Marine water striders (Heteroptera, Gerromorpha) of the Indo-Pacific: cladistic biogeography and Cenozoic palaeogeography

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Abstract

More than 140 species of marine water striders (Heteroptera, Gerromorpha), representing three families and 11 genera, are distributed throughout the Indo-Pacific region. The largest genera are: *Hermatobates* (Hermatobatidae), *Halovelia*, *Haloveloides*, *Xenobates* (Veliidae), *Asclepios*, *Halobates*, *Rheumatometroides*, and *Stenobates* (Gerridae). Marine water striders live in estuaries, mangroves, intertidal coral reef flats, and on the sea surface near coral reefs and rocky coasts. Adult marine water striders are always wingless but may disperse along coasts and chains of islands. Five species of sea skaters, *Halobates*, have colonized the surface of the open ocean. The present work updates and extends previous work on the cladistic biogeography of Indo-Pacific marine water striders. The method of paralogy-free subtree analysis developed by Nelson and Ladiges is applied to taxon-area cladograms for four monophyletic groups, and the results are combined to yield general area cladograms depicting the relationships between eight areas of endemism of the Indo-Pacific region. Finally, hypotheses of area relationships are discussed in the light of available knowledge about the distribution of fossil marine water striders, the Cenozoic palaeogeography of the Indo-Pacific region, and the palaeoecology of mangroves and reef-building corals.

Introduction

The Indo-Pacific comprises land areas bordering the Indian and west Pacific Oceans (Fig.1) and has traditionally been divided into the Ethiopian, Oriental, and Australian regions. Studies using the methods of cladistic biogeography (Nelson and Platnick, 1981; Humphries and Parenti, 1986; Humphries *et al*., 1988), however, do not support this division (*e.g*., Schuh and Stonedahl, 1986; Andersen, 1991a; Muona, 1991; Parenti, 1991; Vane-Wright, 1991; Boer, 1995;

Boer and Duffels, 1996). In general, patterns of distribution seem to be compatible with a set of hierarchical relationships between more restricted areas of endemism. These are quite similar to those delimited by Gressitt (1956) and Gressitt *et al*. (1961), although the areas of the Indian Ocean were not recognized as part of their 'Pacific' region. Malesia (as defined by Whitmore, 1981, 1987) is seemingly not a genuine, monophyletic area of endemism (Andersen, 1991a).

Most studies of Indo-Pacific biogeography have been based upon terrestrial animals and plants. In this chapter, the results of biogeographical studies of a group of marine insects belonging to the heteropterous infraorder Gerromorpha are presented. Although the majority of the about 1,600 gerromorphan species are limnic, about 180 species belonging to five families and seven subfamilies occur in the marine environment and reach their greatest diversity in the Indo-Pacific region (Andersen and Polhemus, 1976; Andersen, 1982; Cheng, 1985). The present work updates and extends previous works on the cladistic biogeography of Indo-Pacific marine water striders (Andersen, 1991a, 1991b; Andersen and Weir, 1994a, 1994b). The method of paralogy-free subtree analyses (Nelson and Ladiges, 1996) is applied to taxon-area cladograms for four monophyletic groups of marine water striders and the results are combined to yield general area cladograms depicting the relationships between areas of endemism of the Indo-Pacific region. Finally, the hypotheses of area interrelationships are discussed
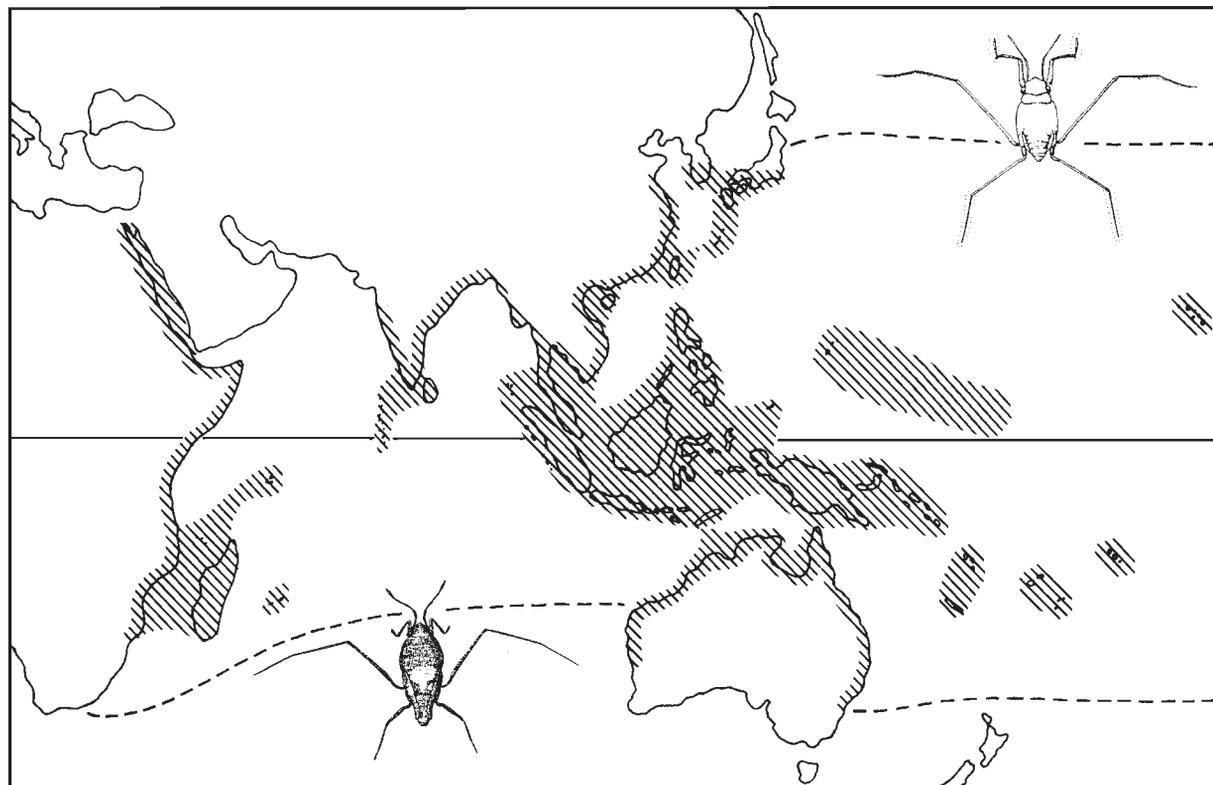
Fig.1. The Indo-Pacific with distribution of nearshore species of marine water striders (hatched areas) and distributional boundaries of oceanic *Halobates* (dashed line). Insertions show *Halovelia malaya* Esaki, length 2.5 mm (bottom left) and *Halobates sericeus* Eschscholtz, length 3.4 mm (top right).

in the light of available knowledge about the Cenozoic palaeogeography of the region (Boer, 1995; Boer and Duffels, 1996; Packham, 1996; Hall, 1996, and references therein).

