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Fossiliferous Cretaceous Amber from Myanmar (Burma): Its Rediscovery, Biotic Diversity, and Paleontological Significance

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CONTENTS

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ABSTRACT

Amber from Kachin, northern Burma, has been used in China for at least a millennium for carving decorative objects, but the only scientific collection of inclusion fossils, at the Natural History Museum, London (NHML), was made approximately 90 years ago. Age of the material was ambiguous, but probably Cretaceous. Numerous new records and taxa occur in this amber, based on newly excavated material in the American Museum of Natural History (AMNH) containing 3100 organisms. Without having all groups studied, significant new records and taxa thus far include the following (a † refers to extinct taxa): For Plants: An angiosperm flower (only the third in Cretaceous amber), spores and apparent sporangia of an unusual but common fungus, hepatophyte thalli and an archegoniophore of Marchantiaceae, and leafy shoots of *Metasequoia* (Coniferae). *Metasequoia* is possibly the source of the amber. For Animals: Mermithidae and other Nematoda; the oldest ixodid tick (a larval *Amblyomma*); bird feathers; and the only Mesozoic record of the Onychophora ("velvet" worms), described as †***Cretoperipatus burmiticus*****,** n. gen., n. sp. (Peripatidae). Poinar's classification of the Onychophora is substantially revised. Still largely unstudied, the fauna of mites (Acari) and spiders (Araneae) appears to be the most diverse ones known for the Mesozoic. For Insecta: Odonata indet. (wing fragment); Plecoptera indet.; new genera of Dermaptera, Embiidina, and Zoraptera (the latter two as the only definitive Mesozoic fossils of their orders). Within Hemiptera, there are primitive new genera in the Aradidae, Hydrometridae, Piesmatidae, Schizopteridae, and Cimicomorpha (Heteroptera), as well as in †Tajmyraphididae (Aphidoidea), and †Protopsyllidiidae. An adult snakefly (Raphidioptera: †Mesoraphidiidae) is the smallest species in the order, and new genera occur in the Neuroptera: Coniopterygidae, Berothidae, and Psychopsidae, as well as larvae of apparent Nevrorthidae. Coleoptera are largely unstudied, but are probably the most diverse assemblage known from the Cretaceous, particularly for Staphylinidae. An adult lymexylid, the most primitive species of *Atractocerus*, is the first Mesozoic record of the family. In Hymenoptera there are primitive ants (Formicidae: Ponerinae n. gen., and †*Sphecomyrma* n.sp [Sphecomyrminae]), the oldest record of the Pompilidae, and significant new records of †Serphitidae and †Stigmaphronidae, among others. Diptera are the most diverse and abundant, with the oldest definitive Blephariceridae and mosquito (Culicidae), as well as new genera in the Acroceridae, Bibionidae, Empidoidea; a new genus near the enigmatic genus *Valeseguya*, and an unusual new genus in the †Archizelmiridae. †*Chimeromyia* (Diptera: Eremoneura), known previously in ambers from the Lower Cretaceous, is also represented.

The stratigraphic distribution of exclusively Mesozoic arthropods in Burmese amber is reviewed, which indicates a probable Turonian-Cenomanian age of this material (90–100 Ma). Paleofaunal differences between the NHML and AMNH collections are discussed, as is the distinct tropical nature of the original biota. Burmese amber probably harbors the most diverse biota in amber from the Cretaceous, and one of the most diverse Mesozoic microbiotas now known.

INTRODUCTION

Of all the world's amber deposits, perhaps none has more mystique than those from northern regions of Myanmar. "Burmite," along with jadeite from nearby mines, was exported to China since at least the first century A.D. for use in jewelry and carved objets d'art (Laufer, 1906; reviewed in Grimaldi, 1996; Zherikhin and Ross, 2000). Baltic amber had been prized for 10 millennia before this in northern Europe, but in Asia the proximity of Burmese amber, and probably its deep red color, hardness, and glassy polish, made it particularly sought along with ivory and jade. Use of it as a precious and semiprecious substance abruptly ended, though, by approximately 1940, and despite the work of an insightful entomologist made 80 years ago, its scientific significance has been confused and only recently recognized.

The first significant geological investigation of Burma's amber was by Noetling (1892, 1893), who reported the most productive sites in the Hukawng Valley of the northern state of Kachin, specifically southwest of Maingkhwan (26°20′N, 96°36′E). Four other regions in Burma have historically yielded amber (reviewed in Zherikhin and Ross, 2000), but none as prolific and commercially exploited as in the Hukawng Valley. Noetling mentioned inclusions of insects and plants, and perceptively noticed that the newly excavated amber pieces appeared weathered and may have been transported some distance before redeposition. H.L. Chhibber visited the Hukawng Valley in 1930, and made many additional observations. He reported the amber to occur in thin lignite seams among clays and shales (Chhibber, 1934). The larger, transparent pieces of amber were buried between 10–15 m, and to reach it miners excavated narrow shafts with walls supported by bamboo screens. Beyond this depth, ground water would fill the shaft. Presence of the foraminiferan *Nummulites biarritzensis* indicated a middle Eocene age of the sediments, though Chhibber acknowledged that the amber was possibly reworked from older sediments. He also reported that amber was mined most abundantly near the villages of Khanjamaw (26°15′50″N, 96°33′37″E), Ladummaw (26°11′19″N, 96°28′48″E), and Lajamaw (26°15′N, 96°28′E). His observation that some areas reported by Noetling were pocked with abandoned mines may have led to the popular notion that the mining of Burmese amber, by and large, was depleted or abandoned (e.g., Fraquet, 1987).

According to the records of the Geological Survey of India, 82,000 kg of Burmese amber were excavated between 1898–1940 (summarized by Zherikhin and Ross, 2000). Curiously, only one collection of Burmese amber is known that was made for scientific purposes. This collection consists of 117 pieces containing approximately 1200 organisms in the NHML. It was assembled by R.C.J. Swinhoe of Mandalay between 1915 and 1916, and sent to a prolific entomologist in Colorado, T.D.A. Cockerell (1866–1948). Cockerell is renowned for having written nearly 4000 articles on various subjects (Weber, 1965), but particularly the systematics of living and fossil insects. Between 1916 and 1921, Cockerell published 13 papers on 41 new arthropods in Swinhoe's collection, then donated the collection to the NHML. Cockerell described perhaps 7000–8000 species during his lifetime, but also had an uncanny ability to recognize natural relationships among the plethora of taxa with which he worked. As a result, he was able to recognize that the arthropods in Burmese amber (and therefore the amber itself) were older than the surrounding sediments, perhaps even Cretaceous in age:

> They [the arthropods in Burmese amber] are, indeed, related to living forms; but in practically every case to precisely those forms which we have thought of as ancient, as remnants of a very old fauna. So . . . it is difficult to avoid a strong suspicion that the amber, though found in Miocene clay, is actually very much older, conceivably even Upper Cretaceous. (Cockerell, 1917a: 360).

Until approximately the 1960s, the Cretaceous was one of the poorest known geological periods for insects; now there are over 30 major Cretaceous deposits yielding insects (see, for example, the summary in Evenhuis, 1994). Despite this deficiency, and Cockerell's early suggestion that Burmese amber was Cretaceous, there was very little research on the NHML collection between 1921 and 1995, nor were there any recorded attempts to excavate additional Burmese amber for study of the inclusions. In 1995, Alexandr Rasnitsyn, of the Paleotological Institute, Moscow, and Genady Dlussky, of Moscow State University, studied Hymenoptera and specifically ants, respectively, in the NHML collection of Burmese amber. Rasnitsyn (1996b) noted the presence of the extinct Cretaceous family †Serphitidae and the subfamily †Iscopininae (Hymenoptera). Dlussky (1996) described a bizarre ant, †*Haidomyrmex*, from the NHML collection, which he placed in the Cretaceous subfamily †Sphecomyrminae. Mounting evidence that Burmese amber was Cretaceous led to a coordinated study of the NHML collection, organized by Andrew Ross (NHML). Productive as Cockerell was, he touched on but a fraction of the organisms in the NHML collection of Burmese amber. In a recent issue (vol. 56, no. 1) of the *Bulletin of the Natural History Museum* (*Geology Series*) [London], eight papers describe 15 new species of arthropods in six orders from that collection. Therein are also extremely useful summaries of described species in Burmese amber (Ross and York, 2000), and a list of arthropod families (Rasnitsyn and Ross, 2000).

Adding to the renewed interest in Burmese amber, we are able to report a new collection

TABLE 1

Summary of Major Fossiliferous Cretaceous Amber Deposits

Location	Age	Present latitude	Paleo-latitude	References
Burma	?Cenomanian	25.5°N	12°N	Zherikhin and Ross, 2000; this paper
Lebanon	Barremian-Aptian	34°N	10–15°N	Azar, 2000; Scotese, 1991; Zharkov et al., 1995; Channell et al., 1996
New Jersey	Turonian	41°N	40°N	Grimaldi et al., 2000a; Scotese, 1991; Zharkov et al., 1995
Spain	Aptian	43°N	25–35°N	Alonso et al., 2000; Scotese, 1991; Zharkov et al., 1995
W. Canada	Campanian	50°N	55°N	Pike, 1995; Scotese, 1991; Zharkov et al., 1997
Siberia	Albian-Santonian	74°N	60–70°N	Zherikhin and Eskov, 1999; Zharkov et al., 1995, 1997

of fossils in amber assembled from material that was recently excavated from the Hukawng Valley in northern Burma—the only new scientific specimens of the material obtained in over 80 years. The collection contains nearly three times the number of inclusions as the NHML collection, and many new taxa and records not represented in the NHML collection. Moreover, our findings not only corroborate a Cretaceous age of Burmese amber, but also suggest an origin that is probably mid-Cretaceous.

The Cretaceous is one of the most biotically significant periods in the evolution of terrestrial life since the angiosperms explosively radiated in the upper part of the Lower Cretaceous (Crane et al., 1995). Given the great diversity of extant insects intimately associated with angiosperms, evolution of the two groups would presumably be inextricably linked. One study found, however, that there was no increase in the number of insect families in the Cretaceous during or immediately following the angiosperm radiations (Labandeira and Sepkoski, 1993), but in fact there was a slight slump in family numbers. Other taxic analyses found a profound radiation of Cretaceous insects (Jarzembowski and Ross, 1993, 1996; Ross et al., 2000). Phylogenetic studies on speciose families of insect pollinators (Engel, 2001; Grimaldi, 1999), herbivores (Farrell, 1998), and major consumers (Grimaldi and Agosti, 2000; Grimaldi et al., 1997; Thorne et al., 2000) indicated explosive radiation of these groups in the Cretaceous. Disparity in the results is probably due to approaches that use taxic analyses (e.g., numbers of insect families) versus phylogenetic analyses (see Grimaldi, 2000a). Compared to dramatic extinctions of non-avian dinosaurs, ammonites, rudist bivalves, and other taxa by the K/T boundary, extinctions of insects are barely noticeable, and may be obscured by the impressive radiations of insects just prior to this time.

Besides preserving a rich fauna from a biologically important time period, Burmese amber preserves organisms with a lifelike fidelity for which amber is renowned (Grimaldi, 1996). Such complete preservation vastly improves interpretation of extinct species.

Lastly, the location of Burmese amber also makes it highly significant. It is the only major, fossiliferous deposit of Cretaceous amber in southeastern Asia, and one of two of the most southerly deposits of fossiliferous Cretaceous amber. All other major deposits of Cretaceous amber occur between 34° and 74° N latitude (Table 1), but why they are restricted to the Northern Hemisphere is an enigma. Paleolatitude of the Burmese and Lebanese amber deposits (10–15°N) are the most southerly of all major Cretaceous amber deposits. As discussed at the end of this paper, climatic effects from paleolatitude were probably profound. Ages, locations, and references for the major deposits of fossiliferous Cretaceous amber are the following:

Lower Cretaceous: LEBANON and JORDAN, ranging from the Lower to Upper Neocomian (Berriasian to Aptian, and a minor incursion into the Albian; Azar, 2000); SPAIN (Nograro Formation of Alava, upper Aptian and middle Albian; Alonso et al., 2000); and RUSSIA, Taimyr Peninsula of northern Siberia (Ogneva Formation, Aptian to Albian; Zherikhin and Eskov, 1999). Several smaller deposits in Japan and England have also yielded insect fossils (summarized by Grimaldi, 1996; Ross, 1998).

Upper Cretaceous: CANADA (western), Cedar Lake, Manitoba and Medicine Hat, Alberta (McAlpine and Martin, 1969), and Grassy Lake, Alberta (Pike, 1995). The Grassy Lake and Medicine Hat deposits belong to the Foremost Formation, Judith River Group (Campanian, possibly Santonian). RUSSIA: Taimyr Peninsula, Siberia, from Agapa and belonging to the Dolgan Formation (Cenomanian), and from Yantardakh, Kheta Formation (Santonian). Zherikhin and Eskov (1999) also reviewed other localities in the former USSR. USA: New Jersey (Raritan Formation, Turonian; Grimaldi et al., 1989; 2000a). The paleobiota of New Jersey amber is the most diverse one reported thus far, even though the deposit that yielded most of the amber was extremely localized. Very likely the Burmese amber biota will be found to be more diverse than any other Cretaceous amber deposit, including amber from New Jersey.

MATERIALS AND METHODS

Bags of crude amber were purchased by Leeward Capital Corporation, a Calgary-based mining company, from local sources near the village of Tanai. Tanai is on the Ledo Road in Kachin State, close to the historical sources of Burmese amber in the Hukawng Valley (fig. 1). Mining specifically occurs approximately 32 km southwest of Tanai near Noije Bum (‘‘hill’’, approx. 250 m). Since initial exploration in 1999, Leeward has joined with a local Kachin mining company (Buga Company Ltd.) for exploitation of the amber deposits, under the jurisdiction of the Myanmar Ministry of Mines and military officials. Methods of mining the amber remain traditional, just as were described by Chhibber (1934). Apparently, miners need to reach lignitic seams some 30–40 cm thick to obtain the amber, which can occur at depths of up to 12 m. In 2000, nearly 80 kg of crude amber was mined. Samples of various colors were analyzed using Pyrolysis-Gas chromatography (PyGC) and PyGC-Mass Spectroscopy (e.g., Shedrinsky et al., 1991; Grimaldi et al., 2000a), which matched identically to each other and to samples from the NHML collection (A. Shedrinsky, unpubl. data on file in the Invertebrates Division, AMNH). Material from the outcrops of the 1999 and 2000 excavations may be different from that reported by Chhibber (1934) and earlier workers, but their proximity and chemical identity indicates an identical botanical origin with the historical collections and, thus, probably a very similar or identical age.

Approximately 75 kg of raw Burmese amber were shipped to the AMNH by Leeward Capital, where it was treated in lots of approximately 3 kg, using a 50% solution of muriatic acid (HCl) to dissolve veins of calcite that permeated most pieces. This greatly improved visibility into the amber. The amber was then washed thoroughly with water, and carefully screened for organismal inclusions piece by piece. The amber was kept wet during screening in order to improve visibility. Screening was done under a stereoscope (approximately 20× magnification) using transmitted and oblique reflected light. For many pieces, one or more surfaces needed to have a ‘‘window’’ polished into the surficial rind in order to locate and view inclusions. This was done using a Buehler Ecomet water-fed flat lap with abrasive discs (320, 600, 800, 1200 grits). Because Burmese amber is exceptionally hard compared to other ambers, it was generally possible to trim off some amber surrounding an inclusion without the piece splitting or crumbling. Hardness of Burmese amber allows surfaces to be polished with a glassy finish. Trimming was done with a fine (1.5 mm thick) diamond, water-fed, circular trim saw; the sawed surfaces were ground with successively finer grits, and then polished with a 1μm alumina polish. This optimized the penultimate step in preparation: embedding the piece in a highly stable epoxy (Buehler) under vacuum, as described in detail elsewhere (Nascimbene

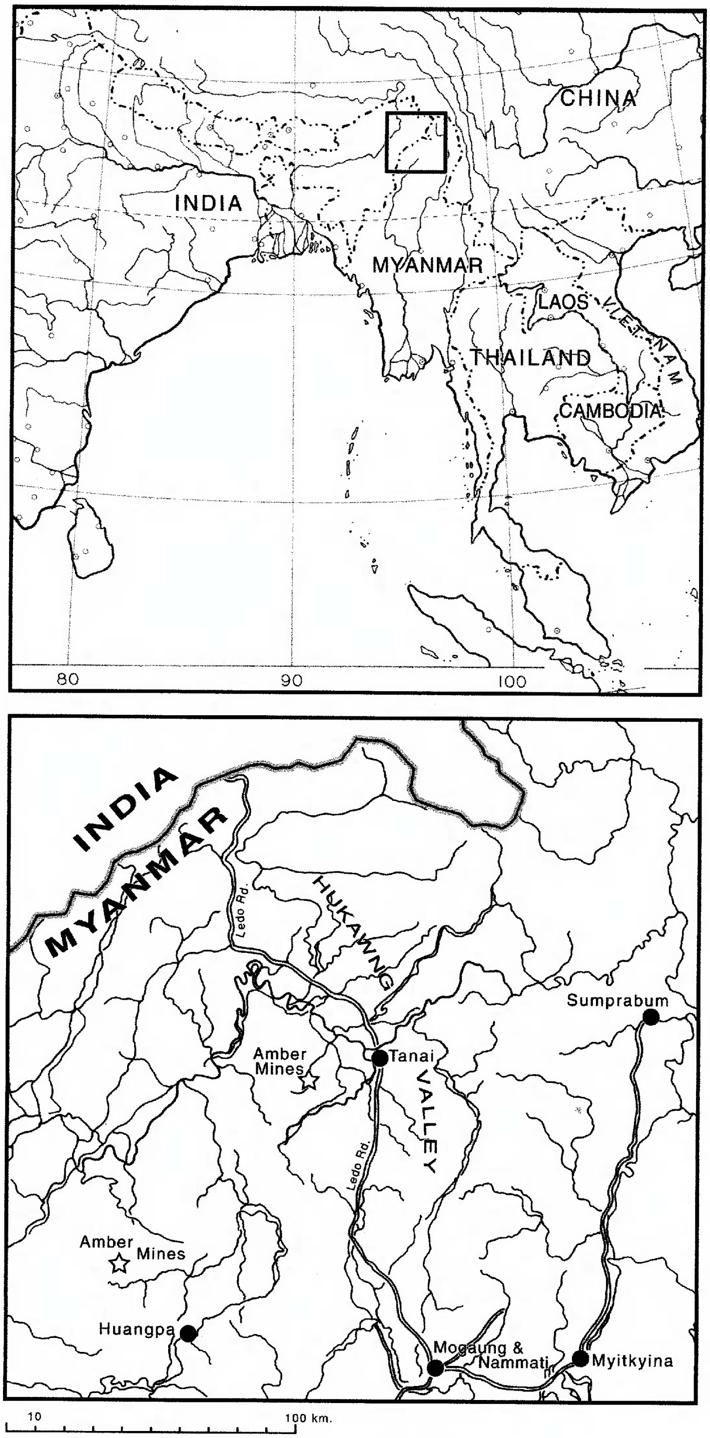

Fig. 1. Location of Burmese amber deposits. **Above**: inset shows approximate area in southeast Asia. **Below**: detail within inset.

and Silverstein, 2000). In this process, epoxy penetrates most fine cracks and thus helps prevent fracturing during the final trimming, grinding, and polishing. Optimal preparations resulted in a cubic shape, with generally no more than a millimeter or two between the inclusion and one or more surfaces of the amber, these surfaces being generally parallel to the plane of critical structures. However, many pieces had multiple inclusions that could not be separated, and this compromises preparation and observation. This appears to be a particular problem with the pieces from the NHML collection, since most inclusions occur in large pieces that were sliced into polished slabs for viewing, but no further.

All AMNH pieces were given unique, sequential numbers; for pieces with multiple inclusions each inclusion was lettered (a, b, c,. . .). Identifications were done, where possible, to at least family level, and a collection of 1200 pieces and 3100 inclusions was catalogued using the database MS Access. Printed or diskette copies of the database are available from the senior author for qualified researchers; an electronic version will eventually be available at www.amnh.org. For taphonomic purposes we included counts of 308 arthropod specimens too partial or degraded to be of systematic use, and so they were not accessioned, cataloged, or databased. Some were identifiable to insect family, or just as ‘‘Insecta incertae sedis’’ or ‘‘Arthropoda incertae sedis’’. Systematic description and discussion of various taxa will be made in separate papers.

RESULTS

TAPHONOMIC OBSERVATIONS

Some 72.21 kg of acid-washed amber (minus the dissolved calcite) yielded, on average, 46 organismal inclusions per kg (a total of 3,408 organisms). This count includes 308 partial specimens, such as isolated wings of insects, as well as specimens too poorly preserved for identification beyond order or to family. Other inclusions (not included in this figure) were plant stellate trichomes (more abundant than in any other Cretaceous ambers studied thus far), bark fibers, wood fragments, and insect frass. Individual pieces of amber varied in color from light, transparent yellow to deep, blood red, but the most abundant kind was an orange-colored amber containing swirls of fine bubbles and different hues. Pyrolysis gas chromatography–mass spectroscopy on the different forms of amber indicate a chemically identical substance (T. Wampler and A. Shedrinsky, unpubl. data), so all of the amber was probably formed by a single species of tree. Botanical identity of the tree that produced Burmese amber is unknown, but presence of diagnostic coniferous compounds indicates it certainly was a conifer, and possibly a cupressaceous tree like *Metasequoia* (see below). Variations may be a result of amount of predepositional exposure and of geothermal energy during deposition (for color), and whether the resin was secreted subcortically or externally (for form). Insects were comparatively rare in the ‘‘swirly’’ amber, and when present they were often distorted from moderate to extreme compression, and often also disarticulated. This type of amber preservation is similar to that in Paleocene amber from Wyoming (Grimaldi et al, 2000b) and putatively Paleocene amber from Sakhalin Island (Zherikhin and Eskov, 1999). For Wyoming amber, it is believed that extremely deep sediments created tremendous pressures, which compressed most organisms and even organic debris within the amber into unrecognizable ‘‘smears.’’ Another type of Burmese amber consisted of flattened, lens-shaped pieces, which rarely contained insects. Insects were most commonly found in pieces shaped like flows or runnels; these compromised no more than 3–4% by mass of all the amber but yielded approximately 85% of the arthropods. Insects in runnel pieces were usually well preserved, and sometimes numerous organisms were found in such a piece merely 3 cm long and 1 cm diameter. Clearly, the runnel pieces were flows of resin secreted in areas or under conditions optimal to entrapment of insects.

TAXONOMIC DIVERSITY

The recent collections have yielded significant new, higher-level taxonomic records for Burmese amber, including several plants, the phyla Nematoda and Onychophora, and nearly 30 families of Arthropoda (table 2). Collectively based on the NHML and AMNH collections, the Burmese amber fauna preserves a remarkable diversity of organisms, including numerous records of earliest occurrence and other significance. We briefly review below those taxa for which at least some family-level identifications were done, and ones we considered especially significant. We have not discussed the following taxa represented in the new AMNH collection, simply because they still require study: Aves (feathers, currently under study by Carla Dove, Smithsonian Institution), Reptilia (skin), Myriapoda, Collembola, Archaeognatha and Thysanura, Ephemeroptera, Odonata (wing fragments only), Blattodea and Mantodea, Auchenorrhyncha, Pscoptera, Thysanoptera, Trichoptera and Lepidoptera.

Kingdom PLANTAE

Plant Antheridia or Fungal Sporangia? The most common organismal inclusion in the material we screened were polyp-shaped structures, ranging in size from 2 to 6 mm in width, which are almost certainly the sporangia of a fungus or possibly plant (figs. 2–7). Similar structures occur in the NHML collection (A.J. Ross, personal commun.). They were never branched or joined at the base, nor were vegetative/leafy structures found associated with them. One type of abundant spore (figs. 8, 9) in this amber must be produced by these sporangia.

The sporangia grew on and through the wood of the tree that produced the amber. Several pieces of amber contained sporangia and thin, delaminated layers of wood containing circular holes the same diameter as the base of nearby sporangia (fig. 3c). Dozens, and up to approximately 100 sporangia, can be found in a piece of amber (fig. 2c). Many pieces contained groups of sporangia arranged radially, with the bulbous ends toward the center (fig. 2c). This suggests that the sporangia were growing in narrow channels into which resin flowed, either in deep grooves in the bark, or within decayed pockets near the surface of wood (fig. 4). Bases of sporangia were very rarely preserved, apparently having decayed when buried with the wood on which they were growing. Thus, the portion of the polyp preserved in the amber almost always has a cross section of the base exposed at the surface. This exposure allowed decay of the internal tissues in most specimens; occasionally specimens were found with intact internal contents.

The sporangia in Burmese amber have no apical ostiole, as is found in some antheridia of hepatophytes having roughly similar shape (e.g., Sphaerocarpaceae). Cuticles were better viewed using scanning electron microscopy (SEM). This was done by taking three pieces with sporangia and cutting a fine groove in each amber piece along various axes close to the sporangium, then splitting them open. This caused fracturing between the cuticle and the amber (fig. 6), or through the sporangium (fig. 7), depending on how the groove was cut. The exposed sporangia were then gold coated for examination using a Zeiss DSM-1 SEM. The external surfaces (cuticle) of the sporangia have a very fine geometric sculpturing, similar to herringbone patterns (fig. 6). Under stereoscope magnifications (50–100×), this pattern resembles fingerprints. Under the SEM at magnifications of 100–1000×, no cellular/epithelial structure was visible, although in some views minute openings, 3–4 μm in diameter, were found in fairly regular distribution (fig. 6b), though nothing resembled stomata.

The interior of well-preserved sporangia was whitish and somewhat granular under stereoscopic magnifications; under the SEM at magnifications of 1,000–3,000× some biological structure was apparent. Significant looking structures were short, fibrous bundles (figs. 7b, f) and small, compressed, irregular "flakes" approximately 5 μm in diameter (figs. 7a, c–e). Serial sections for transmission electron microscopy (TEM) would probably be useful, although if a hymenium were present even at these SEM magnifications columns of paraphyses and asci would be apparent, as is found in the apothecia of certain ascomycetes like *Pyronema*.

Sporangia were always found either completely intact, or dehisced into empty, hemispherical halves (longitudinally; figs. 2, 5). Spores were never found within or oozing out of dehisced sporangia, though clumps of a very distinctive and uniform type of spore

TABLE 2

Numbers of Specimens of Organismal Inclusions in Burmese Amber in the Two Major Collections

Group	Taxon	NHML	AMNH
	Kingdom Plantae		
Musci	Hypnodendraceae	1	[a]
Coniferae	Cupressaceae s.l.	0[a]	3
Fungi?	indet.	many	many
Angiospermae	indet.	0	1
	Kingdom Animalia		
	Phylum Nematoda		
Nematoda	Mermithidae	0	2
Nematoda	indet.	0	20[b]
	Phylum Onychophora		
Onychophora	Peripatidae	0	1
	Phylum Mollusca		
Gastropoda	indet.	1	1
	Phylum Vertebrata		
Aves (feathers)	indet.	0	1
Reptilia (skin)	indet.	1	1
	Phylum Arthropoda		
Acarina	Anystidae	1	
	Bdellidae	2	
	Bdelloidea	1	
	Cheyletidae	5	
	Erythraeidae	25	
	Eupodidae	7	
	Ixodidae	1	1
	indet.	122	206
	TOTAL	164	207
Araneae	Archaeidae		1
	Dictynidae		1
	Eusparassidae	1	
	Lagonomegopidae† ?		1
	Linyphiidae?		1
	Myrmeciidae[c]	3	
	Mysmenidae?		1
	Oonopidae	2	2
	Pisauridae	1	
	Telemidae?		1
	Tetragnathidae	1	
	Theridiidae	1	2
	Thomisidae	1	
	indet.	26	118
	TOTAL	34	128
Chilopoda	indet.	0	3
Diplopoda	Synxenidae	60[b]	3
	Siphonophoridae	0	4
	indet.	1	4
	TOTAL	61	11
Pseudoscorpionida	Cheridiidae	3	
	Olpiidae	1	
	indet.	34	11
	TOTAL	38	11
Scorpionida	indet. (fragments)	1	3
	Class Hexapoda		
Collembola	Sminthuridae	32	5
	indet.	22	50
	TOTAL	54	55
Archaeognatha	Machilidae	1	
	indet.	0	5
	TOTAL	0	5
Thysanura	Lepismatidae	4	0
Ephemeroptera	Prosopistomatidae	1	
	indet.	0	3
Odonata	indet. (fragments)	0	3
Blattodea	Blatellidae	3	
	Polyphagidae	1	
	indet.	54	55
	oothecae	0	3
	TOTAL	58	58
Plecoptera	indet.	0	2
Dermaptera	Labiduridae	1	
	Pygidicranoidea	0	2
	indet.	0	4
Zoraptera	Zorotypidae	0	4
Embioptera	Burmitembiidae†	1	
	indet.	0	2
Isoptera	Hodotermitidae	2	0
	Kalotermitidae	89[b]	7
	Rhinotermitidae	1	0
	TOTAL	92	7
Mantodea	indet.	4	2
Orthoptera	Grylloidea	3	
	indet.	2	3
	TOTAL	5	3
Phasmida?	indet. (eggs)	1	0
Sternorrhyncha	Aleyrodidae	3	6
	Aphidoidea	0	7
	Coccoidea	17	110
	TOTAL	20	146
Auchenorrhyncha	Achilidae	28	
	Aphrophoridae	1	
	Cixiidae	2	
	Fulgoroidea	13	
	indet.	0	47
	TOTAL	44	47
Heteroptera	Aradidae	0	1
	Coreidae	1	0
	Enicocephalidae	6	6
	Hydrometridae	0	1
	Ochteridae	1	0
	Schizopteridae	0	1
	indet.	0	27
	TOTAL	8	36
Hemiptera	indet.	10	
Psocoptera	Compsocidae	1	
	Pachytroctidae	2	
	Psyllipsocidae	4	
	indet.	40	165
	TOTAL	47	165

TABLE 2

(Continued)

Group	Taxon	NHML	AMNH
Lophioneurida	Lophioneuridae†	1	0
Thysanoptera	indet.	13	99
Raphidioptera	indet. (larvae)	1	3? (fragments)
	Mesoraphidiidae†	0	1
Neuroptera	Berothidae	3	34
	Coniopterygidae	0	1
	Osmylidae	1	1
	Osmyloidea	1	1
	Psychopsidae?	0	2
	indet.	1	0
	TOTAL	6	38
Coleoptera	Aderidae	1	
	Anthicidae	1	
	Cantharoidea	2	
	Carabidae? (larva)	1	
	Cerambycidae	1	
	Chrysomelidae?	1	
	Cisidae	1	
	Cleroidea	1	
	Colydiidae	6	
	Cucujidae	4	1
	Dermestidae	2	
	Elateridae	19	12
	Eucinetidae	1	
	Eucnemidae	2	
	Helodidae	1	
	Lathridiidae	1	
	Lymexylidae	0	1
	Melandryidae	2	
	Melyridae	1	
	Microsporidae	1	
	Mordellidae	1	4
	Nitidulidae	1	
	Oedemeridae	2	
	Pselaphidae	6	2
	Ptiliidae	3	48
	Ptilodactylidae	0	1
	Rhipiphoridae	1	1
	Salpingidae	1	
	Scraptiidae	16	
	Staphylinidae	23	55
	Staphylinoidea	2	
	Throscidae	1	
	indet.	89	349
	TOTAL	195	473
Hymenoptera	Bethylidae	31	6
	Braconidae	0	2
	Aulacidae[d]	6	4
Hymenoptera	Chalcidoidea	3	1
	Diapriidae	1	0
	Embolemidae	2	0
	Evaniidae	1	7
	Formicidae	5	4
	Megalyridae	0	1
	Megaspilidae	1	0
	Myrmarommatidae	2	20
	Pelecinidae	1	0
	Pompilidae	0	1
	Scelionidae	23	36
	Sierolomorphidae	0	1
	Serphitidae†	2	27
	Sphecidae	18	7
	Stigmaphronidae†	0	2
	Tiphiidae	2	0
	indet.	4	63
	TOTAL	102	262
Trichoptera	Hydroptilidae	1	
	indet.	0	16
Lepidoptera	Micropterigidae	4	
	indet.	3	5
Diptera	Acroceridae	0	2
	Anisopodidae	0	6
	Archizelmiridae†	0	7
	Apsilocephalidae	1	0
	Blephariceridae	0	1
	Cecidomyiidae	14	141
	Ceratopogonidae	12	204
	Chaoboridae	3	0
	Chimeromyidae†	0	6
	Chironomidae	31	110
	Culicidae	0	1
	Dolichopodidae?	1	0
	Empidoidea	42	80
	Hilarimorphidae	0	1
	Mycetophilidae	15	147
	Phoridae	3	32
	Psychodidae	35	152
	Rhagionidae	2	16
	Scatopsidae	1	50
	Sciaridae	5	6
	Therevidae	1	0
	Tipuloidea	1	28
	indet.	34	218
	TOTAL	201	1210
TOTAL, Arthropods		1198	3012

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[a] A blank indicates that undetermined specimens may belong to the taxon. A zero indicates that all specimens have been identified, and none belong to the taxon.

