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A Revision of Cretaceous Mantises and Their Relationships, Including New Taxa (Insecta: Dictyoptera: Mantodea)

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ABSTRACT

All genera of Cretaceous mantises are reviewed, and diagnoses of some are revised based on re-examination of type specimens. Five new Mantodea are described from Cretaceous deposits on four continents, including: concretions in limestone from the Santana Formation of northeast Brazil (Aptian, 120 Ma), inclusions in amber from the Raritan Formation of New Jersey, USA (Turonian, 90 Ma), and in amber from undetermined formations of Lebanon (Barremian, 125 Ma) and northern Myanmar (Burma) (approximately early Cenomanian to late Albian, 100 Ma). Prior to this, virtually all of the oldest mantises were from five Cretaceous localities in Eurasia. New Mantodea are *Santanmantis axelrodi*, n. gen., n. sp. (Brazil); *Ambermantis wozniaki*, n. gen., n. sp. (New Jersey); *Jersimantis burmiticus*, n. sp. (Myanmar); and *Burmantis asiatica* and *B. lebanensis*, n. gen. and n. spp. (Myanmar and Lebanon, respectively). The first two are based on adults, the last three on nymphs. Cladistic analysis of 26 morphological characters and 20 taxa, including living families and well-preserved fossils, indicates that Cretaceous mantises are phylogenetically basal to all living species and do not belong to the most basal living families Chaeteessidae, Mantoididae, and Metallyticidae. The classification of Cretaceous Mantodea is revised, which includes Santanmantidae, n. fam. and Ambermantidae, n. fam. Stratigraphic and cladistic ranks of taxa, with now improved fossil sampling, indicate that the order Mantodea is relatively recent like Isoptera (termites), with an origin no earlier than Late Jurassic. Superfamily Mantoidea, comprising three families and 95% of the Recent species in the order, radiated in the Early Tertiary to produce the exuberance of forms seen today.

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INTRODUCTION

Few insects have captured the popular imagination like butterflies, certain beetles, and mantises. Sexual cannibalism of the male mantis by his mate, for example, though often exaggerated, actually is a frequent consequence of their voracious and indiscriminate predatory behavior. The common green mantises of temperate regions, like *Mantis religiosa* L., do not reflect the true diversity of the nearly 2300 described species in the order, the great proportion of them occurring in tropical regions. Tropical species mimic, for example, twigs, leaves, flowers, and even ants, which not only prevents detection by other predators but better allows them to ambush prey. As for any impressive group of organisms, an understanding of the relationships and origins of a group can provide unique insight into the evolution of specialized life histories, such as predation. In this respect, perhaps the least appreciated aspect of mantis biology is the fact they are Dictyoptera.

Despite remarkable disparity in structure and habits, roaches, termites, and mantises comprise an indisputably monophyletic group, the Dictyoptera. This is based on molecular (Wheeler et al., 2001) and morphological features (Kristensen, 1975, 1991; Klass, 1997, 1998a, 1998b). Among the more distinctive morphological features defining the group are a perforated tentorium, a reduced to highly vestigial ovipositor largely or entirely hidden in a vestibulum, and eggs laid in a case, the ootheca. Exact relationships of mantises to one of the other two dictyopteran orders, though, is controversial, and three of the four possible hypotheses have been proposed: (1) Mantodea (Blattaria + Isoptera): Hennig (1981), Klass (1997, 1998a, 1998b). (2) (Mantodea + Blattaria) Isoptera: Boudreaux (1979), Thorne and Carpenter (1992), Kambhampati (1996), Wheeler et al. (2001), Vrsansky (2002), Vrsansky et al. (2002). (3) Mantodea + Isoptera + Blattaria (unresolved): Kristensen (1991), Grimaldi (1997).

Thus far no one has hypothesized a sister-group relationship of the two most morphologically modified orders, Mantodea + Isoptera. This ambiguity of relationships has

been due in part to a common assumption that each order is monophyletic. While Isoptera and Mantodea are each clearly monophyletic, traditional and more recent evidence is compelling for a sister-group relationship between termites and certain roaches (Cryptocercidae) (Klass, 1998a, 1998b; Lo et al., 2000), rendering the Blattaria paraphyletic. Such paraphyly, though, has been disputed (Grandcolas, 1994, 1996, 1999; Grandcolas and D'Haese, 2001).

Despite the highly modified morphology of mantises (discussed in detail below), in several important respects they are basal to living roaches and all termites. For example, the main appendages comprising the ovipositor, the gonapophyses and gonoplacs, are least reduced in mantises among the three orders. In basal termites and living roaches the ovipositor is entirely concealed within the vestibulum; in more derived termites, comprising 99% of the species, the ovipositor is essentially lost. In mantises the ovipositor plesiomorphically protrudes from the vestibulum. Also, with a few exceptions (including some extinct species), mantises plesiomorphically have three well-developed ocelli; living roaches and all termites have only the lateral ocelli, with the median one being extremely vestigial or lost altogether (in some termites and roaches all ocelli are lost). The wing venation of mantises, too, is more generalized in some respects than in termites and roaches. Thus, it is highly unlikely that mantises are closely related to any particular group of extant roaches.

Roaches are renowned for their antiquity because of fossils from the Carboniferous (e.g., Carpenter, 1992), an age more than twice that of the oldest known fossils of termites (Thorne et al., 2000) and mantises (this report) from the Cretaceous. Great disparity in ages of the three orders was reconciled by proposals that Paleozoic and Lower Mesozoic fossils are not true roaches but a paraphyletic assemblage of "roachoids," or stem-group Dictyoptera, plesiomorphically possessing a long ovipositor (Hennig, 1981; Grimaldi, 1997). In this respect, Isoptera, Mantodea, and modern roaches are considered derived from some extinct lineage of these roachoids, perhaps in the Jurassic.

The present report explores the earliest

known history of mantises. Unfortunately, phylogenetic relationships among mantises have barely been explored, the most commonly used classification is based largely on the work of Beier (1968). Beier divided the Mantodea into essentially eight families, which are adopted for purposes of this report:

Chaeteessidae: monogeneric (*Chaeteessa*), occurring in Neotropical forests, with very distinctive forefemoral and tibial spines.

Mantoididae: monogeneric (*Mantoida*), also occurring in Neotropical forests.

Metallyticidae: monogeneric (*Metallyticus*), colorful and metallic forms in Asian forests.

Amorphoscelididae: 15 genera, all Old World (Africa, Mediterranean, Asia, Australia), with very distinctive femoral spines and spurs.

Eremiaphilidae: two genera (*Eremiaphila*, *Heteronutarsus*), which are stout-bodied, long-legged forms that are apterous and brachypterous, living in deserts of northern Africa and the Middle East.

Empusidae, Hymenopodidae, Mantidae: 380 genera comprising the superfamily Mantoidea and 95% of all species. Comprises a great diversity of forms in most habitats. Some of the 21 subfamilies of Mantidae are sometimes given family-level status.

Because this report focuses on the relationships of early, Mesozoic fossils, the phylogenetic hypothesis presented here focuses on the basal relationships of mantises, notably families exclusive of the superfamily Mantoidea. Relationships within this diverse group require separate study. Also compromising the study of early mantis evolution is the scarcity of fossils, Mesozoic or otherwise, and many of these until now have been merely wings or fragments thereof. Table 1 is a summary of the known fossil mantises.

There are 17 species-level taxa of Cretaceous Mantodea, and only about 10 Tertiary ones are known, though the available Tertiary specimens are not as well studied and their diversity is much greater. For example, there are approximately eight species of mantises in Miocene Dominican amber alone (D. Grimaldi, unpubl.), most of them nymphs of Mantidae and all undescribed. A Jurassic mantis was recently described on the basis of a very fragmentary wing, specifically just the clavus (Vrsansky, 2002), which, contrary to the original claim, does not possess features specific to Mantodea. The presence of many

crossveins of *Juramantis initialis* Vrskansky, for example, is a feature widespread in Blattoidea from the Paleozoic to the Recent. The large number of known Cretaceous mantises is due mostly to the study by Gratshev and Zherikhin (1993), who described 12 species from productive deposits in central and eastern Eurasia. Of the 17 Cretaceous taxa now known, 10 are compressions or impressions in rocks, and only one is not Eurasian but is from the Cretaceous of Brazil. The Brazilian Cretaceous fossils described herein are the only complete mantises preserved in rock from any geological period; *Cretomantis larvalis* (from the Zaza Formation of Siberia and described herein) is an apparent exuvium of a nymph, so it is missing wings. Three of the rock fossil taxa are simply too fragmentary for any meaningful assessment of relationships. These are *Amorphoscelites sharovi*, *Kazakhophotina corrupta*, and *Vitimiphotina corrugata*, all described by Gratshev and Zherikhin (1993). The first is a foreleg and the last two are merely fragments of wings.

Specimens in amber have finer preservation, typical of this medium (Grimaldi, 1996), but amber biases toward the preservation of smaller organisms, in this case nymphal mantises. Of the eight Cretaceous specimens in amber, five are nymphs. *Chaeteessites* and *Electromantis* in Santonian-aged amber from the Taymyr peninsula of northern Siberia have just the anterior portions of the body preserved. A new genus is described herein for two nearly complete nymphs in mid-Cretaceous amber from Myanmar and in Early Cretaceous amber from Lebanon. *Jersimantis luzzii* and a new species of this genus from Burmese amber are nymphs preserved in their entirety. Two New Jersey amber specimens are portions of adults; one a portion of a wing, the other comprised of wings, pronotum, and dorsal surface of the head. Finally, the finest preserved specimen from the Mesozoic is a small adult in New Jersey amber, *Ambermantis*, described herein.

Despite fragmentary specimens and a meager fossil record, the mantis fossils can provide powerful means for interpretation of evolutionary history when studied in a phylogenetic context (e.g., Smith, 1994). With such an approach, the significance and infor-

TABLE 1
Known Fossil Mantodea

Taxon	Matrix	Parts	Location	Epoch/Series	Age (Ma)	Ref. ^a
CRETACEOUS						
<i>Ambermantis woźniaki</i> ^b	amber	adult	New Jersey	Turonian	90	1
<i>Amorphoscelites sharovi</i>	shale	foreleg	Siberia	Valang-Haut.	135	2
<i>Baissomantis maculata</i>	shale	wings	Siberia	Valang-Haut.	135	2
<i>Baissomantis picta</i>	shale	wings	Siberia	Valang-Haut.	135	2
<i>Burmantis asiatica</i> ^b	amber	nymph	Myanmar	Cenomanian	100	1
<i>Burmantis lebanensis</i> ^b	amber	nymph	Lebanon	Barremian	125	1
<i>Chaeteessites minutissimus</i>	amber	nymph	Siberia	Santonian	85	2
<i>Cretomantis larvalis</i>	shale	nymph	Siberia	Valang-Haut.	135	2
<i>Cretophotina mongolica</i>	shale	wing	Mongolia	Barrem.-Aptian	125	2
<i>Cretophotina serotina</i>	shale	wing	Kazakhstan	Turonian	90	2
<i>Cretophotina tristriata</i>	shale	wings	Siberia	Valang-Haut.	135	2
<i>Electromantis sukatshevae</i>	amber	nymph	Siberia	Santonian	85	2
<i>Jersimantis burmiticus</i> ^b	amber	nymph	Myanmar	Cenomanian	100	1
<i>Jersimantis luzzii</i>	amber	nymph	New Jersey	Turonian	90	3
<i>Kazakhphotina corrupta</i>	shale	wing	Kazakhstan	Turonian	90	2
<i>Santanmantis axelrodi</i> ^b	limestone	adult	Brazil	Aptian	115	1
<i>Vitimiphotina corrugata</i>	shale	wing	Siberia	Valang.-Haut.	135	2
TERTIARY						
<i>Archaeophlebia enigmatica</i>	shale	wing	France	Paleocene	60	4
<i>Arverineura insignis</i>	shale	wings	France	Paleocene	60	4
<i>Chaeteessa</i> sp.	amber	adult	Dom. Republic	Miocene	20	5
<i>Lithophotina floccosa</i>	shale	wings	Colorado	Eocene	45	6
Mantidae spp.	amber	nymphs	Dom. Republic	Miocene	20	5
Mantidae spp.	amber	nymphs	Baltic Region	Eocene	40	5
<i>Mantoida</i> sp.	amber	adult	Dom. Republic	Miocene	20	5
<i>Megaphotina sichotensis</i>	shale	wing	Russia	Oligocene	35	2
<i>Prochaeradodis enigmaticus</i>	shale	wings	France	Paleocene	60	4

^a The most recent, comprehensive reference for the fossils is provided, not necessarily the original reference where descriptions were made. References: 1, this paper; 2, Gratshev and Zherikhin, 1993; 3, Grimaldi, 1997; 4, Nel and Roy, 1996; 5, D. Grimaldi, unpubl.; 6, Sharov, 1962.

^b Species described herein.

mation content of preserved venational characters can be determined, and, in conjunction with chronology, ages of lineages can be better extrapolated. Zherikhin (2002: 276), in the most recent review of mantis fossils, stated "The oldest known fossils [in the Cretaceous] may well represent the early stage of mantid evolution", which contrasts with the estimates of a Late Paleozoic age proposed by Carpenter (1992) and Hennig (1981). With new specimens and this analytical approach, questions like the following can be addressed: Is the apparent young age of the order due to a gap in the fossil record of 100 million years or more, or did mantises evolve

only about 150 Ma? The answer depends in part on how one defines a mantis.

MATERIALS AND METHODS

SOURCES, PREPARATION, AND STUDY OF NEW MATERIAL

Specimens newly reported here derive from three sources: Lower Cretaceous (Aptian-aged) limestone from the Santana Formation, Ceará, Brazil; and mid-Cretaceous ambers from the Raritan Formation of central New Jersey, USA (Turonian), and undefined formations in northern Burma (Myanmar). Additional, previously reported and de-

scribed specimens derive from various deposits as specified later.

Santana Formation fossils include a great diversity of vertebrates and arthropods (Maisey, 1991) and are renowned for their preservation (Grimaldi and Maisey, 1990; Martill, 1988). The rich insect deposits derive from the Crato Member of the Santana Formation, near the town of Nova Olinda in Ceará, northeastern Brazil. Though the Crato Member has not been dated palynologically, its lithology indicates a probable Aptian age. The fossils, including arthropods, are preserved as concretions of iron hydroxide and apatite, so they have relief that is lifelike or nearly so. They have also preserved remarkable details, including soft tissues such as striations of muscle myofibrils. A matrix of soft, fine-grained limestone facilitates preparation with acid digestion, using a weak solution of acetic acid (2% or less), but this technique is complicated by the intricacy of arthropods. With too much acid digestion, fine structures like spines, antennae, and wing veins will disintegrate.

To avoid possible damage from preparation, AMNH 1957 was scanned using ultra high resolution computerized X-ray tomography (UHR CT) to observe critical ventral structures obscured by matrix. The three-dimensional preservation of the fossils, in a matrix with substantially lower density than the concretion, allows the use of this technique. The technique has been described and used very successfully for large insects and small vertebrates preserved in amber (Grimaldi et al., 2000a).

CT scanning used an ACTIS 200/225 Microfocus System (Bio-Imaging Research, Lincolnshire, IL), operating at 150 kV of X-ray energy. Five contiguous image stacks were collected in volume CT mode (cone beam) at a slice thickness of 14 μm . The final reconstructed image resolution was 512 \times 512 pixels. For three-dimensional reconstruction the original dataset was cropped using Scion Image (Scion Corporation, Frederick, MD). Isosurface rendering was done using Imaris Surpass 3.1 (Bitplane AG, Zurich), and volume rendering used Voxblast 3.0 (Vaytek Inc., Fairfield, IA). A rotating, three-dimensional image of AMNH 1957 can be viewed on www.amnh.org/science. While

the resolution was sufficient to determine the size and position of the forelegs and the presence of spines (i.e., their bases), the structure of foreleg spines could not be seen.

Amber specimens from the Cretaceous of central New Jersey, USA, derive from the palynologically-dated Raritan Formation (Turonian). Mantodean specimens reported here come from two closely situated outcrops of equivalent age, in the towns of Sayreville and East Brunswick, Middlesex County. These outcrops have yielded an impressive diversity of fossilized organisms, including various plants; the oldest mushrooms; the oldest true tardigrade, definitive ants, and a parasitiform mite (an argasid soft tick); a plethora of arthropods; and two extremely rare flowers (reviewed in Grimaldi et al., 2000b). Like most amber deposits, amber from the Raritan Formation was deposited in brackish water lagoons and deltas, and in this case the amber was produced by a forest of Cupressaceae in a warm temperate or subtropical environment (Grimaldi et al., 2000b).

Burmese amber has recently been rediscovered (e.g., Grimaldi et al., 2002), with the only fossiliferous collection of the material having been assembled 80 years ago and residing at the Natural History Museum (NHM), London. Historically and presently, the material derives from northern Myanmar, Kachin state, though identity and stratigraphy of the deposits have been confused. Many popular reports indicate this amber is Eocene or younger, which has been attributed to its redeposition in younger deposits. Recent re-study of arthropod inclusions in the NHM collection, though, indicates a Cretaceous age (Rasnitsyn and Ross, 2000; Zherikhin and Ross, 2000). Study of the AMNH collection indicates an age that is probably mid-Cretaceous, perhaps Cenomanian or Turonian (Grimaldi et al., 2002). Most recently, dating based on ammonites and pollen indicates an age of Late Albian for Burmese amber (Cruikshank and Ko, 2002). Moreover, this amber has preserved a biota quite distinct from the prolific deposits of Cretaceous amber in Canada, Siberia, northern Spain, and New Jersey, probably due to its age, paleogeographic isolation, and its formation in a distinctly tropical paleoenvironment. Bur-

mese amber was formed by a conifer, perhaps *Metasequoia*, and is probably the most biotically diverse Cretaceous amber deposit (Grimaldi et al., 2002).

Lebanese amber deposits are the only ones to prolifically yield the oldest insect inclusions, approximately Barremian in age. Other deposits of Lower Cretaceous amber occur, including ones as old as Lebanese amber, but none are so prolific or diverse. Though known for decades (Schlee and Dietrich, 1970), only recently has a systematic study of Lebanese amber been made (Azar, 2000). Dozens of deposits occur throughout Lebanon. Indeed, the formations yielding this amber occur in Jordan and Israel (the “Levantine Amber Belt”), though insects are known in amber only from the former of the two. The source of this amber has popularly been reported as araucarian even though the extinct family Cheirolepidiaceae is the most likely candidate (Azar, 2000). Lebanese amber has yielded a diverse array of arthropod orders and families, with many representing the oldest definitive records of their group (Azar, 2000). This amber is far more brittle and fractured than any other amber, so preparations must be done very carefully.

Inclusions in amber are best observed by grinding and polishing a flat surface close to the inclusion, which reduces most distortion or obscurity from the amber matrix. Unfortunately, unlike soft Dominican amber or hard Baltic amber, most Cretaceous ambers are fractured and brittle, so in order to best observe inclusions the material must be treated prior to trimming and polishing. Pieces from the AMNH collection were embedded in an inert, optically high-quality epoxide resin under vacuum, before any trimming and polishing. The procedure was described in Nascimbene and Silverstein (2000). This technique fills in cracks that otherwise may split through an inclusion during preparation or which obscure observation with reflective surfaces. Even the hard and remarkably durable Burmese amber, which is easily polished, is permeated by fractures, so its preparation and study is greatly improved by epoxy vacuum-embedding. Lastly, epoxy embedding protects the amber from the normal disintegration that occurs via long-term ex-

posure to oxygen and other atmospheric conditions (Grimaldi, 1993).

MORPHOLOGICAL TERMINOLOGY

Names of morphological structures generally follow Snodgrass (1935). For wing venation terminology the system of Kukulová-Peck (1991), used by Nel and Roy (1996), was not used. Snodgrass’s (1935) venation system, which is a refinement of the classic Comstock-Needham system, was used instead. Good justification for use of the Snodgrass system specifically for Mantodea was presented in an early study on mantis wing venation (Smart, 1956). In fact, Smart presented compelling evidence for interpretation of the CuP veins in roaches and mantises. Another important feature of mantis wings, besides venation, is the presence or absence of a thin, sclerotized area obliquely running near the basal branches of veins M and Cu. This feature has been given several names, with the one used here being “pseudovein”.

A hallmark feature of mantises is the pair of raptorial prothoracic legs armed with modified setae. To clarify ambiguity about these various kinds of setae, the following terminology is used throughout this paper (see fig. 1):

Setae are socketed, hairlike, unsclerotized structures, being usually long and fine.

Scales are socketed, flattened setae which can be fan-shaped, lanceolate, or paddle-shaped, with the thickest portion always being several times the width of the base. Ribbing that typically occurs in all setae are particularly well defined on scales.

Spines are socketed, sclerotized structures, slightly to considerably thicker than setae.

Spinules are socketed or apparently unsocketed structures that are very short and stout and have a fine tip.

Spurs are heavily sclerotized, thick spines that have the basal articulation virtually fused to the surrounding cuticle. Spurs often sit atop a tubercle. These are not to be confused with the structures called spurs in Diptera, with are spines in the membrane of the tibial-tarsal joint.

