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REDESCRIPTION OF *MACROPHTHALMUS BOTELTOBAGOE* AND *M. HOLTHUISI* WITH NOTES ON THEIR ECOLOGY (BRACHYURA: OCYPODIDAE)

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A B S T R A C T

Macrophthalmus boteltobagoe (Sakai, 1939) is shown to be specifically distinct from *M. holthuisi* Serène, 1973. The two species differ in many morphological characters and, as well, are shown to prefer different habitats—*M. boteltobagoe* lives in holes in limestone and scrapes algae for food, whereas *M. holthuisi* lives on soft mud around mangroves and is a sediment feeder. These different feeding strategies are reflected in the structure and setation of the claws, and in the conformation of the gastric mills.

Sakai (1939) described *Hemiplax boteltobagoe* based on a single specimen collected from Lan-yu Island, off southeastern Taiwan. Barnes (1976) tentatively placed *Macrophthalmus boteltobagoe* (Sakai, 1939) into the subgenus *Mareotis*, basing his decision on Sakai's description. Barnes (1977), in the concluding paper of his revisionary series, considered *M. boteltobagoe* to be a valid species allied to *M. erato* de Man, 1888, and *M. quadratus* A. Milne Edwards, 1873. Komai *et al.* (1995) examined *Macrophthalmus* in Phuket, Thailand, and established a new subgenus, *Paramareotis*, to include *M. boteltobagoe*, *M. quadratus*, and *M. erato*.

Serène (1973) described his new species *M. holthuisi* based on specimens from the Biak Island, western New Guinea. He considered it to be allied to *M. boteltobagoe*. However, when Barnes (1977) examined newly collected specimens of *M. boteltobagoe* from Okinawa Island, he considered them to be identical to Serène's description and figures of *M. holthuisi*, and therefore considered *M. holthuisi* to be a junior synonym.

Field work by one of us (T.K.) in various localities in the Ryukyu Islands and south to Taiwan has revealed the presence of two distinct species of *Macrophthalmus*, living in different biotopes, which correspond exactly with the original descriptions of both *M. holthuisi* and *M. boteltobagoe*. The identity of our new specimens of *M. boteltobagoe* has been confirmed by comparison with pictures of the holotype now in the Kanagawa Prefectural Museum of Natural History. The species is here redescribed in order to clarify and stabilise its identity. Because of the quite different habitats occupied by these two similar species (rocky shore *versus* muddy mangrove environments), we have taken the opportunity to compare morphological characters of the chelipeds and gastric mills in order to understand how each species has uniquely adapted to its own niche.

MATERIALS AND METHODS

All the specimens of *M. boteltobagoe* and *M. holthuisi* studied here were obtained from the Ryukyu Islands, southern Japan. The gonopods, tips of chelae, and gastric mills were examined using a Scanning Electron Microscope (HITACHI, S–530). Abbreviations: NSMT, National Science Museum, Tokyo; QM, Queensland Museum. Measurements are of carapace breadth (c.b.) followed by carapace length.

SYSTEMATICS

Ocypodidae Dana, 1851
Macrophthalminae Dana, 1852

Macrophthalmus (*Paramareotis*) *boteltobagoe* (Sakai, 1939)
Figs. 1; 2A, C, E, G; 3A; 5A, B; 6A, B; 7A; 8A

Hemiplax boteltobagoe Sakai, 1939: 628–630, text-fig. 99a–d.

Macrophthalmus (*Hemiplax*) *boteltobagoe*—Barnes, 1967: 204 (name only).—Sakai, 1976: 616, 617, text-fig. 338a–d.

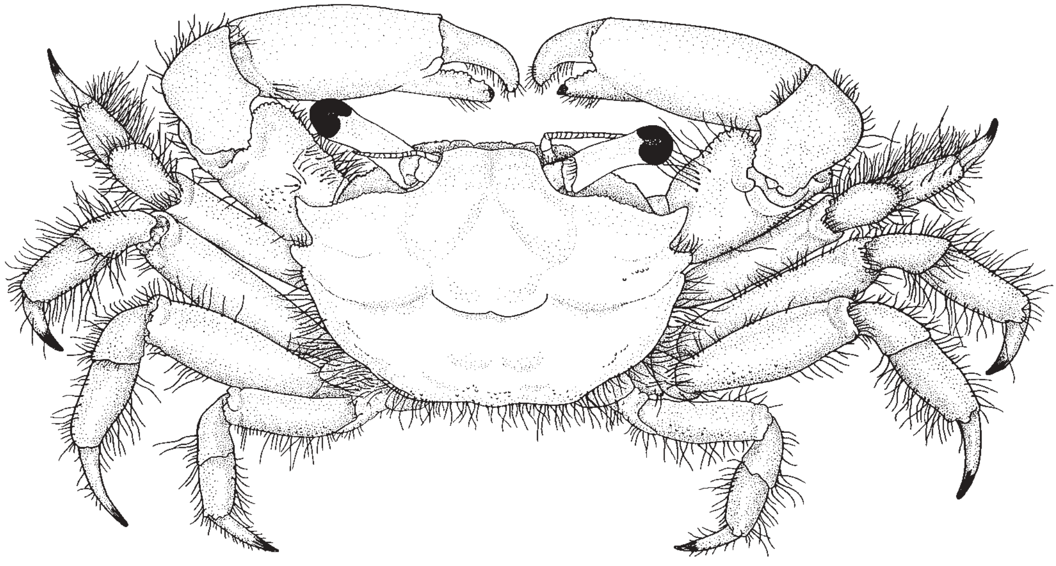

Fig. 1. *Macrophthalmus boteltobagoe* (Sakai, 1939), QM–W24805, ♂ (8.1 mm c.b.).

