

The first Mesozoic microwhip scorpion (Palpigradi): a new genus and species in mid-Cretaceous amber from Myanmar

Michael S. Engel^{1,2} · Laura C. V. Breitenkreuz¹ · Chenyang Cai³ · Mabel Alvarado¹ · Dany Azar⁴ · Diying Huang³

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Abstract A fossil palpigrade is described and figured from mid-Cretaceous (Cenomanian) amber from northern Myanmar. *Electrokoenenia yaksha* Engel and Huang, gen. n. et sp. n., is the first Mesozoic fossil of its order and the only one known as an inclusion in amber, the only other fossil being a series of individuals encased in Pliocene onyx marble and 94–97 million years younger than *E. yaksha*. The genus is distinguished from other members of the order but is remarkably consistent in observable morphological details when compared to extant relatives, likely reflecting a consistent

microhabitat and biological preferences over the last 100 million years.

Keywords Burmese amber · Cenomanian · Chelicerata · Mesozoic · Palpigradi · Taxonomy

Introduction

Among arachnid orders, the one with the least available information regarding their fossil history is the Palpigradi, sometimes known as the microwhip scorpions. This group of truly minute chelicerates, ranging in size from approximately 1–3 mm, has been investigated rather little since their first discovery and description by Grassi and Calandruccio in 1885 (Grassi and Calandruccio 1885; Grassi 1886). Today, nearly 90 species have been documented, and very little information is available regarding refined specifics of their biology, although the fascinating account of the troglobitic *Eukoenenia spelaea* (Peyerimhoff 1902) feeding on heterotrophic cyanobacteria (Smrž et al. 2013) is in contrast to the prevalence of predatory behavior among most non-acarine arachnids (Beccaloni 2009: prominent detritivorous and herbivorous lineages are present among mites (e.g., Walter and Proctor 1999). A considerable amount of basic natural history information is needed for palpigrades, to ascertain the generality of cyanobacterial feeding and other details of their biology.

Understandable for a group with individuals of such diminutive proportions, fossils have not been forthcoming in abundance. Indeed, it takes special modes of preservation in order to preserve with sufficient fidelity the fine details of such a small-bodied arthropod. Remarkably, a rather coarsely preserved compression from the Jurassic Solnhofen Lagerstätte was for a long while considered to be a primitive member of

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- ✉ Michael S. Engel
msengel@ku.edu
- ✉ Diying Huang
dyhuang@nigpas.ac.cn
- Laura C. V. Breitenkreuz
l-breitenkreuz@ku.edu
- Mabel Alvarado
malvarado@ku.edu
- Dany Azar
azar@mnhn.fr

- ¹ Division of Entomology, Natural History Museum, Department of Ecology and Evolutionary Biology, University of Kansas, 1501 Crestline Drive–Suite 140, Lawrence, KS 66045-4415, USA
- ² Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA
- ³ State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, People's Republic of China
- ⁴ Faculty of Sciences II, Department of Biology, Lebanese University, Fanar Matn P.O. Box 26110217, Lebanon

the order. The genus *Sternarthron* Haase 1890a was originally described as a large, primitive arachnid putatively among the Palpigadi (Haase 1890a, b), a placement rather quickly called into question by Handlirsch (1906) but still adopted by various researchers (e.g., Petrunkevitch 1949, 1955; Crowson et al. 1967; Savory 1971, 1974; Rowland and Sissom 1980). Among more current authors, the palpigrade affinities of *Sternarthron* have similarly been questioned (e.g., Carpenter 1992; Harvey 2003), and in fact, *Sternarthron zitteli* Haase represents the nymphal stage of *Chresmoda obscura* Germar 1839 (Orthoptera: Chresmododea) (see Delclòs et al. 2008, who also more extensively review the history and literature on *Sternarthron*). The only other fossil attributed to the order, and the only one correctly placed therein, has been *Paleokoenenia mordax* Rowland and Sissom 1980, represented by a series of individuals preserved in Pliocene lithified travertine from the Onyx marble formation (Rowland and Sissom 1980).

During recent investigations into the diversity of arthropods preserved as inclusions in Burmese amber, a single individual of a minute palpigrade was discovered situated within an internal fracture plane of a much larger piece with inclusions. This individual is the sole fossil of the order from the Mesozoic and predates all previous fossil palpigrades by more than 94–97 million years. This significant find prompted a brief description of the fossil despite the inability to observe several anatomical details, and as the first pre-Neogene representative of its order.

