

The second chthonioid pseudoscorpion (Pseudoscorpiones: Chthoniidae) from mid-Cretaceous Burmese amber: a new genus with unique morphological features and potential Gondwanan affinities

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Abstract. Pseudoscorpions are amongst the oldest terrestrial lineages but there is a major gap in the fossil record between the oldest fossils from the Devonian (ca. 385 million years ago) and rich fossil communities in amber that mostly originate from the Eocene of Europe. Burmese/Myanmar amber (or Burmite) from the middle Cretaceous preserves a diverse community of pseudoscorpions but these remain poorly documented, despite their exceptional preservation and potential to offer unique insights into evolutionary history. Here we describe a new genus and species of pseudoscorpion with a unique morphology of the chelicerae, *Prionochthonius burmiticus* gen. et sp. nov., from Burmese amber. Although some key characters remain obscure, the fossil can be confidently attributed to the basal pseudoscorpion family Chthoniidae, but it cannot be assigned to any extant or other fossil genus. Based on trichobothria patterns, it is most similar to extant genera that are found only in the Southern Hemisphere; findings that are in line with previous studies suggesting Gondwanan origins for at least some of the Burmese amber invertebrates. The fossil provides further evidence for a diverse community of litter- and soil-dwelling pseudoscorpions in the Late Cretaceous that comprises many extinct genera but represents many of the modern families. It also suggests that the diversification of chthoniid pseudoscorpions occurred well before the middle Cretaceous, and that the principle gestalt of its members has changed relatively little over time.

Keywords: Arachnida, Chelonethida, systematics, taxonomy

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Pseudoscorpions are amongst the oldest terrestrial lineages and have a fossil record that extends back to the Devonian, some 385 million years ago (Ma) (Schawaller et al. 1991; Harms & Dunlop 2017). These small (generally 2–8 mm in body length) arthropods occur in most terrestrial ecosystems across the world and are easily recognised by their pincer-shaped pedipalps, but differ from the larger “true” scorpions because they lack the venomous sting (telson) and tail (metasoma). Roughly 3600 species of pseudoscorpions have been described to date, which makes them one of the medium-diverse arachnid orders alongside the harvestmen (Opiliones) and camel spiders (Solifugae). The current classification recognizes 25 Recent families that fall into three major subordinal clades: the Heterosphyronida for basal pseudoscorpions that lack venom glands in the pedipalps and occur primarily in leaf litter habitats and caves; the Atoposphyronida for two families with lobes on the carapace and dorsoventrally flattened bodies; and the Iocheirata for all pseudoscorpions with venom glands (Benavides et al. 2019). The latter group also occurs in habitats other than leaf litter or soil, such as tree bark or under rocks, and many species have noteworthy biological traits such as complex mating dances and phoresy as a means of dispersal. Recent dated molecular analyses have suggested that the present-day families diverged sometime in the Mesozoic, suggesting that pseudoscorpions are a prime example of relative morphological stasis over long periods of time (Harms & Dunlop 2017; Benavides et al. 2019).

Despite their atiquity, pseudoscorpions have a sparse fossil record and there is a gap of more than 290 million years between the Devonian fossils from the famous Gilboa Formation in New York (Schawaller et al. 1991) and fossils in various amber deposits from the Lower Cretaceous. The gap may be due to small body size and presence in concealed habitats that render fossilisation processes rather unlikely, such as leaf litter or soil, but we do know that the oldest pseudoscorpion *Dracochela deprehendor* Schawaller, Shear & Bonamo, 1991 from Gilboa was a ground-dwelling pseudoscorpion without venom glands that shared all the autapomorphic features of this order, but lacked the silk-spinning gland on the mouthparts that is possessed by all modern-day pseudoscorpions (Judson 2012). When venom- and silk glands evolved remains unclear, as is the origin of many of the complex biologies and ecologies found in some taxa.

The fossil history of pseudoscorpions was recently reviewed (Harms & Dunlop 2017) and there are 50 valid species belonging to 14 of the 25 extant families. All except one fossil species have been described from amber sources and there is a strong bias in the fossil record towards families which reside close to tree bark or roots, a source of resin. The fossil record for the litter-dwelling fauna is much scarcer and in the basal suborder Heterosphyronida (comprising the single superfamily Chthonioidea) only a handful of species have been documented, primarily from European Baltic amber that is either of early to middle Eocene (e.g., Wolfe et al. 2016) or of late Eocene age (Sadowski et al. 2017). Only one fossil,



Figure 1A–B.—*Prionochothonius burmiticus* gen. et sp. nov., holotype and only known specimen: A. the amber piece containing the specimen. B. the SR μ CT model derived at the Deutsches Elektronen-Synchrotron. Scale bars: A = 2.5 mm, B = 1 mm.

Weygoldtiella plausus Harvey, Cosgrove, Harms, Selden, Shih & Wang, 2018 has been described recently from the Lower Cretaceous of Myanmar and placed in the Chthoniidae, which is one of the two chthonioid families (Harvey et al. 2018). This fossil displays many unique morphological features that set it aside as a stem-group member of the Heterosphyronida, but also has all of the diagnostic features for the Chthoniidae, highlighting relative morphological stasis for ca. 100 Ma but simultaneously providing insights into character variability and polarity in this ancient fauna. Burmese amber, from which this fossil originates, has been recognised in recent years as the most important source of invertebrate fossils from the Cretaceous (e.g., Selden & Ren 2017) and, in contrast to other Cretaceous ambers, preserves a rich and diverse community of pseudoscorpions which remains essentially undocumented except for *W. plausus*, *Protofeaella peetersae* Henderickx & Boone, 2016 and two additional species that were described almost a century ago (see Cockerell 1917, 1920).

