SOME PSELAPHIDAE INHABITING THE MANGROVE FORESTS OF SINGAPORE AND THAILAND, WITH DESCRIPTION OF A NEW GENUS AND EIGHT NEW SPECIES

Yasuhiko Tanokuchi

ABSTRACT. - Eight new species in five genera are described, one of the genera being new. The mangrove fauna of Pselaphidae seems to be rich and entirely novel. This material is largely associated with mud-lobster (Thalassina) mound systems which provide very uneven topography. Most species are however fully intertidal. The intertidal forms have dense pilosity, long appendages and large eyes, and are flightless. Some speculations are made on the significance and consequences of this.

INTRODUCTION

Recently, Professor D.H. Murphy of the National University of Singapore and his colleagues have carried out a survey which aims to understand the ecosystem and fauna of mangrove forest. When I visited the University in 1987, he told me that pselaphid beetles were often walking on the ground in mangrove forest at low tide. Later, I had an opportunity to visit the Mandai mangrove forest in Singapore accompanied by him, and collect there. I have also been given pselaphid beetles collected in the survey. On examination, it was found the material from Singapore included seven species, all undescribed, in five genera one of which is new. In this paper are described the new genus and eight new species in all, including one belonging to the same new genus from mangrove in Thailand. Singapore locality codes refer to a map published in Murphy & Lee (in press).

The holotypes will be preserved in the Department of Entomology, British Museum (Natural History), London, United Kingdom, and the paratypes will be preserved in the author's private collections for the present.

Abbreviations used in this article are as follows: HW greatest width of head (including eyes); PW — greatest width of pronotum; PL — length of pronotum, measured along the mid-line; PA — width of pronotal apex; PB — width of pronotal base; EA — width of elytral apex; EW — greatest width of elytra; EL — length of elytra, measured along suture; SL — shoulder length of elytra; AAW — apical width of abdominal tergite 1 between lateral sulci.

Arthromelus quadratus, new species

(Figs. 1-3, 12)

Material. -Holotype - &, under decayed wet leaves plastered firmly against level sandy ground between *Thalassina* mounds, mangrove forest, Mandai Kechil, site MK3, Singapore, leg. D. H. Murphy, 18.vi.1987.

Paratypes - 3 δ , 10° , same data as holotype; 5 δ , 2° , same locality as holotype, leg. D. H. Murphy, 19.xi.1987.

Description. - Length: male (Fig. 1) 1.3 mm, female 1.4 mm (from apical margin of clypeus to apex of last abdominal tergite), greatest width: 0.5 mm.

Body small and parallel-sided with large quadrate head, small prothorax and fairly large hind body. Colour dark brown to yellowish brown, while apical segments of antennae, palpi and apices of legs are yellowish brown. Body surface covered with short and dense pubescence; elytra vaguely foveolate. Inner wing narrowed.

Head large, quadrate, evidently wider than long, and parallel-sided behind antennal tubercles, with large eyes and widely emarginate base; vertical field moderately convex and faint mid-striation; frontal furrows deep throughout and divergent posteriad with small foveae at a little behind middle; sides subparallel though lateral vertical carinae emarginate, with eyes extended, large and fully three times as long as genae in male; frons emarginately depressed; antennal tubercles gently convex with obtusely reflexed margin continuous with clypeus; clypeus gently protruding, with margin more or less sharpened at tip and angulate on each side, bearing a spatulate protuberance on the middle portion in male; labrum fairly transverse, but rapidly tapering towards shallowly emarginate tip in male; maxillary palpi (Fig. 12) short, but apical segment almost as long as lateral margin of head; antennae slender, reaching to about the middle of elytra, with scape compressed cylindrical and tip dentate, segment 2 five-eighths as long as scape, segment 3-10 somewhat globate, segments 3-6 and 8 nearly same in size, segment 7 a little larger than each of them, the length of the club of last three segments 4:5:9.

Pronotum subcordate and moderately convex, slightly narrower than head, a little wider than long, widest at about middle, and more strongly contracted towards apex than towards base; PW/HW 0.64+, PW/PL 1.14+=, PW/PA 1.60, PW/PB 1/40+; surface moderately convex between lateral striae though compressed at base in front of basal carinae, which have complicated sinuations: a transverse sinuation on each side, a strongly emarginate one surrounding the compression at middle and a contracted one posteriad; lateral striae subparallel except in feebly emarginate middle portion; sides abruptly protruding just behind anterior margin to basal third, each being bordered by feeble arcuation and slight obliquity between obtuse angles in front and behind, and then narrowed towards base, which is feebly arcuate with narrow rim; apex almost straight though middle portion sinuate, being provided with indistinct narrow rim. PB/PA 1.12+; lateral surfaces each with a longitudinal stria at middle, bearing two foveoli near base on each side across the striation.

Elytra subquadrate, transverse, widest at about three-fifths from base though almost parallel-sided, and slightly divergent behind shoulders towards apices; EW/PW 1.58+, EW/EL 1/22+, EA/SL 1.10+; surface gently convex, with broad sutural convexity gradually narrowed towards apex, bearing two deep foveae on each elytron near base and faint discal stria feebly arcuate, reaching to apical third; shoulders rather gently convex, each end posteriad edged with carina and groove; prehumeral borders almost straight and

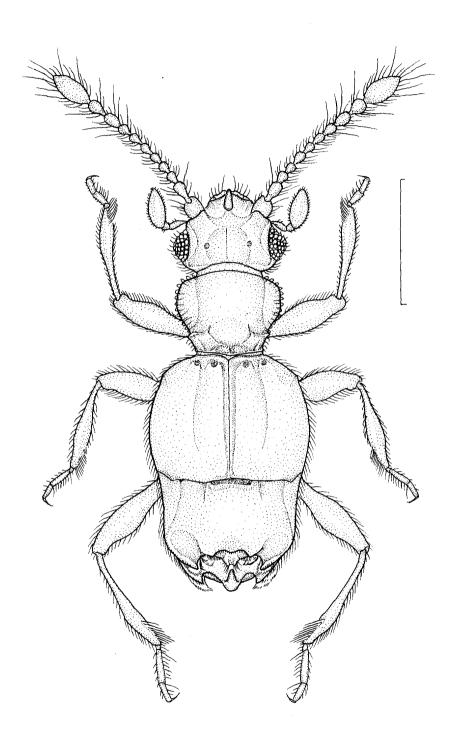
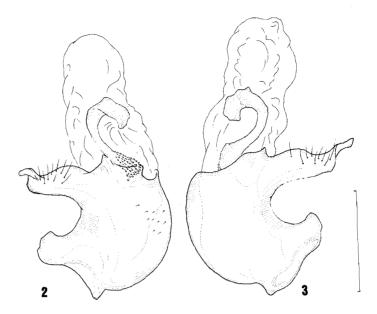


Fig. 1. Arthromelus quadratus, new species. Male. Scale: 0.4 mm.



Figs. 2-3. Male genitalia of Arthromelus quadratus, new species. 2, left lateral view, 3, right lateral view. Scale: 0.1 mm.

oblique; sides widely arcuate, continuous with feebly sinuate apical margin; lateral carinae in contact with the margin of shoulders.

Abdomen relatively short, obtusely rounded posteriad and surface gently convex on disc; tergite 1 transverse, narrower than elytra, about four-fifths as long as elytra, with basal carinae separated by half length of disc and lateral striae divergent behind basal third; tergites 1 and 2 with conspicuous secondary sexual characters in male: tergite 1 deeply grooved on extremity with shallowly ovate depression on each side of surface, posterior border deeply emarginate with sinuation and produced into a small protuberance in the groove; tergite 2 flattened and produced into a plate, whose border is deeply emarginate at each side of the middle capitate protuberance.

Legs stout and relatively long, with second segment of meso- and meta-tarsi prolonged.

Male genital organ (Figs. 2, 3) small and heavily sclerotized. Aedeagus one-third as long as elytra, more or less bowl-shaped, moderately curved ventrad, with a large process produced preapically and large orifice opening at both ends; base shortly cylindrical, though somewhat extended on the ventral side, and provided with large basal orifice at posterior end; ventral process broad, slightly attenuated with sinuation, the apical portion narrowly produced into a twisted lobe blunt at the extremity, bearing nine short setae on apical half. Inner sac armed with an elongate recurved copulatory piece about two-thirds as long as adeeagus, its basal portion with sclerotized teeth and apex down turned.

