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An orb-weaver spider (Araneae, Araneidae) from the early Eocene of India

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Abstract.—A new fossil spider is described from the early Eocene (Ypresian) Palana Formation (54 to 57 Ma) at the Gurha opencast lignite mine, near Bikaner, western Rajasthan, India. It is the first report of a nonamber fossil spider from India. The fossil is referred to the modern genus *Nephila* Leach, 1815, but with hesitation because, while its habitus is similar to that genus, it lacks the behavioral synapomorphies that distinguish the genus.

Introduction

The golden orb-weaver genus *Nephila* Leach, 1815 is renowned for its enormous orb webs constructed with distinctive gold-colored silk, for its extreme sexual size dimorphism (females are gigantic compared to the males), and for being a conspicuous inhabitant of tropical forests (Kuntner et al., 2013). Some two dozen species are recognized in the genus, together with several subspecies (World Spider Catalog, 2018). Golden orb weavers inhabit tropical and subtropical regions throughout the world, and the enormous, permanent webs of the females serve as microecosystems for a variety of kleptoparasites and other cohabitants (Vollrath, 1987; Tso and Severinghaus, 1998; Agnarsson, 2003, 2010; Harvey et al., 2007).

Nephila and related genera (presently including *Clitaetra* Simon, 1889, *Herennia* Thorell, 1877, *Nephilengys* Koch, 1872, and *Nephilingis* Kuntner in Kuntner et al., 2013) were placed in the family Araneidae Clerck, 1757 by Simon (1894), together with other orb weavers, and close to the tetragnathines (Kuntner et al., 2008). They remained in Araneidae until Levi (1986), with doubt, and then Coddington (1990) transferred the nephilines and tetragnathines into the family Tetragnathidae Menge, 1866. The nephiline genera were raised to family status (Nephilidae Simon, 1894) in the work of Kuntner (2006), where they remained (but closer to araneids than tetragnathids, e.g., Pan et al., 2004; Álvarez-Padilla and Hormiga, 2011; Su et al., 2011) until Dimitrov et al. (2017) returned these genera to the family Araneidae as subfamily Nephilinae, a result also supported by Wheeler et al. (2017).

Despite the large size of the females, most fossil nephilines described are males in amber, mainly because of the need of adult males to wander from their webs to seek out the sedentary females. The youngest fossil nepheline described is *Minutunguis silvestris* Wunderlich, 2011, a male in Quaternary Madagascan copal. Miocene Dominican amber contains five species of *Nephila*, all males, described by Wunderlich (1982, 1986), and Wunderlich (2004) described nine male nephilines from Eocene Baltic and Bitterfeld amber, which he referred to three new genera: *Eonephila* Wunderlich, 2004, *Luxurionephila* Wunderlich, 2004, and *Palaeonephila* Wunderlich, 2004. The only female nephiline known hitherto from the Cenozoic Era is *Nephila pennatipes* Scudder, 1885, from Eocene beds at Florissant, Colorado. This species most closely resembles the one described here in size and geological age. Mesozoic nephilines include the males *Cretaraneus vilaltae* Selden, 1990 from the Early Cretaceous of Spain, *Geratonephila burmanica* (Poinar in Poinar and Buckley, 2012) from mid-Cretaceous Burmese amber, *C. liaoningensis* Cheng, Meng, and Wang in Cheng et al., 2008 from the Early Cretaceous of China, and *C. martensnetoi* Mesquita, 1996 from the Early Cretaceous of Brazil. However, the age of *Geratonephila* was disputed by Wunderlich (2015), who synonymized the genus with *Nephila*. From his long experience of working with Burmese amber, during which time he had never seen a nephiline in the deposit, Wunderlich (2015) considered that *Geratonephila* was more likely from the Dominican Republic, of Miocene age, in which deposit the modern genus is quite common; he suggested it might belong to *Nephila tenuis* Wunderlich, 1986. Similarly, the two spiders from the Early Cretaceous of China and Brazil are most likely not nephilines but were placed in the genus *Cretaraneus* because of their Cretaceous age.