Acronyms throughout the paper refer to the following repositories:

AMNH American Museum of Natural History,
New York

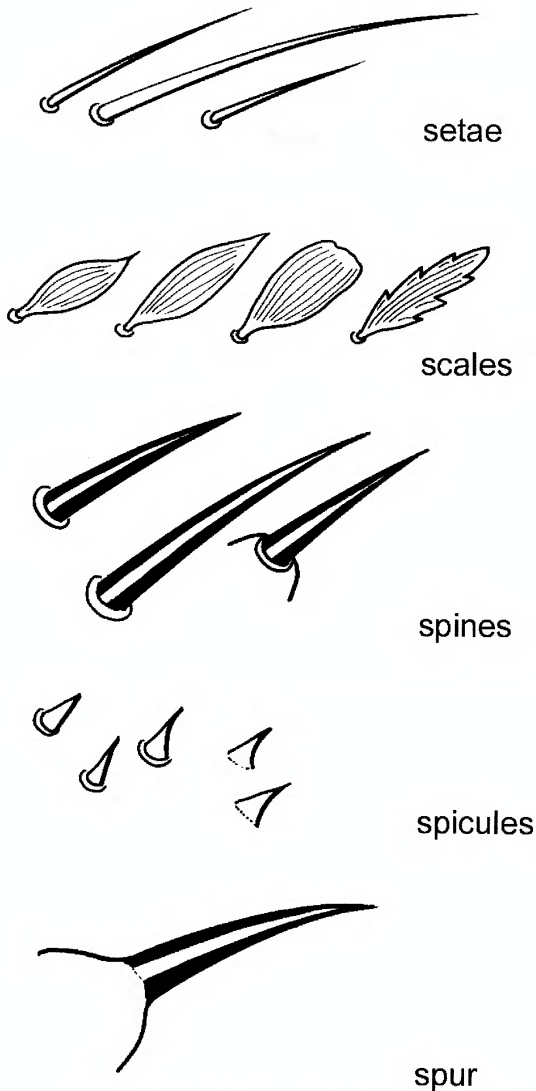


Fig. 1. Significant setal modifications on mantis forelegs and terminology used in this study.

PIN Paleontological Institute of the Russian Academy of Sciences, Moscow
 SMNS Staatliches Museum für Naturkunde, Stuttgart

SYSTEMATICS

One goal of this work is to examine the relationships of Mesozoic and living mantises, and a revised classification reflecting these relationships is presented at the end of this paper. Taxonomy and definitions of taxa are treated first, in alphabetical order of genera.

Ambermantis, new genus

DIAGNOSIS: Spination of forefemur similar to *Mantoida*, except that *Ambermantis* pleiomorphically lacks discoidal spines. Derived features are the following: extremely long foretarsi, forebasitarsus longer than foretibia. Extremely long hindlegs, with length of hindtibia plus tarsi equal to length of body; cerci long, with 20 segments.

TYPE SPECIES: *A. wozniaki*, n. sp., Cretaceous of New Jersey.

INCLUDED SPECIES: Monotypic.

ETYMOLOGY: Directly from amber, itself a derivative of *ambra* (L.), in reference to the mode of preservation of three known specimens, all adults.

Ambermantis wozniaki, new species

Figures 2a, 3, 4

Archimantis zherikhini Vrsansky, 2002a: 6 (misidentification of specimen AMNH NJ90cc: see comments below).

Jantarimantis zherikhini (Vrsansky), 2002b: 1 (replacement name for preoccupied *Archimantis* Saussure).

DIAGNOSIS: As for genus.

DESCRIPTION: Taken largely from holotype specimen, which is nearly complete. Body length of holotype (including cerci) 15 mm, some coloration patterns preserved. Holotype specimen only missing portions of antennae, left mid- and hindlegs. Species identity of paratypes based on similar wing venation. Paratype specimen (AMNH NJ-90cc: fig. 2b, 4c) has wings, most of the pronotum, and dorsal part of the head preserved, with total body length (from front of head to tip of wings, excluding antennae) of 13 mm, forewing length 9.5 mm. Specimen of a forewing exposed on surface of the amber may belong to this species; it was studied using an SEM (fig. 4a, b).

Head: Considerably wider (by approximately 1.5×) than pronotum; in frontal view overall shape triangular, with broad vertex and narrow oral region. Eyes very large, with broad frontal field, inner margins close to scape. Eyes egg-shaped in frontal view, narrow end ventrally; eyes round in lateral view. All 3 ocelli present, very close, large; median one slightly smaller and lying nearly between scapes. Pair of small, blackish, ovate stig-

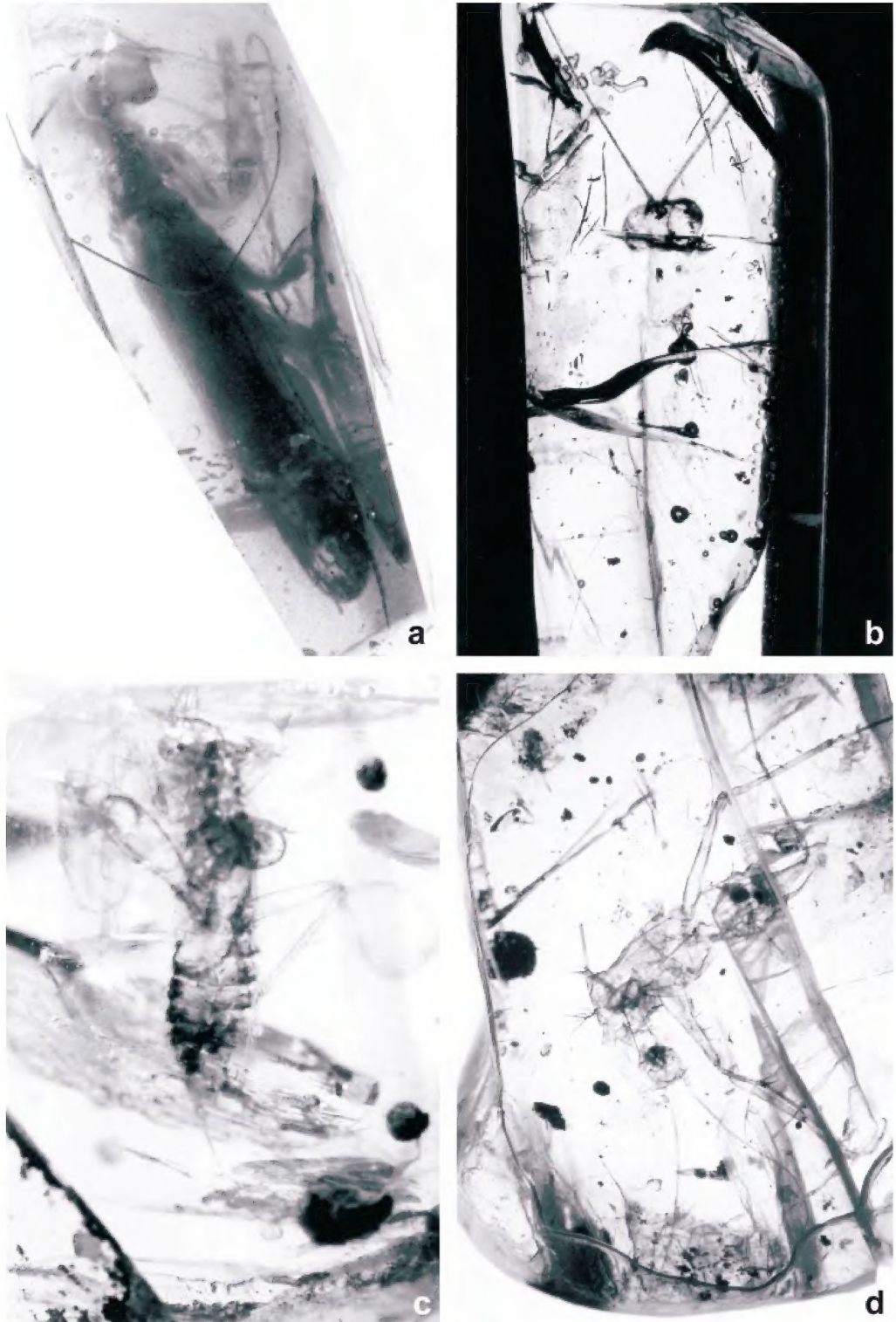


Fig. 2. Photomicrographs of Mantodea in Cretaceous ambers. **a.** *Ambermantis wozniaki*, new species, holotype AMNH NJ1085, in New Jersey amber. **b.** Paratype, *ibid.*, AMNH NJ90cc. **c.** *Jersimantis burmiticus*, holotype AMNH Bu170, in Burmese amber. **d.** *Burmantis asiatica*, holotype, in Burmese amber. For scales, refer to illustrations of specimens.

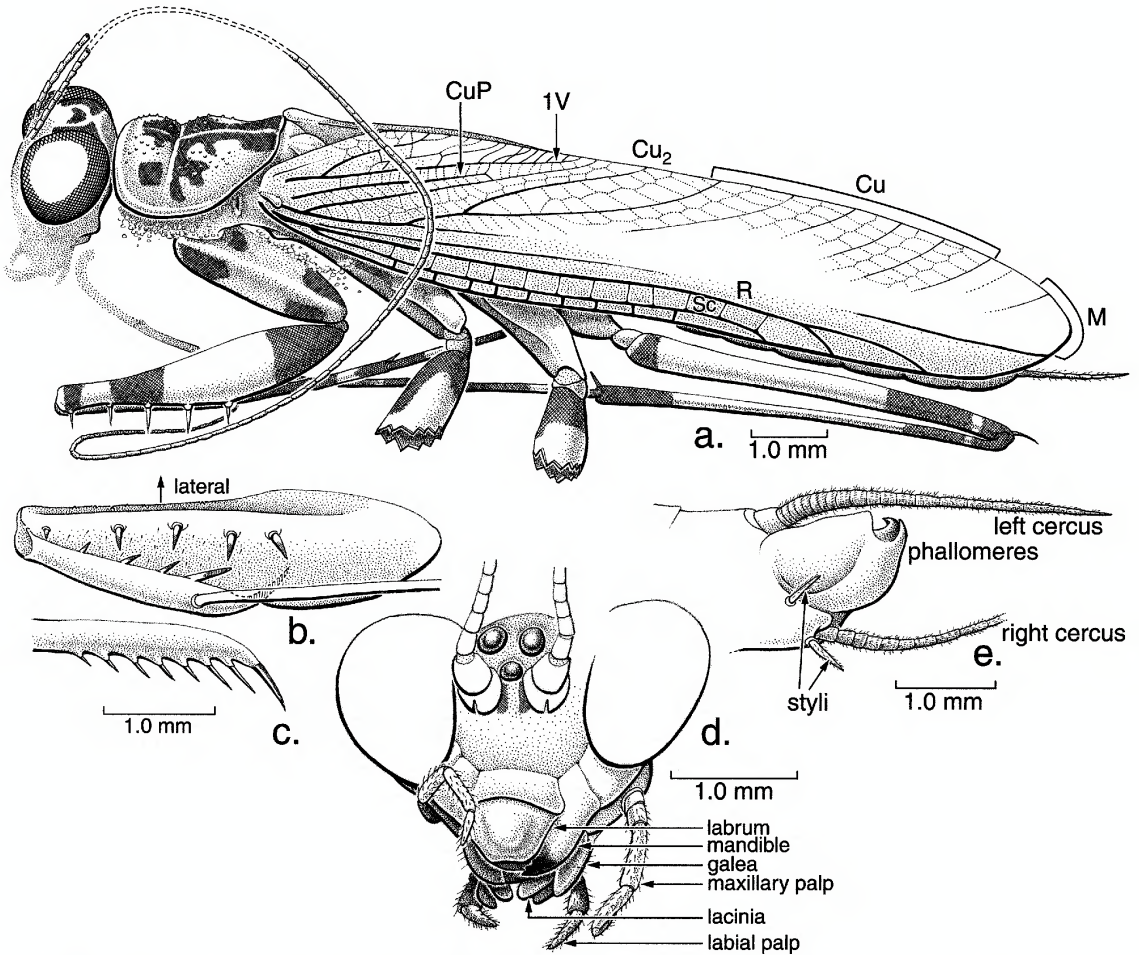


Fig. 3. *Ambermantis wozniaki*, new species, holotype (AMNH NJ1085), in New Jersey Cretaceous amber. **a.** Habitus of entire animal, oblique left lateral view. **b.** Left foreleg, ventral view of femur with folded tibia and basitarsomere. **c.** Foretibia, showing spination of mesal edge. **d.** Frontal view of head. **e.** Male genitalia.

mata occur just below median ocellus and between scapes. Antenna flagellate and extremely long, longer than body (16 mm); flagellomeres filiform and gradually tapering in diameter apicad. Mouthparts fully discernable. Clypeus relatively shallow, depth half that of labrum. Labrum roughly triangular in shape, with shallow lobe in middle. Left mandible, pair of well-developed galeae and laciniae present. Maxillary palp 5-segmented, total length quite long, approximately equal to length from tip of labrum to base of antenna. Labial palp 3-segmented, approximately half the length of maxillary palp, apical palpomere with tapered, darkened tip.

Thorax: Pronotum with dark maculations, length approximately 1.2–1.3× the width, with distinct transverse groove and scattered pimples on dorsal surface. Lateral margins of pronotum turned downward, covering perhaps half of pleura; posterior margin slightly upturned. Forelegs with coxa and femur having maculated pattern, as figured. Forecoxa long, length 0.6× that of femur. Forefemur stoutest of femora, distal half 0.4× thickness of basal half of femur. Spination of forefemur seen best in left leg of holotype. Ventral surface of forefemur with 2 rows of spines; a row of 5 spines on lateral edge, distal spine half the size of others; row of 10 spines on

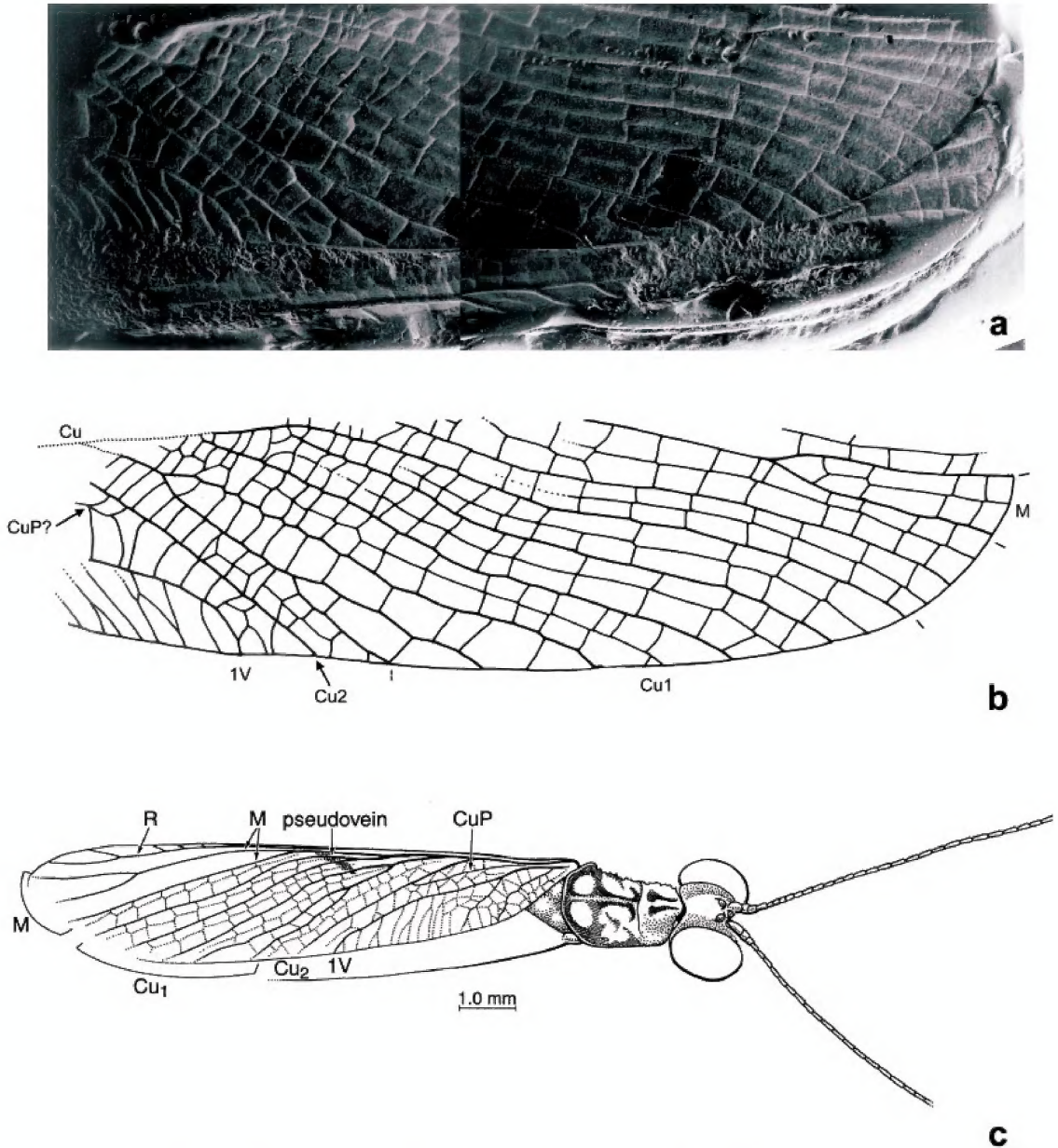


Fig. 4. *Ambermantis wozniaki*, new species, in New Jersey amber. **a, b.** Scanning electron micrograph of an isolated, imprinted wing on the surface of the amber (*a*), with diagram of the venation (*b*). **c.** Paratype, AMNH NJ90cc, a cast/imprint of the dorsal half of the specimen on the surface of the amber; the ventral half was missing.

mesal edge, slightly smaller than lateral spines. Forefemur with groove to receive apical spur of tibia, and patch of fine setulae (the "brush") on mesal surface near distal end; another patch of fine, but longer setulae on ventromesal surface. Foretibia $0.6 \times$

length of femur; with large apical spur having basal articulation to tibia barely discernible, length of spur $0.2 \times$ length of entire tibia. Forebasitarsus articulated on tibia considerably preapically, articulation point near penultimate spine. Foretibia with 2 rows of

spines on ventral (adpressed) surface, lateral row of 4 spines and mesal row of 7 spines. Tibial spines are thin and sharp, gradually shorter proximad. Foretarsi with dark banding, very long, longer than forefemur; forebasitarsomere longer than tibia, with small apical spur. Right midleg of holotype mostly preserved; coxa and base of femur with dark maculation; midtibia slightly longer than midbasitarsomere. Midfemur stout, nearly as thick as forefemur. Hindlegs extremely long; tibia and tarsus equal in length to body, hindtibia equal to length of hindfemur + trochanter, with small apical spur. Hindfemur slender, with small, sharp, slightly curved spiniform seta projecting from apex. Hindfemur and tibia with dark banding at each end.

Wings long and narrow, extended to tip of abdomen but with cerci projecting. Forewing with dark maculations (not illustrated), length approximately $4.5\times$ the width. Hindwing not visible. Venation derived from holotype and paratype AMNH NJ90cc. Forewing: Sc long, approximately $0.7\times$ length of wing, with 9 crossveins joining to C; R with single, short dichotomous fork at apex; M with 3 significant branches (best seen in NJ90cc), first fork near middle of wing, second fork between first one and wing apex; Cu_1 with 5–7 main branches, a long intercalary vein present between each; vein 1V (first vannal vein [Smart, 1956]) present, curved, not fused to Cu_2 ; CuP fused to Cu_2 . Numerous short crossveins present.

Abdomen: Cerci long, with 20 segments, segments longer apicad. Subgenital plate typical, pair of short styli on its posterior margin; ventral lobe large, apical process typical of Mantodea.

TYPE SPECIMENS: Holotype: male, AMNH NJ1085, NEW JERSEY: Middlesex County, Sayreville, Raritan Formation, Upper Cretaceous (Turonian) (Grimaldi et al., 2000b), collected by Joseph Wozniak. Specimen is in a piece of turbid, light yellow amber (fig. 2a), which had been trimmed to a size just slightly larger ($18 \times 8 \times 6$ mm) than the mantis, for optimal viewing. Still, some portions were obscured by turbidity or by milky froth coating parts of the specimen. The amber piece had deep cracks in it, so it was embedded in epoxy after trimming, then re-embed-

ded. All epoxy was trimmed within 1 mm of the surface of the amber. Paratype: AMNH NJ90cc, NEW JERSEY: Middlesex County, East Brunswick, Raritan Formation (Grimaldi et al., 2000b). This is a partial specimen comprised of a dorsal impression of head and wings (figs. 2b, 4c), and it is one of over 30 inclusions found in a remarkable piece of amber, including the oldest definitive mushrooms (Grimaldi et al., 2000).

ETYMOLOGY: Patronym, in honor of the collector and donor of the beautiful holotype specimen, Joseph Wozniak. This is the largest insect preserved in New Jersey amber, though portions of what were larger insect specimens also occur in this amber.

COMMENTS: The holotype specimen (AMNH NJ1085) was mentioned and figured in Grimaldi et al. (2000b: fig. 43g) and is the best-preserved mantis from the Mesozoic. It superficially resembles *Mantoida*, but lacks important synapomorphies, such as the discoidal spines that occur on the forefemur of virtually all living mantises. Spination of the forefemur, in fact, is relatively simple. *Ambermantis* also has several odd features, perhaps the most striking being the extremely long hindlegs. In most mantises, even extremely gracile ones, the length of the hindtibia + tarsus is generally about one-half the body length. *Eremiaphila* is exceptional because the body is very short and stout and the legs stiltlike, an extreme specialization for dwelling in sandy habitats. No other mantis has hindlegs as long as *Ambermantis*. Less exceptional but still distinctive are the long cerci in *Ambermantis*. The number of cercal segments in *Ambermantis* is 20 and in *Chaeteessa* 23–25, but in most other mantises there are 8–12, including the most basal fossil forms, where the cerci are preserved (in *Eremiaphila* the cerci are quite reduced). However, there are species in the Mantidae that also have many cercal segments (i.e., *Theopompella*, 26–28; *Choerododis*, 20–22).

