NEW NOTES ON HOLOTHYRIDA (ANACTINOTRICHID MITES)

by

L. VAN DER HAMMEN
Rijksmuseum van Natuurlijke Historie, Leiden

With 28 text-figures

ABSTRACT

In the present study of the Anactinotrichid order Holothyrida, five species are dealt with: *Australothyrus ocellatus* nov. gen., nov. spec. (family Allothyridae) from Queensland, Australia; *Hammenius* (*Leiothyrus*) *holthuisi* nov. subgen., nov. spec. and *Hammenius* (*Thonius*) *montanus* nov. spec. (family Holothyridae), both from New Guinea; and *Holothyrus coccinella* Gervais and *Holothyrus legendrei* nov. spec. (family Holothyridae), both from Mauritius. The paper includes detailed studies of the morphology, a study of the postembryonic development, a reclassification of the species of the family Holothyridae, and notes on the relationships of the order Holothyrida.

CONTENTS

I. INTRODUCTION

In the course of my comparative morphological studies of mites, I published three papers on representatives of the Anactinotrichid order Holothyrida (Van der Hammen, 1961, 1965, 1968). In my study on the classification of mites (Van der Hammen, 1972) and in my comparative study of the Cryptognomae (Van der Hammen, 1979), a chelicerate subclass which includes Anactinotrichida, the Holothyrida are also mentioned. The present paper is a

continuation of the previous studies, and a completion of the preparatory investigations for the third part of the Glossary of Acarological Terminology, which will be devoted to Holothyrid terminology (cf. also Van der Hammen, 1976, 1980). It is subdivided into nine sections, and deals with five species of Holothyrida: an interesting new species of Allothyridae from Queensland, Australia; two new species of Holothyridae from New Guinea; and two species of Holothyridae from Mauritius (one of which is new). Much attention is paid to Holothyrid morphology, to the postembryonic development, to the classification of species of the family Holothyridae (the subdivison of the family into genera and subgenera), and to the relationships of the order Holothyrida.

Lehtinen (1981) recently introduced several new taxa, based on data from literature and on a study of three species from South America and New Guinea. Travé (1982: 199–200) pointed to the premature character of Lehtinen's subdivision of the family Holothyridae (some of Lehtinen's supposed generic characters are even variable at the species level). It now appears that other characters (the secondary sexual characters of *Thonius*) were not completely understood by Lehtinen, because he had not studied both sexes. In the present paper, Lehtinen's classification is modified.

Travé (1982) published an interesting study of the behaviour of *Thonius braueri* (Thon) (the species is regarded here as a representative of an unnamed subgenus of *Hammenius*). Travé fed his specimens on cheese and egg-yolk (they refused to eat living and dead specimens of various microarthropods, including eggs and larvae, and various kinds of vegetable food). It is not impossible that the natural food of Holothyridae consists of snails (not mentioned by Travé).

Several authors have given a survey of the species of Holothyrida (Thon, 1906; Womersley, 1935; Van der Hammen, 1961; Lehtinen, 1981; Travé, 1982). None of these surveys is complete, for which reason the following catalogue of the species (which includes the results of the present paper) is prepared.

Family Allothyridae: *Allothyrus constrictus* (Domrow, 1955) (Queensland, Australia), *Allothyrus* (?) *australasiae* (Womersley, 1935) (Australia, New Zealand), *Australothyrus ocellatus* Van der Hammen nov. spec. (Queensland, Australia).

Family Neothyridae: *Neothyrus ana* Lehtinen (1981: 5, figs. 1–10) (Peru).

Family Holothyridae: *Holothyrus coccinella* Gervais (1842: xlvi; cf. also Gervais, 1844: 233, pl. 34 fig. 7) (Mauritius), *Holothyrus legendrei* Van der Hammen nov. spec. (Mauritius), *Hammenius* (*Hammenius*) *fujuge* Lehtinen (1981: 6, figs. 12–15, 18–29) (New Guinea), *Hammenius* (*Hammenius*) *ingii*

Lehtinen (1981: 6–7, figs. 11, 16–17) (New Guinea), *Hammenius* (*Hammenius*) *niger* (Thon, 1905: 6; cf. also Thon, 1906: 716–718, pl. 29 fig. 17) (Seychelles), *Hammenius* (*Thonius*) *longipes* (Thorell, 1882: 25–30, pl. 4 figs. 12–17; synonym: *Holothyrus longipes* var. *ferrugineus* Thorell, 1882) (New Guinea), *Hammenius* (*Thonius*) *grandjeani* (Van der Hammen, 1961) (New Guinea), *Hammenius* (*Thonius*) *montanus* Van der Hammen nov. spec. (New Guinea), *Hammenius* (*Leiothyrus*) *holthuisi* Van der Hammen nov. spec. (New Guinea), *Hammenius* (?*Leiothyrus*) *nitidissimus* (Thorell, 1882: 30–31, pl. 4 fig. 18; synonym: *Holothyrus scutifer* Thorell, 1882: 31–32, pl. 4 fig. 19) (New Guinea), *Hammenius* (unnamed subgenus) *braueri* (Thon, 1905: 6; cf. also Thon, 1905a: 585; 1905b; 1906: 681–713, figs. A-D. pl. 28 figs. 1–10, pl. 29 figs. 11–15) (Seychelles). Incertae sedis: *Holothyrus armatus* Canestrini (1897: 472) (New Guinea), *Holothyrus expolitissimus* Berlese (1923: 121) (New Caledonia; possibly a species of the subgenus *Leiothyrus*), *Holothyrus gardineri* Warburton (1913: 359) (Seychelles), *Holothyrus seychellensis* Thon (1906: 718–719, pl. 29 figs. 18–19) (Seychelles), and *Holothyrus testudineus* Butler (1876: 444) (Rodriguez). It may be added here that Hughes (1959: 86, 159, explanation of plates) mentions *Holothyrus gervaisi* (Thon) a species of which I could not find the original description; it could be a manuscript name. I remember having seen Holothyridae from Ceylon in the collection of the British Museum (Natural History); this could be the species mentioned by Hampson & Green (1892).

I have much pleasure in expressing my gratitude to Dr. Valerie Davies (Queensland Museum, Fortitude Valley, Australia) and Prof. Dr. R. Legendre (Laboratoire de Zoologie, Montpellier, France), who generously placed at my disposal the Holothyrid material collected by them in Queensland and Mauritius.

II. On a new genus and species of the family Allothyridae

During the Mt. Bellenden Ker Expedition of the Queensland Museum, Fortitude Valley, Australia, thirty-five specimens of Holothyrida have been collected, which were kindly sent to me for study by Dr. Valerie Davies. The specimens belong to species of the family Allothyridae. Five nymphs (one specimen from an altitude of 100 m, four specimens from an altitude of 1560 m) are not studied here. They probably belong to two different species, are pale in colour (less sclerotized than the adults), and are characterized by the presence of sternapophyses and short idiosomatic setae, and the absence of eyes. Thirty specimens belong to an interesting new species which is charac-

terized, among others, by the presence of eyes. This species is regarderd here as a representative of a new genus *Australothyrus*. A diagnosis of the genus, and a detailed description of the new species, are included in the present section.

Australothyrus nov. gen.

Allothyridae characterized by the presence of one pair of eyes, the absence of sternapophyses, and the absence of sexual dimorphism in the legs.

Type-species: *Australothyrus ocellatus* nov. spec.

Australothyrus ocellatus nov. spec.
(figs. 1–15)

Material. – Mt. Bellenden Ker (17°16′S 145°51′E), Northeast Queensland, altitude 1560 m, 25–31 October 1981. – 21 ♂, 6 ♀ (among which the female holotype and the male allotype); altitude 1500 m, 10 April 1979. – 1 ♂, 1 ♀.

Mt. Bartle Frere, South Peak (17°24′S 145°49′E), Northeast Queensland, altitude 1620 m, 6–8 November 1981. – 1 ♂.

All material was from rainforest litter. The holotype, the male allotype and the greater part of the paratypes are in the Queensland Museum (registration numbers QM S1318–1322); four paratypes are in the Rijksmuseum van Natuurlijke Historie, Leiden.

Measurements. – Male and female are of equal size; the length is about 2.4 mm, the breadth 1.3 mm. The lengths of the legs (of the female represented in figs. 11–12, 14–15; there are no striking differences, in this respect, between male and female) are the following: leg I 2.3 mm, leg II 2.0 mm, leg III 2.1 mm, leg IV 2.9 mm.

Habitus and colour. – The adult specimens of the species are relatively robust mites, with legs about as long as the body. The cuticle is glossy, and presents numerous small tubercles (associated with setae) and large, smooth sigilla. The colour of the adult specimens is reddish brown.

Tegument. – The tuberculate areas (not the sigilla) of the dorsal shield are covered with cerotegument and adhering dirt; ventrally, the cerotegument layer can be particularly well-developed in the sternal concavities and at the posterolateral border of the ventral shield. Each tubercle of the idiosomatic microsculpture is associated with a spiniform seta, and contains a cupuloid (a rounded sensory organ, resembling a cupule, and probably homologous with a lyrifissure). Numerous pores of tegumentary glands are present in the areas between the tubercles.

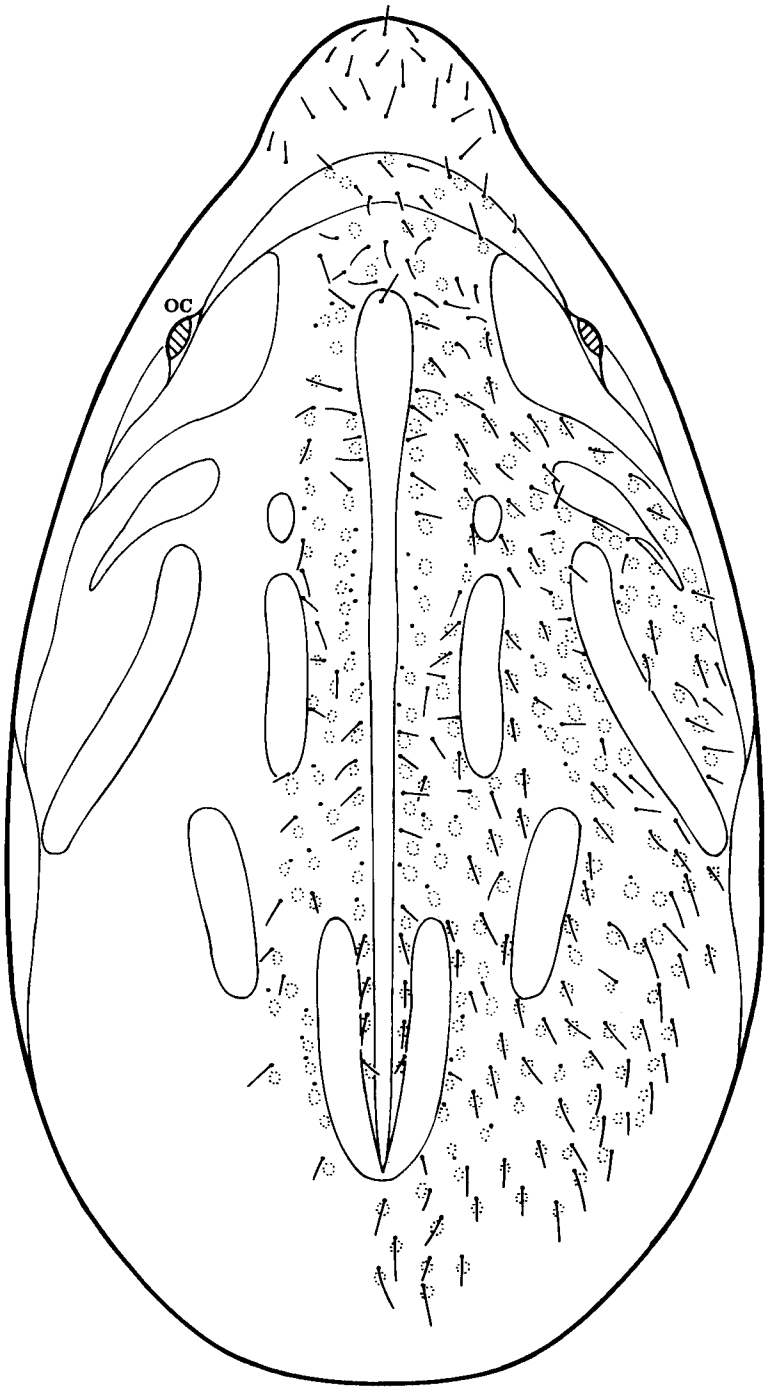

Fig. 1. *Australothyrus ocellatus* nov. spec., dorsal view of adult female, × 75.

Dorsal shield (figs. 1, 2A). – The dorsal shield is oval in shape, with the largest width about the middle; it is narrowed in the rostral region. The large sigilla of the dorsal shield are arranged in a characteristic pattern. There is an elongate unpaired median sigillum which is relatively very long. It is flanked, in the median and posterior part, by pairs of oval sigilla. There are some three pairs of oblique elongate laterodorsal sigilla, and five pairs of rounded posteromarginals. There are, moreover, some scattered smaller sigilla. The areas between the sigilla present tubercles, setae and pores of tegumentary glands; there are, however, no tubercles in the rostral part of the idiosoma. Although the sigillotaxy presents elements of a segmental arrangement, it is strongly different from the ancestral segmentation pattern as present in Opilioacarida.

There is one pair of eyes (figs. 1, 2A, 6A) in the anterolateral region of the dorsal shield. Each eye consists of a cornea (a transparent, rounded, convex part of the cuticle, functioning as a lens), situated in a rounded light spot of the cuticle. The lateral stigma is surrounded by a peritreme (fig. 2A). There are, on either side, two orifices of large glands: one posteriorly of the eye, and one posteriorly of the peritreme (fig. 2A). The orifice behind the eye is situated in a light spot (its duct is even visible through the cuticle); it probably constitutes the orifice of an excretory gland. The orifice behind the peritreme (the so-called stigma 2) is connected with a colourless tube (similar to that of the anterior orifice), and not with a chitinous atrium (as in Holothyridae) previously supposed to represent a respiratory organ. This confirms the conclusion, recently drawn by Travé (1982: 205–206), that the organ represents an excretory gland. According to Dr. David Lee (personal communication), one can observe, in living Allothyrids, a drop of liquid being excreted in this area.

Ventral shield (fig. 3). – The ventral shield is contiguous with the sternal shield; it surrounds the anal region and the posterior part of the genital region. It presents tubercles with cupuloids and setae, which are arranged in oblique rows; some twelve rows can be distinguished, and these could represent traces of the original segmentation (in this case, the anal opening would be in segment XIX as in Opiliocarida). A marginal row of long setae is present in the lateral and posterior part of the shield. Numerous pores of tegumentary glands are present, scattered among the tubercles. The peridium has the same position as in other species of Allothyridae (behind coxa IV). A layer of glandular cells, lining part of the internal wall of the peridium, seems to be present; each of these cells is connected with a papilla (fig. 6C, D).

Anal region. –The anal opening is covered by a pair of anal shields; these can be closed by strong muscles. Each of the shields presents a tubercle, some six setae, and pores of tegumentary glands (fig. 3).

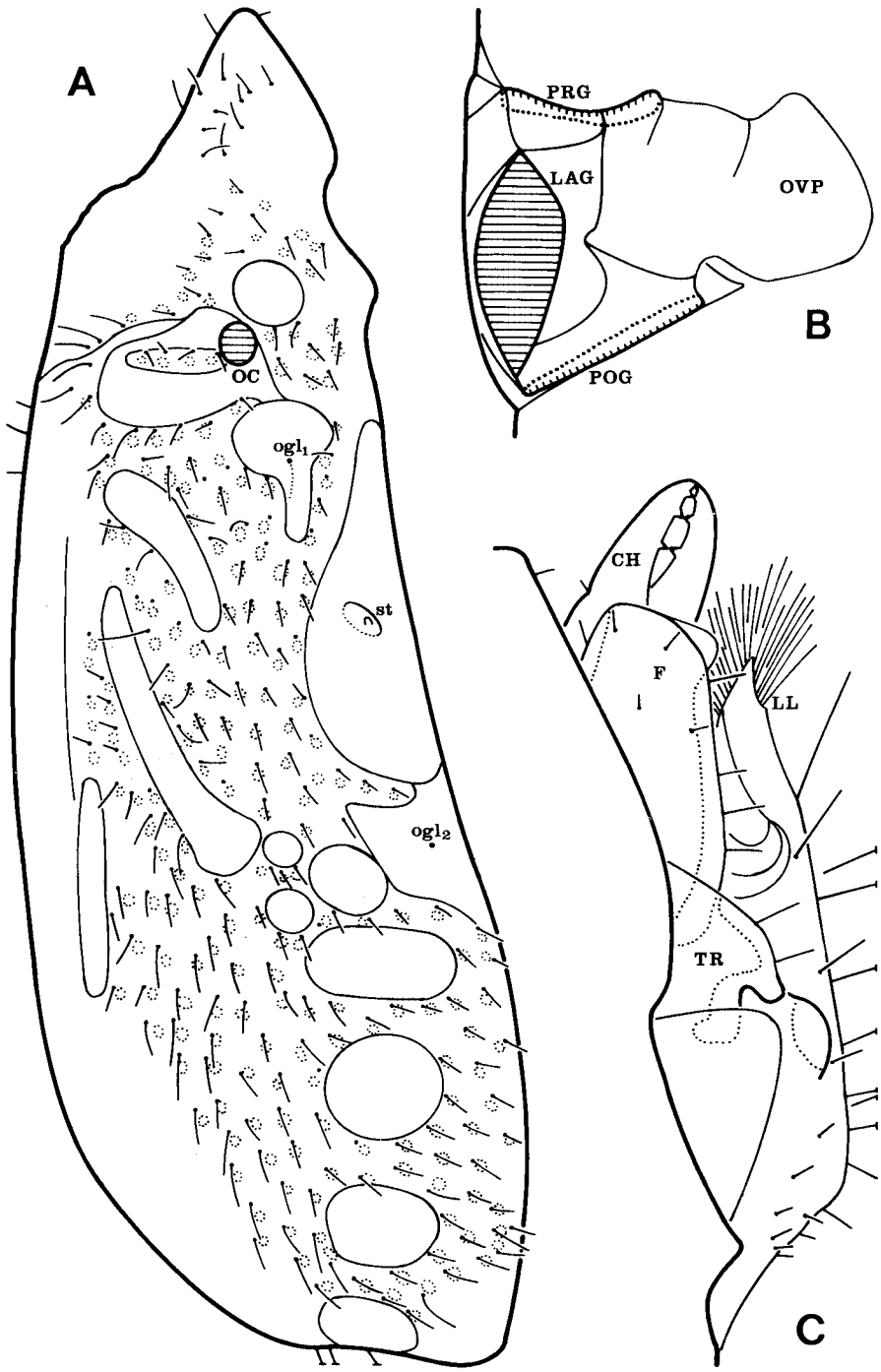

Fig. 2. *Australothyrus ocellatus* nov. spec., adult female; A, lateral view of dorsal shield; B, lateral view of evaginated ovipositor; C, lateral view of gnathosoma in camerostome; A, B, × 75; C, × 176.