Macrophthalmus (*Mareotis*) *boteltobagoe*—Barnes, 1977: 270, 271.—Takeda, 1981: 74.—Huang *et al.*, 1992: 148, 149, fig. 8.

Macrophthalmus (*Paramareotis*) *boteltobagoe*—Komai, Goshimo, and Murai, 1995: 139, 140.

Material Examined.—NSMT Cr.8060, 3 ♂♂ (7.2 × 5.7, 6.5 × 4.6, 3.0 × 2.2 mm), 4 June 1974, coll. by Y. Nakasone, Minatogawa, Okinawa Is., Japan; QM–W24805, ♂ (8.1 × 5.6 mm), Horikawa, Tamagusuku, Okinawa Is., Ryukyus, 18 Aug. 1990, coll. T. Kosuge; QM–W24806, ♂ (7.3 × 5.2 mm), same data as QM–W24805; QM–W24807, ♀ (7.6 × 5.2 mm), same data as QM–W24805; QM–W24808, 5 ♂♂ (8.3 × 5.9, 7.9 × 5.6, 8.9 × 6.2, 6.5 × 4.9, 8.4 × 5.6 mm) same data as QM–W24085; QM–W24809, 5 ♂♂ (4.0 × 2.8, 6.1 × 4.2, 5.0 × 3.7, 3.9 × 2.9, 4.7 × 3.4 mm), 5 ♀♀ (4.6 × 3.4, 5.5 × 4.1, 4.8 × 3.5, 4.2 × 3.1, 4.7 × 3.5 mm), Taketomi Is., Aug. 1998, coll. T. Kosuge; QM–W24903, 5 ♂♂ (7.0 × 4.9, 5.5 × 3.9, 5.8 × 4.2, 4.1 × 2.9, 4.5 × 3.3 mm), 3 ♀♀ (6.4 × 4.8, 5.4 × 3.8, 5.0 × 3.4 mm), Minatogawa, Gushikami, Okinawa Is., Ryukyus, 15 Sept. 1993, coll. T. Kosuge; QM–W24906, ♂ (5.0 × 3.5 mm), Asato, Nakagusuku Bay, Okinawa Is., Ryukyus, 12 June 1990, coll. T. Kosuge.

Description.—Carapace with greatest carapace breadth across exorbital angles; width about 1.4 (1.33–1.46) times length. Front deflexed, bilobed, with well-defined median groove, 0.25 times maximum carapace width, lateral margins divergent posteriorly. Upper orbital border granular, moderately sinuous. Ocular peduncle relatively stout, of moderate length, not projecting beyond tip of exorbital angle. Lower orbital border (Fig. 2C) with inner half consisting of ridge composed of 19 or 20 rounded granules; granules followed by broad, rounded, projecting lobe with outer slope much longer than inner; major lobe confluent with smaller projecting triangular lobe positioned below middle of cornea, outer slope of smaller lobe bearing none to several small pointed granules; separated from exorbital angle by broad, smooth sulcus. Female lower orbital border granular, granules becoming slightly larger and more spaced laterally; without lobes developed. Central region of epistome with distinct median projection. Margin of carapace slightly convergent posteriorly; lateral margin relatively straight. Three anterolateral teeth, first two distinct, third indistinct. Exorbital angle pronounced, narrow, triangular, curved forward, broadly separated from second lateral tooth by deep U-shaped sulcus; second tooth triangular, projecting outwards in line with exorbital angle, and slightly forwards. Third tooth at base of second lateral tooth, weak, granular, separated by small notch. Dorsal surface finely granular, granules more conspicuous anterolaterally, forming fine epibranchial line, and 2 or 3 very short, granular, posterobranchial ridges; regions moderately well defined, with variable, but sparse, covering of setae. Lateral margins fringed with short setae; setae longer on second and third lateral teeth.

