

# A marine water strider (Hemiptera: Veliidae) from Dominican amber

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A fossil water strider, *Halovelina electrodominica* sp. n., is described from the Oligo-Miocene Dominican amber based upon a couple seemingly trapped while they were mating. This is the first fossil record of the genus *Halovelina* (Haloveliinae, Veliidae) and, since most living haloveliine water striders are marine, probably also the first record of a marine insect from amber. Extant haloveliines are confined to the Indo-West Pacific region and the Dominican amber species therefore represent another example of remarkable geographical extinction in the Caribbean during the late Tertiary.

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## Introduction

Water striders (Heteroptera, infraorder Gerromorpha) are common insects found on water surfaces in freshwater habitats throughout the world (Andersen 1982). In addition, more than 150 species occur in marine habitats such as mangroves, intertidal zones of coral reefs, and on the near-shore sea surface (Andersen & Polhemus 1976). Five species of sea skaters, *Halobates*, are the only insects which have successfully colonized the surface of the open ocean (Andersen & Polhemus 1976; Cheng 1985; Andersen 1991b). It is estimated that the marine environment was colonized more than a dozen times during the evolution of the Gerromorpha (Andersen 1982, 1995). The marine habit is also an ancient adaptation as indicated by a fossil *Halobates* from the Middle Eocene (geological age about 45 myr) of present-day northern Italy (Andersen et al. 1994).

The large amber deposits from the Dominican Republic (Hispaniola, Greater Antilles) are renowned for the taxonomic diversity and preservation quality of their insect inclusions. Most Dominican amber insects belong to terrestrial groups (Poinar 1992; Grimaldi 1996), but a few

aquatic insects have been described, including the water strider *Electrobates spinipes* Andersen & Poinar (1992) (Gerridae, Electrobatinae).

Based upon two specimens from Dominican amber, we here describe the first fossil species belonging to the water strider subfamily Haloveliinae (Veliidae). The extant fauna of this group is confined to the Indo-West Pacific region and contains two freshwater genera, *Entomovelina* Esaki and *Strongylovelina* Esaki (Andersen 1982), and three exclusively marine genera, *Halovelina* Bergroth, *Haloveloides* Andersen, and *Xenobates* Esaki. Marine haloveliines have radiated extensively in habitats of intertidal coral, rocky, and mangrove coasts in the Indo-West Pacific (Andersen 1989a, 1989b, 1991a), but have never been recorded from the eastern Pacific Ocean, the Caribbean Sea, or from coasts bordering the Atlantic ocean.

This represents the first record of a marine insect from amber. The only previous record of a marine animal in amber is Grimaldi (1996: 66), who illustrated a small intertidal crab (probably belonging to the family Grapsidae) captured in a piece of Dominican amber.

## Material and methods

Two veliid specimens (Figs 1-2), a male and a female, enclosed in a piece of yellow amber weighing 0.22 grams. The piece is semicircular with the greatest length = 12 mm, the greatest width = 7 mm, and the greatest thickness = 2.5 mm. The amber piece containing the fossils originates from the northern mountain ranges in the Dominican Republic. The exact age of these deposits is still not known, and estimates based on microfossil and chemical analyses have produced a range from 15-20 Myr (Iturralde-Vincent & McPhee 1996) to 30-45 Myr (Cepek *in* Schlee 1990).

The piece is polished, highly transparent, with few impurities, cracks and fissures. The veliids are located superficially, the male positioned on top of the abdomen of the female, and plainly visible from above. All appendages of the female and all legs of the male preserved *in situ*. The head and most of thorax of the male are abraded because of the superficial location of the specimen. The piece also contains parts of antennae and legs probably belonging to other specimens of the same species.



Fig. 1. *Halovelvia electrodominica* sp. n. Type specimens from Dominican amber. Scale 0.5 mm (Photo by G.O. Poinar, Jr.).

