ACTA ENTOMOLOGICA
MUSEI NATIONALIS PRAGAE
ISSN 1804-6487 (online) – 0374-1036 (print)

2025
65(2): 313–332
doi: 10.37520/aemnp.2025.024
www.aemnp.eu

RESEARCH PAPER

Immature stages of the tiger beetle *Cylindera* (*Plectographa*) *apiata apiata* (Coleoptera: Cicindelidae) and analysis of primary chaetotaxy

Juan Ignacio URCOLA[1,2,*)], Matías Ricardo URCOLA[1,2)], Sergio ROIG-JUÑENT[3,4)] & Mariano Cruz MICHAT[1,2)]

[1)] University of Buenos Aires, Faculty of Exact and Natural Sciences, Department of Biodiversity and Experimental Biology, Laboratory of Entomology, Av. Int. Guiraldes 2160, C1428EGA, Buenos Aires, Argentina; e-mail: urcola@bg.fcen.uba.ar
[2)] Institute of Biodiversity and Experimental and Applied Biology (IBBEA), CONICET-UBA, Buenos Aires, Argentina; e-mail: marianoide@gmail.com
[3)] Argentine Dryland Research Institute of the National Scientific and Technical Research Council (IADIZA-CONICET), Mendoza, Argentina; e-mail: saroig@mendoza-conicet.gob.ar
[4)] Cátedra de Ecología, Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Mendoza, Argentina
*) corresponding author; e-mail: jiu7_arg@hotmail.com; ORCID: https://orcid.org/0000-0002-5684-2464

Accepted:
9th September 2025

Published online:
10th December 2025

Abstract. The larval instars and pupa of *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825) are redescribed and illustrated, including morphometric and chaetotaxic characters. The larval ground pattern for the chaetotaxic characters is presented, based on instar I larva of *C. apiata apiata*. For chaetotaxic homologization, comparisons with other adephagan families were performed. The primary chaetotaxy of cicindelid larvae is very similar to that described for Carabidae, and both are distinguished from the aquatic adephagan families by the presence of seta TR8 and pore COb; additionally, they are characterized by the presence of long setae on the apices of the antenna (setae AN4–6) and galea (MX8–9). On the other hand, Cicindelidae differ from Carabidae in the presence of setae PA20–22 on the parietal and setae FE7–8 on the femur, the absence of pores COc–e on the coxa, and by having a single seta on the pretarsus, a condition unique to Cicindelidae. The habitat where both adults and larvae of *C. apiata apiata* were collected is described and illustrated, and the phenology of the species is briefly discussed.

Key words. Coleoptera, Adephaga, Cicindelidae, ground plan, larva, morphometry, pupa, sensilla, taxonomy, tiger beetles, Argentina, Neotropical Region

Zoobank: http://zoobank.org/urn:lsid:zoobank.org:pub:B805A2FD-2144-4D6B-B514-4E1B1A9DE7B2

Introduction

Tiger beetles (Adephaga: Cicindelidae) are arguably one of the most popular and well-studied insect families (Pearson & Vogler 2001), yet knowledge of their larval morphology remains sparse worldwide. Most cicindelid larvae are unidentifiable to species, even though biologically and ecologically they are often more important than adults as habitat indicators and for evaluating the viability and dynamics of populations (Pearson et al. 2015). The identification of tiger-beetle larvae is a persistent challenge because most of the larvae are unknown, descriptions being available for only about 40% of the genera and 10% of the species (Putchkov 1994), and taxonomic keys are limited in scope (Gwiazdowski et al. 2020). Most larval descriptions emphasize morphological characters, focusing only on certain structures, such as the pronotal disc, the median and inner hooks of the fifth abdominal segment, the ninth eusternum, and the pygopod, but lack a comprehensive treatment of the chaetotaxy (e.g., Arndt & Putchkov 1994, Spomer et al. 2008, Brust et al. 2009, Putchkov et al. 2019, Gwiazdowski et al. 2020, Putchkov & Markina 2020).

The system of nomenclature for larval primary chaetotaxy of adephagan beetles, developed over the past 40 years based on the work of Bousquet & Goulet (1984) in Carabidae, documents the complex arrangement of setae and pores on the cuticle of the larvae, which exhibits distinct distribution patterns at various taxonomic levels. This system has proven to be highly valuable in providing characters for taxonomic distinction and phylogenetic analysis in several hydradephagan families, namely Aspidytidae, Dytiscidae, Gyrinidae, Haliplidae, Hygrobiidae, Meruidae,

and Noteridae (e.g., Alarie et al. 2004, 2011; Alarie & Bilton 2005; Michat et al. 2017, 2020; Urcola et al. 2019; Alarie & Michat 2023). Paradoxically, however, studies on the chaetotaxy of geadephagan families have not received as much attention as those conducted on their aquatic counterparts.

The genus *Cylindera* Westwood, 1831 has a worldwide distribution and is currently known to include 11 subgenera (Šafránek & Amaya 2021). It is a problematic group that requires a comprehensive taxonomic revision, as many taxa were inconsistently treated in the literature, and species complexes are present (Moravec & Šafránek 2025). Moreover, phylogenetic studies have demonstrated that it is polyphyletic (Duran & Gough 2019). Therefore, the genus-group classification will likely be revised in future studies.

The only known larvae of *Cylindera* subgenus *Plectographa* are those of *C. apiata* (Dejean, 1825; Brazil), *C. gormazii* (Redd, 1871; Chile) and *C. suturalis* (Fabricius, 1798; Brazil) (Zikan 1929, Cekalovic & Reyes 1985, Adis et al. 1998, Arndt et al. 2002). However, these studies provided brief descriptions and, as mentioned above, did not perform a comprehensive analysis of the chaetotaxy. *Cylindera* (*Plectographa*) *apiata* has two subspecies, both distributed in the Neotropical Region: *Cylindera apiata apiata* occurs in Brazil, Uruguay, and Argentina (Wiesner & Bandinelli 2014, Pett et al. 2022), whereas *C. apiata claussenii* (Putzeys, 1845) is known from Paraguay and Brazil (Freitag & Barnes 1989). In this last country, both subspecies are sympatric in the state of Rio de Janeiro (Freitag & Barnes 1989). In Argentina, *C. apiata apiata* is the most commonly encountered tiger beetle, occurring in the north and central regions (Wiesner & Bandinelli 2014). In this paper, we study the larvae of this subspecies, for the first time including a detailed chaetotaxic treatment of a cicindelid larva following current standards used in larval descriptions of other adephagan families (cf. references above). The objectives of this study therefore are: 1) to describe and illustrate all larval instars and pupa of *C. apiata apiata*; 2) to establish the ground plan of larval features for the subgenus *Plectographa*; 3) to describe in detail its primary chaetotaxy; and 4) to compare the larval characters of Cicindelidae with those of other adephagan families and discuss relevant findings.

Material and methods

Material examined. Thirty-two specimens of instar I, two of instar II, seven of instar III and three pupae of *C. apiata apiata* were used for the descriptions. The larvae were identified using two different methods: rearing under laboratory conditions and association with adults. On one hand, larvae were obtained by rearing adults (Fig. 1B) collected in the following localities of Argentina: Buenos Aires Province, Centinela del Mar (38°26′S; 58°13′W, elevation 15 m a.s.l.), 15–16.xii.2023 and Córdoba Province, Villa Ciudad Parque (31°52′S; 64°32′W, elevation 773 m a.s.l., Fig. 1), 5.x.2023 and 31.i.2024. Thirty-two specimens of instar I were obtained, two of which molted to instar II. On the other hand, at the same site described above in Córdoba Province, adults were found on 30.ix.2024 and a portion of soil containing active burrows was excavated using a shovel. The extracted soil was carefully examined in a white tray, allowing the collection of larvae of instar III and pupae. It is worth noting that *C. apiata apiata* was the only species of the genus collected at this site. The immature stages were killed by immersion in boiling water for about 10–15 seconds and preserved in 96% ethanol.

Methods. Larvae were cleared in lactic acid, dissected, and mounted on glass slides with polyvinyl-lacto-glycerol. Observation (at magnifications of up to 1000×) and drawings were made using an Olympus CX41 compound microscope equipped with a camera lucida. The drawings were scanned and digitally edited. For SEM imaging, nine larvae of instar I were superficially cleaned with a soft brush and sonicated for 4 minutes in a solution of warm water and detergent. To further remove particles, the samples were sonicated for 4 minutes with commercial window cleaner solution. Specimens were then dehydrated in a graded series of ethanol, infiltrated with hexamethyldisilazane, and air dried overnight. The specimens were mounted on stubs with copper tape and sputter-coated with gold-palladium. SEM images were taken with a Zeiss GeminiSEM 360 scanning electron microscope in the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina.

Habitus photographs of the instar III and pupa were taken with a Nikon D800e digital camera equipped with Nikon AFS VR Micro-NIKKOR 105mm f/2.8G IF-ED and Raynox MSN-202 lenses (Tokyo, Japan). The images were stacked using Helicon Focus 6.7.1 Pro software (Kharkiv, Ukraine) and digitally edited. The material is stored in the collection of the Laboratory of Entomology, University of Buenos Aires, Argentina.

Morphometric analysis. The following measurements were recorded for the larvae of all instars, with their respective abbreviations in parentheses. Total length (TL), head length (HL) (measured medially from anterior margin of frontoclypeus to posteroventral margin of parietal), maximum head width (HW), length of frontoclypeus (FRL) (from anterior margin to the joint of coronal and ecdysial sutures), maximum occipital foramen width (OCW), coronal suture length (COL), length of mandible (MNL) (measured from laterobasal angle to apex), width of mandible (MNW) (maximum width measured at base). Length of antenna (A), galea (GA), maxillary palpus (MP), and labial palpus (LP) were obtained by summing the lengths of the individual segments; each segment is denoted by the corresponding letter(s) followed by a number (e.g., A1, first antennomere). Pronotum length (PNL) (total pronotum length, measured medially), maximum pronotum width (PNW). Length of leg (L), including the longest claw (CL), was derived by adding the lengths of the individual segments; each leg is denoted by the letter L followed by a number (e.g., L1, prothoracic leg). Trochanter length includes only the proximal portion; the distal portion is included in the femur length. Legs were considered as being composed of six segments (Lawrence 1991). Median hook length (MHL) (measured from laterobasal angle to apex). Length of the pygopod (PYG) (measured dorsally along midline

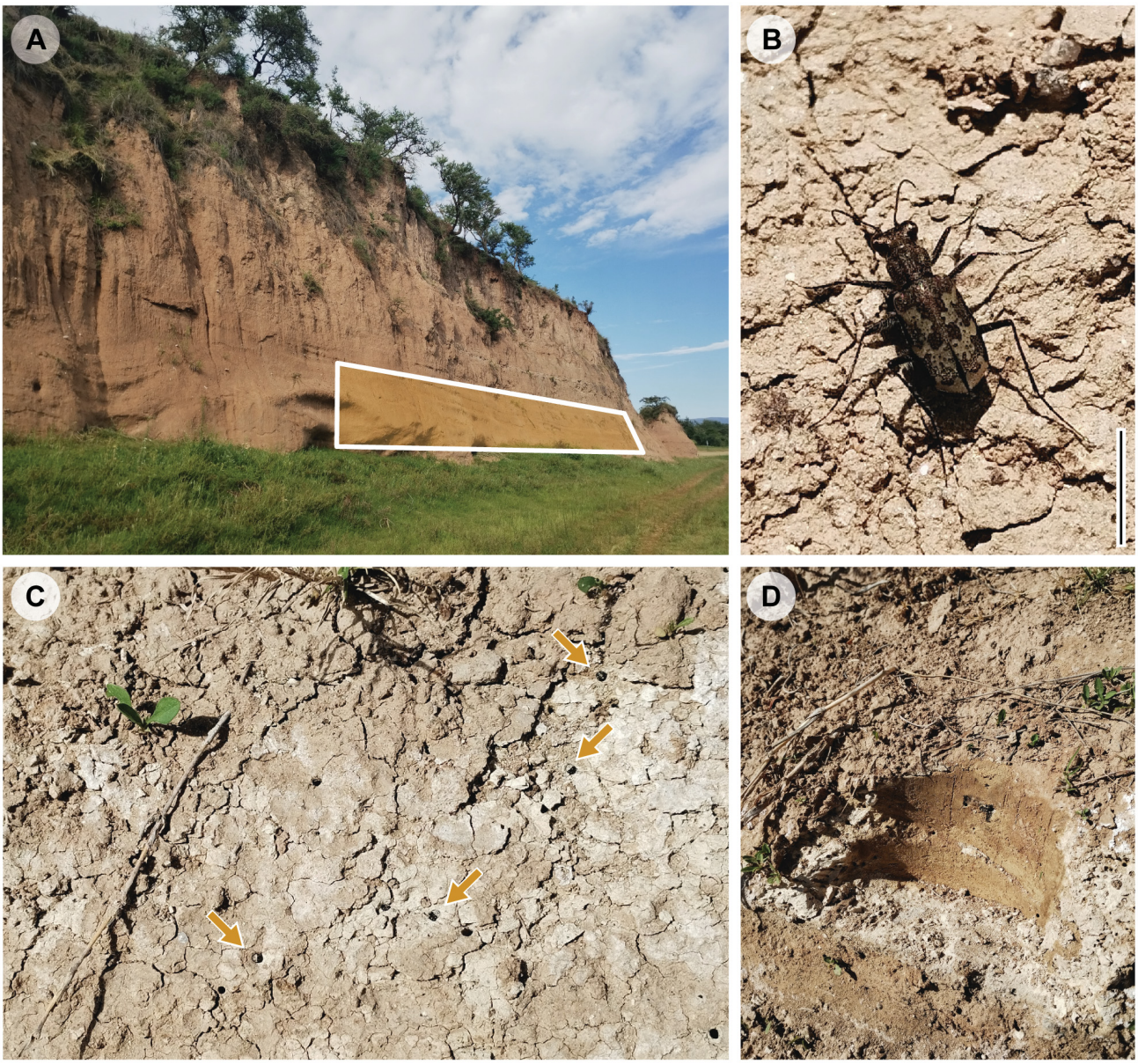

Fig 1. Habitat of *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), Villa Ciudad Parque, Córdoba Province, Argentina. A – general view of the cliff (orange area = zone where the adults and larvae were primarily found). B – adult of *C. apiata*. C – larval burrows at the base of the cliff (orange arrows = the heads of larva of *C. apita* at the entrance of their burrows). D – area where the soil was removed and from which instar III and pupae were obtained. Scale bar = 5.0 mm.

from anterior to posterior margin). These measurements were used to calculate several ratios that characterize body shape. The terminology, abbreviations, measurements, and ratios used for pupae follow those established by Serrano (1991) and Roza & Mermudes (2017).

