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# Fine structure of the trichobothrium of *Heterochthonius gibbus* (Oribatida, Enarthronota, Heterochthoniidae) with remarks on adjacent setae

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## Abstract

The trichobothridium (bothridium and bothridial seta) of the enarthronote mite *Heterochthonius gibbus* is described using scanning and transmission electron microscopy. The cuticular wall of the bothridium shows three recognizable regions an external (distal) smooth part, a central region with a complex structured wall, and an internal (proximal) smooth part beginning where the bothridium bends sharply ending in the setal insertion. The central wall is provided with many tubules or chambers, which in the most distal region are filled with a secretion but otherwise are empty (likely filled with air). Distinct chambers separated by septa are not evident. The bothridial seta is similarly bent and is inserted in a proximal cuticular ring via only a few suspension fibers. Two dendrites terminating with tubular bodies innervate the bothridial seta. The dendrites are distally surrounded by a thick dense dendritic sheath. The overall structure of the trichobothrium, with a simple sharp bend, presents an intermediate condition compared with the straight trichobothrium of early derivative oribatid mites and the double-curved, S-shaped base found in more evolved taxa. The adjacent interlamellar and exobothridial setae are also provided with two dendrites terminating with tubular bodies and thus are mechanosensitive touch receptors.

Keywords bothridial seta | bothridium | mechanoreceptor | sensillus | ultrastucture

## 1. Introduction

Trichobothria are mechanosensitive sensilla functioning as vibro- or anemoreceptors. They consist of a variously shaped bothridial seta which is inserted in a deep cavity, the bothridium (e.g., Hammen 1980). Trichobothria are known from terrestrial arthropods including certain myriapods, some insects and most arachnids (e.g., Foelix 1985, Moritz 1993, Dunger 1993, Kinzelbach 2003). With regard to mites, it is remarkable that trichobothria are only exceptionally present in Anactinotrichida (= Parasitiformes s.l.), but are quite common in Actinotrichida (= Acariformes) (Alberti 2006, Krantz 2009). They may occur on appendages as well as on the body and have mostly a filiform shape. But this is not the case in Oribatida, where a great diversity of form occurs, ranging from filiform to globose or pectinate shapes (e.g., Vitzthum 1940/43, Balogh & Mahunka 1983, Evans 1992, Alberti et al. 1994, Alberti & Coons 1999, Weigmann 2006, Norton & Behan-Pelletier 2009).

In oribatid mites, the trichobothria are distinctly and characteristically placed as one pair on the prodorsum. Interestingly, there are only a few exceptions in Oribatida where the trichobothria of adult mites are rudimentary or entirely lost – evidently secondarily. These are species having achieved an aquatic life (e.g., Vitzthum 1943, Weigmann 2006). The bothridial


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seta is mostly placed in a straight and upright manner within the bothridium, but this is also conspicuously modified in most oribatid mites, where the base of the bothridial seta is S-shaped, corresponding to a similarly formed bothridium (e.g., Alberti et al. 1994, Weigmann 2006, Norton & Behan-Pelletier 2009). Straight or intermediate forms have been reported only in some oribatid mites usually considered to be early derivative, i.e. Palaeosomata (= Palaeosomatides) and some Enarthronota (= Enarthronotides) (e.g., Grandjean 1954, Balogh & Mahunka 1983, Norton & Behan-Pelletier 2009, Norton & Fuangarworn 2015).

The enarthronote mite *Heterochthonius gibbus* (Heterochthoniidae) is rather exceptional within Oribatida for several reasons, including possession of three primary eyes on its prodorsum (Alberti & Moreno-Twose (2012) and four pairs of dermal glands in its hysterosoma (Alberti & Moreno Twose 2016). We here present the first study on a further important sensory structure, the trichobothria, of these remarkable mites using scanning and transmission electron microscopy.

## 2. Materials and methods

About 20 adult specimens of *Heterochthonius gibbus* (Berlese, 1910) were collected near Grindelwald (Switzerland) in summer 1994 from a rotten tree-stump at about 1500 m above s.l. from samples extracted with Berlese-funnels. A number of specimens were transferred to 70 % ethanol for use in scanning electron microscopy (SEM). The specimens were dehydrated using graded ethanols and transferred into dichlordifluormethan, critical point dried using liquid $CO_2$ as final medium. They were mounted on Al-stubs, coated with gold and examined with a Philips SEM 505. Some other specimens wer fixed and dehydrated as for TEM (see below), then embedded in styrol methacrylate (Weissenfels 1982) and sectioned with the ultramicrotome. After reaching regions of interest (using semi-thin sections for orientation), sectioning was stopped and the specimens were removed from the block by dissolving the embedding medium in xylol. The specimens were then treated as described above for SEM.

For transmission electron microscopy (TEM), specimens were transversely cut into halves and fixed in ice-cold 3.5 % glutaraldehyde (pH 7.4, phosphate buffer 0.1M) for two hours. After rinsing with buffer solution, the tissues were postfixed with 2 % $OsO_4$ aqueous solution. After rinsing again, specimens were dehydrated with graded ethanols and embedded in Araldite using propylenoxide as intermedium. Ultrathin sectioning (70 nm) was done with a Leica UCT using a Diatome diamond knife. 100 mesh copper grids provided with a Pioloform-film were used to bear the sections. The sections were stained with uranylacetate and lead citrate (Reynolds 1963) and studied with a JEOL JEM-1011 transmission electron microscope. For general orientation semithin sections (400 nm) were stained according to Richardson et al. (1960) and studied with a compound light microscope (LM). For more technical information see Alberti & Nuzzaci (1996).