The specimens were studied directly or by immersing the piece of amber in vegetable oil, using fiber optic reflected and incandescent transmitted light. All measurements are given in mm and were made using a ocular micrometer. Total length was measured from the tip of the head to the end of the abdomen. Measurements of antennal segments 3 and 4 include the basal internode. Length of the femur is measured along the anterior margin of the segment and does not include the trochanter.

## Taxonomy

### *Halovelvia electrodominica* sp. n.

*Etymology.* – The specific name pertains to the inclusion of the species in Dominican amber (electrum).

*Type material.* – Holotype, apterous ♀, contained in a piece of amber originating from the northern mountain ranges in the Dominican Republic (Hispaniola); holotype catalogued under the code HE-4-28 and deposited in the Poinar collection of amber maintained at Oregon State University, Corvallis, Oregon, U.S.A.

Paratype, apterous ♂, enclosed in the same piece of amber as holotype, same code and repository as holotype.

*Description.* – Size: Holotype, apterous ♀, length 1.5, greatest width 0.7. Paratype, apterous ♂, length >0.8 (head and most of thorax missing), greatest width 0.6.

Color and vestiture: Dark brownish. Basal part of dorsal head surface and median part of pronotum paler. Antennae and legs brownish. Head (Fig. 3) with two long bristles in front of eyes and two long, curved bristles (os) inserted between the facets of each eye. Antennal segments with dense, short pubescence. Thorax furnished with a dense pile of short, erect hairs (most easily observed along the margins of pro- and mesonotum). Pubescence of leg segments chiefly short and oppressed. Anterior margin of middle femur with a row of long, pale hairs, each hair being shorter than femur width. The row continues on middle tibia and tarsus.

Apterous female (Figs 1-2): Subovate, length about 2x greatest width across thorax (1.50: 0.74). Head (Fig. 3) much shorter than wide across eyes (0.38: 0.49), slightly deflected anteriorly. Compound eyes small and globular, diameter less than half width of interocular space (0.11: 0.28). Antennae about 0.6x length of insect (1.50: 0.95); lengths of segments 1-4: 0.29: 0.18: 0.24: 0.24; first segment curved and slightly thicker than seg-

