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The oldest chthonioid pseudoscorpion Arachnida: Pseudoscorpiones: Chthonioidea: Chthoniidae: A new genus and species from mid-Cretaceous Burmese amber[☆],[☆☆]

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ABSTRACT

Pseudoscorpions are an ancient lineage of arachnids but have a scarce fossil record, presumably because these animals are small (2–8 mm in body length) and live in habitats where they do not fossilize easily. This is particularly the case for one of the more basal lineages, the superfamily Chthonioidea, which are common and diverse in leaf litter habitats across the world but have only been described in the fossil record from some specimens in Baltic, Dominican and Chiapas ambers. Here, we describe and illustrate the oldest pseudoscorpion of the superfamily Chthonioidea from the mid-Cretaceous (lowermost Cenomanian, ca. 99 Mya) amber of northern Myanmar and extend the known fossil record of this diverse superfamily from the Eocene into the Cretaceous. Fragments that suggest a diverse pseudoscorpion fauna have been recorded in Myanmar (Burmese) amber but this is only the fourth pseudoscorpion fossil described from this ancient amber type. The single adult female specimen is substantially older than the next oldest fossil chthonioids, which were described from Baltic amber (ca. 44–49 Mya), and displays small but significant differences to other chthonioids, such that we describe a new genus and species, *Weygoldtiella plausus* gen. et sp. nov. The placement of the trichobothria on the chelal hand suggests it can be attributed to the family Chthoniidae, but important morphological features are obscured in the fossil which obfuscates hypotheses regarding its nearest relatives. The specimen, although imperfectly preserved, has no known Recent relatives in this area or elsewhere in the diverse chthonioid fauna, and may represent an extinct lineage. Overall, this fossil is another example of the diverse arachnid community preserved in Burmese amber that includes lineages that are now extinct here and of considerable biogeographic interest, e.g. ricinuleids, and fauna which is essentially modern, e.g. solifuges.

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1. Introduction

Members of the arachnid order Pseudoscorpiones are small (generally 2–8 mm in body length) and occur in most terrestrial ecosystems around the world, with the exception of the polar regions. With ca. 3600 described species, they represent one of the medium-diverse arachnid orders (Harvey, 2002, 2007). The current classification recognizes 27 families and more than 460 genera
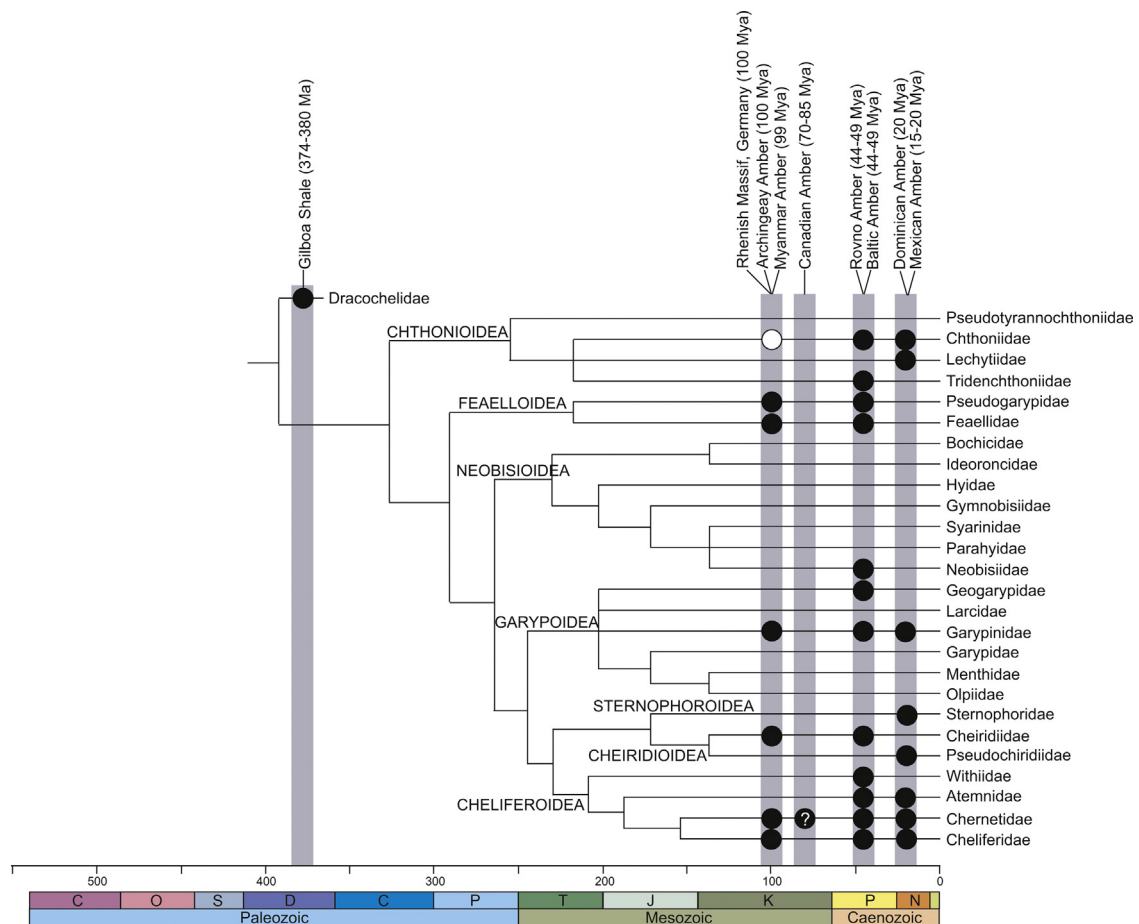
**Fig. 1.** Phylogeny of the order Pseudoscorpiones based on various sources (e.g. Harvey, 1992; Harvey et al., 2016; Judson, 2012; Murienne et al., 2008). Known fossils are depicted with circles, with *Weygoldtiella plausus* gen. et sp. nov. shown in white. The divergence dates are entirely speculative, and have not been tested analytically.

(see Harvey, 2013 and subsequent papers). Phylogenetic hypotheses regarding the relationships of pseudoscorpions suggest that the extinct Devonian family Dracochelidae is a stem-group pseudoscorpion (Judson, 2012), and that the remainder can be divided into three major clades. The superfamily Chthonioidea, a group that comprises litter or soil-dwelling and hypogean species without venom glands in their pedipalpal fingers, is normally regarded as an early-branching group of pseudoscorpions. They have been postulated as the sister-group to all other pseudoscorpions (Chamberlin, 1931), or they resolve basal to the Iocheirata, which contains the majority of species and have venom glands in one or both of their chelal fingers (Harvey, 1992; Murienne et al., 2008).