Fig. 3. *Australothyrus ocellatus* nov. spec., adult female; A, ventral shield with anal and part of genital opening; B, seta, cupule, and orifice of tegumentary gland of ventral shield; A, × 141, B × 550.

Genital region. – The female genital region is covered by four shields (fig. 3, 4): a pregenital, a pair of laterogenitals, and a postgenital. The postgenital shield is the largest; it is not markedly constricted in the anterior part, and slightly wider than long. The pregenital shield is much wider than long; the laterogenital shields are narrow. The shape of the female genital area is strongly different from that in *Allothyrus constrictus* (Domrow), in which the pregenital shield is triangular, the postgenital shield markedly constricted behind anterior horns, and the laterogenital shields rather broad; it is more related to that in *Allothyrus australasiae* (Womersley), in which the postgenital shield is, however, much longer than wide. The four shields present tubercles (with cupuloids), setae and scattered pores of tegumentary glands.

The male genital region (fig. 5) is covered by the usual two shields; these present tubercles (with cupuloids), setae and pores of tegumentary glands. There is no concave epiandrium.

Sternal region (figs. 4,5). – The sternal region presents a transverse sternal groove (with tubercles, cupuloids, setae and pores) in the anterior part of the sternal region, a transverse intersegmental area (with thin cuticle, and without tubercles) at the border of segments IV and V (between acetabula II and III) and a pair of sternal cavities (with tubercles, cupuloids, setae and pores) between coxae III. The last-mentioned cavities are particularly concave in the lateral part, where they extend in posterior direction. There are no internal sternal apodemes, and no sternapophyses.

Gnathosoma. – In rest, the gnathosoma is situated in the camerostome (figs. 2C, 8B). It can be completely extended, as well as bent in ventral direction (perpendicular to the idiosoma) (fig. 6A); these particular movements of the gnathosoma (which are also found in ticks) are associated with the presence of a subcapitular apodeme and its tendons (and of muscles inserted on the base of the cheliceral frame). There is an internal continuation of the cervix (a capitular apodeme) which supports the invaginated chelicerae; no muscles are, however, inserted on this apodeme.

There are two pairs of dorsal infracapitular setae ($1dm_1$, $1dm_2$), as in the Opilioacarid *Paracarus hexophthalmus* (Redikorzev); the posterior of the two setae ($1dm_2$) is small. The corniculus is more or less cone-shaped, without lateral tooth. The paired orifices of the infracapitular glands are in the posterior part of the cervix, close to the line of attachment of the cheliceral frame (as in Opilioacarida, Ixodidae and Oribatida) (fig. 7A). The ventral infracapitular setae (fig. 7B) are numerous (eighteen, on either side, in the figured specimen). The subcapitular gutter is narrow. The labrum is long and tapering, and presents papillae (particularly in the terminal part). The lateral lips are also

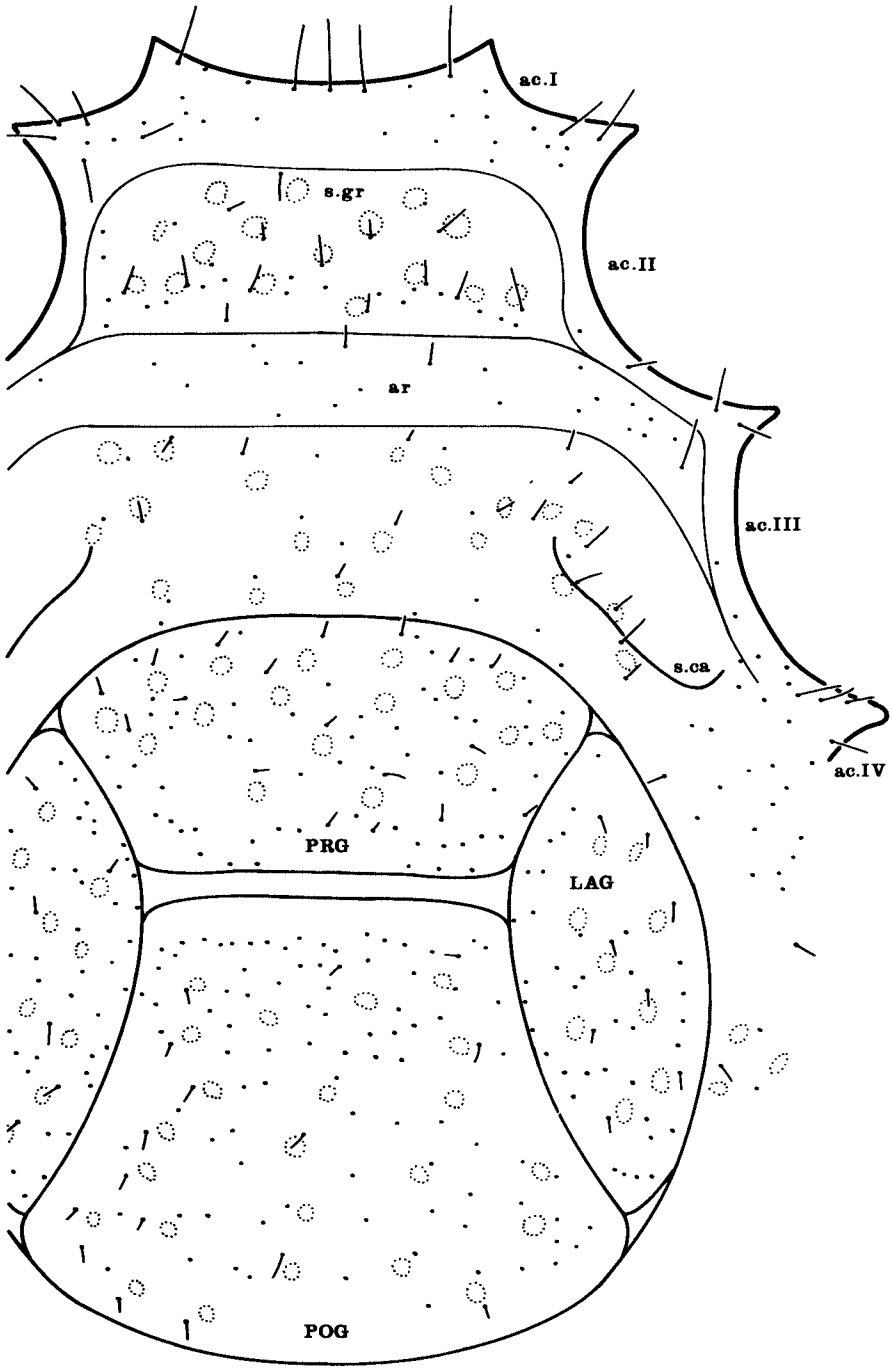

Fig. 4. *Australothyrus ocellatus* nov. spec., ventral view of sternal and genital region of adult female; × 176.

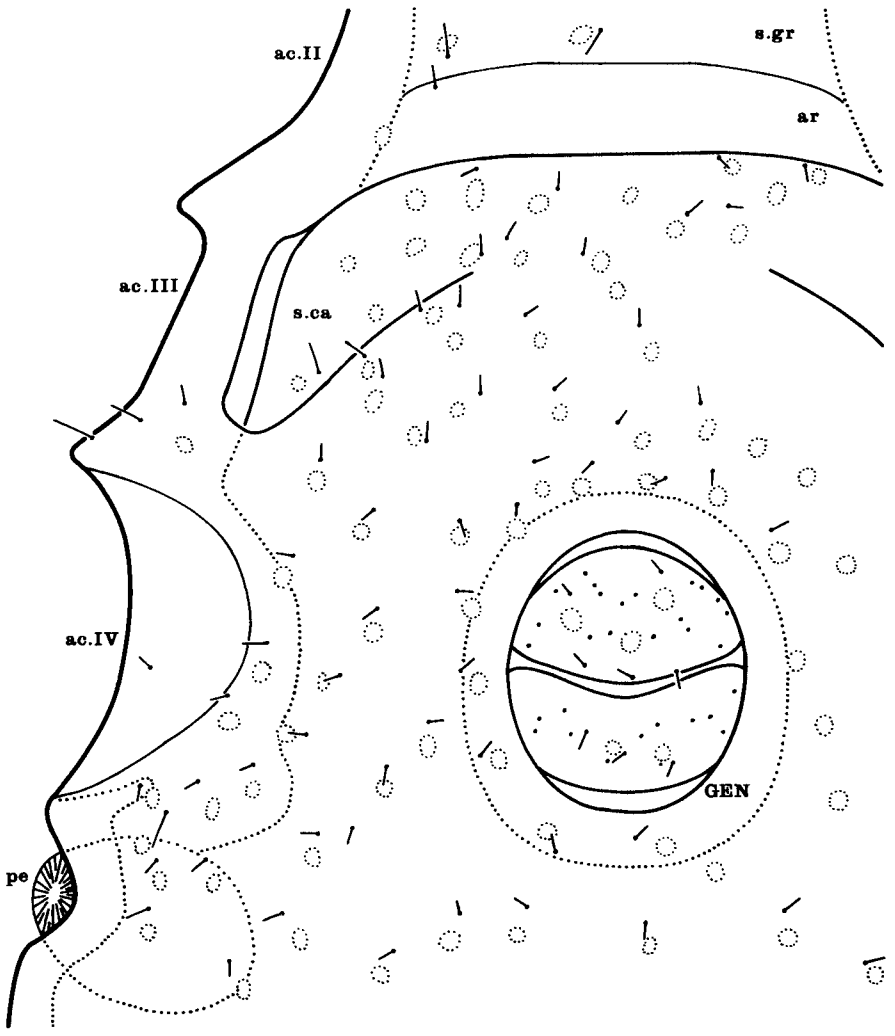

Fig. 5. *Australothyrus ocellatus* nov. spec., ventral view of genital and part of sternal region of adult male; × 176.

tapering; they present long papillae in the dorsal, lateral and ventral parts (fig. 8A, C). As in other Allothyridae, there is a large, lateral apophysis, associated with an apophysis on the palpal trochanter.

Chelicera (fig. 9A, B). – The chelicera is long, and consists of three segments (trochanter, body of chelicera, and apotele) as in other Holothyrida. There are two cheliceral setae, as in *Allothyrus constrictus*: ch_1 (with dorsal position) and ch_2' (with paralaterodorsal position); they are apparently homo-

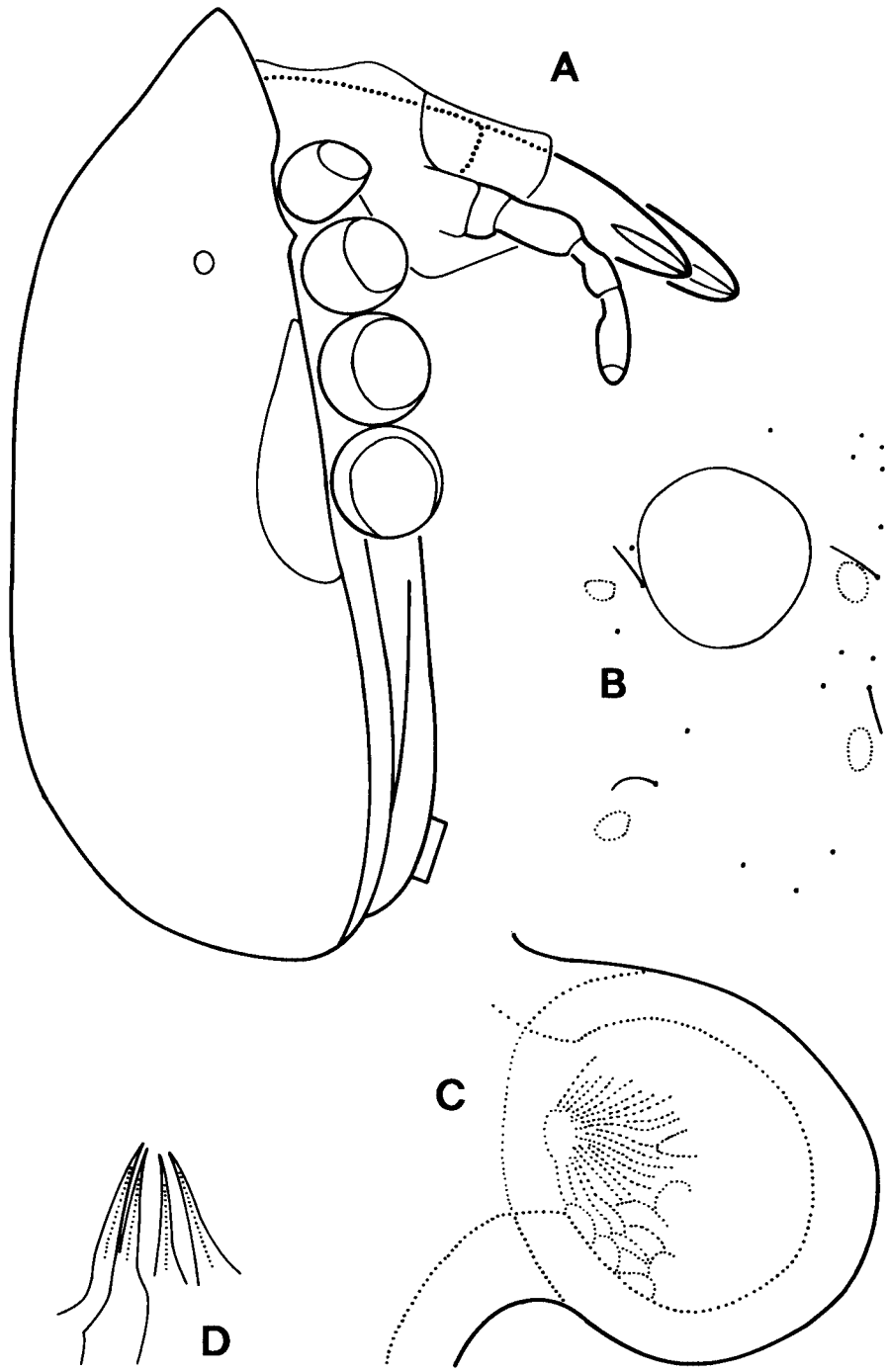

Fig. 6. *Australothyrus ocellatus* nov. spec.; A, lateral view of adult male with extended gnathosoma; B, lateral view of ocular region of adult female (same orientation as figs. 2A, 6A); C, internal (=dorsal) view of left peridium of adult female; D, detail of peridium with supposed glandular cells and papillae; A, × 55; B, × 330; C, × 368; D, × 736.

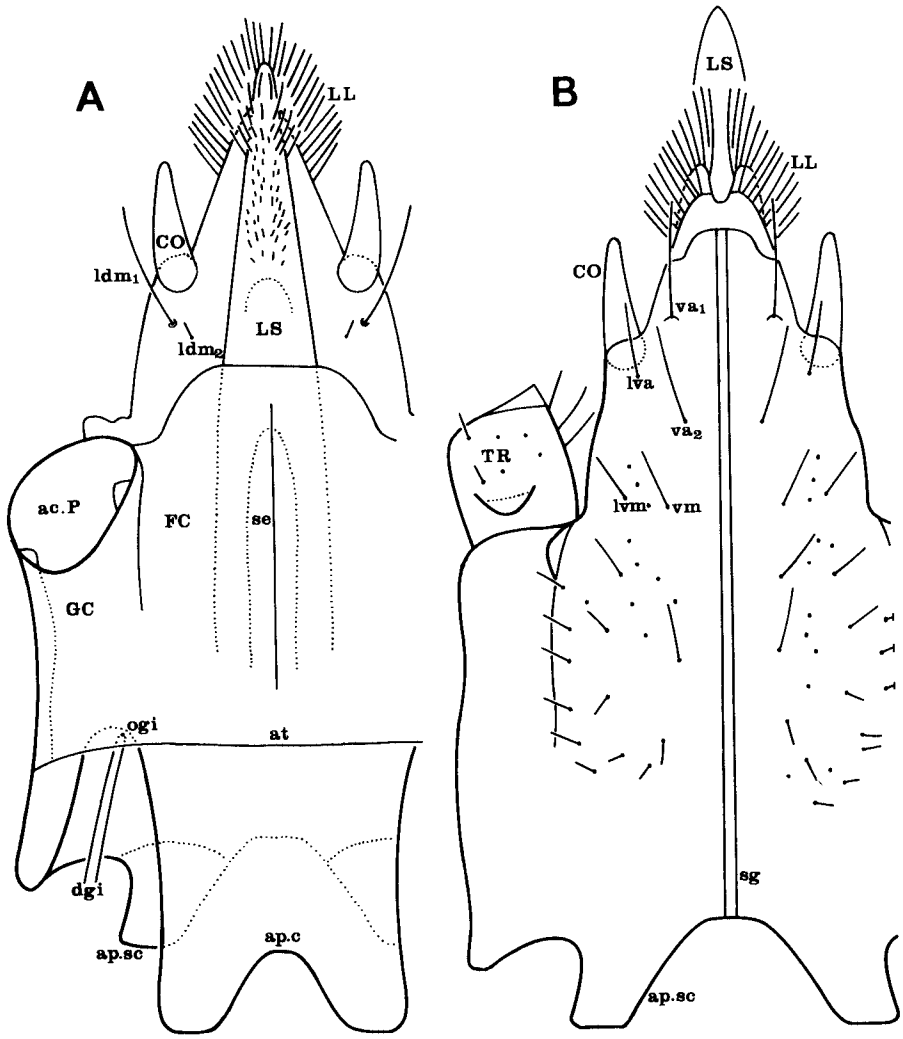

Fig. 7. *Australothyrus ocellatus* nov. spec., infracapitulum of adult female; A, dorsal view; B, ventral view; A, B, × 176.

logous with ch_1'' and ch_2' in Opilioacarida. The dorsal lyrifissure *id* is situated between the two setae (as in Opilioacarida); the antiaxial lyrifissure *iα* is situated near the antiaxial articulation point of the apotele and the body of the chelicera. Both jaws of the chela present three large teeth and rows of very small teeth.

