

Morphology of a new Panguoidea species (Hymenoptera: Aculeata) supports Panguidae as an early-diverging stinging wasp lineage

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Received 15 December 2025; received in revised form 10 February 2026; accepted 10 March 2026

Available online 13 March 2026

Abstract

A new species, *Pangu yehui* Zhang and Rasnitsyn, n. sp., is described from the mid-Cretaceous (early Cenomanian) Kachin amber (Myanmar), which could be assigned to the family Panguidae (superfamily Panguoidea). Detailed morphology of the sting supports the position of Panguoidea as a basal clade within the infraorder Aculeata. Specifically, the presence of a sting with valvelli of distinctive morphology supports attribution to Aculeata and the fore wing with 2m-cu crossvein precludes its attribution to Chrysidoidea. Furthermore, the external position of metasomal tergum 7 and the equal number of antennomeres in both sexes differentiate it from the clade Apoidea + Vespoidea. A new genus *Ceropangu* n. gen. with *Burmusculus mutatus* Li et al., 2024 as its type species is systematically described, and an updated key to genera and species of Panguidae is also provided.

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Keywords: Aculeate wasps; Cretaceous; Kachin amber; Myanmar; Panguidae; Wasp sting

1. Introduction

The superfamily Panguoidea comprising a single family, Panguidae, with four described species of three genera, is a small extinct group of wasps restricted to the Cretaceous (Barremian to Cenomanian: ca. 125–99 Ma; Grimaldi et al., 2019; Zhuang et al., 2024). This group is known only from two amber deposits: the Wealden and Kachin ambers of southern England and northern Myanmar respectively (Fig. 1; Li et al., 2019, 2020; Jouault, 2025). Panguidae

are generally regarded as occupying a basal position within the infraorder Aculeata diverging before the split between Chrysidoidea and the clade Apoidea + Vespoidea, because they lack synapomorphies diagnostic of these latter groups (Li et al., 2019, 2020).

In particular, Chrysidoidea typically retain antennae that are not sexually dimorphic in antennomere number (except for some Sclerogibbidae, in which the number of polymerised flagellomeres differs between sexes) and have an external, non-invaginated seventh metasomal tergum in females (except for several distal segmented internationalised in both sexes of Chrysidae). In contrast, Apoidea + Vespoidea are characterised by sexually

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dimorphic antennae (usually 12-segmented in female and 13-segmented in male rarely further reduced in number in each sex; Rasnitsyn, 1988) and by a permanently invaginated and specialised female seventh tergum (cf. Oeser, 1961; Rasnitsyn, 1980 for detail). Chrysidoidea are further defined by the loss of the 2m-cu crossvein in the forewing, at least one r-m crossvein, and the hindwing jugal lobe. The latter represents a delimited or even detached area posterior of anal area that is common in Apoidea + Vespoidea. The jugal lobe is lost in chrysoid wings and often seemingly replaced there by the anal lobe that may look similarly except that it is folding up at rest whilst the jugal lobe is folding down).

These inferences, however, are based on limited material and require further evidence and testing. Recent phylogenomic analysis recovers Chrysidoidea as paraphyletic with respect to Apoidea + Vespoidea, even though the particular pattern varies from one publication to another (Branstetter et al., 2017; Blaimer et al., 2023; Song et al., 2024). Should this pattern be confirmed by future research, the classification presented above would require revision (Branstetter et al., 2017; Blaimer et al., 2023). Nevertheless, such changes are unlikely to affect the hypothesis that Panguoidea occupies a ‘basal position’ within Aculeata.

The well-preserved panguid wasp described here, revealing fine details of the aculeate-type sting apparatus, represents a significant new discovery. It not only expands the known diversity of the group but also provides critical morphological evidence to better resolve the taxonomic position and evolutionary significance of Panguoidea. A new monotypical genus of Panguidae is established herein for *Burmusculus mutatus* Li et al., 2024 originally described in the vespoid family Burmusculidae (Li et al., 2024).

2. Material and methods

The piece of Kachin amber with the wasp described below was obtained from amber mines situated in the Hukawng Valley of Kachin State, Myanmar (26°29'N, 96°35'E). The age of Kachin amber was estimated as 98.79 ± 0.62 Ma using U-Pb zircon dating of the volcanoclastic matrix, which suggests the earliest Cenomanian age (Shi et al., 2012; Yu et al., 2019).

