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The First Cretaceous Rhinotermitidae (Isoptera): A New Species, Genus, and Subfamily in Burmese Amber

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ABSTRACT

A new subfamily, genus, and species, *Archeorhinotermitinae*, *Archeorhinotermes rossi*, from Burmese amber, dated as Turonian-Cenomanian (90–100 mya) of the Cretaceous period, are described and figured. Comparisons are made between the other subfamilies of the Rhinotermitidae and the new subfamily. This is the first fossil record of the family Rhinotermitidae from the Cretaceous.

INTRODUCTION

Termites, comprising some 2900 species, are, of all the insects, arguably the most ecologically significant group. Reviews by Bignell and Eggleton (2000), Wood (1978), and Wood and Sands (1978) summarized evidence for their prodigious consumption and breakdown of cellulose, particularly in the world's tropics. In grasslands and forests, termites generally account for more carbon mineralization than any other organisms except fungi, as well as for-

the production of soil, or humification. Represented overwhelmingly today by the "higher" termites, family Termitidae, in terms of both numbers of species (70% of all termites) and biomass, termites have a global impact on the cycling of carbon and nutrients in terrestrial environments. Therefore, the origins and earliest diversification of the order Isoptera are hardly trivial considerations. Prior to termites, for example, how were significant quantities of terrestrial cellulose processed?

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The oldest termites occur in the Early and Late Cretaceous, between 135 and 70 mya (reviewed by Thorne, Grimaldi, and Krishna, 2000). During this time, termites were rare and represented almost exclusively by the basal families Mastotermitidae, Hodotermitidae, and Termopsidae, which were more widespread and apparently more diverse than at present. The only Cretaceous fossils of the “dry wood” family Kalotermitidae are *Kalotermites swinhoei* (Cockerell) and *K. tristis* (Cockerell), in Burmese amber (Williams, 1968). The family Kalotermitidae appears to be phylogenetically intermediate between the basal termite families Mastotermitidae, Hodotermitidae, and Termopsidae, and the higher Termitidae (Donovan, Jones, Sands, and Eggleton, 2000; Kambhampati and Eggleton, 2000; Thompson, Kitade, Lo, and Crozier, 2000). Here, we report the first Cretaceous record—also in Burmese amber—of the family Rhinotermitidae, which is the sister group to the termitid radiation (*idem.*). As such, this is the most recently derived termite group known from the Cretaceous. Ironically, the Cretaceous rhinotermitid we describe here has resided in a major museum for nearly a century.

The order Isoptera presumably originated in the Late Jurassic, ca. 150 mya (Thorne, Grimaldi, and Krishna, 2000), although no specimens are known from this period. The discovery of this fossil rhinotermitid, approximately 100 mya in age, indicates that the diversification of termite families apparently was condensed within the first 40–50 million years of isopteran evolution, with the major exception of the Termitidae, the oldest fossils of which are from the Eocene and may indeed reflect an explosive radiation that was very recent.

Fossils in amber from Myanmar (formerly Burma) were first known through the work of the prolific entomologist T.D.A. Cockerell, who published 13 papers alone on arthropods in Burmese amber (summarized by Ross and York, 2000). These studies were based on a collection of Burmese amber presented to Cockerell, who subsequently donated it to the Natural History Museum (NHM), London, ca. 1920. Between that time and 1990 the collection received little attention, and then was systematically studied by Andrew

Ross and colleagues. Recent reports on the systematics of arthropods in the NHM collection of Burmese amber (reviewed by Zherikhin and Ross, 2000; Rasnitsyn and Ross, 2000) confirm Cockerell’s suspicion that Burmese amber is Cretaceous, not Eocene or even Miocene as commonly believed. Most recently, a larger and more diverse collection was assembled at the American Museum of Natural History (AMNH). Study of the inclusions in this collection indicates an age of Burmese amber of probably Cenomanian to Turonian (90–100 mya) (Grimaldi, Engel, and Nascimbene, 2002). The new rhinotermitid is a specimen unique to the NHM collection.

FAMILY RHINOTERMITIDAE FROGGATT

Archeorhinotermitinae, new subfamily

TYPE GENUS: *Archeorhinotermites*, new genus, by original designation and monotypy.

