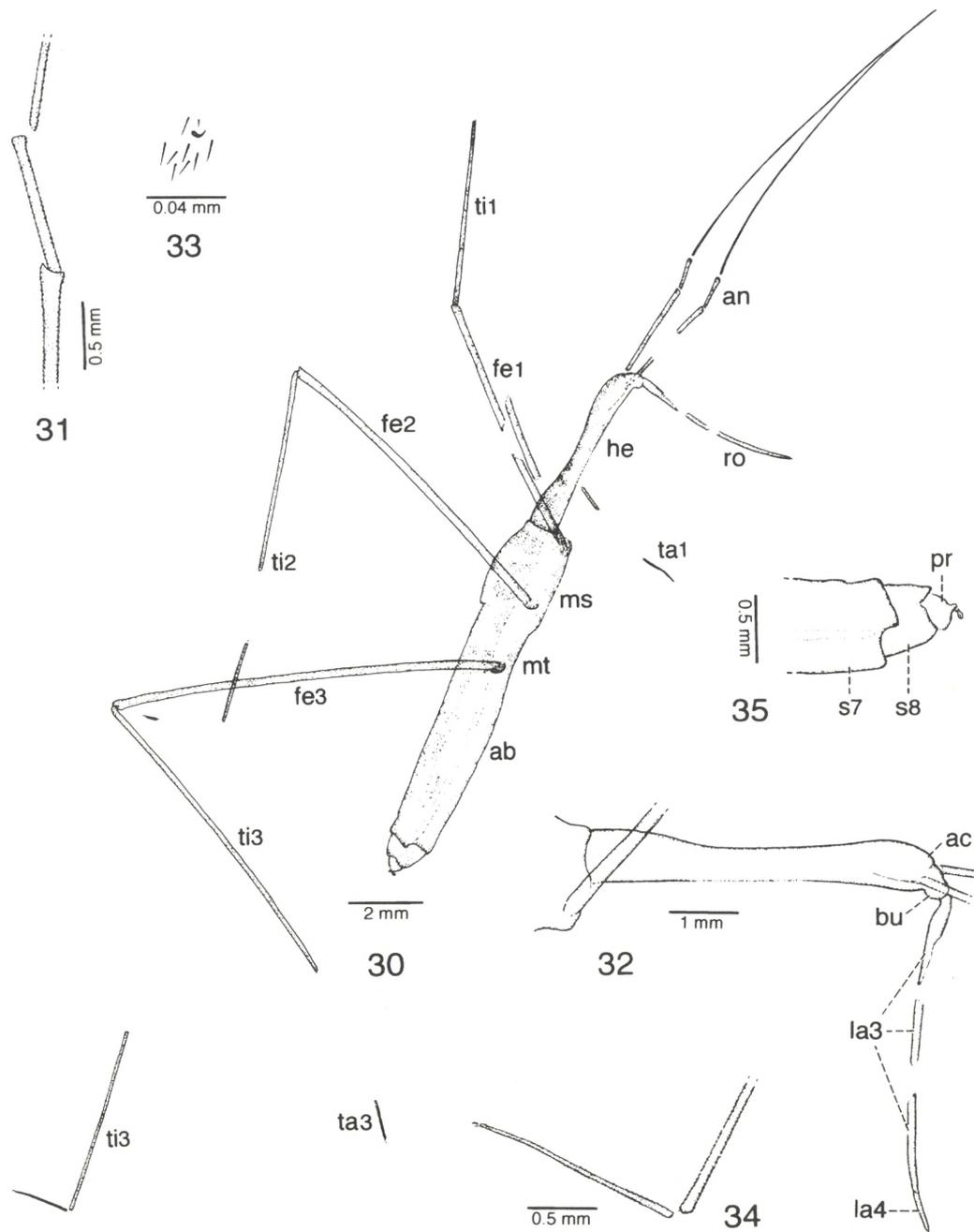
Almost complete specimen, probably a macropterous female (Fig. 107). Locality data: Vester Sundby, Mors, Denmark, 1975, M. Sørensen leg. Part marked "922A", counterpart marked "922B". Geological data: cementstone, probably ash-layer series Nos. +25 to +30. Holotype deposited in GMUC (Nos. MGUH 15912A & B).

Description

Holotype. Almost complete specimen, probably a macropterous female, fairly well preserved in both part (Fig. 107) and counterpart. The insect has been impressed in a lateral position. Cuticular remains blackish; an unpigmented, median longitudinal region present on thorax and abdomen.

Body elongate (Fig. 30), length (from tip of head to end of abdomen) 15.8 mm. *Head* (Fig. 30, he) very long, length 5.0 mm from anterior margin of thorax to apex. Dorsal and ventral outline of head fairly distinct (Fig. 32); exact position of eyes not known and ratio of ante- and postocular parts of head therefore unknown. Anterior region of head slightly

swollen, showing protruding anteclypeus (Fig. 32, ac) and semicircular ventral lobes or bucculae (bu), probably concealing basal segments of rostrum. Traces of pubescence visible in some parts of the head (Fig. 33), composed of slender hairs and a few stouter, hook-shaped hairs. Antennae (Fig. 30, an) inserted close to the apex of head, second and especially the first segment much stouter than third segment, covered by numerous fine hairs (Fig. 31). Lengths of antennal segments 1-3 (perhaps incomplete; segment 4 probably missing): 3.1, 1.0, and 10 mm. Rostrum (Fig. 30, ro) very long and slender, 4.8 mm, slightly swollen at base, tapering to pointed apex; third rostral (or labial) segment (Fig. 32, la3) very long, perhaps more than 6x length of fourth segment (la4). *Thorax* relatively short, length (from anterior margin of prothorax to point of insertion of hind legs) 4.1 mm; length of pronotum 2.8 mm. Distances between points of insertion of front and middle legs 2.0 mm, and of middle and hind legs 1.9 mm. *Legs.* Femora of right side almost intact (Fig. 30): front femur (fe1) 7.5 mm, middle femur (fe2) 9.3 mm, and hind femur (fe3) 11 mm; tibiae incomplete and only approximate lengths can be given: front tibia (ti1) 9 mm, middle tibia (ti2) 10 mm, and hind tibia (ti3) 13 mm; front tarsi (Fig. 30, ta1) and middle tarsi incomplete, but perhaps 1 and 2 mm, respectively; hind tarsus (Fig. 30, ta3) intact, 1.7 mm, very slender, tapering from base to apex (Fig. 34); segments of tarsus (probably three in number) not discernible; claws very small. Leg segments covered with a pubescence of fine hairs. *Wings.* No traces of wings although the specimen probably is macropterous (as indicated by the distinctly arched pronotum). *Abdomen* (Fig. 30, ab) rather high in lateral view, but this may be the result of compression; total length of abdomen (from point of insertion of hind legs to abdominal end) 6.7 mm; an unpigmented, median longitudinal band



Figs 30-35. *Eocenometra danica* Andersen. 30, macropterous female holotype. 31, apex of antennal segments 1 and 2. 32, outline of head, lateral view. 33, chaetotaxy of head. 34, apex of hind tibia and hind tarsus. 35. Abdominal end, lateral view (redrawn from Andersen 1982a).

on the abdomen may indicate the connexival margin; intersegmental sutures of abdomen invisible except for one (probably between sternum 2 and 3). *Genital segments* probably protracted in the specimen at hand. Apex of abdomen (Fig. 35) showing hind margin of segment 7 (s7) with distinctly pointed connexival corner; segment 8 (s8), and proctiger (pr).

Geological horizon

Fur Formation (ash-layer series No. +30). Paleocene-Eocene transition, 55-54 Ma.

Distribution

The holotype is from Vester Sundby, Mors, northern Jutland, Denmark (see map, Fig. 5).

Remarks

The reconstruction of *Eocenometra danica* (Figs 28-19) shows a relatively large hydrometrid (15.8 mm) with extremely long and slender antennae and legs, thereby resembling extant species of the genus *Bacillometra* (see, e.g. Andersen 1982b: fig. 206).

Eocenometra longicornis sp. nov.
(Figs 36-37, 108-109)

Material examined

Holotype

Almost complete specimen, probably a macropterous female (Fig. 108), preserved as compression fossil in two blocks. Locality data: Stolleklint, Fur, Denmark, date and year unknown, H. Madsen leg. Part and counterpart marked "16-3925". Geological data: shale, ash-layer series No. -25. Holotype deposited in GMUC.

Paratype

Almost complete specimen, probably a macropterous female (Fig. 109). Locality data: Stolleklint, Fur, Denmark, date and year unknown,

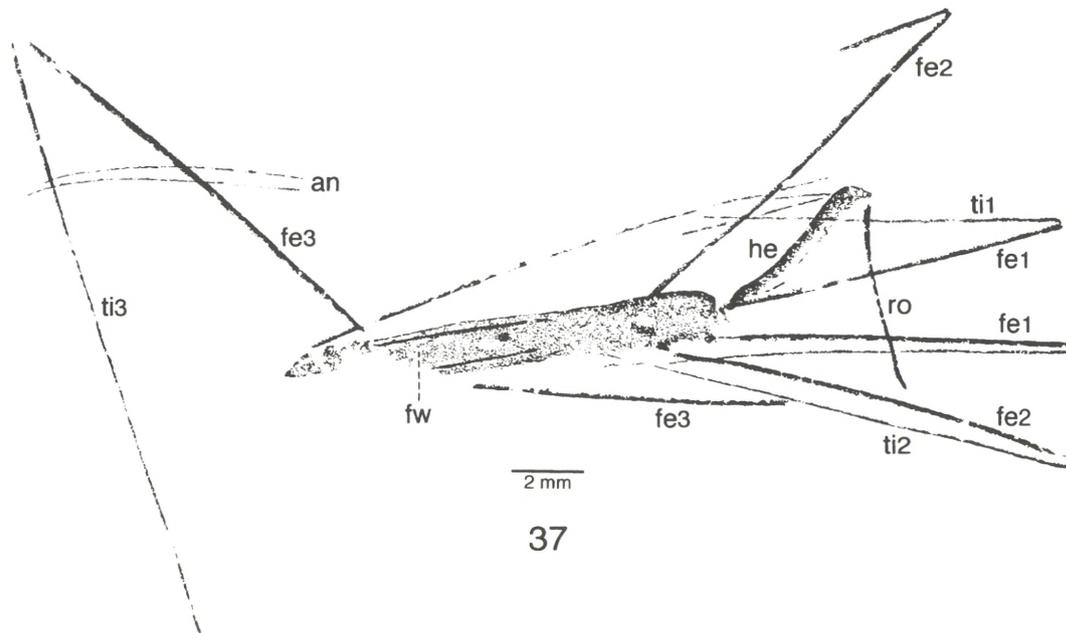
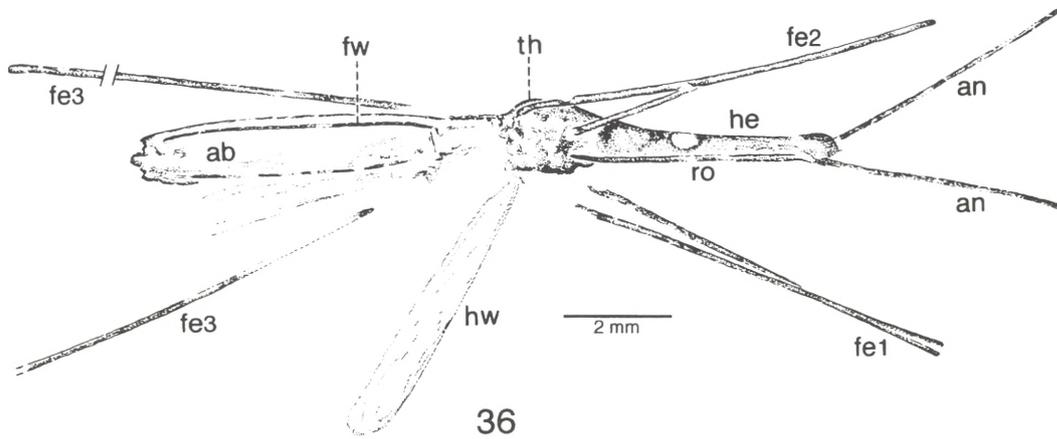
H. Madsen leg. Part marked "16-4634" (no counterpart). Geological data: laminated clay, ash-layer series No. -31 or lower. Paratype deposited in GMUC.

Description

Holotype. Almost complete specimen, probably a macropterous female, fairly well preserved (Figs 36 and 108). Head and thorax impressed in an oblique lateral position, the abdomen in a dorso-ventral position. Cuticular remains blackish.

Body elongate, length (from tip of head to end of abdomen) 13.2 mm. *Head* (Fig. 36, he) fairly distinct and very long, length 4.5 mm from anterior margin of thorax to apex; an unpigmented, roundish area about 1.5 mm in front of thorax probably indicates the position of the compound eye; ratio of ante- and postocular parts of head thus 5 : 3. First antennal segment (an) very long, about 5 mm, much stouter than the other segments; second segment not visible; third segment incomplete but at least 5.5 mm long. Rostrum (ro) closely appressed against ventral side of head, 4.8 mm long. *Thorax* (Fig. 36, th) relatively short, length (from anterior margin of prothorax to point of insertion of hind legs) about 3.5 mm; length of pronotum about 2 mm. *Legs* incompletely preserved. Front femora (Fig. 36, fe1) 7.2 and 7.5 mm; middle femur (fe2) more than 8 mm; and hind femur (fe3) 12.5 mm. Front and middle tibiae not preserved, hind tibia more than 11.5 mm; Tarsi not preserved. *Wings* partly preserved; a pair of dark subparallel lines on top of abdomen (Fig. 36, fw) are probably the two major longitudinal veins of the forewing; an indistinct structure extending laterally from the body (hw) is probably the displaced hind wing. *Abdomen* (Fig. 36, ab) fairly distinct, length about 5 mm; abdominal end showing short, lateral connexival corners and median, blunt proctiger.

Paratype. Probably a macropterous female



Figs 36-37. *Eocenometra longicornis* sp. nov. 36, macropterous female holotype, oblique dorsal view; distal antennal segments omitted and hind femora cut off. 37, macropterous paratype, oblique lateral view.

(Figs 37 and 109). The body is preserved in a dorso-ventral position, the head in an oblique lateral position, slightly inclined in relation to thorax. The abdominal end is partly obscured, but the body length is approximately 13.6

mm. Head (he) 4.6 mm long; only the dorsal outline of the head distinct; first antennal segment 4.1 mm, much stouter than the incompletely preserved antennal segment 3 (an); segment 2 not visible. Rostrum (ro) partly ex-

tended from tip of head, 5 mm long. Boundary between thorax and abdomen indistinct, combined length of thorax and abdomen 9-11.5 mm. Legs incompletely preserved. Front femur (fe1) about 10 mm, middle femur (fe2) 11-11.3 mm, and hind femur (fe3, displaced) 12 mm; front tibia (ti1) 9.5-10.5 mm, middle tibia (ti2) 11.5 mm, and hind tibia 13.5-16.5 (ti3, probably including tarsus); tarsi not visible. Wings (fw) indistinct; a pair of dark, subparallel lines on top of the abdomen is possibly the longitudinal veins of the forewing.

Geological horizon

Ølst and Fur Formations (ash-layer series nos. -25 to -31 or below). Paleocene-Eocene transition, 55-54 Ma.

Distribution

The types are from Stolleklint on the island Fur, northern Jutland, Denmark (see map, Fig. 5).

Remarks

Eocenometra longicornis sp. nov. is slightly smaller (13.2-13.6 mm) than *E. danica* (15.8 mm). This is not an expression of sexual dimorphism (generally, males are smaller than females in hydrometrids) since both types of *E. longicornis* probably are females. The most important distinguishing character of the new species is its distinctly longer antennae, in particular the first segment, which is subequal in length to the head (not nearly so in *E. danica*). The legs are also relatively longer, with middle and hind femora almost as long as the body length.

Subfamily *Limnobotodinae* Esaki

Genus *Palaeometra* gen. nov.

Type species: *Palaeometra madseni* Andersen sp. nov.; by present designation.

Diagnosis and description

Relatively small water measurer, length 5.1 mm, with elongate head and body, and slender antennae and legs. Ground colour chiefly blackish.

Head (Figs 41-42, he) prolonged, slightly longer than thorax (as measured from anterior margin of prothorax to point of insertion of hind legs), almost twice as long as pronotum; head in lateral view swollen in basal and apical parts. Antennae (an) slender, longer than head; first antennal segment probably relatively short, only about one fourth of head length; remaining segments thread-like. Rostrum (ro) slender and long, probably slightly shorter than head length.

Thorax relatively short and stout; pronotum (Figs 41-42, pn) almost two-thirds total length of thorax (measured as above), distinctly arched above in lateral view. Mesothorax (ms) and metathorax (mt) of about the same length; points of insertion of legs on thorax almost equally spaced apart longitudinally.

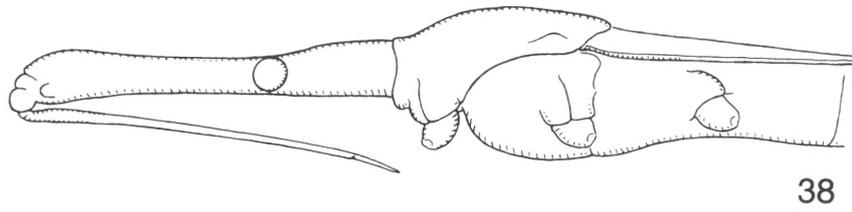
Legs slender; front femur (Fig. 41, fe1) a little more than one fourth of body length; relative length of middle femur unknown; hind femur (fe3) about two fifths of body length; front tibia (ti1) and hind tibia (ti3) very slender, front tibia distinctly longer than front femur; structure of middle tibia and tarsi of all legs unknown.

Wings probably relatively narrow, forewing (Fig. 41, fw) with a few, predominantly longitudinal veins.

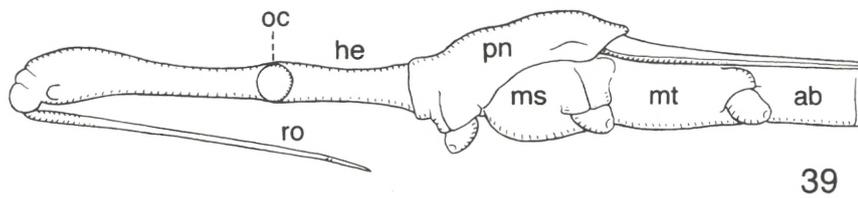
Abdomen (Figs 41-42, ab; as measured from the point of insertion of hind leg to abdominal end) about 0.67x body length (excluding the head), relatively broad. Abdominal end broadly rounded, connexival corners not pointed. Structure of genital segments unknown.

Distribution and geological horizon

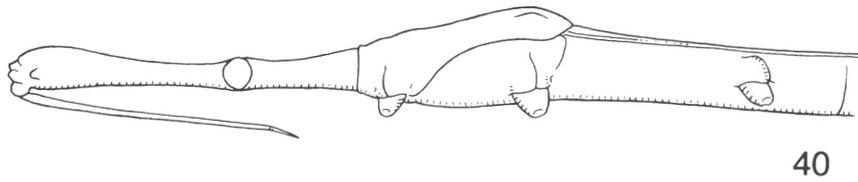
Fur, western Limfjord area, northern Denmark (Fig. 5). Fur Formation. Paleocene-Eocene transition, 55-54 Ma (Fig. 4).



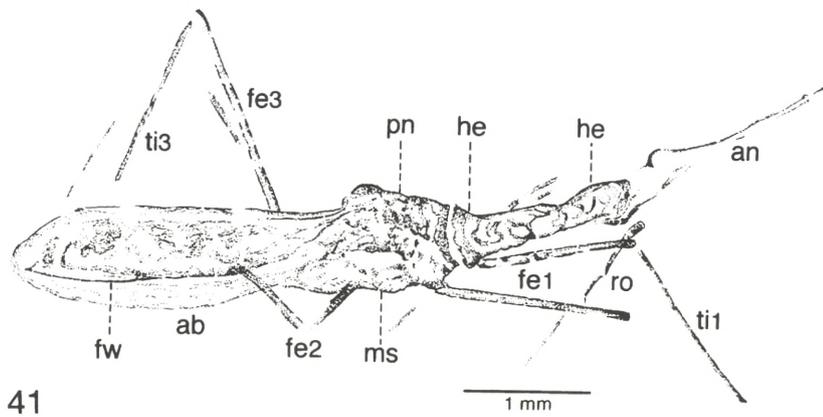
38



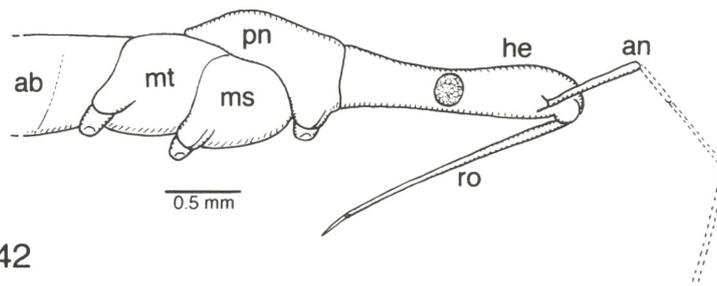
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41



42

Figs 38-40. Head and thorax of fossil and extant Hydrometrinae, lateral view; antenna and legs omitted. 38, *Eocenometra*. 39, *Bacillometra*. 40, *Hydrometra*. Figs 41-42. *Palaeometra madseni* gen. et sp. nov. 41, macropterous holotype, lateral view. 42. Head and thorax, lateral view (reconstruction); legs omitted.

Remarks

The prolonged head capsule with eyes displaced towards middle, elongate thorax, and slender antennae and legs classify *Palaeometra* gen. nov. in the family Hydrometridae. The forewing venation seems to be quite similar to that of the Hydrometrinae (see above), but the head is shorter and the abdomen broader than in most species belonging to this subfamily. Habitually, the fossil genus resembles the extant genus *Limnobatodes* Hussey (1925) and is therefore provisionally classified with this genus in the subfamily Limnobatodinae Esaki (1927).

Palaeometra madseni sp. nov.

(Figs 41-42)

*Material examined**Holotype*

Almost complete macropterous specimen (Fig. 41). Locality data: Stolleklint, Fur, Denmark, 21.i.1994, Henrik Madsen leg. Part and counterpart marked "16-A2920". Geological data: striped cementstone, ash-layer series No. -25. Holotype deposited in GMUC.

Description

Holotype. Almost complete specimen; head, most of thorax, and some leg segments in counterpart. Sex not determined. The insect has been impressed in an oblique lateral position. Cuticular remains blackish. Fig. 41 is based upon the most complete impression supplemented with details from remains preserved in the counterpart.

Body elongate, length (from tip of head to end of abdomen) 5.1 mm. *Head* (Fig. 41, he) prolonged, length 1.5 mm from anterior margin of thorax to apex. Dorsal and ventral outline of head fairly distinct, posterior and anterior parts of head slightly swollen; an unpigmented, roundish area in the middle of the head probably marks the position of the com-

pound eye; ratio between the ante- and post-ocular parts of head 3 : 2.5. Antennae (Fig. 41, an) slender, inserted close to the apex of head, at least 2 mm long but probably incomplete; first antennal segment possibly 0.3-0.4 mm long, the length of other antennal segments unknown. Rostrum (Fig. 41, ro) incomplete, but at least 0.9 mm long and slender. *Thorax* relatively short and stout, length (from anterior margin of prothorax to point of insertion of hind legs) 1.3 mm or slightly shorter than head; pronotum (Fig. 41, pn) distinctly arched dorsally, length about 0.8 mm. Distances between points of insertion of front and middle legs about 0.7 mm, and of middle and hind legs about 0.6 mm. *Legs.* Femora relatively slender: front femora (Fig. 41, fe1) 1.5-1.6 mm, middle femur (fe2) broken and incomplete, but at least 1.5 mm, and hind femur (fe3) about 2.1 mm; tibiae incomplete and only approximate lengths can be given: front tibia (ti1) 1.7 mm and hind tibia (ti3) more than 1.5 mm; tarsi not visible. *Wings.* The distinctly arched pronotum (Fig. 41, pn) suggest that the specimen is macropterous; indistinct traces of forewing (fw) venation on top of abdomen. *Abdomen* (Fig. 41, ab) relatively broad, distinctly widened across middle, rounded apically; total length of abdomen (from the point of insertion of hind legs to the apex) about 2.3 mm. Genital segments not discernible.

Geological horizon

Fur Formation (ash-layer series No. -25). Paleocene-Eocene transition, 55-54 Ma.

Distribution

The holotype was collected at Stolleklint on Fur, northern Jutland, Denmark (see map, Fig. 5).

Remarks

See under generic description (above).

Family **MACROVELIIDAE** McKinstry

Genus *Daniavelia* gen. nov.

Type species: *Daniavelia morsensis* Andersen sp. nov.; by present designation.

Diagnosis and description

Medium-sized gerromorphan bugs, with elongate body and moderately long and slender antennae and legs. Cuticular remains of body dark brownish, legs pale.

Head (Figs 43 and 45, he) elongate, extended in front of eyes, but distinctly shorter than thorax (as measured from anterior margin of prothorax to point of insertion of hind legs). Eyes probably relatively small, distinctly removed from the anterior margin of prothorax (pn). Antennae (an) slender, about half the length of whole insect; first antennal segment distinctly shorter than head, slightly thicker than remaining segments; second and third segment subequal in length to first segment, fourth segment slightly shorter. Structure of rostrum unknown.

Thorax relatively short and stout, about one third length of whole insect, distinctly widened across metaceta-bula. Pronotum (Figs 43 and 45, pn) probably large, with posteriorly extended lobe. Middle legs inserted on thorax slightly closer to hind legs than to front legs. Metaceta-bula (mt) situated laterally on thorax.

Legs moderately slender, femora thickest in basal third, tapering towards apex, without spinous hairs. Front femur (Figs 43 and 45, fe1) about one fifth of the body length, middle femur (fe2) slightly longer, hind femur (fe3) longest, more than two thirds of body length. Tibiae slender, without spinous hairs; front tibia (ti1) and middle tibia (ti2) slightly longer than their respective femora. Tarsi of front and middle legs relatively short, each with three segments (Fig. 44, ta); first tarsal segment very

short, second segment subequal (front leg) or slightly longer (middle leg) than third segment; claws small, falcate, inserted on apex of tarsi (Fig. 44); structure of hind tarsus unknown.

Wings probably relatively broad; forewing (Figs 43 and 45, fw) with a few, predominantly longitudinal veins.

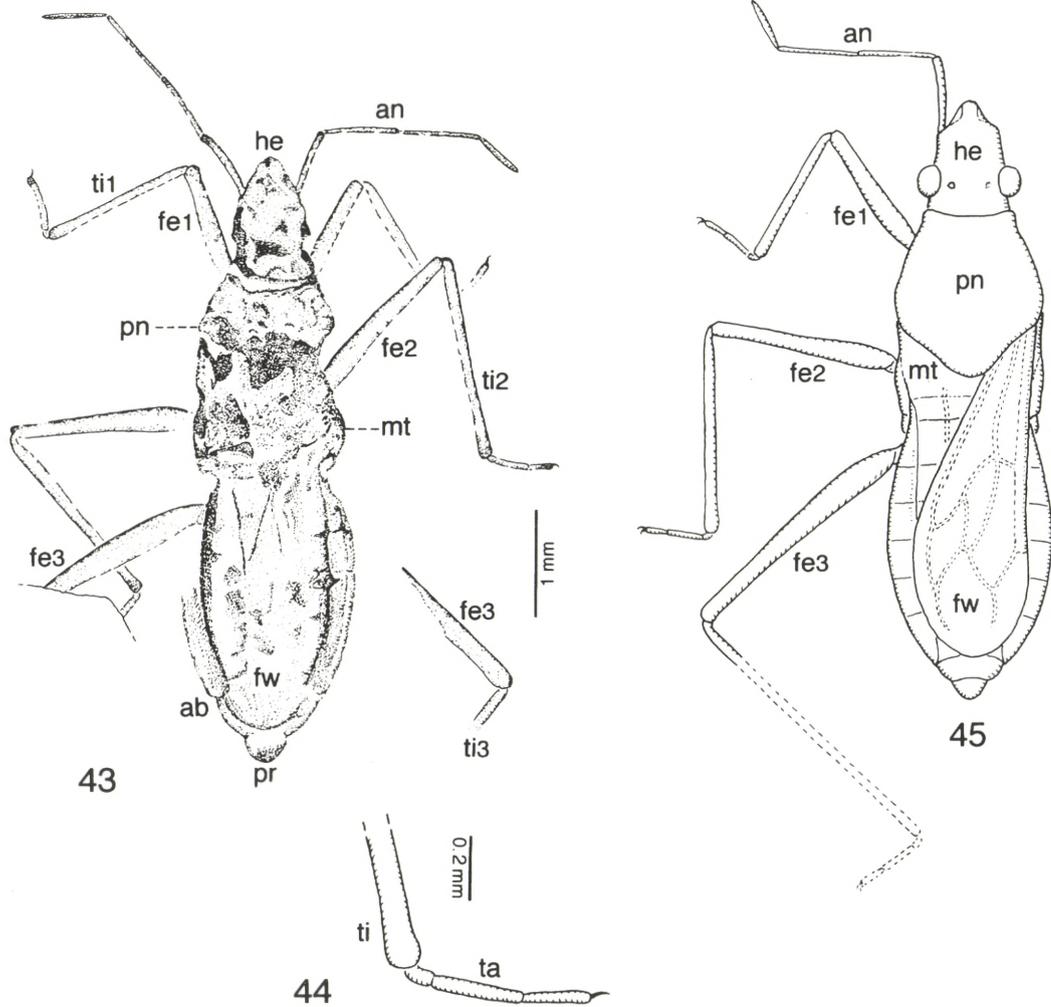
Abdomen (Fig. 43, ab; as measured from the point of insertion of hind leg to abdominal end) almost half length of whole insect, with broadly rounded lateral margins. Abdominal end broadly rounded, connexival corners not prominent. Female genital segment relatively small, proctiger (pr) large and broadly rounded; no signs of large ovipositor.

Distribution and geological horizon

Mors, western Limfjord area, northern Denmark (Fig. 5). Fur Formation, Paleocene-Eocene transition, 55-54 Ma (Fig. 4).

Remarks

A reconstruction of the type-species of *Daniavelia* based on the description above is shown in Fig. 45. The most important features are the elongate head capsule with eyes removed from the anterior margin of prothorax, the large pronotal lobe which covers the mesonotum, the reduced forewing venation, and the relatively slender antennae and legs. The thorax structure excludes the fossil from the family Mesoveliidae. Besides, mesoveliids (e.g. *Mesovelia* spp.) have dark spines on their tibia and a well developed female ovipositor, structures which should be visible on a compression fossil. *Daniavelia* shares many of the characters of the extant species *Macrovelia horni* (Uhler) (Polhemus & Chapman 1979; Andersen 1982b) and may be classified in the family



Figs 43-45. *Daniavelia morsensis* gen. et sp. nov. 43, macropterous female holotype, dorsal view. 44, apex of middle tibia and middle tarsus. 45, macropterous female, dorsal view (reconstruction); antennae and legs of right side and wings of left side omitted.

Macroveliidae. Admittedly, this decision is based on rather weak evidence and since the diagnostic features for the macroveliids (e.g. egg shell with 3-7 micropyles) cannot be observed in fossils, the classification is provisional.

Daniavelia morsensis sp. nov.
(Figs 43-45, 110)

Material examined

Holotype

Almost complete macropterous specimen, probably female (Figs 43 and 110). Locality data: Ejerslev Molergrav, 2.i.1993, Henrik Madsen leg. Part marked "14M-4081" (no counterpart). Geological data: cementstone, ash-layer No. +15. Holotype deposited in GMUC.

Description

Holotype. Almost complete specimen; probably a female impressed in a dorso-ventral position (Figs 43 and 110). Cuticular remains of body dark brown; antennae and legs pale, femora with numerous dark punctures.

Body elongate, length (from tip of head to end of abdomen) 5.7 mm. *Head* (Fig. 43, he) moderately prolonged, length 1.2 mm from anterior margin of thorax to apex. Outline of head (except eyes) fairly distinct, anterior margin protruding, rounded. Positions of compound eyes probably marked by a semicircular indentation on each side of head, slightly anterior to base of head; interocular width of head 0.6 mm. Both antennae (Fig. 43, an) preserved, inserted slightly before apex of head; antennal segments slender, relative lengths of antennal segments 1-4: 0.7, 0.7, 0.75, and 0.6 mm (left) or 0.65, 0.7, 0.75, and 0.5 (incomplete?). Rostrum not visible. *Thorax* relatively short and stout, length (from anterior margin of prothorax to point of insertion of hind legs) 1.8 mm or distinctly longer than head, maximum width (across metacetaabula) 1.4 mm. Pronotum (Fig. 43, pn) indistinct, but probably with large, posteriorly produced pronotal lobe. Distances between points of insertion of front and middle legs about 1.2 mm, and of middle and hind legs about 0.8 mm. *Legs.* All femora preserved, basally thickened (width 0.2-0.25 mm), tapering in width distally; front femur (Fig. 43, fe1) about 1.2 mm, middle femur (fe2) 1.6-1.7 mm, and hind femur (fe3) 2.1 mm. Front tibia (ti1) and middle tibia (ti2)

preserved, length 1.4 and 1.9 mm, respectively. Tarsal structure of front and middle legs distinct (Fig. 44), tarsal length 0.6; length of front tarsal segments 1-3: 0.1, 0.25, and 0.25 mm; length of middle tarsal segments 1-3: 0.1, 0.3, and 0.2 mm. *Wings.* The relatively broad anterior thorax suggests that the specimen is macropterous; possible traces of forewing venation (Fig. 43, fw) on top of abdomen. *Abdomen* (Fig. 43, ab) very broad, distinctly widened across middle (1.6 mm); total length of abdomen (from the point of insertion of hind legs to the abdominal apex) about 2.7 mm. Fairly distinct lateral, longitudinal sutures between mediotergites and laterotergites (together forming the connexivum). Intersegmental sutures indistinct, but lateral indentations towards abdominal apex probably marks the anterior limit of segment 7 (0.4 mm long). Connexiva not forming spines or angular corners posteriorly. *Genital segments* distinctly protruding from abdominal end, proctiger (Fig. 43, pr) broadly rounded.

Geological horizon

Fur Formation (ash-layer series No. +15). Paleocene-Eocene transition, 55-54 Ma.

Distribution

The holotype was collected in Ejerslev Molergrav on Mors, northern Jutland, Denmark (see map, Fig. 5).

Remarks

See under generic description (above).

Other Cenozoic Gerromorpha

Family **GERRIDAE** Leach

Water striders, pondskaters

Subfamily **Gerrinae** Leach

Genus *Limnopor* Stål

Limnopor Stål, 1868: 395-396. – Andersen & Spence, 1992: 756-757.

Type species: *Gerris rufoscutellatus* Latreille, 1807; designation by monotypy.

Diagnosis

Relatively large water striders, length 7.0-19.7 mm. Body elongate and slender. Antennae long, more than half the body length; first segment more than 1.3x head length; second and third segments together at least 1.2x length of first segment; fourth segment longer than third. Adults usually macropterous (long-winged). Pronotal lobe reddish brown; median yellowish stripe of anterior pronotum extending onto pronotal lobe. Metasternal scent orifice circular, not situated on tubercle; metathorax without lateral evaporative grooves. Front femora relatively slender in both male and female. Hind femora distinctly longer than middle femora. Posterior corners of abdominal connexiva produced into long spines. Nymphs (particularly the third and fourth instars) dark with longitudinal pale stripes.

Distribution and habitats

Holarctic. The six extant species have the following distribution (Andersen & Spence 1992): *L. rufoscutellatus* (Latreille): northern Eurasia,

Alaska, and northwestern Canada; *L. genitalis* (Miyamoto): northern Japan, Kurile Islands, and southern Sakhalin; *L. esakii* (Miyamoto): East Asia; *L. dissortis* (Drake & Harris): northern and eastern North America; *L. notabilis* (Drake & Hottes): western North America; and *L. canaliculatus* (Say): eastern North America.

Species of *Limnopor* are typically inhabitants of stagnant freshwater bodies including the most temporary ones (Andersen & Spence 1992). All species except one, *L. canaliculatus*, are monomorphic long-winged, and are known to be strongly migratory with the potential of spreading their reproductive efforts over several habitats, each of a rather temporary nature.

Limnopor wilsoni sp. nov.
(Figs 47-53, 111-112)

Material examined

Holotype. Macropterous male (Fig. 111); complete specimen in lateral view, including most of antennae and legs. Compression fossil in tuffaceous shale. Locality data: Driftwood Creek E. of Smithers, British Columbia, Canada, 1969-71, M. V. H. Wilson leg. Horizon: Middle Eocene. Holotype deposited in ROM (ROM 31036).

Paratypes

No. 1. Fifth instar nymph (Fig. 112); complete specimen in dorsal view, including most of antennae and legs. Compression fossil in tuffaceous shale.

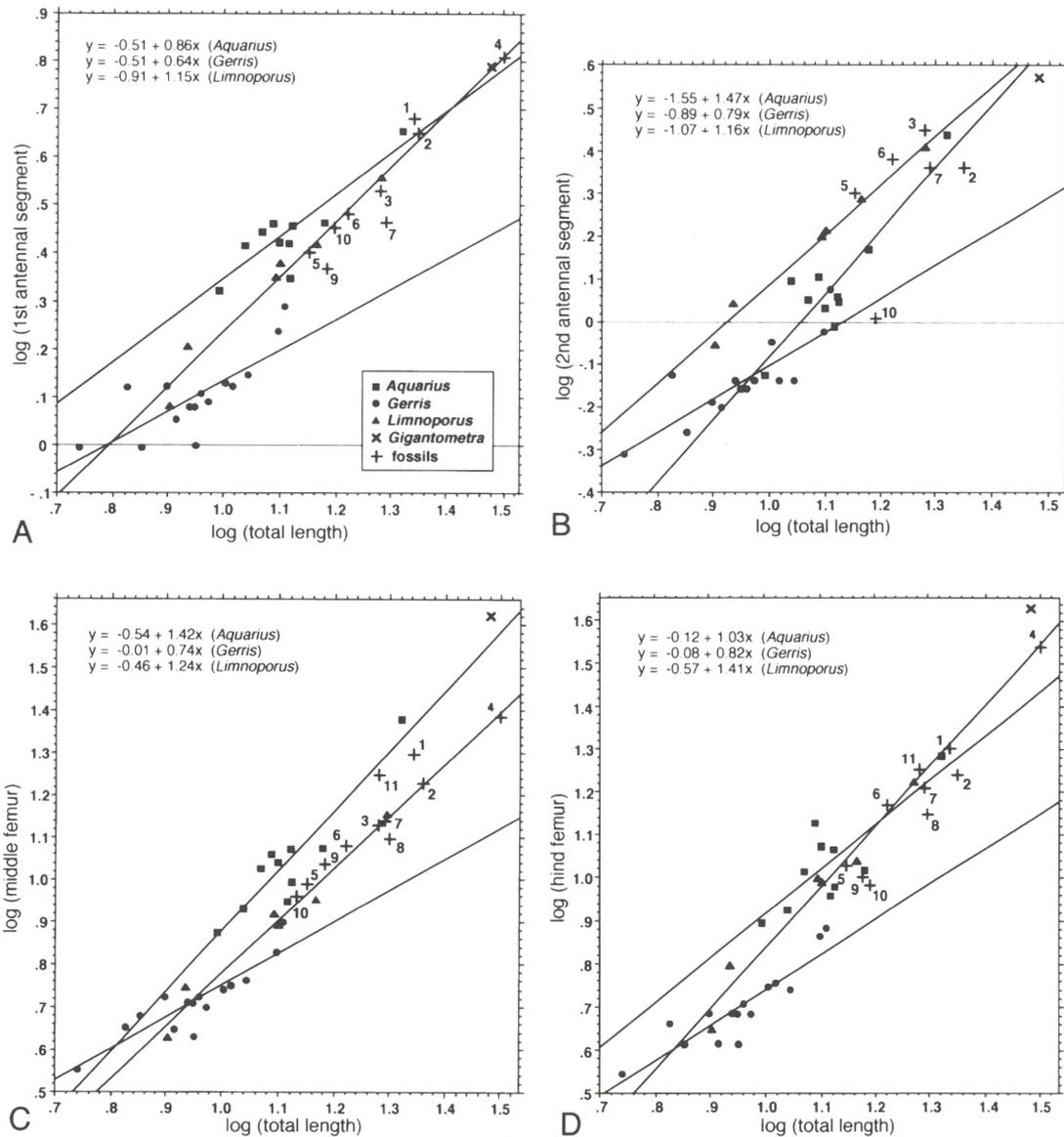


Fig. 46. Measurements of fossil Gerrinae compared with extant *Gigantometra gigas* (China), *Aquarius*, *Gerris*, and *Limnoporus* spp., all plotted against total length (logarithmic scales). Regression lines drawn for extant genera (expressions in upper part of diagram). A, first antennal segment; B, second antennal segment; C, middle femur; D, hind femur. Fossil species nos: 1, *P. furens* sp. nov., holotype; 2, *P. furens* sp. nov., paratype No. 2; 3, *P. furens* sp. nov., paratype No. 3; 4, *Palaeogerris grandis* sp. nov., holotype; 5, *P. mikkelseni* sp. nov., holotype; 6, *P. mikkelseni* sp. nov., paratype No. 2; 7, *Limnoporus wilsoni* sp. nov.; 8, *Telmatrechus stali* (Scudder), type; 9, *T. defunctus* (Handlirsch), specimen from Quilchena; 10, *Aquarius lunpolaensis* (Lin), type; 11, *Aquarius* sp. from Caucasus.

faceous shale. Locality data: Driftwood Creek E. of Smithers, British Columbia, Canada, 1969-71, M. V. H. Wilson leg. Horizon: Middle Eocene. Paratype deposited in ROM (No. 31065).

