

A Revision of *Heteromurus* s. str.
(Insecta: Collembola: Entomobryidae)¹

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ABSTRACT

The revision includes descriptions of five of the seven species, a key to all the species and a phyletic analysis of the taxon. Complete synonymy and geographic distribution are detailed for all the taxa H. caucasicus and H. mexicanus are new synonyms of H. major H. hexophthalmus and H. tetrophthalmus are new synonyms of H. sexoculatus and H. nitidus respectively.

INTRODUCTION

The genus *Heteromurus* Wankel 1860 includes four subgenera: the nominal subgenus, *Verhoeffiella* Absolon 1900b, *Alloscopus* Börner 1903, and *Heteromurtrella* Mari Mutt 1979a. *Alloscopus* was reviewed by Mari Mutt (1978a). The status of *Verhoeffiella* and its five species is uncertain, very few specimens are in collections and these are not available for study. All species of *Verhoeffiella* are troglotic and only one has been collected (once) since its description. A meaningful revision of this taxon must await the discovery of specimens for the study of important characters not mentioned in the original descriptions.

This paper presents a revision of the nominal subgenus, *Heteromurus* s. str., in which I recognize two species groups and seven species. The edaphic *H. gigans* and the cavernicolous *H. noseki* were described recently (Mari Mutt and Stomp 1980) and will not be dealt with here except for their inclusion in the key to the species of the subgenus.

The *nitidus* group includes *H. nitidus*, *noseki* and *peyerimhoffi*; the *major* group houses *H. major*, *gigans* and *variabilis*. Species of the *nitidus* group share the following characteristics: a double row of smooth setae along inner margin of tibiotarsi, a double row of smooth erect setae along dorsum of manubrium and a pair of similar setae upon the proximal dorsal portion of the dentes; only smooth setae on the labial triangle and rest of venter of head; 2&2, 1&1, or eyes absent, and all the species occur in caves two being restricted to this habitat. Species of the *major* group share the following characteristics: only ciliated setae upon tibiotarsi and manubrium; labial triangle and rest of venter of head with smooth setae and ciliated setae; 8&8 eyes, and all the species are edaphic.

The seventh species, *H. sexoculatus*, is intermediate between these otherwise clear-cut groups. It presents: only ciliated setae upon the tibiotarsi; a double row of smooth erect setae along dorsum of manubrium and a pair of similar setae upon the dentes; labial triangle with smooth or ciliated setae; 3&3 eyes, and it occurs both inside and outside caves (troglophilic). Following the results of a preliminary phyletic analysis (see section on phylogeny), I have placed *sexoculatus* in the *major* group.

A series of abbreviations are used throughout this paper to indicate the depository of specimens. These are: BMNH-British Museum (Natural History), Department of Entomology, Cromwell Rd., London SW7 5BD, England; HJG-H.J. Gough collection, Jealott's Hill Research Station, Brecknell Berkshire RG 12 6 EY, England; INHS-Illinois Natural History Survey, Division of Faunistics Surveys, Natural Resources Bldg., Urbana, Illinois 61801; JAB-J.A. Barra collection, Institut de Zoologie, 12 rue de l'Université, 67000 Strasbourg, France; JAMM-J.A. Mari Mutt collection, Department of Biology, University of Puerto Rico, Mayaguez, Puerto Rico 00708; KAC-K.A. Christiansen collection, Department of Biology, Grinnell College, Grinnell, Iowa 50112; LSU-

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Leningrad State University, Laboratory of Entomology, Biological Research Institute, Leningrad, USSR; MNHN Museum National d'Histoire Naturelle, Ecologie Générale, 4 Avenue du Petit Chateau, 91800 Brunoy, France; NS-N. Stomp collection, Athénée Grand-Ducal de Luxembourg, 24 boulevard Pierre Dupong, Luxembourg; NZNM-New Zealand National Museum, Private Bag, Wellington, New Zealand; PAS-Polish Academy of Sciences, Institut of Systematic and Experimental Zoology, Stawkowska 17, Krakow, Poland; SAS-Slovak Academy of Sciences, Institute of Virology, Bratislava 9, Czechoslovakia; USNM-United States National Museum of Natural History, Department of Entomology, Smithsonian Institution, Washington, D.C. 20560. WNE-W.N. Ellis collection, Zoology Museum, University of Amsterdam, Netherlands.

PHYLOGENY

The most important procedure of cladistic analysis is the determination of the ancestral (plesiomorphic) and derived (apomorphic) states of each character used. To solve this problem the worker must frequently go outside his group to more primitive taxa in order to study there the expressions of the characters concerned.

The work of Szeptycki (1972, 1979) and my own suggests that the Orchesellinae are the most primitive entomobryids and that their closest relatives outside of this family lie in the subfamily Isotominae of the Isotomidae. Comprehensive comparative studies in this group are unfortunately lacking. The worker finds that he has more than enough characters to separate the species but not enough for which the ancestral and derived states can be determined with much certainty.

Based on the examination of some isotomids and of scattered literature on this group, I have tentatively designated ancestral and derived states for nine characters in the subgenus.

Ancestral Alternative

1. 8&8 eyes
2. edaphic
3. unguis up to 2.5 x width of tibiotarsus at level of tenent hair
4. mucronal teeth normal
5. microchaetae abundant, scales not so abundant
6. setae of labial triangle smooth
7. setae of PLQ smooth
8. tibiotarsi with smooth setae
9. dorsum of manubrium with smooth setae

Derived Alternative

- 1a. 3&3
- 1b. 2&2, 1&1 or absent
2. in caves
3. 3.3 x width of tibiotarsus at same level
4. teeth modified (Fig. 17)
5. microchaetae scarce, scales very abundant
- 6a. smooth and ciliated
- 6b. all setae ciliated
- 6c. smooth setae, ciliated setae, and scales
7. ciliated
8. all setae ciliated
9. all setae ciliated

The decision to regard smooth setae as ancestral to ciliated setae is most important. Figure 1 presents the proposed phyletic relationships of the seven species of *Heteromurus* s. str. Note the trichotomy in the *major* group; the ancestral and derived states of more characters must be determined to solve it.

TAXONOMY

Genus *Heteromurus* Wankel

Heteromurus Wankel 1860: 203. Placed on the Official List of Generic Names in Zoology with the name number 2034 by the International Commission on Zoological Nomenclature, opinion 1064 (ICZN 1976).

Ptenura Templeton 1844: 306. Placed on the Official List of Rejected and Invalid Names in Zoology with the name number 2074 by the International Commission on Zoological Nomenclature, opinion 1064 (ICZN 1976).

Templetonia Lubbock 1862: 595. Absolon 1900a: 192.

Typhlopodura Absolon 1900b: 428. Kseneman 1937: 69-70. Gisin 1944: 96. Gisin 1960: 237. Salmon 1964: 133, 487.

Euheteromurus Börner 1901: 64. Salmon 1964: 131, 478.

Heteromurodes Absolon 1901: 12. Salmon 1951: 25. Salmon 1964: 131, 478.

Propemesira Salmon 1942: 59. Salmon 1945: 71. Salmon 1964: 131, 478.

Type Species: Heteromurus margaritarius Wankel 1860: 203, by monotypy. Name of species placed on the Official List of Specific Names on Zoology with the name number 2584 by the International Commission on Zoological Nomenclature, opinion 1064 (ICZN 1976).

Subgenus *Heteromurus* s. str.

