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## Whipspiders (Arachnida: Amblypygi) in amber from the Early Eocene and mid-Cretaceous, including maternal care

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**Abstract.** Two new genera and species of fossil whipspiders (Chelicerata: Arachnida: Amblypygi) are described from Tertiary and Cretaceous ambers of southern Asia. *Paracharonopsis cambayensis* Engel & Grimaldi, new genus and species, preserved in Cambay amber of Ypresian age from western India is the first Tertiary and Asian fossil of the Paleoamblypygi, a highly relict taxon that includes the Late Carboniferous genus *Graeophonus* Scudder and the living West African species *Paracharon caecus* Hansen. *Paracharonopsis cambayensis* is one of the few examples in Cambay amber of a biotic connection to Africa; most taxa show widespread or Laurasian distributions. *Kronocharon prendinii* Engel & Grimaldi, new genus and species, is the first Cretaceous amber whipspider and putatively a sister group to the Phrynoidea (= Apulvillata). The holotype female of *K. prendinii* is preserved with the remains of three nymphs near her, documenting the Early Cretaceous presence of the extended maternal care so distinctive for the order, and a behavioral repertoire widespread among arachnids.

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### INTRODUCTION

Given the predatory habits of virtually all arachnids, the class is often overlooked in terms of their considerable diversity of social behaviors. Nonetheless, varying degrees of cooperative behavior and parental care have evolved independently throughout their long history, ranging from the extended care of immatures by solitary mothers to large, perennial societies in which individuals collectively work to build and

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maintain a nest, capture and feed on large prey, and raise offspring that may or may not be the direct brood of the caregiver (e.g., Benton, 1991; Shivashankar, 1994; Warburg, 2000; Machado, 2002; Rayor & Taylor, 2006; Lubin & Bilde, 2007; Del-Claro & Tizo-Pedroso, 2009). One of the more impressive groups in which parental care is documented is the order Amblypygi (whipspiders). These seemingly fearsome animals can at times be relatively large, and their elongate, thin legs (the anteriormost of which are modified into whiplike tactile and olfactory appendages), give them an even larger appearance, ranging from 5–45 mm (in some *Heterophrynus* Pocock at about 30 mm in body length, the hyper-elongate antenniform legs can extend maximally to a span of nearly 60 cm!). They have a dorsoventrally compressed body, with a large, broadly-rounded carapace, and frequently long, ventrally-spined pedipalps that are used in prey capture (Weygoldt, 2000). The pedipalps and whiplike forelegs are also used in complex courtship displays and highly-ritualized male-male antagonistic interactions (e.g., Weygoldt, 2000, 2002, 2009; Prendini *et al.*, 2005). While females are noteworthy mothers, carrying their eggs in a sac under the opisthosoma, brooding them for up to three and a half months, fathers are not so involved and depart shortly after the female has picked up the spermatophore. As immatures hatch, they move to the dorsal surface and cluster on her opisthosoma, covering the tagma in a characteristic fashion. During the moulting periods of her young, the mother finds a concealed location and remains motionless as her prenymphs moult and their cuticles harden. Prenymphs that fall from the mother do not survive. Once the prenymphs moult to the protonymphal stage, they depart from their mother, although in a few species the young may stay for a bit longer (Weygoldt, 2000). Although not truly 'social', such parental investment is noteworthy and is certainly more developed among whipspiders than has historically been credited to the order (refer to Rayor & Taylor, 2006).

Whipspiders are ancient, with definitive evidence of their occurrence extending to the Late Carboniferous (Scudder, 1876, 1890; Pocock, 1911; Petrunkevitch, 1913; Dunlop *et al.*, 2007), although cuticular fragments from the Late Devonian are consistent with Amblypygi (Selden *et al.*, 1991) (Table 1). From the Mesozoic there is a single species, known from the Early Cretaceous Crato Formation of Brazil (Dunlop & Martill, 2001; Dunlop & Barov, 2005). Aside from species in Early Miocene amber of the Dominican Republic and Mexico (Petrunkevitch, 1971; Schawaller, 1979, 1982; Poinar & Brown, 2004), which mostly belong to modern genera, and one putatively from Aix-en-Provence, France (Keferstein, 1834; Gourret, 1887), there are no other documented fossil occurrences. It is therefore significant to report herein two new genera and species of fossil whipspiders preserved in amber – one from the Early Eocene Cambay amber of western India and a second from the earliest Cenomanian-latest Albian of Myanmar. The Eocene species is noteworthy as it belongs to a relic group, the Paleoamblypygi, otherwise known from several Carboniferous representatives and the sole modern species *Paracharon caecus* Hansen, an enigmatic, blind taxon living in termite nests in Guinea-Bissau (Hansen, 1921; Weygoldt, 2000). The species in Burmese amber is remarkable for the preservation of an adult female with several nymphs clustered near her body, documenting the early presence of maternal care in this lineage. Both species are described, figured, and their significance discussed herein.

## MATERIAL AND METHODS

The age (Eocene: Ypresian), biotic diversity, and botanical origin of Indian amber has been reviewed by Rust *et al.* (2010), while those of Burmese amber (earliest Ceno-

