

Diversity in the maxillipede dentition of *Mecistocephalus* centipedes (Chilopoda, Mecistocephalidae), with the description of a new species with unusually elongate denticles

Lucio Bonato^{1,3}, Alessandro Minelli^{2,4}

^{1,2} *Dipartimento di Biologia, Università degli Studi di Padova, Via Ugo Bassi 58b, I-35131 Padova, Italy*

³ *E-mail: lucio.bonato@unipd.it*

⁴ *E-mail: alessandro.minelli@unipd.it*

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Abstract

As a contribution to investigate the interspecific diversity in the large genus *Mecistocephalus* Newport, 1843 with respect to these centipedes' predatorial role in soil tropical communities, we compared the patterns of maxillipede denticles in 32 species of the genus, and studied all published relevant information. All *Mecistocephalus* species share a conservative pattern of six distinct denticles on the mesal side of the four articles of each maxillipede. Current views on centipede phylogeny suggest that the basic pattern in *Mecistocephalus* originated from an ancestral array of fewer denticles, by addition of other denticles on the first and fourth articles of the maxillipede. These patterns are not affected by sexual dimorphism, and intraspecific variation for denticle position, size and shape is negligible, but for minor allometry determining a relative increase of the size of some denticles with respect to the maxillipedes during growth. Species differ mainly in size, shape, and orientation of most denticles. Remarkably larger and unusually shaped denticles are found in a hitherto undescribed species from the Seychelles, which is described in this paper as *M. megalodon* n. sp.

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Introduction

Centipedes (Chilopoda) are important predators in most soil communities throughout the world and,

among centipedes, geophilomorphs are especially adapted to creep in the interstices of litter and soil. Common to all centipedes is the unique functional specialisation of the first pair of trunk appendages as poisonous, stinging maxillipedes (also called forcipules or prehensors), which are used to catch prey as well as to keep enemies at distance. Maxillipedes project forwards from below the head, and are used in grasping, poisoning and manipulating other arthropods, earthworms, and probably a larger array of soil animals (Lewis, 1981; Edgecombe and Giribet, 2007).

Out of more than two hundred known genera of geophilomorph centipedes, *Mecistocephalus* Newport, 1843 is one of the richest, comprising more than 130 named species, but many other species still await description or are expected to be discovered after further field research (Bonato *et al.*, 2003). *Mecistocephalus* represents a well-defined clade, clearly diagnosed by many peculiar morphological traits, including a very broad maxillipede segment and especially the remarkably elongated maxillipedes (Fig. 1), which distinctly overreach the anterior margin of the head. *Mecistocephalus* species occur almost exclusively in the tropical and subtropical regions of Africa, Asia and Oceania, where they are often dominant in the centipede communities of forest soils. Recent taxonomic and faunistic investigations contribute to a more adequate understanding of the morphological diversity in the genus (Bonato and Minelli, 2004; Bonato *et al.*, 2004; Uliana *et al.*, 2007).

Despite the ecological impact of *Mecistocephalus* centipedes as predators in many soil communities, our knowledge is fully speculative with respect to their dietary spectrum, their predatory behaviour and other biological aspects of their trophic role, as well as with respect to possible differences between species. In-

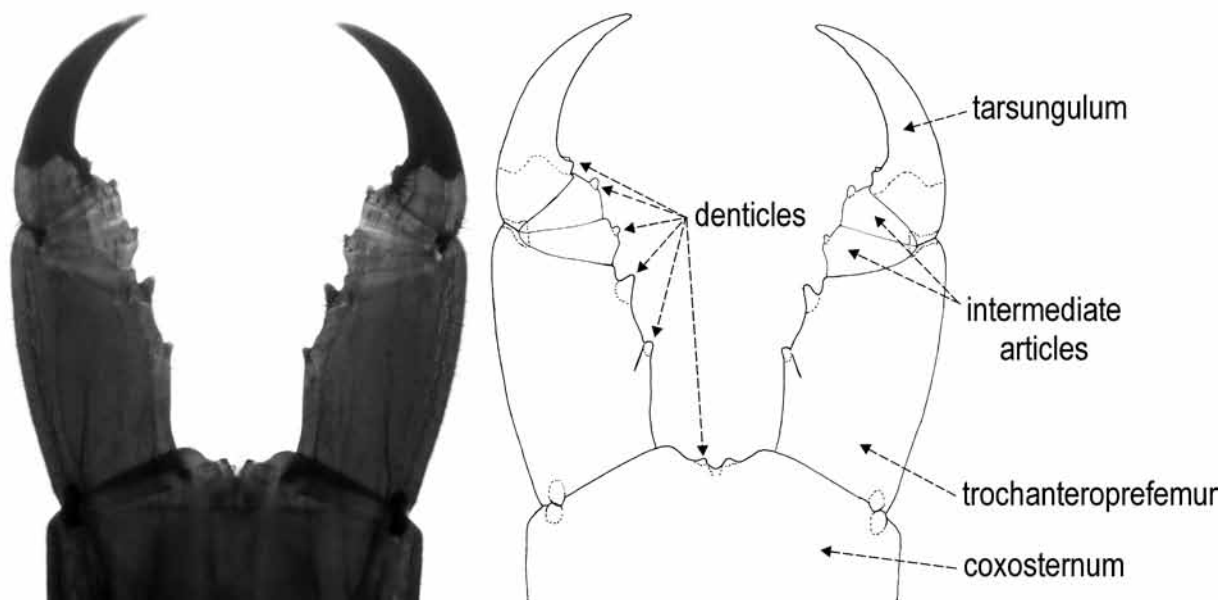


Fig. 1. Structure and shape of the maxillipedes in *Mecistocephalus*: microscopic photograph of the maxillipedes, ventral view, of a specimen of *M. marmoratus* Verhoeff, 1934 (♂, 50 mm, from Beililungshan, Taiwan, coll. MB), and interpretative line-drawing. Descriptive terms for structural elements are indicated.

deed, the interspecific variation in morphological traits that are clearly related to the feeding behaviour has not been adequately explored and documented. Among these traits is the pattern of the sclerotised projections on the mesal side of the maxillipede articles (Fig. 1). All these projections are here referred to as denticles, irrespective of their shape or size, but have been variously called teeth, tubercles, nodes or nodules. Due to the particular position of the condyles between the articles, the maxillipedes perform adduction and abduction on a sub-horizontal plane only and, as a consequence, their mesal denticles are directly involved in the grasping mechanics. Therefore, variation in the pattern of denticles is expected to affect prey selection and efficiency in holding prey.

Even though the maxillipedes of all known *Mecistocephalus* species share a common ground structure and a quite conserved overall shape, preliminary observations have disclosed some interspecific variation in the arrangement, shape and size of the denticles. Published information on such diversity is fragmentary and heterogeneous in quality, because only some authors recognised the interspecific diagnostic value of the pattern of maxillipede denticles (*e.g.*, Crabill, 1970) and therefore their aspect has been hitherto described and illustrated

adequately only for a small number of species.

