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A new species of maimetshid wasp (Insecta: Hymenoptera) in Siberian Cretaceous amber

Une nouvelle espèce de guêpe maimetshide (Insecte: Hyménoptère) dans l'ambre crétacé de Sibérie

Vincent Perrichot[a,*], Evgeny E. Perkovsky[b]

[a] *CNRS UMR 6118 Géosciences & OSUR, Université Rennes 1, Campus de Beaulieu bât. 15, 263 avenue du Général Leclerc, 35042 Rennes cedex, France*
[b] *Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, ul. Bogdana Khmel'nitskogo 15, Kiev, 01601, Ukraine*

[*] Corresponding author. *E-mail address:* vincent.perrichot@univ-rennes1.fr

Abstract

A new fossil wasp belonging to the extinct evaniomorphan family Maimetshidae is described from Santonian amber of Yantardakh, in the Taimyr Peninsula, northern Siberia. *Iberomaimetsha pallida* sp. nov., is represented by a single female and is distinguished from the other two species of the genus most notably in its wing venation. A modified key to the world Maimetshidae is proposed to include the new species.

Keywords: Insecta, Evaniomorpha, Maimetshidae, Taimyr amber, Santonian

Résumé

Une nouvelle guêpe fossile appartenant aux Maimetshidae, une famille éteinte d'Evaniomorphes, est décrite de l'ambre santonien de Yantardakh, dans la Péninsule du Taimyr, en Sibérie du Nord. *Iberomaimetsha pallida* sp. nov., est représentée par une unique femelle et se distingue essentiellement des deux autres espèces du genre par sa nervation alaire. Une clé modifiée des Maimetshidae du monde est proposée pour inclure cette nouvelle espèce.

Mots clés: Insecte, Evaniomorphe, Maimetshidae, ambre du Taimyr, Santonien

1. Introduction

Cretaceous ambers from the Taimyr Peninsula, in northern Siberia, have yielded a diverse array of fossil hymenopterans, and 40 species have been described in 18 families since the first descriptions of crabronid, chrysidoid, and ichneumonid wasps more than 40 years ago (Evans, 1973; Townes, 1973). Among the recorded families, the extinct Maimetshidae was erected to accommodate the single species *Maimetsha arctica* known only from the Santonian amber of Yantardakh (Rasnitsyn, 1975). It was initially considered to be an intermediate between Megalyridae and Ceraphronoidea (Rasnitsyn, 1975), but recently the results of a genus-level phylogenetic analysis of Megalyridae and other evaniomorphan families retrieved Maimetshidae as sister to Trigonalyidae, yet with an uncertain classification within the Evaniomorpha (see details in Vilhelmsen et al., 2010).

The family had remained monotypic until the recent discoveries of an additional ten genera and twelve species from both imprint fossils and amber inclusions, all Cretaceous in age (Perrichot et al., 2004, 2011; Rasnitsyn and Brothers, 2009; Perrichot, 2013). Remarkably, maimetshids are now recorded from all major Cretaceous amber deposits except that of New Jersey (Raritan Formation), but they remain poorly documented as imprint fossils even from insect-rich rock deposits such as those of the Early Cretaceous Yixian Formation in northeastern China. More than four decades after the first collecting of amber in the Taimyr Peninsula, a new expedition has been realized in 2012 by members of the Borissiak Paleontological Institute and the Institute of Developmental Biology of Moscow (Rasnitsyn et al., 2016). More than 3000 new arthropod inclusions have been retrieved, mostly from the Santonian deposit of Yantardakh, among which two specimens that are assignable to Maimetshidae. One specimen is too poorly preserved for assignment to any genus, whereas the other one displays sufficient features for comparison with other known fossils of the family. A first examination revealed that it differs from *Maimetsha*, the type-genus and only other maimetshid described from Taimyr amber (Rasnitsyn, 1975). Instead, the new specimen appeared very similar to the two known species of *Iberomaimetsha*, a genus which was recently described from Albian Spanish amber (Perrichot et al., 2011). The Siberian morphotype, differing from the Spanish species mostly in its wing venation, is described herein as a new species. A modified key for the identification of the world Maimetshidae is also proposed.