Adults 2-5 mm. Pigment absent, restricted to eye patches, or more or less evenly distributed throughout specimen. Most species with variable color pattern. Pigment, when present in preserved specimens, dark-blue (in *nitidus* sometimes orange). Legs scaled (except in *peyerimhoffi*). Antennae about $\frac{1}{2}$ length of head and body combined. Apex of Ant. 5 with pin seta, without apically hooked setae. Eyes 8&8, 3&3, 2&2, 1&1, or absent, number constant intraspecifically (except in *nitidus* where last 3 combinations occur). Head macrochaetotaxy identical for all species (Fig. 28); Ps and S₀ absent, 2 P setae². Labral papillae of type II (4 thick conelike papillae without apical process-Fig. 11), of type III (outer pair rounded, slightly domelike; inner pair strongly conelike-Fig. 18-19), or absent. Labial chaetotaxy variable intra- and interspecifically; posterior row with all setae smooth, all ciliated, smooth setae and ciliated setae, or some setae substituted by scales (*gigans*). Setae of maxillary palp similar in all species (Fig. 27). Differentiated seta of outer labial papilla short and slender (Fig. 4) or long and thick at base (Fig. 16, 25, 30). Postlabial quadrangle (PLQ- 4 setae, 2 on each side of median cleft, behind labial triangle - Fig. 29), of smooth or ciliated setae depending on species; other setae of venter of head smooth or ciliated, both types present in some species. Tibiotarsi, in *nitidus* group, with a double row of smooth setae along inner margin, all leg segments with ciliated setae. Ungues bi-, tri-, or quadri-dentate; all types present in *nitidus*, more than one type may be present in other species. Unguiculus almost always with an outer tooth that is never winglike. Inner margin of unguiculus toothless. Tenent hair apically lanceolate or clavate, both types in some species. Body macrochaetotaxy identical for all species (Fig. 5) except for second thoracic segment (Th. 2) of *peyerimhoffi* (Fig. 22). First abdominal segment (Abd. 1) of adults without macrochaetae. Dorsum of furcula interspecifically with or without smooth erect setae. Dental spines absent. Mucro with basal spine (except in some *nitidus*).

Diagnosis. Mari Mutt (1979a) presented a key to the subgenera of *Heteromurus* which details the differences between these taxa. Briefly, the nominal subgenus may be separated from *Verhoeffiella* by the presence of annulations on Ant. 5 (on both Ant. 4 and Ant. 5 in *Verhoeffiella*); and from *Alloscopus* and *Heteromurtrella* by the lack of macrochaetae on Abd. 1 of adult *Heteromurus* s. str. and by the absence of head seta S₀ in members of the nominal subgenus. In addition, *Alloscopus* and *Heteromurtrella* are strictly tropical.

²The system for naming head setae was proposed by Mari Mutt (1979b) and is detailed therein.

Geographic Distribution. The subgenus is essentially holarctic with most species living in Europe. Figure 33 presents the distribution of *H. major* and *nitidus*; the range of all but one of the other species falls within these.

Key to Species

1. Inner margin of tibiotarsi with rows of smooth setae; eyes 2&2, 1&1 or absent 2
Tibiotarsi without smooth setae (with exception of seta opposite tenent hair of metathoracic legs, which is present throughout subfamily); eyes 8&8 or 3&3 4
2. Th. 2 (Fig. 22) with 6 posterior setae; head and body with many microchaetae and few scales; scales absent from Ant. 3 and legs; unguis (Fig. 26) very long, about 3.3x width of tibiotarsus at level of tenent hair; antennae long, 0.6-0.8x length of head and body combined; caves in northern Algeria *peyerimhoffi* Denis 1937
Th. 2 (e.g., Fig. 5) with 4 posterior setae; head and body with few microchaetae and many scales; scales on Ant. 3 and legs; unguis shorter, about 2.5x width of tibiotarsus at level of tenent hair (Fig. 31); antennae shorter, 0.4-0.5x length of head and body combined 3
3. Apical mucronal tooth greatly elongated (Fig. 17); eyes absent; scales opaque, gray; Romanian cave *noseki* Mari Mutt and Stomp 1980
Mucro normal; eyes 2&2, 1&1 or absent; scales hyaline or opaque; if opaque, light to dark brown; geographic distribution as in figure 33 *nitidus* (Templeton) 1835
4. Eyes 3&3; venter of head mostly with smooth setae; dorsum of manubrium with smooth setae; differentiated seta of outer labial papilla clearly surpassing apex of its papilla (Fig. 16); Middle East and Mediterranean region *sexoculatus* Brown 1926
Eyes 8&8; venter of head mostly with ciliated setae; dorsum of manubrium without smooth setae; differentiated seta of outer labial papilla at most reaching apex of its papilla, usually not so long (Fig. 4, 10) 5
5. Labral papillae of type II (Fig. 11); seta E(L₂ in original description) of labial triangle most often ciliated Fig. 12); all other setae of posterior labial row ciliated; USSR (Tajikistan) *variabilis* Martynova 1974
Labral papillae of type III (Fig. 18-19) or absent; seta E of labial triangle smooth; at least 1 other seta of posterior labial row also smooth 6
6. Labral papillae of type III (Fig. 18-19); length of adults up to 5.0 mm; individuals over 2.3 mm with scales on base of labium (see Mari Mutt and Stomp 1980); pigment scarce, very light, restricted to Ant. 4-5; Portugal *gigans* Mari Mutt and Stomp 1980
Labral papillae absent; length of adults up to 3.0 mm, most frequently up to 2.5 mm; scales absent from base of labium; pigment more abundant (Fig. 2, 3), seldom restricted to Ant. 4-5; geographic distribution as in figure 33 *major* (Moniez) 1889

Descriptions

Note: The literature on *H. nitidus* and *major* is too extensive to be listed here. Up to early 1978 the first species was mentioned in 626 publications and the second in 125. All these references are detailed by Mari Mutt (1978b). A large number of references published before 1961 are listed by Salmon (1964). I have detailed herein, for the aforementioned names, their full synonymy and those references considered more relevant. Full synonymy and all the references are included for the other species except for some papers by Zonev, dealing with *H. sexoculatus*, which I have not obtained.

Heteromurus (Heteromurus) major (Moniez)

Templetonia major Moniez 1889: 26-27. Moniez 1890: 68-69.

Heteromurus major (Moniez). Absolon 1901: 11-12. Börner 1901: 76-78, pl. 2, Fig. 9.
Denis 1923: 56-57. Denis 1924: 276-280. Handschin 1942: 425-428, 443, 445.

Stach 1967: 394, 409-411, pl. 33. Hühner 1970: 8-9, Fig. 22-28. Ellis 1974: 123-124. Martynova, Chelnokov and Rasulova 1974: 66, 67. Ellis 1976: 310.
Ptenura major (Moniez). Salmon 1964: 479.
Heteromurus caerulescens Börner 1903: 156. Denis 1925: 212. Salmon 1954: 122. Mari Mutt 1980: 544.
Ptenura caerulescens (Börner). Salmon 1964: 479.
Heteromurus melitensis Stach 1924: 115, pl. 1, Fig. 13, Stach 1967: 409, 410, 411.
Ptenura melitensis (Stach). Salmon 1964: 479.
Heteromurus mexicanus Handschin 1928: 545. NEW SYNONYMY.
Ptenura mexicana (Handschin). Salmon 1964: 479.
Heteromurus caucasicus Chelnokov 1974: 70, 71; in Martynova, Chelnokov and Rasulova 1974. NEW SYNONYMY.
Lepidocyrtus lundbladi Agrell 1939: 5-6. Gisin 1948: 125. Gama 1959: 33. Gama 1961: 14, 15.

Habitus as in figures 2 & 3, see also Stach 1967: plate 33, Fig. 1 and Stach 1924: plate 1, Fig. 13 (as *melitensis*). Length up to 3.0 mm, generally up to 2.5 mm. Coloration variable; typical pattern (Fig. 2) composed of pigment distributed throughout antennae (more conspicuous on Ant. 3-5), anterior and lateral portions of head, anterior $\frac{1}{2}$ of mesonotum, lateral margins of Th. 2 - Abd. 1, and throughout legs, especially on femora and tibiotarsi; light pigment sometimes along borders of body segments. Lighter and darker (Fig. 3) individuals, as well as all intergrades, may occur sympatrically. Antennae about 0.4x length of head and body combined. Eyes 8&8 on dark patches, eyes g&h reduced in diameter (Fig. 7). Labral papillae absent (see Stach 1967: plate 33, Fig. 2). Chaetotaxy of labial triangle (Fig. 6, see also Martynova et. al. 1974: 67, Fig. 1 and Huther 1970: 10, Fig. 27) variable, A₁, A₂ and E smooth; posterior row with 4-6 ciliated setae or 1 (seldom 2) smooth setae. Differentiated seta of outer labial papilla short, slender, not reaching apex of its papilla (Fig. 4). Setae of PLQ and most other setae on venter of head ciliated. Tibiotarsi without smooth setae. Ungues quadridentate (Fig. 8), seldom tridentate. Unguiculus with small outer tooth. Tenent hair apically clavate. Body macrochaetotaxy typical of subgenus (Fig. 5, see also Huther 1970: 10, Fig. 22). Furcula without smooth setae. Mucro with basal spine.

