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Publication Date

2004-06-30

THE MARINE INSECT *HALOBATES* (HETEROPTERA: GERRIDAE): BIOLOGY, ADAPTATIONS, DISTRIBUTION, AND PHYLOGENY

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Abstract Among the million or so insect species known, only a few thousand are found in marine habitats. The genus *Halobates* is almost exclusively marine and is unique in having the only known species to live in the open ocean. Of the 46 *Halobates* species described, only five are completely oceanic in habitat, with the majority of species living in coastal areas associated with mangroves or other marine plants. This review presents a brief historical account of the genus and provides information on various aspects of its life history, ecology, special adaptations, distribution, and biogeography. Distribution maps of the five oceanic species as well as several of the more widely distributed coastal species have been updated. The phylogeny and evolution of *Halobates* based on morphology and recent molecular data are also discussed. A key to all known species of *Halobates* and related genera and a checklist of all species and their distributions are included as appendices.

Introduction

The oceans have always held a great fascination to us. Many great voyages were launched to explore the oceans and what lies beyond. A great variety of marine organisms were collected and described during these voyages, but insects appear to have received little attention. Although they are the most abundant animals on land, insects are relatively rare in marine environments (Cheng 1976). However, a few thousand insect species belonging to more than 20 orders are considered to be marine (Cheng & Frank 1993, Cheng 2003). The majority of marine insects belong to the Coleoptera, Hemiptera, and Diptera, and they can be found in various marine habitats. However, the only insects to live in the open ocean are members of the genus *Halobates*, commonly known as sea-skaters. They belong to the family Gerridae (Heteroptera), which comprises the common pond-skaters or water-striders. Unlike most of its freshwater relatives, the genus *Halobates* is almost exclusively marine. Adults are small, measuring only about 0.5 cm in body length, but they have rather long legs and may have a leg span of 1.5 cm or more (Figure 1). They are totally wingless at all stages of their life cycle and are confined to the air–sea interface, being an integral member of the pleuston community (Cheng 1975). One may wonder how such tiny insects have managed to live in the open sea, battling waves and storms. In life, sea-skaters appear silvery. On calm days ocean-going scientists have probably seen them as shiny spiders skating over the sea surface. It is not known whether ancient mariners ever saw them, and no mention of their presence has been

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Oceanography and Marine Biology: An Annual Review 2004, **42**, 119–180

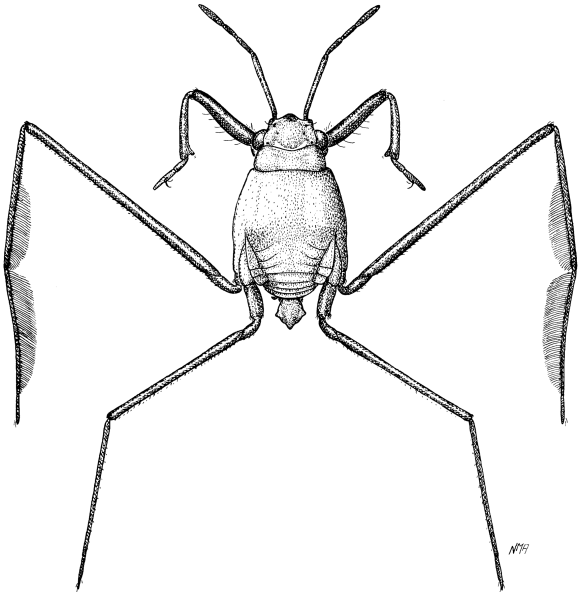

Figure 1 *Halobates* (s. str.) *micans* Eschscholtz, male, body length = 4.4 mm. (From Andersen & Polhemus 1976.)

found in the logs of Christopher Columbus's (1451–1506) ships or other ships that sailed to and from the New World.

Forty-six species of *Halobates* are now known. Five are oceanic and are widely distributed in the Pacific, Atlantic and the Indian Oceans. The remaining species occur in nearshore areas of tropical seas associated with mangroves or other marine plants. Many are endemic to islands or island groups (Cheng 1989a). This review presents a brief historical account of *Halobates* and updates what is known about their biology, special adaptations, distributions, evolution and phylogeny. Earlier literature on *Halobates* can be found in Cheng (1985). A key to *Halobates* species and related genera and a checklist of all species with their known distributions are given in Appendices 1 and 2.

Historical background

The first *Halobates* specimens were collected by an Estonian doctor, Johann Friedrich Eschscholtz, during a round-the-world expedition on the Russian vessel *Rurik* between 1815 and 1818. He erected the genus *Halobates* in 1822 and described three species: *H. micans*, *H. sericeus*, and *H. flaviventris* (Eschscholtz 1822). All three species remain in good standing. The first monograph on *Halobates*, published in 1883 by Buchanan White, contained 11 species, including 6 new species collected during the Challenger expedition (1873–1876). Sporadic accounts of this curious marine insect have appeared in various scientific or popular publications and a number of new species were added in the next 80 yr. However, no serious efforts had been made to study the biology of *Halobates* except for a detailed account on the eggs and oviposition substrata by Lundbeck (1914). This was based largely on an extensive collection deposited at the Zoological Museum, University of Copenhagen, by the well-known Danish zoologist Japetus Steenstrup.

The taxonomy of *Halobates* was in a mess until Jon Herring took it up as a thesis project. The publication of a monograph (Herring 1961) based on his thesis research was the first thorough review on the genus. It contained a concise historical account of its discovery, a list of early references in the literature, maps showing distributions of all known species, and a discussion of the origin and phylogeny of the genus. He also redescribed each species and listed their synonyms, added 14 new species, and constructed a key to the 38 species he recognised. In addition, he made the first attempt to study the life history and development of the coastal *H. hawaiiensis*. With Herring's untangling of the taxonomic confusion, the way was cleared for further research on *Halobates*. However, it appears that for many years no entomologists took the challenge. The first oceanographer to do so was a Russian marine biologist, Anatoly Ivanovich Savilov, who compiled data on *Halobates* collected from 250 stations in the Pacific Ocean during expeditions on the Research Vessel (R/V) *Vityaz* between 1957 and 1961. He mapped the known distributions of all five pelagic species in the Pacific and discussed various physical and biological factors that could be responsible for limiting the ranges of the species (Savilov 1967). His untimely death in 1969 terminated further work on the subject. The first American oceanographer to take any substantial interest in *Halobates* was Rudolf Scheltema at the Woods Hole Oceanographic Institution (WHOI). He published a popular article in *Oceanus* (Scheltema 1968) and mapped the distribution of *H. micans* in the Atlantic Ocean based on samples collected on various WHOI expeditions between 1966 and 1968. Two reviews were subsequently published by Cheng (1973a, 1985), in which information and literature on *Halobates* were discussed in some detail. Since the 1980s, much of the research on *Halobates* has been carried out by the present authors, either independently or in collaboration with other colleagues.

Morphology and systematics

General morphology and key characters

Halobates are medium-size insects rarely measuring more than 6.5 mm long. They are dull-coloured, but owing to light interference in the hair layers surrounding their bodies, they usually appear greyish or silvery (Figure 24A, p. 142). The eyes are well developed, with a multitude of facets. The long, thin antennae have four segments. The body is suboval with relatively short pro- and metathorax but greatly prolonged mesothorax (Figure 1, Figure 2). The abdomen is greatly shortened in both sexes. Genital segments of the male are composed of a broad, tubular segment 8 (Figure 3A and B, s8) carrying a pair of styliform processes posteriorly directed along its ventral side (Figure 3B, st). Enclosed in segment 8 is a suboval pygophore (= segment 9, pg), which is covered by a large, plate-shaped proctiger (= segment 10 + 11, pr). Genital segments of the female are much shorter, composed of a large segment 8 with a pair of gonocoxa on its ventral side and a suboval proctiger protruding from its posterior margin (Figure 2A).

Modifications of the external male genital segments have been widely used for species identification in *Halobates* (Herring 1961). However, detailed comparative studies on their genital morphology have revealed additional characters of both taxonomic and phylogenetic importance (Andersen 1991a). The male organ is composed of a proximal, sclerotised *phallotheca* (Figure 4, ph) and a distal *endosoma*. The latter is further divided into a membranous *conjunctivum* (co) and a *vesica* (ve) armed with sclerotised pieces. In species of the subgenus *Hilliella* (Figure 5A), the vesica has a median, ring-like sclerotised structure composed of separate dorsal (ds) and ventral sclerites (vs). In addition, there are two pairs of lateral sclerites (ls1, ls2). Similar structures were found in *Asclepios* species (Andersen 1991a) and in *Austrobates rivularis*, the limnic sister group of *Halobates* (Andersen & Weir 1994a).

Species of the subgenus *Halobates sensu stricto* (s. str.) can be separated into two major groups based on their vesical armature. One group (Figure 5D) has retained the separate dorsal and ventral sclerites, as well as two pairs of lateral sclerites. To this group belongs *H. poseidon*, *H. robustus*, *H. mariannarum*, *H. princeps*, etc. In the second group (Figure 5B and E) the dorsal and ventral sclerites are fused, and the latter is perforated by a characteristic, diamond-shaped hole. Most species have only one pair of lateral sclerites (although there are two pairs in *H. maculatus* and *H.*

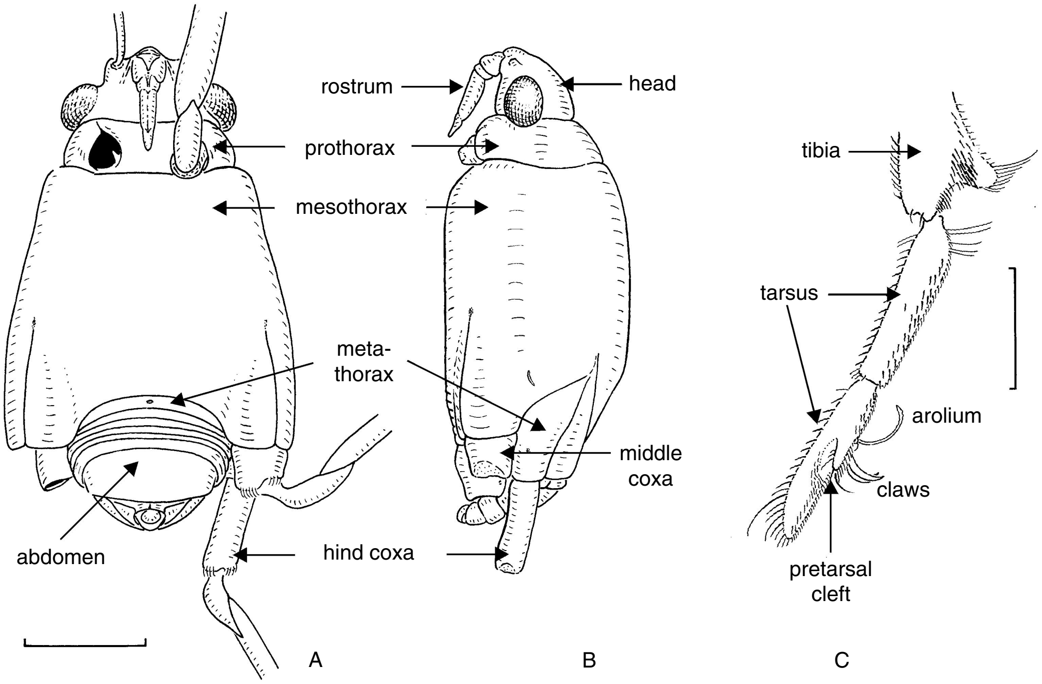

Figure 2 *Halobates* sp., adult female. (A) Ventral view; (B) lateral view, most of antennae and legs omitted; (C) front tarsus and apex of tibia. Scale bars = 1 mm (A and B), 0.4 mm (C). (Modified from Andersen & Polhemus 1976.)

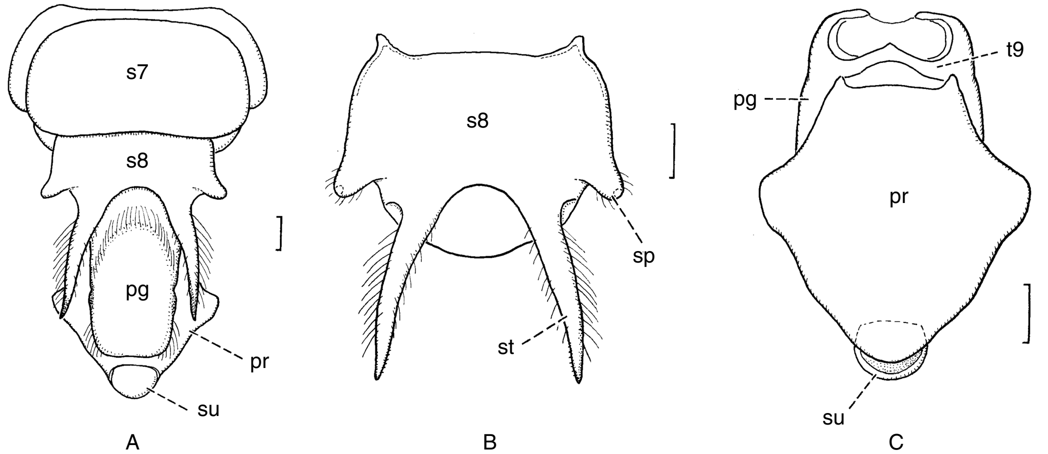

Figure 3 *Halobates* (*Hilliella*) *mjobergi* Hale, male genital segments. (A) Ventral view of abdominal end; (B) ventral view of segment 8, showing spiracular (sp) and styliform processes (st); (C) dorsal view of pygophore (pg) and proctiger (pr), also showing tergum 9 (t9) and subanal plate (su). All scale bars = 0.1 mm. (Modified from Andersen 1991a.)

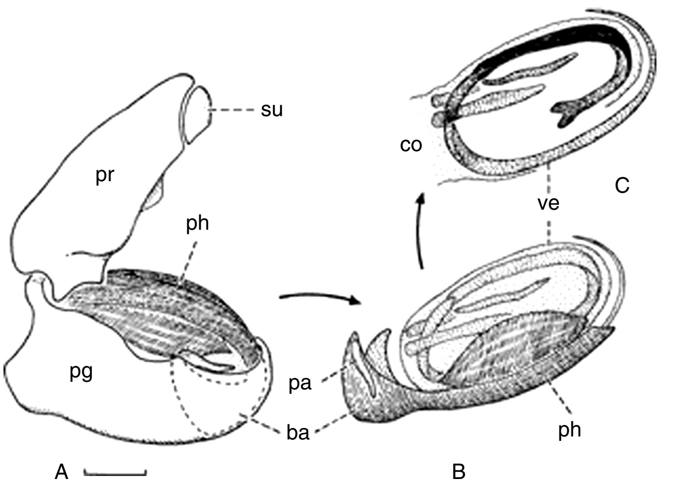

Figure 4 *Halobates* (*Hilliella*) *mjobergi* Hale, male genital segments (slightly schematised). (A) Oblique lateral view of pygophore (pg), proctiger (pr), subanal plate (su), and phallus (ph) lying upside down within pygophore; (B) basal apparatus (ba) with parameres (pa), and phallus removed from pygophore; (C) vesica (ve) removed from phallotheca and everted from conjunctivum (co). Scale bar = 0.1 mm. (Modified from Andersen 1991a.)

proavus; Figure 5C). This latter group includes *H. hayanus*, *H. flaviventris*, *H. zephyrus*, *H. darwini*, and the five oceanic species. In addition, female genital segments and reproductive organs, in particular those of the ovipositor and gynatrial complex, are also of phylogenetic importance (Andersen 1982, 1991a).

In addition to Herring's key (1961) for the identification of 38 species of *Halobates*, regional keys are available for the Indian Ocean (Andersen & Foster 1992), Australia (Andersen & Weir 1994b), and Singapore and Peninsular Malaysia (Cheng et al. 2001). Appendix 1 provides a revised, comprehensive key to all 46 described species of *Halobates* as well as species of the related genera *Austrobates* (one species) and *Asclepios* (three species).

Functional morphology

The overall structure of *Halobates* deviates from the generalised insect plan in several ways. Most of its modifications are adaptations towards locomotion on the water surface, which necessitates specialisations in the thoracic skeleton and musculature, structures of the legs, and water-repellent features of body and legs (Andersen 1976, 1977, 1982, Andersen & Polhemus 1976).

The fine structure of the body surface of *Halobates,* as revealed by scanning electron microscopy (Cheng 1973b, Andersen 1977), comprises two kinds of hairs inserted in sockets (Figure 6 and Figure 7). The first kind (Figure 8, a) is 20–30 µm long, about 1 µm wide at the base, and inclined at angles of 20–40˚. These hairs are evenly distributed over the body surface at densities of 8000–12,000 per mm^2, forming a regular carpet 6–10 µm thick. The second kind (Figure 8b) is slightly longer, more erect, with densities of 4000–5000 per mm^2. Beneath them, there is a velvety undercoat, absent from the antennae and legs, consisting of hook-like microtrichia (Figure 8c) 1.5 µm high, 0.5 µm wide at the base, and 0.6–1.5 µm wide at the tip. Their bases often have slender outgrowths. The density of these microtrichia is very high, $6–7 \times 10^5$ per mm^2. The elaborate body hair layers help to prevent *Halobates* from being wetted when they are accidentally submerged or wetted by mist or rain (Cheng 1985). When a sea-skater is submerged in water it carries a layer of air held by the hair layers, rendering it buoyant so that it can surface rapidly. Once on the sea

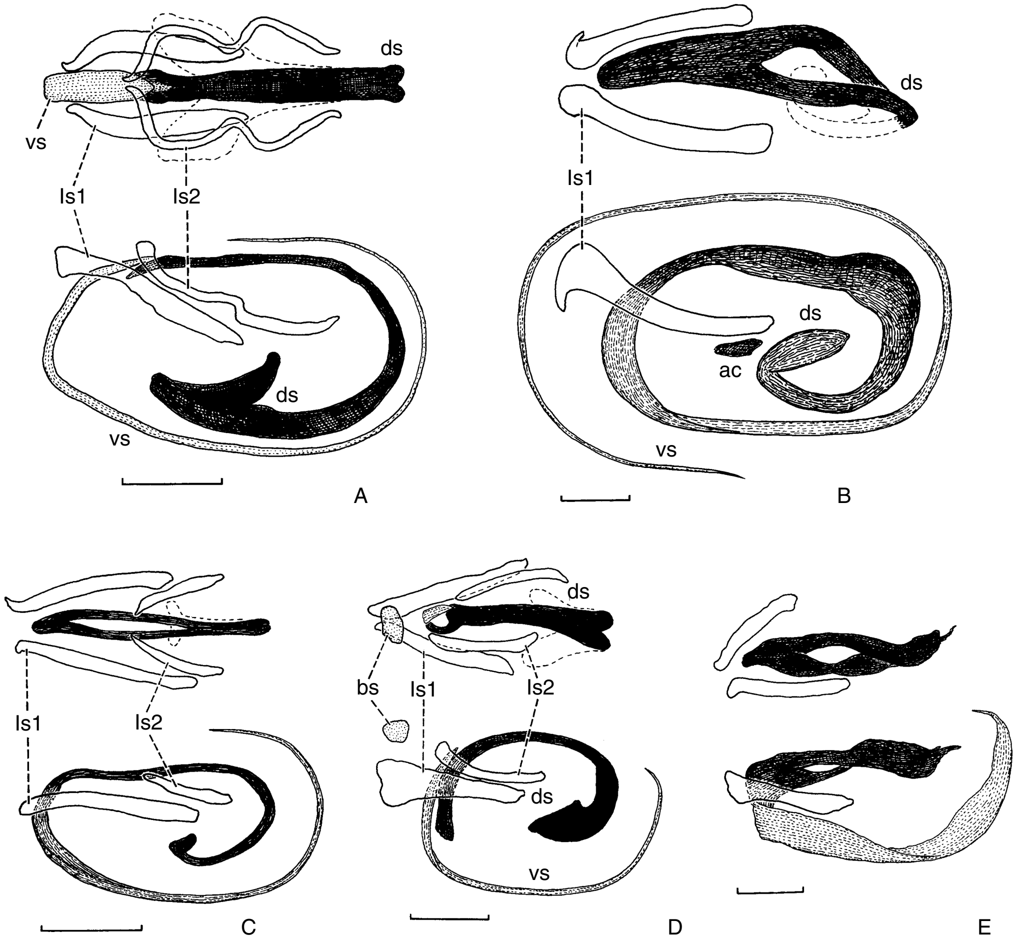

Figure 5 *Halobates* spp., vesical armature of male phallus; for each species shown in dorsal (top) and lateral view (bottom), shading of sclerites conventionalised: dorsal sclerite (ds) shown black, ventral sclerite (vs) stippled, basal plate (bs) dotted, and lateral sclerites (ls1 and ls2) without shading. (A) *H.* (*Hilliella*) *mjobergi* Hale; (B) *H.* (s. str.) *micans* Eschscholtz; (C) *H.* (s. str.) *maculatus* Schadow; (D) *H.* (s. str.) *poseidon* Herring; (E) *H.* (s. str.) *darwini* Herring. All scale bars = 0.1 mm. (Modified from Andersen 1991a.)

surface, water droplets fall away rapidly, leaving the insect quite dry. However, the hydrofuge property of this hair layer is not permanent. Upon prolonged exposure to water the hairs will finally become wetted and the submerged insect may have great difficulty in regaining its position on the sea surface. If, on the other hand, the insect is allowed to groom and become dry in the air, the hair coat can resume its former unwettable condition. Grooming is effected by specialised hair-like structures on the front tibiae (Andersen & Polhemus 1976, Andersen 1977).

The thorax of *Halobates* is well sclerotised, forming a rigid box that limits longitudinal deformations. The legs are adapted for different functions. The short and stout front legs help to support the body while the insect is at rest, or serve for grasping and holding prey during feeding, or the female during copulation. The long and slender middle legs propel the body like oars beating in synchrony while the hind legs are chiefly used for steering and supporting the body when the middle legs are lifted off the surface. The insertion of the middle and hind legs on the sides of the meso- and metathorax, far from the front legs, allows extremely wide movements of these legs. Claws, present on all legs, are inserted preapically on the terminal tarsal segment (Figure 2C).

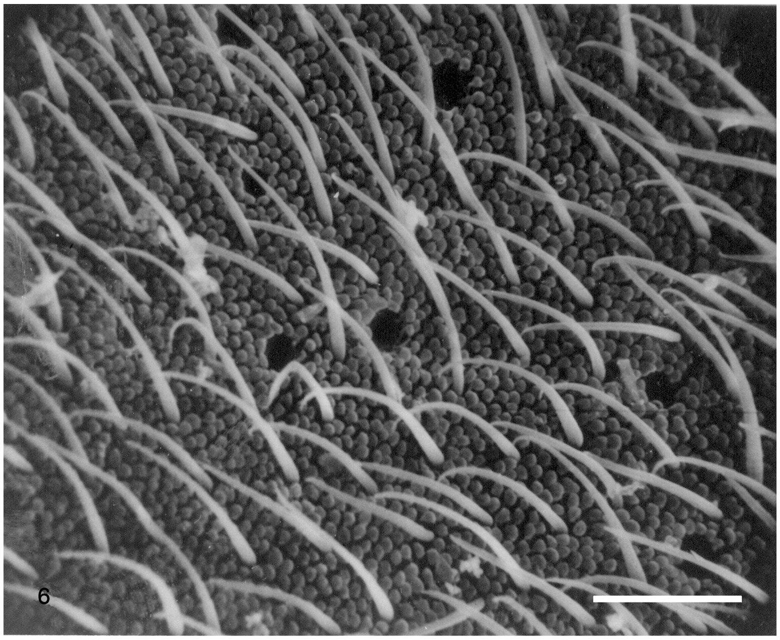

Figure 6 Scanning electron micrograph of thoracic region of *Halobates proavus* showing cuticular hair layers. Scale bar = 10 µm. (Reproduced from Cheng 1973b.)

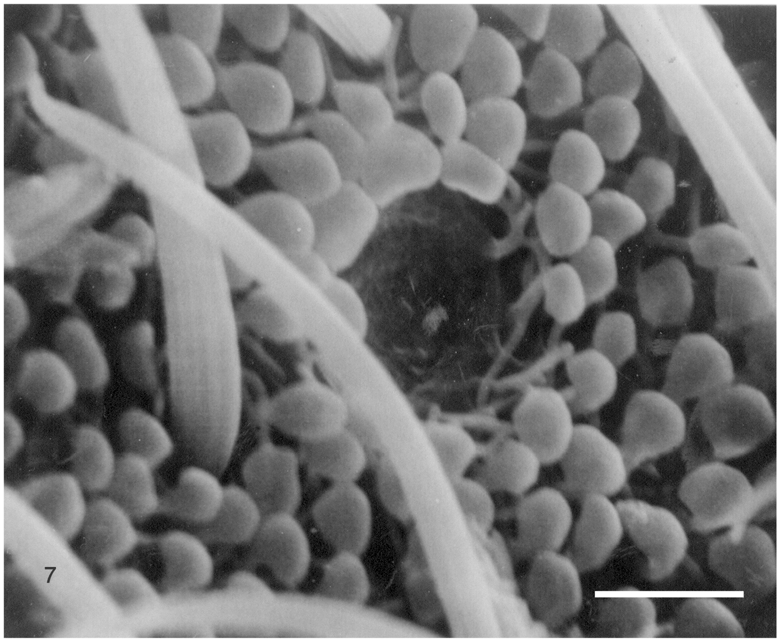

Figure 7 As above, showing mushroom-like microtrichia and pit. Scale bar = 1 µm. (Reproduced from Cheng 1973b.)