DIAGNOSIS: Left mandible (fig. 1b) with a long, prominent, fingerlike apical tooth and three marginal teeth of approximately equal size, the apical tooth much longer than the three marginal teeth; fourth marginal tooth pointed and clearly visible from above (visible only in side view in living species of Rhinotermitidae); outer margin with a prominent protuberance posterior to apical tooth. Right mandible (fig. 1b) with a small subsidiary tooth at base of upper margin of first marginal tooth; second marginal tooth prominent, equal in length to first marginal tooth, with its tip at the same level and its posterior margin with a medium-sized cutting edge (longer in all other subfamilies of the Rhinotermitidae). Wings reticulate, without hairs or bristles. Forewing scale covering hindwing scale (characteristic of the Rhinotermitidae). Forewing (fig. 1d) with median vein simple, as strongly sclerotized as radial sector, and running midway between radial sector and cubitus.

DISCUSSION: This new subfamily has a number of features characteristic of the imago caste of the Rhinotermitidae: (1) Reticulate wings; (2) a large forewing scale, overlapping the hindwing scale (a feature absent only in the Psammotermitinae); (3) the fontanelle and ocelli present; (4) the left imago mandible with three marginal teeth; (5) the right imago

mandible with a subsidiary tooth at the base of the upper margin of the first marginal tooth; and (6) four-segmented tarsi. However, it differs from all the presently known subfamilies of the Rhinotermitidae—*Psammotermitinae*, *Coptotermitinae*, *Heterotermitinae*, *Termitogetoninae*, *Prorhinotermitinae*, *Rhinotermitinae*, and *Stylotermitinae*—in its distinctive mandibular dentition: the left mandible has a long, prominent apical tooth, longer than in any of the other subfamilies, with a distinct protuberance on its outer margin, close to the apical tooth, and the first, second, and third marginal teeth are almost equal in length (in all of the other subfamilies, except for the *Rhinotermitinae*, the first marginal tooth is smaller than or subequal to the second and third marginal teeth); the right mandible has a well-developed second marginal tooth, with its anterior margin extending forward as far as the tip of the first marginal tooth and its posterior margin much shorter than in all the other subfamilies.

Except for its specialized mandibular dentition, most characters in the new subfamily are primitive: the head is densely pilose; the eyes are relatively large and protruding beyond the head; the ocelli are large and separated from the eye; the fontanelle is small; the postclypeus is not arched; the wings are reticulate; in the forewing, the median and cubitus are as strongly sclerotized as the radial sector; and the tibial spur formula is apparently 3:2:2.

In addition to the general distinctions noted above, *Archeorhinotermitinae* differs from the individual subfamilies of the Rhinotermitidae in a number of other characters. It differs from *Psammotermitinae* (fig. 3a), which includes the genera *Psammotermes* and *Glossotermes*, in the following respects: the eyes are larger; the postclypeus is flat (faintly convex in the *Psammotermitinae*); the forewing scale is longer and overlaps the hindwing scale; the median and the cubitus are separate through the entire length of the forewing (fused as a single vein in the first half and separating from each other in the middle of the wing in *Psammotermitinae*).

The new subfamily differs from *Coptotermitinae* (fig. 3b), which includes the genus *Coptotermes*, as follows: the eyes are smaller; the fontanelle is closer to the posterior

margin of the head (near the middle of the head in *Coptotermitinae*); the postclypeus is broad and flat (vs. narrow and faintly arched); the pronotum is narrow (as wide as the head in *Coptotermitinae*); the forewings are reticulate and not hairy; in the forewing the median and the cubitus are as well sclerotized as the radial sector, and the median runs midway between the radial sector and the cubitus (both weakly sclerotized, with the median running close to the cubitus and branched apically in *Coptotermitinae*).

Archeorhinotermitinae is distinguished from *Heterotermitinae* (fig. 3c, d), which includes the genera *Reticulitermes* and *Heterotermes*, in several respects: the head is roundish (oval, with parallel sides in *Heterotermitinae*); the fontanelle is situated close to the hind margin of the head (vs. near the middle of the head); the ocelli are large and prominent (barely visible in *Heterotermitinae*); in the forewing the median and the cubitus are as well sclerotized as the radial sector, and the median runs midway between the radial sector and the cubitus, without branches (both weakly sclerotized, with the median running close to the cubitus and branched apically in *Heterotermitinae*).

The new subfamily differs from *Termitogetoninae* (fig. 3e), which includes the genus *Termitogeton*, as follows: the head is roundish (dorsoventrally very flat, with the sides converging anteriorly and the hind margin sinuate in *Termitogetoninae*); the anterior margin of the pronotum is even (with a projection in the middle in *Termitogetoninae*); the forewings have few hairs (thickly hairy in *Termitogetoninae*); and the median is well developed and sclerotized (vs. absent or indistinct).

