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A review of Burmese amber arachnids

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Abstract. Fossils from the mid-Cretaceous (c. 99 Ma) Myanmar (Burma) amber include all extant orders of Arachnida, including the earliest representatives of Schizomida, Parasitiformes, and Palpigradi. Schizomids are figured from Burmese amber herein for the first time. The most abundant and diverse arachnid order is the Araneae, with 38 families, 93 genera, and 165 species recorded to date. The araneofauna is dominated by haplogynes and palpimanoids, whilst araneoids are rare and members of the RTA clade absent. The arachnofauna is typical of a tropical rainforest habitat, which concurs with evidence from other Burmese amber biota.

Keywords: Burmite, Cenomanian, Cretaceous, Mesozoic, Myanmar

Amber from Myanmar (Burma), sometimes known as burmite, has been known for more than 2000 years in Asia. According to Laufer (1907), amber was most probably traded between the *Ai lao*, the many tribes of the present-day Chinese province of Yunnan, and Burma during the first century AD. Later Chinese writings described the amber trade, and it was first mentioned in European literature in the 17th Century by the Portuguese Jesuit Fr Alvarez Semedo (1643, see also 1655). Further details about the history of burmite can be found in Zherikhin & Ross (2000) and Poinar et al. (2008). Burmite is increasingly sold today for its spectacular inclusions of plants, animals, and fungi. Burmese amber hosts an abundant and diverse biota, including: bryophytes, ferns, gymnosperms, angiosperms, fungi, molluscs, onychophorans, vertebrates, nematodes, and arthropods. Burmese is not the oldest amber with arthropod inclusions, but it is one of the most prolific sources today.

The first Burmese amber arachnid inclusions were reported by Cockerell (1917a,b, 1920), from material sent by R.C.J. Swinhoe of Mandalay (Zherikhin & Ross 2000): the pseudoscorpions *Electrobisium acutum* Cockerell, 1917b and *Amblyolpium burmiticum* (Cockerell, 1920), and the acariform mite *Cheyletus burmiticus* Cockerell, 1917. At that time, the age of the amber was unknown; the pieces occur in a clay of Miocene (5–23 Ma) age, but Cockerell (1917a,b) suggested that they may have been reworked from much older deposits, perhaps even Upper Cretaceous. However, interest in Burmese amber waned after the flow of material ceased, and was only re-ignited at the turn of the 21st Century, when material started to become widely available again, and modern dating showed it to be of mid-Cretaceous (99 Ma) age. After 1920, no more arachnids were described from burmite until 2002 (Grimaldi et al. 2002; Lourenço 2002) (Fig. 1). Thereafter, new species have been reported most years, with exceptionally large numbers of arachnids, mainly spiders, described by Jörg Wunderlich in his large tomes on the fauna (Wunderlich 2008b, 2012a,b, 2015a,b, 2017a,b) (Fig. 1).

GEOLOGY

Burmese amber today comes from a single locality in remote Upper Burma, at Noije Bum hill, Hukawng Valley, northern Myanmar (see location map in Kania et al. 2015). The amber mine and its geological setting was described in detail by Cruickshank & Ko (2003). The amber is dug out by hand, by local Kachin people, in pits along the narrow exposures. Annual production of amber depends on market conditions. It reached 11,000 kg per annum in 1906 (Cruickshank & Ko 2003), but has only reached 500 kg per year more recently (Poinar et al. 2008).

The Indian geologist Noetling (1893) thought its age was Miocene, on account of the similarity of the greenish clays to Miocene rocks nearby. He did record an ammonite in a loose pebble during his visit, but considered it came from further afield. An Eocene (c. 34–56 Ma) age for the strata was proposed by Stuart (1923), based on the presence of the large foraminiferan *Nummulites*, a conclusion supported by Chhibber (1934). Later workers, e.g., Zherikhin & Ross (2000), considered the age of the amber to be Cretaceous, based on its insect content, but thought the pieces were reworked into Eocene-age sediments. Sahni & Sastri (1957) described another foraminiferan, the Cretaceous *Orbitolina*, from the area, but thought that these fossils, too, were derived inclusions in Eocene sediments. It was the detailed study by Cruickshank & Ko (2003) which showed the host clays to be Cretaceous in age. They discovered an *in situ* ammonite during their visit, reported the results of palynological investigations, and re-evaluated the misconceptions of previous workers. More recently, the age of Burmese amber has been dated radiometrically to 98.79 $\pm$ 0.62 Ma based on U-Pb zircon dating of the volcaniclastic matrix (Shi et al. 2012).

Burmese amber varies from deep red in color, through orange (the commonest, Fig. 2A), to light, transparent yellow, commonly containing fine bubbles (Grimaldi et al. 2002). Some pieces are flattened and lens-shaped, but rarely contain animal inclusions. Arthropods are most commonly found in pieces shaped like flows or runnels; these comprise no more than 3–4% by mass of all the amber studied by Grimaldi et al.

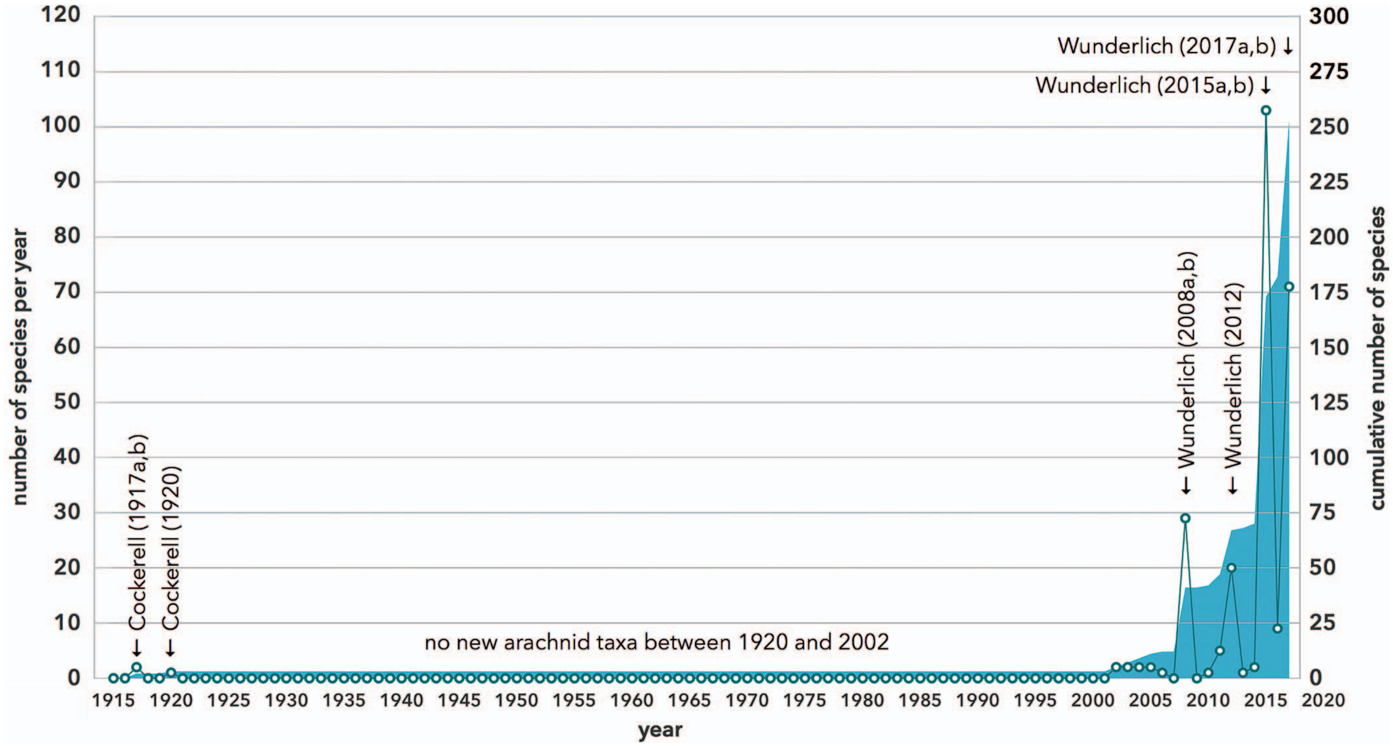

Figure 1.—Graph showing number of fossil arachnid species described from Burmese amber each year from 1917 to the present day (○), and cumulative curve (color). Landmark papers indicated. Data mainly from Dunlop et al. (2017), updated.

(2002) but yielded approximately 85% of the arthropods. In general, arthropod remains occur at the rate of about 46 inclusions per kg of extracted amber. Regarding the source of the resin, spores of both Araucariaceae and Taxodiaceae, both of which contain species which are copious resin producers today, have been found in the amber (Cruickshank & Ko 2003). More recently, nuclear magnetic resonance studies have suggested that the source is most likely an araucariacean tree similar to the modern New Zealand Kauri pine, *Agathis* (Poinar et al. 2007). However, it was pointed out by Grimaldi & Ross (in press) that leafy shoots of *Metasequoia* (Cupressaceae) are common in Burmese amber pieces, so that is a further possibility.

The Myanmar amber locality lies within the West Burma terrane (Broly et al. 2015), which was considered to have rifted off from northwest Australia in the Late Jurassic (156 Ma) and drifted northwards, finally colliding with the Eurasian marginal Sibumasu terrane at around 80 Ma (Heine & Müller 2005; Seton et al. 2012). In this scenario, the amber forest bearing the arachnid fauna was living at the time on an island which had separated from Australia some 75 million years earlier. However, more recent ideas of Metcalfe (2013) suggest that the West Burma terrane formed part of a continent which separated from Australia in the Devonian as the Paleo-Tethys Ocean opened, and then collided with Eurasia (including the North and South China blocks) by Jurassic times. In the latter scenario, the arachnid fauna spread onto the West Burma terrane from Eurasia sometime between Jurassic and mid-Cretaceous times.