[b] Based on multiple individuals in one or several pieces.

[c] Myrmeciidae is preoccupied by subfamily Myrmeciinae (type genus *Myrmecia* Fabricius, 1804), in the ants (family Formicidae, order Hymenoptera). The current correct name is Corinnidae. Also Eusparassidae is currently Sparassidae.

[d] The Gasteruptiidae listed by Rasnitsyn and Ross (2000) are here listed under Aulacidae. Also, unlike Rasnitsyn, we do not classify the Aulacidae as a subfamily within the Gasteruptiidae.

† Extinct.

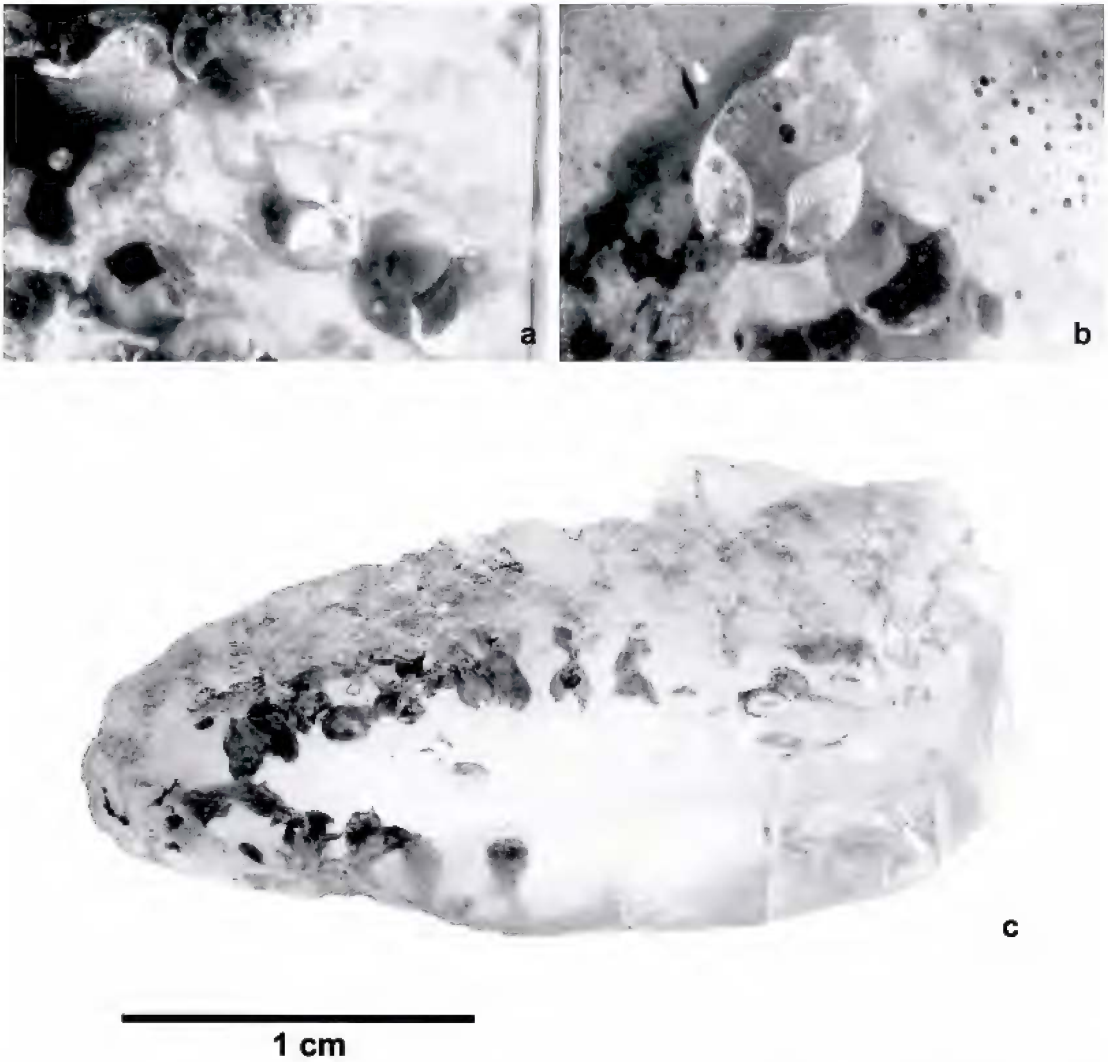

Fig. 2. Photomicrographs of sporangia. **a, b.** Dehisced sporangia. **c.** Cross section through an amber piece, showing sporangia growing on the perimeter of the flow.

were common in the amber, or layers of these spores occurred where they adhered to a fresh resin surface before being covered by another flow of resin (fig. 8). In fact, the spores and sporangia very rarely occurred in the same piece of amber, but the abundance of these two types of inclusions makes their common identity quite probable. Some of the better preserved dehisced sporangia contained a U-shaped structure, suggestive of a spring mechanism for the explosive rupture of the sporangium (fig. 5). The spores are quite large (diameters ranging from 40–70 μm, mean of 45 μm), have an irregular shape, and an apparently thick coat (SEM, fig. 9) without sculpturing (fig. 9). There is no evidence of the spores being trilete or even monolete. Often found proximal to ruptured spores are small nucleated cells, some of which occur in tandem of two or three and forming a bacilliform shape (figs. 8a, b, c). Diameter of the cells is approximately 0.15–0.20× the diameter of the spore.

Though no apparent hymenium was found in longitudinally exposed sporangia, it is most likely that the sporangia are the apothecia of xylophagous ascomycete fungi, or possibly the sporangia of a myxomycete, like

Fig. 3. Sporangia of a probable fungus (not to the same scale). Specimens in c show circular holes in wood or bark fibers adjacent to the sporangia, indicating they grew directly on the amber tree.

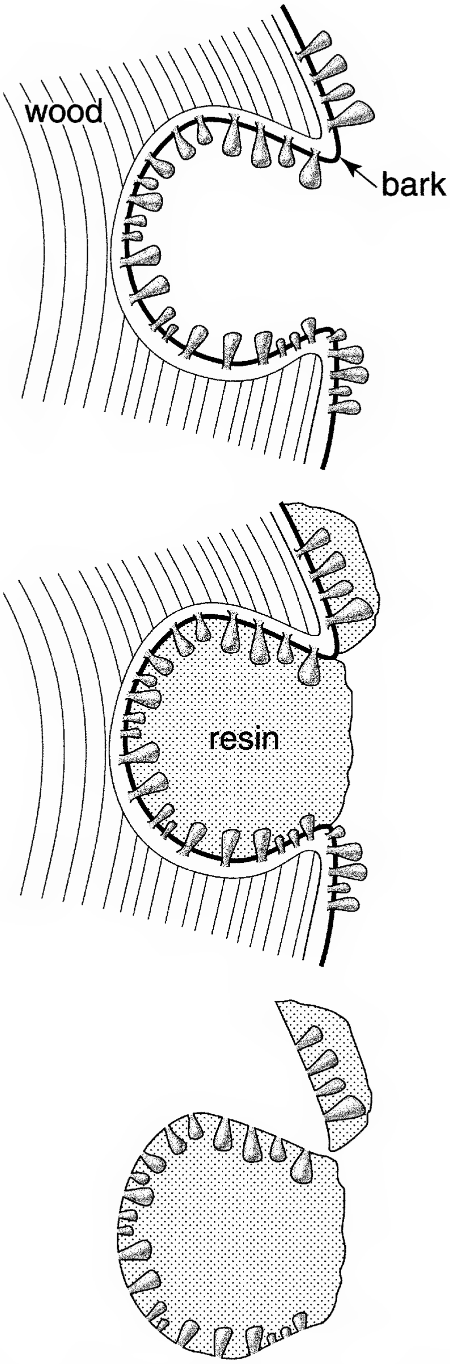

Fig. 4. Possible sequence for the preservation of sporangia in a radial array. **Top**: the sporangia grow on the surface of the wood within grooves and cavities, into which resin flows and encapsulates the sporangia (middle). **Bottom**: wood decays around the hardened resin during burial.

Lycogala. The sporangia are very doubtfully plants, since no epithelial cell structure nor vegetative structures were ever found with them, as always occur with hepatophytes and bryophytes, for example. Also, no elaters were found among the numerous spores, which are distinctive, spiral, asexual cells of hepatophytes that aid in the dispersal of dehisced spores. Although elaters are not found in the Ricciaceae, they occur in all other hepatophytes. The sporangia also lack features distinctive of other similarly shaped plant sporophytes, such as the operculum in *Sphagnum*. Isolated thalli of hepatophytes do occur, rarely, in Burmese amber (below).

An explosive discharge of spores by these sporangia, as suggested by the U-shaped spring mechanism, may explain why spores and polyps are rarely found together: spores were probably dispersed far from the polyps, such that it would have been very unlikely for a resin flow to have enveloped polyps in the moment of spore discharge. *Pyronema* and other "cup" fungi also have explosive discharge of spores.

Hepatophyta (*Hepatopsida*): Several specimens of liverwort thalli have been recently found (e.g., AMNH Bu11; fig. 10a), as well as a portion of a distinctive sporophyte. The thalli are *Frullania*-like jungermannialeans, with saclike ventral lobes (lobules), which in extant forms facilitate water storage. *Frullania* and related genera grow on tree bark and other substrates that encounter water stress. Though the fossils are not necessarily related to *Frullania*, their presence in amber and the possession of lobules indicate they also grew on the surface of tree trunks. Specimen AMNH Bu324 is apparently an isolated archegoniophore of a *Marchantia*-like liverwort (fig. 10b). The structure is star-shaped with 10 "arms" (archegoniophores of extant Marchantiaceae possess 9–11), and 1.5 mm in diameter. Because the structure is black (carbonization occurs in some amber fossils), reflective lighting is insufficient to detect the typical presence of rhizoids or scales on the lower surface or air chambers and pores on the upper surface. The thalli distinctive to many Marchantiaceae (having polygonal air chambers with a central pore, gemma cups, etc.) have not been found in Burmese amber, but the distinctive shape of this isolated

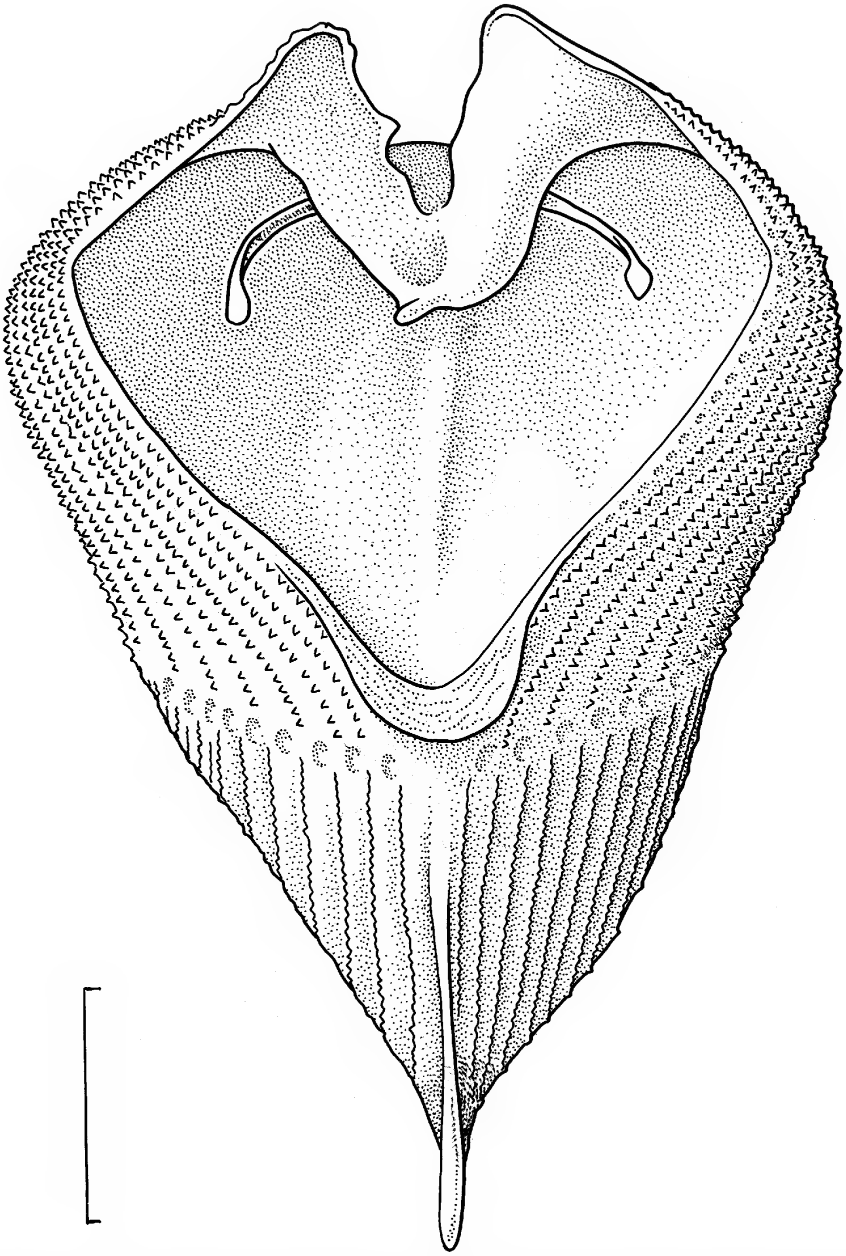

Fig. 5. Detail of a typical sporangium in Burmese amber. Specimen is dehisced, revealing a thin, straplike structure within. The structure is possibly a hinge involved in explosive discharge of spores. Scale is 1.0 mm.

structure allows this taxonomic assignment with some confidence. Though fossils of hepatophytes are rare, particularly from the Mesozoic and Paleozoic, the group is ancient, with the oldest definitive taxa being from the Devonian (reviewed in Kenrick and Crane, 1997).

Bryophyta: In the AMNH collection are two specimens of leafy shoots of a moss with a growth form like *Polytrichum* and *An-*

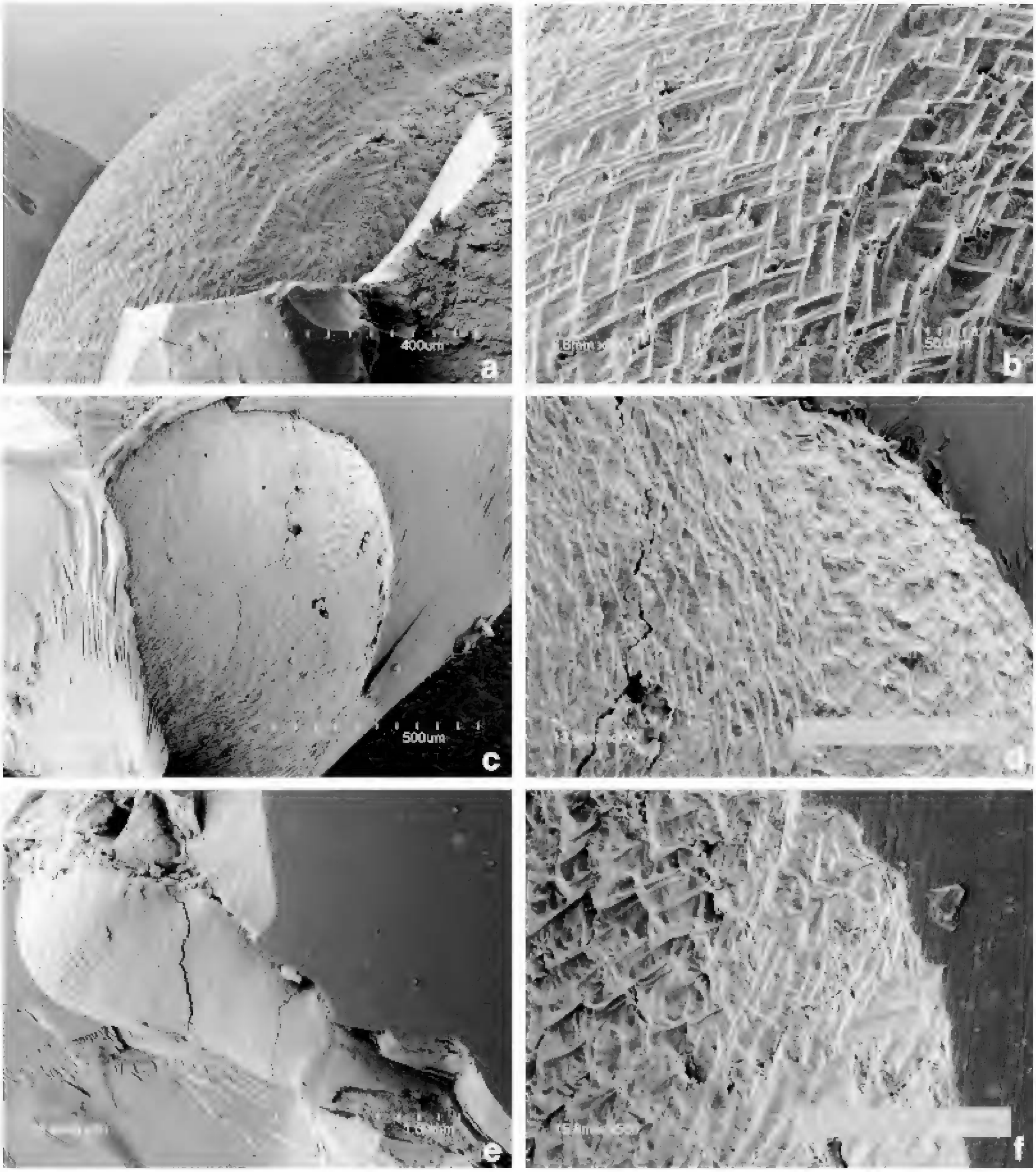

Fig. 6. Scanning electron micrographs of exposed cuticular surfaces of three sporangia in Burmese amber. **a, c,** and **e** show most of the sporangium; **b, d,** and **f** are details of cuticular surfaces of each specimen, respectively.

dreaea. The shoots are among the largest inclusions in the AMNH collection, 34 mm in length. Long-stalked sporophytes with apical capsules, so typical of bryophytes, have not been found. A specimen of *Hypnodendron* occurs in the NHML collection. Like hepatophytes, Mesozoic and Paleozoic bryophytes are rare, but occur since at least the Devonian.

Pterophyta: The presence of leptosporangiate ferns (e.g., Polypodiaceae) is indicated by several sporangia distinctive to this group in pieces AMNH Bu342 and Bu731 (e.g., fig. 11). The sporangia have the typical ribbed

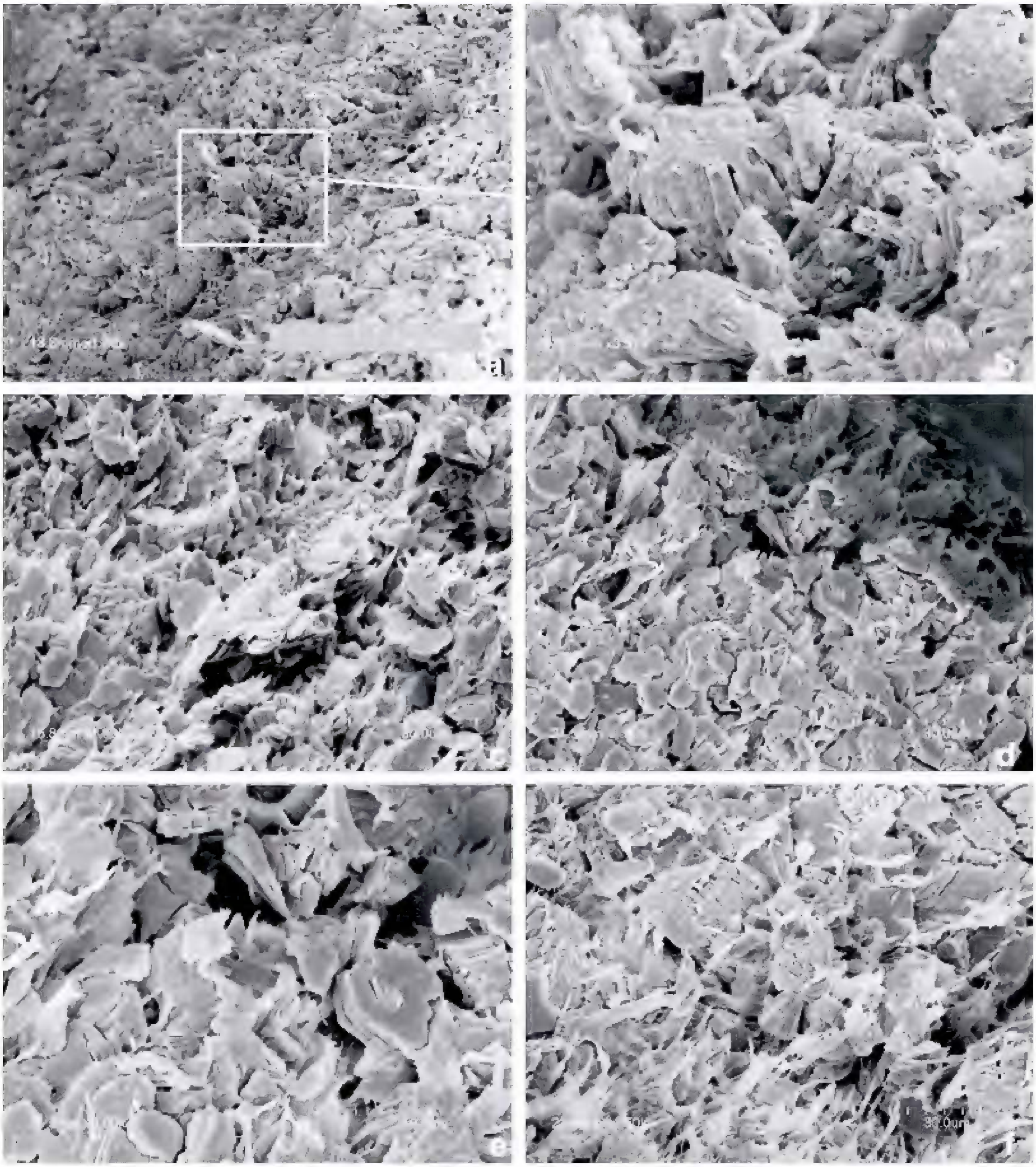

Fig. 7. Scanning electron micrographs of exposed interior contents of three sporangia in Burmese amber (1000–3500×).

annulus, attached to a dehisced, membranous, sac-like portion. Diameters of the dehisced sporangia are approximately 220 μm. Annulate sporangia first appear in the Lower Carboniferous, and are among the earliest evidence of pterophytes. By the Upper Carboniferous, pterophytes were diverse and abundant (reviewed in Kenrick and Crane, 1997).

Coniferae: AMNH Bu794 contains two impressive fragments of leafy shoots of "dawn redwood," *Metasequoia* (Taxodiaceae, or Cupressaceae s.l.) (fig. 12). One shoot is 5 cm long, the other is 1.7 cm, and they bear two rows of opposite leaflets so distinctive to this genus of "living fossils". (*Metasequoia*, like the coelacanth, was first

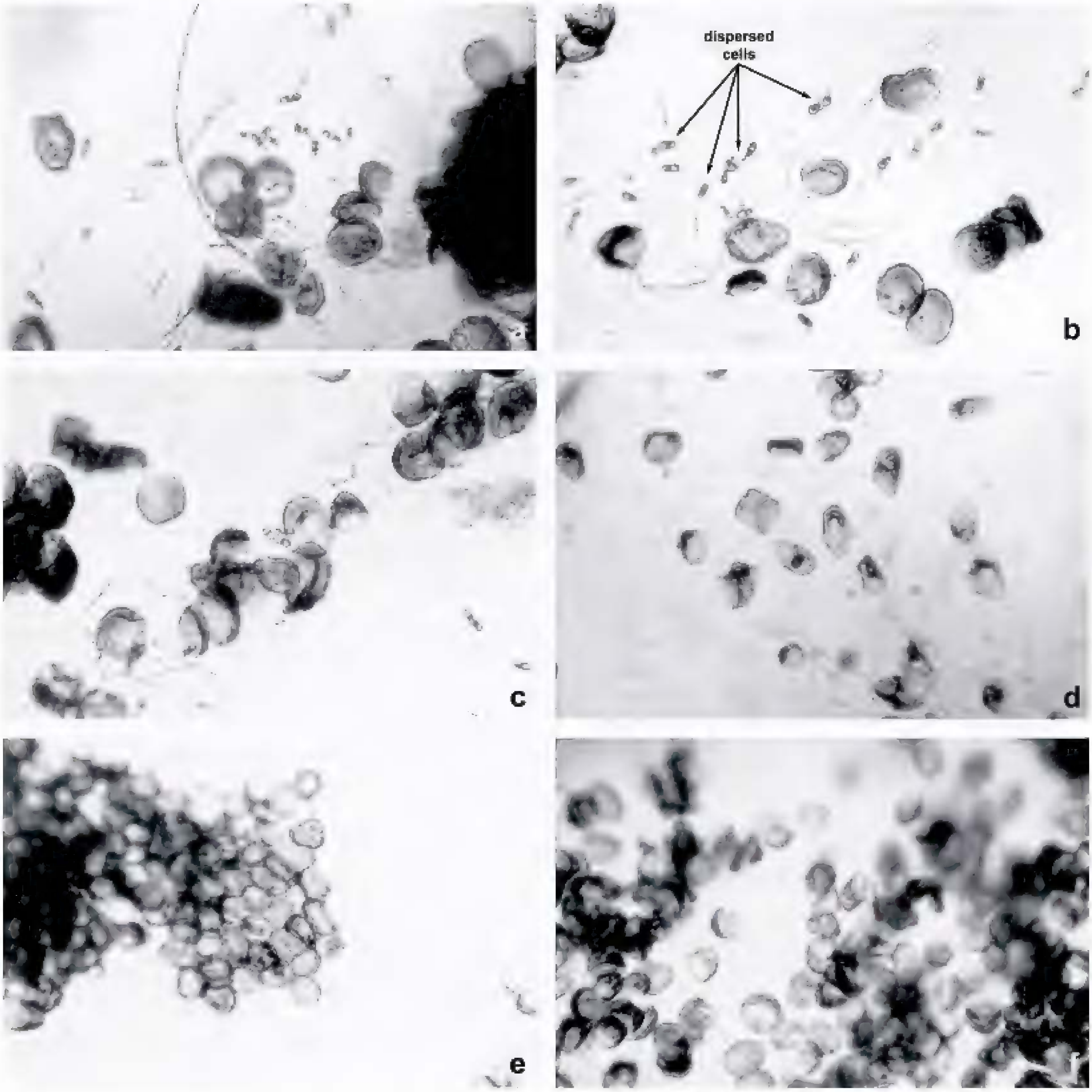

Fig. 8. Photomicrographs of abundant type of spore in Burmese amber, probably produced by the unusual fungal sporangia (figs. 2–7). **a-c.** showing nucleated cells that derive from the spores. Spores are often found in thick clumps (**e, f**). Diameter of spores is approximately 50 μm.

known from fossils about a century before the sole living species was discovered; the tree was later found growing in southern China.) The leaves are shorter, broader, and more crowded than occurs in the most widespread, Cretaceous species, *M. †occidentalis*; also, the Burmese amber species has the tips of the leaves broadly rounded, not pointed as in *M. †occidentalis*. This is the only type of conifer inclusion found in the AMNH collection of Burmese amber. *Metasequoia* has been definitively associated with several types of fossil resins, from the Paleocene of Axel Heiberg Island, Canadian arctic (Anderson and LePage, 1995), and from the Cretaceous of peninsular Alaska (D. Grimaldi, unpubl. data). Chemical analyses of Burmese amber have yet to be compared to these other samples. Though inference of botanical origin based on botanical inclusions can be misleading, it does offer rare macrofossil evidence about possible botanical origins. *Meta-*

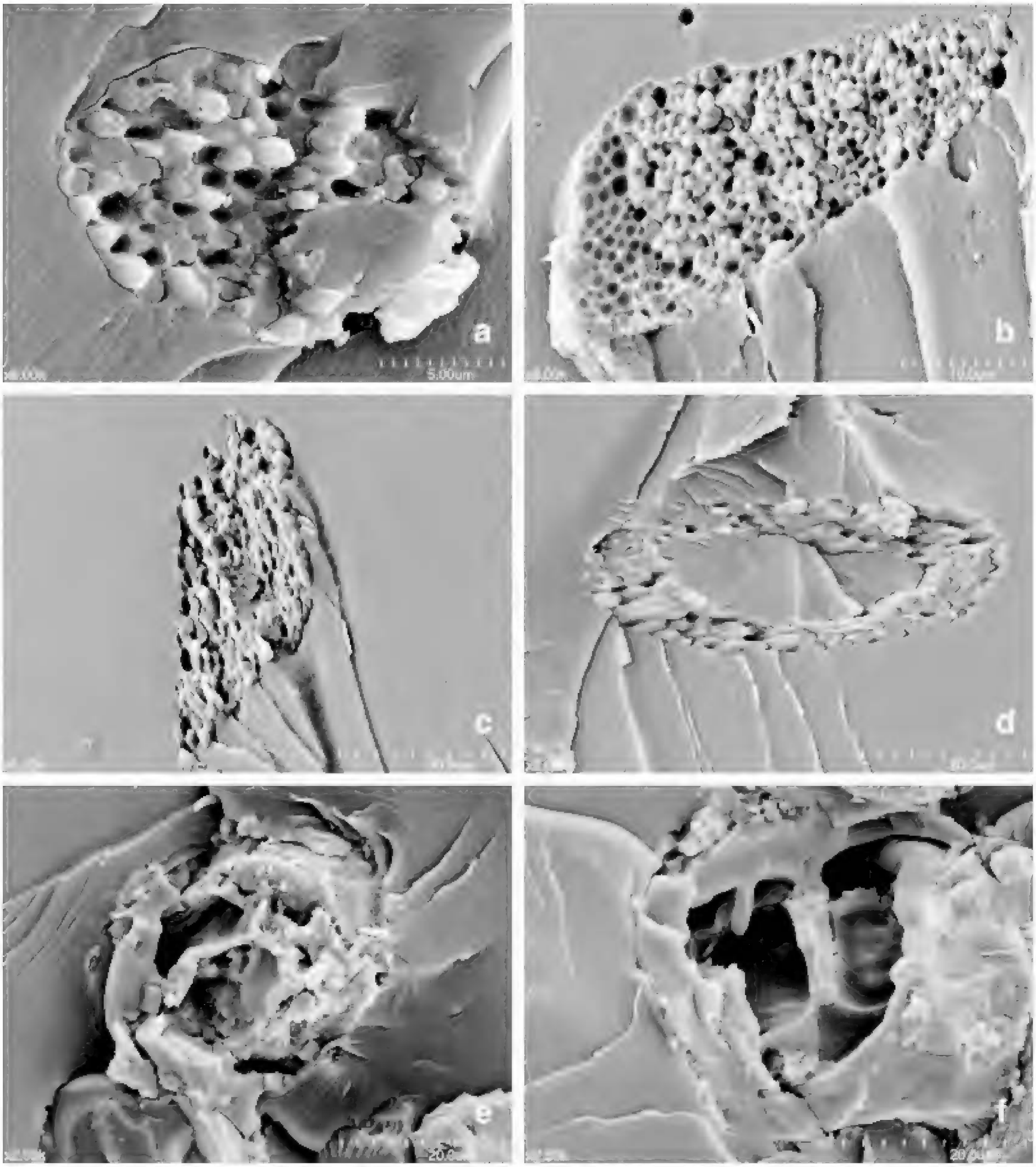

Fig. 9. Scanning electron micrographs of spores (fig. 8) with interior contents exposed on freshly fractured surfaces of amber (1500–6000×).

sequoia should be seriously considered as a possible source of Burmese amber.