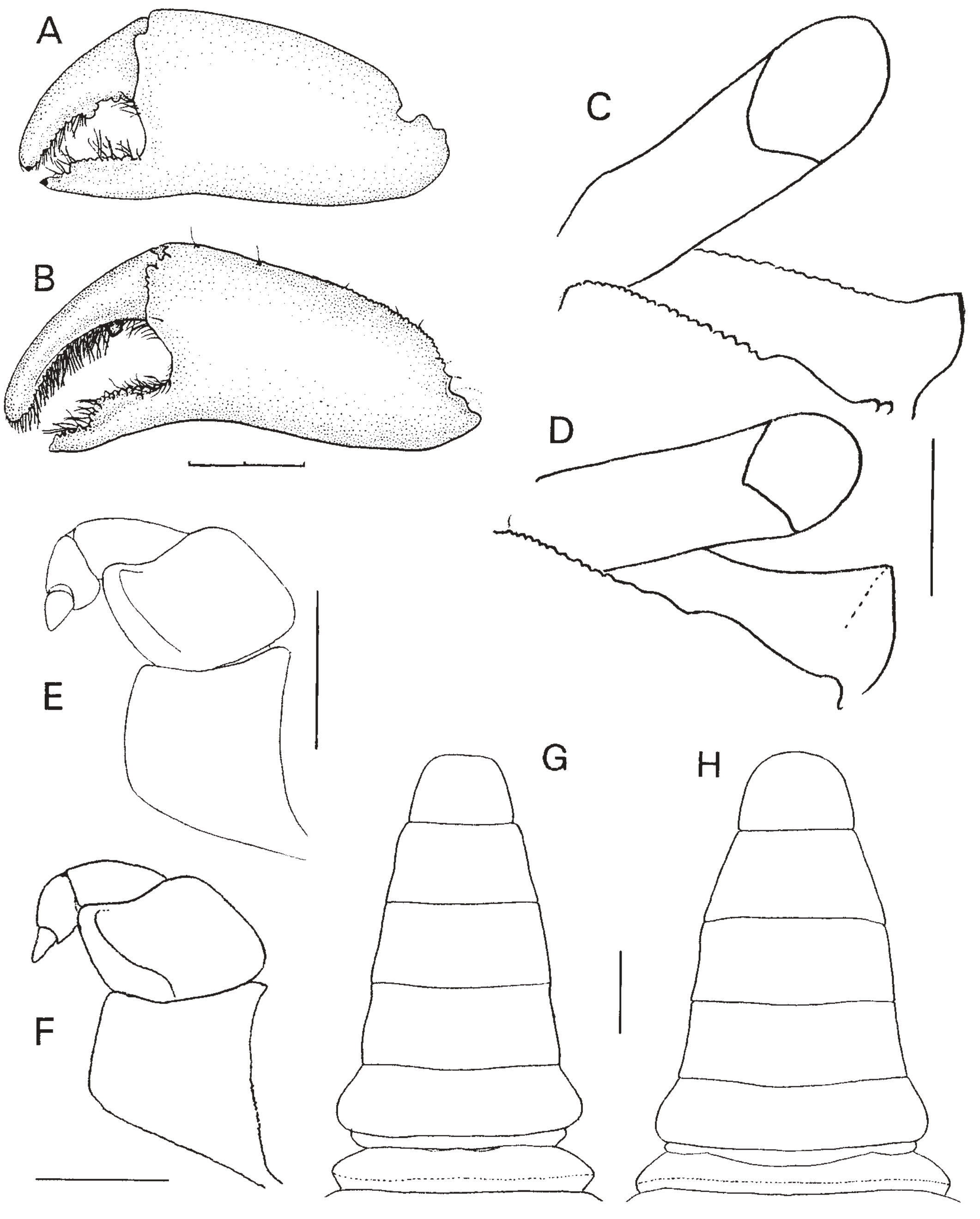

Fig. 2. A, C, E, G: *Macrophthalmus boteltobagoe* (QM–W24805); B, D, F, H: *Macrophthalmus holthuisi* (QM–W24810). A, B, male chelae; C, D, orbits, showing structure of stridulatory crests on infraorbital margin; E, F, third maxillipeds; G, H, male abdomens. Scale lines: A, B = 2 mm; C–H = 1 mm.

Third maxilliped (Fig. 2E) with merus slightly smaller than ischium. Internal margin of ischium straight, external margin slightly concave; internal margin of merus slightly convex, outer margin with slight median concavity.

Male cheliped merus with broad distal convexity on inner margin, otherwise unarmed;

inner margin with moderately long, raised, oblique crest arising from near proximal end and reaching almost level with middle of inner margin, apparently stridulatory but not obviously corneous as in other species; long feathery setae may obscure crest. Carpus subrectangular, widening distally, about 1.4 times longer than wide; inner angle produced into blunt spine. Palm relatively stout and moderately swollen, height about half length (including fixed finger) (Fig. 2A). Inner surface unarmed, smooth, without setae. Outer surface microscopically granular, appearing smooth, upper and lower margins rounded, without granular rows. Fingers relatively short. Fixed finger not deflexed; shallow concavity on lower margin of palm behind base of fixed finger; outer surface appearing smooth; inner margin with row of long setae over distal half; cutting margin with raised row of pointed granules extending over proximal two-thirds of finger. Tips of fingers corneus. Dactylus stout, only slightly curved; outer surface smooth, or microscopically granular; upper margin rounded; cutting margin with one prominent tooth positioned at about proximal third, usually single but sometimes bearing accessory tooth; second small prominent tubercle between main tooth and base; lower surface of finger bearing prominent setae over distal half. Female cheliped poorly developed, short; lacking differentiated teeth on fingers; without stridulatory ridge on merus.

Walking legs relatively short and stout. Third walking leg (measured dorsally) about 1.2 times maximum carapace width; merus about 3 times longer than wide; propodus about 2.1 times longer than wide. Surface of leg segments sparsely and finely granular, granules becoming coarser and denser along dorsal and ventral margins; subdistal tooth on dorsal margins of meri poorly defined. Legs sparsely covered with long setae; first walking leg with thick fur of setae on ventral surface of propodus and distoventral end of carpus.

Male abdomen (Fig. 2G) moderately narrow; third segment about 3.7 times wider than long, slightly narrower than first segment. Male first gonopod with apical process forming a simple flange (Fig. 3A).

Remarks.—The holotype of *Macrophthalmus boteltobagoe* is now housed in the Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa, Japan (Registration No. NH107888). According to the picture in the published catalogue of the donated T. Sakai specimens (Muraoka, 1998), it appears that the holotype specimen is now missing all limbs except for two legs on the left-hand side. It is clear, however, that our specimens are conspecific with the type.

At the localities in the Ryukyu Islands where *M. boteltobagoe* has been found during the present study (and as reported in Kosuge (1991)), offshore coral reefs form a barrier preventing rough wave action from reaching the landward platforms where the crabs occur. On shores where the landward platform is more directly exposed to waves, the cover of blue-green algae and sediments is absent, and the crabs are also not present. Lan-yu Island, the type locality recorded by Sakai (1939), is surrounded by fringing reefs, but the intertidal limestone platforms are more directly washed by wave action than is preferred by this species in the Ryukyu Islands. Lan-yu Island was visited by one of the authors (TK), in April 1993, but *M. boteltobagoe* was not found even though its likely habitat was inspected carefully. Further, Huang *et al.* (1992) also mentioned that there have been no further collections of *M. boteltobagoe* made in this region since the type specimen. The holotype was sent to T. Sakai via two different people, so it is possible that there may have been a mistake made concerning the original locality. It is also possible that the habitat at Lan-yu Island is only marginally suitable, but on rare occasions a few specimens of *M. boteltobagoe* are able to become established. The presence of the species on Lan-yu Island must therefore remain in question pending its possible future recollection.