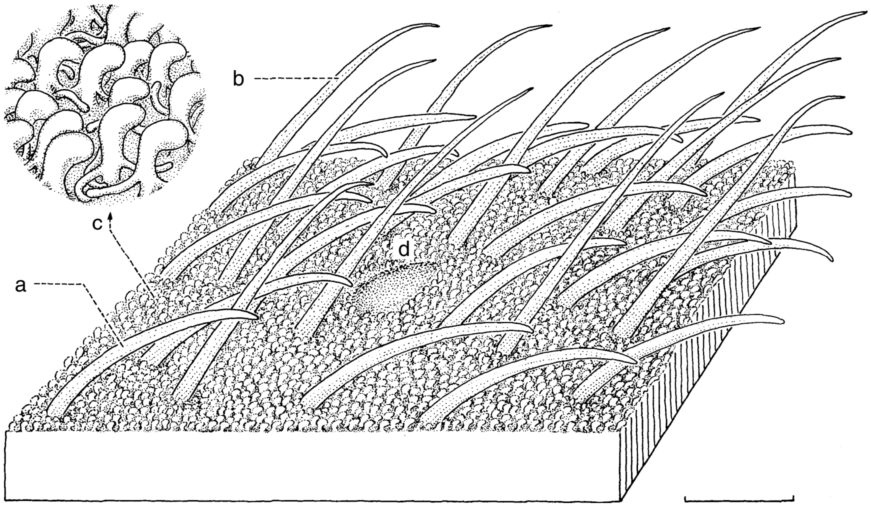

Figure 8 Schematic diagram of *Halobates* cuticle showing surface fine structures. (a) Inclined type of macrohair; (b) erect type of macrohair; (c) undercoat of microtrichia, to the left shown at higher magnification; (d) cuticular pit. Scale bar = 0.01 mm. (Reproduced from Andersen & Polhemus 1976.)

When resting, the body of the sea-skater is elevated above the water, and only the distal segments of the legs are in contact with the surface film. An individual *Halobates* weighing 4 mg requires a total line of contact of about 0.25 cm in order to be supported on the surface film. Because *Halobates* can make vertical jumps from the water surface to a height of several centimetres (Cheng 1985), the thrust produced by the legs may briefly exceed 10 times the weight of the insect. The specialised long hairs ensure a corresponding increase in the area of contact (Andersen 1976). The middle tibia and tarsus of *Halobates* are provided with a fringe of long hairs (Figure 1), which in the oceanic species may reach a length of 0.5 mm. In a few species of coastal *Halobates*, and also in *Asclepios*, the hair fringe is shorter and is limited only to the middle tibia (Miyamoto & Senta 1960, Andersen & Polhemus 1976).

Leg movements and hydrodynamics of locomotion in some freshwater gerrids have been studied by cinematography (Andersen 1976, Hu et al. 2003). The middle legs push against the steep front of a surface wave generated by the insect itself. This requires that the legs move backwards somewhat faster than the speed of the wave. The long middle legs and the powerful leg muscles enable the insect to achieve a high angular velocity by using the water surface as a starting block. By this jump-and-slide movement, a water-strider may quickly achieve a velocity of 0.8–1.3 m s^{-1}. The slide following the initial jump may increase the distance covered by 5–10 times. Recordings of movements in *H. robustus* (Foster & Treherne 1980) indicate a similar mechanism in sea-skaters.

Life history and biology

Oviposition, egg and nymphal development

The life history of *Halobates* includes the egg, five juvenile instars (called nymphs), and the adult stage (Andersen & Polhemus 1976, Cheng 1981). The eggs are oval and the shells are finely and densely porous with an inner spongy layer. There is a single micropyle at the anterior end. They are large (measuring 0.8–1.3 mm long and about 0.5 mm wide) compared with the body of the female, which rarely exceeds 5 mm. The number of mature or semimature eggs in the body cavity of a gravid female may range from 2–20 (Cheng 1985). To accommodate all these eggs, the abdomen has to expand to nearly twice its normal length, while the thoracic cavity is also packed with eggs (Andersen & Polhemus 1976, Cheng & Pitman 2002). Lundbeck (1914) first pointed out that eggs of *Halobates* could be divided into several categories on the basis of size and structure of the shell surface. He found eggs dissected from females of *H. micans*, *H. sericeus*, and *H. sobrinus* to be smooth, but those of others, e.g., *H. germanus*, to be sculptured (Figure 9 and Figure 10).

Female *Halobates* have a very complicated internal reproductive system (the gynatrial complex) for the acceptance and distribution of sperm and fertilisation of eggs (Andersen 1982, 1991a). Recent experimental studies on the function of this system in limnic water-striders (Campbell & Fairbairn 2001) showed that sperms are transferred in a coherent, coiled mass and moved rapidly to the very long spermathecal tube, the primary storage organ. Before fertilisation, the very long spermatozoan (as long as or longer than the egg) is transferred into the fecundation canal and fertilises the egg when it passes the fertilisation chamber prior to oviposition. The elaborate gynatrial complex probably enables the female to control the distribution of sperm and fertilisation of the eggs (Heming-Van Battum & Heming 1986).

In general, coastal *Halobates* lay their eggs on submerged rocks or vegetation. They are deposited at or slightly above the water level and are glued by a gelatinous substance with their dorsal side to the substratum. They are creamy white or translucent when newly laid but later, when the embryo becomes visible through the shell, the egg turns bright orange and the eyes appear as a pair of reddish spots. The appendages are light brown. The long middle and hind legs are neatly folded around the end of the abdomen. During eclosion the shell is split open lengthwise by an embryonic egg-burster, which remains attached to the embryonic cuticle and is left behind after eclosion.

Observations on a coastal species, *H. fijiensis*, revealed that oviposition on turtle grass, coralline algae, or coral rubble occurred only during low spring tides (Foster & Treherne 1986). The eggs were laid singly and glued to the substratum. The maximum number laid by a female

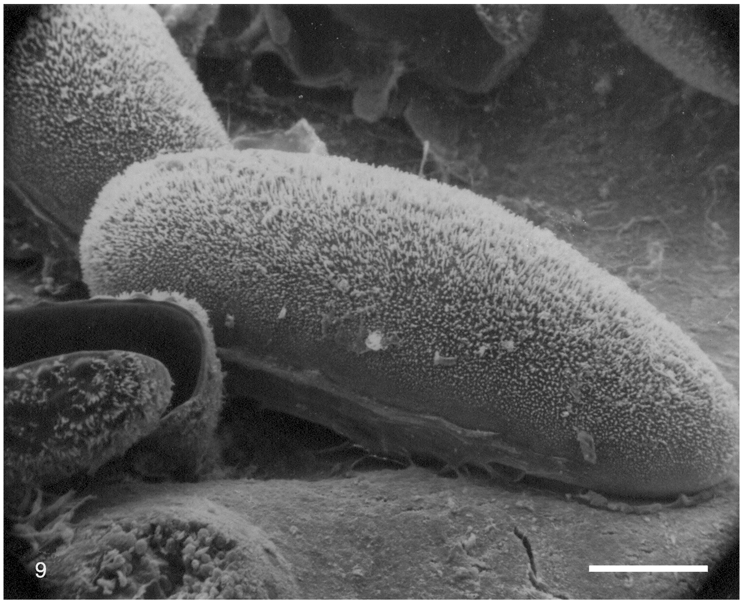

Figure 9 Scanning electron micrograph showing surface sculptures of eggshell of *Halobates germanus*. Scale bar = 0.2 mm. (Reproduced from Andersen & Polhemus, 1976, Water-striders (Hemiptera: Gerridae, Veliidae, etc.), in *Marine Insects*, L. Cheng (ed), Amsterdam: North-Holland Publishing Company, pp. 187–224.)

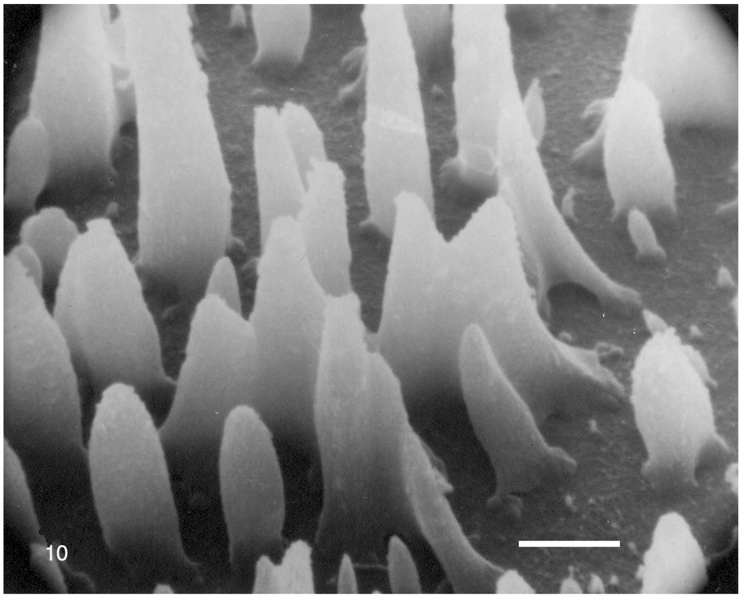

Figure 10 As in Figure 9, showing projections on surface of eggshell. Scale bar = 3 μm. (Reproduced from Andersen & Polhemus 1976.)

was 11. Oceanic *Halobates* have to lay their eggs on any floating material encountered by the female, e.g., seeds, seabird feathers, bits of plastic,pieces of wood, mollusc shells, and even pumice and tar lumps (Figure 24B, p. 142). The most unusual substrata were shells of living atlantid heteropods. Seapy (1996) found from 2–4 *H. sericeus* eggs attached to 139 atlantid shells belonging to eight species. *Atlanta turriculata* was the most common substratum, bearing 71% of the eggs. Most of the eggs he observed were orange and at various stages of development. He also found 16 empty capsules left by nymphs that had already hatched. It was rather curious that all the eggs were found only on shells of adult males. The shells measured 1.3–1.7 mm in diameter, barely big enough for the attachment of four *Halobates sericeus* eggs. *Atlanta turriculata* normally lives in the water column and only comes up to the sea surface to swarm. The choice of such a substratum might indicate that there was a severe shortage of flotsam available for oviposition. Andersen & Foster (1992) reported egg masses deposited on both sides of a cuttlefish shell (*Sepia pharaonis*) collected in the Gulf of Mannar, between India and Sri Lanka, and concluded they had probably been laid by hundreds of *Halobates micans*. During an expedition to the eastern tropical Pacific Ocean Cheng & Pitman (2002) found a plastic gallon jug covered with *H. sobrinus* eggs. The mass was about 15 egg layers deep and was estimated to consist of some 70,000 eggs. Assuming each female normally may not lay more than 10 eggs, the jug must have been used by more than 7000 females. This provides further evidence for a shortage of oviposition substrata for *Halobates* at sea.

Eggs of the oceanic *H. sobrinus* kept at 25°C on board ship hatched in 9–10 days. Those kept at 22°C did not hatch even after 20 days, and it is not known how long eggs kept at such lower temperatures would remain viable. When brought back to the laboratory and kept at 20°C, they took up to 30 days to hatch, suggesting that egg development is temperature dependent (Cheng 1985).

The newly hatched nymph is very feeble but after it has stretched its legs and become tanned (about 30 min after hatching) it becomes very active. However, when the eggs are submerged and hatch underwater the nymphs may spend 1–2 h trying to break through the surface film.

There are five nymphal stages, each lasting from 7–10 days. During each postembryonic moult the old cuticle splits open along a Y-shaped suture above the head and thorax. The total development time from egg to adult may be up to 2 months. Nymphs are similar to adults except they are smaller, paler, and lack differentiation in tarsal and genital segments. It is not known how long the adults live, but they have been kept alive in the laboratory for more than 1 month. Analyses of *H. micans* samples collected from the Atlantic Ocean over a period of about 70 days have shown that although the proportions of nymphs of different stages varied in time and space, no clear seasonal progression was detected (Cheng & Holdway 1995).

Mate location, mating, and seasonality

How the sexes find one another to mate is not known. Although males of some freshwater gerrids use surface ripples to attract females (Wilcox 1979), this process has never been observed in *Halobates*. Females of a related marine insect, *Trochopus plumbeus* (Veliidae), were found to be highly attracted to males or male extracts, indicating the presence of sex attractants (Cheng & Roussis 1998). However, when extracts of either sex were presented to adults of *Halobates hawaiiensis* of the same or opposite sex, both attraction and repulsion were observed (Tsoukatou et al. 2001); perhaps behavioural responses of the adults are governed by their physiological states.

Mating pairs of *H. robustus* (Figure 24C, p. 142), a coastal species endemic to the Galápagos Islands, were seen to form dense aggregations (Birch et al. 1979). However, in another coastal species, *H. alluaudi* in the Seychelles, aggregations consisted mostly of nymphs and few adult males but no females (Cheng 1991). It is likely that mating aggregations are formed only in species with definite breeding seasons. Mating pairs may remain in copula for several hours, e.g., *H. robustus*, *H. nereis*, and *H. mariannarum* (L.C., personal observations). Females of *H. fijiensis* have been observed to mate with more than one male (Foster & Treherne 1986) but it is not known whether this is common for all species.

The functional significance of the complex male terminalia of *Halobates* is poorly understood. Pairs preserved "in copula" are generally rare, indicating that the genital contact between sexes is not persistent enough to endure when the specimens are killed and preserved. In copulating pairs of *H. maculatus*, however, in the absence of phallic contact the gonocoxa of the female is "pinched" between the right styliform process and the pygophore of the male (Andersen 1991a). Recently, there has been much interest in the evolution of mating strategies and sexual selection in water-striders (Spence & Andersen 1994, Arnqvist 1997). Mating systems reflect the classical distinction between male and female interest: male reproductive success varies directly with the number of copulations, whereas that of females depends on the production of viable eggs. This conflict often results in vigorous premating struggles where the female tries to throw off the male. Structural and behavioural adaptations of males to subdue females as well as counteradaptations of females to resist mating have been reported (Andersen 1997). In *Halobates*, the duration of the mating process varies. In *H. fijiensis*, the contact between the two sexes is brief (Foster & Treherne 1986), whereas in *H. robustus* (Figure 24C) the male stays mounted on the female for many hours (Foster & Treherne 1982). In *H. whiteleggei* and *Asclepios shiranui* the male grasps the female's abdomen and trails behind the female before or after copulation (Miyamoto 1937; N.M.A., unpublished). So, at least some sea-skaters have prolonged mate guarding without genital contact, as frequently observed in limnic water-striders (Andersen 1982, Spence & Andersen 1994).

Ecology and special adaptations

Feeding and food

Halobates are predacious fluid feeders. Their mouthparts are of the piercing and sucking type found in other hemipterous insects. The rostrum consists of a four-segment, sheath-like labium enclosing two pairs of long stylets, the outer mandibular and the inner maxillary pair (Cheng 1974, Andersen 1982). The rostrum is usually held pointing backwards under the head and is swung forward when the insect is feeding. The tip of the rostrum is equipped with sensory hairs that aid in the localisation of suitable spots for penetration of the prey. The serrated tips on the mandibular stylets are used for piercing the integument of the prey. The feeding tube is formed by the highly extensible maxillary stylets held together by hairs (Cheng 1974). Body tissues of the prey are liquefied by salivary enzymes before being sucked up.

The main prey items of coastal *Halobates* species are terrestrial insects that have fallen onto the water surface, whereas those of oceanic species consist largely of small zooplankton organisms trapped at the sea surface (Cheng 1974, 1985). Cannibalism is not uncommon and usually involves adults or older nymphs feeding on younger nymphs. In certain freshwater *Gerris* species females were found to be more cannibalistic than males (Nummelin 1989, Cárcamo & Spence 1994). Frequency of cannibalism depends on availability of food and places for younger nymphs to hide (Spence & Cárcamo 1991). Likewise, Ohman & Hirche (2001) have found in an oceanic copepod population that during periods of low food concentration there was density-dependent egg mortality, which was attributed to cannibalism by adult females and late-instar juveniles and may serve to limit populations in times of food shortage.

Food for *Halobates* may be difficult to come by on the open ocean. Comparative studies on lipids of *H. sericeus* and its brackish (*Rheumatobates aestuarius*) and freshwater (*Gerris remigis*) relatives indicated that the amount of neutral triglyceride lipids, which are stored as a food reserve, was much higher in *Halobates sericeus* (Lee & Cheng 1974). Thus this oceanic species was able to withstand much longer periods of starvation. All three gerrids and a coastal species, *H. hayanus*, were also found to store polyunsaturated fatty acids (PUFAs) derived from their food (Lee & Cheng 1974, Nichols & Johns 1983). Although in their study Lee & Cheng (1974) found that the amount of structural phospholipids was about the same for all species analysed, the 22:6 fatty acid was found only in *H. sericeus*, probably as an adaptation to its oceanic life (Figure 11). Another coastal species, *H. fijiensis*, was found to conserve and replace losses in structural PUFAs, which are essential in maintaining membrane integrity in marine animals, by using metabolic pools of neutral lipids (Holland et al. 1983).

Predators

Halobates are agile animals and can move at speeds of 1 m s^{-1} (Cheng 1985). Any potential predators of these sea-skaters must be able to move quickly. The robber fly *Clinopogon scalaris* (Diptera: Asilidae) was observed to capture only first- or second-instar nymphs of *Halobates fijiensis* but not adults or older nymphs (Foster & Treherne 1986). Small birds, lizards, and surface-feeding fishes have also been seen to feed occasionally on coastal *Halobates* (Cheng 1985). The most common predators of oceanic *Halobates* are seabirds, notably small, agile noddies and petrels (Cheng & Harrison 1983, Imber et al. 1995). Six fish species commonly associated with flotsam have been found to contain *Halobates* in their guts, but it was common in only one species, the trevally *Caranx sexfasciatus* (Carangidae), where it was found in 52 of 85 specimens examined (Senta et al. 1993). Actual predation on any open-ocean *Halobates* species has not been observed; the predators are known only from examination of gut contents of seabirds or surface-feeding fishes. However, the small neustonic crab *Planes minutus* (Crustacea: Brachyura) has been observed to

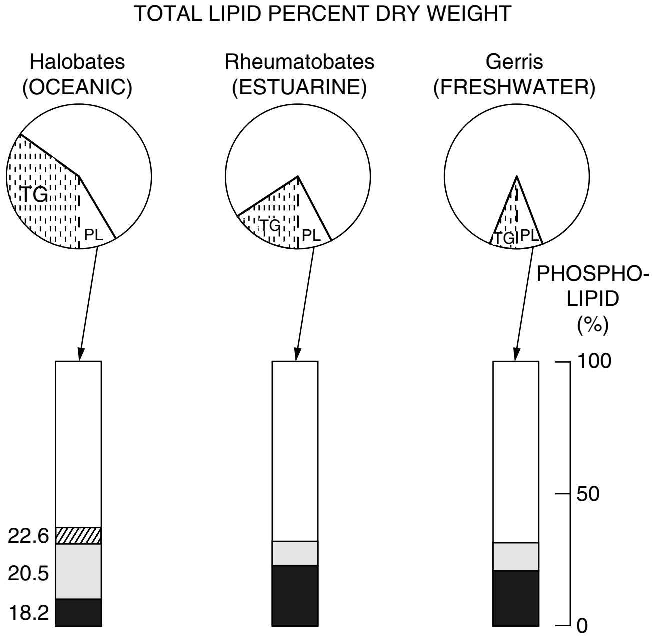

Figure 11 Schematic diagram showing percent dry weight of triglycerides (TG) and phospholipids (PL), and composition of polyunsaturated fatty acids in *Halobates*, *Rheumatobates* and *Gerris*. See text for further explanations.

feed on *Halobates* associated with flotsam as well as scraping off and eating eggs laid on tar balls (Davenport 1992). *Halobates* may also be accidentally ingested by sea turtles (Witherington 2002 and personal communication).

Temperature preference

The occurrence and abundance of any of the five oceanic *Halobates* species on a given water mass may be influenced by sea surface temperatures. Most specimens were collected in tropical areas where the seawater temperatures are above 20˚C. A few caught in cooler waters have been considered to be strays. It is not known whether there are different temperature preferences for each species. The distribution of *H. micans* in the Atlantic Ocean is evidently limited by the 21˚C isotherm (Scheltema 1968). During sampling along a transect across the Atlantic Ocean no specimens of this species were caught in waters between 15 and 20˚C. The highest numbers were caught in waters at 28˚C (Cheng & Holdway 1995), while in the northeastern Atlantic they were absent from waters below the 22˚C isotherm (Cheng et al. 1986). In the Pacific Ocean, where we recorded sea surface temperatures between 20.9 and 30.2˚C, the highest numbers of *H. sericeus* were found at 25˚C and those of *H. sobrinus* at 28˚C (Cheng & Holdway 1995). In the Banda Sea, where large numbers of *H. germanus* were collected, the average sea surface temperature was 29.6˚C (Cheng et al. 1990). This species is also abundant in the Red Sea (Baars & Cheng, unpublished data) where surface temperatures range between 25 and 30˚C. The absence of *Halobates* species from the Mediterranean at the present time is likely due to the low water temperatures (below 20˚C) during much of the year.

UV protection

Sea-skaters are exposed to solar radiation during daylight hours in the open ocean, where there is nowhere to hide. They must therefore possess some means of protection from UV damage. Examination of cuticle sections of *H. sericeus* revealed a dark UV-absorbent layer that excludes practically all transmissions at wavelengths between 260 and 320 nm (Cheng et al. 1978). This layer was much thicker and darker in *H. sericeus* compared to related brackish water (*Rheumatobates aestuarius*) or freshwater (*Gerris remigis*) gerrids (Figure 12). The chemical nature of this highly UV-absorbent material has not been determined. However, preliminary analyses have indicated the presence of four microsporin-like amino acids (MAAs): mycosporine-glycine, shinorine, Porphyra-334, and palythine. The MAAs were found in substantial amounts in the cuticles of two oceanic species, *H. germanus* and *H. micans* (79.6 and 128.5 μg g^{-1} dry wt, respectively), in only trace amounts in *H. flaviventris*, and not detectable in *H. nereis*, both coastal species (Karentz & Cheng, unpublished data).

In general, oceanic species of *Halobates* (both adults and nymphs) are darker in colour than nearshore species, which can often be found under the shade of mangroves or other overhanging vegetation during the day (Cheng 1991). Species of *Asclepios* or *Hilliella*, which are limited to coastal mangrove areas, are pale brown with limited dark brown markings. Such differences in colouration may be attributable to adaptations to UV exposure in their respective habitats.

Environmental considerations

Fine particles of certain heavy metals are continually deposited on the ocean surface, although our knowledge of the distribution and concentrations of such particles on the open ocean is only fragmentary. Concentrations of cadmium, lead, zinc, nickel, iron, and copper were generally higher in several species of *Halobates* than in other marine invertebrates (Cheng et al.

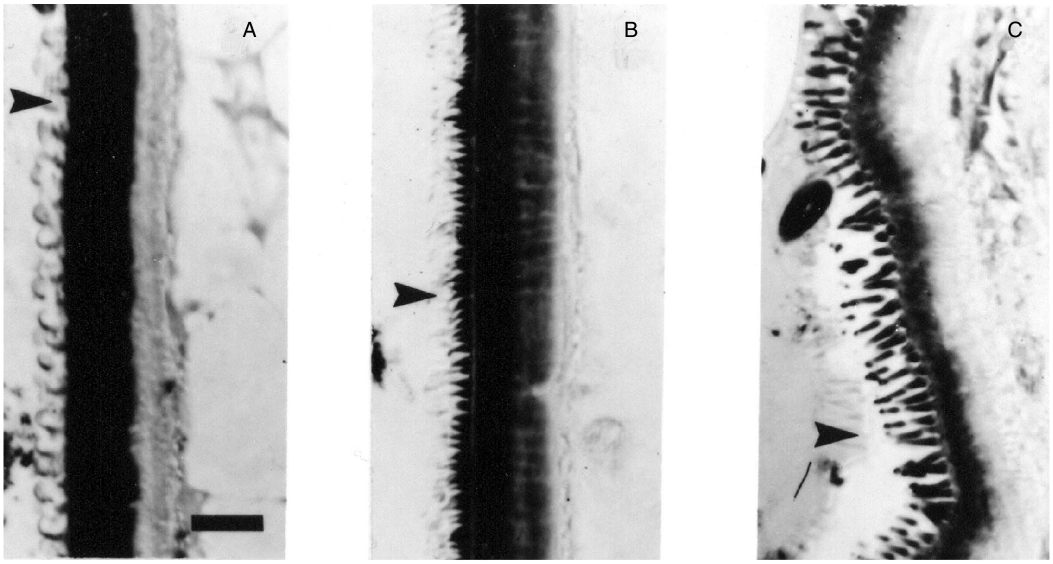

Figure 12 UV photomicrograph taken at 280 nm of thin sections of cuticles of (A) *Halobates sericeus*, (B) *Rheumatobates aestuarius*, and (C) *Gerris remigis*. Arrows point to outer surface of cuticle; scale bar = 5 μm. (Reproduced with permission from Cheng et al., 1978, *Limnology and Oceanography* **23**, 554–556.)

1976, 1979). Cadmium was taken up from the sea surface by drinking (Schulz-Baldes & Cheng 1979) and then transmitted to the seabird predators (Cheng et al. 1984). Cadmium concentrations in *H. micans*, collected from a wide area in the Atlantic Ocean, were found to correlate well with primary production values, especially in equatorial upwelling areas (Schulz-Baldes 1989, 1992). *Halobates* spp., almost the only known marine animals to inhibit the sea–air interface, would seem to be potentially useful as indicators of heavy metals or other pollutants at the sea surface.

