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The systematics and biology of the genus Neotrombidium Leonardi are reviewed and discussed. A generic description is presented for larvae and post-larvae of Neotrombidium, together with descriptions of two new species, N. cleronyssus and N. tenebrionyssus. The biology and life history of N. tenebrionyssus are described, with notes on rearing and host specificity.

The adults and larvae of N. tricuspidum Borland, and adults of N. armatum André, elongatum André, and indosinensis André are compared with the newly described species. Neotrombidium gracilipes Womersley is excluded from the genus Neotrombidium, since its affinities lie outside this genus. Neotrombidium helladicum Cooreman is tentatively synonymized with N. indosinensis André.

A study of the systematic placement of the genus

Neotrombidium necessitated a re-evaluation of the familial concepts within the Trombidioidea. It is proposed that the families Trombiculidae Ewing, Leeuwenhoekiidae Womersley, Trombellidae Feider, Peritremotrombidiidae Feider, Stigmotrombidiidae Feider, and Johnstonianidae Newell be reduced to no more than subfamilial levels, within the inclusive family Trombidiidae Leach. It is also proposed that the superfamily Trombidioidea be composed of the family Trombidiidae and the so-called Hydrachnellae, based on common morphological characteristics.

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GEORGE SINGER

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APPROVED:

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Associate Professor of Entomology
In Charge of Major

Redacted for Privacy

Chairman of Department of Entomology

Redacted for Privacy

Dean of Graduate School

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INTRODUCTION

The intermediate position of the genus Neotrombidium between the families Trombidiidae Leach and Trombiculidae Ewing presents a situation in need of clarification. A lack of a critical definition for the larval stages of Neotrombidium species has also caused confusion and synonymies. The genus Neotrombidium was previously defined with certainty, only on the basis of post-larval characteristics. This study will present a more inclusive definition for the genus, and will call attention to the need for more critical revisional work within the Trombidioidea as a whole.

SYSTEMATICS

Materials and Methods

Methods and materials dealing with the rearing and life history studies will be treated under a separate heading. Specimens were mounted in Hoyer's fluid (=André's fluid), on standard glass slides. Dissection and remounting of specimens was carried out, where necessary, to more clearly interpret given structures. Measurements were made with a fixed, calibrated ocular micrometer. Illustrations were made with the aid of a microprojector. Details were then checked and corrected under phase contrast microscopy, prior to inking. A heavy type of vellum tracing paper, obtained from the Glasner Art Supply Company, 48 West 48th Street, New York 36, New York, was used for the final inking. This paper allowed repeated corrections to be made on the final inked figure, without smearing or blotting.

In addition to material representing two new species, N. cleronyssus and tenebrionyssus, the types of N. tricuspidum, indosinensis, elongatum, armatum, and Monunguis streblida were studied, and described and illustrated where necessary.

The mounting technique employed during this study was essentially the following: Preservation of specimens in 90% alcohol until the red color had dissolved away.

This prevented oil and color globules from remaining in the final preparation. Clearing of specimens in Nesbitt's fluid, by introduction of specimens into the cold clearing fluid and heating to fuming (just prior to boiling), then cooling prior to mounting. Specimens could not be allowed to remain in Nesbitt's for more than four hours, because of a tendency for specimens to weaken and disintegrate on handling. Cooling prior to mounting reduced the tendency for specimens to contract on immersion into the mountant. Cleared specimens which could not be mounted after cooling were transferred to a solution of 3% glycerine in 40% alcohol, in an unstoppered vial. Storage in this solution prevented the weakening effect of the clearing agent, prevented the hardening effect of alcohol, and allowed for infiltration with glycerine. Glycerine-infiltrated specimens were more easily handled for dissection and mounting.

Hoyer's mounting medium was used in all slide preparations.

Systematic Position of the Genus Neotrombidium

Neotrombidium was erected as a subgenus of Trombidium, in the family Trombidiidae, by Leonardi (1902, not 1901). Berlese (1912) elevated Neotrombidium to generic status. Thor (1935a) included Neotrombidium in his Ottoniinae. Thor (1935b) substituted the name

Microtrombidiinae for Ottoniinae, a preoccupied name. Thor and Willmann (1947) retained Thor's concept, although earlier, Womersley (1945a), calling attention to the close relationship between Neotrombidium adults and adults of Leeuwenhoekia, removed Neotrombidium from the Microtrombidiinae. In Womersley (1945b) the genus Neotrombidium was redefined, using the adult of N. barringunense Hirst as the type species and assigned to the newly proposed Leeuwenhoekiidae Womersley.

Baker and Wharton (1952) again listed Neotrombidium in the Microtrombidiinae, although on the basis of their key (p. 174), Neotrombidium adults would be included in the Trombiculidae. Womersley's Leeuwenhoekiidae was not recognized by Baker and Wharton.

Wharton (1938) described the larval Monunguis streblida. In Wharton (1947a) the larval Monunguis was synonymized with Neotrombidium by the fact that M. streblida resembled specimens of trombidioid larvae collected in association with Neotrombidium adults. This observation by Wharton apparently prompted Womersley (1954a) and Audy (1954) to place the larval Neotrombidium Leonardi (not Hirst) in the Apoloniinae (Leeuwenhoekiidae of Womersley, Trombiculidae of others). It should be noted that the data presented by Audy (1954, p. 165) for the larval Neotrombidium represents Monunguis streblida, not the larva of Neotrombidium, as he assumed. The

importance of this point will be shown subsequently.

Southcott (1954a) was the first to correlate the larva with the adult for a Neotrombidium species, N. barringunense, through actual rearing. The larval N. barringunense was placed in the Leeuwenhoekiidae. Borland (1956) correlated the larva and adult for N. tricuspidum, but left the genus unassigned, "until the taxonomy of related genera becomes better known, and until family levels are drawn along more definite lines."

Southcott (1957a) reviewed the genus and discussed some of its affinities to the Trombidioidea, placing it tenuously in the Leeuwenhoekiidae, a family concept which Southcott did not accept. The familial concept of Womersley's Leeuwenhoekiidae is still in a state of flux. Baker and Wharton (1952), Audy (1954), Southcott (1957a), Crossley (1960), Zumpt (1961), and others, do not accept Womersley's concepts. André (1958), Cooreman (1960), Vercammen-Grandjean (1965b), and others, find the concept useful.

Feider (1955) elevated the genus Neotrombidium to the level of a subfamily in his "Stigmotrombidiidae", a family designation which has not been accepted by most acarine taxonomists. A literature survey does not tend to clarify the problem of where to assign the genus Neotrombidium.

Species Included in Neotrombidium

1. N. ophthalmicum (Berlese).
   Trombidium ophthalmicum Berlese, 1888, Bulletino della Società Entomologica Italiana 20:179.

2. N. furcigerum Leonardi.
   Neotrombidium furcigerum Leonardi, 1902, Zoologischer Anzeiger 25:17.

3. N. tridentifer (Ewing).
   Rhyncholophus tridentifer Ewing, 1909, Transactions of the Academy of Sciences of St. Louis 18:56.

4. N. barringunense Hirst.
   Neotrombidium barringunense Hirst, 1928, Annals and Magazine of Natural History 1:563-564.

5. N. tenuipes (Womersley).
   Cockingsia tenuipes Womersley, 1954, Studies from the Institute for Medical Research, Federated Malaya States 26:115-117.

6. N. tricuspidum Borland.
   Neotrombidium tricuspidum Borland, 1956, Journal of the Kansas Entomological Society 29:29-35.

7. N. elongatum André.
   Neotrombidium elongatum André, 1958, Publicação Culturais, Companhia Diamantes de Angola, Museo do Dundo 35:112-114.

8. N. armatum André.
   Neotrombidium armatum André, 1958, Publicação Culturais, Companhia Diamantes de Angola, Museo do Dundo 35:115.

9. N. indosinensis André.
   Neotrombidium indosinensis André, 1960, Acarologia 2:324-326.
   Neotrombidium helladicum Cooreman, 1960, Bulletin et Annales de la Société Royale d'Entomologie de Belgique, 96:195-204.

10. N. neptunium Southcott.
    Neotrombidium tridentifer Southcott, 1957, Transactions of the Royal Society of South Australia 80:157-164.
    Neotrombidium neptunium Southcott, 1961, Australian Journal of Zoology 9:412.

11. N. gracilare Womersley.

    Neotrombidium gracilare Womersley, 1963, Transactions of the Royal Society of South Australia 86:150-152.

12. N. samsinaki Daniel.
    Cockingsia samsinaki Daniel, 1963, Acarologia 4:576-581.

13. N. tenebrionyssus n.sp.

14. N. cleronyssus n.sp.

Berlese (1888) described Neotrombidium ophthalmicum from an unique Paraguayan adult specimen. Leonardi (1902) described N. furcigerum from an Argentinian adult specimen. In his description, Leonardi erected the subgenus Neotrombidium for furcigerum, which was included in Trombidium at the time. The original description follows:

> 43° Trombidium furcigerum Leon. n.sp. - miniaceum (?), et cutulis; abdomine toto pilis in furcam lange triramosam defermatis induto, cephalothorace crista metopica destituto pilisque breviter cylindricis desevestuto; oculo in quoque latere unico; palporum unguibus apice tribus.
>
> Propter oculos tantum binos, cephalothorace crista metopica nulla, aliisque characteribus in subgenere Neotrombidium species mihi videtum inserinda.
>
> Ad: 1,900 long.
> Habitat: Unicum vidi exemplu ad St. Pedro de Colalao collectum.

The triramous configuration of the idiosomal setae in adult trombidioids was considered by Berlese to have generic value. In Berlese (1912), Neotrombidium was elevated to generic rank, Neotrombidium ophthalmicum was redescribed, and additional data were presented by which ophthalmicum and furcigerum could be distinguished.

Ewing (1909) described N. tridentifer from the adult, collected in Illinois, U.S.A. Ewing's description and illustrations are useless below the generic level and, regrettably, the type material has been misplaced and lost (Dr. E. W. Baker, personal communication, 1963).

Hirst (1928) described, but did not illustrate, N. barringunense from an adult Australian specimen. In Hirst (1929), N. barringunense was illustrated and mention was made of its abundance in Australia. Neotrombidium barringunense was later mentioned briefly by Womersley (1936). Womersley (1945b) critically redescribed barringunense, and included a list of Australian localities from which the species was known. The larva of barringunense was carefully described and illustrated by Southcott (1954a), who was the first to correlate the larva and adult for a Neotrombidium species.

The genus Cockingsia was proposed for the larval N. tenuipes by Womersley (1954a). Southcott (1957a) synonymized Cockingsia with Neotrombidium on rather conclusive evidence. Womersley (1963c) upheld this

synonymy.

Borland (1956) described the larva and adult of N. tricuspidum from Kansas and North Carolina, U.S.A. Southcott (personal communication, 1963) suggested that tricuspidum may be a synonym of Ewing's tridentifer. Ewing's types will have to be re-examined in order to clarify the status of tricuspidum.

Southcott (1957a) described N. tridentifer from adults collected in association with N. barringunense adults in Australia. A problem of homonymy arose when Southcott (1961, p. 412) discovered N. tridentifer (Ewing, 1909), an easily overlooked description. In order to correct this homonymy, Southcott renamed his tridentifer, N. neptunium.

André (1958) described N. elongatum and armatum from adults collected in Angola. André (1960) described N. indosinensis from Indochina. In the same year, Cooreman (1960) described N. helladicum from one adult specimen collected in Greece, and included an excellent review of the genus Neotrombidium. Cooreman's N. helladicum is here considered a synonym of André's indosinensis. A study of André's paratype of indosinensis showed that the idiosomal setae are indistinguishable from those of helladicum (contrary to André's illustration). The shape and measurements of tarsus I, as well as a comparison of

the description and illustration of helladicum with a paratype of indosinensis, indicates that the two are conspecific.

Womersley (1963c) described N. gracilare from postlarval specimens collected from bat caves in Australia. Womersley was able to distinguish between nymphs, females and males. However, he did not present much data by which these different instars may be characterized. A short incomplete review and a key to some of the adult forms of Neotrombidium were included in his paper.

Recently, Daniel (1963) described a new larval species, Cockingsia samsinaki. Daniel was apparently misinformed, following Audy (1954) and Womersley (1954a), in his statements that Neotrombidium larvae bear a 7:7:7 leg segmentation and that N. tenuipes shows spiracles and tracheae. These discrepancies appear surprising in view of the fact that Southcott (1957a), a paper included in Daniel's bibliography but apparently not consulted, indicated that Neotrombidium larvae have a 7:6:6 leg segmentation, and that N. tenuipes does not show spiracles and tracheae. Cockingsia samsinaki is included in Neotrombidium and Cockingsia, by virtue of its synonymy with Neotrombidium, (see Southcott, 1957a and Womersley, 1963c) is a nomen rejectum.

Neotrombidium tenebrionyssus is a new species

described from larvae, nymphs and adults, collected from a species of tenebrionid beetles in Kansas and other eastern states, U.S.A., and laboratory reared. A separate section is devoted to the study of the biology and life history of this species.

Neotrombidium cleronyssus n.sp. is described from two larval specimens collected from a clerid beetle in Arizona, U.S.A. These specimens were studied but not described by Borland (1956), discussed by Southcott (1957a), and mentioned by Womersley (1963c).

Species Incorrectly Assigned to Neotrombidium

1. N. vietsi Oudemans.
   Neotrombidium vietsi Oudemans, 1929, Entomologische berichten 7:397-399. (synonym of Valgothrombium valgum (George)).

2. N. streblida (Wharton).
   Monunguis streblida Wharton, 1938, Carnegie Institution of Washington, Publication 491:150-151 (represents a genus distinct from Neotrombidium).

3. N. gracilipes Womersley.
   Neotrombidium gracilipes Womersley, 1963, Records of the South Australian Museum, 14:473-476 (represents a genus distinct from Neotrombidium).

Wharton (1938) described Monunguis streblida. In Wharton (1947a), Monunguis was synonymized with Neotrombidium. Womersley (1954a) and Southcott (1954a, 1957a) also synonymized Monunguis with Neotrombidium.

Borland (1956) and Cooreman (1960) suggested that Monunguis was a genus distinct from Neotrombidium. More recently, Womersley (1963a) reviewed the taxonomic position of Monunguis streblida, considering Monunguis to represent a genus distinct from Neotrombidium. This concept appears valid. Monunguis streblida is considered to represent a genus distinct from Neotrombidium on the basis of its 7:7:7 leg segmentation and idiosomal neotrichy.

Neotrombidium gracilipes was described by Womersley (1963b) from one unique larval specimen from an Australian bat cave. Womersley was impressed by the fact that the post-larval instars of N. gracilare and the larval gracilipes were collected from similar habitats. This suggested that they might be conspecific. The lack of substantiating correlative data prompted Womersley to describe the larval gracilipes as a species distinct from gracilare. Womersley's N. gracilipes is considered to belong in a genus distinct from Neotrombidium on the basis of its idiosomal neotrichy and palp tarsal chaetotaxy. Womersley's specimen requires re-examination in order to determine its true generic affinities.

Definition of Terms and Comparative Morphology

Setal Classification

The necessity for placing heavy emphasis on chaetotaxy in attempting to evolve a working acarine classification appears obvious. What is not obvious is how to go about it.

Discussions of various attempts at evolving a workable system of setal nomenclature and the problems involved in their application have been presented by the following, non-inclusive list of authors: Southcott (1961), Crossley (1960), Newell (1957), Wharton et al (1951), Grandjean (1934, 1935, 1939, 1940, 1946, etc.). A review and discussion of all procedures and problems involved in a system of setal classification would be entirely beyond the scope of this study. Therefore, discussion of setal nomenclature will be restricted to the extent of its relevance.

During the course of this study, and throughout my experience in Acarology, I have been impressed by the degree of subjectivity indicated in the definitions of so-called setal types. A review of the papers listed above will make this point clear. An attempt at using any of these systems objectively has proven quite frustrating.

Subdividing seate on the basis of filament structure, or supposed structure, causes some confusion in definition. Presence or absence of an internal lumen

within the setal filament has been suggested and used in setal classifications. This is an impossible criterion to use. For example, the idiosomal setae of free-living laelaptids (Mesostigmata) are heavily sclerotized and either show no appreciable lumen or a very narrow one, while in the rhinonyssids (a closely related family) the homologous setae show weak sclerotization and a large lumen. In Campylothrombium (Trombidiidae) species the idiosomal setae show an enlarged lumen. These setae are assumed to be homologous to the ventral and most of the appendicular setae which either lack or have a narrow lumen.

Classifying setae on the degree of plumosity appears to be based upon subjective values. Typically "nude" setae are often found to be slightly scaled or spiculated under oil immersion preparations. Degree of plumosity has often been shown to vary between specimens and between instars of a given species.

Setae referred to as "solenidia" may or may not appear to bear "striae" (see Vercammen-Grandjean, 1965a). Presence of "striae" is therefore not an adequate criterion by which to characterize solenidia.

Many setal classifications include attempts at characterizing given setae on the basis of supposed function, even though no adequate knowledge is yet available to indicate function.

Separation of setae on the basis of presence or absence of "actinochitin" or birefringence also appears

to be an artificial and subjective criterion. This view is taken after many unsuccessful attempts at using this system to characterize given setae. Our knowledge of the molecular structure of the arthropod exoskeleton is very scant, as is our knowledge of the origin, development, and actual function of given setal types. Furthermore, the treatment of specimens for microscopical examination tends to alter the physical and chemical properties of the exoskeleton. The works of Grandjean (1935, etc.), indicating that differences in setal structure on the basis of selective staining and birefringence are demonstrable, are no doubt of value at the species level. However, when these differences (presence or absence of "actinochitin" in setae) are used as major phylogenetic criteria (see Zachvatkin, 1952, and Evans et al, 1961) then I must take exception. When Evans et al (1961) use these concepts to state that setae lacking in "actinochitin" can not be homologized with setae bearing "actinochitin", then I again take exception. It is my contention that setae on the body or appendages of a mite can, and should be, homologized with similar setae found anywhere in the phylum Arthropoda and related phyla. A definition of the term homologous refers to two or more structures of common or similar basic origin, regardless of subsequent functional modification. Presence or absence of "actinochitin", if such a substance exists, is considered to represent a functional modification, such as the

tanning of the cuticle.

In addition, excess stress has been placed on minute differences in setal structure and position without adequate regard for genetic variability within each given species. I would prefer to look for other characters by which to more clearly delineate taxa. The concepts proposed by Grandjean and elaborated upon by Newell and others, although probably being of considerable value, are unnecessarily complicated and specialized.

A setal classification for the Acarina should not be attempted without a thorough review of the works of Owen (1963), Roth and Willis (1951), Snodgrass (1935, 1956), Lees and Picken (1945), Schwartzkopff (1964), Hodgson (1964), and many others who have and are contributing to a knowledge of physiology and morphology of arthropod sensory structures.

The Acarina does not represent an isolated group of organisms, bearing structures peculiar to itself alone. The development of structures in the Acarina parallels that of other groups throughout the Arthropoda and related phyla.

Setal Types

In making descriptions, I found it possible, in nearly all cases, to separate setae into two basic categories which seem to be fundamental. The criteria employed in setting up these categories stress the relationship between the setal filament and its base.

These two major categories are illustrated in Pritchard and Baker (1955, p. 6) and are redescribed as follows:

Type I. Typically thick-walled filaments, with slightly expanded proximal ends, extending into, and articulating with, a setal base in a ball-and-socket arrangement. These are the prominent setal types found on the idiosoma and appendages, corresponding to the "tactile setae" of Pritchard and Baker, and the "scobalae" of Southcott (1961).

Evolution of this setal type appears to occur in two general directions: 1) Variations in the morphology of the filament, including smooth, plumose, branched, spine-like (=tibial claw of Trombidiformes) setae, etc. Differences in the idiosomal filament structure is employed in the generic classification of many post-larval trombidiid forms; 2) Variations in the morphology of the setal socket, into structures such as bothridia, masti-setae, pseudostigmata, etc. An increase in complexity of the setal socket is usually accompanied by a relative modification of the setal filament. In this respect, I agree with Southcott (1961, definition of Mastala, p. 604), that the appendicular bothridia are but modifications of the "typical" body and leg setae (scobalae of Southcott). Carrying this concept further, it becomes impossible to clearly distinguish between scobalae and the dorsal propodosomal sensillae of Trombidiformes. This fact is illustrated in the Pachygnathoidea, the Tydeidae, and the Ereynetidae (sensu Fain, 1957), where it is difficult to

distinguish the sensillae from other dorsal idiosomal setae in many species. Newell compounds the confusion by suggesting that setae should be identified, not on appearance, but on supposed evolution and location. Newell (1957, p. 399) stated that the anterior scutal setae in some larval forms of the genus Lassenia are indistinguishable from the lateral scutal setae, and that evolution in the anterior scutal setae has gone from sensillae to typical scutal setae. This strengthens my belief that type I setae grade indistinguishably from the "normal type" body setae to bothridiae, sensillae, etc.

Type II. Thin-walled, apically blunted filaments, immovably fused to the surface of a tympanum-like setal base. Examples of this type are usually found on the distal appendicular segments in arthropods, corresponding to the "sensory setae" of Pritchard and Baker, and "solenidia" of others. Modifications of this setal type appear to occur in two general directions: 1) Variations in the length and shape of the filaments; 2) Sinking of the setal base so that its seta arises from a "sensory pit", as in the Rhagidial Organ (Eupodiidea) and the Ereynetal Organ (Fain, 1962). Snodgrass (1956) illustrated and discussed similar "pit organs", referring to

them as Sensillae Basiconica.

My definition appears to coincide, in part at least, with that of Evans et al (1961).

Microsetae. Placement of the microsetae into either one or the other of these two setal groupings has not been feasible due to their minute size. It is therefore proposed to refer to them simply as microsetae, and to indicate their appearance and morphology in illustrations.

Conclusions. Type I setae will be referred to as scobalae (scobala, singular), taking this term from Southcott (1961), but giving it a more general meaning than that originally proposed for it by Southcott. This is done in order to avoid inventing new terms and further confusing the problem of setal terminology. The term sensilla will be retained, since its use is universally accepted, but it is defined as a modified scobala. It is regrettable that Claperede's term pseudostigmata has become synonymous with sensilla, trichobothrium, etc., when the restricted meaning of this term actually refers only to the dorsal propodosomal sensillae in the Camisiidae and Phthiracaroidea (Oribatei) (see Grandjean, 1934). The use of the terms pseudostigmata and pseudostigmatic organ should be discouraged when referring to the dorsal propodosomal sensillae in the Trombidiformes.

