New Genera and Species of Maimetshidae (Hymenoptera:Stephanoidea s.l.) from the Turonian of Botswana, with Comments on the Status of the Family

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New genera and species of Maimetshidae (Hymenoptera: Stephanoidea s.l.) from the Turonian of Botswana, with comments on the status of the family

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ABSTRACT

Three new genera and four new species, all assigned to Maimetshidae, are described from the Turonian (U. Cretaceous) of Orapa in Botswana (southern Africa), viz., Afrapia globularis gen. et sp. n., A. variicornis sp. n., Afroniania robusta gen. et sp. n., and Maimetshorapia africana gen. et sp. n. The genera Andyrossia Rasnitsyn & Jarzembowski, 2000 from the Barremian (L. Cretaceous) of the Weald Clay (southern England) and Guyotemaimetsha Perrichot, Nel & Néraudeau, 2004 from the Albian (L. Cretaceous) of France are also transferred to Maimetshidae. Cretogonalys Rasnitsyn, 1977 from the Cenomanian (U. Cretaceous) of northern Siberia may also belong here. These results extend the known duration of Maimetshidae over the entire middle part of the Cretaceous (from the Barremian to the Santonian), its geographic distribution over the western half of the Old World (from northernmost Siberia to westernmost Europe and southern Africa), and its taxonomic diversity to at least six genera and seven species, with the diversity possibly centred in Africa. The taxonomic and phylogenetic positions of Maimetshidae are discussed.

KEY WORDS: Hymenoptera, Maimetshidae, Megalyridae, Trigonalidae, Botswana, Orapa, Turonian, fossil insects.

INTRODUCTION

The lower Upper Cretaceous (Turonian) deposits at Orapa, Botswana, resulted from the Kimberlitic eruption that formed a crater about 91 Mya, followed by accumulation of the fossiliferous sediments there (for details see Brothers & Rasnitsyn 2003; Gernon et al. 2009; and references therein). The Orapa insect fossil assemblage is rich and diverse, being currently the most important source of information about mid-Cretaceous insects in the southern hemisphere (reviewed by Brothers & Rasnitsyn 2003). Unfortunately, our knowledge of the Orapa hymenopterans is very poor as yet, being limited, besides the above general review, to the descriptions of two vespid wasps (Brothers 1992, Brothers & Rasnitsyn 2008), several ants (Dlussky et al. 2004), one evaniid and one proctotrupomorph parasitic wasp (Rasnitsyn & Brothers 2007). The Orapa hymenopteran assemblage includes fossils of primary importance for understanding the higher-level evolution of the order. The present paper is devoted to fossils shedding more light on the early history of the stephanoid s.l. parasitic wasps, as concerning the origin of the important extant insect parasites, Ceraphronidae and Megaspididae.

MATERIAL AND METHODS

The new fossils reported on herein are currently housed in the Bernard Price Institute of Palaeontology (BPI) at the University of the Witwatersrand, Johannesburg, South Africa. The figures include some composite photographs prepared by reversing and superimposing the image of the counterpart on that of the part, where possible; this produced images containing more information than either source alone.

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TAXONOMY

Superfamily Stephanoidea Leach, 1815 *sensu lato*

The superfamily Stephanoidea is taken in the broad sense, as proposed by Rasnitsyn (1980, 1988, 2002; sometimes named incorrectly as Ceraphronoidea Haliday, 1833), that is, including Ceraphronoidea *s.str.* (Ceraphronidae, Megaspilidae, and the extinct Cretaceous Stigmaphronidae), as well as Megalyridae, Trigonalidae, Stephanidae, and the extinct Cretaceous Maimetshidae. The reasons are outlined in the papers referred to above.

Family Maimetshidae Rasnitsyn, 1975


Type genus: *Maimetsha* Rasnitsyn, 1975 (monobasic).

