# A review of the genus Mystrium (Hymenoptera: Formicidae) in the Indo-Australian region 

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#### Abstract

Indo-Australian species of the amblyoponine ant genus Mystrium Roger are reviewed. Three species are recognized in the region, and two of them, which were found in Indonesia (Papua and West Papua Province), are described as new species: Mystrium maren sp. nov. and Mystrium leonie sp. nov. Worker diagnoses and illustrations of the three species and a tabular key are given.


Key words: Formicidae, Amblyoponinae, Mystrium, Indo-Australian, Indonesia

## Introduction

The genus Mystrium Roger is morphologically very peculiar within the poneromorph subfamily group and has the following combination of characteristics: the very wide head; spatulate or squamate hairs on the head; and long, narrow mandibles with a double row of teeth on the inner margins. Monophyly of the genus is strongly supported by a recent molecular phylogenetic study (Saux et al. 2004). Besides their bizarre morphology Mystrium ants have also evolved some unique biological traits. They have a unique defense mechanism in which they snap their mandibles to generate a powerful strike (Gronenberg et al. 1998; Moffett 1986). Molet et al. (2006) demonstrated that, in some species of Mystrium known from Madagascar, normal queens are replaced by wingless reproductives which are smaller than workers. Because Mystrium are rarely encountered, information on their general biology, ecology and behavior remains sparse. They are presumably predaceous like other species of the subfamily Amblyoponinae, although no direct evidence is available (Brown 1960).

The genus was erected by Roger (1862) with the description of the queen of M. mysticum. There are few species, all of which occur in the rainforests of the Old World. Most species are found in tropical Africa: six of them are restricted to Madagascar (and its adjacent islands, i.e. the Malagasy region sensu Bolton 1994) and one is recorded from continental Africa. Mystrium camillae Emery 1889 is widespread in the Indo-Australian region. Xu (1998) recently described $M$. oculatum from southern China, but we do not regard it as a distinct species. Since the first revision of Menozzi (1929) only Brown (1960) made some revisionary notes on the genus. Here we describe two new species of Mystrium from Papua and West Papua Province, Indonesia, and provide a review of the species known from the Indo-Australian Region.

## Material and methods

All illustrations with extended focus were produced using Syncroscopy Auto-Montage (v. 5.0) software based on source images which were taken using a JVC KY-F70 digital camera mounted on a Leica Z6 APO microscope (fig. 1-9 \& 13-15) or a Leitz Diaplan compound microscope (fig. 10-12).

Specimens were examined and measured using a Leica MZ16 microscope at magnifications of up to 115 x with a calibrated micrometer. All metric measurements were recorded to the nearest 0.001 mm , rounded to two decimal places for presentation, and given in millimeters. Morphological terminology follows Bolton (1994). The terms for integument sculpture follow Harris (1979). Abbreviations and definitions of measurements and indices are:

HL Head length: maximum longitudinal length from the anteriormost portion of the clypeus (including clypeal teeth) to the midpoint of a line connecting the posteriormost points of the occipital lobes in full-face view.
HW Head width: maximum width of head in full-face view taken just behind the bases of anterolateral spines.
CI Cephalic index: HW/HL x 100.
SL Scape length: maximum straight line of the antennal scape excluding condyle and neck in frontal view.
SI Scape index: SL/HW x 100.
ML Mandible length: In dorsal view the trulleum (basin-shaped depression near the base of the mandible) is separated from the distal part of the mandible by a carina which continues laterally. The mandible length is measured in dorsal view as the straight line from this carina to the apex of the mandible.
WL Weber's length: the diagonal length of the mesosoma in lateral view from the anteriormost point of the pronotum to the posteriormost point of the metapleuron.
PW Pronotal width: maximum width of the pronotum in dorsal view.

Abbreviations of the specimen depositories are:

MCSN Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy (formerly MSNG)
MZB Museum Zoologicum Bogoriense, Cibinong, Bogor, Java, Indonesia
SMNK Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany
SWFC Insect Collection at the Department of Forest Protection, Southwest Forestry College, Kunming, Japan

## Species accounts

## Mystrium camillae Emery

Fig. 1-3, 10, 13

Mystrium Camillae [sic] Emery, 1889: 491, pl. 10, figs. 1-3. Syntype worker and queen: Myanmar (as "Birmania": Bhamò (Fea) [MCSN] (not examined; photographs of syntype worker and queen examined on AntWeb (www.antweb.org): CASENT0102123 (worker), CASENT0102124 (queen)).
Mystrium camillae Emery subsp. javana Karawaiew, 1925: 73, figs. $1 \& 2$. Syntype worker: Java, limestone mountain near Tjampea, no. 2389, 2 workers on the ground, under leaves (Karawaiew) (not examined). Synonymy by Brown, 1960: 170.
Mystrium camillae; Menozzi, 1929: 535-536, fig. 9. Revision of the genus and key to species.