PALEONTOLOGY

The first reviews of Burmese amber arthropods were by Ross & York (2000), who listed the published (type and figured) specimens to that date, and Rasnitsyn & Ross (2000), who listed the families represented in the collections of the Natural History Museum, London (BMNH), including both published and unpublished specimens. The BMNH housed the only scientific collection of Burmese amber at the time, collected early in the 20th Century by R.C.J. Swinhoe (Grimaldi et al. 2002). At the turn of the 21st Century, the arachnid list consisted of one unidentified scorpion (figured in Ross 1998); four specimens of two published pseudoscorpion species (Cockerell 1917a, 1920), and 34 unidentified; 164 mites and ticks, including at least six families, the majority (122) unidentified, and one published (Cockerell 1917b); and 36 spiders in 7 families, but 26 unidentified. The four orders of arachnids known from Burmese amber numbered 239 specimens out of a total of 1198 arthropods in the collection (~20%). Grimaldi et al. (2002) included both BMNH and American Museum of Natural History (AMNH) specimens in their survey, the latter collection having been made in the ensuing two years and amounting to three times as many plant and animal inclusions as those listed for London. These authors added three scorpion fragments, 11 undetermined pseudoscorpions, 207 mites (206 undetermined and one tick), and 128 spiders (10 specimens in eight families, 118 undetermined), making a total of four scorpions, 49 pseudoscorpions, 371 mites and ticks, and 162 spiders: 586 arachnid specimens altogether. A survey by Ross et al. (2010) produced

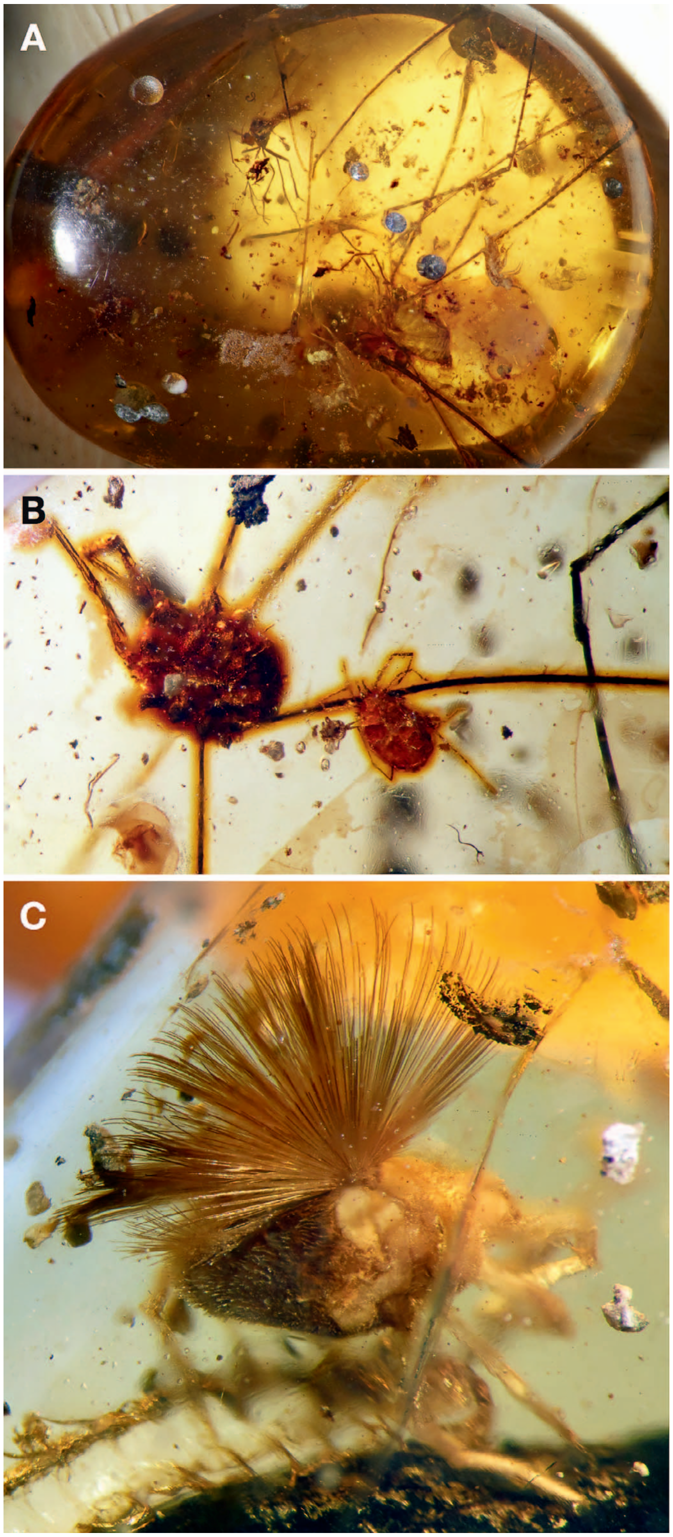

Figure 2.—A. Typical polished cabochon of Burmese amber, containing arthropod inclusions as well as bubbles and debris; B. Acariformes attached (or adjacent?) to the leg of an opilionid; B. Undescribed Acariformes.

the first Opiliones Sundevall, 1833 (two species: Giribet & Dunlop 2005; Poinar 2008), the first described scorpions (two species: Lourenço 2002; Santiago-Blay et al. 2004), two more mites (Poinar & Brown 2003; Poinar & Buckley 2008), and 19 spider species (Penney 2003a, 2004a, 2005; Wunderlich, 2008b). Rasnitsyn et al. (2016) surveyed all Cretaceous ambers, with a supplementary chart listing many recently identified but undescribed arachnids, especially acariform mites. Ross (2017) has published an online list of Burmese amber biota, including arachnids, based on Ross et al. (2010) updated to include the most recent records. Table 1 is a list of families and described species of arachnids recorded from Burmese amber, updated from Ross (2017). Unless otherwise stated, all specimens illustrated here are held in the collections of the College of Life Sciences, Capital Normal University, Beijing.

Order Acariformes Zachvatkin, 1952

While a great many mites are known from Burmese amber (e.g., listed by Kartsev & Makarova in Rasnitsyn & Ross 2000, and Rasnitsyn et al. 2016) (Figs. 2B,C), only two have been described in the literature: *Cheyletus burmiticus* Cockerell, 1917b, and *Protoresinacarus brevipedis* Khaustov & Poinar, 2010. *Cheyletus burmiticus* was placed in the modern family Cheyletidae Leach, 1815, which also contains fossil mites from the Eocene Baltic amber (Koch & Berendt 1854) and Green River (Bradley 1931) deposits. Cheyletidae Leach, 1815 is a large family of mites belonging to the Parasitengona Oudemans, 1909; they are mostly free-living predators but some are permanent ectoparasites of small mammals and birds at the present day. Regarding *C. burmiticus*, Bochkov & Sidorchuk (2016) concluded that it is a heteromorphic male of a free-living cheyletid.

Protoresinacarus brevipedis was placed in the extant, previously monotypic family Resinacaridae Mahunka, 1975 (cohort Heterostigmatina Berlese, 1899, superfamily Pyemotoidea Oudemans, 1937) by Khaustov & Poinar (2010). The specimens occur adjacent to a mantispid neuropteran, *Doratomantispa burmanica* Poinar, 2011 (in Poinar & Buckley 2011), from which the authors concluded that the mites were phoretic.

A great many specimens of acariform mites in Burmese amber are undescribed and available for study. A list of identified families was provided by Sidorchuk in the supplementary information of the paper by Rasnitsyn et al. (2016).

Order Amblypygi Thorell, 1882

The first Burmese amber amblypygid to be described was *Kronocharon prendinii* Engel & Grimaldi, 2014. Two additional species were described by Wunderlich (2015a): *K. engeli* Wunderlich, 2015 and *K. longicalcaris* Wunderlich, 2015. Interestingly, the holotype of *K. prendinii* is an adult female preserved with three nymphs in the same piece of amber, inferring the possible antiquity of maternal care in these animals. An undescribed specimen of *Kronocharon* is illustrated here (Fig. 3). Fossil amblypygids are known from the Carboniferous of Europe and North America, the Cretaceous (Dunlop & Martill 2002), and Cenozoic ambers (Dunlop et al. 2017). These nocturnal animals inhabit crevices in bark, under

Table 1.—List of families and described species of arachnids recorded from Burmese amber. Data mainly from Ross (2017), updated. Note: some of these determinations are erroneous; see text for details.

Arachnida (12 orders, 87 families, 123 genera, 213 species)
Acariformes (15 families, 2 genera, 2 species)
Anystidae
Archaeorchestidae
Bdellidae
Caeculidae
Cheyletidae
Cheyletus burmiticus Cockerell, 1917b
Enantioppiidae?
Eremaeidae
Erythraeidae
Eupodidae
Gymnodameidae
Malaconothridae?
Neoliodidae
Oribatellidae
Oribotritiidae?
Resinacaridae
Protoresinacarus brevipedis Khaustov & Poinar, 2010
Tuckerellidae
Amblypygi (1 genus, 3 species)
Family *incertae sedis*
Kronocharon engeli Wunderlich, 2015a
Kronocharon longicalcaris Wunderlich, 2015a
Kronocharon prendinii Engel & Grimaldi, 2014
Araneae (38 families, 93 genera, 165 species)
Archaeidae
Burmesarchaea alissa Wunderlich, 2017b
Burmesarchaea caudata Wunderlich, 2017b
Burmesarchaea crassicaput Wunderlich, 2017b
Burmesarchaea crassichaelae Wunderlich, 2017b
Burmesarchaea gibber Wunderlich, 2017b
Burmesarchaea gibberoides Wunderlich, 2017b
Burmesarchaea grimaldii (Penney, 2003a)
Burmesarchaea longicollum Wunderlich, 2017b
Burmesarchaea longissipes Wunderlich, 2015b
Burmesarchaea pilosus Wunderlich, 2015b
Burmesarchaea propinqua Wunderlich, 2017b
Burmesarchaea pseudogibber Wunderlich, 2017b
Burmesarchaea pustulata Wunderlich, 2017b
Burmesarchaea quadrata Wunderlich, 2017b
Burmesarchaea speciosus Wunderlich, 2008b
Eomysmauchenius dubius Wunderlich, 2017b
Eomysmauchenius septentrionalis Wunderlich, 2008b
Filiauchenius paucidentatus Wunderlich, 2008b
Planarchaea kopp Wunderlich, 2015b
Planarchaea oblonga Wunderlich, 2017b
Planarchaea ovata Wunderlich, 2017b
†Burmadictynidae
Burmadictyna clava Wunderlich, 2015b
Burmadictyna excavata Wunderlich, 2015b
Burmadictyna pectin Wunderlich, 2008b
Burmadictyna postcopula Wunderlich, 2017b
Eodeinopis longipes Wunderlich, 2017b
†Burmascutidae
Burmascutum aenigma Wunderlich, 2008b
†Burmathelidae
Burmathele biseriata Wunderlich, 2017b
Corinnidae?
†Cretaceothelidae
Cretaceothele lata Wunderlich, 2015b

Table 1.—Continued.

