

FIRST ULTRASTRUCTURAL OBSERVATIONS ON THE TARSAL PORE ORGAN OF *PSEUDOCCELLUS PEARSEI* AND *P. BONETI* (ARACHNIDA, RICINULEI)

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ABSTRACT. Due to their relative rareness and restricted distribution, little is known about the ultrastructure of ricinuleids. In particular, sense organs have not been the subject of electron microscopic research until now. Ricinuleids use their forelegs to explore their surroundings with tentative movements. The distal tarsomeres of legs I and II of two cavernicolous Mexican species, *Pseudocellus pearsei* from the Yucatán Peninsula and *Pseudocellus boneti* from Guerrero, were examined in this study with light microscopy, scanning (SEM) and transmission electron microscopy (TEM). A conspicuous feature of the distal tarsomeres of legs I and II is a single circular opening that extends as a deep tube-like pit into the tarsus. This pore organ is lacking in the 6-legged larvae. Comparable organs are present in Araneae, Scorpiones, Amblypygi and Anactinotrichida. The tarsal organs of the mentioned groups possess several types of sensilla (olfactory, thermo- and hygrosensitive and mechanosensitive). The pore organ is located in the distal third of the dorsal half of the tarsus. In longitudinal sections it shows a long oval shape. In cross sections it is nearly circular. The pore organ contains a large number of long, slightly curved setae. These setae are localized on the bottom and the lower two thirds of the wall of the pit and project into the lumen. The upper third of the wall is free of setae and shows folds which extend parallel to the opening. All setae inside the pit seem to be of the same type. In sections they show a complex inner structure and likely represent chemoreceptive wall pore single-walled (wp-sw) sensilla. This indicates a possible olfactory function. The pore organ is underlain by numerous gland cells which represent characteristics of unicellular “class I” gland cells.

Keywords: Tarsus, ultrastructure, sensory organs

The order Ricinulei Thorell 1892 is one of the smallest arachnid groups. Only 56 recent species, all belonging to the family Ricinoididae Ewing 1929, have been described. The recent species are divided into three genera. *Ricinoides* Ewing 1929 is from Western Central Africa, and *Cryptocellus* Westwood 1874 and *Pseudocellus* Platnick 1980 are both from Central America. Ricinuleids inhabit humid layers of soil and litter in tropical rainforests or caves (Cooke 1967; Mitchell 1970; Adis et al. 1989). They pass through 5 postembryonic life stages: a 6-legged larva, 3 nymphal stages (proto-, deuto- and tritonymph) and the adult stage (Mitchell 1970).

Most available studies about ricinuleids are taxonomic (Mitchell 1970). The knowledge about their internal morphology is based on

relatively few old fundamental studies (e.g., Hansen & Sørensen 1904; Millot 1945, 1949). Until recently, little has been known about the ultrastructure of ricinuleids as there have been few scanning and transmission electron microscopic studies on this animal group (for SEM see Legg 1976, 1977; Dumitresco & Juvara-Bals 1977; Platnick & Shadab 1976, 1977; Harvey 1984; Adis et al. 1999; for TEM see Alberti & Palacios-Vargas 1984; Ludwig & Alberti 1990; Ludwig et al. 1994). In particular, sensory organs have not been subjected to electron microscopic research until now. Ricinuleids use their forelegs, especially the elongated second leg, to explore their surroundings with tentative movements (Pollock 1967). Hence the presence of different sensilla on the distal tarsomeres of the forelegs can be

expected. Some authors identified different types of setae and other surface structures on the tarsi and expected them to be sensilla (e.g., Hansen & Sørensen 1904; Pittard & Mitchell 1972; Dumitresco & Juvara-Bals 1973, 1976; Legg 1976), but information about their ultrastructure and possible function are still not available. In the present work, we intend to present the first ultrastructural study of the pore organ of the foreleg tarsi of Ricinulei.