No. 2. Fifth instar nymph; complete specimen in dorsal view, including most of antennae and legs. Compression fossil in tuffaceous shale. Locality data: Smithers, British Columbia, Canada, date unknown, M. V. H. Wilson leg. Horizon: Middle Eocene. Paratype deposited in Institute of Biological Sciences, University of Edmonton.

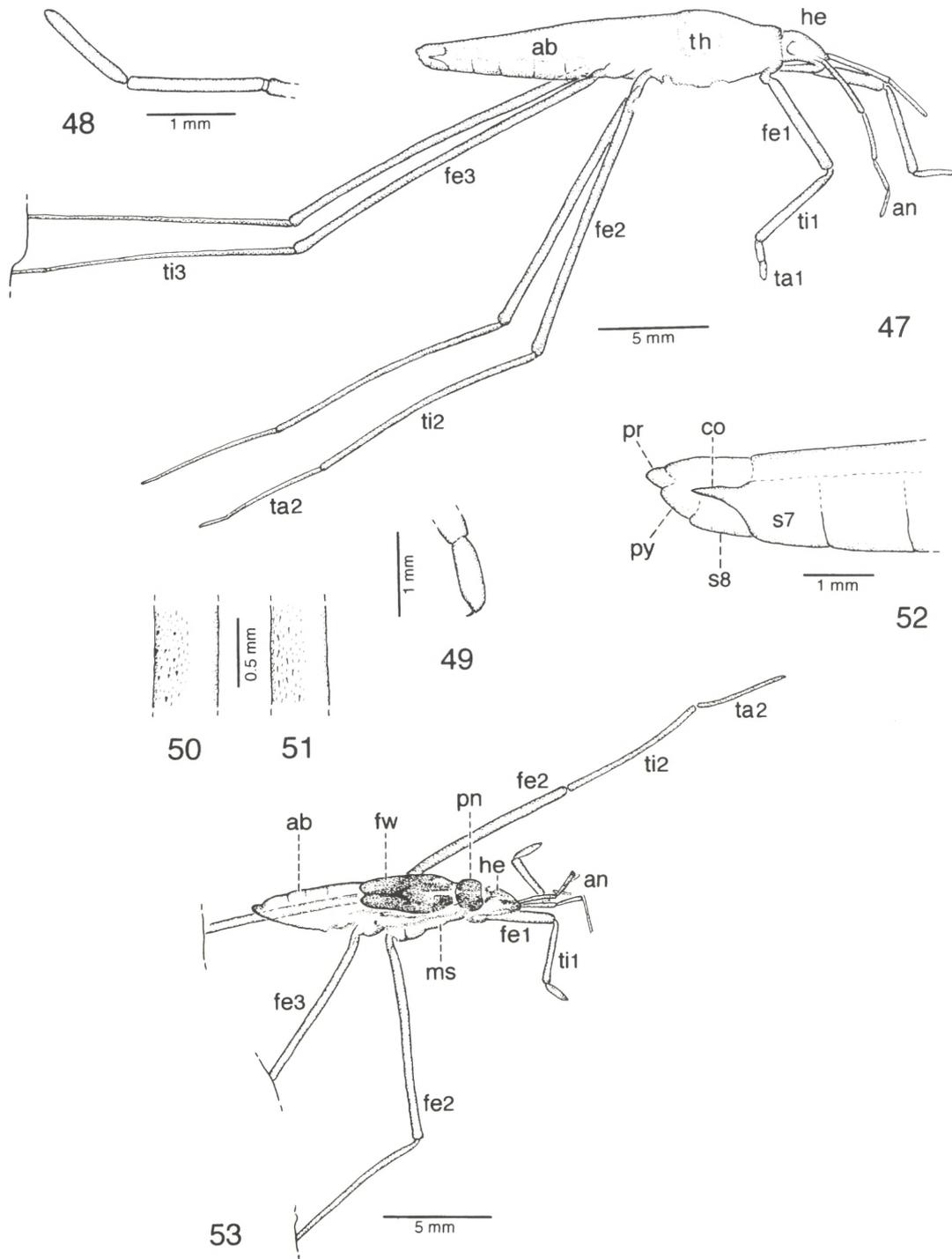
Description

Holotype. Macropterous male preserved in lateral position (Figs 47 and 111). Legs except tarsal segments of hind legs, one antenna, and two basal segments of another antenna present. Cuticular remains black.

Body elongate, length (from tip of head to abdominal end) 19.3 mm. *Head* (Fig. 47, he) relatively short (2.3 mm). Length of antennal segments 1-4: 2.9, 2.3, 1.5, and 1.25 mm; thus, fourth antennal segment slightly shorter than third segment (Fig. 48). Rostrum incomplete, its apex probably reaching anterior part of mesosternum. *Thorax* (Fig. 47, th). Pronotum not well delimited but probably covering mesonotum. Mesothorax relatively long, distance between pro- and mesocoxae 5.2 mm, or about one fourth of body length. Distance between meso- and metacoxae 2.1 mm. *Legs* (Fig. 47). Front femur (fe1) 4.9 mm long and relatively slender throughout, about 0.6 mm wide. Front tibia (ti1) 4.3 and 4.7 mm, straight and slightly widened towards apex. Front tarsi (ta1) 1.9 and 2.0 mm; first and second tarsal segments (Fig. 49) 1.0 and 0.85 mm, respectively. Middle femur (Fig. 47, fe2) 13.7 mm long, or about 0.7x body length, relatively stout, 0.5 mm wide. Middle tibiae (ti2) 11.3 and 11.5 mm long or little more than 0.8x middle femur. Middle tarsus (ta2) 6.3 and 6.5 mm long;

first and second tarsal segments 4.9 and 1.4 mm, respectively. Hind femur (fe3) 16.3 mm or distinctly longer than middle femur; greatest width 0.4 mm. Hind tibia (ti3) 11.5 mm or 0.7x hind femur. Hind tarsus incomplete. Chaetotaxy of middle and hind femora quite distinct (Figs 50-51); there are three kinds of hairs: (1) numerous small, slender hairs which form a dense pile on the entire surface; (2) scattered, larger hairs, chiefly on ventral surface; and (3) scattered spinous hairs on the ventral parts of middle femur. *Wings* not distinct but probably folded over the back of abdomen. *Abdomen* (Fig. 47, ab) relatively long, measuring about 9.1 mm from hind coxae to abdominal end. Intersegmental sutures between sterna fairly distinct; lengths of sterna 4-7: 1.5, 1.5, 1.4, and 1.0 mm; postero-lateral corner of abdominal segment 7 (Fig. 52, s7) produced into a slender connexival spine (co), about 0.7 mm long. *Male genital segments* (Fig. 52) relatively large, protruding from pre-genital abdomen with more than length of sternum 7 (1.6 mm); segment 8 (s8) probably subcylindrical, ventral length slightly less than dorsal length; pygophore (py) partly withdrawn into segment 8; proctiger (pr) small and blunt.

Paratype No. 1. Fifth instar nymph, probably a female, preserved in dorso-lateral position (Figs 53 and 112). Antenna (Fig. 53, an) except distal segments and legs except distal parts of hind legs, present. Cuticular remains brownish; pro- and mesonotum except in middle and wing-pads, blackish. Body elongate, length (from tip of head to abdominal end) 12.1 mm. Head length 1.6 mm. Length of antennal segments 1-3: 2.0, 1.4, 1.0 (?) mm. Rostrum not visible. Pronotum (pn) relatively short, 1.3 mm. Mesonotum (ms) about 2.6 mm long; distance between pro- and mesocoxae 3.4 mm, or a slightly more than one fourth of body length; distance between meso- and metacoxae 1.5 mm. Front femur (fe1) 3.4 mm



Figs 47-53. *Limnoperus wilsoni* sp. nov. 47, macropterous male holotype, lateral view. 48, distal antennal segments. 49, apex of fore tarsus. 50, chaetotaxy of middle femur. 51, chaetotaxy of hind femur. 52, abdominal end. 53, fifth instar nymph (paratype), dorsal view.

long, moderately thickened, 0.5 mm wide. Front tibiae (ti1) 2.9 and 3.1 mm, straight and slightly widened towards apex. Front tarsus 1.2 mm. Middle femur (fe2) 9.2 mm long, or about 0.75x body length, relatively stout, 0.4 mm wide. Middle tibia 7.0 mm long or about 0.75x middle femur. Middle tarsus (ta2) 4.4 mm long; tarsal segments not differentiated. Hind femur (fe3) incomplete but more than 7.9 mm long; not as thick as middle femur. Hind tibia and tarsus incomplete. Forewing-pads (fw) distinct, 2.1 mm long. Abdomen (ab) extended, measuring 4.9 mm from hind coxae to abdominal end. Intersegmental sutures between abdominal terga partly visible. Genital segments indistinct, proctiger small, blunt.

Paratype No. 2. Fifth instar nymph, probably a male, preserved in dorsal position. Antenna and legs except hind tibia and tarsus of left side, present. Cuticular remains brownish; pro- and mesonotum except in middle and wing-pads, blackish. Description and measurements made from photograph (courtesy of M. V. H. Wilson, Edmonton). Body elongate, length 13.3 mm. Head length 1.5 mm. Length of first antennal segment 2.3 mm, second and third segments together 2.7 mm, and fourth segment 1.1 mm. Pronotum relatively short, 1.4 mm. Distance between pro- and mesocoxae 3.3 mm, or about one fourth of body length. Front femur 3.7 mm long, moderately thickened. Front tibia 3.3 mm, straight and slightly widened towards apex. Front tarsus 1.4 mm. Middle femora 10 and 10.4 mm long, or about 0.75x body length, relatively stout. Middle tibia 7.8 mm long or 0.75x middle femur. Middle tarsus 4.8 mm long. Hind femora 10.4 and 11 mm long. Hind tibia and tarsus together 10 mm long. Forewing-pads distinct, about 3 mm long. Abdomen extended, measuring 5.2 mm from hind coxae to abdominal end. Genital segments indistinct, proctiger blunt.

Geological horizon

Lower/Middle Eocene, 52-47 Ma (Wilson 1977, 1978a).

Distribution and palaeoecology

Driftwood Creek E. of Smithers, British Columbia, Canada (see map, Fig. 2). Lacustrine environment. At this locality, Wilson (1977: 1143) states that "the water striders are one of the most common insects." The Eocene insect fauna of British Columbia contains representatives of 30 families in seven orders (Wilson 1977, 1978a). In numbers of individuals it is dominated by Bibionidae (Diptera) of the genus *Plecia*, although locally Gerridae, large Homoptera, and Ichneumonidae (Hymenoptera) are abundant. According to palaeobotanical evidence, the Middle Eocene climate in British Columbia was warm temperate, with wet summers and dry winters (Wilson 1978a).

Remarks

The holotype and paratype No. 1 were illustrated by Wilson (1977: 1143-1144, figs 3 B, C.) and identified as belonging to the water strider subfamily Gerrinae. Based on detailed comparison with extant species, Andersen *et al.* (1993) placed them in the genus *Limnoporus*. The adult male specimen (Fig. 109) compares favourable with species of this genus (in particular *L. notabilis*). The second and third antennal segments taken together are clearly longer than the first segment. The antenna, however, are not quite half as long as the body length and the fourth antennal segment is shorter than the third segment. The fossil shares the following characters with members of the *L. rufoscutellatus* group (*L. dissortis*, *genitalis*, *notabilis*, and *rufoscutellatus*): (1) first middle tarsal segment more than half the length of middle tibia, and (2) hind tibia subequal in length to middle tibia.

Paratype No. 2 was illustrated by Wilson (1988: fig. 9C; 1996: fig. 18.2E). The two fifth

instar nymphs from Smithers compares favourably with samples of fifth instar nymphs of *L. notabilis*, except that the middle and hind femora are distinctly longer. However, the relative shortness of the first antennal segment as compared with the second and third antennal segments, and the apparent overall slimness of the body excludes the fossil nymph from the genus *Aquarius* (see below).

To further clarify relationships of *L. wilsoni* sp. nov. to extant members of the *L. rufoscutellatus* group, Andersen *et al.* (1993) undertook a principal component analysis (PCA) using 19 linear measurements that could be made on the fossilised adult specimen. Most measurements of the fossil are correlated with its large size, and so the first principal component score of the fossil compares favourably with those for *L. notabilis* males. Length of the fourth antennal segment loaded most heavily on the second PCA axis. Although the second axis explains only about 6% of the variation in the data set, the score for the fossil clearly separates it from any of the four modern species.

Wilson (1977: fig. 3D) also illustrated a second water strider nymph from Driftwood Creek E. of Smithers, British Columbia (Royal Ontario Museum No. 31057), which he (with some reservation) classified as belonging to the family Veliidae. Judging from the illustration, however, this specimen clearly belongs to the Gerridae on account of its long and slender middle and hind legs, shape of body, etc. The size (about 5 mm) and absence of distinct wing-pads indicate that the specimen could be a third instar nymph of *L. wilsoni* sp. nov.

Genus *Telmatrechus* Scudder

Telmatrechus Scudder, 1890: 351. – Andersen, 1982b: 415.

Type species: *Hygrotrechus stali* Scudder, 1879; subsequent designation (Andersen 1982b: 415).

Diagnosis

Relatively large water striders, length 15.0-19.8 mm. Body elongate (Fig. 55) but usually more robust than in *Limnoporus* or *Palaeogerris* gen. nov. Antennae (an) subequal to or shorter than half the body length; first segment more than 1.3x head length; second and third segments together subequal in length to first segment; third segment shorter than second. Pronotal lobe (pn) long with posterior margin broadly rounded. Adults wing dimorphic, apterous (wingless) or macropterous (long-winged). Front femora (fe1) relatively robust. Middle tibiae (Fig. 54, ti2) subequal to or slightly shorter than middle femora (fe2). Hind (fe3) femora subequal to middle femora. Posterior corners of abdominal connexiva produced into short spines (co).

Distribution and geological horizon

British Columbia, Canada, and Wyoming, U.S.A. (see map, Fig. 2). Lower/Middle Eocene, 52-47 Ma.

Remarks

Scudder (1890) erected the genus *Telmatrechus* stating that it is “closely related to *Hygrotrechus* Stål [= *Aquarius* Schellenberg], and, combining as it does many of the features of this genus and *Limnotrechus* Stål [= *Gerris* Fabricius], may well have been the lineal predecessor of both.” (Scudder 1890: 351). The distinguishing characters mentioned by Scudder were: first antennal segment only a little longer than second segment; eyes not prominent; thorax relatively shorter than in *Aquarius*; legs very long with tibiae of each pair of legs about as long as the femora of the same legs, posterior lateral edges of abdominal segment 7 produced, forming connexival spines.

Species of *Telmatrechus* share the large body size, middle tibiae being almost as long as middle femora, and presence of connexival spines, with most extant species of *Aquarius* and *Lim-*

noporus species. If Scudder's interpretation of antennal structure is correct, *Telmatrechus* differs from *Aquarius* in the relatively longer second antennal segment and from *Limnoporos* in the middle and hind femora being subequal in length.

Handlirsch (1910: 126) stated that "The genus *Telmatrechus* established by Scudder on this species [*Gerris stali*] is not well founded". However, the antennal structure does not justify the synonymisation of *Telmatrechus* with *Aquarius*.

Telmatrechus stali (Scudder)

Hygrotrechus stali Scudder, 1879: 183-184B.

Telmatrechus stali (Scudder, 1879). – Scudder, 1890: 351-353, Plate 2, figs. 11 and 12.

Descriptive notes

The type specimens of this species are from British Columbia, Canada, and were collected three miles up the north fork of the Similkameen River (Scudder 1879). Scudder (1890) gives a fairly detailed description of his species based upon two adult and one immature specimen. He gives the body length as 19.75 mm, stating that "The insect is of about the same size as our *H[ygrotrechus] remigis* (Say)". However, *Aquarius remigis* measures only 11.5-16 mm (Andersen 1990). The antennae are characterised as being nearly (perhaps quite) as long as the head and thorax together (6.5 mm). and (Scudder 1890: 351-352) "the first antennal joint would seem, from the position of the others, to be shorter than in *Hygrotrechus*". The front femora are described as "stout", 5 mm long, as long as front tibiae. The middle and hind legs are "very slender" with the following dimensions: middle femur, 12.5 mm; middle tibia, 14 mm; hind femur, 14 mm; and hind tibia, 11 mm. Scudder finds traces of wings on both adult specimens, but his illustrations (1890: plate 2, figs. 11 and 12) do not show this very clearly and the specimens could equally

well be apterous. The abdominal end of one adult specimen (1890: plate 2, fig. 11) seems to be distorted and the "pair of stout lappets" probably represents the proctiger and the gonapophyses of the female. The connexival spines are distinct, but since the genital segments seems to be extended in the specimen illustrated by Scudder (1890: plate 2, fig. 11), the spines probably surpass the middle of the first genital segment.

Geological horizon

Lower/Middle Eocene, 52-47 Ma (Wilson 1977, 1978a).

Distribution and palaeoecology

Similkameen River, British Columbia, Canada (see map, Fig. 2). The Eocene insect fauna of British Columbia was described by Wilson (1977, 1978a). According to palaeobotanical evidence, the Middle Eocene climate in British Columbia was warm temperate, with wet summers and dry winters (Wilson 1978a).

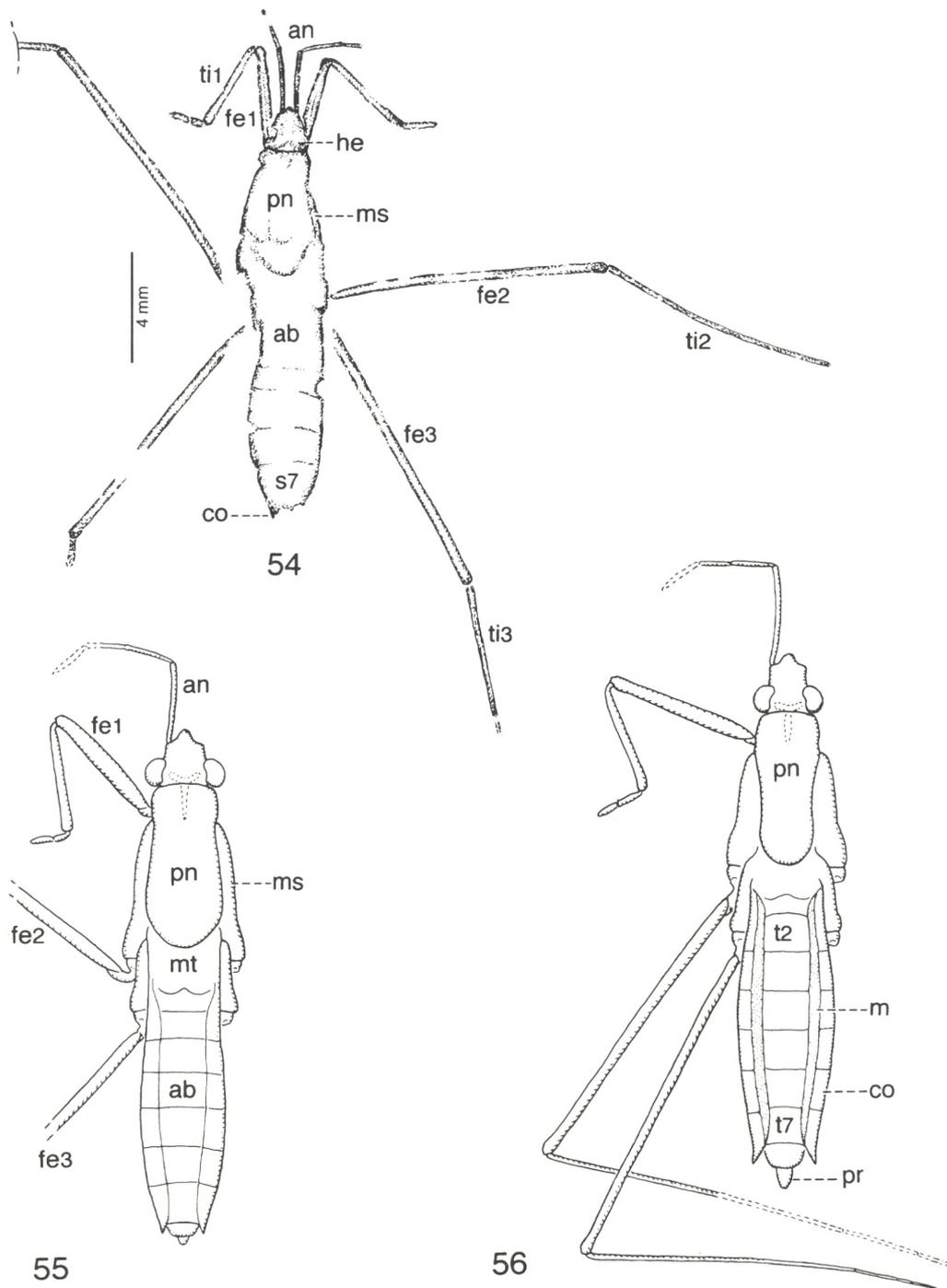
Telmatrechus parallelus Scudder

Telmatrechus parallelus Scudder, 1890: 353, Plate 4, fig. 1.

Descriptive notes

Original description (Scudder 1890) based on two specimens from Twin Creek [Green River], Wyoming, U.S.A. Scudder (1890: 353) states that this species "differs markedly from the preceding [*T. stali*] (with which it agrees in size) in the almost perfectly parallel sides of the abdomen". Scudder gives the following measurements for this species: length of body, 20 mm; width of thorax, 2.75 mm; front femora, 5-5.5 mm; front tibiae, 5-5.5 mm; middle femora, 11-13 mm; hind femora, 13-15 mm.

Judging from the illustration of one specimen (Scudder 1890: plate 4, fig. 1), I suggest that the relatively narrow abdomen is an arti-



Figs 54-56. *Telmatrechus defunctus* (Handlirsch). 54, apterous female from Quilchena, dorsal view. 55. Apterous female, dorsal view (reconstruction); distal parts of middle and hind legs of left side and antenna and legs of right side omitted. Fig. 56. *Aquarius lun-polaensis* Lin; apterous female, dorsal view (reconstruction); antenna and legs of right side omitted.

fact because most of the lateral parts of the abdominal tergites (the laterotergites) are missing.

Geological horizon

According to Wilson (1978a: 14), the Green River Formation, Wyoming, ranges in age from the Lower Eocene to Middle Eocene, 52-47 Ma.

Distribution and palaeoecology

Twin Creek [Green River Formation], Wyoming, U.S.A. (see map, Fig. 2). Wilson (1978a: 14-15, table 1) provides an overview of the insect faunas of the Green River Formation. Palaeobotanical evidence suggests that climates during the deposits of this formation ranged from tropical to subtropical.

Telmatrechus defunctus (Handlirsch) comb. nov.
(Figs 54-55, 113-114)

Gerris defuncta Handlirsch, 1910: 126-127, figs 34-35. – Nel & Paicheler, 1993: 81.

Descriptive notes

Handlirsch (1910) described this species from an almost complete specimen (including counterpart) from Quilchena, British Columbia, Canada, which he said (p. 126) “doubtless represents an apterous form, the body, including the head, measuring 15 mm in length.” Antennal segment 1 much longer than head; antennal segments 1 and 3 subequal, both about one third longer than segment 2. Front femur barely one third length of middle femur, slightly longer than front tibia. Middle femur as long as thorax and abdomen together; middle tibia about two fifths length of femur. Hind femur as long as head and body together; hind tibia barely two thirds of femur. Abdomen exhibits the slightly projecting corners of the preanal (7th) segment.

I have photographs (Figs 113-114; courtesy of Rolf Mathewes, Simon Fraser University,

Canada) of another specimen from Quilchena, collected in 1988. The essential features of this (probably apterous) specimen are depicted in Fig. 54. Body length is about 15 mm. Length of head (he) 1.6 mm. Pronotum (pn) is not well defined but probably measures about 4.5 mm. The abdomen (ab; as measured from the hind margin of pronotum to its apex) is about 9 mm long. Antennae (an) incomplete, antennal segments (1-3): 2.3, 1.5, and 0.6 mm (possibly incomplete). Both front legs are preserved; front femur (fe1) 3.8 mm, front tibia (ti1) 3.3, front tarsus 1.2 mm (first and second tarsal segment 0.7 and 0.5 mm, respectively). Middle legs incomplete; femora (fe2) measuring 10 and 11 mm, middle tibia (ti2) more than 8 mm long. Hind legs incomplete; femur (fe3) 10 mm, hind tibia (ti3) more than 5 mm long. The structure of the abdominal end is obscured, but there seems to be a very short connexival spine (co).

Geological horizon

Lower/Middle Eocene (not Oligocene as stated by Nel & Paicheler 1993), 52-47 Ma (Wilson 1977, 1978a).

Distribution and palaeoecology

Recorded from Quilchena [near Merritt], British Columbia, Canada (Handlirsch 1910) (see map, Fig. 2). Lacustrine environment (Wilson 1977; 1978a).

Remarks

Handlirsch (1910: 127) ends his description of this species by stating that: “These dimensions sufficiently characterise the species, and prove it to be distinct from *G[erris] stali*.” The relatively long first antennal segment and middle tibiae excludes *Telmatrechus defunctus* from the genus *Gerris* (Andersen 1993b). The large and relatively robust body, the relatively long second antennal segment, absence of wings, and the presence of small, but distinct connexival

spines, suggest that this species belongs to the extinct genus *Telmatrechus* rather than any of the extant genera of large, northern temperate water striders (*Aquarius* and *Limnoporus*).

Genus *Aquarius* Schellenberg

Aquarius Schellenberg, 1800: 25. – Andersen, 1990: 45.

Hygrotrechus Stål, 1868: 395. Synonymised by Kirkaldy, 1906: 155.

Type species:

Aquarius: *Cimex najas* De Geer, 1773; subsequent designation (ICZN, Opinion 247/1954).

Hygrotrechus: *Cimex najas* De Geer, 1773; designation by monotypy.

Diagnosis

Relatively large water striders, length 8.0-26.5 mm. Body elongate but usually more robust than in *Limnoporus* or *Palaeogerris* gen. nov. Antennae subequal to or shorter than half the body length; first segment more than 1.3x head length; second and third segments together usually shorter than first segment; fourth segment shorter than third. Adults usually apterous (wingless), rarely macropterous (long-winged) or brachypterous (short-winged). Pronotal lobe uniformly dark; median yellowish stripe of anterior pronotum not extending onto pronotal lobe. Metasternal scent orifice transverse ovate, situated on a tubercle; metathorax without lateral evaporative grooves. Front femora relatively robust, especially in the male, usually uniformly dark. Hind femora usually shorter than middle femora. Posterior corners of abdominal connexiva produced into spines. Nymphs variable in colour, but never dark with longitudinal pale stripes.

Distribution and habitats

Cosmopolitan. The majority of the 17 described, extant species are distributed in Eur-

asia and North America (Andersen 1990). A few species occur in the southern hemisphere, viz. Australia (2 species; Andersen & Weir 1997), Africa, and South America (both with a single species).

Species of *Aquarius* have a rather diverse habitat use, life history, and behaviour (Andersen 1990). Several species are inhabitants of flowing (lotic) freshwater bodies and these are usually wing dimorphic with the flightless (apterous) adult form being much more frequent than the long-winged (macropterous) form. The largest species, *A. elongatus* (Uhler) from East Asia, a monomorphic long-winged species, inhabits stagnant waters and exhibits a complex sexual behaviour (Hayashi 1985).

Remarks

Water striders belonging to *Aquarius* are most easily recognised upon their large and rather robust body, moderately thickened front femora, fairly distinct connexival spines, and above all on the relative lengths of the antennal segments (second and third segments together subequal to or shorter than first segment). The extinct genus *Telmatrechus* (see above) shares several of the characters and may be the sister-group of *Aquarius* (see phylogeny section below).

Aquarius lulpolaensis (Lin) comb. nov. (Fig. 56)

Gerris lulpolaensis Lin, 1981: 345, fig. 1, plate 1.

Descriptive Notes

Lin (1981) described this species from the "grey-yellow paper shale of the Miocene lake deposits", Lulpola Basin, Baingoin county, Xizang [Tibet], China. The type specimen is probably deposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, P.R. China.

The following descriptive notes are chiefly

based on the excellent photograph accompanying the original description (Lin 1981: plate 1). The reconstruction (Fig. 56) has been made from this photograph. The type is a well preserved adult specimen, probably an apterous female, impressed in a dorso-ventral position. All appendages except distal antennal segments, middle tibiae and tarsi preserved. The body length (from tip of head to end of abdomen) is about 15.5 mm, greatest width (across mesoacetabula) about 3.2 mm. Head length 1.6 mm; eyes not visible. Lengths of antennal segments 1-3: 2.8, 1.1, and 0.9 mm (fourth segment absent). Pronotum length about 3.9 mm, pronotal lobe (pn) indistinct but probably covering mesonotum. Lengths of leg segments (femur, tibia, tarsus): front leg: 4.1, 3.1, and 1.5 mm; middle leg: 9.2, >6.5 mm (tibia incomplete, tarsi absent); hind leg: 9.6, 7.4, and 2 mm. Front femora slightly thicker than middle femora which are thicker than hind femora. First and second segments of front tarsi 0.7 and 0.8 mm, respectively. Abdomen 9.2 mm long and 2.7 mm wide; mediotergites separated from laterotergites (connexiva, co) by unpigmented, probably membranous longitudinal band (m) on each side of abdomen. Lengths of abdominal tergites (t2): 1: 0.5 mm; 2-6: each 1.1 mm; and 7: 0.9 mm. Seventh and last laterotergites each produced into a short but distinct connexival spine. Genital segments probably extended, proctiger (pr) elongate.

Geological horizon

Miocene, 24-5 Ma.

Distribution

Lunpola Basin, Baingoin County, Xizang [Tibet], China (see map, Fig. 2).

Remarks

Lin (1981: English summary, p. 348) placed this fossil species in the genus *Gerris*, comparing it with *G. defuncta* Handlirsch and stating that it

differs in the shape of the head, the different structure of the genital segments, and the antennae. In my opinion, however, the Miocene species from Tibet clearly belongs to the genus *Aquarius* based on the following characters (Andersen 1990, 1995c): 1, first antennal segment much longer than 1.3x head length; 2, first antennal segment distinctly longer than second and third segments together; and 3, terminal abdomen with connexival spines. In addition, the size of the fossil (15.5 mm) falls within the known range of body length for extant *Aquarius* spp. (Andersen 1990), but above the range for extant *Gerris* spp. (Andersen 1993b).

A. lunpolaensis (Lin) is superficially very similar to females of the extant water strider species *A. najas* (De Geer), a common inhabitant of flowing waters throughout the western Palearctic region. In this species, the female abdomen swells as the ovarian eggs ripen. This phenomenon is termed *hypogastry* (see Andersen 1982b: 318) and is facilitated by the inflation of membranes connecting the median (mediotergite) and lateral sclerites (laterotergites) of the female abdominal dorsum. The unpigmented, longitudinal bands (Fig. 56, m) separating the mediotergites and laterotergites may indicate the presence of such membranes in the female specimen of *A. lunpolaensis*. The structure of the terminal abdomen is quite similar to that of *A. najas* (see Andersen 1990: fig. 53) which also occurs in an apterous adult form (the most frequent one in most populations of the extant species). The middle and hind femora of *A. lunpolaensis*, however, are relatively shorter in the latter than in *A. najas* (Fig. 46, C-D) which justifies the separate specific status of the Miocene fossil.

Aquarius (?) sp. – Miocene, Caucasus

Material examined

Incomplete specimen, probably an apterous female, labelled "Northern Caucasus, Stavropol,

18 km W Sengeleevskoye lake, Vishniovaya river". Part and counterpart marked "224/39", deposited in PIM.

Descriptive notes

Incomplete specimen, probably an apterous female, preserved in lateral position. Head, anterior thorax, and most of abdomen preserved; body length 19.0 mm. Antennae and front legs missing; middle femur 17.9 mm, middle tibia about 12 mm; hind femur 17.6 mm. Abdomen except anterior part preserved; length of sternites 3 and 4, 1.6 mm, sternite 7, 0.8 mm; connexival spines distinct, pointed, length 0.8 mm, almost reaching end of genital segments.

Geological horizon

Karagan Formation. Miocene, 24-5 Ma (Y. Popov, personal communication).

Distribution

Northern Caucasus, Russia (see map, Fig. 3).

Remarks

The relative lengths of the middle and hind femora (Fig. 46, C-D) compare favourably with females of *Aquarius elongatus* (Uhler) from East Asia (body length 20-26 mm, middle femora 20-24 mm, hind femora 19-21 mm), but the missing information on the antennal structure does not permit a more accurate identification of this fossil.

Subfamily **Electrobatinae** Andersen & Poinar

Genus ***Electrobates*** Andersen & Poinar

Electrobates Andersen & Poinar, 1992: 258-261.

Type species: *Electrobates spinipes* Andersen & Poinar, 1992; by original designation and monotypy.

Diagnosis and description

Small water striders (Figs 120-123), length 2.5-3.6 mm, body subovate. Colouration predominantly black above with pale markings on head and pronotum; ventral surface pale.

Head (Fig. 58) rather long, length in middle about 0.8x greatest width across eyes, widened posteriorly and in front of eyes, with slightly protruding clypeus (cl) on anterior margin. Three pairs of cephalic trichobothria (ct) placed equidistantly on head surface. Eyes globular, only covering antero-lateral angles of pronotum; inner margins slightly sinuated. Ocular setae short, length only about diameter of two eye facets. Antennal tubercles conspicuous, situated in front of and distinctly removed from eyes (Fig. 62). Antennae (Fig. 58, an) slender and long, about 0.8x body length; first segment longest, with three long, subapical spinous hairs; second segment distinctly longer than third, second and third segment together longer than first; fourth segment slender, as long as second segment. Ventral lobes (= gular lobes) of head small. Rostrum short and stout (Fig. 62, ro), its apex extending to prosternum; first and second labial segment subequal in length; third segment straight, about twice as long as fourth segment.

Thorax. Pronotum (Figs 57 and 62, pn) slightly shorter than head in middle; slightly narrower than head including eyes. Mesonotum (mn) about twice as long as pronotum, sides almost straight (male) or broadly rounded (female); posterior margin slightly sinuate, laterally connected to margin of abdominal connexiva (cn) and metacetabular groove (ag). Metanotum with transverse, thickened line (tl) situated slightly behind posterior margin of mesonotum. Female mesonotum (Fig. 62, ms) with median longitudinal sulcus dividing the sclerite into lateral parts connected by a hairy membrane (m). Metathoracic spiracle (Figs 57 and 62, sp) inconspicuous, oriented nearly cephalo-caudally. Only apterous form known.

Legs. Front leg (Figs 59 and 62) short and stout; femur distinctly thickened basally, tapering in width distally; tibia slightly widened in middle, especially in male (Fig. 59); first tarsal segment about half as long as second segment; claws long, surpassing apex of tarsus. Trochanter and femur of front leg armed beneath with dense row of short spines and a few longer spinous hairs; tibia armed with a row of short spines. Middle femur (Fig. 60) longer than the body length, armed beneath with rows of spines; tibia distinctly shorter than femur; tarsi more slender than tibiae. Hind femur subequal in length to middle femur, but distinctly more slender; armed beneath with small spines. Relative lengths of tarsal segments and size and shape of claws of middle and hind legs unknown.

Abdomen. Male abdomen (Fig. 57) short, not longer than pro- and mesonotum together. Basal abdominal mediotergites steeply depressed behind transverse, thickened line (tl) across metanotum. A pair of lateral, transverse impressions probably marks the anterior limit of tergite 1; intersegmental sutures between tergites 2-3 indistinct, those between tergites 4-7 distinct. Connexiva (cn) very broad, almost vertical. Genital segments (Figs 57 and 61) large; segment 8 (s8) posteriorly widened. Pygophore (py) ovate. Proctiger (pr) with long, lateral process (lp) on each side, directed ventrad and cephalad. parameres not visible and probably small or absent. Female abdomen very short (Fig. 62), abdominal end barely extends beyond coxae of hind legs. Connexiva probably broad and vertically raised. Sterna 3-6 very short, sternum 7 (s7) about three times as long as sternum 6, posterior margin straight. Gonocoxae (gx) large, rectangular; proctiger (pr) button-like, protruding.

Distribution and geological horizon

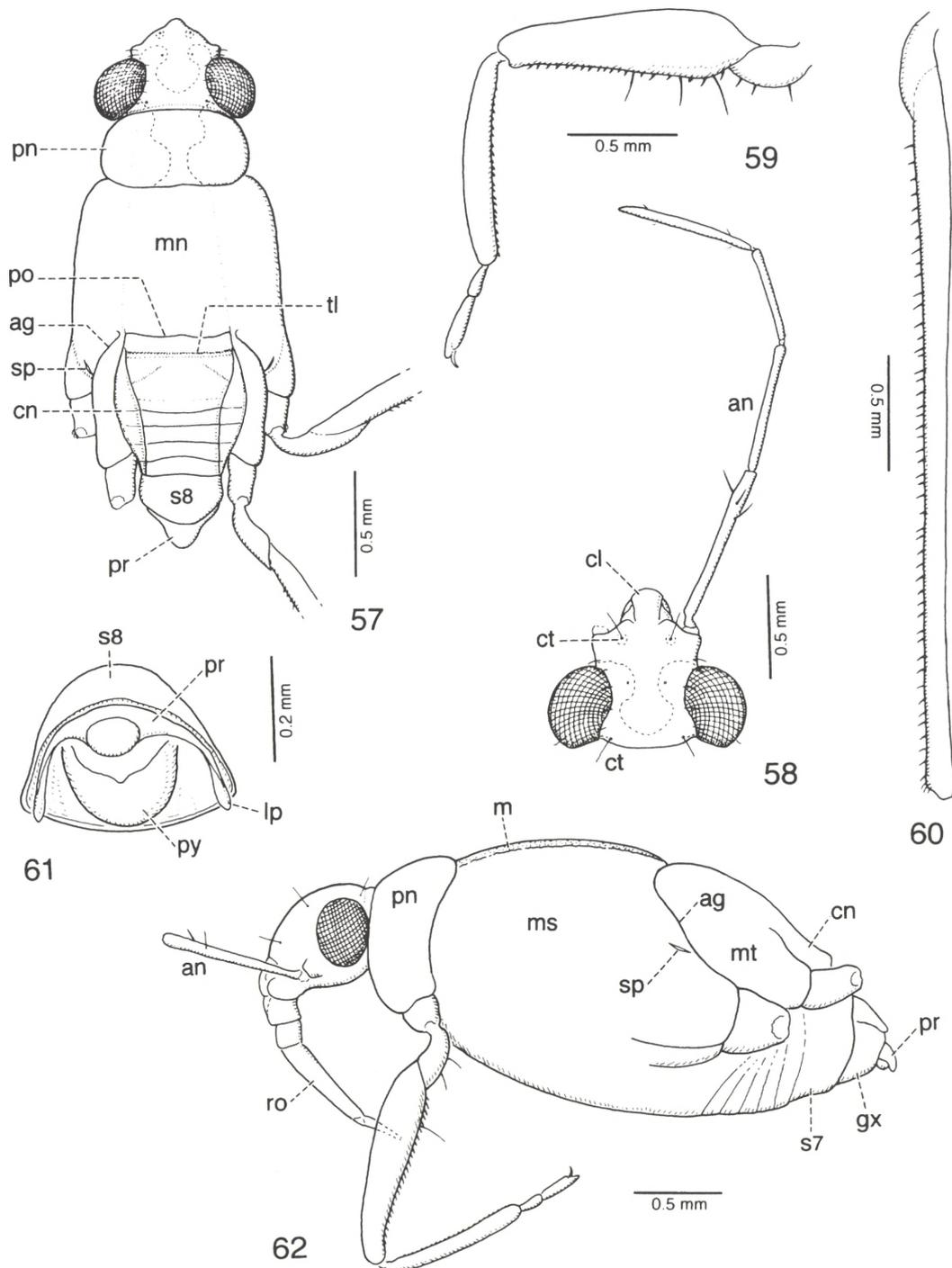
Dominican Republic, Hispaniola (see map, Fig. 2). Oligocene/Miocene, 30-20 Ma. The ex-

act age of these deposits is still not known, and estimates based on microfossil and chemical analyses have produced a range from 20-15 Ma (Iturralde-Vincent & McPhee 1996) to 45-30 Ma (Cepek in Schlee 1990).