Deinopidae
Deinopedes tranquillus Wunderlich, 2017b
Dipluridae
Cethegoides patricki Wunderlich, 2017b
Phyxioschemoides collembola Wunderlich, 2015b
†Eopsilodercidae
Eopsiloderces loxosceloides Wunderlich, 2008b
Eopsiloderces serenitas Wunderlich, 2015b
Loxoderces curvatus Wunderlich, 2017b
Loxoderces longicymbium Wunderlich, 2017b
Loxoderces rectus Wunderlich, 2017b
Praepholcus huberi Wunderlich, 2017b
†Fossilcalcaridae
Fossilcalcar praeteritus Wunderlich, 2015b
Hersiliidae
Burmesiola cretacea Wunderlich, 2011
Burmesiola daviesi Wunderlich, 2015b
Spinasilia dissoluta Wunderlich, 2015b
Hexathelidae
Alioatrax incertus Wunderlich, 2017b
†Lagonomegopidae
Albiburmops annulipes Wunderlich, 2017b
Archaelagonops propinquus Wunderlich, 2015b
Archaelagonops salticoides Wunderlich, 2012b
Archaelagonops scorsum Wunderlich, 2015b
Burlagonomegops eskovi Penney, 2005
Cymbiolaganops cymbiocalcar Wunderlich, 2015b
Lagonoburmops plumosus Wunderlich, 2012b
?*Lagonomegops tuber* Wunderlich, 2015b
Lineaburmops beigeli Wunderlich, 2015b
Lineaburmops hirsutipes Wunderlich, 2015b
Myanlagonops gracilipes Wunderlich, 2012b
Parviburmops brevipalpus Wunderlich, 2015b
?*Parviburmops bigibber* Wunderlich, 2017b
?*Paxillomegops brevipes* Wunderlich, 2015b
?*Paxillomegops comutus* Wunderlich, 2017b
Paxillomegops longipes Wunderlich, 2015b
Picturmegops signatus Wunderlich, 2015b
Planimegops parvus Wunderlich, 2017b
Leptonetidae
Palaeoleptoneta calcar Wunderlich, 2012b
Palaeoleptoneta crus Wunderlich, 2017b
†Micropalpimanidae
Micropalpimanus poinari Wunderlich, 2008b
†Mongolarachnidae
Longissipalpus cochlea Wunderlich, 2017b
Longissipalpus magnus Wunderlich, 2015b
Longissipalpus maior Wunderlich, 2015b
Longissipalpus minor Wunderlich, 2015b
Pedipalparaneus seldeni Wunderlich, 2015b
Mysmenidae?
Nephilidae?
'*Nephila*' *burmanica* (Poinar & Buckley, 2012)
Oecobiidae
Retrooecobius chomskyi Wunderlich, 2015b
Retrooecobius convexus Wunderlich, 2015b
Zamilia aculeopectens Wunderlich, 2015b
Zamilia antecessor Wunderlich, 2008b
Zamilia quattuormammillae Wunderlich, 2015b
Oonopidae
Burmorchestina acuminata Wunderlich, 2017b
Burmorchestina biangulata Wunderlich, 2017b
Burmorchestina plana Wunderlich, 2017b
Burmorchestina pulcher Wunderlich, 2008b

Table 1.—Continued.

Burmorchestina pulcheroides Wunderlich, 2017b
Burmorchestina tuberosa Wunderlich, 2017b
Palpimanidae
†Parvithelidae
Parvithele muelleri Wunderlich, 2017b
Parvithele spinipes Wunderlich, 2017b
Pulvillothele haupti Wunderlich, 2017b
†Pholcochyroceridae
Autotomiana hirsutipes Wunderlich, 2015b
Pholcochyrocer altipecten Wunderlich, 2017b
?*Pholcochyrocer baculum* Wunderlich, 2012b
Pholcochyrocer guttulaeque Wunderlich, 2008b
Pholcochyrocer pecten Wunderlich, 2012b
Spinicreber antiquus Wunderlich, 2015b
Spinipalpus vetus Wunderlich, 2015b
†Plumorsolidae
Burmorsolus nonplumosus Wunderlich, 2015b
Pseudorsolus crassus Wunderlich, 2015b
†Praearaneidae
Praearaneus bruckschi Wunderlich, 2017b
†Praeterleptonetidae
Biapophyses beate Wunderlich, 2015b
Crassitibia longispina Wunderlich, 2015b
Crassitibia tenuimana Wunderlich, 2015b
Curvitibia curima Wunderlich, 2015b
Groehnianus burmensis Wunderlich, 2015b
Hypotheridiosoma falcata Wunderlich, 2015b
Hypotheridiosoma paracymbium Wunderlich, 2012b
Palaeohygropoda myanmarensis Penney, 2004a
Parvispina tibialis (Wunderlich, 2011)
Praeterleptoneta spinipes Wunderlich, 2008b
Spinipalpitibia maior Wunderlich, 2015b
Psilodercidae
Aculeatosoma pyritmutatio Wunderlich, 2017b
Leclercera ellenbergeri Wunderlich, 2015b
Leclercera longissipes Wunderlich, 2012b
Leclercera sexaculeata Wunderlich, 2015b
Leclercera spicula Wunderlich, 2012b
Priscaleclercera paucispina Wunderlich, 2017b
Priscaleclercera brevispina Wunderlich, 2017b
Proterpsiloderces longisetae Wunderlich, 2015b
?*Psiloderces filiformis* Wunderlich, 2012b
Segestriidae
Denticulsegestria rugosa Wunderlich, 2015b
Myansegestria caederens Wunderlich, 2015b
Myansegestria engin Wunderlich, 2015b
Parvosegestria longitibialis Wunderlich, 2015b
Parvosegestria obscura Wunderlich, 2015b
Parvosegestria pintgu Wunderlich, 2015b
Parvosegestria triplex Wunderlich, 2015b
Sparassidae?
†Spatiatoridae
Spatiator putescens Wunderlich, 2015b
Telemidae
?*Telemophila crassifemoralis* Wunderlich, 2017b
Tetrablemmidae
Bicornoculus levis Wunderlich, 2015b
Brignoliblemma bizarre Wunderlich, 2017b
Brignoliblemma nala Wunderlich, 2017b
Brignoliblemma paranala Wunderlich, 2017b
Cymbioblemma comiger Wunderlich, 2017b
Electroblemma bifida Selden, Zhang & Ren, 2016c
?*Eogamasomorpha clara* Wunderlich, 2015b
Eogamasomorpha hamata Wunderlich, 2017b
?*Eogamasomorpha unicomis* Wunderlich, 2017b
Eogamasomorpha nubila Wunderlich, 2008b
Eoscaphiella ohlhoffi Wunderlich, 2011
Furcembolus andersoni Wunderlich, 2008b
Furcembolus crassitibia Wunderlich, 2017b
Furcembolus grossa Wunderlich, 2017b
Furcembolus longior Wunderlich, 2017b
Longissithorax myanmarensis Wunderlich, 2017b
Longithorax furca Wunderlich, 2017b
Palpalpaculla pulcher Wunderlich, 2017b
Praeterpaculla armatura Wunderlich, 2015b
Praeterpaculla biacuta Wunderlich, 2015b
Praeterpaculla dissolata Wunderlich, 2015b
Praeterpaculla equester Wunderlich, 2015b
Praeterpaculla tuberosa Wunderlich, 2015b
Saetosoma filiembolus Wunderlich, 2012b
Uniscutosoma aberrans Wunderlich, 2015b
Tetragnathidae?
Thomisidae?
Theridiosomatidae
Leviunguis bruckschi Wunderlich, 2012b
Theridiidae
Cretotheridion inopinatum Wunderlich, 2015b
Uloboridae
Bicalamistrum mixtum Wunderlich, 2015b
Burmuloborus antefixus Wunderlich, 2015b
Burmuloborus parvus Wunderlich, 2008b
?*Burmuloborus prolongatus* Wunderlich, 2015b
Furculoborus patellaris Wunderlich, 2017b
Kachin fruticosus Wunderlich, 2017b
Kachin fruticosoides Wunderlich, 2017b
Microuloborus birmanicus Wunderlich, 2015b
Ocululoborus curvatus Wunderlich, 2012b
Palaeomiagrammopes vesica Wunderlich, 2008b
Paramiagrammopes cretaceus Wunderlich, 2008b
Paramiagrammopes longiclypeus Wunderlich, 2015b
Paramiagrammopes patellidens Wunderlich, 2015b
Propterkachin magnooculus Wunderlich, 2017b
†Vetiatoridae
Pekkachilus vesica Wunderlich, 2017b
Vetiator gracilipes Wunderlich, 2015b
Opiliones (3 families, 3 genera, 3 species)
Epedanidae
Petrobunoides sharmai Selden, Dunlop, Giribet, Zhang & Ren, 2016
†Halithersidae
Halitherses grimaldii Giribet & Dunlop, 2005
Stylocellidae
Palaeosiro burmanicum Poinar, 2008
Palpigradi (1 family, 1 genus, 1 species)
Eukoeneniidae
Electrokoenenia yaksha Engel & Huang, 2016
Parasitiformes (4 families, 4 genera, 4 species)
Argasidae
Ixodidae
Amblyomma sp.
Amblyomma birmitum Chitimia-Dobler et al., 2017
Compluriscutula vetulum Poinar & Buckley, 2008
Cornupalpatum burmanicum Poinar & Brown, 2003
Opilioacaridae
?*Opilioacarus groehni* Dunlop & Oliveira Bernardi, 2014
Polyaspididae
Pseudoscorpiones (4 families, 3 genera, 3 species)
Cheiridiidae

Table 1.—Continued.

Electrobisium acutum Cockerell, 1917a
Chernetidae
Feaellidae
Protofeaella peetersae Henderickx, 2016
Garypinidae
Amblyolpium burmiticum (Cockerell, 1920)
Ricinulei (4 families, 4 genera, 7 species)
†Hirsutisomatidae
Hirsutisoma acutiformis Wunderlich, 2017b
Hirsutisoma bruckschi Wunderlich, 2017b
Hirsutisoma denticulata Wunderlich, 2017b
†Monooculricinuleidae
Monooculricinuleus incisus Wunderlich, 2017b
Monooculricinuleus semiglobolus Wunderlich, 2017b
†Poliocheridae
?*Poliochera cretacea* Wunderlich, 2012b
†Primoricinuleidae
Primoricinuleus pugio Wunderlich, 2015b
Schizomida
Scorpiones (7 families, 9 genera, 22 species)
Buthidae
Archaeoananteroides maderai Lourenço, 2016 in Lourenço & Velten (2016b)
Chaerilidae
Electrochaerilus buckleyi Santiago-Blay, Fet, Solegrad & Anderson, 2004
†Chaerilobuthidae
Chaerilobuthus birmanicus Lourenço, 2015f
Chaerilobuthus bruckschi Lourenço, 2015f
Chaerilobuthus complexus Lourenço & Beigel, 2011
Chaerilobuthus enigmaticus Lourenço, 2015d
Chaerilobuthus gigantosternum Lourenço, 2016a
Chaerilobuthus longiaculeus Lourenço, 2013
Chaerilobuthus schwarzi Lourenço, 2015 in Lourenço & Velten (2015)
Chaerilobuthus serratus Lourenço, 2016a
†Palaeoburmesebuthidae
Betaburmesebuthus bellus Lourenço, 2016b
Betaburmesebuthus bidentatus Lourenço, 2015c
Betaburmesebuthus fleissneri Lourenço, 2016 in Lourenço & Velten (2016)
Betaburmesebuthus kobberti Lourenço, 2015 Lourenço & Beigel (2015)
Betaburmesebuthus larafleissnerae Lourenço, 2016 in Lourenço & Velten (2016c)
Betaburmesebuthus muelleri Lourenço, 2015c
Palaeoburmesebuthus grimaldii Lourenço, 2002
Palaeoburmesebuthus ohlhoffi Lourenço, 2015f
†Palaeoeuscorpiidae
Archaeoscorpius cretacicus Lourenço, 2015e
Burmesescorpiops groehni Lourenço, 2016a
†Palaeotrilineatidae
Palaeotrilineatus ellenbergeri Lourenço, 2012
†Sucinolourencoidae
Sucinlourencous adrianae Rossi, 2015
Solifugae (1 genus, 1 species)
Family *incertae sedis*
Cushingia ellenbergeri Dunlop, Bird, Brookhart & Bechly, 2015
Thelyphonida (1 family, 2 genera, 2 species)
Thelyphonidae
Mesothelyphonus parvus Cai & Huang, 2016
Family *incertae sedis*
Burmathelyphonia prima Wunderlich, 2015a

Figure 3.—Undescribed specimen of the amblypygid *Kronocharon* Engel & Grimaldi, 2014, scale bar = 1 mm.

stones, and in caves, generally in humid tropical and subtropical regions of the world.