Type II setae will be referred to as solenidia, because of the well established meaning of this term.

Problems of clear definition arise only when attempts are made to construct a hierarchy of setal types beyond the differences outlined above. It is suggested that setae be clearly illustrated and located on the specimen, before any comparisons are made.

Idiosomal Setae

Setal length and fine structure often varies, depending on the location of each given seta on a given specimen. The more detailed a comparison is made between setae, the more important the exact location of each seta becomes. In the post-larval instars of Neotrombidium species, setal measurements and illustrations are given for setae anterior and posterior to the propodosomal sensillary region, on the posterior idiosomal margin, and immediately anterior to the genital aperture (Plate 14). Although some species of Neotrombidium may be identified by the size and structure of the post-larval idiosomal setae, these characters are difficult to measure and interpret. Other, more obvious, morphological differences must be looked for in differentiating between species.

Numbering of the larval idiosomal setal rows and designating given series as ventrals or dorsals are of

dubious value. Dorsal idiosomal setae in Neotrombidium larvae, and in many trombidioid larvae, are set in characteristically convex rows. This convex pattern is often modified as the starved larva reaches full engorgement, resulting in some confusion when comparing setal rows of starved and engorged larvae of the same species. Confusion also results when comparing setal row counts done by different authors. Southcott (1954a) described a 6:4:4:2:4 row pattern of idiosomal setae in N. barringunense, while Womersley (1954a) arrived at a pattern of 2:4:4:4:4:2 for N. tenuipes. Borland (1956) indicated a pattern of 6:4:6:2:2:2 for N. tricuspidum, while Daniel (1963) recorded N. samsinaki as having a 2:4:4:6:6 pattern. An examination of the illustrations of these specimens indicates a definite similarity of setal row pattern between N. barringunense and tenuipes, and N. tricuspidum and samsinaki, the differences being found in the interpretations of the different authors.

Slide preparations of fully engorged larval Neotrombidium species frequently produce specimens which show some of the posterior dorsal setae located on the ventral idiosomal region. Adherence to rigid dorsal and ventral counts would result in a distorted interpretation in such cases. Added to this problem is the fact that the post-anal larval setae in Neotrombidium larvae appear

identical to those characteristically found on the dorsum, while the peri-anal and sternal setae are morphologically distinct from the dorsals.

The idiosomal setal patterns are extremely variable throughout the Trombidioidea, including many instances of neotrichy. Under these circumstances, it appears dubious that a standardized system of idiosomal setal row counts, such as used in the Tetranychidae, for example, would be feasible or useful. Complete and detailed illustrations of the larval instars should accompany each new species description. In this way, the setal rows and numbers would be made more useful in species comparisons.

Audy (1954, p. 148-9) discussed what he referred to as "organizer fields" (using this term in the embryological sense), which influence the larval idiosomal setation. He suggested that several "fields" exist which are influenced, each by a different "organizer", thereby ascribing taxonomic importance to the differences between the different "fields." These "fields" include the following setal groups: median scutals (MS), anterolateral scutals (AL), posterolateral scutals (PL), dorsal hysterosomals (DS), humerals (HS), post anals (PS), and the ventrals (VS). This appears to be a valuable concept, calling attention to characters which may otherwise be overlooked in some species. In Neotrombidium, the DS

and the PS have been found to be identical morphologically. The ventrals are considered to represent the sternals and the perianals. The anal valve setae, when present, are considered to represent a different "field" from that of the ventral series, since their morphology appears distinct from that of the ventrals (Plate 1). The median coxal I and the coxal II and III setae appear to share close morphological similarities with the sternals and perianals. This is obvious in N. tenebrionyssus (Plate 1). In N. cleronyssus and tricuspidum there appears to be no appreciable difference between the median and lateral scutal setae and the other dorsal hysterosomals. In N. tenebrionyssus the median and lateral scutals show a difference in morphology, and the scutals are very distinctly different from the other dorsal setae (Plate 2).

Appendicular Setae

The presence of one or two setae on coxa I of larval trombidioids has been found to have specific value. In some species, the median coxal seta may be located in the sternal membrane, rather than on the coxal scleroma. In N. tricuspidum, this character appears to be variable. Borland's description states, "Coxa I with two setae, the inner long, whiplike, ...; this seta located on innermost coxal rim and possibly on the venter in some

specimens." Borland's illustration shows this mesal seta situated on coxa I. A re-examination of two of Borland's larval types clearly showed the mesal seta to be located on the membrane adjacent to the coxal rim (Plate 19, A). Engorged specimens may show this seta to be further from the coxal rim, than would be the case with starved specimens. In N. tenebrionyssus, barringunense, samsinaki, and tenuipes, the mesal coxal seta appears to be included in, or contiguous with, the coxal rim. Neotrombidium cleronyssus has the inner coxal seta set on the sternal membrane (Plate 15). The positioning of the inner coxal I seta, with respect to the coxal rim, must be considered with caution if it is to be used as a species character.

The presence, shape, and number of appendicular setae, especially solenidia, sensillae, and microsetae, have been used extensively in the larval trombiculid classification. Detailed illustrations and descriptions of these appendicular setae are in many cases indispensable for characterizing given species of larval trombiculids. The literature, however, does not allow for detailed comparative studies of all larval appendicular setae in Neotrombidium species. Observations are therefore limited to the material at hand, N. tricuspidum, tenebrionyssus, and cleronyssus, with additional information from the literature, where available.

Characterizing appendicular sensillae, or so-called masti-setae, is useful only when these setae are considerably modified from other adjoining setae. In Neotrombidium larvae, there appears to be a gradation between these sensillae and the adjoining scobalae. No purpose would be served, therefore, by distinguishing between these setal types, for the three species discussed. The numbers of scobalae on the appendicular tarsi and tibiae indicate specific differences as listed in the following chart:

	tricuspidum	cleronyssus	tenebrionyssus
Tarsus I	18	20	20
Tibia I	7	8	8
Tarsus II	10	9	15
Tibia II	6	6	7
Tarsus III	10	10	15
Tibia III	6	6	7

The appendicular microsetae in Neotrombidium larvae, although sometimes difficult to locate, are of taxonomic value. The microsetae are usually located dorso-distally on tarsi, tibiae, and genuae I and II. The genual microsetae are not associated with a solenidion, as they are in the tarsal and tibial segments. In N. cleronyssus the tarsal I microseta is located posterior to the dorsal solenidion, as it is also for tarsus II, (Plate 17). In N. tenebrionyssus, tricuspidum, samsinaki, and

barringunense, the tarsus I microseta is located distal to the dorsal solenidion (Plate 3). I was unable to detect a microseta on tibia II in N. cleronyssus.

Tarsal Claws

The larval appendicular tarsal segments in Neotrombidium characteristically bear one claw. This character, however, is not in itself diagnostic for the genus, since it is shared by Audyana Womersley 1954, Mackerrasiella Womersley 1954, Monunguis Wharton 1938, and others. In N. tenebrionyssus the tarsal claws are spatulate in the larva (Plate 3), simple in the other larvae studied.

The post-larval N. tenebrionyssus, and elongatum show the claws to be finely haired (Plate 11, A). In N. tricuspidum (Plate 11, B) the claws are more strongly rayed. Neotrombidium indosinensis showed smooth claws. The outer member of each pair of tarsal claws was found to be slightly larger than the inner member. Some specific differences were found when adult claw measurements were taken.

	arma-tum	tricus-pidum	elong-atum	indosi-nensis	tenebrio-nyssus
Claws I	13/17μ	27/28μ	24/26μ	10/13μ	25/27μ
Claws II		33/37μ	33/38μ	21/25μ	37/39μ
Claws III		37/39μ	33/38μ	23/28μ	38/40μ
Claws IV		39/42μ	33/38μ	25/28μ	38/40μ

Anus

Presence or absence of anus, anal valves, and anal setae appear to be valuable specific larval characters that have been given little consideration. In N. tenebrionyssus (Plate 1), barringunense, and tenuipes, anal valves and associated anal setae are present. In N. tricuspidum (Plate 19) and cleronyssus (Plate 15), the anal opening, valves, and setae are absent. Daniel's N. samsinaki is illustrated showing an anal opening but no valves or setae. Such an obvious series of characters deserves more attention.

Palps

Palpal chaetotaxy has been used extensively to characterize trombidioid species. Descriptions of several adult Neotrombidium species weigh heavily upon this one character. Specific characters presented by the post-larval palp, in Neotrombidium, have been found to include the following: 1) Accessory tibial spines (=stout spine scobalae) grading into simple scobalae (N. indosinensis and armatum), or only one accessory tibial spine distinct from the other tibial scobalae (N. elongatum, tenebrionyssus, and tricuspidum); 2) One tibial spine set at internal base of tibial claw (N. indosinensis and armatum), or absent (N. tenebrionyssus, tricuspidum, and elongatum).

An examination of a series of N. tenebrionyssus post-larvae indicated that the numbers of accessory tibial spines, smooth scobalae, as well as the numbers of femoral and genual scobalae were occasionally variable from one specimen to the next, and from nymph to adult of the same specimen. Plate 5, A, B, C and D, represents the palps of one adult female and of her nymphal exuvium. The nymphal palp tibia is abnormal, with several accessory spines and no external sensilla, while the palp of the resulting adult represents the normal condition. Cases of several accessory tibial spines grading into the simple scobalae were also found in one adult male specimen.

The palpal smooth scobalae tend to grade imperceptably into spiculated scobalae. André (1960) described the palp tibial scobalae in N. indosinensis as being smooth, while an examination of one of his types showed these setae to be slightly spiculated. The dorsal setae on the palpal, as well as the leg segments, are usually stouter and differently shaped than are the setae found ventrally on these same segments. However, these setae tend to grade into one another along the lateral margins of these segments. The strict taxonomic use of subtle variations in the setal morphology of the appendages should be attempted only when large series of specimens are available for comparison and when the differences

are clearly obvious.

Taxonomic characters found on the palps of post-larval Neotrombidium species, and probably also many other trombidioid species, must be weighed with caution, because of the variability of these structures and the subjectivity involved in their interpretation.

Larval Neotrombidium species bear palps which appear to be almost identical, with respect to the types, numbers, and placement of setae, varying only with respect to the degree of filament plumosity (Plates 4, A, B; 18, B; 19, C).

Genitalia

The paired sclerites surrounding the genital apertures of adult trombidioids have been named by Newell (1957) and Feider (1959). The inner sclerites are referred to as "genital sclerites" (Newell) or "centrovalves" (Feider), and the outer valves as "paragenital sclerites" (Newell) or "epivalves" (Feider). Moss (1962) used a combination of these two terminologies, "genital valves" for the inner sclerites, and "paragenital valves" for the outer sclerites. The terms "genital valves", or "genital sclerites", if applied loosely refer to both the inner and outer sclerites. Attempting to give these terms a restricted meaning will no doubt lead to confusion. Therefore, the terminology proposed by Feider

is considered to be the more practical of the terminologies proposed, and the term "genital valves" is applied to the total valve complex associated with the genital aperture.

In Neotrombidium, the genital aperture is flanked by centrovalves and epivalves. Two pairs of genital discs are located internal to the centrovalves in both nymphs and adults. The sexes are clearly distinguishable in the adult instars. In males, the centrovalves are characteristically shaped (Plate 8), and there is present an internal sclerotized structure (Plates 9 and 10). Females show more simplified centrovalves (Plate 7), and lack an internal sclerotized structure.

The scobalae of the adult centrovalves show sexual, as well as specific differences. In N. tricuspidum, males have from 16 to 18 spiculated scobalae on each centrovalve, set in single, double and triple rows. Females of tricuspidum have from 12 to 17 spiculated scobalae set in one row. In N. tenebrionyssus, males have from 20 to 30 spiculated scobalae on each centrovalve, set in single, double, and triple rows, while females have from seven to nine scobalae, set in one single row. In one male paratype specimen of N. indosinensis, the centrovalves were found to have only seven to eight scobalae on each valve, set in single and double rows.

Nymphs of N. tenebrionyssus show a reduction in the number of genital valve setae (Plate 6, B). This was found to be an aid in characterizing mounted specimens of nymphs from females of the same species.

Propodosomal Sensillae

The structure of the dorsal propodosomal sensillae in larval and post-larval instars has been found to show subtle specific differences. Larvae of N. tricuspidum show sensillae which are minutely scaled, while post-larvae show distally branching sensillae (setulate). Larvae and post-larvae of N. tenebrionyssus and adults of elongatum show distally setulate sensillae. Smooth sensillae are found in adults of N. indosinensis. The sensillae of N. cleronyssus are minutely scaled.

Scutum

The dorsal propodosomal scutum of trombidioids has been given considerable taxonomic and phylogenetic weight. Newell (1958) discussed the relationship of the crista metopica to the rest of the scutum, calling attention to the fact that the crista is only a strengthening part of the scutum, to which muscles insert. Newell suggested that the portions of the scutum periferal to the crista may illustrate valuable taxonomic differences. In post-larval Neotrombidium species, the crista and its associated sensillary area are not diagnostic at the

species level. However, diagnostic specific characters are available in the shape and size of the nasus and the shape of a posterior prolongation of the sensillary region. Both these structures have been overlooked in some species descriptions.

In N. tenebrionyssus, tricuspidum, and elongatum (Plate 22), the posterior scutal prolongations present clear specific differences. The nasus shape, size and morphology is a helpful species character, if used with caution, since thin preparations tend to flatten this structure. The chaetotaxy of the nasus is subject to frequent variation, from the normal two uniramous spiculated scobalae to one or three.

Diagnosis of the Genus Neotrombidium Leonardi, 1902

Trombidium (Neotrombidium) Leonardi, 1902, Zoologische Anzeiger 25:17.

Cockingsia Womersley, 1954, Studies from the Institute for Medical Research, Federated Malaya States 26:115-117.

Characters Held in Common by Post-Larval Instars

Idiosoma characteristically clothed with trifurcated setae. Two pairs of genital discs (acetabula) internal to centrovalves. Crista (scutum) narrow, extending anteriorly into a sclerotized protuberance, the nasus. Nasus projecting beyond propodosoma, bearing one pair of anteriorly-directed uniramous spiculated setae. Dorsal propodosomal sensillae attenuated, arising from

contiguous bases set near caudal extreme of crista. Idiosoma characteristically elongated, constricted at level of coxae IV, into a "figure-eight" shape (mounted preparations may obscure this constriction), due to muscle insertions into this region. Two pairs of genital sclerites present, clothed in uniramous spiculated setae, although occasional bifurcated and trifurcated setae present on epivalves. Anal valves with uniramous spiculated setae and occasional bifurcated and trifurcated setae. Ventral hypostome basally with uniramous spiculated setae, distally with four pairs of simple scobalae, the lateral-most pair corresponding to the "galeal setae". Usually one pair of eye lenses distinct, dorsal to coxae I (second pair may be distinct, reduced or absent). Spiracular and tracheal system absent. Palp tarsus with a basal-ventral solenidion. Palp tibia with an external sensilla set at base of tibial claw.

Adult Female

Centrovalves simple, with setae set medially in one row. Internal sclerotized apparatus absent.

Adult Male

Centrovalves widened caudally, tapering anteriorly, with setae set posteriorly, in more than one row. Internal sclerotized apparatus present, apparently of characteristic morphology.

Nymph

As in female, except with about half as many setae set on epivalves and anal valves. Sexes apparently indistinguishable in nymphal instar.

Larva

Leg tarsi terminating in one claw. Leg segmentation 7:6:6. Scutum with an antero-median projection extending over chelicerae, bearing two setae (corresponding to nasus of post-larval instars). Scutal sensillae thin, attenuated. Idiosomal neotrichy absent, with 16 pairs of setae, set in orderly rows (apparently only 14 pairs in N. barringunense and tenuipes). One pair of setae anteromedian to coxae III. One pair of setae associated with anal valves, or setae and valves absent. Coxa II and III with one seta. Coxa I with two setae (mesal seta may be set in integument of sternum). Basifemur I with two scobalae. Two pairs of eyes present, flanking caudal margins of scutum. Tracheal system absent. Palp tarsus with six scobalae and one basal inner solenidion. Idiosoma constricted posterior to coxae III due to muscle insertions in that region. Urstigma present, associated with coxa I. Parasitic under the elytra of Coleoptera.

Neotrombidium tenebrionyssus n.sp.

Holotype Female

Length 1620μ , width 875μ . Scutum with nasus slightly larger than sensillary area (Plate 22 , A). Crista length from anterior of sensillary region to posterior of nasus 163μ, width 22.9μ. Crista prolonged posteriorly from sensillary area by 40μ. Scutal sensillae thin, basally spiculated and distally setulate, 95μ long. Idiosomal setae characteristically trifurcated, 19 to 22μ long anterior to sensillary region, 26μ long posterior to sensillary region, 26μ long at caudal margin of idiosoma, 16μ long anterior to genital aperture (Plate 14, A). Epivalves 216μ long, each with about 50 spiculated setae (Plate 7). Centrovalves with seven to nine uniramous spiculated setae set in a single row. Anal valves 68μ long, each with about 13 spiculated setae (Plate 6, C). Tarsus I 204μ long, 64μ wide. Tibia I 136μ long, 54μ wide. One pair of eye lenses dorsal to coxae I. Tarsus I with claws about 26μ long, other tarsal claws 38 to 40μ long, faintly rayed (Plates 11, A; 12, and 13). Palp tibia with one accessory spine dorsal to tibial claw (Plate 5, A, B).

Allotype Male

Similar to holotype female, except for following: Length 1250μ, width 750μ. Crista length from sensillary region to nasus 149μ. Epivalves 143μ long, each with about 70 spiculated setae (Plate 8). Centrovalves each with about 34 spiculated setae set in single, double, and triple rows. Internal sclerotized genital apparatus present (Plates 9 and 10). Tarsus I 180μ long, 58μ wide. Tibia I 118μ long, 51μ wide.

Nymph

Similar to holotype female except for following: Length 1000μ , width 620μ. Crista length from sensillary region to nasus 95μ. Epivalves 142μ long, each with about 22 spiculated setae (Plate 6, B). Centrovalves each with from three to six spiculated setae set in single rows. Anal valves 44μ long, each with five or six spiculated setae (Plate 6, A). Tarsus I 122μ long, 49μ wide. Tibia I 74μ long, 40μ wide. Claws of tarsus I 22μ long, other tarsal claws about 34μ long.

Morphotype Larva

Unengorged length 161μ, width 149μ (Plates 1 and 2). Engorged specimens measured to 1000μ long, 625μ wide. Scutum with anterior nasus containing two unusually branched setae (Plate 4, B). Lateral scutal setae

typically trifurcated, occasionally with one antero-lateral seta branched four times. Scutum punctated and areolated as figured. Sensillae attenuated and distally setulate. Idiosomal setae set in small platelets, in distinct convex rows, dorsal hysterosomals and postanals spiculated, perianals and sternals smooth and medially dialated. Coxae I with mesal setae set on coxal scleroma, smooth, medially dialated, and longer than sternals or perianals. Antero-lateral coxa I seta elongated and spiculated. Other coxal setae similar to, but slightly longer than sternals and perianals. Anal valves present, with one pair of curved, spiculated setae. Tarsal claws dialated medially (Plate 3). Palp and chela (flattened) as figured (Plate 4). Tarsus I 72μ long, 26μ wide. Tibia I 46μ long, 23μ wide. Leg chaetotaxy as figured (Plates 1 and 3), with microsetae on tarsi, tibiae, and genuae I and II. Microseta on tarsus I placed distal to solenidion.

Type Locality and Host Data

Montgomery County State Park, seven miles south of Independence, Kansas, U.S.A. Eighteen live engorged larvae were collected from under the elytra of one live Alobates pennsylvanica (DeG.) (Coleoptera: Tenebrionidae), found under the bark of an elm log, October 14, 1961. The holotype female was reared from one of these larvae.

The holotype female produced an F_1 generation from which the morphotype larva, and a number of nymphs and adults were subsequently reared.

Remarks

The type series comprised 11 adult females, nine adult males, 18 nymphal exuvia, eight nymphs, 40 unengorged F_1 larvae, and 35 assorted field collected engorged larvae. This species is widely distributed throughout the U.S.A., apparently host specific on A. pennsylvanica (see biological accounts).

Larvae are recorded from A. pennsylvanica collected in New York, Pennsylvania, Iowa, Arkansas, and Kansas. Alobates pennsylvanica is reported from eastern Canada to Mexico, and as far west as Kansas, although one specimen at the Oregon State University Entomological Museum, Corvallis, Oregon, is recorded from Tangent, Oregon. A survey of the host beetle throughout its range (from September to January, at which time the beetles harbor the mites, and the beetles congregate under dead bark) would give an accurate index of the range of N. tenebrionyssus. Although adults of N. tricuspidum were commonly collected from under bark in the vicinity of Lawrence, Kansas, no post-larval instars of N. tenebrionyssus have been recorded in field collections.

This species is named N. tenebrionyssus because of its close relationship with a tenebrionid host.

Neotrombidium cleronyssus n.sp.

Holotype Larva

Engorged and extremely flattened (Plates 15 and 16), length 875μ, width 625μ. Scutum with lateral setae similar to dorsal hysterosomals. Scutum punctated and areolated as figured, with anteromedian area containing AM setae more heavily sclerotized than rest of shield. Sensillae attenuated, minutely scaled (Plate 18, C). Ventral idiosomal setae longer and finer than ventrocaudals and dorsals. Coxa I with mesal seta set in sternal membrane. Coxal setae similar to sternals. Anal valves and associated anal setae absent. Palp and chelae as figured (Plate 18, A, B). Tarsus I 69μ long, 27μ wide. Tibia I 46μ long, 23μ wide. Leg chaetotaxy as figured (Plates 15, 16 and 17), with microseta on tarsus I posterior to solenidion, and microseta on tibia II apparently absent.

