The earliest palpimanid spider (Araneae: Palpimanidae), from the Crato Fossil-Lagerstätte (Cretaceous, Brazil)

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Abstract.   The Crato Formation (Lower Cretaceous) of Brazil is well known for an exceptionally preserved terrestrial arthropod fossil assemblage. Spiders are relatively abundant, but few have been formally described. A fossil spider belonging to the family Palpimanidae, araneophageous ground-dwelling spiders with distinctly robust front legs, is preserved with the dorsal side hidden within the rock matrix. For the first time, micro-computed tomography (micro-CT) was used to image a fossil spider preserved in a rock matrix, to reveal the dorsal side of this specimen, revealing the eye arrangement, a useful taxonomic character in most spiders, and a deflated abdomen, likely the result of taphonomic processes. The specimen possesses other distinguishing characteristics of Palpimanidae, including an inflated first leg femur, a heavily sclerotized scutum, and a reduced number of spinnerets (2) surrounded by a sclerotized ring. The spider has eight eyes with the lateral pairs extremely close together, a trait suggestive of the subfamily Chediminae. The specimen also possesses an unusual first leg patella with a retrolateral excavation and a thorn-like projection. A new genus is erected, and the spider is named *Cretapalpus vittari* gen. et sp. nov. A phylogenetic analysis including extant species from each of the subfamilies within Palpimanidae places the fossil at the base of Chediminae + Otiothopinae. This is the earliest reported fossil palpimanid and first chedimine from South America. A fossil chedimine in South America is not surprising because the South American and African plates were still relatively close during the Early Cretaceous.

Keywords: Mesozoic, paleobiogeography, Palpimanoidea, systematics

The Palpimanidae is a small family (18 genera, 157 species) of nocturnal, ground-dwelling spiders whose members occur mainly in tropical and subtropical regions of the world, except Australia (Jocqué & Dippenaar-Schoeman 2006; World Spider Catalog 2021). They are characterized by an extremely thick cuticle on all parts of the body except the opisthosoma (even here, there are commonly sclerotized scuta) and enlarged front legs. By this means, they stalk and capture other spiders as prey, yet are armored against retaliatory bites (Cerveira & Jackson 2005; Pekár et al. 2011). Palpimanidae is historically a poorly studied group but, recently, several genera have been revisited or newly described.

Spiders from the Cretaceous Fossil-Lagerstätte (locality of exceptional fossil preservation) of Crato, Brazil, are relatively numerous but, hitherto, few have been described (Mesquita 1996; Selden et al. 2006; Raven et al. 2015). Here, we present a single specimen of a palpimanid from this locality. It is the oldest member of the family and the first Mesozoic record; the previously known oldest, and only known fossil occurrence of Palpimanidae, are three juvenile specimens of the extant genus *Otiothops* MacLeay, 1839 from the Neogene Dominican amber (Wunderlich 1988); a possible palpimanid has also been reported from mid-Cretaceous Burmese amber (Wunderlich 2017). Nevertheless, the superfamily Palpimanoidea has representatives dating back to the Jurassic period (Penney 2004; Selden et al. 2008; Selden & Dunlop 2014; Wunderlich 2015; Selden et al. 2019 and references therein), so the existence of the nominate family in the early Cretaceous is not improbable. Palpimanoidea, especially the family Archaeidae, has received much more attention in phylogenetic studies. Little work has been done on phylogenetic relationships specifically within Palpimanidae (Wood et al. 2012).

The family Palpimanidae is divided into three subfamilies: Chediminae, Otiothopinae, and Palpimaninae (Platnick 1975, 1985). The specimen described here is referred to the subfamily Chediminae, a clade known today only from Africa across to south Asia (Zonstein & Marusik 2013). The fossil possesses closely spaced lateral eyes, a characteristic commonly used for placement in Chediminae. No extant specimens of Chediminae have been discovered from South America; however, the presence of a fossil specimen in Brazilian sediments is not unexpected, given that the South American and African continents were still in close proximity in the early Cretaceous, and other fauna from the Crato beds show similar affinities to present-day African clades, e.g., Solifugae, Scorpiones (Selden & Shear 1996; Menon 2007).