## 3. Results

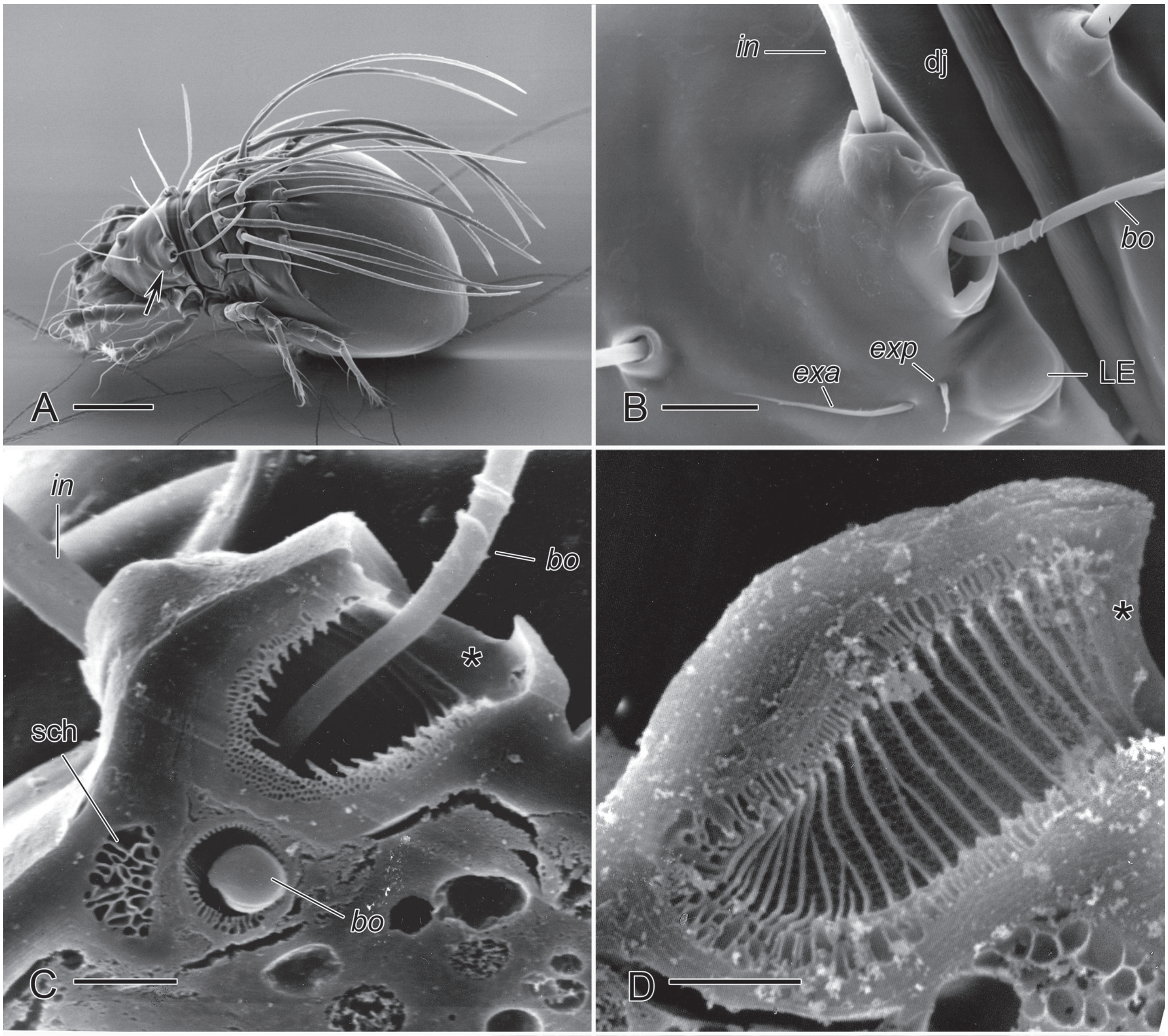
The trichobothrium of *H. gibbus* is positioned on a cuticular elevation close to the posterior border of the prodorsum just above the lateral eye (Fig. 1A, B). Each elevation bears beside the trichobothrium an interlamellar seta, slightly medial to the trichobothrium. Two very small and smooth setae – the anterior and posterior exobothridial setae – are placed ventral to the trichobothrium and anterior of the lateral eye. These tiny setae are inserted movably in a small socket and innervated by two dendrites terminating with tubular bodies (Fig. 2A, B).

The interlamellar seta is filiform and slightly pilose. Like the exobothridial setae, it inserts in a simple socket and is innervated by two dendrites terminating with tubular bodies (Fig. 2D–F).

The bothridial seta of the trichobothrium is distinctive on the cuticular elevation in having a slightly fusiform shape and being distally pilose. Proximally, close to the bothridium, the thin shaft has a short helical ridge.