Biogeography and distribution

Historical biogeography

The general distribution range of *Halobates* covers the entire Indo-Pacific region, except for *H. micans*, which is also found in the Atlantic Ocean and the Caribbean. This wide range reflects not only the widespread occurrence of the five open-ocean species but also that of several endemic coastal species, e.g., in the Red Sea and the Galápagos Islands. It is therefore difficult to delimit a place of origin for the genus *Halobates* based upon the present distribution of its species. The current practice of historical biogeography depends largely upon reliable phylogenetic reconstructions, but biogeographical scenarios are further complicated by the interplay between events of vicariance, dispersal, and extinction (Andersen 1991b, 1998a, 1999, Andersen et al. 1994). As evident from the reconstructed phylogeny of *Halobates* and its allies (Figure 13), the sister group of *Halobates* is *Austrobates* which is endemic to Cape York Peninsula in northeastern Australia. Within the *Halobates* clade, the sister group of all other *Halobates* species is the subgenus *Hilliella*, with three species distributed along the coasts of tropical northern Australia and adjacent Papua New Guinea (Andersen & Weir 1994b).

Phylogenetic evidence supports the hypothesis that *Halobates* diverged from its sister group *Austrobates* somewhere in the area that now constitutes the northernmost part of the Australian continent. Recent fossil evidence (Andersen et al. 1994) indicates that *Halobates* had evolved before the Middle Eocene (45 million yr ago, MYA), when Australia was part of eastern Gondwanaland. The sister group of *Austrobates* + *Halobates* is the genus *Asclepios*, which is distributed along the coasts of South and East Asia (Andersen 1982, Polhemus & Cheng 1982, Andersen & Foster 1992). Assuming that the actual distribution of *Asclepios* also represents the ancestral area for this genus, Andersen & Weir (1994a) hypothesised that the vicariance event separating *Austrobates* + *Halobates* from *Asclepios* took place somewhere between Asia and Australia. Contrary to conventional views, there may have been continental fragments of Gondwanan origin between Australia and mainland Asia during the late Cretaceous and early Tertiary periods. Members of the tribe Metrocorini, the closest relatives of the Halobatini, are widely distributed in the Afro-tropical region and in South and East Asia, but largely absent from the Australian region. Taking the present distribution of the freshwater relatives of sea-skaters into account, it seems likely that the first members of the tribe Halobatini originated in eastern Gondwanaland, perhaps in areas that now comprise the Indo-Australian region.

The 43 species belonging to the subgenus *Halobates* s. str. fall into two major clades (monophyletic groups), marked A and B in the reconstructed phylogeny (Figure 14). Clade B contains the five oceanic species (*H. germanus*, *H. micans*, *H. sericeus*, *H. sobrinus*, and *H. splendens*) but also some of the most widespread coastal species (*H. calyptus* + *H. hayanus* and *H. flaviventris* + *H. hawaiiensis*). There has evidently been an unequal propensity for dispersal among these two clades in the course of the evolution of *Halobates*.

Oceanic *Halobates* probably evolved in the Indo-Pacific because their nearshore relatives (*H. calyptus* + *H. hayanus* and *H. flaviventris* + *H. hawaiiensis*) are widespread within this area. It is noteworthy that the pantropical *H. micans* is closely related to two species, *H. sobrinus* and *H. splendens*, both of which are confined to the eastern tropical Pacific Ocean. *H. micans* probably

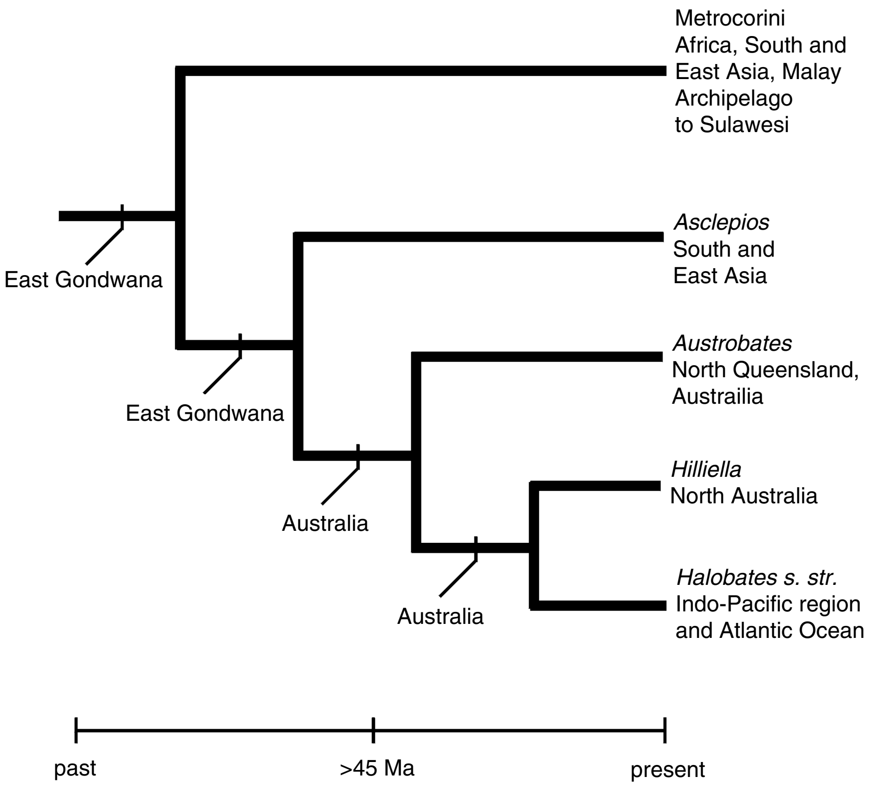

Figure 13 Distributions of Metrocorini and genera and subgenera of Halobatini superimposed on a reconstructed phylogeny. Hypothesised distribution of ancestral species marked on internodes. Timescale below with indication of minimum age of *Halobates* as estimated from the oldest fossil species of the genus. See text for further explanations. (Reproduced with permission from Andersen & Weir 1994a.)

diverged from *H. splendens* in the central or eastern part of the Pacific Ocean, and later dispersed across the Pacific to the Indian Ocean. The tendency of one oceanic species, *H. germanus*, to stay closer to the coasts than other oceanic species (Cheng 1989b) indicates that the oceanic habit might have evolved in a gradual way. This scenario is preferable to a more dramatic one, which imagines populations of coastal species washed or blown out to sea, and somehow finding sufficient food and oviposition sites for sustaining their populations there.

General distribution pattern

The majority of the 46 extant species of *Halobates* are found in the tropical parts of the Indo-West Pacific region, roughly between latitudes 30˚N and 30˚S (Herring 1961, Cheng 1985, 1989b). *H. robustus* (endemic to the Galápagos Islands) and the oceanic species *H. sobrinus*, *H. splendens* (eastern Pacific Ocean), and *H. micans* (Atlantic Ocean, the Caribbean Sea, and eastern Pacific Ocean) are the only sea-skaters that occur outside this region. The present distribution of coastal *Halobates* species more or less coincides with the distribution of reef-building corals and mangrove trees, which require relatively high seawater temperatures (Andersen 1998b, 1999). There is, however, a complete absence of nearshore *Halobates* in the Atlantic Ocean, where coastal mangrove areas are colonised by species of *Trochopus* (Veliidae) (Cheng & Roussis 1998).

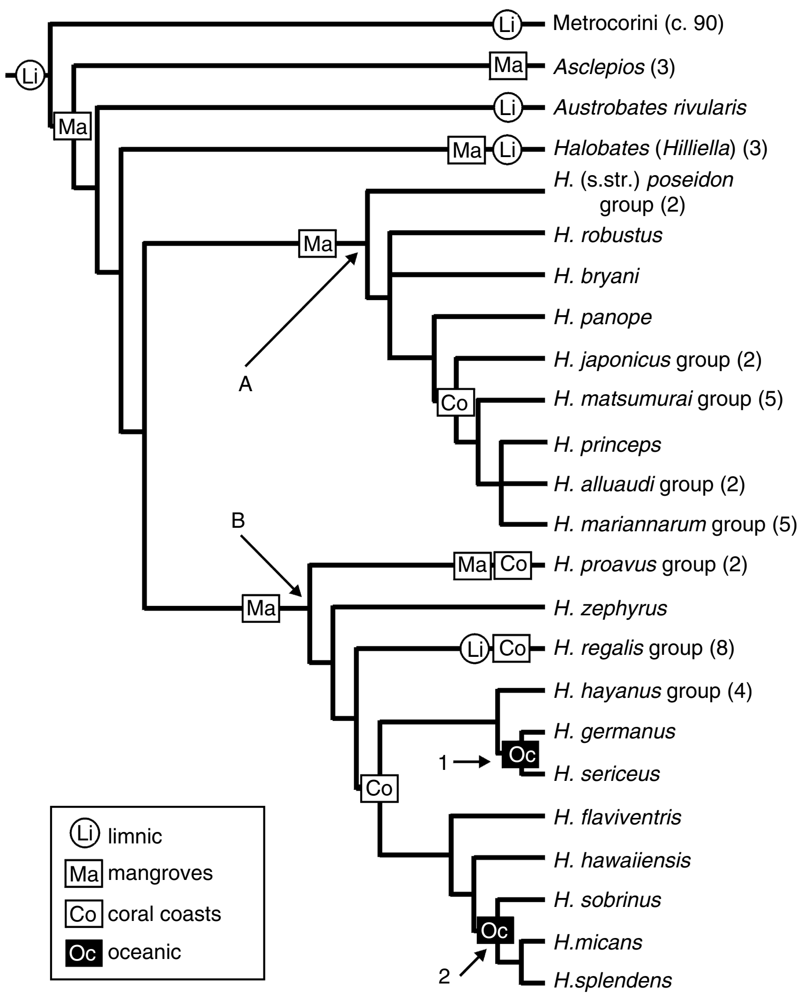

Figure 14 Cladogram showing phylogenetic relationships between the genera of Halobatinae and between subgenera, species, and species groups of *Halobates* (numbers of species in parentheses), the latter divided into clades A and B. Optimisation of states of preferred habitats as indicated on internodes. Two independent origins of oceanic species are marked 1 and 2. Definitions of species groups of *Halobates*: *H.* (*Hilliella*) = *H. lannae*, *H. mjobergi*, *H. robinsoni*; *H. alluaudi* group = *H. alluaudi*, *H. tethys*; *H. hayanus* group = *H. calyptus*, *H. formidabilis*, *H. hayanus*, *H. trynae*; *H. japonicus* group = *H. galatea*, *H. japonicus*; *H. mariannarum* group = *H. fijiensis*, *H. katherinae*, *H. kelleni*, *H. mariannarum*, *H. salotae*; *H. matsumurai* group = *H. browni*, *H. elephanta*, *H. esakii*, *H. matsumurai*, *H. nereis*; *H. poseidon* group = *H. melleus*, *H. poseidon*; *H. proavus* group = *H. maculatus*, *H. proavus*; *H. regalis* group = *H. acherontis*, *H. darwini*, *H. dianae*, *H. herringi*, *H. murphyi*, *H. peronis*, *H. regalis*, *H. sexualis*, *H. whiteleggei*. See text for further explanations. (Modified from Andersen & Weir, 2003.)

Distribution of coastal species

Coastal *Halobates* may be assigned to a number of monophyletic species groups (Andersen 1991b), each showing a characteristic distribution pattern. The subgenus *Hilliella*, with three species (*H. lannae*, *H. mjobergi*, and *H. robinsoni*), is confined to Australia and adjacent Papuasia (New Guinea, Solomons; Figure 15), as are most species belonging to the *Halobates regalis* group (*H. acherontis*, *H. darwini*, *H. dianae*, *H. herringi*, *H. murphyi*, *H. peronis*, *H. regalis*, *H. sexualis*, and

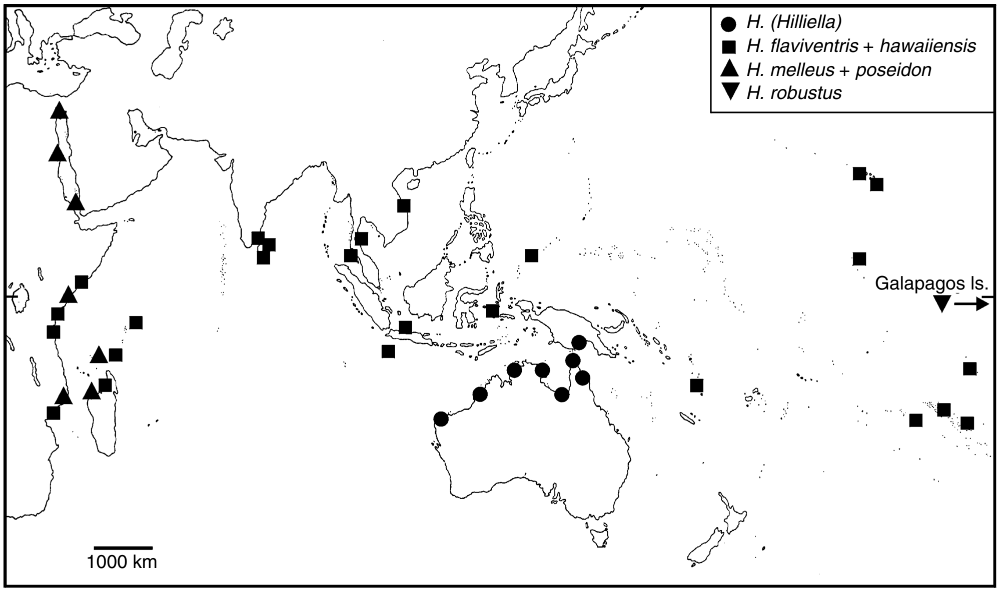

Figure 15 Distribution of *Halobates* (*Hilliella*) (three species), *H. flaviventris* + *H. hawaiiensis*, *H. melleus* + *H. poseidon*, and *H. robustus* (Galápagos Islands).

H. whiteleggei) (Figure 16). The *H. matsumurai* group, with five species (*H. browni*, *H. elephanta*, *H. esakii*, *H. matsumurai*, and *H. nereis*), ranges from India through Southeast and East Asia to New Guinea and the Solomons (Figure 17). The *H. poseidon* group, with two species (*H. melleus* and *H. poseidon*), is distributed along the coasts of the Red Sea and East Africa (Figure 15). The latter distribution is shared with *H. alluaudi*, which has its closest relative, *H. tethys*, in Mauritius (Figure 18). The *H. japonicus* group, with two species (*H. galatea* and *H. japonicus*), are found along the coasts of India and Japan (Figure 16). Finally, the *H. mariannarum* group, with five species (*H. fijiensis*, *H. katherinae*, *H. kelleni*, *H. mariannarum*, and *H. salotae*), is distributed along island coasts of the western Pacific Ocean (Figure 17). Several of the above-mentioned species have fairly limited distributions, e.g., *H. robustus* (Galápagos Islands; Figure 15), *H. kelleni* (Samoa), *H. salotae* (Tonga), *H. bryani* and *H. fijiensis* (Fiji Islands), and *H. panope* (New Caledonia; Figure 18).

A few coastal sea-skaters are relatively widespread. The distribution of *H. princeps* ranges from Borneo and the Palau Islands to the northern coast of Australia (Figure 17). *H. hayanus* and its sibling species *H. calyptus* are distributed from the Red Sea in the west to the Solomon Islands in the east, and from the Philippines to Australia (Figure 18). *Halobates flaviventris* and its close relative *H. hawaiiensis* have an even broader distribution, ranging from East Africa to the islands of the central Pacific Ocean (Figure 15). The two species of the *H. proavus* group (*H. maculatus* and *H. proavus*) occur widely in the Indo-Australian area (Figure 16). Finally, *H. mariannarum* is found throughout Micronesia (Figure 17).

Distribution of oceanic species

The ranges of oceanic *Halobates* species is well defined (Savilov 1967, Cheng 1989b) with a high degree of zoogeographical constancy (Cheng & Holdway 1995). All five species are found in the Pacific Ocean. *Halobates micans* (Figure 19) is the only cosmopolitan species, with a general range between latitudes 40°N and 40°S. However, it has a much narrower range in the Pacific Ocean, being replaced at latitudes greater than 15°N and 15°S by *H. sericeus* (Figure 20), which has a disjunct, amphi-tropical distribution (Cheng 1997). *Halobates germanus* (Figure 21) is found

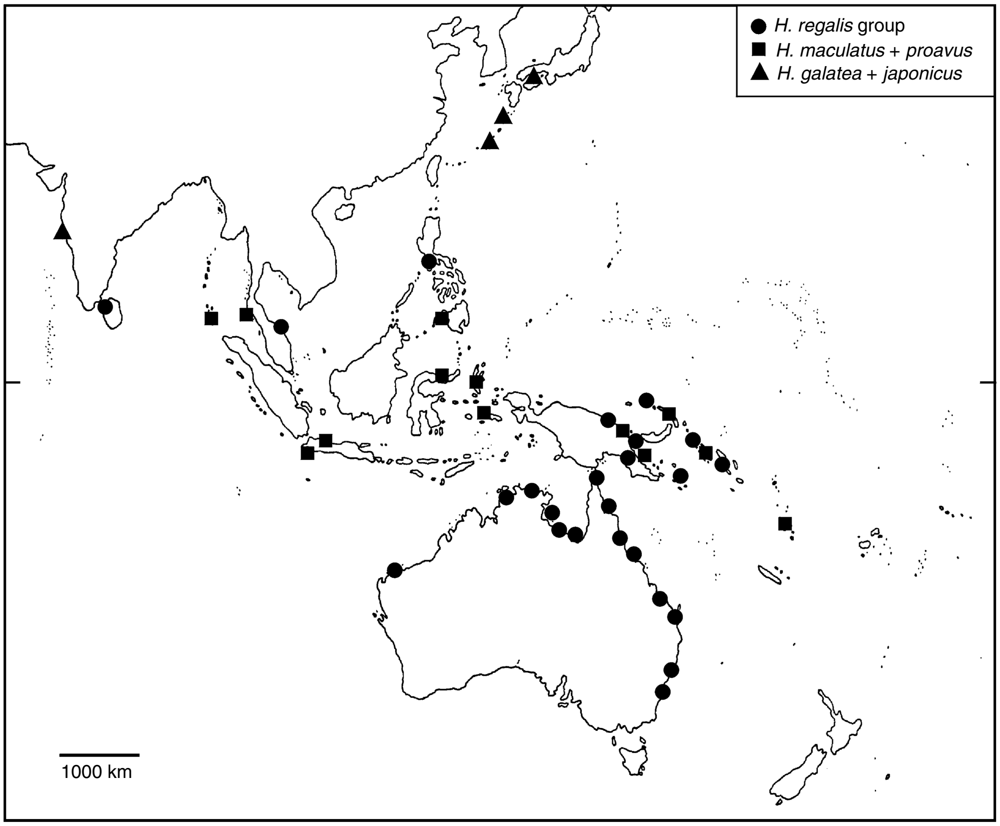

Figure 16 Distribution of the *Halobates regalis* group (nine species), *H. maculatus* + *H. proavus* and *H. galatea* + *H. japonicus*.

in both the Indian and Pacific Oceans. In the Indian Ocean it occurs nearer to the coast than *H. micans* and is very abundant in the Red Sea as well as in the Gulf of Aden, where *H. micans* is absent (Baars and Cheng, unpublished data). In the Pacific Ocean *H. germanus* occurs only in the western half, among islands in the Indo-Pacific, and has not been collected east of longitude 120˚W (Figure 19). The remaining two species, *H. sobrinus* (Figure 22) and *H. splendens* (Figure 23), are both confined to ocean areas off the coasts of Central and South America, and have not been collected in areas west of 130˚W. The former is a more northern species, occurring between latitudes 20˚N and 5˚S, whereas the latter is found farther south, between latitudes 10˚N and 30˚S. Although there are overlaps between the ranges of the four species in the Pacific Ocean, areas of high population density of each species appear to be quite separate (Cheng & Shulenberger 1980). On the whole, the distributions of *Halobates* species appear to agree with broad surface circulation patterns (Cheng 1989b).

Frequency and abundance

On ocean-going expeditions *Halobates* specimens are usually caught by deploying either a neuston net (Figure 24D) or a manta net, which skims over the sea surface (Brown & Cheng 1981). In tropical seas these insects are very common. In the EASTROPAC study they were caught in 30% (498 of 1649) of all surface net tows (Cheng & Shulenberger 1980). This is likely to be an underestimate of their abundance as the net used was an ordinary plankton net with a circular opening that was towed half submerged at a speed of 1.5 m s^{-1} (3 knots). Because the sea-skaters can move

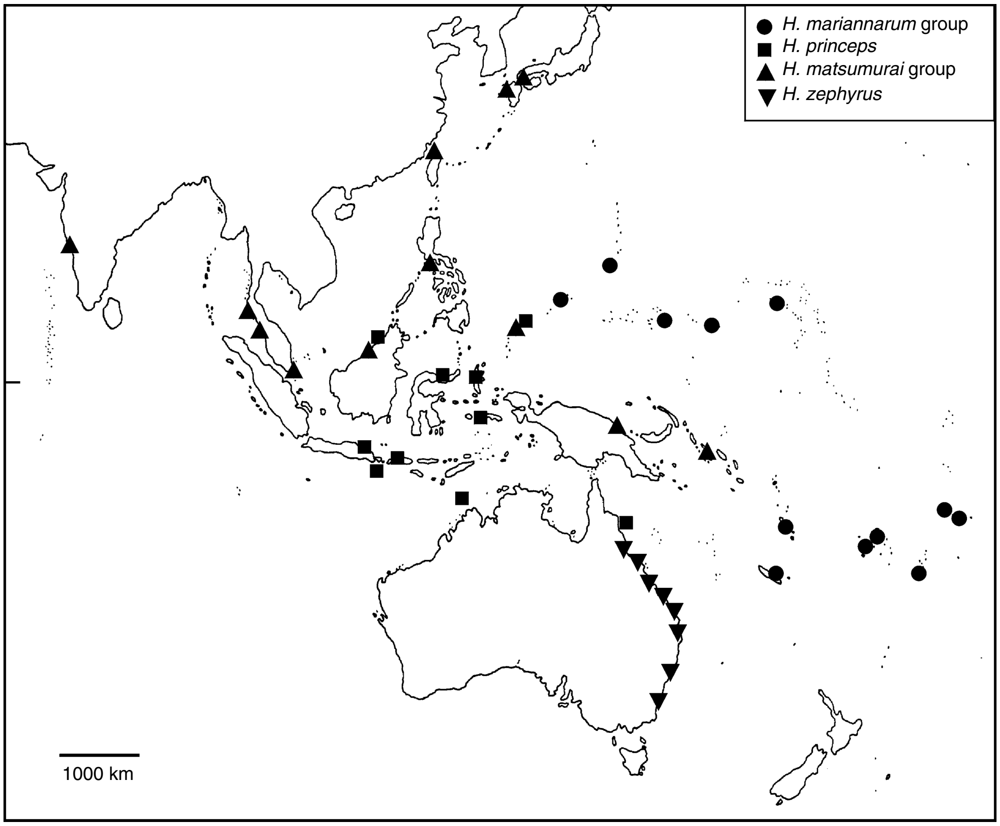

Figure 17 Distribution of the *Halobates mariannarum* group (five species), *H. matsumurai* group (five species), *H. princeps*, and *H. zephyrus*.

at about 1.0 m s^{-1} and have good eyesight, they can probably skate away from approaching nets. During other expeditions where a faster towing speed was used (4 knots), the insects have been caught in well over 50% (62% – Stoner & Humphris 1985; 82% – Cheng et al. 1990; 63% – Cheng & Holdway 1995) or even up to 98% (Cheng 1997) of the tows. In general, more insects were caught during night tows than day tows (Cheng & Shulenberger 1980), up to a fourfold difference in some cases (Cheng et al. 1990). This day/night difference is attributed to net avoidance (Cheng 1973c). However, no significant difference between day and night catches was found for all five *Halobates* species sampled during the "Eye of the Wind" expedition across the Atlantic and Pacific Oceans, probably due to smaller sample sizes and larger variances (Cheng & Holdway 1995).

The number of insects caught per tow varied greatly. In general, more than 50% of the tows yielded less than 10 insects. The majority of the tows would yield 20–50 insects, with a few in the hundreds One of the highest catches was one 220-min night tow that netted 589 insects (of which 584 were *H. germanus*) in the Banda Sea (Cheng et al. 1990). It is obvious that occurrences of *Halobates* in the open sea are very patchy. It is not known how the patches are formed, how they are maintained, or whether they are of a temporary or semipermanent nature.

