European Journal of Taxonomy 511: 1–100
https://doi.org/10.5852/ejt.2019.511
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2019 · Kolicka M.

Monograph

urn:lsid:zoobank.org:pub:8FDAD45D-1B7D-446F-8B34-026EDF192210

Gastrotricha – not only in sediments: new epiphytic species of Chaetonotida from the Jubilee Greenhouse of the Botanical Garden in Kraków

Małgorzata KOLICKA

Department of Animal Taxonomy and Ecology, Institute of Environmental Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland.
Email: kolicka@amu.edu.pl

urn:lsid:zoobank.org:author:550BCAA1-FB2B-47CC-A657-0340113C2D83

Abstract. Although Gastrotricha have previously been recorded in bottom sediments of greenhouses as well as in micro-reservoirs of Bromeliaceae, palm houses provide a more specific microhabitat for these animals that often originate from different regions of the world. This paper presents an investigation of gastrotrich assemblages associated with aquatic plants. Eight species of the epiphytic chaetonotids were found in the Jubilee Greenhouse of the Botanical Garden in Kraków (Poland), including three species new to science, *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov., *C.* (*Hystricochaetonotus*) *horridus* sp. nov. and *C.* (*H.*) *inaequabilis* sp. nov. Two other species are new to Poland, *C.* (*C.*) *paucisquamatus* Kisielewski, 1991 and *C.* (*Zonochaeta*) *cestacanthus* Balsamo, 1990, both recorded here for the first time outside their *terra typica*. These observations confirm that greenhouses and palm houses provide many ecological niches and favourable conditions for the development of a number of unintentionally introduced species which cannot be found outside their original climate conditions.

Keywords. Alien species, *Chaetonotus*, new species, new records, palm house.

Kolicka M. 2019. Gastroticha – not only in sediments: new epiphytic species of Chaetonotida from the Jubilee Greenhouse of the Botanical Garden in Kraków. *European Journal of Taxonomy* 511: 1–100.
https://doi.org/10.5852/ejt.2019.511

Introduction

The beginning of the 20th century can be described as a period of very dynamic growth of urban areas throughout the world. This process is directly connected not only with the growing number of areas covered by compact housing but also with globalisation and the unification of environments (Ignatieva 2010). Palm houses and greenhouses are a frequent and common element in many major European cities. Many such structures were built as early as in the 18th and 19th centuries, and they hosted exhibitions of exotic vegetation species and ornamental elements (e.g., volcanic lava, boulders, logs), which were often brought from different natural environments (Britton 1896; Ignatieva 2010). New, modern palm houses and greenhouses were also created in the 20th and 21st centuries, using plant species from own agriculture, botanical stores or exchanges between palm houses. Regardless of the type of greenhouse, many animals species (both local and foreign) could have been brought in a random and uncontrolled manner together with the plants, seeds, soil, litter and other components of the exhibitions (e.g., Kolicka

et al. 2015). Palm houses provide these accidentally introduced organisms with specific conditions for colonisation and habitation that are different from outside anthropic habitats, e.g., municipal parks or squares (e.g., Duggan & Duggan 2011; Zawierucha *et al*. 2013). Due to the high temperatures and humidity kept at a constant level, they create favourable conditions for the formation of stable and numerous populations of invertebrates which function in an unchanged form for many years (e.g., Kolicka *et al*. 2013). Because of that, palm houses and greenhouses are often regarded as 'tropical islands' in a moderate climate (e.g., Zawierucha *et al.* 2013). These 'islands', as habitats that are distant and isolated from their natural counterparts and other greenhouses, could be a perfect place for research on newly introduced, alien communities of species and the new areas they occupy as well as on variability within and among isolated populations separated from their source habitats.

Studies on palm house gastrotrichs have previously been conducted in Poznań, Łódź (Poland) and Copenhagen (Denmark) (Kolicka *et al.* 2013; Kolicka 2014, 2016), and these microinvertebrates seem to be a constant element of these artificial habitats. However, previous research always concerned the bottom sediments or microreservoirs formed in the axils of Bromeliaceae. Species of Gastrotricha are components of benthic, epibenthic and epiphytic communities. All these habitats need to be the subjects of conducted analyses, as otherwise a false conclusion might be reached that greenhouse faunas do not reflect all the types of environments that these animals occupy in natural conditions. In inland waters, gastrotrichs are a common, abundant group of invertebrates, crucial in meiofauna communities of all types of aquatic and semi-aquatic ecosystems (e.g., Kisielewski 1997a). In nature, they are an important element of the benthic communities (they occur in particularly large abundance in bottom sediments that are very rich in organic matter) as well as of the epiphytic fauna (e.g., Balsamo & Todaro 2002; Balsamo *et al.* 2014).

Taxonomic studies of Gastrotricha have so far mainly focused on the species of benthic communities, both from greenhouses and natural environments. Investigations focusing only on communities of submerged plant fauna remain scarce (e.g., Kisielewski 1981, 1991; Nesteruk 2000, 2004, 2010, 2011). However, analyses of bottom sediments from reservoirs or stations with a rich aquatic vegetation reveal a much higher abundance and species richness of gastrotrichs (e.g., Kisielewski 1986). This may be caused by mixing sediment and vegetation faunas or it may be linked with an increased production of organic matter from decaying plants. Analyses of mixed material (collected, for example, by using a net from the surface of the bottom and submerged plants) also indicate a large number of recorded species (e.g., Balsamo *et al.* 2014). Nonetheless, comparative studies on the gastrotrichofauna of submerged plants and bottom sediments show distinct differences in species composition and the dominance structure of various taxa. The number of common taxa between these two habitats is low, the dominant taxa are different, and the species number and diversity are higher in bottom sediments than in aquatic plants (Nesteruk 2004, 2011).

In my research, I have focused on analysing the composition of the gastrotrich epiphytic fauna forming in an anthropic habitat of the Jubilee Greenhouse of the Botanical Garden in Kraków (Poland). I would like to see whether this artificial habitat provides favourable conditions for Gastrotricha communities and to compare the results of this observation with previous data on palm house chaetonotids from bottom sediments as well as from microreservoirs formed in the axils of bromeliads (Kisielewski 1991; Kolicka *et al*. 2013, Kolicka 2014, 2016).

Material and methods

Study area

Samples were collected at the Jubilee Greenhouse of the Botanical Garden in Kraków (50°03′38″ N, 19°57′30″ E). This greenhouse was built in the years 1959–1966 in the southern part of the Botanical

Garden of Jagiellonian University. The Jubilee Greenhouse comprises 8 departments, viz. the section of the palm house, of carnivorous plants, of aquatic and semi-aquatic plants, of useful tropical plants, of cycads, of desert and semi-desert plants and the nursery section. The research area was the aquatic and semi-aquatic plant section, with large water reservoirs (Fig. 1). These reservoirs with bottom sediments are an exposition place for many plants and some small, ornamental fish species. The submerged plants in this tank come from seeds imported from natural habitats, exchanged between palm houses or from the Botanical Garden's own nursery, whereas the fish come from aquarium shops. Most of the vegetation is cultivated directly in the bottom sediments, but some of the plant species grow in pots immersed in the reservoirs. Manure is added to these pots twice a year. The reservoirs are cleaned once a year, the plants are at that time transferred to a tank in the nursery section, while the water and half of the sediments are exchanged for new ones. The sediments in the aquatic reservoir and pots come from the local area whereas the fresh water for the tank is taken from a municipal water supply. The temperature in this section does not fall below 23°C during the year.

Fig. 1. Study area. **A**. The inside of Jubilee Greenhouse at the Botanical Garden in Kraków. **B**. Sampling site.

Sampling and documentation

Samples of aquatic plants were taken two times (15 November 2013 and 17 April 2014) from water reservoirs at the Jubilee Greenhouse of the Botanical Garden in Kraków. During both sampling sessions, the material was collected at the same spots from three stations within the reservoirs. However, between these sessions the plant arrangement was changed and the samples were collected from different plants during the first and second sampling (see Table 1). Samples of submerged vegetation were collected by picking the plants and squeezing water out of them thoroughly into a container, rinsing and squeezing them one more time, and then picking fresh, non-squeezed plants and placing them in a 1000 cm^3 container. Water plant samples were collected using the standard method for gastrotrichofauna research due to the limited effectiveness of other methods (Kisielewski 1997a). Within 5 days of collecting the material, a total of 5 cm^3 of water from the vegetation was analysed under an Olympus SZ51 stereo microscope. All specimens were observed, photographed and documented alive under an Olympus BX41 compound microscope (Tokyo, Shinjuku, Japan) equipped with phase contrast and an Array Artcam 300 digital camera (Tokyo, Shinjuku, Japan). Morphometric characters were measured in cellSens Entry 1.12 software (Olympus). All measurements are given in micrometres (µm) and all formulas used are given as a percentage (%) (Kisielewski 1981, 1991, 1997a; Hummon *et al.* 1992).

Table 1. Sampling sites with specified aquatic plant species.

Site	Session 1 (15 Nov. 2013)	Session 2 (17 Apr. 2014)
I	*Myriophyllum verticillatum* L.	*Myriophyllum verticillatum* L.
II	*Elodea nuttallii* (Planch.) H.St.John	*Myriophyllum verticillatum* L.
III	*Limnophila sessiliflora* Blume	*Elodea nuttallii* (Planch.) H.St.John

Morphological analyses

Morphological characters were only measured if they were amenable to accurate measurement. Because of the generally low taxonomic usefulness of preserved gastrotrichs, each specimen was documented using a set of photomicrographs and each holotype was additionally documented with detailed schematic drawings (all deposited in the Natural History Collections at Adam Mickiewicz University, Poznań = NHC). The International Code of Zoological Nomenclature allows for such a documentation of types in article 73.1.4 (The International Commission on Zoological Nomenclature 1999), even if the documented specimen no longer exists. The taxon descriptions follow the convention of Hummon *et al.* (1992), in which the distance of a morphological character from the anterior end is expressed as percentage units (U) of the animal's total length. In the descriptions of new species in this paper, the measurements of width of different body sections were omitted because they would be strongly influenced by the pressure of the coverglass on the studied live specimens. The identification of gastrotrichs, their morphological study and terms follow Kisielewski (1981, 1991, 1997a) and Kolicka *et al.* (2016). The terms describing the shape of the furcal branches and furcal indentation follow Roszczak (1969). This paper uses the following formula to describe the distribution of scales:

$$\text{Ratio of scale distribution} = \frac{\text{total number of longitudinal alternating rows of scales}}{\text{number of scales in central longitudinal rows}} \times 100\%$$

as well as the pharynx formulae according to Kisielewski (1991):

$$a = \frac{\text{width of anterior thickening}}{\text{pharynx length}} \times 100\% \qquad n = \frac{\text{width of pharyngeal narrowing}}{\text{pharynx length}} \times 100\%$$

$$m = \frac{\text{width of middle pharynx}}{\text{pharynx length}} \times 100\% \qquad p = \frac{\text{width of posterior thickening}}{\text{pharynx length}} \times 100\%$$

and the pharynx-to-intestine length ratio according to Kolicka *et al.* (2016):

$$I = \frac{\text{pharynx length}}{\text{intestine length}} \times 100\%$$

The use of these formulae allows for the objective comparison of these morphological features between different taxa and the demonstration of scale distribution and detailed pharynx shape in a numerical manner. The pharynx-to-intestine length ratio helps estimate the age of specimens, thus avoiding misclassification by analysing juvenile, subadult and adult individuals together. Juvenile and subadult specimens have a significantly higher I-ratio than adults, usually for representatives of *Chaetonotus* at > 70% and 55%–70%, respectively. In this paper, the following abbreviations were used: D = dorsal; DL = dorsolateral; L = lateral; LV = ventrolateral; V = ventral, sensu Kolicka *et al*. (2016, see S1 and S2).

Results

The analysed material consisted of 208 specimens belonging to three genera, two subgenera and nine species, including three species that are new to science, namely *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov., *C.* (*Hystricochaetonotus*) *inaequabilis* sp. nov. and *C.* (*H.*) *horridus* sp. nov. Two other species

recorded at the Jubilee Greenhouse of the Botanical Garden in Kraków turned out to be new to Poland; the first species, *C.* (*C.*) *paucisquamatus* Kisielewski, 1991, was described from and is only known from Brazil; the second newly reported species, *C.* (*Zonochaeta*) *cestacanthus* Balsamo, 1990, was described from Italy and was previously recorded only in that country. Another species that was found, namely *C.* (*H.*) *hystrix* Mečnikow, 1865, is well known in Poland and is considered as a taxon with a worldwide distribution. The last two of the recorded species were identified as *Lepidodermella* aff. *squamata* (Dujardin, 1841) and *Heterolepidoderma* aff. *majus* Remane, 1927. These taxa were defined as species with an unclear taxonomic rank because they corresponded well with the original description, but possessed a single character that differed from previous records (see the 'Remarks' section for these species). Live euglenids were present inside the intestines of 4 out of 208 specimens (see Kisielewska *et al*. 2015). In all the samples, rotifers (representatives of Monogononta and Bdelloidea), ostracods and rare polychaetes were observed as accompanying fauna.

Phylum Gastrotricha Mečnikow, 1865
Order Chaetonotida Remane, 1925 [Rao & Clausen 1970]
Suborder Paucitubulatina d'Hondt, 1971
Family Chaetonotidae Gosse, 1864 (*sensu* Leasi & Todaro 2008)
Subfamily Chaetonotinae Gosse, 1864 (*sensu* Kisielewski 1991)

Genus ***Chaetonotus*** Ehrenberg, 1830

Type species

Trichoda larus Müller, 1773 (= *Chaetonotus larus* (Müller, 1773)).

Terra typica

Denmark.

Remarks on genus

This is a polyphyletic taxon, with only one apparently monophyletic subgenus (*Chaetonotus* (*Zonochaeta*) Remane, 1927); it encompasses 175 nominal freshwater species and 44 nominal marine species (Kånneby *et al*. 2012, 2013; Todaro 2018). Present in benthic, interstitial, periphytic and rarely semi-planktonic habitats (Kisielewski 1997a).

Subgenus ***Chaetonotus*** s. str. Ehrenberg, 1830

Type species

Trichoda larus Müller, 1773 (= *Chaetonotus larus* (Müller, 1773)).

Terra typica

Denmark.

Remarks on subgenus

This is clearly a polyphyletic subgenus in terms of molecular data (Kieneke *et al.* 2008; Kånneby *et al.* 2012, 2013); it encompasses 84 nominal freshwater and 4 nominal marine species (Kieneke & Schmidt-Rhaesa 2015; Todaro 2018). Present in benthic, interstitial, periphytic and rarely also in semi-planktonic habitats (Kisielewski 1997a).

Chaetonotus* (*Chaetonotus*) *invitatus sp. nov.
urn:lsid:zoobank.org:act:5350662C-4565-4EB6-96B0-4742ED038286
Figs 2–11, A1–A2; Tables 2, A1–A2

Diagnosis

Slender, bottle-shaped, body measuring from 174.6 to 194.7 μm in length. Head five-lobed, cephalion, epipleurae and hypopleurae clearly demarcated in head outline. Hypostomium kidney-shaped with horn-like protuberances anterolaterally and pair of reinforcements near anterior edge. Two additional plates beyond posterior hypostomium edge. Ocellar granules absent. In mouth ring, two weak cuticular teeth arising from anterior pharynx region. All scales one-lobed, with shallow to deep posterior notches, keeled and spined. Scales distributed in 23–25 single longitudinal rows (5–7D+4DL+6L+4LV+4V) with 25–27 scales in central row. Scales strongly differing morphologically in body areas. Scales located close to one another and with overlapping edges on furcal base and furcal appendages. Spines basally bent and thick, subsequently strongly and gradually tapering towards hair-like end, ventral spines hair-like along entire length. Lateral spines more strongly curved than dorsal and dorsolateral ones. Length of spines gradually increases from dorsal, dorsolateral, lateral and ventrolateral surfaces towards ventral surface and from head towards widest trunk region. Dorsally on posterior trunk region, two or three scales with longer and thicker spines. Dorsally and dorsolaterally on posterior trunk region, on furcal base and furcal appendages, scales with shorter spines, with rudimentary spines or without any spine. Dorsolaterally on furcal appendages, one pair of scales with long, rigid and spike-like spines reaching to furca inner indentation. Furcal appendages with two pairs of scales with long, thick parafurcal spines tapering to their ends. Ventral interciliary field covered with semirectangular plates on pharyngeal region and one-lobed, keeled scales on intestine region. Four pairs of ventral interciliary field terminal scales. Pharynx narrow, with anterior and posterior dilatations. Intestine straight without anterior section differing in form and morphology.

Etymology

From the Latin '*invitatus*' = 'invited', referring to the artificial place to which it was transferred.

Material examined

Holotype

POLAND • adult; Kraków, Botanical Garden, Jubilee Greenhouse, site 1; 50°03′38″ N, 19°57′30″ E; 15 Nov. 2013; M. Kolicka leg.; NHC-GCCI-20-1-25/h (photomicrographs, also in the author's collection).

Paratypes

POLAND • 24 adults, 5 subadults, 5 juveniles; same collection data as for holotype; NHC-GCCI-20-26-100/p (photomicrographs, also in the author's collection).

Description

Habitus. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. has a slender, bottle-shaped body (Figs 2, 5). The head is wide and the neck constriction is strongly marked. The neck gradually tapers to the beginning of the trunk (ca U38) (Figs 2, 5). The trunk is only slightly wider than the head and gradually dilates from ca U39 to ca U59, where it is at its maximum width. Then it gradually tapers slightly towards a weakly demarcated furcal base (from U85) (Fig. 2). The furcal indentation is parabolic in shape. The furcal branches are set apart and point slightly outwards (Figs 6G–H, 8). The adhesive tubes are long, slightly bent, narrow and very gradually taper slightly towards their ends. The adhesive tube ends are blunt (Figs 2, 6G–H, 8).

Fig. 2. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Schematic drawings. **A**. Dorsal body view. **B**. View of internal morphology. **C**. Ventral body view. Light grey areas indicate the areas of the insertion of ciliary bands.

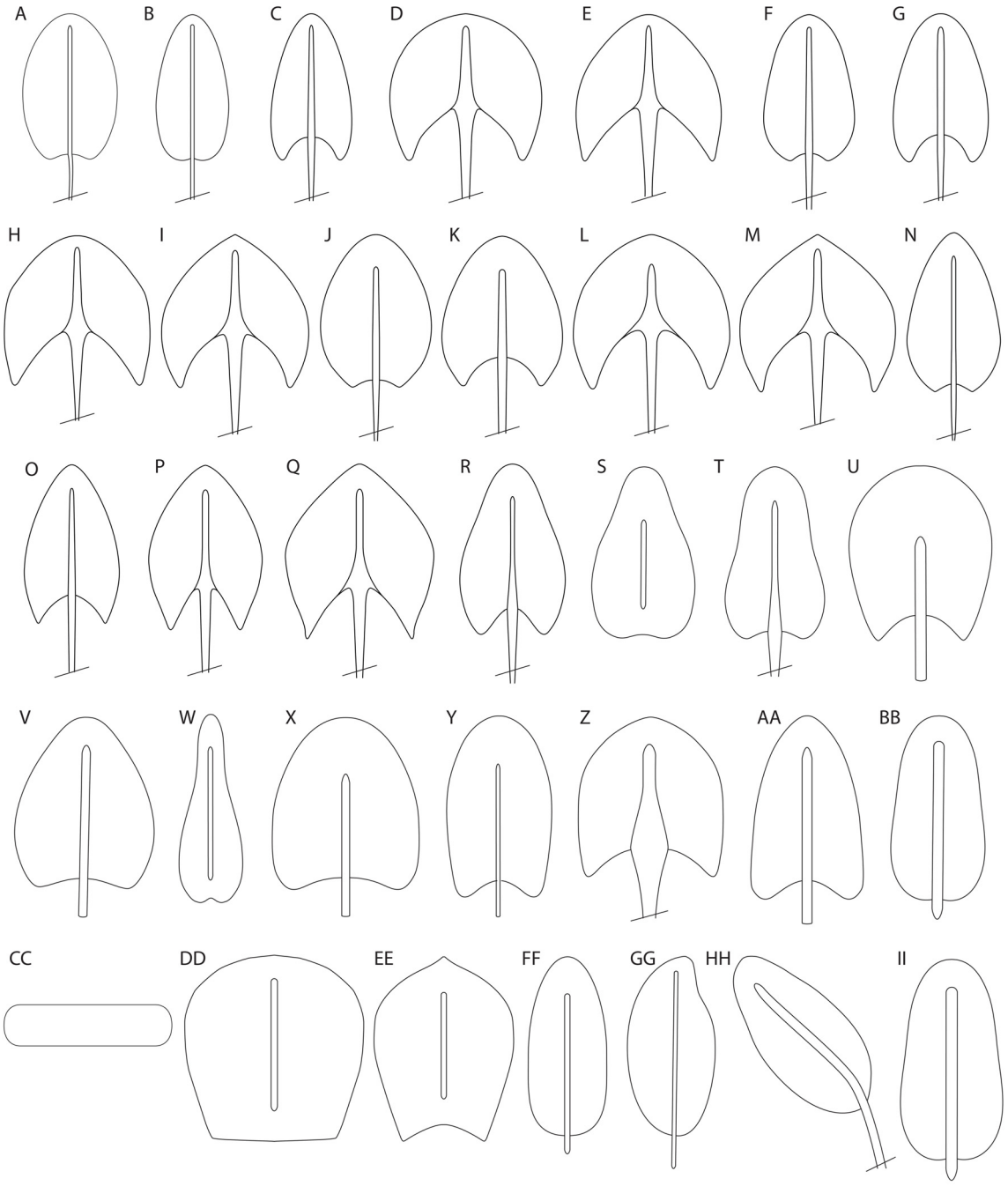

Fig. 3. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Schematic drawings of the scales. **A**. Head anteriormost dorsal scale (scale 1). **B**. Head dorsal scale (scale 2). **C**. Head dorsolateral scale (scale 3). **D**. Head lateral and ventrolateral scale (scale 4). **E**. Head ventral scale (scale 5). **F**. Anterior neck dorsal scale (scale 6). **G**. Anterior neck dorsolateral scale (scale 7). **H**. Anterior neck lateral and ventrolateral scale (scale 8). **I**. Anterior neck ventral scale (scale 9). **J**. Posterior neck dorsal scale (scale 10). **K**. Posterior neck dorsolateral scale (scale 11). **L**. Posterior neck lateral and ventrolateral scale (scale 12). **M**. Posterior neck ventral scale (scale 13). **N**. Trunk dorsal scale (scale 14). **O**. Trunk dorsolateral scale (scale 15). **P**. Trunk lateral and ventrolateral scale (scale 16). **Q**. Trunk ventral scale (scale 17). **R**. Scale 18. **S**. Scale 19. **T**. Scale 20. **U**. Scale 21. **V**. Scale 22. **W**. Scale 23. **X**. Scale 24. **Y**. Scale 25. **Z**. Scale 26. **AA**. Scale 27. **BB**. Scale 28. **CC**. Scale 29. **DD**. Scale 30. **EE**. Scale 31. **FF**. Scale 32. **GG**. Scale 33. **HH**. Scale 34. **II**. Scale 35.

Head. The head is five-lobed, long and parabolic. The cephalion (U1–U7) is long and wide, it is visible on the dorsal head surface as an inverted, rounded triangle. It is clearly demarcated in the body outline and its dorsal edge is free and does not adhere to the head surface (Fig. 7A–B). The pleurae are large, convex and clearly demarcated in the head outline, the hypopleurae are only slightly larger than the epipleurae (Fig. 2). Between the epipleurae and hypopleurae, deep notches are present. The epipleurae (U3–U7) are located on the dorsal, dorsolateral, lateral and ventrolateral surfaces, whereas the hypopleurae (U8–U12) cover the dorsal, dorsolateral, lateral, ventrolateral and ventral surfaces in such a manner that their greatest portion is located on the ventral side. The hypostomium is kidney-shaped and has two horn-like protuberances placed anterolaterally and a pair of strong reinforcements near its anterior edge (U3–U6) (Figs 2C, 6B). One pair of additional plates is located posterolaterally to the hypostomium, at U6–U7. These plates are wide and short and their lateral edges extend to the edges of the ventral epipleurae (Fig. 6B). Two pairs of cephalic ciliary tufts are present. The anterior tufts emerge laterally between the cephalion edge and the dorsal edge of the epipleurae (at U3). The anterior tufts consist of 5 cilia which are bent and short, and their length increases from the first to the last cilium (Table A1). The posterior tufts have 5 cilia each and emerge laterally between the epipleurae and the hypopleurae (at U7–U8). Cilia in the posterior tufts are long and nearly straight and their length increases from the first cilium to the last, long cilium (Table A1). Ocellar granules are absent. The mouth ring is located terminally at U1–U3, is wide and has long, strong finger-like reinforcements as well as very long cuticular inner hairs (Figs 2, 9A–B). Inside the mouth ring, two small and weak cuticular teeth arising from the anterior pharynx region are present (Fig. 9B–C). Suboral bristles emerge in three pairs of tufts, laterally to the mouth ring, near the lateral edges of the hypostomium and in lines below the additional hypostomium plates (Fig. 2C).

Scales. The body is covered with one-lobed scales that adhere along their entire surface to the cuticle (Figs 3, 6–7). The scales have a straight keel and are egg-shaped with very weak posterior notches to very deep posterior notches. The scales are distributed in 23–25 longitudinal alternating rows

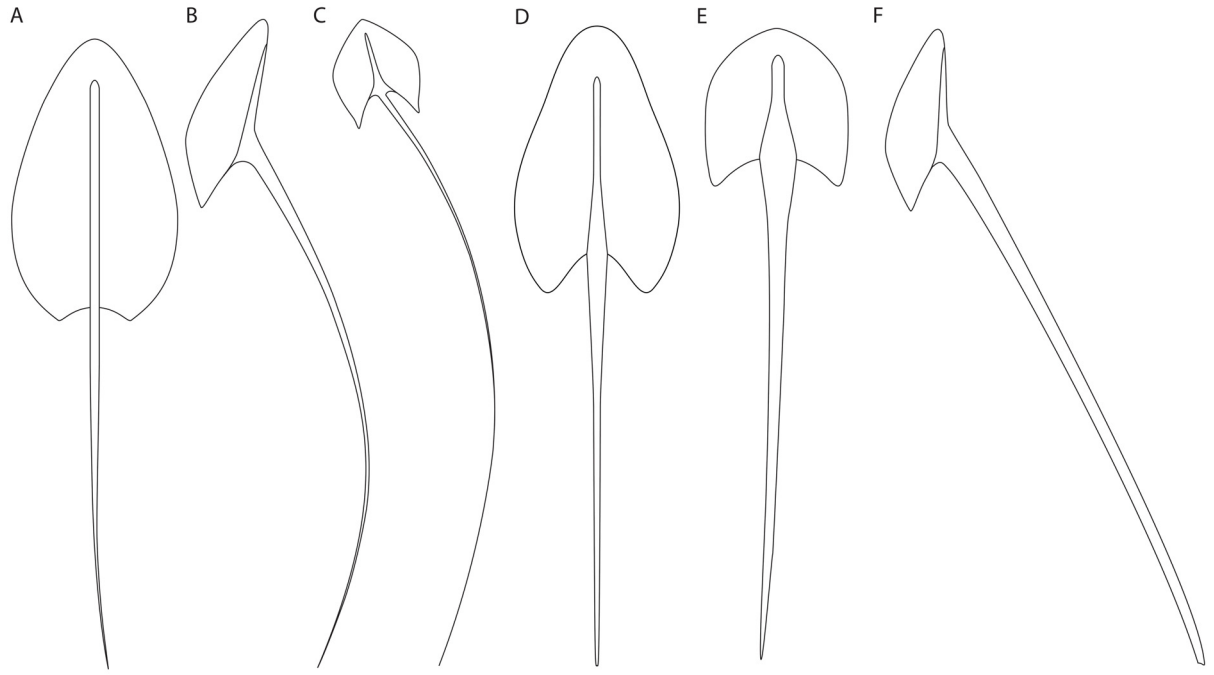

Fig. 4. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Schematic drawings of the spine types. **A**. Dorsal and dorsolateral spine type. **B**. Lateral and ventrolateral spine type. **C**. Ventral spine type. **D**. Scale 18 spine type. **E**. Dorsolateral furcal appendage spine type. **F**. Parafurcal spine type.

Table 2. Main morphometric characters of *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. N = number of specimens analysed; Range = the smallest and the largest structure found among all specimens measured. All measurements in micrometers (μm).

Characters	N	Holotype	Range of adult paratypes
Body length	23	193.18	174.64–194.66
Furca length	22	33.17	31.14–34.45
Adhesive tube length	22	18.97	16.39–19.20
Number of scales in central longitudinal row	25	27	25–27
Total noumber of longitudinal alternating rows of scales	25	25	23–25
Head scales length × width	22	1.94–4.94 × 1.91–4.23	1.58–5.19 × 1.60–4.91
Neck scales length × width	22	2.55–6.29 × 3.02–5.71	2.08–7.09 × 2.46–6.44
Trunk scales length × width	22	3.57–8.78 × 2.79–5.97	2.84–9.38 × 2.22–7.39
Head spines length	22	3.88–24.11	3.31–26.39
Neck spines length	22	6.37–27.41	5.03–31.86
Trunk spines length	22	10.09–31.06	7.84–34.26
Mouth ring diameter	22	8.43	7.58–9.47
Pharynx length	23	56.84	51.02–59.64

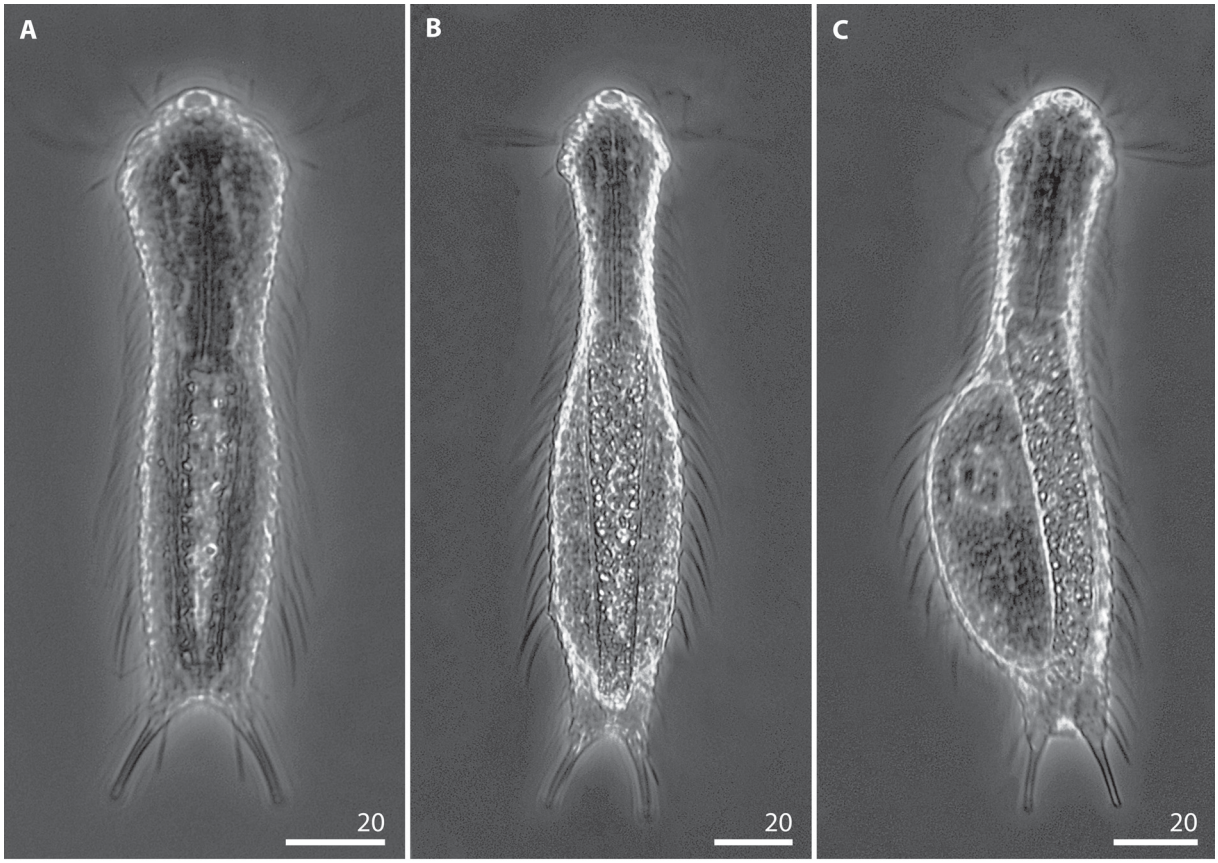

Fig. 5. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Habitus. Phase contrast microphotographs. **A**. Juvenile specimen. **B**. Adult specimen. **C**. Specimen with mature egg.

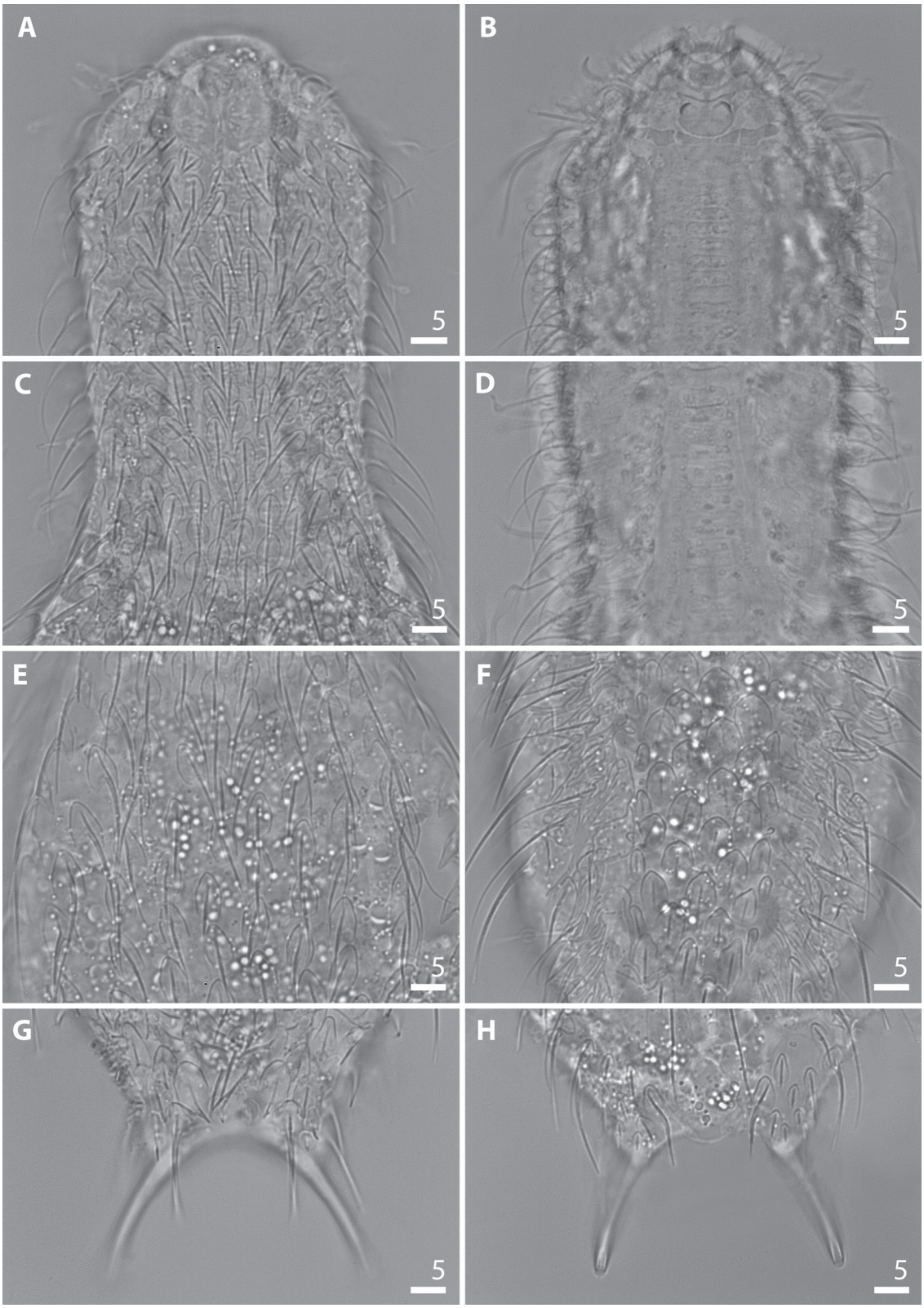

Fig. 6. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Bright field microphotographs. **A**. Head, dorsal view. **B**. Head, ventral view. **C**. Neck, dorsal view. **D**. Neck, ventral view. **E**. Trunk, dorsal view. **F**. Trunk, ventral view. **G**. Furca base and furcal appendages, dorsal view. **H**. Furca base and furcal appendages, ventral view.

(5–7D+4DL+6L+4LV+4V) with 25–27 scales in the central row. The longitudinal rows of scales run straight and are arranged in parallel to one another from the top of the head to the widest body region. Dorsally and dorsolaterally on the posterior trunk region, furca base and furcal appendages, the scales are arranged in rounded arcs and in a rosette (Figs 2, 7C–D, 8A). The scales are located close to one another, but on the head, neck and anterior and central trunk part they do not overlap. The edges of the scales overlap only on the furcal base and furcal appendages (Figs 2, 8A). The scales show morphological diversity throughout the particular body regions in terms of shape and size (Fig. A1). The head anteriormost scales are situated near the posterior edge of the cephalion. These scales are oval with shallow posterior notches (scale 1; Fig. 3A). The remaining head dorsal scales (scale 2; Fig. 3B) are more elongated and have shallower posterior notches. The head dorsolateral scales (scale 3; Fig. 3C) become shorter than the dorsal scales and have deeper posterior notches. The head lateral and ventrolateral scales (scale 4; Fig. 3D) become more semi-rounded, shorter and wider than the dorsolateral ones and possess deep posterior notches, whereas the ventral scales are smaller, wide and have more pointed anterior edges (scale 5; Fig. 3E). On the neck, the scales are shorter and wider than the scales on the head area (scales 6–9; Fig. 3F–I) and their size gradually increases towards the trunk region (scales 10–13; Fig. 3J). The neck dorsal scales (scales 6 and 10; Fig. 3F, J) are egg-shaped and possess weak posterior notches. The neck dorsolateral scales (scales 7 and 11; Fig. 3G, K) become gradually larger than the dorsal scales and have deeper posterior notches. The neck lateral and ventrolateral scales (scales 8 and 12; Fig. 3H, L) become more semi-rounded and deeply posteriorly notched. They are wider and gradually larger than the dorsolateral ones, whereas the ventral scales (scales 9 and 13; Fig. 3I, M) are

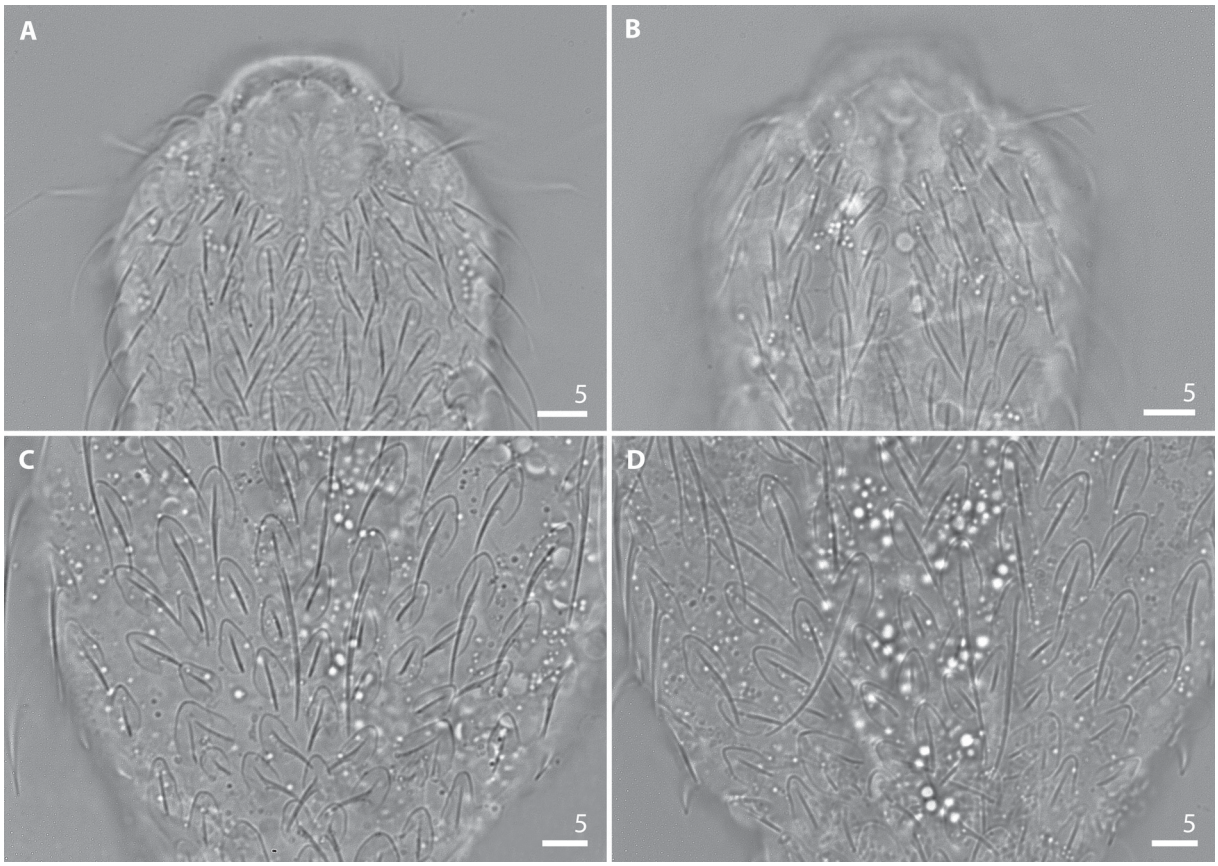

Fig. 7. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Bright field microphotographs. **A**. Detail of dorsal head view of adult specimen. **B**. Detail of dorsal head view of juvenile specimen. **C**. Dorsal view of posterior trunk region of specimen with two scales 17. **D**. Dorsal view of posterior trunk region of specimen with three scales 17.

smaller, wide and have more pointed anterior edges (Fig. 2C). The trunk dorsal scales (scale 14; Fig. 3N) from the anterior to posterior trunk part are egg-shaped, but with a more tapered anterior edge than the neck scales. These scales have weak posterior notches. The trunk dorsolateral scales (scale 15; Fig. 3O) become gradually larger than the dorsal scales and have deeper posterior notches. The trunk lateral and ventrolateral scales (scale 16; Fig. 3P) become more oval, gradually larger and wider than the dorsolateral ones, have a more pointed anterior edge and possess deep posterior notches. The trunk ventral scales (scale 17; Fig. 3Q) are smaller, shorter and wider, have more pointed anterior edges and a very deep posterior notch (Figs 2A, 6F). The scales in the ventral longitudinal row located closest to the ciliary band are distinctly smaller than the other scales and their anterior edge is oriented towards the bands at an angle of ca 40° (Figs 2C, 6B, D, F, H). Dorsally on the trunk posterior region (at U73–U77), two or three slightly larger scales with deeper posterior notches and much longer and stronger spines are present (scale 18; Fig. 3R). Near the scales with longer and stronger spines and posteriorly to them (at U75–U80), smaller, trifle pear-shaped scales are located with weak posterior notches, straight keels and without spines (scale 19; Fig. 3S). Subsequently, on U80–U85, dorsally on the posterior trunk region, 8 scales, that are triangle-shaped with strongly rounded edges, with clear posterior notches and a straight keel and spine, are situated (scale 20; Fig. 3T). On the dorsal posterior trunk region, one pair of small, semirounded scales with a straight keel and a short, straight spine is located in the notch of a pair of double keeled scales with trunk sensory bristles (at U82–U83) (scale 21; Fig. 3U). Dorsolaterally on the posterior trunk region and furcal base, two pairs of small semi-triangular scales with strongly rounded edges and shallow posterior notches, straight keels and straight rudimental spines are present (at U84–

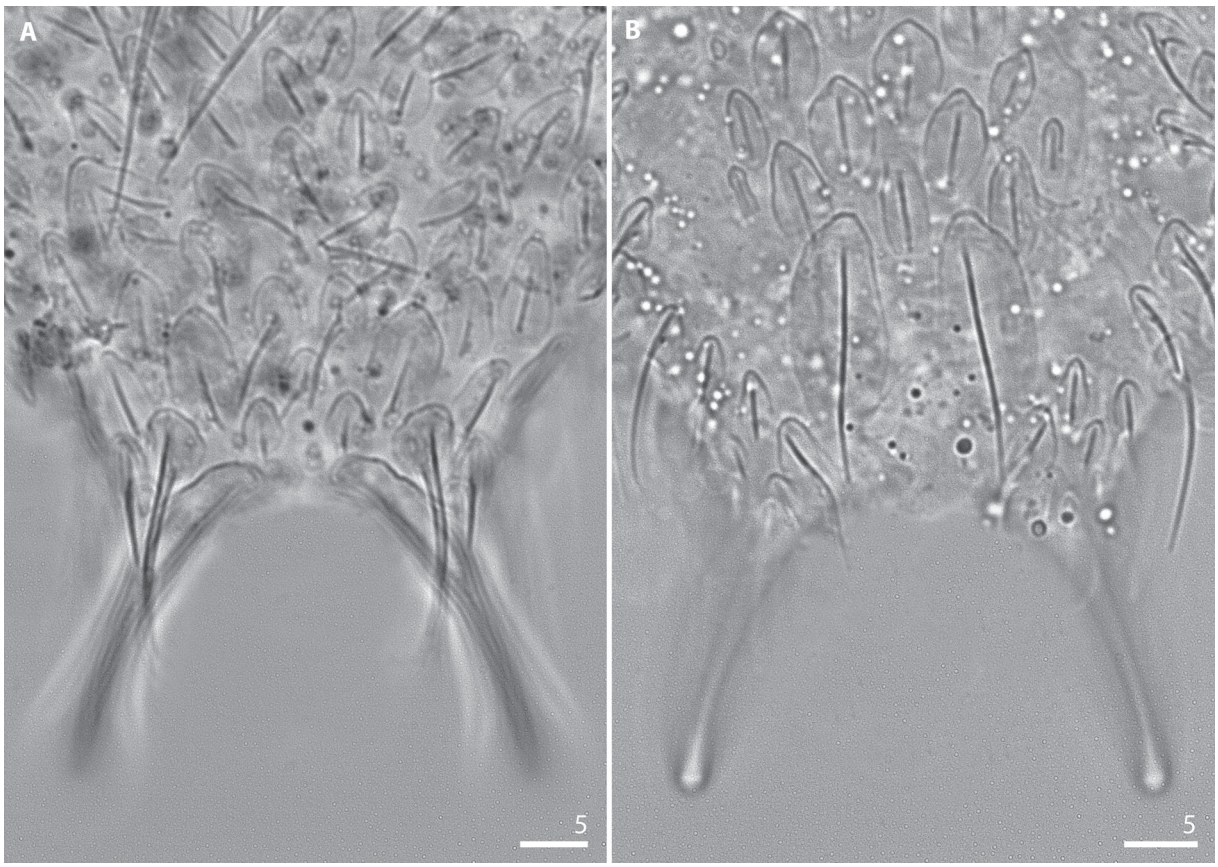

Fig. 8. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Bright field microphotographs. **A**. Dorsal view of the posterior trunk region, furca base and furcal appendage scales. **B**. Ventral view of the posterior trunk region, furca base and furcal appendage scales.

