

## Research article

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# Electrocambalidae fam. nov., a new family of Cambalidea from Cretaceous Burmese amber (Diplopoda, Spirostreptida)

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**Abstract.** A new family, Electrocambalidae fam. nov. of the suborder Cambalidea is described from Cretaceous Burmese amber based on two new genera, *Electrocambala* gen. nov. and *Kachincambala* gen. nov. with four new species, *Electrocambala ornata* gen. et sp. nov., *E. cretacea* gen. et sp. nov., *Kachincambala muelleri* gen. et sp. nov. and *K. distorta* gen. et sp. nov. The specimens are described combining classical light microscopy with drawings and photography, and modern micro-computed tomography ( $\mu$ CT). Morphological characters otherwise obscured are examined and visualized by creating volume renderings and 3D-segmentations from  $\mu$ CT data. Electrocambalidae fam. nov. is characterized by the following character combination: (1) a forward shift of leg pair 3, resulting in an apparently legless 3<sup>rd</sup> body ring, (2) presence of metazonal setae, and (3) extensive pilosity on the head. Although some of these characters are shared with other Juliformia they are unique in this combination. The described fossils are the oldest and first Mesozoic Spirostreptida and Cambalidea known and ca 70 million years older than previous records of the group.

**Keywords.** Myanmar, fossil, micro-CT, gonopods, evolution.

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## Introduction

Millipedes (Diplopoda Gervais, 1844), which comprise more than 11 000 described extant species (Sierwald & Bond 2007; Brewer *et al.* 2012; Enghoff *et al.* 2015), were among the first fully terrestrial animals (Selden & Read 2007; Shear & Edgecombe 2010; Kenrick *et al.* 2012), and are as detritivores (Crawford 1992; Cárcamo *et al.* 2000) and soil-forming organisms (Crossley 1977) essential for terrestrial ecosystems – a role they have played probably unchanged since the Paleozoic (Shear & Kukalová-Peck

1990). From the Paleozoic only representatives of extinct orders are known (Wilson & Anderson 2004; Wilson 2006), among them the giant *Arthropleurida* *Waterlot*, 1934, which could reach a length of up to 2 m and were the largest land arthropods that ever lived (Edgecombe 2015). For the whole Mesozoic only few millipede fossils are known, which leaves a gap in our knowledge of millipede evolution. Most of the Mesozoic millipede fossils known are from the Cretaceous Burmese amber deposits of Myanmar and can be placed in extant orders (Rasnitsyn & Golovatch 2004; Liu *et al.* 2017; Wesener & Moritz 2018; Jiang *et al.* 2019; Moritz & Wesener 2019; Stoev *et al.* 2019; Su *et al.* 2020), while only few millipedes are recorded from other Mesozoic deposits (Fritsch 1910; Martynov 1936; Mulleried 1942; Dzik 1975, 1981; Jell 1983; Duy-Jacquemin & Azar 2004; Shear *et al.* 2009).

Burmese amber from the Hukawng Valley in Kachin State, Northern Myanmar, has a long history of exploitation (Grimaldi *et al.* 2002; Cruickshank & Ko 2003). It is dated to the early Cenomanian age in the Upper Cretaceous ( $98 \pm 0.63$  ma, Shi *et al.* 2002). In recent years Burmese amber yielded many discoveries and inclusions important for our understanding of arthropod evolution. The oldest known and first Mesozoic fossils of various millipede taxa were found trapped in Burmese amber, like those of the orders *Callipodida* Pocock, 1894 (Stoev *et al.* 2019), *Platydesmida* de Saussure, 1860 (Moritz & Wesener 2019), *Siphoniulida* Pocock, 1894 (Liu *et al.* 2017) and *Siphonophorida* Newport, 1844 (Jiang *et al.* 2019). Furthermore, a great diversity of undescribed millipedes has been recorded from Burmese amber, among which are several millipedes belonging to the spirostreptidan taxon *Cambalidea* Cook, 1895 (Wesener & Moritz 2018).

*Spirostreptida* Brandt, 1833 belong to the *Juliformia* Attems, 1926, millipedes in which sternites, pleurites and tergites are fused completely into a rigid ring (Enghoff 1984; Blanke & Wesener 2014) (with the exception of some *Nemasomatidae* Bollman, 1893, which have free sternites on anterior segments (Enghoff 1984)). The relationship of the *Spirostreptida* to the other two *Juliformia* taxa, *Julida* Brandt, 1833 and *Spirobolida* Bollman, 1893 (Verhoeff 1910; Sierwald & Bond 2007; Blanke & Wesener 2014), as well as the internal relationship and the monophyly of the *Spirostreptida* are controversial (e.g., Jeekel 2004; Korsós & Johns 2009). Classically, the *Spirostreptida* are divided into two subgroups, the *Spirostreptidea* Brandt, 1833 and the *Cambalidea* (Enghoff *et al.* 2015). The *Cambalidea* or “*Cambaloidea*” (Jeekel 2004), with more than 250 species and 60 genera, have been in a constant flux basically since 1900 (Attems 1900) and their classification and monophyly remains unclear despite efforts by numerous authors (Verhoeff 1932; Mauriès 1977, 1983, 1987, 1992; Hoffman 1980; Shelley 2003, 2007; Jeekel 1985, 2004). Every worker on the group seems to develop their own system of internal classification of the *Cambalidea*, none of them based on a phylogenetic analysis. The *Cambalidea* are placed either in an order of its own (Mauriès 1983), as a subgroup of the *Spirostreptida* (Hoffman 1980; Shelley 2003; Jeekel 2004; Enghoff *et al.* 2015) or *Julida* (Mauriès 1977), or split between the *Spirostreptida* and *Julida* (Mauriès 1992). Since no classification of the group is based on a phylogenetic analysis, we refrain here from proposing another classification, but follow the system by Jeekel (2004) and Enghoff *et al.* (2015) which treats all five families (or main groups), the *Cambalidae* Bollman, 1893, *Cambalopsidae* Cook, 1895, *Choctellidae* Chamberlain & Hoffman, 1950, *Iulomorphidae* Verhoeff, 1924, and *Pseudonannolenidae* Silvestri, 1895 of equal rank as part of the order *Spirostreptida*. Here, we describe a sixth group from Cretaceous amber.

## Material and methods

### Abbreviations

- BuB = collection number of inclusions in the collection of Patrick Müller  
 CT = computed tomography  
 ZFMK = Zoological Research Museum A. Koenig, Leibniz Institute for Animal Biodiversity, Bonn, Germany  
 ZFMK-MYR = collection number of the Myriapoda collection at the ZFMK

**Table 1.** Material studied. Abbreviations: BuB = identifier in the collection of Patrick Müller; PM = Patrick Müller; ZFMK = Zoological Research Museum A. Koenig; ZFMK-MYR = identifier in the Myriapoda collection of the ZFMK.

Species	Specimen	Status	Dep.
<i>Electrocambala ornata</i> gen. et sp. nov.	ZFMK-MYR7369	holotype	ZFMK
<i>Electrocambala ornata</i> gen. et sp. nov.	ZFMK-MYR7370	paratype	ZFMK
<i>Electrocambala ornata</i> gen. et sp. nov.	BuB1825	–	PM
<i>Electrocambala ornata</i> gen. et sp. nov.	BuB1962	–	PM
<i>Electrocambala cretacea</i> gen. et sp. nov.	ZFMK-MYR7370	holotype	ZFMK
<i>Electrocambala</i> sp.	BuB1990	–	PM
<i>Kachincambala distorta</i> gen. et sp. nov.	ZFMK-MYR7368	holotype	ZFMK
<i>Kachincambala muelleri</i> gen. et sp. nov.	ZFMK-MYR10225	holotype	ZFMK
<i>Kachincambala</i> sp.	ZFMK-MYR6121	–	ZFMK
<i>Kachincambala</i> sp.	BuB1115	–	PM
<i>Kachincambala</i> sp.	BuB4098	–	PM
Electrocambalidae sp.	BuB1144	–	PM

### Specimens and data deposition

Specimens are from the private collection of Patrick Müller (Table 1). All type material were transferred to the collection of the ZFMK. Measurements of the amber pieces were made using a digital caliper.

All data generated is deposited in Morphobank (O’Leary & Kaufmann 2011) under project number 3903 and can be accessed via the following link: <http://morphobank.org/permalink/?P3903>.

### Drawings

Line drawings were made using a camera lucida mounted on a Olympus BX51 light microscope (Olympus Corporation, Tokyo, Japan), with 40–400× magnification. Line drawings were transformed to ink on transparent paper, with PIGMA MICRON 04, 03 and 005 ink pens (Sakura, Hayward, USA). Line drawings were scanned and edited in Inkscape ver. 1.0.1.

### Photography

Photographs of the studied specimens were made using a Canon EOS 7D camera mounted on a magnifier lens, to obtain images at different focus-levels. Image stacking was performed in Zerene Systems Stacker (ver. 1.04).