Archeorhinotermitinae differs from *Prorhinotermitinae* (fig. 5), which includes the genus *Prorhinotermes*, in having its fontanelle closer to the hind margin of the head (in the middle of the head or close to the postclypeus in *Prorhinotermitinae*); the postclypeus flat and not arched (vs. considerably enlarged); the pronotum narrow (vs. wider than the head); the median and the cubitus are separate and sclerotized (vs. weak and fused); and the tibial spurs number 3:2:2 (vs. 2:2:2).

Archeorhinotermitinae is distinguished from *Rhinotermitinae* (fig. 4a–c), which includes the genera *Achorhinotermes*, *Dolichorhinotermes*,

Macrorhinotermes, *Parrhinotermes*, *Rhinotermes*, and *Schedorhinotermes*, as follows: the head is smaller; the postclypeus is flat (very strongly arched and medially projecting in Rhinotermitidae); and the fontanelle is small and without a median groove in front (vs. a median groove extending from the fontanelle up to or near the end of the labrum).

The new subfamily differs from Stylotermitinae (fig. 4d), which includes *Stylotermes* and the exclusively fossil genus *Parastylotermes*, in the following respects: the forewing membrane is moderately reticulate, without crossveins (highly reticulated, with several crossveins in Stylotermitinae); the postclypeus is flat (vs. weakly to strongly swollen); the cubitus has 11 branches (vs. 19–23 branches); and the tarsus has four segments (three in Stylotermitinae).

Archeorhinotermes, new genus

TYPE SPECIES: *Archeorhinotermes rossi*, new species, by original designation and monotypy.

DIAGNOSIS: Head small, roundish. Eyes large, proportionate to head, oval. Ocelli large. Fontanelle present, small, close to hind margin of head. Postclypeus somewhat flat, not prominently arched. Mandible dentition and wing venation as described under subfamily diagnosis.

ETYMOLOGY: The genus name is a combination of Greek *archo-* (ancient, primeval) and the stem of the family Rhinotermitidae + *-termes*, the common generic suffix in the Isoptera.

Archeorhinotermes rossi, new species

IMAGO (figs. 1, 2; table 1): Head, antennae, and pronotum light brown, wing scale brownish, lighter than head, legs light yellow. Head moderately covered with long bristles, longest about 0.18 mm; upper margin of forewing scale with several short bristles; costal margin and radial sector with a few barely visible short bristles; tergites and sternites densely covered with long bristles; fore, middle, and hind tibia with several long, thin bristles; inner margin of middle and hind tibia with a row of additional short, thicker bristles; tarsal segments with several long bristles. Head small, roundish, slightly

TABLE 1
Measurements (mm) of Holotype Imago of
Archeorhinotermes rossi, new species

Length of head to tip of labrum	0.77
Width of head	0.69
Maximum diameter of eye	0.24
Minimum diameter of eye	0.13
Maximum diameter of ocellus	0.09
Ocellus from eye	0.04
Length of labrum	0.23
Width of labrum	0.23
Length of postclypeus	0.10
Length of forewing scale	0.64
Length of forewing with scale	4.39
Width of forewing	0.97
Length of middle tibia	0.39
Length of hind tibia	0.56

longer than wide. Eyes medium-sized, oval, not bulging much beyond head. Ocelli large, separated from eyes. Fontanelle present, appearing closer to hind margin than to postclypeus. Labrum oblong, with lateral margins faintly rounded. Postclypeus narrow, not prominently arched. Pronotum tucked under head, not clearly visible, but appearing narrower than head. Left mandible with a prominent rounded projection near the apical tooth; apical tooth long and prominent, longer than first, second, or third marginal tooth, with outer margin sinuate; first, second, and third marginal teeth almost equal in length; molar prominence pointed, appearing as a fourth marginal tooth. Right mandible with a subsidiary tooth at base of upper margin of first marginal tooth (characteristic of Hodotermitidae, Termopsidae, and Rhinotermitidae); second marginal tooth prominent, equal in length to first marginal tooth, posterior margin with a medium-sized cutting edge (longer in all other rhinotermitids). Antennae broken, with 13+ articles; second subequal to third; third and fourth subequal. Tibial spurs very hard to distinguish from thick bristles at end of tibia, appear to be 3:2:2. Tarsus with four articles. Arolium absent. Cerci with two articles. Forewing membrane reticulate, particularly between branches of cubitus; R_1 and R_2 absent; R_s simple, unbranched, running close to the fused subcosta and costal margin; median arising from a common stem with R_s , inside wing scale, unbranched, running almost midway between R_s and cubitus, appearing joined to cubitus,

close to apical margin; cubitus arising independently from inside wing scale, with 11 branches, fourth with a sub-branch.

