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To cite this version:

Corentin Jouault. Mid-Cretaceous Burmese amber pelecinid wasps (Hymenoptera, Pelecinidae) support the hypothesis of an Asian origin of the family. Annales de Paléontologie, 2021, 107 (1), pp.102464. 10.1016/j.annpal.2020.102464 . insu-03142566

HAL Id: insu-03142566

https://insu.hal.science/insu-03142566v1

Submitted on 17 Feb 2021

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Mid-Cretaceous Burmese amber pelecinid wasps (Hymenoptera, Pelecinidae) support the hypothesis of an Asian origin of the family

Les guêpes pélécinides de l'ambre birman du Crétacé moyen (Hymenoptera, Pelecinidae) soutiennent l'hypothèse d'une origine asiatique de la famille

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ABSTRACT.

A new species of pelecinid wasp, *Eopelecinus marechali* sp. nov., is described and figured from mid-Cretaceous Burmese amber based on a single well-preserved female specimen. Contrary to *Eopelecinus inopinatus* Jouault et al., 2020a, unique other *Eopelecinus* known from this deposit, the new species is based on a complete female specimen. This discovery confirms that the Pelecinidae were highly diverse during the Cretaceous and highlights the underestimated diversity of the genus *Eopelecinus* in Burmese amber biota. *Eopelecinus marechali* sp. nov. differs from all other *Eopelecinus* species by its unique metasomal ratio. A summary on the fossil pelecinid species with distributions and ages is provided. Based on the particular geological history of the West Burmese Terrane and the fossil record of the family, the hypothesis of an Asian origin of the family is discussed. The records of *Eopelecinus* in both Laurasia and Burmese amber biota, during the mid-Cretaceous, suggest that possible transfers of fauna have taken place between these two geological blocks.

Une nouvelle espèce de guêpe pélécinide, *Eopelecinus marechali* sp. nov., est décrite et figurée à partir de l'ambre birman du Crétacé moyen sur la base d'un seul spécimen femelle bien conservé. Contrairement à *Eopelecinus inopinatus* Jouault et al., 2020a, l'unique autre *Eopelecinus* connu de ce gisement, la nouvelle espèce est basée sur un spécimen femelle complet. Cette découverte confirme que les Pelecinidae étaient très diversifiés durant le Crétacé et met en évidence la diversité sous-estimée du genre *Eopelecinus* dans le biote de l'ambre birman. *Eopelecinus marechali* sp. nov. diffère de toutes les autres espèces d'*Eopelecinus* par son ratio métasomal unique. Un résumé des espèces de pélécinides fossiles avec leur répartitions et leur âges est fourni. Sur la base de l'histoire géologique particulière du terrane birman occidental et du registre fossile de la famille, l'hypothèse d'une origine asiatique de la famille est discutée. Les enregistrements d'*Eopelecinus* en Laurasia et dans l'ambre de Birmanie, au Crétacé moyen, suggèrent que des transferts de faunes aient pu avoir lieu entre ces deux paléo-continents.

Key words. New species, *Eopelecinus*, Fossil record, Paleobiogeography

Mots clefs: Nouvelle espèce, *Eopelecinus*, Registre fossile, Paléobiogéographie

1. Introduction.

Pelecinid wasps Hymenoptera in having a long, thin, pluri-segmented metasoma with elongated, untelescoped segments (Goulet and Huber, 1993). All the pelecinid females possess a very long (up to 7 cm, in extant taxa) metasoma, used to lay eggs directly on scarab larvae buried in the soil (Mason, 1984; Johnson and Musetti, 1999).

The Pelecinidae fossil record is rich, dating back to the Jurassic (China, Kazakhstan, and Mongolia) and their highest species diversity occurred during the early Cretaceous (http://fossilworks.org, accessed 10 October 2020). However, their extant record is limited to three species (Mccravy, 2008). The numerous Mesozoic genera were widely distributed in Laurasia but are, to date,

unknown from all Gondwana deposits. They clearly decreased in diversity after the Cretaceous with only two described Cenozoic species from Baltic amber and Kishenehn Formation (Brues, 1933; Engel, 2002; Greenwalt and Engel, 2014) and an undescribed specimen from the Eocene Sakhalin amber possibly belonging to the genus *Pelecinopteron* (Kozlov, 1974; Johnson, 1998).

This peculiar fossil distribution, together with the only phylogenetic analysis proposed for the family, led to hypothesize an Asian origin for the family (Shih et al., 2010). However, the recent descriptions of Pelecinidae from the Burmese amber biota (Engel et al., 2013; Guo et al., 2016a; Jouault et al., 2020a) may challenge this assumption. The West Burmese Terrane displays a peculiar geological history (Seton et al., 2012; Westerweel et al., 2019) questioning the fauna origin of its biota. Some taxa described from this amber deposit support Gondwana affinities (de Sena Oliveira et al., 2016; Jouault and Nel, 2020; Poinar, 2018) while numerous other families and orders suggest an island endemism, first pointed by Zhang et al. (2018) but also by Rasnitsyn and Ohm-Kuhnle (2018). Finally, it is not impossible that taxa with efficient flight abilities might have been able to cross the broad ocean separating West Burmese Terrane from Laurasia before their collision during the Late Cretaceous (Gumovsky et al., 2018; Martynova et al., 2019). The lack of recent exhaustive phylogenetic analysis of extant and fossil pelecinid wasps and of clear apomorphies supporting the extinct Iscopininae, have led Engel et al. (2013) to synonymize this subfamily with Pelecinidae. This synonymization has been accepted by recent most publications (Guo et al., 2016a,b; Jouault et al., 2020a) and is followed herein.

In this paper, *Eopelecinus marechali* sp. nov. is described and figured from a single well-preserved female. A discussion on the origin of the family is proposed based on the pelecinid fossil record and the geological history of the West Burmese Terrane.

2. Material and methods.

The amber piece containing the specimen studied herein derives from the deposits of Noije Bum in the Hukawng Valley (26◦ 29′ N, 96◦ 35′ E), Kachin State, northern Myanmar (see detailed map in Grimaldi and Ross, 2017: Fig. 2). Radiometric data established an early Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing sediments (Shi et al., 2012). Some ammonites found in the amber- bearing bed and within amber corroborates a late Albian/early Cenomanian age (Cruickshank and Ko, 2003; Yu et al., 2019).

The amber piece was prepared using a diamond disk and polished with a grinder polisher (Buehler EcoMet 30) by using a very thin silicon carbide sanding paper (grit size = 7000). The holotype of *Eopelecinus marechali* sp. nov. is housed in the amber collection of the Geological Department and Museum (IGR) of the University of Rennes, France, under the collection number IGR.BU-019. The specimen was examined using a Leica MZ APO stereomicroscope. Photographs have been taken with a Canon 5D Mark II camera, and are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using HeliconFocus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software.