Order Araneae Clerck, 1757

By far the largest number of arachnids recorded in Burmese amber belong to this order (some 165 described species in 93 genera), mainly due to the work of Wunderlich (2008a,b, 2011a, 2012b, 2015b, 2017b). The first spiders described from Burmese amber, however, were by Penney (2003a, 2004a, 2005, 2006a). Of the 38 spider families found in the amber, 16 are extinct. The first Mesozoic member of the primitive suborder Mesothelae Pocock, 1892 was described by Wunderlich (2015b) as *Cretaceothele lata* Wunderlich, 2015b (Fig. 4B). Later, Wunderlich (2017b) described three new genera, including the first adult males, and placed the Cretaceous mesotheles in three new extinct families: Burmathelidae Wunderlich, 2017b (Fig. 4A), Cretaceothelidae Wunderlich, 2017b, and Parvithelidae Wunderlich, 2017b. Mesotheles are known today only from south-east Asia, including China and Japan, but are known from the Euramerican region which was tropical in the Carboniferous and Permian periods (Dunlop et al. 2017).

A number of mygalomorphs are known in Burmese amber, including members of Hexathelidae Simon, 1892, Atypidae Thorell, 1870, Dipluridae Simon, 1889 (Fig. 4C), and the extinct Fossilcalcaridae Wunderlich, 2015b. They are repre-

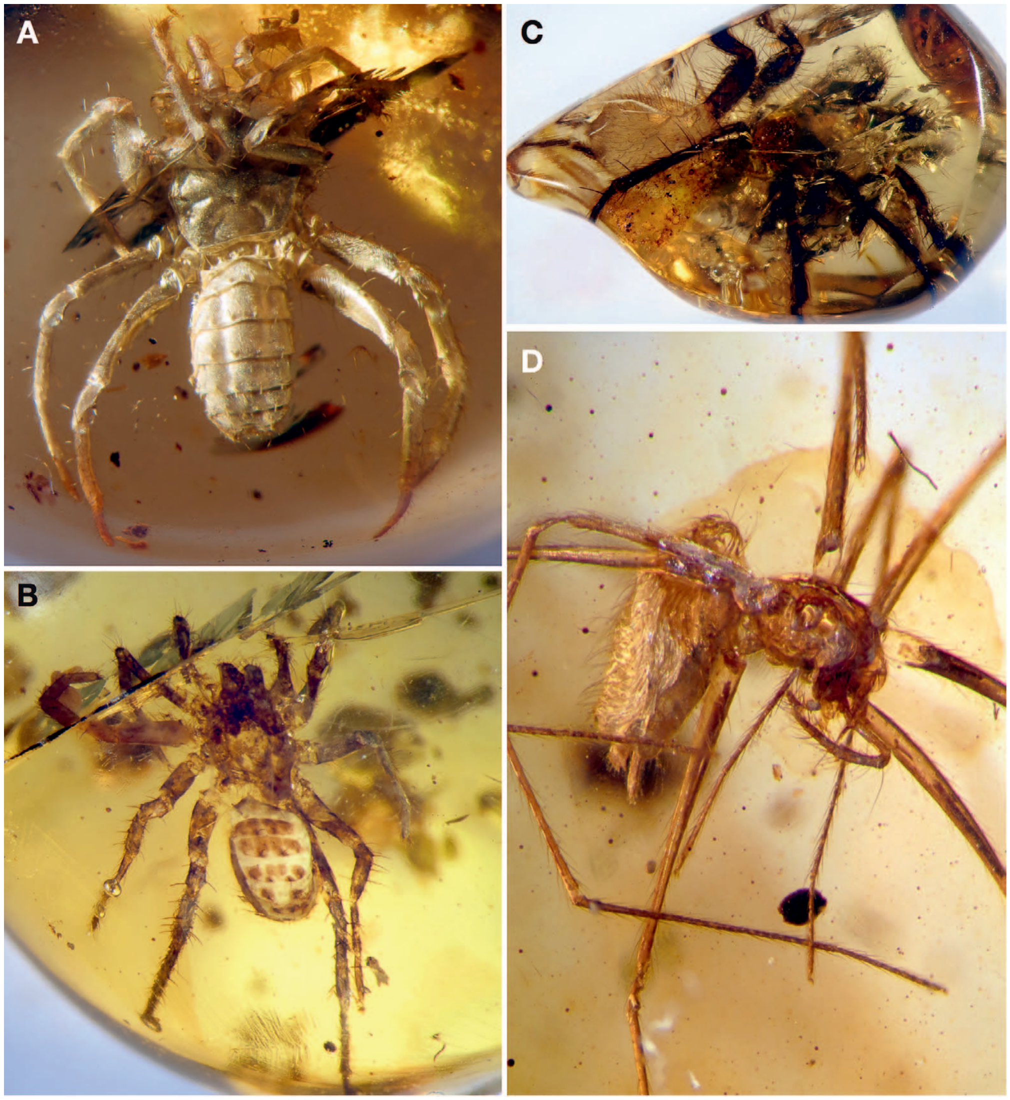

Figure 4.—Mesothele, mygalomorph and haplogyne Araneae in Burmese amber. A. Mesothele spider (possibly *Burmathele* Wunderlich, 2017), dorsal view; B. Mesothele spider (possibly *Cretaceothele* Wunderlich, 2015), dorsal view; C. Mygalomorph spider (Dipluridae?); D. Ochyroceratid spider.

sented predominantly by adult males (no females but some juveniles and exuviae), presumably because adult males leave their retreats to search for females.

Among araneomorph spiders, the haplogynes are well represented in the Burmese amber biota, with some 88 species in 45 genera. Four extinct families of haplogynes erected by Wunderlich are known exclusively from Burmese amber: Praeterleptonetidae Wunderlich, 2008b, Pholcochyroceridae Wunderlich, 2008b, Eopsilodercidae Wunderlich, 2008b, and Plumorsolidae Wunderlich, 2008b. As has been mentioned elsewhere (Selden & Penney 2010), Wunderlich's fossil families are generally diagnosed by unclear characters or combinations of characters of related families; they have never been tested cladistically, and the plethora of new names which result from inadequate description serves to muddle rather than elucidate relationships of these fossil spiders. Mongolarachnidae Selden, Shi & Ren, 2013 was established for a Jurassic genus of possibly orb weavers from China; Wunderlich (2015b, 2017b) added two new genera and five species from Burmese amber to this family, which he (Wunderlich 2015b) also moved to the Haplogynae. Among living haplogynes, members of Ochyroceratidae Fage, 1912 (including Psilodercidae Deeleman-Rheinhold, 1995; Fig. 4D), Tetrablemmidae O. Pickard-Cambridge, 1873, Oonopidae Simon, 1890, and Segestriidae Simon, 1893 are well represented (Figs. 5A,C,D). Ochyroceratids and tetrablemmids are exclusively tropical/subtropical families, oonopids are most diverse in the tropics, while segestriids are cosmopolitan in range.

Among the 33 araneomorph families reported in Burmese amber, 13 are extinct. Micropalpimanidae Wunderlich, 2008b, Burmascutidae Wunderlich, 2008b, Burmadictynidae Wunderlich, 2017b, and Vetiatoridae Wunderlich, 2017b were erected for a few Cretaceous amber forms. Lagonomegopidae Eskov & Wunderlich, 1994 is a large family of spiders only known from Cretaceous ambers. Its name derives from its most characteristic feature: two large eyes on the anterolateral

