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Two New Species of Nicoletiidae (Zygentoma, "Apterygota," Insecta) in Dominican Amber

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ABSTRACT

Trinemurodes antiquus, n. sp., and *Trinemurodes miocenicus*, n. sp., from Dominican amber (ca. 20 Ma) are the first fossil species of the family Nicoletiidae. They can be placed in the genus *Trinemurodes* (subfamily Subnicoletinae) with two extant species living in the Malesian area (Su-

matra and the Moluccas), making these the only known New World species of the genus. The rarity of the Nicoletiidae in the fossil record contrasts with other families of Zygentoma (Ateluridae, Lepidotrichidae, Lepismatidae), probably a result of their more edaphic mode of life.

INTRODUCTION

The Dominican amber is very rich in inclusions of insects (Schlee, 1984; Poinar, 1992). From the order Zygentoma (= Thysanura sensu stricto), Mendes recently described a new species of the genus *Ctenolepisma* (Lepismatidae) (Mendes, in press) and a new genus and species of the Ateluridae (*Archeatelura sturmi* Mendes, 1997). The members of the last-named family can be distinguished by their small body size (ca. 3–5 mm), droplike form, and very short caudal

appendages. The great majority of the species in this family are probably myrmeco- or termitophilous. The species described here are the first fossil representatives of the Nicoletiidae. Members of this family lack eyes and possess a slender body with long, flexible caudal appendages. They live in the soil, in accumulations of humus, or in caves, as a rule independent of ants and termites. Like other inclusions in Dominican amber, these fossils should be approximately 20 Ma old

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(Grimaldi, 1995; Iturralde-Vinent and MacPhee, 1996). Species of another family of the Zygentoma (Lepidotrichidae) are known from the Baltic and the Bitterfeld amber (*Lepidothrix pilifera* Menge, 1854) and an extant species was found in the coastal forests of northern California (*Tricholepidion gertschi* Wygodzinsky, 1961). Their habitus is similar to the Nicoletiidae but they differ in the presence of complex eyes, the absence of a subgenital plate, the morphology of the ovipositor, and the chaetotaxy of the penis. The animals presented here, two fully developed and fairly well-preserved females, raise questions about the systematic position and the evolution of the Nicoletiidae and the Zygentoma in general.

MATERIALS, METHODS, ACKNOWLEDGMENTS

The amber (weight 2.3 g) with the specimen of *Trinemurodes antiquus* also contains a well-preserved beetle of the family Ptilodactylidae (length 4 mm) and parts of two Coleoptera larvae. Fossil Nicoletiidae are very rare compared to the numbers of other "Thysanura" found in 117 inclusions of Dominican amber (61 inclusions from the Sturm collection, 27 Poinar coll., 25 AMNH coll., 4 Museum Naturkunde, Stuttgart coll.): 2 Nicoletiidae, 9 Ateluridae, 4 Lepismatidae, 102 Archaeognatha (all belonging to 1 species of *Neomachilellus*). We wish to thank Dr. D. Grimaldi of the AMNH for the loan of the interesting inclusions of the two nicoletiid specimens. The two amber pieces were reshaped and the sides polished. For examining specimens, Euparal (artificial resin) was applied to the surface with a cover glass, and a combination of illumination from above and below with magnifications up to 200 \times .

SYSTEMATICS

Trinemurodes antiquus, new species

(figs. 1–21)

DIAGNOSIS: The species can be identified by the combination of the following characteristics: Empodium and scales absent, lateral claws smooth, tibia I with 2 stout, short setae; urosternites I–VII entire, II–VII with 1 + 1 vesicles each, II–IX with small stylets; subgenital plate trianguloid; all setae pointed

or apically rounded; distal article of labial palp distinctly longer than wide; ovipositor stout, with about 10 articles and short normal setae only, inner distal area of gonapophyses IX spinulate.

DESCRIPTION: The specimen is fairly well preserved. Difficulties in observation result from a strong curvature and a light twist of the body, by a gas bubble passing through nearly the whole body, and other bubbles and foreign particles near the head and the caudal end.

Head (figs. 1–7): Width of head = 0.64 mm, capsule with many macrochaetae on dorsal and lateral sides. Antennae broken, scapus and pedicellus not detectable, preserved parts of the flagellum with few setae of medium size, not clearly arranged in transverse rings. Mandibles with three strongly chitinized distal teeth. Maxillae: Lacinia with two dark teeth and a comblike prostheta; galea with two apical papillae (probably the apical sensillae) and a lateral row of setae; maxillary palps with five articles; distal end of fifth article with denticulate apical conules; ratio length of articles 5 : 4 : 3 : 2 = 1 : 0.7–0.75 : 0.8 : 0.75. Labium: proximal part not visible; distal article of palp clavate, one side with the usual sensory papillae.

Thorax (figs. 8–10): Tergites I–III (ca. 0.8–0.9 mm wide) on laterocaudal margin with macrochaetae (up to 0.21 mm long); setae on surface up to 0.08 mm, on caudal margin not distinctly longer. Legs with four tarsal articles and two thin claws; tibia of leg I with two stout, short setae having distal end rounded; empodium apparently absent, on distal end of one tarsus II a seta similar to an empodium appears but on three other tarsi (2 \times leg I, 1 \times leg II), which were clearly visible, an empodium was absent; length of coxa II = 0.53 mm; ratio length of coxa : femur : tibia : tarsus of leg II = 1 : 0.67 : 0.51 : 0.52, coxae with some very long setae (up to 0.28 mm); maximum length of tarsi on legs I/II/III = 0.33/0.38/0.44 mm.