The only female Cretaceous nephilines known are several large, undescribed specimens from the Early Cretaceous Crato Formation of Brazil, one of which was figured by Dunlop and Penney (2012, fig. 93). A giant female spider from the mid-Jurassic Daohugou Fossil-Lagerstätte of China was originally described as *Nephila jurassica* Selden, Shih, and Ren, 2011. However, shortly after its description, a giant male was discovered in the same beds, which was considered to be conspecific with *N. jurassica*; the species was placed in the new genus *Mongolarachne* Selden, Shih, and Ren, 2013 and removed from Nephilinae. Kuntner et al. (2013) had already

determined, using molecular dating methods, that *N. jurassica* was unlikely to be a nephiline, but possibly a stem orbicularian, where *Mongolarachne* was placed by Selden, Shih, and Ren (2013). Dimitrov et al. (2017) remained unconvinced of the conspecificity of the male and female of *Mongolarachne*, but their analysis nevertheless recovered a younger origin for the genus *Nephila*.

In this paper, we describe a new fossil as a possibly juvenile female *Nephila*, from the early Eocene Palana Formation of the Gurha opencast lignite mine, western Rajasthan, India. The only fossil spiders known from India are from the Cambay amber, which is approximately coeval with the Palana Formation. Rust et al. (2010) listed four families (Mimetidae, Pholcidae, Thomisidae, and Uloboridae) in Cambay amber. Of these, the mimetid was described in more detail (but not named, being a juvenile) as the oldest known member of the Mimetidae Simon, 1881 by Penney et al. (2012). The fossil described here is therefore the first nonamber fossil spider known from India and provides additional data to the known distribution of fossil nephilines.

Geologic setting

The Gurha opencast lignite mine is situated about 70 km southwest of Bikaner (72.52269°E, 27.5229°N) (Fig. 1). The general geology of the subsurface Gurha lignite mine (Fig. 2) consists of a basement pebbly ash bed, a whitish-gray ash bed that is not in bedded form and also associated with lignite, followed by the Palana Formation, which consists of lignite (4.5 m) at the base, carbonaceous shale (3.80 m) intercalated with a thin siliceous clay nodular bed, a fine laminated pale-yellowish-gray shale associated with a thin band of dirty maroon sandstone (12.00 cm), variegated clay (6.00 m), carbonaceous shale, (3.70 m), variegated shale (3.50 m), and maroon shale (3.00 m), respectively. The thicknesses of these beds are variable in the opencast lignite mine, including lignite. The Palana Formation is overlain by the Kolayat Formation, which consists of variegated clays or fuller's earths (9.50 m), which is overlain by dirty yellow ferruginous sandstone with lenses of clay and sandy shale (5.50 m) and gritty sandstone and lime kankar (7.50 m) of the Jogira Formation, and the top is Recent alluvium and soil (3.88 m). The sedimentological and paleontological data suggest that the Palana Formation was deposited in a fluvio-lacustrine environment with influence of volcanism at the base. The Palana Formation is richly fossiliferous with plant leaves, rare fishes, and invertebrates. The characteristic pollen assemblages, *Sastripollenites trilobatus* (Venkatachala and Kar, 1969), *Ratariacolporites plicatus* (Kar, 1985), *Clavaperiporites jacobii* (Ramanujam, 1966), *C. densus* (Thanikaimoni et al., 1984), *Triangulorites bellus* (Kar, 1985), *Dermatobrevicolporites exaltus* (Kar, 1985), and *Kielmeyerapollenites eocenicus* (Sah and Kar, 1974), reported from the Palana Formation indicate an early Eocene (Ypresian) age (Shukla et al., 2014). A similar pollen assemblage is also known from the early Eocene Naredi Formation of the Kutch Basin (Kar and Saxena, 1981; Kar, 1985) and the Cambay Formation of the Cambay Basin (Kumar, 1996; Rao et al., 2013); a late Paleocene–early Eocene age was reported for the lignites and associated sediments of Rajasthan in general (Kar and Sharma, 2001).