Acronyms for measurements and indices are listed below: HL: maximum head length measured laterally from anteriormost point of head capsule to posteriormost point of vertex; HW: maximum head width measured at eyes level (eyes included); AL: antennal length (length of all antennomeres combined); ED: maximum diameter of eye as measured in lateral view of head to show full surface of eye; PW: pronotum width in dorsal view; ML: mesosomal length measured in lateral view from anterior surface of pronotum to posterior extension of propodeum; WH: mesosoma height (in side view, maximum height measured from lowermost point of mesopleuron (in front of middle coxa) to dorsal edge of mesosoma); MIL: maximal length of first metasomal segment; MIH: maximal height of first metasomal segment; MIIL: maximal length of second metasomal segment;

MIIH: maximal height of second metasomal segment; CI: cephalic index (HL/HW × 100); AI: antennal index (AL/HW × 100); OI: ocular index (ED/HL × 100).

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3. Systematic paleontology

Order Hymenoptera Linnaeus, 1758

Suborder Apocrita Gerstaecker, 1867

Superfamily Proctotrupoidea Latreille, 1802

Family Pelecinidae Haliday, 1840

Genus *Eopelecinus* Zhang et al., 2002

Type species: *Eopelecinus vicinus* Zhang et al. 2002, other species: Table 1.

Eopelecinus marechali sp. nov.

Figs 1 and 2

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Material. Holotype IGR.BU-019 (a nearly complete specimen, with only apex of left antenna and left forewing damaged, in a rectangular piece of amber measuring 8 × 10 × 2 mm).

Locality and horizon. Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid- Cretaceous.

Etymology. The specific epithet is a patronym honoring my friend Arthur Maréchal for his 23rd birthday. The specific epithet is to be treated as a noun in a genitive case.

Diagnosis. Eopelecinus marechali sp. nov. differs from all known *Eopelecinus* species in having a unique metasomal segment ratio: 1.0; 0.96; 0.87; 0.83; 0.64; 0.52; first segment the longest but only slightly longer than second one; metasomal segments decreasing in size from first to apical one

(inmm): 0.78; 0.75; 0.68; 0.65; 0.5; 0.41; vertex strongly concave; propodeum coarsely reticulate; head hemispherical, apical flagellomere nearly twice as long as pre-apical one; small size ca. 4.75 mm; 14 antennomeres.

Description. Female; male unknown.

Head (Figs. 1 and 2A and B). Hypognathous, hemispherical (CI: 76), wider than long, widest in posterior third in dorsal view; mandibles dentate, oriented ventrally; compound eye large, nearly oval; vertex strongly concave, with three ocelli forming a triangle (hard to define due to the preservation in amber). Antennae 14 antennomeres (Fig. 2B), antenna filiform (probably flattened during fossilization process); scape 0.12 mm, pedicel 0.08 mm, F1 0.06 mm, F2 to F10 all ca. 0.07 mm (preservation does not allow differentiation of lengths), F11 0.08 mm, F12 0.13 mm; scape narrow basally, slightly widened apically, 2.15× longer than wide, slightly shorter than apical flagellomeres; pedicel globular, narrower basally, slightly longer than wide; first flagellomere narrower basally than apex of pedicel, gradually increasing in width apically, more than twice as long as wide; remaining flagellomeres similar to first one except apical one with rounded apex and twice as long as pre-apical flagellomere (laterally deformed due to preservation).

Mesosoma (Figs. 1 and 2A) 0.8 mm long, apparently rectangu- lar; pronotum extremely short; mesonotum nearly straight; notauli not clearly visible, metanotal suture conspicuous; mesonotum and propodeum separated by a deep constriction; propodeum coarsely reticulate (Fig. 2A). Fore and mid legs both shorter than hind leg. Fore leg: profemora 0.37 mm long, protatibia: 0.31 mm long, metabasitarsus 0.1 mm long, combined tarsi length ca. 0.28 mm. Mid leg: mesofemora 0.25 mm long, mesotatibia: 0.38 mm long, mesobasitarsus 0.12 mm long, combined tarsi length ca. 0.37 mm. Hing leg: metafemora 0.5 mm long, metatibia: 0.41 mm long, metabasitarsus 0.15 mm long, combined tarsi length ca. 0.45 mm. Tibial spur formula 1-2-2. Tarsal claws unarmed. Arolium present. Forewing (Fig. 2D) 1.5 mm long, with thin costal area; pterostigma short, longer than wide, and broa-

dest in its apical third, with posterior margin arched; covered with microsetae. Hind wing 0.8 mm long, without any veins; covered with microsetae.

Metasoma elongated (Figs. 1 and 2A and C). First metasomal segment 0.78 mm long, elongated, trapezoidal and broadest slightly before its mid-length; tergite and sternite of first metasomal segment convex laterally and dorso-ventrally, slightly shorter than mesosoma and slightly broader basally than apically, without conspicuous sculpture; other metasomal segments tubuliform, slender and slightly arched medially, shortening and thinning toward metasomal apex, respective length (mm): 0.75; 0.68; 0.65; 0.5; 0.41. Apical-most segment needle-shaped maybe due to apices of ovipositor and ovipositor sheaths exerting slightly from the apex (Fig. 2C).

Color pattern. Colors black to dark brown (as preserved in amber). Legs (assumed) lighter than rest of body.

Measurements (in mm): HL 0.38; HW 0.50; AL 1.10; ED 0.22; PW 0.34; ML 0.63; WH 0.37; MIL 0.78; MIH 0.23; MIIL 0.75; MIIH 0.08; MIIIL 0.68; MIIIH 0.07; CI 76; AI 220; OI 57.

4. Discussion

4.1. *Systematic placement and phylogenetic assumption*

The new specimen described herein is undoubtedly assigned to the genus *Eopelecinus* based on the reduced wing venation (viz. forewing with only veins C and R present), pterostigma short with sides subparallel, pronotum medially short, propodeum reticulate, and metasoma with one broad basal segment and others tubular. Among *Eopelecinus* species, *Eopelecinus marechali* sp. nov. can be easily distinguished by the unique metasomal ratio (see differential ratio for all species in Jouault et al., 2020a: tabl. 1), relatively smaller size, antennae 14-segmented, and head with posterior margin conspicuously concave. It differs from (see. inventor and date in Table 1) *E. inopinatus*, *E. mecometasomatus* in having the second metasomal segment shorter than the first. It also differs from *E. eucallus*, *E. fragilis*, *E. laiyangicus*, *E. mesomicrus*, *E. minutus*, *E. pusillus*, *E. shan-*

gyuanensis, *E. tumidus*, and *E. yuanjiawaensis* in having the second metasomal segment only slightly shorter than first one (vs. conspicuously shorter). *Eopelecinus marechali* sp. nov. differs from *E. giganteus*, *E. leptaleus*, *E. hodoiporus*, *E. exquisitus*, *E. scorpioideus*, *E. huangi*, *E. similaris*, and *E. vicinus* by its conspicuously smaller size (4.75 vs. respectively 20.6, 14.2, 13.3, 18.3, 15.7, 30.8, 8.2, 13.8 mm). *E. hodoiporus* Zhang, 2005 is the only other *Eopelecinus* species possessing a "similar" metasomal ratio but it differs from *Eopelecinus marechali* sp. nov. in having a rounded head without conspicuous concave vertex (vs. clearly hemispherical with deep posterior concavity in *Eopelecinus marechali* sp. nov.), and also by its temporal range (Aptian vs. upper Albian–Cenomanian).