Chaetotaxy analysis. Primary (present in first-instar larva) and secondary (added in later instars) setae and the so-called pores were distinguished in the cephalic capsule, head appendages, legs, and pygopod. Sensilla were coded by two capital letters, in most cases corresponding to the first two letters of the name of the structure on which they are located, and a number for setae or a lowercase letter for pores. Setae and pores present in instar I larvae were identified and labeled by comparison with the ground plan of chaetotaxy of Cicindelidae (Bousquet & Goulet 1984) and other adephagan families: Aspidytidae (Alarie & Bilton 2005), Carabidae (Bousquet & Goulet 1984), Dytiscidae (Alarie & Michat 2023), Gyrinidae (Michat et al. 2017), Haliplidae (Michat et al. 2020), Hygrobiidae (Alarie et al. 2004), Meruidae (Alarie et al. 2011), Noteridae (Urcola et al. 2019), and Trachypachidae (Bousquet & Goulet 1984). Due to their position and small size, setae at the apices of the maxillary and labial palpi are extremely difficult to distinguish under an optical microscope. As a result, they are not well represented in the line drawings.

Data curation from citizen science platforms. Occurrence records from iNaturalist (www.inaturalist.org) were carefully curated prior to inclusion in this study. Only records with clear photographs from localities where the subspecies is known to occur were considered.

Results

Description of the immature stages of *Cylindera apiata apiata*

Instar I (Figs 2–9; Tables 1, 3). ***Color.*** Dorsal surface of cephalic capsule and protergite dark brown with a light coppery-bronze sheen; ventral surface of cephalic capsule, antennae, maxilla, labium, and legs light brown; mandibles light brown with darker distal portion; meso- and metatergite grayish-brown; abdomen testaceous, with abdominal sclerites and last segment grayish-brown; abdominal humps light brown.

Structure. *Body*. Long, cylindrical, curved ventrally towards the abdominal apex (Fig. 7A). Measurements and ratios that characterize body shape are shown in Table 1.

Head. Hyperprognathous; cephalic capsule (Figs 2, 7–8A) strongly enlarged and sclerotized, rounded laterally, slightly concave in dorsal view, strongly convex in ventral view; maximum width at level of stemmata; occipital foramen relatively small, dorsal margin deeply indented, reaching posterior margin of frontoclypeus; ecdysial sutures sinuate, separated from occipital foramen by very short coronal suture; posterior tentorial pits transverse, close to each other; gular suture ends in T-shaped groove (Figs 2B, 8A); basal part ventrally W-shaped (Figs 2B, 8A); six stemmata of different size on each side, stemmata 1 and 2 the largest, similar in size, stemmata 4 and 6 reduced, whitish. Frontoclypeus with 2–4 spine-like egg bursters near posterior margin; nasale shovel-shaped, anterior margin rounded medially, sinuous laterally; ridge on posterior region U-shaped, well separated from ridge on posterior region of parietal (Figs 2A, 7B). *Antenna* (Figs 3A–B) short, robust, shorter than HW, composed of four antennomeres; A1 and A2 longest and widest; A3 slightly shorter than A1; A4 shortest, slightly shorter than A3. *Mandibles* (Fig. 3C) symmetrical; prominent, relatively slender; basal half robust, distal half curved inwards, narrowing to pointed apex; inner margin smooth with strong tooth at mid-length. *Maxilla* (Figs 3D–E): cardo small, subtriangular; stipes well developed, subcylindrical, with spine basally and membranous area distally on inner margin, and strongly sclerotized bar on distal ventral margin; galea well developed, as long as maxillary palpus, first galeomere fused to palpifer dorsally, second galeomere shorter and slenderer than first galeomere; palpifer differentiated from stipes; palpus long, robust, composed of three palpomeres, MP1 shortest, MP3 longest. *Labium* (Figs 3F–G): prementum well developed, subrectangular, longer than broad, ventrally with bipartite sclerite on each anterolateral angle and single sclerite on posterior region; palpus short, robust, composed of two palpomeres, LP1 longer than LP2; LP1 with three ventroapical spines, external one longest; ligula subrectangular, with sinuous anterior margin and rounded lateral margins, with dorsal surface entirely covered with short spinulae (Fig. 3H), and ventral surface with several minute spinulae on distal portion (Fig. 3I).

Thorax. Pronotum pentagonal, strongly enlarged, with anterolateral angles slightly protruding forward (Figs 4A, 7A); meso- and metanotum subtrapezoidal, subequal in length, smaller, more rounded, and less sclerotized than pronotum; all tergites with sagittal line; meso- and metasterna with ventral plate between coxae. *Legs* (Figs 4B–C, 5, 9A–B) short, composed of six articles, L1 and L3 subequal in length, L2 slightly shorter; coxa and femur elongated, tibia and tarsus very short, pretarsus with two long, stout, slightly curved claws, posterior claw shorter than anterior claw; pro- and mesocoxae with less sclerotized area on anterodistal portion (Fig. 4B).

Abdomen ten-segmented, membranous with sclerotized and setaceous areas; segments I–IV and VI–IX subequal; segment V distinctly modified, as an "abdominal hump" (Fig. 7A), posterior and lateral parts of tergite V fused, with anterior part separate, and two hooks between them; median hook large, curved, directed outwards; inner hook

Table 1. Measurements and ratios for the larval instars of *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825).

Measure	Instar I (n = 3)	Instar II (n = 2)	Instar III (n = 3)
TL (mm)	3.60–5.20	6.14–6.67	11.83–13.40
HL (mm)	0.85–0.88	1.30–1.34	1.75–1.83
HW (mm)	0.86–0.90	1.35–1.43	2.05–2.08
FRL (mm)	0.50–0.55	0.75–0.79	0.93–1.03
OCW (mm)	0.48–0.50	0.65–0.69	1.60–1.63
HL/HW	0.98–0.99	0.94–0.96	0.84–0.89
FRL/HW	0.58–0.61	0.52–0.59	0.45–0.50
HW/OCW	1.79–1.80	2.07–2.08	1.26–1.30
COL/HL	0.01–0.02	0.01	0.01
FRL/HL	0.59–0.63	0.56–0.61	0.51–0.59
A/HW	0.47–0.52	0.44–0.47	0.45–0.47
A1/A3	1.14–1.19	0.94–1.13	1.36–1.45
A2/A3	1.24–1.33	1.33–1.38	1.27–1.60
A4/A3	0.80–0.90	0.69–0.70	0.64–0.73
MNL/MNW	2.71–2.95	2.64–2.83	2.88–3.38
MNL/HL	0.63–0.69	0.64–0.67	0.64–0.68
A/MP	2.56–2.65	2.84–3.05	3.13–3.29
GA2/GA1	0.77–0.84	0.81–0.82	0.72–0.78
GA/MP1	11.25–12.00	11.43–12.67	11.00–12.22
MP1/MP3	0.18–0.20	0.25–0.33	0.30–0.36
MP2/MP3	0.45–0.50	0.58–0.66	0.70–0.80
MP/LP	0.94–1.00	0.85–0.86	0.88
LP1/LP2	1.06–1.13	1.33–1.36	1.36–1.46
PNW/PNL	1.56–1.72	1.62–1.63	1.58–1.62
L3 (mm)	1.30–1.36	2.08–2.23	3.10–3.14
L3/L1	1.00–1.04	1.08–1.15	1.06–1.13
L3/L2	1.10–1.14	1.17	1.13–1.17
L3/HW	1.50–1.54	1.46–1.65	1.49–1.53
CO/FE (L3)	1.34–1.43	1.45–1.49	1.38–1.39
TI/FE (L3)	0.25–0.26	0.28–0.32	0.23–0.25
TA/FE (L3)	0.14–0.16	0.16	0.12–0.13
CL/TA (L3)	2.50–2.88	2.17–2.45	2.36–2.42
MHL (mm)	0.30–0.31	0.47–0.52	0.74
PYG (mm)	0.24–0.25	0.45–0.55	0.60–0.65
PYG/HW	0.27–0.29	0.31–0.40	0.29–0.31

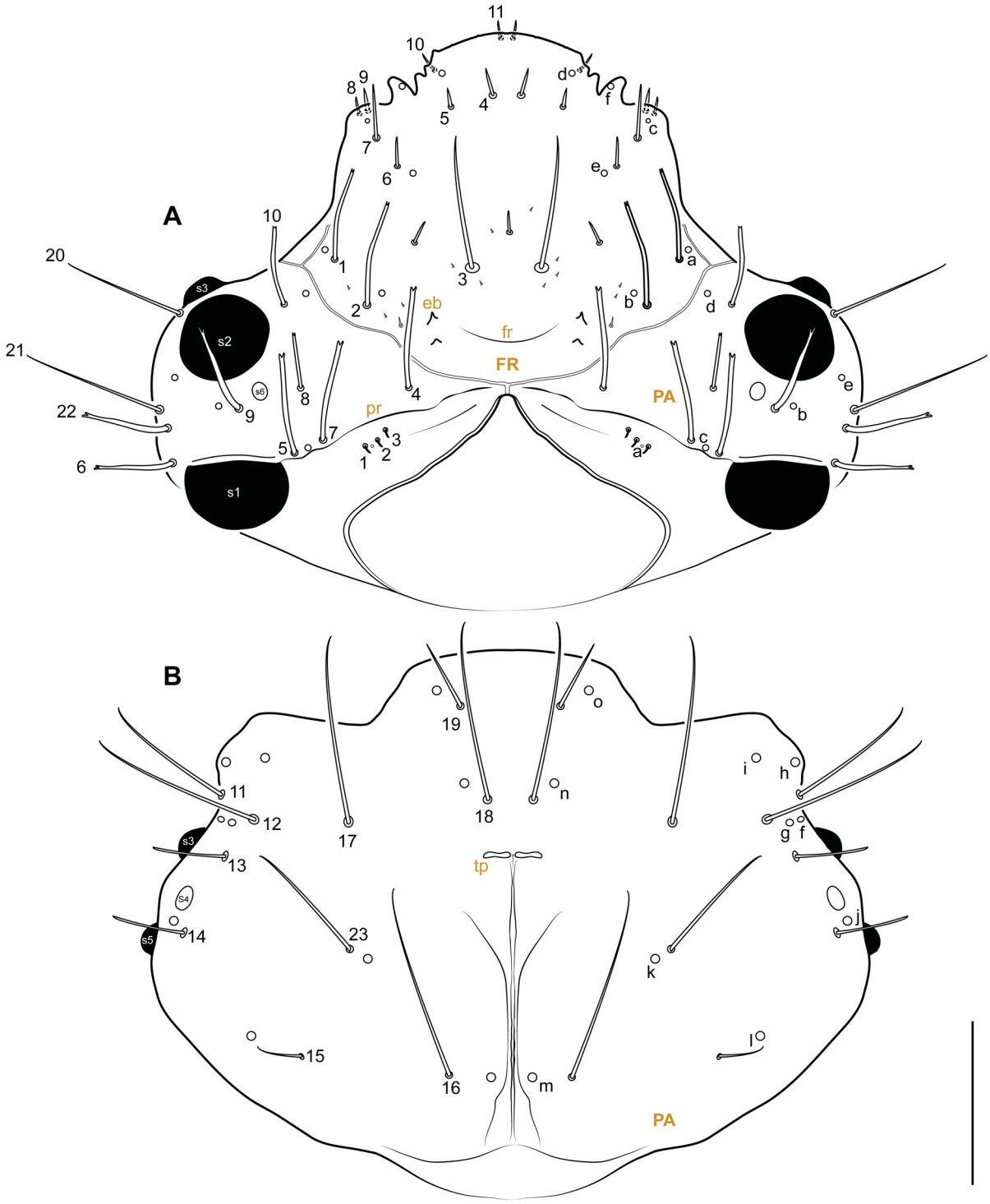

Fig. 2. *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), instar I. A – cephalic capsule, dorsal view. B – cephalic capsule, ventral view. Numbers and lowercase letters indicate primary setae and pores respectively. Abbreviations: FR – frontoclypeus; PA – parietal; eb – egg burster; fr – ridge on the posterior part of frontoclypeus; pr – ridge on the posterior part of parietal; s – stemmata; tp – tentorial pit. Scale bar = 0.25 mm.

small with spine-like projection shorter than lateral setae (Fig. 4D); pygopod short, conical (Figs 6, 9C); urogomphi absent.