Distribution.—Lan-yu Island (presumed type locality); Ryukyu Islands.

Habitat and Ecology.—As described in Kosuge (1991), *Macrophthalmus boteltobagoe* inhabits limestone rocky shores utilizing holes drilled into the limestone by other boring animals, e.g., sipunculans. This crab prefers the middle intertidal zone where the rock surface is covered by blue-green algae and fine sediments. The most densely populated sites are in shallow depressions where sea water remains for 2 or 3 hours after the

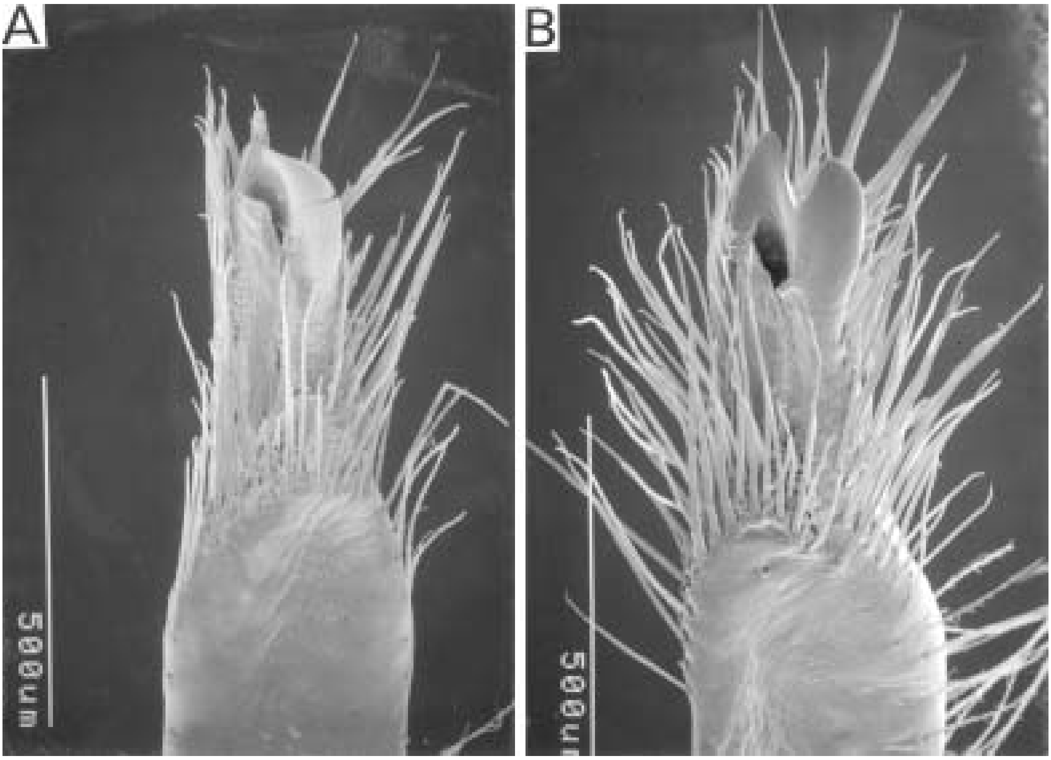

Fig. 3. Scanning electron micrographs of apex of male first gonopods: A, *Macrophthalmus boteltobagoe* (QM–W24806); B, *Macrophthalmus holthuisi* (QM–W24811).

site is exposed. The crabs forage by scraping the surface algae while still wet, but return to their burrows once the surface dries.

Macrophthalmus (*Paramareotis*) *holthuisi* Serène, 1973
Figs. 2B, D, F, H; 3B; 4; 5C, D; 6C, D; 7B; 8B

Macrophthalmus holthuisi Serène, 1973: 99–106, text-fig. 1a, b, pl. 1, fig. A–C, pl. 2, fig. A, B.—Barnes, 1976: 147–150; 1977: 270, 271.

Material Examined.—QM–W24811, ♂ (8.9 × 6.4 mm), mouth of the Shiira-gawa River, Iriomote Is., Ryukyus, 14 Jul 1996, collected by T. Kosuge; QM–W24812, ♀ (8.5 × 6.4 mm), same data as QM–W24811; QM–W24813, 5 ♂♂ (8.6 × 6.1, 6.5 × 4.9, 4.4 × 3.5, 7.4 × 5.3, 7.6 × 5.5 mm), 5 ♀♀ (8.9 × 6.4, 8.4 × 6.3, 8.2 × 6.0, 9.0 × 6.4, 8.7 × 6.2 mm), same data as QM–W24811; QM–W24904, 5 ♂♂ (9.8 × 6.8, 7.6 × 5.5, 10.8 × 7.4, 7.4 × 5.4, 6.6 × 4.9 mm), 5 ♀♀ (8.6 × 6.3, 8.2 × 5.7, 8.2 × 6.0, 9.4 × 6.6, 7.9 × 5.7 mm), Mihara, Iriomote Is., Ryukyus, 14 Jul 1996, collected by T. Kosuge; QM–W24905, 5 ♂♂ (11.4 × 7.9, 8.6 × 6.3, 10.3 × 7.5, 6.6 × 4.8, 7.8 × 5.7 mm), 5 ♀♀ (10.3 × 7.6, 9.1 × 6.9, 8.9 × 6.6, 7.6 × 5.8, 7.5 × 5.7 mm), Anparu, Nagura, Ishigaki Is., Ryukyus, 30 May 1998, collected by T. Kosuge; QM–W24810, ♂ (8.9 × 6.4 mm), same data as QM–W24905.