Jantarimantis zherikhini (Vrsansky) was very recently described as a mantis on the basis of two incomplete specimens in New Jersey amber in the AMNH (he originally used the preoccupied generic name *Archimantis*) (Vrsansky, 2002a, b). The two specimens are not even in the same order. What Vrsansky called specimen “M1” (the holotype of *J. zherikhini*) is actually a roach of

the extinct, unusual family Umenocoleidae. A small series of completely preserved umenocoleid adults in New Jersey amber are in the AMNH collection, so all of these, including the holotype of *Jantarimantis zherikhini*, will be treated in another paper. What Vrsansky labelled "AMNH M2" and as "additional material" (not even as a paratype) is specimen AMNH NJ90cc, properly described herein and named as a paratype of *Ambermantis wosniaki*. During Vrsansky's 1995 visit to the AMNH, the completely preserved holotype of *Ambermantis wosniaki* had not yet been discovered.

Genus *Amorphoscelites* Gratshev and Zherikhin

Amorphoscelites Gratshev and Zherikhin, 1993: 163. Type Species: *A. sharovi* Gratshev and Zherikhin, 1993: 163 (Early Cretaceous, Russia). By original designation.

DIAGNOSIS: Poorly known genus based on a single isolated foreleg (PIN 3064/8586), originally defined by Gratshev and Zherikhin on the basis of the following significant features: coxa long; femur fairly stout, 3 times as long as broad (length, including trochanter, 4.6 mm), inner surface sculptured and with flat tubercles, ventrally with two longitudinal rows of small spines. Tibia fairly long (length, including apical spur $0.7 \times$ length of femur), inner surface with numerous, minute denticles or spicules; apical spur large, with tarsus articulated at its base.

INCLUDED SPECIES: Monospecific.

COMMENTS: The specimen is clearly mantodean but far too incomplete for phylogenetic analysis or classification. Structure of the foreleg differs from *Amorphoscelidae* by this family possessing a small spine in the middle of the femur and with a very long tibial spur, and often possessing few if any other spines (even minute ones). *Amorphoscelites* has no such spine preserved, numerous fine spines or spicules, and the foretibia is of standard size for mantises.

Genus *Baissomantis* Gratshev and Zherikhin

Baissomantis Gratshev and Zherikhin, 1993: 159. Type Species: *B. picta* Gratshev and Zherikhin,

1993: 159 (Early Cretaceous, Russia). By original designation.

DIAGNOSIS: Known only as isolated wings from the Cretaceous of Russia, and defined by Gratshev and Zherikhin largely on the basis of the following significant features: R with 1 or 2 branches, ending at costal margin just beyond Sc; RS separate from R, multi-branched; M with 2 or 3 branches; Cu_2 strongly arched. Wings with patterning. Subsequent study by the author indicates a pseudovein is absent.

INCLUDED SPECIES: *B. picta*; *B. maculata* Gratshev and Zherikhin, 1993 (figs. 5a, 6).

COMMENTS: The absence of a pseudovein, though not mentioned by Gratshev and Zherikhin, is highly significant, and would make this genus plesiomorphic to true mantises.

Burmantis, new genus

DIAGNOSIS: Distinguished from other genera known as nymphs in amber (*Chaeteesites*, *Electromantis*, *Jersimantis*) most readily by the distinctive foreleg structure: femur with ventromesal row of 5–6 stout, short spines, alternating with shorter ones; 3 long spines on ventrolateral edge; with dense, fine pilosity in ventral furrow. Forefemoral brush present, but setae not scalelike. Foretibia with mesal row of thick spines increasing in size distad (fine setae laterally); apex of tibia with two long, thick, spinelike setae, but not spurlike (observed only in type species). Forebasitarsomere slightly longer than foretibia; at least midocellus present (these two features observed only for the type specimens)

TYPE SPECIES: *B. asiatica*, n. sp.

INCLUDED SPECIES: *B. asiatica*, *B. lebanensis*, n. sp.

ETYMOLOGY: Directly from Burma, former name of the country of Myanmar, from where the type species derives; and mantis, a typical suffix in the order.

Burmantis asiatica, new species

Figures 2d, 7, 8

DIAGNOSIS: Differs from *Burmantis lebanensis* as given in the diagnosis of that species, below.

DESCRIPTION: Based on a single specimen,

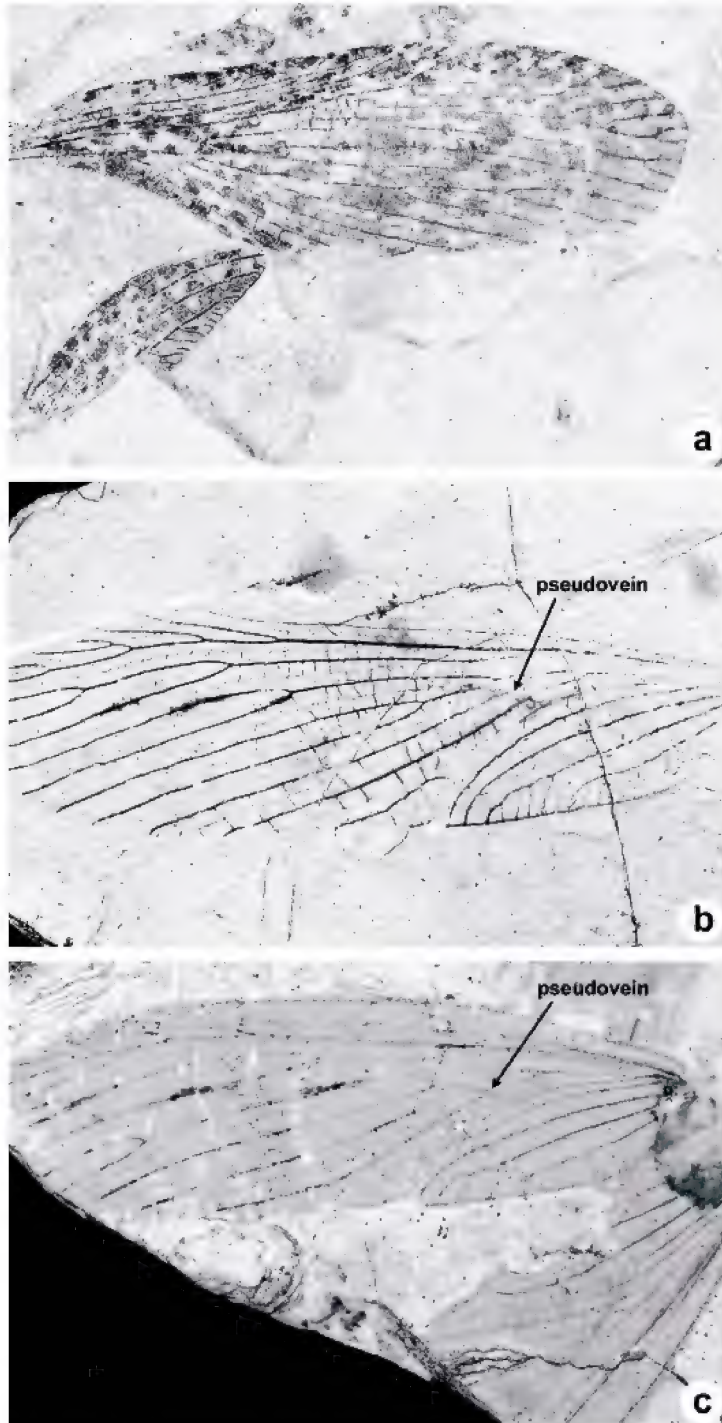
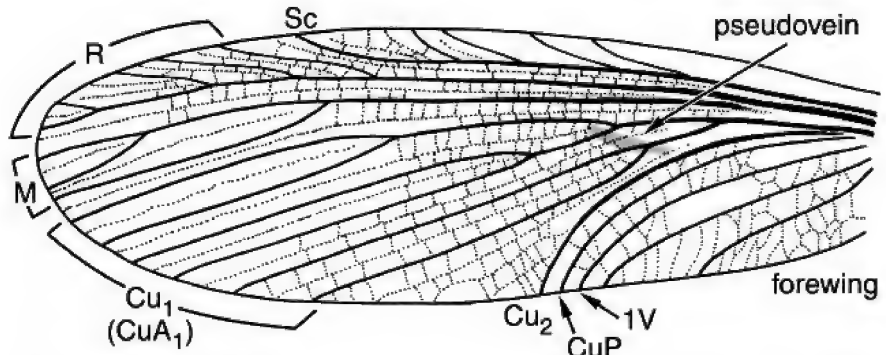
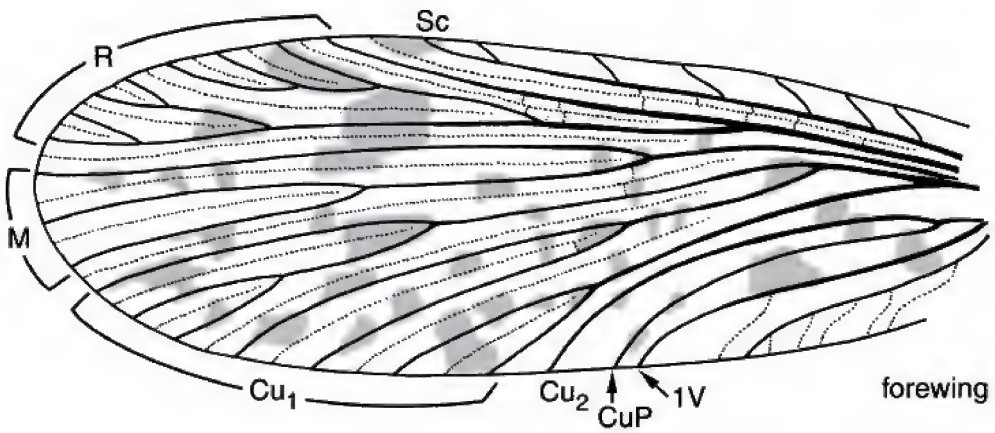
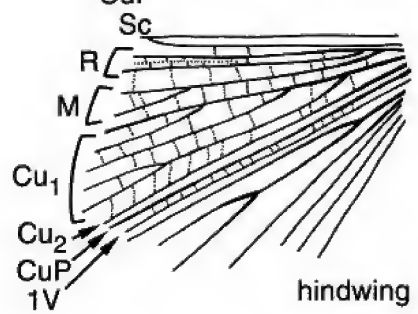


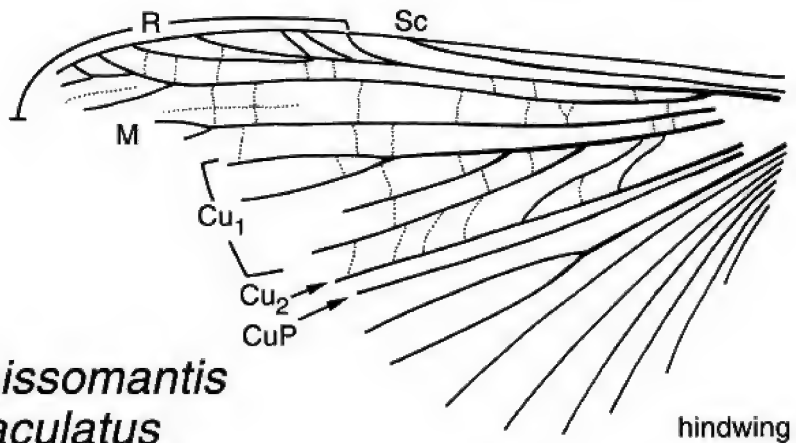
Fig. 5. Wings of Eurasian Cretaceous mantises. **a.** *Baissomantis picta* Gratshev and Zherikhin, PIN 1989/2486. **b, c.** *Cretophotina* spp. **b.** *Cretophotina tristriata* paratype, PIN 1989/2487. **c.** *Cretophotina tristriata* holotype, PIN 3064/8585. Original photographs.



Cretophotina tristriata



Baissomantis maculatus



which is a nymphal exuvium. Since the cuticle is cleared, and with the thin amber preparation made, it was possible to study the specimen under compound microscopy at 100 \times . Portions of the body are collapsed and difficult to reconstruct, but even coloration patterns and microscopic structures like sensilla are observable. *Head*: Eyes large, but only partially preserved. Median ocellus present but lateral ones not apparent (perhaps a preservational artifact). Frons slightly bulbous; frontoclypeal suture well developed. Clypeus and labrum preserved (as figured); mandibles well developed, with heavily sclerotized teeth (dentition of right mandible figured), comparison between left and right mandibles (i.e., slight asymmetry) not possible. Labial palps preserved, 3-segmented; maxilla preserved, lacinia sharp and sclerotized, toothlike. Maxillary palps not preserved or apparent. Antenna long, flagellate; scape with a thin sclerite in the socket membrane ventrally; pedicel rounded apically; flagellomere 1 long, its length greater than that of scape + pedicel; basal flagellomeres very short and compact (lengths less than width), gradually lengthened apicad, with lengths 3–4 \times the width.

Thorax: Crushed and distorted in places; pronotum difficult to reconstruct, but antepnotum apparently split away from rest of pronotum, and most of pronotum is split in half. Pronotum was apparently quadrate in shape, with mottled coloration, and possesses minute, sharp, spiculelike setulae scattered over surface. Similar setulae scattered over surface of wing pads, less so on other sclerites. Legs: Very well preserved. Forecoxa relatively short, length approximately twice the greatest width; articulation of forecoxa to prothorax is broad, seemingly with modest mobility; forecoxa with small knob on ventrolateral margin. All trochanters small. Forefemur large, basal third slightly inflated and bulbous, width of femur gradually tapered apicad. Base of each femur with small patch of 20–25 minute sensilla. Ventromesal sur-

face of bulbous base of forefemur, and ventral surface of basal half of forefemur, with dense, fine, erect pubescence. Ventrolateral edge of forefemur with 3 long, stiff, sclerotized spines, their lengths approximately equal to width of femur; each spine on a low tubercle. Ventromesal edge of forefemur, distal to bulbous base, with row of 18 short, spinelike setae; basalmost one (number 1) and numbers 3, 5, 7, and 9 thick; spines 2, 4, 6, 8, and 10–18 approximately half the thickness of others. No discoidal spines present. Mesal surface of forefemur with patch of scattered spicules (“brush”) near middle; spicules are slightly thickened, but not scaliform as in all living Mantodea (i.e., fig. 8a). Foretibia with 2 ventral rows of spines on distal two-thirds of tibia; mesal row with 8 thicker spines, lengths of which gradually increased distad, apicalmost spine nearly 3 \times width of tibia. Row of ventrolateral spines thinner, only apical spine large. Large apical spines of foretibia not situated on lobe of tibia that projects beyond tarsal articulation (fig. 8a), as occurs in all Mantodea except *Chaeteessa*. Forebasitarsomere length slightly less than foretibia. More distal foretarsomeres poorly preserved or lost. Midfemur stout, width twice that of fore- or hindfemora, with longitudinal ventral groove; dorsal apex of midfemur with a short spine. Hindlegs long; femur slightly longer than tibia, apex of hindfemur ventrally incised and dorsally with short spine. Apex of hindtibia with pair of short spines ventrally; dorsally with small lobe. Hind basitarsomere longer than remaining tarsomeres. Length of hindtibia and tarsus 4.8 mm, approximately same length as body exclusive of cerci.

Abdomen: Short, broad, tergites with minute, spiculelike setulae. Cerci well developed, with broad base and tapered apicad to fine point; approximately 12 segments, most with long, fine setae (as figured for apical segments). No genitalic structures visible.

TYPE SPECIMEN: Holotype is a nymph, AMNH, MYANMAR: Kachin, amber mines

←

Fig. 6. Wings and venation of selected Mantodea from the Lower Cretaceous of Russia. *Cretophona tristriata* (forewing and portion of hindwing), and *Baissomantis maculatus* (fore- and hindwings). Original drawings.

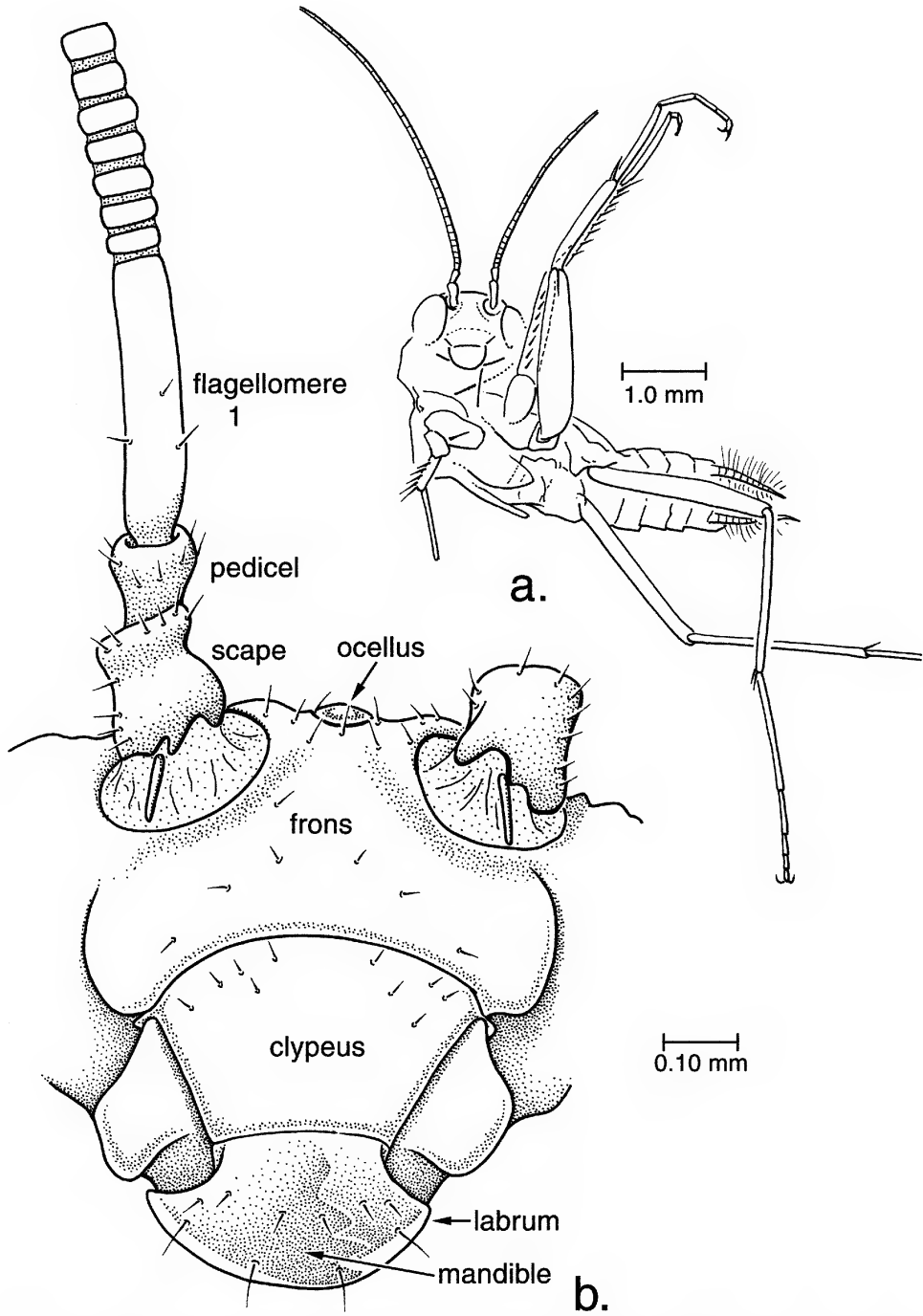


Fig. 7. *Burmantis asiatica*, new species (holotype). **a.** General outline of body. **b.** Frontal view of face.