Mystrium oculatum Xu, 1998: 161, figs. 1 \& 2. Holotype worker: China: Yunnan Province, Mengla County, Menglun Town, Bakaxiaozhai (Xu Zheng-hui) [SWFC] (not examined; photographs of paratype examined on AntWeb (www.antweb.org): CASENT0104982 (worker)). New synonymy.

Material examined. Indonesia: Sumatra: Lampung, Tulang Bawang, Gn. Tanggang, $05^{\circ} 43.933^{\prime} \mathrm{S}$, $105^{\circ} 06.598^{\prime}$ E, 580 m ( 1 worker, 9.VIII.2006, A. Riedel) [SMNK]; Sumatra: Lampung, Tulang Bawang, Gn. Tanggang, $05^{\circ} 43.938^{\prime} \mathrm{S}, 105^{\circ} 06.440^{\prime} \mathrm{E}, 580 \mathrm{~m}$ (5 workers, 9.VIII.2006, A. Riedel) [SMNK]; Java: Jawa Barat, Ciamis, Gn. Sawal, Batu Cakra, $07^{\circ} 14^{\prime} 55^{\prime \prime} \mathrm{S}, 108^{\circ} 15^{\prime} 46^{\prime \prime} \mathrm{E}, 990 \mathrm{~m}$ (1 worker, 1.X.2005, A. Riedel) [SMNK]. Malaysia (West): Negri Sembilan, Simpang Pertang, Pasoh Forest Reserve, 0259' N, 102¹9' E (1 worker, 29.III.1992, K. Rościszewski) [SMNK]; MALAYSIA (WEST): Terengganu, Lake Kenyir, 04ํ $58^{\prime} \mathrm{N}$, $102^{\circ} 49^{\prime}$ E, 300-400m (22 workers, 7.-12.VII.2001, A. Schulz) [SMNK].

Measurements and indices. Workers: HL $0.81-1.75$, HW $0.85-1.64$, CI $88-105$, SL $0.50-1.00$, SI 5464, ML 0.52-1.75, WL 0.91-1.49, PW 0.47-0.80 ( $\mathrm{n}=31$ ).

Diagnosis (worker). The following character combination differentiates M. camillae from all its congeners in the Indo-Australian region: the apex of each mandible distinctly expanded and rounded in lateral view, with a more or less triangular and caudally directed tip on the inner side; outer face of labrum entirely covered with a weakly developed, irregular rugoreticulum; maxillary palps 4-segmented; the second segment of the maxillary palp shorter than the basal (first) segment and less than half as broad as the basal segment; antennal segment III shorter than twice its width; each anterolateral corner of the head produced into a short, nearly triangular, pointed spine; dorsum of head with rugose-reticulate cuticular sculpture and spatulate hairs; minute compound eyes; petiolar node not broader than twice its length measured in dorsal view.

Distribution. Widely distributed in the Indo-Australian region and neighboring countries. Recorded from Australia, Brunei, China, India, Indonesia, Malaysia, Myanmar, Papua New Guinea, the Philippines and Singapore.

Comments. Brown (1960, p. 170) gave no justification for the synonymy of M. camillae subsp. javana under M. camillae but the differences between the taxa given in the description of Karawaiew (1925) fall within the variation of the senior synonym. The most important difference between the taxa - the shape of the mandible apex - depends on the angle from which the mandible is viewed. The triangular tip is highly variable in the specimens examined and often worn out. The number of truncated teeth at the anterior clypeal margin varies from 6-7 in the specimens we have seen and thus is not a character to distinguish the taxa. In most cases there is a toothless gap between the left and right group of these teeth (but see the specimens from Northern Australia depicted on AntWeb [CASENT0172841, CASENT0172082]. From Karawaiew’s description it is clear that he never had a specimen of $M$. camillae at hand but made his judgment of the species just from the description and the drawings of Emery (1889).