Description.—Greatest carapace breadth across third anterolateral teeth; width about 1.4 (1.26–1.46) times length. Front deflexed, bilobed, with shallow median groove, about 0.26 times maximum carapace width, lateral margins divergent posteriorly. Upper orbital border finely granular, sinuous. Ocular peduncle relatively stout, of moderate length, not projecting beyond tip of exorbital angle. Lower orbital border with inner half consisting of ridge composed of 7–12 rounded granules; granules followed by broad, rounded, projecting lobe with outer slope much longer than inner; major lobe confluent with smaller projecting triangular tooth positioned below exorbital angle; separated from exorbital angle by broad smooth sulcus (Fig. 2D). Female lower orbital border granular, granules becoming slightly larger and more spaced laterally; without lobes developed. Central region of epistome with distinct median projection. Lateral margin of carapace moderately convex. Three anterolateral teeth, all distinct. Exorbital angle pronounced, broad, triangular,

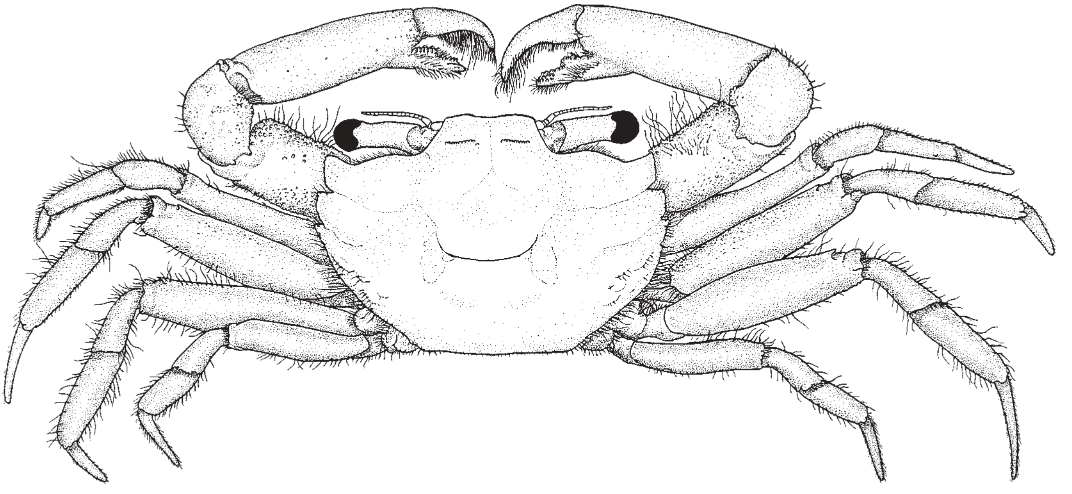

Fig. 4. *Macrophthalmus holthuisi* Serène, 1973, QM–W24810, ♂ (8.9 mm c.b.).

curved forward, separated from second lateral tooth by narrow V-shaped sulcus; second tooth similar in shape and size to first. Third tooth smaller, sharply projecting, clearly separated by broad V-shaped incision. Dorsal surface mostly smooth; pair of slightly raised, finely granular postfrontal crests; finely granular, low epibranchial ridges; 3 or 4 short, granular, posterobranchial ridges; regions moderately well defined; without setae except for sparse, very short setae on posterobranchial region. Lateral margins fringed with short setae; setae longer on second and third lateral teeth.

Third maxilliped (Fig. 2F) with merus slightly smaller than ischium. Internal margin of ischium straight, external margin slightly concave; internal margin of merus slightly convex, outer margin with slight median concavity.

Male cheliped with merus elongated, markedly projecting beyond anterolateral margins; with broad distal convexity on inner margin, otherwise unarmed; inner margin granular, with short, raised, slightly oblique, corneous, stridulatory crest towards proximal end; long feathery setae may obscure crest. Carpus subrectangular, widening distally, about 1.3 times longer than wide; inner angle pointed, granular, but not produced into distinct spine. Palm relatively stout and moderately swollen, height less than half (about 0.45 times) length (including fixed finger); inner surface unarmed, mostly smooth, but becoming granular towards inferior proximal part; without setae proximal to fingers; outer surface smooth, upper and lower margins rounded. Fingers moderately long, dactyl about three-quarters length of palm in midline. Fixed finger deflexed; outer surface appearing smooth; inner upper part covered with mat of long feathered setae; cutting margin granular, with strongly differentiated, raised, elongate tooth medially. Tips of fingers corneous. Wide proximal gape. Dactylus moderately stout, only slightly curved; outer surface smooth; upper margin rounded; cutting margin with one prominent peg-like tooth near base; prominent thick narrow mat of feathered setae distal to tooth, clearly visible from front (Fig. 2B).

Female cheliped poorly developed, short; lacking differentiated teeth on fingers; without stridulatory ridge on merus.

Walking legs relatively narrow and elongated. Third walking leg (measured dorsally) about 1.5 times maximum carapace width; merus about 4 times longer than wide; propodus about 2.9 times longer than wide. Surface of leg segments smooth, finely granular along dorsal and ventral margins; subdistal tooth on dorsal margins of meri sharp, well defined. Legs sparsely covered with long setae; first walking leg with conspicuous covering of short setae on proximal half of merus, and a thick fur of long setae on ventral surface of propodus, dactylus, and distal end of carpus.