METHODS

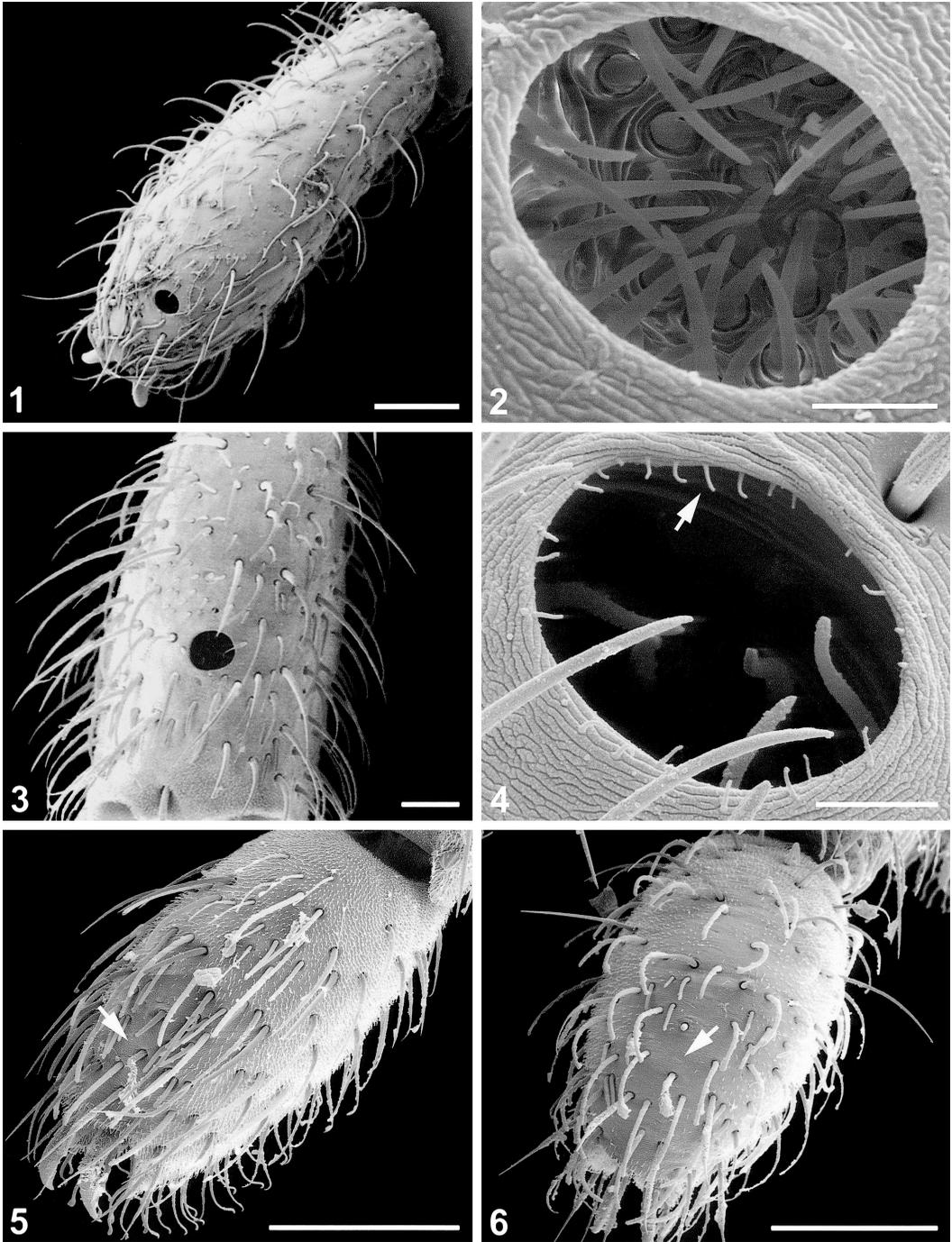
The distal tarsomeres of leg I and II of two cavernicolous Mexican species were examined in this study. Specimens of *Pseudocellus pearsei* (Chamberlin & Ivie 1938) from Yucatan peninsula were collected in three different caves, Gruta Actún Chen (Quintana Roo; 20° 20' 13" N & 87° 20' 45" W), Gruta X-Caret (Quintana Roo; 20° 33' 54" N & 86° 58' 49" W) and Gruta Sabac-Ha (Yucatán; 20° 10' 18" N & 89° 16' 03" W). *Pseudocellus boneti* (Bolivar and Pieltain 1941) from Guerrero was collected in the caves Grutas de Acuitlapán (Mexico; 18° 38' 00" N & 99° 31' 55" W). Both species have been found in bat guano or under flat stones. For SEM, 7 specimens of *P. pearsei* (1 larva, 1 protonymph, 1 deutonymph, 3 adult males and 1 adult female) and 4 specimens of *P. boneti* (1 larva, 1 tritonymph and 2 adult males) stored in ethanol (70%) were dehydrated in graded ethanols, critical-point dried and coated with gold-palladium. Examination was performed on a LEO DSM 940. For TEM the distal tarsomeres I and II of 5 specimens of *P. pearsei* (3 deutonymphs and 2 adult males) were dissected in ice-cold Sørensen phosphate buffer (pH 7.4; 0.1 M) and then fixed in 3.5% glutaraldehyde buffered in Sørensen phosphate buffer overnight. Further processes included postfixation with OsO₄ (2%) for two hours, rinsing in buffer, dehydration in graded ethanols and embedding mainly in Spurr's medium (Spurr 1969) and alternatively in Epon-Araldite. Ultrathin sectioning with a Diatome diamond knife took place on a Leica Ultracut. Sections were stained with saturated uranylacetate (in 70% methanol) for 5 minutes and lead citrate according to Reynolds (1963) for 15 minutes. The sections were examined with a Zeiss EM 10 A. For general orientation semithin sections (400–700 nm) were used which were stained according to Richardson et al.