Remarks

Andersen & Poinar (1992) discussed the relationships of *Electrobates* in great details. The fossil genus has a superficial resemblance to gerrids belonging to the subfamily Trepobatinae (Matsuda 1960; Andersen 1982b). Among the characters shared are that the intersegmental suture between meso- and metanotum is represented dorsally in apterous forms by posterior margin of mesothoracic postnotum (Fig. 57, po), the long, lateral processes of the male proctiger (Fig. 61, lp; shared with the tribes Naboandolini and Stenobatini), the median, longitudinal sulcus dividing the female mesonotum into two sclerites connected by a hairy membrane (Matsuda 1960: fig. 1038). The monophyly of the Trepobatinae is, among other characters, defined by the thickened middle femora which are distinctly shorter than middle tibia and the almost dorso-ventrally oriented metathoracic spiracle. The middle femora of *Electrobates* are definitely longer than their middle tibiae and thereby similar to the leg structure of most gerrids. The orientation of the metathoracic spiracle in *Electrobates* (Figs 57 and 62, sp) is also different from that of trepobatines. Thus, the fossil gerrids do not qualify as members of the subfamily Trepobatinae. Thus, the similarities between *Electrobates* and some trepobatines may be either symplesiomorphies or homoplasies.

In the reconstructed phylogeny of the Gerridae (Andersen 1982b: fig. 480), the subfamilies Rhagadotarsinae and Trepobatinae (in that order) represent the two basal branches of the cladogram. Among the characters used as synapomorphies for the higher branches of the cladogram, *Electrobates* shares the relatively



Figs 57-62. *Electrobates spinipes* Andersen & Poinar. 57, apterous male holotype, dorsal view; antennae and most of legs omitted. 58, head of apterous male, dorsal view; left antenna omitted. 59, left fore leg of apterous male. 60, middle trochanter and femur of apterous male. 61, Abdominal end of apterous male, caudal view. 62, Apterous female paratype, lateral view; distal antennal segments and most of middle and hind legs omitted (redrawn from Andersen & Poinar 1992).

short ocular setae (less than the diameter of four eye facets). In addition, the basal segment of the front tarsus is more than one third the length of second segment (shorter in both Rhagadotarsinae and Trepobatinae). *Electrobates* has retained the plesiomorphic state of dorsal thorax structure (intersegmental suture between meso- and metanotum straight).

The transverse line in front of the abdomen of *Electrobates* (Fig. 57, tl) is superficially similar to the secondary, transverse line across metanotum found in members of the Neotropical subfamily Charmatometrines (Andersen 1982b: fig. 444). In addition to this character, the charmatometrines are, e.g. characterised by the apical processes of front tibiae, and metathorax having lateral grooves leading from the scent orifice to evaporative areas on metacetabula.

The spine-carrying antenna, modified front legs, and shortened female abdomen are characters found in some members of the Oriental subfamily Eotrechinae, especially *Amemboia* (*Amembooides*) spp. (Polhemus & Andersen 1984). The thoracic structure of eotrechines is, however, quite different from that observed in *Electrobates*.

Andersen & Poinar (1992: 263 and fig. 11) concluded that *Electrobates* cannot be placed in any of the extant subfamilies of Gerridae. In some characters, the fossil genus is more derived than any member of the Rhagadotarsinae and Trepobatinae. In others characters it is more primitive than any member of the Charmatometrines, Gerrinae, Eotrechinae, Cylindrostethinae, Ptilomerinae, and Halobatinae. *Electrobates* was therefore placed as sister-group to all gerrid subfamilies except the Rhagadotarsinae and Trepobatinae. On these grounds, Andersen & Poinar (1992) erected a new subfamily, Electrobatinae, with *Electrobates* as its type genus.

Electrobates spinipes Andersen & Poinar
(Figs 57-62, 120-123)

Electrobates spinipes Andersen & Poinar, 1992:
261, figs 1-10. – Poinar, 1992: 114, plate 7.

Material examined

Holotype

Apterous male (Fig. 122). In piece of Dominican amber (26 x 17 x 10 mm) originating from a mine near El Valle, Cordillera Oriental, eastern Dominican Republic, Hispaniola. Holotype deposited in GOPC.

Paratype

Apterous female (Fig. 123), in same piece of amber as holotype; deposited with holotype.

Other material examined

Apterous male in piece of Dominican amber together with remains (pieces of detached legs) of a female (Andersen & Poinar 1992: 265). Deposited in GOPC.

Description

Holotype. Apterous male (Figs 57 and 122), length 2.5 mm, greatest width (across mesoacetabula) 1.0 mm. Body predominantly black dorsally and pleurally. Dorsal head surface with a yellow U-shaped marking along posterior margin and inner margins of eyes. Pronotum with anteriorly widened yellow band in middle. Front femora pale, ventrally darkened; tibiae and tarsi dark. middle and hind legs dark. Ventral surface of insect pale.

Body subovate. *Head* length in middle 0.58 mm; width (across eyes) 0.70 mm; eye width 0.22 mm or two thirds of interocular space. Antennal segments 1-4: 0.62, 0.48, 0.38, and 0.50 mm. *Thorax.* Median length of pronotum 0.35 mm and of mesonotum 0.69. *Legs.* Lengths of leg segments (femur, tibia, first tarsal segment, second tarsal segment): front leg 0.96, 0.80, 0.12, and 0.25 mm; middle leg: 2.75 and 2.05 mm (tarsus incomplete); hind femora incomplete, tibiae and tarsi missing. Front trochanter (Fig. 59) armed beneath with three spines.

Front femur distinctly thickened basally, tapering in width distally, slightly curved in dorsal view; ventral margin of front femur armed with dense row of short, dark spines and a few longer spinous hairs. Front tibia slightly widened in middle, inner margin armed with row of short spines. Middle femur (Fig. 60) and hind femur armed beneath with a row of short spines. *Abdomen*. Length including genital segments 1.0 mm; abdominal tergites 4-7 subequal in length (0.06 mm). Structure of genital segments, see generic diagnosis; length of genital segments 0.35 mm; lateral processes of proctiger 0.18 mm.

Paratype. Apterous female (Figs 62 and 123), length 3.6 mm, greatest width 1.8 mm. Colouration as in male. Head structure as in male. Lengths of antennal segments 1-4: 0.80, 0.62, 0.48, and 0.58 mm. Length of pronotum 0.45 mm, mesonotum 1.08; latter with scattered, suberect bristle-like hairs. Length of leg segments (femur, tibia, first tarsal segment, second tarsal segment): front leg: 0.98, 0.88, 0.12, and 0.22 mm; middle leg: 3.55 and 2.45 mm (tarsus incomplete); hind leg: 3.45 mm (hind tibiae incomplete, tarsi missing). Armature of legs as in male. Abdomen including genital segments) about 1.25 mm; abdominal sternites 4-6 subequal in length (0.05-0.08 mm), sternum 7 much longer (0.25 mm). Genital segments, see generic diagnosis.

Geological horizon

Dominican amber, Oligocene/Miocene, 30-20 Ma (see above).

Distribution and palaeoecology

Dominican Republic, Hispaniola (see map, Fig. 2). The palaeoenvironment of Dominican amber insects has been thoroughly discussed by Poinar (1992) and Grimaldi (1996). Dominican amber was formed from extinct species of *Hymenaea* trees (Leguminosae, Caesalpinioidea) and recent studies have revealed an ex-

ceedingly rich extinct fauna including almost every type of insect life form.

The close association of a conspecific male and female specimen in the same piece of amber (Figs 120-121) was taken as the earliest evidence of mate guarding in a water strider species (Andersen & Poinar, 1992: 265; see also below).

Remarks

See under generic heading (above)

Subfamily **Halobatinae** Bianchi

Genus *Halobates* Eschscholtz – Sea skaters, ocean striders

Halobates Eschscholtz, 1822: 106.

Euratas Distant, 1911: 146. Synonymised with *Halobates* by Esaki, 1929: 417.

Fabatus Distant, 1911: 147 [nymph]. Synonymised with *Euratas* by Annandale and Kemp, 1915: 183.

Type species:

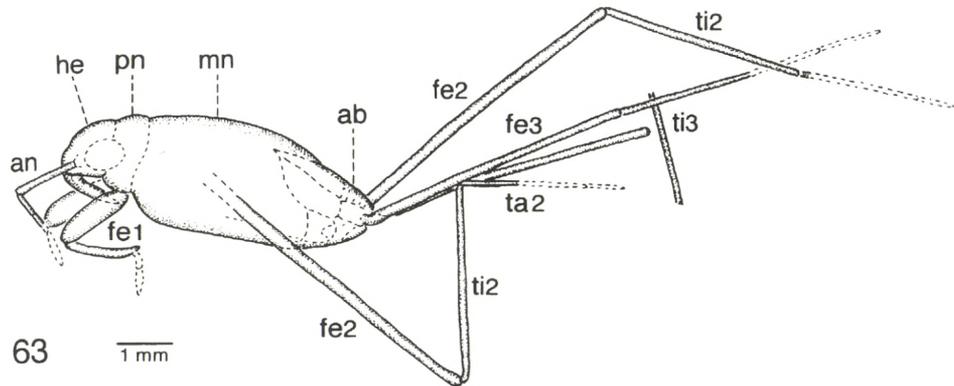
Halobates: *Halobates micans* Eschscholtz, 1822; subsequent designation by Laporte (1832: 24).

Euratas: *Euratas formidabilis* Distant, 1911; designation by monotypy.

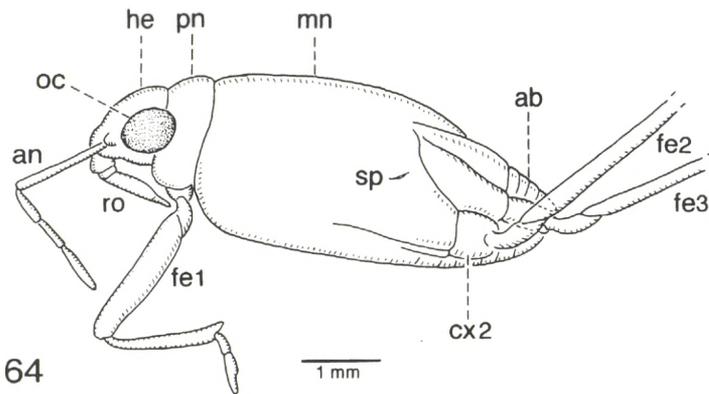
Fabatus: *Fabatus servus* Distant, 1911; designation by monotypy.

Diagnosis

Relatively small water striders, length 3.2-6.5 mm, with broad thorax and short abdomen. Chiefly dark-coloured or silver-grey species without extensive pale markings except on venter (immature specimens have more extensive pale body areas). Yellow markings on head usually restricted to a basal, crescent-shaped mark; if most of the head yellow, then the male front femora are unarmed beneath. Intersegmental suture between meso- and metanotum incomplete, usually reduced to a pair of lateral V-sha-



63



64

Figs 63-64. *Halobates ruffoi* Andersen, Farma, Minelli & Piccoli. 63, apterous female holotype, lateral view; body and appendages drawn *in situ*; reconstructed parts shown as stippled lines. 64, head, thorax, left fore leg, and bases of left middle and hind legs of apterous female, lateral view (full reconstruction) (redrawn from Andersen *et al.* 1994).

ped pits. Male front femora rarely with ventral spines or tubercles. First segment of front tarsus variable in length. Males with eighth abdominal segment wider than long, with rounded, tuberculate, or finger-like spiracular processes; styli-form processes present, usually long and slender. Male proctiger usually pentagonal in outline, produced or dilated laterally.

Distribution and habitats

Five species of *Halobates* are widespread in tropical oceans and live permanently on the sea surface. There are an additional 38 *Halobates* species in sheltered coastal waters throughout

the tropical Indo-Pacific (Herring 1961; Andersen & Polhemus 1976; Cheng 1985; Andersen 1991a). Their distribution seems more or less to coincide with the distribution of reef-building corals and mangroves which require a relatively high sea temperature. Adult sea skaters are always wingless but may disperse along coasts, chains of islands and, occasionally, across wider stretches of open sea.

Remarks

The abdomen of adult *Halobates* is reduced in size relative to the thorax and the middle and hind legs seem to be inserted near the abdomi-

nal end of the insect. Although several groups of gerrids are similar in this respect, workers not familiar with this group of insects have classified fossils with short abdomen in the genus *Halobates*. Gerrid nymphs from Baltic amber have previously been assigned to this genus (Germar & Berendt 1856; Larsson 1978), an error which was already pointed out by White (1883: 14) in his monograph on sea skaters. Scudder (1885) first placed specimens of his *Metrobates aeternalis* (Scudder 1890) in *Halobates*. Finally, Lin (1981) described *Halobates bagonensis* from the Miocene deposits of the Lunpola Basin, Tibet. In my opinion, neither of these fossils are correctly classified (see further discussion below). So far, only the following fossil *Halobates* has been recognised.

Halobates ruffoi Andersen, Farma, Minelli & Piccoli
(Figs 63-64, 106)

Halobates ruffoi Andersen, Farma, Minelli & Piccoli, 1994: 480-483, figs. 1-2.

Material examined

Holotype

Apterous female (Fig. 106), from Bolca near Verona, Italy. Catalogue Nos IG 24526 (part) and IG 24527 (counterpart), in Museo Civico di Storia Naturale, Verona, Italy.

Description

Holotype. Almost complete specimen, probably and apterous female, preserved in a lateral position (Figs 63 and 106).

Body ovate in lateral view, length 5.8 mm, maximum height 2.3 mm. *Head* moderately extended (Figs 63-64, he), its length a little less than one fifth of the body length; dorsal side describing an even curve. Traces of a large, ovate compound eye (Fig. 64, oc) partly overlapping prothorax (pn). Basal 2-3 segments of antenna preserved in front of head (Figs 63-64,

an); first antennal segment measures 1.7 mm, about two and a half times as long as second segment. Indistinct traces of maxillary and mandibular plates and probably also of the socket of left antenna. Clypeus slightly arched with possible traces of labrum below. Rostrum (ro) preserved in a position folded under the head, fairly stout, a little longer than head; rostrum apparently with four segments of which the third segment is the longest. *Thorax*. Pronotum (Figs 63-64, pn) shorter than head, dorsally arched and posteriorly delimited by a curved line. Sutures between mesonotum (mn) and metathorax indistinct but together they are probably more than one third of the body length. Ventral margin of meso-metathorax almost straight, rounded anteriorly. No traces of wings. *Legs*. Front leg much shorter than body as well as middle and hind legs; front femur (Fig. 64, fe1) robust, measuring 1.9 mm; front tibia more slender than femur, measuring at least 1.4 mm; tarsus not preserved. Middle leg much longer than body; middle femur (fe2) measures 6.1-6.6 mm (left side; inaccuracy due to indistinct displacement of femur) or 6.5 mm (right side); middle tibia (ti2) 4 mm (left) or 3.5 mm (right); tarsus (ta2) incomplete. Hind leg a little shorter and more slender than middle leg; left hind femur (fe3) measures 5.1 mm and hind tibia (ti3) at least 2.4 mm (incomplete?); hind tarsus missing. Acetabula, coxae, and trochanters of all legs indistinct. *Abdomen* (Figs 63-64, ab) indistinctly delimited from meso-metathorax, but probably much shorter than the thorax (as judged by the positions of the two posterior legs); abdominal segments indistinctly visible dorsally, abruptly deflected toward abdominal end. Terminal abdominal segments apparently not enlarged or otherwise differentiated.

Geological horizon

The fossil originates from the deposit "Pesciara di Bolca", in the province of Verona, northeast-

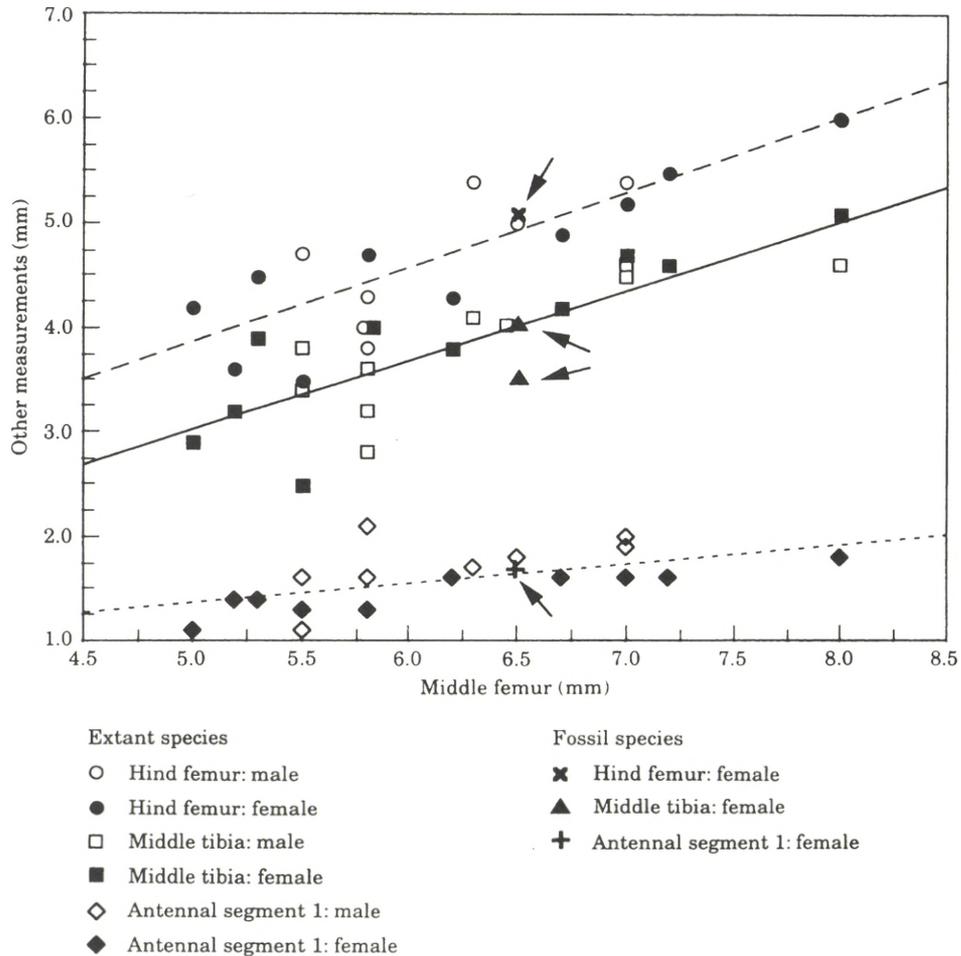


Fig. 65. Scatter diagram showing variation of selected measurements (length of hind femur, middle tibia, and antennal segment 1) of 10 extant species of *Halobates* and the extinct species *Halobates ruffoi* Andersen *et al.* (points indicated by arrows). Length of middle femur used as independent variable. Regression lines (measurements for males and females combined) are shown for hind femur (broken line), middle tibia (unbroken line), and antennal segment 1 (dotted line) (reproduced with permission from Andersen *et al.* 1992).

ern Italy. It is imprinted in a whitish, fine-grained limestone rich in fossils of marine animals, especially fish. The geological age of this deposit is about 45 Ma, on the borderline between Middle and Upper Eocene (Andersen *et al.* 1994, and references therein).

Distribution and palaeoecology

Bolca near Verona, northern Italy (see map,

Fig. 3). The fauna of marine fish from the 'Pesciara di Bolca' is very similar to the present fauna of the Indo-West Pacific region. Part of the Bolca formation contains also remains of plants, jellyfish, a few mollusks, crabs, lobsters, terrestrial insects, crocodiles, and bird feathers. No colonial corals have been found in the Bolca area, but fossil coral reefs of more or less the same age are found in deposits only a few

kilometers away. This indicates water surface temperatures not lower than 20° C, that is, above the tolerance level of extant *Halobates* species. In somewhat younger sediments from Colli Berici, 30 km from Bolca, pollen from mangrove trees has been recovered. Thus, it is estimated that the Eocene climate was tropical in the Veneto area where Bolca is situated (Andersen *et al.* 1994, and references therein).

Remarks

Andersen *et al.* (1994) classified this fossil in the gerrid subfamily Halobatinae by the following combination of characters: Body relatively short and stout. Eyes large, partly overlapping prothorax. First antennal segment much longer than any of the following three segments. Rostrum relatively short and stout. Prothorax shorter than head. Meso- and metathorax not distinctly delimited from each other, together much longer than prothorax. No traces of wings in adult. Middle leg longer than hind leg, both inserted towards the end of body. Femora longer than tibiae in the two posterior pairs of legs. Abdomen distinctly shortened, much shorter than thorax.

The subfamily Halobatinae comprises both limnic species (tribe Metrocorini) and marine species (tribe Halobatini), the latter belonging to the genera *Asclepios* and *Halobates* (Herring 1961; Andersen & Polhemus 1976; Cheng 1985; Andersen 1991b). The presence of the fossil gerrid in a marine sediment favours its classification in one of the marine genera. It is true that flying insects are frequently blown out from land and deposited on the sea surface, but the wingless state of the fossil specimen ex-

cludes this possibility.

The three extant species of *Asclepios* measure 3.0-4.0 mm in body length while *Halobates*-species show a size range of 3.0-6.5 mm with most species within the range of 4.0-5.5 mm. The fossil specimen measures 5.8 mm in body length, which is toward the upper limit of the range for *Halobates* species. Fig. 65 shows a scatter diagram of selected measurements from individuals of ten extant species of *Halobates*. Middle femur length was chosen as the independent variable instead of body length, because the latter, especially in females, depends on the state of filling of the abdomen (food, eggs). Most of the points for measurements on the fossil specimen (Fig. 65) are situated close to the regression lines for the measurements of the first antennal segment, hind femora, and middle tibiae (left and right side) upon middle femora. These and other measurements recorded in the description above corroborate the classification of the fossil specimen in the genus *Halobates*.

The fossil does not reveal enough structural details to permit a closer comparison with extant sea skaters. However, from its size alone, *Halobates ruffoi* compares favourably with the coastal species *H. formidabilis* (Distant) (4.6-5.5 mm) from India, Sri Lanka, and the Maldives, *H. alluaudi* Bergroth (5.0-5.8 mm) from the Seychelles, and *H. princeps* White (6.0-6.6 mm) from the Indo-Malay archipelago. In view of its age, we find it unlikely that the fossil *Halobates* belongs to any of these extant species. The fossil species is larger than any open-ocean species, e.g. *H. micans* Eschscholtz (4.0-4.5 mm) or *H. splendens* Witlaczil (4.5-5.0 mm).

Family **GERRIDAE** Leach, *incertae sedis*

Metrobates (?) *aeternalis* Scudder

Metrobates aeternalis Scudder, 1890: 353-354. – Andersen, 1982b: 250.

Descriptive notes

Described from three specimens (syntypes), of which one immature, from the Florissant Formation, Colorado, U.S.A. Types probably deposited in the Royal Ontario Museum, Ottawa, Canada. Scudder (1890: 353-354) states: "Body considerably elongated, but solely by the prolongation of the mesonotum, which is about twice as long as broad, thus separating at considerably distance the front and aft legs; the abdomen is no longer than the width of thorax and tapers rapidly to a point; the wings are slender, pupæform, ovate pads ..., these do not clearly appear on all specimens. The head is not well preserved on any specimen". The following measurements are given: Length of body 7 mm; width, 1.75 mm; length of front femora, 2 mm; tibiae, 1.6 mm; tarsi, 1.1 mm; middle femora, 4.25-6 mm; tibiae, 4.3 mm; tarsi, 2+ mm; hind femora, 3.5-5.5 mm; and tibiae 4 mm.

Geological horizon

The Florissant Formation has commonly been dated as Lower Oligocene, 37-30 Ma (Wilson 1978a), but more recent evidence suggests that this formation may be Upper Eocene or about 40 Ma (M. Wilson, personal communication).

Distribution and palaeoecology

Colorado, U.S.A. (see map, Fig. 2). The Florissant fauna is the best known, most prolific, and most diverse of the North American Paleogene insect faunas (Scudder 1890; Wilson 1978a). The climate was warm temperate to subtropical according to the evidence of fossil

floras. The evidence from the composition of the insect fauna is in accord with this interpretation, but the evidence is conflicting as to whether the climate was wet or dry (Wilson 1978a: 17-18).

Remarks

Scudder (1890) does not give any particular reason for placing his new species in the genus *Metrobates* Uhler. This genus belongs to the gerrid subfamily Trepobatinae (Matsuda 1960) and includes 14 extant species distributed in North, Central, and South America (Polhemus & Polhemus 1993). Species of *Metrobates* are above all characterised by having a short and broad, more or less strongly dorso-ventrally flattened body, very short abdomen, and middle femora distinctly shorter than tibiae. *M. aeternalis* does not share any of these characters.

Instead, I here offer an alternative interpretation of these fossils. When viewed upside down, the excellent figure by Scudder (1890: plate 22, fig. 15) has a distinct resemblance to a cast skin (exuvium) of a gerrine water strider, possibly belonging to *Limnoporus* or the extinct genus *Telmatrechus* (see above). The middle and hind legs are pointing obliquely backwards, a position typically found in exuviae. The pale area in the middle of the thorax probably marks the ecdysial line. Judging from the dimensions given by Scudder (1890: 354), the exuvium may belong to a fourth instar nymph or to a fifth instar nymph from which an apterous adult individual has emerged.

Gerris (?) *protobates* Cockerell

Gerris protobates Cockerell, 1927: 592.

Descriptive notes

The original description by Cockerell (1927) was based upon an incomplete specimen from the Florissant Formation, Colorado, U.S.A., deposited in the Natural History Museum, London. In his description, Cockerell (1927: 592) states "Similar to modern species; brown; body of usual form (abdomen missing); frontal angle of head broad, about a right angle; first antennal joint 3 mm.; length of head and thorax about 8 mm., width of thorax about 2 mm.; measurements of legs in mm.: anterior femur 3.5, its tibia 3; middle femur 8, its tibia 6; hind femur 7.4. A very ordinary species, which differs from Scudder's extinct genus *Telmatrechus* by having the tibiae conspicuously shorter than the femora. Among modern species it falls near the common *G. marginatus*, Say."

Geological horizon

Florissant Formation, Upper Eocene age, about 40 Ma (see under *Metrobates (?) aeternalis*, above).

Distribution and palaeoecology

Colorado, U.S.A. (see map, Fig. 2). Notes on the palaeoenvironment of the Florissant fauna are given under *Metrobates (?) aeternalis* (above).

Remarks

The length of the first antennal segment (3 mm) and combined length of head and thorax (8 mm) indicate that the fossil specimen must have been much larger than the extant, North American *Gerris marginatus* (Say) which has a body length of 9-11 mm (Andersen 1993b). The original description is insufficient to place this fossil species more precisely.

Gerris (?) parabdrominalis Theobald

Gerris parabdrominalis Theobald, 1937: 254, plate 19, figs. 19-20, plate 3, fig. 18.

Note

Theobald (1937) described this fossil species from the Lower Oligocene (37-30 Ma) of Kleinkemps near Mulhouse, Rhein Valley, France (see map, Fig. 3). I agree with Nel & Paicheller (1993: 81) that the description and discussion by Theobald (1937) is too inadequate to justify the classification of this species in the genus *Gerris*.

Gerris (?) sp. – Eocene, Germany

Gerris (nymph). Lutz, 1991: 120.

Note

Lutz (1991: 120) recorded a wingless gerrid (probably a nymph) from the Middle Eocene of Messel near Darmstadt (see map, Fig. 3), preliminary identified as belong to the genus *Gerris* Fabricius. The specimen was found together with notonectid nymphs, dytiscid and nematoceran larvae, as well as cladocerans, indicating a lacustrine palaeoenvironment. Closer examination of the gerrid nymph is necessary to confirm its identity.

Halobates (?) bagonensis Lin

Halobates bagonensis Lin, 1981: 346, fig. 2, plate 2.

Descriptive Notes

Lin (1981) described this species from the "grey-yellow paper shale of the Miocene lake deposits", Lunpola Basin, Baingoin county, Xizang [Tibet], China (see map, Fig. 2). The type specimen is probably deposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, P.R. China.

The following descriptive notes are chiefly based on the photograph accompanying the original description (Lin 1981: plate 2). The type is impressed in a slightly distorted position. Head (carrying a pair of antennae), a broad thorax, and a short pointed abdomen, can

be differentiated. Middle and hind femora and middle tibiae preserved *in situ*, other appendages displaced or lost. Body length (from tip of head to end of abdomen) about 8 mm, greatest width about 4 mm. Antennae (perhaps incomplete) about 4 mm long; individual segments not visible. The very broad thorax is composed of two lateral, dark parts separated by a wide unpigmented median part. Length of middle femora 9.8-10 mm and of middle tibiae 7.9 mm; length of hind femora about 9 mm. Abdomen very short, about 3 mm long.

Geological horizon

Miocene, 24-5 Ma.

Distribution

Lunpola Basin, Baingoin County, Xizang [Tibet], China (see map, Fig. 2).

Remarks

Li (1981: English summary, p. 348) placed this fossil species in the marine genus *Halobates* Eschscholtz stating "*Halobates alpinus* [error for *bagonensis*] sp. nov. is similar to *H. micans* Eschsch, the former being distinct from the latter in the structure of thorax, antennae and rostrum."

The dimensions of this fossil do not match any living or fossil species of *Halobates* (Herring 1961; Andersen *et al.* 1994). *H. micans* only measures 3.5-4.6 mm and even the largest species, *H. princeps* White, does only reach a body length of 6.0-6.7 mm. The leg segments of extant *Halobates* spp. have the following ranges of lengths: middle femur, 5-8 mm; middle tibia, 2.5-5 mm; and hind femur, 3.5-6 mm. thus, the leg segments of the fossil form are much longer than would be expected for a species belonging to the genus

Halobates. During the Miocene the northern part of Tibet was nowhere near the coastlines of any ocean (Smith *et al.* 1994). It is therefore quite unlikely that the fossil form should belong to any group of marine water striders.

An alternative interpretation of this Miocene fossil from Tibet is, that it represents the cast skin (exuvium) of a large freshwater gerrid. The wide pale area in the middle of the thorax may represent the middorsal, ecdysial opening through which the following instar emerges. The very short abdomen also resembles the nymphal condition. Judging from the dimensions of the exuvium, it may belong to a fifth instar nymph from which an apterous adult individual has emerged, possibly belonging to the extinct species *Aquarius lunpolaensis* (Lin) which was found in the same deposits and geological horizon (see above).

Halobates (?) sp. – Baltic amber

Note

Germer & Berendt (1856: 19, plate 2, fig. 8) illustrated a "Larva *Halobates*" from Baltic amber (Eocene/Oligocene, 40-35 Ma) which obviously is a (fourth instar?) nymph belonging to a species of *Gerris* or an allied genus. Gerrid nymphs from baltic amber classified as *Gerris* are described earlier in this work. Bachofen-Echt (1949: 172) stated (in translation) "three species of the genera *Gerris* and *Metrobates* in amber". I have been unable to find any reference to a record of *Metrobates* (copied by Spahr 1988: 9) from amber and therefore suspect that Bachofen-Echt (1949) by mistake used this name instead of *Halobates*.

Family VELIIDAE Brullé

Water crickets, riffle bugs

Subfamily Haloveliinae Esaki

Genus *Halovelia* Bergroth – Coral bugs

Halovelia Bergroth, 1893: 277. – Andersen, 1989a: 83-84.

Type species: *Halovelia maritima* Bergroth, 1893; designation by monotypy.

Diagnosis

Small or very small water striders, length 1.7-2.6 mm; adults always apterous (wingless). Body usually subovate, chiefly dark coloured, covered by a thick, greyish pilosity. Head and pronotum without extensive pale markings. Head much shorter than wide, moderately deflected in front of eyes; eyes globular but relatively small, width of each eye less than 0.3x interocular width. Antennae long and slender, usually 0.6-0.8x body length; segment 1 usually subequal to or slightly shorter than segment 4; segment 3 longer than segment 2. Pronotum very short; suture between pro- and mesonotum usually obscured laterally. Dorsal boundaries between meso- and metathorax and between metathorax and abdominal terga indistinct. Ventral sutures of thorax and abdomen distinct; metathoracic scent channels extending laterally and obliquely backward. Front tibia of male with a grasping comb composed of a compact row of short spines along the inner margin. Mesotrochanters prolonged; middle femur very long, usually more than 0.5-0.6x body length, usually with short pubescence along anterior margin; middle tibia and tarsus very slender and long. Hind femur relatively short, usually thickened

proximally. Abdomen short with broadly rounded sides in male, longer and usually with more straight sides in female. Male genital segments relatively large but withdrawn into pregenital abdomen and only slightly protruding from abdominal end; parameres large and symmetrically developed. Hind margin of sternum 7 of female usually produced in middle. Female genital segments clearly visible behind tergum 7; proctiger cone- or button-shaped, usually concealed beneath tergum 8.

Distribution and habitats

The genus *Halovelia* contains 31 described species (Andersen 1989a, 1989b) which are distributed throughout the Indo-West Pacific region, ranging from the Red Sea and east coast of Africa (including Madagascar) to the islands of the West Pacific Ocean as far east as Samoa. The discovery of a fossil *Halovelia* in the Caribbean was quite unexpected, representing an enormous extension of the geographical range of this group.

Most species of *Halovelia* are found on intertidal coral reef flats (hence the name coral bugs), on the surface of tidal pools among stands of *Porites* and *Acropora* corals on the mid-reef flat, but only rarely on the inner-reef flat or towards the outer reef margin. They have also been recorded from rocky coasts without corals. *Halovelia* species are occasionally found in mangrove habitats, especially when these border coasts fringed by coral reefs, but are otherwise replaced by species of the genus *Xenobates* Esaki in such habitats. The coral bugs

usually appear when the tide recedes, in particular upon the surface of shallow pools around or beneath blocks of coral or porous rock. When the tide rises, both adults and nymphs retreat to cavities and holes in such blocks and stay submerged during high tide, surrounded by an air bubble.

Remarks

The genus *Halovelgia* was monographed by Andersen (1989a, 1989b). It is separated from the genus *Xenobates* by the presence of a grasping comb on the male front tibia and the concealed male genital segments. In addition, most *Halovelgia* species have almost uniformly dark head and pronotum, without extensive pale markings. The body is covered by a dense clothing of short pubescence (which may appear greyish in some parts), but never by silvery pubescence forming definite spots. The middle femora and tibiae are covered by short pubescence but only rarely have a hair fringe along their anterior margins.

Halovelgia electrodominica Andersen & Poinar
(Figs 66-72, 118-119)

Halovelgia electrodominica Andersen & Poinar,
1998: 1-9.

Material examined

Holotype, apterous female (Fig. 118), contained in a piece of amber (12 x 7 x 2.5 mm) originating from the northern mountain ranges in the Dominican Republic (Hispaniola); holotype catalogued under the code HE-4-28 and deposited in GOPC.

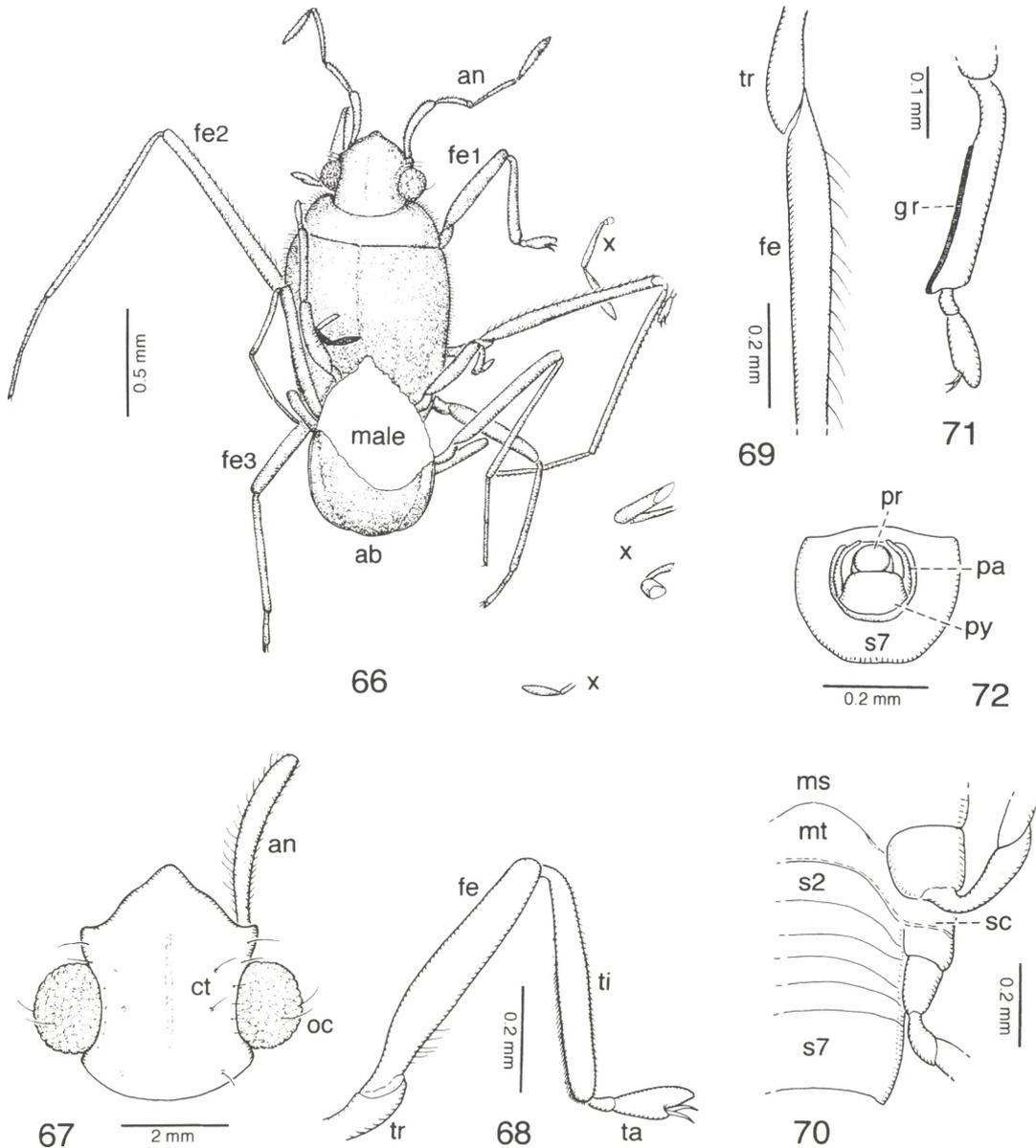
Paratype, apterous male (Fig. 118), enclosed in the same piece of amber as holotype, same code and repository as holotype.

Description

Holotype. Apterous female (Figs 66 and 118), length 1.5, greatest width 0.7. Body subovate,

length about 2x greatest width across thorax (1.50: 0.74). Colour chiefly dark brownish, basal part of dorsal head surface and median part of pronotum paler; antennae and legs brownish.