In this paper, we describe the second chthonioid pseudoscorpion from Burmese amber which displays a mix of morphological characters not recorded for the order before, other characters that allow statements about the evolution of Heterosphyronida, and some insights into the possible biogeographical origins of this amber.

METHODS

Preservation.—The described fossil is included in an oval piece of Burmese amber (Fig. 1A) in the private collection of Carsten Gröhn (Hamburg) and has been lodged with the Geological-Paleontological Museum in Hamburg (Registration Number GPIH4865). The piece comprises several syninclusions, namely two midges (Nematocera), one undetermined beetle, and several trichomes. The amber itself is not heavily oxidized and darkened, which is the case with some Burmese amber pieces that have been thermally altered. Yet, the pseudoscorpion fossil is partly darkened and indicates that at least some thermal degradation has occurred. The dorsal side of the fossil is well preserved but white emulsion covers most of its ventral side, including the coxal area and the

genital region. Both pedipalps are partly obstructed by air bubbles which stem back to the time of initial preservation, and the underlying features are not visible. Otherwise the fossil is complete and no body parts are missing.

Preparation and taxonomy.—The amber was coated with polyurethane resin (Acrüdur R40, Adolf C. C. Rüegg GmbH & Co.) and photographed in oil (“Bübchen Baby Öl”, Hermes Pharmazeutische Fabrik GmbH) to minimize light reflections. Some angles were also sanded with 1200 and 4000 grit abrasive paper to improve imaging results. Habitus photos were taken using a Canon EOS 5D Mark III with a 65 mm lens (magnification setting 2.5) and a Canon EOS 7 Mark II with a microscopic lens (magnification 5 \times) mounted on a BK Plus Lab System by Dun, Inc., and stacked using Zerene stacker (Zerene Systems LLC 2016). Morphological details were imaged using a Leica M205 stereomicroscope and stacked using the software LAS X (Leica Application Suite X, Version 3.0.1.1.15878). Scale bars and measurements were taken using the integrated function in this software. Image editing and plate compilation was done in Gimp Version 2.10.12 (online at <https://www.gimp.org>) and Krita Version 4.1.5 (online at <https://krita.org/>).

To reduce obstruction of morphological structures by bubbles and artifacts, the amber piece was also scanned using Synchrotron radiated micro-computed tomography (SR μ CT) data at Deutsches Elektronen-Synchrotron (DESY), at the Petra III facility, beamline P05, with a scanning energy of 25 keV. See Müller et al. (2019) for details on imaging procedures. In short, the amber piece was mounted on a stub using beeswax and rotated around its own axis by the machine, taking high-resolution shots from all angles. The software package Amira (Version 6.0.1) was used to edit the raw data and calculate the three-dimensional model. SR μ CT could not resolve the obstructed structures (Fig. 1B), possibly because of strong chemical modification of the amber due to the maturation processes that resulted in very weak absorption contrast (Tafforeau et al. 2006).

The terminology of morphological structures and measurements (in millimeters) mostly follows Chamberlin (1931), except for the measurements of the femur and patella of leg IV (Chamberlin & Chamberlin 1945), the terminology of

pedipalp and leg segments (Harvey 1992) and nomenclature of the trichobothria (Harvey 1992). The classification scheme of pseudoscorpions follows the recent transcriptomic analyses of Benavides et al. (2019). Determination of the life stage (juvenile or adult) follows Harvey (1992) and the taxonomic literature for chthoniid pseudoscorpions.

BURMESE AMBER

Burmese amber is one of the most important geological archives for terrestrial arthropods from the Cretaceous and comprises representatives of all present-day arachnid orders (reviewed by Selden & Ren (2017): recently complemented by Müller et al. (2019) with the first detailed description of a member of the Schizomida). This amber is mined in the Hukawng Valley in northern Myanmar. According to a recent study by Smith & Ross (2018), the age of the amber can be estimated to ca. 100 Ma. Thus, Burmese amber originated at the Albian-Cenomanian transition, an interval of increasing global temperatures culminating into one of the warmest phases during the past 150 Ma (Friedrich et al. 2012).

There are several hypotheses about the geographical position of the West Burma terrane at this time, of which two are discussed by Selden & Ren (2017, with additional references therein). One hypothesis claims a separation of the terrane during the Devonian and a collision with Eurasia during the Jurassic, so that the amber forest would have been part of Eurasia during the Cretaceous. This view is to some degree supported by Müller et al. (2019) in connection with the paleobiogeography of schizomids. Another hypothesis is that the West Burma terrane separated from Australia during the Jurassic and collided with Eurasia at ca. 80 Ma, so that Burmese amber may represent a mid-Cretaceous island flora and fauna with Gondwanan faunal elements. Recently, Westerweel et al. (2019) postulated, based on paleomagnetic data, that the Burma terrane was part of an island arc that was isolated during the Cenomanian, at a position around 10° in the southern latitudes.

SYSTEMATICS

Suborder Heterosphyronida Chamberlin, 1929

Family Chthoniidae Daday, 1888

Subfamily Chthoniinae Daday, 1888

Remarks.—The superfamily Chthonioidea is the most basal extant pseudoscorpion clade (Benavides et al. 2019) and the new fossil can unequivocally be assigned to this taxon because it shares the principal diagnostic characters: presence of trichobothria *ib* and *isb* on the dorsum of the chelal hand, the fused metatarsi and tarsi of legs I and II, and the absence of venom glands in both chelal fingers. The Chthonioidea includes two families: the Chthoniidae and the Pseudotyranochthoniidae. The latter family can be excluded because in that family trichobothria *ib* and *isb* of adult specimens are situated dorsally near the base of the chelal fingers. Both trichobothria are situated in a medial or basal position in the Chthoniidae, a position shared by the fossil, and assignment to this family is straightforward.