Palp (fig. 10). – The palp consists of the usual six segments: trochanter, femur, genu, tibia, tarsus and apotele. There are no fringed setae on the genu,

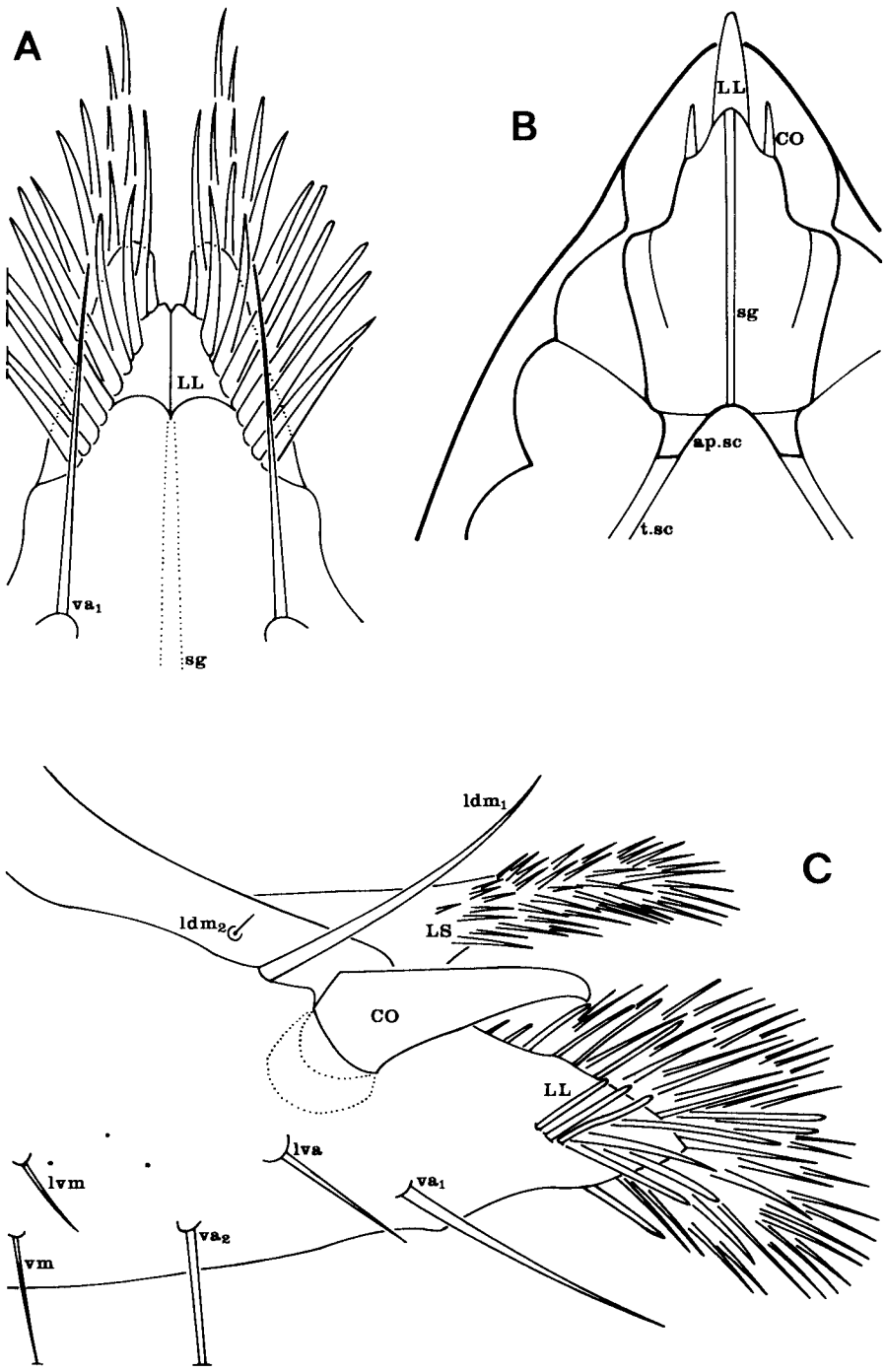

Fig. 8. *Australothyrus ocellatus* nov. spec., infracapitulum of adult female; A, ventral view of distal part; B, ventral view of gnathosoma in camerostome (sternal shield removed); C, lateral view of terminal part (labrum raised); A, × 470; B, × 75; C, 368.

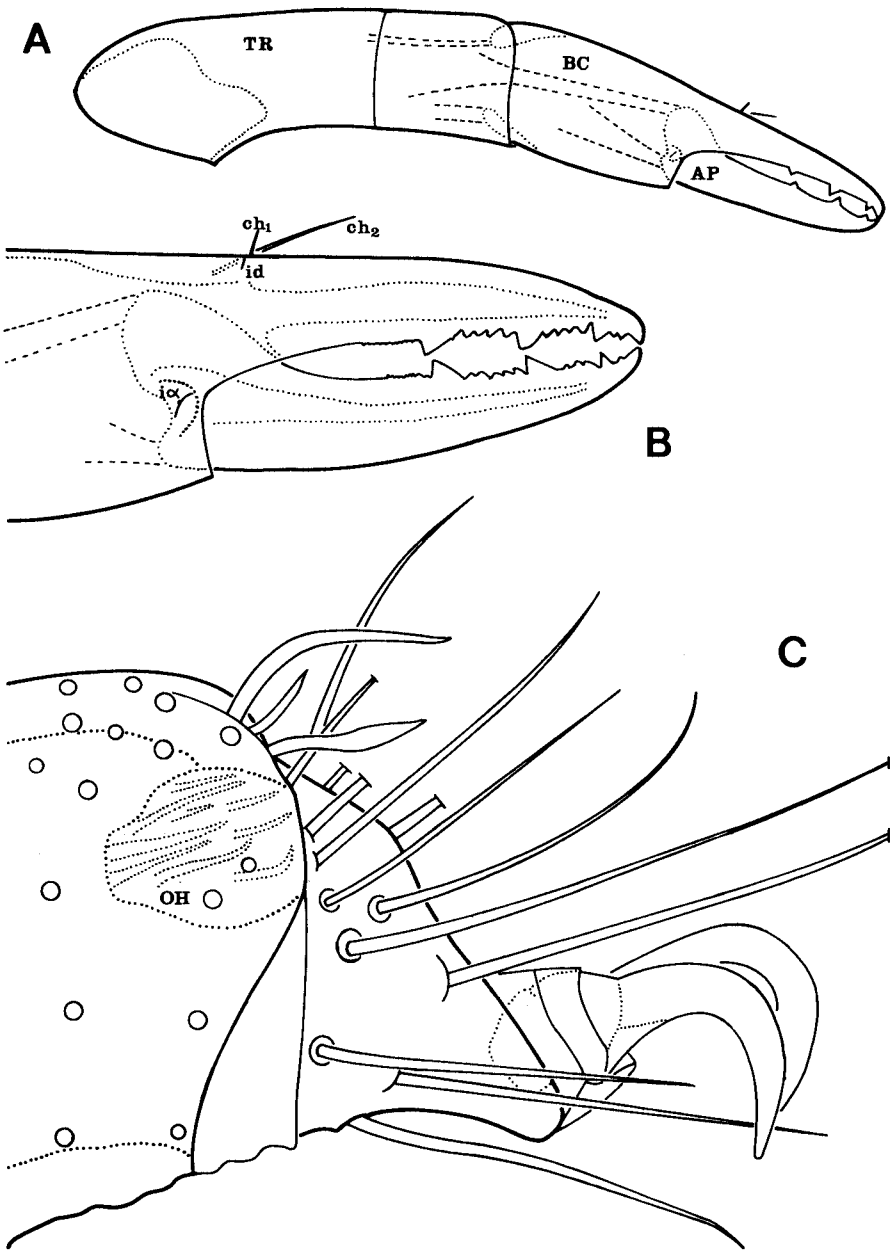

Fig. 9. *Australothyrus ocellatus* nov. spec., adult female; A, B, lateral (antiaxial) view of right chelicera; A, trochanter, body of chelicera and apotele; B, chela; C, lateral (posterior) view of terminal part of right leg I; A, × 75; B, × 176; C, × 736.

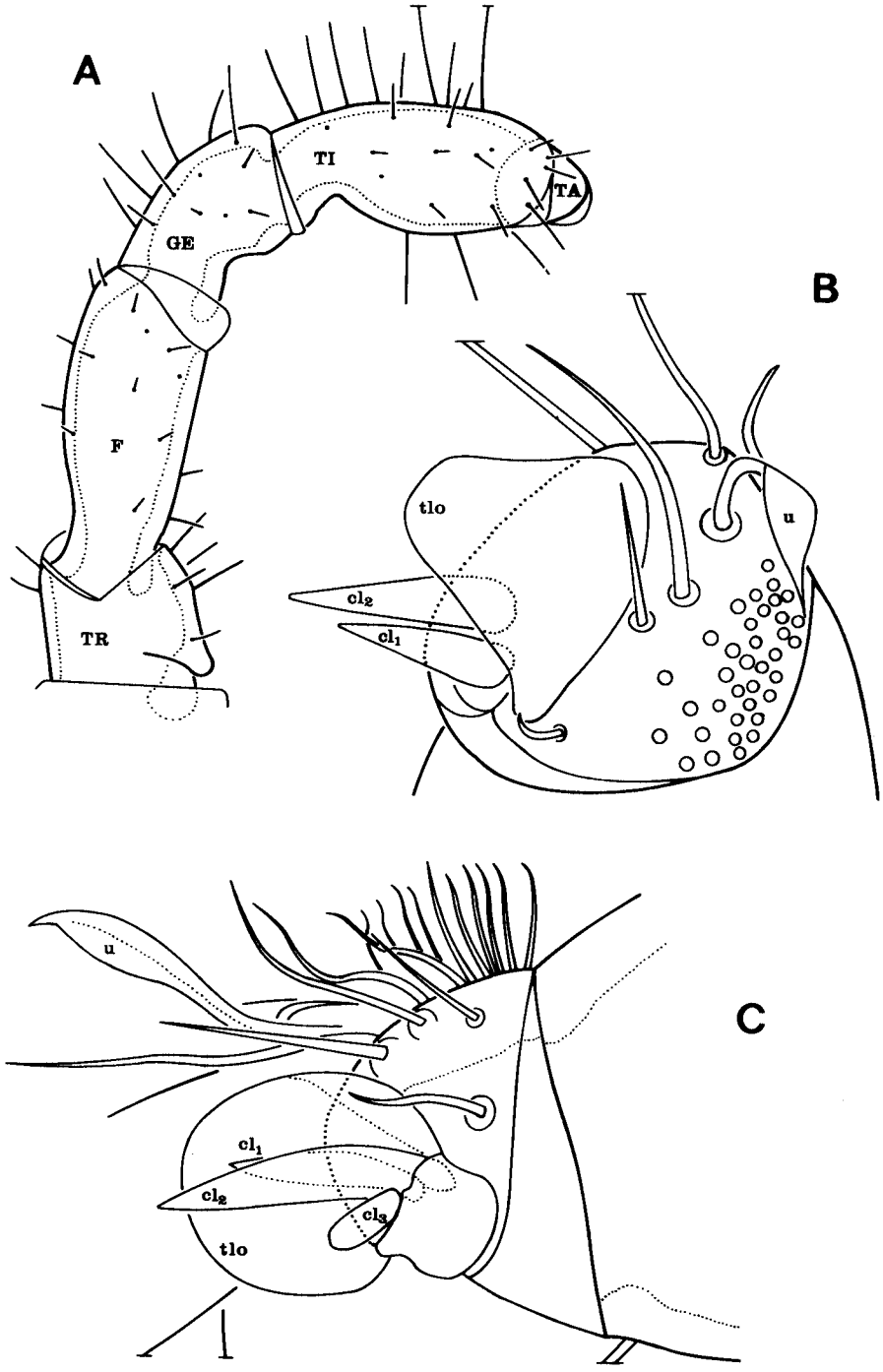

Fig. 10. *Australothyrus ocellatus* nov. spec., right palp of adult female; A, lateral (antiaxial) view; B, C, tarsus and apotele; B, dorsal view; C, lateral (paraxial) view; A, × 176; B, C, × 736.

and there is no paraxial brush (a group or comb of stiff setae) on the tibia. The relatively small tarsus presents, among others, a dorsal area of hollow setae, and a large curved dorsodistal sensory seta with broad, lanceolate terminal part. The paraxial part of the tarsus presents a membraneous lobe. The apotelic claw (with paraxial position) is tripartite: the median and the more antiaxial part are normally developed, but the more paraxial part is small, rounded and membraneous.

Legs (figs. 11–15). – Leg IV is slightly longer than the body, leg I about as long, and legs II and III slightly shorter. There is no sexual dimorphism in shape and chaetotaxy of the legs. All legs consist of coxa, trochanter, basi- and telofemur (separated by a basifemoral ring), genu, tibia, tarsus and apotele. In legs II-IV, the tarsus is subdivided, by a basitarsal ring, into basi- and telotarsus. Leg I is subdivided, as in other Allothyridae, into a bathrotarsus and a very small apicotarsus. Haller's organ (fig. 9C), situated in the dorsoterminal part of the bathrotarsus, contains a number of sensory phaneres. The area dorsally of it presents also several sensory phaneres (among which one with a broad, lanceolate terminal part). All segments present many setae (particularly numerous in the tarsus) and pores (orifices of tegumentary glands). The ambulacrum presents a bidactyl claw and, in legs II-IV, a pulvillus and a pretarsus with one pair of laterodorsal setae.

Relationships. – The relationships of the family Allothyridae are discussed in my study of *Allothyrus constrictus* (Domrow) (Van der Hammen, 1968: 268–269). *Australothyrus ocellatus* distinctly belongs to the family Allothyridae because of: the tuberculate tegument; the presence of a peridium; the great number of infracapitular setae; the simple cone-shaped corniculus; the long, tapering labrum; the tapering lateral lips; the presence of associated apophyses on infracapitulum and palpal trochanter; the presence of two cheliceral setae; the absence of fringed setae on the palpal genu, and the absence of a brush (a group or comb of stiff setae) on the palpal tibia; the subdivision of tarsus I into bathro- and apicotarsus, and the dorsodistal position, in the bathrotarsus, of Haller's organ.

Australothyrus ocellatus is related to *Allothyrus australasiae* (Womersley) because of the absence of sternapophyses, and because of the shape of the female genital area; Womersley's drawing of the terminal part of the palp (Womersley, 1935: pl. 8 fig. 4) suggests, moreover, the presence of a membraneous lobe on the palpal tarsus. *Australothyrus ocellatus* differs from *Allothyrus australasiae* by the presence of eyes, the smaller size, the absence of sexual dimorphism in the legs, and the shape of the apotelic claw of the palp (one of the parts is small and membraneous). *Australothyrus ocellatus* differs from *Al-*

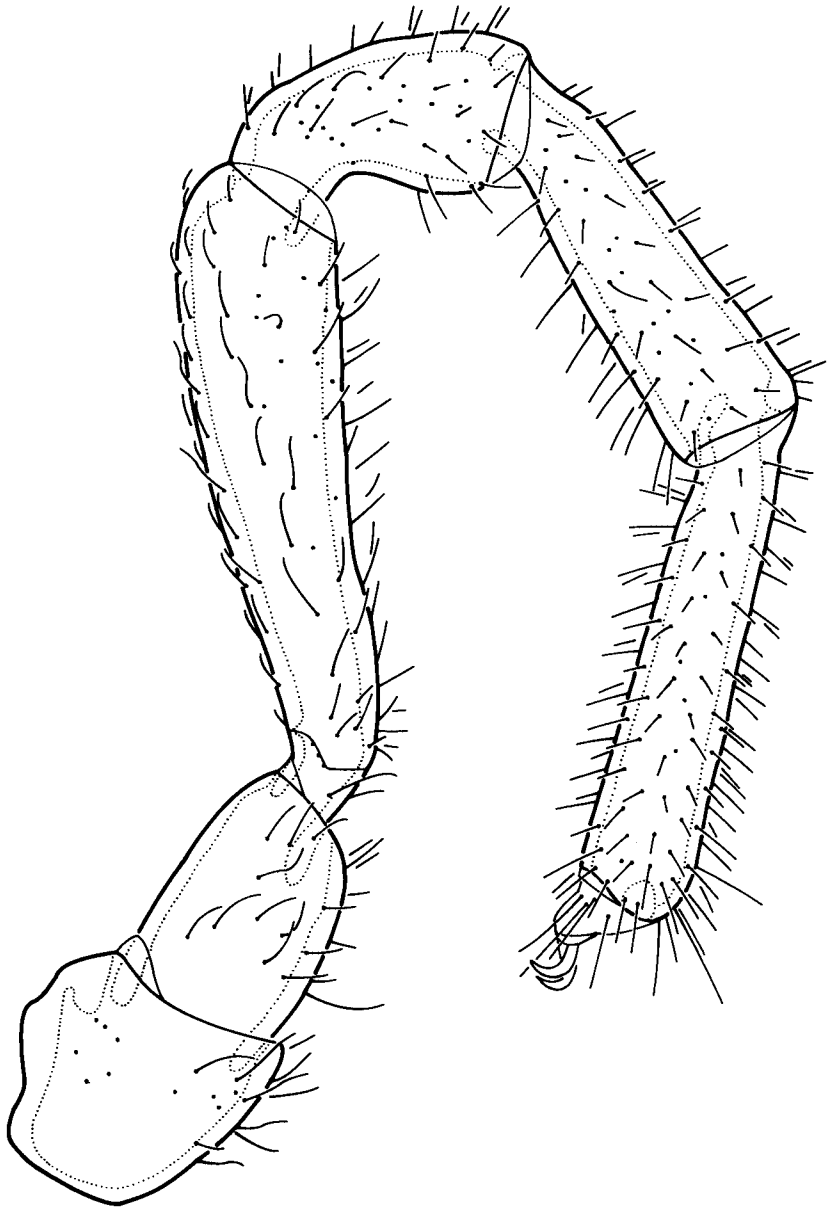

Fig. 11. *Australothyrus ocellatus* nov. spec., lateral (posterior) view of right leg 1 of adult female (part of the terminal setae omitted); × 141.

