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TAXONOMIC STATUS OF THE NEOTROPICAL CAECILIAN GENERA BRASILOTYPHLUS TAYLOR, 1968, MICROCAECILIA TAYLOR, 1968 AND PARVICAECILIA TAYLOR, 1968 (AMPHIBIA: GYMNOPHIONA: SIPHONOPIDAE)

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ABSTRACT — We review the taxonomic history and assess the status of three genera of siphonopid caecilians from South America. Evidence from dentition and squamation suggest that *Microcaecilia* is paraphyletic with respect to *Parvicaecilia*. To avoid this paraphyly we propose to relegate the latter to the synonymy of the former. We find no evidence warranting any change in the taxonomic status of *Brasilotyphlus* at this time. We provide a rediagnosis of *Microcaecilia* and a key to the fourteen currently recognized species.

Key words: Caecilian genera, *Brasilotyphlus*, *Microcaecilia*, *Parvicaecilia*, neotropics, synonymy, key, paraphyly.

INTRODUCTION

In his monographic revision of caecilian taxonomy, Taylor (1968) established the three Neotropical genera, Brasilotyphlus, Microcaecilia and Parvicaecilia, for several small and poorly-known species that had previously been included in Gymnopis Peters 1874. These differed from Taylor's conception of Gymnopis sensu stricto in lacking inner mandibular (= splenial) teeth. According to Taylor (1968, but see also Taylor, 1971; Nussbaum and Hinkel, 1994; Wilkinson et al., 2004) Brasilotyphlus had characters suggesting an affinity to the African genus Boulengerula Tornier, 1896 (diastemata between the vomerine and palatine teeth, a terminal keel) and the other genera differed from each other in whether the eve is covered by bone (Microcaecilia) or not (Parvicaecilia). Maciel et al. (2009) and Maciel and Hoogmoed (2011a) have suggested that Brasilotyphlus does not differ much from Microcaecilia and perhaps they should be considered synonyms. Here we review the history of the taxonomy of these genera. We present evidence that some Microcaecilia, including the type species Dermophis albiceps Boulenger 1882, are more closely related to Gymnopis nicefori Barbour, 1924, the type species of Parvicaecilia, than they are to some other species of

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Microcaecilia, entailing paraphyly of *Microcaecilia* as currently conceived and we propose a taxonomic revision to avoid this paraphyly. In contrast, we find no clear evidence of a relationship between *Brasilotyphlus* and *Microcaecilia* that would prompt any additional taxonomic revision at this time.

MATERIALS AND METHODS

We have examined type specimens of all but two of the 16 species currently included in the genera *Brasilotyphlus*, *Microcaecilia* and *Parvicaecilia*, including the type species of each genus (see Appendix). Most observations were made with the aid of a stereo dissecting microscope. Some light microscope assisted observations of teeth employed the Nussbaum technique and scales were sought using the methods described in Wilkinson *et al.* (2013). We have relied entirely upon Donnelly and Wake (2013) for information regarding *M. savagei* and Taylor (1968) for information on *P. pricei*. For scanning electron microscopy (SEM) using a Hitachi S2500 operating at 15kV, samples were first prepared using a two-step cleaning process involving overnight immersion on a rotor in 2% KOH followed by the same in 16% glycerol, and subsequently dehydrated in a graded acetone series and air-dried in an oven for 4 days to further shrink tissue and increase visibility of the proximal parts of tooth crowns. All specimens were mounted on metal stubs and sputter coated with a thin layer of gold-palladium.

Historical Narrative

The taxonomic history of the species with which we are here concerned begins with Duméril's (1863) description of *Rhinatrema unicolor* from Cayenne in French Guiana. Peters (1879) subsequently transferred this species to his genus *Gymnopis*, which was otherwise known only from Central America, in part because the eye is clearly visible in the type species of *Rhinatrema* Duméril and Bibron 1841 but is concealed under bone in *R. unicolor*. The next relevant species description is that of *Dermophis albiceps* from Ecuador, with Boulenger's (1882) assignment of this species to *Dermophis* Peters, 1879 (also known otherwise only from Central American species) reflecting the visibility of its eye. After a hiatus of more than 40 years, Barbour (1924) described *Gymnopis nicefori* based on a specimen from Colombia in which the eye was completely invisible. All of these authors indicated incorrectly (either explicitly through their descriptions or implicitly through their generic diagnoses) that these species had two rows of teeth in the lower jaw.