Angiospermae: Angiosperms from the Cretaceous are known mostly from dissociated pollen in sedimentary strata and compression-fossilized leaves, occasionally as compression-fossilized flowers. The most informative Cretaceous specimens are fusainized flowers in clays, preserved with complete relief and microscopic fidelity (e.g., Crane and Herendeen, 1996; Crane et al., 1995; Crepet and Nixon, 1998). Fusainized Cretaceous flowers are diverse, but oddly consistently small (2–4 mm). Only two flow-

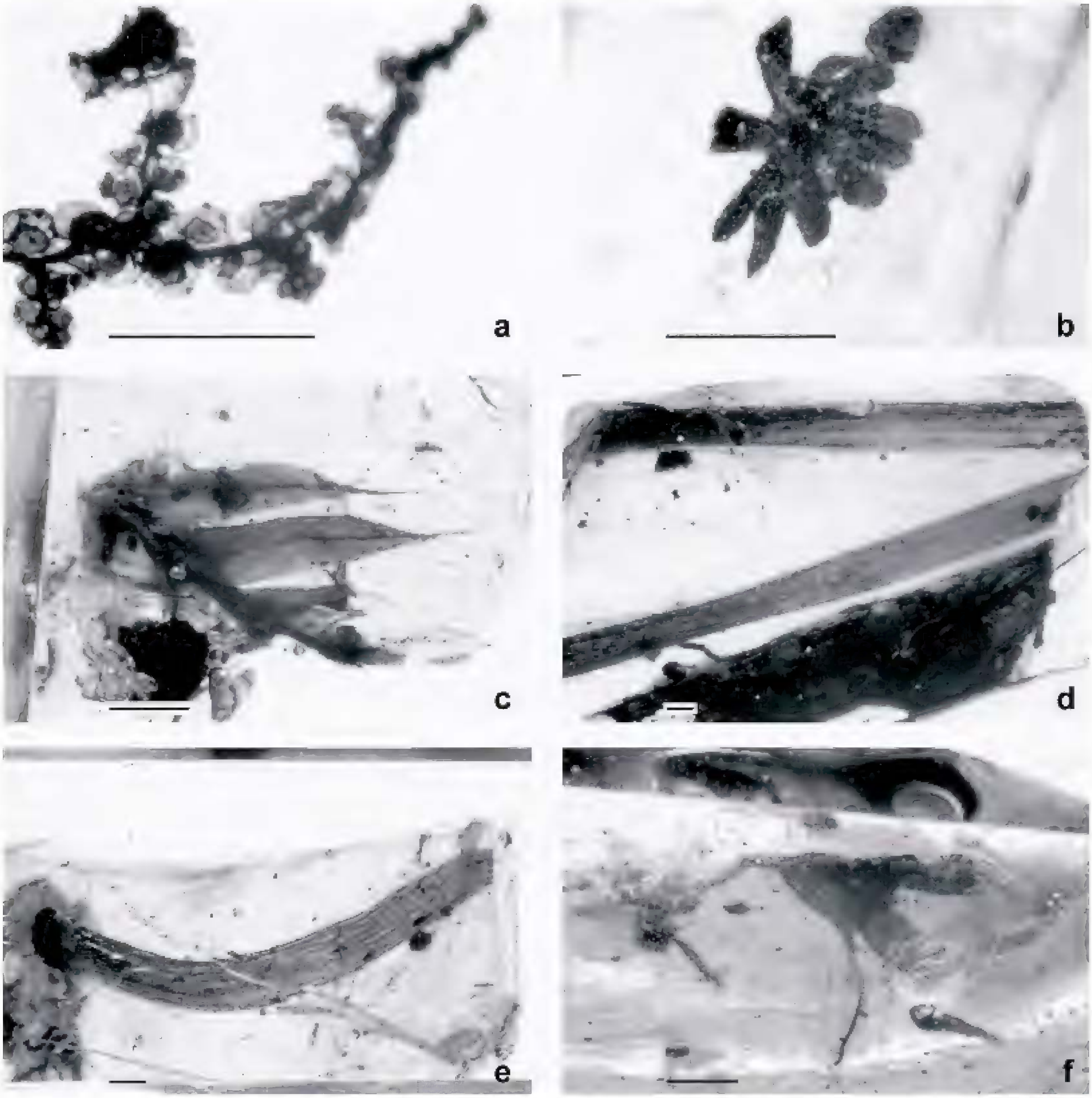

Fig. 10. Plant inclusions in Burmese amber. **a.** Portion of hepatophyte, AMNH Bu11. **b.** Probable archegoniophore of Marchantiaceae (Hepatophyta), AMNH Bu324. **c.** Portion of undetermined leafy shoot, AMNH Bu181. **d, e.** Portions of long leaf blades of undetermined plants, AMNH Bu204, 205, respectively. **f.** Angiosperm flower, AMNH Bu338.

ers are known in Cretaceous ambers, one a partial specimen in Burmese amber of undetermined identity (AMNH Bu338, figs. 10, 13). Typical of the fusainized Cretaceous flowers, AMNH Bu338 is small, approximately 5 mm diameter. Only three petals are preserved, though it appears to have been pentamerous, since the area where two petals were apparently attached was lost at the surface. The petals possess a faint reticulate venation. No obvious reproductive parts like stamens or pistils can be seen (they may have become detached), though the center of the corolla has several rounded areas (ovules?). The other Cretaceous amber flower is a finely preserved, complete inflorescence of a primitive fagalean in New Jersey amber (Grimaldi et al., 2000a). There are also several unidentified, small angiosperm leaves in the AMNH Burmese amber collection.

Fig. 11. Photomicrographs of fern leptosporangium in Burmese amber, AMNH Bu342.

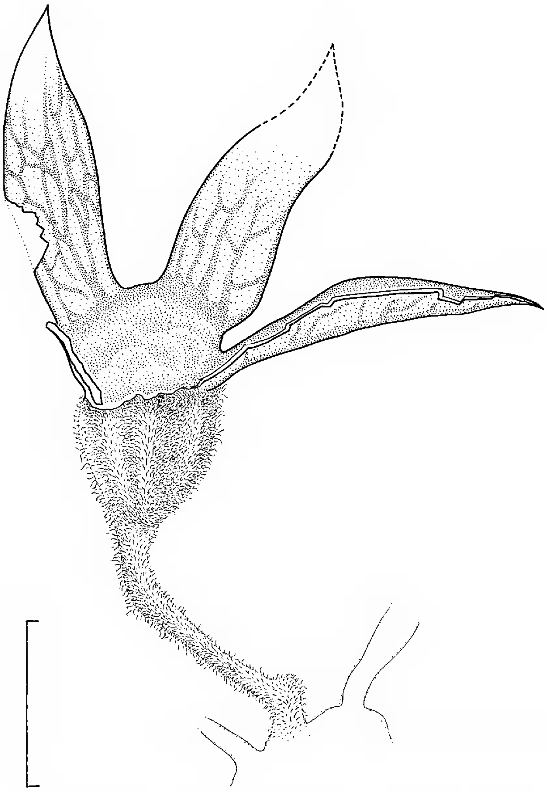

Fig. 13. Detail of angiosperm flower in Burmese amber, AMNH Bu338. Scale is 1.0 mm.

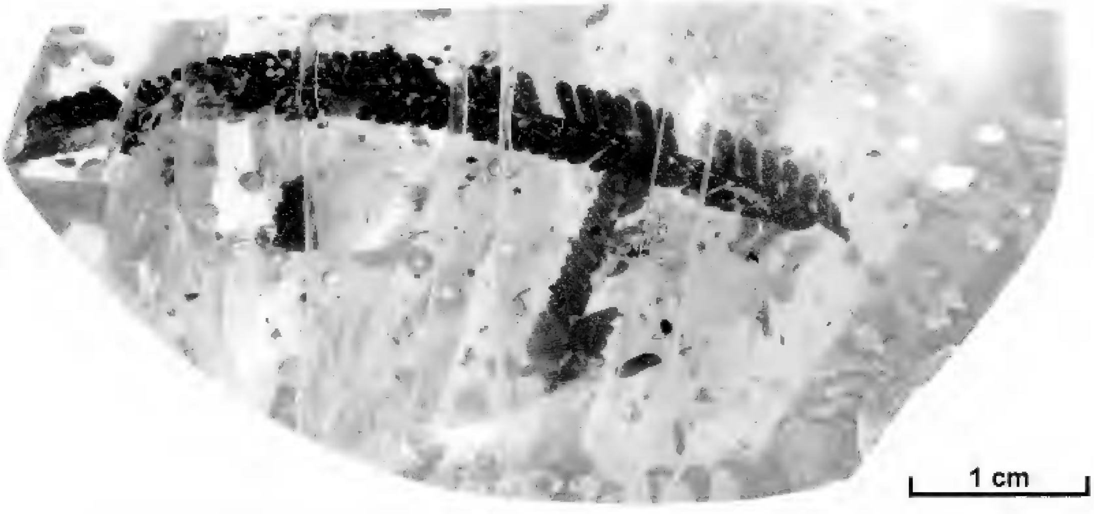

Fig. 12. Leafy shoots of *Metasequoia* sp. in Burmese amber, AMNH Bu794b.

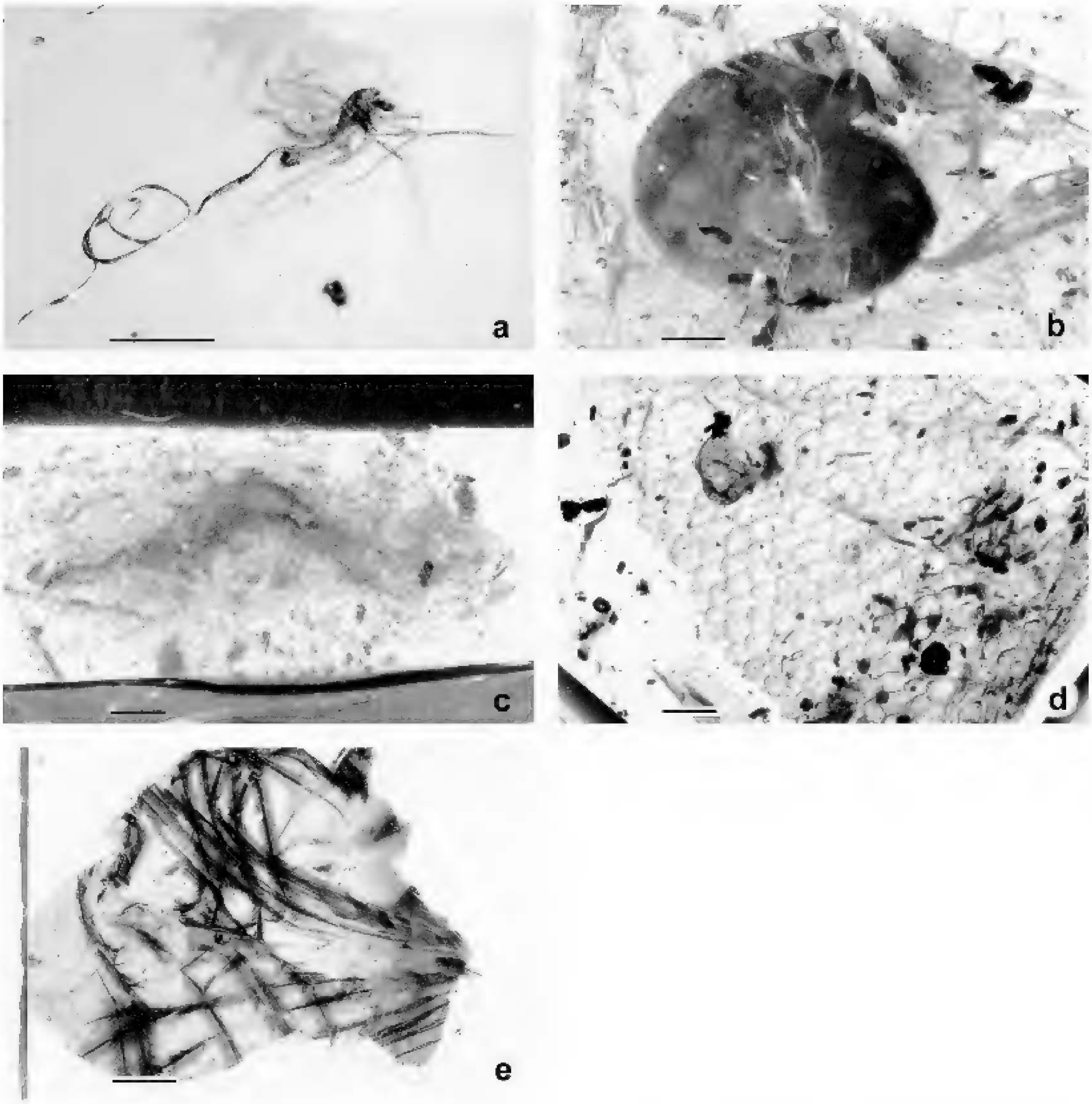

Fig. 14. Various animal remains in Burmese amber. **a.** Two mermithid nematode parasites emerging from abdomen of a female chironomid midge, AMNH Bu320. **b.** Snail, AMNH Bu099. **c.** Onychophoran, *Cretoperipatus burmiticus* holotype (cf. fig. 17), AMNH Bu218. **d.** Reptile skin, AMNH Bu337. **e.** Bird feathers, AMNH Bu183. Scale is 1.0 mm.

Kingdom ANIMALIA

Phylum Nematoda

Nematodes occur rarely in amber, particularly in Cretaceous ambers. The oldest fossil nematode is reported from Lebanese amber (Poinar et al., 1994), which belongs to the Mermithidae, a family to which belong two exceptionally well-preserved specimens in the AMNH Burmese amber collection (AMNH Bu320). Mermithids are obligate, internal parasites of terrestrial and freshwater arthropods (especially insects), some crustaceans, molluscs, and annelids. During their preparasite, postparasite, and adult stages they are free-living (Rubzov, 1972). In the extant fauna there are 32 genera and approximately 200 described species, but are too

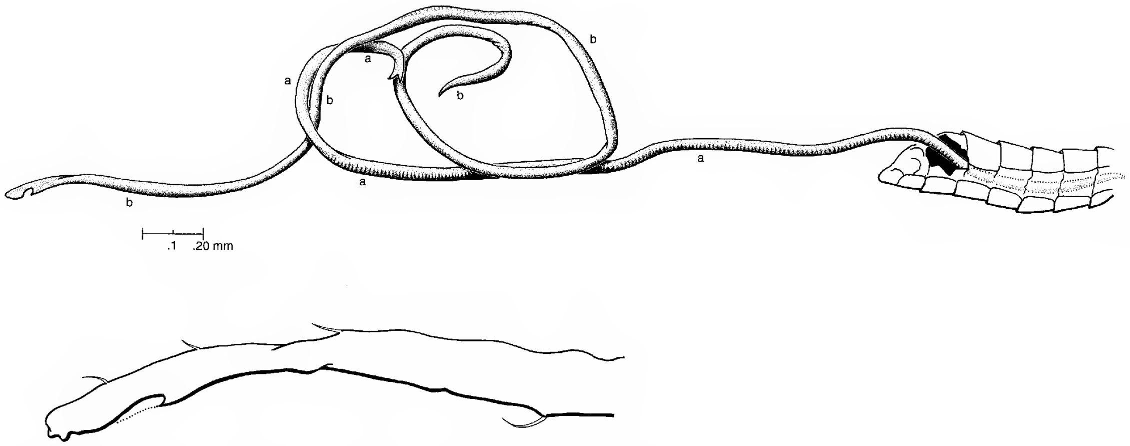

Fig. 15. Detail of AMNH Bu320, two mermithid nematodes (**a, b**) captured while emerging from the abdomen of a female chironomid midge. Detail shows array of spicules on apex of specimen b.

poorly surveyed to determine actual diversity.

Both nematodes in specimen AMNH Bu320 were preserved while emerging from the abdomen of a female chironomid midge (figs. 14a, 15), a family of common mermithid hosts today (Rubzov, 1972; Nickle, 1972). These new specimens are the only other Cretaceous record of the Mermithidae besides †*Heleidomermis libani* in Lebanese amber (Poinar et al., 1994). †*Heleidomeris libani* was described on the basis of a coiled, putatively postparasitic juvenile female (the sex "suggested" by its length), in the abdomen of a female chironomid inclusion. It was placed into this extant genus on the basis of morphological characteristics (final molt in the host, absence of cuticular cross fibers, and lack of a tail projection), and host type (Ceratopogonidae). Poinar et al. (1994) attributed a modern genus of mermithids in the Lower Cretaceous to the morphological conservatism of nematodes, though morphological simplicity by nature is conservative. Body proportions of the coiled specimen are within the range of two extant species of *Heleidomermis*. Interestingly, with the exception of *Leptoconops* (the most primitive living genus of Ceratopogonidae), all genera of ceratopogonids in Lebanese amber are phylogenetically basal and extinct (Borkent, 2000). On this basis, one might expect the Lebanese amber mermithid to likewise be an extinct genus.

The AMNH specimens are very similar in width (approximately 50 μm) and length (3.3 and 3.4 mm). One end of specimen "a" is still enclosed in the midge's abdomen; one end of specimen "b" has at least four preapical spicules (fig. 15). The other nematodes in Burmese amber are approximately 20 minute individuals of undetermined identity (430–520 μm length) in a single piece of amber, AMNH Bu020.

Despite remarkable preservation, nematodes in amber are unlikely to be a significant source of information for the evolutionary history of this group. They are extremely rare in Cretaceous ambers, and definitive fossils (amber or otherwise) are unknown from earlier periods, even though the group is probably at least Cambrian in age judging from the ages of related phyla. The fossils contribute useful information on the minimum ages of particular lineages (e.g., Mermithidae) and their host associations.

Phylum Mollusca

Though molluscs are abundant in the marine record, fossils of terrestrial taxa are relatively sparse. Shells of terrestrial gastropods occur sporadically in Cenozoic ambers, but only three records are known in Cretaceous ambers. A species of possibly the family Pupillidae occurs in Lebanese amber (Roth et al., 1996). Burmese amber contains the other two Cretaceous records. Neither the

NHML (figured in Ross, 1998: fig. 59) nor the AMNH (Bu009) specimens have been identified. The AMNH specimen is slightly oblong in shape and rather large (5.03 × 3.53 mm)(fig. 16). Six fecal pellets near the aperture indicate that the snail was preserved while it was alive.

Phylum Onychophora

The significance of the single new specimen (AMNH Bu218; figs. 14d, 17) in this phylum is exceptional. Several enigmatic, marine fossils from the Cambrian, such as †*Aysheaia* and †*Xenusion* from the Burgess shale[4]have been attributed to the Onychophora[5] (e.g., Dzik and Krumbiegel, 1989; Ramsköld and Hou, 1991). The overall structure of these fossils is similar to that of extant onychophorans, but given the lack of preserved details and their marine origin (all modern onychophorans occur in tropical or subtropical forests) it is probably best to consider the Cambrian taxa as stem-group onychophorans in a Superphylum Lobopodia (Snodgrass, 1938). AMNH Bu218 is the earliest definitive and only Mesozoic fossil of the phylum.

Only the anterior half of the specimen is preserved, the posterior half having been decomposed. Portions of the anterior half, particularly the head, are extremely distorted by compression. Nonetheless, the ventral mouth surrounded by peribuccal papillae, a finely annulate body with dermal papillae, and five preserved pairs of lobopods make the identity of the specimen in this phylum unquestionable (fig. 17). Although with less than optimal preservation, the specimen is further identifiable as a species of the modern, circumtropical family Peripatidae. The lobopods are particularly informative and allow identification of the specimen as unlike any modern peripatid genus. Unique within the family is the combination of three spinous pads (the third subequal in size to the first two and undivided by a urinary papilla), a single distal papilla, and five basal papillae (the basalmost two more weakly developed). The foot structure of AMNH Bu218 is apparently autapomorphic and without clear homologues to any lineage of extant peripatids, thus justifying formal description of a new taxon. Morphological terminology follows that of Storch and Ruhberg (1993).

Cretoperipatus Engel and Grimaldi, new genus

TYPE SPECIES: †*Cretoperipatus burmiticus*, new species.

DIAGNOSIS: A true onychophoran (i.e., terrestrial, with antennae, ventral mouth with entognathous jaws, oral papillae, paired lobopods each with a pair of terminal claws) of the family Peripatidae, having the following characteristics: Approximately 12 complete annuli on each segment or less (no incomplete annuli), annuli not fusing laterally; integumental papillae with round bases and of variable sizes. Nephridial opening present at base of legs. Coxal organ not apparent on any leg. Crural papilla not present on preserved legs (pairs 1–3); consistent with assignment to Peripatidae in which crural papillae are found in the posterior segments. Three spinous pads present distally on leg; third (i.e., basalmost) spinous pad not divided by nephroporous (urinary) papilla on any leg; third spinous pad approximately subequal in size to first and second spinous pads. Five basal papillae present (two basalmost papillae weakly developed) and a single distal papilla present on posterolateral border; claws strong, elongate, and curved.

ETYMOLOGY: The new genus group name

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[4] Ramsköld and Chen (1998) unnecessarily proposed the name Alphonychophora for a group including *Aysheaia* (and, tentatively, *Xenusion*, *Luolishania*, and *Onychodictyon*). The name Protonychophora had already been proposed by Hutchinson (1930) and modified by Hou and Bergström (1995), for a group including *Aysheaia* and *Xenusion*. Rather than emending and using this name to correspond with their phylogeny, Ramsköld and Chen (1998: 143) argued that, so as to avoid confusion, they would employ new names based on the "phylotaxonomy" of de Queiroz and Gauthier (1994). A proliferation of names—particularly ones not defined by characters—contributes even more serious confusion to a literature that "... abounds in names ..." (Ramsköld and Chen, 1998: 142), one criticism that these authors have about a formal Linnean taxonomy. A critique of the misguided attempts of "phylotaxonomy" is provided by Nixon and Carpenter (2000).

[5] This grouping is sometimes referred to as Phylum Lobopodia with two classes; Xenusia for the likely paraphyletic, marine Cambrian fossils, and Onychophora for the terrestrial lineages (e.g., Hou and Bergström, 1995). As mentioned in the text, we prefer to consider xenusians as stem-group Onychophora.

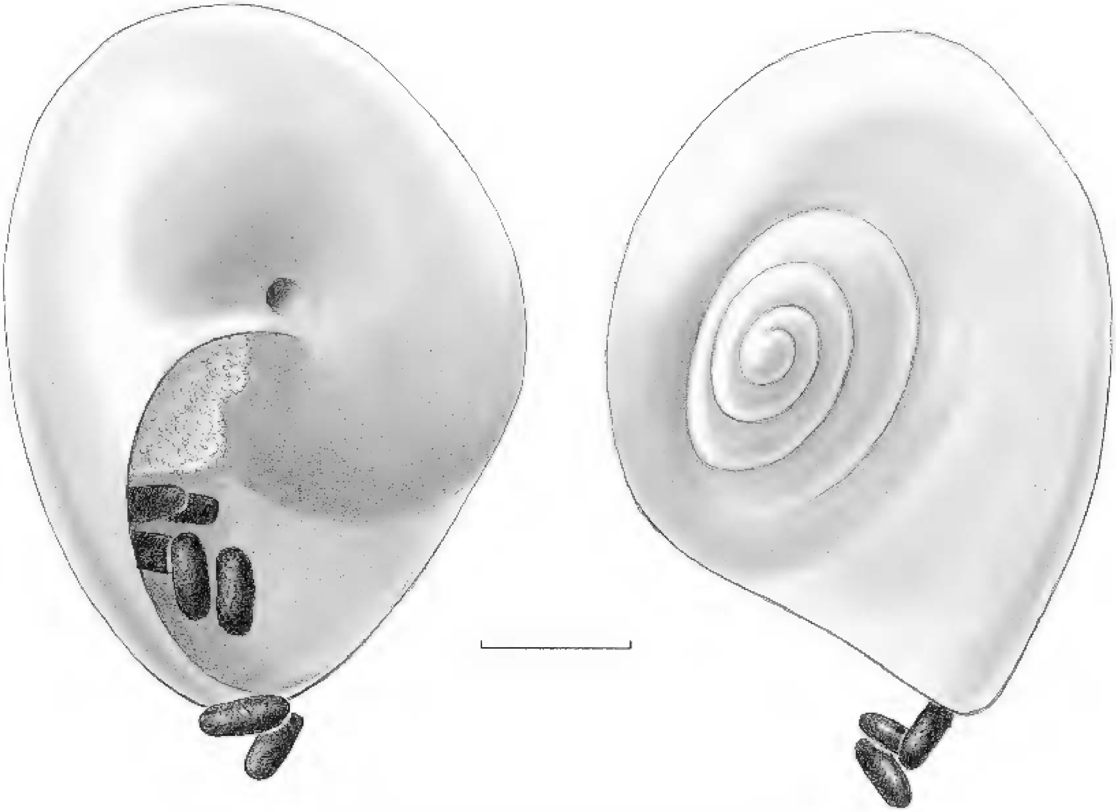

Fig. 16. Detail of snail AMNH Bu009, opposite sides. Scale is 1.0 mm.

is a combination of *creto-* (in reference to the Cretaceous) and *Peripatus* (type genus of the family).

COMMENTS: Feet and claws were not included in the original descriptions for most fossils in the phylum, including the Carboniferous †*Helenodora* (Thompson and Jones, 1980), which may be just a taphonomic artifact. Nonetheless, Poinar (2000) stated (by inference) that claws in the fossils were definitely absent, and on this basis he classified the Tertiary amber fossils †*Tertiapatus* and †*Succinipatopsis* as intermediate between living velvet worms and early Paleozoic forms (Poinar, 2000). To accommodate his interpretation, he placed the amber genera in a separate order, ''†Ontonychophora,'' intermediate between an order ''Euonychophora'' (for the living families Peripatidae and Peripatopsidae) and an order ''†Udeonychophora'' (for the Paleozoic forms). This is peculiar for several reasons. First, virtually all well-studied insects in Miocene Dominican amber belong to modern genera or to extinct genera nearly identical to living taxa, and those in Eocene Baltic amber belong almost exclusively to modern families (e.g., Larsson, 1978). Second, the Cretaceous fossil here clearly belongs in the living family Peripatidae, with clearly defined feet.

The ''absence'' of claws in †*Tertiapatus* and †*Succinipatopsis* is almost certainly an artifact of preservation (likely true as well of the dubiously assigned †*Helenodora*). For example, the feet of Onychophora are retractile, and most ethanol-preserved modern species (e.g., AMNH collection, pers. obs.) have feet retracted with claws frequently protruding. Thus, we consider the original descriptions of †*Tertiapatus* and †*Succinipatopsis* flawed, and place the Udeonychophora and Ontonychophora as newly synonymized under Euonychophora (NEW SYNONYMY). Status of Tertiapatidae and Succinipatopsidae must await competent examination of those amber fossils, since critical characters were omitted

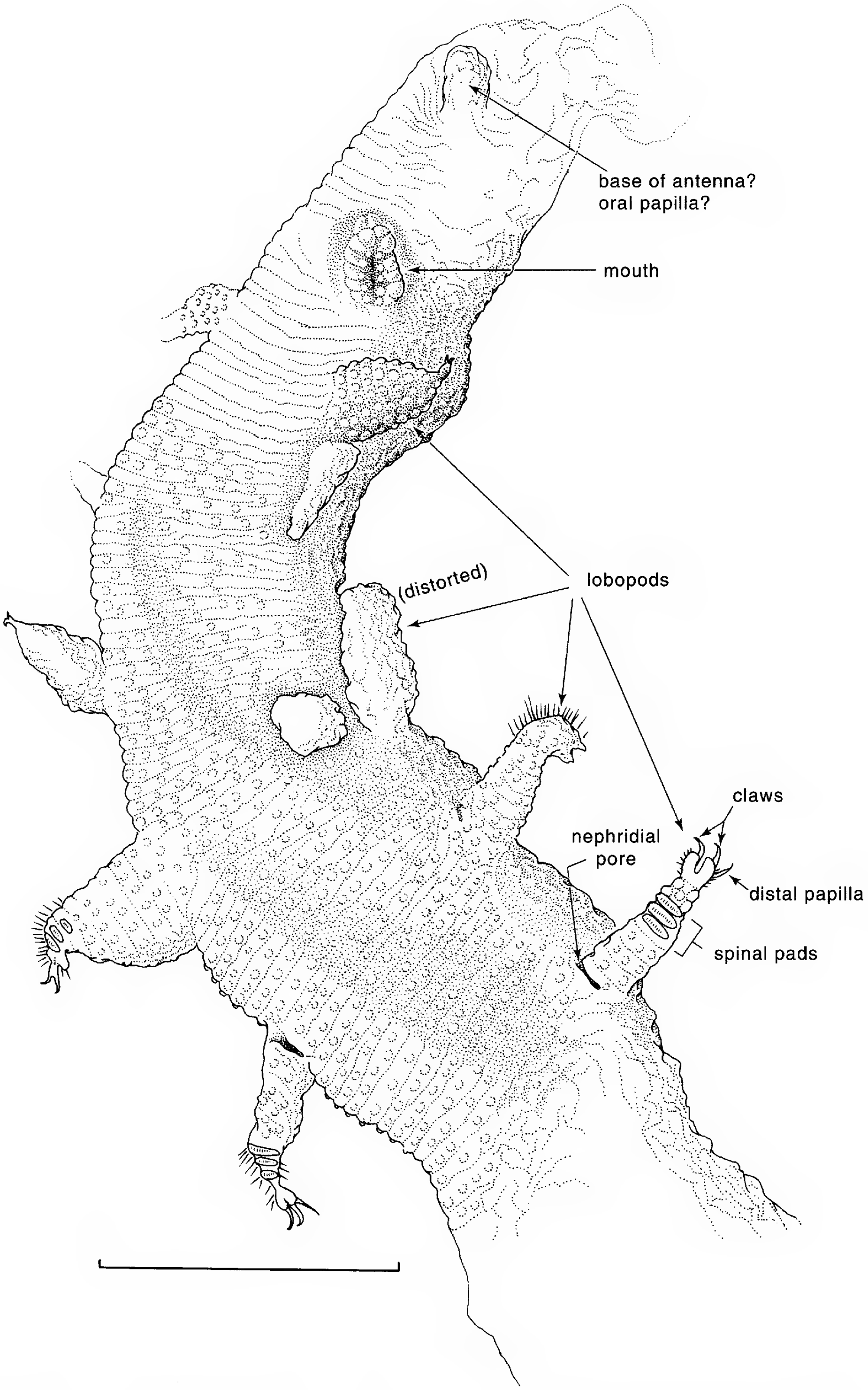

Fig. 17. *Cretoperipatus burmiticus* n. gen., n. sp., holotype, AMNH Bu218. Scale is 1.0 mm.

from the original descriptions and illustrations. Given that we have a Cretaceous species in the living family Peripatidae, extinct families of Onychophora from the Eocene and Miocene are highly improbable. A Cretaceous member of the Peripatidae is consistent with an ancient, Cambrian origin of Lobopodia. This record is also further evidence of the tropical paleoenvironment in which Burmese amber was produced.

Cretoperipatus burmiticus Engel and Grimaldi, new species

Figures 14d, 17

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: The above description characterizes the genus and species (ICZN, 1999: Art. 13.4). To the generic description we add the following minor measurements (based on the third pair of feet): foot length 0.15 mm; distance between second and third pairs of lobopods (as measured from middle of lobopods) 0.69 mm, distance between third and fourth pairs 0.77 mm.

HOLOTYPE: Sex indeterminate; AMNH Bu218; Myanmar (Burma), Kachin, Tanai Village (on Ledo Road, 105 km NW Myitkyina).

ETYMOLOGY: The specific epithet is a reference to Burmite, the amber from which this fossil originates.

PHYLUM ARTHROPODA

SUBPHYLUM CHELIERATA

CLASS ARACHNIDA

ORDER ACARI

Because of the small size of mites, and the microscopic details required for identification, useful fossils of them occur mostly in amber. Remains of Devonian mites are exceptional for their age and cuticular preservation (Kethley et al., 1989; Norton et al., 1988). Mites occur in probably all Cretaceous ambers, but Burmese amber contains the greatest abundance and diversity. Lebanese amber contains Anystidae, Bdellidae, Erythraeidae, Erythracaridae, and Smarididae (Azar, 2000), the first three also occurring in Burmese and New Jersey ambers. Rasnitysn and Ross (2000) (identifications by A.L. Kartsev and O.L. Makarova) also reported Cheyletidae and Eupodidae in Burmese amber. Most acarines from the AMNH collection have yet to be studied, but it appears that the Burmese amber fauna of Acari is likely the most diverse one for the Mesozoic (e.g., fig. 20).

Particularly significant acarines in Burmese amber are two specimens of Ixodida, or ticks (NHML In. 19125 and AMNH Bu325 [fig. 20f]), both juveniles. The AMNH specimen belongs to the large, extant cosmopolitan genus *Amblyomma* (Hans Klompen, personal commun.). Unfortunately, taxonomic features of larval ixodids are few, so attempting to place these fossils within a phylogenetic scheme of living taxa would be extremely difficult. The only other Cretaceous parasitiform is a finely preserved juvenile of the "soft-tick" family Argasidae, in New Jersey amber (Klompen and Grimaldi, 2001). Its apparent close relationship to living species in *Carios* indicates it was probably a parasite of birds or feathered dinosaurs.