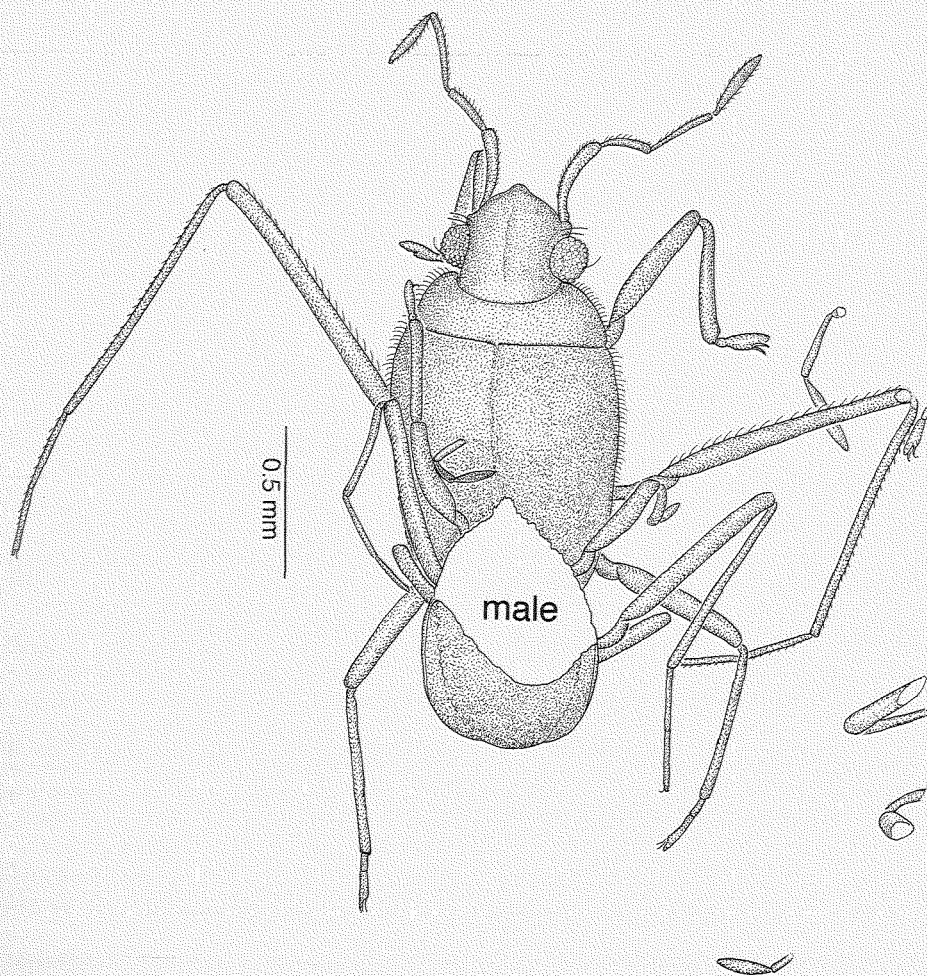
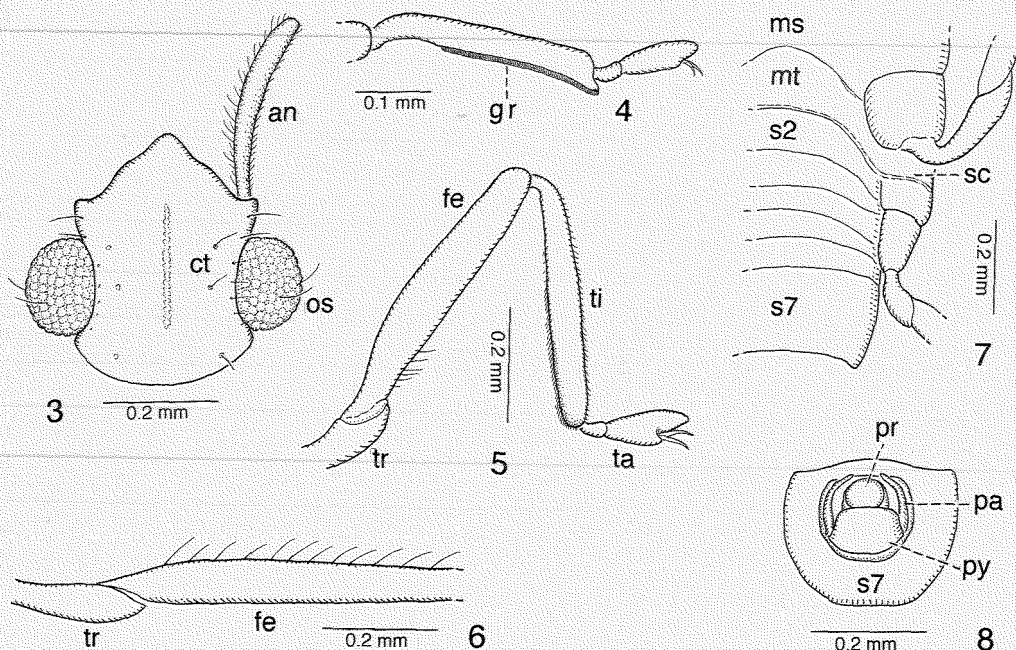


Fig. 2. *Halovelia electrodominica* sp. n. Dorsal habitus of female holotype and male paratype *in situ*. Head and most of thorax of male abraded. Antennal and legs segments of other individuals to the right.

ments 2-3; fourth segment fusiform. Rostrum slender, apex just surpassing prosternum. Thorax. Pronotum very short, in middle less than half length of head (0.14: 0.38); 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 with anterior margin produced in middle (Fig. 7, mt), median length 0.13. Median scent orifice indistinct; lateral scent channels (sc) running along posterior margin, ending on metacetabula. Legs.