Chaetotaxy. *Head*. Frontoclypeus (Figs 2A, 7B): Medial portion of anterior margin with one short hair-like seta (FR11); lateral margin with three short hair-like setae (FR8, FR9, FR10) and three pores (FRc, FRd, FRf); central portion with two hair-like setae (FR4, FR5) on distal third and one long hair-like seta (FR3) and three additional short spine-like setae at mid-length; lateral portion with two hair-like setae (FR6, FR7) and one pore (FRe) on distal half and two spatulate setae (FR1, FR2) and two pores (FRa, FRb) on basal half; posterior portion with 6–7 minute additional setae. Parietal (Figs 2A–B, 7B, 8A): Dorsal surface with two hair-like setae (PA20, PA21), and two spatulate setae (PA6, PA22) on lateral

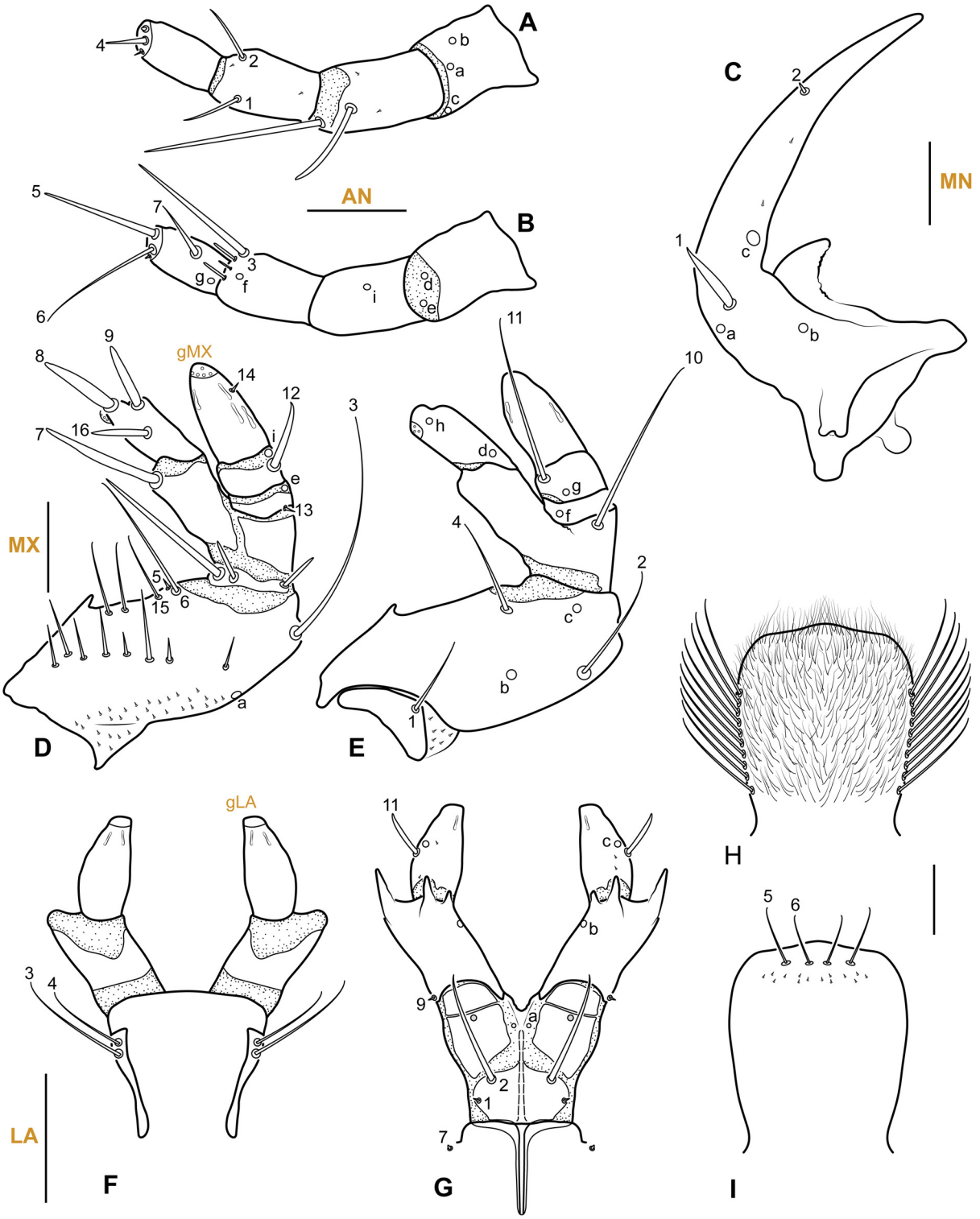

Fig. 3. *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), instar I. A – left antenna, dorsal view. B – right antenna, ventral view. C – left mandible, dorsal view. D – right maxilla, dorsal view. E – left maxilla, ventral view. F – labium, dorsal view. G – labium, ventral view. H – ligula, dorsal view. I – ligula, ventral view. Numbers and lowercase letters indicate primary setae and pores respectively. Abbreviations: AN – antenna; gLA – labial group; gMX – maxillary group; LA – labium; MN – mandible; MX – maxilla. Scale bars = 0.1 mm.

margin, one spatulate seta (PA10) and one pore (PAd) on anterior portion, five spatulate setae (PA4, PA5, PA7, PA8, PA9) and three pores (PAb, PAc, PAe) on medial portion, and three short spine-like setae (PA1, PA2, PA3) and one pore (PAa) on basal region. Ventral surface with four hair-like setae (PA11, PA12, PA13, PA14) and five pores (PAf, PAg, PAh, PAi, PAj) on anterolateral region, three hair-like setae (PA17, PA18, PA19) and two pores (PAn, PAo) on central portion of anterior half, and three hair-like setae (PA15, PA16, PA23) and three pores (PAk, PAl, PAm) on central portion of posterior half. *Antenna* (Figs 3A–B, 8B). A1 with three pores (ANa, ANb, ANc)

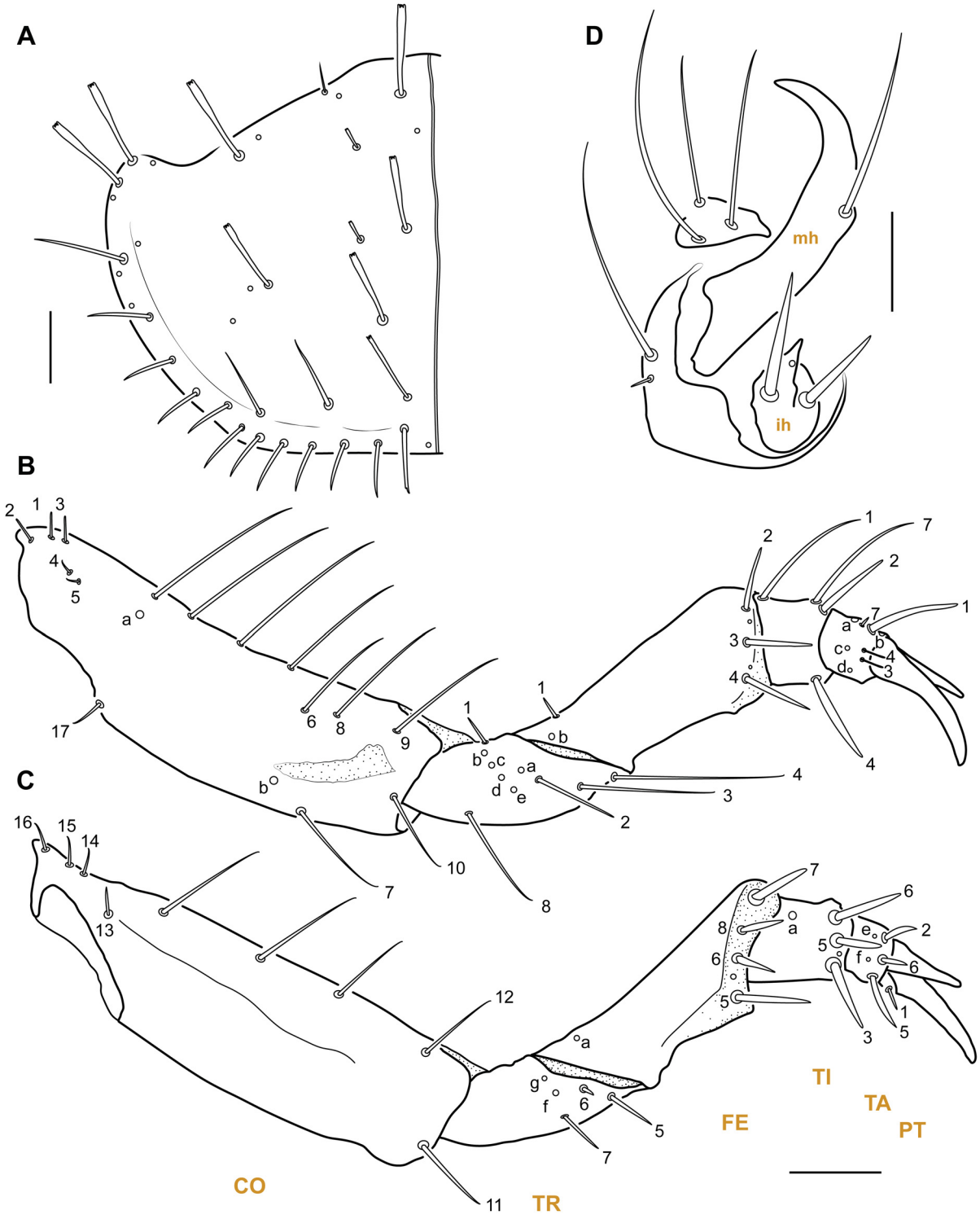

Fig. 4. *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), instar I. A – pronotum, dorsal view (left half). B – left prothoracic leg, anterior view. C – right prothoracic leg, posterior view. D – abdominal tergite V, dorsal view (left half). Numbers and lowercase letters indicate primary setae and pores respectively. Abbreviations: CO – coxa; FE – femur; PT – pretarsus; TA – tarsus; TI – tibia; TR – trochanter; ih – inner hook; mh – median hook. Scale bars = 0.25 mm for Fig. 4A and 0.1 mm for Figs B–D.

on dorsal surface and two pores (ANd, ANe) on ventral surface; A2 with one pore (ANi) on ventromedial region, and two additional hair-like setae and 0–2 minute sensilla on dorsodistal region; A3 with two spine-like setae (AN1, AN2) and 0–2 minute sensilla on dorsal surface, and one hair-like seta (AN3), three short additional spine-like setae and one pore (ANf) on ventrodistal margin; A4 with one hair-like seta (AN7) and one pore (ANg) on ventral surface, and three hair-like setae (AN4, AN5, AN6) and three minute sensilla at apex. *Mandible* (Figs 3C, 8C). Dorsal surface with one seta (MN1) and three pores (MNa, MNb, MNc) on basal half, and one very short seta (MN2) and

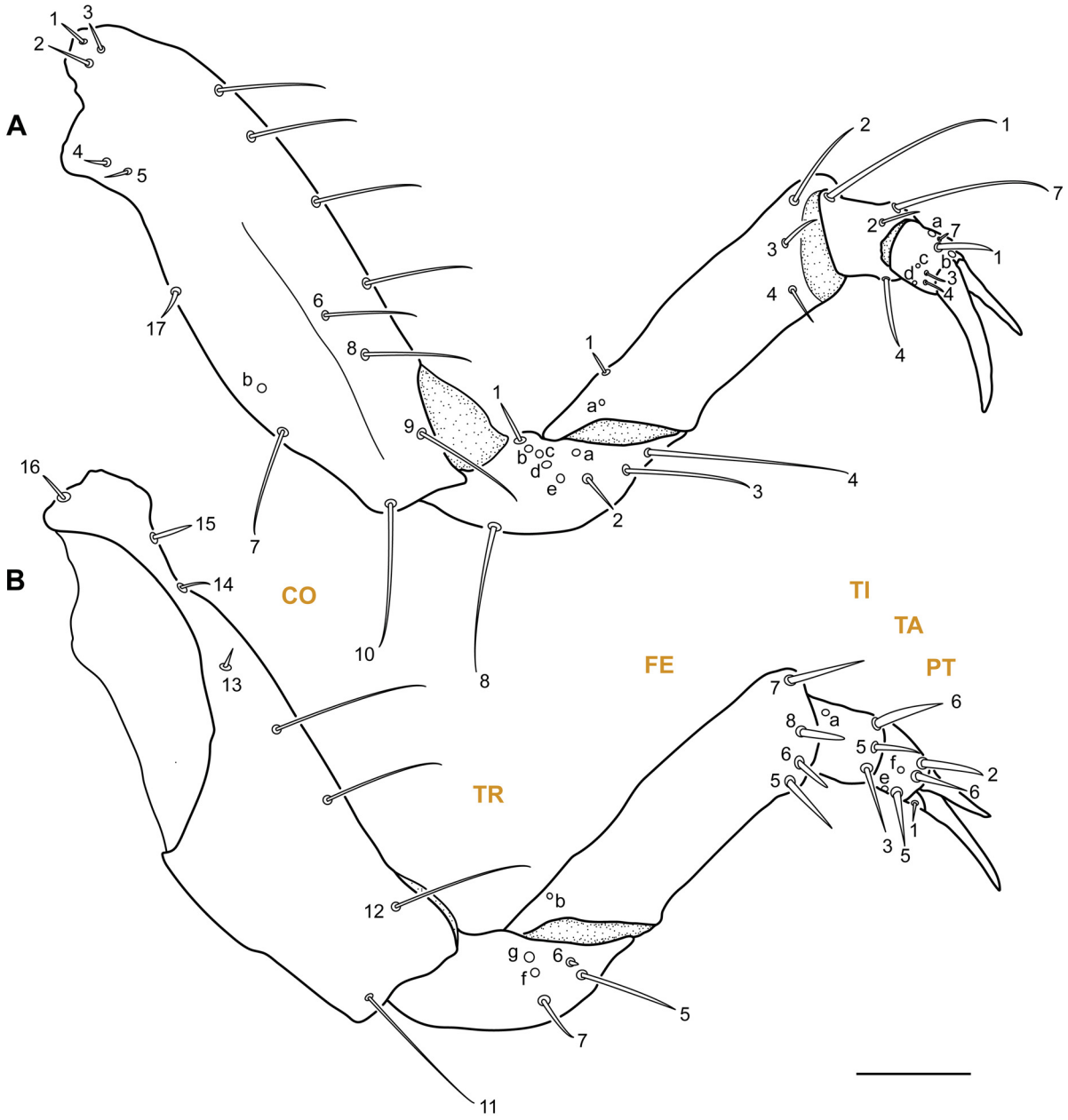

Fig. 5. *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), instar I. A – left metathoracic leg, anterior view. B – right metathoracic leg, posterior view. Numbers and lowercase letters indicate primary setae and pores respectively. Abbreviations: CO – coxa; FE – femur; PT – pretarsus; TA – tarsus; TI – tibia; TR – trochanter. Scale bar = 0.1 mm.

