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Immature stages of Taenioderini (Coleoptera: Scarabaeidae: Cetoniinae): a report of hidden morphological diversity

Tomáš VENDL[1)], Dominik VONDRÁČEK[1)], Vítězslav KUBÁŇ[2)] & Petr ŠÍPEK[1,*)]

[1)] Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic

[2)] Department of Entomology, National Museum, Cirkusová 1740, CZ-193 00 Praha 9 - Horní Počernice, Czech Republic

*) Corresponding author; e-mail: sipekpetr80@gmail.com

Abstract. Here we present the first observations on the immature stages of the cetoniid tribe Taenioderini (Coleoptera: Scarabaeidae). The larvae of *Chalcothea neglecta* Ritsema, 1882, *Coilodera diardi* (Gory & Percheron, 1833), *C. penicillata* Hope, 1831, *Euselates cineraceus* (Gory & Percheron, 1833), *E. laoticus* Mikšić, 1974, *Meroloba suturalis* (Snellen van Vollenhoven, 1858), *Plectrone tristis* (Westwood, 1842) and an undetermined species belonging to *Taeniodera idolica* Janson, 1909 species group are described and illustrated, their morphology is compared with the immature stages of the other Cetoniinae. Brief observations on biology and ecology are given. Larvae of Taenioderini show a remarkable morphological diversity. An intra-generic variability in the body pilosity, presence and development of various structures (e.g. the palidium of raster) is documented. Larvae of Taenioderini are morphologically highly variable, as compared to other all Cetoniinae tribes.

Key words. Scarabaeoidea, white grubs, saproxylic, immature stages, description, morphology, southeastern Asia

Introduction

The Cetoniinae tribe Taenioderini represents a poorly known, however, species-rich group of flower beetles. The group is distributed in the eastern Palaearctic and Oriental Regions, with a single genus intruding into the Australian Region (Krikken 1984). The tribe was established by Krikken (1984), to accommodate the former members of Mikšić's (1976) Gymnetini subtribes Taenioderina and Chalcotheina. Krikken (1984) hypothesised both groups closely

related and listed the following apomorphies defining the tribe Taenioderini: (1) pronotum with weak basomedian lobe; (2) scutellum mostly exposed, scutellar sides straight or convex; (3) absence of horns and other extremities on head; (4) dorsal midline of body (pronotum-scutellum-elytral base) flattened. He also pointed out that some of the above-mentioned characters link the Taenioderini with another oriental tribe, the Phaedimini.

In agreement with Mikšić (1976), Krikken (1984) maintained the subtribal status of the Taenioderina with 18 genera, and the Chalcotheina with 11 genera, respectively (the recent numbers of genera in both subtribes are 15 and 13 genera, respectively; Sakai & Nagai 1998, S. Jákl pers. comm. 2013). The key characters separating both subtribes are the presence of 'juxtasutural striola' (present in Chalcotheina, absent in Taenioderina) and characters of dorsal body surface (glabrous in Chalcotheina; with dense pilosity, tomentum or velutinous-cretaceous in Taenioderina). While all recent studies focus solely on taxonomy of adults, nothing is known about the ecology, immature stages or phylogenetic relationship of the group (Šípek & Král 2012).

Recently, we had the opportunity to breed several Taenioderini species using either field collected specimens, or, as for *Plectrone tristis* (Westwood, 1842) obtained from beetle breeders. Larvae of eight species from six genera were obtained, representing both aforementioned subtribes. The aims of the study are: (1) to provide detailed morphological information on the immature stages of Taenioderini; (2) to provide observation on their biology and life cycle; and (3) to discuss and compare the observed variability of morphological characters.

Material and methods

With exception of *Plectrone tristis*, all material was field collected by the authors during several collection trips to southeastern Asia. All described larvae were obtained by the rearing of adult beetles, with the exception of *Coilodera penicillata* Hope, 1831, whose field-collected larvae were partially preserved for description and partially reared into adults (preserved larvae were compared with respective larval cast skins of hatched adults).

Where possible, adult beetles were determined to species-level and their identification was verified by S. Jákl (Prague, Czech Republic). The larvae of *Taeniodera* sp. were obtained from a single female belonging to *T. idolica* Janson, 1909 species group and, therefore, species determination is impossible. However either *T. salvazai* (Bourgoin, 1924) or *T. zebraea* Fairmaire, 1893 are the most likely candidates (S. Jákl, pers. comm. 2013).

Adult beetles were kept in standard laboratory conditions in 5–10 litre transparent plastic containers, filled with a 20 cm layer of substrate, composed of decaying leaf litter (beech, oak) and soft rotten wood (large pieces and crushed material). Adults were abundantly supplied with ripe banana and the container was sprayed with water every 2–3 days.

The terminology for larval description follows Hayes (1929), Böving (1936) and Ritcher (1966). Antennomeres I–IV were labelled with the respective abbreviations 'an I – an IV.' In order to give the most accurate information on chaetotaxy, the hair-like setae of the cranium and other structures were classified by their relative size into two groups: medium to long (80–300 μm) and minute or small (5–40 μm or less). For a detailed schematic figure, refer to Šípek et al. (2008). Morphological observations and measurements were made using Olympus

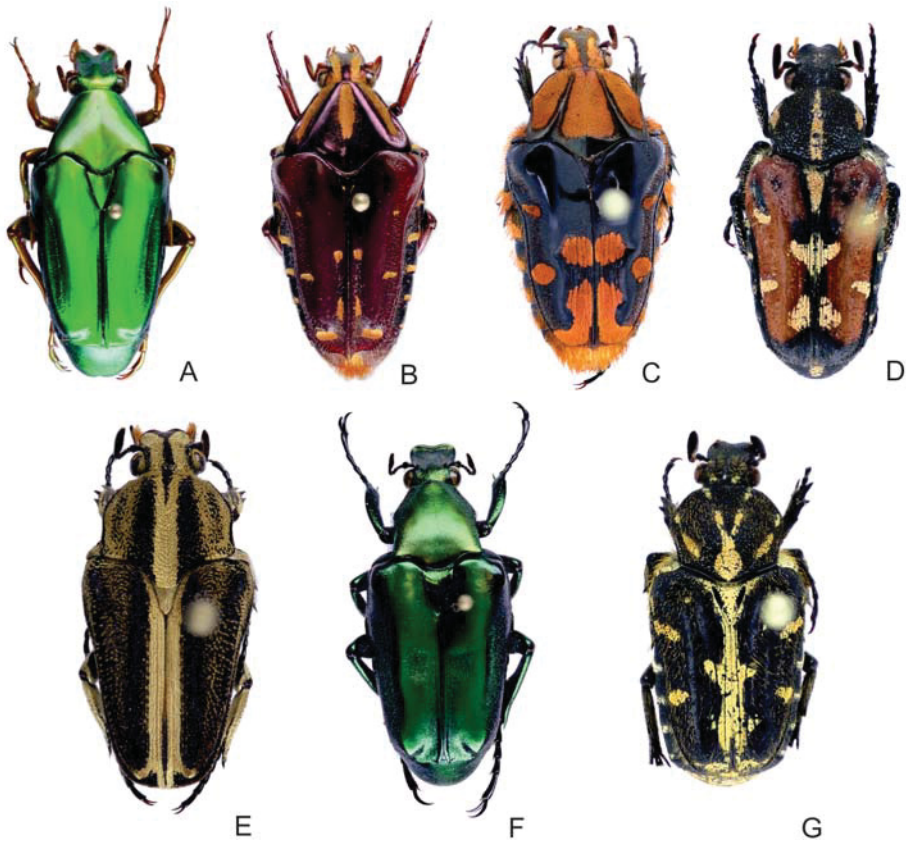

Fig. 1. Habitus of adult Taenioderini which larvae are describe in this paper. A – *Chalcothea neglecta* Ritsema, 1882. B – *Coilodera diardi* (Gory & Percheron, 1833). C – *C. penicillata* Hope, 1831. D – *Euselates laoticus* Mikšić, 1974. E – *Meroloba suturalis* (Snellen van Vollenhoven, 1858). F – *Plectrone tristis* (Westwood, 1842). G – *Taeniodera* sp. Figures not to scale.

SZX9 and Olympus BX 40 dissecting microscopes, both equipped with an Olympus Camedia 5060 digital camera. Mouthparts were dissected and some mounted on slides in Liquide de Swan (e.g., Švácha & Danilevsky 1986). Photographs were taken using a Canon 550D digital camera, equipped with a Canon MP-E 65/2.8 MACRO lens with 5:1 optical magnification. Partially focused images of each specimen were combined using Zerene photo stacker software (Zerene systems LLC, Richland, USA). Structures examined with the JEOL 6380 scanning electron microscope were first cleaned in 10% lactic acid for 24 hours, dried using critical point drying and mounted on aluminium plates. All pictures were digitally enhanced using Adobe Photoshop CS4.

The specimens included in this study are deposited in the following collections:

CUPC Department of Zoology, Charles University, Prague, Czech Republic (P. Šípek);
NMPC National Museum, Prague, Czech Republic (M. Fikáček, J. Hájek).

Larval morphology

Tribe Taenioderini Krikken, 1984

Diagnosis of Taenioderini based on larval characters. Larva scarabaeiform, cranium yellowish, pale brown or reddish-brown, body whitish. Abdominal segments IX and X fused dorsally, ventrally separated by incomplete groove.

Head capsule (Fig. 3). Surface of cranium glabrous or with weak microsculpture, yellowish, pale brown or red-brown; antennifer, postclypeus and labrum darker; area around frontoclypeal suture and apices of mandibles usually black. Epicranial suture extending between frontal suture; frontal sutures more or less bisinuate. Epicranial insertions of antennal muscles indistinct, feebly developed or apparent. Anterior and exterior frontal setae minute or absent. Clypeus subtrapezoidal to rectangular, membranous anteclypeal part narrow, not wider than 1/3 of entire clypeal area. Postclypeus sclerotized, with one anterior and one exterior clypeal setae. Stemmata present, well developed.

Antennae (Figs 3; 9E–L). Tetramerous (an I–IV), relative length of antennomeres (an): an I > an IV > an II > an III or an I ≥ an IV > an II > an III; an I about as long as an II and an III combined or slightly longer. Ventro-apical projection of ANIII with single sensory spot. An IV with numerous dorsal and ventral sensory spots and single apical sensoric field.

***Labrum*.** Symmetrical, anterior margin trilobed with numerous setae. Clithra present. Dorsal surface with two transverse rows of setae and additional pair of exterior labral setae on each side.

Epipharynx (Figs 4A–H; 12A–F). Haptomerum: Zygum convex, with arcuate or angulate row of approximately 15 stout setae and several similar setae on mesal margin. Sensilla of zygum grouped in two groups distad to the row of stout setae, or in single field on a more or less projecting cone. Haptomeral process and proplegmata absent. Acroparia: External margin of medial labral lobe with four to five long setae on ventral side and three to four setae on dorsal side. Lateral labral lobes with three to seven long setae. Setae of acanthoparia on a more or less distinct tubercle, increasing in size towards apex. Plegmata absent. Chaetoparia asymmetric, setae in more or less distinct longitudinal rows or irregularly scattered on chaetoparia, medial rows with stout, spine-like setae. Dexiotorma straight, robust or narrowed, right pternotorma present or widely reduced. Laeotorma usually reduced (entirelly developed only in *Chalcothea neglecta* Ritsema, 1882 and *Plectrona tristis*), left pternotorma triangular or rectangular, large. Haptolachus: Sense cone well developed or reduced to low cob-like tubercle, sclerotized plate (right nesium) absent. Plate-shaped sclerite present. Haptolachus posteriad with two pairs of pore-like setae on each side. Phoba and crepis absent.

Mandibles (Figs 6A–O; 7A–O; 8A–O; 9A–C; 13F–L). Asymmetrical, dorsomolar and ventromolar setae present on both mandibles, stridulatory area absent in *P. tristis*, strongly reduced in *C. neglecta*, in all other species consists of about 20 transversal ridges. Left mandible with four, right mandible with three scissorial teeth.

Maxilla (Figs 5; 12G–M). Dorsomedial surface of stipes with oblique row of more than five well sclerotized spine-shaped or drop-shaped stridulatory teeth and anterior truncate process (blunt tubercle, Fig. 12M). Galea and lacina entirely fused forming mala, galeo-lacinial suture indistinct, entirely absent on ventral face. Galear portion of mala with single falcate uncus

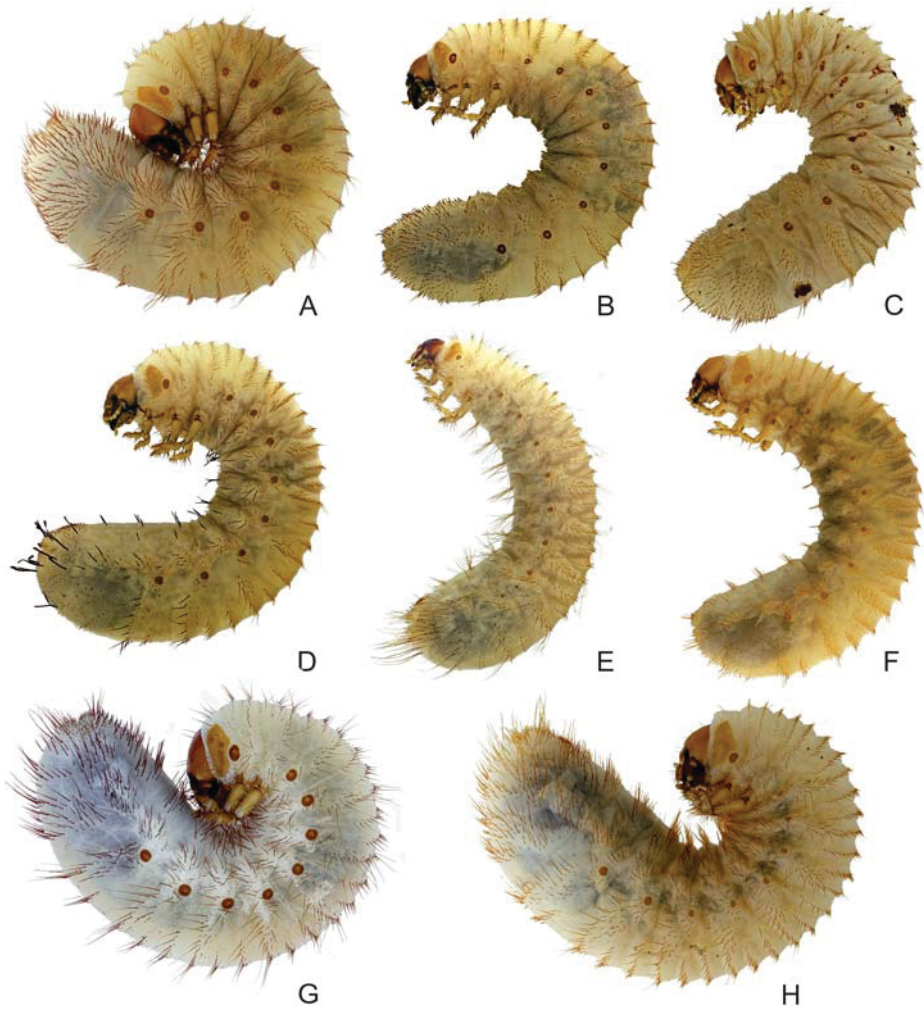

Fig. 2. Third instar larvae of Taenioderini. A–H – habitus. A – *Chalcothea neglecta*. B – *Coilodera diardi*. C – *C. penicillata*. D – *Euselates cineraceus*. E – *E. laoticus*. F – *Meroloba suturalis*. G – *Plectrone tristis*. H – *Taeniodera* sp. Figures not to scale.

and several long and stout hair-like setae in longitudinal rows; lacinia with one or two unci, subapical uncus, if present, small and indistinct. Maxillary palpi tetramerous, penultimate palpomere with two setae.