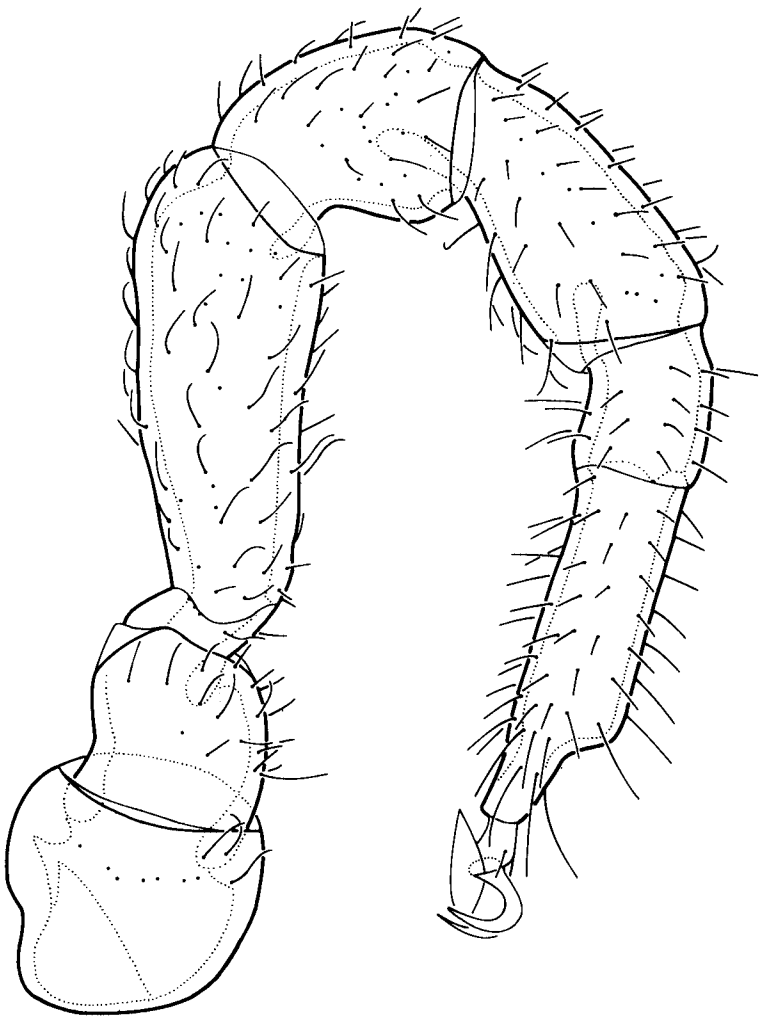

Fig. 12. *Australothyrus ocellatus* nov. spec., lateral (posterior) view of right leg II of adult female; × 141.

lothyrus constrictus (Domrow) by the larger size, the presence of eyes, the spiniform idiosomatic setae, the shape of the female genital area, the absence of sternapophyses, the shape of the apotelic claw of the palp (quadripartite in *Allothyrus constrictus*), and the absence of sexual dimorphism in the legs.

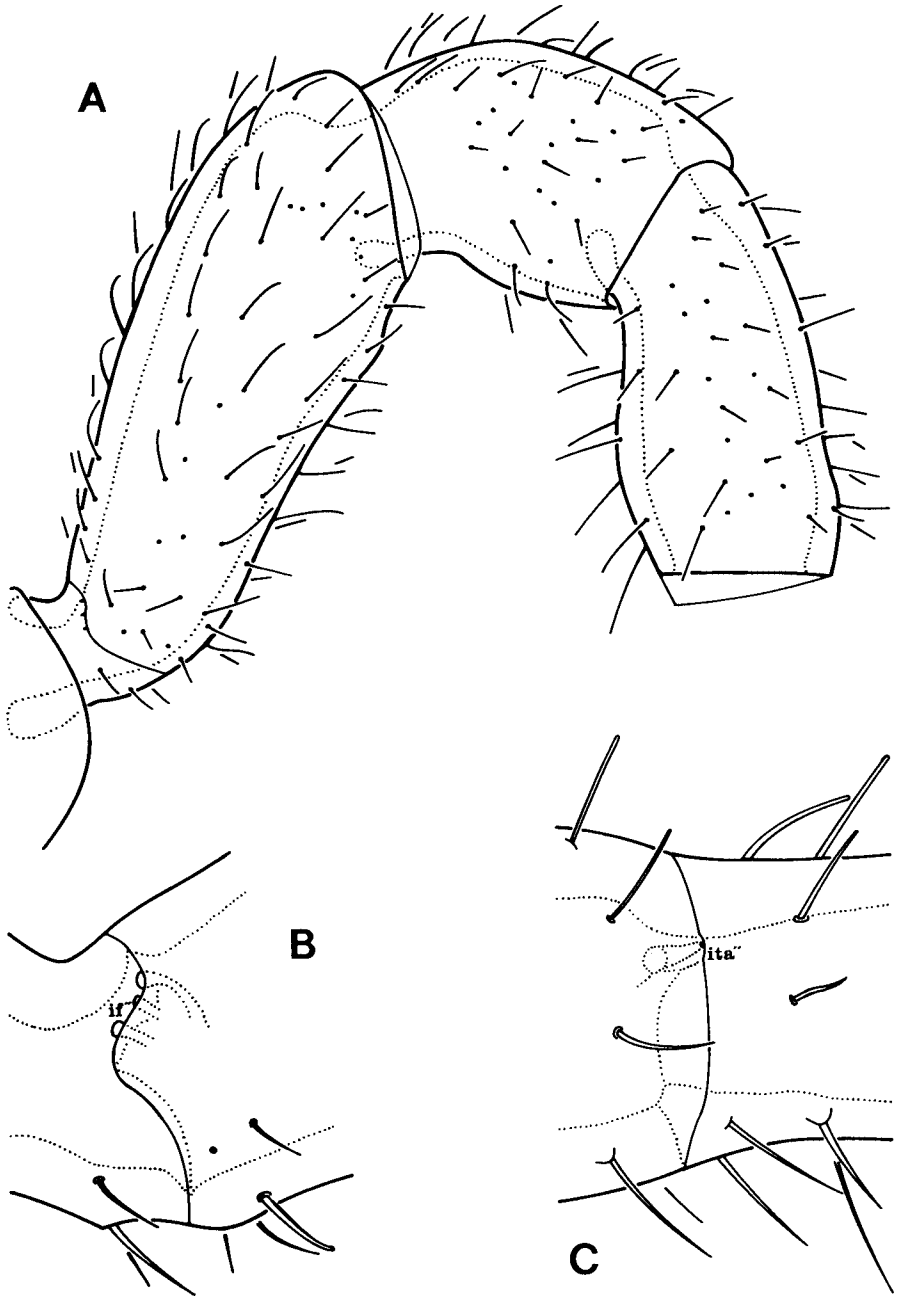

Fig. 13. *Australothyrus ocellatus* nov. spec.; A, lateral (posterior) view of femur, genu and tibia of right leg II of adult male; B, C, lateral (posterior) view of details of right leg III of adult female; B, basifemoral ring; C, basitarsal ring; A, × 176; B, C, × 368.

Fig. 14. *Australothyrus ocellatus* nov. spec.; lateral (posterior) view of right leg III of adult female; × 141.

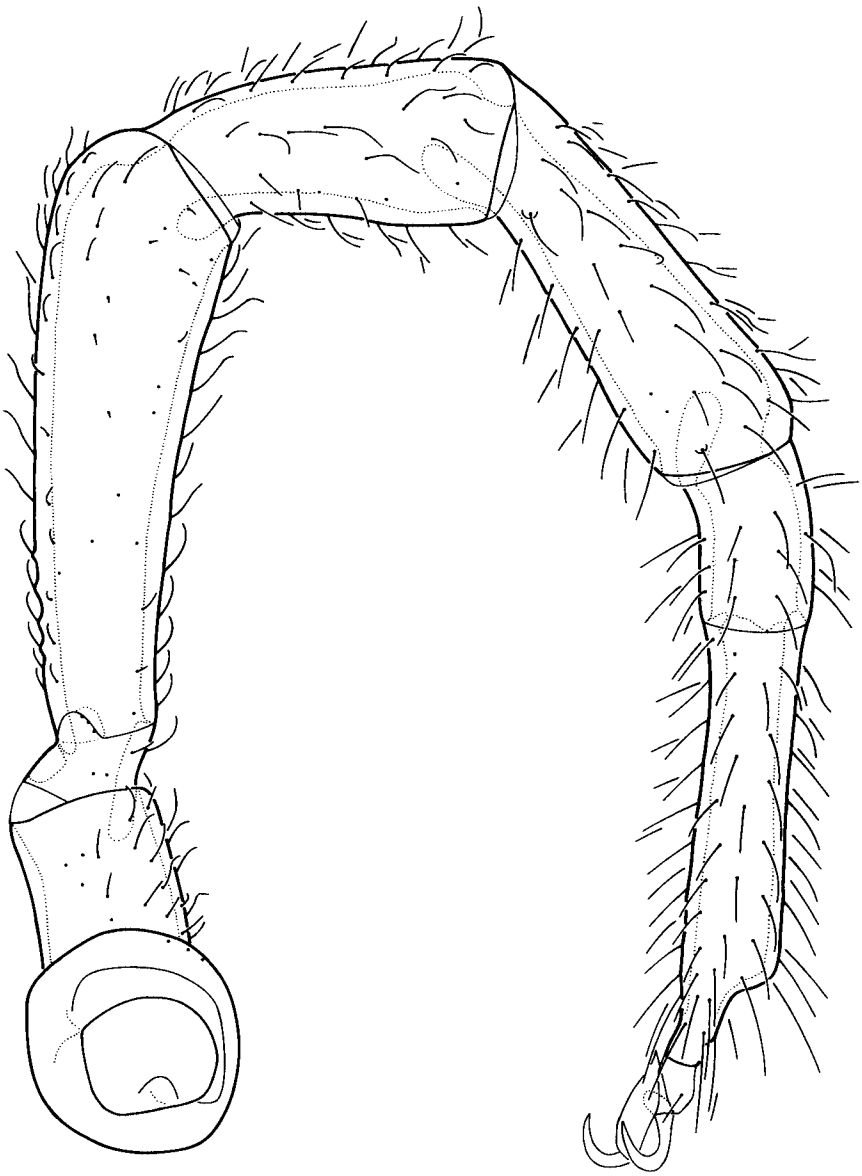

Fig. 15. *Australothyrus ocellatus* nov. spec.; lateral (posterior) view of right leg IV of adult female; × 118.

III. On two new species of Holothyridae from New Guinea

Among the unidentified Arachnid collections of the Rijksmuseum van Natuurlijke Historie, Leiden, I discovered two undescribed species of Holothyridae from the Wissel lakes area, former Netherlands New Guinea. They are described in the present section. Both species are classified with the genus *Hammenius*, but are representatives of two different subgenera, one of which is new.

Leiothyrus nov. subgen.

Relatively small, reddish brown Holothyridae of the genus *Hammenius*, with very glossy and convex idiosoma. Infracapitulum holotrichous. Chelicera with one dorsal seta. Palpal tibia with paraxial comb of stiff setae; palpal genu with one paraxial fringed seta; palpal trochanter with apophysis associated with an apophysis of the coxal region. All legs longer than the body; leg I of the male with long pulvillus, legs II-IV with ventral spines and spinules. Male epiandrium shallow. Type-species: *Hammenius* (*Leiothyrus*) *holthuisi* nov. spec.

The present new subgenus is related to the subgenus *Thonius* because of some of the characters of palp and legs mentioned above (by which they differ from *Holothyrus*). It is different from *Thonius* by the reddish brown colour, the smaller measurements and the presence of apophyses of the coxal region and the trochanter of the palp; tibiae II-III lack, moreover, the large ventrodistal spine present in the males of *Thonius*.

Holothyrus nitidissimus Thorell (synonym: *Holothyrus scutifer* Thorell, which represents the female of *nitidissimus*) probably also belongs to the subgenus *Leiothyrus*; the type-material of this species was collected by D'Albertis near the Fly River in the southern part of New Guinea. D'Albertis ascended the Fly River as far as the foothills of the Central Mountain Range. It is possible that his Holothyrids were collected at that point (cf. D'Albertis, 1880). It is interesting that *Thonius* (*Leiothyrus*) *holthuisi* was collected south of the watershed in the Central Mountain Range. According to Thorell's description (cf. Thorell, 1882: 30–32, pl. 4 figs. 18–19), his species is also small (3–3.25 mm), reddish brown and very glossy, although the legs are much shorter; the coxal region of the palp is described as slightly dilated. *Holothyrus expolitissimus* Berlese (from New Caledonia) could be another representative of the new subgenus.

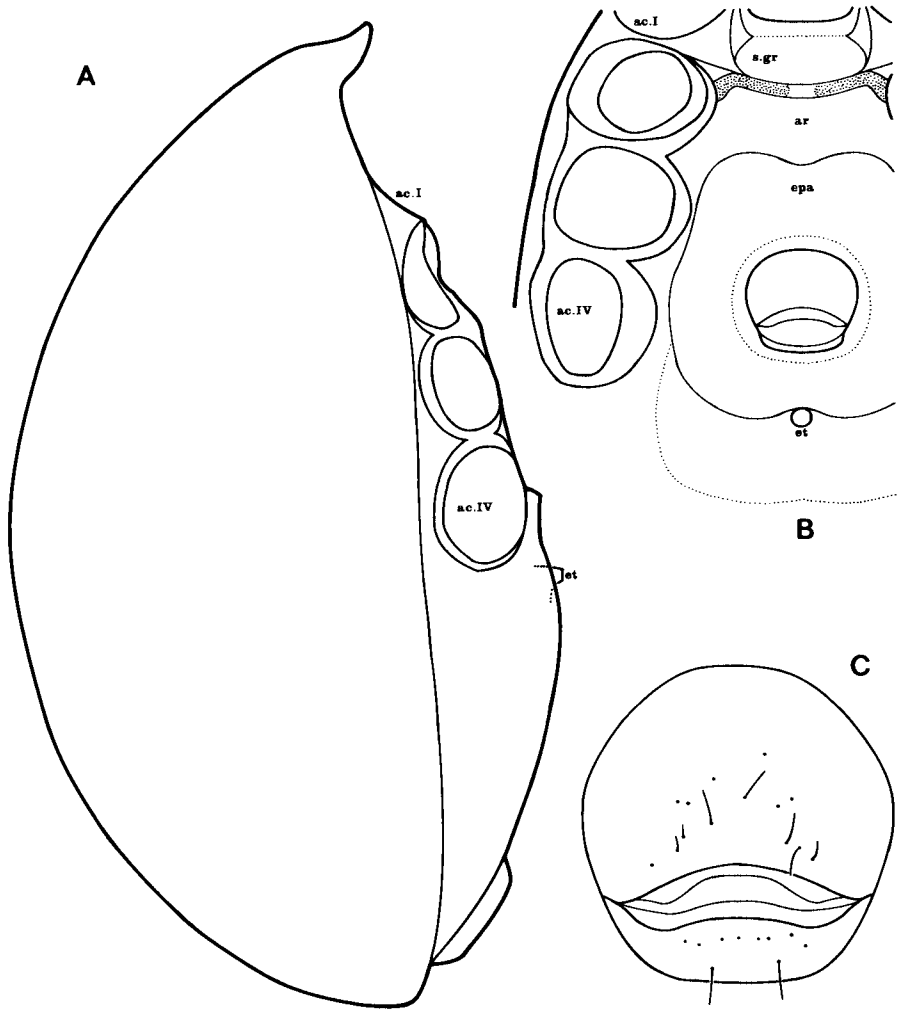

Fig. 16. *Hammenius* (*Leiothyrus*) *holthuisi* nov. spec., adult male; A, lateral view of idiosoma; B, ventral view of sternal and genital region (epiandrium); C, genital opening; A, B, × 37; C, × 107.

Hammenius (Leiothyrus) holthuisi nov. spec.
(figs. 16–19)[1]

Material. – Hills along lake Paniai, near the mouth of the river Dimija (altitude about 1750 m), Wissel lakes area, former Netherlands New Guinea, 5

[1] The species is dedicated to my colleague Dr. L.B. Holthuis, who collected the type-material of this new species.

