Invertebr. Taxon., 1994, **8**, 861–909

The Sea Skaters, Genus *Halobates* Eschscholtz (Hemiptera : Gerridae), of Australia: Taxonomy, Phylogeny and Zoogeography

Nils Møller Andersen[A] *and Tom A. Weir*[B]

[A] Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark.
[B] CSIRO Division of Entomology, GPO Box 1700, Canberra, ACT 2601, Australia.

Abstract

The sea skaters, genus *Halobates* Eschscholtz, include the only known oceanic insects, although most species of *Halobates* are found in sheltered coastal waters. The present paper deals with the 11 species known from Australian waters, divided into two subgenera, *Hilliella* China and *Halobates* s. str., and the latter into 5 species-groups. Characters found useful in forming these species-groups include: interocular width of head, head colour markings, relative lengths of fore tarsal segments, mesotibio-tarsal hair fringe, structure of male genital segments, and vesical armature. The cladistic relationships among species and species-groups are analysed and discussed. A key to the species of Australian *Halobates* is provided. All species endemic to Australia are redescribed and their distribution recorded and mapped. Taxonomic and distributional notes are given for the remaining species. *H. (Hilliella) lannae* is described as new from the Northern Territory, and the synonymies *H. australiensis* Malipatil (= *H. hayanus* White) and *H. ashmorensis* Malipatil (= *H. princeps* White) are verified. Finally, we discuss the ecological diversity and zoogeography of Australian sea skaters.

Introduction

The sea skaters, comprising the genus *Halobates* Eschscholtz, include the only known oceanic insects: five species are distributed in all tropical oceans and a further 38 species have been recorded from sheltered coastal waters of the Indo-Pacific (Herring 1961; Andersen and Polhemus 1976; Andersen 1982, 1991*a*; Cheng 1985; Polhemus and Polhemus 1991; Andersen and Foster 1992). The first species of *Halobates* recorded from Australia was *H. whiteleggei* Skuse (1891), which was described from Sydney Harbour. Additional species were described by Carpenter (1892), Hale (1925), Herring (1961), Polhemus (1982), Polhemus and Cheng (1982), and Malipatil (1988). Walker (1893), Mackerras (1950), Marks (1971), and Cheng and Schmitt (1982) reported on the biology and ecology of Australian sea skaters. The recent discovery of a freshwater relative of sea skaters, *Austrobates rivularis* Andersen & Weir (1994), in Cape York Peninsula, Queensland, has underscored the importance of the Australian fauna in understanding the evolution and historical biogeography of sea skaters.

We hope that the present work will encourage both marine biologists and entomologists to collect *Halobates* in Australia by helping them to assign their specimens to the correct species. All species endemic to Australia are redescribed and a new species, *H. lannae*, sp. nov., is described from the Northern Territory. Descriptive notes and illustrations are given for widespread species found in Australian waters. A key to *Halobates* species of Australia is provided and their distributions along the coasts of Australia are mapped. The cladistic relationships of Australian sea skaters are analysed and discussed in relation to a

0818-0164/94/040861$20.00

reconstructed phylogeny of *Halobates* (Andersen 1991*b*). Finally, we discuss the biology, ecology, and zoogeography of Australian sea skaters in relation to present knowledge about the phylogeny and distribution of these marine insects.

Materials and Methods

The present study is based upon material of sea skaters from marine localities of Australia borrowed from the institutions listed as repositories below. The identification of new material has been greatly facilitated by reference to specimens deposited in the Zoological Museum, University of Copenhagen, which houses one of the largest collections of marine water striders in the world (including the Lanna Cheng collection). Other major collections, in particular those of the Natural History Museum, London, and the John T. Polhemus collection, Englewood, Colorado (now belonging to the National Museum of Natural History, Washington, D.C.), have been studied by the senior author.

Coastal species of sea skaters can easily be collected in nearshore, marine habitats (estuaries, mangroves, intertidal coral reefs) by using a light-weight fishing net with a fine-meshed nylon or other rapid-drying bag. Species of marine water striders including *Halobates* are strongly attracted to light and a particularly productive collecting method is the use of a light-source at night suspended over the side of a boat or from the end of a pier. The open-ocean species may be collected in this way from a boat, or may be picked up after storms when they are stranded on beaches. Specimens should be placed immediately in 70% alcohol, which should be replaced within 24 h to ensure that sea water and salt dust are removed or dissolved.

Sea skaters can be stored permanently in 70% alcohol, although specimens often become discoloured after a lengthy period of storage. Dry mounting of synoptic series is therefore advisable. The general coloration of the body, usually described as silver-grey or black, may depend upon the manner in which specimens have been preserved. In dry-preserved specimens, a drop of alcohol is often useful to bring out the extent and pattern of the yellow markings of the head, which otherwise may be obscured by the pubescence.

Methods for dissecting and examining the male genitalia of *Halobates* are described by Andersen (1991*b*). The terminology used for the male terminalia is explained in that paper and below. All measurements are given in millimeters. Total length and body width are given as ranges for all individuals examined. Other measurements are given for a single specimen: either holotype, lectotype, representative paratype, or other specimen (if no type material is available). As a measurement of size, the total length is not quite reliable since the last 3–6 abdominal segments are connected by membranes and can be extended to a varying degree. The method of calculating the ratio between interocular head width and eye width is explained below. The length of the femora is measured along the dorsal side of the limb, not including the trochanters.

In the taxonomy section, complete descriptions are given for those *Halobates* species that are endemic to Australia. For widespread species occurring in Australian waters, descriptive notes and illustrations are given to facilitate their identification. The senior author has been able to examine holotypes or other type material for most nominal species covered in this paper. The synonymical bibliographies under the taxonomic headings include synonyms and any additional papers dealing with Australian species. Other useful references are given by Herring (1961), Andersen and Polhemus (1976), Cheng (1985), and Andersen (1991*b*).

Abbreviations for Repositories:

AMS	Australian Museum, Sydney, Australia
ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia
BMNH	The Natural History Museum (formerly British Museum, Natural History), London, UK
BPBM	Bernice P. Bishop Museum, Honolulu, USA
JTPC	John T. Polhemus collection, Englewood, Colorado, USA (belonging to the National Museum of Natural History, Washington, D.C.)
NRS	Naturhistoriska Riksmuseet (Natural History Museum), Stockholm, Sweden
NTMD	Northern Territory Museum, Darwin, Australia
QMB	Queensland Museum, Brisbane, Australia
RNHL	Rijksmuseum van Natuurlijke Historie (National Museum of Natural History), Leiden, The Netherlands
SAMA	South Australian Museum, Adelaide, Australia
SMEK	The Snow Entomological Collection, University of Kansas, Lawrence, Kansas, USA
UMO	University Museum, Oxford University, Oxford, UK

UQIC University of Queensland Insect Collection, Brisbane, Australia
USNM National Museum of Natural History, Washington, D.C., USA
WAM Western Australian Museum, Perth, Australia
ZMUC Zoological Museum, University of Copenhagen, Denmark

Genus ***Halobates*** Eschscholtz

Halobates Eschscholtz, 1822: 106.—White, 1883: 23; Matsuda, 1960: 299; Herring, 1961: 240.
Euratas Distant, 1910: 146.—Esaki, 1929: 417 (synonymy with *Halobates*).
Fabatus Distant, 1910: 147 [nymph].—Annandale and Kemp, 1915: 183 (synonymy with *Euratas*).

Type species: *Halobates micans* Eschscholtz, 1822, by subsequent designation (Laporte 1832: 24); *Euratas* Distant: *Euratas formidabilis* Distant, 1910, by monotypy; *Fabatus* Distant: *Fabatus servus* Distant, 1910, by monotypy.

Diagnosis

Length 3·2–6·5. Chiefly dark coloured or silver-grey species without extensive pale markings except on venter (immature specimens have more extensive pale body areas). Yellow markings on head usually restricted to a basal, crescent-shaped mark; if most of the head yellow, then the male fore femora are unarmed beneath. Intersegmental suture between meso- and metanotum incomplete, usually reduced to a pair of lateral V-shaped pits. Male fore femora rarely with ventral spines or tubercles. First segment of fore tarsus variable in length. Males with eighth abdominal segment wider than long, with rounded, tuberculate, or finger-like spiracular processes; styliform processes present, usually long and slender. Male proctiger usually pentagonal in outline, produced or dilated laterally.

Comments

China (1957) proposed the subgenus *Hilliella* for *Halobates mjobergi* Hale (type species) and *H. apicalis* Esaki. Character states used to define this subgenus were the absence of a hair fringe on the first segment of the middle tarsus, the pale stripes on the fore and middle femora and tibiae, and the hairy processes of the eighth abdominal segment in the male. More recently, Polhemus and Cheng (1982) also placed *H. zephyrus* Herring in *Hilliella* because of its supposed relationship with *H. mjobergi*. However, Andersen (1991*b*) showed that *H. zephyrus* is more closely related to the *regalis* group. The taxonomic status of the subgenus *Hilliella* as defined by China (1957) is problematical. *Halobates apicalis*, one of the species originally assigned to his subgenus, clearly belongs to the South and East Asian genus *Asclepios* (Andersen 1991*b*). However, contrary to Andersen (1991*b*), we feel that other diagnostic characters of *Hilliella* justify its status as a valid subgeneric entity, being the sister-group of all other *Halobates* (Fig. 3).

Species-groups

Halobates is a large genus with 43 described species which can be arranged in a number of monophyletic species-groups (Andersen 1991*b*). The Australian fauna includes species belonging to 5 of the 13 species-groups recognised by Andersen (1991*b*), namely the *mjobergi*, *regalis*, *hayanus*, *micans* and *princeps* groups. These groups only partly conform with the species-groups delimited by Herring (1961). Below, we erect a separate group for *H. zephyrus*, formerly included in the *regalis* group.

In this section we describe a number of characters used to group the species of *Halobates* and explain the terminology used in the key and species descriptions.

Characters Used to Group Species

Interocular width of head

Herring (1961: key, p. 241) used the ratio between interocular width of head and the width of an eye to separate the open-ocean species (ratio greater than 4) from coastal

species of *Halobates* (ratio 3·0–3·5). Herring (1961: fig. 108) indicated that the relevant measurements should be taken along an imaginary line across the base of the head, perpendicular to the longitudinal body axis. Since the inner margins of the eyes are diverging posteriorly, the ratio is then calculated by dividing the *maximum* interocular width by the *minimum* width of an eye. However, as pointed out by Polhemus and Polhemus (1991: 7), this procedure will place individuals (especially females) of some coastal *Halobates* species in the open-ocean group. This apparently misled Malipatil (1988) when he described two new species of *Halobates* from Australia (subsequently synonymised with *H. hayanus* White and *H. princeps* White; see below). In addition, the individual variation is relatively large, as seen from the following ratios in 10 males: *H. germanus* White (open-ocean species), range 3·9–4·8 (mean value 4·6); and *H. hayanus* (coastal species), range 3·0–3·7 (mean value 3·4). In the present paper, we calculate the ratio between interocular width and eye width as defined by Herring (1961) [but not Polhemus and Polhemus (1991)], but avoid using the ratio in the key.

Head colour markings

H. mjobergi (Fig. 5) has its dorsal head surface yellow except for a central dark stripe. Similar colour markings are found in *H. zephyrus* (Fig. 24), and in most species of the *regalis* group. In other species, the pale, lateral stripes are interrupted in the middle (Fig. 33). Most other species of *Halobates* have the pale colour reduced to a crescent-shaped marking at the base of the head (Fig. 70). This reduction has gone further in the open-ocean species, *H. micans* Eschscholtz, *H. sericeus* Eschscholtz and *H. germanus*, where the pale markings are reduced to a pair of small triangles close to the anterior margin of the pronotum (Fig. 88).

Fore tarsus

The relative length of the two segments of the fore tarsus is an important taxonomic character in *Halobates* (Herring 1961). However, before using relative measurements, one must take into account that different segments often grow at different rates (allometry). In the Gerridae, the length of the first tarsal segment usually increases at a steeper rate than that of the second segment (Matsuda 1960). By comparing *Halobates* males of different size, Andersen (1991*b*) observed that the fore tarsal ratio varies between 0·3 (*H. maculatus* Schadow, length 3·0) and 1·7 (*H. princeps*, length 6·2), as predicted. Thus, this character is of doubtful value in grouping species. There are, however, some deviating species: *H. mjobergi* and *H. zephyrus* have the smallest fore tarsal ratio, 0·2–0·3, although they are not the smallest species (3·3–4·0).

Mesotibio-tarsal hair fringe

One of the distinct features of the legs of *Halobates* is a fringe of long hairs along the ventral surface of the middle tibia and tarsus (Fig. 48) (called 'swimming hairs', e.g. by China 1957). Already White (1883) noticed that coastal species of *Halobates* have mesotibio-tarsal fringes with shorter hairs than open-ocean species like *H. sericeus* and *H. micans*. This difference is excellently illustrated by Miyamoto and Senta (1960). However, another open-ocean species, *H. germanus*, has a relatively narrow mesotibio-tarsal hair fringe, although it is wider than in the coastal species. The hair fringe is limited to the middle tibia in *H. mjobergi* and *H. lannae* (Fig. 1), a state shared with some (but not all) *Asclepios* species (Andersen 1991*b*).

Male genital segments

The male abdomen of *Halobates* is relatively short. Most of the pregenital abdominal segments are reduced in length, but the genital segments are prolonged and very conspicuous (Fig. 2, pr). The eighth abdominal segment is cylindrical, usually as wide as long (Figs 2, 7, t8; Fig. 9, s8). The dorsal hind margin is roundly produced in most species. Each of the spiracles of the eighth segment is typically placed upon a *spiracular process* (Fig. 9, sp). The ventral hind margin of the segment is concave, with a pair of slender *styliform*

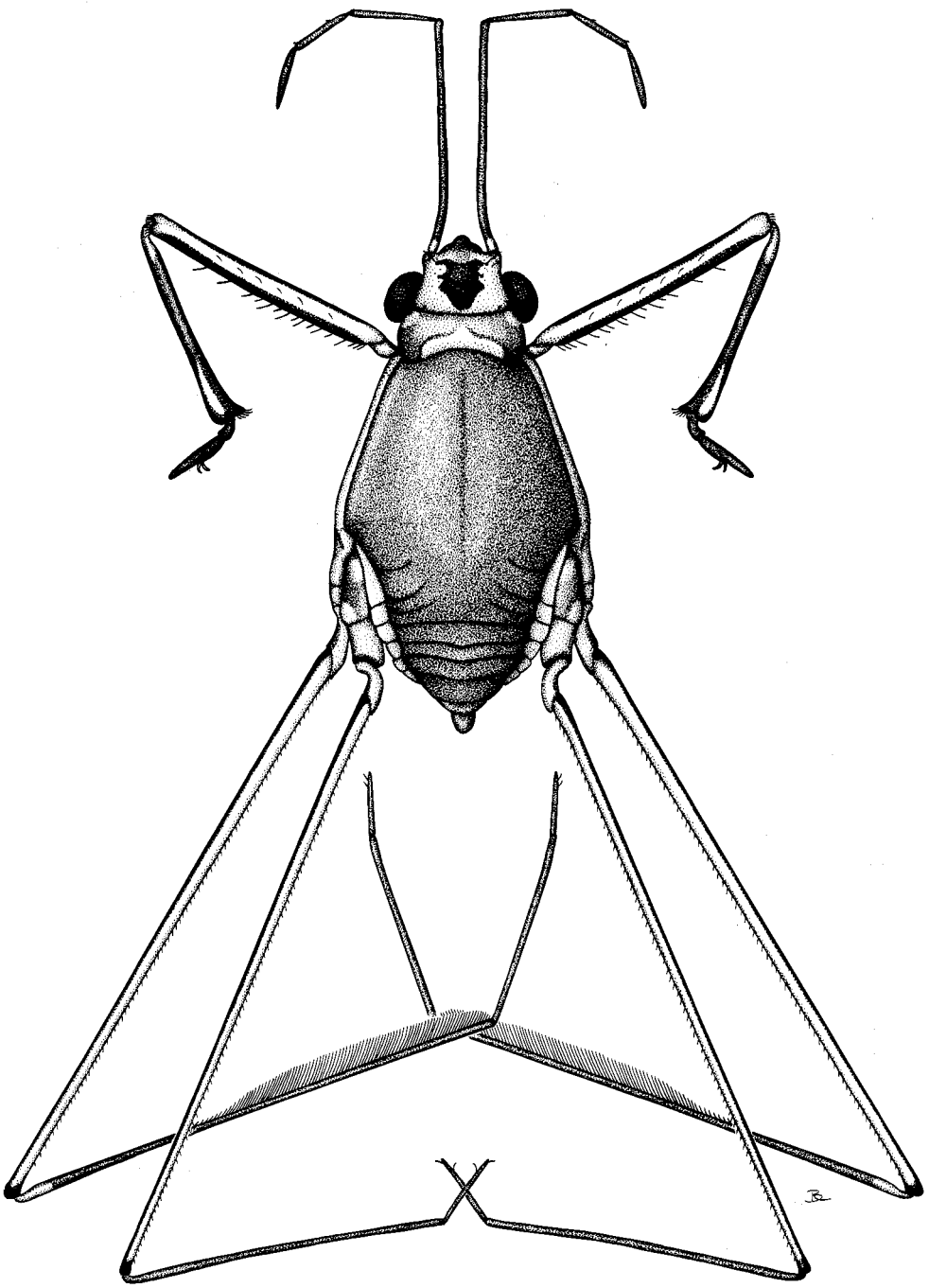


Fig. 1. *Halobates lannae*, habitus of apterous ♀ from Darwin, Northern Territory. Length of body 4·6 mm.

processes (Figs 8, 9, st) varying in relative length, degree of asymmetry, orientation, shape of apices, etc. The *pygophore* (= segment 9; Fig. 9, py) is subovate in ventral outline in most species. It is boat-like and its tergal part is reduced to a narrow proximal bridge.

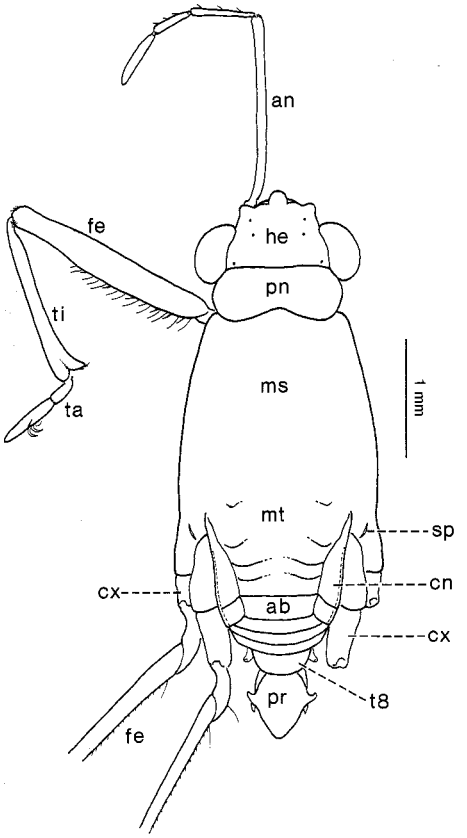


Fig. 2. *Halobates darwini*, dorsal structure of ♂; distal parts of middle and hind legs and appendages of right side omitted. Abbreviations: ab, abdomen; an, antenna; cn, abdominal connexivum (laterotergites); cx, coxae of middle and hind legs; fe, femora; he, head; ms, mesonotum; mt, metanotum; pn, pronotum; pr, abdominal terminalia (proctiger); sp, metathoracic spiracle; t8, abdominal segment 8; ta, tarsus; ti, tibia.

The phallic organ (see below) is inside the pygophore when not distended. The pygophore carries a pair of slender *parameres* in *H. mjobergi* (Fig. 11) and *H. lannae* (Fig. 20). These are absent in all other *Halobates* species. The *proctiger* (segment 10+11) lies on top of the pygophore (Figs 7, 8, pr). It is plate-like, usually pentagonal in outline, with its lateral margins more or less produced in many species. The proctiger was called tergum 9 by Herring (1961).

While the genital segments of *H. mjobergi* (Figs 7–9) and *H. lannae* (Figs 16–18) appear to be strictly symmetrical, various degrees of asymmetry are observed in other *Halobates* species. The highest degree of asymmetry is found, e.g. in *H. darwini* (Figs 49–51), *H. herringi* (Figs 63–65), and *H. micans* (Figs 78–80).

Vesical armature

The phallic organ is composed of two parts (Andersen 1991*b*: fig. 3): a proximal *phallotheca* and a distal *endosoma*. The latter is again divided into a membranous *conjunctivum* and a *vesica*, which has an armature of sclerotised pieces. The structure of the vesical sclerites has proved very useful for placing species in monophyletic species-groups and in clarifying the phylogenetic relationships between them (Andersen 1991*b*).

In order to examine the vesical armature, the phallus first has to be removed from the pygophore. The endosoma is then pushed or pulled out of the phallotheca by means of a fine needle. The ground plan structure is probably close to that found in *Halobates mjobergi* (Figs 12, 13). The most conspicuous structure is an axial, heavily sclerotised, rod-like *dorsal sclerite* (ds). Its apical part is recurved, describing a semicircle, and has a widened and furcated apex. The dorsal sclerite is proximally closely associated with the less sclerotised *ventral sclerite* (vs) which is very long, band-shaped, and distinctly tapering toward the apex. There are two pairs of *lateral sclerites*, of which the first pair

(ls1) are relatively stout while the second pair (ls2) are long and slender. In addition to this armature, the vesica usually has more or less diffuse sclerotised areas or bands in the cover surrounding the dorsal, lateral and apical parts of the vesica. Some of the 'sclerotised pieces' illustrated by China (1957: fig. 3*e*) are of this nature.

The vesical armature of *H. mjobergi* appears to be strictly symmetrical. This state is probably the primitive state within the Halobatini (as well as in most other Gerridae). In all other species of *Halobates* examined, the vesical armature is more or less asymmetrically developed and the structure and number of sclerites vary. In the Australian endemic *H. zephyrus* (Figs 30, 31), the widespread coastal *H. hayanus* (Figs 75, 76), and the open-ocean species *H. micans*, *H. sericeus*, and *H. germanus* (Andersen 1991*b*: figs 4*E*, 5*A*), the dorsal sclerite of the vesica is perforated by an ovate or diamond-shaped hole and there is only one pair of lateral sclerites (Figs 75, 76, ls1), homologous with the first pair of *H. mjobergi*.

In species belonging to the *regalis* group, including several endemic to Australia, the vesical armature is quite similar to that of the previous species-groups except that the distal part of the dorsal sclerite is modified (Figs 38, 39, 45, 46) or more or less reduced (Figs 53, 54, 67, 68).

As the only species from Australian waters, *H. princeps* belongs to the species-groups where the vesica has an armature composed of a basal sclerite, a solid non-perforated dorsal sclerite, and two pairs of lateral sclerites (Andersen 1991*b*: fig. 6).

Cladistic Relationships

A reconstructed phylogeny for the genus *Halobates* was presented by Andersen (1991*b*), based upon cladistic analyses using the parsimony program Hennig86 (Farris 1988). The preferred cladogram of relationships between monophyletic species-groups of *Halobates* (groups with Australian species in boldface) is shown in Fig. 3. It is especially worth noticing that the *mjobergi*-group (= subgenus *Hilliella*) is sister-group to all other species of the genus and that most Australian *Halobates* species belong to only one of the two major clades of the reconstructed phylogeny of sea skaters. In this section, we will try to clarify the cladistic relationships between species belonging to the *regalis* group, which includes about half of the Australian *Halobates* species.