U87) (scale 22; Fig. 3V). Laterally on the posterior trunk region and on the furcal base, at U82–U88, two pairs of narrow, elongated pear-shaped scales with very weak posterior notches are present. These scales have long straight keels but are not spined (scale 23; Fig. 3W). Dorsally on the furcal base and furcal appendages at U85–U88, three semi-rounded scales with weak posterior notches, straight keels and short spines are present (scale 24; Fig. 3X). Laterally to them (to scales 24), on the dorsal furcal base, one pair of large (5.4–9.1 × 3.2–5.3 μm), oval scales with a shallow posterior notch, straight keel and a short, straight spine is situated (at U84–U87) (scale 25; Fig. 3Y). Dorsolaterally on the furcal appendages at U87–U89, one pair of large, rounded scales with prominent posterior notches is present (scale 26; Fig. 3Z). These scales have straight keels and long, rigid spines. Laterally to this pair of scales (to scales 26) at U88–U89, two pairs of small (2.6–6.1 × 1.8–4.1 μm), oval-shaped scales with a shallow indentation and straight keels and spines are present (scale 27; Fig. 3AA). On the lateral surface of the furcal appendage, two pairs of scales with parafurcal spines are present. The first pair is located at U88–U89 and the second one, i.e. the last pair of furcal lateral scales, is located at U90–U91. Both pairs are similar in shape to the posterior trunk scales (Figs 2, 6G). Ventrolaterally and ventrally on the furcal appendages and furcal base, two pairs of small (2.2–5.3 × 1.4–2.8 μm) oval scales without any posterior notches are present (at U85–U88). These scales have straight keels and straight rudimentary spines (scale 28; Fig. 3BB).

Spines. All spines emerging from the posterior scale region have no lateral denticles. The dorsal, dorsolateral (Fig. 4A), lateral and ventrolateral (Fig. 4B) spines are basally bent and thick, and subsequently strongly and gradually taper towards the slightly bent hair-like ends. The spines arising from the lateral,

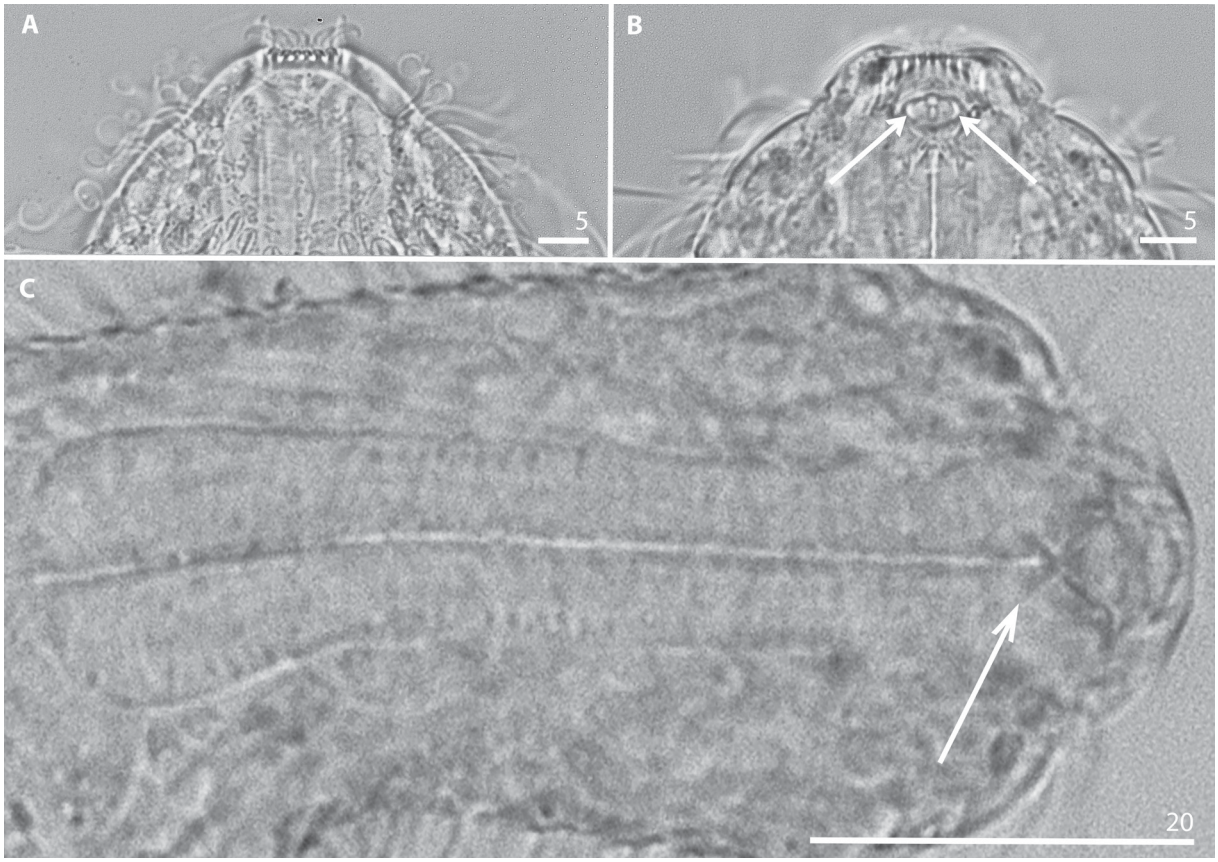

Fig. 9. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Adult specimen. Bright field microphotographs. **A**. Detail of the mouth ring, dorsal view. **B**. Detail of the mouth ring, internal view. **C**. Detail of the pharynx.

ventrolateral and ventral scales are much more strongly bent than the dorsal and dorsolateral spines. The ventral scale spines are hair-like along their entire length (Fig. 4C). The length of the spines gradually increases from the head towards the widest body region (from 3.9–24.1 to 10.1–31.1 μm). Then the length of the dorsal spines gradually shortens to the posterior trunk region. Moreover, the length of the spines gradually increases from the dorsal surface, along the dorsolateral, lateral, ventrolateral and ventral surfaces towards the ciliary bands (head: from 1.6–7.4 to 13.3–26.4 μm; neck: from 5.0–10.7 to 15.9–31.9 μm; trunk: from 7.8–16.5 to 19.6–34.3 μm) (Table A1). On the dorsal posterior trunk region, two or three spines of different types are present (arising from scales 18). These spines are much longer (16.6–20.0 μm) and stronger than the other dorsal spines and taper to blunt ends (Figs 2A, 6C–D). The spines arising from the dorsal and dorsolateral posterior trunk and furcal base scales (namely from scales 20, 22, 24, 27) are thick and straight, tapering to blunt ends (Fig. 4D). The posteriormost lateral trunk spines (16.1–25.1 μm) do not vary in length from the other lateral spines in the posterior trunk region. From the dorsolateral furcal appendage scales (scale 26) arise very long (14.5–18.4 μm), thick, rigid, basally bent and spike-like spines that extend to the inner furcal indentation (Figs 2A, 4E, 6G, 8A). These spines taper slightly to pointed ends. Two pairs of parafurcal spines, emerging from the lateral scales of the furcal appendages (at U88–U89 and at U90–U91), are thicker and longer (11.3–13.5 μm) than the other lateral body spines (Fig. 4F). These spines are basally bent and taper slightly towards their pointed ends (Figs 6G, 8A).

Dorsal sensory bristles. This species has three pairs of dorsal sensory bristles. The first pair is located on the head, directly between the lateral edge of the cephalion and the epipleurae (at U4), and emerges from small, round papillae. The second pair of sensory bristles is located on the neck (U19) and emerges

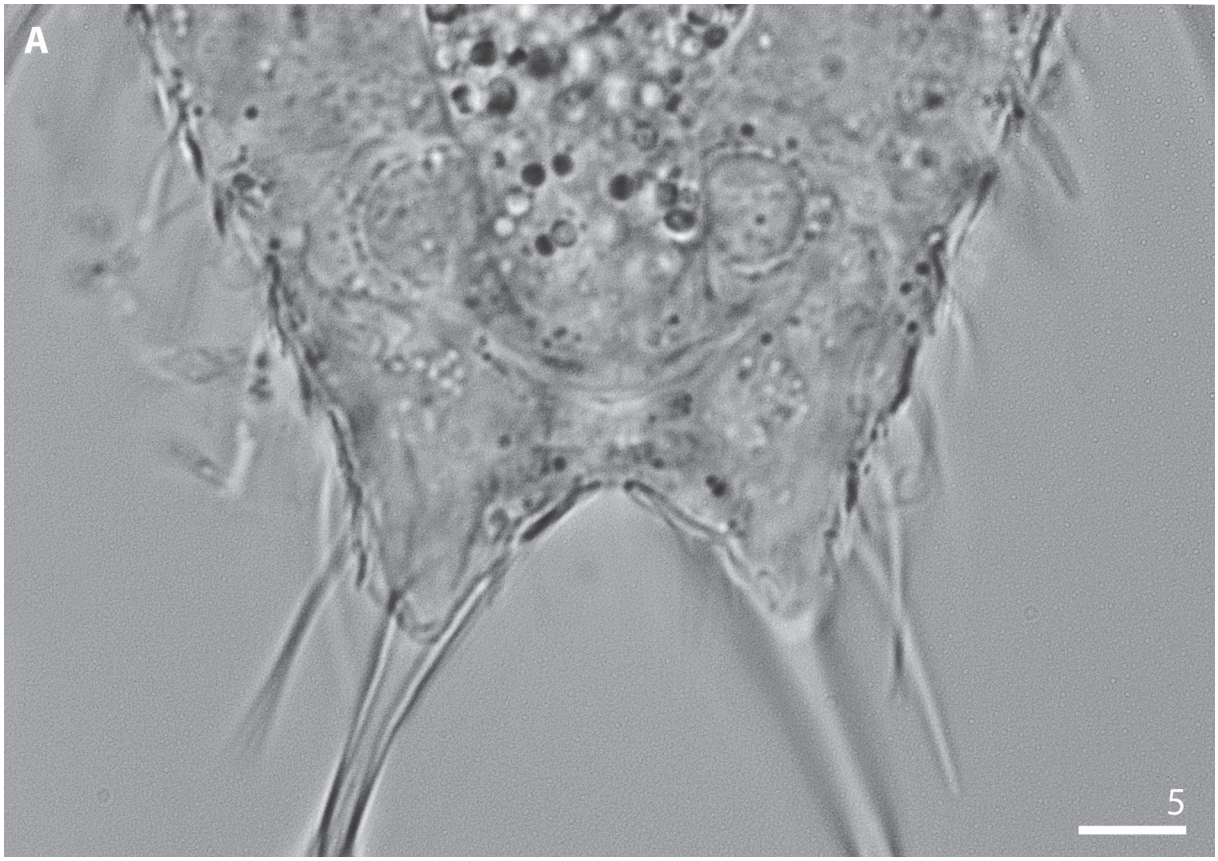

Fig. 10. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Detail of internal morphology. Bright field microphotography. X-organ.

from small, rounded papillae. The third posterior pair of sensory bristles emerges from the double-keeled scales located on the posterior trunk region at U81–U83. These scales are shaped like triangles with strongly rounded edges and a deep posterior notch. The keels of these scales are slightly bent, not connected and pass into rudimentary spines (Figs 2A, 8A).

Ventral ciliary bands and ventral interciliary field. Longitudinal ventral ciliary bands begin at U8 and run back to U86 (Figs 2C, 6B, D, F, H). On the head, at ca U8–U10, the ciliary bands are merged and lie close to the hypopleurae. The ventral interciliary field scales are distributed in single (on the pharyngeal region) and 5–7 (on the intestinal region) longitudinal alternating rows, with 29–33 scales in the central row, including 15–18 plate-like scales and 14–17 one-lobed scales. The entire pharyngeal region (from U10 to U31) is covered with short, wide plates (scale 29; Fig. 3CC) and their size gradually increases from the anterior to the posterior end (from 1.0–1.7 × 1.9–3.5 μm to 2.6–5.2 × 7.1–11.4 μm). On the intestinal region, one-lobed scales with overlapped edges are present (from U32 to U84). On the anterior part of the intestinal region the scales are semi-rectangular in shape, have weak keels and their posterior edges are straight, without posterior notches (scale 30, Fig. 3DD). Towards the furcal base the keels become more pronounced and on the edges of the anterior scales small, horn-like perturbances begin to appear; the posterior edges become notched (scale 31; Fig. 3EE). The last alternating row of interciliary field scales is of a different type, i.e., they are oval in shape without posterior notches, have straight keels and present rudimentary spines (scale 32; Fig. 3FF). The longitudinal row of ventral field scales closest to the ventral ciliary bands has significantly smaller and narrower scales than in the central rows. The first pair of terminal scales on the ventral interciliary field is large (14.8–17.1 × 6.6–8.1) and located at U84–U87. They are oval, asymmetrical in shape, possess a straight keel and a straight,

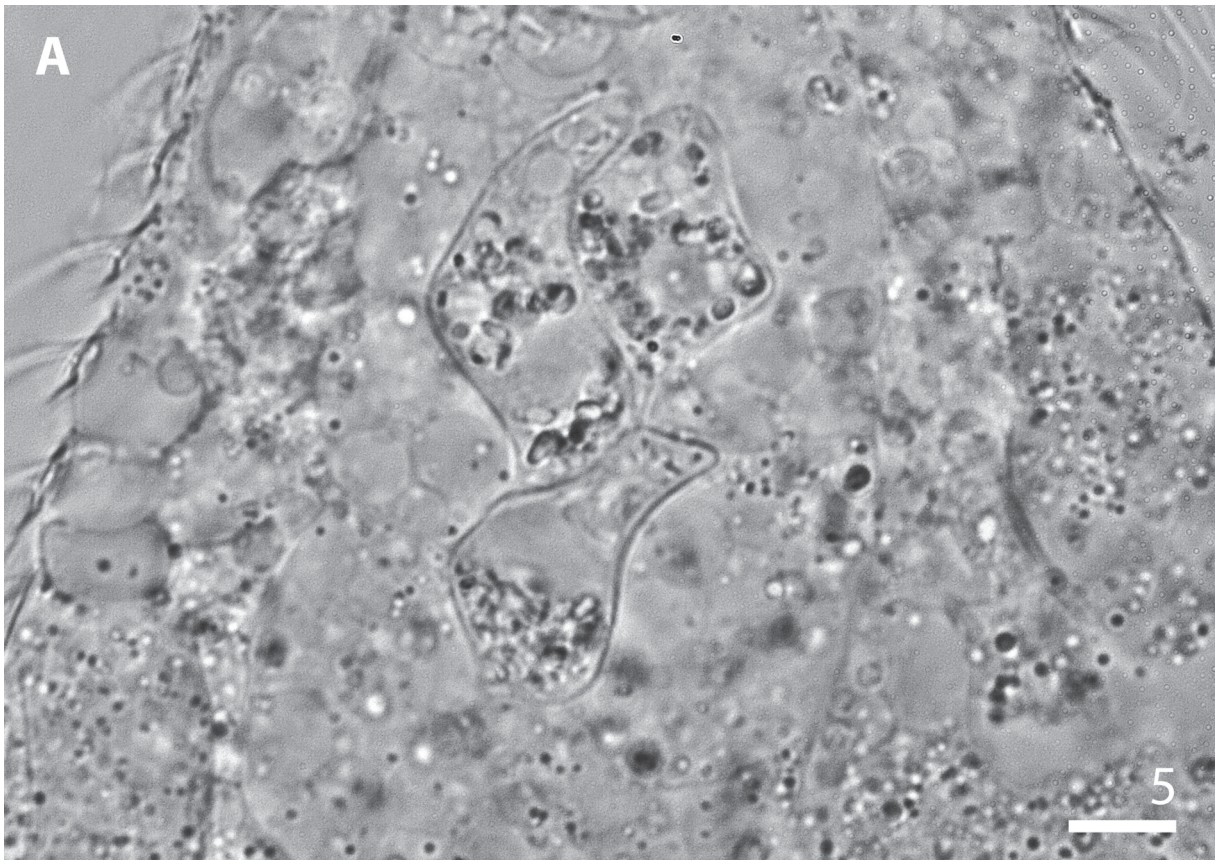

Fig. 11. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Adult specimen. Bright field microphotography. Living euglenids inside intestine.

thick spine (scale 33; Fig. 3GG). The second pair of terminal scales on the ventral interciliary field is located on the furcal appendages (at U86–U88). These scales are oval in shape, have long, straight keels and thick, curved spines reaching to the internal furcal indentation (scale 34; Fig. 3HH). The first and second pairs slightly overlap. The third (at U87–U88) and fourth (at 88–U89) pairs are definitely small (2.0–4.8 × 1.3–3.0 μm), egg-shaped, are located on the furcal appendages, and have straight keels and rudimentary spines (scale 35; Fig. 3II).

Internal morphology. The pharynx (from U2 to U31) is narrow and has marked anterior and posterior dilatations. The posterior dilatation is stronger than the anterior one (Fig. 9C). In the anterior dilatation, weak cuticular reinforcements are located in the form of two straight, connected rods (at U4). The pharynx is connected through the pharyngeal–intestinal junction by the straight intestine (running from U32 to U86). The pharyngeal–intestinal junction is clearly demarcated, short and wide (U32) (Fig. 2B). The intestine does not have a separate, different anterior section. The X-organ of this species (observed in one specimen) is located at U84–U86 near the terminal part of the intestine. It is bilobed, built from two extensions enveloped in a thin coat and connected by a thinner band located below the intestine end, at the ventral surface (Fig. 10). The extensions have a granular appearance. The thin coat and the cellular bridge connecting the extensions have a smooth and homogeneous structure. The sperm packets of this species were not observed.

Remarks

Because of the long pharynx in relation to the length of the body and intestine, the pharynx–intestine ratio (I) has high values in this species. Juvenile and subadult specimens have a pharynx–intestine ratio (I) higher than 65%, rather than higher than 55%, as is usually observed in other species. In juvenile specimens, the first head scales from each dorsal longitudinal row are located under the free dorsal cephalion edges, whereas in adults they are nto located under the cephalion but below their dorsal edges (Fig. 7A–B). Of the 25 reported adults, one individual had a large, developing egg (Fig. 5C) and another possessed a distinct X-organ (Fig. 10). Four specimens had live, motile euglenids inside their intestine (Fig. 11) and were listed in an earlier paper as *Chaetonotus* (*Chaetonotus*) sp. 1 (Kisielewska *et al.* 2015).

Differential diagnosis

Of all the 92 currently known nominal representatives of the subgenus *Chaetonotus* (*Chaetonotus*) Ehrenberg, 1830, *C.* (*C.*) *invitatus* sp. nov. most closely resembles *C.* (*C.*) *maximus* Ehrenberg, 1830, *C.* (*C.*) *microchaetus* Preobrajenskaja, 1926, *C.* (*C.*) *similis* Zelinka, 1889, *C.* (*C.*) *heterospinosus* Balsamo, 1978, *C.* (*C.*) *laroides* Marcolongo, 1910 and *C.* (*C.*) *polyspinosus* Greuter, 1917. Of all 32 species belonging to the subgenus *Hystricochaetonotus* Schwank, 1990, *C.* (*H.*) *trispinosus* Balsamo, 1990 seems to be the most similar to the newly described taxon, whereas of all the currently known 22 nominal representatives of the subgenus *C.* (*Primochaetus*) Kisielewski, 1997b, the new species most closely resembles *C.* (*P.*) *mutinensis* Balsamo, 1978. *Chaetonotus* (*C.*) *maximus, C.* (*C.*) *microchaetus, C.* (*C.*) *similis, C.* (*C.*) *heterospinosus, C.* (*C.*) *laroides, C.* (*C.*) *polyspinosus* and *C.* (*P.*) *mutinensis* are the most similar to the newly described species in terms of: body shape similarity, range of body length, range of pharynx length, range of adhesive tube length, presence of a scale of a different type on the dorsal and dorsolateral surfaces on the furcal base, presence of rigid, long spines on the furcal appendages and a similar type of terminal scales on the ventral interciliary field. *Chaetonotus* (*H.*) *trispinosus* was selected for comparison with *C.* (*C.*) *invitatus* sp. nov. due to its similarity in terms of having three larger scales with longer and stronger spines present on the dorsal posterior trunk region, length variation of large spines on different body sides and by the presence of scales of a different type on the dorsal and dorsolateral surfaces of the furcal base. Despite the fact that these eight species have the highest number of common features with the newly described species, they are significantly different from *C.* (*C.*) *invitatus* sp. nov. – most strikingly by scale type and shape variation, spine types

and length variation. Comparisons between the new species and the most morphologically similar taxa are summarised in Table A2. Taxa chosen for the differential diagnosis often occur in different regions of the world and are presented very differently by various researchers. Thus, a different description/specification or taxonomic classification of theoretically the same species may suggest that we are dealing with a very large range of plasticity of these taxa or with a larger number of undiagnosed, separate species. To avoid any doubts in comparisons with *C.* (*C.*) *invitatus* sp. nov., only the original descriptions of these species and three of the most detailed papers with morphological data were used (Balsamo 1983; Schwank 1990; Kisielewski 1997a). For information regarding *C.* (*P.*) *mutinensis*, only original data are considered in the differential diagnosis.

Chaetonotus* (*Chaetonotus*) *paucisquamatus Kisielewski, 1991
Figs 12–13; Table 3

Chaetonotus (*Chaetonotus*) *paucisquamatus* Kisielewski, 1991: 40–42, figs 47–50.

Locus typicus

Brazil.

Material examined

POLAND • 1 adult; Kraków, Botanical Garden, Jubilee Greenhouse, site 1; 50°03′38″ N, 19°57′30″ E; 15 Nov. 2013; M. Kolicka leg.; NHC (photomicrographs, also in the author's collection).

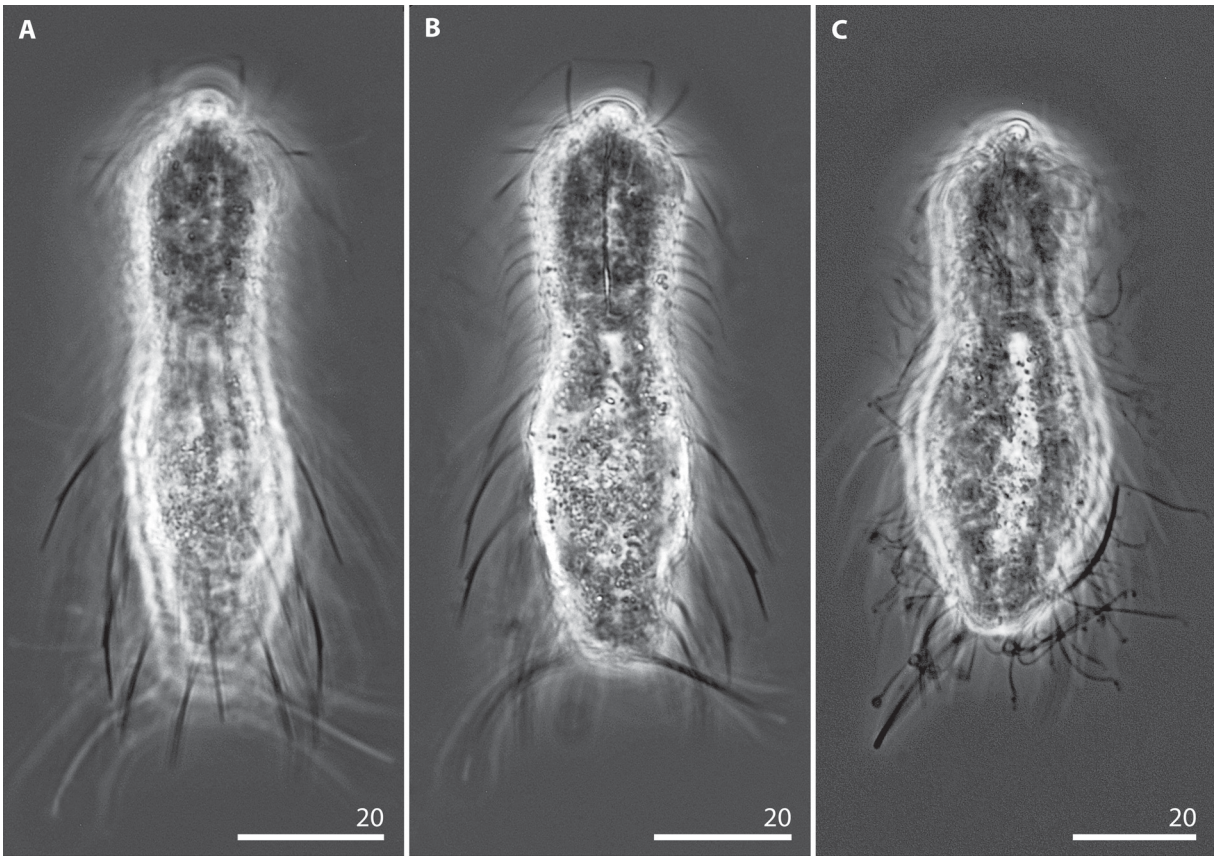

Fig. 12. *Chaetonotus* (*Chaetonotus*) *paucisquamatus* Kisielewski, 1991. Adult specimen. Phase contrast microphotographs. **A**. Dorsal body view. **B**. View of internal morphology. **C**. Ventral body view.

Table 3. Main morphometric characters of *Chaetonotus* (*Chaetonotus*) *paucisquamatus* Kisielewski, 1991. All measurements in micrometers (μm). NA = data not available.

Characters	According Kisielewski (1991)	Adult specimen
Body length	121.00–154.00	114.76
Furca length	NA	36.74
Adhesive tube length	25.00–40.00	27.82
Number of scales in central longitudinal row	9 (head and neck: 5; trunk: 4)	14 (head and neck: 9; trunk: 5)
Total number of longitudinal alternating rows of scales	9	9
Length of cephalic cilia (anterior tuft)	NA	9.49–21.98
Length of cephalic cilia (posterior tuft)	NA	12.97–24.34
Head scales length × width	NA	3.09–4.37 × 3.13–4.14
Neck scales length × width	NA	4.62–6.56 × 3.90–6.26
Trunk scales length × width	8.00–12.50 x 10.00	7.31–13.33 × 7.01–11.72
Head dorsal spines length	NA	1.24–4.03
Head ventral spines length	NA	6.28–8.49
Neck dorsal spines length	4.00–4.50	4.18–14.70
Neck ventral spines length	NA	9.83–20.06
Trunk dorsal spines length	23.00–35.00	23.70–26.70
Trunk ventral spines length	NA	20.86–24.29
Length of rearmost lateral spines	12.00–21.50	19.05
Neck dorsal sensory bristles length	NA	19.96
Posterior dorsal sensory bristles length	NA	23.36
Number of scales in central longitudinal row on ventral interciliary field	NA	13
Total number of longitudinal alternating rows of scales on ventral interciliary field	NA	7
Ventral interciliary field scales length × width	NA	2.83–4.62 × 2.20–3.18
Terminal ventral interciliary field scales length × width	NA	7.41 × 4.02
Mouth ring diameter	3.20–3.50	3.39
Pharynx length	27.50–34.00	30.81
Intestine length	NA	52.90

Distribution

This species was previously known only from Brazil, namely from water reservoirs, silt sediments and aquatic vegetation (Kisielewski 1991).

Remarks

The specimen found in the Jubilee Greenhouse in Kraków is consistent with the detailed description of *Chaetonotus* (*Chaetonotus*) *paucisquamatus* Kisielewski, 1991. The presence of only one specimen does not allow for a thorough comparison and for conclusions to be drawn; however, the individual observed in Poland differed slightly from the original description by: its smaller body size (Table 3); a larger number of scales in the central longitudinal row than in the original description (Table 3); the presence of thin, rounded scales on the ventral interciliary field, increasing in size and isolation from the cuticle towards the posterior trunk region, where the scales possessed weak keels; and the presence of one pair of elongated, elliptical and keeled ventral terminal scales. These differences may result from

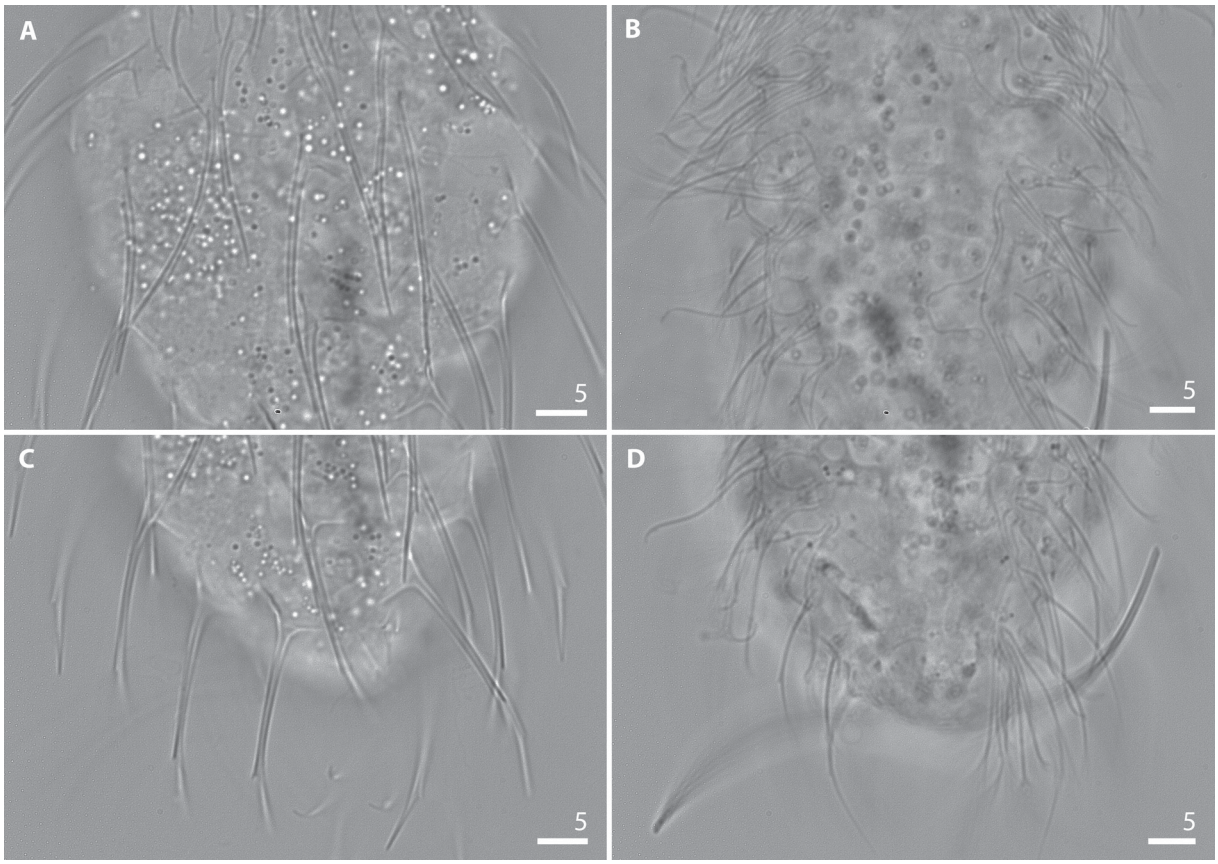

Fig. 13. *Chaetonotus* (*Chaetonotus*) *paucisquamatus* Kisielewski, 1991. Adult specimen. Bright field microphotographs. **A**. Anterior trunk, dorsal view. **B**. Anterior trunk ventral view. **C**. Posterior trunk dorsal view. **D**. Posterior trunk, ventral view.

phenotypic variation caused, e.g., by different developing conditions. Due to the lack of any differences in the other taxonomic characteristics, there are no grounds to conclude that the recorded individual represents a separate species.

Subgenus ***Hystricochaetonotus*** Schwank, 1990

Type species

Chaetonotus hystrix Mečnikow, 1865.

Terra typica

Russia.

Remarks on subgenus

A polyphyletic subgenus in terms of molecular data (Kånneby *et al.* 2013), it encompasses 28 nominal freshwater species and 10 marine species (Todaro 2018). Present in benthic and periphytic habitats (e.g., Kisielewski 1997a).

Chaetonotus* (*Hystricochaetonotus*) *hystrix Mečnikow, 1865
Figs 14–15

Chaetonotus hystrix Mečnikow, 1865: 451, fig. 7.

Locus typicus

Russia.

Material examined

POLAND • 21 adults, 3 subadults, 7 juveniles; Kraków, Botanical Garden, Jubilee Greenhouse, sites 1–3; 50°03′38″ N, 19°57′30″ E; 17 Apr. 2014; M. Kolicka leg.; NHC (photomicrographs, also in the author's collection).

Distribution

Chaetonotus (*Hystricochaetonotus*) *hystrix* Mečnikow, 1865 is considered a cosmopolitan and common species recorded worldwide from highly differing habitats (lakes with different trophic structures, mountain springs, fertile ponds, peat bogs, brackish estuarine waters) (Kisielewski 1991). Outside Europe, it is known from Brazil (Kisielewski 1991), Israel (Kisielewski 1997b), Japan (Saito 1937) and Paraguay (Daday 1905).

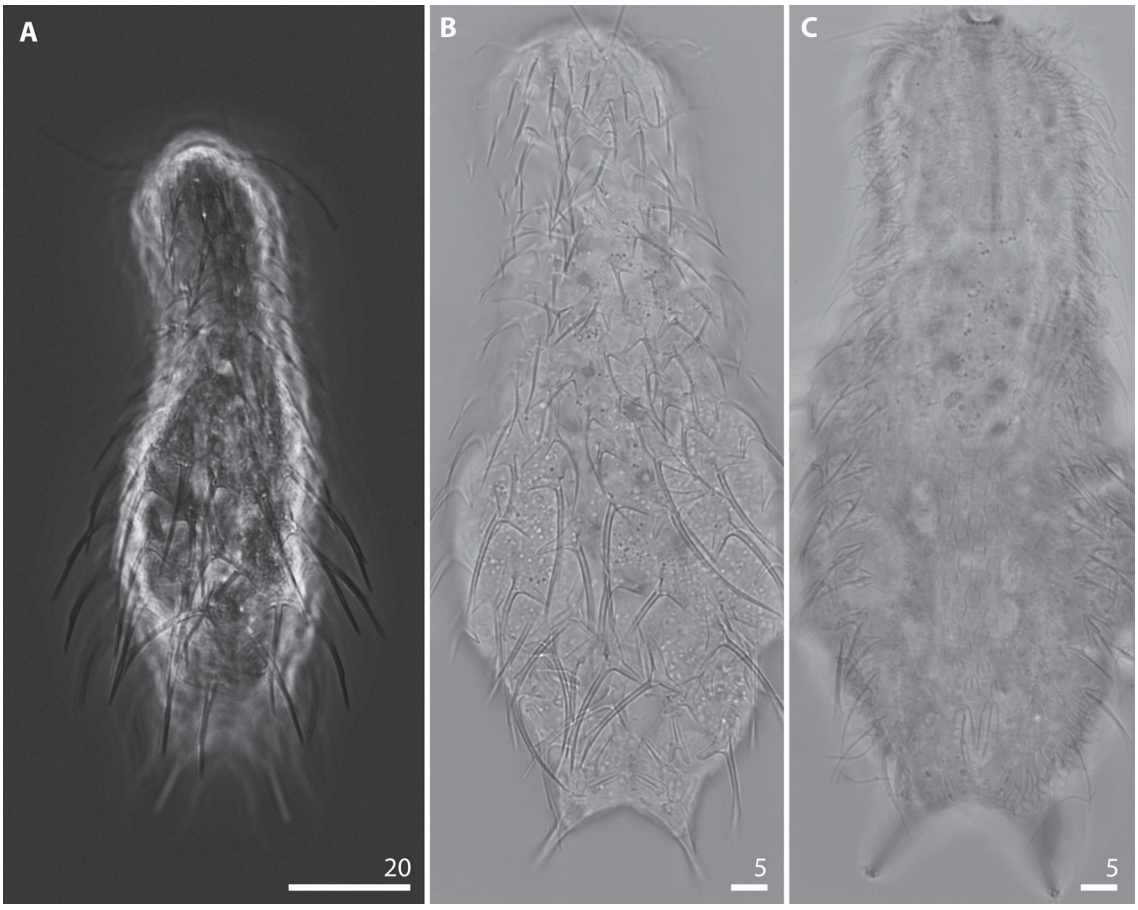

Fig. 14. *Chaetonotus* (*Hystricochaetonotus*) *hystrix* Mečnikow, 1865. Adult specimen. **A**. Habitus, phase contrast microphotograph. **B**. Dorsal scales, bright field microphotograph. **C**. Ventral scales, bright field microphotograph.

Remarks

The specimens examined here correspond very well with the original description (Figs 14–15). All their morphometric characteristics are within the ranges given in the literature for this species (Rudescu 1967; Roszczak 1969; Balsamo 1983; Schwank 1990; Kisielewski 1984, 1997b). The total body length of adult specimens varied from 107.4 to 128.6 μm; length of pharynx was between 27.6

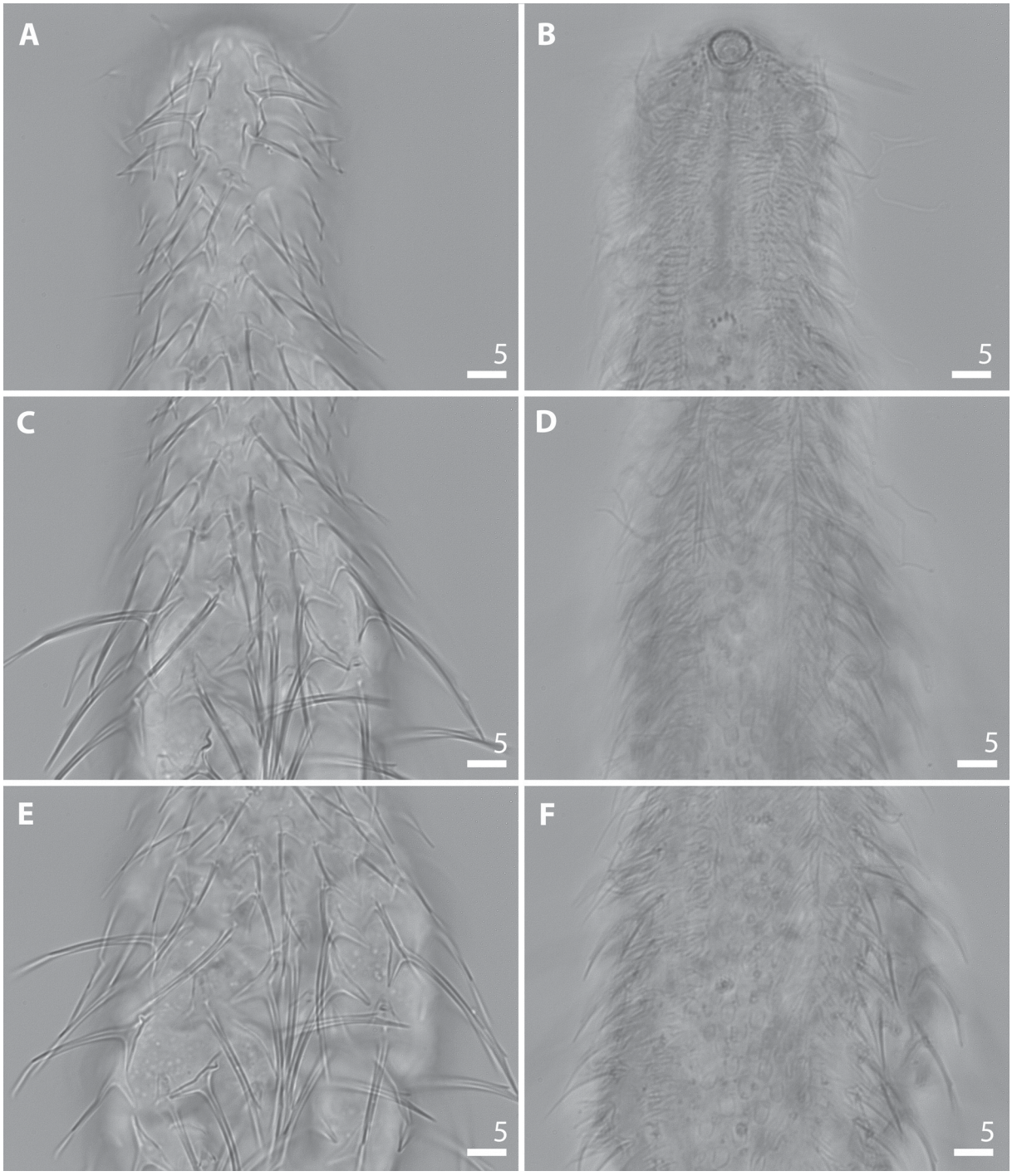

Fig. 15. *Chaetonotus* (*Hystricochaetonotus*) *hystrix* Mečnikow, 1865. Adult specimen. Bright field microphotographs. **A**. Head dorsal spines. **B**. Head ventral spines. **C**. Neck and trunk dorsal spines. **D**. Neck and trunk ventral spines. **E**. Trunk dorsal spines. **F**. Trunk ventral spines.

and 32.7 μm; length of intestine from 56.1 to 81.9 μm; there were 15–17 total longitudinal rows of scales (5–7D+2DL+2L+4LV+2V), with 13–17 scales in the central row. The total body length of juvenile specimens varied from 86.9 to 105.4 μm; length of pharynx was between 28.6 and 32.4 μm; length of intestine from 37.9 to 52.6 μm; there were 13–17 total longitudinal rows of scales (5–7D+2DL+2L+2–4LV+2V), with 13–17 scales in the central row. Among the adults, two had a large, developing egg, while one had an X-organ and two packages of sperm.

Chaetonotus* (*Hystricochaetonotus*) *horridus sp. nov.
urn:lsid:zoobank.org:act:478175BF-E4D8-48BC-AE73-2032127AB69D
Figs 16–25, A3–A6; Tables 4, A3–A4

Diagnosis

Stocky body, measuring from 107.8 to 134.0 μm in length. Head five-lobed, cephalion narrow, hypopleurae slightly larger in size than epipleurae. All cephalic plates weakly demarcated in head outline. Hypostomium small, rectangular in shape. Ocellar granules absent. Almost all scales three-lobed and keeled. Scales distributed in 15–21 total longitudinal rows (3D+2–4DL+4–6L+4LV+2–4V), with 13–15 scales in central row. Scales strongly differ morphologically in various body areas. On dorsal trunk area, large scales with very long, thick spines with a strong, very prominent lateral denticle. Two pairs of posteriormost trunk lateral scales with long, thick spines with strong lateral denticle. Remaining scales with simple, shorter and thinner spines or on central dorsal trunk area and on furcal appendages with rudimentary spines or without spines. Parafurcal spines absent. Spines on ventral surface hair-like, with narrow, delicate lamellae along entire length. Entire ventral interciliary field covered with plate-like scales. Three pairs of ventral interciliary field terminal scales. Pharynx wide, with pronounced anterior and posterior dilatations. Intestine straight without anterior section differing in form and morphology.

Etymology

From the Latin '*horridus*' = 'hairy', referring to the very long and strong trunk spines.

Material examined

Holotype

POLAND • adult; Kraków, Botanical Garden, Jubilee Greenhouse, site 1; 50°03′38″ N, 19°57′30″ E; 15 Nov. 2013; M. Kolicka leg.; NHC-GCHH-22-1-25/h (photomicrographs, also in the author's collection).