SPECIMEN AND TYPE LOCALITY: Imago (holotype) in amber, NHM, Department of Palaeontology number In. 20160, received from R.C.J. Swinhoe, July 1920. Myanmar (Burma): ?Hukawng Valley. Spherical piece of amber, 10 mm in diameter, with a 2-mm wide hole bored through center (originally a bead), containing one termite (as above), one Cecidomyiidae, one Acarina, one Auchenorrhyncha nymph, four Coleoptera (?family), one Coleoptera (Mordellidae), one Heteroptera (Saldidae), two Diptera (Ceratopogonidae), and one male Coccoidea. The holotype is deposited in the Department of Palaeontology (Invertebrates), Natural History Museum, London. Burmese amber is dated as Upper to Middle Cretaceous, probably Turonian–Cenomanian (90–100 mya) by Grimaldi, Engel, and Nascimbene (2002).

ETYMOLOGY: This species is named in honor of Andrew Ross, Curator of Fossil Arthropods, Department of Palaeontology, Natural History Museum, London, and an authority on Burmese amber.

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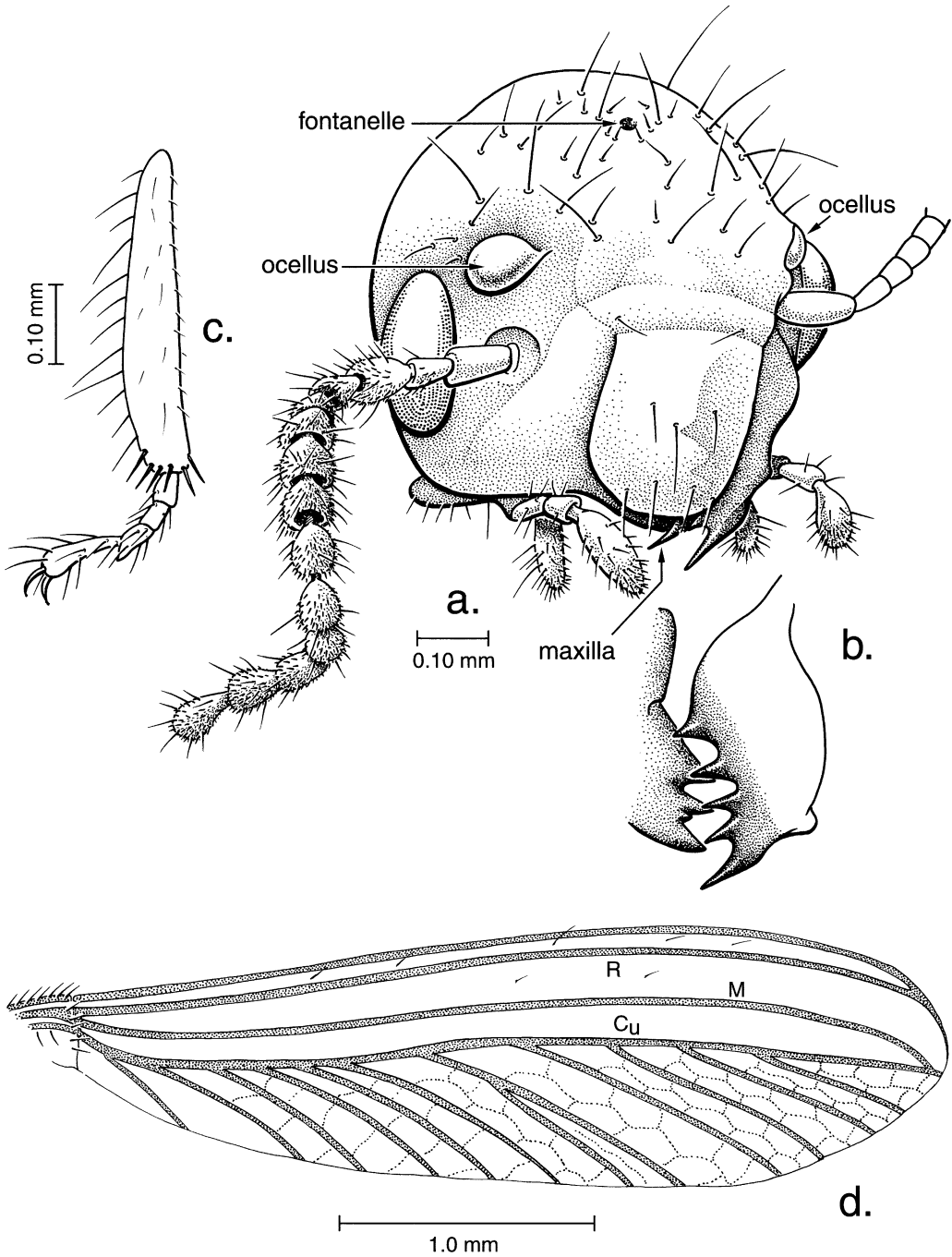