### Micro-CT and 3D-visualization

For non-invasive 3D-visualization of the specimens,  $\mu$ CT-scans were performed using a SKYSCAN 1272 (Brucker microCT, Kontich, Belgium) and the accompanying Control Software ver. 1.1.7 (Brucker microCT, Kontich, Belgium). All scans were performed with Flat Field Correction = ON and Geometrical Correction = ON. Other scanning-parameters were adjusted to achieve optimal settings for each specimen. For scanning parameters see Morphobank. Reconstruction, ring-artefact reduction, misalignment compensation and beam-hardening correction were performed in NRecon ver. 1.7.0.4 (Brucker microCT, Kontich, Belgium). For one specimen (ZFMK-MYR7368)  $\mu$ CT data were obtained in 2017 at the storage ring PETRA III (DESY, Hamburg, Germany) at Beamline P05 (Haibel *et al.* 2010; Greving *et al.* 2014; Wilde *et al.* 2016) operated by the Helmholtzzentrum Geesthacht. Volume rendering and measurements were performed in Drishti ver. 2.6.3 (Limaye 2012). Gonopods of male specimens were segmented in ITK-Snap ver. 3.4.0 (Yushkevich *et al.* 2006) and rendered in Blender ver. 2.77.

## Results

### Class **Diplopoda** Gervais, 1844

The specimens belong to the Diplopoda based on the following characters: diplosegments; gnathochilarium present.

### Subclass **Helminthomorpha** Pocock, 1887

The specimens belong to the subclass Helminthomorpha based on the following characters: gonopods present; ozopores lateral; mandibular base divided.

### Superorder **Juliformia** Attems, 1926

The specimens are identified as members of the superorder Juliformia based on the following characters: totally fused body rings; leg pairs 8 and 9 modified to gonopods; collum enlarged.

### Order **Spirostreptida** Brandt, 1833

The specimens are identified as members of the extant order Spirostreptida based on the following character combination: architecture of anterior body rings, with a not completely fused 4<sup>th</sup> body ring; body ring 4 seemingly legless; gnathochilarium with stipites not mesally fused and spanning along whole length of gnathochilarium.

### Suborder **Cambalidea** Cook, 1895

The specimens are identified as members of the extant suborder Cambalidea based on the following character combination: anterior and posterior gonopod well-developed; gnathochilarium with eumentum and promentum.

### **Electrocambalidae** fam. nov.

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Figs 1–5

### **Type genus**

*Electrocambala* gen. nov.

### **Diagnosis**

The new family *Electrocambalidae* fam. nov. differs from the suborder Spirostreptida by the structure of the gnathochilarium, with a separate eumentum and promentum, as well as by the presence of two pairs of gonopods. *Electrocambalidae* fam. nov. differs from the cambalidean families Choctellidae and Pseudonannolenidae by the presence of well-developed posterior gonopods (Fig. 1B, G). The new family differs from the Choctellidae and Iulomorphidae by having distinctly arched metazonites from body ring 6 onwards, and long body rings with a length/diameter ratio >0.7 (Fig. 1B–C). *Electrocambalidae* fam. nov. differs from the Iulomorphidae by the presence of a relatively large first leg pair in the males (Figs 1D, 4E). The new family differs from the families Cambalidae, Cambalopsidae and Pseudonannolenidae (in which ozopores start from body ring 5) by the ozopores starting from body ring 6 (Figs 1B, 5C). *Electrocambalidae* fam. nov. differs from the Cambalidae and Cambalopsidae by the absence of tubercles

on the metazonites. *Electrocambalidae* fam. nov. differs from other species of the order Spirostreptida in the combination of the following characters: (1) leg pair 3 moved anteriorly, resulting in a seemingly legless body ring 3 in addition to the legless body ring 4 (Fig. 1B), (2) presence of setation on the posterior margin of the metazonites, and (3) pilosity on the head is not restricted to the labrum, but extends further up frontally on the head (Figs 1D, 3E, 5D).

### Etymology

The family name is derived from the Latin word ‘*electrum*’ meaning ‘amber’ and the taxon Cambalidea, to which the studied fossils belong.

### Other genera included

*Kachincambala* gen. nov.

### *Electrocambala* gen. nov.

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Figs 1–3

### Type species

*Electrocambala ornata* gen. et sp. nov.

### Diagnosis

*Electrocambala* gen. nov. differs from *Kachincambala* gen. nov. by the presence of an accessory spine on the tarsus (Figs 1E, 3G). The anterior gonopod carries two rounded coxal lobes, the coxite is as long as the telopodite, and the outer lobe of the coxite is  $\frac{1}{3}$  as long as the inner lobe. The apex of the posterior gonopod is curved anteriorly, creating an open channel (Fig. 1G–H).

### Etymology

As for the family. Feminine.

### Other species included

*Electrocambala cretacea* gen. et sp. nov.

### *Electrocambala ornata* gen. et sp. nov.

[urn:lsid:zoobank.org:act:E66F551F-57A6-4FF6-BD95-C06FD4AD3627](https://zoobank.org/act:E66F551F-57A6-4FF6-BD95-C06FD4AD3627)

Figs 1–2

### Diagnosis

*Electrocambala ornata* gen. et sp. nov. differs from *Electrocambala cretacea* gen. et sp. nov. by the presence of net-like ornamentation on the ventral half of the prozonite (Fig. 1F), V-shaped striae laterally on the collum (Fig. 1D) and the absence of longitudinal ridges on the body rings. Metazonite on ventral half with 7 longitudinal striae. Metazonite from body ring 4 onwards distinctly arched (Fig. 1A). Body rings 2–5 narrower than collum and following body rings (Fig. 1B). Anterior gonopod coxite more than twice as long as wide, with inner lobe longer than outer lobe, telopodite narrow, as long as coxite. Posterior gonopod simple, as long as anterior gonopod, projecting between inner and outer lobes of anterior gonopod (Fig. 1G–H).

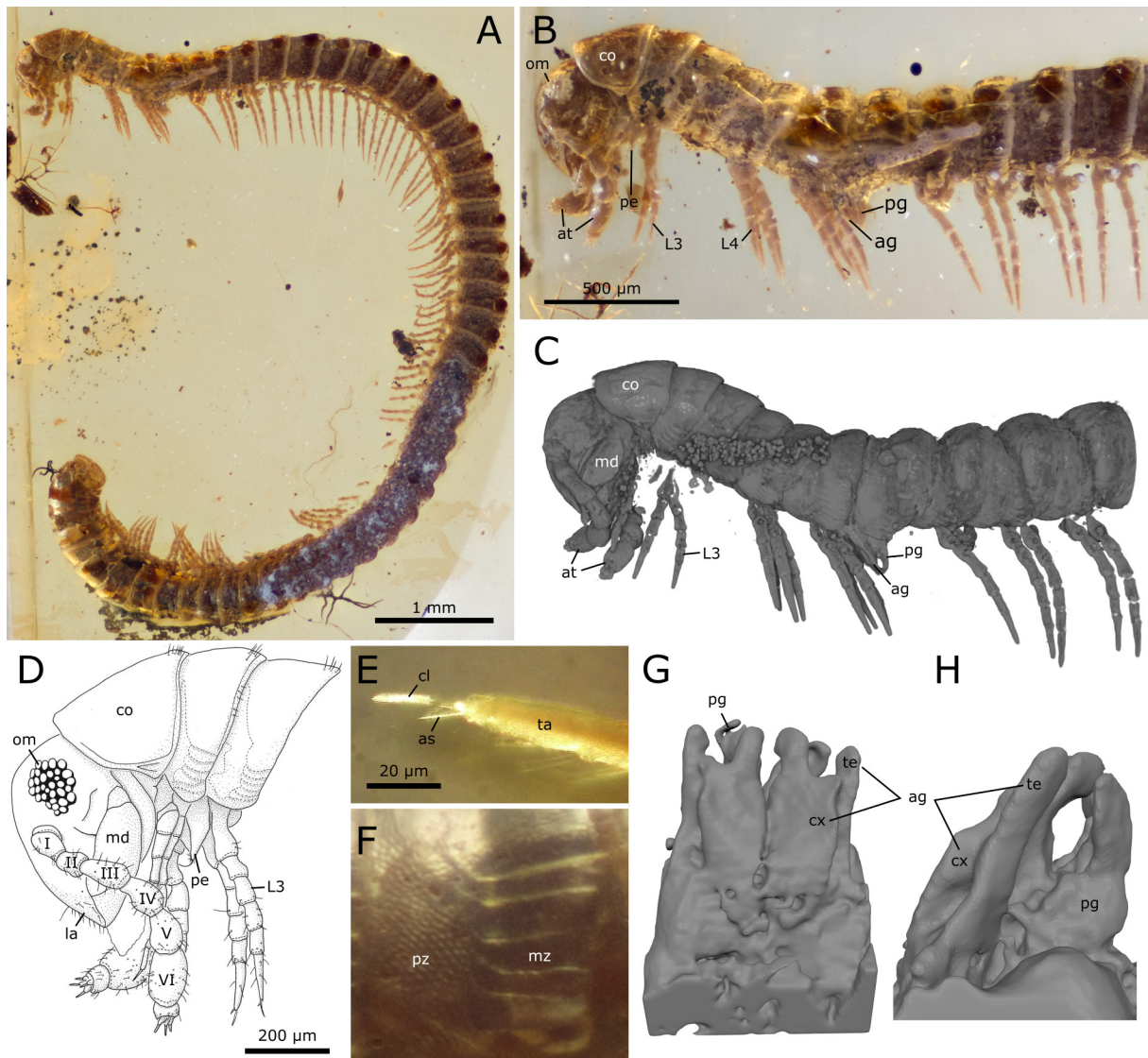
### Etymology

From the Latin word ‘*ornatus*’ meaning ‘ornamented’ in reference to the net-like ornamentation and striae on the body rings of the species. Noun in apposition.