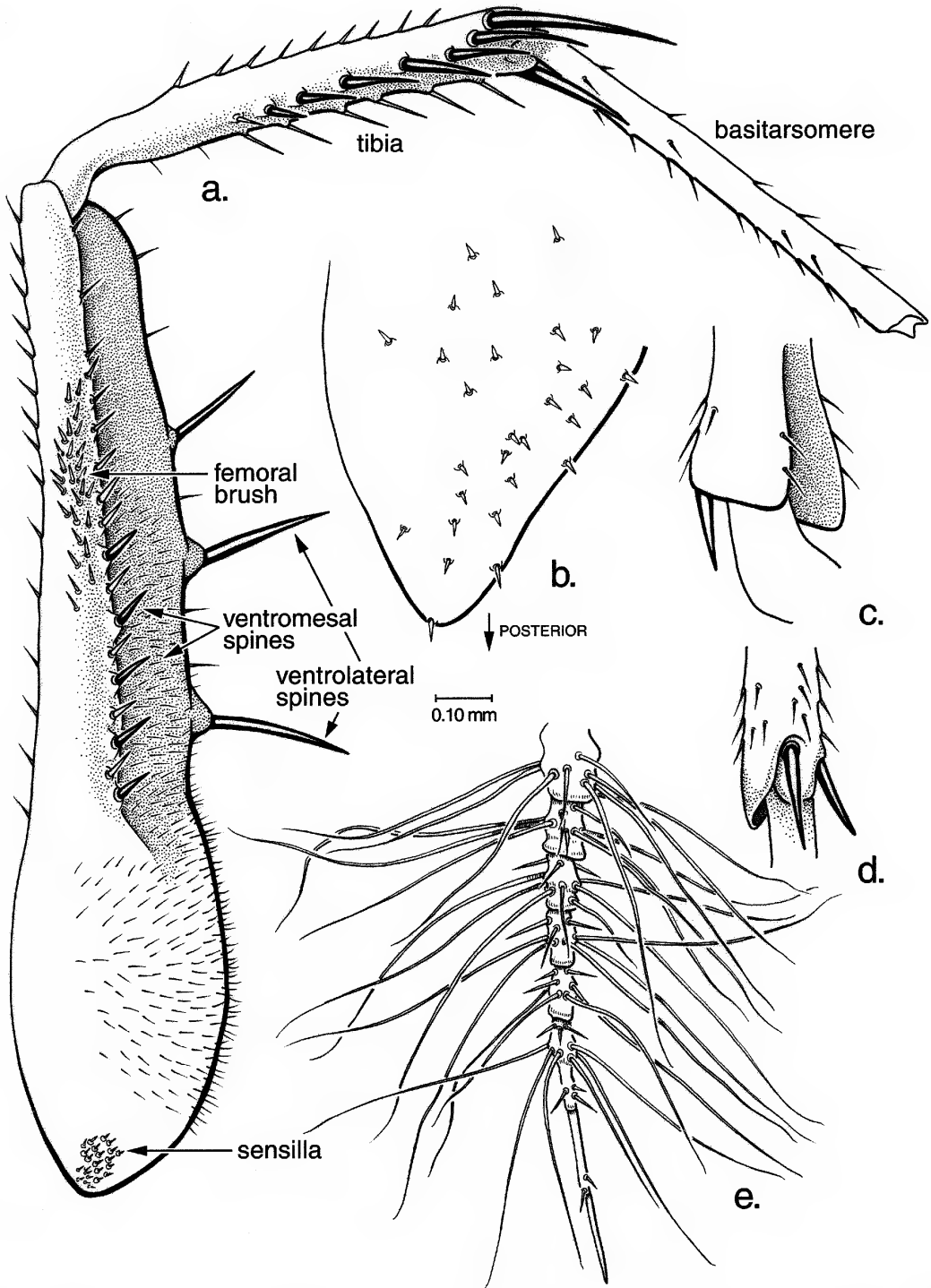


Fig. 8. *Burmantis asiatica*, new species (holotype). **a.** Portion of left foreleg, including femur, tibia, and basitarsomere. **b.** Wing pad. **c.** Apex of hindfemur. **d.** Apex of hindtibia. **e.** Cercus.

near Tanai and Myitkyina. The specimen is in a clear yellowish piece of amber containing scattered bits of debris, stellate trichomes, two staphylinoid beetles, and a berthid neuropteran. The piece is slightly rectangular, 10×14 mm, and was trimmed and polished to 3 mm thickness and parallel to the plane at which the body of the insect is preserved.

ETYMOLOGY: Referring to the Asian locality of the fossil.

COMMENTS: Exquisite preservation of the forelegs reveals a tibial spination that is plesiomorphic: there are no discoidal spines, the setulae of the forefemoral brush are not particularly dense or scaliform in shape, and the tibial spines are not particularly large or thick (in the extant basal genus *Chaeteessa* these spines virtually form a basket). The fossil is apomorphic to *Chaeteessa* and *Chaeteessites minutissimus* in at least one important respect: a long forebasitarsomere (character 13, below).

Burmantis lebanensis, new species

Figure 9

DIAGNOSIS: Differs from *B. asiatica* by having fewer (4, vs. 10) small spines on the forefemur alternating among thick ones; pronotum and some other sclerites covered with small tubercles, instead of minute spiculelike setulae; cerci shorter and with 9–10 (vs. 12) segments, and without very long setae apically.

DESCRIPTION: Based entirely on a single nymphal exuvium. *Head*: Eyes large, but proportions not preserved, nor are ocelli. Mandibles heavily sclerotized, but dentition not visible. Scape and pedicel as in *B. asiatica*; first flagellomere long, length about equal to 4–5 other, basal flagellomeres. Length of flagellomeres gradually and greatly increased distad. *Thorax*: Pronotum too distorted to reconstruct shape, but it and several other sclerites covered with small irregular tubercles (wing pads are smooth). *Legs*: Foreleg: Most of right one preserved; left one lost. Coxa very short, with deep mesal incision; femur tapered distad, ventral surface with dense, fine pubescence on proximal half; femur with two ventral rows of spines, ventromesal row with 5 thick, short, sclero-

tized spines alternating with 4 smaller, less sclerotized ones; ventrolateral row with 3 long spines, a minute one distally. Forefemoral brush present (seen vaguely in dorsal view of specimen), but details (i.e., number and shape of scales) not visible. Only proximal half of tibia preserved, bearing 6 spines increasing in length distad. Right midleg and hindfemur preserved, plus portion of left mid- and hindleg. Mid- and hindfemora fairly stout; midtibia very thin, length equal to that of midfemur. Length of midtarsi equal to length of midtibia; length of hindtibia approximately $1.6 \times$ length of midtibia. *Abdomen*: Largely lost or crumpled. Pair of styles is present; cerci fairly short, with a thick base and tapered to a fine point. Total number of cercal segments not discernable (basal ones obscured).

HOLOTYPE: AMNH L26, in amber from LEBANON: near Bcharré, collected by Antoun Estephan (Early Cretaceous, approximately Barremian). The amber piece is clear, transparent yellow; it was embedded in epoxy and trimmed to separate one piece containing a scelionid wasp, the other containing the mantis nymph and another parasitoid wasp.

ETYMOLOGY: Referring to Lebanon, the source country of the Lower Cretaceous amber.

COMMENTS: Foreleg structure of this species and *B. asiatica* leaves little doubt about their close relationship. The forefemur has similar proportions, with a depressed ventral surface having dense, fine setulae mostly on the basal half. There are two rows of spines, one on the ventromesal edge, the other on the ventrolateral edge. The ventromesal row has 5 strong, sclerotized, short spines, each separated by smaller, less sclerotized spines. The ventrolateral row has three long spines at the middle of the femur. Only the basal half of the tibia is preserved in *B. lebanensis*, but the spination that is preserved is very similar to that of *B. asiatica*.

Genus *Chaeteessites* Gratshev and Zherikhin

Chaeteessites Gratshev and Zherikhin, 1993: 157.

Type Species: *C. minutissimus* Gratshev and Zherikhin, 1993: 157 (Siberian amber [Santonian]). By original designation.

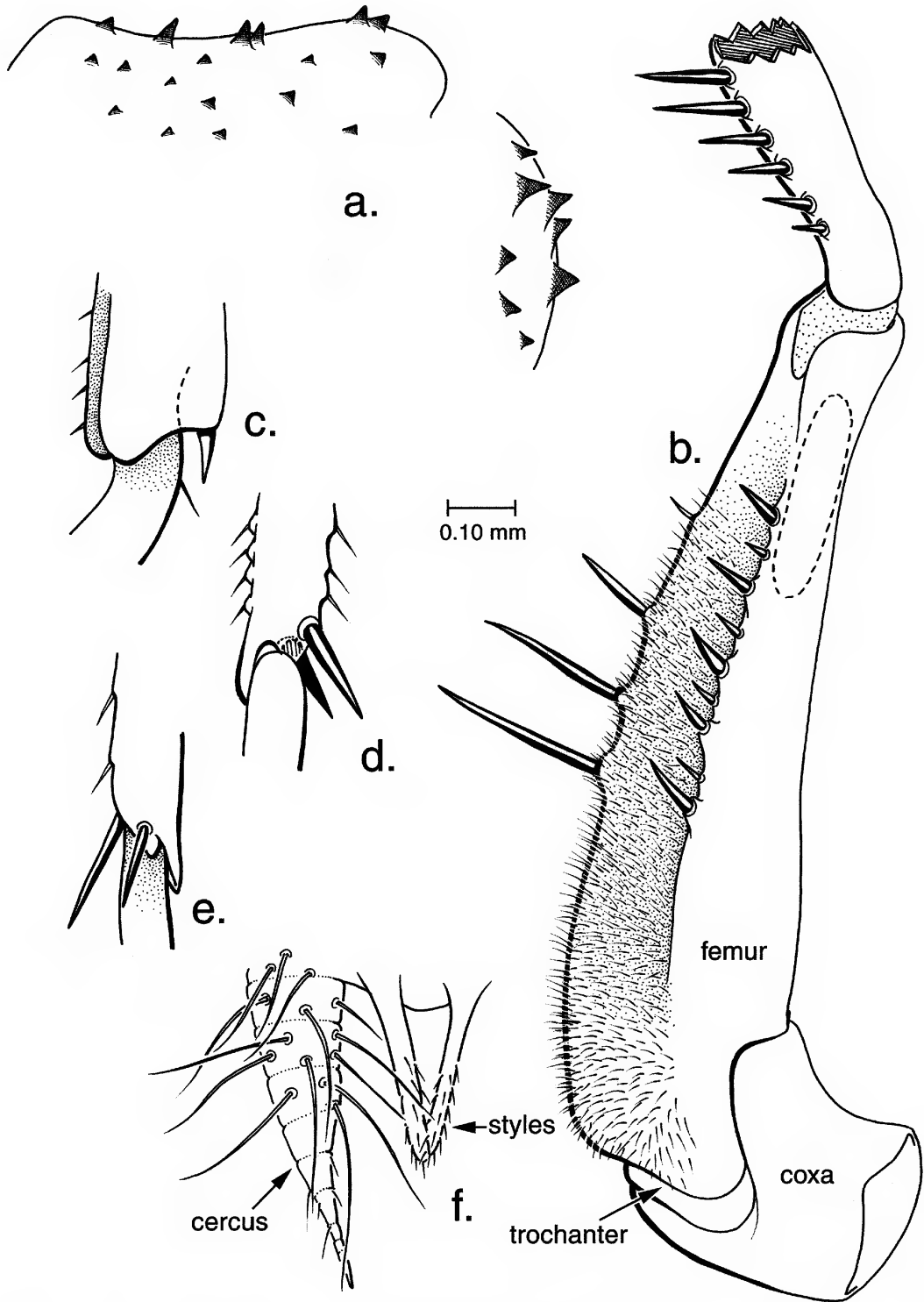


Fig. 9. *Burmantis lebanensis*, new species, holotype AMNH L26. **a.** Portions of pronotum, showing surface structure. **b.** Forefemur and basal portion of tibia. Area within dashed line is typical location of brush, which is obscure here. **c-e.** Apices of midtibia (*c*), hindtibia (*d*), and hindbasitarsomere (*e*). **f.** Left cercus and pair of styles.

DIAGNOSIS: Known only as a partial nymph in Cretaceous amber from northern Siberia, defined mostly on the basis of distinctive spination of forelegs: Foretibia with two ventral rows of spines, ones in mesal row thicker, apex of tibia with pair of large spines but neither of them a spur nor situated on a process of the tibia that extends past the tarsal joint; femur ventrally with 3 long, very fine setae (no spines), no discoidal spines.

INCLUDED SPECIES: Monotypic.

COMMENTS: Gratshev and Zherikhin (1993: 157) originally defined the genus as a "collective" one for "chaeteessids of uncertain generic placement". The unique specimen is comprised of the anterior third of a nymph (fig. 10a, b) in a small chip of Siberian amber, preserving details of the foreleg (fig. 11). Preservation of the specimen does not allow observation of ocelli, so their presence is unconfirmed. The forefemoral brush is apparently absent, but this is difficult to be certain of given preservation of the specimen.

Genus *Cretomantis* Gratshev and Zherikhin

Cretomantis Gratshev and Zherikhin, 1993: 161.

Type Species: *C. larvalis* Gratshev and Zherikhin, 1993: 161 (Early Cretaceous, Russia). By original designation.

DIAGNOSIS (revised from Gratshev and Zherikhin): The genus is based on the compression of a single but complete nymph, which apparently is an exuvium (PIN 3064/8511, holotype, figs. 12, 13). A stout-bodied nymph with forefemora stout and apparently having a ventral furrow, with furrow bordered mesally with row of 8–12 spines and 3–4 short spines or spicules. Mesal row of femoral spines preserved as small, rounded mounds, probably small tubercles that were the bases of spines. Foretibia short ($0.7\times$ length of femur) and stout, with large apical spine or spur (basal articulation obscure); with mesal row of 8–10 stout spines, lateral row of 5 smaller spines. Forebasitarsus extremely short, ca. $0.20\times$ length of foretibia. Midfemur with 2 ventral rows of spicules or minute spines; hindfemur short and stout, only $1.2\times$ length of foretibia. Hindtibia only ca. $1.1\times$ length of hindfemur. Cerci short, approximately same size as styli.

INCLUDED SPECIES: Monotypic.

COMMENTS: Several aspects of the original diagnosis were found to require some revision (Gratshev and Zherikhin, 1993: 161): only one apical tibial spine/spur is preserved, so "apical pair [of spines] strongly differentiated" cannot be corroborated; the large, apical spine of the tibia is not "placed beyond tarsal articulation"; and the foretarsi are not longer than the tibia.

Head structures are difficult to determine, which may be due to the specimen being an exuvium with a crumpled cuticle. Three terminal abdominal appendages are preserved in the specimen, a pair of finer ones with at least 5 segments, and a slightly thicker one (presumably one of a pair). Distinguishing styli from cerci is ambiguous.

Genus *Cretophotina* Gratshev and Zherikhin

Cretophotina Gratshev and Zherikhin, 1993: 150.

Type Species: *C. tristriata* Gratshev and Zherikhin, 1993: 150 (Early Cretaceous, Siberia). By original designation.

DIAGNOSIS: Known only on the basis of wings from the Cretaceous of Eurasia, defined originally by Gratshev and Zherikhin on the following significant features: costal field distinctly wider than field between Sc and R; R apically with 5–8 terminal branches; M with 2–3 branches; CuA with 6–10 terminal branches, posterior branch separated from main stem; Cu₁ distinctly curved. Re-examination by myself indicates the pseudovein is present.

INCLUDED SPECIES: *C. tristriata* (figs. 5c, 6); *C. mongolica* Gratshev and Zherikhin, 1993; and *C. serotina* Gratshev and Zherikhin, 1993.

COMMENTS: Gratshev and Zherikhin (1993) omitted mention of a very important feature in *Cretophotina*: the presence of a short pseudovein near the basal forks of M and Cu₁ (figs. 5b, c; 6), found in all mantis wings save *Baissomantis*. The paratype of *Cretophotina tristriata* (PIN 1989/2487) and the holotype (PIN 3064/8585) (fig. 6) have venational differences that strongly suggest different species. The paratype has M 3-branched (vs. 2), the 2nd vein of Cu₁ with a short, apical branch (vs. none), the basal branching of Cu₁ dichotomous (vs. apparent-

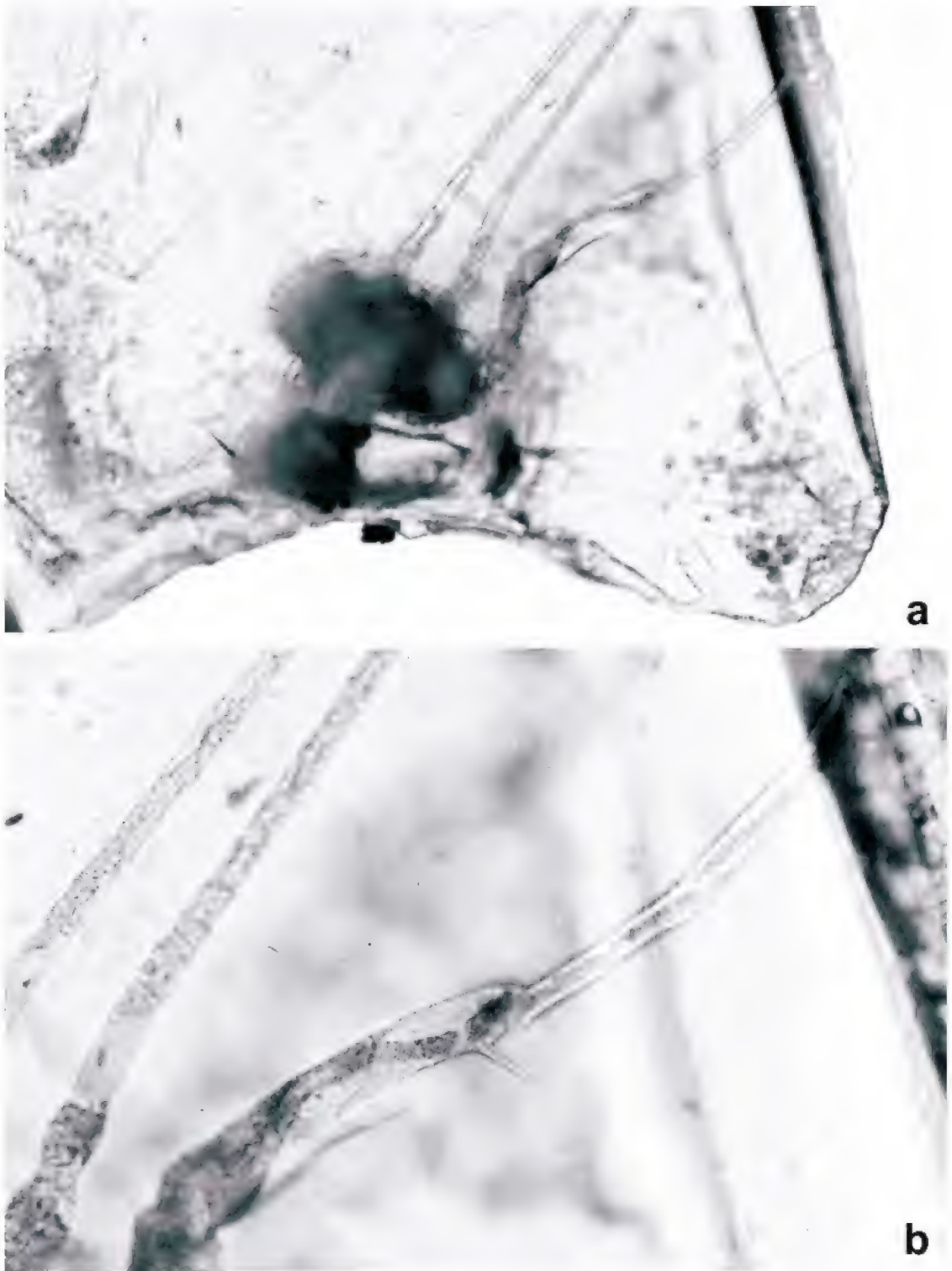


Fig. 10. Photomicrographs of holotype of *Chaeteessites minutissimus* Gratshev and Zherikhin, a partial nymph in Siberian amber, holotype PIN 3311/603. **a.** Entire specimen. **b.** Detail of foretibia. Original photographs.

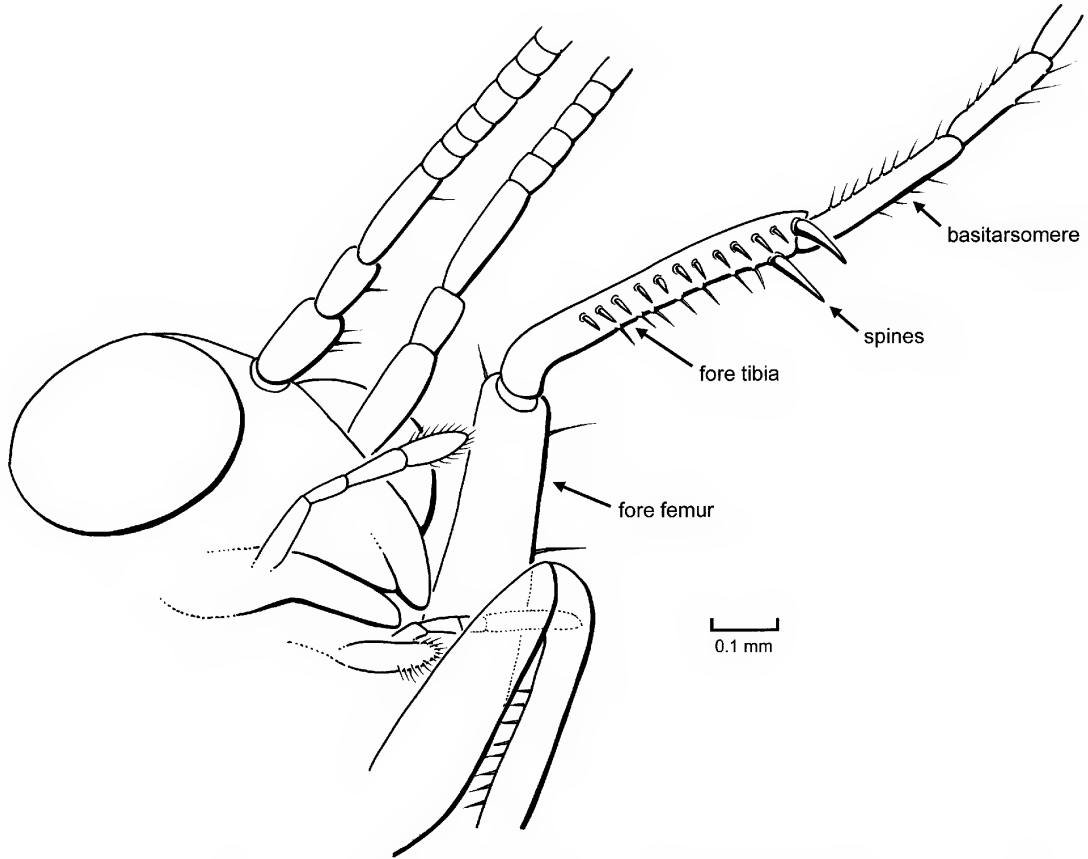


Fig. 11. Drawing of *Chaeteessites minutissimus* holotype.

ly pectinate in the holotype), and CuP is complete (vs. incomplete).