Diagnosis: Head without ocular carina, without subantennal groove accommodating antennal base. Vertex with (in type genus) or without longitudinal median sulcus. Antenna filiform, with scape not elongate, flagellomeres variable in number (known as at least 14 to 17). Mandible with four teeth (mandibles perhaps rarely asymmetrical, with 4 and 3 teeth). Pronotum short mediad, mesoscutum with notauli and medial sulcus, axillae meeting anterior to scutellum or separated by prescutellar impression. Propodeum areolate. Forewing with costal space moderate to wide; vein C and pterostigma present; basal sections of RS and M subequal in length, not continuously aligned (not forming smooth basal vein); marginal cell closed, wide (not triangular), moderately short to moderately long; cells 2rm and/or 3rm closed; cell 1mcu closed, small, distant from 2rm (by at least 0.7× length of 1m–cu); cell 2mcu open (at most delimited by spectral 2m–cu crossvein); 1cu–a antefurcal. Hind wing with no posterobasal lobe; with 4 or 5 distal hamuli; basal cell (1rm) closed; free apex of RS stub-like, short; free apices of M and Cu short or absent, that of A absent. Legs unmodified, with trochantelli, spurs 1-2-2, tarsomeres 5-5-5, claws with preapical tooth. Metasoma rather short, compact, not much sculptured, attached low on propodeum, with first segment forming small articulatory ring, second segment the longest, apical sternum of female elongate, nearly reaching metasomal apex. Ovipositor external but not long, sheaths shorter than metasoma, not fitting tightly to ovipositor (often preserved loose).

Genera included: *Maimetsha* Rasnitsyn, 1977 (type genus) from the Santonian of northern Siberia; *Andyrossia* Rasnitsyn & Jarzembowski, 2000 (= Arossia Rasnitsyn & Jarzembowski, 1998, nom. preocc.) from the Barremian of the Weald Clay (southern England); *Guyotemaimetsha* Perrichot, Nel & Néradeau, 2004 from the Albian of southwestern France (based on their figures and description), and the three new genera described below from the Turonian of Botswana, all mid- and late Cretaceous in age. The undescribed fossil from the Albian Álava amber in Spain (misidentified as Trigonaliidae in Delclòs *et al.* 2007, fig. 4F) also belongs here. Furthermore, based on the available characters, the incompletely preserved *Cretogonalys* Rasnitsyn, 1977 from the Cenomanian of northern Siberia (Rasnitsyn 1977) also may be a member of Maimetshidae. Its asymmetrical mandibles with 3 and 4 teeth are more characteristic of Trigonaliidae, but the venation as far as is known is more typical of Maimetshidae. Unfortunately, the metasomal base is insufficiently preserved to reveal the presence or absence of a small ring-like basal segment. If a genus of Maimetshidae, *Cretogonalys* can be distinguished...
from the other genera in having both 2rm and 3rm cells enclosed (the former not petiolate) and in its slender stature.

Taxonomic position: The small ring-like first metasomal segment limits attribution of the family either to the superfamily Stephanoidea s.l. (including Ceraphronoidea s.str.) or to the infraorder Proctotrupoforma; this is additionally supported by the low metasomal articulation (excluding Evanioidea), distinct costal space (excluding Ichneumonoidea) and external ovipositor (excluding Aculeata). The wide, but not triangular, marginal cell excludes Proctotrupoforma, which additionally differs in having either the hind wing with no enclosed cells (all but Mesoserphidae), or a normal (not ring-like) first metasomal segment (Mesoserphidae). In the superfamily Stephanoidea s.l., only the families forming the Ceraphronoidea s.str., viz., extant Ceraphronidae and Megaspilidae and extinct (Cretaceous) Stigmaphronidae (Engel & Grimaldi 2009), are similar in having the first metasomal segment small and ring-like. All of those differ, however, in having the wing venation far more reduced (with no veins preserved beyond R and no enclosed cells), two foretibial spurs, and internal ovipositor. Of the remaining stephanoid families, Maimetshidae is most similar (except in the form of the first metasomal segment) to Trigonalidae (except that the latter has the forewing with cell 2rm close to 1mcu and vein 2m–cu tubular, the ovipositor rudimentary and internalized, and several other modifications related to reproductive biology; see e.g. Carmean & Kimsey 1998) and Megalyridae (particularly to its archaic Mesozoic subfamily Cleistogastrinae, sometimes considered as a separate family, e.g., by Shaw 1988). In comparison with the two subfamilies of Megalyridae, Maimetshidae shares with Cleistogastrinae well developed notauli, more complete venation (forewing with 2rm enclosed and M+Cu tubular, hind wing with enclosed cells) and variable flagellomere number (14–17 or more, in contrast to always 12 in Megalyrinae; 8–19 in Cleistogastrinae). In addition to the form of the first metasomal segment, Maimetshidae differs from all Megalyridae in having the 1cu–a crossvein antefurcal. Although Maimetshidae is generally most similar to Megalyridae and particularly to Cleistogastrinae, all the similarities are of a plesiomorphic nature, while its own putative synapomorphies, and particularly the form of the first metasomal segment, link it to the Ceraphronoidea s.str. That is why we consider Maimetshidae as forming a morphological and possibly phylogenetic transition between Cleistogastrinae and Ceraphronoidea s.str.