Paratypes

POLAND • 80 adults, 30 subadults, 9 juveniles; same locality as holotype; sites 1–3; 15 Nov. 2013 and 17 Apr. 2014; M. Kolicka leg.; NHC-GCHH-22-21-60/p (photomicrographs, also in the author's collection).

Description

Habitus. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. has a stocky body that is slightly bottle-shaped (Figs 16, 19). Its head is only slightly wider than the neck and the neck constriction is weakly demarcated. The neck gradually tapers from the head (from U17) to the beginning of the trunk (ca U31). The trunk is slightly wider than the head and gradually dilates from ca U32 to ca U59, where it is at its maximum width. Then it gradually tapers towards the narrow furcal base (from U79) (Figs 16, 19). The furcal base is clearly demarcated and narrow. The furcal indentation is V-shaped. The furcal branches are set widely apart and point outwards to the widest trunk region (Figs 16, 19). The adhesive tubes are straight, fairly thick and slightly tapered towards the blunt ends (Figs 16, 19).

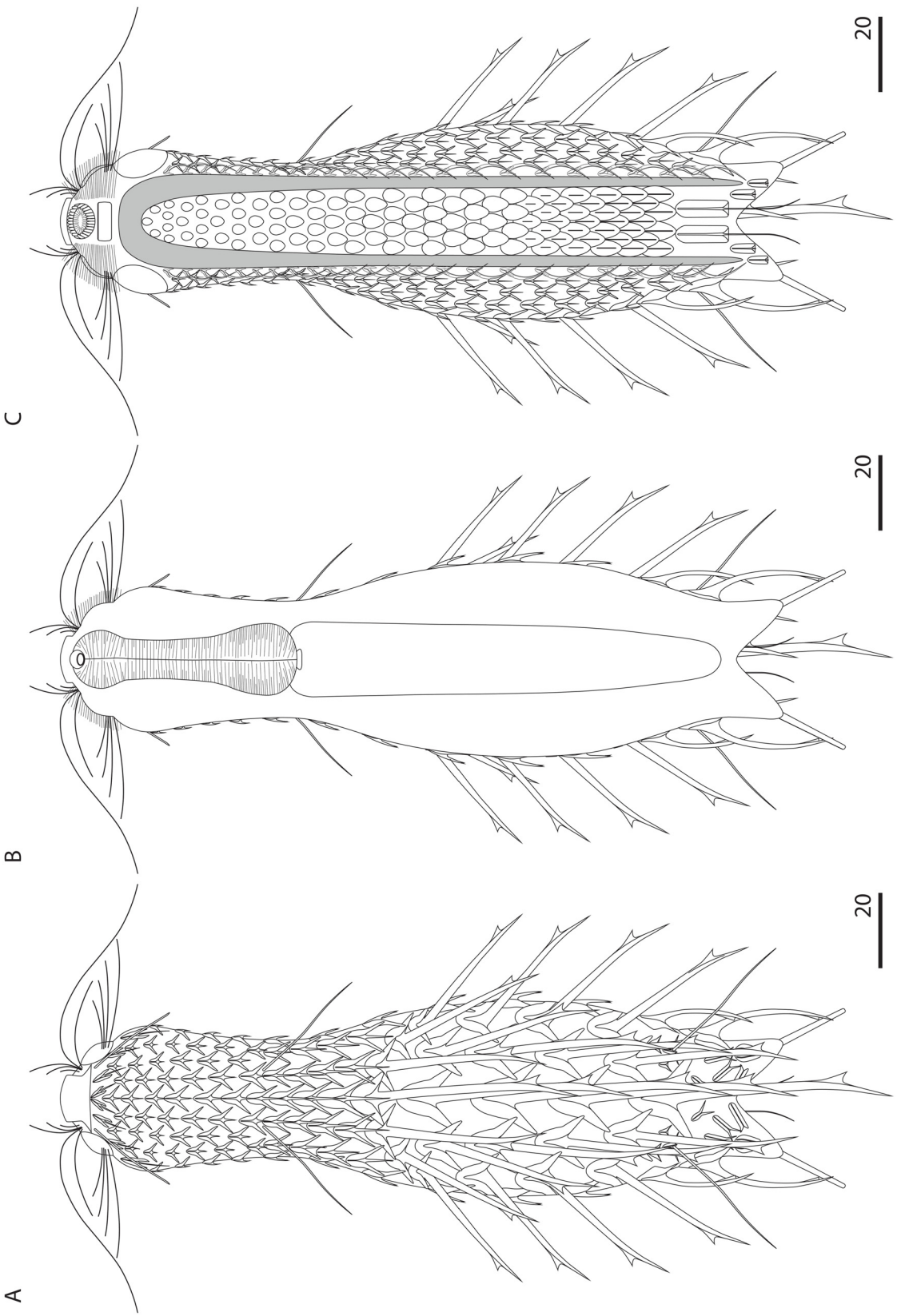

Fig. 16. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Schematic drawings. **A**. Dorsal view. **B**. View of internal morphology. **C**. Ventral view. Light grey areas indicate the areas of insertion of ciliary bands.

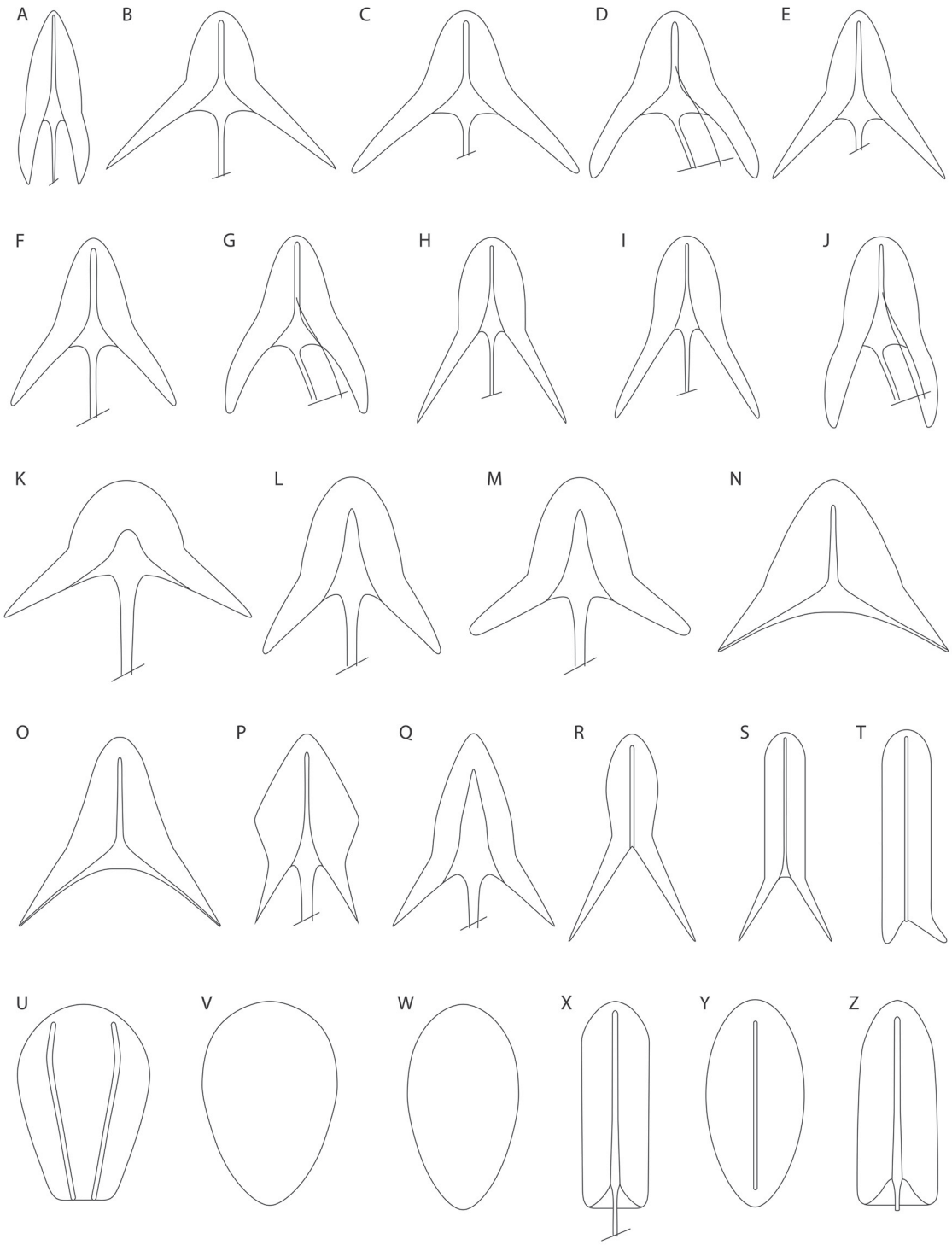

Fig. 17. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Schematic drawings of the scales. **A**. Head anteriormost scale (scale 1). **B**. Head dorsal scale (scale 2). **C**. Head dorsolateral, lateral and ventrolateral scale (scale 3). **D**. Head ventral scale (scale 4). **E**. Neck dorsal scale (scale 5). **F**. Neck dorsolateral, lateral and ventrolateral scale (scale 6). **G**. Neck ventral scale (scale 7). **H**. Trunk dorsal scale (scale 8). **I**. Trunk dorsolateral, lateral and ventrolateral scale (scale 9). **J**. Trunk ventral scale (scale 10). **K**. Scale 11. **L**. Scale 12. **M**. Scale 13. **N**. Scale 14. **O**. Scale 15. **P**. Scale 16. **Q**. Scale 17. **R**. Scale 18. **S**. Scale 19. **T**. Scale 20. **U**. Scale 21. **V**. Scale 22. **W**. Scale 23. **X**. Scale 24. **Y**. Scale 25. **Z**. Scale 26.

Head. The head is five-lobed, short and semicircular in shape. The cephalion (U1–U4) is narrow, short, with straight dorsal edge. It adheres to the head along its entire length and rapidly extends near the dorsal edge (Fig. 20A). The epipleurae (U4–U7) are slightly arched and weakly demarcated in the head outline. They are located on the dorsal, dorsolateral and lateral sides and are slightly visible on the ventrolateral head side. The hypopleurae (U8–U14) are slightly larger in size than the epipleurae and located entirely on the ventrolateral and ventral head sides (Figs 16, 20A–B). They are not visible in dorsal body view. On the dorsal head surface, between the lateral edges of the cephalion and epipleurae there is a prominent space, their edges meeting only in the cephalion extension place. Deep notches are present between the cephalion and epipleurae and between the epipleurae and hypopleurae. The hypostomium (U6–U7) is short, rectangular, with a slightly reinforced anterior edge (Figs 16C, 20B). Two pairs of cephalic ciliary tufts are present. The anterior tufts emerge in the area between the cephalion and epipleurae on the dorso-terminal head surface (ca U3) and consist of 5 cilia. The anteriormost cephalic cilium is very short and the length of the cilia in the anterior tuft gradually increases from the anteriormost to the fourth cilium. The fourth cilium in the anterior tufts is very long, the longest in both pairs of tufts, while the fifth, posteriormost cilium is much shorter. The posterior tufts (at U6–U7) have 4 cilia each and emerge on the ventral head side, above the anterior edge of the hypopleurae. The length of the cilia in the posterior tuft gradually increases from the anteriormost to the fourth cilium. Ocellar granules are not present. The mouth ring is large, wide and located subterminally at U2–U5. It has very strong, long reinforcements and long inner hairs (Figs 16C, 20B). Suboral bristles are located in two tufts located beneath and laterally to the mouth ring and reaching beyond the hypostomium end (between U3 and U7).

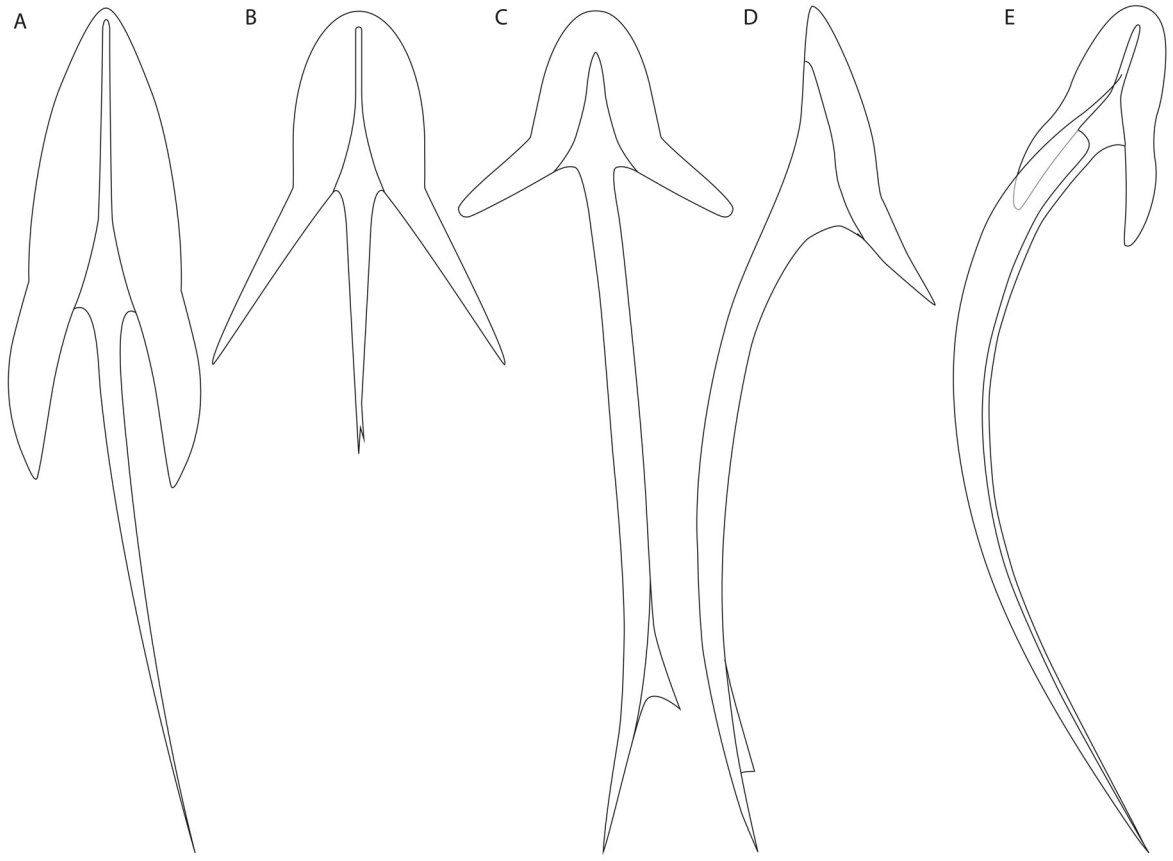

Fig. 18. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Schematic drawings of the spine types. **A**. First type of spines. **B**. Second type of spines. **C**. Third type of spines. **D**. Fourth type of spines. **E**. Fifth type of spines.

Scales. The entire body, except for one pair of scales on the furcal appendages, is covered with three-lobed scales that adhere to the cuticle along their entire surface (Fig. A6). All scales have a strong keel and are shaped like triangles. The scales are distributed in 15–21 total longitudinal alternating rows (3D+2–4DL+4–6L+4LV+2–4V), with 13–15 scales in the central row. The central longitudinal rows of scales begin on the head directly beneath the posterior edge of the cephalion. On the head and anterior neck region the scales are located far from one another, on the posterior neck and anterior trunk region the scales are located gradually closer, but still at a distance to the other scales and not juxtaposed. The dorsolateral, lateral, ventrolateral and ventral trunk scales are located at a distance from the other scales, whereas the dorsal trunk scales and scales on the furcal appendages have slightly overlapping posterolateral edges (Fig. 20). The head anteriormost scales are situated near the posterior edge of the cephalion and epipleurae. The dorsal anterior scales are located aslant, whereas the dorsolateral scales are arranged parallel to the longitudinal body axis. These scales are elongated and their central lobes are long, trilobed and have very long keels. Their posterolateral lobes are slightly separated, narrow, slanted downward and create a narrow, deep V-shaped posterior scale notch (scale 1; Fig. 17A). The remaining scales of the head are significantly wider. The central lobes of these scales become shorter and simultaneously the posterolateral lobes become slightly longer, whereas their keels are shorter. The posterolateral lobes are directed diagonally downward and laterally; they create a deep and wide posterior scale notch (scale 2; Fig. 17B). The anterior neck scales become gradually longer than the head scales. Their central lobes become longer and the posterolateral lobes are more separated and directed more downward and create a wide and deep V-shaped posterior scale notch (scale 5; Fig. 17E). From the neck towards the trunk, the scale size gradually increases (from 2.8–3.5 × 2.4–3.2 to 5.2–6.4 × 5.1–5.9 μm). All of the anterior trunk scales and dorsolateral, lateral, ventrolateral and ventral trunk scales on the

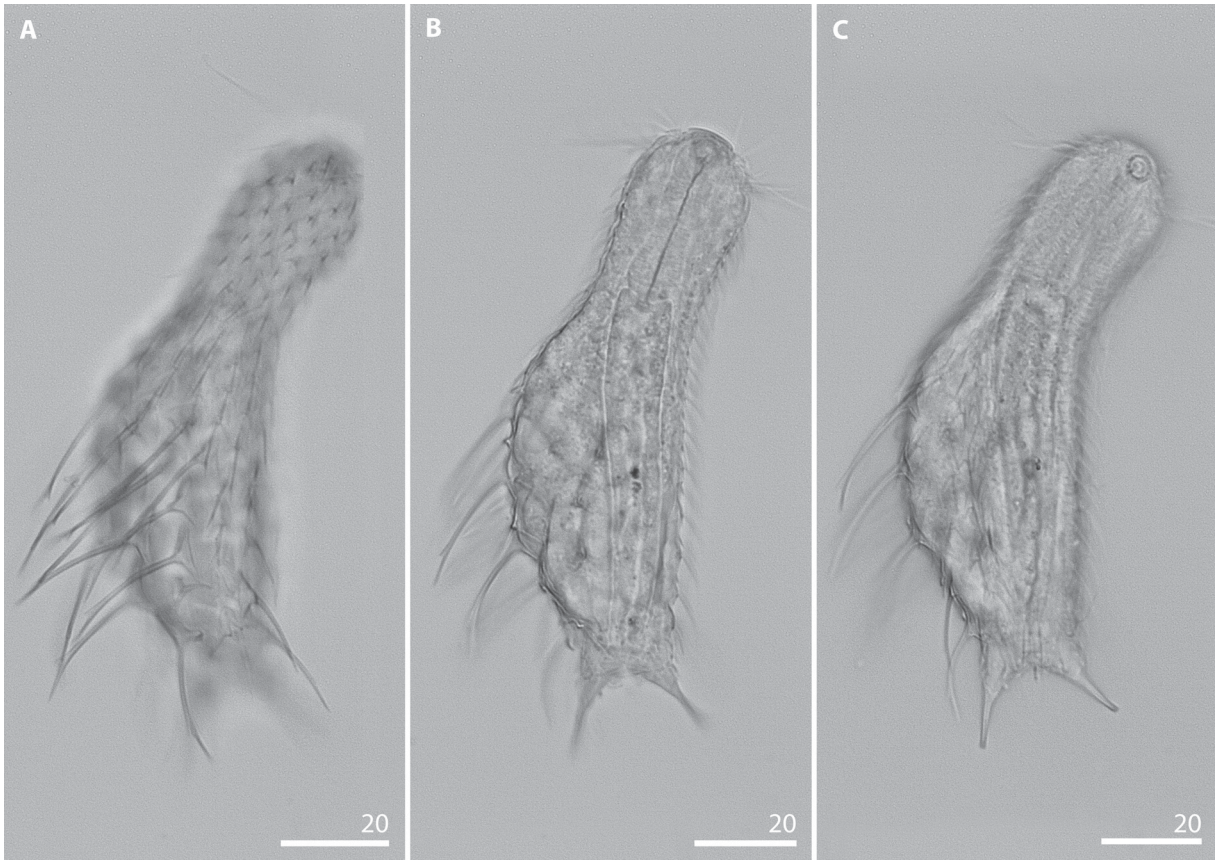

Fig. 19. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Adult specimen. Bright field microphotographs. **A**. Dorsal body view. **B**. View of internal morphology. **C**. Ventral body view.

central and posterior body region have a wide and rounded anterior central lobe and clear, separate, long, narrow and sharp posterolateral lobes. The posterolateral lobes are directed diagonally downward and are slightly lateral; they create a deep V-shaped posterior scale notch (scale 8; Fig. 17H). The size of these scales increases from the anterior trunk region to the widest body region (from 3.0–4.1 × 2.1–3.3 to 5.6–9.7 × 4.68–8.43 μm) (Figs 20, 23). Dorsally and dorsolaterally from ca U37 to U73 and dorsally to U81, larger and thick, different scales are located with very long and strong spines (Figs 16, 20, 22). The first of the different, larger scales from each longitudinal dorsal and dorsolateral row are triangular in shape, their central lobes are short, wide and pass seamlessly into posterolateral lobes that are directed very wide apart. The posterior edge of this scale is almost straight and only very narrowly notched. Its keel starts from the half-length of the central lobe and is very pronounced and high, strongly triangular in shape (scale 11; Fig. 17K). The subsequent large scales (located from U41 to U73) are triangular in shape, with rounded edges, and their central lobes are longer and have longer keels. The posterolateral lobes of these scales are more rounded, directed slightly more downward and create a wide V-shaped posterior scale notch (scale 12; Fig. 17L). The posteriormost scale of the dorsal and dorsolateral large scales with long, strong spines is located in the central longitudinal row of scales at U78 to U81 (Figs 17A, 19A, 22B). This scale is wide and its central and posterolateral lobes are rounded. The posterior edge of this scale is almost straight and only very narrowly notched. Its keel is very pronounced and high, strongly triangular in shape (scale 13; Fig. 17M). Anteriorly to the double keeled scales with trunk dorsal sensory bristles, on the dorsal and dorsolateral trunk region, three pairs of keeled and spineless scales are located at U73–U77. Two of these three pairs are located more anteriorly and laterally than the third pair and are triangular in shape, their posterolateral lobes are weakly separated, and their keels are strong and reach from the anterior part of the central lobes to the ends of the

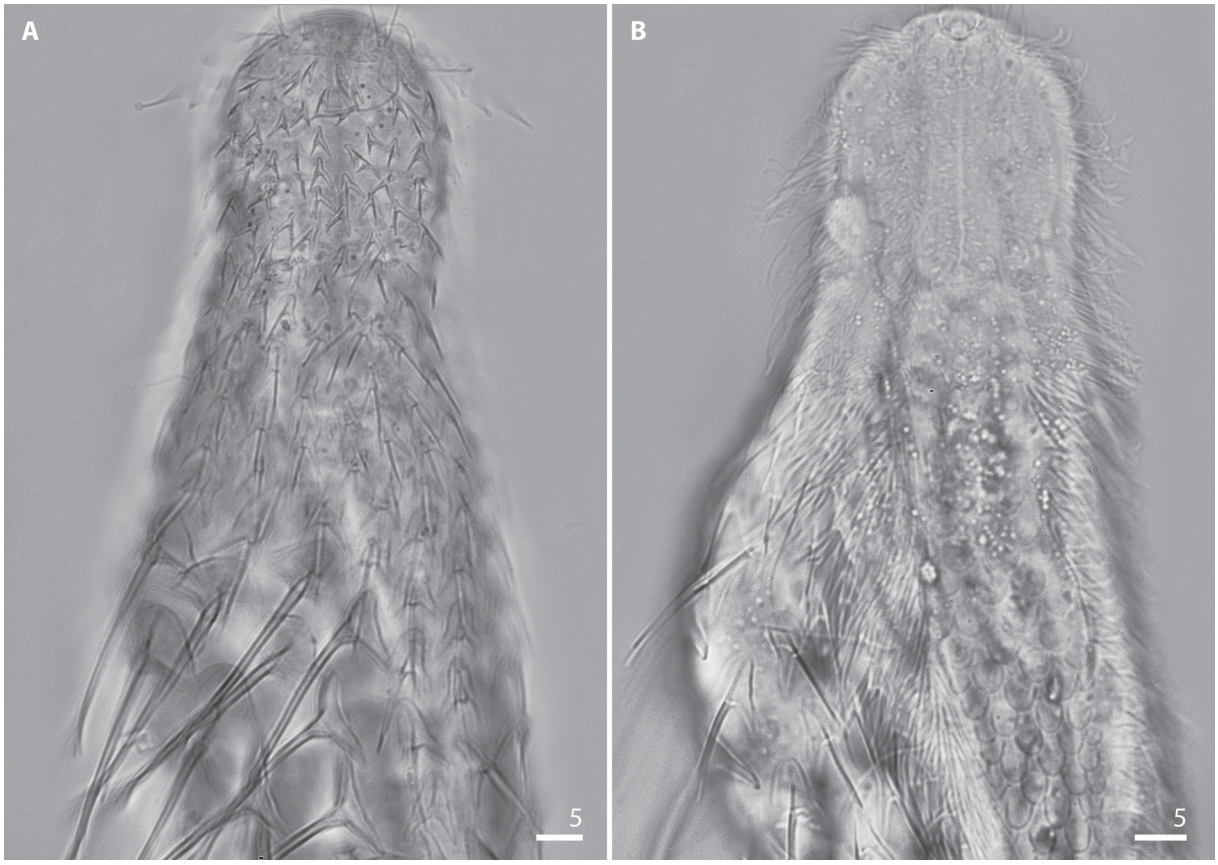

Fig. 20. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Adult specimen. Bright field microphotographs. **A**. Scales, dorsal view. **B**. Scales, ventral view.

posterolateral lobes. The posterior notches of these scales are shallow and semicircular (scale 14; Fig. 17N). The third pair of these scales, located at U75–U77, is wider and possesses shallower posterior notches (scale 15; Fig. 17O). On the lateral surface of the posterior trunk region, one pair of the second to last trunk scales is located at U69–U75. These scales are large and have a long, wide, and anteriorly clearly pointed central lobes with strongly rounded lateral edges. Their posterolateral lobes are clearly separated from the central lobes, are long and have sharp edges. These posterolateral lobes are directed diagonally downward (scale 16; Fig. 17P). The scales have strong keels and strong, long spines. Posteriorly to them, on the posterior trunk region and furcal base, the last pair of trunk lateral scales is situated at U76–U82. This pair of scales is large (7.4–11.7 × 5.3–8.9 μm); its scales have a long, wide and anteriorly strongly pointed central lobes and straight posterolateral lobes that are triangular. The posterolateral lobes of these scales are directed diagonally wide apart, downward and laterally, creating a wide and shallow V-shaped posterior scale notch. These scales have a very strong keel and strong, long spines (scale 17; Fig. 17Q). One pair of small (2.2–7.0 × 1.6–4.5 μm) three-lobed scales, shaped like triangles with strongly rounded anterior lobes and with straight, narrow and long posterolateral lobes, is located diagonally on the dorsal surface of the furcal base (at U81–U83). These scales have long, thin keels and are spineless. Their posterior edge notches are V-shaped and very deep (scale 18; Fig. 17R). Two pairs of three-lobed, elongated and narrow scales are located on the dorsal surface of the furcal base and furcal appendages (at U82–U86). These scales have wide and rounded central lobes and straight, narrow posterolateral lobes located diagonally downward which create narrow, deep V-shaped posterior

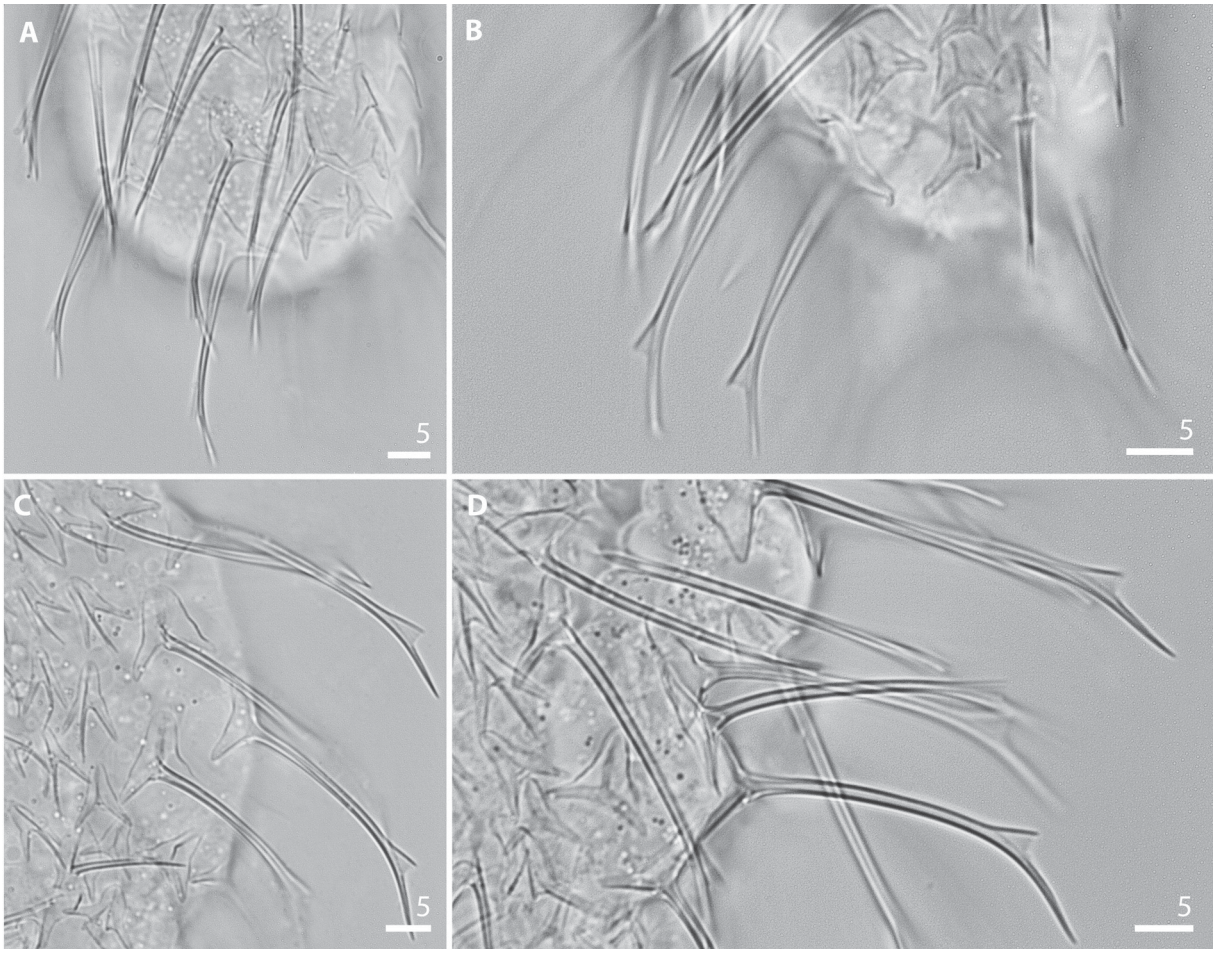

Fig. 21. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Adult specimen. Bright field microphotographs. **A**. Trunk spines, dorsal view. **B**. Trunk spines, dorsolateral view. **C–D**. Trunk spines, lateral view.

scale notches. Their keels are long and thin and the scales are spineless (Fig. 22B). The scales are diagonally arranged and directed towards the central body axis (scale 19; Fig. 17S). One pair of slightly three-lobed, narrow, asymmetrical scales is located on the dorsal surface of the furcal appendages. These scales are shaped like strongly elongated ovals, with a slightly triangular posterior notch. This pair of scales has long keels running along their length and does not have a spine (scale 20; Fig. 17T). They are located at U86–U88, slightly diagonally to the central body axis. Dorsolaterally at the furcal appendages, one pair of scales with two keels is located (at U86–U89). These scales are oval in shape and do not have any posterior notches or spines. Their keels are long and slightly bent (scale 21; Fig. 17U). The edges of the furcal appendage scales are slightly overlapping (Fig. 22). The size of the scales gradually decreases slightly from the dorsal, dorsolateral, lateral, ventrolateral and ventral surfaces towards the ciliary bands (head: from 3.2–5.2 × 3.2–6.2 to 2.2–4.1 × 2.1–3.9 μm; neck: from 4.5–6.4 × 4.1–5.9 to 2.8–4.6 × 2.4–4.1 μm, trunk: from 5.3–9.7 × 4.1–8.4 to 3.0–5.5 × 2.1–4.6 μm) (Table A3). Furthermore, the edges of the dorsolateral, lateral, ventrolateral and ventral scales gradually become slightly more rounded towards the ciliary bands as compared to the edges of the dorsal scales (Figs 16, 20). Scales arranged in the ventral longitudinal row located closest to the ciliary bands are smaller than the scales of the other rows, and their anterior edge is oriented towards the bands at an angle of ca 20°.

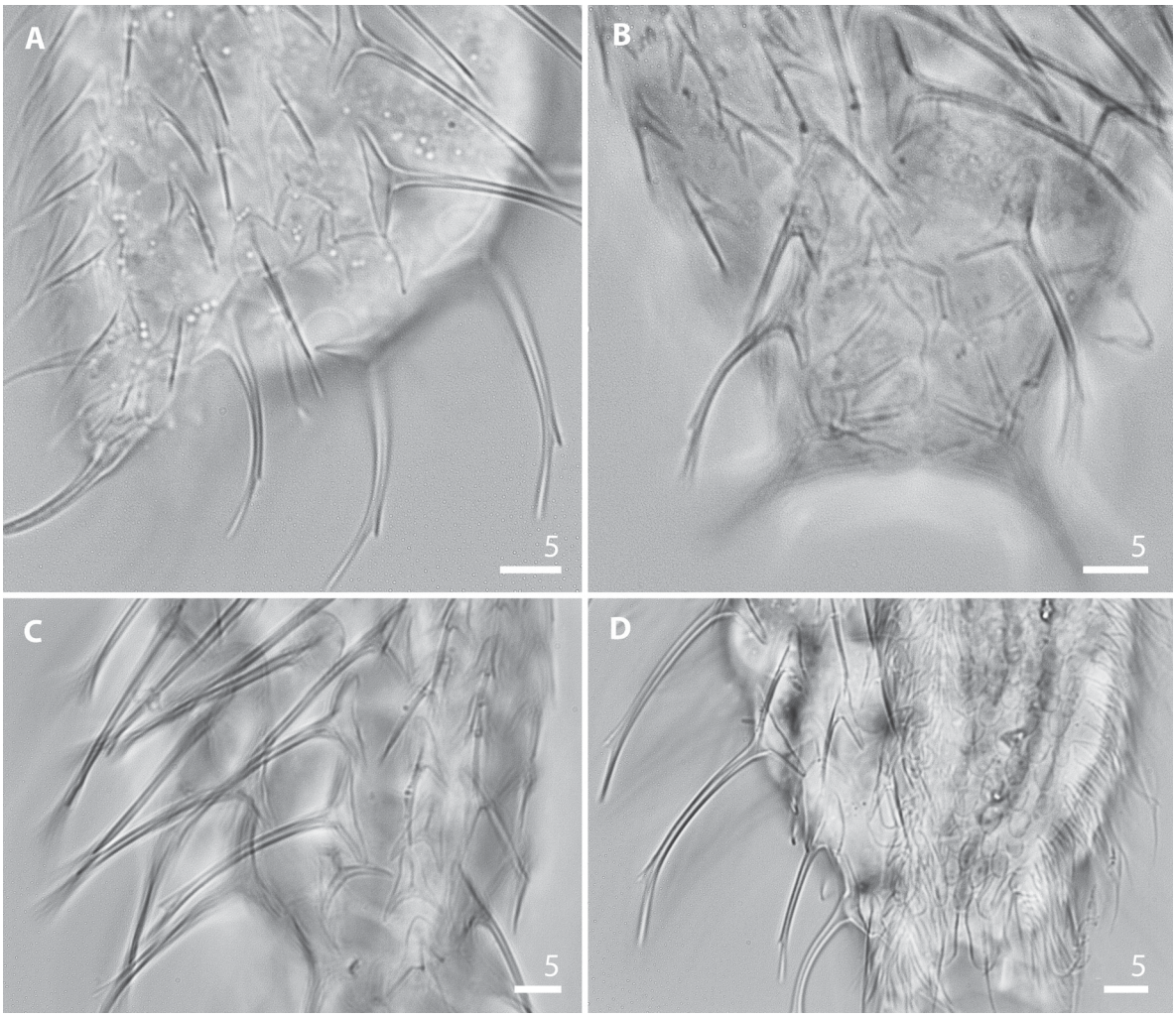

Fig. 22. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Adult specimen. Bright field microphotographs. **A**. Posterior trunk, furca base and furcal appendage, scales lateral view. **B**. Posterior trunk, furca base and furcal appendage scales, dorsal view. **C**. Central and posterior trunk scales, dorsal view. **D**. Posterior trunk, furca base and furcal appendage scales, ventral view.

Table 4. Main morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. N = number of specimens analysed; Range = the smallest and the largest structure found among all specimens measured. All measurements in micrometers (μm); all indicators given as a percentage (%) and italicized.

Characters	N	Holotype	Range of adult paratypes
Body length	70	131.69	107.77–134.01
Furca length	70	25.51	21.74–25.90
Adhesive tube length	70	12.43	9.67–13.04
Number of scales in central longitudinal row	81	15	13–15
Total number of longitudinal alternating rows of scales	81	21	15–21
Head scales length × width	15	2.82–5.23 × 2.66–5.20	2.17–5.30 × 2.05–6.20
Neck scales length × width	15	3.24–6.37 × 2.75–5.91	2.77–6.37 × 2.35–5.91
Trunk scales length × width	15	3.49–13.43 × 2.62–13.37	3.03–13.43 × 2.12–13.37
Head spines length	15	1.86–13.73	0.44–13.78
Localization of lateral denticle on head spines	15	*15.054–32.630*	*13.699–32.653*
Neck spines length	15	5.12–16.49	2.45–16.49
Localization of lateral denticle on neck spines	15	*25.502–29.323*	*19.818–29.448*
Trunk spines length	15	7.88–19.58	4.97–19.54
Localization of lateral denticle on trunk spines	15	*21.053–31.124*	*21.053–32.937*
Long trunk spines length	15	16.65–31.75	11.59–34.14
Localization of lateral denticle on trunk long spines spines	15	*23.039–31.937*	*17.969–34.785*
Length of trunk posteriormost pair of lateral spines	15	20.09	13.87–20.09
Localization of lateral denticle on trunk posteriormost pair of lateral spines	15	*31.210*	*24.942–34.785*
Mouth ring diameter	70	6.45	5.48–7.04
Pharynx length	70	33.20	27.03–33.58

Spines. In this species, five main types of spines may be distinguished (Fig. 18). The first type of spine bends slightly along its entire length and tapers towards the end, without lateral denticles. This type of spine emerges from the anteriormost head dorsal scales (Fig. 18A). The second type of spine is basally bent, tapering towards their ends, with a weak lateral denticle. These spines emerge from the dorsal, dorsolateral, lateral and ventrolateral head, neck and anterior trunk region scales and laterally and ventrolaterally on the remaining scales of the trunk part (Fig. 18B). The length and thickness of the spines gradually increase from the head towards the widest body region (ca U59) (from 1.8–13.7 to 7.9–19.6 μm). Moreover, their length gradually increases towards the ventrolateral surface (head: from 0.4–5.6 to 0.7–6.1 μm; neck: from 2.5–8.3 to 3.4–10.1 μm; trunk: 5.0–11.1 to 5.7–17.0 μm) (Table A3). The third type of spine is very long and thick, straight, with a prominent, deeply notched lateral denticle. The spines emerge from large (scales 11, 12 and 13), thick dorsal and dorsolateral trunk scales (from ca U37 to ca U73), are the longest (18.9–35.5 μm) and thickest body spines and have the most prominent lateral denticle (Fig. 18C). From scales 13, located on the posterior trunk region (at U78–U81), arise the last long dorsal and dorsolateral long spines (Fig. 21). These spines are slightly shorter than the preceding long spines and their lateral denticle is less prominent (18.9–27.2 μm). The fourth type of spine is long, thick, slightly bent and with a clearly marked lateral denticle (Fig. 18D). This type of spine arises from the second to posteriormost trunk pair of lateral scales located at U69–U75 and from the posteriormost trunk pair of lateral scales located at U76–U82 (Fig. 22A–B). The posteriormost pair of trunk spines is longer (13.9–20.1 μm) and thicker than the second to posteriormost pair of lateral

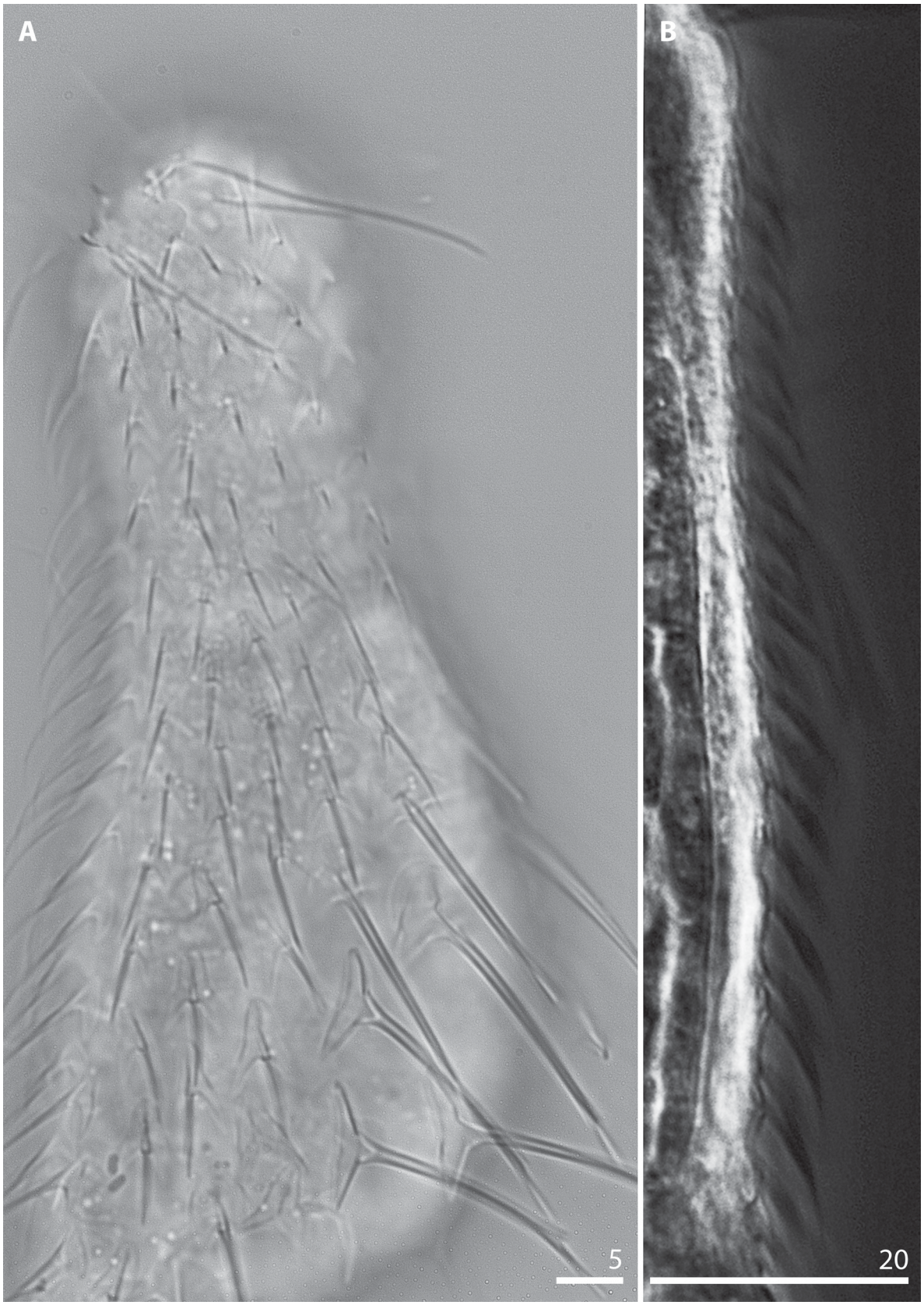

Fig. 23. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Adult specimen. **A**. Spines lateral view, bright field microphotograph. **B**. Spines with lamellae, phase contrast microphotograph.