(1960). All sections and voucher specimens are housed in the Zoological Institute & Museum of the University of Greifswald.

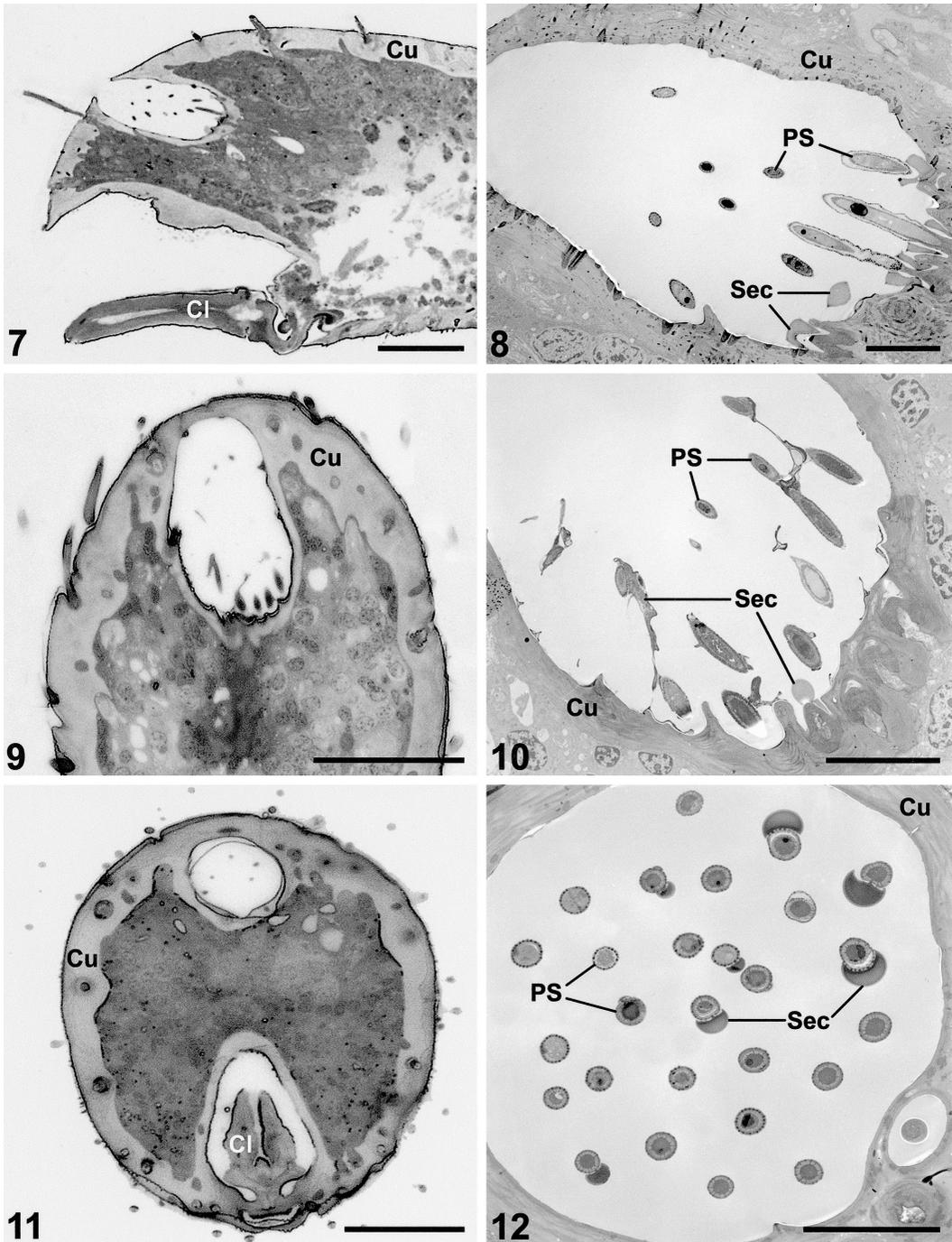
RESULTS

The pore organ is located in the distal third of the dorsal half of the distal tarsomeres of legs I and II (Figs. 1, 3). The width of the opening is about 32 μm in *P. pearsei* and 36 μm in *P. boneti* (Figs. 2, 4). The edge of the opening differs slightly in both species. In *P. pearsei* the edge is smooth without any projections (Fig. 2), while in *P. boneti* there are some short and thin microtrichae which project radially into the center of the opening (Fig. 4). Except for the larvae (Figs. 5, 6), this structure is present on the forelegs of each investigated life stage and both sexes of *P. pearsei* and *P. boneti*. The pore organ extends as a deep tube-like pit into the tarsus. In longitudinal sections it shows a long oval shape (Figs. 7–10). In cross sections it is nearly circular (Figs. 11, 12). Sexual dimorphism could not be observed in the present material.