Abdomen (figs. 11–21): Urotergites I–X with pointed setae, especially long on the distolateral margin, short to medium sized on rest of tergal area with a slight tendency to become longer near caudal margin; urotergite X subtrapezoidal, not much shortened, the hind border not clearly concave. Urosternites

II–IX with stylets, length of stylet IX = 0.17 mm, stylets II–VIII = 0.09–0.11 mm; urosternites II–VI with 1 + 1 exsertile vesicles each, VII with 1 + 1 pseudovesicles; I–VII entire (not divided); all urosternites with short to medium sized pointed setae, nearly evenly distributed; trianguloid subgenital plate present. Ovipositor 0.9 mm long with more than 10 articles, gonapophyses IX with small terminal appendages and spinulate inner area near the distal end; specialized setae on the outer surface absent. Terminal filament and cerci reaching little more than half length of body; each distal article with a ring of long thin setae (up to 0.25 mm) near distal end; one cercus with a long terminal seta, terminal filament and the other cercus with a short distal point.

TYPE AND ONLY KNOWN SPECIMEN: Female, body length 5.8 mm; DOMINICAN REPUBLIC, specific locality unknown, inclusion of Miocene amber, age ca. 20 Ma; deposited in AMNH: DR-10-313.

ETYMOLOGY: From the Latin term *antiquus* (old) in allusion to the fact that the specimen is a fossil representative of the family Nicoletiidae.

DISCUSSION: Description and determination of the species are made difficult by the existence of only a female specimen (generally in this group the males have more specific characteristics than the females), the poor preservation of some parts (antennae, labium, abdominal segment X), and by air bubbles and detritus within the body or near it.

The occurrence of entire urosternites eliminates the fossil from the Nicoletiinae and the Cubacubaninae (Mendes, 1988, 1994). The presence of a prostheca, a subgenital plate, and the spinulate inner wall of gonapophyses IX exclude the amber specimen from the Protrinemurinae. The entire first urosternite points clearly to its inclusion in the Subnicoletiinae. In the Nicoletiinae this sclerite is divided into one submedian sternite plus 1 + 1 lateral coxites. *Trinemurodes* (Silvestri, 1916, Subnicoletiinae) is otherwise the unique nicoletioid genus whose pretarsus lacks an empodium. The generic identity of the Dominican amber fossil mainly reflects an absence of knowledge of the male sexual features. Therefore, the classification of the animal under the genus *Trinemurodes* must

be considered tentative. Additional material from the same locality would be of great interest. The genus *Trinemurodes* was previously known to occur only as two living species in Sumatra (*T. malayanus* Silvestri, 1916) and in the Moluccas islands (*T. mertoni* Paclt, 1961). *Trinemurodes malayanus* (the female sex of this species is not described) is devoid of stylets on urosternite II; also, article 3 of labial palp is more clavate and the caudal margin of tergite X more concave. *Trinemurodes mertoni*, although it has abdominal stylets from urosternite II on, shows a clear subapical tooth on each of the tarsal claws. Furthermore, urotergite X seems clearly shorter in the Moluccan species and the macrochaetae of abdominal tergite IX show quite a different distribution in *T. mertoni* and in *T. antiquus*, n. sp., and the distal article of the labial palp has a different form.

Trinemurodes miocenicus, new species

(figs. 22–33)

DIAGNOSIS: The species can be identified by the combination of the following characteristics: Empodia and scales absent, lateral claws denticulate on the distal convex part; tibia and femur (at least on legs II) with two long, cylindrical, slightly curved setae each; urosternites I(?)–VII entire, II(?)–VII with 1 + 1 vesicles each, II–IX with stylets; subgenital plate trianguloid; all setae pointed or apically rounded; article 3 of labial palps somewhat longer than wide; ovipositor short with ca. nine articles and with two long distal setae, distal part apparently without spinulate area (for variability of the ovipositor see below under Abdomen).

DESCRIPTION: The specimen is well preserved; only the structure of the mandibles, the proximal parts of maxillary and labial palps, and the abdominal sternocoxite I could not be seen clearly.

Head (figs. 23, 24): Maximum width 0.53 mm, max. length 0.5 mm; on dorsal and lateral sides with some long bristles (up to 0.32 mm long); length of antennae 2.3 mm, ratio width of scapus : length = 0.6; pedicellus with some long setae (up to 0.21 mm), ratio width : length = 0.8; articles of flagellum with two rings of setae each, the proximal one protruding more, 2–3 terminal articles

enclosed by gas bubbles. Mandibles with at least three terminal teeth. Maxillary palps with long article 5, ratio length of articles 5 : 4 : 3 : 2 = 1 : 0.5–0.6 : 0.7–0.8 : 0.7–0.8; distal end of article 5 with some denticulate sensilla; galea and lacinia not clearly visible. Article 3 of labial palp somewhat longer than wide, ratio 1 : 0.7; with the usual sensory papillae on the inner side.