Relatively few intensive collections of *Halobates* have been made in the Indian Ocean compared with the Atlantic and the Pacific. Of the two species known from the Indian Ocean, *H. germanus* seemed to occur in greater abundance than *H. micans* (Cheng 1973d), especially in the Gulf of Aden (Sagaydachnyy 1975). In the Arabian Sea, a few specimens of each species, comprising both adults and nymphs, were caught in plankton samples (Pathak et al. 1999). Both species have also been collected from seas around Aldabra and nearby atolls (Polhemus 1990, Polhemus & Polhemus

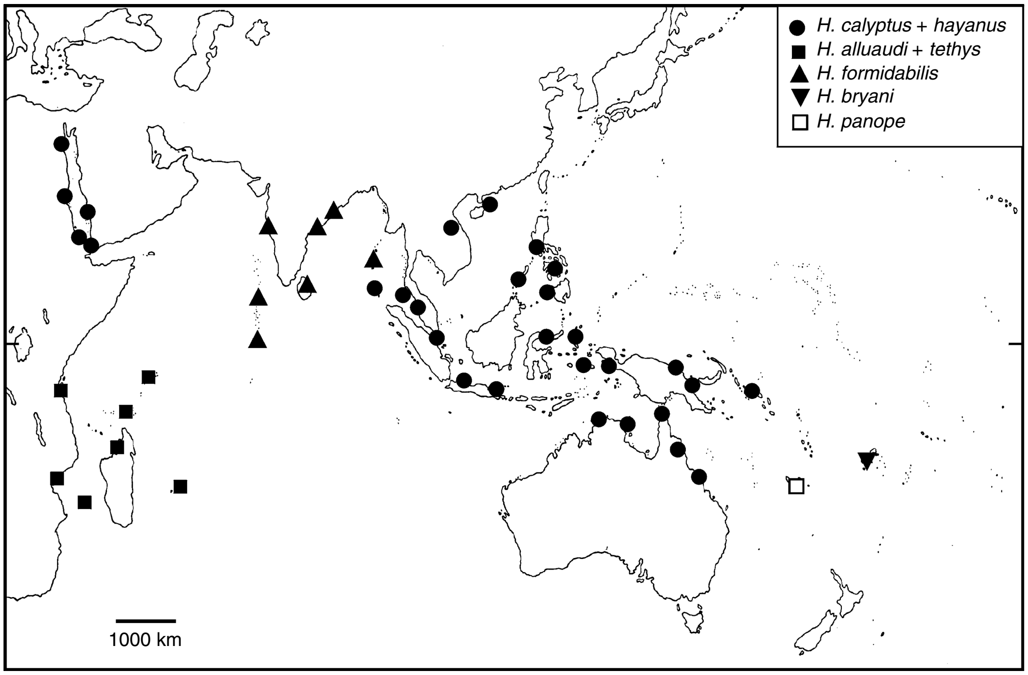

Figure 18 Distribution of *Halobates calyptus* + *H. hayanus*, *H. alluaudi* + *H. tethys*, *H. formidabilis*, *H. bryani*, and *H. panope*.

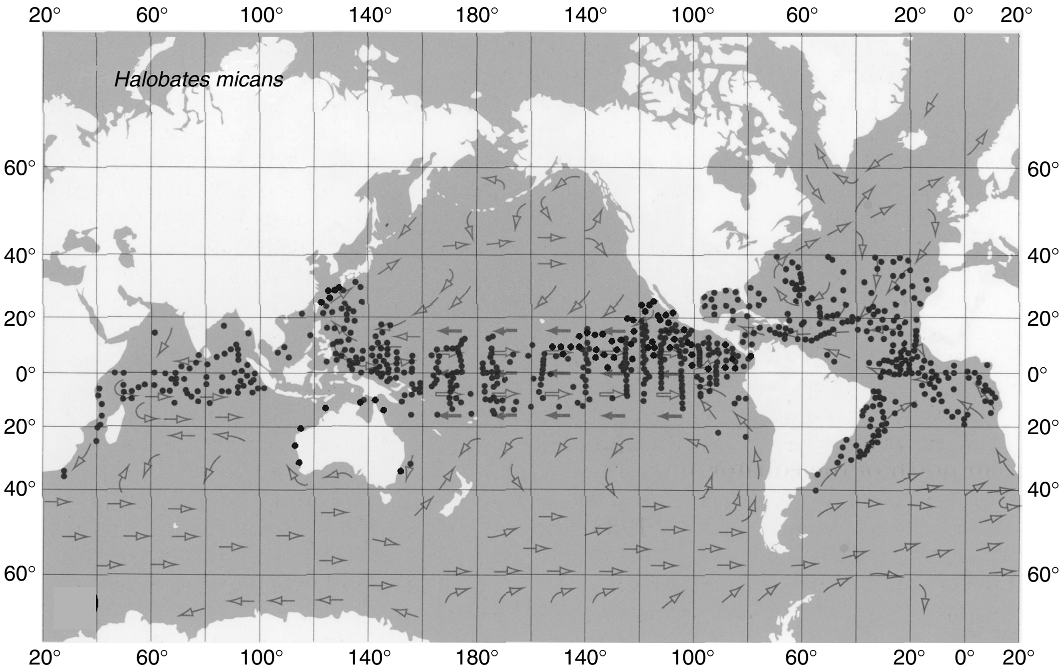

Figure 19 World distribution of *Halobates micans*. (Modified from Cheng 1989b).

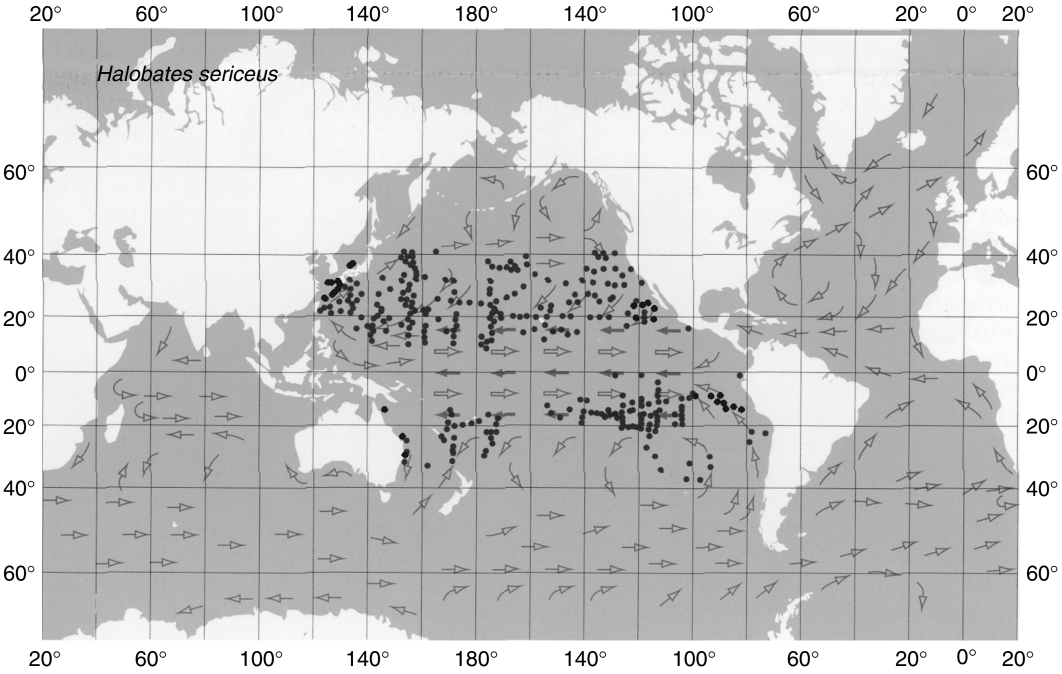

Figure 20 World distribution of *Halobates sericeus*. (Modified from Cheng 1989b.)

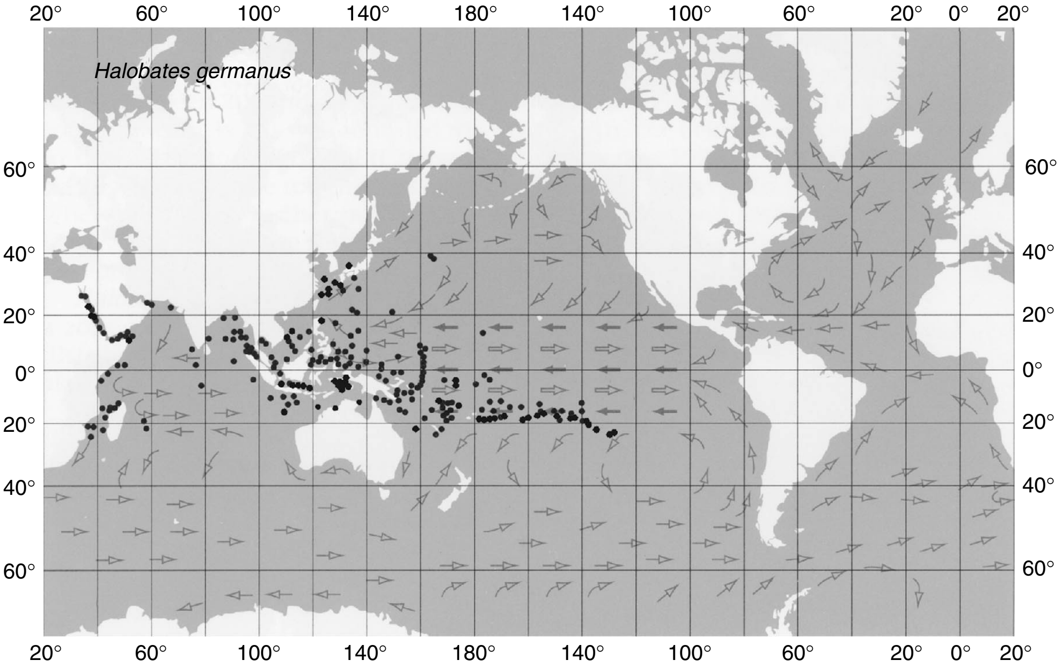

Figure 21 World distribution of *Halobates germanus*. (Modified from Cheng 1989b.)

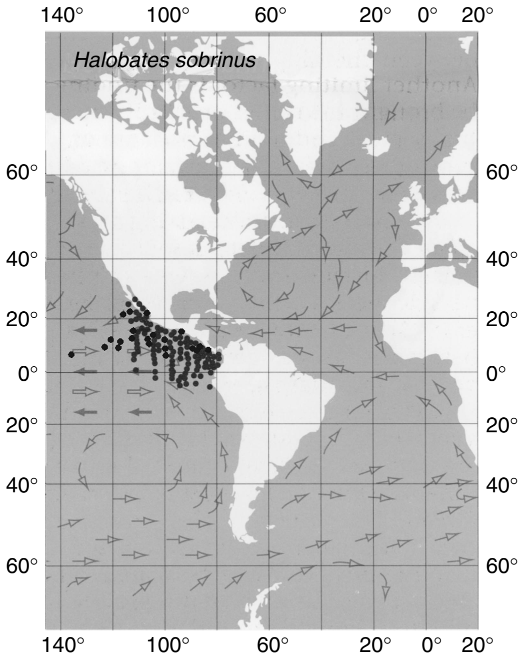

Figure 22 World distribution of *Halobates sobrinus*. (Modified from Cheng 1989b.)

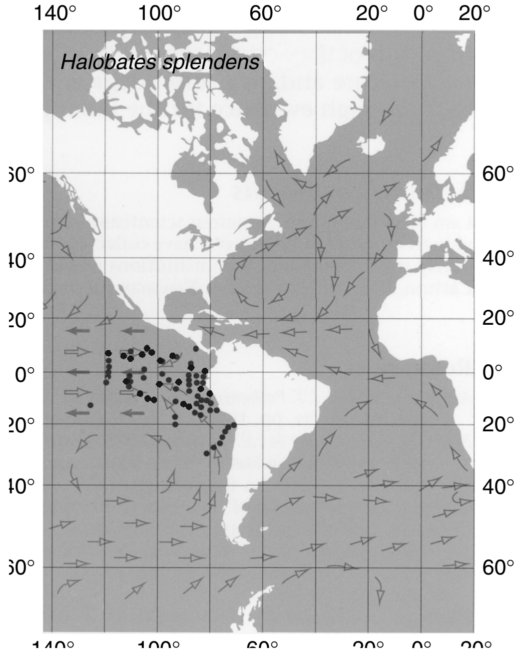

Figure 23 World distribution of *Halobates splendens*. (Modified from Cheng 1989b.)

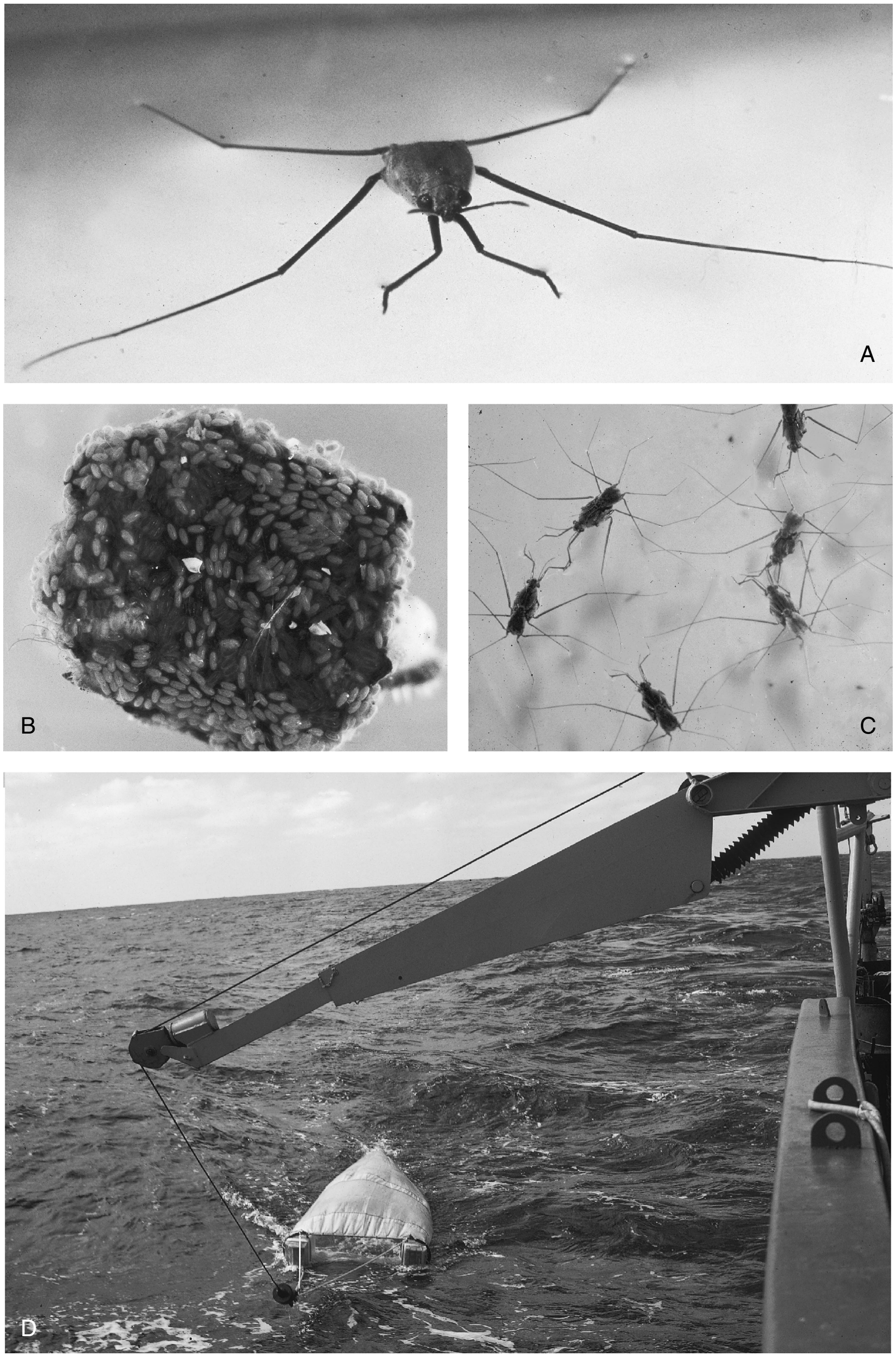

Figure 24 (See colour insert following p. 56.) (A) Live *Halobates robustus* female resting on seawater. (Photo by A.A. Benson.) (B) Live *Halobates* eggs on tar lump. (Photo by L. Cheng.) (C) Mating pairs of *H. robustus*. (Photo by A.A. Benson.) (D) Neuston net being towed from research vessel. (Photo by L. Cheng.)

1991). During two seasonal cruises in the Banda Sea a total of 2089 specimens of both species was caught (Cheng et al. 1990). Of these, 2095 (91%) were *H. germanus*, and almost all of them were caught during the NW monsoon (February/March 1985). Only 194 specimens of *H. germanus* (but not a single *H. micans* specimen) were caught during the SE monsoon (August 1984). It is not known what factors were responsible for such dramatic seasonal changes in the numbers of *Halobates* caught. They may be related to oligotrophic conditions or upwelling in local waters. It is also interesting to note that the mean density of *H. germanus* in the area bore an inverse relationship to surface chlorophyll concentration (Cheng et al. 1990), although the significance of this relationship is yet to be elucidated.

One of few long-term studies on *H. micans* was carried out by Stoner & Humphris (1985), who analysed data from a 7-yr survey (1977–1984) in the northwest Atlantic, covering an area from the coasts of North and Central America to the northern and eastern regions of the Caribbean Sea. The highest abundance was found in the southern Sargasso Sea, between 15 and 25°N in latitude and 50 and 60°W in longitude, with an average density of about 20 insects per tow. In general, insect occurrence and abundance appeared to remain stable over the study period except in the southern Sargasso Sea, where significantly higher numbers were observed during 1978–80 (17–24 vs. 1–4 insects per tow) than in later years.

Population composition and age distribution

Analyses of net catches from different ocean areas showed that the population structure of oceanic *Halobates* is highly variable. The proportions of adults and nymphs as well as the composition of nymphs of various instars tended to vary from tow to tow during any particular cruise. Although no distinct seasonality could be determined for any area sampled, there appeared to be a seasonal succession of developmental stages in the Gulf of Mexico (Cheng & Wormuth 1992). First-instar nymphs were least common (Cheng & Holdway 1995, Ikawa et al. 2002), except when there was, presumably, a mass hatching or active breeding in the area sampled (Cheng & Schulz-Baldes 1981, Cheng & Wormuth 1992). Since newly hatched nymphs measure only about 1 mm in body length and 0.5 mm wide, it is quite likely that some were not retained in the nets (0.5 mm mesh), especially when the towing speed exceeded 4 knots (2 m s^{-1}) (Cheng et al. 1990).

High-density patches normally consisted of adults and nymphs of various developmental stages, with adults accounting for 50% or more of the individuals in many samples. In the majority of tows there were almost equal numbers of adult males and females (Cheng & Holdway 1995, Ikawa et al. 2002). However, a dramatic difference in population structure was observed in the Banda Sea where within a week adult abundance dropped from 78% to less than 5% in the same area (Cheng et al. 1990).

Absolute densities of *Halobates* in the open ocean are difficult to determine. Various calculations from net catches are likely to be underestimates due to net avoidance by the insects, or overestimates due to aggregation. However, such density calculations from different sources are useful in providing comparative data.

Some of the estimates of population density for various *Halobates* species are presented in Table 1. In the Atlantic region the mean densities of *H. micans* ranged from a low of 2.4×10^3 km^{-2} to a high of 208×10^3 per km^2. As a general rule, densities appear to vary with sea surface temperatures and latitudes (Cheng & Wormuth 1992), but other environmental factors, such as frontal systems, may also be important.

Population studies of nearshore *Halobates* species have been carried out in only a few species. Nymphs, especially those of the first two stages, often occur in dense aggregations among mangrove roots where they are presumably relatively safe from predators. Older nymphs and adults often venture out into open waters in groups of two or three individuals. Dense aggregations composed of adults and nymphs in various proportions have been observed in several species. In the Galápagos

Table 1 Density estimates of oceanic *Halobates* species

Ocean basin or area	*Halobates* species	Latitude (°N or °S)	Max* or mean density (10^3 km^{-2})	Primary reference
East Atlantic	*micans*	10–15°S	43	Cheng & Schulz-Baldes 1981
		5–10°S	137	
		0–5°S	208	
		0–5°N	55	
		5–10°N	115	
Caribbean	*micans*	12°N	53*	Stoner & Humphris 1985
		10–20°N	7.0	
		20–35°N	2.4	
Northeastern Atlantic	*micans*	35°N	12.6*	Cheng et al. 1986
Gulf of Mexico	*micans*	27°N	39	Cheng & Wormuth 1992
Eastern tropical Pacific	*micans*	10°S–20°N	2.0*	Cheng & Shulenberger 1980
	sericeus	15–20°N	1.0*	
	sobrinus	05°S–20°N	10.0*	
	splendens	20°S–10°N	0.4*	
Indian Ocean (Banda Sea)	*germanus* (Aug)	04°S	3.1, 28.4*	Cheng et al. 1990
	germanus (Feb)	05°S	15.3, 71.7*	
	micans (Feb)	04°S	2.0	
Western Pacific Ocean	*micans*	13–18°N	3.0	Ikawa et al. 2002
	sericeus	14–20°N	7.0	

Islands, aggregations of *H. robustus* with densities reaching as high as 120 m^{-2} consisted almost entirely of mating pairs (Birch et al. 1979). In Fiji, dense patches of *H. fijiensis* consisted mostly of nymphs belonging to the first through fourth instars, with almost no individuals from the fifth instar and less than 1% adults (Foster & Treherne 1986). Group sizes differed markedly between high and low tides. At high tide most of the insects occurred singly or in groups of 10 or less, whereas at low tide no individuals occurred singly and about half of the populations were in groups of 200 or more individuals. In the Seychelles, a dense aggregation composed of several thousand individuals of *H. alluaudi* consisted mainly of males (Cheng 1991). Patch sizes and compositions differ greatly from species to species, probably depending on reproductive activity in the population.

Dispersal

Because *Halobates* are totally wingless and do not have the ability to dive, the dispersal of oceanic *Halobates* is largely dependent on physical forces, predominantly surface currents and winds acting at the sea–air interface. Owing to the difficulties involved in carrying out experimental studies on *Halobates* at sea, there is no direct evidence on how such forces may act in their dispersal. Presumably the insects are able to move against surface currents or winds below a certain magnitude, but these have yet to be determined. Theoretical calculations based on oceanic diffusion indicated that this force alone would be sufficient to disperse a patch of *Halobates* from a point of origin to a distance of 1250 km in just 60 days (Ikawa et al. 1998). Thus an individual found off the coast of California could theoretically be carried across the Pacific Ocean in about 2 yr, if it could live that long. From a population standpoint this would mean that oceanic diffusion alone could bring about substantial gene mixing over the entire range of a species' distribution. Furthermore, oceanic diffusion could also increase the encounter rates among individuals and thus promote mate location and mating (Ikawa et al. 1998). Evidence from nucleotide variations among oceanic *Halobates* does not contradict this hypothesis. Andersen et al. (2000) found no significant association between nucleotide divergence and geographical distance in populations of *H. germanus* in the western Indian Ocean or in *H. micans* populations inhabiting the Atlantic, Pacific, or Indian Ocean. In fact, the same haplotype was shared by two *H. micans* individuals collected from locations in the Pacific Ocean more than 15,000 km apart (Figure 25, sites 6 and 8, and 6 and 9).

Dispersal mechanisms for coastal *Halobates* species have not been studied. Clearly coastal currents must be the most important agents. These species, which depend on anchored substrata for oviposition, must have rather different life strategies from their oceanic cousins. If they are washed out to the open ocean they are not likely to survive. In the Galápagos Islands, we noted that populations of *H. robustus* maintained stations with reference to the shore during tidal cycles. Somehow they were able to prevent themselves from being carried out to open waters by ebbing tides (Birch et al. 1979).