Xu (1998: 161, figs. $1 \& 2$ ) notes in his description of M. oculatum that this species is close to M. camillae but differs from it by: "small eyes present; central dorsum of hat flat; metanotal groove only shallowly depressed; declivity of propodeum flat, not depressed; anterodorsal angle of petiolar node more extruding." All examined specimens of $M$. camillae possess minute compound eyes. The presence of eyes was already noted in the original description of M. camillae by Emery (1889) and again in Menozzi's revision. Therefore, the presence of eyes in M. oculatum cannot be regarded as a diagnostic character to distinguish it from $M$. camillae. All other diagnostic characters given for M. oculatum by Xu vary much among individuals of $M$. camillae. The morphology of $M$. oculatum as described by Xu (1998: 161-162, figs. $1 \& 2$ ) and shown by photographs of a paratype of M. oculatum on AntWeb (www.antweb.org: CASENT0104982) falls well within the range of morphological variation exhibited by the examined specimens of $M$. camillae. Additionally, all but one metric character of $M$. oculatum fall into the range of $M$. camillae. The exception is CI, which is slightly higher.


FIGURES 1-3. Mystrium camillae (specimen from W-Malaysia: Lake Kenyir): 1—head frontal view, 2—dorsal view, 3-lateral view.

## Mystrium leonie Bihn \& Verhaagh, new species

Fig. 4-6, 11, 14

Type material. Holotype: Worker. Indonesia: Papua Province, Jayawijaya, near Elelim, $03^{\circ} 49^{\prime} \mathrm{S}, 139^{\circ} 24^{\prime}$ E, 750 m a.s.l., December 2004 (leg. A. Riedel), deposited at MZB.

Measurements and indices. Holotype worker: HL 2.26, HW 2.45, CI 108, SL 1.63, SI 66, ML 2.80, WL 2.50, PW 1.18.

Diagnosis (worker). The following character combination differentiates $M$. leonie from all its congeners: the apex of each mandible only slightly expanded and subtruncate; outer face of labrum with an irregular rugoreticulum; maxillary palps 3-segmented; the second segment of the maxillary palp longer than the basal (first) and third segment, respectively; antennal segment III at least twice as long as broad; antennal scape broadened in its distal part, this part ventrally tapering into a lamella; each anterolateral corner of the head produced into a long and pointed spine; dorsum of head with rugose-reticulate cuticular sculpture and clavate hairs; minute compound eyes.

Description (worker). General morphology of worker as shown in figures 4-6. Head wider than long; posterior margin of head in full-face view deeply and roundly emarginate. Each anterolateral corner of head produced into a forward directed, long and curved spine. Mandibles long and slender, basal $2 / 3$ straight, distal $1 / 3$ incurved; the inner margin with two staggered, longitudinal rows of hamulus-like teeth, each row with 14 teeth; the teeth of the lower row larger than those of the upper row; the apex of each mandible only slightly expanded and subtruncate; the medioventral corner of the apex with an additional tooth; distal $3 / 4$ on dorsal side and distal half on ventral side of each mandible with a longitudinal carina.

Labrum (fig. 14) about twice as wide as long; its distal margin convex with a median, broad emargination; outer (ventral) face of labrum entirely foveolate-reticulate, and partly overlaid by an irregular rugoreticulum; this rugoreticulum is restricted to the distal half of the outer face of the labrum.

Maxillary palps 3 -segmented (fig. 11); the second segment longer than the basal (first) and the distal (third) segment; basal (first) segment cylindrical, its diameter only slightly larger than the diameter of the second segment. Labial palps 3-segmented.

Anterior clypeal margin convex with 8 truncated teeth; the teeth evenly spaced along the clypeal margin, without a median toothless gap. Antennal scape (antennal segment I) in dorsal view (as in fig. 4) curved only weakly in its distal part, distal part broadened; in frontal view (perpendicular to dorsal view) scape evenly curved with its predistal part broadened ventrally, tapering into a lamella, apex of scape bends dorsad thus forming a concavity on the dorsal side of the scape. Each of antennal segments II-VIII longer than broad; antennal segment III at least twice as long as broad; antennal segments IX-XII (the four distal segments) forming a weak club. Compound eyes minute, consisting of 7-10 ommatidia, situated near the midpoint of the sides of the head.

In lateral view, the dorsal outline of the mesosoma almost flat; promesonotal suture wide and deeply depressed, metanotal groove indistinct. Mesosoma in dorsal view distinctly constricted between pronotum and propodeum. Propodeal spiracle directed laterocaudad. Hind tarsus, when five tarsal segments combined, only slightly longer than hind tibia. Petiolar node in dorsal view more than twice as broad as long. Subpetiolar process expanded anteroventrally and forming a rounded apex. Gastral segment I less than twice as broad as long, nearly as broad as segment II.