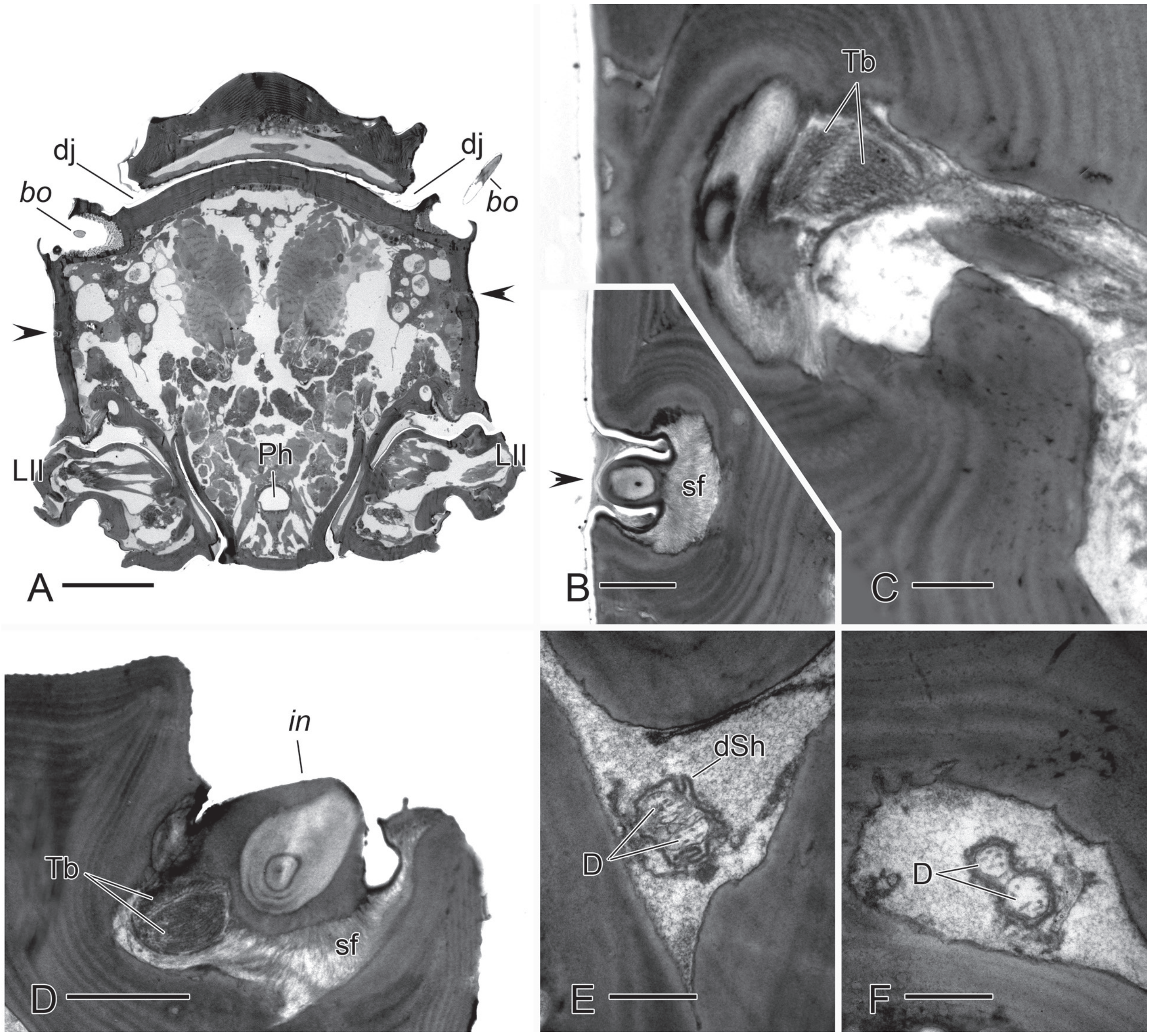
Looking with SEM into the bothridium, its walls exhibit intricate sculpturing (Fig. 1C, D), which is more evident in specimens in which the bothridium is partly cut open. Distally the bothridial wall is smooth, but more proximally it is very intricately structured with circular ridges (described as internal striation by Grandjean 1928), some of which branch (Fig. 1D). Between the ridges numerous small tubules or chambers reach deeper into the cuticle. In their proximal region, the bothridial seta and bothridium are sharply bent ventrolaterad, so that the insertion of the seta is positioned more peripherally than the bend itself (Figs 1C, 3, 4, 5A). The bothridium has proximally a small side-chamber that is provided with a less finely sculptured wall and directed anteriorly (Figs 3B–D, 4C, 5A). The tubules are replaced by wider, irregularly shaped chambers.

The sections reveal other details. The structured wall of the bothridium shows a short zone just proximal to the distal smooth wall, in which the tiny tubules are filled with a substance of medium electron-density (Figs 4C, 5). More proximally, the tubules and chambers appear mostly empty. Close to the insertion of the bothridial seta, the cuticle of the bothridium becomes very thin (Figs 3B–D, 4C, 6A). The seta is a massive structure except for its most proximal part (Fig. 3F). It inserts in the depth of the bothridium within a proximal ring of rather thick cuticle (Figs 3E–G, 4, 5A, 6A, B) to which the slightly broadened inner end of the seta is connected by a thin layer of suspension fibers. From the proximal ring and the setal base an electron-dense sheath extends deeper into the mite, tightly surrounding the two tubular bodies of the two dendrites that innervate the bothridial seta (Figs 3G, 6A–F). More proximally, the sheath disintegrates into irregularly arranged dense sheets and strands. The outer segments of the dendrites reach the base of the seta from a ventro-antero direction running around the bent bothridium (Figs 3B–G). They are surrounded by a wide outer receptor lymph cavity and continue proximally into the inner dendritic segment via a short ciliary segment provided with two basal bodies (Fig. 6H, I). The auxiliary (enveloping) cells do not show peculiarities, such as extended microvilli. We were not able to trace the more proximal somata and axons.




▲ **Figure 1**: SEM figures of *Heterochthonius gibbus*. (**A**) Lateral view of mite. Arrow points to trichobothrium. Scale bar: 100 µm. (**B**) Detail showing cuticular elevation with trichobothrium and interlamellar seta and adjacent region. Scale bar: 10 µm. (**C**) Region of bothridum opened by sectioning. Note that the base of bothridial seta is bent and the wall of the bothridium shows a complex sculpture. * indicates the smooth external (distal) part of the bothridium. A side chamber of the bothridium is formed. Scale bar: 5 µm. (**D**) Wall of bothridium with its complex sculpture. Note the circular ribs branching. * indicates distal smooth wall of the bothridium. Scale bar: 5 µm.

Abbr.: ***bo*** – bothridial seta, **dj** – dorsosejugal furrow, ***exa*** – anterior exobothridial seta, ***exp*** – posterior exobothridial seta, ***in*** – interlamellar seta, **LE** – lateral eye, **sch** – side chamber of bothridium.