Evolution and phylogeny

Origin of sea-skaters

It has been estimated that the colonisation of the marine environment by gerromorphan bugs probably occurred independently at least 14 times (Andersen 1999). The most successful insects are water-striders and their allies in the infraorder Gerromorpha. More than 10% of the 1800 known

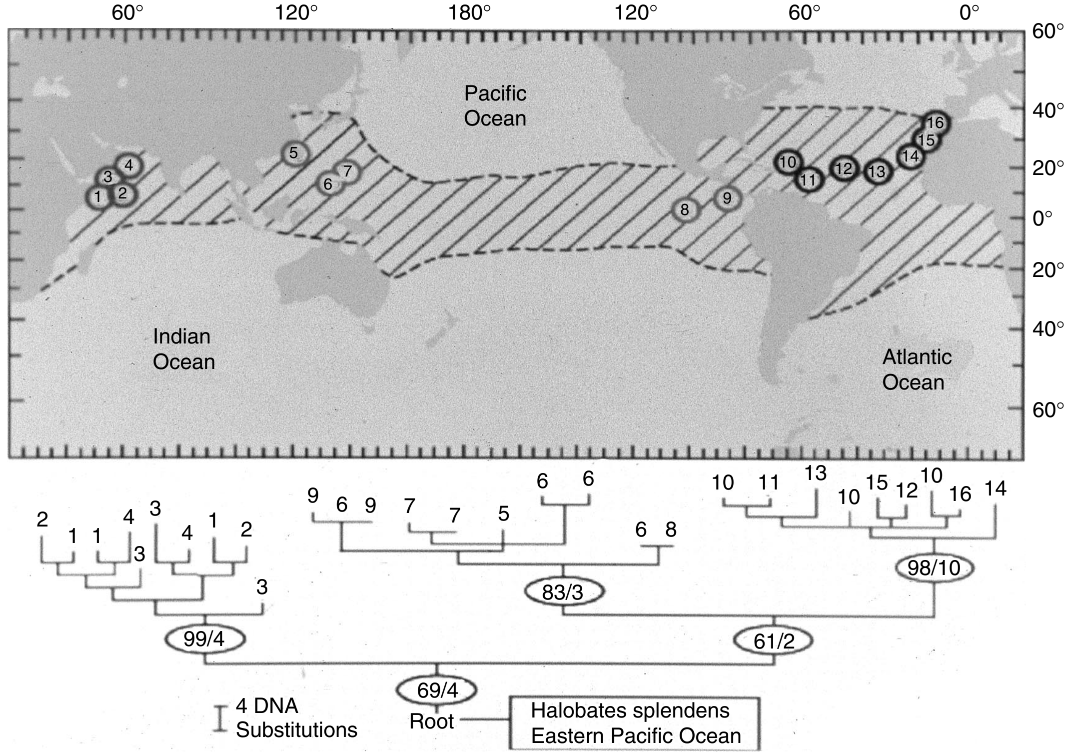

Figure 25 Phylogram of *Halobates micans* showing three mtDNA lineage groupings, one for each ocean. Tree is based on consensus of 372 most parsimonious trees for 29 specimens representing 27 distinct haplotypes, with *H. splendens* as outgroup (for details, see Andersen et al. 2000). Bootstrap support (%) and Bremer (1994) support values are given on major branches. Range of species' distribution shown by dashed lines. Numbers on terminal branches correspond to sites of samples sequenced shown in numbered large dots, with locations within 1–3° of latitude or longitude combined.

species (belonging to 5 families, 7 subfamilies, and 25 genera) are marine (Andersen & Polhemus 1976, Andersen 1982). *Halobates* belongs to one of the most advanced subfamilies of the Gerridae, which evolved at least some 55 MYA (Andersen 1998a). A fossil *Halobates* (Figure 26A and B) was found in northern Italy, suggesting that marine habitats were invaded by members of the Gerridae more than 45 MYA (Andersen et al. 1994). Estuaries and mangrove swamps were undoubtedly the ancestral habitats from which some species diversified to colonise other marine habitats, including the open ocean. Although obligatorily flightless, marine water-striders are structurally very similar to their freshwater relatives where winged adults occur, although sometimes infrequently. Physiological and behavioural rather than morphological specialisations are likely to

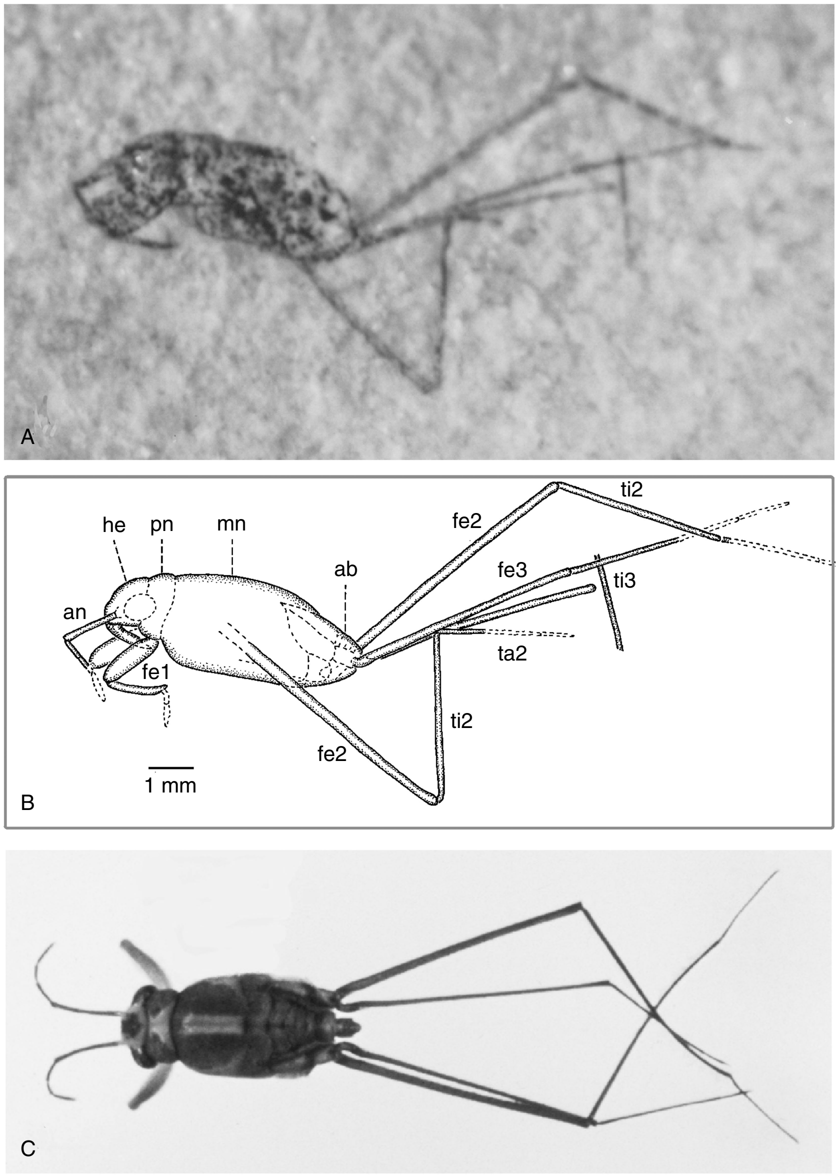

Figure 26 (A) Fossil *Halobates* in the collection of Museo civico di Storia naturale, Verona. (Photo by F. Faracci.) (B) Reconstruction of fossil *Halobates*. (Modified from Andersen et al. 1994.) (C) Male of *Austrobates rivularis*. (Photo by N.M. Andersen.)

have been key innovations in the transition from limnic to marine habitats. The oldest and most species-rich water-strider clades originated in the Indo-West Pacific, where there are 3.5 times as many species of marine water-striders as in the Atlantic, Caribbean, and eastern Pacific put together. This diversity anomaly is explained historically by region-specific differences in the origin and proliferation of clades, in differences of palaeoclimate and palaeogeography, and in their propensity for dispersal between regions (Andersen 1999).

Phylogeny

There has been much speculation about the evolution of sea-skaters, particularly how, when, and where the oceanic species achieved their unique way of life (Cheng 1989a, Andersen 1991a, 1999, Andersen et al. 1994, Andersen & Weir 1994a). Evolutionary questions like these can be answered only through inference based on reliable hypotheses about phylogenetic relationships among the species involved. In his monographic revision of the *Halobates* genus, Herring (1961) recognised several species groups and depicted relationships among them in a phylogenetic diagram. However, some of these groups were based on plesiomorphic (i.e., nonderived) characters, and may therefore not be monophyletic in the strict sense. Andersen (1991a) presented the first attempt to reconstruct the phylogeny of *Halobates*. Using cladistic methods applied to a suite of morphological characters, with emphasis on male and female genitalia, the species of *Halobates* were partitioned into a number of monophyletic species groups (Andersen 1991a, Andersen & Weir 1994a,b). The most basal of these groups is the subgenus *Hilliella* China, whereas species of the subgenus *Halobates* s. str. fall into two clades, each with about the same number of species. Until quite recently, the sister group of *Halobates* was thought to be *Asclepios* (with three species, all marine, in South and East Asia). However, the recently described limnic species *Austrobates rivularis* (Figure 26C), from northeastern Australia, has proven to be even more closely related to *Halobates* (Andersen & Weir 1994a). These three genera constitute the tribe Halobatini. The other halobatine tribe, Metrocorini, comprises about 90 species, all living in lotic freshwater habitats throughout the Ethiopian and Oriental regions. The age of the divergence between Halobatini (or at least the genus *Halobates*) and Metrocorini is inferred, from the fossil *Halobates* species from Italy, to be at least 45 MYA (Andersen et al. 1994).

Herring (1961) recognised an open-ocean group of *Halobates* composed of *H. micans*, *H. sobrinus*, *H. splendens*, *H. germanus* and *H. sericeus*, and suggested that this group is monophyletic. Andersen (1991a) questioned this since his cladistic analysis gave the result that the oceanic species *H. sobrinus*, *H. micans* and *H. splendens* are more closely related to the nearshore species *H. flaviventris* and *H. hawaiiensis* than to the two other oceanic species, *H. germanus* and *H. sericeus*. This implies two possible evolutionary scenarios: (1) the oceanic way of life evolved only once, and *H. flaviventris* + *H. hawaiiensis* have reverted to nearshore habitats; or (2) the oceanic habit has been acquired twice, independently.

Damgaard et al. (2000) scored 19 species of *Halobates*, *Austrobates rivularis*, and one species each of the genera *Asclepios* and *Eurymetra* (outgroup representing the Metrocorini) for the same suite of morphological characters as those used by Andersen (1991a). A phylogenetic (cladistic) analysis of these data yielded a single most parsimonious tree. A molecular data set was obtained from the same 22 species by sequencing 780 bp from the 3' end of the mitochondrial gene encoding cytochrome oxydase subunit I (COI). Unweighted parsimony analyses of this molecular data set gave one tree with weak support for most branches. Because of a potential for considerable homoplasy in third-codon positions, especially due to saturation of A–T transitions, the COI gene appears to be excellent for phylogenetic comparisons of not too distantly related species of insects, but less so for comparisons between genera and higher taxa (Damgaard et al. 2000). The phylogeny of *Halobates* and allied genera depicted in Figure 14 is based on both morphological characters and molecular data. The sequence of evolution of the major clades (*Asclepios*, *Austrobates*, *Halobates* (*Hilliella*), *Halobates* (s. str.)) is well supported by morphological synapomorphies. Species of *Halobates* (s. str.) fall into two clades (A and B on Figure 14): one embracing species and species groups between the *H. poseidon* group and the *H. mariannarum* group, and the other containing all species between the *H. proavus* group and *H. splendens* group. Monophyly of the group composed by the oceanic species *H. sobrinus*, *H. splendens*, and *H. micans* is well supported by molecular data. The other, composed by the oceanic species *H. germanus* and *H. sericeus*, and the nearshore species *H. hayanus*, is also well supported. Finally, the molecular data strongly support the hypothesis proposed by Andersen (1991a) that *H. flaviventris* (and its morphological sibling species *H. hawaiiensis*) is more closely related to some oceanic species than to other nearshore *Halobates*.

Phylogeography of Halobates micans

Halobates micans is the only oceanic species to be found in all three major oceans of the world. Although adults from the Atlantic, Pacific, and Indian Oceans are morphologically indistinguishable, molecular data from mtDNA indicate that the three populations are genetically different (Figure 24). Present-day Atlantic and Pacific *H. micans* populations are now separated by the Isthmus of Panama (promoting genetic isolation). However, although we expected individuals to be able to move freely between the broadly interconnected Indian and Pacific Oceans (permitting genetic mixing), this is contradicted by our findings. Mitochondrial DNA sequences from Indian Ocean *H. micans* differed more from those of Atlantic and Pacific sites (mean sequence divergences of 4.16 and 4.19%, respectively) than did those between the Atlantic and the Pacific (mean of 3.44%) (Andersen et al. 2000).

Based on the Indo-Pacific location of its most closely related coastal species, *H. hawaiiensis* Usinger and *H. flaviventris* Eschscholtz (Andersen et al. 2000), oceanic *H. micans* probably evolved somewhere in that region and then spread to the Atlantic (Andersen 1999). Closure of the Isthmus of Panama would have interrupted gene flow between Atlantic and Pacific marine populations (Knowlton & Weigh 1998). That closure was gradual, beginning ~13 MYA (Haug & Tiedemann 1998). Since *Halobates* is strictly a surface dweller, presumably only the final closure (~2.7 MYA) would have separated the populations on the two opposite sides of the isthmus. We therefore assume that the observed genetic divergence between Atlantic and Pacific populations of *H. micans* began after the final closure.

The seaway for surface–water exchange between the tropical Pacific and Indian Oceans (around the Indonesian Archipelago) is believed to have closed ~8 MYA. This event isolated formerly well-mixed populations and caused east–west disjunct distributions of many formerly widespread pan-tropical marine species, e.g., planktonic foraminiferans (Kennett et al. 1985). This could also account for the observed genetic divergence between Pacific and Indian Ocean populations of *H. micans*. Although that seaway is now open again, various “reunited” fish and mollusc populations seem to continue as distinctly separate sister populations (Randall 1999), indicating that secondary contact of previously isolated populations does not necessarily lead to interbreeding. The apparent genetic divergence of *H. micans* between ocean basins without any apparent phenotypic differentiation over the past several million years may be somehow related to the unique physical habitat and ecology of this species. It is well established that genetic divergence predates speciation among some lineages (see recent reviews by Avise 2000, Nei & Kumar 2000), although we might expect some morphological difference in *H. micans* to have occurred since the separation of major ocean basins. Based on the present results, it seems reasonable to expect that biological diversity among populations of *Halobates* may be more cryptic than previously realised. This appears to be true also for *Cyclothone*, a genus of widely distributed deep-sea fishes (Miya & Nishida 1997). Further molecular genetic studies of this ocean-skater may throw new light on processes of speciation in the open ocean.

Evolution

Establishing a reliable phylogeny helps to answer important questions about the evolution of sea-skaters and, in particular, of their oceanic way of life. Optimisation at different stages of habitat colonisation (limnic, mangrove swamp, coral coast, oceanic) on the reconstructed phylogeny of *Halobates* and allied genera lends support to the following scenario (Figure 14). Since all of the c. 90 species belonging to the tribe Metrocorini live in lotic freshwater habitats, it is hypothesised that ancestral sea-skaters from such limnic habitats invaded nearshore marine habitats, probably through estuaries and coastal mangroves, where the three known species of *Asclepios* now live (Cheng & Hill 1980). The existence of limnic species such as *A. rivularis*, *Halobates* (*Hilliella*) *robinsoni* (Andersen & Weir 2003), and *H.* (s. str.) *acherontis* (Polhemus 1982) suggests that either the marine environment has been invaded more than once or, more likely, marine lineages have recolonised freshwater habitats independently several times. The oceanic way of life in some *Halobates* species probably evolved at least twice (Figure 14, marked 1 and 2). This hypothesis, well supported by molecular data, is more parsimonious than the one that includes only one original transition to the open ocean, but three independent reversals to nearshore habitats in *H. hayanus*, *H. flaviventris*, and *H. hawaiiensis* (Damgaard et al. 2000). Using data based on secondary metabolites extracted from cuticles of *Halobates*, Petrakis et al. (2003) reconstructed a phylogenetic tree which was congruent with that of Damgaard et al. (2000). Chemical differences between coastal an oceanic *Halobates* species correlated well with their evolutionary history.

Concluding remarks

Knowledge of the marine insect genus *Halobates* has grown greatly since its first discovery some 200 yr ago. It is represented by a fossil at least 45 million yr old. There are two discrete groups, coastal and oceanic, each with different life strategies. Within each group there are distinct distribution patterns that reflect the phylogeny of species groups. The oceanic species present challenging problems on phylogeny and gene flow between populations. Advances in molecular techniques will be useful in helping in future studies. Although much is known about the biology of *Halobates*, it is still not known what the newly hatched nymphs feed on in the open ocean, how long the adults live, how the sexes locate each other, and what limits their occurrence and abundance in any particular patch of ocean. Clearly there is scope for much further research.

Under the pen name "A. Square," Edwin A. Abbot wrote a science fiction essay entitled "Flatland" (1884), in which he posited the existence of creatures living paradoxically in a two-dimensional world. It was fanciful, of course, and we may be sure that he never imagined that there could be any creatures living in such an environment. And yet, that is just how the oceanic species of *Halobates* live, at the air–sea interface. They can neither fly over one another nor dive under one another. Admittedly, when excited they can jump a few centimetres into the air, but in comparison with the vastness of their territories, extending thousands of kilometres in all directions, the height of such brief saltations into the third dimension can be considered negligible. They cannot lay their eggs on anything solid unless they can encounter it floating in their two-dimensional world. If they needed to communicate with one another, they could do so by specific patterns of ripples (although so far this has been demonstrated only for their relatives on freshwater ponds) or by pheromones. Furthermore, because it would seem uneconomic to waft their scents upon the sea breezes (which would soon dissipate them), or dissolve them in the waters on which they skate (which could also be expected to dissipate them uneconomically), they would ideally have to use systems of surfactant pheromones that could spread over the surfaces on which they skate. This is, in fact, what they probably do, as has been recently discovered for *Trochopus*, a coastal relative of *Halobates* (Cheng & Roussis 1998). How they speciate, in a contiguous two-dimensional environment that lacks any evident barriers like mountain ranges, can only be surmised. Perhaps explanations will be found when molecular biological data can be properly evaluated. Such odd insects merit much more attention than they customarily receive from entomologists, many of whom, indeed, are unaware of the very existence of sea-skaters, even though the largest world collection of *Halobates* is housed at the Zoological Museum of the University of Copenhagen, where several thousand samples are available for study. A website on *Halobates* was created (Andersen 2002) and is maintained and updated on a regular basis.

Acknowledgements

Our research on *Halobates* would not have been possible without the help of numerous colleagues who collected samples for us from various parts of the world. They are too numerous to list. We would like to extend to them all our heartfelt gratitude. We also thank Josh Fluty for technical assistance in data plotting and Ralph A. Lewin for constructive criticisms on the manuscript. Essential background research for this review was supported by the Danish Natural History Research Council (grants 21-00-0180 and 21-02-0502 to N.M.A.) and the Scripps Institution of Oceanography (to L.C.).

Dr. Nils Møller Andersen passed away on 12 May 2004, at age 63. His death was totally unexpected. I have lost a dear friend and colleague, and marine entomology has lost one of its staunchest supporters. Nils was Curator of Exopterygote Insects and chair of the Entomology Department, Zoological Museum, University of Copenhagen, and also Editor-in-Chief of Insect Systematics & Evolution. He was a highly regarded and internationally known aquatic heteropterist and has published extensively. Many of his publications will remain as standard references for years to come. Some examples of his exquisite and accurate illustrations can be seen in this work.

Nils and I have shared a common interest on aquatic insects for almost 40 years. This review on *Halobates* was the culmination of our collaborative research on the most unique of all marine insects. We complemented each other in our expertise, he on systematics and evolution, and I on ecology and distribution. I insisted that his name appeared first in this review to reflect that this is truly a joint effort. He grudgingly agreed – that his name starts with A and mine with C helped settle the matter. It was extremely fortunate that we were able to complete this review in time. It will be a fitting tribute to his memory.

Lanna Cheng

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APPENDIX 1

Key for the Identification of *Halobates* Eschscholtz and Related Genera (Hemiptera-Heteroptera: Gerridae)[1]

COMPILED BY NILS MØLLER ANDERSEN

Collecting and identifying *Halobates*

Coastal *Halobates* species can easily be collected in nearshore, marine habitats (estuaries, mangroves, intertidal coral reefs) by using a lightweight fishing net with a fine-mesh nylon or other rapid-drying bag. 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. Oceanic species are generally collected by towing a neuston net or by using a dip net on a research vessel. They may also 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 salt crystals have been dissolved and removed.

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 colouration 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. The pilosity of dark, suberect hairs on the thorax used to characterise some species is most readily observed by tilting the specimen to obtain an oblique view.

The morphological terminology used in the keys is explained in Figure A1 through Figure A7. The body of a sea-skater is composed of the head, pronotum, fused meso- and metanotum, and abdomen. The head carries the antenna and, beneath, the short rostrum. The forelegs are relatively short and robust. The middle and hind legs are long and slender. A distinct feature of the legs of sea-skaters is a fringe of long hairs along the ventral surface of the middle tibia and tarsus (Figure A20). As a rule, coastal species have meso-tibio-tarsal fringes with shorter hairs than oceanic species. The hair fringe is limited to the middle tibia in species of the subgenus *Hilliella* (Figure A15), a state shared with some (but not all) species of *Asclepios*. The tarsi have two segments (hind tarsus has only one segment in some species). The relative lengths of the fore tarsal segments vary: as a rule, segment I of large species is subequal to or longer than segment II.

The male abdomen of *Halobates* is relatively short (Figure A1). Most of the pregenital abdominal segments are reduced in length, but the genital segments are prolonged and very conspicuous. Most parts of the male genitalia vary extensively in shape, structure, degree of asymmetry, etc., and are most useful for identifying species. The abdominal segment 8 is cylindrical, usually as wide as it is long (Figure A2). 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 (Figure A2). The ventral hind margin of the segment is concave, with a pair of slender styliform processes (Figure A3) varying in relative length, degree of asymmetry, orientation, shape of apices, etc. The pygophore (= segment 9, Figure A3) is subovate in ventral outline in most species. It is boat shaped with its tergal part reduced to a narrow strip. The proctiger (segments 10 + 11) lies on top of the pygophore (Figure A3 and Figure A4). It is plate-like, usually pentagonal in outline, with its lateral

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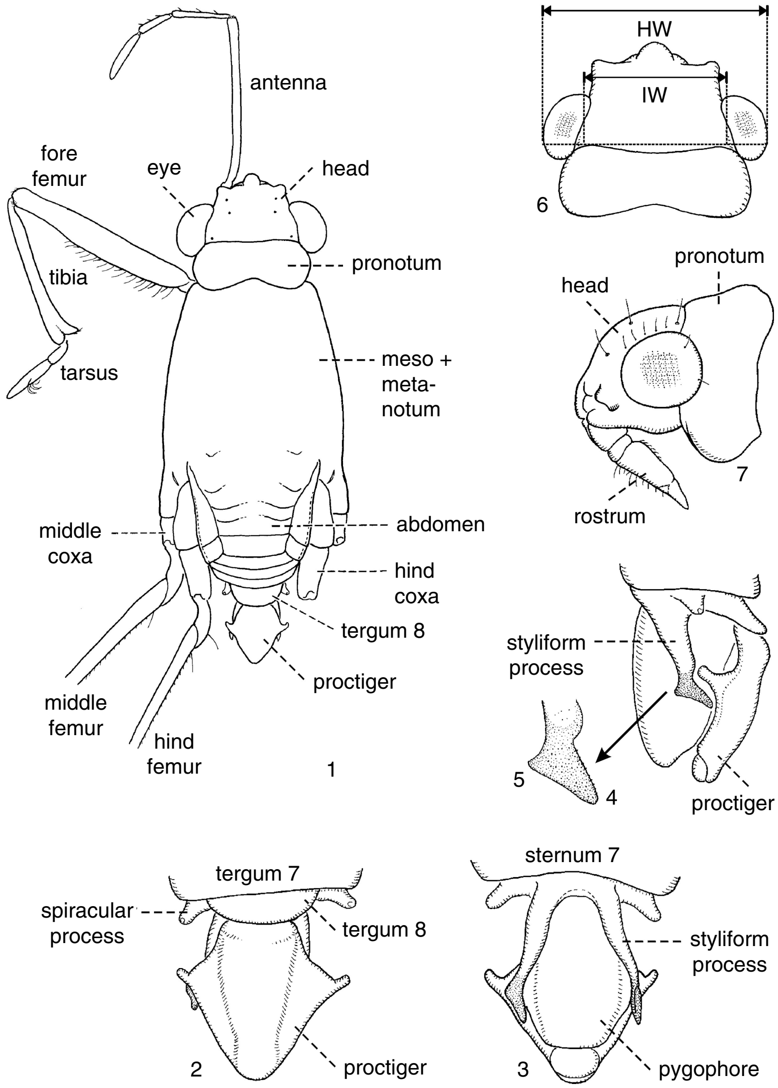
[1] *Illustrations from Andersen & Weir 1994a,b are reproduced with permission of CSIRO PUBLISHING from Invertebrate Taxonomy, **8**, 1–15, 861–909.*



Figures A1–A7 *Halobates darwini*, male. (1) Dorsal view, antenna and legs of right side, and distal parts of middle and hind legs omitted. (2) Dorsal view of abdominal end. (3) Ventral view of abdominal end. (4) Lateral view of abdominal end. (5) Apex of styliform process. (6) *Halobates* sp. Dorsal view of head and pronotum showing measurements of head width (HW) and interocular width (IW). (7) *Austrobates rivularis*. Lateral view of head and prothorax, antenna omitted. (1–6 modified from Andersen & Weir 1994b; 7 modified from Andersen & Weir 1994a.)

margins more or less produced in many species. The proctiger was incorrectly identified as tergum 9 by Herring (1961).

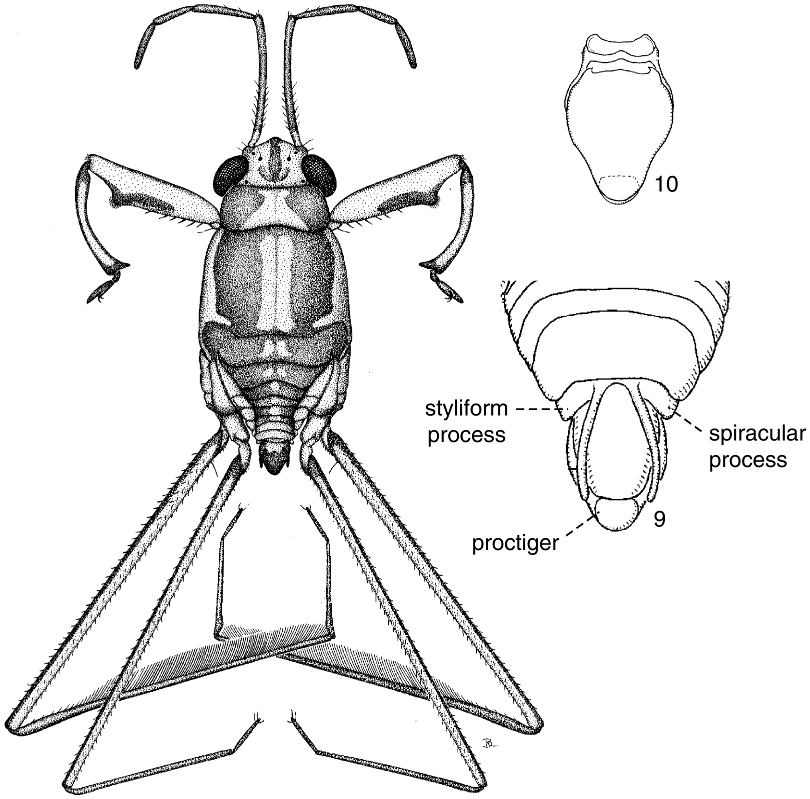
Most measurements used in the key are self-explanatory. The length is measured from the tip of the head to the end of the abdomen. Egg-filled females may have their abdomens distended, thus exaggerating the length. The eye width is obtained by subtracting the interocular width (IW, Figure A6) from the head width and then dividing by 2. The length of the femur is measured along the dorsal side of the limb, not including the trochanter (the segment between the coxa and the femur).