Dunn (1942) revised the American caecilians and considered *Dermophis* to be a junior synonym of *Gymnopis*. His rediagnosis of the latter included (p. 462) "few or no teeth in inner mandibular row" and "eye visible or invisible, in orbit or under bone". Subsequently, Dunn (1944) described *G. pricei* from Colombia, in which the eye is visible, without mentioning anything about the teeth, and Dunn (1945) described *G. braziliensis* from Amazonian Brazil, in which the eye is not visible and no inner mandibular teeth could be discerned. Roze and Solano's (1963) description of *G. rabei*, a species from Venezuela in which the eyes are not visible and there are no inner mandibular teeth, brought the number of South American members of *Gymnopis* to six, all of which were distinguishable primarily on the basis of differences in annulation. Taylor (1968)

removed the South American species from *Gymnopis* and partitioned them into three new genera, with *Brasilotyphlus* receiving *braziliensis*, *Microcaecilia* receiving *albiceps* (the type species), *rabei* and *unicolor*, and *Parvicaecilia* receiving *nicefori* (the type species) and *pricei*.

Taylor's (1968) diagnosis of *Brasilotyphlus* included three features that he considered suggested an affinity with the African *Boulengerula* and seemingly distinguished it from both *Microcaecilia* and *Parvicaecilia*: strong diastemata between the palatine and vomerine teeth, vomerine teeth forming a short semicircle and a weak vertical keel on terminus of body. In contrast, his diagnoses included only a single difference, the eye under bone or not, that distinguished *Microcaecilia* from *Parvicaecilia* respectively, with *Brasilotyphlus* also having the eye, if present, concealed under bone.

Taylor's (1969) description of *M. supernumeraria*, based on a single specimen supposedly from southeastern Brazil, was accompanied by the claim (p. 313) that the species of Microcaecilia "agree in the following generic characters: eye, if present, concealed under bone, lacking an eye socket; tentacular aperture far from nostril in about what would be a normal position for the eye in a caecilian. The line of the mouth seen laterally curves down; the number of premaxillary-maxillary teeth generally reduced, the series not extending back to level of internal nares. The splenial teeth are entirely absent. Scales are present in the primary and secondary grooves at least in much of body; many connective tissue scales may be present." In retrospect this list seems to be more a description of features of the new species M. supernumeraria than of the genus as a whole such that features that are of interest because they were not previously considered diagnostic do not bear scrutiny. Thus it is clear both from both Roze and Solano (1963) and Taylor (1968, see especially his Fig. 294) that neither the number of premaxillary-maxillary teeth (PMs) nor the extent of the PM series are greatly reduced in *M. rabei* and that the margin of the mouth is not noticeably down turned in this species. In his atlas of caecilian squamation, Taylor (1972) reports that while subdermal scales occur in *M. albiceps* and *M.* supernumeraria they (p. 1036) "may be absent in some other forms placed in this genus". He does not report the presence or absence of subdermal scales in Brasilotyphlus or Parvicaecilia in the same work but does make plain that Parvicaecilia and Microcaecilia differ principally in their orbits.

Nussbaum and Hoogmoed (1979) described *M. taylori*, as well as providing information on some other species, from Suriname. Their new species was readily diagnosed because it completely lacked secondary annular grooves but this feature required, and Nussbaum and Hoogmoed (1979) provided, a rediagnosis of the genus. Nussbaum and Wilkinson (1989) offered comparative diagnoses for *Brasilotyphlus*, *Microcaecilia* and *Parvicaecilia* based on a set of core characters they relied upon for diagnosing most "caeciliaid" genera. Wilkinson and Nussbaum (2006) all but repeated these diagnoses, only changing that of *Microcaecilia* very slightly to accommodate that some *Microcaecilia* have a terminal keel, one of the features previously considered to distinguish *Brasilotyphlus* from the other two genera. In both the latter pairs of diagnoses *Microcaecilia* and *Parvicaecilia* are differentiated solely on the basis of whether the eye is under bone or not.