STRATIGRAPHY AND PALEOECOLOGY

The specimen comes from one of the quarries in the Nova Olinda Member of the Crato Formation around the town of Nova Olinda, Cearà Province, northeastern Brazil. The Nova Olinda member is at the base of the Crato Formation and is composed of alternating laminated limestones and mixed carbonate and clastic beds (Martill & Heimhofer 2007). An accepted age of late Aptian (115–120 Ma) for the Crato Formation is based on palynological data (Heimhofer & Hochuli 2010). The depositional environment is interpreted as a stratified lake with hypersaline bottom waters in a semi-arid to arid environment (Heimhofer et al. 2010). The lake basin was the result of extensional tectonics when active rifting was separating the South American and African continents during the early Cretaceous (Martill 2007).
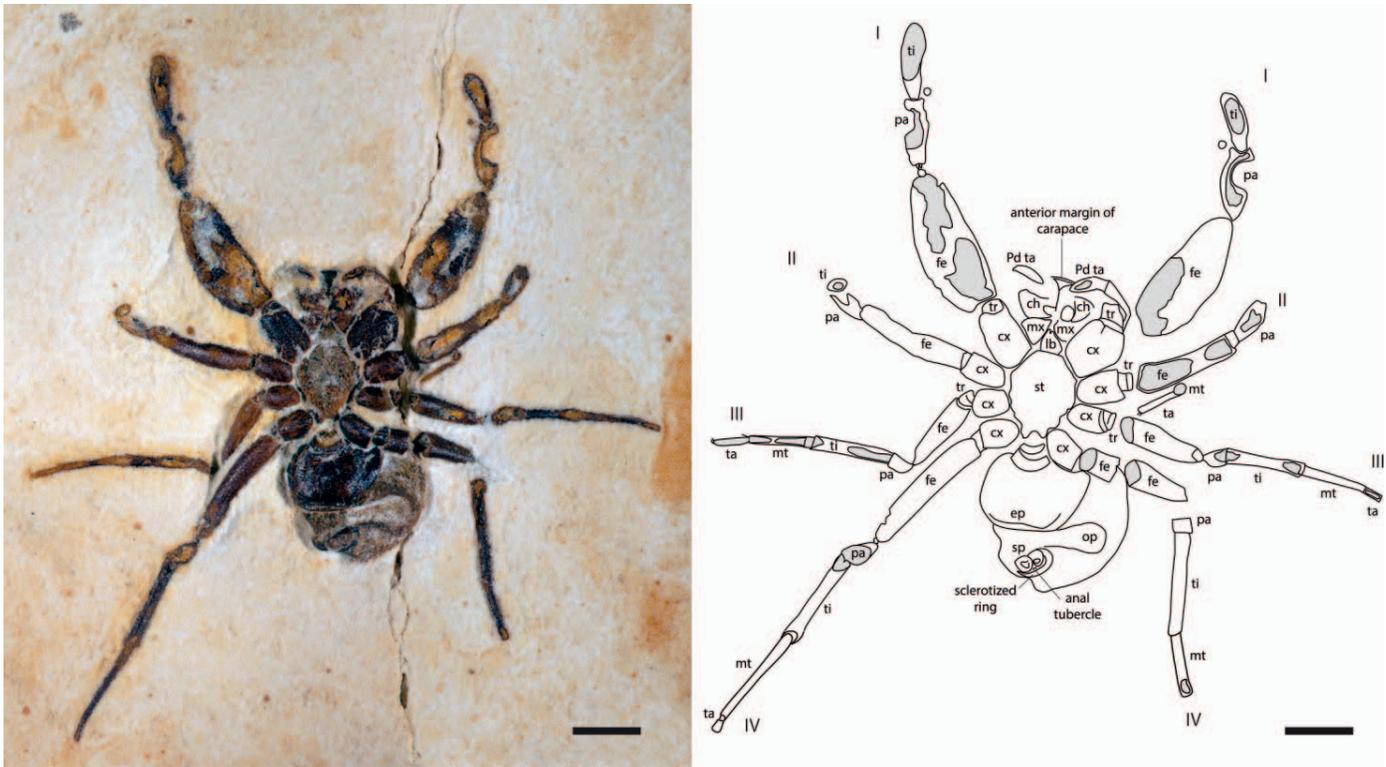
Figure 1.—*Cretapalpus vittari* gen. et sp. nov. Photograph and interpretative drawing of ventral side. Gray areas represent missing cuticle. Scale bar = 1 mm.