2. Material and methods

The studied specimen is preserved in amber from Yantardakh, in the Taimyr Peninsula, Krasnoyarsk Region, northern Siberia (Fig. 1). This is the largest and best-studied insect-bearing site of the Kheta Formation that is exposed along the Romanikha and Maimecha rivers. The Yantardakh site is a cliff on the right bank of the Maimecha river, 3 km upstream of its mouth (GPS coordinates: 71º18′26′′N 99º33′46′′E). The amber containing the specimen was collected in 2012 from the top of the Kheta Formation, among lignitic lenses interbedded within sandstones, and is Santonian in age (Zherikhin and Sukatsheva, 1971; Rasnitsyn et al., 2016).

The specimen is contained in a small piece of clear orange amber that was polished in order to remove the weathered surface and provide an optimal view of the fossil. Photographs were taken under both incident and transmitted light using a Canon 5D Mark II camera attached to a Leica MZ APO stereomicroscope, and stacks of photographs taken at different focal planes were merged using HeliconFocus software (HeliconSoft Ltd.). Line drawings were made with a

camera lucida and digitally processed using Illustrator CS5 software. Measurements were made using the ocular micrometre of the stereomicroscope. The morphological terminology follows that used and illustrated by Perrichot et al. (2011) for Maimetshidae.

3. Systematic palaeontology

Family MAIMETSHIDAE Rasnitsyn, 1975

Genus ***Iberomaimetsha*** Ortega-Blanco, Perrichot & Engel, 2011.

Type species. *Iberomaimetsha rasnitsyni* Ortega-Blanco, Perrichot & Engel, 2011, p. 433, figs. 5-7.

Included species. *Iberomaimetsha nihtmara* Ortega-Blanco, Delclòs & Engel, 2011; *I. pallida* Perrichot & Perkovsky, sp. nov.; *I. rasnitsyni* Ortega-Blanco, Perrichot & Engel, 2011.

The generic diagnosis by Ortega-Blanco, Perrichot & Engel (in Perrichot et al. 2011) is followed.

Iberomaimetsha pallida Perrichot & Perkovsky, sp. nov.

Figs. 2–3

Type material. Holotype PIN 3311/1360 (female), in amber of Yantardakh, Taimyr Peninsula, Krasnoyarsk Region, northern Siberia; upper Kheta Formation, Santonian. Preserved in a small piece of orange amber measuring 4 × 3.5 × 2 mm, and contacting the amber surface so that the left side of body is largely missing. Housed in the Borissiak Paleontological Institute (PIN) of the Russian Academy of Sciences, Moscow.

Etymology. The specific epithet is derived from the Latin *pallidus* and refers to the pale, depigmented integument of the holotype.

Diagnosis. The new species has the following unique combination of characters within the genus: mandibles asymmetrical, right 4-toothed, left 3-toothed (*vs.* symmetrical, each 3-toothed in *I. rasnitsyni*); forewing with pterostigma linear (*vs*. slightly widening apically in *I. rasnitsyni*), vein 2Rs+M shorter than 1m-cu and shorter than cell [1Rs] (*vs*. longer in *I. nihtmara*); vein 2m-cu arising just basad to 2rs-m (*vs*. at midlength between 1rs-m and 2rs-m in *I. rasnitsyni*); cell [1M] rhomboidal, nearly as large as [2Cu] (*vs.* smaller than [2Cu] in *I. nihtmara*); apicalmost abscissa of Cu arising from almost apical posterior margin of [2Cu] (*vs*. at midlength of [2Cu] in *I. rasnitsyni*); hind wing vein Rs with first section very short, straight, more-or-less orthogonal to chord length of wing (*vs*. long, sinuate, oblique in *I. rasnitsyni*).

Description. *Female*. Integument densely covered with short, recumbent pubescence.