Hypopharyngeal sclerome (Figs 5; 12N–O). Asymmetrical with strong protruding hypopharyngeal process. Tufts of tegumentary expansions (= phoba, *sensu* Böving 1936) present on left lateral lobe. Tegumentary expansions of right central part of scleroma either present, absent or individually variable (e.g. present in one specimen, absent in another).

Ligula (Figs 5; 13A–E). Dorsal surface with group of approximately 10–15 hair-like setae on each side; paramedial longitudinal row of three to five stout setae and proximal transverse row of several campaniform or conical setae. Labial palpi bimerous.

Thorax (Figs 2A–H). Prothorax with single dorsal lobe, meso- and metathorax with three well developed lobes. Each dorsal sublobe of thoracic segments with one row of medium long to long setae along with several short setae irregularly scattered anterior to the row. Prothoracic sclerite covering almost whole lateral portion of prothorax. Mesothoracic spiracle (Figs 6P–T; 7P–R) with C-shaped respiratory plate; bullar opening constricted or wide open. All pairs of legs (Figs 9M–T) subequal. Pretarsi conical to cylindrical in shape with two setae, claw present or greatly reduced (Figs 7S–T; 8P–T; 9D).

Abdomen (Figs 2A–H; 10; 11). Nine-segmented. Abdominal segments IX and X fused, fusion line is visible on the ventral side. Dorsa of abdominal segments I–VI with three, segments VII and VIII with two sublobes respectively. Each sublobe bearing one to three (four) rows of setae. Setae in anterior rows short, posterior row with distinctly longer setae.

Abdominal pilosity often species-specific, from long hair-like setae (*Euselates laoticus* Mikšić, 1974) to long stout (*Chalcothea neglecta*), spatulate (long or short; *Coilodera diardi* (Gory & Percheron, 1833), *E. cineraceus* (Gory & Percheron, 1833)) to hamate (*Coilodera penicillata*). Abdominal spiracles similar to mesothoracic spiracle, but smaller. Ultimate abdominal segment usually densely setose. Anal slit transverse.

Raster (Fig. 10). Palidium present or absent, if present than monostichous (few irregular pali may be scattered around main row), composed of approximately 10–22 pali arranged in single U-shaped row or two parallel rows respectively. Septula opened posteriorly.

Chalcothea neglecta Ritsema, 1882

(Figs 2A; 3A; 4A; 5A; 6A–C,P; 7J–L,S; 9E,M; 10A; 11A; 12A,D,G; 13A,F)

Material examined. 7 third instar larvae reared from adults obtained in: **MALAYSIA: Perak Sultanate:** Cameron Highlands, road between Tapah and Tanah Rata, Batu (= mile 19), 4°22.121′N 101°20.012′E, 600–660 m a.s.l., 13.–19.v.2011, local collector leg.; 3 third instar cast skins obtained from larvae reared to adults: same locality and date, P. Šípek & D. Vondráček leg.

Description of third instar larva. ***Body*** (Fig. 2A). Length 53.0–67.0 mm, dorsoventral interval of abdominal segments slightly larger than in thoracic segments (thus abdominal segments appear slightly thicker, abdominal segment VIII is the thickest). Body, especially on ventral side, covered with numerous stiff, brown setae. Dorsal part of thorax and abdomen covered with more slender and shorter setae.

Head capsule (Fig. 3A). Maximum width 4.2–4.6 mm, surface of cranium with indistinct micro-sculpture, yellowish or reddish brown, parts of epicranium with numerous darker irregular spots. Frontal sutures moderately sinuated. Epicranial insertions of antennal muscles distinct (visible as dark spot proximal to the frontal suture slightly above the level of anterior epicranial setae). Cranial chaetotaxy summarized in Table 1. Anterior and exterior frontal setae absent.

Antennae (Figs 3A; 9E). Relative length of antennomeres I–IV (an I–IV): an I ≥ an IV > an II > an III), ultimate antennomere with 9–14 dorsal and 11–18 ventral sensory spots.

Epipharynx (Figs 4A; 12A,D). Haptomerum: Zygum convex, with arcuate or angulate row of 13–18 stout conical setae and medial row of another four to six stout setae. Sensilla

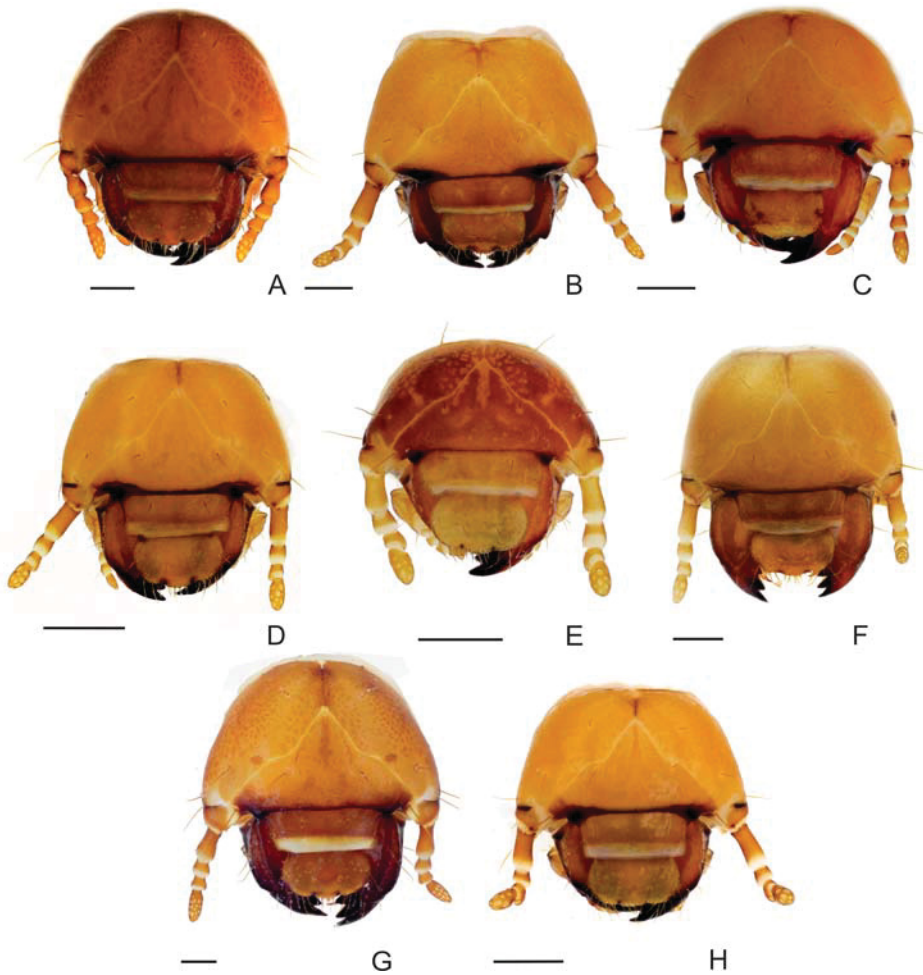

Fig. 3. Third instar larvae of Taenioderini. A–H – cranium. A – *Chalcothea neglecta*. B – *Coilodera diardi.* C – *C. penicillata.* D – *Euselates cineraceus.* E – *E. laoticus.* F – *Meroloba suturalis.* G – *Plectrone tristis.* H – *Taeniodera* sp. Scale bars: Figs 3A–H = 1mm.

of zygum grouped in two groups distad to the row of stout setae. Acroparia: Lateral lobes of epipharynx with three to four long setae, medial lobe with four and four to five setae on ventral and dorsal side, respectively. Acanthoparia with three to five large tubercles each with single seta; the size of the tubercles, as well as the length of setae, increasing towards apex (of epipharynx).

Chaetoparia: Asymmetric, right side with single regular row of long stiff setae and four to five irregular rows, left side with one regular and three to four irregular rows. Right side of chaetoparia with approximately 40–60, left with 30–40 setae respectively. Pedium large. Dexiotorma somewhat crooked, robust, but narrowed toward medial end, right pternotorma

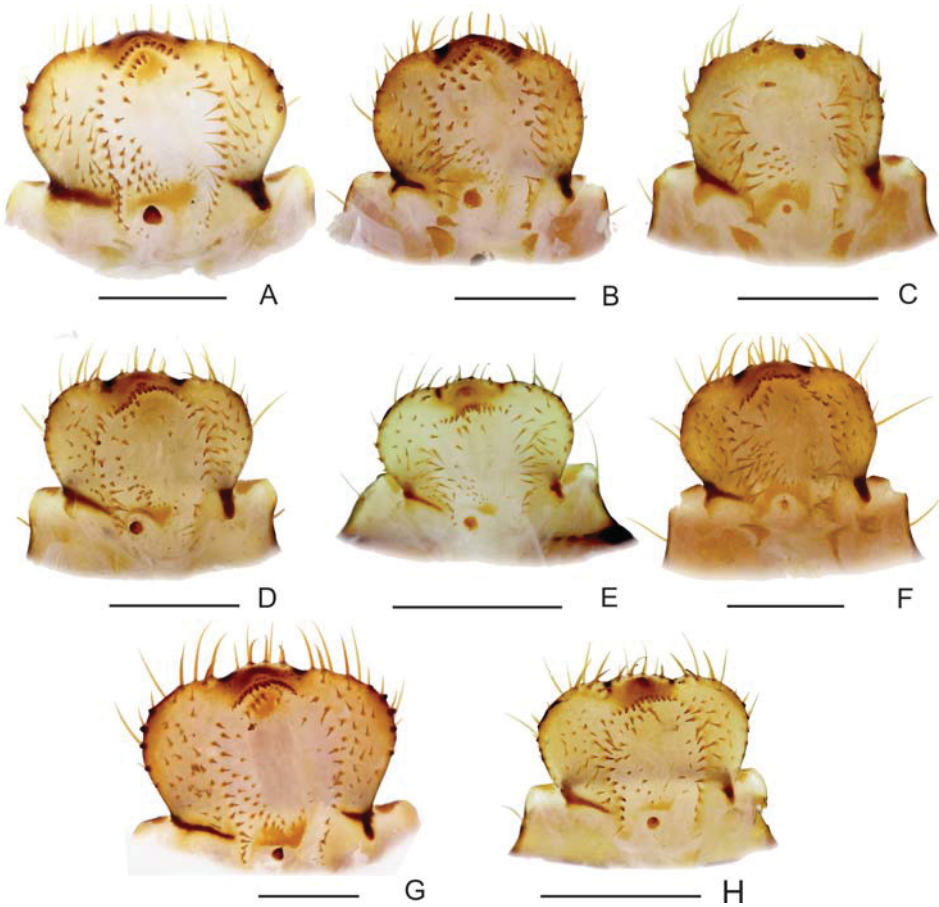

Fig. 4. Third instar larvae of Taenioderini. A–H – epipharynx. A – *Chalcothea neglecta*. B – *Coilodera diardi*. C – *C. penicillata*. D – *Euselates cineraceus*. E – *E. laoticus*. F – *Meroloba suturalis*. G – *Plectrone tristis*. H – *Taeniodera* sp. Scale bars = 1 mm.

only indicated. Laeotorma present. Haptolachus: Sense cone large, broad at the base, conical, almost pointed at the tip, with four pores. Plate-like sclerite large, occupying almost the entire area between sense cone and the regular rows on both sides of chaetoparia. Sensilla of haptolachus organized in two groups (both with two sensilla), each group is located proximal to the end of the respective regular row of stiff setae of chaetoparia.

Mandibles (Figs 6A–C; 7J–L; 13F). Stridulatory area very small, with approximately five to seven indistinct ridges. Scrobis with two to three lateral setae. Longitudinal furrow present, extending towards apex of mandibles, with two prominent lateroapical setae and one or two posterior setae (occasionally absent). Right mandible with three scissorial teeth, the middle tooth blade-shaped, occasionally with small incision or processus.

