The coral bugs, genus *Halovelia* Bergroth (Hemiptera, Veliidae). II. Taxonomy of the *H. malaya*-group, cladistics, ecology, biology, and biogeography

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Marine bugs of the genus *Halovelia* Bergroth inhabit intertidal coral reefs and rocky coasts along the continents and islands bordering the Red Sea, Indian Ocean, and western Pacific Ocean as well as island groups and atolls in these areas. In Part I of this work, the genus *Halovelia* was redescribed together with five previously known species; fifteen new species were described. In the present part, two previously known species are redescribed and eight species described as new, all belonging to the *H. malaya* Esaki-group: *H. sulawesi* sp.n. (Sulawesi); *H. abdominalis* sp.n. (Java, West Malaysia); *H. nicobarensis* sp.n. (Nicobar Islands); *H. convexa* sp.n. (Maldive Islands); *H. poissoni* sp.n. (Kenya, Tanzania); *H. seychellensis* sp.n. (Seychelles, Madagascar); *H. depressa* sp.n. (Madagascar); and *H. mauricensis* sp.n. (Mauritius). A key to the species of the *H. malaya*-group is included.

Using the computer programs PAUP and Hennig86, a cladistic analysis of relationships between the species of *Halovelia* was performed. Other genera of Haloveliinae were used as outgroup taxa. 46 characters (each with 2-4 states) are listed. The cladistic analysis of the character state matrix yields 18 equally parsimonious cladograms, each 155 steps long. The preferred cladogram is evaluated both by characters and by clades. An account is given of the ecology and biology of the coral bugs, chiefly based upon original observations by the author. The distributions of each of the 30 species of *Halovelia* are mapped and discussed. The historic biogeography of the species is analysed using two different methods of cladistic (or vicariance) biogeography: component and parsimony analysis. Reduced area cladograms are produced for most species-groups as well as a summary cladogram for these groups. The biogeographic history of *Halovelia* is discussed in the light of these results and compared with the biogeography of other marine Haloveliinae, the marine Gerridae, and other groups of Indo-Pacific animals.

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The genus *Halovelia* Bergroth (1893) belongs to the semiaquatic bugs (Hemiptera, Gerromorpha). Most species inhabit the intertidal zone of coral reefs (Andersen & Polhemus 1976; Andersen 1982). It is therefore suggested that they are given the trivial name *coral bugs*.

In Part I of the present work (Andersen 1989), a new concept of the genus *Halovelia* was presented. As a result it was necessary to transfer a few *Halovelia* species to the genus *Xenobates* Esaki (1927) and to erect a new genus for *Halovelia papuensis* Esaki (1926) which will be described in a forthcoming paper (Andersen *in prep.*). In addition to the 9 described species, 14 species of *Halovelia* were described as new to science.

In Part II (the present), the species belonging to the *H. malaya*-group are described. In addition to the previously known species *H. malaya* Esaki (1930) and *H. pauliani* Poisson (1956), 8 species are described as new to science. The results of a cladistic analysis of relationships (using the computer programs PAUP and Hennig86) between the 30 species of *Halovelia* are presented and the most parsimonious cladograms evaluated. A reconstructed phylogeny of the genus is presented and discussed. The ecology and biology of coral bugs is reviewed, partly based upon the authors own observations. Species of *Halovelia* occur in the Indo-Pacific area, along the continents and larger islands bordering the Red Sea, the Indian Ocean, and the western Pa-

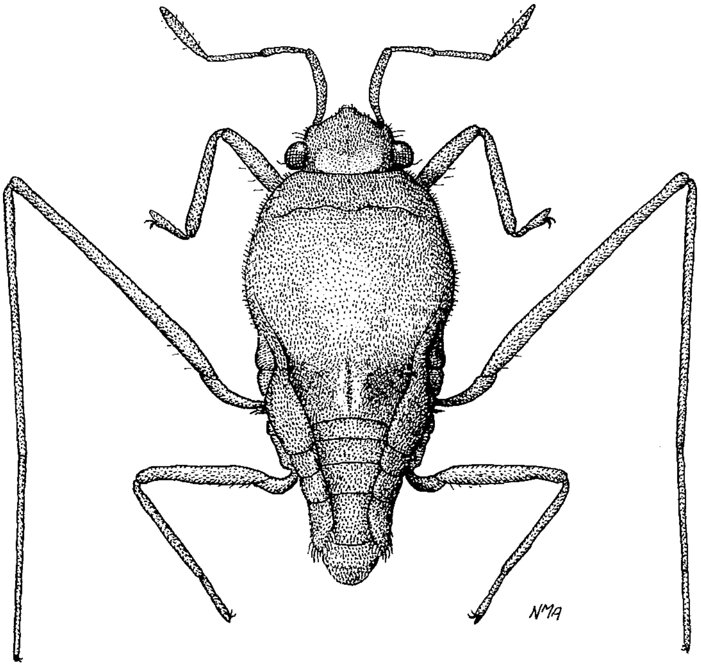


Fig. 1. *Halovelia malaya* Esaki, female, Phuket Island, Thailand.

cific Ocean, as well as on island groups or atolls in these areas. Based upon the reconstructed phylogeny of the genus, its historical biogeography is analysed by two different methods of cladistic (or vicariance) biogeography and the biogeographic history of *Halovelia* is discussed.

Material and methods for the present work are described in Part I which also includes a list of depositories (with abbreviations used) and acknowledgments. Dr J.T. Polhemus, Englewood, Colorado, read and criticized an earlier version of the entire manuscript. Dr W.A. Foster, Cambridge, and Dr J.P. Duffels, Amsterdam, read the parts on ecology and biology, and on biogeography, respectively. The paper has been improved by their valuable comments, for which I am most grateful.

TAXONOMY

Key to the species of the *Halovelia malaya*-group

Males (male of 22. *sulawesi* sp.n. unknown)

1. Antennal segment 3 distinctly longer than segment 2 (ratio 1.2:1 or more). Madagascar .... 29. *depressa* sp.n. (p. 192)
– Antennal segment 3 subequal to or only slightly longer than segment 2 (ratio less than 1.2:1) 2
2. Smaller species, total length less than 1.6 mm. Maldive Islands, Mauritius .... 25. *convexa* sp.n. (p. 186) and 30. *mauricensis* sp.n. (p. 193)
– Larger species, total length more than 1.6 mm 3
3. Abdominal venter slightly but distinctly depressed in middle. Clasper (Fig. 29). Tanzania, Kenya .... 27. *poissoni* sp.n. (p. 190)
- Abdominal venter not modified 4
4. Dorsal vesical sclerite with simple base (Fig. 11). Java, West Malaysia, Nicobar Islands .... 23. *abdominalis* sp.n. (p. 184) and 24. *nicobarensis* sp.n. (p. 186)
– Dorsal vesical sclerite with bifid base (Fig. 8) 5
5. First antennal segment distinctly longer than head. Ile Europa, Mozambique Channel .... 26. *pauliani* Poisson (p. 188)
– First antennal subequal to or shorter than head ... 6
6. Total length about 2.0x greatest width across thorax. West Malaysia, Thailand .... 21. *malaya* Esaki (p. 181)
– Total length less than 2.0x greatest width across thorax. Seychelles, Madagascar .... 28. *seychellensis* sp.n. (p. 191)

Females

1. Antennal segment 3 distinctly longer than segment 2 (ratio 1.2:1 or more) 2
– Antennal segment 3 subequal to or only slightly longer than segment 2 (ratio less than 1.2:1)...... 3

2. Middle trochanter with distinct tubercles on anterior margin (Fig. 18). Sulawesi .... 22. *sulawesi* sp.n. (p. 183)
- Middle trochanter not modified as above. Madagascar .... 29. *depressa* sp.n. (p. 192)

3. Small species, total length equal to or less than 2.1 mm. Thoracic dorsum strongly raised in middle (Fig. 37), furnished with long, suberect pubescence 4
- Larger species, total length more than 2.1 mm; if less then thoracic dorsum only moderately raised and pubescent 5

4. Mesonotum evenly depressed posteriorly and continuing as a broad, median ridge on metanotum and basal abdominal terga (Fig. 36). Maldive Islands .... 25. *convexa* sp.n. (p. 186)
- Mesonotum abruptly depressed towards abdominal tergum, without median ridge on metanotum and basal abdominal terga (Fig. 46). Mauritius............ 30. *mauricensis* sp.n. (p. 193)

5. Connexiva not meeting each other above midline of abdominal dorsum (Figs. 12 and 21) 6
- Connexiva meeting each other above midline of abdominal tergum.......................... 7

6. Metanotum and basal abdominal terga laterally depressed, forming a median tumescence (Fig. 21). Nicobar Islands... 24. *nicobarensis* sp.n. (p. 186)
- Metanotum and basal abdominal terga laterally depressed but not forming a median tumescence or ridge (Fig. 12). West Malaysia, Thailand. ... . 21. *malaya* Esaki (p. 181)

7. Basal abdominal terga grooved in middle (Fig. 19). Thoracic dorsum not raised (Fig. 20). Thoracic pleuron not impressed Java, West Malaysia. .... 23. *abdominalis* sp.n. (p. 184)
- Basal abdominal terga not grooved in middle. Thoracic dorsum raised. Thoracic pleuron impressed posteriorly. 8

8. Mesonotum raised in anterior third (Fig. 39), strongly narrowed posteriorly (Fig. 38). Lateral impressions of thorax and basal abdomen deep. Ile Europa, Mozambique Channel............ .... 26. *pauliani* Poisson (p. 188)
- Mesonotum more or less distinctly raised in middle, only moderately narrowed posteriorly. Lateral impressions of thorax and basal abdomen shallow................................. 9

9. Mesonotum strongly convex in lateral view (Fig. 41), forming a strongly pubescent "hump" Tanzania, Kenya.. 27. *poissoni* sp.n. (p. 190)
- Mesonotum less convex in lateral view (Fig. 43), without a strongly pubescent "hump". Seychelles, Madagascar... 28. *seychellensis* sp.n. (p. 191)

21. *Halovelia malaya* Esaki

Figs. 1-8, 12-15.

Halovelia malaya Esaki, 1930: 18-20, fig. 3 (description; type area: Pulau Angsa, Malay Peninsula); China 1957: 355-356 (descriptive notes, key).

Type material examined: Holotype ♀, *Paratype* ♀, Pulau Angsa, West Coast of Malay Peninsula, October 10th, 1926, E. Seimund, in British Museum (Natural History), London.

Other material examined: THAILAND: 1♂ 2♀♀, South Thailand, Phang Nga, 6.ii.1982, Claus Nielsen (ZMUC); 57♂♂ 62♀♀, Phuket Island, Phuket Marine Biological Center, near the jetty, 22.iii.1975, Claus Nielsen (ZMUC); 9♂♂ 12♀♀ (1♂ 1♀ in copula) and several nymphs, same locality, January 1976, Claus Nielsen (ZMUC); 3♂♂ 4♀♀, same locality, St. 45, 27.v.1977, G. Høpner-Petersen (ZMUC); 3♂♂ 9♀♀, same locality, on water surface; at end of pier, 2200h, high tide, 6.vi.1977, G. Høpner-Petersen (ZMUC); 1♂ 4♀♀, same locality, S. of pier, rockpools at low tide, 23.ii.1982, Mogens Andersen (ZMUC); 11♂♂ 7♀♀, same locality, reef flat S. of pier; low tide, 16-17h, 15.i.1987, N. M. Andersen (ZMUC); 47♂♂ 120♀♀ and several nymphs, same locality, reef flat, pools at low tides, 26-28.i.1987, N. M. Andersen (ZMUC); 4♂♂ 7♀♀, Phuket, PMBC, night light by pier, 17.X.87, Lanna Cheng & Ralph Lewin (ZMUC); 8♂♂ 2♀♀, Phuket, PMBC pier, night light, 20.X.87, Lanna Cheng & Ralph Lewin (ZMUC); 1♂ 2♀♀, Phuket, PMBC, low tide under pier, 21.X.87, Lanna Cheng & Ralph Lewin (ZMUC); 2♂♂ 1♀ 4 nymphs, Phuket, Mangrove NW of PMBC, low tide, 4.xi.1987, Mogens Andersen (ZMUC). WEST MALAYSIA: 10♂♂ 7♀♀ 1 nymph, Malay Penin: West Coast, Pulau Angsa, Oct. 10 1926, E. Seimund, F.M.S. Mus. (BMNH); 17♂♂ 57♀♀, Malaya, Negeri Sembilan, 12 km S. of Port Dickson, in lagoon pools at low tide, III.16.1983, Schuh & Massee (AMNH); 29♂♂ 19♀♀, Negeri Sembilan, 10 km S. of Port Dickson, CL 2060, VIII-15-85, J.T. & D.A. Polhemus (JTPC).

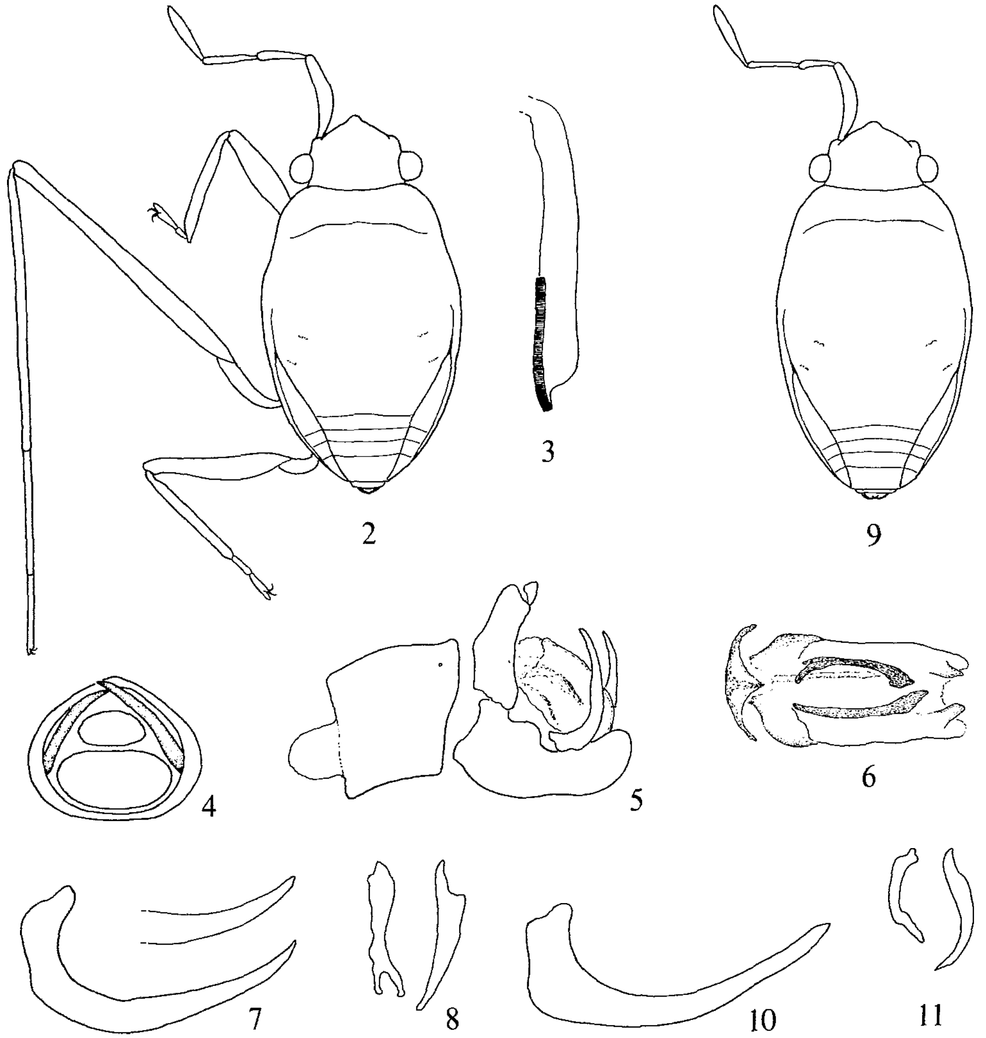
Diagnosis: Recognized by the structure of the female abdomen, especially the medial, pilose area on basal abdominal terga and the connexiva which are basally erect and thickened, distally inflexed upon abdominal dorsum.

Description

Size. ♂♂: length 1.78-1.95 mm, width 0.92-0.98 mm; ♀♀: length 2.30-2.55 mm, width 1.02-1.05 mm.

Colour. Black or dark brown with greyish pubescence which is longer and more dense on posterior thoracic dorsum and entire abdomen (♂) or anterior and lateral parts of abdominal dorsum (♀). Female connexiva terminated by long, whitish hairs. A large yellowish brown spot at base of head. Antennae and legs dark brownish.

Structural characters. Male (Fig. 2) elongate ovate, length about 2.0x greatest width across thorax (147:74). Head length about 0.6x head width across eyes (30:50); eye width about 0.25x width of head between eyes (9:33). Relative lengths of antennal segments (1-4): 31:19:20:27; segment 1 subequal in length to head, distinctly thicker than segment 4 (7:5); segment 2 subequal in length to segment 3. Hind margin of pronotum indistinct in lateral



Figs. 2-11. 2-8. *Halovelia malaya* Esaki. (2. Male, dorsal view. 3. Left fore tibia of male. 4. Male abdominal end, caudal view. 5. Male genital segments, lateral view. 6. Phallus, dorsal view. 7. Left clasper; dorsal aspect of blade above. 8. Vesical sclerites). 9-11. ***Halovelia abdominalis*** sp.n. (9. Male body, dorsal view. 10. Left clasper. 11. Vesical sclerites).

parts. Relative lengths of leg segments (femur :tibia:tarsus): fore leg: 49:41:17; middle leg: 118:109:88; and hind leg: 59:46:21. Grasping comb (Fig. 3) about 2/5 length of fore tibia (17:41); middle femur about 0.8x total length; relative lengths of middle tarsal segments (1:2): 52:36; hind femur slightly thicker than middle femur (9:8). Abdominal venter not modified. Genital segments as illustrated (Fig. 5); claspers relatively short, barely crossing each other dorsal to the genital capsule (Fig. 4); blade of each clasper (Fig. 7) slender and regularly curved both dorsad and mesad, apex pointed; vesical sclerites (Fig. 8).

Female (Fig. 12) fusiform, length 2.3x greatest width across thorax (193:84). Head structure as in male except that antennal segment 1 is more slender; length of antennal segments (1-4): 30:20:23:29. Thoracic dorsum moderately raised in middle of mesonotum (Fig. 13), pubescence distinctly longer on metanotum and medially on basal abdominal terga. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 53:43:21; middle leg: 128:113:93; hind leg: 60:50:25. Mesotrochanter not modified; middle femur 0.65x total length; hind femur only slightly thicker than middle femur. Abdomen tapering in width posteriorly; basal abdominal terga slightly depressed laterally but not forming a median tumescence; pleura with shallow, lateral impressions which originate on metapleura; connexiva basally thickened and vertically raised, posteriorly inflexed upon abdominal dorsum, converging but not meeting each other; tergum 8 produced and distally deflected, concealing proctiger.

Distribution and habitat

West coast of the Malayan Peninsula. So far recorded from West Malaysia (Pulau Angsa and Negeri Sembilan) and Thailand (Phang Nga and Phuket Island). The author collected this species in great numbers on an intertidal reef flat at the Phuket Marine Biological Center near Laem Pan Wah, on the Southeast coast of Phuket Island, Thailand. At low tide, specimens could be found among coral rubble and larger coral blocks, and on small tidal pools among most dead stands of *Porites*- and *Acropora*-corals. It was also found among the rocks along the jetty and below the pier. A few specimens were seen in tidal pools on the rock surfaces along the coast. The species was also found in the mangroves NW of the PMBC. At Port Dickson, Negeri Sembilan, West Malaysia, *H. malaya* was found on a rocky coast (Polhemus, field notes).

Discussion

The original description of this species by Esaki (1930: 18-20) was based upon two females from Pulau Angsa at the West coast of the Malay Peninsula. I have examined a series of specimens (from BMNH) which carry the same label as the types and which include both males and females, the latter matching Esaki's description and figure.

Despite the clear statement by Esaki (l.c.) about the sex of the types (also the statement "Male is unknown", p. 20), China (1957: 355, Table II) gave measurements of a "Type ♂" of *H. malaya* Esaki. This male probably belongs to the same series as examined by me but is not a type.

Polhemus (1982:8) compared *H. malaya* with his *Halovelia* (*Colpovelia*) *angulana* from Australia, N.T. (now transferred to the genus *Xenobates*; Andersen *in prep.*). However, the male characters of *H. malaya* mentioned do not apply to this species, but perhaps to an undescribed genus and species related to "*Halovelia*" *papuensis* Esaki (Andersen *in prep.*).

The males of the *Halovelia malaya*-group are difficult to separate since the relative measurements of antennae and legs as well as the structure of claspers are more or less the same. However, the different shapes of the vesical sclerites (Figs. 8, 11, 24, 28, 32, and 35) may assist in the identification of males not accompanied by females.

22. ***Halovelia sulawesi* sp.n.**

Figs. 16-18.

Type area: Cape Dadepo, Sulawesi Utara Province, Sulawesi.

Type material examined: SULAWESI: *Holotype* ♀, Sulawesi Utara Province, Cape Dadepo, 8 km W. of Malibago, CL 2112, mangroves behind reef, IX-8-85, J.T. & D.A. Polhemus, in the British Museum (Natural History), London, property of the Museum Zoologicum Bogoriense, Bogor, Indonesia. - *Paratypes*: 2♀♀, same locality and date as holotype (JTPC).

Diagnosis: Similar to *H. malaya* Esaki but females of the new species are separated by their relatively longer antennal segment 3 (more than 1.2x segment 2), anteriorly raised thoracic dorsum, tuberculate mesotrochanter, and slightly more incrassate hind femora.

Etymology: Named for the type area, Sulawesi.

Description

Size. ♀♀: length 2.09-2.16 mm, width 0.90-0.94 mm.

Colour. Black with greyish pubescence which is longer and more dense on posterior mesonotum, metanotum, anterior and lateral parts of abdominal dorsum (♀); female connexiva terminated by long, pale yellowish hairs. A large yellowish brown spot at base of head. Antennae and legs blackish.

Structural characters. *Male* unknown.

Female (Fig. 16) fusiform, length about 2.3x greatest width across thorax (167:72). Head length about 0.65x head width across eyes (31:47); eye width slightly more than ¼ width of head between eyes (9:30). Relative lengths of antennal segments (1-4): 28:18:24:29; segment 1 slightly shorter than head, subequal in thickness to segment 4; segment 2 distinctly shorter than segment 3. Hind margin of pronotum indistinct in median and lateral parts. Thoracic dorsum distinctly raised (Fig. 17), greatest height before middle of mesonotum; metanotum slightly depressed laterally; erect pubescence distinctly longer on pronotum and anterior mesonotum. Relative lengths of leg segments (femur: tibia:tarsus): fore leg: 53:46:20; middle leg: 119:107:83; and hind leg: 58:45:22. Mesotrochanter (Fig. 18) with distinct tubercles on anterior margin; middle femur about 0.7x total length; relative lengths of middle tarsal segments (1:2): 48:35; hind femur distinctly thicker than middle femur (9:7). Abdomen tapering in width posteriorly; basal abdominal terga distinctly depressed laterally, forming a low, median tumescence; pleura only slightly impressed; connexiva basally thickened and vertically raised, posteriorly inflexed upon abdominal dorsum, meeting each other above tergum 7; tergum 8 produced and distally deflected, concealing proctiger.

Distribution and habitat

Only known from Sulawesi (Sulawesi Utara Province). The type specimens were collected in mangroves behind a coral reef at Cape Dadepo, Sulawesi Utara Province (Polhemus, field notes).

Discussion

Although only known from the 3 female types, these are so distinct that they undoubtedly belong to a separate species. The structure of the female abdomen (connexiva basally raised and thickened) clearly places the new species in the *H. malaya*-group, but the relatively long antennal segment 3 (more than 1.2x segment 2) and tuberculate mesotrochanter separate the new species (at least in the female sex) from any other species belonging to this group.

23. ***Halovelia abdominalis*** **sp.n.**

Figs. 9-11, 19-20.

Type area: Onrust Island off Djakarta, Java.

Type material examined: INDONESIA: *Holotype* ♀, Onrust, Java Sea, 4.v.1929, collecting from boat on surface at artificial light, Th. Mortensen, in the Zoological Museum, University of Copenhagen. - *Paratypes*: 136♂♂ 13♀♀, same locality and date as holotype (BMNH, JTPC, ZMUC). WEST MALAYSIA: 9♂♂ 7♀♀, Pahang, P. Tioman, rockpools at low tide, 19.x.1985, Lanna Cheng (ZMUC).

Diagnosis: Recognized by the long and very narrow female abdomen with connexiva inflexed upon abdominal dorsum throughout their length. The medially grooved basal abdominal terga also separate this species from *malaya* Esaki and *nicobarensis* sp.n.

Etymology: Characterized by the structure of the female abdomen.