Etymology. - The species name refers to the large, quadrate head.

Remarks. - This small species was gregarious under wet dead leaves which lay sparsely on the mangrove forest floor beside eroding *Thalassina* mounds at about 2.5 m. above chart datum. At this level the ground is inundated about 40 times per month and is

continuously exposed for at most four consecutive days in a cycle. The collections were made in day-time. At no time was this species seen active on the surface, though they dispersed rapidly when the leaf was lifted. Whether A. quadratus is nocturnal has not been established. However it has large eyes, long antennae and well developed palpi for its genus which may indicate nocturnal habits. The long pubescence may hold air when immersed.

Batriscenites celer, new species

(Figs. 4-6, 10)

Material. - Holotype: &, Mandai Besar site MB3, Singapore, leg. D. H. Murphy, 13.viii.1987.

Paratypes: 1 & 7 \(7 \), same data as holotype; 3 \(9 \), same locality as holotype, leg. D. H. Murphy, 18.vi.1987; 64 \(8 \), 35 \(9 \), running on sides and lower part of *Thalassina* mounds, mangrove forest, Mandai Kechil site MK3, Singapore, leg. Y. Tanokuchi, 19.xi.1987; 2 o, running on sides and lower part of *Thalassina* mounds, mangrove forest, Mandai Kechil site MK3, Singapore, leg. D. H. Murphy, 19.xi.1987.

Description. - Length: male (Fig. 4) 2.1-2.2 mm, female 2.2-2.3 mm (from apical margin of clypeus to apex of last abdominal tergite), greatest width 0.7-0.8 mm.

Relatively large species, with elongate appendages and hind body. Colour dark reddish brown and polished, but antennae, legs and palpi more or less yellowish brown. Body surface more or less granulate, covered with long and dense pubescence. Inner wings are present, though less developed.

Head large, subquadrate, slightly wider than long and hardly convex above, with frontal furrows shallow throughout and slightly divergent in front and behind; vertical field rather gently convex with faint carina along mid-line and lateral foveoli at basal fourth; sides shortly oblique, having very large eyes which posses two-thirds in sides and extended, and lateral vertical carinae subparallel though emarginate preapically; antennal tubercles moderately convex with roundly reflexed margin; frons gently depressed, continuous with obtuse clypeus, the border feebly angulate on each side; labrum transverse, tapering towards emarginate tip in male; maxillary palpi (Fig. 10) elongate due to segments 2 and 4, each equal to the combined length of antennal segments 1-3, and with apical segment swollen; antennae long and stout, reaching half length of body or a little more with scape broad towards apex, last three segments forming a obscure club, segment 9 inflated a little before middle, segment 10 enlarged preapically and last segment slenderly ovate, the length of segments decrease in the order of 11>1>9>10>7=2>3=4=5=6>8.

Pronotum subcordate, almost as wide as head, a little wider than long, usually widest at about two-thirds from base, and more strongly contracted towards apex than towards base; PW/HW 1.03+, PW/PL 1.04+, PW/PA 2.06+, PW/PB 1.38+; surface moderately convex between lateral striae, which are very slightly convergent towards apices with gentle sinuation, having shallowly transverse sulcus with feeble emargination at middle and small two foveli on each basal side; sides rather strongly arcuate at apical two-thirds, and then contracted with reflexed border towards posterior ends; base reflexed and almost straight except for feebly arcuate middle portion; apex almost straight, PB/PA 1.50.

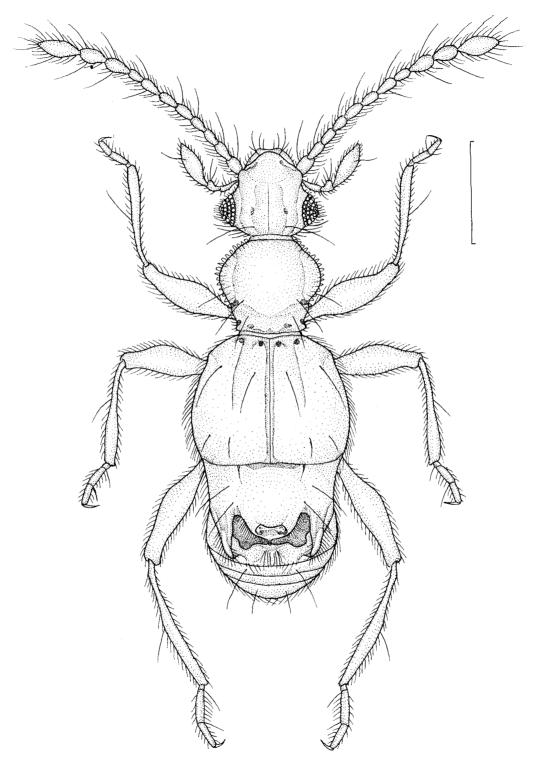
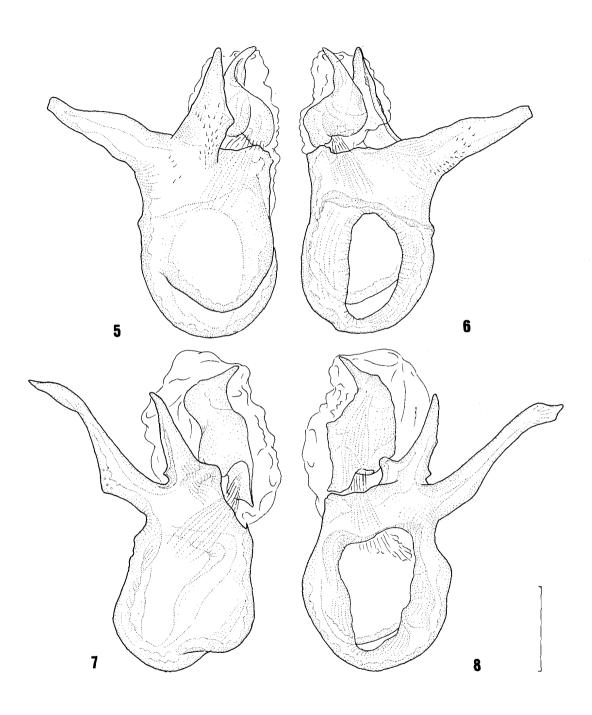


Fig. 4. Batriscenites celer, new species. Male. Scale: 0.5 mm.



Figs. 5-8 Male genitalia of Batriscenites spp. 5-6 B. celer, new species; 7-8 B. humicola, new species 5.7, dorsal view; 6, 8, ventral view.

Grant Stew, 6, 8, ventral view.

Elytra subquadrate, transverse, widest at about apical third and gently divergent behind shoulders; EW/PW 1.30+, EW/EL 1.18+, EA/SL 1.20+; surface moderately convex, though compressed in basal middle and behind shoulders, with sutural convexity narrowly parallel-sided, and each elytron bearing two small lateral foveae near base, of which the outer one is produced into a sulcoid impression, reaching to three-fifths from base; shoulders moderately convex and bordered by strongly arcuate carinae behind with prehumeral borders oblique; sides either very feebly emarginate or obliquely straight behind shoulders, and widely arcuate towards apices; base oblique with rounded margin, apices slightly rounded on each elytral margin. Mesocoxal cavity protuberant and flabelliform behind the middle constriction. Metasternum depressed along mid line, more strongly so in male than in female.

Abdomen relatively narrow, elongate and gradually tapering towards apex in female, but abruptly contracted in male behind segment 1, and surface gently convex; tergite 1 narrow but transverse, with basal carinae being separated by a half width of tergite 1, slightly narrowed apically with reflexed sides in female, and in male, gently dilated and transversely grooved at apical third, the upper surface produced into an arm-like ridge on each side and a strongly arcuate median lobe with an apical pit, and the under surface more or less flattened with a transverse excavation.

Legs stout and elongate.