A recent burst of descriptions of new species has included a second species of *Brasilotyphlus* (Maciel *et al.*, 2009) and seven new *Microcaecilia* from Brazil and the Guyana Shield (Wilkinson *et al.*, 2009, 2013; Wilkinson and

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Kok, 2010; Maciel and Hoogmoed, 2011a,b, 2013; Donnelly and Wake, 2013): more than doubling the number of species of Microcaecilia in less than five years. Maciel et al. (2009) provided an extended diagnosis of Brasilotyphlus, reporting that the terminal keel may be present or absent, and suggested that Brasilotyphlus and Microcaecilia might be synonyms. Maciel and Hoogmoed (2011a) provided an extended diagnosis of Microcaecilia and, with respect to the single diagnostic difference that they considered separated Brasilotyphlus and Microcaecilia (the presence or absence of vomeropalatine diastemata), they further suggested (p. 18) that "This slight difference and the number of character states shared between species in both genera suggest that these two genera are possibly synonymous". In none of these most recent works have the authors been concerned with Parvicaecilia and none of the additional features mentioned in more recent diagnoses of *Microcaecilia* are known to additionally differentiate it from Parvicaecilia. Wilkinson et al. (2011) transferred Brasilotyphlus, Parvicaecilia and Microcaecilia to the family Siphonopidae and gave brief diagnoses that are dependent on the differences in the vomeropalatine diastemata and the condition of the eye and orbit for distinguishing these genera.

In summary, Taylor (1968) distinguished *Microcaecilia* and *Parvicaecilia* on the basis of the eye being covered by bone in *Microcaecilia* and in an open orbit in *Parvicaecilia* and distinguished *Brasilotyphlus* on the basis of its distinctive vomeropalatine teeth (VPs). No further characters that differentiate these genera have been discovered in the more than 50 years since their original description.

Paraphyly of Microcaecilia

Wilkinson et al. (2009) identified two groups of Microcaecilia, one group with the two presumed derived traits of monocuspid VPs and short PM rows that do not extend as far posterior as the choanae (Fig. 1A) and another group with their presumed plesiomorphic alternates, namely longer (extending posteriorly beyond the choanae) PM series and bicuspid VPs (Fig. 1B). The first group includes the type species M. albiceps together with M. supernumeraria and M. unicolor. The second group includes M. rabei, M. taylori, and M. grandis to which can be added the more recently described species *M. marvaleewakeae*, M. rochai, M. iyob and M. dermatophaga. Wilkinson et al. (2009) highlighted that while these differences provided evidence of the closer relationship of the first group of species, and that the second group "currently lacks any putative synapomorphies and may be paraphyletic." A further species, M. trombetas, is intermediate in having long PM series and monocusped VPs (Maciel and Hoogmoed, 2011b; pers. obs) and the same condition is also reported for M. savagei (Donnelly and Wake, 2013). Taken at face value, this intermediate condition would place these species outside the first group but closer to it than to the second group. We note that Maciel and Hoogmoed (2011a) reported that the VPs of *M. taylori* may be either bicuspid or monocuspid within a single individual but they illustrated only the bicuspid condition. In the type material of this species that we have examined the VPs appear to all be bicuspid.

Both species of *Brasilotyphlus* have bicuspid VPs (Maciel *et al.*, 2009) and their PM series are not as short (they include several elements on each maxilla) as they are in those *Microcaecilia* that have short PM series (with at most two elements on each maxilla). In contrast, both species of *Parvicaecilia* have short PM series, and at least the type species *P. nicefori* also has monocuspid VPs.

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Sharing these derived characters with some but not all species of Microcaecilia is evidence of the paraphyly of the latter. It is neither the only nor the most impressive evidence. Whereas most species of *Microcaecilia* have relatively simple conical and recurved tooth crowns in their single mandibular (= dentary) tooth series (Fig. 1C), Greven (1986) reported the presence of highly distinctive serrated teeth in M. unicolor (see Fig. 1D-E). Until now the condition in other Microcaecilia or the potentially closely related species of Brasilotyphlus and Parvicaecilia has not been reported, but we have found very similar serrated teeth to be characteristic also of M. albiceps and P. nicefori. In contrast, the B. brasiliensis and all other Microcaecilia (with the exception of M. supernumeraria) that we have examined lack these serrations and they are not reported for any of the species we have been unable to examine. Given their rarity elsewhere (i.e., among potential caecilian and batrachian outgroups) the presence of serrations is derived and the overall similarity of the mandibular tooth crown morphology in those species of *Microcaecilia* and *Parvicaecilia* with serrated teeth (including the type species of both genera) suggests that their serrations are homologous and derived. This feature thus provides additional strong evidence that M. albiceps and M. unicolor are more closely related to P. nicefori than they are to most other Microcaecilia and to Brasilotyphlus and thus that *Microcaecilia* is paraphyletic with respect to *Parvicaecilia*. The lower jaws of the unique holotype of *M. supernumeraria* are lost and we have not examined any P. pricei and thus we do not know the condition of the mandibular teeth in these species.