Notable fauna from this deposit include fish and pterosaurs, but terrestrial invertebrates like insects dominate the fossil assemblage (Martill et al. 2007). Spiders are relatively abundant, although rarer than insects. The preserved arachnofauna provides an interesting insight into the paleoenvironment. The presence of solifuges supports the semi-arid climate interpretation; however, other fossilized arachnids like scorpions and amblypygids suggest possibly more humid conditions (Selden & Shear 1996; Dunlop & Martill 2001; Menon 2007). There were likely a variety of environments relatively close to the Crato paleolake from which organisms could be transported. Most of the arachnids in the deposit are spiders, with many resembling aerial web-weaving spiders.

METHODS

Materials.—The specimen was donated to PAS by the Chapada do Araripe Paleontological Research Center and National Department of Mineral Production (CPCA-DNPM) for the purpose of research and teaching. The specimen consists of a part only, in ventral view, with some legs extended, others partly (e.g., left leg III, right leg IV) or fully (e.g., right leg II) flexed (Fig. 1). The distal podomeres of some legs are absent, presumably lost with the counterpart; these are: metatarsus and tarsus of leg I, tibia to tarsus of leg II, left (on the right, the tarsus of leg II is present, folded back alongside the proximal part of the leg, Fig. 1), and most of the tarsi of legs III (right) and IV; left leg III is complete to the tip of the tarsus. The cuticle of the fossil is preserved in a buff-colored, finely laminated limestone (Plattenkalk) by replace-

ment with goethite (hydrated iron oxide); a finely tuberculate surface sculpture can be seen on external surfaces (e.g., on the ventral scutum, Fig. 1), and the sternum has a coarsely tuberculate sculpture. Within the matrix, spines and setae can be seen at the margins of podomeres (e.g., right tibia and metatarsus IV, Fig. 1). Within the specimen, cavities are partly filled with calcite crystals, though some pale tan, fibrous material (e.g., in right femur II, Fig. 1) likely represents replaced muscle. The exceptional preservation of the insects in the Nova Olinda Member has recently been described by Barling et al. (2015). These authors showed that the goethite seen in specimens in weathered matrix has actually replaced other iron minerals, which are present in the un-weathered samples. Nevertheless, the mineralization has replaced the original organic material in remarkably fine detail. Palpimanids have a distinctively thick cuticle (Pekár 2011, table 3), and so this specimen is preserved quite three-dimensionally, except for the soft parts of the opisthosoma, which are deflated and folded, especially when viewed in 3D (Fig. 2). The deflated abdomen is likely the result of taphonomic processes related to osmosis and the hypersaline bottom waters of the Crato paleolake (Downen et al. 2016).

Methods.—The specimen was studied using a Leica M205C stereomicroscope, photographed with a Canon EOS 5D MkII digital camera attached to the microscope and captured with DSLR Assistant software (www.kaasoft.com) on an Apple MacBook Pro computer. Drawings were made using a drawing tube attached to the microscope. Photographs were manipulated using Adobe Photoshop software, and final drawings were made using Graphic (www.graphic.com). All
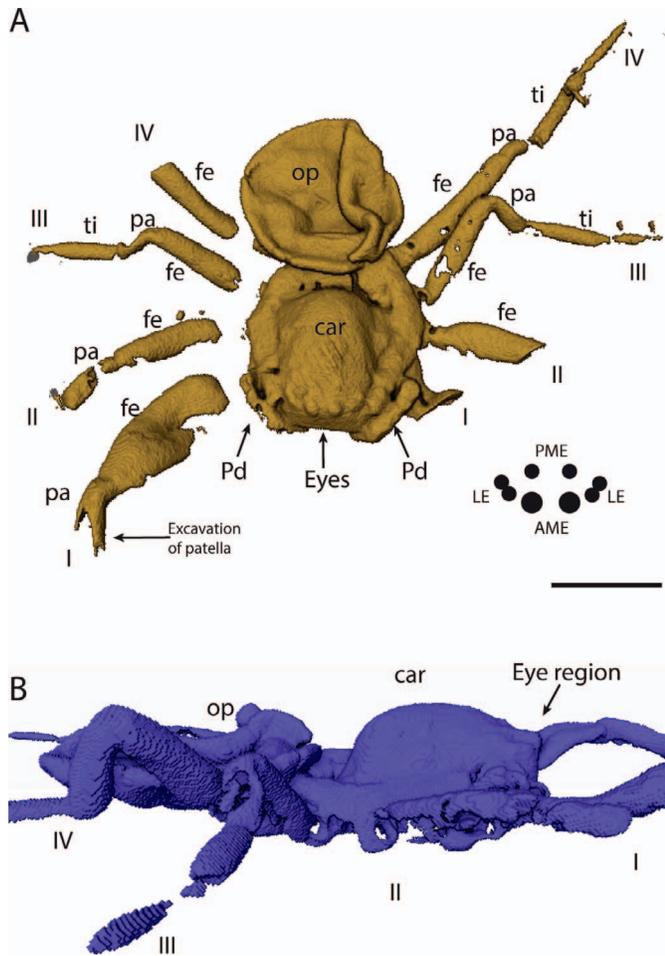
Figure 2.—*Cretapalpus vittari* gen. et sp. nov. 3D rendered volume of the fossil. (A) In dorsal view, the carapace, eye pattern, pedipalps, patella excavation, and deflated abdomen are visible. (B) Lateral view. Scale bar = 1 mm.