According to the phylogenetic analysis of Shih et al. (2010), mainly based on wing venation, the genus *Allopelecinus* was proposed as the putative sister lineage of *Eopelecinus*; but the numerous genera and species described since this first analysis question these affinities. Additionally, some genera formerly comprised only a reduced number of species while they are today represented by many species with polymorphic characters (Shih et al., 2010).

Rasnitsyn (1969, 1980) proposed a theory on a general trend among Hymenoptera consisting in the miniaturization, reduction of venation, enlargement of pterostigma, and reduction of number of flagellomeres, during the evolution of the whole order. This trend has been documented in Aculeata, and non-Aculeata wasps based on fossil specimens (e.g. Jouault et al., 2020b; Li et al., 2015), but it seems to be less obvious for the extant taxa (Vargas et al., 2020). If we apply Rasnitsyn's hypothesis to *Eopelecinus*, species of *Eopelecinus* with 14 antennomeres would have occupied relatively diverging positions in the genus phylogeny of the genus while species with 15 antennomeres would have occupied more inclusive positions. Thereby, *Eopelecinus marechali* sp. nov. (with 14 antennomeres) would likely belong to the recently diverged Eopelecinus sub-group including: *Eopelecinus marechali* sp. nov., *E. inopinatus*, *E. exquisitus*, *E. giganteus*(?), *E. hodoiporus*, *E. huangi*, *E. laiyangicus*, *E. mesomicrus*, *E. pusillus*, *E. scorpioideus*, *E. shangyuanensis*, *E. tumi-*

dus, and *E. vicinus* which all possess 14 antennomeres or less. Within this sub-group, it seems that another sub-group, having more recently diverged, emerges on the basis of an antenna with 13 antennomers (*E. laiyangicus*(?), *E. mesomicrus*(?), *E. pusillus*). This assumption fits with the various ages of the different *Eopelecinus* species: most species with 15 antennomeres are early Cretaceous, while the younger, mid-Cretaceous species had 14 antennomeres. It is therefore likely that *Eopelecinus* species with 13 antennomeres will be discovered in the Cretaceous deposits. It remains that an analysis of the relationships between the *Eopelecinus* species is challenging, since most of them only differs in their metasomal ratio and possesses reduced wing venation. It therefore appears that a complete study of the pelecinid phylogeny is necessary, but that falls outside the objective of the present study.

4.2. *Burmese pelecinid and paleobiogeography*

The presence of *Eopelecinus* in the mid-Cretaceous Burmese amber gives new clues to investigate the paleobiogeography of the genus, on the basis of the geological history of the West Burmese Terrane. During the Lower Jurassic, this Terrane was located near the Australian block in East Gondwana (Seton et al., 2012; van Hinsbergen et al., 2012) and separated from East Laurasia (Asian region) by the Meso-Tethys Ocean. Previous studies estimated that the West Burmese Terrane brake away from the Australian block (with Indian block) between the Late Jurassic and the Lower Cretaceous (Heine et al., 2004; Heine and Müller, 2005), but more recent studies agree on a separation dated back ca. 125 Ma; the Terrane being an isolated island only after ca. 120 Ma (Metcalfe, 1990, 1996; Scotese, 2014; Westerweel et al., 2019). During the mid-Cretaceous, the West Burmese Terrane was isolated geographically and occupied an island position in the Tethys Ocean between Asia and the Indian block, far from both of them (Westerweel et al., 2019), during more than 20 Ma (Heine et al., 2004; Seton et al., 2012).

On this basis, two evolutionary scenarios are possible to explain the presence of Pelecinidae in the Burmese amber biota (Fig. 3): Burmese pelecinid wasps originated from Laurasia and later migrated to Burmese Terrane (Fig. 3, arrow 2); or originated from Gondwana (Fig. 3, arrow 1). The fossil record and the repartition of the extant Pelecinidae would be in accordance with the first hypothesis because of the numerous genera and species described from Laurasia, while the current fossil record in Gondwana is null (Table 1). The lack of pelecinid wasps described from Gondwana is surprising since numerous Hymenoptera are known from the Crato Formation in Brazil known to be among the best documented Aptian insect Konservat Lagerstätte (Martill, 1993; Martill and Bechly, 2007; Milaisey, 1991) and is contemporary with the Chinese, Russian and Mongolian deposits. They are also absent from the Turonian deposit of Orapa (Botswana) where more than 2000 insect fossils are known (Brothers and Rasnitsyn, 2003), strengthening a Laurasia origin for the family.

The numerous records of pelecinid wasps inhabiting the Northern hemisphere (Laurasia) during the late Jurassic and Cretaceous, when India was located in Southern hemisphere (Heine et al., 2004; Seton et al., 2012) or latter was an island completely isolated from any continental land masses (Westerweel et al., 2019), would refute a “out-of-India” hypothesis (Karanth, 2006), in which India was as a raft bringing Gondwanan lineages to Southeast Asia. It also appears very unlikely that Burmese amber pelecinid was a Gondwanan-derived population that had migrated via India since the latter had a hostile paleoclimate during the Cretaceous (Spicer et al., 1996). Additionally, if a population of Pelecinidae had survived in India, it seems likely that some representatives would be present today in Madagascar and/or Australia since these geological blocks were connected together with West Burmese Terrane before the Gondwana breakup (Heine et al., 2004; Seton et al., 2012). It is not the case. The record of *Eopelecinus*, which is to date the most specious genus of the family, widely distributed in Asia before the Cenomanian, strengthens the possible latter migra-

tions from Laurasia to the West Burmese Terrane (Fig. 3). All these geological data agree with the phylogenetic analysis of Shih et al. (2010) pointing the Pelecinidae origin from the Asiatic region.

The distribution of extant pelecinid species may be explained by the persistence of Laurasian populations in North America (recorded in Raritan amber, and by extant species; Engel and Grimaldi, 2006) and latter migrations from North America to South America. In fact, before the establishment of the Isthmus of Panama, a series of islands was present between North America and South America during the Miocene (O'Dea et al., 2016) allowing transfer of flying invertebrates between the North America and the South America.

5. Conclusion.

The highly specialized metasoma of extinct pelecinid wasps are similar to those of the three extant representatives of the family, suggesting similar parasitic behaviors on scarab larvae (Bennett, 2003). The pelecinid fossil record (particularly that of the genus *Eopelecinus*), combined with the description of *Eopelecinus marechali* sp. nov., and the peculiar geological history of the West Burmese Terrane suggest that the origin of the family is likely in Laurasia and particularly in Asia during the Jurassic period. Unlike some other taxa, the shapes and sizes of pelecinids may have played a key role in their lift and favored their transport from continent to the Burmese paleo-island via air currents. Thereby, pelecinid wasps are maybe the testimonies of a late fauna input during mid-Cretaceous period. Future complete phylogenetic analyses, combined with models that estimate ancestral areas with dated phylogenies, current species distribution, and time-stratified paleogeographic matrices may helped to ensure these hypotheses.

Acknowledgements

I am grateful to the editor Prof. Didier Néraudeau for managing the manuscript. I sincerely thank the reviewers: Prof. André Nel and Prof. Alexandr. P. Rasnitsyn for their valuable comments on thismanuscript.