In this paper, we explore the diversity in the arrangement, size and shape of the maxillipede denticles within the genus *Mecistocephalus* after comparatively examining a significant percentage of the species, as well as integrating all available published information for all known species. Within this comparative analysis, we also document a remarkable array of unusually elongate denticles in a species recently discovered in the Seychelles, which is described here as new.

Material and methods

For the circumscription and species composition of the genus *Mecistocephalus*, we refer to the most recent comprehensive treatments (mainly Minelli, 2006; updated by Uliana *et al.*, 2007, and Bonato and Minelli, in press). Accordingly, *Mecistocephalus* is considered here to include *Brachyptyx* Chamberlin, 1920, *Dasyptyx* Chamberlin, 1920, *Ectoptyx* Chamberlin, 1920, *Formosocephalus* Verhoeff, 1937, *Fusichila* Chamberlin, 1953 and *Megalacrus* Attems, 1953; the identity of all these nominal genus-group taxa has been already discussed (Bonato *et al.*, 2003, 2004; Uliana *et al.* 2007).

We took into account all species currently considered valid within *Mecistocephalus* (following Minelli, 2006, and subsequent papers). However, we excluded the nominal species *Mecistocephalus pilosus* Wood, 1862, because its inclusion in the genus *Mecistocephalus* is uncertain.

Intraspecific variation in the pattern of maxillipede denticles, particularly with respect to changes during growth and inter-individual variation, was tested in two species for which large series of specimens of different body length were available to study, namely *M. karasawai* Uliana, Bonato and Minelli, 2007 (82 specimens, body length 11–55 mm, from Kyushu and Ryukyu islands; collections NSMT and MB; see below for abbreviations) and *M. diversisternus* (Silvestri, 1919) (37 specimens, body length 20–55 mm, from Honshu, Ryukyu islands, and Taiwan; collections HWC, MB, TT).

Interspecific variation in the pattern of maxillipede denticles was assessed by comparing 32 species. Species were selected in order to represent all different morphologically recognizable groups or clades within *Mecistocephalus*, based on previous phylogenetic and taxonomic studies (Bonato *et al.*, 2003; Bonato and Minelli, 2004; Uliana *et al.*, 2007). A total of 1 to 5 specimens were examined for each species. As far as possible, in order to control for possible allometric effects and other changes during growth, we selected specimens with body length in the range of 3–5 cm and maxillipede coxosternum width in the range of 1.2–2.0 mm (values found in adult specimens of most species of *Mecistocephalus*). Furthermore, in order to check for possible sexual dimorphism, we examined both males and females for each species, whenever available.

Maxillipedes were examined through light microscopy, after removing the head. Specimens were cleared under ethylene glycol and mounted on temporary slides, in ventral view, following standard procedures for geophilomorphs (Pereira, 2000; Foddai *et al.*, 2002). Photographs were taken for each specimen by means of a digital camera applied to a microscope Leica DMLB, after standardizing the position of the specimen and the photographic conditions; for each specimen, a series of 4 to 8 photographs taken at different focal planes was assembled using the software CombineZM (Hadley, 2008). Profiles of the mesal margin of the maxillipedes were drawn based on the photographs obtained, and superimposed according to alternative criteria; lack of obvious landmarks along the profile did not allow applying quantitative morphometric approaches.

A complete survey of the literature on *Mecistocephalus* was also performed, in order to retrieve all published information on the pattern of maxillipede denticles of different species, through either descriptions or illustrations of representative specimens. Information based on specimens overtly misidentified (often under the names *M. punctifrons*, *M. maxillaris* or *M. insularis*; see Bonato and Minelli, 2004) was considered after emending the identification whenever possible.

The evolution of major features in the pattern of maxillipede denticles in the family Mecistocephalidae was inferred by optimizing selected characters on the only available phylogenetic tree of the family (Bonato *et al.*, 2003), following the parsimony criterion and applying both AccTran and DelTran options.

For descriptive purposes, we followed the traditional morphological terminology (as illustrated in Fig. 1), even though it rests on possibly unwarranted assumptions on the homology between the articles of the maxillipedes and those of the walking legs.

Abbreviations for collections: BM = Bishop Museum, Honolulu; CAS = California Academy of Sciences, San Francisco; HLD = Hessisches Landesmuseum, Darmstadt; HWC = H.-W. Chang, National Sun Yat-Sen University, Kaohsiung, Taiwan; LD = L. Deharveng, Univ. P. Sabatier, Toulouse; MB = A. Minelli and L. Bonato, Univ. Padova; MVR = Museo civico di Storia naturale di Verona; NHML = Natural History Museum, London; NSMT = National Science Museum, Tokyo; PB = P. Beron, Bulgarian Academy of Sciences, Sofia; SI = Smithsonian Institution, National Museum of Natural History, Washington; SM = Senckenberg Museum, Frankfurt am Main; TT = T. Tanabe, Kumamoto University, Kumamoto; VD = K. Van Damme, Ghent Univ.; ZMC = Zoological Museum, Copenhagen Univ.

Results and discussion

The basic pattern of maxillipede denticles

Common to most species of *Mecistocephalus* is an array of denticles on the mesal side of each maxillipede, comprising (Fig. 1):

- two denticles on the trochanteroprefemur, one distal to the other; the basal denticle emerges proximal to a weak furrow that runs transversally on the mesal side of the trochanteroprefemur (such furrow was hypothesised to correspond to a putative ancestral articulation between two distinct articles; Crabill,

1970); the distal denticle emerges just proximal to the distal end of the trochanteroprefemur;

- a single denticle on each of the two intermediate articles;
- two denticles close to the basis of the tarsungulum, one dorsal to the other.

Of all these denticles, those on the trochanteroprefemur are the largest, those on the tarsungulum the smallest; of the trochanteroprefemoral denticles, the distal one is usually more conspicuous than the basal one; in the same way, of the denticles of the intermediate articles, the distal one is usually larger than the basal one.

With respect to the resting position of the maxillipedes, all denticles are projecting antero-mesally.

In addition to the denticles along the appendages, two paired denticles emerge on the anterior margin of the coxosternum, from a shallow sinus between the maxillipedes (Fig. 1).

Intraspecific variation

Examination of conspecific specimens of different body size of two representative species of *Mecistocephalus* showed that number, arrangement and shape of the denticles do not change significantly during growth. Instead, the relative size of the basal trochanteroprefemoral denticle increases slightly with respect to the other denticles and the maxillipede as a whole, at least in *M. karasawai*. A comparable allometry was already found in *M. tahitiensis* by Silvestri (1919). Independent from body size, we found only minor inter-individual variation in the size of denticles within each of the species examined.