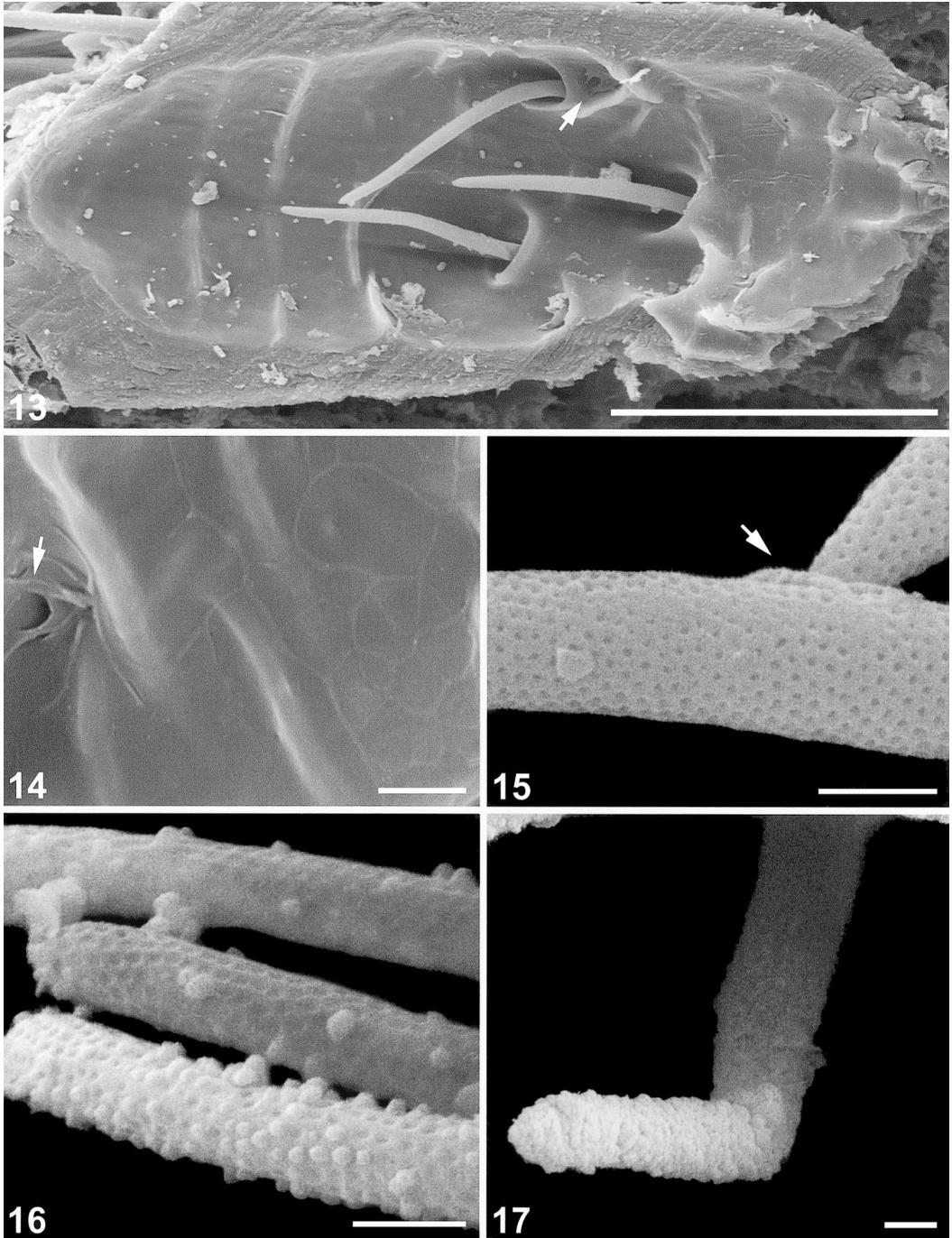
In both species the pore organ contains a large number of long slightly curved setae. These setae are localized on the bottom and the lower two thirds of the wall of the pore organ and project into the lumen but do not reach the opening (Figs. 2, 4, 13). The upper third of the wall is free of setae and shows folds which extend parallel to the opening (Fig. 13, 14). Some small openings in the wall are visible (Fig. 13, 14). In SEM micrographs, the setae show a great number of wall pores (Fig. 15) but in some parts of the shaft the openings of these pores are covered by droplets of different size (Figs. 16, 17). In *P. pearsei* all setae inside the pore organ seem to be of the same type (Fig. 12). Sections reveal the complex wall of these setae. It consists of two layers: a thick inner wall with up to 25 pores per section and a thin outer wall with a similar number of pores which are plugged by electron dense bodies (Figs. 18–20). Some setae are partly surrounded by secretions (Figs. 19). This is very evident in the basal part of the pore organ where most of them arise (Figs. 23, 26). The sockets of the setae are inflexible (Fig. 26). The setae are innervated by 4–7 outer dendritic segments (Figs. 21, 22). These are surrounded by an enveloping cell and many densely arranged microvilli (Fig. 21). The latter are formed by the tormogen cell which



Figures 1–6.—Distal tarsomeres. 1. Tarsus II of *Pseudocellus pearsei* (adult male). Scale bar = 100 μm . 2. Pore organ opening of that tarsus. Scale bar = 10 μm . 3. Tarsus I of *Pseudocellus boneti* (adult male). Scale bar = 50 μm . 4. Opening of the pore organ of tarsus I of *P. boneti* (tritonymph). Note the small microtrichiae (arrow). Scale bar = 10 μm . 5. Tarsus I of *P. pearsei* (larva). Scale bar = 100 μm . 6. Tarsus II of *P. pearsei* (larva). Scale bar = 100 μm . Note the dorsofrontal region of the tarsi without pore organ (arrows).



Figures 7–12.—Light and TEM micrographs of the pore organ of *Pseudocellus pearsei*. 7. Sagittal section of tarsus II. Scale bar = 50 μm . 8. Detail of pore organ with longitudinal and oblique sections of sensilla. Scale bar = 10 μm . 9. Horizontal section of tarsus I. Scale bar = 50 μm . 10. Detail of the pore organ base and some oblique sections of sensilla. Scale bar = 10 μm . 11. Transversal section of tarsus I. Scale bar = 50 μm . 12. Detail of the lumen with cross sections of sensilla. Scale bar = 10 μm . Abbreviations: Cl = claw, Cu = cuticle, PS = pore organ-sensilla, Sec = secretion.