References

Bennett, A.M.R., 2003. Host location behaviour in Pelecinus polyturator (Hymenoptera: Pelecinidae). Journal of the Entomological Society of Ontario 134, 131–134.

Brothers, D.J., Rasnitsyn, A.P., 2003. Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana: a preliminary review. African Entomology 11, 221–226.

Brues, C.T., 1933. The Parasitic Hymenoptera of the Baltic Amber. Bernstein-Forschungen 3, 4–178.

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21, 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5

de Sena Oliveira, I.S., Bai, M., Jahn, H., Gross, V., Martin, C., Hammel, J.U., et al., 2016. Earliest onychophoran in Amber Reveals Gondwanan Migration Patterns. Current Biology 26, 2594–2601, http://dx.doi.org/10.1016/j.cub.2016.07.023.

Duan, Y., Cheng, S.L., 2006. A new species of Pelecinidae (Insecta, Hymenoptera, Proctotrupoidea) from the Lower Cretaceous Jiufotang Formation of western Liaoning. Acta Palaeontologica Sinica 45, 393–398.

Engel, M.S., 2002. The fossil pelecinid *Pelecinopteron tubuliforme* Brues in Baltic amber (Hymenoptera: Pelecinidae). Journal of Hymenoptera Research 11, 5–11.

Engel; M.S., Grimaldi, D.A., 2006. A Diminutive Pelecinid Wasp in Cretaceous Amber from New Jersey (Hymenoptera: Pelecinidae). Northeastern Naturalist 13, 291–297.

Engel, M.S., Grimaldi, D.A., Ortega-Blanco, J., 2013. *Zoropelecinus zigrasi*, a pelecinid wasp in mid-Cretaceous amber from Myanmar (Hymenoptera: Pelecinidae). Novitates Paleoentomologicae 4, 1–10. https://doi.org/10.17161/ np.v0i4.4571.

Feng, H., Shih, C.K., Ren, D., Liu, C.X., 2010. New male pelecinid wasps (Hymenoptera: Pelecinidae) from the Yixian Formation of western Liaoning (China). Geologica Carpathica 61, 463–468. https://doi.org/10.2478/v10096-010-0028-x

Goulet, H., Huber, J.T., 1993. Hymenoptera of the world: An identification guide to families. ed. Agriculture Canada, Ottawa, Ontario, 680 pp.

Greenwalt, D.E., Engel, M.S., 2014. A diminutive pelecinid wasp from the Eocene Kishenehn Formation of northwestern Montana (Hymenoptera: Pelecinidae). Novitates Paleoentomologicae 8, 1–9. https://doi.org/10.17161/np.v0i8.4750

Grimaldi, D., Ross, A., 2017. Extraordinary lagerstätten in amber, with particular reference to the Cretaceous of Burma. In: Fraser, N.C. & Sues, H.-D. (Eds.), Terrestrial conservation lagerstätten: Windows into the evolution of life on land. Dunedin Academic Press, Edinburgh, pp. 287–342.

Gumovsky, A., Perkovsky, E.E., Rasnitsyn, A.P., 2018. Laurasian ancestors and "Gondwanan" descendants of Rotoitidae (Hymenoptera: Chalcidoidea): What a review of Late Cretaceous Baeomorpha revealed. Cretaceous Research 84, 286–322. https://doi.org/10.1016/ j.cretres.2017.10.027

Guo, L.C., Shih, C.K., Li, L.F., Ren, D., 2016a. New pelecinid wasps (Hymenoptera: Pelecinidae) from Upper Cretaceous Myanmar amber. Cretaceous Research 67, 84–90. https://doi.org/ 10.1016/j.cretres.2016.01.009.

Guo, L.C., Shih, C.K., Li, L.F., Ren, D., 2016b. New pelecinid wasps (Hymenopter: Pelecinidae) from the Yixian Formation of western Liaoning, China. Cretaceous Research 61, 151–160. https://doi.org/10.1016/j.cretres.2016.01.009.

Heine, C., Müller, R.D., 2005. Late Jurassic rifting along the Australian North West Shelf: margin geometry and spreading ridge configuration. Australian Journal of Earth Sciences 52, 39–27 https://doi.org/10.1080/08120090500100077

Heine, C., Müller, R.D., Gaina, C., 2004. Reconstructing the lost eastern Tethys ocean basin: convergence history of the SE Asian margin and marine gateways. Geophysical Monograph Series 149, 1–18. https://doi.org/10.1029/149GM03

Johnson, N.F., 1998. The fossil pelecinids *Pelecinopteron* Brues and *Iscopinus* Kozlov (Hymenoptera: Pelecinidae). Proceedings of the Entomological Society of Washington 100, 1–6.

Johnson, N.F., Musetti, L., 1999. Revision of the proctotrupoid genus *Pelecinus* Latreille (Hymenoptera: Pelecinidae). Journal of Natural History 33, 1513–1543.

Jouault, C., Nel, A., 2020. The oldest record of window fly supports a Gondwanan origin of the family (Diptera: Scenopinidae). Palaeoentomology 3, 483–491. https://doi.org/10.11646/palaeoentomology.3.5.6

Jouault, C., Ngô-Muller, V., Pouillon, J.-M, Nel, A., 2020a. Taxonomic additions to the pelecinid wasps (Hymenoptera, Pelecinidae) of the 'mid-Cretaceous' Burmese amber. Cretaceous Research 104505. https://doi.org/10.1016/j.cretres.2020.104505

Jouault, C., Ngô-Muller, V., Pouillon, J.-M., Nel, A., 2020b. New Burmese amber fossils clarify the evolution of bethylid wasps (Hymenoptera: Chrysidoidea). Zoological Journal of the Linnean Society, zlaa078. https://doi.org/10.1093/zoolinnean/zlaa078

Karanth, K.P., 2006. Out-of-India Gondwanan origin of some tropical Asian biota. Current Science 90, 789–792.

Kozlov, M.A., 1974. An Early Cretaceous ichneumon of the family Pelecinidae (Hymenoptera: Pelecinoidea). Paleontological Journal 7, 136–138.

Li, L.F., Rasnitsyn, A.P., Shih, C.K., Ren, D., 2015. A new genus and species of Praeaulacidae (Hymenoptera: Evanioidea) from Upper Cretaceous Myanmar amber. Cretaceous Research 55: 19–24. https://doi.org/10.1016/j.cretres.2015.01.007

Liu, C.X., Shih, C.K., Ren, D., 2009. The earliest fossil record of the wasp subfamily Pelecininae (Hymenoptera: Proctotrupoidea: Pelecinidae) from the Yixian Formation of China. Zootaxa 2080, 47–54. https://doi.org/10.11646/zootaxa.2080.1.4

Liu, C.X., Gao, T.P., Shih, C.K., Ren, D., 2011. New pelecinid wasps (Hymenoptera: Proctotrupoidea: Pelecinidae) from the Yixian Formation of western Liaoning, China. Acta Geologica Sinica 85, 749–757. https://doi.org/10.1111/j.1755-6724.2011.00480.x

Mccravy K.W., 2008. Pelecinid Wasps (Hymenoptera: Pelecinidae). In: Capinera J.L. (eds) Encyclopedia of Entomology. Springer, Dordrecht. pp. 177. https://doi.org/10.1007/978-1-4020-6359-6_2834

Martill, D.M., 1993. Fossils of the Santana and Crato Formations, Brazil. Field guides to fossils, 5, The Palaeontological Association, London, 159 pp.