Lengths of leg segments (femur: tibia: tarsus): fore leg: 0.46: 0.41: 0.16; middle leg: 0.88: 0.85: 0.53; hind leg: 0.54: 0.53: 0.20. Fore femur (Fig. 5, fe) with almost the same width throughout; fore tibia (ti) widened and slightly curved, with a row of short, spinous hairs on the inner surface; fore tarsus (ta) with two segments with basal segment much smaller than second segment (0.04: 0.13). Middle trochanter (Fig. 6, tr) long (0.15); femur (fe) about 0.6x length of insect, slightly thickened basally (0.06); tibia and tarsus very slender and long; lengths of middle tarsal segments 1-2: 0.29: 0.24. Hind leg segments much shorter than those



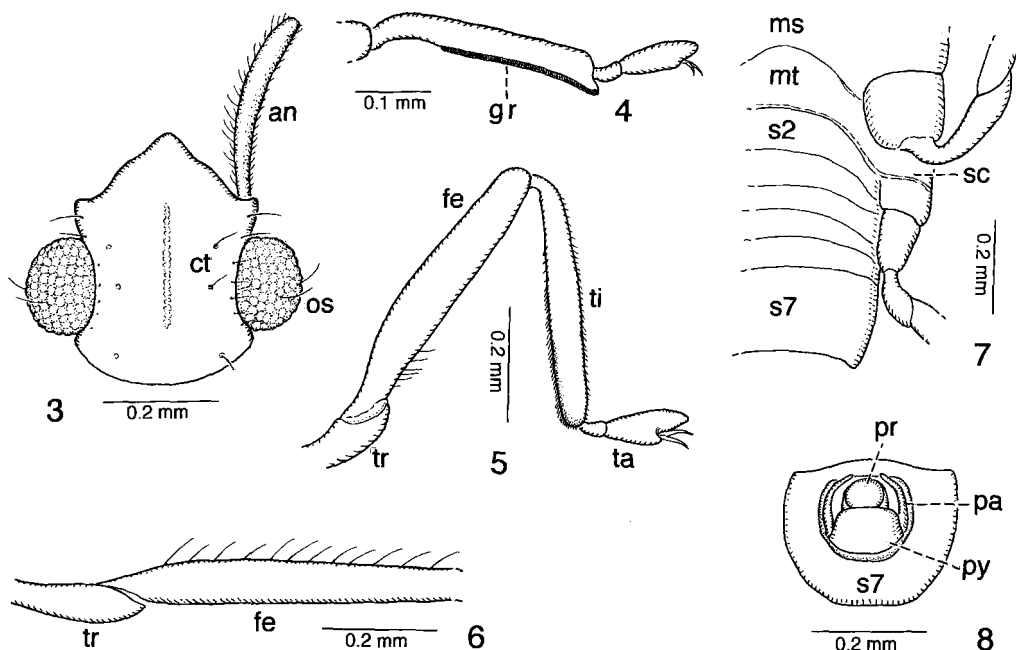
Figs 3 – 8. *Halovelia electrodominica* sp. n.: (3) head and first antennal segment (right side) of female in dorsal view; (4) left fore tibia and tarsus of male; (5) right fore leg of female; (6) base of right middle femur of female; (7) posterior thorax and abdomen of female in ventral view (only left half shown); (8) abdominal end and genital segments of male in caudal view. Abbreviations: an, antenna; ct, cephalic trichobothria; fe, femur; gr, male grasping comb; ms, mesosternum; mt, metasternum; os, ocular setae; pa, paramere; pr, proctiger; py, pygophore; s2, s7, abdominal sternum 2 and 7; sc, scent channel; ta, tarsus; ti, tibia; tr, trochanter.

of middle leg; lengths of hind tarsal segments 1-2: 0.06: 0.14. Claws small but distinct, inserted preapically on all tarsi. Abdomen relatively short with indistinct segmentation on dorsal side; ventral segmentation fairly distinct; median lengths of sternites 2-7: 0.09: 0.07: 0.06: 0.06: 0.06: 0.16; genital segments obscured.