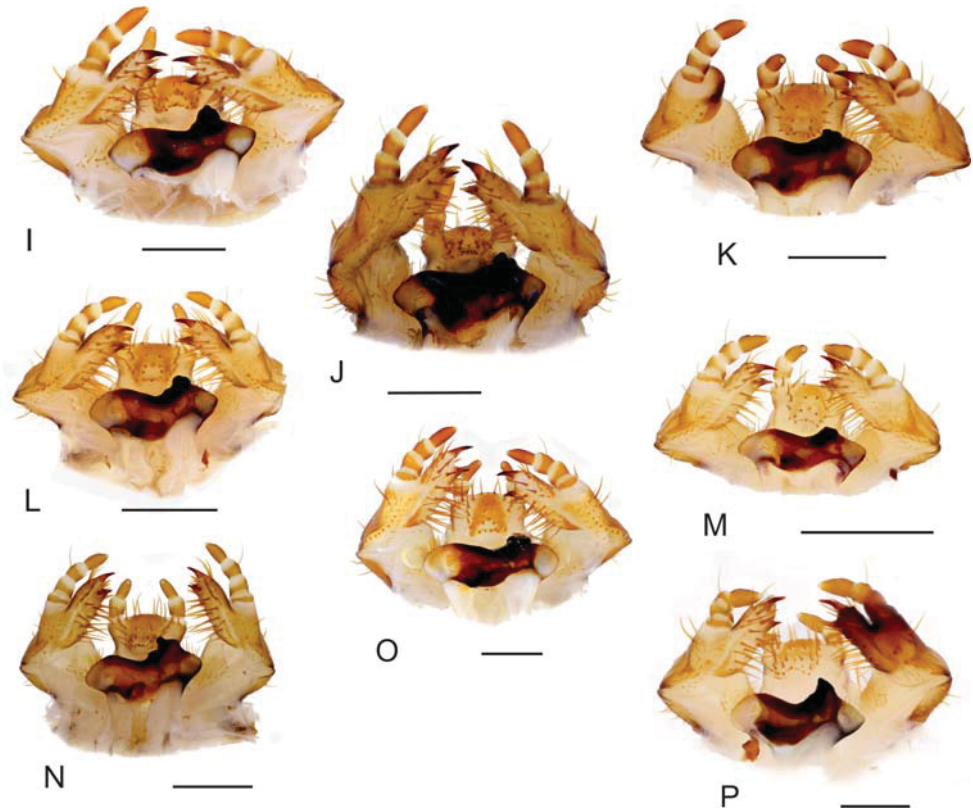

Fig. 5. Third instar larvae of Taenioderini. A–H – maxillo-labial complex. A – *Chalcothea neglecta*. B – *Coilodera diardi*. C – *C. penicillata*. D – *Euselates cineraceus*. E – *E. laoticus*. F – *Meroloba suturalis*. G – *Plectrone tristis*. H – *Taeniodera* sp. Scale bars = 1 mm.

Maxilla (Figs 5A; 12G). Dorsal surface of cardo and labacoparia with four to eight, 16–24 setae, respectively. Ventral surface of cardo and labacoparia with three and 8 to 13 stiff setae respectively. Dorsal surface of stipes with approximately 16 slender hair-like setae and one or two anterolateral stout setae. Maxillary stridulatory apparatus on stipes with six to eight drop-like or obtuse stridulatory teeth (in dorsal aspect, Fig. 12G) and one blunt tubercle. Ventral surface of stipes with single proximal and two distal setae (long and stout, arranged in transverse row). Galear portion of mala in dorsal aspect beside large falcate uncus with three to five large stiff and two to five medium sized hair-like setae respectively. Lacinial part of mala with around twenty mostly long and stiff setae. Lacinial uncus beside large pointed claw with minute second pointed tip and two conical, stout setae. Ventral surface of mala with two longitudinal rows of three setae; setae of the exterior row long and stiff, setae of the interior row shorter and stout.

Hypopharyngeal sclerome (Fig. 5A). Around ten tegumentary expansions (phoba-like processes) present on the left lateral lobe of hypopharynx, the presence of tegumentary expansions on right medial portion scleroma individually variable.

Ligula (Figs 5A; 13A). Dorsal surface with two lateral groups of around 10 hair-like setae (each group consist of longitudinal and oblique row), two paramedial setae at the apical margin and central group of setae and sensilla. This group is composed of two paramedial rows of approximately four stout, conical setae, and transverse, basomedial row with two bulbose setae on each side and two paramedial conical setae.

Thorax (Figs 2A; 6P; 7S; 9M). Prothoracic sclerite with approximately six to eight setae on the anteroventral margin and another one or two setae in the posterio-dorsal area. Each sublobe of prothorax dorsal with single sparse row of mostly long or medium-long setae. Thoracic spiracle (Fig. 6P) 0.9 × 0.63 mm (height × width), bullar opening narrow, arms of respiratory plate almost concealed. Respiratory plate with approximately 50 holes across diameter. Pretarsus (Fig. 7S) conical with minute pointed tip and two apical setae.

Abdomen (Figs 10A; 11A). Abdominal chaetotaxy more developed than on thorax, each dorsal sublobe of abdominal segments I–VIII with two to three rows of setae. Setae in anterior row(s) short or medium-sized, posterior row also with several long setae. Dorsum of abdominal segment IX–X, as well as the entire ventral part of abdomen covered by stiff medium-long to long setae. Spiracles on abdominal segments I–V elongate, similar to thoracic spiracle, abdominal spiracles on segments VI–VIII almost circular.

Raster (Figs 10A; 11A). Rows of pali absent, tegilla fused, covered with numerous medium-long hamate setae. Ventral anal lip with rows of numerous short apically recurved setae.

Coilodera diardi (Gory & Percheron, 1833)

(Figs 2B; 3B; 4B; 5B; 6D–F,Q; 7M–O,T; 9F,N; 10B; 11B; 12B,E,H; 13B,G)

Material examined. 5 third instar larvae reared from adults obtained in: **MALAYSIA: Perak Sultanate:** Cameron Higlands, road between Tapah and Tanah Rata, Batu (= mile 19), 4°22.121′N 101°20.012′E, 600–660 m a.s.l., 13.–19.v.2011, local collector leg.

Description of third instar larva. ***Body*** (Fig. 2B). Length 54.0–61.0 mm, dorsoventral interval of abdominal segments slightly larger than in thoracic segments (thus abdominal segments appear to be slightly thicker, abdominal segments VII and VIII are the thickest). Body only with short and few medium-sized setae. Setae on the dorsal side of body (with the exception of the ultimate segment) hair-like, setae of the ultimate abdominal segment and the ventral parts of body apically recurved, spatulate.

Head capsule (Fig. 3B). Maximum width 5.0–5.4 mm, glossy, yellowish brown or pale brown. Frontal sutures bisinuated. Epicranial insertions of antennal muscles indistinct, dorsally bordered with thin sickle-shaped line. Cranial chaetotaxy summarized in Table 1. Anterior and exterior frontal setae with minute single seta or absent.

Antennae (Figs 3B; 9F). Relative length of antennomeres I–IV (an I–IV): an I > an IV > an II > an III), ultimate antennomere with five to ten dorsal and 8–14 ventral sensory spots.

Epipharynx (Figs 4B; 12B,E). Haptomerum: Zygum convex, more or less protruding, with angulate row of 15–18 stout conical setae and several similar setae proximad to the row. Sensilla of zygum grouped in single group at the top of haptomerum. Acroparia: Lateral lobes of epipharynx with three to five long setae, medial lobe with four and four to five setae on ventral and dorsal side respectively. Acanthoparia with five to seven setae surrounded by

moderately swollen base (or tubercle); the size of the tubercles as well as the setae increasing towards apex (of epipharynx).

Chaetoparia: Asymmetric, right side composed of approximately 30–45 setae in three to five longitudinal rows and medial field (proximad to plate-shaped sclerite). Left side with approximately 30 setae in three to four rows. Both parts of chaetoparia with medial, more or less regular row of prominent long setae. Pedium large. Dexiotorma somewhat crooked, right pternotorma well developed. Laeotorma absent, left pternotorma well developed. Haptolachus: Sense cone (Fig. 12E) knob-like (low, but considerably broad at the base), with four pores. Plate-like sclerite large, occupying almost the entire area between sense cone and the regular rows on both sides of chaetoparia, however it can be less distinct in some specimens.

Mandibles (Figs 6D–F; 7M–O; 13G). Stridulatory area well developed, with approximately twenty ridges (ridges in the proximal third less distinct and narrow). Scrobis with two to three lateral setae. Longitudinal furrow absent. Apical half of mandibles in dorsal aspect with two lateral setae and mediolateral depression (proximad to the base of the third scissorial tooth). Lateral outline of both mandibles with prominent external tooth.

Maxilla (Figs 5B; 12H). Dorsal surface of cardo and labaocoparia with seven to eight, 28–34 setae, respectively. Ventral surface of cardo and labacoparia with two or three and 8 to 12 stiff setae, respectively. Dorsal surface of stipes with approximately 16 slender hair-like setae and one or two anterolateral stout setae. Maxillary stridulatory apparatus on stipes with six to seven spine-like stridulatory teeth (in dorsal aspect, Fig. 12H) and one blunt tubercle. Ventral surface of stipes with single proximal and one distal seta. Galear portion of mala in dorsal aspect beside large falcate uncus with four to five large stiff and three to five medium sized hair-like setae respectively. Lacinial part of mala with around 15–20 mostly long and stiff setae. Lacinial apex with single triangular uncus with two short conical, stout setae at the base and another single long, conical setae next to it. Ventral surface of mala with two longitudinal rows of three to four (seven) setae; setae of the exterior row long and stiff, setae of the interior row shorter and stout.

Hypopharyngeal sclerome (Fig. 5B). Around five tegumentary expansions (phoba-like processes) present on the left lateral lobe of hypopharynx, the presence of tegumentary expansions on right medial portion scleroma individually variable.

Ligula (Figs 5B; 13B). Dorsal surface with two lateral groups of around 10 hair-like setae, two paramedial setae at the apical margin and central group of setae and sensilla. This group is composed of two paramedial rows of approximately three stout and conical setae, and transverse, basomedial row with seven to eight conical setae.

Thorax (Figs 2B; 6Q; 7T; 9N). Prothoracic sclerite with four (three) setae on the anteroventral margin and another single seta in the posterio-dorsal area. Each sublobe of prothorax dorsally with one or two rows of mostly short or medium-long setae interspersed with few long, hair-like setae. Thoracic spiracle (Fig. 6Q) 0.93 × 0.59 mm (height × width), bullar opening narrow, arms of respiratory plate almost concealed. Respiratory plate with approximately 30 holes across diameter. Venter of thorax and legs with spatulate setae. Pretarsus (Fig. 7T) conical with large falcate tip and two apical setae.

Abdomen (Figs 2B; 10B; 11B). Each dorsal sublobe of abdominal segments I–VIII with

two to three rows of setae. Setae in anterior row(s) short or medium-sized, posterior row also with several long setae. Dorsum of abdominal segment IX–X, as well as the entire ventral part of abdomen covered with spatulate medium-long setae. Spiracles on abdominal segments I–VI elongate, similar to thoracic spiracle, abdominal spiracles on segments VII–VIII almost circular.

Raster (Figs 10B; 11B). Rows of pali absent, tegilla fused, covered with numerous short or medium-long spatulate setae.

Coilodera penicillata Hope, 1831

(Figs 2C; 3C; 4C; 5C; 6G–I,R; 8A–C,P; 9G,O; 10C; 11C; 12I; 13H)

Material examined. One third instar larva and two third instar larva cast skins collected at: **TAIWAN:** in the vicinity of Taroko National Park, 17.–19.v.2008, P. Jedelský & I. Hrdý leg.

Description of third instar larva*. ***Body*** (Fig. 2C). Length 54.0 mm (n = 1), dorsoventral interval of abdominal segments slightly larger than in thoracic segments (thus abdominal segments appear to be slightly thicker, abdominal segments VII and VIII are the thickest). Chaetotaxy of body generally short with few medium-sized setae. Setae on the dorsal side of body (with the exception of the last segment) hair-like, setae of the ultimate abdominal segment and the ventral parts of body hamate.

Head capsule (Fig. 3C). Maximum width 4.3 mm, glossy, pale brown. Frontal sutures bisinuated. Epicranial insertions of antennal muscles indistinct. Cranial chaetotaxy summarized in Table 1.

Antennae (Figs 3C; 9G). Relative length of antennomeres I–IV (an I–IV): an I > an IV > an II > an III), ultimate antennomere with eight dorsal and ten ventral sensory spots (n = 1).

Epipharynx (Fig. 4C, malformed specimen!). Haptomerum: Zygum convex, more or less protruding, with arcuate row of 15 stout conical setae and several similar setae proximad to the row. Sensilla of zygum grouped in single group at the top of haptomerum. Acroparia: Lateral lobes of epipharynx with four to five long setae, medial lobe with four and four to five setae on ventral and dorsal sides, respectively. Acanthoparia with four to six setae surrounded by swollen base (or tubercle); the size of the tubercles as well as the setae increasing towards apex (of epipharynx).

Chaetoparia: Asymmetric, right side composed of approximately 30 setae in irregular rows and medial field (proximad to plate-shaped sclerite). Left side with approximately 20 setae. Both parts of chaetoparia with medial, more or less regular row of prominent long setae. Dexiotorma straight, right pternotorma well developed. Laeotorma strongly reduced, left pternotorma well developed. Haptolachus: Sense cone knob-like with four pores. Plate-like sclerite large, occupying almost the entire area between sense cone and the regular rows on both sides of chaetoparia.

Mandibles (Figs 6G–I; 8A–C; 13H). Stridulatory area well developed, with approximately 20 ridges (ridges in the proximal third less distinct and narrow). Scrobis with two to five lateral setae. Longitudinal furrow absent. Apical half of mandibles in dorsal aspect with two

* Haptomerum, acroparia and chaetoparia malformed in depicted specimen, the description of epipharynx thus based solely on cast skin.

lateral setae and mediolateral depression (proximad to the base of the third and fourth scissorial tooth). Lateral outline of both mandibles with obtuse tubercle.

Maxilla (Figs 5C; 12I); parts of left maxilla malformed in depicted specimen). Dorsal surface of cardo and labacoparia with five and 20–30 setae, respectively. Dorsal surface of stipes with 15 slender hair-like setae and one anterolateral stout setae. Maxillary stridulatory apparatus on stipes with five spine-like (or drop-like on the malformed maxilla, see Fig. 12I) stridulatory teeth and one blunt tubercle. Galear portion of mala in dorsal aspect beside large falcate uncus with nine large, mostly stiff setae. Lacinial part of mala with 13 mostly long and stiff setae. Lacinial apex with single triangular uncus.

Hypopharyngeal sclerome (Fig. 5C). Three tegumentary expansions (phoba-like processes) present on the left lateral lobe of hypopharynx; tegumentary expansions on right medial portion of scleroma present.

Ligula (Fig. 5C). Dorsal surface with two lateral groups of around 12–14 hair-like setae, and central group of setae and sensilla. This group is composed of two paramedial rows of approximately three to four stout and conical setae, and transverse, basomedial row with eight conical setae.

Thorax (Figs 2C; 6R; 8P; 9O). Prothoracic sclerite with four (three) setae on the anteroventral margin and another single seta in the posterio-dorsal area. Each sublobe of prothorax dorsal with one or two rows of mostly short or medium-long setae interspersed with few long, hair-like setae. Thoracic spiracle (Fig. 6R) 0.84 × 0.45 mm (height × width), bullar opening broad, the distance between the lobes of the C-shaped respiratory plate equals the maximum diameter of the respiratory plate. Respiratory plate with approximately 16–35 holes across diameter. Venter of thorax with hamate setae. Pretarsus (Fig. 8P) conical with large falcate tip and two apical setae.