Head hypognathous, transverse, its width approximately 1.2× its height, about twice as broad as long; compound eyes oval, bulging; vertex without longitudinal median sulcus; occipital carina present, fine; ocelli distant from compound eyes, median ocellus separated from lateral ocelli by approximately one ocellar diameter, lateral ones separated from each other by about two ocellar diameters; anterior half of frons with a faint longitudinal sulcus; antennae filiform, inserted in shallow depression between compound eyes, closer to each other than to compound eye margin; toruli ring-like, distinctly raised, separated from each other by half a torulus diameter; radicel distinct, drop-shaped; scape compact, laterally compressed, approximately as long as high and twice as long as broad, with base distinctly convex, apex shallowly concave; pedicel inserted eccentrically into scape's apical concavity, 0.72× length of scape; 14 flagellar articles cylindrical in shape and progressively shortening, except apical flagellomere which is 1.7× as long as penultimate one and pointed apically; first two flagellomeres longest, thrice as

long as broad, 1.9× length of pedicel; penultimate flagellomere barely longer than broad; clypeus transverse, convex, anterior clypeal margin strongly convex; mandibles approximately as high as long, with outer margin strongly convex; left mandible with three teeth triangular, subequal in length; right mandible with apical tooth largest, sickle-shaped, following three teeth triangular, nearly half as long as apical tooth; maxillary and labial palps with five and three palpomeres visible, respectively.

Mesosoma compact, about 0.85× as long as high; mesoscutum abruptly truncate anteriorly to form a flat, nearly vertical surface, bordered by an oblique carina at anterolateral corners, with low dorsal convexity; anterior vertical portion of median mesoscutal sulcus crenulate, the remaining portion simple; notauli anteriorly deeply impressed, crenulate, and slightly diverging to reach anterolateral mesoscutal corners; axillae separated anteriorly by distinct groove, remaining mesoscutellum not visible; propodeum areolate, abruptly sloping posteriorly; mesopleuron with anterior and ventral margins foveolate; metapleuron with anterior margin simple, ventral margin foveolate. Forewing hyaline; veins 2rs-m and 2m-cu apparently spectral, visible only when playing with incident light; other veins tubular; prestigma incrassate; vein 1R short, about 0.8× length of pterostigma; first abscissae of Rs and M subequal in length, their fusion slightly angled; vein 2Rs+M 0.5× length of Rs+M; 2Rs distinctly arched around its basal third; apices of M and Cu not preserved in type specimen. Hind wing venation poorly visible, with only Sc+R and R sclerotized; apical portion of Rs straight, about twice as long as basal portion. Metacoxa distinctly larger than pro-and mesocoxae, all with broad bases and roughly conical in shape; all legs with tibia approximately subequal to femora in length, with basitarsus only slightly shorter than combined length of subsequent tarsomeres; protibial spur gently curved, biseriate apically; two mesotibial spurs short and stout; metatibial apex with one long and one short apical spurs, as well as comb-like row of 5–6 short spicules; apicoventral margin of all tarsomeres 1–4 with a distinct plantar lobe (female character; also called tarsal plantula or tarsal pulvillus); pretarsal claws serrate; arolium large.

Metasoma compact, apparently shorter or as long as mesosoma (but apical metasomal sclerites not preserved); first tergum largest, about thrice length of second tergum, strongly narrowed anteriorly to form short peduncle inserted low on propodeum; following terga not discernible or missing.

Measurements (in mm). Estimated body length 2.2–2.3; head height (excl. mandibles) 0.71, width (incl. eyes) 0.87; scape length 0.14, pedicel length 0.10, lengths of flagellomeres 0.19/0.19/0.18/0.16/0.14/0.13/0.11/0.10/0.10/0.10/0.09/0.09/0.07/0.13; forewing length *ca*. 2.00; mesosomal length 0.80; preserved metasomal length 0.74.