Apterous male (Figs 1-2), incompletely preserved (head and anterior thorax missing): Body probably broadly ovate with greatest width across posterior thorax (0.56). Head missing. One incomplete antenna present, segments 2-4: 0.09: 0.13: 0.14; fourth segment fusiform. Thorax incomplete. Legs. Lengths of leg segments (femur: tibia: tarsus): fore leg: 0.39: 0.31: 0.14; middle leg: 0.56: 0.61: 0.44; hind leg: 0.43 (tibia and tarsus missing). Fore femur slender and slightly curved, tibia with long grasping comb (Fig. 4, gr) along inner surface, occupying distal 2/3 of tibia

(0.22). Lengths of middle tarsal segments 1-2: 0.25: 0.19. Other leg structures as in female. Abdomen 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 as long as sterna 5 and 6 together. Genital segments (segments 8-10) completely withdrawn into the pre-genital abdomen. As seen in caudal view, a pair of fairly long parameres (Fig. 8, pa) inserted laterally on the pygophore (py), curved dorsal and almost meeting each other above proctiger (pr).

*Distribution and geological background.* – Dominican Republic, Hispaniola, Greater Antilles. Age probably 20-30 Myr (Oligocene/Miocene).



Figs 3 – 8. *Halovelia electrodominica* sp. n.: (3) head and first antennal segment (right side) of female in dorsal view; (4) left fore tibia and tarsus of male; (5) right fore leg of female; (6) base of right middle femur of female; (7) posterior thorax and abdomen of female in ventral view (only left half shown); (8) abdominal end and genital segments of male in caudal view. Abbreviations: an, antenna; ct, cephalic trichobothria; fe, femur; gr, male grasping comb; ms, mesosternum; mt, metasternum; os, ocular setae; pa, paramere; pr, proctiger; py, pygophore; s2, s7, abdominal sternum 2 and 7; sc, scent channel; ta, tarsus; ti, tibia; tr, trochanter.

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## Discussion

*Classification and phylogeny.* – The following characters are important in assessing the taxonomic position of the two fossil insects:

- (1) Very small, wingless insect, female length only 1.5 mm.
- (2) Dorsal head surface with indistinct median, longitudinal impression.
- (3) Eyes relatively small, less than half width of interocular space.
- (4) Antennae relatively long and slender; first segment slightly longer than third segment; second segment slightly shorter than third segment.
- (5) Pronotum of apterous form much shorter than head length, without pale spots or marks.
- (6) Mesonotum prolonged; dorsal intersegmental suture between meso- and metanotum indistinct.
- (7) Metasternum with lateral scent channels close to hind margin; channels curved backward towards metacetaula.
- (8) Fore tibia of male with grasping comb.
- (9) All tarsi with two segments.
- (10) Claws inserted before apex of second tarsal segment.
- (11) Middle trochanter greatly prolonged.
- (12) Middle femur slender and very long, about 0.6x length of insect.
- (13) Middle tarsus prolonged, length about 0.6x middle tibia; first tarsal slightly longer than second segment.
- (14) Hind femur much shorter than middle femur.
- (15) Male genital segments withdrawn into pre-genital abdomen; male parameres slender and long, curved dorsad above proctiger.

The general structure and especially characters 7, 8, and 10 place the insects in the gerromorphan family Veliidae (Andersen 1982). The combination of the characters 1, 5, 6, 9, and 11–14 are diagnostic for the subfamily Haloveliinae. 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 (character 3), first antennal segment longer than third segment (character 4), the genera *Strongylovelia* Esaki and *Entomovelina* Esaki (both limnic) can be excluded. Among the remaining three genera (all

marine), the uniformly colored pronotum (character 5), the grasping comb of the male fore tibia (character 8), and the concealed male genital segments (character 15) identify the fossils as members of the genus *Halovelia*. 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 character, however, is shared with at least one species of *Halovelia*, *H. fosteri* Andersen (1989a: 113), which is endemic to Fiji. We therefore conclude that the fossil species belongs to the haloveliine genus *Halovelia*. The extinct species is smaller than most living species approaching the size of *H. polhemii* Andersen, length 1.6 mm (female) and 1.3–1.4 (male). Unique characters of *H. electrodominica* sp. n. are the median, longitudinal furrow of the mesonotum and the row of spinous hairs on the inner side of fore tibia in the female.