Abdomen (Figs 2C; 10C; 11C). Each dorsal sublobe of abdominal segments I–VIII with two to three rows of setae. Setae in anterior row(s) short or medium-sized, posterior row also with several long setae. Dorsum of abdominal segments IX–X, as well as the entire ventral part of abdomen covered with hamate setae. Spiracles on abdominal segments I–VI elongate, similar to thoracic spiracle, abdominal spiracles on segments VII–VIII almost circular.

Raster (Figs 10C; 11C). Palidium monostichous (however with few pali scattered around the main row), pali arranged in single elongate U-shaped row. Septula opened posteriorly, about two times longer than broad. Tegilla fused, with numerous short or medium-long hamate setae.

Euselates cineraceus (Gory & Percheron, 1833)

(Figs 2D; 3D; 4D; 5D; 6J–L,S; 8D–F,Q; 9H,P; 10D; 11D; 12J; 13C,I)

Material examined. 14 third instar larvae reared from adults reared from field collected larvae at: **MALAYSIA: Perak Sultanate:** Cameron Highlands, road between Tapah and Tanah Rata, Batu (= mile 19), 4°22.121′N 101°20.012′E, 600–660 m a.s.l., 12.iii.2010, P. Šípek leg.

Description of third instar larva. ***Body*** (Fig. 2D). Length 38.0–49.0 mm, dorsoventral interval of abdominal segments slightly larger than in thoracic segments (the abdominal segment VIII is the thickest). Chaetotaxy sparse, with three distinct types of setae: Short or medium long hair-like setae on dorsal sublobes and the venter of the ultimate segment; long, stiff or

slightly flattened setae on legs, ventral part of body and the dorsa of abdominal segments VII and VIII and oblanceolate* long setae on the ultimate abdominal segment; the last two types of setae, dark brown or black, the first pale brown.

Head capsule (Fig. 3D). Maximum width 3.8–4.0 mm, glossy, yellowish or pale brown. Frontal sutures bisinuated. Epicranial insertions of antennal muscles indistinct. Cranial chaetotaxy summarized in Table 1. Anterior and exterior frontal setae with minute single seta or absent.

Antennae (Figs 3D; 9H). Relative length of antennomeres I–IV (an I–IV): an I > an IV > an II > an III), ultimate antennomere with four to eight dorsal and 7–12 ventral sensory spots.

Epipharynx (Fig. 4D). Haptomerum: Zygum convex, more or less protruding, with arcuate row of 16–18 stout conical setae and few setae proximad to the row. Sensilla of zygum grouped in single group distad to the row. Acroparia: Lateral lobes of epipharynx with three to five long setae, medial lobe with eight setae. Acanthoparia with five to nine setae surrounded by moderately swollen base (or tubercle); the size of the tubercles as well as the setae increasing towards apex of epipharynx.

Chaetoparia: Asymmetric, right side composed of approximately 40–60 setae in three to five longitudinal rows and medial field (proximad to plate-shaped sclerite). Left side with approximately 30–40 setae in two to three rows. Both parts of chaetoparia with medial, more or less regular row of prominent long setae. Pedium large. Dexiotorma straight, right pternotorma well developed. Laeotorma absent, left pternotorma well developed.

Haptolachus: Sense cone conical, almost pointed. Plate-like sclerite large, occupying almost the entire area between sense cone and the regular rows on both sides of chaetoparia, however, it can be less distinct in some specimens.

Mandibles (Figs 6J–L; 8D–F; 13I). Stridulatory area well developed, with approximately 20–25 ridges (ridges in the proximal half less distinct and narrow). Scrobis with three to five lateral setae. Longitudinal furrow absent. Apical half of mandibles in dorsal aspect with two lateral setae and mediolateral depression (proximad to the base of the third scissorial tooth). Lateral outline of both mandibles without prominent external tooth.

Maxilla (Figs 5D; 12J). Dorsal surface of cardo and labacoparia with four to eight, 15–23 setae respectively. Ventral surface of cardo and labacoparia with two to five and 5–14 stiff setae respectively. Dorsal surface of stipes with 11–19 slender hair-like setae and one anterolateral stout seta. Maxillary stridulatory apparatus on stipes with more or less regular row of six to eight spine-like stridulatory teeth (in dorsal aspect, Fig. 12J) and one or two blunt tubercles. Ventral surface of stipes with single proximal and single distal stout seta. Galear portion of mala in dorsal aspect beside large falcate uncus with four to five large stiff and one to three medium-sized hair-like setae, respectively. Lacinial part of mala with around 13–19 mostly very long and stiff setae. Lacinial apex with two unci (subapical uncus however small and reduced) and with conical, stout setae. Ventral surface of mala with two longitudinal rows of two to four (seven) setae; distal setae of the exterior row long and stiff, distal setae of the interior row shorter and stout.

* The extraordinary oblanceolate setae were present only in third instar larvae, first and second instar larvae have 'normal' cetoniinae pilosity.

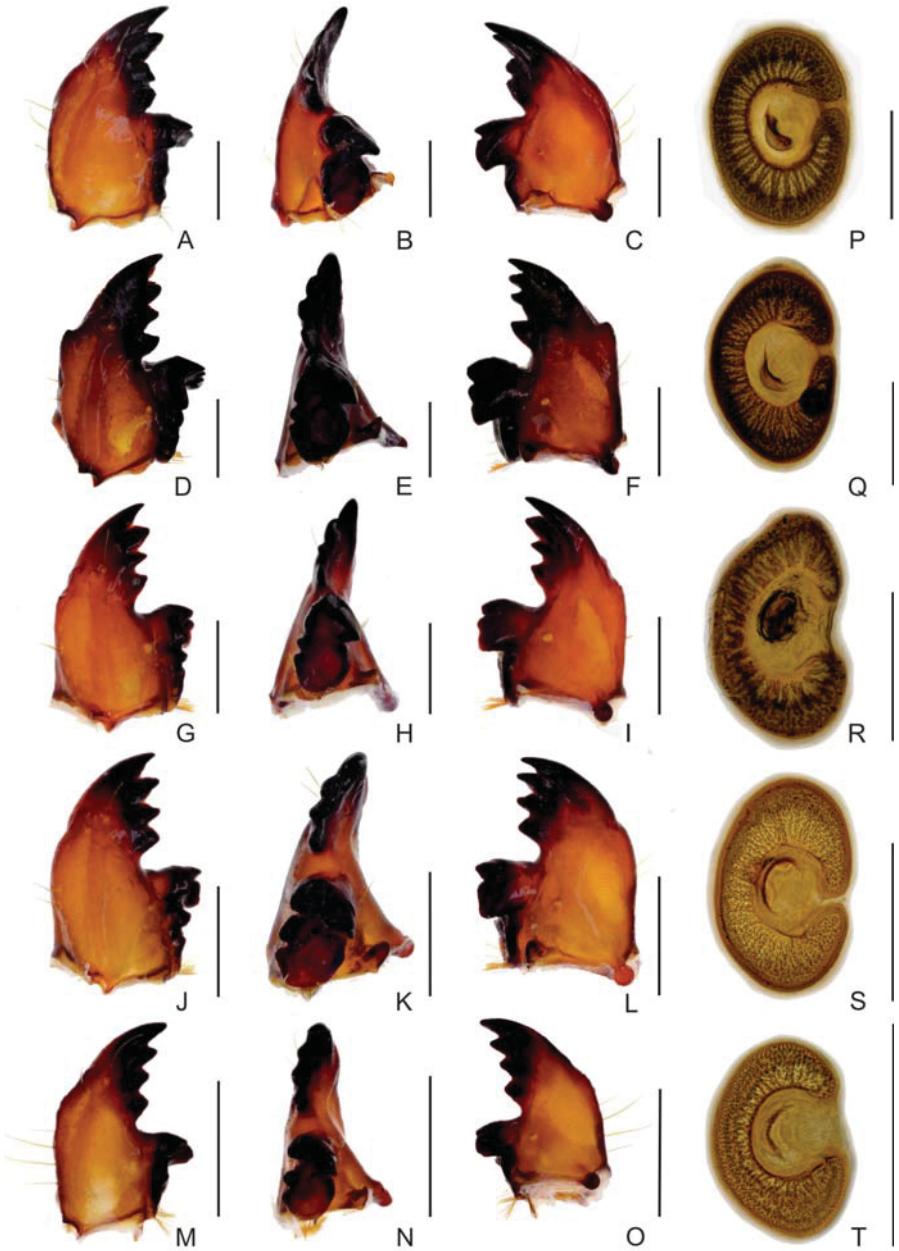

Fig. 6. Third instar larvae of Taenioderini. A–O – left mandible (dorsal, medial and ventral aspect), P–T – thoracic spiracle. A–C,P – *Chalcothea neglecta.* D–F,Q – *Coilodera diardi.* G–I,R – *C. penicillata.* J–L,S – *Euselates cineraceus*. M–O,T – *E. laoticus.* Scale bars: Figs A–O = 1mm; Figs P–T = 0.5 mm.

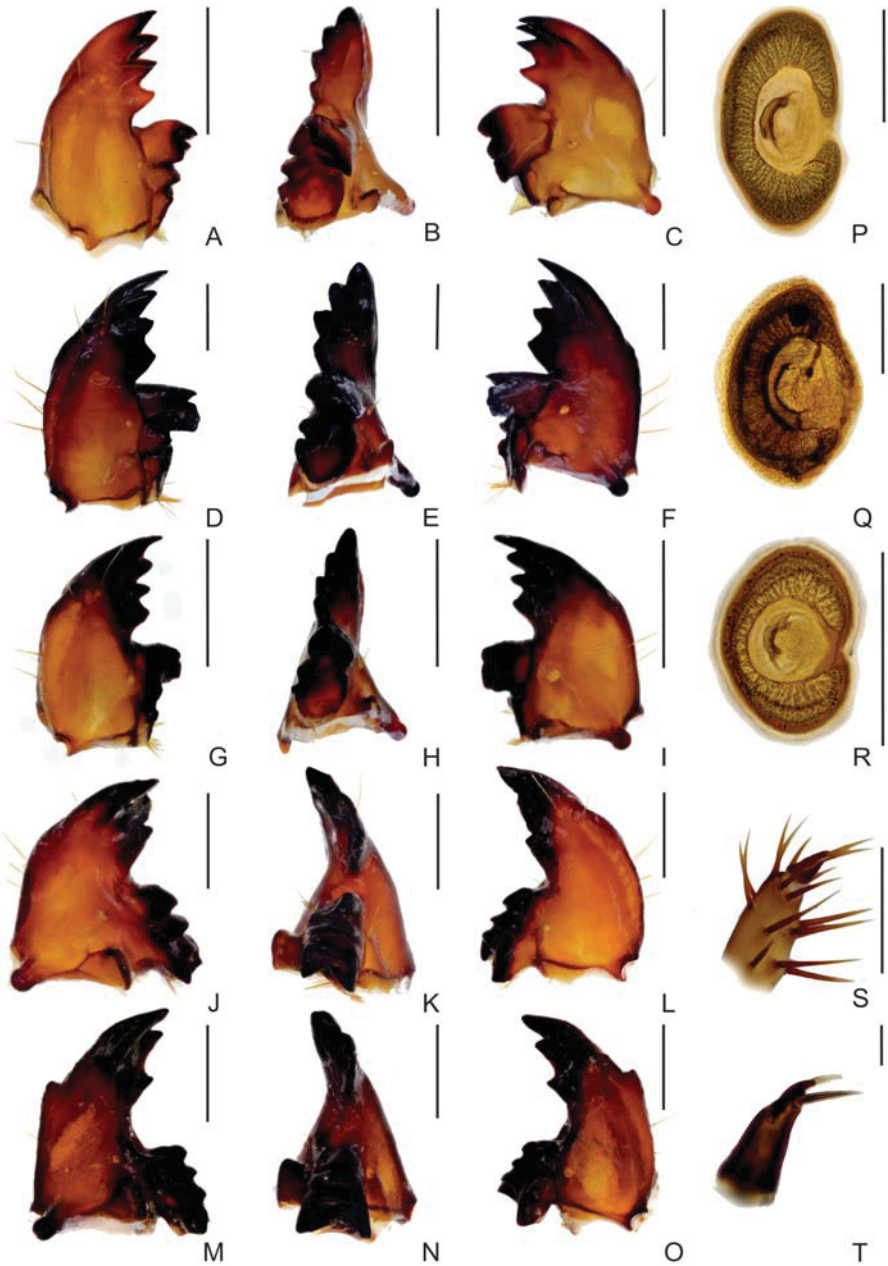

Fig. 7. Third instar larvae of Taenioderini. A–I – left mandible (dorsal, medial and ventral aspect), J–O – right mandible (ventral, medial and dorsal aspect), P–R – thoracic spiracle, S–T – pretarsus. A–C,P – *Meroloba suturalis*. D–E,Q – *Plectrone tristis*. G–I,R – *Taeniodera* sp. J–L,S – *Chalcothea neglecta*. M–O,T – *Coilodera diardi*. Scale bars: Figs A–O,S = 1 mm; Figs P–R = 0.7 mm; Fig. T = 0.1 mm.