The Chthoniidae presently comprises three subfamilies: Chthoniinae, Lechytiinae and Tridenchthoniinae. Lechytiinae

can be excluded because the amber fossil has only two trichobothria on the chelal hand but Lechytiinae has more than two trichobothria. The assignment of the fossil to either Chthoniinae or Tridenchthoniinae is more difficult because several relevant characters (i.e., the coxal blades and the intercoxal tubercle) are not visible. Chamberlin (1931) separated both taxa by the orientation of the spiracles, or the sclerotization of the female genital area. None of these morphological features are visible in our specimen. This leaves us with other characteristics, such as the number of setae on the carapace that were noted by Beier (1932). The fossil has 18 rather long setae on the carapace, which is a very common pattern in Chthoniinae but not in Tridenchthoniinae, where more and shorter setae are common. On the other hand, the basal position of *ib* and *isb* is rather reminiscent of Tridenchthoniinae whereas in most (but not all) Chthoniinae genera, these are situated medially on the chelal hand. With some uncertainty remaining, our specimen is assigned here to the Chthoniinae and its possible affinities discussed below.

The fossil differs from other chthoniid genera found in the area today. From *Lagynochthonius* Beier, 1951 and *Tyrannochthonius* Chamberlin, 1929 it differs by the basal position of *ib* and *isb*, a feature that also sets it apart from the genera *Austrochthonius* Chamberlin, 1929, *Chthonius* C.L. Koch, 1843 and *Pseudochthonius* Balzan, 1892 that occur elsewhere. It differs further from *Congochthonius* Beier, 1959, *Sathrochthonius* Chamberlin, 1962 and *Sathrochthoniella* Beier, 1976 – the most similar extant genera – by the presence of five distal teeth on the lateral side of the moveable cheliceral finger, a feature that is not known from any chthoniid species today. The specimen also differs from the chthoniid genus *Weygoldtiella* Harvey, Cosgrove, Harms, Selden, Shih & Wang, 2018 that was established for a fossil species in Burmese amber by the basal position of *ib* and *isb*, and the peculiar serrations of the fixed cheliceral finger, amongst other features.

Genus *Prionochthonius* gen. nov.

Type species.—*Prionochthonius burmiticus* sp. nov..

Etymology.—The generic name is derived from the teeth on the outer margin of the moveable chelicera finger that is reminiscent of a saw [*prioni*, Greek, saw].

Diagnosis.—This genus is a member of the subfamily Chthoniinae in the pseudoscorpion family Chthoniidae that differs from both extant and fossil genera by the combination of four characters: (i) chelicera with tooth-like serrations on the distal margin of the moveable finger; (ii) trichobothria *isb* and *ib* situated in a basal position on the dorsal surface of the chelal hand; (iii) dentition of chela on moveable finger with small, pointed and contiguous teeth; and (iv) fixed finger similar but teeth more rounded and some occasionally marginally larger.

Prionochthonius burmiticus sp. nov.

(Figs. 1–6)

Type material.—*Holotype adult, gender unknown.* MYANMAR: *Burmese amber:* Hukawng Valley, Upper Cretaceous (lowermost Cenomanian) (GPIH4865, ex Gröhn collection No. 11204).

Etymology.—The specific epithet refers to Burmese amber or Burmite, from which the fossil originates.



Figure 2A–B.—*Prionochthonius burmiticus* gen. et sp. nov.: A. photograph, dorsal view. B. photograph, ventral view. Scale bars = 1 mm.

Diagnosis.—Movable finger of the chela with approximately 80 small, pointed and contiguous teeth; fixed finger similar but teeth more rounded and marginally larger; chelicera with five distinct serrations on the lateral side of the moveable finger; carapace with 18 setae and one pair of corneate eyes only; pedipalp femur long and slender (about $5.5 \times$ longer than broad, about 0.70 in length); chela length about 1.00.

Description.—*Color* (Figs. 2A, B): yellow to red brown, partly with darker spots. Legs of a lighter color, carapace dark brown and oxidized. Broad areas on the dorsal carapace and smaller spots on the chelicerae and tergite VI reflect silver.

Chelicera (Figs. 4A, B, 5A, B, 6A, B): hand with 6 acuminate setae; moveable finger with 1 seta (Fig. 5A), presence of a galea uncertain, if present very inconspicuous and forming a blunt knob distal to the cheliceral serrations, serrula interior not visible but serrula exterior on moveable finger rather elongated and narrow with at least 16 comb-like blades, these distally separated from the finger. Moveable finger without teeth except for a small, blunt tooth above the median and another tooth near the end of the finger (Fig. 5B); 5 teeth distal on the lateral side of the moveable finger, distally decreasing in size and with tips distally inclined (Fig. 6). Most distal tooth only slightly elevated. Fixed finger with 10 uneven