Head (Figs 67 and 119) much shorter than wide across eyes (0.49 mm). Eyes (oc) small and globular, diameter less than half width of interocular space. Antennae (an) with dense, short pubescence, about 0.6x length of insect; lengths of segments 1-4: 0.29, 0.18, 0.24, and 0.24 mm; first segment curved and slightly thicker than segments 2-3; fourth segment fusiform. Rostrum slender, apex just surpassing prosternum. *Thorax* (Fig. 66) furnished with a dense pile of short, erect hairs (most easily observed along the margins of pro- and mesonotum). Pronotum very short (0.14 mm), in middle less than half length of head; posterior margin of pronotum distinct throughout, reaching sides of thorax. Mesonotum much longer than pronotum (exact length cannot be measured) with sides regularly curved; a longitudinal furrow or impression in middle of mesonotum. Metasternum (Fig. 70, mt) with anterior margin produced in middle, median length 0.13 mm. Median scent orifice indistinct; lateral scent channels (sc) running along posterior margin, ending on metacetabula. *Legs*. Lengths of leg segments (femur, tibia, tarsus): front leg: 0.46, 0.41, and 0.16 mm; middle leg: 0.88, 0.85, and 0.53 mm; hind leg: 0.54, 0.53, and 0.20 mm. Front femur (Fig. 68, fe) with almost the same width throughout; front tibia (ti) widened and slightly curved, with a row of short, spinous hairs on the inner surface; front tarsus (ta) with basal segment much smaller than second segment (0.04 and 0.13 mm, respectively). Middle trochanter (Fig. 69, tr) long (0.15 mm); femur (fe) about 0.6x length of insect, slightly thickened basally; tibia and tarsus very slender and long; lengths of middle tarsal segments 1-2: 0.29 and 0.24 mm. Anterior margin of middle femur with a row of



Figs 66-72. *Halovelvia electrodominica* Andersen & Poinar. 66, apterous female holotype and male paratype drawn *in situ*; head and anterior thorax of male abraded; remains of antenna and legs of other specimens marked with an x. 67, head and first segment of right antenna of female, dorsal view. 68, right fore leg of female. 69, trochanter and base of right middle femur of female. 70, right side of posterior thorax and abdomen of female, ventral view. 71, left fore tibia and tarsus of male. 72, abdominal end of male, caudal view (redrawn from Andersen & Poinar 1998).

long, pale hairs, each hair being shorter than femur width; the row continues on middle tibia and tarsus. Hind leg segments much shorter

than those of middle leg; lengths of hind tarsal segments 1-2: 0.06 and 0.14 mm. Claws small but distinct, inserted preapically on all tarsi. *Ab-*

domen relatively short with indistinct segmentation on dorsal side; ventral segmentation fairly distinct; median lengths of sternites 2-7 (Fig. 70, s2 and s7): 0.09, 0.07, 0.06, 0.06, 0.06, and 0.16 mm; genital segments obscured.

Paratype. Apterous male (Figs 66 and 118), length >0.8 mm (head and most of thorax missing), greatest width 0.6 mm. Body probably broadly ovate with greatest width across posterior thorax. Colour as in holotype. Head missing. One incomplete antenna present, segments 2-4: 0.09, 0.13, and 0.14 mm. Thorax incomplete. Lengths of leg segments (femur, tibia, tarsus): front leg: 0.39, 0.31, and 0.14 mm; middle leg: 0.56, 0.61, and 0.44 mm; hind leg: 0.43 mm (tibia and tarsus missing). Front femur slender and slightly curved, tibia with long grasping comb (Fig. 71, gr) along inner surface, occupying distal 2/3 of tibia. Lengths of middle tarsal segments 1-2: 0.25 and 0.19 mm. Other leg structures as in female. Abdomen (Fig. 66) short with indistinct segmentation on dorsal side; longitudinal sutures delimiting the paratergites from the sternites are distinct along the sides of abdomen. Abdominal venter simple; segmentation partly obscured; sternum 7 (Fig. 72, s7) as long as sternite 5 and 6 together. Genital segments (segments 8-10) completely withdrawn into the pregenital abdomen. As seen in caudal view, a pair of fairly long parameres (pa) inserted laterally on the pygophore (py), curved dorsal and almost meeting each other above proctiger (pr).

Geological horizon

Dominican amber. Oligocene/Miocene, 30-20 Ma (see above under *Electrobates*).

Distribution and palaeoecology

Dominican Republic, Hispaniola, Greater Antilles (see maps, Figs 2 and 90). An intriguing question is how a marine insect became trapped in resin. One possible explanation

could be that the resin-producing *Hymenaea*-trees grew along the coast of Oligo-Miocene Hispaniola (Iturralde-Vinent & MacPhee 1996) and drops of resin fall upon a porous block of coral where individuals of *Halovelina electrodominica* were aggregating. Alternatively, sea level changes or high tides may have resulted in the ocean flooding the land and bringing the haloveliines with them.

The two specimens of *H. electrodominica* were seemingly trapped when mating. The male is positioned on top of the abdomen of the female (Figs 66 and 118). The left front leg is stretched forward and the tibial grasping comb (Fig. 71, gr) pressed against the side of the female's pronotum. The hind leg of the same side is curled around the female's hind femur. Seemingly, both leg postures are a function of the male's struggle to uphold his grip of the female. In extant *Halovelina* species, the male rides passively on the back of the (usually larger) female for an extended period of time after copulation, thus guarding his sperm. Permanent genital contact is only observed in species of the *H. bergrothi* Esaki group (Andersen 1989a) where the male inserts one of his very long and slender parameres into the genital opening of the female (Andersen 1989b: figs 61-63).

Remarks

Andersen & Poinar (1998) thoroughly discussed the relationship of *H. electrodominica*. The very short pronotum, prolonged mesothorax, two-segmented tarsi, and very long and slender middle legs are diagnostic for veliid subfamily Haloveliinae (Andersen 1982b; 1989a). There are five extant genera of this subfamily which are keyed out by Andersen (1992: 391). Since the head is not strongly deflected anteriorly, eyes less than half as wide as the interocular space, first antennal segment longer than third segment, the genera *Strongy-*

lovelia Esaki and *Entomovelina* Esaki (both limnic) can be excluded. Among the remaining three genera (all marine), the uniformly coloured pronotum, the grasping comb of the male front tibia, and the concealed male genital segments classify the fossils as members of the genus *Halovelina*. The only characters which associate the fossils with the genus *Xenobates* Esaki are the slightly larger eyes (eye diameter almost 0.4x interocular width) and the row of bristle-like hairs along the anterior margin of the middle femora. The last mentioned charac-

ter, however, is shared with at least one species of *Halovelina*, *H. fosteri* Andersen (1989a: 113), which is endemic to Fiji. Andersen & Poinar (1998) therefore concluded that the fossil species belongs to the haloveliine genus *Halovelina*. The extinct species is smaller than most living species approaching the size of *H. polthemi* Andersen, length 1.6 mm (female) and 1.3-1.4 (male). Unique characters of *H. electrodominica* are the median, longitudinal furrow of the mesonotum and the row of spinous hairs on the inner side of front tibia in the female.

Family VELIIDAE Brullé, *incertae sedis*

Genus *Stenovelina* Scudder

Stenovelina Scudder, 1890: 349-350.

Type species: *Stenovelina nigra* Scudder, 1890; designation by monotypy.

Diagnosis

Body robust, ovate. Head rounded subquadrate, about half as large as pronotum. Eyes moderately large, located at base of head. Antennae with four segments, first and fourth segments longest, second shortest. Pronotum faintly set off from the rest of thorax, more than twice as wide as long. Whole thorax pentagonate, posteriorly widened. Legs short and stout; front legs about half as long as the other leg pairs, hind legs longest. Middle and hind femora subequal in length; hind tibia longer than middle tibia. Tarsi three-segmented, last (third) segment a little shorter than the others. Abdomen oval, the last two segments sometimes produced. No trace of wings.

Distribution and geological horizon

Florissant Formation, Colorado, U.S.A. Upper Eocene, about 40 Ma (see under *Metrobates* (?) *aeternalis*, above).

Remarks

Scudder's original description of this genus is not very precise. There are two illustrations (Scudder 1890: plate 22, figs 8 and 14) of specimens belonging to the type species, *Stenovelina nigra*. One of these (plate 22, fig. 14) shows an insect habitually quite similar to veliids of the genus *Rhagovelina* Mayr (subfamily Rhagoveliinae China & Usinger). In this genus, however, the middle legs are the longest pair of legs and their tarsi are prolonged with the last tarsal segment deeply cleft, provided with an elaborate swimming fan (Andersen 1982b: fig. 290). On the other hand, the very short antennae of the fossil form sets it apart from most veliids, including *Rhagovelina*. A closer study of the large material assigned to this genus by

Scudder (1890) may reveal details that permit a more precise classification of *Stenovelia*. Until then, I prefer to treat this taxon as a veliid genus of uncertain affinity.

Stenovelia nigra Scudder

Stenovelia nigra Scudder, 1890: 350, plate 22, figs. 8 and 14.

Descriptive notes

Scudder's description is based on 23 specimens (syntypes), from the Florissant Formation, Colorado, U.S.A. Types probably deposited in the Royal Ontario Museum, Ottawa, Canada. The original description (Scudder 1890: 350) says: "Whole body uniformly dead black; the pigment in some cases has broken in flakes from the legs, especially the middle and hinder pairs, giving them a mottled appearance which is

purely accidental. The whole body, including the legs, uniformly smooth, with no trace of hairs or spines.

Length of body, 3.75 mm; breadth, 1.65 mm; length of antennae, 1.1 mm; front femora, 0.75 mm; tibiae, 0.75 mm; tarsi, 0.35 mm; middle femora, 1.2 mm; tibiae, 1.3 mm; tarsi, 0.8 mm; hind femora, 1.2 mm; tibiae, 1.4 mm; tarsi, 0.8 mm."

Geological horizon

Florissant Formation, Upper Eocene, about 40 Ma (see under *Metrobates* (?) *aeternalis*, above).

Distribution and palaeoecology

Colorado, U.S.A. (see map, Fig. 2). (See also above under *Metrobates* (?) *aeternalis* Scudder).

Remarks

See under generic heading (above).

Family **HYDROMETRIDAE** Billberg

Marsh treaders, water measurers

Subfamily **Hydrometrinae** Billberg

Genus *Limnaxis* Germar

Limnaxis Germar in Germar & Berendt, 1856: 19. – Popov, 1996: 212-213.

Type species: *Limnaxis succini* Germar & Berendt, 1856; designation by monotypy.

Diagnosis and description

Body elongate, length 5-6 mm. Surface of pronotum and lateral parts of head covered by

scattered "pimples" (small, circular or ovate, pale plate-like structures). Head distinctly prolonged, about one third of body length; antocular part of head longer than postocular part. Eyes small but distinct, located behind middle of head; ocelli absent. Antenniferous tubercles very small; first and second antennal segments relatively short, subequal in length, both distinctly shorter than third segment. Rostrum long and slender, reaching middle coxae. Pronotum relatively short, almost 1.5x as wide

as long; sides of pronotum slightly diverging posteriorly. Metanotum very small, middorsal sulcus very short. Only micropterous and apterous adult forms known. Legs slender without conspicuous pilosity; hind femora not reaching tip of abdomen. Second and third tarsal segments subequal in length; claws distinct but very small, inserted apically on tarsi. Abdomen widened, with very broad laterotergites; mediotergites about as wide as long.

Distribution and geological horizon

Baltic amber, probably from northern Germany (see map, Fig. 3). Eocene/Oligocene, 40-35 Ma.

Remarks

The type species of this genus, *Limnaxis succini*, was originally classified in the family Gerridae (= Hydrodromici Burmeister) by Germar & Berendt (1856: 19) stating: "Bei dem ersten Anblick findet man grosse Aehnlichkeit mit der zu den Reduvinen gehörigen Gattung *Pygolampis*, aber es besitzt doch noch grössere Uebereinstimmung mit der zu den Hydrodromicis gerechneten Gattung *Limnobates*." (in translation: "At first glance one finds great similarity with the reduvine genus *Pygolampis*, but it has even greater correspondence with the gerrid genus *Limnobates* [= *Hydrometra*]"). The first sentence probably has caused subsequent authors (Handlirsch 1908; Keilbach 1982; Spahr 1988) to include the genus in the family Reduviidae.

I agree with Popov (1996) in that *Limnaxis* should be classified in the family Hydrometriidae, chiefly on account of the very elongate shape of the head and very long and slender rostrum. The relatively short first and second antennal segments affiliate the genus with the subfamily Hydrometrinae. Among the four hydrometrine genera, *Limnaxis* shares the relatively short metathorax with *Bacillometra*, *Chaetometra*, and *Dolichocephalometra*. The eyes are

also reduced in the last two genera, both monotypic and endemic to the Marquesas Islands in the Central Pacific Ocean. *Limnaxis* differs from both genera in the dorsal sculpturation of thorax and head and the very broad laterotergites.

Limnaxis succini Germar & Berendt

Limnaxis succini Germar & Berendt, 1856: 19, pl. 3, figs. 18a-c. – Popov, 1996: 213-214, fig. 1.

Descriptive notes

Described by Germar & Berendt (1856) on a micropterous male from Baltic amber. The holotype is not very well preserved, its dorsal side partly obscured by a opal substance. Type deposited in Paläontologisches Museum, Museum für Naturkunde der Humboldt Universität, Berlin, Germany (Type Katalog No. 7338). Popov (1996: 213-214, fig. 1) examined and re-described the holotype as follows:

"Body length 5.1 mm; greatest width (across) abdomen 1.2 mm. General coloration brownish gray. Head slightly less than 3 times longer than wide across eyes, weakly broadened in front of eyes before the level of antennae, narrowed before and behind eyes, and again broadened at the base of head; antecular part of head 1.5 times longer than postocular one. Eyes small but distinct, almost semiglobular, occupying horizontal and latero-dorsal position, as wide as semicircular space and about 1.5 times wider than long, seen from above. Antennae, located [inserted] almost ventrally; ratio of antennal joints I-III (IVth joint broken): 9.5: 9.5: 20 (10). Rostrum broken. Pronotum half of head length, nearly 1.5 times wider than long, with convex lateral sides, hind margin straight; metathorax like a very small triangle; middorsal sulcus equal to metathorax length. Relative length of leg segments (femur incl. trochanter, tibia, tarsus): front legs are broken;

middle leg: 30: 36: 7; hind leg: 44: 53: 9. Tarsal segment I shortest, II and III segment equal size in middle (1: 3: 3) and hind (1: 4: 4) legs. Length of abdomen 2.8 mm, width 1.1 mm; laterotergite (connexiva) and mediotergite of equal width."

To this description could be added that the head, pronotum, and metapleura are covered by numerous, scattered "pimples". Wing rudiments slightly surpass the hind margin of metanotum. Male genital segment(s) conspicuous.

Geological horizon

Baltic amber, Eocene/Oligocene, 40-35 Ma.

Distribution

Northern Germany (see map, Fig. 3).

Remarks

Popov (1996: 214) states that "The type species [*L. succini*] distinctly differs from the other species of this genus *L. hoffeinsi* n. sp. by the larger eyes, the more basal position of the eyes (eyes located clearly behind the middle of head) and by the shorter hind legs (hind femora not reaching apex of abdomen)."

Limnaxis hoffeinsi Popov

Limnaxis hoffeinsi Popov, 1996: 214, fig. 2, pl. 1, figs. 1-2.

Descriptive notes

Described on an apterous female holotype from Baltic amber. Deposited in the collection of H.W. and C. Hoffeins, Hamburg (No. 521). Popov (1996: 214-215) gives the following description:

"Body length 5.3 mm. General coloration silver gray. Head 3 times longer than wide across eyes, weakly broadened at top and at base; antocular part of head 1.2 times longer than postocular one. Eyes very small, distinctly re-

duced and flattened, occupying lateral position, as wide as long. Ratio of antennal joints I-II (III and IV joints broken): 9.5: 9.5 (7...). Pronotum 1.7 times of head length, almost 1.5 times wider than long, hind margin straight. Relative length of leg segments (femur, tibia, tarsus): front leg: 36: 38: 8; middle leg: 32: 37: 8; hind leg: 46: 56: ? Length of abdomen 2.8, width 1.1 mm; femora distinctly thickened at [their] bases."

Geological horizon

Baltic amber, Eocene/Oligocene, 40-35 Ma.

Distribution

Northern Germany (see map, Fig. 3).

Remarks

Popov (1996: 215) states: "This species mainly differs from the type species *L. succini* by the position of the reduced eyes, and by the longer hind femora thickened at [their] bases and, reaching the apex of the abdomen. Note: The strongly reduced eyes and their median position on the head as well as the long hind femora thickened at [their] bases may probably justify to establish a separate genus for this species. However, the fact that there exist only a single [specimen] which beyond that is relatively poor[ly] preserved prevents us from making a final conclusion."

Genus *Metrocephala* Popov

Metrocephala Popov, 1996: 215.

Type species: *Metrocephala anderseni* Popov, 1996; original designation.

Diagnosis and description

Body elongate (Figs 73-74), length not more than 5 mm. Dorsal body surface smooth. Head (he) much prolonged, length about one third of body length; head widened in front of eyes,

anteocular part distinctly longer than postocular part, and clearly longer than pronotum. A pair of small but distinct tubercles on dorsal side of head, just in front of pronotum; each tubercle carry a long and thin trichobothrium (as illustrated by Popov 1996: plate 2, fig. 2). Eyes moderate in size, semiglobular; ocelli absent. Antennae (an) long, first antennal slightly shorter than second segment; third segment about twice the length of second; fourth segment longest. Rostrum (ro) long and slender, reaching middle coxae. Pronotum (pn) relatively short, length almost 1.3x greatest width, sides almost parallel. Front femur (fe1) and tibia about as long as middle femur (fe2) and tibia; hind femur (fe3) and tibia distinctly longer. Basal segment of tarsi shortest, second and third longest. Only micropterous form known. Abdomen (ab) distinctly widened across middle. Male genital segments (s8) conspicuous behind pregenital abdomen.

Distribution and geological horizon

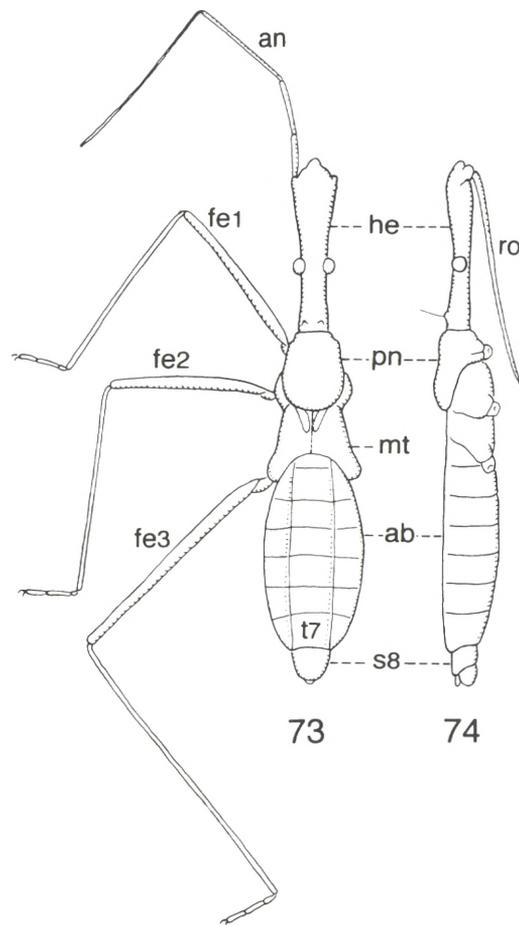
Baltic amber and Bitterfeldt amber from Northern Germany (see map, Fig. 3). Eocene/Oligocene, 40-35 Ma.

Remarks

The presence of a pair of cephalic trichobothria inserted on small tubercles in the posterior part of the head clearly indicates that *Metrocephala* belongs to the gerromorphan family Hydrometridae. Other structures discussed under *Limnaxis* also apply here. *Metrocephala* differs from *Limnaxis* by the shape of the head (postocular part not widened), the slightly larger eyes, the almost parallel-sided pronotum, and by the smooth dorsal surface of body.

Metrocephala anderseni Popov

Metrocephala anderseni Popov, 1996: 215, fig. 3, pl.2, figs. 1-3. – Wichard & Weitschat, 1996: fig. 11, plate 7 (as *Metrocephala andersoni* Popov).



Figs 73-74. *Metrocephala anderseni* Popov (reconstruction). 73, apterous male, dorsal view; antenna and legs of right side omitted. 74, apterous male, lateral view; antennae and legs omitted.

Descriptive Notes

Original description (Popov, 1996) based on the micropterous male holotype from Baltic amber, Coll. Scheele (No. 52); deposited in Geologisch-Paläontologisches Institut der Universität Hamburg, Germany (type Katalog No. 3750). Two additional specimens (paratypes) were also examined, including a micropterous female (Popov 1996: fig. 3) from “Bitterfeldt amber”, deposited in Paläontologisches Museum, Museum für Naturkunde der

Humboldt Universität, Berlin (Type Katalog No. 8).

Popov (1996: 215-216) gives the following diagnosis and description: "Body length 4.7 mm (male) and 4.3 mm (female); greatest width (1.1 mm) near boundary of the posterior quarter of abdomen. General coloration dark metallic, appendages ferrous. Head slightly less than 3 times longer than wide across eyes, weakly broadened in front of eyes before the level of antennae; anteocular part of head 1.36 times longer than postocular one. Eyes as wide as interocular space; about 1.3 times longer than wide, seen from above. Antenniferous tubercles small, located latero-ventrally; ratio of antennal joints I-IV: 10: 11: 22: 34 (male); joint I slightly thicker, others very thin. Rostrum long and slender, reaching middle coxae; 2nd segment much longer than others taken together. Pronotum 1.7-1.8 times of head length, 1.3 times wider than long; metacoxae formed a very small triangular elevated area (holotype) or a very narrow strip (paratype). Relative lengths of leg segments of holotype (femur: tibia: tarsus): front leg: 25 (broken); middle leg: 25: 37: 8; hind leg: 40: 54: 9.5 (1.5: 4.5: 3.5); tarsal segment I shortest; II longest. length of abdomen 2.3 mm, width 1.1 mm; abdominal laterotergites (connexivum) slightly wider than mediotergites.

"Note: The female from Bitterfeldt amber differs from the male from Baltic amber by the slightly smaller size (4.3 mm), the shape of the metathorax (very narrow strip) and by the coloration of tibiae (ferrous) in all leg pairs. Whether these small differences are due to sexual dimorphism or to individual variability must remain an open question because the material is very scarce and the specimen not well preserved."

Geological horizon

Baltic amber and Bitterfeldt amber (see map, Fig. 3). Eocene/Oligocene, 40-35 Ma.

Distribution and palaeoecology

Northern Germany. Accounts on the palaeoenvironment of Baltic amber are provided by Larsson (1978) and Poinar (1992).

Remarks

A reconstruction of *Metrocephala anderseni* (Figs 73-74) was made from the original description and illustrations of the male holotype (Popov 1996). This species has a certain resemblance with the extant species *Chaetometra robusta* (Hungerford) and *Dolichocephalometra pacificus* (Van Duzee), both from the Marquesas Islands, southern Pacific Ocean (see Andersen 1982b: figs 185 and 186), except for the relatively shorter head and larger eyes.

Genus *Protobacillometra* Nel & Paicheler

Protobacillometra Nel & Paicheler, 1993: 80.

Type species: *Protobacillometra oligocenica* Nel & Paicheler, 1993; by original designation and monotypy.

Diagnosis

Body elongate, thirteen times as long as wide. Head very long, as long as thorax and three times as long as pronotum, slightly thickened at base and towards apex. Eyes large, their diameter more than interocular width of head; ocelli absent. Antennae long, but less than twice the head length; first segment stout, slightly shorter than second segment; third segment longest, fourth segment as long as second segment. Pronotum relatively short and parallel-sided, its width about two thirds of its length. Legs inserted on thorax at about equal distances from each other. Legs long and slender, femora not thickened basally. Front femora almost reaching apex of head; hind legs about as long as body; hind femora not reaching abdominal end. Mediotergites of abdomen much longer than wide.

Distribution and geological horizon

Provence, southern France (see map, Fig. 3).
Upper Oligocene, 30-24 Ma.

Remarks

Nel & Paicheler (1993: 81) discussed the systematic position of *Protobacillometra* in detail and concluded that the extinct genus was closest to the hydrometrine genera *Bacillometra* and *Hydrometra*. Referring to the cladogram of relationships between hydrometrid genera (Andersen 1977a), Nel & Paicheler (1993: 81) concluded (in translation): “*Protobacillometra* probably represents the sister-group of *Bacillometra* with which it shows most affinity, or the sister-group of the two genera *Bacillometra* + *Hydrometra*.” I agree that the very elongate head and body, the long and extremely slender legs, and especially the relatively short first antennal segment place *Protobacillometra* in the subfamily Hydrometrinae. The relatively short thorax (metathorax not prolonged) affiliates the fossil form with *Bacillometra*, but its antennae and legs are shorter than those of the three extant species of the latter genus (Andersen 1982b).

Protobacillometra oligocenica Nel & Paicheler

Protobacillometra oligocenica Nel & Paicheler,
1993: 80-81, figs. 92-95.

Descriptive notes

Holotype (part and counterpart) from “série de gypse d’Aix”, Aix-en-Provence, France, Coll.

Nel; deposited in Institut de Paléontologie du Muséum National d’Histoire Naturelle, Paris (MNHN-LP-R.07893). The following extract (in translation) from the original description (Nel & Paicheler 1993: 80-81) will characterize the fossil species:

Insect preserved in dorsal position, body length 10.68 mm, width 0.84 mm. Head 2.82 mm long and 0.34 mm wide; antecular part of head 1.86 mm, postocular part 0.96 mm. Diameter of an eye 0.22 mm, interocular distance 0.15 mm. Antennae 5.05 mm long; lengths of antennal segments 1-4: 0.50, 0.93, 2.54, and 1.08 mm. Length of thorax 2.8 mm; pronotum 0.93 mm long and 0.68 mm wide. Lengths of femora and tibiae: front leg: 3.10 and 2.02 mm; middle leg: 3.56 and 2.50 mm; hind leg: 4.28 and 4.18 mm. Only hind tarsus preserved, 0.71 mm long, with three segments measuring 0.25, 0.25, and 0.21 mm, respectively; claws very small. Abdomen 3.16 mm long; longitudinal sutures between sternites and tergites visible.

Geological horizon

Found in the formation “Gypse d’Aix” at Aix-de-Provence, France. Upper Oligocene, 30-24 Ma (Nel & Paicheler 1993).

Distribution

Provence, southern France (see map, Fig. 3).

Remarks

See under the generic heading (above).

Family **HYDROMETRIDAE** Billberg, *incertae sedis*

Limnobates (= *Hydrometra*) *prodromus* Heer

Limnobates (= *Hydrometra*) *prodromus* Heer, 1865: 392. Nomen nudum (Nel & Paicheler 1993: 82).

Note

This species was recorded by Heer (1865) from Miocene deposits at Oeningen in Baden, Germany, without any illustrations or descriptive notes except for the statement that the fossil form had a certain resemblance to *Limnobates* (= *Hydrometra*) *stagnorum* L. Declared *nomen nudum* by Nel & Paicheler (1993).

Family **HEBRIDAE** Amyot & Serville

Velvet water bugs, Sphagnum bugs

Subfamily **Hebrinae** Amyot & Serville

Genus *Stenohebrus* Polhemus

Stenohebrus Polhemus, 1995: 78-79.

Type species: *Stenohebrus glaesarius* Polhemus, 1995; by original designation and monotypy.

Diagnosis and description

Small, macropterous bugs with elongate oval body (Fig. 75). Head long, porrect, only slightly declivent but narrowed anteriorly. Eyes globose, exerted and very prominent, located adjacent to prothorax. Ocelli obscured, but probably present. Antennal tubercles very large, produced laterally to outer eye level; antennae about half as long as body; segment 1 stout, shorter than head; segment 2 more slender, about half as long as segment 1; segments 3

and 4 flagelliform, set with scattered long hairs; segment 4 subdivided by a "false joint". Ventral head surface with long carinate buccula which are produced anteriorly. Rostrum very long, reaching beyond posterior coxae. Pronotum (pn) longest on midline, with anterior collar, prominent humeri, and strongly bilobed hind margin. Mesoscutellum short, metanotal elevation (mt) triangular, rounded distally, shallowly notched on apex; median carina not visible. Paired, ventral carinae of thorax (rostral groove) well developed, parallel throughout, continuing separately onto base of abdominal venter. Femora stout; tibia slender, unarmed except for spur of stiff hairs distally; tarsi two-segmented, first segment shortest, second segment distally set with long hairs. Claws long and very slender, with prominent basal spur. Fore-

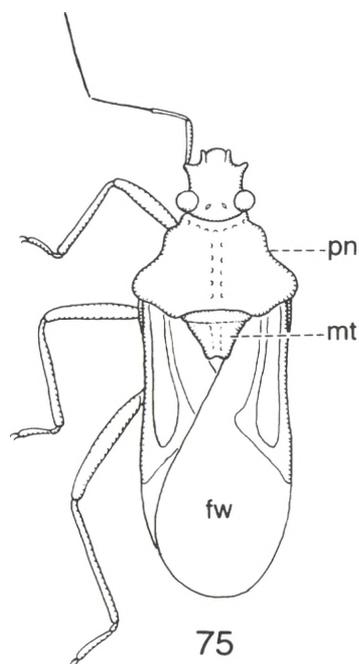


Fig. 75. *Stenohebrus glaesarius* Polhemus, dorsal view (reconstruction); antenna and legs of right side omitted.

ing (fw) with two prominent, basal veins forming a closed cell along anterior margin. Abdomen longer than broad, not depressed ventrally. Female first gonocoxa large, prominent.

Distribution and geological horizon

Mexican (Chiapas) amber, Mexico (see map, Fig. 2). Oligocene/Miocene, 30-20 Ma (Hurd et al. 1962; Poinar 1992).

Remarks

Polhemus (1995: 79) discussed the relationships of this fossil genus as follows: "This genus differs from known extant hebrids by the protuberant eyes, strongly laterally produced antennal tubercles, long slender claws, and apparent lack of arolia. *Stenohebrus* is most similar to *Hebrometra* Cobben, sharing the basal spur on the claws, but in the latter the rostral cavity

[rostral groove] is closed posteriorly and the bucculae are reduced, not produced posteriorly, whereas in *Stenohebrus* the rostral cavity is open posteriorly, and the bucculae are well developed and strongly produced posteriorly."

I have previously (Andersen 1981, 1982b) discussed the phylogenetic relationships between the extant genera of the Hebridae. *Stenohebrus* is difficult to place because information on some critical characters (fine structure of antennae, female gynatrial complex) are missing. There is no doubt, however, that the fossil genus belongs to the subfamily Hebrinae. Since the fourth antennal segment has a "false joint", and the paired, ventral carinae of thoracic venter are parallel throughout, *Stenohebrus* is probably most closely related either to the worldwide distributed genus *Hebrus* Curtis or to *Hebrometra* from East Africa. Polhemus (1995: 79) suggested that the laterally produced antennal tubercles ally *Stenohebrus* with *Hebrus* subgenus *Timasielloides* Poisson from the Ethiopian and Oriental regions, but that other features place it closer to *Hebrometra*.

Stenohebrus glaesarius Polhemus

Hebrus sp. Poinar, 1992: 114, fig. 61.

Stenohebrus glaesarius Polhemus, 1995: 79-80, figs 1-3.

Descriptive notes

Original description (Polhemus 1995) based on a female specimen contained in a piece of cut and polished amber from Chiapas, Mexico. Holotype deposited in the Palaeontological Museum, University of California, Berkeley, U.S.A. (C. Mus. Paleo. No. 12894). I have not seen the holotype and the following descriptive notes are extracted from Polhemus (1995).

Holotype. Macropterous female, length 1.83 mm, greatest width 0.67 mm. Elongate oval, apparent ground colour brownish black; legs, ros-

trum, and antennae brownish. Head length 0.30 mm, width across eyes 0.28 mm. Eyes moderately large, exerted, with about 30 ommatidia; eye width (0.06 mm) less than half width of interocular space (0.16 mm). Lengths of antennal segments 1-4: 0.18, 0.14, 0.26, and 0.11 + 0.26 mm; pseudoarticulation in middle of segment 4 broad but indistinct. Length of pronotum 0.35 mm; anterior collar set off with a row of pits. Length of mesoscutellum 0.05 mm; metanotal elevation 0.16 mm long and 0.30 mm wide. Lengths of leg segments (femur, tibia, tarsus): front leg: 0.35, 0.37, and 0.15 mm; middle leg: 0.41, 0.41, 0.17 mm; hind leg: 0.53, 0.53, 0.18 mm; first tarsal segment (0.03 mm) much shorter than second segment (0.12-0.15 mm). Forewings long, reaching tip of abdomen; "clavus" (posterior part of wing) lightly tinged with brown; "corium" (basal part of wing) smoky, indistinct; "membrane" (distal part of wing) fumose, with paler spot near distal angle of closed proximal cell. First gonocoxae large, plate-like, covering all but triangular proctiger.

Geological horizon

Mexican (Chiapas) amber, Oligocene/Miocene, 30-20 Ma.

Distribution and palaeoecology

Chiapas, Mexico (see map, Fig. 3). Polhemus (1995: 79-80) states: "The slender claws with a prominent basal spur are similar to semiaquatic bugs living on damp earth or hygropetric habitats, e.g. *Hebrometra* spp., *Ochterus* spp. [Ochteridae], thus it seems likely that this species ranged away from the waters edge."

Remarks

The reconstruction (Fig. 75) was made from photographs in Poinar (1992) and Polhemus (1995). From the original description (Polhemus 1995: 79) one may get the impression that the antennae have five segments. However, the fourth and last segments of most hebrids are subdivided by a "false joint" (see Andersen 1982b: fig. 114), but all Hebridae have four antennal segments like other gerromorphans. See also above under the generic description.

Class **Insecta**, *incertae sedis*

Genus *Palaeovelina* Scudder

Palaeovelina Scudder, 1890: 349, plate 22, fig. 13.

Type species: *Palaeovelina spinosa* Scudder, 1890; designation by monotypy.

Descriptive notes

Scudder (1890: 349) gave a rather detailed description of this genus, e.g. "Head much as in *Microvelina*, small, subtriangular, with rounded angles, a little broader than long, plunged to

the eyes in the roundly emarginate prothorax..." "Thorax pentagonal, the sides subequal, the lateral faces straight, the front concave, the posterior faces still more concave but a little shorter than the others, the median posterior process not reaching far back, rather acute.", and "Hind legs very short, only reaching the tip of abdomen, the femora and tibiae of nearly equal length, the tarsi longer than either, the tibiae and first tarsal joint both armed at the tip with prominent delicate spines, the tarsi three-jointed."

In the description of the type species Scudder (1890: 349) further writes: "The legs are pretty thickly beset with fine, stiff hairs, the apical spines of the tibia and first tarsal joint about as long as the width of the joint, the tibiae also with an apical or preapical spur fully twice as long."

Distribution and geological horizon

Florissant Formation, Colorado, U.S.A (see map, Fig. 2). Upper Eocene, about 40 Ma (see under *Metrobates (?) aeternalis*, above).

Remarks

The hind legs are unusually short and the hind tarsus (being longer than tibia) is unusually long for veliids. Most important, the presence of apical spines on the tibia and first tarsal segment, and a apical and preapical spur on the tibia, set *Palaeovelina* apart from any living gerromorphan. Therefore, I very much doubt that Scudder's genus can be classified in any family of Gerromorpha.

Palaeovelina spinosa Scudder

Palaeovelina spinosa Scudder, 1890: 349, Plate 22, fig. 13.

Note

Description and illustration (Scudder 1890: 349, plate 22, fig. 13) based on a single specimen from the Florissant Formation, Colorado, U.S.A. Type probably deposited in the Royal Ontario Museum, Ottawa, Canada. Length 3.65 mm, width 1.85 mm, length of hind femur 0.8 mm, tibia 0.8 mm, tarsi 1.2 mm. Other characters, see generic description (above).

Geological horizon

Florissant Formation, Upper Eocene, about 40 Ma (see under *Metrobates (?) aeternalis*, above).

Distribution and palaeoecology

Colorado, U.S.A. (see map, Fig. 2). The palaeoenvironment of the Florissant fauna was discussed above (under *Metrobates (?) aeternalis*).

Remarks

See under generic heading (above).

Velia (?) bouati Meunier

Velia (?) bouati Meunier, 1914: 191, fig. 3.

Insecta, *incertae sedis*. – Nel & Paicheller, 1993: 79.

Note

Meunier (1914) described this species based on several specimens contained in a plate of laminites from the Upper Oligocene "Gypse d'Aix", Aix-en-Provence, Bouches-du-Rhone, France (see map, Fig. 3). The type(s) should be deposited in the Museum d'Aix-en-Provence, France, but Nel & Paicheller (1993: 79) consider the material lost. However, Nel (personal communication) now tells me, that the material was bought by the Los Angeles County Museum and that the type of this species probably is deposited there. The original description (Meunier 1914) is too brief and inadequate and the photo of the specimens of very bad quality. Nel & Paicheller (1993: 79) consider these fossils for indeterminate. It is not even certain that they should be classified in the Heteroptera. I therefore agree with Nel & Paicheller (1993) that *Velia bouati* Meunier (1914) should be treated as Insecta, *incertae sedis*.

Gerris (?) sp. – Oligocene, France

Note

A fossil insect recorded as *Gerris* sp. by Serre (1829) from the Upper Oligocene of Aix-en-Provence, Bouches-du-Rhone, France, is probably not a gerrid. Nel & Paicheller (1993: 82) mention that the type of *Megalomerium serratum*

Theobald (1937) (classified in the family Berytidae; Heteroptera, *incertae sedis* according to Nel 1992) carry the label (probably written by Serre): “Hémiptère. Gerris. Gerris ou Ploiaria Latreille. Genera”. Therefore, this may be the specimen referred to as “*Gerris* sp.” by Serre (1829).

The author of *Gerris*, I.C. Fabricius (1794) was responsible himself for some confusion about the taxonomic meaning of this genus name. In later writings (Fabricius 1803), he applied this name to various heteropterous bugs with long and slender body and legs (e.g. in the families Alydidae, Berytidae, and Reduvi-

dae). Instead, Fabricius and other authors of the early 19th century used the name *Hydrometra* Latreille for “true” gerrids.

***Gerris* (?) sp.** – Oligocene, Germany

Note

Statz (1950) recorded an almost complete larva (nymph) of Gerridae (?) from the Middle Oligocene diatomite, Rott-am-Siebengebirge, Germany (see map, Fig. 3). Nel & Paicheler (1993: 82) recommended a revision of this specimen in order to verify its classification in *Gerris*.

Mesozoic Gerromorpha

Family **VELIIDAE** Brullé, *incertae sedis*

Water crickets, riffle bugs

Veliiidae sp. – Lower Cretaceous, Australia

Veliid indet. Jell & Duncan, 1986: 143, figs. 24A, 25A-C.

Descriptive notes

Jell & Duncan (1986) described this fossil form based on two specimens from the Koonwarra fossil bed (Korumburra group), South Gippsland, Victoria, Australia (see map, Fig. 2). The specimens are deposited in the Palaeontological Collection, Museum of Victoria, Melbourne (NMVP103235 and 103236). The original description says (Jell & Duncan 1986: 143):

“NMVP103235 dorsoventrally compressed, 3

mm long, with hind tibia 2.4 mm long. Head triangular, with bulging lateral eyes, produced anteriorly to obtuse angle. Antennae long, thin, apparently with few segments (not clearly defined except for two long basal segments). Pronotum about half as long as wide, with anterior and posterior margins transverse. Mesonotum and metanotum not clearly differentiated, together longer than pronotum. legs all long, thin, with femora obviously wider than tibiae, with hind leg distinctly longest. Abdomen tapering markedly to apex, with wide doublure; segments transverse and short anteriorly, becoming longer towards posterior; sixth segment more than half as long as wide.”

Distribution and geological horizon

Koonwarra fossil bed (Korumburra group). Lower Cretaceous (Aptian), about 120 Ma.

Distribution and palaeoecology

South Gippsland, Victoria, Australia (see map, Fig. 3). Jell & Duncan (1986: 112-113) suggested that the palaeoenvironment of this site "formed a shallow part of, or was periodically linked with, a larger body of water (e.g. a lake) from which it received a periodic repopulation of its aquatic fauna." and "Conditions within this environment were of the still-water type, or nearly so, for most of the period of sedimentary deposition." The insect fauna of this fossil bed consists of "1, the resident lake fauna with preservation of whole larvae as well as moulted cuticles; 2, a transported stream fauna of moulted cuticles of larvae that dwelt in the inflow stream; and 3, a terrestrial component floundering onto the lake surface and dying there outspread under the stress of surface tension." Jell & Duncan (1986: 113) further suggested: "The fauna of the lake was apparently very similar to that of present-day, shallow, cold, freshwater lakes of southeastern Australia and Tasmania."