**Table 1.** Supraspecific, hierarchical classification of Recent and fossil Amblypygi.

Order AMBLYPYGI Thorell	
Suborder PALEOAMBLYPYGI Weygoldt	
Family <i>Incertae sedis</i>	
Genus † <i>Sorellophrynus</i> Harvey	Carboniferous (Mazon Creek)
Genus † <i>Thelyphrynus</i> Petrunkevich	Carboniferous (Mazon Creek)
Superfamily Paracharontoidea Weygoldt	
Family Paracharontidae Weygoldt	
Genus † <i>Graeophonus</i> Scudder	Carboniferous (Mazon Creek, Cape Breton, Coseley)
Genus <i>Paracharon</i> Hansen	
Genus † <i>Paracharonopsis</i> , n. gen.	Eocene (Indian amber)
Suborder EUAMBLYPYGI Weygoldt	
Infraorder Charinina Weygoldt	
Superfamily Charinoidea Quintero	
Family Charinidae Quintero	
Genus <i>Catageus</i> Thorell	
Genus <i>Charinus</i> Simon	
Genus <i>Sarax</i> Simon	
Infraorder Neoamblypygi Weygoldt	
Superfamily Charontoidea Simon	
Family Charontidae Simon	
Genus <i>Charon</i> Karsch	
Genus <i>Stygophrynus</i> Kraepelin	
Clade Unidistitarsata, n.	
Genus † <i>Kronocharon</i> , n. gen.	Cretaceous (Burmese amber)
Superfamily Phrynoidea Blanchard [= <i>Apulvillata</i> Quintero]	
Family Phrynichidae Simon	
Genus <i>Damon</i> Koch	
Genus <i>Euphrynichus</i> Weygoldt	
Genus <i>Musicodamon</i> Fage	
Genus <i>Phrynichodamon</i> Weygoldt	
Genus <i>Phrynichus</i> Karsch	
Genus <i>Trichodamon</i> Mello-Leitão	
Genus <i>Xerophrynus</i> Weygoldt	
Family Phrynidae Blanchard	
Genus <i>Acanthophrynus</i> Kraepelin	
Genus † <i>Britopygus</i> Dunlop & Martill	Cretaceous (Crato Limestone)
Genus † <i>Electrophrynus</i> Petrunkevich	Miocene (Mexican amber)
Genus <i>Heterophrynus</i> Pocock	
Genus <i>Paraphrynus</i> Moreno	
Genus <i>Phrynus</i> Lamarck	Miocene (Dominican & Mexican amber)
<i>Incertae sedis</i>	
?Genus † <i>Ecchosis</i> Selden & Shear	Devonian (Gilboa, New York)

manian near the Albian boundary: Shi *et al.*, 2012) have been summarized by Grimaldi *et al.* (2002). Both specimens were polished to permit clear views of the inclusions from multiple angles – dorsal, oblique lateral, and frontal in the case of the Indian specimen, and dorsal and ventral for the individuals in Burmese amber. Cambay amber is a dammar-type resin and required embedding in EpoTek-301 epoxy for preparation and study. CT scanning of the two pieces was not attempted. Cambay amber inclusions

routinely are either not discernible or barely discernible at all using micro-CT or even nano-CT techniques. Burmese amber inclusions are usually slightly more resolved with CT scanning, but most features in the unique specimen could be observed with a light microscope. Inclusions in Cambay amber can be extracted (Mazur *et al.*, 2014), but this leaves highly fragile specimens susceptible to deterioration and is not advised for truly unique material.

For the descriptions, morphological terminology generally follows that of Weygoldt (1996, 2000), including spine nomenclature. Summaries of the higher classification of Amblypygi are provided by Weygoldt (1996, 2000), Prendini (2011), and in table 1, while the most recent catalog of the species was given by Harvey (2003).

## SYSTEMATIC PALEONTOLOGY

Order Amblypygi Thorell  
Suborder Paleoamblypygi Weygoldt  
Family Paracharontidae Weygoldt

*Paracharonopsis* Engel & Grimaldi, new genus

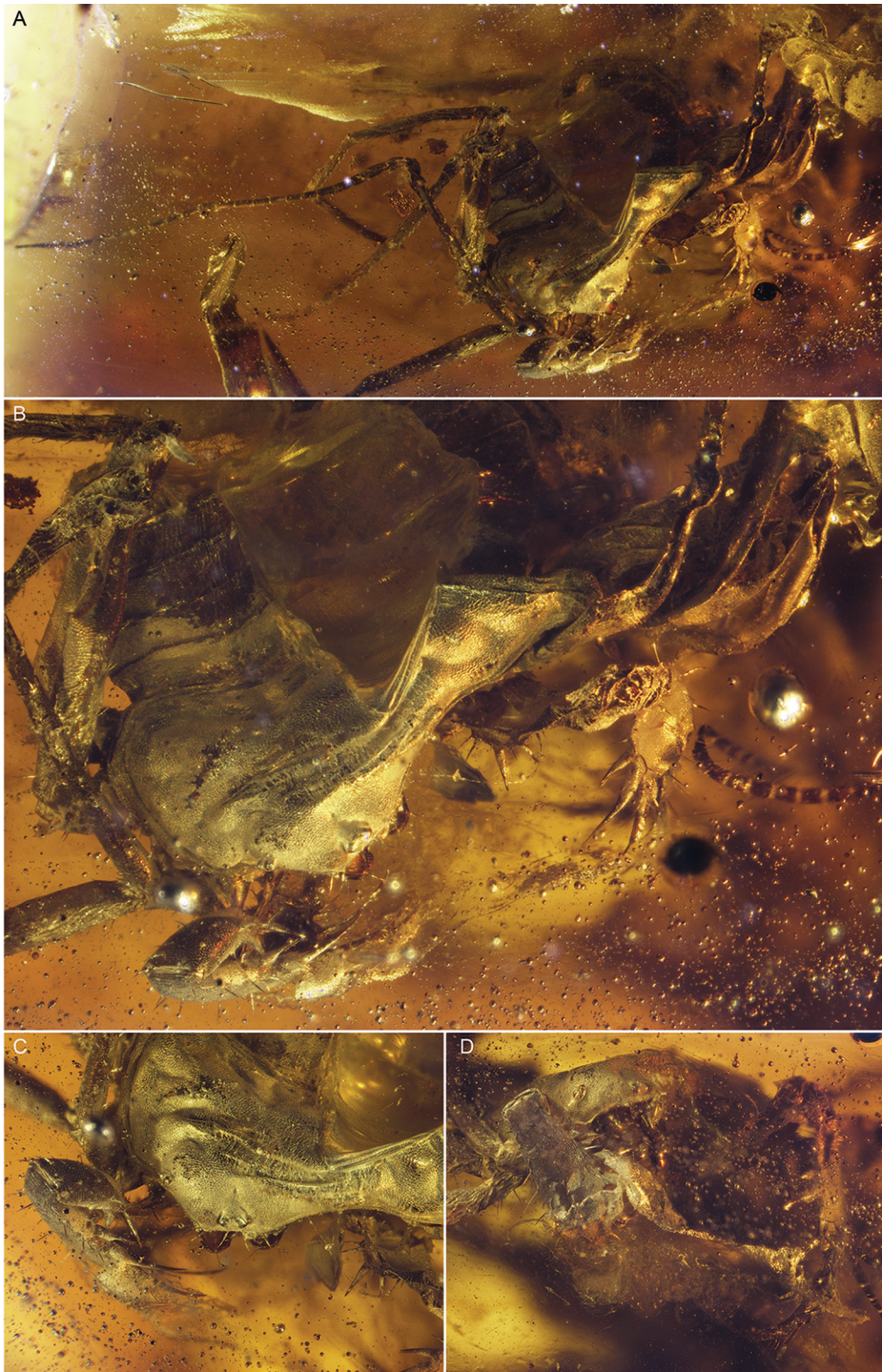
ZooBank: urn:lsid:zoobank.org:act:902BF22B-3438-4483-9237-E1189C8DC0B5

DIAGNOSIS: *Paracharonopsis cambayensis* Engel & Grimaldi, new species.