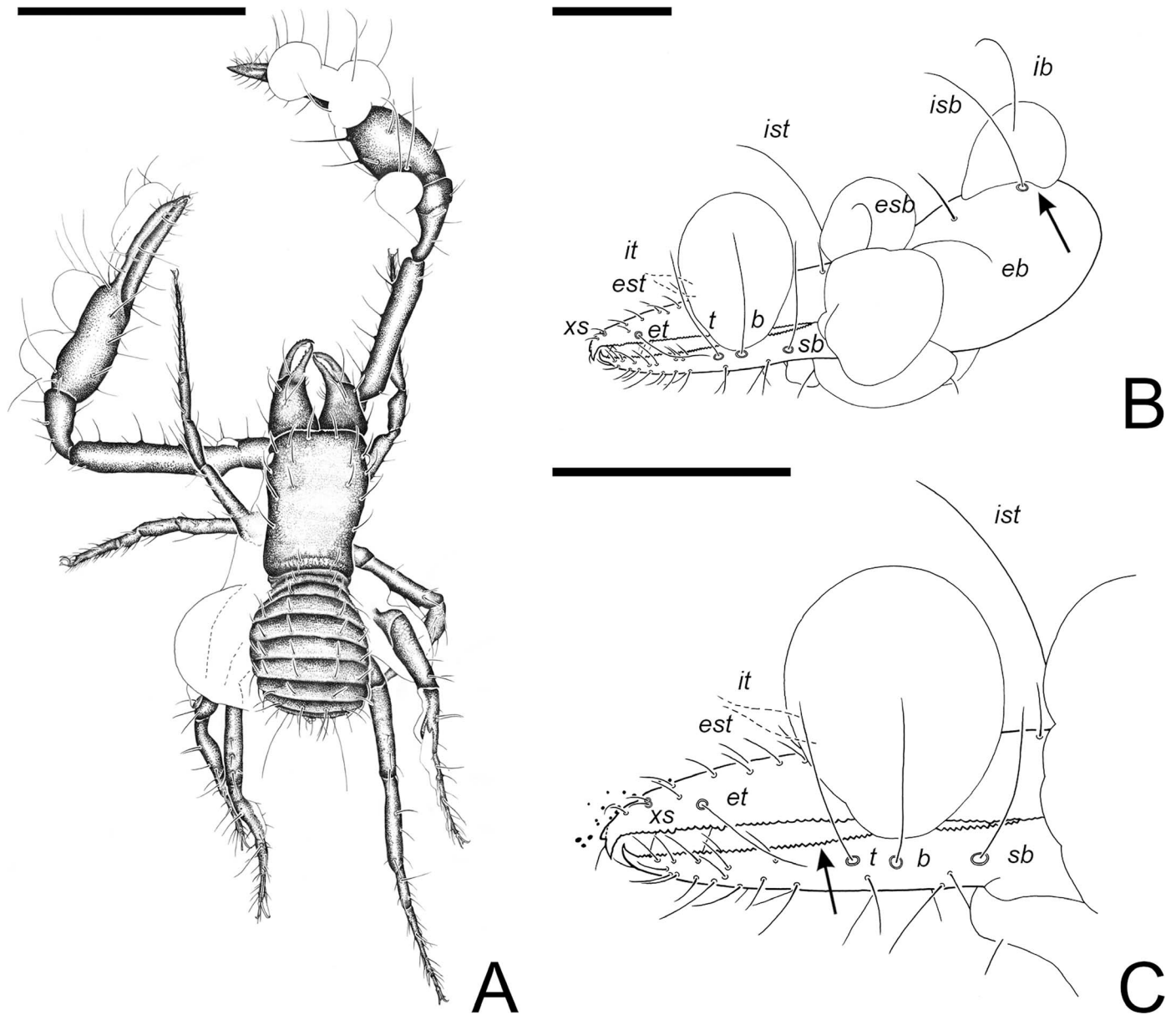


Figure 3A–C.—*Prionochothonius burmiticus* gen. et sp. nov.: A. illustrated model showing artifacts and preservation state. B. right chela in retrolateral view showing trichobothria patterning. C. detail of the right chela tip with trichobothria pattern emphasized. Scale bars: A = 1 mm, B, C = 0.25 mm.

teeth, including a larger median tooth that is inclined distally and the remaining 8 smaller teeth in a proximal row that extends to the base. Rallum comprising 10 long blades in two rows; areole of elliptical form. Due to the preservation of the fossil the form of the blades cannot be determined but they are most likely pinnate.

Pedipalp (Figs. 3B, C): all setae acuminate; femur 5.54, patella 2.43, chela 4.50, hand 2.13 x longer than broad; finger 1.12 x longer than hand. Patella calyciform. Setae on the medial side of the femur longer and more frequent than on lateral side. Chelal hand with spine-like setae (Figs. 2, 3A). Trichobothria *ib* and *isb* situated dorsally close to the base of the hand. Fixed chelal finger with 6 trichobothria plus shorter duplex trichobothria (*xs*); moveable finger with 4 trichobothria.

Trichobothria *eb*, *esb* and *ist* are visible and present at the base of the fixed finger; *est* and *it* on both hands are obstructed but presumed to be closer to *et* than to *ist*; *et* is at least twice as far away from *it* as from *xs* (Fig. 3C). The knob on the tip of the finger as seen in Fig. 3C is likely a product of surrounding debris. Trichobothria *sb*, *b* and *t* are close to each other and presumably in the middle of the moveable finger; *b* is about twice as far from *sb* as from *t*; *st* is presumably distal of the usual basal position although the exact position cannot be determined; distance from *st* to *sb* presumed to be nearly twice the distance from *st* to finger base. All trichobothria filiform and acuminate.

Cephalothorax (Figs. 4C, D, 5C, D): rectangular carapace 1.34 x longer than broad and narrowed posteriorly; with