Remarks

Jell & Duncan (1986: 143) give the following remarks: "The body resembles that of members of the Gerridae but differs in the hind leg being longer than middle leg and in femora not being extremely narrow. The shape of the head is characteristic of the Veliidae and although the hind leg is longer than is usual in that family we assign the specimen to the Veliidae rather than the Mesoveliidae."

If this fossil form is correctly assigned to the family Veliidae it provides us with a minimum age, not only for the Veliidae, but also for the origin of the other large gerromorphan family, the Gerridae. The incomplete nature of the specimens, however, makes the interpretation and classification extremely difficult. Apomorphic characters of the Veliidae most likely to be preserved in compression fossils are (Andersen 1982b): 1, head broad, deflected in front of eyes; 2, ocelli absent (except in *Ocellovelia* China & Usinger); 3, first antennal segment usually longer than fourth; 4, middle and hind legs inserted laterally on thorax; 5, front tibia with grasping comb (at least in male); 6, middle tibia with row of long trichobothria-like hairs; 7, claws inserted preapically on tarsi. In addition, the middle legs are longer than the hind legs in many veliid groups. Veliids are, among other characters, separated from gerrids by their relatively shorter thorax and shorter and more robust middle and (in particular) hind femora.

The description and illustrations of the fossil "Veliid indet." from the Koonwarra Fossil Bed (Jell & Duncan 1986: 143, fig. 24A, 25A-C), only provide few clues to its systematic position. The habitus of the fossil is definitely veliid-like, and its relative short and broad head also support Jell & Duncan's family assignment. On the other hand the legs, in particular the hind pairs, are longer and more slender than typical for veliids, and the structure of the tarsi (including the point of insertion of claws) is unknown. In conclusion, I accept (with some reservation) that this Lower Cretaceous form is placed in the family Veliidae. Additional specimens showing more of the diagnostic features listed above are highly desirable.

Family **HYDROMETRIDAE** Billberg

Marsh treaders, water measurers

Hydrometridae sp. – Lower Cretaceous, Brazil

Note

Through the courtesy of André Nel, Paris, I have been able to see a manuscript draft with the description of a fossil Hydrometridae from the Lower Cretaceous (Aptian, about 120 Ma) Santana Formation, Araripe Basin, Brazil (see map, Fig. 2). Since this species will be described in a forthcoming paper by A. Nel and Y. Popov, I have been permitted to supply the following notes relevant in the present context.

The species is apterous (wingless), with very long and slender head, body, and legs. Eyes

ovate, prominent, located in posterior third of head; anteocular part of head more than twice as long as postocular part. Antennae long, first antennal segment a little shorter than second segment. Pronotum with subparallel sides, slightly longer than anteocular part of head. Meso- and metathorax of about same length. Abdominal mediotergites longer than broad.

Nel (personal communication) concludes that the fossil belongs to the family Hydrometridae and probably is a member of the Hydrometrinae or has a sister group relationship to this subfamily. So far, this is the oldest known fossil hydrometrid.

Family **MESOVELIIDAE** Douglas & Scott

Pondweed bugs

Genus *Duncanovelia* Jell & Duncan

Duncanovelia Jell & Duncan, 1986: 143.

Type species: *Duncanovelia extensa* Jell & Duncan, 1986; by original designation and monotypy.

Diagnosis

Jell & Duncan (1986: 143) characterize this fossil genus as “Mesoveliid with elongate head, with eyes situated near midlength of head, with antennae of four long segments, with thoracic

segments relatively short, subequal although becoming slightly longer to posterior.”

To this may be added that the fourth antennal segment is shorter than the basal three segments, that metanotum is roughly triangular, and that the first tarsal segment is very short. Only apterous form known.

Distribution and geological horizon

Victoria, Australia. Koonwarra fossil bed (Koorumburra group) (see map, Fig. 2). Lower Cretaceous (Aptian), about 120 Ma.

Remarks

The reconstruction (Fig. 76) of an apterous female was based upon the photographs and drawings presented by Jell & Duncan (1986). The authors noted the superficial resemblance of this genus to members of the heteropteran families Nabidae and Alydidae from which it is said to differ in its shorter pronotum (Fig. 76, pn); it also resembles some Miridae but the combination of short pronotum and long scape (first antennal segment) is said to distinguish it from that family. Jell & Duncan (1986: 143) assign the fossil to the Mesoveliidae "on

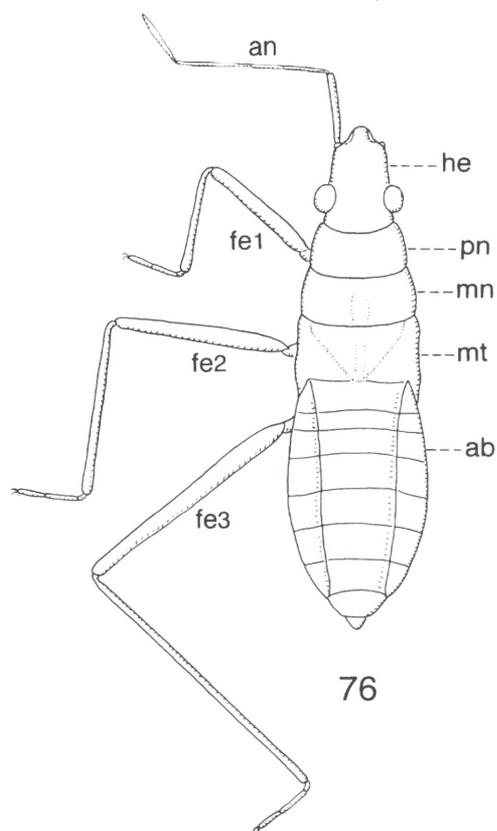


Fig. 76. *Duncanovelia extensa* Jell & Duncan, apterous female, dorsal view (reconstruction); appendages of right side omitted.

the overall similarity but in particular, similar pronotum, head shape, and legs".

Duncanovelia resembles a number of heteropteran groups, including the family Lygaeidae and their relatives (Schuh & Slater 1995), but the relatively long first antennal segment excludes it from most families of Cimicomorpha. If Jell & Duncan's interpretation of the relative lengths of tarsal segments is correct, the fossil genus is also excluded from most Pentatomorphan families where the first tarsal segment usually is much longer than the other segments. The interpretation of the thorax structure is difficult. Jell & Duncan (1986: 143) state "pronotum transverse, half as long as wide" meaning that the pronotal lobe is reduced, exposing the mesonotum. The thoracic segments are said to be "subequal although becoming slightly longer to posterior". Judging from Jell & Duncan's illustrations of the fossils (in particular the camera lucida sketch, fig. 24B), the metanotum should be roughly triangular, thus resembling the scutellum of many heteropterous bugs (including some Mesoveliidae; Andersen 1982b: figs. 69-70). However, a scutellum is never present in the apterous adult form. An alternative interpretation could be that the fossils are winged adults, with a large pronotal lobe and a triangular scutellum; the wings may either have been lost or have left no traces during fossilization. However, without having examined the fossils myself, I prefer to accept the interpretations provided by Jell & Duncan, which classify *Duncanovelia* as belonging to the Mesoveliidae.

Apart from the unique dorsal structure of the thorax, the head structure also deviates from most living mesoveliids (Andersen 1982b). The eyes are distinctly removed from the base of head, a condition only observed in those mesoveliids where the eyes are reduced (e.g. *Cavaticovelia aaa* (Howarth & Gagné and *Cryptovelia terrestris* Andersen & Polhemus). The relatively short fourth antennal segment is

also unique. Extant mesovelids are currently classified in two subfamilies, Madeoveliinae and Mesoveliinae (Andersen 1982b). The apterous form is only found in the latter and *Duncanovelia* may therefore belong in the subfamily Mesoveliinae.

Duncanovelia extensa Jell & Duncan

Duncanovelia extensa Jell & Duncan, 1986: 143-144, figs 24B, 25D-F.

Descriptive notes

Jell & Duncan (1986) described this fossil species based on a holotype and paratype from the Koonwarra fossil bed (Korumburra group), South Gippsland, Victoria, Australia (see map, Fig. 2). The types are deposited in the Palaeontological Collection, Museum of Victoria, Melbourne (Holotype NMVP27044 and paratype NMVP103237). The original description says (Jell & Duncan, 1986: 143-144):

“Body heavily sclerotized (so presumably an adult), 5 mm long, thin, with long legs. Head long, with anteriorly rounded frons produced forward in front of laterally placed antennal insertions; eyes prominent, situated laterally near midlength of head; antennae 4-segmented, all segments long, basal three subequal, apical

segment shorter and slightly expanded. Thoracic segments distinct; pronotum transverse, half as long as wide, slightly drawn out at anterolateral corners, with gently convex lateral margins. Legs long and thin, increasing slightly in length from front to hind legs, femur slightly wider towards base, tibia longer than femur; tarsus 3-segmented, basal segment very short, second twice as long as apical, tarsal claws terminal. Wings absent. Abdomen with distinct segmentation, fourth and fifth segments longest; two well-separated longitudinal grooves delimiting lateral flanges; terminalia not clearly discernible but apparently those of a male in NMVP27044 [holotype] with a median, subapical, more heavily sclerotized area.”

Geological horizon

Koonwarra fossil bed (Korumburra group). Lower Cretaceous (Aptian), about 120 Ma.

Distribution and palaeoecology

South Gippsland, Victoria, Australia (see map, Fig. 2). Notes on palaeoenvironment given by Jell & Duncan (1986: 113-114; see above under Veliidae – Cretaceous, Australia).

Remarks

See under the generic heading (above).

Infraorder **Gerromorpha** (?), *incertae sedis*

Engynabis tenuis Bode

Engynabis tenuis Bode, 1953: 130-131, 355, pl. 6, fig. 111. – Popov & Wootton, 1977: 348, fig. 25.

Descriptive notes

This Lower Jurassic fossil from Mecklenburg, Germany, was classified as belonging to the infraorder Gerromorpha by Popov & Wootton (1977). I have not examined the holotype (deposited in Mineralogisch-Geologisches Institut

der Technische Hochschule Braunschweig, Germany) and the following notes are based on the redescription and illustration provided by Popov & Wootton (1977: 348, fig. 25).

Length 4.5 mm, width 1.3 mm. Head perfect, slightly longer than broad, with large eyes; antennae missing. Pronotum with a narrow anterior collar, the remaining part of pronotum circular with four large indentations. Scutellum short and narrow. Legs missing. Forewings slender, particularly at the base, with reduced venation. R close to the costal margin, radial cell more heavily sclerotized, or pigmented, than the rest of the remigium. R and M separate within the basal quarter of the wing, both unbranched. M and CuA may be joined by two cross-veins. Clavus very narrow, not projecting from the hind margin of the wing.

Distribution and geological horizon

Hondelago near Braunschweig, Mecklenburg, Germany (see map, Fig. 2). Lower Jurassic (Lower Toarcian or Upper Liassic), about 190 Ma.

Remarks

Engynabis tenuis has several structural details not found in any living gerromorphan (for comparisons, see Andersen 1982b), e.g. the anterior collar of pronotum, indentations of pronotum, and a forewing venation with a sclerotized or pigmented radial cell and a distinct

clavus. A triangular scutellum (or similar structure) is only present in members of the families Mesoveliidae and Hebridae. The presence of two cross-veins in the forewing resembles the venation found in some Hydrometridae. On these grounds, I find the conclusions by Popov & Wootton (1977: 350) too far reaching: “*Engynabis* is clearly a member of the Gerromorpha (Gerroidea) and is probably closely related to *Karanabis* Becker-Migdisova, from the Upper Jurassic of Karatau, Kazakhstan. An account of this group is in preparation, and further evaluation of *Engynabis* must await its publication. It is enough to note here that it is the oldest known gerromorpha, and that it also now provides the earliest direct evidence of surface-film predation in insects (cf. Wootton, 1972)”.

Gerromorpha (?) – Lower Cretaceous, Brazil

Note

Grimaldi & Maisey (1990: fig. 1D) published a photograph of a “Gerromorpha?” from the Lower Cretaceous (Aptian, about 120 Ma) Santana Formation, Araripe Plateau, northeastern Brazil (see map, Fig. 3). The specimen seems to be well preserved (legs present), with a rather stout body. If the scale of this picture is correct, the insect should be about 8.5 mm long and about 3.5 mm wide. Further study of this specimen is necessary to verify its classification in the Gerromorpha.

Phylogeny and the fossil record

General principles and methods

Cladistics and fossils

The evolutionary history or phylogeny of a group of organisms is the most useful, general reference system in evolutionary biology. A phylogeny is usually presented as a dichotomously branching diagram as shown by a simple example (Fig. 77, A). In this case, a number of species (A-F) evolved through a series of dichotomous splitting of ancestral species, for example a_0 and a_1 . Species and other taxa are distinguished by way of their characters (traits, features). Any character can be viewed as a set of alternative conditions called character states. In a phylogenetic context, we distinguish between ancestral and derived states of a character.

Cladistics is a set of principles and methods for reconstructing phylogenies on basis of shared, derived character states. Organisms that share many derived character states are grouped more closely together than organisms that do not. The phylogenetic relationships between organisms are shown by a branching, tree-like diagram called a *cladogram* (Fig. 77, B). The cladogram is usually constructed so that the number of implied character changes are minimised. The rationale behind this procedure is that the hypothesis that requires fewest assumptions about character changes is to be preferred. This is also called the principle of parsimony (see, e.g. Smith 1994).

Modern principles and methods of cladistics are founded upon "Phylogenetic systematics" developed by the German zoologist Willi Hennig (Hennig 1966; Nelson & Platnick 1981; Forey *et al.* 1992; Smith 1994). Following the terminology developed by Hennig (1966), the

ancestral state of a character is called a *plesiomorphy* and the derived state is called an *apomorphy*. It is important to realise that plesiomorphy and apomorphy are relative, not absolute concepts. A character state which is apomorphic for a set of species may be plesiomorphic for a subset of these species.

Without knowing the true phylogeny of a group of organisms, the only method of reconstructing this phylogeny is to use the historical information embedded in the characters of these organisms. In the present example (Fig. 77, B), each of the species A-F are described by either the plesiomorphic or apomorphic state for character nos 1-7. Only similarities in relatively derived or apomorphic character states can be used to reconstruct the phylogenetic relationships between organisms. Hennig (1966) introduced the term *synapomorphy* for similarity in the derived state(s) of a character. Alternatively, similarity in the ancestral state of a character was termed *symplesiomorphy*.

A *monophyletic group* or *clade* is a group of species that shares a common ancestor exclusive to them. That is, the most recent ancestor of the group is not shared by any species outside the group. In the present example, D + E + F is a monophyletic group of species that evolved from a common ancestor (Fig. 77, A: a_1). The group A + B + C is not a monophyletic group because it excludes some species (D, E, and F) that evolved from their most recent common ancestor (a_0). Such groups are also termed *paraphyletic* groups. Two monophyletic groups, or a monophyletic group and a single species, are *sister groups* if they are each other's closest relatives, that is sharing a common ancestor exclu-

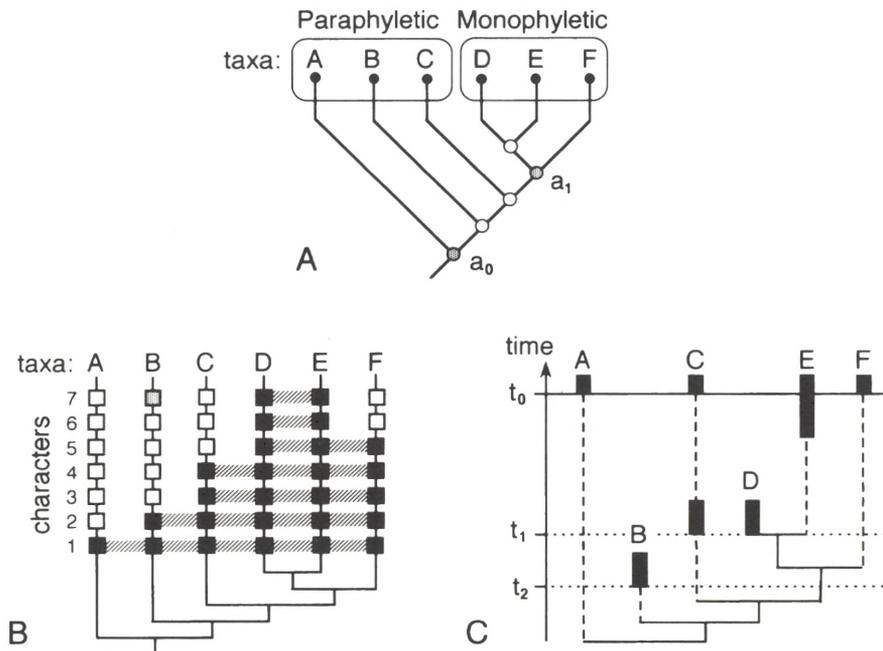


Fig. 77. Cladogram and phylogenetic tree for six taxa (A - F). A, definition of paraphyly and monophyly. B, cladogram with characters used in its construction; open box = plesiomorphy, shaded or filled box = apomorphy, hatched cross-bars = synapomorphies. C, phylogenetic tree showing same relationships between taxa A-F as (B), but also the temporal distributions of fossils (heavy branches) and minimum times of divergence between sister taxa inferred by fossils (unbroken branches). Further explanations in text.

sive to them. Together, sister groups form a more inclusive monophyletic group. A phylogeny can therefore also be described as a nested or hierarchic set of monophyletic groups.

A cladogram of relationships between species A-F (Fig. 77, B) is constructed by grouping species into monophyletic groups, each supported by one or more synapomorphies. Examples of such groups in the cladogram are D + E (supported by apomorphic states of character nos 6 and 7), D + E + F (character No. 5), C + D + E + F (character nos 3 and 4), etc. This method also reconstructs the most likely sequence of branching events or nodes in the phylogeny of species A-F. Unfortunately, character state distributions are not always that simple. In character No. 7, the apomorphic state has seemingly evolved twice independ-

dently of each other, in B and D + E. This is the third kind of similarity, convergence or parallelism, collectively termed *homoplasy*. Most difficulties in reconstructing phylogenies stem from problems in distinguishing homoplasies from synapomorphies. The acceptance of the parsimony criterion serves to maximise the congruence of characters (nested sets of synapomorphies) and to minimise character conflict when incongruence due to homoplasy is present.

Generally, fossil taxa are difficult to compare with extant taxa, in particular when diagnostic characters are hidden in morphological structures which are impossible to observe in most fossils. This is especially the case when the fossils are preserved in rocks, petrified or as casts or moulds. Insects enclosed in amber usually

reveal more details (see, e.g. Andersen & Poinar, 1992) and recent advances in molecular systematics open the exciting possibility of extracting DNA from amber insects (e.g. DeSalle *et al.* 1992; but see Austin *et al.* 1997). Although fossils can play a crucial role in understanding the phylogeny of a groups of organisms with both extant and fossil species (for examples see, e.g. Smith, 1994), most cladograms will have to be based on characters gathered from extant species. This is certainly the case with the cladograms presented below.

Phylogenetic tree

In agreement with, e.g. Eldredge & Cracraft (1980) and Smith (1994), I here use the concept of *phylogenetic tree* to denote a cladogram calibrated against the fossil record. A phylogenetic tree (Fig. 77, C) combines the results of a cladistic analysis (presented as a cladogram, Fig. 75, B) with biostratigraphic data, using the fossil record to date the earliest appearances of taxa with apomorphic character states and thus establish the time by which each branch of the cladogram must have come into existence.

The example cladogram (Fig. 77, B) presents the reconstructed phylogeny for species only known from extant material (A and F), species with both extant and fossil material (C and E), and species known only as fossils (B and D). In the phylogenetic tree (Fig. 77, C), the range of each species is shown in relation to a time scale (t_0 = present). Since sister groups have evolved by the splitting of one ancestral species, such groups have by definition the same time of origin. For example, the species D and E are sister groups, and the fossil specimen(s) of D (recorded at time t_1) determine not only the minimum age of this extinct species, but also of the lineage leading to the extant species E. The extra stratigraphic range added to the observed range of fossils represents a *range extension* (Smith 1994: 138). Like-

wise, the split between the extinct species B and the monophyletic species group C + D + E + F must have occurred at the time t_2 or earlier. By applying such *ad hoc* assumptions about range extensions, minimum ages can be assigned to lineages with an incomplete fossil record.

In a phylogenetic context, the word *extinction* cannot be used without specification. Only monophyletic groups can go extinct because these are the only groups that consist of *all* descendants of a common ancestor. By definition, paraphyletic groups cannot be extinct since they exclude at least some descendants of a common ancestor. For example, even if the extant species A and C (Fig. 77, C) ceased to exist, their most recent common ancestor (Fig. 77, A: a₀) still have living descendants (E and F).

Heteroptera

Cladogram

The Heteroptera or true bugs has since long been well established as a monophyletic group within the insect order Hemiptera (Schuh & Slater 1995). This suborder was divided by the pre-evolutionary entomologist Dufour (1833) into three major groups: Hydrocorisae (aquatic bugs), Amphibiocorisae (semiaquatic bugs), and Geocorisae (terrestrial bugs). This classification roughly divides heteropterous insects according to their preferred habitats, but is strongly typological since it is based on only one set of characters. Leston *et al.* (1954) introduced the terms Cimicomorpha and Pentatomomorpha in the first formalised attempt to recognise natural groups within the non-monophyletic Geocorisae. This work stimulated other attempts to document the monophyly of higher groups within the Heteroptera, resulting in the recognition of seven such groups (termed infraorders): Enicocephalomorpha, Dipsocoromorpha, Gerromorpha, Nepomor-

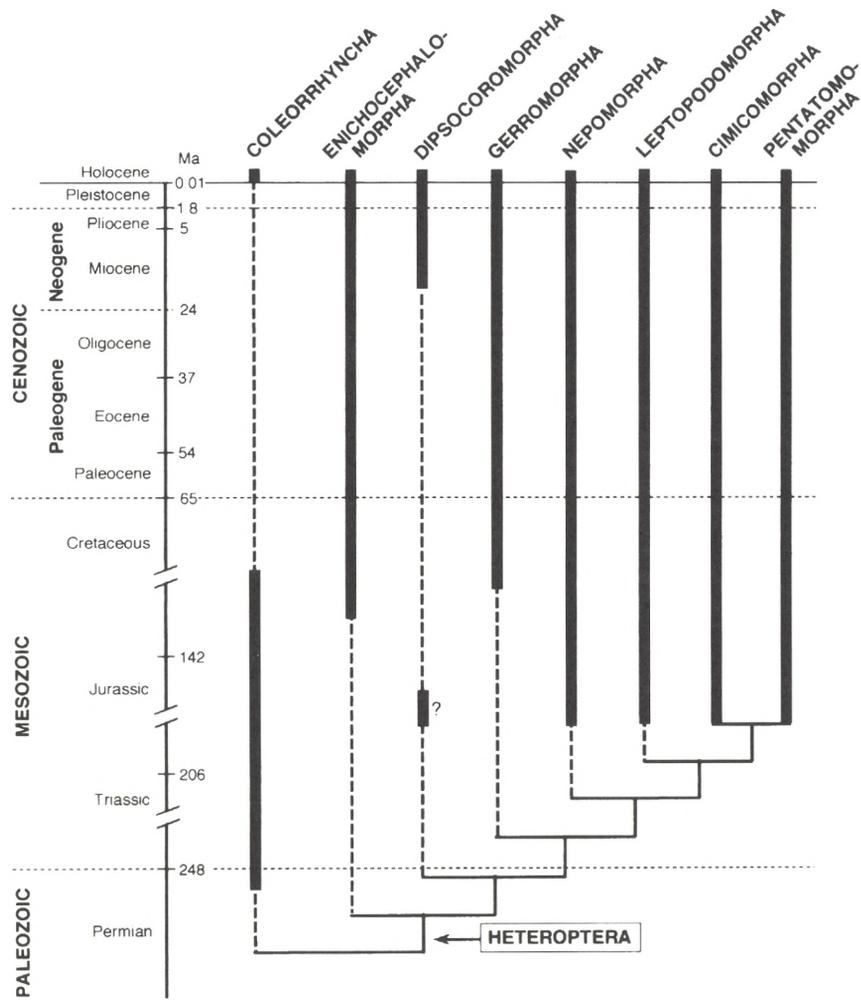


Fig. 78. Phylogenetic tree for the infraorders of Hemiptera-Heteroptera with the Coleorrhyncha (Peloriidae) added. Temporal distributions of fossils indicated by heavy branches; range extensions inferred from fossils shown by unbroken branches; range extension inferred from sister group relationships shown by broken branches. Further explanations in text.

pha, Leptopodomorpha, and Pentatomomorpha (Stys & Kerzhner 1975; Schuh 1986; Schuh & Slater 1995).

The first documented higher-level cladogram for the seven infraorders was that of Schuh (1979), mostly based on character data drawn from the works of Cobben (1968, 1978) on the morphology and evolution of the Heteroptera. The relationships suggested by Schuh

(1979) have been widely accepted (e.g. Andersen 1982b, 1995b; Stys 1985; CSIRO 1991). Schuh (1979) did not present arguments for the apomorphy of the morphological characters used in his cladogram. Recently, however, Wheeler *et al.* (1993) published 18s nuclear rDNA sequences for 29 hemipteran species, representing all infraorders and six outgroup taxa, i.e., the Psocoptera and various groups of

non-heteropteran Hemiptera. Their cladogram, based on combined molecular and morphological data, has been translated into a phylogenetic tree (Fig. 76). Following Schlee (1969) and Carver *et al.* (in CSIRO 1991), the small, southern hemisphere group Coleorrhyncha (Peloriidae) is depicted as sister group of the Heteroptera.

Whereas the Heteroptera undoubtedly is a monophyletic group, the monophyly of the group "Homoptera-Auchenorrhyncha (cicadas, leafhoppers, etc.), has recently been questioned, based on both morphological (Wootton & Betts 1986; Bourgoin 1993; Mahner 1993; Kristensen 1995) and molecular evidence (e.g. Sorensen *et al.* 1995). Thus, it is very likely that the Heteroptera plus Coleorrhyncha are more closely related to the Fulgoromorpha than to the Cicadomorpha, i.e., the two groups comprising the traditional homopteran group "Auchenorrhyncha".

Phylogenetic tree

The fossil record of the Heteroptera was reviewed by Handlirsh (1906-1908) and Carpenter (1992). The phylogenetic tree (Fig. 78) shows the range of the fossil record for the seven heteropteran infraorders. Species classified in the Cimicomorpha, Pentatomomorpha, and Leptopodomorpha have been recorded from the Lower Jurassic. The Nepomorpha (true aquatic bugs) has a quite extensive fossil record (Popov 1971; Nel & Paicheler 1993), which also extends back to the Early Jurassic. Thus the minimum age for these four infraorders is the same, 180-190 Ma.

Popov & Wootton (1977: 348) assigned the genus *Engynabis* Bode from the Lower Jurassic of Germany to "*Gerromorpha incertae sedis*", a decision which has been seriously questioned above. According to the evidence presented in this work, the oldest fossils classifiable in the infraorder Gerromorpha are from the Lower Cretaceous (Aptian) of Australia (Jell & Duncan

1986) and Brazil (A. Nel, personal communication). Since the Gerromorpha is sister group of heteropteran infraorders with an estimated minimum age that is much older, the geological range of the Gerromorpha can be extended back to the Early Jurassic or earlier (Fig. 78).

The oldest fossil Dipsocoromorpha (Dipsocoridae) is from Mexican amber (Oligocene/Miocene) (Wygodzinsky 1959). It is true, however, that Popov & Wootton (1977) assigned the extinct family Cuneocoridae (Hand-

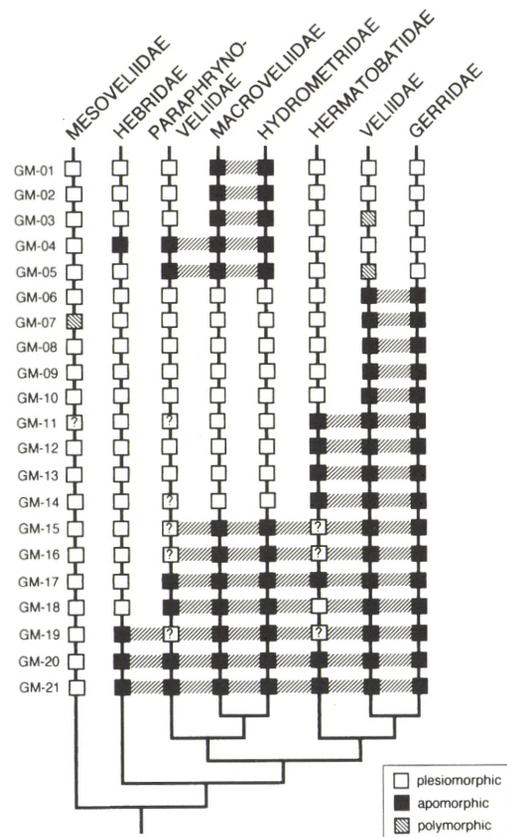


Fig. 79. Cladogram of relationships between the families of Gerromorpha. States of character numbers GM-01 - GM-21 listed in Table 3; box with question mark indicates missing observation, synapomorphies connected by hatched cross-bars. Further explanations in text.

lirsch 1925) from the Lower Jurassic to this infraorder, but this classification needs verification. Fossil Enicocephalomorpha (Enicocephalidae) are now known from Lebanese amber (Lower Cretaceous, Albian – Aptian) and from Dominican amber (Oligocene/Miocene) (Grimaldi *et al.*, 1993), suggesting a minimum age for this infraorder to about 120 Ma. Following the same line of argumentation as for the Gerromorpha (see above), however, the geological age of both the Dipsocoromorpha and Enicocephalomorpha can be extended back to the Early Jurassic or earlier.

In recent time, the Coleorrhyncha, the sister group of the Heteroptera, are only represented by a small number of species belonging to the family Peloriidae and distributed in Australia, New Zealand, and Chile. Popov & Shcherbakov (1991), however, convincingly demonstrated that the extinct families Progonocimicidae (late Permian – early Cretaceous time) and Karabasiidae (Jurassic) could be classified in the Coleorrhyncha. In that case, the minimum age of the sister group of the Heteroptera is about 260 Ma (Fig. 78).

Using both palaeontological and molecular evolutionary evidence, Sorensen *et al.* (1995) argued that the major euhemipteran lineages (Hemiptera except the Sternorrhyncha) already were in existence during late Permian time, more than 250 Ma ago. The present phylogenetic and biostratigraphic evidence (as presented in Fig. 78) imply that the heteropteran infraorders evolved during early Mesozoic time, probably within a relatively short time span.

Gerromorpha

Cladogram

The phylogenetic relationships between the gerromorphan families were analysed and discussed by Andersen (1982b: 253-259). The cladogram (Fig. 79) presents these relationships with the characters supporting each clade (ple-

sio- and apomorphic states for each character listed in Table 3).

The sister group relationship between Macroveliidae and Hydrometridae is supported by the elongate shape of the head with eyes distinctly removed from the anterior margin of prothorax (GM-01), the dorsal location of the metathoracic spiracle (GM-02), and the structure of the basal abdominal tergites (GM03). The idea of a close relationship between the Macroveliidae and Hydrometridae, especially the subfamily Heterocleptinae, was suggested by China & Usinger (1949) and revived by Stys (1976). The discovery of the primitive hydrometrid genus *Veliometra* Andersen (1977a) bridged the morphological gap between the Macroveliidae and Hydrometridae. The close relationship between these two families and the small family Paraphrynoveeliidae was suggested by Andersen (1978) based on shared structures of the ventral head region (GM-04) and metathorax (GM-05). The two described species of *Paraphrynoveelia* are only known in the apterous (wingless) adult form and the missing observations for structures associated with wings complicate a correct placement of the Paraphrynoveeliidae.

The sister group relationship between the large gerromorphan families Veliidae and Gerriidae is strongly supported by several synapomorphies (Fig. 79), including the structure of the salivary pump (GM-06), preapical insertion of claws (GM-07), asymmetrical parempodia (GM-08), presence of evaporative grooves on metathorax (GM-09), and loss of abdominal scent apparatus (GM-10). The close relationships between the two families was suggested by previous workers (e.g. China & Usinger 1949; China 1957), who found it difficult to separate veliids and gerrids on diagnostic characters, chiefly because of the great structural variation observed among the Veliidae.

The relationship of the exclusively marine family Hermatobatidae was discussed by Andersen (1982b: 259). Previous authors (e.g.

Table 3. List of characters of the families of Gerromorpha with their plesiomorphic (p) and apomorphic (a) states.

GM-01.	Location of eyes: close to anterior margin of prothorax (p); distinctly removed from anterior margin of prothorax (a).
GM-02.	Location of metathoracic spiracle on thorax: laterally (p); dorsally (a).
GM-03.	Paired, longitudinal ridges of abdominal tergum: at most reaching abdominal tergum 3 (p); also reaching tergum 4 (a).
GM-04.	Ventral lobes of head (buccula): not protruding (p); protruding in front of and hiding the basal labial segments(s) (a).
GM-05.	Metepisternal process: absent (p); present, directed anteriorly (a).
GM-06.	Salivary pump: isoradial (p); laterally inflected from behind (a).
GM-07.	Insertion of claws on tarsi: apically (at least in middle and hind legs) (p); preapically in all legs (a).
GM-08.	Parempodia (pretarsal structures): symmetrical (p); asymmetrical (a).
GM-09.	Evaporative grooves on metathorax: short or absent (p); long, ending with a hair tuft on metepisternum (a).
GM-10.	Abdominal scent apparatus: present (p); absent (a).
GM-11.	Embryonic egg-buster (if present): paired, clypeal (p); unpaired, median clypeal or frontal (a).
GM-12.	Intercalary sclerites of labial (rostral) segments: absent (p); present, between segments 3 and 4 (a).
GM-13.	Gynatrial sac: not glandular (p); with glandular cells (a).
GM-14.	Number of ovarioles in each ovary: 5 or 7 ovarioles (p); 4 ovarioles (a).
GM-15.	Pronotal lobe (winged form): short and broad, hind margin concave or straight (p); produced backwards in middle, covering mesonotum and (sometimes) part of metanotum (a).
GM-16.	Mesoscutellum (winged form): present (p); absent (a).
GM-17.	Metasternal scent reservoir: lined with glandular cells (p); not lined with glandular cells (a).
GM-18.	Metasternal scent reservoir: without sclerotizations (p); with sclerotizations (a).
GM-19.	Mesoscutellum (winged form): large, triangular (p); reduced to narrow transverse plate or rudimentary (a).
GM-20.	Metathoracic spiracle: situated ventro-laterally on thorax (p); latero-dorsally on thorax (a).
GM-21.	Insertion of coxae: close to ventral midline of thorax (p); displaced laterally on thorax, separated by a rostral groove (a).

China 1957) treated this taxon as a member of the Gerridae, chiefly based on its superficial resemblance to the likewise marine genus *Halobates*. The hermatobatids are, however, more plesiomorphic than both the Veliidae and Ger-

ridae in the characters used to support the sister group relationship between these two families (Fig. 79). Species belonging to the Hermatobatidae share the clypeal embryonic egg-burster (GM-11) with the veliids, but since the

frontal egg-burster of the Gerridae is assumed to have evolved from the clypeal type (Cobben 1968: 318), this character may be a synapomorphy for the three families. The presence of intercalary sclerites between labial segments 3 and 4 (GM-12), a glandular gynatrial sac of the female gynatrial complex (GM-13), and only four ovarioles in each ovary (GM-14) are other synapomorphies supporting the relationship of the Hermatobatidae.

Macropterous (winged) adults of the Macroveliidae, Hydrometridae, Veliidae, and Gerridae have the notal part of pronotum produced backwards, forming a so-called pronotal lobe covering mesonotum and median part of metanotum (GM-15). The mesoscutellum is re-

duced or absent (GM-16). These character states cannot be scored for the families Paraphrynoveliidae and Hermatobatidae where only the apterous (wingless) adult form is known. Gerromorphan families except the Mesoveliidae and Hebridae share an apomorphic structure of the metasternal scent apparatus, in particular the non-glandular reservoir (GM-17) and presence of sclerotisations associated with the accessory scent gland (GM-18). These characters support (as synapomorphies) the relationship between these six gerromorphan families (Fig. 79).

The family Hebridae comprises a very distinct group and its monophyly is supported by several autapomorphies (Andersen, 1982b:

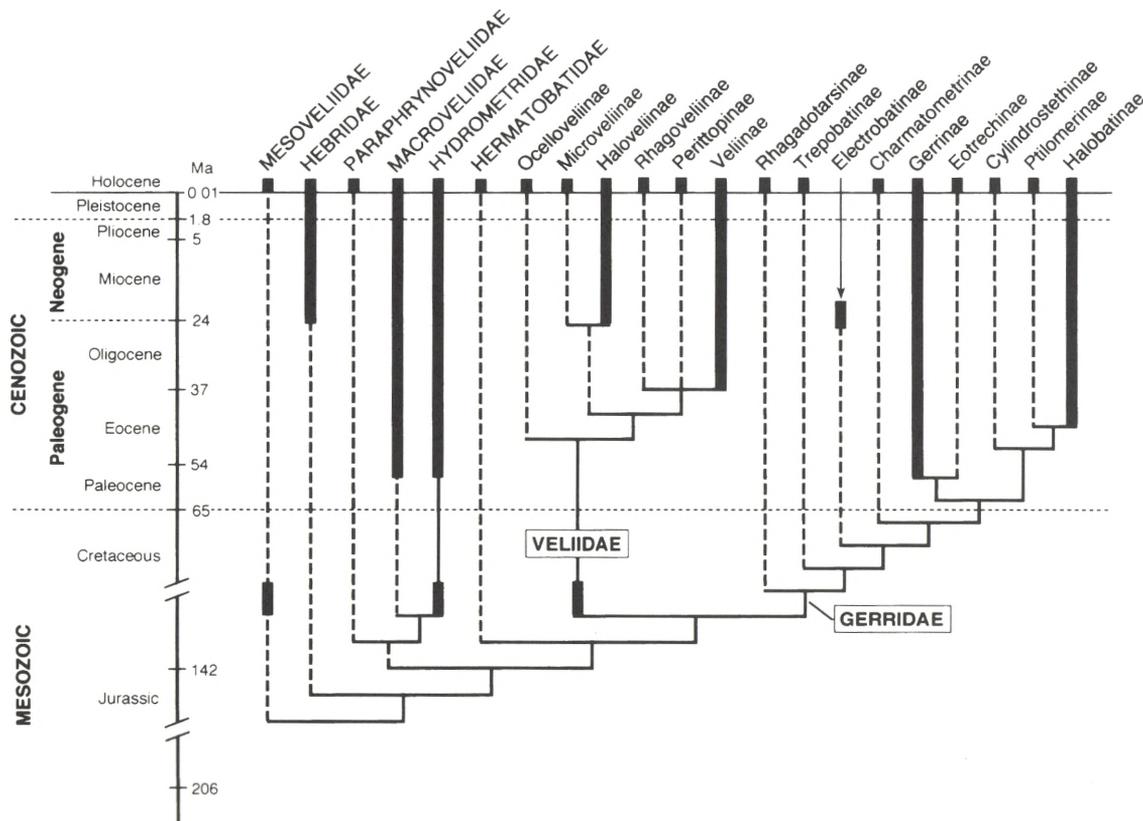


Fig. 80. Phylogenetic tree for the families of Gerromorpha and subfamilies of Veliidae and Gerridae. For explanations of symbols, see Fig. 78. Further explanations in text.

255). Hebrids are more apomorphic than members of the family Mesoveliidae in having a reduced mesoscutellum (GM-19), a latero-dorsal location of the metathoracic spiracle (GM-20), and lateral displacement of the coxae on thorax (GM-21).

The family Mesoveliidae has always been considered quite distinct from other families of Gerromorpha and even removed completely from the infraorder by some authors (for references, see Andersen 1982b). However, since all mesoveliids share most of the apomorphic characters used to support the Gerromorpha as a monophyletic group, this family has subsequently been treated as a genuine member of the infraorder (Andersen 1982b: 253). Mesoveliids, however, are more plesiomorphic than other gerromorphans in having a more generalised thorax structure (including a well-developed mesoscutellum), a metathoracic scent reservoir lined with glandular cells, etc. The Mesoveliidae therefore assume a basal position within the Gerromorpha as shown in the cladogram of relationships between the gerromorph families (Fig. 79).