Our observations suggest that the pattern of maxillipede denticles in *Mecistocephalus* species is indeed affected by some intraspecific variation, but this can be regarded as

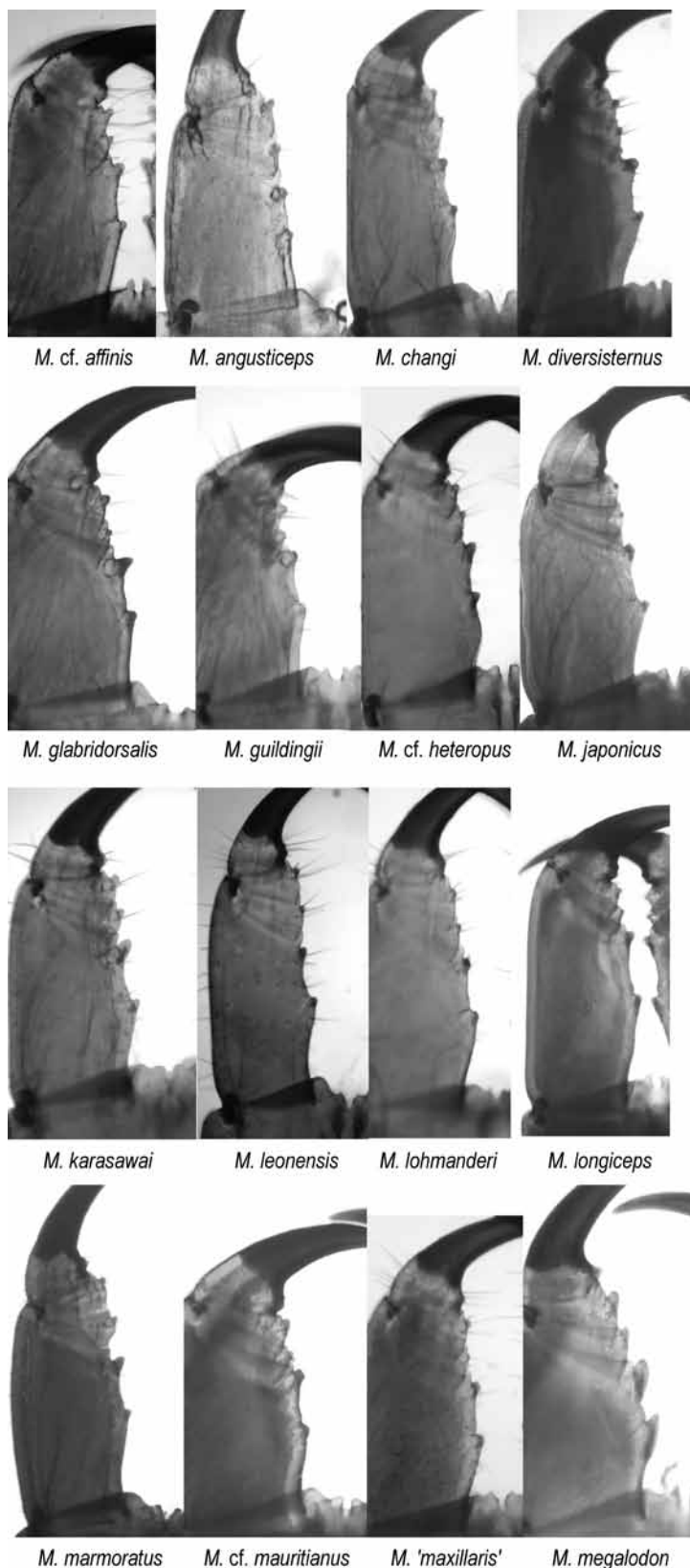
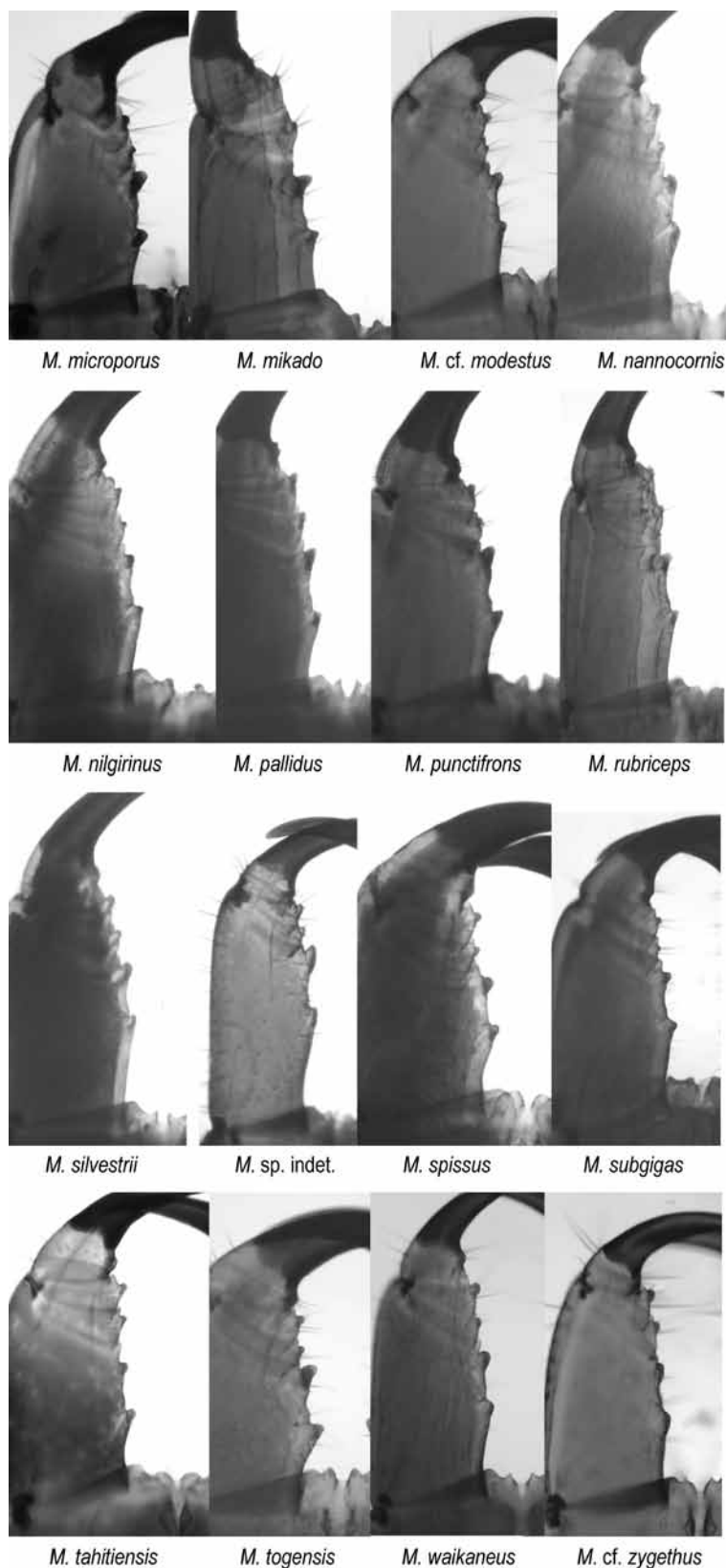


Fig. 2. Diversity in the maxillipede denticles between *Mecistocephalus* species: microscopic photographs of the right maxillipede, ventral view, of representative specimens. Species are illustrated according to the alphabetic order. Data on specimens are given in Appendix 2.



negligible compared to interspecific differences. Published information for other species is consistent with this assumption. However, as the relative size of the denticles may actually change with growth, we performed our comparison between species after controlling, as far as possible, for the body size of the specimens examined (see Material and methods).