Figures 13–17.—Surface of the pore organ integument and the pore organ-sensilla. 13. Longitudinal section of the pore organ of tarsus I of *Pseudocellus pearsei* (adult female) with three lateral inserted sensilla and a gland opening (arrow). Scale bar = 30 μm . 14. Detail of the integument with folds and a gland opening (arrow). Scale bar = 3 μm . 15. The sensilla shaft of *P. pearsei* with many wall pores. Note the damaged area (arrow). Scale bar = 1 μm . 16. Some sensilla with numerous droplets covering the wall pores. Scale bar = 1 μm . 17. Pore organ-sensillum of *Pseudocellus boneti* with a totally covered surface. Scale bar = 1 μm .

produces the slightly electron dense receptor lymph (Figs. 21, 26). A dendritic sheath is lacking. The dendritic segments terminate in the basal part of the shaft. Pore tubules beneath the wall pores are lacking. The apical part of the shaft is completely filled with receptor lymph of different electron densities (Fig. 18).

Large gland cells which are formed by modified epidermal cells occur between the sensilla forming cells (Figs. 23, 26). The glands appear sack-like and each one forms a large secretion reservoir which is filled with an almost electron lucent material (Figs. 23, 26). Large nuclei, numerous mitochondria, secretion vesicles and microvilli, which project into the reservoirs, are present in these cells (Figs. 23, 26). The secretion seems to be delivered through at least 1 pore, partly filled with granular material, into the lumen of the tarsal pore organ (Figs. 24, 25) but it can not be excluded that a gland cell exhibits more than 1 pore.