Male genital organ (Figs. 5, 6) large and rather heavily sclerotized. Aedeagus about half as long as elytra, cup-shaped, parallel-sided though more or less expanded towards large apical orifice, and widely convex on dorsal surface, forming two protrusions, with two processes prolonged on the apical right side and base rounded; basal part hardly expanded, about two-thirds as long as aedeagus and apical walls truncate with largely ovate basal orifice; long process extended on right side, gradually narrowed towards apex with truncate tip, and short process prolonged in front, which is sharpened and internal margin angulate in the middle portion. Inner sac armed with a large copulatory piece; copulatory piece heavily sclerotized, about half as long as aedeagus, attenuated and twisted, with the apical part thinly prolonged and arcuate.

Etymology. - The specific epithet is Latin for "swift", referring to the high activity shown by these beetles once the ground is exposed by low tide.

Remarks. - The forest floor at the site shows the very uneven topography typically associated with *Thalassina*. The depressions contained mixed leaf litter and wood on wet soil, with streams and pools edged by soft mud. There, B. celer was running actively together with mid-sized ants but showed no association with them. This relatively large species is characterized by fairly large eyes, narrow abdomen, reduced inner wings, long pubescence on surface and elongate appendages (see DISCUSSION).

The genus *Batriscenites* was placed by Jeannel (1952) near the large genus *Batriscenites* as currently defined, by the conformation of appendages, secondary sexual characters and genital organs, but differ from described forms. Notably, the basal orifice of aedeagus only opens ventrally and is closed on the dorsal surface which has a two-stepped convexity; the inner sac armature is distinctive and the copulatory piece rather large. Whether to consider these as conservative or advanced features is undecided. Many problems still remain in the systematics of this genus complex which may require further subdivision.

Batriscenites humicola, new species

(Figs. 7-9)

Material. - Holotype - &, site MK3, on Thalassina mounds, mangrove forest, Mandai Kechil, Singapore, leg. D. H. Murphy, 18.vi.1987.

Paratypes: 1 &, 14, same data as holotype.

Description. - Length: male (fig.9) 2.2-2.3 mm, female 2.4-2.5 mm (from apical margin of clypeus to apex of last abdominal tergite), greatest width: 0.7-0.8 mm.

Externally similar to *B. celer*, new species, but appearing longer on average due to prolonged thorax and abdomen, the head evidently constricted at eye field, and elytra more broad towards apices, with slender appendages and more flattened surface. Markedly different from the preceding species in the conformation of male genitalia and appearance of secondary sexual characters. Colour light reddish brown, though antennae and legs more or less yellowish; apical segments of antennae, palpi and tarsi yellowish brown. Surface as in *B. celer*.

Head as in *B. celer*, but vertical field rather gently convex throughout, with frontal furrows vague, bearing vertical foveae at basal two-fifths and median carina conspicuous; sides fairly constricted at a level of large eyes, and then dilated at antennal tubercles; frons less depressed, continuous with strongly arcuate clypeus; maxillary palpi elongate, with segment 2 slender, and terminal segment the longest, widest at apical third; antennae slender and longer than those of *B. celer*, reaching at three-fifths from base of elytra, with segment 2 rather strongly narrowed near base and segment 9 gently expanded in preapical portion, the length of segments decrease in the order of 11>1>9=10>5=7>2=3=4=6=8.

Pronotum similar to B. celer, though slightly longer than wide and widest at about middle or little before that level, sides moderately extended and its margin arcuate at apical two thirds, surface gently convex though more or less compressed in middle portion, bearing usually shallow fovea near base, vague basal transverse carina and lateral striations, which are very faint and feebly arcuate; PW/HW+ 1.04, PW/PL+ 0.94, PW/PB 1.38+, PB/PA 1.50; Elytra larger than B. celer, though otherwise similar to that of the latter; EW/PW 1.62+, PW/PL 1.18+, EA/SL 1.32+; surface less convex and more smooth on disc, bearing distinct discal striae, which are subparallel to mid line and either reaching to about middle or a little beyond that level; prehumeral borders oblique and sides more divergent posteriad than those of B. celer; apical margin of each elytron feebly emarginate. The mesocoxal protuberance transversely fan-shaped, in contact with shallow sulcus at metasternum. Abdomen more elongate than that of B, celer due to prolonged segment l with a little more elevated disc, and segments 2-4 gradually contracted towards apex, though each segment more or less inflated at middle portion; second sexual characters appeared on tergites I-2: tergite I slightly narrowed towards apex and reflexed sides forming another plate in male, apical margin of which widely arcuate, but abruptly reflexed at middle portion forming obtuse peak, tergite 2 very short with bi-convex margins in male. Legs as in B. celer, though longer due to elongate tarsi.

Male genital organ (Figs. 7, 8) basically similar to that of *B. celer* differing in details. Aedeagus fairly large, about three-fourths as long as elytra, expanded in the middle portion and slightly attenuated, with dorsal surface two-stepped in the basal third; basal part expanded and emarginate on apical walls, with basal orifice somewhat oblong; dorsal margin of apical orifice emarginate; narrow process prolonged, being inclined to the right

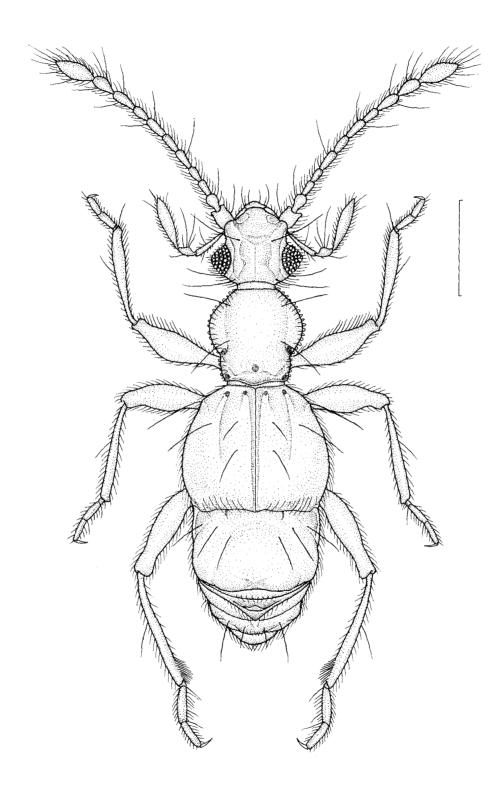
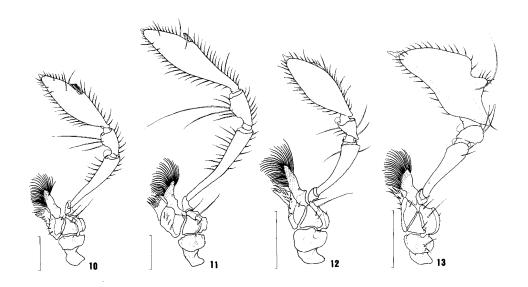


Fig. 9. Batriscenites humicola, new species. Male, Scale: 0.5 mm.



Figs. 10-13. Maxilla of pselaphid spp., ventral views. 10, Batriscenites celer, new species; 11, Batrisocenus foveiterminalis, new species; 12, Arthromelus quadratus, new species; 13, Berlara bella, new species.

with terminal dilatation and rather short process obliquely extended in front, apex narrowly sharpened and base protuberant both on internal and external margins. Inner sac armed with fairly large copulatory piece; copulatory piece broad, two-thirds as long as aedeagus, somewhat gutter-shaped, with apex narrowly produced on left face.