Comments. Although it is preferable not to propose new synonyms unless specimens of the taxa concerned are studied, it is my opinion that the name *H. caucasicus* should not have been proposed. According to its author, *caucasicus* is to be separated from *major* by its pigmentation, size, and labial chaetotaxy. The expression of all these characters in *caucasicus* falls within the range of variability of *major*. *H. caucasicus* was apparently described from a single specimen.

I have received from Dr. F. Bonet ten specimens of *Heteromurus* from near the type locality of *H. mexicanus* Handschin 1928. The specimens agree in most respects with Handschin's description and in all but one aspect with the description of *major* (Mexican specimens are light blue and more evenly pigmented). The original description of *mexicanus*, which did not include diagnosis, presents a color pattern more like that of typical *major* than seen in Bonet's specimens.

The synonymy between *H. major* and *caerulescens* has been proposed several times but frequently preceded by a question mark (e.g., Handschin 1942, Gisin 1960). I have studied a paratype of *caerulescens*, deposited at the BMNH, and can find no difference between it and *major*. As Denis (1924: 279-280) pointed out, *caerulescens* was described at a time when the identity was not clear; Börner (1901) having misconceived Moniez's species. The main difference between both species, according to Börner's description, is the presence of 8&8 eyes in *caerulescens*. Denis (1924) studied the types of *major* and found 8&8 eyes.

Material Examined. JB: FRANCE, Provenze, May 1977, J.A. Barra, col., 27 specimens. MNHN: FRANCE, Boungta-Reine, Seine, Feb. 4, 1945, over 70 specimens. PAS: BULGARIA, Ost. Rica, 850 Bistrice, April 18, 1936, L. Drenowski, col., 8 specimens. BULGARIA, Warna, Aug. 20, 1937, L. Drenowski, col., 4 specimens. HUNGARY, south of Budapest, Simontornya, Kom. Tolna, 24 specimens. MALTA, 1925, Gatto, col., 35 specimens (identified as *H. melitensis* by Stach). WNE (all collected by W.N. Ellis): FRANCE, var. Gossin, April 29, 1975 (1975-076), 1 specimen. FRANCE, van Gorge de Verden, April 26, 1975 (1975-004), 3 specimens. SPAIN, Mallorca, Arta, Feb. 2, 1975 (1975-004), 2 specimens. As preceding but Lluch Alcami, Nov. 11, 1975

(1975-279), 2 specimens. GREECE, Crete, Knossos, Oct. 24, 1972 (1972-242, see Ellis 1976: 223 for full locality data), 2 specimens. As preceding but 1972-195, 1 specimen. Drosia, Oct. 23, 1972 (1972-226), 1 specimen. Rhodes, Lindhos, April 15, 1970 (1970-010, see Ellis 1974: 107 for full locality data), 3 specimens. Kalathos, April 5, 1970 (1970: 022, 2 specimens.) INHS. MEXICO, Federal District, Aug. 15, 1953, A. Barrera, col., 10 specimens identified as *H. mexicanus* by Bonet. Also in the INHS are several specimens from some of the localities listed above. JAMM. Some specimens from the above localities.

The present author has no information about the whereabouts of the types of this species.

Geographic Distribution (Fig. 33): Known from one or more localities in the following countries: Algeria (north), Austria, Bulgaria, Chile (Mallueco Province, 36-40° s. lat.), Czechoslovakia, France (mainland, Yeu, Corsica), Germany, Greece (Crete, Rhodes), Hungary, Italy (mainland, Molara, Tavolara, Tuscan Archipelago), Mexico, Palestine Region, Portugal (mainland, Madeira, Azores), Romania, Spain (mainland, Canary Islands, Annobon Island-Gulf of Guinea), Switzerland, USSR (Azerbaijan SSR), Yugoslavia.

Womersley (1934: 472) cites this species from Sierra Leone and Morocco. His records are presented in a table without references and are omitted from the preceding list.

The only records of this species outside Europe and the Mediterranean region are: 1) Annobon Island, Gulf of Guinea (Selga 1962, 1 specimen). This record probably represents an introduction during the colonization by Spain. 2) Chile, Mallueco Province, south of the tropic of Capricorn (Rapoport & Rubio 1968, 1 specimen). This record could represent an introduction to a climate similar to that of the Mediterranean region. 3) Southern Mexico, vicinity of Mexico City (Handschin 1928, as *H. mexicanus* and this paper, see material examined). This record lies in the nearctic region and could represent an introduction or remnants of a once wider distribution.

Heteromurus (Heteromurus) variabilis Martynova

Heteromurus variabilis Martynova 1974: 66, 68-70, 71; in Martynova, Chelnokov and Rasulova 1974.

Length to 2.5 mm. Color pattern variable, ranges from heavily pigmented (Fig. 9, see also Martynova et al. 1974: 68, Fig. 2a) to practically unpigmented individuals (Martynova et al., *loc. cit.* Fig. 2b). Ant. 1-3 unpigmented; Ant. 4-5 at least lightly pigmented, frequently deeply pigmented creating a striking pattern. Antennae about 0.4x length of head and body combined. Eyes 8&8 on dark patches. Labral papillae of type II (Fig. 11); all papillae similar, short, conelike, apically pointed, unlike type II papillae in subgenus *Heteromurtrella*. Chaetotaxy of labial triangle (Fig. 12) variable; all setae of second row ciliated, seta E (L₂ in original description) most frequently ciliated. Differentiated seta of outer labial papilla as in figure 10. Setae of PLQ and most other setae on venter of head ciliated. Tibiotarsi without smooth setae. Methathoracic claws as in figure 13, basal pair of unequal teeth placed halfway along inner lamellae. Tenent hair apically clavate. Furcula without smooth setae. Mucro with basal spine.

Material Examined. PAS: USSR, Tajikistan, 20 km north of Dushambe, May 18, 1972, in detritus, Paupowski, col., 5 specimens.

Type material (not examined) is deposited at the LSU.

Geographic Distribution (Fig. 33): Known only from Tajikistan, USSR.

Heteromurus (Heteromurus) sexoculatus Brown

Heteromurus sexoculatus Brown 1926: 212, 213-214. Handschin 1942: 428-429.

Denis 1948: 49. Gisin 1960: 238. Gruia 1964: 203. Gruia 1969: 165, 166, 167.

Ellis 1974: 124. Ellis 1976: 310-311.

Heteromurus major var. *sexoculatus* Brown. Ellis 1974: 124.

Ptenura sexoculata (Brown). Salmon 1964: 483.

Heteromurus hexophthalmus Denis 1948: 48. Delamare Deboutteville 1952: 77. Cassagnau & Delamare Deboutteville 1955: 383. Gisin 1960: 238. NEW SYNONYMY.
Ptenura hexophthalma (Denis). Salmon 1964: 479.

Length to 2.1 mm. Pigment restricted to eye patches. Antennae not over 0.4 x length of head and body combined. Eyes 3&3 on characteristic patches (Fig. 14, 15). Labral papillae absent. Chaetotaxy of labial triangle variable; posterior row with 2-4 setae, all of which may be smooth or ciliated. Differentiated seta of outer labial papilla as in figure 16. Setae of PLQ and other setae on venter of head smooth except for few ciliated setae ventro-laterally on head. Tibiotarsi without smooth setae. Ungues tri- or quadri-dentate (Fig 20); unguiculus with small outer tooth (not mentioned in original description). Tenent hair apically lanceolate or clavate. Manubrium dorsally with at least 4 pairs of smooth erect setae (Fig. 21); base of dentes dorsally with 1 pair of these setae. Mucro with basal spine.