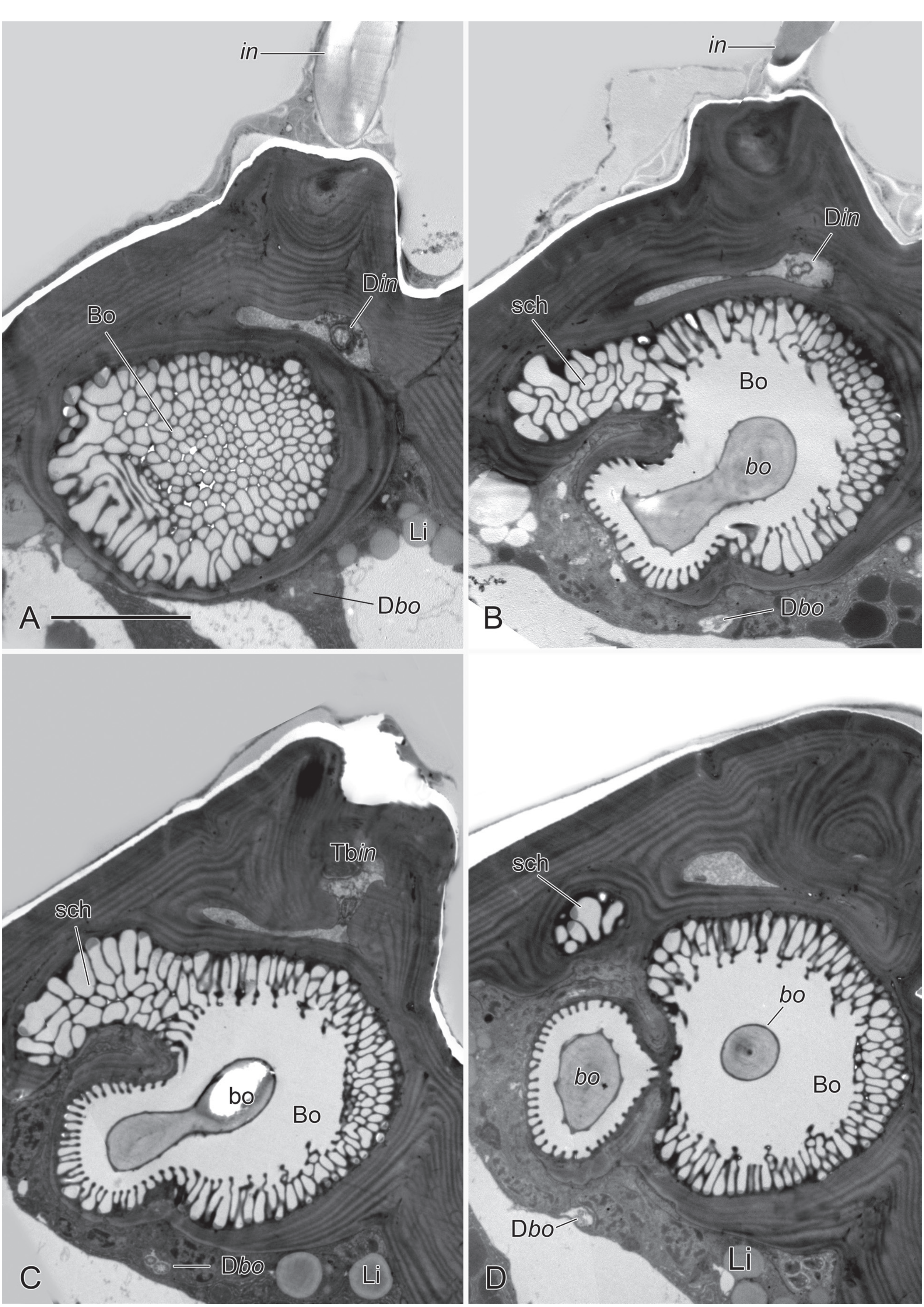



▲ **Figure 2**. TEM figures of *Heterochthonius gibbus*. (**A**) Cross section through proterosoma level with the trichobothria (section slightly posterior of interlamellar setae). Arrowheads point to insertion sites of exobothridial setae. Scale bar: 20 µm. (**B**) The exobothridial seta, due to the suspension fibers, is movably inserted (compare left arrowhead in Fig. 2A). Scale bar: 1 µm. (**C**) Slightly more posterior section, showing the tubular bodies of the exobothridial seta. Scale bar: 0.5 µm. D–F: Interlamellar seta. (**D**) Base of interlamellar seta with suspension fibers and two tubular bodies. Scale bar: 2 µm. (**E**) Slightly more proximal, the dendrites are surounded by irregular sheets of the dendritic sheath. Scale bar: 0.5 µm. (**F**) The two dendrites close to the more proximally located ciliary segment. Scale bar: 0.5 µm.

Abbr: ***bo*** – bothridial seta, **D** – dendrite (outer segment), **dj** – dorsosejugal furrow, **dSh** – dendritic sheath, ***in*** – interlamellar seta, **LII** – leg II, **Ph** – pharynx, **sf** – suspension fibers, **Tb** – tubular body.

► **Figure 3**. Series of parasagittal sections through trichobothrium starting from the inner (median) side towards a more outer (lateral) region. Anterior is left. All but D are from the same specimen. All figures in same scale as shown in Fig. A and E: Scale bar: 5 µm. (**A**) The distal chamber of the bothridium is tangentially sectioned. Note interlamellar seta and its innervation. (**B**) The bothridal seta is sectioned where it bends into the proximal chamber of the bothridium. Note small side chamber. (**C**) Almost same as in Fig. 3B but tubular bodies of the interlamellar seta are visible. (**D**) The bent bothridial seta is sectioned twice. Note that the cuticular wall structure of the proximal chamber (left) of the bothridium is much simpler than that of the distal chamber (right). Side chamber is disappearing.