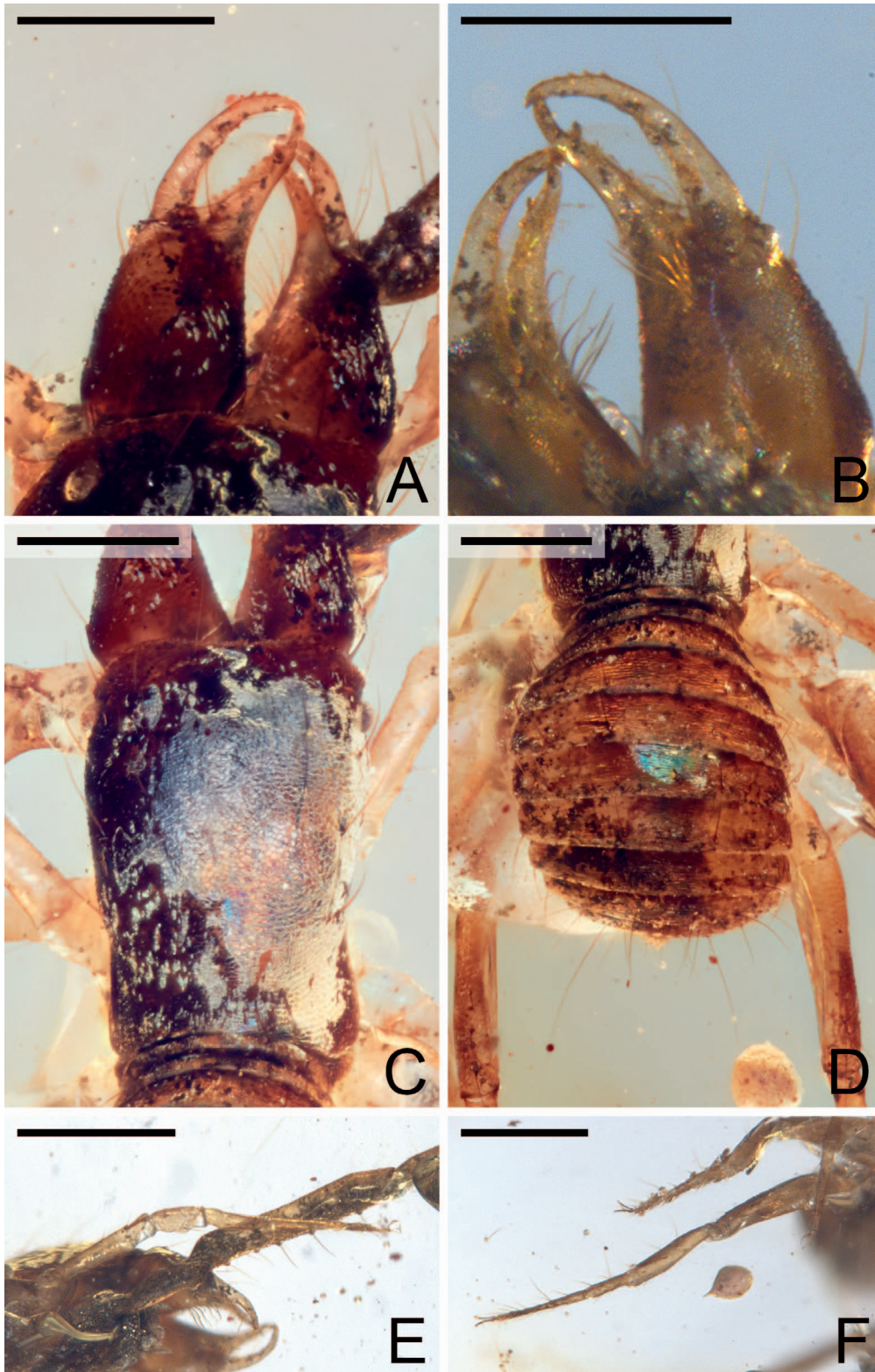


Figure 4A–F.—*Prionochthonius burmiticus* gen. et sp. nov.: Photographs of A. left chelicera, dorsal view. B. left chelicera, ventral view. C. carapace in dorsal view. D. abdomen in dorsal view. E. right leg I, trochanter not fully visible, ventral view. F. right leg IV, parts of femur not visible, trochanter not visible, ventral view. Scale bars: A, B = 0.25 mm, C, D = 0.25 mm, E, F = 0.5 mm.