The key is only applicable to adults, which in sea-skaters are completely wingless and may be confused with juveniles (called nymphs), in particular fourth or fifth instars. Nymphs, however, can be distinguished from adults by their softer and paler integuments, distinct colour patterns on the thorax and abdomen, one-segment tarsi, and undifferentiated male genitalia.

Key to genera of Subfamily Halobatinae (Gerridae: Halobatini)

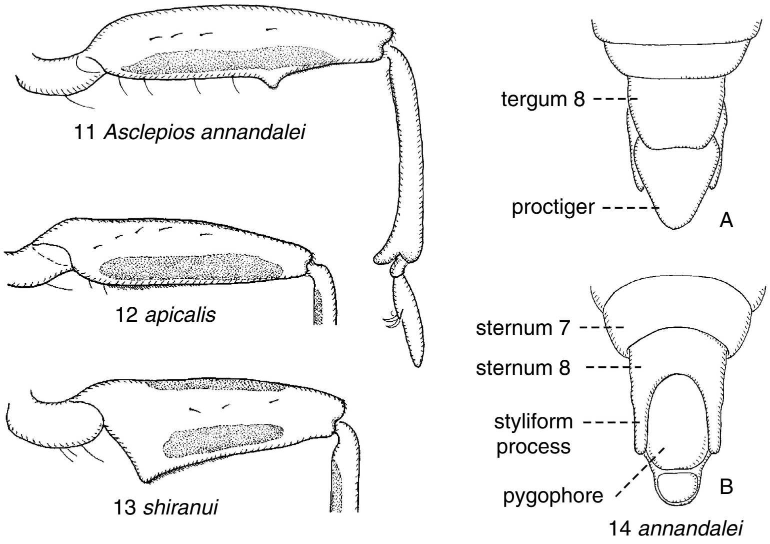
1. Dorsal surface of body chiefly dark, pale markings usually limited to head and pronotum (Figure A16 to Figure A19). Intersegmental suture between meso- and metanotum indistinct or absent (Figure A1). Male fore femora usually relatively simple, if modified on ventral surface, then proctiger (segment 10) of male, pentagonal in outline (as in Figure A2, etc.). Predominantly marine. .... *Halobates* Eschscholtz

– Dorsal surface of body with extensive pale markings on head, thorax, and abdominal dorsum (Figure A8). Intersegmental suture between meso- and metanotum distinct. Male fore femora more or less modified, incrassate basally or with a prominent tubercle on ventral surface (Figure A8, Figure A11 to Figure A13). Proctiger (segment 10) of male rounded (Figure A10 and Figure A14A). Freshwater or marine. 2



8 *Austrobates rivularis*

Figures A8–A10 *Austrobates rivularis*. (8) Male. (9) Ventral view of abdominal end. (10) Dorsal view of proctiger. (Modified from Andersen & Weir 1994a.)



Figures A11–A14 *Asclepios* spp., males. (11) *A. annandalei*, foreleg. (12) *A. apicalis*, fore femur. (13) *A. shiranui*, fore femur. (14) *A. annandalei*, dorsal (A) and ventral (B) views of abdominal end.

2. Segment 8 of male is longer than it is wide (Figure A14B); spiracles not situated on lateral tubercles; ventral styliform processes short and stout, almost parallel. Mangrove swamp or lagoon. .... *Asclepios* Distant
– Segment 8 of male is wider than it is long (Figure A9); spiracles situated on low, lateral tubercles; ventral styliform processes long and slender, diverging. [One species: *A. rivularis* Andersen & Weir; length, 3.1–3.3 mm (♂), 4.2–4.4 mm (♀).] Freshwater stream. .... *Austrobates* Andersen & Weir

Key to species of *Asclepios* Distant

1. Fore femur of male thickest in middle, with a tubercle on ventral surface (Figure A11). Both middle tibia and tarsus with ventral hair fringe. Length, 3.0 mm (♂), 4.4 mm (♀). .... *A. annandalei* Distant
– Fore femur of male thickest in basal part, without a tubercle on ventral surface. Only middle tibia with ventral hair fringe. 2
2. Basal part of male fore femur strongly widened, more than twice as broad as distal end (Figure A13). Length, 3.5 mm (♂), 4.0 mm (♀). ....*A. shiranui* Esaki
– Basal part of male fore femur moderately widened, much less than twice as broad as distal end (Figure A14). Length, 3.0 mm (♂), 3.5 mm (♀). ....*A. apicalis* (Esaki)

Key to species of *Halobates* Eschscholtz

1. Length of fore tarsal segment I, 0.3 times or less that of segment II. Middle femur at most 1.05 times longer than hind femur. 2
– Length of fore tarsal segment I, more than 0.3 times that of segment II. Middle femur 1.1 times or more longer than hind femur. 5

2. Body brown or yellow with posterior margin of pronotum, most of thoracic pleura, and prominent stripes on femora paler (Figure A15). Apices of male styliformprocesses slender and curved (Figure A21 to Figure A23) (subgenus *Hilliella* China). 3

– Body dark brown to black with most of thoracic pleura dark and only bases of anterior femora yellow. Apices of male styliform processes slender and straight (Figure A24). Length, 3.6–4.0 mm (♂), 4.2–4.5 mm (♀) [Head with prominent pale markings along inner margins of eyes (Figure A17). Fore femur of male distinctly constricted in distal third.] .... *H.* (s. str.) *zephyrus* Herring

3. Male fore femur depressed ventrally at distal quarter with an elongate patch of stiff hairs. Proctiger of male widest across middle. [Apices of styliform processes simple (Figure A21). Female meso- and metanotum with scattered, long dark bristles.] Length, 3.3–3.8 mm (♂), 3.4–4.2 mm (♀). .... *H.* (*Hilliella*) *mjobergi* Hale

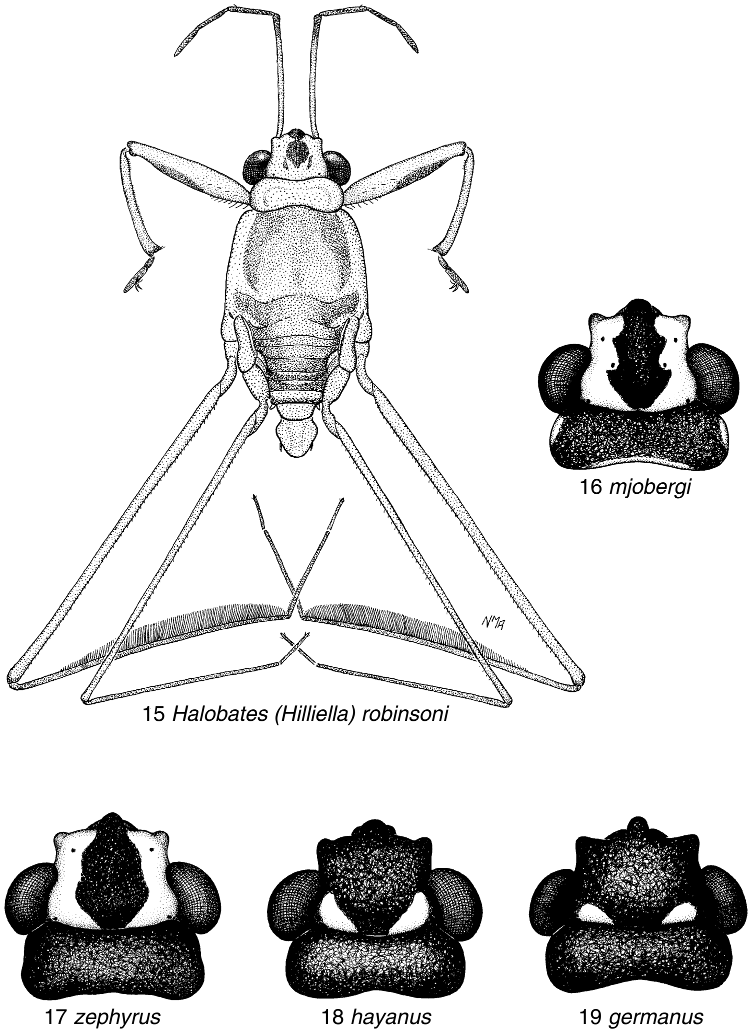
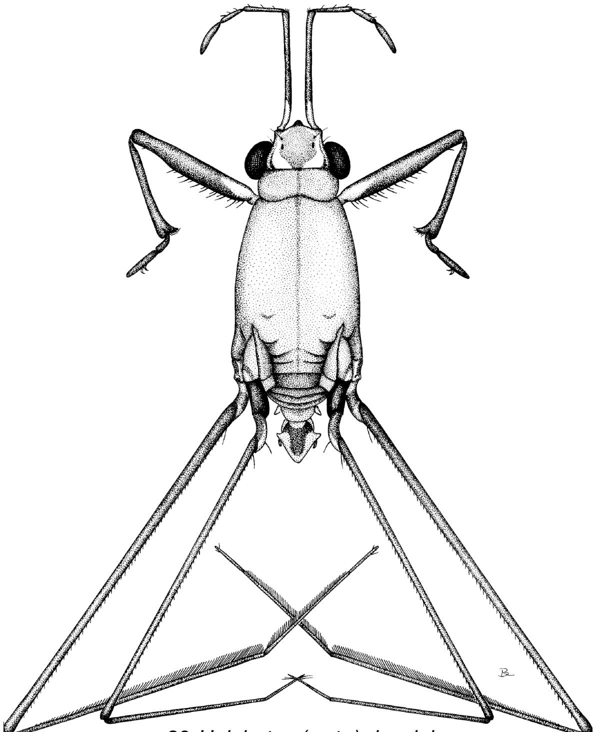


Figure A15 *Halobates* (*Hilliella*) *robinsoni*, male. **Figures A16–A19** Colour pattern of dorsal head and pronotum. (16) *H.* (*Hilliella*) *mjobergi*. (17) *H.* (s. str.) *zephyrus*. (18) *H.* (s. str.) *hayanus*. (19) *H.* (s. str.) *germanus*. (15 modified from Andersen & Weir 2003; 16–19 modified from Andersen & Weir 1994b.)



20 *Halobates (s.str.) darwini*

Figure A20 *Halobates* (s. str.) *darwini*, male. (Modified from Andersen & Weir 1994b.)

– Fore femur of male not modified ventrally, tapering slightly toward apex. Proctiger of male widest at basal third (Figure A22 and Figure A23). 4

4. Proctiger of male distinctly produced laterally at basal third; apices of styliform processes slightly widened and pointed (Figure A22). Thorax and abdomen dark brown dorsally. Female meso- and metanotum without dark bristles. Length, 4.1–4.5 mm (♂), 4.3–4.7 mm (♀). .... *H.* (*Hilliella*) *lannae* Andersen & Weir

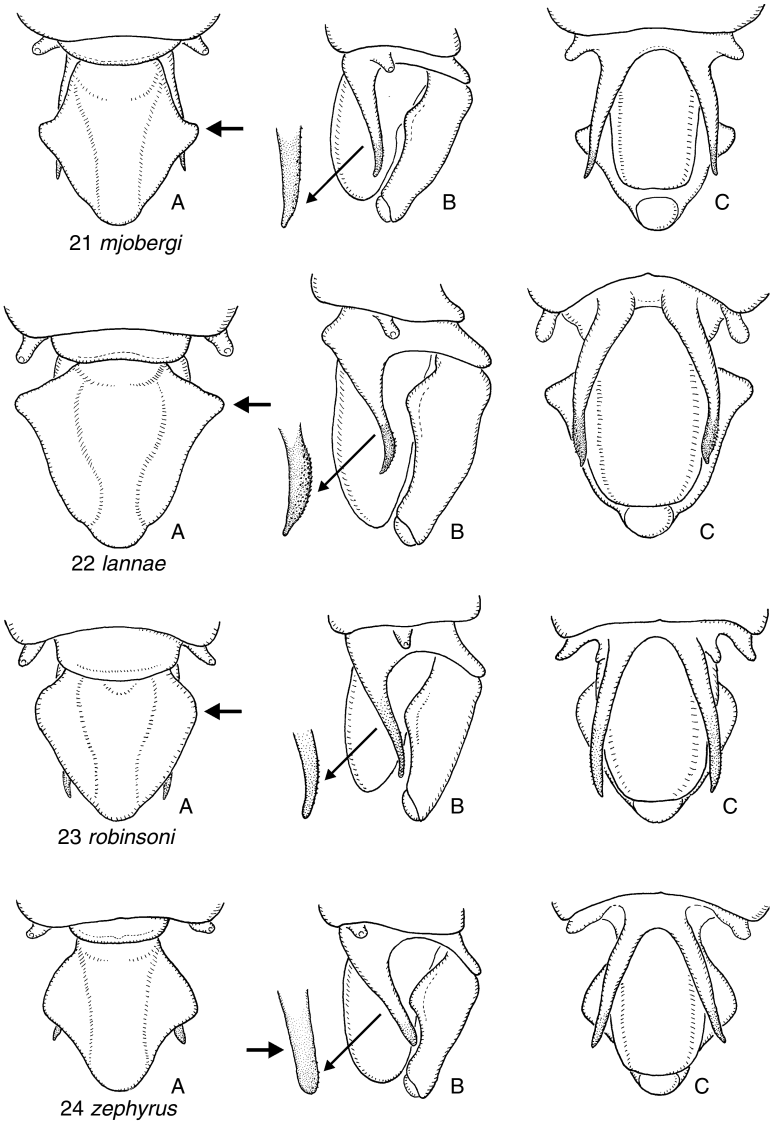
– Proctiger of male widened but not distinctly produced laterally at basal third; apices of styliform processes simple and blunt (Figure A23). Thorax and abdomen brown or yellowish brown dorsally. Female meso- and metanotum with scattered long, dark bristles. Length, 3.6 mm (♂), 4.4–4.5 mm (♀). ....*H.* (*Hilliella*) *robinsoni* Andersen & Weir

5. Yellow marking on head reduced to a pair of triangular markings at the base (Figure A19). Body, including thoracic and abdominal venter, uniformly dark. Interocular width of head subequal to or more than 3.6 times the width of an eye (see Figure A6). Oceanic species. 6

– Yellow marking on head more extensive, with prominent yellow stripes along eyes (Figure A16) or reduced to a pair of crescent-shaped spots between eyes (Figure A18), occasionally with a yellow spot at the base of antennae. Conspicuous yellow or brown markings on some parts of venter. Interocular width of head less than 3.6 times the width of an eye. Coastal species. 10

6. Larger species, length more than 4.1 mm (♂), 3.9 mm (♀). Styliform processes of male asymmetrical (Figure A25 to Figure A27). 7

– Smaller species, length less than 3.9 mm (♂, ♀). Styliform processes of male more or less symmetrical (Figure A28 to Figure A29)..9

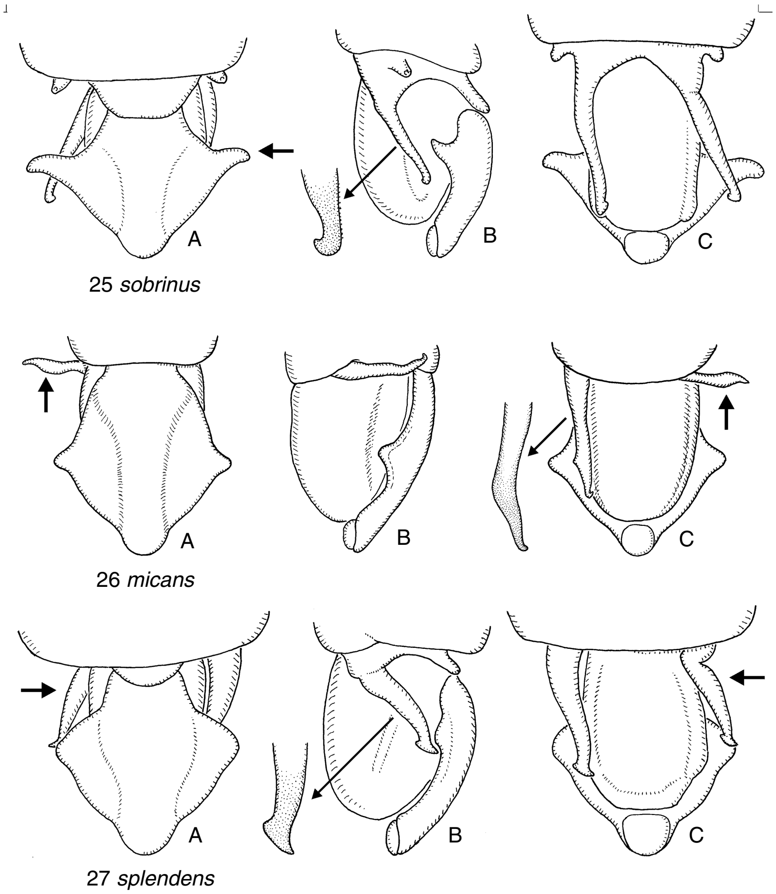


Figures A21–A24 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (21) *H.* (*Hilliella*) *mjobergi*. (22) *H.* (*H.*) *lannae*. (23) *H.* (*H.*) *robinsoni*. (24) *H.* (s. str.) *zephyrus*. (21, 22, and 24 modified from Andersen & Weir, 1994b; 23 from Andersen & Weir 2003.)

7. Hind femur long, more than 0.8 times as long as middle femur, and at least twice as long as hind tibia. Male proctiger relatively short and broad, with lateral finger-like protuberance (Figure A25). Length, 4.4 mm (♂), 4.0 mm (♀). ...... *H.* (s. str.) *sobrinus* White

– Hind femur short, less than 0.8 times as long as middle femur and less than twice as long as hind tibia. Male proctiger as broad as long, without lateral protuberance as above (Figure A26 to Figure A27). 8

8. Fore tarsal segment I shorter than segment II. Left styliform process of male bent abruptly upward at a right angle (Figure A26). Length, 4.1–4.6 mm (♂), 3.9–4.6 mm (♀). .... *H.* (s. str.) *micans* Eschscholtz



Figures A25–A27 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left (25 and 27) or right (26) styliform process shown at higher magnification. (25) *H.* (s. str.) *sobrinus*. (26) *H.* (s. str.) *micans*. (27) *H.* (s. str.) *splendens*. (26 modified from Andersen & Weir 1994b.)

– Fore tarsal segment I subequal to or slightly longer than segment II. Left styliform process of male bent outward but not at right angle (Figure A27). Length, 5.0 mm (♂), 4.5 mm (♀)..*H.* (s. str.) *splendens* Witlaczil

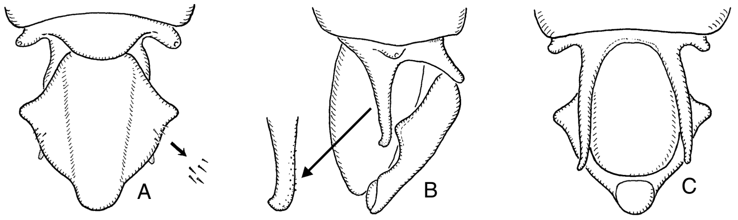
9. Antennal segment I 0.5 times as long as segment IV. Fore tarsal segment I about 0.4 times longer than segment II. Male terminalia (Figure A28). Length, 3.2–3.6 mm (♂), 3.0–3.4 mm (♀)...*H.* (s. str.) *sericeus* Eschscholtz

– Antennal segment I much more than 0.5 times as long as segment IV. Fore tarsal segment I about 0.6 times longer than segment II. Male terminalia (Figure A29). Length, 3.3–3.8 mm (♂), 3.5–3.9 mm (♀). .... *H.* (s. str.) *germanus* White

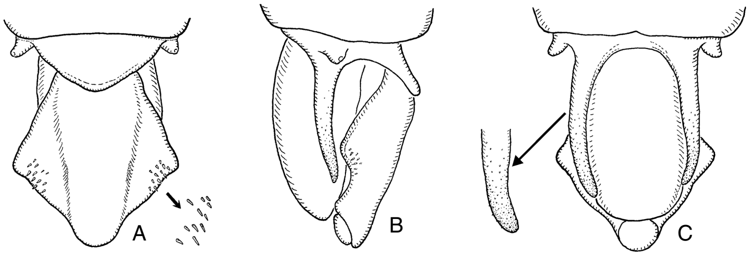
10. Fore tarsal segment I subequal to or longer than segment II. 11

– Fore tarsal segment I shorter than segment II..33

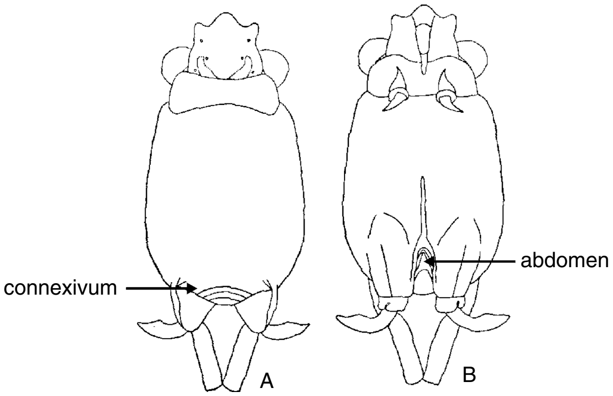
11. Male abdominal segment 8 enclosed within the enlarged, tubular segment 8. [Male genital segments usually rotated about 90° relative to rest of the body.] Right styliform process very short and deformed (Figure A31 to Figure A33). Female abdominal venter with a triangular pocket into which apex of abdomen may be fitted; venter often with a longitudinal fold, sometimes extending forward to prothorax (Figure A30). 12



28 *sericeus*



29 *germanus*



30 *salotae*

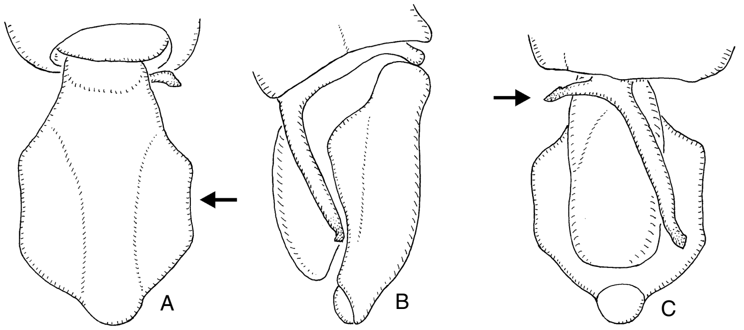
Figures A28–A29 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (28) *H.* (s. str.) *sericeus*. (29) *H.* (s. str.) *germanus*. **Figure A30** *H.* (s. str.) *salotae*, female in dorsal (A) and ventral (B) views; antenna and most of legs omitted. (28 and 29 modified from Andersen & Weir 1994b; 30 modified from Herring 1961.)

– Male abdominal segment 8 clearly visible, never enclosed within a tubular segment 8. Right styliform process may be short, but not deformed as above. Female abdominal venter without triangular pocket or longitudinal fold. 14

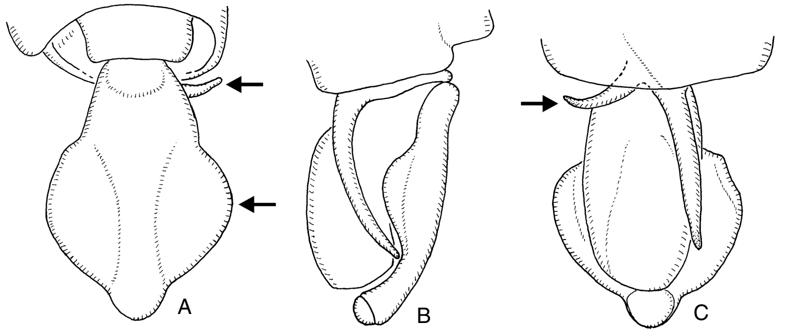
12. Male proctiger parallel sided (Figure A31). Female connexiva forming two large triangles (Figure A30). No black bristles on anterior margin of meso- and metanotum. Length, 5.5 mm (♂), 4.4 mm (♀). .... *H.* (s. str.) *salotae* Herring

– Male proctiger more or less shield shaped, sides not parallel (Figure A32 and Figure A33). Female connexiva not as above. Black bristles may be present on anterior margin of meso- and metanotum. 13

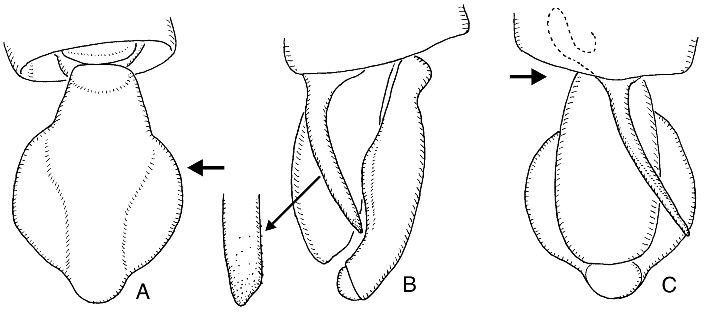
13. Right styliform process of male curved at apex and visible from above (Figure A32). Female very broad posteriorly, body width between hind coxae wider than head between eyes. Stout black bristles present on anterior margin of meso- and metanotum. Length, 6.5 mm (♂), 5.0 mm (♀). .... *H.* (s. str.) *katherinae* Herring



31 *salotae*



32 *katherinae*



33 *fijiensis*

Figures A31–A33 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (31) *H.* (s. str.) *salotae*. (32) *H.* (s. str.) *katherinae*. (33) *H.* (s. str.) *fijiensis*.