### Type material

#### Holotype

MYANMAR • ♂; Kachin State, Hukawng Valley, Mid-Cretaceous Burmese amber inclusion; formerly in the collection of Patrick Müller (BuB1151); ZFMK-MYR7369.



**Fig. 1.** *Electrocambala ornata* gen. et sp. nov., holotype, ♂ (ZFMK-MYR7369). **A.** Habitus, lateral view, photograph. **B.** Head and anterior body rings, lateral view, photograph. **C.** Head and anterior body rings, lateral view, volume rendering. **D.** Head and anterior body rings, lateral view, drawing. **E.** Tarsus of midbody leg, photograph. **F.** Midbody ring, photograph. **G.** Gonopods, frontal view, segmentation. **H.** Gonopods, lateral view, segmentation. Abbreviations: ag = anterior gonopod; as = accessory spine; at = antennae; cl = claw; co = collum; cx = coxite; L = leg; la = labrum; md = mandible; mz = metazonite; om = ommatidia; pe = penis; pg = posterior gonopod; pz = prozonite; ta = tarsus; te = telopodite.

### Paratype

MYANMAR • 1 ♀; same collection data as for holotype; formerly in the collection of Patrick Müller (BuB1142); ZFMK MYR7370.

### Other material examined

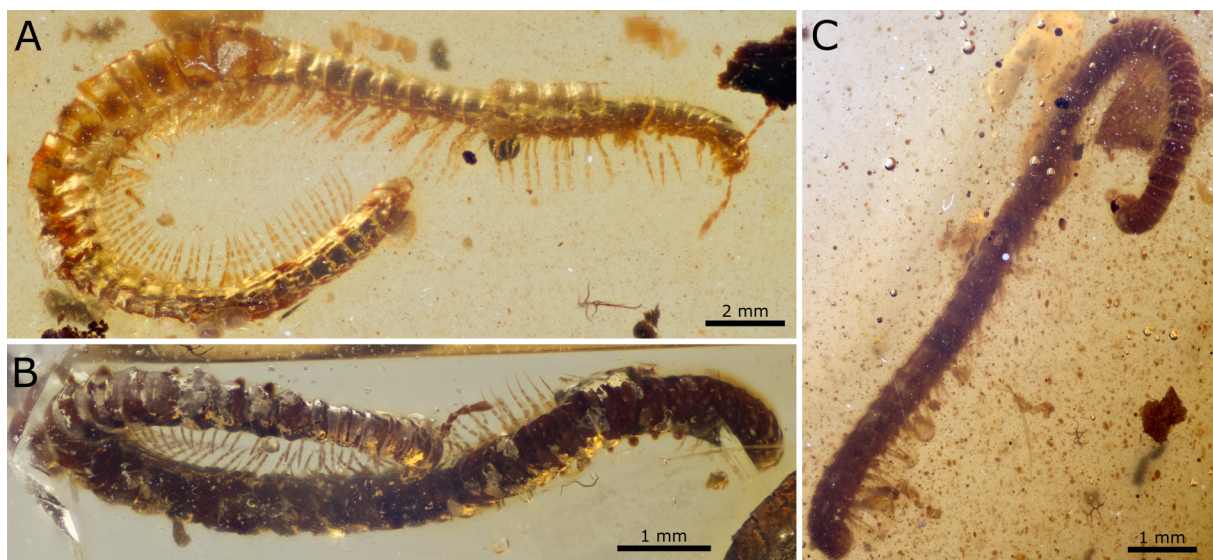
MYANMAR • 1 ♂; same collection data as for holotype; in the collection of Patrick Müller (BuB1962)  
• 1 ♀; same collection data as for holotype; in the collection of Patrick Müller (BuB1825).

### Description

**HABITUS.** At least up to 46+6 (holotype, ZFMK-MYR7369) body rings (Fig. 1A) (ZFMK-MYR7370 = 42+3; BuB1825 = 40+4; BuB1962 = 45+4); body cylindrical, slender, up to at least 14.7 mm long, diameter 0.5 mm, males smaller. Colour light to dark brown, posterior margin of metazonites light grey.

**HEAD.** As wide as collum and body ring 6 onwards, wider than body ring 2–5 (Fig. 1B–C). Labrum and front of head with setae (Fig. 1D). 32/21 ommatidia (21 probably an artefact) arranged in circular patch. Incisura lateralis present, closed. Antennae reaching to posterior margin of body ring 4, with 7 antennomeres, covered by setae, 6>3>4=5>1>2>7, with four apical sensory cones. Antennomeres 5 and 6 broader (Fig. 1D). Labrum tridentate. Mandible base divided into small cardo and large stipes (Fig. 1C–D). Gnathochilarium with eumentum and promentum, stipes along whole length of gnathochilarium, lamella lingualis not completely separated by promentum, not reaching to eumentum.

**TRUNK.** Collum only slightly curved, projecting over posterior margin of head (Fig. 1B–D). Collum with small triangular process projecting ventrally, reaching to height of upper margin of mandibular base, with 2 striae touching anterior forming a V (Fig. 1D). Body rings totally fused from body ring 5 onwards. Anterior four body rings with sternites free from pleuro-tergites. Prozonite separated from metazonite by constriction. Metazonite from body ring 6 onwards distinctly arched and wider than prozonite (Fig. 1C). Prozonite ventrally with net-like ornamentation (Fig. 1F). Metazonite ventrally with up to 7 longitudinal striae (Fig. 1F). Posterior margin of metazonites with 2–3 rows of setae (Fig. 1D). Ozopores from body ring 6 onwards lateral on metazonite, at middle height of body ring (Fig. 1B). Midbody rings (9) ca 0.7 times as long as diameter.



**Fig. 2.** *Electrocambala ornata* gen. et sp. nov., other material, photographs. A. ♂ (BuB1962). B. ♀ (BuB1825). C. Paratype, ♀ (ZFMK MYR7370).

**LEGS.** First two leg pairs surrounded by first pleuro-tergite (collum), leg pair 3 surrounded by 2<sup>nd</sup> pleuro-tergite close to 3<sup>rd</sup> pleuro-tergite, body rings 3 and 4 seemingly legless, from body ring 5 onwards 2 leg pairs per body ring (Fig. 1B–C). Midbody legs with coxa, prefemur, femur, postfemur, tibia, tarsus. Tarsus > prefemur = femur > postfemur > tibia > coxa. Podomeres with few setae. Tarsus with tarsal claw and accessory spine (Fig. 1E). Leg pairs 1 and 2 without accessory spine. Coxa of 2<sup>nd</sup> leg pair inserts medial of coxa of 1<sup>st</sup> leg pair.

**POSTERIOR BODY RINGS.** Preanal ring without epiproct projecting, with 5 longitudinal lateral grooves and setae. Anal valves with at least 10 marginal setae and up to 8 setae on surface. Subanal scale not projecting over anal valve. Posterior 3–6 body rings legless (Fig. 1A).

**MALE SEXUAL CHARACTERS.** Smaller and more slender than females (Figs 1A, 2A vs Fig. 2B–C). In male 1<sup>st</sup> leg pair present, reduced in size not in segmentation, without tarsal claw. Penis with wide base and curved tip, with short setae (Fig. 1D). Anterior (8<sup>th</sup> leg) and posterior gonopod (9<sup>th</sup> leg) well-developed, on body ring 7 (Fig. 1B–C). Anterior gonopod coxite flat with two rounded apical lobes (inner and outer lobe), telopodite as long as inner coxal lobe, inserting at base of coxa, with few setae. Presence of flagellum unknown. Posterior gonopod as long as anterior gonopod, with rounded tip. Apex curved anteriorly, creating an open channel. Anterior surface with possible remnant of seminal groove reaching up to apex (Fig. 1G–H).

**FEMALE SEXUAL CHARACTERS.** Larger and wider than male (Fig. 2B–C). First leg pair reduced in length and broadened. Vulva not sufficiently preserved for description.

### Remarks

*Electrocambala ornata* gen. et sp. nov. was discovered in one case (ZFMK MYR7370) in the same amber stone as a specimen of *Electrocambala cretacea* gen. et sp. nov. described below, showing that both species lived in temporal and geographical sympatry, not unlike recent species of the Cambalopsidae in SE Asia (e.g., Likhitrakarn *et al.* 2020).