Serrated teeth also occur in some species of the genus *Caecilia* but the serrations are far smaller than in *Microcaecilia* and *Parvicaecilia*, are more likely to occur on both anterior and posterior flanks, and are less proximally restricted (Fig. 1F). The morphological dissimilarity of the macroserrated teeth of *Microcaecilia* and *Parvicaecilia* and the microserrated teeth of some *Caecilia* together with evidence that *Caecilia* and *Microcaecilia* are not closely related (*e.g.*, Frost *et al.*, 2006; Roelants *et al.* 2007; San Mauro *et al.*, 2012; Zhang and Wake, 2009) argues against the homology of these different forms of serrations.

Microcaecilia supernumeraria's specific epithet refers to the presence beneath the skin of many subdermal scales. These scales are distinct from the annular scales that occur in pockets in the dermis of all currently known *Microcaecilia* and *Parvicaecilia*. They are small roundish scales found in the connective tissue between the dermis and the external muscular sheath. In addition to *M. supernumeraria*, subdermal scales are present also in *M. albiceps* and in *P. nicefori*. They are reported as not present in *M. trombetas* (Maciel and Hoogmoed, 2011b) and we have sought but not found them in *B. braziliensis*, *M. dermatophaga*, *M. grandis*, *M. iyob*, *M. marvaleewakeae*, *M. rabei*, *M. taylori* and *M. unicolor*. Subdermal scales are another unusual and presumed derived feature the distribution of which provides evidence that some *Microcaecilia*, including the type species, are more closely related to the type species of *Parvicaecilia* than they are to most other *Microcaecilia*. Subdermal scales have an otherwise patchy but restricted and presumably independently derived distribution in the caeciliid genera *Caecilia* and *Oscaecilia* (Taylor, 1972).

Taken together the single squamation and three dental characters provide congruent evidence supporting the conclusion that *Microcaecilia*, as currently conceived, is paraphyletic with respect to *Parvicaecilia*. This evidence is incongruent with the one character that has been relied upon to distinguish

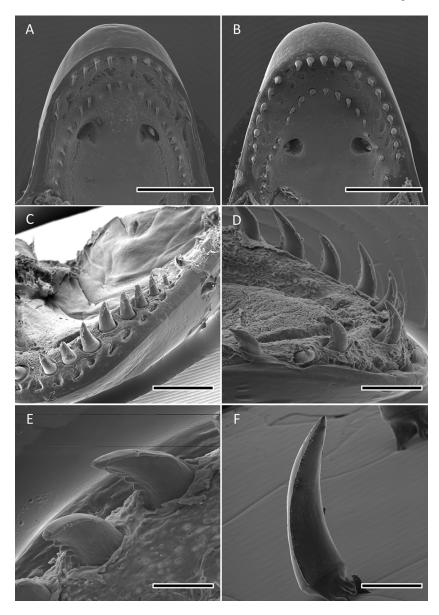


FIGURE 1 — Scanning Electron Micrographs showing major differences in dentition of *Mirocaecilia* species (A) palates of *Microcaecilia unicolor* (MW 5590) showing short PM series and monocuspid VPs, scale bar = 1 mm, (B) *Microcaecilia* sp. (UMMZ 214086) showing long PM series and bicuspid VPs, scale bar = 1 mm, (C) lower jaw of *Microcaecilia* sp. (UMMZ 214086) showing simple mandibular tooth crowns, scale bar = 0.48 mm, (D) lower jaw of *Microcaecilia unicolor* (MW 5590) showing serrated mandibular tooth crowns, scale bar = 250 μm, (E) single mandibular tooth crown of *M. unicolor* (MW 5590), scale bar = 120 μm, (F) single, microserrated PM tooth crown of *Caecilia tentaculata* (MW 3341), scale bar = 0.5 mm.

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the genera, the condition of the orbit. The latter character varies substantially, and thus appears to have evolved independently multiple times, within the Gymnophiona (Nussbaum and Wilkinson, 1989; Wilkinson, 1997). It also seems to provide a little less reliable differentiation than it perhaps once seemed. Thus, although the eye is mostly in an open orbit in *P. nicefori*, it is partially covered by bone posteriorly. Conversely, in *M. albiceps* the eye is mostly, but not completely, covered by bone.