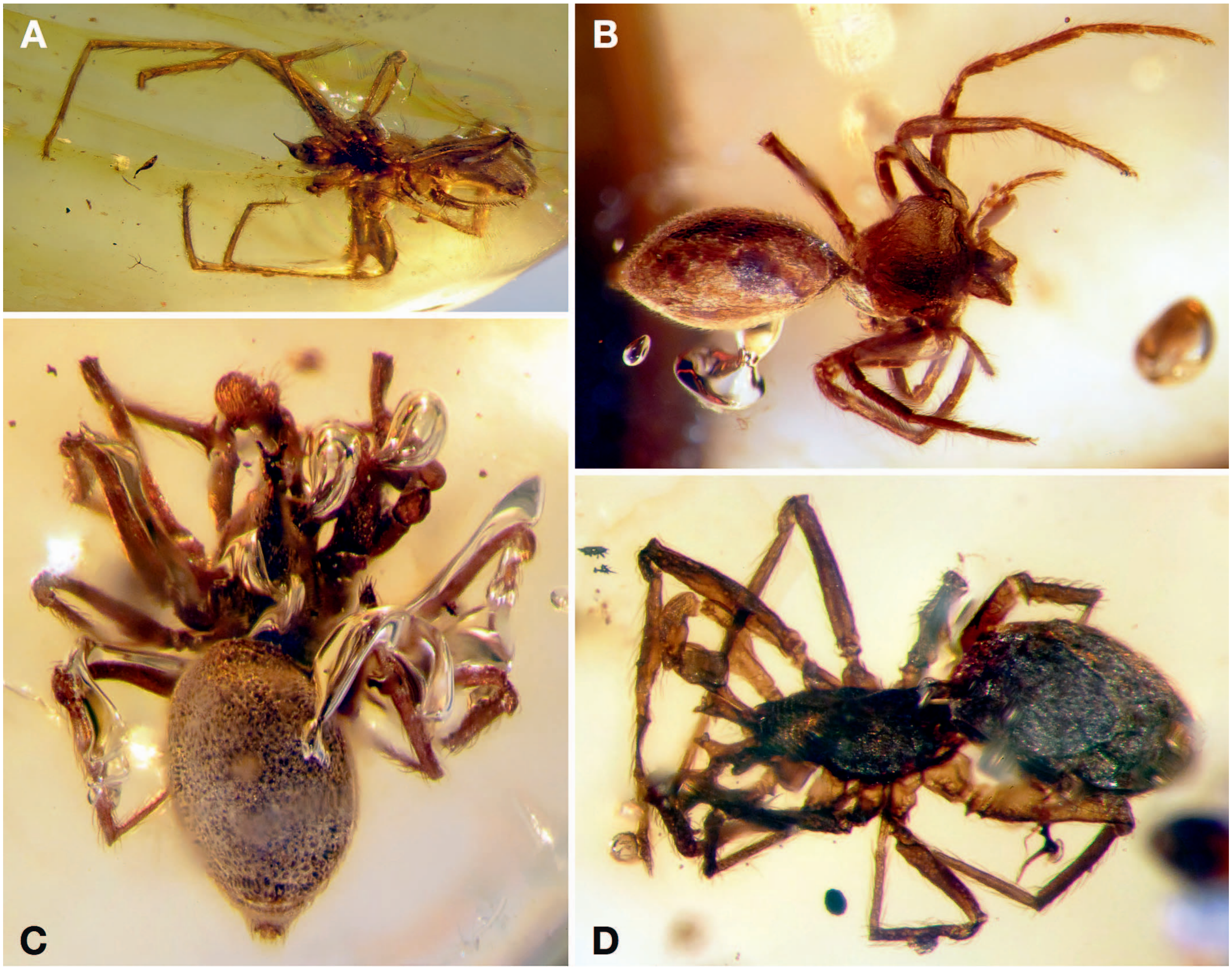

Figure 5.—Haplogye and entelegyne Araneae in Burmese amber. A. Segestriid; B. Lagonomegopid; C. Tetrablemmid *Electroblemma bifida* Selden, Zhang & Ren, 2016c, holotype, dorsal view; D. *Electroblemma bifida*, paratype, dorsolateral view.

flanks of the carapace, a character unknown in any other fossil or extant spider family. Eighteen species in 11 genera are known from Burmese amber (Wunderlich 2015b, 2017b) (Fig. 5B). Spatiatoridae Petrunkevitch, 1942 is a family erected for a Baltic amber genus, to which Wunderlich (2006, 2008a, 2011b) added further Baltic species and two from Burmese amber (Wunderlich 2015b). Wunderlich (2017b) erected a new family, Vetiatoridae, to accommodate *Vetiator* Wunderlich, 2015b, formerly included in Spatiatoridae, and a new genus, *Pekkachilus* Wunderlich, 2017b. A large number of Burmese amber entelegynes belong to the superfamily Palpimanoidea (*sensu* Wood et al. 2012). In addition to species in the Micropalpimanidae, Lagonomegopidae and Spatiatoridae already mentioned, there are 23 species in the extant family Archaeidae C.L. Koch & Berendt, 1854 (which, incidentally, was first described from fossils in Baltic amber). Palpimanoids are relatively common and diverse in the Mesozoic compared to the present day, with species known from the Jurassic and Cretaceous periods, as well as Cenozoic deposits.

Oecobiidae Blackwall, 1862 and Hersiliidae Thorell, 1870 are represented in the Burmese amber by five and three species, respectively. Members of both of these families are ground, rock and bark dwellers. Among cribellate orb weavers in Burmese amber, there are five described species in Wunderlich's (2017b) extinct family Burmadictynidae, 14 in the extant Uloboridae Thorell, 1869, and the possible deinopid *Deinopedes tranquillus* Wunderlich, 2017. Like palpimanoids, cribellate orb weavers are relatively common and diverse among Mesozoic spiders, with species known from the Jurassic as well as the Cretaceous and Cenozoic.

There are a few, mainly doubtful, records of araneoids from Burmese amber. Wunderlich (2008b:644) recorded a juvenile "Araneoidea fam. indet.". Wunderlich (2015b) described a supposed theridiid, *Cretotheridion inopinatum* Wunderlich, 2015, in a new subfamily, Cretotheridiinae Wunderlich, 2015, distinguished from all other theridiids by the lack of a theridioid tarsal comb of serrate bristles (a synapomorphy for Theridiidae Sundevall, 1833 + Nesticidae

Simon, 1894: Griswold et al. 1998) and the lack of a prosomal–opisthosomal stridulatory organ (common in theridiids). One member of the Theridiosomatidae Simon, 1881, *Leviunguis bruckschi* Wunderlich, 2012, has been described from Burmese amber, though many more species await description according to Wunderlich (2017b), and this family is also known from other Cretaceous deposits (Selden 2010; Penney 2014). Finally, *Geratonephila burmanica* Poinar *in* Poinar & Buckley, 2012 was described by Poinar & Buckley (2012) as a member of the Nephilidae Simon, 1894 (recently returned to Araneidae Simon, 1895 by Dimitrov et al. 2017). Poinar & Buckley (2012) proposed that this was the first evidence of sociality among spiders in the fossil record because there are two specimens which they considered were conspecifics. Penney (2013) considered that, while their description of the holotype as a nephiline was correct, the evidence of sociality was unproven (see also reply by Poinar & Buckley 2013). Wunderlich (2015b) synonymized *Geratonephila* with Recent *Nephila* Leach, 1815, agreed with the comments of Penney (2013) that there was no evidence that the two specimens were conspecific, nor that it showed sociality. From his long experience of working with Burmese amber, during which time he had never seen a nephiline in the deposit, Wunderlich (2015b) considered that the amber was more likely from the Dominican Republic, of Miocene age, in which deposit *Nephila* is quite common, and suggested it might belong to *Nephila tenuis* Wunderlich, 1986.

The RTA clade (Dionycha, Lycosoidea, Amaurobioidea, Dictynoidea: Sierwald 1990; Coddington & Levi 1991), is known from the Mesozoic only from questionable records, including some in Burmese amber, although its roots likely extend back to that era (Dimitrov et al. 2017). For example, the questionable juvenile thomisid listed in Rasnitsyn & Ross (2000) is more likely to be a lagonomegopid. Wunderlich 2008b: 652) described a molted skin as "Araneae indet. (RTA-clade?)" and, in the same article, several questionable Dictynidae O. Pickard-Cambridge, 1871. Wunderlich (2017b) added another doubtful member of the RTA clade from an immature male in Burmese amber. It is likely that this enormous group of spiders did not radiate until late in the Mesozoic, and many of its constituent families (e.g., Thomisidae Sundevall, 1833, Salticidae Blackwall, 1841) did not appear until the Cenozoic.

Order Opiliones Sundevall, 1833

Three genera and species of harvestman have been described from Burmese amber, yet many more are now available for study. *Halitherses grimaldii* Giribet & Dunlop, 2005 (Figs. 6A,C,D) was the first Mesozoic harvestman to be accurately described and named (previously recorded examples, not in amber, are either misidentified non-arachnids, or so poorly preserved as to be identifiable only as Opiliones). *Halitherses* was placed by Sharma & Giribet (2014) in Nemastomatidae Simon, 1879 (in the suborder Dyspnoi Hansen & Sørensen, 1904), but was later moved in its own extinct family, Halithersidae Dunlop, Selden & Giribet, 2016 following the discovery of a beautifully preserved penis (Dunlop et al. 2016) (Fig. 6C,D). Shear & Warfel (2016) have suggested that this family may belong within the superfamily Acropsopilionoidea Roewer, 1923.

Palaeosiro burmanicum Poinar, 2008 was the first Mesozoic record of the suborder Cyphophthalmi, and also the oldest record of the group; the oldest records prior to this are in Eocene Baltic and Bitterfeld ambers and were placed in the modern genus *Siro* Latreille, 1796 (Dunlop & Giribet 2003; Dunlop & Mitov 2011). *Palaeosiro* was originally placed in the European/North American family Sironidae before being transferred to the Southeast Asian family Stylocellidae by Giribet et al. (2012).

Petrobunoides sharmai Selden et al., 2016a (Figs. 6E,F) was described as the oldest member of the suborder Laniatores Thorell, 1876, and its first Mesozoic record; younger laniatoreans are known from Eocene Baltic and Miocene Dominican ambers (Cokendolpher & Poinar 1992; Ubick & Dunlop 2005). Selden et al. (2016a) placed *Petrobunoides* in the extant family Epedanidae Sørensen, 1886, which occurs today exclusively in south-east Asia, with a few species reaching as far north as Nepal and southern China (Kury 2007). Several additional Laniatores species are known from Burmese amber (Fig. 6B), which await formal description.

Order Palpigradi Thorell, 1888

Fossil palpigrades are extremely rare. Older references mentioned *Sternarthron zitteli* Haase, 1890 from the Altmühltal Formation (Solnhofen Limestone) of southern Germany, but this has been shown to be an insect nymph (Delclòs et al. 2008). Apart from the Burmese specimen mentioned below, the only other fossil palpigrade is *Paleokoenenia mordax* Rowland & Sissom, 1980, from the Pliocene Onyx Marble Formation (a cave deposit) of Arizona. Hence, the discovery of a fossil palpigrade in Burmese amber extended the fossil record of the group by some 95 million years. *Electrokoenenia yaksha* Engel & Huang in Engel et al. 2016 (Fig. 7A, B) was placed in the family Eukoeneniidae Petrunkevitch, 1955, the larger of the two extant families (4 genera, 85 named species; Giribet et al. 2014).

Order Parasitiformes Reuter, 1909

The Parasitiformes is the smaller of the two mite orders, and only 16 fossil species have been described (Dunlop et al. 2017), from strata of Cretaceous to Quaternary age. Of these, four are from the Burmese amber. ?*Opilioacarus groehni* Dunlop & Bernardi, 2014 is the oldest record of the suborder Opilioacarida Zachvatkin, 1952 (Fig. 7C), one of the most primitive acarine groups, whose members resemble tiny harvestmen. It was the third fossil opilioacarid to be described, others being known from Eocene Baltic amber (Dunlop et al. 2004, 2010).

A larval tick, *Amblyomma* sp., was identified by Klompen (in Grimaldi et al. 2002) and, most recently, a new species of *Amblyomma* has been described (Chitimia-Dobler et al. 2017). Two more larval ticks were described from the amber: *Cornupalpatum burmanicum* Poinar & Brown, 2003 and *Compluriscutata vetulum* Poinar & Buckley, 2008. All of these specimens belong to the modern family of hard ticks Ixodidae Koch, 1844 (suborder Ixodida Leach, 1815). Poinar (2015) has described patches of *Rickettsia*-like cells from the body cavity of the larval tick *Cornupalpatum burmanicum*.