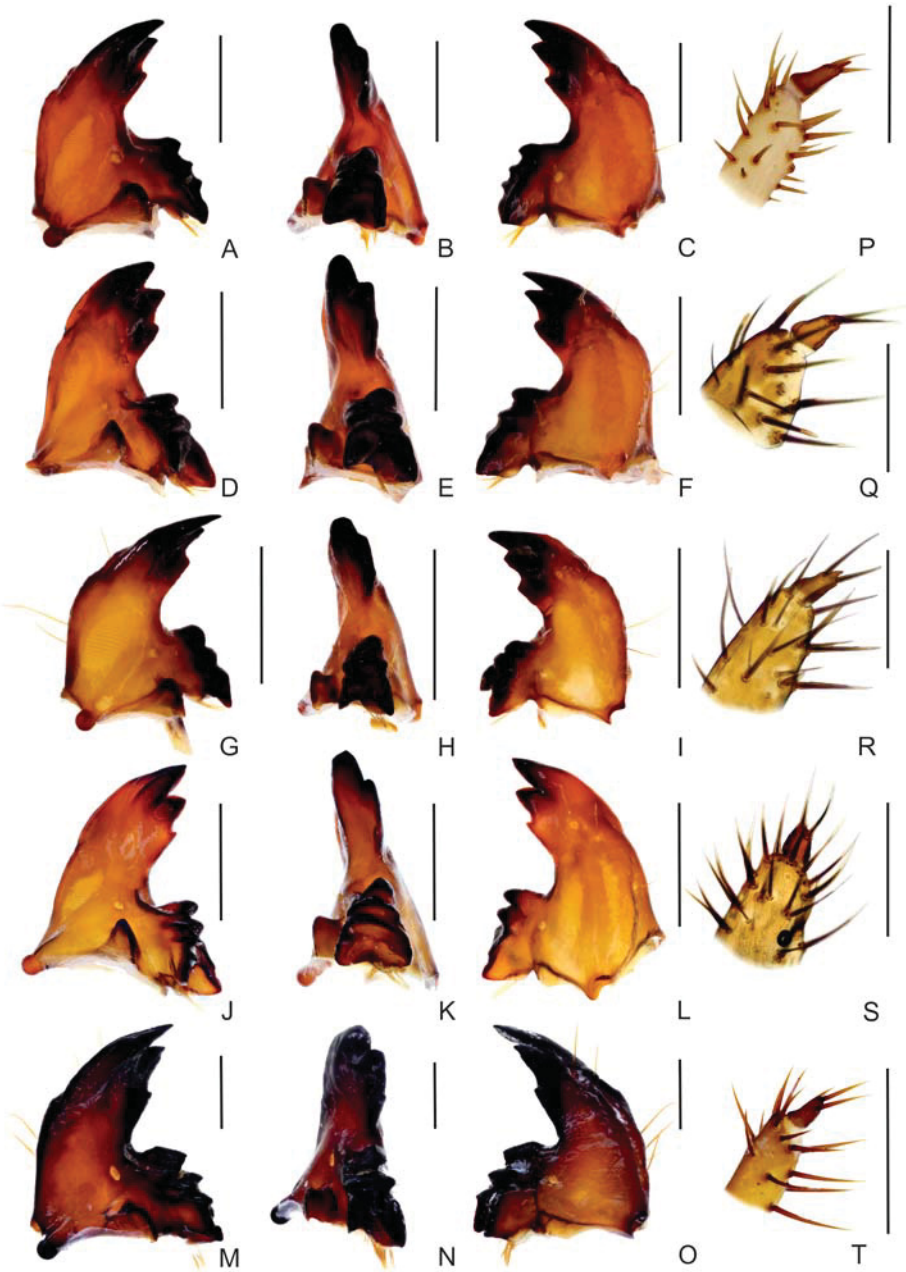

Fig. 8. Third instar larvae of Taenioderini. A–O – right mandible (ventral, medial and dorsal aspect), P–T – pretarsus. A–C,P – *Coilodera penicillata.* D–F,Q – *Euselates cineraceus.* G–I,R – *E. laoticus*. J–L,S – *Meroloba suturalis*. M–O,T – *Plectrone tristis*. Scale bars: Figs A–P,T = 1 mm; Figs Q–S = 0.5 mm.

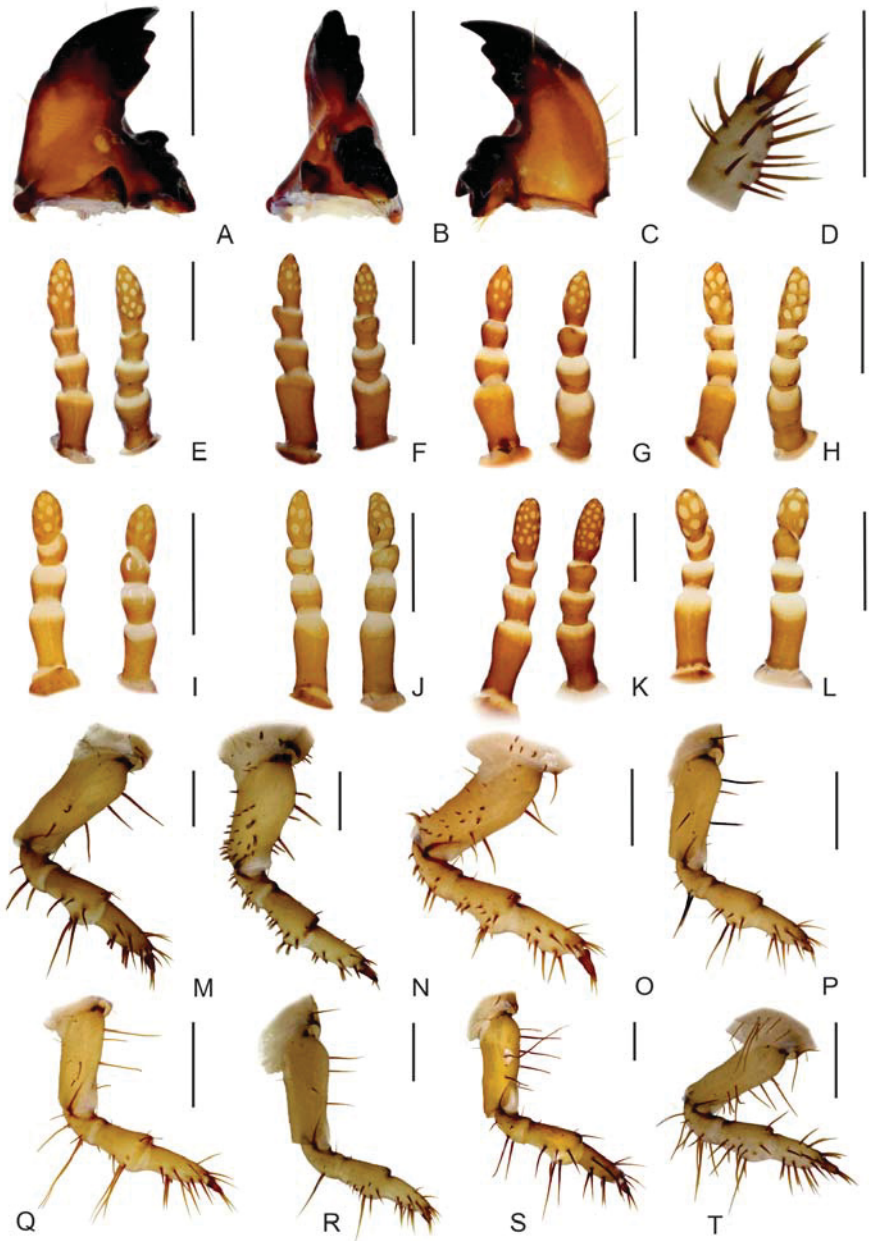

Fig. 9. Third instar larvae of Taenioderini. A–C – right mandible (ventral, medial and dorsal aspect), D – pretarsus, E–L– antenna (dorsal and ventral aspect), M–T – metathoracic leg: A–D – *Taeniodera* sp. E,M – *Chalcothea neglecta*. F,N – *Coilodera diardi*. G,O – *C. penicillata*. H,P – *Euselates cineraceus*. I,Q – *E. laoticus*. J,R – *Meroloba suturalis*. K,S – *Plectrone tristis*. L, T – *Taeniodera* sp. Scale bars = 1 mm.

Hypopharyngeal sclerome (Fig. 5D). Four to five tegumentary expansions (phoba-like processes) present on the left lateral lobe of hypopharynx, tegumentary expansions on right medial portion of scleroma present.

Ligula (Figs 5D; 13C). Dorsal surface with two lateral groups of nine hair-like setae, two paramedial setae at the apical margin and central group of setae and sensilla. This group is composed of two paramedial rows of three stout and conical setae, and transverse, basomedial row with four conical and four to six campaniform setae.

Thorax (Figs 2D; 6S; 8Q; 9P). Prothoracic sclerite with seven to ten setae on the antero-ventral margin and another two setae in the posterio-dorsal area. Each sublobe of prothorax dorsally with one row of mostly medium-long or long setae interspersed with few short setae. Thoracic spiracle (Fig. 6S) 0.7 × 0.4 mm (height × width), bullar opening narrow, arms of respiratory plate almost concealed. Respiratory plate with approximately 20–40 holes across diameter. Venter of each thoracic segment with four to six prominent dark setae (usually one pair of long and several medium-long or short setae present). Similar setae also on coxa. Pretarsus (Fig. 8Q) conical with falcate tip and two apical setae.

Abdomen (Figs 2D; 10D; 11D). Each dorsal sublobe of abdominal segments I–VIII with one row of mostly medium long setae, however, short and long setae also present. Dorsum of abdominal segment VII–VIII, as well as venter, and spiracular and pleural areas of all abdominal segments with several prominent dark stiff setae. Spiracles on abdominal segments I–V elliptical, similar to thoracic spiracle, abdominal spiracles on segments VI–VIII almost circular.

Raster (Figs 10D; 11D). Palidium monostichous (however with few pali scattered around the main row), approximately 25 pali arranged in single elongate U-shaped row. Septula opened posteriorly, about three times longer than broad. Tegilla fused, with numerous short, stout, apically recurved setae, ventral and dorsal anal lip with dense rows of similar setae. The ultimate abdominal segment with sparse but prominent dark oblanceoate setae.

Euselates laoticus Mikšić, 1974

(Figs 2E; 3E; 4E; 5E; 6M–O,T; 8G–I,R; 9I,Q; 10E; 11E; 12F,K,N; 13J)

Material examined. 2 third instar larvae reared from eggs laid by adults collected in: **LAOS: Houa Phan Province:** 20°13′09–19″N 103°59′54″–104°00′03″E, Mount Phou Pane, 1480–1510 m a.s.l., 1.–16.vi.2009, V. Kubáň leg.

Description of third instar larva. ***Body*** (Fig. 2E). Length 27.0–34.0 mm, dorsoventral interval of body segments gradually increasing toward the penultimate segment; penultimate and ultimate segment distinctly thicker than the previous segments. Chaetotaxy more or less sparse, however with numerous long or extremely long setae, giving the larva 'hairy appearance', the longest setae present on the ultimate abdominal segment.

Head capsule (Fig. 3E). Width 2.9 (n = 1), brow with pale spots, clypeus and labrum yellow. Frontal sutures bisinuated. Epicranial insertions of antennal muscles visible as pale depressions. Cranial chaetotaxy summarized in Table 1. Anterior and exterior frontal setae with minute single seta.

Antennae (Figs 3E; 9I). Relative length of antennomeres I–IV (an I–IV): an I > an IV > an II > an III), ultimate antennomere with eight dorsal and nine ventral sensory spots (n = 1).

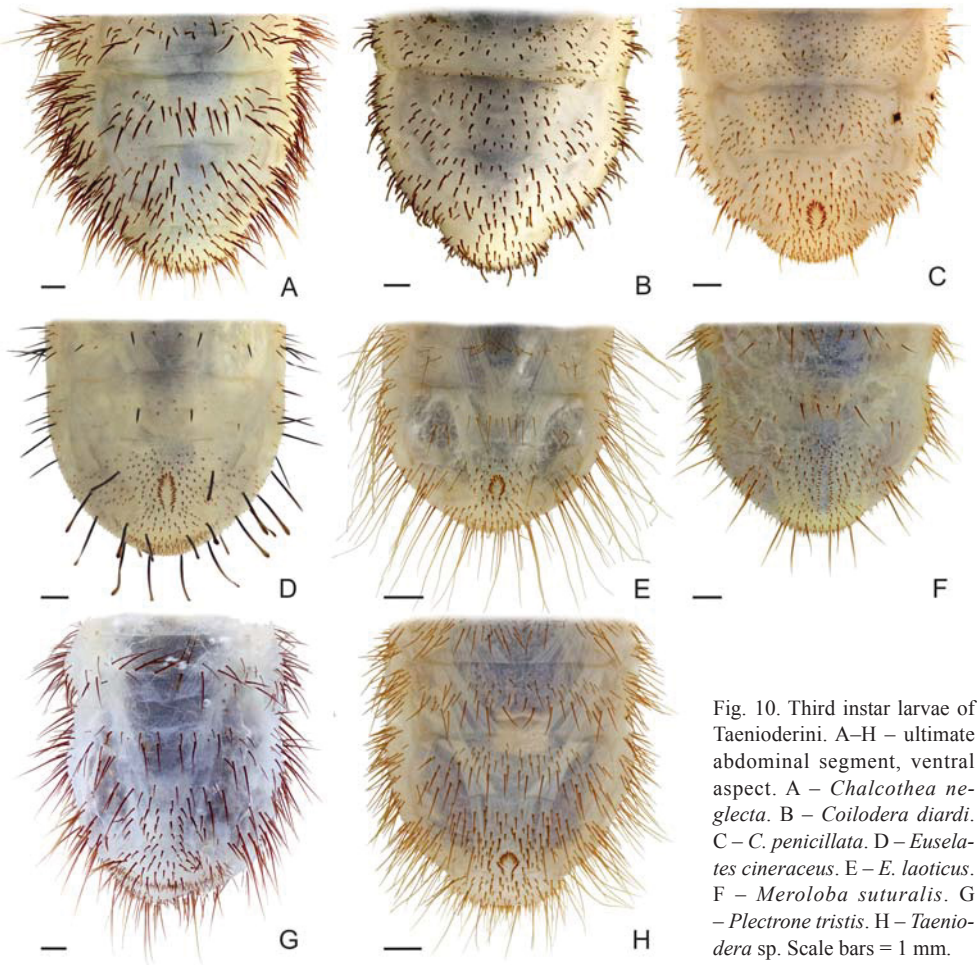

Fig. 10. Third instar larvae of Taenioderini. A–H – ultimate abdominal segment, ventral aspect. A – *Chalcothea neglecta*. B – *Coilodera diardi*. C – *C. penicillata*. D – *Euselates cineraceus*. E – *E. laoticus*. F – *Meroloba suturalis*. G – *Plectrone tristis*. H – *Taeniodera* sp. Scale bars = 1 mm.

Epipharynx (Figs 4E; 12F). Haptomerum: Zygum convex, more or less protruding, with arcuate row of approximately 14 stout conical setae and few setae proximad to the row. Sensilla of zygum grouped in single group on more or less prominent cone. Acroparia: Lateral lobes of epipharynx with four to five long setae, medial lobe with eight setae. Acanthoparia with five to six setae surrounded by moderately swollen base (or tubercle); the size of the tubercles as well as the setae increasing towards apex of epipharynx.