Sex-related differences were not found in any of the species examined. More generally, sexual dimorphism in *Mecistocephalus* is very slight in the external morphology, but for the genital region: consistent differences between sexes have to date only been detected in the maximum body size (females growing slightly larger than males) and the elongation of antennae (these are slightly more elongate in males than in females) (Bonato and Minelli, 2004). Furthermore, no case of sexual differences in the external morphology of maxillipedes has been reported for any geophilomorph species.

Interspecific diversity and the unusual pattern of maxillipede denticles in M. megalodon n. sp.

Direct examination of 32 representative species of *Mecistocephalus* (Fig. 2) and study of all published information for all species in the genus revealed interspecific diversity in the following features.

The denticles on the anterior margin of coxosternum are always present, but variable in relative size (from almost inconspicuous, *e.g.*, in *M. angusticeps*, to very large, *e.g.*, in *M. affinis*), shape (from stout and rounded, *e.g.*, in *M. tahitiensis*, to sharply pointed, *e.g.*, in *M. silvestrii* and *M. megalodon n. sp.*), and degree of forward projection from the coxosternal margin (from not distinctly projecting because emerging from inside a deep concavity, *e.g.*, in *M. glabri-dorsalis*, to conspicuously projecting, *e.g.*, in *M. affinis*).



Fig. 3. Diversity in the denticles of the trochanteroprefemur in *Mecistocephalus* species: superimposed profiles of the mesal margin of the right trochanteroprefemur in representative specimens of 32 species, taken from the microscopic photographs in fig. 2. Alternative superimpositions have been obtained selecting different landmarks (empty circles, indicated by arrows): (a) the distal bases of the two denticles; (b) the distal basis of the basal denticle and distal end of the mesal margin of the trochanteroprefemur. The profile of *M. megalodon* n. sp. is indicated by a thicker line.

The denticles on the trochanteroprefemur are variable in relative size with respect to the article (from very tiny, *e.g.*, in *M. zygethus*, to much larger, *e.g.*, in *M. karasawai*), general shape (for example, stout with rounded tip, in *M. waikaneus*; stout with flattened tip and thus with an angulated profile, *e.g.*, in *M. japonicus*; long with pointed tip, *e.g.*, in *M. marmoratus*), especially in the orientation (usually projecting straight in mesal-anterior direction, *e.g.*, in *M. rubriceps*, but sometimes distinctly bending mesally, *e.g.*, in *M.*

glabridorsalis, or instead straight projecting anteriorly, *e.g.*, in *M. megalodon* n. sp.) and aspect of the mesal profile (from concave, *e.g.*, in *M. togensis*, to almost straight, *e.g.*, in *M. pallidus*, or convex, *e.g.*, in *M. megalodon* n. sp.; sometimes peculiarly sinuous, *e.g.*, in *M. punctifrons*) (see also Fig. 3 for a direct comparison of profiles).

According to the literature, the basal denticle of the trochanteroprefemur is apparently so inconspicuous in some species that it has been described and illustrated as virtually absent in *M. conspicuus* Attems, 1938 (Attems, 1938; Lewis, 1991), *M. manazurensis* Shinohara, 1961 (Shinohara, 1961: fig. 5), and *M. satumensis* Takakuwa, 1938 (Takakuwa, 1938: fig. 4). Peculiar conditions are reported for a few other species: both denticles are illustrated as unusually very slender in *M. momotoriensis* Takakuwa, 1938 (Takakuwa, 1938: fig. 2); the distal denticle is illustrated as remarkably expanded in *M. insularis* (Lucas, 1863) (Brölemann, 1926: fig. 167); both denticles are distinctly curved backwards and thus appearing hook-like in *M. uncifer* (Silvestri, 1919) (Silvestri, 1919).

Also the denticles on the intermediate articles are always present but variable in relative size with respect to the maxillipedes (from very tiny, *e.g.*, in *M. japonicus*, to much larger, *e.g.*, in *M. heteropus* and *M. megalodon* n. sp.), general shape (usually stout with rounded tip, *e.g.*, in *M. microporus*, but sometimes more swollen and projecting, *e.g.*, in *M. waikaneus*, or stout with flattened tip, *e.g.*, in *M. lohmanderi*). As a rule, size and shape of these denticles correlate with those of the denticles on the trochanteroprefemur.

The denticles at the basis of the tarsungulum are variable in relative size with respect to the maxillipede, but also in their apparent number (from two distinct denticles, *e.g.*, in *M. marmoratus*, to a single shallow bulge, *e.g.*, in *M. tahitiensis*). Additional projections on the tarsungulum are known for one species only, *M. aethelabis* Bonato and Minelli, 2004: in the single known specimen, each tarsungulum bears a peculiar shallow projection at about the mid-length of the internal margin (Bonato and Minelli, 2004).

A new species recently discovered in the Seychelles, described below as *M. megalodon* n. sp. (Appendix 1; fig. 6), is remarkable in its pattern of maxillipede denticles. With respect to the diversity hitherto known and here comparatively assessed for the whole genus *Mecistocephalus*, *M. megalodon* n. sp. appears exceptional in the relative elongation, and therefore the overall size, of the whole set of denticles (Fig. 4). Particularly unusual are also the profile, and thus the