For this analysis, we scored 16 characters for the Australian species of the *regalis* group, namely *H. acherontis*, *H. darwini*, *H. herringi*, *H. regalis*, *H. whiteleggei*, and *H. zephyrus*. We also included *H. murphyi* Polhemus & Polhemus (Papua New Guinea), *H. peronis* Herring (Philippines, New Guinea, Solomon Islands), and *H. sexualis* Distant (West Malaysia, Sri Lanka) which belong to the same species-group. *H. hayanus* and *H. mjobergi* were selected as outgroups. The characters and their states are listed below. Since Hennig86 has no option for analysing character-state trees, the apices of the styliform processes are described by way of two characters (Nos 10 and 11). The distribution of character states for all terminal taxa are shown in Table 1.

Definition of Characters and States

0. Dummy character (to adjust character numbering in Hennig86 to start with No. 1).
1. Head with extensive pale markings bordering the eyes (0); pale markings interrupted in middle (1); pale markings reduced to a crescent-shaped mark extending forward toward the eyes (2).
2. Antennae relatively long, 0·75× or more the length of male (0); antennae shorter, 0·67× or 0·5× the length of male (1).
3. First segment of male fore tarsus less than 0·3× second segment (0); 0·3–0·4× second segment (1); first segment more than 0·4× second segment (2).
4. Meso-metanotum of male without bristles (0); with scattered, stiff black bristles (1).
5. Meso-metanotum of female without bristles (0); with scattered, stiff black bristles (1).
6. Middle and hind femora subequal in length (0); middle femur distinctly longer than hind femur (1)

7. Styliform processes widely separated at base (0); arising from a common base (1).
8. Styliform processes of about same length (0); slightly different in length (1).
9. Apices of styliform processes simple and straight (0); apices modified (1).
10. Apices of styliform processes simple and pointed (0); simple but blunt (1); otherwise shaped (2).
11. Apices of styliform processes simple, pointed or blunt (0); widened (1); boot-shaped (2).
12. Proctiger symmetrical (0); more or less asymmetrically developed (1).
13. Lateral extensions of proctiger rounded or subparallel (0); distinctly produced, more or less pointed (1); finger-like produced (2); as before, but drawn out to slender spines.
14. Dorsal sclerite of vesica not perforated (0); perforated in proximal half or in middle (1); perforated in distal half (2).
15. Apical, recurved part of dorsal sclerite shorter than half length of dorsal sclerite (0); longer than half length of dorsal sclerite (1); reduced (2).
16. Apex of dorsal sclerite strongly enlarged (0); widened, but relatively small (1); reduced (2).
17. Ventral sclerite band-shaped but not distinctly wider than dorsal sclerite (0); distinctly wider than dorsal sclerite (1).

Table 1. Character state matrix for species of the *Halobates regalis* group and three outgroup species, *H. mjobergi*, *H. hayanus* and *H. zephyrus*

Meaning of characters and character states explained in the text

Character nos	0 0	0 1	0 2	0 3	0 4	0 5	0 6	0 7	0 8	0 9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7
H. regalis	–	1	0	2	0	1	1	1	1	1	2	1	0	1	1	1	2	0
H. whiteleggei	–	0	0	1	0	1	1	1	1	1	2	1	1	1	1	1	1	0
H. sexualis[A]	–	1	1	1	0	?	1	1	1	1	2	1	0	2	1	2	2	1
H. peronis[A]	–	1	1	1	0	0	1	1	1	1	2	2	0	2	1	2	2	1
H. murphyi[A]	–	1	1	1	0	1	1	1	1	1	2	2	0	2	1	?	?	?
H. darwini	–	1	1	2	1	1	1	1	1	1	2	2	1	2	1	2	2	1
H. acherontis	–	1	1	2	1	1	1	1	1	1	2	2	1	2	1	2	2	1
H. herringi	–	1	1	2	0	1	1	1	1	1	2	2	1	3	1	2	2	1
H. mjobergi	–	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
H. hayanus	–	2	0	2	0	0	1	0	0	1	0	0	0	0	1	1	1	0
H. zephyrus	–	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0

[A] Extra-Australian species.

The analysis was performed using the *ie** (implicit enumeration) command of Hennig86, which guarantees to find all most parsimonious trees for the data set in question. Only one tree was found, 32 steps long, with a consistency index of 0·75 and a retention index of 0·82. The relationships derived from this tree, with character changes (denoted by character number and character state) placed upon branches (internodes) are shown in Fig. 4.

Even though *H. hayanus* was explicitly selected as one of the two outgroups, the analysis places this species in the ingroup while *H. zephyrus* is connected to the outgroup node. The reason is that *H. zephyrus* is more plesiomorphic than *H. hayanus* in the colour pattern of the head (1), very short first tarsal segment (3), middle and hind femora subequal in length (6), and more simple styliform processes (9). However, since the primary objective of the analysis was to clarify the relationships within the *regalis* group (with *H. zephyrus* tentatively included), the relationships between *H. hayanus* and these species must remain unsettled as depicted in Fig. 3. The results of the cladistic analysis (Fig. 4) emphasise, however, the uniqueness of *H. zephyrus* among Australian *Halobates* species.

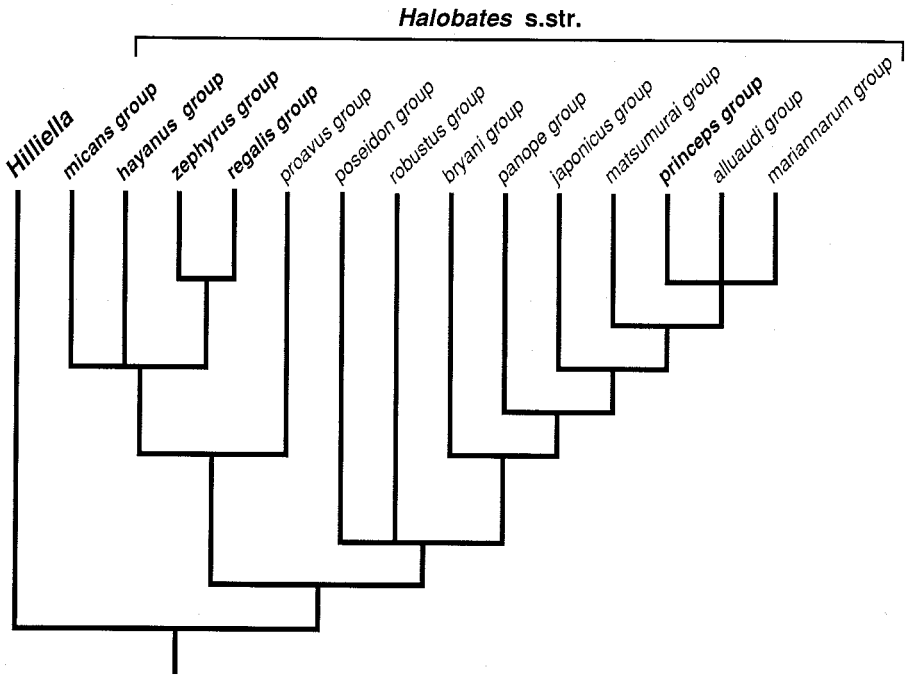


Fig. 3. Cladistic relationships between species-groups of *Halobates* (based upon Andersen 1991*b*). Species-groups with Australian species in boldface.

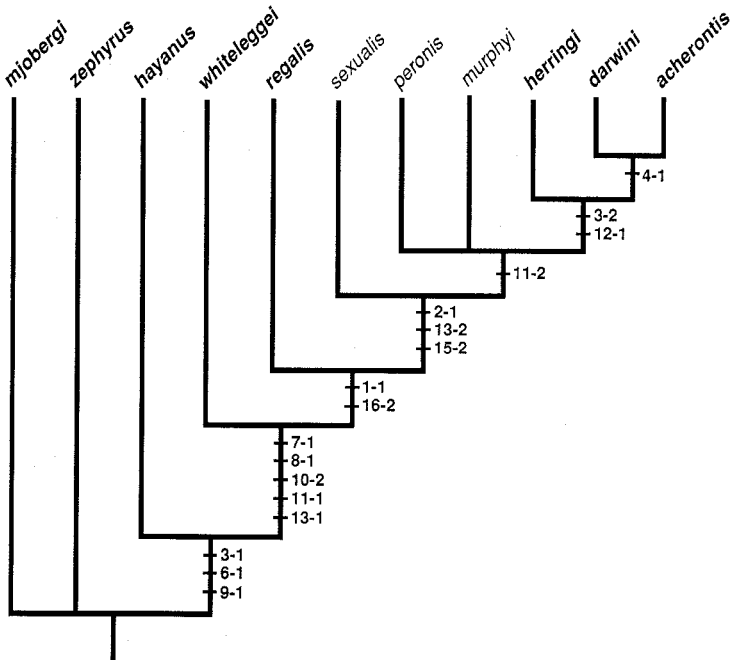


Fig. 4. Cladistic relationships between *Halobates* species belonging to the *zephyrus* and *regalis* groups. Australian species in boldface. Meaning of character-numbers and character-states explained in the text.

Key to the Australian Species of *Halobates* Eschscholtz

1. Body length 5·8–6·2 (♂ and ♀). Male proctiger pentagonal, with a recurved prominence on lateral angle (Fig. 94). Fore femur of male with a tubercle beneath ..... *H. princeps* White
   Body length at most 5·5. Structure of male proctiger not as above. Fore femur of male unarmed 2
2. First segment of fore tarsus shorter than 0·3× second segment. Middle femur at most 1·05× longer than hind femur 3
   First segment of fore tarsus longer than 0·3× second segment. Middle femur 1·1× or more longer than hind femur 5
3. Brown and yellow species usually with posterior margin of pronotum, most of thoracic pleura, and prominent stripes on femora, yellow (Fig. 1). Apices of male styliform processes slender and curved (Figs 8–10, 17–19) (subgenus *Hilliella* China) 4
   Dark brown to black species with most of thoracic pleura dark and only bases of anterior femora, yellow. Apices of male styliform processes slender and straight (Figs 27–29) ..... *H. zephyrus* Herring
4. Body length 3·3–3·8 (♂) or 3·4–4·2 (♀). Male fore femur depressed ventrally in distal fourth with an elongate patch of stiff hairs (Fig. 6). Female meso-metanotum with scattered, long dark bristles. Male terminalia (Figs 7–10) .. *H. mjobergi* Hale
   Body length 4·1–4·5 (♂) or 4·3–4·7 (♀). Male fore femur not modified ventrally, tapering in width toward apex (Fig. 15). Female meso-metanotum without long scattered dark bristles. Male terminalia (Figs 16–19) ..... *H. lannae*, sp.nov.
5. Yellow coloration on head extensive, with prominent yellow stripes along eyes (Fig. 24) or reduced to a crescent-shaped mark extending forward toward the eyes (Fig. 70), occasionally with a yellow spot at the base of antennae (Fig. 33). Conspicuous yellow or brown markings on some parts of venter. Near-shore species 6
   Yellow coloration on head reduced to a pair of triangular markings at the base (Fig. 88). Body including thoracic and abdominal venter, uniformly dark. Open-ocean species 11
6. Proctiger of male with a patch of spinous dark hairs on each side, styliform processes almost symmetrical, apices slender and diverging (Figs 71–74). Female meso-metanotum without dark bristles ..... *H. hayanus* White
   Proctiger of male without a patch of spinous dark hairs on each side, styliform processes neither symmetrical nor diverging apically, apices stout. Female meso-metanotum with scattered, dark bristles 7
7. Both male and female completely yellow beneath. Apices of styliform processes of male stout, but not boot-shaped (Figs 37, 44). Hind trochanters of female pilose, but without a tuft of long hairs 8
   Male not completely yellow beneath, thoracic venter darkened. Apices of styliform processes of male boot-shaped (Figs 52, 60, 66). Hind trochanters of female with a tuft of long hairs 9
8. First segment of fore tarsus 0·5× (♂) or 0·6× (♀) longer than second segment. Male terminalia (Figs 34–37). Hind coxae of female shorter, only about 2·0× as long as wide ..... *H. regalis* Carpenter
   First segment of fore tarsus 0·4× (♂) or 0·5× (♀) longer than second segment. Male terminalia (Figs 41–44). Hind coxae of female very long, about 3·0× times as long as wide ..... *H. whiteleggei* Skuse
9. Lateral projections of male proctiger finger-like but relatively short (Figs 49, 57). Male meso-metanotum with scattered stiff, black bristles 10
   Lateral projections of male proctiger finger-like and long (Figs 63–65). Male meso-metanotum without scattered stiff, black bristles ..... *H. herringi* Polhemus & Cheng
10. Body length 4·5–4·8 (♂) or 4·3–4·8 (♀). Meso-metanotum with few short, dark bristles (Fig. 55) ..... *H. darwini* Herring
    Body length 3·8–4·2 (♂) or 3·8–3·9 (♀). Meso-metanotum with numerous long, dark bristles (Fig. 61). ..... *H. acherontis* Polhemus
11. Body length 4·4 (♂), 4·0 (♀) or more. Styliform processes of male strongly asymmetrical, left process bent abruptly upwards at a right angle, apices modified (Figs 78–81. ..... *H. micans* Eschscholtz

Smaller species, length less than 4·0 (♂) or 3·8 (♀). Styliform processes of male almost symmetrical, apices simple 12

12. Second antennal segment 0·5× as long as fourth segment. First segment of fore tarsus about 0·4× longer than second segment. Male terminalia (Figs 83–86) .... *H. sericeus* Eschscholtz

Second antennal segment much more than 0·5× as long as fourth segment. First segment of fore tarsus about 0·6× longer than second segment. Male terminalia (Figs 89–92) ..... *H. germanus* White

Subgenus ***Hilliella*** China

Hilliella China, 1957: 342 (as subgenus). — Andersen, 1991*b*: 47 (synonymy with *Halobates*).

Type species: *Halobates mjobergi* Hale, 1925 by original designation (China 1957).

Diagnosis

Length 3·3–4·7. Colour dark brown with extensive yellow markings on head, pronotum, pleura, legs, and venter. First segment of fore tarsus much shorter than second segment. Distal half of middle tibia with hair fringe, fringe about 2·5× as wide as tibia; tarsal segments without hair fringe. Hind tarsal segments fused. Male terminalia: styliform processes of segment 8 and proctiger symmetrical. Parameres present. Vesical armature symmetrical; dorsal sclerite not perforated, 2 pairs of lateral sclerites. Female terminalia: gonocoxae relatively large, partly exposed, proctiger button-shaped, protruding.

Halobates (Hilliella) mjobergi Hale

(Figs 5–14)

Halobates mjobergi Hale, 1925: 12. — Herring, 1961: 274.
Halobates (Hilliella) mjobergi. — China, 1957: 342; Polhemus, 1982: 7.

Material Examined

Holotype. ♂, Western Australia, 'Broome, June 16th, 1911, E. Mjöberg' (NRS).

Paratypes. 1♂, 1♀, 'Broome, N. V. Austr., Mjöberg' (SAMA).

Other material examined. **Northern Territory:** 1♂, Darwin, among mangrove roots, 26.ii.1982, J. R. Hanley (NTMD); 5♂, 3♀, Darwin, Frances Bay, CL914, 13.xii.1977, J. T. Polhemus (ANIC, JTPC, UQIC, ZMUC); 3♂, 2♀, Darwin, Ludmilla, in brackish water among mangroves, 22.iii. 1982, M. B. Malipatil (NTMD); 5♂, 2♀, 1 nymph, Darwin, Ludmilla Ck, mouth, 18.ii.1987, R. Hanley and R. Williams (NTMD); 1 nymph, same loc., mangrove mudflat, 18.ii.1987, R. Hanley and R. Williams (NTMD); 1♂, Ludmilla Ck nr Darwin, among mangrove roots, 26.ii.1982, J. R. Hanley (NTMD); 4♂, 1 nymph, same loc., in mangroves, 22.iii.1982, J. R. Hanley (NTMD); 1♂, 1♀, Inglis I., 11·59 S 136·18 E, 29.i.1988, H. Larson (NTMD); 13♂, 5♀, + many nymphs, Coral Bay, Port Essington, 19.vii.1981, no collector (NTMD); 5♂, 2♀, Woods Inlet, 12·29 S 130·46 E, 10.iii.1988, P. Alderslade (NTMD); 16♂, 8♀, + many nymphs, W. Alligator Mouth, 12·11 S 132·16 E, 20–22.vii.1979, G. Monteith and D. Cook (QMB). **Queensland:** 12♂, 9♀, + many nymphs, Cape York, 6–10.vi.1969, G. B. Monteith (ANIC); many ♂, ♀, and nymphs, Roonga, 10·43 S, 142·25 E, amongst mangroves and in sea, 17.x.1992, T. Weir, P. Zborowski (ANIC); 1♀, Portland Roads, CL1751, 24.viii.1983, J. T. and D. A. Polhemus (JTPC); 2♂, 2♀, Somerset Bay, mangroves, CL1763, 28.viii.1983, J. T. and D. A. Polhemus (JTPC, ZMUC); 6♂, 6♀, Mornington I., Appel Channel, June 1960, P. Aitken and N. B. Tindale (SAMA). **Western Australia:** 2♂, 3♀, Monte Bello I, South Hermite, mangrove swamp, 25.viii.1952, F. L. Hill (BMNH); 15♂, 11♀, + many nymphs, same loc., 12.xi.1953, T. G. Campbell (AMS).

Description

Size. ♂, length 3·3–3·8, body width 1·65–1·8, head width 1·15–1·3; ♀, length 3·4–4·2, body width 2·1–2·3, head width 1·2–1·4.

Colour. Body chiefly brown with greyish pubescence and extensive yellow markings. Head yellow with a central dark stripe. Antennae dark brown with base of each segment yellow. Pronotum uniformly brown or more or less extensively margined with yellow (Fig. 5). Meso-metanotum and abdominal terga brown, connexiva with yellow markings. Thoracic pleura and entire thoracic and abdominal venter, yellow. Fore femora and tibia (Fig. 6), middle and hind femora, yellow with longitudinal dark stripes; remaining leg segments brownish. Male proctiger yellow with more or less extensive brown median part. Styliform processes with dark apices.

Male structure. Body oval, length about 2·1× maximum body width (3·52 : 1·65). *Head* between eyes about as long as wide (0·68 : 0·70), interocular width about 2·9× width of an eye (0·70 : 0·24). Antenna 0·9× length of the body (3·08 : 3·52). Lengths of antennal segments (1–4): 1·45 : 0·52 : 0·55 : 0·55. *Thorax.* Pronotum 3·6× wider than long (1·00 : 0·28) and 0·4× length of head on the median line (0·28 : 0·68). Sides of meso-metanotum rounded, gradually diverging to maximum width across the middle acetabula, without prominent dark bristles. *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 1·82 : 1·25 : 0·12 : 0·45; middle leg, 4·60 : 3·78 : 1·50 : 0·55; hind leg, 4·68 : 2·15 : 0·55 (I+II). Fore femora moderately robust (Fig. 6), widest across the middle (0·22); ventral margin impressed in distal fourth; an elongate patch of dark, stiff hairs just before impression. Fore femora with 5–8 long, black bristles on ventral margin and 3–4 bristles on external surface. First segment of fore tarsus very short, about 0·3× length of second segment. *Terminalia* (Figs 7–11). Styliform processes slender, symmetrical, and diverging; both apices visible from above, pointed, and with dark denticles (Fig. 10). Proctiger pentagonal in outline, as broad as long, lateral margins distinctly produced in middle. Parameres present, slender and sinuate (Fig. 11). Vesical armature symmetrical (Figs 12–13); dorsal sclerite prolonged distally with prominent recurved apex; band-shaped ventral sclerite long, separated from dorsal sclerite; 2 pairs of lateral sclerites, pieces of second pair long, slender and sinuately curved, meeting each other above dorsal sclerite.

Female structure. Body broadly oval, length about 1·7× maximum body width (3·78 : 2·22). *Head* between eyes slightly shorter than wide (0·80 : 0·82), interocular width 3·2× width of an eye (0·82 : 0·26). Antenna about 0·9× length of the body (3·30 : 3·78). Lengths of antennal segments (1–4): 1·52 : 0·62 : 0·55 : 0·60. *Thorax.* Pronotum 3·4× wider than long (1·10 : 0·32) and 0·4× length of head on the median line (0·80 : 0·32). Meso-metanotum with obscure, slender dark brown bristles scattered over its surface (most easily seen when viewed from behind). *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 2·12 : 1·60 : 0·12 : 0·55; middle leg, 4·88 : 4·10 : 1·68 : 0·58; hind leg, 4·80 : 2·48 : 0·62 (I+II). First segment of fore tarsus about 0·2× second segment. Hind coxae 1·6× as long as wide (0·45 : 0·28).

Variation. Individuals from Hermite Island (Monte Bello Islands, W.A.) have almost uniformly brown pronotum (as Fig. 5, bottom) and are significantly larger (♂, length 3·7–3·8, mean = 3·74, $n = 10$) than individuals from Northern Territory localities (♂, length 3·3–3·6, mean = 3·45, $n = 10$).

Distribution and Habitats

Halobates mjobergi was described by Hale (1925) from Broome, north-western Australia, and later recorded from Hermite Island (China 1957) and Frances Bay near Darwin (Polhemus 1982). The material examined by us indicates that *H. mjobergi* has a wider distribution in northern Australia (Fig. 14), extending from the Cape York Peninsula, through coastal areas of the Northern Territory, to the Monte Bello Islands, Western Australia. It is also known from Daru Island, Western Province, Papua New Guinea (J. Polhemus, unpublished new record). *H. mjobergi* is a mangrove-inhabiting species that lives amongst roots of mangrove trees in saltwater lagoons and swamps (Hale 1925; China 1957; Polhemus 1982).