Remarks: Shaw (1988, 1990, 2007; see also Grimaldi & Engel 2005) synonymised Maimetshidae (based on Maimetsha only) under Megalyridae: Dinapsini. His only positive arguments were that “Maimetsha is characterized as having a more reduced pattern of forewing venation (Rasnitsyn 1975), which is in fact very similar to that of some modern megalyrids, such as Ettschellsia. In particular, Maimetsha has Rs curving towards the wing margin to form a short radial cell, very similar to the short radial cell that characterizes the Dinapsis+Ettschellsia lineage of dinapsine megalyrids. This indicates that Maimetsha should be classified in the Megalyridae. … In Maimetsha the Rs of the hindwing is reduced to a short stub (Rasnitsyn 1975); therefore, the genus can be assigned to the Dinapsinae [later Dinapsini] on the basis of this character.” (Shaw 1988: 109). Both observations are correct but not very convincing because both characters represent a part of the miniaturization syndrome. This is a set of modifications resulting in the formation of a wide vein-free zone along the outer and posterior margins of the
functional wing (joined fore- and hind wings in the case of the hymenopterons) which commonly accompanies evolutionary reduction of body size in winged insects (Rasnitsyn 1980). Both characters emphasised by Shaw (1990) as placing Maimetsha in Dinapsini (his characters 9 and 10) appear to us as possibly wrongly polarised, with the putative derived states involving development of veins otherwise lost; if so, the shared states would be symplesiomorphies. Opposed to these is a set of characters implying a possible sister-group relationship between Maimetshidae and Megalyrinae (= Megalyridae excluding Cleistogastriinae). This set includes a number of synapomorphies of Megalyrinae for characters which are plesiomorphic in Maimetshidae, e.g., the head with subocular groove (absence of the groove demonstrated in Maimetsha (Rasnitsyn 1975, fig. 87a, c, d), in Guyotemaimetsha (Perrichot et al. 2004, fig. 2), and inferred in the new taxa described below), reduced and stabilized number of flagellomeres (12) (variable in Maimetshidae), lost notauli (present in Maimetshidae), forewing with M+Cu lost as a tubular vein and 2r–m and 3r–m both lost (M+Cu tubular, 2r–m and 3r–m present in ground plan and never both lost in Maimetshidae), and hind wing with M+Cu and A lost and no closed cells (M+Cu and A present, and cells rm and cuda closed in Maimetshidae). Furthermore, there is a potential synapomorphy of Maimetshidae and Ceraphronoidea s.str. in having the first metasomal segment reduced to a small articulatory ring (best described by Perrichot et al. 2004: 161, and visible in their photo, fig. 1B) (not so modified in Megalyridae s.l.). This makes the proposal by Shaw (1988, 1990) to synonymise Maimetshidae under Dinapsini in Megalyridae s.str. inappropriate. Shaw’s (1990) cladistic analysis included only characters relevant to his concept of Megalyridae (incidentally, there are three errors in his coding for Maimetsha, which should be 100?002021?12?0??212). If the matrix were expanded in taxa and characters to include Cleistogastriinae and Ceraphronoidea, as well as the other genera now assigned to Maimetshidae, we are confident that the results would differ; such an analysis is beyond the scope of this paper, however. Meanwhile, we prefer to retain Maimetshidae as a family in its own right, for the reasons outlined above.

Key to genera and species of Maimetshidae

1 Forewing cells 2rm and 3rm both present (2rm sometimes incompletely delimited); flagellomere number variable (unknown for Andyrossia). .................................................. 2
   - Forewing cells 2rm and 3rm not simultaneously present; 14 flagellomeres ....... 6

2 Second abscissa of RS+M (distal to 1m–cu) shorter than 1m–cu
   .......................................................... Andyrossia joyceae (Rasnitsyn & Jarzembowski)
   - Second abscissa of RS+M (distal to 1m–cu) subequal to or longer than 1m–cu ...
     .......................................................... Afromaimetsha robusta sp. n.