measurements are in millimeters and were made from the drawings using Graphic. Measurements of paired organs are means of left and right. Note that, because of the three-dimensional preservation, it is not possible to get accurate measurements for some podomeres— posterior femora and patellae in particular—and the distorted opisthosoma defies accurate measurement.

The sample was cut with a Dremel saw into a rectangular prism to minimize the amount of matrix. The dorsal side of the specimen was imaged using an FEI HeliScan micro-CT scanner in the Earth, Energy and Environment Center (EEEC) at the University of Kansas, Lawrence KS. The specimen was mounted upright on a stub with double-sided sticky tape and rotated through the x-ray beam for approximately eight hours (Supplemental Material, online at https://dx.doi.org/10.1636/JoA-S-19-059.s1). The data were reconstructed using qmango software (Thermo Fisher Scientific). Segmentation and 3D visualization were conducted in PerGeos Software for Digital Rock Analysis at the University of Kansas. Measurements of 3D images were made using PerGeos Software and Adobe Photoshop.

Cladistic analysis and character matrices.—Two analyses were conducted. The fossil and four other palpimanid genera

were scored into the matrix used in Selden et al. (2019, supplemental material), which is based on the matrix used in Wood et al. (2012, appendix 2). The analysis also used the same methods as in Selden et al. (2019). The analysis employed MrBayes v3.2.6 and generated a majority rule consensus tree. The tree was imported into FigTree v1.4.4 and manipulated for visuals. The character matrix (online at https://dx.doi.org/10.1636/JoA-S-19-059.s2) and associated code for the analysis is included as a NEXUS file in Supplementary Files (online at https://dx.doi.org/10.1636/JoA-S-19-059.s3). A second analysis was run using PAUP* v4.0a (build 167) (Swofford 2003). In this analysis, only palpimanid genera and one outgroup were included to examine relationships within Palpimanidae. This simple phylogenetic analysis based on morphological characters was conducted to determine to which subfamily the fossil spider belongs. The fossil specimen, although exceptionally preserved, lacks many useful visible characters that are observed in extant specimens such as genitalia, the fovea, and details of the chelicerae. Morphological characters were chosen primarily based on what is visible in the fossil and by characters used to distinguish the three subfamilies. Characters of extant palpimanids were taken from descriptions and figures from previous literature. A simple heuristic search (Optimality criterion = parsimony) returned 14 trees and a 50% majority-rule consensus tree. The trees were manipulated in FigTree v1.4.4 for visuals.

Taxon sampling.—The Crato specimen was compared with palpimanids described in the recent literature. The phylogenetic analysis based on the Selden et al. (2019) matrix included the fossil specimen and four additional palpimanid genera: *Chedimanops* sp. (see Zonstein & Marusik 2017b), *Levymanus* sp. (see Zonstein & Marusik 2013), *Steriphopus* sp. (see Simon 1887), and *Otiothops* sp. The smaller analysis focusing explicitly on Palpimanidae was based on seven taxa. Species from each of the three subfamilies were included in descriptive comparisons and the simple phylogenetic analysis. Chedimininae is the most diverse subfamily with regard to number of genera (11), but only four species, each from a separate genus, were included here. From Chedimininae: *Levymanus gershomi* Zonstein & Marusik, 2013; *Steriphopus macleayi* (O. Pickard-Cambridge, 1873); *Diaphorocellus isalo* Zonstein & Marusik, 2020; and *Scelidocteus taitave* Oketch & Li, 2020. *Palpimanus* Dufour, 1820 (Palpimaninae) and *Otiothops* (Otiothopinae) are the most species-rich genera. From Otiothopinae: *Otiothops chiaque* Cala-Riquelme, Quijano-Cuervo & Agnarsson in Cala-Riquelme et al., 2018; *Otiothops atalaia* Castro, Baptista, Grismado & Ramírez, 2015; *Notiothops* sp. (see Platnick et al. 1999); and *Fernandezina jurubatiba* Castro et al., 2015. Palpimaninae only contains three genera: *Palpimanus*, *Ikuma* Lawrence, 1938, and *Badia* Roewer, 1961. *Palpimanus* was already included in the Selden et al. (2019) and Wood et al. (2012) matrices. No taxonomic work exists for *Ikuma* and *Badia* beyond the 1960s, so *Palpimanus processigor* Strand, 1913 was used. The outgroup was represented by *Huttonia palpimanoides* O. Pickard-Cambridge, 1880 (Huttoniidae). Huttoniidae has been included in previous molecular and morphological phylogenetic analyses, and is commonly recovered as the sister group to Palpimanidae (Wood et al. 2012).