Genus *Electromantis* Gratshev and Zherikhin

Electromantis Gratshev and Zherikhin, 1993: 162. Type Species: *E. sukatshevae* Gratshev and Zherikhin, 1993: 163 (Late Cretaceous, Siberia). By original designation.

DIAGNOSIS: Known only as partial remains of a nymph in amber (fore- and midlegs, ventral portions of head and thorax)(PIN 3631/7), with the following distinctive features: forefemur incrassate (greatest width $0.3\times$ the length), with pubescent ventral furrow, bordered by 2 rows of fine spines; foretibia short, length (excluding apical spine) $0.5\times$ length of femur, with one large and one smaller apical spines. Larger apical tibial spine $0.6\times$ length of tibia; smaller apical spine $0.6\times$ length of larger one; apical spines

at apex of tibia (no projection beyond articulating bases). Foretibia with 2 rows of approximately 7 small spines, increased in size distad. Forebasitarsomere slender, slightly shorter than tibia.

INCLUDED SPECIES: Monotypic.

COMMENTS: Proportions of the forefemur and foretibia, and spination of each, distinguish this genus from *Amorphoscelites*, *Burmantis*, *Cretomantis*, and *Jersimantis*.

Genus *Jersimantis* Grimaldi

Jersimantis Grimaldi, 1997: 6. Type Species: *J. luzzii* Grimaldi, 1997: 6 (mid-Cretaceous [Turonian] of New Jersey) (fig. 14 herein). By original designation.

DIAGNOSIS (emended): Plesiomorphically as in *Chaeteessites minutissimus*, with forefemur having ventral row of 3–4 long, fine, stiff setae (no spines); apex of foretibia with two spines (one large, one small), having



Fig. 12. Photomicrograph (original) of *Cretomantis larvalis* Gratshev and Zherikhin, holotype (PIN 3064/8511).

well-defined articulation points but no spur at the apex of a tibial extension. Differs from *Chaeteessites* by lacking a medial row of foretibial spinules (instead there are just fine, stiff setae); differs from *Amorphoscelites*, *Cretomantis*, and *Electromantis* by having a slender forefemur and by spination of the foreleg. Apomorphically with vertex bulbous, ocelli absent.

***Jersimantis burmiticus*, new species**

Figures 2c, 15

DIAGNOSIS: Differs from *J. luzzi* by having bulbous vertex with finely reticulate (vs. smooth) surface; pronotum with pair of low paramedian ridges (vs. none); stiff foretibial setae thicker; ventral surface of forefemur without fine, dense setulae; cerci with 10

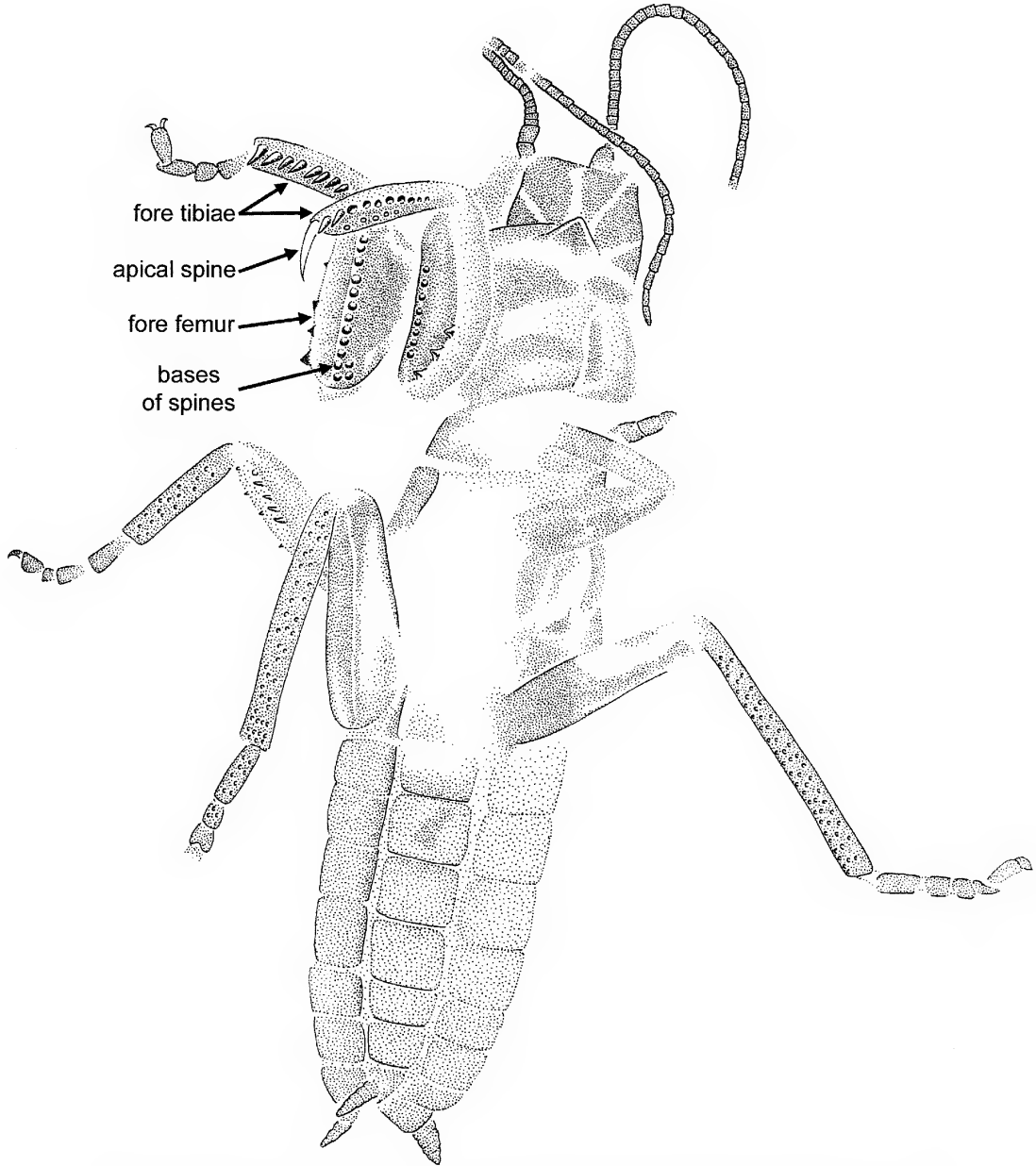


Fig. 13. Drawing (original) of *Cretomantis larvalis* holotype, showing details.

segments (vs. 3) that are highly differentiated (described below).

DESCRIPTION: Based entirely on the unique, nymphal specimen, which is completely preserved save for distal flagellomeres (lost at surface of amber). Body length 3.50 mm, including cerci. Specimen is observable dorsally, ventrally, and frontally. Portions of the cuticle are transparent, allowing observation

of some usually microscopic or concealed features (i.e., absence of forefemoral brush).

Head: Broad, approximately $1.7\times$ width of pronotum. Eyes large, exophthalmic, with large frontal field. Vertex bulbous, having fine pattern of reticulations on surface; ocelli absent. Mouthparts largely obscured, all but basal segments of palps lost.

Thorax: Pronotum comparatively small

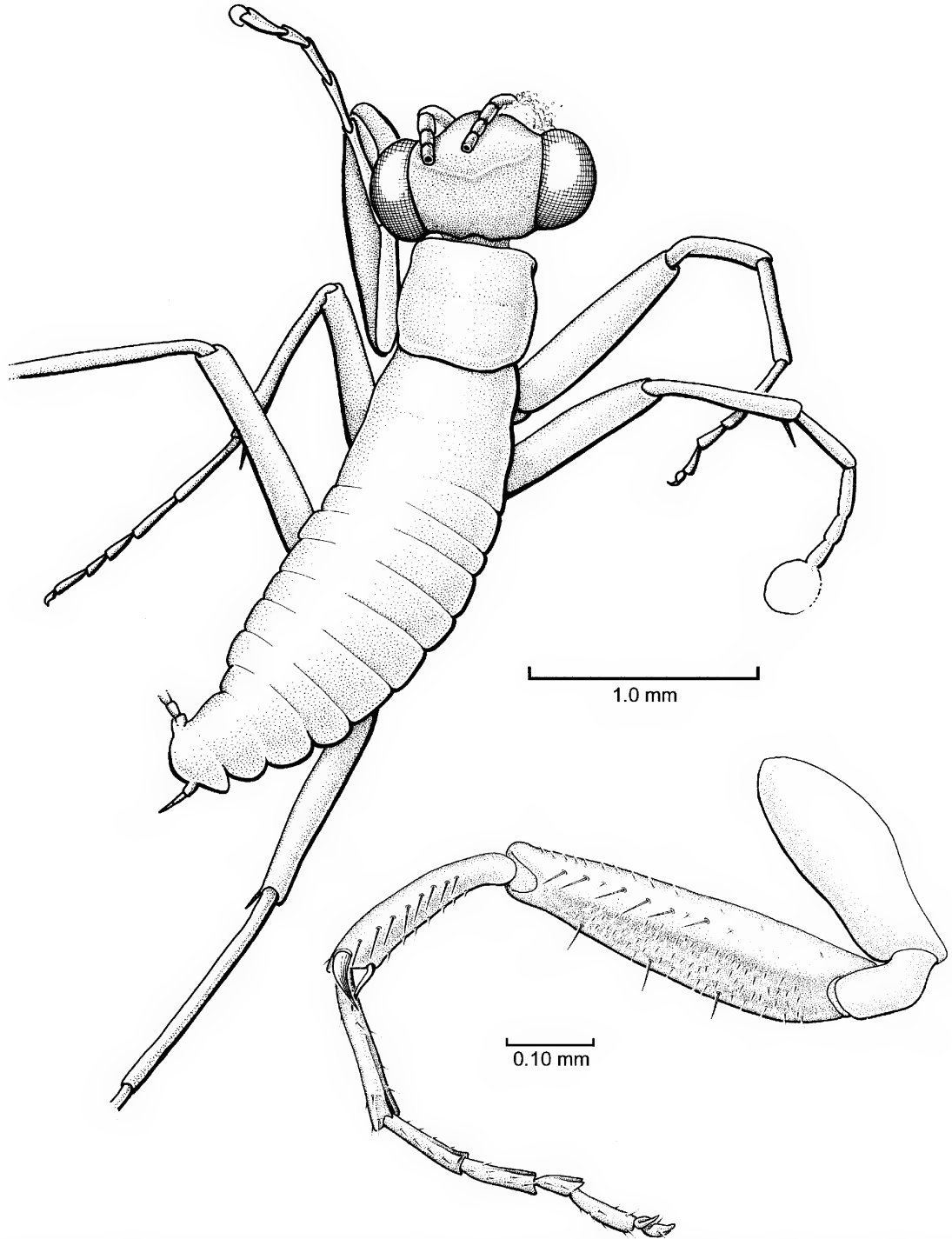


Fig. 14. Nymph in New Jersey amber, *Jersimantis luzzii* holotype (AMNH NJ425) (from Grimaldi, 1997).

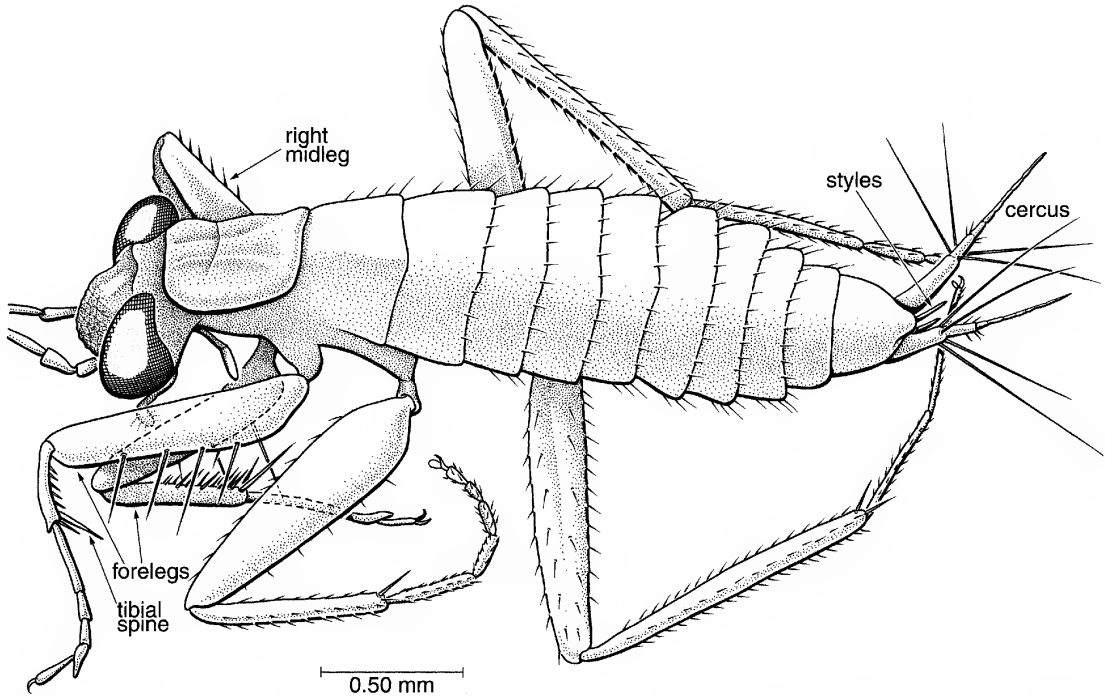


Fig. 15. *Jersimantis burmiticus*, new species (holotype), AMNH Bu170, oblique dorsal view, in mid-Cretaceous amber from Myanmar.

for mantises, length only slightly more than ($1.25\times$) the width; transverse groove present; with pair of slight, paramedian ridges extended approximately three-quarters the pronotal length. Pronotum with sides curved slightly downward, though not extended along pleura. Legs: Robust, hind pair longest (approximately $1.7\times$ length of forelegs). Foreleg with coxa small, forefemur stout (though no thicker than midfemur); tibia and tarsi slender. Forefemur approximately $1.5\times$ the length of foretibia, $1.3\times$ the length of foretarsi. Forefemur with ventro-lateral row of 4 long, fine, stiff setae; no thick setae or spines, nor dense patch of fine setae on inner surface. Foretibia with two ventral rows of sharp, stiff setae; setae on inner row thicker, spiculate, approximately 6 in row; apex of tibia with pair of thick, stiff, long setae with well-defined articulation. Inner foretibial spine longest, length approximately $3\times$ the width of tibia. All legs with 5 tarsomeres, tarsomere 4 with pulvillar lobe extended ventrally $0.4\times$ length of pretarsus. Midleg with short, fine setae; tibia with pair of fine apical setae on

ventral surface, length of longest seta twice the width of tibia. Hind legs long and slender, lengths of femur and tibia equal.

Abdomen: Only 8 segments visible. Pair of short styli between cerci, attached to terminal sternite. Styli extended slightly past midlength of first cercal segment. Cerci very distinctive: 10 segments, basal segment large, nearly one-third length of cercus, with whorl of 4 long, fine, stiff setae at apex; apical 9 segments with basal one largest, having whorl of 4 small setae at apex; distal 8 segments small, tapered apicad to fine point.

TYPE SPECIMEN: Nymph, AMNH Bu170, MYANMAR: Kachin, from mines near Tan-ai, ex: Leeward Capital Corp. 1999. The specimen is in a piece of dark, transparent amber, $15 \times 14 \times 7$ mm, which contains 9 other arthropod inclusions: 1 Cecidomyidae, 1 Psychodidae, 2 *Chimeromyia* (Diptera), 2 Auchenorrhyncha, 1 Coleoptera, 2 larvae. The mantis nymph is slightly distorted by dorsoventral compression of the body and frontal compression of the head.

ETYMOLOGY: From Burma (Myanmar).

Genus *Kazakhophotina* Gratshev and Zherikhin

Kazakhophotina Gratshev and Zherikhin, 1993: 156. Type Species: *K. corrupta* Gratshev and Zherikhin, 1993: 156 (Upper Cretaceous, Kazakhstan). By original designation.

DIAGNOSIS: Known only as a portion of a wing (PIN 2383/150), defined originally by Gratshev and Zherikhin on basis of the following most significant features: costal field (between Sc and C) distinctly wider than subcostal one (between Sc and R); no intercalary veins between Sc and R; R with 6 apical branches; M 2-branched; CuA with 4 or more branches.

INCLUDED SPECIES: Monotypic.

COMMENTS: The unique specimen on which the genus is based is too incomplete and distorted to include in a phylogenetic analysis and classification.

Santanmantis, new genus

DIAGNOSIS: A primitive type of mantis with tips of wings apomorphically extended well beyond apex of the abdomen (by more than one-third the wing length); venation reduced, such that vein M has only 2 main branches (vs. 3 or 4 found in other primitive mantises) and only 4 main branches of vein CuA (vs. generally 5 or more). Most distinctive is the very long pseudovein: instead of a sclerotized area restricted to the basal fork of M and Cu₁, it is a tubular vein extending from this region through veins CuA₂, CuP, and anal veins and nearly reaching margin of anal lobe. The genus possesses the following combination of plesiomorphic characters: prothorax short; pronotum wider than long, nearly discoid; at least middle femur (and probably hindfemur) with ventral row of spines; mid- and hindlegs long and thin; forewings tegminous (at least the proximal half), as in roaches, with 4 main branches off vein R, CuP vein (claval furrow) deep and strongly curved; genitalia (possibly ovipositor) protruding from terminal segments (not internal).

TYPE SPECIES: *S. axelrodi*, new species.

INCLUDED SPECIES: Monotypic.

ETYMOLOGY: From Santana Formation (Brazil), the provenance of the type specimen and species.

Santanmantis axelrodi, new species

Figures 16–24

DIAGNOSIS: As for the genus, given above.

DESCRIPTION: Gross aspects of ventral structures were observed using HRCT scans of the holotype specimen (figs. 18, 19). Measurements of various parts are given in table 2. Specimens from the SMNS (Staatliches Museum für Naturkunde, Stuttgart) have provisional numbers.

Head: Antennae filiform, at least basal 8–10 flagellomeres with lengths 2.5× the width; scape and pedicel small. Eyes large, situated frontally and somewhat laterally, with a large postoccipital space. Distance between eyes wide, equal to width of eye. Ocelli present, but seen in only one specimen (SMNS 172). Head hypognathous, mouthparts (mandibles, labrum) narrow compared to dorsal region of head.

Thorax: Short, prothorax not lengthened as in more derived mantises. Pronotum wider than long, its length 0.70–0.75× its width (as seen in AMNH 1957, SMNS 112, and 174), the surface evenly covered with fine punctations (perhaps sockets of lost hairs), with two slightly raised areas. Variation in the shape of the pronotum, from nearly discoid in the holotype to quadrate in some paratypes, appears due to preservational differences. Forelegs observed using HRCT on holotype: held frontally, tibiae and femora folded against each other, femoro-tibial joint barely reaching to level of posterior margin of eyes, presence of spines on either one or both segments suggested by HRCT, though details not discernable. Apex of each foretibia apparently with a spur, though cannot discern whether the spur has a well-defined articulation (i.e., fig. 19). Forecoxae not visible. Mid- and hindlegs long and slender; proportions as given in table 2. Midcoxae not visible, but hindcoxae (observed with HRCT) small, situated medially, contiguous. No spines apparent on hindfemora or hindtibiae, but row of at least 4 ventral spines occur on midfemur (visible dorsally). Forewings tegminous (especially basal half), long and narrow, extend well past apices of cerci. Pseudovein uniquely long among mantises: a tubular vein extending from this region through veins CuA₂, CuP, and anal veins and

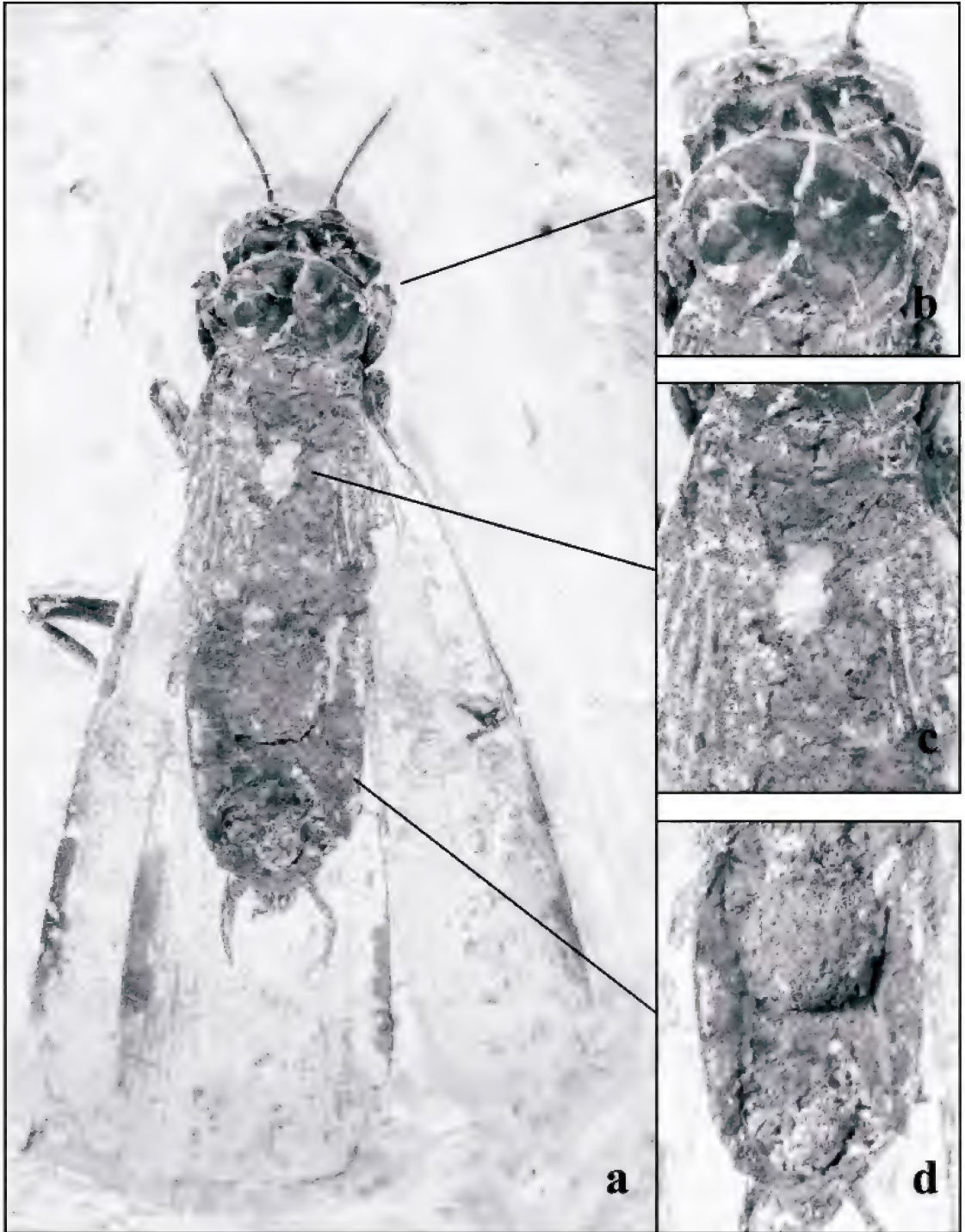


Fig. 16. Photomicrographs of *Santanmantis axelrodi*, new species, holotype (AMNH 1957), in Early Cretaceous limestone from the Santana Formation of Brazil. **a.** Dorsal view of cleaned specimen. **b.** Detail of head and pronotum. **c.** Detail of bases of wings. **d.** Detail of abdomen, showing the crop contents in relief.