Chaetoparia: Asymmetric, right side composed of approximately 45 setae in irregular longitudinal rows and medial field (proximad to plate-shaped sclerite). Left side with approximately 30 setae in three irregular rows. Pedium large. Dexiotorma straight, right pternotorma absent (only slightly indicated). Laeotorma strongly reduced, however present, left pternotorma well developed.

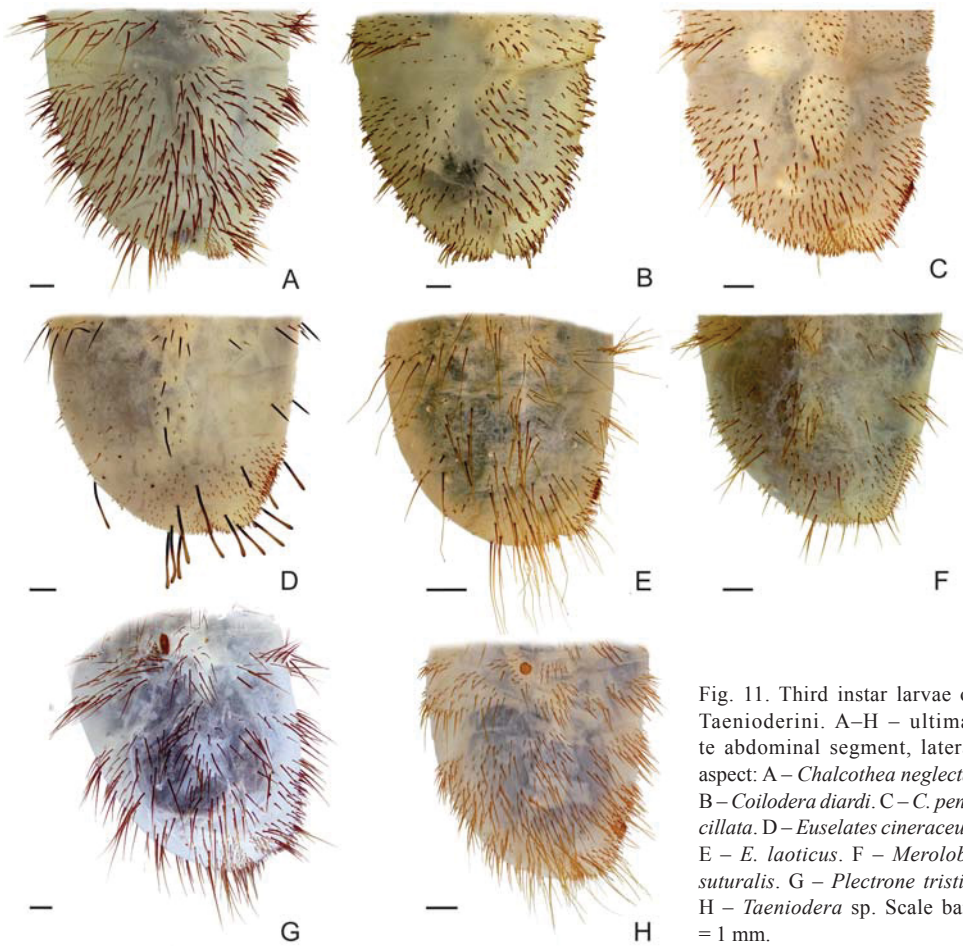

Fig. 11. Third instar larvae of Taenioderini. A–H – ultimate abdominal segment, lateral aspect: A – *Chalcothea neglecta*. B – *Coilodera diardi*. C – *C. penicillata*. D – *Euselates cineraceus*. E – *E. laoticus*. F – *Meroloba suturalis*. G – *Plectrone tristis*. H – *Taeniodera* sp. Scale bars = 1 mm.

Haptolachus: Sense cone low, cob-like. Plate-like sclerite reduced.

Mandibles (Figs 6M–O; 8G–I; 13J). Stridulatory area well developed, with approximately 20–25 ridges. Scrobis with two to five lateral setae. Longitudinal furrow absent. Apical half of mandibles in dorsal aspect with two lateral setae and mediolateral depression (proximad to the base of the third scissorial tooth). Lateral outline of both mandibles without prominent external tooth.

Maxilla (Figs 5E; 12K). Dorsal surface of cardo and labacoparia with four to six and 10 setae, respectively. Dorsal surface of stipes with 13–14 slender hair-like setae and one anterolateral stout seta. Maxillary stridulatory apparatus on stipes with four to five spine-like stridulatory teeth (in dorsal aspect, Fig. 12K) and two blunt tubercles. Galear portion of mala in dorsal aspect beside large falcate uncus with five large stiff and three to four medium-sized hair-like setae, respectively. Lacinial part of mala with around 15 mostly long

and stiff setae. Lacinial apex with two unci (subapical uncus however small and reduced) and with conical, stout setae.

Hypopharyngeal sclerome (Figs 5E; 12N). Four to five tegumentary expansions (phoba-like processes) present on the left lateral lobe of hypopharynx, tegumentary expansions on right medial portion of scleroma absent.

Ligula (Fig. 5E). Dorsal surface with two lateral groups of nine hair-like setae, two paramedial setae at the apical margin and central group of setae and sensilla. This group is composed of two paramedial rows of three stout and conical setae, and transverse, basomedial row with three to conical and six campaniform setae.

Thorax (Figs 2E; 6T; 8R; 9Q). Prothoracic sclerite with anterior row of approximately 20 hair-like setae and posterior row of four to five setae. Each sublobe of prothorax dorsally with one row of mostly medium-long or long setae interspersed with few short setae. Thoracic spiracle (Fig. 6T) 0.6 × 0.3 mm (height × width), bullar opening broad, distance between the arms of respiratory plate equals the widest diameter of respiratory plate. Respiratory plate with approximately 15 holes across diameter. Venter of each thoracic segment with row of numerous long hair-like setae. Pretarsus (Fig. 8R) cylindrical with small falcate tip and two apical setae.

Abdomen (Figs 2E; 10E; 11E). Each dorsal sublobe of abdominal segments I–VIII with one or two rows short and long hair-like setae. Setae of ventral and lateral parts of body extremely long. Spiracles on abdominal segments I–VII similar to the thoracic spiracle in shape and size, spiracle of abdominal segment distinctly smaller.

Raster (Figs 10E; 11E). Palidium monostichous (however with few scattered pali around the main row), approximately 20–25 pali arranged in single U-shaped row. Septula opened posteriorly, about two times longer than broad. Tegilla fused, with approximately 15 hamate setae. Hamate setae also present on the ventral anal lip. The ultimate abdominal segment with numerous extremely long hair-like setae especially on sides.

Meroloba suturalis (Snellen van Vollenhoven, 1858)

(Figs 2F; 3F; 4F; 5F; 7A–C,P; 8J–L,S; 9J,R; 10F; 11F; 12L,O; 13D,K)

Material examined. 7 third instar larvae reared from adults collected in: **MALAYSIA: Borneo Island:** Sabah Sultanate: Kinabatangan River Reserve, Sukau (Kota Kinabatangan), 5°31′13″N 118°17′41″E, 50 m a.s.l., 20.–22. ii.2010, P. Šípek leg.

Description of third instar larva. ***Body*** (Fig. 2F). Length 43.0–51.0 mm, dorsoventral interval of body segments increasing slightly towards the penultimate body segment (thus abdominal segments appear to be slightly thicker; abdominal segments VII and VIII are the thickest). Body with numerous setae; setae of ventral and dorsal body parts of equal shape and size.

Head capsule (Fig. 3F). Maximum width 3.5–3.7 mm, smooth, yellowish brown. Frontal sutures deeply bisinuated. Epicranial insertions of antennal muscles indistinct. Cranial chaetotaxy summarized in Table 2. Anterior and exterior frontal setae with minute single seta.

Antennae (Figs 3F; 9J). Relative length of antennomeres I–IV (an I–IV): an I > an IV > an II > an III), ultimate antennomere with three to seven dorsal and six to nine ventral sensory spots.

Epipharynx (Fig. 4F). Haptomerum: Zygum convex, more or less protruding, with angulate or arcuate row of 17–19 stout conical setae and several similar setae proximad to the row. Sensilla of zygum grouped in two groups distad to the row. Acroparia: Lateral lobes of epipharynx with three to five long setae, medial lobe with four and four to five setae on ventral and dorsal side, respectively. Acanthoparia with four to eight setae; the size of setae increasing towards apex of epipharynx. Chaetoparia: Asymmetric, right side composed of approximately 45–60 setae, left side with around 28–33 setae in three to four rows. Both parts of chaetoparia with medial, more or less regular row of prominent long setae. Pedium large, with isolated row of two to five slender setae on the left side. Dexiotorma straight, right pternotorma well developed. Laeotorma absent, left pternotorma well developed.

Haptolachus: Sense cone small, conical, with four pores. Plate-like sclerite large, horse--shoe shaped.

Mandibles (Figs 7A–C; 8J–L;13K). Stridulatory area well developed, distinctly paler than the other parts of ventral mandibular face, with approximately ten regular ridges, bordered with numerous irregular rugosities at both proximal and distal margin of field. Scrobis with one or two lateral setae. Longitudinal furrow shallow. Lateral outline of both mandibles without external tooth. Scissorial teeth of left mandible subequal, large; right mandible with two large and one small scissorial tooth.

Maxilla (Figs 5F; 12L; 12O; 13D). Dorsal surface of cardo and labacoparia with zero to four, 13–20 setae, respectively. Ventral surface of cardo and labacoparia with zero to three and 5–14 setae, respectively, labacoparia often with one or two stiff setae. Dorsal surface of stipes with approximately 14–19 slender hair-like setae, one anterolateral stout seta may be present. Maxillary stridulatory apparatus with row of five to eight spine-like stridulatory teeth and one blunt tubercle (Fig. 12L), in some specimens some stridularory teeth outside the row. Ventral surface of stipes with single proximal and two distal setae. Galear portion of mala in dorsal aspect beside large falcate uncus with six (seven) large stiff and three to five medium-sized hair-like setae, respectively. Lacinial part of mala with around 16–18 mostly extremely long and stiff setae. Lacinial apex with single triangular uncus with short, conical seta at the base and another long, stout, conical seta next to it. Vental surface of mala with two longitudinal rows of four to five setae; setae of the exterior row long and stiff, setae of the interior row shorter and stout.

Hypopharyngeal sclerome (Figs 5F; 12O). Four tegumentary expansions (phoba-like processes) present on the left lateral lobe of hypopharynx, tegumentary expansions on right medial portion of scleroma present.

Ligula (Figs 5F; 12O; 13D). Dorsal surface with two lateral groups of around 10 hair-like setae, two paramedial setae at the (ventro-) apical margin and central group of setae and sensilla. This group is composed of two paramedial rows of three stout, conical setae, and transverse, basomedial row with seven to eight conical or campaneiform setae.

Thorax (Figs 2F; 7P; 8S; 9R). Prothoracic sclerite with four to seven setae on the antero-ventral margin and another two to four setae in the posterio-dorsal area. Each sublobe of prothorax dorsal with one or two rows of medium-long and long setae interspersed with few short setae. Thoracic spiracle (Fig. 7P) 0.93 × 0.50 mm (height × width). Bullar opening distinct,

approximately 0.1 mm wide, arms of respiratory plate thus well separated. Respiratory plate with approximately 20–40 holes across diameter. Venter of thorax (and the first abdominal segment) with paramedian pair of stiff setae, similar setae found also on legs. Pretarsus (Fig. 8S) conical, with two apical setae, falcate tip or similar structures absent.

Abdomen (Figs 2F; 10F; 11F). Each dorsal sublobe of abdominal segments I–VIII with two to three rows of setae. Setae in anterior row(s) short or medium-sized, posterior row also with several long setae. Venter of abdominal segments II–IX with several long stiff setae. Dorsum of abdominal segments IX–X, with numerous short to long setae. Spiracles on abdominal segments I–VI elongate, similar to thoracic spiracle, abdominal spiracles on segments VII–VIII almost circular, arms of respiratory plate almost concealed.

Raster (Figs 10F; 11F). Pali, short, spine-like, smaller than setae of tegilla. Palidium monostichous, with approximately 20 pali arranged in two almost parallel rows, closed at the proximal end. Teges almost entirely separated by rows of pali. Septula opened posteriorly, about six times longer than broad. Tegilla with numerous apically recurved, pointed setae. Setae of the dorsal and ventral anal lip same as those on the dorsal abdominal lobes.

Plectrone tristis (Westwood, 1842)

(Figs 2G; 3G; 4G; 5G; 7D–F,Q; 8M–O,T; 9K,S; 10G; 11G)

Material examined. 5 third instar larvae reared from adults obtained in February 2013 from the beetle breeder O. Jahn (Sušice, Czech Republic), collecting data and locality are not available.

Description of third instar larva. ***Body*** (Fig. 2G). Length 56.0–68.0 mm (n = 3, larvae not fully grown), dorsoventral interval of abdominal segments slightly larger than in thoracic segments (thus abdominal segments appear to be slightly thicker, abdominal segments VII and VIII are the thickest). Body, especially on ventral side, covered with numerous stiff, brown setae. Setae on both dorsal and ventral part of thorax and abdomen subequal in size and shape.

Head capsule (Fig. 3G). Maximum width 5.6–7.1 mm, surface of cranium with indistinct microsculpture, yellowish or reddish brown, parts of epicranium with numerous darker irregular spots. Frontal sutures bisinuated. Epicranial insertions of antennal muscles very distinct, dorsally emarginated with sickle-like line. Cranial chaetotaxy summarized in Table 2. Anterior and exterior frontal setae absent or composed of one or two minute setae.

Antennae (Figs 3G; 9K). Relative length of antennomeres I–IV (an I–IV): an I ≥ an IV > an II > an III), ultimate antennomere with 15–20 dorsal and 17–23 ventral sensory spots.

Epipharynx (Fig. 4G). Haptomerum: Zygum convex, with arcuate row of 15–17 stout, pointed setae and medial row of another five to eight stout setae. Sensilla of zygum in single row distad to the row of stout setae. Acroparia: Lateral lobes of epipharynx with four to five long setae, medial lobe with eight setae. Acanthoparia with four to five large tubercles each with single seta; the size of the tubercles, as well as the length of setae, increasing towards the apex of epipharynx.