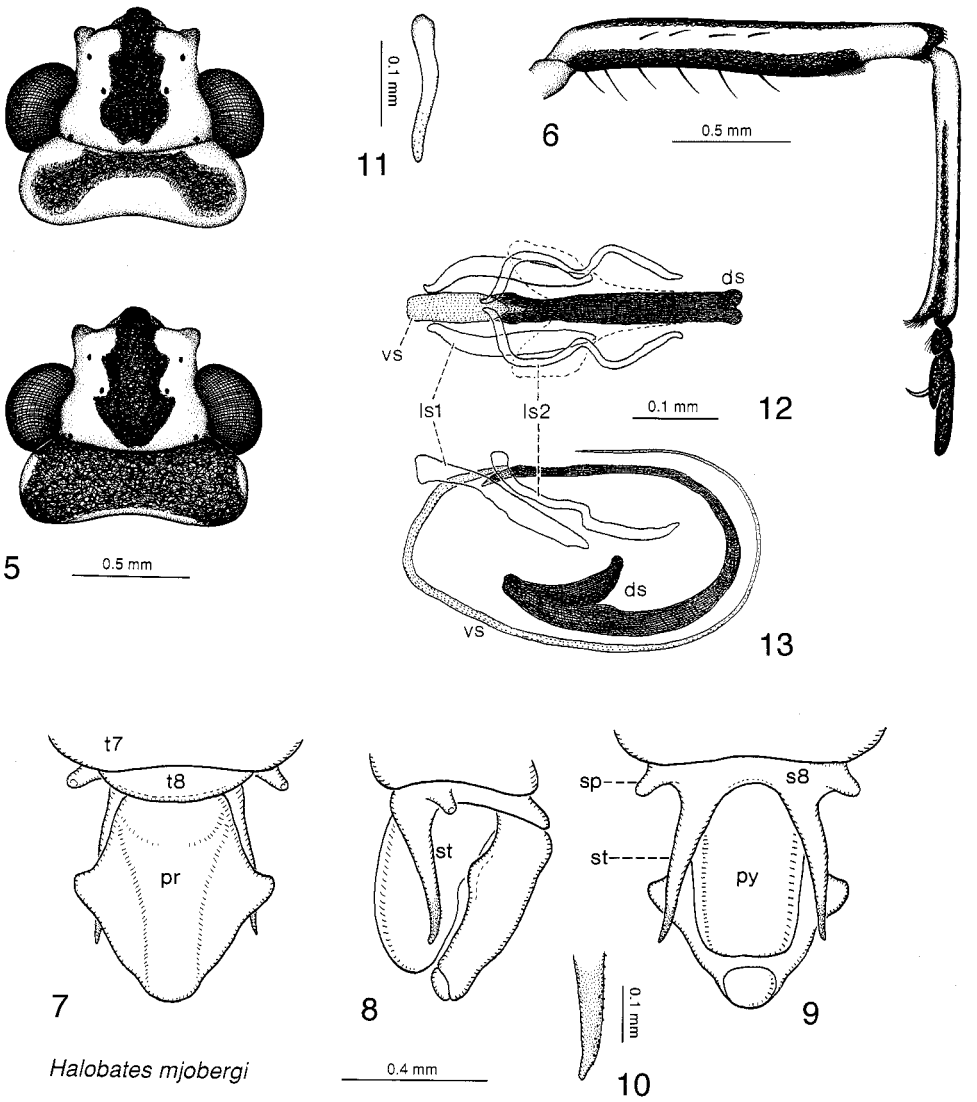


Fig. 5. *Halobates mjobergi*, head and pronotum; two colour-forms. **Fig. 6.** *Halobates mjobergi*, ♂ right fore leg. **Figs 7–11.** *Halobates mjobergi*, ♂ terminalia. *7*, dorsal view; *8*, lateral view; *9*, ventral view; *10*, apex of styliform process; *11*, left paramere. Abbreviations: pr, proctiger; py, pygophore; s8, sternum of abdominal segment 8; sp, spiracle of 8th abdominal segment; st, styliform process; t7, t8, tergum part of abdominal segment 7 and 8. **Figs 12–13.** *Halobates mjobergi*, ♂ vesical armature: *12*, dorsal view; *13*, lateral view. Abbreviations: ds, dorsal sclerite; ls1, ls2, first and second pair of lateral sclerites; vs, ventral sclerite.

Comments

The excellent original description and illustrations of *H. mjobergi* (Hale 1925: 12–14, fig. 7) leave no doubt about the identity of this species. China (1957: 342–5, figs 1–3) illustrated structural details of the legs and male terminalia, pointing out the absence of a mesotarsal hair fringe, which is otherwise present in *Halobates* species. China initially placed *H. mjobergi* in the genus *Asclepios*, but finally erected a separate subgenus, *Hilliella*, for *H. mjobergi* (see Andersen 1991*b*; and discussion above).

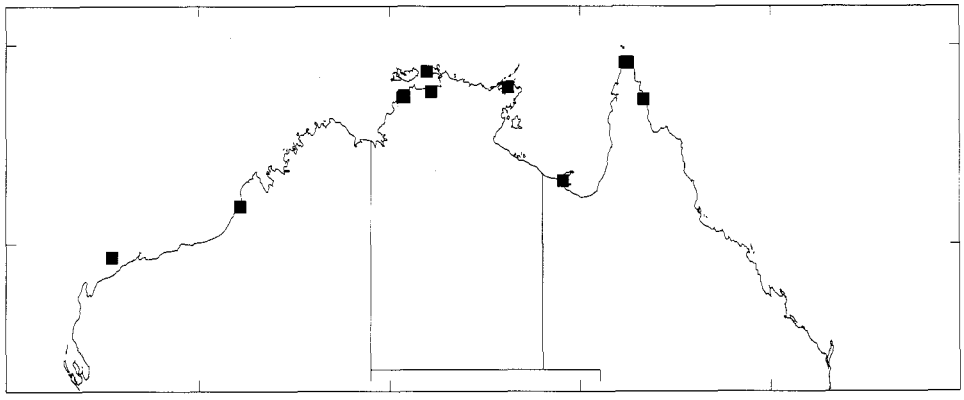


Fig. 14. *Halobates mjobergi*, distribution.

Halobates (Hilliella) lannae, sp. nov.

(Figs 1, 15–23)

Material Examined

Holotype. ♂, Northern Territory, Darwin, Frances Bay, CL914, 13.xii.1977, J. T. Polhemus (ANIC).

Paratypes. **Northern Territory:** 11♀, same label data as holotype (ANIC, JTPC, ZMUC); 1♂, Darwin, East P, in tidal pool, 3.ix.1981, J. Hanley (NTMD); 1♂, 2♀, Inglis I., 11·59 S, 136·18 E, 29.i.1988, H. Larson (NTMD). **Western Australia**: 2♀, 1♂, Wapet Ck, Exmouth Gulf, Feb. 1957 (WAM).

Description

Size. ♂, length 4·1–4·5, body width 1·8–2·0, head width 1·3–1·45; ♀, length 4·3–4·7, body width 2·1–2·5, head width 1·3–1·5.

Colour. Body above chiefly dark brownish. Head yellow with broad, median dark marking. Antennae dark except base of first segment. Pronotum more or less extensively light brownish posteriorly (Fig. 1). Meso-metanotum brown with darker median stripe. Abdominal terga brown, connexiva with yellow markings. Coxae, trochanters, and femora yellow with dark, longitudinal stripes on femora; tibiae and tarsi chiefly dark. Pleural areas of meso-metathorax including mesoacetabula, triangular spots above spiracles, lower half of metacetabula, and entire thoracic and abdominal venter pale yellow. Styliform processes of male terminalia with dark apices; proctiger dark in middle; pygophore pale.

Male structure. Body oval, length about 2·4× maximum body width (4·35 : 1·80). *Head* between eyes longer than wide (0·78 : 0·72), interocular width 2·5× width of an eye (0·72 : 0·29). Antenna very long, about 0·85× length of the body (3·80 : 4·35). Lengths of antennal segments (1–4): 1·82 : 0·70 : 0·60 : 0·68. *Thorax.* Pronotum 3·2× wider than long (1·05 : 0·32) and about 0·4× length of head on the median line (0·32 : 0·78). Sides of meso-metanotum rounded, gradually diverging to maximum width across middle acetabula. Meso-metanotum without prominent bristles. Metasternum swollen around scent orifice. *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg,: 2·10 : 1·55 : 0·15 : 0·55; middle leg, 5·38 : 4·28 : 1·68 : 0·55; hind leg, 5·15 : 2·52 : 0·65 (I+II). Fore femora incrassate (Fig. 15), widest across the middle, tapering towards the apex, with 16–20 long, black bristles on ventral margin and 4 or 5 bristles on external surface. Fore tarsus 0·45× length of fore tibia (0·70 : 1·55); first tarsal segment about 0·3× length of second segment. *Terminalia* (Figs 16–20). Styliform processes symmetrical, proximally

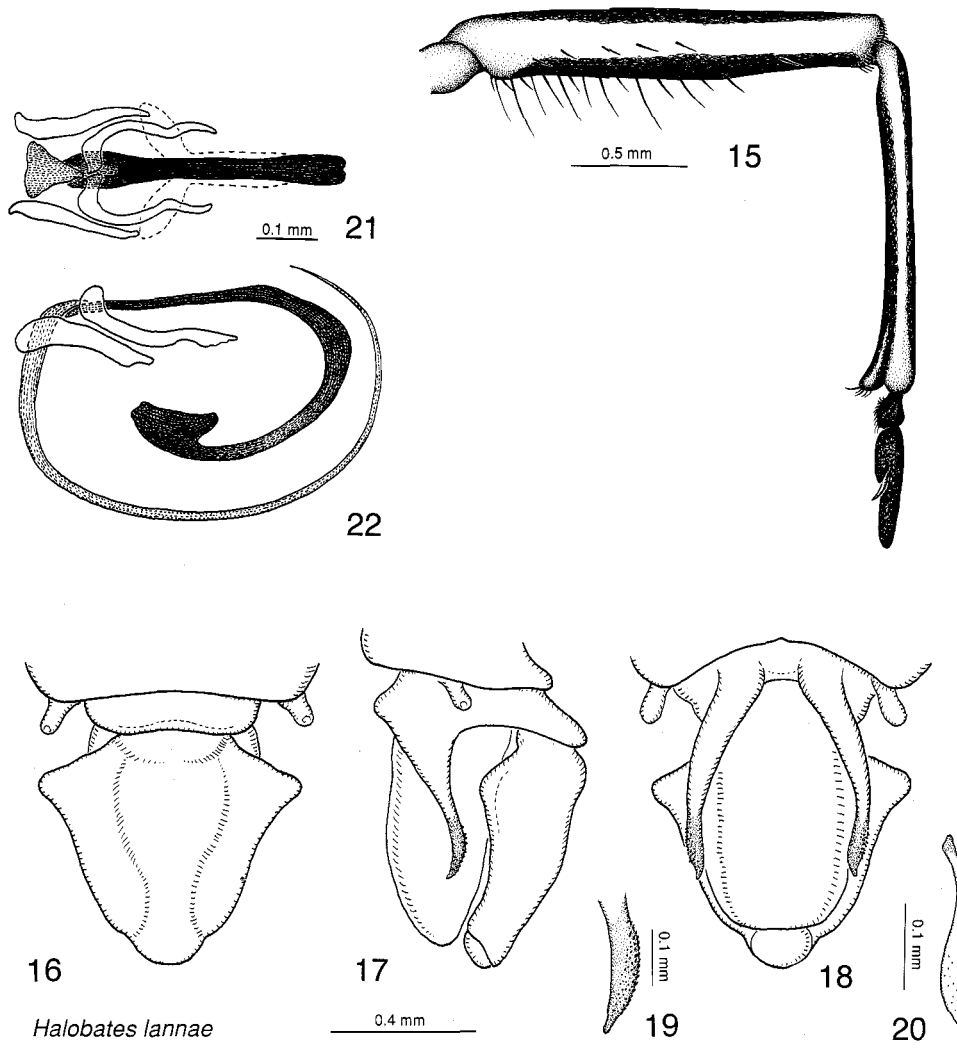


Fig. 15. *Halobates lannae*, ♂ right fore leg. **Figs 16–20.** *Halobates lannae*, ♂ terminalia: *16*, dorsal view; *17*, lateral view; *18*, ventral view; *19*, apex of styliform process; *20*, left paramere. **Figs 21–22.** *Halobates lannae*, ♂ vesical armature: *21*, dorsal view; *22*, lateral view.

thickened, with slender and curved distal parts which are not visible from above; apices furnished with numerous dark denticles (Fig. 19). Proctiger triangular to pentagonal in outline, slightly wider than long, lateral margins distinctly produced in basal half; posterior margin produced in middle. Parameres present but weakly sclerotised, slender and sinuate, thickened distally (Fig. 20). Vesical armature symmetrical (Figs 21, 22); dorsal sclerite strongly produced distally with prominent recurved apex; long, band-shaped ventral sclerite separated from dorsal sclerite; 2 pairs of lateral sclerites, second pair long, slender and sinuately curved, meeting each other dorsally.

Female structure. Body broadly oval (Fig. 1), length about 1·9× maximum body width (4·72 : 2·48). *Head* between eyes longer than wide (0·88 : 0·82), interocular width 2·7× width of an eye (0·82 : 0·30). Antenna about 0·9× length of the body (4·38 : 4·72). Lengths of antennal segments (1–4): 2·25 : 0·82 : 0·65 : 0·65. *Thorax.* Pronotum 3·4× wider than long (1·20 : 0·35) and 0·4× length of head on the median line (0·35 : 0·88).

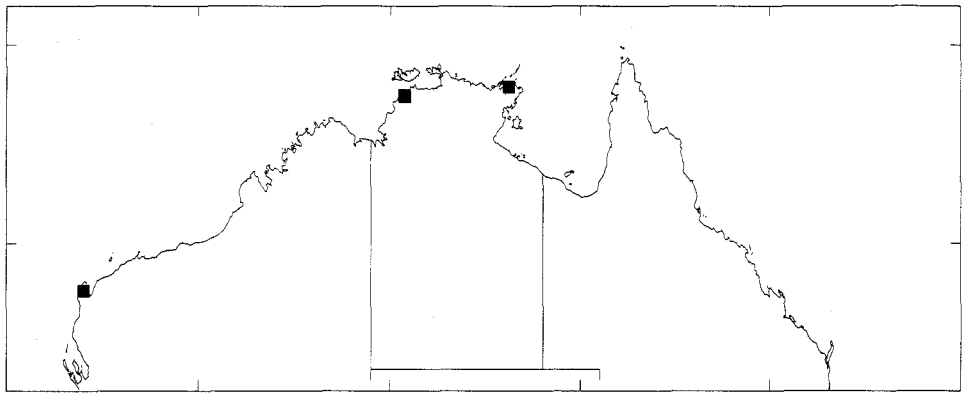


Fig. 23. *Halobates lannae*, distribution.

Sides of meso-metanotum rounded, gradually diverging to maximum width across posterior meso-metanotum or middle acetabula. Meso-metanotum with dense, suberect pubescence but without scattered, long bristles. *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 2·52 : 2·00 : 0·20 : 0·68; middle leg, 6·05 : 4·68 : 1·90 : 0·60; hind leg, 5·95 : 3·00 : 0·68 (I+II). Fore femora moderately robust, widest across the middle (0·28), with numerous black bristles on ventral margin. Fore tarsus about 0·45× fore tibia (0·88 : 2·00); first tarsal segment 0·3× length of second segment. Hind coxae about 1·3× as long as wide. *Terminalia.* Gonocoxae large and partly exposed. Proctiger rounded, protruding.

Distribution and Habitat

Halobates lannae, sp. nov., is so far known only from a few localities in the Northern Territory and Western Australia (Fig. 23). It has previously been collected together with *H. mjobergi* in both Inglis Island and Frances Bay near Darwin (Polhemus 1982) and probably inhabits mangroves, as does the latter species (see above). Future studies should be directed toward clarifying the ecological segregation of these closely related species.

Comments

Named for Dr Lanna Cheng, Scripps Institution of Oceanography, in recognition of her outstanding work on the biology of sea skaters. *Halobates lannae* is closely related to *H. mjobergi* and easily confused with this species. The most useful characters separating the two species are:

(1) *H. lannae* is a distinctly larger species (♂, 4·1–4·5; ♀, 4·3–4·7) than *H. mjobergi* (♂, 3·3–3·8; ♀, 3·4–4·2);

(2) the male fore femur of *H. lannae* (Fig. 15) is gradually tapering in width towards the apex, not distinctly constricted in distal fourth as in *H. mjobergi* (Fig. 6) which also has an elongate patch of stiff hairs just before the constriction;

(3) the shape of the male proctiger is quite different in the two species (compare Figs 7 and 16);

(4) the female meso-metanotum of *H. lannae* has a dense pilosity of short, suberect hairs but not longer, scattered bristles like *H. mjobergi* (most easily seen when the meso-metanotum is viewed from behind).

Subgenus ***Halobates*** Eschscholtz, s. str.

See generic diagnosis above.

The *zephyrus* Species-group

Following the results of the cladistic analysis (Figs 3–4), a separate species-group is erected for the Australian species *Halobates zephyrus*, a small (body length 3·6–4·5) species

with prominent yellow markings on the head, the first segment of the fore tarsus much shorter than the second segment, relatively simple, slightly asymmetrical male terminalia, and vesical armature of the male with a perforated dorsal sclerite and one pair of lateral sclerites.

Halobates (H.) zephyrus Herring

(Figs 24–32)

Halobates zephyrus Herring, 1961: 276.
Halobates (Hilliella) zephyrus.—Polhemus and Cheng, 1982: 224.

Material Examined

Holotype. ♂, Queensland, Bribie I., 26.xii.1930, H. Hacker, in the C. J. Drake Coll., USNM [not examined].

Paratype. 1♂, Queensland, Moreton Bay, 1.i.1953, T. E. Woodward (AMS).

Other material examined. **New South Wales:** 2♂, 1♀, Brunswick Hds, Jan. 1961, K. R. Norris (ANIC); 2♂, 1♀, Pittswater [Pittwater], 20 mls [= 32 km] north of Sydney, Saltwater lagoon, Coasters retreat, Ap. 1966, J. Child (ANIC, ZMUC); 8♂, 10♀, Candlagan Ck nr Mossy Pt, 10.i.1978, P. S. Lake (ANIC). **Queensland:** 1♂, 2♀, Bribie I., 26.xii.30, H. Hacker (USNM); 1♂, Brisbane, 17.iv.1965, B. Cantrell (UQIC); 4♂, 3♀, Gladstone, Auckland Ck, 18.v.1976, L. Cheng (ANIC, ZMUC); 10♂, 12♀, + many nymphs, Carlisle I., tidal ck, 9–17.xii.1986, S. R. Monteith (QMB); 2♂, 1♀ 1 nymph, Don R. mouth at Bowen, 6.xi.1969, T. Weir (ANIC); 5♂, 3♀, Moreton Bay, 1.i.1953, T. E. Woodward (UQIC); 41♂, 38♀ + many nymphs, Myora, Nth Stradbroke I., in saltwater amongst mangroves, 28.ii.1969, T. Weir (ANIC); 13♂, 26♀, Myora, same loc., ex mangroves and sea, 28.ii.1969, T. Weir (UQIC); 3♂, 1♀ + many nymphs, Townsville, 3-mile Ck, 16 and 20.vii.1976, L. Cheng (ZMUC); 2♂, 2♀, Townsville estuary, CL1713, 12.viii.1983, J. T. and D. A. Polhemus (JTPC); 3♂, 3♀, Proserpine R. mouth, incoming tide, 5.xi.1969, T. Weir (ANIC); 2♂, 4♀, 8 nymphs, Fraser I., Wanggoolba Ck mouth, 25·27 S, 153·00 E, amongst mangroves, 25.xi.1993, G. Cassis and P. Stys (AMS); 3♂, 5♀, Brisbane R., M. Ward (SAMA); 1♂, 1♀, mouth of Brisbane R., in mangroves, M. Ward (SAMA).

Description

Size. ♂, length 3·6–4·0, body width 1·6–1·75, head width 1·25–1·4; ♀, length 4·2–4·5, body width 2·2–2·5, head width 1·4–1·45.

Colour. Body above chiefly brown to black with yellow markings. Head with prominent yellow or brownish yellow markings along sides of head between eyes (Fig. 24). Antennae dark brown with base of first segment yellow. Posterior margins of abdominal tergites 5–7 yellow, connexiva chiefly dark. Almost entire thoracic and abdominal venter yellow. Legs dark brownish, proximal third of fore femora with prominent yellow stripe (Fig. 25). Male proctiger brown with paler lateral parts. Styliform processes with brownish apices.

Male structure. Body oval, length about 2·3× maximum body width (3·68 : 1·62). *Head* between eyes slightly shorter than wide (0·72 : 0·80), interocular width 3·2× width of an eye (0·80 : 0·25). Antenna 0·8× length of the body (2·92 : 3·68). Lengths of antennal segments (1–4): 1·38 : 0·58 : 0·45 : 0·52. *Thorax.* Pronotum 2·9× wider than long (1·12 : 0·38) and about half as long as head on the median line (0·38 : 0·72), distinctly swollen postero-laterally. Meso-metanotum anteriorly abruptly roundly angled, gradually increasing to maximum width across the middle acetabula. No prominent bristles on meso-metanotum. *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 1·72 : 1·32 : 0·15 : 0·52; middle leg, 4·20 : 3·52 : 1·67 : 0·58; hind leg, 4·08 : 1·90 : 0·62 (tarsus I+II). Fore femora moderately incrassate (Fig. 25), widest across the middle, distinctly

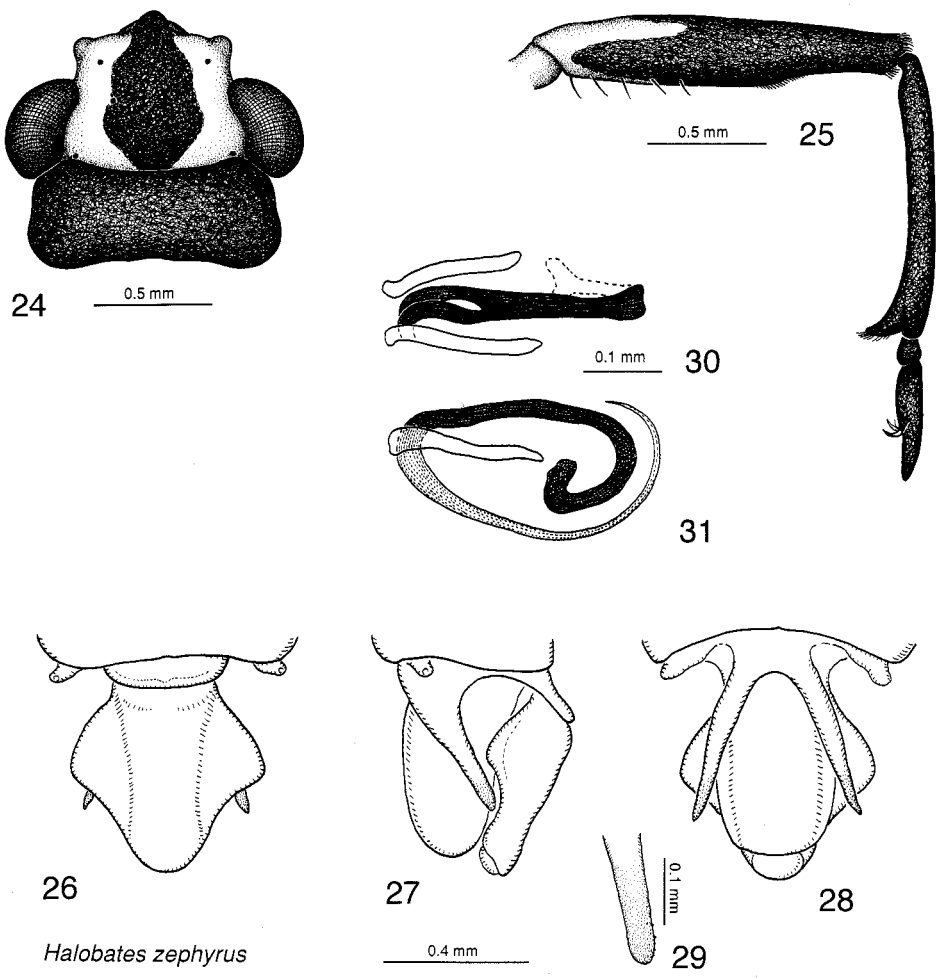


Fig. 24. *Halobates zephyrus*, head and pronotum. **Fig. 25.** *Halobates zephyrus*, ♂ right fore leg. **Figs 26–29.** *Halobates zephyrus*, ♂ terminalia: *26*, dorsal view; *27*, lateral view; *28*, ventral view; *29*, apex of styliform process. **Figs 30–31.** *Halobates zephyrus*, ♂ vesical armature: *30*, dorsal view; *31*, lateral view.

constricted in distal third, with 5 or 6 short, black spinous hairs on ventral margin but none on external surface. First segment of fore tarsus about 0·3× length of second segment. Middle femur only slightly longer than hind femur. *Terminalia* (Figs 26–29). Styliform processes slender and almost symmetrical; apices both visible from above, flattened and with a few dark denticles (Fig. 29). Proctiger pentagonal in outline, about as broad as long (0·50:0·48), lateral margins broadly produced basally. Parameres absent. Vesical armature asymmetrical (Figs 30–31); dorsal sclerite perforated basally, with distal, recurved part long and expanded toward apex; ventral sclerite short, band-shaped, fused with dorsal sclerite; one pair of slender, lateral sclerites.