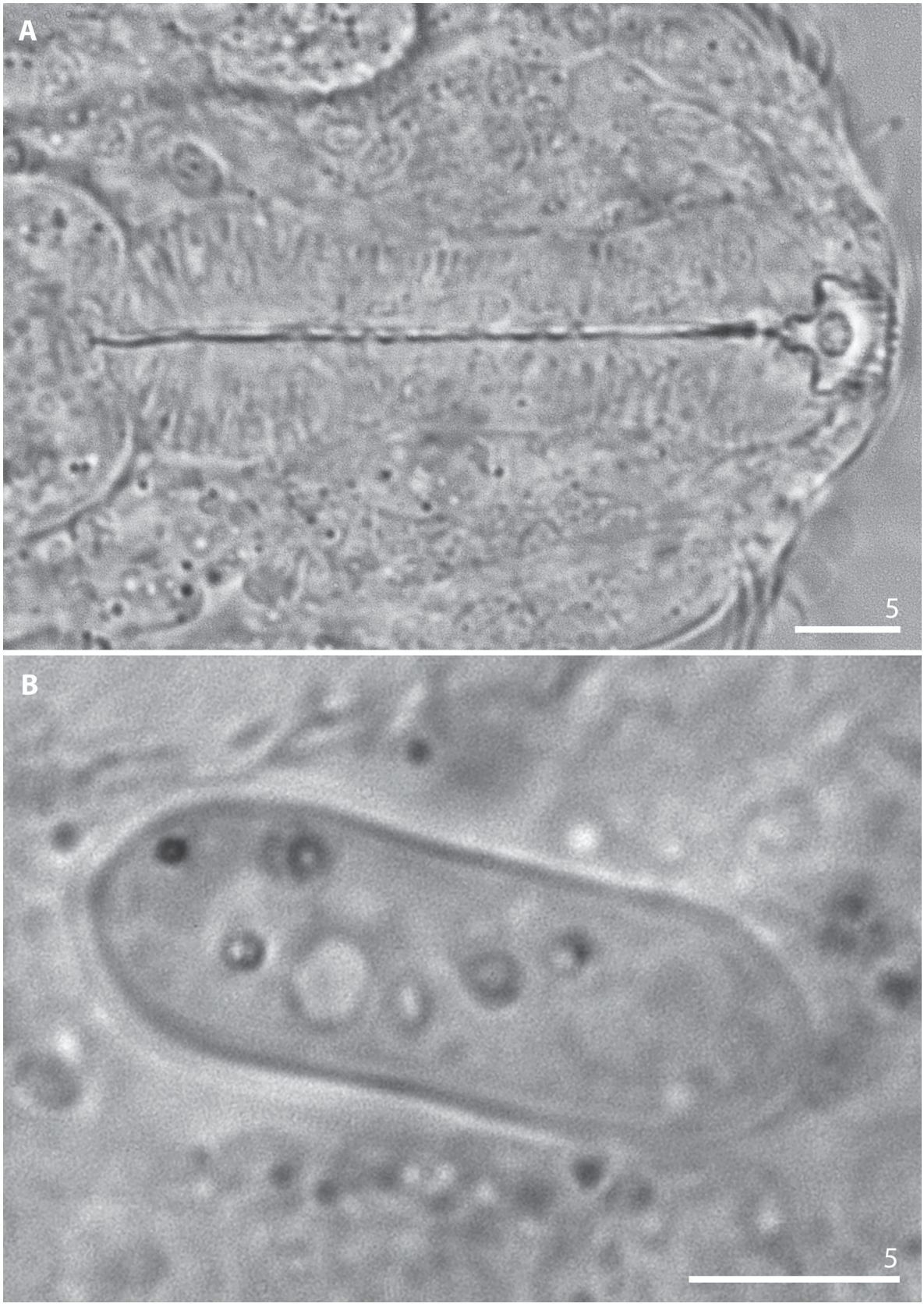

Fig. 24. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Adult specimen. Bright field microphotographs. **A**. Detail of pharynx. **B**. Crescent-like formation inside body integument.

spines (11.6–16.7 μm) (Table A3), and their lateral denticles are more prominent and deeply notched (Fig. 22A–B). The fifth type are long (7.2–19.5 μm), thin, hair-like spines with narrow, delicate lamellae along their entire length. These spines arise on the ventral surface, from scales arranged in one pair of longitudinal rows located closest to the ciliary bands (Fig. 18E). The lamellae are the widest here, ca one-third of the length of the spine, and taper towards the end of the spines (Fig. 21B).

Dorsal sensory bristles. This species has three pairs of dorsal sensory bristles (Fig. 16A). The first, anterior pair is located on the dorsal surface of the head at U5, beyond the dorsolateral cephalion edges, whereas the second pair of sensory bristles is located on the dorsal surface of the posterior neck region at U27. The first and the second pairs emerge from small, spherical papillae. The third, posterior pair of sensory bristles is located dorsally and dorsolaterally on the posterior trunk and emerges from the three-lobed, double-keeled scales at U76–U79. The keels of these scales are connected in the centre of the scales, and the scales are shaped like double, sharp triangles with long, narrow posterolateral lobes set very wide apart and a double, deep posterior notch (Figs 16A, 22B).

Ventral ciliary bands and ventral interciliary field. On the ventral surface, the longitudinal ciliary bands begin at U8 and run back to U87 (Fig. 16C). On the head region (from ca U8 to ca U11) the ciliary bands are merged (Fig. 16C) and subsequently are divided into two separate bands arranged parallel to one another. The entire ventral interciliary field is covered by plate-like scales. They are distributed in 7 longitudinal rows with 14–23 scales in the central row (Figs 16C, 19C, 22D). The ventral interciliary field anterior scales are partially recessed on the cuticle and isolation from the cuticle increases towards the posterior body part. The anterior scales are rounded to inverted egg-shaped (scale

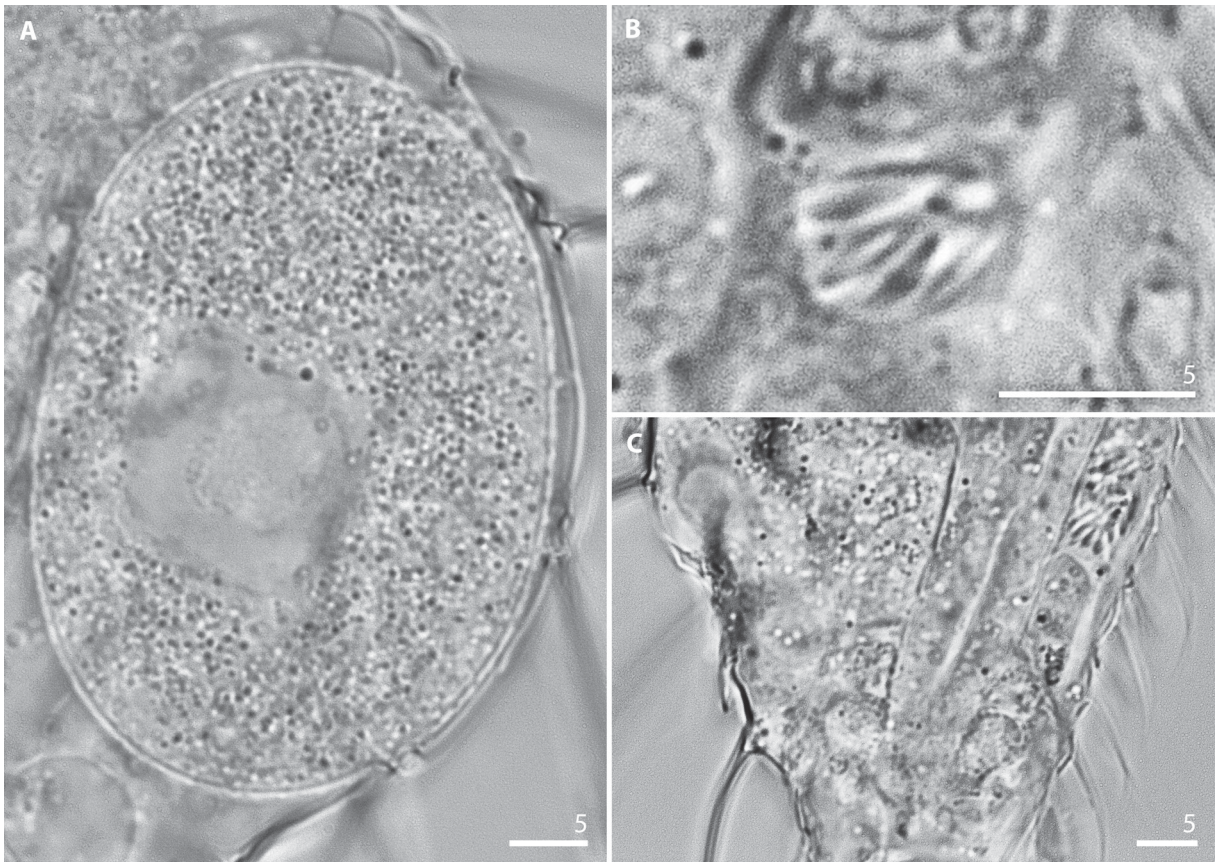

Fig. 25. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Detail of the internal morphology. Bright field microphotographs. **A**. Mature egg. **B**. Sperm pocket. **C**. X-organ and sperm pocket.

22; Figs 17V, 20B), and towards the posterior body region the scales become gradually larger and more elongated (scales 23–24; Fig. 17W–X). The posterior ventral interciliary field region scales (at U73–U79) are elongated, oval in shape, and have straight and thin keels (Figs 20F, 22D). From the anterior to posterior body region, the distances between the scales decrease, and beyond half the trunk length the scales start to overlap (Fig. 20D, F). Three pairs of ventral interciliary field terminal scales are present. The first pair (at U79–U85) is elongated and rectangular, with rounded anterior edges (scale 25; Fig. 17Y). They have a long, narrow keel and a long, thin and straight spine extending beyond the internal furcal indentation. The second and third pairs (at U86–U89) are elongated and rectangular, with rounded anterior edges (scale 26; Fig. 17Z). These pairs have long, narrow keels and possess short, rudimentary spines that only slightly extend towards the posterior scale edge (Fig. 22D).

Internal morphology. The pharynx (from U2 to U30) is wide and has distinct, marked, rounded anterior and posterior dilatations. The posterior dilatation is wider than the anterior one (Fig. 24A). The pharynx is connected through the pharyngeal–intestinal junction to a straight intestine, running from U30 to U84. The pharyngeal–intestinal junction is clearly demarcated, short and narrow (U31). The X-organ of this species (observed in five specimens) is located at U83–U86 near the terminal part of the intestine. It is bilobed, built from two extensions enveloped in a thin coat and connected by a thinner band located below the intestine, at the ventral side. The extensions and the thin coat and the cellular bridge connecting the extensions have a grain-like structure (Fig. 25C). The pair of sperm packets of this species are circular in shape and contain spermatozoids (8–16 per packet) in the form of a short rod. The pair is located at U60–U62 on both sides, juxtaposed to the intestine. When only a single sperm pocket is present, it is irregular in shape, less compact and contains 8–16 spermatozoids. Unpaired sperm pockets, when present, are located at U64–U66, very near the internal trunk wall (Fig. 25C).

Remarks

The total body length of juvenile specimens of *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. varied from 88.8 to 122.9 μm; length of pharynx between 27.6 and 34.2 μm; length of intestine from 36.4 to 58.2 μm; there were 15–21 total longitudinal rows of scales (3D+2–4DL+4–6L+4LV+2–4V), with 11–15 scales in the central row. Out of 69 adults, nine had a large, developing egg, one had a developing egg, an X-organ and a single sperm packet, one had an X-organ and a single sperm packet, whereas two others had an X-organ and two sperm packets and the next one only had a single sperm packet; one had large, crescent-like formations inside the integuments (Fig. 25B) and another had diffuse formations (in both case probably some kind of parasitic structures).

Differential diagnosis

Of all 32 species belonging to the subgenus *Hystricochaetonotus* Schwank, 1990, *Chaetonotus* (*H.*) *horridus* sp. nov. most closely resembles *C.* (*H.*) *acanthophorus* Stokes, 1888, *C.* (*H.*) *balsamoae* Kisielewski, 1997, *C.* (*H.*) *euhystrix* Schwank, 1990 and *C.* (*H.*) *novenarius* Greuter, 1917 (Table A4). *Chaetonotus* (*H.*) *acanthophorus* shares the following characters with *C.* (*H.*) *horridus* sp. nov.: long and strong spines on the dorsal and dorsolateral trunk surfaces; two strong and long anteriormost lateral trunk spines. *Chaetonotus* (*H.*) *balsamoae* and *C.* (*H.*) *novenarius* were selected for comparison with the new species due to their similarity in possessing very long and strong spines with strong, prominent lateral denticles on the dorsal trunk surface. *Chaetonotus* (*H.*) *euhystrix* was selected for comparison with the new species due to its similarity in possessing very long and strong spines with strong, prominent lateral denticles on the dorsal and dorsolateral trunk surfaces; a large mouth ring; a similar number of scales in the central longitudinal row of scales; and type of covering of the ventral interciliary field. Despite the fact that among all of the hitherto known species in this subgenus, those listed above have the highest number of common features with *C.* (*H.*) *horridus* sp. nov., they are significantly different from it – most strikingly by scale type and shape, spine length variation, as well as arrangements of the long trunk dorsal spines and lateral denticle type. In order to avoid any doubts in comparisons with

the new species, only the original descriptions of these species and three of the most detailed papers with morphological data were used (Balsamo 1983; Schwank 1990; Kisielewski 1997a). Comparisons between the new species and the most morphologically similar taxa have been summarised in Table A4.

Chaetonotus* (*Hystricochaetonotus*) *inaequabilis sp. nov.
urn:lsid:zoobank.org:act:82BC94AE-15DD-4A5D-A727-B34013BC6B7A
Figs 26–32, A7; Tables 5, A5–A6

Diagnosis

Stocky body, measuring from 98.2 to 108.5 µm in length. Head five-lobed, cephalion narrow, epipleurae and hypopleurae small. All cephalic plates weakly demarcated in head outline. Hypostomium small, rectangular in shape. Ocellar granules absent. Almost all scales three-lobed. Scales distributed in 15–17 total longitudinal rows (5–7D+2DL+2L+4LV+2V), with 12–13 scales in central row. Scales strongly differ morphologically in various body areas. Nine significantly larger scales on dorsal trunk area with very long, thick spines with a strong lateral denticle. Two pairs of posteriormost trunk lateral scales with long, thick spines with strong lateral denticle. Remaining scales with simple, shorter and thinner spines, or with rudimentary spines, or without spines on central dorsal trunk area and on furcal appendages. Scales with parafurcal spines absent. Spines on ventral surface hair-like, with narrow, delicate lamellae along entire length. Entire ventral interciliary field covered with small scales. Four pairs of ventral interciliary field terminal scales. Pharynx wide, with pronounced anterior and posterior dilatations. Intestine straight without anterior section differing in form and morphology.

Etymology

From the Latin '*inaequabilis*' = 'heterogeneous', referring to the very numerous types of scales on the body.

Type material

Holotype

POLAND • adult; Kraków, Botanical Garden, Jubilee Greenhouse, site 2; 50°03′38″ N, 19°57′30″ E; 15 Nov. 2013; M. Kolicka leg.; NHC-GCHI-23-1-25/h (photomicrographs, also in the author's collection).

Paratypes

POLAND • 6 adults; same locality as holotype; sites 2–3; 15 Nov. 2013 and 17 Apr. 2014; M. Kolicka leg.; NHC-GCHI-23-26-60/p (photomicrographs, also in the author's collection).

Description

Habitus. *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. has a stocky body (Figs 26, 29). Its head is only slightly wider than the neck, and the neck constriction is weakly demarcated. The neck gradually tapers from the head (from U20) to the beginning of the trunk (ca U30) (Figs 26, 29). The trunk is slightly wider than the head and gradually dilates from ca U31 to ca half of its length (U56), where it is at its maximum width. Then it gradually tapers towards the narrow furcal base (from U84) (Figs 26, 29). The furcal base is clearly demarcated and narrow. The furcal indentation is V-shaped. The furcal branches are set narrowly apart and point slightly outwards (Figs 26, 29). The adhesive tubes are relatively short in comparison to the whole body length (Table 5), straight, fairly thick and not tapered towards the blunt ends (Figs 26, 29).

Head. The head is five-lobed, short and semicircular in shape. The cephalion (U1–U3) is narrow, short and straight, on the dorsal body side. It adheres to the head along its entire length and rapidly extends

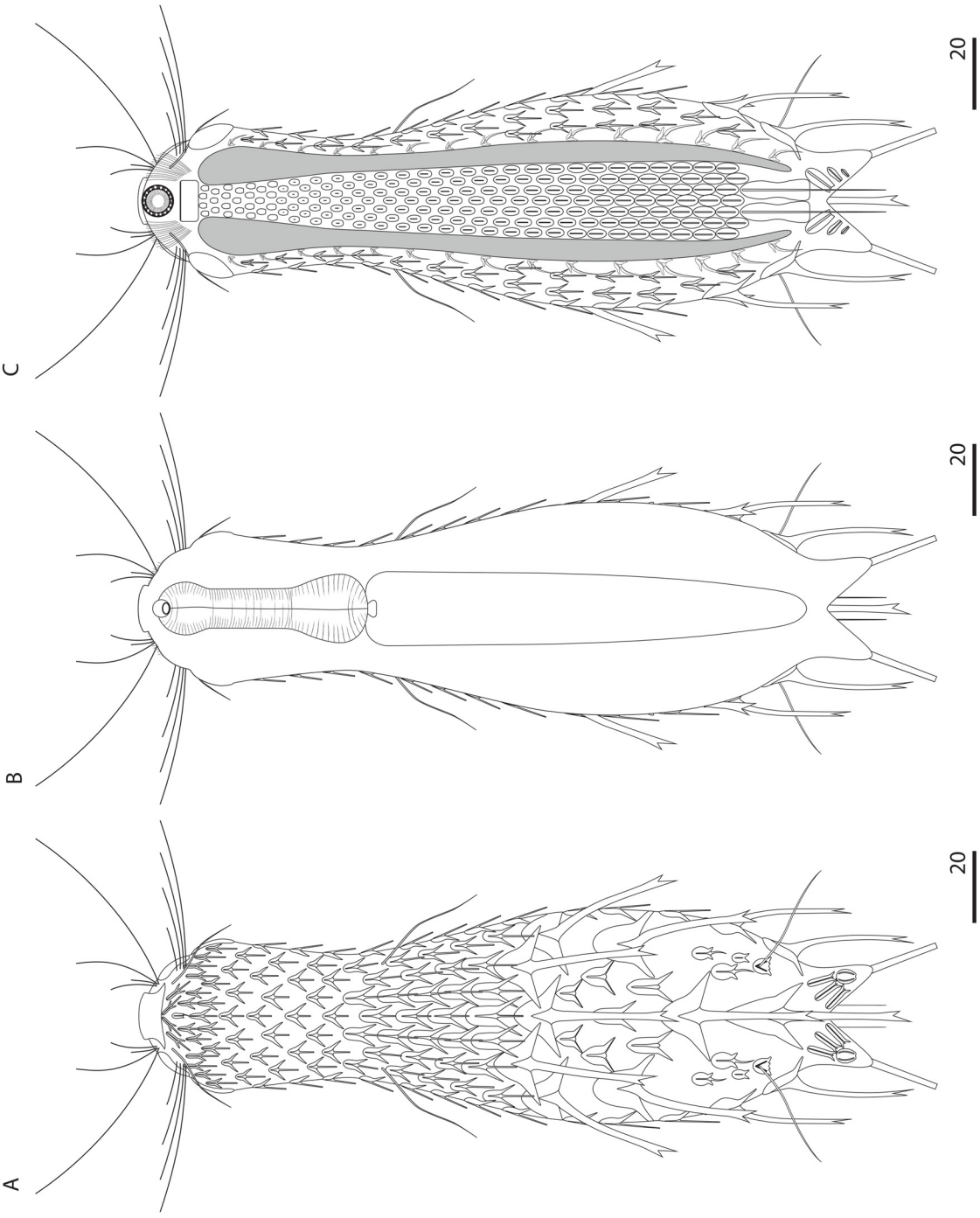

Fig. 26. *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. Schematic drawings. **A**. Dorsal body view. **B**. View of internal morphology. **C**. Ventral body view. Light grey areas indicate the areas of insertion of ciliary bands.

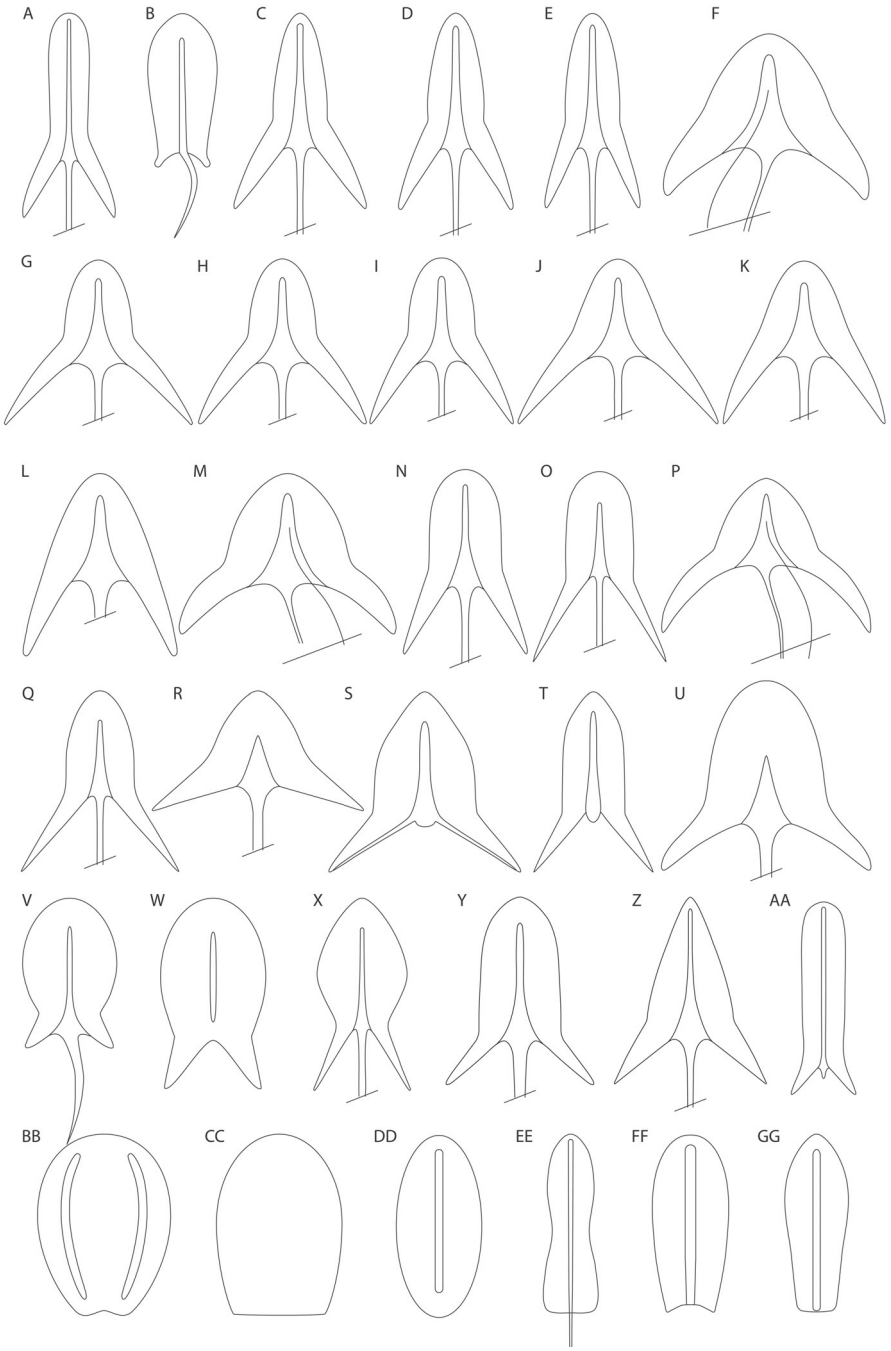

Fig. 27. *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. Schematic drawings of the scales. **A**. Head anteriormost scale (scale 1). **B**. Head anteriormost central scale (scale 2). **C**. Anterior head dorsal scale (scale 3). **D**. Anterior head dorsolateral and lateral scale (scale 4). **E**. Anterior head ventrolateral scale (scale 5). **F**. Head ventral scale (scale 6). **G**. Posterior head dorsal scale (scale 7). **H**. Posterior head dorsolateral and lateral scale (scale 8). **I**. Posterior head ventrolateral scale (scale 9). **J**. Anterior neck dorsal scale (scale 10). **K**. Neck dorsolateral and lateral scale (scale 11). **L**. Neck ventrolateral scale (scale 12). **M**. Neck ventral scale (scale 13). **N**. Posterior neck dorsal scale (scale 14). **O**. Anterior trunk dorsal, dorsolateral, lateral and ventrolateral scale (scale 15). **P**. Trunk ventral scale (scale 16). **Q**. Posterior trunk dorsal, dorsolateral, lateral and ventrolateral scale (scale 17). **R**. Scale 18. **S**. Scale 19. **T**. Scale 20. **U**. Scale 21. **V**. Scale 22. **W**. Scale 23. **X**. Scale 24. **Y**. Scale 25. **Z**. Scale 26. **AA**. Scale 27. **BB**. Scale 28. **CC**. Scale 29. **DD**. Scale 30. **EE**. Scale 31. **FF**. Scale 32. **GG**. Scale 33.

Table 5. Main morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. N = number of specimens analysed; Range = the smallest and the largest structure found among all specimens measured. All measurements in micrometers (μm); all indicators given as a percentage (%) and italicized.

Characters	N	Holotype	Range of adult paratypes
Body length	5	107.91	98.16–108.49
Furca length	5	20.96	20.08–22.05
Adhesive tube length	5	10.05	9.92–10.50
Number of scales in central longitudinal row	5	14	14–15
Total number of longitudinal alternating rows of scales	5	19	19–21
Head scales length × width	5	1.87–5.22 × 1.49–4.86	1.49–5.91 × 1.23–5.01
Neck scales length × width	5	2.39–6.45 × 2.77–5.21	2.07–6.65 × 2.40–5.37
Trunk scales length × width	5	2.82–11.04 × 3.31–13.03	2.28–11.39 × 2.24–13.03
Head spines length	5	0.34–11.42	0.27–12.03
Neck spines length	5	1.76–12.41	1.62–13.60
Trunk spines length	5	3.32–14.62	3.09–15.23
Trunk long spines length	5	11.61–21.61	10.16–21.61
Localization of lateral denticle on trunk long spines spines	5	*10.288–17.399*	*8.780–17.958*
Length of trunk posteriormost pair of lateral spines	5	13.69	11.42–14.02
Localization of lateral denticle on trunk posteriormost pair of lateral spines	5	13.587	12.610–15.149
Mouth ring diameter	5	6.04	5.14–7.07
Pharynx length	5	28.05	26.21–28.29

laterally near the dorsal edge (Figs 26A, 31A). The epipleurae (U3–U7) are small, narrow, slightly arched and weakly demarcated in the head outline. They are visible on the dorsal, dorsolateral and lateral head sides. The hypopleurae (U7–U12) are similar in size to the epipleurae and located entirely on the ventrolateral and ventral head sides (Fig. 26). On the dorsal head surface, between the lateral edges of the cephalion and epipleurae, is a prominent space; their edges meet only in the cephalion extension place. Deep notches are present between the cephalion and epipleurae and between the epipleurae and hypopleurae. The hypostomium (U6–U8) is small, rectangular, with a slightly reinforced anterior edge (Figs 26C, 31B). Two pairs of cephalic ciliary tufts are present. The anterior tufts emerge in the area between the cephalion and epipleurae on the dorso-terminal head surface (at U2–U3) and consist of four cilia. The anteriormost cilium in both anterior tufts is fairly short. The second cilium is short, shorter than the anteriormost one. The third cilium is longer than either of the preceding cilia. The fourth, last cilium in the anterior tufts is very long, the longest in both pairs of tufts. The posterior tufts (at U6–U7) have four straight cilia each and emerge on the ventral head surface, above the anterior edge of the hypopleurae. The length of the cilia in the posterior tuft gradually increases from the anteriormost to the fourth cilium. Ocellar granules are not present. The mouth ring is large and subterminal at U2–U5. It has very strong, granular cuticular reinforcements and short inner hairs (Figs 26C, 29C). Suboral bristles are located in two tufts located beneath and laterally to the mouth ring and reaching half the length of the lateral hypostomium edges (between U5 and U7).

Scales. The entire body, except for one pair of scales on the furcal appendages, is covered with three-lobed scales that adhere to the cuticle along their entire surface (Fig. A7). All scales have a strong, triangular keel and are shaped like triangles with a deep posterior notch. The scales are distributed in 15–17 total longitudinal alternating rows (5–7D + 2DL + 2L + 4LV + 2V), with 12–13 scales in the central

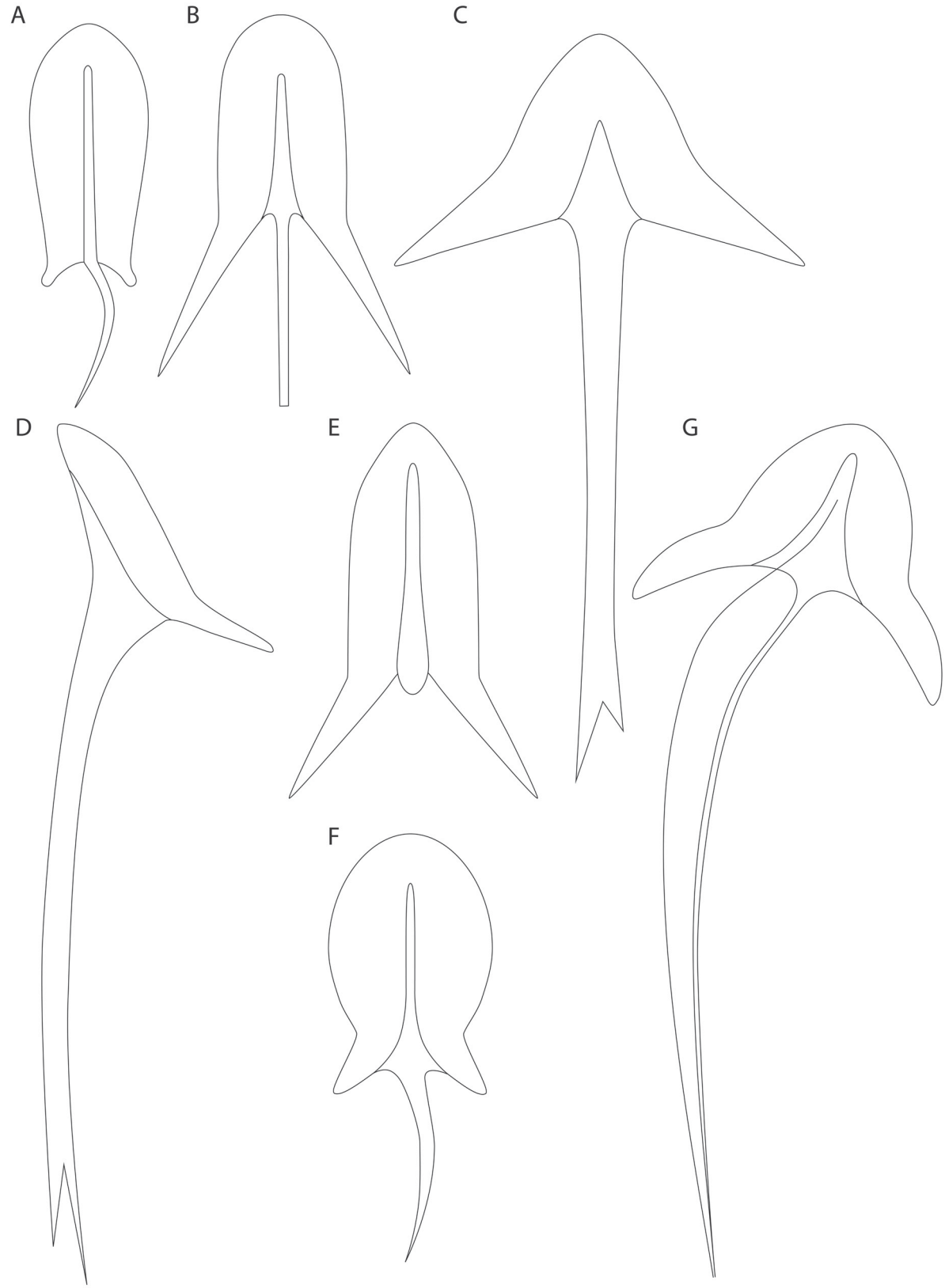

Fig. 28. *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. Schematic drawings of the spine types. **A**. First type of spines. **B**. Second type of spines. **C–D**. Third type of spines. **E–F**. Fourth type of spines. **G**. Fifth type of spines.

row. The longitudinal rows of scales begin on the head directly beneath the posterior edge of the cephalion, epipleurae and hypopleurae. The scales show a strong diversity in size and shape between the various parts of the body. On the head and anterior neck region the scales are located far from each other, while on the posterior neck and anterior trunk region the scales become gradually juxtaposed but do not overlap. The dorsolateral, lateral, ventrolateral and ventral trunk scales are juxtaposed, whereas the dorsal trunk scales and scales on the furcal appendages have overlapping posterolateral edges (Fig. 30). The head anteriormost scales are situated near the posterior edge of the cephalion and epipleurae. The dorsal anterior scales are located aslant, whereas the dorsolateral scales are arranged parallel to the longitudinal body axis. These scales are elongated, their central lobes are long and wide, and they have very long keels. The posterolateral lobes are narrow, slanted downward and create a narrow, deep V-shaped posterior scale notch (scale 1; Fig. 27A). The central anteriormost head scales are located at U5–U6, beneath the aslant arranged scales, are smaller, more rounded and have weaker separate posterolateral lobes (scale 2; Fig. 27B). The remaining scales of the head are wider. The central lobes of these scales become shorter, and simultaneously the posterolateral lobes become slightly longer, whereas their keels are shorter. The posterolateral lobes are directed diagonally downward and laterally and create a deep and wide posterior scale notch (scales 3 and 7; Fig. 27C, G). The anterior neck scales are shorter than the head scales. Their central lobes are wide and short. Their posterolateral lobes are weaker and separate from the central lobes (scale 10; Fig. 27J). The subsequent neck scales become larger but relatively narrower than the preceding neck scales (Table A5). Their central lobes are wide, with strongly rounded anterior edges, whereas their postero-lateral lobes are more separated and directed more downward and create a deep V-shaped posterior scale notch (scale 14; Fig. 27N). The posterolateral lobes of the dorsolateral, lateral and ventrolateral scales of the head and neck become gradually more

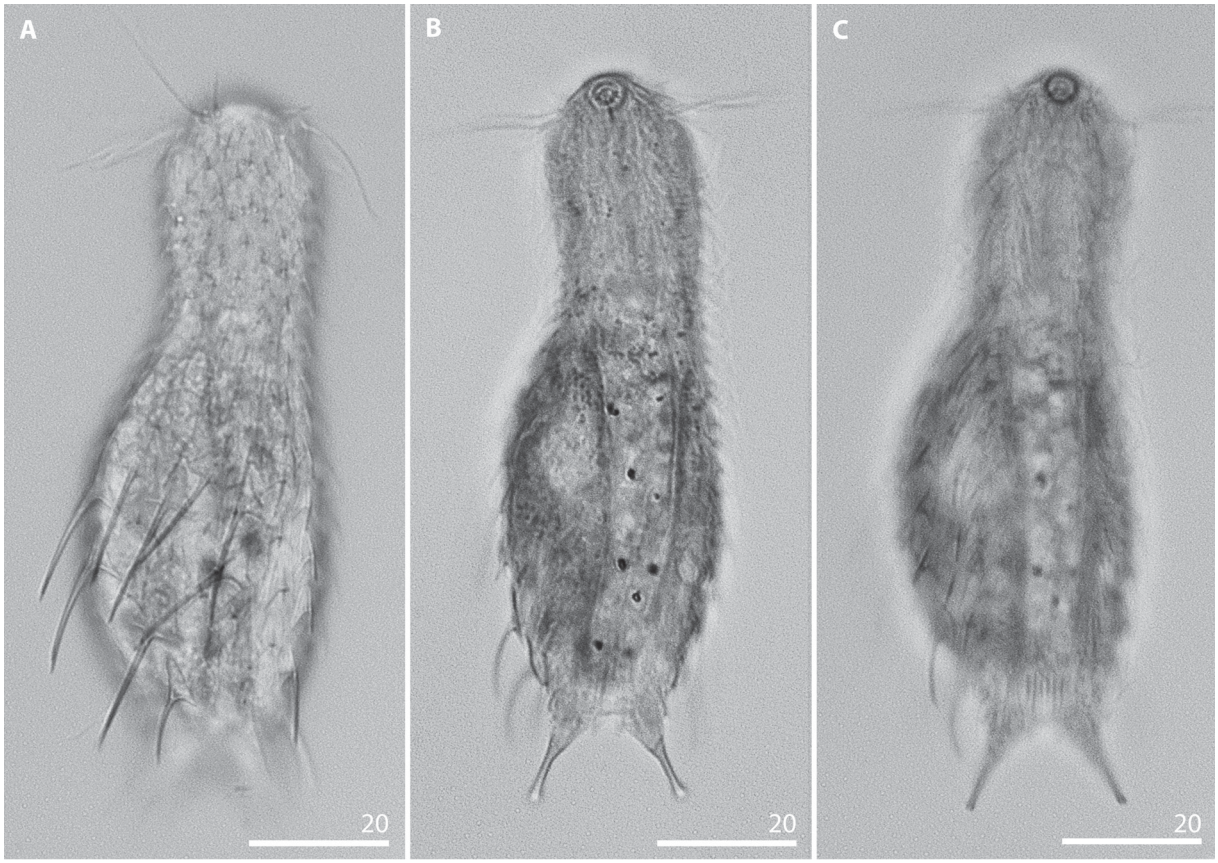

Fig. 29. *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. Adult specimen. Bright field microphotographs. **A**. Dorsal body view. **B**. View of internal morphology. **C**. Ventral body view.

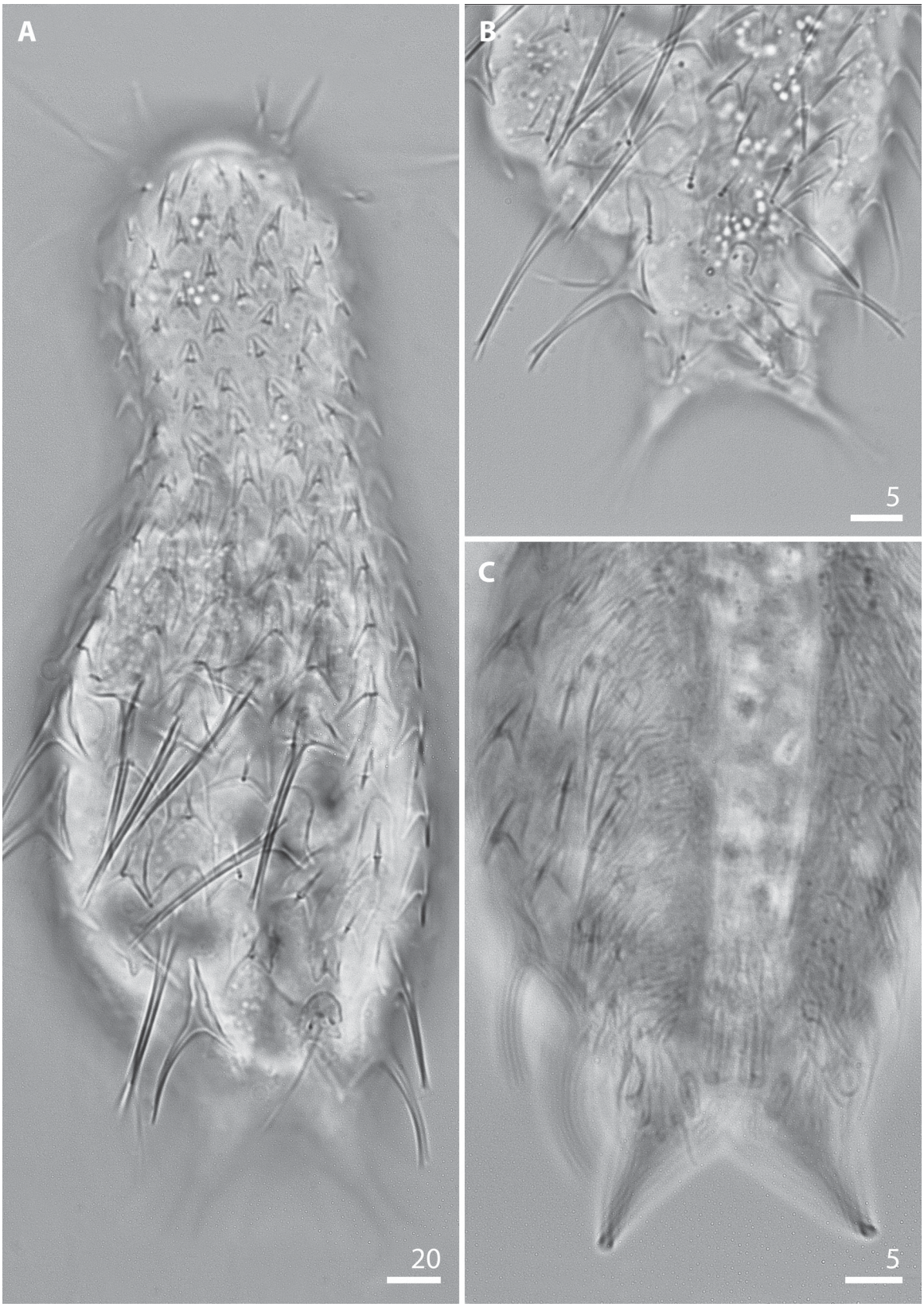

Fig. 30. *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. Adult specimen. Bright field microphotographs. **A**. Scales, dorsal view. **B**. Posterior trunk region, furca base and furcal appendage scales, dorsal view. **C**. Posterior trunk region, furca base and furcal appendage scales, ventral view.

directed downward towards the ciliary bands as compared to the dorsal scales (scales 3–14; Fig. 27C–N). From the neck towards the trunk, the size of the scales gradually increases (from 2.1–2.5 × 2.4–2.9 to 4.2–5.4 × 5.1–6.5 μm). The anterior trunk scales have a wide and rounded anterior central lobe and clearly separate, long, narrow and sharp posterolateral lobes. The posterolateral lobes are directed diagonally downward and slightly laterally, and they create a deep, narrow V-shaped posterior scale notch (scale 15; Fig. 27O). The dorsolateral, lateral and ventrolateral trunk scales, arranged from the central to posterior trunk region (U50 to U83), become gradually larger than the anterior trunk scales (from 2.3–7.1 × 2.7–5.1 to 3.5–8.8 × 4.1–7.1 μm) and they have a more pointed anterior edge of the central lobe and longer, more sharp posterolateral lobes directed more apart and diagonally downward (scale 17; Fig. 27Q). Dorsally, on the central trunk part (at U47–U57), five different scales with very long and strong spines are located in one transverse row. These scales are very large (6.4–13.0 × 5.2–8.3 μm) and very thick. They are triangular, their central lobes are short, wide and pass seamlessly into wide, posterolateral lobes directed very far apart. The posterior edges of these scales are almost straight and only very narrowly notched. Their keels start from the half length of the central lobes and are very pronounced, strongly triangular in shape (scale 18; Fig. 27R). Directly beneath the row of large scales, two pairs of smaller scales with long keels and spiny processes are located (at ca U55–U61). These scales are triangular, have longer central lobes with pointed anterior edges and narrower posterolateral lobes directed slightly more downward (scale 19; Fig. 27S). Posteriorly to these scales, at the centre of the dorsal trunk region, three scales with long keels and spiny processes are located (at U60–U68). These scales are narrower and have longer central lobes than the preceding scales. Their posterolateral

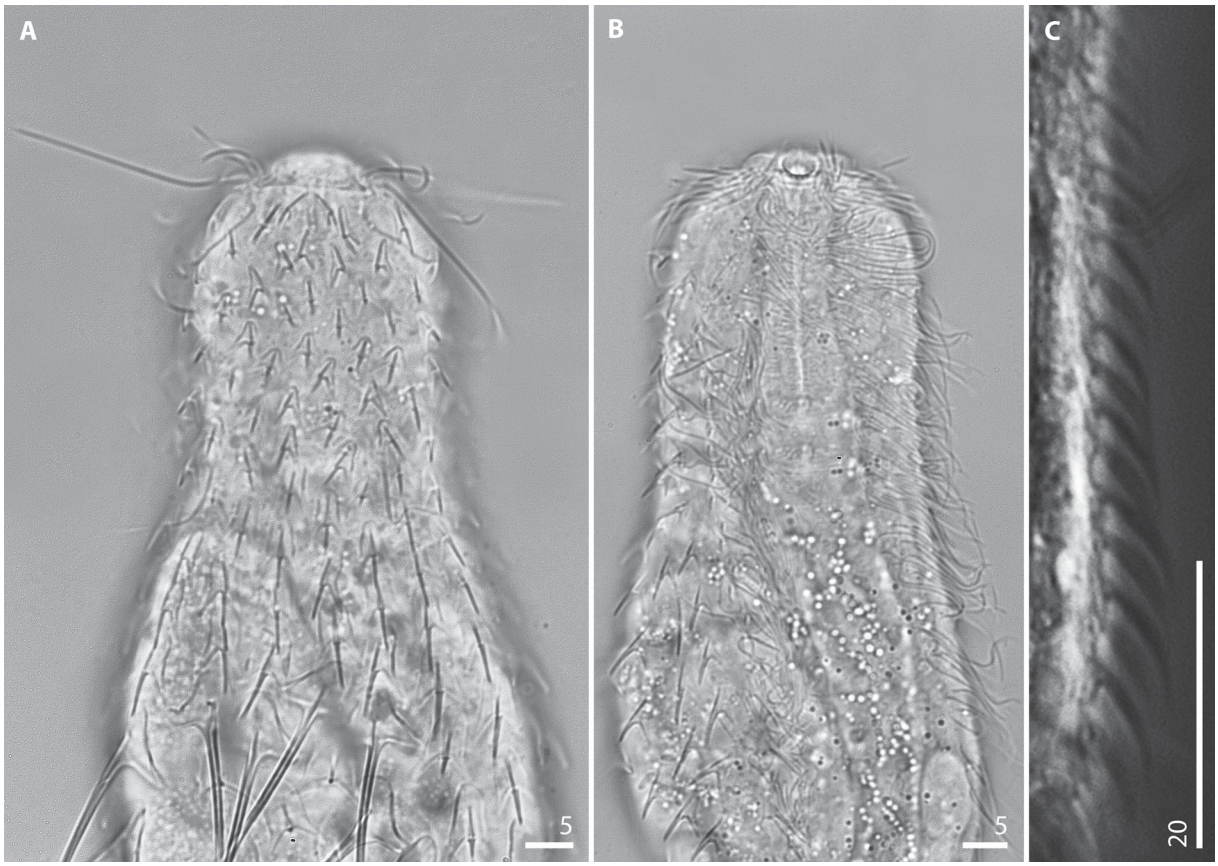

Fig. 31. *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. Adult specimen. **A**. Head, neck, anterior and central trunk spines, dorsal view, bright field microphotograph. **B**. Head, neck, anterior and central trunk spines, ventral view, bright field microphotograph. **C**. Ventrolateral spines with lamellae, phase contrast microphotograph.