Martill, D., Bechly, G., 2007. Introduction to the Crato Formation. In: Martill, D., Bechly, G., & Loveridge, R. (Authors), the Crato fossil beds of Brazil: Window into an ancient world (pp. 3–7). Cambridge: Cambridge University Press.

Martynova, K.V., Olmi, M., Müller, P., Perkovsky, E.E., 2019. Description of the first sclerogibbid wasp (Hymenoptera: Sclerogibbidae) from Burmese (Myanmar) amber and its phylogenetic significance. Journal of Systematic Paleontology 17, 1791-1803. https://doi.org/10.1080/14772019.2018.1551250

Mason, W.R.M., 1984. Structure and movement of the abdomen of female Pelecinus polyturator (Hymenoptera: Pelecinidae). The Canadian Entomologist 116, 419–426.

Metcalfe, I., 1990. Allochthonous terrane processes in Southeast Asia. Philosophical Transactions of the Royal Society of London, A, 331, 625–640. https://doi.org/10.1098/rsta.1990.0094

Metcalfe, I., 1996. Pre-Cretaceous evolution of SE Asian terranes. In: Hall, R. & Blundell, D. (Eds), Tectonic evolution of Southeast Asia. Geological Society Special Publication, 106, 122–97 https://doi.org/10.1144/GSL.SP.1996.106.01.09

Milaisey J.G., 1991. Santana fossils: An illustrated atlas. T.F.H. Publications, New Jersey, USA, 459 pp.

O'Dea, A., Lessios, H.A., Coates, A.G., Eytan, A.R.I., Restrepo-Moreno, S.A., Cione, A.L., Collins, L.S., de Queiroz, A., Farris, D.W., Norris, R.D., Stallard, R.F., Woodburne, M.O., Aguilera, O., Aubry, M.-P., Berggren, W.A., Budd, A.F., Cozzuol, M.A., Coppard, S.E., Duque-Caro, H., Finnegan, S., Gasparini, G.M., Grossman, E.L., Johnson, K.G., Keigwin, L.D., Knowlton, N., Leigh, E.G., Leonard-Pingel, J.S., Marko, P.B., Pyenson, N.D., Rachello-Dolmen, P.G., Soibelzon, E., Soibelzon, L., Todd, J.A., Vermeij, G.J., Jackson, J.B.C., 2016. Formation of the Isthmus of Panama. Science Advances 2, e1600883. https://doi.org/10.1126/sciadv.1600883

Poinar, G, Jr. 2018. Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. Historical Biology, 31, 1304–1309. https://doi.org/10.1080/08912963.2018.1446531

Rasnitsyn, A.P., 1969. The origin and evolution of Lower Hymenoptera. Transactions of the Paleontological Institute. Academy of Sciences of the USSR 123, 1–196 [In Russian].

Rasnitsyn, A.P., 1980. [Origin and evolution of Hymenoptera]. Transactions of the Paleontological Institute. Academy of Sciences of the USSR 174, 1–192 [in Russian].

Rasnitsyn, A.P., 2008. Hymenopterous insects (Insecta: Vespida) in the Upper Jurassic deposits of Shar Teg, SW Mongolia. Russian Entomological Journal 17, 299–310.

Rasnitsyn, A.P., Ohm-Kühnle, C., 2018. *Aptenoperissus* from mid-Cretaceous Burmese amber (Hymenoptera, Stephanoidea, Aptenoperissidae): unexpected diversity of paradoxical wasps suggests insular features of source biome. Cretaceous Research 91, 168–175. https://doi.org/10.1016/j.cretres.2018.06.004

Scotese, C.R., 2014. Atlas of Early Cretaceous Paleogeographic Maps, PALEOMAP Atlas for ArcGIS, volume 2, The Cretaceous, Maps 23–31, Mollweide Projection, PALEOMAP Project, Evanston, Illinois.

Seton, M., Müller, R.D., Zahirovic, S., Gaina, C., Torsvik, T., Shepard, G., Talsma, A., Gurnis, M., Turner, M., Maus, S. & Chandler, M., 2012. Global continental and ocean basin reconstructions since 200 Ma. Earth-Science Review 113, 212–270. https://doi.org/10.1016/j.earscirev.2012.03.002

Shih, C.K., Feng, H., Liu, C.X., Zhao, Y., Ren, D., 2010. Morphology, phylogeny, evolution, and dispersal of pelecinid wasps (Hymenoptera: Proctotrupoidea: Pelecinidae) over 165 million years. Annals of the Entomological Society of America 102, 20–38. https://doi.org/10.1603/AN09043

Shih, C.K., Liu, C.X., Ren, D., 2009. The earliest fossil record of pelecinid wasps (Insecta: Hymenoptera: Proctotrupoidea: Pelecinidae) from Inner Mongolia, China. Annals of the Entomological Society of America 102, 20–38. https://doi.org/10.1603/008.102.0103

Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., et al., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Spicer, R.A., Rees, P.M., Herman A.B., 1996. The Cretaceous vegetation and climate of Asia: some insights. Meomoirs of the Geological Society of India 37, 405–433.

van Hinsbergen, D.J.J., Lippert, P.C., Dupont-Nivet, G., McQuarrie, N., Doubrovine, P.V., Spakman, W., Torsvik, T.H., 2012. Greater India Basin hypothesis and a two-stage Cenozoic collision between India and Asia. Proceedings of the National Academy of Sciences of the United States of America 109, 7659–7664. https://doi.org/10.1073/pnas.1117262109

Vargas, J.M.R., Colombo, W.D., Azevedo, C.O., 2020. Revisited phylogeny of Scleroderminae (Hymenoptera: Bethylidae) reveals a plastic evolutionary history. Arthropod Systematics & Phylogeny 78, 217–243. https://doi.org/10.26049/ASP78-2-2020-02

Westerweel, J., Roperch, P., Licht, A., Dupont-Nivet, G., Win, Z., Poblete, F., Ruffet, G., Swe, H.H., Thi, M.K., Aung, D.W., 2019. Burma Terrane part of the Trans-Tethyan arc during collision with India according to palaeomagnetic data. Nature Geoscience, 12, 863–868. https://doi.org/10.1038/s41561-019-0443-2

Yu, T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F., Zhang, H., Wang, B., Dilcher, D., 2019. An ammonite trapped in Burmese amber. Proceedings of the National Academy of Sciences of the USA, 116, 11345–11350. https://doi.org/10.1073/pnas.1821292116

Zhang, H.C., Rasnitsyn, A.P., 2004. Pelecinid wasps (Insecta, Hymenoptera, Proctotrupoidea) from the Cretaceous of Russia and Mongolia. Cretaceous Research 25, 807–825. https://doi.org/10.1016/j.cretres.2004.08.002

Zhang, H.C., Rasnitsyn, A.P., Zhang, J.F., 2002. Pelecinid wasps (Insecta: Hymenoptera: Proctotrupoidea) from the Yixian Formation of western Liaoning, China. Cretaceous Research 23, 87–98. https://doi.org/10.1006/cres.2002.0301

Zhang, J.F., 2005. Eight new species of the genus Eopelecinus (Hymenoptera: Proctotrupoidea: Pelecinidae) from the Laiyang Formation, Shandong Province, China. Paleontological Journal 39, 417–427.