Materials and methods

The specimen was recovered by hand picking from the thin, laminated, pale gray shale bed of the Palana Formation exposed in the Gurha opencast lignite mine (Figs. 1, 2), Bikaner District, Rajasthan. The Palana Formation has yielded abundant plant remains and rare fish fossils (work in progress). The specimen was studied using a Leica MZ-6 microscope, and photographs were taken using a Nikon D5500 DSLR camera and Olympus digital micropad 777. Photographs were manipulated in Affinity Photo (affinity.serif.com), and drawings were made from the photographs using Autodesk Graphic (graphic.com) on an Apple MacBook Pro computer. All measurements are in millimeters and were made from the drawings using the tools in Graphic. Measurements of paired organs are means of left and right of the specimen.

Repository and institutional abbreviation.—The specimen is deposited in the Department of Geology, HNB Garhwal University Srinagar Uttarakhand, India.

Systematic paleontology

Abbreviations.—Roman numerals I, II, III, IV = walking leg numbers; ch = chelicera; cx = coxa; fe = femur; L = length; lb = labium; mt = metatarsus; op = opisthosoma; pa = patella; Pd = pedipalp; ta = tarsus; ti = tibia; tr = trochanter; W = width.

Class Arachnida Lamarck, 1801
Order Araneae Clerck, 1757
Family Araneidae Clerck, 1757
Subfamily Nephilinae Simon, 1894
Genus *Nephila* Leach, 1815

Type species.—*Aranea pilipes* Fabricius, 1793.

Remarks.—The specimen described here is identified as a possible *Nephila* on the basis of its relatively large size, the elongate, pyriform shape of the opisthosoma, the long, slender legs with legs I, II, and IV being extremely long while leg III is relatively shorter (nearly half the length of the other legs), and the shape of the sternum and labium (Figs. 2, 3; compare with Murphy and Roberts, 2015, pl. 116). The slightly thickened proximal and distal ends of the tibiae, especially of legs III and IV (Fig. 3) are typical of *Nephila*; compare, for example, Figure 3.1 with the ventral view of *N. pilipes* in Thakur and Tembe (1956, pl. I, fig. 2, as *N. maculata*). Its small size suggests that it is an immature, and the shape of the opisthosoma together with the lack of swelling of the distal pedipalp podomeres suggest it is a female (see Discussion).

Nephila? sp.

Description.—Immature female (Figs. 3, 4). Body length (including ch) 10.25. Labium subtriangular in outline, with rounded anterior border, wider than long (L 0.32 mm, W 0.53 mm, ratio 0.61); sternum subtriangular, widest at