Morphological Characters.—The 10 morphological characters used in the cladistics analysis are listed below. Each character state is coded as (0) or (1), with (?) representing an unknown. All characters are coded as (0) for their state in *Huttonia*.

1. Leg I: (0) not inflated, (1) inflated.
2. Size of leg I patella: (0) fe/pa > 1.25, (1) fe/pa ≤ 1.25
3. Distance between lateral eyes (ALE-PLE): (0) > 0.01, (1) < 0.01.
4. Distance between posterior median eyes (PME): (0) > 0.01, (1) < 0.01.
5. PME size: (0) subequal to other eyes, (1) larger than other eyes.
6. Anterior eye row shape: (0) straight or recurved, (1) procurved.
7. Tegular sclerites: (0) present, (1) absent.
8. Labium shape: (0) labium longer than wide, (1) labium as long as wide.
9. Maxillae shape: (0) rotated so distal edge is convergent, (1) not rotated so project forward.
10. Conductor of male pedipalp: (0) present, (1) absent.

Abbreviations: AME, anterior median eye(s); car, carapace; ch, chelicera; cp, clypeus; cx, coxa; fe, femur; L, length; lb, labium; LE, lateral eye(s); mt, metatarsus; mx, maxilla; op, opisthosoma; pa, patella; Pd, pedipalp; PME, posterior median eye(s); sp, spinnerets; st, sternum; ta, tarsus; Th, thorn; ti, tibia; W, width. Repository abbreviation: KUMIP, University of Kansas Natural History Museum, Department of Invertebrate Paleontology.

SYSTEMATIC PALEONTOLOGY

Order Araneae Clerck, 1757
Suborder Opisthothelae Pocock, 1892
Infraorder Araneomorphae Smith, 1902
Superfamily Palpimanoidea *sensu* Wood, 2012
Family Palpimanidae Thorell, 1870

Remarks.—The characters of the family which place the fossil in the Palpimanidae are: inflated first leg (all podomeres from coxa to at least tibia are swollen in comparison with other legs); free labium; single pair of spinnerets (presumably anterior), surrounded by a sclerotized ring; sternum scutiform, coarsely tuberculate, with extensions between coxae (Platnick 1975; Jocqué & Dippenaar-Schoeman 2006).

Genus *Cretapalpus* gen. nov.

Type species.—*Cretapalpus vittari* sp. nov. (monotypic).
Diagnosis.—Distinguished from all other palpimanids by the patella of the first leg, which is short, excavated retrolaterally, and bears a distal prolateral apophysis.
Etymology.—After the Latin *creta* for chalk and *palpus* for the palp-footed spiders.

Cretapalpus vittari sp. nov.
(Figs. 1–3)

'Palpimanid spider' Selden & Penney, 2017: 113 fig. 16.