Fig. 1. Holotype imago of *Archeorhinotermes rossi*, n. sp. **a**, dorsal view of head; **b**, dorsal view of mandibles; **c**, ventral view of middle tibia and tarsus; **d**, dorsal view of forewing.



Fig. 2. Photomicrograph of the holotype imago of *Archeorhinotermes rossi*, n. sp.

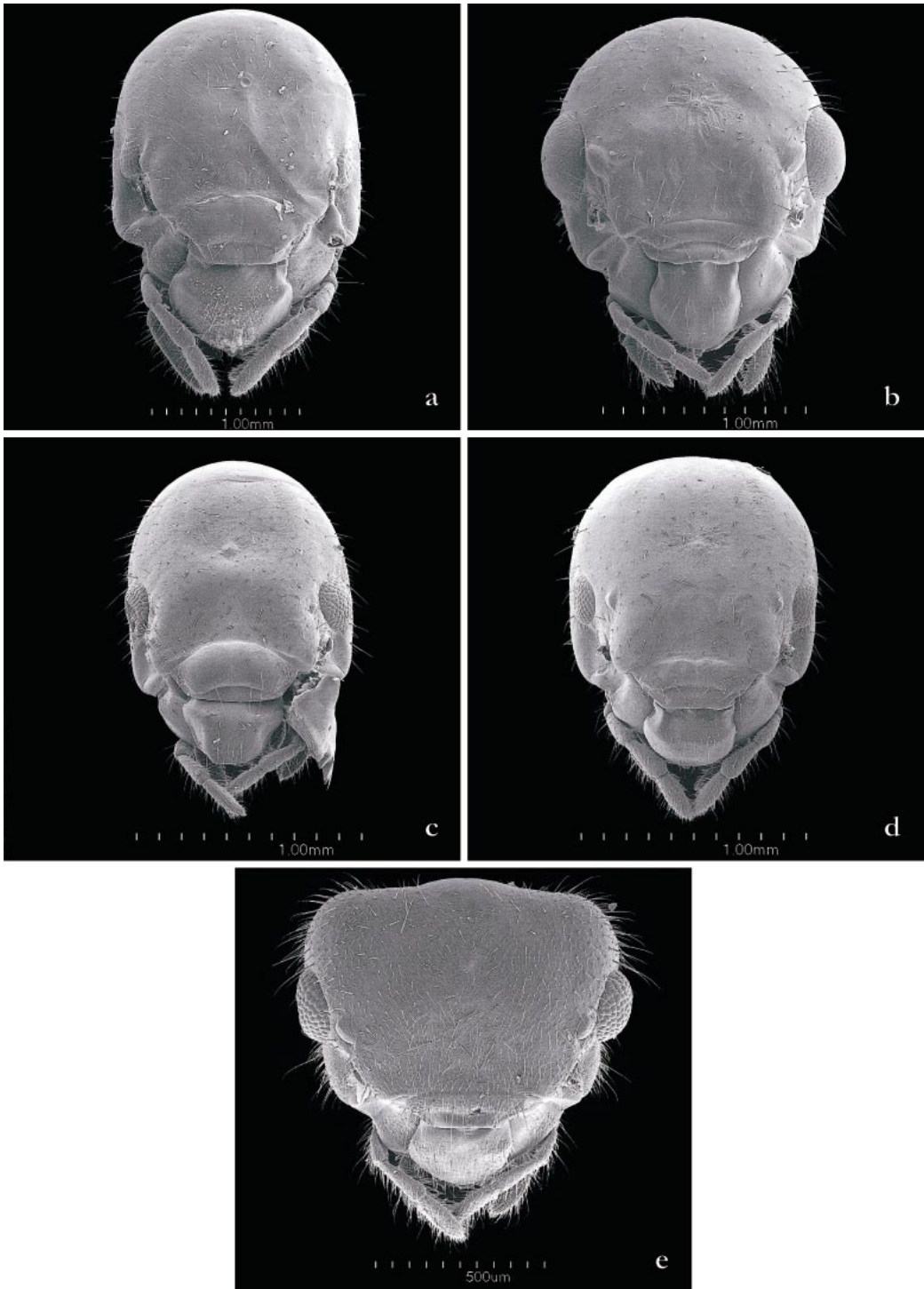


Fig. 3. Scanning electron micrographs. Dorsal view of head of imagoes: **a**, *Psammotermes allocerus* Silvestri); **b**, *Coptotermes curvignathus* Holmgren); **c**, *Heterotermes platycephalus* Froggatt); **d**, *Heterotermes* (*Reticulitermes* *flavipes* (Kollar)); **e**, *Termitogetoninae* (*Termitogeton umbilicatus* (Hagen)).