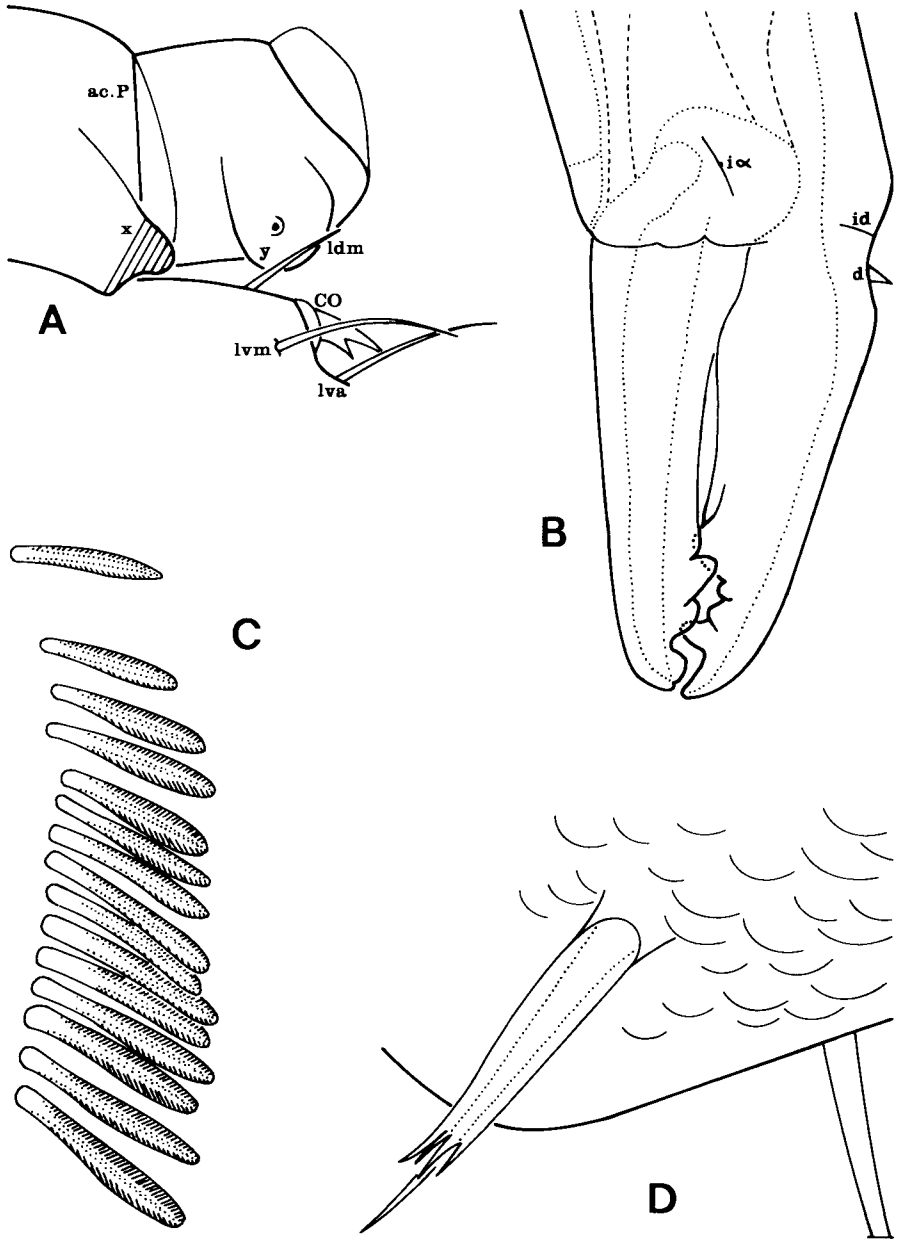

Fig. 17. *Hammenius* (*Leiothyrus*) *holthuisi* nov. spec., adult male; A, lateroventral view of part of gnathosoma with coxal region and trochanter of palp, corniculus and three infracapitular setae; B, lateral (antiaxial) view of terminal part of right chelicera; C, paraxial comb of stiff setae of right palpal tibia; D, lateral (paraxial) view of terminal part of right palpal genu with fringed seta; A, × 176; B, C, × 366; D, × 687.

January 1955, from litter on steep slope, leg. Dr. L.B. Holthuis. – 1 ♂ (holotype), 1 small nymph.

Measurements. – The length of the idiosoma of the adult male is 3.5 mm, the breadth 2.3 mm, the height 1.9 mm. All legs are longer than the idiosoma; the length of legs I and IV of the adult male is 6.0 mm, the length of legs II and III 4.5 mm.

Habitus and colour. – Small reddish brown Holothyrid with very glossy and convex idiosoma and very long legs. The ventral shield presents scattered dots and setae.

Tegument. – The reddish brown colour of the species is caused by the colour of the cuticle. In the lateral and posterior parts of the dorsal region (and also in the ventral region) scattered subcuticular grains of darker pigment are present.

Dorsal shield. – Muscle insertions are not indicated by distinct sigilla but, in the lateral and posterior regions, by small areas devoid of subcuticular pigment grains. The distribution of these areas is more or less similar to the sigillotaxy of *Australothyrus*.

Ventral region. – The ventral shield, which includes the sternal and the genital regions (cf. fig. 16) is very convex. The transverse sternal groove and the epiandrium are shallow. The sternal groove is bordered posteriorly by a ridge. The shape of the epiandrium is represented in fig. 16B; the posterior border is not very distinct, but there is a strong epiandrial tooth of which the lateral aspect is represented in fig. 16A. The male genital opening presents the usual two valves (fig. 16C); it is about as wide as long.

Gnathosoma. – The infracapitulum is holotrichous, as in other Holothyridae: it presents a pair of corniculi and seven pairs of infracapitular setae (*va, vm, vp, lva, lvm, lvp, ldm*). The coxal region of the palp presents a distinct apophysis (fig. 17A), associated with an apophysis of the palpal trochanter.

Chelicera. – The chelicera presents one dorsal seta (as in other Holothyridae) and the usual two lyrifissures (*id* and *iα*). The chela presents teeth of unequal shape and size, in the distal part of the jaws (fig. 17B).

Palp. – There is a paraxial comb of fifteen stiff setae on the tibia (fig. 17C) and a single paraxial fringed seta in the distal part of the genu (fig. 17D). As mentioned above, the palpal trochanter presents an apophysis associated with an apophysis in the coxal region of the palp (fig. 17A).

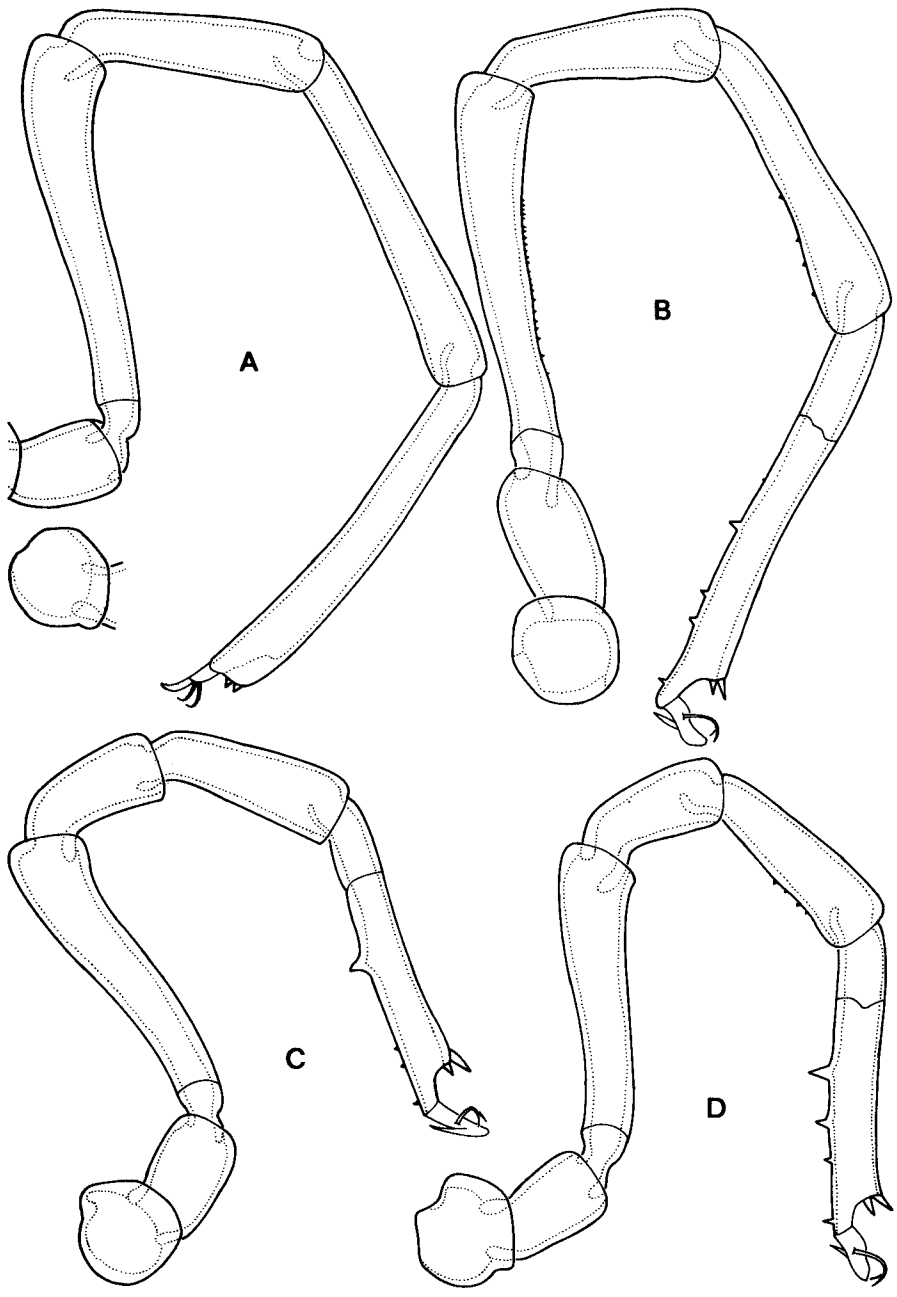

Fig. 18. *Hammenius* (*Leiothyrus*) *holthuisi* nov. spec., adult male; lateral (posterior) view of right legs I–IV; A, leg I (coxa represented separately); B, leg IV; C, leg II; D, leg III; A–D, × 37.

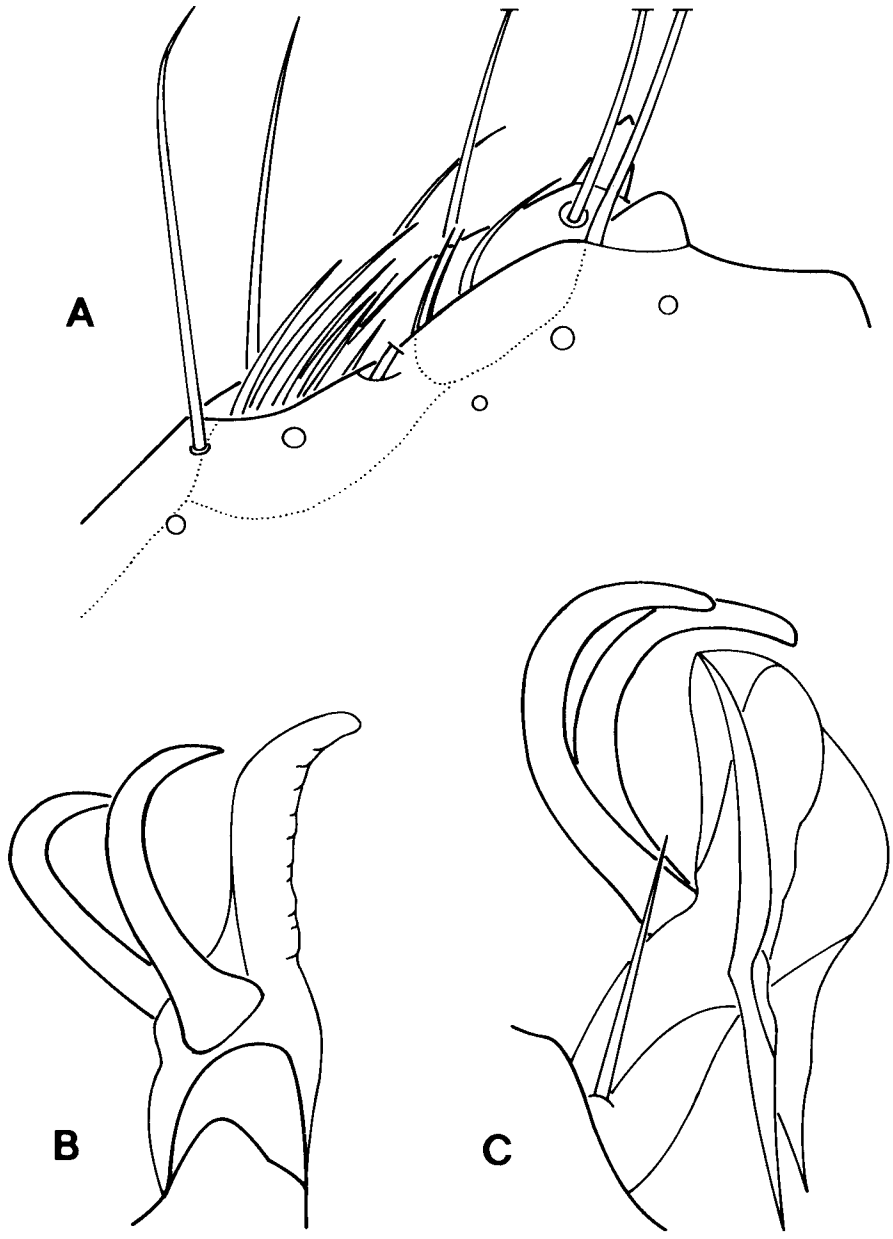

Fig. 19. *Hammenius* (*Leiothyrus*) *holthuisi* nov. spec., adult male; A, Haller's organ of right leg I, lateral (posterior) view; B, ambulacrum of right leg I, lateral (posterior) view; C, ambulacrum of right leg II, lateral (posterior) view; A–C, × 366.

Legs. – All legs are longer than the idiosoma. Legs I and IV are of equal length, and much longer than legs II and III (which are also of equal length). Leg I (fig. 18A) is characterized by the absence of spines and spinules, the absence of a basitarsal ring (as in other Holothyrida), the presence of a long pulvillus (fig. 19B; it is a character of males of the family Holothyridae), and the usual presence of Haller's organ (fig. 19A). Leg II (fig. 18C) presents ventrally one large tarsal spine and three tarsal spinules. Leg III (fig. 18D) presents ventral tibial spinules and three or four ventral tarsal spines. Leg IV (fig. 18B) presents ventral femoral and tibial spinules and four ventral tibial spines (in the right leg moreover one spinule). The pulvillus of legs II-IV (fig. 19C) presents the usual two posteroventral branches.

Hammenius (Thonius) montanus nov. spec.
(figs. 20–22)

Material. – Surroundings of lake Paniai (altitude about 1750 m), Wissel lakes area, former Netherlands New Guinea, September 1939, leg. The Royal Netherlands Geographical Society's Expedition. – 1 ♂ (holotype), 4 ♀ (female allotype and paratypes).

Measurements. – Length of the idiosoma of the adult male, and of two of the adult females, 5.3 mm, breadth 4.0 mm. All legs longer than the idiosoma. The lengths of the legs in the male are the following: leg I 10.7 mm, legs II and III 7.5 mm, leg IV 10.6 mm. The lengths of the legs in two females are the following: leg I 10.4 and 10.2 mm, leg II 7.6 mm, leg III 7.5 and 7.8 mm, leg IV 10.8 and 8.6 mm (leg IV of the second female, which is abnormally short on both sides, could be a case of regeneration).

Habitus and colour. – Large, dark brown Holothyrid with very long legs. Dorsal shield moderately convex; tegument moderately glossy.

Tegument. – The microsculpture of the dorsal shield is indistinctly vermiculate. Scattered dots and small setae are particularly discernable in the genital region. The brown colour of the cuticle is obscured by the presence of dark subcuticular pigment grains.

Dorsal shield. – Muscle insertions are indicated by lighter areas in the dark-coloured shield. The pattern of insertion is more or less similar to that of *Australothyrus*.

