Curculio Institute
WEEVIL *News* ISSN 1615-3472
WEEVIL *News* **1. April 2022** **No. 99**

Morphology, instar determination and larval biology of *Otiorhynchus* (*Otiorhynchus*) *coecus coecus* Germar, 1823 and pupal morphology of *O. (Nihus) carinatopunctatus* (Retzius, 1783) and *O.* (*Postaremus*) *nodosus* (O. F. Müller, 1764) from Central or Northern Europe (Coleoptera, Curculionidae, Entiminae)

by
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With **30** figures and **28** drawings on **15** plates

Manuscript received: 15. September 2021
Accepted: 20. March 2022
Internet (open access, PDF): 01. April 2022

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Abstract. The mature larva and pupa of *Otiorhynchus* (*Otiorhynchus*) *coecus coecus* Germar, 1823 are re-described and illustrated with full chaetotaxy. The pupae of *O.* (*Nihus*) *carinatopunctatus* (Retzius, 1783) and *O.* (*Postaremus*) *nodosus* (O. F. Müller, 1764) are described for the first time. In *O. coecus* a number of 6 larval instars was determined using an improved method initially based on Dyar's law. The life-cycle of *O. coecus coecus* is visualized. Finally, upgraded keys for selected mature *Otiorhynchus* larvae and pupae are given.

Keywords. Weevil, Curculionoidea, chaetotaxy, immature stages, bionomics, life-cycle, development, growth factor, European region, identification key.

Introduction

The present paper is a continuation of our studies focused on morphology and biology of developmental stages of soil–dwelling weevils with special regard to *Otiorhynchus* Germar, 1822 species (see Gosik & Sprick 2012a, 2012b, 2013 and Gosik et al. 2016). We deal in this contribution with three *Otiorhynchus* species, *O. coecus coecus* Germar, 1823 (syn. *O. niger* (Fabricius, 1775)), *O.* (*Postaremus*) *nodosus* (O.F. Müller, 1764) (syn. *O. dubius* Strøm, 1783) and *O.* (*Nihus*) *carinatopunctatus* (Retzius, 1783), long time known under the name of *O. scaber* (Linnaeus, 1758), of which the holotype had proved to belong to another genus, *Trachyphloeus* Germar, 1817, now *Romualdius* Borovec, 2009 (Borovec 2009; Alonso-Zarazaga et al. 2017). The aim of our paper was to describe the pupae of three and the larva of one species, to determine the number of larval instars, if possible, to explain the life-cycle of one species, and to provide keys to all immatures treated in this paper.

Otiorhynchus coecus coecus [**Fig 1A**] is a polyphagous bisexual species that prefers coniferous and especially spruce forests in the Alps and the Carpathians. It is widely distributed in the central parts of Europe, ranging to France in the West and to Lithuania, Poland, Bulgaria and Ukraine in the East (Alonso-Zarazaga et al. 2017). It is mainly found in the mountains. In Germany the lower mountain range is nearly completely inhabited, and there are also some scattered sites in the northern lowlands where it is found preferably in moor forests. Main host and food plant of *O. coecus* is Norway spruce (*Picea abies* (L.) H. Karst.), but in literature there are also data about use of other conifers (e.g., the introduced *Pseudotsuga menziesii* (Mirb.) Franc.), deciduous trees (mainly *Alnus glutinosa* (L.) Gaertn., and *Betula*), shrubs (*Rubus idaeus* L.), and dwarf shrubs (*Vaccinium myrtillus* L.). Occasionally it was observed on further tree genera such as *Abies, Acer, Carpinus, Fagus, Fraxinus, Pinus, Sorbus* and on herbaceous plants with well–developed rhizomes (*Cicerbita, Petasites*). It was found noxious in various young tree plantations (Dieckmann 1980; Hoffmann 1950; Koch 1992; Schindler 1958). Schindler (1958) stated that – in the Harz Mts –, if *Alnus glutinosa* or *Pseudotsuga menziesii* grew close to *Picea abies*, the adult weevils moved there indicating preference over *Picea*.

Fig. 1A–D. A, B: *Otiorhynchus coecus coecus*; C: *O. carinatopunctatus*; D: *O. nodosus* adults.

Biology and morphology of developmental stages were previously studied by some authors. Information about deposition and shape of eggs, the first and a middle larval instar were given by Van Emden (1950 and 1952). Descriptions of the mature larva and the pupa were published by Schindler (1958). Scherf (1964), the last author dealing with this topic, compiled all available data.

Otiorhynchus carinatopunctatus [**Fig. 1B**] is another polyphagous species that inhabits temperate and moderately cool climate zones. Its main occurrence may be in the boreal forests of Europe west of the Ural Mts., in the Pyrenees, the Alps, the Carpathians and north of them and in great parts of the northern Balkans. It inhabits mixed and coniferous forests of hillsides and mountains, and it is also present in wet deciduous forests of the lowlands; one time it was recorded from anthropogenic environments (botanical garden). It feeds mainly on young trees and bushes such as *Picea abies, Pinus sylvestris* L., *Corylus avellana* L., *Larix europaea* Mill., *Rosa, Rubus, Salix aurita* L., *S. cinerea* L., *Populus tremula* L., *Taxus baccata* L. and on perennial herbs, e.g. *Alchemilla, Potentilla reptans* L., *Rumex* and *Tussilago farfara* L. (Palm 1996 and own observations). *O. carinatopunctatus* was treated as a model species of parthenogenesis with diploid (bisexual), triploid and tetraploid populations (Suomalainen 1961, Saura et al. 1976, Stenberg et al. 2000, Stenberg et al. 2003). - All these species are absent from the Mediterranean zone with Iberian Peninsula, Italy south of the Alps and Greece. A description of the larva was given by Van Emden (1952), but without any collecting or breeding dates.

Otiorhynchus nodosus [**Fig. 1C**] is a polyphagous species that prefers cool climate conditions. It is present in great parts of Northern and Northwestern Europe including Iceland, Ireland, Faeroe Islands, Scandinavia, Northern Russia and Northwestern Siberia (Alonso-Zarazaga et al. 2017, Legalov 2010). It is also known to occur in Greenland (Szekessy 1936). In the central parts of Europe and on the Balkans the montane and alpine zones are inhabited. As it occurs in treeless areas in the North and in the high mountains, many perennial herbs are inhabited, such as *Dryas octopetala* L., *Rumex acetosa* L., *Saxifraga hirculus* L., *Trifolium repens* L., and, as in the previous species, the dwarf shrub *Vaccinium myrtillus* (Palm 1996). One time we found this species in the Bavarian Forest under *Maianthemum bifolium* (L.) F.W. Schmidt showing conspicuous feeding marks [**Figs 2A, B**], and a search revealed several adult specimens of this species.

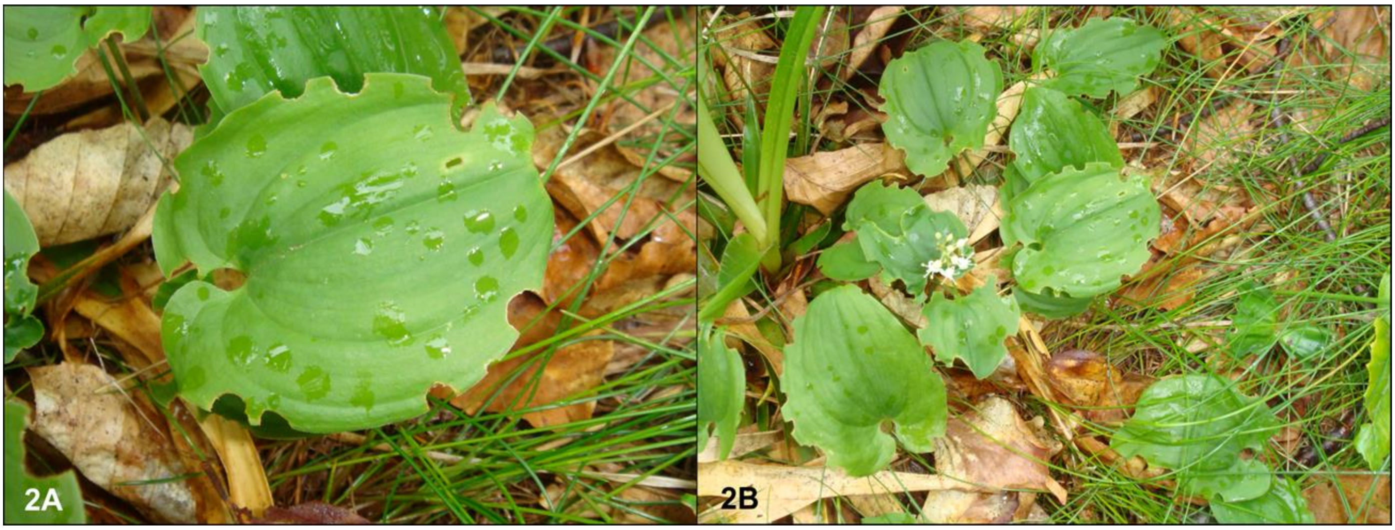

Fig. 2A, B. *Maianthemum bifolium* with feeding marks probably made by *Otiorhynchus nodosus* (several adults hidden below the plants).

O. nodosus has parthenogenetic tetraploid populations in the northern part of its range and a bisexual population in the southern parts (e.g. Alps, German low mountain areas) (Szekessy 1936). No information was found about presence and distribution of a triploid population. A description of the larva was given by Willis (1964: 200ff.), but without any information about the number of larval instars.

Fig. 3A–D. *Otiorhynchus coecus coecus*, field investigation. A: habitat of *O. coecus coecus* in the Harz Mountains; B: searching for immatures between the roots of *Vaccinium myrtillus*; C: pupa; D: adult on spruce.

4 Morphology of immatures, instar determination and biology of 3 *Otiorhynchus* species

Materials

Otiorhynchus coecus coecus [**Figs 3A–D**]

<u>Breeding conditions and origin of immatures</u>
Larvae and pupae used for description were reared and collected between the roots of young *Picea abies* plants and in soil under blueberries (*Vaccinium myrtillus*) bearing well developed feeding marks at the leaf margins. They were caused by the adult weevils collected previously and at the same time when digging for larvae (on *Picea* feeding marks were less conspicuous).

A breeding was carried out in the Julius–Kühn–Institut (JKI) in Braunschweig in a climate chamber (light 12 hours, temperature 18 ºC). In 2015, 9 adults (5 ♂, 4 ♀), collected in the National Park Harz, Niedersachsen, Riefensbeek, "Auf dem Acker" on 24.07.2015, were placed on 31.07.2015 in the JKI in 4 flowerpots with *Chaenomeles x superba* (Frahm) Rehder, *Corylus avellana*, *Prunus laurocerasus* L. 'Van Nes' and *Rubus idaeus* L.

In 2016, 9 adults (5 ♂, 4 ♀) were collected on 12.05.2016 in the National Park Harz, Niedersachsen, Torfhaus, Marienbruch, and they were placed in flowerpots with different plants in the JKI on 23.05.2016: two pots with *Acer platanoides* L., one with *Euonymus fortunei* (Turcz.) Hand.–Mazz. 'Emerald'n Gold', and one with *Thuja occidentalis* L. 'Smaragd'. Due to suffering plants the breeding in the first pot with *Acer platanoides* was terminated on 23.09.2016, and in the second on 03.11.2016; the remaining larvae were set in the flowerpot with *Euonymus fortunei*. To obtain L_1 larvae adults were kept in boxes in the lab in Hannover. Adults were previously collected also in the Harz Mountains.