Comment. This specimen displays all diagnostic features of *Iberomaimetsha* as given by Ortega-Blanco, Perrichot, and Engel (in Perrichot et al., 2011), except for the notauli slightly diverging anteriorly to reach the anterolateral mesoscutal corners (*vs*. notauli apparently parallel in *I. nihtmara*, unknown in *I. rasnitsyni*). Parallel notauli have already been found in *Afrapia* and *Maimetshorapia*, two maimetshid genera from the Turonian of Botswana (Rasnitsyn and Brothers, 2009). When present in recent and extinct Hymenoptera, however, notauli are most generally not parallel but oblique longitudinal lines converging posteriorly on the mesoscutum (Gauld and Bolton, 1988; Goulet and Huber, 1993). In our opinion, this feature can be variably perceived in fossil wasps preserved in amber depending on the orientation of the specimen during examination, i.e. if not in full dorsal view, or if the mesosoma is distorted. None of the type specimens of *Iberomaimetsha nihtmara* that were used for the description is exposed in full dorsal view, and all have their notauli more or less visible (for example, see Perrichot et al.,

2011: fig. 8A) so it remains possible that these were in fact at least slightly diverging anteriorly. Therefore, the parallel *vs*. slightly oblique condition of this character alone can hardly justify separate genera. We prefer to keep a conservative approach and assign the Siberian fossil to *Iberomaimetsha* (but see conclusion).

4. Modified key to world genera and species of Maimetshidae

1. Forewing with three submarginal cells, i.e., cells [1Rs] and [2Rs] both present, [2Rs] delimited apically either by tubular or nebulous cross-vein 2rs-m (Perrichot et al., 2011: figs. 5, 12D) …… **2**
—. Forewing with two submarginal cells, i.e., cells [1Rs] and [2Rs] not simultaneously present (Perrichot, 2013: fig. 3) ……..……. **11**
2(1). Forewing 1m-cu basad to second free abscissa of Rs such that 2Rs+M present (Perrichot et al., 2011: fig. 7) …….. **3**
—. Forewing 1m-cu effectively confluent with second free abscissa of Rs such that 2Rs+M absent (Perrichot et al., 2011: figs. 11, 12) (Hauterivian-Barremian, Lebanon) …… ..... ***Ahiromaimetsha najlae*** **Perrichot, Azar, Nel & Engel**
3(2). Forewing 2Rs+M (second abscissa Rs+M, distal to 1m-cu) shorter than 1m-cu (Perrichot et al., 2011: figs. 7, 12D) ……..……. **4**
—. Forewing 2Rs+M subequal to or longer than 1m-cu (Perrichot et al., 2011: figs. 10, 14) ……..……..…….. **6**
4(3). Forewing cell [2Rs] not widened anteriorly; prestigma incrassate, about as long as 1Rs; 2m-cu present; pterostigma linear or slightly widening apically ……..…. **5**
—. Forewing cell [2Rs] widened anteriorly; prestigma linear, longer than 1Rs; 2m-cu absent; pterostigma linear **(**Rasnitsyn et al., 1998: fig. 13) (Barremian, England) .... ***Andyrossia joyceae*** **(Rasnitsyn & Jarzembowski)**
5(4). Mandibles symmetrical, 3-toothed; forewing pterostigma slightly widening apically; 2m-cu arising at midlength of [2Rs]; apical section of Cu arising at midheight of [2Cu]; hind wing vein Rs long, oblique to anterior wing margin (Perrichot et al., 2011: figs. 5–7) (Albian, Spain) ..... ***Iberomaimetsha rasnitsyni*** **Ortega-Blanco, Perrichot & Engel**
—. Mandibles asymmetrical, right 4-toothed, left 3-toothed; forewing pterostigma linear; 2m-cu arising just basad to 2rs-m; apical section of Cu arising at posterior margin of [2Cu]; hind wing vein Rs short, orthogonal to anterior wing margin (Fig. 3) (Santonian, Siberia) ……..... ***Iberomaimetsha pallida*** **Perrichot & Perkovsky, sp. nov.**
6(3). Forewing cell [1Rs] not reduced, 1rs-m longer than 3Rs (abscissa of Rs distad 1rs-m; Perrichot et al., 2011: fig. 10); pedicel, where known, not curved **7**
—. Forewing cell [1Rs] greatly reduced, 1rs-m much shorter than 3Rs (abscissa of Rs distad 1rs-m); pedicel arched (Perrichot et al., 2011: figs. 13, 14) (Campanian, Canada) .... ***Ahstemiam cellula*** **McKellar & Engel**
7(6). Notauli more or less parallel (Perrichot et al., 2011: fig. 9) **8**
—. Notauli strongly diverging anteriorly (Rasnitsyn and Brothers, 2009: fig. 7b) (Turonian, Botswana) ..... ***Afromaimetsha robusta*** **Rasnitsyn & Brothers**
8(7). Forewing Rs originating well before pterostigma, prestigma about as long as or longer than 1Rs (Perrichot et al., 2011: figs. 9, 10) **9**