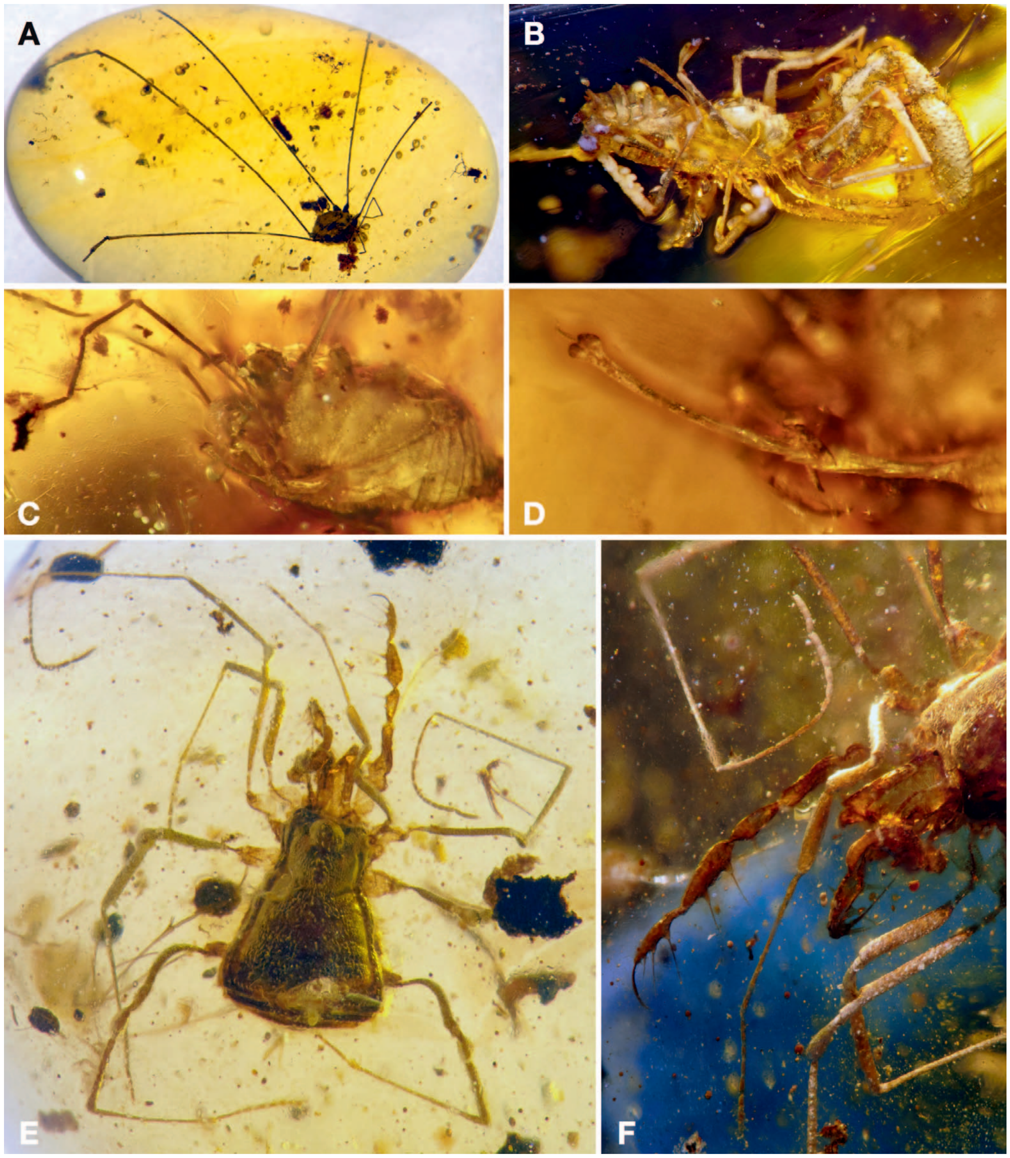

Figure 6.—Opiliones in Burmese amber. A. *Halitherses grimaldii* Giribet & Dunlop, 2005 in an amber cabochon; B. Undescribed Laniatores; C. *Halitherses grimaldii* side view of body; D. *Halitherses grimaldii* detail of extended penis (see Dunlop et al. 2016); E. The oldest described Laniatores, *Petrobunoides sharmai* Selden et al., 2016a, holotype, dorsal view; F. *Petrobunoides sharmai*, left frontal view, showing chelicerae, pedipalps, and parts of legs I and II.

Order Pseudoscorpiones Latreille, 1817

Two pseudoscorpions from Burmese amber were described early in the twentieth century by Cockerell (1917a, 1920): *Electrobisium acutum* Cockerell, 1917a and *Amblyolpium burmiticum* (Cockerell, 1920). *Electrobisium* was placed in the extant Neobisiidae Chamberlin, 1930 by Cockerell (1917a), but Judson (1997, 2000) moved it to another extant family, Cheiridiidae Hansen, 1894. *Amblyolpium burmiticum*, originally placed in the extant genus *Garypus* L. Koch, 1873, was placed in another extant genus, *Amblyolpium* Simon, 1898, in the extant family Garypinidae Daday, 1889.

More recently, a third species was described: *Protofeaella peetersae* Henderickx in Henderickx & Boone, 2016. Henderickx & Boone (2016) placed this species in Feaellidae Ellingsen, 1906, pointing out that the superfamily Feaelloidea Ellingsen, 1906 constitutes the most primitive group within the pseudoscorpions, according to the study of Murienne et al. (2008). Judson (2017) studied an additional adult male of *Protofeaella* and considered it to be most likely a stem-group feaellid.

Judson (2000) mentioned the presence of fragmentary specimens of Chthonioidea and Cheliferoidea in the material housed in the BMNH. Many more pseudoscorpion specimens from Burmese amber (Fig. 8) are undergoing study at present, so a much greater diversity of this order is to be expected in the near future.

Order Ricinulei Thorell, 1876

Ricinulei is a small order of arachnids with extremely thick cuticle which live in tropical forests and caves. The first

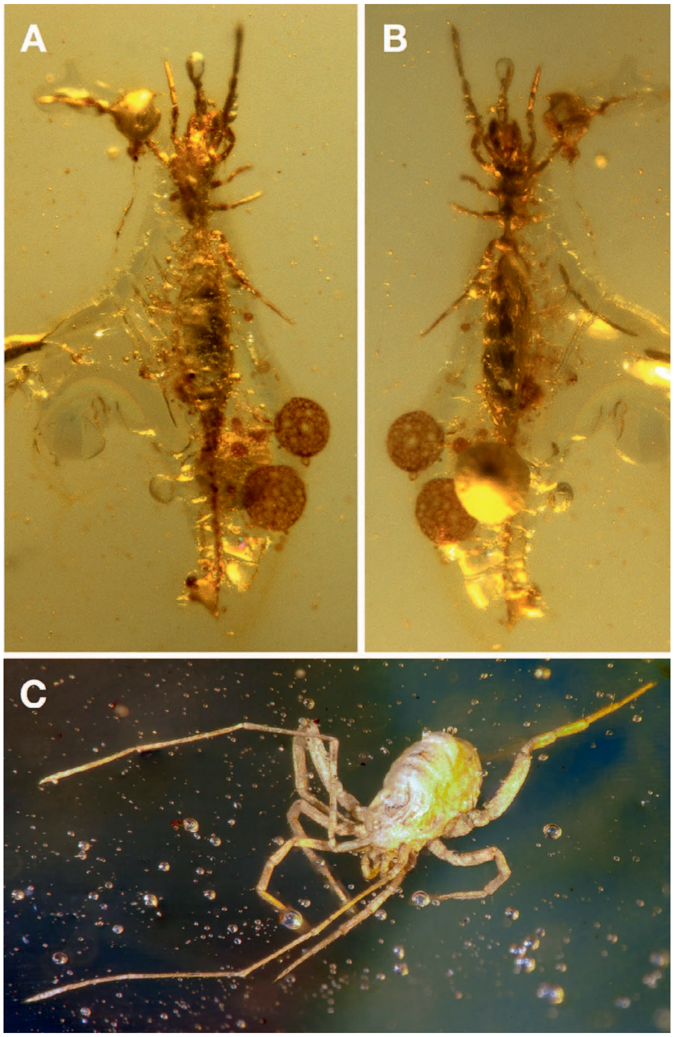

Figure 7.—Palpigradi and Parasitiformes in Burmese amber. A. Oldest known palpigrade, *Electrokoenenia yaksha* Engel & Huang, 2016, holotype, dorsal view; B. Same, ventral view. Specimen in the collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. C. Parasitiformes: Opilioacarida.

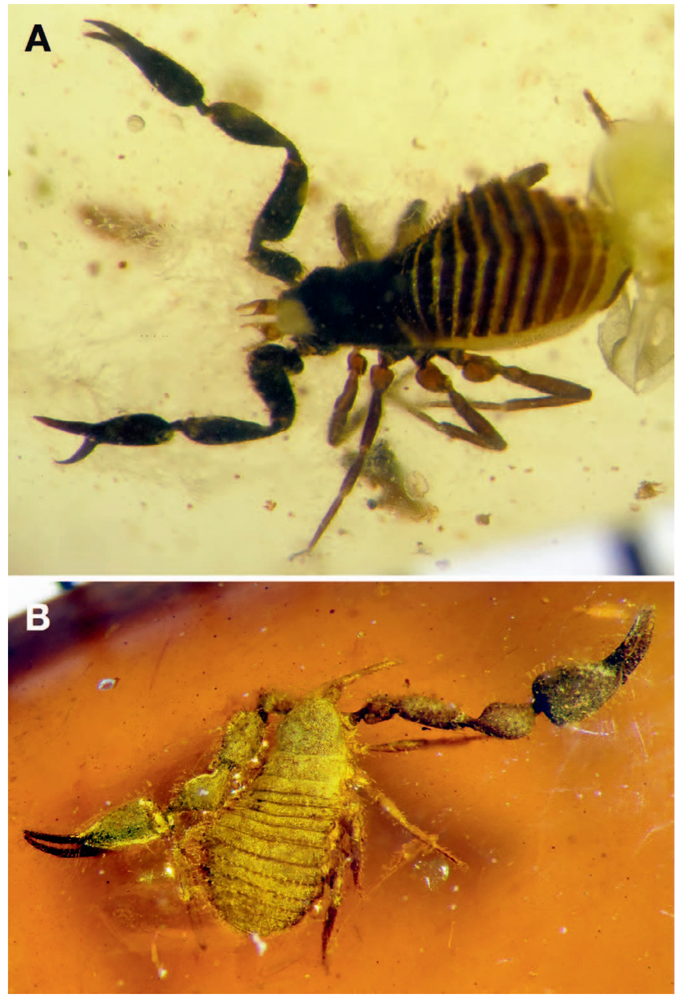

Figure 8.—Pseudoscorpiones in Burmese amber. A. Undescribed pseudoscorpion (Withiidae?); B. Undescribed pseudoscorpion (Chernetidae?).

species ever described was a fossil, mistaken for a beetle: *Curculioides ansticii* Buckland, 1837. Ricinulei occur today only in Central America and the Caribbean region (including Texas caves), and in West Africa. Until recently, fossil Ricinulei were known only from the Carboniferous. Wunderlich (2012a) described the first Mesozoic ricinuleid specimens as Ricinulei indet. and ?*Poliochera cretacea* Wunderlich, 2012a (Fig. 9C). Later, Wunderlich (2015a) described another new genus and species as *Primoricinuleus pugio* Wunderlich, 2015a (Figs. 9A, B). Both of these Burmese amber species were known only from nymphs. Wunderlich (2015a) rearranged the higher classification of Ricinulei to accommodate unusual aspects of *Primoricinuleus*, which lacks visible opisthosomal segmentation and bears a reduced or absent fixed finger on the pedipalp. In Wunderlich's (2015a) scheme, all ricinuleids, living and extinct, would be in one suborder: Posteriorricinulei Wunderlich, 2015a, except for *Primoricinuleus*, for which the new suborder Primoricinulei Wunderlich, 2015a was erected. However, examination of the specimen (Wunderlich coll. F2635/BU/CJW) indicates that the pedipalp fixed finger is present on the right side. Nevertheless, the pedipalp morphology is unlike that seen in other ricinuleids, and the lack of obvious segmentation (although there are paired spots on the ventral surface where sulci would occur in other ricinuleids) is unusual, but probably not sufficient to place the nymphal specimen in its own suborder.