Marine water striders and their distribution

General

More than 140 species of marine water striders, representing three families and 11 genera, are distributed throughout the Indo-Pacific region. They live in estuaries, mangroves, intertidal coral reef flats, and on the sea surface near coral reefs and rocky coasts (Fig.1). Five species of sea skaters, *Halobates*, have colonized the surface of the open ocean (Cheng, 1985, 1989). Adult marine water striders are always wingless but may disperse along coasts, chains of islands and, for a few species of *Halobates*, possibly across wider stretches of open sea. Although some species belonging to the genera *Halovelia* and *Halobates* are widespread, most species of

marine water striders have rather restricted areas of distribution.

Hermatobates

The genus *Hermatobates* contains eight described species, but a taxonomic revision is required. The biology of these odd marine insects was studied by Foster (1989), who named them coral treaders because they live on the tidal flats of coral reefs. Both adults and nymphs retreat to holes in porous blocks of dead coral during high tides. *Hermatobates* is unique (Andersen, 1982), belonging to its own family, one of few exclusively marine insect families. It has no close freshwater relatives and it is difficult to trace its geographical origin. *Hermatobates* species are found along continental coasts and islands throughout the Indo-Pacific. Widespread species are *H. djiboutensis* Coutière and Martin (Red Sea, East Africa, Seychelles, Maldives), *H. marchei* Coutière and Martin (Ryukyu Islands, Philippines, Indonesia, Australia, islands of the

West Pacific), and *H. hawaiiensis* China (Hawaiian Islands and islands of Central Pacific). *H. breddini* Herring (Caribbean) is the only species found outside the Indo-Pacific region.

Halovelia

The subfamily Haloveliinae belongs to the Veliidae, one of the most speciose families of water striders, with more than 600 species. Most haloveliines are marine. Freshwater relatives belong to two genera: *Entomovelia* with one described and some undescribed species in Burma, Malaya and Borneo, and *Strongylovelia* with several, mostly undescribed, species in the Indo-Australian region. The marine Haloveliinae have been classified into three genera, *Halovelia*, *Xenobates*, and *Haloveloides* (Andersen, 1989a, 1989b, 1992; Lansbury, 1989, 1996). So far, 45 species have been described, but during the past 10 years, marine haloveliines have been collected in many new localities, increasing the number of known species to more than 60.

Species of *Halovelia* or coral bugs inhabit the intertidal zone of rocky coasts or coral reefs where they can be found on the surface of tidal pools. At high tide they retreat to holes in blocks of coral or other porous rocks where they rest, surrounded by an air bubble, until the next low tide (Andersen, 1989b). The 32 described species of the genus *Halovelia* range from the Red Sea and East African coast to the West Pacific islands as far as Samoa (Andersen, 1989a, 1989b). Species belonging to the *H. esakii* group occur along the coasts of the Philippines, Sulawesi, New Guinea, the Solomons, northern Australia, and the Fiji and Tonga Islands. Species of the *H. bergrothi* group have a similar distribution but two species are widespread in Australia and the islands of the West Pacific, respectively. Two closely related species, the *H. lannae* group, are found on both sides of Wallace's line. Species belonging to the *H. malaya* group are found along the coasts of East Africa, southern Asia, and island groups of the Indian Ocean.

Xenobates and Haloveloides

Species of *Xenobates* typically live in mangroves where they can be found on the surface of tidal canals. Until recently this genus was thought to be monotypic, but now more than 25 species have been collected throughout the Indo-Australian region. Other species have been placed in *Halovelia* (China, 1957; Polhemus, 1982; Lansbury, 1989). A preliminary classification of *Xenobates* species has revealed a number of monophyletic species groups (Andersen, unpublished). The *X. seminulum* (Esaki) group (with four species) occurs in Maluku, northern New Guinea, the Bismarck archipelago and Solomon Islands. A related species group is found in Maluku, Sulawesi, southern Philippines, Java, Singapore, and Sri Lanka. Another group occurs in Maluku, Sulawesi, southern Philippines, North Borneo, and Malaya. Eight species of *Xenobates*, most of them undescribed, are found along the coast of tropical Australia (Andersen and Weir, unpublished). Finally, *X. loyaltiensis* (China) is endemic to New Caledonia and the Loyalty Islands.

A separate genus, *Haloveloides*, with seven species, was erected for the '*Halovelia*' *papuensis* Esaki group (Andersen, 1992). It is closely related to *Xenobates* but some species have left the protecting mangroves and live on the sea surface at some distance from the coast (Lansbury, 1996). One species is found in areas of the Sunda shelf, another one in Sulawesi, Maluku, and southern Philippines, three species in Palawan and Luzon, and another two species in northern New Guinea, the Bismarck archipelago and the Solomons.

Stenobates and Rheumatometroides

Another large family of water striders, the Gerridae, with more than 500 species, contains several groups of marine species. The tribe Stenobatini has 21 mangrove-inhabiting species in Malesia (Polhemus and Polhemus, 1996). They belong to the subfamily Trepobatinae and are related to the freshwater genus *Naboandelus* found in Africa, India, and SE Asia (Andersen, 1982; Polhemus and Polhemus, 1993). *Stenobates* (10 species) is distributed from Singapore to Australia, while the distribution of *Rheumatometroides* (7 species) ranges from Singapore to the Solomons. *Thetibates* (2 species) and the monotypic genera *Pseudohalobates* and *Stenobatoides* have more restricted distributions within Malesia.

Halobates and Asclepios

The subfamily Halobatinae, tribe Halobatini, contains the well-known sea skaters, genus *Halobates*, with 42 described species (Herring,

1961; Polhemus and Polhemus, 1991; Andersen and Foster, 1992; Andersen and Weir, 1994b). Most species are confined to coastal, marine habitats such as estuaries, mangroves and coral reefs. Freshwater relatives belong to the tribe Metrocorini (Andersen, 1982) and live in running freshwater throughout Africa, South and SE Asia, and the Malay archipelago, including Sulawesi (Polhemus, 1990). The closest relatives of *Halobates* are *Austrobates*, a monotypic, freshwater-inhabiting genus endemic to the Cape York peninsula, Australia (Andersen and Weir, 1994a), and *Asclepios* with three species distributed along the coasts of SE and East Asia. These genera are more primitive than *Halobates* in some characters but otherwise difficult to separate from the most primitive species, *H. mjobergi* Hale and *H. lannae* Andersen and Weir, found in tropical Australia (Andersen and Weir, 1994b).

A cladistic analysis of *Halobates* (Andersen, 1991b), allows the definition of a number of monophyletic species-groups, each showing a characteristic distribution pattern. Most species of the *H. regalis* Carpenter group occur in tropical Australia but two species (*H. zephyrus* Herring and *H. whiteleggei* Skuse) live along the coast of New South Wales as far as 100 km south of Sydney. There is considerable distributional overlap between species. *H. peronis* Herring, ranging from the Philippines to the Solomons, and *H. sexualis* Distant, from Sri Lanka and Malaya, are both closely related to species from Australia (*H. darwini* Herring and *H. herringi* Polhemus and Cheng).