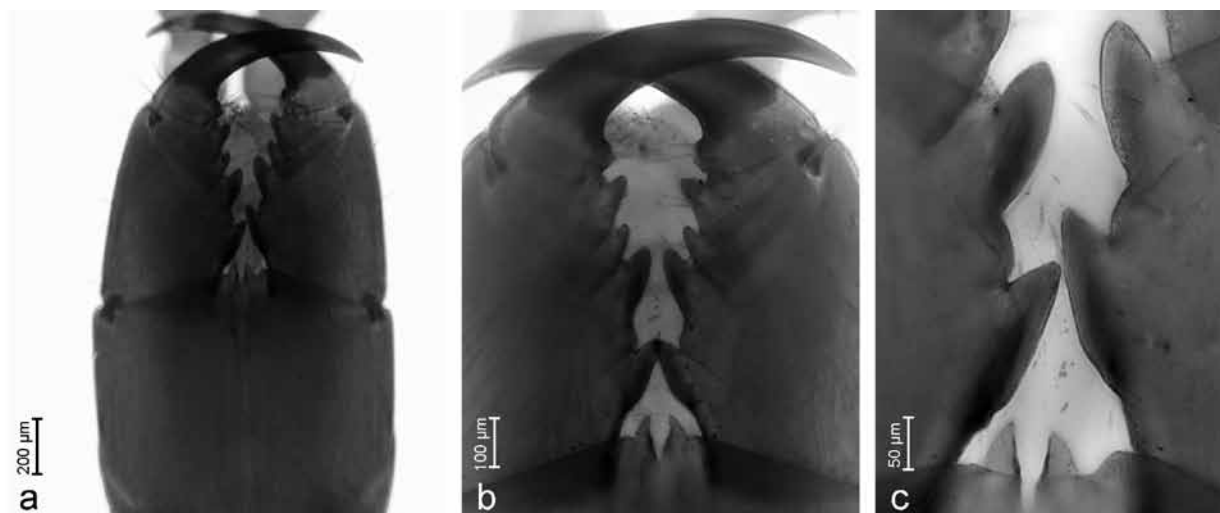


Fig. 4. Maxillipede denticles of *Mecistocephalus megalodon* n. sp.: a, maxillipede segment; b, internal margin of maxillipedes; c, denticles of the trochanteroprefemur. Microscopic photographs taken in ventral view from two ♂♂, both 32 mm long, from Aride, Seychelles islands, II-1999, J. Cadbury leg., coll. MB (a, c from a specimen, b from the other specimen).

overall shape, of the denticles of the trochanteroprefemur (Figs 3, 4): the profile of the basal denticle appears approximately 'securiform' (axe-shaped), whereas that of the distal one appears more 'lanceolate' (lance-shaped). Out of all known species of *Mecistocephalus*, these profiles resemble in some respect those found in another species only (still undescribed, Fig. 2), but in the latter species the denticles are much smaller than in *M. megalodon* n. sp.

The evolutionary differentiation of a species with very elongated maxillipede denticles within a clade characterised by moderately elongated denticles, as observed in the case of *M. megalodon* n. sp., probably parallels similar evolutionary transitions that have occurred in a few other lineages of geophilomorphs, distantly related to each other. An example is provided by *Schendyla armata* Brölemann, 1901 (Schendyliidae), which is characterised by a very elongated subconic denticle emerging at the distal end of the trochanteroprefemur (Brölemann, 1930), as opposed to the less conspicuous denticles in all other species in the genus *Schendyla* Bergsøe and Meinert, 1866.

Evolution of maxillipede denticles in the mecistocephalids

An analysis of the evolutionary changes that gave rise to the diversity currently observed in *Mecistocephalus* is hindered by the lack of resolution of the internal phylogeny of the genus obtained by Bonato *et al.*

(2003). Instead, the evolutionary origin of the general pattern of maxillipede denticles that is common to all extant species of Mecistocephalidae, and therefore most probably ancestral to the genus, may be traced back by extending the comparative analysis to all major clades recognised in the family Mecistocephalidae, as well as to the most closely related lineages, namely the Adesmata and the Scolopendromorpha, and exploiting the available genus-level phylogeny of the family (Fig. 5).

Common to all mecistocephalids, and therefore featuring as the ancestral condition of the family, is the presence of a pair of denticles on the coxosternal margin and a denticle on the trochanteroprefemur that corresponds to the distal one of the two present in *Mecistocephalus*. This condition could be a plesiomorphic trait, as possibly homologous sclerotised projections are present in the same position in different Adesmata and Scolopendromorpha, but this remains uncertain as a large variation occurs within both these two groups and their internal phylogeny remains broadly unresolved (Edgecombe and Giribet, 2004, 2007; Koch *et al.*, 2009).

Also the presence of denticles on the intermediate articles could be ancestral to the whole family Mecistocephalidae, but the variation observed within different genera suggests that those intermediate denticles could have undergone multiple evolutionary losses and gains. Even less clear is whether a basal denticle on the tarsungulum is ancestral to the whole family