### Measurements and taphonomy

#### ZFMK-MYR7369

**AMBER DESCRIPTION.** Amber flat, semi-circle, 15.45 × 6.6 × 2.84 mm, polished, yellow, clear transparent.

**SYNINCLUSIONS.** Soil particles, stellate hairs, plant parts, Acari.

**TAPHONOMIC FEATURES.** Body curved as in defence (Fig. 1A). Defence fluid released from anterior body rings, form transparent dark brown bubbles above ozopores (Fig. 1B). Field of ommatidia damaged on left side. Gonopods everted (Fig. 1B). Anal-valves open (Fig. 1A). Body laterally slightly flattened. Body rings 26–38 damaged on right side and from leg pair 10 onwards right leg missing (artefact from polishing) (Fig. 1A).

#### ZFMK-MYR7370

**MEASUREMENTS.** 14.5 mm long, 0.5 mm in diameter.

**AMBER DESCRIPTION.** Amber flat, oval-shaped, 48.3 × 29.5 × 7.4 mm, polished, yellow, reddish transparent.

**SYNINCLUSIONS.** Soil particles, sporangia of fungi, bark, wood fibre, leaves, Diptera, Coleoptera, *Electrocambala cretacea* gen. et sp. nov., small brown droplets.



TAPHONOMIC FEATURES. Anterior body coiled as in defence (Fig. 2C). Field of ommatidia visible, but single ommatidia not distinguishable. Setation only partially preserved. Legs only partially preserved, mostly decayed (Fig. 2C). Vulva visible, but poorly preserved. Surrounded by brownish film.

**BuB1825**

MEASUREMENTS. 14.7 mm long, 0.5 mm in diameter.

AMBER DESCRIPTION. Amber flat, semi-circle,  $18.23 \times 9.09 \times 4.05$  mm, polished, yellow to reddish, clear transparent, with fissures.

SYNINCLUSIONS. Sporangia of fungi, stellate hairs.

TAPHONOMIC FEATURES. Anterior body bent as in defence. Secretion of defence fluid (Fig. 2B). Setation not preserved. Legs only partially preserved (Fig. 2B). Characters partly obscured by body. Amber with fissure.

**BuB1962**

MEASUREMENTS. 11.9 mm long, 0.3 mm in diameter.

AMBER DESCRIPTION. Amber cuboid,  $12.28 \times 5.57 \times 3.29$  mm, polished, yellow, clear transparent. From larger piece, includes 5 pieces.

SYNINCLUSIONS. Soil particles, sporangia of fungi, stellate hairs, parts of arthropod appendages.

TAPHONOMIC FEATURES. Anterior body bent as in defence (Fig. 2A). Head damaged, antennae deformed, legs only partially preserved (Fig. 2A), anal valves of preanal ring missing, body rings 9–12 and 21–31 damaged.

*Electrocambala cretacea* gen. et sp. nov.

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Fig. 3

**Diagnosis**

*Electrocambala cretacea* gen. et sp. nov. differs from *Electrocambala ornata* gen. et sp. nov. by the presence of at least two lateral ridges on the body rings (Fig. 3C), a prozonite without net-like ornamentation and a collum without lateral striae. Ommatidia arranged in rows (Fig. 3E). Male gonopods unknown.

**Etymology**

‘*Cretacea*’ in reference to the Cretaceous, the geological period to which the Burmese amber deposits are dated. Noun in apposition with a free ending.

**Type material**

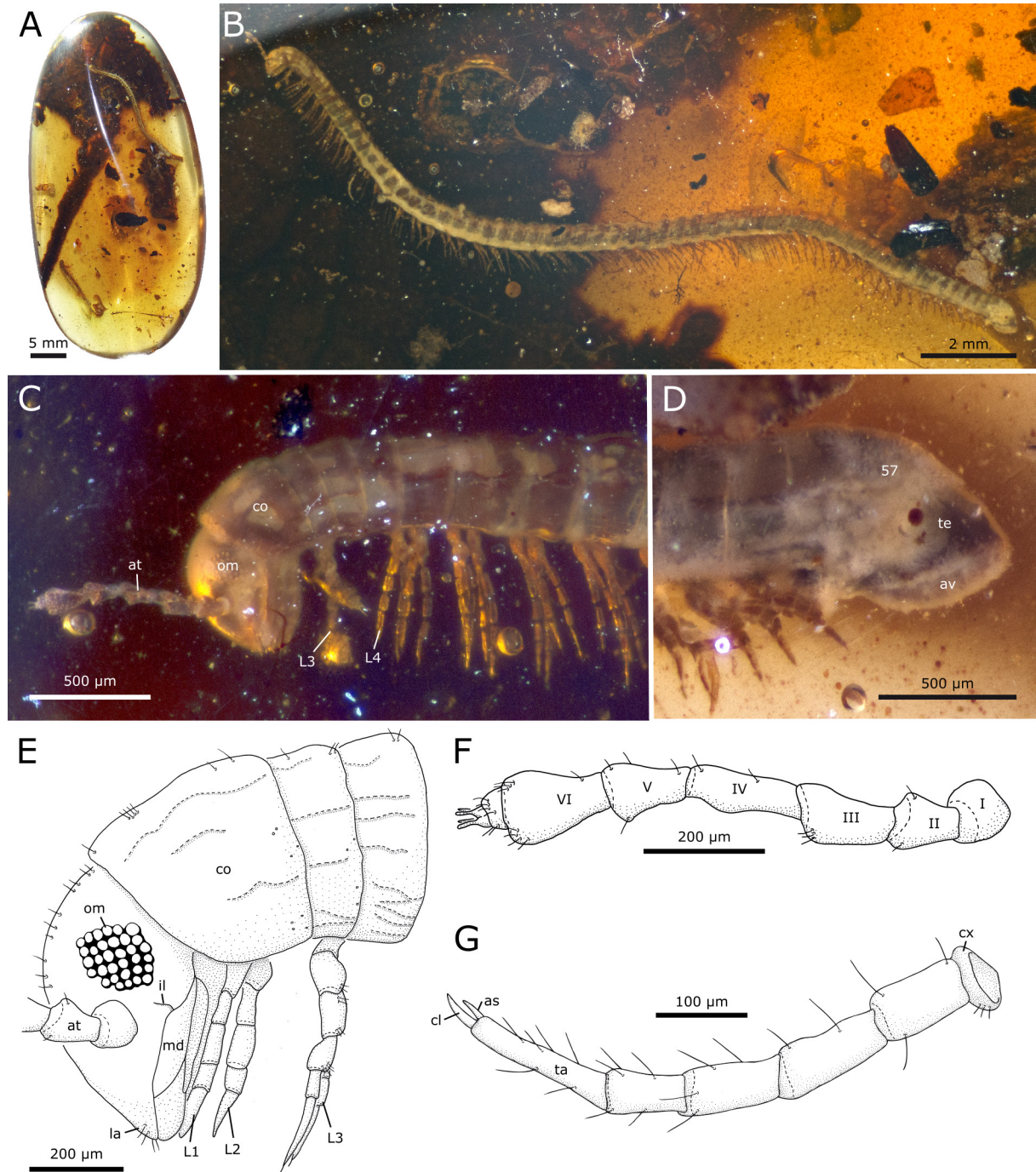
**Holotype**

MYANMAR • ♀; Kachin State, Hukawng Valley, Mid-Cretaceous Burmese amber inclusion; formerly in the collection of Patrick Müller (BuB1142); ZFMK-MYR7370.

**Description**

HABITUS. 55+3 body rings; body cylindrical, slender, up to at least 17.9 mm long, 0.6 mm in diameter. Colour brown to greyish (Fig. 3B).

HEAD. As wide as collum and body rings 6 onwards, wider than body rings 2–5 (Fig. 3C). Head and labrum with setae. 31/? ommatidia (left side obscured) arranged in 6 rows, posterior 4 rows with 6 ommatidia,



**Fig. 3.** *Electrocambala cretacea* gen. et sp. nov., holotype, ♀ (ZFMK-MYR7370). **A.** Amber piece, photograph. **B.** Habitus, lateral view, photograph. **C.** Head and anterior body rings, lateral view, photograph. **D.** Telson and posterior body rings, lateral view, photograph. **E.** Head and anterior body rings, lateral view, drawing. **F.** Antenna, drawing. **G.** Midbody leg, drawing. Abbreviations: 57 = body ring 57; as = apical spine; at = antennae; av = anal valve; cl = claw; co = collum; cx = coxa; il = incisura lateralis; L = leg; la = labrum; md = mandible; om = ommatidia; ta = tarsus; te = telson.

row 5 (counted from posterior) with 5, anterior row with 4 ommatidia. Incisura lateralis present, closed (Fig. 3E). Antennae reaching to body ring 5, with 7 antennomeres, covered by setae, 6 = 4 > 3 > 5 > 2 > 1 > 7, with 4 sensory cones (Fig. 3F).