Female structure. Body broadly oval, length about 1·9× maximum body width (4·48:2·32). *Head* between eyes as long as wide (0·88:0·88), interocular width 3·1× width of an eye (0·88:0·28). Antenna about 0·7× length of the body (3·20:4·48). Lengths of antennal segments (1–4): 1·55:0·60:0·50:0·55. *Thorax.* Pronotum 3·5× wider than long (1·22:0·35) and 0·4× length of head on the median line (0·35:0·88). Sides of meso-metanotum rounded, gradually diverging to maximum width across the posterior

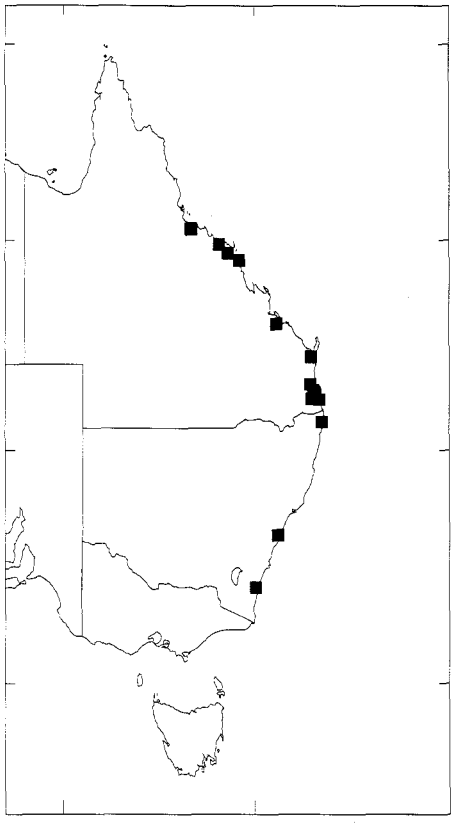


Fig. 32. *Halobates zephyrus*, distribution.

mesonotum or middle acetabula. Meso-metanotum with numerous slender, brown bristles scattered over its surface (most easily seen when viewed from behind). *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 2·22 : 1·68 : 0·20 : 0·70; middle leg, 4·92 : 4·10 : 1·88 : 0·65; hind leg, 4·52 : 2·42 : 0·70 (I+II). First segment of fore tarsus about 0·3× length of second segment. Hind coxae about 1·5× as long as wide (0·48 : 0·32).

Distribution and Habitats

Halobates zephyrus was described from Bribie Island and also recorded from Moreton Bay, south-eastern Queensland (Herring 1961: 276). Polhemus and Cheng (1982: 224) recorded this species from Gladstone and Townsville, further north in Queensland. The available material shows that *H. zephyrus* has a wide distribution in eastern Australia (Fig. 32) including New South Wales, where it was collected in saltwater lagoons at Pittwater, North of Sydney, together with *H. whiteleggei* (see below), as well as at Mossy Point, south of Sydney. *H. zephyrus* inhabits mangroves in bays and river mouths.

Comments

Herring (1961: 277) suggested a close relationship between *H. mjobergi* and *H. zephyrus* and Polhemus and Cheng (1982: 224) placed both species in the subgenus *Hilliella.* However, Andersen (1991*b*: 47) showed that from the characters of the male terminalia (especially the vesical armature), *H. zephyrus* is more closely related to the *regalis* group, if not a member of that group.

H. zephyrus can be distinguished from other Australian species of *Halobates* with extensive yellow markings on the head by the shape of the male fore femora (Fig. 25), the shape of the proctiger, and the relatively slender styliform processes. In the female,

H. zephyrus can be separated from *H. whiteleggei* by the much shorter first segment of the fore tarsi and shorter hind coxae (see below).

The *regalis* Species-group

This species-group includes five Australian *Halobates* species as well as *H. peronis* Herring from the Solomon Islands and the Philippines, *H. murphyi* Polhemus & Polhemus from Papua New Guinea, and *H. sexualis* Distant from Malaysia and Sri Lanka (Andersen and Foster 1992). The *regalis* group comprises small or medium-sized species with or without prominent yellow markings on the head. The first segment of the fore tarsus is always shorter than the second segment. The styliform processes and proctiger of the male are more or less asymmetrical. Vesical armature is asymmetrical with a perforated dorsal sclerite and one pair of lateral sclerites; distal, recurved part of the dorsal sclerite is usually reduced. The cladistic relationships between species are analysed above (Fig. 4).

Halobates (H.) regalis Carpenter

(Figs 33–40)

Halobates regalis Carpenter, 1892: 144, pl. 13.—Hale, 1925: 13; China, 1957: 345; Herring, 1961: 283.

Material Examined

Holotype. ♀, Queensland, 'Torres Strait' (BMNH).

Paratype. 1♂, Queensland, Mabuiag [in Torres Strait] (BMNH).

Other material examined. **Queensland:** 2♂, 1♀, same label data as holotype (BMNH); 3♀, Thursday I. Hbr, skating on surface of sea, 30.x.1922, A. R. McCullock (AMS); 1♂, 2♀, Thursday I. Hbr, skating on surface of sea, 30.x.1928, A. R. McCullock (AMS); 2♂, 3♀, Bedarra I., on seawater, 12.viii.1976, D. C. Geijskes (RNHL, ZMUC). **Western Australia:** 8♂, 6♀, Monte Bello Is, South Hermite, Oct. 1952, G. Wedd (BMNH, JTPC).

Description

Size. ♂, length 4·3–4·7, body width 2·0–2·3, head width 1·4–1·5; ♀, length 4·8–5·2, body width 2·6–2·8; head width 1·5–1·6.

Colour. Body above dark brown to black with silver-gray pubescence. Head with crescent-shaped yellow markings, anteriorly reaching middle pair of trichobothria (Fig. 33). Antennal tubercles, base of first antennal segment yellow, rest of antenna dark brownish. Posterior margins of abdominal terga 5–7 yellow, connexiva dark. Entire thoracic and abdominal venter yellow. Legs dark brownish, base of fore femora yellow. Male proctiger brown with paler lateral parts. Styliform processes with black apices.

Male structure. Body oval, length about 2·2× maximum body width (4·30 : 1·98). *Head* with interocular width about 3·4× width of an eye (0·90 : 0·26). Antenna about 0·8× length of the body (3·35 : 4·30). Lengths of antennal segments (1–4): 1·80 : 0·58 : 0·42 : 0·55. *Thorax.* Pronotum 3·1× wider than long (1·18 : 0·38) and about half as long as head on the median line (0·38 : 0·80). Meso-metanotum anteriorly abruptly roundly angled, gradually diverging to maximum width across the middle acetabula. No bristles on meso-metanotum. *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 2·20 : 1·60 : 0·35 : 0·68; middle leg, 5·60 : 4·18 : 1·90 : 0·58; hind leg, 5·02 : 2·48 : 0·68 (tarsus I+II). Fore femora moderately incrassate, widest across the middle, distinctly tapering towards the apex, with 3 or 4 black spinous hairs on ventral margin and none on external surface. First segment of fore tarsus about 0·5× length of second segment. *Terminalia* (Figs 34–37). Styliform processes subcylindrical, robust, and slightly asymmetrical; apices of both processes visible from above, widened in lateral view and with numerous dark

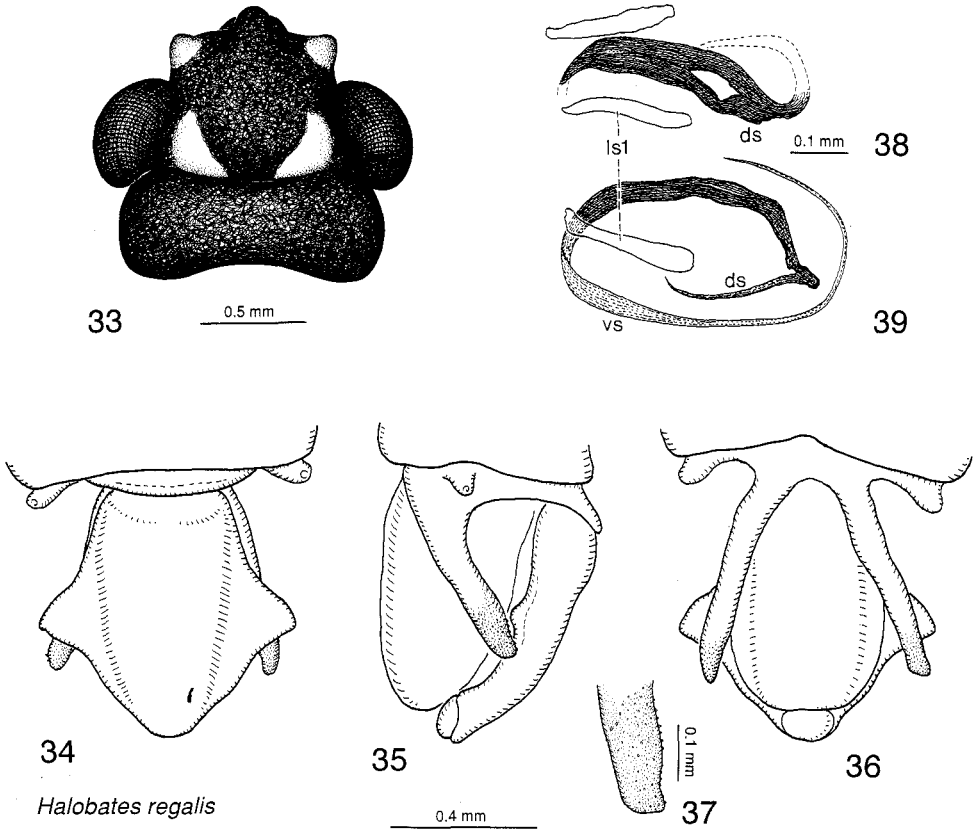


Fig. 33. *Halobates regalis*, head and pronotum. **Figs 34–37.** *Halobates regalis*, ♂ terminalia: *34*, dorsal view; *35*, lateral view; *36*, ventral view; *37*, apex of styliform process. **Figs 38–39.** *Halobates regalis*, ♂ vesical armature: *38*, dorsal view; *39*, lateral view. Abbreviations: ds, dorsal sclerite; vs, central sclerite; ls1, first pair of lateral sclerites.

denticles (Fig. 37). Proctiger pentagonal in outline, symmetrical, about as broad as long (0·70 : 0·66); lateral margins produced in middle. Vesical armature asymmetrical (Figs 38, 39); dorsal sclerite perforated in middle, distal recurved part long, tapering to thread-like apex; slender ventral sclerite fused with dorsal sclerite.

Female structure. Body broadly oval, length about 1·8× maximum body width (4·82 : 2·68). *Head* with interocular width 3·3× width of an eye (0·95 : 0·29). Antenna about 0·7× length of the body (3·38 : 4·82). Lengths of antennal segments (1–4): 1·80 : 0·58 : 0·42 : 0·58. *Thorax.* Pronotum 3·5× wider than long (1·22 : 0·35) and 0·4× length of head on the median line (0·35 : 0·85). Sides of meso-metanotum gradually diverging to maximum width across the middle acetabula. Meso-metanotum with numerous stiff dark bristles scattered over its surface (easily seen in oblique view). *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 2·45 : 1·98 : 0·52 : 0·82; middle leg, 6·02 : 4·62 : 2·20 : 0·68; hind leg, 5·22 : 2·90 : 0·88 (tarsus I+II). First segment of fore tarsus longer than in male, more than half as long as second segment. Hind coxae about twice as long as wide (0·58 : 0·28).

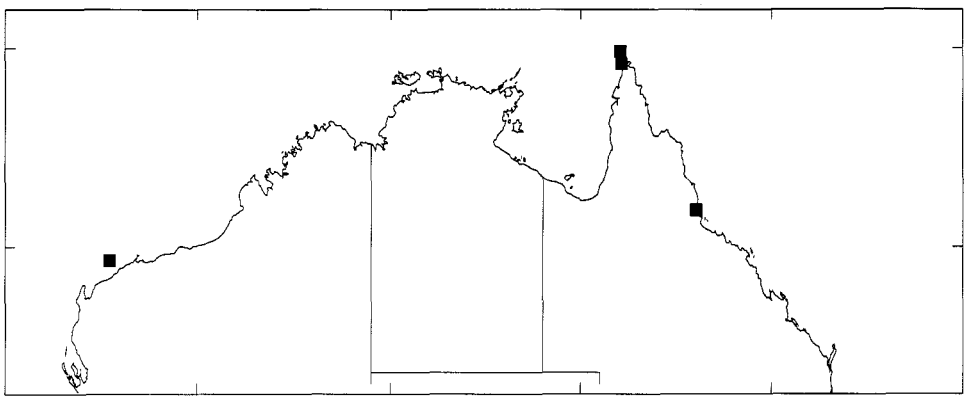


Fig. 40. *Halobates regalis*, distribution.

Distribution and Habitat

Halobates regalis was described by Carpenter (1892) from the island of Mabuiag (Murray Islands) in the Torres Strait. Hale (1925: 13) recorded *H. regalis* from the Arafura Sea and Port Darwin, but since there are no specimens available in the collections of AMS, we assume that Hale simply cited the observations by Walker (1893: 229) referring to that species. However, there are no specimens of *H. regalis* in BMNH from these localities and Walker may have seen specimens of other *Halobates* species instead. Herring (1961: 284) studied six female specimens of *H. regalis* from Thursday Island, near Cape York. We have seen a series from this locality (in AMS) which in addition to *H. regalis* includes three females of the widespread *H. hayanus* (see below). Thus, *H. regalis* was known only from the northernmost part of Queensland until China (1957: 345) quite unexpectedly recorded it from the Monte Bello Islands, Western Australia. The senior author has examined specimens from this locality in BMNH and can confirm China's identification. On account of the few and disjunct records (Fig. 40), *H. regalis* seems to be a rare or elusive species and nothing is known about its preferred habitat. Since it has been taken together with *H. hayanus*, however, it probably inhabits the intertidal zone of coral reefs rather than mangroves.

Comments

Carpenter's (1892) description and illustrations are adequate to separate *H. regalis* from other Australian sea skaters. The yellow markings on the head (Fig. 33) are reduced in comparison with the previous and following four species. The relatively long first segment of the fore tarsus and shape of the male styliform processes and proctiger (Figs 34–37) separate *H. regalis* from all other species, including *H. hayanus* (see below).

Halobates (H.) whiteleggei Skuse

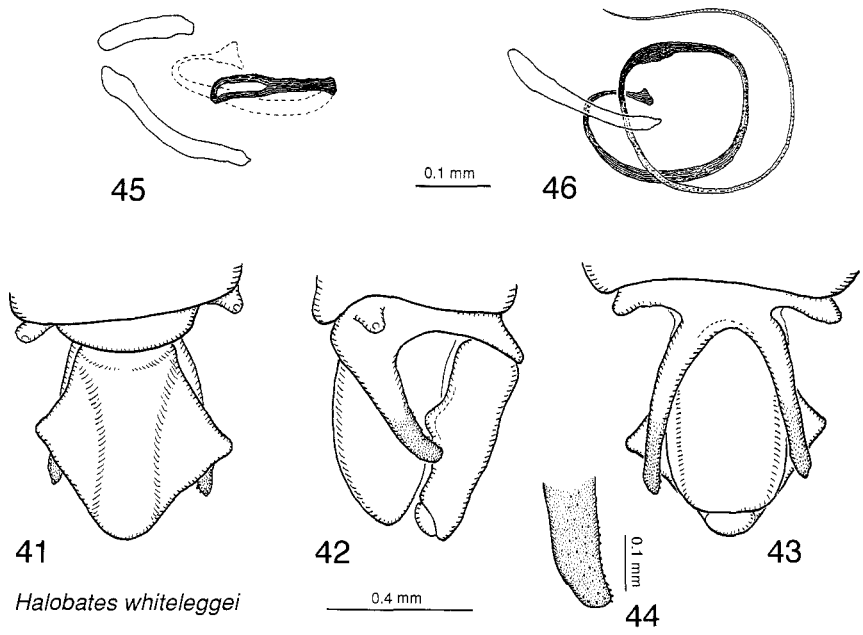
(Figs 41–47)

Halobates whiteleggei Skuse, 1891: 174. – Skuse, 1893: 44; Herring, 1961: 277.

Material Examined

Holotype. ♂, New South Wales, Port Jackson, in AMS [not examined].

Other material examined. **New South Wales:** 1♂, 4♀, Gundamaian, Port Hacking, K 60624, 12.iii.1927, T. G. Campbell (AMS); 7♂, 5♀, Pittswater [Pittwater], 20 mls North of Sydney, saltwater lagoon, Coasters retreat, Apr. 1966, J. Child (ANIC, ZMUC). **Queensland:** 19♂, 16♀ + many nymphs, Myora, North Stradbroke I., Moreton Bay, saltwater pools at edge of mangroves,



Figs 41–44. *Halobates whiteleggei*, ♂ terminalia: *41*, dorsal view; *42*, lateral view; *43*, ventral view; *44*, apex of styliform process. **Figs 45–46.** *Halobates whiteleggei*, ♂ vesical armature: *45*, dorsal view; *46*, lateral view.

1.i.1953, T. E. Woodward (ANIC, UQIC); 4♂, 8♀, same loc., ex mangroves and sea, 28.ii.1969, T. A. Weir (UQIC).

Description

Size. ♂, length 3·7–4·0, body width 1·7–1·8, head width 1·3–1·35; ♀, length 4·2–4·9, body width 2·45–2·6, head width 1·4–1·5.

Colour. Body above chiefly dark brown to black with yellow markings. Head with prominent yellow markings along sides of head between eyes. Antennae dark brown with first segment yellow proximally. Posterior margins of abdominal terga 5–7 yellow, connexiva chiefly dark. Entire thoracic and abdominal venter yellow. Legs brownish, fore femora yellow proximally. Male proctiger brown with paler lateral parts. Styliform processes with shiny black apices.

Male structure. Body oval, length about 2·2× maximum body width (3·85 : 1·75). *Head* with interocular width 3·4× width of an eye (0·85 : 0·25). Antenna about 0·8× length of the body (2·98 : 3·85). Lengths of antennal segments (1–4): 1·60 : 0·48 : 0·38 : 0·52. *Thorax.* Pronotum 3·2× wider than long (1·12 : 0·35) and about half as long as head on the median line (0·35 : 0·72). Meso-metanotum anteriorly abruptly roundly angled, gradually diverging to maximum width across the middle acetabula. No bristles on meso-metanotum. *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 1·82 : 1·35 : 0·22 : 0·60; middle leg, 5·00 : 3·85 : 1·88 : 0·65; hind leg, 4·30 : 2·30 : 0·72 (tarsus I+II). Fore femora moderately incrassate, widest across the middle, tapering towards the apex, with 2 or 3 black spinous hairs on ventral margin and none on external surface. First segment of fore tarsus about 0·4× length of second segment. *Terminalia* (Figs 41–44). Styliform processes relatively short and stout, asymmetrically developed with right process slightly longer than left process; apices of both processes visible from above, flattened and with numerous dark denticles (Fig. 44). Proctiger pentagonal in outline, but slightly asymmetrical, a little broader than long (0·56 : 0·50); lateral margins produced in middle. Vesical armature asymmetrical

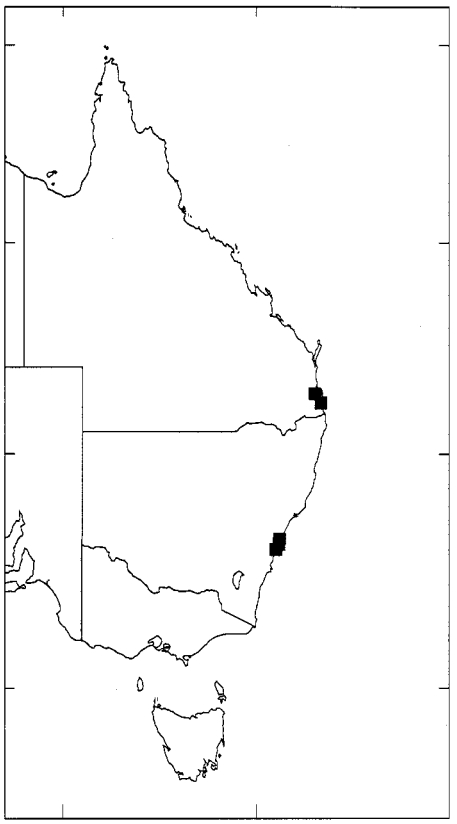


Fig. 47. *Halobates whiteleggei*, distribution.

(Figs 45, 46); dorsal sclerite perforated basally, distal recurved part slender and very long with slightly widened apex; long, slender ventral sclerite fused with dorsal sclerite.

Female structure. Body broadly oval, length about 1·8× maximum body width (4·55 : 2·52). *Head* with interocular width 3·9× width of an eye (0·98 : 0·25). Antenna about 0·7× length of the body (3·15 : 4·55). Lengths of antennal segments (1–4): 1·60 : 0·55 : 0·42 : 0·58. *Thorax.* Pronotum 3·9× wider than long (1·25 : 0·32) and 0·4× length of head on the median line (0·32 : 0·82). Sides of meso-metanotum gradually diverging to maximum width across the middle acetabula. Meso-metanotum with numerous stiff dark bristles scattered over its surface (easily seen when viewed from behind). *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 2·32 : 1·78 : 0·42 : 0·85; middle leg, 5·72 : 4·25 : 2·25 : 0·70; hind leg, 4·38 : 2·82 : 0·85 (tarsus I+II). First segment of fore tarsus longer than in male, about half as long as second segment. Hind coxae very long, about 3 times as long as wide (0·85 : 0·28).

Distribution and Habitat

Halobates whiteleggei was described by Skuse (1891) from Tarban Creek, Parramatta River, and Middle Harbour, Port Jackson, both localities in modern Sydney Harbour. Herring (1961: 277) recorded it from Port Hacking, NSW, and Bribie Island and North Stradbroke Island, south-eastern Queensland. The known localities are mapped in Fig. 47. *H. whiteleggei* inhabits saltwater lagoons at the edge of mangroves where individuals occur in 'schools' close to the shore, usually in sheltered spots. Skuse (1891: 176) reported a large percentage of mating adults in April.

Comments

The excellent description and illustrations of *H. whiteleggei* Skuse (1891) leave no doubt about the identity of this species. *H. whiteleggei* can be distinguished from other Australian species of *Halobates* with extensive yellow markings on the head by the shape of the proctiger (Fig. 41) and the relatively short and robust styliform processes of the males (Figs 42–44), and the very long hind coxae of the females. The last-mentioned character and the relatively longer first segment of the fore tarsus are useful to separate females of *H. whiteleggei* and *H. zephyrus* when these occur in mixed samples.

Halobates (H.) darwini Herring

(Figs 48–56)

Halobates darwini Herring, 1961: 278.—Polhemus, 1982: 5.

Material Examined

Holotype. ♂, Northern Territory, label data 'Port Darwin, 92–14', date and collector unknown, in BMNH.