Species belonging to the *H. princeps* White group occur throughout the Indo-West Pacific region. Most species are endemic to single islands or island groups. There is one subgroup of closely related species in the Indian Ocean (*H. alluaudi* Bergroth group) including the west coast of India, and another subgroup (*H. mariannarum* Esaki group) on islands of the western Pacific. *H. princeps* White, the sister taxon of these subgroups, is widely distributed in Malesia. Many *Halobates* species are endemic to single islands or island groups like *H. robustus* Barber (Galapagos), *H. kelleni* Herring (Samoa), *H. salotae* Herring (Tonga), *H. bryani* Herring and *fijiensis* (Fiji), and *H. tethys* Herring (Mauritius), but a few coastal species are widespread like *H. hayanus* White (Red Sea to New Guinea) and *H. flaviventris* Eschscholtz (East Africa to Vanuatu).

Five species of *Halobates* spend their entire life on the surface of the open ocean, sometimes hundreds of kilometres from the nearest coast (Cheng, 1985, 1989): *H. germanus* White (Indian Ocean, West and Central Pacific Ocean), *H. sericeus* Eschscholtz (Pacific Ocean), *H. sobrinus* White (East Pacific Ocean, off the coasts of Middle America), *H. splendens* Witlaczil (East Pacific Ocean, off the coast of South America), and *H. micans* (all tropical oceans). Herring (1961) considered this group monophyletic but the cladistic analysis of *Halobates* (Andersen, 1991b) shows that two oceanic species are closer to some coastal, but widespread species (*H. flaviventris* and *hawaiiensis* Usinger), than to other oceanic species.

Methods

Areas of endemism

For the present study, the Indo-Pacific region is divided into eight areas of endemism following Andersen (1991a: Fig.9). These areas are delimited as follows (with abbreviations used throughout the chapter and in the figures):

Australia (Aust): The coasts of the Australian continent, but also including southern New Guinea, New Caledonia, and Vanuatu (New Hebrides).

East Asia (EAsi): The coasts of continental Asia including Vietnam, China, and Korea, Taiwan, Japan, and Ryukyu Islands.

Indian Ocean (IndO): Red Sea, East African coast, Madagascar, Seychelles, Mascarenes, Maldives, and west coast of India.

Malayan (Mala): East coast of India, Burma, Thailand, Cambodia, Malaysia, Singapore, and Indonesia as far east as Wallace's line.

Papuasia (Papu): Northern New Guinea, Belau (Palau Islands), the Bismarck archipelago, and Solomon Islands.

Philippines (Phil): The Philippine Islands.

Sulawesi (Sula): Sulawesi (Celebes), the Lesser Sunda Islands (except Bali), and Maluku (the Moluccas).

West Pacific (WPac): Islands of the west Pacific Ocean as far east as Samoa and the Hawaiian Islands.

Analytical methods

For each monophyletic group of marine water striders, the distributions of species or species groups were recorded as taxon-area cladograms
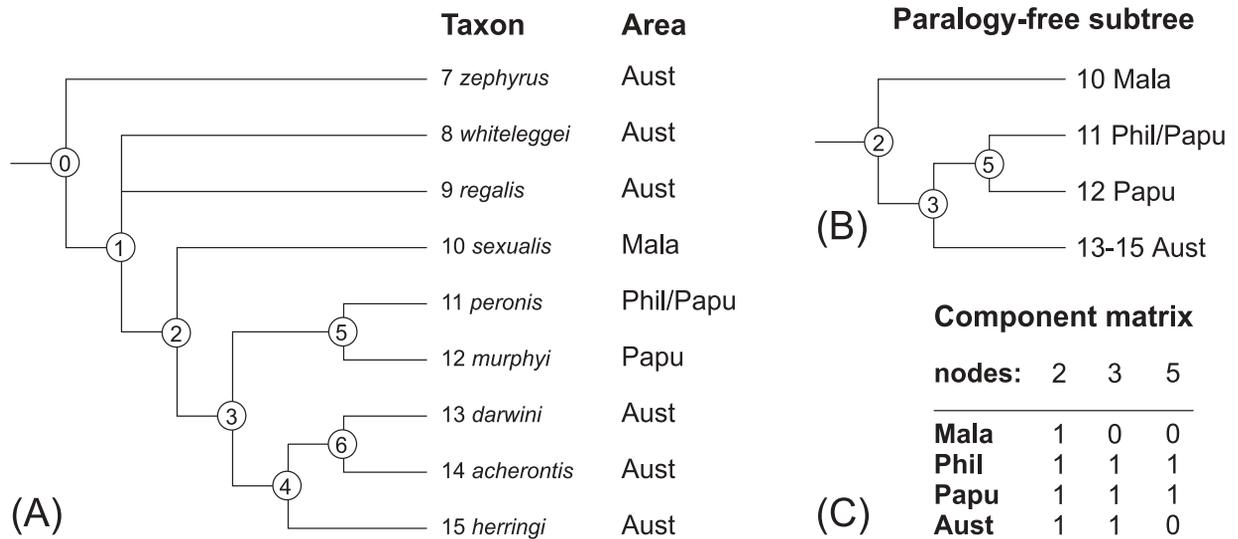
Taxon	Area
7 *zephyrus*	Aust
8 *whiteleggei*	Aust
9 *regalis*	Aust
10 *sexualis*	Mala
11 *peronis*	Phil/Papu
12 *murphyi*	Papu
13 *darwini*	Aust
14 *acherontis*	Aust
15 *herringi*	Aust

(A)

Paralogy-free subtree

10 Mala
11 Phil/Papu
12 Papu
13-15 Aust

(B)

Component matrix

nodes:	2	3	5
Mala	1	0	0
Phil	1	1	1
Papu	1	1	1
Aust	1	1	0

(C)

Fig.2. Paralogy-free subtree analysis. (A) Taxon-area cladogram for *Halobates zephyrus* and the *H. regalis* group (Gerridae, Halobatinae). (B) Paralogy-free subtree derived from (A). (C) Component matrix derived from the nodes of (B). Further explanation in text.

of the eight areas of endemism defined above. Two methods of biogeographic analysis were applied to these taxon-area cladograms. First, they were subjected to component analysis (Nelson and Platnick, 1981; Humphries and Parenti, 1986) using the computer program COMPONENT, version 1.5 (Page, 1989, 1990). The cladograms were analyzed by the options *Build* and Assumption 0, 1, and 2 (which stipulate different ways of treating widespread taxa). The results are cladograms showing the relationships between the eight areas of endemism. The options *Compare*, *Consensus*, and *Strict* were used in cases which yielded more than a single area cladogram, obtaining a strict consensus cladogram for all possible area cladograms.

Second, the taxon-area cladograms were analyzed by the method of paralogy-free subtree analysis (Nelson and Ladiges, 1996). The subtree algorithm builds subtrees from a taxon-area cladogram, starting at each terminal node and progressing to the base of the cladogram. A node (taxon) that relates organisms that, as different taxa, do not overlap in geographic distribution is associated with the non-overlapping geographic data. A node (taxon) that relates organisms that overlap in distribution is deemed paralogous (analogous to the molecular phenomenon) and is not generally associated with geographic data.