Comments. It is with some hesitation that I have synonymized *H. hexophthalmus* to *sexoculatus*. That both "species" are close can be gathered from one of Denis's (1948: 48) statements on the relationship between his new species and *sexoculatus*: "*Ces differences sont plus que suspectes et la reunion des deux especes est possible*". The main difference is the shape of the eye patch; in *sexoculatus* all eyes are surrounded by pigment (Fig. 14) but in *hexophthalmus* the patch is divided in two (Fig. 15).

I have studied French specimens identified as *H. hexophthalmus* and specimens from Rhodes and Crete called *H. sexoculatus* (Ellis 1974, 1976). Besides the aforementioned difference, all *hexophthalmus* have only smooth setae on the labial triangle (smooth and ciliated setae in *sexoculatus*), and all ungues are tridentate (quadridentate in *sexoculatus*).

It is tempting to separate both species but there is no assurance that Ellis' specimens are really *sexoculatus* (the types of *sexoculatus* are apparently lost, see Ellis 1976: 311). The original description of Brown's species and the redescription by Handschin (1942) figured lanceolate tenent hairs and tridentate ungues like *hexophthalmus* at hand. The relative position of the eyes of *sexoculatus* (Brown 1926: 212, Fig. 25) is also as in *hexophthalmus* under study. If two species with 3&3 eyes are present, a new name may have to be proposed for Ellis' specimens while retaining *sexoculatus* and *hexophthalmus* as synonyms.

Material Examined. MNHH: FRANCE, 27 Tuzet, Terreau Nimes Gird, maïsson deyrôle, 10 specimens. 12 Tuzet, 1 specimen (all the preceding specimens are identified as *hexophthalmus*). WNE: GREECE, Rhodes, Lindhos, April 10, 1970, soil sample of moderately damp, crumbly loam, in a shadowed olive garden (1970-006), W.N. Ellis, col., 1 specimen. Crete, Festós, along Geropotamus, Oct. 16, 1972, rather dry crumbly loam with many roots and stones in a small bush along Geropotamus, consisting of *Vitis*, *Punica* and *Ficus*; with little undergrowth of geophytes (1972-227), W.N. Ellis, col., 1 specimen. All Greek material was identified as *sexoculatus* by Ellis.

Geographic Distribution: As *sexoculatus*-Mesopotamia (Iraq), Palestine region, Greece (Central Crete, Rhodes), Romania (caves). As *hexophthalmus*-France, Lebanon.

Heteromurus (Heteromurus) peyerimhoffi Denis

Heteromurus peyerimhoffi Denis 1937: 87. Gisin 1960: 239. Stomp 1974: 112-113.
Ptenura peyerimhoffi (Denis). Salmon 1964: 483.

Length to 2.7 mm. Pigment restricted to eye patches. Scales absent from Ant. 3-5, legs, and collophore. Ant. 1-2 with few (1-4) scales, manubrium scaled sparsely. Scales hyaline, apically rounded or truncated, not fusiform. Microchaetae abundant throughout antennae, dorsum of head and body, legs, and furcula. Antennae long, about 0.6-0.9x length of head and body combined. Ant. 5 annulated, Ant. 4 not annulated but most dorsal setae arranged in whorls. Eyes 2&2 on small dark patch. Labral papillae absent. Chaetotaxy of labial triangle as in figure 24, all setae smooth. Differentiated seta of outer labial papilla long (Fig. 25). Setae of PLQ and most other setae on venter of head smooth. Tibiotarsi with double or triple row of smooth setae along inner margin. Femora with some smooth setae. Ungues (Fig. 26) unusually long, slender, with a pair of short basal teeth. Unguiculus with very small outer tooth. Tenent hair short, apically lanceolate. Body macrochaetotaxy typical of subgenus except for posterior half of Th. 2 (Fig. 22). Dorsum of manubrium with smooth setae arranged as in figure 23. Mucro with inconspicuous basal spine,

apical mucronal tooth markedly longer than subapical.

Comments. This species stands no chance of confusion with any other member of the subgenus. Its claw structure reminds of *H. (Verhoeffiella) hispanicus* and *H. (V.) longicornis* but the presence of eyes and nonannulated Ant. 4 separates the species from members of that subgenus.

Other diagnostic features, aside from claw structure, are the chaetotaxy of Th. 2, presence of many microchaetae on head and body, number and arrangement of smooth setae on dorsum of manubrium, and the long antennae.

Material Examined. NS: ALGERIA, Djurdjura, glacial caves, on snow, 2 °C., summer of 1972, F. Delhez, col. (locality no. 2 in Stomp 1974: 113), 6 specimens. As preceding but P13, 15, 17; Petit Bousoil cave, 17 specimens. INHS, JAMM: 2 specimens each from the second locality.

Type material (not seen) should be at the MNHN.

Geographic Distribution: Algeria, known only from the glacial caves of Djurdjura.

Heteromurus (Heteromurus) nitidus (Templeton)

Podura nitida Templeton 1835:94.

Ptenura nitida (Templeton). Templeton 1844: 306. Salmon 1945: 71. Salmon 1964: 131-132, 478, 480-483.

Isotoma nitida (Templeton). Nicolet 1847: 375. Kolenati 1858: 133 (as *nitidens*).

Templetonia nitida (Templeton). Lubbock 1862: 595, 596. Lubbock 1873: 13, 18, 142, 143, plate 20.

Templetonia (Heteromurus) nitida (Templeton). Theobald 1910: 193.

Beckia nitida (Templeton). McIntire 1873: 5.

Choreutes nitidus (Templeton). Elditt 1854: 20-21.

Heteromurus nitidus (Templeton). Megnin 1888: 261. Absolon 1901: 11, 12. Denis 1924: 280-282. Denis 1931: 12-13. Bonet 1931: 272-276, 283, 284, 350, 354, 356, 387. Mills 1934: 77. Denis 1934: 93-96. Denis 1935: 343-344. Delamare Deboutteville 1944: 29-30. Gisin 1944: 90, 97. Maynard 1951: 179, 184-185, 189. Yosii 1961: 26. Szeptycki 1972: 341, 342, 359, 364, 371, 372. Szeptycki 1979: 14, 19, 20, 36, 37, 49, 55, 56, 57, 59, 72, 73, 81, 85, 88, 83, 136, 137, 154, 164, 171, 187, 190, 198, 199.

Heteromurus (Heteromurus) nitidus (Templeton). Strouhal 1939: 263. Grindbergs 1960: 51.

Heteromurus (Heteromurus) nitidus margaritarius (Templeton). Grindbergs 1960: 51.

Heteromurus nitidus margaritarius (Templeton). Stach 1929: 295. Gruia 1976: 95, 101.

Heteromurus nitidus margaritaceus (Templeton). Paclt 1957: 273.

Heteromurus nitidus paucidentatus Stach 1929: 295. Gruia 1976: 90, 101.

Heteromurus nitidus quadriocellata Kseneman 1934: 14-15, 20. Gisin 1960: 239. Gruia 1976: 100.

Heteromurus nitidus albicans Durkop 1934: 508.

Heteromurus nitidus brevicornis Bonet 1934: 180-182, 185.

Heteromurus nitidus armapollerae Massera 1952: 32-33. Gilsin 1960: 239.

Heteromurus margaritarius Wankel 1860: 203. Absolon 1900a: 191, 192. Paclt 1972: 414. Bellinger & Ellis 1972: 213.

Heteromurus (Templetonia) margaritarius Wankel. Absolon 1900a: 192. Absolon 1901c: 12.

Degeeria margaritacea Nicolet 1842: 75.

Heteromurus hirsutus Absolon 1899a: 317. Absolon 1899b: 493, 495-496. Absolon 1901c: 8-12, plate 1. Cassagnau & Delamare Deboutteville 1955: 367. Paclt 1972: 414.

Ptenura hirsuta (Absolon). Salmon 1964: 479.

Heteromurus tetrophthalmus Börner 1903: 156. Stach 1922: 109, 122. Denis 1930: 94 (as *tatraphthalmus*). Gisin 1944:97. Gisin 1960: 239. Stomp 1974: 109-113, 114.
NEW SYNONYMY.