The amber specimen was trimmed, polished and photographed by Dr. Dmitry D. Vorontsov (PIN RAS, Moscow). It was studied using a Leica M165C stereomicroscope with a Leica DFC 420 camera. For imaging, a compound microscope Nikon E-800 with dry (4×, 10×) and water-dip optics (40×) was used. The images were obtained under a combination of bright field and incident illumination. Stacks of images, comprising multiple focal planes, were acquired with an Olympus OM-D E-M10II camera and processed with Helicon Focus version 7.6.2. The morphological terminology used in this study follows those of Li et al. (2020).

The type material is housed at the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Acad-

emy of Sciences. All taxonomic acts established herein are registered in ZooBank (see below). The electronic publication is registered with LSID urn: lsid: zoobank.org:pub:96C74ECA-DEA2-439E-ABBB-CFB076B194AA.

3. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Suborder Apocrita Gerstaecker, 1867

Superfamily Panguoidea Li, Rasnitsyn, Shih and Ren in Li et al., 2019

Family Panguidae Li, Rasnitsyn, Shih and Ren in Li et al., 2019

Genus *Pangu* Li, Rasnitsyn, Shih and Ren in Li et al., 2019

Type species: *Pangu yuangu* Li, Rasnitsyn, Shih and Ren in Li et al., 2019.

Other species: *Pangu antiquum* Li, Rasnitsyn, Shih and Ren in Li et al., 2020; and *Pangu yehuii* Zhang and Rasnitsyn, n. sp.

Pangu yehuii Zhang and Rasnitsyn, n. sp.
(Figs. 1–3)

LSID: urn: lsid: zoobank.org:act:88F2D482-A83D-4FFB-945F-5B7716D5B273.

Etymology: The species name is dedicated to Mr. Ye-Hui Zhang, in recognition of his invaluable donation of amber specimens that advances palaeoentomologic research.

Holotype: Female NIGP 209712. Kachin amber, mid-Cretaceous. Well-preserved, complete insect with some debris partially obscuring the head. Metasoma slightly distorted (Fig. 2A): apical segments somewhat extracted, apex open, tergum 7 apparently turned down and hardly visible in lateral aspect, and sting visible almost completely. Syninclusia: Psocoptera, unidentified insect fragment.

Material: In addition to the holotype, a non-paratype specimen (NIGP 14062), a female, also from Kachin amber, is also referred to here. This specimen was initially and tentatively identified as Trigonaliidae due to its imperfect preservation (Zhang et al., 2018).

Diagnosis: Female only (male unknown). Head thicker (in side view), with eye less than twice as long as wide. Antenna with scape in widest aspect much narrower than first flagellomere long. Propodeum and first metasomal tergum short, strongly convex, propodeum angular between dorsum and declivity, with the former shorter than the latter. 2r-m meeting RS distal of 2r-rs.

Description: Body with fine punctation, particularly fine on mesosoma sides and on metasoma, especially toward its apex (Fig. 1A). Integument colour rather pale (yellowish) with antennae, mesosomal dorsum, distal triangular spots of metasomal terga 1-2 and basal spots of terga 3-5, second valvifer and ovipositor sheath dark; tarsi infuscate. Vestiture mainly weak except conspicuous on mandible, tibiae, tarsi, distal metasomal segments apically and ovipositor sheaths (see below for detail).