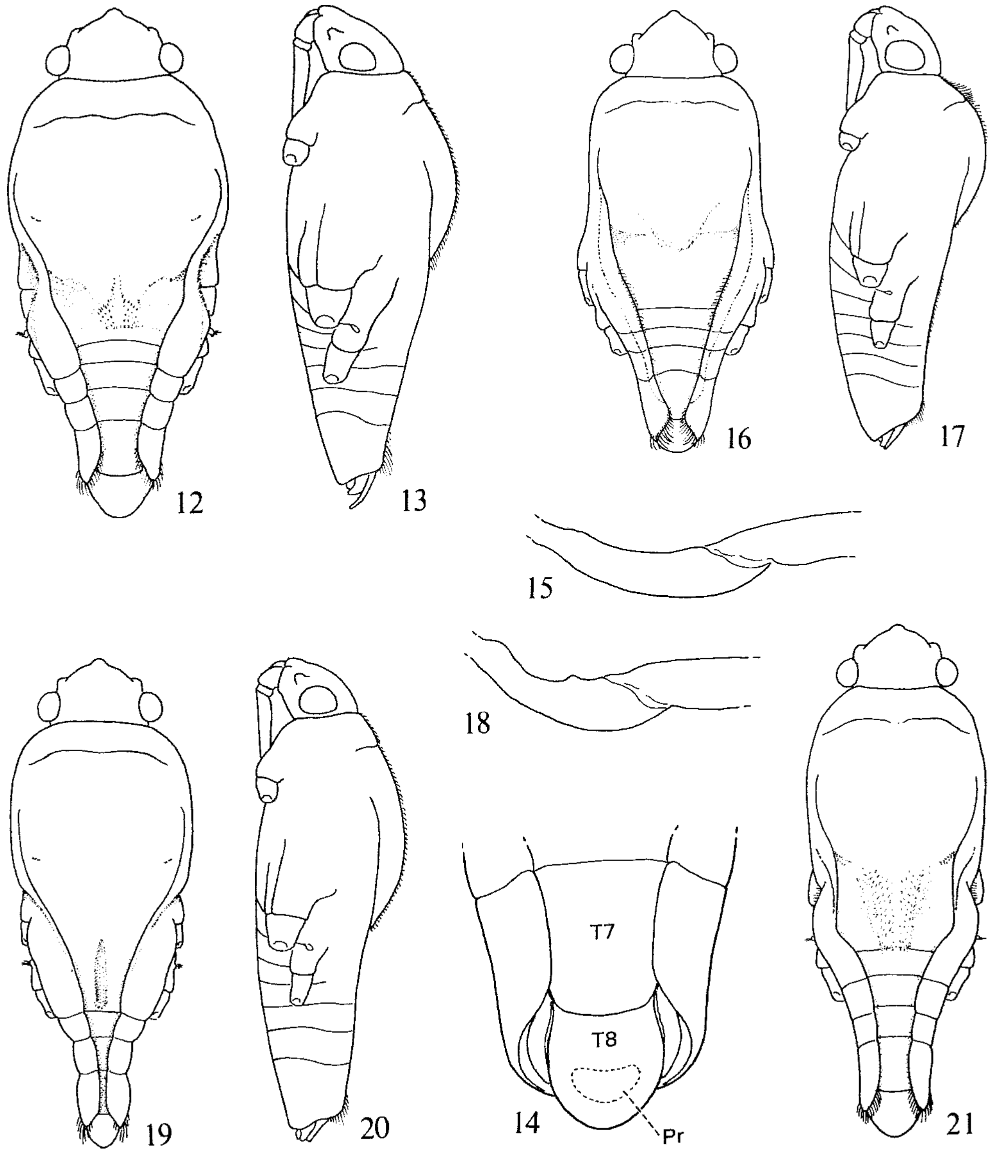
Description

Size. ♂♂: length 1.72-1.85 mm, width 0.88-0.91 mm; ♀♀: length 2.38-2.52 mm, width 0.92-1.00 mm.

Colour. Black or dark brown with a greyish pubescence which is longer and more dense on abdominal dorsum (♂) or first three abdominal terga (♀). Female connexiva terminated by long, whitish hairs. A large obscure, yellowish brown spot at the base of head. Antennae and legs brownish.

Structural characters. *Male* (Fig. 9) elongate ovate, length about 2.0x greatest width across thorax (148:73). Head length about 0.6x head width across eyes (29:47); eye width about 0.25x width of head between eyes (8:32). Relative lengths of antennal segments (1-4): 30:18:19:24; segment 1 subequal in length to head, slightly thicker than segment 4 (6:5); segment 2 subequal in length to segment 3. Hind margin of pronotum indistinct laterally. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 51:42:17; middle leg: 122:107:86; and hind leg: 57:46:21. Grasping comb about 2/5 length of fore tibia (16:42); middle femur about 0.8x total length; relative lengths of middle tarsal segments (1:2): 50:36; hind femur as thick as middle femur (8:8). Abdominal venter not modified. Claspers relatively long, crossing each other dorsal to the genital capsule; blade of each clasper (Fig. 10) slender and regularly curved both dorsad and mesad, apex pointed; vesical sclerites (Fig. 11).

Female (Fig. 19) elongate ovate, length about 2.6x greatest width across thorax (191:74). Head structure as in male except that antennal segment 1 is more slender; length of antennal segments (1-4): 29:18:19:25. Thoracic dorsum slightly raised in middle of mesonotum (Fig. 20), pubescence longer on lateral and posterior parts of mesonotum, metanotum, and basal abdominal terga. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 51:40:19; middle leg: 121:106:84; hind leg: 57:47:22. Middle



Figs. 12-21. 12-15. *Halovelia malaya* Esaki. (12. Female body, dorsal view. 13. Female body, lateral view. 14. Female abdominal end, dorsal view. 15. Right trochanter of female). 16-18. *Halovelia sulawesi* sp.n. (16. Female body, dorsal view. 17. Female body, lateral view. 18. Right trochanter of female). 19-20. *Halovelia abdominalis* sp.n. (19. Female body, dorsal view. 20. Female body, lateral view). 21. *Halovelia nicobarensis*. Female body, dorsal view. Abbreviations: Pr, proctiger (concealed); T7, T8, abdominal terga 7 and 8.

femur 0.6x total length. Abdomen distinctly tapering in width posteriorly and very narrow; basal four terga with a longitudinal, median groove; pleura with rather deep, lateral impressions which originate posteriorly on mesopleura; connexiva basally thickened, inflexed upon abdominal dorsum, converging throughout and meeting each other above tergum 5-7; tergum 8 produced and distally deflected, concealing proctiger.

Distribution and habitat

Probably southern Sundaic. So far recorded from northern Java (Onrust Island off Djakarta) and the east coast of West Malaysia (Tioman Island). In the last mentioned locality, the species was found in rock pools at low tide (Cheng *in litt.*).

24. ***Halovelia nicobarensis*** **sp.n.**

Fig. 21.

Type area: Nancowry, Nicobar Islands.

Type material examined: NICOBAR ISLANDS: *Holotype* ♀, Anchorage Nancowry, St.319, 20.30-5.30h, 6-7.v.1951, Galathea, in the Zoological Museum, University of Copenhagen. - *Paratypes*: 1♂ 2♀♀, same locality and date as holotype (ZMUC).

Diagnosis: Female very similar to *H. malaya* Esaki, but separated by the narrower abdomen, the longer median pilose area on basal abdominal terga, the anteriorly subparallel connexiva, etc.

Etymology: Named for the type locality, the Nicobar Islands.

Description

Size. ♂: length 1.95 mm, width 0.94 mm; ♀♀: length 2.48-2.60 mm, width 0.96-0.98 mm.

Colour. The reddish brown colour of the type specimens is most certainly a result of long term storage in alcohol. The distribution of greyish pubescence in both male and female as described in *H. malaya* Esaki.

Structural characters. Male elongate ovate, length about 2.1x greatest width across thorax (156:75). Head length about 0.7x head width across eyes (35:52); eye width about 0.25x width of head between eyes (9:34). Relative lengths of antennal segments (1-4): 32:20:21:23; segment 1 slightly shorter than head, distinctly thicker than segment 4 (7:5); segment 2 subequal in length to segment 3. Hind margin of pronotum indistinct in lateral parts. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 51:42:18; middle leg: 127:115:85; and hind leg: 65:46:21. Grasping comb slightly more than 2/5 length of fore tibia (19:42); middle femur about 0.8x total length; relative lengths of middle tarsal segments (1:2): 52:33; hind femur distinctly thicker than middle femur (10:8). Abdominal venter not modified. Claspers relatively long, crossing each other dorsal to the genital capsule; shape of each clasper as in *H. malaya* Esaki.

Female (Fig. 21) elongate ovate, length about 2.6x greatest width across thorax (198:77). Head structure as in male except that antennal segment 1 is more slender; length of antennal segments (1-4): 30:20:22:27. Thoracic dorsum moderately raised in middle of mesonotum, pubescence longer on lateral and posterior parts of mesonotum and on metanotum and basal abdominal terga. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 56:43:20; middle leg: 129:114:89; hind leg: 63:50:24. Middle femur 0.65x total length. Abdomen distinctly tapering in width posteriorly and rather narrow; basal abdominal terga depressed laterally on each side of a slightly raised, median area; pleura with rather deep, lateral impressions which originate on metapleura; connexiva basally thickened, vertically raised, and subparallel, posteriorly inflexed upon abdominal dorsum, subparallel but not meeting each other above tergum 5-7; tergum 8 produced and slightly deflected, concealing proctiger.

Distribution

Probably endemic to the Nicobar Islands.

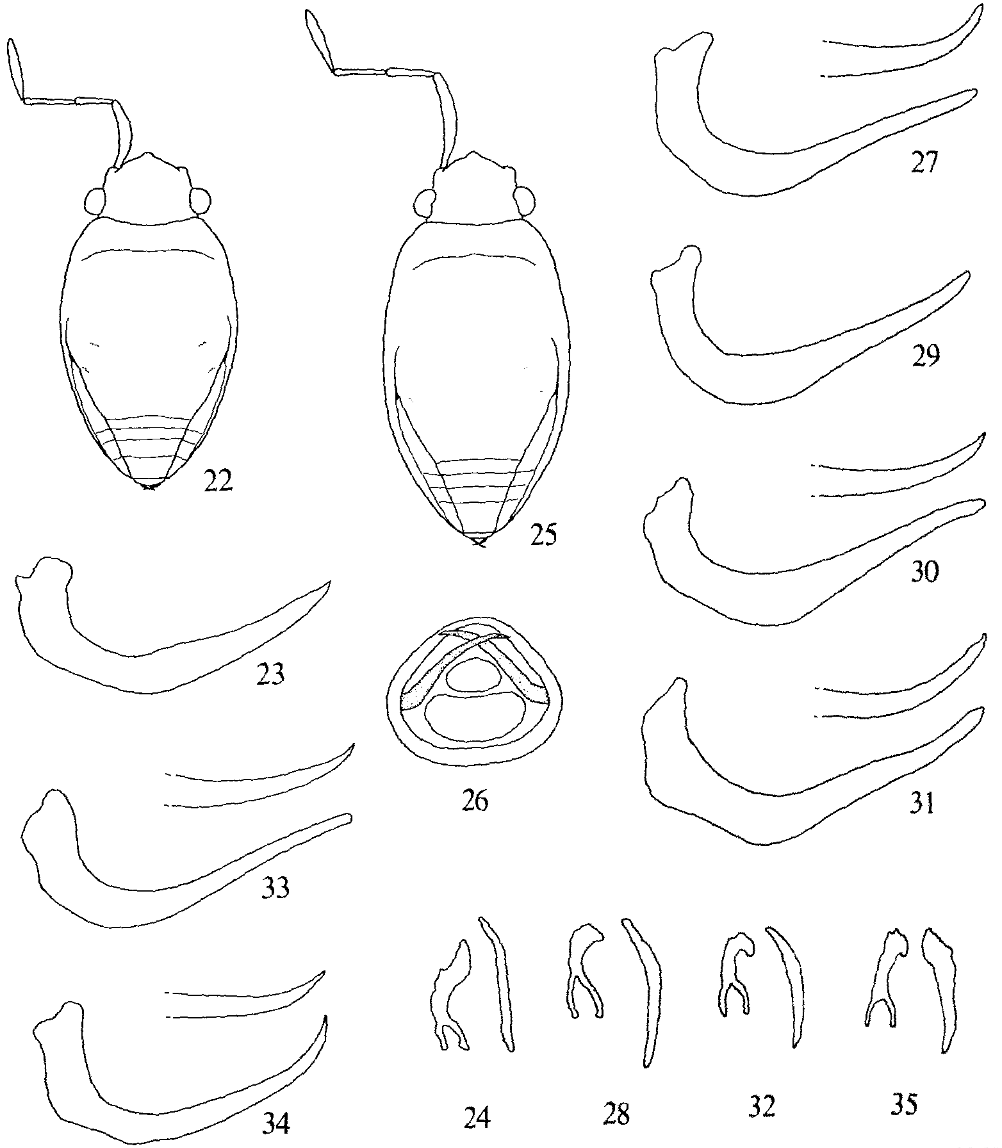
25. ***Halovelia convexa*** **sp.n.**

Figs. 22-24, 36-37.

Type area: Gan Island, Addu Atoll, Maldive Islands.

Type material examined: MALDIVE ISLANDS: *Holotype* ♀, Gan I., Addu Atoll, 13.iii.1959, in shallow pools left in coral, 20 yds from deep water, 200 yds from land, W.W.A. Phillips, in the British Museum (Natural History), London.- *Paratypes*: 13♂♂ 9♀♀, same locality and date as holotype (BMNH); 13♂♂ 8♀♀, same locality, 20.ii.1959, shallow tidal pool; 2♂♂ 6♀♀, Bushy I., Addu Atoll, 11.iii.1959, at low tide in shallow water amongst coral; 7♂♂ 9♀♀, Willingtli I., Addu Atoll, 22.i.1959, from shallow pools on reef at low tide; 9♂♂ 5♀♀, Doonidu I., North Male Atoll, 25.ix.1958, in small pools on reef at low tide, all collected by W.W.A. Phillips (BMNH, ZMUC).

Diagnosis: Recognized by the strongly convex and pilose female mesonotum which is evenly depressed posteriorly



Figs. 22-35. 22-24. *Halovelia convexa* sp.n. (22. Male body, dorsal view. 23. Left clasper. 24. Vesical sclerites). 25-28. *Halovelia pauliani* Poisson. (25. Male body, dorsal view. 26. Male abdominal end, caudal view. 27. Left clasper. 28. Vesical sclerites). 29. *Halovelia poissoni* sp.n. Left clasper. 30-31. *Halovelia seychellensis* sp.n. (30. Left clasper (Seychelles). 31. Same (Madagascar). 32. Vesical sclerites). 33. *Halovelia depressa* sp.n. Left clasper. 34-35. *Halovelia mauricensis* sp.n. (34. Left clasper. 35. Vesical sclerites).

and continuing as a broad, median ridge on metanotum and basal abdominal terga; connexiva inflexed upon abdominal terga throughout their entire length.

Etymology: Characterized by the strongly convex female thorax.

Description

Size. ♂♂: length 1.55-1.65 mm, width 0.85-0.90 mm; ♀♀: length 1.95-2.15 mm, width 0.90-0.98 mm.

Colour. Black or dark brown; thoracic and abdominal dorsum (♂) or base of abdominal dorsum (♀) with dense greyish pubescence. Female connexiva terminated by prominent groups of whitish hairs. A brownish yellow spot at base of head. Antennae and legs dark brownish.

Structural characters. Male (Fig. 22) subovate, length about 1.8x greatest width across thorax (132:73). Head length about 0.6x head width across eyes (29:48); eye width about 0.25x width of head between eyes (8:32). Relative lengths of antennal segments (1-4): 30:18:19:26; segment 1 subequal in length to head, distinctly thicker than segment 4 (6:4); segment 2 subequal in length to segment 3. Hind margin of pronotum indistinct in lateral parts. Relative lengths of leg segments (femur :tibia:tarsus): fore leg: 47:38:16; middle leg: 95:82:62; and hind leg: 51:38:20. Grasping comb almost ½ length of fore tibia (18:38); middle femur about 0.7x total length; relative lengths of middle tarsal segments (1-2): 36:26; hind femur slightly thicker than middle femur (8:7). Abdominal venter not modified. Claspers relatively long, crossing each other dorsal to the genital capsule; blade of each clasper (Fig. 23) slender and only slightly curved dorsad, more distinctly curved mesad, apex pointed; vesical sclerites (Fig. 24).

Female (Fig. 36) fusiform, length about 2.2x greatest width across thorax (173:79). Head structure as in male except that antennal segment 1 is more slender; length of antennal segments (1-4): 27:17:20:28. Thoracic dorsum distinctly raised in middle of mesonotum, strongly convex in lateral view (Fig. 37), evenly depressed posteriorly and continuing as a broad, median ridge on basal abdominal terga; thoracic dorsum furnished with long, erect pubescence which is longest on posterior part of mesonotum, on metanotum, and on basal abdominal terga. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 49:38:19; middle leg: 101:91:71; hind leg: 49:42:20. Middle femur almost 0.6x total length. Abdomen tapering in width posteriorly; basal abdominal terga slightly depressed on each side of median ridge; pleura with shallow, lateral impressions which originate on metapleura; connexiva basally thickened and inflexed upon abdominal dorsum throughout their entire length, subparallel and not meeting each other; tergum 8 produced and almost horizontal, forming a roof above the genital segments.

Distribution and habitat

Probably endemic to the Maldive Islands. Phillips (1959) gives a brief account of the habitat of the new species in the Addu Atoll, Maldive Islands. He only found the species (l.c., p. 246) in "clear weedless pools left by the receding tide on the outer aspects of the reefs, often 200 feet or more from the shore."

Discussion

China (*in* Phillips l.c.) states that the specimens collected by W.W.A. Phillips in Addu Atoll, Maldive Islands (p. 246, footnote no. 2) were "Closely allied to *Halovelia amphibia* Bergroth from the Zanzibar coast and possibly conspecific." However, the new species is far from *amphibia* as a comparison between the descriptions and figures of the two species readily will show.

26. ***Halovelia pauliani*** Poisson

Figs. 25-28, 38-39.

Halovelia pauliani Poisson, 1956: 252-255, figs. 11-12 (description; type area: Ile Europa, Mozambique Channel); Poisson 1965: 141-142 (description of ♂).

Type material: *Syntypes* 2♀♀, Ile Europa, R. Paulian, 10-12-48, repository unknown (not examined).

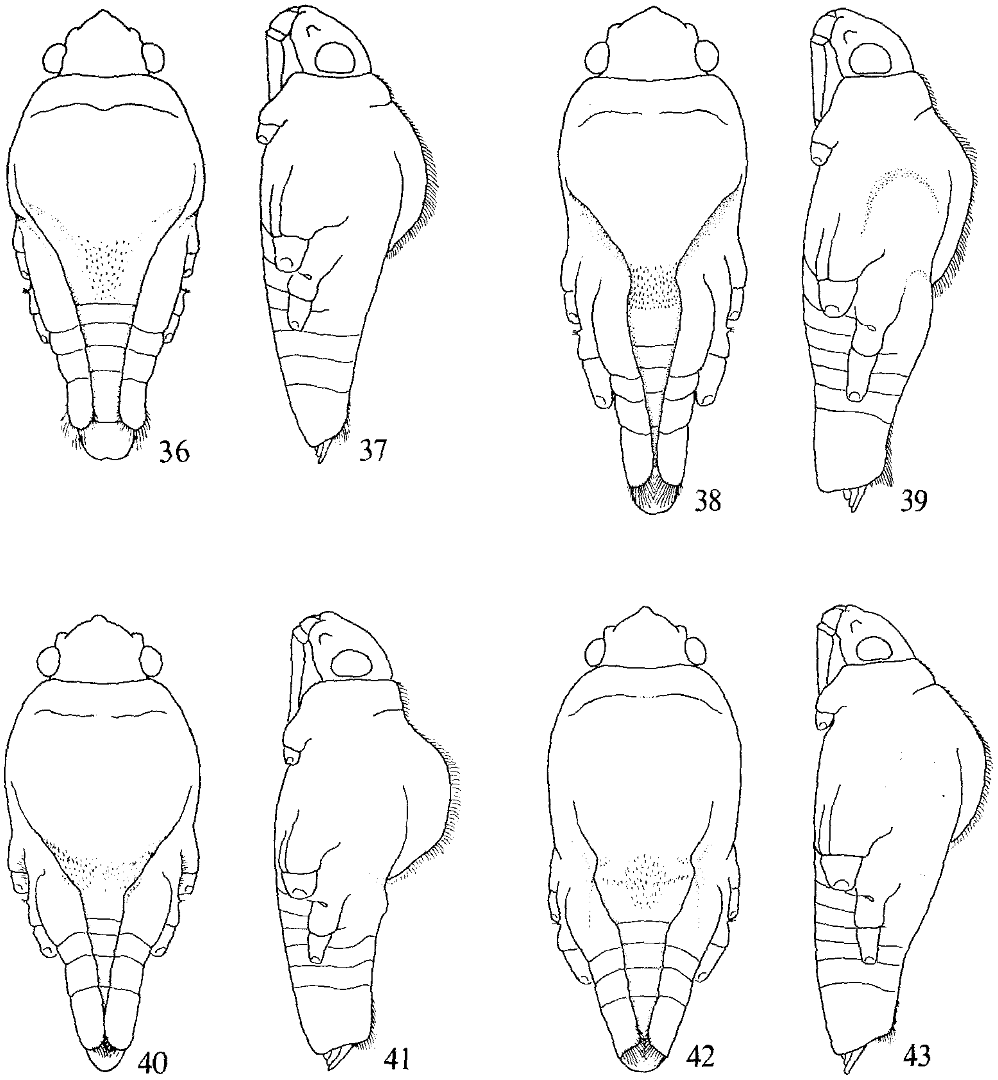
Material examined: MADAGASCAR: Numerous ♂♂ and ♀♀, Ile Europa, Legendre, 1964 (USNM, ZMUC).

Diagnosis: Female recognized by the modifications of thorax and abdomen, especially the posteriorly narrowed, pilose thoracic dorsum, deep, lateral impressions on posterior thorax and abdominal base, and distinctly tapering abdomen with connexiva inflexa upon abdominal dorsum. Male recognized by the relatively long antennal segment 1.

Description

Size. ♂♂: length 1.80-1.88 mm, width 0.93-0.98 mm; ♀♀: length 2.35-2.48 mm, width 0.90-0.95 mm.

Colour. Blackish with greyish pubescence which



Figs. 36-43. 36-37. *Halovelia convexa* sp.n. (36. Female body, dorsal view. 37. Female body, lateral view). 38-39. *Halovelia pauliani* Poisson. (38. Female body, dorsal view. 39. Female body, lateral view). 40-41. *Halovelia poissoni* sp.n. (40. Female body, dorsal view. 41. Female body, lateral view). 42-43. *Halovelia seychellensis* sp.n. (42. Female body, dorsal view. 43. Female body, lateral view).

is longer and denser on abdomen (♂), or with long, pale hairs on posterior mesonotum, metanotum and base of abdominal tergum and abdominal end (♀). Female connexiva terminated by long, whitish hairs. A large brownish yellow spot at the base of head. Antennae and legs blackish.

Structural characters. Male (Fig. 25) elongate ovate, length almost 2.0x greatest width across thorax (148:76). Head length about 0.6x head width across eyes (30:51); eye width about 0.25x width of head between eyes (9:34). Relative lengths of antennal segments (1-4): 36:21:22:28; segment 1 distinctly longer than head, thicker than segment 4 (7:5); segment 2 subequal in length to segment 3. Hind margin of pronotum indistinct in lateral parts. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 50:45:18; middle leg: 118:107:74; and hind leg: 60:47:20. Grasping comb about 2/5 length of fore tibia (18:45); middle femur about 0.8x total length; relative lengths of middle tarsal segments (1:2): 44:30; hind femur slightly thicker than middle femur (9:8). Abdominal venter not modified. Claspers relatively long, crossing each other dorsal to the genital capsule (Fig. 26); blade of each clasper (Fig. 27) slender and almost straight, distinctly curved mesad, apex pointed; vesical sclerites (Fig. 28).

Female (Fig. 38) elongate ovate, length 2.6x greatest width across thorax (198:77). Head structure as in male except that antennal segment 1 is more slender; length of antennal segments (1-4): 32:20:23:29. Thoracic dorsum distinctly raised with greatest height slightly before middle of mesonotum (Fig. 39), slightly depressed and distinctly narrowing posteriorly; dorsum furnished with long erect pubescence which is longest on posterior part of mesonotum, on metanotum and basal abdominal terga. Mesopleura distinctly impressed. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 52:44:20; middle leg: 127:112:81; hind leg: 58:52:24. Middle femur about 0.6x total length. Abdomen distinctly tapering in width posteriorly; basal abdominal terga forming a median tumescence; pleura with deep, lateral impressions which originate on mesopleura; connexiva basally thickened and vertically raised, inflexed upon abdominal dorsum posteriorly, converging and meeting each other above tergum 7; tergum 8 produced and more or less deflected, concealing proctiger.

Distribution

Only recorded from the small Île Europa which is situated in the Mozambique Channel, about halfway between the East coast of Africa and Madagascar.