Abbr.: **Bo** – bothridium, ***bo*** – bothridial seta, **D*bo*** – dendrites of the bothridium, **D*in*** – dendrites of the interlamellar seta, **dj** – dorsosejugal furrow, **dSh** – dendritic sheath, ***in*** – interlamellar seta, **Li** – lipid inclusion, **pri** – proximal cuticular ring into which the bothridial seta is inserted, **RCA** – receptor lymph cavity, **sch** – side chamber of bothridium, **Tb*in*** – tubular bodies of dendrites innervating interlamellar seta, **Tb*bo*** – tubular bodies of dendrites innervating the bothridial seta.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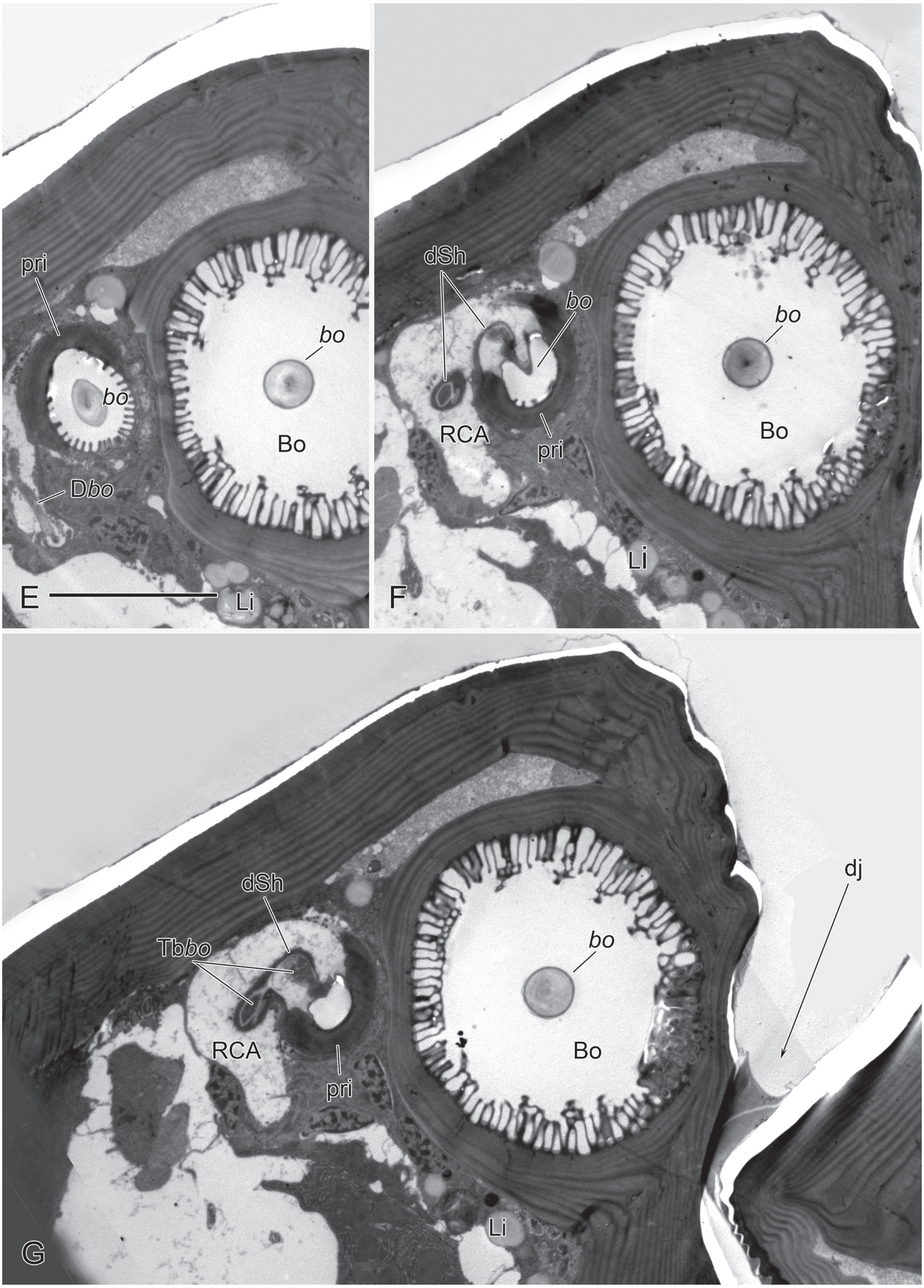
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## 4. Discussion

The trichobothrium of *Heterochthonis gibbus* is only the second of an oribatid mite studied extensively by TEM. In general form, it shows an intermediate condition with regard to the proximal parts of seta and bothridium. In most oribatid mites both components show an S-shape, but these structures are upright in the early derivative Oribatida such as Palaeosomata (Grandjean 1954) and some Enarthronota, e.g., the recently described *Nanohystrix hammerae* (Norton & Fuangarworn 2015). This straight shape of seta and bothridium is considered to be plesiomorphic since it occurs also in other actinotrichid mites as well as in other Arachnida (e.g., Moritz 1993, Foelix 1985). In *H. gibbus* the bothridial seta and the bothridium is sharply bent proximally, but only once. It has been suggested that the peculiar arrangement of bothridial setae in the more derivative oribatid mites increases the protection of the sensillum and may also improve its sensitivity (Alberti et al. 1994, Alberti & Coons 1999, Norton & Fuangarworn 2015).

It seems very likely that the intricate structures of the cuticular wall of the bothridium evolved to keep the seta movable, a capability indispensable to perceive vibrations. Thus it is obviously necessary to keep the bothridium clean and full of air. This is achieved by the fine structures formed by the cuticle proper as is the case in *H. gibbus* (and apparently also in *Nanohystrix hammerae*; Norton & Fuangarworn 2015) and/or by a specialized cerotegument as, e.g., in *Acrogalumna longipluma* (Alberti et al. 1994, Alberti & Coons 1999, Norton & Fuangarworn 2015). In addition, other secretions may be involved. The very distinct distal region in the bothridium of *H. gibbus* seems remarkable in this respect. The substance filling the cuticular tubules in that region may represent a hydrophobic lipid secretion. A similar substance was observed in the bothridium of *Eulohmannia ribagai* (Alberti et al. 1997). It is not known where it comes from, but it may be secreted from the epithelium that underlies the bothridium, particularly where the cuticle is very thin. In contrast to most more derivative oribatid mites, the bothridium of *H. gibbus* is not divided into several chambers by prominent cuticular septa leaving only restricted openings through which the borthridial seta curves (e.g., *A. longipluma*; Alberti et al. 1994). The circular ridges present in *H. gibbus* are much smaller and far more numerous, although the most proximal area, internal to the bend of the bothridium, shows a simplified wall sculpture.