Pseudoscorpions have a sparse fossil record compared with other more commonly preserved arachnid groups such as spiders and mites, but belong to the oldest terrestrial lineages due to the presence of a stem-group pseudoscorpion, *Dracochela* Schawaller et al., 1991, from the Gilboa mudstones of New York in the USA and from the Middle Devonian (Givetian, ca. 390 Mya) (Judson, 2012; Schawaller et al., 1991). Pseudoscorpions do not fossilize easily and there is a huge gap of almost 290 million years in the fossil record, with the second-oldest fossils coming from the mid-Cretaceous amber deposits. The fossil history of these animals was reviewed recently (Harms and Dunlop, 2017) and there are currently 49 valid fossil species belonging to 16 of the 26 extant families. Pseudoscorpions represent a case of evolutionary stasis and almost all fossils can be assigned to Recent genera or families, with the exclusion of the Devonian fossils that belong to the stem-group. There is a strong bias in the fossil record towards families which reside close to the amber source, such as groups that live under tree bark.

The only known and described fossil chthonioids, a group that is common in litter-dwelling habitats around the world, are from Cainozoic (Cenozoic) amber deposits (Fig. 1), including *Chelignathus kochii* Menge, 1855, *Chthonius mengei* Beier, 1937 and *C. pristinus* Schawaller, 1978 from Eocene Baltic amber (44–49 Mya) (Beier, 1937; Koch and Berendt, 1854; Menge, 1855; Schawaller, 1978), *Pseudochthonius squamosus* Schawaller, 1980 and *Lechytia tertiaria* Schawaller, 1980 from Miocene Dominican amber (ca. 25 Mya) (Schawaller, 1980), and *Paraliochthonius miomaya* from Miocene Mexican amber (Judson, 2016). The fossil record for this group does thus not extend beyond the Eocene (Baltic amber 44–49 Mya) and there is a major gap of about 340 million years between these fossils and the oldest pseudoscorpion fossil *Dracochela* which shares with the Chthonioidea several plesiomorphic features and has been interpreted as a stem-group pseudoscorpion (Judson, 2012).

We report here on a fossilized adult female chthonioid pseudoscorpion embedded in Myanmar (Burmese) amber (also referred to as Burmite), which more than doubles the age of the superfamily Chthonioidea and the family Chthoniidae. Burmese amber is perhaps one of the most interesting amber depots because it is one of the oldest [ca. 99 Mya, see also Shi et al. (2012)] and contains rich assemblages of arthropods (Grimaldi et al., 2002), including several arachnid orders (Selden and Ren, 2017). Fossil pseudoscorpions from this amber were initially described in the early 20th century (Cockerell, , 1920) but there has been a long gap and only recently have more pseudoscorpions been described including the enigmatic *Protofeaella peetersae* Henderickx, 2016 (Henderickx and Boone, 2016) which highlights some interesting features of character evolution within another ancient superfamily, the Feael-
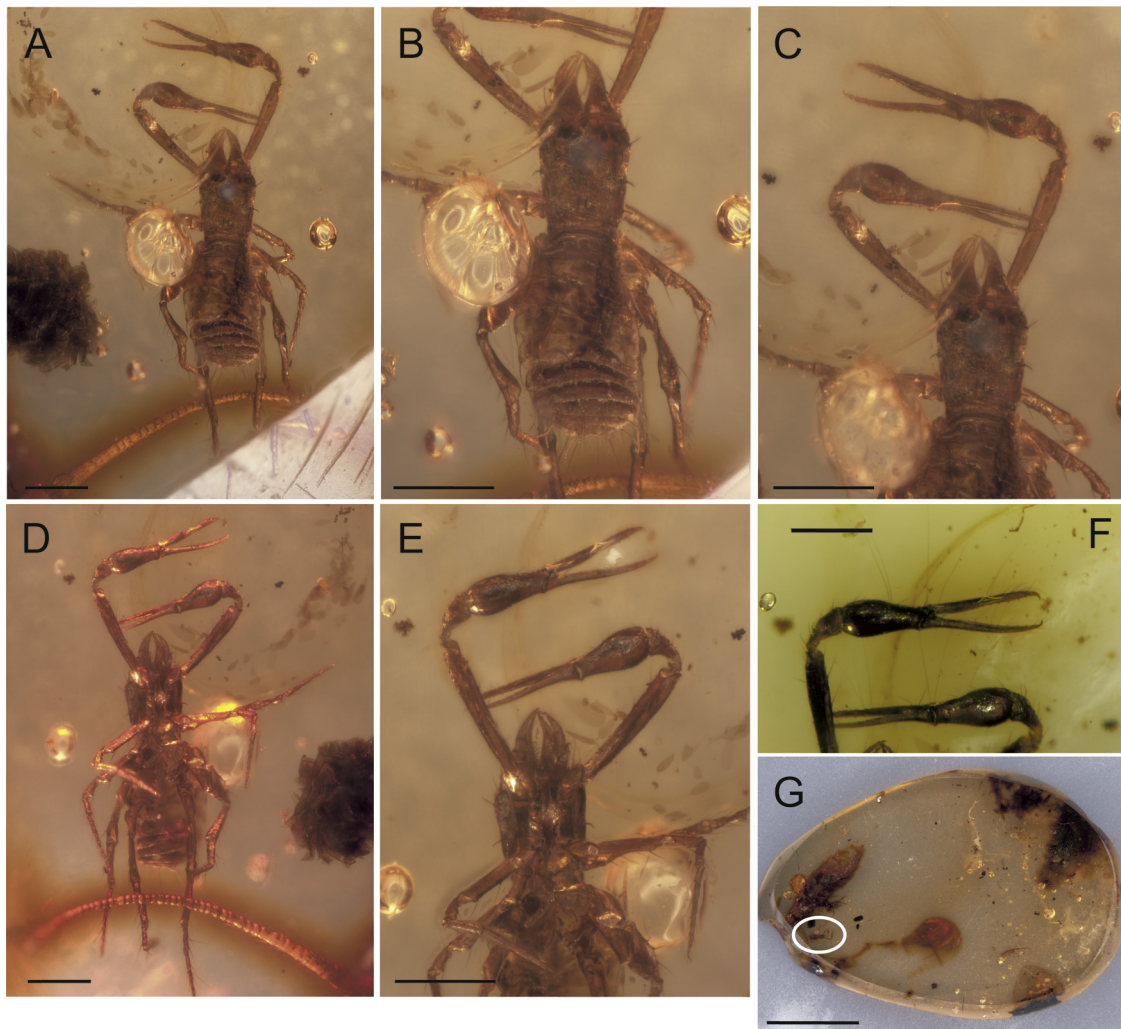
Fig. 2. Images of the female holotype of *Weygoldtiella plausus* gen. et sp. nov.: A. Dorsal view; B. Body, dorsal view; C. Cephalothorax and pedipalps, dorsal view; D. Ventral view; E. Cephalothorax and pedipalps, ventral view; F. Pedipalps, ventral view; G. The entire piece of amber with the pseudoscorpion highlighted. Scale lines = 0.25 mm (Figs A–E), 0.2 mm (Fig. F), 5 mm (Fig. G).