Other material examined. **Northern Territory:** 10♂, 9♀, Darwin, Frances Bay, CL914, 13.xii.1977, J. T. Polhemus (ANIC, JTPC, UQIC, ZMUC); 4♂, 2♀, 1 nymph, 3 mls [= 4·8 km] N mouth of Finniss R., 27.vii.1971, T. Weir and A. Allwood (ANIC); 1♂, 8♀, Vanderlin I. 15·45 S, 137·04 E, sandshells, seagrass, 0–1 m, HL 88–20, 22.vii.1988, H. Larson and W. Houston (NTMD); 1♀, Ck of east side of Vanderlin I., 15·45 S 137·04 E, 1♀, 22.vii.1988, H. Larson (NTMD); 1♀, W Alligator Mouth, 12·11 S, 132·16 E, 10–22.vii.1979, G. Monteith and D. Cook (QMB); 6♂, 3♀, Woods Inlet, 12·29 S, 130·46 E, 10.iii.1988, P. Alderslade (NTMD). **Queensland:** 2♂, Mornington I., Appel Channel, June 1960, P. Aitken and N. B. Tindale (SAMA).

Description

Size. ♂, length 4·5–4·8, body width 1·7–1·9, head width 1·35–1·4; ♀, length 4·3–4·8, body width 2·2–2·4, head width 1·4–1·45.

Colour. Body above chiefly dark brown to black with greyish pubescence (Fig. 48). Head with yellow stripes along sides of head between eyes (as Fig. 24), or each stripe interrupted in middle (as Fig. 33). Antennae dark brown with first segment yellow proximally. Posterior margins of abdominal terga 5–7 yellow, connexiva chiefly dark. Acetabula and abdominal sternum (♂) or entire thoracic and abdominal venter yellow (♀). Legs brownish, fore femora yellow proximally. Male proctiger dark brown with paler lateral parts. Styliform processes with shiny black apices.

Male structure. Body elongate oval, length about 2·5× maximum body width (4·78 : 1·88). *Head* with interocular width 3·1× width of an eye (0·85 : 0·28). Antenna about 0·6× length of the body (2·90 : 4·78). Lengths of antennal segments (1–4): 1·52 : 0·50 : 0·35 : 0·52. *Thorax.* Pronotum 2·9× wider than long (1·10 : 0·38) and about half as long as head on the median line (0·38 : 0·78). Meso-metanotum anteriorly abruptly roundly angled, gradually diverging to maximum width across the middle acetabula. Meso-metanotum with scattered short, black bristles on each side of its median line (Fig. 55; easily seen in oblique view). *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 1·90 : 1·40 : 0·25 : 0·58; middle leg, 5·38 : 3·60 : 1·55 : 0·48; hind leg, 4·42 : 2·12 : 0·58 (tarsus I+II). Fore femora moderately incrassate (Fig. 48); 5 or 6 black spinous hairs on ventral margin and 2 or 3 hairs on external surface. First segment of fore tarsus about 0·4× length of second segment. *Terminalia* (Figs 49–52). Styliform processes relatively stout, asymmetrically developed, and with boot-shaped apices furnished with numerous dark denticles (Fig. 52); apex of left process flattened in the vertical plane, visible from above; apex of right process twisted to almost horizontal plane. Proctiger pentagonal to triangular in dorsal outline, but slightly asymmetrical, a little broader than

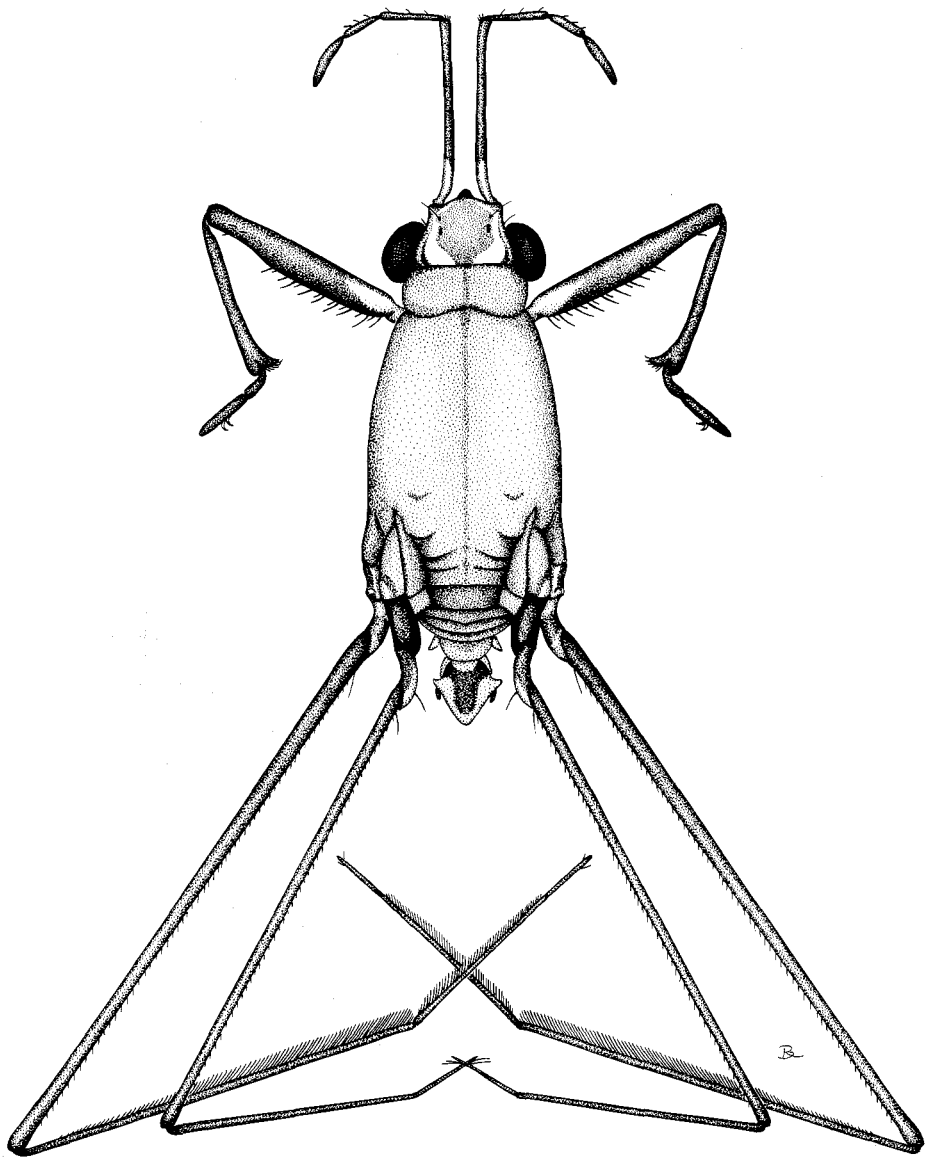
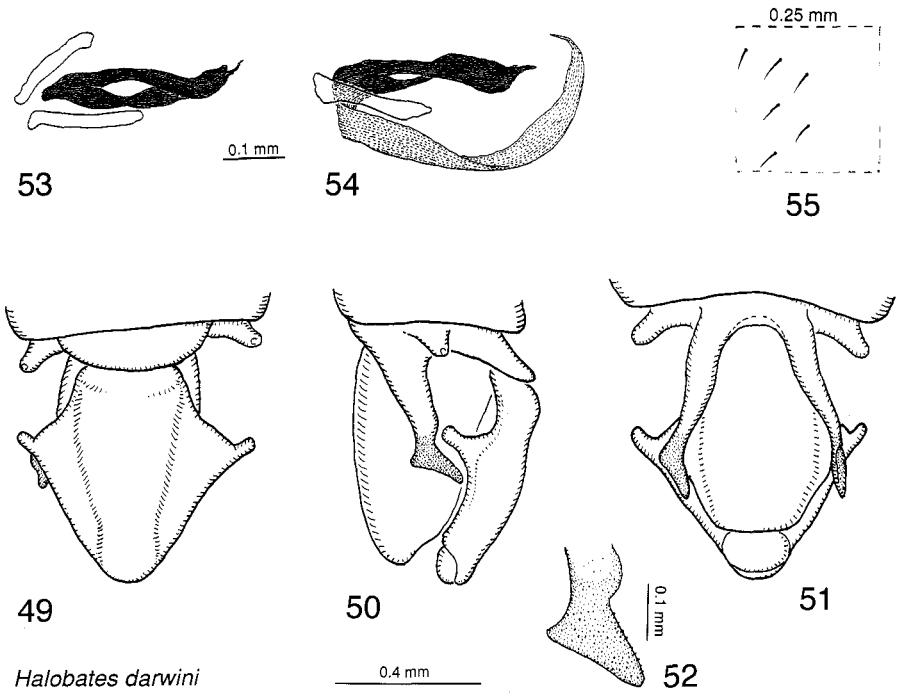


Fig. 48. *Halobates darwini*, habitus of apterous ♂ from Darwin, Northern Territory. Length of body 4·7 mm.

long (0·66:0·59); lateral margins finger-like produced in middle, each process curved downward. Vesical armature asymmetrical (Figs 53, 54); dorsal sclerite perforated in middle, distal part reduced, bifid and pointed; relatively short, band-shaped ventral sclerite fused with dorsal sclerite.

Female structure. Body oval, length about 2·0× maximum body width (4·70:2·32). *Head* with interocular width about 3·0× width of an eye (0·85:0·29). Antenna about 0·6× length of the body (2·72:4·70). Lengths of antennal segments (1–4): 1·38:0·50:0·35:0·50. *Thorax.* Pronotum 3·9× wider than long (1·12:0·38) and 0·5×

length of head on the median line (0·38 : 0·82). Sides of meso-metanotum gradually diverging to maximum width across the middle acetabula. Meso-metanotum with scattered stiff, dark bristles on each side of its median line (easily seen in oblique view). *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 2·08 : 1·60 : 0·32 : 0·65; middle leg, 5·22 : 3·70 : 1·65 : 0·50; hind leg, 4·22 : 2·25 : 0·65 (tarsus I+II). First segment of fore tarsus longer than in male, about half as long as second segment. Hind coxae about twice as long as wide (0·58 : 0·28); hind trochanters with a tuft of long, golden hairs.



Figs 49–52. *Halobates darwini*, ♂ terminalia: *49*, dorsal view; *50*, lateral view; *51*, ventral view; *52*, apex of styliform process. **Figs 53–54.** *Halobates darwini*, ♂ vesical armature: *53*, dorsal view; *54*, lateral view. **Fig. 55.** Bristles on mesonotum (♂).

Distribution and Habitats

Halobates darwini was described from Darwin, Northern Territory (Herring 1961) and also recorded from Groote Eylandt by Polhemus (1982 : 5). We have seen specimens from several localities along the coast of the Northern Territory and from Mornington Island, northern Queensland (Fig. 56). In Frances Bay near Darwin, this species was collected by Polhemus (1982: 5) 'in port area close to mangroves and some miles distant at the edge of thick mangrove stands bordering the bay'.

Comments

H. darwini has a more elongate body shape than the previously mentioned species, especially in the male. This species is also distinguished by the presence of scattered, stiff black hairs on the meso-metanotum in both males and females, and by the very characteristic male terminalia (Figs 49–52). The female was unknown when Herring (1961) characterised his *H. darwini* as closely related to *H. whiteleggei*. However, the females of the two species can easily be separated by the tuft of hairs on the hind trochanters of the former species and the very long hind coxae of the latter species. *H. darwini* is very closely related to *H. acherontis* (see discussion below).

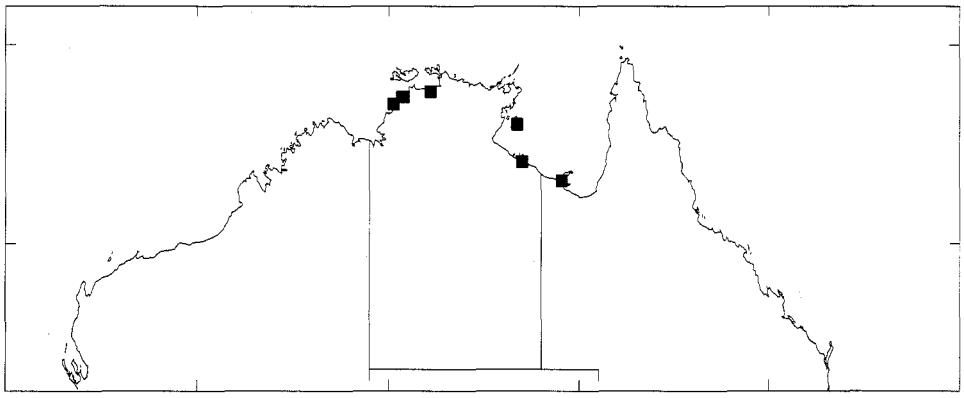


Fig. 56. *Halobates darwini*, distribution.

Halobates (H.) acherontis Polhemus

(Figs 57–62)

Halobates acherontis Polhemus, 1982: 6.

Material Examined

Holotype. ♂, Northern Territory, 'Daly River about 70 miles [= 112 km] above mouth, CL906, XII-11–1977, J. T. Polhemus' (ANIC).

Paratypes. 7♂, 3♀, same label data as holotype (ANIC, JTPC, UQIC, ZMUC).

Description

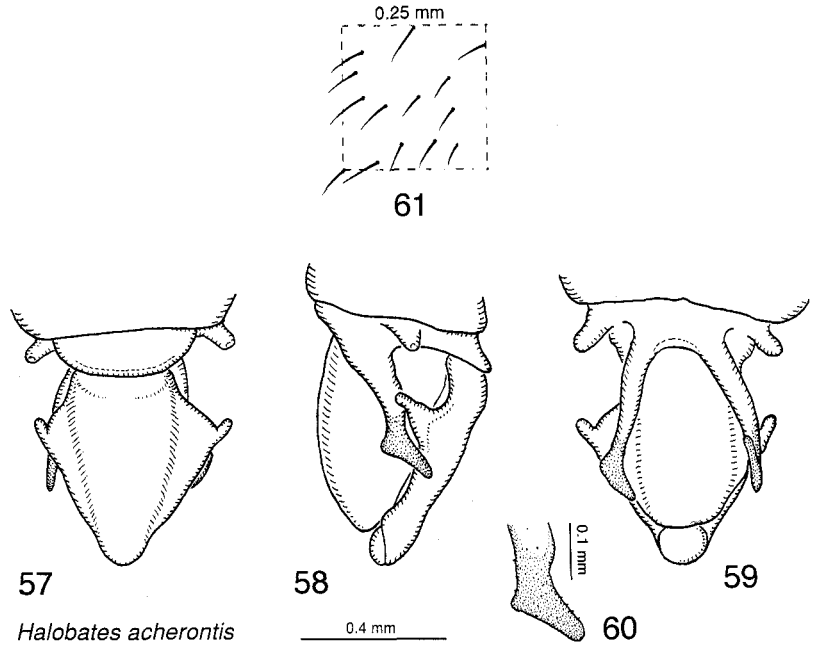
Size. ♂, length 3·8–4·2, body width 1·5–1·65, head width 1·25–1·3; ♀, length 3·7–3·9, body width 1·9–2·0, head width 1·3.

Colour. Body above chiefly dark brownish to rufous with greyish pubescence. Head with yellowish brown stripes along sides of head between eyes (as Fig. 24). Antennae dark brown with base of first segment yellow. Posterior margins of abdominal terga 5–7 yellow, connexiva chiefly dark. Acetabula and abdominal sternum (♂) or entire thoracic and abdominal venter yellow (♀). Legs brownish, basal half of fore femora yellow. Male proctiger dark brown with paler lateral parts. Styliform processes with dark brown apices.

Male structure. Body oval, length about 2·4× maximum body width (3·90 : 1·65). *Head* with interocular width 2·7× width of an eye (0·75 : 0·28). Antenna 0·65× length of the body (2·53 : 3·90). Lengths of antennal segments (1–4): 1·33 : 0·43 : 0·33 : 0·45. *Thorax.* Pronotum 3·2× wider than long (0·95 : 0·30) and less than half as long as head on the median line (0·30 : 0·70). Meso-metanotum anteriorly abruptly roundly angled, gradually diverging to maximum width across the middle acetabula. Dorsal and pleural parts of meso-metathorax with numerous long, black bristles (Fig. 61). *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 1·62 : 1·22 : 0·22 : 0·45; middle leg, 4·82 : 3·08 : 1·30 : 0·38; hind leg, 3·60 : 1·78 : 0·50 (tarsus I+II). Fore femora moderately incrassate; 6–8 black spinous hairs on ventral margin and 2 or 3 hairs on external surface.

First segment of fore tarsus 0·5× length of second segment. *Terminalia* (Figs 57–60). Very similar to those of *H. darwini*; styliform processes asymmetrically developed, with boot-shaped apices (Fig. 60) twisted in different planes. Proctiger slightly asymmetrical, as broad as long (0·52 : 0·52); lateral margins finger-like, produced in middle, each process curved downward. Vesical armature almost identical to that of *H. darwini*.

Female structure. Body oval, length about 2·0× maximum body width (3·75 : 1·90). *Head* with interocular width about 2·7× width of an eye (0·75 : 0·28). Antenna about 0·6× length of the body (2·32 : 3·75). Lengths of antennal segments (1–4): 1·12 : 0·42 : 0·32 : 0·45. *Thorax.* Pronotum 3·3× wider than long (0·98 : 0·30) and a little less than 0·5× length of head on the median line (0·30 : 0·65). Sides of meso-metanotum gradually diverging to maximum width across the middle acetabula. Dorsal and pleural areas of meso-metanotum with scattered stiff, dark bristles as in male. *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 1·80 : 1·40 : 0·22 : 0·48; middle leg, 4·58 : 3·28 : 1·40 : 0·40; hind leg, 3·62 : 1·80 : 0·50 (tarsus I+II). First segment of fore tarsus about half as long as second segment. Hind coxae about twice as long as wide (0·50 : 0·22); hind trochanters with a tuft of long, pale hairs.



Figs 57–61. *Halobates acherontis*, ♂ terminalia: *57*, dorsal view; *58*, lateral view; *59*, ventral view; *60*, apex of styliform process. **Fig. 61.** Bristles on mesonotum (♂).

Distribution and Habitat

Halobates acherontis is known only from the type series from Daly River, Northern Territory (Fig. 62), collected about 112 km above the mouth of the river. According to Polhemus (1982: 6), this species 'was abundant in various reaches of the Daly River, in midstream where the current was estimated at 5 knots, a habitat similar to that of *Metrobates* Uhler in the New World. *H. acherontis* was absent from the still portions of the river and backwaters, being replaced there by *Rhagadotarsus kraepelini* Breddin. Aside from a few specimens of *Limnogonus* Stål, these were the only water striders seen on the

river'. Polhemus saw his species as the first freshwater *Halobates*, although no information about the salinity of the water was given. It is true, however, that no other sea skater has been recorded at such a great distance from the sea. It should be interesting to know more about the distribution of populations along the course of the Daly River, the range of salinities at which the species occur, and, eventually, how *H. acherontis* interacts in distribution and ecology with *H. darwini*.

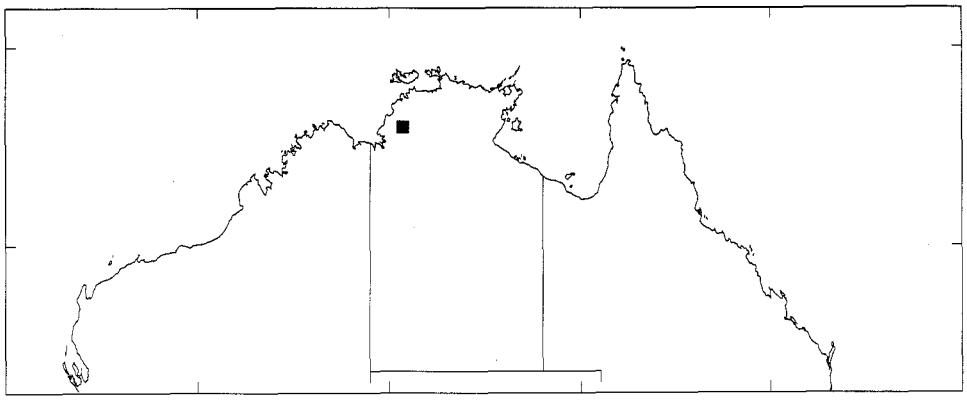


Fig. 62. *Halobates acherontis*, distribution.

Comments

H. acherontis was described by Polhemus (1982: 6) with the comment 'I believe that *H. acherontis* is a sibling species with *H. darwini*, to which it is very similar.'. He gave a number of characters to separate the two species, of which the following are the most reliable:

(1) *H. acherontis* is a smaller and more ovate species (♂, length 3·8–4·2, width about 1·6; ♀, length 3·8–3·9, width 1·9–2·0) than *H. darwini* (♂, length 4·5–4·8, width 1·7–1·8; ♀, length 4·3–4·8, width 2·2–2·4).

(2) *H. acherontis* has much more numerous and slightly longer black bristles on dorsal and pleural areas of meso-metathorax than *H. darwini* (compare Figs 55 and 61).

We are unable to verify the other diagnostic characters of *H. acherontis* mentioned by Polhemus (1982: 6), namely the presence of dark conical setae on the pronotum, relatively longer middle femora, and different shape of the proctiger. Based upon the available material, the characteristics of *H. acherontis* fall outside the range of known variation of *H. darwini*. Although the differences between these two species are less significant than between other Australian *Halobates*, we still maintain the specific status of *H. acherontis*.

Halobates (H.) herringi Polhemus & Cheng

(Figs 63–69)

Halobates herringi Polhemus and Cheng, 1982: 224.

Material Examined

Holotype. ♂, Queensland, 'Gladstone, Auckland Creek, 18.v.1976, L. Cheng' (ANIC).

Other material examined. **Northern Territory:** 3♂, 1♀, Woods Inlet, 12·29S, 130·46E, 10.iii.1988, P. Alderslade (NTMD). **Queensland:** 1♂, Coopers Ck, 18 mls [= 38 km] N of Daintree R., 21–22.vi.1969, G. B. Monteith (ANIC); many ♂ and ♀, Coopers Ck estuary N of Cape Tribulation, CL1734, 17.viii.1983, J. T. and D. A. Polhemus (JTPC); 2♂, 3♀ + many

nymphs, Daintree R., 13.xi.1969, T. Weir (ANIC); 70♂, 5♀ + nymphs, MacMillan R., 11·56 S, 143·58 E, mouth of river amongst mangroves, 28.v.1994, P. Zborowski (ANIC); many ♂ and ♀, Daintree Ferry, N of Mossman, CL1731, 17.viii.1983, J. T. and D. A. Polhemus (JTPC); 2♂, 2♀, Deeral Landing, Lower Mulgrave R., CL1724, 15.viii.1983, J. T. and D. A. Polhemus (JTPC, ZMUC); 2♂, 1♀, Horn I., intertidal ck, CL1767, 30.viii.1983, J. T. and D. A. Polhemus (JTPC, ZMUC).