Andersen (1989b) presented the results of a cladistic analysis of 30 species of *Halovelia* using the other four haloveliine genera as outgroups. A character data set of 46 characters were analyzed using the parsimony program PAUP, version 2.4 and 30 equally parsimonious trees were obtained, each 153 steps long and with a consistency index of 0.373. Analyzing the same data set with Hennig86 yielded 144 trees, each 152 steps long and  $ci = 0.37$ . Based upon an evaluation of characters supporting different nodes, one of the 153-steps trees was preferred.

Because of the excellent state of preservation of the type specimens of *Halovelia electrodominica* sp. n., 37 of the original 46 characters can be scored and added to the data set of Andersen (1989b). Only character nos 1, 14, 26, 39, and 42–46 have to be entered as missing data (as question marks, '?'). A Hennig86 analysis of this data set yields 72 equally parsimonious trees, each 158 steps long and  $ci = 0.36$ . All trees have *H. electrodominica* as sister group of a clade composed by the 30 extant species of *Halovelia*. The cladogram (Fig. 9) shows the phylogenetic position of *H. electrodominica* sp. n. in relation to the species groups of *Halovelia* defined by Andersen (1989b) as well as the other extant genera of the Haloveliinae.

*Biology and ecology.* – The two specimens of *Halovelia electrodominica* sp. n. were seemingly



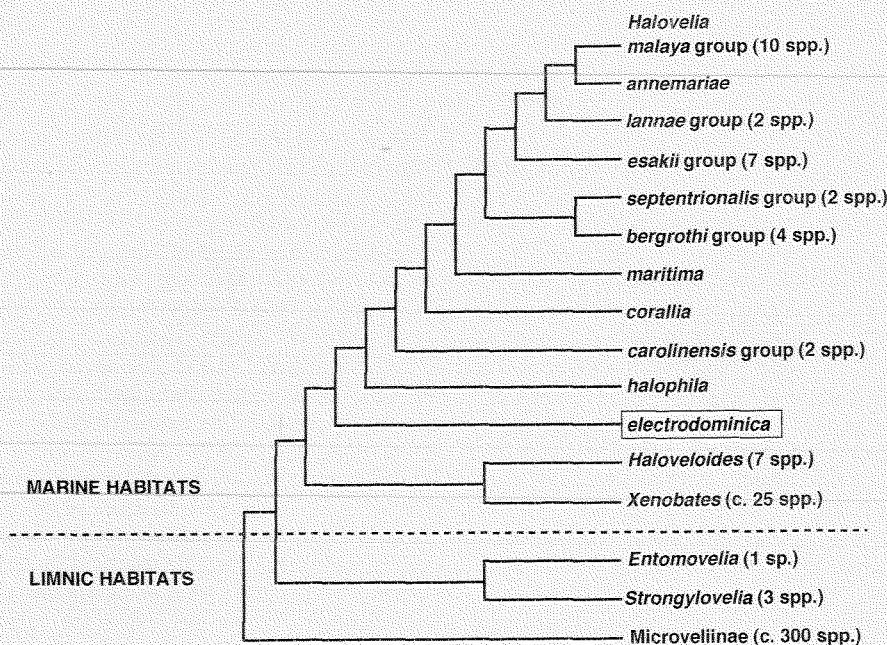


Fig. 9. Cladogram of phylogenetic relationships between species and species groups of *Halovelia*, other genera of the subfamily Haloveliinae, and its sister group Microveliinae. Numbers of species in brackets. The box highlights the position of the Dominican amber species *H. electrodominica* sp. n. Dotted line separates lineages with species living in limnic and marine habitats.

trapped when mating. The male is positioned on top of the abdomen of the female (Figs 1-2). The left fore leg is stretched forward and the end of tibia 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 *Halovelia* 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* group (e.g., *H. hilli* China from Australia) where the male inserts one his very long and slender parameres into the genital opening of the female (Andersen 1989b: figs 61-63).