ORDER SCORPIONES

Despite the antiquity of this group, from the Lower Devonian (i.e., Størmer, 1977), there are remarkably few Mesozoic fossils of scorpions. The Lower Cretaceous limestone of Brazil's Santana Formation contains several described and undescribed taxa, and is probably the most diverse Mesozoic fauna known. Despite the relief and microscopic preservation for which even the Santana Formation fossils are well known, systematic placement of the Mesozoic rock fossils is hampered by so few available characters. Only one virtually complete scorpion occurs in Cretaceous amber—a specimen of a buthoid (missing only the tip of the tail) in a private collection of Lebanese amber (Lourenço, 2001). Though no complete scorpion has yet been found in Burmese amber, a fragment of one is in the NHML collection (In. 20174; Ross, 1998: fig. 100), and two additional, isolated fragments occur in our material (AMNH Bu215c, 710). These fragments are a dorsal sclerite of the telson, and a sting with part of the telson (fig. 19). The fragments allow no definitive identification subordinate to the rank of order, but indicate that

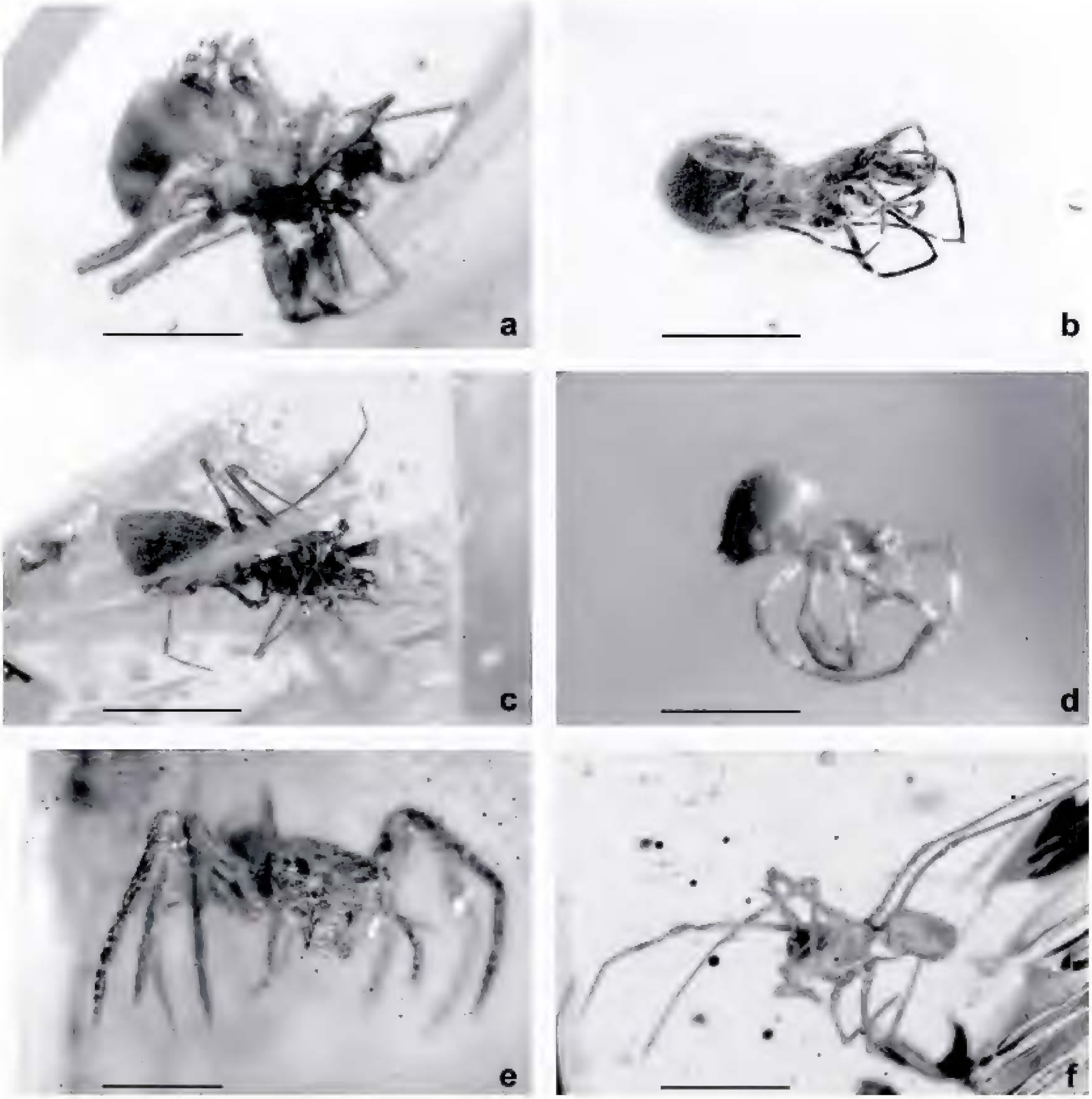

Fig. 18. Select spider (Araneae) specimens in the AMNH collection of Burmese amber. **a.** Male? Mysmenidae/?Aranaeidae, AMNH Bu234. **b.** Family indet., AMNH Bu252. **c.** Male Archaeidae, AMNH Bu256. **d.** Araneoidea family indet., AMNH Bu258. **e.** Lagonomegopidae, AMNH Bu707. **f.** Family indet. Scales are 1.0 mm.

there is significant potential with Burmese amber for another complete Cretaceous scorpion to surface.

ORDER PSEUDOSCORPIONES

Like mites, these small arthropods require microscopic details for accurate identification, and cuticular remains of them also occur from the Devonian (Schawaller et al., 1991). Cretaceous amber contains the only Mesozoic specimens of the group. Three specimens are known from Lebanese amber (Azar, 2000) and four specimens, mostly fragmentary, occur in New Jersey amber (Grimaldi, unpubl. data). Burmese amber has fossilized two species that have been described, though several more exist. Cockerell (1917a, 1920) described †*Electrobisium acu-*

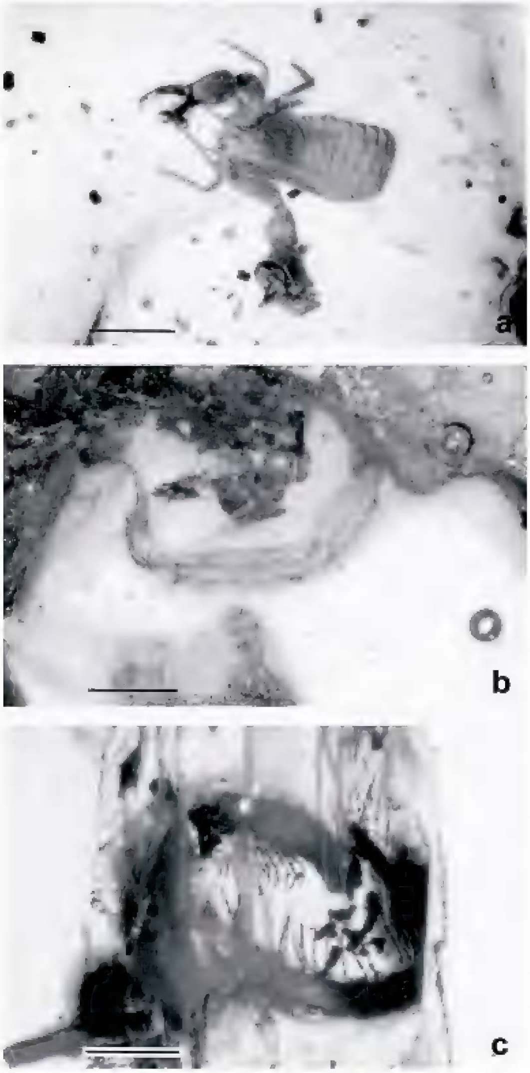

Fig. 19. Various chelicerates and tracheates in Burmese amber. **a.** Pseudoscorpion, AMNH Bu230. **b.** Scorpion tail, AMNH Bu710. **c.** Millipede, AMNH Bu206. Scale is 1.0 mm.

tum and †*Garypus burmiticus* from the NHML collection, and Judson (2000) recently revised one of those species based on Cockerell's material. According to Judson, †*Electrobisium acutum* is closely related to several species in the extant genus *Cryptocheridium* Chamberlin (Cheridiidae), which may not be a monophyletic genus. †*Garypus burmiticus* is probably a species of the extant genus *Amblyolpium* Simon (Olpiidae). The only other species of pseudoscorpion reported from Cretaceous amber is an unnamed chernitid in Canadian amber (Schawaller, 1991). Burmese amber contains the most abundant and diverse fauna of Mesozoic pseudoscorpions, with 38 specimens in the NHML collection (four of the pieces contained 5, 6, 6, and 11 specimens alone), and 11 in the AMNH, many of them fragmentary (fig. 19a).

Order Araneae

Spiders are among the most ancient land animals, with Devonian fossils of true Araneae and their close, extinct relatives, the †Trigonotarbida. Nonetheless, the well-preserved specimens in Cretaceous amber offer unique insight into Mesozoic Araneae. Provisional identifications to family of many of the better-preserved specimens in the AMNH collection indicates at least eight families (David Penney, unpubl.): Archaeidae (AMNH Bu256), Dictynidae (Bu714, juvenile),? †Lagonomegopidae (Bu707, juvenile),? Linyphiidae (Bu716, male),? Mysmenidae/?Araneidae (AMNH Bu234), Oonopidae (Bu706, juvenile; and Bu708, male?),? Telemidae (Bu712, juvenile), and Theridiidae (Bu676, juvenile; and Bu713, male). These are but 8% of the 128 spider specimens in the Burmese amber at the AMNH, so the list is minimal. Rasnitsyn and Ross (2000) listed seven families in the NHML collection. Families in common to both collections are the Oonopidae and Theridiidae; unique to the NHML collection are the Sparassidae (=Eusparassidae), Corinnidae (=Myrmecidae), Pisauridae, Tetragnathidae, and Thomisidae. Thus, at least 11 families of Araneae occur in Burmese amber, which is probably the most diverse Mesozoic deposit for the Araneae.

Burmese amber taxa representing the oldest apparent fossils of particular families are the Theridiidae, Dictynidae, Linyphiidae, and? †Lagonomegopidae. If AMNH Bu234 is an araneid, this would be the oldest one in amber and possibly in the fossil record (the attribution being uncertain of †Juraraneidae Eskov [from the Jurassic of Transbaikalia] to the Araneidae). The oldest Oonopidae occurs in Lebanese amber (D. Penney, unpubl.). The †Lagonomegopidae (AMNH Bu707) has a

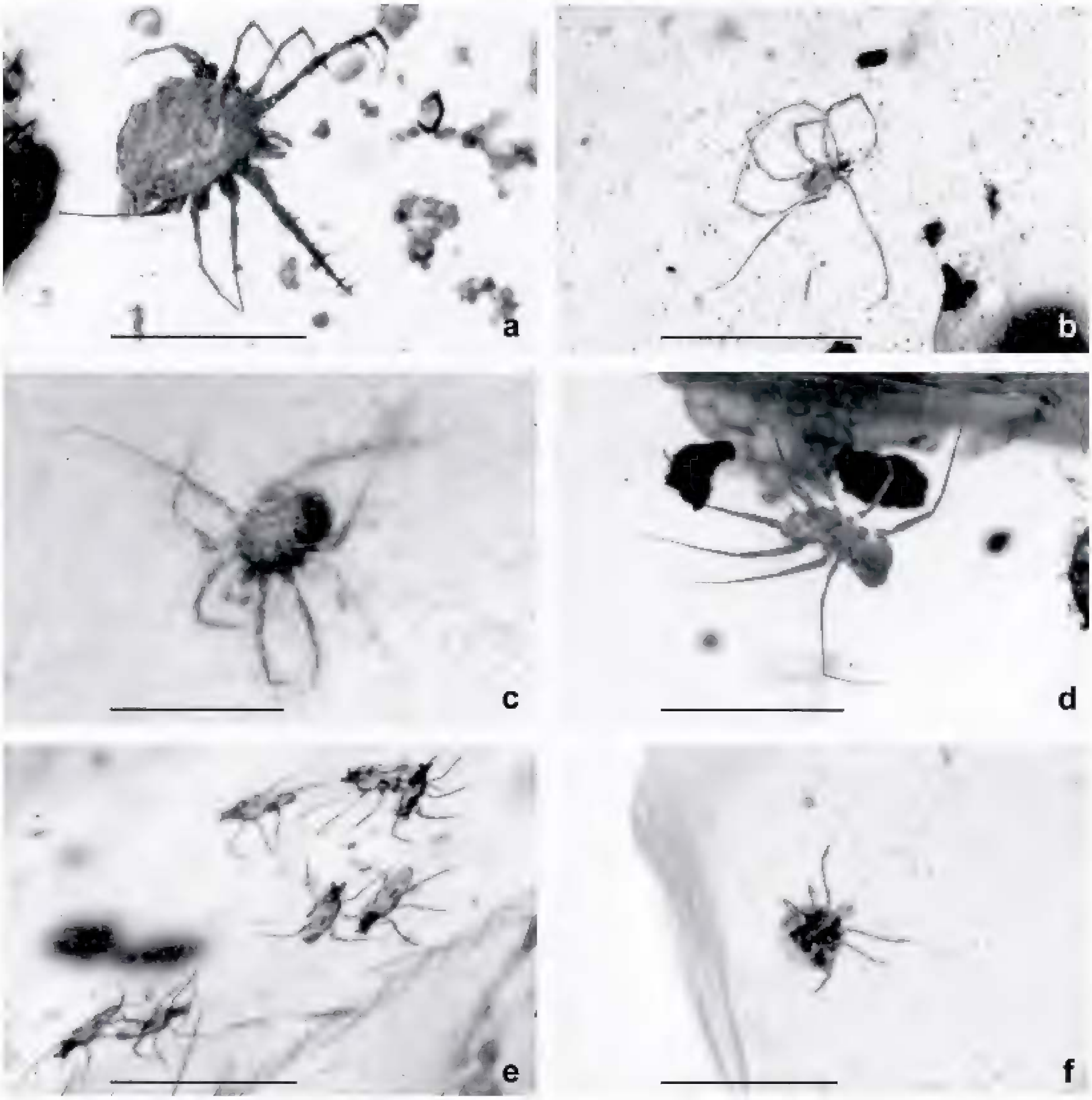

Fig. 20. Representative Acari in Burmese amber. **a.** AMNH Bu342. **b.** AMNH Bu516. **c.** AMNH Bu519. **d.** AMNH Bu009. **e.** AMNH Bu582. **f.** Juvenile tick (Ixodida), genus *Amblyomma*, AMNH Bu325. Scale is 1.0 mm.

body form closely resembling a salticid, but instead of having a pair of large, forward-directed anterior median eyes, these have a pair of large anterolateral eyes. Salticidae are the most diverse spider family. The oldest true salticid, and only Cretaceous one, is in New Jersey amber (AMNH NJ835; D. Penney, personal comm.). †Lagonomegopidae are known in amber from Siberia and New Jersey.

A particularly exciting record is AMNH Bu256, an excellently preserved male of the primitive and relict family Archaeidae. The family today is restricted to southern Africa, Madagascar, and Australia. Archaeidae was originally discovered in 1854 by Koch and Berendt, occurring in Baltic amber, and a specimen is also known from the Jurassic of Kazakhstan (Eskov and Golovatch, 1986). The implications of Baltic, and now Burmese, records for a group showing classic austral disjunction was discussed by Eskov and Golovatch (1986) and Grimaldi (1992).

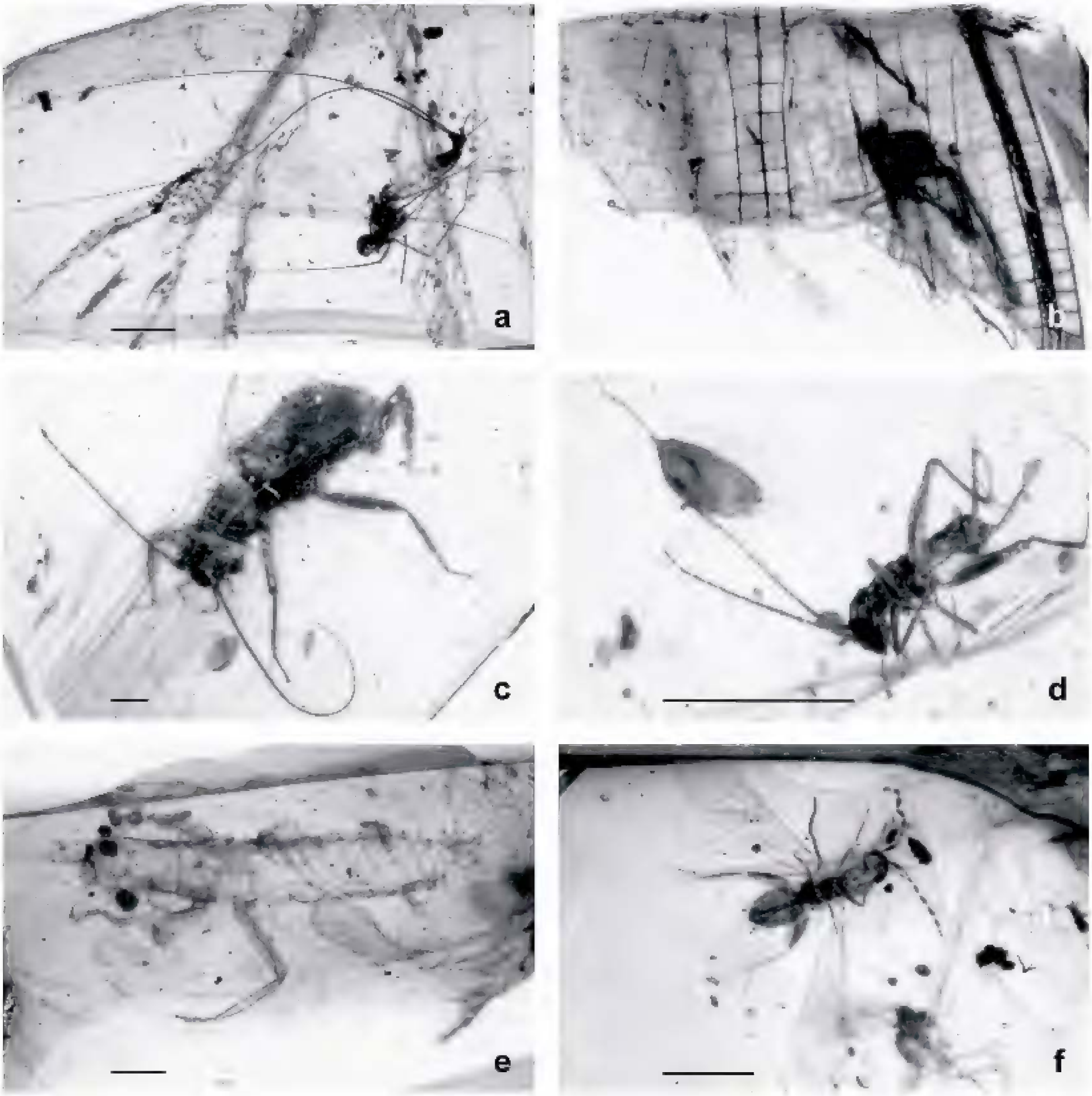

Fig. 21. Assorted paleopterous and lower Neoptera insects in Burmese amber. **a.** Ephemeroptera, AMNH Bu303. **b.** Portion of wing of Odonata with rhagionid fly, AMNH Bu031. **c.** Plecoptera, AMNH Bu269. **d.** Orthoptera: nymphal Grylloidea, AMNH Bu323. **e.** Orthoptera (Grylloidea?), AMNH Bu278. **f.** Zoraptera: *Zorotypus* n. sp., AMNH Bu341a. Scales are 1.0 mm.

CLASS INSECTA

ORDER ORTHOPTERA

Insects of this order are rare in both the NHML and AMNH collections of Burmese amber, with five and three specimens, respectively. The NHML specimens were identified as Grylloidea, but only one of the AMNH specimens may belong to this group. AMNH Bu323 (fig. 21d) is an early instar nymph of what appears to be a tettigonioid. AMNH Bu278 (fig. 21e) is much more unusual, having an elongate head and body, three tarsomeres, and cerci without segmentation, similar to what is found in the Phasmida. The specimen, however, possesses no definitive characters of the Phasmida, but may belong to the Grylloidea (Erich Tilgner, personal commun.). For example, the posterior tentorial arms lack tubercles near the posterior tentorial pits distinctive for Phasmida; the probasisternum is shaped like an "x" (as in Orthoptera and some lower Neoptera), and is not a broad plate as in Phasmida; the arolia are absent (present in Phasmida); and small stalked scales occur at the base of the cerci (occurring, for example, in some grylloids, but not in Phasmida). Also, the hind femora appear to be saltatorial, as they are narrowed dorsally and have the trochanters virtually fused to them, and the second tarsomere is lobed (as in some grylloids). The oldest *definitive* Phasmida are from the Lower Tertiary (reviewed by Tilgner, 2001), though they should occur by the Jurassic. Various Mesozoic fossils have been described as Phasmida, and some plausibly belong to this order, but they do not possess definitive features of Phasmida. Rasnitysn and Ross (2000) record phasmid eggs in the NHML collection but these require confirmation. The Grylloidea extend to the Triassic (reviewed by Carpenter, 1992).

ORDER ZORAPTERA

This is a small circumtropical insect order of only 32 modern species. Distributions of a few species (i.e., *Zorotypus hubbardi* Caudell, *Z. sinensis* Hwang, and *Z. medoensis* Hwang) extend to warm temperate regions. Relationships of the order have been controversial, the most recent hypothesis being that the Zoraptera are most closely related to the webspinners, order Embiidina (Engel and Grimaldi, 2000). The only zorapteran fossils known were several very rare specimens in Miocene Dominican amber (Poinar, 1988; Engel and Grimaldi, 2000), so the discovery of four Burmese amber specimens is of considerable significance.

The Burmese amber fossils are the oldest fossils of the order, and further remarkable in that three of the specimens (AMNH Bu44o, 341a, and 966a, the first one being apterous) each represent an extinct species in the living genus *Zorotypus*. Species are clearly definable by segmentation of antennae and spination of the hind femur. Another specimen, AMNH Bu182 is a distinctive new genus with apomorphic metafemoral spination and male genitalia, but plesiomorphic for the hind wing venation. The presence of several species of Zoraptera in Burmese amber is further evidence that the Burmese amber forests were tropical. Systematics of the Burmese amber Zoraptera have been treated in detail in a separate article (Engel and Grimaldi, 2002).

ORDER EMBIIDINA

As for Zoraptera, the Embiidina in Burmese amber are the only Mesozoic, and also the oldest definitive, fossils of the order. Embiidina are rare in Dominican and Baltic ambers; they are correspondingly rare in Burmese amber, with two specimens in the AMNH (Bu200, and Bu227; fig. 22a), and one described specimen in the NHML (In. 19132; Ross and York, 2000: fig. 4), which is the holotype of †*Burmitembia venosa* Cockerell. The best preserved AMNH specimen (Bu227) is a male and is generically distinct from Cockerell's specimen and represents either an independent lineage within Burmitembiidae, or a separate, yet undescribed family. Both the male terminalia and wing venation are completely unlike that of *B. venosa* or modern families (Engel and Grimaldi, unpubl.). The second AMNH specimen (Bu200) preserves only the forelegs and apical portion of a wing of an embiid. As such, it is unassignable to family but is undoubtedly a webspinner owing to the distinctive glandular foretarsus.

A Permian fossil of a putative Embiidina was reported by Kukalová-Peck (1991: fig. 6.19B). The figure of the specimen is consistent with the overall shape of embiids, such as the homonomous wings with narrow bases, and apparently asymmetrical male genitalia (characteristic though not unique to the order, e.g., Grylloblattodea). The geological distribution of related orthopteroid and polyneopteran lineages makes the existence of Permian Embiidina certainly feasible. However, the venation (which is distinctive for all living Embiidina) is obscure in that specimen, and it is unclear if genitalic asymmetry is due to incomplete preservation. The hallmark synapomorphy of the Embiidina is a pair of swollen, glandular foretarsi, which are not preserved in the Permian fossil but are revealed in microscopic detail in the Burmese amber specimens.

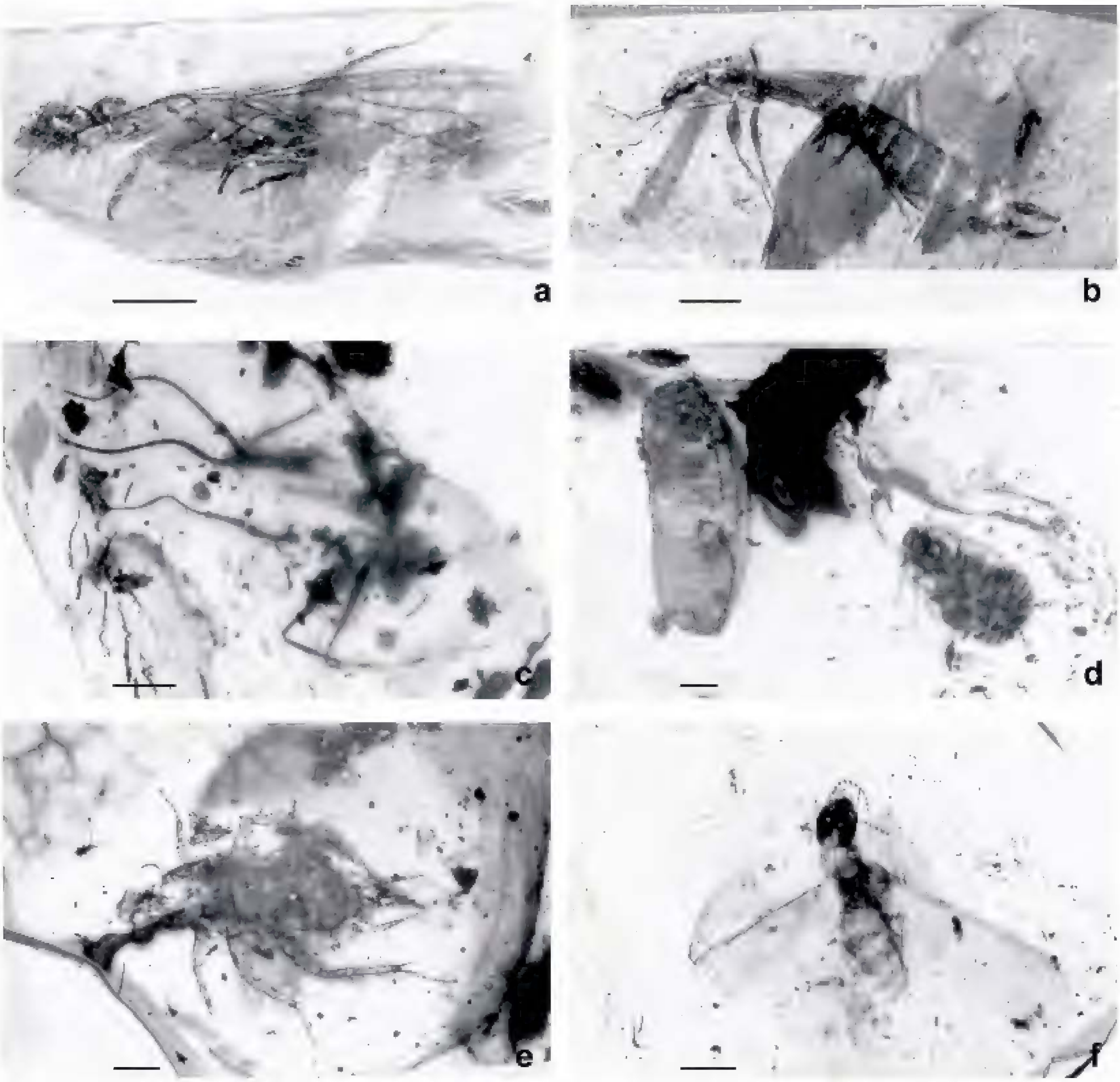

Fig. 22. Assorted lower Neoptera and dictyopteran insects in Burmese amber. **a.** Embiidina, new genus, AMNH Bu227. **b.** Dermaptera (Pygidicranoidea), AMNH Bu274. **c.** Partially preserved nymphal? Mantodea, with exceptionally long cerci, AMNH Bu155. **d.** Blattodea, ootheca (left) and nymph (right), AMNH Bu322. **e.** Blattodea nymph, AMNH Bu202. **f.** Isoptera: *Kalotermes* (?*swinhoei*), AMNH Bu313. Scales are 1.0 mm.

ORDER PLECOPTERA

The cosmopolitan order Plecoptera, or stoneflies, comprises approximately 2000 species whose naiads typically live on or under stones in cool, flowing freshwater, and which leave the water for the final moult to an imago. The order is plesiomorphic in overall structure, perhaps not surprising considering their relatively basal position in neopteran phylogeny and their ancient geological occurrence and geographical distribution. Plecoptera may even be the living sister group to all other Neoptera (e.g., Zwick, 1980). Taxa assigned to the Plecoptera date back to the Lower Permian (e.g., Carpenter, 1992: as Order Perlaria), and are known on the basis of both adults and naiads. The two major clades of stoneflies, Arctoperlaria and Antarctoperlaria (Zwick, 1980, 2000) probably reflect an ancient, pangaean distribution early in the order's history.

Although species of several modern families are known from Tertiary amber of northern Europe and the Dominican Republic (Weitschat and Wichard, 1998; Stark and Lentz, 1992), none have previously been recorded from Cretaceous amber. Diverse Cretaceous Plecoptera preserved in rocks have been described by Sinitschenkova (1987). The two Burmese amber specimens in the AMNH are the oldest stoneflies in amber, and the most completely preserved Mesozoic Plecoptera. The higher-level systematics of Plecoptera is relatively well established (Zwick, 2000), which will facilitate interpretation of these specimens.

ORDER DERMAPTERA

Like the Zoraptera and Embiidina, the earwigs (Dermaptera) are an autapomorphic, isolated order of Polyneoptera. Their true phylogenetic position remains obscured, but it is for just such lineages that early fossils will prove most critical for elucidating relationships. To date, no such analysis incorporating information from extinct groups has been undertaken, although Haas (1995) has evaluated various character systems for Dermaptera phylogeny.

Numerous compression fossils of earwigs have been described from deposits ranging in age from the Lower Jurassic to the Miocene (e.g., Whalley, 1985; Ping, 1935; Vishniakova, 1980; Popham, 1990; Carpenter, 1992, Zhang, 1994). Three undescribed and putatively Dermaptera elytra from the Upper Triassic of Australia occur in the NHML collections (A.J. Ross, personal commun.). Several Cenozoic amber fossils from Eocene Baltic amber (Burr, 1911) have been described, and ones also occur in Miocene Dominican amber (Schlee, 1980; AMNH and NHML collections). Several compression fossil species from the Upper Jurassic and Lower Cretaceous of Asia were placed in an extinct suborder, the †Archidermaptera, which plesiomorphically have segmented cerci, pentamerous tarsi, and retain venation (albeit reduced) on their tegmina (Bey-Bienko, 1936; Carpenter, 1992). All other fossils are of the suborder Forficulina (sometimes referrred to as the "true earwigs"), with the typical synapomorphies of reduced tarsi, unsegmented cerci, and veinless tegmina, among other characters.

Four specimens of Forficulina are known from Cretaceous amber, two unstudied ones in Lebanese amber and two in Burmese amber. The first Burmese amber specimen known is the holotype of *Labidura electrina* Cockerell (NHML In. 20146; Ross and York, 2000: fig. 2); the second is an adult female pygidicranoid in the AMNH collection (Bu274: fig. 22b). The NHML specimen is not well preserved and its assignment to the living genus *Labidura* may be incorrect, as suspected by Cockerell (1920), owing to an apparent unbent pygidium, though it may be labidurid of some sort. The AMNH specimen is remarkably well preserved, easily recognizable as a pygidicranoid and distinct from Cockerell's species. Interestingly, the Pygidicranoidea is the basalmost superfamily of the suborder Forficulina (Haas, 1995). The other two living suborders are Hemimerina and Arixeniina and are, not surprisingly, unknown from the fossil record. Both are ectoparasitic on mammals, the Arixeniina on molossid bats in southeast Asia, and Hemimerina on certain rodents in Africa. At least Arixeniina is well established to be a monophyletic derivative of the Forficulina and should be reduced in rank to a family of this latter group (e.g., Popham, 1965, 1985). It would not be suprising if Hemimerina were likewise found to be subordinate within an existing taxon of Forficulina.

Modern pygidicranoid species have a roughly pantropical distribution, occurring in southeast Asia, central Africa and Madagascar, and Central and South America (e.g., Popham, 2000). Some additional species of Pygidicranidae also occur in southern Africa and Australia, including Western Australia. The AMNH specimen intermingles some characters of the pygidicranoid families and perhaps represents a distinct lineage of this superfamily. Although several Lower Cretaceous and younger fossils from Asia have been described as pygidicranoids, none of them preserve characters that could definitively place them in this superfamily (e.g., see discussion by Willmann, 1990).

ORDER ISOPTERA

This order is of global ecological significance in the processing of lignocellulosic plant matter and in humification (e.g., Wood and Sands, 1978; Bignell and Eggleton, 2000). The group appears to be relatively young, with the oldest fossils occuring in the Lower Cretaceous (reviewed in Thorne et al., 2000). With the exception of Burmese amber, all Cretaceous termites belong to the primitive families Hodotermitidae, Termopsidae, and possibly the Mastotermitidae. This stratigraphic occurrence corresponds with recent and even traditional phylogenetic hypotheses of isopteran families: Mastotermitidae (Hodotermitidae (Termopsidae (Kalotermitidae (all other termites)))) (e.g., Donovan et al., 2000; Thompson et al., 2000). The Burmese amber termites are of great significance because they are definitive Kalotermitidae from the Cretaceous, though kalotermitids putatively occur in Lebanese amber (A. Nel, personal commun.).