Discussion

Poisson (1956: 252-255) described this species on "2 femelles aptére" from "Île Europa (R. Paulian), 10-12-48". The new species was described in the journal published by l'Institut Scientifique de Madagascar, Tananarive. Although not specifically stated, the type specimens presumably were to be deposited in that institution (now Parc de Tsimbazaza). However, the types are not in the collections of that institution (D.A. Polhemus *pers. comm.*) and their present place of deposition is unknown. The R.A. Poisson collection (now divided between the U.S. National Museum, Washington, D.C., and the Zoological Museum, University of Copenhagen) contains a long series of specimens from the type locality, labelled "Île Europa, Legendre, 1964". These are not types, but since they have been identified by Poisson (Poisson 1965: 141-142) and match his description and figures, there can be no doubt about the identity of the species. That Poisson (l.c.) named 2 males and 3 females from this series 'Type' is not justified. If the two female syntypes proved to be lost, a neotype should be chosen from the series collected by Legendre.

China (*in* Phillips 1959), when mentioning *Halovelia amphibia* Bergroth from the Zanzibar coast, states (p. 246, footnote no. 2) "Poisson has recently (1956) redescribed this species from Madagascar under the name *H. paulians* [sic])." However, Poisson's species is far from *amphibia* as a comparison between the descriptions and figures of the two species readily will show.

27. ***Halovelia poissoni*** **sp.n.**

Figs. 29, 40-41.

Halovelia pauliani Poisson; Polhemus & Cheng 1982: 222 (records Sange Island, Tanzania).

Type area: Sange Island, Tanzania.

Type material examined: TANZANIA: *Holotype* ♀, Mkwaja, Sange Island, III.10.1979, J.T. Polhemus, CL994, in the U.S. National Museum of Natural History, Washington, D.C. - *Paratypes*: 6♂♂ 5♀♀, same data as holotype (JTPC); 4♀♀, Pangani, 50 km S. of Tanga, Oct. 1987, J. Strange (ZMUC); 1♂ 2♀♀, Pangani, low tide, pool in mangrove, 4.ii.1988, J. Strange (ZMUC); 1♂ 1♀, Pangani, low tide, open water, 5.ii.1988, J. Strange (ZMUC); 2♂♂ 2♀♀, Zanzibar, Kisimkasi, 13.vi.1979, seawater pools at low tide, Michael Stoltze (ZMUC). KENYA: 1♂, Kenya, River Athi, Bushwackers' Camp, 29.iii. 1964, E.S. Brown (BMNH); 1♂, Turtle Bay nr Malindi, sea level, 21.viii.1963, E.S. Brown (BMNH); 8♂♂ 5♀♀, South Kenya, Kisite Island, pools on coral reef at low tide, 11.ii.1985, Mogens Andersen (ZMUC); 1♀, Mombasa, Drani Beach, Mixed with brown algae on beach after windy night, VI.6.1985, Matti Nummelin (ZMUC); 1♀, Wasini Island, in pool in mangrove at low tide, 12.ii.1985, T.G. Nielsen & S.J. Hørsted (ZMUC).

Diagnosis: Female easily recognized by the strongly raised thoracic dorsum which forms a pilose "hump". Male separated from *pauliani* Poisson and *seychellensis* sp.n. by its more distinctly depressed abdominal venter.

Etymology: Named in honour of R.A. Poisson, the foremost author of semiaquatic bugs of the Ethiopian region.

Description

Size. ♂♂: length 1.72-1.80 mm, width 0.92-0.98 mm; ♀♀: length 2.12-2.32 mm, width 0.90-0.94 mm.

Colour. Blackish with greyish pubescence which is longer and denser on abdomen (♂), or with long, pale hairs on posterior mesonotum, metanotum and base of abdominal tergum and abdominal end (♀). Female connexiva terminated by long, whitish hairs. A large brownish yellow spot at the base of head. Antennae and legs blackish.

Structural characters. Male elongate ovate, length about 1.8x greatest width across thorax (140:76). Head length about 0.7x head width across eyes (35:49); eye width slightly more than 0.25x width of head between eyes (9:31). Relative lengths of antennal segments (1-4): 31:20:21:24; segment 1 shorter than head, slightly thicker than segment 4 (6:5); segment 2 subequal in length to segment 3. Hind margin of pronotum indistinct in lateral parts. Relative lengths of leg segments (femur :tibia:tarsus): fore leg: 45:39:17; middle leg: 105:102:76; and hind leg: 55:43:22. Grasping comb slightly more than 2/5 length of fore tibia (18:39); middle femur 0.75x total length; relative lengths of middle tarsal segments (1:2): 43:33; hind femur slightly thicker than middle femur (9:8). Abdominal venter slightly but distinctly depressed in middle. Claspers relatively long, crossing each other dorsal to the genital capsule; blade of each clasper (Fig. 29) slender and almost straight, slightly curved mesad, apex pointed; vesical sclerites as in *seychellensis* sp.n. (Fig. 32).

Female (Fig. 40) elongate fusiform, length 2.4x greatest width across thorax (182:76). Head structure as in male except that antennal segment 1 is more slender; length of antennal segments (1-4): 30:19:20:25. Thoracic dorsum very distinctly raised as a "hump" with greatest height in middle of mesonotum (Fig. 41), steeply depressed and distinctly narrowing posteriorly (Fig. 40); thoracic dorsum furnished with long erect pubescence which is longest in middle and posterior part of mesonotum and on metanotum. Mesopleura distinctly impressed. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 49:40:18; middle leg: 111:101:74; hind leg: 54:43:23. Middle femur about 0.6x total length. Abdomen distinctly tapering in width posteriorly; basal abdominal terga medially raised; pleura with deep, lateral impressions which originate on mesopleura; connexiva basally thickened and vertically raised, inflexed upon abdominal dorsum posteriorly, converging and meeting each other above tergum 7; tergum 8 produced and more or less deflected, concealing proctiger.

Distribution and habitat

East coast of Africa; recorded from Kenya (Malindi, Mombasa, Kisite Island, Wasini Island) and Tanzania (east coast S. of Tanga, Zanzibar, Sange Island). Polhemus & Cheng (1982) recorded the new species (as *H. pauliani* Poisson) from Sange Island, Tanzania, (p. 222) from "a sheltered area adjacent to steep, sharp rocks on a very small island that is part of an offshore reef." Many specimens were taken together with *Halobates* spp. and a *Hermatobates* sp.

28. *Halovelia seychellensis* sp.n.

Figs. 30-32, 42-43.

Type area: Mahé, Seychelles.

Type material examined: SEYCHELLES: *Holotype* ♂, Seychelles, Mahé, Ruin at Bel Ombre, 17.viii.1985, Lanna Cheng, in the Zoological Museum, University of Copenhagen. - *Paratypes*: 5♂♂ 2♀, same locality and date as holotype; 4♂♂ 2♀♀, Mahé, Anse Aux Pins, at light, 18.viii.1985, Lanna Cheng (ZMUC); 15♂♂ 2♀♀, Mahé, Bean Valley Bay, Near shore pool, 20.viii.1985, Lanna Cheng (ZMUC); 3♂♂, Mahé, Bean Valley Bay, 20.viii.1985, Lanna Cheng (ZMUC); 1♂, Praslin, Baie Ste. Anne, at light, 4.ix.1985, Lanna Cheng (ZMUC); 10♂♂ 1♀, Praslin, La Reserve, Anse Petit Cour, at light, mid-tide, around pier, 3.ix.1985, Lanna Cheng (ZMUC). MADAGASCAR: 80♂♂ 28♀♀, Diego Suarez Prov., rocky coast at Courrier Bay, 40 km NW. of Diego Suarez, CL 2279, XI-14-86, J.T. & D.A. Polhemus (JTPC, ZMUC).

Diagnosis: The female is separated from *pauliani* Poisson by the wider posterior mesonotum and from *poissoni* sp.n. by the less convex and pilose thoracic dorsum; the lateral impressions of thorax and basal abdomen are also more shallow.

Etymology: Named for the type locality, the Seychelles.

Description

Size. ♂♂: length 1.68-1.85 mm, width 0.88-0.92 mm; ♀♀: length 2.12-2.28 mm, width 0.92-0.98 mm.

Colour. Blackish with greyish pubescence which is longer and denser on abdomen (♂), or with long, pale hairs on posterior mesonotum, metanotum and base of abdominal tergum and abdominal end (♀). Female connexiva terminated by long, whitish hairs. A large brownish yellow spot at the base of head. Antennae and legs blackish.

Structural characters. Male elongate ovate, length about 1.9x greatest width across thorax (134:71). Head length about 0.7x head width across eyes (34:46); eye width about 0.25x width of head between eyes (8:31). Relative lengths of antennal segments (1-4): 29:17:19:25; segment 1 slightly longer than head, thicker than segment 4 (6:4); segment 2 slightly shorter than segment 3; Hind margin of pronotum indistinct in lateral parts. Relative lengths of leg segments (femur:tibia: tarsus): fore leg: 47:37:16; middle leg: 107:100:74; and hind leg: 51:41:19. Grasping comb slightly less than 2/5 length of fore tibia (14:37); middle femur about 0.80x total length; relative lengths of middle tarsal segments (1:2): 42:32; hind femur slightly thicker than middle femur (8:7). Abdominal venter slightly depressed. Claspers relatively long, crossing each other dorsal to the genital capsule; blade of each clasper slender and almost straight, slightly curved mesad, apex pointed (Figs. 30-31); vesical sclerites (Fig. 32).

Female (Fig. 42) elongate fusiform, length 2.2x greatest width across thorax (172:77). Head structure as in male except that antennal segment 1 is more slender; length of antennal segments (1-4): 26:18:21:25. Thoracic dorsum distinctly raised in middle of mesonotum (Fig. 43), regularly depressed and only slightly narrowing posteriorly (Fig. 42); thoracic dorsum furnished with short erect pubescence which is longest in middle and posterior part of mesonotum and on metanotum. Mesopleura distinctly impressed. Relative lengths of leg segments (femur:tibia:tarsus): fore leg: 50:37 :19; middle leg: 119:110:85; hind leg: 55:48:23. Middle femur about 0.7x total length. Abdomen distinctly tapering in width posteriorly; basal abdominal terga medialy raised; pleura with rather deep, lateral impressions which originate on mesopleura; connexiva basally thickened and vertically raised, inflexed upon abdominal dorsum posteriorly, converging and meeting each other above tergum 7; tergum 8 produced and more or less deflected, concealing proctiger.

Distribution and habitat

Recorded from the Seychelles (Mahé, Praslin) and northern Madagascar (Diego Suarez Province). The new species was taken on a rocky coast without much coral at Courrier Bay, 40 km NW. of Diego Suarez, Madagascar (Polhemus, field notes).

Discussion

The specimens from Madagascar (Diego Suarez) differ from those from the Seychelles by having a less distinctly pilose female thoracic dorsum and more slender and distinctly curved male claspers (Figs. 30-31). There are agreement in all other characters, including the vesical sclerites of the male and abdominal structure of female.

29. ***Halovelia depressa*** **sp.n.**

Figs. 33, 44-45.

Type area: Le Grotte, Tulear Province, Madagascar.

Type material examined: MADAGASCAR: *Holotype* ♀, Tulear Prov., Le Grotte, 20 km S. of Tulear on St. Augustin rd., 8-10 m, CL 2293, XI-28-86, J.T. & D.A. Polhemus, in the U.S. National Museum of Natural History, Washington, D.C. - *Paratypes*: 1♂ 2♀♀, same data as holotype (JTPC).

Diagnosis: The female is separated from those of *pauliani* Poisson, *poissoni* sp.n., and *seychellensis* sp.n. by its much less modified thorax which is only moderately raised and pubescent dorsally and not distinctly impressed laterally.

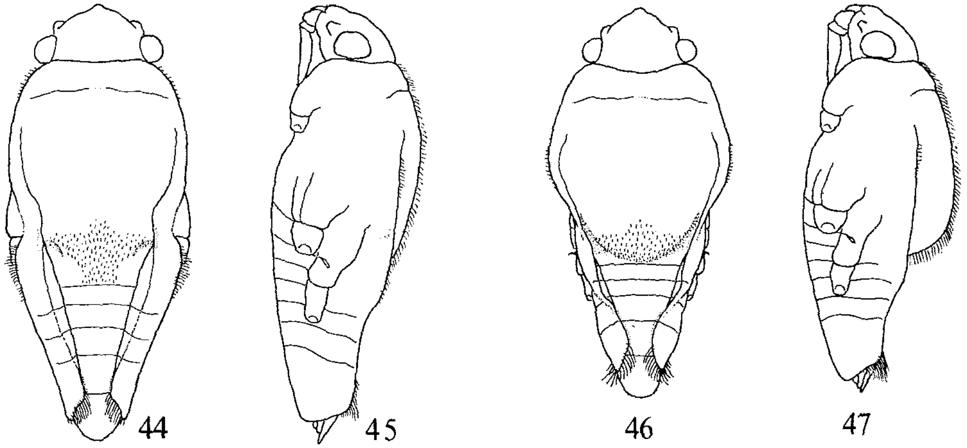
Etymology: Named for the relatively depressed female thorax.

Description

Size. ♂: length 1.58 mm, width 0.84 mm; ♀♀: length 2.08-2.25 mm, width 0.82-0.85 mm.

Colour. Blackish with greyish pubescence which is longer and denser on abdomen (♂), or with long, pale hairs on metanotum and base of abdominal tergum (♀). Female connexiva terminated by long, pale hairs. A brownish yellow spot at the base of head. Antennae and legs blackish.

Structural characters. Male elongate ovate, length about 1.9x greatest width across thorax (126:67). Head length about 0.7x head width across eyes (31:45); eye width about 0.25x width of head between eyes (8:30). Relative lengths of antennal segments (1-4): 30:16:21:25; segment 1 about as long as head, thicker than segment 4 (6:4); segment 2 distinctly shorter than segment 3; Hind margin of pronotum indistinct in lateral parts. Relative lengths of leg segments (femur:tibia: tarsus): fore



Figs. 44-47. 44-45. *Halovelia depressa* sp.n. (44. Female body, dorsal view. 45. Female body, lateral view). 46-47. *Halovelia mauricensis* sp.n. (46. Female body, dorsal view. 47. Female body, lateral view).

leg: 43:38:15; middle leg: 94:86:63; and hind leg: 48:39:17. Grasping comb a little more than 2/5 length of fore tibia (16:38); middle femur about 0.75x total length; relative lengths of middle tarsal segments (1:2): 37:26; hind femur slightly thicker than middle femur (8:7). Abdominal venter not modified. Claspers relatively long, crossing each other dorsal to the genital capsule; blade of each clasper slender and almost straight, slightly curved mesad, apex pointed (Fig. 33); vesical sclerites as in *seychellensis* sp.n.

Female (Fig. 44) elongate fusiform, length about 2.5x greatest width across thorax (166:66). Head structure as in male except that antennal segment 1 is more slender; length of antennal segments (1-4): 27:17:23:27. Thoracic dorsum only moderately raised in middle of mesonotum (Fig. 45), regularly depressed towards metanotum and basal abdominal terga; mesonotum not narrowing posteriorly; thoracic dorsum furnished with erect pubescence which slightly longer on posterior part of mesonotum, metanotum, and basal abdominal terga. Mesopleura not impressed. Relative lengths of leg segments (femur: tibia:tarsus): fore leg: 47:40:19; middle leg: 101:95:68; hind leg: 51:45:23. Middle femur about 0.6x total length. Abdomen distinctly tapering in width posteriorly; basal terga not raised; pleura with lateral, shallow impressions which originate on metathorax; connexiva basally thickened and raised, inflexed upon abdominal dorsum posteriorly, converging and almost meeting each other above tergum 7; tergum 8 produced and more or less deflected, concealing proctiger.

Distribution and habitat

Only known from the type locality, Le Grotte, Tulear Province, Madagascar. The locality was a seaside limestone sinkhole with overhanging walls and tidally influenced freshwater spring within. The new *Halovelia*-species was found in a freshwater springpool while *Halobates* sp. occurred on the ocean outside (Polhemus, field notes).

30. *Halovelia mauricensis* sp.n.

Figs. 34-35, 46-47.

Type area: Pointe d'Esny estuary, Flacq District, Mauritius.

Type material examined: MAURITIUS: *Holotype* ♀, Flacq District, Pointe d'Esny mangrove estuary, CL 2227, X-20-86, J.T. & D.A. Polhemus, in the U.S. National Museum of Natural History, Washington, D.C. - *Paratypes*: 44♂♂ 38♀♀, same data as holotype (JTPC, ZMUC); 28♂♂ 19♀♀, Black River District, reef at Big Black River Bay, CL 2224, X-20-86, J.T. & D.A. Polhemus (JTPC).

Diagnosis: The female is separated from *pauliani* Poisson and *seychellensis* sp.n. by the strongly raised and pubescent thoracic dorsum which is abruptly depressed towards abdomen. It differs from *convexa* sp.n. by lacking the median keel on the basal abdominal terga.

Etymology: Named for the type locality, the island of Mauritius.

Description

Size. ♂♂: length 1.38-1.42 mm, width 0.80-0.84 mm; ♀♀: length 1.86-1.94 mm, width 0.86-0.92 mm.

Colour. Blackish with greyish pubescence which is longer and denser on abdomen (♂), or with long, pale hairs on posterior metanotum and base of abdominal tergum (♀). Female connexiva terminated by long, pale hairs. A brownish yellow spot at the base of head. Antennae and legs blackish.

Structural characters. *Male* subovate, length about 1.75x greatest width across thorax (113:65). Head length about 0.65x head width across eyes (29:43); eye width 0.25x width of head between eyes (7:28). Relative lengths of antennal segments (1-4): 26:17:20:25; segment 1 slightly shorter than head, slightly thicker than segment 4 (5:4); segment 2 slightly shorter than segment 3. Hind margin of pronotum indistinct in lateral parts. Relative lengths of leg segments (femur:tibia: tarsus): fore leg: 39:35:14; middle leg: 84:70:51; and hind leg: 45:36:18. Grasping comb a little more than 2/5 length of fore tibia (15:35); middle femur about 0.75x total length; relative lengths of middle tarsal segments (1:2): 29:22; hind femur as thick as middle femur (7:7). Abdominal venter depressed from sternum 6 and backwards. Claspers relatively long, crossing each other dorsal to the genital capsule; blade of each clasper slender, distally curved both dorsad and mesad, apex pointed (Fig. 34); vesical sclerites (Fig. 35).

Female (Fig. 46) elongate fusiform, length about 2.2x greatest width across thorax (149:69). Head structure as in male except that antennal segment 1 is more slender; length of antennal segments (1-4): 26:17:21:26. Thoracic dorsum distinctly raised with greatest height in posterior part of mesonotum (Fig. 47), continuing onto basal abdominal terga; mesonotum tapering in width posteriorly (Fig. 46); thoracic dorsum furnished with long erect pubescence which is longest in posterior part of mesonotum and on metanotum. Mesopleura not impressed. Relative lengths of leg segments (femur :tibia: tarsus): fore leg: 43:39:17; middle leg: 91:80:59; hind leg: 48:41:21. Middle femur about 0.7x total length. Abdomen distinctly tapering in width posteriorly; dorsum abruptly depressed behind basal terga; pleura with lateral, shallow impressions; connexiva basally thickened and raised, inflexed upon abdominal dorsum posteriorly, converging and almost meeting each other above tergum 7; tergum 8 produced and more or less deflected, concealing proctiger.

Distribution and habitat

Probably endemic to the island of Mauritius. At the Pointe d'Esny mangrove estuary, Flacq District, the new species (together with *Halobates* sp.) was taken from an isolated patch of mangroves, from around mangrove roots and rocks. It was also found at the rock jetty and offshore reef at Big Black River Bay, Black River District (Polhemus, field notes).

CLADISTIC ANALYSIS

Methods

The cladistic analysis was performed using the program PAUP (Phylogenetic Analysis Using Parsimony by D.L. Swofford, Illinois Natural History Survey), version 2.4, run on the RC900 microcomputer (80386/80387 microprocessor) of the Zoological Museum, University of Copenhagen. This program infers phylogenies using the principle of maximum parsimony (see, e.g., Wiley 1981). Additional analyses were performed using the program Hennig86 (by J.S. Farris, State University of New York at Stony Brook), version 1.5. Unlike PAUP, this program eliminates trees that are identical due to zero-length branches.

Taxa incl. outgroups

The ingroup taxa were all 30 species of the genus *Halovelia* as previously described. As outgroup taxa were selected the type species of the three other genera of Haloveliinae, viz., *Xenobates seminulum* (Esaki), *Strongylovelia formosa* Esaki, and *Entomovelia doveri* Esaki. *Halovelia papuensis* Esaki was selected as representative of a new genus to be described in a forthcoming paper (Andersen *in prep.*).

For most species all of the 46 characters could be scored. The exceptions were *Halovelia amphibia* Bergroth and *sulawesi* sp.n. (only female characters) and *H. solomon* Andersen (only male characters). This resulted in a number of "missing data" scores in the data matrix (marked by a ?). A few characters (e.g., character 25) depend upon the possession of certain states for other characters (e.g., character 24, state 0). Such non-comparable characters were also scored as "missing". The data matrix is presented in Table 1.

Table 1. Character data set for *Halovelia* spp. and outgroups (31-34, marked by *). Missing character states marked by ?.

			1	1	2	2	3	3	4	4	5
Character nos =	0	5	0	5	0	5	0	5	0	5	0
1. *maritima*		00100	11000	00100	01100	20001	00010	11101	10111	01101	1
2. *amphibia*		?0100	11001	001?0	01100	000??	?001?	?0000	10???	????0	0
3. *carolinensis*		01100	11001	00100	01100	00001	00010	00000	10110	00100	0
4. *halophila*		00100	11001	00000	01100	00000	00010	00000	10100	00000	0
5. *corallia*		00110	11001	00000	01100	00000	00010	00000	10110	00001	1
6. *bergrothi*		10110	11001	00001	11111	00002	11010	00000	10121	10010	0
7. *hilli*		10110	11001	00001	11110	00001	11010	00000	10121	10010	0
8. *heron*		10110	11000	00001	11110	20002	11010	00100	10121	10000	0
9. *fijiensis*		10110	11001	00001	11111	00001	11010	00000	10101	00010	0
10. *septentrionalis*		10110	11100	00011	11100	20001	11011	02102	10121	00011	1
11. *inflexa*		00110	11000	00001	11100	20001	11010	02102	10121	02101	1
12. *esakii*		00110	11100	00010	11100	00001	11011	00101	10101	01101	1
13. *polhemi*		00110	11100	00010	11100	00001	11011	00101	10101	01101	1
14. *solomon*		??110	11???	?0010	11???	???01	1?011	0????	??100	0210?	?
15. *novoguinensis*		01110	11111	10010	11111	20101	11010	12102	10111	01101	1
16. *fosteri*		00100	01111	11000	01111	20100	11011	00100	10100	00101	0
17. *tongaensis*		00110	11011	00010	11110	20001	11010	00100	10101	01101	1
18. *annemariae*		01110	11000	00010	11110	00101	11010	01101	10110	00001	1
19. *lannae*		01110	11000	00011	11110	00100	11010	01101	10111	02001	1
20. *wallacei*		01110	11000	00011	11100	00001	11010	01001	10111	02001	1
21. *malaya*		01110	11000	00011	11100	00001	11010	02112	12100	00001	1
22. *sulawesi*		?1110	11100	000?0	11100	000??	?111?	?2112	11???	????1	1
23. *abdominalis*		01110	11000	00011	11100	01001	11010	02213	11110	00001	1
24. *nicobarensis*		01110	11000	00011	11100	10001	11010	02112	12110	00001	1
25. *convexa*		01110	11010	00011	11110	10002	11010	02112	11100	00001	1
26. *pauliani*		01110	11000	00011	11110	21101	11010	12113	12100	00001	1
27. *poissoni*		01110	11010	00011	11120	21101	11010	12113	12100	00001	1
28. *seychellensis*		01110	11000	00011	11110	20101	11010	02113	12100	00001	1
29. *depressa*		01110	11000	00010	11100	00001	11010	02112	12110	00001	1
30. *mauricensis*		01110	11010	00011	11110	20001	11011	02112	11110	00001	1
31. *Xenobates*	*	00001	00000	01000	11000	0001?	11000	00000	10000	00000	0
32. *H.papuensis*	*	00000	01001	00011	11000	0001?	11001	00002	00000	00100	0
33. *Entomovelia*	*	00201	01000	01000	00000	0001?	01000	00000	00100	00000	0
34. *Strongylovelia*	*	00200	00001	10000	00010	0001?	11000	02001	00100	00000	0

Characters

Characters were selected to describe as much as possible of the observed morphological variation in the 30 known species of *Halovelia*. The observed range of relative measurements was arbitrarily divided into states (usually only 2 or 3). Out of 46 characters, 9 characters describe differences between outgroup and ingroup taxa. These characters therefore have the same score for all species of *Halovelia*.

Where possible, the states of a character were ordered into a transformation series, and coded as 0 (plesiomorphic), 1, 2...n (most apomorphic). For a small number of characters with more than two states, it was uncertain what was the most appropriate ordering of the states. Such characters were analysed as unordered. Unordered characters are indicated below by an asterisk (*) and the coding of their states 0, 1, 2...n carries no connotation of polarity.

It should be stressed, however, that parsimony programs like PAUP and Hennig86 do not require polarity decisions to be made for the characters beforehand. Including the outgroup taxa in the analysis, the program decides character polarities based on the same parsimony criterion used in constructing the tree.