loidea (Judson, 2017). Many more fragments of pseudoscorpions in Burmese amber have been noted over the years (e.g. Xia et al., 2015) but have not been described. In fact, the presence of Chthonioidea in Burmese amber was first noted by Judson (2000) but have not been formally documented or described. The discovery of a more complete fossil allows for a first description of chthoniids from Burmese amber and extends the known fossil range of this lineage by more than 45 million years from the Eocene to the mid-Cretaceous.

Three other pseudoscorpions have been described from Burmese amber (Harms and Dunlop, 2017; Selden and Ren, 2017) and all can be attributed to established families: *Electrobisium acutum* Cockerell, 1917 in the family Cheiridiidae, see Judson (2000); *Amblyolpium burmiticum* (Cockerell, 1920) in the family Garypinidae, see Judson (1997) and *Protofeaella peetersae* Henderickx and Boone, 2016 in the family Feaellidae, see Henderickx and Boone (2016) and Judson (2017). The only other named Cretaceous pseudoscorpion is *Heurtaultia rossiorum* Judson, 2009 from Lower Cretaceous amber collected in Archingeay-Les Nouillers, France (Judson, 2009), but other unidentified pseudoscorpions from Lebanese, Álava, New Jersey and Canadian ambers have been mentioned or illustrated in several publications (e.g. Delclòs et al., 2007; Grimaldi, 1996; Grimaldi et al., 2002; Judson, 2017; Schawaller, 1991; Whalley, 1980).

The aim in this paper is to describe the fossil chthonioid from Burmese amber and to assess its taxonomic position. Although it can be assigned to the family Chthoniidae, there are sufficient morphological differences to postulate that it is sufficiently different from all other Chthoniidae in this region and warrants the description of a new, monotypic genus. However, we are unable to identify a close relative among the Holocene fauna and it appears to represent an extinct lineage.

2. Materials and methods

The fossil treated in this study is included in a small piece of amber from the amber mine in the Hukawng Valley in northern Myanmar (see map in Kania et al., 2015). The age of the amber has been estimated to a maximum of 98.79 ± 0.62 Mya using U–Pb zircon dating (Shi et al., 2012) and the site was close to a marine shore that experienced nearby volcanic activity (Ross et al., 2010; Shi et al., 2012). The piece of amber is oval in shape, 19.5 mm long and 13 mm wide, and has been polished on both faces to near the dorsal and ventral surfaces of the pseudoscorpion (Fig. 2G). The amber possesses several other inclusions including plant debris and some isolated insect remains such as a leg and an antenna, as well as two air bubbles next to the specimen. These intrusions do not,
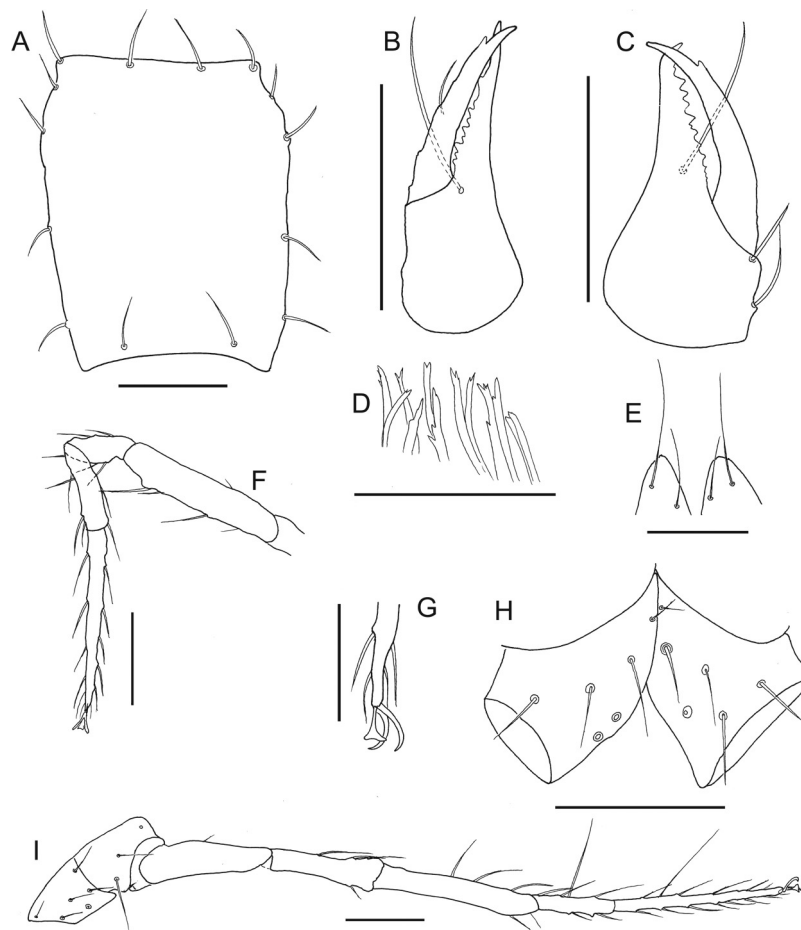
Fig. 3. Illustrations of the female holotype of *Weygoldtiella plausus* gen. et sp. nov.: A. Carapace, dorsal view; B. Right chelicera, ventral view; B. Left chelicera, ventral view; D. Left rallum, lateral view; E. Distal setae of manducatory process; F. Right leg I, lateral view; G. Tip of left tarsus I, lateral view; H. Coxae of fourth pair of legs, ventral view; I. Left leg IV, ventral view. Scale lines = 0.1 mm (Figs A–C, F–I), 0.05 mm (Figs D, I).

however, significantly impede the view of any morphological features. Many regions of the specimen, such as the chela, chelicerae, posterior coxae, abdomen and legs are relatively clear and easy to observe, but others are opaque and thus render some structures difficult to discern. This is particularly true of the cephalothorax where the carapace and the coxal region are obscured. Indeed, the coxae are folded inwards and important morphological features are obscured (see below).