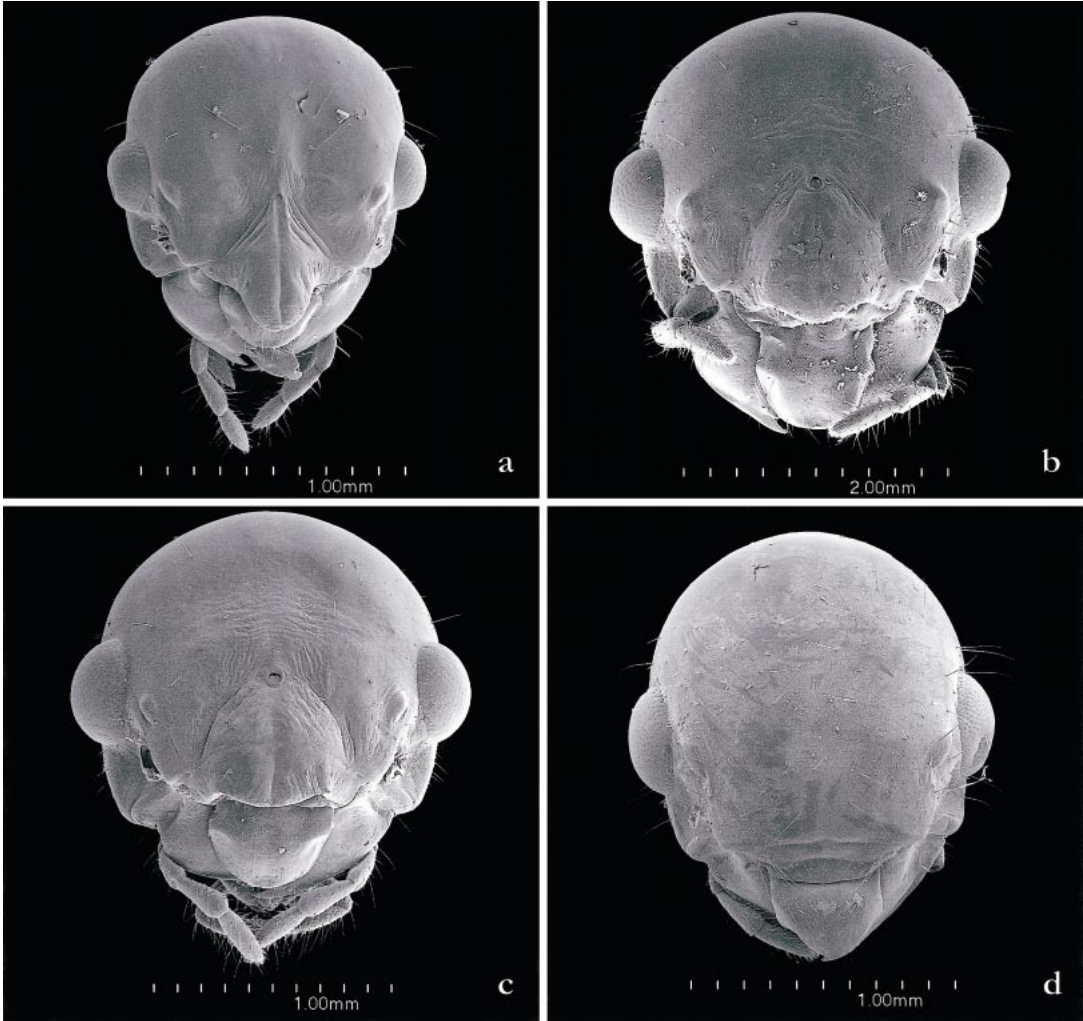


Fig. 4. Scanning electron micrographs. Dorsal view of head of imagoes: **a**, Rhinotermitinae (*Dolichorhinotermes longilabius* (Emerson)); **b**, Rhinotermitinae (*Schedorhinotermes* sp. A. from the Indomalayan Region); **c**, Rhinotermitinae (*Schedorhinotermes* sp. B, from