The following characters were used:

Size and body proportions

1 Male length more than 75 pct. of female length (0) / less than 75 pct. of female length (1).

2 Female total length less than 2.0x greatest width of body (0) / more than 2.0x greatest width of body (1).

Colour

3*Head with large, V-shaped, pale marking between eyes (0) / head at most with basal roundish pale spot (1) / head with other kinds of markings (2).

4 Parts of pronotum paler than rest of thorax (0) / pronotum dark as rest of thorax (1).

5 Thoracic and/or abdominal dorsum without definite spots of silvery pubescence (0) / with definite spots of silvery pubescence (1).

6 All femora uniformly dark (1) / at least basal part of fore femora pale (0).

Vestiture

7 Antennal segment 2 with a few erect bristles (0) / antennal segment 2 without such bristles (1).

8 Pubescence of female pronotum short (0) / pubescence of female pronotum distinctly longer than pubescence of meso- and metanotum (1).

9 Pubescence of female mesonotum short (0) / pubescence of female mesonotum distinctly longer than pubescence of rest of thoracic dorsum (1).

10 Pubescence of female metanotum and basal abdominal terga long and distinctly greyish (0) / pubescence of metanotum and basal abdominal terga not differentiated in length and/or colour (1).

11 Female mesopleura with tufts of long hairs (1) / without such tufts of long hairs (0).

12 Middle femora and tibiae with a row of long, suberect hairs along anterior margin (1) / middle leg without such hairs (0).

Head incl. antennae

13 Eye width more than 0.20x interocular width of head (0) / less than 0.20x interocular width of head (1).

14 Antennal segment 1 of male distinctly shorter than head length (0) / subequal to or longer than head length (1).

15 Ratio of antennal segment 3 and segment 2 more than 1.2:1 (0) / less than 1.2:1 (1).

Thorax

16 Hind margin of pronotum distinct throughout (0) / hind margin of pronotum more or less obsolete laterally and/or medially (1).

17 Lateral sutures between pro- and mesothorax distinct (0) / sutures obsolete (1).

18 Mesonotum of female laterally with longitudinal clefts extending forward from connexiva to at least middle of mesonotum (1) / lateral clefts much shorter (0).

19 Thoracic dorsum of female at most moderately raised (0) / distinctly raised above level of head and thorax (1) / as before but mesonotum forming a "hump" (2).

20 Greatest height of female thorax located at or slightly before middle of mesonotum (0) / greatest height located distinctly before the middle of mesonotum (1).

21*Posterior thoracic dorsum of female regularly depressed towards abdominal dorsum (0) / as before, continuing as a broad median tumescence or ridge onto abdominal dorsum (1) / abruptly depressed towards abdominal dorsum (2).

22 Female meso- and metanotum distinctly narrowed posteriorly (1) / not modified as described (0).

23 Meso- and/or metapleura of female impressed (1) / thorax without lateral modifications (0).

Legs

24 Fore tibiae of male with grasping comb composed of a row of densely set spines (0) / without grasping comb (1).

25*Grasping comb of male fore tibia less than 2/7 of fore tibial length (0) / between 2/7 and 3/7 (1) / more than 3/7 of fore tibial length (2).

26 Middle femur length of male less than 0.60x total length (0) / more than 0.60x total length (1).

27 Middle femur length of female less than 0.50x total length (0) / more than 0.50x total length (1).

28 Middle trochanter of female tuberculate (1) / not tuberculate (0).

Abdomen

29 Intersegmental sutures between basal 3 abdominal terga obsolete (1) / at least anterior suture of tergum 3 distinct (0).

30 Male abdominal venter with basal tumescence (1) / without basal tumescence (0).

31*Male abdominal venter not depressed (0) / depressed medially below level of thoracic venter (1) / depressed and medially grooved (2).

32*Female abdomen in dorsal view with sides broadly rounded or slightly converging posteriorly (0) / sides subparallel, at least in anterior parts (1) / sides distinctly converging, especially in posterior parts (2).

33*Basal abdominal terga of female not modified (0) / laterally depressed on each side of midline (1) / medially grooved (2).

34 Basal abdominal pleura of female abdomen laterally impressed (1) / female abdomen not modified as described (0).

35 Female connexiva obliquely raised throughout (0) / vertically raised but not inflexed (1) / raised and inflexed, at least in posterior parts, but not meeting each other above posterior terga (2) / as before but connexiva meeting each other above posterior terga (3).

36 Female sternum 7 with hind margin straight or only slightly produced in middle (0) / with hind margin distinctly produced in middle (1).

37 Anterior parts of female connexiva thickened, inner margins distinctly sinuate (2) / as before but inner margins straight or almost so (1) / female connexiva not modified as described (0).

Male genitalia

38 Male genital segments distinctly protruding from pregenital abdomen (0) / genital segments withdrawn into pregenital abdomen, barely visible behind segment 7 (1).

39 Clasper length less than 0.40x head width (0) / between 0.40x and 0.50x head width (1) / more than 0.50x head width (2).

40 Clasper simple falciform (0) / not simple falciform (1).

41 Blade of clasper regularly curved or straight (0) / abruptly turned mesad distally (1).

42*Blade of clasper circular or ovate (0) / horizontally flattened in cross-section (1) / vertically flattened in cross-section (2).

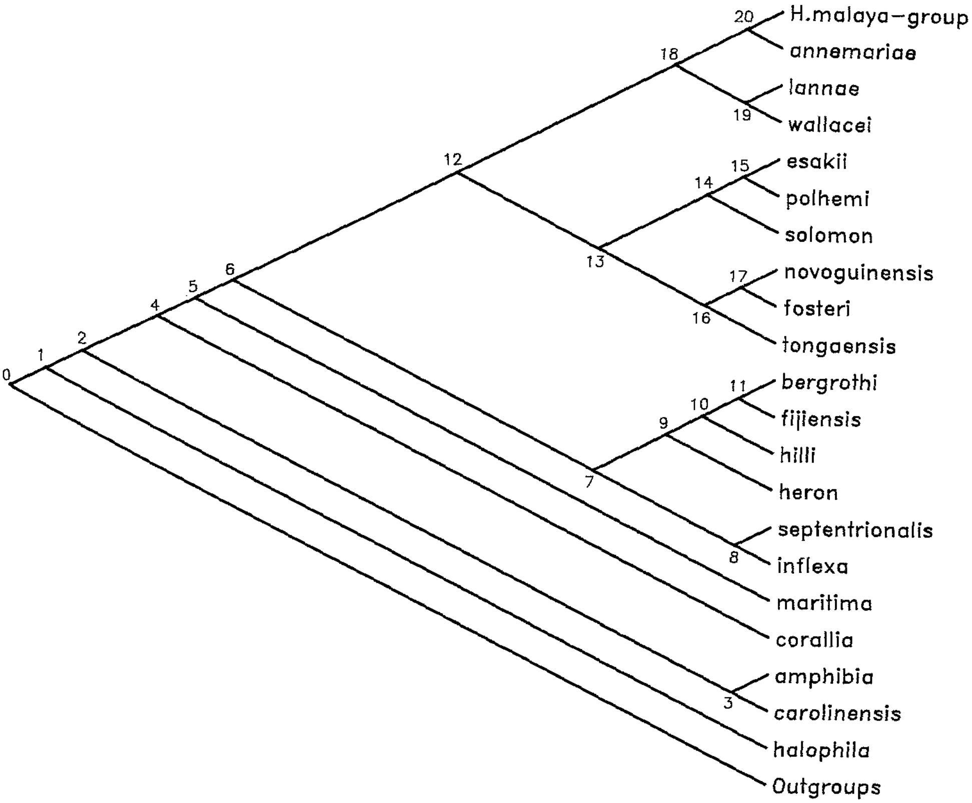


Fig. 48. The 155-step cladogram of relationships between the species of *Halovelia* (except the *H. malaya*-group and outgroups). Numbers denote clades referred to in the text.

43 Apex of clasper pointed (0) / blunt (1).
44 Apex of clasper straight (0) / hook-shaped (1).

Female genitalia

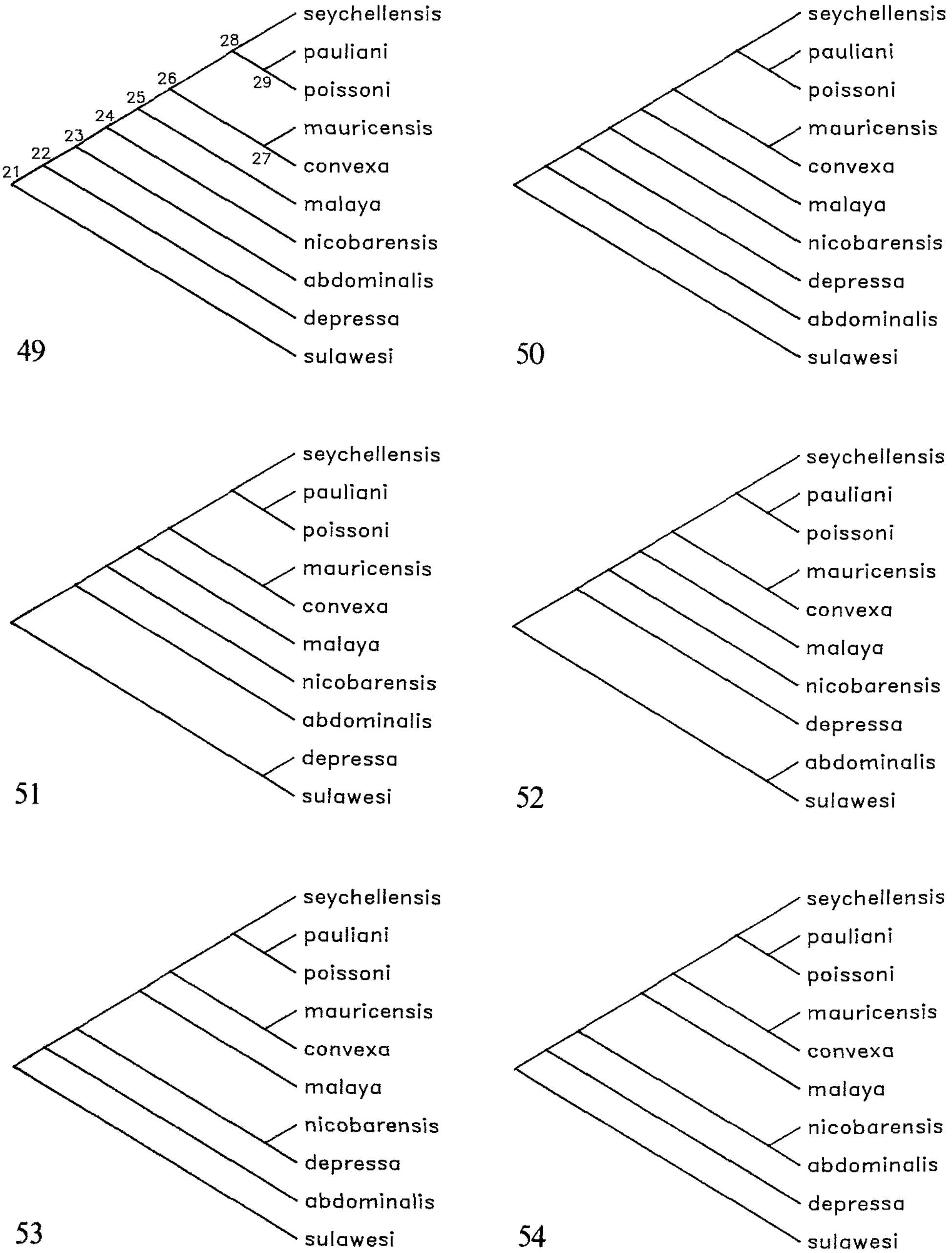
45 Tergum 8 not longer than half of its width (0) / distinctly longer than half of its width (1).
46 Proctiger exposed behind tergum 8 (0) / concealed beneath tergum 8 (1).

Analytical procedure

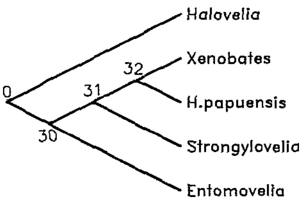
In the complete data set (34 taxa by 46 characters; see Table 1), species 13. *polhemi* is identical to 12. *esakii* in all character states, and species 14. *solomon* is only scored for 31 male characters. In order to reduce the computing time, these two species were deleted from the data set. Initially, this reduced data set (32 taxa by 46 characters) was analysed using PAUP. A simple Wagner tree was constructed with ROOT = OUTGROUP using the addition sequence CLOSEST and setting HOLD (the number of trees held in memory at any one step of tree construction) equal to one. No branch-swapping was employed. The result was a single cladogram of 155 steps and a consistency index (Kluge & Farris 1969) of 0.368.

This cladogram was used as input to a branch-swapping analysis (using the option SWAP = GLOBAL), with the MULPARS option to check for the existence of multiple, equally-parsimonious cladograms. A total number of 30 trees of length 153 and a consistency index of 0.373 was found.

The topological differences between these 30 cladograms were evaluated. They consisted of two sets of subcladograms. One set of 10 differed only



Figs. 49-54. The six different subcladograms for the *Halovelia malaya*-group. Numbers denote clades referred to in the text.



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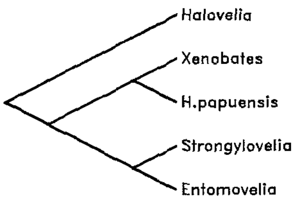

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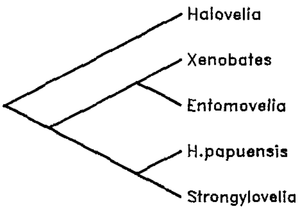

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Figs. 55-57. The three different subcladograms for the outgroups of *Halovelia*. Numbers denote clades referred to in the text.

in the relative position of species within the *H. malaya*-group, especially 22. *sulawesi*, 23. *abdominalis*, 24. *nicobarensis*, and 29. *depressa*. Another set of 3 subcladograms differed in the relative position of the four outgroup taxa (31-34, Figs. 55-57). A strict consensus cladogram for these 30 cladograms depicts the relationships between the two sets of taxa as unresolved (multifurcating branches). Using the options CHGLIST and APOLIST of PAUP, lists of character state changes and apomorphies, respectively, were produced.

The same data set was analysed using Hennig86. First, the tree calculation option MHENNIG* (which applies branch-swapping to any initial trees) was applied with OUTGROUP = taxa 31-34. Two trees of length 152 were found and stored in an internal tree file. Next, the option BB* (which applies extended branch-swapping to the trees in the current tree file and stores all shortest trees) was applied and a total number of 144 trees of length 152 and a consistency index of 0.37 was found. The 144 cladograms consisted of several sets of subcladograms. As before, one set of 3 differed in the relative position of the four outgroup taxa. Neglecting these differences, 48 different subcladograms were recognized, composed by a set of 2 differing in the relative positions of the taxa 2. *amphibia* + 3. *carolinensis*, 4. *halophila*, and 5. *corallia*, a set of 4 differing in the relative positions of the taxa 18. *annemariae*, 19. *lannae*, and 20. *wallacei*, and, finally, a set of 6 differing in the positions of species within the *H. malaya*-group.

The most important differences between the 152-step cladograms calculated by Hennig86 and the 153-step cladograms produced by PAUP, are the relative positions of the taxa 1. *maritima*, 10. *septentrionalis* + 11. *inflexa*, and 12. *esakii*. Both the 152-step and 153-step cladograms were evaluated using the tree editor XX ("Dos Equis") of Hennig86. The character states for the hypothetical ancestor of the outgroup + ingroup taxa differ only in the characters 24 and 25, and for the ingroup taxa only in the characters 26 and 27. For these characters, the alternative polarization 1→0 of states was implied by the 152-step cladograms. Since these alternative hypotheses of character polarizations are rejected for the reasons stated in the character analysis (below), all of the 152-step cladograms are rejected in favour of the 153-step cladograms.

A second analysis was performed on a restricted data set, with the outgroup taxa (31. *Xenobates*, 32. *papuensis*, 33. *Strongylovelia*, and 34. *Entomovelia*) excluded. The reduced data set was analysed using the same procedure as above. The cladograms were rooted using ROOT = ANCESTOR with species 4. *halophila* selected as hypothetical ancestor. A number of 10 equally parsimonious cladograms were found, with the length 121 steps and a consistency index of 0.388. This means that 32 or 21% of the steps on the original 153-step cladograms occurred outside the genus *Halovelia*. The 10 cladograms were a subset of the 153-step cladograms repeating the 10 different topologies for the *H. malaya*-group.

When the same data set was analysed using Hennig86, only 6 different cladograms of length 121 steps were found. These are a subset of the 10 different topologies for the *H. malaya*-group just mentioned, eliminating 4 topologies which are identical because of zero-length branches. These six subcladograms are shown in Figs. 49-54.

Finally, the species 13. *polhemi* and 14. *solomon* were added to the data set and to the 153-step cladogram on the same branch as 12. *esakii*. The reasoning behind this decision is given below. The length of this cladogram was calculated as 155 steps with a consistency index of 0.368. The 155-step cladogram (without the *malaya*-group) is shown in Fig. 48. Adding the subcladograms for the *malaya*-group (Figs. 49-54) and the outgroups (Figs. 55-57), 18 different cladograms of length 155 steps can be recognized.

Evaluation of the preferred cladogram

The preferred cladogram of relationships between the 30 species of *Halovelia* and the 4 outgroup species is 155 steps in length. It consists of the subcladograms in Fig. 48 (*Halovelia* except the *malaya*-group), Fig. 49 (*malaya*-group), and Fig. 55 (outgroups). The relationships depicted for the outgroups are only preliminary.

The character data set (Table 1) comprises 38 two-state characters, 8 three-state characters, and one four-state character. This gives a minimum of 57 steps based on these characters (since no character is constant in all OTU's). The length of 155 steps of the preferred cladogram indicates that there are many cases of homoplasious evolution (convergences or reversals) along the branches of the cladogram. Homoplasies weaken cladistic hypotheses. One of the purposes of the following discussion is to sort out those characters which in general or in particular cases corroborate hypotheses of relationships between the species of *Halovelia*.

The list of character changes along the branches of the preferred cladogram implies alternative polarizations of transformation series for some characters. Comments on these and a few other characters follow. The clade numbers refer to Figs. 48, 49, and 55.

3 It was believed that the extensive pale marking of the dorsal head surface found in some of the outgroups (species 31-32) was the plesiomorphic state. However, the alternative polarization 1→2→0, of character states is suggested.

4 The pronotum of most *Halovelia*-species is dark as the rest of the dorsum. Since the outgroups (31-34) all have more or less extensive pale markings on pronotum, the pale pronotal hind margin found in the *Halovelia*-species 1-4 is probably the plesiomorphic state. Species 16. *fosteri* has also pale dorsal markings, not only on pronotum but also on the pleural and ventral body surfaces. It is hypothesized that the change in coloration has evolved along with a shift in ecology in this species, from an exposed (intertidal reef) to a more shaded type of habitat (mangrove).

6 The comments given for character 4 also apply to this character.

7 The presence of a few erect bristles on the basal antennal segments is characteristic of many veliids. These are present in the outgroups 31. *Xenobates* and 34. *Strongylovelia* but never observed in *Halovelia*. Although an alternative polarization is suggested, I maintain that the presence of such bristles is plesiomorphic within the study group.

10 The long and distinctly greyish pubescence of the female metanotum and basal abdominal terga is found in many *Halovelia*- species and in the outgroups 31. *Xenobates* and 33. *Entomovelia*. This was believed to be the plesiomorphic state, but the cladistic analysis suggests the alternative polarization, 1→0. Following that suggestion, the character weakly support the monophyly of clade 5 (species 1 + 6-30). But since it has reversed twice in the cladogram (clades 10 and 16), this character is not very reliable.

15 The ratio of antennal segment 3 and segment 2 is a useful key character in *Halovelia*. The outgroups (except 31. *papuensis*) have segment 3 distinctly longer than 2 which is the plesiomorphic state. However, since the apomorphic reduction in the length of segment 3 has taken place several times (clades 7, 19, and 23), this character is not very reliable.

17 The retention of pleural sutures between pro- and mesothorax in the outgroups 33. *Entomovelia* and 34. *Strongylovelia* is clearly plesiomorphic compared to the absence of these sutures in other haloveliines including *Halovelia*. The suggestion that the polarization may be reversed is rejected.

18 The mesonotum of all *Halovelia*-species has lateral clefts extending forwards from the abdominal connexiva. These clefts, which are especially well developed in females, are not found in any of the outgroups. The suggestion that this is the plesiomorphic state is therefore rejected.

21 The posterior thoracic dorsum of female is modified in several species of *Halovelia*. These modifications are synapomorphic for certain species-groups, viz., clades 7, 16, and 26, but since reversals also occur, these synapomorphies are rather weak.

24 Although the character distribution on the cladogram suggests otherwise, the presence of a grasping comb on the male fore tibiae is undoubtedly the plesiomorphic state. This structure is characteristic of most veliids including all species of *Halovelia*. In the other haloveliine genera (31-34), the grasping comb is secondarily reduced.

25 The relative length of the tibial grasping comb varies considerably in *Halovelia*-species. The cladogram suggests that the transformation series should be read 0→1→2, i.e., by increasing relative length. There are, however, several convergencies and reversals in this character which is not very reliable.

26 The middle legs are prolonged in all haloveliines and distinctly longer than the hind legs. This is one of the synapomorphies for the genera of Haloveliinae. Within the genus *Halovelia*, the middle femur being less than 0.6x total length in the male is taken as the plesiomorphic state.

27 Similarly, the relative length of the female middle femur being more than 0.5x total length was considered plesiomorphic within *Halovelia*. However, this assumption is not supported by the character state distribution in the cladogram. But since it applies to the

male (previous character), the alternative polarization of character states is rejected.

29 The presence of intersegmental sutures between abdominal terga 1-3 is undoubtedly plesiomorphic although the cladistic analysis suggests otherwise. These sutures are obsolete in all *Halovelia*-species and a synapomorphy for the genus.

35 The structure of the female abdominal connexiva is an important diagnostic character for many *Halovelia*-species. In its plesiomorphic state, the connexiva are obliquely raised throughout. The next state of the transformation series is probably the vertically raised but not inflexed connexiva (clade 5). The connexiva have then been raised and inflexed upon abdominal dorsum (clades 8 and 21), and finally meet each other above posterior terga (clade 28 and species 23. *abdominalis*. An alternative to the transformation series 0→1→2→3 is the series 0→2 leading to species 15. *novoguinensis*. Parallel changes has occurred in the outgroups 30. *Xenobates* and 32. *papuensis* and there are also cases of the reversed change 1→0.

38 It was believed that the distinctly protruding male genital segments was the plesiomorphic state in the haloveliines. However, an alternative interpretation is that the more or less concealed genital segments found in all *Halovelia*-species as well as in the outgroups 33. *Entomovelia* and 34. *Strongylovelia* may be the plesiomorphic state.

39 The male claspers are always well developed in the haloveliines, but their relative length is quite variable. It appears that the lengthening or shortening of the claspers has taken place several times and the character is generally not very reliable. The very long clasper found in species of the *bergrothi*-group (clade 6, species 6-11), except 9. *fijiensis* (secondarily shortened) is, however, a strong synapomorphy.

42 The blade of the clasper is primitively circular or ovate in cross-section. One transformation series has lead to a horizontally flattened blade (state 1), which characterizes 1. *maritima*, 11. *inflexa*, and species of the *esakii*-group (clade 13, species 12-17) except 14. *solomon* (state 2) and 16. *fosteri* (reversed). The other series have produced a vertically flattened blade (state 2), which is found in 14. *solomon* and 19. *lannae* + 20. *wallacei* (clade 19).

45 The female tergum 8 is primitively almost quadrangular but has been prolonged in most species of *Halovelia* (clade 4) and deflected to conceal proctiger. Species belonging to clade 9 (species 6-9) have secondarily acquired the plesiomorphic state.

The following evaluation of the preferred cladogram (Figs. 48, 49, and 55) is clade-oriented. Each clade (identified by the number attached to the nodes of the cladogram) is discussed in turn, with particular reference to the synapomorphies that support its monophyly. Alternative hypotheses of relationships are also discussed. The characters are referred to by their numbers in the list of characters. Figures in brackets denote the state.

Clade 1: The monophyly of the genus *Halovelia* is supported by the synapomorphies 6(1), 17(1), 18(1), 29(1), and 36(1). The absence of pleural sutures between pro- and mesothorax (17) and of sutures between abdominal terga 1-3 (29) are significant. However, the strongest synapomorphy is the presence of lateral clefts on mesonotum extending forwards from the abdominal connexiva (18; especially well developed in females). Such clefts are not found in any other haloveliine genus.

Clade 2: The monophyly of *Halovelia*-species except 4. *halophila* is weakly supported by 39(1).

Clade 3: The relationship between species 2. *amphibia* and 3. *carolinensis* is supported by the synapomorphies 13(1), 25(1) and 43(1). The last one is weakened by the lack of knowledge of male characters in *amphibia*. The eyes of these species are relatively smaller than in other *Halovelia*-species, except 1. *maritima*.