0–2 minute sensilla on distal half. *Maxilla* (Figs 3D–E, 7B, 8C–D). Cardo with one hair-like seta (MX1); dorsal surface of stipes with transverse row of 7–10 hair-like additional setae on central portion, one long hair-like seta (MX6), 2–3 hair-like setae (MX15 and 1–2 additional setae) and one short spine-like seta (MX5) on internal margin, one hair-like seta (MX3) and one pore (MXa) on external margin, and three additional setae on sclerotized bar; ventral surface of stipes with one hair-like seta (MX4) near internal margin, two pores (MXb, MXc) on central portion and one hair-like seta (MX2) on external margin; GA1 with one seta (MX7) on anterointernal angle; GA2 with one seta (MX16) on dorsal surface, two pores (MXd, MXh) on ventral surface, and two setae (MX8, MX9) and a sensillar field on apex; palpifer with one long seta (MX10) on ventral surface; MP1 with one minute seta (MX13) and one pore (MXe) on dorsal surface, and one pore (MXf) on ventral surface; MP2 with one seta (MX12) and one pore (MXi) on dorsodistal portion, and one hair-like seta (MX11) and one pore (MXg) on ventral surface; MP3 with one minute seta (MX14) on dorsoexternal margin, a few placoid sensilla on surface, and several minute sensilla at apex (gMX). *Labium* (Figs 3F–G, 8E). Postmentum with one seta (LA7) on lateral margin; prementum with two hair-like setae (LA3, LA4) on dorsolateral margin, and one short seta (LA1), one long seta (LA2) and one pore (LAa) on ventral surface; LP1 with one short seta (LA9) and one pore (LAb) on ventral surface; LP2 with one spine-like seta (LA11) and one pore (LAc) ventrally at mid-length, 1–2 minute sensilla and three placoid sensilla on surface,

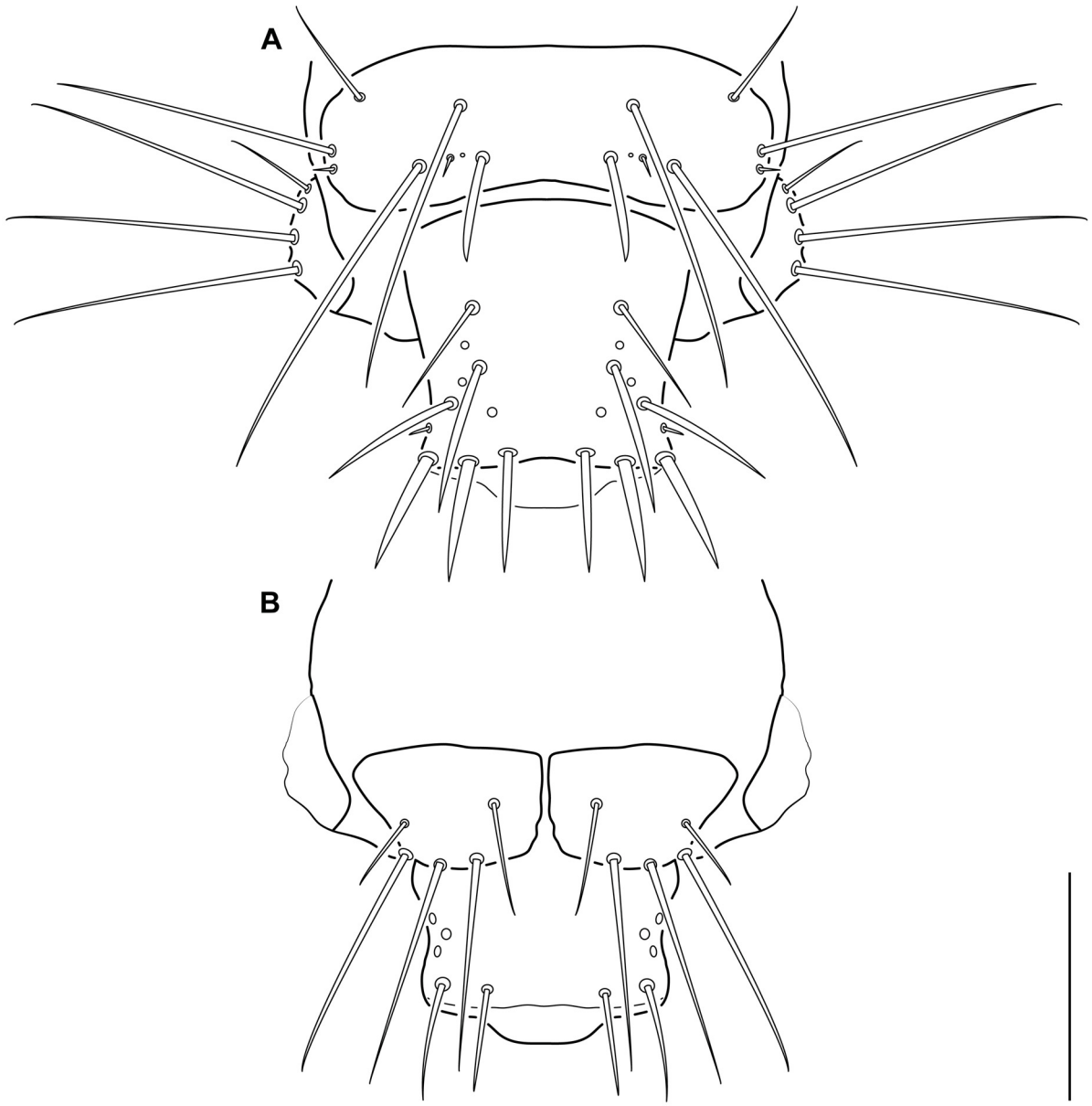

Fig. 6. *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), instar I. A – abdominal segment IX and pygopod, dorsal view. B – abdominal segment IX and pygopod, ventral view. Scale bar = 0.20 mm.

and several minute sensilla at apex (gLA), dorsal surface of ligula (Fig. 3) with ten hair-like setae on lateral margin; ventral surface of ligula (Fig. 3I) with two hair-like setae (LA5, LA6). *Thorax*. Protergite (Figs 4A, 7) with short hair-like seta, two spatulate setae and two pores on anterior margin, two spatulate setae and two pores on anterolateral angle, five hair-like setae and three pores on lateral margin, six hair-like setae, one spatulate seta and one pore on posterior margin, and two short spatulate setae, four long spatulate setae, two hair-like setae and four pores on disc. *Legs* (Figs 4B–C, 5, 9A–B). Anterior surface of coxa with six short setae (CO1, CO2, CO3, CO4, CO5, CO17) and one pore (COa) on proximal portion, five hair-like setae (CO6, CO7, CO8, CO9, CO10) and one pore (COb) on distal portion, and 2–4 additional hair-like setae (3–4 / 2 / 4 on pro-, meso- and metathoracic leg, respectively) on dorsal margin; posterior surface of coxa with four short setae (CO13, CO14, CO15, CO16) on proximal portion, 2–3 additional hair-like setae (3 / 2 / 3 on pro-, meso- and metathoracic leg respectively) at mid-length, and two hair-like setae (CO11, CO12) on distal portion; anterior surface of trochanter with one short seta (TR1) on dorsal margin, three setae (TR3, TR4, TR8) on ventral margin, and one seta (TR2) and five pores (TRa, TRb, TRc, TRd, TRe) on central portion; posterior surface of trochanter with three setae (TR5, TR6, TR7) and two pores (TRf, TRg) on distal region; anterior surface of femur with one seta (FE1) and one pore (FEb) on proximal portion, and three setae (FE2, FE3, FE4) and 0–2 minute sensilla on distal portion; posterior surface of femur with one pore (FEa) on proximal portion, and four setae (FE5, FE6, FE7, FE8) and 0–1 minute sensilla on distal margin; anterior surface of tibia with three setae (TI1, TI2, TI7) on dorsal margin, and one seta (TI4) on ventral margin; posterior

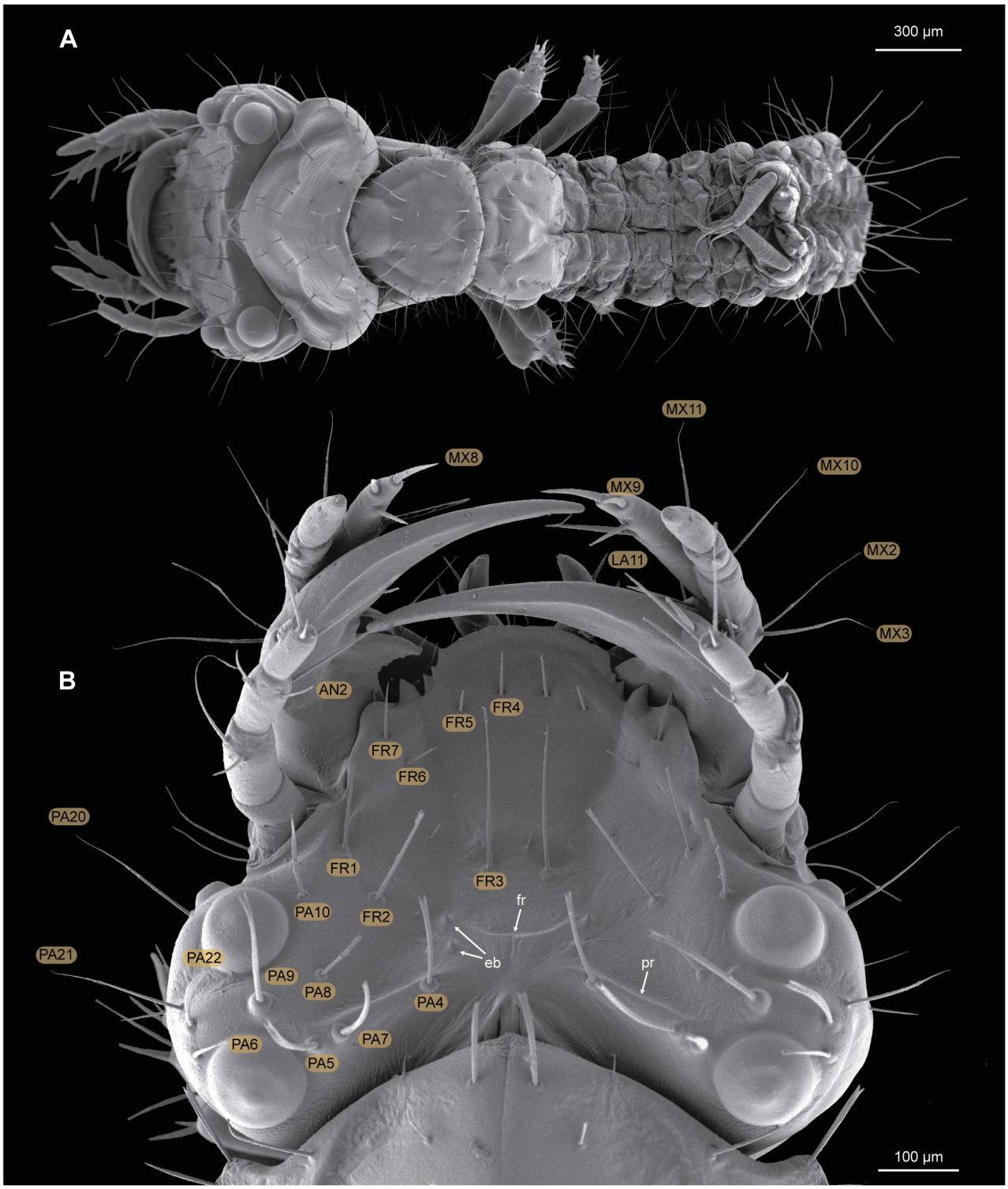

Fig. 7. *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), SEM images of instar I. A – habitus, dorsal view. B – cephalic capsule, dorsal view. Numbers and lowercase letters indicate primary setae and pores respectively. Abbreviations: AN – antenna; FR – frontoclypeus; MX – maxilla; PA – parietal; eb – egg burster; fr – ridge on the posterior part of frontoclypeus; pr – ridge on the posterior part of parietal.