—. Forewing Rs originating close to pterostigma, prestigma much shorter than 1Rs; prestigma incrassate, swollen apically and broader than basal abscissa of Rs (Rasnitsyn and Brothers, 2009: fig. 8b) (Turonian, Botswana) .... ***Maimetshorapia africana*** **Rasnitsyn & Brothers**

9(8). Prestigma linear and similar to basal abscissa of Rs; 15 to 19 flagellomeres (Rasnitsyn and Brothers, 2009: figs. 1, 2); 2m-cu absent (Genus *Afrapia*) ……..…… **10**

—. Prestigma incrassate; 2m-cu present, nebulous; 14 flagellomeres (Perrichot et al., 2011: figs. 8, 9) (Albian, Spain) .. ***Iberomaimetsha nihtmara*** **Ortega-Blanco, Delclòs & Engel**

10(9). Pterostigma shorter (about 0.8x) than distance between base of Rs and 2r-rs (Rasnitsyn and Brothers, 2009: fig. 1b) (Turonian, Botswana) .... ***Afrapia globularis*** **Rasnitsyn & Brothers**

—. Pterostigma as long as or longer than distance between base of Rs and 2r-rs (Rasnitsyn and Brothers, 2009: fig. 2b) (Turonian, Botswana) .... ***Afrapia variicornis*** **Rasnitsyn & Brothers**

11(1). Forewing cell [1Rs] anteriorly petiolate; hind wing with free apex of Cu; vertex without medial longitudinal line; compound eyes bulging; tarsal plantulae present in females (unknown in *Maimetshasia*) (Perrichot, 2013: figs. 1–3) ……..……..….. **12**

—. Forewing cell [1Rs] anteriorly sessile; hind wing without free apex of Cu; vertex with medial longitudinal line; compound eyes not bulging, almost following head contour; tarsal plantulae absent (Rasnitsyn, 1975: fig. 87, pl. IV, figs. 14a, 14b) (Santonian, Siberia) ..... ***Maimetsha arctica*** **Rasnitsyn**

12(11). Forewing cell [1M] rhombic, with M and 1m-cu nearly parallel; 2Rs+M longer than Rs +M; short stubs reminiscent of 2rs-m present, i.e., abscissa of Rs distad of r-rs composed of 4Rs and 5Rs, distinctly angled (Perrichot, 2013: figs. 1, 3A) ……..…… **13**

—. Forewing cell [1M] trapezoidal, with M and 1m-cu strongly converging posteriorly; 2Rs +M shorter than Rs+M; 2rs-m entirely absent, i.e., abscissa of Rs distad of r-rs composed only of 4Rs, continuously arched (Perrichot, 2013: figs. 2, 3B) (Cenomanian, Myanmar) ……. ***Maimetshasia kachinensis*** **Perrichot**

13(12). Face distinctly concave; right mandible surpassing left one by its entire apical tooth when closed; antenna with pedicel inserted deeply into scape's apex, in male with flagellomeres elongate (never as broad as long); forewing 4Rs (abscissa of Rs distad r-rs) shorter than r-rs (Perrichot, 2013: figs. 1, 3A) (Cenomanian, Myanmar) …… ……..…….. ***Burmaimetsha concava*** **Perrichot**

—. Face weakly concave; mandibles overlapping apically when closed (their apical teeth aligned); antenna with pedicel inserted apically on scape, in male with flagellomeres compact (penultimate one as broad as long); forewing 4Rs (abscissa of Rs distad r-rs) longer than r-rs (Perrichot et al., 2011: figs. 1–4) (latest Albian/earliest Cenomanian, France) ..... ***Guyotemaimetsha enigmatica*** **Perrichot et al.**