Ptenura tetrophthalma (Börner). Salmon 1964: 483.

Heteromurus cavernicolus Ionesco 1915: 222. Bonet 1931: 353.

Heteromurus gradgensis Denis 1933: 212. Denis 1934: 93. Denis 1935: 331. Denis 1936: 263-265. Denis 1938: 145. Gisin 1960: 239.
Podura crystallina Müller 1776: 183.
Isotoma crystallina (Müller). Parona 1878: 584.
Heterotoma crystallina (Müller). Bourlet 1839: 396. Gervais 1844: 377.
Orchesella crystallina (Müller). Nicolet 1847: 366.
Templetonia crystallina (Müller). Lubbock 1873: 143.
Aetheocerus crystallinus (Müller). Bourlet 1842: 32.
Sinella cavernicola Carpenter 1895: 30.
Templetonia cavernicola (Carpenter). Carpenter 1897: 229. Absolon 1901c: 11, 12, 13.
Templetonia americana Harvey 1892: 57. Mills 1934: 77.
Heteromurus americanus (Harvey). Absolon 1901: 12.
Lepidocyrtus marmoratus Packard 1873: 36. Mills 1934: 77. Gisin 1960: 239.
Pseudosinella kemneri Agrell 1936: 27. Gisin 1944: 155. Gisin 1948: 125. Gisin 1960: 239.
Propemesira duoculata Salmon 1942: 59. Salmon 1945: 71.
Troglosinella clayae Salmon 1955: 25. Gisin 1960: 239. Salmon 1964: 482.

Habitus typical of subgenus (see Lubbock 1873: plate 20 (color) and Delamare Deboutteville 1955: 454, Fig. 1-photograph). Length to 3.0 mm. Pigmentation variable, typical pattern of orange pigment distributed more or less evenly throughout head and body. Pigment sometimes absent or restricted to eye patches, which may be orange or black. Antennae about 0.4x length of head and body combined. Eyes 2&2, 1&1 or absent. Head macrochaetotaxy (Fig. 28) typical of subgenus. Labral papillae absent. Chaetotaxy of labial triangles as in figure 29; all setae smooth, posterior row (excluding E) of 3-4 setae. Differentiated seta of outer labial papilla long, clearly surpassing apex of its papilla (Fig. 30). All setae of venter of head (including PLQ) smooth. Tibiotarsi with 2 rows of strong smooth setae along inner margin, number of setae increases with size of specimen. Ungues (Fig. 31) bi-, tri-, or quadridentate; most often tridentate. Unguiculus usually with well developed tooth beyond middle of outer lamella, tooth sometimes absent. Tenent hair apically lanceolate or clavate, both types sometimes on same specimen. Dorsum of manubrium with double row of smooth erect setae, 1 pair of these setae on proximal dorsal portion of dentes. Mucro sometimes without basal spine.

Comments. Although this species is quite variable with respect to some characters (e.g., pigmentation, number of eyes, number of teeth on unguis and unguiculus, shape of tenent hair) other features are constant and permit rapid recognition. The *nitidus* group of species is characterized by: only smooth setae on labial triangle and rest of venter of head, double row of smooth setae along inner margin of tibiotarsi and the presence of smooth setae on dorsum of manubrium. From *H. peyerimhoffi*, *nitidus* can be readily separated by the ratio of length of unguis to width of tibiotarsus at level of tenent hair. From *noseki* it can be separated immediately by the shape of the mucro.

The use of latinized names for varieties is undesirable and incorrect since such names are intended for subspecies which by definition must be geographically isolated. None of *H. nitidus*' seven varieties (a key to which is given by Gisin 1944) can be considered as subspecies. Bonet (1931) found specimens of the varieties *quadriocellata* (2&2 eyes), *margaritarius* (eyes absent) and of the nominal variety (1&1) within the same colony. I have found specimens with bidentate (*paucidentata*) and tridentate (nominal variety) unguis in the same population. Similar observations were made by Delamare Deboutteville (1944), Denis (1924, 1931) and Gama (1962). The name *Heteromurus nitidus callaticola* Gruia 1965 (again cited by the same author in 1969) is unavailable as it violates article 45 c, e of the Rules of Zoological Nomenclature which declares unavailable latinized names proposed for varieties after 1960.

Although *H. tetrophthalmus* has been mentioned in 28 publications (17 of which cite new records), the only comprehensive description of the species is the original one (Stach 1922 and Stomp 1974 added descriptive notes). This situation probably arose because the only difference

between *tetraphthalmus* and *nitidus* (e.g., see Gisin 1944, 1960) is the absence of the unguicular tooth in *tetraphthalmus*.

I have studied a paratype of *tetraphthalmus* (kept in the BMNH) and it complies with Börner's description. Some of the specimens recorded by Stomp (1974) from northern Algeria were also studied and no unguicular tooth was found. Specimens reported by Delamare Deboutteville (1946) from Portugal must be referred to *nitidus* because the unguiculi possess a clear outer tooth. Although *nitidus* and *tetraphthalmus* are troglomorphic and the geographic range of the latter falls within the former's, they have not been collected together (or perhaps they have but specimens have received only one name).

Whether Börner's *tetraphthalmus* ought to be considered separate from *nitidus* or not depends on the importance assigned to the absence of the unguicular tooth. Faced with such a variable species as *nitidus* I am treating *tetraphthalmus* as a synonym of *nitidus*. An experimental approach, such as that used by Hale & Rowland (1978) to help distinguish species of the *Onychiurus armatus* group, would be a most welcome contribution towards settling the taxonomic status of *tetraphthalmus*.

Material Examined. BMNH, Germany, Frauenburg, Marburg, July 1901, BM 1907-130, C. Börner det., 3 specimens. CZECHOSLOVAKIA, Pacina Cave, Popovopolje, Herzegovina, Aug. 20, 1937, R.S. Hawes, col., BM 1937-88, 1 specimen. BULGARIA, Temna Docapka, Karlova Regn., Aug.-Sept. 1967, on clay, W. Maxwell, col., BM 296 AB 1899, 1 specimen. SWITZERLAND, Chateau du Bols, rotten lichenous fallen bark, May 19, 1963, P.N. & B.K. Lawrence, cols., 1849, 1 specimen. GREECE, Crete, Aug. 20, 1967, Birmingham University Speleological Society expedition, BU 110, 1 specimen. GREECE, northwest region, Perama n. Loannine, moss on electric light stalagmite, May 23, 1971, T. Clay, col., 1 specimen. IRELAND, Bantry County, Jan. 28, 1953, under stones in pasture, 178, BM 1953-91, 1 specimen. CLARE, Pollnagollum, Gunmana cave, July 7, 1960, pool in pothole, 769, P.N. Lawrence, col., 1 specimen. CLARE, near Ballyvaghna, ¼ km west of Newtown Castle, Aug. 5, 1960, ivy humus foot of 6 meter cliff, 742, P.N. Lawrence, col., 1 specimen. HOLLAND, near Amsterdam, edge of Zuider Zee, Aug. 1, 1951, under stones, BM 1951-459, 1 specimen. ENGLAND, Huntshire, Monks Wood, Sould pond, March 14, 1973, on bank of pond, 3147-51, P.N. Lawrence, col., 2 specimens. SURREY, Godston mine, mid-April 1969, BM/832, BM 1969-221, W. Maxwell, col., 1 specimen. NORTHUMBERLAND, Pegswood, water pollution research laboratory, 1967, BM 1968-418, 1 specimen. CAMBRIDGE, Feb. 4, 1925, under board in garden, C.H. Jackson, col., 1 specimen. KENT, Chiselhurst caves, Nail Box chalk mine, April 3, 1955, BM 145, P.N. Lawrence, col., 3 specimens. SOMERSET, Dundry stone mines, near Bristol, dark zone, Ato/10, 2 specimens. LINCOLNSHIRE, Fiskerton, water pollution research laboratory, Sept. 20, 1966, BM 1966-418, 1 specimen. ITALY, Palmi (Calabria), under stone in olive grove, April 9, 1902, C. Börner, col., 1 paratype of *H. tetraphthalmus*, BM 1907-130.