Ventral region. – The transverse sternal groove is rather shallow. The area posteriorly of the sternal groove presents a posteromedian convexity which is particularly well-developed in the male (less distinct in the female). The male

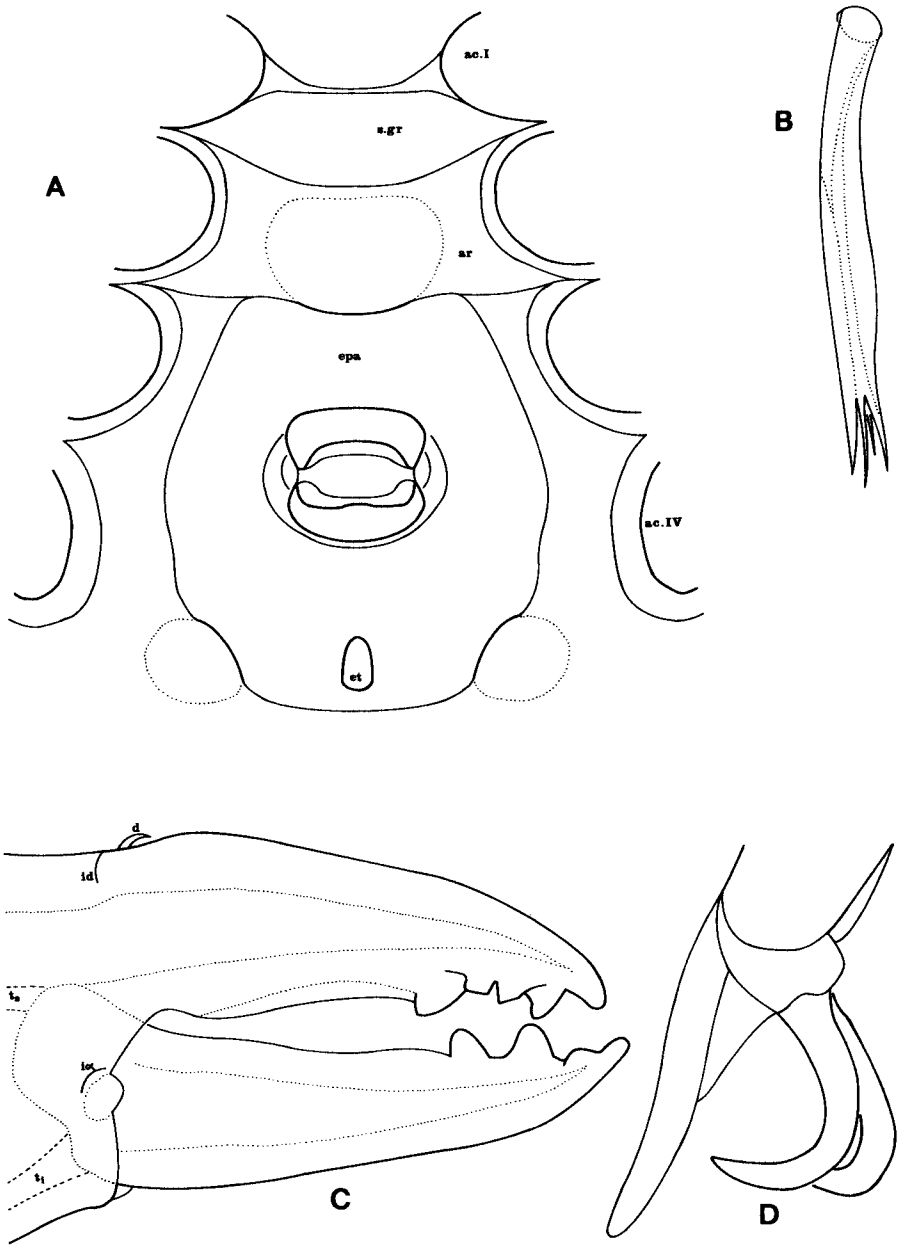

Fig. 20. *Hammenius* (*Thonius*) *montanus* nov. spec., adult male; A, ventral view of sternal and genital region; B, paraxial fringed seta of palpal genu; C, lateral (antiaxial) view of chela of right chelicera; D, lateral (posterior) view of ambulacrum of right leg I; A, × 37; B, × 455; C, D, × 246.

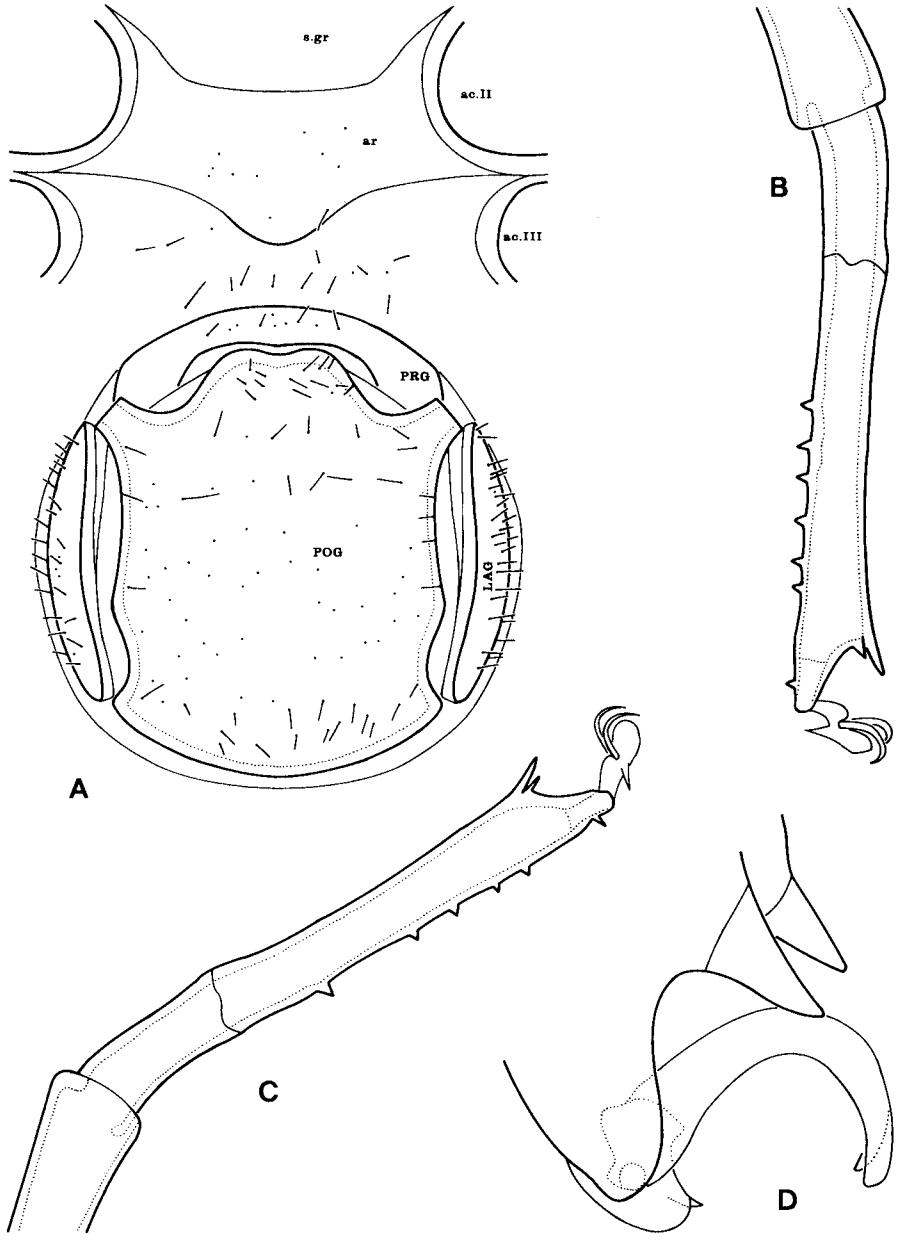

Fig. 21. *Hammenius* (*Thonius*) *montanus* nov. spec., adult female; A, ventral view of part of sternal and genital region; B, lateral (posterior) view of distal part of tibia, tarsus and ambulacrum of right leg II; C, lateral (posterior) view of distal part of tibia, tarsus and ambulacrum of right leg III; D, lateral (posterior) view of ambulacrum of right leg I; A–C, × 246.

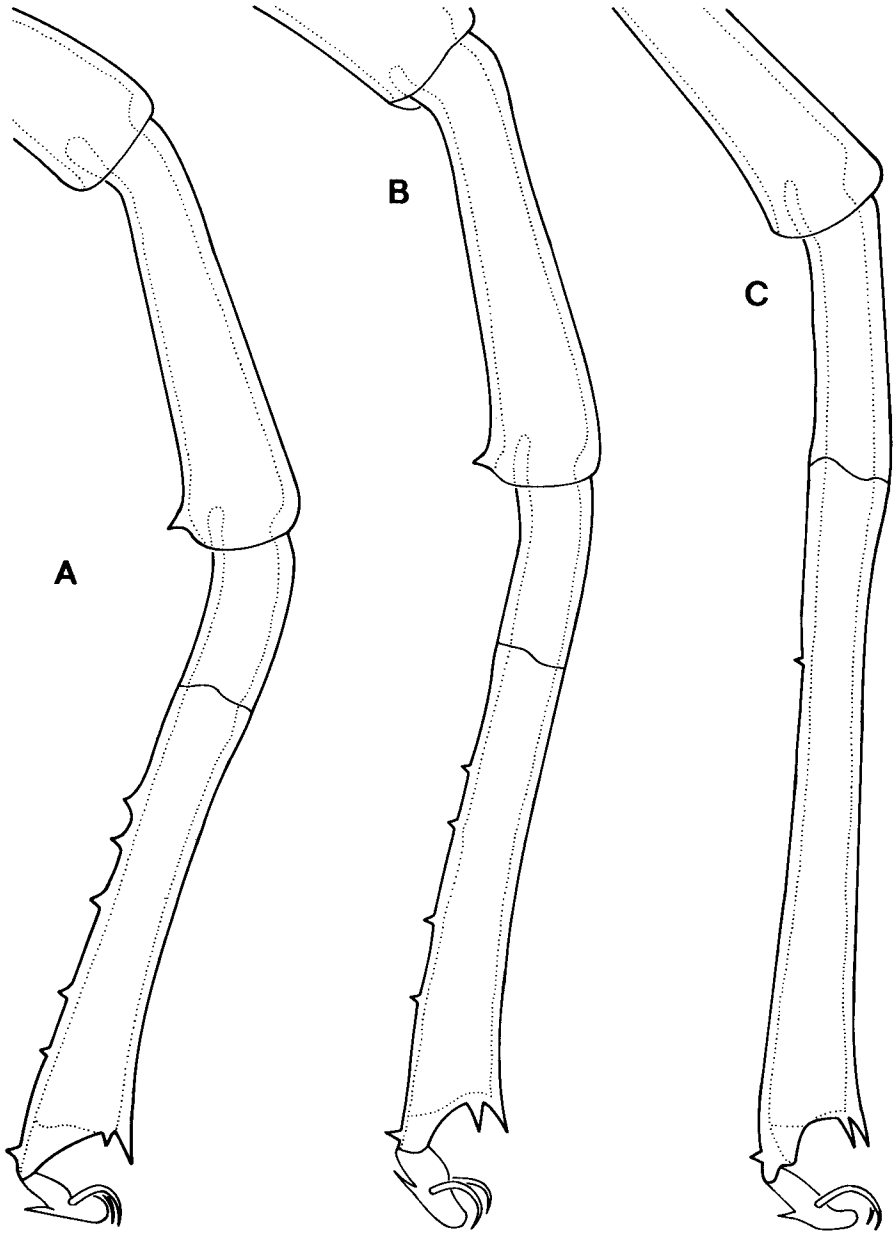

Fig. 22. *Hammenius* (*Thonius*) *montanus* nov. spec., adult male, lateral (posterior) view of distal parts of legs II–IV (setae omitted); A, distal part of genu, tibia, tarsus and ambulacrum of leg II; B, distal part of genu, tibia, tarsus and ambulacrum of leg III; C, distal part of tibia, tarsus and ambulacrum of leg IV; A–C, × 44.

epiandrium is bordered, in the anterior part, by the above-mentioned convexity; a pair of convexities is found near the posterolateral border. The epiandrial tooth is long, but rather low (fig. 20A). The shape of the male genital opening is broadly elliptical; the genital valves are closed by a single pair of long tendons. The female genital region is represented in fig. 21A; it is covered by the usual four shields (a small pregenital, a pair of narrow laterogenitals and large postgenital, of which the anterior part has a characteristic shape).

Gnathosoma. – The infracapitulum is holotrichous, as in other Holothyridae.

Chelicera. – The chelicera presents the usual characters of the family Holothyridae: a single dorsal seta, two lyrifissures (*id* and *iα*), and a chela with teeth of unequal shape and size in the distal part of the jaws (fig. 20C).

Palp. – The palp presents a paraxial tibial comb of numerous stiff setae (21–22 in the male specimen). The palpal genu presents a single paraxial fringed seta (fig. 20B).

Legs. – The ratio length of the legs: length of the idiosoma is about 2 in the case of legs I and IV, and about 1.4 in the case of legs II and III. The distal parts of legs II-IV are represented in fig. 22. The measurements (in mm) of respectively coxa, trochanter, femur, genu, tibia, tarsus, and ambulacrum, in legs I-IV of the single male and one of the females (mentioned between brackets) are the following. Leg I: 0.319 (0.382), 0.645 (0.655), 2.627 (2.555), 1.645 (1.527), 2.609 (2.527), 2.727 (2.591), 0.164 (0.136). Leg II: 0.382 (0.418), 0.527 (0.555), 1.973 (2.018), 0.900 (0.900), 1.282 (1.282), 2.091 (2.082), 0.327 (0.309). Leg III: 0.500 (0.509), 0.436 (0.473), 1.927 (1.891), 0.955 (0.927), 1.364 (1.336), 2.027 (2.091), 0.273 (0.273). Leg IV: 0.545 (0.418), 0.591 (0.645), 2.636 (2.873), 1.364 (1.364), 2.182 (2.136), 2.936 (3.064), 0.336 (0.309). Leg I does not present ventral spines. Legs II and III of the male (fig. 22A–B) present one large ventrodistal tibial spine (absent in the female) and 4–6 ventral telotarsal spines (also present in the female; cf. fig. 22B–C). Leg I of the male presents a long pulvillus (fig. 20D); it is absent in the female (fig. 21D). In legs II–IV, the pulvillus presents the usual two posteroventral branches.

Affinities and diagnostic characters. – The species is related to *Hammenius* (*Thonius*) *longipes* (Thorell) and *Hammenius* (*Thonius*) *grandjeani* (Van der Hammen), from which it is particularly different by the measurements (length 4.3 mm in *grandjeani*, 6.5 mm in *longipes*), the number of setae of the tibial comb of the palp (14–15 in *grandjeani*; the number of setae is, however, not known for *longipes*), and the shape of the male genital area (no epiandrial tooth in *grandjeani*, a rounded tooth in *longipes*; no striking marginal convexities in both species).

IV. Supplementary description of Holothyrus coccinella Gervais

Material of *Holothyrus coccinella* Gervais, received from the late Dr. J. Vinson (The Mauritius Institute, Port Louis, Mauritius) and from Prof. Dr. R. Legendre (Laboratoire de Zoologie, Montpellier, France), enabled me to study details not mentioned in my previous study of the species (Van der Hammen, 1965), among which secondary sexual characters, and characters of the postembryonic development. The results of this study are summarized in the following description.

Holothyrus coccinella Gervais, 1842
(figs. 23–25)

Material. – Mauritus, Mt. Pouce, 7 December 1965, leg. Dr. J. Vinson. – 1 ♂, 3 ♀, 7 immature specimens. Mauritius, mixed sample from two localities (forêt du Pouce, forêt Machabée), January 1961, leg. Prof. Dr. R. Legendre, M. Mamet & Dr. J. Vinson. – 8 ♂, 9 ♀, 34 immature specimens.

Measurements. – The lengths of my adult specimens (males and females) vary from 4.4 to 5.5 mm. The lengths of the legs of an adult male of 5.0 mm are the following: leg I 8.0 mm, leg II 6.0 mm, leg III 6.3 mm, leg IV 8.0 mm.

Male genital region. – The epiandrium (fig. 23A) is shallow (in contradistinction to the sternal groove, which is deep); it is more or less pentagonal, although the posterior border is rather indistinct. There is no epiandrial tooth. The male genital opening is wider than long. The area, which anteriorly borders the epiandrium, is slightly convex in the median part.

Gnathosoma. – The duct of the infracapitular gland is, on either side, in the coxal vault; the orifice is close to the line of attachment of the cheliceral frame to the infracapitulum. A taenidium extends, from the orifice, in anterior direction (it constitutes, more or less, the border between cervix and large lateral ridges).

Palp. – The paraxial brush of the palpal tibia consists of a group of 25–33 setae.

Legs. – As in other species of Holothyridae, leg I of the male (fig. 23B) presents a long pulvillus, whilst pulvillus I is reduced to a vestige in the female (fig. 23C). In the female of *H. coccinella*, the ungues of leg I are, moreover, much heavier than in immature and male specimens (this secondary sexual character of the female is not known from species of *Hammenius*).

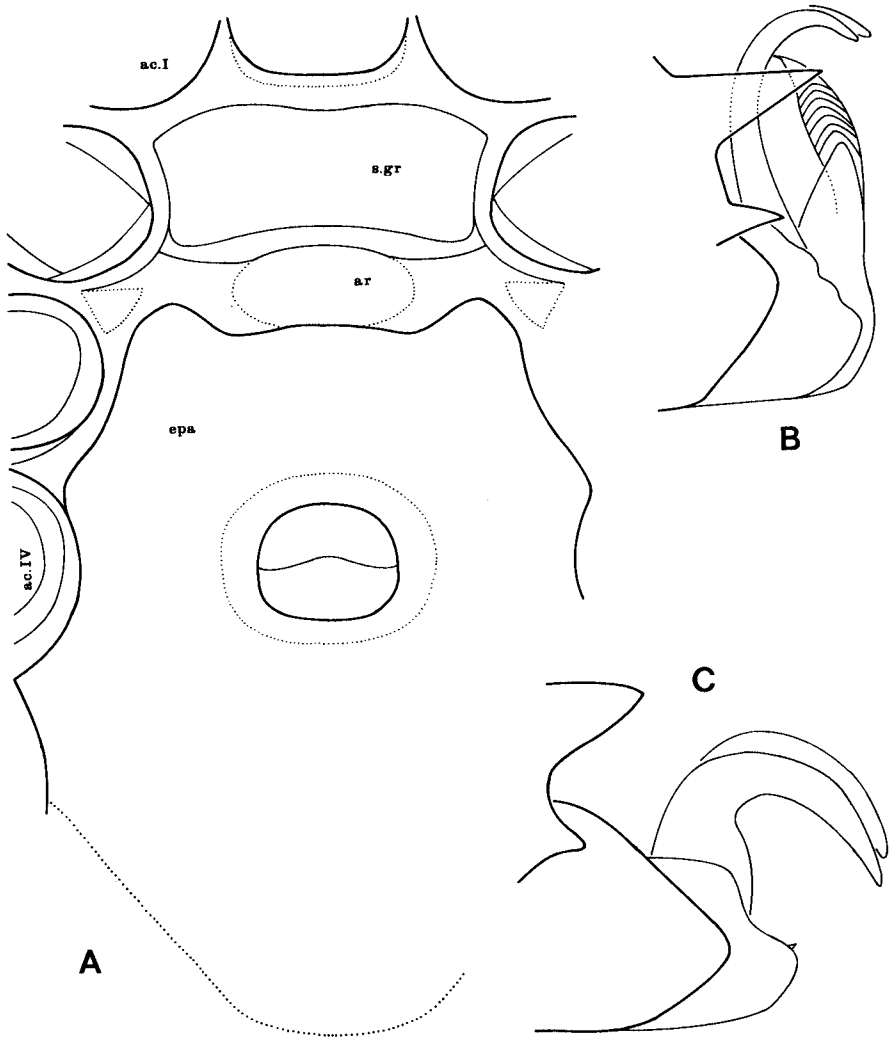

Fig. 23. *Holothyrus coccinella* Gervais; A, ventral view of sternal and genital region of adult male; B, C, lateral (posterior) view of terminal part of tarsus and ambulacrum of right leg I; B, adult male; C, adult female; A, × 44; B, C, × 295.