The specimen is lodged in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNU) and was examined with a Leica MZ16A dissecting microscope and an Olympus BH–2 compound microscope, and illustrated with the aid of a drawing tube. Whole body images were taken with a digital camera attached to the MZ16 using Leica Automontage version 3.7.0 software. Measurements were taken at the highest possible magnification using an ocular graticule. Terminology and mensuration largely follow Chamberlin (1931), with the exception of the nomenclature of the pedipalps, legs and with some minor modifications to the terminology of the trichobothria (Harvey, 1992), chelicera (Judson, 2007) and faces of the appendages (Harvey et al., 2012).

Synchrotron transmission X-ray microscope (TXM) at BL01B1 beamline of the Taiwan Light Source (TLS) in Hsinchu, Taiwan was used for providing high-resolution X-ray photographs in this study. TXM had been demonstrated to reveal more detail features of fossils than either high-resolution X-ray micro-CT or standard optical microscopy (Wang et al., 2017; Wang et al., 2015). These fine features can provide much more meaningful information about the fossils. A superconducting wavelength shifter source is used for providing a photon flux of 4×10^{11} photons s^{-1} (0.1% bw)$^{-1}$ in the energy range of 5–20 keV in this beamline. A monochromator utilizing a pair of Ge(111) crystals selected monochromatic X-rays with an energy from 8 to 11 keV. The image of the specimen was magnified using a Fresnel zone plate, which provides about 60 nm spatial resolution. A Zernike phase ring installed at the back focal plane of the zone plate was used for performing phase contrast images for imaging of low X-ray absorption materials. Optical microscopes are the most popular tools for observing fossils embedded inside amber, however, visible light often cannot pass through the fossils. This method restricts the observation to part of the specimen surface; some fine features of specimens may be blocked by the body itself that cannot be observed through amber. We use TXM, which utilized high-penetration hard X-ray, to obtained phase contrast X-ray images of the pseudoscorpion embedded inside amber in this work to prevent some of the above disadvantages. The image contrast of the specimen's chitinous features was increased using the phase contrast mode of TXM, even though the absorption coefficient of chitin is very low for hard X-ray. The halo effect (features with bright ring artifact) showed in phase contrast images can further increase the visibility of specimen fine structures. By rotating the specimen observation angles, three-dimensional spatial relations between fine features were identified. The field of view of the TXM is $15 \times 15 \ \mu m^2$. A millimeter-scale field of view was produced by stitching images from a series of observation positions.

3. Systematics

Order Pseudoscorpiones de Geer, 1778
Superfamily Chthonioidea Daday, 1889
Family Chthoniidae Daday, 1889
Subfamily Chthoniinae Daday, 1889
Genus *Weygoldtiella* gen. nov
ZooBank LSID: urn:lsid:zoobank.org:act:E03F5641-14E3-4868-B1A6-18B870EFCA4A

4. Type species

4.1. Weygoldtiella plausus *sp. nov*

4.1.1. Etymology

The generic epithet is to honour the German arachnologist, Dr Peter Weygoldt for his outstanding papers and books on pseudoscorpion embryology and development in the 1960s and 1970s.

4.1.2. Diagnosis

The genus *Weygoldtiella* differs from all other chthonioid genera in four characters: the teeth of both chelal fingers are mostly diastemodentate, but those located on the basal portion of both fingers are juxtadentate and on a slightly raised keel (Fig. 4B, 4C); the swelling on the chelal hand where the movable finger inserts (Fig. 4C); the elongated chelicerae (Figs. 3B, C); and the medial setae of the manducatory process are about half the length of the lateral setae (Fig. 3E). The genus further differs from other chthoniid genera that are present in this area today, in particular *Lagynochthonius* and T*yrannochthonius* by the position of the medial setae in the anterior setal row of the carapace which are widely spaced in *Weygoldtiella* gen. nov and close to the mid-line in *Lagynochthonius* and T*yrannochthonius*.

4.1.3. Description

Chelicera (Fig. 3A, B): rather elongated, slender; with unknown number of setae on hand, but all visible setae acuminate; movable finger with 1 submedial seta (*gls*); rallum of 12 bipinnate blades arranged in 2 rows (Fig. 3D); lamina exterior absent; galea subdistal.

Pedipalp (Fig. 4A–C): femur long and slender. Patella calyciform. Fixed chelal finger with 8 trichobothria, plus duplex trichobothria (*dt*); movable chelal finger with 4 trichobothria; *eb*, *esb* and *ist* situated at base of fixed finger; *est* and *it* situated in distal half of fixed finger, much closer to *et* than to *ist*; *it* slightly distal to *est*; trichobothria *ib* and *isb* situated on dorsum of hand, slightly distal of middle; *sb*, *b* and *t* situated close to each other slightly distal to middle of movable finger; *b* closer to *t* than to *st*; *st* situated near base of finger; all trichobothria filiform and acuminate. Dorsum of chelal hand and fixed finger without curved microsetae (presumed chemosensory setae); chelal hand and fingers without spine-like setae; chelal hand flask-shaped and with swelling where the movable finger inserts (Fig. 4A–C). Movable finger without large internal apodeme. Venom apparatus absent in both chelal fingers. Chelal teeth: fixed finger with several diastemodentate teeth, plus smaller, low teeth situated on a low keel; movable finger with several diastemodentate teeth, plus smaller, low teeth.