DESCRIPTION: Carapace with medioanterior prolongation (Figs. 1B, 2A), prolongation shorter and broader than in *Paracharon* Hansen and *Graeophonus* Scudder, apex truncate, apicolateral margins distinctly concave as a result of prolongation (Figs. 1B, 2A), lateral margins faintly convex, posterior margin deeply concave; median eye tubercle present (absent in *Paracharon*) (Fig. 2A); lateral eyes paired (not a triad) (Figs. 1C, 1D, 2A, 2C), on lateral extremity of medial prolongation of carapace (absent in *Paracharon* and apparently in *Graeophonus*). Pedipalp femur and tibia relatively short (as in other Paleoamblypygi), femur slightly shorter than tibia (Fig. 2A), femur with two anterior-dorsal spines (Fig. 2A) (as in other Paracharontidae, a putative synapomorphy uniting the members of this family: Dunlop *et al.*, 2007), two anterior-ventral spines present (Fig. 2A), anterior-ventral spines larger than anterior-dorsal spines; tibia with anterior-dorsal row composed of four spines, gradually longer from proximal to apical (Figs. 1C, 2A) (fewer tibial spines in other Paleoamblypygi); basitarsus with two dorsal spines (Fig. 2A), apicalmost spine longest, one ventral spine; distitarsus divided into basal part and terminal claw (apotele) (Fig. 2A), basal part with long dorsal spine, no ventral spine (ventral spine present in *Paracharon*), with distinct cleaning organ on inner surface, without prominent setal row proximal to cleaning organ. Walking legs with basitibia (fourth pair of legs) undivided; distitibia IV with reduced number of trichobothria (13 versus over 20) (Fig. 2D); second tarsomere apically divided to give appearance of 'five' tarsomeres (Fig. 2D); oblique slit on fourth tarsomere absent; pulvilli present (Fig. 2D).

ETYMOLOGY: The new genus-group name is a combination of *Paracharon*, type genus of the family Paracharontidae, and the suffix *-opsis*, meaning, "look like". The gender of the name is feminine.

COMMENTS: In all other Amblypygi the lateral eyes, when present, are composed of a triad. It is apparent in all views of the holotype that there are only two lateral eyes, a noticeable apomorphy for the fossil.



**Figure 1.** Holotype (Tad 456) of *Paracharonopsis cambayensis*, new genus and species, in Ypresian amber from the Cambay Basin, Gujarat, India. **A.** dorsal view of entire specimen as preserved, with left of carapace extremely distorted due to compression (refer to discussion in text). **B.** Close up from A. **C.** Detail of carapace and right pedipalp in dorsal view. **D.** Frontal view.



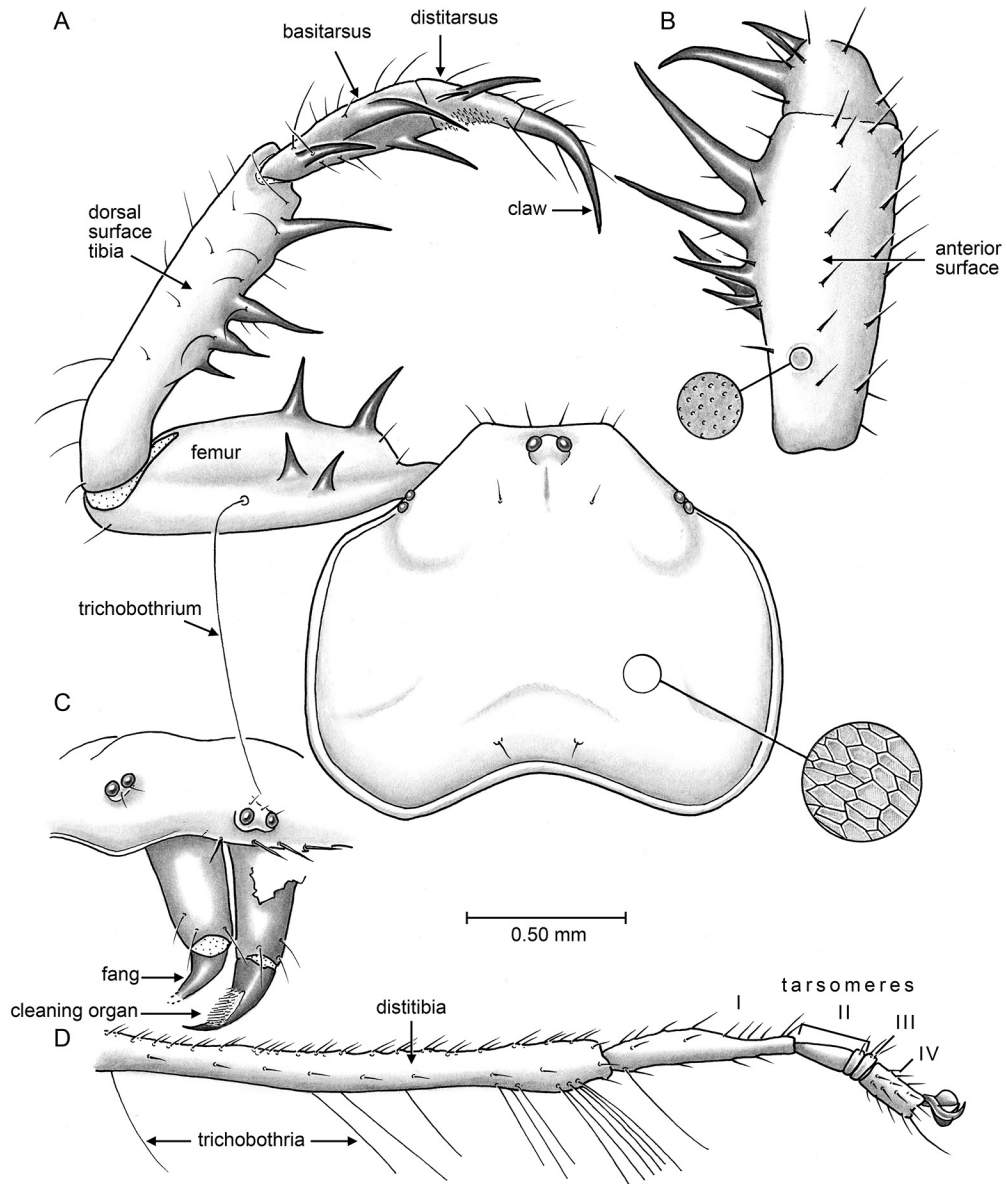
*Paracharonopsis cambayensis* Engel & Grimaldi, new species

ZooBank: urn:lsid:zoobank.org:act:86A3F4AC-7E3C-4CF7-AB6D-1788EC6FCCB4

(Figs. 1–2)

DIAGNOSIS: As for the genus (*vide supra*).