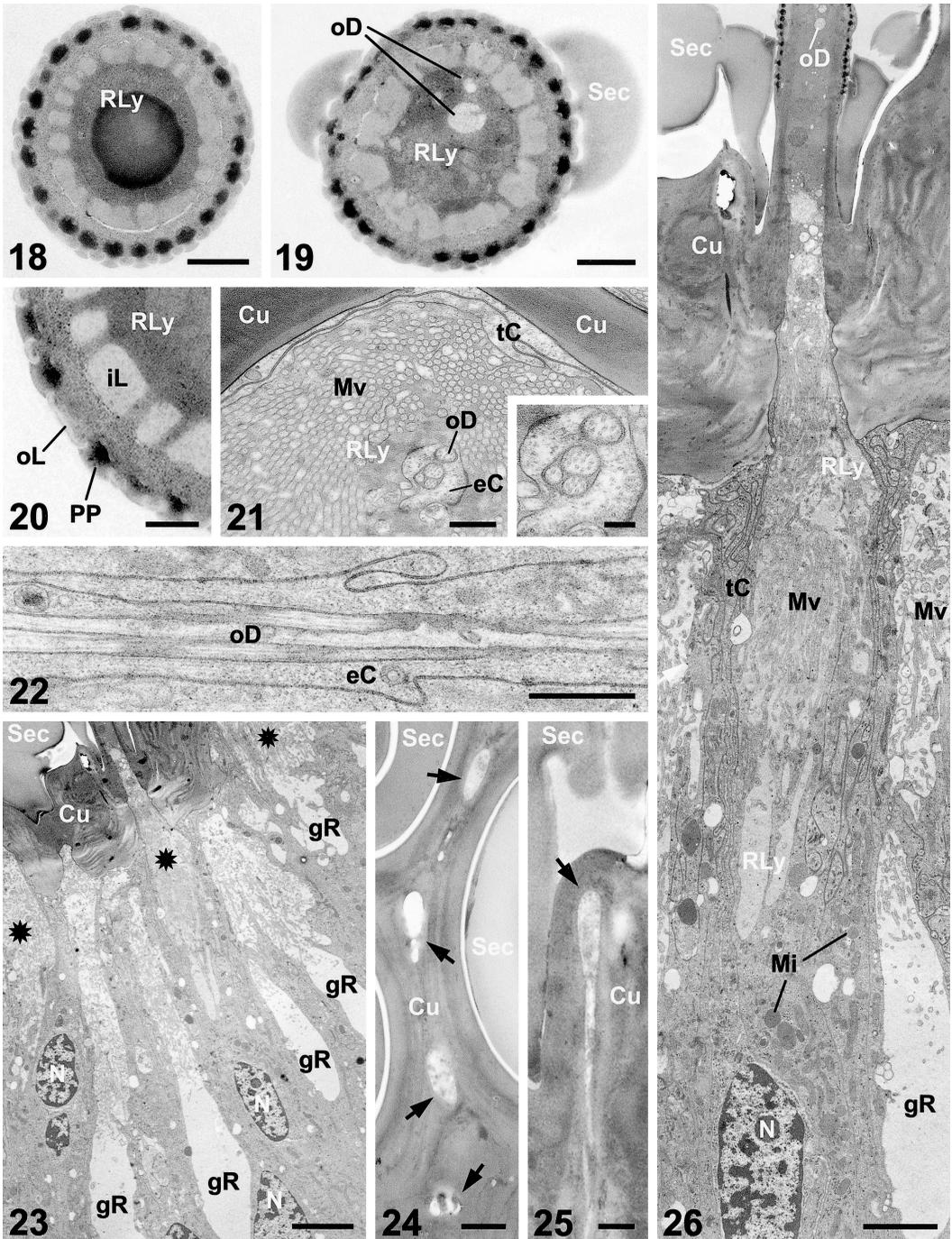
DISCUSSION

The first short description of the tarsal pore organ was given by Pittard & Mitchell (1972). They named it "deep pit" and found that this structure is not present in the larva but on the distal tarsomeres of leg I and II of all further life stages. Our observations confirm these results for *P. pearsei* and partly for *P. boneti*. Dumitresco & Juvara-Bals (1973) suggested the "organe tarsal" may be comparable to the tarsal organs of other Arachnida. These are present in Araneae, the tarsal organs on palps and walking legs (e.g., Blumenthal 1935; Foelix & Chu-Wang 1973), Scorpiones (Foelix & Schabronath 1983), Amblypygi (Foelix et al. 1975) and in Anactinotrichida, the well known Haller's Organ on tarsus I of Ixodida and Holothyrida and the telotarsal organ on tarsus I of Opilioacarida (summarized by Alberti & Coons 1999; Coons & Alberti 1999). The tarsal organs of the mentioned groups possess several types of sensilla. Olfactory, thermo/hygrosensitive and mechanosensitive receptors could be identified in numerous studies.

The tarsal pore organ of ricinuleids shows similarities to the proximal part of Haller's organ, the capsule, in Ixodida. These capsules bear 2–7 sunken sensilla (see Foelix & Axtell 1972; Coons & Alberti 1999) which have olfactory function. According to the concepts of

pore structures and the function of arthropod sensilla (e.g., Altner 1977; Altner & Prillinger 1980; Tichy & Barth 1992; Steinbrecht 1997; Hallberg & Hansson 1999), three main types of olfactory sensilla are known: 1) single-walled sensilla with simple wallpores, 2) single-walled sensilla with plugged wallpores and 3) double-walled sensilla with spoke canals. Single-walled sensilla with plugged wallpores are present in the capsule of Haller's organ (Foelix & Axtell 1972). The wall of the