Fig.2A shows an example of a taxon-area cladogram for the monophyletic *Halobates*

regalis (Gerridae, Halobatinae) group with its outgroup species *H. zephyrus*. The terminal taxa 13-15 are all endemic to Aust which therefore is the only geographic data associated with nodes 4 and 6. The distribution of taxon 11 (Phil/Papu) and 12 (Papu) overlaps. Node 5 is therefore paralogous in the strict sense, yet node 5 evidently relates Phil more close to Papu than to the areas Mala and Aust. Following Assumption 2 (which treats areas for widespread taxa as redundant and not necessarily indicating close area relationships), the widespread distribution of taxon 11, *H. peronis*, can be reduced to Phil and node 5 thereby made paralogy-free. Likewise, the nodes 2 and 3 (Fig.2A) are paralogy-free, associated with the geographic information Mala/Phil/Papu/Aust and Phil/Papu/Aust, respectively. In contrast, nodes 0, 1, and 2 are paralogous because the area Aust already is associated with the more terminal nodes 4 and 6. Thus, the original taxon-area cladogram (Fig.2A) yields only one, fully resolved paralogy-free subtree (Fig.2B) showing unique relationships between the areas Aust, Mala, Phil, and Papu.

A component matrix can be derived from each subtree by scoring geographical information associated with the subtree nodes (Fig.2C). Matrices derived from two or more subtrees can be combined and subjected to a parsimony analysis using programs like Hennig86 (Farris, 1988) or PAUP (Swofford, 1993). For each analysis, the result is given as the number of most
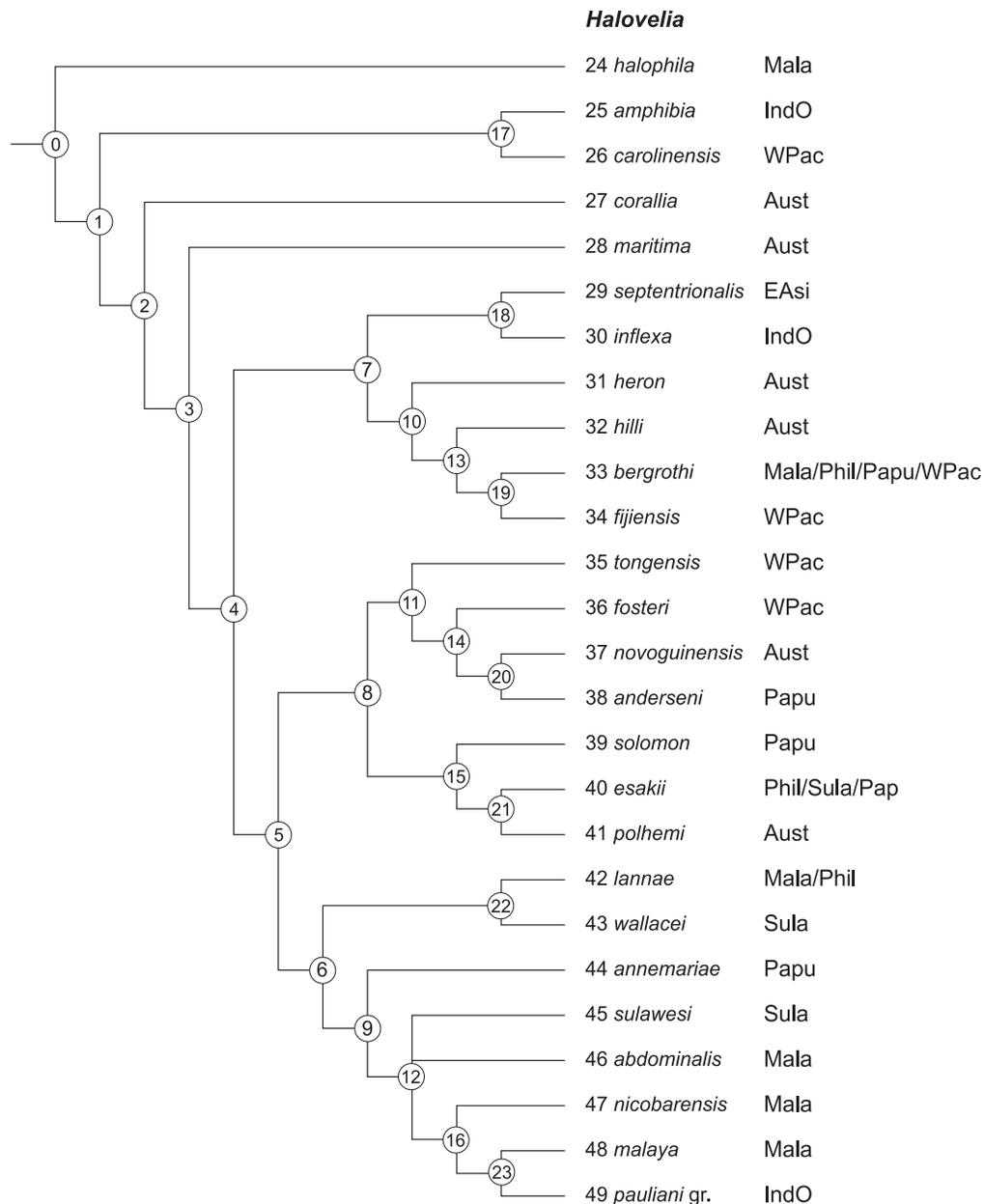
Halovelia

24 *halophila*	Mala
25 *amphibia*	IndO
26 *carolinensis*	WPac
27 *corallia*	Aust
28 *maritima*	Aust
29 *septentrionalis*	EAsi
30 *inflexa*	IndO
31 *heron*	Aust
32 *hilli*	Aust
33 *bergrothi*	Mala/Phil/Papu/WPac
34 *fijiensis*	WPac
35 *tongensis*	WPac
36 *fosteri*	WPac
37 *novoguinensis*	Aust
38 *anderseni*	Papu
39 *solomon*	Papu
40 *esakii*	Phil/Sula/Pap
41 *polhemi*	Aust
42 *lannae*	Mala/Phil
43 *wallacei*	Sula
44 *annemariae*	Papu
45 *sulawesi*	Sula
46 *abdominalis*	Mala
47 *nicobarensis*	Mala
48 *malaya*	Mala
49 *pauliani* gr.	IndO

Fig.3. Taxon-area cladogram for species of *Halovelia* (Veliidae, Haloveliinae). Further explanation in text.

parsimonious trees, length, consistency index (ci), and retention index (ri) of these trees. The geographical information may also be scored as three item statements (Nelson and Ladiges, 1991), but parsimony analyses of matrices of component data and three item statements usually yield the same trees (Nelson and Ladiges, 1996). This is not the case, however, for the taxon-area cladogram used as an example above (Fig.2A). A parsimony analysis for three item statements yields two area cladograms, viz.,

(Mala (Aust (Phil, Papu))) and (Aust (Mala (Phil, Papu))). This suggests that the area Aust may have a dual history.

Results

Hermatobates

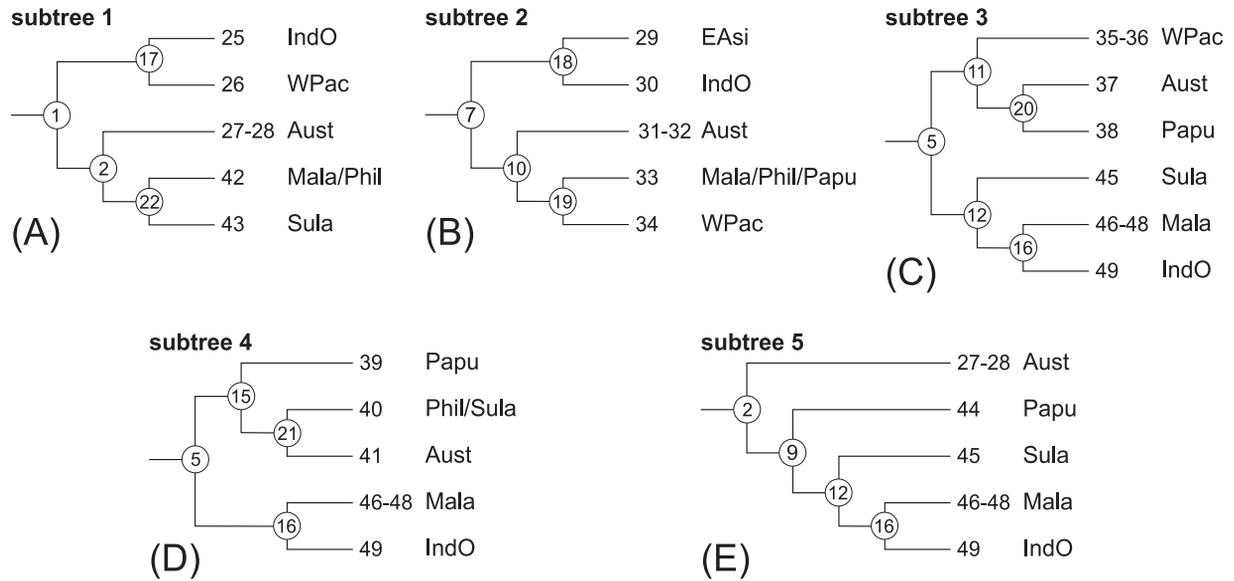Classified as a family of its own (Hermatobatidae), *Hermatobates* is probably the oldest group

Fig.4. Paralogy-free subtrees derived from the taxon-area cladogram for *Halovelia* (Fig.3). Further explanation in text.

of marine water striders. Knowledge about the phylogenetic relationships between the species of *Hermatobates* is not available at present, precluding a cladistic biogeographical analysis. The occurrence of one species in the Caribbean indicates that the genus was already widely distributed before the final closure of the Isthmus of Panama (since 5 Ma), and probably much earlier than this event.

Halovelia

The taxon-area cladogram for *Halovelia* (Fig.3) has 26 terminal taxa. Five species occurring in East Africa and various Indian Ocean islands are joined in the *H. pauliani* group. For subtree analysis, informative nodes of the taxon-area cladogram for *Halovelia* (Fig.3) are 7, 9, and 10-23. Five paralogy-free subtrees (Fig.4) can be derived from this cladogram using assumption 2 when distributions overlap. The component matrix for the nodes of individual subtrees is given in Table 1. Parsimony analysis of this matrix give 9 trees (length = 22, c_i = 59, and r_i = 60). All of these trees have IndO and EAsi as sister-areas. The relationships between other areas vary and are unresolved in a strict consensus tree (Fig.7A). The COMPONENT analysis for *Halovelia* yields 4 trees (assumption 0), 30 trees (assumption 1), and 11 trees (assumption 2), all resulting in highly unresolved consensus trees for the 8 areas involved.

Xenobates and Haloveloides

Species of *Xenobates* are only recorded from Mala, Phil, Sula, Papu, and Aust. Three paralogy-free subtrees (nos. 6-8) can be derived from a preliminary taxon-area cladogram for *Xenobates* (Andersen, unpublished) using assumption 2. The taxon-area cladogram for *Haloveloides* (Andersen, 1992) has 7 terminal taxa with the same distributional areas as *Xenobates* (except Aust). Only one subtree can be derived from this cladogram. The component matrix for the nodes of individual subtrees for *Xenobates* and *Haloveloides* is listed in Table 1. Parsimony analysis of this matrix gives one, completely resolved tree (length = 20, c_i = 70, and r_i = 62). In contrast, the COMPONENT analysis for *Xenobates + Haloveloides* yields 2 trees (assumption 0), 3 trees (assumption 1), and 6 trees (assumption 2), all resulting in highly unresolved consensus trees for the 5 areas involved.

Stenobates and Rheumatometroides

Species of the five genera of the tribe Stenobatini are only recorded from Mala, Phil, Sula, Papu, and Aust. A preliminary taxon-area cladogram for species belonging to the tribe Stenobatini (Andersen, unpublished) has 22 terminal taxa. Three paralogy-free subtrees (nos. 9-

Table 1. Component matrices for subtrees derived from taxon-area cladograms for marine water striders. Nodes of subtrees nos. 1 - 19. OG = "outgroup" area. Further explanation in text.

	Halovelia					*Xenobates & Haloveloides*				Stenobatini			Halobatini						
Tree No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Node	012	111	1112	112	011	001	001	011	00	000	001	001	1112	1112	0112	012	11	0012	1122
	272	089	1260	561	926	296	496	518	24	489	494	375	3673	3673	9673	182	49	7963	1734
OG	000	000	0000	000	000	000	000	000	00	000	000	000	0000	0000	0000	000	00	0000	0000
IndO	010	010	0110	010	111	???	???	???	??	???	???	???	1010	1010	1010	???	??	0000	1101
Mala	101	101	0110	010	111	111	111	100	11	110	100	111	1111	1111	1111	010	00	1111	1010
EAsi	???	010	????	???	???	???	???	???	??	???	???	???	1111	1111	1111	010	??	1111	1010
Phil	101	101	????	101	???	111	111	111	00	000	000	111	????	????	????	101	11	????	????
Sula	101	???	0100	101	110	110	110	111	10	101	110	100	1110	1110	1110	101	??	1110	1101
Papu	???	101	1001	100	100	000	000	101	11	101	111	000	1110	1110	1110	101	11	1110	1101
Aust	100	000	1001	101	000	100	100	000	??	110	111	110	0000	0000	1000	100	10	1100	0000
WPac	010	101	1000	???	???	???	???	???	??	???	???	???	0010	0010	0000	101	??	1000	1100

11) can be derived from this cladogram using assumption 2. The component matrix for the nodes of individual subtrees for the Stenobatini is listed in Table 1. Parsimony analysis of this matrix gives two trees (length = 14, ci = 64, and ri = 54). The strict consensus tree is only partly resolved, with Phil as the basal area and Sula and Papu as sister areas. The COMPONENT analysis yields 1 tree (assumption 0 and 1) and 14 trees (assumption 2), the latter resulting in a completely unresolved consensus tree for the 5 areas involved. The trees resulting from applying assumptions 0 and 1 are different, placing Aust close to either Papu/Sula or Mala/Phil, respectively.