– Right styliform process of male flattened, its apex lanceolate, not visible from above (Figure A33). Female only as broad through hind coxae as width of head through eyes. No stout black bristles on meso- and metanotum. Length, 5.8 mm (♂), 4.5 mm (♀). ....*H.* (s. str.) *fijiensis* Herring

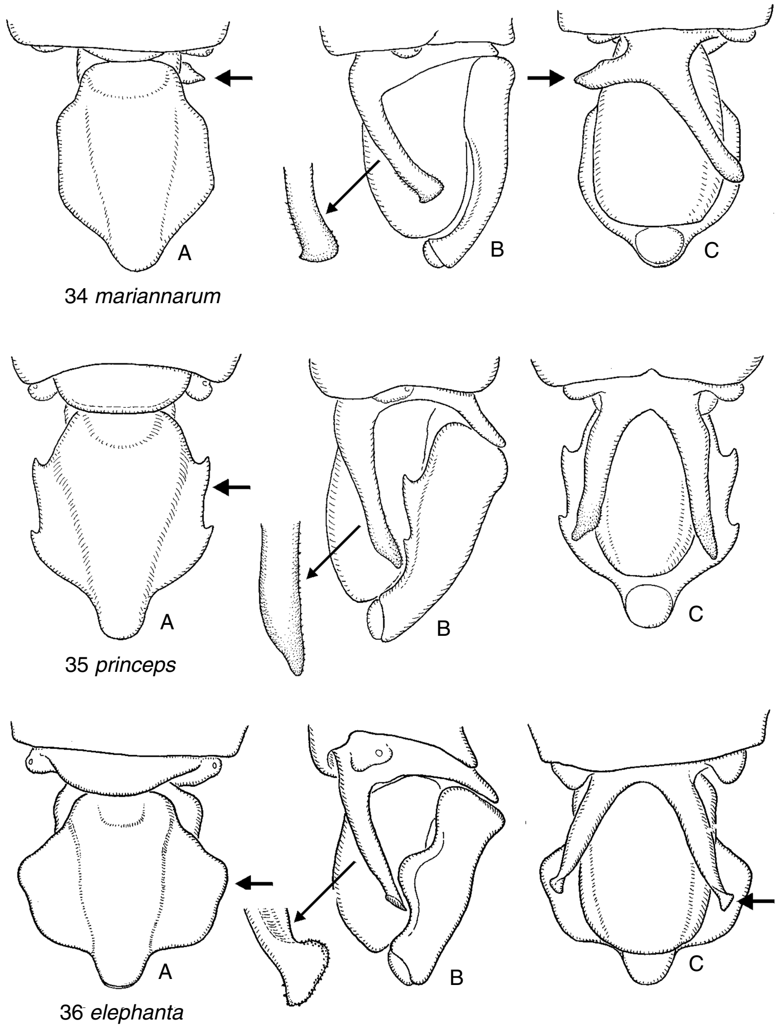
14\. Males. 15

– Females..24

15\. Right styliform process much shorter than left process and directed outward (Figure A34). Length, 4.5 mm. ....*H.* (s. str.) *mariannarum* Esaki

– Right styliform process not as above, similar to left process..16

16\. Proctiger of male broadly expanded laterally, with subparallel sides (Figure A35 to Figure A39)..17



Figures A34–A36 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (34) *H.* (s. str.) *mariannarum*. (35) *H.* (s str.) *princeps*. (36) *H.* (s. str.) *elephanta*. (35 modified from Andersen & Weir 1994b; 36 modified from Andersen & Foster 1992.)

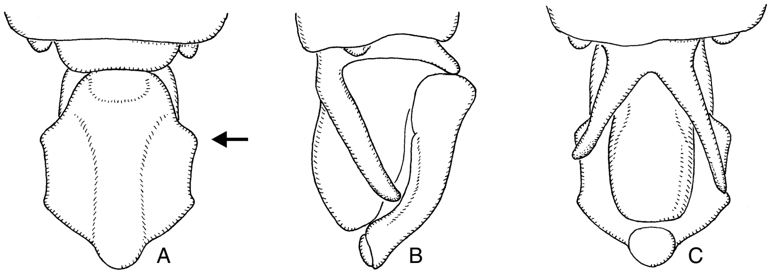
– Proctiger at most slightly expanded laterally, usually protruding but never parallel sided (Figure A40 to Figure A43). 21

17\. Proctiger with two pointed prominences on each side (Figure A35). Fore femur with a tubercle beneath. [Large species, length, 6.0–6.3 mm.] .... *H.* (s. str.) *princeps* White

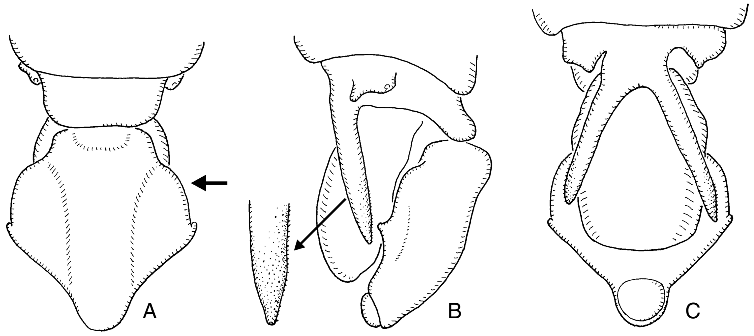
– Proctiger with no pointed prominences (Figure A36 and Figure A37) or with only one pointed prominence on each side (Figure A38 and Figure A39). Fore femur not modified as above. 18

18\. Proctiger with rounded posterolateral angles (Figure A36). Apices of styliform processes slender, spatulate, and twisted. Length, 5.4–5.7 mm .... *H.* (s. str.) *elephanta* Andersen & Foster

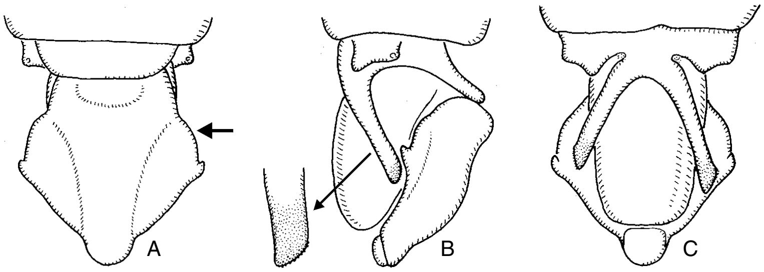
– Proctiger with sharp posterolateral angles (Figure A37 to Figure A39). Apices of styliform processes not twisted. 19



37 *kelleni*



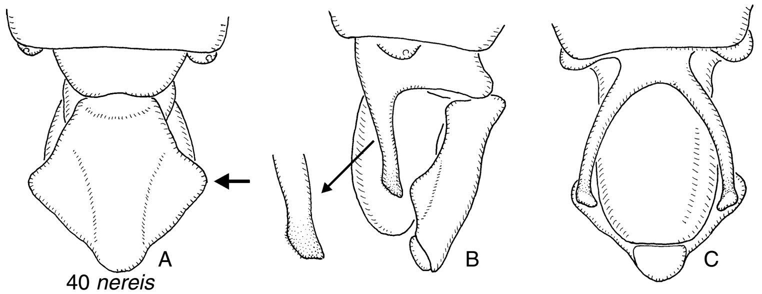
38 *alluaudi*



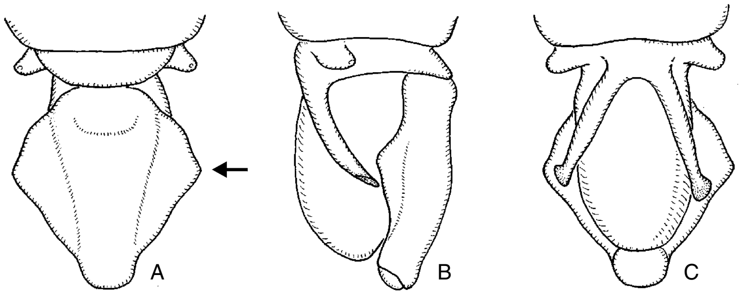
39 *tethys*

Figures A37–A39 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (37) *H.* (s. str.) *kelleni*. (38) *H.* (s. str.) *alluaudi*. (39) *H.* (s. str.) *tethys*.

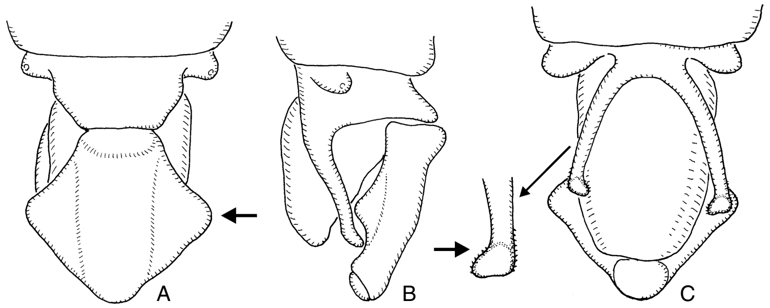
19. Proctiger much longer than broad, anterolateral angles pointed (Figure A37). Length, 4.5 mm. .... *H.* (s. str.) *kelleni* Herring
– Proctiger about as broad as long, anterolateral angles rounded (Figure A38 and Figure A39). Length, 5.0–5.8 mm. 20
20. Apices of male styliform processes tapered (Figure A38). Length, 5.0 mm. .... *H.* (s. str.) *alluaudi* Bergroth
– Apices of male styliform processes blunt (Figure A39). Length, 5.3 mm. .... *H.* (s. str.) *tethys* Herring
21. Small species, length, 5.5 mm or less. Male terminalia (Figure A40). ....*H.* (s. str.) *nereis* Herring
– Large species, length, 5.6 mm or more. 22
22. Oval species, much wider at the bases of legs than at anterior margin of mesonotum. Male terminalia (Figure A41). Length, 5.6 mm................. *H.* (s. str.) *matsumurai* Esaki
– Cylindrical, parallel-sided species; hardly, if at all, wider at the bases of middle and hind legs than at anterior margin of mesonotum..23



40 *nereis*



41 *matsumurai*



42 *esakii*

Figures A40–A42 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (40) *H.* (s. str.) *nereis*. (41) *H.* (s. str.) *matsumurai*. (42) *H.* (s. str.) *esakii*.

23\. Apices of styliform processes expanded, flattened, and shiny (Figure A43). Length, 6.0 mm.. *H.* (s. str.) *esakii* Miyamoto

– Apices of styliform processes not expanded or flattened as above (Figure A42). Length, 6.5 mm. .... *H.* (s. str.) *browni* Herring

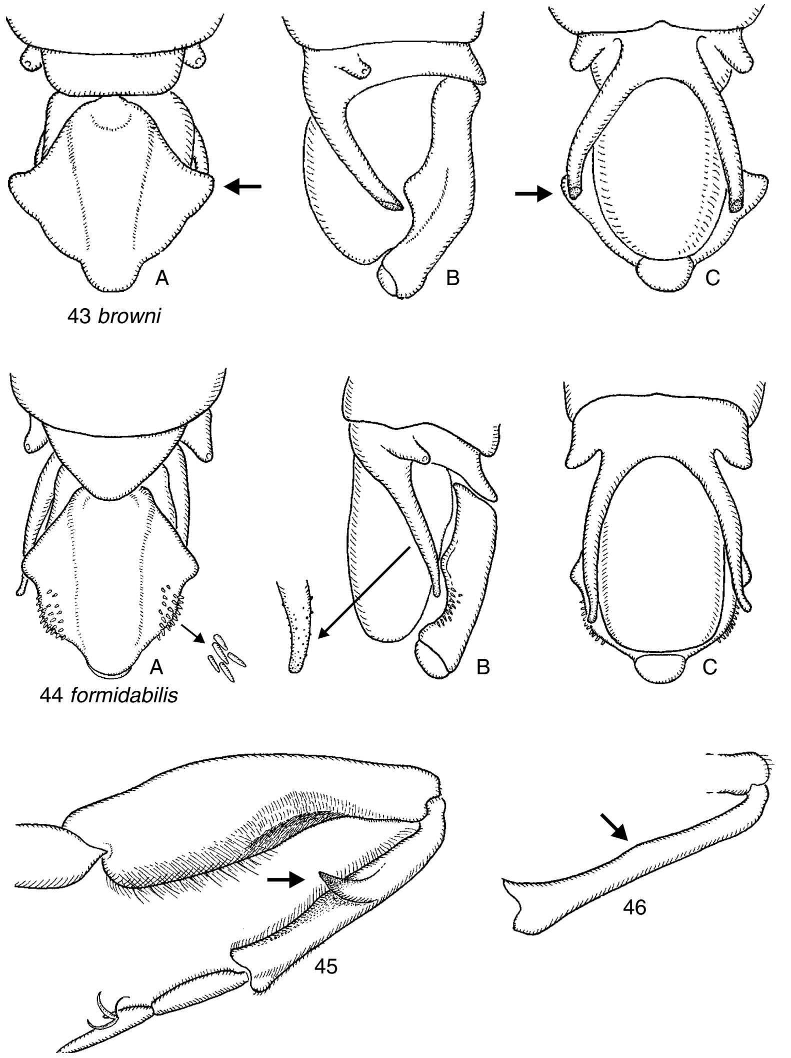
24\. Thorax in side view strongly arched and abruptly slanted downward toward abdomen. Connexiva curved inward, their edges posteriorly divergent. Length, 4.7 mm. .... *H.* (s. str.) *kelleni* Herring

– Thorax and connexiva not modified as above...25

25\. Hind coxae much shorter than acetabula. Small species, length not more than 4.5 mm (♀). .... *H.* (s. str.) *mariannarum* Esaki

– Hind coxae subequal to or longer than acetabula. Larger species, length over 4.5 mm (♀). 26

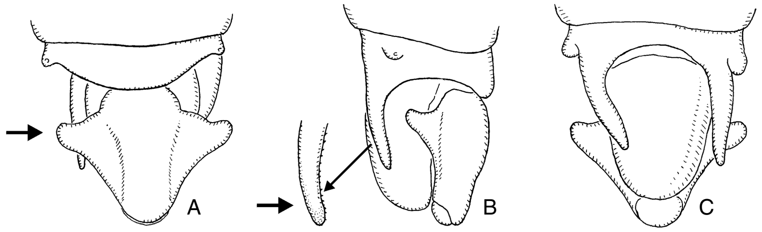
26\. Black bristles on meso- and metanotum quite dense and covering all but mid-dorsal area. Thorax in side view strongly arched. Length, 5.0 mm (♀). *H.* (s. str.) *alluaudi* Bergroth



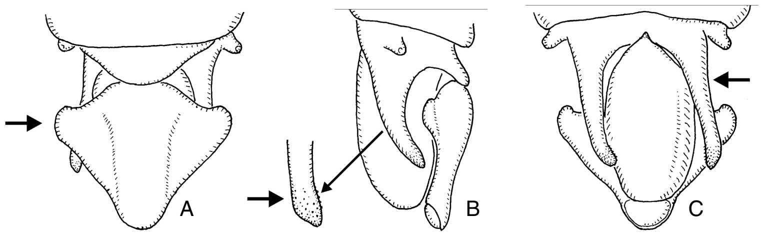
Figures A43–A46 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (43) *H.* (s. str.) *browni*. (44–46) *H.* (s. str.) *formidabilis*. (45) Left foreleg of male. (46) Fore tibia of female. (44–46 modified from Andersen & Foster 1992.)

– Black bristles on meso- and metanotum, if present, not extending laterally to bases of acetabula. Thorax in side view not arched. 27
27. Fore tarsal segment I at least 1.4 times as long as segment II. 28
– Fore tarsal segment I less than 1.4 times as long as segment II. 29
28. Uniformly blue-black. Meso- and metanotum with scattered black bristles. Length, 6.1–6.7 mm. .... *H.* (s. str.) *princeps* White
– Uniformly black. Meso- and metanotum laterally with densely set black bristles. Length, 5.5–5.7 mm (♀). .... *H.* (s. str.) *elephanta* Andersen & Foster
29. Body elongate-cylindrical, greatest width at posterior margin of hind acetabula. Larger species, length, 6.0 mm or more. 30
– Body oval, greatest width well in front of posterior margin of hind acetabula. Smaller species, length much less than 6.0 mm. 31

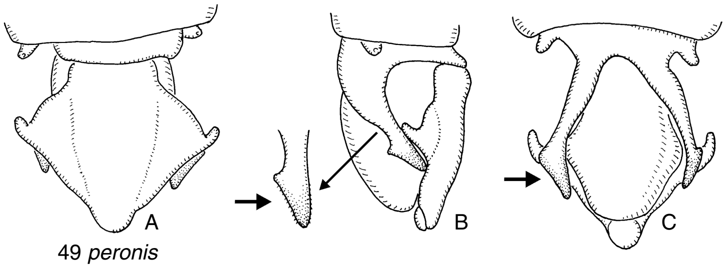
30. Meso- and metanotum with scattered black bristles. ....*H.* (s. str.) *esakii* Miyamoto
– Meso- and metanotum without black bristles. .... *H.* (s. str.) *browni* Herring
31. Stout black bristles present on meso- and metanotum. Large species, over 5.0 mm long. ....*H.* (s. str.) *matsumurai* Esaki
– Stout black bristles present on some parts of meso- and metanotum. Smaller species, length, 5.0 mm or less. 32
32. Stout black bristles on anterior half of meso- and metanotum. Antennal segments II and IV not subequal. Fore tarsal segment I about 1.3 times as long as segment II. ....*H.* (s. str.) *tethys* Herring
– Stout black bristles absent on anterior half of meso- and metanotum, only a small patch on sides of posterior half. Antennal segments II and IV subequal. Fore tarsal segment I about 1.1 times as long as segment II. ....*H.* (s. str.) *nereis* Herring
33. Fore femur of male strongly incrassate, fore tibia with a long spinous process on inner margin (Figure A45); pronotum distinctly swollen. Male terminalia (Figure A44). Inner margin of fore tibia of female sinuate (Figure A46). Length, 4.6–5.2 mm (♂), 4.7–5.5 mm (♀). ....*H.* (s. str.) *formidabilis* (Distant)
– Fore femur and tibia of male not modified as above; pronotum not distinctly swollen. Inner margin of fore tibia of female straight. 34
34. Fore tarsal segment I, 0.6 times or less length of segment II. 35
– Fore tarsal segment I, more than 0.6 times length of segment II. 51
35. Male proctiger subtriangular (Figure A47 and Figure A48). Fore tarsal segment I, 0.3 times (♂) or 0.4 times (♀) as long as segment II. 36
– Male proctiger more or less pentagonate, never triangular. Fore tarsal segment I, more than 0.3 times (♂) or 0.4 times (♀) as long as segment II. 37
36. Males with black bristles along sides of meso- and metanotum. Male styliform processes slender (Figure A47). Female thorax with a mid-dorsal, longitudinal groove lined with black spines on both sides and an orange stripe. Length, 3.5 mm (♂), 4.5 mm (♀). ....*H.* (s. str.) *proavus* White
– Males without black bristles along sides of meso- and metanotum. Male styliform processes stouter with the left strongly curved (Figure A48). Female thorax without groove or orange stripe but with scattered black bristles on anterior margin of meso- and metanotum. Length, 3.0 mm (♂), 3.8 mm (♀). ....*H.* (s. str.) *maculatus* Schadow
37. Apices of styliform processes boot shaped (Figure A49 to Figure A57). 38
– Apices of styliform processes variable but never boot shaped. 44
38. Male and female meso- and metanotum with scattered dark bristles. 39
– Male and female meso- and metanotum without dark bristles. 41
39. Male proctiger almost symmetrical (Figure A50). Lengths of styliform processes unequal, right much longer than left. Length, 3.8–4.3 mm (♂,♀). ....*H.* (s. str.) *dianae* Zettel
– Male proctiger distinctly asymmetrical (Figure A52 and Figure A53). Lengths of styliform processes about the same. 40
40. Meso- and metanotum with few short dark bristles (Figure A55). Male terminalia (Figure A52). Length, 4.5–4.8 mm (♂), 4.3–4.8 mm (♀). ....*H.* (s. str.) *darwini* Herring
– Meso- and metanotum with numerous long dark bristles (Figure A56). Male terminalia (Figure 53). Length, 3.8–4.2 mm (♂), 3.8–3.9 mm (♀). ..... *H.* (s. str.) *acherontis* Polhemus
41. Male proctiger distinctly asymmetrical, lateral finger-like projection on the right very much longer than the left (Figure A54). Length, 4.0–5.1 mm (♂,♀). ....*H.* (s. str.) *herringi* Polhemus & Cheng
– Male proctiger almost symmetrical, lateral finger-like projection on the right not much longer than the left (Figure A49, Figure A51, Figure A57). 42



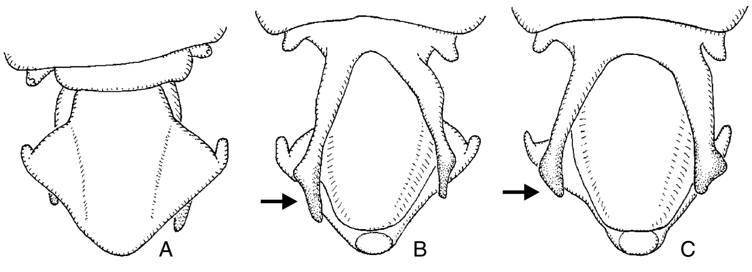
47 *proavus*



48 *maculatus*



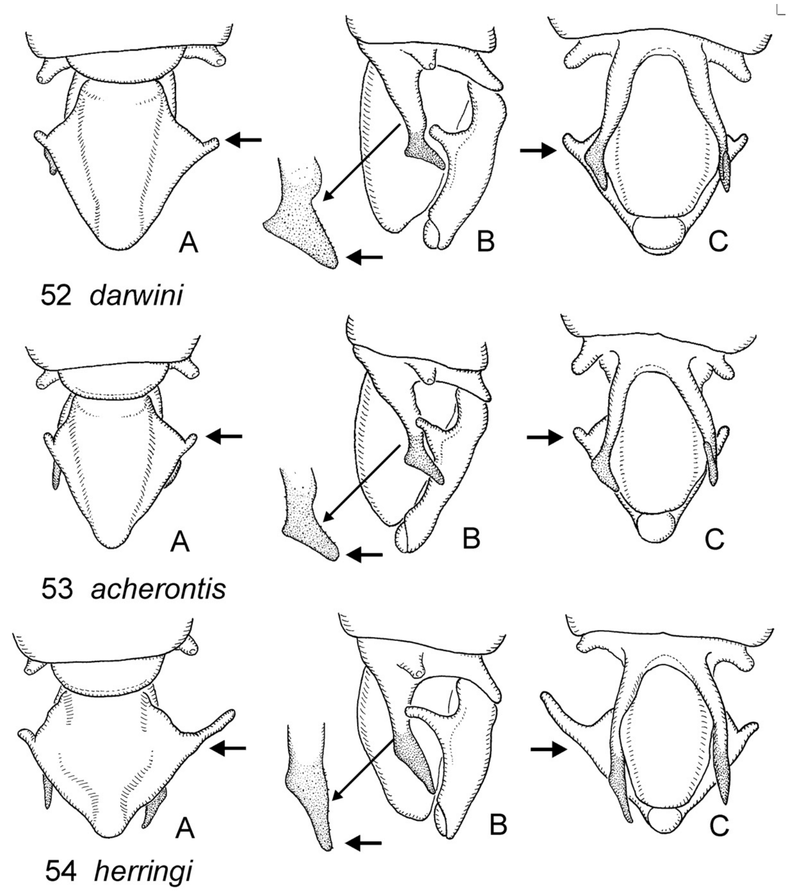
49 *peronis*



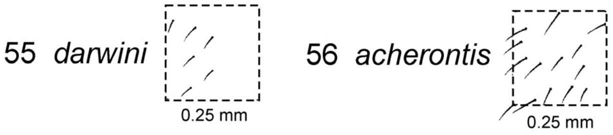
50 *dianae* 51 *murphyi*

Figures A47–A51 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (47) *H.* (s. str.) *proavus*. (48) *H.* (s. str.) *maculatus*. (49) *H.* (s. str.) *peronis*. (50) *H.* (s. str.) *dianae*. (51) *H.* (s. str.) *murphyi*.

42. Apices of styliform processes almost symmetrical, only slightly widened (Figure A57). Length, 3.5 mm (♂,♀). .... *H.* (s. str.) *sexualis* Distant
– Apices of styliform processes asymmetrical, distinctly widened (Figure A49 and Figure A51). 43
43. Small species, length, 3.8–4.2 mm (♂,♀). Male terminalia (Figure A49). ....*H.* (s. str.) *peronis* Herring
– Large species, length, 4.5 mm (♂), 4.6 mm (♀). *H.* (s. str.) *murphyi* Polhemus & Polhemus
44. Both male and female completely yellow beneath. 45
– Male not completely yellow beneath, thoracic venter dark. 46



Figures A52–A54 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (52) *H.* (s. str.) *darwini*. (53) *H.* (s. str.) *acherontis*. (54) *H.* (s. str.) *herringi*.