Cephalothorax: carapace (Fig. 3A) slightly longer than wide, tapering slightly posteriorly; eyes or eyespots not visible; with at least 7 pairs of setae arranged 6: 2: 2: 4; number of lyrifissures not determined; presence or absence of epistome not determined; antero-median pair of setae not closely appressed to mid-line. Manducatory process with 2 setae, both acuminate, lateral seta longer than medial seta.
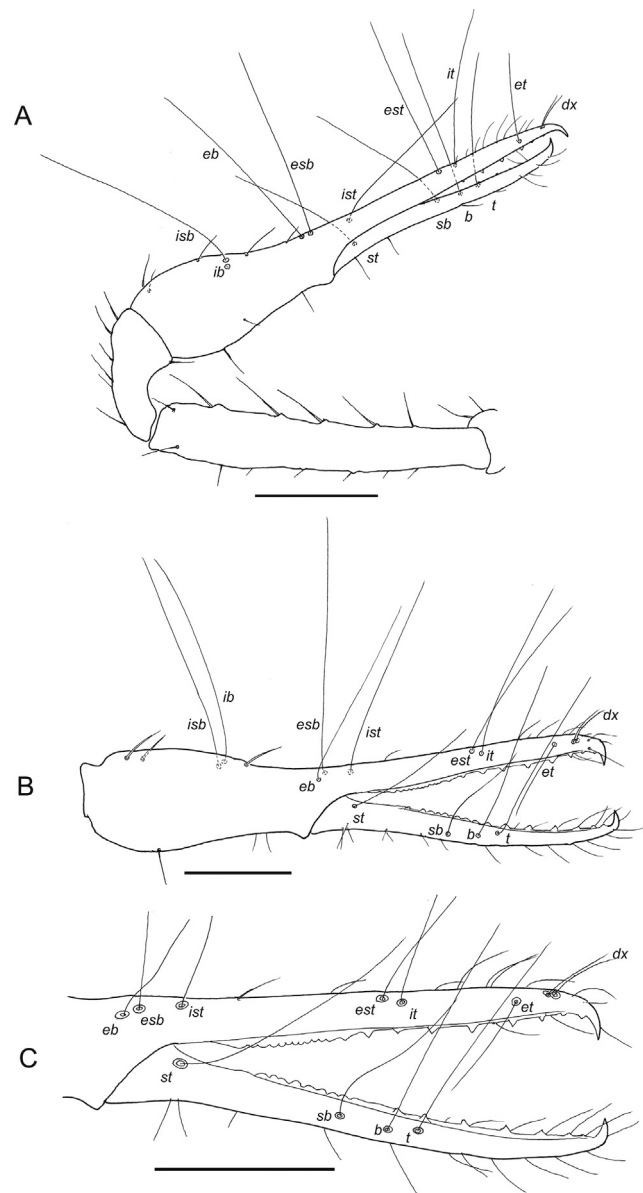

Fig. 4. Illustrations of the female holotype of *Weygoldtiella plausus* gen. et sp. nov.: A. Left pedipalp; B. Right chela, lateral view; C. Right chelal fingers, lateral view. Scale lines = 0.25 mm (Fig. A), 0.1 mm (Figs B, C).

Abdomen (Fig. 2B): pleural membrane papillostriate. Tergites and sternites without median suture line; each median tergite with 4 setae. Spiracles not visible.

Genitalia: not visible.

Legs (Fig. 3F, I): heterotarsate, i.e. metatarsi and tarsi of anterior legs fused; femora I and II much longer than patellae I and II; femora III and IV shorter than patellae III and IV; metatarsi III and IV with long sub-basal tactile seta; tarsi III and IV with long sub-basal tactile seta; arolium shorter than claws; claws simple, not modified.

4.1.4. Remarks on systematic position

The relationships of the Chthonioidea are currently unresolved and will require further research to achieve a taxonomic arrangement that reflects the phylogeny of the group. The Chthonioidea currently comprise four families: Chthoniidae, Lechytiidae, Pseudotyrannochthoniidae and Tridenchthoniidae (Harvey, 2013). While the Pseudotyrannochthoniidae clearly represent the sister-group to the remaining chthonioids (Harvey et al., 2016; Murienne et al.,
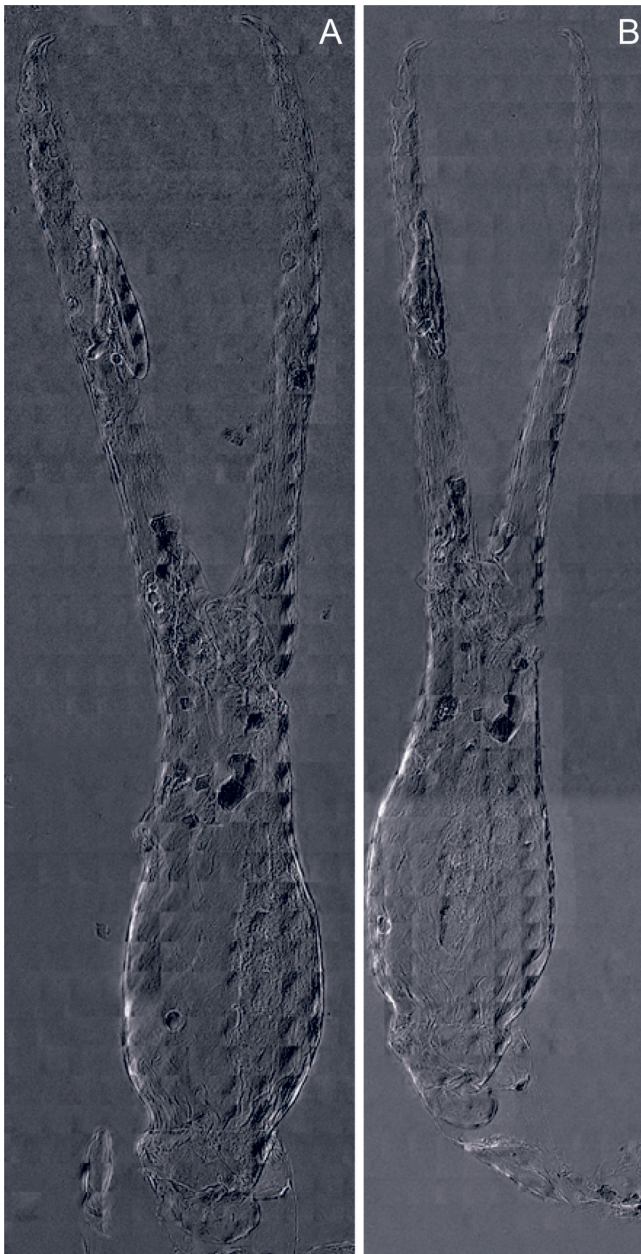
Fig. 5. Nano-CT scan images of the right chela of the female holotype of *Weygoldtiella plausus* gen. et sp. nov.: A. Lateral view; B. Lateral view, with 30° rotation.