pore organ-setae of *P. pearsei* differs in structural details from the main types described above and also from the capsule-sensilla of Ixodida. Although wall pores with some kind of pore plugs are clearly present, the complex thin outer layer (Figs. 18–20), which may consist of another type of secretion instead of cuticle, makes it difficult to assign the pit-setae to one type of sensilla. Foelix & Axtell (1972) described a thin layer of "extracellular material" which often covers the capsule-sensilla, but this layer has no complex structure. It is not clear whether this layer consists of receptor lymph or other secretions but the authors note that it was only prominent after simultaneous glutaraldehyde-OsO₄ fixation which was not performed in this study. Indeed the phenomenon of droplets appearing on the surface of sensilla (Figs. 16, 17) is explained as dried receptor lymph (Foelix & Schabronath 1983). Altner (1977) pointed out that pore structures exist which do not fit to the classification system of sensilla types. However, the presence of wall pores and innervating dendrites (Figs. 15–22) in the pore organ-setae of *P. pearsei* indicate an olfactory function. The limited material does not allow the reconstruction of the exact innervation pattern (e.g. number and organization of neurons) of this organ. Therefore further investigations are needed. According to Foelix & Axtell (1972) and with regard to the more or less endogenous living of ricinuleids we believe that the tarsal pore organ serves, similar to the capsule of Haller's organ of Ixodida, mainly as a protective device for numerous olfactory sensilla, which could easily be damaged mechanically if been exposed to the tarsal surface. However, only electrophysical proofs can verify the sensory function of an organ (see e.g., Dumpert 1978; De Bruyne & Guerin 1994).