Male abdomen (Fig. 2H) moderately broad;

third segment about 4.1 times wider than long, distinctly narrower than first segment. Male first gonopod with apical process deeply bilobed (Fig. 3B).

Remarks.—Serène (1973) recorded *M. holthuisi* from the mangroves of Biak Island, western New Guinea. Our present specimens, from the Yaeyama Group in the Ryukyu Islands, are also exclusively associated with mangroves, and thus it appears that the species is specialised for this habitat.

Barnes (1977) proposed that *M. holthuisi* be considered a junior synonym of *M. boteltobagoe,* after examining specimens he believed to be *M. holthuisi* collected by Y. Nakasone in 1977 from the Yuhi River, Okinawa Island. There are no mangroves in the Yuhi River, but limestone bedrock exists at the mouth, which is the perfect habitat for *M. boteltobagoe.* Except for Barnes' record there have been no other verified *M. holthuisi* specimens recorded from Okinawa Island. We were able to examine the specimens discussed by Barnes, now lodged in the National Science Museum, Tokyo (three males, NSMT Cr.8060), and found them to be true *M. boteltobagoe,* not *M. holthuisi.* This was unexpected because Barnes (1977: 270) clearly stated that his specimens differed in a number of points from the type description of Sakai but were absolutely identical to the detailed description and figure of *M. holthuisi* given by Serène, such that "but for their geographical separation . . . the specimens could well have come from the same population." The differences between the two species are, however, quite striking, and the original descriptions and figures of both species are clear and accurate.

Distribution.—Biak Island, western New Guinea (type locality), north to the Yaeyama Group, Ryukyu Islands, Japan.

Habitat.—In the present study, *M. holthuisi* was found in shallow depressions occurring at the fringe of mangroves composed of *Rhizophora stylosa* Griffith, 1854, and *Bruguiera gymnorhiza* (L.) Lamarck. Fallen mangrove leaves usually occurred in depressions, and crabs walk in and out from below the leaves. The crabs do not appear to have a particular burrow in which to take refuge. It was observed that the crab feeds by scooping the sediment.

Discussion

Serène (1973) remarked that *M. holthuisi* was most closely related to three other species that apparently are able to stridulate, viz., *M. erato* De Man, 1888, *M. quadratus* A. Milne Edwards, 1873, and *M. boteltobagoe* (Sakai, 1939). Of these species, Serène noted that the stridulatory ridge was placed in a different position on the merus of *M. holthuisi* than on *M. erato* or *M. quadratus* which were themselves similar. The exact position of this ridge in *M. boteltobagoe* was not known at that time, but the present observations have found that it is very similar in its placement to *M. holthuisi,* suggesting a close affinity between these two species. All four species were later included in a new subgenus, *Paramareotis,* by Komai, Goshima, and Murai (1995).

Paramareotis is defined by: carapace subquadrate; front relatively wide (more than 0.2 times width of carapace), not strongly constricted at bases of ocular peduncles; posteromedian margin of epistome more or less convex, anterior buccal cavity with sharp median ridge; third maxilliped with merus shorter than ischium; ocular peduncles relatively stout; males with a stridulatory structure consisting of lobules on lateral part of lower orbital border and a corneous crest on inner margin of merus of cheliped (Komai *et al.,* 1995).

With the recognition of *Macrophthalmus holthuisi* as being a valid species, there are now four species included in *Paramareotis. Macrophthalmus boteltobagoe* and *M. holthuisi* have been the most easily confused but can be readily separated by the following characters.

1. In *M. boteltobagoe* maximum carapace width is between the first and second anterolateral teeth, but in *M. holthuisi* the maximum carapace width is between the third anterolateral teeth (even more accentuated in females) (cf., Figs. 1, 4).
2. The shape of the lower orbital margin differs in both species (cf., Fig. 2C, D).
3. The fixed finger of the chela is relatively straight in *M. boteltobagoe* but obviously deflexed in *M. holthuisi* (cf., Fig. 2A, B).
4. The chela is relatively shorter in *M. boteltobagoe* (cf., Fig. 2A, B).
5. The fingers of the chelipeds of *Macrophthalmus boteltobagoe* and *M. holthuisi* are shown in Figs. 2A, B, 5, 6. Males of *M. botel-*