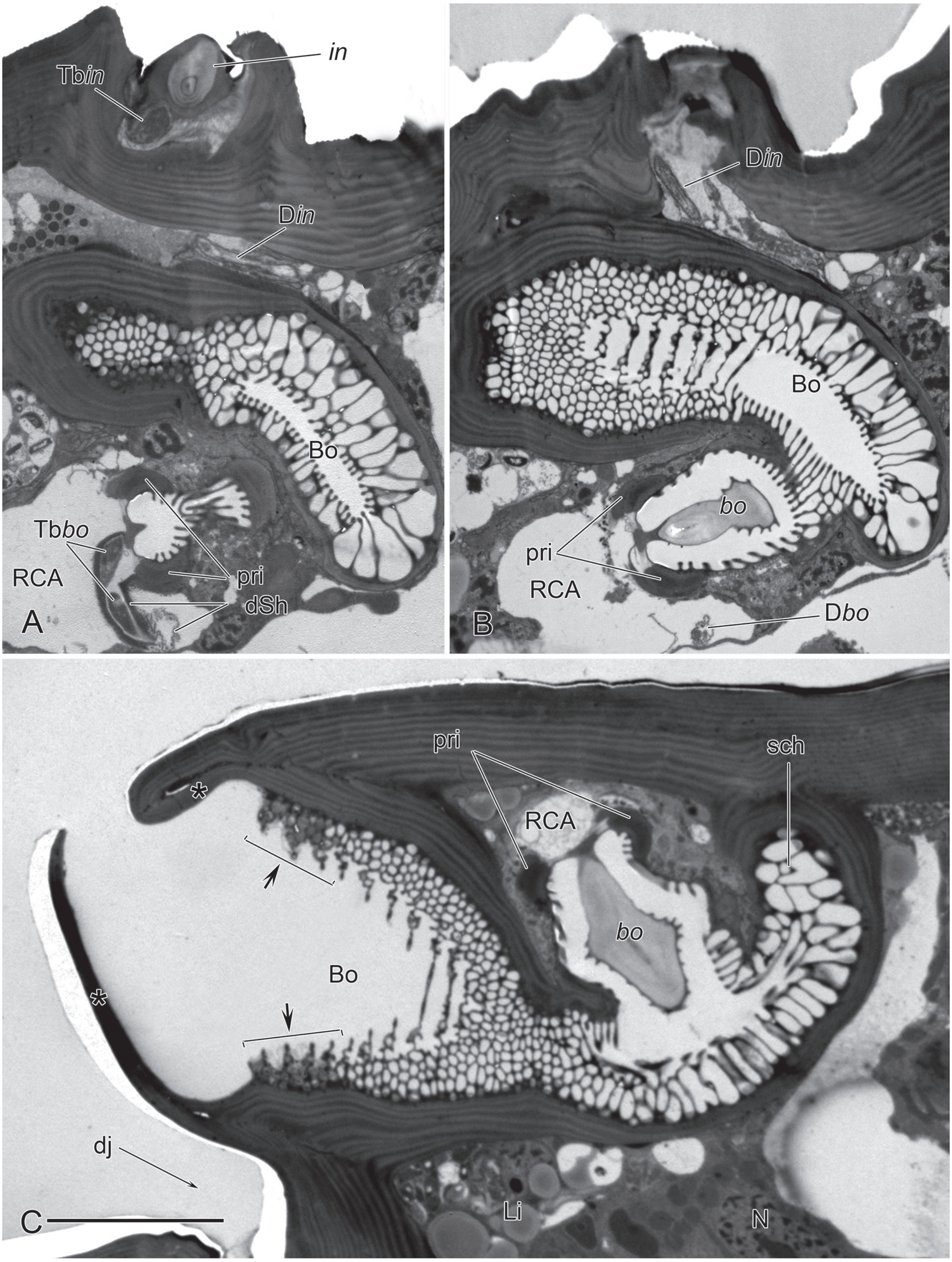
The side-chamber branching from the bothridium of *H. gibbus*, perhaps also seen by Grandjean (1928) according to his drawing, presents a further aspect. Its function is not really clear, but it may be compared with the various porose structures associated with the bothridium in some other oribatid mites, e.g., the bothridial sacs and tubular brachytracheae found in certain Crotonioidea and Phthiracaroidea, which are thought to help gas exchange in the prosoma or keeping the bothridium clean by ventilation (Grandjean 1939, Alberti et al. 1997, Norton & Alberti 1997, Norton et al. 1997). The side-chambers may represent a starting point to more effective structures as found in the just-mentioned taxa.

The innervation by two dendrites with two tubular bodies seems to be a general feature of all mechanosensitive setae in Actinotrichida (Alberti & Coons 1999, Alberti 2006). Only the tiny supracoxal setae *e* may differ, but these setae are insufficiently studied (Alberti et al. 2011). As in *Acrogalumna longipluma* we observed only one of the tubular bodies contacting the setal base. The other tubular body terminates slightly more proximally. It may be significant that the electron-dense sheath surrounding the tubular bodies of the trichobothria of *A. longipluma* as well as of *Heterochthonius gibbus* is rather thick (called dense tubes by Alberti et al. 1994, Alberi & Coons 1999), continuous and smooth. This contrasts with other mechanosensitive sensilla in which this sheath forms more or less distinct semicircular structures projecting against the tubular bodies (Alberti et al. 1994, Alberti & Coons 1999, Alberti & Dabert 2012, Alberti & Kitajima 2014, Alberti & Moreno Twose 2016). However, with so few studies any generalization would be premature. Also of interest is the fact that the auxiliary cells of the trichobothria of both *H. gibbus* and *A. longipluma* are not provided with long microvilli, which were very obvious in other mechanosensory cells studied in *H. gibbus* (Alberti & Moreno Twose 2016). Unfortunately nothing is known about these cells, neither from *A. longipluma* nor any other oribatid mite.

Evidently, these sensilla are highly specialized mechanoreceptors, likely reacting to airborne stimuli. In *Acrogalumna longipluma* the base of the bothridial seta is oval, suggesting a directional preference (Alberti et al. 1994, Alberti & Coons 1999), but this was not observed in *Heterochthonius gibbus*. In any case the structure of the trichobothria supports the interpretation of this species as early derivative, representing at least in some traits an intermediate step in the evolution of Oribatida.

(◄ continued figure 3) (**E**) The bothridial seta close to its insertion within a cuticular ring. The dendrites of the trichobothrium run dorsally to reach the insertion site of the bothridial seta. (**F**) The dendrites have formed tubular bodies and are close to the insertion of the bothridial seta. The dendritic sheath is formed. (**G**) Connection of dendrites and the dendritic sheath with the base of the bothridial seta.