The two termite species described by Cockerell from the Burmese amber in the NHML were revised by Williams (1968), and are now known to belong to the Kalotermitidae: *Kalotermes †swinhoei* (Cockerell) and *Kalotermes †tristis* (Cockerell). At least one specimen in the AMNH collection is *K. †swinhoei* (fig. 22f) or near this species, but most of the other seven specimens are difficult to evaluate because they are either too partial or poorly preserved. There is also a specimen belonging to a very unusual, undescribed genus of Rhinotermitidae in the NHML collection (K. Krishna and D. Grimaldi, unpubl. data). This specimen is of exceptional significance as the first Cretaceous representative of the "higher" termites, families Rhinotermitidae + Termitidae.

Occurrence of Kalotemitidae in the mid-Cretaceous, possibly Cenomanian, indicates divergence of the basal four families of Isoptera by this time. Isoptera have yet to be found in the Jurassic[6], despite intensive study of Upper Jurassic deposits from Eurasia. This suggests that earliest diversification of termites in the Lower Cretaceous was quite rapid. Kalotermitidae are often referred to as "dry wood" termites, since they excavate galleries in dry, dead wood, in which they house their small colonies and where they feed. Though most abundant and diverse in tropics around the world, they also occur in temperate regions. The tropical nature of the Burmese amber paleobiota may account for the rare presence of Kalotermitidae among Cretaceous amber deposits.

ORDER HEMIPTERA

†Protopsyllidiidae: This is a large, diverse family of putatively sternorrhynchan affinities, occurring from the Permian to Lower Cretaceous (reviewed in Carpenter, 1992). Two specimens, in amber from the Upper Cretaceous of Burma and New Jersey, are the most recent occurrence of the group.

Specimen AMNH Bu137 (fig. 24e) is an entirely preserved male, but slightly cleared and compressed in parts. Specimen AMNH NJ623 is a beautifully preserved female. Both belong to an apomorphic new genus of the family. The genus could be characterized by veins of the forewings having rows of stiff, thick, erect setae on the upper surface (the hind wing is completely bare); the margin of the forewing has a fringe of long setae, which are slightly longer and thinner than the setae along the veins. Such setae have been reported from *†Aphidulum steoptilium* Shcherbakov, known from compression fossil wings from the Lower Cretaceous of Mongolia, though its marginal setae were much smaller and fewer, possibly dislodged (Shcherbakov, 1988). *†Aphidulum* occurs in the Lower Cretaceous of Mongolia and Lower Purbecks of Dorset, England (Coram et al., 1994). The Lower Purbecks is now known to be Lower Cretaceous rather than Upper Jurassic (Rasnitsyn et al., 1998). These last two occurrences were the most recent records of the family. Venation of the two amber specimens is very similar and consistent with protopsyllidiids, though missing the small apical fork of R (as also occurs in *†Aphidulum*). Venation of the new genus differs most from *†Aphidulum* by hav-

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[6] Ren (1995) described six genera of putative Hodotermitidae and Termopsidae from wing remains from the Yixian Formation of Beipiao, southern China. Originally believed to be Upper Jurassic, this Formation is now better known to be Lower Cretaceous, probably Barremian in age (ca. 120 Ma; Barrett, 2000).

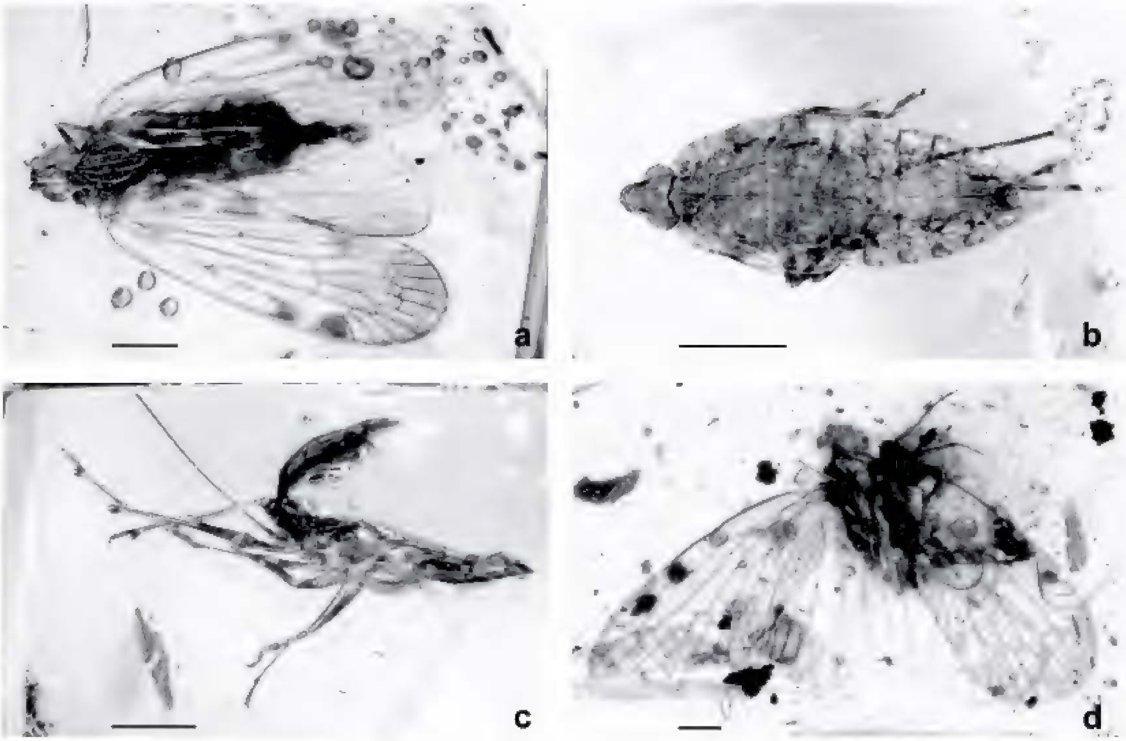

Fig. 23. Assorted adult and nymphal Auchennorhyncha (Hemiptera) in Burmese amber. **a.** AMNH Bu511. **b.** AMNH Bu964. **c.** AMNH Bu510. **d.** AMNH Bu512. Scales are 1.0 mm.

ing a three-branched M, instead of two branches. Carpenter (1992) placed †*Aphidulum* into Hemiptera incertae sedis; Shcherbakov (1988) placed the genus in the †Protopsyllidiidae.

The new genus is highly apomorphic in many other respects. The vertex of the head bristles with numerous long, thick, stiff setae. The meso- and metathoracic legs are long and slender, but the prothoracic legs are about half the length and with a row of spine-like setae on the ventral surface of the femur. Tarsomeres are 2–3–3. The antenna is long and slender, with eight flagellomeres, and the clypeus has a distinctive pair of long, stiff, projecting setae. The probosocis appears typically sternorrhynchan-auchenorrhychan, being extremely opisthognathous and ending at the third pair of coxae. The eyes are extremely large. After comprehensive study, these two unique specimens will clearly reveal a great deal about the phylogenetic affinities of this unusual extinct group.

Suborder Sternorrhyncha

Coccoidea: Though they represent only about 1% of the arthropods in the NHML collection (Rasnistyn and Ross, 2000), Coccoidea were 3.6% of all inclusions in the AMNH collection of Burmese amber. Most specimens are winged males (e.g., fig. 24f); apterous females are very rare in any amber. Because of their minute size (<1 mm body length), amber is the only consistently informative type of fossil for this group. The only other Cretaceous amber deposit with a comparable abundance of coccoids is from New Jersey, which contains eight families and genera, and at least 12 species (Koteja, 2000), representing at least 10% of all organismal inclusions in that amber (Grimaldi et al., 2000a). Burmese amber preserves the next most abundant and diverse record for the group. The proportions of Coccoidea in all other Cretaceous ambers are far less than 1%.

There are two interesting ecological pat-

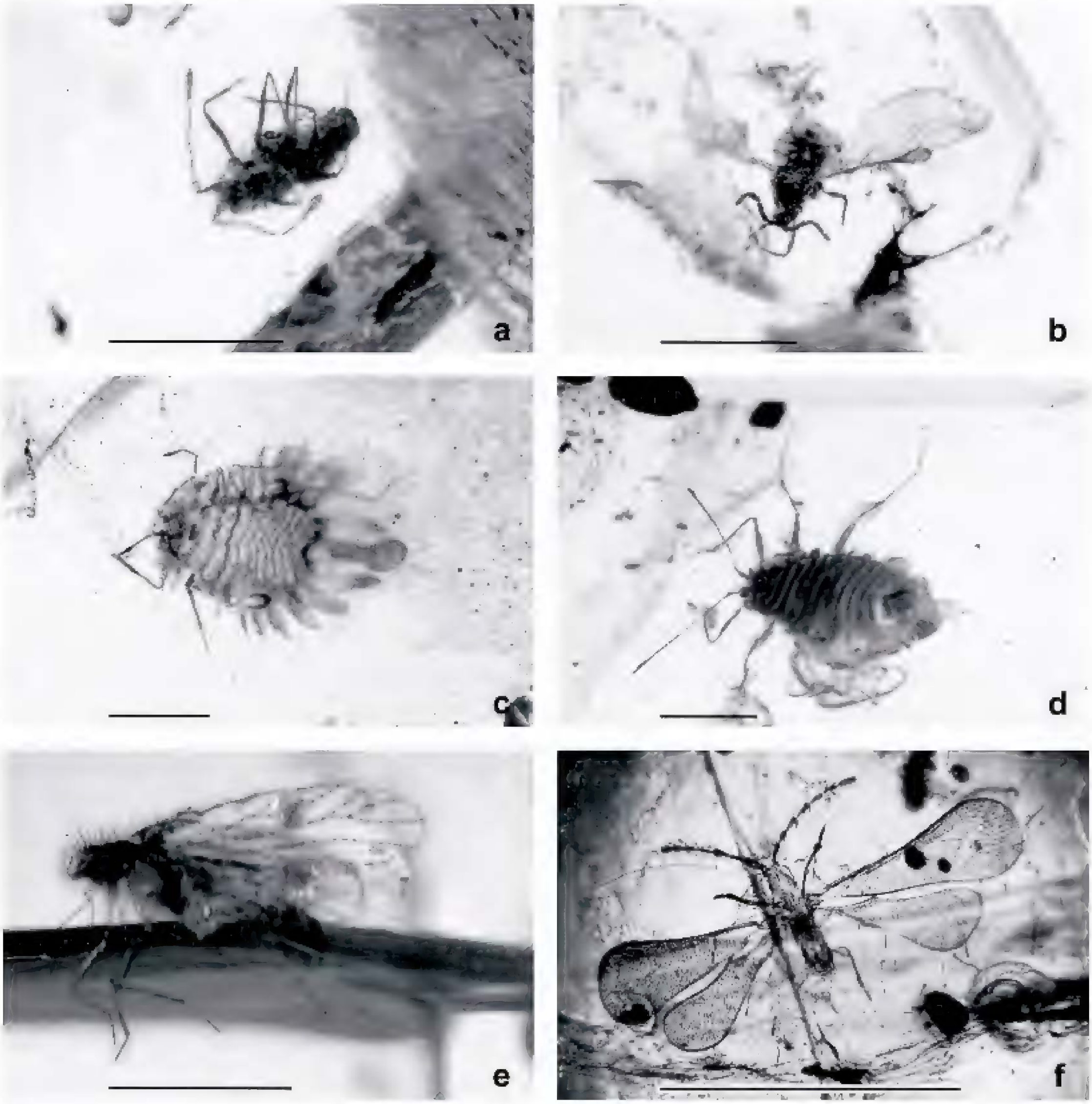

Fig. 24. Assorted adult and nymphal Sternorrhyncha (Hemiptera) in Burmese amber. **a–d**: Aphidoidea. **a.** nymph, AMNH Bu007. **b.** alate (Tajmyraphididae), AMNH Bu963. **c.** nymph, AMNH Bu1094. **d.** nymph, AMNH Bu962. **e.** Protopsyllidiidae, AMNH Bu137. **f.** Coccoidea male, AMNH Bu114. Scales are 1.0 mm.

terns shared between Burmese and New Jersey amber, both involving Coccoidea. First, Aphidoidea (aphids) in both these ambers are very rare (<0.5%), in contrast to the abundance of aphids in Siberian and Canadian ambers (5, 10% [Yantardakh, Kresty/Zhdanikha] and 35–40%, respectively). This may reflect the more tropical paleoclimates of the New Jersey and Burmese ambers, since today coccoids are more abundant in tropical than temperate forests—a distribution opposite that of aphids. Secondly, New Jersey (Grimaldi, 2000b) and Burmese ambers both have an impressive abundance of predatory Berothidae (see below, Neuroptera).

Aphidoidea: Aphids are an ancient group that extend to the Triassic (two species), have modest diversity in the Jurassic (six species), and first become abundant and diverse in the Cretaceous (70 species, ten families [eight extinct]). Despite this antiquity, they seem to have undergone a major radiation in the mid-Tertiary, as a result of proliferation of the Aphididae (representing 55% of extant species) on the Asteraceae (composits) and Poaceae (grasses)(Heie, 1996). In fact, Heie (1996) hypothesized extinction of Mesozoic aphids (presumably mostly conifer feeders) near the K/T boundary or in the early Tertiary, resulting from floras dominated by conifers to ones dominated by angiosperms.

No Aphidoidea are reported in the NHML collection, but eight specimens are in the AMNH collection (0.2% of all inclusions). This low abundance is comparable to what is found in the Lebanese and New Jersey ambers. Five of the specimens are alates (AMNH Bu022, 188, 963, 1300, and 1301). The remainder of the specimens comprises nymphs, all of which bear waxy terminal filaments (e.g., fig. 24c). Affinities of the nymphs have yet to be determined, but all of the alates belong to the extinct family Tajmyraphididae (fig. 24b), known otherwise in amber from northern Siberia, western Canada, and Lebanon (e.g., Heie and Azar, 2000). Among alates there are approximately five species in three genera. All bear typical features of the Tajmyraphididae: seven antennal segments (five flagellomeres); abdomen simple; apically rounded (not bilobate); no siphunculi; wing venation with short pterostigma, Rs originating at distal half of pterostigma, M with only two branches and stem originating in proximal half of pterostigma, CuA and CuP widely separated, CuP nearly perpendicular to main vein. In one species (AMNH Bu188), the rostrum projects well beyond the apex of the abdomen; the rostrum of another species (AMNH Bu1301) ends at the abdominal apex (in the other species the rostrum cannot be observed).

Though not nearly as diverse as aphid paleofaunas from Siberia and Canada, five species represented by five alates indicate a diverse aphid community in Burmese amber. Their rarity in Burmese amber, though, is very similar to that in the other major Cretaceous amber deposits from low paleolatitudes. This pattern suggests tropical rarity of aphids in the Cretaceous, as is found today.

Suborder Heteroptera

Enicocephalidae: Several specimens exist of this family in the AMNH and NHML collections (AMNH Bu110a, 131a, 212e, 268, 451a, and 960a)(e.g., figs. 25a, b). Cockerell (1917a, 1917b) described four fossil species from the NHML collection alone: †*Disphaerocephalus constrictus*, *D. macropterus*, *D. swinhoei*, and †*Paenitotechys fossilis*. The original specimens of these species have been redescribed in detail by Štys (1969), but identities of the AMNH specimens have yet to be determined.

Enicocephalidae should be expected from the Triassic, but the oldest fossils are from the Lower Cretaceous, specifically Neocomian amber from Lebanon (Grimaldi et al., 1993; Azar et al., 1999). The specimens in Burmese amber are among the only other enicocephalids known from the Cretaceous, since they have not yet been found in ambers from Canada, New Jersey, Siberia, or Spain. The family Enicocephalidae[7] is the sister group to the rest of the Heteroptera (Schuh and Slater, 1995). Since definitive Nepomorpha occur in the Upper Triassic, we should expect Enicocephalidae to be at least this old and perhaps Lower Triassic to Upper Permian in age. Small size may obscure their recognition in sedimentary matrix.

Schizopteridae: This is a new family record for Burmese amber, not represented in the NHML collection. Specimen AMNH Bu720a (fig. 25c) is more finely preserved than the others (AMNH Bu87f, 723c, 965), showing features typical of the family. For example: forewings tegminal, barely differentiated into a corium and membrane, with distinctive venation; antennal segments one and two short; forewing without C or medial fractures; parameres long, fingerlike, and asymmetrical. The family belongs to the Dipsocoromorpha, which also includes the families Stemmocryptidae (Australia), Hypsip-

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[7] Enicocephalidae is sometimes split into the Aenictopecheidae and Enicocephalidae s.s. (Štys, in Schuh and Slater, 1995). This appears to be unnecessary splitting, since the group appears definitively monophyletic, based alone on the bilobed head (with hind lobe bearing ocelli) and the foreleg structure (tarsi spinose, strongly chelate, apical tarsomere with pair of subequal claws). It is highly unlikely that these unique structures evolved convergently in Aenictopecheidae and Enicocephalidae.

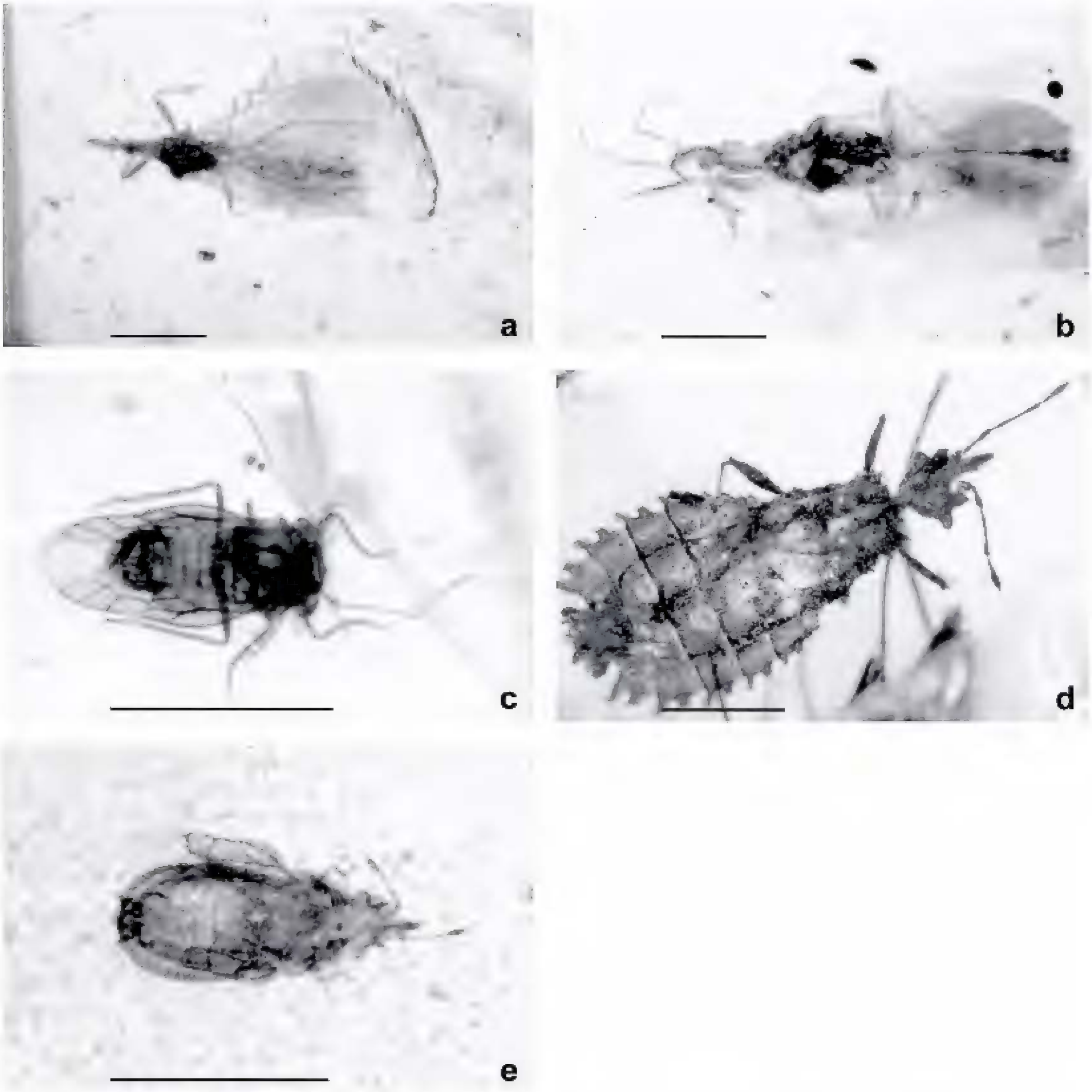

Fig. 25. Assorted Heteroptera in Burmese amber. **a, b**: Enicocephalidae. **a.** AMNH Bu268. **b.** AMNH Bu960. **c.** Schizopteridae, AMNH Bu720. **d.** Aradidae, n. gen., AMNH Bu167. **e.** Piesmatidae, AMNH Bu958. Scales are 1.0 mm.

terygidae (Africa, Asia), Ceratocombidae (cosmopolitan, mostly tropical), and Dipsocoridae (cosmopolitan). The Dipsocoromorpha is one of the most primitive groups in the Heteroptera, as reflected by the extensive venation. Relationships appear to be as a sister group to the Neoheteroptera (sensu Schuh and Slater, 1995): Enicocephalidae (Dipsocoromorpha (Neoheteroptera)). The fossil record is sparse, with the only other Mesozoic fossils being undescribed species in Neocomian amber from Lebanon. Like Enicocephalidae, their small size (0.8–2.0 mm) may obscure or prevent preservation of dipsocoromorphs in sedimentary matrices.

Hydrometridae: The Gerromorpha is a group of approximately 1600 extant species in eight families, commonly called the semiaquatic bugs and including the familiar water striders (Gerridae), water measurers (Hydrometridae), and less familiar forms. Specimen AMNH Bu1098 is unique, and only the

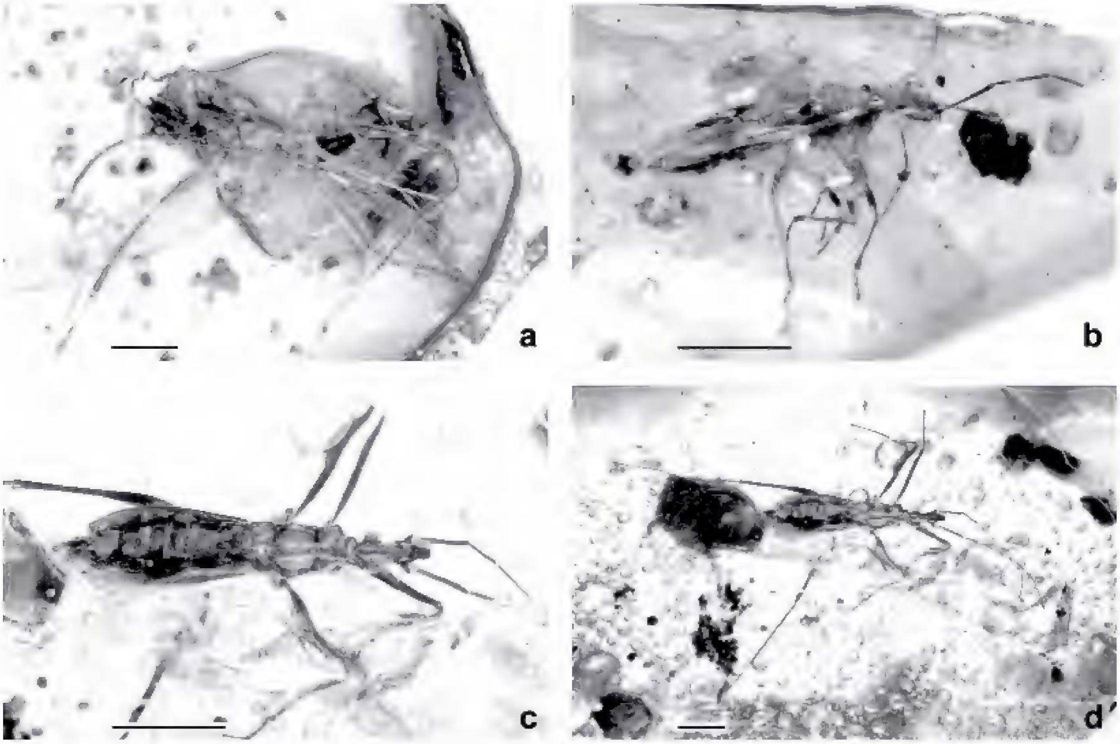

Fig. 26. Assorted Heteroptera in Burmese amber. **a.** Family near Cimicidae, AMNH Bu728. **b.** Family indet., AMNH Bu1092. **c, d**: Hydrometridae, n. gen., detail of body and entire habitus, AMNH Bu1098b.

fourth definitive Mesozoic gerromorphan (as the only one in Mesozoic amber it is also the most completely preserved Mesozoic fossil of the infraorder; fig. 26c, d). The specimen is well preserved, although a lateral view is obscured. Typical of the Gerromorpha, the bug possesses long legs and well-developed pairs of trichobothria on the head. Typical of the Hydrometridae it has three pairs of head trichobothria, a prolonged head, long legs and antennae, and reduced wing venation (N.M. Andersen, personal commun.). The specimen is brachypterous and has vestigial ocelli, which are correlated features. The posterior two pairs of trichobothria have extremely long trichs (the posterior pair tuberculate), and there is a slight preapical articulation of the second antennal segment into the first. These features indicate the fossil is probably within the Heterocleptinae, the most primitive subfamily of Hydrometridae. Heterocleptines are represented by two extant genera: *Veliometra* (Brazil), and *Heterocleptes* (western and central Africa, with three species; and one species on Borneo). The fossil appears to be the most primitive known hydrometrid, living or extinct (N.M. Andersen, personal commun.).

Andersen (1998) recently monographed the fossil Gerromorpha, including descriptions of various new taxa from the Paleocene of Denmark. Based on the phylogenetic position of the Gerromorpha as the sister group to the Panheteroptera (Nepomorpha + Leptopodomorpha + Pentatomorpha + Cimicomorpha [Schuh and Slater, 1995]), they should be present in the Triassic. Definitive Nepomorpha occur in the Triassic. Oddly, the only Mesozoic Gerromorpha are three Cretaceous records: †*Duncanovelia* (Mesoveliidae: Koonwarra bed, Aptian of Australia), †*Cretaceometra brasiliensis* Nel and Popov (Hydrometridae: Santana Formation, Aptian of Brazil), and a possible Veliidae also from Koonwarra. Interestingly, the Santana Formation fossil is apparently a hydrometrine, or at least sister group to this derived subfamily.

Andersen's (1998) phylogenetic analysis of the fossils and closely related living families allows an excellent basis for extrapolating ages. He estimated Jurassic divergence of most gerromorphan families, so clearly there are huge gaps in the fossil record of this group of Heteroptera. Though some tropical hydrometrids live among vegetation distant from water, most species of this related families live on the water surface or among emergent vegetation, so there would presumably be far better representation of gerromorphs in lacustrine fossil beds. Hydrometridae are cosmopolitan; two closely related families are relict, with only two and three species each from Chile and western North America (Macroveliidae), or southern Africa (Paraphyrnoveliidae). Andersen (1998) hypothesized divergence of these three families in the Lower Cretaceous, with apparent Hydrometrinae already appearing by the Aptian. Thus, by the mid-Cretaceous, the primitive fossil in Burmese amber probably represented a relict taxon. Description and discussion of the unique fossil is provided elsewhere (Andersen and Grimaldi, 2002).

Aradidae: One finely preserved specimen (AMNH Bu167; fig. 25d) represents a new genus of the Aradidae, having the plesiomorphic presence of pulvilli, as well as a long clypeus, free and unfused mediotergites III–VI, and lack of metapleural scent gland openings. The only other Mesozoic aradid is *Aradus* †*creticus* from the Cenomanian of northeast Siberia (Kormilev and Popov, 1986). Aradids are highly flattened pentatomorphan bugs with approximately 1800 species in 211 genera, the greatest diversity being in southeastern Asia (Schuh and Slater, 1995). They live among forest floor leaf litter and under the bark of injured, dying, or dead trees, where they feed on fungal mycelia. Some species of *Aradus* feed on the phloem and xylem of *Pinus* and *Larix*. A separate article treats this unique specimen (Heiss and Grimaldi, 2002).

Piesmatidae: A tiny species is represented by a unique specimen (AMNH Bu958, fig. 25e), which is typical for the family with the dorsal surface of the head, pronotum, and most of the forewings covered with a dense, fine, areolate punctation. Ocelli cannot be distinguished (they are present in modern species), but elongate mandibular plates and a "dorsal crest" on the head are also distinctive for the family. The ventral view affords excellent observation of the abdomen, in which trichobothria should be observable if present. None appear to be present, or there are only a few, reduced trichobothria—another feature of the family. This is the only Mesozoic piesmatid, which is not unusual based on their small size alone. Phylogenetic position of the family in the Pentatomorpha makes a Cretaceous fossil of considerable significance for the phylogeny and chronology of the "higher" Heteroptera (Panheteroptera, sensu Schuh and Slater, 1995). There are 50 extant species in six genera. The family is cosmopolitan and where known all are phytophagous, with many on Chenopodiaceae, some on *Acacia*, and various other angiosperm families.

Cimicomorpha, near Cimicidae: Specimen AMNH Bu728 is very peculiar and apparently a very primitive relative of extant Cimicidae (bed bugs). The specimen is compressed and distorted, but apparently was a broad, flat bug, similar in shape to extant Cimicidae (figs. 26a, 27). Like Cimicidae, it has a dense vestiture of fine, long setae, as well as a spinelike aedeagus. A stiff seta occurs just posterior to the eye (seen for its right eye), as is found in the primitive subfamily Primicimicinae (Usinger, 1966). Otherwise, the bug is entirely plesiomorphic to the Cimicidae. There are long basal portions of the male genitalia (well preserved and visible through the sheer cuticle), which is similar to the condition in other cimicomorphs; extant Cimicidae have quite short genitalia. Also, legs are fairly long (not as short as in Cimicidae), and the rostrum extends to the hind coxae (in Cimicidae it generally extends at best to the first pair of coxae). Most striking of all is the macropterous condition, albeit with weakly sclerotized hemelytra. A clavus, cuneus, and medial fracture are present, though the membrane is too faint to observe. Wings are as densely pubescent as the rest of the body.

Extant Cimicidae are parasitic on bats and certain birds, particularly swifts and swallows (Apodidae, Hirundinidae), although

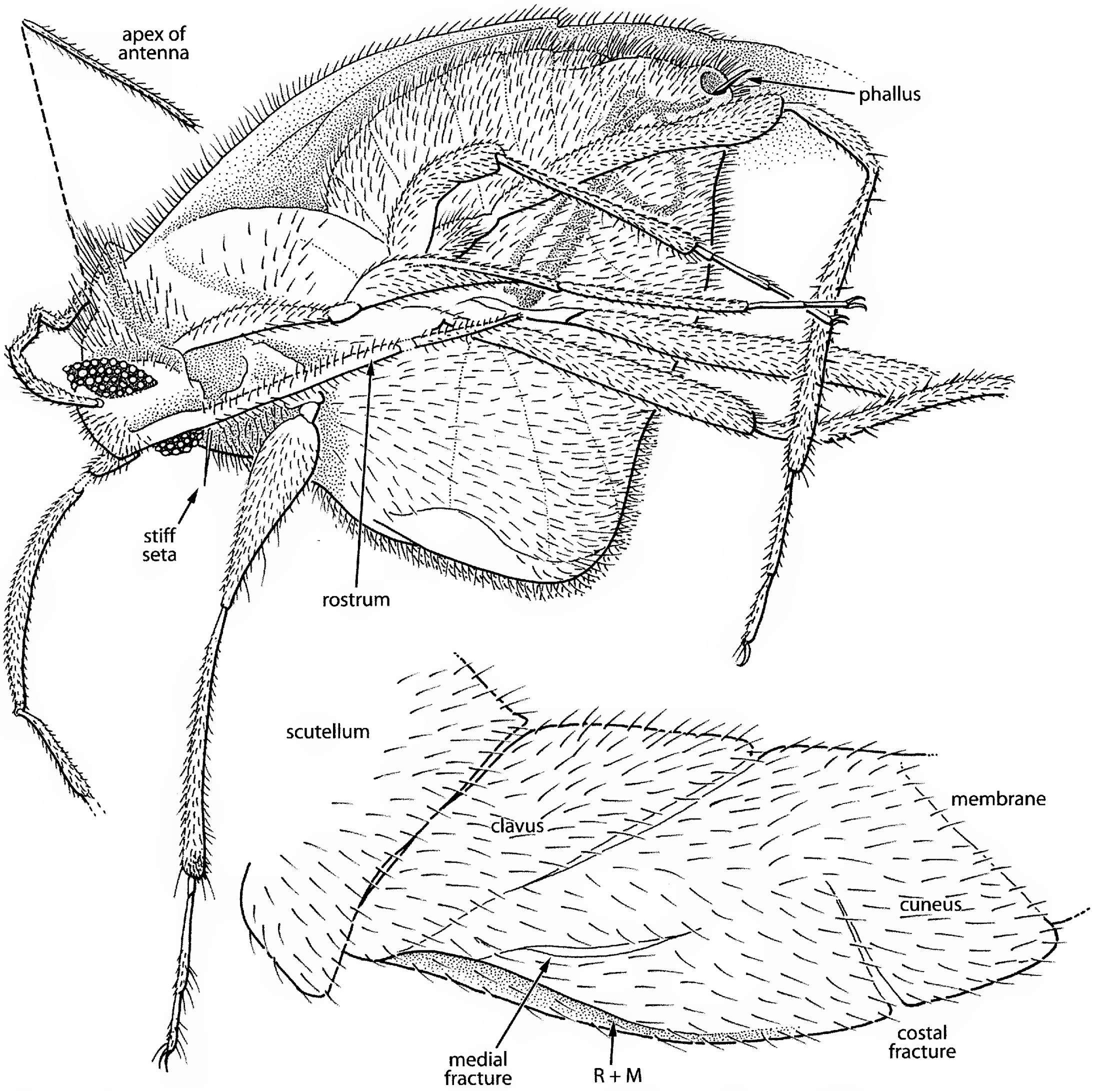

Fig. 27. AMNH Bu728, family near Cimicidae. Ventral view, with dorsal view of hemelytra.

some other bird families are also parasitized (summarized in Usinger, 1966). Vestiture of the fossil species *suggests* it was parasitic, but if so, its host was almost certainly some type of bird. The earliest fossil bats are from the Eocene, and perhaps first evolved in the Paleocene (Simmons and Geisler, 1998).