Halobates and Asclepios

The taxon-area cladogram for the three genera of the tribe Halobatini (including *Austrobates*; Fig.5) has 29 terminal taxa. Only *Halobates germanus* and *flaviventris* were included from the chiefly oceanic *H. micans* group, either because they are widespread (*H. micans* and *H. sericeus*) or because their distribution falls outside the Indo-Pacific region (*H. sobrinus* and *splendens*). *H. robustus* is endemic to the Galapagos Islands which also is outside the boundary of the Indo-Pacific region (but see discussion below). Informative nodes of the taxon-area cladogram (Fig.5) are 12, 14, 16, 17, 18, 19, 22, 23, 24. Seven paralogy-free subtrees (Fig.6, A-G) can be derived from this cladogram using assumption 2 when distributions overlap. For example, geographic data associated with

node 18 overlaps with data associated with node 22. Since Mala is part of a widespread distribution of taxon 40 (*H. proavus*), the geographic data at node 22 are reduced to Phil/Sula/Papu/WPac.

The component matrix for the nodes of individual subtrees (Fig.6, A-G) for the Halobatini is given in Table 1. A parsimony analysis of this matrix give 5 trees (length = 33, ci = 75, ri = 81). All trees have Aust, WPac, and IndO (in that order) in a basal position and Mala and EAsi as sister areas. The relationships between Mala/EAsi, Phil, Sula, and Papu vary and are unresolved in a strict consensus tree (Fig.7B).

The COMPONENT analysis for the Halobatini yields 2 trees under assumption 0 with a consensus tree showing EAsi, WPac, Sula, and Aust (in that order) in basal positions and the relationships between Mala, Phil, and Papu unresolved. No less than 819 trees are found under assumption 1 which gives a completely unresolved consensus tree. Finally, 17 trees are found under assumption 2 with a unresolved strict consensus tree except for a close relationship between EAsi and Mala.

All groups combined

Halovelia and the two genera of Halobatini occur in all of the eight areas of endemism considered here. When the informative subtree nodes for these taxa are analyzed together, one fully resolved tree is found (Fig.7, C; length = 61, ci = 62, and ri = 65).

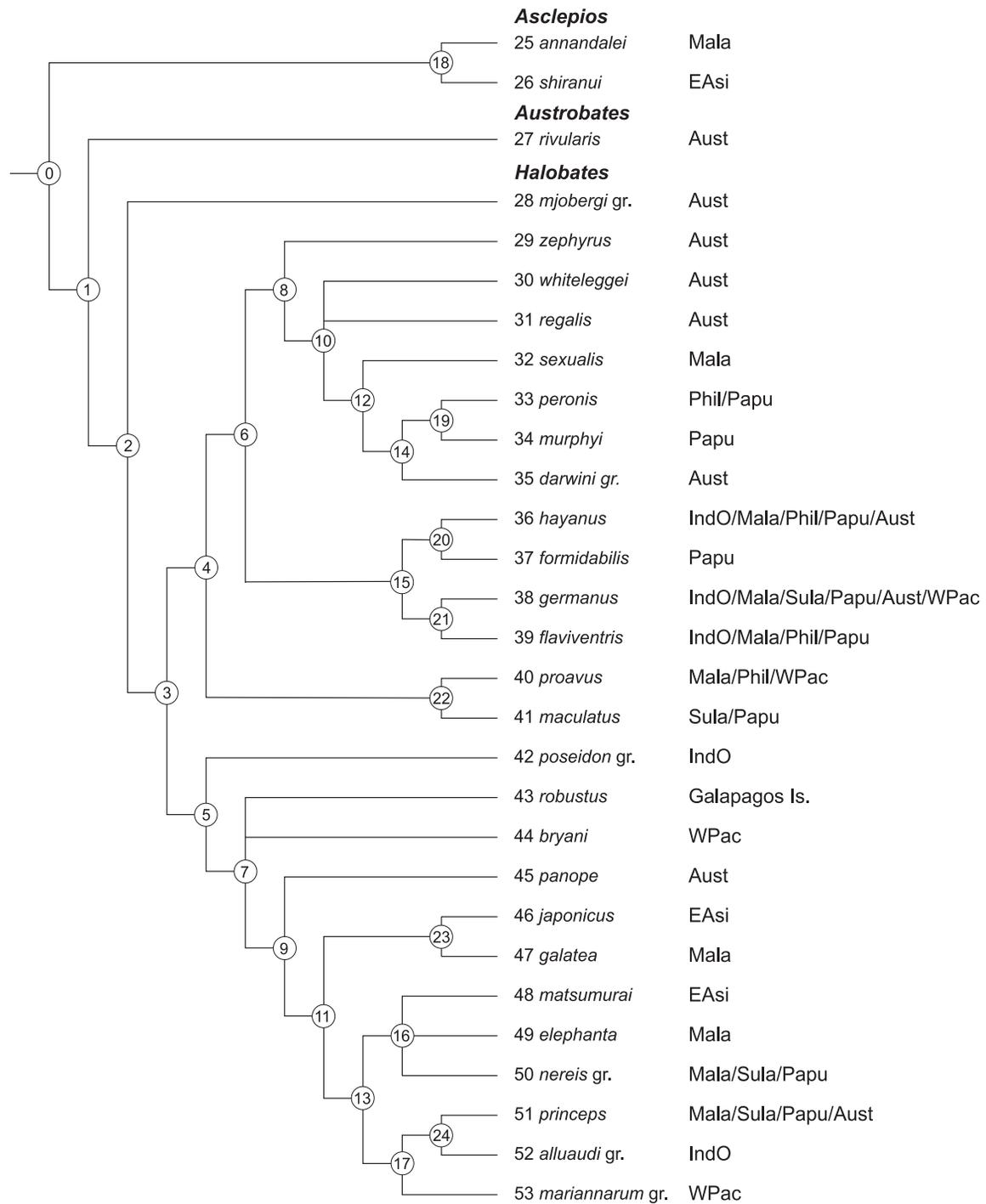*Xenobates*, *Haloveloides*, and the five genera

Fig.5. Taxon-area cladogram for species of *Asclepios, Austrobates,* and *Halobates* (Gerridae, Halobatinae). Further explanation in text.

of Stenobatini only occur in five out of the eight areas of endemism (EAsi, IndO, and WPac excluded). A parsimony analysis of informative subtree nodes for these genera yields two trees (length = 37, ci = 62, and ri = 48). The consensus

tree (Fig.7D) is partly resolved.