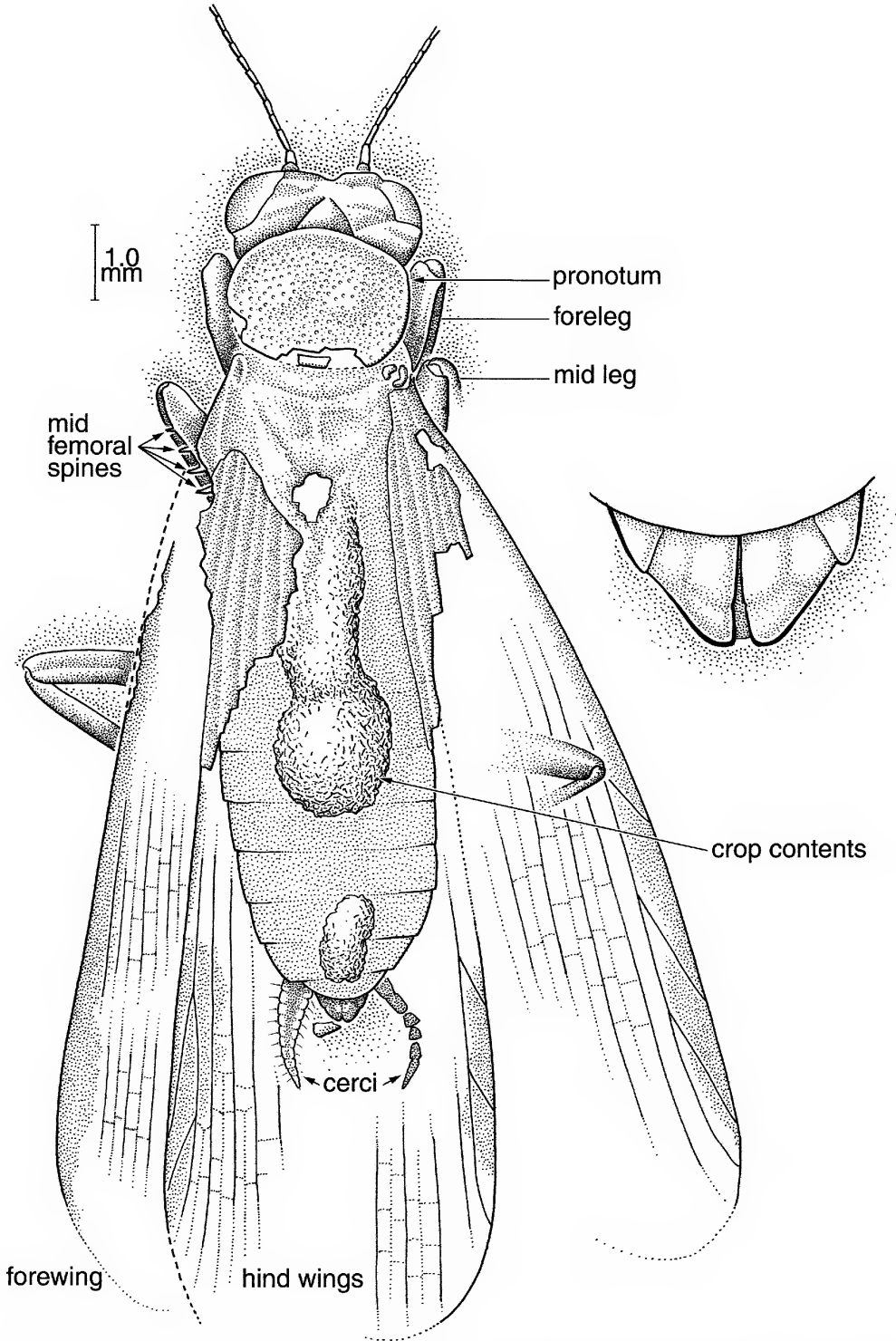


Fig. 17. Illustrated rendering of *Santanmantis axelrodi*, holotype, with detail of terminalia.

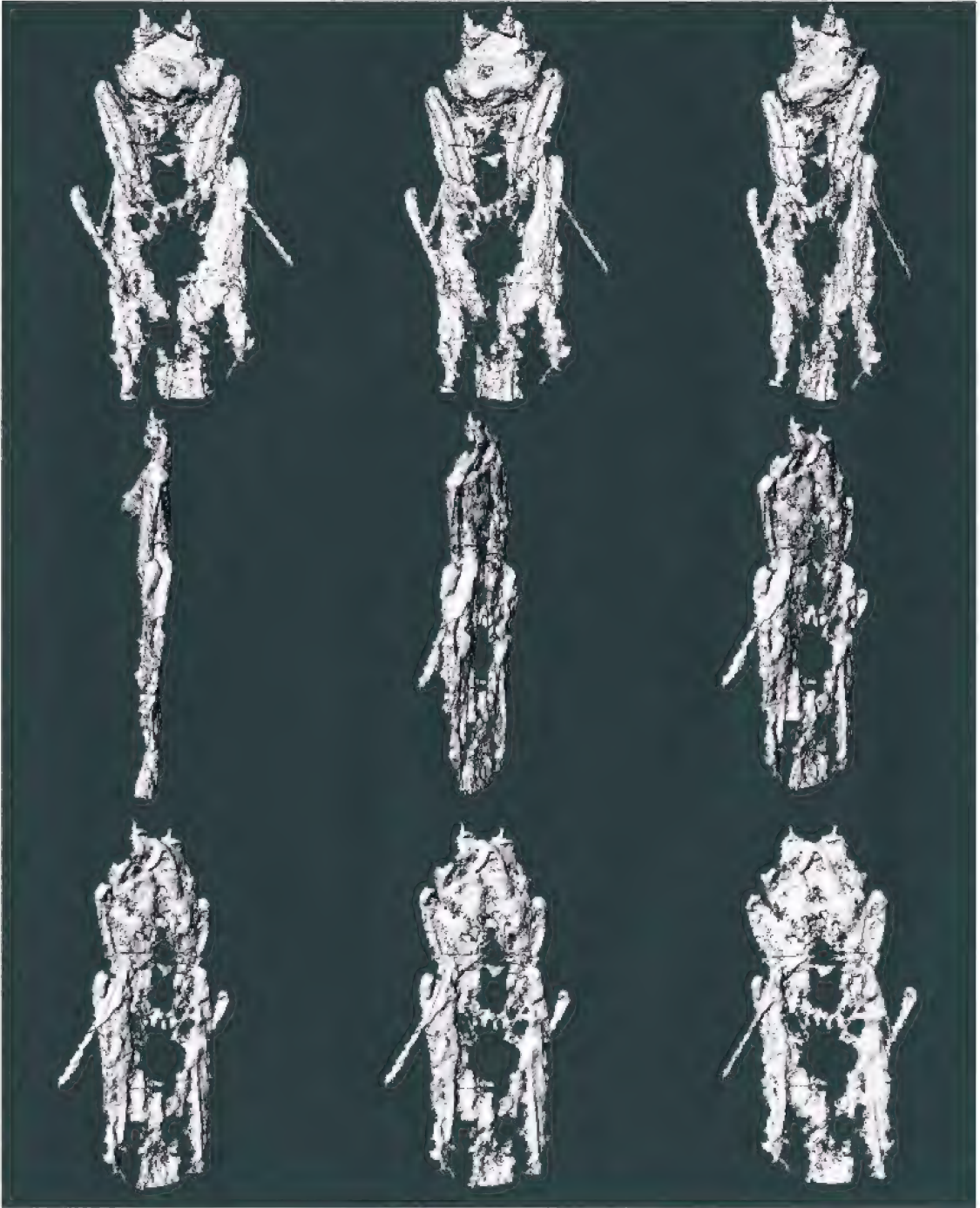


Fig. 18. High-resolution CT scans of the holotype of *Santanmantis axelrodi* (AMNH 1957), showing various views of the anterior half. **Top:** Completely ventral (left, to oblique ventral, right). **Middle:** Completely lateral (left) to oblique lateral (right) (note great compression of the specimen). **Bottom:** Dorsal view, oblique (left) to completely dorsal (right). See text for description of methods and parameters.

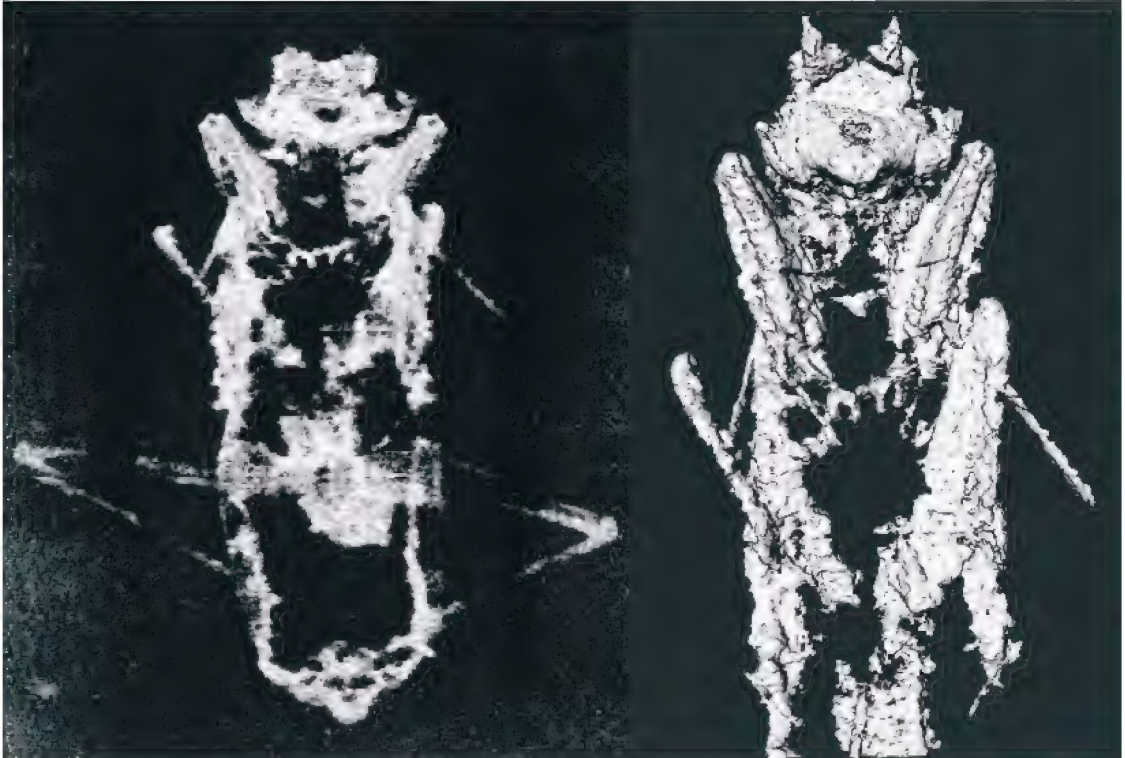


Fig. 19. High-resolution CT scans of holotype of *Santanmantis axelrodi*. *Left*: a volume-rendering of complete specimen, exposing more of the long, slender hindlegs. *Right*: a more detailed, surface-rendered view of the ventral surface of the anterior half (cf. fig. 18). The rounded topography of the specimen and lack of spines and other fine structures are due to the resolution of imaging (14 μm), not the actual preservation. The bases of some spines on the foretibia and femur are visible.

nearly reaching margin of anal lobe. Wing lengths slightly longer than total length of body with cerci and exclusive of antennae (body length/forewing length = 0.82–0.94); wing length approximately four times the width (table 2). Fore- and hindwings homonomous, though anal regions (i.e., presence of expansive fan on hindwing) were not preserved. Forewing venation: Vein Sc long, ends at level of middle of wing; R pectinate, with 5–6 main branches, including an apical fork (some branches are forked). Vein M is a simple fork, its base proximal to the end of Sc. Cu_1 with 4 main branches, bases of 2 most proximal branches very close. Claval furrow at CuA_2 well developed, being strongly arched and defined in relief (e.g., figs. 20c, 22c, f). CuP incomplete, distally shortened, with free end not joining CuA_2 ; A with two main branches. Only a portion of

hindwing tip was preserved (SMNS 112: fig. 23).

Abdomen: Relatively short and stout, length approximately 1.3 \times the width. Contents of a distended crop and portions from midgut were preserved in two specimens (AMNH 1957 and SMNS 115) (see below). Cerci typically blattoid, well developed, 1.05–1.37 mm long and tapered apicad to fine point; with approximately 10 visible segments (best seen in left cercus of holotype), each segment with long fine setae. Ovipositor (gonapophyses, gonoplacs) protrudent, but short and broad; flanked by pair of small, triangular subgenital plates and with two pairs of small, mounded areas dorsally.

TYPE AND OTHER SPECIMENS: All are from Brazil: Ceará, Crato Member of the Santana Formation (Aptian: Lower Cretaceous).

Holotype, AMNH 1957 (figs. 16–19): A

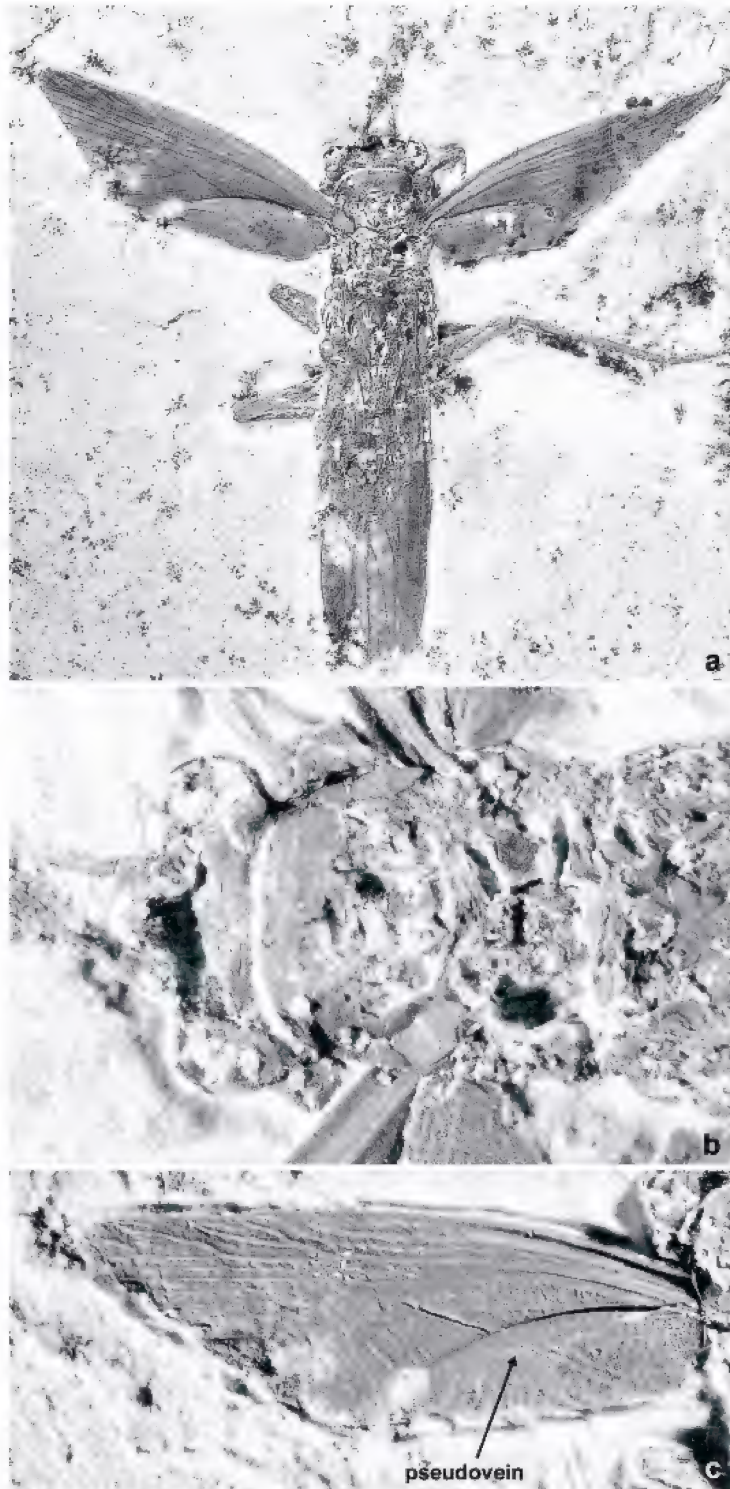


Fig. 20. Paratype of *Santanmantis axelrodi*, AMNH 1956. **a.** Complete specimen, dorsal view. **b.** Detail of head and pronotum. **c.** Detail of left forewing. The membranous apical half of both forewings were not preserved.



Fig. 21. Santana Formation Mantodea in the SMNS. **a.** Paratype of *Santanmantis axelrodi*, SMNS 115. **b.** SMNS 114, probably a different species (see text). **c.** Paratype of *Santanmantis axelrodi*, SMNS 113. Photos of *b* and *c* are courtesy of Dr. Günter Bechly (SMNS).

complete specimen, though the wing venation of this specimen is not as well preserved as in AMNH 1956, SMNS 112, 113, and 115. Proportions of various body structures indicate it is the same species as the other specimens. HRCT scanning of the holotype further revealed features not seen in the paratypes, particularly of the head and forelegs.

Paratype, AMNH 1956 (figs. 20, 24): A beautifully preserved, complete adult with

forewings spread but hindwings folded over the abdomen. Apical third of forewings lost, probably because they are membranous; preservation of remaining, sclerotized portions of forewings excellent, showing significant relief. Pronotum subdiscoid; portions of femur and tibia of right foreleg exposed (but not revealing spines), as are portions of mid- and hindlegs.

Paratype, SMNS 112 (fig. 22a): A beau-



Fig. 22. *Santanmantis axelrodi* paratypes. **a–c.** SMNS 112, showing dorsal habitus (*a*), detail of head and pronotum (*b*), and base of forewing with claval furrow (*c*). **d–f.** SMNS 172, showing habitus (*d*), detail of head and pronotum (*e*), and base of forewing (*f*) with raking light that depicts claval furrow in relief.

tiful specimen with dorsal surface preserved; forewings spread and nearly completely preserved; hindwings folded and covered beneath abdomen. Pronotum preserved (fig. 22b); portions of right midfemur exposed and most of right hindtibia and tarsus. Abdomen well preserved, though cerci barely discernable.