Type Locality and Host Data

Brown's Canyon, Baboquivari Mountains, Arizona, U.S.A., July 18, 1949. Collected from Cymatodera peninsularis Schffr. (Coleoptera: Cleridae), by Werner and Nutting.

Remarks

This species is described from two larval specimens. The name N. cleronyssus is given this species in order to call attention to its relationship with a clerid host.

BIOLOGY

Introduction

Berlese (1888) described Neotrombidium ophthalmicum from one adult specimen collected in rotten leaf litter, from Paraguay. Neotrombidium tridentifer was collected from under bark in Illinois by Ewing (1909). Neotrombidium barringunense was described by Hirst (1928) from one adult specimen collected under the bark of a Eucalyptus tree in South Australia. Hirst (1929), Womersley (1936, 1945b), and Southcott (1954a, 1957a) showed that N. barringunense adults could be collected in large numbers from under the bark of "gum" and Eucalyptus trees in Australia. Wharton (1947a) called attention to a species of Neotrombidium recorded from under bark in North Carolina, U.S.A. This species was apparently later described by Borland as N. tricuspidum. Borland recorded this species as being commonly found under bark of trees in the eastern United States. Southcott (1957a) recorded N. neptunium (=tridentifer Southcott) adults from under bark and leaf litter in South Australia. André (1958) recorded two N. elongatum adults from under bark, and one adult N. armatum from forest leaf litter, in Angola. Neotrombidium indosinensis (=helladicum Cooreman) was recorded from one adult specimen collected in a briny grotto in Greece by Cooreman (1960). Womersley (1963c)

described the adult N. gracilare from ten specimens collected in bat caves of New South Wales, Australia.

The larval forms of Neotrombidium species have been recorded from the following hosts:

N. tricuspidum Borland, 1956, Monochamus carolinensis Oliv. (Coleoptera:Cerambycidae), eastern U.S.A.

N. tenuipes (Womersley, 1954), (Coleoptera:Cerambycidae), Malaya.

N. samsinaki (Daniel, 1963), Cerambyx cerdo L. (Coleoptera:Cerambycidae), Bohemia.

N. cleronyssus n.sp., Cymatodera peninsularis Schffr. (Coleoptera:Cleridae), Arizona, U.S.A.

N. tenebrionyssus n.sp., Alobates pennsylvanica (DeG.) (Coleoptera:Tenebrionidae), eastern U.S.A.

Biological studies of Neotrombidium species have been limited to the works of Southcott (1954a) and Borland (1956). Both these authors succeeded in obtaining larvae from gravid Neotrombidium females, but were unable to continue the life cycle beyond that point. The successful laboratory rearing of the full life cycle of N. tenebrionyssus n.sp. has been accomplished, and is discussed below.

Materials and Methods Employed in Biological Studies

Eighteen engorged larvae of N. tenebrionyssus were found parasitic under the elytra of a specimen of Alobates pennsylvanica, collected under the bark of an elm log in Montgomery County State Park, seven miles south of Independence, Kansas, U.S.A., October 14, 1961.

From these engorged larvae, adults and a succeeding F_1 generation of adults were reared. A second collection of six engorged larvae, from three specimens of A. pennsylvanica, Douglas County, Kansas, March 3, 1963, was reared to adults only. F_1 larval specimens were allowed to engorge on their natural host and were then reared to F_1 adults in three successive rearings, involving ten, three, and five larvae. In a fourth attempt, involving ten larvae, the beetle host died before larval engorgement could be completed, and the larvae did not develop further. Larvae were made to detach from the host by the decapitation of the host. Removal of the mites by other means usually resulted in injury to the mite. The engorged larvae did leave the host, but after a long period of attachment. Their forced removal from the host was done to speed up the study during the F_1 rearings.

Attempts were made to rear larval N. tenebrionyssus on the following Coleoptera, commonly found under bark in eastern Kansas: Penthe obliquata (Fabr.) (Melandryidae), Popilius disjunctus (Ill.) (Passalidae), Alaus oculatus (L.) (Elateridae), Megalodachne fasciata (Fabr.) (Erotylidae), Chion cinctus (Drury) (Cerambycidae), and Tenebrio molitor L. (Tenebrionidae). From four to 18 larval N. tenebrionyssus, starved for at least three days, were placed under the elytra of each beetle

specimen. The beetles were kept isolated and were checked after several days, to determine whether mite attachment had occurred.

The following live material was supplied to the nymphs of N. tenebrionyssus, in an attempt to induce feeding and development to the adult instar: Eggs and first instars of Collembola (Entomobryidae), eggs and first instar larvae of Musca domesticae, eggs of Thyridopteryx sp. (Psychidae), Brewer's yeast, pieces of fresh T. molitor larvae and adults, and eggs of T. molitor. Berlese extractions of frass from under bark yielded the following material, which was supplied to the nymphs: Eggs and larvae of species of laelaptid, acarid, and oribatid mites, ant eggs, assorted live and dead Collembola, and assorted small dipteran larvae. Lipovsky (1954) presents a list of food material used in the rearing of trombiculid mite post-larvae.

Rearing of N. tenebrionyssus was accomplished with deep cavity slides, containing a plaster-charcoal (9:1 ratio) substrate. Several deep scratches in this substrate afforded a retreat for the mites. The cavity slides were sealed with a 15 mm. square coverslip, secured with freezer tape. The cavity slides were stacked in a humidor, constructed from a five-inch-diameter finger bowl, the inside glass surface covered

with a plaster-charcoal mixture. A square of blackened plate glass was used for a lid. Water was added to the substrate as it was needed.

Beetle hosts were housed in finger bowl humidors, or plastic petri dishes, with a filter paper substrate. Attempts at rearing Alobates pennsylvanica in the laboratory were unsuccessful. Tenebrio molitor colonies were set up and maintained in gallon jars, using dry housefly larval rearing medium, or bran for food. Pieces of vegetables, apples, and Brewer's yeast cake were added from time to time as a food supplement, primarily for the adult beetles.

Moist Brewer's yeast cake was found to be an excellent food source for maintaining adults of tenebrionid and erotylid beetles. The yeast cake was stored at 40°F and fed by packing into one-dram shell vials. In this way, spoilage of the yeast from mold and desiccation was effectively eliminated by the feeding of the beetles. Generally, all the yeast was consumed as the beetles ate their way into the shell vials.

Eggs of T. molitor were obtained by placing several beetles in a cardboard cylinder (1/2-pint liquid measure), with the bottom replaced by a screen (eight meshes to the inch). Tissue paper strips were added as a substrate which the beetles could crawl under. Brewer's yeast was

added as food. The cylinder was placed screen-end down over a petri dish lid. Eggs dropped through the screen on to the petri dish, were flooded off in a drop of water, and then transferred to the mite cells. Egg breakage was a problem during handling, due to the extremely tacky and fragile nature of the chorion. Ruptured eggs were discarded, in order to discourage mold growth in the mite cells.

Mites and beetle eggs were handled with a fine, moistened brush. Observations and handling of live material were accomplished with the aid of a binocular dissecting microscope. Illustrations were made using the dissecting microscope, fitted with an ocular grid. Developmental times are given for laboratory temperatures averaging 72°F.

Laboratory Observations on the Life History of *N. tenebrionyssus* and Descriptions of Some Developmental Stages

Egg

Color carmine-orange, elyptical in shape, 245μ long, 160μ wide. Egg exterior heavily stippled, bearing minute wart-like protuberances.

After from 11 to 16 days from oviposition, the egg shell ruptured, exposing the developing deutovum (Plate 23,A). Bulges were evident at this time, corresponding

to the developing larval appendages. The crimson eyes of the larva soon became evident and the exposed portion of the deutovum changed to a yellowish-white, while the rest of the idiosoma retained an orange color.

Emergence of the larva took place from 18 to 20 days after development of the deutovum. A total of from 20 to 40 days (averaging 32 days) elapsed between oviposition and eclosion.

Larva

Larvae were active after emergence, wandering about the cell, occasionally forcing their way out from under the coverslip sealing the cell. After about three days the larvae tended to become somewhat quiescent, apparently probing the substrate with their mouthparts. They would temporarily resume active movements after being disturbed with the bristles of a brush.

Larvae were not observed to show the peculiar questing responses exhibited by some trombiculid larvae (Jones, 1950). Exposure of the larvae to their natural beetle host seemed to induce no outward change in the behavior of the larvae, possibly due in part to the unnatural conditions of the laboratory. Larvae wandered over their beetle host, occasionally returning to the substrate. Starved larvae seemed to show a greater tendency towards probing the beetle with their mouthparts

than did freshly emerged larvae. A definite preference was shown by the larvae for probing at the juncture between the abdomen and the elytra. Larvae tended to attach themselves near the anterior abdominal spiracles of the host beetle, possibly because of an attraction to the spiracles, or also possibly because of a thigmotactic response to the overlying wings.

The 18 fully engorged larvae obtained at the onset of this study, October 14, 1961, began to detach naturally from January 8 until February 26, 1962, at which time the beetle was showing signs of weakening. The beetle died on February 26th, still harboring one larva, which developed into a nymph; the other larvae had all detached. These larvae had been in association with their beetle host in excess of 117 days, having been fully engorged when the beetle host was collected.

A set of ten F_1 generation larvae detached after the death of their host, 79 days after attachment. These larvae all developed into nymphs. Two other beetles, with three and five larvae respectively, were decapitated after 16 and 25 days of larval attachment. These larvae detached and developed into nymphs. Ten F_1 larvae were allowed to engorge for nine days on one host beetle, after which time the beetle died and the larvae detached. None of these larvae had fully engorged, and none of them developed further. This would tend to

indicate that larval N. tenebrionyssus require a minimum of about 14 days of attachment to their host, A. pennsylvanica, in order for sufficient engorgement to take place to allow for further development.

Detached, engorged larvae moved about actively, becoming quiescent after entering a suitable crack or irregularity of the substrate. Touching the front legs with a brush tip resulted in avoidance reactions. Touching the scutum and sensillae induced the larvae to elevate their front legs. The distended opisthosoma was capable of elevation, depression, and lateral movements. Dorso-ventral contractions of the hysterosoma were commonly observed.

After from one to seven days, the detached larva assumed a quiescent attitude, with the legs outstretched on the substrate. The idiosomal muscles relaxed, and the body became rounded and, after about 12 hours, very turgid (Plate 23, B). Relaxation of the muscles preceded their lysis and reabsorption, while turgidity of the specimen probably resulted from water uptake. These conclusions were reached after the following observations: Several active specimens of engorged larvae were obtained from a dead, desiccated A. pennsylvanica. These larvae were of a darker red color than usual, and were considerably flattened. After one day in the high humidity environment of the rearing cells, the larval

idiosoma was found to have enlarged and the intensity of the red color was reduced. This would tend to indicate that water had been taken up, either directly from the substrate and/or by absorption from the air. Engorged specimens of N. tenebrionyssus larvae, fixed in alcohol, cleared in Nesbitt's, and mounted in a modified Hoyer's fluid, distinctly showed the presence of idiosomal muscles and their origins and insertions. Distended akinetic larvae, when treated in a like manner, showed that the idiosomal muscles were becoming lysed.

As development proceeded, the appendages became translucent white, as their tissues became lysed and re-absorbed. From three to six days after quiescence and distention, the appendages flexed and the larval exo-skeleton took on a shrivelled, rugose texture (Plate 23, C). This developmental stage is referred to as nymphochrysalis, protonymph, prepupa, pupa I, larvopupa, nymphophane, etc. The nymph emerged from eight to 14 days later, leaving behind a larval exuvium which also contained the chrysalis exuvium. A chrysalis exuvium was also detected within the duetovum, and also within the following nymphal pupal stage. Total developmental time, from larval quiescence until nymphal emergence required from 11 to 20 days, at room temperature.

Nymph

A total of 31 nymphs were reared in the laboratory. Nymphs were found to be predatory. At least one engorgement on a Tenebrio molitor egg was required for completion of development to the adult instar. Repeated engorgement occurred if additional eggs were supplied.

The observed developmental time from nymphal emergence until nymphal pupation varied from a recorded minimum of ten days to a maximum of 214 days. The protraction of developmental time was due to an extended period of starvation, during which time various food substances were tried in an attempt to induce nymphal feeding (these foods were listed in a preceding section). No morphological, behavioral, nor developmental anomolies were observed to occur due to a protraction of developmental time.

The quiescent pupal period of the nymph, known as postnymphal pupa, pupa II, preadult, tritonymph, teleiochrysalis, etc., developed in much the same way as did the preceding larval pupa. The nymph became quiescent, with appendages outstretched, muscles relaxed, and the idiosoma distended. From three to eight days later, the legs assumed a curled attitude, their contents having become lysed and reabsorbed. The pupal appendages were then clearly evident (Plate 23, D). The appendages of

the adult developed within these pupal appendages.

The adult emerged from nine to 13 days after development of the pupal appendages. Total time from quiescence until adult emergence varied from about 11 to 21 days.

Adults

Twenty-one adults, 12 females and nine males, were reared in the laboratory. The adults were found to be predaceous on T. molitor eggs. Sexing of live specimens was done according to size, since males were found to be relatively smaller than females. This sexing technique was far from infallible, especially when applied to engorged and partly engorged specimens. An attempt was made to pair off the two sexes, two or more specimens to each cell.

One pair of adults mated and the female began ovipositing. It is assumed that mating occurred through spermatophore transfer (Lipovsky et al, 1957; Moss, 1960), although this was not observed. None of the other females became gravid. It is believed that in Neotrombidium, as in other trombidioid species, virgin females do not produce eggs.

Eggs apparently developed in separate batches. The female produced one clutch of eggs after each engorgement. Oviposition would then commence until all the

eggs had been deposited. A total of five egg clutches were recorded, amounting to more than 243 eggs, for the one gravid female. All the eggs hatched into normal appearing larvae.

Eggs were deposited singly, up to a maximum of 13 eggs per day. After oviposition, each egg was rolled about on the substrate with the use of the female's palps. As the egg was rolled, it tended to collect debris which adhered to the chorion. Each egg was subsequently deposited in a crack or other irregularity of the substrate. A similar behavior was noted by Wharton (1946) for Ascoschongastia indica (Hirst).

Two adult females lived for over three years. These two specimens were starved for long periods before engorgement. The male specimen used in the one successful mating attempt died after 153 days. The female specimen which mated and produced the F_1 generations lived for 366 days after emergence from the nymphal pupa, and completed her final clutch of eggs 64 days before death. Four other adults lived for from 122 to 446 days. The other adults were killed and mounted earlier in the study.

Notes on Post-Larval Behavior

The post-larval instars were not found to exhibit aggressive behavior, in contrast to the findings of

Moss (1960) for Allothrombium lerouxi. Cannibalism was noted in only two cases, one involving two nymphs, the other involving two adults. The pierced nymph pupated and developed into a normal adult. The adult healed, showing a slight dimple at the site of puncture. In neither case was much fluid extracted from the punctured specimen.

Orientation towards T. molitor eggs appeared to be at random up to about one mm distance. At that point the post-larval instar either showed repulsion or attraction to the egg. Feeding occurred by insertion of the hypostome into the egg, penetration apparently aided by the sharp chelicerae. Engorgement was rapid, resulting in considerable idiosomal distention.

Post-larval instars were frequently observed preening themselves. Pretarsal regions of the legs were frequently cleaned by the use of the gnathal appendages. The body was curled dorsoventrally to allow the gnathal elements to clean regions of the lateral and ventral idiosoma and appendages. The dorsal and ventral idiosomal regions were rubbed against the substrate while the mites were inside the deep scratches of the substrate.

Host Specificity and Feeding

Exposure of the post-larval instars to a selection of live material (see methods and materials section)

indicated that these instars had a degree of specificity for tenebrionid eggs. Tenebrio molitor eggs supplied all the nutritional requirements necessary for completion of two generations of mites. No abnormal development was noted in any instar during laboratory rearing. It is assumed that tenebrionid, and possibly other beetle eggs, may be successfully utilized by N. tenebrionyssus post-larvae in nature.

A study was undertaken to analyze the host specificity of the starved larvae of N. tenebrionyssus. Methods employed in this phase of the study were discussed in an earlier section. No larval mites were recorded from under the elytrae of Penthe, Popilius, Alaus, Megalodachne, or Chion, two days after introduction of the mites. Penthe obliquata was found to harbor a predaceous female laelaptid mite under its elytra. The effect that this mite may have had on N. tenebrionyssus larvae was not determined.

When T. molitor was tried as a potential host, the following data were recorded: February 23, 1963, placed six mite larvae under elytra of teneral T. molitor adult (mites were starved for eight days), under conditions of low relative humidity. February 25, placed ten assorted larvae on same host. February 28, noticed five mites crawling along the beetle's venter, two mites desiccated

on substrate. Added water to substrate to elevate relative humidity. March 3, lifted beetle elytra and recorded three larvae partly engorged, attached to membrane of beetle abdomen. March 5, one partly engorged larva moving about on substrate, beetle with one unattached starved larva, one unattached partly engorged larva, and one attached partly engorged larva on abdomen under elytra. March 7, one partly engorged larva attached to axillary region of left wing, and one dead starved larva under elytra. March 11, partly engorged unattached larva on right part of abdomen, left wing showing black spot in axillary region. May 12, partly engorged larva on right portion of beetle abdomen, beetle with black melanized area at site of mite feeding, mite accidentally lost during handling of beetle. The dorsal abdominal region of the T. molitor individual used in the preceding experiment is illustrated in Plate 24. The black melanized spotting is believed to be indicative of attempts by N. tenebrionyssus larvae to feed on this host, and a reaction of T. molitor to this parasitism. Such pigmentation was not observed for any of the other experimental hosts, nor for the natural host, A. pennsylvanica.

Extensive field collections of A. pennsylvanica adults during the three-year period of 1961 - 1963, in

Douglas County, Kansas, U.S.A., indicated that parasitism by the larvae of N. tenebrionyssus occurred quite regularly throughout the host population (about one beetle in four or five). Larval mites were not recorded from other beetles. It was observed that, in Kansas, N. tenebrionyssus larvae overwinter on their host, probably detaching during warm days in the spring. August collections showed some partly engorged larvae, while the collections from September to March showed only fully engorged larvae. Alobates pennsylvanica adults were collected only infrequently from May until August, suggesting that a different habitat may be utilized by the beetles at this time. The few beetles collected from May until August were free of mites.

DISCUSSION AND CONCLUSIONS

That the trombidiods comprise a highly variable group of organisms is indicated by the problems inherent in their classification. Attempts at classifying the larval trombiculid forms illustrate and confirm the existence, and some degree, of this genetic plasticity.

The larval leg segmentation has been a subject of considerable study by trombiculid taxonomists. The division of some or all of the larval leg femora has been used as an important criterion in the subfamilial and generic divisioning of trombiculids. Audy (1954) indicated that rigid enforcement of this leg character resulted in several unnatural groupings. Audy felt that divisioning of the leg femora may have been developed independently among different groups of trombiculids, suggesting that this criterion not be used as a subfamilial character. Womersley (1954c) discussed this character of femoral divisioning, concluding that the appearance of a 7:6:6 leg segmentation in trombiculines (typically with 7:7:7 segmentation) is not of generic importance. Audy (1957) agreed with these conclusions.

The positioning of lateral scutal setae off the scutal scleroma, and the inclusion of dorsal-hysterosomal setae by an encroachment of the scutal scleroma, have been used as important criteria to delineate genera in

trombiculid larvae. Womersley (1954b) and Audy (1954, p. 149), however, found that the use of the positioning of lateral scutal setae and scutal encroachment on to the hysterosoma did not bear generic significance, and doubtfully subgeneric value.

The use of palpal claw furcation in the larval trombiculid classification was found by Womersley (1954c) to be unreliable for generic characterization. Crossley (1960), in contrast, found that this character held generic value in characterizing some trombiculid nymphs.

Emphasis has been placed on the armament of the cheliceral blade in the larval trombiculid classification. Due to the minute details involved, this has often been found to be a somewhat subjective criterion, often impossible to characterize without illustrations of exacting detail. Audy (1954) found that a stress placed upon the character of chela toothed, allowed several unrelated species to be included under the genus Schöngastia.

Some larval species of Whartonia, Odontacarus, Leeuwenhoekia, and others, are known to have spiracles and tracheae. The use of these structures in the systematization of trombiculids has been of minor consequence, since these structures appear to be recurrent. Brennan and Dalmat (1959) showed that in the genus Leeuwenhoekia,

the presence of stigma and tracheae separates the subgenus L.(Leeuwenhoekia) from L.(Comatacarus). In the larval Whartonia nudesetosa (Wharton) spiracles and tracheae are obvious, while in W. womersleyi Brennan and Dalmat, these structures are not present.

Adults of several trombidioid genera have spiracles and tracheae associated with the chelicerae. As with the larval classification, presence or absence of these structures has not been given much taxonomic weight (except for Feider, 1955). The presence of taenidiae in the salivary ducts of trombidioid post-larvae has caused some confusion by their resemblance to tracheal structures. Mitchell (1962a), in his study of the musculature of Blankaartia ascoscutellaris (Walch), referred to these salivary ducts as tracheae. This oversight was corrected in Mitchell (1962b). A review of the salivary structures in Allothrombium is found in Moss (1962).

A system of biometrical measurements, utilizing direct measurements and length/width ratios of tarsus I, or other leg segments, in relation to measurements or ratios of other structures, has been attempted in the trombiculid classification. The value of these measurements have been questioned by Crossley (1960) and others, who maintain that the flattening of structures through mounting procedures gave rise to exaggerated readings.

Variation in tarsal lengths and widths have been poorly analyzed for given species. Where these studies have been attempted, the variations have been found to be excessive for species characterization (see Michener, 1946). No comprehensive study has yet been attempted to show that these biometrical comparisons are as infallible as taxonomic tools, as they are tedious. Audy (1954) called attention to the fact that the stress placed upon the "standard measurements", "has produced workers which both encourage superfluous measurements or unfortunate omissions." A stress on the "standard measure", at the expense of detailed, complete illustrations and descriptions, should be discouraged.

Supposed host specificity has been used in the trombiculid larval classification as a generic criterion. The fact that a new species is recorded from a new and unusual host, or from a new host site, seems to encourage taxonomists to erect new supra-specific taxa.