Clade 4: Synapomorphies for *Halovelia* spp. except species 2-4 are 4(1), 45(1), and 46(1). The two last characters describe the structure of the female tergum 8 which has been prolonged and deflected to conceal proctiger. However, since species 1. *maritima* and species belonging to clade 9 (species 6-9) have secondarily acquired the plesiomorphic state (0), these synapomorphies are rather weak.

Clade 5: Synapomorphies for *Halovelia* spp. except species 2-5 are 10(0), 25(1), 33(1), 35(1), and 40(1), but most of these are rather weak. The *Halovelia*-species (1-5) considered so far are characterized mostly by primitive (plesiomorphic) character states. The body outline (dorsal view) is broadly ovate in both sexes, the female thorax is at most only moderately convex dorsally (19), and her abdomen is unspecialized (32-35), i.e., sides regularly curved, connexiva obliquely raised, metanotum and basal abdominal tergites not modified; tergum 8 of female is relatively broad and short, exposing proctiger behind (45-46). First and foremost are the middle legs distinctly shorter than in other *Halovelia* (26-27), being less than 0.6x (♂) or 0.5x (♀) total length of insect. The hind margin of pronotum is usually distinct throughout (16), reaching the lateral margins of body (dorsal view) in 1. *maritima*, 2. *amphibia*, and 3. *carolinensis*.

Clade 6: Synapomorphies for *Halovelia* spp. except species 1-5 are 16(1), 26(1), and 27(1). The two last characters describe the lengthening of the middle femora which is the strongest synapomorphy for the species 6-30.

Clade 7: The *H. bergrothi-group* is a very distinct, monophyletic group composed by the species

6. *bergrothi*, 7. *hilli*, 8. *heron*, 9. *fijiensis*, 10. *septentrionalis*, and 11. *inflexa*. This group is characterized by the synapomorphies 1(1), 15(1), 21(2), and 39(2). The most important of these are male characters, the females being relatively plesiomorphic. The size difference between the sexes is significant, the male length being less than 75% of the female length (1). The male claspers are much prolonged in 6. *bergrothi*, 7. *hilli*, 8. *heron*, 10. *septentrionalis*, and 11. *inflexa* (39). The shorter but distally hook-shaped claspers of male 9. *fijiensis* are probably derived by secondary shortening from the much longer type (the copulatory mechanism is the same in this species as in 6. *bergrothi*; see p. 209).

Clade 8: The relationship between species 10. *septentrionalis* and 11. *inflexa* is supported by 32(2) and 35(2), both describing modifications of the female abdomen.

Clade 9: The monophyly of the group composed by 6. *bergrothi*, 7. *hilli*, 8. *heron*, and 9. *fijiensis* is supported by 19(1), 35(0), 41(1), 45(0), and 46(0) of which the distinctly raised female thoracic dorsum (19) is the strongest. Three of these character changes are interpreted as reversals.

Clade 10: The close relationships between 6. *bergrothi*, 7. *hilli*, and 9. *fijiensis* is supported by 10(1), 21(0), 33(0), and 44(1). Only the hook-shaped apex of the male clasper (44) is a strong synapomorphy for this species-group. In the cladogram (Fig. 48), species 8. *heron* is placed as sister-group of this clade mainly because of its less modified male claspers. However, if this is a secondary condition derived from the state observed in *bergrothi* or *hilli*, an alternative hypothesis may be that *heron* is sister-species of *hilli*. This adds 3 extra steps to the cladogram.

Clade 11: The relationship between 6. *bergrothi* and 9. *fijiensis* is supported by 20(1), the greatest height of the female thorax being located distinctly before the middle of mesonotum.

Clade 12: The *Halovelia*-species 12-30 form a monophyletic group supported by the synapomorphy 14(1), the first antennal segment of the male being distinctly longer than the head. This group may appear to be weakly founded, but it also comprises the *Halovelia*- species with the most apomorphic females.

Clade 13: The *H. esakii*-group is composed by the species 12. *esakii*, 13. *polhemi*, 14. *solomon*, 15. *novoguinensis*, 16. *fosteri*, and 17. *tongaensis*. The monophyly of this group is supported by the synapomorphies 8(1), 39(0), 42(1), and 43(1). The suberect pubescence of the female thoracic dorsum is distinctly longer on the pronotum than on the meso-metanotum (8). The male claspers are modified, flattened in either the vertical or horizontal plane (42), and with blunt instead of pointed apices (43).

Clade 14: A group composed by 12. *esakii*, 13. *polhemi*, and 14. *solomon* (only the male is known and its placement is therefore tentative). A synapomorphy for this group is 30 (1), the presence of a basal tumescence on the male abdominal venter.

Clade 15: The species 12. *esakii* and 13. *polhemi* are identical in the characters used in the cladistic analysis. The two species are separated by other characters described in the taxonomical part (Andersen 1989).

Clade 16: The monophyly of a group composed by 15. *novoguinensis*, 16. *fosteri*, and 17. *tongaensis* is supported by 9(1), 10(1), 19(1), 21(2), and 35(0). The strongest synapomorphies are the strongly raised and pilose thorax (9, 10, and 19) and basally modified abdominal dorsum of the female (21).

Clade 17: The relationship between 15. *novoguinensis* and 16. *fosteri* is supported by 11(1), 20(1), and 23(1) which all describe modifications of the female thorax. *H. fosteri* is one of the most deviant species of the genus (pale colour, middle femora with a row of bristles on anterior margin, etc.) but the female has mesopleural hair tufts (11) and impressions (23), and an anteriorly raised thoracic dorsum quite similar to the female of *novoguinensis*.

Clade 18: The monophyly of a group composed by species 18-30 is supported by 2(1) and 32(1). The female body is elongate, more than 2.0x greatest width (2) and the sides of abdomen are subparallel (at least basally) and/or posteriorly converging (32).

Clade 19: The close relationship between 19. *lannae* and 20. *wallacei* is supported by 15(1) and 42(2). Especially the long, horizontally flattened male clasper (42) is a strong synapomorphy.

Clade 20: The relationship between 18. *annemariae* and species of the *H. malaya*-group (species 21-30) is weakly supported by 40(0), the reversal of the male clasper from non-falciform to falciform shape. An alternative hypothesis is that *annemariae* forms a monophyletic group together with 19. *lannae* and 20. *wallacei*. This only adds one extra step to the cladogram and is based upon the following synapomorphies. The female abdomen has a characteristic structure, almost parallel-sided in basal part (32), abruptly narrowing in distal part, the connexiva being almost erect throughout (35); the female thorax is more or less convex dorsally; the male claspers are prolonged, falciform in *annemariae*, horizontally flattened in *lannae* and *wallacei* (42).

Clade 21: The *H. malaya*-group is the largest and most firmly established monophyletic species group composed by the species 21. *malaya* Esaki, 22. *sulawesi*, 23. *abdominalis*, 24. *nicobarensis*, 25. *convexa*, 26. *pauliani*, 27. *poissoni*, 28. *seychellensis*, 29. *depressa*, and 30. *mauricensis*. This group is above all characterized by several female synapomorphies 32(2), 34(1), 35(2), and 37(1), while the males are relatively plesiomorphic. The female abdominal pleurae are basally impressed (34), and their sides are strongly converging, especially posteriorly (32); the connexiva are raised and inflexed upon abdominal dorsum, at least posteriorly (35), and the connexiva anteriorly are more or less thickened (37).

Clades 22-26 (Fig. 49): As previously discussed, the relationships within the *H. malaya*-group are partly unresolved. This is especially true for the species 21. *malaya*, 22. *sulawesi* (only females known), 23. *abdominalis*, 24. *nicobarensis*, and 29. *depressa*. Most of the character changes in clades 22-26 are too weak as synapomorphies to warrant any definite statements about relationships. However, the species *malaya* and *nicobarensis* appear to be closely related, perhaps even sister-species.

Clade 27: The relationship between 25. *convexa* and 30. *mauricensis* is supported by 9(1), dorsal pubescence of female thorax prolonged, and 21(2), posterior thorax of female abruptly depressed towards abdominal dorsum.

Clade 28: The monophyly of the group composed by 26. *pauliani*, 27. *poissoni*, and 28. *seychellensis* is supported by 23(1), female meso- and metapleurae impressed, and 35(3), inflexed connexiva of female meeting each other above posterior terga.

Clade 29: The relationship between 26. *pauliani* and 28. *poissoni* is supported by 22(1), female meso- and metanotum distinctly narrowed posteriorly, and 31(1), male abdominal venter medially depressed.

Clades 30-32: The outgroups 31. *Xenobates*, 32. *H. papuensis*, 33. *Entomovelia*, and 34. *Stronglyovelia* share the apomorphies 3(2), 24(1), and 27(1). However, since the cladistic analysis primarily was designed to clarify the relationships between the species of *Halovelia*, nothing can be said about the exact relationships between the outgroups and *Halovelia*. The cladistics of the Haloveliinae will be analysed and discussed in a forthcoming paper (Andersen *in prep.*). The present analysis (which does not include all relevant characters) suggests a close relationship between *Xenobates* and '*Halovelia*' *papuensis* (Fig. 55). That *Halovelia* is shown as sister group of all other haloveliines is an effect of its status as the ingroup of the analysis.

ECOLOGY AND BIOLOGY

The first account on the biology of a *Halovelia*-species is by Esaki (1924) who gave notes on the habitat, food, locomotion, copulation, etc., of *H. septentrionalis* Esaki (first identified by Esaki as *H. maritima* Bergroth). It is, however, Kellen (1959) who has published the most comprehensive treatment of the natural history of a single species, *H. marianarum* Usinger (= *H. bergrothi* Esaki), in Samoa. In January-February, 1987, the author spent three weeks at the Phuket Marine Biological Center near Laem Pan Wah, on the southeast coast of Phuket Island, Thailand. During that period, I was able to study the ecology and biology of *H. malaya* Esaki in some detail. If not otherwise stated, the following account is based upon original observations.

Habitats

I have suggested the trivial name *coral bugs* for species of the genus *Halovelia* because most species appear to be associated with coral reefs. That such an association exists is evident from glancing through the lists of material in the taxonomical sections of this work and also from field notes accompanying the samples (in particular those furnished by J.T. Polhemus). For each species, this information has been summarized under the heading 'Distribution and habitat'.

H. malaya Esaki was abundant on intertidal reef flats at the Phuket Marine Biological Center, Thailand (Fig. 64). These localities have been described by Ditlev (1978) with particular reference to the zonation of corals (Scleractinia). Most of the present study was carried out on the reef flats situated south of the pier at the PMBC. Along the beach, rocks are exposed during low tide with numerous pools of sea water on the rock surface. Outside the beach rocks there is a c. 60 m wide inner reef flat covered by mud, sand, stones and pebbles, and strewn with blocks of dead *Porites*-coral. There are no living corals. The mid-reef flat is 20 to 40 m wide. The dominant coral species are *Porites lutea* which forms micro-atolls with compact but irregular surfaces, and *Acropora hebes* or *A. pulchra* which forms 2-3 m stands of branching colonies. In between these dominant corals there are tidal pools with species of *Fungia, Favia, Goniastrea,* etc. The reef crest is situated c. 120 m from the beach and has developed as a large *Porites lutea*-block with smaller stands of *Acropora hebes/pulchra.* The reef edge, which is only exposed during extreme low tide, is dominated by dense ramose-growth forms of various coral-species.

The distribution of *H. malaya* in the area was studied by almost daily observations around low tide in various parts of the area just described. Individuals were never observed on the innermost 20-30 m, mostly covered by mud and without larger blocks of dead coral. Outside this zone, individuals were found among pebbles, stones, and larger blocks, especially in the shallow pools of water around and beneath such blocks. They occurred singly or in groups of 3-8.

H. malaya was also found on the water surface in small tidal pools among stands of *Porites*- and *Acropora*-corals on the mid-reef flat. They occurred mostly singly or in groups of 2-5 although the exact number was difficult to estimate, especially when the bugs were found close to branching *Acropora*-colonies. Few individuals were seen towards the outer margin of the exposed reef where small waves washed around the coral stands.

Along the concrete walls of the jetty where rockboulders are piled up, the coral bugs were rather abundant on the water in between stones. Under the pier, small groups of 10-20 individuals were found moving about on the sheltered water surface. Finally, groups of 2-5 individuals were seen in tidal pools on the rockfaces along the coast.

Other species of *Halovelia* have been recorded from rocky coasts without corals. Esaki (1924: 32-33) found *H. septentrionalis* abundantly on the surface of sea-water among rocks on the coast at Misaki near Tokyo, Japan. At Tansui, northern Taiwan, the same species occurred on small pools and streams among rocks near the coast exposed at ebbtide. Kellen (1959: 53-55) found *H. bergrothi* inhabiting a restricted area on the edges of a shallow lagoon in the southern part of Tutuila, Samoa. The area was bordered by mangroves, old lava beds, and numerous black volcanic rocks about a foot in diameter. There were no coral rocks in the area but the mouth of the lagoon was protected by a fringing reef. The lagoon experienced about a 3.5 foot tide and most of the scattered volcanic rocks were alternately submerged and exposed.

When mangroves occur close to intertidal coral reefs or rocky coasts, species of *Halovelia* may also be found in the vicinity of mangrove trees. Few species have been found exclusively in mangroves. *H. fosteri* Andersen was collected in a channel in mangroves at Laucala Bay and in a mangrove lagoon at Vuda, Viti Levu (localities described by Foster & Treherne 1986). This species is paler than other *Halovelia* and it is hypothesized that the change in coloration has evolved along with a shift in ecology in this species, from an exposed (intertidal reef) to a more shaded type of habitat (mangrove).

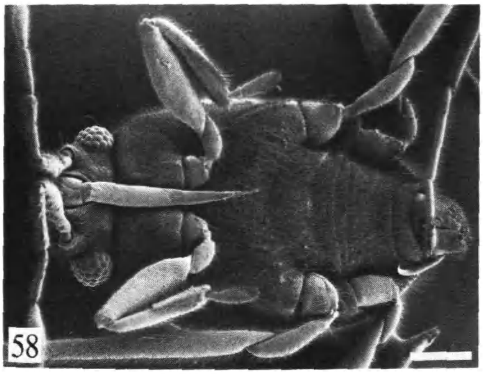
Kellen (1959: 55) observed a very distinct seasonality in the abundance of *H. bergrothi.* During the months December to February the veliids were much more abundant than in any other time of the year. During these months groups comprised of over 300 individuals were occasionally found together in schools covering several square feet on the surface of water. Similar concentrations of *H. bergrothi* were reported by Dr L. Cheng (*in litt.*) in New Georgia, Solomon Islands, where the bugs formed "rafts" of about 2-3 m wide and over 50 m long with densities estimated at 20-50/m^2.

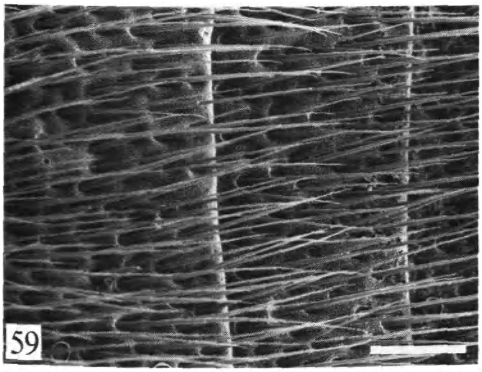
Individuals of *Halovelia* and ocean skaters, *Halobates*, do often occur in mixed schools. Kellen (1959) reported that *H. bergrothi* and a species of *Halobates* frequently were found together upon the water surface. Mixed schools or "flotillas" of *Halovelia fijiensis* and *Halobates fijiensis* Herring were also observed in the Fiji Islands (Foster *in litt.*).

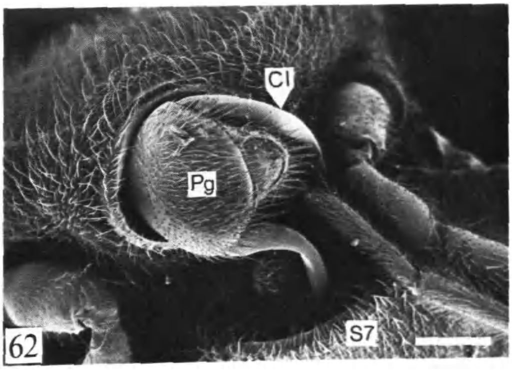
Distribution in relation to tide

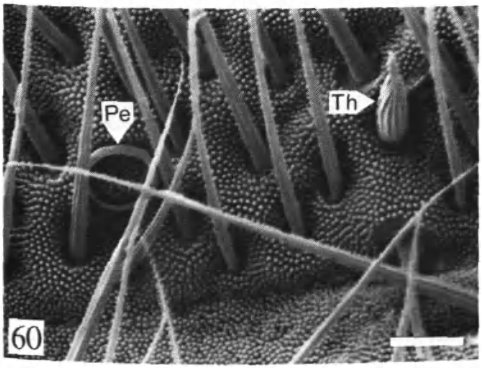
On the southeastern corner of Phuket Island, the sea shows tidal fluctuations of 1-3 m. During the study period (14-30 January 1987), the maximum daily range occurred towards the end of the period, where the exposed reef area at lowest tide extended about ⅔ towards the end of the pier (c. 200 m).

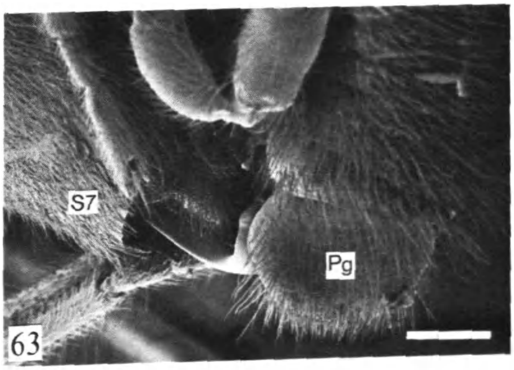
The distribution of *H. malaya* in relation to the tide was especially studied on the mid-reef flat strewn with blocks of dead *Porites*-coral (Fig. 64). The first individuals were observed after the blocks had emerged. As the tide receded the number of bugs visible on the reef flat increased, especially











Figs. 58-63. *Halovelia bergrothi* Esaki. Scanning Electron Photomicrographs. 58. Male, ventral view; scale 200 μm. 59. Surface structure of male abdominal venter; scale 20 μm. 60. Fine structure of body surface; scale 5 μm. 61. Copulating pair, lateral view; scale 200 μm. 62. Genital segments of copulating pair, caudal view; male pygophore rotated 90°; scale 100 μm. 63. Same, lateral view; scale 100 μm. Abbreviations: Cl, male clasper; Pe, peg-plate; Pg, pygophore (segment 9) of male; S7, abdominal sternum 7 of female; Th, thorn-like outgrowth.

upon the water surface of the shallow pools around or beneath the blocks. By turning 0.5-1 m blocks upside down, groups of 10-40 individuals were found sitting in holes on the subsurface of the block (Fig. 66). Such holes are made by several species of boring bivalves (Mollusca) which infest *Porites*-corals rather heavily in the area (Nielsen 1976, 1986). The sizes of the holes (Fig. 67) varied between 0.5 and 2 cm in diameter and 2-5 cm in depth.

One particular block was kept under observation during most of the study period (Fig. 66). The number of bugs found in one hole (diameter 1.5 cm, depth 3 cm) varied between 10 and 40, even at lowest tide. At the end of the period, this particular hole was flushed with 70% alcohol and its content was analysed. Most living bugs had left the hole, but there was still 5 live nymphs (3rd-5th instar). However, the inner surface of the hole was covered by numerous exuviae (c. 60, counting only the head capsules). There were also live nymphs and exuviae of a *Hermatobates*-species.

Although the coral blocks were not inspected when completely submerged, the bugs were found in their holes in blocks half covered with water by the receding tide (Fig. 65). There is therefore no doubt that both adults and nymphs of *H. malaya* retreat to cavities and holes in these blocks and stay submerged during high tide, covered by 1-2 m of sea water. My observations also indicate that at least some of the bugs stay in their hole during low tide, while others leave the hole but stay close to the block. However, movements by both adults and nymphs away from the coral block were frequently observed. It was not possible to determine how many of the bugs resting in the hole were more or less permanent "residents", i.e. retreated to the same hole during successive high tides.

Kellen (1959: 55-56) made similar observations for *H. bergrothi* in Samoa. At high tide the bugs were concealed in small air pockets trapped in the holes of submerged volcanic rocks and were never found swimming on the water. In the laboratory, conditions created by ebbing tides were simulated by slowly submerging rocks with veliids resting in their holes. The bugs were immediately encapsulated in air bubbles and made no attempt to escape. When the tide began to wane and parts of the rocks holding veliids became exposed, the insects freed themselves from the air pockets and began to move around on the water. As the receding tide continued to wane, however, leaving rocks in the tidal zone completely exposed on a mud flat, the veliids left the water and once again crawled into the holes of the rocks. A second period of activity was produced by the raising tide when the rocks were again about half submerged. According to Kellen's observations, the coral bugs only have four relatively short periods of activity (about 6 hours out of every 24 hours) dictated by the tidal cycle.

When submerged into water, both adults and nymphs of *Halovelia* are surrounded by a distinct, silverish layer of air. The cuticular surface of these bugs have structures which probably are adaptations associated with life in a moist environment as well as regular submergence in the tidal environment. These structures are disclosed on scanning photomicrographs (Figs. 58-61) and were described and compared with similar structures in other semiaquatic bugs by Andersen (1977). Most conspicuous is the layer of macro-hairs covering almost all parts of the body at densities of 10.000-15.000/mm². Each hair is 30-40 μm long, inserted in a socket in the cuticular surface. Closer to the body surface is a dense layer of minute cuticular outgrowths (microtrichia). These are simple pegs, 0.5-1 μm long, found at densities of 30-40 x 10^5/mm².

Locomotion

Kellen (1959: 56 and 60) gave a fine account on the locomotory behaviour of *H. bergrothi*. My observations on *H. malaya* concur with Kellen's. Coral bugs move about in different ways depending upon the substrate. On the water surface, they move by simultaneous strokes of the middle legs. Each stroke brings the insects forward for 0.5-2 cm's distance in a jerky although very fast progression over the water surface. In those veliids, (e.g. *Velia*-species) which also move by simultaneous strokes of their middle legs (termed "rowing"), the movement on the water surface usually seems more smooth. In their way of locomotion, coral bugs resemble the true waterstriders, the Gerridae, which perform jump-and-slide movements on the water surface (Andersen 1976, 1982). Both adults and nymphs of *Halovelia* are also capable of moving very fast upon solid substrates, like sand, pebbles, or the surface of a rock or piece of coral. Usually the three pairs of legs are used for walking or running, the long middle legs being used with the same dexterity as the much shorter fore and hind legs. Occasionally, however, when moving short distances, the bug folds the middle legs close to the body and only the fore and hind legs are used. These veliids are also

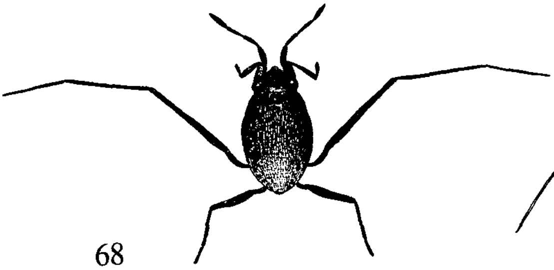
Figs. 64-67. Photographs of habitats of *Halovelia malaya* Esaki, Phuket Island, Thailand, taken by the author. 64. Intertidal reef flat south of the PMBC-pier at lowest tide. 65. Same area about two hours before low tide with emerging coral blocks. 66. Block of dead *Porites*-coral turned upside down. Note sea cucumber. 67. Holes made by boring bivalves on surface of coral block; scale 2 cm.

able to jump or leap for distances of several cm's. The middle legs are used for this kind of movement. Again, this is a very gerrid-like behaviour whereas jumping has never been observed in other veliids.

The locomotory behaviour of *H. malaya* was studied in various parts of the intertidal reef area described above. On the surface of tidal pools, each individual was seen moving about in a very characteristic, angular pattern. Although being in almost constant motion, the movements were usually confined to a limited area of surface. When the bug was close to the edge of the pool, the size of this area was small, while an individual moving about in the middle of the pool covered a much larger area. The locomotory behaviour of each individual thus seems to be determined by the features of the immediate surroundings.

Observations of *H. malaya* on the mid-reef flat strewn with blocks of dead coral indicated, that both adults and nymphs may disperse widely during low tide, by running and jumping over the flat of mud, sand, and pebbles. Although the bugs move towards the light in the laboratory, they were often seen to seek shelter in dark places in the field.

Like other marine gerromorphans, *Halovelia*-species are attracted to a light source during night. Dr L. Cheng has with great success used artificial light to attract and collect these insects in many localities.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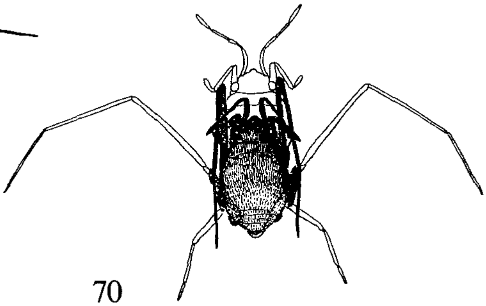
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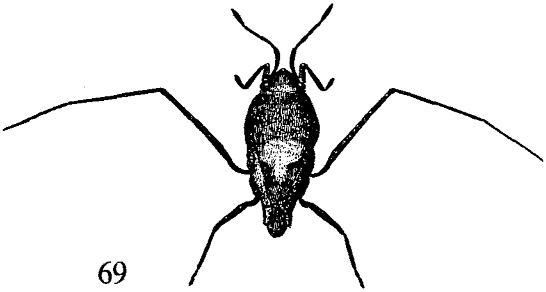
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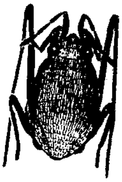
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Figs. 68-71. *Halovelia malaya* Esaki drawn from field sketches and photographs. 68. Male on water surface. 69. Female on water surface. 70. Copulating pair; female shown white, male black. 71. Male in resting posture.