HJG: ENGLAND, Surrey, Godston mine, Oct. 17, 1970, on rotten wood, H.J. Gough, col., 5 specimens. DEVON, Rockhouse caves, lower central tunnel, Oct. 10, 1970, W.G.R. Maxwell col., 2 specimens. BERKSHIRE, Jealott's Hill, surface of pond, May 26, 1967, 1 specimen. BERKSHIRE, Bradfield, hazel litter, Sept. 27, 1970, W. Wilkinson, col., 1 specimen. SOUTH DEVON, Badford cave, on surface of pool, March 17, 1974, H.J. Gough, col., 3 specimens. SPAIN, Picos de Europa, Cueva Dobros, 410 m from entry, Aug. 1972, H.J. Gough, col., 4 specimens.

INHS: USA, Iowa, Ames, Sept. 2, 1933, on a cellar, 57 specimens. CANADA, Ontario, Arrprior, Sept., with earthworms on garden bed, Macnamara, col., 9 specimens.

JAB: FRANCE, Grotte de Bartharram, April 6, 1968, 5 specimens. STRASBOURG, June 15, 1966, 2 specimens.

KAC: USA, Iowa, Dubuque Co., Dubuque, Billboard cave, 1483, 1 specimen. MAINE, York Co., 453, 1 specimen. NEW YORK, Columbia Co., 2218, Polk, Norton & Culver, cols., 1 specimen. NEW YORK, Jefferson Co., Glenn Park, Labyrinth cave, 1891, 1 specimen.

MNH: ITALY, Paitone-Brescia, Buco del Frate, Feb. 10, 1940, M. Pavan, col., 53 specimens. PORTUGAL, Lapa de Saldada, A. de Barros Machado, col., 16 specimens identified as *H. tetraphthalmus* by Delamare Deboutteville 1946. CASA DE MOURA, Cesaride Peniche (d. Lisboa), Aug. 23, 1943, A. de Barros Machado, col., 1 specimen.

NS: FRANCE, Catacoubes de Paris, J.-M. Thibaud, col., 13 specimens. ALGERIA, Maudabee Mac 3 cave, F. Delhez, col., 5 specimens identified as *H. tetraphthalmus* by Stomp 1974. Ifri Smedane cave (placed on the foot of a mountain, properly said this is not a glacial cave), IS 1, 12 °C., 3 specimens (labeled *H. nitidus* but treated as *H. tetraphthalmus* by Stomp 1974).

NZNM: NEW ZEALAND, Wellington, under the linoleum in a dwelling, D.K. Ross, col., 1 paratype of *Propemesira duoculata* Salmon.

PAS: BULGARIA, Warva, Aug. 20, 1927, L. Drenowski, col., 8 specimens. Magura cave, near Rabisa, Sept. 8, 1948, 10 specimens. SPAIN, Pyrenees, Santa Isabel station cave, Oct. 8, 1935, G. Santander, col., 10 specimens. Pyrenees, Cueva de Santian, Oct. 5, 1935, Stammer, col., 6 specimens.

SAS: CZECHOSLOVAKIA, Moravian Karst, 18K, June 12, 1973, Zacharda, col., 5 specimens.

USNM, ENGLAND, on potatoes intercepted at Philadelphia (USA), Oct. 17, 1952, 52-12594, 11 specimens. HOLLAND, on lily bulbs intercepted at New York, Sept. 26, 1934, no. 28571, 1 specimen. FRANCE, hickory leaf, lot. 36-29776, Aug. 17, 1936, 1 specimen. USA, New York, Rochester, March 30, 1947, under stone, R. Maynard, col., 16 specimens reported upon by Maynard (1951).

The type material for this species is apparently lost.

Geographic Distribution (Fig. 33): Holarctic with exception of one record from Argentina (Bonet 1934, as *H. nitidus* var. *brevicornis*), one from Chile (Rapoport & Rubio 1968), and one from New Zealand (Salmon 1942, as *Propemesira duoculata*).

My collection contains two Peruvian specimens identified as *H. nitidus* by Winter (1963: 509, collection 34a) but they are *H. (Heteromurtrella) schoetti* Denis 1931, species previously known from Costa Rica and Guatemala. Although Winter (1963) recorded *nitidus* from various other localities, it is likely that they are all *schoetti* or another species of the subgenus *Heteromurtrella*.

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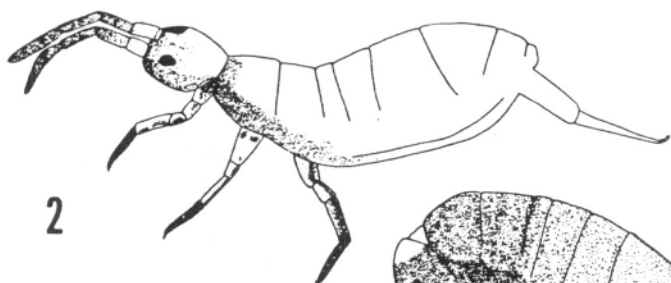
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Legends for the Figures

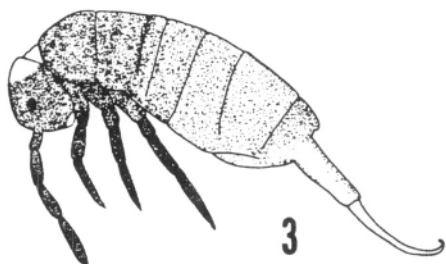
1. Phyletic diagram for the species of *Heteromurus* s. str., see text for explanation.
- 2-8. *H. (H.) major*. 2. Habitus of lightly pigmented specimen. 3. id., more thoroughly pigmented form; both specimens from same population. 4. Outer labial papilla. 5. Body macrochaetotaxy, each dot represents a seta. 6. Chaetotaxy of labial triangle. 7. Arrangement of eyes. 8. Metathoracic claws.
- 9-13. *H. (H.) variabilis*. 9. Habitus and distribution of violet pigment. 10. Outer labial papilla. 11. Labral papillae. 12. Chaetotaxy of labial triangle. 13. Metathoracic claws.
- 14-16, 20-21. *H. (H.) sexoculatus*. 17. *H. (H.) noseki*. 18-19. *H. (H.) gigans*. 14. Arrangement of eyes of specimen from Crete labeled *H. sexoculatus* (det. Ellis). 15. Arrangement of eyes of specimen from France labeled *H. hexophthalmus* (det. Denis). 16. Outer labial papilla. 17. Mucro. 18. Outer labral papilla, lateral view. 19. Labral papillae. 20. Metathoracic claws. 21. Manubrium and proximal portion of dens showing distribution of smooth erect setae, lateral view.
- 22-27. *H. (H.) peyerimhoffi*. 22. Body macrochaetotaxy, each dot represents a seta. 23. Manubrium and dorsal portion of dentes detailing distribution of smooth erect setae, dorsal view. 24. Chaetotaxy of labial triangle. 25. Outer labial papilla. 26. Metathoracic claws. 27. Maxillary palp.
- 28-32. *H. (H.) nitidus*. 28. Head macrochaetotaxy; each dot represents a seta, P = posterior group. 29. Chaetotaxy of labial triangles and positions of setae forming the postlabial triangle (PLQ). 30. Outer labial papilla. 31. Metathoracic claw; unguis may have 2-4 inner teeth, tenent hair may be apically lanceolate or clavate. 32. Chaetotaxy of labial triangle.
33. Geographic distribution of *H. (H.) major*, *nitidus* and *variabilis*.

Ancestor of *HETEROMURUS* s. str.