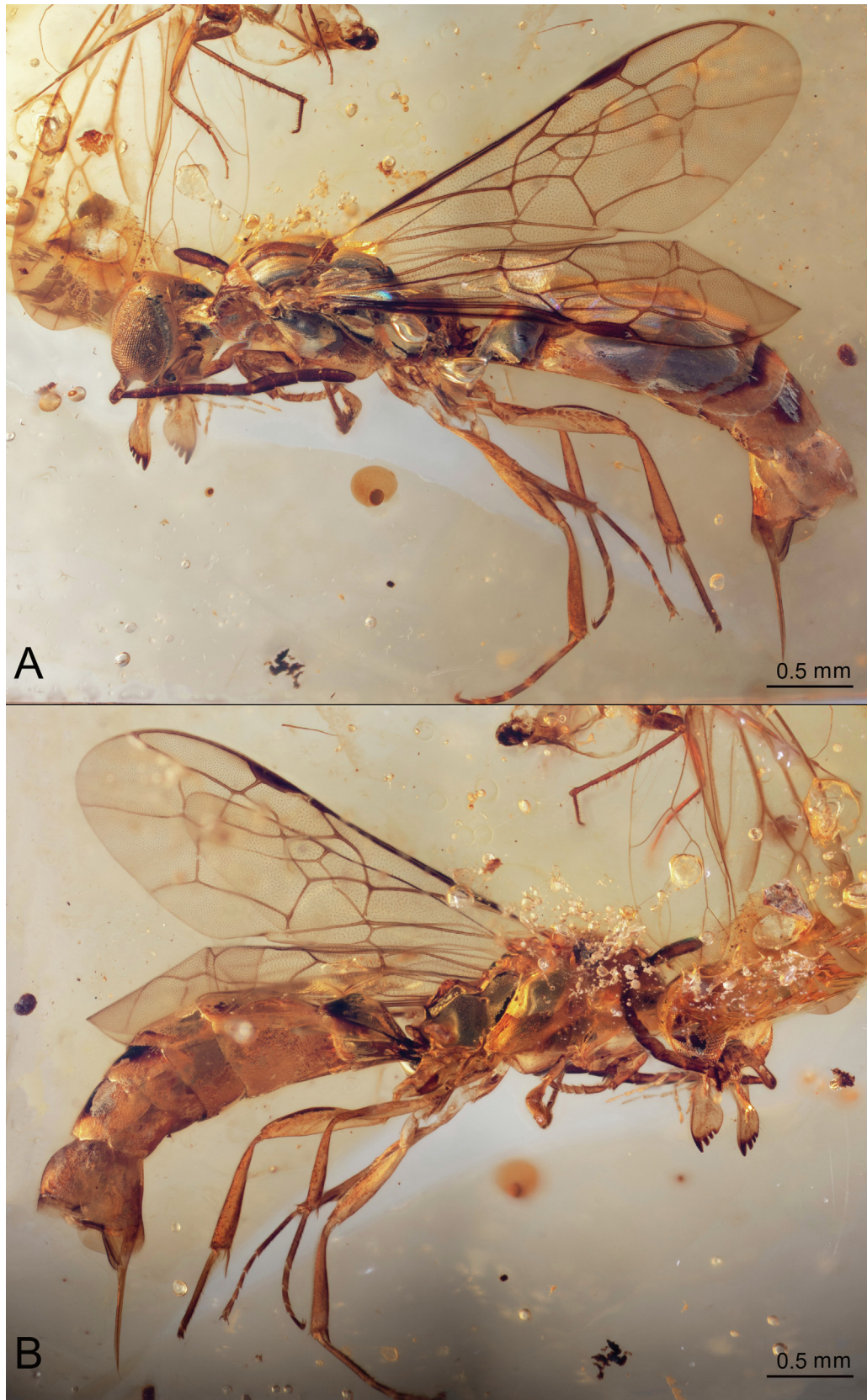


Fig. 1. *Pangu yehuii* Zhang and Rasnitsyn, n. sp., holotype NIGP 209712. (A) Habitus, oblique left aspect. (B) Habitus, oblique right aspect showing, *inter alia*, left antenna and right maxillary palp.