Material and methods

The single individual was located in a larger piece of amber and lying within a small, internal fracture which reflected much light making it difficult to see the specimen which was easy to overlook. The palpigrade was isolated from the remainder of the block and prepared into a thin, square chip of amber of a couple of millimeter thickness and of approximately 5.3-mm length and width, and was stabilized in a surrounding disc of epoxy. After preparation the amber piece was then suitable for examination under the compound microscope with both transmitted and reflected light, and utilizing an Olympus SZX-12 stereomicroscope and BX-41 compound microscope. We also employed confocal laser scanning microscopy (CLSM) using a Zeiss LSM 710 with 10× objectives and using a laser at 488 nm. In spite of the preparation, the fine fractures in the amber surrounding the inclusion as well as the placement of additional organic matter and small layers of trapped air near the integument in some places (Figs. 1 and 3c) rendered finer details of some features such as chaetotaxy difficult to see, and thereby limited comparisons with extant relatives. For some structures, a direct view was not possible, and so precise measurements were not obtainable, but relative proportions to other sclerites were attempted. Despite these setbacks, the



Fig. 1 Photomicrographs of holotype (NIGP 163253) of *Electrokoenenia yaksha* Engel and Huang, gen. n. *et* sp. n., in mid-Cretaceous amber from northern Myanmar. **a** Dorsal view. **b** Ventral view

significance of a 100-million-year-old palpigrade warranted documentation and description (Grimaldi and Engel 2007). The format and terminology for the description generally follow that of Rowland and Sissom (1980) and van der Hammen (1982). Following van der Hammen (1982), we have numbered body segments through the entire length of the body (rather than with separate numbering schemes within each tagma as used by Rowland and Sissom (1980)). Analogous to that partially employed by Engel and Grimaldi (2014), we have used a subscript annotation to indicate particular serial appendages (c, p, and 1–4 indicating chelicera, pedipalp, and walking legs 1–4, respectively), with Roman numerals distinguishing subdivisions within podites (e.g., “tarsomere₃ II” denotes the second tarsomere of the third walking leg). Condé (1996), Harvey (2003), and Prendini (2011) have summarized the current classification of the order. The age, biotic diversity, and composition of Burmese amber have been reviewed by Grimaldi et al. (2002) and Shi et al. (2012). The nomenclatural acts established herein are registered under ZooBank LSID urn:lsid:zoobank.org:pub:3F5095F6-FFB7-4488-9F8D-5528F8CFB8A2.

Results

All authors contributed to the development of the project and text discussion; in addition, MSE discovered the fossil in the amber piece, and worked on the comparative analysis,

descriptions, photography, and illustrations; DYH did initial amber sorting and preparation, and contributed to the descriptions, photography, and CLSM; LCVB and MA worked on imaging and illustrations; CYC contributed to initial amber sorting and preparation and CLSM; DA worked on extensive final preparation of the amber to make close observation possible.

Systematic paleontology

Order Palpigradi Thorell 1888

Family Eukoeneniidae Petrunkevitch 1955

Genus *Electrokoenenia* Engel and Huang, gen. n.

Type species *Electrokoenenia yaksha* Engel and Huang, sp. n.

Diagnosis Propeltidium with anterodorsal cone, with anterolateral margins of propeltidium tapering gently away from cone to the widest point of carapace at about tangent of coxae₁, then margins slightly constricted and tapering to posterior end; frontal organ rounded and U-shaped, with distinct concavity between rounded lateral “arms;” prosomal sterna exceedingly difficult to observe but apparently with only five sterna, apparent fused sterna II + III articulating with the coxae of anterior two pairs of walking legs broadest. Opisthosoma (segments VII–XVII) without ventral sacs and sterna without protuberances; segments XV–XVII (pygidial segments) tapering rapidly in width such that segment XVII is distinctly narrower than width of segment XV; segment XV distinctly wider than segment XVII, about 1.7× as wide as segment XVII, segment XV slightly narrower than segment XIV, segment XIV about 1.5× as wide as segment XV; setation of pygidial segments (XV–XVII) not discernible (possibly absent); flagellum only slightly shorter than opisthosoma, with 11 roughly moniliform articles, each flagellar article longer than wide (ranging from about 1.7–2.1 times as long as wide), not compact, those medially slightly more slender than those basally or apically, each flagellar article with apical whorl of several long, simple setae, individual setae longer than length of an individual article.