Head and posterior face of propodeum, dorsa of mesosoma, petiolar node and gastral segment I rugosereticulate; anterodorsal part of head between scape insertion and lateral spine with longitudinal rugae; outer face of each mandible with evenly spaced, oblique rugae; distal part of antennal scape with strong rugae; coxae with strong rugae; dorsa of gastral segments I and II with longitudinal rugae, which are sparsely interconnected by transverse ridges; rugae finer on gastral segment II than on segment I; helcium and girdling constriction of gastral segment II scrobiculate. Intervals between rugae with fine foveolate-reticulate


FIGURES 4-6. Mystrium leonie (holotype, worker): 4-head, frontal view, 5-dorsal view, 6-lateral view.
microsculpture; strength of microsculpture varies greatly among body parts: distinct on anterodorsal and mediodorsal faces of head, on lateral faces of mesosoma, in promesonotal depression, on posterior face of propodeum, on anterior face of petiole, on all gastral segments including the presclerites and on legs; microsculpture on posterodorsal and ventral faces of head, and on dorsa of mesosoma and petiolar node very shal-
low and obscure, i.e. these areas nearly smooth (the less-microsculptured areas were mostly hidden under soil particles, that stuck on the integument [or possibly a mixture of soil particles and integumental secretion], and became visible only after cleaning).

Dorsum of head, antennal scape, antennal segments II-VIII, mesosoma, petiole and dorsum of gaster with decumbent to suberect, bluntly pointed, clavate setae; posterodorsal margin of gastral segments I-IV with a row of subdecumbent, longer and narrower clavate setae; pygidium with both clavate and simple hairs; setae on ventral face of head appressed and simple; hairs on ventrum of gaster subdecumbent and simple; antennal segments IX-XII densely covered with decumbent, simple hairs and a few simple, erect hairs.

Most body parts dark brown to black, except for anterior part of head, mandibles, antennae and gaster which are of a variable lighter, rusty brown color; coloration of legs changing gradually from black coxae to yellow brown distal tarsal segments; integument mostly dull, but the less-microsculptured areas somewhat shining.

Queen and male unknown.
Etymology. Named in dedication to Leonie Geeltje Aimée Wiegel, the daughter of M. Verhaagh, being as unique as this species known from a single specimen. The specific epithet is to be treated as a noun in apposition.

Distribution. The single known specimen was extracted from a leaf litter sample taken in an old growth rainforest near Elelim.

Comments. Species of the genus Mystrium in Madagascar show two distinct reproductive strategies and relevant colony structures (Molet et al. 2006). In some species (e.g. M. rogeri Forel 1899) each colony has a single dealate queen with a larger thorax than workers but with mandibles similar to those of the workers. In colonies of other species (e.g. "M. `red"" in Molet et al. 2006) winged queens are missing and half of the female adults belong to wingless reproductives which are smaller and allometrically distinct from workers. Because of the lack of nest series we cannot know the reproductive strategy adopted by M. leonie. But we can eliminate the possibility that the described specimen of $M$. leonie is not a worker but a wingless reproductive because wingless reproductives in Mystrium have reduced mandibles which are inappropriate for hunting. The holotype of $M$. leonie has well-developed mandibles.

Much of the holotype specimen, and especially the dorsum, is covered with a tightly adhering layer that is presumably soil and/or detritus. This layer in combination with the overall cryptic behavior probably acts as a camouflage for foragers in the leaf litter.

## Mystrium maren Bihn \& Verhaagh, new species

Fig. 7-9, 12, 15

Type material. Holotype: Worker. Indonesia: West Papua Province, Waigeo Island, near Urbinasopen, Gunung Susu, $0^{\circ} 22^{\prime} 45^{\prime \prime} \mathrm{S}, 131^{\circ} 15^{\prime} 10^{\prime \prime} \mathrm{E}, 350-450 \mathrm{~m}$ a.s.l., January 2001 (leg. A. Riedel), deposited at MZB. PARATYPE: worker from the same collection as holotype, deposited at SMNK.

Measurements and indices. Holotype worker: HL 2.46, HW 2.72, CI 111, SL 1.84, SI 68, ML 2,81, WL 2.73, PW 1.37; Paratype worker: HL 2.34, HW 2.64, CI 113, SL 1.71, SI 65, ML 2.81, WL 2.62, PW 1.35.