Taxonomy

Although Maciel and Hoogmoed (2011a) consider the difference between *Brasilotyphlus* and *Microcaecilia* to be slight we do not think it is insubstantial. The VP diastemata of *Brasilotyphlus* are very large and are associated with: 1. laterally splayed palatine teeth the posteriormost elements of which appear to be more in series with the PMs than with the vomerine teeth; 2. semi-circular vomerine series; and 3. choanae that are relatively far posterior. Each of these additional associated features serves to help distinguish *Brasilotyphlus* from *Microcaecilia*. Our understanding of relationships of these forms would benefit from recollection of *Brasilotyphlus* to secure tissue samples and phylogenetic analysis of molecular data. In the absence of any clear evidence that *Brasilotyphlus* as a synonym of *Microcaecilia*.

However, in order to remove the paraphyly of *Microcaecilia* with respect to *Parvicaecilia* some taxonomic revision is required. In the absence of more detailed understanding of the interrelationships of their species, this can best be achieved by relegating either *Microcaecilia* or *Parvicaecilia* to the synonymy of the other. Neither *Microcaecilia* nor *Parvicaecilia* has priority leaving the choice to the first reviser. We prefer to maintain *Microcaecilia* for three reasons: the type species is a relatively better known species (represented by more specimens in more repositories), it requires the fewest nomenclatural changes (two versus twelve), and there are fewer reports on species of *Parvicaecilia* Taylor to be a junior subjective synonym of *Microcaecilia* Taylor. Diagnoses and synopses of *Parvicaecilia* and *Microcaecilia* were provided most recently by Wilkinson *et al.* (2011). We offer the following:

Microcaecilia Taylor, 1968 *Parvicaecilia* Taylor, 1968 new synonym.

Type species.—*Dermophis albiceps* Boulenger, 1882, by original designation. Diagnosis.—The only siphonopids with scales and lungs and without substantial diastemata between the vomerine and palatine teeth.

Content.—14 species: *M. albiceps* (Boulenger, 1882), *M. dermatophaga* Wilkinson, Stauro, Gower and Sherratt, 2013, *M. grandis* Wilkinson, Nussbaum and Hoogmoed, 2009, *M. iyob*, Wilkinson and Kok 2010, *M. marvaleewakeae* Maciel & Hoogmoed, 2013, *M. nicefori* (Barbour, 1928) new combination, *M. pricei* (Dunn, 1944) new combination, *M. rabei* (Roze and Solano, 1963), *M. rochai* Maciel and Hoogmoed, 2011, *M. savagei* Donnelly & Wake, 2013, *M. supernumeraria* Taylor, 1970, *M. taylori* Nussbaum and Hoogmoed, 1979, *M. trombetas* Maciel and Hoogmoed, 2011, *M. unicolor* (Duméril, 1863).

Distribution.—Brazil, Colombia, Ecuador, French Guiana, Guyana, Suriname, Venezuela.

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Remarks.—Progress in caecilian systematics has been hampered by unstable foundations at the generic and specific levels (Nussbaum and Wilkinson, 1989; Wilkinson and Nussbaum, 2006). While the present revision succeeds in removing the clear paraphyly of *Microcaecilia* with respect to *Parvicaecilia*, none of the characters of *Microcaecilia sensu lato* are understood to be uniquely derived such that monophyly of the genus remains a tentative hypothesis in need of testing with additional data. As conceived here, *Microcaecilia* differs from Caecilita Wake and Donnelly, 2009 in having lungs, from *Brasilotyphlus* in lacking vomeropalatine diastemata and from other siphonopids in having scales, all of which are plesiomorphic features.

All but one Microcaecilia are from the Amazon Basin or further north. The single exception, M. supernumeraria, is reported as being from "Sao Paulo" but its provenance is uncertain. We find that *M. supernumeraria* is rather similar to *M. nicefori* and we are not completely confident that they are specifically distinct. In our key (see below) we were only able to distinguish these nominal species through reference to the density of subdermal scales. And yet we know too little about intra- and interspecific variation in these enigmatic scales to be sure that the observed differences in representatives of these nominal species are not due to ontogenetic, sexual or other polymorphism occurring within a single species. Similarly, *M. trombetas* and *M. savagei*, which are both known only from their holotypic specimens, seem sufficiently alike and difficult to separate as to warrant further investigation of their taxonomic status. Maciel and Hoogmoed (2011a) considered the type series of *M. taylori* from Suriname and several populations from south of the Amazon river to be conspecific, simultaneously increasing the known variation within this species to substantially greater than for any other Microcaecilia. We would like to see this hypothesis of conspecificity tested. We have employed the presence or absence of a dorsal transverse groove on the first nuchal collar in our key but note that Maciel and Hoogmoed (2013) reported the absence of this feature in c. 16% of 160 Brazilian specimens of M. taylori.