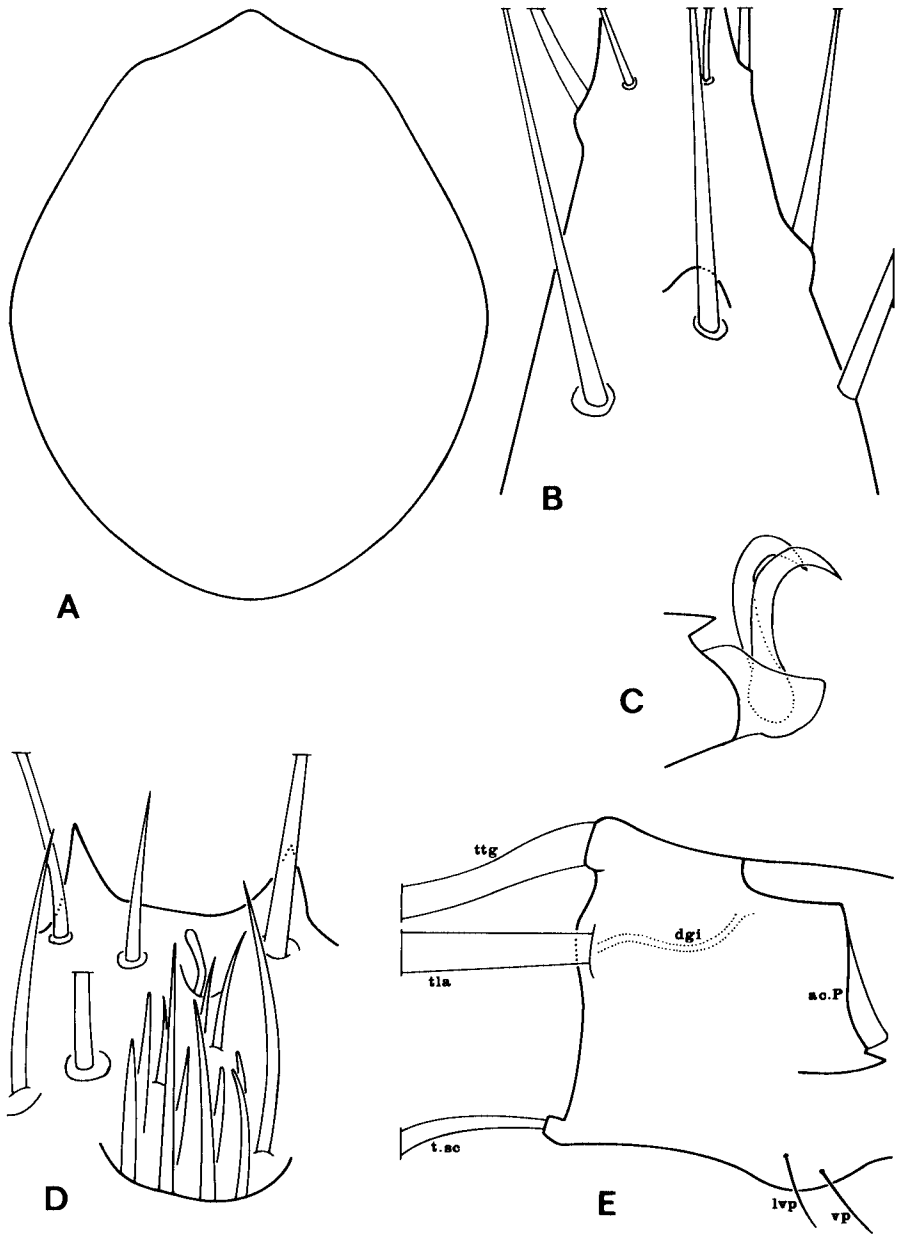

Fig. 24. *Holothyrus coccinella* Gervais, smallest known instar; A, dorsal view of idiosoma; B, dorsal view of distal part of tarsus IV; C, lateral (posterior) view of distal part of tarsus and ambulacrum of leg I; D, dorsal view of Haller's organ; E, lateral view of basal part of gnathosoma; A, × 42; B, D, × 550; C, × 295; E, × 141.

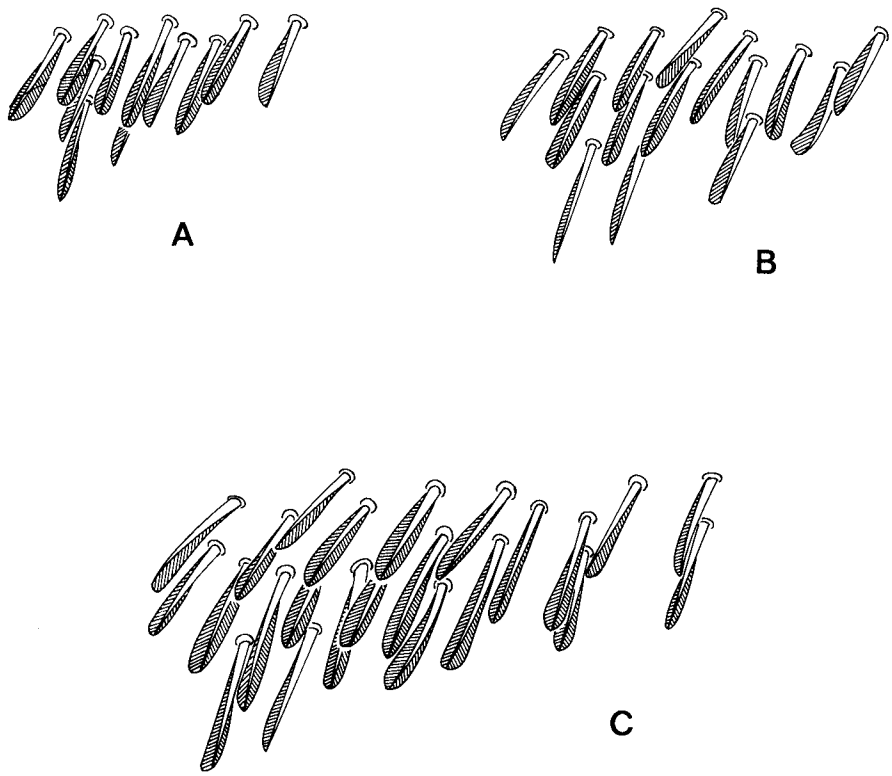

Fig. 25. *Holothyrus coccinella* Gervais, lateral (paraxial) view of brush of right palpal tibia; A, protonymph; B, deutonymph; C, tritonymph; A–C, × 295.

Postembryonic development. – The 41 immature specimens of my material belong to four groups of distinctly different size. The idiosomatic lengths of these groups range from 1.7–1.8, 2.1–2.3, 2.6–2.8 and 3.4–4.4 respectively. Three groups can be distinguished by the number of setae in the paraxial brush of the palpal tibia (fig. 25). In the first and second size class it presents 10–11 setae, in the third 15–16, and in the fourth 19–23 (in the adult, the number ranges from 25–33). I could find no morphological differences (besides size) between representatives of the first and second size class (I did, however, not make a detailed comparative study of leg chaetotaxy). The smallest instar could represent an octopod larva; the other instars certainly represent proto-, deuto- and tritonymph. The length of most of the tritonymphs ranges from 3.4–3.6 mm. The idiosoma of the smallest instar (fig. 24A) presents already the characteristic broad shape of the adult. Some characters of the gnathosoma can easily be studied in this instar: the duct of the infracapitular gland, and the presence of three pairs of gnathosomatic tendons, viz., a

pair inserted on the base of the tegulum, a lateral pair, and the tendons of the subcapitular apodeme (fig. 24E). In leg I of the smallest instar, Haller's organ is already completely developed (fig. 24D; cf. Van der Hammen, 1965: fig. 9C, D), and the ambulacrum presents a reduced pulvillus and slender ungues (fig. 24C). In leg IV of the smallest nymph, the number of dorsodistal teeth of the tarsus is reduced (fig. 24B): the lateral teeth are absent, and the median tooth is reduced to a rounded tubercle.

V. A NEW SPECIES OF THE GENUS HOLOTHYRUS FROM MAURITIUS

Among the material of *Holothyrus coccinella* collected by Prof. Dr. R. Legendre and his collaborators in Mauritius, I discovered a few specimens of a much smaller species which appears to be new. It is the second species of the genus *Holothyrus* in its present restricted sense. It is described below.

Holothyrus legendrei nov. spec.
(figs. 26–28)[1]

Material. – Mauritius, mixed sample from two localities (forêt du Pouce, forêt Machabée), January 1961, leg. Prof. Dr. R. Legendre, M. Mamet & Dr. J. Vinson. – 2 ♂, 4 ♀, 2 nymphs (probably tritonymphs). Unfortunately, the material from the two localities has not been preserved separately. The new species is apparently much less common than *Holothyrus coccinella*, and probably occurs at one of the two localities only.

Measurements. – Length of one of the males 3.0 mm, breadth 2.1 mm; length of one of the females 3.3 mm, breadth 2.3 mm; ratio length: breadth in both specimens 1.4. Lengths of the legs of the female of 3.3 mm: leg I 4.0 mm, leg II 3.1 mm, leg III 3.0 mm, leg IV 4.2 mm.

Habitus and colour. – A small, reddish brown, relatively narrow Holothyrid (fig. 26A) with rather flat idiosoma and relatively short legs. Newly hatched specimens (and nymphs) are pale brown.

Tegument. – The reddish brown colour of the species is caused by the colour of the cuticle.

Ventral region. – The epiandrium (fig. 26C) is shallow and relatively narrow; the lateral borders are more or less parallel. The posterior border is not

[1] Dedicated to Prof. Dr. R. Legendre (Laboratoire de Zoologie, Montpellier, France), who, together with his collaborators, collected the type-material of this new species.

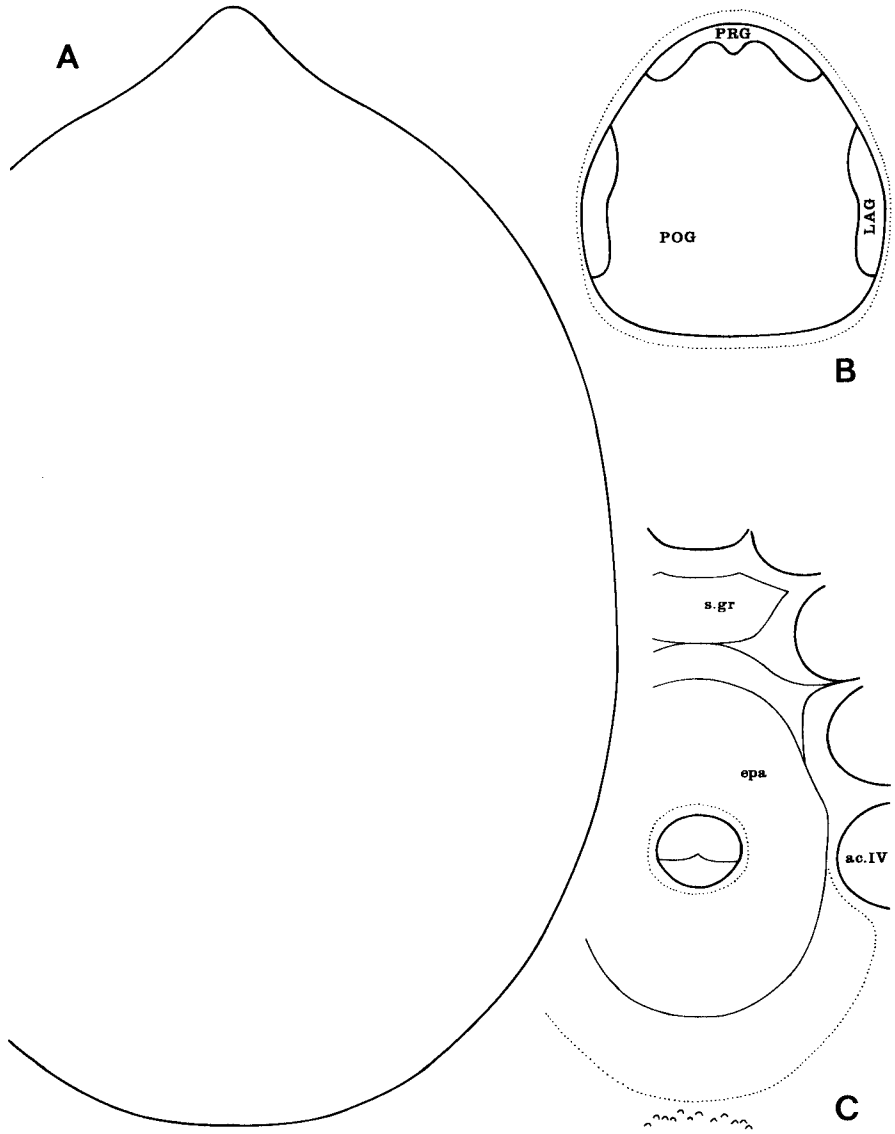

Fig. 26. *Holothyrus legendrei* nov. spec., adult; A, dorsal view of idiosoma of female; B, female genital region; C, sternal and genital region (epiandrium) of male; A–C, × 44.

very distinct, and there is no epiandrial tooth. The female genital region (fig. 26B) consists of the usual four shields; the anterior border of the postgenital shield presents a median indentation.

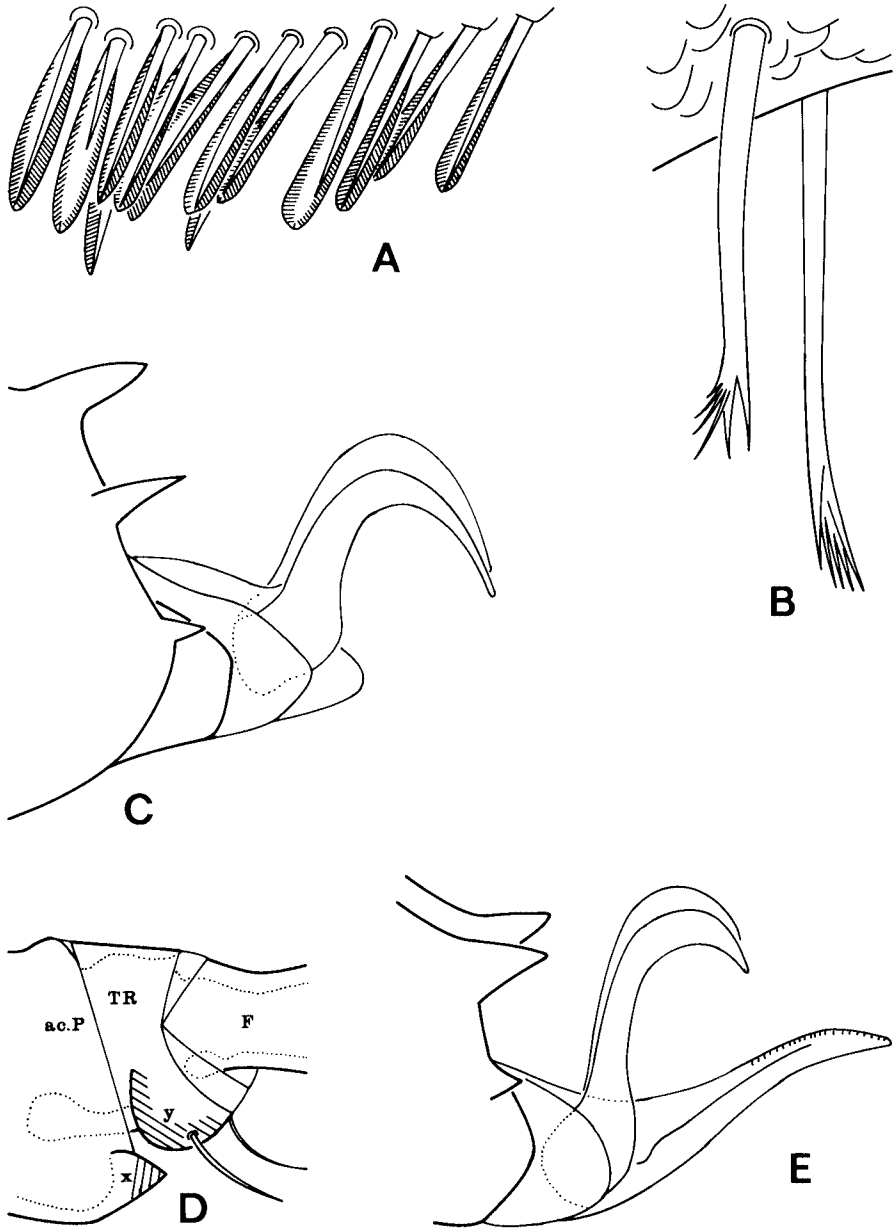

Fig. 27. *Holothyrus legendrei* nov. spec., adult; A, tibial brush of right palp of female; B, fringed setae of right palpal genu of female (paraxial view); C, lateral (posterior) view of distal part of tarsus and ambulacrum of right leg I of female; D, lateral view of acetabulum and base of right palp; E, lateral (posterior) view of distal part of tarsus and ambulacrum of right leg I of male; A, C, E, × 368: B, × 687; D, × 176.