Paratype, SMNS 113 (fig. 21c): A beautifully displayed adult with the forewings

spread, revealing virtually all of the forewing venation (fig. 23). A color photograph of the specimen is in an exhibition catalog (Bechly, 2001), where the specimen was identified as a chaeteessid. Portions of hindwing venation preserved, though no diagnostic details evident. Dorsal portions of head damaged. Prothorax appears to be saddle-shaped with anterior edge emarginate. A portion of what appears to be a midleg protrudes from under

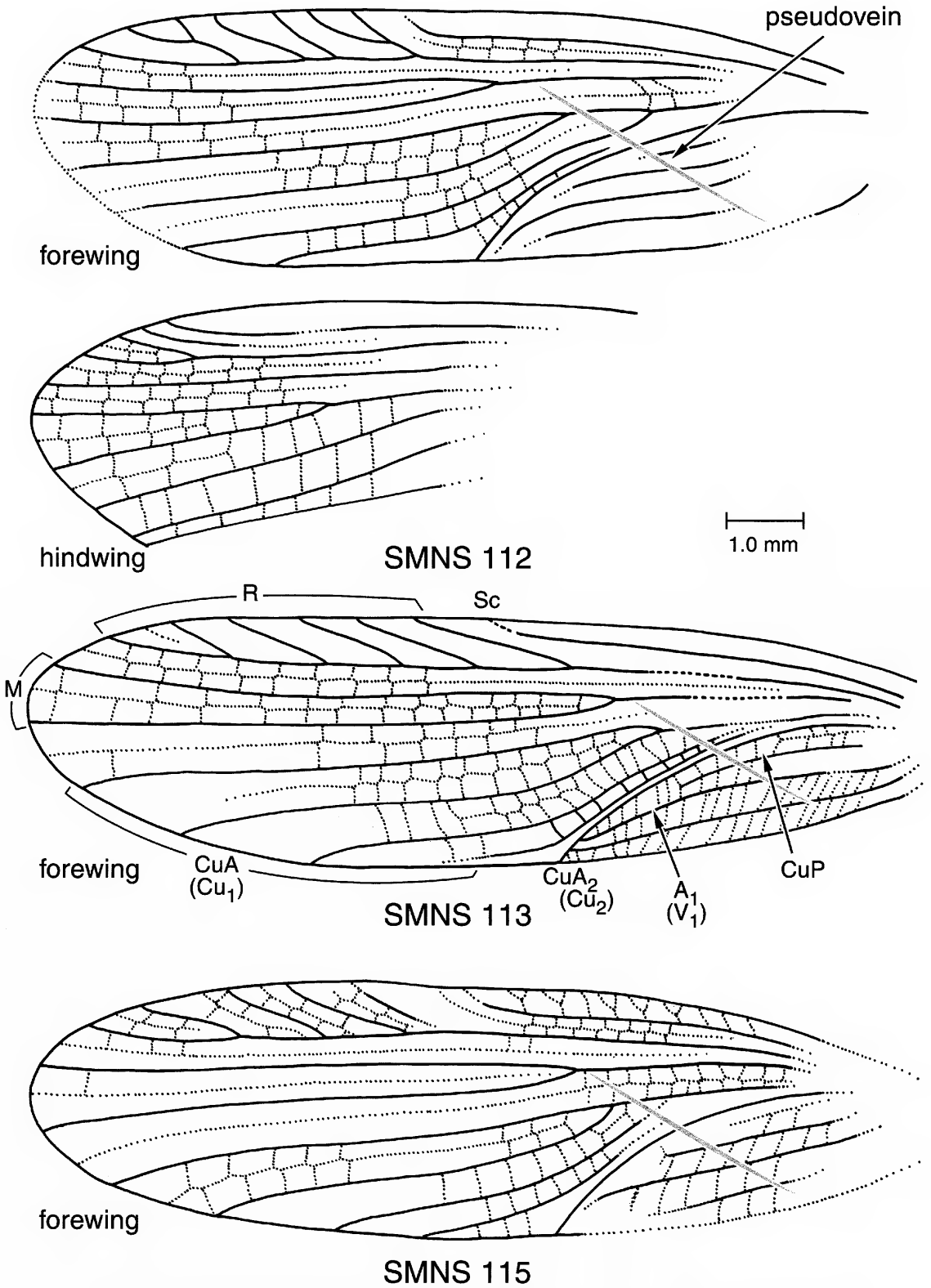


Fig. 23. Wing venation of *Santanmantis axelrodi* paratypes, showing slight variation.

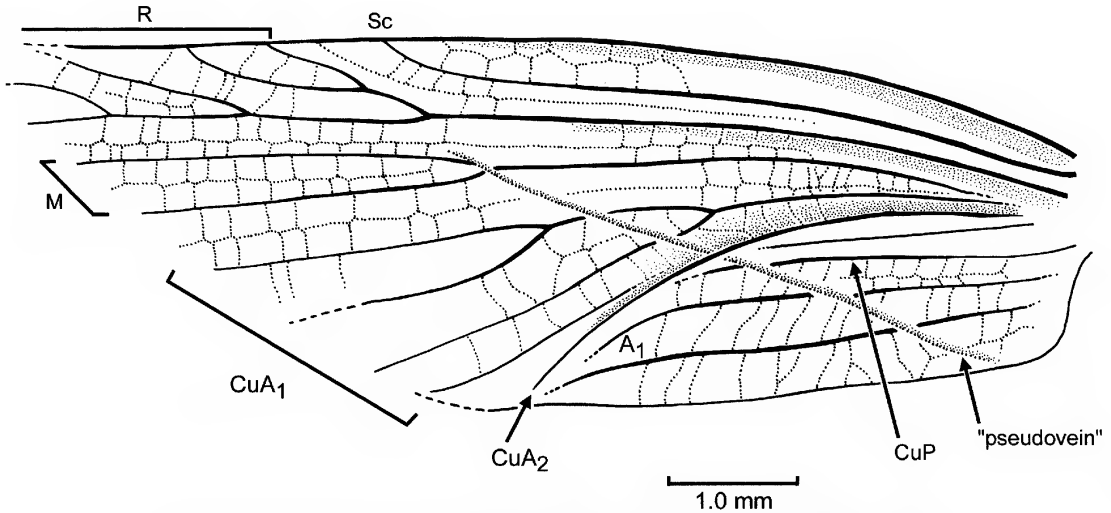


Fig. 24. Left wing of *Santanmantis axelrodi* paratype, AMNH 1956.

left forewing. Portions of what is probably left hindleg are exposed, including distal portion of femur; a long, thin tibia; and tarsi. Small spines occur along one edge of tarsi and apical portion of tibia. Forelegs not visible; probably folded beneath head and pronotum, buried in matrix.

Paratype, SMNS 115 (figs. 21a, 23): Headless specimen with ventral surface ex-

posed; right forewing is spread, revealing venation. What appears to be the left fore- and hindwings are spread out, but overlapping venation makes venation difficult to discern. Abdomen broad, filled with material (probably ingestate); portions of legs preserved: right hindleg (femur and tibia only), base of left hindleg; left midleg (femur + tibia + tarsus). What appears to be left midfemur has

TABLE 2
Measurements of *Santanmantis axelrodi* Specimens (in mm)

	AMNH		SMNS				
	1957	1956	112	113	114	115	172
Body length (exclusive of cerci)	11.3	10.16	9.7	-	10.2	-	9.5
Pronotum width	2.4	2.35	2.0	-	-	-	2.2
Pronotum length	1.8	1.71	1.4	1.5	-	-	1.5
Head width	2.5	2.64	2.2	-	2.4	-	2.7
Forewing length	12.0	-	11.8	13.0	-	12.0	11.1
Forewing width (greatest)	-	2.83	3.1	3.5	-	3.2	3.1
Hindwing length	11.4	-	11.3	13.0	-	-	10.8
Length wings extended past tip of abdomen	4.5	3.67	5.5	-	3.5	-	4.6
Legs							
Midfemur length	-	2.53	-	-	-	3.1	-
Midtibia length	-	4.00	-	-	-	4.1	-
Midtarsus length	-	-	-	-	-	2.7	-
Hindfemur length	4.6 ^a	-	-	-	-	2.7	-
Hindtibia length	4.8 ^a	-	4.1	4.6	-	-	-
Hindtarsus length	-	-	2.3	-	-	-	-
Cercus length	1.4	-	-	-	-	-	1.0

^a Structures hidden in matrix, measured from HRCT images.

row of at least 8 short, ventral spines. Most of thorax is scraped away, so the pronotum is not preserved, nor are forelegs.

Paratype, SMNS 172 (fig. 22d–f): Dorsal surface is exposed; wings poorly preserved (venation barely discernable, though revealing a deep claval furrow [fig. 22f]). Left forewing outstretched, left hindwing and right fore- and hindwings folded over abdomen. Abdomen well preserved, including left cercus. Best portions of specimen are head and pronotum (fig. 22e).

SMNS 114: A complete adult (fig. 21b) with ventral surface exposed and wings folded, so venation not preserved. The forelegs appear to have a short, stout femur and tibia, rather different from the HRCT scans of the holotype, which is why this specimen was not assigned as a paratype of the species. Its apparent pedunculate eyes may be due to the matrix lying over the central front portion of the face.

ETYMOLOGY: Patronym in honor of Dr. Herbert Axelrod, for his interest with Santana fossil insects and his generosity to the AMNH.

DISCUSSION: The holotype and five paratypes clearly represent a new genus of basal mantis, not placement in the basal living family Chaeteessidae (Bechly, 2001: 56) (see cladistic analysis, below). These specimens represent one of two superbly preserved Cretaceous mantis species. *Santanmantis* lacks synapomorphies distinct to all living mantises, including *Mantoida* and *Chaeteessa*, as given in the diagnosis. *Santanmantis* is distinct from *Baissomantis* (L. Cretaceous, Eurasia), which has more dichotomous branching in R (vs. pectinate), more branches in CuA_1 (5 or 6, vs. 4), a complete CuP (figs. 23, 24), and no pseudovein. The two groups, though, have distinct plesiomorphic similarities, particularly the strongly arched claval furrow—a condition intermediate between roaches and more derived mantises. The extremely long wings (or, conversely, a very short abdomen) in *Santanmantis* are unusual, as most fully winged Mantodea and Blattodea have the tips of the wings extended to the apex of the abdomen or slightly beyond. In *Santanmantis* the wings extend well beyond the abdominal apex by more than one-third the wing length. This condition is in-

termediate between what is found in Isoptera and the rest of the Dictyoptera.

A preserved and full crop in the type specimen offered an apparent opportunity to confirm if the diet of *Santanmantis* was indeed predatory. Crop contents of mineralized insect fossils are sometimes well preserved (e.g., Krassilov and Rasnitsyn, 1999), and this was especially expected for this specimen given the preservation of relief, of tissues, and even cellular structures in Santana fossils (Grimaldi and Maisey, 1990; Martill, 1988). Small fragments of the crop contents were studied using the AMNH Zeiss DSM-1 SEM, in order to scrutinize for fragments of plant or animal remains. If present, fragments of plant or arthropod cuticle would have been preserved, as these are particularly durable, but no biological structure was recognized in these samples. Though *Santanmantis* was clearly predatory (and possibly a scavenger as well), the crop of this specimen may have been filled with soft tissues.

Genus *Vitimiphotina* Gratshev and Zherikhin

Vitimiphotina Gratshev and Zherikhin, 1993: 154.

Type Species: *V. corrupta* Gratshev and Zherikhin, 1993: 155 (Early Cretaceous, Russia). By original designation.

DIAGNOSIS: Known only as portions of wings (PIN3064/8587, 3064/419), defined originally by Gratshev and Zherikhin on the basis of the following most significant features: wing with extensive dark patterns; R with single apical fork; M 2-branched, close to R but then strongly divergent; CuA with 6 apical branches.

INCLUDED SPECIES: Monotypic.

COMMENTS: The incomplete specimens on which the genus is based are too poorly known to include in a phylogenetic analysis and classification.

PHYLOGENY OF BASAL MANTISES

Characters used for a cladistic analysis were external, comprising features of the head, wings, and legs. Spination of the forelegs accounts for significant characters; fortunately, there is little ontogenetic change between nymphs and adults in mantis spination. A more exhaustive search for characters

would involve the male and female genitalia (i.e., LaGreca, 1954; Klass, 1997, 1998a) and even internal features (Klass, 1998b, for the proventriculus). Preliminary results indicate that there is significant variation in shape and structure of sclerites of the prothoracic and cervical region of Mantodea (D. Grimaldi, unpubl. data). Characters gleaned from this portion of the body must await a more detailed comparative study since most of these characters would not be observable in fossils, particularly because they are so intricate. The extreme asymmetry in dictyopteran male genitalia, for example, has even led to considerable controversy about homologous structures in this part of the body (e.g., Grandcolas, 1996; Klass, 2001), though the work by Klass on innervation and musculature of genitalic structures has helped to clarify problems. Accurate identification of genitalic features among a broad array of mantises is a very large project out of scope for the present one. Moreover, many characters seen in the earliest mantis fossils (e.g., presence/absence of forefemoral brush, well-developed and strongly curved claval furrow) represent variation that does not occur in living mantises.

CHARACTERS

1. Blattodean-type discoid pronotum is reduced, not covering the head. Plesiomorphically, it is as occurs in most living and Paleozoic roaches, which is large enough to shield most of the head or even sometimes the whole head in dorsal view.
2. Forelegs raptorial, spiny, and folded under the thorax at rest, with associated movable forecoxa. Plesiomorphically, the forelegs are not differentiated from the others and are used in walking.
3. Eyes large, exophthalmic, with a large frontal field. Plesiomorphically, the eyes do not occupy the entire lateral surface of the head, nor are they bulging with a large frontal area, and they usually have the fronto-mesal margin emarginate.
4. Loss or great reduction of the claval furrow, wherein vein CuA₂ runs in the tegminous forewing. Plesiomorphically, this furrow is very distinctive and well developed (e.g., figs. 20c; 22c, f).
5. Midfemur without spines along its length. Plesiomorphically, the midfemur has spines, as in roaches and in *Santanmantis*.
6. Mid and hindlegs are long and slender and are the only legs involved in walking, or at least appear structurally so. Plesiomorphically, all three pairs of legs are involved in locomotion, and the mid- and hindlegs are not particularly longer or more slender than the fore pair.
7. Claval furrow in the forewing is not arched, at best it is slightly curved and often straight. The plesiomorphic situation is found in most modern roaches (some, like Plectopterinae, have lost this feature), in Paleozoic roachoids, and some of the most basal, Cretaceous mantises (e.g., figs. 5, 6, 20, 22–24).
8. At the base of the hindwing is a small but fully formed crossvein, r-cu. Plesiomorphically this vein is absent. As would be expected, this character is virtually impossible to see in fossils. Only two Cretaceous fossils have the basal portions of the hindwings preserved (*Cretophotina tristriata* and *Baissomantis maculatus*, fig. 6), but preservation of the r-cu crossvein in both is ambiguous or obscure.
9. In the region near the middle of veins M and Cu of the forewing is an oblique, thickened (and sometimes pigmented) structure, called the “pterostigma” by some authors, or “pseudovein” (Nel and Roy, 1996) (figs. 4c, 5b, c; 6; 20c; 23, 24). This structure is actually a thickened, sclerotized area of the wing membrane and not a vein. It is not homologous to the true pterostigma in insects, which is located at the apex of the radial vein near the wing margin and usually has more discrete edges. In the Early Cretaceous *Santanmantis* from Brazil the pseudovein is very long, extending from the basal forks of M and Cu and through CuP and nearly to the margin of the anal lobe. Contrary to comments by Nel and Roy (1996), the pseudovein is not “special” to *Chaeteessa*, but is present in various forms throughout Mantodea. Plesiomorphically, this structure is absent. Since it is a sclerotized structure, its apparent absence in compression-fossil wings is usually not ambiguous.
10. Forewing with vein R simple or at best with 2 main branches. Plesiomorphically, the radial field is large, comprised of 3–4 main branches of R. *Metallyticus* is the only extant genus with 3 branches of R; presumably this is a reversal.
11. Pronotal shape is square or rectangular, with sides usually down turned (saddle-shaped). Plesiomorphically, the pronotum

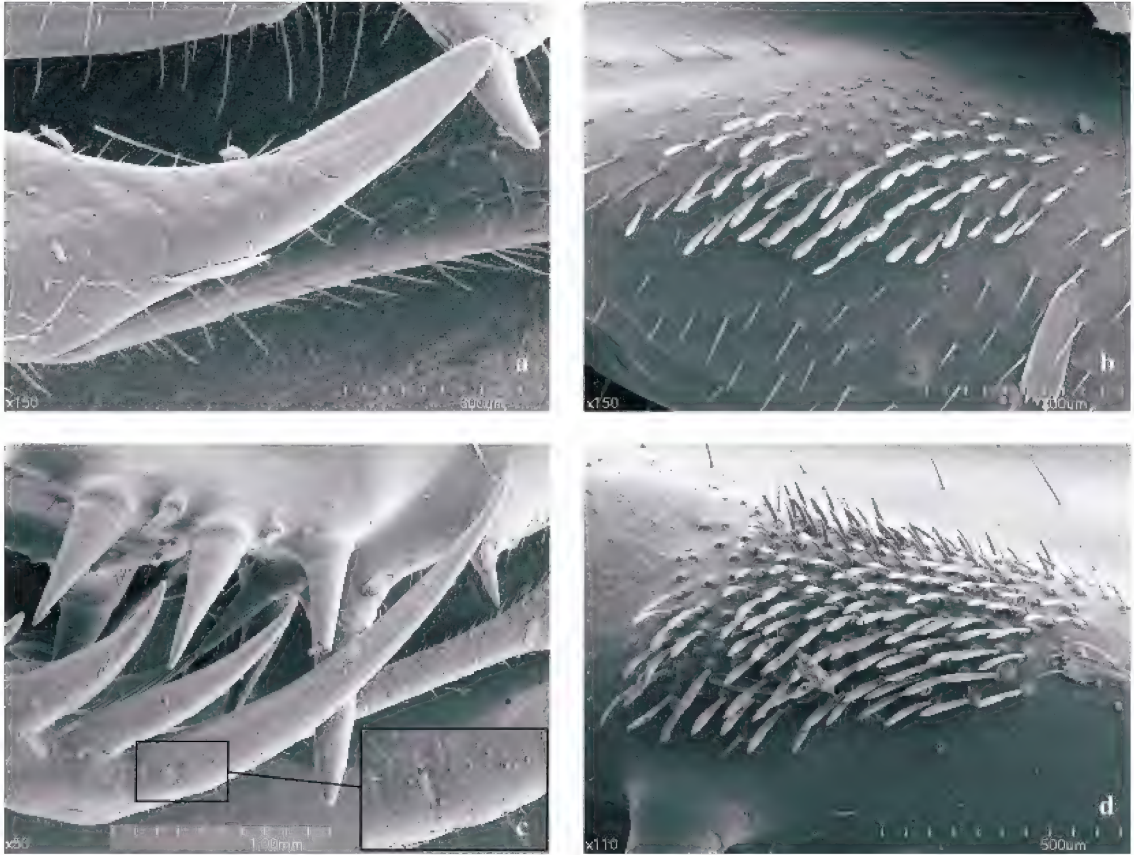


Fig. 25. Scanning electron micrographs of tibial spur (**a**, **c**) and femoral brush (**b**, **d**) in a “lower” mantis (*Amorphoscelis*: **a**, **b**), and a “higher” mantis (*Pseudocreobotra*: **c**, **d**). Note the barely discernible suture between the spur and tibia in **c** (in detail).

is discoid (rounded or nearly so), as occurs in most extant roaches and Paleozoic roachoids. Caution must be used in observing this feature. The first specimen of *Santanmantis* studied here (the holotype) had an apparently discoid pronotum, but subsequent study of additional specimens revealed the pronotum to be slightly to distinctly quadrate, so the shape of the holotype’s pronotum was probably slightly deformed.

12. Forefemur with a patch of fine, short setae or spinules on inner surface, nearer the distal end (the forefemoral “brush”) (fig. 25). Plesiomorphically, the brush is absent.
13. Forebasitarsomere long, its length equal to or greater than (sometimes considerably so) the length of the foretibia (without the spur). Plesiomorphically, the length of this basitarsomere is 0.5–0.7× the foretibial length, as is found in *Chaeteessa* and some of the Cretaceous mantises, though some

Mantoidea have secondarily evolved a reduction of this segment.

14. Forefemur with discoidal spines present, usually 3–4 located on the ventral surface at the proximal end and between the mesal and lateral rows of spines. Plesiomorphically, these are absent.
15. Forefemur with a lateral row of 4–5 spines and a mesal row of generally 8 or more similar spines. This is a fairly conservative arrangement in Mantodea, with the most notable exceptions being cases of extreme modification. *Amorphoscelis*, for example, has lost most of the forefemoral spines. Plesiomorphically, spines do not occur, with the femur armed merely with stiff setae, as in *Burmantis*, *Chaeteessites*, and *Jersimantis*.
16. Foretibia with a large apical, articulated spine, or a spur on the inner surface. Plesiomorphically the spine or spur are absent.
17. Foretibia with a distinctive, long, apical

- spur (sometimes called the "claw") on the inner surface. This spur is typically heavily sclerotized, with its articulated base barely discernable (fig. 25c) and situated at the apex of an extension of the tibia that projects well beyond the tibial-tarsal joint. Plesiomorphically, the spur is absent, or there is a large, spinelike, articulated seta in this spot, sometimes also with a smaller one on the outside surface.
18. Hind wing with vein 1V (A1) lost (Smart, 1956). Plesiomorphically, it is present, as is found in the living genera *Chaeteessa* and *Metallyticus*.
 19. All three ocelli are lost. Plesiomorphically, all three ocelli are present (as in most Mantodea or basal Neoptera), or at least the two lateral ocelli (as in roaches and most termites). Care must be taken in assessing this feature in nymphal mantises, as ocelli are minute and often obscured.
 20. Forewing with vein PCu incomplete (Smart, 1956), not extended to wing margin. Plesiomorphically, it is complete, as is found in *Mantoida*, *Metallyticus*, and Baisomantidae. Some Hymenopodidae and Mantidae have a complete CuP, but this is obviously a reversal of the groundplan state of an incomplete CuP found among virtually all living mantises.
 21. Females with wings reduced or absent. Plesiomorphically, the females have wings as well developed as in males.
 22. A metathoracic hearing organ is present that is morphologically unique in insects (Yager and Hoy, 1986; Yager, 2000). The structure occurs ventrally, with the external opening being a slit between the hindcoxae. The tympana of the hearing organ are comprised of a pair of drop-shaped areas of cuticle recessed into the groove, which oppose each other. Mantises are auditory cyclops and tone deaf, distinguishing neither directionality nor frequency of sound. Plesiomorphically, the groove and tympana exist, but specialized tracheal sacs and sensilla that magnify and transduce the sounds are absent (Yager, 2000).
 23. Pronotum is elongate, with a length 2–20× its width. Plesiomorphically, the length is barely longer than the width.
 24. Cerci are long, with at least 20 segments. Plesiomorphically there are 8–15 segments, as found in roaches and most other mantises. Some Mantodea have significant reduction of the cerci (e.g., *Eremiaphila*, no doubt an adaptation for the extreme conditions of its habitat); some Mantidae have more than 20, but this is clearly secondarily derived.
 25. The setae in a patch or brush on the forefemur are flattened and scalelike, which occurs in all living Mantodea. The plesiomorphic state, where the setae are only slightly thickened, occurs in *Burmantis asiatica* (fig. 8a), observation of which is a result of unusually good preservation. In this fossil the brush is microscopically visible, and the setae are barely flattened and least modified among all other mantises. Scanning electron microscopy of brush setae in various living mantises indicates that the setae are always flattened and scaliform (fig. 25b, d), or have a shape that is featherlike.
 26. The forefemur has a row of 5 ventromesal spines and 3 long ventrolateral spines. This is a feature that occurs in *Burmantis* species. Plesiomorphically, the forefemur has just stiff, sharp setae (as in *Jersimantis*) or numerous spines arranged as in *Mantoida*, *Chaeteessa*, and *Ambermantis*.