The modifications in tarsal claws of larval trombidioids suggest considerable genetic plasticity throughout the group. In Neotrombidium larvae the tarsal claws are single, as they are in some unrelated trombelline species, while apparently closely related forms of these two groups have two or three claws. The use of these characters has been fairly limited to the generic and specific level.

A few variations in the life histories of trombidioids appear noteworthy. Eutrombicula (=Vatacarus) ipoides (Southcott) was found to lack the nymphal instar. The larvae are nasal parasites in certain sea snakes (see Vercammen-Grandjean, 1960a). Species of Microtrombidium were found to have several post-larval molts (Michener, 1946a). Southcott (1945) found that in Microtrombidium hirsutum eggs hatched directly into nymphs. Knowledge of life history data may be found useful in arriving at more natural species groupings.

Perplexing variability between larval and adult morphologies have been discussed by Michener (1946b), Audy (1954), Newell (1957), and others. Michener found clear morphological differences between the nymphs of Trombicula attenuata, alleei, and velascoi; however, he could not always distinguish between these species on larval characters. Audy found that the larvae of Heaslipia gateri, Trombicula hastata, and T. consueta were distinct, while the nymphs were difficult to separate. Newell found that one major generic and subfamilial character separating johnstonianids from other trombidioids, the presence of two propodosomal sensillae, was variable between the larvae and adults of Lassenia and Diplothrombium species. In larvae of Lassenia, Newell claimed to recognize an anterior pair of sensillae, which are absent in the adult. In Diplothrombium

monoense, the adults bear two pairs of sensillae, while the larvae apparently only show one pair.

The structures considered to have the greatest taxonomic value in the post-larval trombidioid instars were first discussed by Berlese (1912). With the exception of our present larval classification, the methods set forth by Berlese are still very strongly adhered to today. The palpal armature has been given strong consideration in characterizing taxa on the generic and specific levels. However, it is becoming increasingly apparent that, in several groups of trombidioids, the palpal chaetotaxy is of little value by itself at the species level, due to specific variability, similarities between different species, and subjectivity in the interpretation of characters. This is regrettable, since so many species descriptions of post-larval trombidioids rely heavily upon this one character. Crossley (1960) presents a review of this subject, as it relates to some trombiculid nymphs.

The presence, number, or absence of eyes has been suggested to be of supra-specific value within the trombidioids. Subsequent material has shown that these characters are, in themselves alone, not of supra-specific value. Closely related species may show two, one, or no eye lenses in the post-larval instars. Audy (1954) indicated that in Euschongastia lacunosa, nymphs

were sometimes found with conspicuous eye spots. These same specimens, when mounted, did not have eye lenses.

The spacial relationship between the larval coxa I and coxa II has caused some confusion within the Trombidioidea. Southcott (1954b) erected the genus Vatacarus for a species of trombiculid which showed coxa I to be separated from coxa II. In Southcott (1957b) the family Vatacaridae was proposed for this monotypic genus. Vercammen-Grandjean (1960a) found that the coxal separation in the larval Vatacarus was a result of distention during engorgement, since unengorged specimens were found to have coxae I and II contiguous. On the basis of other characters, the genus Vatacarus was shown to be a synonym of Eutrombicula. Womersley (1963a) discussed this character of coxal separation with reference to Monunguis streblida, again in (1963b), for his N. gracilipes, concluding, in 1963b, that the character of coxal separation is limited to the specific level. The above review, together with a study of starved and engorged specimens of N. tenebrionyssus, indicates that the character of coxal separation is the natural consequence of engorgement and flattening of the specimen during mounting, therefore bearing no taxonomic significance whatever.

From these and other observations, it seems evident

that the trombidioids represent a highly variable group of organisms, with considerable gene-pool plasticity. This results in recurrence of similar characters in apparently unrelated groups, parallelism, divergence of characters from related groups, and convergence of characters from distantly related groups. Mention of the Hydrachnellae may be pertinent. Here is an example of how terrestrial trombidioids successfully invaded the fresh water habitat, and from which the gene flow between terrestrial forms and aquatic forms has apparently been severed for some time. Availability, and subsequent exploitation of new niches, by a highly plastic and successful group of organisms, has produced as diverse a fauna as the terrestrial trombidioids and the aquatic Hydrachnellae.

These findings suggest that a more conservative approach be taken in the systematics of the Trombidioidea, with emphasis on more biological work, greater emphasis on studying morphological variations within the group, and more detailed descriptive work. The Trombidioidea apparently comprise a rather close-knit assemblage of species, with similarities in genetic make-up. Excessive concern with separating species and supraspecific categories on minor differences and variations has resulted in a complex of excessively subdivided

artificial groupings, which are then difficult to set into a meaningful hierarchy of taxa. The result is a proliferation of monotypic taxonomic units, and supra-generic categories which can not be clearly characterized. Dividing this large group of species into poorly definable family categories results in the fragmentation of knowledge, the proliferation of confusing terminologies, and a clouding of the natural relationships between the different species groupings.

The problems involved with having two classifications evolving simultaneously, that of the post-larval instars on the one hand, and the larval instars on the other, has caused considerable concern and discussion by Crossley (1960), Audy (1954), Vercammen-Grandjean (1960b), and others. Neither one nor the other approach should be stressed at the expense of the other. Trombidioid larvae have tended to evolve in different directions from that of the post-larvae. Such a phenomenon would tend to reduce competition between the immature stages and adults of a given species or group. There may also be a tendency towards a reduction in mortality from the selective pressures of predation, unfavorable physical environmental conditions, temporary unavailability of food, etc. Apparent independent evolution of the larvae and adults of a given group of organisms tends to

increase the adjustability of the group as a whole, and may give the group an added advantage in survival. Disadvantages of this type of evolution obviously also occur, for with over-specialization there is the ever present danger of extinction.

The gene-pool of a given species, or group, must have a different composition from one group to the other, otherwise the respective groups could not merit separation. The expression of characters of a given group of organisms is governed by its gene-pool make-up. This would result in the fact that the larvae and post-larvae of a given group of trombidioids should have characters in common within the respective group, as opposed to other groups. In other words, larval characters should delineate related groups of individual specimens or species, corresponding to similar limits set up for the post-larval instars. Once both larval and adult characters are known, then it makes no difference whether larval or adult characters are stressed. Adult and larval characters share equal importance, since they both, together or independently, illustrate the gene-pool composition.

The family Trombiculidae was proposed by Ewing (1944a) for a group of trombidioids whose larvae are parasitic on vertebrates. The fact that the erection of this family was based upon weak grounds is shown by

Womersley's attempts at justifying its retention by erecting the Leeuwenhoekiidae, as a catch-all for those species which overlapped between the Trombidiidae and the Trombiculidae. Womersley had considerable experience with the taxonomy of both the larval trombiculids and adult trombidiids, a fact which has been overlooked by some taxonomists who specialize on larval trombiculids. By erecting the Leeuwenhoekiidae, Womersley apparently attempted to maintain Ewing's family concept. Womersley's Leeuwenhoekiidae has met with mixed response, rejection on the one hand by many trombiculid taxonomists, but acceptance on the other hand by trombidiid taxonomists.

Wharton (1947b) and Baker and Wharton (1952) suggested that trombiculid larvae may be characterized by the fact that the ventral hypostomal setae (palp-coxal setae) originate posterior to the palp trochanterofemoral segment. This single morphological character has subsequently been found to be non-diagnostic, being also found in some trombellinae species, Vercammen-Grandjean (1955). Crossley (1960), and others, have stated that the only working separation between the Trombiculidae and the Trombidiidae is based upon host data. Trombiculid larvae are parasitic on vertebrates, while trombidiid larvae are parasitic on invertebrates. This appears to be a poor criterion for separating organisms

into two different families, especially when larvae are collected free in nature. The criterion for distinguishing between these two families presents an insurmountable barrier to the study of post-larval trombidioids. The separating of morphologically indistinguishable groups on the basis of host date, a character which was shown by Audy (1950, 1956) to be non-diagnostic for several trombiculid species, is a procedure which has not been followed by workers in other trombidiform groups. The Ereynetidae (sensu Fain, 1957) includes a large assemblage of mites which are obligate parasites in the nasal passages of vertebrates (Speleognathinae and Lawrencarinae), and an assemblage of free-living, and insect and mollusc associated species (Ereynetinae). The family Eupodidae includes the genus Benoinyssus Fain,1958, which was found parasitic in the nasal passages of a snake. Other described representatives of this family are predaceous. The family Pterygosomidae includes several genera of obligate lizard parasites, and other genera of species parasitic on insects. It is suspected that the elevation and retention of the family Trombiculidae is strongly based upon the fact that many trombiculid larvae are of medical importance to man and to domestic animals,(Ewing, 1944b). Still, this is not enough of a criterion for justifying the retention of this family.

It is therefore proposed that the families Trombiculidae Ewing, 1944 and Leeuwenhoekiidae Womersley, 1945 not be considered as valid taxonomic entities.

Newell (1957) erected the family Johnstonianidae on the basis of the fact that he considered the group to be a closely related assemblage of "primitive" species. His arguments that the genera included in his Johnstonianidae merit familial rank are not justified. Newell's speculation on the primitiveness of johnstonianids is interesting, but not verifiable. Evolution may, and frequently does, go in several directions, with advanced trombidioids parasitizing so-called primitive hosts such as insects or amphibians, and so-called primitive trombidioids parasitizing mammals. The geological table tells us nothing about the evolution of trombidioids. Again, the relationship of larva to host may evolve in any direction. Ascribing "primitiveness" to one type of larval behavior, or habitat preference of the postlarvae is of little value. With the degree of variability noted throughout the Trombidioidea, it appears that the morphology of the johnstonianids does not differ that markedly from other trombidioids to warrant familial status. Finally, Newell's characterization of the family Johnstonianidae is not adequately diagnostic for separating it from other related trombidioids. The

morphological data at Newell's disposal would seem to make the earlier subfamilial concepts of Thor's Johnstoniinae inconclusive and in need of re-evaluation, rather than suggesting the elevation of a new family category on these same discrepancies.

Feider (1955) is an extensive study of the Trombidioidea in which he erected three new families, several new subfamilies, one genus, and several new species. Feider elevated the family Trombidiidae (sensu Thor and Willmann, 1947) to the rank of superfamily, something which was done much earlier. Having erected his new superfamily "Trombidoidea", Feider then proposed the families Trombellidae, Peritremotrombidiidae, and Stigmotrombidiidae. The family category Trombidiidae was dropped without explanation, and the families Trombiculidae and Leeuwenhoekiidae were apparently not known to Feider.

Feider's familial concepts are unique in that they weigh heavily on the presence, absence, and shape of the stigmatal and tracheal system in trombidioid adults. Other workers have given the tracheal system of trombidioids little taxonomic significance, since these morphological structures are believed to be recurrent throughout the group. Feider's work is unique also, for it illustrates an original classification scheme,

evolved without consideration of current work in the group, in which the genera of the Trombiculidae, Leeuwenhoekiidae, and Johnstonianidae are not recognized as deserving familial rank on strictly morphological considerations.

Finally, the question of the aims and methods of classification, both generally and specifically, as regards the Trombidioidea should be considered. The ascribing and cataloging of taxonomic entities is in many ways similar to the cataloging of books in a library. It is a method by which organisms may be correctly identified, so that all known information pertinent to their taxonomy, biology, etc. may be found. An attempt must be made to utilize indices which will give the easiest and clearest means for characterizing a given taxonomic entity, and distinguishing it from all others. Often this must be done at the expense of evolutionary relationships, resulting in a classification which is referred to as "artificial". Classifications which attempt to correlate taxa on the basis of evolutionary relationships are referred to as "natural". Clearly, a system of classification for any given group of organisms should distinguish the various taxonomic

levels in a clear, objective manner and also indicate the phylogenetic relationships of the organisms within each taxon to each other and to related taxa. The objectives of systematics are therefore two-fold, to classify and to indicate evolutionary trends or relationships.

It is generally accepted that taxonomists classify organisms, in part at least, through inductive and intuitive reasoning. When working with a group of organisms which, at least to some degree, share the same sensory acuteness and macroenvironment with the taxonomist, then the experience and judgment of the taxonomist is of considerable value at arriving at a system of classification for these organisms. However, when the taxonomist deals with organisms such as the acarines, which must adapt to highly restrictive microhabitats, habitats to which human senses are not attuned, then considerable supplemental knowledge is required to reach sound taxonomic conclusions. It generally is accepted that little knowledge is yet available of the sensory

physiology, behavioral ecology, or life history of most acarine species. Little is known about the composition and succession of the innumerable microhabitats in which mites occur. Scant knowledge exists of the degree of morphological and physiological variability inherent in any acarine species. Less is understood of the means by which this variability serves a given species population in allowing it to subsist and/or reproduce in various changing microhabitats. The meager fossil record has divulged no new information by which evolutionary trends in the Acarina may be assessed.

Without this type of knowledge, the acarologist is left with only subjective induction and intuition, by which to set limits for the various taxonomic levels in the Acarina. Human subjectivity also influences the means by which structures or groups of acarines are considered "primitive" or "advanced". Until such time that physiological, ecological, morphological, and paleontological information indicate evolutionary trends, the acarologist must attempt to make order out of the many varieties and variations of mites through, what seem to be, arbitrary means. If arbitrary indices are to be set up, then they should be set up by clear and objective standards. Since acarine taxonomy is based upon cleared specimens on slides, then criteria utilized for their

classification should be based upon morphological differences and similarities which are clearly evident under microscopical preparations, not supposed evolutionary relationships. It appears questionable whether evolutionary and phylogenetic speculation should be allowed to disrupt systematic order. A workable artificial classification is considered to be far superior to a non-workable natural classification.

When two or more classifications evolve simultaneously for the same group of organisms, and when both these classifications evolve from different and non-substantiated premises, the result is bound to lead to confusion. The classification of the Trombidioidea is based excessively upon premises and assumptions which have not been substantiated. If trombidioid taxonomy is to be considered a science, then a scientific approach is required. Until such time no advantage can be gained by fragmenting obviously related and overlapping groups of organisms into family units, until the relationships between the species and genera are more clearly understood and defined. This would require more detailed and inclusive studies of the life histories and morphologies of the included species.

In conclusion, it is proposed that the families Trombiculidae Ewing , 1944 , Leeuwenhoekiidae Womersley

1945, Trombellidae Feider, 1955, Stigmotrombidiidae Feider, 1955, Peritremotrombidiidae Feider, 1955, and Johnstonianidae Newell, 1957, be given no more than subfamilial rank in the family Trombidiidae Leach, 1814, and that the many trombidiid genera be carefully re-evaluated and critically redefined so that generic relationships may be more clearly understood throughout the group. Furthermore, it appears universally accepted by acarologists that the Hydrachnellae Latreille, 1802 (an artificial ecological grouping) represent an offshoot from ancestors of the family Trombidiidae (see Southcott, 1961, p. 406-407). Morphological similarities between these two groups are obvious. It is believed that the systematics of both these two related groups may be more clearly understood if they are brought together under a common taxonomic category. It is proposed, therefore, that the superfamily Trombidioidea be applied to include the one family Trombidiidae and the ecological unit referred to as the Hydrachnellae.

SUMMARY

1. A literature review and morphology study show that the genus Neotrombidium may be included in either of three trombidioid families -- Trombidiidae Leach, Trombiculidae Ewing, or Leeuwenhoekiidae Womersley. This fact, together with a knowledge that the family categories proposed within the Trombidioidea are based upon unverified premises, suggested the need for a re-evaluation and reinterpretation of these family categories. The Leeuwenhoekiidae Womersley, Johnstonianidae Newell, Trombiculidae Ewing, Trombellidae Feider, Stigmotrombidiidae Feider, and Peritremotrombidiidae Feider are considered to be invalid as family categories. Elevation of these taxa to family levels has resulted in an evolution of conflicting terminologies and classification schemes for obviously related and morphologically overlapping species and supraspecific groups. The family Trombidiidae Leach is redefined to include all the recorded terrestrial trombidioid species, following Berlese (1912) and Thor and Willmann (1947). The ecological grouping, Hydrachnellae, which has been shown to bear a close phylogenetic relationship with the terrestrial trombidioids, is included along with the family Trombidiidae, to comprise the superfamily

Trombidioidea. It is believed that this new concept of the Trombidioidea will bring this large, ill-defined, assemblage of species groups into a clearer perspective.

2. The genus Neotrombidium is reviewed and redefined through a re-examination of the types of N. armatum André, N. elongatum André, N. indosinensis André, N. tricuspidum Borland, Monunguis streblida Wharton, and description of two new species, N. tenebrionyssus and N. cleronyssus. A generic diagnosis is presented which supplements previous knowledge, by defining the genus on the basis of the larval, nymphal, adult male, and adult female instars. The species examined exhibited several new morphological features by which they may be more easily distinguished.

The genus Neotrombidium includes the following species: ophthalmicum Berlese, furcigerum Leonardi, tridentifer Ewing, barringunensis Hirst, tenuipes (=Cockingsia tenuipes Womersley), tricuspidum Borland, elongatum André, armatum André, indosinensis André (=N. helladicum Cooreman), neptunium Southcott (=tridentifer Southcott), gracilare Womersley, samsinaki (=Cockingsia samsinaki Daniel), tenebrionyssus n.sp., cleronyssus n.sp.

Species incorrectly assigned to Neotrombidium include N. vietsi Oudemans (=Valgothrombium valgum (George)), N. streblida (=Monunguis streblida Wharton) and

N. gracilipes Womersley (not a Neotrombidium species).

3. The setal nomenclature, as it applies to the Acarina in general, and the terrestrial trombidioids in particular, is discussed and re-evaluated. Setal types are subdivided into two basic groupings, on the relationship between the setal filament and the setal socket. Filaments extending into, and articulating with the setal base, in a ball-and-socket arrangement are referred to as "scobalae" (after Southcott, 1961). Filaments arising from the surface of a tympanum-like base are referred to as "solenidia".

4. The life history of Neotrombidium species is reviewed, together with a detailed study of the bionomics of N. tenebrionyssus n.sp. A technique was developed for rearing N. tenebrionyssus in the laboratory. The larvae were allowed to engorge on their natural host, Alobates pennsylvanica (DeG.) (Coleoptera:Tenebrionidae). Nymphs and adults fed upon the eggs of Tenebrio molitor Lin. (Tenebrionidae).

Neotrombidium tenebrionyssus is dioecious, with fertilized (probably through spermataphore transfer) females ovipositing after each engorgement. Two hundred and forty-three eggs required an average of 32 days for larval emergence, at laboratory temperatures. A deutoval stage preceded the larva. A minimum of

about 14 days of feeding on A. pennsylvanica was required before the larvae could continue development to the nymph. Thirty-one nymphs emerged from larvo-pupae after from 11 to 20 days. Nymphs entered pupation after at least one engorgement on a T. molitor egg, from ten to 214 days after emergence from the larvo-pupa. The nympho-pupa required from 11 to 21 days before adult emergence. Twenty-one adults, 12 females and nine males, were obtained. One of these laboratory-reared females supplied 243 eggs, from which an F_1 generation of adults was reared.

5. Neotrombidium tenebrionyssus n.sp. shows a degree of host specificity towards tenebrionid beetles. Larval mites were commonly collected from under the elytra of Alobates pennsylvanica, and laboratory-reared larvae placed upon this host readily engorged and completed development. The larvae were placed upon several other potential beetle-host species. Unsuccessful attempts at feeding on T. molitor were observed. No indication of feeding was noted on the other beetle species. The post-larval instars refused a large assortment of nutrient material, but readily accepted T. molitor eggs.

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APPENDIX

PLATES

Plate

1. N. tenebrionyssus larva, ventral aspect.
2. N. tenebrionyssus larva, dorsal aspect.
3. N. tenebrionyssus larva. A, tarsus and tibia I. B, tarsus and tibia II. C, tarsus and tibia III.
4. N. tenebrionyssus larva. A, external aspect of palp. B, dorsal aspect of palp. C, chela. D, scutum.
5. N. tenebrionyssus. A, internal aspect of adult female palp. B, ventral hypostome and external aspect of adult female palp. C, internal aspect of nymphal palp. D, external aspect of nymphal palp.
6. N. tenebrionyssus. A, anus of nymph. B, genital aperture of nymph. C, anus of adult female.
7. N. tenebrionyssus adult female, genital aperture.
8. N. tenebrionyssus adult male, external aspect of genital aperture.
9. N. tenebrionyssus adult male, internal aspect of genital aperture.
10. N. tenebrionyssus adult male. A, posterior aspect of male organ. B, lateral aspect of male organ. Not to scale.
11. A, claws on tarsus IV of adult female N. tenebrionyssus. B, claws on tarsus IV of adult female N. tricuspidum. C, chela of adult N. tenebrionyssus. D, chela of nymphal N. tenebrionyssus.

12. N. tenebrionyssus adult male, legs I and II.

13. N. tenebrionyssus adult male, legs III and IV.

14. N. tenebrionyssus idiosoma of adult female. A, idiosomal setae of N. tenebrionyssus. B, N. indosinensis. C, N. elongatum. D, N. tricuspidum.

15. N. cleronyssus larva, ventral aspect.

16. N. cleronyssus larva, dorsal aspect.

17. N. cleronyssus larva. A, tarsus and tibia I. B, tarsus and tibia II. C, tarsus and tibia III.

18. N. cleronyssus larva. A, chela. B, palp. C, scutum.

19. N. tricuspidum larva, ventral aspect.

20. N. tricuspidum larva. A, dorsal aspect. B, chela. C, palp.

21. N. tricuspidum larva. A, tarsus, tibia and genu I. B, tarsus and tibia II. C, tarsus and tibia III.

22. Scuta. A, N. tenebrionyssus adult female holotype. B, N. tricuspidum adult female. C, N. elongatum adult female.

23. N. tenebrionyssus. A, dorsal and lateral aspects of deutovum. B, dorsal aspect of distended akinetic larva. C, ventral aspect of larvo-pupa. D, ventral aspect of nympho-pupa.

24. Dorsal aspect of abdomen of Tenebrio molitor specimen used in host specificity studies, indicating feeding sites of N. tenebrionyssus larvae.

Plate 1.