Description

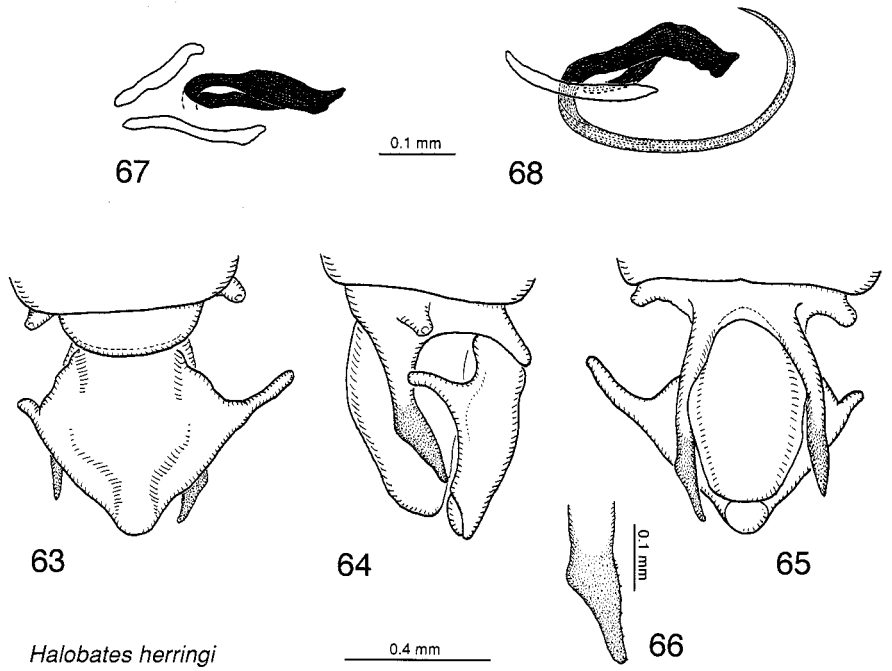
Size. ♂, length 4·0–4·4, body width 1·5–1·9, head width 1·2–1·4; ♀, length 4·1–5·1, body width 2·1–2·7, head width 1·35–1·6.

Colour. Body above chiefly dark brown to black with greyish pubescence. Head with brownish yellow stripes along sides of head between eyes, interrupted in middle (as Fig. 33). Antennae dark brown with basal $\frac{1}{3}$ of first segment yellow. Posterior margins of abdominal terga 5–7 yellow, connexiva chiefly dark. Acetabula and abdominal sternum (♂) or entire thoracic and abdominal venter yellow (♀). Legs dark brownish, base of fore femora brownish yellow. Male proctiger dark brown to black. Styliform processes with shiny black apices.

Male structure. Body elongate oval, length about 2·4× maximum body width (3·90 : 1·60). *Head* with interocular width 2·8× width of an eye (0·72 : 0·26). Antenna 0·65× length of the body (2·52 : 3·90). Lengths of antennal segments (1–4): 1·22 : 0·48 : 0·35 : 0·48. *Thorax.* Pronotum 3·3× wider than long (0·98 : 0·30), less than half as long as head on the median line (0·30 : 0·70). Meso-metanotum anteriorly abruptly roundly angled, gradually diverging to maximum width across the middle acetabula. Meso-metanotum without black bristles. *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 1·60 : 1·28 : 0·20 : 0·45; middle leg, 4·50 : 3·42 : 1·48 : 0·48; hind leg, 3·90 : 1·82 : 0·52 (tarsus I+II). Fore femora moderately incrassate; 6 or 7 black spinous hairs on ventral margin and 3 or 4 hairs on external surface. First segment of fore tarsus about 0·4× length of second segment. Middle femur distinctly longer than hind femur. *Terminalia* (Figs 63–66). Styliform processes relatively stout, asymmetrical, right process distinctly longer than left process; apices of both processes visible from above, boot-shaped, furnished with numerous dark denticles (Fig. 66); apical part of right process twisted to almost horizontal plane. Proctiger pentagonal to triangular in dorsal outline, but strongly asymmetrical, distinctly broader than long (0·75 : 0·50); lateral margins finger-like produced in middle, each process curved downward, right process much longer than left process. Vesical armature (Figs 67, 68) similar to that of *H. darwini*, except that the dorsal sclerite is shorter and one of the lateral sclerites much longer than the other.

Female structure. Body oval, length about 1·9× maximum body width (5·12 : 2·65). *Head* with interocular width about 3·2× width of an eye (0·95 : 0·30). Antenna about 0·65× length of the body (3·38 : 5·12). Lengths of antennal segments (1–4): 1·60 : 0·62 : 0·50 : 0·65. *Thorax.* Pronotum 3·5× wider than long (1·32 : 0·38) and 0·4× length of head on the median line (0·38 : 0·90). Sides of meso-metanotum gradually diverging to maximum width across the middle acetabula. Meso-metanotum with scattered stiff, dark bristles (easily seen in oblique view). *Legs.* Lengths of segments (femur : tibia : tarsus I : tarsus II): fore leg, 2·32 : 1·88 : 0·45 : 0·85; middle leg, 6·00 : 4·48 : 2·05 : 0·85; hind leg, 4·65 : 2·72 : 0·80 (tarsus I+II). First segment of fore tarsus longer than in male, about half as long as second segment. Hind coxae about twice as long as wide (0·65 : 0·30); hind trochanters with a tuft of long, pale hairs.

Variation. This species seems to vary in size between localities. The smallest individuals examined are from Deeral Landing, Lower Mulgrave River (♂, length 3·9–4·0; ♀, length 4·1–4·3), the largest individuals from Horn Island (♂, length 4·2–4·4; ♀, length 5·1).



Figs 63–66. *Halobates herringi*, ♂ terminalia: *63*, dorsal view; *64*, lateral view; *65*, ventral view; *66*, apex of styliform process. **Figs 67–68.** *Halobates herringi*, ♂ vesical armature: *67*, dorsal view; *68*, lateral view.

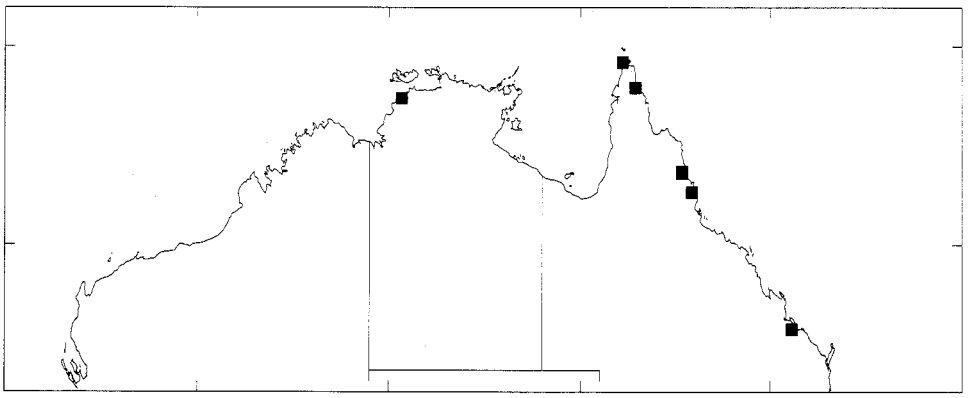


Fig. 69. *Halobates herringi*, distribution.

Distribution and Habitat

Halobates herringi was described from Gladstone, south-eastern Queensland (Polhemus and Cheng 1982), but we have seen specimens from several localities in northern Queensland, between Cairns and Cape York (Fig. 69), and from one locality in the Northern Territory. This species inhabits mangroves in estuaries and intertidal creeks.

Comments

The peculiar structure of the male terminalia (Figs 63–66), with extremely long digitate lateral projections of the male proctiger, separates *H. herringi* from all other Australian

Halobates species, including its closest relatives, *H. darwini* and *H. acherontis*. In mixed samples of *H. herringi* and *H. zephyrus* from Queensland mangroves, females of the former may be easily distinguished by the less extensive, brownish yellow markings of the head, where the lateral, pale stripes are interrupted in the middle (as Fig. 33).

The *hayanus* Species-group

This species-group includes three species (Andersen 1991*b*: 45), of which the widespread *H. hayanus* also occurs in Australian waters. Species are of intermediate size. Colour is chiefly dark, the head with a crescent-shaped yellow mark. The first segment of the fore tarsus is slightly shorter than the second segment. Styliform processes of the male are directed outward at apices; the proctiger with lateral groups of spinous hairs. Vesical armature is asymmetrical, with a perforated dorsal sclerite and one pair of lateral sclerites; the distal, recurved part of the dorsal sclerite is prominent.

Halobates (H.) hayanus White

(Figs 70–77)

Halobates hayanus White, 1883: 52, pl. 1, fig. 8.—Herring, 1961: 284.
Halobates frauenfeldanus White, 1883: 57.—Herring, 1961: 284 (synonymy with *H. hayanus*).
Halobates incanus Witlaczil, 1886: 5.—Herring, 1961: 284 (synonymy with *H. hayanus*).
Halobates australiensis Malipatil, 1988: 157.—Andersen, 1991*b*: 45 (synonymy with *H. hayanus*).

Material Examined

H. hayanus, holotype. ♂, 'Red Sea, 90·5' (BMNH).

H. australiensis, holotype. ♂, Northern Territory, label data 'Bay S of Sphinx Head, Marchinbar I., Wessel Is., 11·12S 136·41E, 20.ii.1984, H. Larson' (NTMD).

Paratype. 1♂, Northern Territory, 'rock pool, East Point beach, Darwin, 15.iii.1987, W. Houston' (NTMD).

Other material examined. **Northern Territory:** 1♀, Beer Eetar I., 12·37S, 130·24E, 1♀, 22.iv.1987, H. Larson (NTMD); 1♀, Darwin, in seawater at front of NT Museum, 30.xi.1989, D. White (NTMD); 5♂, 2♀, Elcho I., Settlement, 12·02S, 135·33E, 5♂, 2♀, 31.i.1988, H. Larson (NTMD); 2♂, Inglis I., 11·59S 136·18E, 29.i.1988, H. Larson (NTMD); **Queensland:** 3♂, 3♀ + nymphs, Low Isles, Gt Barrier Reef, pools, low tide and N end mangroves, 11, 13 and 23.viii.1954, M. T. Mackerras, E. N. Marks (UQIC); 3♂, 4♀ + nymphs, Magnetic I., Cockle Bay, 9.vii.1976, L. Cheng (ZMUC); 1♂, 6♀, Palm I., 20.xii.1930–6.i.1931, I. M. Mackerras (ANIC); many ♂ and ♀, Portland Roads, CL1751, 24.viii.1983, J. T. and D. A. Polhemus (JTPC); 1♂, 1♀ + nymphs, Roonga Pt, 10·43S, 142·25E, amongst mangroves and in sea, 17.x.1992, T. Weir, P. Zborowski (ANIC); 3♀, Thursday I. Hbr, skating on surface of sea, 30.x.1922, A. R. McCullock (AMS); 1♀, Townsville, 15.x.1919, G. F. Hill (SAMA); 1♂, 8 nymphs, Torres Strait, Horne I. [Horn I.], on sea, C. T. McNamara (SAMA).

Description

Size. ♂, length 3·7–4·2, body width 1·6–1·9, head width 1·2–1·35; ♀, length 4·1–4·6, body width 2·15–2·5, head width 1·3–1·4.

Colour. Uniformly blue-black above with silver-grey pubescence. Yellow coloration limited to base of first antennal segment, crescent-shaped marking on head between eyes (Fig. 70), acetabula, and entire abdominal venter; female mesosternum with a median stripe extending forward to fore coxae and entire medial surface of fore femora, yellowish.

Structure. Body oval, 2·2× (♂) or 1·8× (♀) as long as wide across middle acetabula. Interocular width of head about 3·4× width of an eye. Fourth antennal segment about

1·2× as long as third segment. No stiff black bristles on meso-metanotum of either sex. First segment of fore tarsus short, 0·5–0·6× as long as second segment. *Male terminalia* (Figs 71–74). Styliform processes almost symmetrical; long, slender, and directed outward at apices. Proctiger pentagonal in outline, a little broader than long; lateral margins produced in middle, bearing groups of dark spinous hairs on each side. Vesical armature asymmetrical (Figs 75, 76); dorsal sclerite perforated, distally prolonged and recurved, with hammer-shaped apex; short, band-shaped ventral sclerite fused with dorsal sclerite basally; 1 pair of lateral sclerites.

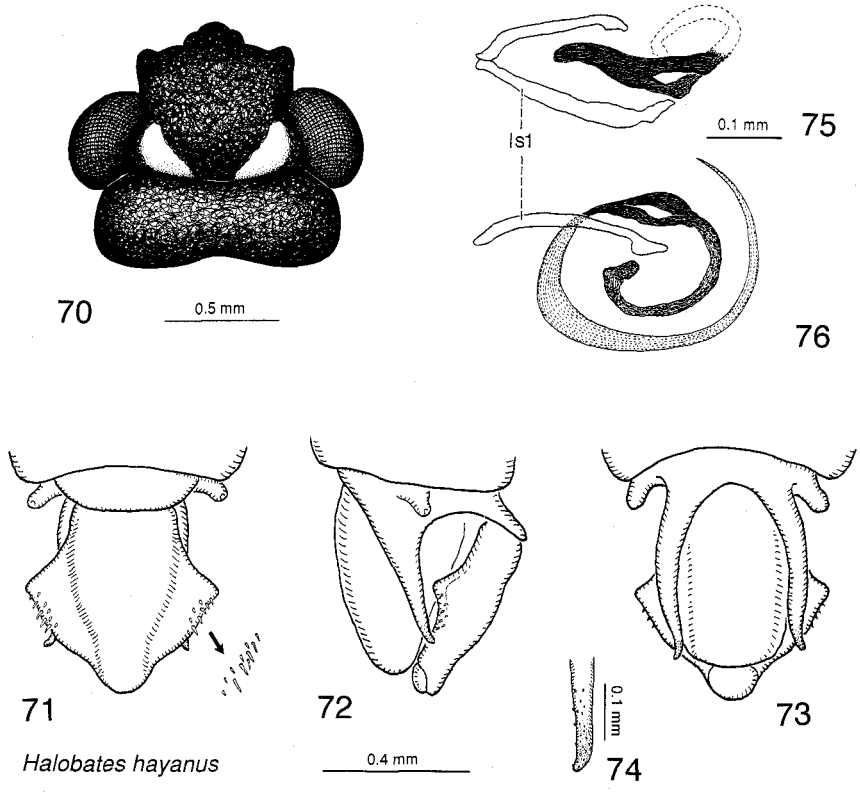


Fig. 70. *Halobates hayanus*, head and pronotum. **Figs 71–74.** *Halobates hayanus*, ♂ terminalia: *71*, dorsal view; *72*, lateral view; *73*, ventral view; *74*, apex of styliform process. **Figs 75–76.** *Halobates hayanus*, ♂ vesical armature: *75*, dorsal view; *76*, lateral view.

Distribution and Habitat

Halobates hayanus was described from the Red Sea, near Aden (White 1883), but Herring (1961: 284, fig. 4) showed that it is widely distributed in the Indo–West Pacific region, including Queensland: Prince of Wales Island and Low Island, Great Barrier Reef. The material examined by us adds a number of localities from the Northern Territory and Queensland (Fig. 77). *H. hayanus* is most frequently found in pools on intertidal reef flats and on the sea surface off coral coasts.

Comments

Malipatil (1988: 187) described *Halobates australiensis* from Marchinbar Island, Wessel Island group, Northern Territory. His original description and illustrations are excellent

and led Andersen (1991*b*: 45) to synonymise Malipatil's species with *H. hayanus*. After examining the holotype of *H. australiensis*, we can now confirm that it is conspecific with *H. hayanus*.

H. australiensis was synonymised with *H. calyptus* Herring (1961) by Polhemus and Polhemus (1991: 7). The senior author (NMA) has examined a series of paratypes of *H. calyptus* from Tubajon Bay, Dinigat Island, Philippines (in ZMUC) and can confirm most of the characters given by Herring (1961: 286 and key, p. 245) to separate this species from *H. hayanus*. Above all, *H. calyptus* is larger (♂, length 4·4, width 1·5; ♀, length 5·0, width 2·3) and distinctly more slender, with almost parallel-sided thorax. The structure of the male terminalia of the two species is practically identical. However, we believe that the differences between *H. calyptus* and *H. hayanus* justify specific separation. In any case, the holotype of *H. australiensis* falls clearly inside the known range of variation of *H. hayanus*.

H. hayanus is easily separated from other Australian *Halobates* species by the structure of the male terminalia, especially the distally diverging styliform processes (Fig. 73) and lateral groups of spinous hairs on the proctiger (Fig. 71). Females can be recognised by the yellow medial surface of the fore femora and wedge-shaped yellow mark on the mesosternum.

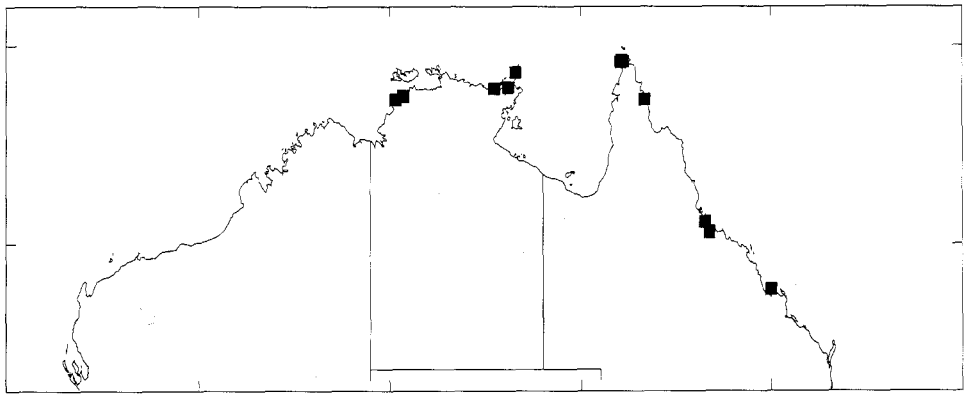


Fig. 77. *Halobates hayanus*, distribution.

The *micans* Species-group

This group comprises the five open-ocean species of *Halobates* (Herring 1961), of which three species (*H. micans*, *H. sericeus* and *H. germanus*) occur in Australian waters. Andersen (1991*b*: 44) included two coastal species as well: *H. flaviventris* Eschscholtz and *H. hawaiiensis* Usinger. These species are of small or intermediate size. They are uniformly dark including the venter; yellow markings of the head are usually greatly reduced. Eyes are relatively small. The first segment of the fore tarsus is shorter than the second segment. Styliform processes of the male are more or less asymmetrically developed. Vesical armature is strongly asymmetrical with a perforated dorsal sclerite and one pair of lateral sclerites. Female gonocoxae are relatively small and concealed by sternum 7; the proctiger is deflected, and usually hidden from dorsal view.

Halobates (H.) micans Eschscholtz

(Figs 78–82)

Halobates micans Eschscholtz, 1822: 107, pl. 2, fig. 3.—Herring, 1961: 246.
Halobates streatfieldanus Templeton, 1836: 230, pl. 22, fig. A.—Herring, 1961: 246 (synonymy with *H. micans*).

Halobates wullerstorffi Frauenfeld, 1867: 458, pl. 12, fig. 5.—Dahl, 1893: 6 (synonymy with *H. micans*); Skuse, 1893: 44.
Halobates inermis Dahl, 1893: 6, figs 4, 5, 7, 8.—Herring, 1961: 246 (synonymy with *H. micans*).

Material Examined

H. micans. Types not located. Herring (1961: 248) states that the types of Eschscholtz's species probably are in the collections of the Dorpat Museum [Tartu, Estonia].

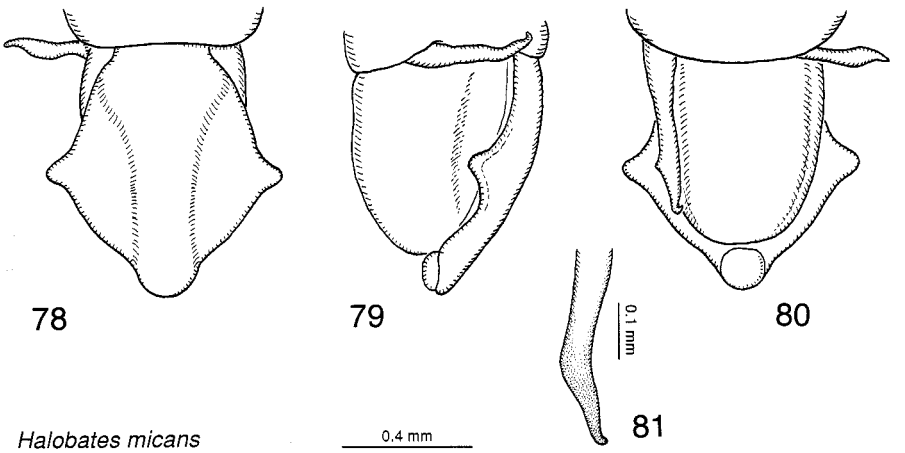
H. streatfieldanus, *H. wullerstorffi* and *H. inermis.* Types not located.

Other material examined. **New South Wales:** 1♂, 1♀, Maroubra Bay, K 14710, Apr. 1892, no collector (AMS). **Northern Territory:** 1♂, 1♀ + nymphs, Cartier Reef, 5.vi.1992, B. Russell (NTMD); 3♀, 1 nymph, Wessel Is, Rimbija I., 11·01 S, 136·45 E, on sand dunes 100 m from water, 3–14.ii.1977, T. A. Weir (ANIC). **Queensland:** 1♂, 1♀, Coral Sea off Lizard I., ex neuston net, 10.ii.1985, J. M. Leis (AMS); 1 nymph (5th instar), 4 km S of Somerset, rock pools in sea splash zone, 15.x.1992, T. Weir, P. Zborowski (ANIC). **Western Australia:** 1♂, 1♀, in towing net off W coast of Australia, no date, F. Wagstaff (AMS); 1♂, 1 nymph, Murchison R., no date or collector (WAM); 12♂, 15♀, Cottesloe Beach, in storm drift, 1.viii.1959, R. P. McMillan (WAM); 1♀, 1 nympth, Cottlesloe, no date or collector (WAM).

Description

Size. ♂, length 4·1–4·6, body width 2·0–2·15, head width 1·4–1·5; ♀, length 3·5–4·6, body width 2·25–2·5, head width 1·45–1·6.

Colour. Uniformly blue-black with fine greyish pubescence. Antennae, legs, and proctiger with an iridescent metallic sheen. Yellow coloration of head limited to a pair of triangular marks at base, not extending forward to middle of eyes (as Fig. 88). Bases of antennae and legs brownish. Venter uniformly dark.



Figs 78–81. *Halobates micans*, ♂ terminalia: *78*, dorsal view; *79*, lateral view; *80*, ventral view; *81*, apex of right styliform process.

Structure. Body oval, 2·2× (♂) or 2·0× (♀) as long as wide across middle acetabula. Eyes relatively small, interocular width of head more than 4·5× width of an eye. Second

antennal segment 0·6–0·7× as long as fourth segment. No black bristles present on thorax or acetabula of either sex. Fore femora of male incrassate; first segment of fore tarsus about 0·7× as long as second segment. Middle and hind femora very stout. *Male terminalia* (Figs 78–81). Styliform processes strongly asymmetrical, left process short, bent abruptly at right angles and extending outward, visible from above; right process almost straight; apices of both processes shoe-shaped (Fig. 81). Proctiger pentagonal in outline (Fig. 78), about as broad as long; lateral margins produced in middle. Vesical armature as illustrated by Andersen (1991*b*: fig. 5*A*).