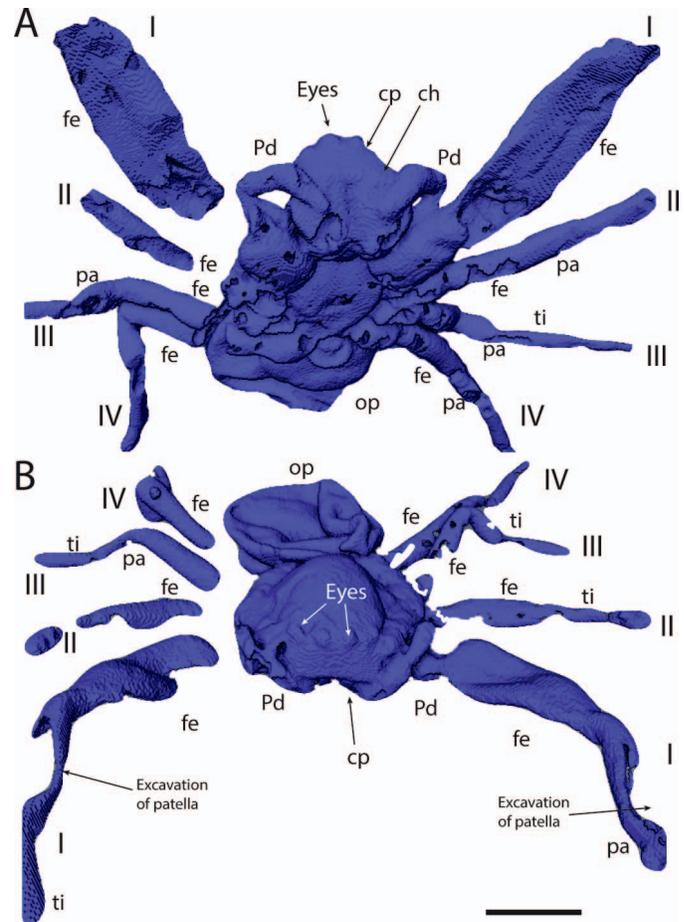**Etymology.**—Named for the Brazilian singer, songwriter, and drag queen Pabllo Vittar.

Figure 3.—*Cretapalpus vittari* gen. et sp. nov. 3D rendered volume of the fossil. (A) Oblique view of anterior and ventral showing clypeus, chelicerae, eyes, and palps with unmodified tarsi. (B) Head-on view of anterior showing excavations on patella of the first leg. Scale bar = 1 mm.

Type material.—Holotype subadult male, only known specimen, part only, KUMIP 374705, from Nova Olinda Member of the Crato Formation; Early Cretaceous (late Aptian) age; quarry at Nova Olinda, Cearà Province, Brazil; deposited in the University of Kansas Natural History Museum, Department of Invertebrate Paleontology.
Diagnosis.—As for the genus.
Description.—Carapace suboval in outline, narrowing slightly anteriorly, anteriorly truncated in dorsal and lateral view, steeply sloping posteriorly. Labium triangular, as long as wide, and notched distally. Maxillae stout, almost as long as wide, tapering distally. Sternum scutiform, heavily tuberculated, extensions around coxae and pedicle attachment. Eye region slightly projected forward. Eight eyes in two rows; AE row slightly recurved, PE row slightly recurved. AME largest (diameter = 0.19, 2× diameter of other eyes), other eyes subequal (average = 0.82). Distance between AME 0.11. Distance between AME and ALE 0.12. Distance between lateral eyes < 0.01. Clypeus height 0.39 (2× diameter of AME). Chelicerae 2× long as clypeus height. Patellae short, with excavation > ½ their length. Distal prolateral apophysis on patellae 0.29 long. Opisthosoma
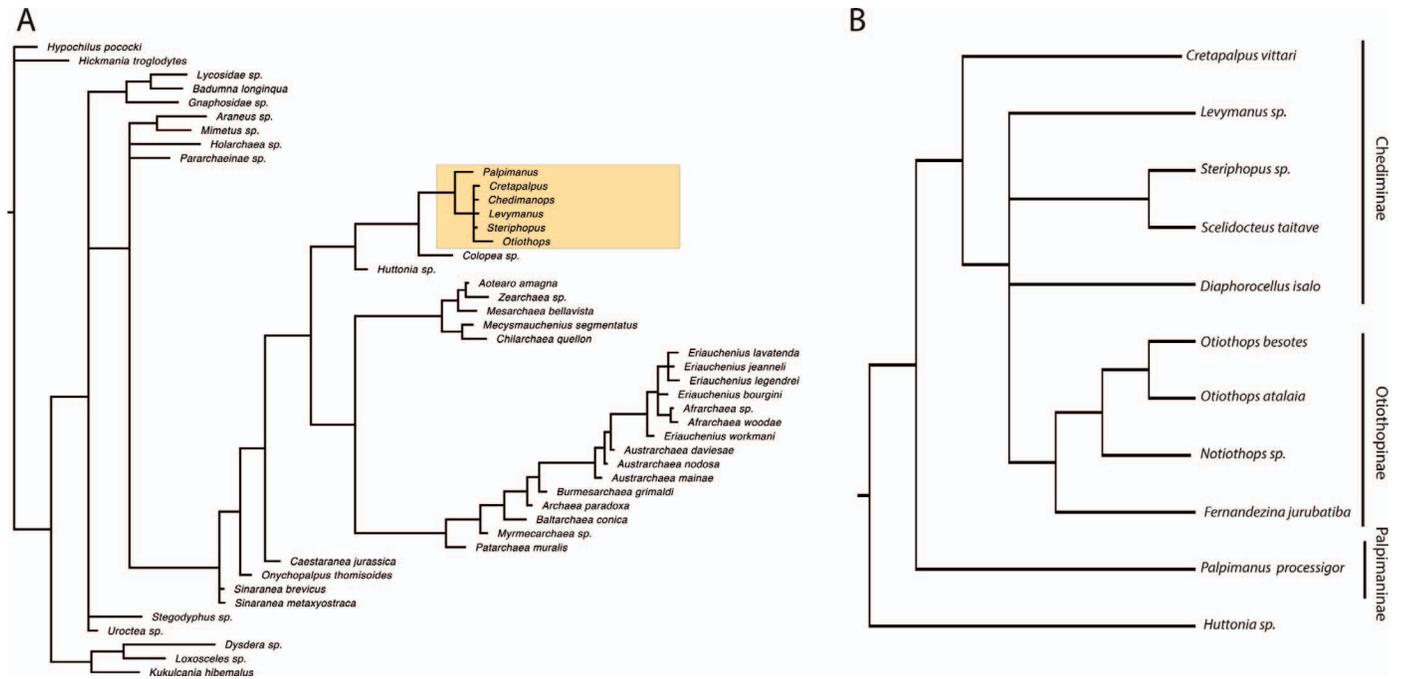
Figure 4.—Phylogeny of extant genera and *Cretapalpus vittari* gen. et sp. nov. (A) Phylogenetic reconstruction based on Selden et al. (2019) matrix. All palpimanid genera except *Palpimanus* are unresolved as a polytomy. (B) 50% Majority-rule consensus phylogeny of palpimanid genera with subfamilies indicated.