A parsimony analysis of the complete component matrix (Table 1) yields only two trees (length = 103, ci = 59, ri = 55). One tree (Fig.7E) has Aust, WPac, and IndO (in that order) in ba-
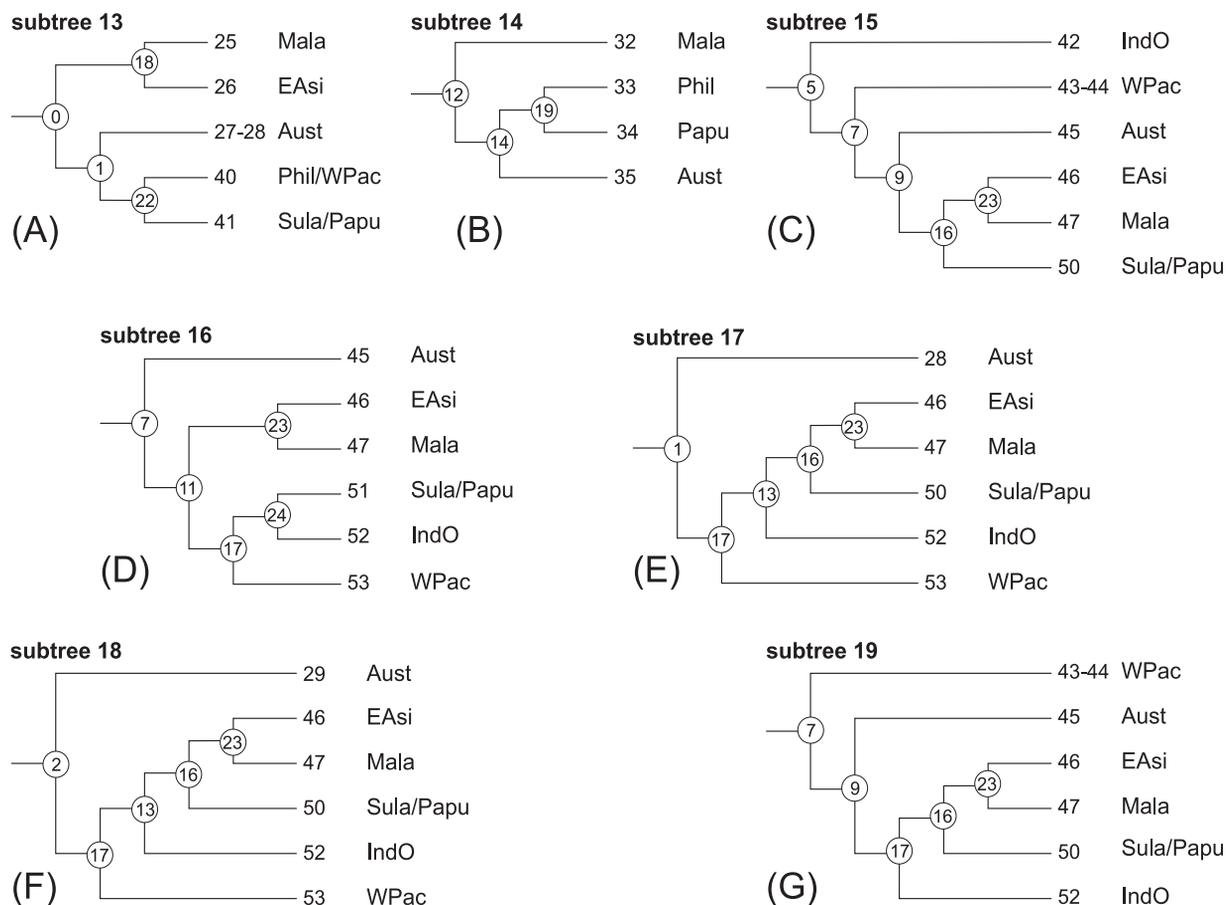
Fig.6. Paralogy-free subtrees derived from the taxon-area cladogram for *Asclepios*, *Austrobates*, and *Halobates* (Fig.5). Further explanation in text.

sal positions. The other tree (Fig.7F) has Aust, WPac, and Papu (in that order) in basal positions and IndO in a position close to the sister areas Mala and EAsi.

Discussion

Parsimony analyses of matrices derived from individual (not combined), paralogy-free subtrees generally yield cladograms with better resolution among areas than COMPONENT analyses of taxon-area cladograms for the same groups. While a strict consensus of the most parsimonious area cladograms for *Halovelia* (Fig.7A) is largely unresolved, a hierarchic structure is more apparent in the cladograms for the other groups of marine water striders, although the area relationships are not completely congruent. When data for *Halovelia* and the Halobatini are combined, the area relationships among all

eight areas are completely resolved (Fig.7C). When data for *Xenobates*, *Haloveloides*, and the Stenobatini are combined, the tree shows partly resolved area relationships among the areas Aust (Australia), Mala (the Malayan subregion), Papu (Papuasia), Phil (Philippines), and Sula (Sulawesi) (Fig.7D).Combining data for all four groups of marine water striders yields two, completely resolved area cladograms (Fig.7, E-F) which only differ in the position of IndO (Indian Ocean) in relation to the areas Papu, Sula, Phil, and Mala/EAsi (East Asia).