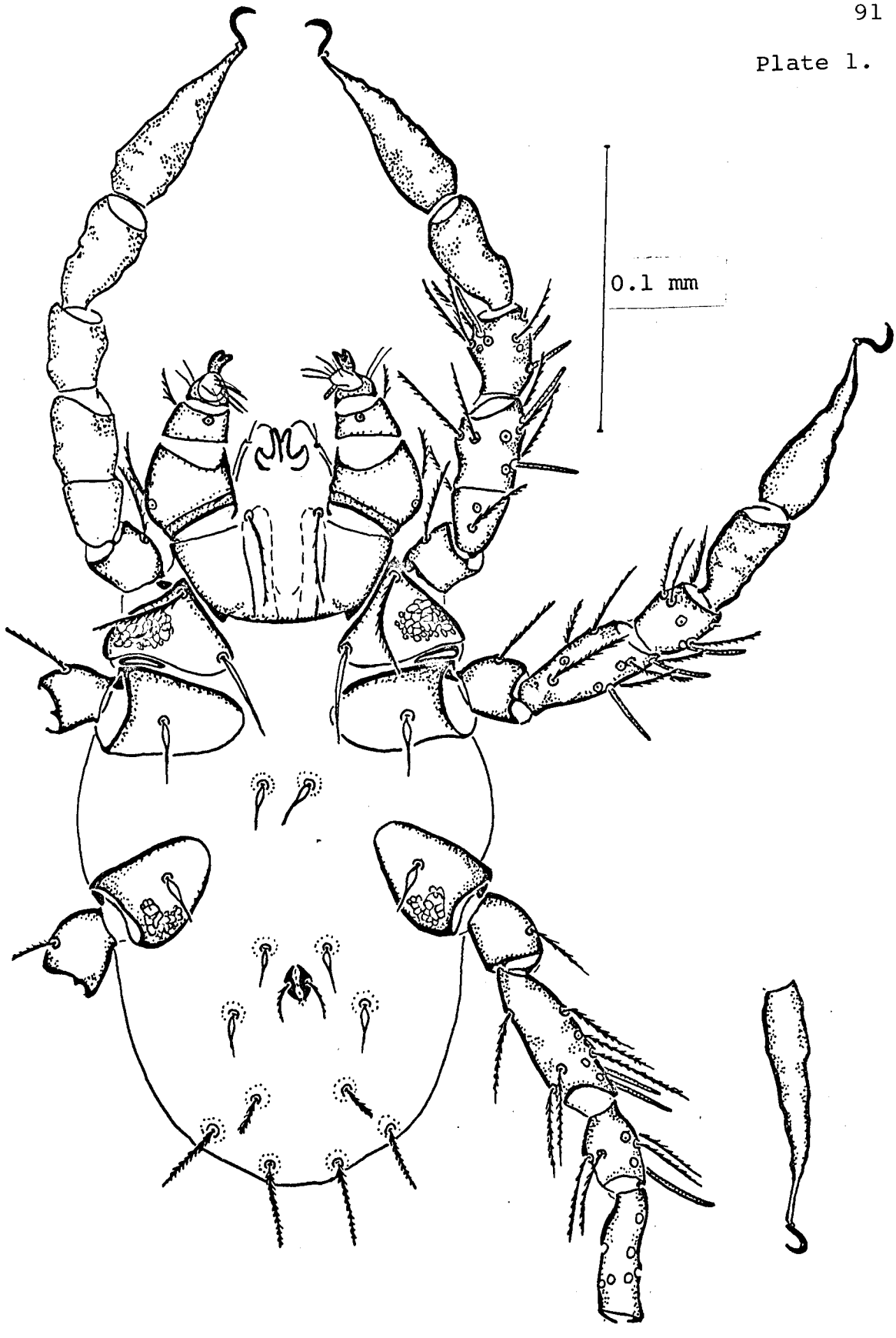


Plate 2.

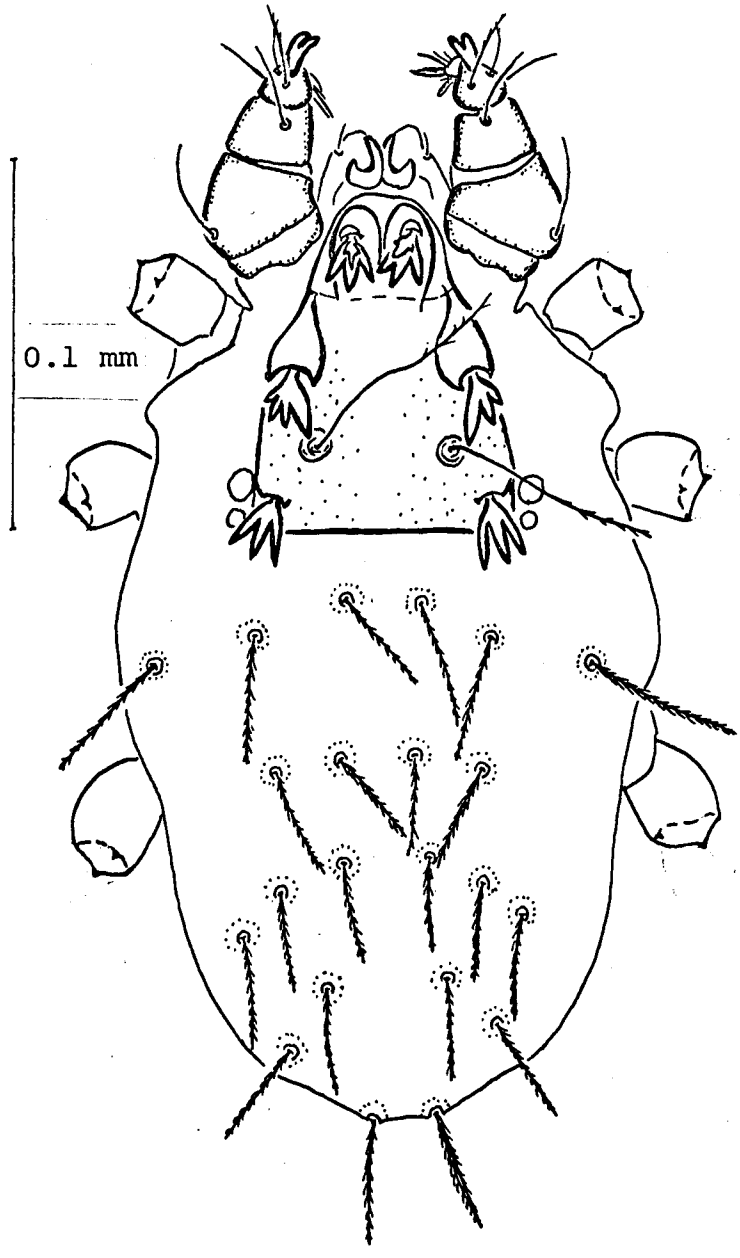
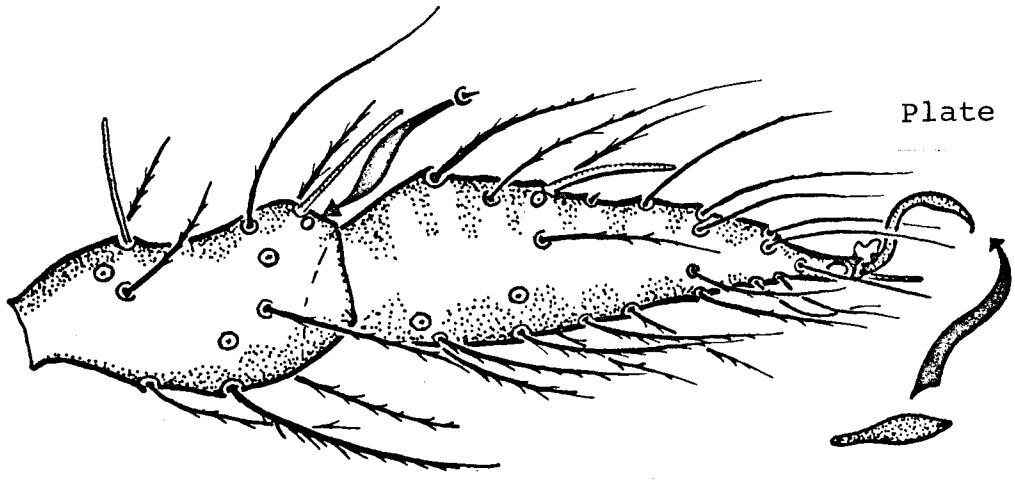
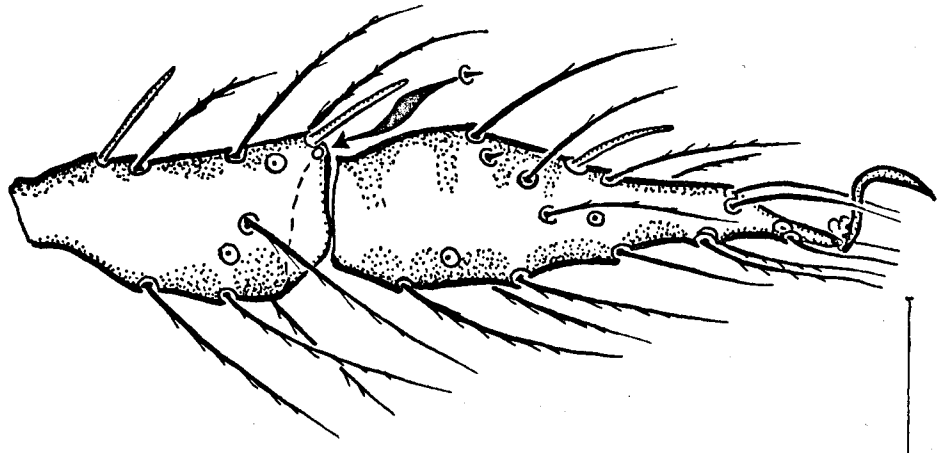


Plate 3.

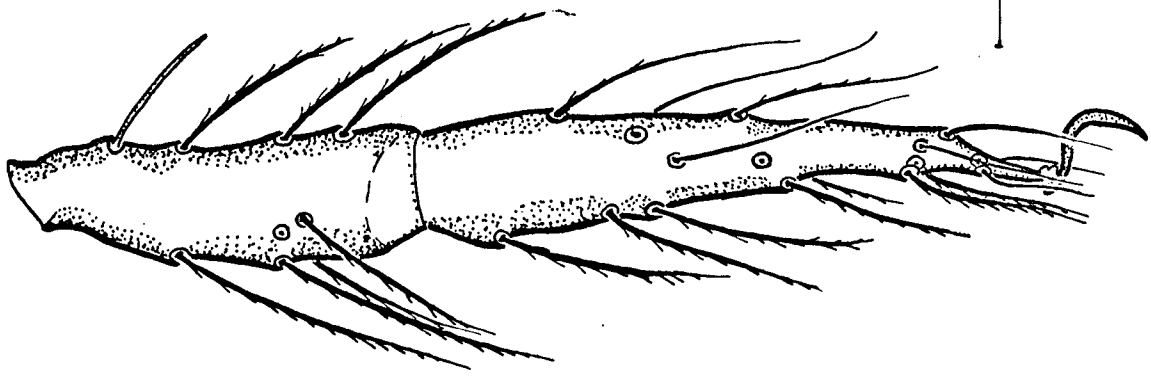


A. tarsus and tibia I.



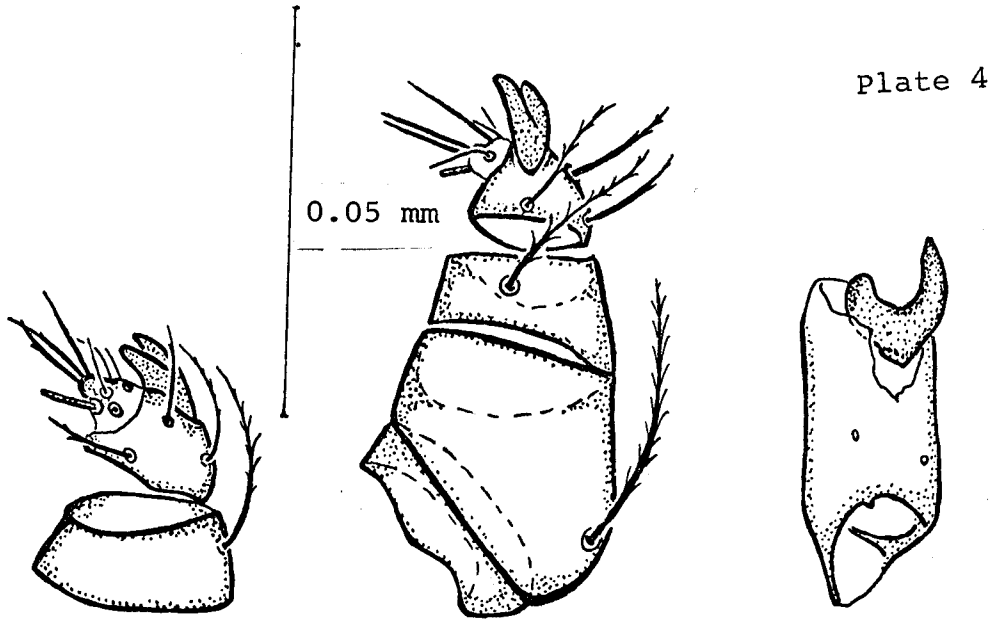
B. tarsus and tibia II.

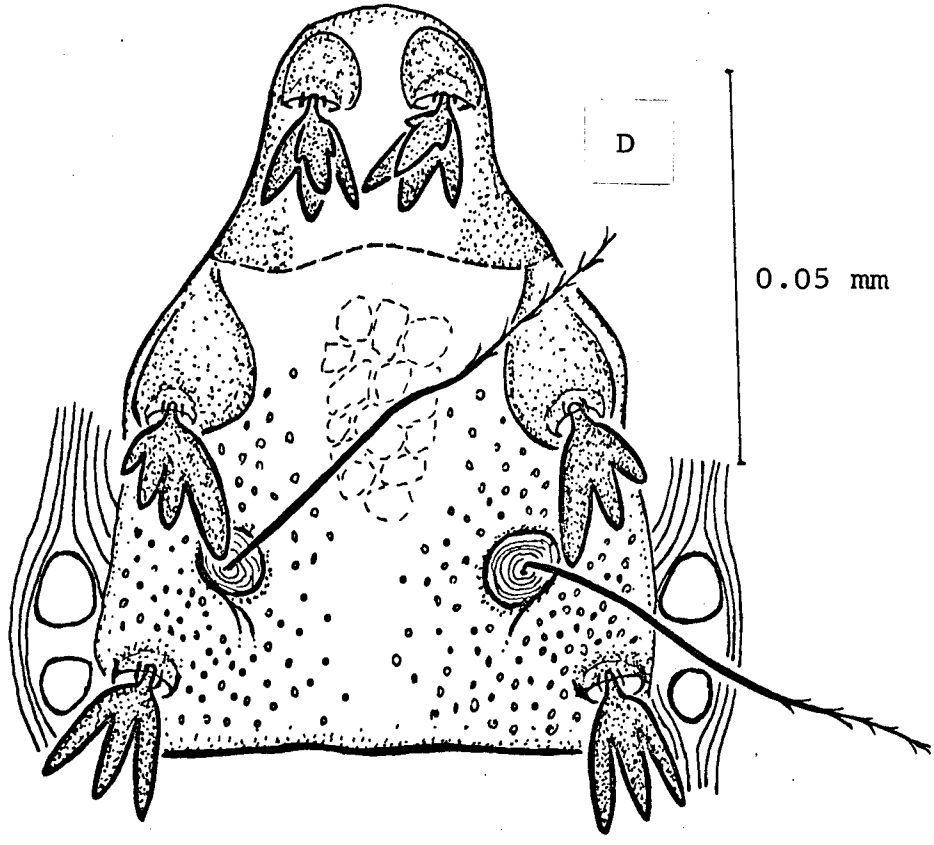
0.05 mm



C. tarsus and tibia III.

Plate 4.





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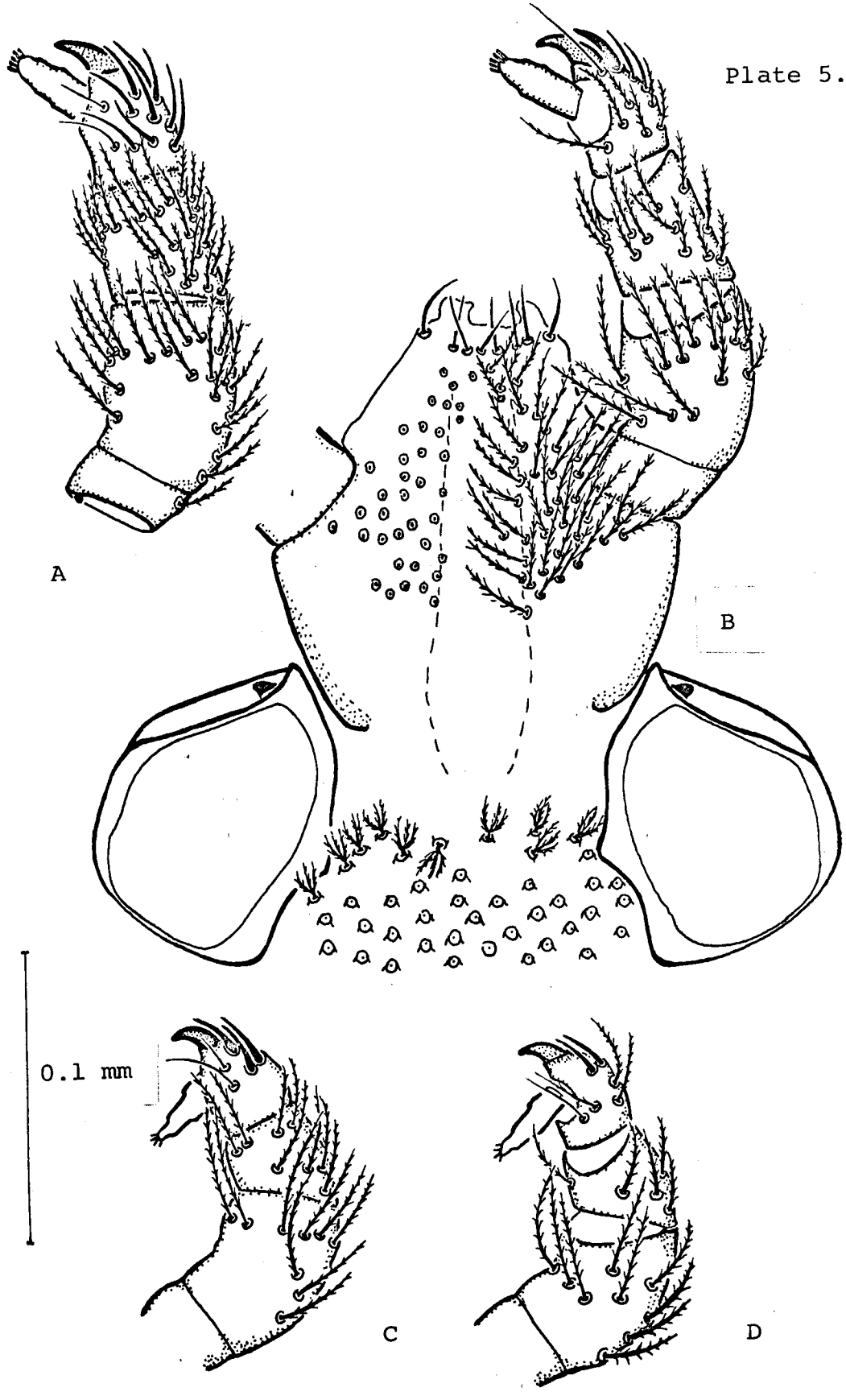