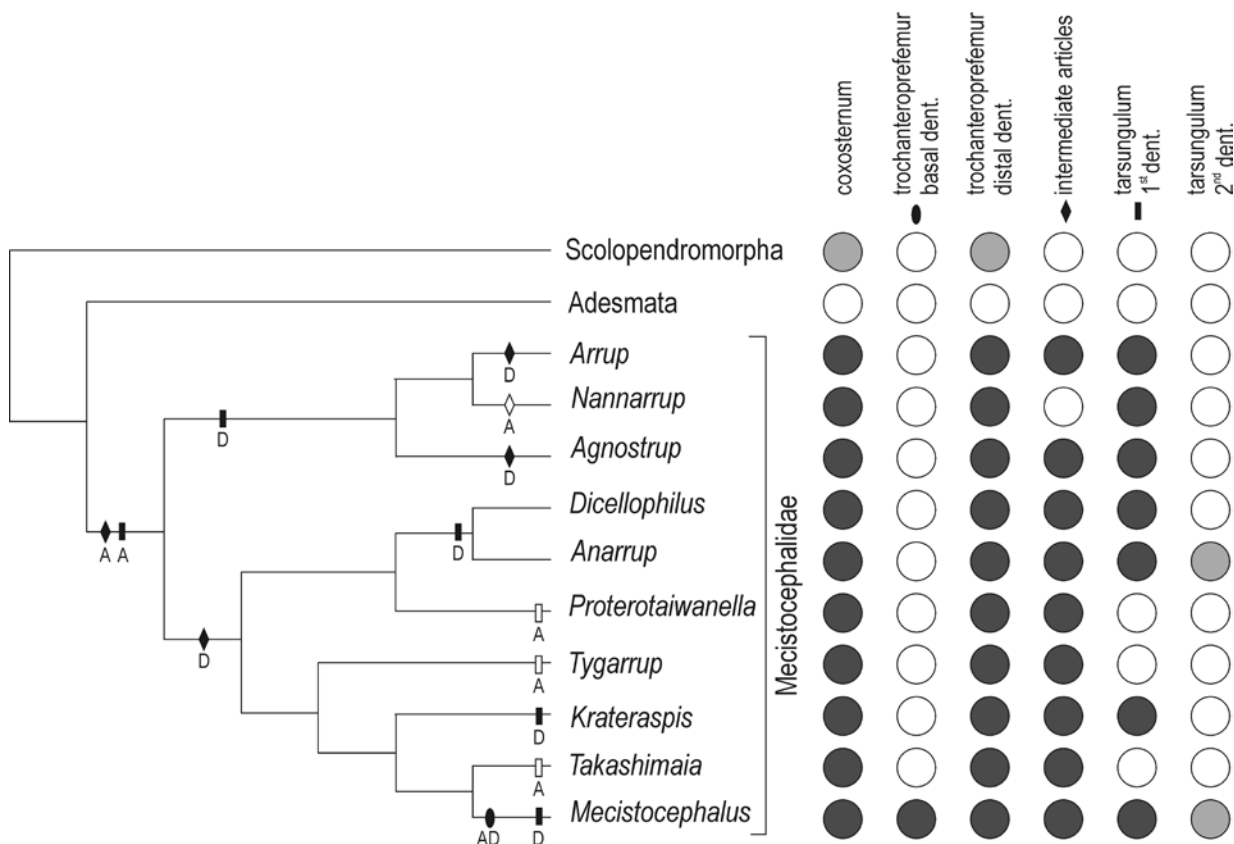


Fig. 5. Evolution of the pattern of maxillipede denticles in the Mecistocephalidae. Presence of denticles (dent.) in different positions is scored for each clade (when variability is present within a clades, the most probable ancestral condition for the clade is considered): black-filled = present; grey-filled = uncertain; empty = absent. Transitions reconstructed under AccTran (A) or DelTran (D) options are marked on the tree by different symbols (empty for reversal). Sources: phylogeny from Bonato *et al.* (2003); ancestral characters states for Adesmata and Scolopendromorpha mainly based on Foddai and Minelli (2000), Edgecombe and Giribet (2004, 2007), and Koch *et al.* (2009).

and went lost in some clades, or has been repeatedly acquired by different clades (Fig. 5).

Most probably, the basal denticle on the trochanteroprefemur originated at the root of the *Mecistocephalus* clade. It is lacking in all other mecistocephalids, even though a shallow bulge in a few species of *Arrup* (Uliana *et al.*, 2007) could be interpreted as corresponding in position to the basal denticle of *Mecistocephalus*, however not affecting our evolutionary inference. If confirmed, the putative lack of this basal denticle in a few species of *Mecistocephalus* could be explained by secondary loss, as at least one of these species (*M. conspicuus*) came out nested within many other congeneric species in the phylogenetic analysis by Bonato *et al.* (2003). Worth noting is that a similar basal trochanteroprefemoral denticle is present in some other lineages of Adesmata, *e.g.*, within the Aphilo-

dontidae and the Geophilidae, which however are only distantly related to Mecistocephalidae (Edgecombe and Giribet, 2004, 2007) and therefore an independent origin may be assumed.

The presence of a pair of basal denticles, instead of a single one, at the basis of each tarsungulum originated at the root of either *Mecistocephalus* or a subclade of this genus. Indeed, a pair of distinct denticles were detected in another mecistocephalid species, *Anarrup flavipes* (Attems, 1930) (Bonato *et al.*, 2003) and could be a common feature of the small, very distinct genus *Anarrup* Chamberlin, 1920. However, this is most probably due to evolutionary convergence, as *Anarrup* is only distantly related to *Mecistocephalus*, whereas the most closely related genera *Takashimaia* Miyosi, 1955 and *Krateraspis* Lignau, 1929 have only a shallow bulge at the basis of the tarsungulum.

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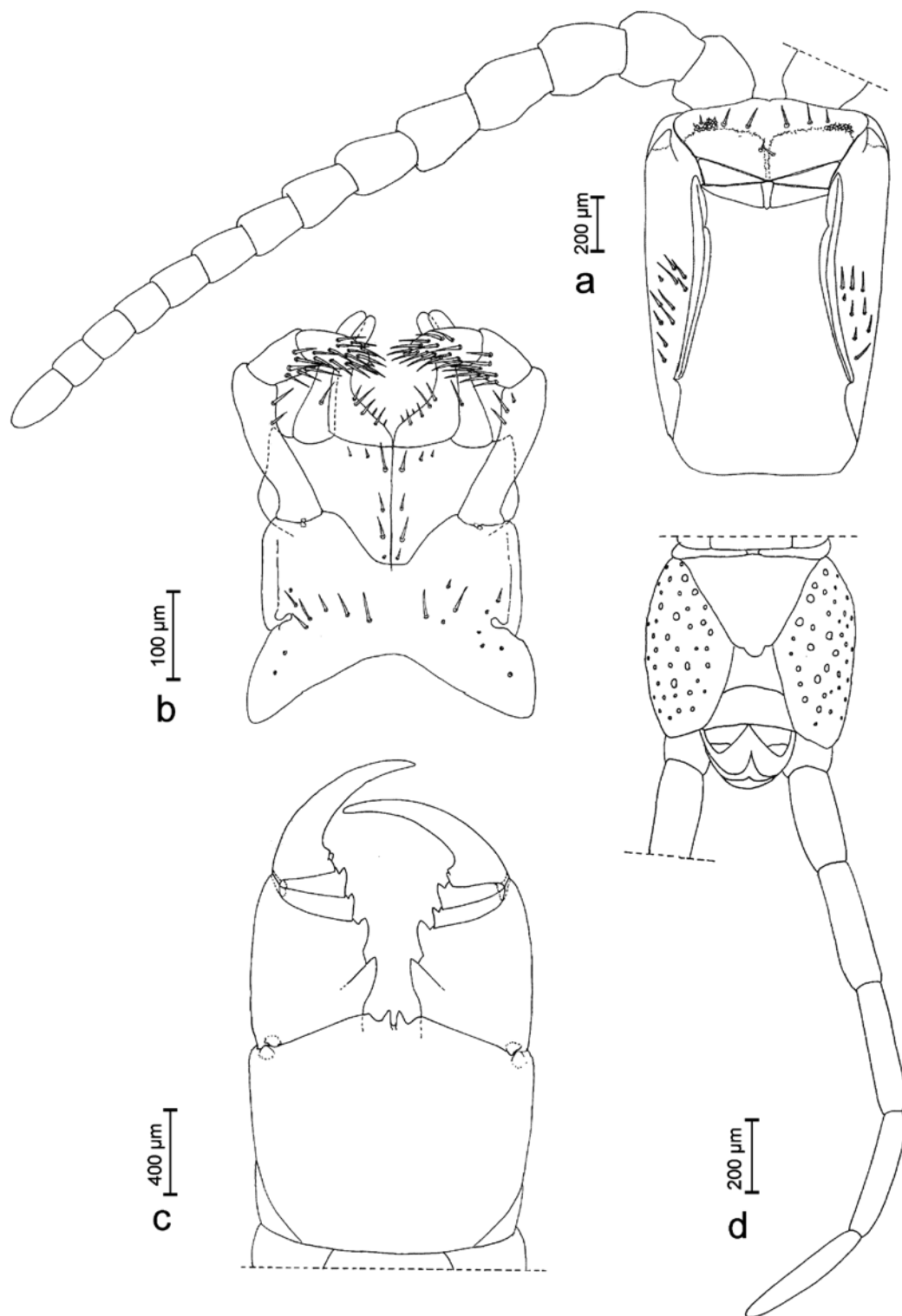


Fig. 6. *Mecistocephalus megalodon* n. sp., holotype (♀, adult, 45 mm long; from Aride, Seychelles islands, 0 m a.s.l., II-1999, J. Cadbury leg.). a, cephalic capsule and right antenna, ventral view (maxillary complex and mandibles detached; antennal setae and left antenna not drawn; clypeal areolation drawn only in part). b, maxillary complex, ventral view. c, maxillipede segment, ventral view. d, last leg-bearing segment and posterior tip of the trunk, ventral view (distal part of the right leg lacking; setae not drawn).