5. Conclusion

Iberomaimetsha is the first maimetshid genus known to occur in both the Lower and the Upper Cretaceous, and from two widely distant localities (Fig. 4). The 13 known species have a broad geographical distribution, but further palaeontological investigations are yet necessary for a better understanding of the origin and evolution of this extinct family of wasps, particularly through a phylogenetic analysis based on the morphological characters of the fossils. Indeed, the

key provided therein is not fully satisfactory as *Iberomaimetsha* is split into two couplets. It is possible that *Iberomaimetsha* will not be retrieved as monophyletic, and *I. nihtmara* could well belong to another genus distinguished, among others, by the forewing vein 2Rs+M longer than 1m-cu and the notauli parallel. But more taxa will be necessary before a phylogenetic analysis can be performed, and it is preferable to maintain the current diagnosis of *Iberomaimetsha* unmodified until a phylogenetic argument can be found.

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Figures

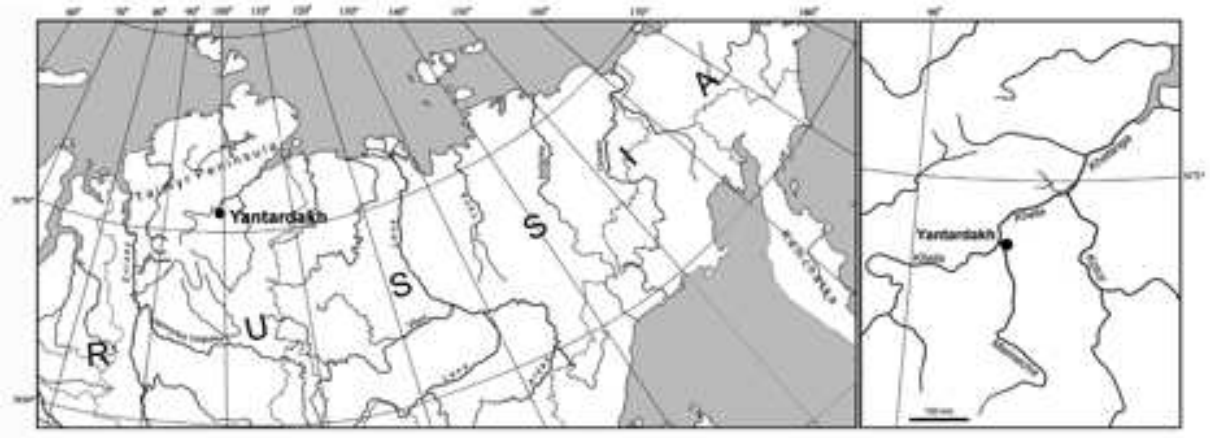

Fig. 1. Maps showing the Taimyr Peninsula and the location of Yantardakh.
Cartes montrant la Péninsule du Taimyr et la localisation de Yantardakh.