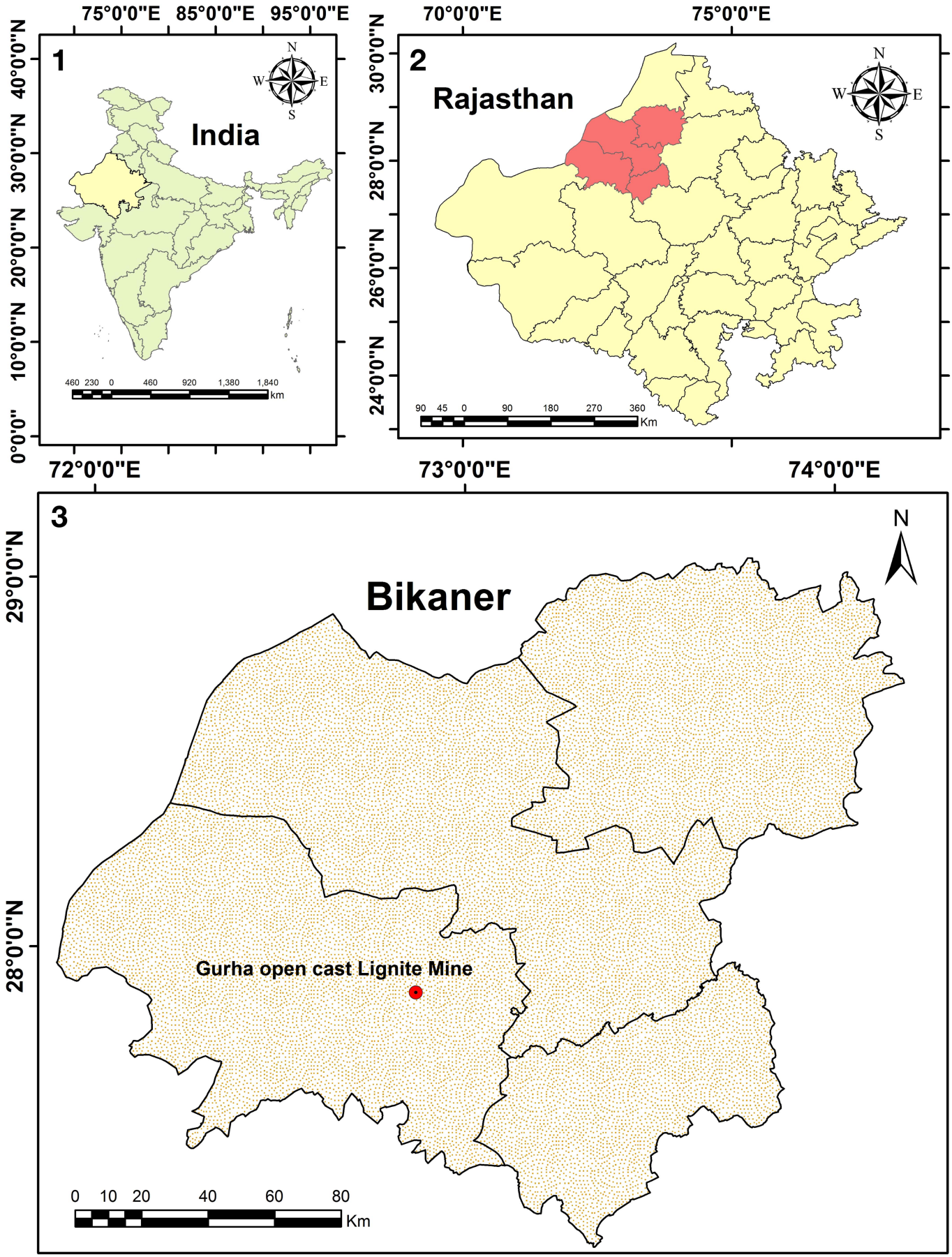

Figure 1. Location map of the Gurha opencast lignite mine, near Bikaner, western Rajasthan, India: (**1**) map of India showing location of Rajasthan; (**2**) map of Rajasthan, showing location of Bikaner district; (**3**) map of Bikaner district showing location of the Gurha opencast lignite mine.