Appendix 1

Description of *Mecistocephalus megalodon* n. sp.

Holotype: ♀, adult, 45 mm long; from Aride (Seychelles islands), 0 m a.s.l., II-1999, J. Cadbury leg., coll. NHML.

Other material examined: 3 ♂ and 3 ♀, sub-adults to adults, 24 to 37 mm long, from Aride (Seychelles islands), 0 m, II-1999, J. Cadbury leg.; 1 ♀, sub-adult, 26 mm long, from Aride (Seychelles islands), XI-2000; 1 ♂, sub-adult, 23 mm long, from Aride (Seychelles islands), 20-III-2002; 1 ♂, adult, 30 mm long, from Cousine (Seychelles island), 0 m, 13-III-1998, J. Kelly leg., coll. MB.

Diagnosis: a *Mecistocephalus* species with invariantly 49 leg-bearing segments; head and most anterior trunk segments reddish brown, contrasting with the paler yellow remaining trunk; areolate part of the clypeus without non-areolate insulae; clypeus with about three pairs of setae on the areolate part, arranged in an almost transverse row, and a pair of setae in the plagulae, close to the mid-longitudinal areolate stripe, at about 1/3 of medial length of the stripe; buccae with setae on the posterior half only; maxilliped cerrus absent; denticles on the anterior margin of the maxilliped coxosternum and on the mesal side of the maxillipedes very elongate, pointed and projecting forwards; each tarsungulum with two distinct basal denticles; sternal mid-longitudinal sulcus anteriorly furcate, with an obtuse angle; sternum of the last leg-bearing segment sub-triangular, wider than long, with a distinct medial posterior projection.

Description of the holotype (see also Fig. 6).

Condition of the specimen. Body in four pieces: head without maxillae; maxillary complex; anterior part of the trunk (including the most anterior 35 leg-bearing segments); posterior part of the trunk (including the most posterior 14 leg-bearing segments). Some legs lacking, including the distal part of the right leg of the last pair.

Color (in alcohol): head and most anterior trunk segments reddish brown, gradually but distinctly changing into yellow in the remaining body, without dark patches.

Cephalic capsule. Head plate 1.6 times as long as wide; frontal line rounded. Antennae 3.3 times as long as the head width. Apical sensilla about 10 μ m long, with a distinct transverse crown-like projection at about 1/3 of the length. Club-like sensilla on the external sides of antennal articles VII-XIV of both antennae, and on the internal sides of antennal arti-

cles IX-XIV of the right antenna and XI-XIV of the left antenna. Clypeus about 2.5 times as wide as long; areolate part without smooth insulae; mid-longitudinal extent of the plagulae about half of the clypeus; three pairs of setae approximately aligned inside the areolate part, and another pair flanking closely the areolate mid-longitudinal stripe at about 1/3 of medial length of the stripe; no evident sensilla or pores on the clypeus. Labrum: anterior ala subtriangular, medially reduced to a point; posterior ala with medial margins convergent posteriorly, their postero-medial corners slightly projecting; posterior margin of each side-piece uniformly slightly convex, without crenulation and without hair-like projections. Spicula distinctly bent medially; each bucca with eight setae, in the posterior half only.

Mandibles. Each mandible with 12 well-developed lamellae; first lamella with six teeth; average intermediate lamella with about 30 teeth; basal tooth of the mandible rounded, not overreaching the first tooth of the first lamella, with margin only sparsely scalloped.

First maxillae. Coxosternum with 4 paramedian pairs of setae, and a few other setae close to the anterior margin; antero-external corners slightly projecting. Each medial projection about 2.0 times as long as wide, with eight-nine setae on the basal part, and distal lobe almost uniformly narrow. Each telopodite about 3.4 times as long as wide, slightly sinuate along the external margin, with two setae on the basal part, the distal part almost uniformly narrow.

Second maxillae. Coxosternum about 1.4 times as wide as long; total length about 2.0 times the mid-longitudinal length; wide medial band and posterior marginal band uniformly areolate, without non-areolate areas; many scattered setae on the posterior half. First article of telopodite about 4.9 times as long as wide; with two-three setae. Third article about 2.4 times as long as wide, with many setae; apical claw well developed.

Maxilliped segment. Tergum about 1.3 times as wide as long, its exposed part about 1.4 times as wide as long, with a distinct mid-longitudinal groove. Pleurites with a well sclerotised dorsal ridge, the anterior tip not particularly elongate. Exposed part of coxosternum about 1.2 times as wide as long; cerrus absent; no condylar projections; anterior margin with a pair of elongate, pointed denticles. Trochanteroprefemur about 1.4 times as long as wide, with two

well developed denticles, the basal one only slightly smaller and its margin less convex than the distal one; each of the intermediate articles with a well developed denticle, that on the third article larger than the other, both distinctly smaller than those of trochanteroprefemur; tarsungulum with two subconic basal denticles, the dorsal one more projecting than the other. Poison calyx reaching about 0.6 of the length of trochanteroprefemur.

Leg-bearing trunk. A total of 49 leg-bearing segments. Sternal sulcus furcate, anterior angle between the branches from about rectangular on a few most anterior segments to about 120° wide on the other segments. Length of leg I about half of that of leg II.

Last leg-bearing segment. Tergum subrectangular, about 1.7 times as long as wide. Sternum subtriangular, about 1.2 times as wide as long; the lateral margin strongly converging backwards, almost straight, only slightly sinuous; a distinct medial posterior rounded

projection; dense setae on the posterior half. Each coxopleuron about 1.8 times as long as the sternum, covered with tens of scattered pores of various size. Telopodite about 2.0 times as long as that of the preceding leg, with a tiny sub-apical spine.

Posterior tip of the trunk. Gonopods well developed, subtriangular, bi-articulate, almost touching each other at the basis. A pair of anal pores.