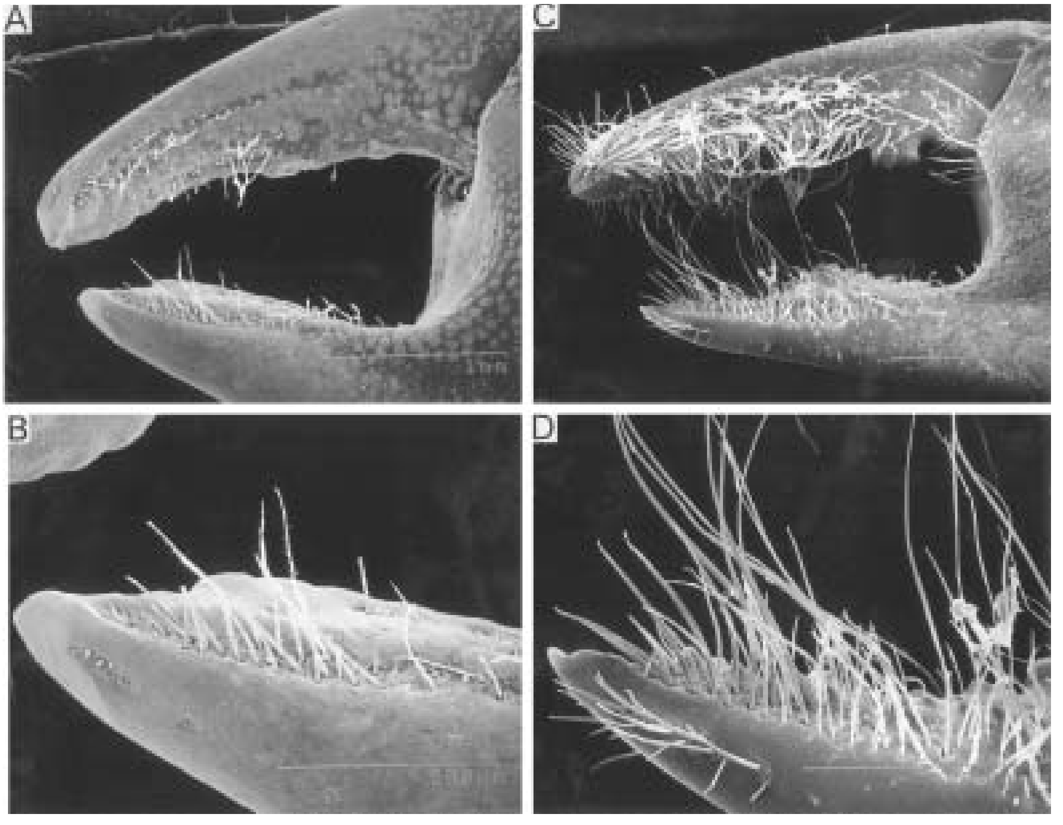

Fig. 5. Scanning electron micrographs of male chelae: A, B, *Macrophthalmus boteltobagoe* (QM–W24806); C, D, *Macrophthalmus holthuisi* (QM–W24811).

tobagoe have a few rows of relatively short setae on the mobile and immobile fingers, whereas in *M. holthuisi* the inner surfaces of both fingers are densely covered by mats of longer setae. In female *M. boteltobagoe,* the mobile finger has a row of stout setae on the inner edge, and another short row of 5–7 setae near the tip. Similarly, in female *M. holthuisi,* there are corresponding rows of setae, but these are relatively longer and thinner.

6. Both species have chitinous cusps capping the finger tips, particularly obvious in females. In female *M. boteltobagoe,* the cusp is short and restricted more to the distal end (shown as partly detached in Fig. 6B). However, in *M. holthuisi,* the cusp on the immobile finger forms a thin blade extending much further back along the cutting margin.

7. Tooth on cutting margin of fixed finger of chela is low and occasionally almost obsolete in *M. boteltobagoe*, whereas it is high and clearly defined in *M. holthuisi.*

8. Subdistal tooth on dorsal margin of meri of walking legs is poorly defined in *M. boteltobagoe* but strong and obvious in *M. holthuisi.*

9. The walking legs are noticeably shorter in *M. boteltobagoe* than in *M. holthuisi*. Third walking leg about 1.2 times maximum carapace width *versus* 1.5 times; merus of third walking leg about 3 times longer than wide *versus* 4 times; propodus of third walking leg about 2 times longer than wide *versus* 3 times.

10. Male gonopods differ: *M. boteltobagoe* has the apex forming a simple flange (Fig. 3A), whereas *M. holthuisi* has the apex deeply bilobed (Fig. 3B).

Differences in Claw Morphology

Wada (1982) compared the claw morphology of the ocypodids *Ilyoplax pusilla* (de Haan, 1835) and *Scopimera globosa* (de Haan, 1835). He found that *I. pusilla* has tufts

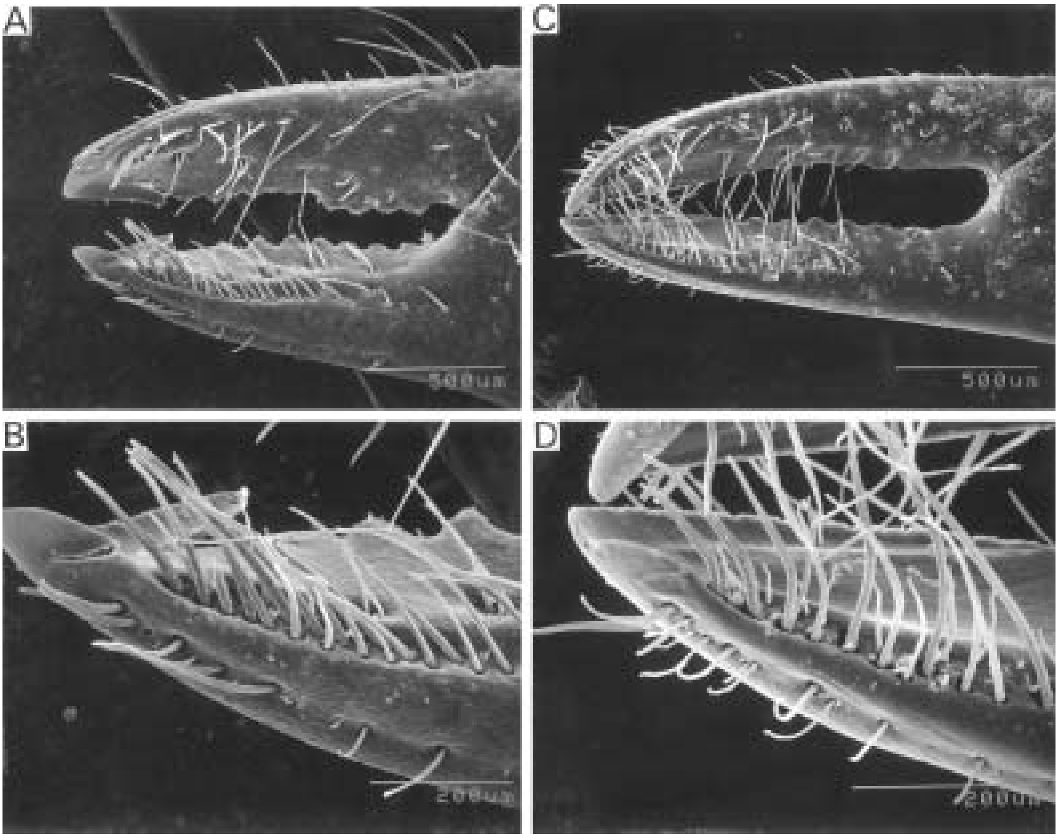

Fig. 6. Scanning electron micrographs of female chelae: A, B, *Macrophthalmus boteltobagoe* (QM–W24807); C, D, *Macrophthalmus holthuisi* (QM–W24812).