surface of tibia with one pore (TIa) on proximal portion, and three setae (TI3, TI5, TI6) on distal margin; anterior surface of tarsus with three short setae (TA3, TA4, TR7), one long spine-like seta (TA1) and four pores (TAa, TAb, TAc, TAd) on distal half; posterior surface of tarsus with three setae (TA2, TA5, TA6) and two pores (TAe, TAf) on distal half; pretarsus with one seta (PT1) on basoventral portion. *Abdomen*. Abdominal tergite V (Figs 4D, 7) with three hair-like setae on anterior part, one hair-like seta and one short seta on posterolateral part, two setae and one pore on inner hook, and one hair-like seta on median hook. Abdominal tergite IX (Fig. 6A) with one short spine-like seta and two long setae on lateral margin, and one short spine-like seta, one long spine-like seta, two very long

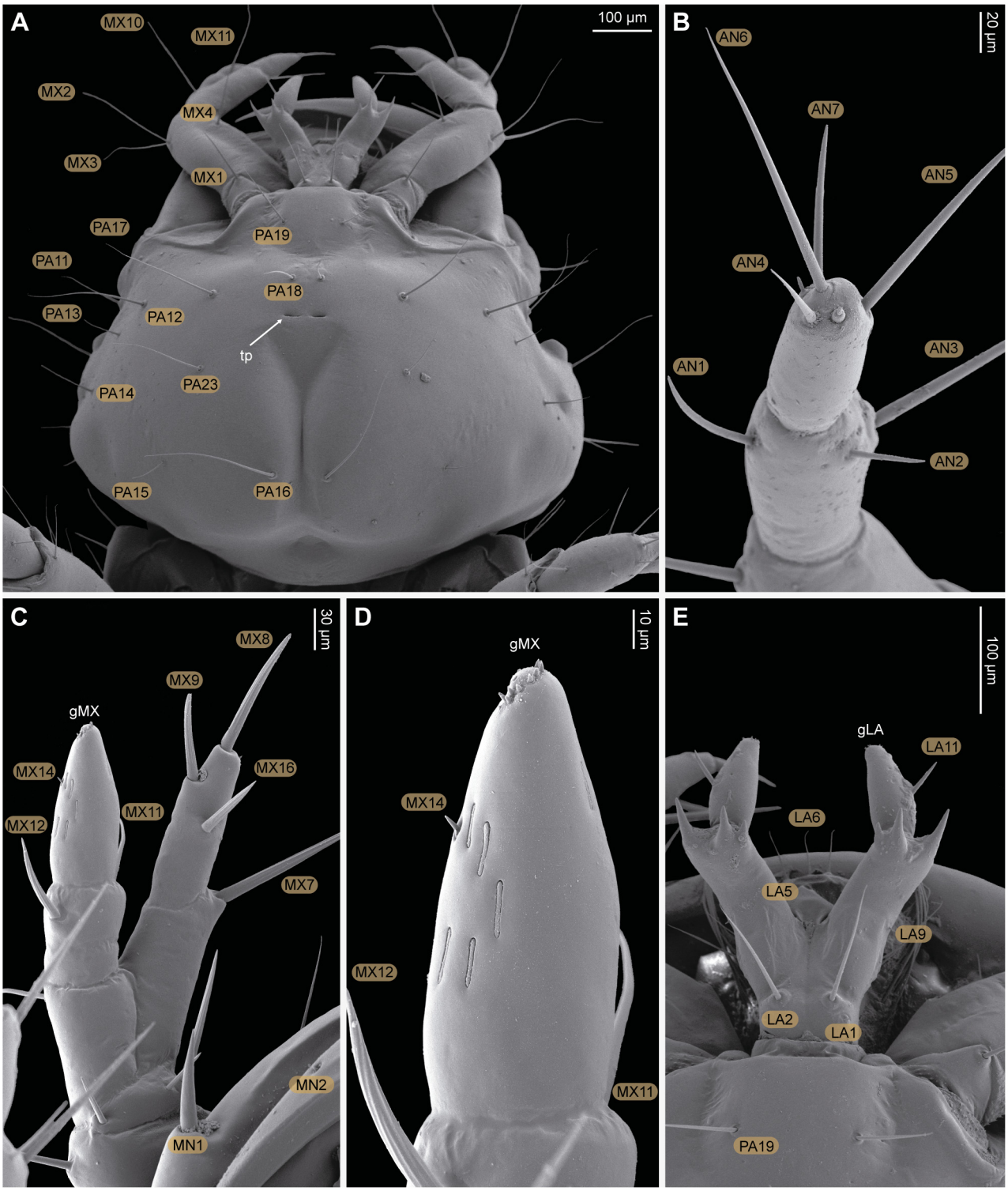

Fig. 8. *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), SEM images of instar I. A – cephalic capsule, ventral view. B – antenna, dorsofrontal view. C – maxilla and portion of mandible, dorsal view. D – maxillary palpomere 2, dorsal view. E – labium, ventral view. Numbers and lowercase letters indicate primary setae and pores respectively. Abbreviations: AN – antenna; FR – frontoclypeus; gLA – labial group; gMX – maxillary group; LA – labium; MN – mandible; MX – maxilla; PA – parietal.

setae and one pore on central portion. Abdominal sternite IX (Fig. 6B) with two hair-like setae on mid-length and three hair-like setae on posterior margin. Dorsal surface of pygopod (Figs 6A, 9C) with one short seta, three long setae and 3–4 pores on lateromedial region, and three long setae on distal margin; ventral surface of pygopod (Fig. 6B) with three pores on lateromedial region and two long setae on distal margin.

Instar II (Fig. 10A; Tables 1–3). As for instar I except for the following features:

Color. Head and protergite with more intense coppery bronze coloration.

Structure. *Body*. Measurements and ratios that characterize body shape are shown in Table 1. *Head*. Egg

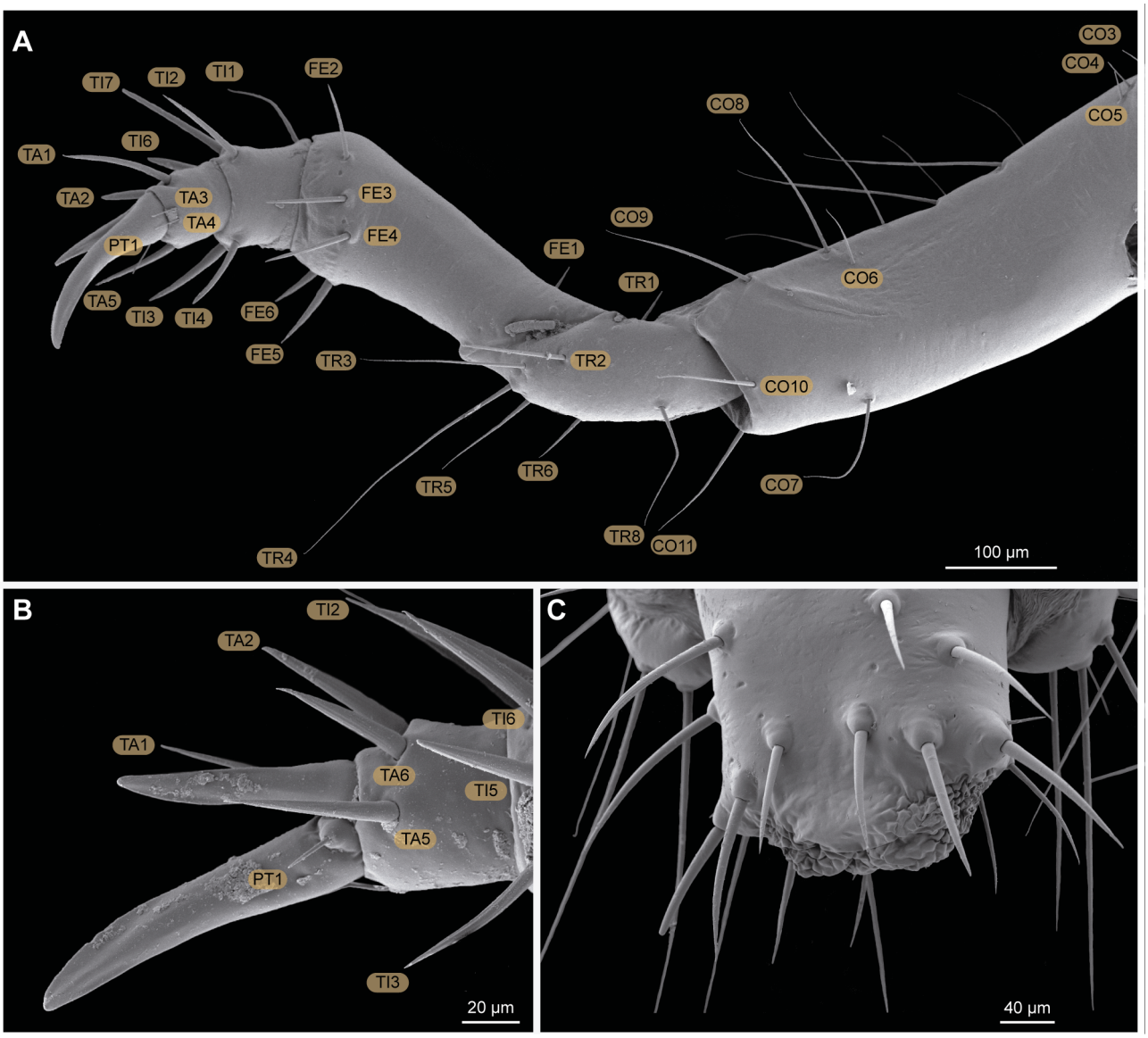

Fig. 9. *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), SEM images of instar I. A – prothoracic leg, anterior view. B – apex of mesothoracic leg, ventral view. C – pygopod, dorsal view. Numbers and lowercase letters indicate primary setae and pores respectively. Abbreviations: CO – coxa; FE – femur; PT – pretarsus; TA – tarsus; TI – tibia; TR – trochanter.

bursters absent. *Abdomen*. Anterior part of tergite V more developed, formed by three plates (two anterior and one laterointernal) (Fig. 10A).

Chaetotaxy. *Head*. Frontoclypeus with two short secondary setae near FR4 and FR5, and 2–4 minute secondary sensilla on anterior portion, 5–7 short secondary setae and 10–12 minute secondary sensilla on basal half, and one hair-like secondary seta near coronal suture; dorsal surface of parietal with one short secondary seta near PA10, one short secondary seta near PA4, two spatulate secondary setae near PA9, and one secondary seta on lateral margin between PA20 and PA21; ventral surface of parietal with one hair-like secondary seta near PA18, five hair-like secondary setae on distal half, and two hair-like secondary setae near gular suture; A1 with one short secondary seta on dorsal surface, three long secondary setae on internal margin, and one hair-like secondary seta on external margin; A2 with one secondary seta on dorsal surface and three secondary setae on ventral surface; dorsal surface of mandible with two spine-like secondary setae near MN1 (one on dorsal surface and the other on external margin), five spine-like secondary setae on posterior region (one on external margin), 10–13 minute secondary sensilla on surface; stipes with 6–8 hair-like secondary setae on dorsal surface, 1–2 hair-like secondary setae and 2–3 short conical secondary setae on ventrointernal margin, one long hair-like secondary seta between MX2 and MX3, 2–3 short secondary setae on ventroexternal margin, and 3–4 short secondary setae on posterointernal angle; GA1 with one secondary seta on internal margin; GA2 with two secondary setae on dorsal surface; palpifer with three secondary setae on dorsal surface; LP1 with three secondary setae on dorsodistal margin and one secondary seta on ventrodistal margin. *Thorax*. Protergite with five secondary setae on anterior margin, five secondary setae on anterolateral angle, three secondary setae on lateral

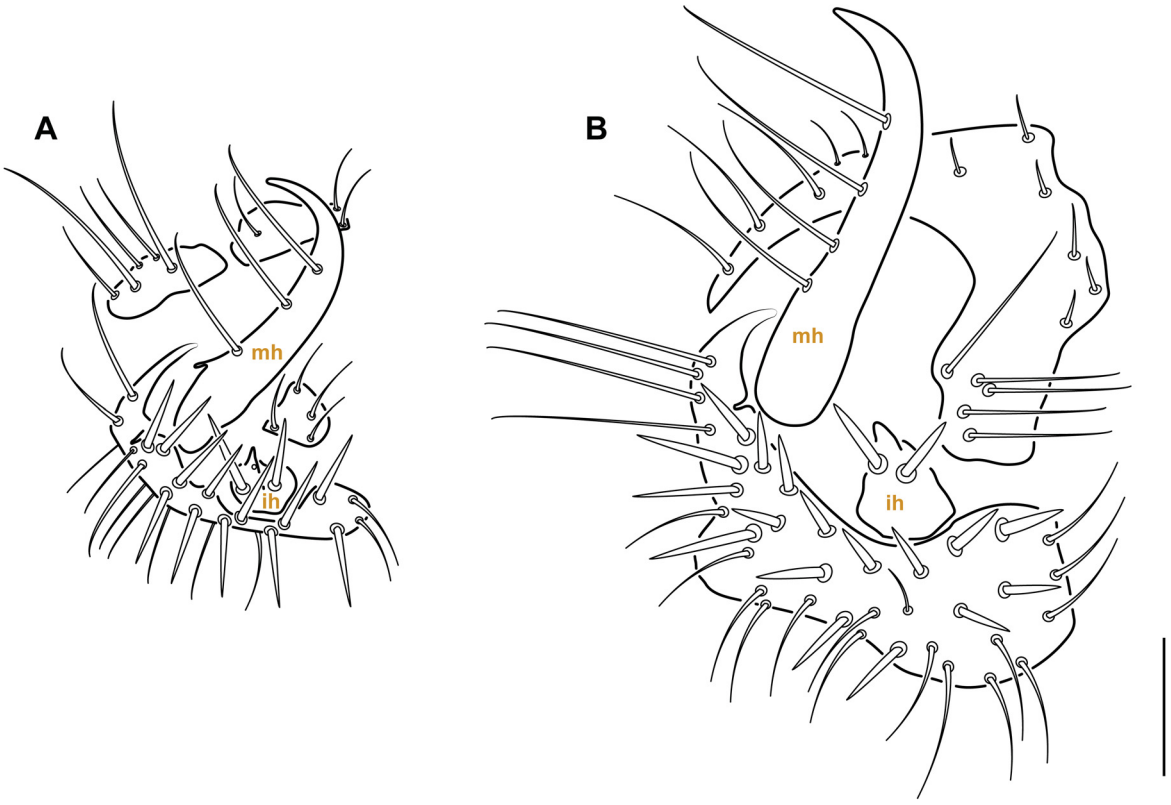

Fig. 10. Abdominal tergite V of *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), dorsal view (left half). A – instar II. B – instar III. Abbrevitions: ih – inner hook; mh – median hook. Scale bar = 0.25 mm.

margin, ten secondary setae on posterior margin, and two long secondary setae, eight short secondary setae and four secondary pores on disc; secondary leg setation detailed in Table 2. *Abdomen*. Abdominal segments I–IX with several secondary setae; abdominal tergite V (Fig. 10A) with nine hair-like secondary setae on anterior region (two on anteroexternal plate, three on anterointernal plate, and four on lateroexternal plate), 12 spine-like secondary setae and 10 hair-like secondary setae on posterolateral region, and two hair-like secondary setae on median hook; dorsal surface of pygopod with five secondary setae on basal half, 2–3 secondary setae on distal half; ventral surface of pygopod with 7–8 hair-like secondary setae on posterior half.