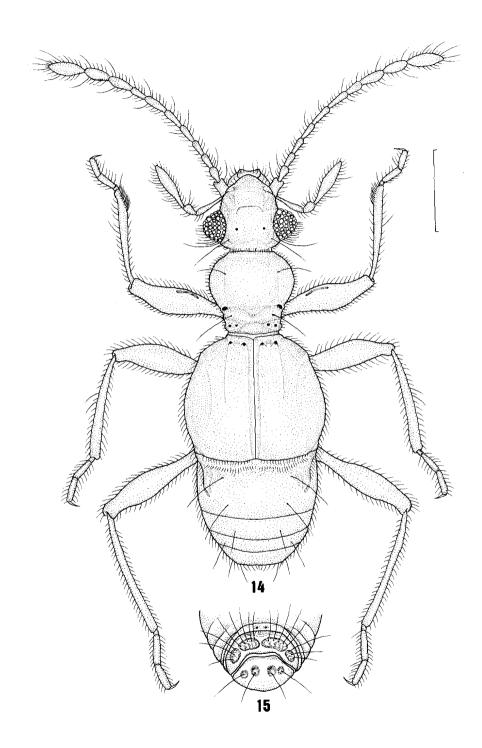
Etymology. - The name "humicola", from the Latin "humus" for ground, and "incolere" - to dwell, refers to the surface running habits of the species.

Remarks. - Batriscenites humicola was collected together with the preceding species which it resembles but is larger with longer antennae and maxillary palpi and more protruding large eyes. It is easily distinguishable from B. celer by the flattened head, vague lateral striations on pronotum, the elongate maxillary palpi, the long tarsi, combination of secondary sexual characters on dorsum and the structure of male genital organ which shows broader walls on ventral surface, strongly convex dorsal surface, slender process and prolonged copulatory piece. Though closely related to B. celer in the structure of male genitalia, it shows a different combination of secondary sexual characters in the male. Other species of the genus show the male characters only on first abdominal tergite, but B. humicola has sexual modification of both first and second tergites.

Batrisocenus foveiterminalis, new species

(Figs, 11, 14-18)

Material. - Holotype - &, funnel extraction using naphthalene repellant, of wet litter from a gulley between *Thalassina* mounds, Mandai Besar mangroves site MB3, Singapore, leg. D. H. Murphy, 24.x.1987.



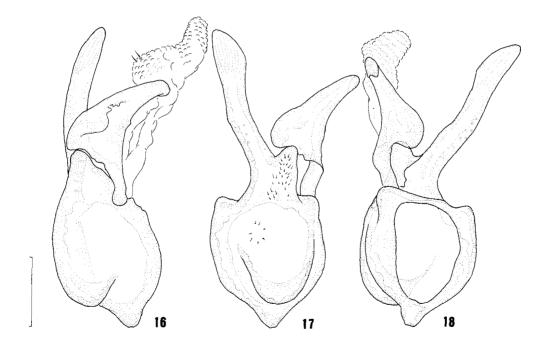
Figs. 14-15. Batriscocenus foveiterminalis, new species. Male. 14, general view; IS, ventral view of abdomen. Scale: 0.5 mm.

Paratypes: $4 \ 3$, $10 \ 4$, same data as holotype; $5 \ 3$, $9 \ 4$, same locality as holotype; leg. D. H. Murphy, 14.xi.1987.

Description. - Length: 2.3-2.4 mm (from apical margin of clypeus to apex of last abdominal tergite), greatest width: 0.7-0.8 mm.

Slightly larger than the preceding species and more elongate in body form, recognized by the flattened head with conspicuous eyes, small prothorax, long hind body, and elongated appendages. Colour reddish brown, shiny, faintly yellowish on appendages; palpi, apical segments of antennae and tarsi yellowish brown. Body surface covered densely with short pubescence, especially so on the surface of abdominal tergite I, and with sparse long setae. Inner wings are present though less developed.

Head large, subtriangular, slightly wider than long and gently depressed in front with large eyes; field of vertex hardly convex throughout, with median carina faint and small foveae at basal two-sevenths; sides slightly narrowed apically with widely arcuate genae; eyes very large and projecting, fringed with dense pubescence behind; antennal tubercles gently convex with arcuate margin; frons shallowly depressed and smoothly continuous with clypeus, whose margin is sharply arcuate; labrum transverse, with sides rounded and apical margin deeply emarginate; maxillary palpi (Fig. II) elongate, especially segments 2 and 3, the latter inflated a little beyond middle; antennae very long, reaching apical fifth of elytra, with segments 1-8 cylindrical, but segments 2-8 each slightly enlarged apically, last three segments forming a club, segment 9 shortly expanded preapically, segment 10 inflated a little before middle, and the length of segments decrease in the order of ll>10>7=9>1=5>6>2=3=4=8.



Figs. 16-18. Male genitalia of *Batrisocenus foveiterminalis*, new species. 16, lateral view; 17, dorsal view; 18. ventral view. Scale; 0.1 mm.

Pronotum cordate, almost as long as wide and as wide as head, widest at about three-fifths from the base, and evidently more contracted towards apex than towards base; PW/HW 1.00. PW/PL 1.00, PW/PA 1.88+, PW/PB 1.44+; surface moderately convex between lateral striae, though more or less compressed behind, with lateral striae gently arcuate and slightly divergent in front, transverse impression vaguely sinuate, bearing foveoid depression at basal fourth on mid-line, two foveoli situated on either side behind basal convexity which is broadened by arcuation and acumination postlaterad; sides moderately arcuate in apical two-thirds, slightly constricted just behind arcuations, and then more or less dilated towards posterior ends; apex almost straight with faintly broad rim; base feebly emarginate with very obtuse posterior angle on each side, PB/PA 1.28+.

Elytra transverse, widest at two-thirds from base, and gently dilated behind shoulders; EW/PW 1.56+, EW/EL 1.10+, EA/SL 1.18+; surface rather strongly convex though more or less compressed in front and lateral portions, with sutural convexity narrow, small foveae situated at base on either side and discal striae parallel to mid-line, reaching five-ninths from base; shoulders gently convex and more or less angulate at posterior ends due to a faint groove, though almost effaced in female; prehumeral borders very long, oblique and very feebly emarginate; sides oblique with border almost straight behind shoulders; and subparallel sides continuous with rounded distal ends; base narrow. Metasternum widely depressed; mesocoxa protuberant triangularly behind the constriction, with margin arcuate.

Abdomen relatively short, rather abruptly contracted towards apex, with gently convex surface and sparse long setae; tergite I distinctly narrower than elytra, more or less constricted near base with gently convex disc; tergite 5 conspicuous, trapezoid and incurved ventrally, bearing four foveae in a row in male, each provided with a long seta; sternite I with somewhat compressed surface at middle portion; sternite 4 with a pair of small foveae in the middle portion in male; sternite 5 deeply emarginate on apical margin, its surface being occupied by four excavatioms with long setae in male (Fig. 15).

Legs thick and long, due to prolonged femora; forefemora bears short sulcus at middle on internal face.

Male genital organ (Figs. 16-18) large, elongate and heavily sclerotized. Aedeagus about four-sevenths as long as elytra, being composed of broad basal part, prolonged apical lobe and arcuate laminate piece, which is articulated at left shoulder in aedeagus, with basal orifice at the ventral side; surface strongly convex to two protrusions in the middle portion; basal orifice largely ovate with thick walls, which is expanded ventrally, forming shoulders in front and with obtusely produced extremity; apical lobe extended in front, produced into a long process on right face with laminate tip; laminate piece fairly large, almost as long as the basal part, each end twisted and turned down.

Etymology. - The species name "foveiterminalis" refers to the distinctive pits on the terminal abdominal segment of the male.

Remarks. - The type locality is 2.5 m. above chart datum and the type specimens were collected following a tide of 2.9 m. The sample also contained Crustacea that require regular immersion, notably *Microrchestia* sp. (Amphipoda), *Hansenolana anisopous* and *Excirolana* sp. (Isopoda). The latter in an intermittent ectoparasite of fish, which indicates the intertidal conditions under which *B. foveiterminalis* lives.

Batrisocenus foveiterminalis can be regarded as belonging to the genus Batrisocenus in the sense of Jeannel (1949, 1952) by the conformation of male genitalia. It bears two

prolonged styles and inner sac in these styles is not armed. In secondary sexual characters of male, however, the present species shows significant differences from other members of the genus. *Batrisocenus foveiterminalis* shows modified last abdominal tergite and sternite, without modification of antennal segment 3 or abdominal tergite 3-4.