Feeding

Coral bugs are predators or scavengers. Several instances of feeding were observed in *H. malaya.* In one case, an adult female was seen feeding on a black-blue springtail (*Anurida* sp., Collembola). The prey was pierced by the mouthpart stylets and carried on the tip of the rostrum. Potential prey were mites (Acari) and springtails which were abundant on the beach rocks as well as on the irregular surface of coral blocks. Other bugs were seen feeding upon a dead *Halobates hyanus* B. White and an exuvia of a *Hermatobates* sp. (fourth instar). *Halovelia* probably also feeds upon various small dipterans which were abundant on the intertidal reef. Land insects blown out onto the reef may also form an essential part of their diet. Kellen (1959: 60) found *H. bergrothi* attacking leafhoppers washed from grass growing on shore and fed a laboratory colony with grasshopper nymphs. According to Esaki (1924: 33) the bulk of the food of *H. septentrionalis* was small planctonic crustaceans.

The locomotory behaviour described above may be part of the feeding behaviour of coral bugs. When the bugs moved about on the surface of tidal pools in their characteristic, angular patterns, they were seen to stop from time to time, examining various floating objects in search for prey.

Sexual behaviour

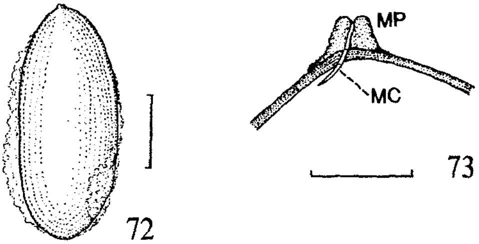
Copulation in *H. malaya* was observed very frequently during the study period. In a copulating pair, the male rides on the back of the female, resting in the depression on her posterior thorax and abdomen, grasping her thorax with his fore and hind legs. The grasping combs of the fore tibiae (see Andersen 1989: figs. 5, 9) probably have the function of securing a firm grip. Like in many other semiaquatic bugs, the actual act of copulation and sperm transfer probably only takes short time but the male stays on the back of the female for a much longer time. During that period, the male fights off other males attempting to copulate with the female thereby increasing the chance that his sperm cells fertilize the eggs. Copulating females were noticeably slower in their movements than single females. They may therefore be more exposed to predation. However, although some females were seen resisting the mounting attempts of males, most females observed in the study area were taken by a male.

Although males of *H. malaya* seem very persistent in their copulatory behaviour, they appear not to be physically attached to the female with any part of their genital apparatus during most of the sexual act. When caught by a net, copulating pairs usually separated after a while. In *H. bergrothi* and other species of the *bergrothi*-group, males riding on the back of females are always genitally attached (Fig. 62). Close examination shows that one of the very long claspers is hooked into the opening between the first gonocoxae of the female (Fig. 63). The pairs usually remain united even when captured and killed in alcohol. Kellen (1959: 60) found only a few males riding females unattached genitally. In these instances the male always occupied a more anterior position on the back of the female.

The various modifications of the female thorax and abdomen described and illustrated in the taxonomical parts of the present work are most certainly adaptations associated with the kind of sexual behaviour described above. Similar structural adaptations are found in a number of veliids (see Andersen 1982 for a review).

Oviposition

The author did not succeed in finding deposited eggs of *H. malaya* in the study area in Phuket. It was predicted, however, that females oviposit in the same cavities and holes where they rest during high tide (see above). Dr Claus Nielsen, Zoological Museum, University of Copenhagen, has presented me with a small piece of *Porites*-coral chopped off a larger block in the study area. This piece has a hole, presumably made by a boring bivalve. In the bottom of the hole there are 10 eggs of the same size as ripe ovarian eggs of *H. malaya*. The eggs are scattered over the surface area of the hole (c. 1.2 x 1 cm), only three eggs are deposited close together. Most are empty egg-shells with a longitudinal eclosion split. Others have an almost circular opening in one end which may be caused by egg predators (small crabs?). One developing egg is present (Fig. 72), 0.64 mm long and 0.30 mm wide, in which the very characteristic micropylar projection can be observed. Thus, there is no doubt that these eggs were deposited by a *Halovelia*-species. The eggs are deposited lengthwise and probably glued to the substrate like eggs of other veliids (Andersen 1982: fig. 6). In the same piece of coral there is a group of eggs deposited by a *Hermatobates* species. These are larger and placed in an upright position (op.cit., p. 241).



Figs. 72-73. Egg structure of *Halovelia malaya* Esaki. 72. Deposited egg; scale 200 µm. 73. Optical section of micropylar region of ripe ovarian egg; scale 50 µm. Abbreviations: MC, micropylar canal; MP, micropylar projection.

In the laboratory, Kellen (1959: 61) kept adult *H. bergrothi* alive for several months. During that period, eggs were found deposited singly in small holes in pieces of volcanic rocks, usually about half an inch above the water surface, where they were kept moist by water absorbed by the porous surface of the rock.

Andersen (1982: 137, fig. 240) described and illustrated the structure of the ripe ovarian egg of a *Halovelia*-species. The micropylar projection terminates in four minute lips. In contrast to other veliids (except *Trochopus*, another marine group), there is only one micropyle with a transverse canal which run parallel to the inner surface of the shell for a short distance. The shell surface has a fine, hexagonal sculpturation. The same structure of micropylar projection and micropyle is found in *H. malaya* (Fig. 72) but the shell surface has a fine, tuberculate sculpturation.

Miyamoto (1957: 78) recorded only two ovarioles in each ovarium of female *H. septentrionalis* Esaki while he found four ovarioles in *Strongylovelia formosa* Esaki, the usual number for the Veliidae. The eggs of *Halovelia malaya* are large (0.6-0.7 mm) compared to the female body length (2.3-2.6 mm). Only 6-8 ripe eggs were dissected from mature females and the eggs occupied almost all available space in their thorax and abdomen. Like other small gerromorphan bugs, *Halovelia*-females probably deposit their eggs more or less continuously (Andersen 1982: 318).

Development

Kellen (1959: 61-62) gave a detailed account of the development in *Halovelia bergrothi* Esaki. The incubation period of the eggs was estimated to 18 days

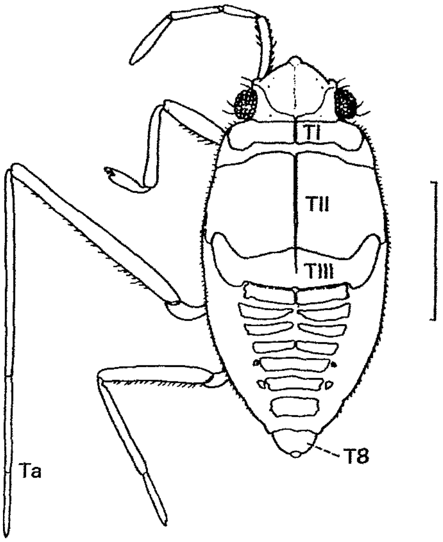


Fig. 74. *Halovelia malaya* Esaki, female fifth instar nymph; scale 1 mm. Abbreviations: TI, TII, TIII, pro-, meso-, and metanotum; T8, abdominal tergum 8; Ta two-segmented middle tarsus.

at 25° C. The prolarva has a median, pointed egg-burster which is used during eclosion to perforate the egg shell along half the length, resulting in a narrow split through which the nymph escapes. Several nymphs were reared to the adult stage. At an average ambient temperature of 25° C the duration of each of the five instars was as follows (average number of days): first instar 7.8; second instar 6.5; third instar 6.4; fourth instar 7.3; and fifth instar 11.4. The nymphs always moulted while resting on the sides of pieces of rocks immediately above the water surface. Kellen describes the moulting process which lasts about half an hour. Newly emerged adults generally remain resting until the adult colour is obtained after about two and a half hours. Kellen illustrates (op. cit., fig. 5) and gives detailed measurements of all of the five nymphal instars of *H. bergrothi*. The growth rates for the femur and tibia of middle legs are larger than the growth rates for head, antennae, and rostrum.

Based upon my observations of *H. malaya*, I can confirm the presence of five nymphal instars (fifth instar female nymph illustrated, Fig. 74). The accumulation of exuviae belonging to several instars (see above) inside the holes in coral blocks, indicates that the nymphs tend to moult while resting in these holes, probably in between tides.

BIOGEOGRAPHY

Distribution of the species of *Halovelia*

The maps in Figs. 75-80 show the distributions of each of the 30 species of *Halovelia*. The total distribution of the genus can be characterized as Indo-West Pacific. In the direction from west to east the coral bugs range from the Red Sea and East African coast to the West Pacific islands as far as the Samoan Islands. In the direction from north to south they range from Japan to southwestern Australia, between the latitudes of about 35° N and 35° S.

Although more than 4.000 specimens have been examined from about 120 localities, there is still shortage of material from many areas of the Indo-Pacific. Marine water striders have been inadequately collected, e.g., in Vanuatu (New Hebrides), Irian New Guinea, Moluccas, Caroline Islands, northern Australia, Lesser Sunda Islands, Java, Sumatra, Gulf of Siam, East Asia, in the Red Sea, and along the coasts of Burma and India. New distributional records and perhaps even new species may turn up in future collections from these and other places.

Most species of *Halovelia* distributed along the continents and islands bordering the Indian Ocean belong to the *malaya*-group of species. *H. malaya* itself is confined to the west coast of the Malayan Peninsula while *nicobarensis* is known only from the Nicobar Islands (see map, Fig. 78). *H. convexa* is endemic to the Maldives and *mauricensis* to the island of Mauritius (map, Fig. 79). *H. seychellensis* is found both on the Seychelles and Madagascar (see map, Fig. 80). *H. poissoni* occurs along the east coast of Kenya and Tanzania, while *pauliani* is only known from the small Ile Europa in the Mozambique Channel between Africa and Madagascar. *H. depressa* is probably restricted to Madagascar. The only species belonging to the *malaya*-group which occur east of the Malacca Strait are *abdominalis* (southeastern coast of the Malayan Peninsula and Java) and *sulawesi* (Sulawesi) (map, Fig. 78).

H. annemariae is known from northeastern New Guinea and the Solomon Islands (see map, Fig. 77). *H. lannae* occurs at the coast of Singapore and adjacent Malayan Peninsula, Java, North Borneo, and the southern Philippines (Palawan and Mindanao). The closely related *wallacei* is known from the Lesser Sunda Islands (Sumbawa) and northeastern Sulawesi.

In the *esakii*-group, the most widely distributed species is *esakii* itself (map, Fig. 76), occurring from

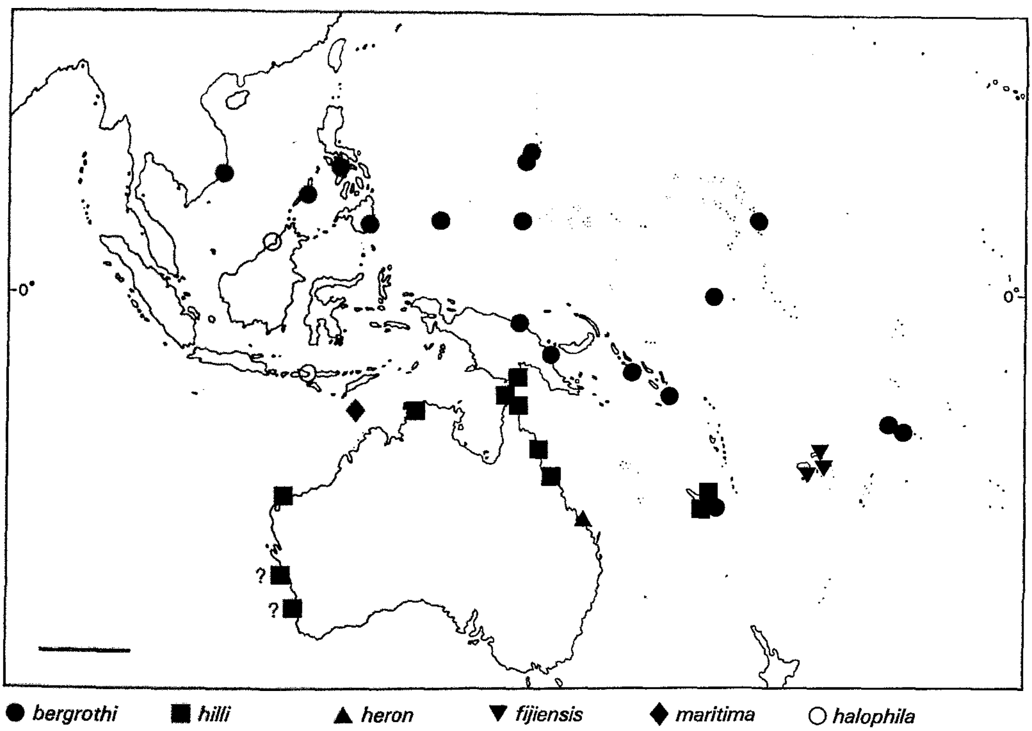


Fig. 75. Distribution of *Halovelia* spp. in the Indo-Australian and West Pacific areas. Scale of map 1,000 km.

the Philippines, Sulawesi, and Sumbawa in north and west, through the Palau Islands and Biak (northern Irian), to the Solomon Islands. The related *polhemi* occurs in northern Australia. *H. solomon* is only known from San Cristobal in the Solomon Islands (map, Fig. 77). The other species belonging to this group are *novoguinensis* from southeastern New Guinea, *fosteri* from Viti Levu, and *tongaensis* from Tongatabu. The last two species are probably endemic to the Fiji and Tonga Islands, respectively (map, Fig. 76).

The *bergrothi*-group has the widest distributional range of all species-groups. *H. inflexa* is so far the only species of coral bugs recorded from the Red Sea (map, Fig. 79). *H. septentrionalis* has the northernmost distribution (see map, Fig. 78), occurring along the coasts of Honshu, the islands South of Japan (South West Islands and Ryukyu Islands), and Taiwan. *H. bergrothi* is the most widely distributed species of the genus (see map, Fig. 75). It has been recorded from the east coast of the Asian continent (Vietnam), the Philippines, the islands of Micronesia (Mariana Islands, Caroline Islands, Marshall Islands, Nauru Island), northern coast of New Guinea, the Solomon Islands, and the Samoan Islands. A single specimen is also present from New Caledonia. *H. hilli* occurs on the southeastern coast of New Guinea and along the coast of adjacent northern Queensland, as far south as 20° S (Townsville). It is recorded from New Caledonia (incl. the Loyalty Islands) and probably also occurs on the atolls of the Coral Sea. The same species is found along the coast of Northern Territory and Western Australia, probably as far south as 35° S (Perth). The related *heron* has only been found on Heron and Bedara Island, Southern Queensland. Finally, *fijiensis* is known from several islands in the Fijis.

The species of *Halovelia* not assigned to any monophyletic species-group are scattered throughout the whole distributional range of the genus. *H. maritima* has only been found on the small Cartier Island between Australia and Timor (map, Fig. 75). *H. carolinensis* is only known from a few specimens from the Caroline Islands and perhaps from the

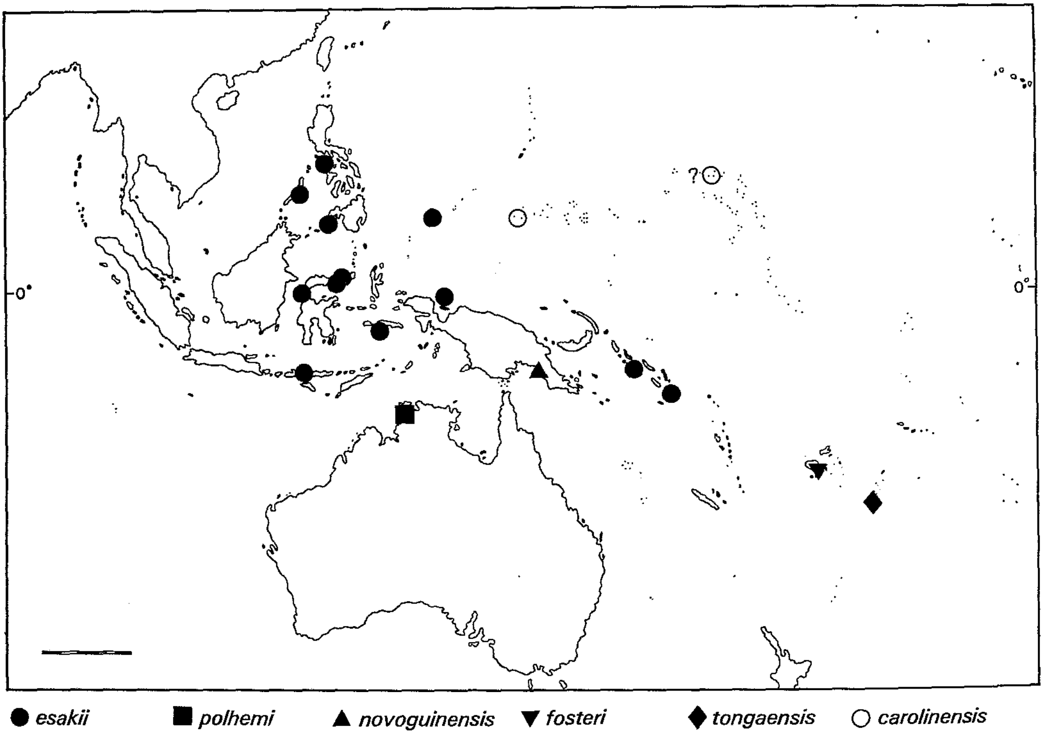


Fig. 76. Distribution of *Halovelia* spp. in the Indo-Australian and West Pacific areas. Scale of map 1,000 km.

Marshall Islands (map, Fig. 76). *H. halophila* occurs at Sumbawa and Sabah, North Borneo (map, Fig. 75). *H. corallia* is known from both sides of the Torres Strait, in southeastern New Guinea and the Cape York Peninsula (map, Fig. 77). Finally, *amphibia* is recorded from Zanzibar and northern Madagascar (map, Fig. 79).

Historic biogeography

During the past decade there has been a growing recognition of the importance of hierarchic patterns of relationships among geographical areas instead of similarity relations in studies of the historic biogeography of animals and plants. The methods designed to disclose these hierarchic patterns are the core of *cladistic* (or *vicariance*) *biogeography*, an approach which has been outlined, e.g., in the books by Nelson & Platnick (1981) and Humphries & Parenti (1986). What is needed to apply these methods are: 1) monophyletic groups whose included species have restricted distributions, and 2) cladistic analyses for these groups that resolve the interrelationships of the included species at the level of which they are endemic (Schuh & Stonedahl 1986).

Based upon cladograms of relationships between species we can construct taxon-area cladograms of supposed relationships between geographical areas. From congruent cladograms for various unrelated groups we can derive a biogeographical pattern. Historic biogeographical analysis constitutes the search for such patterns. It follows from this approach, that geological hypotheses of area relationships are no more or less reliable than area cladograms derived from biological data.

The cladistic relationships between the species of *Halovelia* have been analysed and discussed earlier in this paper. The preferred cladogram (Figs. 48 and 49) depicts a number of monophyletic species groups. A taxon-area cladogram is obtained by substitution of the species names in the cladogram of relationships between species with the names of the

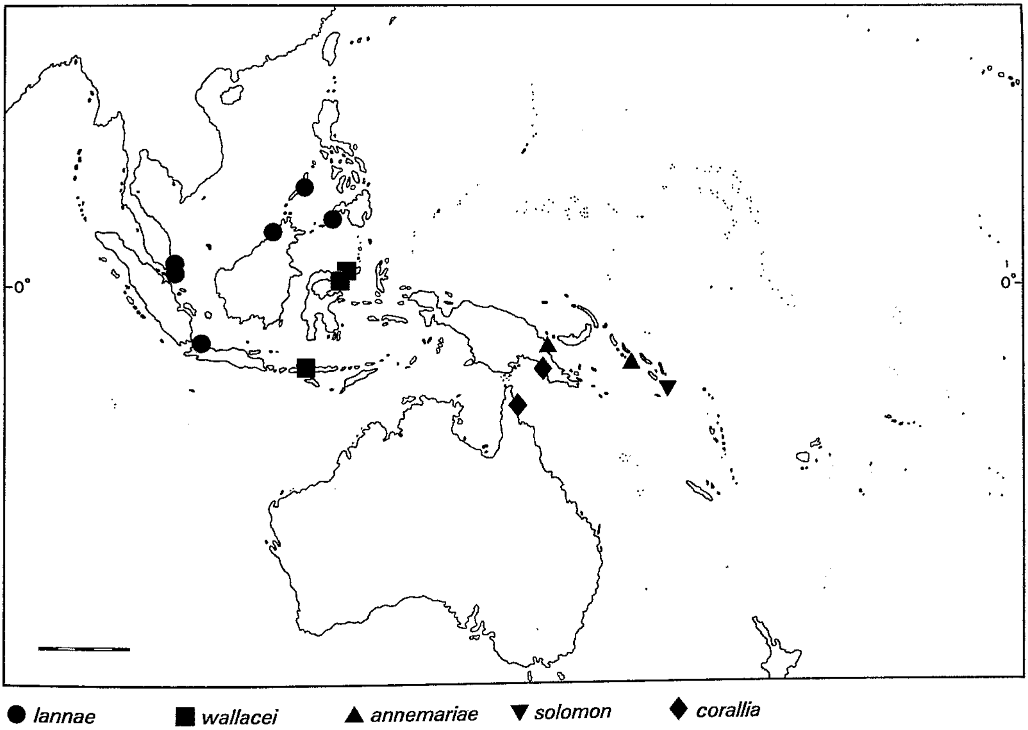


Fig. 77. Distribution of *Halovelia* spp. in the Indo-Australian and West Pacific areas. Scale of map 1,000 km.

geographical areas occupied by these species. The relationships between the different areas inhabited by the *Halovelia*-species were analysed by way of two methods, *component analysis* and *parsimony analysis*. The results of these analyses are the basis of a discussion of the biogeographical history of the genus *Halovelia*, followed by comparisons with the biogeography of other marine Haloveliinae, the marine Gerridae of the Indo-Pacific, and other groups of animals inhabiting the Indo-Pacific region.

Component analysis

For analytical purposes, the following groups of *Halovelia* were treated separately: 1) *malaya*-group + *annemariae* + *lannae*-group; 2) *esakii*-group; and 3) *bergrothi*-group. Although these groups are closely related to each other (probably in the way presented in the cladogram, Fig. 48), each monophyletic group has a unique history of evolution which justifies that the historical biogeography of each group is analysed separately.

The recorded distributions of the *Halovelia*-species as depicted in the taxon-area cladograms (Figs. 81-83) has been reduced to a limited number of areas occupied by a monophyletic species-group or a single species found nowhere else (areas of endemism). These areas are listed in Table 2. For the matter of simplification, the distributions of species of the *malaya*-group occurring in the Indian Ocean including East Africa are combined (as area 1). N. Borneo is combined with the Philippines (as area 5) because the only species recorded from N. Borneo, *H. lannae*, also occurs in the Philippines. Sumbawa and the Moluccas have no endemics and are joined with Sulawesi (as area 6). New Caledonia is joined with Queensland (area 13) for the same reason. The areas considered for the widespread species *H. bergrothi* were also limited for practical reasons (see discussion below). The simplified taxon-area cladograms are shown in Figs. 84, 86, and 89.

Even with the above-mentioned modifications the taxon-area cladograms show several cases of redundancy, i.e., areas appearing on more than one

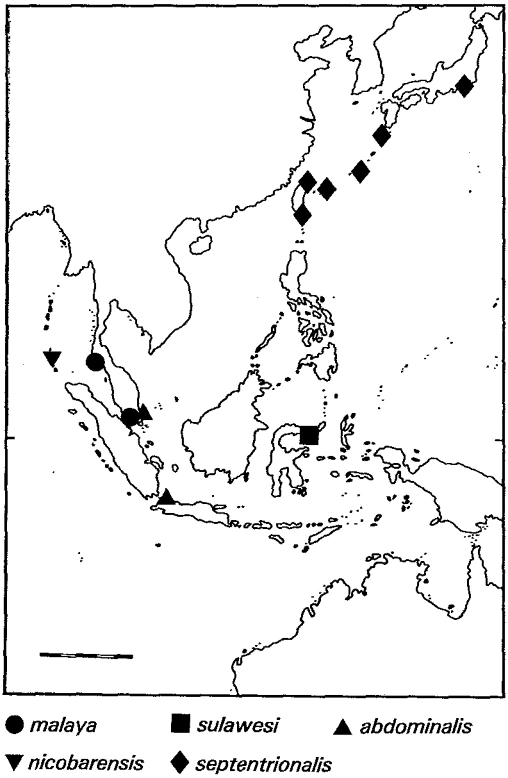


Fig. 78. Distribution of *Halovelia* spp. in East and Southeast Asia. Scale of map 1,000 km.

terminal branch. The three groups of *Halovelia* have only partly overlapping distributional ranges. There are therefore several of the areas of endemisms (Table 2) which are missing from each of the taxon-area cladograms (Figs. 81-84, 86, and 89). Finally, several species of *Halovelia* are widespread, i.e., they occur in more than one area, either because of dispersal or failure to respond (e.g., by speciation) to a vicariance event. Such problems may cause incongruence between different area cladograms and are dealt with under different assumptions in biogeographical component analyses (Nelson & Platnick 1981; Humphries & Parenti 1986).