Phylogenetic tree

Combining the cladogram of relationships between the the families of Gerromorpha (Fig. 79) with biostratigraphic evidence produces a phylogenetic tree describing the evolution of the families of Gerromorpha (Fig. 80).

Previously, the genus *Eocenometra* (Paleocene – Eocene transition) was thought to be the oldest member of the family Hydrometridae, but the recent discovery of an indisputable hydrometrid species from the Lower Cretaceous (Aptian) of Brazil sets the minimum age of this family to about 120 Ma. The fossil genus *Daniavelia* gen. nov. (Paleocene – Eocene transition) was classified in the family Macroveliidae with some reservation. Irrespective of the correctness of this taxonomic decision, the minimum age of the Macroveliidae is inferred to be the

same as for its sister group, the Hydrometridae. The origin of the family Paraphrynoveliidae, with only two extant species, can be extended back to the same time period or earlier.

The genus *Electrovelia* gen. nov. (Baltic amber, Eocene/Oligocene) is the oldest reliable fossil member of the family Veliidae, setting the minimum age of this family to 40–35 Ma. Lower Cretaceous (Aptian) fossils from Australia classified as veliids (without subfamily-assignment) extends the possible origin of the family much further back in geological time (120 Ma). The oldest members of the family Gerridae belong to the genus *Palaeogerris* gen. nov. (Paleocene-Eocene transition), thus setting the minimum age of this family to 55–54 Ma. However, since its sister group, the Veliidae, possibly is at least 120 Ma old (see above), the Gerridae may have originated in the early Cretaceous or before that (Fig. 80).

The true minimum age of the family Hebridae is determined by the Oligocene/Miocene genus *Stenohebrus*. Compared with the inferred ranges of the Veliidae and Gerridae (see above), the range of the Hebridae can be extended much further back. The same applies to the family Hermatobatidae which only has extant species. Finally, *Duncanovelina* from the Lower Cretaceous of Australia sets a possible minimum age of origin of the family Mesoveliidae. Since this family represents the basal branch of the cladogram (Fig. 79), it can be concluded that the infraorder Gerromorpha is at least 120 Ma old (Fig. 80; but see under Heteroptera, above).

Our present knowledge about the evolution of the major groups of Gerromorpha is seriously hampered by the scarcity of well-preserved Mesozoic fossils, especially from the Cretaceous. Semiaquatic bugs are less likely to be preserved as inclusions in amber than terrestrial insects and so far none of the localities for Cretaceous amber (e.g. Siberia, Lebanon, or New Jersey) have produced any gerromor-

phans. Many semiaquatic bugs are quite difficult to recognise as compression fossils. However, species belonging to the families Hydrometridae and Gerridae are so characteristic that they might be recognised more easily in existing or future collections of Mesozoic insect fossils.

Hydrometridae and Macroveliidae

Cladogram

The phylogeny of the Hydrometridae was discussed by Andersen (1977a, 1982b: 125-126) who presented a cladogram of relationships between genera. That work was prompted by the discovery and subsequent description of the species *Veliometra shuhi* Andersen (1977a) which narrowed the morphological gap between the most specialised hydrometrids and other gerromorphan bugs. *Veliometra* shares a number of apomorphic characters with the genera of Hydrometridae, in particular with the genus *Heterocleptes*, thus qualifying as a member of this monophyletic family. The cladogram (Fig. 81) shows the relationships between living and fossil genera of the family Hydrometridae with the extant genus *Macrovelia* (Macroveliidae) and the extinct genus *Daniavelia* added (plesiomorphic and apomorphic states of characters listed in Table 4).

The sister group relationship between *Veliometra* and *Heterocleptes* (subfamily Heterocleptinae) is supported by the very long posterior pair of cephalic trichobothria which are inserted on prominent elevations close to the anterior margin of prothorax (HY-01) and by the preapical articulation between the second and third antennal segments (HY-02).

Dolichocephalometra and *Chaetometra* are two monotypic genera described by Hungerford (1939) from the Marquesas Islands in the eastern South Pacific. The two genera have several characters in common, e.g. the distinctly reduced eyes (HY-03). The genus *Bacillometra* was

described by Esaki (1927) and separated from its closest relative *Hydrometra* on account of its stouter body, relatively shorter and broader thorax, sulcated venter, and long femora which are thickened at base. Most of these characters are plesiomorphies, but the sister group relationship between these two genera is supported by the elongate shape of thorax (HY-04) and narrow abdominal mediotergites (HY-05). The four above-mentioned, extant genera constitute the subfamily Hydrometrinae, the monophyly of which is supported by the relatively long anteocular part of the head (HY-06), short first antennal segment (HY-07), and loss of the metasternal scent apparatus (HY-08).

The monotypic genus *Limnobotodes* was recognised as a hydrometrid by Hussey (1925) based on its prolonged head, a rostrum with only two visible segments (the two basal segments being hidden by the buccula), and a forewing venation similar to that of *Hydrometra*. In the cladogram (Fig. 81), this genus (classified in its own subfamily, Limnobotodinae) is shown as sister group of the Hydrometrinae sharing the presence of spinous macro-hairs (HY-09; see Andersen 1982b: plate 6, figs A-B), absence of ocelli (HY-10), a narrow, parallel-sided pronotal lobe (HY-11), reduced forewing venation (HY-12), absence of paired, longitudinal ridges on the abdominal tergum (HY-13), and loss of the abdominal scent gland (HY-14).

With the addition of plesiomorphic genera like *Veliometra* and *Heterocleptes*, the prolonged head capsule (HY-15) and apical modification of the fourth antennal segment (HY-16) are the most important synapomorphies supporting the monophyly of the Hydrometridae. The arguments in favour of a sister group relationship between the families Hydrometridae and Macroveliidae were discussed above. One of the most obvious synapomorphies is the elongate shape of the head capsule with the eyes distinctly removed from the anterior margin of prothorax (HY-17). The family Macroveliidae

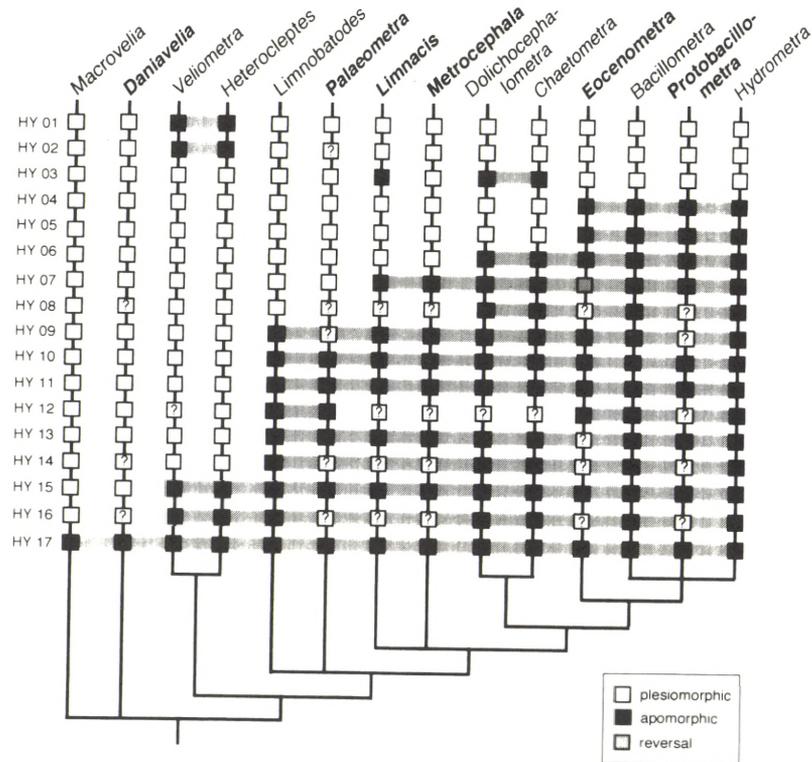


Fig. 81. Cladogram of relationships between the genera of Hydrometridae and Macroveliidae; names of fossil genera in boldface. States of character numbers HY-01 - HY-17 listed in Table 4. For explanations of symbols, see Fig. 79. Further explanations in text.

is composed of three monotypic genera, *Macrovelia* McKinstry and *Oravelia* Drake & Chapman, both from western North America, and *Chepuvelia* China from Chile. Only the first mentioned genus is included in the cladogram (Fig. 81).

In the previous sections of this work, five extinct genera were classified in the family Hydrometridae and their relationships with living genera discussed. Placing fossil forms in a cladogram of relationships between extant genera is a difficult task since many of the relevant characters cannot be observed in fossils, not even in those found as amber inclusions. *Protobacillometra* shares many characters with *Bacillometra* (Fig. 81), but since all of these are plesiomorphic in relation to *Hydrometra*, the relation-

ships between the fossil genus and the two extant genera cannot be resolved. *Eocenometra* is also a typical hydrometrine in most characters. Since the antennae are unusually long in this genus, the prolongation of the first segment (HY-07) is interpreted as a character reversal. *Limnaxis* and *Metrocephala* have the same antennal structure of extant Hydrometrinae (HY-07), but are more plesiomorphic in the structure of their head (HY-06). These two extinct genera are therefore placed as possible sister groups to other genera of the Hydrometrinae (Fig. 81).

Palaometra gen. nov. shares several apomorphic characters with the hydrometrine genera (Fig. 81), including the forewing venation (HY-12), but was classified in the subfamily Limnobotodinae on account of its relatively short head

and broad abdomen. The relationships of this fossil genus, however, cannot be resolved in relation to other hydrometrid genera except *Veliometra* and *Heterocleptes*. *Daniavelia* gen. nov. is clearly more plesiomorphic than any of the fossil or living genera classified in the family Hydrometridae. On account of its head structure (HY-17), *Daniavelia* most likely belongs in the macroveliid-hydrometrid lineage (Fig. 81), but since the diagnostic features for the macroveliids (e.g. egg shell with 3-7 micropyles) cannot be observed in fossils, its more exact phylogenetic position cannot be settled.

Phylogenetic tree

By transforming the cladogram of relationships between fossil and extant genera of Hydrometridae and Macroveliidae (Fig. 81) into a phylogenetic tree (Fig. 82), the following inferences can be made. *Protobacillometra* (Upper Oligocene) sets the minimum age for the clade composed by the extant genera *Bacillometra* and *Hydrometra* to about 30 Ma. If the phylogenetic position of *Eocenometra* (Paleocene-Eocene transition) is correct, however, the possible origin of this clade is much older, at least 55-54 Ma. The Eocene/Oligocene fossils *Lim-*

Table 4. List of characters of genera belonging to the families Hydrometridae and Macroveliidae with their plesiomorphic (p) and apomorphic (a) states.

HY-01.	Posterior pair of cephalic trichobothria: moderately long, at most inserted on low tubercles (p); very long, inserted on prominent rounded elevations (a).
HY-02.	Articulation between second and third antennal segments: apical (p); preapical (a).
HY-03.	Size of eyes: large (p); distinctly reduced (a).
HY-04.	Width of thorax: More than half of median length (p); less than half of median length (a).
HY-05.	Width of abdominal mediotergites: more than half of median length (p); less than half of median length (a).
HY-06.	Anteocular part of head: less than 1.25x pronotal length (p); more than 1.25x pronotal length (a).
HY-07.	Length of first antennal segment: distinctly longer than second segment (p); subequal to or shorter than second segment (a).
HY-08.	Metasternal scent gland: present (p); absent (a).
HY-09.	Macro-hairs of body: setiform (p); spinous (a).
HY-10.	Ocelli: present (p); absent (a).
HY-11.	Pronotal lobe: with strongly diverging sides (p); with almost parallel sides (a).
HY-12.	Forewing venation: complex (p); reduced to two longitudinal veins and 1-2 cross-veins (a).
HY-13.	Paired, longitudinal ridges of abdominal tergum: present (p); absent (a).
HY-14.	Abdominal scent gland: present (p); absent (a).
HY-15.	Postocular part of head: subequal to or shorter than the eye diameter (p); much longer than the eye diameter (a).
HY-16.	Fourth antennal segment: not modified apically (p); with apical invagination and sensorial structures (a).
HY-17.	Location of eyes: close to anterior margin of prothorax (p); distinctly removed from anterior margin of prothorax (a).

nacis and *Metrocephala* clearly belong to the subfamily Hydrometrinae but these genera are relatively younger (40-30 Ma) than *Eocenometra*. The genus *Palaeometra* gen. nov. (Paleocene-Eocene transition) undoubtedly belongs to the Hydrometrinae, whereas its relationships to the hydrometrid subfamilies are more uncertain. Most significant is the recently discovered hydrometrid from the Lower Cretaceous (Aptian) of Brazil which either belongs to the Hydrometrinae or is the sister group of that subfamily (A. Nel, personal communication). This important finding sets the minimum age of the subfamily Hydrometrinae as well as of the family Hydrometridae to about 120 Ma (Fig. 82). Irrespective of the correct placement of *Daniavelia* gen. nov. (Paleocene-Eocene transition), the minimum age of the family Macroveliidae is also inferred to be about 120 Ma, or the same

as for its sister group, the Hydrometridae.

Veliidae

Cladogram

The Veliidae is a large and structurally quite diverse family (Andersen 1982b). The South African genus *Ocellovelia* China & Usinger (1949) and most species of the subfamilies Veliinae and Microveliinae are in general morphology quite similar to the Macroveliidae and *Veliometra*, the most plesiomorphic member of the Hydrometridae. On the other hand, the Haloveliinae, Rhagoveliinae, and several species of Microveliinae are highly evolved insects with many apomorphic structures.

Andersen (1982b: 177-183) discussed the phylogenetic relationships between the subfamilies of the Veliidae as depicted in the clado-

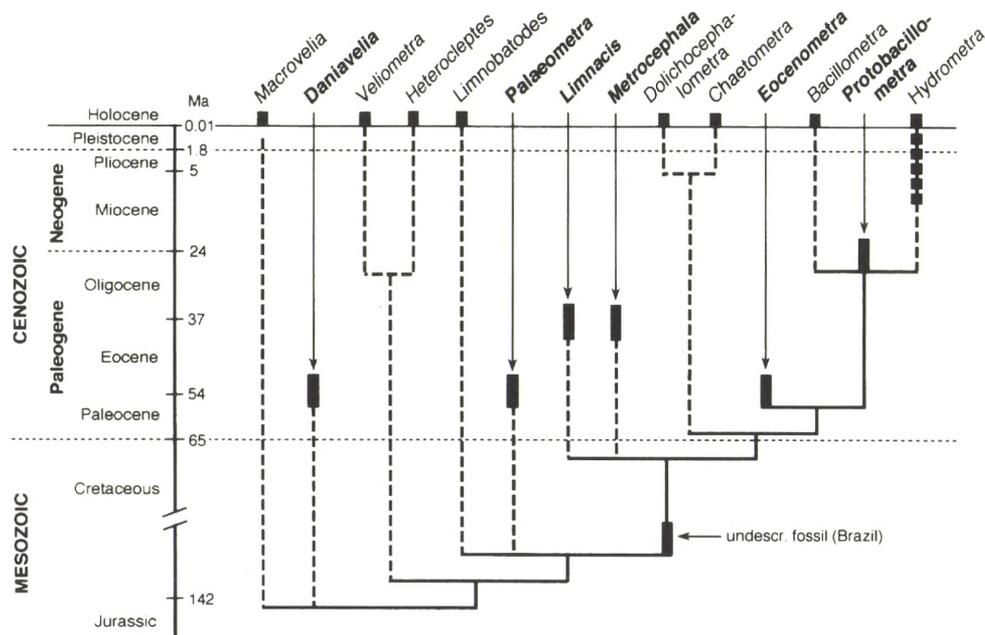


Fig. 82. Phylogenetic tree for the genera of Hydrometridae and Macroveliidae; names of fossil genera in boldface. For explanations of symbols, see Fig. 78. Further explanations in text.

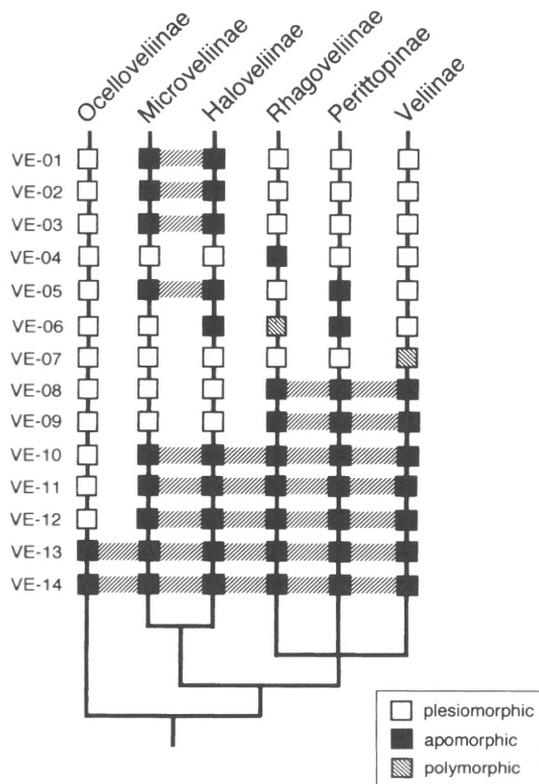


Fig. 83. Cladogram of relationships between the subfamilies of Veliidae. States of character numbers VE-01 - VE-14 listed in Table 5. For explanations of symbols, see Fig. 79. Further explanations in text.

gram (Fig. 83; plesio- and apomorphic states of characters listed in Table 5). The sister group relationship between the Microveliinae and Haloveliinae is supported by the structure of the salivary pump (VE-01), tarsal segmentation (VE-02 and VE-05), and female gynatrial complex (VE-03). The subfamily Microveliinae has a unique 1-2-2 segmentation of tarsi and includes some of the smallest gerromorphan bugs (1-2 mm long). Species of the subfamily Haloveliinae are habitually much like members of the Gerridae and were actually classified in that family by Esaki (1926, 1930). More than half of the haloveliine genera and species are marine.

The monophyly of a clade composed by the

subfamilies Rhagoveliinae, Perittopinae, and Veliinae is supported by the structure of the female ovipositor (VE-08) and gynatrial complex (VE-09), but their mutual relationships are unresolved. The two species of *Ocellovelia* are the only veliids which have retained the ocelli (VE-10). Other plesiomorphic features of this genus is the complex forewing venation (VE-11), and well defined second gonocoxae (VE-12). The apomorphic states of these characters support the sister group relationship between the subfamily Ocelloveliinae and the remaining veliid subfamilies (Fig. 83). The monophyly of the Veliidae is supported by a number of characters (Andersen 1982b: 177), e.g. head deflected in front of eyes (VE-13) and male front tibia with grasping comb (VE-14).

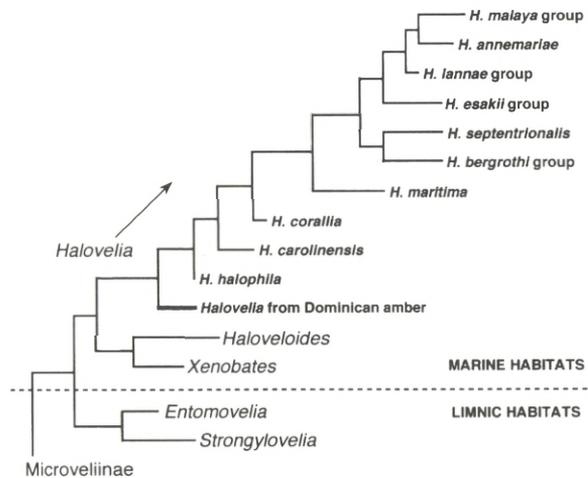


Fig. 84. Cladogram of relationships between species and species groups of *Halovelia*, other genera of the subfamily Haloveliinae (Veliidae), and its sister group Microveliinae. Numbers of species in brackets. The box highlights the position of the Dominican amber species *H. electrodominica* Andersen & Poinar. Dotted line separates lineages with species living in limnic and marine habitats (redrawn from Andersen & Poinar 1998).

Phylogenetic tree

The cladogram of relationships between the subfamilies of Veliidae (Fig. 83) was transformed into a phylogenetic tree (Fig. 80), but only two known fossils can be classified in the extant veliid subfamilies. *Halovelvia electrodominica* was recently described by Andersen & Poinar (in press) from Dominican amber (Oligocene/Miocene). When the characters of the fossil species were added to a character data matrix based on extant species (Andersen 1989b), the fossil species assumed a position as the most basal branch of *Halovelvia* (Fig. 84). Thus, the minimum age of this genus, as well as the subfamily Haloveliinae, is 30-20 Ma (Fig. 80). The minimum age of the sister group Microveliinae is also inferred to be 30-20 Ma, although no fossil microveliines are known so far.

Electrovelvia gen. nov. from Baltic amber (Eocene/Oligocene) was classified in the Veliinae, setting a minimum age for this subfamily to 40-35 Ma (Fig. 80). By range extension, the same minimum age can be assigned to the subfamilies Rhagoveliinae and Perittopinae, both without known fossils. So far, *Electrovelvia* is the oldest fossil taxon which can be classified in the Veliidae with absolute certainty. However, the family probably originated long before the time when Baltic amber was formed (Eocene/Oligocene) as indicated by possible veliid fossils from the Lower Cretaceous of Australia (Fig. 80).

Gerridae*Cladogram*

The family Gerridae is species-rich but comprises a morphologically rather homogeneous group of very specialised insects. Andersen (1982b: 233-239) discussed the phylogenetic relationships between the subfamilies of Gerridae as presented in the cladogram (Fig. 85; plesio- and apomorphic states of characters listed in Table 6). The sister group relationship between the Halobatinae and Ptilomerinae is

supported by the reduction of the number of cephalic trichobothria from four to three pairs (GE-01) and by the bilobed second gonapophyses (GE-02). The subfamily Cylirostethinae was included as a tribe in the Gerrinae by Matsuda (1960), but the characters used in support for this classification are plesiomorphies. The Gerrinae *sensu* Matsuda (1960) is therefore a paraphyletic group. Instead, the Cylirostethinae forms a monophyletic group with the Ptilomerinae and Halobatinae, sharing the relatively short and stout rostrum (GE-03) and apical process of front tibia (GE-07).

The sister group relationship between the subfamilies Gerrinae and Eotrechinae is supported by the structure of the first gonapophyses (GE-04) and the female gynatrial complex (GE-05). Cladograms of relationships between genera have been presented for the Eotrechinae (Polhemus & Andersen 1984) and Gerrinae (Andersen 1995c). The subfamily Charmatometrinae is perhaps more plesiomorphic than any other gerrid subfamily and was also included in the Gerrinae *sensu* Matsuda (1960). Andersen (1982b: 238), however, suggested that the Charmatometrinae is the sister group of the above mentioned five gerrid subfamilies on account of the state of the lateral intersegmental suture between meso- and metathorax (GE-09).

Species belonging to the subfamilies Rhagadotarsinae and Trepobatinae have ocular setae that are longer than four eye facets (GE-10), a simple dorsal, intersegmental suture between meso- and metanotum (GE-11), and a relatively short first segment of the front tarsi (GE-12), all inferred to be plesiomorphic character states. The apomorphic state of these characters therefore support the monophyly of a group composed by the gerrid subfamilies except the Rhagadotarsinae and Trepobatinae (Fig. 85). The subfamily Trepobatinae is a rather homogeneous and well defined monophyletic group which share the reduced ventral lo-

Table 5. List of characters of the subfamilies of the family Veliidae with their plesiomorphic (p) and apomorphic (a) states.

VE-01. Salivary pump: without sclerite (p); with dark sclerite in dorsal wall (a).
VE-02. Middle and hind tarsi: with 3 segments (p); with 2 segments, first segment formed by fusion of primitive first and second segments (a).
VE-03. Fecundation pump of gynatrial complex: absent (p); present (a).
VE-04. Last segment of middle tarsus: simple (p); deeply cleft, with hairy or plumose swimming fan (a).
VE-05. Fore tarsus: with 3 segments (p); with 2 or 1 segment (a).
VE-06. Fore wing venation: 4 closed cells (p); 2 closed cells, apical veins reduced (a).
VE-07. Fore tibia of female: without grasping comb (p); with grasping comb (a).
VE-08. Second gonapophyses: at most with fringes of simple or branched hairs (p); with feathered outgrowths (a).
VE-09. Fecundation canal of gynatrial complex: long (p); reduced or rudimentary (a).
VE-10. Ocelli: present (p); absent (a).
VE-11. Fore wing venation: with 6 closed cells (p); with less than 6 closed cells (a).
VE-12. Second gonocoxae: separated (p); fused medially (a).
VE-13. Shape of head capsule: head extended in front of eyes (p); head deflected in front of eyes (a).
VE-14. Male fore tibia: without grasping comb (p); with grasping comb (a).

bes of head (= buccula) (GE-13), absence of second gonocoxae (GE-14), and membranous second gonapophyses (GE-15) with all other gerrids except the Rhagadotarsinae. Finally, the monophyly of the Gerridae is supported by a number of characters (Andersen 1982b: 233), e.g. the prolonged mesothorax, rotation of mesocoxal and metacoxal axes to an almost horizontal state (GE-16), and the reduction of the number of tarsal segments from three to two (GE-17).

The relationship of the extinct genus *Electrobates* from Dominican amber was discussed by Andersen & Poinar (1992: 262-263). Based upon observable characters, it cannot be placed in any of the extant gerrid subfamilies. It shares apomorphic character state with some or all Trepobatinae (see above), with the Charatometrinae (GE-06), and with the Gerrinae, Eotrechinae, Cylindrostethinae, Ptilomerinae,

and Halobatinae (GE-10 and GE-12). Andersen & Poinar (1992) in conclusion proposed *Electrobates* as sister group of all gerrid subfamilies except the Rhagadotarsinae and Trepobatinae (Fig. 83) and erected a separate subfamily, Electrobatinae, for the Dominican amber genus.

Phylogenetic tree

The cladogram of relationships between fossil and extant subfamilies of Gerridae (Fig. 85) can be transformed into a phylogenetic tree (Fig. 80). Since the elongate body, prolonged mesothorax, and long and slender middle and hind legs makes gerrids easily recognisable, a fair amount of fossils have been recorded. A fossil sea skater, *Halobates*, was described by Andersen *et al.* (1994) from Middle Eocene deposits of northern Italy, thus setting the minimum age for the subfamily Halobatinae to

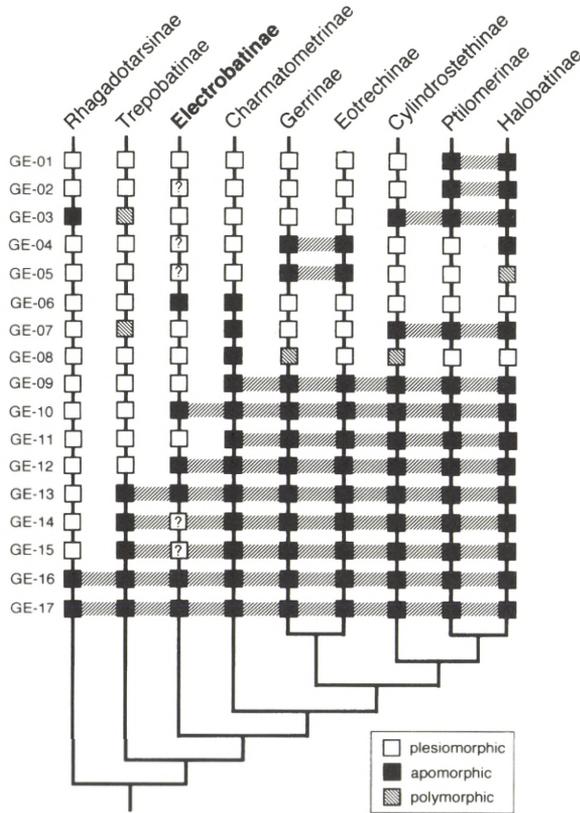


Fig. 85. Cladogram of relationships between the subfamilies of Gerridae. States of character numbers GE-01 - GE-17 listed in Table 6. For explanations of symbols, see Fig. 79. Further explanations in text.

about 45 Ma (Fig. 80). The same age can be applied to its sister group, the Ptilomerinae. The oldest fossil gerrids are the three species of *Palaeogerris* gen. nov. described above (Paleocene - Eocene transition). They were classified in the subfamily Gerrinae which has an almost continuous fossil record from that period to the present. The minimum age for the Gerrinae is 55-54 Ma and the same must apply to its sister group, the Eotrechinae (Fig. 80).

The genus *Electrobates* from Dominican amber (Oligocene/Miocene) represents a lineage which became extinct sometimes during the Neogene. Although the actual age of the fossil taxon is 30-20 Ma, the range of that lineage can be extended much further back (Fig. 80). The minimum age of the entire family is determined by the age of the oldest fossil forms which with certainty can be classified as gerrids. However, if its sister group, the Velidae, evolved more than 120 Ma ago, the same time of origin can be hypothesized for the Gerridae.

Gerris and allied genera

Cladogram

The genera *Aquarius*, *Gerris*, and *Limnoporus* include the majority of the water strider species occurring in the northern, temperate region, and several species have been subject to extensive ecological and behavioural studies during the past two decades (for a review, see Spence & Andersen 1994). In order to create a phylogenetic framework for such studies, the relationships between genera and species have been analysed and clarified (Andersen 1990, 1993b, 1995c; Andersen & Spence 1992). The current hypothesis of relationships between *Aquarius*, *Gerris*, *Limnoporus*, and the monotypic genus *Gigantometra* is presented in the cladogram (Fig. 86; plesio- and apomorphic states of characters listed are in Table 7). These genera form a clade within the subfamily Gerrinae supported by the proximity of the metathoracic spiracle to the wing bases (GI-13).

The sister group relationship between *Aquarius* and *Gerris* is supported by the relatively shorter antennae (GI-06), absence of a median pale stripe on pronotal lobe (GI-07), and the relatively thickened front femora of both male and female (GI-08). The elevated anterior margin of pronotum (GI-09), carinated pronotal lobe (GI-10), and absence of evaporative scent

Table 6. List of characters of the subfamilies of the family Gerridae with their plesiomorphic (p) and apomorphic (a) states.

GE-01. Number of cephalic trichobothria: four pairs (p); three pairs (a).
GE-02. Apices of second gonapophyses: simple (p); bilobate (a).
GE-03. Relative length of rostrum: long and slender, reaching mesosternum (p); short and robust, apex not reaching mesosternum.
GE-04. Inner lobe of first gonapophysis: membranous (p); sclerotized (a).
GE-05. Gynatrial gland: undivided (p); divided in two lateral glandular areas (a).
GE-06. Base of abdominal tergum: not modified (p); with secondary transverse line in front of first abdominal tergum (a).
GE-07. Apical process of fore tibia: absent (p); present (a).
GE-08. Evaporative scent grooves on metasterno-pleura: present (p); absent (a).
GE-09. Lateral intersegmental suture between meso- and metathorax: present (p); indistinct or lost (a).
GE-10. Length of ocular setae: longer than four eye facets (p); shorter than four facets (a).
GE-11. Dorsal, intersegmental suture between meso- and metanotum: straight (p); V- or U-shaped (a).
GE-12. First segment of fore tarsus: less than one third the length of second segment (p); more than one third the length of second segment (a).
GE-13. Ventral lobes of head (= buccula): present (p); absent (a).
GE-14. Second gonocoxae: present (p); absent (a).
GE-15. Second gonapophyses: chiefly sclerotized (p); chiefly membranous (a).
GE-16. Meso- and metathorax: Subequal in length, coxal axes oblique (p); mesothorax prolonged, coxal axes horizontal (a).
GE-17. Number of tarsal segments: three segments (p); two segments (a).

grooves on metasterno-pleura (GI-11), place *Limnopus* as the sister group of these two genera. This hypothesis has recently been corroborated by molecular data (Sperling *et al.* 1997; Jakob Damgaard and Felix Sperling, personal communication).

Two extinct genera, *Palaeogerris* gen.nov. and *Telmatrechus*, are members of the same clade as the three principal holarctic genera (see above). The evaluation of the phylogenetic relationships of fossil form is impeded by missing observations of crucial characters. *Telmatrechus*, however, shares the unique antennal structure (GI-05) with the genus *Aquarius*. Species of *Palaeogerris* are more plesiomorphic than the tree extant, holarctic genera in several characters,

but share the shape of the metasternal scent orifice (GI-02) and relatively long hind femora (GI-12; also found in some *Aquarius*) with *Limnopus*. Placing *Palaeogerris* as a sister group of the latter genus, however, requires a number of homoplasies (convergences or reversals) and is therefore not justified. The relationship of *Palaeogerris* is therefore depicted as unresolved in the cladogram (Fig. 86).

Phylogenetic tree

The cladogram of relationships between *Gerris* and allied genera (Fig. 86) can be transformed into a phylogenetic tree (Fig. 87) with the range of known fossils inserted. The oldest fossil species classified in the genus *Aquarius* is from the

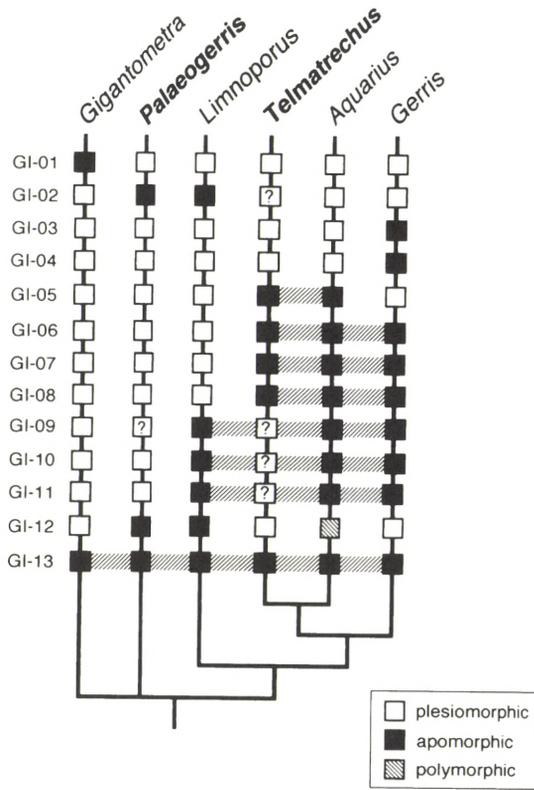


Fig. 86. Cladogram of relationships between *Gerris* and related genera of the subfamily Gerrinae (Gerridae). States of character numbers GI-01 - GI-13 listed in Table 7. For explanations of symbols, see Fig. 79. Further explanations in text.

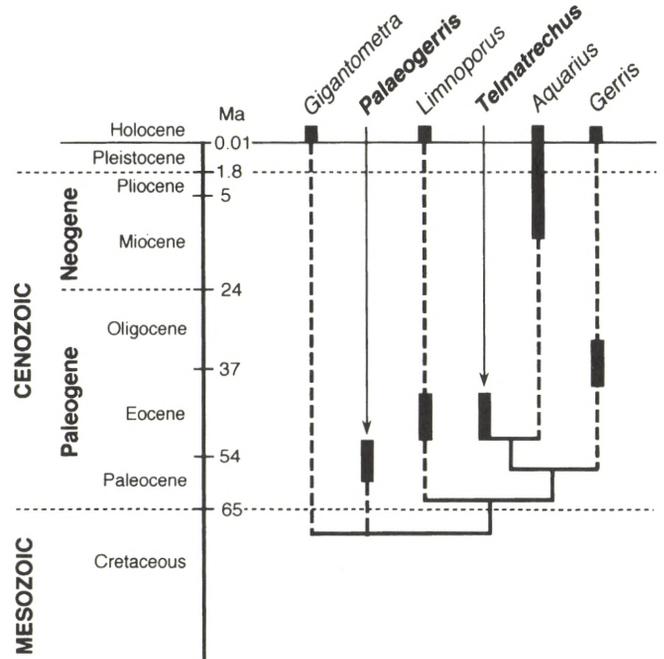


Fig. 87. Phylogenetic tree for *Gerris* and related genera of the subfamily Gerrinae (Gerridae); names of fossil genera in bold-face. For explanations of symbols, see Fig. 78. Further explanations in text.

Miocene, or 5-20 Ma ago. However, if the sister group of this genus is the extinct genus *Telmatrechus* (Middle Eocene), the minimum age of *Aquarius* is inferred to about 50 Ma and the separation of the extant genera *Aquarius* and *Gerris* must have occurred at about this time or earlier. A couple of gerrid nymphs from Baltic amber (Oligocene/Eocene) assigned to *Gerris* suggest 40-35 Ma as the minimum age for this genus.

Andersen *et al.* (1992) classified a Middle Eocene fossil gerrid as belonging to the genus *Limnoporos* (described above as *L. wilsoni* sp. nov.), setting a minimum age for this genus to

about 50 Ma. This estimated minimum divergence time for *Limnoporos* and allied genera is about tenfold earlier than those based on mtDNA and allozyme data using the assumptions of a standard molecular clock (Sperling & Spence 1990; Sperling *et al.* 1997).

The extinct species of *Palaeogerris* gen. nov. are the oldest members of the clade shown in Fig. 87. They occur at Paleocene – Eocene transition, setting a minimum age of the clade to 55-54 Ma which is also the estimated minimum divergence time for *Gigantometra* and the principal genera of Holarctic water striders.

Table 7. List of characters of *Gerris* and allied genera (Gerridae, subfamily Gerrinae) with their plesiomorphic (p) and apomorphic (a) states.

-
- GI-01. Relative length of male hind leg: shorter than middle leg (p); much longer than middle leg (a).
- GI-02. Shape of scent orifice: transverse ovate (p); circular (a).
- GI-03. Length of first antennal segment: more than 1.3x head length (p); less than 1.3x head length (a).
- GI-04. Connexival spines (posterior corners of laterotergites 7): absent (p); present (a).
- GI-05. Combined length of second and third antennal segments: distinctly longer than first segment (p); subequal to or shorter than first segment (a).
- GI-06. Relative length of antennae: subequal to or longer than half of body length (p); shorter than half of body length (a).
- GI-07. Median pale stripe on pronotal lobe: present (p); absent (a).
- GI-08. Fore femur of female: slender, about as thick as middle femur (p); distinctly thicker than middle femur (a).
- GI-09. Anterior margin of pronotum behind eyes: not elevated (p); elevated (a).
- GI-10. Median, longitudinal carina of pronotal lobe: absent (p); present (a).
- GI-11. Evaporative scent grooves on metasterno-pleura: present (p); absent (a).
- GI-12. Relative length of hind femur: distinctly shorter than middle femur (p); subequal to or longer than middle femur (a).
- GI-13. Location of metathoracic spiracle: more than its own length from wing base (p); less than its own length from wing base (a).
-

Phylogenetic classification and fossils

General principles and methods

Crown groups and stem groups

A cladogram can be translated to a nested or hierarchical set of relationships between taxa and groups of taxa. Ideally, only monophyletic taxa should be recognised in cladistic classifications. Some cladists require that every monophyletic group is recognised and named in the classification and that sister groups should be given the same taxonomic rank (see, e.g. Hennig 1966). For any sizeable number of taxa, however, the number of higher taxon names will increase. Some authors advocating this method (e.g. De Queiroz & Gauthier 1990, 1992) therefore abandon the traditional Linnean hierarchy of categorical names (order, family, subfamily, etc.). An alternative (and less radical) approach is based on the principle of *phyletic sequencing* which does not require that every monophyletic group is formally named (see, e.g. Wiley, 1981). Instead it is prescribed, that taxa listed in sequence have the same taxonomic rank. This convention have been applied to the current classification of gerromorphan bugs (Andersen, 1982b).

When reconstructing the phylogenetic relationships of a group, fossils should not be treated as different from extant organisms. When it comes to translating a cladogram into a classification, however, fossils may pose a special problem. Because of their incomplete state of preservation, many fossils cannot be scored for all the characters (synapomorphies) that normally are required to diagnose extant, monophyletic groups. A fossil group, such as a genus, is commonly defined by a smaller subset of these characters and may be paraphyletic with respect to its extant sister group. The problem of placing fossil taxa in phylogenetic classifica-

tions can be illustrated by the distinction between crown groups and stem groups first made by Hennig (1969) and formalised by Jeffries (1979; see also Smith 1994).