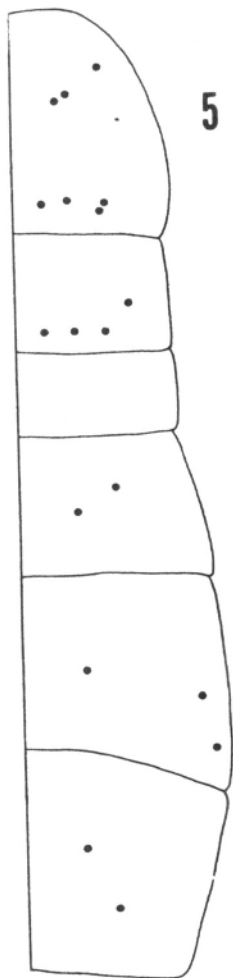


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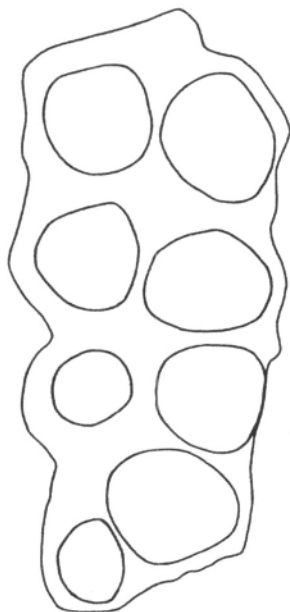
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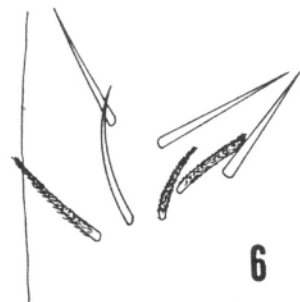
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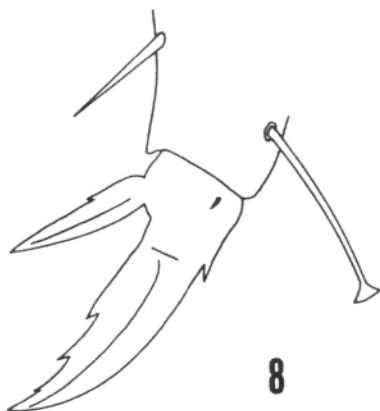
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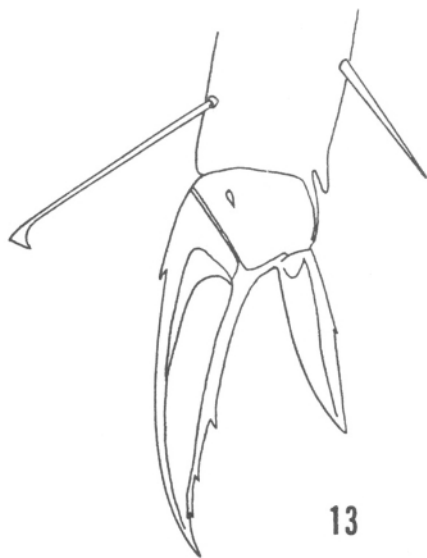
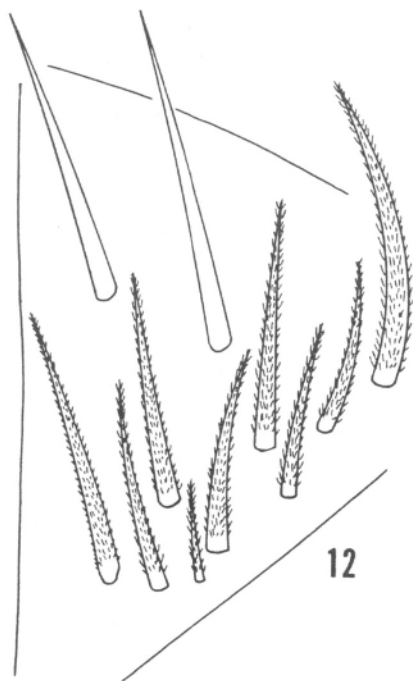
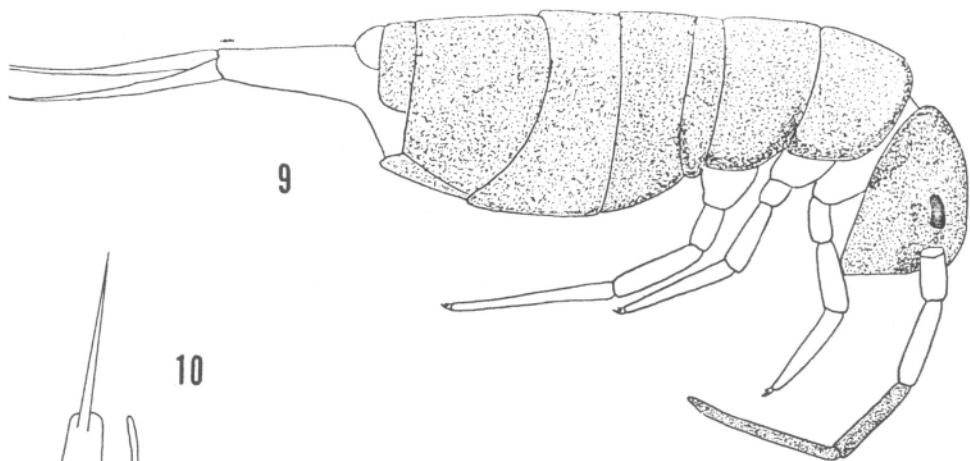
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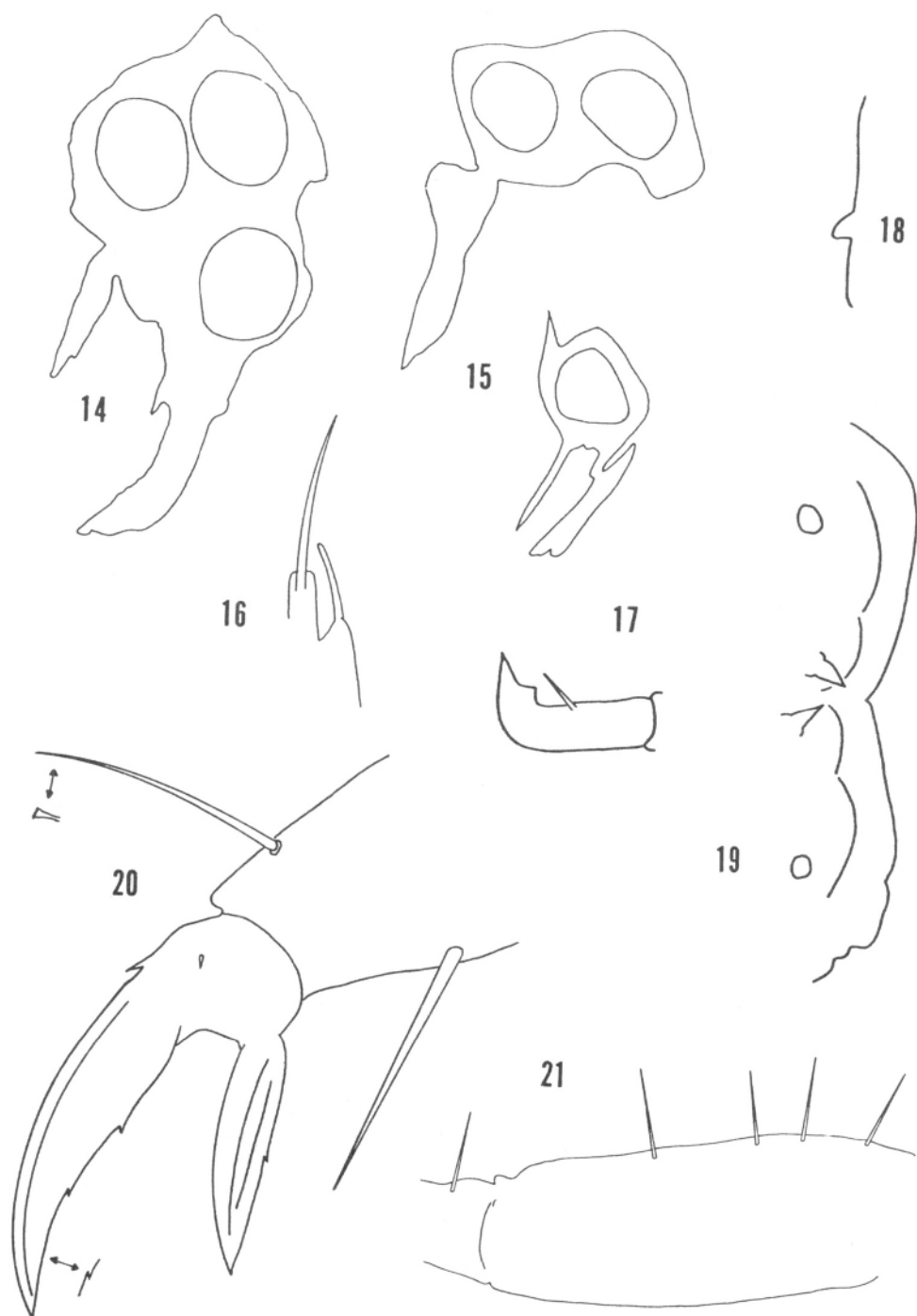