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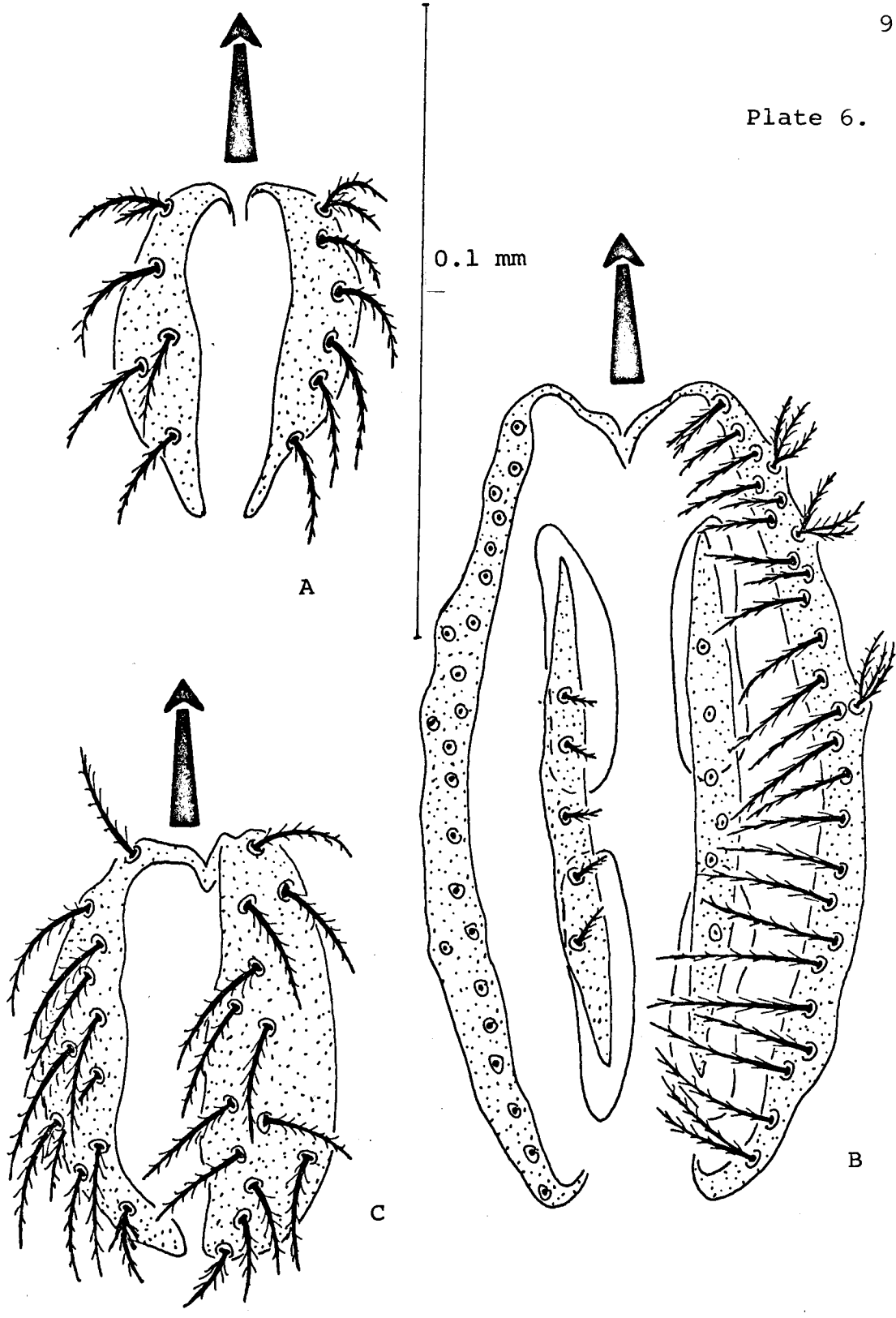
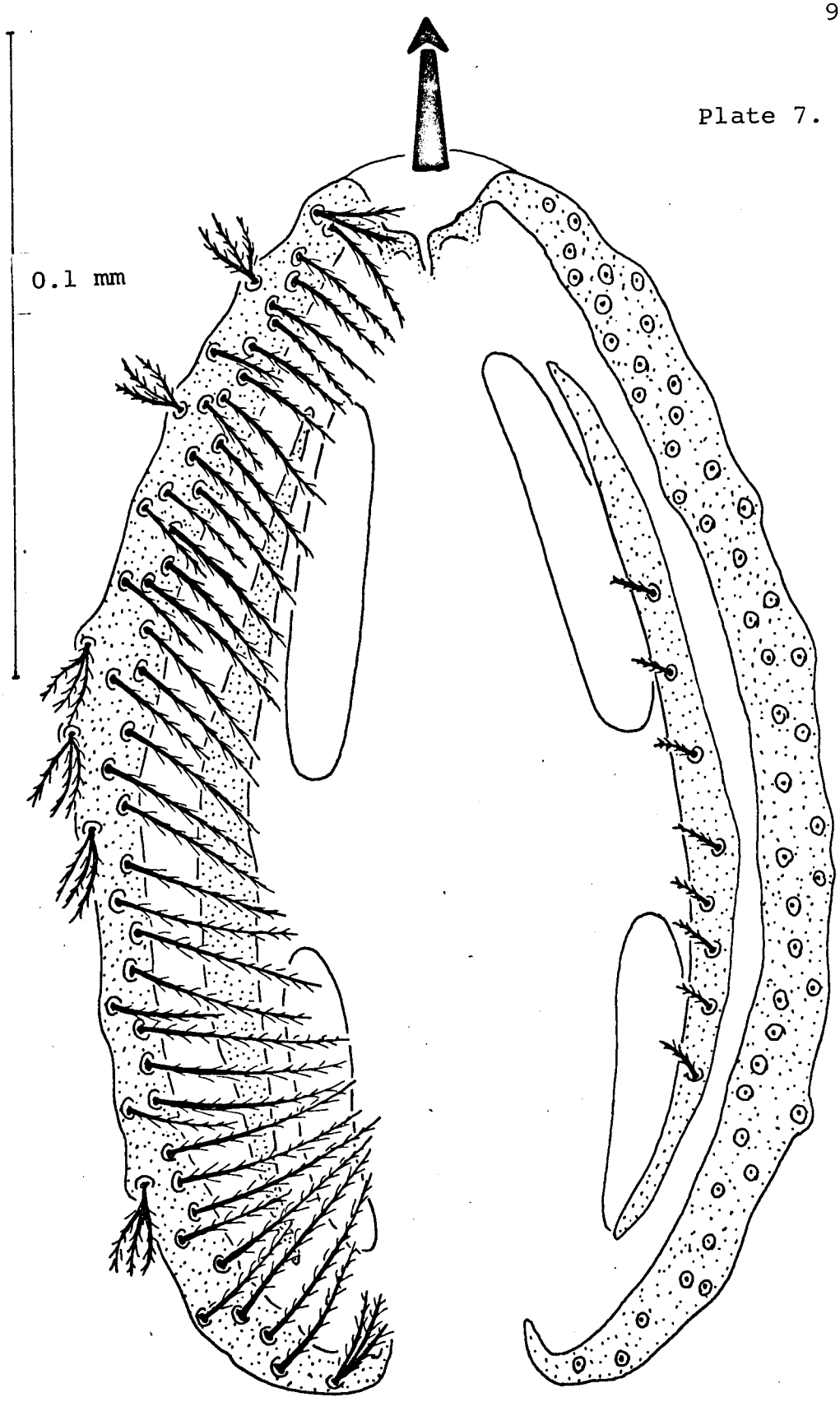


Plate 7.



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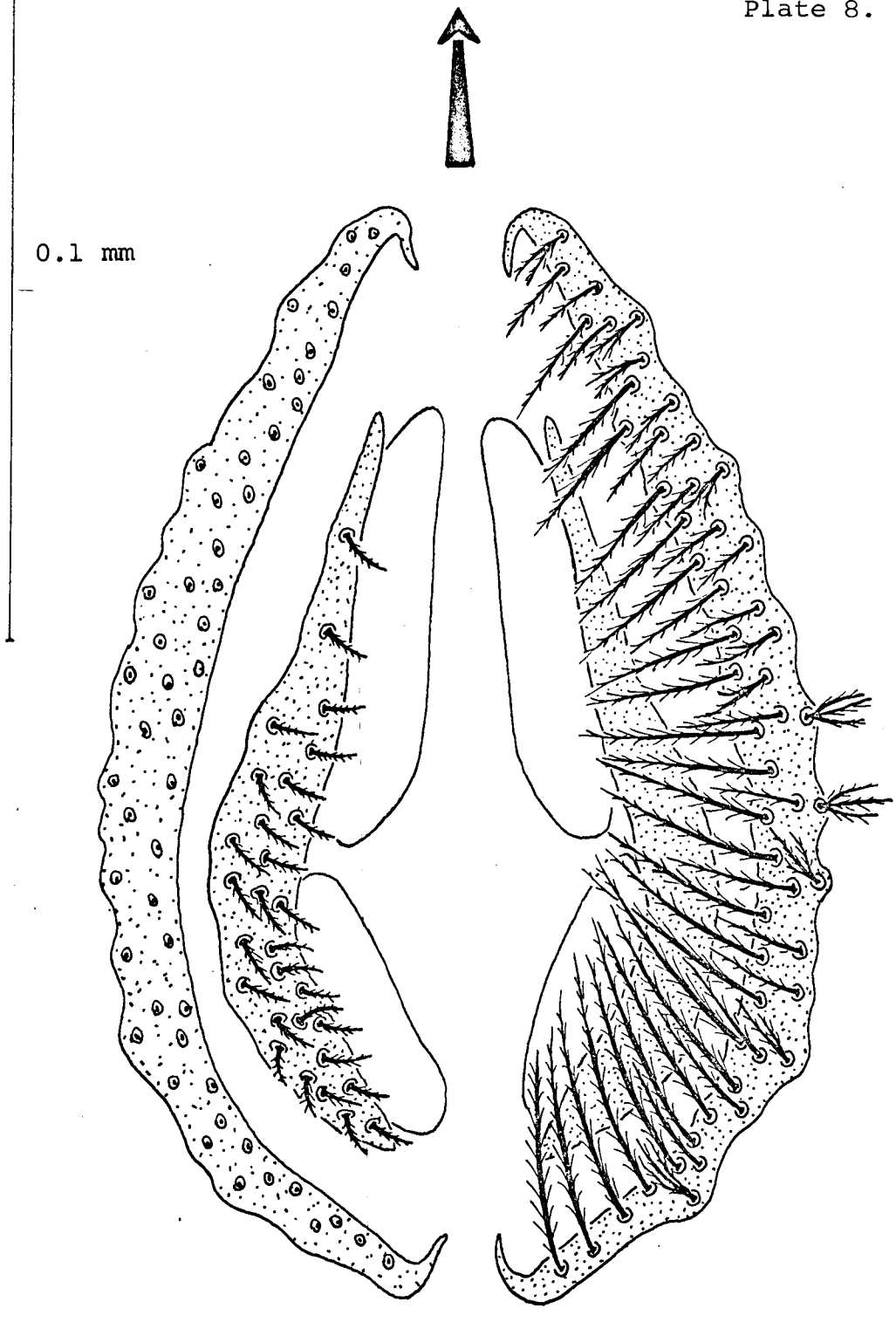

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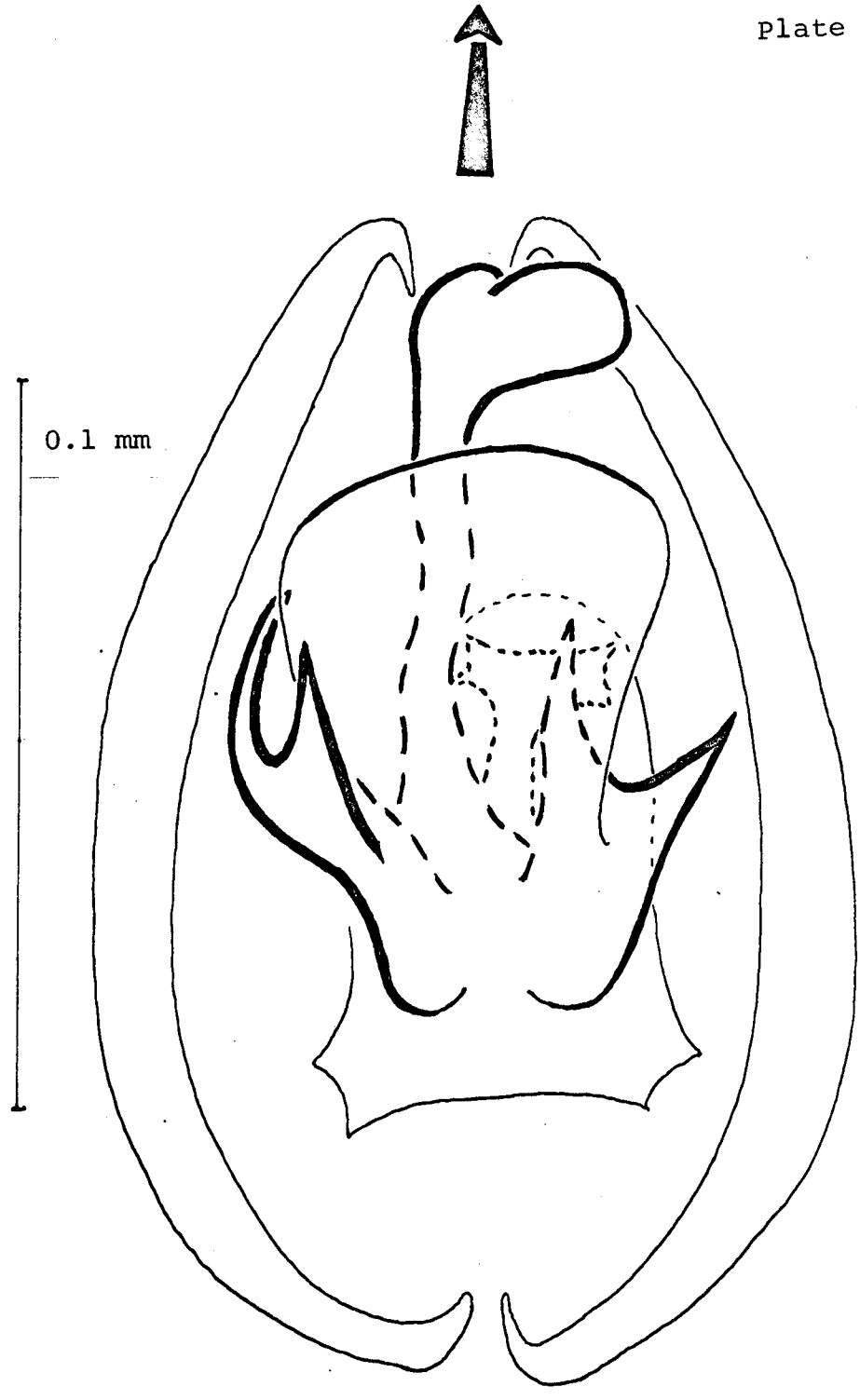

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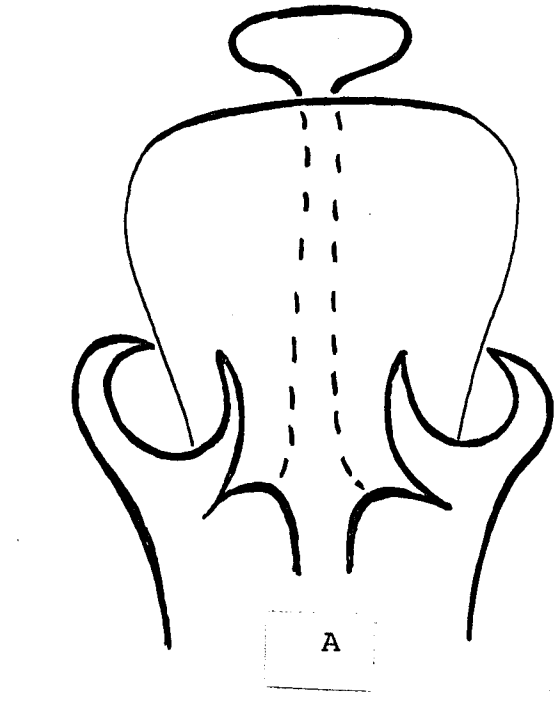

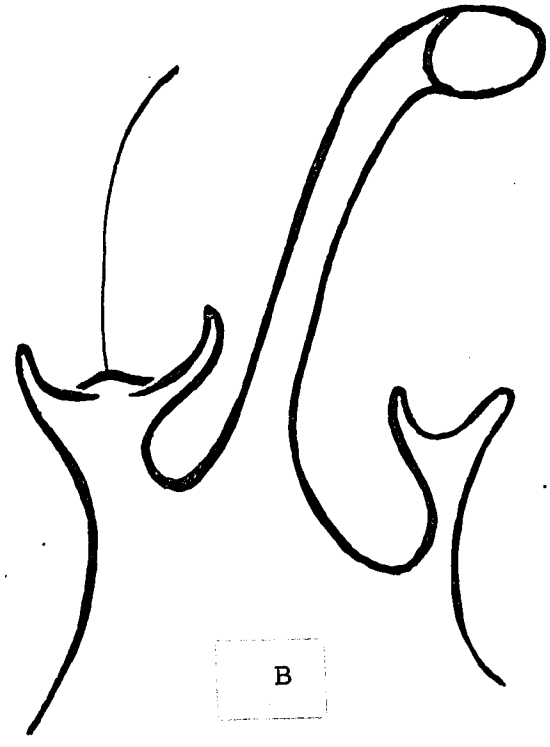

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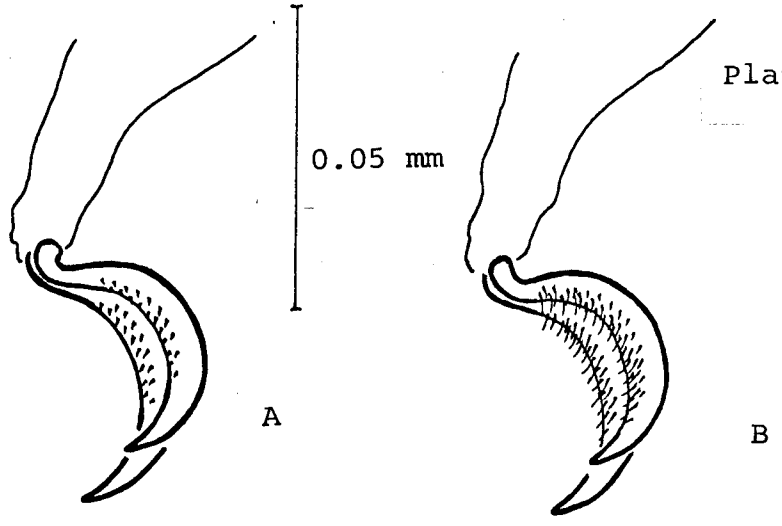

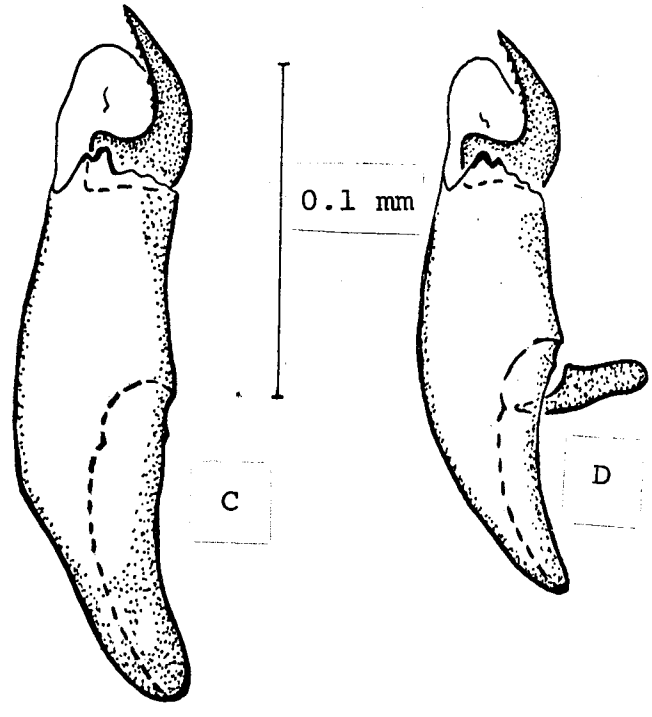

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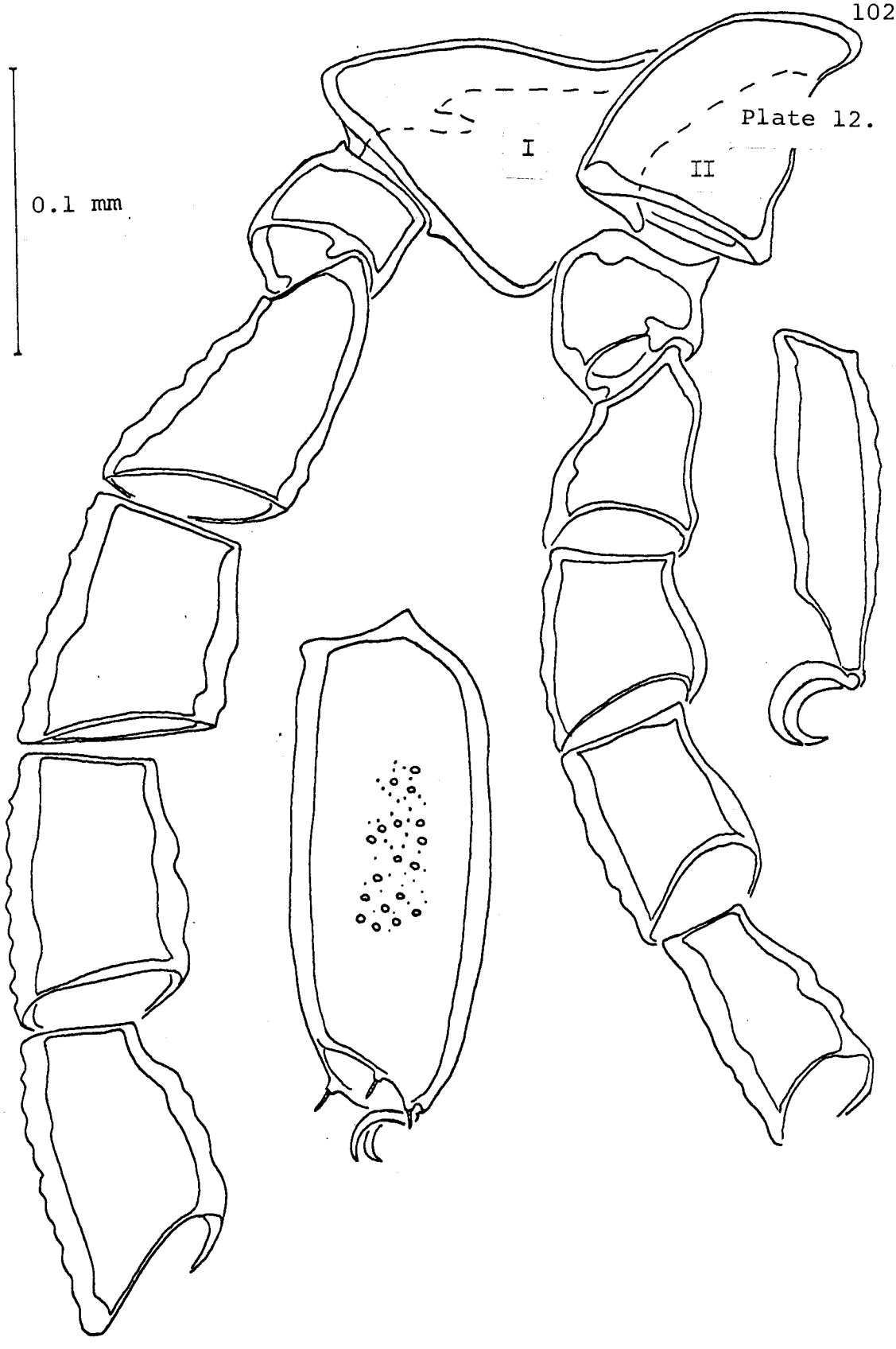