Berlara bella, new species

(Figs. 13, 19-22)

Material. - Holotype - ♂, mangrove forest, Mandai Kechil, Site MK3, Singapore, leg. Y. Tanokuchi, 19.xi.1987

Paratypes: 7 & 7, 8 & 9, same data as holotype; 1 & 9, funnel extraction of wet litter, Mandai Besar Site MB3, leg. D. H. Murphy, 14.xi.1987 (together with *B. foveiterminalis*).

Description. - Length: 1.5-1.6 mm (from apical) margin of clypeus to apex of last abdominal tergite), greatest width: 0.5 mm.

Small species with elongate hind body and conspicuous secondary sexual characters on palpi and metafemora. Colour brown to yellowish brown, but more yellowish in apical part of appendages and apices of head and abdomen. Body surface smoothly polished, covered with short pubescence, which is regular on hind body and irregular on fore body. Inner wings are well developed.

Head large, quadrate but somewhat rounded in female, convex above with feebly emarginate base; vertical area smooth, feebly convex throughout with small foveae at middle; sides subparallel with feebly arcuate genae and conspicuously large eyes, which are fairly protruding, larger in male than in female; frons, smoothly continuous with clypeus in female, though rather strongly compressed in male with arcuate border anteriad; antennal tubercles small and hardly convex, more or less extended in male with oblique margin, but rounded in female; clypeus quadrate; labrum transverse, with margin either almost straight or feebly arcuate; maxillary palpi (Fig. 13) relatively long, with terminal segment more or less falcate, simply elongate in female, though very large in male, almost two-thirds as long as head, and grooved at basal half on dorsum with feebly emarginate base and bi-angulate at middle external face; antennae slender except for last three segments, which form conspicuous club, reaching at about one-fourth from base of elytra, with segment 1-8 cylindrical, the length of segments decrease in the order of l>2=5>3=6=7>4>8, segments 9-10 globular though armed with protuberance in male, segment 10 fairly transverse and last segment the largest and semi-ovate.

Pronotum subcordate, about as wide as head in male, a little narrower than head in female due to smaller eyes, evidently wider than long, widest at apical two-fifths and a little more contracted towards apex than base; PW/AW 1.00+ (3), 1.08+ (4), PW/PL 1.20, PW/PA 1.60, PW/PB 1.32+; surface gently convex throughout, with large lateral foveae situated at basal thirds and median carinae faint, reaching basal fourth; sides shortly oblique in front, produced, with margin arcuate though more or less rounded anteriorly, and then gradually contracted towards base, which is bordered by narrowly transverse impression and gently arcuate margin, PB/PA 1.20+; apex almost straight in middle portion with vaguely broad rim.

Elytra slightly transverse, relatively narrow, widest at about a little behind middle and rather moderately divergent behind with almost straight apical margin; EW/PW 1.51+, EW/EL 1.06+, EW/SL 1.40+; surface gently convex, though more or less flattened at

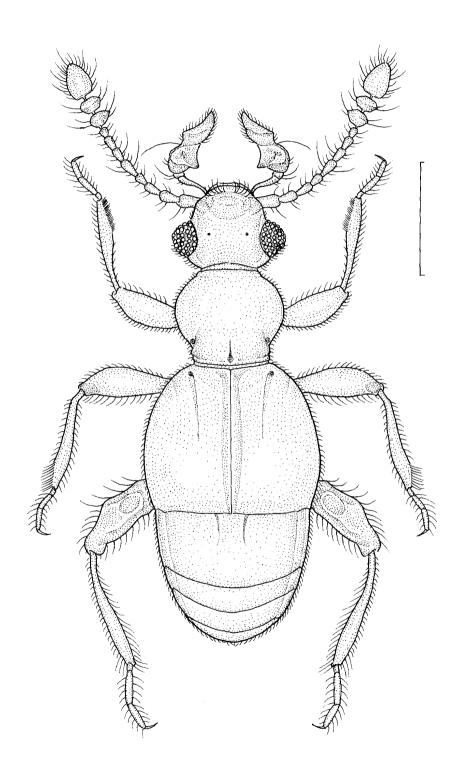
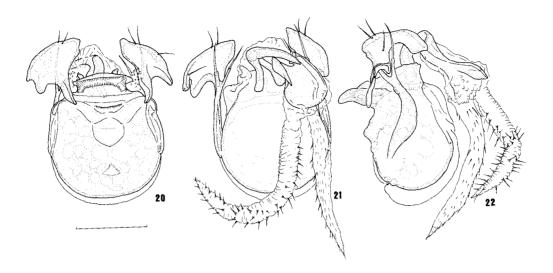


Fig. 19. Berlara bella, new species. Male. Scale 0.4 mm.



Figs. 20-22. Male genitalia of *Berlara bella*, new species. 20, ventral view; 21, dorsal view; 22, lateral view. Scale: 0.1 mm.

middle portion and compressed near base, with sutural convexity broad, a small fovea on each elytron close to shoulder and faintly impressed discal line reaching three- eighths from base; shoulders hardly convex in male, but effaced in female, with prehumeral borders shortly rounded though oblique; sides feebly arcuate and base emarginate. Mesosternal shield short and swollen just before mesocoxal cavity; behind the constriction of mesocoxal cavity transversely protuberant with arcuate margin; metasternum compressed in hind half in female, but bordered and shallowly grooved through abdominal sternite in male.

Abdomen relatively long, nearly as long as elytra, gradually tapering and contracted towards distal end with parallel-sided rims, and disc gently convex throughout; tergite I evidently narrower than elytra, regularly narrowed towards apex with gently elevated lateral rims, AAW/ABW 0.89+, and surface more or less flattened in middle portion, with basal carinae subparallel and extending to middle, its bases being separated by about two-ninths the width of disc; sternite I with large fovea on either side near base.

Legs short and stout; femora fairly inflated, especially so in metafemora in male, which is abruptly dilated at apical four- ninths, and on compressed and grooved on its external face with ovate concavity in middle portion and margin slightly concave; tibia enlarged preapically.

Male genital organ rather large and moderately sclerotized. Aedeagus ovoid, about half as long as elytra; basal part rounded with small basal orifice on ventral surface; apical part constricted before apical orifice, bearing on each side a obliquely produced protuberance; ventral face of apical orifice extending to a laminate plate, and convex on apical half. Inner sac armed with large copulatory piece; innersac rather narrow and furcate at apex of copulatory piece, extending slenderly tubular with sharp apices, of which right one sparsely spinose and left one sparsely ciliate; copulatory piece heavily sclerotized, very large, strongly bent dorsad, with basal part furcate and apical part spatulate. Styles iointed a little behind middle portion to the ventrolateral side of aedeagus, extending

beyond aedeagus, narrowly arcuate in lateral view and each furcate in apical third, with apices provided with setae and contact with fairly large pieces, which are attenuated with long process and three short setae.

Etymology. The specific epithet is the adjective in apposition from the Latin "bella" - pretty.

Remarks. - When collected from the Mandai Kechil site, this small species occupied a different habitat different from the other four species found there. Most parts of the site are below water at high tide, whereas the tops of mounds remain above water. These upper parts are usually covered with mosses or algae and are cracked. Berlara bella was found walking on these higher parts or hiding in the cracks, never walking on the lower part even at low tide. Presence of a specimen in the wetter sample from MB3 might be contamination due to disturbance.

This species differs from the others described here in having well developed inner wings, short antennae and short, robust legs. In these respects, it may be less specialised for intertidal conditions (see DISCUSSION).

GENUS MANGALOBYTHUS, NEW GENUS

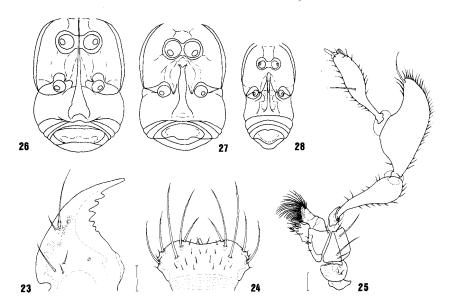
Type species: Mangalobythus furcifer, new species

Description. - Body broad and surface rather flattened with elongate antennae and legs; Head and prothorax smooth on dorsum, elytra slightly divergent and abdomen semi-ovate.