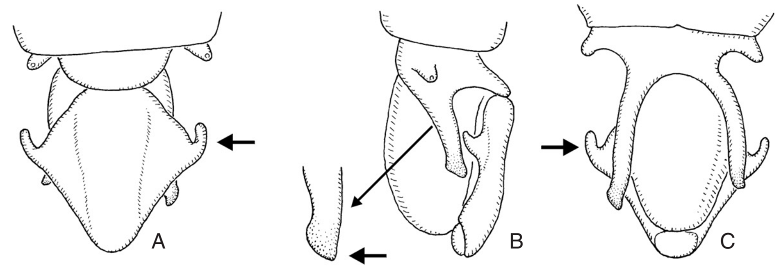
Figures A55–A56 Part of mesonotum with dark bristles. (55) *H.* (s. str.) *darwini*. (56) *H.* (s. str.) *acherontis*. (Modified from Andersen & Weir 1994b.)

45. Fore tarsal segment I, 0.5 times (♂) or 0.6 times (♀) length of segment II. Male terminalia (Figure A58). Hind coxae of female shorter, only about 2.0 times as long as wide. Length, 4.3–5.2 mm (♂,♀). .... *H.* (s. str.) *regalis* Carpenter

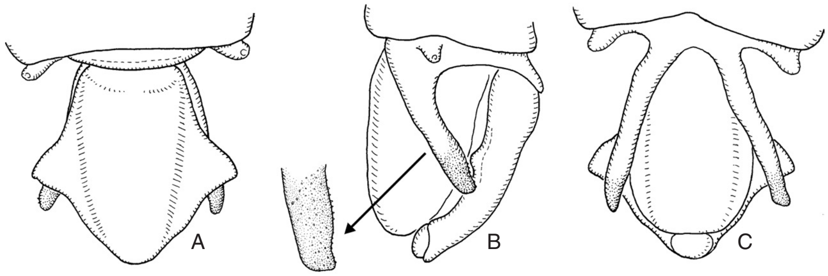
– Fore tarsal segment I, 0.4 times (♂) or 0.5 times (♀) length of segment II. Male terminalia (Figure A59). Hind coxae of female very long, about 3.0 times as long as wide. Length, 3.7–4.9 mm (♂,♀). .... *H.* (s. str.) *whiteleggei* Skuse

46. Male and female with scattered black bristles on meso- and metanotum. Male terminalia (Figure A60). Length, 3.5–4.0 mm (♂), 4.2–4.5 mm (♀). .. *H.* (s. str.) *robustus* Barber

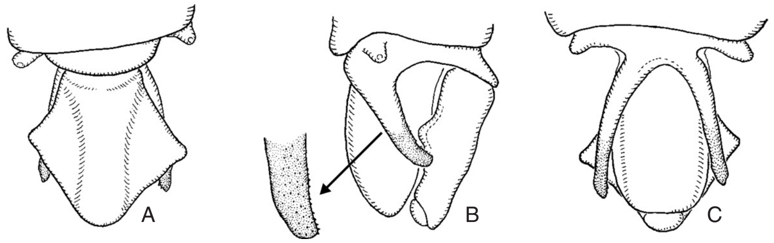
– Male and female without scattered black bristles on meso- and metanotum. 47



57 *sexualis*



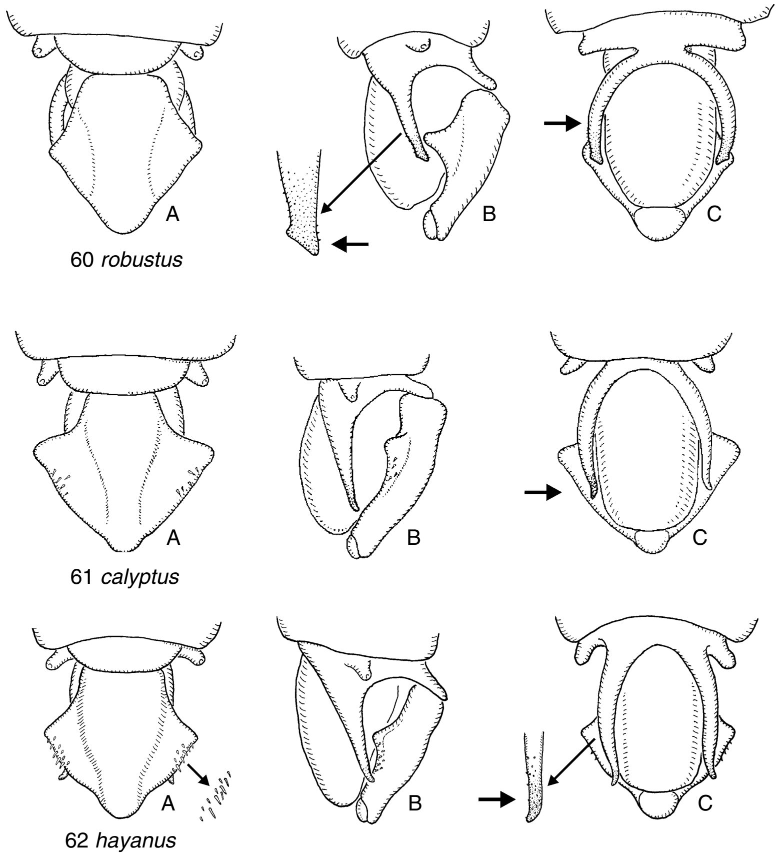
58 *regalis*



59 *whiteleggei*

Figures A57–A59 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (57) *H.* (s. str.) *sexualis*. (58) *H.* (s. str.) *regalis*. (59) *H.* (s. str.) *whiteleggei*. (58 and 59 modified from Andersen & Weir 1994b.)

47. Male proctiger with a distinct patch of black spines on each side (Figure A61 and Figure A62). Styliform processes almost symmetrical, their apices diverging (Figure A66). Female more than 4.3 mm long. 48
 – Male proctiger without patch of black spines or with only a group of small spines (Figure A61). Styliform processes not symmetrical and not diverging apically. Female less than 4.3 mm long. 49
48. A pair of V-shaped sutures delimiting mesonotum from metanotum. Posterolateral margins of male pronotum swollen. Male terminalia (Figure A61). Female elongate-cylindrical, over twice as long as broad; base of antennae dark; no pale yellow stripe on fore femora. Length, 4.4–5.0 mm (♂,♀). .... *H.* (s. str.) *calyptus* Herring
 – No sutures delimiting mesonotum from metanotum. Posterolateral margins of male pronotum not swollen. Male terminalia (Figure A62). Female more rounded, hardly twice as long as broad; base of antennae yellow; pale yellow stripe on fore femora. Length, 3.7–4.6 mm (♂,♀). ....*H.* (s. str.) *hayanus* White



Figures A60–A62 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left (60) or right (62) styliform process shown at higher magnification. (60) *H.* (s. str.) *robustus*. (61) *H.* (s. str.) *calyptus*. (62) *H.* (s. str.) *hayanus*. (62 modified from Andersen & Weir 1994b.)

49. Styliform processes of male diverging posteriorly, apices slender (Figure A63). Female without black bristles on hind acetabula. [Small brown species, length, 3.3–3.5 mm (♂,♀).] .... *H.* (s. str.) *bryani* Herring

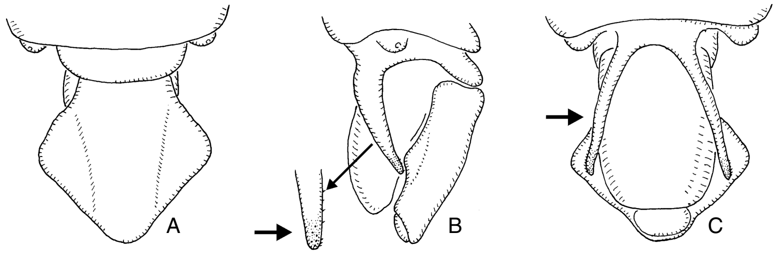
– Styliform processes of male converging posteriorly, apices expanded (Figure A64 and Figure A65). Female with a group of stout black bristles on hind acetabula. 50

50. Yellow marking on head extensive, extending uninterrupted to bases of antennae (see Figure 16), leaving a lyre- or arrow-shaped spot in center. Male terminalia (Figure A65). Length, 3.0–4.4 mm (♂,♀). .... *H.* (s. str.) *melleus* Linnavuori

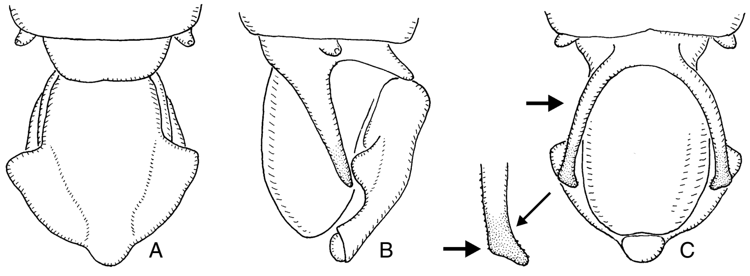
– Yellow marking on head usually crescent shaped, never reaching bases of antennae (see Figure A18), occasionally with yellow spots at bases of antennae. Male terminalia (Figure A64). Length, 3.7–4.0 mm (♂,♀). .... *H.* (s. str.) *poseidon* Herring

51. Left styliform process curved outward, visible from above (Figure A66 to Figure A68). Female with yellow colouration of venter limited to abdominal segments and sometimes middle acetabula. 52

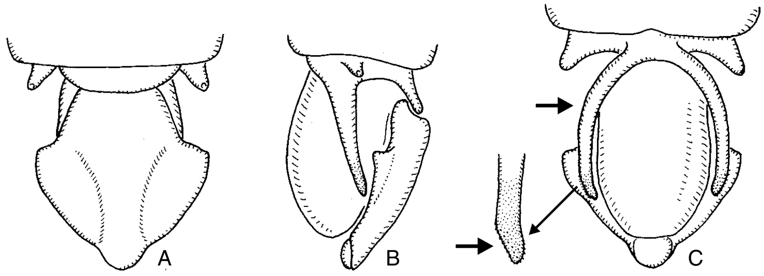
– Left styliform process not curved outward, not visible from above (Figure A69 to Figure A71). Female with yellow colouration of venter more extensive, usually extending forward to bases of forelegs. 54



63 *bryani*



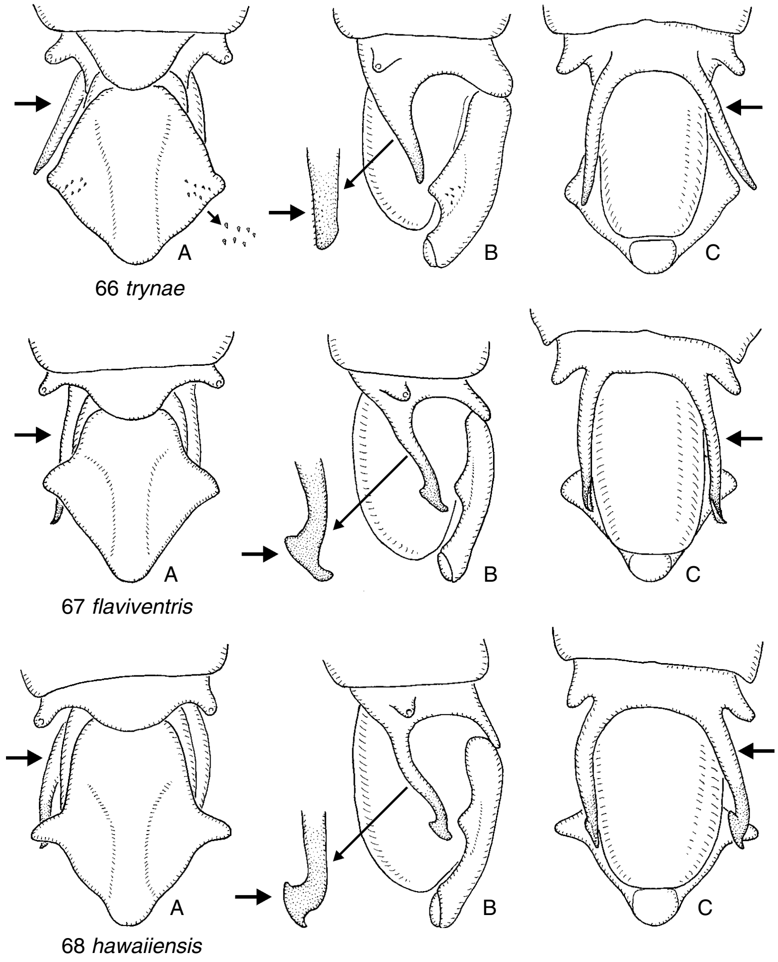
64 *poseidon*



65 *melleus*

Figures A63–A65 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left (63) or right (64 and 65) styliform process shown at higher magnification. (63) *H.* (s. str.) *bryani*. (64) *H.* (s. str.) *poseidon*. (65) *H.* (s. str.) *melleus*.

52. Apices of styliform processes of male simple (Figure A66). Proctiger with lateral groups of minute spine-like hairs. Length, 4.3–4.5 mm (♂,♀). .... *H.* (s. str.) *trynae* Herring
– Apices of styliform processes of male, shoe shaped (Figure A67 and Figure A68). Proctiger without lateral groups of spine-like hairs. 53
53. No dense, stiff black bristles on hind acetabula. Undersurface of middle acetabula with a wide yellow band. Male terminalia (Figure A67). Hind coxae of female short and straight, never 1.5 times as long as fore tarsal segment I. Length, 4.2–4.6 mm (♂,♀). .... *H.* (s. str.) *flaviventris* Eschscholtz
– Dense, stiff black bristles present on hind acetabula. Undersurface of middle acetabula without a wide yellow band. Male terminalia (Figure A68). Hind coxae of female elongate and curved, at least 1.5 times as long as fore tarsal segment I. Length, 4.2–4.8 mm (♂,♀). .... *H.* (s. str.) *hawaiiensis* Usinger
54. Right styliform process of male curved outward and visible from above (Figure A69); lateral edges of male proctiger rounded. Female with median triangular area on meso- and metasternum, entire abdominal venter, and basal third of fore femora, yellow. Length, 5.0–5.7 mm (♂), 4.7–4.9 mm (♀). .... *H.* (s. str.) *galatea* Herring



66 *trynae*

67 *flaviventris*

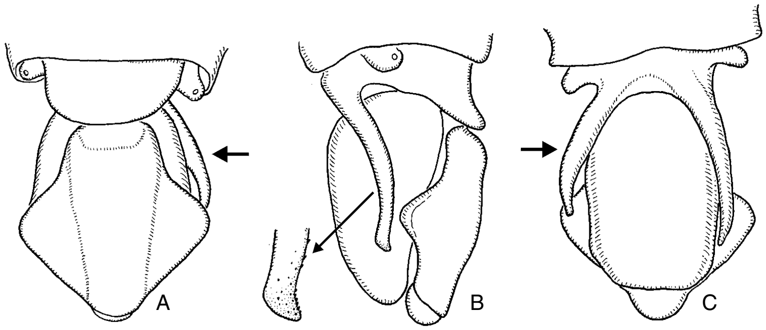
68 *hawaiiensis*

Figures A66–A68 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (66) *H.* (s. str.) *trynae*. (67) *H.* (s. str.) *flaviventris*. (68) *H.* (s. str.) *hawaiiensis*.

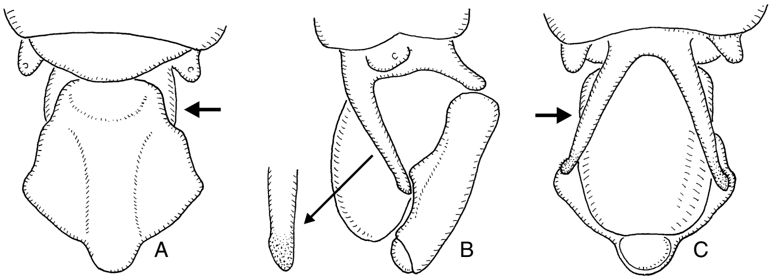
– Right styliform process of male not curved outward and not visible from above (Figure A70 and Figure A71); lateral edges of male proctiger angular. Yellow colouration of female venter more limited, basal parts of fore femora dark. 55

55. Large species, length, 5.0–5.2 mm (♂, ♀). Male terminalia (Figure A70). Female without black bristles on meso- and metanotum. .... *H.* (s. str.) *japonicus* Esaki

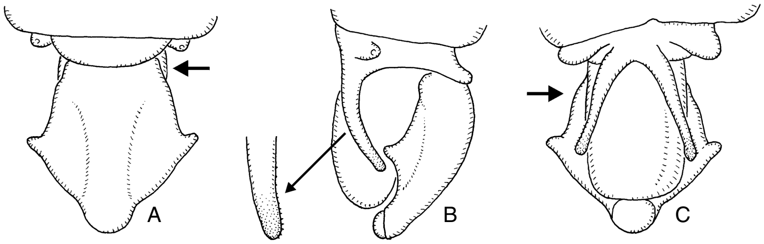
– Small species, length, 3.6–4.0 mm (♂, ♀). Male terminalia (Figure A71). Female usually with black bristles on meso- and metanotum. ....*H.* (s. str.) *panope* Herring



69 *galatea*



70 *japonicus*



71 *panope*

Figures A69–A71 *Halobates* spp., abdominal end of male in dorsal (A), lateral (B), and ventral (C) views, with apex of left styliform process shown at higher magnification. (69) *H.* (s. str.) *galatea*. (70) *H.* (s. str.) *japonicus*. (71) *H.* (s. str.) *panope*. (69 modified from Andersen & Foster 1992.)

APPENDIX 2

Species checklist and distribution of *Halobates* and allied genera (Heteroptera: Gerridae)

Synonyms listed by Herring (1961) have been updated. Unpublished, new distributional records from the authors and from J. T. Polhemus (with permission) are marked with asterisks (*). Locations not checked by us are marked with question marks (?).

Genus ***Asclepios*** Distant, 1915

Asclepios annandalei Distant, 1915 — India (Calcutta, Tamil Nadu), Malaysia (Sabah*), Singapore, Sri Lanka, Thailand (Phuket)

Asclepios apicalis Esaki, 1924 — Taiwan, Vietnam*

Asclepios shiranui coreanus Esaki, 1930 — China (Hong Kong), Korea

Asclepios shiranui shiranui Esaki, 1924 (syn. *Asclepios coreanus miyamotoi* Esaki, 1937) — Japan (Honshu, Kyushu)

Genus ***Austrobates*** Andersen & Weir, 1994

Austrobates rivularis Andersen & Weir, 1994 — Australia (Queensland)

Genus ***Halobates*** Eschscholtz, 1822

Subgenus ***Halobates*** Eschscholtz, 1822

Halobates acherontis Polhemus, 1982 — Australia (Northern Territory)

Halobates alluaudi Bergroth, 1893 — Aldabra and Cosmoledo Atolls, Ile Europa, Kenya, Mozambique*, Madagascar*, Seychelles (Curieuse, La Dique, Mahé, Praslin)

Halobates browni Herring, 1961 — Solomon Is. (New Georgia Is.)

Halobates bryani Herring, 1961 — Fiji Is.

Halobates calyptus Herring, 1961 — Indonesia (Bacan, Ceram*, Halmahera*, Irian Jaya, Sulawesi), Papua New Guinea, Philippines (Dinigat, Leyte, Luzon, Mindanao, Mindoro), Solomon Is.*

Halobates darwini Herring, 1961 — Australia (Northern Territory, Queensland), Papua New Guinea

Halobates dianae Zettel, 2001 — Philippines (Luzon)

Halobates elephanta Andersen & Foster, 1992 — Andaman Sea, India (Mumbai)

Halobates esakii Miyamoto, 1967 — Brunei, Indonesia (Halmahera*), Singapore*, Thailand (Phuket)

Halobates fijiensis Herring, 1958 — Fiji Is.

Halobates flaviventris Eschscholtz, 1822 (syn. *Halobates eschscholtzi* Herring, 1961) — Aldabra and Cosmoledo Atolls, Comores, Ethiopia, Ile Europa, Kenya, Madagascar, Mozambique*, Seychelles (Amirantes), Somalia, Tanzania, Caroline Is. (Palau Is.), Christmas Is., India (Bay of Bengal), Indonesia (Java, S. Moluccas), Sri Lanka, Thailand (Phuket, Gulf of Thailand), Vanuatu, Vietnam

Halobates formidabilis (Distant, 1910) — Andaman Is., Andaman Sea, India (east coast), Maldives, Sri Lanka

Halobates galatea Herring, 1961 — Arabian Sea, India (Goa), Sri Lanka*

Halobates germanus White, 1883 — Indian Ocean, West and central Pacific Ocean, Aldabra and Cosmoledo Atolls, Australia (Northern Territory, Queensland, Western Australia), China, India (Bay of Bengal), Iran, Japan, Madagascar, Malaysia (Johore), Maldives, Red Sea (Israel, Oman, Saudi Arabia), Singapore, Somalia

Halobates hawaiiensis Usinger, 1938 — Hawaiian Is., Marquesas Is., Society Is., Tuamotu Arch.

Halobates hayanus White, 1883 (syn. *Halobates australiensis* Malipatil, 1988) — Australia (Northern Territory, Queensland), China*, Indonesia (Bali, Irian Jaya, Java, Sulawesi*, Moluccas), Malaysia (Johore), Nicobar Is., Papua New Guinea, Philippines (Luzon, Mindanao, Palawan), Red Sea (Djibouti, Egypt, Saudi Arabia, Sudan, Yemen), Singapore, Thailand (Phuket), Vietnam

Halobates herringi Polhemus & Cheng, 1982 — Australia (Northern Territory, Queensland), Indonesia (Irian Jaya)

Halobates japonicus Esaki, 1924 — Japan (Amami-Oshima, Iriomote Is., Miyako Is., Ryukyu Is., Shikoku)

Halobates katherinae Herring, 1958 — Loyalty Is., New Caledonia, Vanuatu*

Halobates kelleni Herring, 1961 — American Samoa (Tutuila), Western Samoa (Upolu)

Halobates maculatus Schadow, 1922 — Bismarck Arch., Indonesia (Sulawesi*), Papua New Guinea, Solomon Is. (Florida Is., New Georgia Is., Rennell Is.)

Halobates mariannarum Esaki, 1924 — Caroline Is. (Kusaie, Palau Is., Ponape, Truk, Yap), Mariana Is. (Guam, Rota), Marshall Is. (Arno Atoll)

Halobates matsumurai Esaki, 1924 — China (Chusan Is.), Japan (Honshu, Kyushu), Korea, Taiwan

Halobates melleus Linnavuori, 1971 (syn. *Halobates mangrovensis* Schmidt & Müller, 1973) — Red Sea (Erithrea*, Israel, Sudan, Yemen*)

Halobates micans Eschscholtz, 1822 — Atlantic Ocean between 40°N and 30–40°S, Caribbean Sea, Indian Ocean between 20°N and 10–40°S, western Pacific Ocean between 30°N and 5°S, central and eastern Pacific Ocean between 20°N and 20°S; Aldabra & Cosmoledo Atolls, Australia (New South Wales, Northern Territory, Queensland, Western Australia), Cape Verde Is., China, Japan, Sri Lanka, Taiwan, Gulf of Mexico

Halobates murphyi Polhemus & Polhemus, 1991 — Indonesia (Irian Jaya), Papua New Guinea

Halobates nereis Herring, 1961 — Caroline Is. (Palau Is.), Papua New Guinea

Halobates panope Herring, 1961 — New Caledonia

Halobates peronis Herring, 1961 — Bismarck Arch.*, Solomon Is. (Florida Is., New Georgia Is., San Cristobal, Santa Isabel)

Halobates poseidon Herring, 1961 — Aldabra and Cosmoledo Atolls, Kenya, Madagascar*, Mozambique*, Tanzania

Halobates princeps White, 1883 (syn. *Halobates ashmorensis* Malipatil, 1988) — Australia (Northern Territory, Queensland), Caroline Is. (Palau Is.), Malaysia (Penang?, Sabah), Indonesia (Halmahera, Java, Madura, S. Moluccas, Sulawesi, Sumbawa*), Solomon Is.

Halobates proavus White, 1883 — Indonesia (Bacan*, Ceram, Halmahera, Java, Sulawesi), Malaysia (Pahang, Penang), Nicobar Is., Philippines (Mindanao), Singapore, Solomon Is., Thailand (Phuket), Vanuatu

Halobates regalis Carpenter, 1892 — Australia (Queensland, Western Australia)

Halobates robustus Barber, 1925 — Galápagos Is.

Halobates salotae Herring, 1961 — Tonga Is. (Tongatapu)

Halobates sericeus Eschscholtz, 1822 — Pacific Ocean between 40 and 5°N and between 5 and 40°S; Australia (Lord Howe Is., Queensland), China, Hawaiian Is., Japan (Honshu), Vietnam

Halobates sexualis Distant, 1903 — Malaysia (Kelantan?), Sri Lanka

Halobates sobrinus White, 1883 — East Pacific Ocean between 30°N and 5°S, Colombia, Costa Rica

Halobates splendens Witlaczil, 1886 — Southeast Pacific Ocean between 10°N and 30°S, Chile

Halobates tethys Herring, 1961 — Mauritius

Halobates trynae Herring, 1964 — Malaysia (Negeri Sembilan*), Nicobar Is., Thailand (Phuket), Singapore*

Halobates whiteleggei Skuse, 1891 — Australia (New South Wales, Queensland)

Halobates zephyrus Herring, 1961 — Australia (New South Wales, Queensland)
Subgenus ***Hilliella*** China, 1957
Halobates lannae Andersen & Weir, 1994 — Australia (Northern Territory, Western Australia)
Halobates mjobergi Hale, 1925 — Australia (Northern Territory, Queensland, Western Australia), Papua New Guinea
Halobates robinsoni Andersen & Weir, 2003 — Australia (Western Australia)