ORDER NEUROPTERIDA

Suborder Neuroptera

The lacewings (Neuroptera, Planipennia) are today represented by approximately 17 families and 6000 species occurring in all habitats and on all continents except Antarctica. The order has a long geological history, extending into the Permian and with considerable diversity of early Mesozoic families. Despite the relatively common occurrence of Neuroptera as compression fossils in the Mesozoic, usually with only wings preserved, the order has not been well represented as amber inclusions. The most diverse amber fauna is that of the mid-Eocene Baltic amber, although new taxa are regularly discovered in that amber and basic monographic work is ongoing (Engel, 1999). Neuroptera are rare in Miocene Dominican amber, which contains two orders, seven families, and 13 species (Engel and Grimaldi, in prep.). Neuroptera have a sporadic occurrence in Cretaceous ambers. Rasnitsyn and Ross (2000), for example, listed only a few specimens in the NHML collection of Burmese amber. The most diverse fauna in Cretaceous amber known thus far is from New Jersey (Grimaldi, 2000b), though it is likely that the Burmese fauna will be more diverse for this order. Like the New Jersey amber fauna, the AMNH collection of Burmese amber contains a remarkable number of neuropteran specimens and taxa. In particular, it includes adult or immature representatives of the Berothidae, Rhachiberothidae, Osmylidae, Coniopterygidae, Nevrorthidae, and Psychopsidae (the latter three not in the NHML collection; Engel, in prep.).

The berothids are particularly abundant in Burmese amber and are generally more diverse and common in Cretaceous ambers than in Tertiary ambers. Rasnitsyn and Ross (2000) listed only three berothids (i.e., inclusive of Rhachiberothidae, of which one specimen, In. 20177, is representative), out of 1198 arthropod inclusions in the NHML collection (0.2%). In the Burmese amber at the AMNH, berothids are much more common, with 34 specimens, representing some 1% of all arthropod inclusions. Of the specimens studied thus far in New Jersey amber, there are five species and three genera of berothids, representing nearly 2% of all organismal inclusions. Only one or two specimens of Berothidae have been found in each of the other Cretaceous ambers, in which coccoids are also rare. Where plants have large infestations of coccoids, the larvae and adults of these small lacewings are commonly found preying among the aggregations, so the berothids in New Jersey and Burmese ambers probably were feeding on the abundant coccoids.

The Rhachiberothidae is a group of raptorial lacewings today restricted to sub-Saharan Africa. Interestingly, their discovery in Burmese amber (NHML In. 20177 [M.S. Engel *in* Rasnitsyn and Ross, 2000] and an AMNH specimen) bolsters the evidence for a Cretaceous age of Burmese amber. Fossil rhachiberothids are known only from the Cretaceous of the Northern Hemisphere (e.g., in amber from France, Lebanon, New Jersey, and now Myanmar), so this group was once globally distributed.

Several dustywing specimens (Coniopterygidae; e.g., AMNH Bu198: fig. 28a) represent another index taxon for the Cretaceous age of Burmese amber. They possess the plesiomorphic arrangement of three branches to vein M, similar to *Glaesoconis* and *Apoglaesoconis*, which occur only in the Cretaceous (Grimaldi, 2000b; Engel, in press). Like berothids, coniopterygids also feed as larvae and adults on sessile sternorrhynchans such as Coccoidea.

Suborder Raphidioptera

The Mesozoic record of snakeflies (Raphidioptera) is quite extensive, but specimens in amber are exceedingly rare. At present only one species, †*Mesoraphidia luzzii* Grimaldi, of the extinct family †Mesoraphidiidae, is described from Cretaceous amber (from New Jersey; Grimaldi, 2000b). Mesoraphidiids and other Raphidioptera are diverse and common in Mesozoic rocks but defined largely on the basis of wing venation and therefore not entirely comparable with the modern classification of snakeflies, which is based heavily on genitalic structures (Aspöck et al., 1991). The order today is relict, consisting of approximately 206 described species in two families (the Inocelliidae and Raphidiidae), with a disjunct Holarctic distribution.

The discovery of a second adult snakefly (AMNH Bu092: fig. 28c) is significant for several reasons. First, this is only the second record of an adult, mesoraphidiid snakefly in Cretaceous amber, and so provides detailed character information for a family otherwise known only from compression fossils. Second, AMNH Bu092 and †*M. luzzii* are the only mesoraphidiids from the Late Cretaceous, all other fossils being from the Lower Cretaceous and Jurassic (Engel, 2002). Third, the specimen is further documentation of the past occurrence of snakeflies in tropical habitats. Today the order is restricted to temperate regions of the Northern Hemisphere (Aspöck et al., 1991; Aspöck, 1998). Snakefly fossils, however, have been recov-

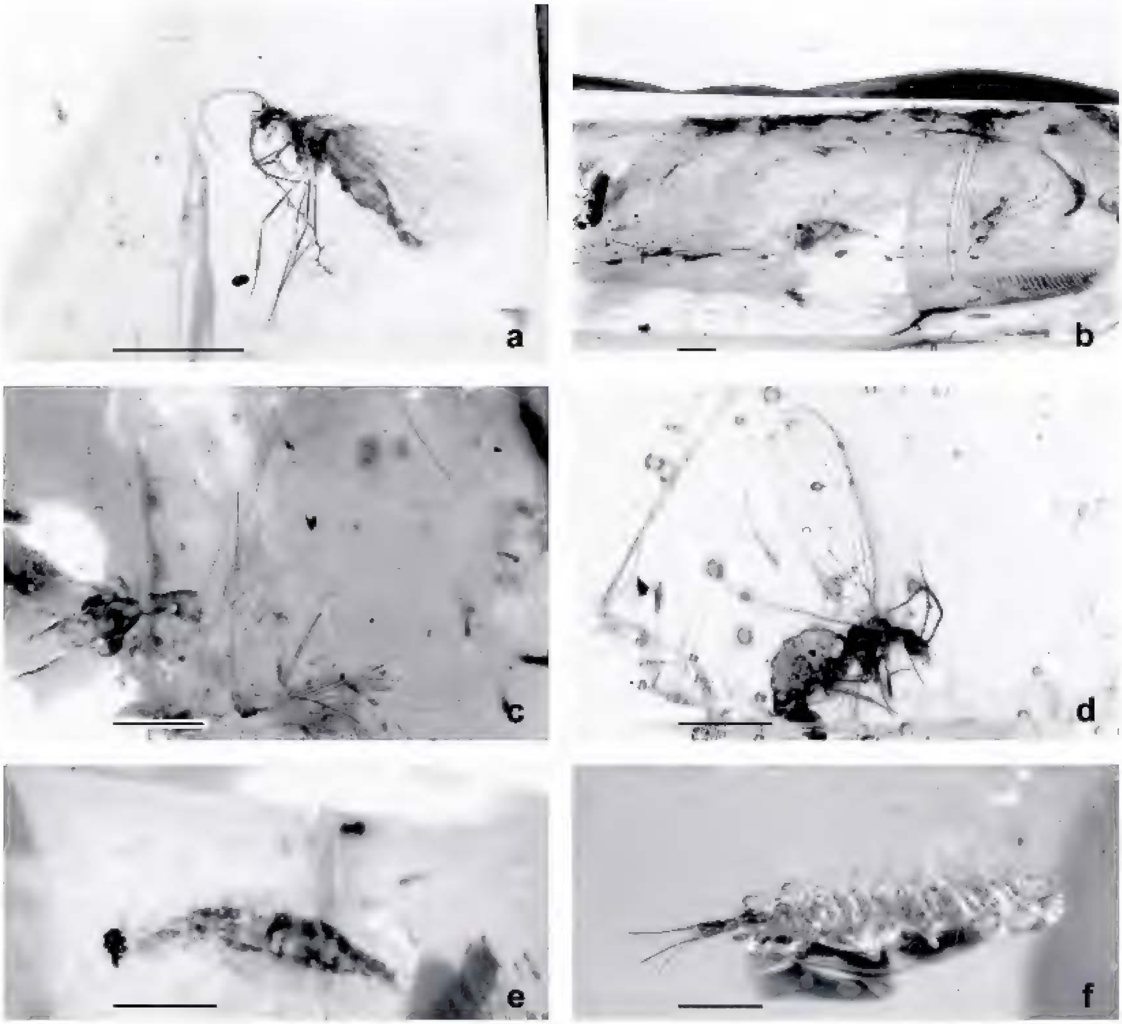

Fig. 28. Assorted Neuropterida in Burmese amber. **a.** Coniopterygidae, AMNH Bu198. **b.** Psychopsidae (wings), AMNH Bu309. **c.** Partial adult Raphidioptera, n. gen. in the Mesoraphidiidae†, AMNH Bu092. **d.** Berothidae, AMNH Bu1291. **e.**? Nevrorthidae (larva), AMNH Bu1297. **f.**? Osmylidae (larva), AMNH Bu267. Scales are 1.0 mm.

ered from subtropical paleoenvironments of the Southern Hemisphere (e.g., Oswald, 1990), as well as tropical to subtropical regions elsewhere during the Cretaceous. The tropical origin of the Burmese amber paleobiota is discussed towards the end of this paper. What factors might have led to the extinction of Southern Hemisphere and tropical snakeflies is not entirely understood (Aspöck, 1998). Baltic amber snakeflies (Engel, 1995), for example, indicate that tropical or subtropical snakeflies survived into the early Tertiary, although they perhaps were relict even at that time.

Last, the significance of AMNH Bu092 is its uniquely small size. The forewing length of the specimen is 4.26 mm, the smallest of any raphidiopteran living or extinct! In the NHML Burmese amber collection is a raphidiopteran larva, undetermined to family (In. 20150), but perhaps a mesoraphidiid. The NHML specimen is significantly larger than the AMNH adult (body length 13.83 mm) and the two are likely not congeneric.

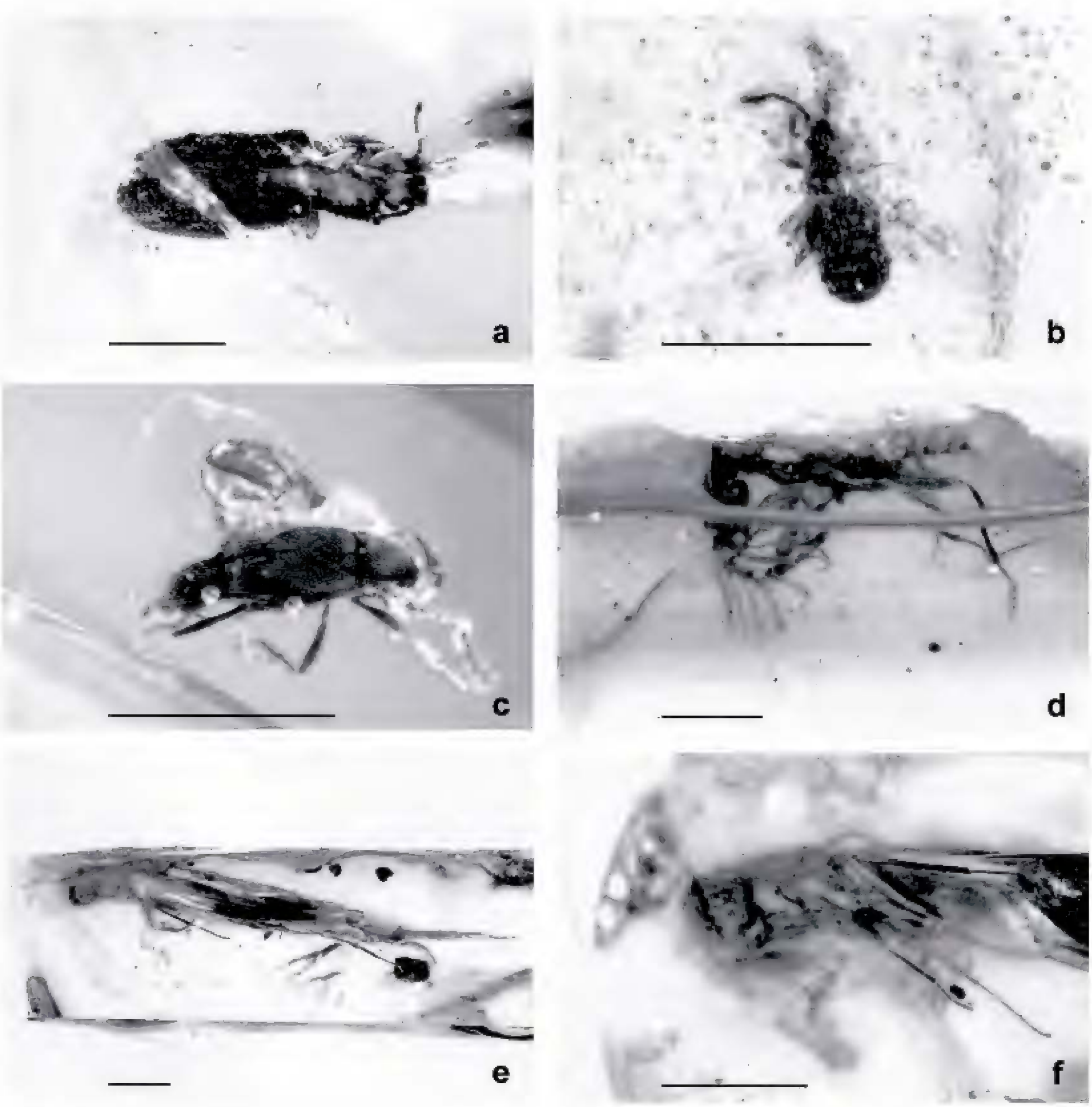

Fig. 29. Assorted Coleoptera in Burmese amber. **a.** Cupedoidea, AMNH Bu345. **b, c**: Staphylinoidea. **b.** AMNH Bu248. **c.** AMNH Bu259. **d.** Rhipiphoridae, AMNH Bu368. **e, f.** Lymexylidae, habitus and detail of anterior end. Scales are 1.0 mm.

A separate article provides further details of these specimens (Engel, 2002).

ORDER COLEOPTERA

There is a far greater diversity of beetles in Burmese amber than in any other Cretaceous amber (e.g., figs. 29–31). Azar (2000) listed 19 families in Lebanese amber; Grimaldi et al. (2000a) listed ten families in New Jersey amber, though the great majority of specimens are still unstudied. In contrast, Rasnitsyn and Ross (2000) listed 28 families in the Burmese amber at the NHML (also with many specimens still undetermined), representing 6% of all organismal inclusions (4% and 8% for Lebanese and New Jersey amber, respectively).

Many beetles in Cretaceous ambers are small, with body lengths 1–3 mm. Since the systematics of Coleoptera is highly depen-

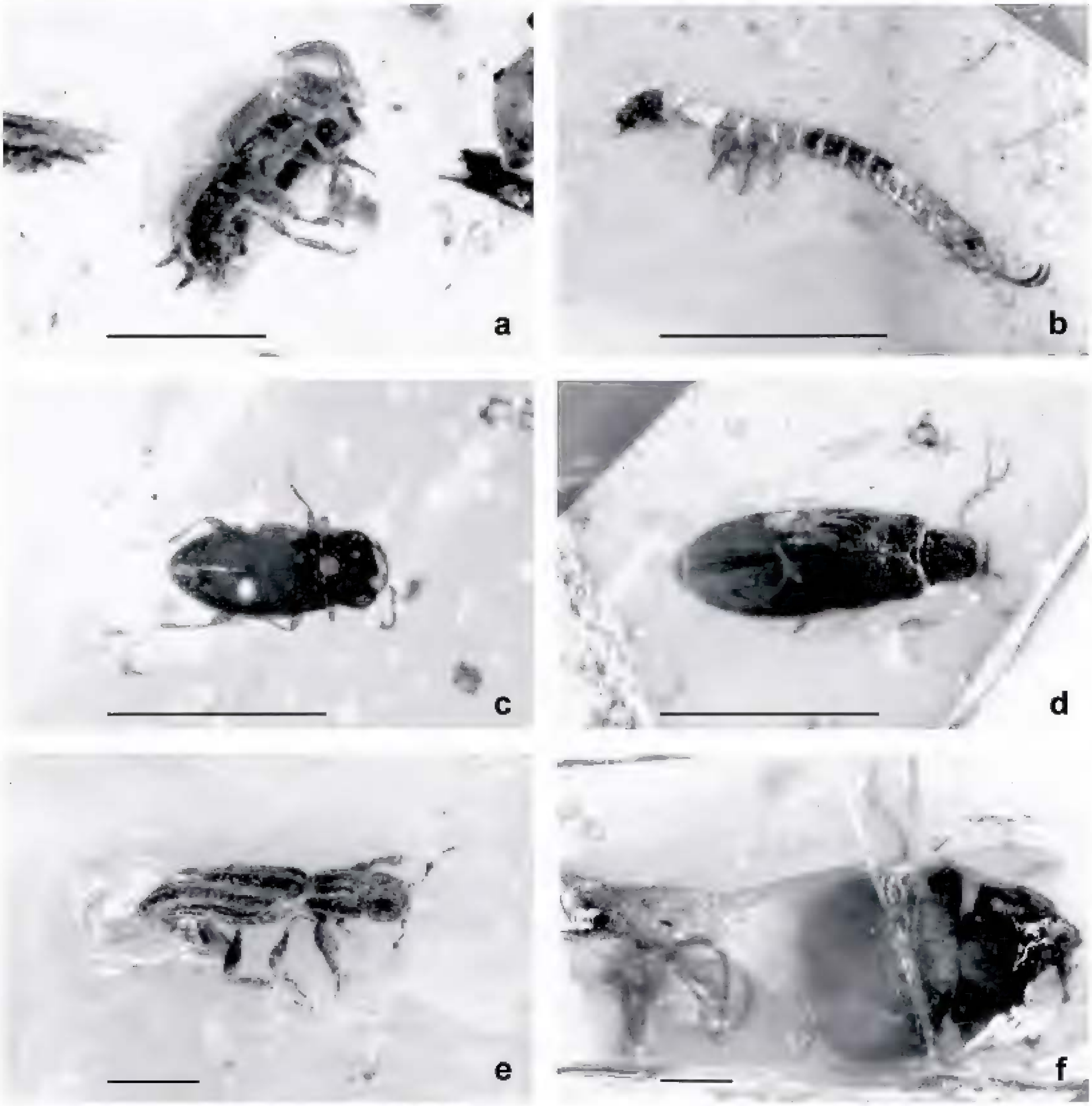

Fig. 30. Assorted Coleoptera in Burmese amber. **a.** Horned beetle (Ciidae?), AMNH Bu232. **b.** Larva, family undetermined, AMNH Bu366. **c.** Family indet., AMNH Bu062. **d.** Family indet., AMNH Bu069. **e.** Family near Platypodidae?, AMNH Bu235. **f.** Family indet., AMNH Bu236.

dent on minute features, like the segmentation and structure of palps and tarsomeres, and hind wing venation is generally not preserved or observable in beetle fossils, preservation in rock greatly compromises the systematics of fossil beetles. Carpenter (1992), for example, listed 234 genera of Coleoptera as incertae sedis, and several hundred more as doubtfully assigned to modern genera, the great majority of all of these being rock fossils. Thus, the Burmese Coleoptera fauna appears to have unique significance, and compliments other diverse, Mesozoic rock-fossil faunas, such as from the Jurassic of Karatau, Kazakhstan (Arnol'di et al., 1977). Of the families Rasnitsyn and Ross (2000) listed, eight have records from the Jurassic, or even the Triassic. All other families in their list are the only or among the few records from the Mesozoic.

Unfortunately, only a small proportion of the AMNH Coleoptera has been identified to

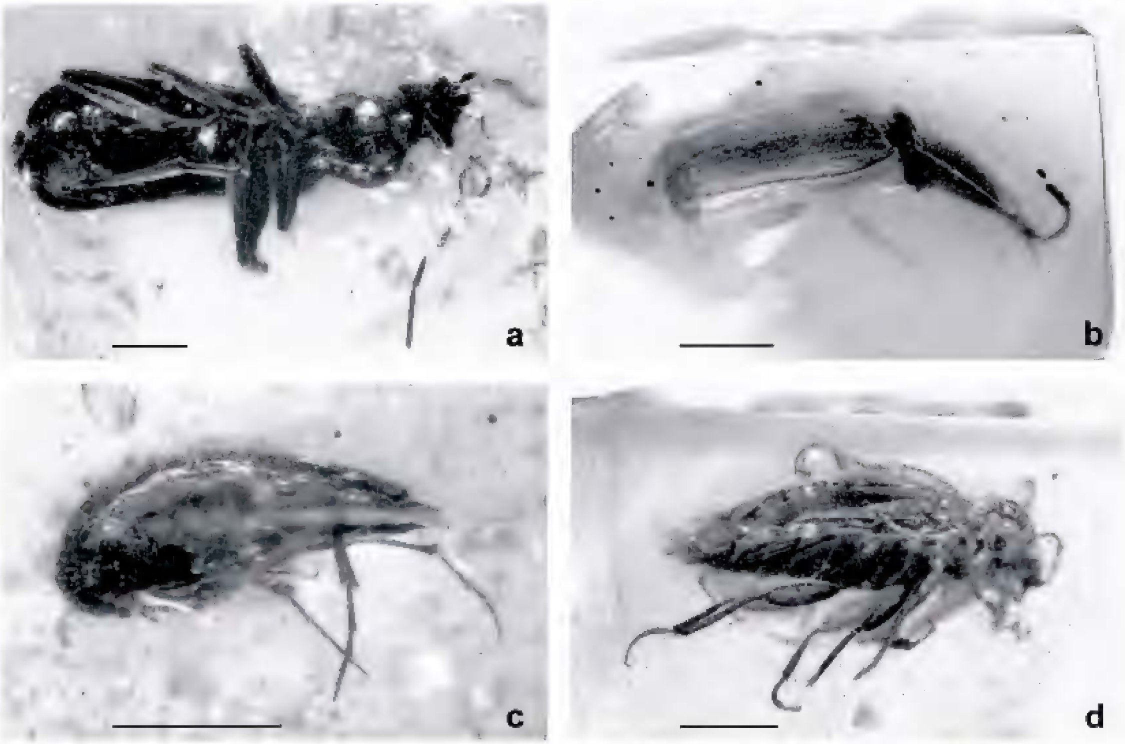

Fig. 31. Assorted Coleoptera in Burmese amber. **a.** Family indet., AMNH Bu257. **b.** Family indet., AMNH Bu284. **c.** Mordellidae, AMNH Bu363. **d.** Family indet., AMNH Bu367. Scales are 1.0 mm.

family as yet, so we present below only the most obvious and significant records.

Staphylinidae: Beetles of this family are known from the Triassic (Fraser et al., 1996) and Jurassic (Tichomirova, 1968), but the Burmese fauna is probably the most abundant and diverse Mesozoic one of this huge extant family (e.g., figs. 29b, c).

Lymexylidae: A unique record for Burmese amber is a single specimen in the AMNH (fig. 29e, f), the only Mesozoic fossil known for the Lymexylidae. Wheeler (1986) monographed the genera in the family and studied their phylogenetic relationships. By the impressive standards of present beetle diversity, the Lymexylidae is a very modest group, with only seven extant genera and about 50 species. The family, however, has been of considerable interest because of controversial relationships, largely due to their unusual long, soft bodies, reduced elytra, and many other derived features. Definitive assignment of the Burmese amber specimen to the pantropical genus *Atractocerus* is based on its extremely brachypterous elytra; short, spindle-shaped antennae; female maxillary palp organs; and lack of tibial spurs. Of the 23 described species, 14 occur in Asia. Wheeler (1986) concluded that there was little correspondence between phylogenetic relationships of lymexylid genera, their distributions, and geological relationships of the continents (“area cladograms”). He attributed the widespread distribution of *Atractocerus* to dispersal, and that it “may be later in origin” (Wheeler, 1986: 198). The new fossil establishes that *Atractocerus* is of sufficient age for its distribution to have been affected by continental drift. This is merely permissive evidence for tectonic vicariance, for even if past distributions of the genus were affected by drifting continents these may have been erased by dispersal. Phylogenetic relationships hypothesized by Wheeler are *Hylecoetus* + [(*Atractocerus* + *Lymexylon*) + all other genera], so a definitive Cretaceous species of *Atractocerus* is consistent with Crowson's (1981) suggestion of a Jurassic origin of the family.

ORDER HYMENOPTERA

Hymenoptera are relatively common inclusions in amber, including Burmese amber, but this is primarily true for the groups of smaller, parasitoid wasps. The NHML collection contains representatives of the Diapriidae, Embolemidae, Megaspilidae, Mymarommatidae, Pelecinidae, Scelionidae, Serphitidae, Evaniidae, Aulacidae (listed as Gasteruptiidae in Rasnitsyn and Ross, 2000), undetermined Chalcidoidea, and of the aculeate families Bethylidae, Tiphiidae, Formicidae, and Sphecidae. The AMNH collection contains representatives of all of these families except for the Tiphiidae, Pelecinidae, and Megaspilidae, while adding to this list records of Stigmaphronidae, Megalyridae, and Pompilidae. The families Serphitidae and Stigmaphronidae are significant stratigraphic indicators, as both families are known only from Cretaceous ambers.

It is not surprising that the Burmese amber inclusions are all apocritans, as symphytans are exceptionally rare in all Cretaceous ambers (specimens known only from Siberian, New Jersey, and Spanish ambers). The xylophagous symphytans are a paraphyletic assemblage of families from which the parasitoid Apocrita arose, specifically with the parasitic superfamily Orussoidea being the extant sister group to the Apocrita. Owing to the diversity of Mesozoic symphytans, particularly from the Upper Jurassic and Lower Cretaceous, and the association of most of them with trees, it is unusual that symphytans are actually rare in amber.

Among the non-aculeate lineages, it is little wonder that the Scelionidae are among the most abundant in Burmese amber. Scelionids (e.g., figs. 32a, b) are diverse and common in all Cretaceous amber deposits and typically outnumber all other Hymenoptera inclusions. Scelionids appear to have experienced their greatest diversity in the Mesozoic and dwindled in diversity during the Cenozoic. The presence of evaniids in Burmese amber, a group that is today exclusively parasitoids of cockroach oothecae, probably relates to the abundance of Blattodea in Burmese amber.

Pompilidae: The AMNH collection contains a single specimen of an enigmatic and remarkably autapomorphic pompilid (fig. 33f). The specimen is excellently preserved and exhibits some peculiar modifications of the head capsule that have no apparent functional significance (Engel et al., in prep.). Today pompilids are principally ectoparasitoids of spiders, although a few species develop on species of other arachnid orders. The family occurs throughout the world but primarily in the tropics. This is the oldest definitive record of the Pompilidae.

Formicidae: Among the most interesting aculeate Hymenoptera in Burmese amber are the ants (family Formicidae). Two genera and species have been described from the NHML collection (In. 19125 and In. 20182), and are the holotypes of †*Burmomyrma rossi* and †*Haidomyrmex cerberus*, respectively (Dlussky, 1996). †*Haidomyrmex* has mandibles unique for the Formicidae, and was described as belonging to the †Sphecomyrminae, the most primitive subfamily of ants and which is exclusively Cretaceous in occurrence (Grimaldi et al., 1997; Grimaldi and Agosti, 2000). The ocelli, mandibles, and scape were inconsistent with other sphecomyrmines, so Grimaldi et al. (1997) indicated only that †*Haidomyrmex* "may" be in this primitive subfamily, pending more conclusive evidence. †*Burmomyrma* is based on a fragmentary specimen, so relationships are uncertain. In the AMNH collection is another unusual ant (AMNH Bu014), which also has distinctive mandibles, a slight constriction between the first and second segments of the gaster (as in Ponerinae), and a gracile body with very long legs (fig. 33d). Another specimen, AMNH Bu351 (figs. 33e, 34), is a definitive sphecomyrmine, possessing the distinctively long second funicular segment (first flagellomere), but the plesiomorphically short scape. If Burmese amber is Cenomanian in age, as is hypothesized (see Discussion, below), these would be the oldest definitive ants.

Sphecoidea: The diversity of spheciform wasps in Burmese amber is remarkable (Antropov, 2000). This fact, plus the tropical paleoenvironment of Burmese amber, makes

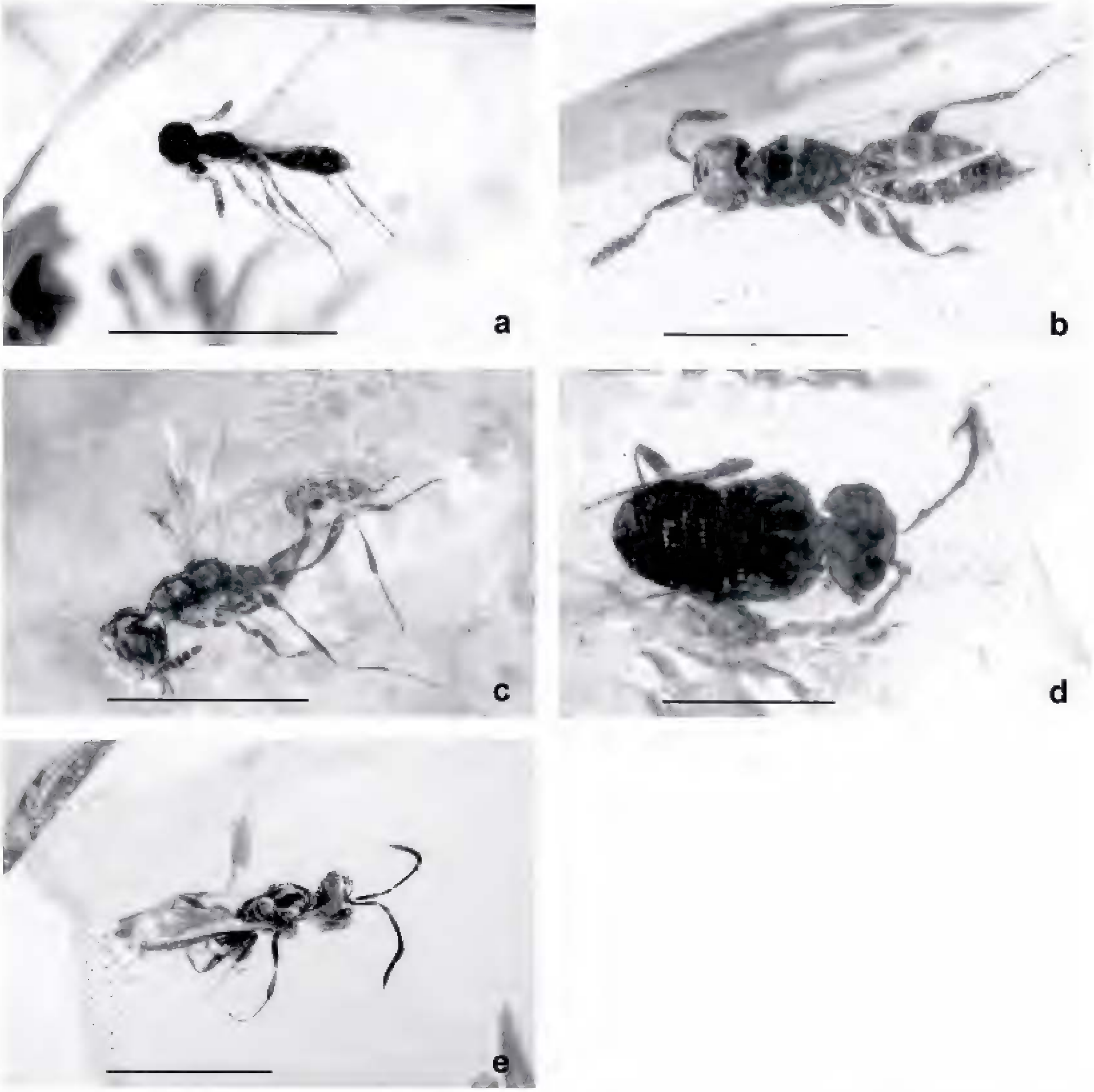

Fig. 32. Assorted Hymenoptera in Burmese amber. **a, b**: Scelionidae. **a.** AMNH Bu224. **b.** AMNH Bu282. **c.** Serphitidae, AMNH Bu313. **d.** Family indet., AMNH Bu049. **e.** Family indet., AMNH Bu089. Scales are 1.0 mm.

the possibility quite tantalizing of discovering a fossil bee (Apoidea) in this amber. Presently, the only definitively Cretaceous bee is a single specimen preserved in putatively Maastrichtian-aged amber from New Jersey (Michener and Grimaldi, 1988; Engel, 2000). The spheciforms in Burmese amber (e.g., fig. 33c) consist of forms intermingling traits of several subfamilies, as well as definitive representatives of the Ampulicinae and Pemphrodoninae. No crabronines (i.e., the lineage most closely related to the bees [Prentice, 1998; Melo, 1999]) are known from Burmese amber.