TRUNK. Collum slightly curved, covering posterior margin of head. Collum laterally without striae (Fig. 3C, F). Body rings totally fused from body ring 5 onwards, anterior four body rings with sternite free from pleuro-tergite. Metazonites from body ring 6 onwards distinctly arched and wider than prozonite (Fig. 3C). Body rings with several longitudinal ridges. Metazonites ventrally with at least 5 longitudinal striae, posterior margin with 1 or 2 rows of setae (Fig. 3E), ozopores start lateral from body ring 6.

LEGS. Body ring 4 legless, from body ring 5 onwards 2 leg pairs per body ring. Midbody legs with coxa, prefemur, femur, postfemur, tibia, tarsus. Podomeres with few setae. Tarsus > femur > postfemur = prefemur > tibia > coxa. Tarsus with tarsal claw and accessory spine (only visible on well preserved legs separated from body, other legs partly decomposed). Podomeres with setae (Fig. 3G). 1<sup>st</sup> and 2<sup>nd</sup> leg pair shorter and stouter than midbody legs (Fig. 3G).

POSTERIOR BODY RINGS. Preanal ring without epiproct projecting, with marginal setae. Subanal scale not projecting over anal valve. Posterior body rings and anal valves covered by fungi (Fig. 3D).

MALE. Unknown.

### Measurements and taphonomy

MEASUREMENTS. 17.9 mm long, 0.6 mm in diameter.

AMBER DESCRIPTION. Amber flat, oval-shaped, polished, 48.3 × 29.5 × 7.4 mm, yellow, reddish transparent (Fig. 3A).

SYNINCLUSIONS. Same as in ZFMK-MYR7370 (*Electrocambala ornata* gen. et sp. nov.).

TAPHONOMIC FEATURES. From body ring 8 onwards body rings and anal valves partially covered by white, filamentous substance. Only right side of anterior body visible, left side obscured by leaf, several legs detached, next to body (Fig. 3B).

### *Electrocambala* gen. nov. sp.

#### Material examined

MYANMAR • 1 ♀; Kachin State, Hukawng Valley, Mid-Cretaceous Burmese amber inclusion; in the collection of Patrick Müller (BuB1990).

### Measurements and taphonomy

MEASUREMENTS. 8.4 mm long, 0.5 mm in diameter.

AMBER DESCRIPTION. Semicircle, 15.5 × 1.1 × 2.6 mm. Polished, yellow transparent.

SYNINCLUSIONS. Soil particles, sporangia of fungi, stellate hairs, small brown droplets.

TAPHONOMIC FEATURES. Specimen hollow, only sclerotized parts preserved. Only anterior 35 body rings preserved. From body ring 6 onwards only right half preserved. Cracks in amber filled by minerals.

### Remarks

This specimen is not sufficiently preserved to identify it as either one of the two species described above, or as a third species. This specimen was identified as a member of *Electrocambala* gen. nov. based on the following character combination: legs with accessory spine, gap between leg pair 3 and leg pair 4.

### *Kachincambala* gen. nov.

[urn:lsid:zoobank.org:act:D64F73BD-381E-4028-B362-EA1DE2B6442F](https://zoobank.org/urn:lsid:zoobank.org:act:D64F73BD-381E-4028-B362-EA1DE2B6442F)

Figs 4–5

### Type species

*Kachincambala muelleri* gen. et sp. nov.

### Diagnosis

*Kachincambala* gen. nov. differs from *Electrocambala* gen. nov. by the absence of an accessory spine on the tarsus (Fig. 5E) and in the structure of the gonopods (Fig. 4F–G).

### Etymology

‘*Kachin*’, after the Myanmar state of Kachin where the amber deposits are located, and ‘*-cambala*’, a common suffix for names in the Cambalidea. Feminine.

### Other species included

*Kachincambala distorta* gen. et sp. nov.

### *Kachincambala muelleri* gen. et sp. nov.

[urn:lsid:zoobank.org:act:F9CC6697-1E02-4A41-AABA-1E5EE46D7AFA](https://zoobank.org/urn:lsid:zoobank.org:act:F9CC6697-1E02-4A41-AABA-1E5EE46D7AFA)

Fig. 4

### Diagnosis

*Kachincambala muelleri* gen. et sp. nov. differs from the only other species of the genus, *K. distorta* gen. et sp. nov., in gonopod characters. The anterior gonopod coxite is more stout in *K. muelleri* gen. et sp. nov., less than twice as long as wide, while it is more narrow in *K. distorta* gen. et sp. nov. The inner lobe is apically rounded, nearly triangular and bends mesally. The outer lobe of the anterior gonopod is short and broad, oriented more laterally than in *K. distorta* gen. et sp. nov. Telopodite of anterior gonopod is broad, shorter than coxite. Posterior gonopod simple, broad, reaching over inner lobe of coxite.

### Etymology

In honour of Patrick Müller, who granted us access to his large collection of inclusions in Burmese amber for study, which resulted in the discovery of the specimens studied here, and who donated the type material to the ZFMK. Noun in the adjective case.

### Type material

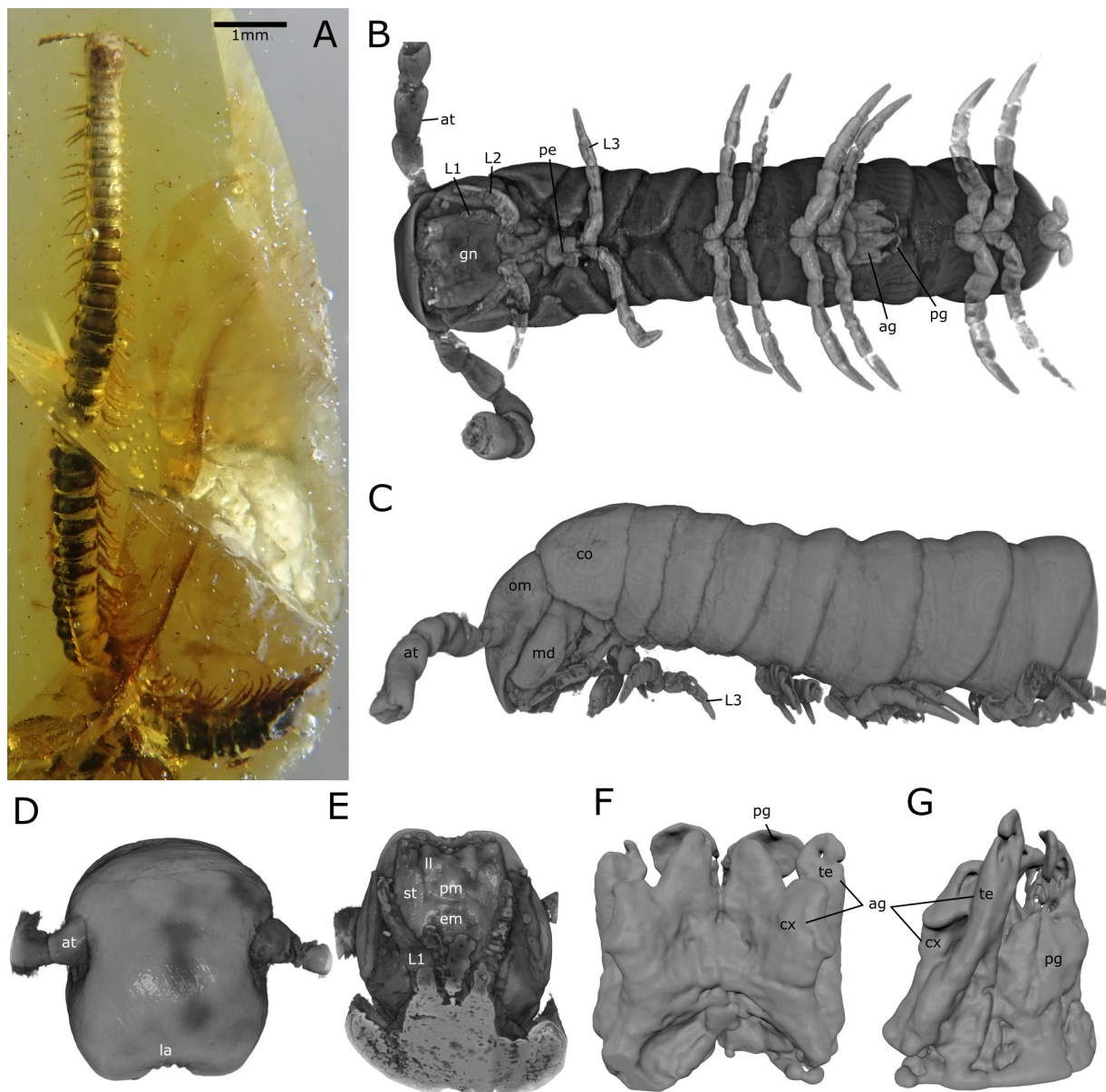
#### Holotype

MYANMAR • ♂; Kachin State, Hukawng Valley, Mid-Cretaceous Burmese amber inclusion; formerly in the collection of Patrick Müller (BuB3757); ZFMK-MYR10225.

### Description

HABITUS. >41 body rings; cylindrical and slender, up to at least 12 mm long and 0.5 mm wide. Colour dark brown to greyish (Fig. 4A–C).