Diagnosis (worker). The following character combination differentiates M. maren from all its congeners: the outer and inner margins of mandibles in dorsal view parallel and sinuate; the apex of each mandible only slightly expanded and subtruncate; outer face of labrum with a bilateral-symmetric rugoreticulum; maxillary palps 4-segmented; the second segment of the maxillary palp longer than the basal (first) segment; antennal segment III at least twice as long as broad; each anterolateral corner of the head produced into a long and pointed spine; dorsum of head with rugose-reticulate cuticular sculpture and spatulate to clavate hairs; minute compound eyes.


FIGURES 7-9. Mystrium maren (holotype, worker): 7-head, frontal view, 8-dorsal view, 9—lateral view.

Description (worker). General morphology of the worker as shown in figures 7-9. Head wider than long; posterior margin of head in full-face view deeply and roundly emarginate. Each anterolateral corner of the head produced into a forward directed, long and curved spine. Mandibles long and slender; the outer and inner margins of each mandible in dorsal view parallel and distinctly sinuate; the inner margin with two staggered,
longitudinal rows of hamulus-like teeth, each row with 12-14 teeth; teeth of the lower row larger than those of the upper row; the apex of each mandible only slightly expanded and subtruncate; the medioventral corner of the apex with an additional tooth; distal $2 / 3$ on the dorsal face and distal half on the ventral face of each mandible with a longitudinal carina.

Labrum (fig. 15) about twice as wide as long; its distal margin convex with a median emargination; outer (ventral) face of labrum entirely foveolate-reticulate, and overlaid by a peculiar pattern of rugae: one ruga running between basolateral corners in an arc which is parallel to the distal margin and divides the outer surface of the labrum into distal and basal areas; additional rugae delimiting symmetrically two roughly rectangular fields on the median portion of the distal area.

Maxillary palps 4-segmented (fig. 12); the basal (first) segment roughly cone-shaped, shorter and much broader than the second. Labial palps 3 -segmented.

Anterior clypeal margin convex with 9 truncated teeth; the teeth evenly spaced along the clypeal margin, without a median toothless gap. Antennal scape (antennal segment I) in dorsal view (as in fig. 7) curved only weakly and broadened in its distal part, in frontal view (perpendicular to dorsal view) strongly curved, with its predistal part ventrally broadened; apex of scape bends only weakly dorsad in this view. Each of antennal segments II-VI longer than broad; antennal segment III at least twice as long as broad; antennal segments IX-XII (the four distal segments) forming a weak club. Compound eyes minute, consisting of $7-10$ ommatidia, situated near the midpoint of the sides of the head.

In lateral view, the dorsal outline of the mesosoma almost flat; promesonotal suture wide and deeply depressed; metanotal groove distinct but shallower and narrower than promesonotal suture. Mesosoma in dorsal view distinctly constricted between pronotum and propodeum. Propodeal spiracle directed laterad. Hind tarsus, when five tarsal segments combined, only slightly longer than hind tibia. Petiolar node in dorsal view about twice as broad as long. Subpetiolar process expanded anteroventrally and forming a rounded apex. Gastral segment I in dorsal view less than twice as broad as long, nearly as broad as the segment II.

Head and dorsa of mesosoma, petiolar node and gastral segment I rugose-reticulate; anterodorsal part of head between scape insertion and lateral spine with longitudinal rugae; lateral face of each mandible with evenly spaced, oblique rugae; coxae with strong rugae; dorsa of gastral segments I and II with longitudinal rugae, which are sparsely interconnected by transverse ridges; rugae finer on gastral segment II than on I; helcium and girdling constriction of gastral segment II scrobiculate; intervals between rugae with fine foveolatereticulate microsculpture; strength of microsculpture varies greatly among body parts: distinct on anterodorsal and mediodorsal faces of head, on lateral faces of mesosoma, in promesonotal depression, on posterior face of propodeum, on anterior face of petiole, on all gastral segments including the presclerites and on legs; microsculpture on posteriodorsal and ventral faces of head, and on dorsa of mesosoma and petiolar node very shallow and obscure, i.e. the areas nearly smooth (the less-microsculptured areas were mostly hidden under soil particles, that stuck on the integument [or possibly a mixture of soil particles and integumental secretion], and became visible only after cleaning).

Dorsum of head, antennal scape, antennal segments II-VII, mesosoma, petiole and dorsum of gaster with decumbent to suberect, bluntly pointed, narrowly spatulate or clavate setae; posterodorsal margin of gastral segments I-IV with a row of subdecumbent, longer and narrower spatulate setae; pygidium with both spatulate and simple hairs; setae on ventrum of head appressed and simple; hairs on ventrum of gaster subdecumbent and simple; antennal segment IX-XII densely covered with decumbent, simple hairs and a few simple, erect hairs.