A *crown group* (Fig. 88, A) is an extant monophyletic group that also may include extinct species with all the diagnostic characters (synapomorphies) of that group, or can be shown to have secondarily lost such characters. In a phylogenetic context, a crown group is composed of the most recent common ancestor of all the extant members of the group and all of its descendants including extinct species, and is therefore monophyletic. A *stem group* (Fig. 88, B) is a group of extinct species possessing one or more of the diagnostic characters of an extant group, but not including all descendants of a common ancestor. A stem group is therefore paraphyletic in a phylogenetic context. Crown groups and stem groups combined constitute a *total group* (Fig. 88, C) which includes all extinct and extant descendants of a common ancestor and therefore is monophyletic.

Fossil species belonging to a crown group can simply be classified with their extant allies in the an existing, monophyletic taxon as exemplified by the fossils *Limnopus wilsoni* sp. nov. and *Aquarius lunpolaensis*. Stem group fossils are those that originated somewhere in the lineage leading to the crown groups, thus sharing its common ancestor, but have not acquired all of the diagnostic characters of this crown group as far as they can be observed on the fossil material. For example, the extinct water striders described and classified above in the genus *Palaeogerris* gen. nov. may actually constitute a paraphyletic stem group with re-

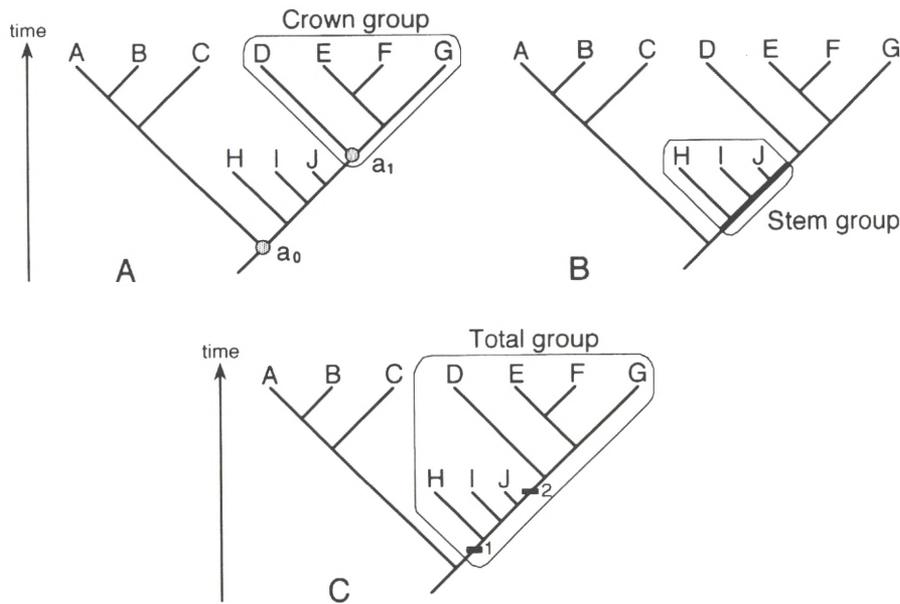


Fig. 88. Cladograms of relationships between seven extant species (A-G) and three extinct species (H-J). A, crown group (D-G). B, stem group (H-J). C, total group (D-J). Further explanations in text.

spect to extant water striders belonging to the monophyletic group composed by *Gerris* and allied genera (Figs 86-87). The same may apply to the extinct genus *Telmatrechus*.

The distinction between crown and stem groups is important for decisions on the time of origin or divergence of monophyletic groups (clades) and for comparisons between such groups. In the example cladogram there are two monophyletic groups of extant species, A + B + C and D + E + F + G (Fig. 88, A). The time of origin of both groups is unequivocally determined by the splitting of their most recent common ancestor (Fig. 88, A: a_0). Adding the fossil species H, I, and J to the crown group D + E + F + G does not change the time of origin of the total group composed by all species D-J (Fig. 88, C).

Michelsen (1996) presented an excellent discussion of the problems posed by incorporating fossils in a phylogenetic classification of extant taxa. Following De Queiroz & Gauthier

(1990, 1992), three principal ways of defining taxa with reference to common ancestry, *node-based*, *stem-based*, and *apomorphy-based* were specified (Michelsen 1996). Referring to a common ancestor as being a node on the cladogram, the definition of a crown group (Fig. 88, A) is node-based whereas the definition of a total group (Fig. 88, C) is stem-based. The contents of apomorphy-based groups change with the synapomorphies used. The apomorphy 2 (Fig. 88, C) delimits the group D + E + F + G, whereas the apomorphy 1 delimits a group that also includes the fossil species H, I, and J. I agree with Michelsen (1996: 448) that using apomorphy-based definitions of clades is an unsatisfactory approach, as it makes decisions upon their time of origin dependent on subjectively selecting one or more characters as being diagnostic for clade membership.

A node-based definition of clades was preferred by Michelsen (1996: 448-449) because it most readily applies to clades with extant spe-

cies and because diagnoses are incompatible with stem-based taxon definitions. Michelsen (1996) further argued that since extant members of sister clades are the product of speciation and extinction events that took place *after* the origin of their latest, common ancestor, it is the time of diversification, not the time of divergence between sister clades that is important in any comparative assessment of evolutionary success of recent, sister group related clades.

A stem-based definition of clades as advocated, e.g. by Hennig (1966, 1969) and Ax (1987) effectively eliminates paraphyletic stem groups. The time of origin or divergence of two sister group related clades like A + B + C and D + E + F + G (Fig. 88, A), is unequivocally determined as the time of splitting (speciation) of their most recent common ancestor a_0 . This is not affected by the inclusion of the fossil species H, I, and J, irrespective of their relative position on the stem leading to the crown group D-G. Only by accepting that monophyletic sister groups have the same time of origin is it possible to make meaningfully comparisons between such groups. I therefore prefer the stem-based definition of clades and have applied it throughout this work.

Plesion

Formally assigning higher category names to all fossil taxa that are members of a stem group might inflate the taxonomic hierarchy if the fossil taxa should be given the same rank as their extant sister groups. Patterson & Rosen (1977) recognised this problem and proposed that all extinct clades constituted *plesions* which could be inserted anywhere within the classification without changing the rank of the crown group(s). Instead of classifying the extinct water strider genus *Electrobates* in its own subfamily, Electrobatinae (Andersen & Poinar 1992), the genus could thus be entered in the existing classification as Plesion (Genus) *Electrobates* Andersen & Poinar.

In the classification of extant genera of the family Hydrometridae based upon the cladogram (Fig. 81), the fossil genera *Limnaxis*, *Metrocephala*, and *Palaeometra* may be entered as plesions, whereas the fossil genus *Protobacillometra* can be entered without this qualification.

Family Hydrometridae Billberg, 1820

Subfamily Heterocleptinae Villiers, 1948

Genus *Heterocleptes* Villiers, 1948

Genus *Veliometra* Andersen, 1977

Subfamily Limnobatodinae Esaki, 1927

Genus *Limnobatodes* Hussey, 1925

Plesion (Genus) *Palaeometra* gen. nov.

Subfamily Hydrometrinae Billberg, 1820

Plesion (Genus) *Limnaxis* Germar, 1856

Plesion (Genus) *Metrocephala* Popov, 1996

Unnamed group 1

Genus *Chaetometra* Hungerford, 1950

Genus *Dolichocephalometra* Hungerford, 1939

Plesion (Genus) *Eocenometra* Andersen, 1982

Unnamed group 2

Genus *Bacillometra* Esaki, 1927

Genus *Protobacillometra* Nel & Paicheler, 1993

Genus *Hydrometra* Latreille, 1796

A classification of fossil Gerromorpha

The following list contains a revised phylogenetic classification of the infraorder Gerromorpha including all fossil taxa down to the level of genus. Geological ranges derived from previous sections of this work are entered when appropriate.

Infraorder **Gerromorpha** Popov, 1977. Lower Cretaceous-Holocene

Superfamily **Mesovelioidea** Douglas & Scott, 1867

Family **MESOVELIIDAE** Douglas & Scott, 1867. Lower Cretaceous-Holocene.

Subfamily **Mesoveliinae** Douglas & Scott, 1867. Lower Cretaceous-Holocene.

Plesion (Genus) *Duncanovelia* Jell & Duncan, 1986. Lower Cretaceous.

Subfamily **Madeoveliinae** Poisson, 1959. Holocene.

Superfamily **Hebroidea** Amyot & Serville, 1843

Family **HEBRIDAE** Amyot & Serville, 1843. Oligocene/Miocene-Holocene.

Subfamily **Hebrinae** Amyot & Serville, 1843. Oligocene/Miocene-Holocene.

Genus *Stenohebrus* Polhemus, 1995. Oligocene/Miocene.

Subfamily **Hyrcaninae** Andersen, 1981. Holocene.

Superfamily **Hydrometroidea** Billberg, 1820

Family **PARAPHRYNOVELIIDAE** Andersen, 1978. Holocene.

Family **MACROVELIIDAE** McKinstry, 1942. Paleocene/Eocene-Holocene.

Plesion (Genus) *Daniavelia* Andersen gen. nov. Paleocene/Eocene.

Family **HYDROMETRIDAE** Billberg, 1820. Lower Cretaceous-Holocene.

Subfamily **Heterocleptinae** Villiers, 1948. Holocene.

Subfamily **Limnobatodinae** Esaki, 1927. Paleocene/Eocene-Holocene.

Plesion (Genus) *Palaeometra* Andersen gen. nov. Paleocene/Eocene.

Subfamily **Hydrometrinae** Billberg, 1820. Lower Cretaceous-Holocene.

Unnamed plesion (Genus). Lower Cretaceous

Plesion (Genus) *Limnaxis* Germar, 1856. Eocene/Oligocene.

Plesion (Genus) *Metrocephala* Popov, 1996. Eocene/Oligocene.

Plesion (Genus) *Eocenometra* Andersen, 1982. Paleocene/Eocene.

Genus *Hydrometra* Latreille, 1796. Miocene?-Holocene.

Genus *Protobacillometra* Nel & Paicheler, 1993. Oligocene.

Superfamily **Gerroidea** Leach, 1815

Family **HERMATOBATIDAE** Coutière & Martin, 1901. Holocene.

Family **VELIIDAE** Brullé, 1836. Lower Cretaceous-Holocene.

Subfamily **Ocelloveliinae** Drake & Chapman, 1963. Holocene.

Subfamily **Microveliinae** China & Usinger, 1949 (1860). Holocene.

Subfamily **Haloveliinae** Esaki, 1930. Oligocene/Miocene-Holocene.

Genus *Halovelia* Bergroth, 1893. Oligocene/Miocene-Holocene.

Subfamily **Rhagoveliinae** China & Usinger, 1949. Holocene.

Subfamily **Perittopinae** China & Usinger, 1949. Holocene.

Subfamily **Veliinae** Brullé, 1836. Eocene/Oligocene-Holocene.

Plesion (Genus) *Electrovelia* Andersen gen. nov. Eocene/Oligocene.

Unnamed plesion (Subfamily) 1

Genus *Stenovelia* Scudder, 1890. Eocene.

Unnamed plesion (Subfamily) 2

Veliidae sp. Lower Cretaceous.

Family **GERRIDAE** Leach, 1815. Paleocene/Eocene-Holocene.

Subfamily **Rhagadotarsinae** Lundblad, 1933. Holocene.

Subfamily **Trepobatinae** Matsuda, 1960. Holocene.

Plesion (subfamily) **Electrobatinae** Andersen & Poinar, 1993. Oligocene/Miocene.

Genus *Electrobates* Andersen & Poinar, 1993. Oligocene/Miocene.

Subfamily **Gerrinae** Leach, 1815. Paleocene/Eocene-Holocene.

Plesion (Genus) *Palaeogerris* Andersen gen. nov. Paleocene/Eocene.

Genus *Limnoporos* Stål, 1868. Eocene-Holocene.

Plesion (Genus) *Telmatrechus* Scudder, 1890. Eocene.

Genus *Aquarius* Schellenberg, 1800. Miocene-Holocene.

Genus *Gerris* Fabricius, 1794. Eocene/Oligocene?-Holocene.

Subfamily **Eotrechinae** Matsuda, 1960. Holocene.

Subfamily **Cylindrostethinae** Matsuda, 1960. Holocene.

Subfamily **Ptilomerinae** Bianchi, 1896. Holocene.

Subfamily **Halobatinae** Bianchi, 1896. Eocene-Holocene.

Genus *Halobates* Eschscholtz, 1822. Eocene-Holocene.

Palaeoecology and palaeobiology

Ecological phylogenetics and fossils

Ecologists and evolutionary biologists have for some time acknowledged the fact that evolution cannot exclusively be explained by studying patterns and processes observable today. Historical perspectives may be achieved by studying fossils, but ecological and biological relations are rarely reflected in the fossil record. More recently, an efficient research protocol designed to gain a historical perspective on ecological problems has evolved through the amalgamation of cladistics and comparative biology (see, e.g. Brooks & McLennan 1991; Harvey & Pagel 1991; Eggleton & Vane-Wright 1994). This approach is most appropriately referred to as *ecological phylogenetics* (Spence & Andersen 1994; Andersen 1996a). Ecological data from extant taxa are combined with phylogenies to reveal patterns of behavioural or ecological adaptations, determine the sequence of changes that have generated these patterns, and infer the evolution of the taxa in question. Brooks & McLennan (1991) consistently denote this research protocol as "historical ecology", a term which sometimes is used for studies of the ecology of fossils (e.g. Wootton 1988). To minimise confusion, I prefer to use the term ecological phylogenetics for the approach outlined in this chapter.

Although the eight families comprising the infraorder Gerromorpha are relatively species-poor (Fig. 89) as compared to insect families in general, the semiaquatic bugs are quite diverse, both in structure, ecology, and behaviour. Using the methods outlined above, I have previously analysed and discussed various aspects of the adaptive evolution of gerromorphan bugs, including the evolution of habitat use (Andersen 1979, 1982b), locomotory struc-

ture and performance (Andersen 1995d), wing polymorphism (Andersen 1994, 1997a), sexual size dimorphism and mating behaviour (Andersen 1994, 1996a, 1997b). The results of these studies are briefly outlined below with discussions of how the fossil record may provide clues to the temporal scale and sequence of various elements of adaptive evolution within the infraorder Gerromorpha.

Palaeoenvironments and habitats

Palaeoenvironments

The composition of fossil biotas is determined by a number of factors united under the concept of *taphonomy*. Based upon a comparative study of some insect-bearing localities from the European Tertiary (Fur Formation, Baltic amber, Rott Formation, and Bitterfeld amber), Kohring & Schlüter (1995) concluded that the occurrence of different taxa is mainly controlled by the mode of life of insects. The size of the fossils may also play a role, although amber-preserved and sediment-preserved taxa cannot be separated clearly on their body sizes. For marine deposits like the Fur Formation, the potential association between the fauna of the source area and sedimentological conditions should be considered.

Paleogene insect faunas of western North America are concentrated in limnic, lacustrine sediments of the Cordillera (Wilson 1977, 1978a, 1978b). Inferred palaeoclimates vary from temperate to tropical, based mostly on palaeobotanical evidence. Wilson (1980, 1988) reconstructed Eocene lake environments of British Columbia, Canada, using evidence from assemblages of autochthonous and al-

lochthonous fish, insect, and plant fossils. Assemblages of fossil insects found in deep-water, off-shore deposits have relatively more Tipulidae and other Diptera as well as water striders (Gerridae) than assemblages found in shallow-water, near-shore deposits. Although taphonomic effects cannot be ruled out, this variation between fossil assemblages may indicate that the Eocene water striders (*Limnoporus wilsoni* sp. nov. and *Telmatrechus* spp.) ventured relatively far from the lake shore, e.g. like the extant pondskater *Aquarius paludum* (Damgaard & Andersen 1996).

The fauna and flora of Baltic amber have been so extensively studied that some reconstruction of the palaeoenvironment is allowed (Larsson 1978; Poinar 1992). The climate varied from subtropical to tropical when the Baltic amber was formed in the Eocene/Oligocene, and the rapid cooling of the climate in the northern hemisphere during the Oligocene could explain the disappearance of the amber-bearing forests. The forests must have been quite humid as the fauna includes many groups which breed in freshwater, both running and still (Ephemeroptera, Plecoptera, Trichoptera, several families of Diptera). The amber-bearing trees must also have been rather close to water as shown by the presence of larvae of may-flies, caddis-flies, water-beetles (Dytiscidae), and aquatic bugs (Corixidae). The gerrid nymphs recorded from Baltic amber (see above) fall into the same line of evidence.

The Paleocene/Eocene Fur and Ølst Formations are marine and the fossiliferous sediments were deposited some distance from the coast. The very large number of insect fossils contained in these formations is therefore remarkable. So far, however, only winged adult insects have been recovered and the commonly accepted hypothesis is that the insects have been caught by the wind when flying over land and carried out to sea where they were forced down upon the water surface (Larsson 1975;

Willmann 1990a; Andersen & Andersen 1996). Investigations of recent faunas have shown that flying insects belonging to many orders are transported far out over the sea by air currents (Bowden & Johnson 1976). The abundance of gerrids (*Palaeogerris* spp.) among fossil insects from the Fur and Ølst Formations may be more than accidental, indicating that migratory flights between habitats were just as common in these Paleogene gerrids as they are in many extant water striders (Andersen 1982b; Andersen & Spence 1992; Spence & Andersen 1994).

Habitats

The about 1,600 extant species of semiaquatic bugs (Gerromorpha) live in a wide range of humid terrestrial and aquatic habitats (Andersen 1982b). No other living group of insects displaying a similar number of species shows such a remarkable diversity of habitat preferences. Most species of Mesoveliidae and Hebridae, several Hydrometridae, and all Macroveliidae live in humid terrestrial and marginal aquatic habitats, e.g. litter on humid soil, spring-fed gravel and stones, tufts of plants, carpets of mosses, and seeping rock-faces with growth of algae. Such habitats are characterised by containing mainly solid matter covered by a thin film of water. They are therefore collectively called *hygropetric* habitats.

True water striders, belonging to the families Veliidae and Gerridae, are highly adapted to a more or less permanent life on the surface of water, either fresh (limnic) or salt (marine), stagnant (lentic) or flowing (lotic). Since water striders are part of the animal community – the pleuston – associated with the surface film of water, these habitats are also called *pleustonic* habitats. In freshwater, the water surface may be more or less extensively covered by mats of algae, emergent plants, and floating leaves of water plants upon which many species of Mesoveliidae, Hydrometridae, and Veliidae live.

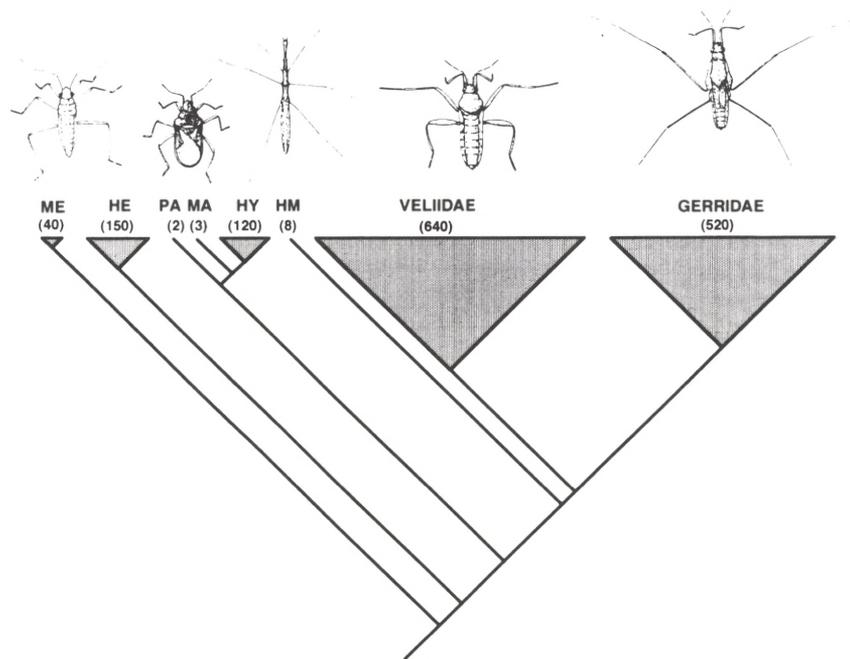


Fig. 89. Cladogram of phylogenetic relationships between the families of Gerromorpha; shaded areas on top of branches proportional to number of extant species (figures in brackets). Selected species inserted above diagram (from left to right): *Mesovelium furcata* Mulsant & Rey; *Hebrus ruficeps* (Thomson); *Hydrometra stagnorum* (Linnaeus); *Velia caprai* Tamanini; *Gerris lacustris* (Linnaeus). Abbreviations of family names: HE, Hebridae; HM, Hermatobatidae; HY, Hydrometridae; MA, Macroveliidae; ME, Mesoveliidae; PA, Paraphrynoveliidae.

Such habitats form a kind of intermediary type between hygropetric and pleustonic habitats called the *intersection* type of habitats (Andersen 1982b).

By superimposing various types of habitats on a reconstructed phylogeny of gerromorph bugs, Andersen (1979, 1982b) showed that the hygropetric type of habitats is ancestral for the Gerromorpha as a whole as well as for the families Mesoveliidae, Hebridae, Paraphrynoveliidae, Macroveliidae, and Hydrometridae. Such habitats is probably also ancestral for the family Veliidae, although most of the about 640 known species of veliids live in pleustonic habitats. Almost all of the about 520 known species of the family Gerridae are pleustonic. Thus, despite the dominance of extant species of Gerromorpha in pleustonic

habitats, ancestral gerromorphans most probably lived in humid terrestrial or marginal aquatic habitats rather than on water surfaces. This is in agreement with hypotheses about the ancestral habitats for other heteropteran infraorders, viz. Dipsocoromorpha and Leptopodomorpha, as well as for the Heteroptera as a whole (China 1955; Polhemus 1985; Cobben 1978).

Habitat uses in fossil insects can usually only be inferred indirectly. For compression or petrified fossils, the depositional environment (e.g. limnic or marine) is most important. The taxonomic and taphonomic nature of other fossils in the assemblage may also provide clues to the palaeoenvironment of the fossil in question. Species of the family Gerridae are so highly specialised to life on the water surface that one hardly

can doubt that Paleogene gerrids (*Palaeogerris* spp., *Telmatrechus* spp.) also were surface dwellers. The only extant gerrids which (secondarily) have acquired a more terrestrial way of life all belong to the Oriental subfamily Eotrechinae and have structural specialisations not found in any fossil gerrid (Andersen 1982b).

Unlike the case of Paleogene Gerridae, it is far from certain that all species of Hydrometriidae were associated with free water surfaces. Several extant hydrometrids live in humid terrestrial habitats (*Heterocleptes* spp. in forest litter; *Chaetometra robusta* and some *Hydrometra* spp. on ferns) and it is quite likely that the extinct hydrometrids *Limnaxis* spp. and *Metrocephala anderseni* lived in similar habitats. The two species of *Eocenometra*, however, may have been pleustonic as suggested by their long legs similar to species of the extant genus *Bacillometra* which inhabit flowing water (Andersen 1982b).

Based on the assumption that the Lower Jurassic fossil *Engynabis tenuis* (see above) was a member of the Gerromorpha, Wootton (1988) hypothesised that the pleustonic habit was an ancient adaptation in heteropterous insects. However, even if the earliest members of the infraorder were that old (which is quite likely), ancestral gerromorphans were probably more terrestrial (hygropetric) than truly aquatic (see above). Only the future discovery of Mesozoic fossils with structural modifications comparable to extant water striders will provide safe evidence for a pleustonic habit in gerromorphans older than the Paleogene.

Note: Because of their superficial similarity with water striders (long, slender body and legs), Jurassic and Cretaceous insects of the family Chresmodidae (Phasmatoidea; Handlirsch 1906-1908) have been supposed to be pleustonic, living on the surface of sea water. Baudoin (1980), however, showed that because of their size (body length 2.5-5 cm), the physical properties of the surface film rule out that

chresmodids could have been supported by the water surface.

Colonisation of marine habitats

Although the majority of gerromorphans live in freshwater habitats, as many as 180 species occur in the marine environment, chiefly in intertidal coastal habitats with mangrove swamps and coral reefs bordering the tropical seas. Five species of sea skaters, *Halobates*, are the only insects that inhabit the surface of the open ocean. (Andersen & Polhemus 1976; Andersen 1991a, 1991b). Marine habitats have probably been colonised about a dozen times independently during the evolution of the Gerromorpha (Andersen 1982b). The small family Hermatobatidae contains only marine species, while the most species-rich genera of marine bugs are *Halovelia*, *Xenobates* (Veliidae-Haloveliinae; Andersen 1989b, 1991a), and *Halobates* (Gerridae-Halobatinae; Andersen 1991b).

Andersen (1991b) discussed the evolution of *Halobates* in the light of a reconstructed phylogeny for the genus. Sea skaters probably invaded marine habitats from lotic freshwater habitats, through estuaries and mangrove swamps. Some species became adapted to living on the near-shore, more exposed sea surface, and ultimately to life on the surface of the ocean. This unique life-style may have evolved from mangrove-inhabiting species becoming gradually better adapted to more exposed sea conditions (Andersen 1991b). The record of the Middle Eocene *Halobates ruffoi* (Andersen *et al.* 1994) sets 45 Ma as the minimum age for the origin of sea skaters and for the evolution of their unique features and way of life.

All living species of *Halovelia* are marine and most of them inhabit the intertidal zone of tropical coasts, usually where these are bordered by coral reefs. During high tides, adults and immatures of *Halovelia* retreat to holes in

coral blocks and stay submerged, surrounded by an air bubble. The complex cuticular surface structures of *Halovelina* probably assist in maintaining this air-store which may function as a physical gill (Andersen 1989b). *H. electrodominica* from Dominican amber (Oligocene/Miocene) has all of the structural features of extant *Halovelina* believed to be adaptations to a marine life (Andersen & Poinar, in press). The presence of remains belonging to several individuals in the same piece of amber suggests a gregarious behaviour only known from *Halovelina* species living on intertidal reef flats (Andersen 1989b). These fossil sets a minimum age of 20-30 Ma for the colonisation of the marine environment by haloveliine water striders.

Adaptations

Locomotion

Semiaquatic bugs are highly diverse in morphological structures associated with locomotion (thorax, legs), reflecting a great variation in locomotory performance and way of life (Andersen 1976, 1982b, 1995d). In addition, most gerromorphans have their body and legs covered by hydrofuge hair layers to prevent wetting (Andersen 1977b). In species belonging to the Mesoveliidae, Hebridae, Paraphrynoveliidae, Macroveliidae, and some Hydrometridae (*Heterocleptes* and *Veliometra*), the thorax and legs are quite generalised, broadly resembling the morphology of most terrestrial bugs and therefore inferred to be ancestral to the infraorder Gerromorpha as well as to the families mentioned above (Andersen 1976, 1982b). Walking on alternating tripods of support is the ordinary way of locomotion in terrestrial bugs (legs belonging to the same segment are moved asynchronously). *Mesovelina*, *Hebrus*, and *Microvelina* move their legs in the same way both on land and water and walking is probably the ancestral type of locomotion in the Gerromorpha (Andersen 1976, 1979, 1982b).

Compared to the ancestral type mentioned above, the thorax is more or less modified in the majority of semiaquatic bugs. Representatives of *Hydrometra* have extremely long and slender head and body, including thorax. The middle legs originate laterally on the thorax, and the mesocoxal axis is vertical, not oblique as in the ancestral state. All femora are extremely slender. The lateral position of the coxae increases the stroke angle of the vertical leg movements whereas the direction of pull of the trochanteral muscles falls almost exactly in the frontal plane (Andersen 1976). The middle legs of many veliids (e.g. *Velia*, *Halovelina*, and *Rhagovelia* spp.) are distinctly longer than the hind legs. Locomotion on the water surface is here performed by *rowing*, where the middle legs perform simultaneous strokes while the two other leg pairs slide on the surface film (Andersen 1976). Species belonging to the Veliidae commonly have less than three tarsal segments and the claws are inserted preapically, that is in a cleft before the apex of the last tarsal segment. Other pretarsal structures include the arolia which in several veliids form swimming fans, alone or together with the modified claws (Andersen 1982b). The most elaborate swimming fan is found in *Rhagovelia* spp. and consists of a fan of feathered hairs which is unfolded during the thrust stroke of the middle legs (Andersen 1976).

The thorax of members of the family Gerriidae is radically modified. The mesothorax is greatly prolonged and the coxal cavities of the middle and hind legs are far removed from those of the front coxae. The mesocoxae and metacoxae are inserted clearly on the sides of thorax and the coxal axes are almost horizontal. The middle and hind legs are long and slender with the middle pair being much longer than the hind pair. The joints of the two posterior pairs of legs allow wide movements of the femora. The tarsi have only two segments with the small claws inserted preapically

on the last segment. Associated with the restructuring of the Gerrid thorax are radical changes of the leg musculature. The most powerful muscles are the mesotrochanteral depressors which produce the horizontal thrust of the middle legs, while the vertical component of the leg movements is produced by the two coxal rotators (Andersen 1976). In many Gerrids (e.g. *Halobates* spp.), the abdomen is reduced in length and the middle and hind legs appear to originate from near the posterior end of the body (Andersen & Polhemus 1976; Andersen 1982b); the action angles of the middle and hind legs are therefore even more extreme.

Gerrids move very fast on the water surface by *skating* (or “jump-and-slide” movements), where the simultaneous power strokes of the middle legs make the insect take off from the water surface (Andersen 1976, 1982b); the movement is extended after touch-down by passive sliding on the almost frictionless surface film (in contrast to leaping in land insects). Contrary to their high locomotory performance on the surface film of water, Gerrids are usually rather helpless when they are forced to move on a solid substrate.

Obviously, fossils cannot provide direct evidence for the locomotory behaviour of the living insect. It is worth noticing, however, that both the distinctive hydrometrid and Gerrid types of thorax and leg morphology already were present and fully developed in the earliest Paleogene (represented by *Eocenometra* spp. and *Palaeogerris* spp., respectively) and that the *Halobates* type probably had appeared before the Middle Eocene. Thus, it is fairly certain that Gerromorphan bugs had colonised the water surface or pleustonic habitat before the end of the Cretaceous.

Wing polymorphism

Most extant semiaquatic bugs exhibit a very distinct polymorphism in the development of

their flight apparatus, usually termed *wing polymorphism*, after its most obvious external expression (Andersen 1982b, 1997a). Most species are dimorphic. Besides the ordinary long-winged or macropterous, flying morph, there are wingless or apterous adult individuals which have no traces of wings. Short-winged (brachypterous) morphs occur in some species. The wing musculature necessary for flight is only present in long-winged individuals.

Ancestral Gerromorphans were probably wing polymorphic, and the loss of the flightless form in some species is most likely secondary (Andersen 1982b). Individuals of early Cretaceous Gerromorphans, *Duncanovelia extensa* and an undescribed hydrometrid from Brazil (see above), were wingless and the wingless form is the only one known for the hydrometrids and veliids from Baltic amber (Eocene/Oligocene) and *Electrobates spinipes* from Dominican amber (Oligocene/Miocene). The Gerromorphans from the Fur and Ølst Formations are all long-winged and have probably been flying when transported out to sea. This does not rule out, however, that they belonged to species which were polymorphic for wing development.

Adult water striders only use flight for dispersal among habitats and, in temperate regions, in connection with hibernation which takes place on land (Andersen 1982b). In species of northern temperate water striders (*Aquarius*, *Gerris*, and *Limnoporus* spp.), there are definite associations between flight loss and the durational stability of habitats, where monomorphic long-winged or seasonally dimorphic species occupy less stable habitats than predominantly wingless species (Andersen 1993a, 1997a; Spence & Andersen 1994). All marine species of Gerromorpha are wingless (Andersen & Polhemus 1976; Andersen 1982b). This probably also applies to the few fossil species mentioned above. Since all ma-

rine water striders have polymorphic freshwater relatives, the complete loss of the winged form associated with the stable marine habitats is easy to understand.

Feeding

Gerromorphan bugs are predators or scavengers feeding on living or dead arthropods, mostly insects (Andersen 1982b). The feeding apparatus is characterised by the serrated maxillary stylets which protrude far beyond the tip of the four-segmented rostrum during feeding, although the rostrum is held in a straight, unflexed position during the act of feeding (Cobben 1978). There is a considerable variation among gerromorphan bugs in morphological features directly or indirectly associated with prey capture and feeding (Andersen 1982b: 292-294). Two distinctive types of predator strategies can be recognised among extant gerromorphans.

The *searching* strategy exemplified by *Hydrometra* spp. which are timid predators which move slowly around, examining cavities and crevices in the vegetation or other floating objects on the water surface in search of something edible. The antennae are long and constantly waved from side to side. The eyes are relatively small. The rostrum is long and can be extended forward, far in front of the front legs which are not raptorial. The prolongation of the maxillary stylets is accomplished by the extreme prolongation of the head (Cobben 1978; Andersen, 1982b).

The *waiting* strategy as exemplified by members of the family Gerridae which utilise the special properties of the water surface as a means of detecting and locating the prey, in much the same way as a spider uses its web. Gerrid water striders can detect and locate live prey trapped in the surface film of water solely by surface vibrations generated by the struggling prey. The eyes are large and the vision is probably important for close-range location of prey.

Once the prey is located, the predator proceeds rapidly to the prey which, depending upon its size, usually is grasped with the raptorial front legs and sucked out through the relatively short rostrum. The maxillary stylets are just as long as in *Hydrometra* although the head capsule is relatively short. The proper operation of the stylets is accomplished by muscles inserted on a pair of very long apodemes arising from the posterior margin of the head and extending far into the thorax (Andersen 1982b).

In a phylogenetic perspective it is interesting that both these types of predator strategies probably were in effect before in earliest Paleogene, the "hydrometrid" type as exemplified by *Eocenometra* spp. and the "gerrid" type as exemplified by *Palaeogerris* spp. The great abundance and diversity of flying insects of the Fur and Ølst Formations (Larsson 1975; Andersen & Andersen 1996) indicates that there was plenty of potential prey for these Lower Paleogene water striders. The recent discovery of an indisputable fossil Hydrometridae from the Lower Cretaceous (Aptian) of Brazil (A. Nel, personal communication) suggests that at least the "hydrometrid" type of predator strategy is very old.

Reproductive biology

Fossils rarely leave any clues from which their reproductive biology can be deduced. Findings of juveniles (nymphs) and cast skins (exuviae) may be taken as evidence of the insects being fossilised while they were part of a breeding population. The female type of *Aquarius lunpolaensis* probably has the abdomen inflated by a large number of ripe eggs (*hypogastry*) as in extant species of the genus *Aquarius* (Andersen 1982b: 318). When it comes to questions about sexual behaviour and mating strategies, some recent fossil findings suggest that modern patterns of variation may have existed for a long time.

Sexual size dimorphism and mating strate-

gies in water striders of the family Gerridae have been subject to a number of both experimental and comparative studies (reviewed by Spence & Andersen 1994; Rowe *et al.* 1994; Arnqvist 1997). Female/male size ratios vary between 0.8 for some species of *Halobates*, *Metrocoris* (Halobatinae), and *Limnometra* (Gerrinae) and 1.8 for *Andersenella binotata* Polhemus & Polhemus (Trepobatinae). The largest extant gerrid, *Gigantometra gigas*, is about 20 times as large as the smallest species belonging to the genus *Naboandelus* (Andersen 1997b).

A large variation in absolute size as well as in F/M ratios are seemingly old traits in gerrids. Males of *Palaeogerris grandis* sp. nov. reached a body length of about 32 mm, thus approaching the size of the largest living gerrids. Within the subfamily Gerrinae, females are usually bigger than conspecific males (Andersen 1994, 1996a, 1997b), but the female/male (F/M) size ratio declines as body size increases in extant species of *Aquarius*, *Gerris*, and *Limnopus*. In other words, males tend to become larger relative to females as the absolute body size increases. This tendency also seems to apply to fossil members of the Gerrinae. In *Palaeogerris furensis* and *grandis* spp. nov. (female length 19.6 and 27 mm, respectively), the F/M size ratio is about 0.9 which compares favourably with F/M ratios calculated for larger species of *Aquarius* and *Limnopus* (Andersen 1994). In some of these large gerrids the small F/M ratio (males larger than females) is associated with territorial behaviour where males defend suitable oviposition sites and attract females by way of surface ripple signals (Hayashi 1985; Spence & Wilcox 1986; Wilcox & Spence 1986).

Water strider males usually exhibit post-copulatory guarding, staying in close contact with the female, usually by riding on her back, after the copulation proper has terminated. By remaining in contact with his mate in the interval

between copulations, the male may prevent takeovers by other males that could lead both to sperm displacement and loss of opportunities to mate again with the same female and fertilise more of her eggs. Females carrying a male, however, experience a reduced foraging activity and are more vulnerable to predation. Selection reducing the cost of loading should therefore favour females that are large relative to their mates.

A pair of *Electrobates spinipes* (from Dominican amber) was found captured in what seems to be a mating situation (Andersen & Poinar 1992). The female measures 3.6 mm or more than 1.4 times the length of the male. The male and female are closely associated (Figs 120-121), with the male situated closely behind and slightly above the female, holding her hind femora with both of his front legs. There is no direct genital contact between the two individuals. Either the male has been dislodged during the process of inclusion in resin, or the pair has formed a "tandem" with the female skating along the water surface and the male passively trailing behind as observed in several extant gerrids.

Extended mate guarding is also observed in many Veliidae. A pair of *Halovelina electrodominica* (Dominican amber) was seemingly trapped when mating (Andersen & Poinar, in press). The male is positioned on top of the abdomen of the female (Figs 66 and 118) with his left front leg stretched forward and the tibia (which has a specialised grasping comb) pressed against the side of the female's pronotum. The hind leg of the same side is curled around the female's hind femur. Seemingly, both leg postures are a function of the male's struggle to uphold his grip of the female. In most extant *Halovelina* species, the male rides passively on the back of the usually larger female for an extended period of time in between copulations.

Historical biogeography

Cladistic biogeography and fossils

Historical biogeography is the study of patterns of spatial distribution of organisms explained by their evolutionary history. Historical explanations of distributional patterns fall into two classes, dispersal models and vicariance models. The classical *dispersal model* postulates that disjunct distributions of organisms can be explained by dispersal over pre-existing barriers such as oceans, mountains, or deserts. The *vicariance model* tries to explain disjunct distributions of related taxa by the appearance of barriers fragmenting ancestral species ranges. According to the dispersal model certain geographical areas were originally devoid of organisms and later colonised from some “source” area, whereas the vicariance model presumes that the organisms evolved *in situ*.

During the past few decades, biogeographical theory and practice have come to rely heavily on advances in biological systematics, in particular phylogenetic systematics or cladistics. Beginning with the works of Hennig (1960, 1966) and Brundin (1966, 1988), the field of *cladistic biogeography* has emerged (Nelson & Platnick 1981; Humphries & Parenti 1986; Humphries *et al.* 1988; Forey *et al.* 1992). Here, data on the geographical distribution of species are integrated with knowledge about the phylogenetic relationships among species and monophyletic groups (clades). Since the Earth and its biota have evolved together, different groups of organisms inhabiting the same geographical area may share a common history. Finally, the developments in the theory of plate tectonics during the 1960s led to the acceptance of the idea that biogeographic patterns may have their causal explanation in past distributions of land masses different from those known to-day.

The application of the methods of cladistic biogeography starts with a taxon-area cladogram where the areas of distribution of species or higher taxa are superimposed upon a cladogram of relationships between taxa (Fig. 90). By applying various tools of analysis, an attempt is then made to transform the taxon-area cladogram into one or more area cladograms where each geographical area appears just once. If area cladograms derived from several unrelated groups of organisms are congruent, one may be confident that these reflect the biogeographic history of the areas (e.g. Enghoff 1995). Recent advances in cladistic biogeography have chiefly been concerned with the refinement of analytical tools (e.g. Morrone & Carpenter 1995; Morrone & Crisci 1995; Nelson & Ladiges 1996). Examples of cladistic biogeography applied to various groups of water striders can be found in works by the present author (Andersen 1982b, 1989b, 1991a, 1995c, 1998).

Chiefly because of the notorious incompleteness of the fossil record, contemporary biogeographers have not paid much attention to fossils as indications of past distributional patterns or extinction as equally important to dispersal and vicariance in shaping the present distribution of organisms (Rosen 1988a). Nevertheless, locality data for fossils may provide important biogeographical information. When a fossil species can be placed in a monophyletic group (clade) also comprising extant species, the distribution of the fossil species can be compared with the known distribution of extant species belonging to the same clade. There are two possible outcomes of such comparisons:

(1) If the fossil locality is inside the distributional range of extant clade members it confirms that the distributional area of the taxon has persisted through geological time and the present distribution of the taxon not necessarily an effect of recent dispersal from some other area.