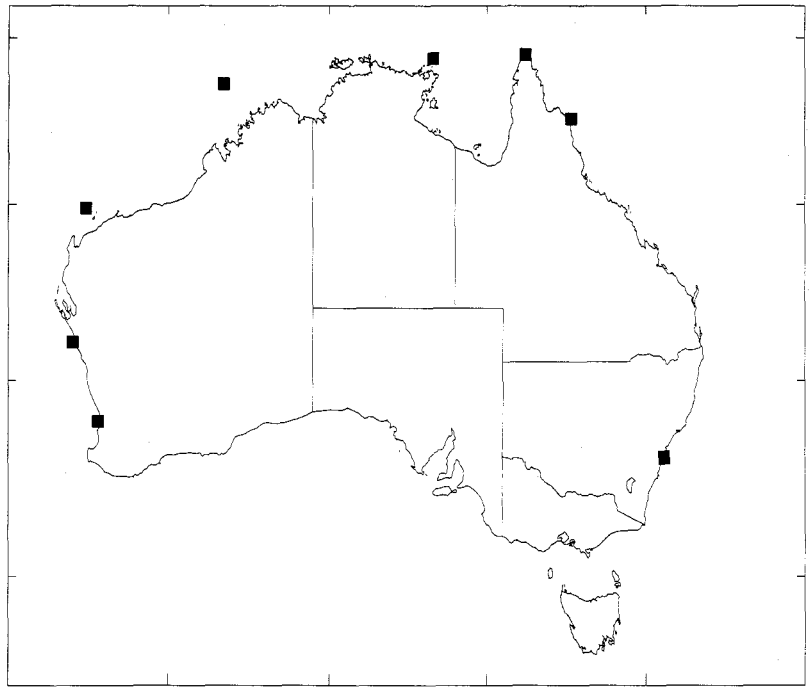


Fig. 82. *Halobates micans*, distribution.

Distribution and Habitats

Eschscholtz (1822) described this species from the South Atlantic and South Pacific Ocean, and Skuse (1893: 44) recorded it (as *Halobates wullerstorffi*) from Port Jackson and Western Australia. *H. micans* is found in the tropical and subtropical parts of the Atlantic, Indian, and Pacific Oceans. In the Central Pacific its distribution appears to be limited to a broad zone on both sides of the equator (Cheng 1989: fig. 1). Herring (1961: fig. 2) and Cheng (1989: fig. 1) mapped records from stations in the Arafura Sea and from the Tasman Sea, some distance off the coast of New South Wales. We can add records from Maroubra Bay near Sydney and Wessel Islands, NT (Fig. 82).

H. micans is an open-ocean species which usually lives at considerable distances from land, and individuals are taken near shore or found on beaches only after severe storms, as probably was the case with the individuals collected at Wessel Islands, on sand dunes 100 m from water. Eggs are deposited, often in huge numbers, on all kinds of floating objects, such as sea-bird feathers, sea-weed leaves, pieces of cork, lumps of tar, and shells of cuttlefish (*Sepia*) (Lundbeck 1914; Andersen and Polhemus 1976; Andersen and Foster 1992).

Comments

Males of *H. micans* can be distinguished from all other Australian *Halobates* by the structure of their terminalia (Figs 78–81). Females can be separated from the other two open-ocean species from Australian waters, *H. sericeus* and *H. germanus*, by their larger size, relatively longer first segment of the fore tarsus, and much stouter middle and hind femora.

Halobates (H.) sericeus Eschscholtz

(Figs 83–87)

Halobates sericeus Eschscholtz, 1822: 108, pl. 2, fig. 4.—Herring 1961: 252.

Material Examined

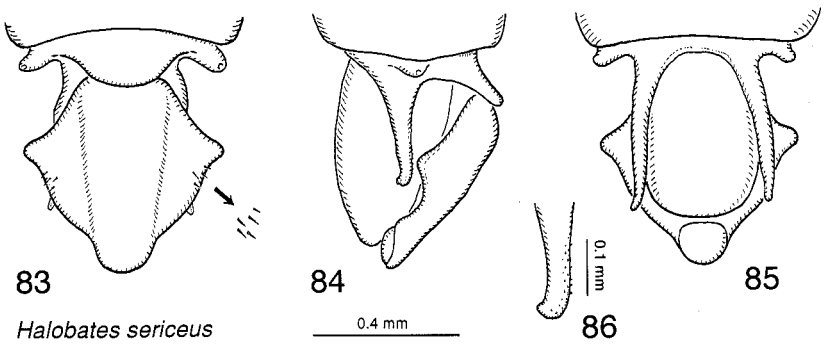
Types. Not located (see note above under *H. micans*).

Other material examined. **Lord Howe Island:** 69♂, 86♀, Blinkie Beach, Oct. 1962, J. Booth (AMS); 1♀, Middle Beach, 5.vi.1963, J. Carrick (AMS). **Queensland:** 2♂, 1♀ + nymphs, Lizard I., off Crystal Beach, 2.vii.1980, L. Cheng and P. D. Schmitt (ZMUC); 3♀ + nymphs, Lizard I., off Coconut Beach, 6.vii.1980, L. Cheng and P. D. Schmitt (ZMUC); 6♂, 7♀+ nymphs, Lizard I., lagoon, 6–13.vii.1980, L. Cheng and P. D. Schmitt (ZMUC); 1♀ + nymphs, Lizard I., off Osprey Islet, 22.x.1979, L. Cheng and P. D. Schmitt (ZMUC); 2♂, 2♀ + nymphs, Lizard I., off Osprey Islet, 2–10.vii.1980, L. Cheng and P. D. Schmitt (ZMUC); 2♂, 2♀ + nymphs, Lizard I., reef flat, 10 and 13.vii.1980, L. Cheng and P. D. Schmitt (ZMUC); 1♀, Low Isles, 21.viii.1954, E. N. Marks (UQIC); 1♀, Low Isles, Gt Barrier Reef, Gap Pt, 24.viii.1954, E. N. Marks (UQIC); 1♂, Pt Cartwright, on rocky shore, caught in froth among high seas, 31.iii.1956, E. N. Marks (UQIC); 1♂, 3♀, 1 nymph, Swains Reef, Gannet Cay, 26.xi.1982, L. Hill (ANIC); 1♂, Pt Lookout, Stradbroke I., common on beach after storm, SE winds for several days, 12.ii.1951, W. D. (SAMA).

Description

Size. ♂, length 3·2–3·6, body width 1·5–1·7, head width 1·15–1·2; ♀, length 3·0–3·4, body width 1·5–1·7, head width 1·1–1·2.

Colour. Uniformly blue-black above with fine greyish pubescence. Antennae, legs, and proctiger reddish brown. Yellow coloration of head limited to a pair of triangular marks at base, not extending forward to middle of eyes (as Fig. 88). Middle coxae, hind acetabulum, and posterior margins of abdominal sterna brownish.



Figs 83–86. *Halobates sericeus*, ♂ terminalia: *83*, dorsal view; *84*, lateral view; *85*, ventral view; *86*, apex of styliform process.

Structure. Body oval, 2·1× (♂) or 1·9× (♀) as long as wide across middle acetabula. Eyes relatively small, interocular width of head more than 4·5× width of an eye. Second

antennal segment very short, only about half as long as fourth segment. No black bristles present on thorax or acetabula of either sex. Fore femora incrassate; first segment of fore tarsus about 0·4× as long as second segment. Middle and hind femora slender. *Male terminalia* (Figs 83–86). Styliform processes slender, almost symmetrical, left process slightly shorter than right process; both processes diverging at apices and visible from above; apices slightly recurved (Fig. 86). Proctiger pentagonal in outline, slightly broader than long; lateral margins produced in middle, with 4–5 spinous hairs on each side (Fig. 83) (easily overlooked except in genital preparations). Vesical armature quite similar to that of *H. germanus*.

Distribution and Habitat

Eschscholtz (1822) described *Halobates sericeus* from the northern Pacific Ocean and it is widely distributed in the Pacific Ocean, except for a broad zone on both sides of the equator (Cheng 1989: fig. 2) where it is replaced by *H. micans*. Herring (1961: fig. 2) and Cheng (1989: fig. 2) mapped records from the Australian east coast, between Brisbane and Sydney. Cheng and Schmitt (1982) recorded *H. sericeus* from around Lizard Island, Great Barrier Reef. We can add records from Swains Reef, Queensland, and Lord Howe Island (Fig. 87).

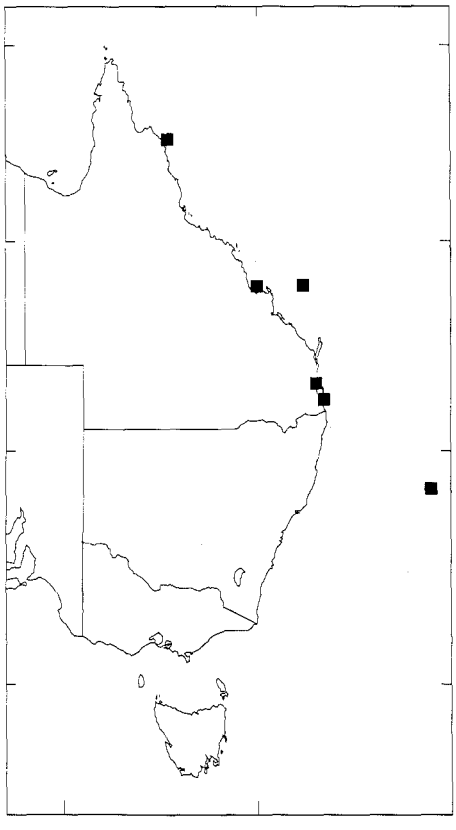


Fig. 87. *Halobates sericeus*, distribution.

H. sericeus is an open-ocean species that usually lives at considerable distances from land. Cheng and Schmitt (1982) found it most abundant in predominantly windward locations at Lizard Island and suggested an effect of south-eastern winds blowing individuals in from oceanic waters beyond the outer barrier reef. The presence of both adults and nymphs (most abundant in July), however, indicates breeding populations.

Comments

H. sericeus can be distinguished from the two other oceanic species from Australian waters, *H. micans* and *H. germanus*, by its small size, relatively short second antennal segment, short first segment of the fore tarsus, and distinctive male terminalia (Figs 83–86).

Halobates (H.) germanus White

(Figs 88–93)

Halobates germanus White, 1883: 50, pl. 1, fig. 6.—Herring, 1961: 253.
Halobates sewelli Imms, 1936: 71.—Herring, 1961: 253 (synonymy with *H. germanus*).

Material Examined

H. germanus, holotype. ♀, 'Pacific 90·4' (BMNH).

H. sewelli, holotype. ♂, 'Arabian Sea, Gulf of Oman' (BMNH).

Other material examined. **Northern Territory:** 1♂, 1♀, 1 nymph, Ashmore Reef, 12·14 S, 122·59 E, at boat anchorage, night light, dip net, 17.iv.1987, G. O'Connor (NTMD); 1♀, Cartier Reef, 5.vi.1992, B. Russell (NTMD); 1♀, Inglis I., 11·59 S, 136·18 E, 29.i.1988, H. Larson (NTMD); 3♂, 3♀ + nymphs, Wessel Is, Marchinbar I., head, Bay S of Sphinx, 11·15 S, 136·38 E, 20–21.ii.1984, H. Larson (NTMD); 13♂, 4♀ + nymphs, Wessel Is, Rimbija I., 11·01 S, 136·45 E, on sand dunes 100 m from water, 3–14.ii.1977, T. A. Weir (ANIC). **Queensland:** 1♂, 4 km S of Somerset, rock pools in sea splash zone, 15.x.1992, T. Weir, P. Zborowski (ANIC). **Western Australia:** 3♂, 5♀ + nymphs, Jos. Bonaparte Gulf, on surface over 39 fathoms, submarine light, dip net, 14.ix.1949, Stanley Fowler (AMS).

Description

Size. ♂, length 3·3–3·9, body width 1·6–1·8, head width 1·25–1·35; ♀, length 3·5–4·0, body width 1·8–2·0, head width 1·25–1·4.

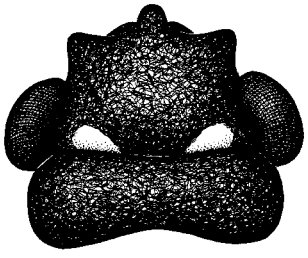
Colour. Uniformly blue-black with fine greyish pubescence. Antennae, legs, and proctiger dark brown to black. Yellow coloration of head limited to a pair of triangular marks at base (Fig. 88), not extending forward to middle of eyes. Bases of middle and hind legs and posterior margins of abdominal sterna, reddish brown.

Structure. Body oval, 2·1× (♂) or 1·9× (♀) as long as wide across middle acetabula. Eyes relatively small (Fig. 88), interocular width of head much more than 4·0× width of an eye. Second antennal segment 0·6–0·8× as long as fourth segment. No black bristles present on thorax or acetabula of either sex. First segment of fore tarsus about 0·6× as long as second segment. Middle and hind femora slender. Hind tarsal segments fused. *Male terminalia* (Figs 89–92). Styliform processes slender, asymmetrical, left process distinctly shorter than right process; both processes converging at their apices (Figs 91–92), neither process visible from above. Proctiger pentagonal in outline, a little broader than long; lateral margins produced in middle, with 10–12 spinous hairs on each side (Fig. 89). Vesical armature as illustrated by Andersen (1991*b*: fig. 4*E*).

Distribution and Habitats

White (1883) described *Halobates germanus* from the northern Pacific Ocean and Celebes Sea and recorded a specimen from the China Sea. Herring (1961: fig. 3) and Cheng (1989: fig. 3) found this species to be widely distributed in the Indo–West Pacific region, and mapped records in Australian waters from the Timor Sea and Torres Strait. We can add Ashmore Reef and Wessel Islands off the coast of the Northern Territory, and Jos. Bonaparte Gulf, Western Australia (Fig. 93).

H. germanus belongs to the group of open-ocean species, but seemingly prefers to stay closer to land than does *H. micans* and *H. sericeus* (Cheng 1989: fig. 3). However, the



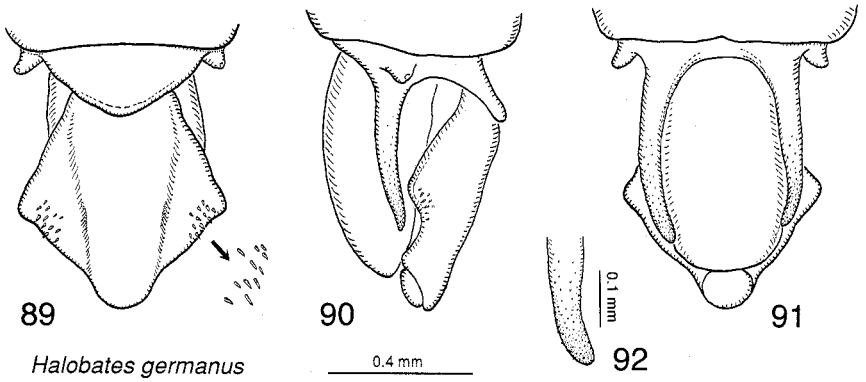


Fig. 88. *Halobates germanus*, head and pronotum. **Figs 89–92.** *Halobates germanus*, ♂ terminalia: *89*, dorsal view; *90*, lateral view; *91*, ventral view; *92*, apex of styliform process.

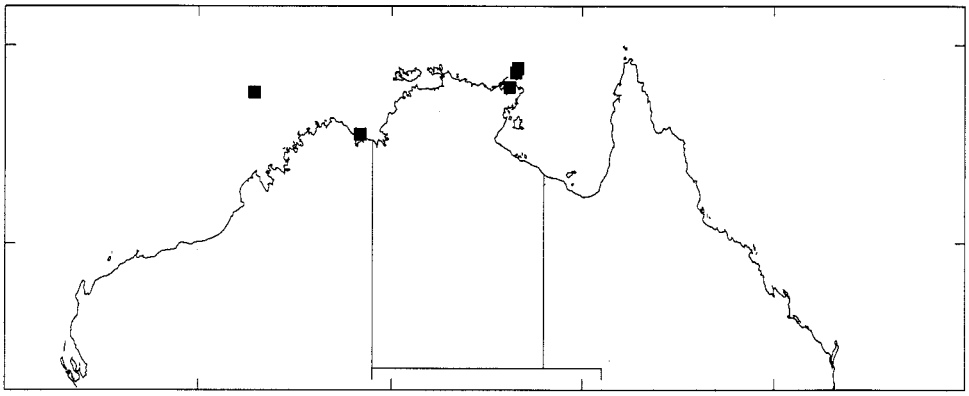


Fig. 93. *Halobates germanus*, distribution.

individuals collected on the Wessel Islands, on sand dunes 100 m from the water, were most likely blown ashore.

Comments

H. germanus can be separated from *H. sericeus* by its larger size, longer second antennal segment, and longer first segment of the fore tarsus. The male terminalia (Figs 89–92) are also quite distinctive.

The *princeps* Species-group

Although *H. princeps* was placed in a species-group of its own (Andersen 1991*b*: 45), this species is closely related to the *H. mariannarum* group (with five species in the West Pacific area including New Caledonia) and the *H. alluaudi* group (with two species along islands of the Indian Ocean). Most of these species are relatively large. The colour is chiefly dark, the head with crescent-shaped yellow markings. The first segment of the fore tarsus is longer than the second segment. Hind tarsal segments are distinctly separated from each other. The styliform processes of the male are more or less asymmetrically developed. Vesical armature is asymmetrical; the basal sclerite is present, the dorsal sclerite not perforated; there are two pairs of lateral sclerites.

Halobates (H.) princeps White

(Figs 94–100)

Halobates princeps White, 1883: 44, pl. 1, fig. 3.—Herring, 1961: 267.
Halobates ashmorensis Malipatil, 1988: 158.—Polhemus and Polhemus, 1991: 7 (synonymy with *H. princeps*); Andersen, 1991*b*: 45 (synonymy with *H. princeps*).

Material Examined

H. princeps, holotype. ♀, label data 'Between Station 212 and 213, Celebes Sea, 90·4' (BMNH).

H. ashmorensis, holotype. ♂, Northern Territory, 'Ashmore Reef, 12·14S 122·59E, at boat anchorage, night light, dip net, 17.iv.1987, G. O'Connor' (NTMD).

Paratypes. 1♂, 1♀, Northern Territory, same label data as holotype (NTMD).

Other material examined. **Northern Territory:** 1♀, Ashmore Reef, at boat anchorage, 12·14S, 122·59E, night light, dip net, 17.iv.1987, G. O'Connor (NTMD); 1♂, Ashmore Reef, West I., at boat anchorage, night light, 20.ix.1987, H. Larson (NTMD); 1♀, Hibernia lagoon, anchorage, 5.x.1992, collector unknown (NTMD). **Queensland:** 1♂, Lizard I., Coconut Beach, 9.ii.1980, L. Cheng and P. D. Schmitt (ZMUC); 1♀, same loc., lagoon, 24.i.1980, L. Cheng and P. D. Schmitt (ZMUC); 2♂, same loc., reef flat, 30.i. and 9.ii.1980, L. Cheng and P. D. Schmitt (ZMUC); 1♀, same loc., off reef flat, 10.i.1980, L. Cheng and P. D. Schmitt (ZMUC); 1♂, same loc., Osprey Islet, 24.i.1980, L. Cheng and P. D. Schmitt (ZMUC); 1♂, same loc., Watsons Bay, 24.i.1980, L. Cheng and J. E. Schmitt (ZMUC); 4♂, 4♀, South Lizard I., 100–200 offshore, night light, 2.ii.1981, B. and L. Goldman (ZMUC).

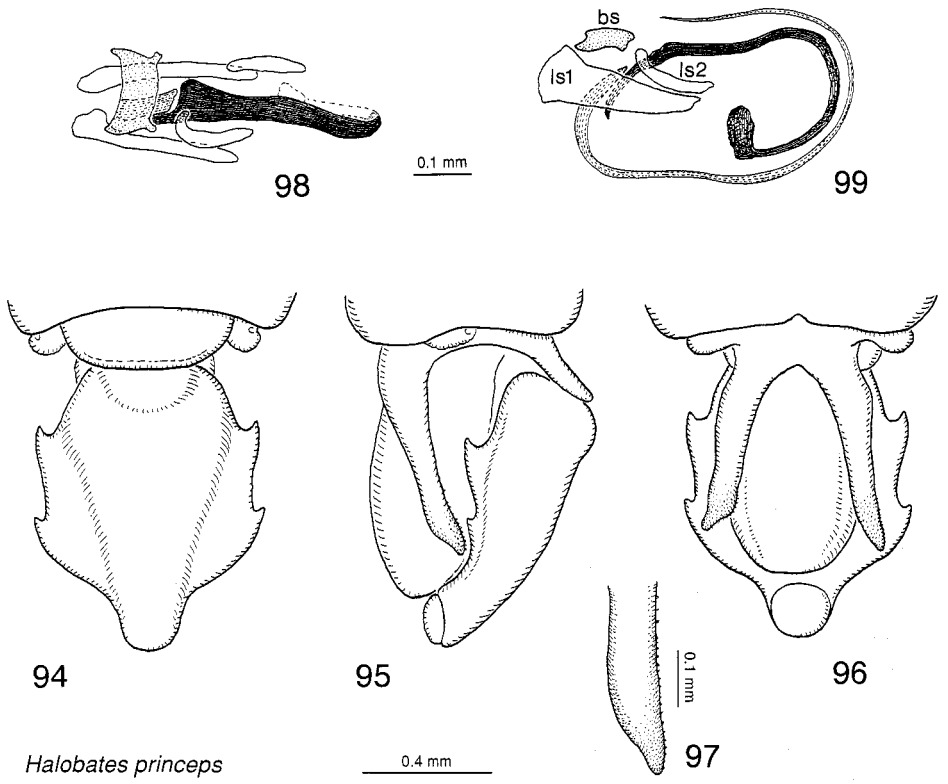
Description

Size. ♂, length 6·0–6·25, body width 2·3–2·5, head width 1·8–1·85; ♀, length 6·1–6·65, body width 2·7–2·9, head width 1·8–1·9.

Colour. Predominantly blue-black with fine greyish pubescence. Antennae, legs, and proctiger black. Yellow coloration of head forming crescent-shaped marking reaching middle of eyes, but not reaching middle pair of trichobothria. Thoracic and abdominal venter chiefly black, posterior margins of abdominal sterna yellowish. Male terminalia brownish beneath.

Structure. Body elongate oval, 2·6× (♂) or 2·3× (♀) as long as wide across middle acetabula. Interocular width of head about 3·8× width of an eye. Antenna $\frac{2}{3}$ as long as body; second antennal segment as long as fourth segment. Meso-metanotum of ♀ with few scattered, stiff hairs along sides; none present in ♂. Fore femora of ♂ incrassate, with a broad tubercle on ventral surface just before middle (see Malipatil 1988: fig. 7); first segment of fore tarsus very long, about 1·7× as long as second segment. *Male terminalia* (Figs 94–97). Styliform processes asymmetrical, broad and flattened, left process much longer than right process; apices not visible from above, with numerous denticles (Fig. 97). Proctiger almost hexagonal in dorsal outline, longer than broad; dorsally swollen near base

in lateral view (Fig. 95); lateral margins of proctiger almost parallel-sided, with 2 pairs of postero-laterally pointed edges. Vesical armature strongly asymmetrical (Figs 98–99); a large basal sclerite; dorsal sclerite prolonged and recurved distally with knob-like apex; slender, ventral sclerite separated from dorsal sclerite basally; 2 pairs of lateral sclerites, first pair distinctly larger than second pair.



Figs 94–97. *Halobates princeps*, ♂ terminalia: *94*, dorsal view; *95*, lateral view; *96*, ventral view; *97*, apex of styliform process. **Figs 98–99.** *Halobates princeps*, ♂ vesical armature: *98*, dorsal view; *99*, lateral view. Abbreviations: bs, basal sclerite; ls1, ls2, first and second pair of lateral sclerites.