Instar III (Figs 10B. 11A; Tables 1–3). As for instar II except for the following features:

Color. Head with bright golden coloration; protergite with broad light brown band along margins. Some larvae have darker abdomen.

Structure. *Body*. Measurements and ratios that characterize body shape are shown in Table 1. *Abdomen*. Anterior part of tergite V more developed, plates fused (Fig. 10B).

Chaetotaxy. *Head.* Frontoclypeus with 1–2 short secondary setae and several minute secondary sensilla on basal half; ventral surface of parietal with one hair-like secondary seta near PA17 and 5–6 hair-like secondary setae along gular suture; A1 with one short secondary seta on internal margin, and one hair-like secondary seta on external margin; A2 with 1–2 secondary setae on dorsal surface; GA1 with one secondary seta on internal margin; palpifer with three secondary setae on dorsal surface; LP1 with one secondary seta on dorsodistal margin. *Thorax*. Protergite with three secondary setae on anterior margin, 10–12 secondary setae on lateral margin, and 1–2 secondary setae on posterior margin; secondary leg setation detailed in Table 2. *Abdomen*. Abdominal segments I–IX with several secondary setae; abdominal tergite V (Fig. 10B) with four hair-like secondary setae on anterior region, 3–5 spine-like secondary seta and 8–9 hair-like secondary setae on posterolateral part, and 0–1 hair-like secondary setae on median hook; dorsal surface of pygopod with four secondary setae on basal half and six secondary setae on distal half; ventral surface of pygopod with 2–3 hair-like secondary setae on posterior half.

Comparative notes on larval instars. Zikan (1929) briefly described the larva of *C. apiata*. Based on its body size and the number of setae on the median hook we infer that it belongs to instar III. He reported a larger body size (17 mm) and a higher number of setae (up to five) on the median hook with respect to the specimens described in this paper. Besides *C. apiata*, *C. gormazii* (instar III; also inferred by us) and *C. suturalis* (instars I and III) are the only other species of the subgenus with larvae described to date (Cekalovic & Reyes 1985, Adis et al. 1998, Arndt et al. 2002). Instar I of *C. apiata apiata* and *C. suturalis* differ in the number of setae on tergite V. While *C. apiata apiata* has three hair-like setae on the anterior part, and one hair-like seta and one short seta on the posterolateral part (Fig. 4D), *C. suturalis* presents two hair-like setae on the anterior part and two hair-like setae on the posterolateral part (Adis et al. 1998). On the other hand, instar III

Fig. 11. *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825), habitus of instar III and male pupa. A, D – lateral view. B – dorsal view. C – ventral view. . Scale bars = 2.0 mm.

of *C. suturalis* has a distinctive metallic green luster on the head and pronotum (Arndt et al. 2002), whereas *C. apiata apiata* has a coppery bronze to golden coloration. No reliable morphological differences could be found to distinguish the mature larvae of *C. gormazii* from those of the other two species. Chaetotaxic characters may potentially provide additional diagnostic features. However, previous descriptions of *C. gormazii* and *C. suturalis* did not emphasize this character system.

A summary of characters useful for identifying larval instars of *C. apiata apiata* is presented in Table 3.

Pupa (Figs 11B–D; Table 4). ***Color.*** Eyes black; body white, with cephalic capsule, head appendages, pro- and mesotergite, wings, and abdominal spines darkened to brown; as the pupa becomes older, the abdomen turns to testaceous (Figs 11B–D).

Structure. *Body*. Measurements and ratios that characterize body shape are shown in Table 4. *Head.* Glabrous; eyes prominent; median frontal boss extending to clypeus; antennae long, extending dorsally between legs; labrum subcircular, wider than long, distal portion unilobed, with lateral margins sinuate. Adult structures, such as the mandibles, labrum, and antennae, are visible beneath the pupal cuticle.

Thorax. Pronotum subrectangular, transverse, clearly narrower than meso- and metanotum, with anterior margin

Table 2. Number and position of secondary setae on the legs of larvae of *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825). Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. Total – total number of secondary setae on the article (i.e., excluding primary setae).

Article	Position	Instar II (n = 2)	Instar III (n = 3)
Coxa	anterodorsal	5–6/5–9/7–8	1–2/0–1/5–6
	posterodorsal	7/5/4	6/1–2 /1–5
	anterodistal	3–4/1–3/2	0–1/1–3/1–2
	posterodistal	2–3/3–5/2–3	0–2/0–1/0–2
	total	17–20/14–22/15–17	7–11/2–7/7–15
Trochanter	anterior	0/1/1	1–2/0/0–1
	posterior	1/2/3	2/0–1/0–3
	anteroventral	6/3–4/4–5	0/2 –3/2–4
	total	7/6–7/8–9	3–4/2–4/2–8
Femur	anterior	3/3/3	1/3/1–3
	posterior	7–8/7–8/6–7	1–5/2–5/1–5
	anterodistal	0/0/0–1	1/0–1/0
	posterodistal	2–3/2/2	0/0/0
	total	12–14/12–13/11–13	3–7/5–9/2–8
Tibia	anterior	3/3/3	1–2/0–1/0

somewhat arcuate, rounded in middle, anterolateral angles slightly prominent; lateral margins sinuate, convergent posteriorly, with series of short hair-like setae; posterior margin with median lobe and series of short hair-like setae; mesonotum subtrapezoidal, broader than long, with sulcus on midline; metanotum subtrapezoidal, smaller than mesonotum, with sulcus on midline; sagittal line well visible on protergite, faintly visible on meso- and metatergite.

Abdomen. Spines on tergites I–IV subequal, with 4–5 hair-like setae on apex; spines of tergite V longer and more robust, twice as long as those on tergites I–IV, with 9–10 hair-like setae on apex.

Comparative notes on pupa. As previously reported by Serrano (1991), several morphological traits distinguish male and female cicindelid pupae. Our observations are consistent with these findings: the first four protarsomeres of males are expanded, which is not observed in females; females have a larger abdominal index (AI = 88.7) compared to males (AI = 74.5–77.0), due to extended segments VI–X; gonocoxae are visible as ventrolateral spurs on the abdominal apex of females, and the apex of aedeagus is visible on the lateral part of the abdominal apex of males. However, we observed that the aedeagus apex is visible on the left side (Figs 11B, C), in contrast to Serrano (1991) who reported it to be on the right side. On the other hand, Zikan (1929) provided a brief description of the pupa of *C. apiata* as follows (translated from German): *"The pupa is 8.9–12 mm long, with 10 abdominal spines (five on each side), the last of which, directed backward, is the longest. This spine ends in three setae, while the others end in a single seta"*. Our observations differ from that description only in the smaller size (TL = 7.3–8.1 mm) and in the higher number of hair-like setae in the abdominal spines (4–5 setae on tergites I–IV, 9–10 setae on tergite V).

Ecological peculiarities. In Villa Ciudad Parque, Córdoba Province, adults and larvae were found inhabiting a cliff about 10 m high near Los Reartes River, where they were concentrated in a specific area (Fig. 1A). During the summer, when adults are recorded in greater numbers, they were also observed near the shores of the river and along the edges of temporary pools that form on the roads. The vertical walls of the cliff seem to be the preferred oviposition sites for females, where larvae later develop. We registered larvae of instars I and II in January (when mating and oviposition were also observed), and larvae of instar III and pupae on September 30, 2024 (no adults were observed). However, the previous year, around the same date (October 5, 2023), adults were collected, suggesting that adult emergence occurs in early spring. Adults of *C. apiata* were previously recorded from November to March (Erwin & Pearson 2008); however, based on our observations and records from the citizen science platform iNaturalist, we can infer that adults of *C. apiata* are observed from early spring (October) to mid-autumn (April) (Fig. 12). It is unknown whether the adults die at the end of the summer or hibernate.

In January 2025, a river flood reached the collection site (Fig. 1), submerging a large portion of the burrows. As many tiger beetle species inhabit riverine habitats worldwide, their usually soil-dwelling, sedentary, and long-lived larvae are exposed to flooding (Zerm & Adis 2003). As an adaptation to hypoxic conditions, some species have larvae that switch to anaerobic metabolism during immersion (e.g., Hoback et al. 2000, Zerm & Adis 2003, Brust & Hoback 2009). This capacity for anaerobic metabolism is likely to occur in *C. apiata*, but could not be confirmed in this study.

Discussion

The larvae and pupae of *Cylindera* (*Plectographa*) *apiata apiata* are redescribed herein, including instars I and II for the first time. Larvae of this species share all characters previously described for *Cylindera* (Putchkov & Arndt 1994, Arndt et al. 2002, Putchkov et al. 2019): i) dorsal surface of cephalic capsule and protergite with metallic lustre; ii) ridge on the posterior part of frontoclypeus U-shaped and distinctly separated from the ridge on the caudal part of parietal (Figs 2A, 7B); iii) gular suture

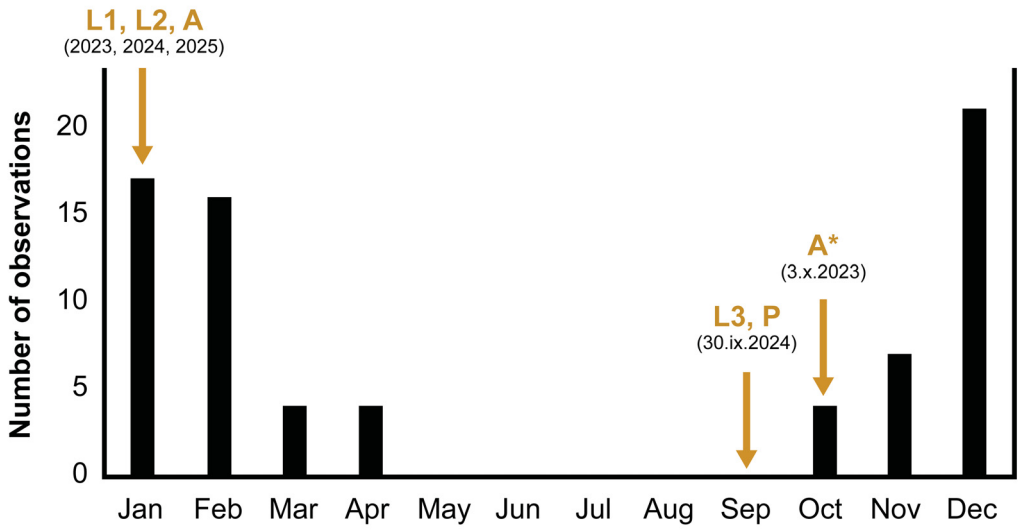

Fig. 12. Number of observations of adults of *Cylindera* (*Plectographa*) *apiata* (Dejean, 1825) per month from iNaturalist (Oct 2014–Feb 2025). Arrows indicate sampling dates in Villa Ciudad Parque, Córdoba Province (Fig. 1). Abbreviations: A – adult; L1 – instar I; L2 – instar II; L3 – instar III; P – pupa. *No check for active burrows was conducted on this date.

ending in a T-shaped groove (Figs 2B, 8A); iv) basal part of cephalic capsule W-shaped ventrally (Figs 2B, 8A); v) maxillary palpomere 1 without spines and setae; vi) labial palpomere 2 with a short spine-like seta at mid-length (Figs 3G, 8E); vii) abdominal segment V with 2 pairs of hooks (Fig. 4D); viii) median hooks at least 2 times longer than inner hooks (Fig. 4D); ix) median hooks of abdominal tergite V arched apically with hair-like setae (Figs 4D, 7A); x) central spine of inner hooks straight and shorter than lateral setae (Fig. 4D).