(2) If the fossil locality is outside the distributional range of extant clade members it indicates that the taxon once had a wider distribution and has now disappeared in some part of its former distributional area.

Thus, fossils may provide important clues to past distributions that may enable us to choose among two or more, equally plausible biogeographical hypotheses. When plotted on palaeogeographical reconstructions of the Earth at a given geological time, the fossil record may also suggest possible pathways of dispersal or vicariance events in the past. In the following, I will discuss the distribution of fossil Gerromorpha in a historical biogeographical perspective.

Historical biogeography of Gerromorpha

Hydrometridae and allied families

The present distribution of the genera belonging to the monophyletic group composed of the families Paraphrynoveleidae, Macroveliidae, and Hydrometridae (excluding *Hydrometra*) is rather disjunct (Andersen 1982b: 357-358). When superimposed upon a cladogram of relationships between genera, the occurrence of *Paraphrynovelelia* in South Africa, *Chepuvelia* in Chile, and *Macrovelia* + *Oravelia* in western North America, as well as the vicariant distributions of the sister taxa *Veliometra* (Brazil) and *Heterocleptes* (western Africa, Borneo) suggest primitive cosmopolitanism for the ancestors of the clade composed by the three families (Fig. 90, A). The addition of fossil genera classified in this clade (Fig. 90, B) give further support to this hypothesis. Despite the fos-

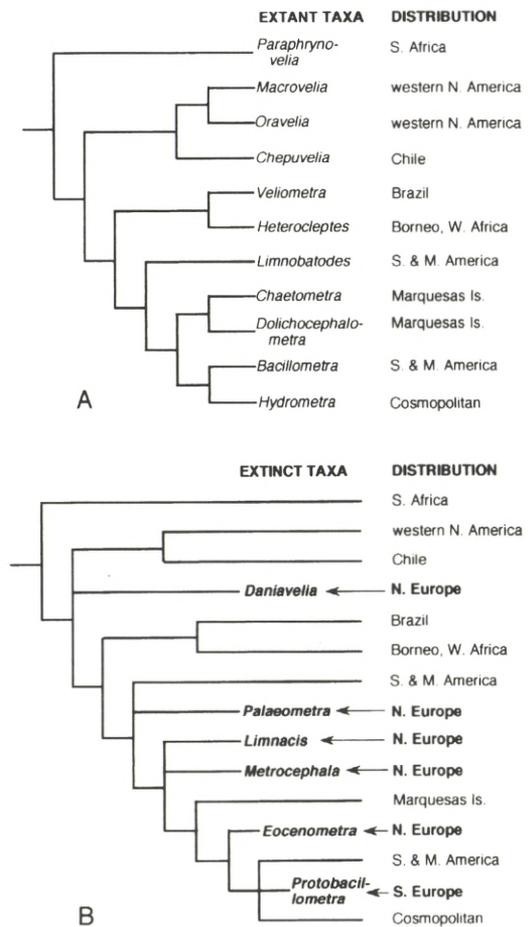


Fig. 90. Taxon-area cladograms for the genera Paraphrynoveleidae, Macroveliidae, and Hydrometridae. Geographical distributions superimposed upon cladogram of relationships between genera. A, taxon-area cladograms for extant genera. B, same with extinct genera included (distribution in boldface). Further explanations in text.

sil record of the group certainly being geographically biased, the fossil data suggest that the Paleogene Europe was inhabited by a rather diverse fauna of hydrometrids whereas at present, this clade is only represented by a few species of the cosmopolitan genus *Hydrometra* (Andersen 1995a).

Gerrine water striders

Water striders belonging to the subfamily Gerrinae are widely distributed in all parts of the World and several genera have distributional ranges covering several zoogeographical regions (Andersen 1975, 1982b). Based on a cladistic analysis of relationships between genera, Andersen (1995c) applied various analytical tools to the distribution of extant genera, hypothesising that ancestral gerrines probably were widespread before the Cretaceous- Paleogene transition. One of the postulated vicariance events were the disruption of ancestral members of the tribe Gerrini by the separation of Gondwanaland and Laurasia in the Late Mesozoic (e.g. Smith *et al.* 1994). One lineage evolved into predominantly palaeotropical genera, whereas another lineage evolved into the predominantly holarctic genera *Aquarius*, *Gerris*, *Gigantometra*, and *Limnoporus* (Andersen 1990, 1993b; Andersen & Spence 1992). The available fossil gerrines from the Paleogene of Eurasia and North America all belong to the latter lineage and thus support the scenario outlined above.

Sea skaters, Halobates

The majority of the 44 extant species of *Halobates* are found in the tropical parts of the Indo-West Pacific region, roughly between latitudes 30° N and 30° S (Herring 1961; Cheng 1985, 1989). *H. robustus* Barber (endemic to the Galapagos Islands) and the open-ocean species *H. sobrinus* White, *splendens* Witlaczil (eastern Pacific Ocean), and *micans* Eschscholtz (Atlantic Ocean, the Caribbean Sea, and eastern Pacific Ocean) are the only sea skaters that occurs outside this region. No living species of *Halobates* have so far been recorded from the Mediterranean. Three species, including the open-ocean species *H. germanus* White, are found in the Red Sea (Schmidt & Müller 1973), but apparently none of these have managed to spread, actively or passively, through the Suez Canal to

the Mediterranean as have other marine organisms. The record of a fossil sea skater, *Halobates ruffoi* Andersen *et al.* (1994), from the Middle Eocene of northern Italy may help understanding of the biogeographical history of sea skaters.

The present distribution of coastal *Halobates* species more or less coincides with the distribution of reef-building corals and mangrove trees which require a relatively high sea temperature. The five open-ocean species of *Halobates* occur in tropical and subtropical waters and their occurrence and abundance on any given water mass is apparently controlled by surface water temperatures, with an optimum temperature range for four eastern Pacific species (including *H. micans*) of 24-28° C (Cheng & Schulenberger 1980). The absence of *Halobates* species from the Mediterranean may in part be due to the surface temperature being below 20° C at certain times of the year whereas the surface temperature of the Red Sea varies between 25 and 30° C.

In the Lower and Middle Eocene, the Mediterranean was connected with the Indo-Pacific Ocean by the Tethys Ocean (see map, Fig. 91), located in present day Turkey, Iraq, and The Persian Gulf. In this period, the Tethys was a wide and continuous ocean, probably with numerous islands. Jaczewski (1972) hypothesised that the pantropical *Halobates micans* dispersed from the Indo-Pacific to the Atlantic Ocean through this Tethyan connection. However, as also pointed out by Jaczewski (1972), there have been other, more recent routes of dispersal to the Atlantic Ocean, e.g. from the Indian Ocean around southern Africa, or from the eastern Pacific Ocean through Middle America, before the closure of the Isthmus of Panama.

Coral bugs, Halovelgia

The genus *Halovelgia* contains 31 described species (Andersen 1989a, 1989b; Lansbury 1996) which are distributed throughout the Indo-

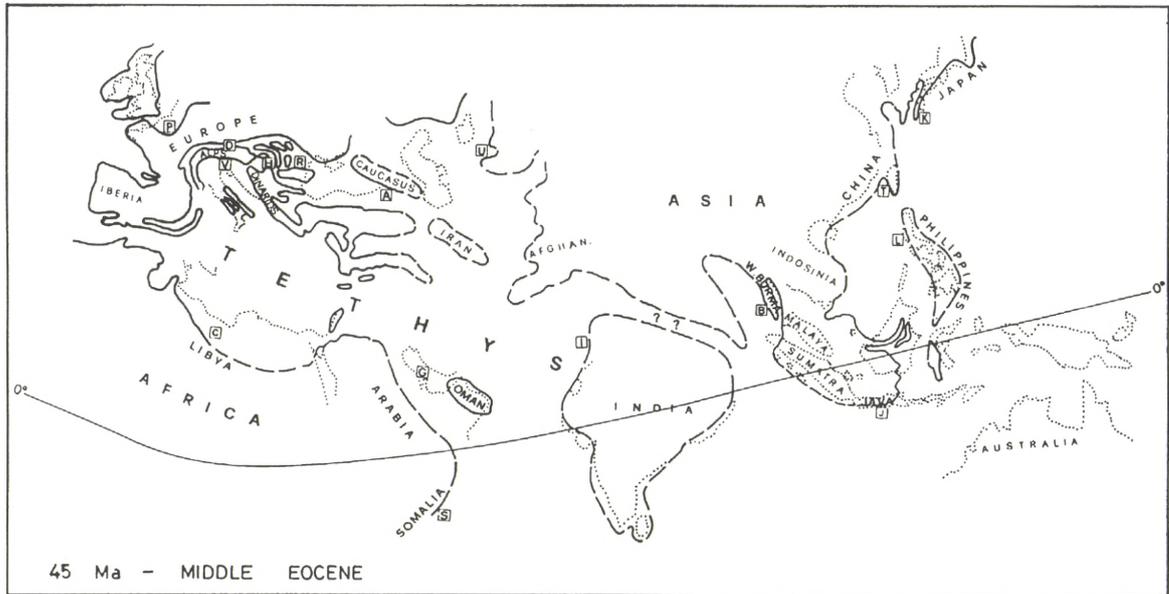


Fig. 91. Palaeogeography of the Mediterranean and the Indian Ocean areas in Middle Eocene, 45 Ma. Capital letters indicate some of the main fossil-bearing sites from the epoch, including Veneto (V) where the fossil sea skater *Halobates ruffoi* Andersen, Farma, Minelli & Piccoli was found (after Piccoli *et al.* 1991).

West Pacific region (Fig. 92), ranging from the Red Sea and east coast of Africa including Madagascar to the islands of the West Pacific Ocean as far east as Samoa. Andersen (1991a) analysed the historical biogeography of marine water striders, and concluded that the present distribution of *Halovelina* reflects both vicariance and dispersal events. The distribution of extant haloveliines suggests that the group originated somewhere in the Indo-Australian region. The two limnic genera, *Entomovelina* and *Strongyloveina*, are found in India, Indo-China, and Malaysia (Andersen 1982b). The distribution of the marine genera *Xenobates* and *Haloveloides* covers the same geographical areas. Most *Halovelina* species found along the coasts of East Africa, Madagascar, and the islands of the Indian Ocean (Mascarenes, Seychelles, and the Maldives) belong to the predominantly Southeast Asian *H. malaya* group (Andersen 1989b) and may have originated in relatively late dispersal and subsequent speciation events. On the other

hand, the disjunct distributions of the most basal clades of *Halovelina* may be relict of an ancient, much wider distribution of the genus.

The finding of an extinct species of coral bugs, *Halovelina electrodominica* Andersen & Poinar (in press) in the Caribbean (Fig. 92) suggests that this genus had a trans-Pacific distribution in the Oligocene-Miocene. Very few extant groups of marine water striders have a distribution comprising both the western and eastern parts of the Pacific Ocean and/or the Caribbean. One species of *Hermatobates* (*Hermatobatidae*) occurs in the Caribbean while the remaining nine species have an Indo-Pacific distribution. The sea skaters, *Halobates* (*Gerridae*), have one endemic species (*H. robustus* Barber) in the Galapagos Islands, while four open ocean species occur along the Pacific coast of Middle and South America (*H. sericeus*, *sobrinus*, *micans*, and *splendens*) or along the Caribbean and Atlantic coasts of these areas (*H. micans*).

The Atlantic/Caribbean/eastern Pacific fauna of marine water striders is in general composed of taxa of low taxonomic rank, i.e., genera with close limnic relatives or species of otherwise limnic genera (Andersen & Polhemus 1976; Andersen 1982b; Polhemus & Manzano 1992). In contrast, the marine water striders of the Indo-West Pacific region generally belong to taxa of higher rank, such as genus-groups or tribes. This seems to follow a general pattern for organisms of tropical shallow seas such as mangrove trees, reef-building corals, and various groups belonging to these communities (Ricklefs & Latham 1993). Since taxonomic rank within a clade coarsely reflects age of origin, water striders probably colonised the marine environment more recently in the Caribbean than in the Indo-West Pacific region.

When and why has *Halovelia* disappeared from the Caribbean? Marine water striders are chiefly confined to the tropics and their distri-

butions seem to be limited by the same temperature regimes as reef-building corals and mangrove trees, i.e. in sea water bounded by the 20° C isotherms. Fossil evidence suggests major changes through the Tertiary in the climatic conditions favouring these shallow water communities. The mangrove palm, *Nyssa*, had an extensive distribution in the Caribbean in early Tertiary and occurred at high latitudes in Europe (Ricklefs & Latham 1993). Throughout much of the Tertiary, the reef coral belt appears to have been latitudinally wider than it is today, though it was noticeably narrowed to something like its present limits by the late Neogene, and was reduced still further during the Pleistocene when it was narrower than today (Rosen 1988b). Although there are several possible explanations for extinction, a drop in the sea temperature during the Miocene may have had a profound effect on stenothermic shallow water organisms such as *Halovelia*.

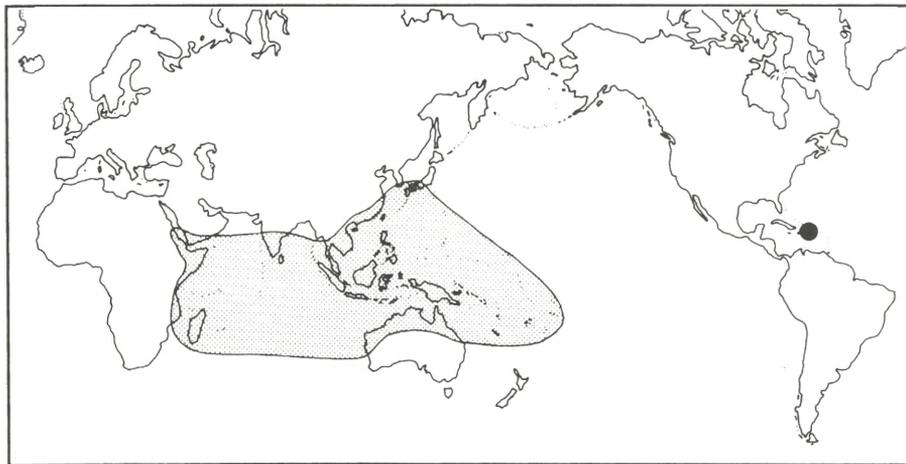


Fig. 92. Distribution of extant species of *Halovelia* (shaded area) and the fossil *Halovelia electrodominica* Andersen & Poinar (dot) (re-drawn from Andersen & Poinar 1998).

Conclusions

Water striders and other semiaquatic bugs (Hemiptera-Heteroptera, Gerromorpha) comprise about 1,600 extant species classified in eight families. So far, about 30 fossil species belonging to six families have been described or recorded, spanning more than 120 million years of geological history. Fossil localities are distributed on all continents except Africa, but are concentrated in Europe. Three sites are of Mesozoic age while 16 can be dated to the Cenozoic. Both lacustrine, marine, and terrestrial deposits are represented, the latter as amber with insect inclusions.

Recent collections of fossils on the islands of Fur and Mors, northern Denmark, reveal an unusually rich fauna of insects, including seven species classified in four genera and three families of Gerromorpha. The fossils are found in sediments belonging to the Fur and Ølst Formations which were deposited in a marine environment at the Paleogene-Eocene transition, 55-54 Ma ago.

Phylogenetic classification is the most useful, general reference system in evolutionary biology. Within the Gerromorpha, phylogenies are now available for most higher taxa, down to the level of subfamilies and tribes, and for the genera and species of several groups. Although the fossil record of water striders is immensely imperfect, the available fossils provide useful insights into the evolutionary history of the group. By applying cladistic principles and methods, fossil taxa can in most cases be placed in phylogenies (cladograms) together with their extant relatives. Cladograms calibrated against the fossil record yield phylogenetic trees which can be used to estimate minimum divergence time of extant monophyletic groups (clades).

The evolutionary history of water striders and other semiaquatic bugs probably began in

the early Mesozoic. The oldest members of the Gerromorpha are of Lower Cretaceous age and belong to the structurally least modified families Mesoveliidae and Veliidae, but also to the more specialised family Hydrometridae. Several genera and species belonging to the structurally most derived family, the Gerridae, occur in Early Paleogene deposits, both in Europe and North America.

Through a research protocol called ecological phylogenetics, ecological data from extant water striders are combined with phylogenies to reveal patterns of adaptations and to infer the history of changes that have generated these patterns. In the most ideal case, fossils can contribute by suggesting most plausible pathways of evolution, minimum ages for the origin of adaptations, etc. In the Gerromorpha, the adoption of life on the water surface probably evolved before the beginning of the Paleogene. The record of a fossil sea skater, *Halobates*, from the Middle Eocene indicates an early invasion of the marine environment by water striders. The feeding strategy exemplified by the most specialised Hydrometridae were probably already present in Lower Cretaceous. Pronounced sexual size dimorphism and mate guarding appeared before the Oligocene/Miocene. On this background, it is a reasonable assumption that semiaquatic bugs displayed most of their present structural and functional diversity at the beginning of the Paleogene.

Within the context of cladistic biogeography, the geographical distribution of fossil species may provide information not available from the distribution of extant taxa or support biogeographical hypotheses based exclusively on the latter. For example, the distribution of fossil Hydrometridae strengthens the assumption of primitive cosmopolitanism in this family.

Available fossils of Gerrinae from the northern Hemisphere support the hypothesis of a Gondwana-Laurasia vicariance during the evolution of this subfamily. The finding of fossil species of the marine genera *Halobates* (Gerridae) and

Halovelgia (Veliidae) in localities outside their present distributional ranges, strongly suggests that extinction has taken place and must be taken into account in studies of historical biogeography.

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Plates 1-8

PLATE 1

Figs 93-96. *Palaeogerris furens* gen. et sp. nov.

93. Male holotype. Skarrehage Molergrav, Mors; Bent S e Mikkelsen leg. (Molermuseet). Scale bar = 5 mm.
94. Head and fore legs of male holotype. Scale bar = 2 mm.
95. Female paratype No. 1 (Fur Museum). Scale bar = 5 mm.
96. Right fore wing of paratype No. 16 (Palaeontological Institute & Museum, Uppsala University). Scale bar = 2 mm.

Photographs by G. Brovad (Figs 93-95) and Y. Popov (Fig. 96).



PLATE 2

Figs 97-99. *Palaeogerris furensis* gen. et sp. nov.

97. Female paratype No. 2 (Palaeontological Institute & Museum, Uppsala University). Scale bar = 5 mm.
98. Same, counterpart. Scale bar = 5 mm.
99. Head, thorax, and basal abdomen of female paratype No. 2 (counterpart). Scale bar = 2 mm.

Photographs by Y. Popov.

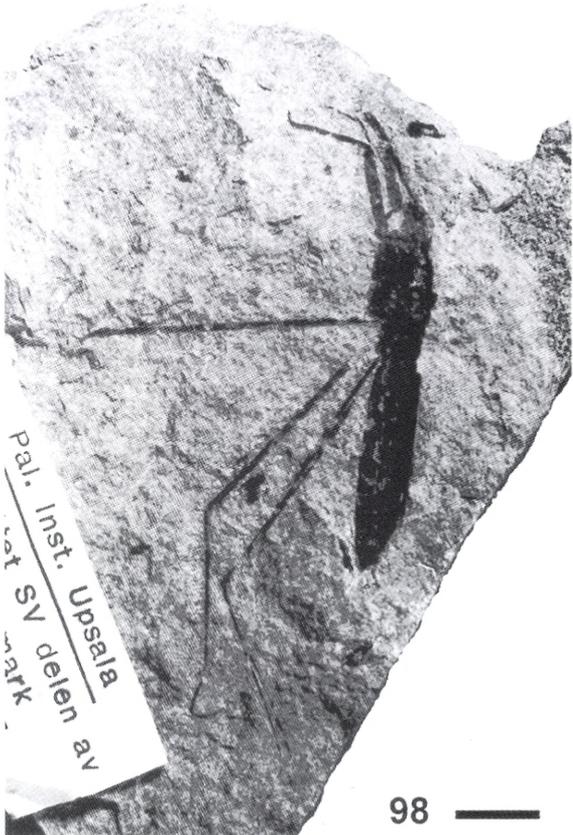
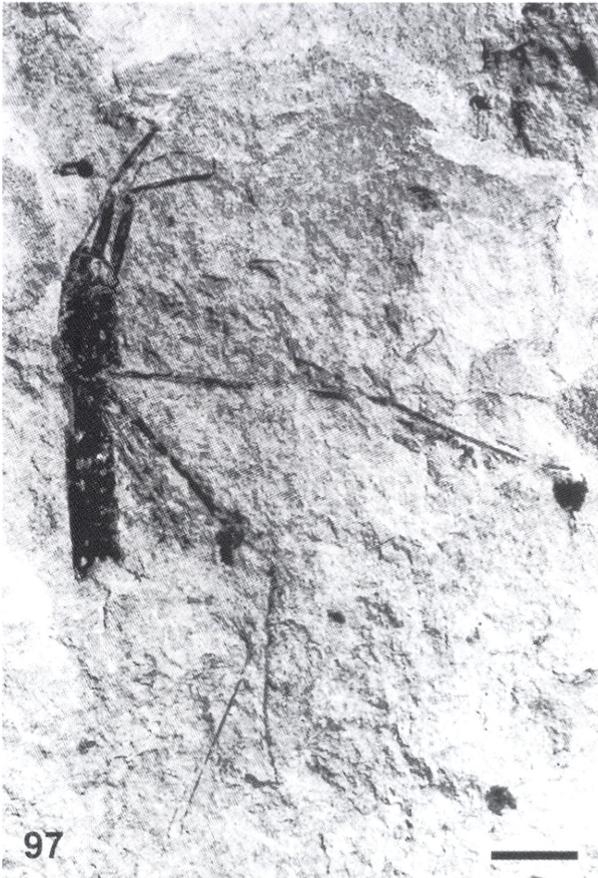


PLATE 3

Figs 100-103. *Palaeogerris grandis* gen. et sp. nov.

100. Male holotype (Fur Museum). Scale bar = 10 mm.
101. Body and bases of antennae and legs of male holotype. Scale bar = 5 mm.
102. Female paratype No. 3 (Geological Museum, University of Copenhagen). Scale bar = 10 mm.
103. Abdominal end of male paratype No. 4. Stolleklint, Fur. Søren Kristensen leg. (Coll. Søren Kristensen, Veksø). Scale bar = 2 mm.

Photographs by G. Brovad.

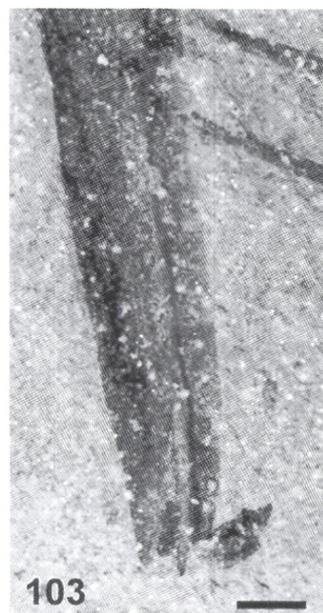
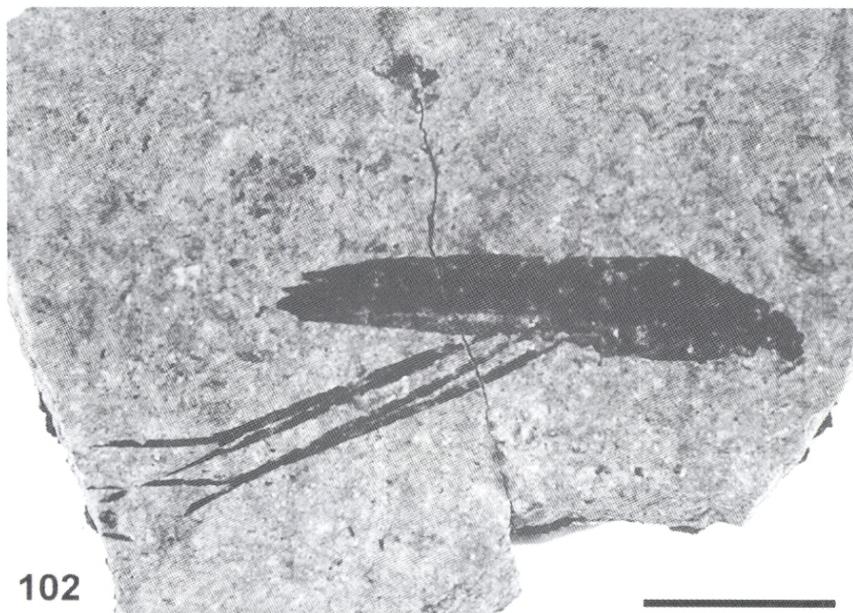
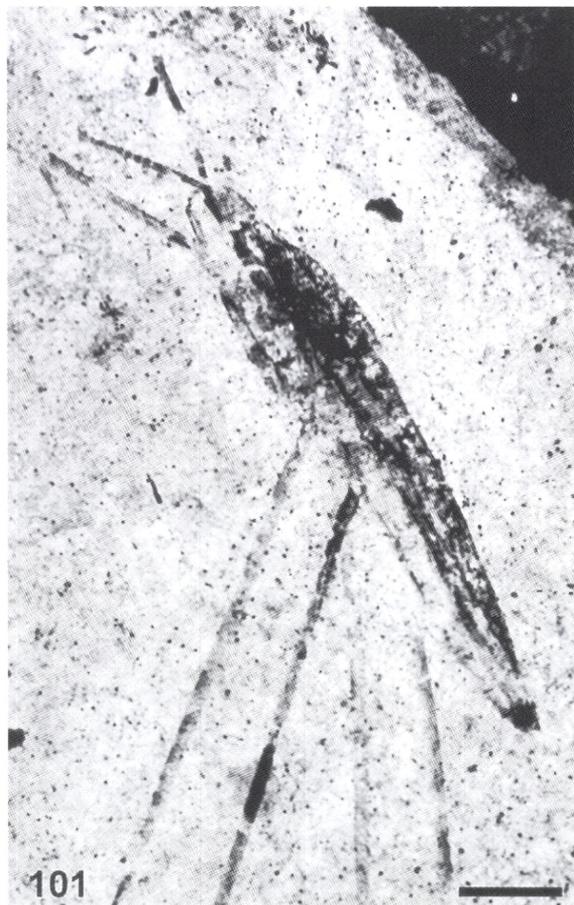


PLATE 4

Figs 104-105. *Palaeogerris mikkelseni* gen. et sp. nov.

104. Holotype. Ejerslev, Mors; Bent S e Mikkelsen leg. (Molermuseet).
Scale bar = 5 mm. 105. Same. Scale bar = 10 mm.

Fig. 106. *Halobates ruffoi* Andersen, Farma, Minelli & Piccoli. Female holotype. Bolca near Verona, Italy. (Museo Civico di Storia Naturale, Verona).
Scale bar = 2 mm.

Photographs by G. Brovad (Figs 104-105) and C. Brogiata (Fig. 106).

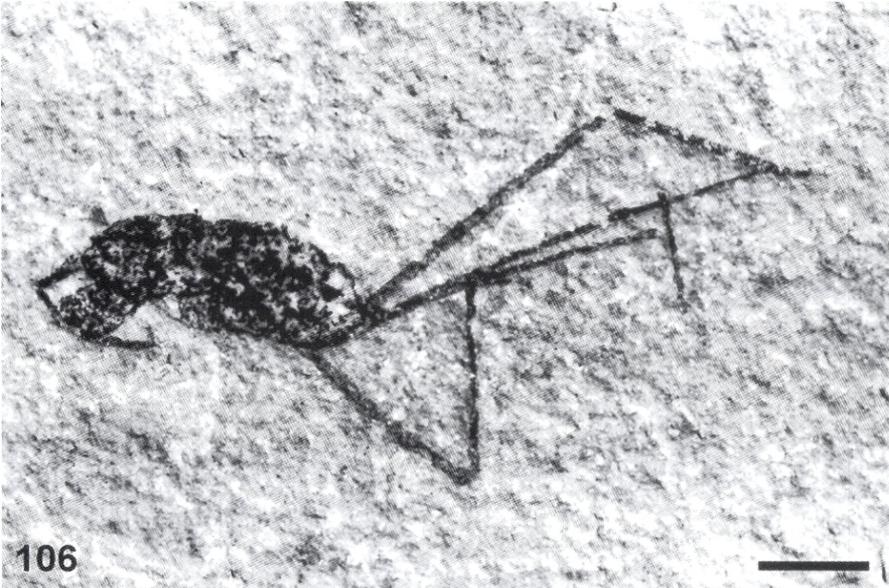
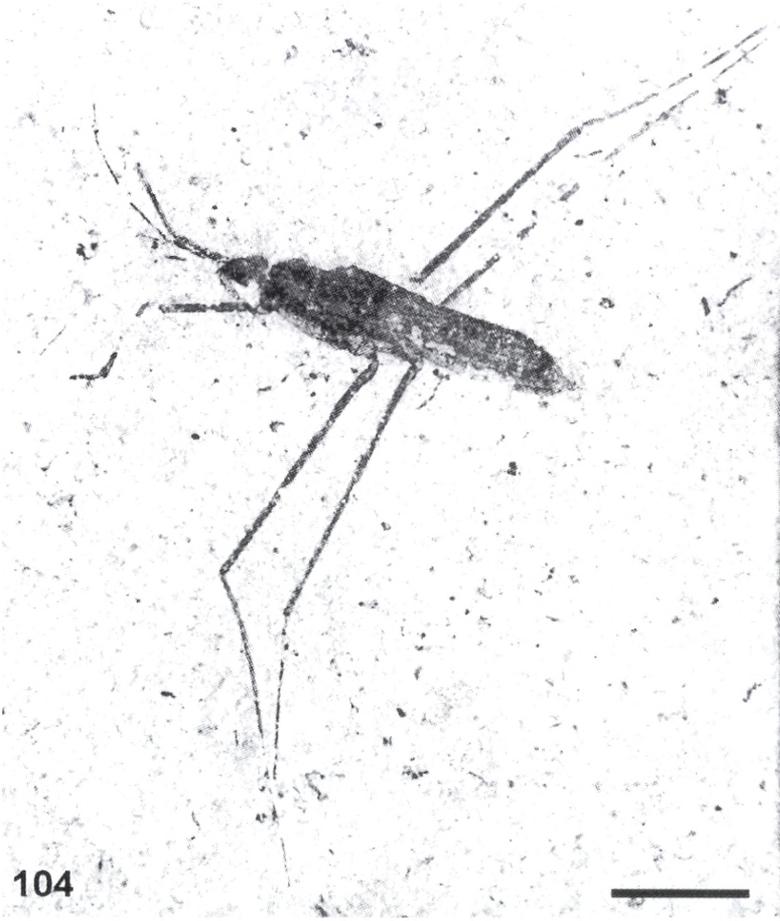


PLATE 5

Fig. 107. *Eocenometra danica* Andersen. Female holotype. Vester Sundby, Mors; M. Sørensen leg. (Geological Museum, University of Copenhagen). Scale bar = 5 mm.

Figs 108-109. *Eocenometra longicornis* sp.n.

108. Female holotype. Stolleklint, Fur; Henrik Madsen leg. (Geological Museum, University of Copenhagen). Scale bar = 5 mm.

109. Paratype. Stolleklint, Fur; Henrik Madsen leg. (Geological Museum, University of Copenhagen). Scale bar = 5 mm.

Fig. 110. *Daniavelia morsensis* gen. et sp. nov. Female holotype. Ejerslev Møllergrav, Mors, Henrik Madsen leg. (Geological Museum, University of Copenhagen). Scale bar = 2 mm.

Photographs by G. Brovad.

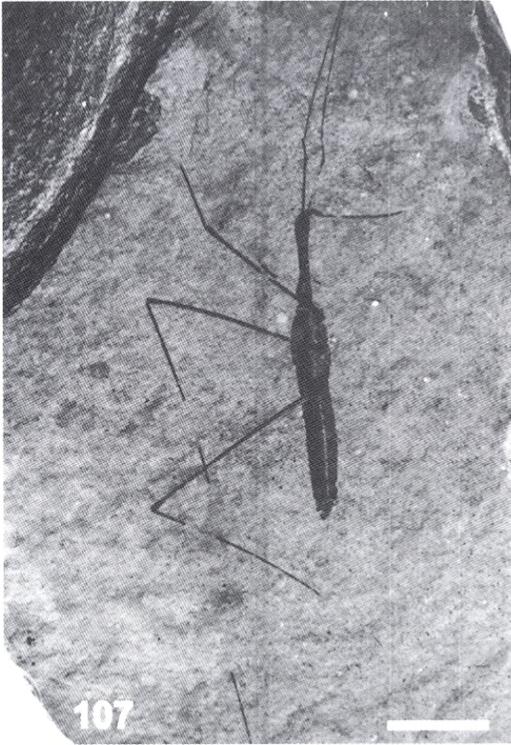


PLATE 6

Figs 111-112. *Limnaporus wilsoni* sp. nov.

111. Male holotype. Driftwood Creek E. of Smithers, British Columbia, Canada; M.V.H. Wilson leg. (Royal Ontario Museum, Ottawa). Scale bar = 10 mm.
112. Fifth instar nymph paratype. Driftwood Creek E. of Smithers, British Columbia, Canada; M.V.H. Wilson leg. (Royal Ontario Museum, Ottawa). Scale bar = 5 mm.

Figs 113-114. *Telmatrechus defunctus* (Handlirsch)

113. Part and counterpart of apterous female. Quilchena, British Columbia, Canada. (Simon Fraser University, Canada). Scale bar = 10 mm.
114. Apterous female (counterpart). Scale bar = 5 mm.

Photographs by G. Brovad (Figs 113-114) and R. Mathewes (Figs 113-114).

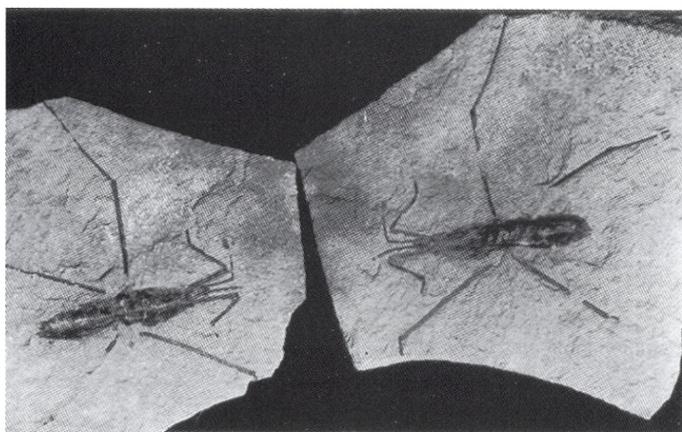
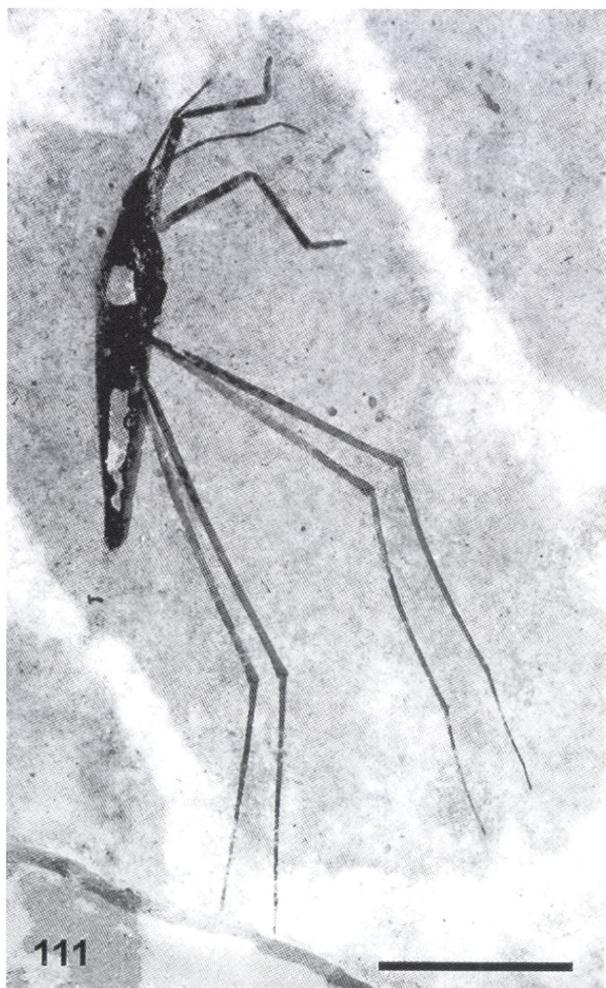


PLATE 7

Fig. 115. *Electrovelia baltica* gen et sp. nov. Apterous holotype. Baltic amber, Denmark; C.V. Henningsen leg. (Zoological Museum, University of Copenhagen, Denmark). Scale bar = 1 mm.

Figs 116-117. *Gerris* sp.

116. Fourth instar nymph. Baltic amber, Denmark; A.K. Andersen leg. (Zoological Museum, University of Copenhagen). Scale bar = 2 mm.
117. Head including antenna of same specimen. Scale bar = 1 mm.

Figs 118-119. *Halovelis electrodominica* Andersen & Poinar.

118. Female holotype and male paratype. Dominican amber, Dominican Republic, Hispaniola, Greater Antilles. (Coll. G.O. Poinar, Jr. Oregon State University, Corvallis, U.S.A.). Scale bar = 1 mm.
119. Head and right fore leg of female holotype. Scale bar = 0.5 mm.

Photographs by the author.

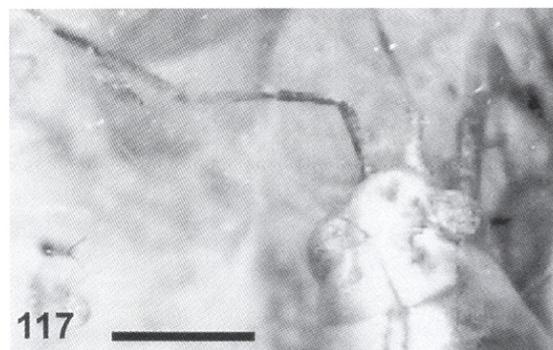
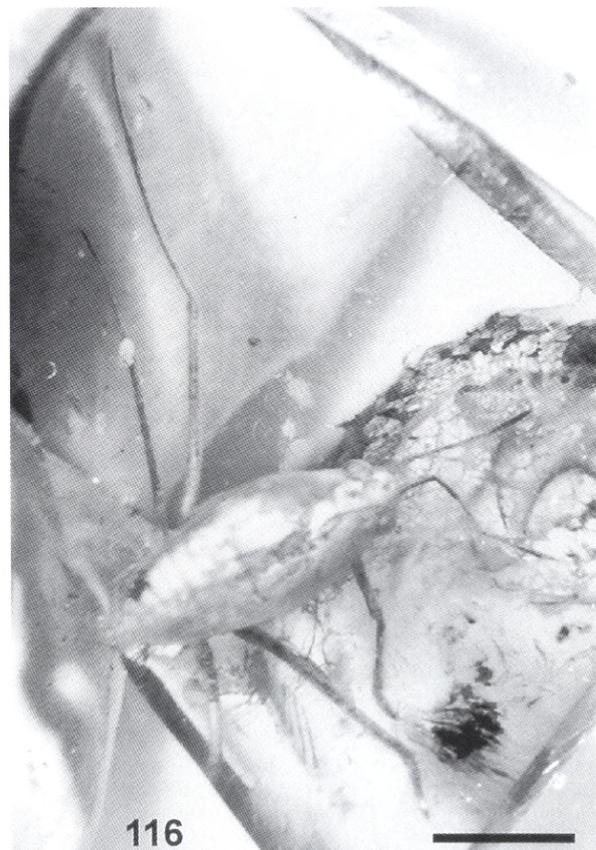


PLATE 8

Figs 120-123. *Electrobates spinipes* Andersen & Poinar.

120. Male holotype and female paratype. Dominican amber, Dominican Republic, Hispaniola, Greater Antilles. (Coll. G.O. Poinar, Jr. Oregon State University, Corvallis, U.S.A.). Scale bar = 1 mm.
121. Same in different view. Scale bar = 1 mm.
122. Male holotype, dorsal view. Scale bar = 1 mm.
123. Female paratype. Scale bar = 1 mm.

Photographs by G.O. Poinar, Jr.



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