Distribution and Habitat

White (1883) described *Halobates princeps* from the Celebes Sea, and Herring (1961: fig. 4) recorded it from Penang, West Malaysia, two localities near Java, the Palau Islands, and from Halmahera in the northern Moluccas. Cheng and Schmitt (1982) recorded *H. princeps* from Lizard Island, North Queensland, a significant eastward extension of its distributional range. We have also seen specimens from Ashmore Reef in the Timor Sea (Fig. 100).

According to Cheng and Schmitt (1982), neuston-net samples of *H. princeps* from Lizard Island consisted of both adults and nymphs, but with only few individuals per sample; the species was found only during January and February. A sample of eight adults was collected by 'night lighting' 100–200 m offshore South Lizard Island. *H. princeps* seems to inhabit more exposed parts of coral coasts, at varying distances from the shore. No information is present to indicate where and under which circumstances *H. princeps* breeds.

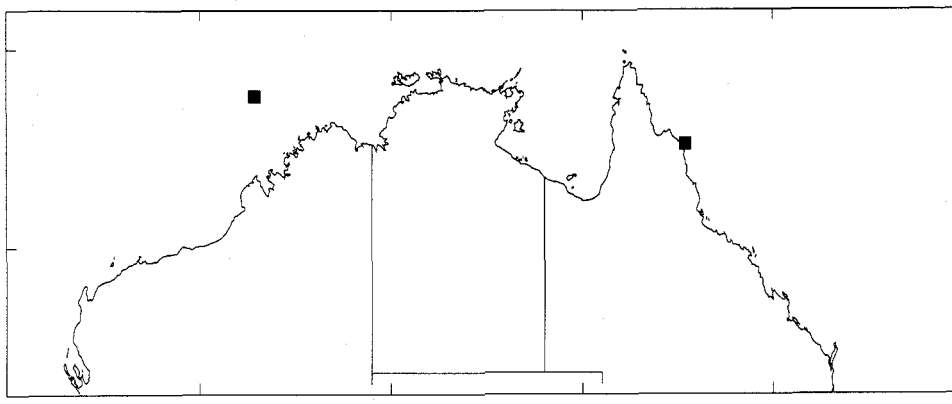


Fig. 100. *Halobates princeps*, distribution.

Comments

H. ashmorensis Malipatil (1988: 158) was described from Ashmore Reef, Timor Sea, and the excellent description and illustrations led both Polhemus and Polhemus (1991: 7) and Andersen (1991*b*: 45) to synonymise Malipatil's species with *H. princeps*. We have now examined the holotype of *H. ashmorensis* and can confirm its identity with that species.

H. princeps is by far the largest species of *Halobates* found in Australian waters (body length 6·0–6·7). The structure of the male terminalia (Figs 94–97) are also very distinctive.

Biology and Ecology

Although the open-ocean species of *Halobates* have attracted most interest, the majority of the 44 described species of sea skaters prefer near-shore, marine habitats. Our knowledge about the biology and ecology of sea skaters is generally quite sparse (Andersen and Polhemus 1976; Cheng 1985). Fortunately, a few coastal species have been studied more intensively during the past decade or so.

Halobates robustus has been studied in the Galapagos Islands (Birch *et al.* 1979; Foster and Treherne 1980, 1982). This species inhabits protected, rocky coasts with mangroves. Adults tend to aggregate in large 'flotillas' very close to mangrove trees or rocks. Nymphs (all instars) are usually found further away from the shore. Mating pairs are very frequently observed and the male (which is smaller than the female) stays with the female for a prolonged period (mate-guarding behaviour). Egg-laying has never been observed but oviposition probably takes place on rocks and/or roots of mangrove trees.

Another coastal species, *H. fijiensis*, has been studied in the Fiji Islands (Foster and Treherne 1986). It inhabits bays and lagoons fringed with mangroves. Younger nymphs are always found in sheltered waters amongst mangroves. Older nymphs and adults are found in more open water, sometimes several hundred metres from the mangroves. Mating pairs are infrequently observed, and the encounter between male and female (male slightly larger than female) is brief. Egg-laying was observed to take place on stands of sea-grass near the low-water mark, at extreme low spring tides. The newly hatched nymphs then have to make their way for several hundred metres to the protecting mangroves.

Most near-shore species of *Halobates* seem to prefer habitats that are sheltered from winds and wave action. Very few species of *Halobates* tolerate more exposed conditions. Observations of the distribution of *H. flaviventris* in Palau, West Caroline Islands (Cheng 1981), and the Aldabra Atoll, Seychelles (Polhemus 1990) suggest that this species aggregates along the *outer* margins of fringing coral reefs.

Five species of sea skaters have successfully colonised the open ocean (Cheng 1989): *H. germanus* (Indian and West Pacific Ocean), *H. sericeus* (Pacific Ocean), *H. sobrinus* (tropical eastern Pacific), *H. micans* (Atlantic, Indian, and Pacific Ocean), and *H. splendens*

(tropical south-eastern Pacific). Both adults and nymphs of these species live permanently upon the sea surface, always at some distance from nearest land. Eggs are deposited on various floating objects (Lundbeck 1914; Andersen and Polhemus 1976).

Although observations of preferred habitats are limited, the species of sea skaters found along the coasts of Australia are probably distributed among different marine habitats as shown on the idealised transect (Fig. 101). *Halobates acherontis* was collected more than 100 km above the mouth of Daly River, Northern Territory (Polhemus 1982). No other sea skaters have been recorded at such a great distance from the sea. Most Australian species inhabit mangroves in river estuaries, tidal creeks, or protected bays. Species like *H. mjobergi*, *H. lannae*, *H. zephyrus*, *H. whiteleggei*, *H. darwini* and *H. herringi* are probably close to *H. robustus* in their way of living (see above). Species inhabiting tidal pools and lagoons along coral coasts like *H. regalis*, *H. hayanus* and *H. princeps* may be ecologically close to *H. fijiensis* (see above). A transitional stage between the near-shore and oceanic way of life in sea skaters is represented by *H. germanus* which usually is found closer to land than the truly open-ocean species, *H. micans* and *H. sericeus* (Cheng 1989; Andersen 1991*b*).

By superimposing different stages of habitat preferences upon a reconstructed phylogeny of *Halobates* and its sister-group, *Asclepios*, Andersen (1991*b*) hypothesised that ancestral sea skaters colonised the sea surface through estuaries and coastal mangroves. This hypothesis was corroborated by the fact that such habitats are preferred by the three *Asclepios* species (Andersen 1991*b*; Andersen and Foster 1992) and by the two species of *Halobates*, subgenus *Hilliella*, the sister-group of all other *Halobates* (Fig. 3). The recent discovery of the limnic *Austrobates rivularis* (Andersen and Weir 1994), a halobatine water strider more closely related to *Halobates* than *Asclepios*, may seem puzzling. However, since organisms may have a wider spectrum of habitat tolerances than those actually preferred, the following scenario was suggested (Andersen and Weir 1994): (a) ancestral Halobatini lived in both limnic and marine habitats; (b) *Asclepios* adopted a preference for marine habitats; while (c) *Austrobates* and *Halobates* evolved from their euryhaline ancestors into species preferring limnic and marine habitats respectively. On the other hand, the supposed freshwater habit of *H. acherontis* (see above) may be a case of habitat reversal since this species is a sibling species of the mangrove-inhabiting *H. darwini*.

The diversification with respect to habitat preferences of adults and nymphs, tolerance toward surface winds and wave action, and in oviposition sites and mating strategies, has made it possible for several species of sea skaters to coexist in the same geographical area as exemplified through recent studies (Polhemus 1990; Andersen and Foster 1992), as well as by the distribution and habitat preferences of Australian sea skaters.

Zoogeography

The zoogeography of *Halobates* reflects both ecological and historical factors. The great majority of *Halobates* species are found in the tropical parts of the Indo–West Pacific region (Cheng 1985). The distribution of near-shore sea skaters in this region seems more or less to coincide with the distribution of reef-building corals and mangroves. Most near-shore *Halobates* species have a limited distribution and some are endemic to particular groups of islands or coastal areas of larger land masses. Adult sea skaters are always wingless but may disperse by surface skating or passive drift along coasts, chains of islands and, occasionally, across wider stretches of open sea. This may account for the wide distribution of a few near-shore species, namely *H. flaviventris*, *H. hawaiiensis*, *H. hayanus* and *H. mariannarum* (Herring 1961).

The distribution of the five oceanic *Halobates* species is now well established (Cheng 1989). They all occur in tropical and subtropical waters where the winter temperature does not fall much below 20°C. Their occurrence and abundance on any given water mass is apparently controlled by surface water temperatures, with an optimum temperature range for four eastern Pacific species (including *H. micans* and *H. sericeus*) of 24–28°C (Cheng and Shulenberger 1980).

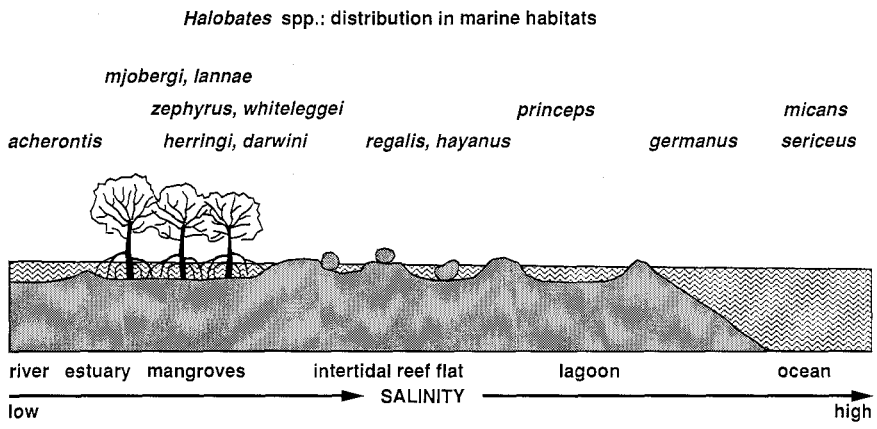


Fig. 101. Habitat preferences of Australian species of *Halobates* indicated by species names above idealised transect of aquatic habitats, from river to open ocean.

Andersen (1991*a*) discussed the historical (cladistic) biogeography of marine water striders. Until quite recently, the genus *Asclepios* was the only other genus of the tribe Halobatini besides *Halobates*. The three described species of *Asclepios* are distributed along the coasts of south-east and east Asia. They are more plesiomorphic than *Halobates* in some characters but otherwise difficult to separate from *H. mjobergi* and *H. lannae* (subgenus *Hilliella*), which together form the sister-group of all other *Halobates* species (Fig. 3). Since *H. mjobergi* and *H. lannae* occur in tropical Australia, Andersen (1991*b*) suggested that *Halobates* originated somewhere in the Indo-Australian region. The discovery of an even closer relative of *Halobates* in Cape York Peninsula, Queensland (*Austrobates rivularis* Andersen & Weir, 1994), further suggests that *Halobates* originated somewhere in the area that now includes the northernmost part of the Australian continent.

The distributions of Australian species of *Halobates* are summarised in Table 2. Most Australian sea skaters occur in the tropical north, but two endemic species, *H. zephyrus* and *H. whiteleggei*, extend along the coast of New South Wales as far south as Sydney. Most endemic *Halobates* species belong to the *regalis*-group, with *H. whiteleggei* confined to eastern Australia and the species-pair *H. darwini* and *H. acherontis* to northern Australia. *H. regalis* and *H. herringi* are found in both areas. Although the comparison between the cladistic relationships (Fig. 4) and distributions of species indicates some east–north-west vicariance in Australia, it is noteworthy that the *regalis*-group also includes non-Australian species, namely *H. peronis*, ranging from the Philippines to the Solomon Islands, *H. murphyi* from Papua New Guinea, and *H. sexualis* Distant, from Sri Lanka and West Malaysia.

The sea skaters endemic to Australia belong to two of the three major clades of *Halobates* (Fig. 3). The third clade is represented by two species in New Caledonia (*H. panope* Herring and *H. katherinae* Herring) and the absence of these or related species in Australia is noteworthy.

Widespread *Halobates* species found in Australia may be either coastal (*H. hayanus* and *H. princeps*) or oceanic (*H. micans*, *H. sericeus* and *H. germanus*). Andersen (1991*b*) showed that two of the five ocean skaters are closer to some coastal, but widespread species, than to other oceanic species. It is most likely that the oceanic species have originated somewhere in the Indo-Pacific and have subsequently dispersed to all tropical areas of the Atlantic, Indian and Pacific Oceans.

In conclusion, the Australian fauna of *Halobates* is ecologically and historically diverse and in several respects unique. Sea skaters are, above all, inhabitants of mangroves and coral reefs, marine communities recognised as extremely vulnerable and threatened by human activities and exploitation (World Conservation Monitoring Centre 1992). Australia

Table 2. Distribution of Australian species of *Halobates*

Species	Australian distribution	Other distribution
	Endemic, coastal species	
H. mjobergi	NT, Qld, WA	Papua New Guinea
H. lannae	NT, WA	—
H. zephyrus	NSW, Qld	—
H. regalis	Qld, WA	—
H. whiteleggei	NSW, Qld	—
H. darwini	NT	—
H. acherontis	NT	—
H. herringi	NT, Qld	—
	Widespread, coastal species	
H. hayanus	NT, Qld	Red Sea, Indo-Australian region
H. princepts	NT, Qld	Indo-Malayan Archipelago
	Widespread, oceanic species	
H. micans	NSW, NT, WA	Atlantic, Indian and Pacific Ocean
H. sericeus	Lord Howe I., Qld	Pacific Ocean
H. germanus	NT, WA	Indian and West Pacific Ocean

holds a significant element of the biological diversity of marine water striders and is capable of making a worthy contribution to their protection and conservation.

Acknowledgments

We thank Dr J. Just, Australian Biological Resource Study, for suggesting the project 'Semiaquatic Bugs of Australia' to us, and especially Dr E. S. Nielsen, CSIRO Division of Entomology, Canberra, for his enthusiasm and invaluable help during the initial phase of our work. We are further indebted to Dr L. Cheng, Scripps Institution of Oceanography, La Jolla, and to Dr J. T. Polhemus, Englewood, Colorado, for donating material of sea skaters and for permission to cite unpublished records. Birgitte Rubaek assisted with the preparation of the illustrations. Thanks are also due to two anonymous referees for valuable comments on the manuscript and to the following persons for permission to study specimens under their care: Dr R. C. Froeschner, USNM; Mr I. Lansbury, UMO; Dr P. Lindskog, NRS; Dr G. B. Monteith, QMB; Dr D. A. Polhemus, BPBM; Dr J. T. Polhemus, JTPC; Miss M. A. Schneider, UQIC; Dr J. van Tol, RNHL; Mr M. D. Webb, BMNH. This work is part of a project supported by grants from the Australian Biological Resource Study, Canberra, and the Danish Natural Science Research Council (Grant No. 11–0090) to the senior author.

References

Andersen, N. M. (1982). The semiaquatic bugs (Hemiptera, Gerromorpha). Phylogeny, adaptations, biogeography, and classification. *Entomonograph* **3**, 1–455.

Andersen, N. M. (1991*a*). Cladistic biogeography of marine water striders (Hemiptera, Gerromorpha) in the Indo-Pacific. *Australian Systematic Botany* **4**, 151–63.

Andersen, N. M. (1991*b*). Marine insects: genital morphology, phylogeny and evolution of sea skaters, genus *Halobates* (Hemiptera, Gerridae). *Zoological Journal of the Linnean Society, London* **103**, 21–60.

Andersen, N. M., and Foster, W. A. (1992). Sea skaters of India, Sri Lanka and the Maldives, with a new species and a revised key to Indian Ocean species of *Halobates* and *Asclepios* (Hemiptera, Gerridae). *Journal of Natural History* **26**, 533–53.

Andersen, N. M., and Polhemus, J. T. (1976). Water-striders (Hemiptera: Gerridae, Veliidae, etc.). In 'Marine Insects'. (Ed. L. Cheng.) pp. 187–224. (North-Holland: Amsterdam.)

Andersen, N. M., and Weir, T. A. (1994). *Austrobates rivularis*, gen. et sp. nov., a freshwater relative of *Halobates* (Hemiptera: Gerridae), with a new perspective on the evolution of seaskaters. *Invertebrate Taxonomy* **8**, 1–15.

Annandale, N., and Kemp, S. (1915). Fauna of the Chilka Lake. Aquatic insects, other than Coleoptera, with notes on some marginal species. *Memoirs of the Indian Museum* **5**, 177–87, pl. 11.

Birch, M., Cheng, L., and Treherne, J. E. (1979). Distribution and environmental synchronization of the marine insect, *Halobates robustus*, in the Galapagos Islands. *Proceedings of the Royal Society of London, Series B* **206**, 33–52.

Carpenter, G. H. (1892). Rhynchota from Murray Island and Mabuiag. Reports on the Zoological collections made in Torres Straits by Professor A. C. Haddon, 1888–1889. *Scientific Proceedings, Royal Dublin Society, N.S.* **7**, 137–46, pls 12–13.

Cheng, L. (1981). *Halobates* (Heteroptera: Gerridae) from Micronesia with notes on a laboratory population of *H. mariannarum*. *Micronesica* **17**, 97–106.

Cheng, L. (1985). Biology of *Halobates* (Heteroptera: Gerridae). *Annual Review of Entomology* **30**, 111–35.

Cheng, L. (1989). Factors limiting the distribution of *Halobates* species. In 'Reproduction, Genetics and Distributions of Marine Organisms'. (Eds J. S. Ryland and P. A. Tyler.) pp. 357–62. (Olsen and Olsen: Fredensborg.)

Cheng, L., and Schmitt, P. D. (1982). Marine insects of the genera *Halobates* and *Hermatobates* (Heteroptera) from neuston tows around Lizard Island, Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* **33**, 1109–12.

Cheng, L., and Shulenberger, E. (1980). Distribution and abundance of *Halobates* species (Insecta: Heteroptera) in the eastern tropical Pacific. *Fishery Bulletin* **78**, 579–91.

China, W. E. (1957). The marine Hemiptera of the Monte Bello Islands, with descriptions of some allied species. *Journal of the Linnean Society of London, Zoology* **40**, 342–57.

Dahl, F. (1893). Die *Halobates*-Ausbeute der Plankton-Expedition. *Ergebnisse der Plankton-Expedition* **2**, G.a., 1–9.

Distant, W. L. (1910). Some undescribed Gerrinae. *Annals and Magazine of Natural History, 8th Series* **5**, 140–53.

Esaki, T. (1929). New or little-known Gerridae. II. Indian species. *Annals and Magazine of Natural History, 10th Series* **4**, 412–19.

Eschscholtz, J. F. (1822). 'Entomographien.' Vol. 1 (1stelieferung). (Berlin.)

Farris, J. S. (1988). 'Hennig86, Version 1·5 Computer Program.' (New York.)

Foster, W. A., and Treherne, J. E. (1980). Feeding, predation and aggregation behaviour in a marine insect, *Halobates robustus* Barber (Hemiptera: Gerridae) in the Galapagos Islands. *Proceedings of the Royal Society of London, Series B* **209**, 539–53.

Foster, W. A., and Treherne, J. E. (1982). Reproductive behaviour of the ocean skater *Halobates robustus* (Hemiptera: Gerridae) in the Galapagos Islands. *Oecologia (Berlin)* **55**, 202–7.

Foster, W. A., and Treherne, J. E. (1986). The ecology and behaviour of a marine insect, *Halobates fijiensis* (Hemiptera: Gerridae). *Zoological Journal of the Linnean Society* **86**, 391–412.

Frauenfeld, G. von (1867). Zoologische Miscellen. 11. Das Insektenleben zur See. *Verhandlungen zoologisches-botanisches Gesellschaft Wien* **17**, 456–60, pl. 12, figs 1–10.

Hale, H. M. (1925). The aquatic and semi-aquatic Hemiptera. Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910–1913. *Arkiv för Zoologi* **17A(20)**, 1–19.

Herring, J. L. (1961). The genus *Halobates* (Hemiptera: Gerridae). *Pacific Insects* **3**, 223–305.

Imms, A. D. (1936). On a new species of *Halobates*, a genus of pelagic Hemiptera. *The John Murray Expedition 1933–34, Scientific Reports, Zoology* **4** [1936–38], 71–8.

Laporte, F. L. de (1832). 'Essai d'une classification systématique de l'ordre Hémiptères (Hémiptères — Héteroptères Latr.).' (Paris.)

Lundbeck, W. (1914). Some remarks on the eggs and egg-deposition of *Halobates*. *Mindeskrift for Japetus Steenstrup* **2(27)**, 1–13.

Mackerras, I. M. (1950). Marine insects. *Proceedings of the Royal Society of Queensland* **61**, 19–29.

Malipatil, M. B. (1988). Two new species of *Halobates* Eschscholtz (Hemiptera: Gerridae) from Australia. *Journal of the Australian Entomological Society* **27**, 157–60.

Marks, E. N. (1971). Australian marine insects. *Australian Natural History* **17**, 134–8.

Matsuda, R. (1960). Morphology, evolution and a classification of the Gerridae (Hemiptera — Heteroptera). *University of Kansas Science Bulletin* **41**, 25–632.

Miyamoto, S., and Senta, T. (1960). Distribution, marine condition and other biological notes of marine water-striders, *Halobates* spp., in the south-western sea area of Kyushu and western area of Japan Sea. *Sieboldia* **2**, 171–86. (In Japanese with English summary.)

Polhemus, D. A. (1990). Heteroptera of Aldabra Atoll and nearby islands, western Indian Ocean, Part 1. Marine Heteroptera (Insecta): Gerridae, Veliidae, Hermatobatidae, Saldidae and Omaniidae, with notes on ecology and insular zoogeography. *Atoll Research Bulletin* **345**, 1–16.

Polhemus, J. T. (1982). Marine Hemiptera of the Northern Territory, including the first fresh-water species of *Halobates* Eschscholtz (Gerridae, Veliidae, Hermatobatidae and Corixidae). *Journal of the Australian Entomological Society* **21**, 5–11.

Polhemus, J. T., and Cheng, L. (1982). Notes on marine water-striders with descriptions of new species. Part I. Gerridae (Hemiptera). *Pacific Insects* **24**, 219–27.

Polhemus, J. T., and Polhemus, D. A. (1991). Three new species of marine water-striders from the Australasian region, with notes on other species (Gerridae : Halobatinae, Trepobatinae). *Raffles Bulletin of Zoology* **39**, 1–13.

Skuse, F. A. A. (1891). Description of a new pelagic Hemipteron from Port Jackson. *Records of the Australian Museum* **1**, 174–7, pl. 27.

Skuse, F. A. A. (1893). Notes on Australian aquatic Hemiptera No. 1. *Records of the Australian Museum* **2**, 42–5, pl. 11.

Templeton, R. (1836). Description of a new hemipterous insect from the Atlantic Ocean. *Transactions of the Entomological Society of London* **1**, 230–1, pl. 22, fig. *a*.

Walker, J. J. (1893). On the genus *Halobates* Esch., and other marine Hemiptera. *Entomologists' Monthly Magazine* **29**, 227–32.

White, F. B. (1883). Report on the pelagic Hemiptera. *Voyage of Challenger, Reports, Zoology* **7**, 1–82.

Witlaczil, E. (1886). Die Ausbeute des 'Pisani' an *Halobates* wäahrend der Erdumseglung 1882–1885. *Wiener entomologisches Zeitung* **5**, 177–82, 231–4.

World Conservation Monitoring Centre (1992). 'Global Biodiversity: Status of the Earth's Living Resources.' (Chapman and Hall: London.)

Manuscript received 17 December 1993; accepted 19 April 1994