As previously mentioned, this study is the first in providing a detailed description of the chaetotaxy of a cicindelid larva. A total of 178 primary sensilla (109 setae and 69 pores) were coded and illustrated (Figs 2–6, 12). It is worth mentioning, however, that the nomenclature system provided here is provisional, given that this is the first genus for which the chaetotaxy has been fully described. Despite this, it is useful to compare the ground plan of primary chaetotaxy of Cicindelidae with those previously provided for other adephagan families, especially with Carabidae, which, together with Trachypachidae, form the monophyletic group collectively known as Geadephaga (McKenna et al. 2019, Beutel et al. 2020, Gustafson et al. 2020, Vasilikopoulos et al. 2021). The comparison with Trachypachidae is difficult due to the lack of comprehensive study on the chaetotaxy of its larvae.

The cephalic capsule chaetotaxy is similar to that described for *Cicindela* (Bousquet & Goulet 1984) and several hydradephagan families (Fig. 13). The parietal pores PAf and PAc, present in *Cylindera* (Fig. 2A), are absent in *Cicindela*. These pores, however, are small and somewhat difficult to see, with one located near the margin and the other close to the base of setae PA8 and PA9. The parietal setae here labeled as PA6, PA20, PA21 and PA22 are present in *Cicindela*. Whereas PA6 is present in all adephagan families, the presence of PA20, PA21 and PA22 is restricted to Dytiscidae (Alarie & Michat 2023). We provisionally consider PA23 (Fig. 2B) a plesiomorphic seta for Cicindelidae, as it is also present in at least one genus of Carabidae (Di Giulio et al. 2021).

The chaetotaxy of the antenna is, in general, similar to that of other adephagan families. The most conspicuous differences are the presence of seta AN7 and the absence of pore ANh. These characteristics are shared by Carabidae and Noteridae (Fig. 13). On the other hand, the antenna has several additional setae. The antennomere 2 bears two long additional setae (Fig. 3B) which are also present in several other cicindelid genera (e.g., Lin 2012, 2014; Putchkov &

Table 3. Morphological characters allowing recognition of larval instars of *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825).

Character	Instar I	Instar II	Instar III
Egg burster	present	absent	absent
Maximum head width	0.86–0.90	1.35–1.43	2.05–2.08
Maximum pronotum width	0.89–0.91	1.44–1.45	2.08–2.38
Setae on antennomere 1	0	5	7–8
Setae on antennomere 2	2	6	8
Setae on galeomere 1	1	2	3
Setae on galeomere 2	3	5	5
Setae on palpifer	1	4	7
Setae on labial palpomere 1	0	3	4
Setae on median hook	1	3	3–4

Markina 2020; Schule et al. 2021), suggesting that they could potentially be considered ancestral traits for Cicindelidae. Additionally, there is a group of three short additional setae near the apex of antennomere 3 (Fig. 3A). It is worth noting that in Carabidae and Trachypachidae, this region contains the sensory appendage of antennomere 3.

Mandible posed no problem in homologation. The mandibles in Cicindelidae, as in Carabidae, Aspidytidae, Hygrobiidae, Noteridae, Trachypachidae and many Dytiscidae, have only two setae (MN1–2) and three pores (MNa–c) (Fig. 3C). However, up to two minute additional sensilla may appear on distal half.

Also, the maxilla presents no major problems for homologation. As in Carabidae and Trachypachidae, the main difficulty arises in the stipes due to the presence of additional setae. We provisionally identified setae MX5, MX6, and MX15, but homologies are difficult to establish due to presence of additional setae on this region of the stipes. The third labial palpomere in cicindelid larvae bears a single seta on the surface, which we interpret as MX14 based on positional homology. This seta can also be observed in some carabid larvae (Moore & Di Giulio 2006, Di Giulio et al. 2021), and is consistently present within Hydradephaga. The same applies to the only seta present on the second galeomere of Cicindelidae larvae, here interpreted as MX16. This seta is also present in Carabidae (Moore & Di Giulio 2006) but within Hydradephaga, it is known to occur only in Noteridae (Urcola et al. 2019). The seta MX13 is present in cicindelid larvae (Fig. 3D) and in all Hydradephaga families but absent in Carabidae and Trachypachidae (e.g., Bousquet & Goulet 1984, Arndt & Beutel 1995, Moore & Di Giulio 2006, Gilgado et al. 2011). It should be noted, however, that this seta is very small and difficult to observe. The pores MXh on the galea and MXi on the second palpomere are also absent in Carabidae but present in Cicindelidae and along Hydradephaga.

The chaetotaxy of the labium is very similar to that described for Noteridae (Urcola et al. 2019). The only difference is the absence of pore LAd in Cicindelidae, similar to the condition found in Carabidae and Gyrinidae (Fig. 13). The setae LA9, present in Cicindelidae, is absent in Carabidae and Trachypachidae (e.g., Bousquet & Goulet 1984, Arndt & Beutel 1995, Saska 2004, Gilgado & Ortuño 2011, Di Giulio et al. 2021).

The chaetotaxy of the legs is, as a rule, very similar to that described for Carabidae (Bousquet & Goulet 1984) and other Adephaga. Both families are distinguished from their aquatic counterparts by the presence of pore COb on the coxa and of seta TR8 on the trochanter. Additionally, Cicindelidae differ from Carabidae in the absence of the pores COc, COd, and COe and in the presence of the setae FE7 and FE8. The presence of a single seta on the pretarsus (Fig. 9B) is unique to Cicindelidae, whereas the other Adephagan families have two setae in this region (PT1 and PT2) (Fig. 13).

The comparison of the chaetotaxy pattern of the last abdominal segment and urogomphus within Adephaga is problematic due to differences in the number of abdominal segments among families, the absence of urogomphi in certain families, and the presence of additional setae in both structures in some taxa.

Table 4. Measurements and ratios for the pupae of *Cylindera* (*Plectographa*) *apiata apiata* (Dejean, 1825).

	Male (n = 2)	Female (n = 1)
Measure		
TL (mm)	7.31–8.08	8.47
HL (mm)	1.46–1.75	1.85
HW (mm)	2.09–2.14	2.19
IOD (mm)	0.58–0.78	0.83
LAL (mm)	0.49–0.54	0.54
LAW (mm)	0.97–1.17	1.24
PNL (mm)	0.88–1.07	0.93
PNW (mm)	1.70–1.75	1.85
MNL (mm)	0.93–1.07	1.02
MNW (mm)	2.29–2.39	2.53
AI–VL (mm)	2.68–3.00	3.02
AVI–XL (mm)	2.00–2.31	2.68
T1L (mm)	0.39–0.46	0.39
T2L (mm)	0.39–0.41	0.49
T3L (mm)	0.36–0.44	0.44
T4L (mm)	0.39	0.44
T5L (mm)	0.80–0.85	1.00
T1W (mm)	1.51–1.70	2.14
T2W (mm)	1.46–2.09	2.05
T3W (mm)	1.75–1.95	2.58
T4W (mm)	2.24–2.24	2.44
T5W (mm)	2.44–2.73	3.17
Setae number		
PAS	0	0
PLS	22–27	21
PPS	14	14
T1	4–5	4
T2	4–5	4
T3	4	4
T4	4–5	4
T5	9–10	9
Ratios		
OI	27.27–37.21	37.78
LAI	41.67–55.00	43.14
PNI	50.00–62.86	50
MNI	40.38–44.90	40.38
AI	74.55–77.24	88.71
SI	44.44–45.00	44.44

In correlation with their life habits, cicindelid larvae are strongly modified morphologically (Arndt et al. 2016), exhibiting many differences from carabid larvae, which are detailed in Putchkov & Cassola (2005). In spite of this, based on the species described here, Carabidae and Cicindelidae share a very similar primary chaetotaxy. The larvae of these two families can be distinguished from those forming the Hydradephaga by the presence of the coxal pore COb and the trochanteral seta TR8 (Fig. 4B), and the conspicuous aspect of setae AN4–7 and MX8–9 (Figs 3A–D). In turn, Cicindelidae differ from Carabidae by the presence of the parietal setae PA20–22 (Fig. 2A) and the femoral setae FE7–8 (Fig. 4C), the absence of pores COc–e, and by having a single seta on the pretarsus, a condition unique to Cicindelidae (Fig. 9B) among the Adephaga. It is worth noting that although setae MX13 and LA9 are present in Cicindelidae and have not been documented in Carabidae (Fig. 13), their presence in the

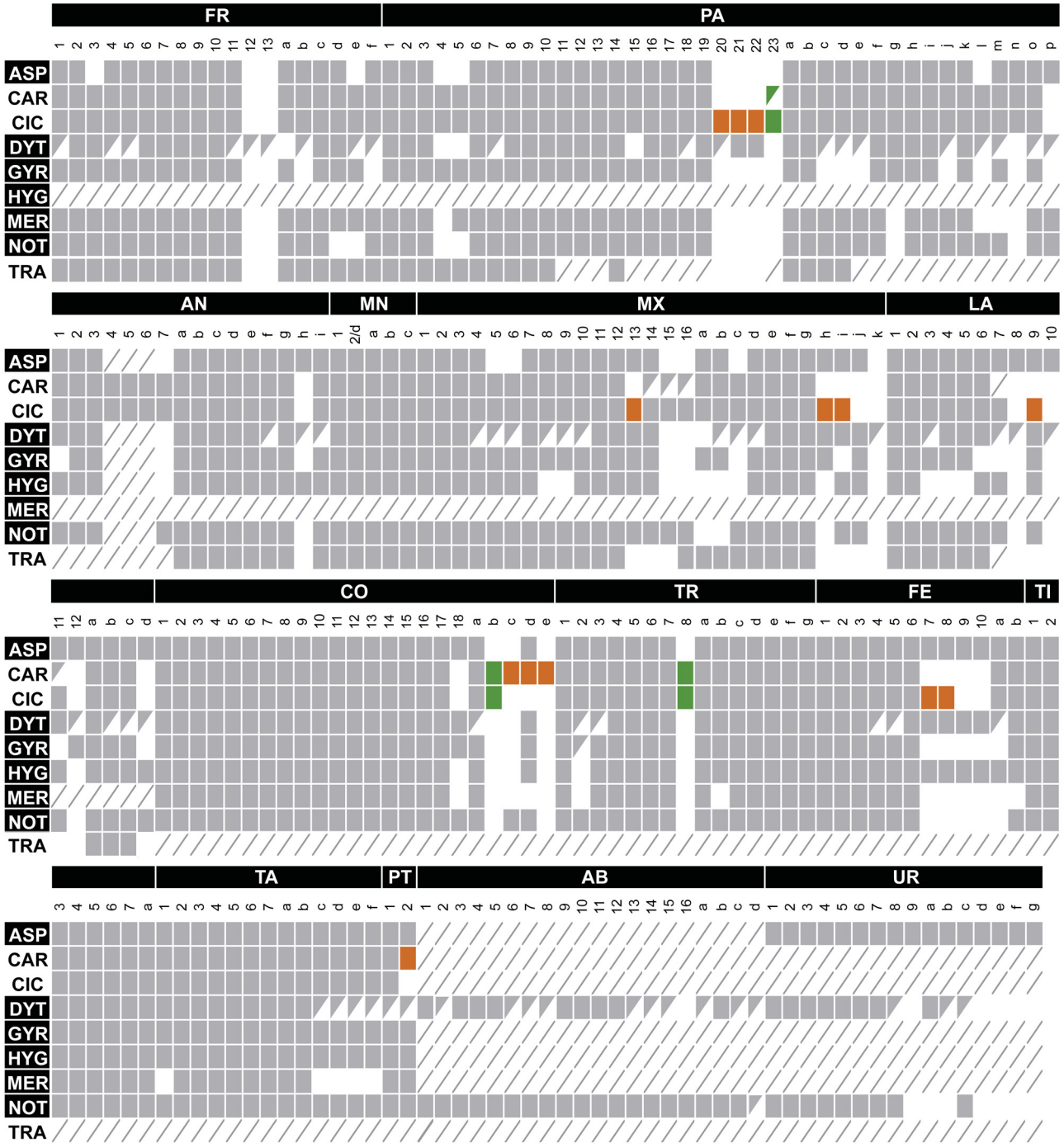

Fig. 13. Setae and pores on the cephalic capsule, head appendages, legs, abdominal segment VIII, and urogomphus of first instars of families of Adephaga (ASP – Aspidytidae; CAR – Carabidae; CIC – Cicindelidae; DYT – Dytiscidae; GYR – Gyrinidae; HYG – Hygrobiidae; MER – Meruidae; NOT – Noteridae; TRA – Trachypachidae); white rectangles, absent; colored rectangles, present (green, characters shared by CAR and CIC; orange, characters differentiating CAR and CIC); gray diagonal band, missing data / not applicable.

latter family should not be excluded given their small size and position, which makes them difficult to observe (particularly MX13).

Acknowledgments

André S. Roza and an anonymous referee are acknowledged for their valuable comments on the manuscript. We sincerely thank Ainara and Ricardo Urcola, Julia Sartini and Valeria Ruiz for their invaluable assistance during the fieldwork, and Florencia Menay for her help in rearing and maintaining the beetles. We would also like to thank Jürgen Wiesner for sharing articles essential to this work. The work of J.I.U. was supported by a postdoctoral scholarship from CONICET. J.I.U., M.R.U., and M.C.M. were supported by the Agencia Nacional de Promoción Científica y Tecnológica under Grant PICT-I-INVI-00460 and by Universidad de Buenos Aires under Grants UBACyT-20020190100240BA, UBACyT-0020220400253BA and FUNDACEN (+4i).

References

ADIS J., PAARMANN W., AMORIM M. A., ARNDT E. & DA ONSECA C. R. V. 1998: On occurrence, habitat specificity and natural history of adult tiger beetles (Coleoptera: Carabidae: Cicindelinae) near Manaus, Central Amazonia, and key to the larvae of tiger beetle genera. *Acta Amazonica* **28**: 247–272.