Zhang, J.F., Rasnitsyn, A.P., 2006. New extinct taxa of Pelecinidae *sensu lato* (Hymenoptera: Proctotrupoidea) in the Laiyang Formation, Shandong, China. Cretaceous Research 27, 684–688. https://doi.org/10.1016/j.cretres.2006.03.001

Zhang, Q., Rasnitsyn, A.P., Wang, B., Zhang, H.C., 2018. Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: a review of the fauna. Proceedings of the Geologists' Association 129, 736–747, http://dx.doi.org/10.1016/j.pgeola.2018.06.004.

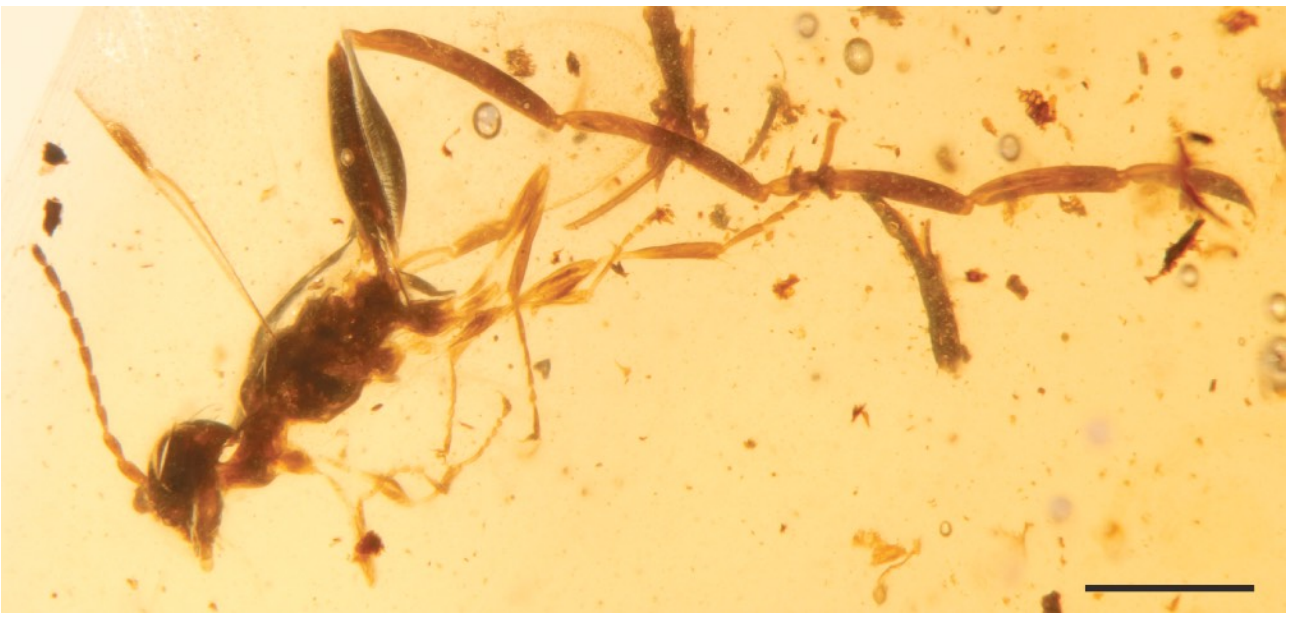

Figure 1: *Eopelecinus marechali* sp. nov., holotype IGR.BU-019. Habitus in left-lateral view. Scale bar: 0.5 mm.

Eopelecinus marechali sp. nov., holotype IGR.BU-019. Habitus en vue latérale gauche. Barre d'échelle: 0.5 mm.

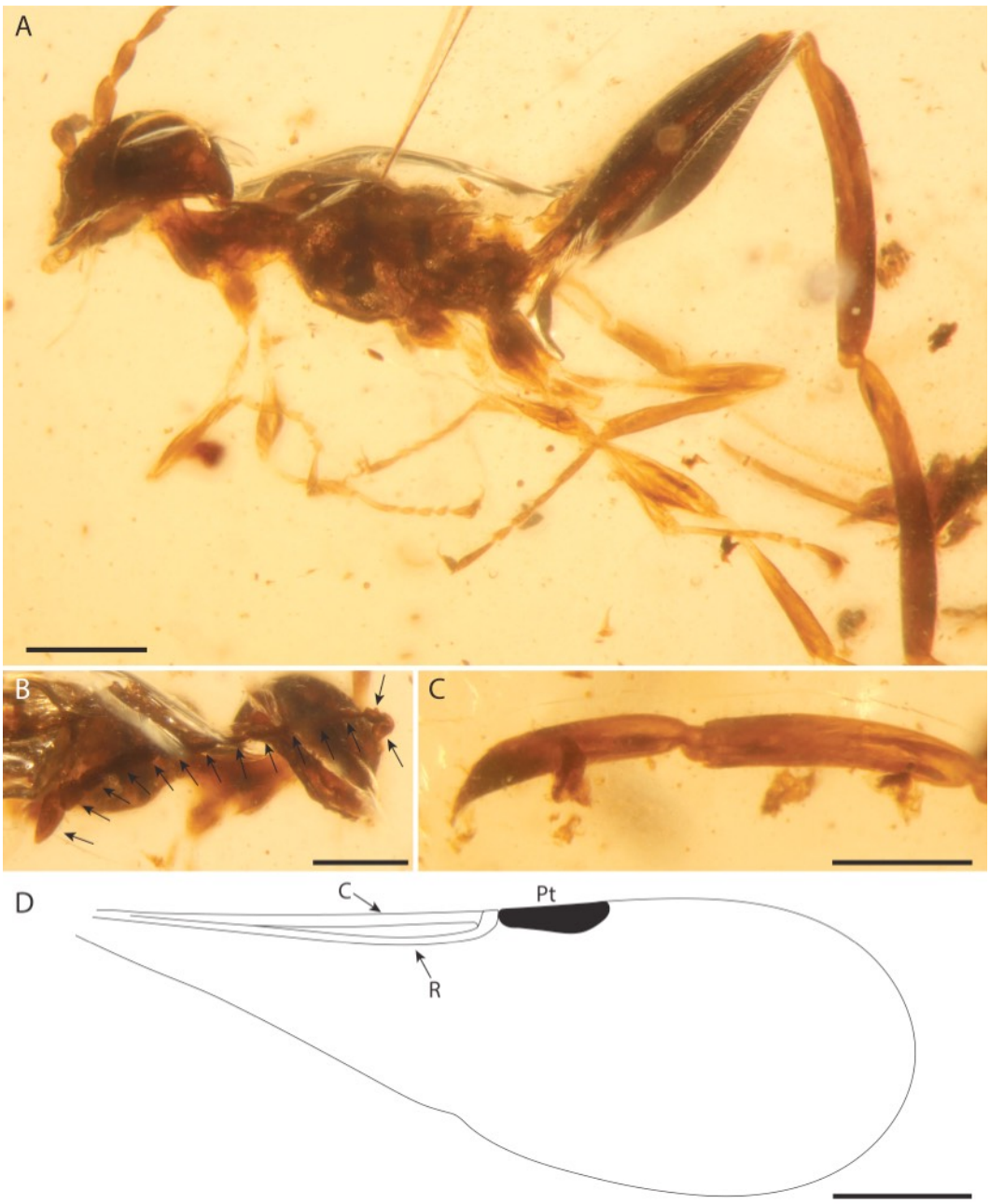

Figure 2: *Eopelecinus marechali* sp. nov., holotype IGR.BU-019. A. Detailed view of mesosoma. B. Right antenna (black arrows pointing each antennomere). C. Apical metasomal segment. D. Line drawing of forewing venation. Pt: pterostigma. Scale bars: 0.25 mm.