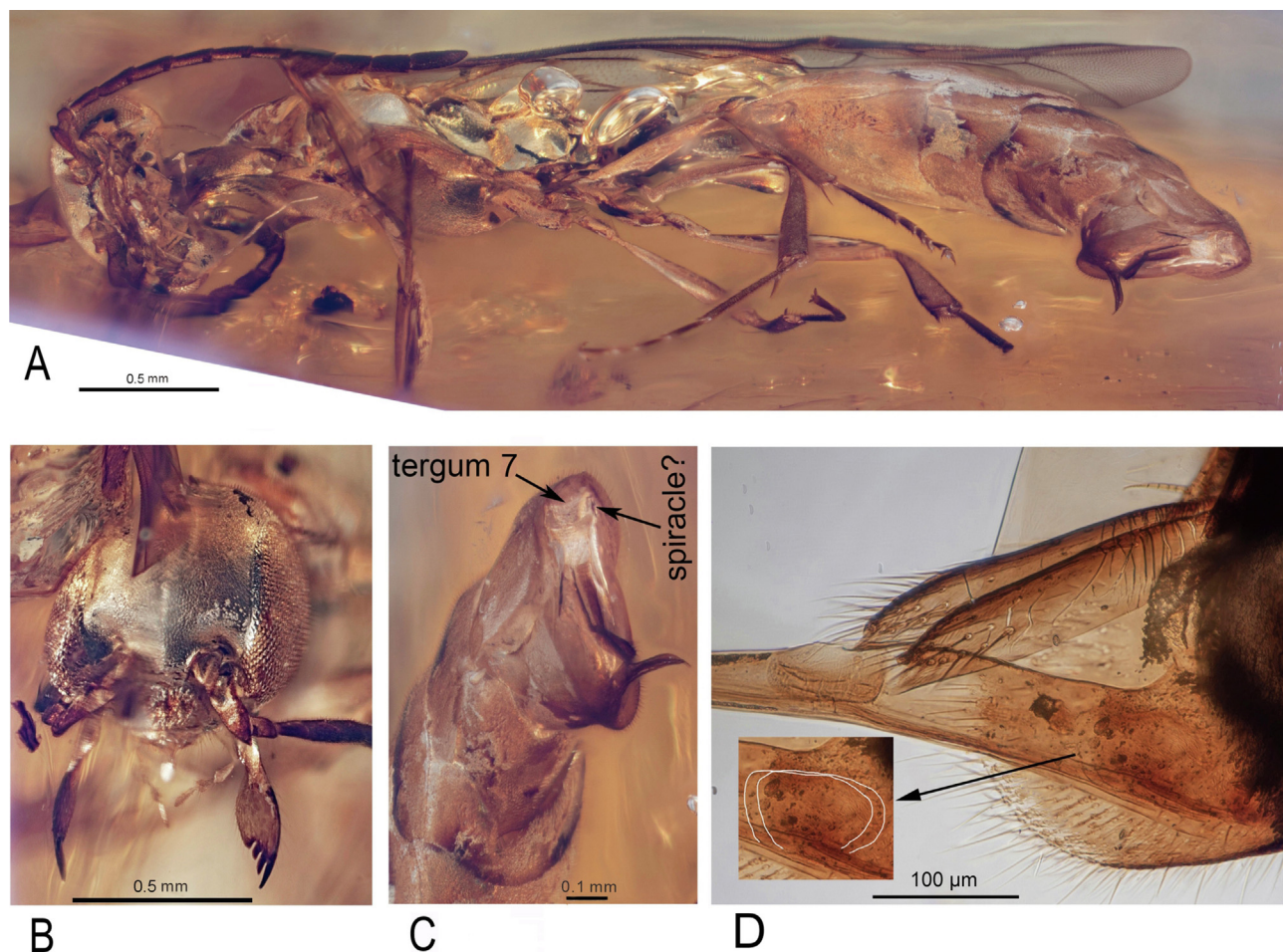


Fig. 2. *Pangu yehuii* Zhang and Rasnitsyn, n. sp., holotype NIGP 209712. (A) Habitus, oblique lower aspect. (B) Head anterior aspect showing mandibles and labial palps. (C) Metasoma rear aspect showing tergum 7 with supposed spiracle. (D) Basal sting with inset showing outlines of valvilli.

Head transverse, with eye occupying most of its side, almost reaching mandibular base, less than twice as long as wide, with inner orbits slightly emarginate, subparallel. Ocelli small, distant from eyes. Occipital carina well-developed dorsally and laterally, fading gradually toward buccal pieces. Postgenal bridge short. Temples narrow. Frons with distinct median line. Antennal foramina open, closer to inner eye margin than to each other, located distinctly below eyes mid-length (Fig. 2B). Clypeus with straight anterior and posterior margins, less than twice as wide as long, with weak but distinct median carina. Antenna with scape and pedicel not inflated, scape in widest aspect much narrower than first flagellomere long about as wide and long as penultimate flagellomere, with radix attached mesally, subbasally, pedicel shorter than first (smallest) flagellomere, attached to scape ventrally, subapically. Flagellomeres becoming longer and thicker apically, apical flagellomere rounded distally; all flagello-

meres with dense, short setae, all with numerous, small, ovate sensilla. Labrum short, almost as wide as clypeus. Mandible spoon-like, narrow in basal half, with widened part somewhat convex outwards, with apical margin oblique (ventral margin longer than dorsal), in plane of mandible articulatory axis (not twisted into rotation plane), armed with long, acute, apical tooth, two shorter, truncate teeth, and wide, thin, smooth basal lobe margined with row of some 12 long and rather stiff setae; lower margin of mandible with numerous even longer and thinner setae (Fig. 2B). Maxillary palps long, with six long and narrow palpomeres (third one widest). Labial palps much shorter than maxillary ones, four-segmented (first one long, thin, second widest, third shortest) (Fig. 2B).