Etymology The generic name is a combination of the prefix *electro-* (*electrum*, meaning, “amber,” and a reference to the discovery of the first amber-preserved palpigrade) and *Koenenia* Grassi and Calandruccio, first generic name in the order albeit preoccupied and thereby succeeded by *Eukoenenia* Börner. The gender of the name is feminine. The generic name is registered under LSID urn:lsid:zoobank.org:act:FF0A399D-52AB-4D00-A805-718F923B014E.

Electrokoenenia yaksha Engel and Huang, sp. n.
(Figs. 1, 2, 3, and 4)

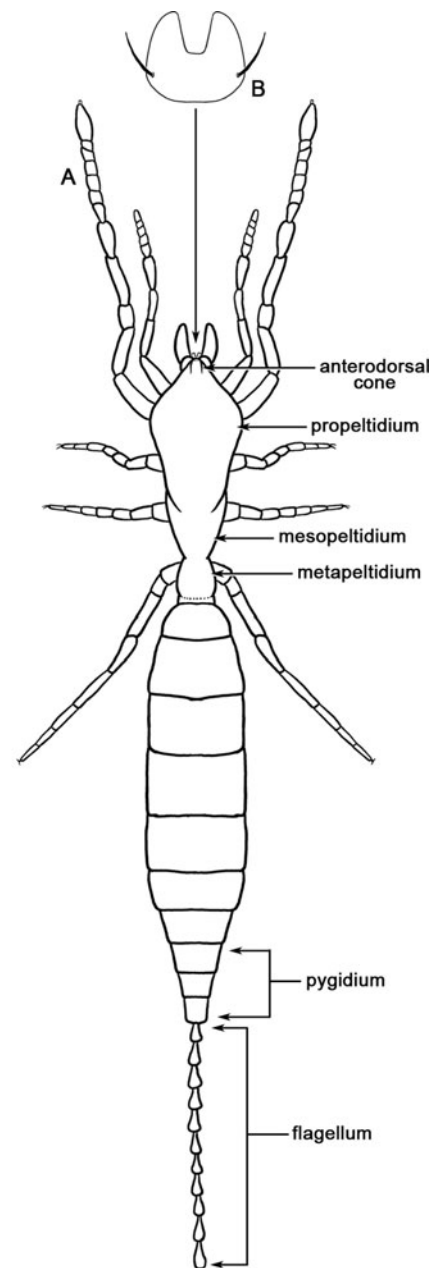


Fig. 2 Reconstructed habitus of *Electrokoenenia yaksha* Engel and Huang, gen. n. *et sp. n.*, with meso- and metapeltidia reconstructed as they appear to have been formed (chaetotaxy omitted). **a** Dorsal habitus. **b** Expanded detail of reconstructed frontal organ

Holotype Possible ♀ (Fig. 1; reconstruction in Fig. 2), NIGP 163253, Albion-Cenomanian boundary, Hukawng Valley, northern Myanmar; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Diagnosis As for the genus (*vide supra*).

Description Generic features with the addition of the following: Total length (as preserved, from anteriormost point of