2008), the available molecular evidence suggests that the families Lechytiidae and Tridenchthoniidae are subsets of the Chthoniidae and should not be recognized as distinct families. These data, albeit based on few exemplars, found that *Lechytia* Balzan, 1892 (Lechytiidae) and *Anaulacodithella* Beier, 1944 (Tridenchthoniidae) formed a clade with the chthoniids *Sathrochthonius* Chamberlin, 1962 and *Pseudochthonius* Balzan, 1892. This result is partially supported by some morphological features, in particular the location of trichobothria *ib* and *isb* near the basal edge of the chelal hand in Lechytiidae, Tridenchthoniidae and *Sathrochthonius*, as well as in *Sathrochthoniella* Beier, 1967 and *Congochthonius* Beier, 1959 (Beier, 1959, 1967) for which sequence data are currently unavailable. In all other Chthoniidae, including *Pseudochthonius*, these trichobothria are situated dorso-medially on the hand, and in all Pseudotyrannochthoniidae they are situated dorso-distally, a seemingly plesiomorphic feature which Pseudotyrannochthoniidae shares with *Dracochela* (Judson, 2012). The dorso-medial

position of *ib* and *isb* is also found in the *Weygoldtiella* gen. nov. and we therefore attribute it to the family Chthoniidae, regardless of whether Lechytiidae and Tridenchthoniidae need to be synonymized.

We also stress that none of the characters used to diagnose this genus are autapomorphic in their own right or carry strong phylogenetic signal. Some of these characters, e.g. pedipalp shape, have been shown to exhibit homoplasy (e.g. Harrison et al., 2014). However, the combination of characters delineates the fossil from all Holocene chthonioids in south-east Asia and highlights a unique morphology that defines this fossil taxon and delineates it from all other fossil pseudoscorpions and the Holocene fauna. It is unclear whether some of the diagnostic characters are autapomorphic or plesiomorphic, because a detailed morphological study and phylogenetic hypothesis of chthoniids is still lacking.

4.1.5. Remarks on preservation

It is unfortunate that some morphological features of major significance in chthonioid systematics are not visible in the specimen, particularly in the coxal region and the genitalia which are obscured and collapsed medially such that the coxal spines and coxal tubercle are not visible. The placement and morphology of coxal spines is a highly significant feature in chthonioid systematics, and help to define certain groups. For example, they are present on coxa I in all Pseudotyrannochthoniidae and the chthoniid genera *Apochthonius* Chamberlin, 1929c and *Kleptochthonius* Chamberlin, 1949 (e.g. Chamberlin, 1929b; Harms and Harvey, 2013; Malcolm and Chamberlin, 1961); on coxae I and II in all Tridenchthoniidae and the chthoniid genus *Aphrastochthonius* Chamberlin, 1962 and most *Pseudochthonius* (e.g. Chamberlin, 1929a, 1962; Chamberlin and Chamberlin, 1945; Mahnert, 1979; Muchmore, 1972; Wagenaar-Hummelinck, 1948); on coxa II in most Chthoniidae (*Austrochthonius* Chamberlin, 1929c, *Chiliochthonius* Vitali-di Castri, 1976, *Congochthonius*, *Drepanochthonius* Beier, 1964, *Francochthonius* Vitali-di Castri, 1976, *Lagynochthonius* Beier, 1951, *Malcolmochthonius* Benedict, 1978, *Mexichthonius* Muchmore, 1975, *Mundochthonius* Chamberlin, 1929c, *Paraliochthonius* Beier, 1956, *Sathrochthoniella*, *Troglochthonius* Beier, 1939, *Tyrannochthoniella* Beier, 1966, *Tyrannochthonius* Chamberlin, 1929c and *Vulcanochthonius* Muchmore, 2000) (Beier, 1939, 1959; e.g. Beier, 1964, 1967; Chamberlin, 1929c; Edward and Harvey, 2008; Muchmore, 2000; Vitali-di Castri, 1976); on coxa II and III in the chthoniid genera *Cantabrochthonius* Zaragoza, 2017, *Chthonius* C.L. Koch, 1843, *Ephippiochthonius* Beier, 1930, *Globochthonius* Beier, 1931, *Hesperochthonius* Muchmore, 1968, *Microchthonius* Hadži, 1933, *Neochthonius* Chamberlin, 1929c, *Occidenchthonius* Zaragoza, 2017, and *Spelyngochthonius* Beier, 1955 (e.g. Zaragoza, 2017); on coxae I, II and III in *Caribchthonius* Muchmore, 1976 and some *Pseudochthonius* (Muchmore, 1976, 1977, 1986); replaced by a hispid area on coxa II in *Sathrochthonius* (e.g. Chamberlin, 1962); or absent in all Lechytiidae (e.g. Muchmore, 1975). The inability to observe the coxal spines in *Weygoldtiella plausus* gen. et sp. nov. hampers our efforts to identity its potential relatives, and further fossils from the Hukawng Valley site will be necessary to ascertain the location and morphology of the spines.

4.2. Weygoldtiella plausus *sp. nov*

Figs. 2–5

ZooBank LSID: urn:lsid:zoobank.org:act:B256BAE4-FFC8-4C1D-B4E4-57C12984C1FB

4.2.1. Etymology

This species is named in honour of Peter Weygoldt's extraordinary scientific contributions [*plausus*, Latin, clap the hands in praise; see Brown (1956)].

4.2.2. Material examined

Holotype female, in piece of Burmese amber collected from the Hukawng Valley, Kachin State, Myanmar (CNU, CNU-PSE-MA2016001). Lowermost Cenomanian, the mid-Cretaceous.

4.2.3. Diagnosis

As for genus.

4.2.4. Description

Chelicera (Fig. 3B, C): rather elongate, slender; hand with unknown number of setae, those setae that are visible are acuminate; movable finger with 1 sub-medial seta; fixed finger with 12 juxtadentate teeth, the basal teeth becoming progressively smaller; movable finger with ca. 8 small juxtadentate teeth; galea small and cylindrical, located sub-distally; rallum consisting of 12 bipinnate blades arranged in 2 rows; scaly projections present on lateral edges of hand and base of the movable finger.