HEAD. As wide as collum and body rings 6 onwards, wider than body rings 2–5. Head and labrum with setae. Labrum with three teeth (Fig. 4D). >30 ommatidia arranged in several rows. Incisura lateralis present, closed. Antennae ca 800 µm long, covered by setae, 7 < 1 < 2 < 4 = 5 < 3 < 6, with four apical sensory cones (Fig. 4B). Mandible base with small cardo ca ¼ of length of large stipes (Fig. 4C). Gnathochilarium with mentum divided in eumentum and promentum, large triangular lamella lingualis, large stipites occupying entire length of gnathochilarium, with inner and outer palp (Fig. 4E).



**Fig. 4.** *Kachincambala muelleri* gen. et sp. nov., holotype, ♂ (ZFMK-MYR10225). **A.** Habitus, dorsal view, photograph. **B.** Head and anterior body rings, ventral view, volume rendering. **C.** Head and anterior body rings, lateral view, volume rendering. **D.** head, frontal view, volume rendering. **E.** Head, ventral view, volume rendering. **F.** Gonopods, frontal view, segmentation. **G.** Gonopods, lateral view, segmentation. Abbreviations: ag = anterior gonopod; at = antennae; co = collum; cx = coxite; em = eumentum; gn = gnathochilarium; L = leg; la = labrum; ll = lamella lingualis; md = mandible; om = ommatidia; pe = penis; pg = posterior gonopod; pm = promentum; st = gnathochilarial stipes; te = telopodite.

TRUNK. Collum large, laterally with triangular extension. Body rings 2–5 narrower than collum and following body rings. Body rings totally fused from body ring 5 onwards, anterior four body rings with sternite free from pleuro-tergite. Body rings from body ring 5 onwards with distinctly arched metazonite and wider than prozonite. Metazonite ventrally with 7–9 striae. Ozopores from body ring 6 onwards positioned ventro-lateral on metazonite (Fig. 4C).

LEGS. Body rings 3 and 4 seemingly legless, from body ring 5 onwards 2 leg pairs per body ring (Fig. 4B). Anterior three leg pairs shorter than following legs but not reduced in segmentation. Midbody legs with coxa, prefemur, femur, postfemur, tibia, tarsus. Podomeres covered by setae. Tarsus > tibia > prefemur = femur > postfemur > coxa. Accessory spine on tarsus absent.

POSTERIOR BODY RINGS. Unknown.

MALE SEXUAL CHARACTERS. Leg pair 1 reduced in size, not in segmentation (Fig. 4A). Anterior gonopod plate-like, coxite with apically rounded inner lobe and shorter outer lobe, which extends laterad. Inner lobe ca two times as long as outer lobe. Telopodite as long as coxite's inner lobe, apically rounded. Presence of flagellum unknown. Posterior gonopod as long as anterior gonopod; apically with rounded lobe extending laterally (Fig. 4F–G).

FEMALE SEXUAL CHARACTERS. Unknown.

### Measurements and taphonomy

MEASUREMENTS. Ca 12 mm long, 0.5 mm in diameter.

AMBER DESCRIPTION. Flat, triangular, 15.5 × 8.9 × 3.0 mm. Yellow transparent with brownish areas close to animal. With crack.

SYNINCLUSIONS. Insect remains, stellate hairs.

TAPHONOMIC FEATURES. Specimen straight. Posterior body rings missing (cut away). Mid body partially obscured by crack. Gonopods everted. Defence fluid released from ozopores (Fig. 4A).

*Kachincambala distorta* gen. et sp. nov.

[urn:lsid:zoobank.org:act:EBD66E4D-D2FB-40EC-B1EC-D429C7465428](https://zoobank.org/act:EBD66E4D-D2FB-40EC-B1EC-D429C7465428)

Fig. 5

### Diagnosis

Forty-two ommatidia arranged in circular patch (Fig. 5A). Anal valve with 8 marginal setae. Male leg pair 1 well-developed (Fig 5D). *Kachincambala distorta* gen. et sp. nov. differs from the only other species of the genus, *K. muelleri* gen. et sp. nov., in gonopod characters: unlike in *K. distorta* gen. et sp. nov., the posterior gonopod of *K. muelleri* gen. et sp. nov. does not possess a lateral lobe apically. On the anterior gonopod, the outer lobe of the anterior gonopod's coxite is nearly as long as the inner lobe in *K. distorta* gen. et sp. nov., while the outer lobe is short and broad, oriented more laterally in *K. muelleri* gen. et sp. nov. Furthermore, the anterior gonopod's telopodite is in *K. distorta* gen. et sp. nov. apically pointed and not rounded as in *K. muelleri* gen. et sp. nov. (Fig. 5F–G).

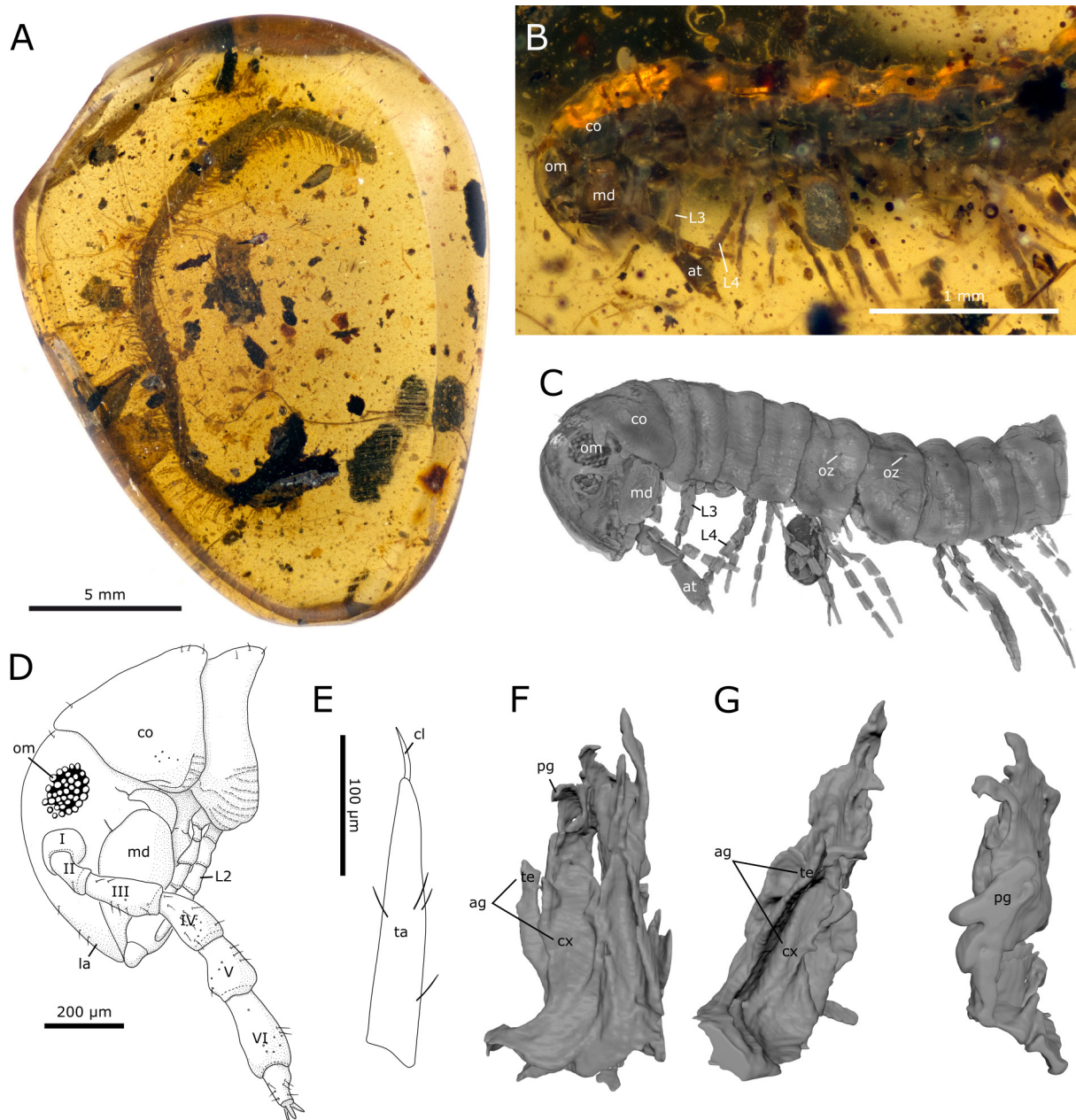
### Etymology

From the Latin word '*distortus*', meaning 'distorted' or 'deformed', referring to the strong deformation of the specimen and especially its gonopods. Noun in the adjective case.

**Type material**

**Holotype**

MYANMAR • ♂; Kachin State, Hukawng Valley, Mid-Cretaceous Burmese amber inclusion; formerly in the collection of Patrick Müller (BuB1839); ZFMK-MYR7368.