Abbr.: **Bo** – bothridium, ***bo*** – bothridial seta, **D*bo*** – dendrites of the bothridium, **D*in*** – dendrites of the interlamellar seta, **dj** – dorsosejugal furrow, **dSh** – dendritic sheath, ***in*** – interlamellar seta, **Li** – lipid inclusion, **pri** – proximal cuticular ring into which the bothridial seta is inserted, **RCA** – receptor lymph cavity, **sch** – side chamber of bothridium, **Tb*in*** – tubular bodies of dendrites innervating interlamellar seta, **Tb*bo*** – tubular bodies of dendrites innervating the bothridial seta.



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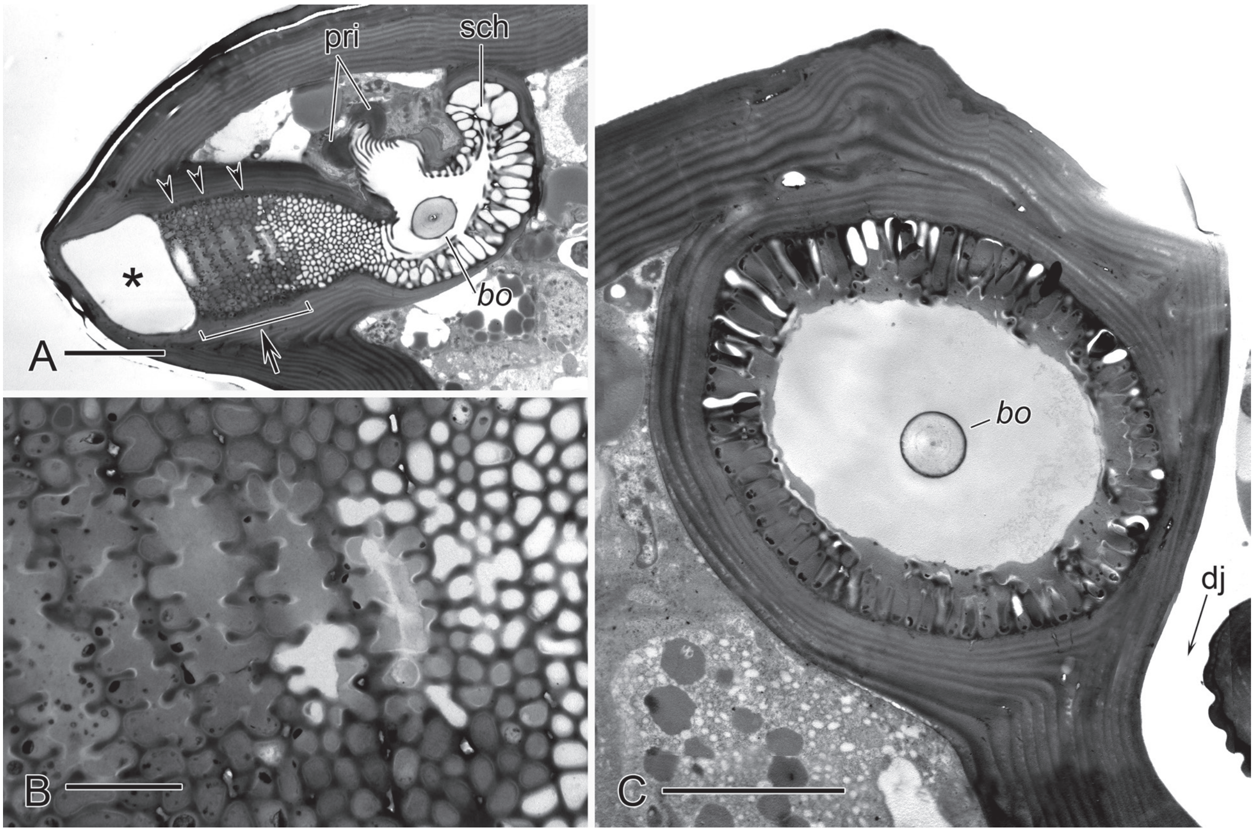
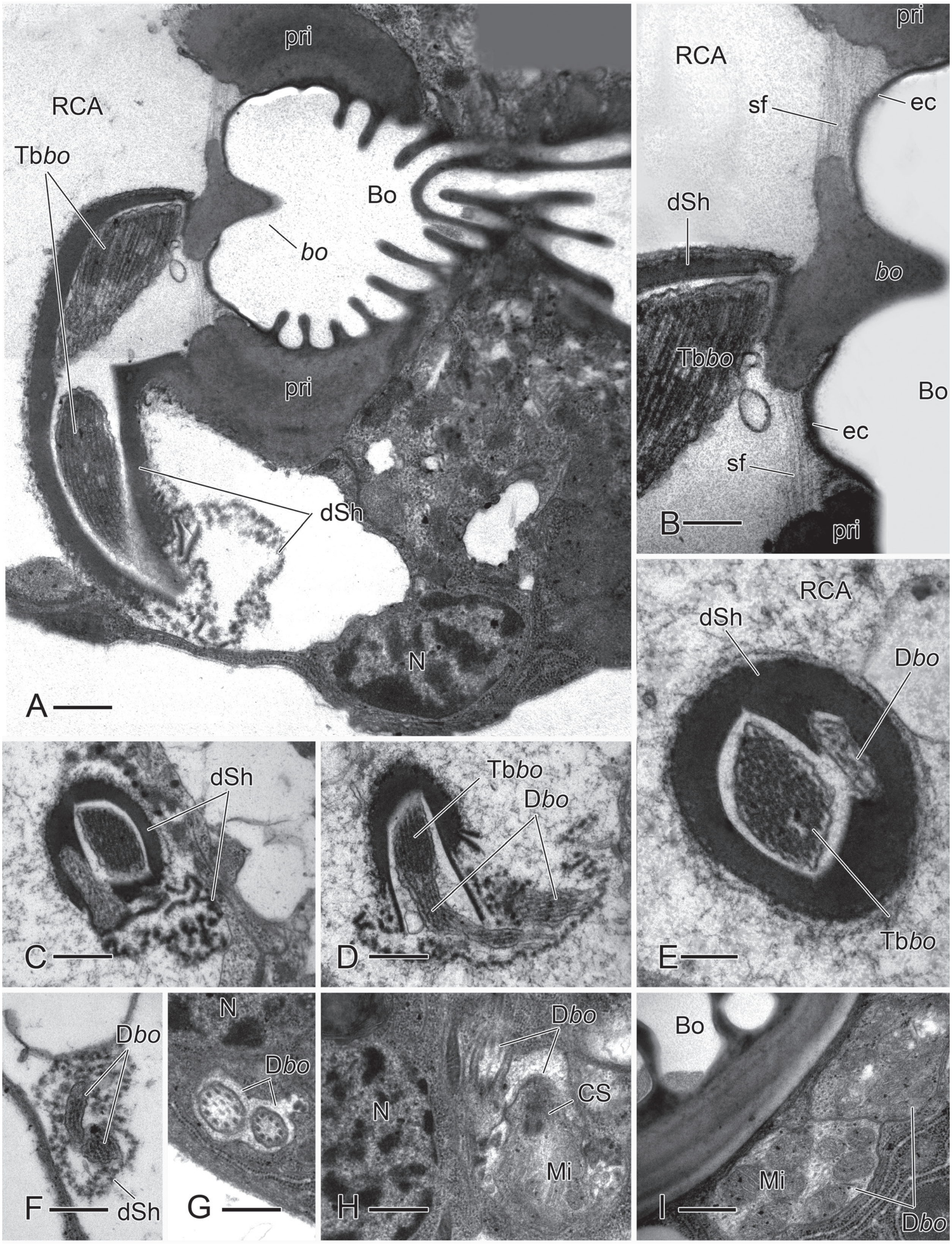