<u>Reared specimens</u>
First instar larvae: 10 ex. were received on 05.07.2015, and 11 ex. on 04.07.2016.
Premature and mature larvae: 1 mature larva, 30.12.2015, flowerpot with *Prunus laurocerasus*; 4 premature and 2 mature larvae, 23.09.2016, from flowerpots with *Acer platanoides*; 2 mature larvae, 03.11.2016, 1 larva from flowerpot with *Acer platanoides* and 1 from flowerpot with *Euonymus fortunei*.
Pupae: 3 ex., 28.12.2016, from the flowerpot with *Euonymus fortunei* that contained also the larvae previously reared, until November, in the *Acer platanoides* flowerpot.

<u>Field–collected specimens</u>
Premature and mature larvae: 2 mature larvae, National Park Harz, Niedersachsen, Torfhaus, Marienbruch, *Picea abies* forest, 23.07.2015, between the roots of *Vaccinium myrtillus*; 7 larvae of different instars, National Park Harz, Niedersachsen, Torfhaus, Marienbruch, old causeway, from under young *Picea abies* bushes, 25.04.2018, leg. P. Sprick & A. Marten.

Otiorhynchus carinatopunctatus [**Figs 4A–D**]

<u>Field–collected specimens</u>
Pupae: 3 ex., *Vaccinia myrtillus*, National Park Harz, Niedersachsen, Sonnenkopf, 700 m, headwater region of Sieber river, 19.07.2018, leg. P. Sprick. In a pitfall trap placed at this site a light-coloured, newly emerged specimen was seen in the trap one day before, and for this reason digging for immature instars seemed promising. Extensive search for several hours revealed only 3 pupae but no larvae: apparently it was almost too late in the season.

Other *Otiorhynchus* species present at this site: *O. coecus coecus*, *O. fagi* Gyllenhal, 1834 (syn. *O. fuscipes* (Olivier, 1807)) and *O. lepidopterus* (Fabricius, 1794).

Otiorhynchus nodosus [**Figs 5A–D**]

<u>Field–collected specimens</u>
Pupae: **2** ex., National Park Harz, Niedersachsen, Kamschlacken: Auf dem Acker, 700 m, 24.07.2015, between the roots of *Vaccinium myrtillus*, leg. P. Sprick.
Other *Otiorhynchus* species present at this site: *O. carinatopunctatus*, *O. coecus coecus*.

Methods

Specimens collected in the field were fixed in 75% ethanol, and thereafter examined under an optical stereomicroscope (Nikon SMZ 1270, Olympus SZ 60 and SZ11). Measurements were made by using calibrated oculars. The following abbreviations were used for larvae: body length (BL), body width (BW) (in abdominal segment 2), and width of the head capsule (HW), and for pupae: body length (BL), body width (BW) (at the level of the middle leg pair) and width of the head (HW).

Fig. 4A–D. *Otiorhynchus carinatopunctatus*, field investigation, feeding and breeding. A: habitat of *O. carinatopunctatus* in the Harz Mountains; B: breeding attempt with *Taxus baccata*; C: feeding test with *Symphoricarpos x chenaultii* Rehder*, Geranium x cantabrigiense* Yeo, and *Deutzia scabra* Thunb. (one notch); D: eggs.

Drawings and outlines were made using a drawing tube (MNR–1) installed on a stereomicroscope (Ampliwal) and processed by computer software (Corel Photo–Paint X7, Corel Draw X7). Photos were taken with the Olympus camera E–M10. General terminology and chaetotaxy follow May (1994), Marvaldi (1997, 1998, 1999), and antennae terminology follows Zacharuk (1985). The nomenclature and taxonomic status of species under discussion based on Alonso-Zarazaga et al. (2017) and Przybycień et al. (2021). These specimens are deposited in the collection of Department of Zoology and Nature Protection, University of Maria Curie–Skłodowska (Lublin, Poland).

Results

Morphological descriptions of immature stages

Morphological abbreviations:
Abd. 1–10–abdominal segments 1–10, **Th. 1–3**–thoracic segments 1–3, **at**–antenna, **clss**–clypeal sensorium, **st**–stemmata, **Se**–sensorium, **sa**–sensillum ampullaceum, **sb**–sensillum basiconicum, **lr**–labral rods, **ur**–urogomphus; setae: ***als***–anterolateral, ***ams***–anteromedial, ***as***–alar (larva), ***as***–apical (pupa), ***cls***–clypeal, ***d***–dorsal (pupal abdomen), ***des***–dorsal (larval head), ***dms***–dorsal malar, ***ds***–discal (pupal prothorax), ***ds***–dorsal (larval abdomen), ***eps***–epipleural, ***es***–epistomal, ***eus***–eusternal, ***fes***–femoral, ***fs***–frontal, ***les***–lateral epicranial, ***ligs***–ligular, ***lrs***–labral, ***ls***–lateral, ***lsts***–laterosternal, ***mbs***–malar basiventral, ***mds***–mandibular, ***mes***–median, ***mps***–maxillary palp, ***os***–orbital, ***pas***–postantennal, ***pda***–pedal, ***pds***–postdorsal, ***pls***–posterolateral, ***pes***–postepicranial, ***pfs***–palpiferal, ***pms***–postlabial, ***prms***–prelabial, ***prns***–pronotal, ***prs***–prodorsal, ***ps***–pleural, ***rs***–rostral, ***sos***–superorbital, ***ss***–spiracular, ***stps***–stipal, ***sts***–sternal, ***ts***–terminal, ***v***–ventral (pupa), ***ves***–ventral (larva), ***vms***–ventral malar, ***vs***–vertical.

Fig. 5A–D. *Otiorhynchus nodosus*, field investigation. A–C: habitat of *O. nodosus* in the Harz Mountains; D: pupa.

Description of the mature larva of *Otiorhynchus coecus coecus*

First instar - head width: 0.375^{12}, 0.362^{1}, 0.350^{5}, 0.387^{1} mm
Medium instars - head width: 0.900^{1}, 1.150^{1}, 1.650^{4}, 1.340^{1} mm
Mature larva - head width: 1.950^{1}, 2.000^{3}, 2.050^{1}, 2.200^{1} mm
Body length: 9.3–10.2 mm, body width: 3.0–3.4 mm, head width: 1.95–2.20 mm.

Body [**Fig. 6A**] slender, slightly curved, rounded in cross section. Prothorax slightly smaller than mesothorax; metathorax as wide as mesothorax. Abdominal segments 1–6 of almost equal length; 7–9 decreasing gradually to the terminal parts of the body; 10 reduced to four anal lobes of almost equal size. Chaetotaxy well developed, setae capilliform, variable in length, dark yellow. Each side of prothorax with 9 *prns* of unequal length (six of them placed on premental sclerite, next three close to spiracle); 2 *ps* and 1 *eus*. Meso– and metathorax [**Figs 6B, C**] on each side with 1 moderately long *prs*, 4 *pds*, variable in length (first, second and fourth moderately, third long), 1 long *as*, 1 long *eps*, 1 *ps* and 1 *eus*. Each pedal area of thoracic segments with 6 *pda*, variable in length. Abd. 1–8 [**Figs 6B–F**] on each side with 1 moderately long *prs*, 5 *pds*, various in length (first and second short, third long, fourth very short, fifth long) and arranged along the posterior margin of each segment, 1 minute and 1 long *ss* (Abd. 8 without *ss*), 2 *eps* and 1 minute and 1 long *ps*, 1 *lsts* and 2 short *eus*. Abd. 9 [**Figs 6C, E, F**] on each side with 3*ds*, first and third moderately long, second very long, all located close to the posterior margin of the segment, 1 long *ps* and 2 short *sts*. Each lateral anal lobe (Abd. 10) with a pair of minute *ts*.

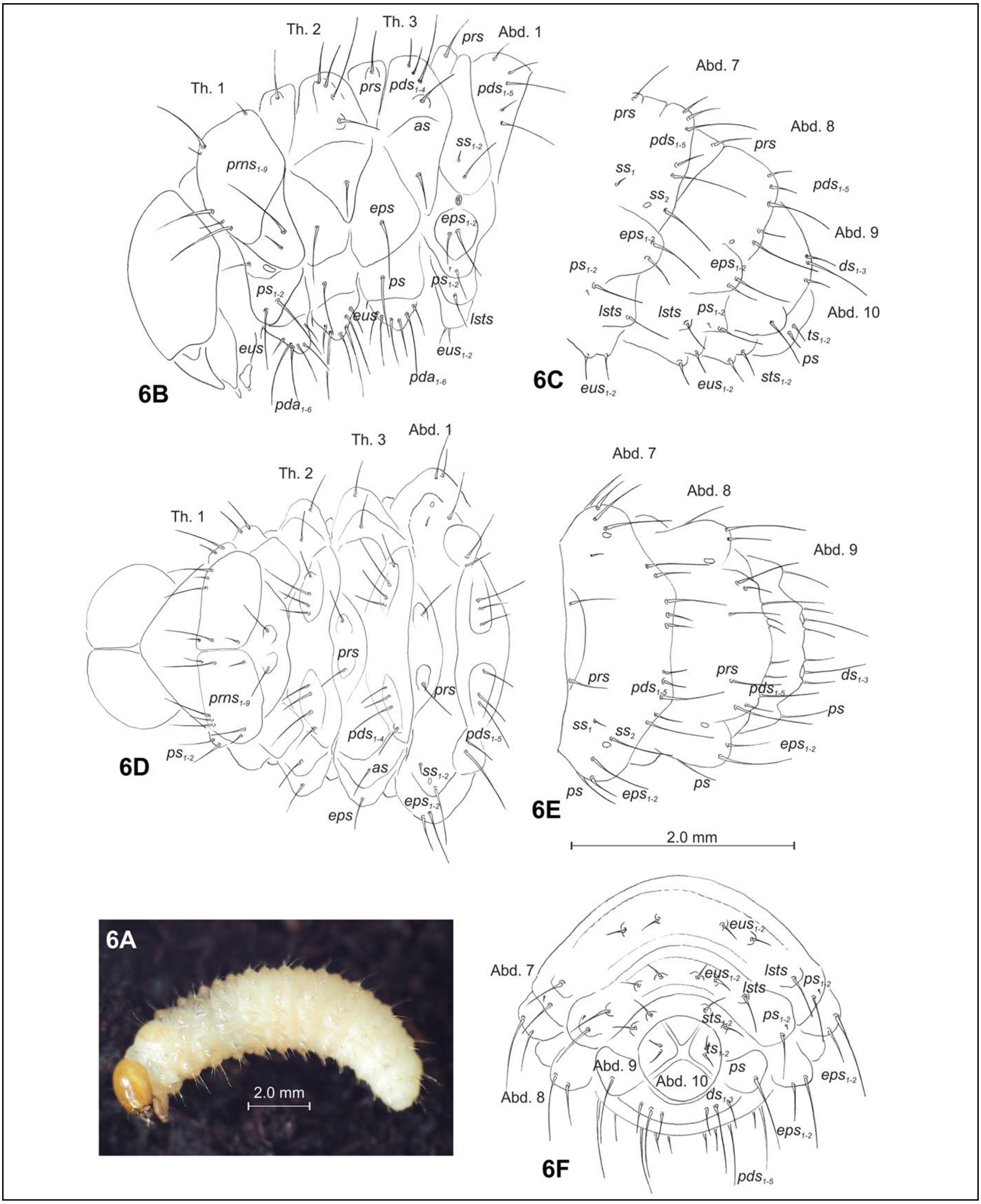

Fig. 6A–F. *Otiorhynchus coecus coecus,* mature larva, habitus and chaetotaxy. A: habitus; B: lateral view of thoracic segments and first abdominal segment; C: lateral view of abdominal segments 7–10; D: dorsal view of thoracic segments and first abdominal segment; E: dorsal view of abdominal segments 7–10; F: apical view of abdominal segments 7–10 (Th. 1–3–thoracic segments, Abd. 1–10–abdominal segments. Setae: *as*–alar, *ps*–pleural, *eps*–epipleural, *ds*–dorsal, *lsts*–laterosternal, *eus*–eusternal, *pda*–pedal, *pds*–postdorsal, *prns*–pronotal, *prs*–prodorsal, *ss*–spiracular, *sts*–sternal, *ts*–terminal).

Head [**Figs 7A, B**] light to dark yellow, suboval, frontal suture distinct, Y–shaped, endocarina absent. Setae on head capilliform. *Des*$_{1,\ 2,\ 3,\ 5}$ equal in length; *des*$_1$ and *des*$_2$ located in the central part of epicranium, *des*$_3$ placed on frontal suture, *des*$_5$ located anterolaterally; *des*$_4$ minute, located close to *des*$_5$. *Fs*$_{4,5}$ equal in length, *fs*$_4$ located anteromedially, *fs*$_5$ anterolaterally, close to epistoma. *Les*$_1$ and *les*$_2$ equal in length, slightly shorter than *des*$_1$. *Ves*$_{1,2}$ short, poorly developed. Postepicranial area with 2 very short *pes*. A pair of small stemmata (st) located anterolaterally on each side of the head. Antennae [**Fig. 8A**] located at the end of frontal suture; antennal segment membranous with cushion–like Se, located medially and with 5 sensilla of different types: 3 sa and 2 sb. Labrum [**Fig. 8B**] almost semicircular, anterior margin slightly sinuously emarginated; 3 pairs of *lrs*, various in length: *lrs*$_1$ long, *lrs*$_2$ very long, *lrs*$_3$ very short; *lrs*$_1$ placed medially, *lrs*$_2$ anteromedially, *lrs*$_3$ anterolaterally. Clypeus [**Fig. 8B**] trapezoid, anterior margin of clypeus straight; two pairs of *cls* reduced, vestigial, located posteromedially; clss clearly visible, placed medially between *cls*. Epipharynx [**Fig. 8C**] with 3 pairs of rod–shaped *als* of almost equal length; 3 pairs of *ams*: *ams*$_1$ and *ams*$_2$ rod–shaped, *ams*$_3$ capilliform; *ams*$_1$ very short, *ams*$_2$ and *ams*$_3$ a third the length of *als*; 2 pairs of rod–shaped *mes* of almost equal length: the first pair placed anteriorly, very close to *ams*, the second pair medially. Anterior margin of epipharynx smooth, medial part serrated due to the presence of thorn–like asperities placed between labral rods. Labral rods rather elongate, converging posteriorly. Mandibles [**Fig. 8D**] curved, moderately narrow, with divided apex (teeth of different length). There is a protruding additional tooth on the cutting edge between the apex and the middle of the mandible; both *mds* capilliform, various in length. Maxilla [**Figs 8F–H**] with 1 *stps* and 2 *pfs* of equal length; mala with 7 finger–like or capilliform *dms* of different size, 4 *vms* [**Figs 8G, H**]; *vms* shorter than *dms*; *mbs* short. Maxillary palpi with two palpomeres, basal with short *mps*; distal palpomere apically with a group of sensilla, each palpomere with a pore. Basal palpomere distinctly wider than distal, both of almost equal length. Praelabium [**Fig. 8F**] heart–shaped, with 1 long *prms*, located medially. Ligula with a pair of capilliform *ligs*. Premental sclerite clearly visible, trident–shaped. Labial palpi two–segmented; apex of distal palpomere with some sensilla; each palpomere with a pore. Basal palpomere slightly wider than distal, both of almost equal length. Postlabium [**Fig. 8F**] with 3 capilliform *pms*, the first pair located anteromedially, the remaining two pairs laterally; *pms*$_1$ and *pms*$_3$ very short, *pms*$_2$ distinctly longer than the others.

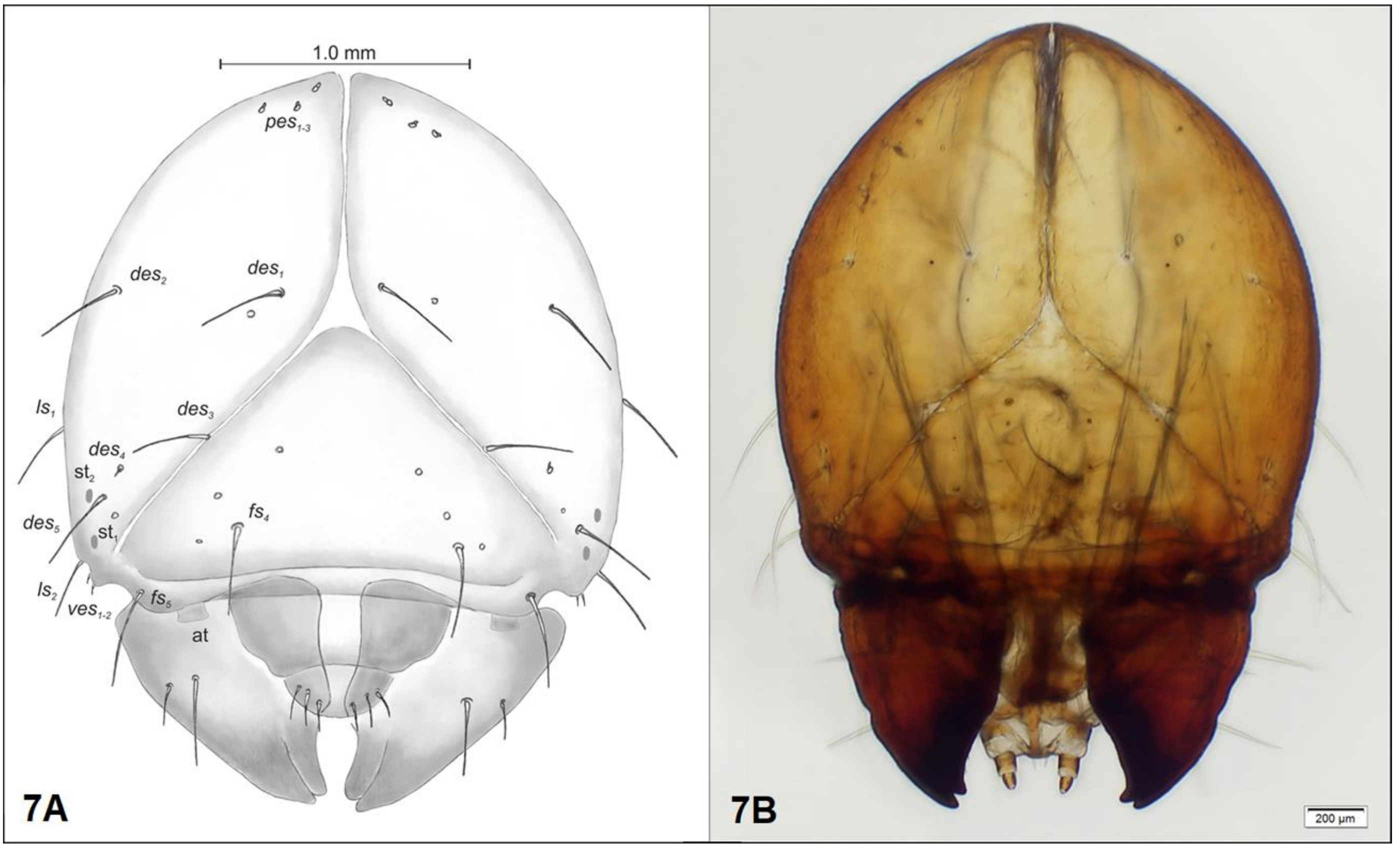

Fig 7A, B. *Otiorhynchus coecus coecus,* mature larva, head A: scheme; B: photo (at–antenna, st–stemmata. Setae: *des*–dorsal epicranial, *fs*–frontal, *les*–lateral epicranial, *pes*–postepicranial, *ves*–ventral).

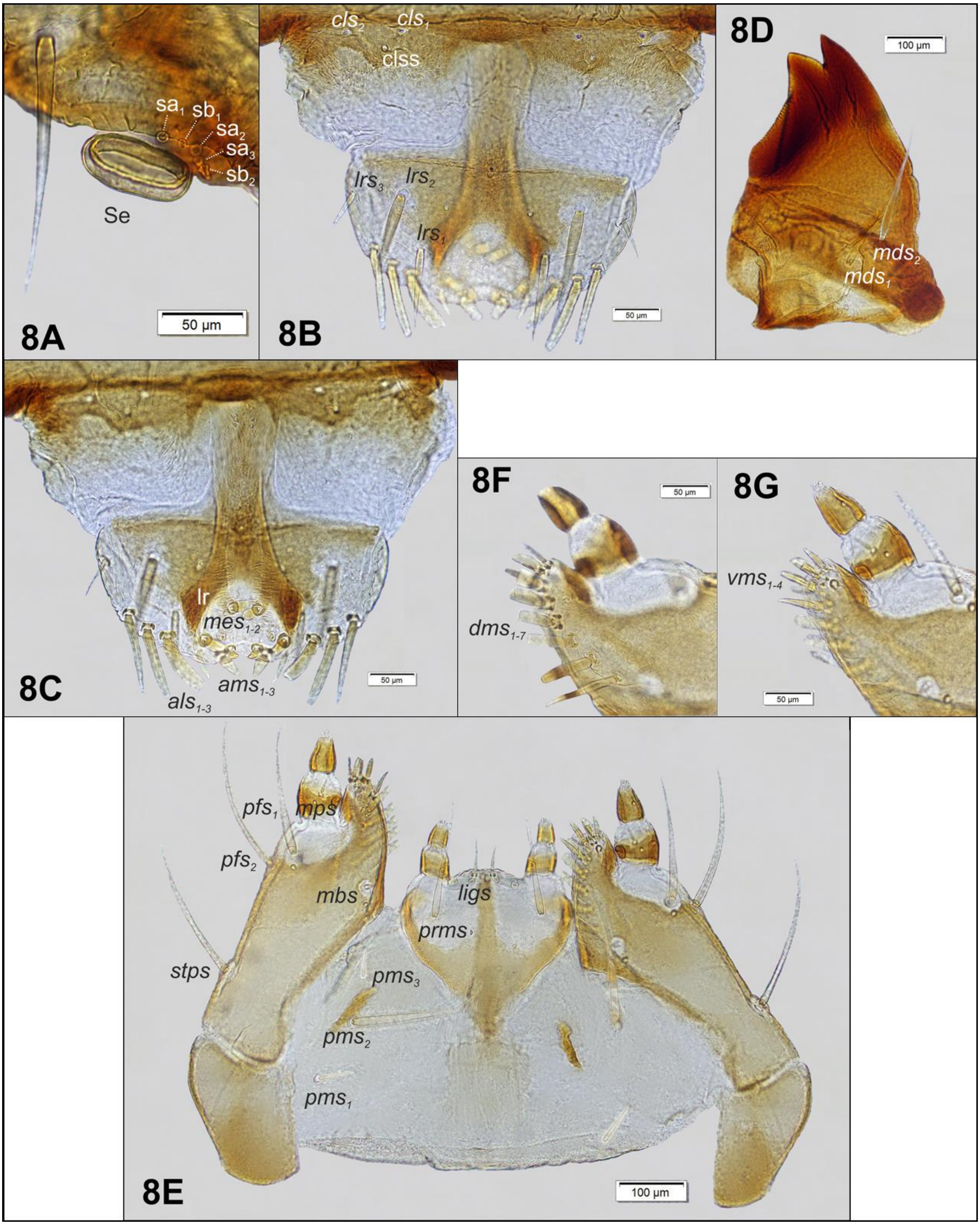

Fig 8A–G. *Otiorhynchus coecus coecus*, mature larva, body parts. A: right antenna; B: clypeus and labrum; C: epipharynx; D: right mandible; E–maxillolabial complex, ventral aspect; F: apical part of right maxilla, dorsal aspect; G: apical part of right maxilla, ventral aspect (clss–clypeal sensorium, lr–labral rods, Se–sensorium, sa–sensillum ampullaceum, sb–sensillum basiconicum. Setae: *als*–anterolateral, *ams*–anteromedial, *cls*–clypeal, *dms*–dorsal malar, *ligs*–ligular, *lrs*–labral, *mbs*–malar basiventral, *mds*–mandibular, *mes*–median, *mps*–maxillary palp, *pfs*–palpiferal, *prms*–prelabial, *pms*–postlabial, *stps*–stipal, *vms*–ventral malar).

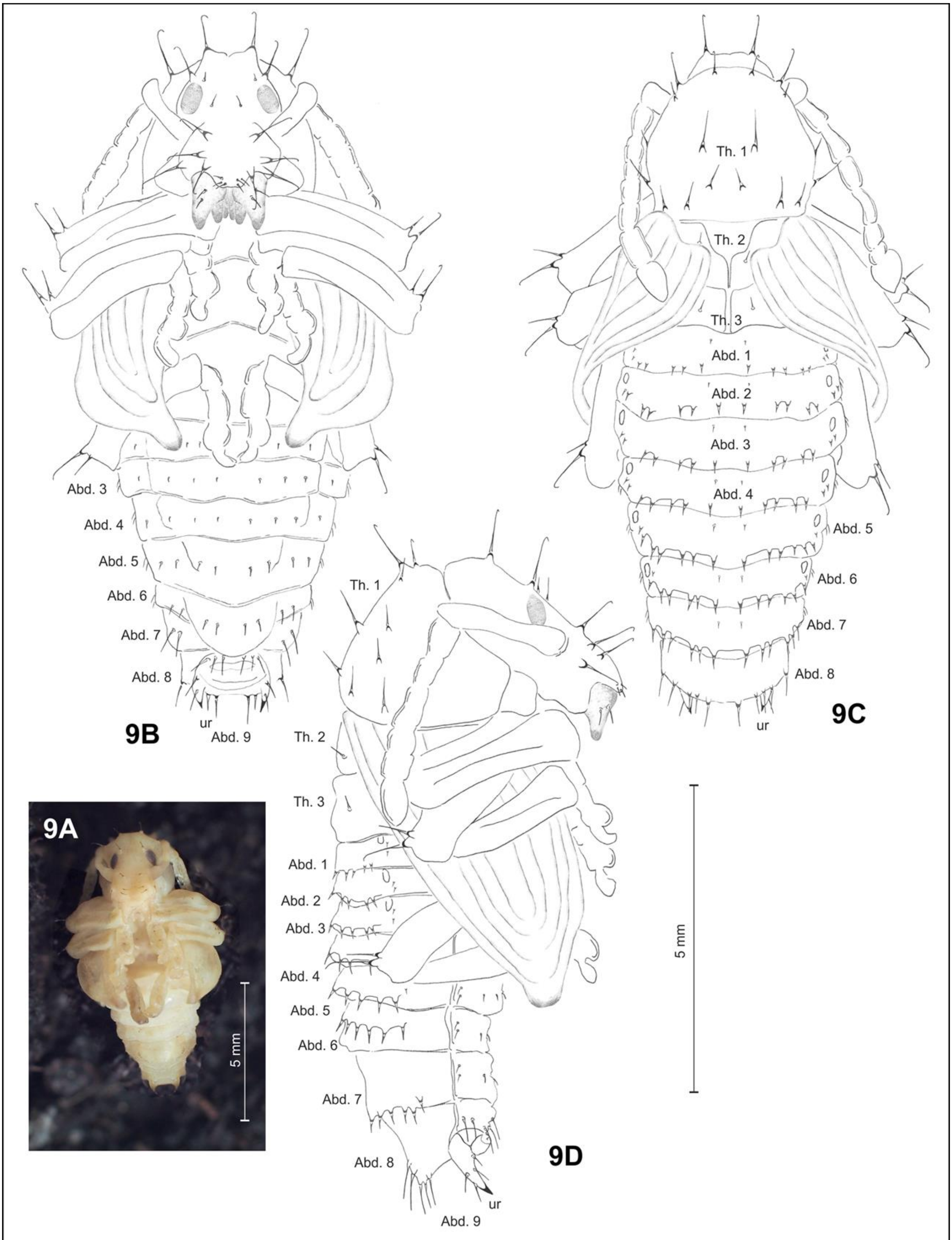

Fig. 9A–D. *Otiorhynchus coecus coecus*, pupa. A: habitus, ventral view; B: ventral view; C: dorsal view; D: lateral view (Th. 1–3–pro–, meso– and metathorax, Abd. 1–9–abdominal segments, ur–urogomphus).

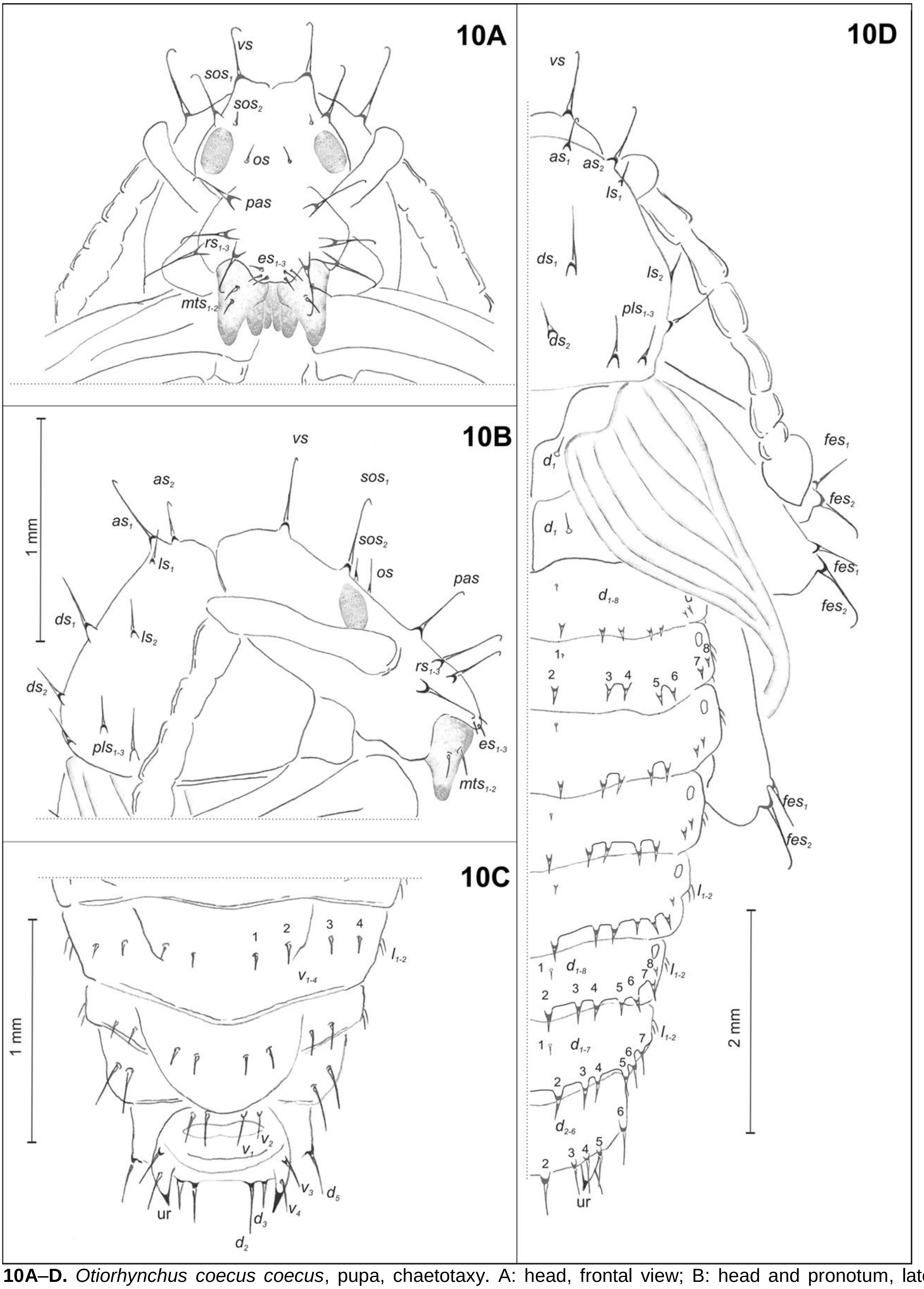

Fig. 10A–D. *Otiorhynchus coecus coecus*, pupa, chaetotaxy. A: head, frontal view; B: head and pronotum, lateral view; C: last abdominal segments, dorsal view; D: dorsal side (ur–urogomphus. Setae: *as*–apical, *d*–dorsal, *ds*–discal, *es*–epistomal, *fes*–femoral, *l, ls*–lateral, *mts*–mandibular theca, *os*–orbital, *pas*–postantennal, *pls*–posterolateral, *rs*–rostral, *sos*–superorbital, *v*–ventral, *vs*–vertical).

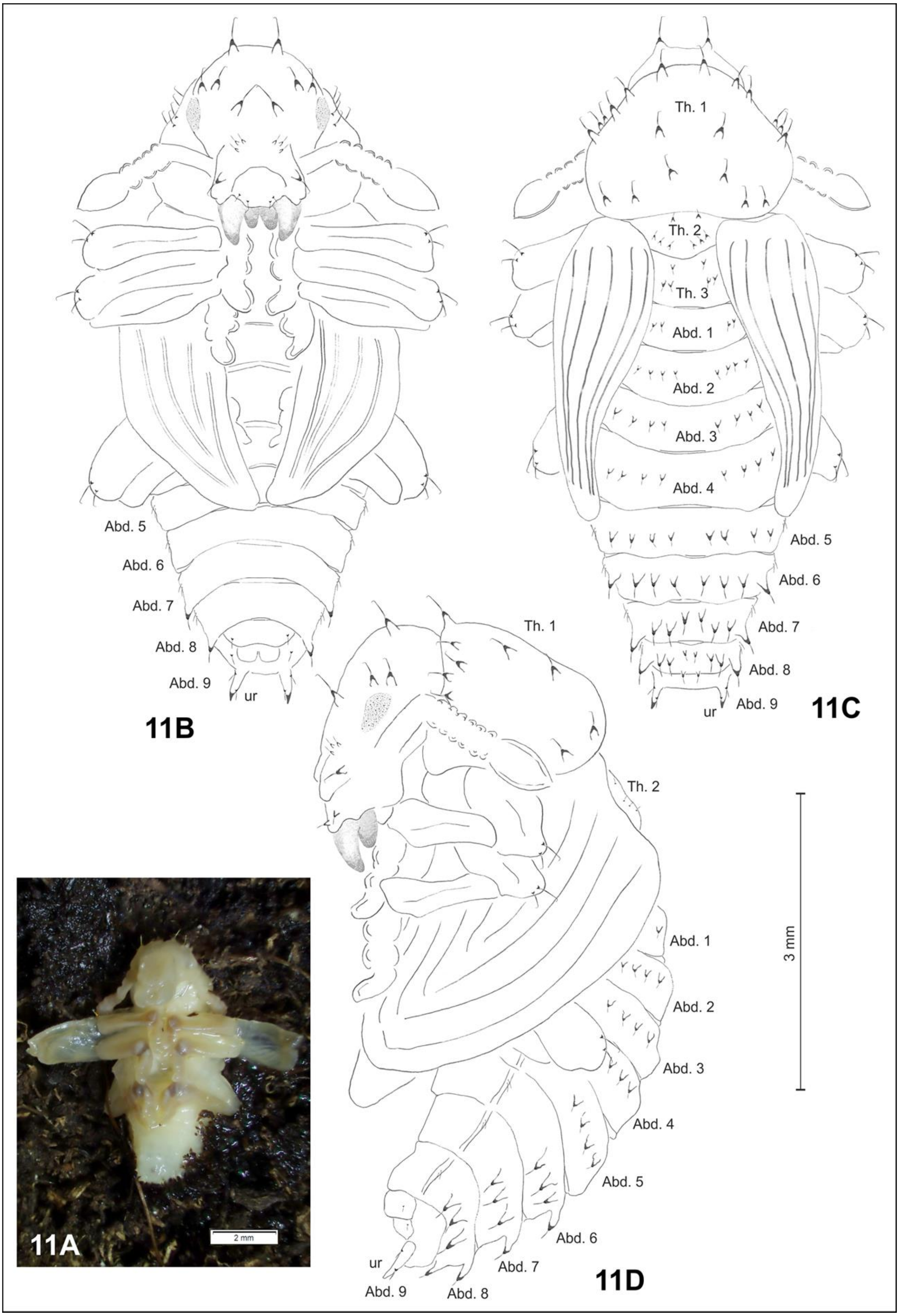

Fig. 11A–D. *Otiorhynchus carinatopunctatus*, pupa. A: habitus; B: ventral view; C: dorsal view; D: lateral view (Th. 1–3–pro–, meso– and metathorax, Abd. 1–9–abdominal segments, ur–urogomphus).

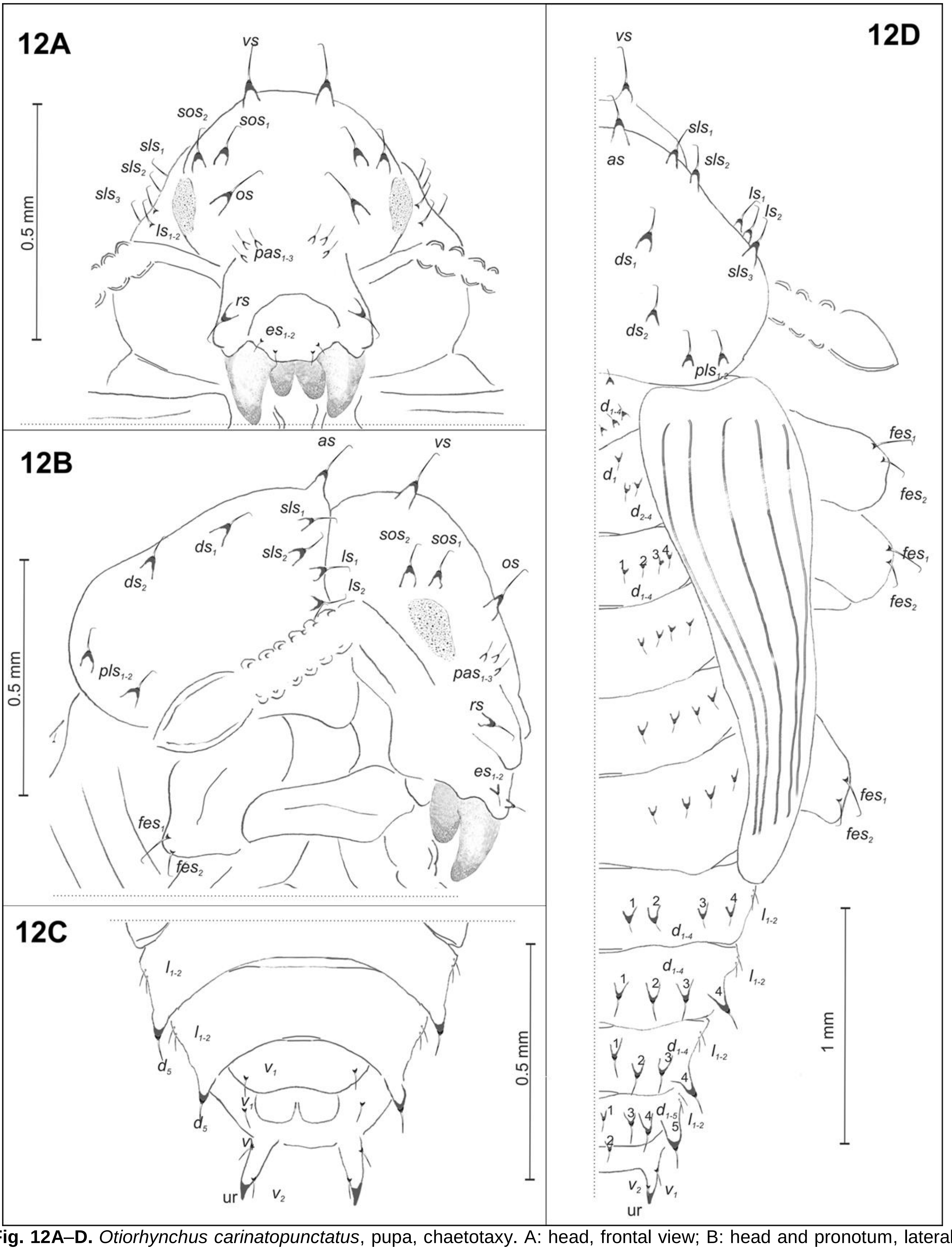

Fig. 12A–D. *Otiorhynchus carinatopunctatus*, pupa, chaetotaxy. A: head, frontal view; B: head and pronotum, lateral view; C: last abdominal segments, dorsal view; D: dorsal side (ur–urogomphus. Setae: *as*–apical, *d*–dorsal, *ds*–discal, *es*–epistomal, *fes*–femoral, *l, ls*–lateral, *os*–orbital, *pas*–postantennal, *pls*–posterolateral, *rs*–rostral, *sos*–superorbital, *v*–ventral, *vs*–vertical).

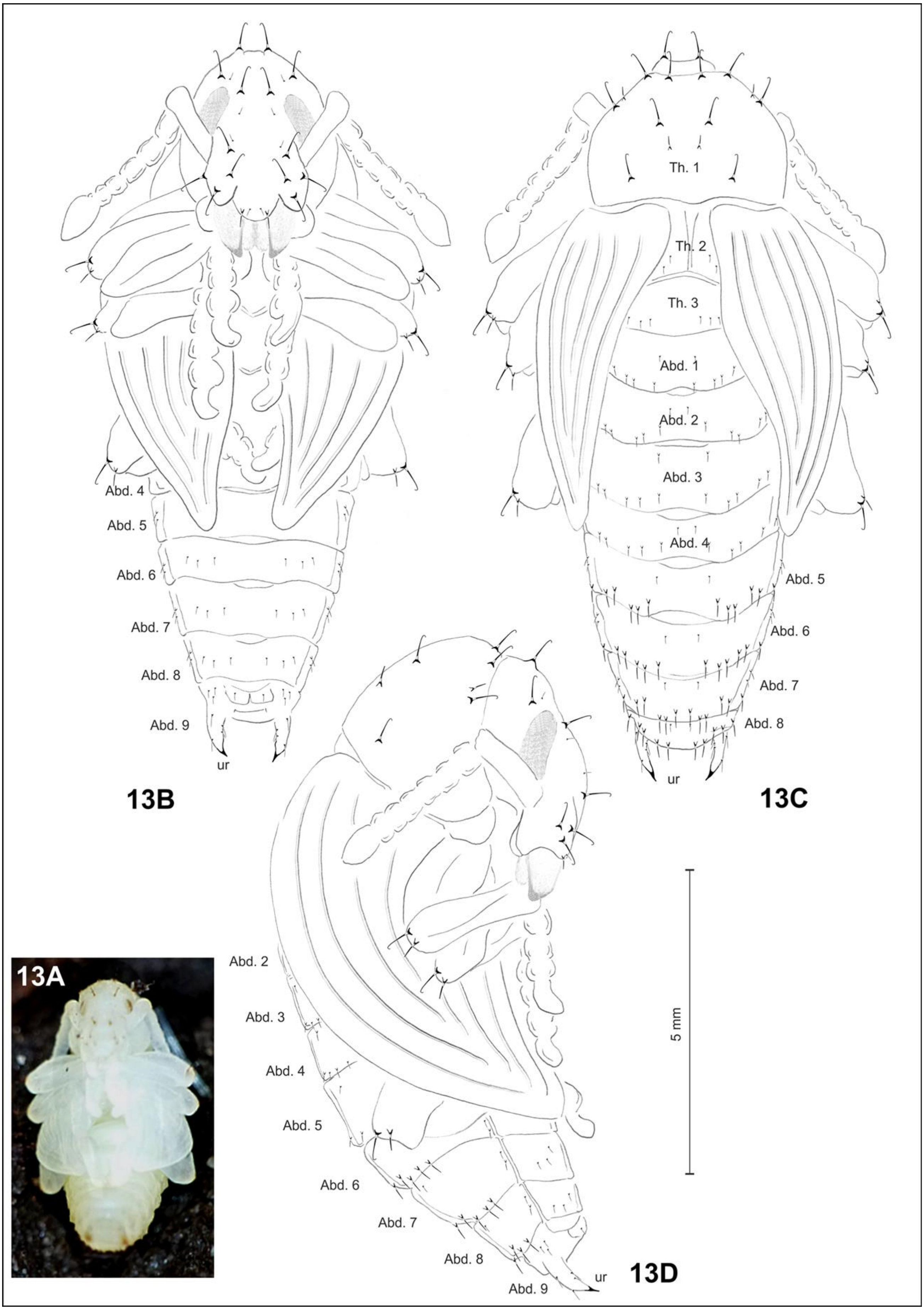

Fig. 13A–D. *Otiorhynchus nodosus*, pupa. A: habitus; B: ventral view; C: dorsal view; D: lateral view (Th. 1–3–pro–, meso– and metathorax, Abd. 1–9–abdominal segments, ur–urogomphus).

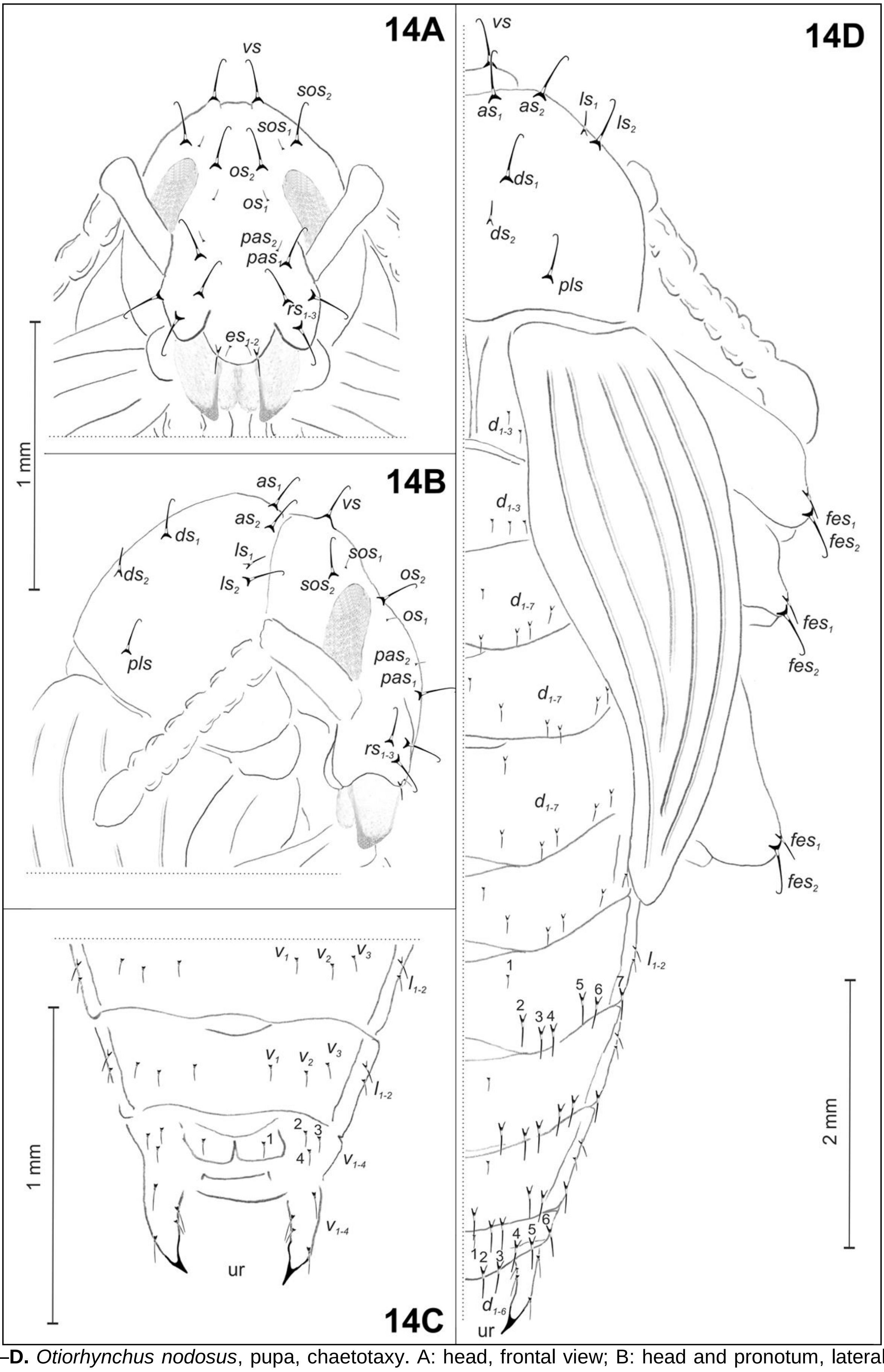

Fig. 14A–D. *Otiorhynchus nodosus*, pupa, chaetotaxy. A: head, frontal view; B: head and pronotum, lateral view; C: last abdominal segments, dorsal view; D: dorsal side (ur–urogomphus. Setae: *as*–apical, *d*–dorsal, *ds*–discal, *es*–epistomal, *fes*–femoral, *l, ls*–lateral, *os*–orbital, *pas*–postantennal, *pls*–posterolateral, *rs*–rostral, *sos*–superorbital, *v*–ventral, *vs*–vertical).

Description of the pupa of *Otiorhynchus coecus coecus*

Measuring data of the three described pupae - Body length: 7.0; 7.7; 8.7 mm; body width: 6.1; 6.2; 6.5 mm; thorax width: 2.3; 2.6; 2.7 mm; head width: 1.80; 1.80; 2.00 mm.

Body rather slender, straight, whitish [**Fig. 9A**]. Cuticle smooth. Rostrum short, 1.2 times as long as wide, extended beyond procoxae. Antennae long and slender. Pronotum almost 1.1 times as wide as long. Abdominal segments 1–4 of almost equal length, segments 5–7 decreasing gradually, 8 semicircular, 9 distinctly smaller than previous segments. Urogomphi moderately long, conical, with sclerotized apical parts [**Figs 9B–D**].

Chaetotaxy well developed, setae various in length and shape: on head, rostrum and thorax capilliform, straight or with a curved apical part; on dorsal parts of abdominal segments capilliform or spine–like. Setae yellowish to brownish, usually located on visible protuberances. Head capsule and rostrum with: 1 *vs*, 2 *sos*, 1 *os*, 1 *pas*, 3 *rs*, and 3 *es*. *Vs*, sos_1, *pas* and $rs_{1–3}$ long, with curved apical parts, placed on protuberances. Sos_2, *os* and *es* very short, straight. Each of mandibular thecae with a pair of short, straight *mts* [**Fig. 10A**]. Pronotum with 2 *as*, 2 *ls*, 2 *ds* and 3 *pls*. $As_{1–2}$ long, with curved apical parts, $ds_{1–2}$ and $pls_{1–3}$ long, straight, $ls_{1–2}$ moderately long, straight [**Fig. 10B**].
Each meso– and metathorax with 1 moderately long seta. Abdominal segments 1–6 with 8 pairs of spine–like $ds_{1–8}$ (first very short, located anteromedially, second to sixth moderately, placed along posterior margin, seventh and eighth, short, to very short located below stemmata), 2 short $ls_{1–2}$ and 4 short $vs_{1–4}$. Segment 7 with 7 $ds_{1–7}$ spine–like (first very short, located anteromedially, next 6 pairs elongate, placed posteriorly), 2 short $ls_{1–2}$ and short 4 $vs_{1–4}$. Segment 8 with 5 capilliform, elongate $ds_{2–6}$, placed along posterior margin, 2 short $ls_{1–2}$ and 4 short $vs_{1–4}$. Segment 9 with 4 pairs of moderately long, capilliform $vs_{1–4}$ [**Fig. 10C**]. Each apex of femorae with 2 *fes*: fes_1 moderately long, straight, fes_2 long with curved apical part [**Fig. 10D**].

Description of the pupa of *Otiorhynchus carinatopunctatus*

Measuring data of the described female pupae - Body length: 4.5; 6.0 mm; body width: 3.3; 3.5 mm; thorax width: 1.8, 2.0 mm; head width: 1.0 mm, 1.05 mm.

Body rather slender, slightly curved, whitish [**Fig. 11A**]. Cuticle smooth. Rostrum short, 1.4 times as long as wide, extended to procoxae. Antennae moderately elongate. Pronotum almost 1.5 times as wide as long. Abdominal segments 1–4 of almost equal length, segments 5–7 decreasing gradually, 8 semicircular, 9 narrow, distinctly smaller than previous segments. Urogomphi short, conical, with sharp, sclerotized apical parts [**Figs 11B–D**].

Chaetotaxy well developed, setae various in length, capilliform, straight or with curved apex. Setae yellow or brown, usually located on prominent protuberances. Head capsule and rostrum [**Fig. 12A**] include 1 *vs*, 2 *sos*, 1 *os*, 3 *pas,* 1 *rs* and 2 *es*. *Vs*, $sos_{1,2}$, *os* and *rs* elongate, with curved apical parts, placed on protuberances. *Pas* and *es* very short, straight. Pronotum [**Fig. 12B**] with 1 *as*, 3 *sls*, 2 *ls*, 2 *ds* and 2*pls*. All pronotal setae elongate, with curved apical parts, placed on protuberances, of almost the same size.

Meso– and metathorax each with four small setae. Dorsal parts of abdominal segments 1–4 with four small, straight setae placed in line in the middle of each segment; segments 5–7 with four elongate, thorn–like setae, placed on distinct protuberances; segment 8 with five setae, d_1 and d_2 of medium length, $d_{3–5}$ prominent, thorn–like, placed on distinct protuberances; segment 9 with 4 pairs of setae: the first placed on gonothecae, the next on urogomphi. Each of abdominal segments 1–8 with 2 small $l_{1–2}$; ventral parts without setae [**Fig. 12C**]. Each apex of femorae with 2 *fes*; fes_1 elongate, fes_2 medium-sized, both with curved apical part [**Fig. 12D**].

Description of the pupa of *Otiorhynchus nodosus*

Measuring data of the two described female pupae - Body length: 7.1 mm, 7.5 mm; body width: 4.0 mm, 4.2 mm; thorax width: 2.0 mm, 2.1 mm; hHead width: 1.1 mm, 1.2 mm.

Body rather slender, slightly curved, whitish [**Fig. 13A**]. Cuticle smooth. Rostrum short, 1.2 times as long as wide, extended beyond procoxae. Antennae very long and slender. Pronotum almost 1.7 times as wide as long. Abdominal segments 1–5 of almost equal length, segments 6–7 decreasing gradually, 8 and 9 distinctly smaller than previous segments. Urogomphi moderately long, conical, with pointed sclerotized apical parts [**Figs 13B-D**].

Chaetotaxy well developed, setae various in length and shape: on head, rostrum and thorax capilliform, straight or with a curved apical part; on dorsal parts of abdominal segments capilliform or spine–like. Setae yellowish to brownish, usually located on visible protuberances. Head capsule and rostrum with: 1 *vs*, 2 *sos*, 2 *os*, 2 *pas*, 3 *rs*, and 2 *es*. *Vs*, sos_2, os_2, pas_1 and $rs_{1–3}$ long, with curved apical parts, placed on protuberances. Sos_1, os_1, pas_2 and es_{1-2} very short, straight [**Fig. 14A**]. Pronotum with 2 *as*, 2 *ls*, 2 *ds* and 1 *pls*. $As_{1–2}$, ls_2, ds_1 and *pls* long, with curved apical parts, ds_2 and ls_1 short, straight [**Fig. 14B**].

Each meso– and metathorax with 3 minute setae. Abdominal segments 1–4 with 7 pairs of minute $ds_{1–7}$ (first located anteromedially, second to sixth moderately, placed along posterior margin, seventh located below stemmata) and 2 minute $ls_{1–2}$. Abdominal segments 5–7 with 7 pairs of $ds_{1–7}$, various in size (first very short, located anteromedially, second to sixth capilliform, placed along posterior margin, seventh capilliform, located below stemmata), 2 minute $ls_{1–2}$ and 3 short $vs_{1–3}$. Segment 8 with 6 setae, various in size (first very short, located anteromedially, second to fifth capilliform, placed along posterior margin), 2 short $ls_{1–2}$ and 3 short $vs_{1–3}$. Segment 9 with 4 pairs of minute $vs_{1–3}$ [**Fig. 14C**]. Each apex of femorae with 2 *fes*: fes_1 moderately long, straight, fes_2 long, with curved apical part [**Fig. 14D**].

Results and Discussion

Addendum to the key to larvae of selected *Otiorhynchus* species of Gosik et al. (2016)

(previous steps as in the original key)

5. Pds_1 and pds_2 on metathorax equal in length. Meso– and metathorax with 2 *as*. Body greyish to brown, cuticle especially on dorsal part covered with triangular cuticular processes and more pigmented than on lateral and ventral parts. Head dark brown, almost rounded. Surfaces of labrum densely covered by thorn–like cuticular processes …….. ………........……….................……….. ***O.* (*Choilisanus*) *raucus* (Fabricius, 1777)**
– Pds_1 on metathorax distinctly longer than pds_2. Meso– and metathorax with 1 *as*. Body white to yellowish, asperities very fine. Head light yellow to brownish. Surface of labrum smooth …………..**5a, b**
5a. Pds_1 on metathorax three times longer than pds_2; pds_2 distinctly shorter than pds_4. Body white to yellowish, asperities very fine. Head without des_4, light yellow, distinctly narrowed bilaterally …………………………………………… …………………...…………………...***O.* (*Pendragon*) *ovatus* (Linnaeus, 1758)**
5b. Pds_1 on metathorax twice as long as than pds_2; pds_2 as long as pds_4. Body yellowish, cuticle smooth. Head with two minute setae (des_{4a} and des_{4b}); yellow, slightly narrowed bilaterally……………………………………………….…….. ………………………………………………………………………………***O. (Podoropelmus) rotundus* Marseul, 1872**

(next steps in the original key)

11. Lms_2 (lrs_2) slightly to clearly longer (maximum 1.33 times) than *lms1* (lrs_1) and lms_3 (lrs_3) ……..**12**
– Lrs_2 twice as long as lrs_1 and lrs_3..**11a, b**
11a. Head without des_4. Clypeus with 1 *cls* only; mala with 4 *dms*. Abd. 8 with one minute ss_1. Lateral anal lobes with 1 *ts* each...***O.* (*Otiorhynchus*) *aurifer* Boheman, 1843**
11b. Head with one minute des_4. Clypeus with 2 *cls*; mala with 7 *dms*. Abd. 8 without *ss*. Lateral anal lobes with 2 *ts* each...***O.* (*Otiorhynchus*) *coecus coecus* Germar, 1823**

Updated key to pupae of selected *Otiorhynchus* species of Gosik & Sprick (2012b)

1. Both pairs of apical setae (as_1 and as_2) of almost the same length……………….......................................…**2**
– Apical seta (as_1) less than a third the length of as_2 or absent...**10**
2. Setae on rostrum and abdomen well visible...**3**
– Rostrum, mouthparts and abdomen without setae……………….............***O.* (*Crataegodes*) *crataegi* Germar, 1824**
3. Rostrum with 1**–**2 pairs of setae...**4**
– Rostrum with 3 pairs of setae……………………………………………....……………………………………..**8**
4. Rostrum with 1 pair of *rs* and 3 pairs of minute *pas* …...***Otiorhynchus* (*Nihus*) *carinatopunctatus* (Retzius, 1783)**
– Rostrum with 2 pair of *rs* and 1 pair of elongated *pas*……………….……………………………..……..…….**5**
5. Abdominal segments 1–4 dorsally with setae …………………………………………………………..……..…**6**
– Abdominal segments 1–4 dorsally without setae ……………………………………………………...…..…..…**7**
6. Abdominal segments 1–4 dorsally with 2 pairs of setae; body length under 5 mm…………………………………… ....***O.* (*Pendragon*) *ovatus* (Linnaeus, 1758)**

– Abdominal segments 1–4 dorsally with 5 pairs of setae; body length over 6 mm………………………………………… ………………………………………..……***O.*** **(*Zustalestus*)** ***rugosostriatus*** **(Goeze, 1777)**
7. Head with 2 *sos*. Pronotum with 3 *ls*, 2 *ds*, without *sls* ………… ***O.*** **(*Podoropelmus*)** ***smreczynskii*** **Cmoluch, 1968**
– Head with 1 *sos*. Pronotum with 1 *ls*, 1 *ds*, and 1 *sls* …………………..***O.*** **(*Podoropelmus*)** ***rotundus*** **Marseul, 1872**
8. All rostral setae (*rs*) equal in size; body length over 7.0 mm…………………………………………...…………….**9**
– *Rs_3* distinctly smaller than *rs_1* and *rs_2*; body length below 6.5 mm; ………. ***O.*** **(*Lolatismus*)** ***porcatus*** **(Herbst, 1795)**
9. Orbital setae (*os*) a third the length of *vs* or absent; pronotum with 2 *pls*; body length (usually) over 9 mm ………… ……………...***O.*** **(*Dorymerus*)** ***sulcatus*** **(Fabricius, 1775)**
– Orbital setae (*os*) present, *os_1* as long as *vs*; pronotum with 1 *pls*; body length up to 7.0 mm ………………………….. …………………………………………………………………………......***O.*** **(*Postaremus*)** ***nodosus*** **(O. F. Müller, 1764)**
10. Urogomphi strongly curved outwards...***O.*** **(*Otiorhynchus*)** ***aurifer*** **Boheman, 1843**
– Urogomphi curved inwards...**11**
11. Each abdominal segment (VII, VIII) with 6 pairs of almost equal length, dorsal setae distributed along the posterior margin...**12**
– Each abdominal segment (VII, VIII) with 5 pairs of almost equal length, dorsal setae distributed along the posterior margin...**13**
12. *Os* elongated, with curved apical part; rostrum with 2 pairs of *es*; *as_1* less than a third the length of *as_2*; *ds_2* and *pls_3* absent; meso– and metathorax without seta.. ....***O.*** **(*Otiorhynchus*)** ***pseudonothus*** **Apfelbeck, 1897 (= *O. salicicola* Heyden, 1908)**
– *Os* short, straight; rostrum with 3 pairs of *es*; *as_1* half the length of *as_2*; *ds_2* and *pls_3* present; meso– and metathorax each with 1 pair of setae ……………………………………………… ***O.*** **(*Otiorhynchus*)** ***coecus coecus*** **Germar, 1823**
13. Pronotum with 1 *as*, 1 *ds* and 1 *pls*. Ocelli almost oval ……………… ***O.*** **(*Otiorhynchus*)** ***armadillo*** **(Rossi, 1792)**
– Pronotum with 2 *as*, 2 *ds* and 2 *pls*. Ocelli narrow, reniform …….. ***O.*** **(*Otiorhynchus*)** ***meridionalis*** **Gyllenhal, 1834**

Sex determination in the pupal stage of weevils

Sex determination of weevil pupae is based on the following set of characters (Park 1934; Thomas 1965; Korman & Oseto 1984; Shukla & Palli 2012). First of all, pupae (unlike the larvae) possess many features present in the adult stage, too. So in the case of species with distinct sexual dimorphism, sex determination in the pupal stage can be based partially on the same features as in the adult stage (e.g., relative length of rostrum or [relative] body size) (Burke 1968). In all other cases sex determination of pupae relies on shape of gonothecae (Anderson 1968; Gosik & Skuhrovec 2011; Gosik & Sprick 2012b; Gosik & Wanat 2014). It seems to be a universal principle in weevils and in all other described beetles that gonothecae of males are undivided but divided in females (Hopkins 1909; Reinecke 1981). This character is generally well visible and easy to detect. On the other hand sex differences of shape of urogomphi or chaetotaxy are rather almost absent, invisible or show at most feeble differences.

Larval instar determination

With the method of Leibee et al. (1980), based on Dyar (1890), adapted by Sprick & Gosik (2014) in *Mitoplinthus* Reitter, 1897 and refined by Gosik et al. (2019), it is possible to determine the number of larval instars of soil–dwelling weevils, if the head widths of the first and the last larval instar of a certain species are known. We used it to check the unusual data of Schindler (1958), who reported about three larval instars in *Otiorhynchus coecus*. According to literature data concerning other *Otiorhynchus* species this is a questionable statement, as Palm (1935) for *O. ligustici*, or La Lone & Clarke (1981) for *O. sulcatus* reported about 6 or 7 larval instars in these similar-sized species. In *O. carinatopunctatus* there are a few data from earlier studies (Sprick & Stüben 2012) to make a first effort. Only in *O. nodosus* no data were available.

Otiorhynchus carinatopunctatus

There are only very few data of preimmature specimens with available head width data: a few photos made during the soil-dwelling project (Sprick & Stüben 2012) of some black spherical eggs and of 2 L_1 larvae on graph paper. From this we could determine the diameter of the eggs by around 0.44 mm and the head width of two L_1 larvae by 0.26 mm and around 0.24 mm (rather blurry part of the photo). The head width of three adults was measured by 0.9, 0.925 and 0.95 mm, and Van Emden (1952) stated the average head width of 4 full-sized larvae with around 1.06 mm. These scattered data allow at least a preliminary larval instar and Growth Factor determination (Table 1).

Table 1. Data for instar determination in *Otiorhynchus carinatopunctatus*

GF: Growth Factor, L_1, L_2, … larval instars, italics: hypothetical (calculated) values; best approximation bold.

GF	**1.44**	**1.43**	**1.42**	**1.41**	**1.40**	**1.39**
L_1	0.25	**0.25**	0.25	0.25	0.25	0.25
L_2	*0.360*	***0.358***	*0.355*	*0.353*	*0.350*	*0.348*
L_3	*0.518*	***0.511***	*0.504*	*0.497*	*0.490*	*0.483*
L_4	*0.746*	***0.731***	*0.716*	*0.701*	*0.686*	*0.671*
L_5	*1.075*	***1.045***	*1.016*	*0.989*	*0.960*	*0.933*
Mature larva*	1.06	**1.06**	1.06	1.06	1.06	1.06
Pupa*	1.025	1.025	1.025	1.025	1.025	1.025
Adult*	0.925	0.925	0.925	0.925	0.925	0.925

*: Mean values of 4 mature larvae (Van Emden 1952), 2 pupae and 3 adult specimens (own data).

From Table 1 it can be concluded that there are **five** larval instars and that the Growth Factor is around **1.43**.

Otiorhynchus coecus coecus

To determine the number of larval instars in *O. coecus*, we measured the head width of L_1 and of mature larvae and used published data from other sources (Table 2). The fully developed eggs of this species are shining black (Schindler 1958).

Table 2: Data available for larval instar determination

Data of mean value in [mm]

Instar	**Mean value ($\bar{x}$)**	**Specimens**	**Source**
L_1	0.42	31	Van Emden (1952)
L_1	0.40	40	Schindler (1958)
L_1	0.368	19	own data
“L_2”	0.83	40	Schindler (1958)
Unknown instar	0.985	2	Van Emden (1952)
“L_3”	1.72	40	Schindler (1958)
Mature larva	2.03	6	own data

Instar determination in *Otiorhynchus coecus coecus* is hampered by the rather discrepant head width data of L_1 larvae from Van Emden (1952) and Schindler (1958) on the one hand and our own data on the other. As there is no obvious explanation for this difference all values have to be taken into account. Hence, we tried to determine the best approximation for larval growth for L_1 HW values of 0.41 mm (Van Emden’s and Schindler’s data combined) and for 0.368 mm (own data) (Table 2) and used GF values between 1.38 and 1.41. Either with HW data of 0.368 mm or 0.41 mm and HW data for mature larvae of 2.03 mm it can be stated that both approximations show that there are **6 larval instars** in *O. coecus coecus*. If the mean HW of L_1 larvae is 0.41 mm, a GF of 1.38 reveals the best approximation; if mean HW is only 0.368 mm, then a GF of 1.41 reveals the best result. These relatively low GF values for larval growth, compared with *O. carinatopunctatus*, may be a consequence of the rather big L_1 larvae of this species. But to this point further research is necessary. And at the moment the question must be left unanswered whether a GF of around 1.38 or of 1.41 may reflect the reality in *O. coecus coecus* best (Table 3).

Our larvae with head widths of 0.9 mm and 1.15 mm should therefore represent the 4th instar, and the larvae of 1.34 mm and 1.65 mm should mark extreme values of the 5th instar, which was calculated to range between 1.45 mm and 1.50 mm (Table 3). It is known that a certain instar, especially in the higher stages, may overlap with neighbouring instars (e.g. Willis 1964 in *Otiorhynchus*, or Lekander 1973 in *Phyllobius*).

"L_2" larvae of Schindler (1958) with measuring data of 0.83 mm (Table 2) may in fact represent a mix of L_3 and L_4 larvae, and his "L_3" of 1.72 mm a mix of L_5 and L_6 larvae (see column 7 of Table 3). This is well comprehensible by the easy to overlook young larval instars which may hide close to or even inside of young roots and are only rarely found during field search, which would be in full accordance with own experience.

If data of Schindler (1958) about larval growth would be correct the GF from L_1 to L_2 is 2.075 (0.4 mm → 0.83 mm) and from Schindler's L_2 to L_3 2.072 (0.83 mm → 1.72 mm; see Table 2). GF values over 2 were never observed in any other Entiminae (e.g. Leibee et al. 1980, Gosik et al. 2019). Moreover, this does not agree with instar data of Palm (1935) or La Lone & Clarke (1981) as already reported (see above).

The error of Schindler (1958) who published a detailed report about the development of *O. coecus coecus* and measured on average 40 larvae of each instar may have been that he dispensed with the graphical representation of his data being at the same time not aware of the validity of Dyar's law.

Table 3. Search for the best approximation of larval growth in *Otiorhynchus coecus coecus*
Yellow columns contain the average value of head width data of L_1 larvae from Van Emden (1952) and Schindler (1958), and blue columns contain our own measuring data (see Table 1) to show the possible ways from the L_1 to the mature larva. Best approximations in both parts bold (vertical) using growth factors (GF) between 1.38 and 1.41. Calculated (= hypothetical) values in italics.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
GF	1.41	**1.41**	1.40	1.40	1.39	1.39	**1.38**	1.38
L_1	0.41	**0.368**	0.41	0.368	0.41	0.368	**0.41**	0.368
L_2	*0.578*	***0.519***	*0.574*	*0.515*	*0.570*	*0.512*	***0.566***	*0.508*
L_3	*0.815*	***0.732***	*0.804*	*0.721*	*0.792*	*0.711*	***0.781***	*0.701*
L_4	*1.149*	***1.032***	*1.125*	*1.010*	*1.101*	*0.988*	***1.078***	*0.967*
L_5	*1.621*	***1.455***	*1.575*	*1.414*	*1.531*	*1.374*	***1.487***	*1.335*
L_6	*2.285*	***2.051***	*2.205*	*1.979*	*2.128*	*1.910*	***2.052***	*1.842*
Mature larva*	2.03	**2.03**	2.03	2.03	2.03	2.03	**2.03**	2.03
Pupa*	1.87	1.87	1.87	1.87	1.87	1.87	1.87	1.87
Adult*	1.76	1.76	1.76	1.76	1.76	1.76	1.76	1.76

*: Mean values of 6 mature larvae, 3 pupae, and 6 adults (3 males, 3 females)

Data on the biology of *Otiorhynchus coecus coecus*

The life-cycle of *O. coecus coecus* is very probably the best-studied in *Otiorhynchus* species absent from anthropogenic environments (Beling 1887, Schindler 1958). So our few development data from breeding and field-collecting could not really expand our knowledge about this species. Thus, present data are summarized and visualized here for the first time [**Fig 15**].

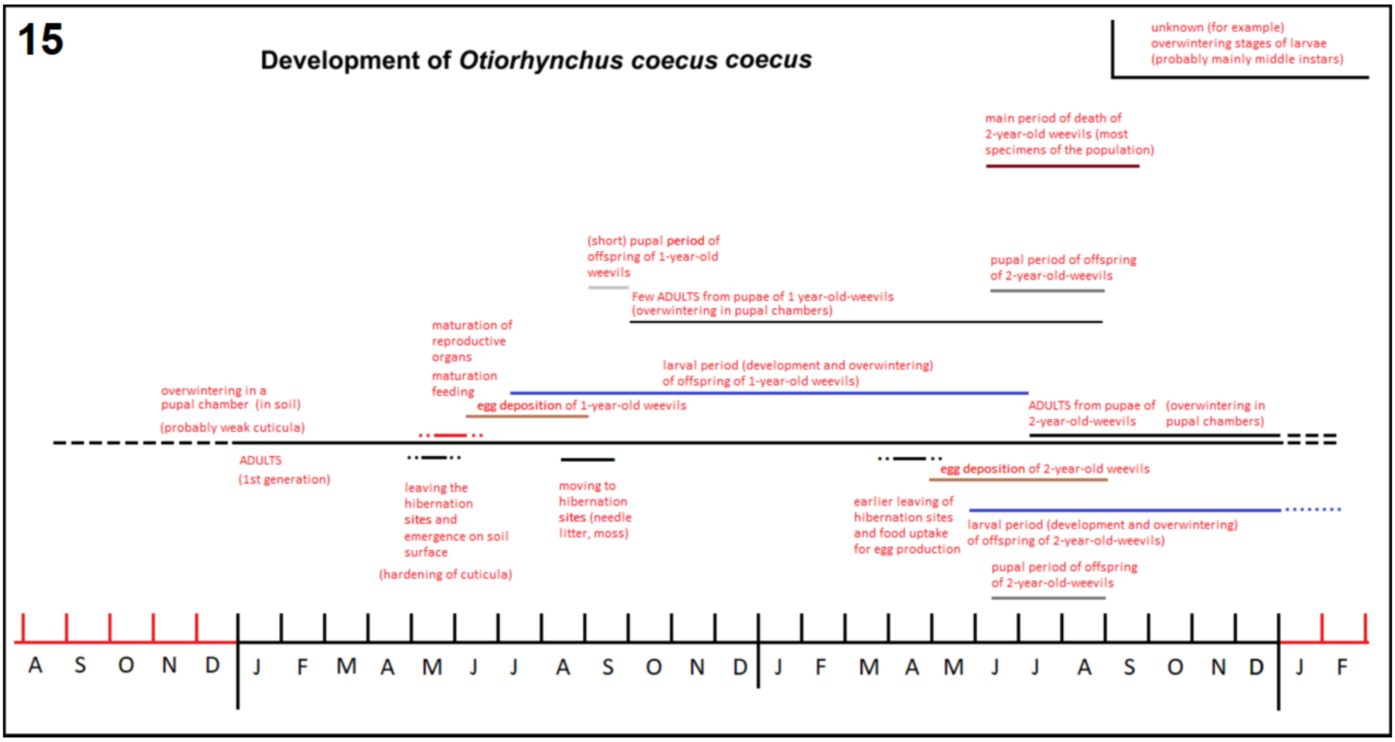

Fig. 15. Development of *Otiorhynchus coecus coecus* Germar, 1823 based mainly on data of Beling (1887) and Schindler (1958).

I. Own data

The best results of our two breeding efforts were received in 2016 with *Acer platanoides*: 2 mature larvae on 23.09. after less than 2 months (breeding was started on 31.07. with the release of adults in breeding cages). The late receipt of 3 pupae, after a breeding period of 5 months in a climate chamber under constant temperature and light conditions, on 28.12., is, however, less understandable. An explanation could be that the transfer of the larvae from the *Acer platanoides* flowerpot to another one with *Euonymus fortunei* in November may have impeded further development. But, on the other hand, this would mean that the time period from 31.07. to 03.11., the date of larva transfer, was not long enough to develop from egg deposition to pupal stage. From these climate chamber data it can be assumed that egg deposition that starts in the beginning of August does not provide adults in the same year, and this is in accordance with field data from Schindler (1958), see below.

II. Data from literature

Life-cycle and development of *Otiorhynchus coecus coecus* that appeared in the 19th and 20th century as noxious species in young *Picea abies* plantations, were already studied and described by Beling (1887) and Schindler (1958) in many details from the Harz Mountains.

Beling (1887) found the first pupae on 30th July (1884) of which some had already black appendages indicating an around 14 days earlier begin of the pupal instar. He received two adults from the taken home pupae on 14.08. and found the first five teneral adults in their pupal chambers in soil two days later in the field, beneath numerous larvae and pupae. In the following year he continued with systematic digging. Between March and June he did not find any pupae, but always larvae, at first premature and in May and June "nearly mature" and later also smaller larvae. The first pupae and certainly mature larvae were found on 11th July. In March and April larvae were accompanied by large numbers of overwintering adults (adults up to mid-April). So, larvae are present during the whole year. The last pupae were found on 17th September, these are present only from July to September. According to Schindler (1958) there is some reason to assume that overwintering larvae produce the first pupae in July and that larvae from eggs deposited in spring produce pupae later (mid–August to September).

Schindler (1958) reported that most of the teneral adults stay in their pupal chambers and emerge early in April of the next year on the soil surface and on the trees. Young weevils need long time for maturation of sexual organs and start with egg deposition in summer of the same or even only in the second year. He also reported that early larvae develop in the same year, and all larvae from eggs deposited after mid–June overwinter and pupate between July and September of the following year. And he continued that main egg deposition takes place in July which would mean that most larvae overwinter.

However, 2-year-old weevils start with egg deposition earlier, usually in mid-May or June around 3 weeks after maturation feeding, and they continue until end of August. - In the lab egg-laying started 3 and 4 weeks after collecting from the overwintering sites in the needle litter, where mainly the older (2-year-old) weevils hibernate. In August, at the latest in September, weevils move to their hibernation sites. The greatest part of the weevils dies in the second year, between June and September, only a few reach the third year, when they die early without continuation of egg deposition.

Schindler (1958) described a similar life-cycle as Beling (1887) but with many additions and a few differences. He reported that most adults of *O. coecus coecus* live up to 2 years, and some also reach the third year but do not continue with egg-laying then. Young adults overwinter in their pupal chambers at depths of 3 cm to 10 cm in soil. After overwintering they emerge later on the soil surface and on the plants than adults that hatched one year before. These old adults overwinter (in the second year) between mosses or in the needle litter that warms up earlier; this is why they are earlier on the trees for maturity feeding and start earlier with egg-laying thus producing more offspring than weevils from the first year.
Beling (1887) reported that the last overwintering adults had left their hibernation sites mid-April. But according to Schindler (1958) the emergence period can be delayed at unfavourable sites for more than four weeks until May. This may be an explanation for a difference between Beling (1887) and Schindler (1958): the first author stated that main egg deposition is in the first half of the year and the second author that it is in the second half. And Beling (1887) was not aware about different behavior and starting conditions of 1- and 2-year-old specimens when emerging from their hibernation sites.

According to Dieckmann (1980), which was thereafter repeated by Burakowski et al. (1993), the life-cycle is extended over 2 years: after egg deposition between May and end of August, larvae begin to feed, overwinter, continue feeding and develop (as "L_3") into the pupal stage between end of July and beginning of September, hatch after 3 – 4 weeks in their pupal chambers, where they stay until next spring and emerge on the trees.

However, this statement can be considered too simplified, because only a small part of the larvae always completes the development cycle in the same year, while the majority hibernates and transforms in the following year. This kind of development seems to be typical for the *O. tenebricosus* (Herbst, 1784) group (see Gosik et al. 2016, Przybycień et al. 2021), but does not show two separate periods of pupation as in species from the lowlands and low altitudes. In the mountains temperatures are apparently too low to allow pupation of hibernating larvae in spring and early summer.

Acknowledgements

We thank Andreas Marten for the permission to search for immature instars of Entiminae on the territory of the National Park Harz. We express our gratitude to dr Roberto Caldara and dr Jiři Krátký for very useful comments to our manuscript.

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