rounded in outline, about as long as wide. Ventral scutum nearly ½ length of opisthosoma and nearly equal to length of sternum, lacking extensions, with heavily sclerotized ring around pedicle.

Measurements: body L 4.71; car L 1.81, W 1.80 (L/W 1.01); op L 2.27, W 2.23 (L/W 1.01); st L 1.33, W 1.01 (L/W 1.32); lb L 0.42, W 0.32 (L/W 1.32); mx L 0.40, W 0.34 (L/W 1.18). Podomere lengths: Pd ta 0.49; leg I cx 0.89, tr 0.89, fe 2.11 (W 0.86, L/W 2.45), pa 1.05, ti ≥1.14; leg II cx 0.64, tr 0.22, fe 1.65 (W 0.42, L/W 3.92), pa 0.67, ta 0.71; leg III cx 0.61, tr 0.31, fe 1.21 (W 0.36, L/W 3.35), pa 0.37, ti 1.19, mt 0.95, ta 0.56; leg IV cx 0.57, fe 2.03 (W 0.41, L/W 4.99), pa 0.62, ti 1.52, mt 1.53. Ventral scutum L 1.18, W 1.49, L/W 0.79.

DISCUSSION

The classification of spiders, especially at the generic and specific level, typically relies on genitalic characteristics of the male and female. This is also true for palpimanid spiders, with recent papers also including the internal structure of the copulatory organs of females (Castro et al. 2015; Zonstein et al. 2016; Zonstein & Marusik 2017a). The specimen described here is a subadult male, indicated by the thorn-like modifications on the front legs and unmodified palps (Fig. 3). Some male palpimanines, like *Palpimanus armatus* Pocock, 1898, possess a thorn-like extension of the cuticle on the femur and patella of the first leg. These features suggest the specimen is a male, and was initially suggestive that the fossil was a palpimanine but, based on characteristics of the eyes and mouthparts, *Cretapalpus* is unlikely to belong to Palpimaninae. Characteristics of the eyes, including size and arrangement, are helpful in understanding the subfamily and phylogenetic placement of *Cretapalpus*. The closely spaced lateral eyes of the Crato specimen are