A reduced area cladogram was constructed from each of the taxon-area cladograms of the three groups of *Halovelia*. In the combined cladogram for the *malaya*-group, *annemariae*, and the *lannae*-group (Fig. 84), area 1 represents most of the *malaya*-group occurring in the Indian Ocean. The taxonomical relationships of *H. depressa* (from Madagascar) are problematical (see section on cladistics of species). It is therefore omitted from the analysis. Since no other species-group occurs in the Indian Ocean, the relationships between the different areas are determined by the taxon-area cladogram for the *malaya*-group (Fig. 81).

The area cladogram for the *malaya*-group, etc., (Fig. 84) contains one trifurcation caused by the unresolved relationships between *abdominalis* (area 4) and *sulawesi* (area 6). Both areas are found in two positions in the cladogram. Redundant information like this is dealt with by considering each case of occurrence separately. This results in two basically different sets of reduced area cladograms, one set with areas 4 and 6 placed as the first branch (Fig. 85a), the other set with these areas placed after the branch terminated by areas 7 and 8 (Fig. 85b).

Two branches of the cladogram (Fig. 84) are terminated by more than one area. In a component analysis widespread species can be treated under

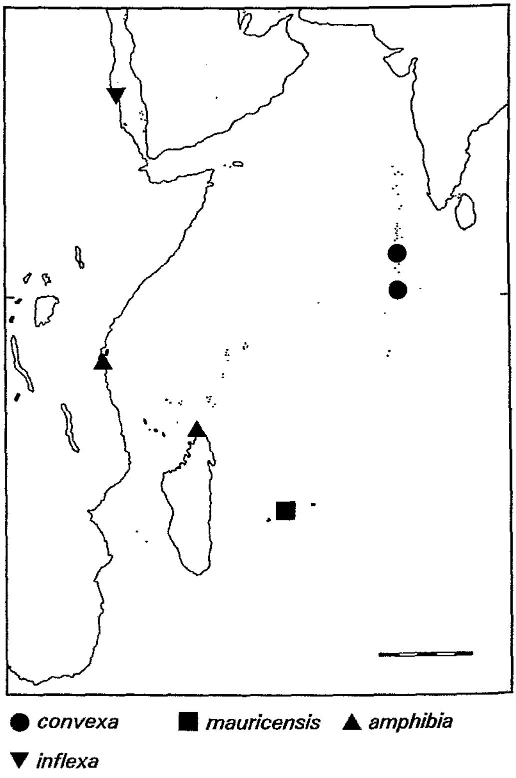


Fig. 79. Distribution of *Halovelia* spp. in East Africa and Indian Ocean. Scale of map 1,000 km.

Table 2. Areas of endemism considered in the biogeographical component analysis for *Halovelia* (see text) with the distribution of species-groups. Area numbers used in Figs. 84-91.

No. Area	Species-groups of *Halovelia*			
	malaya	*esakii*	*bergrothi*	others
1. Indian Ocean	x	-	-	*amphibia*
2. W Malayan Pen.	x	-	-	-
3. Nicobar Is.	x	-	-	-
4. SE Malaya & Java	x	-	-	-
5. N Borneo & Philippines	x	-	-	*halophila*
6. Sulawesi, Moluccas & Lesser Sunda Is.	x	x	-	*halophila*
7. N New Guinea	x	x	x	-
8. Solomon Is.	x	x	x	-
9. SE New Guinea	-	x	x	*corallia*
10. Fiji Is.	-	x	x	-
11. Tonga Is.	-	x	-	-
12. N & W Australia	-	x	x	*maritima*
13. Queensland & New Caledonia	-	-	x	*corallia*
14. East Asia	-	-	x	-
15. Red Sea	-	-	x	-
16. West Pacific	-	-	x	*carolinensis*

two assumptions. Under *assumption 1* all areas occupied by the species are taken as historically related, i.e., representing the true ancestral area of the species. *H. lannae* is found in Java (area 4), N. Borneo, and the Philippines (area 5). This may well represent the true ancestral area of the species. Besides, as discussed in the taxonomical section of this work, there are indications of an incipient differentiation between the populations in SE Malaya, Singapore, and Java on one hand and those in N Borneo and the Philippines on the other hand. Future investigations may show that there are two, closely related species in the area. The same line of argumentation can be applied to the distributions of *H. annemariae* in N New Guinea (area 7) and the Solomon Islands (area 8).

As the result of the component analysis, the reduced area cladogram for the *malaya*-group, *annemariae*, and the *lannae*-group (Fig. 85) contains one quadrifurcation (areas 4, 5, 6, and the rest) and one trifurcation (areas 7, 8, and the rest). With the two alternative positions of these multifurcations (see above), there are a number of equally possible area cladograms derived from the distribution of the species of these groups.

The taxon-area cladogram for the *esakii*-group (Fig. 86) contains one widespread species, *H. esakii*, which is recorded from the areas 5, 6, 7, and 8. In a component analysis, widespread species can also be treated under *assumption 2*. Here the areas

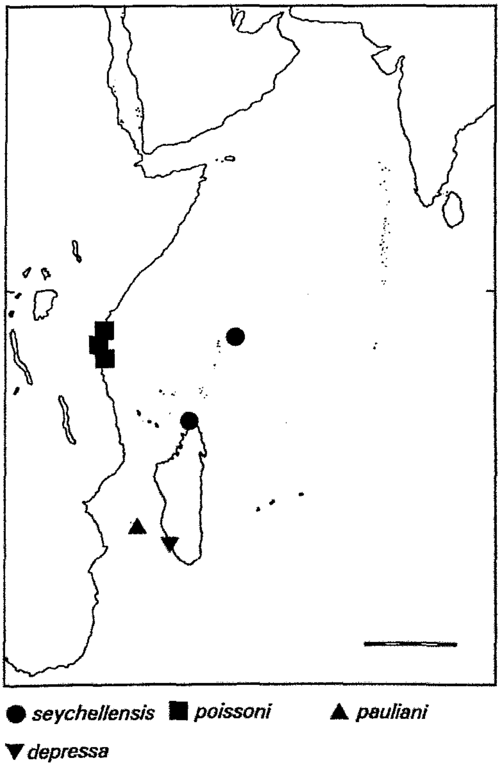


Fig. 80. Distribution of *Halovelia* spp. in East Africa and Indian Ocean. Scale of map 1,000 km.

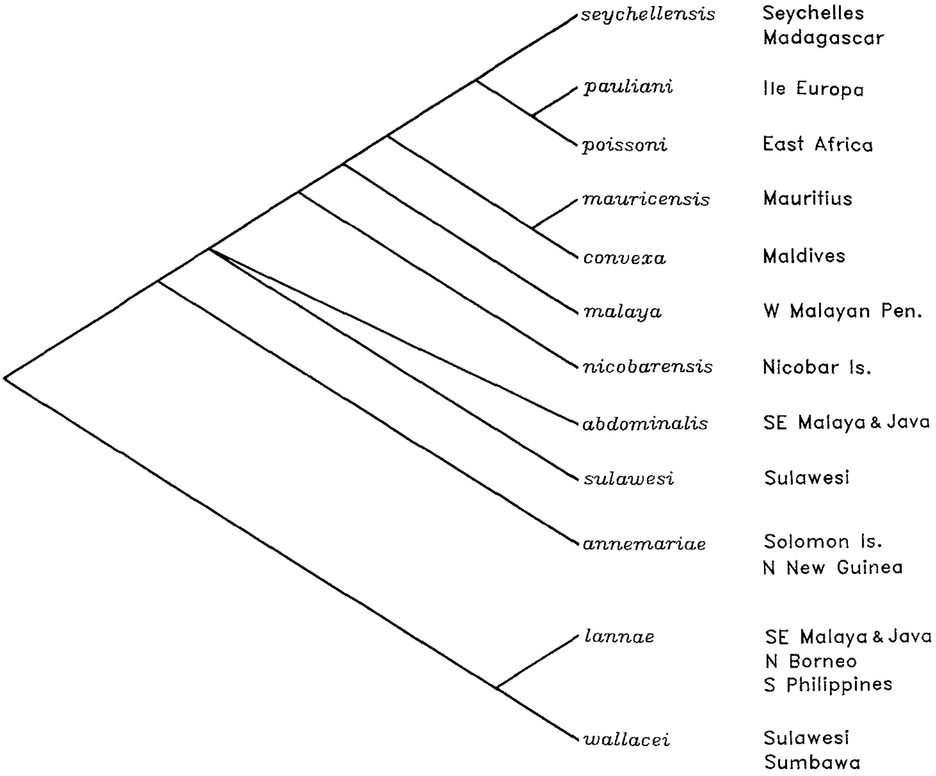


Fig. 81. Cladogram for the *Halovelia malaya*-group (except *depressa* sp.n.), *H. annemariae* Andersen, and the *H. lannae*-group with distribution of species. Further explanation in text.

occupied by a widespread species are not à priori judged as closely related to each other and all except one area are allowed to "float" in the cladogram, i.e., take any position on the branches of the area cladogram. In the reduced area cladogram (Fig. 87), the widespread occurrence of *esakii* results in a multifurcation between the areas 5, 6, 7, 8, and 12. The taxonomical relationships of *H. solomon* (from the Solomons) are problematical and it is therefore not considered in the analysis. The relationships between the areas 9, 10, and 11 are retained in the reduced area cladogram (Fig. 87).

The taxon-area cladogram for the *bergrothi*-group (Fig. 89) contains two widespread species, *H. hilli* and *bergrothi*. The latter is the most widely distributed species of *Halovelia* and its occurrence along many islands of the West Pacific suggests that its present distribution probably is the result of dispersal rather than vicariance. Both widespread species of this group are treated under assumption 2 and the relationships between the areas 5, 7, 8, 9, 10, and 12 are left unresolved in the area cladogram (Fig. 90). Of the two occurrences of area 13, the endemic one (*H. heron*) is preferred. The relationships of areas 14 and 15 are also preserved.

The next step in the component analysis was to combine the reduced area cladograms for different groups in order to achieve more general hypotheses for the areas considered. The three groups of *Halovelia* analysed above have only partly overlapping distributional ranges. There are therefore several areas (Table 2) missing from one or the other of the area cladograms (Figs. 85, 87, and 90). In a component analysis, each missing area can be added to the area cladogram by inserting it in one of all possible positions on the branches of the cladogram. For example, Java (area 4) is missing from the area cladogram for the *esakii*-group (Fig. 87). Java can therefore be inserted in any position on the cladogram, including that next to the Philippines

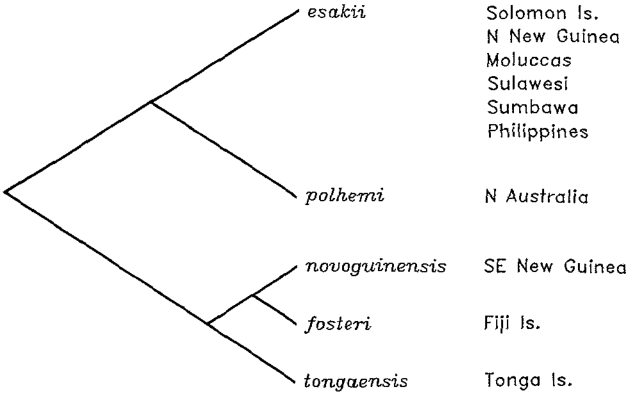


Fig. 82. Cladogram for the *Halovelia esakii*-group (except *solomon* Andersen) with distribution of species. Further explanation in text.

(area 5) or Sulawesi (area 6), which results in partial congruence with one of the cladograms for the *malaya*-group, etc. (Figs. 85a and b).

First, each of the two area cladograms for the *malaya*-group, *annemariae*, and the *lannae*-group (Figs. 85a and b) was combined with the cladogram for the *esakii*-group (Fig. 87). Under assumption 2 the numerous unresolved area relationships for the *esakii*-group cannot be incongruent with the relationships shown by the less widely distributed or endemic species of the *malaya*-group, etc. However, since the relationships between areas 5 and 6 on one hand and areas 7 and 8 on the other hand also are unresolved in Fig. 87, the relationships between these areas remain unresolved. Neither of the two alternative cladograms for the *malaya*-group, etc. (Figs. 85a and b) can be preferred on basis of the relationships shown by the *esakii*-group. There are therefore two alternative summary cladograms of which only one is shown (Fig. 88). The relationships between areas 1-3 are preserved, area 12 is added, whereas areas 9-11 are placed as the first branch of the summary cladogram (Fig. 88).

The same line of argumentation applies when the reduced area cladogram of the *bergrothi*-group (Fig. 90) is combined with the cladogram in Fig. 88. The unresolved area relationships of the former caused by the widespread species do not improve the resolution of the summary cladogram (Fig. 91). Only areas 13-15 are added to the cladogram because they contain endemic species of the *bergrothi*-group. The occurrence of area 10 (the Fiji Islands) is redundant, but since the position of this area in relation to most other areas is unresolved, it cannot be incongruent with the position of area 10 in Fig. 88. Also area 12 shows redundancy, but since the relationships of this area is unresolved for the *bergrothi*-group, its relative position is preserved in the summary cladogram (Fig. 91).

So far, only the taxon-area relationships of the *malaya*-group, *annemariae*, *lannae*-group, *esakii*-group, and the *bergrothi*-group have been considered. The area relationships shown by the remaining species of *Halovelia* (see maps, Figs. 75-80, and Table 1) cannot be analysed since these species do not form monophyletic groups which can be compared with the species-groups analysed above. The only area components suggested for these species are 1) East Africa (*amphibia*) + West Pacific (*carolinensis*), 2) Lesser Sunda Is. + N Borneo (*halophila*), and 3) SE New Guinea + N. Queensland (*corallia*). Only the last component is shared by any other species-group of *Halovelia*.

Parsimony analysis

An alternative analytical method for historical biogeography based upon the principle of parsimony has recently been proposed (Wiley 1988, 1989). Parsimony analysis of area relationships assumes that valid analogies exist between cladistic methods for reconstructing phylogenetic relationships and methods for reconstructing area relationships. The "taxa" of the analysis are the areas of endemism pertinent to the study group. The "characters" are the presence/absence of terminal taxa (species) in

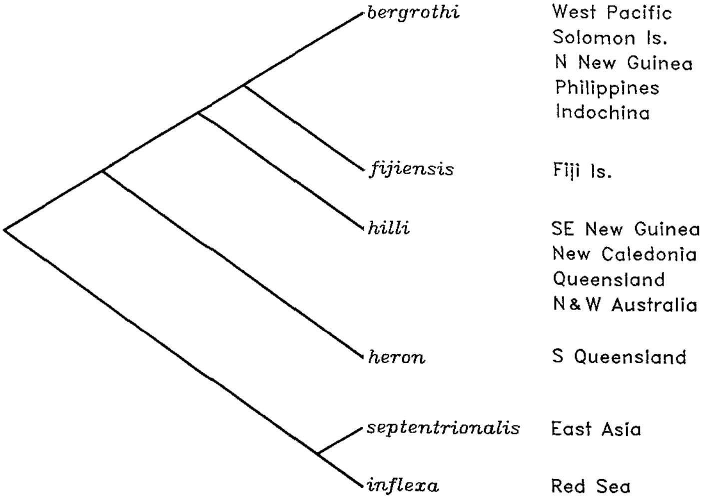


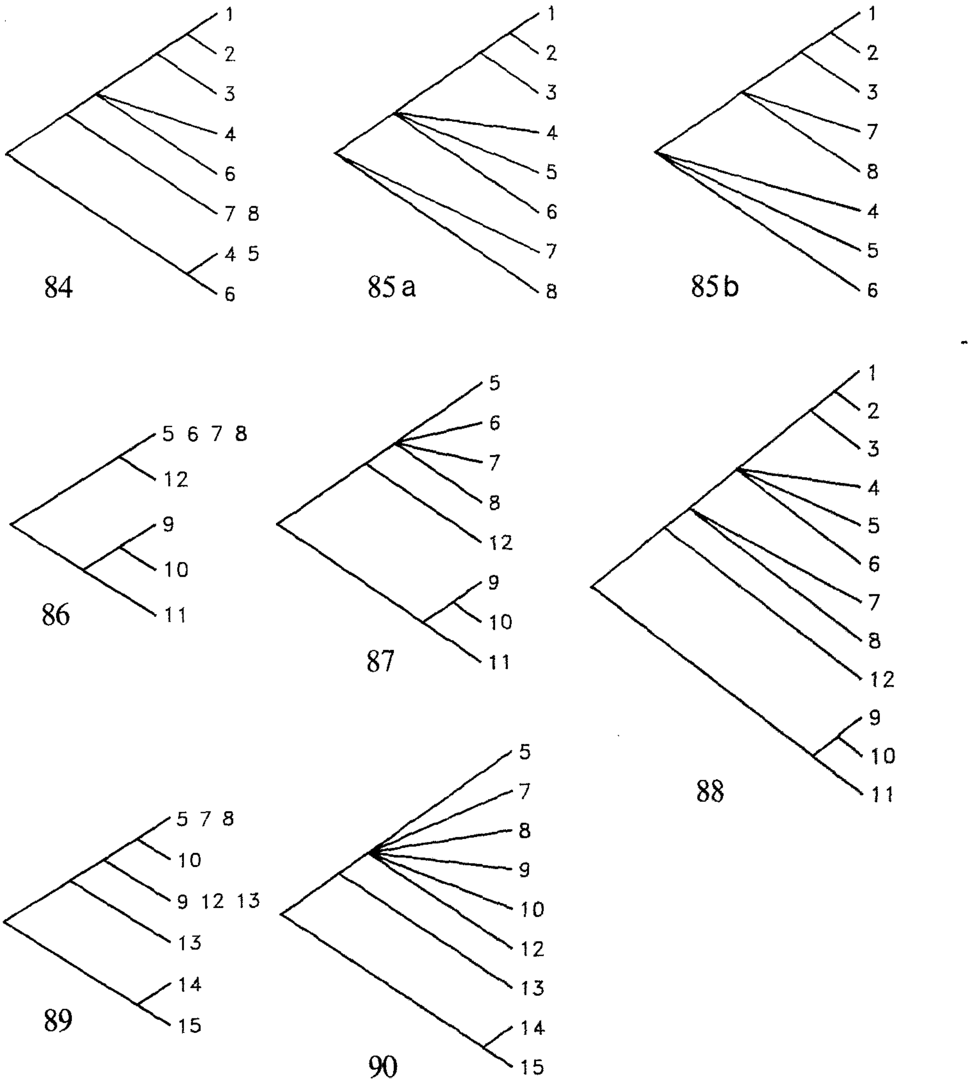
Fig. 83. Cladogram for the *Halovelia bergrothi*-group with distribution of species. Further explanation in text.

these areas as well as the inferred distributions of the hypothetical ancestors in the cladogram of relationships between these species.

The parsimony analysis uses a matrix produced by binary coding. An assumption termed *assumption 0* is used to code the data. It states (Wiley 1988: 529) "that the best estimate of ancestral distributions for any particular group resides in the original phylogeny of that group and the known distributions of members of the group." There are, however, problems involved in this kind of coding. Missing areas, for instance, could be coded either as "absent" or "unknown". The first option implies some knowledge since it is assumed that the taxon is truly missing from the area (this may be justified for terminal taxa but not for ancestors). The second option results in a code that is neutral and should be preferred. The areas occupied by widespread species are coded as "synapomorphies" of areas. This is a major point of difference between the parsimony and component methods.

Using the coding methods outlined above area x taxon matrices were generated for the groups of *Halovelia*-species mentioned above. Terminal species, including widespread ones, were coded as "1" for the areas where they occur, and as "0" for all other areas. Each hypothetical ancestor was coded as "1" for those areas where its descendants occur, and as "9" (the usual convention for missing data in PAUP) for all other areas. In order to root the trees, an ancestral vector of zero values was included in the matrix. The resulting matrices were analysed with PAUP, with the DELTRAN option as recommended by Wiley (1988). For the *malaya*-group, *annemariae*, and the *lannae*-group, the analysis gave 9 equally parsimonious trees (length 14 steps, C.I. = 1.0). Together, these trees give area relationships quite similar to the cladogram in Fig. 85. For the *esakii*-group more than 100 equally parsimonious trees (the MAXTREE limit) were generated (length 12 steps, C.I. = 1.0), but the area relationships are similar to Fig. 87, the many unresolved area relationships taken into consideration. An analysis of the data matrices for the *malaya*-group, etc., and the *esakii*-group together also gave 100 trees (length 28 steps, C.I. = 0.93). The area relationships, however, are significantly different from the summary cladogram obtained by the component analysis (Fig. 88). Besides having a lower degree of resolution, some aberrant area relationships are suggested, e.g., the Fiji and Tonga Islands joined with the Indian Ocean areas. The analysis was not carried on to include the *bergrothi*-group.

While the parsimony analysis gave more or less the same results as the component analysis for species-groups, the method obviously failed to produce acceptable results when these groups were analysed together. The two species-groups analysed have only partly overlapping distributional ranges. This results in numerous missing areas (coded as missing information) when a joined data matrix is produced. In the process of minimizing the length



Figs. 84-90. Taxon-area cladograms and area cladograms for species-groups of *Halovelia*. 84. Taxon-area cladogram for the *malaya*-group (Indian Ocean species combined), *annemariae*, and the *lannae*-group. 85a and b. Two alternative reduced area cladograms for the *malaya*-group, etc. 86. Taxon-area cladogram for the *esakii*-group (except *solomon*). 87. Reduced area cladogram for the *esakii*-group. 88. Summary area cladogram based upon Fig. 85a (the *malaya*-group, etc.) and Fig. 87 (the *esakii*-group). 89. Taxon-area cladogram for the *bergrothi*-group (some areas excluded, see text). 90. Reduced area cladogram for the *bergrothi*-group. For explanation of area numbers, see Table 2. Further explanation in text.

of the tree, data entries coded as "9" are allowed to take any of the values "0" or "1" and areas with many such entries (like the Indian Ocean, Fiji, and Tonga Islands) tend to be placed on the same branch in the most parsimonious tree. Wiley (1988: 530) admits that areas with many missing groups may cause problems and recommends that such areas are taken out of the analysis and added in a post hoc manner according to the evidence associated with them. This is, actually, what a component analysis does. Thus, parsimony analysis seems to have some undesirable effects, at least for the

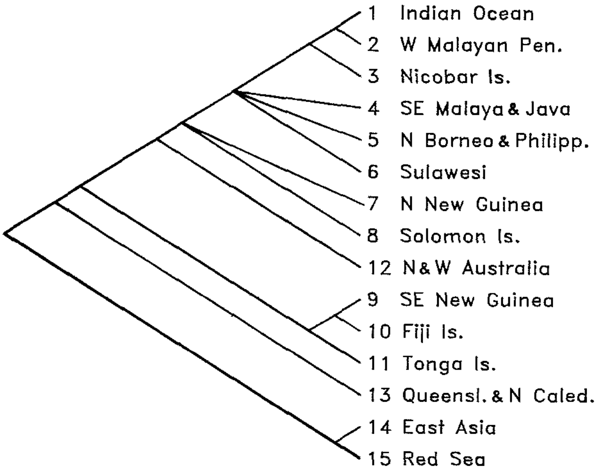


Fig. 91. Summary area cladogram for species-groups of *Halovelia* (from Figs. 88 and 90). For explanation of area numbers, see Table 2. Further explanation in text.

kind of taxon-area relationships analysed in the present work. The conceptual background as well as the methodological approach of parsimony analysis has been severely criticized by Platnick (1988).

Biogeographical history of Halovelia

The result of the component analysis of interrelationships between geographical areas occupied by *Halovelia*-species is our best foundation for speculations upon the biogeographical history of the coral bugs. This history can be described as a sequential number of vicariance events partitioning the ranges of ancestral species, followed by speciation. The resulting pattern may be obscured by extinction, dispersal, and area-hybridization. The component analysis was restricted to the *malaya*-group, etc., the *esakii*-group, and the *bergrothi*-group, i.e., the uppermost or "higher" branches of the taxon cladogram (Fig. 48). The following discussion is therefore chiefly concerned with these groups. The distributional limits of a number of monophyletic species-groups are depicted on the map (Fig. 92).

The genus *Halovelia* probably had its origin in the Indo-Australian region. This region has experienced major fluctuations in the distribution of land and sea throughout the late Mesozoic and Cenozoic eras (see, e.g., Holloway 1979; Duffels 1983, 1986, 1988; and Whitmore 1981, 1987). Obviously, this has greatly influenced the evolution and distribution of animals confined to coastal marine habitats.