Mesosoma with pronotum movably overlapping mesonotum, shallowly emarginate posteriorly, reaching tegulae, with weak spiracular lobe and short, rounded posteroven-tral angle (Fig. 2A). Propleura not elongate neck-like.

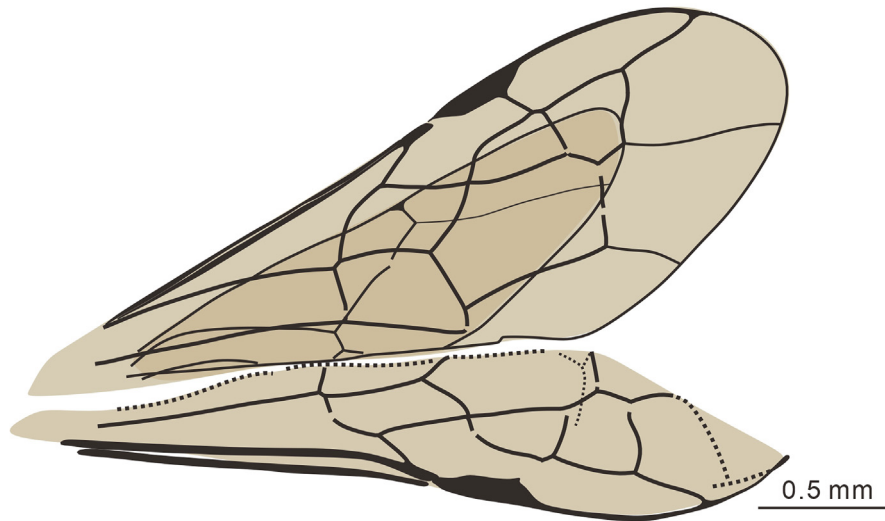
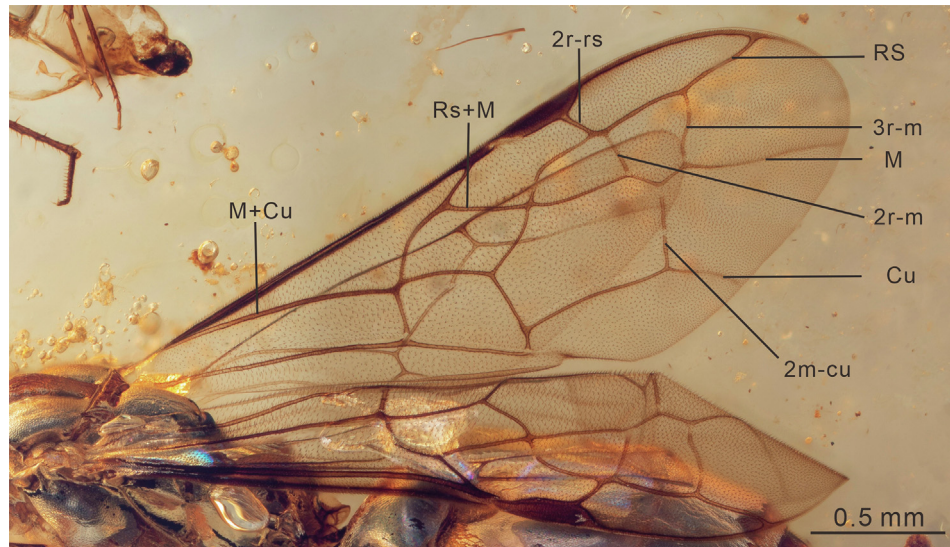


Fig. 3. Venation of *Pangu yehuii* Zhang and Rasnitsyn, n. sp. Fore wing veins labelled, venational symbols standard. Abbreviations: Rs, radial sector; M, media; Cu, cubitus; crossveins r-rs, r-m, m-cu are named according to the two longitudinal veins they connect; fused longitudinal veins M+Cu, Rs+M are designated by the plus sign to indicate the basal confluence of their respective component longitudinal veins.

Mesonotum with deeply impressed notauli, distinctly divergent anteriorly and almost reaching transverse line posteriorly; parapsidal lines long, weakly impressed; prescutellar fovea deep, slightly shortened medially; scutellum narrow, slightly convex, without carinate lateral carinae. Metanotum short in dorsal view (much shorter than mesoscutellum), elevated above wide trough-like metapostnotum. Mesopleuron apparently lacking carinae, with pleural suture delimiting rather wide epimeron, with short transverse depression anterior to mesopleural pit. Metapleuron wide, with weak suture from endophragmal pit near its posterior margin downward (as described by Brothers, 1975, character state 36.3). Propodeum without

distinct metapleural-propodeal suture, with complete lateral carinae, with dorsum short, distinctly angled with, and delimited with transverse carina from, longer declivitous parts, with sublateral carinae on declivitous part only.