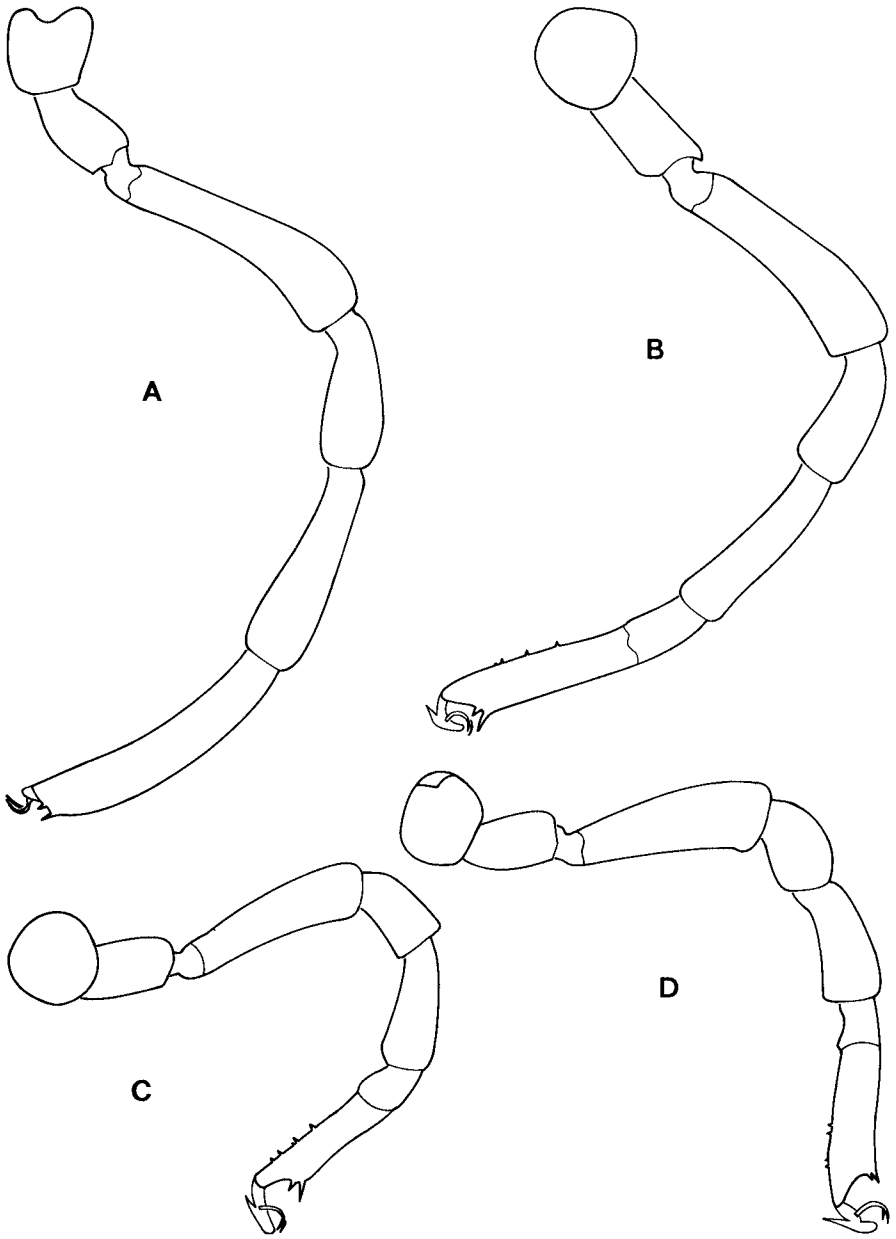

Fig. 28. *Holothyrus legendrei* nov. spec., adult female, lateral (posterior) view of right legs I–IV (setae omitted); A, leg I; B, leg IV; C, leg III; D, leg II; A–D, × 37.

Gnathosoma. – The infracapitulum is holotrichous. The coxal region of the palp presents a distinct apophysis (fig. 27D) associated with an apophysis of the palpal trochanter.

Palp. – The paraxial tibial brush (fig. 27A) consists of 12–13 setae, arranged in two rows (the ventral row consisting of two setae). The palpal genu presents the two paraxial fringed setae characteristic of the genus *Holothyrus* (fig. 27B). As mentioned above, the palpal trochanter (fig. 27D) presents an apophysis associated with an apophysis in the coxal region of the palp.

Legs. – Legs II–III are about as long as the body, legs I and IV only slightly longer. The general shape of the legs is represented in fig. 28. The tarsus of legs II–IV presents a number of small ventral teeth. The ambulacrum of leg I of the male (fig. 27E) presents a long narrow pulvillus; ambulacrum I of the female (fig. 27C) has a reduced pulvillus, whilst the ungues are broadened (although less than in the female of *Holothyrus coccinella*).

Postembryonic development. – The paraxial brush of the palpal tibia of the two nymphs presents 9–10 setae. The nymphs are only slightly smaller than the adults, and probably represent tritonymphs.

VI. The classification of the species of the family Holothyridae

The species of the family Holothyridae (now recorded from Mauritius, Rodriguez, Seychelles, Ceylon, New Guinea, New Caledonia) are all closely related, and distinctly different from species of the families Allothyridae (from Australia, New Zealand) and Neothyridae (from tropical America). They are characterized, among others, by the holotrichous infracapitulum, the radula-shaped labrum, the shape of the corniculus (with tooth), the bipartite apotelic claw of the palp, the shape and position of Hallers's organ (which reminds of that in the ticks), and the secondary sexual characters of the male ambulacrum I (which presents a long pulvillus).

The two species of the genus *Holothyrus* sensu stricto are characterized by the reddish brown colour, the presence of associated apophyses on coxal region and trochanter of palp, the presence on the palpal genu of two fringed setae, the shape of the tibial brush of the palp (a group of setae, not a single row), and the four terminal teeth of tarsus I; a secondary sexual character is constituted by the robust ungues of the female ambulacrum I. It is not impossible that *Holothyrus testudineus* Butler and the undescribed species from Ceylon belong to the same genus. All other species of Holothyridae are tenta-

tively classified with the genus *Hammenius*, characterized by the presence on the palpal genu of one fringed seta, and by the shape of the tibial brush of the palp (a single row of setae, constituting a comb). Three subgenera of this genus are now distinctly characterized: the subgenus *Hammenius* (coxal region of palp without apophysis, genu I of male with large ventral apophysis, tarsus I with four terminal teeth), the subgenus *Thonius* (coxal region of palp without apophysis, distal part of tarsus I with two teeth, tibiae II–III of the male with large ventrodistal spine), and the subgenus *Leiothyrus* (small size, very convex and very glossy idiosoma, coxal region of palp and palpal trochanter with associated apophyses, epiandrium shallow). *Holothyrus braueri* Thon, classified by Lehtinen (1981: 7) and Travé (1982) with *Thonius*, certainly represents a new subgenus (it differs from *Thonius*, among others, by the absence of the large ventrodistal spine of tibiae II–III of the male). As mentioned above, several species of Holothyridae are insufficiently described and cannot be classified here with certainty.

VII. The relationships of the order Holothyrida

On several occasions, I have discussed the relationships of Holothyrida with other groups of Anactinotrichida (Van der Hammen, 1966: 61; 1968: 268–269; 1971: 470–471; 1972: 277–278; 1983 (in press); cf. also Camicas & Morel, 1977: 412). Some of the characters mentioned in these papers are re-discussed in the present section.

It is not impossible that the four pairs of opisthosomatic respiratory organs of Opilioacarida originated from excretory glands[1] and that three of them are homologous with, respectively, the single pair of respiratory organs and the two pairs of supposed excretory organs (orifices $ogl_{1\text{-}2}$) in Holothyrida. The single pair of respiratory organs of Holothyrida is certainly homologous with the single pair found in Gamasida and Ixodina (the homology of the respiratory organs in Argasina is not certain).

The Holothyrid, Opilioacarid and Ixodid tegulum is not produced into a supracheliceral limbus. The last-mentioned limbus is present in most (but not all) Gamasida (cf. Van der Hammen, 1972: 279).

Muscle insertion on a subcapitular apodeme (or the ventral part of the gnathosomatic base) is found in Holothyrida and Ixodida. In both groups the gnathosoma can be completely extended, as well as bent in ventral direction

[1] All respiratory organs in mites could be of glandular origin. In Actinotrichida, tracheae probably originate from groups of tegumentary glands (areae porosae and sacculi) and from accessory glands (in the case of genital tracheae).

(perpendicular to the idiosoma). The functional morphology of gnathosoma movements in other groups of Anactinotrichida is still insufficiently studied.

The paired orifice of the infracapitular glands is generally close to the line of attachment of the cheliceral frame to the infracapitulum; in Gamasida, this orifice can be considerably advanced (salivary styli). The paired ducts of the glands can be found in the coxal vaults of the infracapitulum.

Ancestrally, subcapitular gutter, sternapophyses and orifices of coxal glands are associated structures (as in Opilioacarida). In Gamasida, sternapophysis and subcapitular gutter are still associated with each other. In most Holothyrida (and in Ixodida) the sternapophyses have disappeared.

The apotelic claw of the palp is terminal in Opilioacarida, lateral (paraxial) in Holothyrida and Gamasida, absent in Ixodida. Tibia and tarsus of the palp are separated, but have the shape of a single segment, in Opilioacarida, Holothyrida and Gamasida; they have fused in Ixodida. The tibial brush of the palp in Holothyridae, and the brush of palpal trochanter and femur in Ixodidae, constitute interesting analogies.

Sensory areas in the distal part of leg I are found in all groups of Anactinotrichida, but Haller's organ in ticks (consisting of capsule and trough) has a distinct resemblance to Haller's organ in the family Holothyridae (consisting of a dorsal cavity and an elongated groove). The supposed ancestral condition (telotarsal organ or antiaxial capsule, and dorsal group of sensory setae) is still present in Opilioacarida and Allothyridae.

Evidently, Holothyrida share an important number of ancestral characters with Opilioacarida. They share some interesting derived characters (pertaining to Haller's organ and gnathosoma movements) with Ixodida.

VIII. Sigla

ac.P, acetabulum of palp
ac.I, acetabulum of leg I
ac.II, acetabulum of leg II
ac.III, acetabulum of leg III
ac.IV, acetabulum of leg IV
AN, anal shields
AP, apotele
ap.c, capitular apodeme
ap.sc, subcapitular apodeme
ar, sternal area posteriorly of transverse sternal groove
at, line of attachement of cheliceral frame to infracapitulum

BC, body of chelicera

CH, chelicera
ch_1, ch_2', cheliceral setae
cl_{1-3}, ungues op palpal apotele
CO, corniculus

d, dorsal seta
dgi, duct of infracapitular gland

epa, epiandrium
et, epiandrial tooth

F, femur
FC, cheliceral groove of infracapitulum

GC, large lateral ridge of infracapitulum

GE, genu
GEN, (male) genital shields

i, lyrifissure, cupuloid
id, dorsal lyrifissure of chelicera
if'', posterior (compound) lyrifissure associated with basifemoral ring
ita'', posterior lyrifissure associated with basitarsal ring
iα, antiaxial lyrifissure of chelicera.

LAG, laterogenital shield of female
ldm, ldm_{1-2}, laterodorsal infracapitular setae
LL, lateral lips
LS, labrum
lva, anterior lateroventral infracapitular seta
lvm, median lateroventral infracapitular seta
lvp, posterior lateroventral infracapitular seta

OC, eye
ogi, orifice of infracapitular gland
ogl_{1-2}, orifices of supposed excretory glands
OH, Haller's organ
otg, orifice (pore) of tegumentary gland
OVP, ovipositor

pe, peridium
POG, postgenital shield of female
PRG, pregenital shield of female

s.ca, sternal cavity
se, capitular saddle
sg, subcapitular gutter
s.gr, transverse sternal groove
st, stigma

t_i, inferior tendon of apotele
t_s, superior tendon of apotele
TA, tarsus
TI, tibia
tla, lateral tendon of gnathosoma
tlo, lobe of palpal tarsus
TR, trochanter
t.sc, tendon of subcapitular apodeme
ttg, tendon inserted on base of tegulum

u, distal lanceolate sensory seta of palpal tarsus

va_{1-2}, anterior ventral infracapitular setae
vs, ventral idiosomatic seta
vm, median ventral infracapitular seta
vp, posterior ventral infracapitular seta

x, apophysis of coxal region of palp

y, apophysis of palpal trochanter

IX. References

Albertis, L.M. d', 1880. New Guinea: What I did and what I saw, vol. 2. – London: x + 406 p., text-figs., pls., 1 map.

Berlese, A., 1923. Acarina della Nuova-Caledonia e delle Isole Loyalty. – In: F. Sarasin & J. Roux, Nova Caledonia, A, Zoologie, 3 (1): 115–124.

Butler, A.G., 1876. Preliminary notice of new species of Arachnida and Myriopoda from Rodriguez, collected by Messr. George Gulliver and H.H. Slater. – Ann. Mag. Nat. Hist. (4), 17: 439–446.

Camicas, J.L. & P.C. Morel, 1977. Position systématique et classification des tiques (Acarida: Ixodida). – Acarologia, 18: 410–420.

Canestrini, G., 1897. Nuovi Acaroidei della N. Guinea. – Termész. Füzet., 20: 461–474.

Domrow, R., 1955. A second species of Holothyrus (Acarina: Holothyroidea) from Australia. – Proc. Linn. Soc. N.S.W., 79: 159–162, fig. 1

Gervais, P., 1842. [Une quinzaine d'espèces d'insectes aptères qui doivent presque toutes former des genres particuliers]. – Ann. Soc. Ent. France, 11, Bull. 1842: xlv-lviii.

——, 1844. Acères Phrynéides, Scorpionides, Solpugides, Phalangides et Acarides; Dicères Épizoïques, Aphaniptères et Thysanoures. – In: C.A. Walckenaer, Histoire naturelle des Insectes Aptères, 3: 1–476; Atlas: pls. 22–38, 46–52.

HAMMEN, L VAN DER, 1961. Description of Holothyrus grandjeani nov. spec., and notes on the classification of the mites. – Nova Guinea, Zool., 9: 173–194, figs. 1–9, pl. 6.
——, 1965. Further notes on the Holothyrina (Acarida) I. Supplementary description of Holothyrus coccinella Gervais. – Zool. Meded. Leiden, 40: 253–276, figs. 1–9.
——, 1966. Studies on Opilioacarida (Arachnida) I. Description of Opilioacarus texanus (Chamberlin & Mulaik) and revised classification of the genera. – Zool. Verh. Leiden, 86: 1–80, figs. 1–21.
——, 1968. Stray notes on Acarida (Arachnida) I. – Zool. Meded. Leiden, 42: 261–280, figs. 1–3.
——, 1971. La phylogénèse des Opilioacarides, et leurs affinités avec les autres Acariens. – Acarologia, 12: 465–473, figs. 1–5.
——, 1972. A revised classification of the mites (Arachnidea, Acarida) with diagnosis, a key, and notes on phylogeny. – Zool. Meded. Leiden, 47: 273–292, fig. 1.
——, 1976. Glossaire de la terminologie acarologique, vol. 2. Opilioacarida. – The Hague (Dr. W. Junk): viii + 137 p., tab. 1–3, figs. 1–31, pls. 1–5.
——, 1979. Comparative studies in Chelicerata I. The Cryptognomae (Ricinulei, Architarbi and Anactinotrichida). – Zool. Verh. Leiden, 174: 1–62, figs. 1–31.
——, 1980. Glossary of acarological terminology, vol. 1. General terminology. – The Hague (Dr. W. Junk): viii + 244 p.
——, 1983. Notes on the comparative morphology of ticks (Anactinotrichida: Ixodida). – Zool. Meded. Leiden (in press).
HAMPSON, G.F. & E.E. GREEN, 1892. Remarkable weapons of defence. – Nature, 47: 199.
HUGHES, T.E., 1959. Mites, or the Acari. – London: viii + 225 p., pls. 1–52.
LEHTINEN, P.T., 1981. New Holothyrina (Arachnida, Anactinotrichida) from New Guinea and South America. – Acarologia, 22: 3–13, tab. 1, figs. 1–29.
THON, K., 1905. O Zlazách Holothyridu. Über die Drüsen der Holothyriden. – S.B. Böhm. Ges. Wiss. Prag, 1905 (10): 1–41, figs. 1–4, pls. 1–2. [This paper was not available to me.]
——, 1905a. Neue Luftorgane bei Milben. – Zool. Anz., 28: 585–594, figs. 1–3.
——, 1905b. Über die Coxaldrüse bei Holothyriden. – Zool. Anz., 28: 823–832, figs. 1–3.
——, 1906. Die äussere Morphologie und die Systematik der Holothyriden. – Zool. Jahrb., Syst., 23: 677–724, figs. A–D, pls. 28–29.
THORELL, T., 1882. Descrizione di alcuni Aracnidi inferiori dell' Arcipelago Malese. – Ann. Mus. Civ. Stor. Natur. Gen., 18: 21–69, pls. 4–6.
TRAVÉ, J., 1982. Premières observations sur le comportement de Thonius braueri (Thon, 1906) (Holothyrida). – Acarologia, 23: 199–206, fig. 1.
WARBURTON, C.M.A., 1913. The Acarina of the Seychelles. – Trans. Linn. Soc. (2), Zool., 15: 349–360.
WOMERSLEY, H., 1935. A species of Acarina of the genus Holothyrus from Australia and New Zealand. – Ann. Mag. Nat. Hist. (10), 16: 154–157, pl. 8.