3 Notauli strongly diverging cephalad .................................... Afrapapia gen. n.
   - Notauli more or less parallel ................................................................. 4

4 Vein RS originating close to pterostigma (prestigma much shorter than 1RS); prestigma incrassate (swollen apically and broader than basal abscissa of R) ......
   ........................................................................................................ Maimetshorapia africana sp. n.
   - Vein RS originating well before pterostigma (prestigma about as long as or longer than 1RS); prestigma linear and similar to basal abscissa of R (Afrapia gen. n.)
     ........................................................................................................ 5
Afrapia globularis sp. n.

Etymology: The species name is the Latin adjective for ‘globular’, with reference to the form of each of the head, meso- and metasoma of the holotype.

Description: Ground colour dark (pterostigma and venation slightly less so); legs not distinctly preserved but, by inference, pale. Head rounded, slightly wider than mesonotum, with occipital carina complete or almost so (possibly briefly interrupted above
Figs 1, 2. Afrapia gen. et spp. n.: (1) A. globularis sp. n., holotype BP/2/28003-1 & BP/2/28069-1: (1a) Composite photograph, (1b) Line drawing, with separate wing (not to same scale) to show venational symbols: 1RS, 1RS+M, etc. – sections of respective longitudinal veins; 2r–rs, 3r–m, etc. – crossveins; 3r, 3rm, etc. – cells; pt – pterostigma; mesonotal structures: al – adlateral ("parapsidal") line, mss – medial mesoscutal suture, n – notaulus; (2) A. variicornis sp. n., holotype BP/2/27215, photograph and line drawing. Scale bars = 1.0 mm.
and below). Flagellum at least 15- or 16-segmented, gradually narrowed distad, with segments gradually shortening from almost 3 times as long as wide (first and second) to about 1.5 times so. Pterostigma distinctly shorter than distance between base of RS and 2r–rs; 1RS+M subparallel to 1Cu, starting slightly below midlength of basal vein; cell 3rm subquadrate. Areola small, slightly broader than long. Ovipositor straight, parallel-sided from above, sheath about as long as distance from pterostigmal base to apex of cell 3r. Body length as preserved 3.9 mm, forewing length to apex of cell 3r ca. 2.8 mm, ovipositor sheath 1.1 mm. Male unknown.

Holotype: ♀ BP/2/28003-1 & BP/2/28069-1, almost complete, lacking legs (except indistinct traces), most of hind wings and parts of antennae. BOTSWANA: Orapa; Upper Cretaceous, Turonian.

**Afrapia variicornis** sp. n.

Figs 2–6

Etymology: The species name is from the Latin for ‘variable antenna’, alluding to the variation observed in the specimens as preserved.

Description:

**Female.**

Ground colour dark (pterostigma and venation slightly less so); legs not preserved. Head thick in side view, with large, rounded subquadrate eye, temple moderately narrow (about 0.3 times as wide as eye), apparently not swollen. About ten flagellomeres preserved (several basal and apical ones missing), thin, about twice as long as wide, gradually becoming slightly shorter and a little narrower distad. Hind coxa very large, 2.5 times as long as mid coxa. Propodeum with sides rather closely areolate. Pterostigma as long as distance between base of RS and 2r–rs; 1RS+M subparallel to 1Cu, starting slightly above midlength of basal vein; cell 3rm subquadrate. Ovipositor narrow and short (sheath about as long as pterostigma), slightly arcing down. Body length as preserved 4.3 mm, forewing length to apex of cell 3r about 2.8 mm, ovipositor sheath 0.6 mm.

**Male.**

Legs pale as preserved. Antenna with scape globular, flagellum long and fairly narrow (but thickness and proportions varying according to preservation), probably with about 19 flagellomeres, all elongate except apical one, gradually shortening from more than twice (usually) to about 1.5 times as long as wide or even almost quadrate. Pronotum moderately short centrally, with hind margin only slightly concave. Propodeum with coarse areolation of the type best known in Ichneumonidae but also present in many extinct apocritans including *Maimetsha*; areola broadly rectangular, transverse, area basalis indistinct. Forewing with pterostigma slightly longer than distance between base of 1RS and 2r–rs; 1RS+M slightly oblique or subparallel to 1Cu, starting at about midlength of basal vein or slightly below; cell 3rm about as long as high or slightly longer. Hind wing with no free apex of M and with long distance between RS and M+Cu fork. Body length as preserved 3.1–3.8 mm, forewing length to apex of 3r about 2.2–2.4 mm. Otherwise like female.