†Serphitidae: The presence of this family and the †Stigmaphronidae, which are known only from Cretaceous ambers, provide some of the most compelling evidence for the Cretaceous age of Burmese amber.

The †Serphitidae are an extinct lineage of parasitoid wasps allied to the Proctotrupoidea, Mymmaromatoidea, Chalcidoidea, and

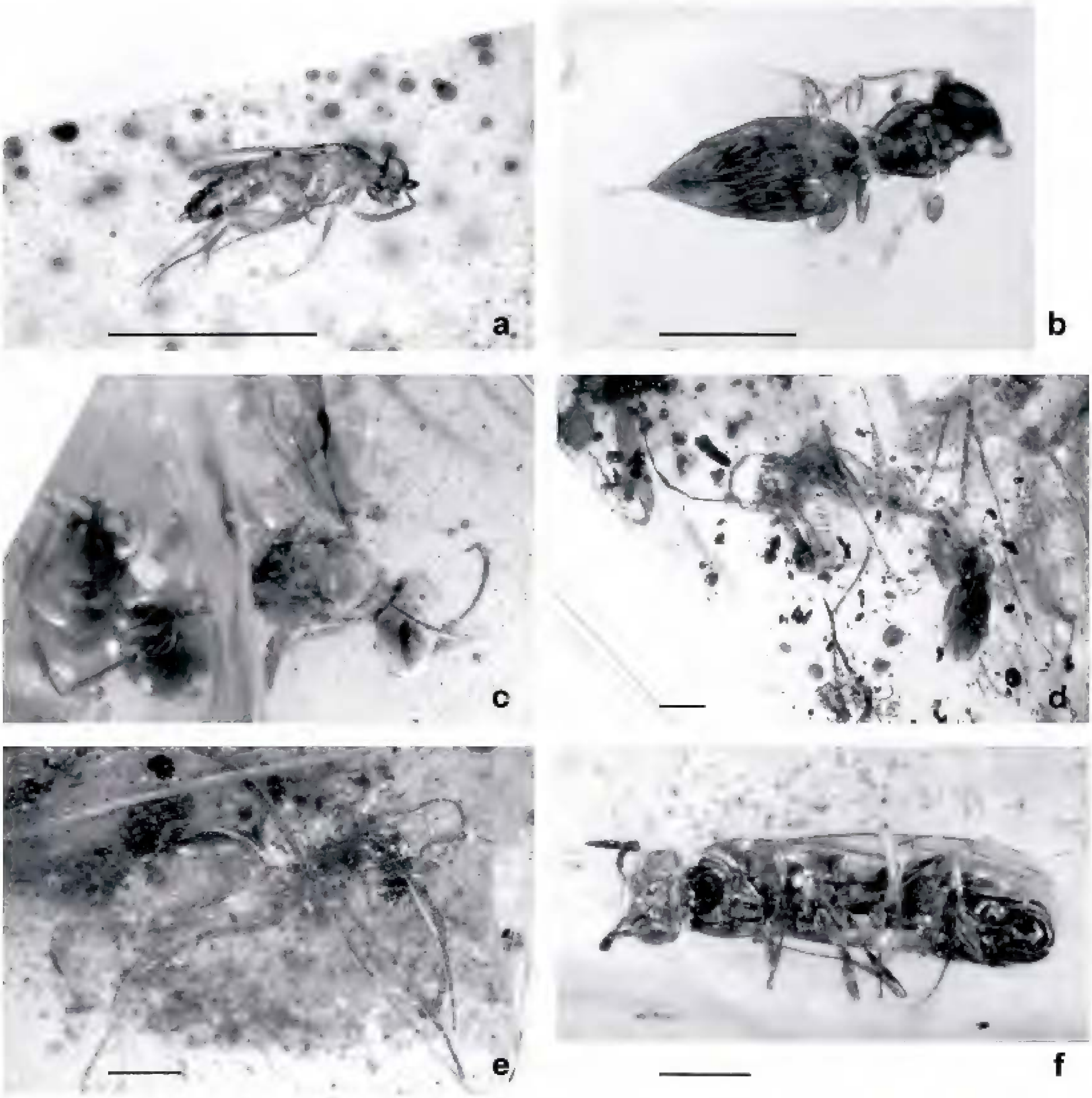

Fig. 33. Apocrita, mostly aculeate (**b-f**), Hymenoptera in Burmese amber. **a.** Stigmaphronidae, AMNH Bu677. **b.** Bethylidae, AMNH Bu047. **c.** Sphecidae. **d, e**: Formicidae. **d.** Ponerinae, n. gen., AMNH Bu014. **e.** *Sphecomyrma* n. sp. (Sphecomyrminae), AMNH Bu351. **f.** Pompilidae, AMNH Bu051. Scales are 1.0 mm.

Platygastroidea. Serphitids are entirely restricted to the Mesozoic and fossils are known only in Cretaceous amber from Siberia, Canada, New Jersey, and northern Spain. The family intermingles traits of several lineages and has been difficult to place in a phylogenetic framework but is perhaps nearest the base of the platygastroids, and with this group as sister to the Mymarommatoidea + Chalcidoidea. In fact, owing to some distinctive characters present in both mymarommatoids and serphitids, the two were once considered a single family (e.g., Kozlov and Rasnitsyn, 1979). In a forthcoming work (Engel et al., in prep.) the serphitids are assigned to a separate superfamily, Serphitoidea near the Platygastroidea, Mymarommatoidea, and Chalcidoidea. The hosts of serphitids are entirely unknown. The discovery of 22 serphitid specimens in Burmese

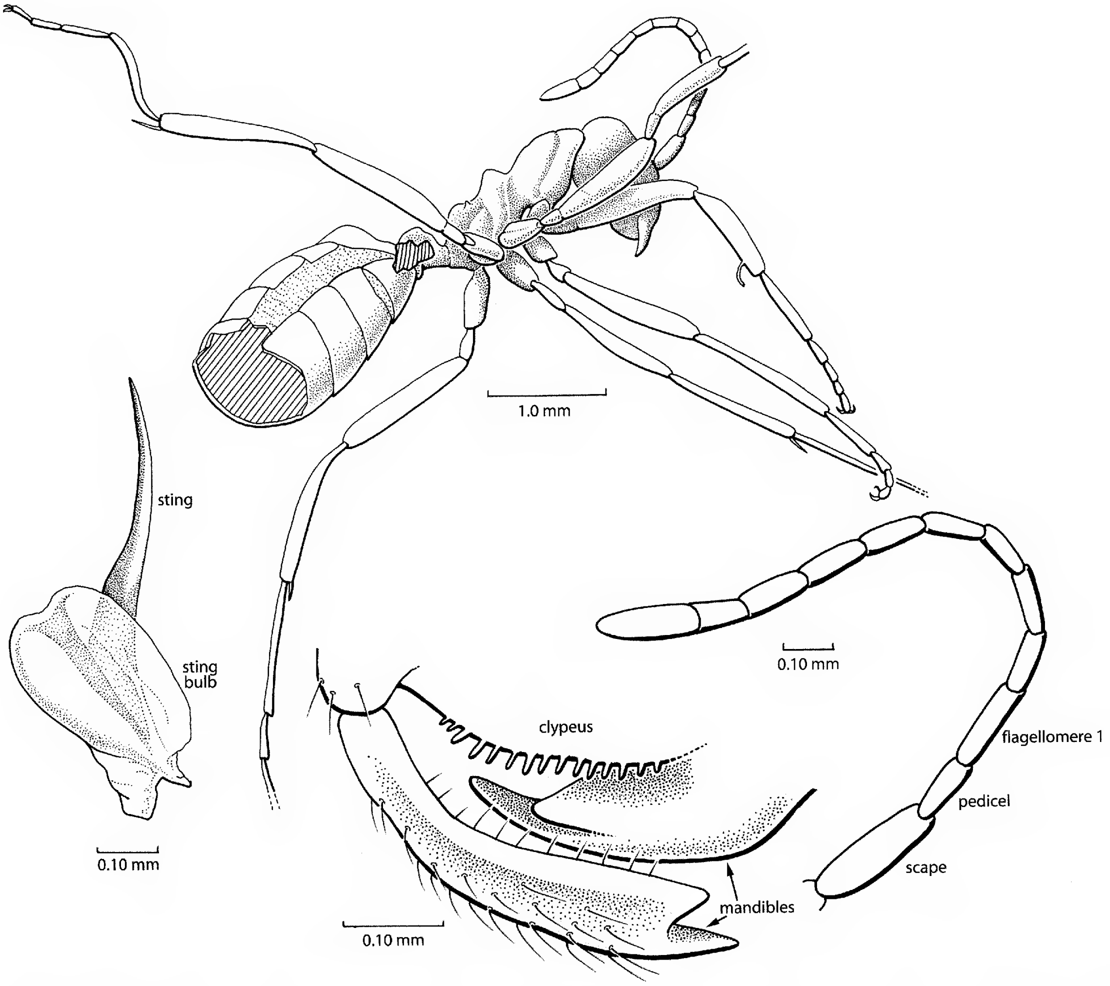

Fig. 34. AMNH Bu351, *Sphecomyrma* sp. (worker), right lateral habitus and details of antenna, mouthparts, and disarticulated sting.

amber in the AMNH, plus two in the NHML collection (one figured by Ross, 1997), strongly reinforces the Cretaceous age of this fossil resin.

†Stigmaphronidae: Burmese amber specimens in this Cretaceous family are unique to the AMNH collection. They are considerably rarer than Serphitidae in Burmese amber, with only two specimens known (AMNH Bu671a, 677). Like the serphitids, the family consists of little-understood parasitoids, known from Cretaceous amber of Siberia, New Jersey, Canada, and Lebanon. Stigmaphronids are related to the superfamily Ceraphronoidea and, in fact, one species was originally assigned to the Ceraphronidae before being recognized as a stigmaphronid (e.g., Muesebeck, 1963). Like the †Serphitidae, the stigmaphronids are best classified in their own superfamily, sister group to the Ceraphronoidea (Ceraphronidae and Megaspilidae).

ORDER DIPTERA

Diptera are the most common and diverse organismal inclusions in ambers, so it is not surprising that so many significant new records and taxa have been found in Burmese amber. As in most other ambers, Cecidomyiidae, Ceratopogonidae, Chironomidae, and Psychodidae dominate in Burmese amber (8% of all inclusions, NHML coll.; 20% of all inclusions, AMNH coll.). Full appreciation of the diversity in each of these families requires detailed, comprehensive study of species and genera, similar to those done on the Ceratopogonidae in Cretaceous ambers (Borkent, 1995; 1996; 2000a, 2000b; Szadziewski, 1994, 2000; Szadziewski and Arillo, 1995; Szadziewski and Schlüter, 1992) and on Cretaceous Brachycera (e.g., Grimaldi and Cumming, 1999).

Blephariceridae: A beautifully preserved male specimen, AMNH Bu310 (fig. 35b), is the only Cretaceous amber fossil of the family. Jarzembowski (1978) reported, but did not formally describe, a compression-fossilized blepharicerid, from the Eocene-Oligocene of the Isle of Wight. Evenhuis (1994) cited Alexander (1958), regarding putative blepharicerids described by Cockerell from several North American deposits as "questionably" in this family, being perhaps Tipulidae or Bibionidae. Hogue (1981) adopted Alexander's decision. The only other blepharicerid fossil is from the Turonian- aged Ola' Formation of Magadan (Upper Cretaceous), *Megathon zwicki* (Lukashevich and Shcherbakov, 1997). Based on wing venation *Megathon* appears related to the living genera *Agathon* and *Bibiocephala*. Blephariceridae is a small extant family, with the habits "confined to areas in the immediate vicinity of rapidly flowing streams" (Hogue, 1981: 193). Larvae are highly modified for clinging to the smooth surfaces of rocks in streams, where they graze on algae and diatoms. Though known principally in temperate areas, blepharicerids also occur throughout the tropics, but usually only in mountainous regions where the streams are cool and clear. Thus, this is an unusual fossil record.

New genus near *Valeseguya* (fig. 35f): *Valeseguya* is a very unusual genus that has been tentatively placed in the Anisopodidae (s.l.) by Colless (1990) and Grimaldi (1991). Its relationships are actually obscure, and may not be at all with the Anisopodidae; it and a new one from Burmese amber probably represents a new family of Diptera. The genus was originally discovered on the basis of two living males from Queensland, Australia, *Valeseguya rieki* (Colless, 1990), which is the only material of the genus known thus far from the extant fauna. Soon thereafter, *V. †disjuncta* was described from a large series of males and females in Miocene amber from the Dominican Republic (Grimaldi, 1991). *Valeseguya †disjuncta* is not particularly rare in Dominican amber, and, indeed, more is known of the extinct than the living species. Females of *V. †disjuncta* are unique in Diptera by possessing a long, fine ovipositor with two valves. The new fossil, AMNH Bu108, also possesses this type of ovipositor (fig. 35f), even with the same bulbous base and bifid tips of the valves. The Burmese fossil, however, is distinctly plesiomorphic relative to the extant and the Miocene species and represents a new genus closely related to the enigmatic Tertiary genus. It has eyes without medial emargination; 15 (vs. 12/14) flagellomeres; only the basal flagellomeres are serrate; and it has a plesiomorphic, more generalized venation (veins M_1 and M_2 have a common stem rather than being connected to the basal cell; the basal cell is much larger; and Sc is complete or nearly so).

Mycetophilidae sensu lato: "Fungus gnats", often classified in six families in the Mycetophiloidea, occur in forested environments in tropical and temperate regions. Larvae of most feed on fungal mycelia, though some are predatory. Rasnitsyn and Ross (2000) recorded 15 specimens in the NHML collection, or slightly more than 1% of all arthropod inclusions; a very similar proportion of these flies is found in New Jersey amber (Grimaldi et al., 2000a). In the AMNH collection of Burmese amber mycetophilids comprise nearly 5% of all arthropod inclusions, with at least eight genera and ten species in the Diadocidiidae, Lygistorrhinidae, and Mycetophilidae s.s. (Vladimir Blagoderov, personal commun.)(e.g., fig. 35e), though much of the material is still unstudied. The lygistorrhinid primitively possesses a very small proboscis; most living species and an Eocene species possess long mouthparts (the exception being *Seguyola*, which has lost the proboscis). Mycetophiloids are known from the Jurassic, but as extinct families only; living families and some genera appeared in the Cretaceous. The abundance of Mycetophilidae s.l. in Burmese amber is approximately the abundance seen in Baltic amber (see catalogue by Evenhuis, 1994).

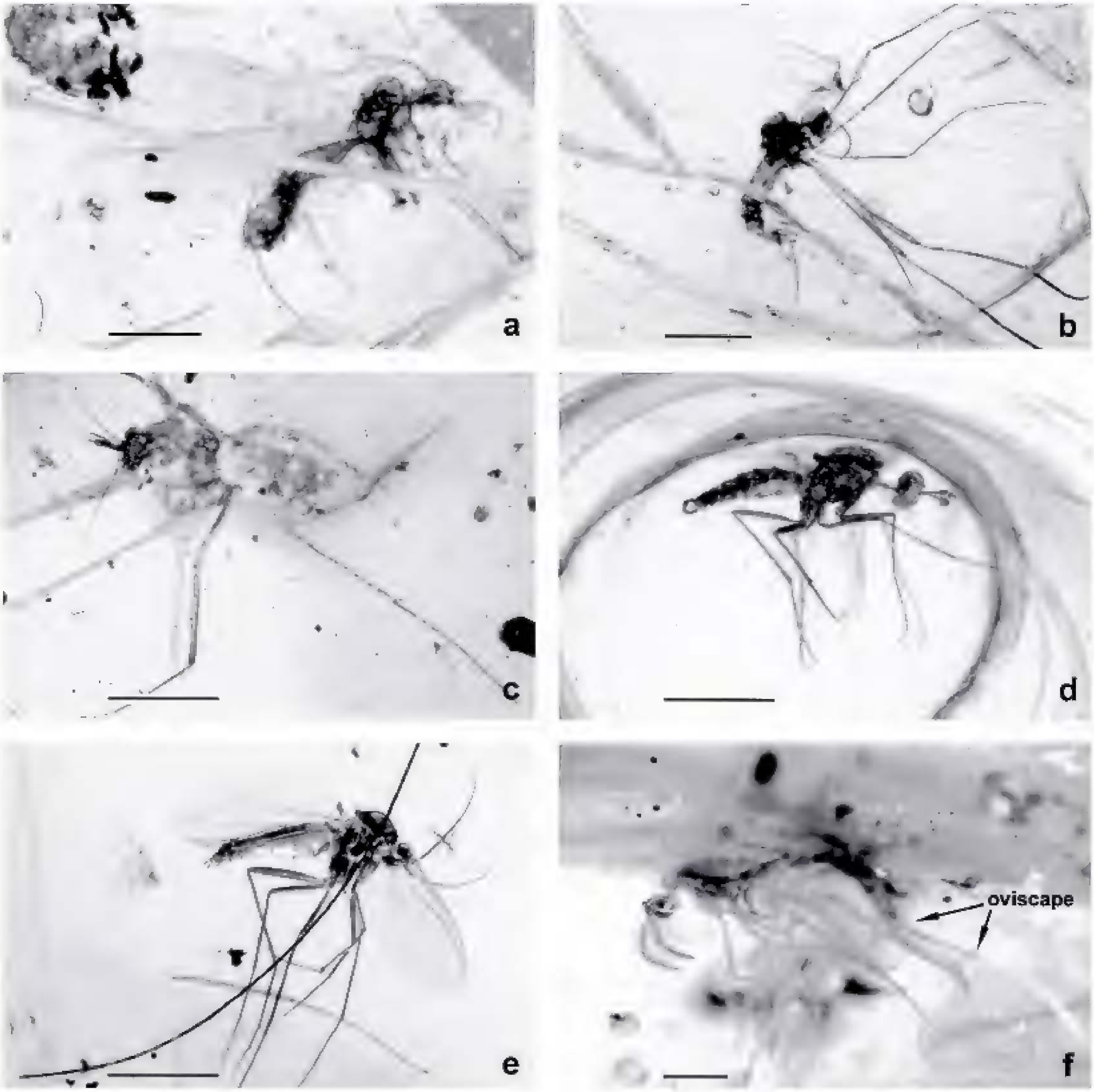

Fig. 35. Assorted nematocerous Diptera in Burmese amber. **a.** Tipulidae, AMNH Bu003. **b.** Blephariceridae, n. gen., AMNH Bu310. **c.** Culicidae, n. gen., AMNH Bu032. **d.** Archizelmiridae, AMNH Bu178. **e.** Mycetophilidae (Macrocerinae), AMNH Bu314. **f.** New genus near *Valeseguya*, AMNH Bu108. Scales are 1.0 mm.

Culicidae: The significance of mosquitoes as vectors of some devastating diseases makes any fossils of them of interest. Evenhuis (1994) reviewed the fossil record of the Culicidae, all substantiated records of described taxa being Cenozoic. Jurassic (compression) fossils attributed to the Culicidae by Bode and Hong are of highly questionable identity. A significant, largely undescribed diversity of Culicidae occurs in Dominican amber, but these belong to modern genera, subgenera, and even species groups. There are only two Cretaceous Culicidae known: one in Canadian amber (Pike, 1995; Poinar et al., 2000), and a new specimen in Burmese amber. The Canadian amber specimen, †*Paleoculicis minutus*, is believed to be closer to the Culicinae than to the Anophelinae or Toxorhynchinae.

The new Burmese specimen, AMNH

Bu032 (figs. 35c, 36), is the most primitive known Culicidae, and perhaps reflects an age significantly older than the Canadian amber specimen. Unlike all other culicids, the Burmese specimen lacks scales on the wing veins, margin of the wings, or anywhere on the body (instead there are setae). Wing venation is rather similar to that of primitive Culicidae and to Chaoboridae (fig. 36), including several recently described in Burmese amber from the NHML, though there are various, small differences with the latter. This is somewhat expected, given the consistent grouping of Chaoboridae + Culicidae as sister groups on the basis of morphological (Wood and Borkent, 1989; Saether, 2000) and molecular (Pawlowski et al., 1997; Miller et al., 1997) phylogenetic studies. Venational similarity between the Burmese fossil culicid and Chaoboridae, thus, is probably symplesiomorphic resemblance.

Most significant is the long proboscis in AMNH Bu032 (fig. 36). Though shorter than in any living culicid, its proboscis is considerably longer than the head, with very long palps that are at least equal to the length of the labium + labellum (this is difficult to determine, since the latter structures are curved). All Chaoboridae have proboscides considerably shorter than the head. The specimen is incompletely preserved, with most of three legs, the entire head, and the right wing preserved. Most of the thorax and abdomen are preserved as an impression on the surface of the amber, though there is enough of the abdomen to determine that the gut contains a mass of granular material, probably a blood meal.

†Archizelmiridae: This is a Mesozoic family, probably basal within the Sciaroidea, which was described on the basis of a wing in rocks from the Upper Jurassic of Karatau (Rohdendorf, 1962). Fortunately, the wing venation is distinctive, consisting of heavy C and R veins, with C ending abruptly at the apex of R_{4+5}; a large basal cell, to which parallel bases of M, CuA_1 and CuA_2 connect; and incomplete anal veins. Though not reported, the group also occurs in Lower Cretaceous sediments from Baissa (Transbaikalia) and the Upper Jurassic of Shara-Teg (Mongolia). The distinctive venation, plus several new species and genera we have examined in New Jersey and Lebanese amber, allowed identification of an unusual archizelmirid species in Burmese amber, based on seven partial and complete specimens in the AMNH. The antenna of the Burmese amber archizelmirid is exceptional among nematocerous Diptera, being remarkably convergent to the aristate antenna of higher Brachycera, especially Eremoneura. Inspection under high (160–400×) magnification, though, reveals the thick, conical base of the antenna to be a compact fusion of 12 flagellomeres, distinguished by slight annuli. The arista is the last one or two flagellomeres, extremely elongated. Interestingly, the antenna of the Karatau species shows little differentiation of flagellomeres; that of the Lebanese amber archizelmirid has flagellomeres strongly but evenly tapered apicad (moreso than is typical in Nematocera); and the New Jersey amber species has an abruptly tapered flagellum, with the apical flagellomere being very thin and equal in length to the preceding eight flagellomeres. This morphocline or transformation series corresponds to the stratigraphic chronology of the species. The Burmese amber archizelmirid is an excellent biostratigraphic indicator of the Cretaceous age of this amber. A separate article discusses Archizelmiridae in detail.

Suborder Brachycera

Recent comprehensive study of Brachycera in Cretaceous ambers (Grimaldi and Cumming, 1999) greatly facilitates study and interpretation of the Burmese fauna. Cretaceous ambers, for example, contain an impressive diversity of Empidoidea (e.g., figs. 38–40), which fossilize poorly in sediments. These ambers also have preserved the best record of earliest Cyclorrhapha. Here we discuss only the taxa of greater stratigraphic or systematic significance.

Acroceridae: AMNH Bu332 (fig. 37c) contains two complete, small specimens of an unusual new genus of "hump-backed" flies, family Acroceridae. This is a small extant family of approximately 50 genera and 500 species, which are larval parasitoids of spiders. Some genera have vestigial mouthparts; others have extremely long proboscides, which they use for feeding from deep

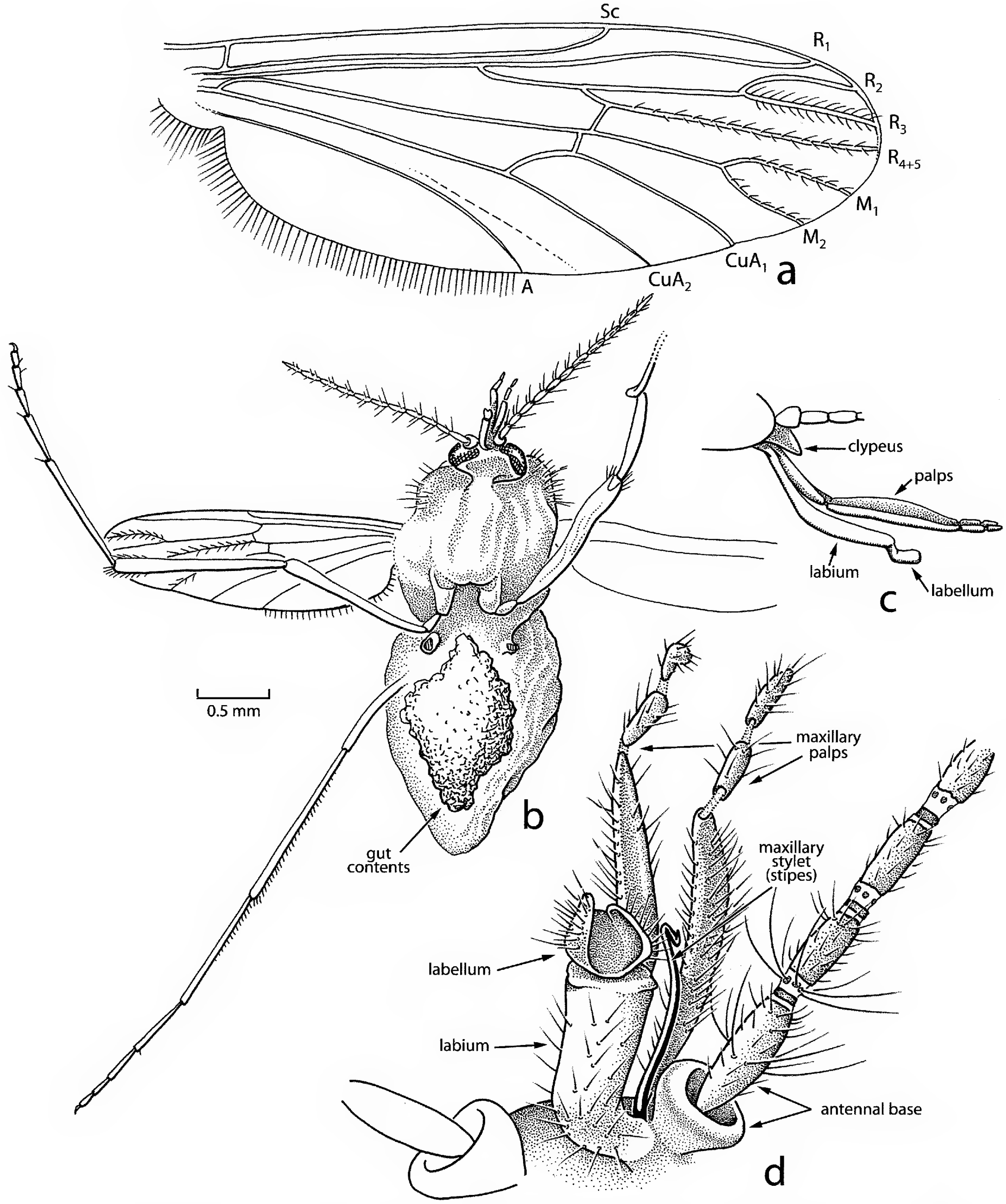

Fig. 36. AMNH Bu032, Culicidae. Ventral habitus and details of proboscis, antenna, and wing.

flowers. These two specimens reveal typical acrocerid features of a large head with large eyes, minute antennae, a strongly humpbacked scutum, very large calypters, finely pleated wing membrane, and various features of wing venation. They have very small mouthparts. Some aspects of the rather complete wing venation are unique for acrocerids, though venation of the Eocene genus †*Glaesoncodes* (in Baltic amber) is readily

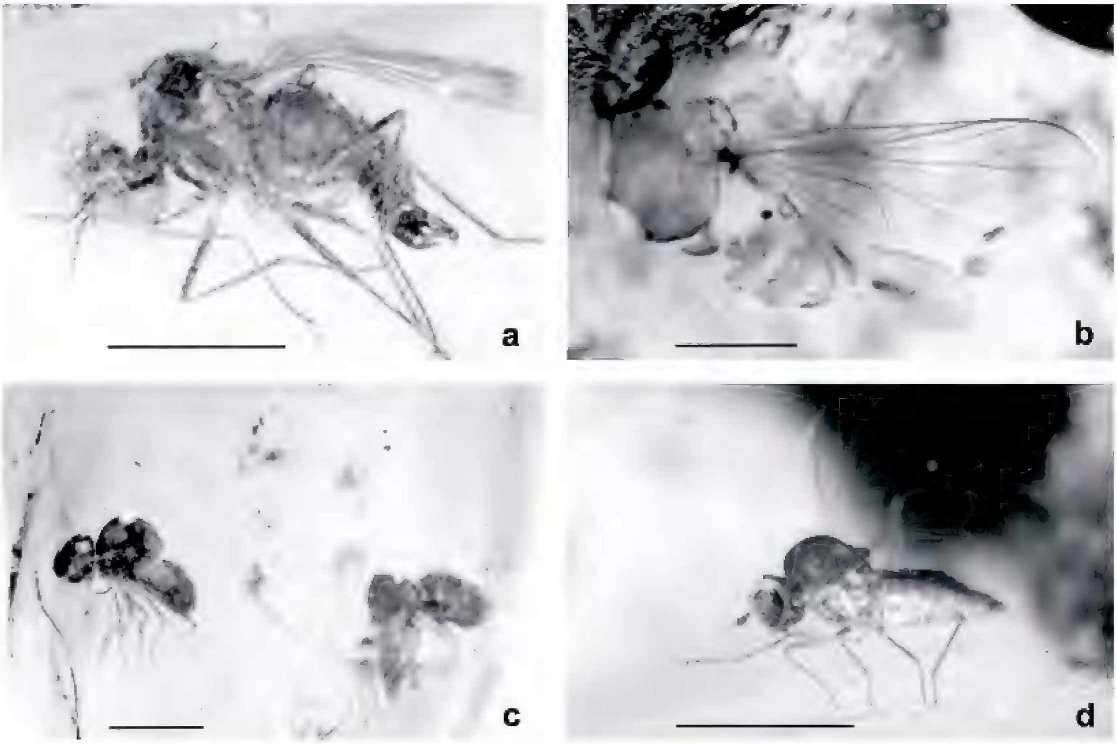

Fig. 37. Assorted lower Brachycera (Diptera) in Burmese amber. **a.** Rhagionidae (male), AMNH Bu128. **b.** Rhagionidae (*Bolbomyia* group), AMNH Bu039. **c.** Acroceridae, n. gen. AMNH Bu332. **d.** *Hilarimorphites* (Hilarimorphidae), AMNH Bu098. Scales are 1.0 mm.

derivable from this Cretaceous genus. In †*Glaesoncodes*, for example, R_{2+3} is lost, the anterior radial cell is very thin, the vein between the discal and posterior radial cells is barely developed, and R_4 and R_5 are widely divergent (as in most modern species), The oldest acrocerid appears to be †*Juracyrtus kovalevi* (Upper Jurassic: Karatau). The original description of †*Juracyrtus* indicates it had a long proboscis, though not well preserved. However, wing venation of †*Juracyrtus* is not of the hovering type, which all long-proboscid acrocerids have, so the putative proboscis of †*Juracyrtus* is probably extraneous material (Grimaldi, 1999). Wing venation of AMNH Bu332 is more complete than in †*Juracyrtus*, and it also possesses several venational features apomorphic to †*Juracyrtus*.

Hilarimorphidae: AMNH Bu098 (fig. 37d) is the third Mesozoic record of the family, the first being from Turonian-aged amber from central New Jersey. The New Jersey and Burmese amber species belong to †*Hilarimorphites* (four species occurring in New Jersey amber). The other Mesozoic hilarimorphid is †*Apystomima*, from the Upper Jurassic Karabastau Formation of Karatau, Kazakhstan (Mostovski, 1999b). Venation of the two genera is very similar, but with †*Apystomima* having peculiarly small wings, and apomorphically with long cerci. AMNH Bu098 is additional evidence for the mid-Cretaceous age of Burmese amber. Hilarimorphidae today comprise 33 mostly Nearctic species, perhaps closely related to the Bombyliidae; alternatively they are the sister group to the Eremoneura (Empidoidea + Cyclorrhapha; D. Yeates, unpubl. data).