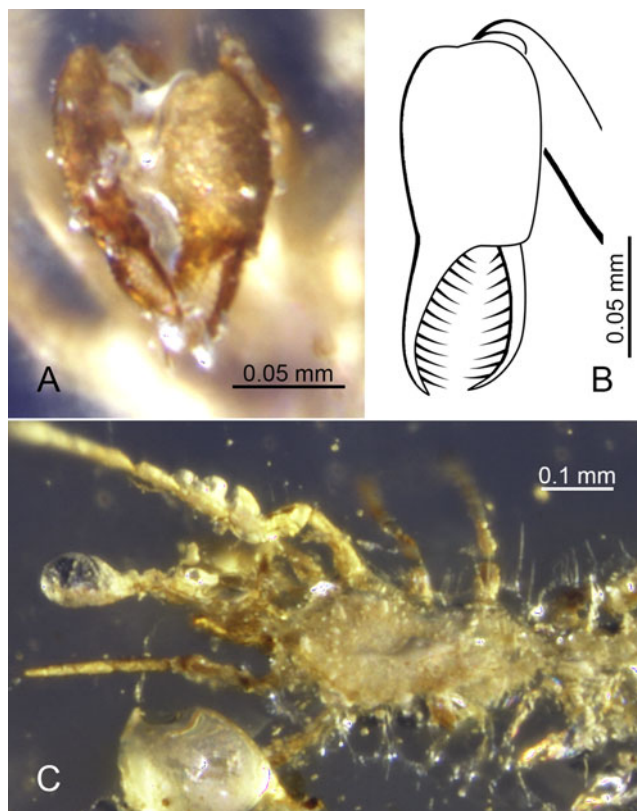


Fig. 3 Details of holotype (NIGP 163253) of *Electrokoenenia yaksha* Engel and Huang, gen. n. *et* sp. n., in mid-Cretaceous amber from northern Myanmar. **a** Frontal view of cheliceral chela as preserved (note that the right chela [left in image] is turned such that its leading edge is more angled toward the viewer, while the left is more in profile). **b** Reconstruction of chela, from observable details. **c** Detail of dorsal surface of prosoma and anterior legs (the *fine lines* radiating from body are not setae but rather minute, reflective fractures within the amber itself resulting from weakness around the inclusion)

prosoma to apex of flagellum) 1.47 mm; integument largely yellowish throughout (except where partly cleared postmortem), with imbricate to microgranulose sculpture; prosomal maximum width (at about apical one-third length) 0.13 mm; prosomal median length 0.35 mm; anterior of propeltidium tapering gently to anterior midpoint, with distinct anterodorsal cone; mesopeltidia not discernible; metapeltidium largely damaged over top of coxae₄. Frontal organ present albeit scarcely visible, near apex of cone of propeltidium (Fig. 2), rounded U-shaped, about as long as wide (Fig. 2b), median concavity of “U” as wide apically as width of lateral “arm” of “U,” depth of concavity about one-half length of total organ length, width of organ about as wide as width of podite X of leg₁; lateral organs not visible.

Appendages on left side damaged and largely missing except chelicera, pedipalp, and leg₁ present. Chelate chelicera with proximal podite_c long and slender, longer than chela (precise measurement not possible as there is no direct lateral view with the structure angled away from all accessible viewpoints); fixed chela podite_c (i.e., secondary podite_c inclusive

of immoveable digit) length 0.13 mm, fixed chela body length excluding immoveable digit 0.08 mm, width 0.05 mm; apotele as long as immoveable digit (Figs. 3a, b, and 4b); immoveable digit with 12–13 long, slender teeth along nearly entire length, apotele with ten long slender teeth along entire length (Fig. 3b); surface setation of cheliceral podites not discernible.

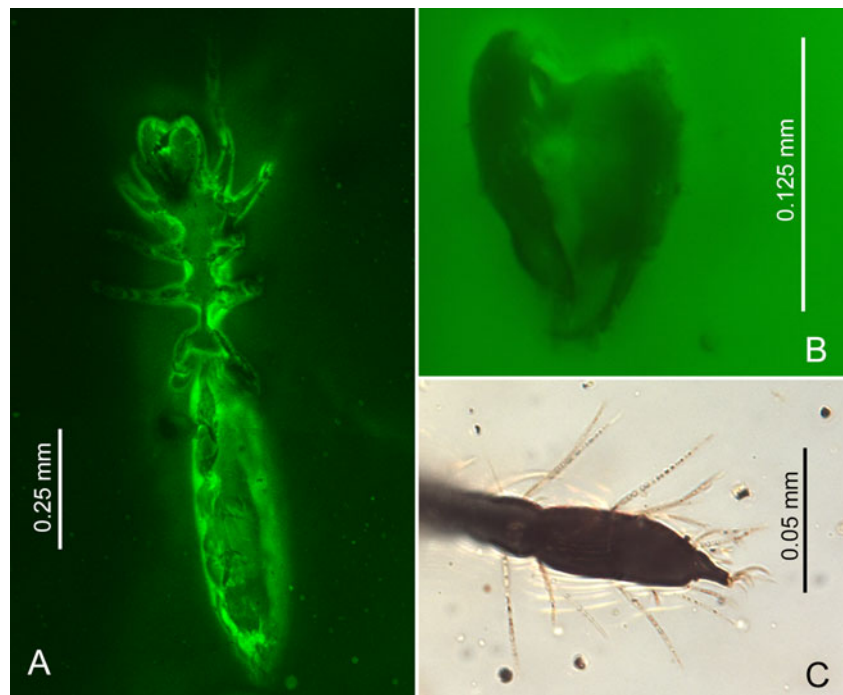
Coxae of all appendages (except chelicera), medially separated by more than their width; coxa_p of pedipalp and leg₁ each about 2.5 times as long as basal width, each tapering in width from base to apex (somewhat conical in appearance); coxa₂ about 1.5 times as long as basal width, tapering slightly along length (with squat appearance); coxa₃ and coxa₄ about 2 times as long as basal width, faintly tapering along length (rather semi-cylindrical in appearance).

Pedipalp femur_p much longer than wide; patella_p cylindrical, slightly longer and narrower than tibia_p, with at least one stiff seta at midlength and three near apex; tibia_p slightly broader than patella_p, with apical half appearing slightly swollen and basal half tapered, with at least a few scattered short setae in apical half; basitarsomere_p I with tapered base, otherwise parallel-sided in apical three-quarters, distinctly narrower than tibia_p, with at least four elongate, stiff setae visible (two near midlength, two near apex), slightly longer than basitarsomere_p II; basitarsomeres_p II and III subequal in length, cylindrical, as wide as basitarsomere_p I, and with similar setation as on basitarsomere_p I; tarsomere_p I as wide as basitarsus_p, about as long as basitarsomere_p III, with at least one long setae near midlength and two near apex; tarsomere_p II (apicalmost) more swollen than tarsomere_p I, approximately 3.5 times longer than wide, longer than tarsomere_p I (tarsomere_p I about two-thirds length tarsomere_p II), apically tapering to pretarsal claws (with fine, short seta just basad and between claws) (Fig. 4c), with at least three elongate lateral setae (one near base, one near midlength, one near apex), and two dorsal elongate setae, first slightly apicad level of midlength lateral seta, second at about level of apical lateral seta.

Leg₁ distinctly longer than pedipalp, about as thick as pedipalpal podites. Trochanter₄ about half as long as coxa₄; femur₄ long, longer than patella₄, patella₄ and more distal podites distinctly more slender than femur₄; patella₄ only slightly shorter than tibia₄; basitarsus₄ about three-quarters length of tibia₄; tarsus₄ divided into two tarsomeres, proximal tarsomere₄ (tarsomere₄ I) about two-thirds length of basitarsus₄, subequal in length to apical tarsomere₄ (tarsomere₄ II); leg chaetotaxy difficult to discern, at least a few long setae at base of each podite from patella through apical tarsomere.

Opisthosoma elongate, largely parallel-sided and compressed (dorsoventrally) as preserved, length 0.63 mm, setae (where discernible) at apex of segments, short and simple; segments X, XI, and XII approximately equal in length and

Fig. 4 Confocal and microphotographic images of holotype (NIGP 163253) of *Electrokoenenia yaksha* Engel and Huang, gen. n. *et* sp. n., in mid-Cretaceous amber. **a** Ventral view of specimen excluding flagellum. **b** Frontal view of chela. **c** Detail of apex of right pedipalp



width, each about 0.16-mm wide, 0.08-mm long; segment IX similar to X but slightly narrower anteriorly and apparently slightly longer medially; segment VIII slightly narrower than IX and distinctly shorter, at most approximately three-quarters length of segment IX; segment XIII slightly shorter and narrower than segment XII; segments XIII and XIV distinctly tapering in width and length toward pygidial segments. Flagellum long, length 0.50 mm, individual flagellar articles each longer than wide, individual widths about 0.014 mm.

Etymology The specific epithet is taken from South Asian mythology where the “yaksha” were nature spirits who held stewardship over the wonders hidden in the earth (such as the wonders of Burmese amber, recovered from their resting place in the earth). The name is treated as a noun in apposition. The species is registered under LSID urn:lsid:zoobank.org:act:4876BF69-92BC-424E-8B3B-BD4A1DEB12D1.

Discussion

The genus is superficially similar to the extant genus *Leptokoenenia* Condé 1965, known from five species in Saudi Arabia, the Republic of the Congo, northern Brazil, and Italy (Souza and Ferreira 2013), and both have rather rounded lateral “arms” to the frontal organ of the propeltidium, although other aspects of the form disagree (e.g., more of a broad concavity between these elements in the fossil). It differs most notably from *Leptokoenenia* by the

more dramatic narrowing of the pygidial segments, and the more slender and long flagellar articles with fewer long setae (typically compact and wider than long and with dense setae in females of *Leptokoenenia*). The large number of elongate “teeth” on the chelicercal digits is distinctive for the genus. Typically, there are between seven and ten such serrations, and they are more tooth-like in form. In the fossil, these are more numerous on the immovable digit (at least 13 visible), while the apotele (moveable digit) bears ten. Moreover, these are elongated into stiff, spinelike structures that form a fine comb along the inner surfaces of each claw. Unfortunately, many of the finer details commonly compared among living palpigrades are simply not visible in the minute fossil (e.g., most chaetotaxy), either owing to its inclusion in the amber (and inability to make preparations closer to the integument or suitable for compound microscopic examination) or due to the nature of preservation (slightly desiccated, bordered by microscopic fractures, and positioned among other organic debris).

Not surprisingly, the morphology of these chelicerates has changed little over the last 100 million years, and although the fossil is considered generically distinct, the differences between the genera of eukoeneiids are rather subtle, with little anatomical disparity across the order. Most arachnid orders extend well into the Paleozoic and can in some groups exhibit similar degrees of conserved morphology over vast expanses of geological time (Dunlop 2010). Indeed, even many behaviors among arachnids are quite ancient, with well-documented occurrences in the Mesozoic (e.g., Engel and Grimaldi 2014). While certain chelicerates are hallmark examples of bradytely (e.g., Norton et al. 1988; Rudkin et al. 2008; Dunlop 2010;

Sidorchuk et al. 2015), much of this conservatism remains unquantified. Such bradytely likely reflects a conserved and stable ecological niche for otherwise generalized organisms (versus a specialized niche which would undoubtedly be associated with concomitant specializations in the organisms occupying them and certainly would be so as those niches change over time, or even disappear!), much as was perceived by Simpson (1953). Indeed, such would seem to be the case for many groups that also appear to exhibit some degree of bradytely whereby each occurs in microhabitats (e.g., subcortical environments) that would be expected to be consistent over long periods of geological time (e.g., Hamilton 1978; Engel and Grimaldi 2002; Cognato and Grimaldi 2008; Chatzimanolis et al. 2013). Living within tropical soils and caves could be argued to fit into such a generalization and this may account for much of the perceived conserved morphology across the order and despite their clear antiquity based on phylogenetic position (Dunlop 2010; Garwood and Dunlop 2014), and now further witnessed by the current fossil, and that what disparity as does exist within the order reflects comparatively minor deviations and specializations. Fortunately, phylogenetic hypotheses are being developed at long last for the palpigrades (Giribet et al. 2014), and these should provide an ultimate framework from which to address some of the evolutionary questions, including bradytely, surrounding these tiny arachnids.

It is hoped that by bringing the discovery of this microscopic fossil to the attention of other researchers, further material might be discovered. Indeed, these tiny, soft-bodied arthropods may be overlooked easily, particularly if placed near other inclusions or debris, or if situated among fissures. The present specimen was at first not noticed owing to its placement among a series of reflective fractures, none of which extended far from the inclusion, in the center of a larger piece. In the unprepared amber piece, the palpigrade appeared only as a slightly darker, thick area at the center of a minute whorl of reflections, with none of the fissures coming near to other inclusions or the edges of the piece, and it was only after more careful examination that the palpigrade could be discerned. This prompted detailed preparation to isolate it from other inclusions that then made it largely observable as well as rendered its study possible. Such preparation will undoubtedly be necessary for any future specimens that are discovered. It is remarkable to consider the circumstances that lead to the entrapment of the current individual. As noted, palpigrades live interstitially in moist habitats such as tropical or subtropical soils or may be littoral, occurring along shores. Species are also found in cave environments and can be troglobitic. While the Burmese amber forest was certainly a moist tropical climate, there was nothing about the piece in which the palpigrade was discovered that suggested it represented a humus fauna, instead including several aerial insects such as small flies and wasps. This does not preclude extended contact

near the forest floor or near the edge of water, but does make it more difficult to understand the taphonomic circumstances that lead to its capture and preservation. Regardless, preservation in amber is perhaps the only medium through which such minute animals could be adequately characterized, their fine features and fragile forms too readily destroyed or rendered unidentifiable in sediments. The present individual leaves the potential for further specimens to be discovered, and in amber deposits throughout the Cretaceous and Tertiary, particularly humid environments such as those of India, the Dominican Republic, Lebanon, and eastern North America, and especially those whose inclusions are more representative of a litter fauna, such as the amber of Archingey in France.

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