DESCRIPTION: Total body length as preserved 2.0 mm. **Carapace.** Anterior margin projected, anteriormost margin flat; this margin with 4 short, spine-like setae. Eyes present; pair of median eyes situated on low tubercle (Figs. 1B, 2A, 2C), width between outer margins of median eyes 150  $\mu\text{m}$ ; paired (2, not 3) lateral eyes on each side; distance between outer margins of frontal eyes and inner margin of ipsilateral eye 330  $\mu\text{m}$ . Carapace width (estimated) 1.40 mm, length (as preserved, along midline) 1.20 mm, depth of posterior emargination 0.20 mm. Lateral and posterior margins of carapace with continuous, well-developed rim. Surface of carapace without minute tubercles — instead entirely covered with fine, irregular, somewhat hexagonal imbrications (Fig. 2A). Ventral surface of prosoma not visible. **Chelicerae.** Held in opisthognathous position; base and fang dark, shiny brown. Base length 340  $\mu\text{m}$ , with paramedian pair of setae near dorsoapical margin, plus scattered smaller setae; presence/absence of ventral denticles and setal brush not visible. Fang length 240  $\mu\text{m}$ ; brush of fine, dense setulae present on mesal surface of fang (absent from tip and base of fang). **Pedipalp.** Stout, color appears dull brown. Coxa not visible; trochanter barely visible, with large ventral spine, apparently without ventral apophysis. Femur with two dorsal spines and two ventral spines, all on basal half of femur; very long trichobothrium on dorsal surface at midlength; femur slightly shorter than tibia. Tibia stout, length 1.00 mm, greatest width (frontally) 360  $\mu\text{m}$ ; dorsal surface with 4 longitudinal rows of short, stiff setae (1 row on mesal margin, 1 median row, 2 rows on/near lateral margin); tibial spine I (apicalmost) length 460  $\mu\text{m}$ , spine II 330  $\mu\text{m}$ , spine III 210  $\mu\text{m}$ , spine IV (proximalmost) 100  $\mu\text{m}$ . Basitarsus length 390  $\mu\text{m}$ ; basal part of distitarsus 360  $\mu\text{m}$ ; claw 400  $\mu\text{m}$ . Basitarsus with 2 dorsal and 1 ventral spines, spine A length 170  $\mu\text{m}$ , spine B 320  $\mu\text{m}$ , spine C 380  $\mu\text{m}$ ; basal part of distitarsus with one prominent dorsal spine, a prominent, stiff, thickened seta proximal to this spine, spine D length 215  $\mu\text{m}$ . Cleaning organ present on mesal surface of proximal half of basal part of distitarsus; row of 12 very fine, minute teeth on inner margin (seen in profile). Claw not fused to distitarsus. **Walking legs.** All legs with four tarsomeres (excluding apotele), second tarsomere divided apically to give appearance of ‘five tarsomeres’ (basitarsus longest article, tarsomere four about as long as tarsomere two; third tarsomere extremely short, as long as apical divided portion of second tarsomere); apoteles with well-developed claws and pulvilli. *Leg 1:* Coxa protruding slightly beyond margin of carapace; trochanter slightly broader than femur and slightly longer than patella; femur length 1.96 mm; tibiotarsus with approximately 45 articles in whip (21 basal articles well preserved in right leg, no trichobothria apparent; *ca.* 45 stretched, deformed articles preserved in left leg). *Leg 2:* Femur too distorted for measurement; patella with 2 short trichobothria; distitibia with 11 trichobothria, trichobothria lengths on distitibia 590–640  $\mu\text{m}$ ; trichobothria on basitarsus 380  $\mu\text{m}$ ; basitarsus length 620  $\mu\text{m}$ ; distitarsus 560  $\mu\text{m}$ ; claw 110  $\mu\text{m}$ . *Leg 3:* Trichobothrium length on distitibia 580  $\mu\text{m}$ ; basitarsus 580  $\mu\text{m}$ ; distitarsus 430  $\mu\text{m}$ ; claw 110  $\mu\text{m}$ . *Leg 4:* Basitibia undivided; distitibia with 13 long trichobothria on dorsal surface (Fig. 2D), one further trichobothrium on first tarsomere (Fig. 2D). **Opisthosoma.** Length (as preserved) 0.93 mm; ventral surface largely not visible (*i.e.*, ventral sac covers, lung slits); some sternites barely visible, quite small.



**Figure 2.** Holotype (Tad 456) of *Paracharonopsis cambayensis*, new genus and species. **A.** Details of carapace and left pedipalp (reconstructed). **B.** Close up of right pedipalp tibia and base of basitarsus. **C.** Frontal view of carapace and chelicerae. **D.** Distal portion of walking leg IV.

**HOLOTYPE:** Tad 456 (Fig. 1A), India: Gujarat, Surat District, Tadmashwar lignite mine, Cambay Shale Formation (Ypresian, *ca.* 52 Ma), coll. D. Grimaldi, P. Nascimbene, H. Singh, 2011; deposited in amber fossil collection, Division of Invertebrate Zoology, American Museum of Natural History, New York.

**PRESERVATION:** The body is largely complete but portions are slightly to extremely distorted by compression, especially the entire left half of the animal (except for the left pedipalp). The left side of the specimen appears as if smeared or stretched (Fig.



**Figure 3.** Ventral view of entire piece containing holotype (JZC Bu150) and nymphs of *Kronocharon prendinii*, new genus and species, in mid-Cretaceous amber from Myanmar.