New Guinea; **d**, Stylotermitinae (*Stylotermes fletcheri* Holmgren, K. & N.).

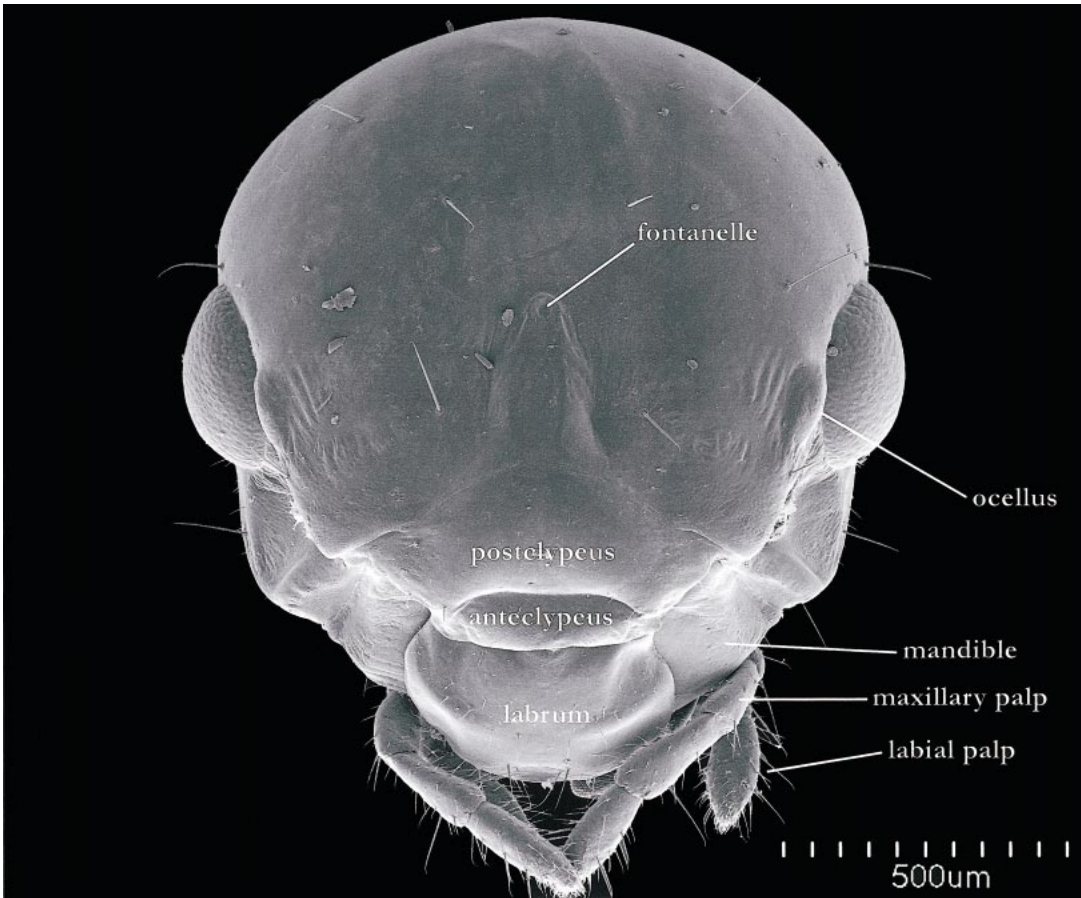


Fig. 5. Scanning electron micrograph. Dorsal view of head of Prorhinotermitinae (*Prorhinotermes flavus* (Bugnion & Popoff)).

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