Wunderlich (2017a) described five more Burmese amber ricinuleids, in two new genera: *Hirsutisoma* Wunderlich, 2017a and *Monooculricinuleus* Wunderlich, 2017a, for which he also created monotypic families. He placed the new families in the suborder Primoricinulei on account of the wide sternum, the large eyes, absence of a median tarsal claw, and the presence of single, long finger on the pedipalp. *Hirsutisoma bruckschi* Wunderlich, 2017b is a complete adult male, showing the characteristic sperm transfer modifications of leg 3, and is the smallest known adult ricinuleid. *Hirsutisoma* shows extreme hairiness for a ricinuleid, particularly on the dorsal opisthosoma. *Monooculricinuleus* is named for the single pair of eyes on a median carapace eye tubercle: an extremely unusual

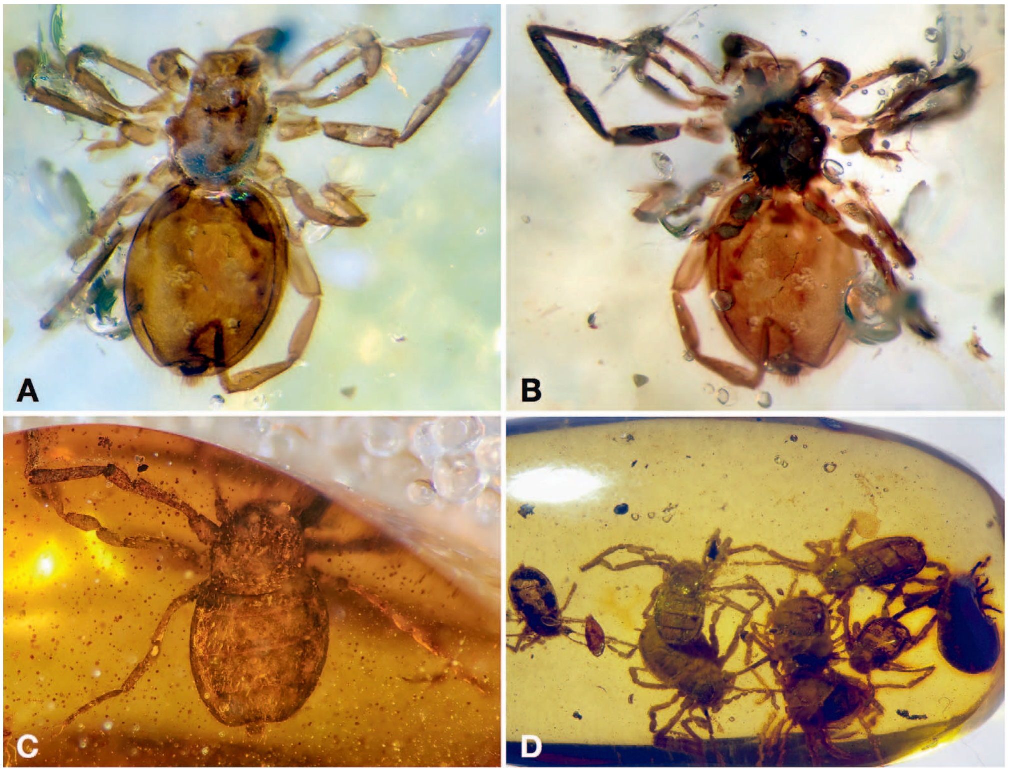

Figure 9.—Ricinulei in Burmese amber. A. *Primoricinuleus pugio* Wunderlich, 2015, dorsal view; B. Same, ventral view; C. ?*Poliochera cretacea* Wunderlich, 2012, dorsal view; D. Aggregation of juvenile ricinuleids in a single amber cabochon.

feature compared to other ricinuleids. However, in a recent communication (Jörg Wunderlich *in litt*., September 19, 2017), it appears that *Monooculricinuleus* is really an opilionid, and so requires redescription.

Ricinuleids are unknown today in Asia, so the presence of high diversity of this order in Burmese amber is evidence for a different, perhaps wider, distribution in the mid-Cretaceous than today, and that the present-day ricinuleid fauna is relict and impoverished compared to that of the past. Some specimens in Burmese amber show aggregations of juveniles (Fig. 9D), a phenomenon which has only recently been described for extant ricinuleids (García et al. 2015).

Order Schizomida Petrunkevitch, 1945

The fossil record of this small group of arachnids is sparse. They have been described only from the so-called Onyx Marble of Arizona, a cave deposit dated at probably Pliocene (c. 2.58–5.33 Ma) (Petrunkevitch 1945; Pierce, 1951), and Dominican amber, which is probably Miocene (c. 5–23 Ma) in age (Krüger & Dunlop 2010). Wunderlich (2015a) mentioned specimens of this order in Burmese amber, and a few dozen specimens have been examined in Burmese amber by the present authors, but none has yet been formally described. The Burmese example figured here (Fig. 10A) is the oldest record of the order, the first record of schizomids from the Mesozoic, and it at least doubles the fossil record of the group. Schizomids inhabit soils, litter and caves mostly in tropical regions.

Order Scorpiones C.L. Koch, 1851

To date, 22 species of scorpion in nine genera have been described from Burmese amber, mainly by Lourenço and colleagues (Lourenço 2002, 2003, 2012, 2013, 2015a,b,c,d,e, 2016a,b; Lourenço & Beigel 2011, 2015; Lourenço & Velten 2015, 2016a,b,c) and most have been placed in extinct buthoid families: Palaeoburmesebuthidae Lourenço, 2015e (7 spp.), Chaerilobuthidae Lourenço & Beigel, 2011 (8 spp.), Palaeotrilineatidae Lourenço, 2012 (1 sp.), Sucinlourencoidae Rossi, 2015 (1 sp.), and one (*Archaeoananteroides maderai* Lourenço, 2016 in Lourenço & Velten 2016b) has been assigned tentatively to the extant Buthidae C.L. Koch, 1837. The other two specimens have been referred to the Chactoidea Pocock, 1893: *Electrochaerilus buckleyi* Santiago-Blay et al., 2004, placed by its describers in a new subfamily of the extant Chaerilidae Pocock, 1893; and *Burmesescorpiops groehni* Lourenço, 2016a, placed in the extinct family Palaeoeuscorpiidae Lourenço, 2003. Fig. 10B shows the holotype specimen of *Betaburmesebuthus bellus* Lourenço, 2016b. It was pointed out by Dunlop & Penney (2012) that the relationships of the Cretaceous fossil scorpions are in need of testing with cladistic methods.

Order Solifugae Sundevall, 1833

The fossil record of Solifugae is very poor. In the Paleozoic, a single, very poorly preserved specimen, *Protosolpuga carbonaria* Petrunkevitch, 1913, from the Carboniferous of Illinois, is referable to this order. Two species are known from

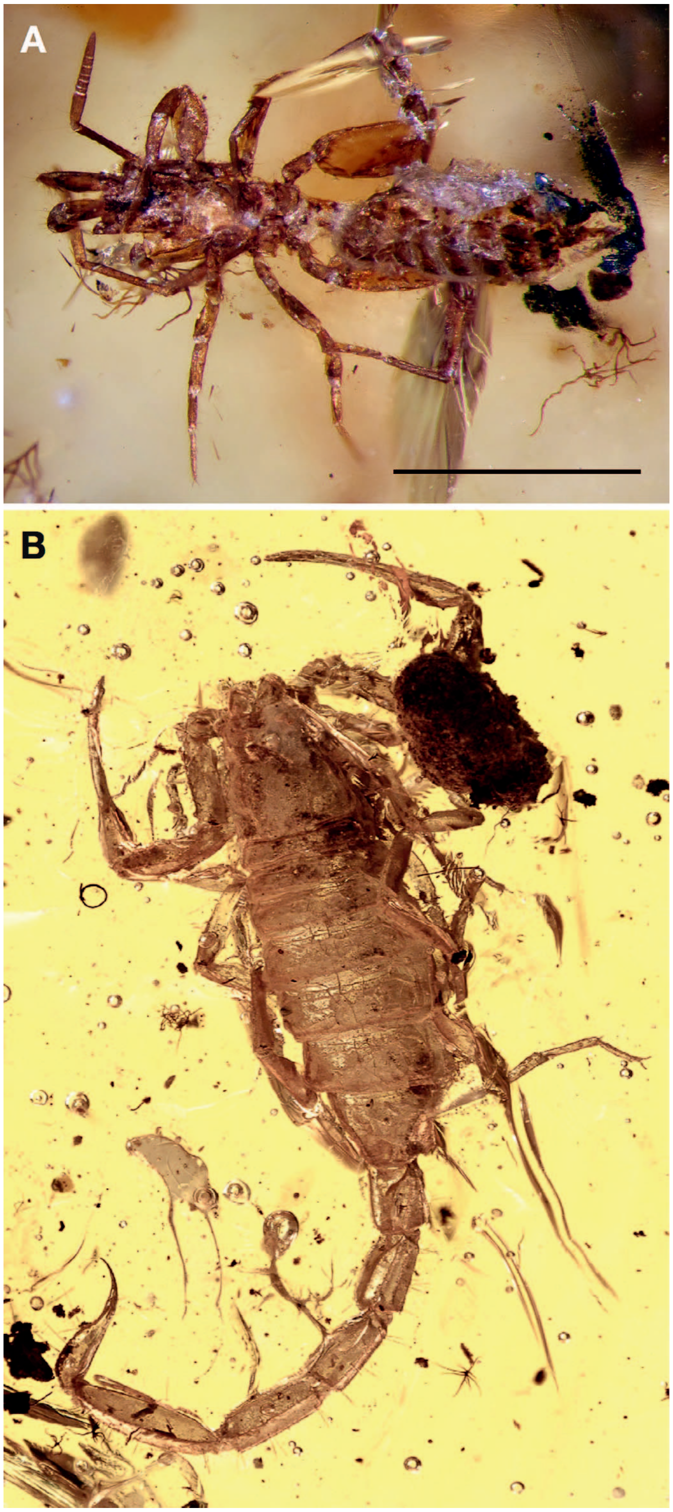

Figure 10.—Schizomida and Scorpiones in Burmese amber. A. Undescribed schizomid specimen, scale bar = 1 mm; B. Scorpion *Betaburmesebuthus bellus* Lourenço, 2016; specimen in the collection of the Museum of the Geological-Palaeontological Institut, University of Hamburg.