Most body parts dark brown to black, except for anterior part of head, mandibles, antennae and gaster which are of a variable lighter, rusty brown color; coloration of legs changing gradually from dark brown coxae to yellow brown apical tarsal segments; integument mostly dull, but the less-microsculptured areas somewhat shining.

Queen and male unknown.


FIGURES 10-15. 10-12. Maxillary palpus (right side): 10—M. camillae (specimen from W-Malaysia: Lake Kenyir), 11-M. leonie (holotype), 12-M. maren (paratype). 13-15. Labrum (ventral side, distal margin at bottom): 13—M. camillae (specimen from W-Malaysia: Lake Kenyir), 14—M. leonie (holotype), 15—M. maren (holotype).

Etymology. Named in dedication to Dr. Maren Scheidhauer, friend of the first author and as beautiful though of low overall resemblance - as this ant. The specific name is an arbitrary combination, to be treated as a noun in apposition.

Distribution. The two known specimens were extracted from a leaf litter sample taken in an old growth rainforest near the summit of Gunung Susu.

Comments. As in M. leonie we cannot determine which reproductive strategy M. maren follows. But we conclude that the described specimen is a worker because wingless reproductives in Mystrium have reduced mandibles which are inappropriate for hunting. This is clearly not the case for the holotype of M. maren.

The holotype and paratype of M. maren show similar camouflage tendencies as described for M. leonie.
Tabular key to Indo-Australian species based on the worker

|  | M. camillae | M. leonie | M. maren |
| :---: | :---: | :---: | :---: |
| Mandibles | Relatively short; the distal $1 / 3$ slightly incurved in dorsal view; the apex of each mandible distinctly expanded and rounded in lateral view, often with a more or less triangular and caudally directed tip at the inner side; dorsal face of each mandible with a carina covering almost its entire length. | Long and slender; basal 2/3 straight, distal $1 / 3$ incurved; the apex of each mandible only slightly expanded and subtruncate in lateral view; distal 3/4 of the dorsal face of each mandible with a longitudinal carina. | Very long and slender; the outer and inner margins of each mandible in dorsal view parallel and distinctly sinuate; the apex of each mandible only slightly expanded and subtruncate in lateral view; distal 2/3 of the dorsal face of each mandible with a longitudinal carina. |
| Maxillary palpi | 4-segmented; the $2^{\text {nd }}$ segment shorter than the $1^{\text {st }} ; 1^{\text {st }}$ segment very broad (fig. 10). | 3-segmented; the $1^{\text {st }}$ segment only slightly broader than the $2^{\text {nd }}$ segment and cylindrical (fig. 11). | 4 -segmented; the $2^{\text {nd }}$ segment longer than the $1^{\text {st }}$; the $1^{\text {st }}$ segment much broader than the $2^{\text {nd }}$ and cone-shaped (fig. 12). |
| Clypeal teeth | 6-7 teeth arranged in 2 groups along the clypeal margin; the 2 groups in most cases separated by a toothless, median gap (fig. 1). | 8 teeth evenly spaced along clypeal margin, without a toothless median gap (fig. 4). | 9 teeth evenly spaced along clypeal margin, without a toothless median gap (fig. 7). |
| Labrum | Weakly developed, irregular rugoreticulum covers entire outer (ventral) face of labrum (fig. 13). | Irregular rugoreticulum on distal half of outer (ventral) face of labrum (fig. 14). | Bilateral-symmetric rugoreticulum on distal half of outer (ventral) face of labrum (fig. 15). |
| Head | With a short, triangular spine on each side. | With a long and curved spine on each side. | With a long and curved spine on each side. |
| Antennae | Length of each segment III-VIII equal to or slightly longer than its maximum width; segment III shorter than twice its width. | Each segment II-VIII longer than its maximum width; segment III at least twice as long as wide. | Each segment II-VIII longer than its maximum width; segment III at least twice as long as wide. |
| Propodeal spiracle | Directed caudad. | Directed laterocaudad. | Directed laterad. |
| Sculpture on posterior face of propodeum | Regular, reticulate microsculpture. | Reticulate microsculpture overlaid by rough rugoreticulum. | Regular, reticulate microsculpture. |
| Petiolar node | Width of node in dorsal view equal to or less than twice its length. | Node in dorsal view more than twice as broad as long. | Node in dorsal view more than twice as broad as long. |

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