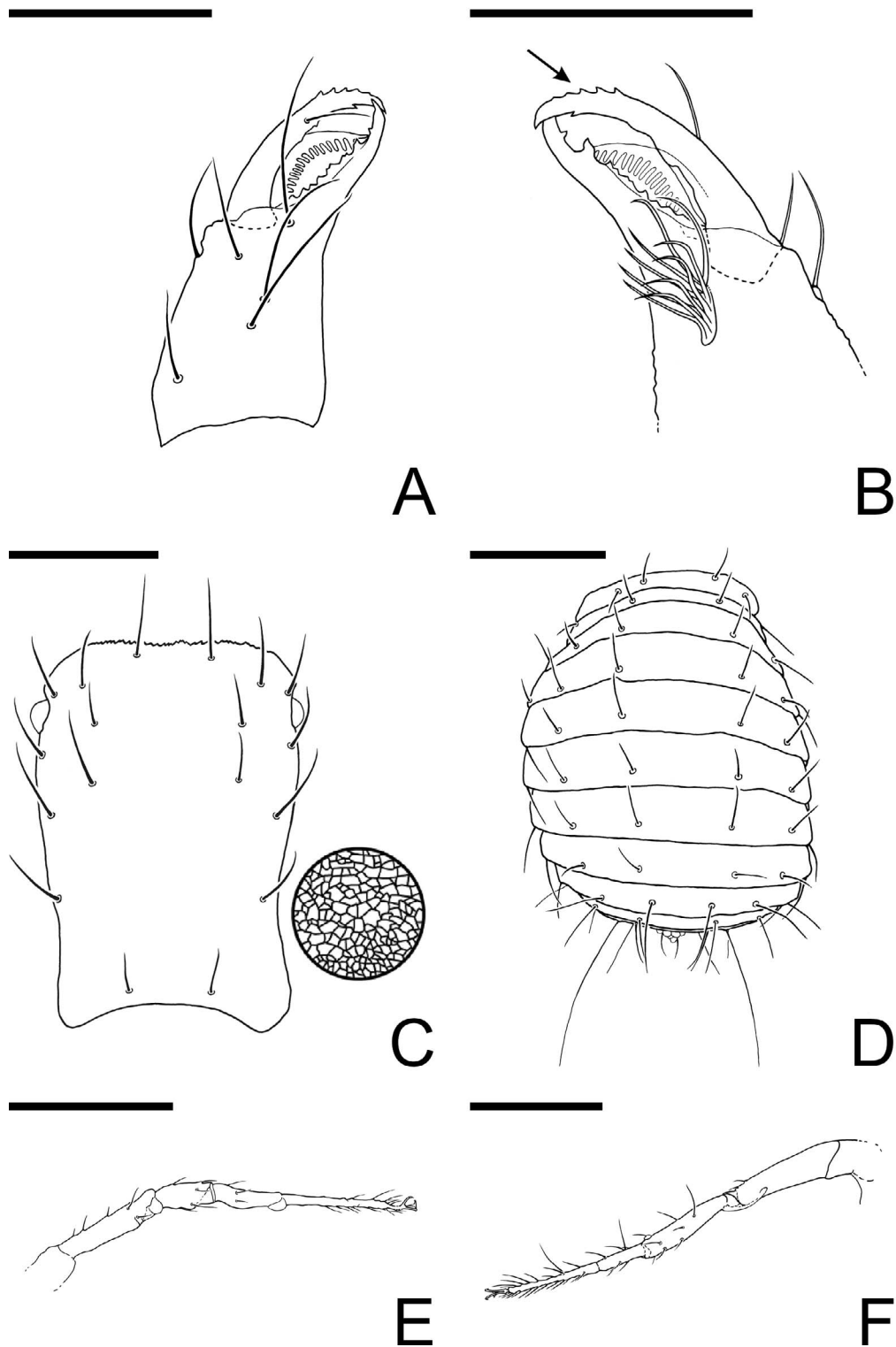


Figure 5A–F.—*Prionochthonius burmiticus* gen. et sp. nov.: Interpretive illustrations of A. left chelicera, dorsal view. B. left chelicera, ventral view. C. carapace in dorsal view, with inset showing surface sculpturing. D. abdomen in dorsal view. E. right leg I, ventral view. F. right leg IV, parts of femur not visible, trochanter not visible, ventral view. Scale bars: A–D = 0.25 mm, E, F = 0.5 mm.

reticulated granulations; anterior carapace margin straight and serrated; epistome indistinctly developed, small and serrated; 1 pair of well-developed corneate eyes (0.07 in diameter); 18 setae arranged 6: 4: 4: 2: 2, the last row of

posterior setae slightly shorter than the other setae. Manducatory process with 2 pairs of acuminate setae, lateral and medial setae of the same length (0.17). Emulsion covers most of the ventral side, the view of the coxal region is

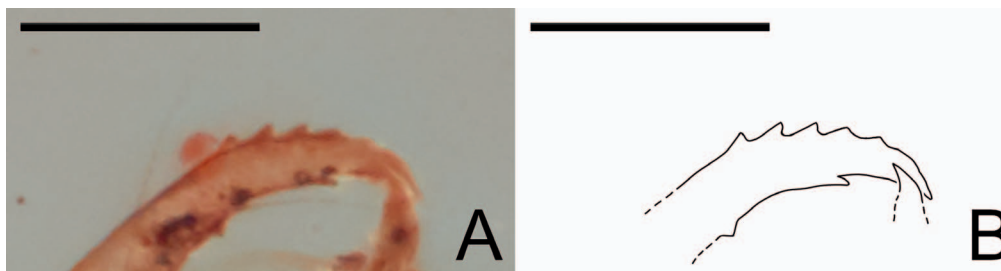


Figure 6A–B.—*Prionochothonius burmiticus* gen. et sp. nov.: A. Photograph of left chelicera tip, dorsal view. B. Interpretive illustration of left chelicera tip, dorsal view. Scale bars = 0.1 mm.

obstructed, coxal blades and intercoxal tubercle are not visible (Fig. 2B).

Abdomen (Figs. 4D, 5D): slightly deformed but length 0.68, width 0.51. Pleural membrane not visible. Tergites undivided, surface longitudinally rippled; setae uniseriate and acuminate; chaetotaxy of tergites I–XI: 4: 4: 6: 6: 6: 6: 6: 6: 4: 4. Tergite XI with 2 remarkably long setae, tergite XII presumably with 2 small setae. Setae on the last three tergites are poorly visible. Sternites, spiracles and genitalia not visible due to the emulsion (Fig. 2B).

Legs (Figs. 4E, F, 5E, F): metatarsi and tarsi of anterior legs fused (Figs. 4E, 5E). Femora longer than patellae on legs I and II and shorter than patellae on legs III and IV; metatarsi III and IV with long sub-basal tactile seta; tarsi III and IV with long sub-basal tactile seta (Figs. 4F, 5F). Arolium marginally shorter than claws, undivided; claws simple, not modified and without serrations.

Dimensions (ratios in parentheses): Body length 1.27 (measured) or ca. 1.39 (with estimated abdomen length); carapace 0.59/0.44 (1.34 x). Chelicera 0.48/0.21, moveable finger 0.25. Pedipalpal trochanter 0.32/0.12 (2.67 x); femur 0.72/0.13 (5.54 x); patella 0.34/0.14 (2.43 x). Chela 1.08/0.24 (4.5 x); hand 0.51/0.24 (2.13 x); finger 0.57/0.04 (14.25 x). Leg I trochanter 0.17/0.11 (1.55 x); femur 0.34/0.08 (4.25 x); patella 0.17/0.08 (2.13 x); tibia 0.21/0.06 (3.5 x); tarsus 0.37/0.02 (18.5 x). Leg IV trochanter not visible; femur and patella ca. 0.56/0.15 (3.73 x); tibia 0.4/0.08 (5 x); metatarsus 0.19/0.05 (3.8 x); tarsus 0.35/0.04 (8.75 x).