Legs ordinary, coxae rather big, mid coxa with basal articulation apparently narrow, trochanters elongate, mid trochantellus distinguishable, femorae short, narrow, tibiae with dense, short pubescent and with crown of apical stiff setae (Fig. 2A). Tibial spur formula 1-2-2. Metatibia with distinct strigil formed by longer (outer) spur and basitarsus, both abundantly setose at faced surfaces. Tarsomeres 1-4 apically, ventrally, and tarsomeres 1 ventrally, with stiff setae, mid and hind basitarsi longer than three middle tar-

someres combined, tarsomere 4 elongate, claws simple, thin, slightly bent, arolium small.

Fore and hind wing venations generally as in type species: Fore wing with 2r-rs oblique, originating at distal third of length of pterostigma, meeting RS distinctly before 2r-m, RS+M ending at or close to 1m-cu, 3r-m sinuate, 2-M+Cu distinct, short, 2m-cu near equidistant from 2r-m and 3r-m along M (Fig. 3). Hind wing with r-m and 1-M near aligned, 1-Cu about half length of cu-a, free ends of M and A lost.

Metasoma not very slender, segment 1 slightly longer than high, tergum 1 strongly convex, with wide laterotergites, sternum 1 in plane with sternum 2. Tergum 2 slightly longer than high, 0.5–0.6× as long as mesosoma without extending propleura, narrowed basally before segment 1; following segments transverse. Sixth tergum with wide distal translucent zone covered with numerous long setae, sixth sternum folded U-like, also with distal zone of long pubescence but without cuticular differentiation, without delimited lateral flaps (or at least not discernible). Metasomal apex opened, seventh tergum apparently visible only in posterior aspect as flat plate without discernible details except possibly a spiracle. Second valvifer rod-like as visible, apically bearing sting sheaths. Sheaths relatively short, entire (not subdivided), apically long-setose (Fig. 2C). Sting of characteristic aculeate form, almost straight (slightly bent downward), smooth apically, with distinct basal bulb enclosing valvilli (“a complex structure comprising a pair of valvilli located on a distinct boss”; Quicke et al., 1992, p. 587; Fig. 2C).

Measurements (in mm): Body length 4.4, head length 0.50, height 0.70, width 0.75, antennomeres 1–12, respectively, 1.26 (1), 0.08 (2), 0.09 (3), 0.12 (4), 0.13 (5), 0.14 (6–9, 11), 0.16 (10), 0.20 (12), mesosoma length 1.7, height 0.83, mid trochanter length 0.14, mid trochantellus length 0.04, mid femur length 0.49, mid tibia length 0.55, mid tarsomeres 1–5, respectively, 0.34 (1), 0.11 (2), 0.09 (3), 0.06 (4), 0.19 (5), hind trochanter length 0.20, hind femur length 0.73, width 0.15, hind tibia length 0.7, hind tarsomeres 1–5, respectively, 0.37 (1), 0.15 (2), 0.12 (3), 0.06 (4), 0.13 (5), forewing length 2.93, width 1.0, metasoma length 2.5, terga 1–6, respectively (apical segments extended telescopically), 0.68 (1), 0.73 (2), 0.44 (3), 0.24 (4), 0.38 (5), 0.5 (6), sting length (tentatively, for base not well seen) 0.95, ovipositor sheath length 0.23.

Remarks: The new species is assigned to Panguoidea because of its unique combination of wing venation characters (i.e., fore wing with 2r-m, 3r-m and 2m-cu, and with 3r-m reclival, hind wing with closed cells, r-m and 1-M aligned and with M lost behind r-m).