Chaetoparia: Asymmetric, right side with single regular row of long stiff setae and five to six irregular rows, left side with single regular and three to four irregular rows of setae. Right side of chaetoparia with approximately 55–70, left with 40–50 setae, respectively. Pedium large. Dexiotorma somewhat crooked, long, narrowed toward medial end, right pternotorma

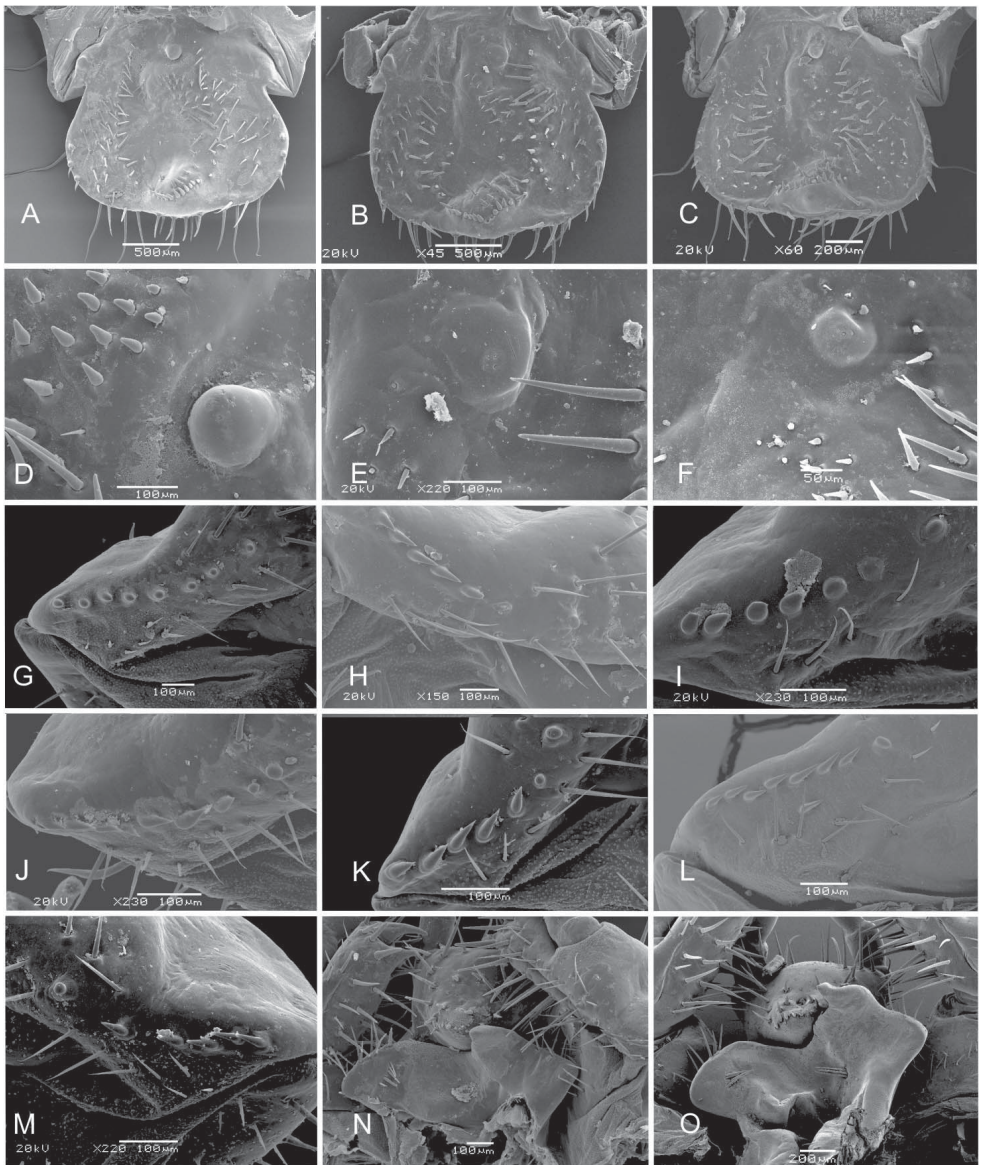

Fig. 12. Third instar larvae of Taenioderini, SEM images. A–C – epipharynx: A – *Chalcothea neglecta*. B – *Coilodera diardi*. C – *Taeniodera* sp. D–F – sense cone (haptolachus, epipharynx): D – *Chalcothea neglecta.* E – *Coilodera diardi*. F– *Euselates laoticus*. G–M – maxillar stridulatory teeth: G – *Chalcothea neglecta.* H – *Coilodera diardi*. I – *C. penicillata*. J – *E. cineraceus*. K – *E. laoticus*. L – *Meroloba suturalis*.M – *Taeniodera* sp. N,O – hypopharyngeal scleroma: N – *E. laoticus*. O – *Meroloba suturalis*.

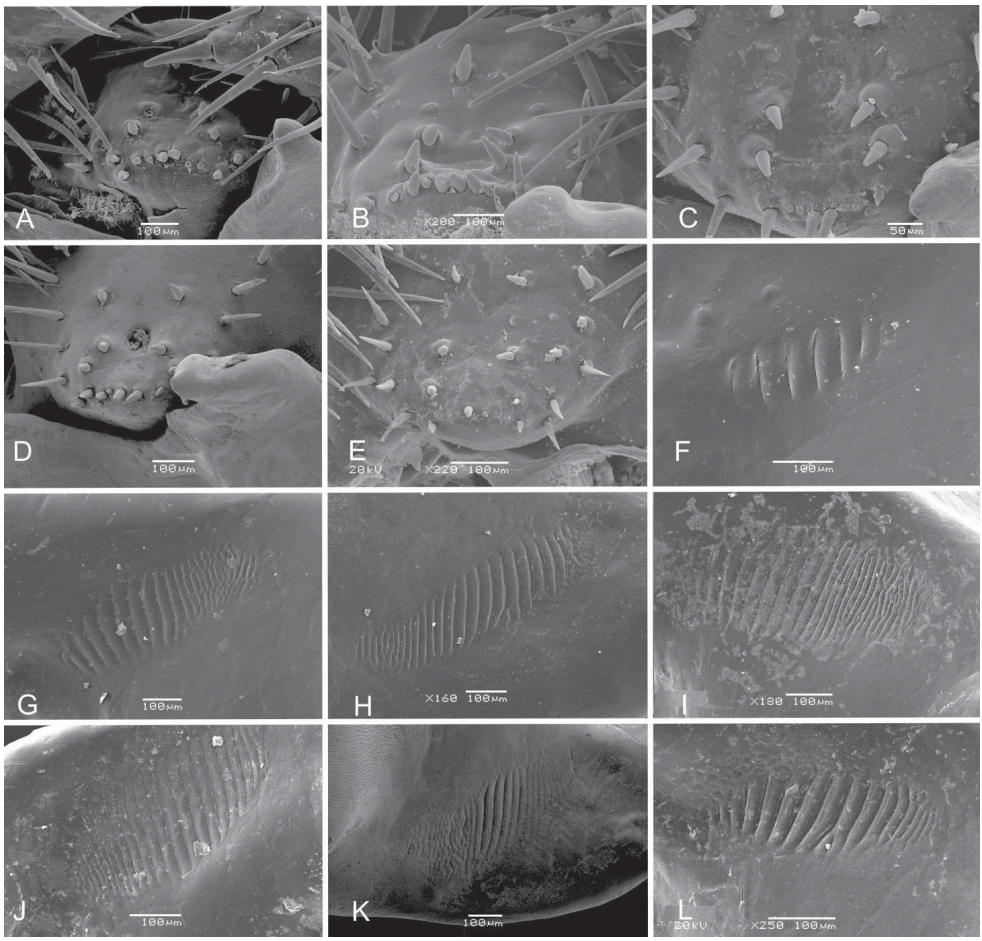

Fig. 13. Third instar larvae of Taenioderini, SEM images. A–E – ligula: A – *Chalcothea neglecta*. B – *Coilodera diardi*, C – *Euselates cineraceus*. D – *Meroloba suturalis*. E – *Taeniodera* sp. F–L – mandibular stridulatory area: F – *Chalcothea neglecta*. G – *Coilodera diardi*. H – *C. penicillata*. I – *E. cineraceus*. J – *E. laoticus*. K – *Meroloba suturalis*. L – *Taeniodera* sp.

absent. Laeotorma present, left pternotorma prolonged. Haptolachus: Sense cone large, broad at the base, conical, almost pointed at the tip. Plate-like sclerite large, occupying almost the entire area between sense cone and the regular rows on both sides of chaetoparia. Sensilla of haptolachus organized in two groups of two sensilla.

Mandibles (Figs 7D–F; 8M–O). Stridulatory area absent, ventral surface of entire mandible smooth, rarely with few irregular ridges. Scrobis with three to four lateral setae. Longitudinal furrow present, extending towards apex of mandibles, with two prominent lateroapical setae and one or two posterior setae (occasionally absent).

Maxilla (Fig. 5G). Dorsal surface of cardo and labacoparia with four to eight stiff and 16–24 slender setae, respectively. Ventral surface of cardo and labacoparia with three to four and six to nine stiff setae, respectively, labacoparia with another 8–15 slender setae. Dorsal surface of stipes with approximately 13–20 slender hair-like setae and one to four anterolateral stout setae. Maxillary stridulatory apparatus on stipes with eight to nine, blunt, conical stridulatory teeth, blunt tubercle absent or of the same shape as the previous teeth. Ventral surface of stipes with single proximal and one to three distal setae (long and stout, arranged in transverse row). Galear portion of mala in dorsal aspect beside large falcate uncus with three to five large stiff and four to eight medium-sized hair-like setae respectively. Lacinial part of mala with around twenty mostly extremely long and stiff setae. Lacinial uncus beside large pointed claw with minute second pointed tip, and two conical, stout setae. Ventral surface of mala with two longitudinal rows of setae; the exterior row with three to five mostly long and stiff setae, the interior row with three short and stout setae.

Hypopharyngeal sclerome (Fig. 5G). Around twenty tegumentary expansions (phoba-like processes) present on the left lateral lobe of hypopharynx, tegumentary expansions on right medial portion of scleroma present in all studied individuals.

Ligula (Fig. 5G). Dorsal surface laterally and anteriorly with two groups of around 11–15 hair-like setae (each group consists of longitudinal and oblique row) and central group of setae and sensilla. The central group is composed of two paramedial rows of two stout, conical setae, and transverse, basomedial row of five to seven conical setae.

Thorax (Figs 2G; 7Q; 8T; 9S). Prothoracic sclerite with approximately eight to twelve setae on the anteroventral margin and another one or two setae in the posterio-dorsal area. Each sublobe of prothorax dorsal with one or two rows of setae (short to long). Thoracic spiracle (Fig. 7Q) 1.1 × 0.8 mm (height × width), bullar opening narrow, not broader than the maximum perimeter of respiratory plate. Respiratory plate with approximately 50 holes across diameter. Pretarsus (Fig. 8T) conical with minute pointed tip and two apical setae.

Abdomen (Figs 2G; 10G; 11G). Each dorsal sublobe of abdominal segments I–VIII with one to three rows of setae. The anterior one or two row(s) irregular, with short setae. Posterior row regular with medium-long and long setae. Setae of abdominal segments IX–X, as well as the setae of the entire ventral body covered slightly stiffer than those on dorsal part. Spiracles on abdominal segments I–III elongate, similar to thoracic spiracle, abdominal spiracles on segments IV–VIII almost circular.

Raster (Figs 10G; 11G). Rows of pali absent, tegilla fused, central part with medium-long hamate setae, other parts with stiff and long hair-like setae. Ventral anal lip with three rows of short apically recurved setae.

Taeniodera sp. (*T. idolica* Janson, 1909 species group)

(Figs 2H; 3H; 4H; 5H; 7G–I,R; 9A–D,L,T; 10H; 11H; 12C, M; 13E,L)

Material examined. 2 third instar larvae reared from eggs laid by adult females collected in: **LAOS: Houa Phan Province:** 20°13′09–19″N 103°59′54″–104°00′03″E, Mount Phou Pane, 1480–1510 m a.s.l., 1.–16.vi.2009, V. Kubáň leg.

Description of third instar larva. ***Body*** (Fig. 2H). Length 35.0 mm, dorsoventral interval of body segments increasing towards the penultimate body segment (thus abdominal

segments appear to be thicker; abdominal segments VII and VIII are the thickest). Body with numerous setae; setae of ventral and dorsal body parts of the same shape, however ventral setae distinctly longer.

Head capsule (Fig. 3H). Maximum width 3.5–3.7 mm, glossy, yellowish. Frontal sutures bisinuated. Epicranial insertions of antennal muscles indistinct. Cranial chaetotaxy summarized in Table 2. Anterior and exterior frontal setae with minute single seta.

Antennae (Figs 3H; 9L). Relative length of antennomeres I–IV (an I–IV): an I > an IV > an II > an III), ultimate antennomere with five dorsal and six ventral sensory spots.

Epipharynx (Figs 4H; 12C). Haptomerum: Zygum convex, more or less protruding, with slightly arcuate row of 12 stout conical setae and several similar setae on the mesal part of zygum. Sensilla of zygum grouped in single group on low tubercle. Acroparia: Lateral lobes of epipharynx with five long setae, medial lobe with four and eight setae. Acanthoparia with seven setae surrounded by small tubercle; the size of setae as well as the size of the tubercle increasing towards apex of epipharynx. Chaetoparia: Asymmetric, right side with approximately 50 setae, left side with around 40 setae. Both parts of chaetoparia with medial, more or less regular row of prominent long setae. Pedium large, with isolated setae at the left side. Dexiotorma straight, slightly bent inwards, right pternotorma poorly developed. Laeotorma absent, left pternotorma well developed.

Haptolachus: Sense cone conical, well developed. Plate-like sclerite subtriangular, relatively small.

Mandibles (Figs 7G–I; 9A–C; 13L). Stridulatory area well developed, distinctly paler than the other parts of ventral mandibular face, with approximately 16–17 regular ridges, ridges at the mesal margin of stridulatory area short, slightly irregular and narrowed. Scrobis with five lateral setae. Longitudinal furrow absent. Lateral outline of both mandibles without external tooth. Scissorial teeth of left mandible subequal, large; right mandible with three teeth, apical tooth large, the two subapical teeth subequal.

Maxilla (Figs 5H; 12M). Dorsal surface of cardo and labaocoparia 8–12, 20–30 setae, respectively. Dorsal surface of stipes with approximately 14–18 hair-like setae and one anterolateral stout seta. Maxillary stridulatory apparatus with row of five to six spine-like stridulatory teeth and one blunt tubercle (Fig. 12M). Galear portion of mala in dorsal aspect beside large falcate uncus with five to six large stiff and three medium-sized hair-like setae, respectively. Lacinial part of mala with around 15–16 mostly extremely long and stiff setae. Lacinial apex with single triangular uncus with short, conical seta at the base and another long, stout, conical seta next to it.