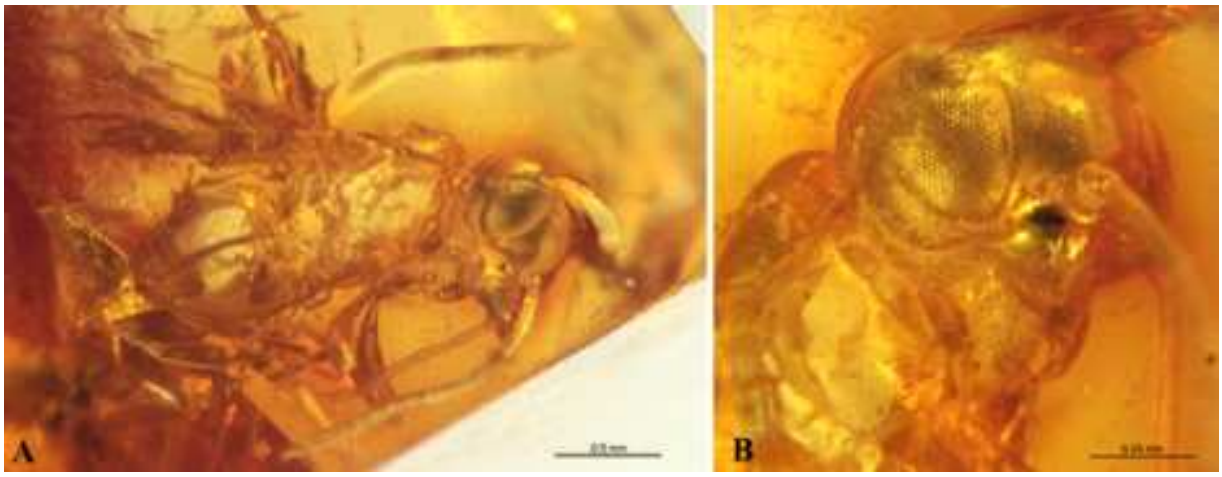

Fig. 2. *Iberomaimetsha pallida* sp. nov., holotype female (PIN 3311/1360). A: habitus in right profile view; B: detail of head.
Iberomaimetsha pallida *sp. nov., holotype femelle (PIN 3311/1360). A: vue de profil; B: détail de la tête.*