of fine setae on the claws that are not present in *S. globosa*. As the claws are the primary food-gathering organ, he interpreted this structural difference to be necessitated by different substrate preferences. *Ilyoplax pusilla* prefers silty substrates, and therefore fine setae on the finger tips would serve to trap fine mud particles during scooping. *Scopimera globosa* is found in sandier habitats, and therefore such setae would not be required and would probably be subject to abrasion.

The claws of *Macrophthalmus boteltobagoe* and *M. holthuisi* similarly show differences in morphology that reflect the different foraging habits forced by the distinctly different substrates on which they live. The fingers of *M. boteltobagoe* are less densely covered by setae than those of *M. holthuisi*. *Macrophthalmus boteltobagoe* inhabits rocky limestone shores, and the tips of its blunt fingers have a short hoof-shaped chitinous cusp for scraping algae and fine sediment layers from the hard surface—for this mode of feeding, a dense covering of setae would be superfluous. In contrast, *M. holthuisi* has long, smooth, elongate cusps, perfect for pulling across, and scooping up, the soft mudflat surface. The dense, fine setae lining the fingers then effectively trap the silt particles and associated organic matter, allowing them to be conveyed to the mouth. It is interesting that two species so similar in gross morphology have developed such different and specialised claws clearly reflecting their different modes of feeding and different habitat preferences. *Macrophthalmus boteltobagoe* still possesses some rows of stout setae on its claw, but it is probable that these primarily perform other functions not related to foraging, e.g., mouthparts grooming.

Gastric Mill

Icely and Nott (1992) showed quite dramatic differences in the structure of the gas-

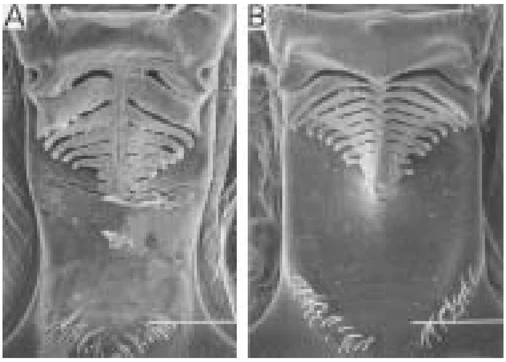

Fig. 7. Scanning electron micrographs of median tooth plate of gastric mill: A, *Macrophthalmus boteltobagoe,* ♂ (QM–W24806); B, *Macrophthalmus holthuisi,* ♂ (QM–W24811).

tric mills of four species of *Uca* (Ocypodidae: Ocypodinae) from a shore in East Africa, relating them to size distribution and organic content of the particles on which they feed.

Similarly, there are conspicuous differences between the two *Macrophthalmus* species studied here. The median tooth in both species has the transverse ridges expanded and relatively closely aligned to provide a smooth surface for the mastication of fine particles; however, in *M. holthuisi* (Fig. 7B), that feeds on very fine particle size sediments, there are 11 transverse ridges (*versus* 9 in *M. boteltobagoe*), and they are relatively narrower, almost meeting centrally. *Macrophthalmus boteltobagoe* (Fig. 7A) scrapes algae from rocky surfaces, and its median tooth is relatively flatter, broader (especially the penultimate posterior ridge), and the transverse ridges are slightly more expanded anteriorly. In *M. holthuisi,* the spines of the lateral teeth are lined with conspicuous, flexible setae (Fig. 8B), which would allow treatment of fine sediment particles in the diet, whereas in *M. boteltobagoe* these spines are almost completely lacking (Fig. 8A).

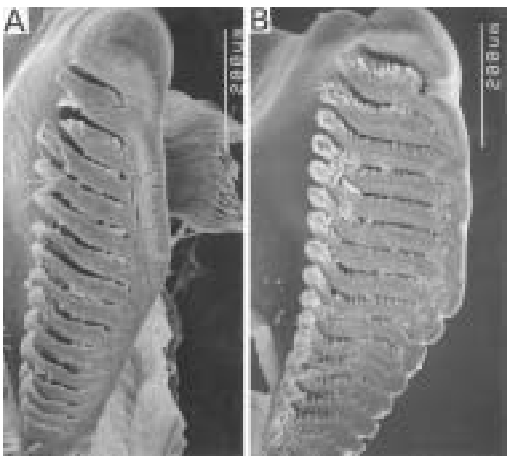

Fig. 8. Scanning electron micrographs of lateral tooth plate of gastric mill: A, *Macrophthalmus boteltobagoe,* ♂ (QM–W24806); B, *Macrophthalmus holthuisi,* ♂ (QM–W24811).

Gastric mill morphology is becoming increasingly useful in showing generic differences in grapsid and other ocypodid crabs (Yang, 1986; K. Sakai *et al.*, in press; M. Türkay, personal communication), but its usefulness in *Macrophthalmus* has yet to be determined and will require an assessment of a broad range of species.

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