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. When mangroves are present, *Halovelia* may also be found in the vicinity of mangrove

trees. Andersen (1989b) studied the biology of *H. malaya* Esaki in Phuket, Thailand. This species was abundant on intertidal reef flats strewn with blocks of dead *Porites*-coral. The surface of such blocks was highly irregular and with numerous holes made by boring bivalves (Mollusca). 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 *Halovelia* probably assist in maintaining this air-store which may function as a physical gill.

The sister group of *Halovelia* (Fig. 9) is a clade composed by the genera *Xenobates* and *Haloveloides* Andersen. Most species are found in pools and channels in estuaries and mangroves, following tidal changes in water level but not becoming submerged during high tide (Lansbury 1996; Andersen & Weir, unpublished). A few species of *Haloveloides* live on the sea surface outside protecting mangroves or reefs, tolerating more exposed conditions as they cruise on the sea sur-

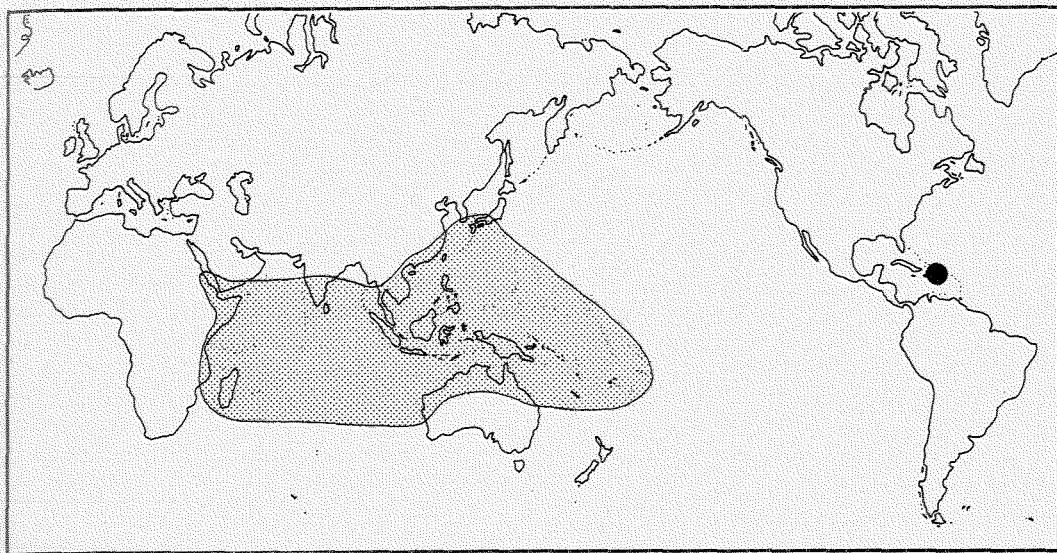


Fig. 10. Distribution of extant species of *Halovelia* (shaded area) and the fossil species *H. electrodominica* sp. n. (dot).

face as far as a couple of kilometers from the coast (Andersen 1992; Lansbury 1996).

Optimization of habitats on the cladogram for the Haloveliinae (Fig. 9), with limnic habitats as the ancestral trait, yields a limnic → mangroves → intertidal reef flats sequence of transitions, with an additional change from mangroves to the near-shore sea surface in some *Haloveloides*. An alternative, equally parsimonious optimization implies independent transitions from limnic habitats to mangroves or reef flats. If this was true, however, the physiological and behavioural adaptations required for life in an intertidal, marine environment should have evolved twice in the subfamily which is a more unlikely (less parsimonious) hypothesis.