**Variation:** Apart from size and venational differences, the greatest variation is seen in the male antennae (relative width and apparent sizes of flagellomeres) but this may be
a reflection of taphonomic influences. The three male specimens are preserved in close
proximity on the same block with other unidentifiable fossils (see fig. 3).

Holotype: ♀ BP/2/27215, almost complete, lacking legs and most of hind wings, antennae incomplete
(Fig. 2). BOTSWANA: Orapa; Upper Cretaceous, Turonian.

Paratypes: 3♂ (?) BP/2/26666-3 & BP/2/28224-3 (most of legs, hind wings and metasomal apex lacking; 
head and most of mesosoma not interpretable; forewings incomplete; body length 3.8 mm; Fig. 4); BP/2/ 
26666-2 & BP/2/28224-2 (head, antenna, mesosoma and wings incomplete; metasomal apex and most of 
legs lacking; body length 3.6 mm; Fig. 5); BP/2/26666-1 & BP/2/28224-1 (incomplete; flagellar and thoracic 
fragments, partial head and metasoma, and most of one fore- and one hind wing preserved; body length 3.1 
mm; Fig. 6). BOTSWANA: Orapa; Upper Cretaceous, Turonian.

Figs 3, 4. Afrapia variicornis sp. n.: (3) Paratypes BP/2/26666-3, 2 & 1, photograph; (4) Paratype BP/2/26666-
3 & BP/2/28224-3, composite photograph and line drawing; a – areola. Scale bars = 1.0 mm.
Figs 5, 6. Afrapia variicornis sp. n.: (5) Paratype BP/2/26666-2 & BP/2/28224-2, composite photograph and line drawing; (6) Paratype BP/2/26666-1 & BP/2/28224-1, composite photograph and line drawing. Scale bars = 1.0 mm.
Afromaimetsha gen. n.

Etymology: The generic name is derived from Africa and the genus *Maimetsha*. Gender feminine.

Type species: *Afromaimetsha robusta* sp. n., by present designation.

Diagnosis: Similar to *Afrapia* except for notaulli distinctly diverging cephalad, first visible metasomal tergum longer (as long as cell 3r), ovipositor slightly longer, and, possibly (not precisely known for *Afrapia*), propleura longer (may form a short but distinct neck in life). No reliable venational differences are known. The characters relevant to the higher taxonomic levels of Stephanoidea are the head with postgenae widely separated (most probably by the lower tentorial bridge), mesopleuron with complete lateral horizontal furrow and with posterior submedial lamella, and postepisternal lobes apparently forming medial midcoxal articulation. The last character may be taken as an indirect indication of a distal position of the articularitary condyle on the midcoxa, the putative synapomorphy of the stephanoid and evanioid clades (Rasnitsyn 1988).

Species included: Type species only.

Comparison: Similar to *Afrapia*, except notaulli diverging and propleura apparently much longer. Differs from *Maimetsha* and *Guyotemaimetsha* in having cells 2rm and 3rm both delimited, from *Maimetsha* also in having RS starting well before the pterostigma.

Remarks: The horizontal midpleural furrow which is similar to that (although incomplete) in *Maimetsha*, and which is rare in other Stephanoidea, may support attribution of the present genus, and *Afrapia* by inference, to Maimetshidae. The broad lower tentorial bridge is unusual for Stephanoidea, generally being replaced by the postgenal bridge there.

Afromaimetsha robusta sp. n.

Fig. 7

Etymology: The species name is Latin for ‘robust’, in reference to the body form.

Description: Ground colour dark (pterostigma and venation slightly less so); legs pale as preserved. Head large. Scape short and broadly cup-like; pedicel short, transverse; flagellum almost uniformly narrow, with 13 flagellomeres preserved, all much longer than wide, longest (3rd and 4th) about 4 times as long as wide, distal-most preserved nearly twice as long as wide. Propodeum with coarse areolation, areola almost twice as wide as long, as long as area basalis, petiolar area narrow. Forewing with pterostigma probably as long as or slightly shorter than distance between base of RS and 2r–rs; RS starting basad of pterostigma, probably by almost its length; 1RS+M parallel to 1Cu, apparently starting at about midlength of basal vein; second abscissa of RS+M (distal to 1m–cu) longer than 1m–cu; forewing cells 2rm and 3rm both present, 3rm subquadrate (appearing slightly different in right and left wing). Metasoma with apical sternum only slightly longer than subapical. Ovipositor arching down, with sheath narrow basally, distinctly widening apicad, longer than distance from pterostigmal base to apex of cell 3r. Body length as preserved 4.9 mm, forewing length to apex of cell 3r about 2.5 mm, ovipositor sheath 1.4 mm.