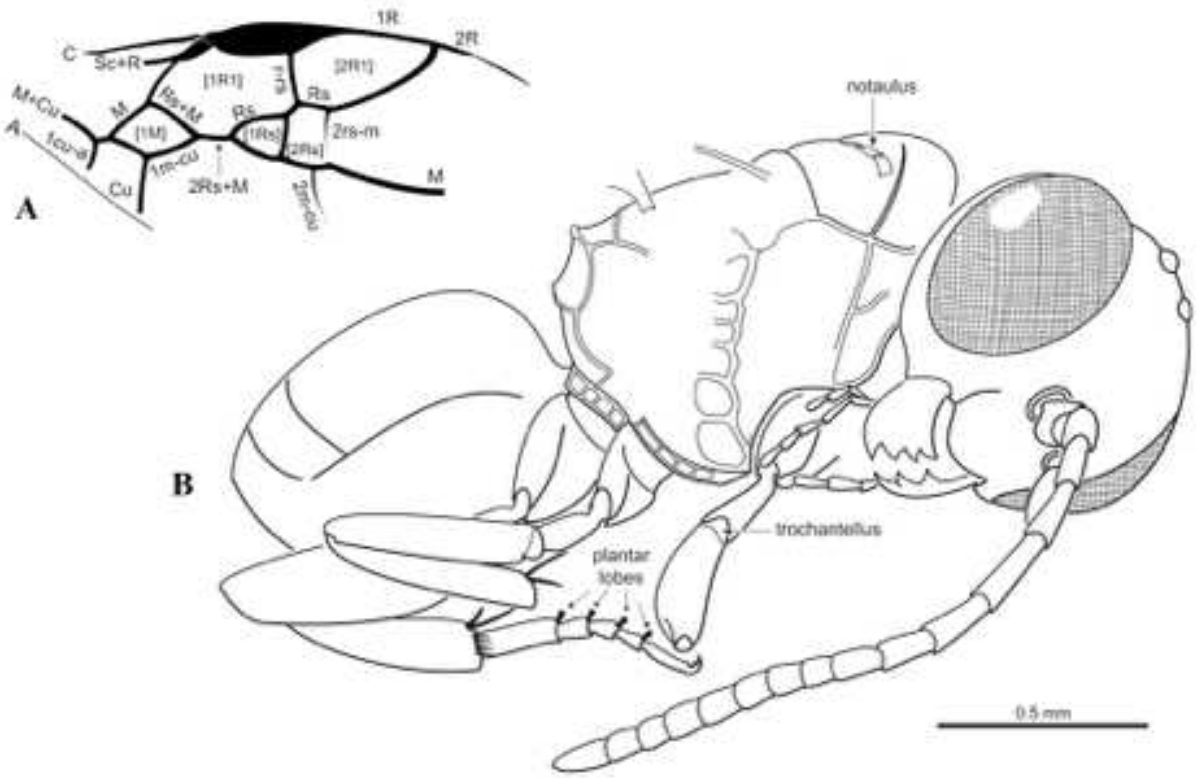

Fig. 3. Illustrations of *Iberomaimetsha pallida* sp. nov. A: forewing venation; B: body in profile view (left legs, left antenna, and right pro- and mesotarsomeres omitted for better clarity). *Illustrations de* Iberomaimetsha pallida *sp. nov. A: nervation de l'aile antérieure; B: corps en vue latérale (pattes gauches, antenne gauche, et pro- et mésotarsomères droits omis pour une meilleure clarté).*

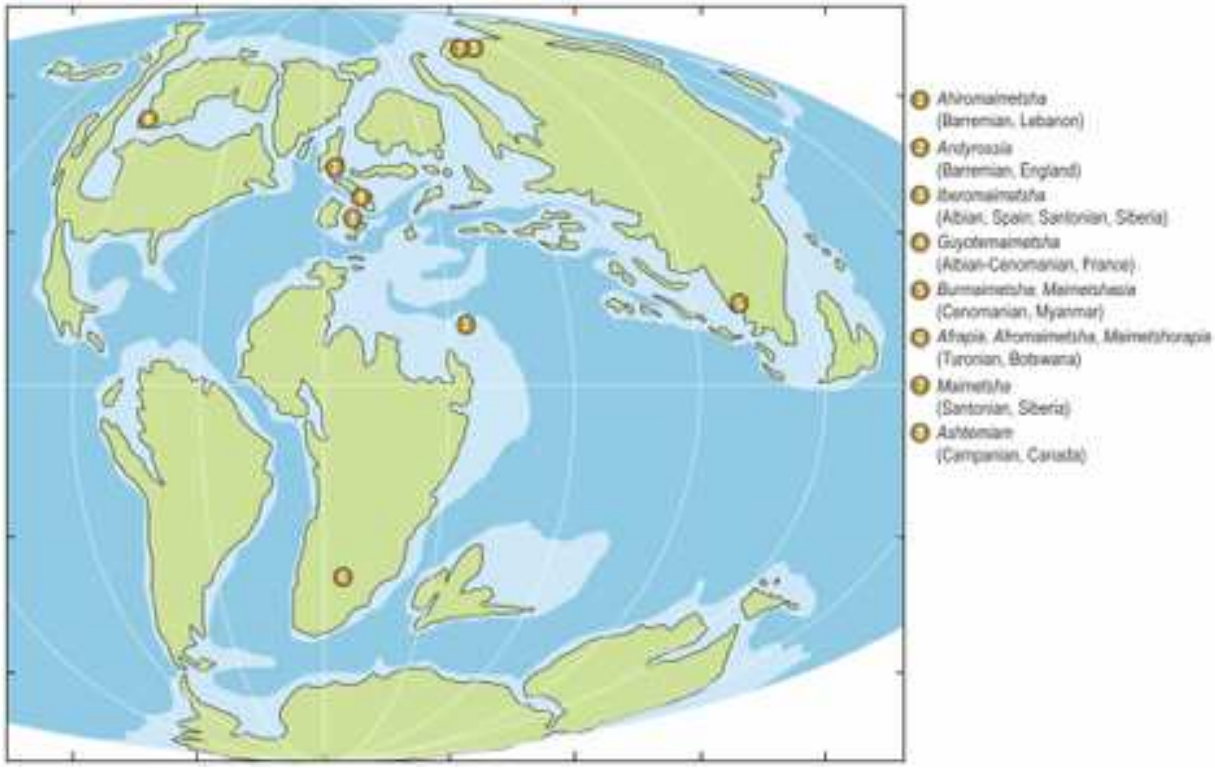

Fig. 4. Distribution of Maimetshidae (Late Early Cretaceous (105 Ma) map modified from Blakey, 2011).
Distribution des Maimetshidae (carte du Crétacé inférieur terminal (105 Ma) modifiée d'après Blakey, 2011).