Pedipalp (Fig. 4A): all setae acuminate; femur 6.36, patella 2.08, chela 5.10, hand 1.95× longer than broad; movable finger 1.32× longer than hand, without large basal apodeme. Patella calyciform, with lyrisfissures not visible. Fixed chelal finger with 8 trichobothria, plus shorter duplex trichobothria (*dt*); movable chelal finger with 4 trichobothria (Fig. 4A–C); *eb*, *esb* and *ist* situated at base of fixed finger; *est* and *it* situated about one areolar diameter apart in distal half of fixed finger, much closer to *et* than to *ist*; *et* situated distally, adjacent to *dt*; *it* slightly distal to *est*; trichobothria *ib* and *isb* situated close together on dorsum of hand, slightly distal of middle; *sb*, *b* and *t* situated close to each other slightly distal to middle of movable finger; *b* closer to *t* than to *st*; *st* situated near base of finger; all trichobothria filiform and acuminate. Dorsum of chelal hand and fixed finger without microsetae (presumed chemosensory setae); chelal hand and fingers without spine-like setae; chelal hand with pronounced swelling where movable finger inserts (Fig. 4A–C). Venom apparatus absent. Chelal teeth: fixed finger with 9 diastemodentate, triangular teeth, plus 12 smaller, low teeth situated on basal keel; movable finger with 6 diastemodentate, triangular teeth, plus 11 smaller, basal, low teeth.

Cephalothorax: carapace (Fig. 3A) ca. 1.18× longer than broad, slightly constricted postero-laterally; eyes or eyespots not visible; epistome not visible; with at least 7 pairs of setae arranged 6: 2: 2: 4; the pre-ocular seta slightly shorter than other setae in anterior row; antero-median seta not situated at base of epistome (Fig. 3A). Manducatory process with 2 acuminate distal setae, lateral seta longer than medial seta (Fig. 3E); coxa IV with 5 setae (Fig. 3H); presence or absence of coxal spines not determined; presence or absence of intercoxal tubercle not determined. Lyriform organs not visible.

Abdomen: pleural membrane papillostriate. Tergites and sternites without median suture line; setae acuminate; posterior segments with several longer setae.

Genitalia: not visible in detail, but not heavily sclerotized.

Legs: femora I and II longer than patellae I and II; metatarsi III and IV with long sub-basal tactile seta; tarsi III and IV with long sub-basal tactile seta; heterotarsate; subterminal tarsal setae not distally serrate; arolium shorter than claws, not divided; claws simple.

Dimensions (mm): Body length ca. 0.785. Pedipalps: femur 0.350/0.055, patella 0.135/0.065, chela 0.485/0.095, hand length 0.185, movable finger length 0.245. Carapace ca. 0.260/0.220.

4.2.5. Remarks

The specimen is interpreted to be an adult female, as it possess the full trichobothrial complement typical of most adult pseudoscorpions (e.g. Chamberlin, 1931; Harvey, 1992; Vachon, 1964) and lacks any obvious male genitalia in the abdominal region. As adult male chthonioids have large internal sclerites and a deep longitudinal cleft in sternite III (e.g. Chamberlin, 1931), it is safe to assume it is a female.

As mentioned earlier, the fossil is imperfectly preserved and certain details are not visible. Additionally, the fossil seems to have several raised areas that appear to be accretions rather than parts of the specimen. Several conical lumps occur on the posterior edges of both coxae of the fourth pair of legs, with five on the left coxa and only one of the left coxa. As they are arranged asymmetrically and are differently coloured to the pseudoscorpion cuticle (Fig. 2), we infer that they are accretions which are typical for many fossils in Burmese amber which has been reformed and thermodynamically altered. The chelae bear similar raised mounds but they clearly represent some sort of resin or other deposit accreted onto the surface of the cuticle (Figs. 2, 5A).

5. Discussion

5.1. Evolution & systematics

The Chthonioidea currently comprise four families: the Chthoniidae, Lechytiidae, Tridenchthoniidae and Pseudotyrannochthoniidae. Chthoniidae is currently known from five named fossil species that were described from Baltic, Dominican and Mexican ambers, whereas the fossil record for Lechytiidae and Tridenchthoniidae is sparse and comprises one fossil species from Dominican and Baltic ambers, respectively (Harms and Dunlop, 2017). Pseudotyrannochthoniidae is not known from any fossils, although this group is presumably Pangaean in origin and present on five continents (Harms and Harvey, 2013). We provide a detailed description for the eighth chthoniid fossil to date, which not only extends the fossil record for this family by more than 45 million years but also provides a record outside the Americas and the Palaearctic. The new fossil cannot add major insights into the evolution of the chthonioid pseudoscorpions but offers a unique combination of characters. Importantly, this is the first chthoniid pseudoscorpion that differs morphologically from Holocene taxa. The two described species of *Chthonius* from Baltic amber (Beier, 1937; Schawaller, 1978) and *Lechytia tertiaria* (Schawaller 1980) from Dominican amber are extremely similar to Holocene forms and points to a fauna that has changed little over time. The present fossil is the first that can potentially aid discussions about character polarity and evolution once there is a detailed morphological study on this group, and once the Holocene fauna of Myanmar and adjacent areas is documented in more detail. One should bear in mind that while other south-east Asian countries are relatively well explored, the Holocene pseudoscorpion fauna of Myanmar is still largely unexplored and that there are only 14 described pseudoscorpion species (Harvey, 2013, 2016), which is doubtlessly due to a lack of detailed studies. Nearby countries such as Malaysia with 38 species and Vietnam with 63 species (Harvey, 2013) suggests that the Myanmar fauna is not completely known. It is not clear at present if *Weygoldtiella* is an extinct genus, belongs to a lineage that still occurs in south-east Asia, or belongs to a group that remains undetected. New genera are not commonly encountered in this region, but the recent discovery of cave-dwelling feaellid pseudoscorpions in Vietnam and Thailand that were previously only known in this area from Burmese amber (Judson, 2017) and a new south-east Asian genus of Ideoroncidae (Harvey, 2016), shows that new taxa continue to be detected. Certainly, this new record differs

significantly from other south-east Asian chthoniid genera, such as *Lagynochthonius* and *Tyrannochthonius*, which represents a new facet of chthoniid morphological diversity. Additional specimens will be needed to further evaluate the status of important characters, such as the coxal spines, genitalia and the presence or absence of an intercoxal tubercle.