Eopelecinus marechali sp. nov., holotype IGR.BU-019. A. Vue détaillé du mesosoma. B. Antenne droite (les flèches noires pointent chaque antennomere). C. Segment apical du metasoma. D. Dessin de la nervation de l'aile antérieure. Pt : ptérostigma. Barres d'échelle : 0.25 mm.

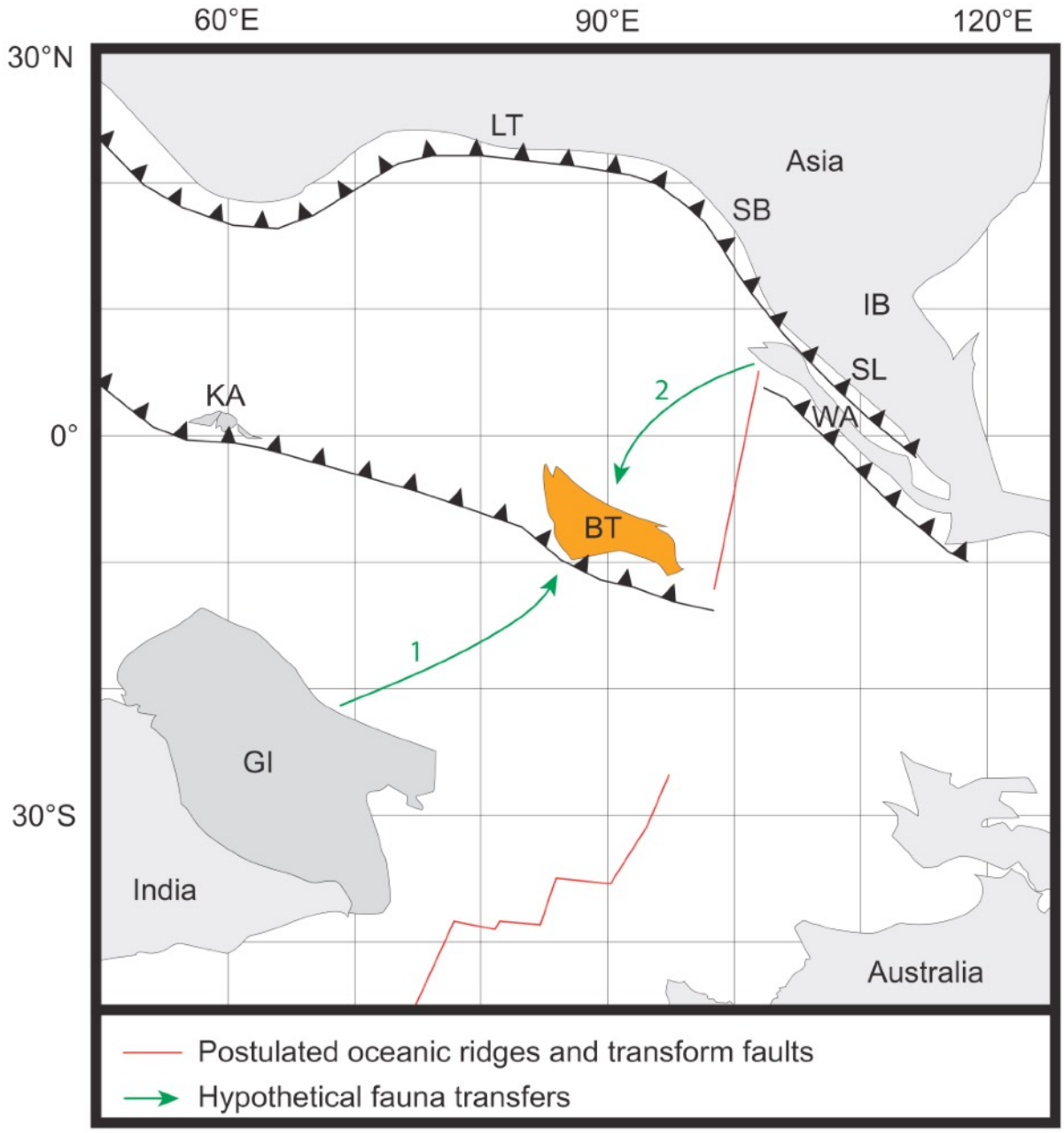

Figure 3: Maps of West Burmese terrane position at 95 Ma with hypothetic fauna transferts (modified from Westerweel et al., 2019: fig 4a).

Carte de la position du terrane birman ouest à 95 Ma avec les hypothétiques transferts de faunes (modifiée d'après Westerweel et al., 2019 : fig 4a).

Table 1: Diversity of fossil Pelecinidae.

Diversité des Pelecinidae fossiles.

Genera / Species	Distribution	Period	Locality / Formation	References
Abropelecinus Feng, Shih, Ren & Liu				
A. annulatus Feng, Shih, Ren & Liu 2010	China	Aptian	Huangbanjigou / Yixian Formation	Feng et al., 2010
A. tytthus Guo, Shih & Ren 2016	Myanmar	Cenomanian	Burmese amber	Guo et al., 2016a
Allopelecinus Zhang & Rasnitsyn				
A. terpnus Zhang & Rasnitsyn 2006	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang and Rasnitsyn, 2006
Archaeopelecinus Shih, Liu & Ren				
A. jinzhouensis Shih, Liu & Ren 2009	China	Callovian/Oxfordian	Daohugou / Daohugou formation	Shih et al., 2009
A. tebbei Shih, Liu & Ren 2009	China	Callovian/Oxfordian	Daohugou / Daohugou formation	Shih et al., 2009
Azygopelecinus Feng, Shih, Ren & Liu				
A. clavatus Feng, Shih, Ren & Liu 2010	China	Aptian	Huangbanjigou / Yixian Formation	Feng et al., 2010
Brachypelecinus Guo, Shih & Ren				
B. euthyntus Guo, Shih & Ren 2016	Myanmar	Cenomanian	Burmese amber	Guo et al., 2016a
Cathaypelecinus Shih, Liu & Ren				
C. daohugouensis Shih, Liu & Ren 2009	China	Callovian/Oxfordian	Daohugou / Daohugou formation	Shih et al., 2009
Eopelecinus Zhang, Rasnitsyn & Zhang				
E. eucallus Zhang 2005	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang, 2005
E. exquisitus Zhang & Rasnitsyn 2004	Russia	Aptian	Baissa / Zaza Formation	Zhang and Rasnitsyn, 2004
E. fragilis Zhang & Rasnitsyn 2004	Mongolia	Valanginian/Barremian	Khutel-Khara / Tsagaantsav Formation	Zhang and Rasnitsyn, 2004
E. giganteus Zhang 2005	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang, 2005
E. hodoiporus Zhang 2005	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang, 2005
E. huangi Liu et al. 2011	China	Aptian	Huangbanjigou / Yixian Formation	Liu et al., 2011
E. inopinatus Jouault, Ngô-Muller, Pouillon & Nel 2020	Myanmar	Cenomanian	Burmese amber	Jouault et al., 2020
E. laiyangicus Zhang 2005	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang, 2005