CLADISTIC ANALYSIS

Table 3 is a matrix of 26 morphological characters for 20 living and fossil taxa (minimum possible steps of 25, maximum possible steps 80). Half of the cells (263 of 520), have missing entries, denoted by a "?". Only two cells of living species have missing entries. These involve *Amorphoscelis* and refer to the spination of the forelegs, which is extremely reduced in this genus. As expected, virtually all missing entries involve fossil taxa, but there is a very uneven distribution of these among the fossils. Rock fossils averaged 17 missing entries (range of 10–20), with the fewest being in the completely preserved *Santanmantis*. Amber fossils averaged 10 missing entries (4–14), with the fewest in *Ambermantis*, preserved in entirety as an adult.

Cladistic analysis used the phylogenetic program WINONA, version 2.0 (Goloboff, 1999), run with a PC having a 256-MHz processor and 40-GB memory. Also used was PAUP version 4 (Swofford, 2002), run on a MacG4 computer with dual processors. Having half of the matrix with missing entries was computationally intensive and significantly complicated the analyses. Analyses in WINONA, for example, yielded more than

TABLE 3
Matrix of Taxa and Characters for Cladistic Analysis

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Santanmantis axelrodi</i>	1	1	1	0	0	1	0	?	1	0	1	?	?	?	?	1	?	?	0	1	0	?	0	0	?	?				
<i>Baissomantis</i> spp.	?	?	?	1	?	?	0	?	0	0	?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?				
<i>Cretophotina</i> spp.	?	?	?	1	?	?	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?				
<i>Jersimantis burmiticus</i>	1	1	1	?	1	1	?	?	?	1	0	0	0	0	1	0	?	1	?	?	?	?	?	0	0	0	0			
<i>Jersimantis luzzii</i>	1	1	1	?	1	1	?	?	?	1	0	0	0	0	1	0	?	1	?	?	?	?	?	0	0	0	0			
<i>Chaeteessites minutissi</i>	1	1	1	?	?	?	?	?	?	1	?	0	0	0	1	0	?	?	?	?	?	?	?	0	?	?	?			
<i>Burmantis asiatica</i>	1	1	1	?	1	1	?	?	?	1	1	1	0	0	1	0	?	?	?	?	?	?	?	0	0	0	1			
<i>Burmantis lebanensis</i>	1	1	1	?	1	1	?	?	?	1	1	?	0	0	1	?	?	?	?	?	?	?	?	0	0	?	?			
<i>Cretomantis larvalis</i>	1	1	?	?	0	1	?	?	?	?	1	?	0	0	1	0	?	?	?	?	?	?	?	0	0	?	?			
<i>Electromantis sukatshev</i>	1	1	1	?	1	?	?	?	?	1	?	1	0	1	1	0	?	?	?	?	?	?	?	0	?	0	?			
<i>Ambermantis wozniaki</i>	1	1	1	1	1	1	1	?	1	1	1	1	1	0	1	1	1	?	0	1	?	?	?	0	1	1	0			
<i>Arverineura insignis</i>	?	1	?	1	?	?	1	?	1	1	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?				
<i>Chaeteessa</i> spp.	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	1	0	0	0	1	0	0	1	1	0		
<i>Mantoida</i> spp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0			
<i>Amorphoscelis</i> spp.	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	0	1	1	0	0	0	0	1	0			
<i>Metallyticus</i> sp.	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0			
<i>Eremiaphila</i> spp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	1	0				
Empusidae spp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0			
Hymenopodidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0			
Mantidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0			

10,000 most parsimonious (MP) trees, with 35 steps. The strict consensus tree was completely unresolved. PAUP analyses were run with the characters ordered and unordered, in each case using 10 replicate analyses with each one having the input of matrix data randomized. Searches for MP trees were terminated after 49,600 trees were found (memory could store no more). The strict consensus of the MP trees was completely unresolved, no doubt a result of the many missing characters, but still very unusual given that significant phylogenetic structure exists for the living families that does not conflict with other parts of the phylogeny.

Two majority-rule (MR) trees were obtained, one for ordered characters and the other for unordered characters, both with significantly resolved topology (fig. 26). Both MR trees yielded poorly supported groupings, such as the following:

1. *Santanmantis* + *Cretomantis* (the former a complete adult, the latter a nymph, with very few shared features);
2. *Baissomantis* as part of a basal pentatomy, even though its wings lack a distinctive syn-

apomorphy (character 9, the pseudovein) common to all other winged mantises;

3. *Ambermantis* as part of a basal polytomy of living families, even though *Ambermantis* lacks a derived venational feature of living families (character 10) and distinctive features of foreleg spination found in the Chaeteessidae, or in all other mantises (character 14, discoidal spines).

Thus, significant aspects of the MR trees were not compelling. An alternative, preferred cladogram was constructed by hand, some portions of which are in agreement with the MR trees, whereas other portions differ considerably (fig. 27). This preferred tree was based on some inference regarding the probability of the existence of synapomorphies not directly observed in some fossils. The more inclusive the synapomorphy, and the more exclusive (i.e., the more recently derived) the taxon, the higher the probability that the taxon possessed the synapomorphy (or secondarily lost the feature). For example, though *Cretophotina* is known only as wings, it is a reasonable hypothesis that this genus possessed raptorial forelegs

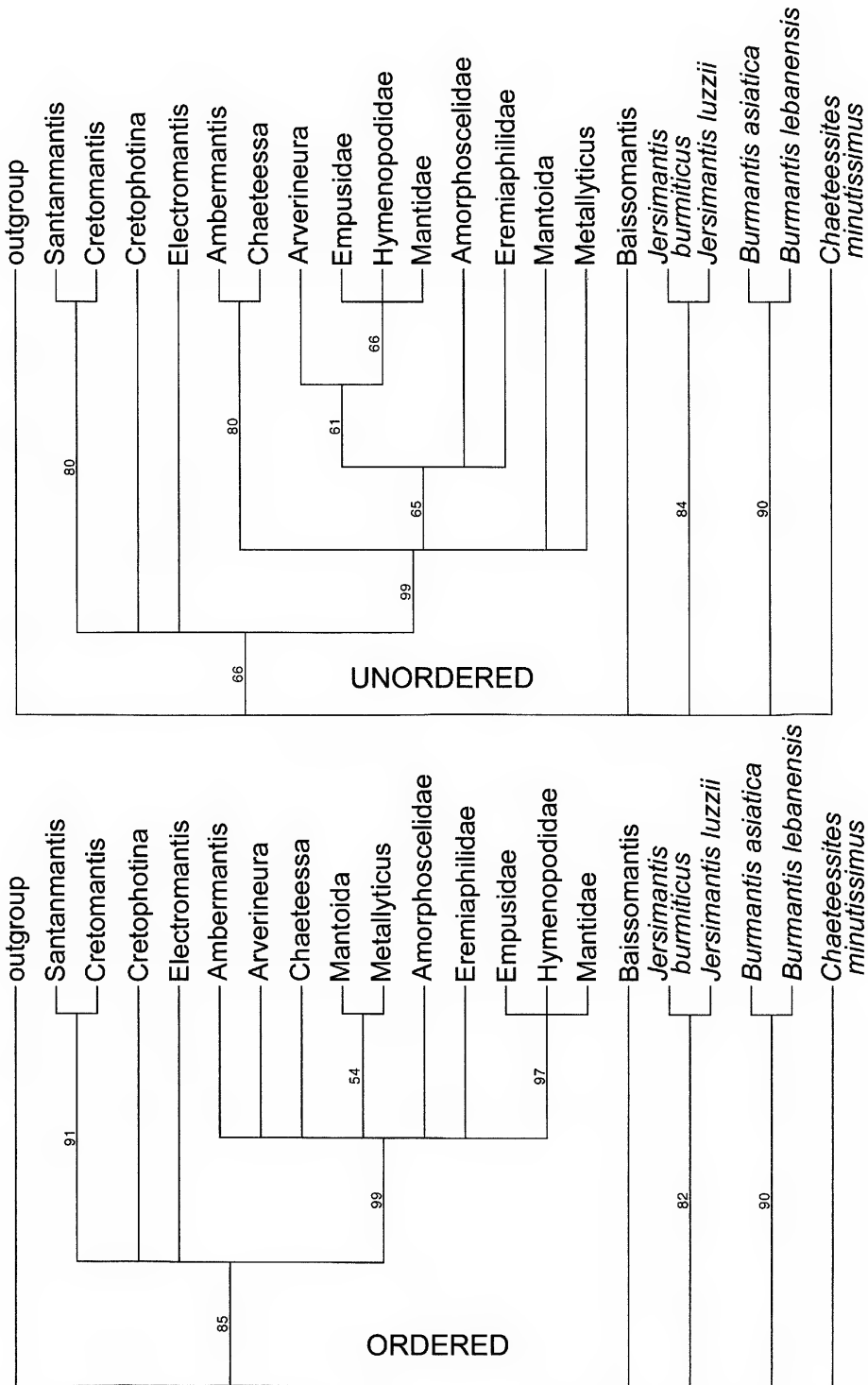


Fig. 26. Majority-rule cladograms (with characters ordered and unordered) (L = 36, CI = 0.72; RI = 0.81) of Cretaceous genera and living families of Mantodea, based on the matrix in table 3. Numbers at nodes are bootstrap values.

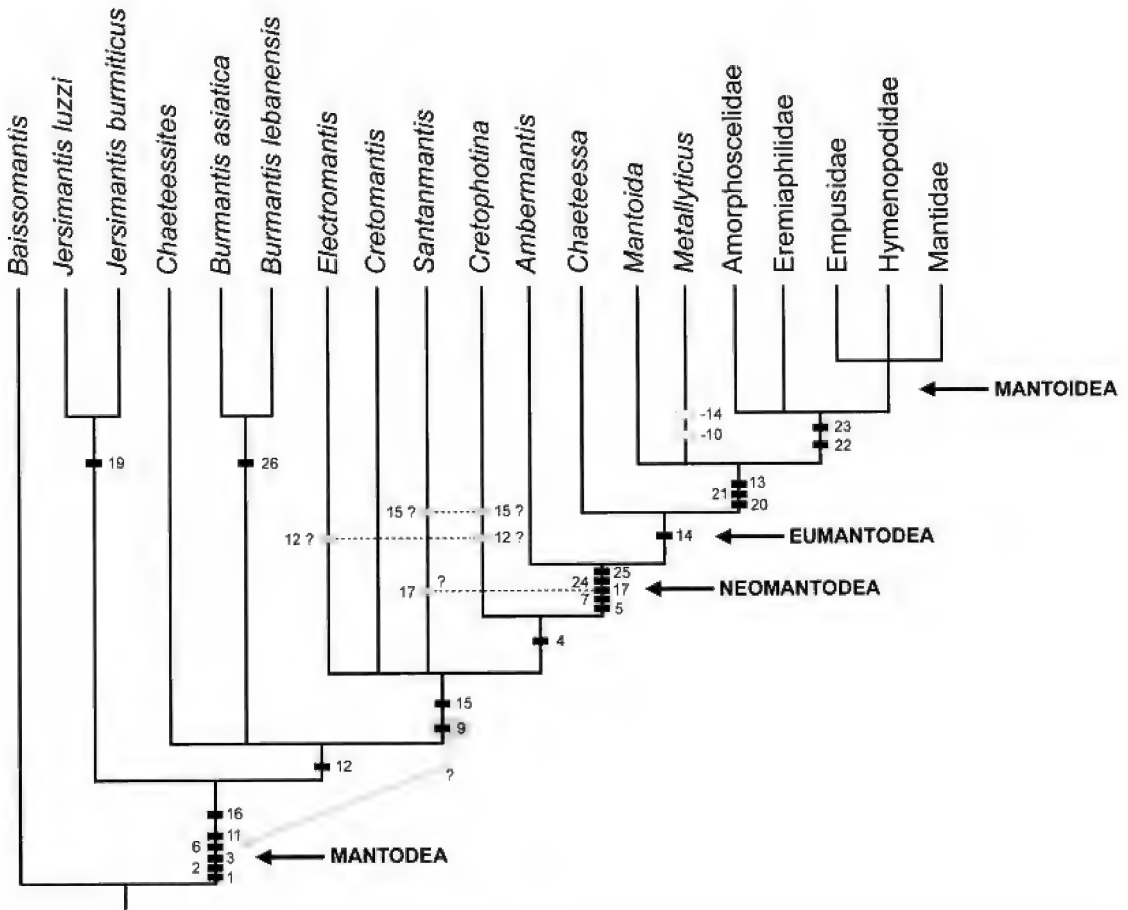


Fig. 27. Preferred cladogram for basal relationships of the Mantodea. Ambiguities in character distribution are indicated by shading. Further work will focus on Eumantodea. See text for discussion.

(character 2) since more basal genera possessed raptorial forelegs. In other words, *Cretophina* possessed certain derived, more exclusive features (i.e., reduction of claval furrow, presence of pseudovein, characters 4 and 9, respectively) highly correlated with having raptorial forelegs. Likewise, it is a reasonable hypothesis that *Cretophotina* had a forefemoral brush, as all but the three most basal genera possess this feature. Conversely, given that the mantis ear (character 22) is present in the Mantoidea but not in basal living families, it is a reasonable hypothesis that the ear did not occur in Cretaceous mantises since they are even more basal on the basis of independent evidence. Assumptions like these are not accommodated in parsimony or majority-rule analyses, but they may be warranted in that they result

in a testable hypothesis, but more importantly one that appears predictive. Certainly, the strict consensus tree, an unresolved bush, is erroneous. Strictly interpreted, the consensus trees depict a simultaneous origin of all mantis groups, even though 135 million years of continuous evolution separates the oldest genus from recent ones. Disciples of strict consensus methods could, alternatively, argue that the data prevent a more resolved hypothesis, but this is tautological and is even contradicted by the high bootstrap values in some clades of the MR trees. As new fossils are gradually discovered, or more completely preserved specimens of described species, there will be significant revision to the preferred phylogenetic tree. Some phylogenetic structure is required for interpretation of the Cretaceous fossils, so the one hypothesis is

offered here simply as the best available working hypothesis.

One potentially problematic aspect of this analysis is the different criteria used in the taxonomy of compression fossil and amber fossil specimens. Only body structures were available for the nymphs in amber, and only venation for the wings preserved in rocks. Thus, it is possible that there may be some synonymy between a few of the taxa in rocks from the Cretaceous of Eurasia (*Baissomantis* and *Cretophotina*) and ones known as nymphs in amber (*Burmantis*, *Chaeteessites*, *Cretomantis*, *Jersimantis*), a possibility that could only be resolved with the discovery of completely preserved adults. It is doubtful, though, that there is significant synonymy here, but any such synonymy would have little effect on the consistent occurrence of basal most mantises in the Cretaceous (see below). Fortunately, too, some stability to the systematics of Cretaceous Mantodea is provided by exquisite preservation of complete, adult *Santanmantis* and *Ambermantis*.

Despite ambiguities with the phylogenetics, new evidence does not support the classification of Cretaceous mantises proposed by Gratshev and Zherikhin (1993):

Family Chaeteessidae:

genus *Cretophotina*
Kazakhaphotina
Vitimiphotina
Chaeteessites (tentatively)
 (+ *Arverineura*, *Chaeteessa*, *Lithophotina*,
Megaphotina: Tertiary/Recent).

Family Baissomantidae:

Baissomantis

Family Cretomantidae:

Cretomantis
Electromantis

Family Amorphoscelidae:

Amorphoscelites
 (+ extant genera)

The following revised classification is proposed, in which *Baissomantis* (Baissomantidae) is considered a sister group to the true mantises, order Mantodea:

ORDER MANTODEA: Pronotum quadrate, saddle-shaped, not covering head; forelegs spined, raptorial, foretibia with large apical spine or spur, with freely moving forecoxae; mid- and hindlegs long, slender, used in walking; forewing with pseudovein.

Family Santanmantidae, new family: as defined for type genus.

Genus *Santanmantis*

Genera Incertae Sedis: *Amorphoscelites*, *Burmantis*, *Chaeteessites*, *Cretophotina*, *Electromantis*, *Jersimantis*, *Kazakhaphotina*, *Vitimiphotina*

SUBORDER NEOMANTODEA (new): Midfemur lacking spines; claval furrow straight or only slightly arched; foretibia with long apical spur; forefemur with patch of small scales on mesal surface.

Family Ambermantidae, new family: as defined for type genus.

Genus *Ambermantis*

INFRAORDER EUMANTODEA (new): All living mantises, which have forefemur with discoidal spines.

Families: Chaeteessidae, Mantoididae, Metallyticidae, Amorphoscelidae, Eremiaphilidae, and superfamily Mantoidea.

The two new families are basal to living families but they also possess unique apomorphies. Baissomantidae is still defined on the basis of plesiomorphic features and, though related to mantises on the basis of wing venational characters, it is not a mantis in the sense defined here. One could propose families for each or most of the Cretaceous genera, but given that characters preserved in the various fossils are not all comparable, it would be imprudent to formally propose any new higher taxonomic names. The two new families described are for taxa that are preserved as complete adults.

Gorochoy (2001: 357) recently commented that "it cannot be excluded that *Ponopterix* and possibly *Umenocoleus* are representatives of a second-oldest branch of Mantina [Mantodea], having a shape of head and pronotum as well as almost raptorial forelegs, similar to mantises." These two genera are roaches of the Cretaceous family Umenocoleidae. Neither *Ponopterix* nor *Umenocoleus* are known to have raptorial forelegs, either "almost" or actually. Also, the very highly modified, tegminous forewings and hindwing venation, the broad abdomen, short mid- and hindlegs, and other features preclude their close relationship to mantises.

CONCLUSIONS

There appears to be no relationship between age and cladistic rank among Cretaceous Mantodea. This can be due to problems in the phylogenetic hypothesis, to in-

adequate taxon and character sampling, or to both. It is assumed that, given sufficient stratigraphic sampling and accuracy of phylogenetic hypotheses, such a correlation would appear. What is highly significant, though, is the fact that Cretaceous mantises are consistently basal phylogenetically to living families, the Eumantodea. The Cretaceous mantises possess plesiomorphic features of venation, the forefemoral brush, forefemoral spines, and/or the foretibial spur. Clearly, mantises are in nascent stages of their evolution in the Cretaceous. True mantises, complete with raptorial forelegs and other diagnostic features like the pseudovein, probably appeared in the Late Jurassic and almost certainly no earlier. In this regard, Zherikhin's (2002) view on the relatively recent age of Mantodea is accurate, and estimates of Paleozoic mantises are extremely excessive.

Independent evidence suggests that the superfamily Mantoidea is actually quite young, perhaps even entirely Tertiary in age. The group is defined by, among other features, the distinctive cyclopean ear (Yager, 2000), which is sensitive to sounds at 25–50 Hz, or the region of bat echolocations. Stereotyped evasive behavior of flying mantises to bat calls indicate that the ear is probably an adaptation for avoidance of bats during nighttime flight (Yager, 2000). Thus, Mantoidea is a group probably not much older than the microchiropteran (insectivorous) bats, which appear suddenly in Lower Eocene strata of Europe, North America, Australia, and Africa (reviewed in Simmons and Geisler, 1998) and further diversified later in the Eocene. Basal relationships of the earliest microchiropteran fossils (Simmons and Geisler, 1998) suggest a Paleocene origin of these mammals, and almost certainly no older. The oldest mantoidean is *Prochaerododis enigmaticus*, from the Paleocene of France (Nel and Roy, 1996), which is based on a portion of a rather distinctive forewing.

Though the Cretaceous mantises have not helped to reveal a close blattodean relative, the revised fossil record provided here, I think, helps clarify the origins and earliest radiation of the mantises. Cretaceous mantises were probably superficially very similar to most species of the basal families Chaetees-

idae, Metallyticidae, and Mantoididae: small, brown, stout-bodied predators, cryptic and scuttling among leaves on the forest floor or on tree trunks. Origins and radiations of the superfamily Mantoidea in the Early Tertiary led to the array of spectacular mantises found today.

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