5.2. Relationships

Weygoldtiella plausus is unusual among chthonioids by the morphology of the chelal teeth of both chelal fingers, which are clearly diastemodentate in the distal two-thirds, but are juxtadentate basally (Fig. 4C). Furthermore, the basal teeth on the fixed finger are raised on a slight keel. We are not aware of any chthonioid with teeth arranged in this way, but perhaps the most similar are the species of *Hesperochthonius*, where the basal teeth are also smaller than the distal teeth (Muchmore, 1968; Zaragoza, 2017). It is also unusual with the presence of a pronounced swelling on the chelal hand where the movable finger inserts (Fig. 4A–C). The third unusual feature is the relative sizes of the paired setae located on the distal end of the manducatory process. The medial setae of *Weygoldtiella plausus* are about half the length of the lateral setae (Fig. 3E), whereas in most other chthonioids the setae are about the same length. The only other character state is where the lateral setae are about one-third the length of the medial setae, which occurs in all Pseudotyrannochthoniidae (e.g. Chamberlin, 1962; Harms and Harvey, 2013; Sakayori, 1999, 2000, 2002; Sato, 1984), as well as in the North American chthoniid genus *Aphrastochthonius* (Muchmore, 1972). This character state appears to be independently derived in these two clades, as the morphology of the lateral seta is different, being straight in Pseudotyrannochthoniidae and curved in *Aphrastochthonius*. The medial seta of *Weygoldtiella plausus* is also straight (Fig. 3E).

Other morphological features, such as the papillostriate pleural membrane and the heterotarsate legs (Fig. 3F, I), are typical chthonioid character states. The state of preservation of the specimen is insufficient to observe the precise details of the setal and lyrifissure patterns that have been recently enumerated by Zaragoza (2017).

5.3. Preservation

The specimen shows little sign of struggling once entombed in the amber. In particular, the pedipalps and legs are in relatively normal positions for a dead pseudoscorpion (Fig. 2), and there is no indication that they are twisted after wriggling in wet amber. Also, the trichobothria of both chelae have the hairs intact and lying normally at right angles to the cuticular surface (Figs. 2F, 4A–C). Both of these aspects may suggest that the specimen was already dead when covered by or falling into the amber.

5.4. Burmese amber pseudoscorpion fauna

The Hukawng Valley is one of the oldest deposits for invertebrates in amber and it is becoming obvious that the pseudoscorpion fauna of Burmese amber is both rich in species and diverse at the systematic level. The pseudoscorpion families that have been previously recorded include "typical" bark-dwelling fauna such as Cheiridiidae, Chernetidae and Garypinidae (Harms and Dunlop, 2017; Xia et al., 2015) but also groups that are typically ground or soil-dwelling fauna, such as Feaellidae (Henderickx and Boone, 2016) and now Chthoniidae. More groups have recently been identified from this amber such as Atemnidae, Hyidae and Ideoroncidae (Harvey, unpublished data) and the detailed study of this material will provide either the first fossil record of these families, or extend the known fossil records for others by millions of years (Fig. 1). The pseudoscorpions found so far in Burmese amber offer

few insights into character evolution as so many can be attributed to crown-group taxa. Similar patterns can be detected in other arachnid faunas, such as solifuges (Bartel et al., 2016; Dunlop et al., 2015) and ticks (Chitimia-Dobler et al., 2017), where fossils are often modern-looking but raise interesting questions of biogeography. Other groups, such as ricinuleids, are only known from the Americas and Africa in the Holocene fauna but occur with astonishing diversity and abundance in Burmese amber (e.g. Wunderlich, 2012) and must have become extinct since the Cretaceous. Overall, the Burmese amber arachnids offer a unique window into the evolution of arachnids during the Cretaceous and highlights a fauna that is already modern in parts but also comprises fossils of unique biogeographic value or the ability to untangle the complex patterns of arachnid evolution at the morphological level. *Weygoldtiella* is a fossil of the latter kind.

5.5. Biogeography

The Burmese amber site is considered to belong to a land-mass known as the West Burma terrane, which rifted from northwest Australia during the Late Jurassic (156 Mya) and drifted northwards, finally colliding with the Eurasian marginal Sibumasu terrane at around 80 Ma (Heine and Müller, 2005; Seton et al., 2012). The ecosystem bearing the fauna now found in the amber was living at the time on an island which had separated from Australia, and the fauna may represent an early off-shoot of a typical Gondwanan fauna. An alternative hypothesis, that the West Burma terrane formed part of a continent which separated from Australia in the Devonian, and collided with Eurasia by the Jurassic, was proposed by Metcalfe (2013). This scenario suggests that the arachnid fauna dispersed onto the West Burma terrane from Eurasia sometime between the Jurassic and the mid-Cretaceous. While it would be desirable to use *Weygoldtiella plausus* to test these competing hypotheses, our inability to observe important morphological characters (see above) precludes an assessment of its affinities and, hence, an appraisal of its biogeographic relationships.

5.6. Palaeoecology

Chthonioid pseudoscorpions are common inhabitants of leaf litter and upper soil environments in many parts of the world, often in high densities, but also occur in subterranean environments and occasionally on tree trunks, in moss and under bark. The modern Holocene chthonioid fauna of south-east Asia consists of only five genera: *Lagynochthonius* and *Tyrannochthonius* of the Chthoniidae, *Lechytia* of the Lechytiidae, and *Compsaditha* and *Ditha* of the Tridenchthoniidae (Harvey, 2013). The new fossil does not appear to be closely related to any of these genera, as trichobothria *ib* and *isb* are located medially on the hand (basally in *Lechytia*, *Compsaditha* and *Ditha*) and the chelal hand lacks dorsal curved microsetae which are present in *Lagynochthonius* and *Tyrannochthonius*. As the south-east Asian chthonioid fauna is relatively well-known, at least at the generic level, we surmise that the new genus *Weygoldtiella* did not survive into the Holocene or remains undetected in the region. There is no evidence to suggest that the present species had an ecology that differed from other chthonioids and it was probably living in moist leaf litter, potentially near bark, and was non-phoretic. The structure of the chelicerae suggests that it was an ambush-hunter and fed on small arthropods, although the chelicerae are longer than in other chthoniids and may suggest that it could handle larger prey.

6. Concluding remarks

The discovery and documentation of a chthonioid pseudoscorpion in Burmese amber doubles the known age of the superfamily

Chthonioidea from the Eocene (44–49 Mya) to the lowermost Cenomanian (99 Mya), even though unidentified chthonioids from Burmese amber have been previously mentioned in the literature (Judson, 2000). The specimen described here as *Weygoldtiella plausus* provides a valuable data point for calibrating phylogenetic analyses of pseudoscorpions. It seems to represent a clade that is not represented in the Holocene fauna, and is quite different to all modern chthonioid genera found locally in south-east Asia.

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