In Ixodida a large multicellular gland beneath the capsule is known (Foelix & Axtell



Figures 18–26.—Ultrastructure of the tarsal pore organ of *Pseudocellus pearsei*. 18. Cross section of a pore organ-sensillum (apical shaft). Scale bar = 0.5 μm. 19. Cross section of the basal shaft with droplets of secretion. Scale bar = 0.5 μm. 20. Detail of the wall. Scale bar = 0.2 μm. 21. Transverse section of a sensillum socket with 4 outer dendritic segments (inset). Scale bars = 0.5 μm, 0.2 μm. 22. Horizontal section of dendrites beneath a sensillum. Scale bar = 1 μm. 23. Horizontal section of the pore organ base with gland cells between the sensilla forming cells (asterisks). Scale bar = 5 μm. 24. Transverse section of pores (arrows) in the integument between sensilla sockets. Scale bar = 0.5 μm. 25. Horizontal section of a pore filled with granular material (arrow). Scale bar = 0.5 μm. 26. Detail of Fig. 23. Scale bar = 2 μm. Abbreviations: Cu = cuticle, eC = enveloping cell, gR = glandular reservoir, iL = inner layer, Mi = mitochondria, Mv = microvilli, N = nucleus, oD = outer dendritic segment, oL = outer layer, PP = pore plug, RLy = receptor lymph, Sec = secretion, tC = tormogen cell.

1972). Their glandular openings were found in the capsule wall. It was suggested that this gland might be the origin of the material surrounding the capsule-sensilla. The large glands beneath the pore organ of *P. pearsei* are supposed to produce the secretion present between the sensilla and on their surface (Figs. 19, 23–26). They are believed to represent enlarged unicellular “class I” epidermal glands according to the classification of Noirot & Quennedy (1974, 1991). Such glands pour their secretions through a simple pore without any special canal formation (Figs. 13, 14, 24, 25). The secretion may support the binding of odorants or probably rinses the sensilla surfaces to keep them clean.

However, some main differences between Haller’s organ of Ixodida and the tarsal organ of ricinuleids are evident. The tarsal pore organ of ricinuleids occurs on leg I and leg II not only on leg I like in ticks and it contains many more sensilla than the capsule of ticks. Furthermore Haller’s organ is present in ixodid larvae but the tarsal pore organ is not present in the larva of ricinuleids. In ticks Haller’s organ is the main receptor for host detection in all life stages (Foelix 1985). Ricinuleids are not parasitic. If olfactory function can be confirmed in the future, detection of other odorants can be expected. Like in Araneae (Dumert 1978) pheromone detection is imaginable, because this might not be important for the larvae. Unfortunately, the knowledge of the biology of these animals, in particular the dynamics between individuals in their habitats is still too poor to enable any suggestions in this case. For these reasons, further investigations including also species of the other two genera and on the biology of Ricinulei are required.

ACKNOWLEDGMENTS

G.T. wishes to express his special thanks to Anja Klann and Peter Michalik for comments and support. He also thanks Romano Dallai, Fabiola Giusti, Valerio Vignoli and all their colleagues at the Department of Evolutionary Biology, Siena for their generous help and kind hospitality. Some specimens of *Pseudocellus pearsei* from Yucatán Peninsula were collected and donated to P.-V. by Mrs. Josiane Lips. All authors appreciate the technical assistance of Christine Putzar and Hartmut Fi-

scher. G.T., P.-V. and G.A. remember Mariano Fuentes Silva who died in April 2004.

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Manuscript received 21 December 2004, revised 20 June 2005.