E. leptaleus Zhang 2005	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang, 2005
E. marechali sp. nov.	Myanmar	Cenomanian	Burmese amber	This study
E. mecometasomatus Zhang 2005	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang, 2005
E. mesomicrus Zhang 2005	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang, 2005
E. minutus Zhang & Rasnitsyn 2004	Mongolia	Valanginian/Barremian	Khutel-Khara / Tsagaantsav Formation	Zang and Rasnitsyn, 2004
E. pusillus Zhang 2005	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang, 2005
E. rudis Zhang & Rasnitsyn 2004	Russia	Aptian	Baissa / Zaza Formation	Zhang and Rasnitsyn, 2004
E. scorpioideus Zhang & Rasnitsyn 2004	Russia	Aptian	Baissa / Zaza Formation	Zhang and Rasnitsyn, 2004
E. shangyuanensis Zhang, Rasnitsyn & Zhang 2002	China	Aptian	Huangbanjigou / Yixian Formation	Zhang et al., 2002
E. similaris Zhang, Rasnitsyn & Zhang 2002	China	Aptian	Huangbanjigou / Yixian Formation	Zhang et al., 2002
E. tumidus Liu et al. 2011	China	Aptian	Huangbanjigou / Yixian Formation	Liu et al., 2011
E. vicinus Zhang, Rasnitsyn & Zhang 2002	China	Aptian	Huangbanjigou / Yixian Formation	Zhang et al., 2002
E. yuanjiawaensis Duan & Cheng 2006	China	Aptian	Yuanjiawa No. 3 quarry, Dapingfang, Chaoyang City / Jiufotang Formation	Duan and Cheng, 2006
Henopelecinus Engel & Grimaldi				
H. pygmaeus Engel & Grimaldi 2006	USA	Turonian	White Oaks Pit (Old Crossman's Clay Pits) / Raritan Formation	Engel and Grimaldi, 2006
Iscopinus Kozlov				
I. baissicus Kozlov 1974	Russia	Aptian	Baissa / Zaza Formation	Kozlov, 1974
I. separatus Zhang & Rasnitsyn 2004	Russia	Aptian	Obeshchayushchiy / Ola Formation	Zhang and Rasnitsyn, 2004
I. simplex Zhang & Rasnitsyn 2004	Russia	Aptian	Baissa / Zaza Formation	Zhang and Rasnitsyn, 2004
?I. suspectus Zhang & Rasnitsyn 2004	Russia	Campanian	Baissa / Zaza Formation	Zhang and Rasnitsyn, 2004
Megapelecinus Shih, Liu & Ren				
M. changi Shih, Liu & Ren 2010	China	Aptian	Huangbanjigou / Yixian Formation	Shi et al., 2010
M. nashi Shih, Liu & Ren 2010	China	Aptian	Huangbanjigou / Yixian Formation	Shi et al., 2010
Pelecinopteron Brues				
P. tubuliforme Brues, 1933	Russia	Priabonian	Baltic amber	Brues, 1933; Kozlov, 1974 (the author indicates that the specimen may belong to *P. tubuliforme* but the material need to be reanalyzed)

Phasmatopelecinus Greenwalt & Engel				
P. leonae Greenwalt & Engel 2014	USA	Lutetian	Disbrow Creek site, Kishenehn / Kishenehn Formation	Greenwalt and Engel, 2014
Praescopinus Rasnitsyn				
P. excellens Rasnitsyn 2008	Mongolia	Tithonian	Shar-Teg, outcrop 443/1 / Sharteg Formation	Rasnitsyn, 2008
Protopelecinus Zhang & Rasnitsyn				
P. deformis Zhang & Rasnitsyn 2004	Mongolia	Aptian	Bon Tsagaan / Dzun-Bain Formation	Zhang and Rasnitsyn, 2004
P. dubius Zhang & Rasnitsyn 2004	Mongolia	Aptian	Bon Tsagaan / Dzun-Bain Formation	Zhang and Rasnitsyn, 2004
P. furtivus Zhang & Rasnitsyn 2004	Russia	Aptian	Baissa / Zaza Formation	Zhang and Rasnitsyn, 2004
P. regularis Zhang & Rasnitsyn 2004	Russia	Aptian	Baissa / Zaza Formation	Zhang and Rasnitsyn, 2004
Sinopelecinus Zhang, Rasnitsyn & Zhang				
S. daspletis Zhang & Rasnitsyn 2006	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang and Rasnitsyn, 2006
S. delicatus Zhang, Rasnitsyn & Zhang 2002	China	Aptian	Huangbanjigou / Yixian Formation	Zhang et al., 2002
S. epigaeus Zhang, Rasnitsyn & Zhang 2002	China	Aptian	Huangbanjigou / Yixian Formation	Zhang et al., 2002
S. hierus Zhang & Rasnitsyn 2006	China	Aptian	Nanligezhuang / Laiyang Formation	Zhang and Rasnitsyn, 2006
S. magicus Zhang, Rasnitsyn & Zhang 2002	China	Aptian	Huangbanjigou / Yixian Formation	Zhang et al., 2002
S. viriosus Zhang, Rasnitsyn & Zhang 2002	China	Aptian	Huangbanjigou / Yixian Formation	Zhang et al., 2002
Scorpiopelecinus Zhang, Rasnitsyn & Zhang				
S. laetus Zhang & Rasnitsyn 2004	Russia	Aptian	Baissa / Zaza Formation	Zhang and Rasnitsyn, 2004
S. versatilis Zhang, Rasnitsyn & Zhang 2002	China	Aptian	Huangbanjigou / Yixian Formation	Zhang et al., 2002
Shoushida Liu, Shih & Ren				
S. infera Guo, Shih & Ren 2016	China	Aptian	Huangbanjigou / Yixian Formation	Guo et al., 2016b
S. regilla Liu, Shih & Ren 2009	China	Aptian	Huangbanjigou / Yixian Formation	Liu et al., 2009
Stelepelecinus Guo, Shih & Ren				

S. longus Guo, Shih & Ren 2016	China	Aptian	Huangbanjigou / Yixian Formation	Guo et al., 2016b
Zoropelecinus Engel & Grimaldi				
Z. periosus Guo, Shih & Ren 2016	Myanmar	Cenomanian	Burmese amber	Guo et al., 2016a
Z. zigrasi Engel & Grimaldi 2013	Myanmar	Cenomanian	Burmese amber	Engel et al., 2013