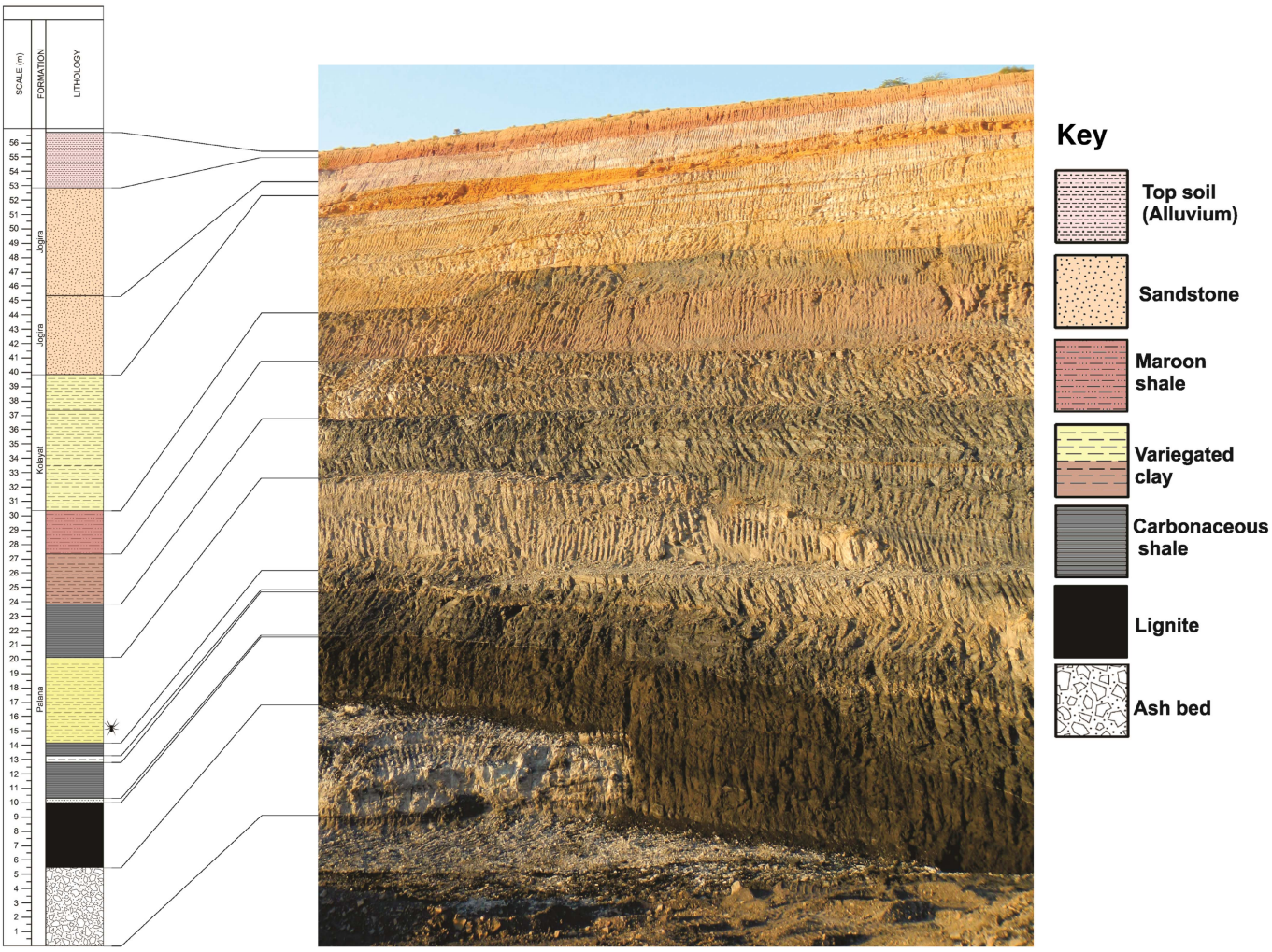

Figure 2. Stratigraphy and lithologies exposed in the Gurha opencast lignite mine, near Bikaner, western Rajasthan, India. Horizon bearing the spider specimen in the variegated clays of the Palana Formation marked on the section, about 15 m from the base.

anterior border, longer than wide (L ~1.0 mm, W ~0.8 mm). Chelicera subequant in outline, L 0.81. Pedipalps slender, short, with tarsal claw; podomere lengths: pa 0.25, ti 0.57, ta 0.72. Legs long, slender, smooth, lacking tufts of setae (gaiters) on tibiae; leg I longest, legs II and IV approximately equal in length, leg III short (leg formula I, IV, II, III). Long podomeres, particularly tibiae of legs III, IV, slightly thickened at proximal and distal ends. Podomere lengths: Leg I cx 0.69, tr 0.18, fe 5.63, pa 1.07, ti 3.60, mt 3.69, total fe–ti 10.29; Leg II cx 0.67, tr 0.24, fe 4.57, pa 0.84, ti 2.82, mt 3.67, total fe–ti 8.23; Leg III cx 0.59, tr 0.23, fe 2.82, pa 0.59, ti 1.29, mt 1.94, total fe–ti 4.70; Leg IV cx 0.71, tr 0.25, fe 4.77, pa 0.90, ti 2.71, total fe–ti 8.38. Opisthosoma nearly twice as long as wide (L 7.17 mm, W 3.65 mm, ratio 1.96), elongate pyriform in outline, greatest width one-third of length from anterior border, connected to prosoma by narrow pedicel.

Material.—Immature female, GU/SP/B-101 (part only), only known specimen, deposited in the Department of Geology, HNB Garhwal University Srinagar Uttarakhand, India, from the early Eocene Palana Formation, Gurha lignite mine, Bikaner, Rajasthan, India.