**Fig. 5.** *Kachincambala distorta* gen. et sp. nov., holotype, ♂ (ZFMK-MYR7368). **A.** Amber piece, photograph. **B.** Head and anterior body rings, lateral view, photograph. **C.** Head and anterior body rings, lateral view, volume rendering. **D.** Head, lateral view, drawing. **E.** Tarsus, drawing. **F.** Gonopods, anterior view, segmentation. **G.** Gonopods, lateral view, segmentation. Abbreviations: ag = anterior gonopod; at = antennae; cl = claw; co = collum; cx = coxite; L = leg; la = labrum; md = mandible; om = ommatidia; oz = ozopore; pg = posterior gonopod; ta = tarsus; te = telopodite.

## Description

**HABITUS.** 56+4 body rings. Body cylindrical, slender, up to at least 20.8 mm in length, 0.4 mm in diameter. Colour grey to brown (Fig 5A).

**HEAD.** As wide as collum and body ring 6 onwards, wider than body rings 2–5. 42/39 ommatidia arranged in circular patch (Fig. 5C). *Incisura lateralis* present, closed. Antennae with 7 antennomeres, reaching to posterior margin of body ring 4, 6=3>4>5>2>1>7, with 4 apical sensory cones (Fig. 5D). Labrum tridentate, with setae. Mandibular base divided in small *cardo* and large *stipes* (Fig. 5D). Gnathochilarium with *eumentum* and *promentum*. Lamella *lingualis* reaching to lower third of *promentum*, not touching *eumentum*. *Promentum* not completely separating the lamellae *lingualis*. *Stipes* of gnathochilarium along whole length of gnathochilarium touching *gula* laterally.

**TRUNK.** Collum only slightly curved, projecting over posterior margin of head, reaching laterally to height of mandibular base (Fig. 5C). Collum ventrally with 6 grooves on posterior margin (Fig. 5D). Body rings totally fused from body ring 5 onwards. Metazonite from body ring 5 onwards distinctly arched, wider than prozonite. Metazonite ventrally with 6 to 9 striae (Fig. 5C). Posterior margin dorsally with few setae (Fig. 5D). Ozopores start on body ring 6. Midbody rings (9) ca 0.8 times as long as diameter (Fig. 5C).

**LEGS.** First two leg pairs surrounded by first pleuro-tergite (collum), leg pair 3 surrounded by 2<sup>nd</sup> pleuro-tergite, body rings 3 and 4 legless, from body ring 5 onwards 2 leg pairs per body ring (Fig. 5C). Midbody legs with coxa, prefemur, femur, postfemur, tibia, tarsus. Podomeres with few setae. Tarsus with one claw, no apical spine (Fig. 5E). Tarsus > prefemur > postfemur > femur = tibia > coxa. Coxa of 2<sup>nd</sup> leg pair inserted medial of coxa of 1<sup>st</sup> leg pair.

**POSTERIOR BODY RINGS.** Preanal ring without epiproct projecting, with few setae. Valves with at least 8 marginal setae. Subanal scale not projecting over valve.

**MALE SEXUAL CHARACTERS.** In males leg pairs 1 and 2 slightly reduced in size but not in segmentation. In leg pair 2 femur > tarsus > tibia = postfemur = prefemur > coxa. Except leg pair 1 with tarsal claw. Coxa of leg pair 2 inserted medial of coxa of leg pair 1. Paired penis located behind leg pair 2, within pouch. Anterior and posterior gonopods on body ring 7 well-developed, retracted into body. Left gonopods highly deformed (Fig. 5F–G). Anterior gonopod with telopodite slightly longer than coxite, apically pointed. Coxite long, slender, with two lobes, outer lobe pointed and nearly as long as inner lobe. Inner lobe apically rounded. Presence of flagellum unknown. Posterior gonopod longer than anterior gonopod, anterior surface of posterior gonopod with possible seminal groove (Fig. 5F–G).

## Measurements and taphonomy

**MEASUREMENTS.** 20.8 mm long, 0.4 mm in diameter (Fig. 5A).

**AMBER DESCRIPTION.** Amber flat, elliptical, 19.7 × 14.8 × 3.9 mm. Polished, yellow transparent (Fig. 5A).

**SYNINCLUSIONS.** Soil particles, plant parts, pollen, antennae, leg parts and cuticle of arthropods.

**TAPHONOMIC FEATURES.** Specimen bend dorsally. Front of specimen laterally flattened (compressed, cuticle partially broken) (Fig. 5A). Left antenna missing (Fig. 5B). Preanal segment damaged.



*Kachincambala* gen. nov. sp.

**Material examined**

MYANMAR • 1 specimen; Kachin State, Hukawng Valley, Mid-Cretaceous Burmese amber inclusion; in the collection of Patrick Müller (BuB1115).

**Measurements and taphonomy**

MEASUREMENTS. 9.0 mm long, 0.3 mm in diameter.

AMBER DESCRIPTION. Rectangular,  $14.2 \times 5.3 \times 2.5$  mm. Polished, yellow, transparent.

SYNINCLUSIONS. Sporangia of fungi, pollen grains, plant parts.

TAPHONOMIC FEATURES. Laterally flattened. Head damaged on both sides, body rings partially damaged on left side. Muscles visible within legs. Amber with fissure along specimen.

**Remarks**

This specimen is identified as a member of *Kachincambala* gen. nov. based on the absence of an accessory spine. The poor preservation of this specimen prevents any assignment to the species of *Kachincambala* described here or to describe it as a new species.

*Kachincambala* gen. nov. sp.

**Material examined**

MYANMAR • 1 ♂; Kachin State, Hukawng Valley, Mid-Cretaceous Burmese amber inclusion; ZFMK-MYR6121.

**Measurements and taphonomy**

MEASUREMENTS. 5.3 mm long, 0.3 mm in diameter, 24+6 body rings.

AMBER DESCRIPTION. Oval, flat,  $6.0 \times 13.5 \times 4.1$  mm. Light yellow, transparent.

SYNINCLUSIONS. Archaeognatha, aphid, Hymenoptera?, mite, stellate hair.

TAPHONOMIC FEATURES. Anterior body rings compressed. Posterior body rings partly polished away.

**Remarks**

This specimen is identified as a member of the Electrocambalidae fam. nov. based on the large gap between leg pairs 3 and 4 and the presence of setae on the head and the posterior margin of the body rings. It is determined as a member of *Kachincambala* gen. nov. based on the absence of an accessory spine. For a detailed description the animal is not sufficiently preserved.

*Kachincambala* gen. nov. sp.

**Material examined**

MYANMAR • 1 ♀; Kachin State, Hukawng Valley, Mid-Cretaceous Burmese amber inclusion; in the collection of Patrick Müller (BuB4098).

### **Measurements and taphonomy**

MEASUREMENTS. 13.0 mm long, 0.4 mm in diameter, 43+3 body rings.

AMBER DESCRIPTION. Triangular, flat, 15.0 × 10.8 × 2.3 mm. Light yellow, transparent.

SYNINCLUSIONS. Stellate hairs.

TAPHONOMIC FEATURES. Anterior body rings compressed. Posterior body rings partly polished away.

### ***Electrocambalidae* fam. nov. sp.**

### **Material examined**

MYANMAR • 1 specimen; Kachin State, Hukawng Valley, Mid-Cretaceous Burmese amber inclusion; in the collection of Patrick Müller (BuB1144).

### **Measurements and taphonomy**

MEASUREMENTS. 13.8 mm long, 0.4 mm in diameter.

AMBER DESCRIPTION. Spherical, flat, 44.4 × 33.6 × 15.9 mm. Polished, yellow, transparent.

SYNINCLUSIONS. Soil particles, bark, Archaeognatha, Diptera, Hymenoptera (wasp, ant).

TAPHONOMIC FEATURES. Body straight. Imprint of body next to specimen. Body dorsally flattened, cuticle partially broken. Layering of amber.

### **Discussion**

#### **Characters of the *Electrocambalidae* fam. nov.**

The family *Electrocambalidae* fam. nov. is distinct from all *Cambalidea* and *Spirostreptidea* by the position of leg pair 3. Leg pair 1 and 2 both appear to be situated on the collum and leg pair 3 is shifted to body ring 2 in the *Electrocambalidae* fam. nov., resulting in an apparently legless third body ring, in addition to the seemingly legless fourth body ring observable in all *Spirostreptida*. This shift of leg pair 3 is the strongest argument in support of the new family, since it also requires modifications of the muscular and tracheal system, associated to the sternites, carrying the legs.