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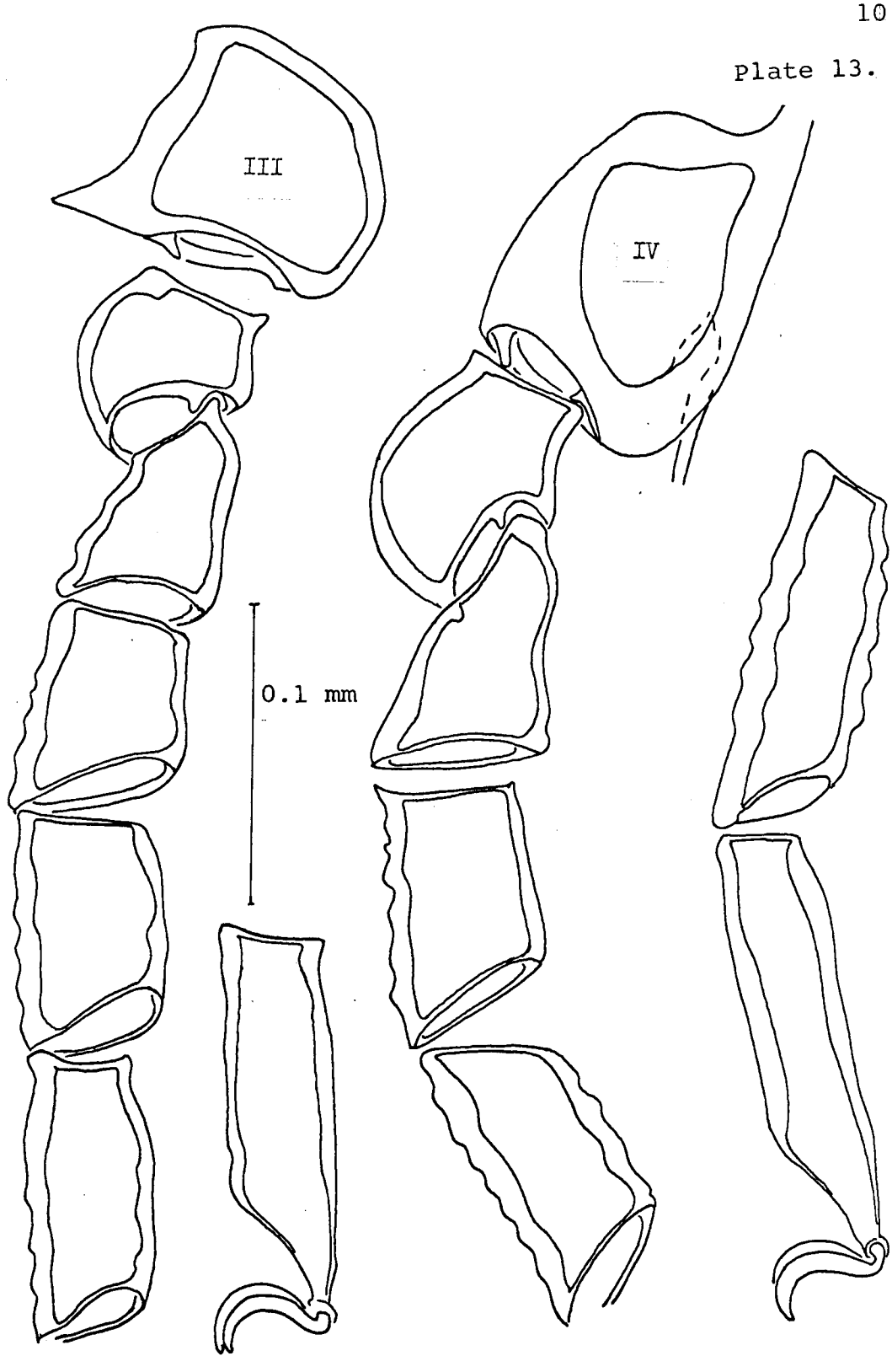

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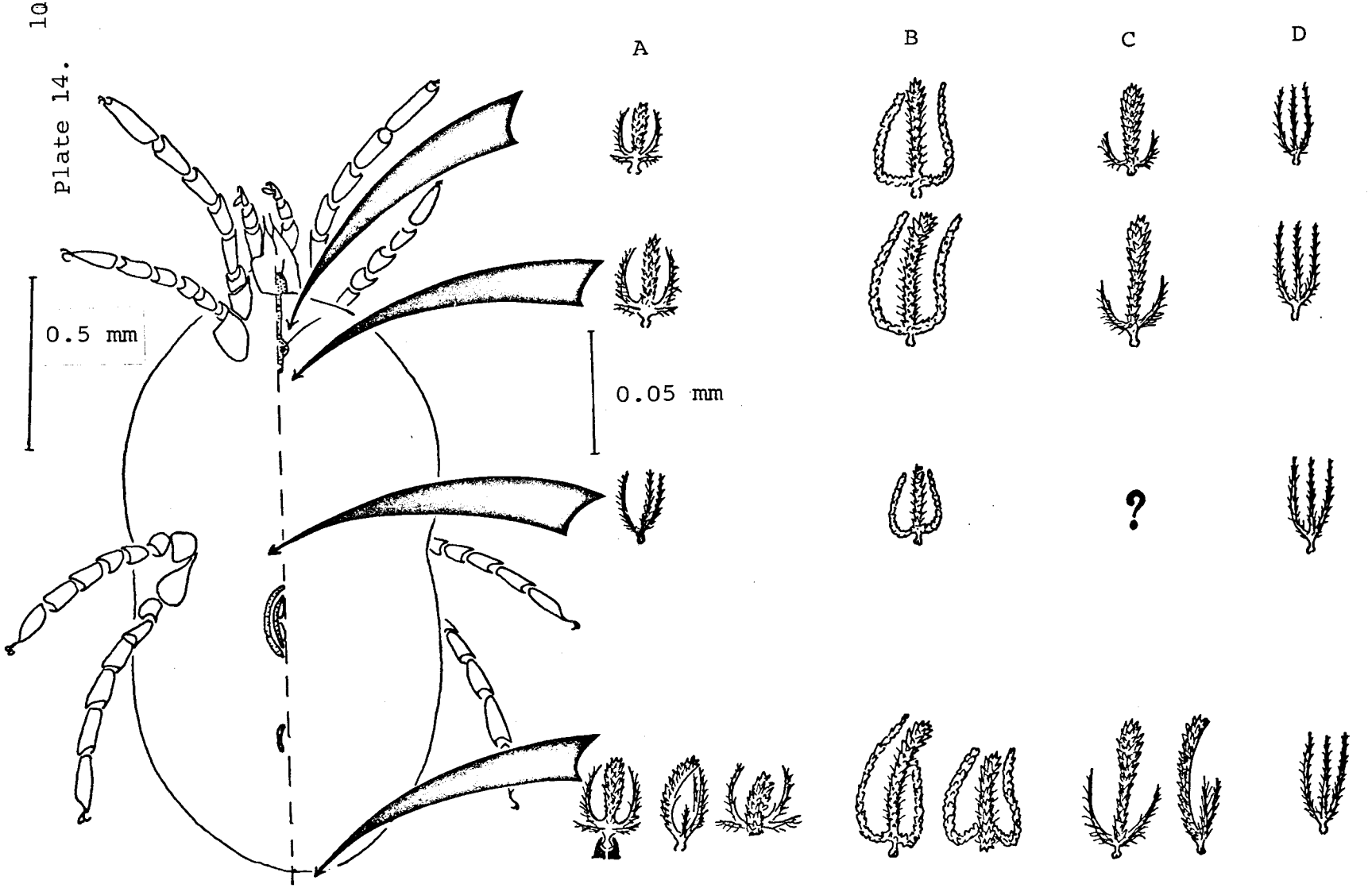

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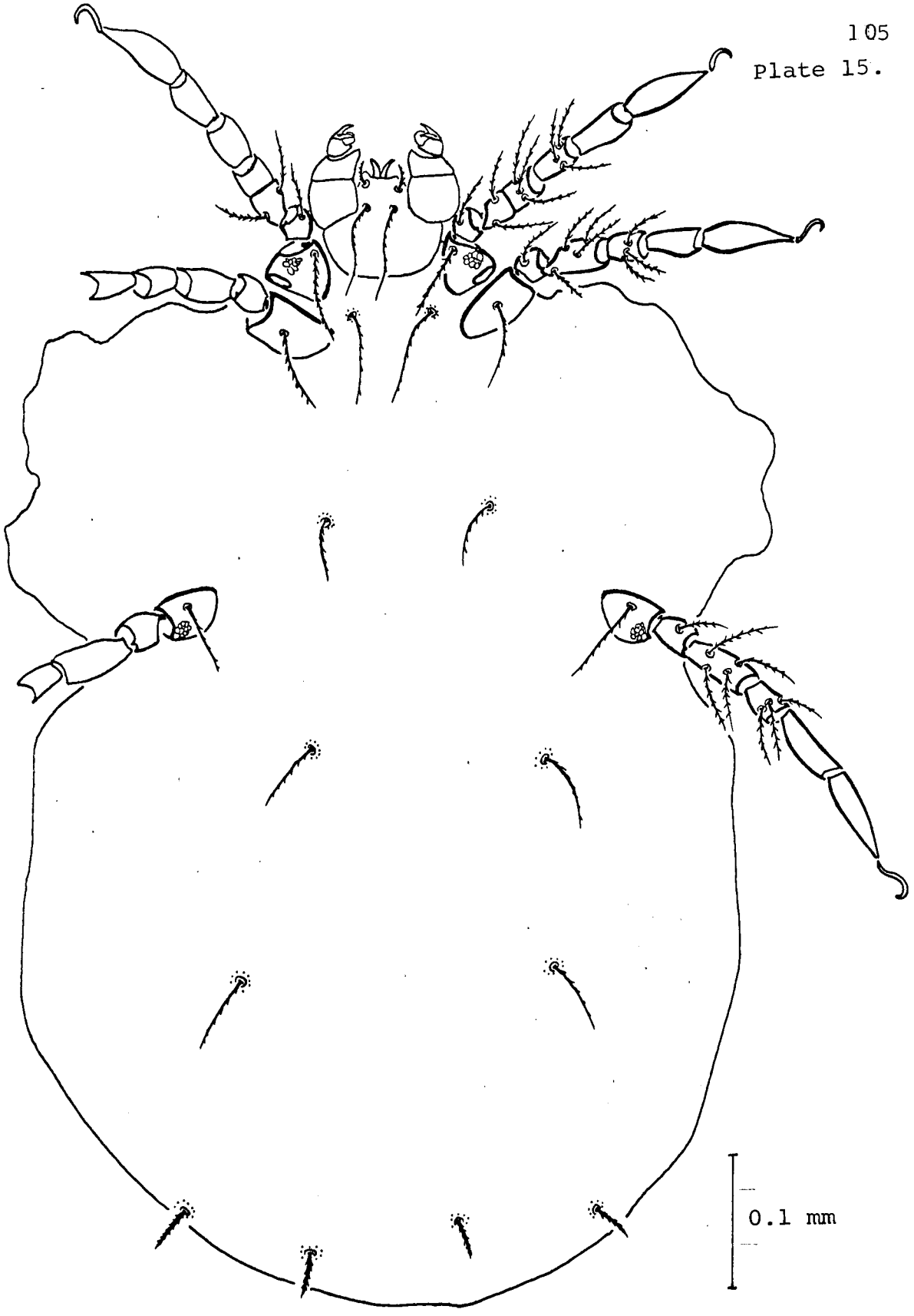

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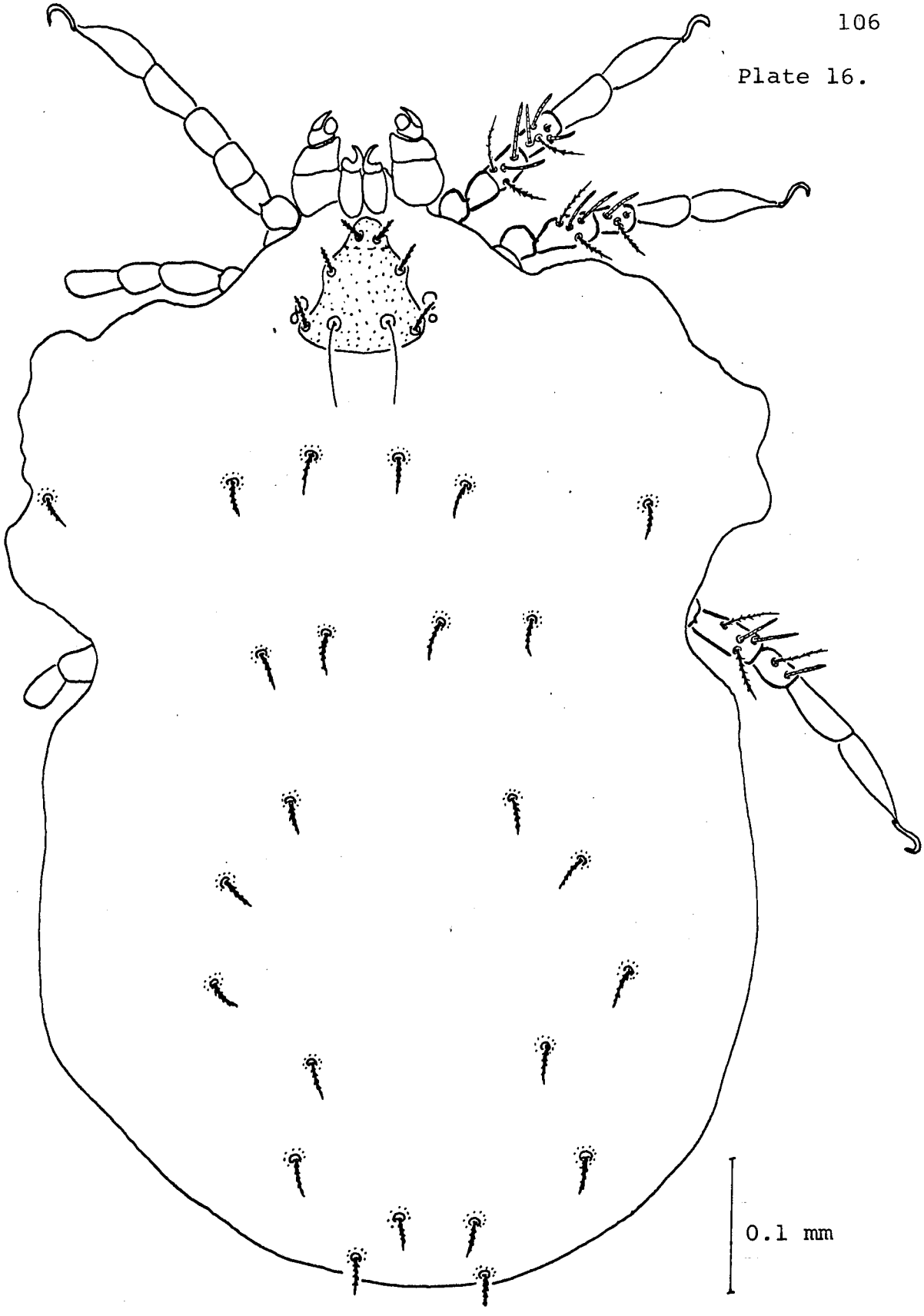

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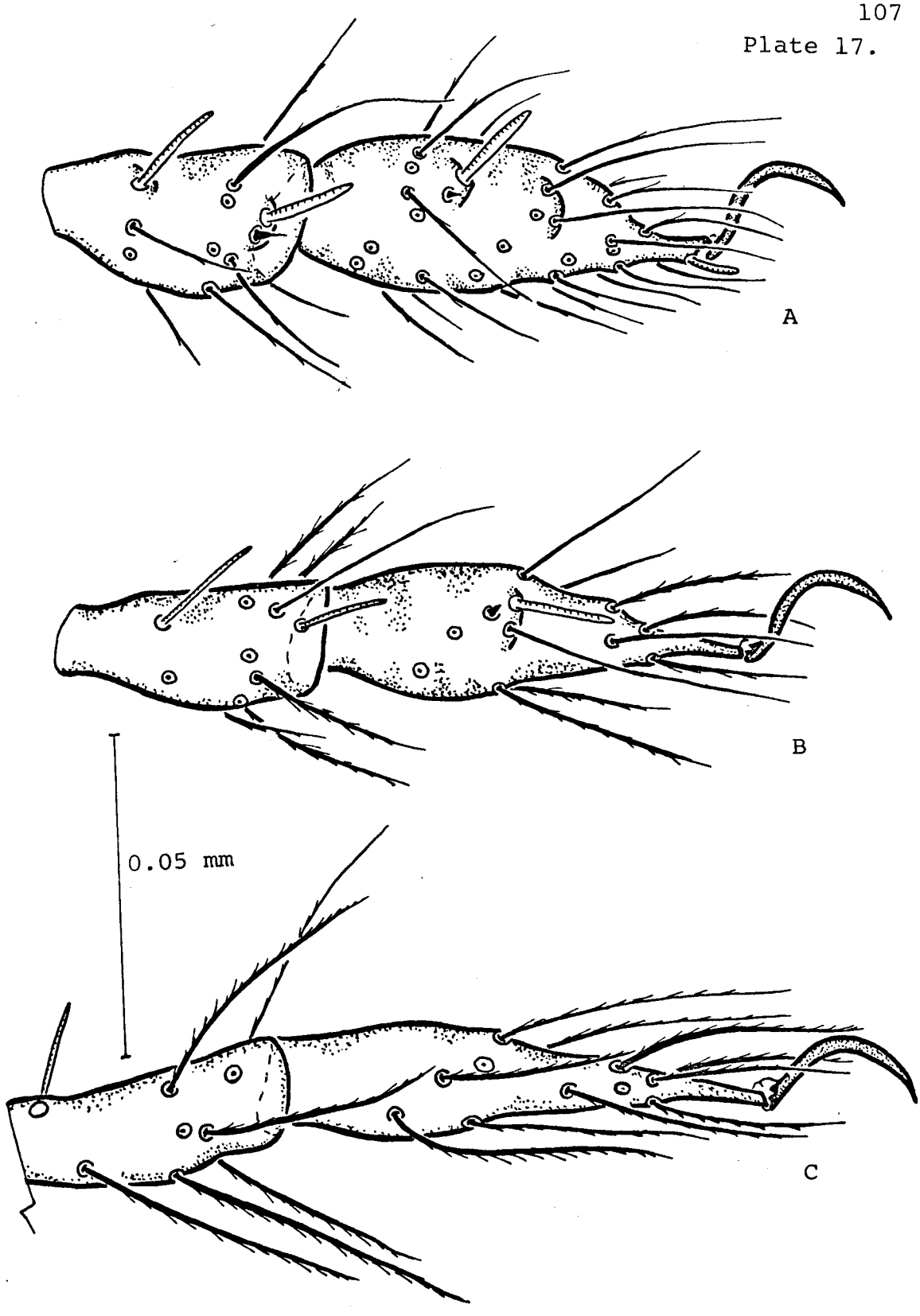

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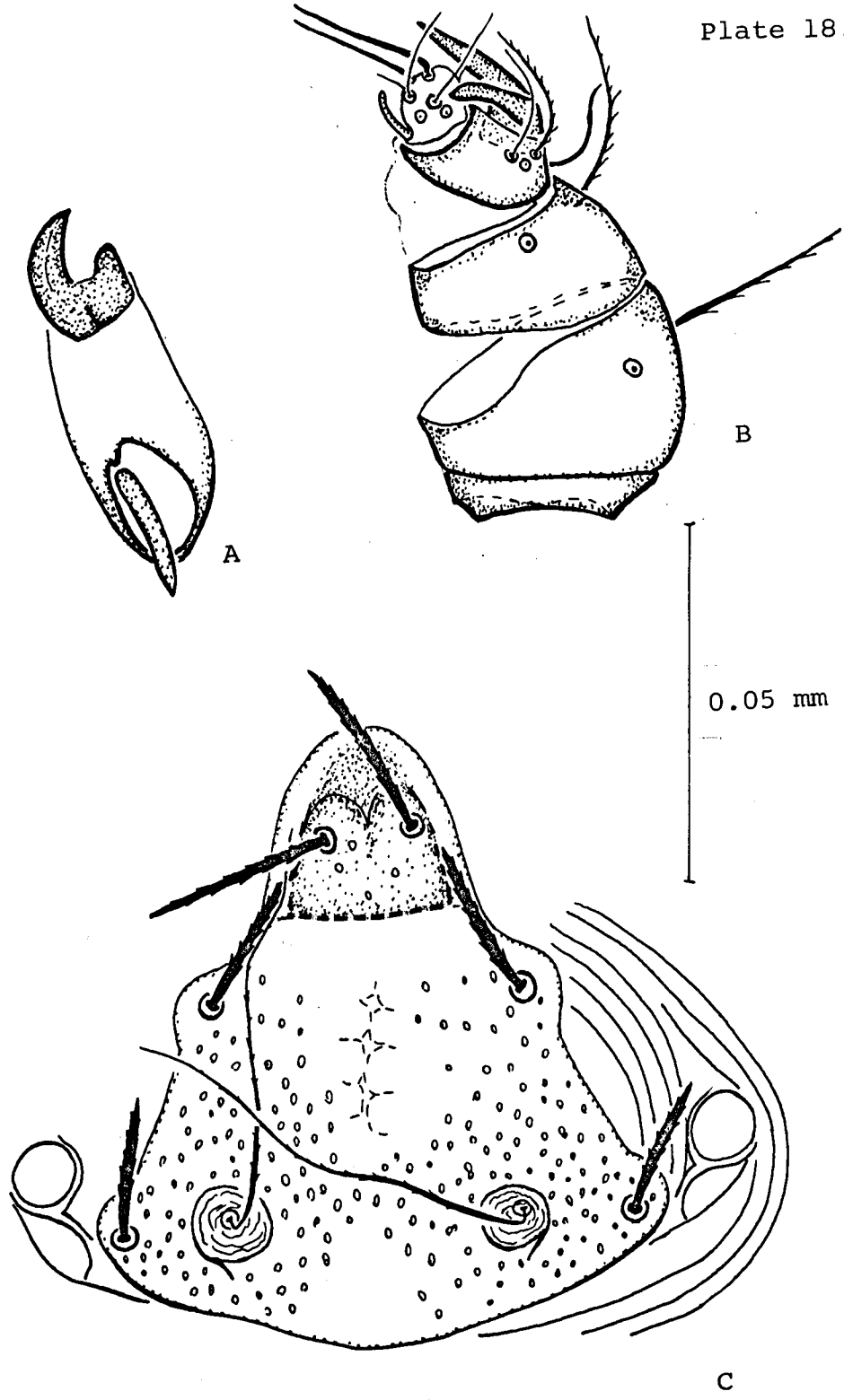