Head large, roundly quadrate, fairly thin, and constricted at the level of eyes, which are large but gently projecting; surface smooth, hardly convex throughout vertical area, though frons more or less compressed; genae produced, antennal tubercles hardly convex with rounded margin; clypeus also less produced, with margin protuberant on each side, and unarcuate; labrum and mandibles produced below; maxilla relatively large, bearing two short setae in about middle part on cardo, a long seta and a short seta near base on stipes, two long setae apically on palpifer and four short setae in two rows and a short seta at inner apex on lacinia; maxillary palpi conspicuous, with segment 2 strongly enlarged apically, segment 3 the largest, produced transversely, semi-crescentic with expanded base, where the small clavate terminal segment articulates; antennae long, submoniliform, with scape cylindrical and apical segment conspicuously elongate, not forming a club.

Pronotum large, transversely cordate, wider than head, and rapidly contracted towards apex than towards base, with surface gently convex and smooth; sides expanded and arcuate anteriorly, then smoothly contracted posteriorly.

Elytra relatively narrow though transverse, and less divergent behind shoulders; shoulders very obtuse though still marked, with prehumeral borders rather long and oblique; sides more or less oblique behind shoulders and then either almost straight or gently arcuate towards preapices; surface gently convex or rather flattened, with sutural convexity broadly lenticulate and two foveae situated on each elytron near the level of shoulders or a little before that portion, of which inner one contacts with sutural convexity and outer one bears a long discal stria. Metasternum in male grooved along mid-line, gradually dilated behind, and protuberant before metacoxal cavity.



Figs. 23-28. Body parts of Mangalobythus spp. 23-26, M. furcifer, new species; 27, M. acutifolius, new species; 28, M. murphyi, new species. 23, mandible in dorsal view; 24, labrum in dorsal view; 25, maxilla in dorsal view; 26-28, hind-body in ventral view.

Abdomen, broad, rather short, rapidly contracted behind segment 1 and curved below with hardly convex disc and broad rims; tergite 1 fairly large with a pair of long basal carinae; sternite 1 in male produced into a longitudinal process, which is prolonged towards fore-body; sternite 5 small, ovate and more or less grooved on surface in male.

Legs stout and long, meso- and meta-femora slender, tibia relatively short and slightly dilated apically, tarsi rather short, and claws very long; fore femora in male fairly inflated on outer face where surface armed with a protuberance or process.

Male genital organ very small, thinly quadrate, either very slightly sclerotized or membraneous. Aedeagus very thin, walls membraneous, and apical orifice large, which is almost wide as aedeagus and opening apically, walls are fully fringed by spines, bearing well developed styles, which usually forms a U-shaped sclerotization with apices provided with long setae. Inner sac indefinite due to membranous aedeagal walls, though either armed with a piece on each side of apical orifice or none at all.

Etymology. The genus name is a compound derived from "mangal", a West African name widely applied to the mangrove forest ecosystem, with the root of the tribal name Bythinini.

Remarks. - Though it belongs to the tribe Bythinini, mainly on structure of male genitalia, this new genus shows no close similarity to any known pselaphid genera. Mangalobythus has not only remarkable characters in the maxillary palpi with segment 3 transversely produced and apical segment inserted subbasally, male characters developed on the outer face in fore femora and process on abdominal sternite I, but is also peculiar in the flattened surface of head, smooth surface of pronotum, the retreated basal foveae on elytra and the slender legs in comparison with its body size.

All known members of the genus inhabit estuarine mangrove forest and are active on the open ground at low tide, both by day and night. Characters such as large eyes,

reduction or absence of inner wings, long pubescence, elongate appendages and the male secondary characters related to mating posture may be adaptive to life in this special environment (see **DISCUSSION**). On the other hand, the male genitalia of *Mangalobythus* have retained a primary condition, that is, aedeagus thin, symmetrical and small, without sclerotized walls, usually bearing U-shaped sclerotized styles. Furthermore, the chaetotaxy of mouthparts may be regarded as still remaining at a primitive stage due to small number of the primary setae. If so, *Mangalobythus* may be considered a relict group isolated by their special environment.

The known species are sufficiently diversified to suggest that an extensive survey of the regional fauna of mangrove Pselaphidae will be needed before relationships between those described can be established.

Mangalobythus furcifer, new species

(Figs. 23-26, 29-31)

Material. - Holotype - & mangrove forest, Mandai Kechil Site MK3, Singapore, leg. Y. Tanokuchi, 19.xi, 1987.

Paratypes: 1 &, mangrove forest, Mandai Besar site MB3, Singapore, leg. D. H. Murphy, 18.vi.1987; 1 & , 1 , mangrove forest, Mandai Besar site MB3, Singapore, leg. D. H. Murphy, 14.xi.1987; 10 & , 6 , same data as holotype; 5 &, 3 , same locality as holotype, leg. D. H. Murphy, 19.xi.1987.

Description. - Length: 2.2-2.3 mm (from apical margin of clypeus to apex of last abdominal tergite), greatest width: 0.7-0.8 mm.

Mid-sized psclaphid beetle, with fairly broad abdomen and elongate appendages. Colour dark reddish brown, though apical segments of antennae, palpi, apical portion of legs and terminal sternites of abdomen more or less yellowish brown. Surface more or less punctulate, and covered with dense pubescence, which is irregular on pronotum and denser at apices of elytra and lateral surface of abdomen. Inner wings are present though reduced.

Head large, transverse quadrate, and flattened above, with sides constricted due to large eyes and with basal margin slightly arcuate; surface either feebly convex or flattened though more or less compressed in front; sides slightly divergent behind antennal tubercles and genae smoothly arcuate, with eyes large and moderately protruding; antennal tubercles hardly convex, with reflected margin continuous with clypeus, which is hardly correct and with margin almost straight at middle; labrum about twice as wide as long, obtusely incised in front, giving a bilobed appearance; maxillary palpi conspicuous, with segment 2 fairly enlarged in apical two-thirds, segment 3 fairly transverse and terminal segment clavate; antennae elongate and stout, submoniliform, reaching at basal three-sevenths of elytra, with cylindrical segment 1 somewhat constricted and about twice as long as segment 2, the length of segments decrease in the order of ll>1>4>2=7>5=6=9=10>3>8, of which segment 5 armed with nail-like protuberance at ventral face apicad in male, and last segment long, fully three times as long as segment 7 but not forming a club.

Pronotum cordate, slightly wider than head, a little wider than long, widest at about two-thirds from base, and more rapidly contracted towards apex than towards base; PW/HW 1.03+, PWPA 1.88+, PW/PB 1.33+; surface gently convex throughout disc, though

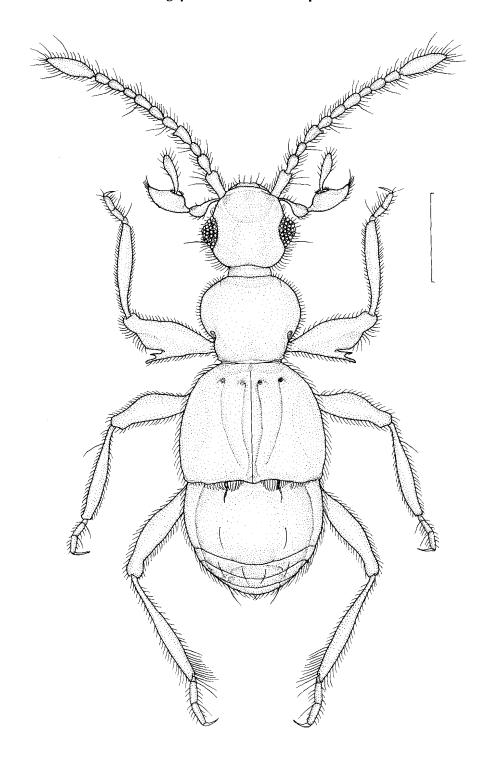
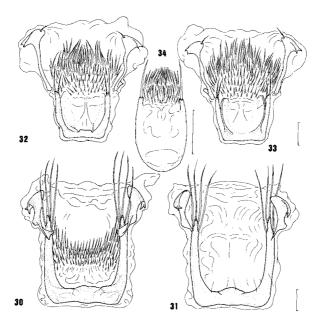


Fig. 29. Mangalobythus furcifer, new species. Male. Scale 0.5 mm.