*Electrocambalidae* fam. nov. shares with the remaining *Spirostreptida* the architecture of the anterior body rings. In the *Electrocambalidae* fam. nov. the pleuro-tergites and sternites of body rings 2 to 4 are not completely fused; thus, the sternites carrying the first three leg pairs are free and separated from the pleuro-tergites. Among the *Juliformia* (*Julida*, *Spirostreptida*, *Spirobolida*), a free leg pair 3 in combination with four not fully fused body rings is only present in the order *Spirostreptida*, as pointed out by Verhoeff (1928–1932) and Mauriès (1992). In the *Julida* and the *Spirobolida* only the anterior three body rings are not totally fused while from body ring 4, which carries a single pair of legs (the third pair in *Julida*, the fourth pair in *Spirobolida*), and onwards, the pleuro-tergites and sternites are totally fused (Verhoeff 1928–1932; Mauriès 1992). The *Julida* have a maximum of only two free leg pairs, while the *Spirobolida* show a special case within the *Juliformia*, with three free leg pairs, despite having only three not fully fused body rings (Verhoeff 1928–1932). Because of the differences in the trunk-ring architecture, Hoffman (1982) did not accept a monophyletic superorder *Juliformia* but placed the *Spirobolida* in its own superorder *Anocheta* Cook, 1895, and the *Julida* and the *Spirostreptida* together with the *Siphoniulida* in the *Diplocheta* Cook, 1895, a placement not recovered in any phylogenetic analyses (e.g., Sierwald *et al.* 2003; Blanke & Wesener 2014).

Electrocambalidae fam. nov. shares with the Julida the metazonital setation of the body rings. Metazonital setation is common in species of the order Julida, which usually bear a single row of setae (Enghoff 1981). In the Spirobolida setation of the body rings is only known from the Typhlobolellidae Hoffman, 1969, a troglobitic family (Enghoff *et al.* 2015). Setae on the margin of the metazonites are characters usually not found in species of the order Spirostreptida (Enghoff *et al.* 2015). The only exceptions can be found in the Cambalidean genera *Hypocambala* Silvestri, 1897, of the family Cambalopsidae, and *Jamilka* Shear, 1973, of the family Cambalidae, which bear single a row of setae or are densely covered by setae on the body rings (Jeekel 1963; Enghoff 1981, Jiang *et al.* 2021). Enghoff (1981) suggested that the metazonital setation in the Julida is a plesiomorphic character, as could also be the case in the here proposed Electrocambalidae fam. nov. Furthermore, in the Electrocambalidae fam. nov. setation of the head is present on the labrum and extends up to the anterior margin of the collum. Within Spirostreptida a similar setation pattern of the head can only be observed in a few species of the genus *Hypocambala* (Jiang *et al.* 2021).

The following characters of the Electrocambalidae fam. nov. are shared with the Cambalidea: (1) the structure of the gnathochilarium, (2) the structure of the gonopods, and (3) developmental characters (euanamorphosis, as indicated by the presence of apodous body rings in front of the telson in mature specimens).

(1) The gnathochilarium of the Electrocambalidae fam. nov. corresponds to the state found in several cambalidean families and differs markedly from the structure found in the Julida and Spirobolida. The gnathochilarium of the Electrocambalidae fam. nov. consists of the lateral stipites, which reach over the full length of the gnathochilarium. A basal eumentum and an anterior, triangular promentum are present at its centre. Although the structure of the gnathochilarium is highly variable within the families of the Cambalidea, the structure seen in the Electrocambalidae fam. nov. can be found in representatives within all cambalidean families (e.g., Schubart 1966 for *Iulomorpha* Porat, 1872; Loomis 1938 for *Tridere* Loomis, 1938; Mauriès 1983, 1987 for *Podoglyphiulus* Attems, 1909 and *Pseudonannolene* Silvestri, 1895). In contrast to the Cambalidea the structure of the gnathochilarium is highly conserved in the suborder Spirostreptidea (Jeekel 1985) and the order Spirobolida (Enghoff *et al.* 2015), which both have an undivided duplomentum, as well as in the order Julida, which has the mentum and the stipites fused (with the exception of Parajulidae Bollman, 1893 (Jeekel 1985)) and differs clearly from the state in the fossil family.

(2) In the Electrocambalidae fam. nov. the 8<sup>th</sup> and 9<sup>th</sup> leg pairs on body ring 7 are both modified to well-developed gonopods. Within the order Spirostreptida this character state can only be found in the suborder Cambalidea, as classified by Hoffman (1980, 1982), consisting of the families Cambalidae, Cambalopsidae and Iulomorphidae. In the Spirostreptidea, Choctellidae and Pseudonannolenidae the 8<sup>th</sup> leg pair is modified, and the 9<sup>th</sup> reduced or absent (Hoffman 1982; Enghoff *et al.* 2015). Furthermore, the Electrocambalidae fam. nov. seem to be opisthospermophorous or amphispemphorous with the posterior gonopod, which possibly shows the remnants of a seminal groove, being involved in sperm transfer. In the orders Julida and Spirobolida, and the families Cambalopsidae and Cambalidae, the posterior gonopod is the functional gonopod (= opisthospermophory) and the anterior gonopod serves as claspers or rarely assists in sperm transfer (= amphispemphorous) (Jeekel 1985 for Cambalidae and Cambalopsidae; Enghoff *et al.* 2015 for Spirobolida and Julida). The Iulomorphidae are amphispemphorous with a tendency towards protospemphory (Jeekel 1985). The families Pseudonannolenidae and Choctellidae, and the suborder Spirostreptidea, which lack a fully developed posterior gonopod, are protospemphorous (Jeekel 1985). Therefore, the ancestral state in the Juliformia is most likely opisthospermophory, with a functional posterior gonopod and an accessory anterior gonopod, as seen in our Electrocambalidae fam. nov., and the shift of the sperm transfer function to the anterior gonopod occurred in the suborder Spirostreptidea, and the families Choctellidae and Pseudonannolenidae.

(3) While most species of the suborder Spirostreptida are hemianamorphic, with body rings only added to a certain stadium, and further moults taking place without an addition of body rings (Enghoff *et al.* 1993), in Cambalidea adults show apodous body rings in front of the telson, suggesting euanamorphosis. Body rings are added with every moult until the death of the animal (Enghoff *et al.* 1993). We suggest that the Electrocambalidae fam. nov. are euanamorphic as well, because males show completely developed gonopods and apodous body rings at the same time. This means that after reaching sexual maturity body rings are still added.

Other characters of the Electrocambalidae fam. nov. are (1) ozopores starting from body ring 6 and (2) a relatively well-developed first leg pair in males. The position of the first ozopores (1) varies within the Juliformia, with few exceptions, between body rings 5 and 6 (Attems 1926; Verhoeff 1928–1932; Enghoff 2015). In the cambalidean families Cambalidae (Reboleira *et al.* 2015), Cambalopsidae (Korsós & Johns 2009), and Pseudonannolenidae (Iniesta & Ferreira 2013a, 2013b) ozopores start on body ring 5, while ozopores start on body ring 6 in Choctellidae (Chamberlin 1918) and Iulomorphidae (Verhoeff 1924; Korsós & Johns 2009), as is the case in the Electrocambalidae fam. nov. A well-developed first leg pair in males (2) can be found in several spirostreptidan taxa (see above). In the studied male specimens the first leg pair was only slightly reduced in size but not in segmentation. Golovatch *et al.* (2007) stated that the cambalopsid species *Glyphiulus costulifer* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007 is probably the most basal representative of the genus because of the nearly unmodified first male legs (Golovatch *et al.* 2007), while Enghoff (1981) regarded the presence of unmodified first legs in Julida as reversals. Therefore, it is not clear whether or not the presence of an unmodified first leg pair in the fossil specimens is a plesiomorphic condition. At the moment the relationship of the Electrocambalidae fam. nov. to the remaining Spirostreptida and Juliformia remains speculative. To clarify the phylogenetic position of the Electrocambalidae fam. nov. a phylogenetic reconstruction including a broad sampling of juliformian taxa is needed.

The fossils were found in the present distributional range of the family Cambalopsidae, which are endemic to South-East Asia (Jeekel 1985; Shelley & Golovatch 2011). This does not necessarily indicate a closer relationship between the new family and the Cambalopsidae, as data on the Mesozoic distribution of the Spirostreptida is lacking.

### **The fossil record of the Spirostreptida**

The here described Electrocambalidae fam. nov. are the oldest known fossils of the order Spirostreptida. Thus, there are no other Spirostreptida fossils known from the Mesozoic, and the only known fossils of the order are *Protosilvestria sculpta* Handschin, 1944 (Cambalidae or Cambalopsidae) from the Oligocene (ca 23.03–33.0 ma) of France (Handschin 1944; Mauriès 1992) and the undescribed pseudonannolenid *Epinannolene* sp., from 20 my old Dominican amber (Santiago-Blay & Poinar 1992). Twelve specimens, four species, two genera and one family are here added to the fossil record of the Spirostreptida, all from Burmese amber dating back to the Cretaceous, ca 99 ma (Shi *et al.* 2012). These fossils are ca 70 my older than the previously oldest known Spirostreptida and narrow the gap between the estimated appearance of the order Spirostreptida and suborder Cambalidea ca 514 ma (Shelley & Golovatch 2011). The fossil record of the Juliformia, as for the Diplopoda in general, remains scarce and fragmentary, but the exceptional preservation of millipedes in Burmese amber offers the opportunity to greatly enlarge the fossil record. In the same way representatives of the other diplopod orders can be expected to be found in Burmese amber and widen our understanding of the evolution of the Diplopoda tremendously.

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