Remarks.—This specimen differs from most other members of the genus in lacking gaiters on the tibiae in the immature female (which this specimen is presumed to be).

Discussion

Phylogenetic relationships.—"When I see a bird that walks like a duck and swims like a duck and quacks like a duck, I call that bird a duck" (quote attributed to James Whitcomb Riley, Indiana poet, 1849–1916). However, what if that supposed duck lacks the synapomorphies of a duck? The analogy is important because the specimen described here shows the general habitus of a *Nephila* but lacks the synapomorphies of that genus, such as sexual dimorphism and web structure (e.g., Scharff and Coddington, 1997; Harvey et al., 2007), which are not identifiable in a fossil. While the elongate abdomen is characteristic of *Nephila*, a similar abdomen shape occurs in some other araneids and tetragnathids. However, the chelicerae of tetragnathids are large, and their legs are very long and thin. One characteristic of *Nephila* (also seen in the specimen described here) that differs from other araneids is the length of the legs: not only is leg III short compared to the others, but also leg IV is as long as leg II.

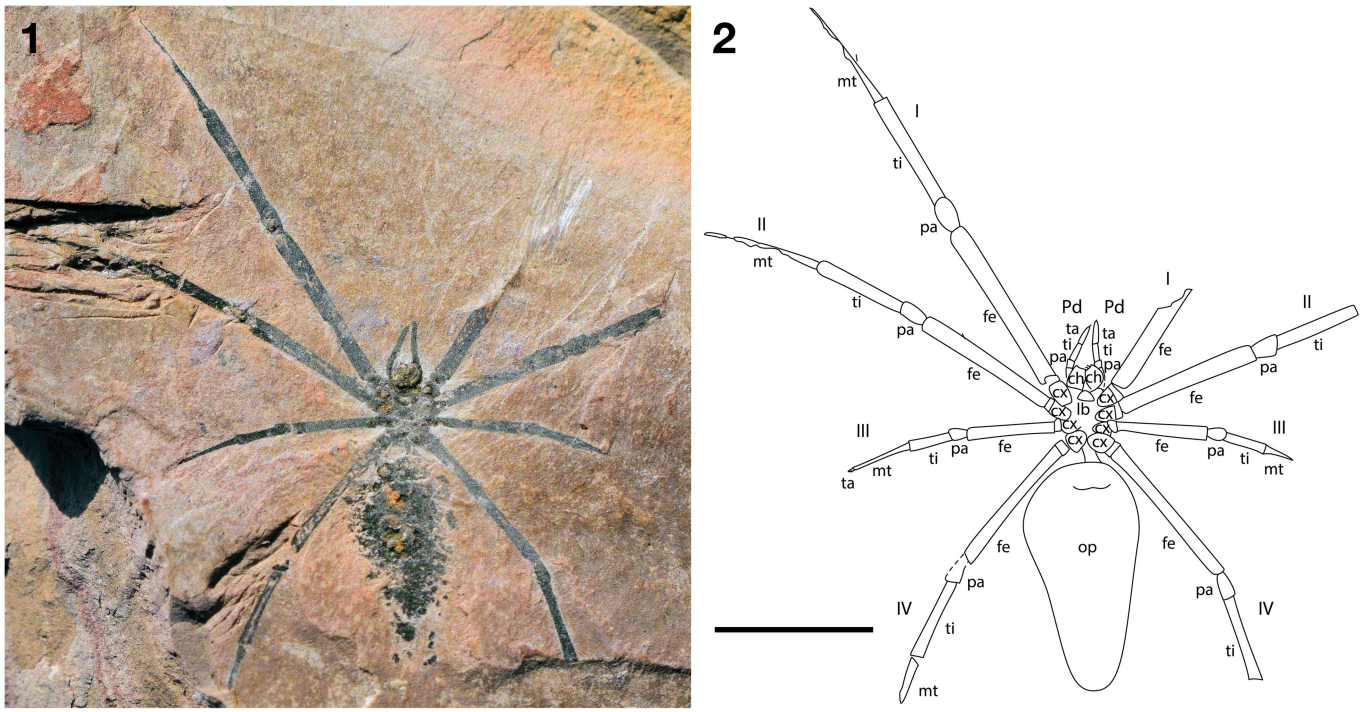

Figure 3. *Nephila*? from the early Eocene (Ypresian) Palana Formation, Gurha opencast lignite mine, near Bikaner, western Rajasthan, India: (**1**) photograph of whole specimen (GU/SP/B-101), ventral aspect; (**2**) explanatory drawing. I, II, III, IV = walking leg numbers; ch = chelicera; cx = coxa; fe = femur; lb = labium; mt = metatarsus; op = opisthosoma; pa = patella; Pd = pedipalp; ta = tarsus; ti = tibia. Scale bar = 5 mm.

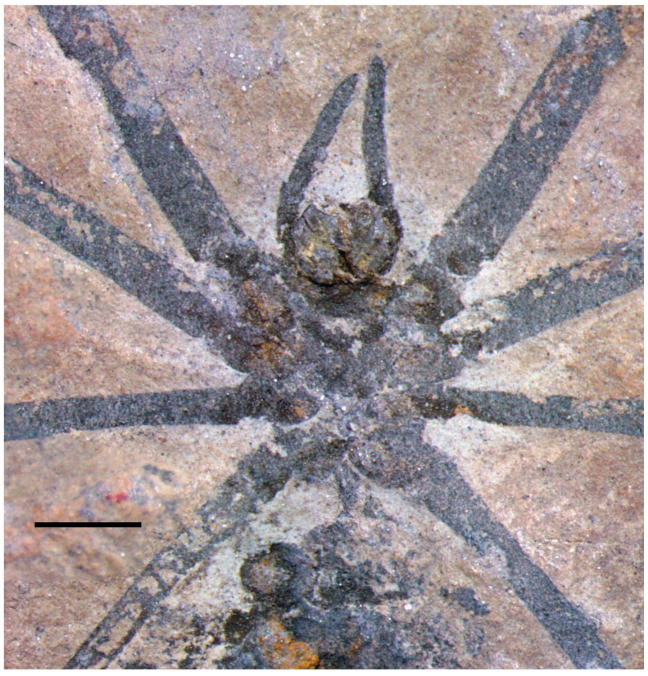

Figure 4. Close-up of ventral prosoma of *Nephila*? (GU/SP/B-101) from the early Eocene (Ypresian) Palana Formation, Gurha opencast lignite mine, near Bikaner, western Rajasthan, India, showing ventral structures of prosoma; for explanatory drawing, see Figure 3.2. Scale bar = 1 mm.

In addition, the metatarsus is longer than the tibia and patella together (e.g., Banks, 1907).