Thorax (figs. 25–28): Maximum width 0.7 mm; tergites near the lateral and on the latero-ocaudal margin with macrochaetae (up to 0.32 mm long), some of them nearly vertical, setae on the surface up to 0.08 mm. Legs with 2 claws, distal part of convex side of claws denticulate (up to 5 small spines), empodium apparently absent, on one tarsus II a strong seta similar to an empodium is present between the claws (fig. 27), but on the other tarsi empodia could not be detected; tibia and femur at least of leg II with 2 stout setae each (ca. 0.08 mm long) having rounded distal ends; length of coxa II = 0.51 mm, of coxa III = 0.63 mm, ratio length of coxa : femur : tibia of leg II = 1 : 0.66 : 0.62; ratio length of coxa : tibia : tarsus of leg III = 1 : 0.8 : 0.75.

Abdomen (figs. 29–33): Urotergites I–X with pointed setae especially long on the distolateral margin (up to 0.3 mm); urotergite X subtrapezoidal, not much shortened, hind border not clearly concave. Urosternites II–IX with stylets (length of stylets IX 0.22–0.24 mm, of VIII 0.11 mm); II(?)–VII with vesicles, I(?)–VII not divided; subgenital plate trianguloid; all urosternites with many short to medium sized pointed setae, nearly evenly distributed. Ovipositor short and stout, apparently with less than 10 articles (0.82 mm long, ratio width : length = 0.15; probably length of ovipositor and number of its articles can increase after reaching sexual maturity: Smith, 1997, in press); distal part apparently without spinulate area but with two long, straight, terminal setae (0.14 mm long); other parts with scattered medium sized setae and a cover of small setae; entire outer surface of ovipositor with a dense cover of tiny spines arranged in rings (similar structures also on some other appendages, e.g., caudal appendages and flagellum). Length of terminal filament = 2.6 mm, of

cerci 2.4 mm; setae on caudal appendages up to 0.32 mm long.

TYPE AND ONLY KNOWN SPECIMEN: Female, body length 4.4 mm; DOMINICAN REPUBLIC, specific locality unknown; inclusion of Miocene amber, age ca. 20 Ma; deposited in AMNH: DR-14-1035.

ETYMOLOGY: The species name refers to the Miocene.

DISCUSSION: At 4.4 mm the specimen has a normal body length within the Nicoletiidae, in which normal body length for adult specimens lies between 2.7 and 9.3 mm. Generally the length of amber specimens is somewhat reduced in connection with shrinking in the amber. Also, the fully developed ovipositor indicates the maturity of the animal. A comparison with *Trinemurodes antiquus* shows that the structure and chaetotaxy of the ovipositor and the tarsal claws are clearly different (*T. miocenicus* has denticulated tips) and that the specimen has to be assigned to a separate species. In other characteristics the two species are very similar: absence of empodia and scales, urosternites I(?)–VII entire, II–IX with stylets, II(?)–VII with 1 + 1 vesicles; subgenital plate trianguloid; tergite X trapezoidal; chaetotaxy on tergites and sternocoxites, form and structure of maxillary and labial palps. On the basis of these similarities both species are assigned to the genus *Trinemurodes*. A definitive classification of the species will be possible if the corresponding males are ever found.

Trinemurodes miocenicus differs from the two extant species especially by the presence of fine spines near the tips of tarsal claws, the short antennae, the different form of article 3 of labial palps, and abdominal tergite X.

DISCUSSION

These two amber species raise a paleogeographic problem, since the two described recent species of the genus live in the Malesian area and no terrestrial connections are known to have occurred in the last 20–30 Ma between America and Australasia. Approximately 20 examples of distribution patterns have been discovered like the one described here: a Dominican amber fossil closely related to an Indopacific taxon. The great majority of distributions, though, are Dominican

amber fossils most closely related to species living in the Caribbean or Central America (D. Grimaldi, personal commun.). This suggests that *Trinemurodes* could have been a much more widely distributed genus and that the two Recent species are relicts. It is highly unlikely that some kind of long-distance dispersal could have occurred.