▲ **Figure 5**. Horizontally (A, B) and sagittally (C) sectioned specimens showing the distal region of the sculptured bothridial wall filled with secretion. (**A**) Overview of a partly tangentially sectioned bothridium. Asterisk indicates region with smooth wall followed internally by sculptured region. Arrow indicates sculptured region with secretion-filled small wall-chambers. Note circular ridges (arrowheads). Scale bar: 5 µm. (**B**) Detail of A showing transition between secretion-filled small chambers and empty chambers. Scale bar: 1 µm. (**C**) The bothridium region with secretion-filled small wall-chambers is visible in cross section here. Scale bar: 5 µm.

Abbr.: ***bo*** – bothridial seta, **dj** – dorsosejugal furrow, **pri** – proximal cuticular ring into which the bothridial seta (not encountered here) is inserted, **sch** – side chamber of bothridium.

◄ **Figure 4**. Cross (A, B, lateral is left) and horizontal (C) sectioned specimens showing insertion site of bothridial seta. All figures in same scale as shown in Fig. 4C. Scale bar: 5 µm. (**A**) The insertion site of the bothridial seta is positioned ventral of that of the interlamellar seta. One tubular body contacts the base of the bothridial seta. (**B**) Slightly more posterior, the bothridial seta is visible and the sharp bent of the bothridium is evident. (**C**) The insertion of the bothridial seta is located close to the anterior wall of the cuticular elevation which bears the bothridial and interlamellar setae. Note side chamber and the smooth (*) and sculptured regions of the bothridial wall. In the distal region of the sculptured wall, the small wall-chambers are filled with secretion (arrows).

Abbr.: **Bo** – bothridium, ***bo*** – bothridial seta, **D*bo*** – dendrites of bothridial seta, **D*in*** – dendrites of interlamellar seta, **dj** – dorsosejugal furrow, **dSh** – dendritic sheath, ***in*** – interlamellar seta, **Li** – lipid inclusion, **pri** – proximal cuticular ring into which the bothridial seta is inserted, **RCA** – receptor lymph cavity, **sch** – side chamber of bothridium, **Tb*in*** – tubular bodies of dendrites innervating interlamellar seta, **Tb*bo*** – tubular bodies of dendrites innervating bothridial seta.




▲ **Figure 6**. Details of the innervation of the trichobothrium of *Heterochthonius gibbus*. (**A**) Detail of Fig. 4A. One dendrite has reached the base of the bothridial seta. Note thick dendritic sheath closely contacting the tubular body. More proximally the dendritic sheath disintegrates into thin sheets and strands. Scale bar: 0.5 µm. (**B**) The bothridial seta is connected to the surrounding proximal cuticular ring only by some suspension fibers and a thin epicuticular layer. Scale bar: 0.2 µm. (**C**) One dendrite is sectioned proximal of its tubular...

## 5. Acknowledgements

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(◄ continued figure 6) body. Scale bar: 0.5 µm. (**D**) The thick dendritic sheath ends abruptly and continues into dense sheets and strands. Scale bar: 0.5 µm. (**E**) Cross section through the dendrites. One contains the dense tubular body (compare Fig. 3F). Scale bar: 0.2 µm. (**F**) The dendrites proximal of the tubular bodies and thick dendritic sheath. Scale bar: 0.5 µm. (**G**) The dendrites more proximally close to the ciliary segment show only peripheral microtubules (compare Fig. 3C). Scale bar: 0.5 µm. (**H**) Dendrites at the ciliary segment containing basal bodies enter the inner segment of the dendrite with mitochondria. Scale bar: 0.5 µm. (**I**) The two inner segments of the dendrites of the trichobothrium with numerous mitochondria (compare Fig. 3A). Scale bar: 0.5 µm.

Abbr.: **Bo** – bothridium, ***bo*** – bothridial seta, **CS** – ciliary segment, **D*bo*** – dendrite innervating bothridial seta, **dSh** – dendritic sheath, **iRCA** – inner receptorlymph cavity, **Mi** –mitochondrium, **N** – nucleus, **pri** – proximal cuticular ring into which the bothridal seta is inserted, **RCA** – receptorlymph cavity, **sf** –suspension fibers, **Tb*bo*** – tubular bodies of the dendrites innervating the trichobothrium.

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