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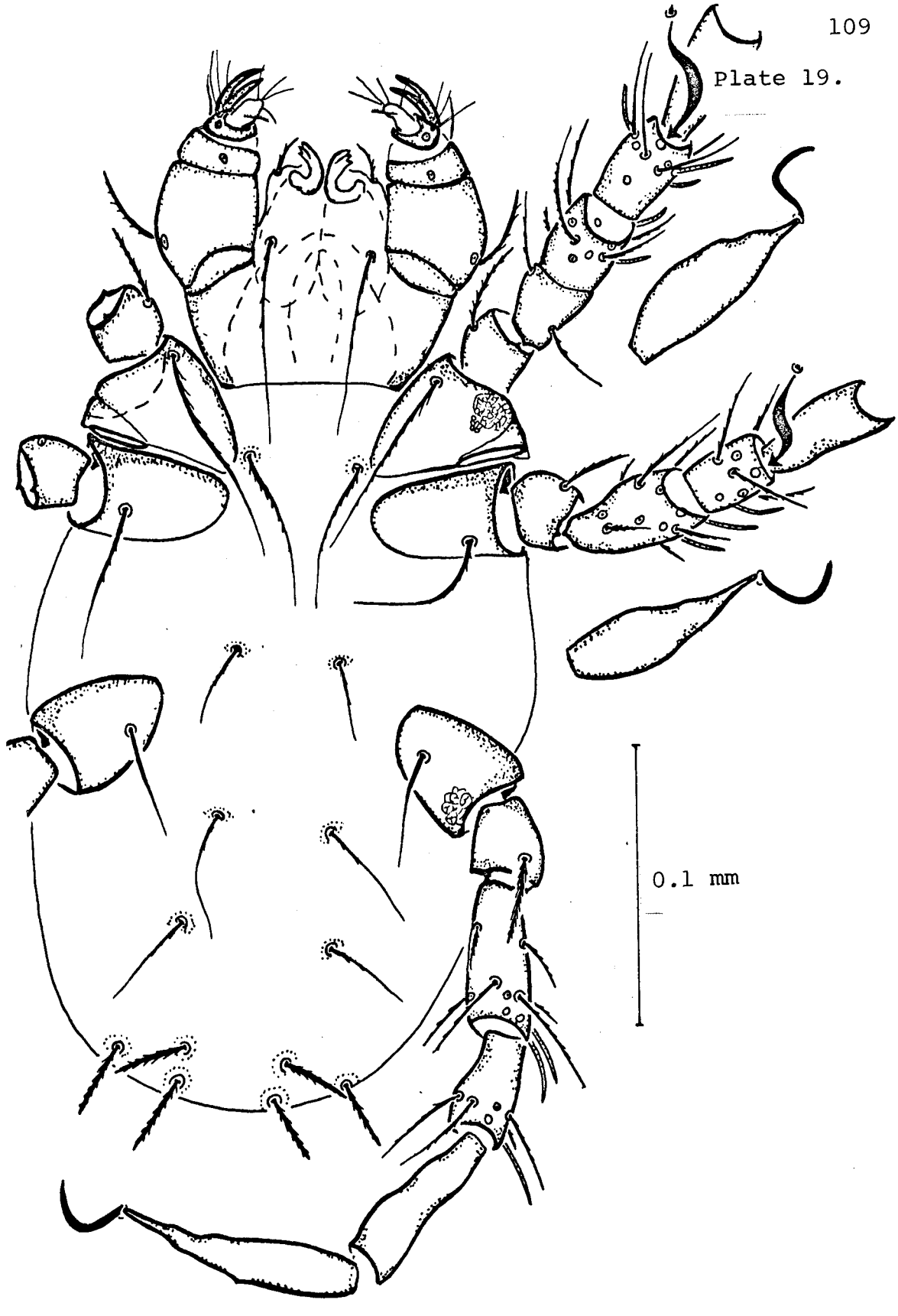

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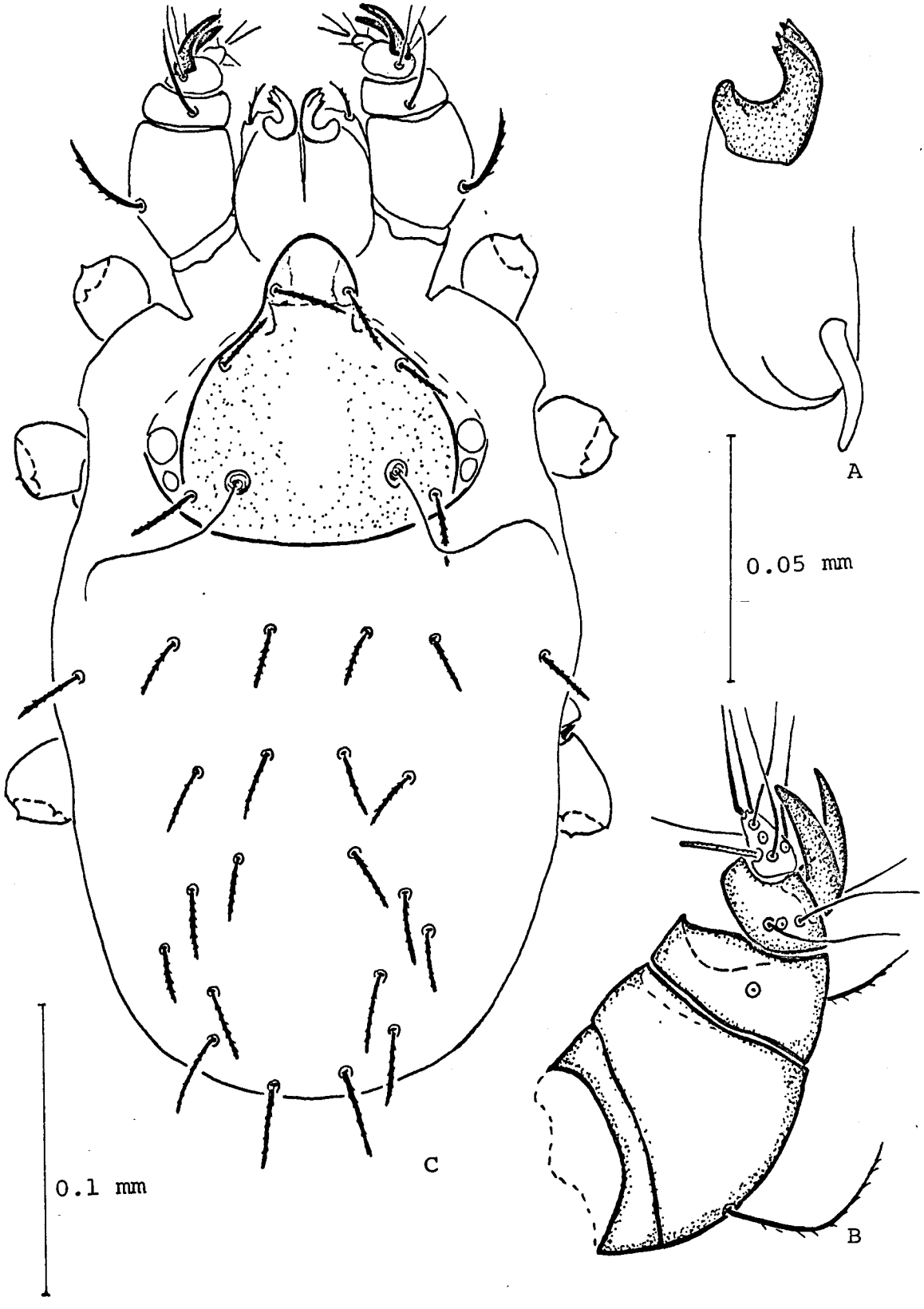

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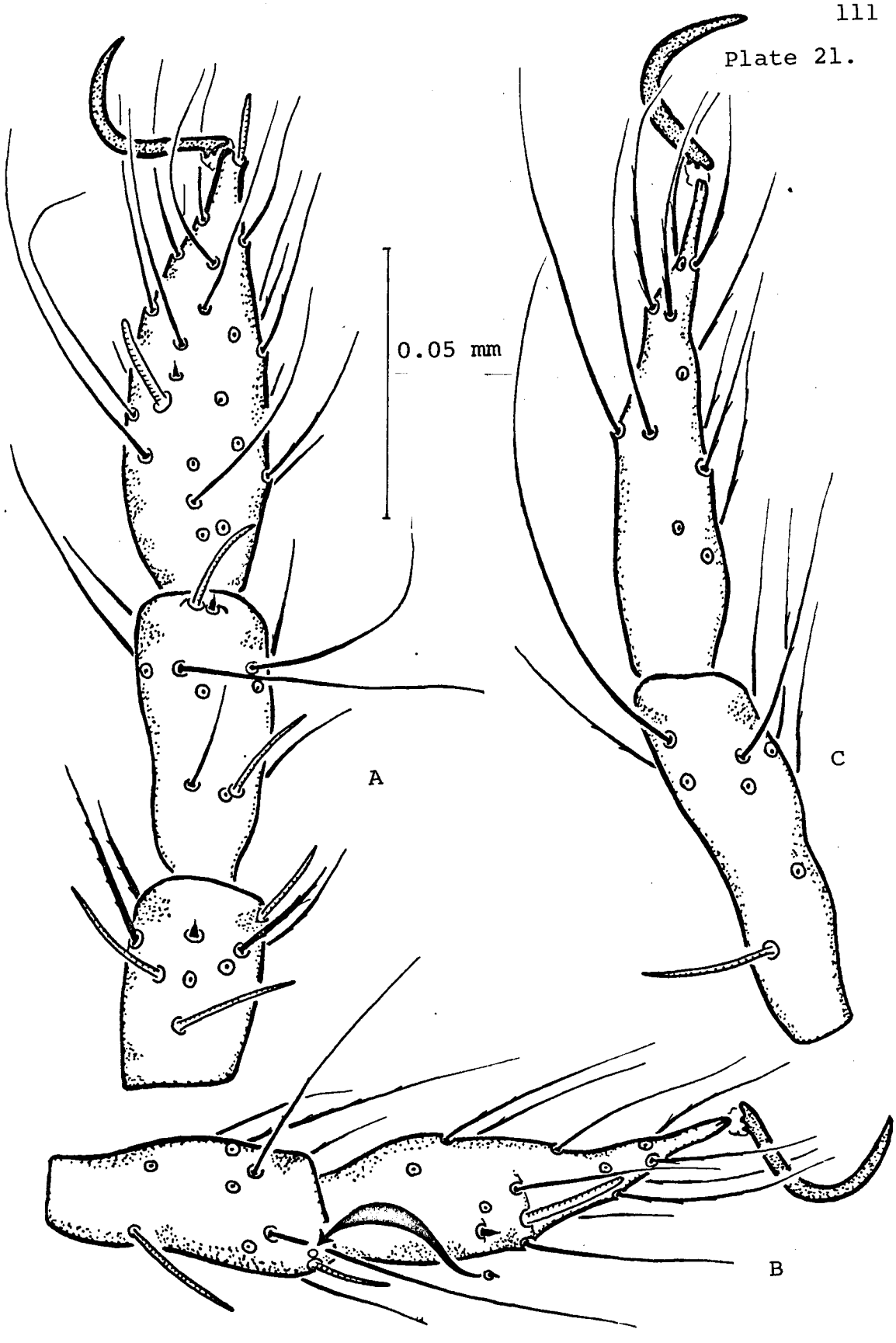

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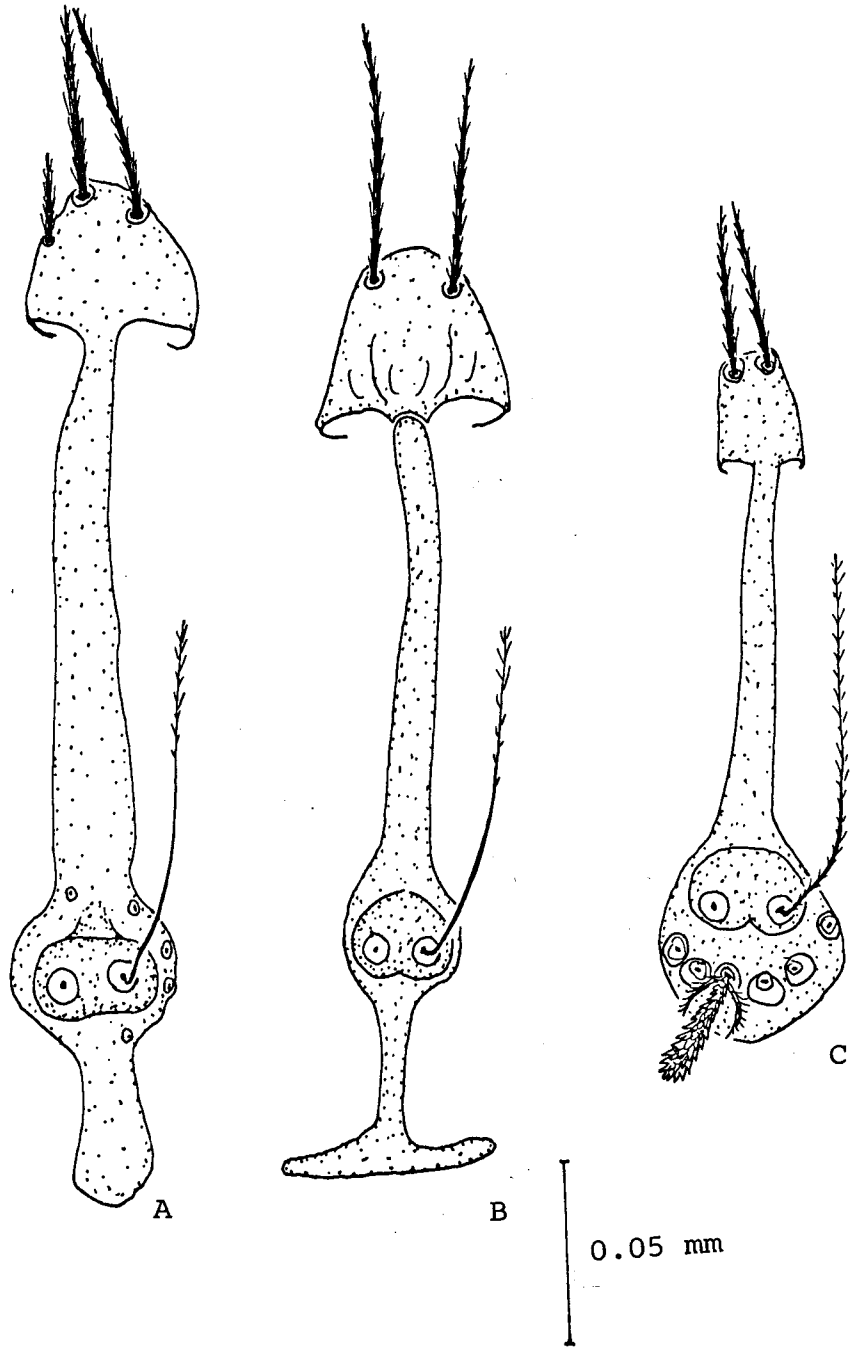

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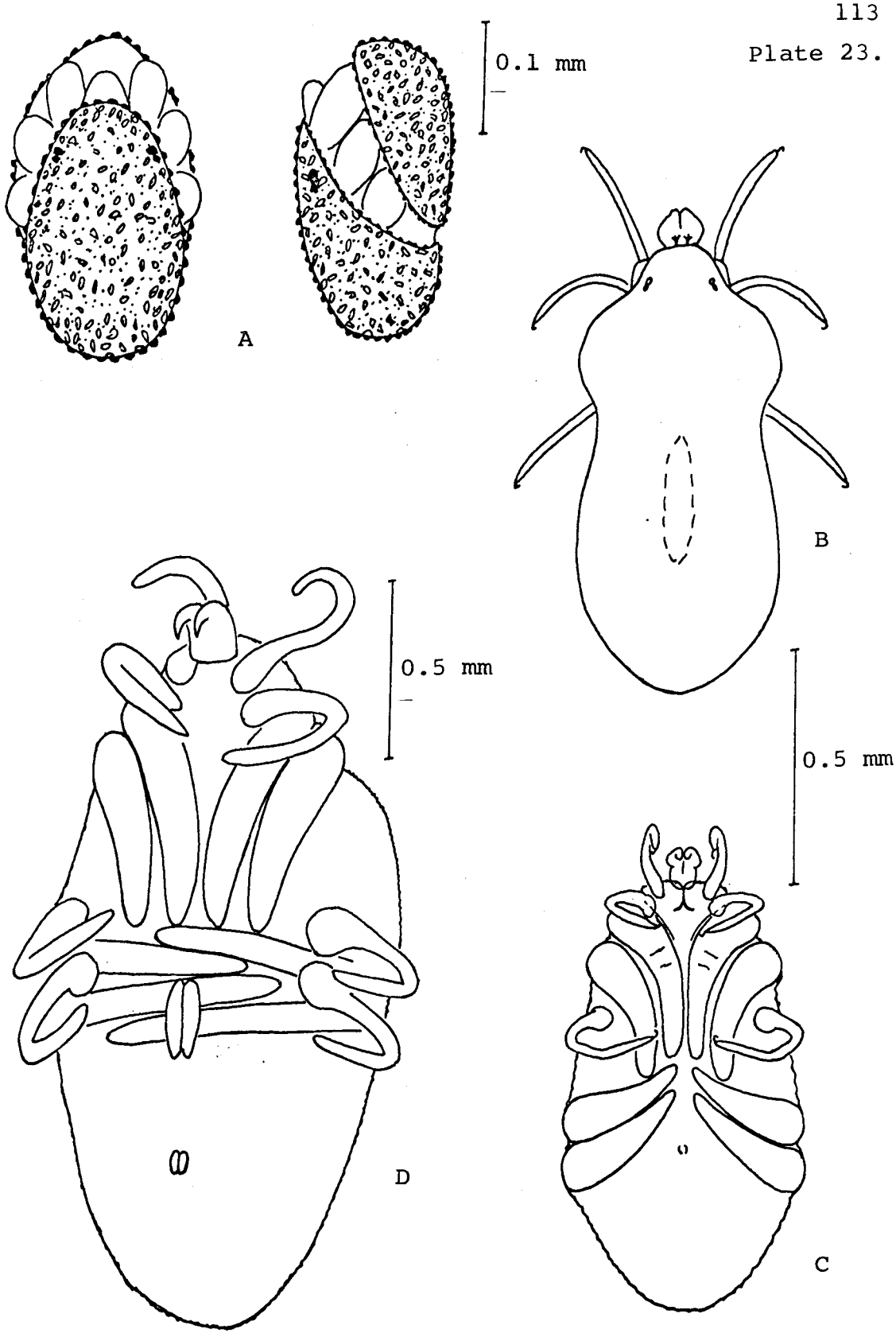
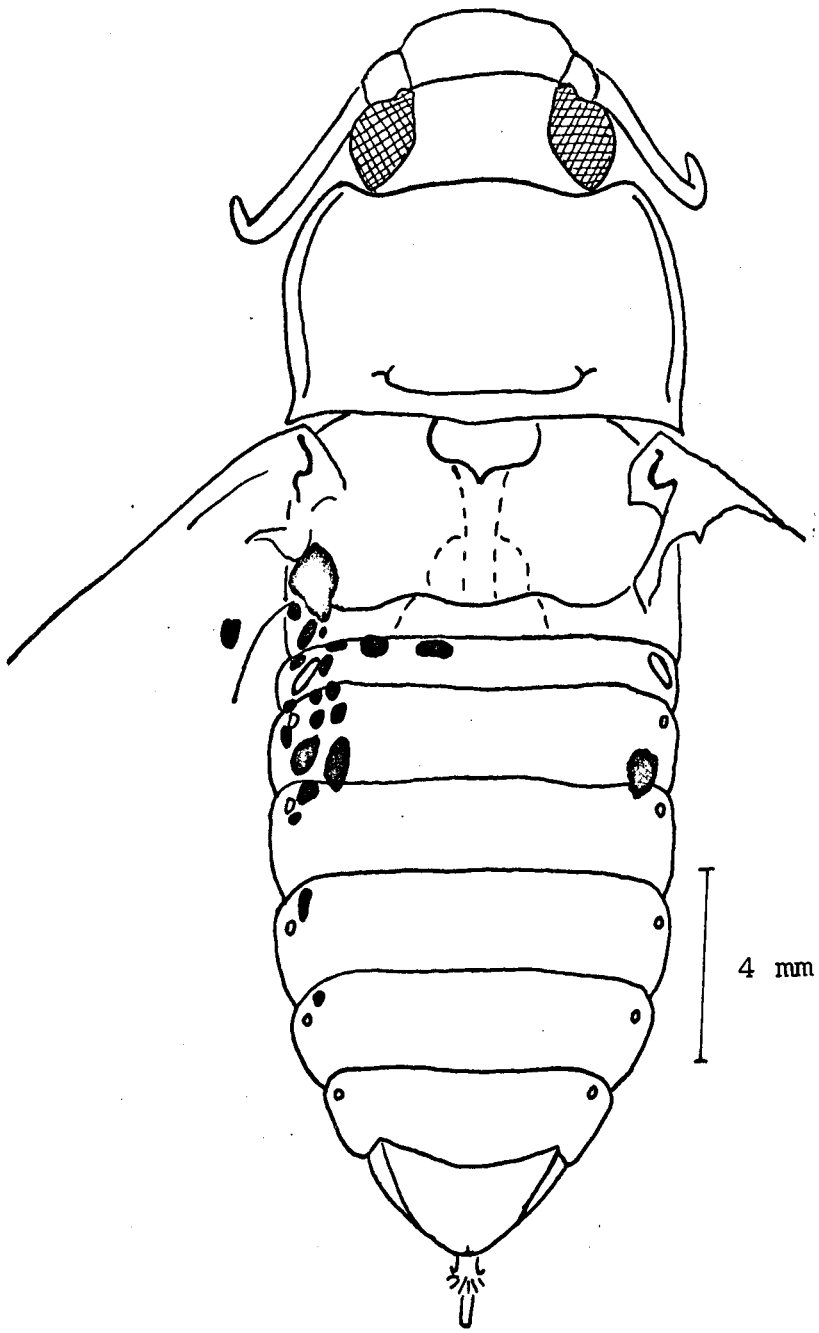
Plate 24.