DISCUSSION

The paleontological record.—Pseudoscorpions have a sparse fossil record and Mesozoic records are exclusively from six Cretaceous amber types in the Northern Hemisphere. Only a handful of pseudoscorpions have been described from these ambers and unidentified records are from Lebanese amber (ca. 125–135 Ma), Álava amber (100 Ma), New Jersey amber (ca. 90–94 Ma) and Canadian amber (72–84 Ma; Harms & Dunlop 2017) whilst one described species, *Heurtaulia rossiorum* Judson, 2009 (Cheliferidae), comes from Archingey amber (ca. 100 Ma) and five described species, *Amblyolpium burmiticum* Cockerell, 1920 (family Garypinidae), *Electrobisium acutum* Cockerell, 1917 (Cheiridiidae), *Protocheiridium judsoni* Porta, Michalik & Proud 2020 (Cheiridiidae), *Protofeaella peetersae* (Feaellidae) and *Weygoldtiella plausus* (Chthoniidae), from Burmese amber (Harms & Dunlop 2017, Porta et al. 2020). Of all Mesozoic records, Burmese

amber stands out because it not only includes a diverse and rich pseudoscorpion community but is also the only deposit that potentially originates in the former Gondwana (Harms & Dunlop 2017, see above). *Prionochothonius burmiticus* is the second chthonioid pseudoscorpion to be described from this amber after *W. plausus*, and together they represent the oldest fossil records of the pseudoscorpion family Chthoniidae, which is a diverse family today with potentially thousands of species from leaf litter habitats and caves across the world. Other fossil records of the Chthoniidae are much younger and come from late Eocene amber types (Baltic and Bitterfeld ambers; see Sadowski et al. 2017 for a discussion on amber ages), and Miocene ambers in the Caribbean region (Dominican and Chiapas amber, ca. 16 Ma). It should be pointed out that all fossils from Caribbean ambers and many from the Eocene amber types can be attributed not just to Recent families but also to extant genera which, again, testifies to the importance of Burmite to understand evolutionary patterns in pseudoscorpions. *Prionochothonius burmiticus* is now the ninth fossil species of the Chthoniidae (Table 1) and of importance in that it displays, amongst other traits, trichobothria patterns of the pedipalp hand and setation patterns on the carapace that are unique to a few Recent genera within the subfamily Chthoniinae. It is also the fifth fossil pseudoscorpion species described from Burmese amber.

Morphology and evolution.—In a recent phylogenomic analysis of pseudoscorpion relationships, Benavides et al. (2019) suggested a number of systematic changes but also proposed ages for the diversification of the main pseudoscorpion clades based on molecular clock data. The superfamily Chthonioidea is now considered the most basal pseudoscorpion lineage and comprises the families Chthoniidae Daday, 1888 and Pseudotyranochthoniidae Beier, 1932, while two previous families, the Lechytiidae Chamberlin, 1929 and Tridenchthoniidae Balzan, 1892 were synonymized with Chthoniidae leading to three sub-families within this family: the Chthoniinae, the Lechytiinae and the Tridenchthoniinae. Dating analyses suggest that these subfamilies diverged in the Mesozoic sometime between the Triassic and Early Cretaceous periods (252–100 Ma).

Like *Weygoldtiella*, the new genus *Prionochothonius* already displays the typical bauplan of chthoniid pseudoscorpions including large chelicerae with a rallum, serrulae, trichobothria patterning of the pedipalps, shape of the legs including fusion of metatarsi and tarsi in legs III and IV, and the number and position of setae on the carapace. Nevertheless, assignment of our fossil to one of the subfamilies is more

Table 1.—The fossil record of the pseudoscorpion family Chthoniidae ordered by amber type and taxonomic identity. Please see Harms & Dunlop (2017) for additional details. Ma = million years ago.

Amber type	Age	Chthoniidae subfamily	Species
Burmese	Late Cretaceous (ca. 100 Ma)	Chthoniinae	<i>Prionochothionius burmiticus</i> gen. et sp. nov.
		Chthoniinae	<i>Weygoldtiella plausus</i> Harvey, Cosgrove, Harms, Selden, Shih & Wang, 2018
Baltic	Late Eocene (ca. 41–34 Ma)	Chthoniinae	<i>Chthonius mengei</i> Beier, 1937
		Chthoniinae	<i>Chthonius pristinus</i> Schawaller, 1978
		Tridenchthoniinae	<i>Chelignathus kochii</i> Menge, 1854
Dominican	Miocene (ca. 16 Ma)	Chthoniinae	<i>Pseudochthonius squamosus</i> Schawaller, 1980
		Lechytiinae	<i>Lechytiia tertiaria</i> Schawaller, 1980
Mexican	Miocene (ca. 16 Ma)	Chthoniinae	<i>Paraliochothionius miomaya</i> Judson, 2016
		Chthoniinae	<i>Tyrannochothionius</i> sp. indet. Judson, 2016

difficult. Many morphological features that characterize the Tridenchthoniidae are not visible in our fossil but some Tridenchthoniinae show up to five simple galeae in nymphs (e.g., the tritonymphs of *Pycnodithella harveyi* Kennedy, 1988) but the cheliceral serrations in *Prionochothionius* are not reminiscent of this feature. Most Tridenchthoniinae also have a large number of relatively short setae on the carapace, with numbers of 30–32 in *Rheodithella* Dashdamirov & Judson, 2004 (Dashdamirov & Judson 2004) being at the lower end. Our fossil has 18 long setae which matches a common pattern in Chthoniinae.

It has to be noted that Beier (1932) generally distinguished Tridenchthoniinae and Chthoniinae, referred to by him as Dithinae and Chthoniinae respectively, by the basal position of the trichobothria *isb* and *ib* on the chelal hand in Dithinae and the medial position of *isb* and *ib* in Chthoniinae, the former pattern also being present in *Prionochothionius*. However, the basal position of the trichobothria *ib* and *isb* is also found in a few Chthoniinae genera, such as *Sathrochothionius*, *Sathrochothioniella* and *Congochthonius*. *Prionochothionius* differs from these three genera by the five distal teeth distal on the lateral side of the moveable chelicera finger and a distinctly longer than broad carapace, from *Congochthonius* by the number of setae on the carapace and abdomen, and from *Sathrochothionius* by the equal length of the setae of the manducatory process, the tactile setae on the tarsi and metatarsi of leg III and IV, the positioning of trichobothria *b* compared to *sb* and *t*, and the number of setae on the tergites.