Description of a male (30 mm long, from Cousine; collection data given above).

Differing from the female holotype only in the posterior tip of the trunk: gonopods bi-articulate, slender, with a rounded tip, well separated from each other by a sub-conic genital projection in between.

Etymology: from ancient Greek *μεγας* (big) and *οδους, οδοντος* (tooth); referring to the unusually large size of the maxillipede denticles.

Appendix 2

Specimens illustrated in Fig. 2.

- M. cf. affinis* Lawrence, 1960: ♂, 32 mm, 49 leg pairs, from Madagascar, III-1969, W.L. Brown leg., coll. SI
- M. angusticeps* (Ribaut, 1914): ♀, 15 mm, 47 leg pairs, from Picard Island, Seychelles, 9-IX-2005, K. Mach & O. Maurel leg., coll. MB
- M. changi* Uliana, Bonato and Minelli, 2007: ♀, 50 mm, 49 leg pairs, from Yungan, Taiwan, date unknown, H.W. Chang leg., coll. MB
- M. diversisternus* (Silvestri, 1919): ♀, 40 mm, 57 leg pairs, from Aono, Minami-izu-machi, Japan, 26-VIII-1978, K. Ishii leg., coll. MB
- M. glabridorsalis* Attems, 1901: ♀, 32 mm, 49 leg pairs, from Mont Plaisir, Silhouette, Seychelles, 11-VIII-2000, J. Gerlach leg., coll. MB
- M. guildingii* Newport, 1843: ♂, 24 mm, 49 leg pairs, from Smith's, Bermuda, 2-IV-1976, collector unknown, coll. NHML
- M. cf. heteropus* Humbert, 1865: ♀, 26 mm, 49 leg pairs, from Dambula, Sri Lanka, 25-XII-1984, P. Beron & S. Andreev leg., coll. PB
- M. japonicus* Meinert, 1886: ♀, 68 mm, 63 leg pairs, from Odamiyama, Japan, 19-VI-1996, E. Yamamoto leg., coll. MB
- M. karasawai* Uliana, Bonato and Minelli, 2007: ♀, 30 mm, 49 leg pairs, from Mt. Nishime, Japan, 13-XI-2001, S. Karasawa leg., coll. MB
- M. leonensis* (Cook, 1896): ♂, 38 mm, 49 leg pairs, from Ribeira Seca, Santiago Id, Cabo Verde, 26-I-1988, P.T. Bailey leg., coll. ZMC
- M. lohmanderi* Verhoeff, 1939: ♀, 29 mm, 49 leg pairs, from La Passe, Silhouette, Seychelles, 16-VII-2000, collector unknown, coll. MB
- M. longiceps* Lawrence, 1960: ♂, 50 mm, 49 leg pairs, from Majakatempo, Madagascar, 25-XI-1959, E.S. Ross leg., coll. CAS
- M. marmoratus* Verhoeff, 1934: ♂, 50 mm, 49 leg pairs, from Beililungshan, Taiwan, date unknown, collector unknown, coll. MB
- M. cf. mauritanus* Verhoeff, 1939: ♀, 52 mm, 49 leg pairs, from Petrin, Mauritius Is., 31-III-1969, W.L. Brown leg., coll. SI
- M. 'maxillaris'* sensu Silvestri (1919): ♀, 38 mm, 49 leg pairs, from Haiku, Maui, Hawaii Ids, 20-III-1967, N.L.H. Krauss leg., coll. BM
- M. megalodon* n. sp.: ♀, 45 mm, 49 leg pairs, from Aride, Seychelles, II-1999, J. Cadbury leg., coll. NHML
- M. microporus* Haase, 1887: ♀, 52 mm, 93 leg pairs, from Cebu, Philippines, 31-I-1980, V. Cottarelli leg., coll. MVR
- M. mikado* Attems, 1928: ♀, 37 mm, 49 leg pairs, from Shiauliouchiou, Taiwan, date unknown, H.W. Chang leg., coll. MB
- M. cf. modestus* (Silvestri, 1919): ♀, 32 mm, 49 leg pairs, from Kuper-Range, Wau, Papua New Guinea, 10-X-1992, A. Riedel leg., coll. CAS
- M. nannocornis* Chamberlin, 1920: ♀, 40 mm, 45 leg pairs, from San Jose, Mindoro, Philippines, III-1945, E.S. Ross leg., coll. CAS
- M. nilgirinus* Chamberlin 1920: ♀, 55 mm, 49 leg pairs, from Koraput, India, 2-II-1962, E.S. Ross & D.Q. Cavagnaro leg., coll. MB
- M. pallidus* (Silvestri 1919): ♂, 40 mm, 49 leg pairs, from Netarhât, India, 11-XI-1961, E.S. Ross & D.Q. Cavagnaro, coll. MB
- M. punctifrons* Newport, 1843: ♂, 50 mm, 49 leg pairs, from 8 mi. NE of Tuni, India, 5-II-1962, E.S. Ross & D.Q. Cavagnaro leg., coll. MB
- M. rubriceps* Wood, 1862: ♂, 41 mm, 49 leg pairs, from Chichijima, Ogasawara, Japan, 18-I-1996, K. Ishii leg., coll. MB
- M. silvestrii* Bonato and Minelli, 2004: ♀, 50 mm, 49 leg pairs, from Kâthgodâm, India, 30-XI-1961, E.S. Ross & D.Q. Cavagnaro leg., coll. MB
- M. sp. indet.*: ♀, 47 mm, 51 leg pairs, from Abd al Kuri, Yemen, 17-18-II-1999, K. van Damme leg., coll. VD
- M. spissus* Wood, 1862: ♂, 42 mm, 45 leg pairs, from Necker, Hawaii Islands, VI-1923, E.H. Bryan leg., coll. BM
- M. subgigas* (Silvestri, 1919): ♀, 75 mm, 49 leg pairs, from Finschhafen, Papua New Guinea, 10-V-1944, E.S. Ross leg., coll. CAS
- M. tahitiensis* Wood, 1862: ♀, 48 mm, 47 leg pairs, from Puerto Princesa, Philippines, 4-II-1981, G.B. Osella & V. Cottarelli leg., coll. MVR
- M. togensis* (Cook, 1896): ♀, 36 mm, 49 leg pairs, from 56 km N of Matadi, Democratic Republic of the Congo, 28-VII-1957, E.S. Ross & R.E. Leech leg., coll. CAS
- M. waikaneus* Chamberlin, 1953: ♂, 23 mm, 49 leg pairs, from Hawaii, Hawaii Ids, 22-I-1974, J. Jacobi leg., coll. BM
- M. cf. zygethus* Chamberlin, 1939: ♀, 36 mm, 51 leg pairs, from Batu Lubang, Halmahera, Indonesia, 24-VII-1988, L. Deharveng & A. Bedos leg., coll. LD