The summary cladogram of relationships between geographical areas (Fig. 91) implies that East Asia (area 14), the Red Sea (area 15), and the eastern part of the Australian continent (area 13) were among the first areas that were isolated within a larger, ancestral area of distribution for the genus *Halovelia*. This is in agreement with the hypothesis that the *bergrothi*-group was the first to branch off among the "higher" groups of the genus (Fig. 48). It seems reasonable to assume that the ancestor of the *bergrothi*-group was widely distributed in the area between continental Asia and Australia-New Guinea.

The first vicariance event separated the *bergrothi*-subgroup and *septentrionalis* + *inflexa*. The disjunct distribution of *inflexa* (Red Sea) and its sister-species, *septentrionalis* (Japan, Ryukyu Islands, Taiwan) may be the result of extinction unless these species are connected by related, but hitherto unknown species along the poorly explored southern coast of continental Asia. Because of the relatively recent origin of the Red Sea, *inflexa* probably became separated earlier along the coast of the Arabian Peninsula or India and later migrated into the Red Sea. In the *bergrothi*-subgroup, *H. heron* (southern Queensland) was possibly the first species to become separated. Despite the wide distributional range of *bergrothi* there is an almost complete vicariance between the species belonging to this subgroup. In the region of New Guinea-Australia, *bergrothi* is the northern species while *hilli* has a southern distribution (see map, Fig. 75). Only in New Caledonia do the two species occur together (probably as a result of secondary dispersal of *bergrothi*, see below). The occurrence of *hilli* in West Australia may also be due to more recent dispersal from east.

The next vicariance events implied by the cladogram (Fig. 91) probably involved SE New Guinea (area 9), the Fiji Islands (area 10), Tonga Islands (area 11), N New Guinea (area 7), and the Solomon Islands (area 8). It is hypothesized that the ancestor of the *esakii*-group were confined to east Malesia (Papua New Guinea, Bismarcks, Solomons) and central Malesia (Irian New Guinea, Moluccas, Sulawesi). The primary vicariance event responsible for the diversification of this group probably was the separation of a southern (SE New Guinea) and a northern (N New Guinea - Solomons, central Malesia) lineage. The first event with an ancestral species spreading to the Fijis and Tongas followed by a succesive speciation which first isolated the Tonga populations, then separated the Fiji and New Guinea populations. While both the Fijis and Tongas are known to be parts of the pre-Miocene Outer Melanesian Arc system (Holloway 1979; Duffels 1988), the distribution of the monophyletic group composed by *novoguinensis*, *fosteri*, and *tongaensis* (see map, Fig. 76) supports the hypothesis that SE New Guinea have Outer Arc relationships (Duffels 1983).

The second vicariance event separated *esakii* (and probably *solomon*), in Papuasia (northern New Guinea, Bismarcks, and Solomons), Moluccas, Sulawesi, and the Philippines, i.e., areas east of Wallace's line. An alternative hypothesis is that this species originated in Papuasia and spread via the north Moluccas - Sulawesi -Sangihe archipelago and/or the Palau Islands to the Philippines, perhaps following the pre-Miocene Outer Melanesian Arc system of islands (Holloway 1979; Duffels 1983). The presence of *polhemi* (which is very closely related to *esakii*) in N Australia could be the result of more recent dispersal (perhaps from the Lesser Sunda Islands) and speciation rather than vicariance as implied by the cladogram (Fig. 91).

Several possible vicariance events may have lead to the separation of the *malaya*-group, *annemariae*, and the *lannae*-group. If Papuasia (areas 7 and 8) was isolated first as implied by the cladogram (Fig. 91), then *annemariae* was separated from the *malaya*-group before the *lannae*-group. This is in conflict with the phylogenetic relationships between these groups (Fig. 48). However, the sister-group relationship of the *malaya*-group and *annemariae* is weakly supported as discussed earlier. An alternative hypothesis is that *annemariae* and the *lannae*-group are sister groups. In that case, a vicariance pattern exists between *annemariae* (Papuasia) and *lannae-wallacei* (Sunda shelf areas and Sulawesi, areas 4, 5, and 6). The distributional gap between *annemariae* and *sulawesi*, the most eastern species of the *malaya*-group, is quite extensive but may be closed by future collections from Moluccas and Irian New Guinea.

It is hypothesized that the *malaya*-group originated somewhere in the central and/or west Malesia. Although the relationship of *abdominalis* (SE Malaya and Java, area 4) and *sulawesi* (Sulawesi, area 6) is unresolved, the occurrence of the first two species on both sides of Wallace's line suggests that the ancestor of the *malaya*-group probably had a distribution which included both west and central Malesia. *H. lannae* and *wallacei* are sister-species which also occur on each side of Wallace's line. *H. lannae* has a Sundaic distribution which includes Palawan and Mindanao in the Philippines. *H. wallacei* occurs on Sulawesi and Sumbawa in the Lesser Sunda Islands. Since these two species are very close, their separation is probably of a relatively recent date.

The ancestral populations of the *malaya*-group occurring west of the Malayan Peninsula were probably separated from the eastern populations relatively early in the history of the genus. *H. malaya* (W Malayan Peninsula, area 2) is most likely the sister-group of all the species occurring in the Indian Ocean and *nicobarensis* (Nicobar Islands, area 3) probably sister-group of this, more inclusive subgroup. The present distribution of species belonging to the *malaya*-group in the central and western part of the Indian Ocean may be explained either by successive fragmentation of the range of a widespread ancestral species, by dispersal from Malesia towards the Indian Ocean, or a combination of these processes. The area relationships for the Indian Ocean species can be read off from Fig. 81. The species *pauliani*, *poissoni*, and *seychellensis* form a monophyletic subgroup with a vicariant distribution along the coasts of East Africa, Madagascar, and the Seychelles. The sister-species *convexa*

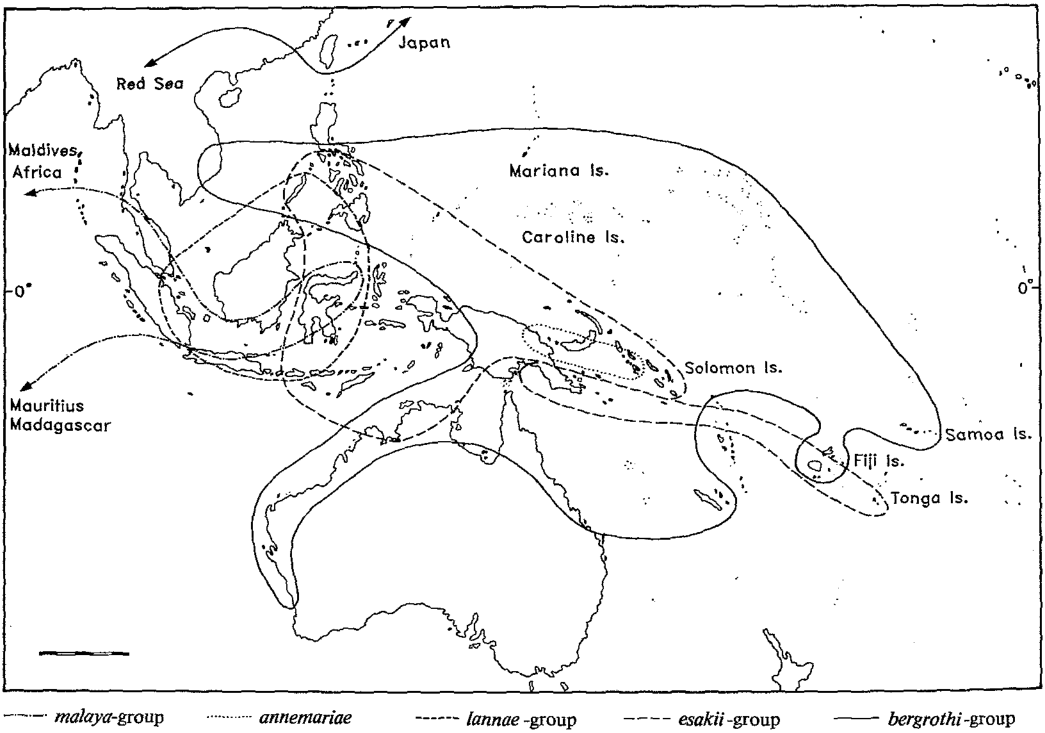


Fig. 92. Distributional limits of some monophyletic species-groups of *Halovelia* in the Indo-Australian and West Pacific areas. Scale of map 1,000 km.

and *mauricensis* are endemic to the Maldives and Mauritius, respectively. All these species share a common ancestor which probably was widely distributed in the central and western parts of the Indian Ocean. The relationship of *depressa* (Madagascar) is unsettled, but it may well belong to the same subgroup as other Indian Ocean species.

The pattern of area relationships produced by the sequence of vicariance events described above may have been significantly modified by extinction and/or dispersal. The present distribution of species belonging to the *malaya*-group along the East African coast and islands of the Indian Ocean could be explained as the result of dispersal from Malesia. The widespread occurrence of *H. esakii* may be the result of dispersal, for example from Papuasia (New Guinea + Solomons) into the Philippines via the northern Moluccas - Sulawesi - Sangihe archipelago and/or the Palau Islands. Likewise, *esakii* could have reached N Australia and produced the closely related *polhemi*. Finally, the occurrence of *bergrothi* in Micronesia and the Samoan Islands is most probably the result of recent dispersal along the chains of islands in the West Pacific, possibly from source areas in the Philippines - Palau - New Guinea regions. The occurrence of this species in New Caledonia is probably also a result of recent dispersal. *H. hilli* may have originated in the Coral Sea and spread to the western coast of Australia after the late Pleistocene opening of the Torres Strait.

Area hybridization, i.e., the invasion of biotas of different origin into a geographical area, may also have modified a more fundamental vicariance pattern of area relationships. From the map (Fig. 92) it is obvious that the three species of *Halovelia* found in the Philippines show both Sundaic (*lannae*), central and east Malesian (*esakii*), and perhaps east Malesian - Australian (*bergrothi*) relationships. It is also interesting that all three species occur on Mindanao and Palawan, i.e., on both sides of Wallace's line as established by Huxley 1868.

A question not addressed so far is the impact of relatively older area patterns underlying the pattern governing present distributions of species. The first branches of the cladogram of relationships between *Halovelia*-species (Fig. 48) all terminates with species that are rare and have quite restricted distributions (*maritima*, *amphibia*, *carolinensis*, *corallia*, and *halophila*). These species are not concentrated in one particular area but scattered throughout the whole Indo-Pacific region (see Table 2 and the maps, Figs. 75-79). The biogeographic inferences based upon the known distribution of these species can only be highly speculative. It is most probable, however, that the distributional pattern of these species is of a relatively old age. The disjunct distributions may be the result of extinction, perhaps following the evolution and subsequent dispersal of competitively superior species of *Halovelia*.

Comparison with other marine Haloveliinae

The phylogenetic analyses of other marine Haloveliinae are in progress (Andersen *in prep.*) and some preliminary results can be presented here. The genus *Xenobates* Esaki has a number of monophyletic species-groups with more or less restricted distributions in Ceylon, the Malayan Peninsula, Singapore, North Borneo, the Philippines, Sulawesi, Moluccas, New Guinea, the Bismarck and Solomon Islands, Australia, and New Caledonia. Most species are single area endemics, a few have wider distributions which cover adjacent areas. No species are shared between Papuasia (northern New Guinea, the Bismarck, and Solomon Islands) and southern New Guinea - northern Australia and between the Sunda shelf areas and the Philippines - Sulawesi - Moluccas areas. Queensland, Australia, has a remarkably high number of endemic species of *Xenobates*.

A new genus has to be erected for *Halovelia papuensis* and several undescribed species (Andersen *in prep.*). The distribution of this genus includes the Malayan Peninsula, Java, Borneo, the Philippines, Sulawesi, Moluccas, and Papuasia. No species have penetrated into southern New Guinea-Australia.

The biogeography of the two other genera of marine Haloveliinae supports most of the hypotheses of area relationships based upon the component analysis of *Halovelia*. The discontinuities between Papuasia and southern New Guinea - northern Australia and between the Sunda shelf areas and the Philippines - Sulawesi - Moluccas areas are repeated. However, since the proportions of single area endemics are higher in these two genera than in *Halovelia*, a much better resolution of area relationships can be expected in component analyses based upon taxon-area cladograms for other marine haloveliines.

The freshwater relatives of the marine haloveliines belong to only two genera: *Entomovelia* Esaki with one described and several undescribed species in Burma, the Malayan Peninsula, and North Borneo, and *Strongylovelia* Esaki with many, mostly undescribed, species throughout the whole Indo-Australian region (Andersen 1982: see map, fig. 619). There is little doubt that the marine haloveliines, including *Halovelia*, have originated from these freshwater relatives somewhere in the Indo-Australian area. More specific hypotheses about the history of evolution of the Haloveliinae must await further cladistic analyses of the group.

Comparison with marine Gerridae

As in the family Veliidae, the marine habit have evolved several times in the large waterstrider family Gerridae (Andersen 1979, 1982; Andersen & Polhemus 1976). The genus *Halobates* Eschscholtz (Gerridae, Halobatinae) contains 46 described species. The taxonomy of the genus is well known, chiefly through the monographic revision by Herring (1961) who also discussed the phylogeny of the genus very briefly and delimited a number of species-groups. He also discussed the relationships of *Halobates* with the four species of *Asclepios* Distant. Herring, however, did not use cladistic methods in his analysis, and some of his species-groups are certainly not monophyletic.

What we need is a cladistic analysis of relationships between the species of *Halobates* and *Asclepios*. This is a major project which is just started and only some preliminary results can be presented here. A number of monophyletic species-groups can be defined, each showing a vicariant pattern of distribution. The most unspecialized species of *Halobates* are found in widely separate geographical areas, in the Red Sea, along the northern coasts of Australia, and in the Galapagos Islands (*robustus* Barber). The four species of *Asclepios* are distributed along the coasts of southern and eastern Asia. They are more primitive than *Halobates* in some characters but otherwise difficult to separate from the most primitive species of that genus.

Most species of *Halobates* are confined to coastal habitats like estuaries, mangroves and coral reefs. The distribution of these species ranges from the Red Sea to the Galapagos Islands in the west - east direction, and from Japan to New South Wales, Australia, in the north - south direction. Many species are endemic to single islands or island-groups. The *Halobates*-species of the Fiji Islands (*fijiensis* Herring and *bryani* Herring) and Tonga Islands (*salotae* Herring) show relationships with New Caledonia and perhaps Australia. The *Halobates*-species of the Maldives (*formidabilis* (Distant) and *galatea* Herring) are also found in India and/or Sri Lanka. Mauritius has an endemic species of *Halobates* (*tethys* Herring) which probably is related to *alluaudi* Bergroth from the Seychelles.

Tropical Australia and especially the coast of Queensland has a number of endemic species of *Halobates* as well as other marine waterstriders. This may be an indication of environmental conditions in the past which prevented dispersal and facilitated speciation. During the Pleistocene, the Sahul shelf formed a land connection between northern Australia and New Guinea, an effective barrier to the dispersal of marine biotas.

A few coastal *Halobates*-species are widespread. *H. flaviventris* Eschscholtz ranges from East Africa to the West Pacific (Vanuatu) and its close relative, *H. hawaiiensis* Usinger, is found along the Central Pacific island-groups (Hawaiian Is., Marquesas Is., Society Is., Taumoto Is.). *H. hayanus* B.-White ranges from the Red Sea to Australia.

Five species of *Halobates* spend their entire life on the surface of the open ocean, sometimes hundreds of kilometers from the nearest coast. These are *germanus* B.-White (Indian and W Pacific Ocean), *micans* Eschscholtz (tropical parts of all oceans), *sericeus* Eschscholtz (Pacific Ocean), *sobrinus* B.-White (E Pacific Ocean), and *splendens* Witlaczil (E Pacific Ocean). Herring (1961) considered this group monophyletic. I am not sure that this is correct. Instead, the oceanic habit may have evolved independently at least twice, and each of two groups of oceanic species could be closer to some coastal species-group than to each other. More comparative studies are necessary to test this hypothesis. Undoubtedly, the oceanic species have originated somewhere in the Indo-Pacific and have subsequently dispersed into all tropical areas of the Atlantic, Indian, and Pacific Ocean.

The freshwater relatives of the marine halobatines belong to the halobatine tribe Metrocorini. These waterstriders all live in running freshwater. They are distributed throughout Africa, South and Southeast Asia, and the Malayan Archipelago including Sulawesi and the Lesser Sunda Islands (Sumbawa, Flores) (Polhemus *pers. comm.*). Undoubtedly, the marine halobatines have their origin somewhere in the Indo-Pacific region, but the question about where can only be addressed after the cladistic analysis has been completed.

Species of the genera *Stenobates* Esaki and *Rheumatometroides* Hungerford & Matsuda (Gerridae, Trepobatinae) are now known to be marine, their species being confined to estuaries and mangrove coasts. These marine waterstriders were previously only known from Singapore (*Stenobates biroi* (Esaki) and *insularis* Polhemus & Cheng) and the Solomon Islands (*Rheumatometroides browni* Hungerford & Matsuda), but several, yet undescribed species are now present from many localities in the Philippines, Sulawesi, Moluccas, Papua New Guinea, and northern Australia (Polhemus *pers. comm.*).

Comparison with other Indo-Pacific animals

Adult marine waterstriders are always wingless and therefore unable to disperse by flight. Most species are confined to coastal habitats which means that a land mass of some size is a major obstacle to their dispersal. On the other hand, they may disperse easily along the coast, along chains of islands, and perhaps even across wider stretches of open sea, floating upon the sea surface. One would expect that such insects have a biogeographic history which is quite different from that of terrestrial organisms, especially those inhabiting inland areas and mountains.

Duffels (1986) discussed areas of endemism of the Indo-Pacific and their interrelationships based upon his studies of the Cicadoidea. He also compared biogeographic patterns found in cicadas with published distributions of various other terrestrial animals. Most important was the repeated discontinuities observed in New Guinea and adjacent areas. Duffels (op.cit.) characterizes New Guinea as "a composite area which is non-monophyletic in a (bio)geographical sense" (p. 333). The biogeography of marine haloveliines is consistent with this view, with strong evidence in favour of an Outer Melanesian Arc pattern, including the northern coast of New Guinea, SE New Guinea, the Solomon, Fiji, and Tonga Islands. An Inner Melanesian

Arc pattern is less marked since there are few endemic species known from southern New Guinea and from New Caledonia, and no marine waterstriders are known from New Zealand. Very few species of marine waterstriders show an Outer - Inner Arc pattern.

Sulawesi and the Moluccas may both be of composite nature. Since marine waterstriders have chiefly been collected in the northern Moluccas and in northern and western Sulawesi, comparisons for these areas are not relevant for the moment.

For the same reasons as stated at the beginning of this section, one would expect a high degree of biogeographic congruence between marine waterstriders and other organisms inhabiting coastal marine habitats. Unfortunately, there are very few studies of marine organisms which make such comparisons possible. Springer (1982) published an excellent analysis of the biogeography of Pacific plate shorefishes. He also reviewed the distribution of other Pacific organisms, chiefly marine invertebrates. Springer (op.cit.) stressed the importance of knowing the sister-group (i.e., cladistic) relationships of his Pacific plate endemics and the distributions of their sister-groups. But since cladistic analyses were and still are very scarce in the literature on marine organisms, comparisons of taxon-area relationships in terms of monophyletic groups and areas of endemism cannot be meaningful. Of the numerous groups of shorefishes and other marine animals mapped by Springer (op.cit.), a few show a distributional pattern quite similar to that of marine waterstriders.

In terms of tectonic plate distributions, very few marine waterstriders, apart from the oceanic species of *Halobates*, occur in localities situated on the Pacific plate. Of *Halovelia*-species only *bergrothi* (a widespread species) and *carolinensis* are found in islands of the West Pacific (Caroline, Marshall, and Samoa Islands). Only the last species may be a Pacific Plate endemic. Most marine waterstriders occur in the boundary zones between the Pacific and Australian plates (northern New Guinea, Bismarck, and Solomon Islands) and between the Philippine, Eurasian, and Australian plates (Philippines, Moluccas, and Sulawesi).

Biogeographic conclusions

The genus *Halovelia* originated in the Indo-Australian region. The summary cladogram of relationships between geographical areas gives some indications of the biogeographic history of the coral bugs. The present distribution of species is the result of a number of vicariance events partitioning the ancestral distributional area of the genus. The resulting pattern has been obscured by extinction, dispersal, and area-hybridization. The most important vicariance events took place in the area between continental Asia and Australia, in New Guinea - eastern Australia, in central Malesia, and in the western Sunda shelf region. The discontinuity between Papuasia (northern New Guinea, the Solomon Islands) and southern New Guinea - Australia is significant, especially when the distribution of other marine Haloveliinae is taken into consideration. An Outer Melanesian Arc pattern including Papuasia and the Fiji and Tonga Islands is demonstrated. SE New Guinea is part of this pattern. Two monophyletic species-groups of *Halovelia* transcend Wallace's line, between the Sundaland and Sulawesi. All of the three Philippine species are found in both Mindanao and Palawan. Area-hybridization is evident in the Philippines. Most species occurring west of the Malayan Peninsula are members of the same monophyletic group. The distribution of *Halovelia*-species terminating the lower branches of the cladogram suggests an older, underlying pattern which has been much obscured by extinction. Current work on the cladistics and biogeography of the marine Haloveliinae and Gerridae will show how far the patterns of biogeographic relationships in marine Gerromorpha are compatible. Comparison of these patterns with those of other groups of animals and plants will reveal the generality of the biogeographic patterns found in marine waterstriders.

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APPENDIX: Check-list (alphabetical) and distribution of the species of the genus *Halovelia* Bergroth (Veliidae, Haloveliinae). (With page references to descriptions in Part I and II of the present work).

Genus *Halovelia* Bergroth, 1893................ I:83

abdominalis Andersen, 1989.
Java, West Malaysia....................... II:184

amphibia Bergroth, 1906.
Zanzibar, Madagascar....................... I:88

angulana Polhemus, 1982 (subgenus *Colpovelia*);
removed from *Halovelia*.................... I:85

annemariae Andersen, 1989.
Solomon Islands, Papua New Guinea. I:115
bergrothi Esaki, 1926.
syn. *marianarum* Usinger, 1946.
syn. *danae* Herring, 1958.
Vietnam, Philippines, Papua New Guinea, Guinea, Solomon Islands, New Caledonia, Mariana Islands, Caroline Islands, Marshall Islands, Nauru Island, Samoa Islands. I:93
carolinensis Andersen, 1989.
Caroline Islands. I:90
convexa Andersen, 1989.
Maldive Islands. II:186
corallia Andersen, 1989.
Papua New Guinea, Australia: Queensland. I:92
danae Herring, 1958; see *bergrothi*.
depressa Andersen, 1989.
Madagascar. II:192
esakii Andersen, 1989.
Solomon Islands, Irian New Guinea, Moluccas, Sulawesi, Lesser Sunda Islands (Sumbawa), Palau Islands, Philippines. I:107
fijiensis Andersen, 1989.
Fiji Islands. I:103
fosteri Andersen, 1989.
Fiji Islands. I:113
halophila Andersen, 1989.
Lesser Sunda Islands (Sumbawa), Borneo (Sabah). I:92
heron Andersen, 1989.
Australia: S. Queensland. I:102
hilli China, 1957.
Australia: Monte Bello Islands, Northern Territory, Queensland, Papua New Guinea, New Caledonia, Loyalty Islands. I:99
inflexa Andersen, 1989.
Sudan, Red Sea. I:106
lannae Andersen, 1989.
Java, Singapore, West Malaysia, Borneo (Sabah), Philippines. I:116
loyaltiensis China, 1957; removed from *Halovelia*.. I:85
malaya Esaki, 1930.
West Malaysia, Thailand. II:181
marianarum Usinger, 1946; see *bergrothi*.
maritima Bergroth, 1893.
Cartier Island, Timor Sea. I:87
mauricensis Andersen, 1989.
Mauritius. II:193
nicobarensis Andersen, 1989.
Nicobar Islands. II:186
novoguinensis Andersen, 1989.
Papua New Guinea. I:112
papuensis Esaki, 1926; removed from *Halovelia*. .. I:85
pauliani Poisson, 1956.
Île Europa, Mozambique Channel. II:188
poissoni Andersen, 1989.
Kenya, Tanzania. II:190
polhemi Andersen, 1989.
Australia: Northern Territory. I:109
septentrionalis Esaki, 1926.
Japan, Ryukyu Islands, Taiwan. I:104
seychellensis Andersen, 1989.
Seychelles, Madagascar. II:191
solomon Andersen, 1989.
Solomon Islands. I:110
sulawesi Andersen, 1989.
Sulawesi. II:183
tongaensis Andersen, 1989.
Tonga Islands. I:115
wallacei Andersen, 1989.
Sulawesi, Lesser Sunda Islands (Sumbawa). I:119

Note added in proof

After the present paper was submitted, Dr W. A. Foster, Cambridge, had the courtesy of sending me samples of a *Halovelia*-species collected by him at Goa, on the west coast of India. The species belongs to the *H. malaya*-group but cannot be identified with any of the 10 species described in the present work. The new species appears to be closely related to *malaya* Esaki and *nicobarensis* sp.n. and will be described in a forthcoming paper.