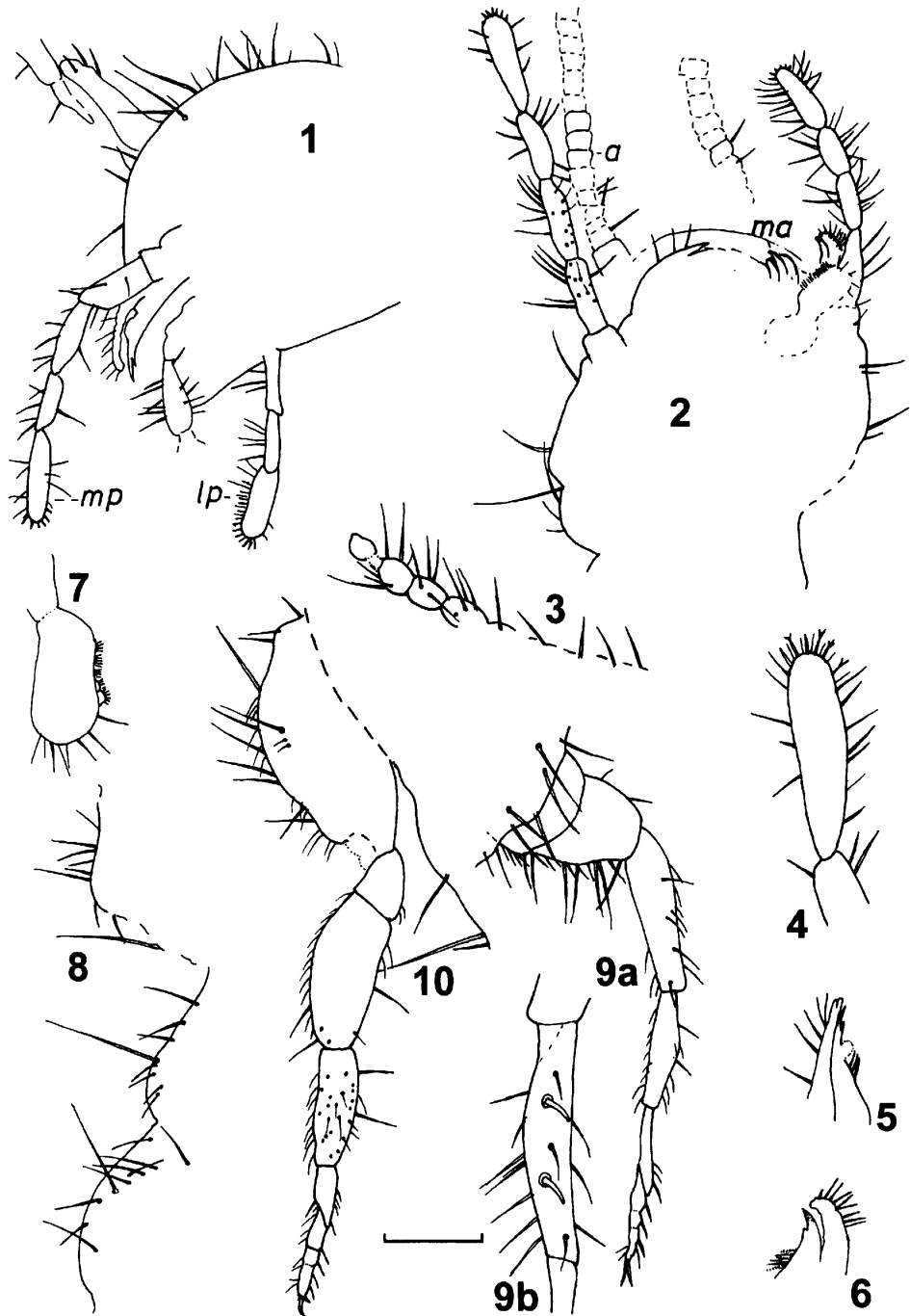
The Nicoletiidae and the sister group, the Ateluridae, are highly specialized taxa, shown by the evolution of two very different forms that are connected by a few transitional types. The original slender habitus, which occurs also in the Maindroniidae and Lepi-

dothrichidae, was obviously modified in the Ateluridae in connection with myrmecophily and termitophily. The close contact with ants and termites requires the shortening of the caudal appendages and antennae and has apparently produced a more rounded body shape in the Ateluridae. Also, in the Nicoletiidae, other characteristics are variable (cf. Mendes, 1994).

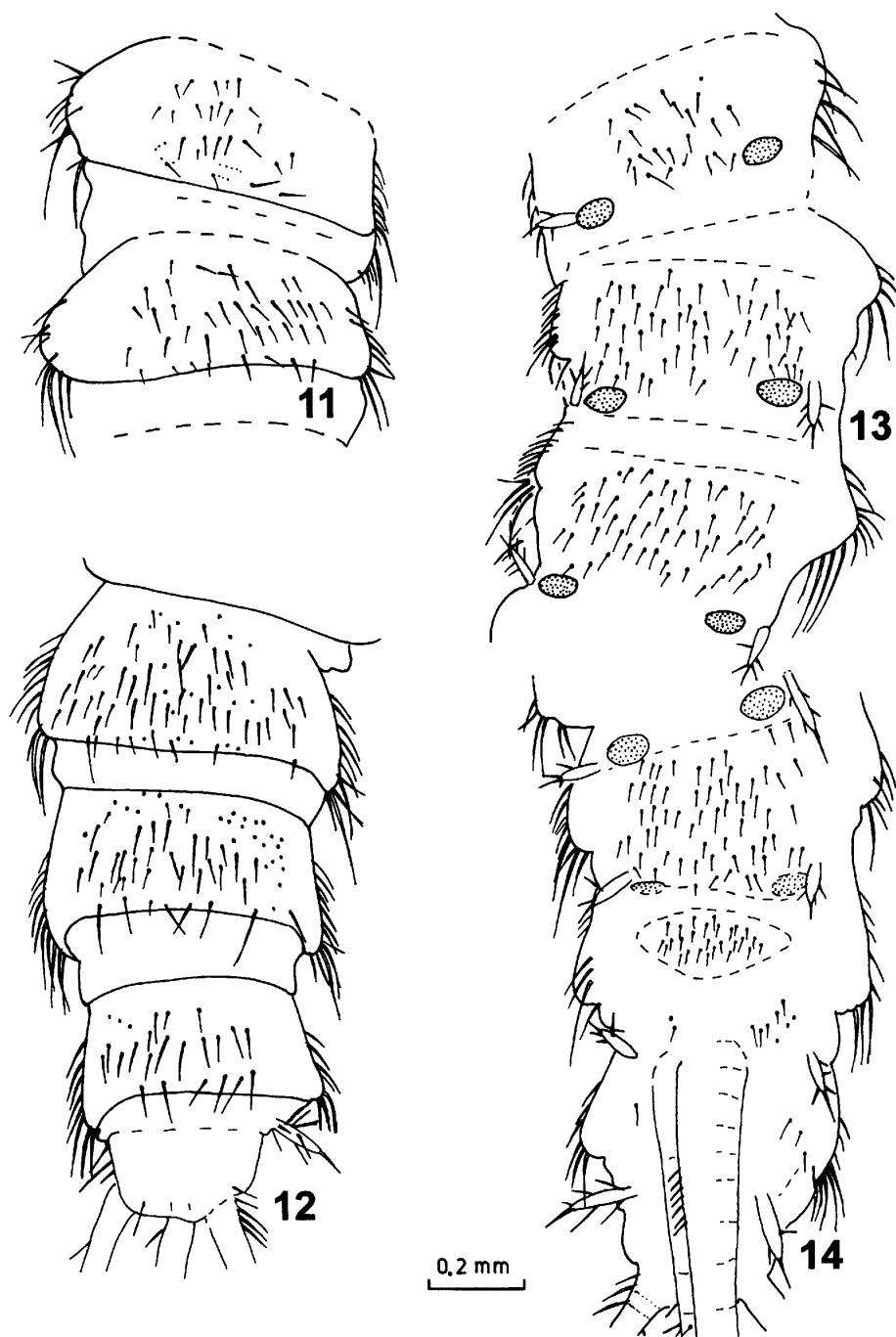
Specimens of *Zygentoma* found in Dominican and Baltic amber reveal that by the Eocene the families Lepismatidae and Lepidothrichidae existed and that even by the Miocene modern genera had evolved.