The new species can be differentiated from *Pangu yuangu* Li et al., 2019 based on the characters:

- Head thick in side view, with eye less than twice as long as wide (Fig. 1A; Zhang et al., 2018, fig. 4) (versus head

thin, with eye more than twice as long as wide; Li et al., 2019, figs. 2,3; Jouault, 2025, figs. 4, 5);

- Scape in widest aspect much narrower than first flagellomere long (Fig. 2B) (versus scape in widest aspect about as wide as first flagellomere long; Li et al., 2019, fig. 2G; Jouault, 2025, fig. 5B);
- Propodeum and first metasomal tergum short and strongly convex, with propodeum angular between short dorsum and longer declivity (Fig. 1B; Zhang et al., 2018, fig. 4) (versus propodeum and first metasomal tergum longer and weakly convex, with propodeum weakly convex over long dorsum and short declivity; Li et al., 2019, fig. 2D; Jouault, 2025, fig. 5C, D);
- Second metasomal tergum 0.5–0.6× as long as mesosoma without extending propleura (Fig. 1B; Zhang et al., 2018, fig. 4) (versus 0.75× as long as mesosoma; Li et al., 2019, fig. 2A; Jouault, 2025, fig. 4A).

Genus *Ceropangu* n. gen.

LSID: urn: lsid: zoobank.org:act:66CCA6B8-AA4C-4C16-8114-26A43037D9DC.

Etymology: The species name combines the genus name *Pangu* and the prefix *cero-* derived from the Greek word *Kéras* meaning antenna and alluding to the 13-segmented antenna.

Type species: *Burmusculus mutatus* Li, Shih and Ren in Li et al., 2024.

Species included: Type species only.

Diagnosis: Antenna 13-segmented, with scape almost as long as eye wide. Mandible short, with two obtuse teeth before basal lobe. Forewing with pterostigma issuing 2r-rs distinctly before its mid-length, 2+3-RS angular at rudimentary 1r-rs, 1m-cu meeting M distal of RS+M fork, 4-M longer than 0.3 of 3r-m length. Hind wing with 1-M angular with r-m and lost behind it.

Remarks: *Ceropangu mutatum* (Li et al., 2024), n. comb. can be assigned to aculeate wasps based on its characteristic general appearance and the female metasoma with the external naked sting and hidden (internal) sheaths (sting is well seen in the photograph even though it is missed in the original line drawing; cf. Li et al., 2024, fig. 2A, B). It can be assigned neither to Burmusculidae nor to Vespidea and Apoidea because it combines 13-segmented antenna and 7 external metasomal terga in female sex. It cannot be assigned to Chrysidoidea because of presence of 2m-cu lost in all Chrysidoidea as coloured vein. Instead, *Ceropangu* n. gen. agrees with Panguidae in having the above combination of 13-segmented antenna and 7 external metasomal terga in female sex, and additionally hind wing with M lost behind r-m and forewing with reclival 3r-m. The new genus differs from all other Panguidae by the long antennal scape, forewing with pterostigma issuing 2r-m distinctly before its mid-length, and hind wing with 1-M angled with r-m.

Key to genera and species of Panguidae (updated from Zhuang et al., 2024):

1	Antenna 13-segmented with scape almost as long as eye wide. Forewing with pterostigma issuing 2r-rs distinctly before its mid-length and 2+3-RS angular at rudimentary 1r-rs. Hind wing with 1-M angled with r-m	<i>Ceropangu mutatum</i> (Li et al., 2024)
	Antenna with scape about half as long as eye wide. Forewing with pterostigma issuing 2r-rs at or behind its mid-length, with 2+3-RS arching and lacking trace of 1r-rs. Hind wing with 1-M aligned with r-m	2
2	Fore wing with 4-M almost as long as 0.25 of 3r-m length. General habitus stouter. Pterostigma issuing 2r-rs at about its mid-length. Antennae when known 13-segmented	3
	Fore wing with 4-M longer than 0.3 of 3r-m length. General habitus more slender. Pterostigma usually with 2r-rs distinctly behind its midlength. Antenna 12-segmented. <i>Pangu</i> Li, Rasnitsyn, Shih and Ren in Li et al., 2019	4
3	Propodeum very short with posterolateral margin with two spines and emargination in-between. Basitarsi distinctly longer than following four tarsomeres combined. Fore wing with 1m-cu meeting M distal of Rs+M fork, 2r-m and 3r-m meeting M very close to 2m-cu (both distances less than 0.25 of 2r-m length). Antenna 13-segmented	<i>Prospheex anthophilos</i> Grimaldi and Engel in Grimaldi et al., 2019
	Propodeum not very short, with lateral margin smooth. Basitarsi distinctly shorter than following four tarsomeres combined. Fore wing with 1m-cu meeting M at Rs+M fork, 2r-m and 3r-m meeting M distant from 2m-cu (both distances more than 0.25 of 2r-m length)	<i>Protopangu valdensis</i> Zhuang, Li, Jarzembowski, Wang and Zhang, 2024
4	Fore wing with pterostigma issuing 2r-rs at about its distal 1/4th, 2r-m meeting Rs before 2r-rs, 3r-m straight. Propodeum with five transverse carinae and with no distinct longitudinal carinae at least on declivity	<i>Pangu antiquum</i> Li, Rasnitsyn, Shih and Ren in Li et al., 2020
	Fore wing with pterostigma issuing 2r-rs well before its distal 1/4th, 2r-m meeting Rs behind 2r-rs, 3r-m sinuate. Propodeum with lateral carinae	5
5	Head thin (in side view), with eye more than twice as long as wide. Scape in widest aspect almost as wide as first flagellomere long. Propodeum and first metasomal tergum weakly convex, propodeum arching in side view rather than angular, with declivity (marked with transverse carina) shorter than dorsum	<i>Pangu yuangu</i> Li, Rasnitsyn, Shih and Ren in Li et al., 2019
	Head thick (in side view), with eye less than twice as long as wide. Scape in widest aspect much narrower than first flagellomere long. Propodeum and first metasomal tergum short, strongly convex, propodeum angular between dorsum and declivity, with dorsum shorter than declivity	<i>Pangu yehuii</i> Zhang and Rasnitsyn, n. sp.