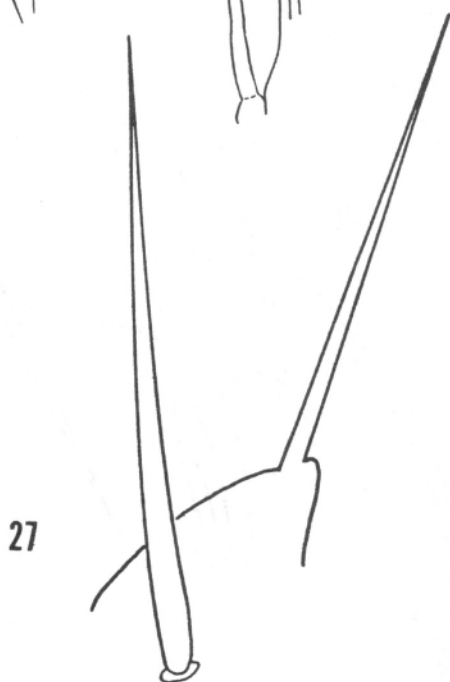
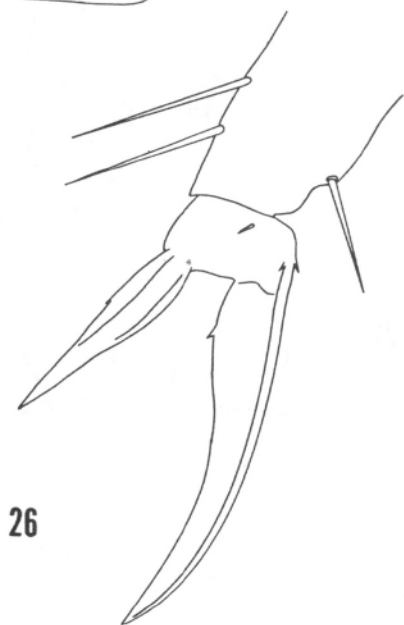
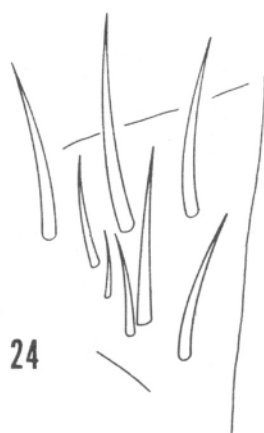
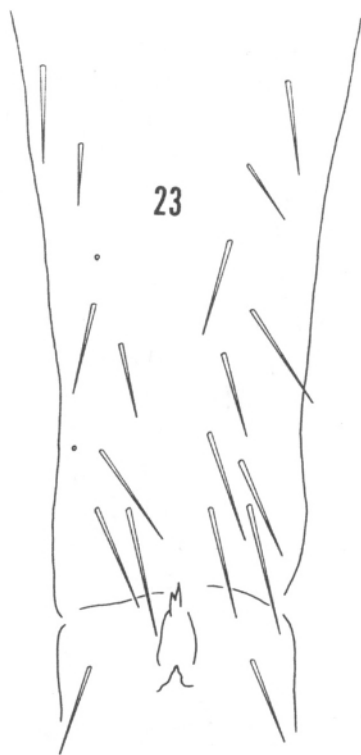
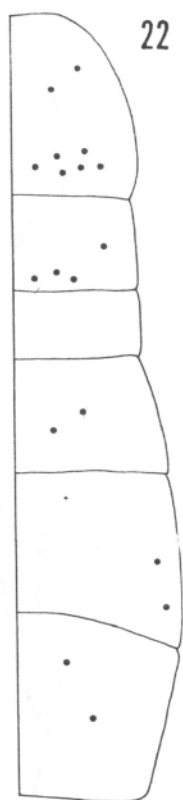
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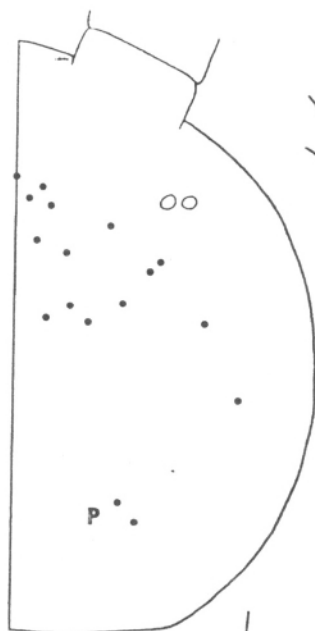


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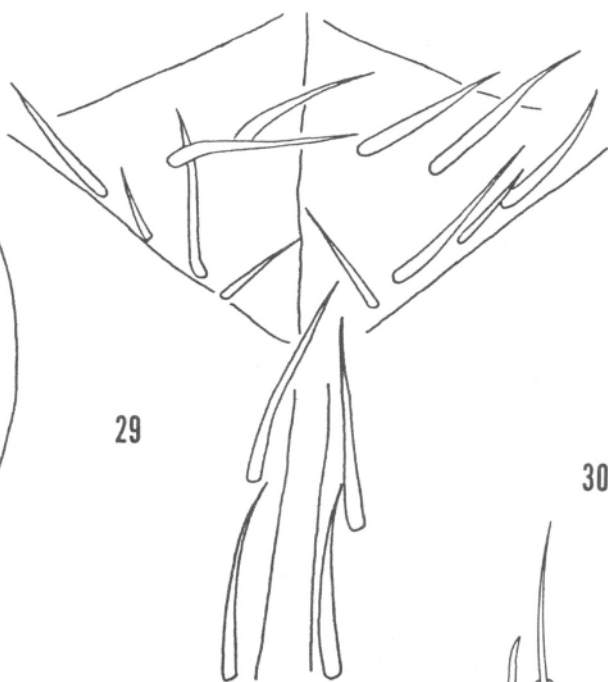








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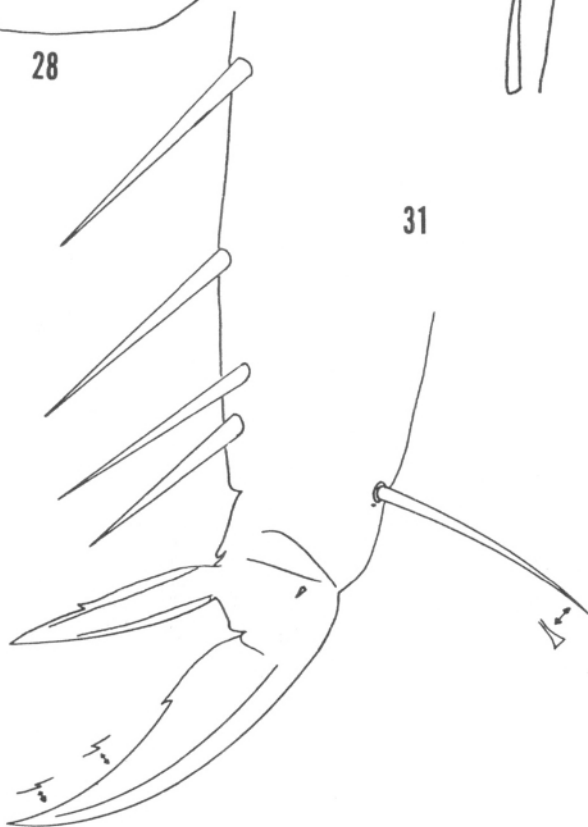


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