Hypopharyngeal sclerome (Fig. 5H). Eight tegumentary expansions (phoba-like processes) present on the left lateral lobe of hypopharynx, tegumentary expansions on right medial portion of scleroma present.

Ligula (Figs 5H; 13E). Dorsal surface with two lateral groups of 11 hair-like setae, two pairs of paramedial setae at the (ventro-) apical margin and central group of setae and sensilla. This group is composed of two paramedial rows of three stout, conical setae, and transverse, basomedial row of three conical and six campaneiform setae.

Thorax (Figs 2H; 7R; 9D,T). Prothoracic sclerite with eight setae on the anteroventral margin and one seta in the posterio-dorsal area. Each sublobe of prothorax dorsal with one

Table 1. Cranial chaetotaxy of larvae of Taenioderini

	Epicranium				Frons				Clypeus		Labrum				
Group of setae:	**DES**	**PES**	**AES**	**EES**	**PFS**	**EFS**	**AFS**	**AAS**	**ACS**	**ECS**	**PLS**	**PMS**	**ELS**	**LLS**	**SMLL**
Chalcothea neglecta															
Long and medium setae	1(2)	-	1	2(3–4)	1	-	-	1	1	1(0)	-	1	2	3–4	8–9
Minute setae	-	1–3	-	(2)	-	-	-	-	-	0–1	3–8	0–3	-	-	-
Coilodera diardi															
Long and medium setae	1	-	1	2	1	-	-	1	1	1	-	1	2	4–6	8–9
Minute setae	3–9	5–10	-	(2)4–12	-	(1)	(1)	-	-	0–1	4–11	(1)	-	-	-
Coilodera penicillata															
Long and medium setae	1(1)	-	1	2	1	-	-	1	1	1	NA	NA	NA	NA	NA
Minute setae	6–8	5–7	-	0–5	-	-	(1)	-	-	-	-	-	-	-	-
Euselates cineraceus															
Long and medium setae	1	-	1	1	1	-	-	1	1	1	-	1	2	5–7	7–8
Minute setae	0–9	0–7	-	1–7	-	(1)	(1)	-	-	-	2–9	(2–3)	-	-	-
Euselates laoticus															
Long and medium setae	1	-	1	1	1	-	-	1	1	1		1	2	5	8
Minute setae	4–6	4–8	-	NA	-	0–1	1	-	-	-	4–5	-	-	-	-
Meroloba suturalis															
Long and medium setae	1(2)	-	1	1	1	-	-	1	1	1	-	1(2)	2	4–6	8
Minute setae	3–8	8–16	-	2–11	-	1	1	-	-	-	4–10	2–5	-	-	-
Plectrone tristis															
Long and medium setae	1	-	1	2	1	-	-	1	1	1	-	1	2	5–6	6–8
Minute setae	0–4	4–5	-	0–3	-	0–2	0–1	-	-	1	5–9	0–1	-	-	-
***Taeniodera* sp.**															
Long and medium setae	1	(1)	1	1	1	-	-	1	1	1	-	1	2	4	7
Minute setae	9–13	9–15	-	NA	-	1	1	-	-	-	1	0–1	-	-	-

Abbreviations: AAS = anterior frontal angle setae; ACS = anterior clypeal setae; AES = anterior epicranial setae; EES = exterior epicranial setae; AFS = anterior frontal setae; DES = dorsoepicranial setae; ECS = exterior clypeal setae; EFS = exterior frontal setae; ELS = exterior labral setae; LLS = setae of lateral labral lobe; SMLL = setae of medial labral lobe; PES = posterior epicranial setae; PFS = posterior frontal setae; PLS = posterior labral setae; PMS = paramedial labral setae. Number in brackets () indicates a rarely occurring stage.

Table 2. Morphological variability of larval Taenioderini: character states of seleceted morphological structures

	Pilosity	Epipharynx: stout setae of haptomerum	Epipharynx: sensilla of haptomerum	Epipharynx: sense cone	Epipharynx: laeotorma	Maxillary stridulatory teeth	External tooth on mandible	Stridulatory area	Lacinial unci	Raster of abdomen
Chalcothea neglecta	uniform, long and stiff setae	13–18 setae in arcuate or angulate row	two groups	prominent, conical and pointed	present	6–8, obtuse, drop-like	absent	reduced with 5–7 indistinct ridges	two	absent
Coilodera diardi	spatulate setae (venter of body + entire abdominal segment)	15–18 setae in angulate row	single group at the apex of haptomerum	reduced, knob-like	absent	6–7, spine-like	present, prominent	approximately 20 well developed ridges	single	absent
Coilodera penicillata	hamate setae (venter of body + entire abdominal segment)	15 setae in arcuate row	single group at the apex of haptomerum	reduced, knob-like	strongly reduced/ absent	5, spine-like	present, obtuse	approximately 20 well developed ridges	single	elliptical
Euselates cineraceus	sparse, with extraordinary long setae on ultimate abdominal segments	16–18 setae in arcuate row	single group	conical, almost pointed	absent	6–8, spine-like	present, prominent	20–25 well developed ridges	two	elliptical/ parallel
Euselates laoticus	prominent oblanceolate setae (ultimate abd. segment), long and stiff setae (venter of body), hair-like setae on remaining body parts	14 setae in arcutae row	single group on a slightly projecting cone	low, cob-like	strongly reduced	4–5, spine-like	absent	20–25 ridges	two (subapical uncus largely reduced)	elliptical
Meroloba suturalis	uniform, hair-like	17–19 setae in arcuate/ angulate row	two groups	small, conical	absent	5–8 spine-like	absent	10 well distinct ridges	single	parallel
Plectrone tristis	uniform, long and stiff setae	15–17 setae in arcuate row	independently in a row	prominent, conical, pointed	present	8–9, blunt, conical	absent	absent	two	absent
***Taeniodera* sp.**	Hair-like, ventral setae distinctly longer	12 setae in almost straight row	Single group on a single tubercle	Conical, well developed	Absent	5-6, spine-like	Absent	16-17 distinct ridges	Two	Elliptical

row of medium-long and short setae. Thoracic spiracle (Fig. 7R) 0.50 × 0.26 mm (height × width). Bullar opening large, distance between the arms of spiracular plate equal to 2/3 of the maximum diameter of spiracular plate. Respiratory plate with approximately 12–20 holes across diameter. Venter of thorax with numerous stiff setae. Pretarsus (Fig. 9D) cylindrical, with two apical setae, apical tip absent.

Abdomen (Figs 2H; 10H; 11H). Each dorsal sublobe of abdominal segments I–VI with one or two rows of short and medium-long setae; if two rows present then the anterior row irregular with only few short setae. Dorsal sublobes of abdominal segments VII and VIII with one to three rows of setae. Venter of abdominal segments I–IX with several long stiff setae organized in transverse rows. Dorsum of abdominal segments IX–X, with numerous short to long setae. Size of the abdominal spiracle gradually increasing caudad, spiracles on abdominal segments I–V elongate, similar to thoracic spiracle, but smaller. Abdominal spiracles on segments VI–VIII almost circular, arms of respiratory plate closer than in the preceding spiracles.

Raster (Figs 10H; 11H). Pali flattened dorsoventrally, lanceolate. Palidium monostichous composed of single horse-shoe shaped row of approximately 20 pali. Teges almost entirely separated by rows of pali. Septula opened posteriorly, about two times longer than broad. Tegilla with numerous apically recurved (subhamate) pointed setae, other ventral parts of abdominal segments VIII and IX covered with long stiff setae. Anal lip surrounded by regular rows of mostly short or medium-long setae.

Note on identification. The larvae belong either to *Taeniodera salvazai* (Bourgoin, 1924) or *T. zebraea* Fairmaire, 1893, however, the exact identification of the specimen is not possible as only females were collected.

Morphological diversity of larval Taenioderini

Larvae of Taenioderini described in the present paper showed a remarkable morphological diversity. The most important examples of such divergences are shown in Table 3. The larvae diverged mainly in the body pilosity, structures of haptomerum of epipharynx (row of stout setae arcuate or angulate; organization of haptomeral sensilla), development of laeotorma and sense cone; mandibular and maxillary stridulatory apparatus, presence or absence of external mandibular tooth, number of unci and development of raster.

Biology of Taenioderini

Based on our observations, Taenioderini do not markedly differ in their ecological preferences from other Cetoniinae *sensu stricto.* We collected either larvae or adults of several species associated with compact, rotten dead wood, often with white fungi. The larvae of *Chalcothea neglecta*, *Euselates cineraceus*, *Coilodera penicillata*, *Plectrone borneensis* Mikšić, 1973, *Ixorida* sp. and *Taeniodera* spp. were found in such conditions. Two females of *Meroloba suturalis* were observed in galleries of passalid beetles in a dead tree trunk near Sukau in Sabah, Borneo. An adult *Clerota brahma* Gestro, 1879 was chopped out of a rotten standing trunk inhabited by passalid beetles and *Odontolabis* sp.

stag beetle (Coleoptera: Lucanidae) in Cameron Highlands, Malaysia. In contrast, only a single larva of *P. borneensis* was found under epiphytic orchids and ferns. In captivity, the larvae developed well on a diet composed of soft, compact pieces of rotten beech (*Fagus* sp.) wood and ground leaf litter of deciduous trees.

Discussion

Morphology. Larvae of Taenioderini described in the present paper show complex morphological diversity (Table 3). The genera not only diverge significantly in several morphological characters, but an intra-generic variability in the presence or absence of important structures (e.g. the palidium of raster in the genus *Coilodera*; Figs 10B,C) was also observed. Because of this morphological variability we failed to identify a clear synapomorphy or combination of diagnostic characters which would allow us to separate the larvae of Taenioderini from other Cetoniinae tribes.

The most interesting feature visible at first sight is undoubtedly the variability in body pilosity (Figs 2, 9, 10). The most extreme example of such variability is found in the last instar of *Euselates cineraceus* larvae (Fig. 10D). While the body pilosity in the first two instars does not vary significantly from a 'common Cetoniinae' type, the last instar larvae have three types of setae: (1) the common hair-like setae on the dorsal portions of body segments; (2) long, stiff setae found especially on legs and ventral body parts and, finally, (3) the striking, extremely long and oblanceolate setae of the ultimate abdominal segment. This pattern of body pilosity seems to be unique among Scarabaeidae. However, the function (if any) of such unusual setae remains unclear. Other unusually variable morphological characters include various structures of the haptomerum and haptolachus on the epipharynx (Fig. 4), stridulatory apparatus on the maxilla and mandibula (Figs 12, 13) and structures of raster (Fig. 10; Table 3).

The reduction in the number of lacinial unci is also noteworthy. The typical character state occurring in almost all Cetoniinae *sensu stricto* are two lacinial unci, however, the larvae of *Coilodera* and *Meroloba suturalis* have a single triangular uncus. A single lacinial uncus is reported in Cetoniinae *sensu stricto* only for representatives of the genus *Euchroea* Burmeister, 1842 by Lumaret & Peyrieras (1982). Based on the images provided by the authors we consider their observation to be more or less doubtful as a second minute uncus is indicated on several illustrations.

The existence of the observed morphological variability in larval Taenioderini is rather unexpected. Generally, larvae of holometabolous insects are expected to be more conservative in their morphological features than their respective adults (due to the absence of direct sexual selection or more general feeding habits, for example). While it is debatable as to whether or not this is true, we have to admit that the current state of knowledge on immature stages of Coleoptera is rather limited and therefore logically biases our perception. On the other hand, when considered in the context of known immature stages from Europe and North America, an unparalleled morphological diversity of immature Taenioderini can be observed. There are several possible explanations for this phenomenon of which we would like to list the following three: (1) the members of this tribe belong to an early lineage/lineages of Cetoniinae, which would imply a longer development time of the respective groups, bringing into question the

monophyly of the tribe; (2) the exceptionally stable conditions of Southeast Asiatic forests led to a high specialisation rate for respective niches, which subsequently leads to high morphological diversity (given that the variable characters have an adaptive function); (3) the evolution rate of morphological characters in immature Taenioderini is higher than in other groups of Cetoniinae. However, it is obvious that none of the listed explanations can be tested without a deeper study of the evolution and ecology of the Cetoniinae and their closest relatives.

Classification of Taenioderini within the Cetoniinae. Krikken (1984) established the tribe Taenioderini by removing the respective subtribes Taenioderina and Chalcotheina from Gymnetini and supported his classification by four synapamorphic characters of the adults (see Introduction). We argue that the shape of the tibiotarsus in larvae of Taenioderini may represent another argument in favour of Krikken's (1984) theory. All of the studied larvae of Taenioderini have a more or less claw-like tibiotarsus with two setae (Figs 7S,T; 8P–T; 9D,M–T), while all of the known larvae of Gymnetini (for a list of described species and references see Šípek & Král 2012) have a blunt cylindrical tibiotarsus with several setae. As shown by Micó et al. (2008, data in matrix) the ancestral state of larval tibiotarsus in Cetoniinae is represented by a falcate claw with two setae, while the derived state is represented by a blunt cylindrical tibiotarsus with several setae (typical for the tribes Cetoniini, Gymnetini and several members of Goliathini: Micó et al. (2008; data in matrix), P. Šípek (unpubl. data).

According to Krikken's (1984) subdivision of Taenioderini, two of the described genera (*Chalcothea*, *Plectrone*) belong to the subtribe Chalcotheina, while the remaining four (*Coilodera*, *Euselates*, *Meroloba* and *Taeniodera*) are members of Taenioderina. On the basis of our results we identified three possible larval characters to support the recent subtribal classification of Taenioderini: (1) the mandibular stridulatory area strongly reduced or absent in representatives of Chalcotheina (Fig. 10F); with about 20 stridulatory ridges in Taenioderina (Figs 10G–L); (2) shape of maxillary stridulatory teeth obtuse or blunt in Chalcotheina (Fig. 12G), spine-like and pointed in Taenioderina (Figs 12J–L); (3) state of development of epipharingeal laeotorma (present in Chalcotheina (Figs 4A,G), absent in Taenioderina (Figs 4B-F,H)). However, these diagnostic traits should be regarded as preliminary due to the limited taxon sampling in the present study and an overall uncertainty of classification and phylogeny of the Cetoniinae *sensu lato.*

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