4. Discussion

The discovery of *Pangu yehuii* Zhang and Rasnitsyn, n. sp. highlights the unexpected diversity of this newly discovered group of basal aculeate wasps. Until recently, Panguidae were thought to be endemic to the insular tropical fauna of the Late Mesozoic West Burma block (Li et al., 2019, 2020). This group now comprises only six species in three genera spanning from the early Barremian (~125 Ma) of southern England (Zhuang et al., 2024) to the earliest Cenomanian (~99 Ma) of northern Myanmar (Grimaldi et al., 2019; Li et al., 2019, 2020; Jouault, 2025).

Panguidae were initially interpreted as a basal lineage within Aculeata based on the following combination of characters: a complete wing venation, notably including crossveins 2r-m, 3r-m and 2m-cu, which typifies non-chrysidoid aculeates (in contrast to Chrysidoidea, which retain at most a single r-m and lack 2m-cu), and the presence of an externally visible seventh metasomal tergum in female, a condition shared with chrysidoids but contrasting with Apoidea + Vespoidea, in which the tergum is hidden and modified (Li et al., 2019). Subsequent discoveries (Li et al., 2020) further showed that panguids possess antennae that are not sexually dimorphic in segment number, again matching the chrysidoid condition and differing from Apoidea + Vespoidea, in which female typically have 12 antennomeres and males 13.

The present specimen provides decisive evidence by preserving a fully developed aculeate sting bearing valvilli and otherwise typical of Aculeata. This observation eliminates any possibilities that Panguoidea represents aberrant non-aculeate parasitic wasps, and instead confirms their status as true stinging wasps. Together, these data support the original hypothesis that Panguoidea forms the sister group to remaining Aculeata.

5. Conclusion

The new species described herein supports the widely held view that Kachin (Burmese) amber from northern Myanmar represents a seemingly inexhaustible and unparalleled source of knowledge about mid-Cretaceous arthropod diversity in terrestrial thermophilous ecosystems (Ross, 2024). The new genus based on a misplaced species in Kachin amber further supports the above inference. These discoveries are particularly significant for the basal aculeate family Panguidae, a group only known since 2019, which has already been remarkable in several respects. First, Panguidae is likely to represent the most basal lineage of true aculeate wasps (those possessing a true sting). Second, they were widely distributed in space and time, that is, on islands in the northern paleo-Atlantic (Isle of Wight) and in the midst of Tethys Ocean (Burma Terrane; Westerweel et al., 2019), and spanning from the early Barremian (ca. 125 Ma) to the early Cenomanian (ca. 99 Ma). Third, and perhaps most strikingly, these basal aculeates were already engaged in trophic and

pollination-related interactions with early angiosperms (Grimaldi et al., 2019). The new species unequivocally demonstrates the aculeate nature of Panguidae.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are deeply thankful to Drs. Yu-Hui Zhuang and Corentin Jouault for their significant contribution during the peer review process. The authors are deeply indebted to Dr. Dmitry D. Vorontsov (Moscow) for his preparation of the fossil for its best quality images. This research was supported by the Shandong Province Natural Science Foundation (Grant No. ZR2020QD022).

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