suggestive of Chediminae. Closely spaced or touching lateral eyes distinguish Chediminae from Palpimaninae, which have widely spaced lateral eyes (Platnick 1981; Zonstein & Marusik 2019). The palpimanines also have an AME/PME ratio of approximately 1.6–1.9, whereas the chedimines possess larger AME to PME. The chedimines *L. germoshi* and *S. macleayi* have an AME/PME ratio of 5 and 2.5, respectively, in *D. biplagiatus* the PME are slightly larger (AME/PME = 0.86), and species of *Chedimanops* Zonstein & Marusik, 2017 lack PME (Zonstein & Marusik 2013; Zonstein et al 2016; Zonstein & Marusik 2017b). The AE row of the Crato specimen and other chedimines appear to be straight or slightly recurved in contrast to the four palpimanines included here, which have an AE row that is procurved. *Palpimanus* has a slightly longer labium and maxillae that fan out distally (Zonstein & Marusik 2019). The mouthparts, labium and maxillae of the Crato specimen closely resemble those of *Levymanus*, a chedimine from Israel (Zonstein & Marusik 2013; Zonstein et al. 2017).

Distinguishing *Cretapalpus* from otiothopine genera is more difficult. Otiothopines lack the tegular sclerites characteristic of chedimines. This feature is not visible in the Crato specimen, but other characteristics visible in the specimen can be compared to genera within the Otiothopinae. Some otiothopines also possess closely spaced or touching lateral eyes like species of *Otiothops* (*O. besotes*, *O. vaupes*, *O. doctorstrange*, and *O. chicaque*; see Cala-Riquelme et al. 2018) but these species, with the exception of *O. chicaque*, also possess closely spaced or touching posterior median eyes, unlike *Cretapalpus* and other chedimines, except for *Diaphorocellus biplagiatius* Simon, 1893 (Brescovit & Bonaldo 1993; Zonstein et al. 2016; Cala-Riquelme et al. 2018; Zonstein & Marusik 2020). The only preserved tarsi are on leg 3 of the left side and leg 2 of the right side (ventral up) and appear to lack

dense claw tufts. This is different from *Otiothops*, which possess dense claw tufts on legs 2–4, but it could be possible that the claw tufts are simply not preserved in the fossil specimen. The AE row of *Cretapalpus* and extant chedimines and otiothopines is mostly straight, with the exception of *Fernandezina* Birabén, 1951, which is recurved. *Fernandezina* also lack the greatly inflated femur of the first leg that *Cretapalpus* and other chedimines possess (Ramírez & Grismado 1996; Platnick et al. 1999).

In a recent molecular phylogenetic analysis, Chediminae was recovered as the most derived group within Palpimanidae and sister to *Palpimanus*, while Otiothopinae, represented by *Otiothops* and *Anisaedus* Simon, 1893 was the most basal (Wood et al. 2018). The phylogeny presented here places *Cretapalpus* within Palpimanidae (Fig. 4). In contrast to the molecular phylogeny, palpimanines are presented here as the most basal in the tree. Otiothopine genera are monophyletic and render Chediminae paraphyletic, with the fossil at the base of Chediminae + Otiothopinae. A thorough and comprehensive phylogenetic analysis of Palpimanidae combining molecular and more robust morphological characters is needed to confidently hypothesize evolutionary relationships at the subfamily level.

Cretapalpus is the first reported Mesozoic occurrence of Palpimanidae and the first chedimine palpimanid reported from South America. Today, chedimines are found throughout Africa, the Middle East, and Southern Asia (Oketch et al. 2020). Otiothopinae has been reported from almost every country in South America, several islands in the Caribbean, as well as a few countries in Africa and Asia (Brescovit & Bonaldo 1993). Palpimaninae has been reported mostly in Africa, the Middle East, and the Mediterranean. During the early Cretaceous, the South American and African continents were still relatively close or partially connected. All subfamilies of Palpimanidae were likely dispersed throughout Gondwana before the breakup of the supercontinent. The reason for the absence of Chediminae in South America today is unknown. It is possible chedimines are present in South America but are rare, and have not yet been observed. Other spider-bearing lacustrine deposits in China and Korea, as well as Burmese amber, have shown the superfamily Palpimanoidea was quite diverse during the Mesozoic (Wunderlich 2008; Park et al. 2019; Selden et al. 2019). As the oldest fossil representative of Palpimanidae thus far, *Cretapalpus vittari* extends the age of the family back 10–13 million years within the Cretaceous.

ACKNOWLEDGMENTS

SUPPLEMENTARY FILES

Supplementary File 1.—microCT parameters, online at https://dx.doi.org/10.1636/JoA-S-19-059.s1

Supplementary File 2.—Palpimanidae, character matrix, online at https://dx.doi.org/10.1636/JoA-S-19-059.s2

Supplementary file 3.—Palpimanoids, nexus file, online at https://dx.doi.org/10.1636/JoA-S-19-059.s3

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