Even though *Prionochothionius burmiticus* gen. et sp. nov. is the second chthoniid genus from Burmese amber, it also differs distinctly from *Weygoldtiella* by the lack of a swelling of the chelal hand where the moveable finger inserts, the basal position of the trichobothria *ib* and *isb*, non-elongated chelicera, a rallum of only ten blades, the five distal teeth distal on the lateral side of the moveable chelicera finger, setae on the manducatory process of the same length, and the number and arrangement of setae on the carapace. We further note the differences from all chthoniid genera that are widespread in south-east Asia today: *Tyrannochothionius* and *Lagynochthonius* of the Chthoniinae, *Lechytiia* Balzan, 1892 of the Lechytiinae and *Compsaditha* Chamberlin, 1929 and *Ditha* Chamberlin, 1929 of the Tridenchthoniinae (Harvey 2013), either because of the basal position of *ib* and *isb* (different in *Tyrannochothionius*, *Lagynochthonius* and *Lechytiia*) or because of the low number of 18 carapace setae (50–80 in

Compsaditha (Chamberlin & Chamberlin 1945) and 54–160 in *Ditha* (Beier 1932)).

We conclude that *Prionochothionius* does not have an exact match in the Recent or extinct pseudoscorpion fauna but is best placed in the kinship of the Chthoniinae genera *Congochthonius*, *Sathrochothionius* and *Sathrochothioniella* because all of these taxa share a basal position of *ib* and *isb* but have relatively few setae (<30) on the carapace. Classification aside, the fossil is congruent with the hypothesis that the diversification of chthoniid pseudoscorpions occurred well before the Late Cretaceous, because it displays the typical gestalt and autapomorphic features of this family.

Biogeography.—The Burmese amber site belongs to the West Burma terrane and there are two major hypotheses considering its paleogeography. Seton et al. (2012) suggested that West Burma belongs to the Argo Abyssal Plain and was rifting from the north-western margin of Australia at around 156 Ma (late Jurassic), moved northwards and sutured to the Sibumasu terrane at around 80 Ma (late Cretaceous); thus, the fauna should be of Gondwanan origin. Metcalfe (2013) suggested an alternative scenario in which the West Burma terrane derived from the Indochina-South China superterrane instead of the Argo Abyssal Plain. Therefore, West Burma would have separated from Gondwana much earlier; the continental blocks interpreted to have separated are North China, South China, Tarim and Indochina (including West Burma). Fauna in this scenario presumably would have been distributed to West Burma from Eurasia in Jurassic and Early Cretaceous times. Although *Prionochothionius burmiticus* cannot be attributed to any extant genera it should be noted, though, that it is morphologically most similar to genera that are found today only in the Southern Hemisphere: *Sathrochothionius* has a putative Gondwanan distribution with species from Australia, New Caledonia, New Zealand and South America (Harvey 1996). *Congochthonius* is known from the Democratic Republic of Congo and *Sathrochothioniella* occurs in New Zealand. All three genera and the fossil genus are united by the basal position of trichobothria *ib* and *isb* on the chelal hand. Unfortunately, some other important morphological features are not visible in our fossil, such as the position and shape of the coxal blades which could not be resolved using Synchrotron radiation, but clearly *Prionochothionius* groups with Gondwanan genera rather than with those found in the Northern hemisphere today, lending some support to Seton's original hypothesis for this amber type. We should emphasize here that this does not exclude the

possibility that the so-called Gondwanan genera mentioned above were more widespread in the past and are confined today to southern latitudes because of excessive Pleistocene extinctions in the Northern hemisphere (see Eskov & Golovatch 1986), a scenario that has been inferred in other taxa, e.g., for archaeid spiders (Wood et al. 2013). We note though that no chthoniids with a basal position of trichobothria *ib* and *isb* on the pedipalp hand are known from the Eocene ambers of Europe and they were likely not present then, unlike archaeid spiders that are diverse in both Baltic and Bitterfeld ambers. So, either we have a true Gondwanan radiation for the complex of genera treated here (*Prionochothonius* and its Recent relatives) or these taxa went extinct at least in Europe before the Eocene. Still Seton's original hypothesis is most congruent with our data for now.

Paleoecology.—Most chthonioid pseudoscorpions live in leaf litter, topsoil and in caves. Some species have been found in specialist habitats such as under rocks in intertidal habitats (e.g., Harvey 2009). They rarely inhabit other habitats such as tree bark, bird or insect nests, which are preferred by other families. Chthoniid pseudoscorpions rarely undertake phoresy on insects or birds, which is a common dispersal mechanism in many other families.

From the data available it appears that *Prionochothonius burmiticus* had a similar ecology to present-day species in this family. The presence of two eyes indicates that this species had some vision and probably lived in the leaf litter or topsoil layer but not in deeper soil or caves. Its relatively large size may suggest a certain moisture-dependence, which is common in similarly-sized chthonioid pseudoscorpions today that are almost exclusively collected from mesic forest habitats (e.g., Harms 2018; Harms et al. 2019). It co-occurred (and probably shared the same habitat) with other chthonioid genera such as *Weygoldtiella plausus* and several other chthoniid species that await formal description. *Prionochothonius* was obviously a member of a very diverse local fauna of leaf litter-dwelling pseudoscorpions. Some features remain enigmatic, such as the function of the curious serrations on the movable finger of the chelicerae. It is possible that the species preyed (partly) on animals that required a modified cheliceral morphology but the exact function of this feature will remain unknown.

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