Few setae or spines are visible on the specimen, yet it is most likely that, were they present, tufts of setae on the tibiae (gaiters) would be visible. Normally, spiders preserved in fluvio-lacustrine environments are well preserved, and spines, setae, and even trichobothria are usually visible in the fossils (e.g., Selden et al., 2013). Tibial tufts are present in most *Nephila* juveniles (e.g., in all Australasian species except *N. pilipes*; Harvey et al., 2007) and are retained into adulthood in the females of a few species (Thakur and Tembe, 1956; Robinson and Robinson, 1973). So the absence of tibial tufts in the fossil is somewhat unusual but not conclusive evidence of it being either an adult or a juvenile.

With its body length of 10.25 mm, were it mature, the fossil would be the smallest *Nephila* known. The contemporaneous *Nephila pennatipes* from the Eocene of Florissant, Colorado, measures 14 mm in body length (Scudder, 1885), which is also small for a *Nephila*. *N. pennatipes* bears tibial gaiters, and it could be a juvenile or adult female. The smallest living *Nephila* is *N. pakistaniensis* Ghafoor and Beg, 2002, whose females range from 10.25 to 13.00 mm (mean 10.81, n = 5), which is similar in size to the Eocene species, but other extant *Nephila* are considerably larger (Kuntner and Coddington, 2009, fig. 1). *N. pakistaniensis* has not been restudied since its first description. The drawings of the body and the internal and external views of the epigyne are clearly copies of figs. 195–197 of Tikader (1982) of the 20 mm long *N. clavata*; the male palp looks quite unlike a *Nephila* palp (there is no long conductor), so *N. pakistaniensis* requires reevaluation. The small size of the fossil, together with the labium being wider than long (it is normally longer than wide, or at least as long as wide; see Murphy and Roberts, 2015, pl. 116), would suggest the specimen is immature and lacks tibial gaiters. It is most likely a female because male nephilines are much smaller than the

females, and some swelling of the distal pedipalp podomores would be expected even in a juvenile male.