lobes are directed clearly downward, creating a V-shaped posterior scale notch (scale 20; Fig. 27T). Laterally to these three scales and posteriorly to the transverse row with wide, large scales, another pair of large scales with very long and strong spines is located (at U60–U66). These scales have longer central lobes, narrower posterolateral lobes directed more downward (7.3–9.2 × 7.2–9.5 μm) and more rounded edges than the preceding large scales (scale 21; Fig. 27U). In the central dorsal longitudinal row, at U67–U74, a single scale of the same type as the large scales from the transverse row at U55–U59 is present (scale 18; Fig. 27R). Laterally to it, at U70–U74, two pairs of smaller scales are located, with one pair after another in the longitudinal row. These scales have a long and strongly rounded central lobe and clearly separated, short and wide posterolateral lobes (Fig. 30B). Of these two scale pairs, the pair situated below (U72–U74) is larger than the upper pair (U70–U72) (scale 22; Fig. 27V). On the posterior trunk region laterally to these rounded scales, directed above the double-keeled scales with trunk dorsal sensory bristles, one pair of small (3.3–4.9 × 2.2–3.3 μm) scales is arranged at U74–U75 (scale 23; Fig. 27W). These scales have a strongly rounded central lobe and posterolateral lobes that are weakly separated from the central lobes, wide, short and directed downward, creating a V-shaped posterior notch. Their keels are strong but short and pass into short spines which do not extend to the posterior edge of the scales. On the lateral surface of the posterior trunk region, one pair of second to last trunk scales is located (at U71–U78). These scales are large (7.4–11.4 × 4.1–6.1 μm) and have a long, wide, strongly rounded and clearly pointed anterior central lobe. Their postero-lateral lobes are strongly separated from the central lobe and have long, narrow and sharp edges that are directed diagonally downward. These scales have strong keels and strong, long spines (scale 24; Fig. 27X). Posteriorly to them, the last pair of trunk lateral scales is situated at the furcal base (at U78–U84). This pair of scales is large (6.4–10.8 × 4.9–8.3 μm); these scales have a long, wide and strongly anteriorly rounded central

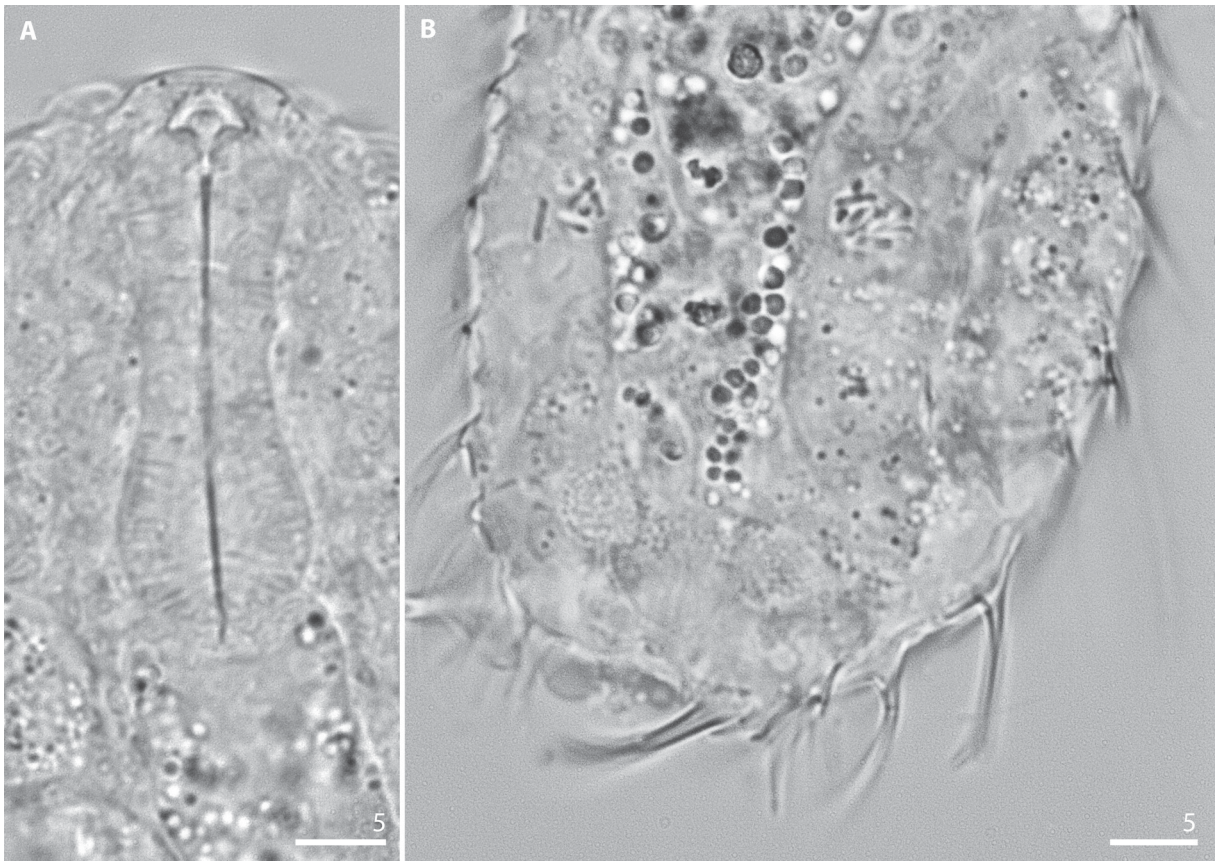

Fig. 32. *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. Adult specimen. Bright field microphotographs. **A**. Detail of pharynx. **B**. X-organ and sperm pockets.

lobe with a very strong and high keel and strong, long spines and short, narrow posterolateral lobes. The posterolateral lobes of these scales are directed diagonally wide apart, downward and laterally, creating a wide and shallow V-shaped posterior scale notch (scale 25; Fig. 27Y). On the dorsal posterior trunk region and furcal base, at U76–U83, one median large scale that is different in type is located. This scale is triangular, has a long and pointed central lobe with a long keel and a long, strong spine, and clearly separate, relatively short postero-lateral lobes directed diagonally downwards (scale 26; Fig. 27Z). On the dorsal surface of the furcal appendages (at U84–U89), three pairs of three-lobed, elongated and narrow scales with long central and short posterolateral lobes are present. These scales have a long keel with a spiny process (scale 27; Fig. 27AA). Dorsolaterally and laterally to the furcal appendages (at U88–U90), one pair of scales with two long and slightly bent keels is present. These scales are oval in shape and have very shallow posterior notches (scale 28; Fig. 27BB). The edges of the scales on the furcal appendage are slightly overlapping (Fig. 30B). The size of the scales gradually decreases from the dorsal, dorsolateral and lateral surfaces towards the ventrolateral surface. The scales in the ventral longitudinal row located closest to the ciliary bands are short and wide, their central lobes are short and their posterolateral lobes are weakly separated. From the head to the widest body region the length of the posterolateral lobes of these scales, as well as their separation from the central lobes, gradually increase. The notches of the posterior edges of these scales are semicircular in shape. The ventral scales are much smaller than the scales of the other rows and their anterior edge is oriented towards the bands at an angle of ca 20°.

Spines. In this species, five main types of spines may be distinguished (Fig. 28). The first type are basally bent spines tapering towards the end, without any lateral denticle (Fig. 28A). These spines emerge from single, central anteriormost head scales located at U5–U6 (Figs 27A, 31A) and from two pairs of dorsal posterior trunk region scales located at U70–U74 (scale 12) (Fig. 27A). The second type are simple spines that do not taper towards the blunt ends and are without any lateral denticle (Fig. 28B). These spines emerge from the dorsal, dorsolateral, most of the lateral and ventrolateral head, neck and anterior trunk region scales and dorsolaterally, laterally and ventrolaterally on the remaining trunk part scales. The length and thickness of the spines gradually increase from the head top towards the widest body region (from 0.3–12.0 to 3.1–15.2 μm) (ca U57). Moreover, their length gradually decreases towards the ventrolateral surface (head: from 0.5–3.1 to 0.3–2.4 μm; neck: from 2.1–5.7 to 1.6–4.4 μm; trunk: from 3.9–8.2 to 3.1–7.1 μm) (Table A5). The third type are very long (11.4–21.6 μm) and thick, straight spines with a prominent lateral denticle (Fig. 28C). Together, nine dorsal spines and four (two pairs) lateral spines of this type are present. Five of them arise from large dorsal trunk scales located in one transverse row at U47–U57 (scale 18) (Figs 29A, 31A–B). The next two spines arise from one pair of dorsal trunk scales located at U60–66 (scale 21) (Figs 29A, 31A–B). The eighth of these long spines arises from the central dorsal scale located at U67–U74 (scale 18) (Figs 29A, 31A–B). This spine is the longest (11.4–21.6 μm) and the thickest body spine and it has the most prominent lateral denticle. The ninth and last of these long dorsal spines arises from the central dorsal scale located at the posterior trunk region and on the furcal base (at U84–U89) (scale 26) (Fig. 31A–B). This spine is slightly shorter than the preceding long spine (11.4–14.2 μm). The two pairs of long lateral spines arise from the trunk second to posteriormost pair of lateral scales (at U71–U78) (scale 24) and from the trunk posteriormost pair of lateral scales (at U78–U84) (scale 25; Figs 28D, 31A–B). The posteriormost pair is longer (11.4–14.0 μm) and thicker than the second to posteriormost pair of lateral spines (10.1–12.7 μm long). The fourth type are short, simple spines (Fig. 28E) or spiny processes without any lateral denticle (Fig. 28F). These spines arise from the central dorsal trunk scales located at U55–U59 and U60–U68 (Fig. 31A), from one pair of trunk dorsal scales located at U74–U75, above the double-keeled scales with the dorsal sensory bristle, and from three pairs of elongated scales located on the dorsal and dorsolateral surface of the furcal appendages at U84–U89 (Fig. 31A). The fifth type are long (7.3–15.2 μm), thin and hair-like, with narrow, delicate lamellae along their entire length (Fig. 28G). These spines arise on the ventral

surface, from scales arranged in one pair of a longitudinal row located closest to the ciliary bands. The lamellae on these spines are widest near the spine base and gradually taper towards the end of the spine (Fig. 31C).

Dorsal sensory bristles. This species has three pairs of dorsal sensory bristles (Fig. 26A). The first, anterior pair is located on the dorsal surface of the head at U5, beyond the dorsolateral cephalion edges, where the second pair of sensory bristles is located on the dorsal surface of the posterior neck at U31. The first and the second pairs emerge from small, spherical papillae. The third, posterior pair of sensory bristles is located dorsolaterally on the posterior trunk region and furcal base and emerges from the small three-lobed scales with two strong keels situated at U77–U79. These scales have keels which are connected in the centre of the scales and have a strongly rounded, wide central lobe and short, weakly separated posterolateral lobes. These scales have a double, shallow posterior notch (Fig. 31A).

Ventral ciliary bands and ventral interciliary field. On the ventral surface, the longitudinal ciliary bands begin at U9 and run back to U82 (Fig. 29C). The ciliary bands are wide, and wider on the head region than on other parts of the body. The entire ventral interciliary field is covered with thin, small scales. They are distributed in seven longitudinal rows, with 21–25 scales in the central row (Figs 30C, 31B). The ventral interciliary field anterior scales are partially recessed on the cuticle and isolation from the cuticle increases towards the posterior body part. On the anterior region the scales have an oval shape with a straight posterior edge and are located far from each other (scale 29; Fig. 27CC). Towards the posterior body region the scales become gradually larger (from 1.4–1.9 × 0.6–1.1 to 3.8–5.2 × 2.7–4.1 μm), more elongated and with a rounded posterior edge (scale 30; Fig. 27DD). The anterior scales are keelless and spineless, but towards the trunk posterior region the keels on the scales become more distinct and the distance between the scales decreases (Figs 26C). Four pairs of ventral interciliary field terminal scales are present. The first pair (at U76–U85) is elongated and has a narrowing halfway along the length of the scale (Fig. 30C). They have a long, narrow keel and a long, thin and straight spine extending beyond the internal furcal indentation (scale 31; Fig. 27EE). The second pair (at U84–U87) is elongated, has a pointed anterior edge and gradually tapers to the posterior end. This pair has long, narrow keels and is spineless (scale 32; Fig. 27FF). The third (at U87–U88) and fourth (at U88–U89) pairs are small, elongated and oval-shaped, with a shallow posterior notch (scale 33; Fig. 27GG). They have a long, straight keel and are spineless. The second, third and fourth pairs of ventral interciliary field terminal scales are situated at the furcal appendages.

Internal morphology. The pharynx (from U3 to U29) is wide and has distinct, marked, rounded anterior and posterior dilatations. The posterior dilatation is wider than the anterior one (Fig. 32A). The pharynx is connected through the pharyngeal–intestinal junction to a straight intestine, running from U29 to U84. The pharyngeal–intestinal junction is clearly demarcated, short and narrow (U29–U30). The X-organ of this species (observed in one specimen) is located at U80–U83 near the terminal part of the intestine. It is bilobed, built from two extensions enveloped in a thin coat and connected by a thinner band located behind the intestine at the ventral side. The extensions, the thin coat and the cellular bridge connecting the extensions have have a grain-like structure. The pair of sperm packets of this species are circular in shape and contain spermatozoids (12 per packet) in the form of a short rod. They are located at U62–U64 on both sides, juxtaposed to the intestine (Fig. 32B).

Remarks

Juvenile specimens of *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. were not observed; furthermore, specimens with large, developing eggs were not present. Out of seven adults, one had an X-organ and two had sperm packets.

Differential diagnosis

Within the subgenus *Hystricochaetonotus*, *Chaetonotus* (*H.*) *inaequabilis* sp. nov. most closely resembles *C.* (*H.*) *enormis* Stokes, 1887, *C.* (*H.*) *schlitzensis* Schwank, 1990, *C.* (*H.*) *octonarius* Stokes, 1887, *C.* (*H.*) *novenarius* Greuter, 1917, *C.* (*H.*) *aemilianus* Balsamo, 1978, *C.* (*H.*) *ferrarius* Schwank, 1990, *C.* (*H.*) *spinulosus* Stokes, 1887 and *C.* (*H.*) *longispinosus* Stokes, 1887. All of these species were chosen for comparison because they possess a set of similar features such as: range of body length; body shape; presence of very long spines on dorsal and/or dorsolateral trunk surfaces; presence of lateral denticle only on the long spines (for *C.* (*H.*) *ferrarius* see Table A6); and absence of parafurcal spines. Moreover, *C.* (*H.*) *enormis* is similar to the new species in having two pairs of furcal base lateral spines which are longer and stronger than the remaining lateral spines. *Chaetonotus* (*H.*) *schlitzensis*, *C.* (*H.*) *octonarius*, *C.* (*H.*) *novenarius*, *C.* (*H.*) *aemilianus*, *C.* (*H.*) *ferrarius* and *C.* (*H.*) *spinulosus* share with *C.* (*H.*) *inaequabilis* sp. nov. the presence of scales without spines or with spiny processes on the central dorsal trunk region. *Chaetonotus* (*H.*) *novenarius* and *C.* (*H.*) *aemilianus* also possess the same number of scales with long spines as the newly described species. Despite the fact that among the hitherto known species in this subgenus, those listed above have the highest number of common features with the newly described species, they are significantly different from *C.* (*H.*) *inaequabilis* sp. nov. – most strikingly by size, type, and shape of the scale coverage as well as the arrangement of scales with long spines. In order to avoid any doubts in comparisons with the new species, only the original descriptions of these species and three of the most detailed papers with morphological data were used (Balsamo 1983; Schwank 1990; Kisielewski 1997a). Comparisons between the new species and the morphologically most similar taxa are summarised in Table A6.

Subgenus ***Zonochaeta*** Remane, 1927

Type species

Chaetonotus succinctus Voigt, 1902.

Terra typica

Germany.

Remarks on subgenus

This is the only subgenus of *Chaetonotus* that seems to be monophyletic in terms of molecular data (Kånneby *et al.* 2013); it encompasses 13 nominal freshwater species (Todaro 2018). It is present in benthic and periphytic habitats (e.g., Kisielewski 1997a).

Chaetonotus* (*Zonochaeta*) *cestacanthus Balsamo, 1990
Figs 33–34; Table 6

Chaetonotus (*Zonochaeta*) *cestacanthus* Balsamo, 1990: 168, fig. 4.

Locus typicus

Italy.

Material examined

POLAND • 3 adults, 1 juvenile; Kraków, Botanical Garden, Jubilee Greenhouse, sites 1–2; 50°03′38″ N, 19°57′30″ E; 15 Nov. 2013 and 17 Apr. 2014; M. Kolicka leg.; NHC-GCZC-24-1-10 (photomicrographs, also in the author's collection).

Distribution

Chaetonotus (*Z.*) *cestacanthus* Balsamo, 1990 was originally described from Italian lakes, namely Lake Chiusi and Lake Bolsena (Balsamo 1990), and next recorded from the volcanic Lake Nemi, also in Italy (Balsamo & Fregni 1995). It has not previously been listed outside of this country.

Fig. 33. *Chaetonotus* (*Zonochaeta*) *cestacanthus* Balsamo, 1990. Adult specimen. Bright field microphotographs. **A**. Scales and spines, dorsal view. **B**. Scales and spines, ventral view.

Fig. 34. *Chaetonotus* (*Zonochaeta*) *cestacanthus* Balsamo, 1990. Adult specimen. **A**. Habitus, phase contrast microphotograph. **B**. Posterior trunk region, furca base and furcal appendages, dorsal view, phase contrast microphotograph. **C**. Posterior trunk region, furca base and furcal appendages, dorsal view, bright field microphotograph.

Table 6 (continued on next page). Main morphometric characters of *Chaetonotus* (*Zonochaeta*) *cestacanthus* Balsamo, 1990. N = number of specimens analysed; NA = data not available; Range = the smallest and the largest structure found among all specimens measured. All measurements in micrometers (μm).

Characters	According to Balsamo (1990)	N	Range of adult specimens	Juvenile specimen
Body length	64.50–80.00	3	87.19–89.11	70.12
Furca length	8.50–11.00	3	14.91–15.77	15.05
Adhesive tube length	NA	3	7.50–8.13	8.06
Number of scales in central longitudinal row	13–14	3	14	13
Total number of longitudinal alternating rows of scales	15	3	15	13
Length of cephalic cilia (anterior tuft)	(8.50–10.50)–(18.50–20.0)	3	(7.85–8.11)–(20.89–22.46)	7.34–18.16
Length of cephalic cilia (posterior tuft)	8.50–10.50	3	(8.24–9.55)–(11.73–16.54)	8.15–11.37
Head scales length × width	3.50–4.20 × 2.50–3.20	3	(2.98–3.19)–(4.67–5.02) × (2.18–2.34)–(3.63–3.83)	2.89–4.22 × 2.09–3.32
Neck scales length × width	3.00 × 2.80	3	(2.56–2.91)–(4.19–4.67) × (2.77–3.19)–(4.10–4.31)	2.34–3.83 × 2.67–3.86
Trunk scales length × width	6.50–8.70 × 5.30–6.50	3	(3.89–4.05)–(9.46–9.59) × (3.26–3.91)–(7.20–7.85)	3.68–5.94 × 3.10–4.72
Scales with long dorsal spines length × width	3.70–4.60 × 3.20–3.70	3	(4.24–4.78)–(4.69–4.95) × (2.89–3.30)–(3.19–3.53)	4.19–4.81 × 3.22–3.46
Median and dorsolateral scales with long spines on posterior trunk region length × width	6.00 × 4.00–6.00	3	(5.68–6.70)–(5.86–7.19) × (5.22–5.88)–(5.42–6.47)	5.03–5.72 × 4.41–4.76
Double keeled scales on furcal appendages length × width	NA	3	4.36–4.93 × 4.04–4.51	3.85 × 3.52
Head dorsal spines length	1.30–2.30	3	(0.39–0.51)–(3.17–4.61)	0.34–3.97
Head ventral spines length	2.00–7.80	3	(3.02–3.81)–(6.14–6.54)	2.84–5.79
Neck dorsal spines length	1.30–2.30	3	(0.31–0.37)–(2.66–2.74)	0.27–2.30
Neck ventral spines length	2.00–7.80	3	(6.23–6.82)–(7.28–7.79)	6.08–7.14
Trunk dorsal spines length	1.30–2.30	3	(2.34–2.49)–(2.81–2.92)	2.12–2.92
Trunk ventral spines length	2.00–7.80	3	(7.47–8.06)–(9.16–10.12)	7.36–9.69
Long dorsal spines length	13.50–17.80	3	19.69–20.61	18.28
Median spine on posterior trunk region length	9.30–11.00	3	8.20–9.66	7.8
Dorsolateral spines on posterior trunk region length	7.20–8.70	3	7.18–7.69	6.61
Head dorsal sensory bristles length	NA	3	9.47–11.21	10.29
Neck dorsal sensory bristles length	8.70–10.20	3	12.95–14.29	12.7
Posterior dorsal sensory bristles length	8.70–10.20	3	14.23–15.62	13.94
Number of scales in central longitudinal row on ventral interciliary field	25–26	3	25–26	23
Total number of longitudinal alternating rows of scales on ventral interciliary field	2	3	2	2

Table 6 (continued). Main morphometric characters of *Chaetonotus* (*Zonochaeta*) *cestacanthus* Balsamo, 1990.

Characters	According to Balsamo (1990)	N	Range of adult specimens	Juvenile specimen
Ventral interciliary field scales length × width	2.50–2.60 × 2.80–3.00	3	(1.93–2.26)–(3.28–3.72) × (2.26–3.25)–(4.59–4.66)	1.72–3.16 × 2.04–4.05
Terminal ventral interciliary field scales I pair length × width	7.60 × 2.7	3	7.25–8.04 × 2.24–2.80	6.63 × 2.43
Terminal ventral interciliary field scales II pair length × width		3	3.10–3.50 × 1.43–1.89	2.79 × 1.39
Mouth ring diameter	NA	3	3.79–3.95	3.82
Pharynx length	20.70–27.00	3	23.26–24.09	24.28
Intestine length	NA	3	45.24–46.70	30.51

Remarks

The original description of *C.* (*Z.*) *cestacanthus* is very detailed (Balsamo 1990) and specimens found in the Jubilee Greenhouse in Kraków correspond well with it. However, the present specimens differ from the original data in being slightly larger (Table 6) and in having three pairs of dorsal sensory bristles instead of two (the additional pair arising on the head, near the dorsal cephalion edge); the first scales of the dorsal longitudinal rows, located near the cephalion and epipleurae, are more elongated and have longer spines than the remaining head scales in comparison to the original description and figures (Figs 33–34); the ventrolateral and ventral scales are similar to the dorsal ones (Fig. 33B), and dorsolaterally on the furcal appendages they have one pair of double-keeled scales, rounded in shape, with shallow posterior notches (Fig. 34B).

Chaetonotus (*Zonochaeta*) *cestacanthus* has previously been recorded only as an element of benthic assemblages in sandy sediments, as well as in sediments rich in detritus, at a station with rich vegetation (Balsamo 1990; Balsamo & Fregni 1995). There have been no reports of this taxon being found in epiphytic or other periphyton communities, although their presence in samples collected near rich aquatic vegetation may suggest that *C.* (*Z.*) *cestacanthus* could also survive in this habitat type.

Genus ***Heterolepidoderma*** Remane, 1927

Type species

Ichthydium ocellatum Mečnikow, 1865 (= *Heterolepidoderma ocellatum* (Mečnikow, 1865)).

Terra typica

Russia.

Remarks on genus

This is regarded as a polyphyletic genus (Kieneke *et al*. 2008; Kånneby *et al*. 2013), which encompasses 22 nominal freshwater species and 10 nominal marine species. It is present in benthic, interstitial and periphytic habitats.

Heterolepidoderma aff. ***majus*** Remane, 1927
Fig. 35

Heterolepidoderma majus Remane, 1927: 313–315, fig. 10.

Locus typicus

Germany.

Material examined

POLAND • 8 adults; Kraków, Botanical Garden, Jubilee Greenhouse, sites 1–2; 50°03′38″ N, 19°57′30″ E; 15 Nov. 2013; M. Kolicka leg.; NHC (photomicrographs, also in the author's collection).

Distribution

Nominal *Heterolepidoderma majus* Remane, 1927 is a species that is widely distributed in Europe, *inter alia* reported from: Bulgaria (Valkanov 1937), France (Kisielewski 1997a), Germany (Remane 1927), Great Britain (Martin 1990), Poland (e.g., Roszczak 1936; Kisielewska & Kisielewski 1986a, 1986b, 1986c), Russia (Tretjakova 1989) and Romania (Rudescu 1967); it has also been reported from Argentina (Grosso & Drahg 1984), Brazil (Kisielewski 1991), Canada (Schwank 1990) and Japan (Sudzuki 1971).

Fig. 35. *Heterolepidoderma* aff. *majus* Remane, 1927. Adult specimen. Bright field microphotographs. **A**. Habitus. **B**. Dorsal view. **C**. Ventral view.

Remarks

The body length of adult specimens of *Heterolepidoderma* aff. *majus* Remane, 1927 varied from 111.1 to 131.4 μm; length of pharynx was between 31.9 and 40.3 μm; intestine length from 60.7 to 72.6 μm; 53–57 total longitudinal rows of scales (19–21D + 10DL + 8L + 8–10LV + 8V), with 23–27 scales in the central row (Fig. 35).

In a previous paper, these specimens were reported as *Heterolepidoderma majus* Remane, 1927 (Kisielewska *et al*. 2015). However, although the specimens seemed to fall within the range of variability as reported by Schwank (1990) and Kisielewski (1997a), the presence of one pair of scales with four keels, nearly parallel to one another, did not allow, after a thorough analysis, the identification of the specimens from the Jubilee Greenhouse as representatives of the nominal species *H. majus*. The question of the species affinities of these individuals demands further analyses and studies of intra- and interspecific variability within *Heterolepidoderma*.

Genus ***Lepidodermella*** Blake, 1933

Type species

Chaetonotus squamatus Dujardin, 1841 (= *Lepidodermella squamata* (Dujardin, 1841)).

Terra typica

France.

Remarks on genus

This polyphyletic genus (Kånneby *et al.* 2012, 2013) comprises 12 nominal freshwater species and one nominal marine species. It is present in benthic, interstitial and periphytic habitats.

Lepidodermella aff. ***squamata*** (Dujardin, 1841)
Fig. 36

Chaetonotus squamatus Dujardin, 1841: 664, fig. 18.

Locus typicus

France.

Material examined

POLAND • 2 adults; Kraków, Botanical Garden, Jubilee Greenhouse, site 2; 50°03′38″ N, 19°57′30″ E; 15 Nov. 2013; M. Kolicka leg.; NHC (photomicrographs, also in the author's collection).

Distribution

Lepidodermella squamata is a widely distributed species or, more precisely, in the light of the current data, it represents sets of cryptic or morphologically similar species noted in Europe, *inter alia* reported from Bulgaria (Valkanov 1937), Germany (Remane 1935–36), Great Britain (Martin 1981), Italy (Mola 1932), Poland (Roszczak 1936; Kisielewska & Kisielewski 1986a, 1986b, 1986c), Romania (Rudescu 1967), Sweden (Kånneby 2011) and Switzerland (Greuter 1917); also reported from Argentina (Grosso & Drahg 1984), Australia (Hochberg 2005), Brazil (Kisielewski 1991), Canada (Schwank 1990), East Africa (Daday 1910), India (Naidu & Rao 2004), Israel (Kisielewski 1999), Japan (Sudzuki 1971), South Korea (Lee & Chang 2000), the United States (Bryce 1924) and Uruguay (Cordero 1918).

Remarks

Lepidodermella squamata (Dujardin, 1841) is one of the four earliest described gastrotrich species (Balsamo *et al*. 2014). This taxon is distributed worldwide and is very common in very different habitats (from freshwater and brackish psammon to micro-reservoirs in bromeliad leaves); however, in light of molecular data and on the basis of morphological evidence, it constitutes not one but at least a few morphologically very similar species, i.e., a complex of pseudocryptic or cryptic species (Fregni *et al*. 1998; Kånneby *et al*. 2012).

Both of the specimens reported here corresponded well with the original species description (Dujardin 1841) and with later records and the emended descriptions by Balsamo (1983) and Kisielewski (1984, 1997a) (Fig. 36). A detailed discussion of the shape of the scales and comparisons between the studied specimens and *L. squamata* in the literature are considerably impeded by the noticeable differences in the shape and distribution of the scales that were presented by various authors and by intraspecific variability (e.g., Rudescu 1967; Roszczak 1969; Balsamo 1983; Schwank 1990; Kisielewski 1997a), but the type and shape of the scales in the main covering remain consistent with Balsamo (1983)

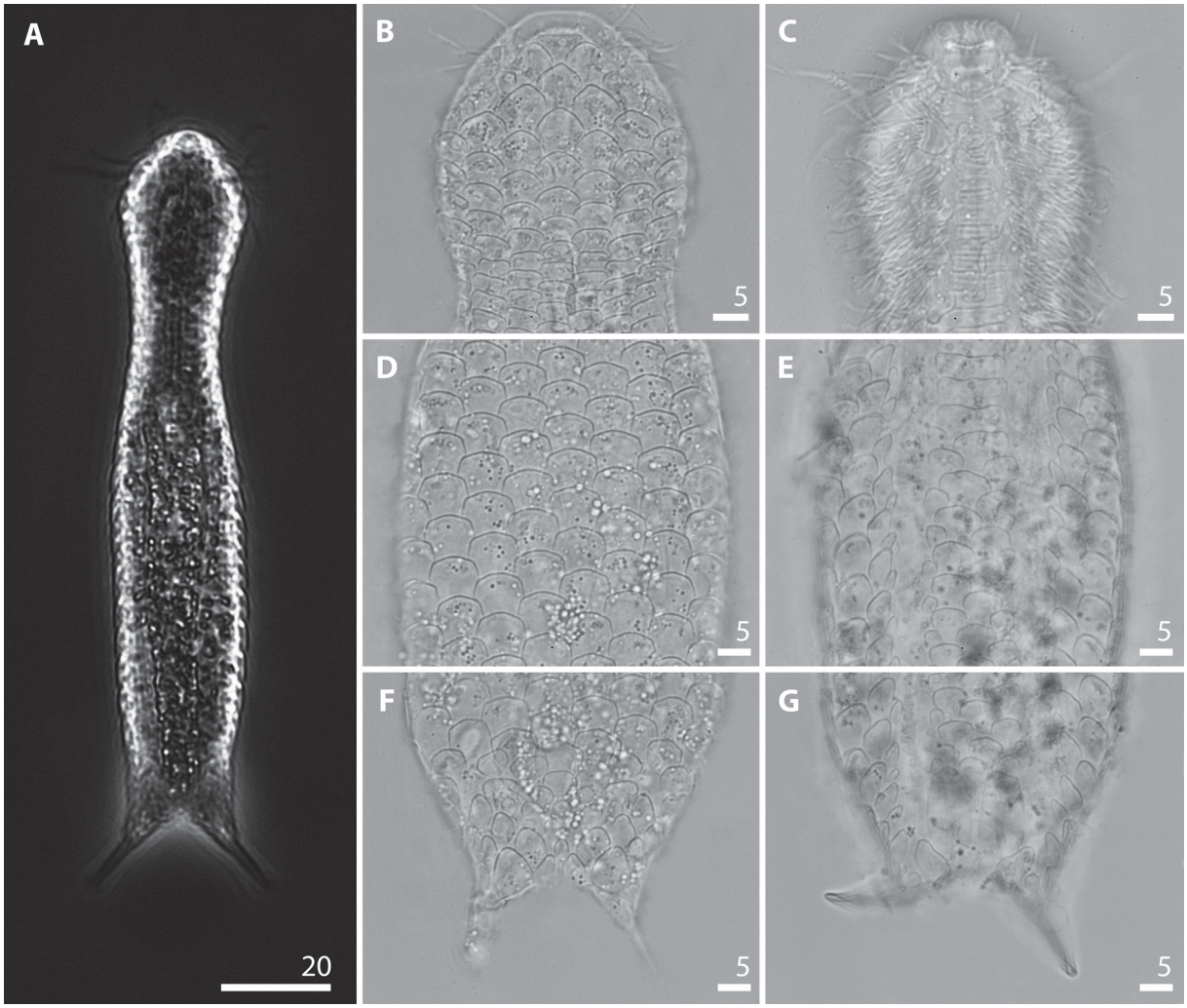

Fig. 36. *Lepidodermella* aff. *squamata* (Dujardin, 1841). Adult specimen. **A**. Habitus, phase contrast microphotograph. **B–G**. Bright field microphotographs. **B**. Head, dorsal view. **C**. Head, ventral view. **D**. Trunk, dorsal view. **E**. Trunk, ventral view. **F**. Posterior trunk region, furca base and furcal appendages, dorsal view. **G**. Posterior trunk region, furca base and furcal appendages, ventral view.

and Kisielewski (1984, 1997a). All of the main morphometric characteristics of *L.* aff. *squamata* are within the range given in the literature (Rudescu 1967; Roszczak 1969; Balsamo 1983; Schwank 1990; Kisielewski 1984, 1997a). The body length of studied adult specimens varied from 146.2 to 153.5 μm; the length of the pharynx from 45.7 to 47.3 μm; the intestine length from 75.5 to 82.1 μm; there were 19 total longitudinal rows of scales (5D+4DL+4L+4LV+2V), with 29–31 scales in the central row. The main clear differences between the studied specimens and *L. squamata* are the possession of one pair of scales with keels and rudimental but rigid spines on the dorsolateral area of the furcal appendages. Scales with keels or spines were listed neither in the original description nor in the main taxonomic reports on *L. squamata*; thus, I could not determine that the specimens undoubtedly belonged to this nominal taxon. Moreover, the present specimens possessed three pairs of dorsal sensory bristles, but this features cannot be a valid diagnostic character, since it was omitted in the original description and most previous works.

Discussion

The epiphytic species found in the Jubilee Greenhouse in Kraków increase the number of Gastrotricha known from Poland to 105 and those known from palm houses to 24 species (see Kolicka 2016). This is also the first recorded presence of gastrotrichs in aquatic plants in an artificial habitat. It is worth emphasising that these chaetonotids were found on vegetation cultivated from seeds or small seedling shoots in reservoirs that were cleaned on a yearly basis, including a partial replacement of the bottom sediment. The species composition changed between the first and second sample collections. The presence of different species could have been caused by two factors, namely the reservoir cleaning which took place between the collection of the samples and the change of plant species arrangement. Perhaps some of the gastrotrich species did not survive the seasonal cleaning and replacement of sediments, or some new taxa from the second sample collection were ones that were unintentionally imported into the Jubilee Greenhouse or were present on different plant species brought from another part of the reservoir. Observations of epiphytic gastrotrichs and species community changes may increase our knowledge of the colonisation abilities of Gastroticha because they suggest three ways of inhabitation of specific plants: 1) the gastrotrichs were brought in their resting egg stages on seeds or seedlings to the reservoir and survived the transfer to the nursery tank during the annual cleaning procedure; 2) gastrotrichs were introduced to the reservoir with the bottom sediments, they grew in abundance and subsequently they also moved to the submerged plants from the benthic communities; 3) the resting eggs of various gastrotrich species were brought yearly to the reservoirs in uncontrolled ways and some taxa found appropriate conditions to live in the bottom sediments while others were able to live only on aquatic vegetation.

Kisielewski (1990) suggested that submerged plants were the last freshwater habitat to be colonised by gastrotrichs after their expansion from marine waters. Possible routes of gastrotrich transfer from sediments to aquatic plants or from aquatic plants to sediments remain unconfirmed. Chaetonotids, as small benthic or epibenthic invertebrates without any free-swimming life stages, possess very limited abilities to actively move long distances. However, the active movement of Gastrotricha into vegetation rooted in a reservoir bottom does not seem to be impossible. On the other hand, transport by the water column itself seems to be a task requiring external factors in the form of water tides or larger, more actively swimming animals which could drag the gastrotrichs or their eggs from the bottom sediments to the submerged plants. The very long spines on the trunk of *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. and *C.* (*H.*) *inaequabilis* sp. nov., as well as the very long lateral to ventral spines in *C.* (*C.*) *invitatus* sp. nov., may be a crucial adaptation to an epibenthic or epiphytic lifestyle. The presence of a long spine could increase the likelihood of elevation from sediments to vegetation and allow this species to stay on submerged plants by increasing the bearing surface (Kisielewski 1991).

The presence of as many as three species that are new to science and two newly recorded species in such a relatively well-studied country as Poland may suggest the foreign origin of the newly found taxa. Although we do not know the place of origin of the new species, the newly observed *Chaetonotus* (*Chaetonotus*) *paucisquamatus* Kisielewski, 1991 and *C.* (*Zonochaeta*) *cestacanthus* Balsamo, 1990 were previously known only from their *terra typica* in Brazil and Italy, respectively. Both regions have a relatively high annual temperature and more stable climatic conditions than those observed in natural Polish habitats (e.g., Hijmans *et al*. 2005). It is possible that these species were accidentally imported to the Jubilee Greenhouse along with the subsoil (potted plants, sand, peat or, less probably, in the manure) or with the water containing fish, and they found appropriate living conditions. It cannot be excluded that the resting eggs of these species are widely spread in a temperate climate zone via natural (air currents, surface runoffs, dispersion with larger animals) or anthropogenic (long-distance transport of goods and people) means, but do not find favourable conditions for development and/or the creation of a stable population (e.g., due to long, cold winters). On the other hand, the taxa recorded in the Kraków greenhouse were not found in any previously studied palm houses (see Kolicka *et al*. 2013; Kolicka 2014, 2016), which may suggest that the aquatic vegetation plays a crucial, habitat-forming role for these chaetonotids. This research could confirm that urban greenhouses may be considered as biodiversity hot-spots in a strongly industrialised world and that they provide conditions for communities composed of species from different habitats and world regions.

Acknowledgements

I thank Prof. Ziemowit Olszanowski and two anonymous reviewers for their kind advice and insightful and helpful comments regarding earlier versions of the manuscript. Special thanks to Małgorzata Kuźnik and Beata Starczewska for preparing the drawings of the new species and the figures used in this paper. I also sincerely thank Mrs. Dorota Wróbel and the staff of the Botanical Garden of Jagiellonian University in Kraków for their kindness and support during collection of the samples. My studies were supported by National Science Centre grant no. 2015/17/N/NZ8/01568 titled 'Gastrotricha in palm houses as a model for research on phenotypic variability and cryptic diversity.' I was also a beneficiary of the Adam Mickiewicz Foundation scholarship scheme.

References

Balsamo M. 1983. Gastrotrichi. *In*: Consiglio Nazionale delle Ricerche (ed.) *Guide per il Riconoscimento delle Specie animali delle Acque interne italiane* 20: 1–92.

Balsamo M. 1990. Gastrotrichs from Lakes Bolsena, Chiusi and Montepulciano (central Italy), with the description of four new species. *Bolletino di Zoologia* 57 (2): 165–178. https://doi.org/10.1080/11250009009355693

Balsamo M. & Fregni E. 1995. Gastrotrichs from interstitial fresh water, with a description of four new species. *Hydrobiologia* 302: 163–175. https://doi.org/10.1007/BF00027040

Balsamo M. & Todaro M.A. 2002. Gastrotricha. *In*: Rundle S.D., Robertson A.L & Schmid-Araya J.M. (eds) *Freshwater Meiofauna: Biology and Ecology*: 45–61. Backhuys Publishers, Leiden.

Balsamo M., Grilli P., Guidi L. & d'Hondt J.-L. 2014. Gastrotricha: biology, ecology and systematics: families Dasydytidae, Dichaeturidae, Neogosseidae, Proichthydiidae. *In*: Dumont H.J.F. (ed.) *Identification Guides to the Plankton and Benthos of Inland Waters* 24. Backhuys Publishers and Margraf Publishers, Weikersheim, Germany.

Britton N.L. 1896. Botanical Gardens. *Science* 4 (88): 284–293.

Bryce D. 1924. The Rotifera and Gastrotricha of Devils and Stump Lakes, North Dakota, USA. *Journal of the Quekett Microscopical Club* 15: 81–108.

Cordero E.H. 1918. Notes sur les Gastrotriches. *Physis* 4: 241–244.

Daday E.V. von. 1905. Untersuchungen über die Süsswasser-Mikrofauna Paraguays. *Zoology of Bulgaria* 44: 72–86.

Daday E.V. von. 1910. Die Süßwasserfauna Deutsch-Ostafrikas. *Zoologica* 23: 56–59.

Duggan I.C. & Duggan K.S. 2011. Are botanical gardens a risk for zooplankton invasions? *Biological Invasions* 13 (12): 2997–3003. https://doi.org/10.1007/s10530-011-9984-z

Dujardin F. 1841. *Histoire naturelle des Zoophytes, Infusoires*. Librairie Encyclopedique de Roret, Paris.

Fregni E., Balsamo M. & Tongiorgi P. 1998. Interstitial gastrotrichs from lotic Italian fresh waters. *Hydrobiologia* 368: 175–187. https://doi.org/10.1023/A:1003250217483

Greuter A. 1917. Beiträge zur Systematik der Gastrotrichen in der Schweiz. *Revue suisse de Zoologie* 25: 35–76. Available from https://biodiversitylibrary.org/page/10710334 [accessed 28 Jan. 2019].

Grosso L.E. & Drahg F. 1984. Gastrotricos dulceacuicolas de la provincia de Tucuman. II. *Chaetonotus majestuosus* n. sp. *Acta Zoologica, Lilloana* 37: 227–230.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978. https://doi.org/10.1002/joc.1276

Hochberg R. 2005. First record of *Polymerurus* (Gastrotricha, Chaetonotida) from Australia with the description of a new species from Queensland and of cuticular ultrastructure in *P. nodicaudus*. *Invertebrate Biology* 124: 119–130. https://doi.org/10.1111/j.1744-7410.2005.00014.x

Hummon W.D., Balsamo M. & Todaro M.A. 1992. Italian marine Gastrotricha: I. Six new and one redescribed species of Chaetonotida. *Bollettino di Zoologia* 59: 499–516.

Ignatieva M. 2010. Design and future of urban biodiversity. *In*: Müller N., Werner P. & Kelcey J.G. (eds) *Urban Biodiversity and Design*: 118–144. Blackwell Publishing, Chichester.

International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature*, Fourth Edition. The International Trust for Zoological Nomenclature, The Natural History Museum, London.

Kånneby T. 2011. New species and new records of freshwater Chaetonotida (Gastrotricha) from Sweden. *Zootaxa* 3115: 29–55.

Kånneby T., Todaro M.A. & Jondelius U. 2012. A phylogenetic approach to species delimitation in freshwater Gastrotricha from Sweden. *Hydrobiologia* 683: 185–202. https://doi.org/10.1007/s10750-011-0956-1

Kånneby T., Todaro M.A. & Jondelius U. 2013. Phylogeny of Chaetonotidae and other Paucitubulatina (Gastrotricha: Chaetonotida) and colonization of aquatic ecosystems. *Zoologica Scripta* 42: 88–105. https://doi.org/10.1111/j.1463-6409.2012.00558.x

Kieneke A. & Schmidt-Rhaesa A. 2015. Gastrotricha. *In*: Schmidt-Rhaesa A. (ed.) *Handbook of Zoology 3. Gastrotricha and Gnathifera*: 1–134. De Gruyter, Berlin, Boston.

Kieneke A., Riemann O. & Ahlrichs W.H. 2008. Novel implications for the basal internal relationschips of Gastrotricha revealed by an analysis of morphological characters. *Zoologica Scripta* 37: 429–460. https://doi.org/10.1111/j.1463-6409.2008.00334.x

Kisielewska G. & Kisielewski J. 1986a. Freshwater Gastrotricha of Poland. II. Gastrotricha from the seaside lakes in the Słowiński National Park. *Fragmenta Faunistica* 30: 183–182.

Kisielewska G. & Kisielewski J. 1986b. Freshwater Gastrotricha of Poland. III. Gastrotricha from the Białowieża Forest and the Białowieża Glade. *Fragmenta Faunistica* 30: 195–215.

Kisielewska G. & Kisielewski J. 1986c. Freshwater Gastrotricha of Poland. V. Gastrotricha of alder woods. *Fragmenta Faunistica* 30: 235–250.

Kisielewska G., Kolicka M. & Zawierucha K. 2015. Prey or parasite? The first observations of live Euglenida in the intestine of Gastrotricha. *European Journal of Protistology* 51: 138–141. https://doi.org/10.1016/j.ejop.2014.12.003

Kisielewski J. 1981. Gastrotricha from raised and transitional peat bogs in Poland. *Monografie Fauny Polski* 11: 1–143.