Caecilians are generally considered poorly known (*e.g.*, Wilkinson, 2012) and relatively little is known of the biology of any species of *Microcaecilia*. The skull of *M. unicolor* was considered from a functional perspective by Renous (1990) without any mention of the unusual crowns of their mandibular teeth. The little information available on reproduction suggests that they are oviparous with altricial hatchlings that feed upon the modified (lipid-rich) outer layer of their mother's skin (Wilkinson *et al.*, 2013). We are aware of some undescribed, and suspect that there are many more undiscovered, species of *Microcaecilia*.

KEY TO THE SPECIES

1. Short premaxillary-maxillary tooth series	
not extending beyond choanae.	2
Long premaxillary-maxillary tooth series	6
2. More than 130 primary annuli	3
Less than 130 primary annuli	4
3. Subdermal scales large and very abundant	
Subdermal scales small and scattered	
4. More than 40 secondary annular grooves	5

Less than 40 secondary annular grooves	pricei
5. Eye visible, body lavender, head paler	
Eye not visible, body blackish, head not much paler	
6. Less than 70 secondary annular grooves	
More than 70 annular grooves	
7. Usually no dorsal transverse groove on first nuchal collar	
Dorsal transverse groove usually present on first nuchal collar.	11
8. More than 15 secondary annular grooves	9
Less than 15 secondary annular groovesderm	atophaga
9. Less than 150 total (primary and secondary)	
annular grooves	10
More than 150 total annular grooves	grandis
10. Less than 70 primary annuli without secondary	
annular grooves	iyob
More than 70 undivided primary annuli	rabei
11. More than 40 secondary annular grooves	rochai
Less than 40 secondary annular grooves	12
12. More than 20 secondary annular groovesmarval	eewakeae
Usually less than 40 secondary annular grooves	taylori
13. Less than 200 annular grooves (primary + secondary)	savagei
More than 200 annular grooves (primary + secondary)t	rombetas

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APPENDIX - Materials examined

Brasilotyphlus braziliensis - American Museum of Natural History (AMNH) 51751 (Holotype), 51749-50, 51752 (Paratopoypes).

B. guarantanus - Museu Paraense Emílio Goeldi, Belém (MPEG) 22382 (Holotype).

Caecilia tentaculata - Natural History Museum, Mark Wilkinson Field Series (MW) 3341; University of Michigan Museum of Zoology (UMMZ) 89459, 177895.

Microcaecilia sp. - UMMZ 214080-90

M. albiceps - The Natural History Museum, London (BMNH) 1946.9.5.32 (Holotype); UMMZ 83051; Museum of Comparative Zoology, Harvard (MCZ) 58411; Kansas University Museum of Natural History (KU) 125300; Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ) 39071.

M. dermatophaga - BMNH 2008.715 (Holotype) BMNH 2008.716 - 722, La Muséum nationale d'Histoire naturelle, Paris (MNHNP) 2010.0190 (Paratypes).

M. *grandis* - Rijksmuseum van Natuurljke Histoire, Leiden (RMNH) 17738 (Holotype), 17736 (Paratype).

M. iyob - Field Museum of Natural History, Chicago (FMNH) 35117 (Holotype).

M. marvaleewakeae – MPEG 21896 (Holotype).

M. nicefori - MCZ 9609 (Holotype), BMHN 1996.91.

M. *rabei* - Museo de Biología, Universidad Central de Venezuela (MBUCV) 5126 (Holotype), 5359 (Paratype).

M. supernumeraria - Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB) 5268 (Holotype).

M. taylori - RMNH 15165a (Holotype), 15165b (Paratype).

M. trombetas – MPEG 26476 (Holotype).

M. unicolor - MNHNP 581 (Lectotype) 581a, 581b, 1991-407, 1903-31, 1903-31A, 1903-30, 1903-32, 1903-32A, 1903-32B, 1903-32D, 1903-33, BMNH 84.12.8.5.0, MW 5590; UMMZ 173394.