A strict consensus of the two, completely resolved area cladograms results in completely unresolved relationships between these areas which is not a fair representation of the information conveyed by the original area cladograms. In general, consensus trees are not well suited to summarize information about relationships between taxa or areas and should therefore be avoided. Instead, one should seek of possible
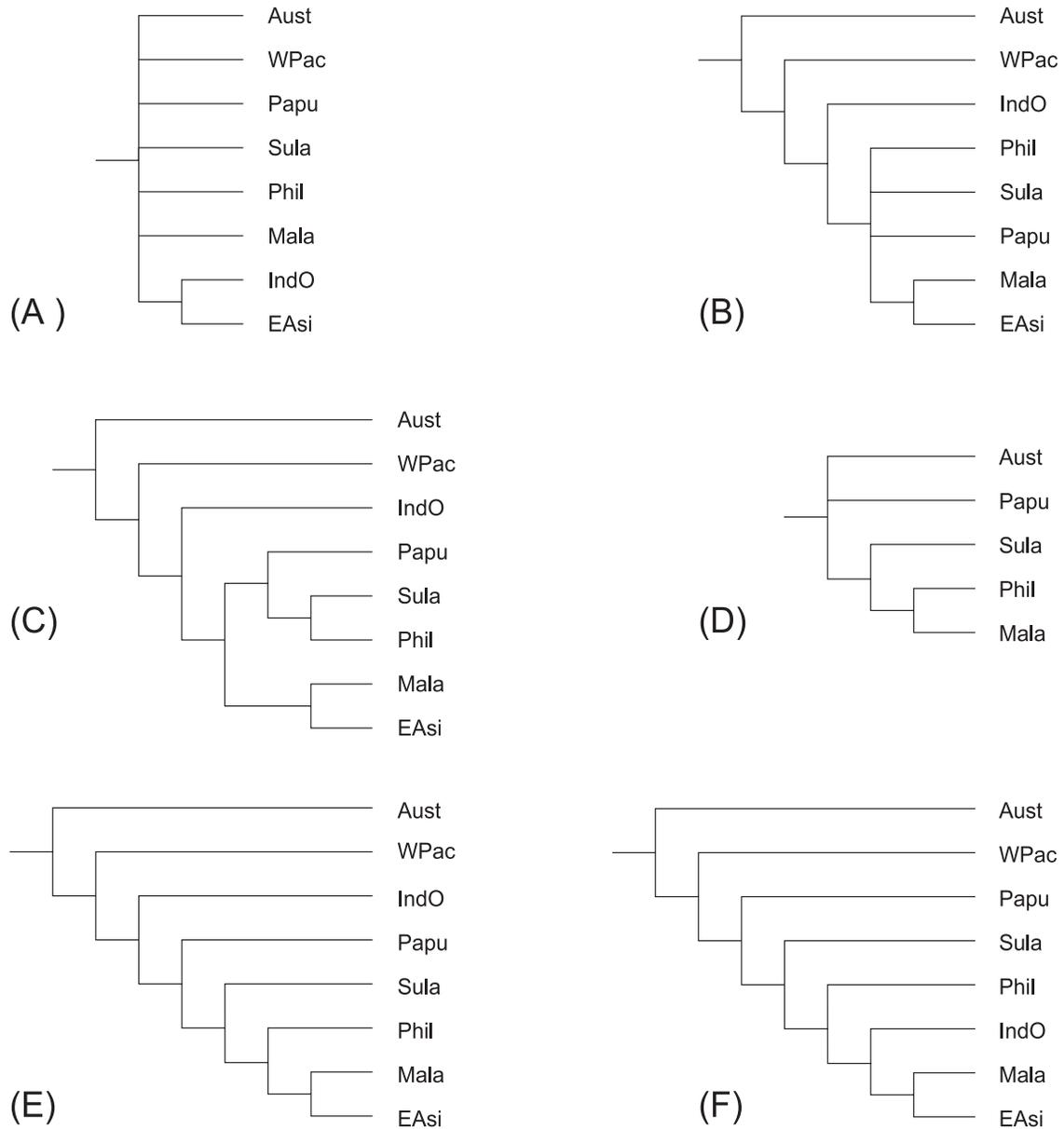
*Fig.*7. Area cladograms for marine water striders. (A) Consensus tree of 9 most parsimonious trees for *Halovelia* (Fig.4 and Table 1). (B) Consensus tree of 5 most parsimonious trees for *Asclepios*, *Austrobates*, and *Halobates* (Fig.6 and Table 1). (C) Most parsimonious area cladogram derived from subtrees for *Halovelia* and the Halobatini (Figs.4, 6, and Table 1). (D) Most parsimonious area cladogram derived from subtrees for *Haloveloides*, *Xenobates*, and the Stenobatini (Table 1). (E) One of two most parsimonious area cladograms derived from subtrees for all groups (Table 1). (F) Another most parsimonious area cladogram. Further explanation in text.

causes for the ambiguous area relationships. Unlike organisms, geographical areas may have more than one history. For example, most *Halovelia* species found along the coasts of East Africa, Madagascar, and the islands of the Indian Ocean (Mascarenes, Seychelles, and the Maldives) belong to the SE Asian *H. malaya* group (Andersen, 1989b) and may represent relatively late dispersal and subsequent speciation. On the other hand, the disjunct distributions of the most basal clades of *Halovelia* may be relicts of an ancient, much wider distribution of the genus as supported by the finding of a fossil *Halovelia* in the Oligo-Miocene Dominican amber (20-30 Ma; Andersen and Poinar, 1997).

Phylogenetic relationships provide clues to the evolution of present-day marine water striders, suggesting the number of independent origins of modern taxa, possible pathways of habitat changes and adaptive evolution, and the approximate geographical location of this evolution. The sister group of the marine Haloveliinae is a clade composed of two limnic genera, *Entomovelia* and *Strongylovelia* found in India, Indo-China, and Malesia (Andersen, 1982). The distribution of *Xenobates* and *Haloveloides* covers the same geographical areas, while the present distribution of *Halovelia* includes the whole Indo-Pacific region. Under the premise that marine species evolved from freshwater species occupying the same or an adjacent geographical area, marine haloveliines probably evolved somewhere in the Indo-Australian region.

The sister group of the Halobatini (Gerridae-Halobatinae) is the tribe Metrocorini with about 80 species distributed in tropical Africa, continental Asia, and the Indo-Malayan archipelago (including Sulawesi). The genus *Asclepios* (with three marine species) is confined to Asia. The sister group of *Halobates* is the monotypic genus *Austrobates*, endemic to tropical Australia (Andersen and Weir, 1994a) where also the most basal clade of *Halobates*, the subgenus *Hilliella* (with two species), is found (Andersen and Weir, 1994b). Under the assumption that ancestral taxa were no more widespread than their descendants, one may hypothesize that *Halobates* evolved along the coasts of Australia-New Guinea and/or in the Indo-Malayan archipelago and subsequently dispersed to other parts of the Indo-Pacific. The record of a Middle Eocene *Halobates* from modern northern Italy (45 Ma; Andersen *et al.*, 1994) suggests that these events took place in the early Tertiary, before the closure of Tethys and the formation of the present-day Middle East.

The most significant palaeogeographic event in the Indo-Pacific region was the northward movement of the Australian continent during the Cenozoic to its collision with an intra-oceanic arc some 25 Ma (Boer, 1995; Boer and Duffels, 1996; Hall, 1996, 1998 this volume; Packham, 1996). Before this event, the subduction of the oceanic lithosphere under the Pacific plate was accompanied with volcanic activity forming an island arc system comprised by present-day central Philippines and northern and southeastern New Guinea. The northward movement of Australia was preceded by continental fragments which form the present-day

Birds Head peninsula of New Guinea and parts of the Moluccas. Throughout most of the Cenozoic, the area between Asia and Australia was not an open ocean, but probably an archipelago of volcanic islands and microcontinents with rapidly changing areas of land and coastline contours. This may have been the perfect conditions for allopatric speciation and diversification among organisms of shallow seas including marine water striders.

Marine water striders are chiefly confined to the tropics, and their distributions seem to be limited by the same temperature regimes as reef-building corals and mangrove trees, i.e., in water bounded by the 20°C isotherms. Fossil evidence suggests major changes throughout the Tertiary in the climatic conditions favouring the presence of organisms of tropical shallow seas, including marine water striders. The mangrove palm, *Nypa*, had an extensive distribution in the Atlantic/Caribbean/East Pacific region in early Tertiary and once occurred at high latitudes in Europe (Ricklefs and Latham, 1993). Throughout much of the Tertiary, the reef coral belt appears to have been wider in latitude than it is today, though it was noticeably narrowed to something like its present limits by the late Neogene, and was reduced still further during the Pleistocene when it was narrower than today. The diversity of corals declined during the Neogene in the Atlantic/Caribbean and rose in the Indo-Pacific region, while in the Mediterranean, reef corals disappeared completely by the end of the Miocene (Rosen, 1988). Information derived from the few fossil marine water striders (Andersen *et al.*, 1994; Andersen and Poinar, 1997), suggests that both *Halovelia* and *Halobates* occupied wider geographical ranges in the past and that extinction may have played a significant role in shaping the present distributional patterns of marine water striders.

Acknowledgements

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