ALARIE Y., BEUTEL R. G. & WATTS C. H. S. 2004: Larval morphology of three species of Hygrobiidae (Coleoptera: Adephaga: Dytiscoidea) with phylogenetic considerations. *European Journal of Entomology* **101**: 293–311.

ALARIE Y. & BILTON D. T. 2005: Larval morphology of Aspidytidae (Coleoptera: Adephaga) and its phylogenetic implications. *Annals of the Entomological Society of America* **98**: 417–430.

ALARIE Y. & MICHAT M. C. 2023: Larval chaetotaxy of world Dytiscidae (Coleoptera: Adephaga) and implications for the study of Hydradephaga. Pp. 17–53. In: YEE D. A. (ed.): *Ecology, systematics, and the natural history of predaceous diving beetles (Coleoptera: Dytiscidae). 2nd Edition.* Springer, Cham, 573 pp.

ALARIE Y., SHORT A. E. Z., GARCÍA M. & JOLY L. 2011: Larval morphology of Meruidae (Coleoptera: Adephaga) and its phylogenetic implications. *Annals of the Entomological Society of America* **104**: 25–36.

ARNDT E. & BEUTEL R. G. 1995: Larval morphology of *Systolosoma* Solier and *Trachypachus* Motschulsky (Coleoptera: Trachypachidae) with phylogenetic considerations. *Insect Systematics & Evolution* **26**: 439–446.

ARNDT E., BEUTEL R. G. & WILL K. W. 2016: Carabidae Latreille, 1802. Pp. 160–188. In: BEUTEL R. G. & LESCHEN R. A. B. (eds.) *Handbook of Zoology, Vol. IV Arthropoda: Insecta. Part 38. Coleoptera. Vol. 1. Morphology and Systematics. 2nd Edition. (Archostemata, Adephaga, Myxophaga, Polyphaga (partim)*. Walter De Gruyter, Berlin, New York, 684 pp.

ARNDT E. & PUTCHKOV A. V. 1994: Description of larvae of the tiger beetle genera *Lophyra*, *Habrodera* and *Nelaphyra* (Coleoptera: Cicindelidae) from Africa. *European Journal of Entomology* **91**: 407–418.

ARNDT E., ZERM M. & ADIS J. 2002: Key to the larval tiger beetle (Coleoptera: Cicindelidae) of Central Amazonian floodplains (Brazil). *Amazoniana* **17**: 95–108.

BEUTEL R. G., RIBERA I., FIKÁČEK M., VASILIKOPOULOS A., MISOF B. & BALKE M. 2020: The morphological evolution of the Adephaga (Coleoptera). *Systematic Entomology* **45**: 378–395.

BOUSQUET Y. & GOULET H. 1984: Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). *Canadian Journal of Zoology* **62**: 573–588.

BRUST M. & HOBACK W. 2009: Hypoxia tolerance in adult and larval *Cicindela* tiger beetles varies by life history but not habitat association. *Annals of the Entomological Society of America* **102**: 462–466.

BRUST M., HOBACK W. & KNISLEY C. B. 2009: Biology, habitat preference, and larval description of *Cicindela cursitans* Leconte (Coleoptera: Carabidae: Cicindelinae). *Coleopterists Bulletin* **59**: 379–390.

CEKALOVIC T. & REYES M. 1985: Descripción de la larva de *Cicindela* (*Plectographa*) *gomarzi* (Red, 1871) (Coleoptera, Cicindelidae). *Boletin de la Sociedad de Biología de Concepción* **56**: 225–229.

DI GIULIO A., MUZZI M. & FATTORINI S. 2021: Description and illustration of the discotelic larvae of *Pachyteles vignai* Deuve, 1999 and *P. digiulioi* Deuve, 1999 from the Otonga cloud forest (Ecuador) (Coleoptera, Carabidae, Ozaenini). *Memorie della Società Entomologica Italiana* **97**: 47–81.

DURAN D. P. & GOUGH H. M. 2019: Unifying systematics and taxonomy: Nomenclatural changes to Nearctic tiger beetles (Coleoptera: Carabidae: Cicindelinae) based on phylogenetics, morphology and life history. *Insecta Mundi* **727**: 1–12.

ERWIN T. L. & PEARSON D. L. 2008: *A treatise on the Western Hemisphere Caraboidea (Coleoptera): Their classification, distributions, and ways of life. Vol II (Carabidae –Nebriiformes 2 – Cicindelitae)*. Pensoft, Sofia, 400 pp.

FREITAG R. & BARNES B. L. 1989: Classification of Brazilian species of *Cicindela* and phylogeny and biogeography of subgenera *Brasiella*, *Gaymara* new subgenus, *Plectographa* and South American species of *Cylindera* (Coleoptera: Cicindelidae). *Quaestiones Entomologicae* **25**: 241–386.

GILGADO J. D., LÓPEZ H., OROMÍ P. & ORTUÑO V. M. 2011: Description of the first larval instar of *Broscus crassimargo* Wollaston, 1865 (Carabidae: Broscini) and notes about the presence of the species in the mesovoid shallow substratum of La Gomera (Canary Islands, Spain). *Entomologica Fennica* **22**: 45–54.

GILGADO J. D. & ORTUÑO V. M. 2011: Biological notes and description of egg and first instar larva of *Carabus* (*Oreocarabus*) *ghilianii* La Ferte-Senectere 1847 (Coleoptera: Carabidae). *Annales de la Société Entomologique de France (Nouvelle Série)* **47**: 444–456.

GUSTAFSON G. T., BACA S. M., ALEXANDER A. M. & SHORT A. E. Z. 2020: Phylogenomic analysis of the beetle suborder Adephaga with comparison of tailored and generalized ultraconserved element probe performance. *Systematic Entomology* **45**: 552–570.

GWIAZDOWSKI R. A., ANDERSEN J. C., KNISLEY C. B., GRIFFIN B. P. & ELKINTON J. S. 2020: First account of phylogeographic variation, larval characters, and laboratory rearing of the endangered cobblestone tiger beetle *Cicindelidia marginipennis*, Dejean, 1831 with observations of their natural history. *Insects* **11 (708)**: 1–19.

HOBACK W. W., PODRABSKY J. E., HIGLEY L. G., STANLEY D. W. & HAND S. C. 2000: Anoxia tolerance of con-familial tiger beetle larvae is associated with differences in energy flow and anaerobiosis. *Journal of Comparative Physiology B. Biochemical, Systemic and Environmental Physiology* **170**: 307–314.

LAWRENCE J. F. 1991: Order Coleoptera. Pp. 144–658. In: STEHR F. W. (ed.): *Immature Insects, Volume 2*. Kendall/Hunt Publishing Company, Iowa, 992 pp.

LIN T. J. 2012: Description of the immatures of the tiger beetles (Coleoptera: Cicindelidae) from Taiwan (I). *Formosan Entomologist* **32**: 71–96.

LIN T. J. 2014: Description of the immatures of the tiger beetles (Coleoptera: Cicindelidae) from Taiwan (II). *Formosan Entomologist* **34**: 97–128.

McKENNA D. D., SHIN S., AHRENS D., BALKE M., BEZA-BEZA C., CLARKE D. J., DONATH A., ESCALONA H. E., FRIEDRICH F., LETSCH H., LIU S., MADDISON D., MAYER C., MISOF B., MURIN P. J., NIEHUIS O., PETERS R. S., PODSIADLOWSKI L., POHL H., SCULLY E. D., YAN E. V., ZHOU X., ŚLIPIŃSKI A. & BEUTEL R. G. 2019: The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences* **116**: 24729–24737.

MICHAT M. C., ARCHANGELSKY M. & ALARIE Y. 2020: Morphology and chaetotaxy of Neotropical *Haliplus* larvae (Coleoptera: Haliplidae). *Revista Mexicana de Biodiversidad* **91 (e913541)**: 1–12.

MICHAT M. C., GUSTAFSON G. T. & BERGSTEN J. 2017: Larval description and chaetotaxic analysis of *Dineutus sinuosipennis* Laporte, 1840, with a key for the identification of larvae of the tribe Dineutini (Coleoptera, Gyrinidae). *ZooKeys* **718**: 95–114.

MOORE W. & DI GIULIO A. 2006: Description and behaviour of *Goniotropis kuntzeni* larvae (Coleoptera: Carabidae: Paussinae: Ozaenini) and a key to genera of Paussinae larvae. *Zootaxa* **1111**: 1–19.

MORAVEC J. & ŠAFRÁNEK O. 2025: Taxonomic revision of the current concept of *Cylindera morio* and allied taxa (Coleoptera: Cicindelidae). *Acta Entomologica Musei Nationalis Pragae* **65 (1)**: 105–147.

PEARSON D. L., KNISLEY C. B., DURAN D. P. & KAZILEK C. J. 2015: *A field guide to the tiger beetles of the United States and Canada: identification, natural history, and distribution of the Cicindelidae*. Oxford University Press, New York, 251 pp.

PEARSON D. L. & VOGLER A. P. 2001: *Tiger beetles: the evolution, ecology, and diversity of the cicindelids*. Cornell University Press, Ithaca, 333 pp.

PETT B. L., WYER R. & SMITH P. 2022: Contributions to the knowledge of tiger beetles in Paraguay, with new country and departmental records (Coleoptera: Cicindelidae). *Fragmenta Entomologica* **54**: 163–170.

PUTCHKOV A. V. 1994: State-of-the-art and world perspectives of studies on tiger beetle larvae (Coleoptera, Carabidae, Cicindelinae). Pp. 51–54. In: DESENDER K., DUFRÊNE M., LOREAU M., LUFF M. L. & MAELFAIT J.-P. (eds): *Carabid beetles. Ecology and Evolution*. Kluwer Academic Publishers, Dordrecht, 476 pp.

PUTCHKOV A. V. & ARNDT E. 1994: Preliminary list and key of known tiger beetle larvae (Coleoptera, Cicindelidae) of the world. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **67**: 411–420.

PUTCHKOV A. & CASSOLA F. 2005: Tiger Beetles deserve separate family status in suborder Adephaga (Coleoptera, Cicindelidae). *Bulletin de la Société Entomologique de France* **110**: 281–293.

PUTCHKOV A. V. & MARKINA T. Y. 2020: The description of the tiger beetle larvae of *Cosmodela aurulenta* (Fabricius, 1801) (Coleoptera, Cicindelidae). *Zootaxa* **4859**: 537–544.

PUTCHKOV A. V., MARKINA T. Y & NITOCHKO M. I. 2019: Larvae of *Cylindera* (*Eugrapha*) *contorta* (Fleutiaux) (Coleoptera: Cicindelidae) and general review of larval features in the subgenus *Eugrapha*. *Zootaxa* **4664**: 412–422.

ROZA A. & MERMUDES J. R. 2017: Tiger Beetles' (Coleoptera: Carabidae, Cicindelinae) pupal stage: current state of knowledge and future perspectives. *Zootaxa* **4226**: 348–358.

ŠAFRÁNEK O. & AMAYA M. 2021: A new species of the genus *Cylindera* (Coleoptera: Cicindelidae) from southern Bolivia with imitating behaviour to co-occurring ants. *Zootaxa* **4980**: 575–582.

SASKA P. 2004: Larvae of the nominotypical subgenus *Amara* (Coleoptera: Carabidae). *Acta Societatis Zoologicae Bohemicae* **68**: 191–234.

SAWADA H. & WIESNER J. 2002: The tiger beetles of Paraguay (Insecta: Coleoptera: Cicindelidae), 67th Contribution towards the knowledge of Cicindelidae. *Coleoptera, Schwanfelder Coleopterologische Mitteilungen* **4**: 285–325.

SERRANO A. R. M. 1991: Description of the pupal stage of tiger beetles (Coleoptera: Cicindelidae) of Castro Marin –Vila Real Santo António Region (Algarve-Portugal). *Elytron, Supplement* **5**: 197–220.

SPOMER S. M., NABITY P. D. & BRUST M. L. 2008: Larval description of *Cicindela* (*Dromochorus*) *pruinina* (Casey) (Coleoptera: Carabidae: Cicindelinae) with notes on habitat and adult behavior. *Coleopterists Bulletin* **62**: 37–41.

URCOLA J. I., ALARIE Y., BENETTI C. J., RODRIGUEZ G. & MICHAT M. C. 2019: Larval morphology and analysis of primary chaetotaxy in the genus *Suphis* Aubé, 1836 (Coleoptera: Noteridae). *Zootaxa* **4619**: 121–138.

VASILIKOPOULOS A., BALKE M., KUKOWKA S., PFLUG J. M., MARTIN S., MEUSEMANN K., HENDRICH L., MAYER C., MADDISON D. R., NIEHUIS O., BEUTEL R. G. & MISOF B. 2021: Phylogenomic analyses clarify the pattern of evolution of Adephaga (Coleoptera) and highlight phylogenetic artefacts due to model misspecification and excessive data trimming. *Systematic Entomology* **46**: 991–1018.

WIESNER J. & BANDINELLI A. 2014: Notes on the tiger beetles (Coleoptera: Cicindelidae) of Argentina. 117. Contribution towards the knowledge of Cicindelidae. *Insecta Mundi* **377**: 1–66.

ZERM M. & ADIS J. 2003: Exceptional anoxia resistance in larval tiger beetle, *Phaeoxantha klugii* (Coleoptera: Cicindelidae). *Physiological Entomology* **28**: 150–153.

ZIKAN J. J. 1929. Zur Biologie der Cicindeliden Brasiliens. *Zoologischer Anzeiger* **82**: 269−414.