Accepting the hypothesis that the marine environment was colonized only once in the Haloveliinae, *Halovelia electrodominica* clearly belongs to a lineage of marine water striders. No living species of *Halovelia* is known to have secondarily invaded freshwater habitats. In addition, the structural features of the amber specimens match all those features of extant *Halovelia* believed to be adaptations to a marine life (Andersen 1982, 1989b). It is therefore quite unlikely that the Dominican species was non-marine. The presence

of a mesofemoral fringe of hairs (shared with the mangrove-inhabiting *Halovelia fosteri* and *Xenobates* spp.) suggests that *H. electrodominica* lived in mangroves. On the other hand, the presence of remains belonging to several specimens in the same piece of amber suggests a gregarious behavior only known from *Halovelia* species living on intertidal reef flats (Andersen 1989b).

How did a marine insect become 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 *Halovelia electrodominica* sp. n. were aggregating. Alternatively, sea level changes or high tides may have resulted in the ocean flooding the land and bringing the haloveliines with them.

**Distribution and biogeography.** – The genus *Halovelia* contains 31 described species (Andersen 1989a, 1989b; Lansbury 1996) which are distributed throughout the Indo-West Pacific region (Fig. 10), 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) analyzed the historical bio-



geography of marine water striders, concluding that the present distribution of *Halovelia* is a reflection of 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 *Strongylovelina*, are found in India, Indo-China, and Malesia (Andersen 1982). The distribution of the marine genera *Xenobates* and *Haloveloides* covers the same geographical areas. Most *Halovelia* species found along the coasts of East Africa, Madagascar, and the islands of the Indian Ocean (Mascarenes, Seychelles, and the Maldives) belong to the Southeast Asian *H. malaya* group (Andersen 1989b) and may represent relatively late dispersal and subsequent speciation. On the other hand, the disjunct distributions of the most basal clades of *Halovelia* may be relictual of an ancient, much wider distribution of the genus.

The finding of an extinct species of *Halovelia* in the Caribbean 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) occur 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 freshwater relatives or species of otherwise limnic genera (Andersen & Polhemus 1976; Andersen 1982; 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 be repetitive of 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). If taxonomic rank reflects age of origin (as commonly believed), water striders probably colonized 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 distributions 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 throughout the Tertiary in the climatic conditions favoring these shallow water communities. The mangrove palm, *Nypa*, had an extensive distribution in the Caribbean in early Tertiary and once occurred at high latitudes in Europe (Ricklefs & Latham 1993). Throughout much of the Tertiary, the reef coral belt appears to have been latitudinal 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 1988). Although there are several possible explanations for extinction, a drop in the sea temperature during Miocene may have had a profound effect on stenothermic shallow water organisms such as *Halovelia*.

Whereas most of the insects found in Dominican amber can be assigned to taxa which show distinct affinities to species found in the Caribbean and adjacent areas to-day (Poinar 1992; Grimaldi et al. 1993; Grimaldi 1996; Michelsen 1996), there are some striking exceptions. The water strider *Electrobates spinipes* Andersen & Poinar (1992) from Dominican amber cannot be classified in any extant subfamily of the Gerridae and has no close relatives in the present fauna of the Caribbean. Species of the ant genus *Leptomyrmex* are restricted to the Indo-West Pacific except for one species described from Dominican amber (Baroni-Urbani & Wilson 1987). Two genera of mycetobiine woodgnats (Diptera, Anisopodidae) distributed in the Old World tropics have been recorded from Dominican amber (Grimaldi 1991). Perhaps the most striking example is the termite genus *Mastotermes* (Krishna & Grimaldi 1991); apart from one Dominican amber species, this genus is only represented by one living species in Australia. The marine water strider genus *Halovelia* can now be added to these examples of remarkable geographical extinction in the Caribbean during the late Tertiary.

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