Paleoecology.—The early Eocene is known for a marked global warming (Zachos et al., 2001, 2003), known as the Paleocene–Eocene Thermal Maximum (Higgins and Schrag, 2006), and at that time the Indian subcontinent was located near the equator (< 10°N) (Shukla et al., 2014). Studies on the flora of Gurha lignite mine indicate a mean annual temperature of ~24°C and a mean annual temperature range of ~10°C. The cold month mean temperature of ~18°C was tropical by today's climate standards but cooler than experienced today at 9°N in southern India at sea level. Similarly, the Gurha mean annual temperature is cooler than that of today (~27°C), and the modern mean annual range of temperature (2.8°C) is smaller (Shukla et al., 2014). Paleobotanical evidence points toward a near-coastal tropical flora of evergreen trees subject to frequent wildfires under a strongly seasonal precipitation (monsoon) regime (Kumar et al., 2016; Spicer et al., 2017). The analysis of Spicer et al. (2017) showed that, at the time of deposition of the Gurha mine sediments, this part of the Indian continent was subject to a seasonal climate more akin to the present-day Intertropical Convergence Zone–influenced Indonesia-Australia Monsoon, rather than the Himalaya-influenced South Asia Monsoon experienced in the region today.

Nephila is found today in tropical and subtropical (occasionally temperate) climates (Su et al., 2011). The presence of a nephiline in the Palana Formation concurs with a subtropical climate. In comparison with the habits of modern *Nephila*, the fossil presumably wove orb webs to catch the insects living in the forest. Undescribed fossils of large insect wings have been recovered from the same horizon, and insects are known from amber in the Cambay Basin (Rust et al., 2010).

Biogeography.—Amber in the nearby Cambay Basin indicates the presence of Dipterocarpaceae at this time, a family of moist tropical forest trees with its current center of biodiversity in Borneo and once thought to have reached India in the Miocene from there. However, the Cambay amber, together with other fossil evidence, indicates a more likely origin for the family in Africa, with the Indian continent transporting the forests to Asia, followed by their subsequent later Cenozoic radiation (Ghazoul, 2016). The insects in Cambay amber show affinities with the much better-known Eocene Baltic amber, with some Recent taxa from Australasia, and with Miocene neotropical ambers (Mexico and Dominican Republic) (Rust et al., 2010). The few spiders known from Cambay amber have yet to be formally described, but belong to widespread families (Rust et al., 2010).

Su et al. (2011) studied the phylogeography of *Nephila* and concluded that the subtropical/temperate clades of the genus were more derived than the tropical ones and that the ancestral range of *Nephila* was Asia or Africa. However, Su et al. (2011) used an earliest date of 20 Ma (Miocene) for the oldest fossil *Nephila*, based on Wunderlich's species from Dominican amber, yet *N. pennatipes* provides an Eocene age of ~35 Ma for an American *Nephila*. The most recent analyses of Su et al. (2011) and Kuntner et al. (2013) retrieved a basal *Nephila* group consisting of the type species *N. pilipes*, found in Asia, and the African *N. constricta*. Indeed, Kuntner et al. (2013) found this small clade to be sister to a group containing not just all other *Nephila* species but also *Nephilingis* and *Clitaetra*. These authors dated the origin of this clade to around 50 to 60 Ma, a time when India was separated from both Africa and Asia, halfway across the Indian ocean. The discovery of a fossil nephiline on the Indian continent adds to the known distribution of fossils of the subfamily. Whether the nephiline was transported on India over its entire journey from Africa (which began in the Cretaceous), or whether it arrived on the Indian continent from Africa, perhaps by ballooning (Su et al., 2011), during its travels, is not known.

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