Kisielewski J. 1984. Three new freshwater gastrotrichs of the genus *Chaetonotus* Ehrenberg (Chaetonotida) from Poland. *Bulletin de l'Académie polonaise des Sciences, Série des Sciences biologiques* 32: 293–301.

Kisielewski J. 1986. Freshwater Gastrotricha of Poland. VII. Gastrotricha of extremely eutrophicated water bodies. *Fragmenta Faunistica* 30: 267–295.

Kisielewski J. 1990. Origin and phylogenetic significance of freshwater psammic Gastrotricha. *Stygologia* 5: 87–92.

Kisielewski J. 1991. Inland-water Gastrotricha from Brazil. *Annales Zoologici* 43: 1–168.

Kisielewski J. 1997a. Brzuchorzęski (Gastrotricha). *Fauna Słodkowodna Polski, Zeszyt* 31: 1–157.

Kisielewski J. 1997b. On the subgeneric division of the genus *Chaetonotus* Ehrenberg (Gastrotricha). *Annales Zoologici* 46: 145–151.

Kisielewski J. 1999. A preliminary study of the inland-water Gastrotricha of Israel. *Israel Journal of Zoology* 45: 135–157.

Kolicka M. 2014. Gastrotricha Mečnikow, 1865 from Copenhagen Palm House – contribution to the knowledge of *Lepidodermella intermedia* Kånneby, Todaro & Jondelius, 2012 (Chaetonotida, Gastrotricha). *Zoosystema* 34 (4): 713–722. https://doi.org/10.5252/z2014n4a1

Kolicka M. 2016. Gastrotrichs in bromeliads – newly recorded *Chaetonotus* (*Hystricochaetonotus*) *furcatus* Kisielewski, 1991 (Chaetonotida) from the Łódź Palm House. *Zoosystema* 38 (1): 141–155. https://doi.org/10.5252/z2016n1a5

Kolicka M., Kisielewski J., Nesteruk T. & Zawierucha K. 2013. Gastrotricha from the Poznań Palm House – one new subgenus and three new species of freshwater Chaetonotida (Gastrotricha). *Zootaxa* 3717 (2): 231–279. https://doi.org/10.11646/zootaxa.3717.2.7

Kolicka M., Dziuba M.K., Zawierucha K., Kuczyńska-Kippen N. & Kotwicki L. 2015. Palm house – biodiversity hotspot or risk of invasion? Aquatic invertebrates: The special case of Monogononta (Rotifera) under greenhouse conditions. *Biologia* 70 (1): 94–103. https://doi.org/10.1515/biolog-2015-0012

Kolicka M., Dabert M., Dabert J., Kånneby T. & Kisielewski J. 2016. *Bifidochaetus*, a new Arctic genus of freshwater Chaetonotida (Gastrotricha) from Spitsbergen revealed by an integrative taxonomic approach. *Invertebrate Systematics* 30: 398–419. https://doi.org/10.1071/IS16001

Leasi F. & Todaro M.A. 2008. The muscular system of *Musellifer delamarei* (Renaud-Mornant, 1968) and other chaetonotidans with implications for the phylogeny and systematization of the Paucitubulatina (Gastrotricha). *Biological Journal of the Linnean Society* 94: 379–398. https://doi.org/10.1111/j.1095-8312.2008.00974.x

Lee J.M. & Chang C.Y. 2000. Freshwater chaetonotid gastrotrichs in Korea. *The Korean Journal of Systematic Zoology* 16: 87–104.

Martin L.V. 1981. Gastrotrichs found in Surrey. *Microscopy* 34: 286–300.

Martin L.V. 1990. Further observations on gastrotrichs in Surrey and a provisional British list. *Microscopy* 36: 415–425.

Mečnikow E. 1865. Über einige wenig bekannte niedere Thierformen. *Zeitschrift für Wissenschaftliche Zoologie* 15: 450–463. Available from https://biodiversitylibrary.org/page/45004241 [accessed 28 Jan. 2019].

Mola P. 1932. Gastrotricha delle acque dolci italiane. *International Review of Hydrobiology* 26 (5–6): 397–423. https://doi.org/10.1002/iroh.19320260504

Naidu K.V. & Rao G.C. 2004. *The Fauna of India and the Adjacent Countries – Gastrotricha*. Zoological Survey of India, Kolkata.

Nesteruk T. 2000. Epiphytic Gastrotricha – species composition and dominance. *Acta Hydrobiologica* 42: 53–57.

Nesteruk T. 2004. Benthic and epiphytic fauna of Gastrotricha in littoral of mesotrophic lake in Łęczna-Włodawa Lakeland, Poland. *Fragmenta Faunistica* 47 (1): 1–6.

Nesteruk T. 2010. Species structure, density and biomass of gastrotrich fauna of elodeids in two lakes of different trophy. *Teka Komisji Ochrony i Kształtowania Środowiska Przyrodniczego* [Teka Commission of Protection and Formation of Natural Environment] 7: 280–289.

Nesteruk T. 2011. Comparison of gastrotrich fauna on elodeids and in bottom sediments of different trophic status (the region Polesie Lubelskie, Estern Poland). *Oceonological and Hydrobiological Studies* 40: 13–21. https://doi.org/10.2478/s13545-011-0012-9

Rao G.C. & Clausen C. 1970. *Planodasys marginalis* gen. et. sp. nov. and Planodasyidae fam. nov. (Gastrotricha Macrodasyoidea). *Sarsia* 42: 73–82.

Remane A. 1927. Beiträge zur Systematik der Süsswassergastrotrichen. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 53: 269–320.

Remane A. 1935–1936. Gastrotricha und Kinorhyncha. *In*: Bronn H.G. (ed.) *Klassen und Ordnungen des Tierreichs, Vol. 4, Section 2, Book 1, Part 2, Issues 1–2*. Akademie Verlagsgesellschaft, Leipzig.

Roszczak R. 1936. Brzuchorzęski (Gastrotricha) zbiorników wodnych okolic Poznania. *Sprawy, Poznańskie Towarzystwo Przyjaciół Nauk* 9: 109–111.

Roszczak R. 1969. Brzuchorzęski (Gastrotricha) środkowej Wielkopolski. *Prace Komisji Biologicznej* 32: 1–92.

Rudescu L. 1967. Gastrotricha. *In*: *Fauna Republicii Socialiste Romania, Trochelminthes* 2 (3). Academia Republicii Socialiste Romania, Bucharest.

Saito I. 1937. Neue und bekannte Gastrotrichen der Umgebung von Hiroshima (Japan). *Journal of Science of the Hiroshima University* 5: 245–265.

Schwank P. 1990. Gastrotricha. *In*: Schwoerbel J. & Zwick P. (eds) *Süsswasserfauna von Mitteleuropa, 3. Gastrotricha und Nemertini*. Gustav Fischer Verlag, Stuttgart, Jena, New York.

Sudzuki M. 1971. Die das Kapillarwasser des Lückensystems bewohnenden Gastrotrichen Japans II. *Bulletin of the Biogeographical Society of Japan* 27 (5): 37–41.

Todaro M.A. 2018. *Gastrotricha*. Available from http://www.marinespecies.org/aphia.php?p=taxdetailsetid=2078 [accessed 2 Aug. 2018].

Tretjakova E.I. 1989. *K poznaniju Fauny presnovodnych Gastrotrich evropejskoj Casti SSSR*. Gosudarstvennyj Komitet SSSR po Narodnomu Obrazovaniju, Redkollegija Zhurnala. *Biologieeskie Nauki* (typescript, 21 pp, ID: udk 595.132).

Valkanov A. 1937. Über die Gastrotrichen Bulgariens. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 70: 171–176.

Zawierucha K., Szymkowiak P., Dabert M. & Harvey M.S. 2013. First record of the schizomid *Stenochrus portoricensis* (Schizomida: Hubbardiidae) in Poland with DNA barcode data. *Turkish Journal of Zoology* 37: 357–361. https://doi.org/10.3906/zoo-1210-9

Manuscript received: 5 August 2018
Manuscript accepted: 13 December 2018
Published on: 2 April 2019
Topic editor: Rudy Jocqué
Desk editor: Danny Eibye-Jacobsen

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Real Jardín Botánico de Madrid CSIC, Spain; Zoological Research Museum Alexander Koenig, Bonn, Germany.

Appendices

Figs A1–A2: *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Figs A3–A6: *Chaetonotus* (*Chaetonotus*) *horridus* sp. nov.

Fig. A7: *Chaetonotus* (*Chaetonotus*) *inaequabilis* sp. nov.

Tables A1–A2: *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Tables A3–A4: *Chaetonotus* (*Chaetonotus*) *horridus* sp. nov.

Tables A5–A6: *Chaetonotus* (*Chaetonotus*) *inaequabilis* sp. nov.

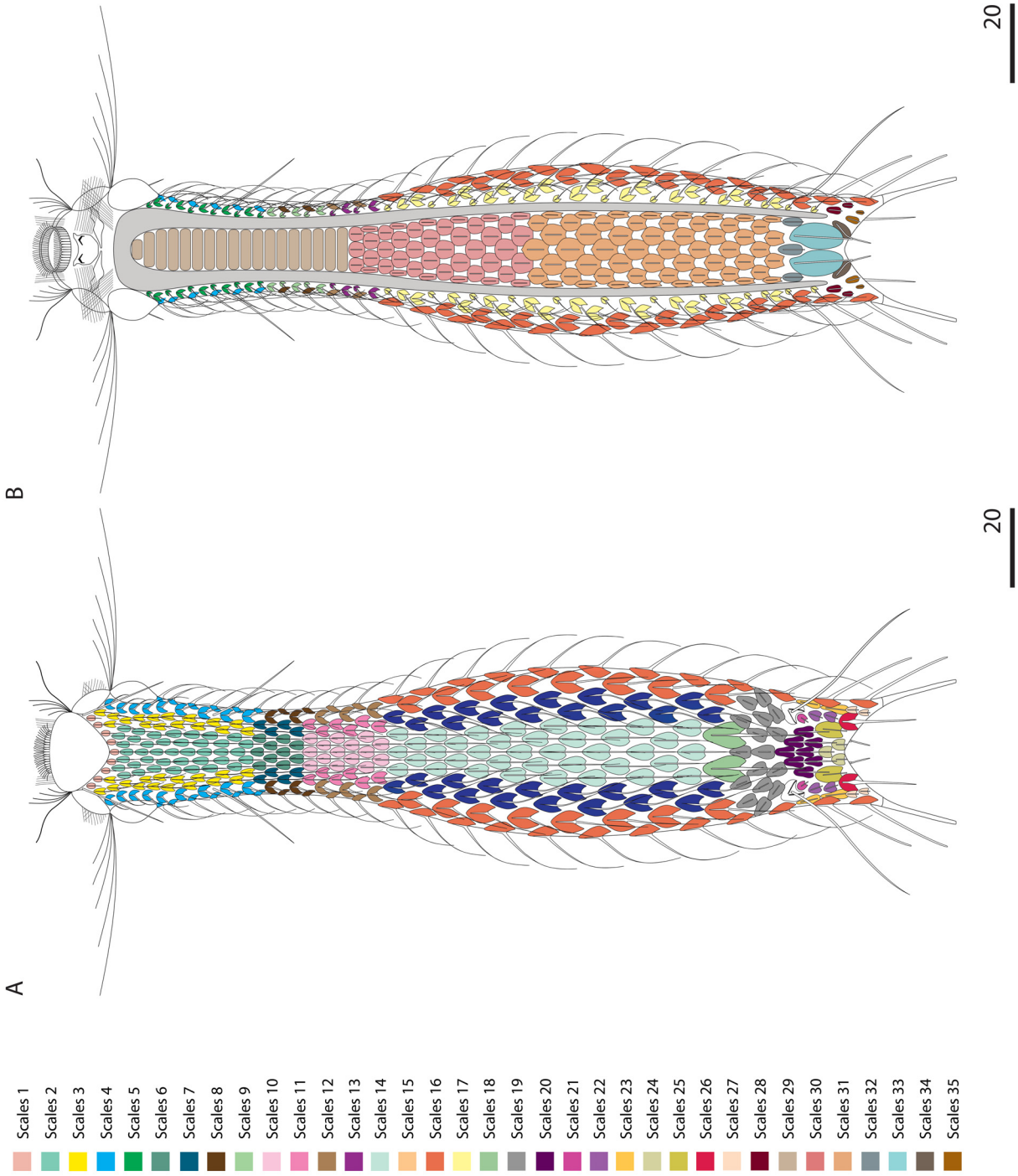

Fig. A1. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Schematic drawings with various types of scales indicated. **A**. Dorsal body view. **B**.Ventral body view. Light grey areas indicate the areas of insertion of ciliary bands.

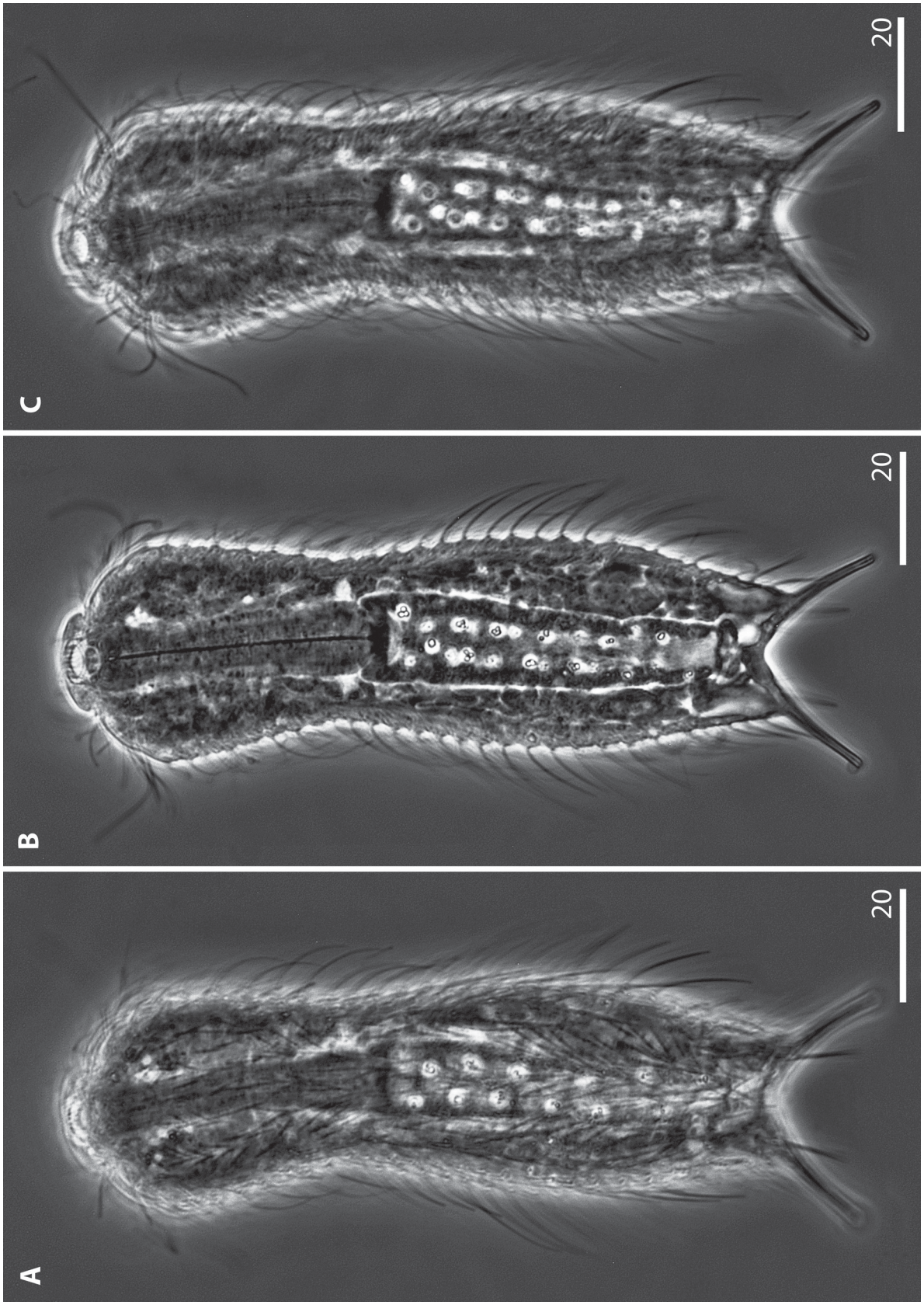

Fig. A2. *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. Juvenile specimen. Phase contrast microphotographs. **A**. Dorsal body view. **B**. View of internal morphology. **C**. Ventral body view.

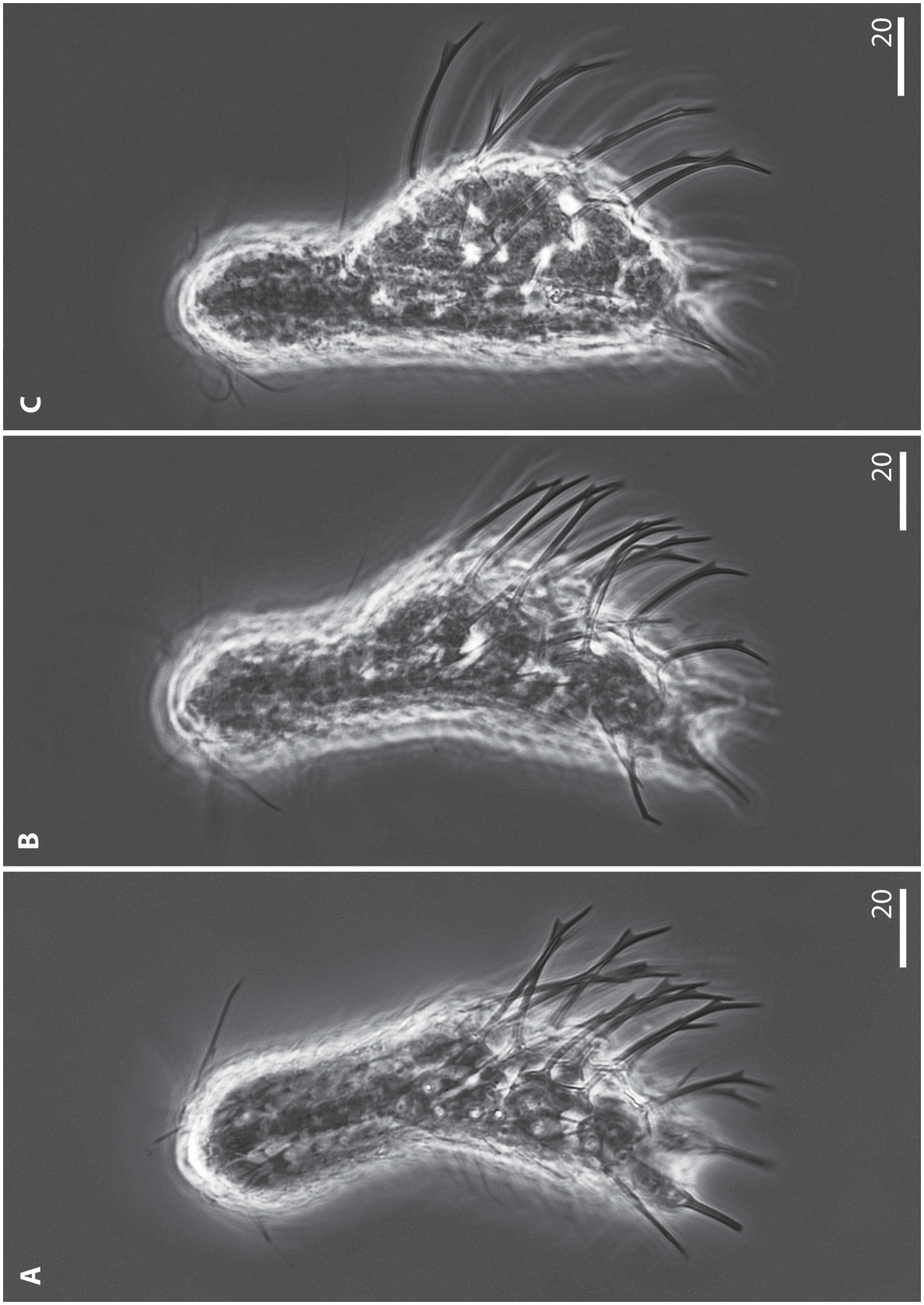

Fig. A3. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Habitus. Phase contrast microphotographs. **A**. Juvenile specimen. **B**. Adult specimen. **C**. Specimen with mature egg.

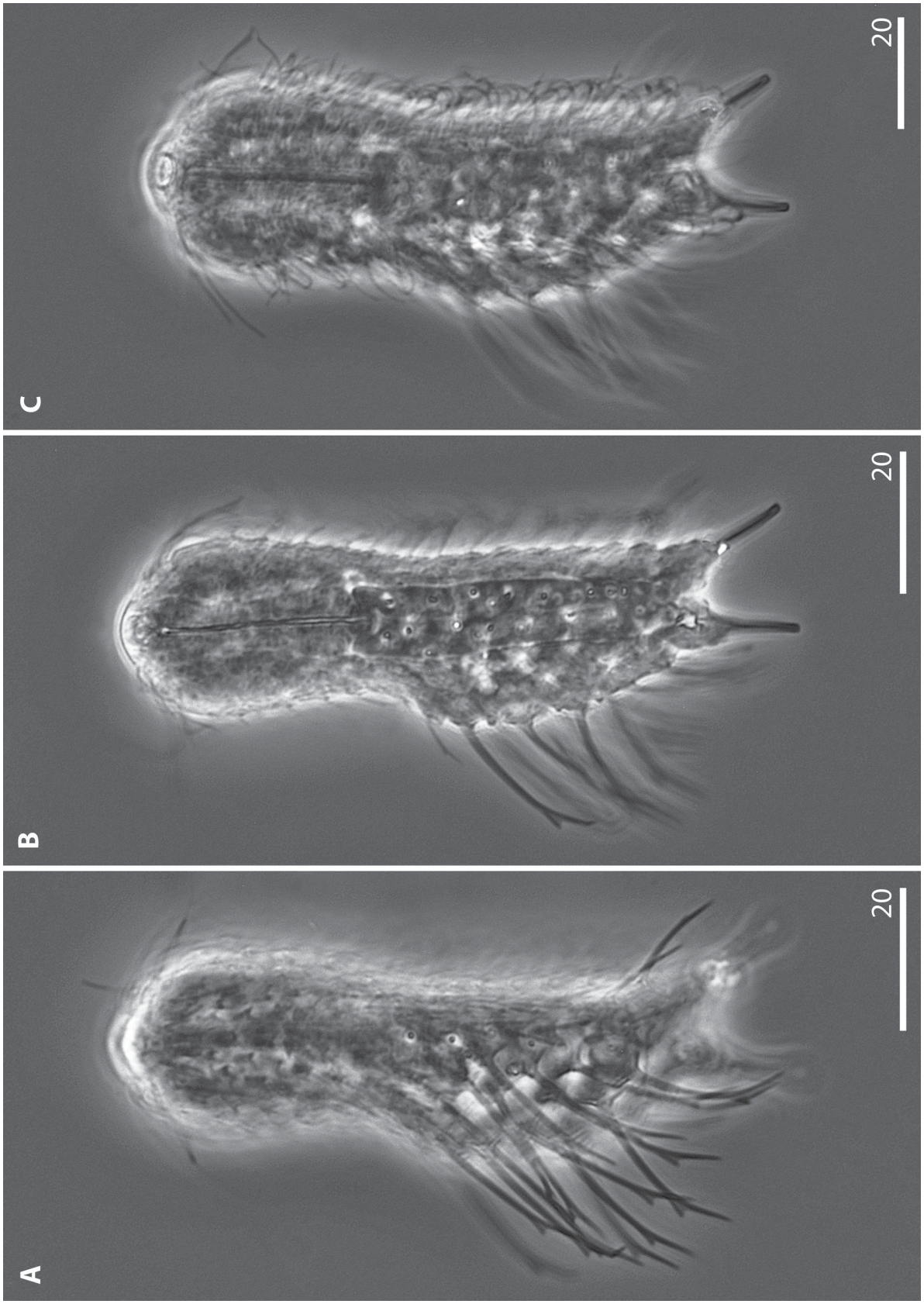

Fig. A4. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Juvenile specimen. Phase contrast microphotographs. **A**. Dorsal body view. **B**. View of internal morphology. **C**. Ventral body view.

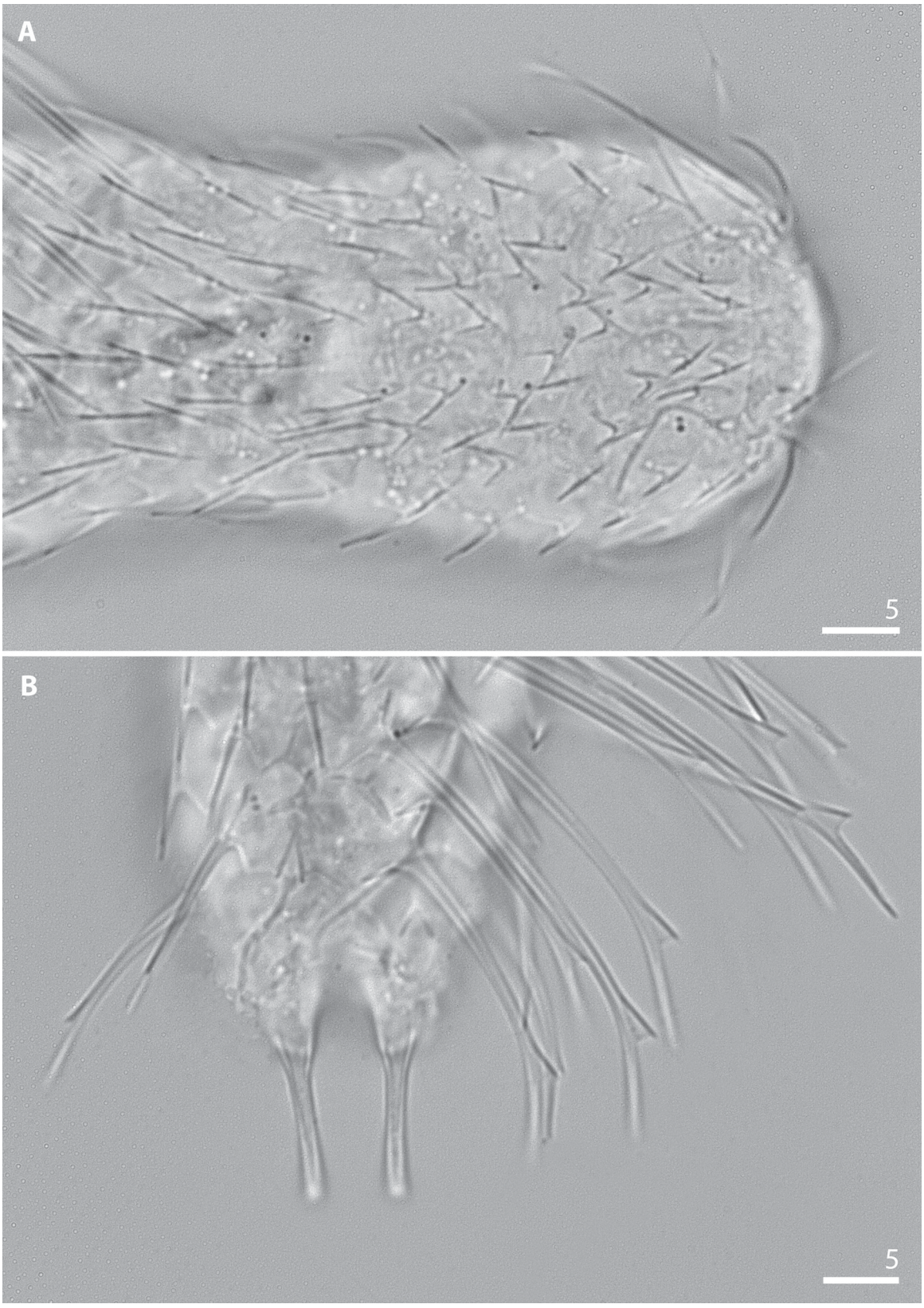

Fig. A5. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Juvenile specimen. Bright field microphotographs. **A**. Head, neck and anterior trunk scales, dorsal view. **B**. Posterior trunk, furca base and furcal appendage scales and spines, dorsal view.

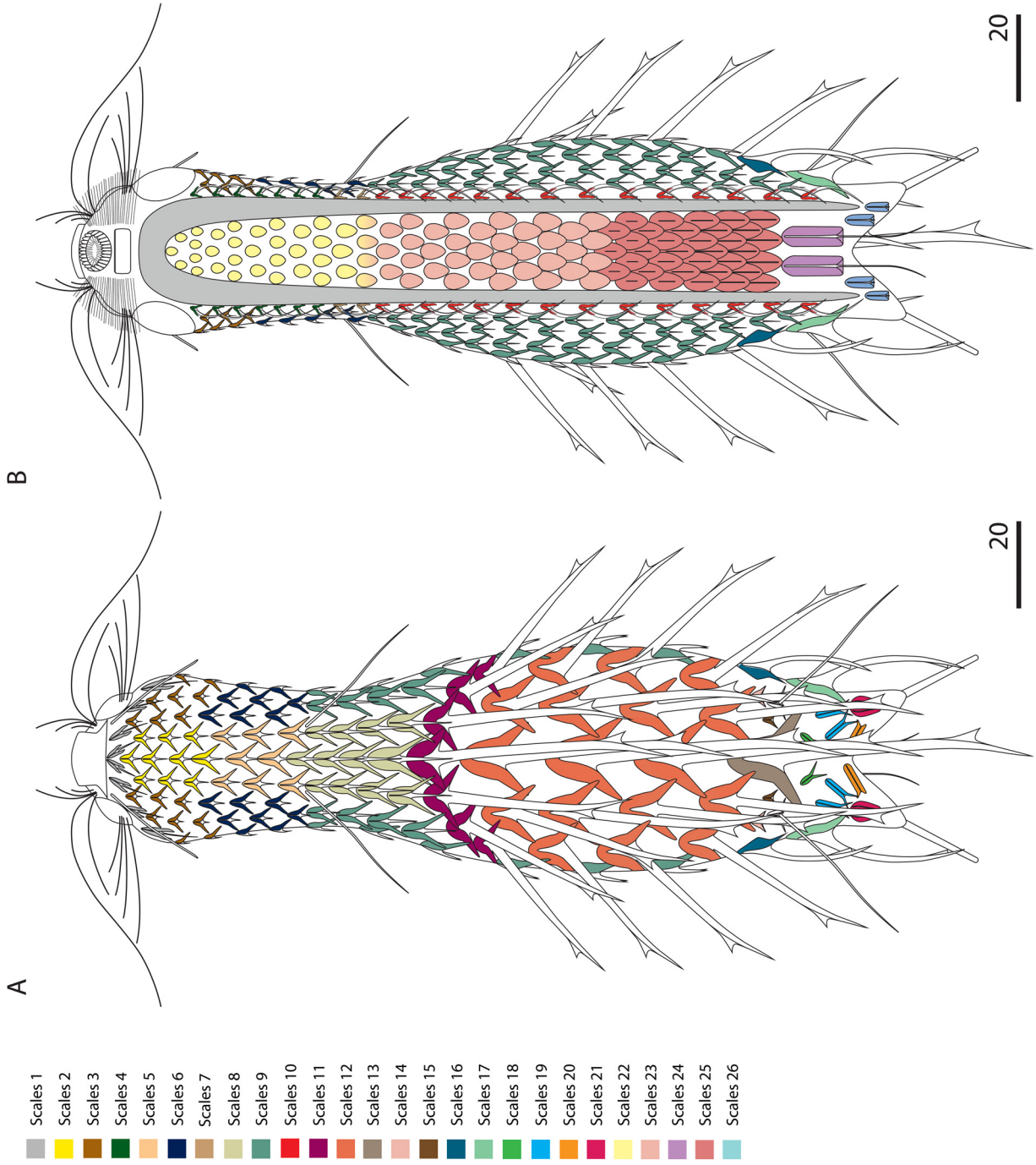

Fig. A6. *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. Schematic drawings with various types of scales indicated. **A**. Dorsal body view. **B**. Ventral body view. Light grey areas indicate the areas of insertion of ciliary bands.

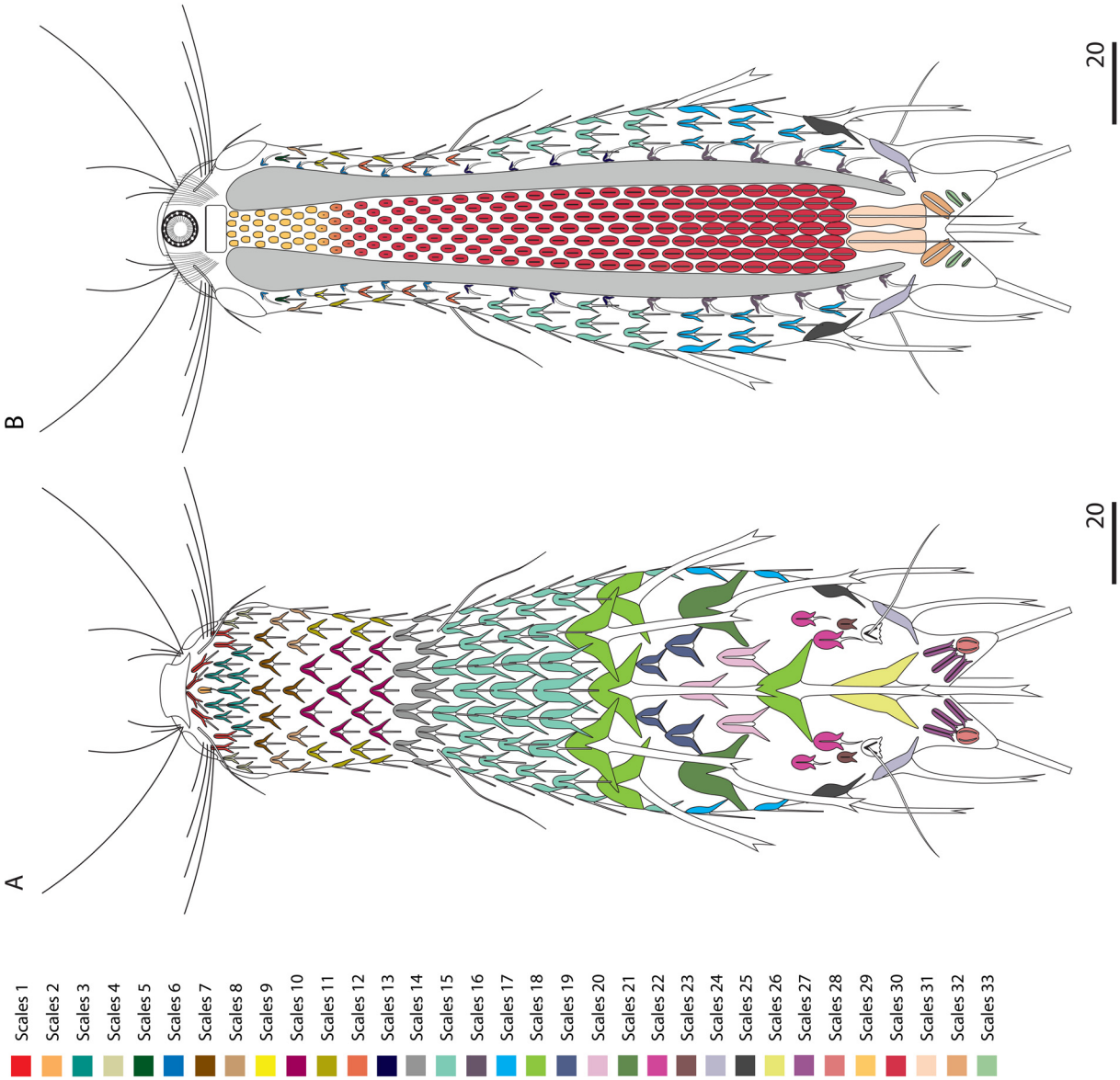

Fig. A7. *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. Schematic drawings with various types of scales indicated. **A**. Dorsal body view. **B**. Ventral body view. Light grey areas indicate the areas of insertion of ciliary bands.

Table A1 (continued on next 5 pages). Detailed morphometric characters of *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. N = number of specimens analysed; Range = the smallest and the largest value found among all specimens measured; SD = standard deviation. All measurements in micrometers (μm); all indicators given as a percentage (%) and italicized. When the range of plural structures in many specimens is given, the first parentheses contain the range of smallest/shortest structures in analysed individuals; the second parentheses contain the range of the largest/longest structures in analysed individuals.

Characters	N	Holotype	Range of adult paratypes	SD	N	Range of juvenile and subadult paratypes	SD
Cephalion length	22	17.15	15.09–18.23	0.856	10	14.49–18.14	0.939
Cephalion width	22	19.11	16.34–20.64	1.205	10	15.41–19.38	1.082
Hypostomium length	22	6.94	4.04–9.11	0.955	10	5.24–8.26	0.910
Hypostomium width	22	9.15	8.75–12.55	1.062	10	8.61–12.58	1.151
Length of cephalic cilia (anterior tuft)	22	6.36–10.28	(4.67–7.27)–(9.47–15.28)	0.644; 1.233	10	(4.67–7.49)–(9.47–12.92)	0.756; 1.015
Length of cephalic cilia (posterior tuft)	22	17.33–33.58	(11.32–18.15)–(24.35–33.58)	1.675; 1.989	10	(11.32–15.28)–(24.35–30.06)	1.295; 1.782
Width of cephalic cilia (anterior tuft)	22	0.58–0.65	(0.49–0.65)–(0.54–0.72)	0.049; 0.049	10	(0.51–0.65)–(0.56–0.69)	0.054; 0.048
Width of cephalic cilia (posterior tuft)	22	0.67–0.72	(0.54–0.81)–(0.58–0.85)	0.061; 0.062	10	(0.57–0.72)–(0.61–0.76)	0.060; 0.059
Width of adhesive tube	23	1.95	1.89–1.97	0.029	10	1.85–1.95	0.037
Ratio of scale distribution	25	*92.593*	*92.000–100.00*	1.546	11	*92.000–109.523*	5.895
Length of head dorsal scales (scales 1 and 2)	22	2.73–4.94	(2.23–2.87)–(4.27–5.19)	0.176; 0.229	10	(2.06–2.37)–(3.74–4.29)	0.106; 0.191
Width of head dorsal scales (scales 1 and 2)	22	1.96–2.82	(1.60–2.06)–(1.83–2.96)	0.125; 0.252	10	(1.48–1.70)–(2.14–2.45)	0.077; 0.107
Length of head dorsolateral scales (scales 3)	22	2.66–4.81	(2.17–2.80)–(4.17–5.05)	0.173; 0.221	10	(2.01–2.31)–(3.26–4.18)	0.102; 0.294
Width of head dorsolateral scales (scales 3)	22	1.91–2.80	(1.56–2.01)–(2.58–4.78)	0.127; 0.543	10	(1.44–1.66)–(1.90–2.43)	0.075; 0.172
Length of head lateral scales (scales 4)	22	2.89–3.74	(2.36–3.04)–(3.37–3.93)	0.189; 0.155	10	(2.18–2.51)–(2.83–3.25)	0.111; 0.159
Width of head lateral scales (scales 4)	22	3.28–4.23	(2.68–3.44)–(3.81–4.45)	0.212; 0.174	10	(2.47–2.85)–(3.20–3.68)	0.127; 0.178
Length of head ventrolateral scales (scales 4)	22	2.81–3.68	(2.28–2.96)–(3.32–4.37)	0.187; 0.252	10	(2.12–2.44)–(2.78–3.20)	0.109; 0.159
Width of head ventrolateral scales (scales 4)	22	3.22–4.14	(2.61–3.39)–(3.74–4.91)	0.214; 0.281	10	(2.43–2.80)–(3.13–3.60)	0.128; 0.180
Length of head ventral scales (scales 5)	22	1.94–2.97	(1.58–2.05)–(2.69–3.53)	0.133; 0.202	10	(1.46–1.69)–(2.24–3.56)	0.078; 0.403
Width of head ventral scales (scales 5)	22	2.21–3.32	(1.80–2.34)–(2.95–3.48)	0.152; 0.129	10	(1.66–1.93)–(2.50–3.98)	0.089; 0.450
Length of neck dorsal scales (scales 6 and 10)	22	3.64–5.83	(3.15–3.82)–(5.04–6.13)	0.174; 0.275	10	(2.76–3.16)–(4.42–5.06)	0.138; 0.221
Width of neck dorsal scales (scales 6 and 10)	22	3.41–4.45	(2.95–3.58)–(3.85–4.66)	0.159; 0.203	10	(2.59–2.96)–(3.37–3.86)	0.129; 0.169
Length of neck dorsolateral scales (scales 7 and 11)	22	4.11–5.98	(3.55–4.32)–(5.17–6.29)	0.190; 0.284	10	(3.12–3.57)–(4.53–5.19)	0.154; 0.227

Table A1 (continued). Detailed morphometric characters of *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD	N	Range of juvenile and subadult paratypes	SD
Width of neck dorsolateral scales (scales 7 and 11)	22	4.21–5.22	(3.64–4.43)–(4.47–5.49)	0.194; 0.288	10	(3.20–3.66)–(3.95–4.53)	0.157; 0.199
Length of neck lateral scales (scales 8 and 12)	22	4.23–6.29	(3.65–4.45)–(5.44–7.09)	0.197; 0.377	10	(3.21–3.67)–(4.76–5.46)	0.158; 0.239
Width of neck lateral scales (scales 8 and 12)	22	4.38–5.71	(3.78–4.61)–(4.94–6.44)	0.204; 0.348	10	(3.32–3.80)–(4.32–4.96)	0.166; 0.216
Length of neck ventrolateral scales (scales 8 and 12)	22	3.91–5.97	(3.37–4.11)–(5.16–6.73)	0.182; 0.366	10	(2.97–3.39)–(4.52–5.18)	0.146; 0.226
Width of neck ventrolateral scales (scales 8 and 12)	22	4.05–5.40	(3.49–4.26)–(4.67–6.10)	0.190; 0.333	10	(3.08–3.63)–(4.09–4.69)	0.181; 0.206
Length of neck ventral scales (scales 9 and 13)	22	2.55–3.49	(2.08–2.68)–(2.77–3.93)	0.153; 0.263	10	(1.94–2.21)–(2.64–3.03)	0.094; 0.133
Width of neck ventral scales (scales 9 and 13)	22	3.02–3.94	(2.46–3.16)–(3.13–4.44)	0.178; 0.297	10	(2.30–2.61)–(2.98–3.42)	0.108; 0.151
Length of trunk dorsal scales (scales 14)	22	5.97–8.08	(5.16–6.53)–(7.32–8.66)	0.324; 0.366	10	(4.53–5.18)–(6.13–7.01)	0.228; 0.307
Width of trunk dorsal scales (scales 14)	22	4.21–4.89	(3.64–4.60)–(4.43–5.18)	0.223; 0.214	10	(3.19–3.65)–(3.71–4.24)	0.161–0.186
Length of trunk dorsolateral scales (scales 15)	22	6.42–8.58	(5.56–7.02)–(7.77–9.20)	0.347; 0.390	10	(4.87–5.76)–(6.51–7.44)	0.294; 0.327
Width of trunk dorsolateral scales (scales 15)	22	4.61–5.19	(3.99–5.04)–(4.70–5.57)	0.247; 0.242	10	(3.50–4.14)–(3.94–4.50)	0.212; 0198
Length of trunk lateral scales (scales 16)	22	6.60–8.78	(5.72–7.23)–(7.95–9.38)	0.358; 0.404	10	(5.01–5.92)–(6.66–7.61)	0.305; 0.340
Width of trunk lateral scales (scales 16)	22	4.88–5.97	(4.23–5.35)–(5.41–6.38)	0.266; 0.276	10	(3.70–4.38)–(4.53–5.17)	0.226; 0.229
Length of trunk ventrolateral scales (scales 16)	22	6.43–8.02	(5.56–7.02)–(7.25–8.59)	0.345; 0.371	10	(4.88–5.77)–(6.10–6.95)	0.298; 0.307
Width of trunk ventrolateral scales (scales 16)	22	4.97–5.93	(4.30–5.43)–(5.36–7.39)	0.267; 0.502	10	(3.76–4.47)–(4.51–5.14)	0.234; 0.228
Length of trunk ventral scales (scales 17)	22	3.57–5.10	(2.84–3.87)–(4.08–5.46)	0.243; 0.381	10	(2.71–3.21)–(3.88–4.42)	0.166; 0.197
Width of trunk ventral scales (scales 17)	22	2.79–3.81	(2.22–3.03)–(3.05–4.08)	0.191; 0.302	10	(2.12–2.51)–(2.90–3.30)	0.125; 0.149
Length of scales 18	22	9.52	6.97–9.81	0.824	10	6.97–8.57	0.467
Width of scales 18	22	5.78	4.23–5.93	0.499	10	4.13–5.20	0.325
Length of scales 19	22	6.22–7.56	(5.44–6.33)–(6.27–7.70)	0.249; 0.369	10	(4.26–5.15)–(4.81–6.08)	0.321; 0.430
Width of scales 19	22	3.91–5.18	(3.32–4.21)–(3.95–5.26)	0.214; 0.415	10	(2.77–3.24)–(3.30–4.17)	0.166; 0.284
Length of scales 20	22	5.21–5.28	(4.51–6.77)–(4.97–6.90)	0.555; 0.524	10	(3.69–4.59)–(3.75–5.07)	0.315; 0.434
Width of scales 20	22	3.67–3.84	(3.15–4.49)–(3.47–4.55)	0.312; 0.269	10	(2.60–3.37)–(2.73–3.69)	0.258; 0.303
Length of scales 21	22	3.68	2.42–3.95	0.375	10	2.42–3.95	0.435
Width of scales 21	22	3.10	2.05–3.34	0.351	10	2.05–3.17	0.326
Length of scales 22	22	5.18–5.82	(4.29–6.04)–(4.68–6.42)	0.497; 0.518	10	(3.67–4.61)–(4.12–4.98)	0.331; 0.299
Width of scales 22	22	3.62–4.02	(3.26–3.98)–(3.49–4.74)	0.203; 0.293	10	(2.56–3.23)–(2.85–3.44)	0.235; 0.207