Holotype: ♀ BP/2/27111-1, almost complete but lacking hind wings and most of legs; head and metasoma incomplete. BOTSWANA: Orapa; Upper Cretaceous, Turonian.
**Maimetshorapia** gen. n.

Etymology. The generic name is derived from Orapa and the genus *Maimetsha*. Gender feminine.

Type species: *Maimetshorapia africana* sp. n., by present designation.

Description: Similar to *Afrapia* except for RS starting almost at base of pterostigma, with intervening prestigma distinctly incrassate, RS apparently somewhat reduced before...
2r–rs unless incompletely preserved, RS+M forking close to 2r–m (cell 2rm relatively short), first visible metasomal tergum as long as cell 3r, and ovipositor sheath probably wide basally and straight, elongately triangular in form. Pronotum, if correctly identified, longer dorsally than in other genera.

Species included: Type species only.

Comparison: Differs from all genera other than *Maimetsha* in having RS starting at or very close to base of pterostigma, and from *Maimetsha* in having the prestigma incrassate, 1RS and 1M almost aligned, marginal cell shorter and wider, all remnants of 2m–cu lost, and ovipositor shorter. Apparently (unless due to imperfect preservation) differs from all other genera in having cell 2rm present but short and with 2RS incomplete.

*Maimetshorapia africana* sp. n.  

**Fig. 8**

Etymology: The species name is Latin for ‘African’.

Description: Ground colour moderately dark, pterostigma and venation less so; antenna and most probably legs pale. Head transverse, apparently with large eyes; temples moderately narrow, convex. Apical 8 flagellar segments narrow, as long to almost twice as long as wide. Propodeum coarsely areolate dorsally, closely so laterally, areola about twice as wide as long, about as long as area basalis. Forewing with 1RS+M parallel to 1Cu, starting at about midlength of basal vein; cell 3rm shorter than high. Ovipositor sheath straight, probably elongately triangular, about as long as valvifers 1+2 and as cell 3r. Body length as preserved 5.3 mm, forewing length to apex of cell 3r about 2.7 mm, ovipositor sheath 0.75 mm.

Holotype: ♀ BP/2/28222-11; almost complete but lacking hind wings, legs, and most of antennae.  
BOTSWANA: Orapa; Upper Cretaceous, Turonian.

**DISCUSSION**

The fossils described above shed some light on the structure, position, and history of the family Maimetshidae, which was previously known from a single specimen from the Upper Cretaceous (Santonian) of northern Siberia (Rasnitsyn 1975). The present material, of only slightly older age (Turonian) but from southern Africa, far extends the family distribution geographically. Additionally, it establishes taxonomic connections between *Maimetsha* and several other taxa of previously doubtful position (*Andyroussia*, *Guyotemaimetsha*, and the above mentioned “Trigonalidae” specimen from the Álava amber), thus resulting in extension of distribution of the family over western Europe (including England, France and Spain), and even farther so stratigraphically, to the Lower Barremian, rather low in the Lower Cretaceous.

The new material extends the morphological diversity of the family as well. It narrows the gap between it and the putatively ancestral taxon Cleistogastrinae (Megalyridae; Rasnitsyn 1988, 2002), particularly in the wing venation (the new genera differ from Cleistogastrinae only in their long 2RS+M and long petiolate 2rm) and in the metasomal structure (the new genera have their longest tergum much shorter than in *Maimetsha* and *Guyotemaimetsha*). Additionally, *Afromaimetsha* demonstrates the formation of an incipient propleural neck, as well as widely separated postgenae with the lower tentorial bridge intervening between them, both these apomorphies unknown elsewhere in Stepha-noidea s.l.
Still more unexpected is the abundance and taxonomic diversity of the southern African Maimetshidae, for the seven fossils were discovered amongst a total of 108 hymenopterons (6.5%; Brothers & Rasnitsyn 2003) and belong to four different species and three distinct genera. In contrast, *Maimetsha* is based on a single specimen among 400 hymenopterons, *Andyrossia* is also a single specimen amongst 25 Wealden hymenopterons (but the small number of specimens implies little about relative abundance), and *Guyotemaimetsha* is based on two conspecific specimens amongst 115 late Albian hymenopterons (Perrichot et al. 2007).

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