Empididae: These small, predatory flies are the most abundant and diverse Brachycera in Cretaceous ambers, including Burma (e.g., figs. 38–40). Among the various genera and species represented in Burmese amber, three are particularly significant. †*Alavesia* (figs. 40a, b) is a distinctive genus of hybo-

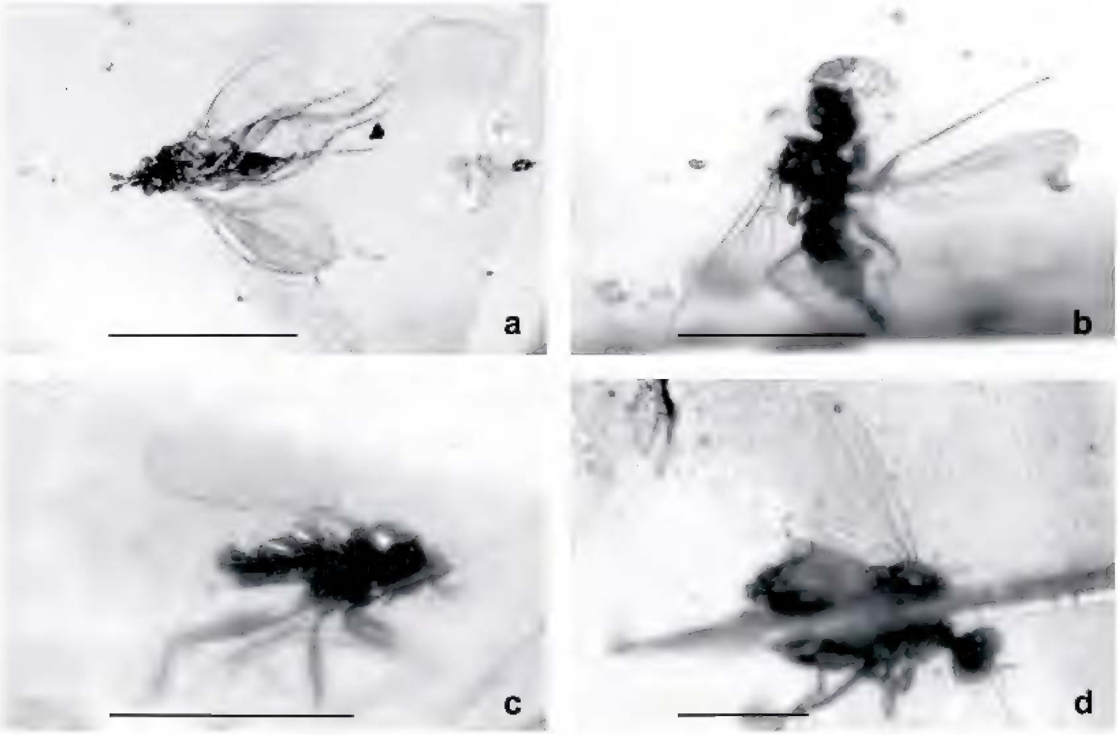

Fig. 38. Assorted Empidoidea in Burmese amber. **a.** Empididae, n. gen. with highly reduced venation, AMNH Bu339. **b.** Empididae, near *Cretoplatypalpus*. **c.** Empididae, near *Cretoplatypalpus*, AMNH Bu169. **d.** Hybotidae, n. gen. near *Meghyperus*, AMNH Bu172. Scales are 1.0 mm.

tine recently described from Aptian-aged amber of northern Spain (Waters and Arillo, 1999). This genus has a very large first flagellomere; a very small, three-segmented arista; and venation with a distinctive, small dm cell and widely divergent veins M_1-CuA_1. †*Nemedromia* is known from one species in New Jersey amber and two in Canadian amber (Grimaldi and Cumming, 1999), with a distinctive new species in Burmese amber. Besides AMNH Bu169 (fig. 38c), †*Cretoplatypalpus* is known from two species: one in Siberian amber (Dolganian Formation: Cenomanian), the other in Canadian amber (Grimaldi and Cumming, 1999).

Dolichopodidae sensu lato: We are including within the large family of long-legged flies the Microphorinae, since detailed morphological studies indicate they are the sister group or stem group to the Dolichopodidae (Chvála, 1983; Ulrich, 1984; Woodley, 1989; J. Cumming and B. Sinclair, unpubl. data). Microphorinae have traditionally been placed within the Empididae or in a family of their own. Although there are only five genera and approximately 70 species of extant Microphorinae, they are strikingly diverse in Cretaceous amber (Grimaldi and Cumming, 1999; unpubl. data), suggesting that the present fauna is relict. An exceptional new taxon of microphorine is represented by AMNH Bu029 and Bu175 (figs. 40c, d). This species has grossly inflated fore femora and tibiae bearing rows of spines, and was probably raptorial like *Ochthera* (Ephydridae) and some genera of Empididae are today. Obscure relationships among living and extinct microphorines precludes estimates of the affinities of the Burmese amber microphorines.

†Chimeromyia: This is an unusual genus that probably deserves a family of its own, possessing features of the Empididae and the Cyclorrhapha (Grimaldi and Cumming, 1999). It is known thus far only from the Lower Cretaceous, based on three species in Lebanese amber and one species in Alava amber. The type genus is distinctive for various veinal reductions or losses (M_2, mcu and

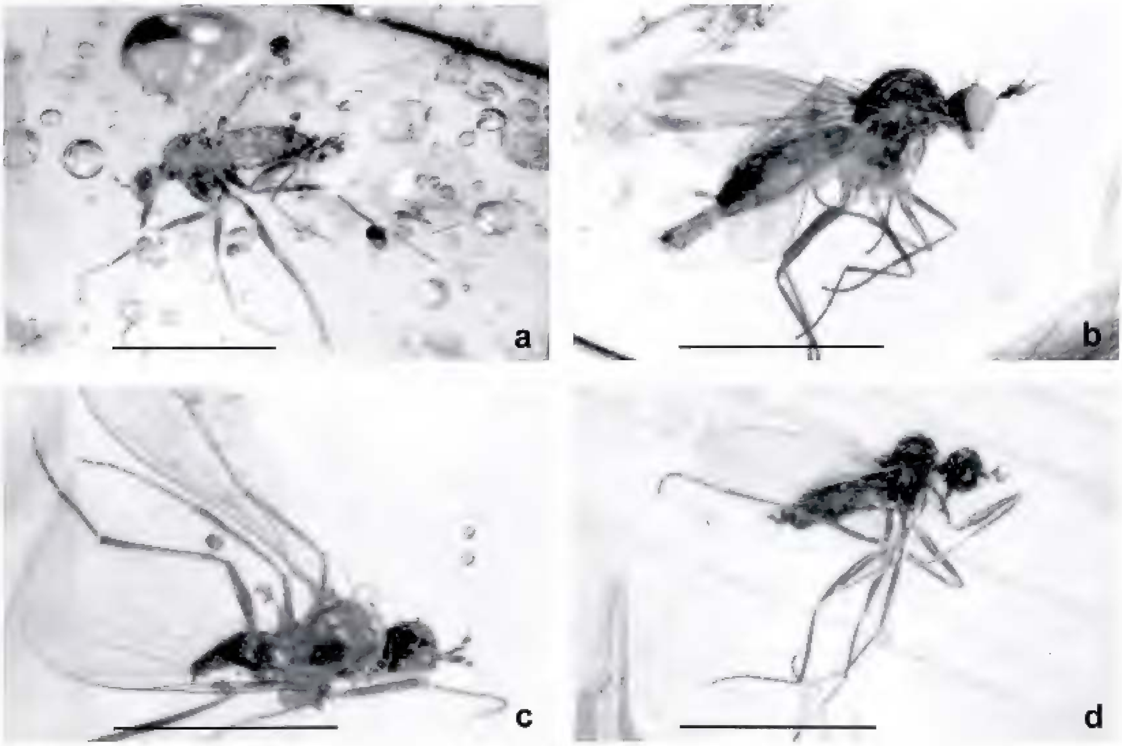

Fig. 39. Assorted Empididae in Burmese amber. **a.** Genus indet. **b.** Trichopezinae, AMNH Bu006. **c.** Genus indet., AMNH Bu339. **d.** Genus indet., AMNH Bu052.

cell d, CuA_2, A, and an anal lobe). Recently, a plesiomorphic new genus has also been found in Alava amber. The new Burmese amber †*Chimeromyia* (figs. 41d, e) is another important index taxon, the age of which would be consistent with a Cenomanian age of Burmese amber.

Phoridae: †*Prioriphora* and several related genera of the most primitive phorids (e.g., †*Euliphora*) occur exclusively in Cretaceous ambers, from Siberia, Canada, New Jersey (these reviewed by Grimaldi and Cumming, 1999), Alava (Arillo and Mostovski, 1999), and Burma (32 specimens in the AMNH: figs. 41a–d). Rasnistyn and Ross (2000) listed "Phoridae" but no generic determination for specimens in the NHML; examination of the specimens by DG indicates they are also †*Prioriphora*. This genus at present is not defined by any apomorphic features (Grimaldi and Cumming, 1999), and may in fact represent a paraphyletic stem-group that is ancestral to the large extant family of true Phoridae, some 5,000 species. Modern subfamilies and genera of Phoridae proliferated in the Tertiary. Occurrence of one or more new species of †*Prioriphora* in Burmese amber is additional evidence for the Cretaceous age of Burmese amber.

CONCLUSIONS

BIOSTRATIGRAPHIC CHRONOLOGY: There is now little doubt about the Cretaceous age of Burmese amber. This is partly revealed by primitive new species groups, like genera, of Zoraptera; Embiidina; Aradidae, Hydrometridae, and Cimicomorpha near Cimicidae (Heteroptera); Lymexylidae (near *Atractocerus*: Coleoptera); and Acroceridae, Culicidae, Lygistorrhinidae, and other Diptera. Many groups still require examination, particularly Amphiesmenoptera (Trichoptera + Lepidoptera; e.g., fig. 42). The only group of surprisingly derived status in the Burmese amber are the kalotermitid termites (which are still quite primitive compared to the "higher" termites Rhinotermitidae and Termiti-

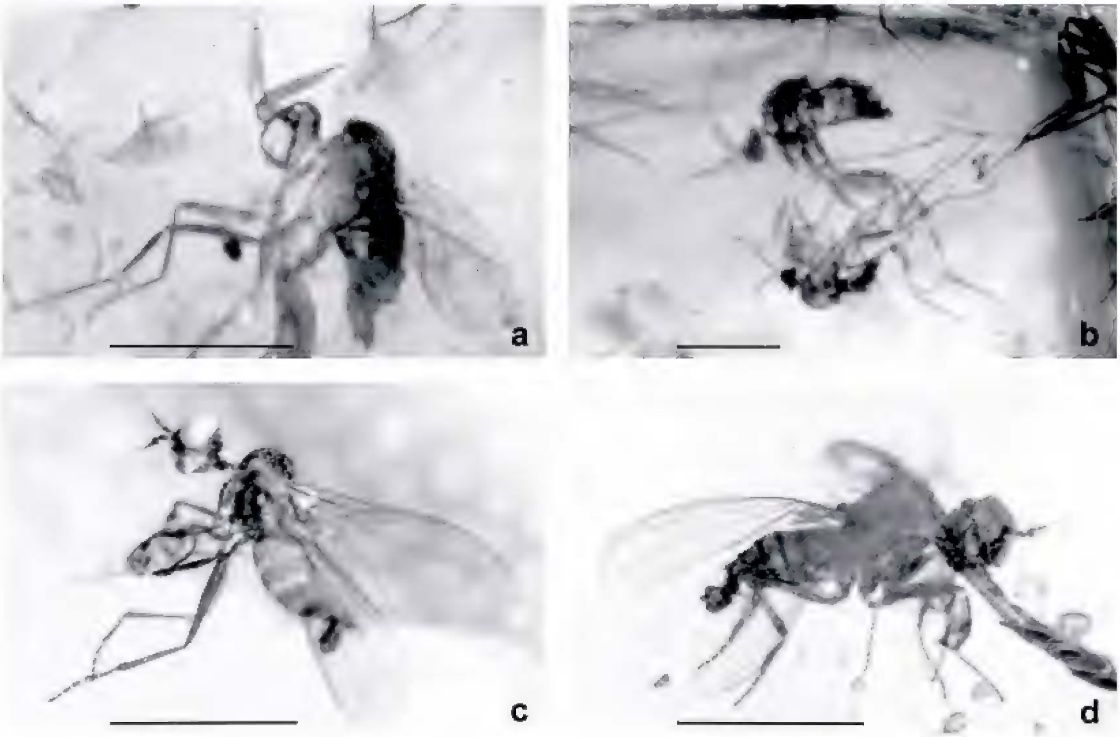

Fig. 40. Empidoidea in Burmese amber. **a, b**: Hybotidae: *Alavesia* n. sp. **a.** AMNH Bu496. **c, d**: Raptorial males of n. sp. of Microphorinae (Dolichopodidae s.l.). **c.** AMNH Bu175. **d.** AMNH Bu029. Scales are 1.0 mm.

dae), and a probable rhinotermitid in the NHML collection. Other evidence provides an estimate for age within Cretaceous epochs.

Figure 43 summarizes the stratigraphic distribution of various Cretaceous insect taxa. This is a minimal sampling, since there are many arthropod taxa that have not been studied sufficiently or at all, which might allow additional chronological inference. Comparing exclusively Mesozoic taxa in Burmese amber with their occurrence in other, well-dated, Late Mesozoic deposits (especially amber), Burmese amber was found to contain an interesting mix of paleofaunal elements from the Upper and Lower Cretaceous. Among the older, Lower Cretaceous (even Jurassic-aged) elements are the †Mesoraphidiidae (Raphidioptera), †Protopsyllidiidae (Hemiptera), and in the Diptera, †Archizelmiridae, †*Chimeromyia*, and †*Alavesia* (Hybotidae; see discussion and references under each of these). The first two families are similar in their occurrence throughout most of the Mesozoic, with the most recent occurrences being in the New Jersey amber. †Archizelmiridae are known from Upper Jurassic and Lower Cretaceous rocks, and in amber from the Lower Cretaceous of Lebanon (Neocomian) and Upper Cretaceous of New Jersey (Turonian). †*Chimeromyia* and †*Alavesia* occur exclusively in Lower Cretaceous ambers, as well as in Burmese amber.

Insect taxa found in Burmese amber that are of intermediate or extensive stratigraphic occurrence in the Cretaceous are the †Tajmyraphididae (Aphidoidea: Sternorrhyncha), †*Hilarimorphites* (Diptera: Hilarimorphidae), and the extinct hymenopteran families †Serphitidae and †Stigmaphronidae. With the exception of †*Hilarimorphites* and a related Jurassic genus, they are known entirely from ambers spanning the Cretaceous from Lebanon to Canada (the latter Campanian). †*Hilarimorphites* has so far been found only in New Jersey and Burmese ambers. Burmese amber also contains elements that are exclusively Upper Cretaceous: the primitive ant

Fig. 41. Assorted eremoneuran Diptera in Burmese amber. **a-c**: *Prioriphora* sp. (Phoridae). **b.** AMNH Bu296. **c.** AMNH Bu005. **d-e**: *Chimeromyia* n. sp. **d.** AMNH Bu298. **e.** AMNH Bu352. **f.** Sciadoceridae n. gen., AMNH Bu499. Scales are 1.0 mm.

genus †*Sphecomyrma*, the empidoid fly genera †*Nemedromia* and †*Cretoplatypalpus*, and the most primitive phorid fly genus, †*Prioriphora*.

Based on the distributions of these index taxa, it is likely that the Burmese amber is mid-Cretaceous in age, approximately Turonian to Cenomanian. This estimate is consistent with the apparently Cenomanian-aged strata that are in close proximity to the amber deposits in northern Burma (summarized by Zherikhin and Ross, 2000). We predict that those strata will eventually reveal the source of Burmese amber.

TAXONOMIC DIVERSITY: Abundance of arthropod groups in the NHML and AMNH collections of Burmese amber is disproportionate, with at least 13 ordinal-level taxa having proportions that differ 3–4 fold (fig. 44). There are five taxa heavily represented in the NHML collection (Rasnitsyn and Ross, 2000), due to numerous individuals in

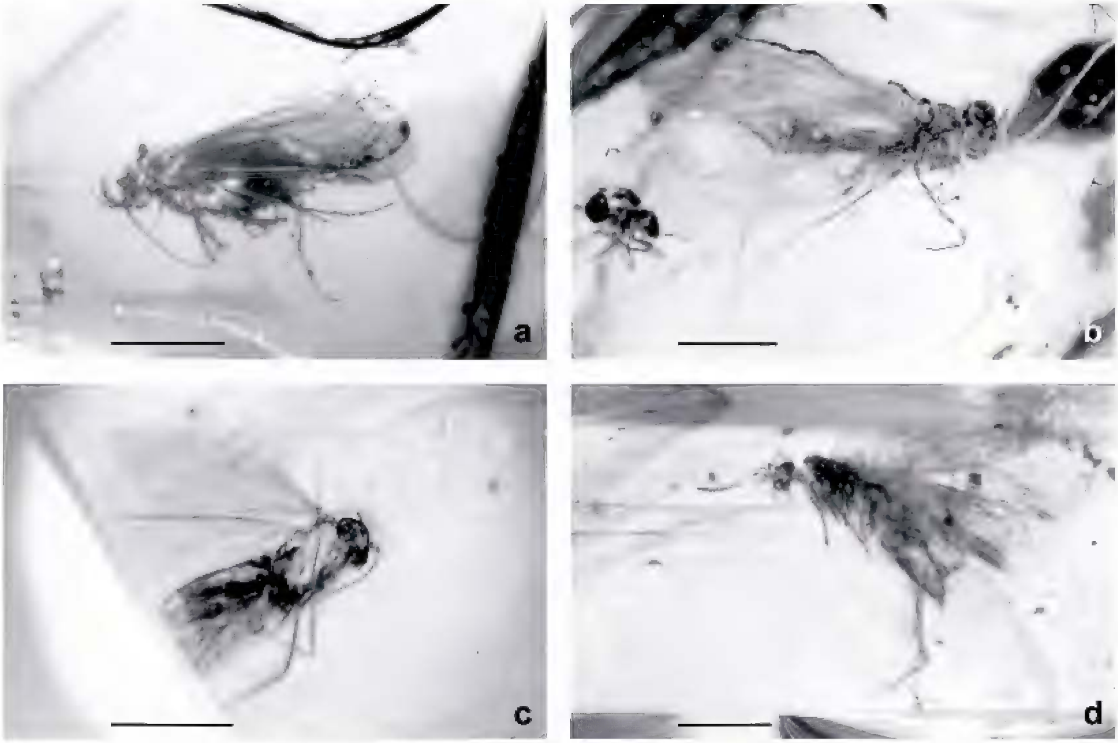

Fig. 42. Assorted Amphiesmenoptera in Burmese amber. **a, b**: Trichoptera, families indet. **a.** AMNH Bu128. **b.** AMNH Bu727. **c.** Lepidoptera (Micropterigidae), AMNH Bu701. **d.** Lepidoptera (Glossata, family indet.), AMNH Bu187. Scales are 1.0 mm.

one or more pieces. These include the following: Acarina (six pieces with 8, 11, 14, and 25 individuals each), Myriapoda (four pieces with 5, 6, 18, and 24 individuals each of Synxenidae), Pseudoscorpionida (four pieces with 5 or more individuals each), Isoptera (three pieces with 11, 15, and more than 50 individuals each), and Auchenorrhyncha (three pieces with 4, 5, and 8 individuals each). This sampling bias is probably related to differences in the sizes of pieces between the two collections. The NHML collection has far fewer pieces (117, less than 10% the number in the AMNH), but they are much larger and were sliced into slabs for viewing inclusions. This mode of preservation is more conducive to capture of aggregations and swarms, particularly of larger species as in Isoptera and Auchenorrhyncha. In contrast, the AMNH collection contains significantly higher proportions of four other orders. These are: Sternorrhyncha (4.8% of all arthropod inclusions vs. 1.7%), Heteroptera (1.2% vs. 0.6%), Neuropterida (1.2% vs. 0.5%), and especially Diptera (40% vs. 16%). The higher abundance in the AMNH collection of Sternorrhyncha is due largely to the Coccoidea (3.6% of all inclusions) and to the Berothidae for the Neuropterida. Though the proportions of Coccoidea in the AMNH collection of Burmese amber is approximately 6% less than in New Jersey amber (10% of all inclusions in that amber), the Burmese amber Coccoidea are still inordinately abundant and diverse compared to all other Cretaceous ambers. As pointed out earlier, the abundance of Berothidae (which prey on Coccoidea) is no doubt related to coccoid abundance—a correlation also seen in New Jersey amber.

The much greater proportions of Diptera seen in the AMNH collection are largely due to a predominance of Ceratopogonidae (6% of all inclusions vs. 1% in the NHML collection), Cecidomyiidae (5% vs. 1%), and Mycetophilidae (5% vs. 1%). Possibly, many

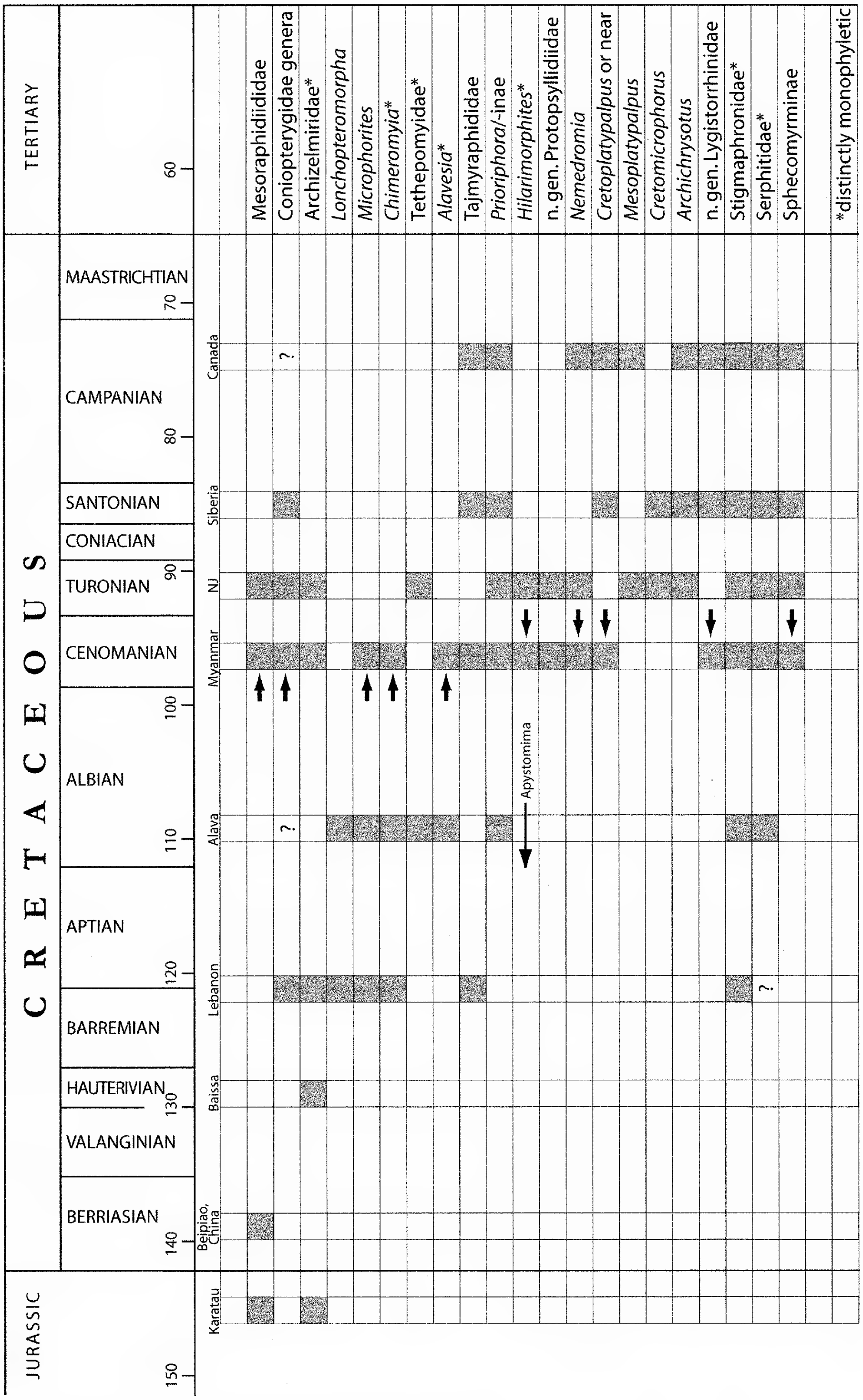

Fig. 43. Stratigraphic occurrence of various Cretaceous insect taxa in major amber deposits. With exception of the Burmese deposits, all have been well dated palynologically. The distributions of these Cretaceous "index taxa" suggest a Turonian-Cenomanian age for Burmese amber.

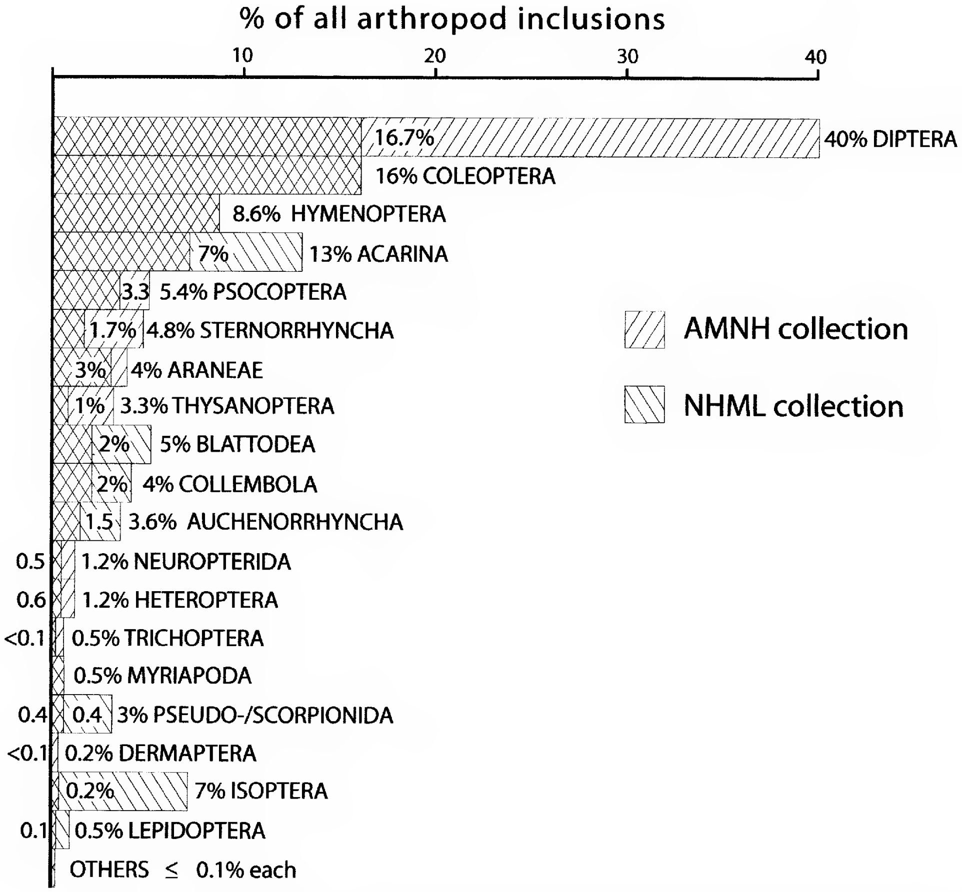

Fig. 44. Proportions of major arthropod taxa in Burmese amber, based on collections in the AMNH and NHML.

of the tiny ceratopogonids and cecidomyiids deep inside the large NHML pieces escaped notice, but this is unlikely given scrutiny to that collection, nor would this account for the Mycetophilidae. Mycetophilid fungus gnats are much larger than cecidomyiids and ceratopogonids, and should be obvious in even large amber pieces containing myriad inclusions. Smaller pieces in general are derived from small resin flows, so it is most likely that the AMNH collection represents a more dispersed medium into which wafted tiny winged arthropods. This explanation would also account for the higher proportion of ptiliids (the smallest of all beetles) in the AMNH collection (1.5% of all inclusions vs. 0.2%). The proportions of Diptera in the AMNH Burmese amber collection are closer to what is seen in other major deposits of amber: 34% in New Jersey amber, 44% in Canadian amber, 50% in Lebanese amber, and 70% in Baltic (Eocene) and Siberian ambers (Azar, 2000; Grimaldi et al., 2000a).

The proportions in the two Burmese amber collections of Hymenoptera and Coleoptera are identical: 8% and 16% of all arthropod inclusions, respectively. For the Hymenoptera, this abundance is slightly lower, but still comparable to that in other ambers: 10% (Baltic), 11% (Lebanese), 13% (Siberian), 14% (Canadian), with 24% of all inclusions in New Jersey amber being Hymenoptera. The preponderance of Hymenoptera in most of these ambers is due to Scelionidae. Very interesting is the very high abundance of Coleoptera in Burmese amber, far higher (16%)

than in any other amber deposit: Canada (1%), Siberia (1.6%), Lebanon (4%), Baltic (5.5%), and New Jersey (8%). Abundance also appears related to diversity. Though the AMNH Burmese amber beetles have not been fully identified, this collection is likely to contain the 30 or more families found in the NHML collection (Rasnitsyn and Ross, 2000)—far more than in any other Cretaceous amber deposit. Clearly, Burmese amber will be of exceptional significance in the fossil record of Coleoptera, particularly for numerous families of tiny Cucujoidea.

Lastly, the minute proportions of ants and termites in Burmese amber relates to an important evolutionary trend of increasing diversity and abundance of these ecologically important eusocial groups, from the Cretaceous to the Tertiary. The 7% estimate of isopteran abundance in the NHML collection is skewed because of preservation of a swarm of one species. The 0.2% abundance of Isoptera in the AMNH collection closely matches their relative abundance in other Cretaceous deposits, not just amber. The same trend is found for ants: though they appeared in the mid Cretaceous (and termites in the Lower Cretaceous), they remained rare, primitive, and very modestly diverse until the Eocene (Grimaldi and Agosti, 2000). Several of the ants in Burmese amber are highly unusual, and the Kalotermitidae and rhinotermitid in Burmese amber represent the most derived Isoptera in the Mesozoic.

PALEOENVIRONMENT: Rasnitsyn (1996a) indicated that the Burmese amber was not formed in a tropical environment. Our results indicate quite the opposite: this amber was formed under conditions that were probably more tropical than any other major deposit of Cretaceous amber. Distinctly tropical taxa found thus far include Onychophora, Zoraptera, Embiidina, Sclerogibbidae, *Atractocerus*, n. gen. near *Valeseguya*, and an impressive diversity and abundance of Coccoidea (with corresponding rarity of the temperate group Aphidoidea).

The Cretaceous has been identified as one of the warmest periods in the last 500 Ma of earth history, and this period has often been regarded as globally tropical. Indeed, according to Spicer et al. (1996) below approximately 40°N average temperatures ranged from 32 to 55°C. Krassilov (1996) indicated that temperate deciduous forest during the mid-Cretaceous occurred north of approximately 55°N latitude. Major Cretaceous amber deposits with paleolatitudes approximately near or below 40°N are Burma (12°), Lebanon (10–15°), northern Spain (25–35°), and New Jersey (40°) (table 1). Based on physiognomic features of fossil plants, however, such high temperatures apparently caused evaporative stress, and lower latitudes had frequent droughts with xeromorphic floras (Spicer et al., 1996; Krassilov, 1996). In these regions, xeric, microphyllous plants like Cheirolepidiaceae (Coniferae) and *Weichselia* ferns predominated, with more mesic forests occurring northerly. Apparently, Cenomanian-aged rainforests were barely developed, except for isolated regions in what are now Colombia and southeast Asia, which were subject to moist air flows from nearby oceans (Spicer et al., 1996; Krassilov, 1996).

Spicer et al.'s (1996) Cretaceous climate model has implications for interpreting the diversity of the Burmese amber paleoenvironment. As we have established, the paleoenvironment was distinctly tropical, which supports their model. While the high diversity of the Burmese amber paleobiota can be attributed to a fully tropical environment at the time, the distinct nature of the paleobiota, with many autapomorphic species, is possibly due to the ecological isolation of this part of Asia during the Cenomanian. Various insect taxa having biogeographic connections to other Cretaceous amber deposits indicate that such isolation was not complete.

Lastly, we have found several taxa in Burmese amber whose Recent distribution is disjunct among or restricted to one of the southern temperate regions: Rhachiberothinae (Berothidae) in southern Africa; Sciadoceridae (Diptera) in southern South America, Australia, and New Zealand; Archaeidae (Araneae) in southern Africa, Madagascar, and Australia; and a new genus near the Australian genus *Valeseguya* (Diptera). This is additional evidence for formerly widespread distributions of "austral" taxa (Grimaldi, 1992), whose Recent distributions have routinely and probably naïvely been interpreted as entirely a vestige of gondwanan drift.

Though our intentions in studying the Burmese amber paleobiota were purely exploratory, we can confirm the insight of Cockerell (1917a) and the later conclusions of Zherikhin and Ross (2000), that Burmese amber is Cretaceous. Originally sought as a precious substance, Burmese amber retains its mystique, but now scientifically as a window to a unique, highly diverse Mesozoic microbiota worthy of intense exploration.

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