Figs. 30-34. Male genitalia of Mangalobythus spp. 30-31, M. furcifer, new species; 32-33, M. acutifolius, new species; 34, M. murphyi, new species. 31, 33, 34, dorsal view; 30, 32, ventral view.

more or less compressed posteriorly, bearing lateral foveae at the level of one-third from base; sides strongly arcuate in front, less so behind middle, more or less distinctly sinuate at about one-sixth from base, and then feebly contracted towards basal angles; apex either straight or slightly arcuate, with broad rim which is provided emarginate striation and compressed surface, PB/PA 1.41+; base slightly reflexed, with margin widely arcuate.

Elytra relatively narrow but transverse, widest at apical half and gradually divergent behind shoulders; EW/PW 1.50+, EW/EL 1.20+, EA/SL 1.35+; surface rather flattened though transversely compressed in basal area, with sutural convexity vaguely broad, two foveae situated on each elytral surface at about the level of shoulder and discal striae inclined to mid line, reaching to three-tenths from base; shoulders feebly convex and widely rounded, with humeral borders very long, almost straight and oblique; sides strongly oblique in apical half, with borders either straight or very feebly arcuate, almost parallel-sided and then rounded at distal ends; base emarginate; apex either straight or slightly emarginate, much wider than base, EA/EB 1.95+. Metasternum in male, longitudinally grooved and acutely projected above in front of each metacoxal cavity and longitudinal plate produced along the mid line through meso-, meta-sternum and sternite l, and gradually dilated towards sternites with bilobed apices continuous with sternite l.

Abdomen broad, rather short, rapidly contracted towards distal end with rather flattened disc and relatively broad rims. Tergite I ample, seven-tenths as long as and a little narrower than elytra with lateral rims, which are narrowed towards apices and hardly elevated, and disc gently convex as a whole, with lateral striae divergent and arcuate, AAW/ABW I/05+, and basal carinae extending to two-ninths from base, its bases being separated by a half width of disc; terminal tergite more or less lanceolate. Sternite I large, elevated and porrect behind with retuse margin in male; terminal sternite transversely oblong, grooved in male as a whole with transverse sulcus posteriad.

Legs stout and long; mesotrochanter somewhat acute at apex in male; forefemora

inflated, especially so in external face, of which middle portion produces obliquely furcate process and protuberant a right angle in the middle portion in male.

Male genital organ rather small and membraneous except for U-shaped styles, which are heavily sclerotized. Aedeagus rectangular, very thin, three-sevenths as long as elytra; apical orifice opening at about middle on ventral side, with walls emarginate and fringed with very dense spines only on dorsal face. Styles slender, two-third as long as aedeagus, thin though thickened at base, more or less reflexed below and slightly narrowed towards apices, each bearing four long setae. Inner sac armed with a piece on either side of apical orifice; copulatory pieces a half as long as styles with slightly arcuate internal face, emarginate external face and twisted behind.

Etymology. - The specific epithet refers to the bifurcate external process of the male front femur. Variation in this feature, presumably involved in copulation, is one of the simplest ways of discriminating species in the genus.

Remarks. - The species is large compared with the following two species. Individuals collected by me at MK3, were actively walking, together with *B. celer* and mid-sized Formicidae on moist intertidal forest floor or concealed under very wet wood.

Mangalobythus furcifer seems to represent a more advanced stage than the following species in the structure of male genitalia: aedeagus is larger and mainly placed on ventral surface of styles, which are heavily sclerotized, the U-shape with thick walls, each apex with four long setae, and copulatory pieces are already modified. Even the male genital organ of this species however, does not suggest any affinities among other Pselaphidae.

Mangalobythus acutifolius, new species

(Figs. 27, 32-33, 35)

Material. - Holotype - &, in cavities in decomposed intertidal Rhizophora log on wet ground, Khlong Ngau Mangrove, 20 km south of Ranong, S.W. Thailand, leg. D. H. Murphy, 14.xi.1987.

Paratype: 1 3, same data as holotype.

Description. - Male: Length: 2.1-2.2 mm (from apical margin of clypeus to apex of last abdominal tergite), greatest width: 0.8 mm.

Externally similar to *M. furcifer* Tanokuchi, but distinctly smaller on average, having obviously smaller prothorax, relatively broad elytra and stouter legs.

Colour light reddish brown, and shiny; palpi apical segments of antennae and legs yellowish brown. Pubescence relatively thick. Inner wings contracted. Head constricted at middle, with genae roundly produced and base either straight or feebly emarginate; sides obtusely angulate just before eyes and emarginate behind each antennal tubercle, which is small and gently convex with rounded margin; clypeus less extended, with margin almost straight at middle; labrum only shallowly emarginate at apex; maxillary palpi fairly large, with segment 3 transversely prolonged and last segment rather gently clavate; antennae long, especially so in terminal segment which is fully fifths times as long as segment 8, the length of segments lessen in the order of ll>1>7=9>2=5>3=4=6=10>8 and the male character effaced, with scape cylindrical and last segment, more or less shell-shaped. Pronotum strongly transverse evidently wider than head, almost equally contracted in front and behind, with apex feebly emarginate without rim and lateral foveae large; sides expanded at apical two-thirds, with margin rather strongly arcuate, though less so in front;

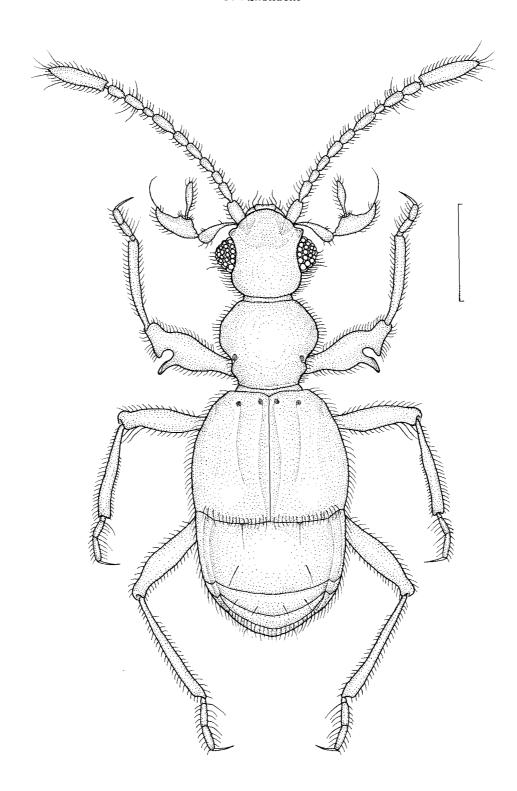


Fig. 35. Mangalobythus acutifolius, new species. Male, from Thailand. Scale: 0.5 mm.

PW/HW I/20+, PW/PL I.30+, PW/PA.PB 2.00+, PB/PA I.0+. Elytra divergent, with prehumeral borders less arcuate, widest posteriad; surface bearing basal foveae at the level a little before shoulders and discal striae reaching at about five-sixths from base; EW/PW I.30+, EW/EL I.20+, EA/SL I.30+. Metasternal acumination before cavity somewhat obtusely produced behind. Abdomen broad with wide lateral rims. Tergite I moderately convex at middle portion, and lateral rims parallel-sided, with lateral striae widely arcuate, AAW/ABW 0.94+, and basal carinae extending to basal third, its bases being separated by about three-sevenths of disc; terminal tergite transversely semi-ovate. Sternite I elevated medially, with margin almost straight, the median portion being a raised longitudinal plate through metasternum with somewhat emarginate apex; terminal sternite depressed as a whole in male. Mesotrochanter cuspidate at apex in male; forefemora in male with a deep notch externally at basal third, its basal margin foliaceous, acutely produced and recurved, and apical margin triangularly angulate.

Male genital organ basically similar to that of *M. furcifer* but significantly different in details. Aedeagus slightly thickened towards apex; apical orifice opened in front, its walls covered with dense spines; styles protruded broadly on ventrolateral side, with arcuate inner walls, two-fifths as long as aedeagus, and each apex bears two setae. Inner sac armed with a slender piece in contact with each style, with dilated tip and bearing a short seta.