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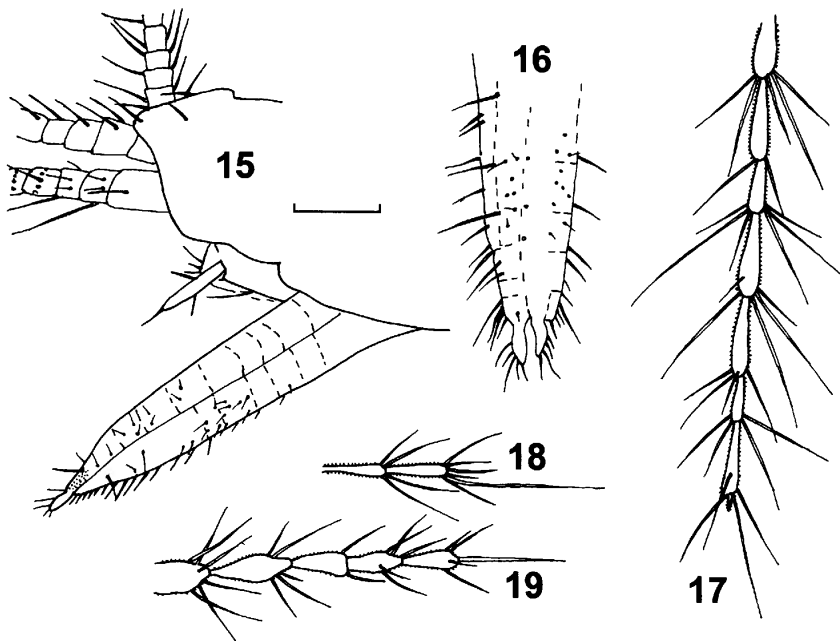
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Figs. 1-10. *Trinemurodes antiquus*, n. sp., female; a = antenna, lp = labial palp, ma = mandible, mp = maxillary palp; scale bar = 0.2 mm for figs. 1, 2, 8, 9a, 10; 0.1 mm for figs. 3-7, 9b. 1. Head, ventrolateral view. 2. Head, ventral view. 3. Parts of flagellum, dorsal view. 4. Distal (fifth) article of maxillary palp, ventral view. 5. Distal part of right maxilla, ventral view. 6. Distal part of left maxilla, ventral view. 7. Distal (third) article of labial palp, ventral view. 8. Lateral margins of thoracic tergites I-III with setae, ventral view. 9a. Leg I, dorsal view; b. tibia, leg I ventral view with 2 stout sensory (?) setae. 10. Leg II, dorsal view.



Figs. 11–14. *Trinemurodes antiquus*, n. sp., female. 11. Urotergites III + IV, dorsal view. 12. Urotergites VII–X, dorsal view. 13. Urosternites II–IV, ventral view, exsertile vesicles dotted. 14. Urosternites VI–X with base of ovipositor, ventral view.



Figs. 15–19. *Trinemurodes antiquus*, n. sp., female; scale bar 0.1 mm for fig. 15, 0.2 mm for figs. 16–19. 15. Distal end of abdomen with ovipositor, lateral view. 16. Distal part of ovipositor, ventral view. 17. Distal end of filum terminale, dorsal view. 18. Distal end of cercus with long terminal seta, dorsal view. 19. Distal end of other cercus, dorsal view.

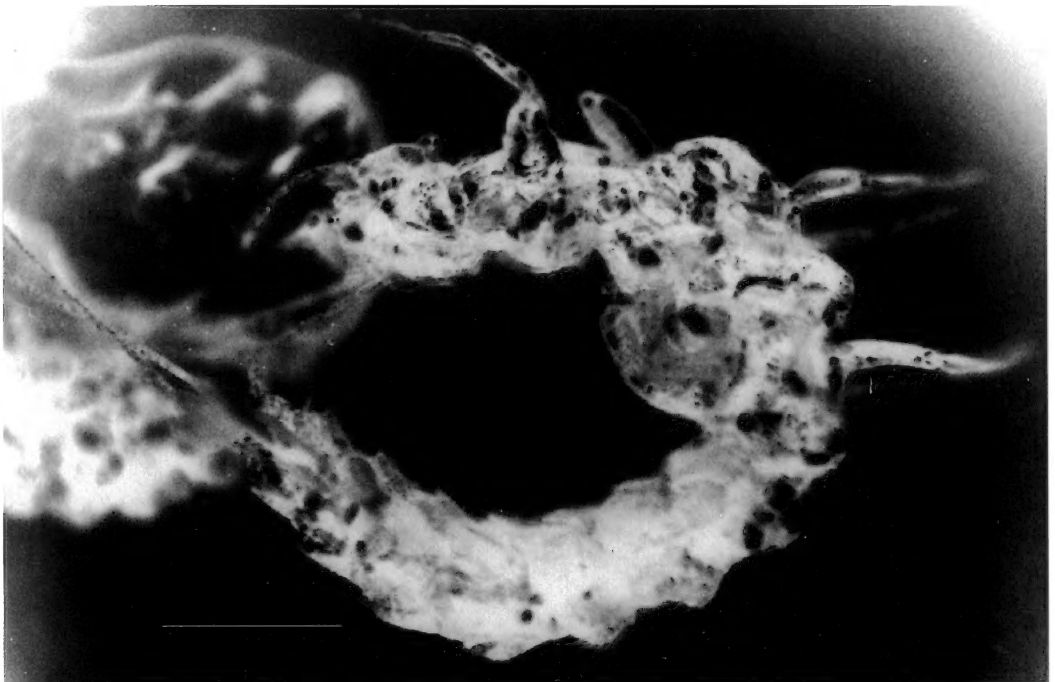


Fig. 20. Photo of *Trinemurodes antiquus* (whole animal), ventral view. Scale bar = 1 mm.

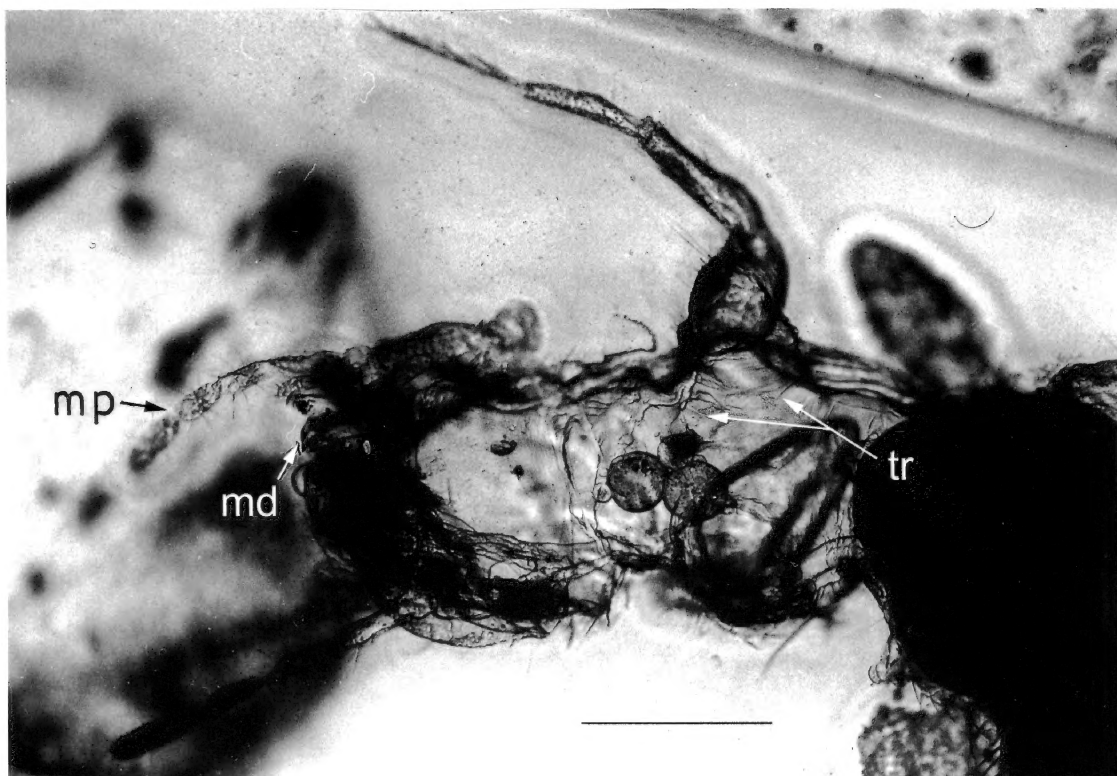


Fig. 21. *Trinemurodes antiquus*, n. sp., female, ventral view; md = mandible, mp = maxillary palp, tr = tracheae. Scale bar = 0.5 mm.

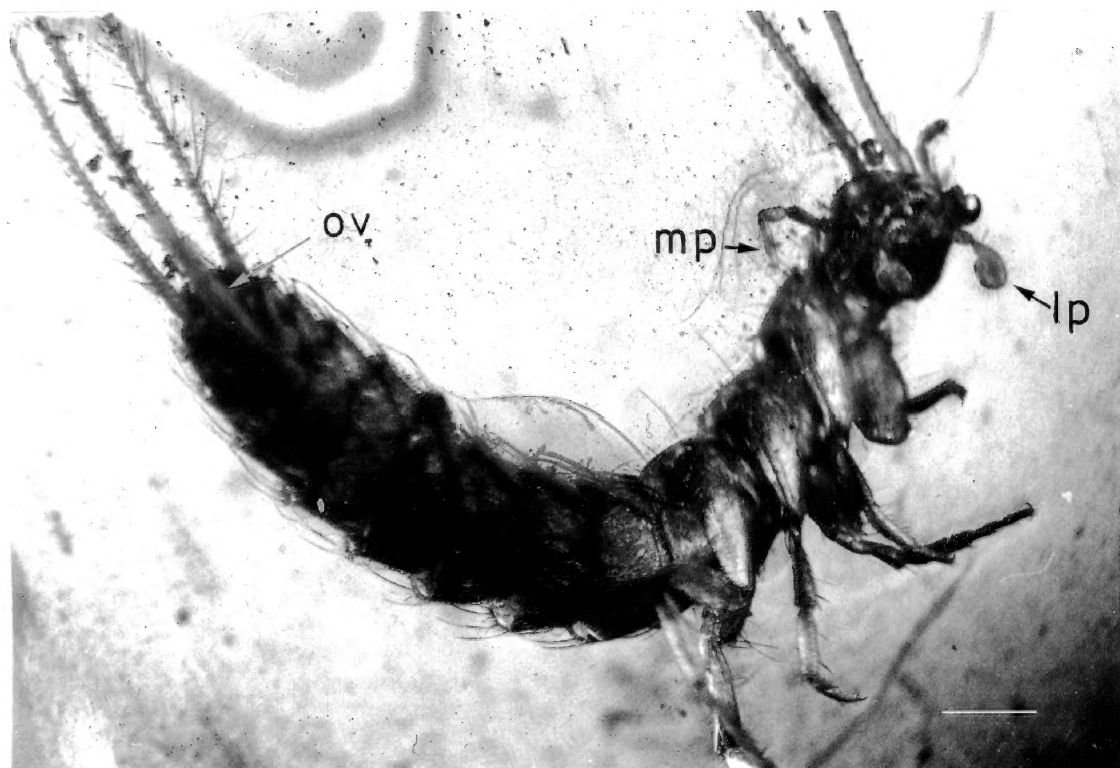
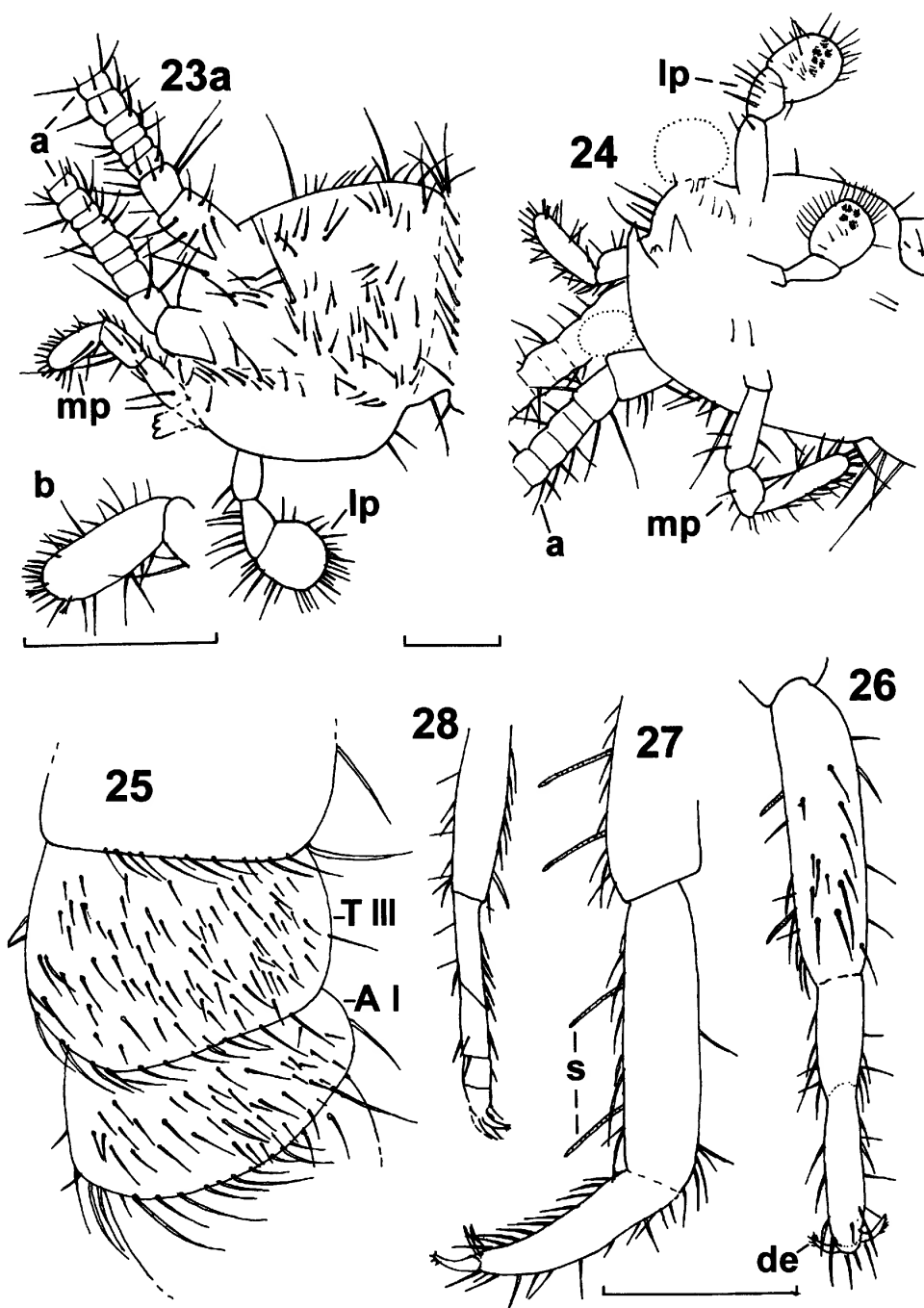
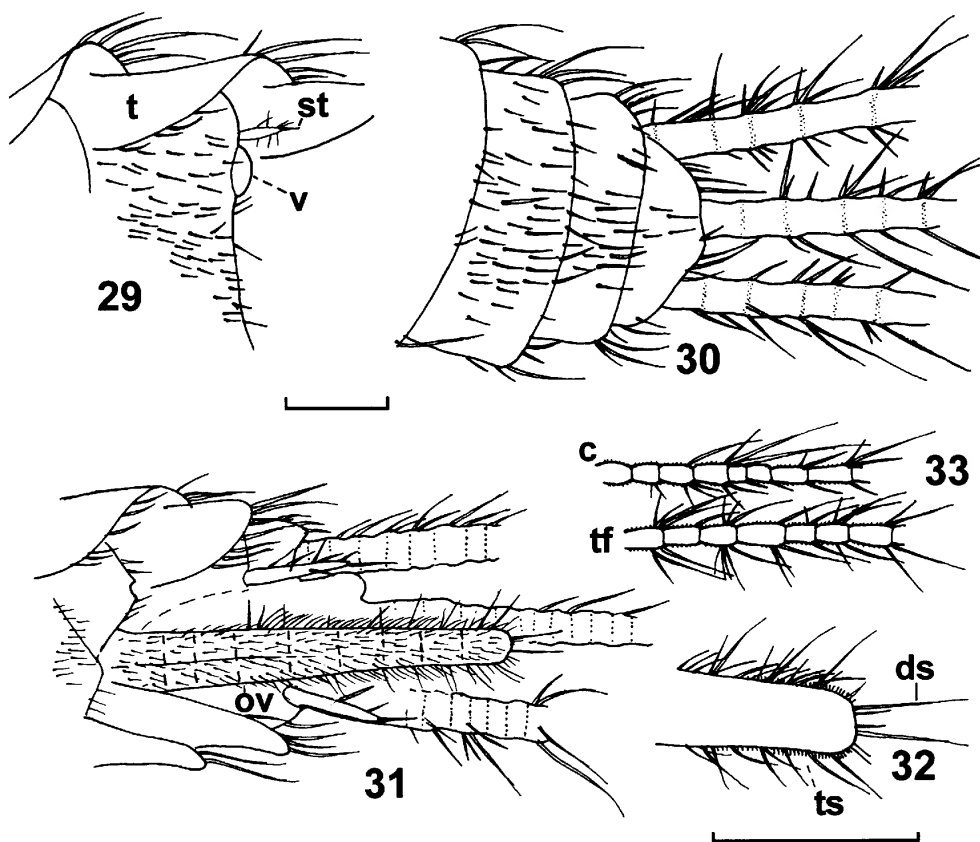


Fig. 22. *Trinemurodes miocenicus*, n. sp., female, ventrolateral view; lp = labial palp, mp = maxillary palp, ov = ovipositor. Scale bar = 0.5 mm.



Figs. 23–28. *Trinemurodes miocenicus*, n. sp., female, body length 4.4 mm; scale lines = 0.2 mm. 23a. Head with bases of antennae (a) and palps, lp = labial palp, mp = maxillary palp, b. Distal article of maxillary palp at higher magnification. 24. Head, ventral view; a = antennae, lp = labial palp with sensory papilla, dotted lines = gas bubbles. 25. Chaetotaxy of tergites, dorsal view; T III = thoracal tergite III, A I = abdominal tergite I. 26. Leg II (right side), tibia + tarsus, dorsal view; de = denticulate claws. 27. Leg II (left side); distal part, dorsal view; s = stout setae. 28. Leg III (left side), tibia + tarsus, ventral view.



Figs. 29–33. *Trinemurodes miocenicus*, n. sp., female, body length 4.4 mm, scale lines 0.2 mm. **29.** Half of sternocoxite V with vesicle (v), stylet (st), and lateral parts of tergites (t). **30.** Tip of abdomen, dorsal view, with tergites VIII–X and bases of caudal appendages. **31.** Tip of abdomen, ventral view, with ovipositor (ov) and basal parts of caudal appendages. **32.** Distal end of ovipositor with distal setae (ds) and cover of tiny spines (ts), ventral view. **33.** Distal parts of cercus (c) and terminal filament (tf).

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