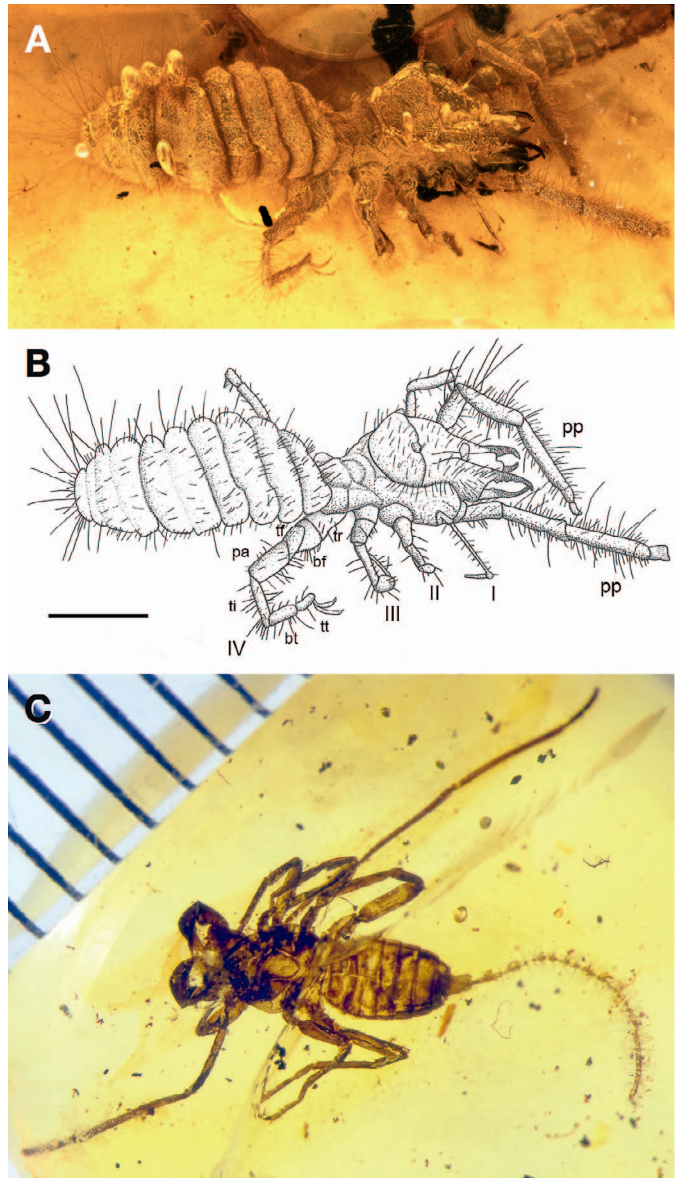

Figure 11.—Solifugae and Thelyphonida in Burmese amber. A. Solifuge *Cushingia* cf. *ellenbergeri* Dunlop et al., 2015, dorsolateral view; B. Same, explanatory drawing; bf basifemur, bt basitarsus, pa patella, pp pedipalp, tf telofemur, tt telotarsus, ti tibia, tr trochanter, legs numbered I–IV, scale bar = 1 mm (from Bartel et al. 2016); C. Undescribed specimen of thelyphonid *Mesothelyphonus parvus* Cai & Huang, 2017, with mm scale.

the Mesozoic: the Burmese amber one mentioned here, and one from the Cretaceous Crato Formation of Brazil (Selden & Shear 1996). Two species are known from Cenozoic ambers, from the Dominican Republic and the Baltic (Poinar & Santiago-Blay 1989; Dunlop et al. 2004, respectively). The single genus and species described from Burmese amber, *Cushingia ellenbergeri* Dunlop et al. 2015 (Fig. 11A, B) was not placed in a family, but it appears to have most characters in common with the living genus *Dinorhax*, which is the only extant species found in south-east Asia, and one of the few solifuges not associated with an arid environment (Dunlop et al. 2015; Bartel et al. 2016). Modern solifuges are associated

Table 2.—Numbers of described species of arachnid orders recorded in Burmese amber compared to other major Cretaceous ambers with arachnids. * Schizomida are recorded herein but as yet undescribed. Data mainly from Dunlop et al. (2017), updated.

ORDER	MYANMAR	LEBANON	NEW JERSEY	SPAIN	CANADA	FRANCE	JORDAN
Acariformes	2			10	2	1	
Amblypygi	3						
Araneae	196	5	3	5	3	2	6
Opiliones	3						
Palpigradi	1						
Parasitiformes	4		1				
Pseudoscorpiones	3					1	
Ricinulei	8						
Schizomida	*						
Scorpiones	22	1				1	
Solifugae	1						
Thelyphonida	2						
TOTAL	244	6	4	15	5	5	6

with arid environments, so their occurrence in ambers derived from humid forests in the Mesozoic and Cenozoic hints at broader habitat tolerances in the past.

Order Thelyphonida Latreille, 1804

Fossil thelyphonids preserved in rock are known from seven species in the Carboniferous of Europe and North America, and one from the Cretaceous of Brazil (Tetlie & Dunlop 2008; Selden et al. 2016b; Dunlop et al. 2017). Two genera and species of thelyphonid (Fig. 11C) are known from Burmese amber: *Burmathelyphonia prima* Wunderlich, 2015a and *Mesothelyphonus parvus* Cai & Huang, 2017. These are the only amber-preserved fossil thelyphonids known, and only the second and third species recorded from the Mesozoic. Thelyphonids are nocturnal hunters which inhabit tropical and subtropical areas of the world today; they are mainly found in forests but are also known from arid regions of the southern states of the USA. The order is absent from Europe and Australia, a single species occurs in Africa, but thelyphonids are common in south-east Asia and the Americas.

DISCUSSION

The first significant point emerging from this survey is that all living arachnid orders are found in Burmese amber. All arachnid orders in burmite have been formally described with exception of the Schizomida, for which this publication is the first to be figured. For Schizomida, Parasitiformes and Palpigradi, the Burmese amber records are the oldest for the group. The most abundant and diverse order recorded from Burmese amber is the Araneae, because there is a bias towards this group in the works of Wunderlich (2008a,b, 2011a, 2012b, 2015b, 2017b). However, it is likely that data for the acarine orders will surpass those of spiders when more work has been done. The diversity of Ricinulei seems extraordinary in comparison with the lack of records from other ambers, but some of this is erroneous (see above), and it is likely that these rarely collected arachnids will turn up elsewhere when more material comes to light (see Table 2). Burmese is the also the only amber to have produced Palpigradi; this, too, can be explained by the sheer numbers of arachnid inclusions discovered in the burmite compared with other ambers.

Second, advancement in our knowledge of mid-Cretaceous arachnofaunas is greatly increased by the sheer numbers of specimens available, compared with Mesozoic occurrences known just a decade ago (Table 2). The abundance of recently described arachnid fossils in Burmese amber will provide a great deal of data to aid phylogenetic studies. The rapid growth in data from the Burmese amber, however, should not allow specimens from other Mesozoic ambers, such as New Jersey and Canadian, to be forgotten. Other Cretaceous ambers with arachnid inclusions exist, although the amber from Ethiopia, originally thought to be Cretaceous in age (Schmidt et al. 2010) has now been shown to be Cenozoic (Coty et al. 2016). Older ambers bearing arachnids come from the Lebanon (c. 130 Ma; Penney & Selden 2002; Penney 2003b; Wunderlich 2008b), Isle of Wight (c. 127 Ma: Selden 2002), Jordan (c. 125–140 Ma: Kaddumi 2007; Wunderlich 2008b, 2012b), sites in Burgos, Cantabria and Teruel, Spain (c. 110 Ma: Alonso et al. 2000; Arillo & Subías 2000, 2002; Penney 2006b; Peñalver et al. 2007; Najarro et al. 2009; Arillo et al. 2009, 2010, 2012, 2016; Saupe et al. 2012), and Charente-Maritime, France (c. 101 Ma: Néraudeau et al. 2002, 2008; Perrichot et al. 2007; Judson 2009; Judson & Mąkol 2009). Younger are: New Jersey (c. 92 Ma: Klompen & Grimaldi 2001; Penney 2002, 2004b; Wunderlich 2011a), Vendée, France (c. 90 Ma: Perrichot & Néraudeau 2014; Sidorchuk et al. 2015; Néraudeau et al. 2017), Taimyr, Russia (c. 85 Ma: Eskov & Wunderlich 1994), Alabama (c. 82 Ma: Bingham et al. 2008), and Canada (c. 78 Ma: McAlpine & Martin 1969; Schawaller 1991; Poinar et al. 1997; Penney 2004c, 2006a; Penney & Selden 2006; McKellar & Wolfe 2010). Stratigraphical charts of these arachnid-bearing amber deposits are provided in Peris et al. (2016, fig. 3) and Rasnitsyn et al. (2016, fig. 1).

Looking at the species present in the Burmese amber, and comparing them with their modern counterparts, it is clear that the amber represents a tropical forest environment. For example, ricinuleids are unknown outside the tropics, with the exception of Texas cavernicole habitats (Gertsch & Mulaik 1939). Among the spider families represented in Burmese amber, Tetrablemmidae and Ochyroceratidae are tropical in distribution and typically forest dwellers. Rasnitsyn (1996) considered that the Burmese amber habit could not be tropical rainforest because of its lack of social insects (termites, bees, and ants). However, termites are known (e.g., Poinar 2009), as are eusocial insects (Yamamoto et al. 2016), and many insects and other biota found in Burmese amber are today restricted to tropical rainforests; e.g., 'passaloid' Coleoptera (Boucher et al. 2016). Grimaldi & Ross (in press) discussed other biota which suggest a tropical rainforest ecosystem, including: abundant liverworts, slime molds, ferns, angiosperms with tropical characteristics (e.g., leaves with drip tips), and onychophorans (Grimaldi et al. 2002; de Sena Oliveira et al. 2016). Burmese amber represents a unique window onto life in a tropical rainforest in the middle of the Cretaceous period, within which its abundant and diverse arachnofauna played a prominent ecological role.

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