Female unknown.

Etymology. - The specific epithet refers to the distinctive profemoral process.

Remarks. - In spite of a close resemblance in external morphology, this species is not very closely related to M. furcifer. It differs in the unarmed antennae and its genitalia, characterized mainly by the dilated aedeagus fringed with spines on apical orifice, somewhat sclerotized basal part and narrow styles, bearing two long setae and slender copulatory pieces.

Mangalobythus murphyi, new species

(Figs. 28, 34, 36)

Material. - Holotype - ♀, under very wet wood at stream side, mangrove forest, Mandai Kechil Site MK3, Singapore, leg. Y. Tanokuchi, 19.xi.1987.

Paratypes: 1 & 19, same locality as holotype.

Description. - Length: 1.3-1.4 mm (from apical margin of clypeus to apex of last abdominal tergite); greatest width: 0.5 mm.

Small species of subparallel habitus, with quadrate head and elongate hind body. Colour yellowish brown to light reddish brown, shiny; palpi, apical segments of antennae and legs light yellowish brown. Body surface smooth and covered densely with short pubescence, which is regularly distributed except on pronotum. Inner wings are absent.

Head transversely subquadrate, slightly constricted at the position of the fairly large eyes, with base very feebly emarginate and genae shortly rounded; surface hardly convex and compressed in frons with vague foveoli at basal thirds; antennal tubercles elevated towards arcuate margin; clypeus almost straight, though produced in middle portion with feeble arcuation; labrum transverse, with margin emarginate; maxillary palpi conspicuous, with segment 2 abruptly enlarged at apex, segment 3 rather short but wide and segment 4

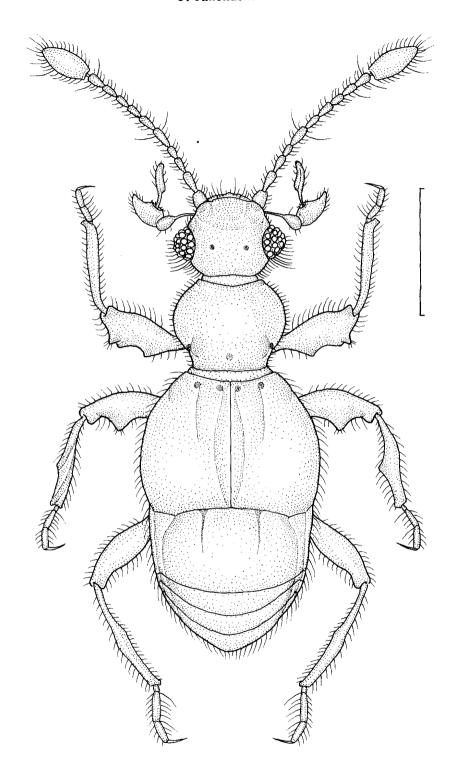


Fig. 36. Mangalobythus murphyi, new species, Male. Scale: 0.4 mm.

enlarged extremely in apical three-fourths; antennae long, stout, reaching apical three-fifths of elytra, and the length of segments lessen in the order of ll>l>2>3=5=6=9=l0>7>4=8, with terminal segment the largest and subconical.

Pronotum cordate, a little wider than head, usually widest at three-fourths from base, and more strongly contracted towards base than towards apex; PW/HW 1.08+, PW/PL 1.25+, PW/PA 1.78+, PW/PB 1.31+, surface slightly convex, but more or less flattened with large lateral foveae at about basal third and vaguely foveoid depression; sides strongly arcuate and smoothly contracted behind; apex feebly emarginate and base almost straight, PB/PA 1.35+.

Elytra large, much wider than pronotum, slightly divergent behind shoulders and widest in about middle; EW/PW 1.52+, EW/EL 1.26+, EA/SL 1.30+; surface rather flattened, but more or less compressed in basal portion, with sutural convexity vaguely broad, small foveae situated close to base and discal striae subparallel to mid-line though incurved near apex, reaching two-thirds from base; shoulders small and almost effaced, with prehumeral borders short and oblique; sides as in M. furcifer; base and apex slightly emarginate. Metasternum in male, deeply fluted or scooped out along mid-line, with either side compressed and protuberant posteriorly.

Abdomen long, a little shorter than elytra, gradually contracted and attenuated towards apex and surface flattened or gently convex, with narrow rims; tergite 1 relatively narrow, slightly tapering apically, lateral rims dilated near base and disc somewhat depressed in basal portion, with lateral striae feebly arcuate, AAW/ABW 0.96+, and basal carinae extending to in about middle of tergite 1, its bases being separated by four-ninths the width of disc; sternite 1 in male producing a long process, which is arcuate and prolonged obliquely towards front with slenderly furcate apices; terminal sternite grooved on the whole in male.

Legs rather long and stout; forefemora enlarged towards apex, with outer face in male depressed at middle with semicircular sulcus and protuberance in apical portion; mesofemora expanded on outer face and less so internal face with are obtuse protuberance at a little behind middle in male; mesotibia in male slightly dilated with a shallow groove.

Male genital organ very small, membraneous as a whole and inner sac without armature. Aedeagus more or less ovate, thin, somewhat lenticulate in lateral view, and about one-fourth as long as elytra; base more or less rounded and apical orifice opening just in front, being covered with dense spines; styles shortly produced on each side of apical orifice, also membraneous, each tip bearing a long seta.

Etymology. - This new species is dedicated to Professor D.H. Murphy, who has collected many new species of Pselaphidae in Singapore and adjacent areas.

Remarks. - This small species, accompanied by M. furcifer was only obtained under very wet wood at the stream. Differing in body size, sculpture of body surface and aedeagal structure, M. murphyi seems less closely related than the preceding two species of the genus especially in conformation of fore-body. In some respects it can be regarded as a primitive species in having the following morphological characters. Its head and pronotum still retain traces of foveolation, middle legs show male characters, and genitalia in a presumed primitive state: the aedeagus wholly membraneous without any copulatory pieces, styles also membraneous and underdeveloped, bearing only one setae on each apex. While probably derived from a common ancestor with the other members of Man-

galobythus, its affinity is less close. Rather than erect a separate genus, I prefer to regard it as a peculiar offshoot within *Mangalobythus* where it is considered to represent its own species-group.

DISCUSSION

Except for Berlara bella, which appears to be largely confined to those parts of the Thalassina mound system which lie above the reach of high tides, all these pselaphid beetles appear to be truly intertidal. They share morphological features that may be adaptive to this habitat. All are more densely pubescent than allied forms from inland situations, which may serve to retain air when inundated. All have unusually long appendages and large eyes. Most are conspicuously fast running forms, very active on the wet ground when the tide is down. Since the ground is free of water for only a few hours in the day and again at night, the hunting time available to these predaceous beetles is very limited. During these few hours, a high activity would have adaptive value. Some species at least are equally active at night (Murphy, personal communication), perhaps because of the need to maximise feeding time. This may correlate with the unusually large eyes.

The flightless condition is more difficult to account for. Perhaps the risk of landing on water is a selective disadvantage. In most mangrove areas, the topography is very flat, an incoming tide advances very rapidly, and insects without a refuge could easily be lost. Only in the localised *Thalassina* mound systems where these beetles are most abundant, is easy escape ensured. For whatever reason it evolved, the flightless condition may greatly reduce dispersal, so that the mangrove fauna may prove to be rich in local species. It is suggestive that none of the Singapore species were found in the Thai mangroves only a few hundred kilometers away, while a different species of the same genus occurred. An extended survey for pselaphids in this poorly investigated habitat is much to be desired.

Acknowledgements. - I wish to thank Professor D.H. Murphy for offering specimens and for reading the original manuscript. Thanks are also due to Professor J. Aoki of the Department of Soil Zoology, Yokohama National University, for his constant guidance. This work could not be accomplished without the encouragement of Dr. R. Yoshii and Dr. K. Sawada. Dr. Yoshii is grateful for support from the Toyota Foundation.

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Address: YT: Department of Soil Zoology, Institute of Environmental Science & Technology, Yokohama National University, Yokohama 240, Japan