Table A1 (continued). Detailed morphometric characters of *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD	N	Range of juvenile and subadult paratypes	SD
Length of scales 23	22	6.32–7.20	(5.64–7.89)–(6.07–8.08)	0.559; 0.614	10	(5.26–6.17)–(5.82–6.53)	0.318; 0.261
Width of scales 223	22	3.15–3.56	(2.61–4.06)–(2.86–4.31)	0.378; 0.427	10	(2.62–3.09)–(2.89–3.24)	0.161; 0.129
Length of scales 24	22	4.11–4.32	(3.42–4.74)–(3.76–5.20)	0.299; 0.375	10	(2.85–3.93)–(2.92–4.38)	0.379; 0.460
Width of scales 24	22	3.28–3.42	(2.72–3.79)–(2.89–4.25)	0.243; 0.306	10	(2.27–3.18)–(2.43–3.45)	0.323; 0.351
Length of scales 25	22	8.67	5.37–9.12	1.123	10	5.37–7.16	0.548
Width of scales 25	22	5.20	3.23–5.31	0.623	10	3.23–4.32	0.336
Length of scales 26	22	5.91	4.52–6.17	0.436	10	4.52–5.79	0.371
Width of scales 26	22	5.71	4.37–5.84	0.381	10	4.37–5.46	0.369
Length of scales 27	22	3.06–3.93	(2.60–3.61)–(3.35–6.14)	0.247; 0.663	10	(1.98–2.93)–(2.41–3.62)	0.377; 0.348
Width of scales 27	22	1.97–2.49	(1.84–2.53)–(2.19–4.08)	0.268; 0.472	10	(1.32–1.85)–(1.55–2.18)	0.211; 0.226
Length of pairs of scales lateral to the furcal appendages	22	4.36–4.53	(3.71–4.55)–(3.88–5.08)	0.231; 0.277	10	(3.39–3.92)–(3.64–4.27)	0.175; 0.220
Width of pairs of scales lateral to the furcal appendages	22	3.88–3.92	(3.31–4.05)–(3.39–4.40)	0.210; 0.246	10	(3.02–3.49)–(3.16–3.70)	0.157. 0.190
Length of scales 28	22	3.68–4.81	(2.18–3.68)–(3.51–5.26)	0.513; 0.533	10	(2.08–3.02)–(2.72–3.65)	0.302; 0.325
Width of scales 28	22	2.04–2.51	(1.37–2.17)–(1.92–2.79)	0.239; 0.249	10	(1.15–1.71)–(1.43–1.90)	0.185; 0.166
Length of head dorsal spines (scales 1 and 2)	22	1.82–6.08	(1.59–2.24)–(4.76–7.38)	0.154; 0.647	10	(1.37–1.64)–(4.58–5.47)	0.090; 0.301
Length of head dorsolateral spines (scales 3)	22	3.72–13.41	(3.25–4.54)–(10.41–16.24)	0.306; 1.442	10	(2.80–3.36)–(10.11–12.06)	0.188; 0.659
Length of head lateral spines (scales 4)	22	12.93–19.09	(10.87–15.78)–(15.37–23.09)	1.158; 1.970	10	(9.73–11.66)–(14.39–17.17)	0.650; 0.941
Length of head ventrolateral spines (scales 4)	22	14.97–20.22	(12.59–18.21)–(16.25–24.28)	1.332; 2.062	10	(11.27–13.50)–(15.24–18.18)	0.752; 0.996
Length of head ventral spines (scales 5)	22	15.76–24.11	(13.25–19.14)–(17.88–26.39)	1.393; 2.431	10	(11.86–14.21)–(18.17–21.63)	0.790; 1.177
Length of neck dorsal spines (scales 6 and 10)	22	6.37–8.81	(5.03–7.75)–(6.86–10.73)	0.676; 0.984	10	(4.82–5.73)–(6.72–7.92)	0.309; 0.411
Length of neck dorsolateral spines (scales 7 and 11)	22	11.33–15.62	(8.95–13.75)–(12.14–19.01)	1.200; 1.747	10	(8.57–10.18)–(11.91–14.04)	0.550; 0.728

Table A1 (continued). Detailed morphometric characters of *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD	N	Range of juvenile and subadult paratypes	SD
Length of neck lateral spines (scales 8 and 12)	22	17.00–23.17	(13.46–20.62)–(18.01–28.18)	1.803; 2.504	10	(12.86–15.28)–(17.66–20.37)	0.825; 1.004
Length of neck ventrolateral spines (scales 8 and 12)	22	18.65–25.45	(14.77–22.30)–(19.81–30.54)	1.922; 2.674	10	(14.11–16.79)–(19.39–22.38)	0.903; 1.111
Length of neck ventral spines (scales 9 and 13)	22	20.07–27.41	(15.86–23.75)–(21.27–31.86)	2.041; 2.720	10	(15.19–18.05)–(20.88–24.11)	0.969; 1.191
Length of trunk dorsal spines (scales 14)	22	10.09–13.62	(7.84–12.27)–(10.57–16.48)	1.122; 1.494	10	(7.69–9.07)–(10.38–12.25)	0.471; 0.636
Length of trunk dorsolateral spines (scales 15)	22	15.07–19.91	(11.70–18.29)–(15.36–23.11)	1.668; 2.022	10	(11.49–13.56)–(15.17–17.91)	0.710; 0.934
Length of trunk lateral spines (scales 16)	22	20.76–24.62	(15.93–25.08)–(19.02–27.87)	2.294; 2.383	10	(15.84–18.69)–(18.76–22.14)	0.978; 1.174
Length of trunk ventrolateral spines (scales 16)	22	22.28–27.12	(17.09–26.34)–(20.90–30.24)	2.373; 2.460	10	(17.02–20.02)–(20.63–24.34)	1.037; 1.281
Length of trunk ventral spines (scales 17)	22	25.58–31.06	(19.63–30.17)–(23.06–34.26)	2.696; 2.887	10	(19.54–22.93)–(23.63–27.86)	1.173; 1.465
Length of spines of scales 18	22	18.52	16.56–20.04	0.976	10	13.43–20.04	1.617
Length of spines of scales 20	22	4.31–5.91	(3.05–5.81)–(5.51–7.35)	0.684; 0.538	10	(2.85–4.21)–(4.59–6.74)	0.439; 0.782
Length of spines of scales 21	22	1.76	1.28–1.82	0.168	10	0.94–1.82	0.233
Length of spines of scales 22	22	1.23–1.43	(1.15–1.38)–(1.25–1.76)	0.083; 0.139	10	(0.90–1.19)–(1.13–1.39)	0.91; 0.077
Length of spines of scales 24	22	0.86–1.03	(0.58–1.48)–(0.84–2.84)	0.279; 0.640	10	(0.56–2.09)–(0.74–0.55)	0.453; 0.528
Length of spines of scales 25	22	1.71	1.10–2.42	0.328	10	1.11–1.51	0.11
Length of spines of scales 26	22	17.47	14.48–18.39	1.046	10	13.04–16.21	1.221
Length of spines of scales 27	22	0.40–0.63	(0.25–0.98)–(0.47–1.43)	0.205; 0.312	10	(0.23–0.75)–(0.45–0.86)	0.186; 0.151
Length of trunk posteriormost pair of lateral spines	22	21.10	16.05–25.10	2.237	10	16.36–19.01	0.854
Length of parafurcal spines	22	12.37–13.14	(11.30–12.98)–(12.04–13.45)	0.421; 0.401	10	(9.61–12.11)–(10.34–12.25)	0.771; 0.552
Length of spines of scales 28	22	0.40–0.63	(0.25–0.98)–(0.47–1.43)	0.205; 0.312	10	(0.23–0.75)–(0.45–0.86)	0.186; 0.151
Head dorsal sensory bristles length	22	18.2	17.31–21.57	1.327	10	15.61–20.99	1.628

Table A1 (continued). Detailed morphometric characters of *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD	N	Range of juvenile and subadult paratypes	SD
Neck dorsal sensory bristles length	22	19.84	18.42–24.17	1.507	10	17.70–22.40	1.443
Posterior dorsal sensory bristles length	22	22.61	20.33–27.96	1.939	10	19.83–23.01	0.973
Number of scales in central longitudinal row on ventral interciliary field	22	33	29–33	0.831	10	25–32	1.038
Total number of longitudinal alternating rows of scales on ventral interciliary field	22	2	5–7	0.770	10	5–7	0.850
Length of ventral interciliary field anterior scales (scales 28)	22	1.21–2.96	(1.03–1.72)–(2.55–5.19)	0.175; 0.674	10	(0.81–1.50)–2.29–2.82)	0.201; 0.174
Width of ventral interciliary field anterior scales (scales 28)	22	2.98–8.53	(1.89–3.48)–(7.13–11.40)	0.457; 1.034	10	(2.06–2.87)–(6.68–8.01)	0.256; 0.446
Length of ventral interciliary field posterior scales (scales 29–31)	22	4.25–8.28	(2.07–4.68)–(6.47–9.85)	0.759; 0.868	10	(2.48–3.56)–(6.42–7.74)	0.323; 0.420
Width of ventral interciliary field posterior scales (scales 30–32)	22	1.96–7.21	(1.09–2.39)–(5.67–11.26)	0.368; 1.216	10	(1.14–1.69)–(4.74–6.82)	0.195; 0.636
Length of terminal ventral interciliary field scales I pair (scales 33)	22	16.28	14.83–17.14	0.619	10	12.23–15.06	0.812
Width of terminal ventral interciliary field scales I pair (scales 33)	22	7.96	6.57–8.06	0.461	10	5.78–6.99	0.437
Length of terminal ventral interciliary field scales II pair (scales 34)	22	6.65	6.17–7.58	0.443	10	5.36–6.46	0.365
Width of terminal ventral interciliary field scales II pair (scales 34)	22	3.32	3.17–4.58	0.346	10	2.87–3.49	0.195
Length of terminal ventral interciliary field scales III pair (scales 35)	22	3.15	2.91–4.80	0.552	10	2.51–3.51	0.266
Width of terminal ventral interciliary field scales III pair (scales 35)	22	1.94	1.79–2.95	0.329	10	1.42–1.96	0.174
Length of terminal ventral interciliary field scales IV pair (scales 35)	22	2.23	2.06–3.56	0.402	10	1.72–2.25	0.174

Table A1 (continued). Detailed morphometric characters of *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD	N	Range of juvenile and subadult paratypes	SD
Width of terminal ventral interciliary field scales IV pair (scales 35)	22	1.51	1.29–2.03	0.212	10	0.93–1.50	0.155
Length of terminal ventral interciliary field scales I pair spines (scales 33)	22	3.66	3.32–5.76	0.748	10	3.09–5.33	0.657
Length of terminal ventral interciliary field scales II pair spines (scales 34)	22	8.22	5.84–9.29	1.033	10	6.15–6.91	0.268
Length of terminal ventral interciliary field scales III pair spines (scales 35)	22	0.67	0.59–0.98	0.132	10	0.47–1.02	0.166
Length of terminal ventral interciliary field scales IV pair spines (scales 35)	22	0.41	0.27–0.64	0.101	10	0.23–0.39	0.053
Width of anterior pharynx thickening (a)	22	10.39	9.78–11.26	0.342	10	8.92–10.99	0.574
Width of pharynx narrowing (n)	22	8.6	7.29–8.98	0.470	10	6.46–8.72	0.557
Width of middle pharynx (m)	22	9.72	8.45–10.50	0.511	10	7.83–9.89	0.568
Width of posterior pharynx thickening (p)	22	12.48	11.67–13.83	0.523	10	11.54–13.62	0.606
Width of intestine junction	22	5.26	4.63–5.91	0.306	10	4.21–5.51	0.386
Intestine length	23	106.04	90.07–106.04	3.990	10	63.54–81.21	5.503
Pharynx formula a	22	18.279	*17.486–21.345*	0.835	10	*18.795–21.427*	0.807
Pharynx formula n	22	15.13	*12.643–15.705*	0.867	10	*13.584–17.001*	1.000
Pharynx formula m	22	17.101	*14.168–18.738*	1.123	10	*15.934–19.283*	1.055
Pharynx formula p	22	21.956	*20.787–26.009*	1.235	10	*21.339–25.568*	1.554
Pharynx–intestine ratio I	22	53.602	*52.173–61.974*	2.548	10	*66.162–80.563*	5.165
Length of mature egg	1	–	74.05	0	–	–	–
Width of mature egg	1	–	33.17	0	–	–	–
Length of X-organ	1	–	13.04	0	–	–	–
Width of X-organ	1	–	21.83	0	–	–	–

Table A2 (continued on next 5 pages). Condensed comparison of the most important differentiating characters among species most similar to *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov. All measurements in micrometres (μm). NA = data not available; – = not applicable.

Character	*C.* (*C.*) *invitatus* sp. nov.	*C.* (*C.*) *maximus*	*C.* (*C.*) *microchaetus*	*C.* (*C.*) *similis*	*C.* (*C.*) *heterospinosus*	*C.* (*C.*) *laroides*	*C.* (*C.*) *polyspinosus*	*C.* (*H.*) *trispinosus*	*C.* (*P.*) *mutinensis*
Body length	174.6–194.7	112.0–330.0	130.0–283.0	176.0–232.0	138.0–210.0	180.0–220.0	194.0–355.0	91.0–99.0	111.0–143.0
Cephalic pleurae	cephalion long and wide, with free dorsal edge; pleurae large, convex and clearly demarcated, hypopleurae slightly larger than epipleurae; epipleurae located on dorsal, dorsolateral, lateral and ventrolateral surfaces, hypopleurae located on dorsal, dorsolateral, lateral, ventrolateral and ventral, greatest portion present on the ventral side; hypostomium with two horn–like anterolateral protuberances and pair of strong anterior edge reinforcements	cephalion narrow; pleurae convex and clearly demarcated, epipleurae and hypopleurae similar in size, located mostly laterally but clearly visible on the dorsal body side; hypostomium with pair of anterior edge reinforcements	cephalion short and wide, pleurae convex and clearly demarcated, hypopleurae slightly larger than epipleurae; epipleurae located on dorsal, dorsolateral, lateral and ventrolateral surfaces, hypopleurae located on dorsal, dorsolateral, lateral, ventrolateral and ventral, greatest portion present on the ventral side; hypostomium with pair of anterior edge reinforcements	cephalion short and wide, pleurae large, convex, clearly demarcated and similar in size; epipleurae and hypopleurae located on mostly laterally; hypostomium with two horn-like anterolaterally protuberances	cephalion short and wide, pleurae convex and clearly demarcated, hypopleurae slightly larger than epipleurae; epipleurae and hypopleurae located mostly laterally; hypostomium not visible	cephalion short and wide, slightly smaller than epipleurae and hypopreuria; all pleurae convex and clearly demarcated, hypopleurae slightly larger than epipleurae; pleurae located mostly laterally but clearly visible on the dorsal body side; hypostomium with two horn–like anterolateral protuberances	cephalion long and wide, convex and clearly demarcated, hypopleurae slightly larger than epipleurae; epipleurae and hypopleurae located mostly laterally; hypostomium with pair of anterior edge reinforcements	cephalion short, wide and slightly extended near the dorsal edge; pleurae flat and clearly demarcated, hypopleurae three times larger than epipleurae; epipleurae located on dorsal, dorsolateral, lateral and ventrolateral surfaces, hypopleurae located on dorsal, dorsolateral, lateral and ventrolateral and ventral, greatest portion present on the ventrolateral side; hypostomium short, semirectangular in shape	cephalion long and wide; pleurae large, convex and clearly demarcated, hypopleurae larger than epipleurae; epipleurae and hypopleurae located on mostly laterally; hypostomium with pair of anterior edge reinforcements
Presence of additional hypostomium plates	present	absent	absent	absent	absent	present	absent	absent	absent
Place of emerging cephalic cilia	anterior tufts: laterally between cephalion edge and the dorsal edge of the epipleurae; posterior tufts: laterally between epipleurae and hypopleurae	anterior tufts: laterally between cephalion and epipleurae; posterior tufts: laterally between epipleurae and hypopleurae	anterior tufts: laterally between cephalion and epipleurae; posterior tufts: laterally between epipleurae and hypopleurae	anterior tufts: laterally between cephalion and epipleurae; posterior tufts: laterally between epipleurae and hypopleurae	anterior tufts: laterally between cephalion and epipleurae; posterior tufts: laterally between epipleurae and hypopleurae	anterior tufts: laterally between cephalion and epipleurae; posterior tufts: laterally between epipleurae and hypopleurae	anterior tufts: laterally between cephalion and epipleurae; posterior tufts: laterally between epipleurae and hypopleurae	anterior tufts: laterally between cephalion and epipleurae; posterior tufts: laterally between epipleurae and hypopleurae	anterior tufts: anterolateral between cephalion and epipleurae; posterior tufts: laterally between epipleurae and hypopleurae

Table A2 (continued). Comparison of species most similar to *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Character	*C.* (*C.*) *invitatus* sp. nov.	*C.* (*C.*) *maximus*	*C.* (*C.*) *microchaetus*	*C.* (*C.*) *similis*	*C.* (*C.*) *heterospinosus*	*C.* (*C.*) *laroides*	*C.* (*C.*) *polyspinosus*	*C.* (*H.*) *trispinosus*	*C.* (*P.*) *mutinensis*
Presence of cuticular teeth in the mouth ring	two small, weak cuticular teeth	absent	absent	absent	absent	absent	absent	absent	absent
Pharynx length	51.0–59.6	50.0–66.0	47.0–63.0	35.0–75.0	46.0–66.0	68.0–70.0	55.0–90.0	26.7–29.0	41.0–58.0
Pharynx shape	pharynx narrow; anterior and slightly wider posterior dilatation	anterior and wider posterior dilatation	anterior and wider posterior dilatation	anterior and wider posterior dilatation	slightly anterior and posterior dilatation	cylindrical, gradually widening to the posterior end	anterior and wider posterior dilatation	cylindrical with weak posterior dilatation	cylindrical with posterior dilatation
Presence of cuticular reinforcements in the pharynx	present (two straight, connected rods)	absent	absent	absent	absent	absent	absent	absent	absent
Anterior intestine section differing in form of morphology	absent	absent	absent	absent	absent	absent	present	absent	absent
Furca length	31.1–34.5	15.0–30.0	16.0–17.0	19.0–39.0	21.0–30.0	27.0–30.0	30.0–55.0	13.6–14.3	16.0–26.0
Adhesive tube length	16.4–19.2	16.0–18.0	16.0–19.0	21.0–23.0	15.0–22.5	15.0–19.0	15.0–26.0	NA	NA
Type of furcal indentation	parabolic in shape	parabolic in shape	parabolic in shape	V-shaped	parabolic in shape	V-shaped	parabolic in shape	parabolic in shape	V-shaped
Number of scales in central longitudinal row	25–27	21–26	31–35	17–27	18–22	28–32	33–70	15–16	22–25
Total number of longitudinal alternating rows of scales	23–25	17–21	30–36	15–23	9–15	11–17	38–47	13	9–12
Type of scales	one-lobed, oval and egg-shaped with very weak posterior notches to deep posterior notches, all scales keeled and spined; strongly varied within body regions	one-lobed with keels and spines, all with posterior notches; shape differentiated within body regions	one-lobed small, with posterior notches, with keels and spines	one-lobed small, with shallow posterior notches, with keels and spines	one-lobed with shallow posterior notches, all scales with keels, some without spines, remaining with spines	one-lobed with wide and concave posterior edge, all scales keeled and spined; varied within body regions	one-lobed, small, triangle-shaped with posterior notches, with keels and spines	one-lobed, trilobate in shape, keeled and spined scales; varied within body regions	one-lobed, oval in shape without posterior notches, with keels and spines

Table A2 (continued). Comparison of species most similar to *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Character	*C.* (*C.*) *invitatus* sp. nov.	*C.* (*C.*) *maximus*	*C.* (*C.*) *microchaetus*	*C.* (*C.*) *similis*	*C.* (*C.*) *heterospinosus*	*C.* (*C.*) *laroides*	*C.* (*C.*) *polyspinosus*	*C.* (*H.*) *trispinosus*	*C.* (*P.*) *mutinensis*
Scales size variation	neck scales smaller, shorter and wider than the head scales; trunk scales become larger and more elongated than neck scales; from dorsal, dorsolateral, lateral to the ventrolateral body surface, scales become shorter and wider; ventral scales much smaller than remaining scales	size gradually increases from the head towards the widest trunk region; on the furcal base and furcal appendage scales strongly varied in size	size similar on the head, neck and trunk; on the furcal base and furcal appendage scales differentiated in size	size gradually increase from the head towards the widest trunk region	strongly varied within body regions. Size gradually increases from the head towards the widest trunk region, on posterior trunk region and furcal base and furcal appendage scales smaller	size gradually increases from the head towards the widest trunk region; on the furcal base and furcal appendage scales strongly varied in size	similar size all over the body	size gradually increases from the head towards the trunk; three scales with long spines on the posterior trunk region larger	size gradually increases from the head towards the posterior trunk region; on the furcal base and furcal appendage scales smaller; ventral scales much smaller than remaining scales
Scale size	head: 1.6–5.2 × 1-6–4.9 neck: 2.1–7.1 × 2.5–6.4 trunk: 2.8–9.4 × 2.2–7.4	6.0–10 × NA	head: NA neck: 3.0 × NA trunk: 3.0–6.0 × NA	head: NA neck: 4.0–6.0 × NA trunk: 11.0–12.0 × NA	head and neck: 5.0–6.0 × NA trunk: 8.0–8.5 × NA	head and neck: 2.0–3.0 × NA trunk: 5.0–8.0 × NA	head and neck: 2.0–4.0 × 3.0–4.0 trunk: 3.0–7.0 × NA	head: 2.9 × 3.1 neck: NA trunk: 3.8 × 3.4	3.0–8.0 × NA
Alignment of scales	located close to another; on the head, neck and trunk do not overlap, scale edges overlap only on the furcal base and furcal appendages	located close to another; their posterolateral parts overlap adjacent scales	located close to another; their posterolateral parts overlap adjacent scales	located close to another; their posterolateral parts overlap adjacent scales	edges of scales overlapping	edges of scales overlapping	located close to another; their posterolateral parts overlap adjacent scales	located far from another; do not overlap	located close to another; their posterolateral parts overlap adjacent scales
Presence of a scale of a different type on the dorsal and dorsolateral surfaces on the furcal base	present	present	present	present	present	present	present	present	present
Scale coverage of the ventral interciliary field	entire ventral interciliary field covered with scales	entire ventral interciliary field covered with scales	entire ventral interciliary field covered with scales	entire ventral interciliary field covered with scales	entire ventral interciliary field covered with scales	entire ventral interciliary field covered with scales	entire ventral interciliary field covered with scales	ventral interciliary field naked except for one pair of ventral terminal scales	entire ventral interciliary field covered with keels

Table A2 (continued). Comparison of species most similar to *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Character	*C.* (*C.*) *invitatus* sp. nov.	*C.* (*C.*) *maximus*	*C.* (*C.*) *microchaetus*	*C.* (*C.*) *similis*	*C.* (*C.*) *heterospinosus*	*C.* (*C.*) *laroides*	*C.* (*C.*) *polyspinosus*	*C.* (*H.*) *trispinosus*	*C.* (*P.*) *mutinensis*
Type of scales on the ventral interciliary field	on pharyngeal region semirectangular plates;on intestine region one-lobed, keeled scales	on anterior pharyngeal region semirectangular plates;on posterior pharyngeal region and intestine region one-lobed, keeled scales with rudimental spines	on pharyngeal region and anterior intestine region semirectangular plates;on intestine region central and posterior region one-lobed, keeled, semirectangular-shaped scales	small, rounded keeled and spined scales	on anterior pharyngeal region small semirectangular in shape, keeled scales;on posterior pharyngeal region and intestine region round in shape, keeled scales	small, rounded keeled scales with rudimental spines	small rounded or elongated keeled scales with rudimental spines from intestine region	–	from the head to posterior trunk region scales small rounded, keelless and spineless; on posterion trunk region scales semitriangular in shape, keeled and with rudimental spines
Number of terminal scales of the ventral interciliary field	4 pairs	1 pair	4 pairs	3 pairs	3 pairs	4 pairs	6 pairs	1 pair	3 pairs
Type of terminal scales on the ventral interciliary field	I pair: large, oval shaped, asymmetrical, without posterior notches, keeled and spined; II pair: oval shaped, without posterior notches, keeled and spined; III and IV pairs: egg-shaped keeled with rudimental spines	oval shaped, asymmetrical, without posterior notches, keeled, spined	I pair: large, oval shaped, asymmetrical, without posterior notches, keeled and spineless; II pair: rounded triangular in shape, with posterior notches, keeled and spined; III and IV pairs: rounded triangular in shape, keeled with rudimental spines	I pair: large, oval shaped, asymmetrical, without posterior notches, keeled and spineless; II pair: rounded triangular in shape, with shallow posterior notches, keeled and spined; III pair: rounded triangular in shape, keeled with rudimental spines	I pair: large, oval shaped, asymmetrical, without posterior notches, keeled and spineless; II pair: rounded triangular in shape, with shallow posterior notches, keeled and spined; III pair: rounded triangular in shape, keeled and spineless	I pair: large, oval shaped, asymmetrical, without posterior notches, keeled and spined; II–IV pairs: rounded triangular in shape, with shallow posterior notches, keeled and spined	I–III pairs: elongated, with very shallow posterior notches, keeled and spined; IV–VI pairs: small, rounded triangular in shape, keeled with rudimental spines	large, semirectangular in shape, keeled and spined	I pair: large, oval shaped, without posterior notches, keeled and spineless; II–III pairs: rounded triangular in shape, with posterior notches, keeled and spined

Table A2 (continued). Comparison of species most similar to *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Character	*C.* (*C.*) *invitatus* sp. nov.	*C.* (*C.*) *maximus*	*C.* (*C.*) *microchaetus*	*C.* (*C.*) *similis*	*C.* (*C.*) *heterospinosus*	*C.* (*C.*) *laroides*	*C.* (*C.*) *polyspinosus*	*C.* (*H.*) *trispinosus*	*C.* (*P.*) *mutinensis*
Spine length variation	spine length gradually increases from dorsal, dorsolateral, lateral and ventrolateral towards the ventral surface and from the head towards the widest trunk region; dorsally on the posterior trunk region two or three longer and thicker spines than neighbouring scale spines	spine length gradually increases from head towards the widest trunk region	spine length slightly, gradually increases from head towards the posterior trunk region; on furcal base and furca appendages spines longer	spine length gradually increases from head towards the widest body region	spine length gradually increases from dorsal, dorsolateral and lateral towards the ventrolateral surface and from the head towards the widest trunk region; on the trunk spines much longer	spine length gradually increases from head towards the widest body region	spine length gradually increases slightly from head towards the widest body region	spine length gradually increases from dorsal, dorsolateral, lateral and ventrolateral towards the ventral surface and from the head towards the trunk; dorsally on the posterior trunk region three longer and thicker spines than neighbouring scale spines; remaining spines on the posterior trunk region, furcal base and furca appendages short	spine length gradually increases from head towards the trunk posterior region
Spine length	head: 3.3–26.4 neck: 5.0–31.9 trunk: 7.8–34.3 (long dorsal spines: 16.6–20.0)	head: 5.0–11.0 neck: 6.0–15.0 trunk: 8.0–17.0	head: NA neck: 2.0–4.0 trunk: 3.0–5.0	head: NA neck: 4.0–6.0 trunk: 18.0–30.0	head and neck: 2.0–9.0 trunk: 14.0–20.5	head and neck: 12.0–16.0 trunk: 20.0–22.0	head: NA neck: 2.0–5.0 trunk: 3.0–10.0	2.0–8.3 (long dorsal spines: 12.5–13.0)	head and neck: 4.0–7.0 trunk: 9.0–22.0
Presence of lateral denticle on the spine	absent	absent	absent	present	present	absent	absent	absent	absent
Presence of hair–like spines on the ventral body surface	present	absent	absent	absent	absent	absent	absent	present	present
Type of posteriormost pair of trunk lateral spines	do not vary from other posterior trunk spines, not longer or thicker	slightly longer and thicker than the other lateral spines	slightly longer than the other lateral spines	slightly longer and thicker than the other lateral spines	shorter than the other lateral spines	slightly longer and thicker than the other lateral spines	longer and thicker than the other spines	longer and thicker than the other spines	slightly shorter than the other posterior trunk lateral spines
Number of rigid, long spines on furcal appendages	1 pair	1–3 pairs	1 pair	2 pairs	2 pairs	2–3 pairs	4–10 pairs	Absent	2 pairs

Table A2 (continued). Comparison of species most similar to *Chaetonotus* (*Chaetonotus*) *invitatus* sp. nov.

Character	*C.* (*C.*) *invitatus* sp. nov.	*C.* (*C.*) *maximus*	*C.* (*C.*) *microchaetus*	*C.* (*C.*) *similis*	*C.* (*C.*) *heterospinosus*	*C.* (*C.*) *laroides*	*C.* (*C.*) *polyspinosus*	*C.* (*H.*) *trispinosus*	*C.* (*P.*) *mutinensis*
Type of parafurcal spines	two pairs of parafurcal spines on lateral surface of furca appendages; long, thick and tapering to their end	longer and thicker than the other spines	longer and thicker than the other spines	longer and thicker than the other spines	similar in length to the trunk spines but more straight	longer and thicker than the other spines	longer and thicker than the other spines	longer and thicker than the other spines	similar in length to posterior trunk lateral spines
Ventral locomotor cilia	two longitudinal bands merged on the head region	two longitudinal bands wider on the head region	two longitudinal bands	two longitudinal bands wider on the head region	two longitudinal bands wider on the head region	two longitudinal bands	two longitudinal bands	two longitudinal bands wider on the head region	two longitudinal bands wider on the head region
Number of dorsal sensory bristles	3 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs

Table A3 (continued on next 5 pages). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. N = number of specimens analysed; Range = the smallest and the largest structure found among all specimens measured; SD = standard deviation. All measurements in micrometers (μm); all indicators given as a percentage (%) and italicized. When the range of plural structures in many specimens is given, the first parentheses contain the range of smallest/shortest structures in analysed individuals; the second parentheses contain the range of the largest/longest structures in analysed individuals.

Characters	N	Holotype	Range of adult paratypes	SD
Cephalion length	20	8.01	7.23–8.87	0.554
Cephalion width	20	9.41	7.64–9.72	0.555
Cephalion maximum width	20	13.98	12.82–14.21	0.322
Hypostomium length	20	2.92	2.36–3.12	0.183
Hypostomium width	20	6.31	5.48–6.63	0.276
Length of cephalic cilia (anterior tuft)	20	3.75–29.59	(3.21–4.48)–(23.75–29.59)	0.349; 1.678
Length of cephalic cilia (posterior tuft)	20	5.59–20.25	(4.79–7.61)–(17.38–21.72)	0.683; 0.965
Width of cephalic cilia (anterior tuft)	20	0.67–0.72	(0.61–0.69)–(0.68–0.78)	0.021; 0.023
Width of cephalic cilia (posterior tuft)	20	0.76–0.83	(0.70–0.79)–(0.79–0.90)	0.020; 0.029
Width of adhesive tube	20	1.83	1.67–1.83	0.041
Ratio of scale distribution	81	140	12.104–16.626	1.169
Length of anteriormost head scales (scales 1)	81	4.39–5.23	(3.37–4.39)–(4.47–5.23)	0.239; 0.189
Width of anteriormost head scales (scales 1)	15	2.19–2.54	(1.68–3.04)–(2.17–3.22)	0.293; 0.272
Length of head dorsal scales (scales 2)	15	4.10–5.17	(3.16–4.10)–(4.43–5.17)	0.216; 0.189
Width of head dorsal scales (scales 2)	15	4.15–5.20	(3.20–5.26)–(4.46–6.20)	0.438; 0.403
Length of head dorsolateral scales (scales 3)	15	3.97–4.96	(3.06–3.97)–(4.25–4.96)	0.211; 0.191
Width of head dorsolateral scales (scales 3)	15	3.98–4.94	(3.07–4.84)–(4.23–5.53)	0.375; 0.304
Length of head lateral scales (scales 3)	15	3.85–4.84	(2.97–3.85)–(4.11–4.84)	0.209; 0.202
Width of head lateral scales (scales 3)	15	3.79–4.78	(2.92–4.37)–(4.10–5.20)	0.307; 0.265
Length of head ventrolateral scales (scales 3)	15	3.49–4.57	(2.69–3.49)–(3.73–4.57)	0.194; 0.212
Width of head ventrolateral scales (scales 3)	15	3.36–4.43	(2.59–4.05)–(3.81–4.72)	0.309; 0.226
Length of head ventral scales (scales 4)	15	2.82–4.13	(2.17–2.82)–(3.39–4.13)	0.152; 0.188
Width of head ventral scales (scales 4)	15	2.66–3.95	(2.05–3.38)–(3.39–3.98)	0.284; 0.166
Length of neck dorsal scales (scales 5)	15	5.30–6.37	(4.54–5.30)–(5.18–6.37)	0.197; 0.308
Width of neck dorsal scales (scales 5)	15	4.78–5.91	(4.09–4.78)–(5.06–5.91)	0.186; 0.236

Table A3 (continued). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD
Length of neck dorsolateral scales (scales 6)	15	5.13–6.01	(4.32–5.13)–(4.88–6.01)	0.218; 0.292
Width of neck dorsolateral scales (scales 6)	15	4.56–5.53	(3.90–4.56)–(4.74–5.53)	0.168; 0.221
Length of neck lateral scales (scales 6)	15	5.07–5.78	(4.10–5.07)–(4.62–5.78)	0.240; 0.291
Width of neck lateral scales (scales 6)	15	4.43–5.27	(3.79–4.43)–(4.38–5.27)	0.172; 0.245
Length of neck ventrolateral scales (scales 6)	15	4.66–5.44	(3.93–4.66)–(4.48–5.44)	0.197; 0.253
Width of neck ventrolateral scales (scales 6)	15	4.02–4.92	(3.44–4.02)–(4.17–4.92)	0.147; 0.212
Length of neck ventral scales (scales 7)	15	3.24–4.57	(2.77–3.46)–(3.92–4.57)	0.167; 0.185
Width of neck ventral scales (scales 7)	15	2.75–4.09	(2.35–3.22)–(3.51–4.09)	0.200; 0.154
Length of trunk dorsal scales (scales 8)	15	7.02–9.71	(5.28–7.02)–(5.64–9.71)	0.424; 0.953
Width of trunk dorsal scales (scales 8)	15	5.52–8.43	(4.10–5.52)–(4.68–8.43)	0.343; 0.878
Length of trunk dorsolateral scales (scales 9)	15	6.88–8.55	(5.00–6.88)–(5.52–8.55)	0.450; 0.711
Width of trunk dorsolateral scales (scales 9)	15	5.34–7.37	(3.87–5.34)–(4.34–7.37)	0.352; 0.709
Length of trunk lateral scales (scales 9)	15	6.41–7.81	(4.87–6.41)–(5.34–7.81)	0.376; 0.582
Width of trunk lateral scales (scales 9)	15	4.93–6.68	(3.69–4.93)–(4.17–6.68)	0.300; 0.587
Length of trunk ventrolateral scales (scales 9)	15	6.29–7.47	(4.64–6.29)–(5.11–7.47)	0.391; 0.558
Width of trunk ventrolateral scales (scales 9)	15	4.79–6.34	(3.47–4.79)–(4.06–6.34)	0.310; 0.535
Length of trunk ventral scales (scales 10)	15	3.49–5.48	(3.03–4.08)–(4.60–5.48)	0.251; 0.267
Width of trunk ventral scales (scales 10)	15	2.62–4.61	(2.12–3.33)–(3.64–4.61)	0.270; 0.259
Length of scales 11	15	8.21–9.02	(5.34–8.21)–(5.56–9.06)	0.885; 0.899
Width of scales 11	15	12.43–13.37	(7.05–12.43)–(7.42–13.37)	1.379; 1.301
Length of scales 12	15	10.74–13.43	(7.44–10.74)–(7.64–13.43)	0.942; 1.354
Width of scales 12	15	10.51–13.22	(7.20–10.51)–(7.42–13.22)	0.874; 1.359
Length of scales 13	15	13.46	7.56–13.46	1.627
Width of scales 13	15	14.24	7.70–14.24	1.869
Length of scales 14	15	7.94–8.46	(4.30–7.94)–(4.54–8.46)	0.893; 0.950
Width of scales 14	15	6.29–6.98	(4.73–6.77)–(4.90–7.16)	0.632; 0.672
Length of scales 15	15	8.38	5.13–8.38	0.839
Width of scales 15	15	10.02	5.05–10.02	1.181

Table A3 (continued). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD
Length of scales 16	15	10.5	6.35–10.50	1.038
Width of scales 16	15	8.21	4.65–8.21	0.942
Length of scales 17	15	11.72	7.41–11.72	1.206
Width of scales 17	15	8.86	5.28–8.86	1.048
Length of scales 18	15	6.98	2.21–6.98	1.291
Width of scales 18	15	4.46	1.58–4.46	0.869
Length of scales 19	15	8.16–9.24	(5.96–8.16)–(6.63–9.24)	0.588; 0.652
Width of scales 19	15	3.03–3.93	(2.04–3.22)–(2.67–3.93)	0.332; 0.310
Length of scales 20	15	7	5.72–7.00	0.441
Width of scales 20	15	2.28	1.76–2.44	0.203
Length of scales 21	15	6.05	3.42–6.05	0.671
Width of scales 21	15	5.88	3.07–5.88	0.637
Length of head anteriormost spines (scales 1)	15	3.26–4.39	(2.24–3.45)–(3.30–5.24)	0.360; 0.550
Length of head dorsal spines (scales 2)	15	1.86–5.04	(0.44–1.86)–(2.38–5.04)	0.394; 0.783
Head dorsal spines length between lateral denticle and spine top (scales 2)	15	0.28–1.63	(0.07–0.28)–(0.54–1.63)	0.061; 0.282
Length of head dorsolateral spines (scales 3)	15	2.03–5.21	(0.48–2.03)–(2.55–5.21)	0.445; 0.800
Head dorsolateral spines length between lateral denticle and spine top (scales 3)	15	0.34–1.70	(0.09–0.34)–(0.57–1.70)	0.067; 0.294
Length of head lateral spines (scales 3)	15	2.48–5.53	(0.59–2.48)–(2.80–5.53)	0.529; 0.819
Head lateral spines length between lateral denticle and spine top (scales 3)	15	0.47–1.77	(0.12–0.47)–(0.64–1.77)	0.096; 0.290
Length of head ventrolateral spines (scales 3)	15	3.05–6.11	(0.73–3.05)–(3.09–6.11)	0.643; 0.869
Head ventrolateral spines length between lateral denticle and spine top (scales 3)	15	0.53–1.84	(0.14–0.53)–(0.70–1.84)	0.103; 0.307
Length of head ventral spines (scales 4)	15	12.31–13.73	(7.16–12.31)–(8.44–13.78)	1.467; 1.479
Lamella width on the ventral head spines (scales 4)	15	0.80–1.44	(0.42–0.94)–(0.65–1.44)	0.143; 0.216
Length of neck dorsal spines (scales 5)	15	5.12–7.39	(2.45–5.72)–(4.66–8.26)	0.916; 1.051
Neck dorsal spines length between lateral denticle and spine top (scales 5)	15	1.48–1.91	(0.66–1.65)–(1.20–2.13)	0.268; 0.270
Length of neck dorsolateral spines (scales 6)	15	5.32–7.97	(2.70–5.94)–(5.03–8.91)	0.921; 1.136
Neck dorsolateral spines length between lateral denticle and spine top (scales 6)	15	1.56–2.05	(0.72–1.74)–(1.29–2.29)	0.281; 0.292
Length of neck lateral spines (scales 6)	15	5.98–8.47	(3.03–6.6.8)–(5.35–9.47)	1.019; 1.204

Table A3 (continued). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD
Neck lateral spines length between lateral denticle and spine top (scales 6)	15	1.72–2.16	(0.81–1.92)–(1.36–2.42)	0.308; 0.309
Length of neck ventrolateral spines (scales 6)	15	6.65–8.98	(3.37–7.43)–(5.68–10.04)	1.097; 1.251
Neck ventrolateral spines length between lateral denticle and spine top (scales 6)	15	1.81–2.22	(0.87–2.02)–(1.40–2.48)	0.321; 0.313
Length of neck ventral spines (scales 7)	15	14.26–16.49	(8.76–14.26)–(10.12–16.49)	1.464; 1.584
Lamella width on the ventral neck spines (scales 7)	15	1.49–1.72	(0.71–1.49)–(1.01–1.72)	0.210; 0.206
Length of trunk dorsal spines (scales 8)	15	7.88–9.96	(4.97–8.82)–(7.06–11.14)	1.121; 1.341
Trunk dorsal spines length between lateral denticle and spine top (scales 8)	15	2.09–3.10	(1.32–2.34)–(2.20–3.47)	0.296; 0.418
Length of trunk dorsolateral spines (scales 9)	15	8.41–10.45	(5.30–9.39)–(7.41–11.69)	1.190; 1.326
Trunk dorsolateral spines length between lateral denticle and spine top (scales 9)	15	2.23–3.25	(1.41–2.49)–(2.30–3.64)	0.314; 0.414
Length of trunk lateral spines (scales 9)	15	8.68–11.12	(5.47–9.68)–(7.89–12.44)	1.233; 1.409
Trunk lateral spines length between lateral denticle and spine top (scales 9)	15	2.30–3.32	(1.45–2.57)–(2.36–3.71)	0.325; 0.425
Length of trunk ventrolateral spines (scales 9)	15	9.11–16.15	(5.74–10.16)–(8.71–16.98)	1.293; 2.436
Trunk ventrolateral spines length between lateral denticle and spine top (scales 9)	15	2.38–3.40	(1.50–2.65)–(2.46–3.84)	0.335; 0.437
Length of trunk ventral spines (scales 10)	15	17.19–19.54	(10.56–17.19)–(12.04–19.54)	1.617; 1.799
Lamella width on the ventral trunk spines (scales 10)	15	1.86–2.14	(1.06–1.86)–(1.24–2.14)	0.224; 0.255
Length of spines of scales 11	15	28.17–29.35	(19.88–29.70)–(22.36–34.14)	2.856; 3.789
Trunk scales 11 spines length between lateral denticle and spine top	15	6.49–7.52	(4.41–7.47)–(5.35–9.08)	0.920; 0.998
Length of spines of scales 12	15	27.07–31.75	(20.14–28.92)–(23.37–35.52)	2.568; 3.945
Trunk scales 12 spines length between lateral denticle and spine top	15	7.08–10.14	(3.75–7.08)–(6.14–10.59)	0.896; 1.211
Length of spines of scales 13	15	24.89	18.94–27.15	1.925
Trunk scales 13 spines length between lateral denticle and spine top	15	6.91	5.19–8.23	0.757
Length of spines of scales 16	15	16.65	11.59–16.65	1.284
Trunk scales 16 spines length between lateral denticle and spine top	15	4.68	2.32–4.68	0.613
Length of trunk posteriormost pair of lateral spines (scales 17)	15	20.09	13.87–20.09	1.564
Trunk posteriormost pair of lateral spines length between lateral denticle and spine base (scales 17)	15	6.27	4.15–6.32	0.698
Length ratio of posteriormost trunk lateral spines	15	15.256	12.104–16.626	1.169
Localization of lateral denticle on dorsal head spines (scales 2)	15	*15.054–32.341*	*(13.699–17.949)–(22.689–32.642)*	1.158; 2.477
Localization of lateral denticle on dorsolateral head spines (scales 3)	15	*16.749–32.630*	*(14.773–23.711)–(22.353–32.653)*	2.357; 2.641

Table A3 (continued). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD
Localization of lateral denticle on lateral head spines (scales 3)	15	*18.952–32.007*	*(15.657–22.689)–(21.053–32.143)*	1.422; 2.830
Localization of lateral denticle on ventrolateral head spines (scales 3)	15	*17.377–30.115*	*(15.745–20.161)–(17.632–30.233)*	1.124; 3.213
Localization of lateral denticle on dorsal neck spines (scales 5)	15	*25.846–28.906*	*(23.558–28.861)–(25.789–29.290)*	1.013; 0.927
Localization of lateral denticle on dorsolateral neck spines (scales 6)	15	*25.721–29.323*	*(24.828–29.268)–(25.691–29.448)*	0.963; 1.227
Localization of lateral denticle on lateral neck spines (scales 6)	15	*25.502–28.763*	*(23.209–25.581)–(27.147–28.861)*	0.594; 0.421
Localization of lateral denticle on ventrolateral head spines (scales 6)	15	*24.722–27.218*	*(19.818–24.799)–(25.486–27.310)*	1.268; 0.521
Localization of lateral denticle on dorsal trunk spines (scales 8)	15	*26.523–31.124*	*(25.796–26.606)–(31.005–31.452)*	0.202; 0.098
Localization of lateral denticle on dorsolateral trunk spines (scales 9)	15	*26.516–31.100*	*(25.221–26.604)–(30.979–31.808)*	0.338; 0.190
Localization of lateral denticle on lateral trunk spines (scales 9)	15	*26.498–29.856*	*(25.00–26.571)–(29.755–32.937)*	0.389; 0.801
Localization of lateral denticle on ventrolateral trunk spines (scales 9)	15	*21.053–26.125*	*(21.053–26.198)–(21.053–32.814)*	2.213; 3.092
Localization of lateral denticle on spines of scales 11	15	*23.039–25.622*	*(17.969–25.152)–(20.395–27.370)*	1.815; 1.844
Localization of lateral denticle on spines of scales 12	15	*26.154–31.937*	*(18.620–26.449)–(23.057–31.937)*	2.056–2.706
Localization of lateral denticle on spines of scales 13	15	*27.762*	*24.213–33.204*	2.580
Localization of lateral denticle on spines of scales 16	15	*28.108*	*18.026–30.015*	3.285
Localization of lateral denticle on posteriormost trunk lateral spines (scales 17)	15	*31.21*	*24.942–34.785*	2.530
Head dorsal sensory bristles length	15	24.53	15.86–24.53	2.053
Neck dorsal sensory bristles length	15	21.56	18.49–24.36	1.532
Posterior dorsal sensory bristles length	15	28.48	19.22–28.48	2.160
Number of scales in central longitudinal row on ventral interciliary field	81	18	15–23	1.992
Total number of longitudinal alternating rows of scales on ventral interciliary field	81	7	7	0
Length of ventral interciliary field scales (scales 22–24)	15	2.43–4.68	(1.48–2.73)–(3.15–5.37)	0.379; 0.622
Width of ventral interciliary field scales (scales 22–24)	15	1.87–4.12	(1.05–2.46)–(2.87–5.14)	0.361; 0.530
Length of terminal ventral interciliary field scales I pair (scales 25)	15	8.71	7.10–8.71	0.419
Width of terminal ventral interciliary field scales I pair (scales 25)	15	3.18	2.44–3.31	0.257
Length of terminal ventral interciliary field scales II pair (scales 26)	15	4.17	2.69–4.69	0.569
Width of terminal ventral interciliary field scales II pair (scales 26)	15	2.7	1.63–2.70	0.288
Length of terminal ventral interciliary field scales III pair (scales 26)	15	3.11	1.82–3.18	0.401
Width of terminal ventral interciliary field scales III pair (scales 26)	15	1.66	1.13–1.67	0.192

Table A3 (continued). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD
Length of terminal ventral interciliary field scales I pair spines (scales 25)	15	14.45	9.78–14.51	1.496
Length of terminal ventral interciliary field scales II pair spines (scales 26)	15	0.61	0.37–1.48	0.281
Length of terminal ventral interciliary field scales III pair spines (scales 26)	15	0.31	0.23–1.47	0.078
Width of anterior pharynx thickening (a)	20	10.14	8.49–10.97	0.614
Width of pharynx narrowing (n)	20	6.42	6.00–7.48	0.356
Width of middle pharynx (m)	20	6.96	6.54–7.77	0.334
Width of posterior pharynx thickening (p)	20	10.32	10.22–11.96	0.539
Width of pharyngeal–intestinal junction	20	3.78	3.17–3.97	0.242
Intestine length	70	74.91	54.58–74.91	3.622
Pharynx formula a	20	*30.542*	*27.378–34.367*	1.768
Pharynx formula n	20	*19.337*	*18.991–23.317*	1.147
Pharynx formula m	20	*20.964*	*20.936–24.221*	1.123
Pharynx formula p	20	*31.084*	*31.084–39.298*	2.288
Pharynx–intestine ratio I	70	*44.32*	*43.759–54.732*	2.515
Length of matured egg	4	–	41.89–46.16	1.907
Width of matured egg	4	–	21.12–29.34	3.815
Length of X-organ	4	–	7.96–10.56	1.209
Width of X-organ	4	–	14.71–17.68	1.521

Table A4 (continued on next 3 pages). Comparison of the most important differentiating characters among species most similar to *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov. All measurements in micrometres (µm). NA = data not available; – = not applicable.