1B) and lies adjacent to a mass of opaque organic debris (?bark), fungal hyphae, and swirls of fine froth and bubbles. The ventral surface of the prosoma and most of the opisthosoma are not visible.

**ETYMOLOGY:** The specific epithet is a reference to the Cambay Basin in which the amber-bearing deposits may be found.

Suborder Euamblypygi Weygoldt  
 Infraorder Neoamblypygi Weygoldt

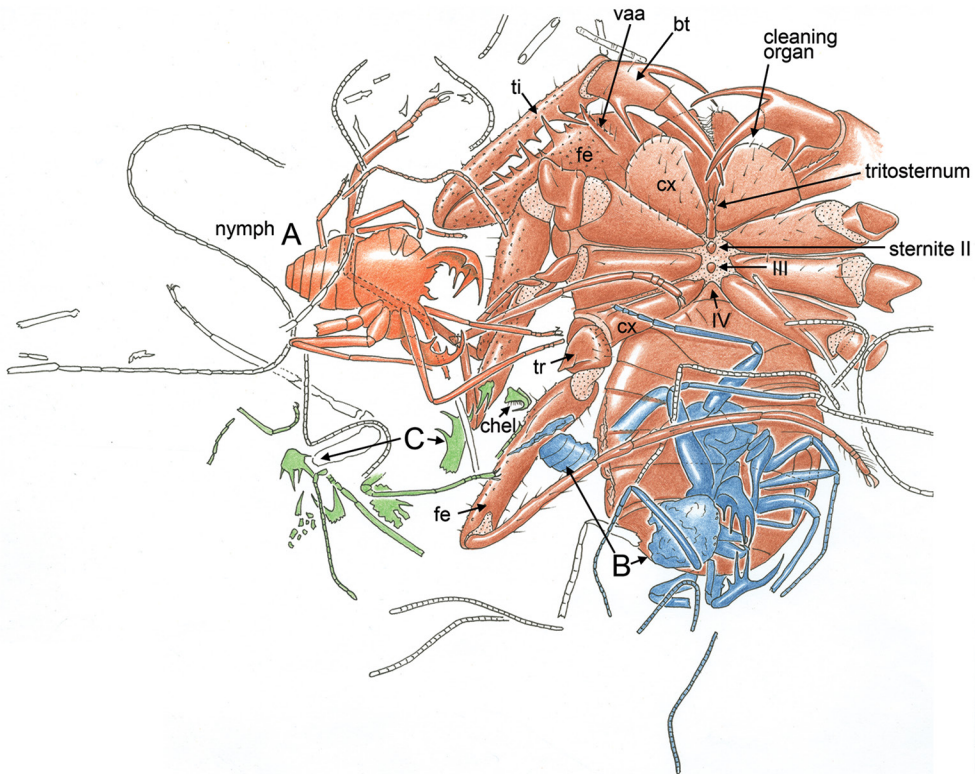
*Kronocharon* Engel & Grimaldi, new genus

ZooBank: urn:lsid:zoobank.org:act:443850E9-B193-4C9A-93EF-0A9C2D8C6223

**TYPE SPECIES:** *Kronocharon prendinii* Engel & Grimaldi, new species.

**DIAGNOSIS:** Carapace subcircular (Figs. 5A, 5C, 6), anterior margin of carapace relatively straight (Figs. 5C, 6), apicolateral angles weakly concave, otherwise lateral margins broadly and gently convex, posterior border weakly concave; median eyes present, set on low tubercle (Figs. 5C, 6), lateral eyes absent but with noticeable, swollen brow where lateral triad would be present (Fig. 6) (a likely apomorphic reduction of eyes). Pedipalp trochanter with distinct ventral, anteriorly-directed apophysis bordered by furrow (Figs. 3, 4, 5B); femur and tibia long (Figs. 3, 4, 6), femur shorter than tibia; femur with anterior-dorsal row of spines absent (typically with one or two dorsal spines) (Fig. 6), with a noticeable, upward-pointed, proximal spine on dorsal surface (Fig. 6), anteroventral row of spines present, seven short spines, two more





**Figure 4.** Map of inclusions and fragments in piece JZC Bu150, showing relative positions of adult female and nymphs A, B, and C.

prominent than others; tibia with anteriodorsal row composed of three elongate spines (Figs. 5C, 6), proximalmost spine shortest, apical two spines relatively equal in length, plus single short spine at apex beyond apicalmost primary spine, anteroventral row of three spines present, proximal two spines short, apicalmost spine longer; basitarsus with single, long, dorsal spine, and single, long, ventral spine; distitarsus not divided, with shallow and short cleaning organ present on inner proximal surface of distitarsus, without prominent setal row proximal to cleaning organ (setal row present in Charontidae). Walking legs with basitibia (fourth pair of legs) divided into two segments, proximal segment more than twice length of apical segment; second tarsomere apically divided to give appearance of 'five' tarsomeres (Fig. 6); oblique slit on fourth tarsomere absent; pulvilli present (Fig. 6).

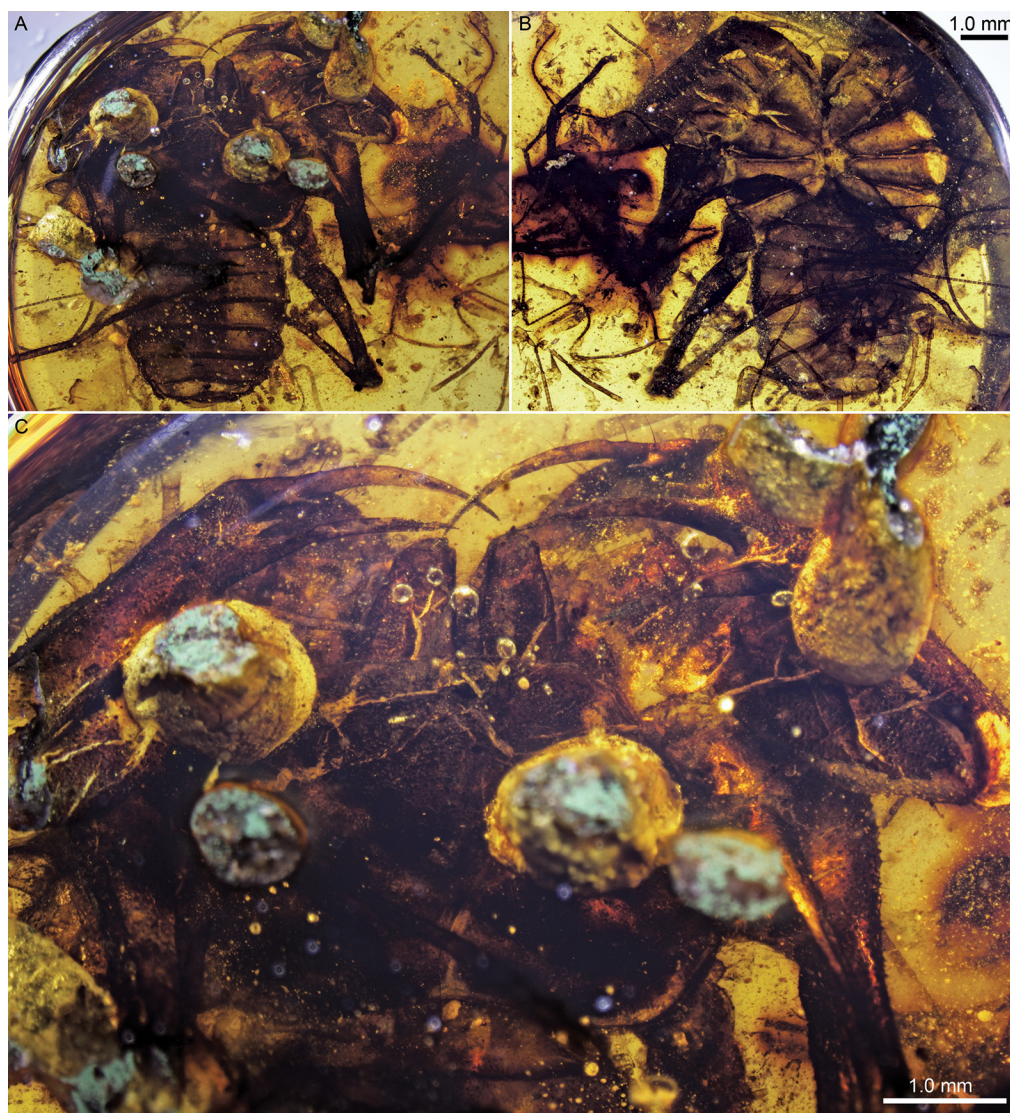
**ETYMOLOGY:** The new genus-group name is a combination of Kronos, father of the primary Olympian gods and a general figure symbolizing aged time, and *Charon*, type genus of the primitive euamblypygid family Charontidae. The gender of the name is masculine.

***Kronocharon prendinii* Engel & Grimaldi, new species**

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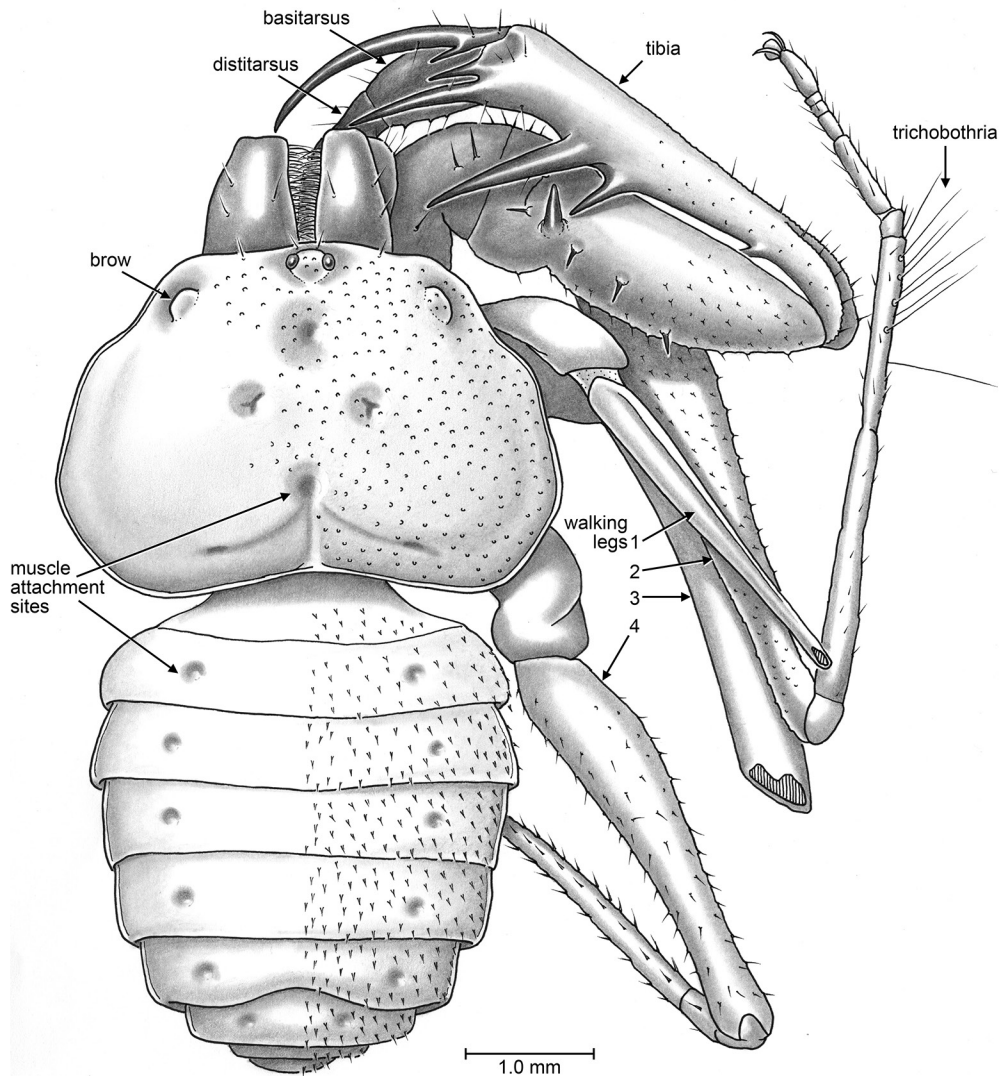
(Figs. 3–6)

**DIAGNOSIS:** As for the genus (*vide supra*).



**Figure 5.** Adult female holotype (JZC Bu150) of *Kronocharon prendinii*, new genus and species. **A.** Dorsal view of entire specimen. **B.** Ventral view. **C.** Detail of carapace and pedipalps in dorsal aspect.

**DESCRIPTION:** Total body length as preserved 6.7 mm (exclusive of pedipalps). **Carapace.** Large, slightly wider than opisthosoma, greatest width 4.18 mm; length (along midline) 2.68 mm. Anterior margin virtually straight and transverse (Figs. 5A, 5C, 6), width of anterior margin 2.00 mm; this margin with four very short, stiff setae, one pair anterior to median eyes, smaller pair just above cheliceral bases. Lateral margins convex; posterior margin weakly concave (Fig. 6), depth of concavity 250  $\mu$ m. Carapace with 6 obvious depressions (marks of internal muscle attachments): median one just posterior to eyes; pair of small triangular, paramedian ones near mid-length; deep, median one 0.60 mm from posterior margin, from which pair of shallow grooves diverge, each ending in small, shallow pit. Pair of frontal eyes on shallow



**Figure 6.** Dorsal view of adult female holotype (JZC Bu150) of *Kronocharon prendinii*, new genus and species.

tubercle, distance between outer margins of frontal eyes  $460\ \mu\text{m}$ . Lateral eyes apparently absent, instead replaced by distinctive 'brow' (Fig. 6); distance between outer margin of frontal eye and inner margin of ipsilateral 'brow'  $680\ \mu\text{m}$  (lateral eyes may be present under brow, but if so, then they are impossible to see). Cuticular surface evenly covered with small, scale-like tubercles, few/none of which bear setulae (Fig. 6). **Prosoma (ventral).** Four sternites present; tritosternum slender, digitate, length  $560\ \mu\text{m}$ ; sternites II and III small, circular; sternite IV not divided, but single, median, triangular sternite lying between coxae<sub>4</sub>. **Chelicerae.** Largely hidden from view, with dorsal surface of basal article visible, surface smooth (no tubercles or rugosity), bearing 3 setae, length of exposed portion of cheliceral base 1.00 mm. Brush of dense, fine setae present (distribution of setae on base and fang not visible; cheliceral denti-



tion also not visible). **Pedipalp.** Large, combined length of segments nearly 11 mm; cuticle evenly covered with small scale-like tubercles, some of which bear 1 minute setula. Coxa (along midline) 1.50 mm; trochanter with large, carina-like, anteriorly-directed ventral apophysis bordered by furrow (Figs. 3, 4, 5B), dorsally with 2 stout setae. Femur length 2.74 mm; dorsal-facing surface with longitudinal row of 5 small, tubercle-like spines (second spine from base is largest); ventrally with row of 7 spines on anterior surface, alternating in size (3 large spines, 4 small ones). Tibia length 3.79 mm; tibial dorsal spine I length 1.52 mm; spine II 1.65 mm; spine III 410  $\mu\text{m}$  (single small spinelet 330  $\mu\text{m}$  in length just apical to spine I). Basitarsus length 1.24 mm; distitarsus length 1.06 mm, shallow and short cleaning organ present proximally (faintly observable in lateral view), with fine microtrichia; tarsal spines: 2.12 mm, 670  $\mu\text{m}$ ; claw length (linear) 310  $\mu\text{m}$ . **Walking legs.** Largely preserved on right half of specimen; on all legs apotele with pair of large claws and large pulvillus. *Leg 1:* trochanter and most of femur preserved (apex lost at surface of amber); femur<sub>1</sub> very slender; portions of whip apparently preserved in amber piece, but disarticulated and scattered (number of articles cannot be determined). *Leg 2:* length of coxa<sub>2</sub> 1.53 mm; femur<sub>2</sub> with small, scale-like tubercles, base stout; patellar-tibial joint appearing immobile; basitibia<sub>2</sub> 2.0 mm long, appears 2-, possibly 3-segmented; distitibia<sub>2</sub> 1.60 mm long, bearing 9 long trichobothria on dorsal surface (1 near middle, 4 pairs on distal half); tarsus<sub>2</sub> with 6 segments, including small (220  $\mu\text{m}$ ) segment at base, second tarsomere 700  $\mu\text{m}$  long, remaining distal tarsomeres (3–6) 810  $\mu\text{m}$  long. *Leg 3:* coxa<sub>3</sub> 1.72 mm long. *Leg 4:* coxa<sub>4</sub> length 1.84 mm, femur<sub>4</sub> length 3.6 mm; basitibia<sub>4</sub> 2-segmented, distal segment 0.28x length of proximal segment. **Opisthosoma.** Broad, flat; length 4.00 mm, width 3.56 mm; entire dorsal surface covered with scale-like tubercles, each tubercle pointed and bearing 1 fine setula. Nine segments visible dorsally (posterior two tergites very short); each segment with pair of slightly depressed, circular, bare areas that mark internal muscle attachments (*ca.* 0.5 mm from lateral margin).

**HOLOTYPE:** ♀ (Fig. 3), JZC Bu150, Myanmar: Kachin, near Myitkyina, Cretaceous (earliest Cenomanian, latest Albian, *ca.* 99 Ma); in James Zigras Collection, indefinitely held in the Division of Invertebrate Zoology, American Museum of Natural History, New York.

**ADDITIONAL MATERIAL:** Fragments of at least three nymphs, same piece of amber as holotype (Fig. 4).

**PRESERVATION:** The amber piece containing the whipspiders is a small, flat, oval piece of 14 mm length x 16 mm width x 3.5 mm thickness (Fig. 3), remarkably containing much of one large specimen and disarticulated remains of at least three nymphs (Fig. 4). Figure 4 is a map of the piece, with color codes for each specimen and for those disarticulated remains that can be associated with certain nymphs (some parts could not be associated with bodies). Descriptive notes on the three nymphs are summarized here. The nymphs are overall about 0.27x the size of the adult female and there are 14 fragmentary segments of whiplike legs, some clearly belonging to the adult female based on thickness and segment size, while the others are of the nymphs. **Nymph A.** Body length *ca.* 1.8 mm; best preserved individual, missing only some appendages; pedipalps separated and well displayed; nymph adjacent to right walking legs III and IV of adult female, four of its appendages extended beneath ventral surface of female; lying perpendicular to and facing female, in same dorsoventral position as female. **Nymph B.** Body length *ca.* 1.8 mm; portions disarticulated, opisthosoma separated from carapace, lying *ca.* 1.3 mm from posterior margin of carapace; still with pedipalps, five walking legs attached to cephalothorax (including basal portions of

each whip), as well as chelicerae; most interesting aspect of this nymph is its position adjacent to ventral surface of posterior portion of adult female's opisthosoma; body of nymph pointing in same direction as nymph A, but dorsoventral orientation of nymph B opposite that of nymph A and adult female. **Nymph C.** Highly fragmentary, essentially consisting of two groups of pedipalp fragments, separated by *ca.* 1.2 mm, an isolated pair of chelicerae lying between these remains and body of female, and some unidentifiable other cuticular fragments.

**ETYMOLOGY:** The specific epithet is a patronym honoring Dr. Lorenzo Prendini of the American Museum of Natural History, a terrific colleague, and a world-class arachnologist and monographer.

## DISCUSSION

The Indian species, *Paracharonopsis cambayensis*, is noteworthy as the first Tertiary and Oriental record of the relic suborder Paleoamblypygi. Virtually all of the Paleozoic occurrences of the order may be assigned to this group, otherwise comprising five Carboniferous species and the living *P. caecus* from tropical Guinea-Bissau. The defining feature of this group is the medioanterior prolongation of the carapace, a trait easily observed in *P. caecus* and *Graeophonus* (Weygoldt, 1996, 2000; Dunlop *et al.*, 2007), but also pedipalp spination and the low number of trichobothria on distitibia<sub>4</sub>. The discovery of a paracharontid in the Ypresian amber of the Cambay Basin attests to the widespread distribution of these animals even as late as the mid-Paleogene, although they were perhaps relic by this time. Further living relicts may persist in unexplored, tropical areas of this region. Although scarcely anything is known of the biology of *P. caecus*, the one record of it consists of specimens collected from deep within a termite nest, suggesting that exploration of such mounds would be fruitful. *Paracharon caecus* is blind and presumably never or rarely leaves the confines of the termite nest. Its association with termites remains unstudied and unfortunately the termites from whose nest it was collected have never been identified or reported. Alternatively, caves and karst landscapes might also host isolated relicts and there are certainly vast areas remaining for exploration. *Paracharon* is a surviving descendant of what was previously a more diverse and globally-distributed group of whipspiders, and the last remnant of a group whose initial radiation was in the Paleozoic.

It is interesting to note that *P. cambayensis* has at least distant ties to a species today occupying westernmost Africa. This further highlights the broad biogeographic connections between Cambay amber arthropods and coeval or surviving relatives in lands as distant as South America and northern Europe (Rust *et al.*, 2010). Many of these examples are indicative of widespread groups occupying continental areas as well as the Indian subcontinent (*e.g.*, Engel *et al.*, 2011a, 2011b; Grimaldi & Singh, 2012; Grimaldi *et al.*, 2013a, 2013b; Engel *et al.*, 2013), which was still marginally separated by shallow waters and archipelagos during the Ypresian (Chatterjee & Scotese, 2010; Chatterjee *et al.*, 2013). It is highly unlikely, however, that *P. cambayensis* were capable of extensive dispersion, particularly over large bodies of water. Given the biology of most Amblypygi, it is more likely that *P. cambayensis* was a relict of a more ancient paracharontid diversity that left behind *P. caecus*, and which occupied Gondwana over 130 million years ago, prior to the rifting of India and Madagascar from the other continents.

At about twice the geological age of *P. cambayensis*, *Kronocharon prendinii* is remarkable as the first Cretaceous amber whipspider. It is further noteworthy in that, unlike the Indian species, *K. prendinii* is a member of the Euamblypygi, the suborder compris-



ing all but one of the over 160 species of living whipspiders (Harvey, 2003; Prendini, 2011). It can even be placed within the Neoamblypygi. Although the genus has primitive features typically associated with the Charinidae (*i.e.*, the prominent and well developed ventral apophysis on the pedipalp trochanter, a noteworthy plesiomorphy), the genus shares more derived traits with the Neoamblypygi, such as the straight anterior margin of the carapace and the apical two dorsal spines of the pedipalp tibia having relatively equal lengths. *Kronocharon* does not belong to the Phrynoidea (= Apulvillata) as evidenced by the presence of pulvilli, absence of the oblique slit on the fourth tarsomere, and the presence of a well-developed ventral apophysis on the pedipalp trochanter. *Kronocharon* cannot be placed within the Charontidae based on the absence of the distinctive row of setae at the base of the cleaning organ on the pedipalp distitarsus. Interestingly, *Kronocharon* would appear to represent a sister group to the Phrynoidea due to the undivided pedipalp distitarsus, the two taxa apparently forming a clade – ‘Unidistitarsata’ (Table 1).

Beyond its rather interesting phylogenetic position, the adult female holotype of *K. prendinii* is preserved with the remains of three nymphs, presumably her offspring, still clustered near or in contact with the venter of her opisthosoma, attesting to the antiquity of maternal care among whipspiders. Parental behavior in the fossil record is perhaps best popularized by records among dinosaurs and mammals, but there are notable examples from among insects such as clusters of nymphal earwigs preserved in Cretaceous amber from France (Engel, 2009), larval cases of leaf beetles initially constructed by the mother (Chaboo *et al.*, 2009), or even ants carrying larval and pupal brood (Weitschat & Wichard, 2002), the latter being more broadly ‘colonial care’ rather than individual maternal care. Given that many parent-offspring interactions do not leave a physical trace, such ephemeral behaviors are difficult, if not impossible, to track in the fossil record. It is therefore all the more dramatic that such an occurrence could be documented in a fossil whipspider, and the oldest of its kind preserved in amber.

Whipspiders typically are found in humid and moist environments such as caves or the leaf litter, rock crevices, and rotten logs of tropical forests, and much less frequently in arid habitats. Certainly both the Burmese and Indian amber forests match well with this general habitat preference, although the specific conditions that would have to be met in order capture such elusive species would certainly have been a rare event. In both cases, the fossil species were likely living among the leaf litter or moist crevices of fallen logs, including those of the amber-producing trees in the environment, thereby bringing them into contact with resin flows at the base of trees or perhaps resin masses in a tree fall. This is also consistent with the occurrence of amber-entombed whipspiders in the ambers of the Dominican Republic and Chiapas, Mexico. This is assuredly the primitive habitat preference for Amblypygi going back to the Carboniferous, and those derived lineages today found in deserts have evolved secondary adaptations to surviving in more xeric environments.

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*Pharciphyzelus lacefieldi* Beckemeyer & Engel, 2011

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