Character	*C.* (*H.*) *horridus* sp. nov.	*C.* (*H.*) *acanthophorus*	*C.* (*H.*) *balsamoae*	*C.* (*H.*) *euhystrix*	*C.* (*H.*) *novenarius*
Body length	107.8–134.0	80.0–110.0	147.0–172.0	150.0–160.0	106.0–193.0
Cephalic pleurae	cephalion short and narrow; straight cut and extended on the dorsal body side; epipleurae slightly arched and located on the dorsal, dorsolateral, lateral side and slightly visible on the ventrolateral head side; hypopleurae slightly larger than the epipleurae and located entirely on the ventrolateral and ventral head sides, not visible from the dorsal body view; between the cephalion and epipleurae and between the epipleurae and hypopleurae deep notches; hypostomium short, rectangular-shaped with a slightly reinforced anterior edge	cephalion short and narrow; epipleurae and hypopleurae similar in size; epipleurae and hypopleurae located mostly laterally; hypostomium not marked	cephalion short and narrow; epipleurae and hypopleurae similar in size; epipleurae and hypopleurae located mostly laterally; hypostomium not marked	cephalion narrow; epipleurae and hypopleurae similar in size; epipleurae and hypopleurae located mostly laterally; hypostomium not marked	cephalion wide and narrow; epipleurae smaller than hypopleurae; epipleurae and hypopleurae located mostly laterally; hypostomium not marked
Place of arising cephalic cilia	anterior tufts: dorso-terminally, in area between the cephalion and epipleurae; posterior tufts: ventrally, above the anterior edge of the hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae
Pharynx length	27.0–33.6	30.0	40.0–46.0	50.0–55.0	27.5–51.0
Pharynx shape	wide; round anterior and wider posterior dilatations	cylindrical expanding towards posterior end	narrow; small, similar in size anterior and posterior dilatations	anterior and wider posterior dilatation	cylindrical expanding towards posterior end
Furca length	21.7–25.9	16.0	25.0–32.0	25.0–35.0	17.0–32.5
Adhesive tube length	9.7–13.0	8.0	19.0–21.0	15.0–16.0	*ca.* 11.0–21.5
Type of furca indentation	V-shaped	V-shaped	helmet-shaped	V-shaped	helmet-shaped
Number of scales in central longitudinal row	13–15	11	16	13	19
Total number of longitudinal alternating rows of scales	15–21	NA	NA	NA	14–15
Type of scales	almost all three-lobed with strong, high, triangular keels, with from strong towards rudimentary spines; shape strongly differentiated within body regions	small, reduced to the triangle, high keels	all three-lobed with triangular keels and spines	all three-lobed with strong, high, triangular keels and strong spines; shape strongly differentiated within body regions	scales one-lobed and three-lobed; with strong, high, triangular keels, with strong or rudimentary spines; shape strongly differentiated within body regions

Table A4 (continued). Comparison of species most similar to *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov.

Character	*C.* (*H.*) *horridus* sp. nov.	*C.* (*H.*) *acanthophorus*	*C.* (*H.*) *balsamoae*	*C.* (*H.*) *euhystrix*	*C.* (*H.*) *novenarius*
Scale size variation	strongly differentiated within body regions; dorsal and dorsolatral scales much larger	NA	scales similar in size	size increases gradually from the head towards the posterior trunk region	strongly differentiated within body regions
Scale size	Head: 2.2–5.3 × 2.0–6.2 Neck: 2.8–6.4 × 2.4–5.9 Trunk: 3.0–13.7 × 2.1–13.4	NA	4.0 × NA	7.0 × NA–15.0 × NA	3.6–6.0 × NA
Alignment of scales	scales on the head and anterior neck region located far from another; on posterior neck and anterior trunk region located gradually closer but still at a distance to the other scales and not juxtaposed; scales on dorsolateral, lateral, ventrolateral and ventral trunk region located at a distance from the other scales, dorsal trunk scales and furcal appendages scales slightly overlap	scales located far from another	scales located far from another	scales located far from another but posteriolateral lobes meet and are juxtaposed	scales on the head located far from another; on neck and anterior trunk region located gradually closer and juxtaposed; trunk scales slightly overlap, furcal base scales juxtaposed and not overlap
Number of scales with long spines	21–29	20	7–9	–	9
Location of scales with long spines	on the trunk and furcal base; dorsally and dorsolaterally from *ca*. U37 to U73 and dorsally to U81, laterally two pairs at U69–U75 and U76–U82	dorsally and dorsolaterally on the trunk, posteriormost trunk lateral spines on the furcal base	dorsally on anterior trunk region	dorsally and dorsolaterally on the trunk	dorsally on anterior trunk region
Presence of a different type of scales on the dorsal and dorsolateral surfaces of the furcal base and furcal appendages	present	absent	absent	present	present
Scale coverage of the ventral interciliary field	entire ventral interciliary field covered by scales	NA	naked pharyngeal region; keels on intestine region s	entire ventral interciliary field covered by scales	entire ventral interciliary field covered by scales
Type of scales on ventral interciliary field	one-lobed; anterior scales egg-shaped, rounded and are rounded towards the posterior body region become gradually larger and more elongated, posterior scales elongated, oval-shaped with straight, thin keels; from the anterior to posterior body region, the distances between the scales decrease, and beyond half the trunk's length the scales start to overlap	NA	only keels visible	one-lobed, rounded, keelless, without overlapping edges	one-lobed, rounded, keelless and spineless

Table A4 (continued). Comparison of species most similar to *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov.

Character	*C.* (*H.*) *horridus* sp. nov.	*C.* (*H.*) *acanthophorus*	*C.* (*H.*) *balsamoae*	*C.* (*H.*) *euhystrix*	*C.* (*H.*) *novenarius*
Number of scales in central longitudinal row on the ventral interciliary field	15–23	NA	NA	NA	40
Total number of longitudinal alternating rows of scales on the ventral interciliary field	7	NA	6–8	NA	4
Number of terminal scales on the ventral interciliary field	3 pairs	NA	2–5 scales	1 pair	1 pair
Type of terminal scales on the ventral interciliary field	I pair: elongated, rectangular-shaped with rounded anterior edges, keeled and with with a long, thin, straight spine; II and III pairs: elongated, rectangular-shaped with rounded anterior edges, keeled and rudimentary spined	NA	scales with keels and simple, long spines	oval, keeled and spineless	elongated, oval-shaped keeled and spined
Spine length variation	anteriormost spines slightly longer than subsequent head spines; spine length and thickness increase gradually from head towards the widest body region; head, neck and anterior trunk spines length gradually increase from dorsal, dorsolateral, lateral and ventrolateral towards to the ventral surface; ventral hair–like spines very long; dorsal and dorsolateral trunk spines very long, thick, rigid; distinctly longer and stronger than remaining spines	head and neck spines short, trunk dorsal and dorsolateral, and posteriormost trunk lateral spines very long	spine length gradually increase slightly from head towards the posterior body region; ventral hair–like spines longer than remaning spines; anterior trunk dorsal spines very long, thick, rigid; distinctly longer and stronger than remaining spines	spine length and thickness increase gradually from head top towards the posterior trunk region; all dorsolateral, lateral, ventrolateral and ventral spines shorter than the dorsal spines, their length gradually decreases towards the ventral surface	anteriormost spines longer than subsequent head spines; spine length and thickness increase gradually from head posterior region towards the anterior trunk region; anterior dorsal trunk spines very long, thick, rigid; distinctly longer and stronger than remaining spines; central and posterior trunk spines short or rudimentary; from lateral and ventrolateral towards ventral surface spines much longer than dorsolateral spines
Spine length	head: 0.4–13.8 neck: 2.5–16.5 trunk: 5.0–19.5 long spines: 11.6–34.1	head: 4.0 long spines: 16.0–24.0	head and neck: 2.5–19.0 posterior trunk: 12.0–32.0 long spines: 30.0–76.0	head and neck: 5.0–7.0 trunk: 50.0–70.0	head: 9.0 neck: NA trunk: 9.0–19.0 long spines: 60.0–85.0
Presence of hair-like spines on the ventral body surface	present	NA	present	absent	absent
Presence of lamellae on ventral spines	present	NA	absent	absent	absent

Table A4 (continued). Comparison of species most similar to *Chaetonotus* (*Hystricochaetonotus*) *horridus* sp. nov.

Character	*C.* (*H.*) *horridus* sp. nov.	*C.* (*H.*) *acanthophorus*	*C.* (*H.*) *balsamoae*	*C.* (*H.*) *euhystrix*	*C.* (*H.*) *novenarius*
Presence and distinctness of lateral denticle on the spines	all spines, except for anteriormost head dorsal spines, furcal appendages spines and ventral surface spines, have lateral denticle; lateral denticle on spine becomes more pronounced from head towards the widest body region; the most prominent, very distinct and deeply notched lateral denticle present on dorsal and dorsolateral trunk spines	dorsal, dorsolateral and posteriormost trunk lateral spines have lateral denticle; lateral denticle on remaining spines not observed	double lateral denticle arranged in single file present only on long, anterior trunk dorsal spines; lateral denticle on remaining spines absent	all spines have lateral denticle; lateral denticle on the spines becomes more pronounced from head towards the posterior trunk region	single or double lateral denticle arranged in single file present only on long, anterior trunk dorsal spines; lateral denticle on remaining spines absent
Localization of lateral denticle on the spines	head: *13.699–32.653* neck: *19.818–29.448* trunk: *21.053–32.937* long spines: *17.969–34.785*	NA	long spines: smaller denticle: *12.000–14.000* larger denticle: *23.000–31.000*	NA	NA
Type of posteriormost pair of trunk lateral spines	longer, stronger and more curved than other lateral spines but shorter thank the trunk dorsal and dorsolateral long spines	longer than other lateral spines	the same as other lateral trunk spines	shorter than other posterior trunk region spines	longer than other lateral spines
Length ratio of posteriormost trunk lateral spines	*24.942–34.785*	NA	NA	NA	NA
Type of last pair lateral spines	–	–	–	shorter than posterior trunk region spines	–
Length ratio of posteriormost parafurcal lateral spines	–	–	–	NA	–
Ventral locomotor cilia	two longitudinal bands merged on the head region	NA	two longitudinal bands almost merged on the head region	two longitudinal bands	NA
Number of dorsal sensory bristles	3 pairs	2 pairs	1 pair	2 pairs	2 pairs

Table A5 (continued on next 4 pages). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. N = number of specimens analysed; Range = the smallest and the largest structure found among all specimens measured; SD = standard deviation. All measurements in micrometers (μm); all indicators given as a percentage (%) and italicized. When the range of plural structures in many specimens is given, the first parentheses contain the range of smallest/shortest structures in analysed individuals; the second parentheses contain the range of the largest/longest structures in analysed individuals.

Characters	N	Holotype	Range of adult paratypes	SD
Cephalion length	5	6.11	6.11–6.94	0.307
Cephalion width	5	7.56	7.03–8.29	0.449
Cephalion maximum width	5	11.68	11.68–12.93	0.492
Hypostomium length	5	2.55	2.55–2.92	0.152
Hypostomium width	5	6.10	5.55–7.19	0.601
Length of cephalic cilia (anterior tuft)	5	4.58–26.81	(4.36–4.99)–(22.66–26.81)	0.239; 1.719
Length of cephalic cilia (posterior tuft)	5	7.41–20.05	(5.22–8.56)–(19.44–20.95)	1.213; 0.562
Width of cephalic cilia (anterior tuft)	5	0.67–0.78	(0.62–0.73)–(0.71–0.81)	0.040; 0.039
Width of cephalic cilia (posterior tuft)	5	0.80–0.91	(0.073–0.83)–(0.80–0.91)	0.036; 0.045
Width of adhesive tube	5	1.43	1.43–1.48	0.019
Ratio of scale distribution	5	*135.714*	*135.714–140.000*	*1.620*
Length of anteriormost head scales (scales 1)	5	4.15–5.22	(3.77–4.54)–(4.13–5.91)	0.305; 0.651
Width of anteriormost head scales (scales 1)	5	2.07–2.65	(1.77–2.26)–(2.12–3.02)	0.187; 0.330
Length of head dorsal cental scales (scales 2)	5	2.76	2.42–3.19	0.305
Width of head dorsal central scales (scales 2)	5	1.49	1.23–1.72	0.189
Length of head dorsal scales (scales 3 and 7)	5	3.81–4.72	(3.08–3.92)–(3.82–4.86)	0.391; 0.470
Width of head dorsal scales (scales 3 and7)	5	3.57–4.86	(2.89–3.67)–(3.93–5.01)	0.364; 0.486
Length of head dorsolateral scales (scales 4 and 8)	5	3.68–4.57	(2.97–3.79)–(3.70–4.71)	0.380; 0.456
Width of head dorsolateral scales (scales 4 and 8)	5	3.34–4.55	(2.70–3.44)–(3.68–4.69)	0.345; 0.456
Length of head lateral scales (scales 4 and 8)	5	3.60–4.24	(2.90–3.71)–(3.43–4.37)	0.375; 0.424
Width of head lateral scales (scales 4 and 8)	5	3.22–4.15	(2.59–3.32)–(3.36–4.28)	0.335; 0.415
Length of head ventrolateral scales (scales 5 and 9)	5	3.28–4.09	(2.64–3.38)–(3.31–4.22)	0.341; 0.435
Width of head ventrolateral scales (scales 5 and 9)	5	2.89–3.87	(2.33–2.98)–(3.13–3.99)	0.305; 0.388
Length of head ventral scales (scales 6)	5	1.87–2.21	(1.49–1.93)–(1.91–2.28)	0.194; 0.152
Width of head ventral scales (scales 6)	5	2.03–2.44	(1.62–2.11)–(2.12–2.52)	0.206; 0.158

Table A5 (continued). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD
Length of neck dorsal scales (scales 10 and 14)	5	4.11–6.45	(3.33–4.24)–(5.23–6.65)	0.420; 0.654
Width of neck dorsal scales (scales 10 and14)	5	3.92–5.21	(3.18–4.04)–(4.22–5.37)	0.398; 0.528
Length of neck dorsolateral scales (scales 11)	5	3.90–6.29	(3.16–4.02)–(5.10–6.49)	0.398; 0.640
Width of neck dorsolateral scales (scales 11)	5	3.66–4.85	(2.97–3.77)–(3.93–5.00)	0.369; 0.493
Length of neck lateral scales (scales 11)	5	3.72–6.07	(3.01–3.83)–(4.92–6.27)	0.380; 0.620
Width of neck lateral scales (scales 11)	5	3.40–4.56	(2.75–3.50)–(3.70–4.71)	0.348; 0.465
Length of neck ventrolateral scales (scales 12)	5	3.51–5.54	(2.84–3.64)–(4.49–5.72)	0.359; 0.565
Width of neck ventrolateral scales (scales 12)	5	3.14–4.09	(2.54–3.26)–(3.31–4.22)	0.320; 0.418
Length of neck ventral scales (scales 13)	5	2.39–3.94	(2.07–2.48)–(3.19–4.09)	0.167; 0.364
Width of neck ventral scales (scales 13)	5	2.77–4.48	(2.40–2.87)–(3.64–4.66)	0.192; 0.411
Length of trunk dorsal scales (scales 15 and 17)	5	6.90–8.48	(5.59–7.11)–(6.87–8.82)	0.701; 0.882
Width of trunk dorsal scales (scales 15 and 17)	5	4.98–6.85	(4.03–5.13)–(5.55–7.14)	0.507; 0.716
Length of trunk dorsolateral scales (scales 15 and 17)	5	6.74–7.86	(5.46–6.95)–(6.37–8.19)	0.687; 0.820
Width of trunk dorsolateral scales (scales 15 and 17)	5	4.74–6.27	(3.84–5.09)–(5.08–6.53)	0.532; 0.653
Length of trunk lateral scales (scales 15 and 17)	5	6.36–7.60	(5.15–6.56)–(6.16–7.92)	0.650; 0.793
Width of trunk lateral scales (scales 15 and 17)	5	4.39–5.97	(3.58–4.53)–(4.84–6.22)	0.441; 0.623
Length of trunk ventrolateral scales (scales 15 and 17)	5	6.08–7.22	(4.92–6.27)–(5.82–7.52)	0.623; 0.763
Width of trunk ventrolateral scales (scales 15 and 17)	5	4.10–5.49	(3.32–4.23)–(4.43–5.72)	0.420; 0.579
Length of trunk ventral scales (scales 16)	5	2.82–4.34	(2.28–2.93)–(3.51–4.51)	0.263; 0.404
Width of trunk ventral scales (scales 16)	5	3.31–5.02	(2.68–3.44)–(4.06–5.22)	0.307; 0.467
Length of scales 18	5	6.78–8.37	(5.04–6.78)–(6.13–8.37)	0.759; 0.955
Width of scales 18	5	10.89–13.03	(6.44–10.89)–(8.37–13.03)	1.729; 1.882
Length of scales 19	5	7.38–8.26	(5.15–7.38)–(6.12–8.26)	0.898; 0.886
Width of scales 19	5	8.10–8.86	(6.26–8.10)–(7.29–8.86)	0.779; 0.777
Length of scales 20	5	9.14–10.40	(6.23–9.14)–(7.53–10.40)	1.118; 1.143
Width of scales 20	5	6.37–7.09	(4.90–6.37)–(5.44–7.09)	0.635; 0.667
Length of scales 21	5	8.97	7.32–9.16	0.740
Width of scales 21	5	8.86	7.20–9.53	0.728
Length of scales 22	5	4.77–6.97	(4.31–4.84)–(5.88–7.11)	0.249; 0.572

Table A5 (continued). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD
Width of scales 22	5	3.84–4.93	(3.48–3.92)–(4.20–5.03)	0.212; 0.330
Length of scales 23	5	4.85	3.27–4.85	0.644
Width of scales 23	5	3.32	2.24–3.32	0.481
Length of scales 24	5	11.04	7.42–11.39	1.765
Width of scales 24	5	5.86	4.13–6.05	0.872
Length of scales 25	5	10.63	6.37–10.80	1.900
Width of scales 25	5	8.19	4.93–8.32	1.453
Length of scales 26	5	10.52	8.12–10.68	1.065
Width of scales 26	5	8.69	6.71–9.03	0.916
Length of scales 27	5	5.89–8.77	(4.43–6.47)–(6.42–8.77)	0.771; 0.925
Width of scales 27	5	2.21–2.67	(1.61–2.28)–(2.05–3.19)	0.284; 0.438
Length of scales 28	5	5.96	4.22–5.96	0.689
Width of scales 28	5	4.18	3.15–4.41	0.489
Length of head anteroiormost spines (scales 1)	5	2.03–3.19	(1.63–2.47)–(2.61–3.45)	0.313; 0.309
Length of head scales 2 spines	5	1.66	1.53–2.92	0.552
Length of head dorsal spines (scales 3 and 7)	5	0.74–2.14	(0.54–1.93)–(1.96–3.07)	0.568; 0.505
Length of head dorsolateral spines (scales 4 and 8)	5	0.68–1.92	(0.50–1.77)–(1.76–2.75)	0.519; 0.452
Length of head lateral spines (scales 4 and 8)	5	0.56–1.80	(0.41–1.48)–(1.66–2.53)	0.439; 0.421
Length of head ventrolateral spines (scales 5 and 9)	5	0.34–1.63	(0.27–0.92)–(1.59–2.35)	0.268; 0.362
Length of head ventral spines (scales 6)	5	8.06–11.42	(7.32–8.95)–(9.59–12.03)	0.679; 0.985
Lamella width on the ventral head spines (scales 6)	5	0.68–1.09	(0.57–0.91)–(0.87–1.09)	0.149; 0.103
Length of neck dorsal spines (scales 10 and 14)	5	2.27–3.96	(2.09–3.26)–(3.67–5.69)	0.533; 0.917
Length of neck dorsolateral spines (scales 11)	5	2.10–3.58	(1.93–3.02)–(3.32–5.14)	0.495; 0.828
Length of neck lateral spines (scales 11)	5	1.88–3.35	(1.73–2.70)–(3.11–4.81)	0.442; 0.775
Length of neck ventrolateral spines (scales 12)	5	1.76–3.08	(1.62–2.53)–(2.86–4.42)	0.414; 0.712
Length of neck ventral spines (scales 13)	5	11.68–12.41	(9.84–12.31)–(10.98–13.60)	0.969; 0.956
Lamella width on the ventral neck spines (scales 13)	5	1.17–1.80	(0.94–1.17)–(1.07–1.80)	0.111; 0.300
Length of trunk dorsal spines (scales 15 and 17)	5	4.21–5.93	(3.91–6.02)–(5.52–8.24)	0.964; 1.280

Table A5 (continued). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD
Length of trunk dorsolateral spines (scales 15 and 17)	5	3.98–5.52	(3.70–5.68)–(5.14–7.67)	0.908; 1.192
Length of trunk lateral spines (scales 15 and 17)	5	3.81–5.37	(3.55–5.44)–(5.02–7.56)	0.868; 1.189
Length of trunk ventrolateral spines (scales 15 and 17)	5	3.32–5.04	(3.09–4.74)–(4.71–7.11)	0.757; 1.120
Length of trunk ventral spines (scales 16)	5	12.68–14.62	(11.19–13.93)–(13.26–15.23)	0.990; 0.868
Lamella width on the ventral trunk spines (scales 16)	5	1.88–2.07	(1.16–1.88)–(1.24–2.18)	0.282; 0.374
Length of spines of scales 18	5	18.08–21.61	(16.15–18.08)–(18.31–21.61)	0.801; 1.436
Trunk scales 18 spines length between lateral denticle and spine top	5	1.86–2.83	(1.49–1.86)–(2.02–2.86)	0.163; 0.348
Length of spines of scales 19	5	0.64–0.72	(0.30–0.64)–(0.51–0.84)	0.128; 0.118
Length of spines of scales 20	5	0.61–0.66	(0.31–0.61)–(0.36–0.97)	0.121; 0.236
Length of spines of scales 21	5	18.79	15.92–18.79	1.260
Trunk scales 21 spines length between lateral denticle and spine top	5	2.28	1.67–2.28	0.222
Length of spines of scales 22	5	3.41–4.75	(2.32–3.41)–(3.44–4.75)	0.430; 0.520
Length of spines of scales 24	5	12.58	10.16–12.73	1.078
Trunk scales 24 spines length between lateral denticle and spine top	5	1.63	1.37–1.71	0.156
Length of trunk posteriormost pair of lateral spines (scales 25)	5	13.69	11.42–14.02	1.028
Trunk posteriormost pair of lateral spines length between lateral denticle and spine base (scales 25)	5	1.86	1.58–1.97	0.147
Length of spines of scales 26	5	11.61	11.39–14.20	1.148
Trunk scales 26 spines length between lateral denticle and spine top	5	2.02	1.66–2.55	0.355
Length of spines of scales 27	5	0.31–0.45	(0.27–0.42)–(0.42–0.55)	0.068; 0.056
Length ratio of posteriormost trunk lateral spines (scales 25)	5	*12.686*	*11.094–12.923*	0.750
Localization of lateral denticle on spines of scales 1	5	*10.288–13.096*	*(8.780–10.504)–(9.839–15.068)*	0.733; 2.136
Localization of lateral denticle on spines of scales 19	5	*12.134*	*10.127–12.477*	1.086
Localization of lateral denticle on spines of scales 24	5	*12.957*	*12.398–13.682*	0.533
Localization of lateral denticle on posteriormost trunk lateral spines (scales 25)	5	*13.587*	*12.610–15.149*	0.938
Localization of lateral denticle on spines of scales 26	5	*17.399*	*12.691–17.958*	2.154
Head dorsal sensory bristles length	5	10.45	9.24–11.76	1.036
Neck dorsal sensory bristles length	5	14.92	14.24–17.93	1.508
Posterior dorsal sensory bristles length	5	18.57	18.28–19.71	0.578

Table A5 (continued). Detailed morphometric characters of *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov.

Characters	N	Holotype	Range of adult paratypes	SD
Number of scales in central longitudinal row on ventral interciliary field	5	25	21–25	1.574
Total number of longitudinal alternating rows of scales on ventral interciliary field	5	7	7	0
Length of ventral interciliary field scales (scales 29–30)	5	1.66–4.42	(1.39–1.91)–(3.82–5.15)	0.190; 0.531
Width of ventral interciliary field scales (scales 29–30)	5	0.79–3.29	(0.62–1.05)–(2.73–4.12)	0.158; 0.552
Length of terminal ventral interciliary field scales I pair (scales 31)	5	8.23	6.92–8.57	0.627
Width of terminal ventral interciliary field scales I pair (scales 31)	5	2.79	2.62–3.04	0.152
Length of terminal ventral interciliary field scales II pair (scales 32)	5	3.98	3.14–4.05	0.401
Width of terminal ventral interciliary field scales II pair (scales 32)	5	1.81	1.41–1.93	0.210
Length of terminal ventral interciliary field scales III pair (scales 33)	5	2.31	2.25–2.68	0.188
Width of terminal ventral interciliary field scales III pair (scales 33)	5	1.27	1.20–1.32	0.044
Length of terminal ventral interciliary field scales VI pair (scales 33)	5	1.84	1.75–2.06	0.113
Width of terminal ventral interciliary field scales VI pair (scales 33)	5	0.90	0.85–0.98	0.053
Length of terminal ventral interciliary field scales I pair spines (scales 31)	5	9.41	7.71–10.69	1.065
Width of anterior pharynx thickening (a)	5	7.98	7.58–9.09	0.610
Width of pharynx narrowing (n)	5	5.31	4.92–7.13	0.929
Width of middle pharynx (m)	5	5.64	5.33–7.40	0.890
Width of posterior pharynx thickening (p)	5	9.83	9.22–11.08	0.758
Width of pharyngeal–intestinal junction	5	2.92	2.51–3.09	0.234
Intestine length	5	61.59	54.61–61.70	3.164
Pharynx formula a	5	*28.449*	*26.965–32.887*	2.180
Pharynx formula n	5	*18.93*	*18.771–25.796*	3.127
Pharynx formula m	5	*20.107*	*20.107–26.773*	2.993
Pharynx formula p	5	*35.045*	*35.045–40.087*	2.281
Pharynx–intestine ratio I	5	*45.543*	*45.543–49.147*	1.561
Length of X-organ	1	–	6.13	–
Width of X-organ	1	–	16.39	–

Table A6 (continued on next 4 pages). Comparison of the most important differentiating characters among species most similar to *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov. All measurements in micrometres (µm). NA = data not available; – = not applicable.

Character	*C.* (*H.*) *inaequabilis* sp. nov.	*C.* (*H.*) *enormis*	*C.* (*H.*) *schlitzensis*	*C.* (*H.*) *octonarius*	*C.* (*H.*) *novenarius*	*C.* (*H.*) *aemilianus*	*C.* (*H.*) *ferrarius*	*C.* (*H.*) *spinulosus*	*C.* (*H.*) *longispinosus*
Body length	98.16–108.49	85.0	125.0	70.0–110.0	106.0–193.0	80.0–103.0	90.0–110.0	60.0–90.0	70.0–160.0
Cephalic pleurae	cephalion short and narrow; straight cut and extended on the dorsal body side; epipleurae and hypopleurae similar in size; epipleurae slightly arched and located on the dorsal, dorsolateral, lateral side and slightly visible on the ventrolateral head side; hypopleurae located entirely on the ventrolateral and ventral head sides, not visible from the dorsal body view; between the cephalion and epipleurae and between the epipleurae and hypopleurae deep notches; hypostomium short, rectangular–shaped with a slightly reinforced anterior edge	cephalion short and narrow; epipleurae and hypopleurae similar in size; epipleurae and hypopleurae located mostly laterally; hypostomium not marked	cephalion short and narrow; epipleurae smaller than hypopleurae; epipleurae and hypopleurae located mostly laterally; hypostomium not marked	cephalion short and narrow; epipleurae smaller than hypopleurae; epipleurae and hypopleurae located mostly laterally; hypostomium not marked	cephalion wide and narrow; epipleurae smaller than hypopleurae; epipleurae and hypopleurae located mostly laterally; hypostomium not marked	cephalion short and narrow; epipleurae and hypopleurae similar in size; epipleurae and hypopleurae located mostly laterally; hypostomium not marked	cephalion short and narrow; epipleurae and hypopleurae similar in size; epipleurae and hypopleurae located mostly laterally; hypostomium not marked	cephalion short and narrow; epipleurae, hypopleurae and hypostomium unrecognizable	cephalion wide and narrow; epipleurae smaller than hypopleurae; epipleurae and hypopleurae located mostly laterally; hypostomium not marked
Place of arising cephalic cilia	anterior tufts: dorso–terminaly, in area between the cephalion and epipleurae; posterior tufts: ventrally, above the anterior edge of the hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae	anterior tufts: dorsoterminal between cephalion and epipleurae; posterior tufts: laterally, between epipleurae and hypopleurae
Pharynx length	26.2–28.3	NA	21.0–23.0	20.0–28.0	27.5–51.0	24.0–29.0	ca 22.5–37.0	20.0–26.0	
Pharynx shape	anterior and wider posterior dilatation	cylindrical expanding towards posterior end	cylindrical with posterior dilatation	cylindrical with posterior dilatation	cylindrical expanding towards posterior end	cylindrical expanding towards posterior end	cylindrical expanding towards posterior end	cylindrical expanding towards posterior end	cylindrical with slight posterior dilatation
Furca length	20.1–22.1	NA	20.0	14.0–18.0	17.0–32.5	10.0–15.0	10.0–15.0	8.0–10.0	15.0
Adhesive tube length	9.9–10.5	NA	10.0	7.0–9.0	ca 11.0–21.5	NA	5.0–7.0	ca 2.0–5.0	6.0–7.0
Type of furca indentation	V-shaped	V-shaped	V-shaped	V-shaped	helmet-shaped	V-shaped	V-shaped	V-shaped	V-shaped
Number of scales in central longitudinal row	14–15	15–16	14	3	19	7–11	7–10	NA	NA

Table A6 (continued). Comparison of species most similar to *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov.

Character	*C.* (*H.*) *inaequabilis* sp. nov.	*C.* (*H.*) *enormis*	*C.* (*H.*) *schlitzensis*	*C.* (*H.*) *octonarius*	*C.* (*H.*) *novenarius*	*C.* (*H.*) *aemilianus*	*C.* (*H.*) *ferrarius*	*C.* (*H.*) *spinulosus*	*C.* (*H.*) *longispinosus*
Total number of longitudinal alternating rows of scales	19–21	NA	NA	3	14–15	7–17	19–20	NA	NA
Type of scales	almost all three-lobed with strong, high, triangular keels, with spines from strong towards rudimentary; shape strongly differentiated within body regions	NA	one-lobed, keeled and spined	one-lobed, rounded in shape with very shallow or straight posterior edge, keeled and with long spines; sub-three-lobed, keeled and spineless	scales one-lobed and three-lobed; with strong, high, triangular keels, with spines strong or rudimentary; shape strongly differentiated within body regions	almost all three-lobed with strong, high, triangular keels, with spines from strong towards rudimentary; shape strongly differentiated within body regions	almost all sub-three-lobed with strong, high, triangular keels, with spines from strong towards rudimentary; shape strongly differentiated within body regions	all three-lobed or sub-three-lobed with keels, with spines from strong towards rudimentary; shape differentiated within body regions	scales sub-three-lobed with keels, with spines from strong towards short; shape differentiated within body regions
Scale size variation	strongly differentiated within body regions; dorsal and dorsolatral scales much larger	NA	size gradually increases from the head towards the widest body region	trunk scales similar in size	strongly differentiated within body regions	strongly differentiated within body regions; dorsal scales much larger	strongly differentiated within body regions; dorsal scales much larger	dorsal trunk scales much larger than remaining scales	NA
Scale size	head: 1.49–5.91 × 1.23–5.01 neck: 2.07–6.65 × 2.40–5.37 trunk: 2.28–10.40 × 2.24–13.03	NA	head and neck: 3.0–5.0 trunk: 7.0–9.0	head: – neck: – trunk: NA	3.6–6.0 × NA	head and neck: 2.0–6.0 × NA trunk: 4.5–8.0 × NA	head and neck: 1.0–5.0 × NA trunk: 1.0–7.0 × NA	NA	NA
Alignment of scales	scales on the head and anterior neck region located far from another; on posterior neck and anterior trunk region located gradually closer but still at a distance to the other scales and not juxtaposed; scales on dorsolateral, lateral, ventrolateral and ventral trunk region located at a distance from the other scales, dorsal trunk scales and furcal appendages scales slightly overlap	scales located far from each other	scales located far from another but dorsally on posterior trunk region juxtaposed	head and neck naked, trunk scales located far from another	scales on the head located far from another; on neck and anterior trunk region located gradually closer and juxtaposed; trunk scales slightly overlap, furcal base scales juxtaposed and not overlap	head or head and neck entirely or partially naked; on remaining body parts scales located far from another	scales located far from another but dorsally on posterior trunk region located closer	body almost naked, scales if present located far from another	body almost naked, scales present only laterally on head, neck, trunk and dorsally and dorsolaterally on trunk centre
Number of scales with long spines	9	13	7	8	9	7–9	5	4–8	7–8

Table A6 (continued). Comparison of species most similar to *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov.

Character	*C.* (*H.*) *inaequabilis* sp. nov.	*C.* (*H.*) *enormis*	*C.* (*H.*) *schlitzensis*	*C.* (*H.*) *octonarius*	*C.* (*H.*) *novenarius*	*C.* (*H.*) *aemilianus*	*C.* (*H.*) *ferrarius*	*C.* (*H.*) *spinulosus*	*C.* (*H.*) *longispinosus*
Location of scales with long spines	dorsally, dorsolaterally and laterally on the trunk and furcal base; five scales dorsally at U47–U57, one pair dorsolaterally at U76–U83, one scaes dorsally at U76–U83, two pairs laterally at U71–U78 and U78–U84, schematic trunk scale arrangement: 5 + 2 + 2 +1	dorsally, dorsolaterally and laterally on the trunk and furcal base; scales arrangement in five alternating rows, schematic trunk scale arrangement: 3 + 4 + 2 +3 +1	dorsally on the trunk, schematic trunk scale arrangement: 2 + 1 + 2 +2	dorsally on the trunk, schematic trunk scale arrangement: 3 + 2 + 3	dorsally on anterior trunk region	dorsally on the trunk in various arrangements	dorsally on the trunk, schematic trunk scale arrangement: 3 + 2	dorsally on the trunk in various arrangements	dorsally and dorsolaterally on the trunk; scales arrangement in two alternating rows, schematic trunk scale arrangement: 3–4 + 4–5
Presence of a scales without or with rudimentary spines on the central dorsal trunk region	present	NA	present	present	present	present	present	present	absent
Presence of a different type of scales on the dorsal and dorsolateral surfaces of the furcal base and furcal appendages	present	NA	present	present	present	present	present	absent	absent
Scale coverage of the ventral interciliary field	entire ventral interciliary field covered with scales	NA	NA	ventral interciliary field naked	entire ventral interciliary field covered by scales	ventral interciliary field naked or covered by scales	covered from end of anterior dilatation of the pharynx to the furcal base	ventral interciliary field naked	ventral interciliary field naked
Type of scales on ventral interciliary field	anteriorly oval-shaped with straight posterior edge, keelless and spineless; posteriorly more elongated, keeled and spineless	NA	NA	–	one-lobed, rounded, keelless and spineless	scale if present, small, one-lobed, oval-shaped, keelless and spineless	one-lobed, rounded, keelless and spineless	–	–
Number of scales in central longitudinal row on the ventral interciliary field	21–25	NA	NA	–	40	7–10	*ca.* 32	–	–
Total number of longitudinal alternating rows of the ventral scales	7	NA	NA	–	4	NA	8–10	–	–

Table A6 (continued). Comparison of species most similar to *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov.

Character	*C.* (*H.*) *inaequabilis* sp. nov.	*C.* (*H.*) *enormis*	*C.* (*H.*) *schlitzensis*	*C.* (*H.*) *octonarius*	*C.* (*H.*) *novenarius*	*C.* (*H.*) *aemilianus*	*C.* (*H.*) *ferrarius*	*C.* (*H.*) *spinulosus*	*C.* (*H.*) *longispinosus*
Number of terminal scales on the ventral interciliary field	4 pairs	NA	NA	absent	1 pair	absent or 1 pair	1 pair	absent	absent
Type of terminal scales on the ventral interciliary field	I pair: elongated with narrowing in half of its length, keeled and spined; II pair: elongated, with the pointed anterior edge, gradually tapers to the posterior end, keeled and spineless; III and IV pairs: elongated, oval-shaped with shallow posterior notch, keeled and spineless	NA	NA	–	elongated, oval-shaped keeled and spined	NA	elongated, oval-shaped keeled and spineless	–	–
Spine length variation	anteriormost spines slightly longer than subsequent head spines; spine length and thickness increase gradually from head towards the widest body region; head, neck and anterior trunk spines length gradually decrease towards to the ventrolateral surface; ventral hair-like spines very long; dorsal and dorsolateral trunk spines very long, thick, rigid; distinctly longer and stronger than remaining spines	head and neck spines short, on lateral surface longer; trunk dorsal, dorsolateral and furcal base lateral spines very long, thick, rigid; distinctly longer and stronger than remaining spines	head and neck spines short, on lateral surface longer; trunk dorsal, spines very long, thick, rigid; distinctly longer and stronger than remaining spines	all spines similar in length	anteriormost spines longer than subsequent head spines; spine length and thickness increase gradually from head posterior region towards the anterior trunk region; anterior dorsal trunk spines very long, thick, rigid; distinctly longer and stronger than remaining spines; central and posterior trunk spines short or rudimentary; from lateral towards ventral surface spines much longer than dorsolateral spines	all spines short except 7–9 distincly longer and thicker dorsal trunk spines	head, neck and anterior trunk region spines short, on lateral surface longer; central trunk dorsal spines very long, thick, rigid; distinctly longer and stronger than remaining spines	all spines short except 4–8 distincly longer and thicker dorsal trunk spines	lateral spines short and thin, dorsal and dorsolateral trunk spines very long, the spines located in second alternating row ca two times longer than spine arrangement in first row
Spine length	head: 0.3–12.0 neck: 1.6–13.6 trunk: 3.1–15.2 long spines: 10.2–21.6	head and neck: 2.0–9.0 trunk: NA long spines: NA	head and neck: 2.0–9.0 trunk: NA long spines: 25.0–30.0	long spines: 24.0–26.0	head: 9.0 neck: NA trunk: 9.0–19.0 long spines: 60.0–85.0	head, neck, trunk: 1.8–5.0 long spines: 18.0–26.0	head, neck, trunk: 2.0–3.0 long spines: 11.0–35.0	long spines: 12.0–25.0	long spines: 20.0–90.0

Table A6 (continued). Comparison of species most similar to *Chaetonotus* (*Hystricochaetonotus*) *inaequabilis* sp. nov.

Character	*C.* (*H.*) *inaequabilis* sp. nov.	*C.* (*H.*) *enormis*	*C.* (*H.*) *schlitzensis*	*C.* (*H.*) *octonarius*	*C.* (*H.*) *novenarius*	*C.* (*H.*) *aemilianus*	*C.* (*H.*) *ferrarius*	*C.* (*H.*) *spinulosus*	*C.* (*H.*) *longispinosus*
Presence of hair-like spines on the ventral surface	present	NA	NA	absent	absent	absent	present	absent	absent
Presence of lamellae on ventral spines	present	NA	NA	absent	absent	absent	present	absent	absent
Presence and distinctness of lateral denticle on the spines	dorsal, dorsolateral and posteriormost trunk lateral spines have lateral denticle; lateral denticle on remaining spines absent	dorsal, dorsolateral and posteriormost trunk lateral spines have lateral denticle; lateral denticle on remaining spines absent	dorsal trunk lateral spines have lateral denticle; lateral denticle on remaining spines absent	dorsal trunk spines have lateral denticle; lateral denticle on remaining spines absent	single or double lateral denticle arranged in single file present only on long, anterior trunk dorsal spines; lateral denticle on remaining spines absent	dorsal trunk and lateral furcal base spines have lateral denticle; lateral denticle on remaining spines absent	long dorsal and lateral or all spines with lateral denticle	long dorsal spines with lateral denticle; lateral denticle on remaining spines absent	dorsal and dorsolateral trunk spines have distinct, strong lateral denticle; lateral denticle on lateral spines absent
Localization of lateral denticle on the spines	long spines: *8.780–17.959*	NA	NA	NA	NA	NA	NA	NA	NA
Type of posteriormost pair of trunk lateral spines	longer than the other lateral spines	longer than the other lateral spines	the same as other lateral spines	–	longer than other lateral spines	the same as or longer than other lateral spines	the same as other lateral spines	the same as or longer than other lateral spines	the same as or longer than other lateral spines
Length ratio of posteriormost trunk lateral spines	*11.094–12.923*	NA	NA	–	NA	NA	NA	NA	NA
Type of last pair lateral spines	–	–	–	–	–	–	–	–	–
Length ratio of posteriormost parafurcal lateral spines	–	–	–	–	–	–	–	–	–
Ventral locomotor cilia	two longitudinal bands wider on the head region	two longitudinal bands	two longitudinal bands	two longitudinal bands	two longitudinal bands	two longitudinal bands	two longitudinal bands	two longitudinal bands	two longitudinal bands
Number of dorsal sensory bristles	3 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs