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THE HYPOTHETICAL GROUND PLAN OF THE ZYGAENIDAE, WITH A REVIEW OF THE POSSIBLE AUTAPOMORPHIES OF THE PROCRIDINAE AND THE DESCRIPTION OF THE INOUELINAE SUBFAM. NOV.

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ABSTRACT. The hypothetical ground plan of the lepidopterous family Zygaenidae is reconstructed based on a review of the apomorphic characters of the Zygaenoidea. Five subfamilies are recognised and their characters discussed in detail: **Inouelinae new subfamily**, Procridinae, Chalcosiinae, Callizygaeninae and Zygaeninae. A review of the possible autapomorphies of Procridinae is provided. The autapomorphic structure in the receptaculum seminis in the spermatheca of the Procridinae females is newly described as **bursa utricularis**.

Additional key words: Zygaenoidea, Zygaenidae, Zygaeninae, Chalcosiinae, Callizygaeninae, Procridinae, Inouelinae **new subfamily**, autapomorphies, morphology, bursa utricularis (**new structure**), chaetotaxy, anal combs, larval spined tubercles, karyotypes, character variability, taxonomy, systematics.

The lepidopterous family Zygaenidae has a world-wide distribution and hitherto has been divided into the four subfamilies: Procridinae, Chalcosiinae, Callizygaeninae and Zygaeninae (Tarmann 2004; Efetov et al. 2014a), to include more than 1,000 species. Alberti (1954) published the first comprehensive revision of the Zygaenidae of the world. However, a new review of the zygaenid characters is urgently needed because a number of new and significant characters of this family have been discovered in the last 60 years. Our views on the phylogeny of the group have improved and many new taxa have been described. Moreover, the status of some groups has changed. In the present work we provide an overview of our contemporary knowledge. We also describe Inouelinae as a new subfamily within the Zygaenidae, and propose a name (*bursa utricularis*) for a newly discovered and outstanding autapomorphic character of the subfamily Procridinae.

Apomorphies of Zygaenoidea

The definition of the superfamily Zygaenoidea is based on only a few characters that might only represent autapomorphies. The discussed characters are: head retractibility, heteromorphosis, forward migration and reduction of head setae, position of microsetae and pores, labral sensilla (see Vegliante & Zilli 2004: 181). However, as Vegliante & Zilli (2004) correctly state most of these characters have not been sufficiently studied throughout all families.

Two characters that may represent possible autapomorphies are:

1. Head of larva (at least in the later instars) retractile (Minet 1986: 300) (Figs. 1–3). It can be discussed if this applies also for Epipyropidae and Cyclotornidae. Our information is based on literature (Common 1990: 304; Epstein et al. 1998: 159) and personal communication with the late Clas M. Naumann and the late I. F. B. Common who both have dealt with these two families in detail. We have not examined the larvae of Epipyropidae and Cyclotornidae ourselves. The parasitic life habits and the morphology of both larvae are unique. The first instar larva of both families is attacking the host (Homoptera) by their piercing mandibles. In this position, the head is extended. When safely fixed to the host, in the later instars, the head is permanently retracted (Davis 1987: 460). Our conclusion is therefore that the head is principally retractile, but this habit is only used once.
2. Position of the 2nd abdominal spiracle of the pupa, which is covered by the wings whereas the 1st abdominal segment is visible (only verified for Epipyropidae, Megalopygidae, Limacodidae, Heterogynidae, Zygaenidae) (Minet 1986: 300; Nielsen & Common 1991: 877; Fänger et al. 2002: fig. 2) (Fig. 4).

The hypothetical 'ground plan' of the family Zygaenidae

We are aware that the term 'ground plan' is a hypothetical construction. It is an assembly of

characters that are supposed to represent plesiomorphies. In comparison with other groups (that are more primitive) many of these characters can, of course, represent apomorphies. For us the 'ground plan' of Zygaenidae is a hypothetical reconstruction of a 'primitive' Zygaenidae that most probably has never existed in that form. However, this hypothetical construction helps to understand the currently observed characters in the different groups of Zygaenidae. Therefore a list of so-called 'primitive characters' for this hypothetical 'ground plan' of the Zygaenidae is compiled below. It is summarized from all known characters of the superfamily Zygaenoidea and in comparison with other Lepidoptera:

- A. Head with ocelli and chaetosemata (Epstein et al. 1998: 171) (Figs. 5, 6) (for discussion, see below).
- B. Compound eyes with interommatidial setae (= interfacetal hairs sensu Scoble 1992: 27) (Tarmann 2004: 13, fig. 18; 19, fig. 53; 25, figs. 90, 91). This character is seen so far only in the Procridinae: in the Artonini in *Pollanisus* Walker, 1854, *Onceroptyga* Turner, 1906, and *Homophylotis* Turner, 1904 (Fig. 7) and in some Procridini (e.g. present in *Adscita* Retzius, 1783) (Figs. 8, 9), but not observed in *Illiberis* Walker, 1854 (Procridini) (Figs. 10, 11) and *Thyrassia* Butler, 1876 (Artonini) (see also Davis 1978: 9, figs. 6, 8, 9). This character is not sufficiently studied in Inouelinae **subfam. nov.** (description see below), Chalcosiinae, Callizygaeninae and Zygaeninae but it has not been found in the so far examined species.
- C. Maxillary palps present, short, with 2 segments (Fig. 12) (Tarmann 2004: 13, fig. 15; 16, fig. 31) (primary situation in Lepidoptera is 5 segments, as still observed in Micropteroidea—see Kristensen 1998: 41) (see Heppner 1998).
- D. Labial palps present, consisting of 3 segments, with sensory organ at tip (Figs. 13–15) (Epstein et al. 1998: 171; Tarmann 2004: 9, 11, 20, figs. 2, 4, 60) (compared with other groups).
- E. Mandibles reduced as in all higher Lepidoptera but still present as small lobes which connect to the anterior margin of the lower subgena by an intersegmental membrane. From the position of this membrane cyanogenic droplets can be released (Fig. 16) (Yen 2003: 305; Tarmann 2004: 23, fig. 76; Yen et al. 2005: 239, fig. 53a).
- F. Proboscis present, unscaled, long, spirally enrolled with muscles (myoglossat), tip with sensory hairs (Figs. 13, 17) (Naumann et al. 1999: 25, text-fig. 22), unpigmented and therefore yellowish.
- G. Antenna biserrate or bipectinate (Figs. 18, 19; Efetov 2001c: figs. 42–67; Efetov 2005b: figs. 2–12).
- H. Antenna tapering towards and pointed at apex (Fig. 20).
- I. Pectinations with setae (sensillae) (Figs. 21, 22) (e.g. Tarmann 2004: 19, fig. 56).
- J. Scapus short, without pecten (Figs. 5, 15) (Epstein et al. 1998: 171; e.g. Tarmann 2004: 19, figs. 2, 12, 57, 59, 77, 87).
- K. Prothorax with paired, strongly sclerotized sac-like patagia and parapatagia (Figs. 23, 24) (Naumann et al. 1999: 26, text-fig. 23; Yen 2003: 307).
- L. Mesothorax with tegulae (Figs. 23, 24) (Naumann et al. 1999: 26, text-fig. 23; Yen 2003: 307).
- M. Metathorax with a wing-thorax-coupling mechanism, as in most ditrysian Lepidoptera (Fig. 25) (Yen 2003: 308; Tarmann 2004: 10).
- N. Forelegs with epiphysis (Fig. 26) (Naumann 1977: 22; Efetov & Tarmann 1994: 91, fig. 29; Efetov 1994a: 56, fig. 5; Efetov 1994b: 119, fig. 6; Efetov 2001a: 42, fig. 1; Efetov 2001c: figs. 70, 71, 81; Efetov 2005a: fig. 101.1).
- O. Tibial spurs 0–2–4 (Fig. 27) (Epstein et al. 1998: 171; Efetov 2001c: figs. 68–82).
- P. Frenate wing coupling mechanism with frenulum and retinaculum, with variable sexual dimorphism (as in most ditrysian Lepidoptera) (Fig. 28) (Yen 2003: 308).
- Q. Wing venation with full set of veins (forewing: C, Sc, R_1 – R_5 , M_1 – M_3 , CuA_1 , CuA_2 , CuP , $1A+2A+3A$ (as basal fork); hindwing: $Sc+R_1$, Rs , M_1 – M_3 , CuA_1 , CuA_2 , CuP , $1A$, $2A$, $3A$) (Fig. 29) (Alberti 1954: pls 44–55; Tarmann 1984: figs. 219–245; Efetov 2001c: figs. 83–87; Efetov 2005b: fig. 13; Yen 2003: 310).
- R. All veins arising evenly spaced from cell (Fig. 29) (Alberti 1954: pls 44–55; Tarmann 1984: figs. 219–245; Efetov 2001c: figs. 84–87; Efetov 2005b: fig. 13).
- S. Medial stem as fully developed vein present in both wings (Fig. 29) (Alberti 1954: pls 44–55; Tarmann 1984: figs. 219–245; Efetov 2001c: figs. 83–87; Efetov 2005b: fig. 13).
- T. CuP completely present (Fig. 29) (Alberti 1954: pls 44–55; Tarmann 1984: figs. 219–245; Epstein et al. 1998: 171; Efetov 2001c: figs. 83–87; Efetov 2005b: fig. 13).
- U. Sc and Rs free in hindwing (Fig. 29) (Alberti 1954: pls 44–55; Tarmann 1984: figs. 219–245; Efetov 2001c: figs. 83–87; Efetov 2005b: fig. 13).
- V. Ultrastructure of wing scales on the 'abwing side' (upperside) with longitudinal ribs and with transverse striae (Fig. 30) (Naumann et al. 1999:

- 30, text-fig. 29f; Yen 2003: 312). In the most primitive Zygaenidae no perforation is developed. This character combination is similar to that of most primitive Lepidoptera (non-glossatan families) (Simonsen 2001; Kristensen & Simonsen 2003: 11).
- W. Abdomen with tortricoid apodemes on sternite 2 (Fig. 31) (Epstein et al. 1998: 172).
 - X. Abdomen of larva, pupa and imagines with a pair of lateral protuberances on segments 2 and 7 (Figs. 32, 33, 34) (Tarmann 1994; Epstein et al. 1998: 172; Tarmann 2004: 33, 50, 218–219, figs. 431, 433, 434; Efetov & Tarmann 2004: 301–303, figs. 1–7; Efetov 2005b: pl. 25, fig. 6).
 - Y. Larva feeding freely on the host-plant (Figs. 35, 36, 37). Not leaf mining.

Possible apomorphies of the family Zygaenidae

1. Cyanogenesis and resistance against cyanides. This character is possibly shared with other groups. Whether it is based on true relationship or just a parallel development is still unclear.
2. Head with ocelli and chaetosemata present (as in some other more primitive ditrysian groups, e.g. Yponomeutoidea and Tortricoidea). This character combination is absent in all other Zygaenoidea. It has also been reported for the Heterogynidae (Scoble 1992: 37, fig. 39). However, Scoble used the South African *Janseola titaea* Druce, 1896, as a model for his figure. Whereas *Heterogynis* species have only sensillae trichodea present (Jordan's first type of chaetosema), *Janseola* has the typical zygaenoid type (Jordan's second type of chaetosema) (Jordan 1923). Zilli (1998: 111) proposed the transfer of *Janseola* to the Zygaenidae, a change that has never been done officially in a separate paper but is correct and the authors agree with A. Zilli's arguments. Moreover, groups that were placed in the Zygaenidae earlier (e.g. Alberti 1954) are now excluded from that family, viz. Anomoeotidae, Himantopteridae, Phaudidae (that are now treated as families) and the genus *Chalcosiopsis* as well as the *Burlacena*-group (see also Yen et al. 2005: 184). Consequently, within the Zygaenoidea the character combination 'head with ocelli and chaetosemata present' applies to the Zygaenidae only (with the five included subfamilies: Inouelinae **subfam. nov.** (see below), Procrinae, Chalcosiinae, Callizygaeninae and Zygaeninae) (Figs. 5, 6).

The chaetosema was first described by Jordan (1923). He found two different forms that he described as 'type one' and 'type two'. Eltringham

(1925) examined the enervation and found that the chaetosema must be a sensory organ. Since then, the chaetosema is also known as Jordan's or Eltringham's organ (Scoble 1992: 36).

In the Zygaenidae the chaetosemata have a special structure consisting of erected scales (that look similar to those that cover the head at the vertex and genae) and setose bristles (sensilla trichodea) situated on a ground-plate and arranged in a typical way (Figs. 6, 38, 39) ('zygaenoid chaetosema', similar to 'second type' of chaetosema sensu Jordan (1923: 7), who figured the chaetosema of a *Micronia* sp. (Uraniidae) (Jordan 1923: pl. 2; Alberti 1954: 164; Naumann et al. 1999: 24, text-fig. 19; Tarmann 2004: 9, 11–25, figs. 6, 17, 26, 33, 44, 52, 61, 88; Yen 2003: 306–307; Yen et al. 2005: 186–187, figs. 15, 16). This 'zygaenoid chaetosema' is here considered to be unique and different from all other chaetosemata known, it could be an apomorphy of the Zygaenidae and Lacturidae (Lacturidae without ocelli!) (Yen et al. 2005: 186, fig. 15G). It differs from the chaetosemata of Uraniidae and Geometridae, by the large number of vertical-standing scales within or beside the sensilla trichodea, arranged either in honeycomb-like clusters around them (Procrinae), with the upright scales and the sensillae scattered between (Chalcosiinae, Callizygaeninae) (Yen et al. 2005: 184, figs. 15, 16) or side by side (Zygaeninae). In Inouelinae **subfam. nov.** (see below) the broad upright scales are arranged in the centre and the papillae trichodea beside them (Yen et al. 2005: 186, fig. 15C). In Uraniidae and Geometridae (both also referred to the 'second type' sensu Jordan (1923)) the sensillae trichodea are also arranged in groups in which some very slender upright scales are scattered. Most other Lepidoptera that have a chaetosema present belong to Jordan's first type without upright scales included beside the sensilla trichodea (Jordan 1923: 7, pl. 2) (see e.g. Horak 2006: 22, fig. 4 for Tortricidae; Scoble 1992: 37, fig. 39 for Heterogynidae).

3. Development of Petersen's gland (a pair of glands close to the ooporus in Zygaeninae and Procrinae of not exactly known function) (Fig. 40). This character is considered to be secondarily reduced in Inouelinae **subfam. nov.** (see below), Chalcosiinae and Callizygaeninae. This gland seems to have an importance for the protection of the eggs against predators, as it is reduced in three Australian genera of Procrinae (viz. *Pollanisus*, *Oncerothyra*, and *Hestiochora*), species of which

protect their eggs with poisonous dart-like scales from an abdominal hair tuft and in Chalcosiinae. The latter have an ovipositor and deposit their eggs into clefts of the bark of twigs and stems and obviously do not need additional protection (Bode & Naumann 1987; Naumann 1988; Naumann et al. 1999: 35, 37, text-fig. 38; Yen 2003: 316; Tarmann 2004: 36).

Possible apomorphies of the subfamily Chalcosiinae

1. Presence of a specialised hindwing-abdominal scent organ consisting of a fold on the first to second abdominal pleurite and a bundle of hair tufts that arises from the anal axillary sclerite of the hindwing and inserts into the pleural fold (Figs. 42–44) (Haase 1888; Tarmann 1992: 34, figs. 42–45; Yen et al. 2005: 229–230, 273, figs. 43–46).
2. Capability of releasing a large amount of cyanogenic protective fluid (often with a hissing sound) as foam from a dorsolateral opening situated between the patagia and parapatagia (Fig. 41). Whether this fluid is stored in cavities within the patagia or parapatagia is not known yet (Yen et al. 2005: 188, 239, fig. 53b).
3. Compound eyes without interommatidial setae (Yen 2003: 306). This character is considered to be a secondary reduction (see ground plan of Zygaenidae above and Figs. 7–11).
4. Chaetosema with upright scales and sensillae trichodea arranged in a mixture amongst each other (see above and for comparison Figs. 38, 39).
5. Tegumen in male genitalia with specialised apodemes (Yen 2003: 314–315, fig. 4).
6. In the females abdominal segments 8–10 transformed into an ovipositor (Yen 2003: 319, fig. 5).
7. Accessory gland on utriculus in receptaculum seminis absent (Yen et al. 2005: 221)

Possible apomorphies of the subfamily Zygaeninae

1. Compound eyes without interommatidial setae (Yen 2003: 306). This character is considered to be a secondary reduction (see ground plan of Zygaenidae above and Figs. 7–11).
2. Chaetosema placed on an elongate oval plate that is situated dorsad (Pryeriini) or laterodorsad/dorsad of ocellus (like an encaved triangle behind the ocellus) (Zygaenini), with a trichose part (main part) and upright scales arranged

around or along side (see Yen et al. 2005: 186, fig. 15D).

3. Development of a characteristic abdominal coremata organ (a pair of eversible brushes on the intersegmental integument between abdominal segments 8 and 9) in the male. This character is secondarily reduced in *Zygaena anthyllidis* Boisduval, 1828, and *Z. loti*-group (Kames 1980; Efetov 2004; 2005b).

Possible apomorphies of the subfamily Callizygaeninae

We know three plesiomorphic characters of the group:

- A. Medial stem in wing venation fully developed.
- B. Lagenae in receptaculum seminis present.
- C. Petersen's gland absent (based on examination of *Callizygaena aurata* only).

Possible apomorphies:

1. Compound eyes without interommatidial setae (Yen 2003: 306). This character is considered to be a secondary reduction (see ground plan of Zygaenidae above and Figs. 7–11).
2. Foretibial epiphysis reduced (Alberti 1954: 217).
3. Bulla seminalis in form of a globular bulb that is connected with the ductus seminalis by a stick-like tubular connection (Alberti 1954: 217) (not sufficiently examined in further species).
4. Development of signum-plates in corpus bursae (Alberti 1954: 217).
5. Abdominal segments 8–10 transformed to form a short ovipositor (Alberti 1954: 375, pl. 15, fig. 3b).

Possible autapomorphies of the subfamily Procridinae

Based on the comparison of all the above-mentioned characters with those found in the Procridinae we consider the following to represent autapomorphies of Procridinae:

1. In the females of Procridinae the spermatheca (= receptaculum seminis) is not divided into a bulb-like lagena and a tube-like utriculus, as in most other known ditrysian Lepidoptera (including the Zygaenidae subfamilies Zygaeninae, Chalcosiinae and Callizygaeninae; not yet clear in Inouelinae **subfam. nov.** due to lack of material), and represented by long tube (utriculus) (Fig. 45), as found in the monotrysian Lepidoptera families. However, we interpret this as a secondary reduction of the lagena, or the lagena is fused with the utriculus (Naumann 1988; Epstein et al. 1998: 173, 175, fig. 10.3.P). Yen (2003: 317), citing Naumann (1988), mentions that a lagena is also absent in the Zygaeninae. This is incorrect, as

in all examined Zygaeninae we found a well-developed lagena present. The terminology for these parts of the spermatheca is slightly confusing, as different authors have transposed these terms (see Kristensen 2003: 436–437). The form of the utriculus (at the position where the lagena is situated in non procridine zygaenids and other Lepidoptera) is always slightly or prominently broadened in Procridinae, forming a bag-like structure. We propose to denote this unique structure in the Procridinae as '*bursa utricularis*' (Fig. 45).

2. Development of a trend to inflate the posterior part of the ductus bursae to form a praebursa (Figs. 45, 46, 47) (Alberti 1954: 155–156, 210, text-figs. 14, 15; Tarmann 1984: figs. 268–270, 275, 278, 279, 282, 319, 320; Efetov 1994a: figs. 6, 7; Efetov 1996b: fig. 2; Efetov 1997a: figs. 6, 12, 16, 18; Efetov 1997b: figs. 16, 22; Efetov 1998a: figs. 9, 15, 21; Efetov 1998b: fig. 3; Efetov 2000: figs. 6, 10; Efetov 2001a: fig. 15; Efetov 2001c: pl. 27, figs. 2, 3, pl. 32, fig. 12, pl. 34, fig. 16, pl. 44, fig. 43; Efetov 2005a: figs. 105.8, 107.1–107.4; Efetov 2005b: pl. 53, figs. 9, 10, pl. 54, figs. 11, 12, pl. 55, fig. 15, pl. 56, figs. 16, 17, pl. 57, fig. 18; Efetov 2006: figs. 8, 11, 17, 26, 32, 47; Efetov & Tarmann 1999b: figs. 3, 4; Efetov & Tarmann 2013b: figs. 7, 8; Efetov & Tarmann 2014a: fig. 5; Efetov & Tarmann 2014b: figs. 26, 27; Efetov & Tarmann 2016a: fig. 10; Parshkova 2007: figs. 1–3; Tarmann 2004: figs. 240–272, 373–377, 419–422, 425). This praebursa can accommodate the spermatophore and functionally partly replaces the corpus bursae. There are often special crests, teeth and spines developed or folded sclerotized walls that help to rupture the spermatophore mechanically. Their structure has little variability within a species but there are remarkable differences between species; therefore they are of high diagnostic value (see e.g. Figs. 46, 47).
3. Wing scales with a specialised ultrastructure (Tarmann 1984a: 17–20; 1984b: 42–64, figs. 81–218; 2004: 28–30, figs. 99–118). The scale ultrastructure between the longitudinal ribs develops from the primitive 'transverse striae'-type (also still preserved in the most primitive Zygaeninae) through the implementation of cross connections first to a 'plate'-type sensu Tarmann (1984: 58–59, figs. 177–188) without perforation and then to a 'central hole'-type sensu Tarmann (1984: 42–47, figs. 81–116), or to a 'grid scale'-type or 'sieve scale'-type sensu Tarmann (1984:

48–49, figs. 117–128) equal to the '*Urania*-type' sensu Kristensen & Simonsen (2003: 11) (Figs. 48–51). The ultimate situation is a 'ladder'-type sensu Tarmann (1984: 51, fig. 140; 53, figs. 150, 152). On the body but not on the wings one can still find scales with the primary ultrastructure of primitive Lepidoptera in the form of 'transverse striae' also in the Procridinae (e.g. on the abdominal hair tuft of females in the Australian genera *Pollanisis*, *Onceroptyga* and *Hestiochora*) (Fig. 30).

4. Female 'calling' with a pheromone distributing organ that is located on abdominal tergites 3, 4 and 5. The release of the pheromone is combined with a characteristic 'calling position' in which the female spreads the wings and exposes these tergites by bending the abdomen downwards (Hallberg & Subchev 1997; Efetov 2001c: 16, 24, 25, pl. 53, figs. 1–7; Nishihara & Wipking 2003: fig. 3). The location of the glands in *Th. ampellophaga* was confirmed by investigations with electron microscopy which showed that the sex pheromone glands are situated on the anterior part of the 3rd–5th abdominal tergites of the females (Hallberg & Subchev 1997). In Figs. 52–57 one can see examples from the tribe Procridini, viz. the genera *Theresimima*, *Rhagades*, *Zygaenoprocris*, *Jordanita*, *Acoloithus*. In the tribe Artonini only *Pollanisis* females (Fig. 58) were observed in such a calling position, which is in a slightly different way from that observed in Procridini females: they spread their wings and expose the dorsal part of the abdomen. The latter is not bent downward but is almost straight; in addition, they vibrate the abdomen at a high frequency, which most likely helps to diffuse the pheromone from the glands (Mollet & Tarmann, pers. obs., 2013; Subchev 2014: 149). An interesting habit was observed by R. Turrent (pers. comm.). In Mexico he has found groups of females calling in a tree or shrub with the males flying around in the species *Triprocris ruemelli* (Druce, 1884) and a so far unidentified species that is related to *Pyromorpha latercula* (H. Edwards, 1882). Zygaeninae have the pheromone-producing glands at the posterior end of the abdomen between abdominal segments 8 and 9 (Tremewan 1985: 97; Naumann et al. 1999: pl. 9, fig. 1). In Inouelinae subfam. nov., Chalcosiinae and Callizygaeninae no such glands have been found so far. Moreover, Yen et al. (2005: 230) reported that calling by females of *Aglaope* (Chalcosiinae) has been observed in

which the female expands and contracts the abdominal segments, possibly to release the pheromone. Koshio & Hikada (1995) studied the sexual behaviour in *Elcysma weswoodi* and found that calling females were motionless and without a distinct calling posture.

The composition of sex attractants is known only for the Procrinae and Zygaeninae. While in Zygaeninae sex attractants are esters of higher alcohols and acetic acid, in Procrinae they are esters of 2-butanol and fatty acids (Subchev et al. 2010; 2012; 2013; 2016; Efetov et al. 2010; 2011; 2014b; 2015b; 2016; Efetov, Hofmann & Tarmann 2014).

5. Chaetosema in a honeycomb-like arrangement. The upright body scales (mainly broad scales) encircle the sensillae trichodea (Figs. 6, 38, 39) (Yen et al. 2005: 186, figs. 15A, 15B; Tarmann 2004: 11–25, figs. 6, 17, 26, 33, 39, 44, 52, 61, 63, 78, 88).

Tribe Artonini

(includes species from the eastern Palaearctic, the Oriental, Australian and Afrotropical regions).

Possible apomorphies:

1. Form of head dorsoventrally compressed with flat occiput (Fig. 14) (Tarmann 2004: 11, fig. 2; 12, fig. 12; 19, fig. 51; 20, fig. 59).
2. Chaetosema extending forward between the compound eye and the ocellus (Fig. 14) (Tarmann 1994; 2004: 11–20, figs. 2, 6, 12, 14, 17, 26, 32, 33, 38, 39, 43, 44, 51, 52, 59, 61).
3. A single unpaired medial spur developed on hind tibia (Fig. 59) (Tothill et al. 1930: 39; Efetov 2005a: figs. 101.5–101.7; Efetov & Tarmann 1996: 202–203, figs. 8–10; Efetov & Tarmann 2008: fig. 4). This character is secondarily reduced in some species (Tarmann 2004: 31, fig. 121a, b; Efetov & Tarmann 2008: fig. 5). A similar unpaired spur is known in the Eriocraniidae and Acanthopteroctetidae (Eriocranioidea) (Kristensen 1998: 51).
4. Valva in male genitalia fan-shaped (Tarmann 1994; 2004: 108–116, figs. 136–185; 136–137, figs. 273, 274, 277, 278; 178–179, figs. 344–355; 205, figs. 402–404; 212, figs. 412, 415), the dorsal and ventral sclerotisations are close together when in a relaxed position but can be remarkably spread when everted from the abdominal end to hold the abdomen of the female (Tarmann, personal observation); the translucent membrane between the dorsal and ventral sclerotisations is folded; this

gives the whole valva a fan-shaped appearance (Fig. 60).

5. Antenna with the pectinations very movable (they can be closed to the shaft when the specimen is disturbed).
6. First instar larva with only one dorsal seta on the first abdominal segment (Fig. 61) (Tarmann 2004: figs. 131.g–131.i; Efetov et al. 2006: figs. 3–7; Efetov & Hayashi 2008: fig. 3) (plesiomorphic variant – 2 dorsal setae on the first abdominal segment).

Tribe Procradini

(includes species from the Palaearctic, Nearctic, Neotropical, Afrotropical regions and the northern parts of the Oriental region).

Possible apomorphies:

1. Lateral protuberances on abdominal segments 2 and 7 reduced in imagines. Only in *Pseudoilliberis kuprijanovi* (Efetov, 1995) and some primitive *Illiberis* species this character is still developed (but all other characters show that these species belong to Procradini). The reduction is considered to be a secondary loss (see ground plan of Zygaenidae above).
2. Larvae develop the ability to live as leaf miners. The more primitive groups of Procradini still have larvae that feed freely on the plants but, step by step, beginning with the earliest instars in *Adscita* Retzius, 1783, the leaf-mining habit starts to become the standard habit. In *Jordanita* Verity, 1946, leaf-mining until the last instar is developed in most species.
3. The integument of adult larvae with sclerotized spined micro- and macrotubercles (unispined or multispined) (Efetov 1994b; 2001c; 2004).

Recently discovered characters in Procrinae

The data on the chaetotaxy of the first instar larvae, structure of sclerotized spined tubercles and anal combs of the adult larvae, and karyotypes are very important for studying the phylogeny and systematics of the Procrinae (Efetov 2001c; 2004; 2005b). A review of these characters is included below.

Chaetotaxy of first instar larva.

The chaetotaxy of the first instar larvae of species of the Zygaenidae is important for the understanding of relationships within this group because there are significant differences in the combinations of setae of genera and some subgenera (Efetov 2001a; 2001c; 2004; 2005b; Efetov et al. 2000; Efetov & Tarmann 1999a).

This character has been studied in different species of the Procrinae, Chalcosiinae and Zygaeninae. In spite of slight variation within a species there are good differences between species groups. Two main types of setae occur: light (*l*) and stronger sclerotized, dark (*d*). The numbers and combinations of dorsal (D), subdorsal (SD) and lateral (L) *l* and *d* setae are apomorphic characters in some groups. Some examples are listed below.

More than two SD setae is an apomorphic character of the genus *Rhagades* Wallengren, 1863 (Fig. 62). Two dark SD setae is an apomorphic character of the subgenus *Tarmannita* Efetov, 2000 that differs it from all other subgenera of the genus *Adscita* Retzius, 1783 (Figs. 63, 64). More than two D setae is a unique character of the subgenus *Roccia* Alberti, 1954, in the genus *Jordanita* Verity, 1946 (Figs. 65, 66).

Multispined micro- and macrotubercles of the larvae of Procrinae

Sclerotized tubercles that are covered with spines (spined tubercles) and situated on the integument of the adult larvae of Procrinae have already been described (Efetov 1994b). These structures have nothing to do with the coronetted tubercles described in the genus *Heterogynis* Rambur, 1837 (Lepidoptera: Heterogynidae) by Chapman (1904) and mentioned also by Vegliante & Zilli (2004). Coronetted tubercles are sclerotized cylinders with the upper end open and bordered with spines (Vegliante & Zilli 2004: figs. 2f, 2g), while spined tubercles have no openings and their function is not secretory. We suppose that the function of spined tubercles is to protect the integument of the larva (like chain armour of soldiers in early times) from injury and from attacks by parasitoids and predators (Efetov 2004).

More detailed investigations (Efetov 2004; 2005a) have shown that there are two types of spined tubercles: micro-tubercles (height less than 0.02 mm) (Figs. 67–70) and macrotubercles (height more than 0.04 mm) (Figs. 67–72). Tubercles of both types can be with one spine (unispined tubercles) (Figs. 67–70) or numerous (3–12 and more) spines (multispined tubercles) (Figs. 67, 68, 70–72).

Efetov & Tarmann (1995; 1999a) showed that multispined macrotubercles (Figs. 70–72) are a synapomorphy of *Zygaenoprocris* Hampson, 1900, *Adscita* Retzius, 1783, and *Jordanita* Verity, 1946.

Studies undertaken by Efetov (2004) in the subfamilies Procrinae (tribes Procrini and Artonini), Chalcosiinae and Zygaeninae revealed that multispined microtubercles are a synapomorphic character of the genera *Theresimima* Strand, 1917, *Rhagades* Wallengren, 1863,

and *Illiberis* Walker, 1854 (Procrinae, Procrini).

The cuticle of the larvae of *Theresimima* + *Rhagades* + *Illiberis* is covered with sclerotized multispined microtubercles and unispined macrotubercles (Figs. 67, 68), while in *Zygaenoprocris* + *Adscita* + *Jordanita*, the combination of unispined microtubercles and multispined macrotubercles is characteristic (Fig. 70). In the genus *Hedina* Alberti, 1954, there is a combination of unispined microtubercles and unispined macrotubercles (Fig. 69) (Efetov 2008).

Moreover, it has also been shown that very important characters are the position of the spines on the tubercles (symmetrical, asymmetrical) and the shape of the apices of the spines (pointed apices, crown-shaped apices). Symmetrical multispined macrotubercles with crown-shaped apices of the spines (Fig. 70) are considered to be a synapomorphic character of the subgenera *Adscita* Retzius, 1783, and *Tarmannita* Efetov, 2000, of the genus *Adscita*. The presence of strongly asymmetrical multispined macrotubercles with crown-shaped apices of the longest spines (Fig. 71) is an apomorphic character of the subgenus *Solaniterna* Efetov, 2004 (Efetov 2004), of the genus *Jordanita*.

Anal combs

Larvae of the Procrinae have a sclerotized comb situated above the anus (the so-called anal comb). While investigating early stages of the Procrinae, we found that the anal combs of the adult larvae in different genera and subgenera of Procrinae have different structures (Efetov 2001c; 2004: figs. 143–189). The anal comb consists of a plate-like base and setae. The most important criterion is the ratio of the height (H) of the base to the length (L) of the central setae (Figs. 73, 74).

It was found that in the genera *Pseudoilliberis* Efetov & Tarmann, 2012, *Illiberis* Walker, 1854, *Rhagades* Wallengren, 1863, and *Jordanita* Verity, 1946, the height of the base of the anal comb is greater than the length of the setae: H/L more than 1 (Fig. 73), while in the genus *Theresimima* Strand, 1917, and subgenera *Adscita* Retzius, 1783, and *Tarmannita* Efetov, 2000, of the genus *Adscita* Retzius, 1783, the situation is reversed: H/L less than 1 (Fig. 74). The high base of the comb (H/L more than 1) is probably a plesiomorphic character, as it is present in the more primitive genera *Pseudoilliberis*, *Illiberis* and *Rhagades*.

The larvae of the genus *Zygaenoprocris* Hampson, 1900, have a reduced anal comb (Fig. 76) (Efetov 2001c; 2004), while in the subgenus *Procriterna* Efetov & Tarmann, 2004, of the genus *Adscita* Retzius, 1783, the anal comb is double (without central part) (Fig. 75). We consider such a double anal comb to be an apomorphic character of *Procriterna*.

In *Zygaenoprocris*, as mentioned above, the anal comb in the adult larva is reduced. This character is here considered to be an autapomorphy of the genus because the anal comb is well developed not only in *Pseudoilliberis*, *Illiberis*, *Theresimima*, *Rhagades*, *Jordanita*, *Adscita* but also in some other genera of the Procridae. The apomorphy of the reduction of the anal comb in adult larva of *Zygaenoprocris* is supported by the fact that it is well developed in larvae of early instars (including the first instar) and is reduced in the last instars (according to observations by the first author on *Z. taftana* (Alberti, 1939)). *Harrisina* Packard, 1864, has no comb at all but only a dark spot at the place where the comb should be. However, *Harrisina* is a very derived genus with even asymmetrical genitalia.

The larvae of Artonini have a combination of three anal combs, consisting of a larger dorsal comb and two smaller lateral combs (Mollet & Tarmann 2010: fig. 7) arranged around the anal orifice. This character was observed in the genera *Pollanisus* and *Thyrassia*.

A thoracic brush organ in males of Artonini

This organ was recently discovered by B. Mollet & G. M. Tarmann in the Australian Procridae genera *Pollanisus* Walker, 1854, *Hestiochora* Meyrick, 1886, and *Onceropeya* Turner, 1906. The structure consists of a bunch of transparent hairs (looking like androconial scales) inserted laterally on each side of the thorax between the prothorax and mesothorax. These hairs are arranged in a weakly sclerotized translucent fold, connected to the posterior part of coxa 1 and the inner skeleton by a fine skin-like diaphragm. The fold covers the densely grouped hairs (20 to 30) and is set distally to allow the “blooming” of these hairs, in the form of a brush or a bouquet, laterally on the outer side of the thorax.

Similar hairs between the forelegs on the prothorax were found in *Amuria* Staudinger, 1887, and *Pseudoamuria* Tarmann, 2004.

During the last years a number of other characters have been discovered in different species and species-groups of Procridae, viz. specialized structures on the juxta (Efetov 1996a; Tarmann & Drouet 2015), unusual shapes of the uncus (Tarmann 1984; Tarmann & Drouet 2015), very long vesica with more than 70 cornuti arranged in a long spiral (Efetov & Tarmann 2013a), pulvinus represented by a long process with strongly sclerotized spines (Efetov 2010), well developed lamina dorsalis (Tarmann 1984), extraordinary shapes of the valvae (Tarmann 1984; Tarmann & Drouet 2015) and the ductus bursae (Efetov 2012) etc.

Karyotypes

As shown by investigations during recent years (Efetov 2001b; 2001c; 2004; Efetov & Tarmann 1999a; Efetov et al. 2004; Efetov et al. 2015a), a study of the karyotypes in the family Zygaenidae provides very interesting results. The modal haploid chromosome number for Lepidoptera is generally 30–31 (Robinson 1971; Lukhtanov & Kuznetsova 1988). In the majority of species studied in the genus *Zygaena* Fabricius, 1775 (subfamily Zygaeninae), the haploid chromosome number is 30 (only in one species it is 29 and for three species both numbers: 30 and 31, were recorded by different authors) (Lukhtanov & Kuznetsova 1988; Tremewan 2006; Efetov & Parshkova 2003; 2004). It seems that this number is ancestral for the genus *Zygaena* (possibly for the subfamily Zygaeninae).

Aglaope infausta (Linnaeus, 1767) (subfamily Chalcosiinae) also has the modal haploid chromosome number 31 (Efetov 2004: fig. 177; Efetov & Parshkova 2004).

However, we found that in many species of the Procridae the haploid chromosome numbers differ from the modal. For example, in species of the subgenera *Roccia* Alberti, 1954, *Tremewanina* Efetov & Tarmann, 1999, and *Jordanita* Verity, 1946, of the genus *Jordanita* Verity, 1946, the haploid chromosome number is 31, while in *Jordanita* (*Solaniterna*) *subsolanata* (Staudinger, 1862) it is 27 (Efetov 2004: fig. 176). The same situation is found in the genus *Adscita* Retzius, 1783. While the majority of species of the subgenera *Adscita* Retzius, 1783, and *Tarmannina* Efetov, 2000, have the haploid chromosome number 31, in *Adscita* (*Adscita*) *jordani* (Naufock, 1921) it is 30 (Efetov 2004: fig. 168), in *Adscita* (*Adscita*) *geryon* (Hübner, 1813) it is 32 (Efetov 2004: fig. 170), and in *Adscita* (*Procriterna*) *subtristis* (Staudinger, 1887) it is 17 (Efetov 2004: fig. 167). The most dramatic differences in chromosome numbers were found in the genus *Rhagades* Wallengren, 1863 (Figs. 79–81). In the primitive species, *Rh.* (*Naufockia*) *brandti* (Alberti, 1938), it is modal (31), but in *Rh.* (*Wiegelia*) *amasina* (Herrich-Schäffer, 1851) it is 12, and in *Rh.* (*Rhagades*) *pruni* ([Denis & Schiffermüller], 1775) it is 47! We consider this increase in the number of chromosomes in *Rh. pruni* to result from polyploidy (Efetov 2001c; 2004). It is also interesting that the number is reduced (compared with the modal) to 25 in *Illiberis* (*Primilliberis*) *rotundata* Jordan, 1907 (Fig. 77), and to 28 in *Theresimima ampellophaga* (Bayle-Barelle, 1808) (Fig. 78). Thus, with the exception of *Rh. brandti*, the modal number in the genera *Rhagades* Wallengren, 1863, *Theresimima* Strand, 1917, and *Illiberis* Walker, 1854, does not occur. Our results confirm that

Procrinae are a unique group in the Zygaenidae from a karyological point of view and investigation of the karyotypes in this subfamily is very important for understanding evolutionary relationships and the systematic position of species in this group.

Results of DNA sequencing

A DNA barcoding project on zygaenid moths (ZYGMO) was activated in 2009 and remains in progress (Efetov et al. 2013; Efetov & Tarmann 2016b; Mutanen et al. 2016). Work initially focused on the Palaearctic Zygaenidae, but species from other regions (South East Asia, Australia, Central and North America, etc.) have also been examined.

We obtained DNA results based on analysis of the 658-bp barcode region of the cytochrome *c* oxidase I (COI) mitochondrial gene involving 1031 sequences of 245 species from 64 genera. Sequence divergences for the barcode region were calculated using the Kimura 2 Parameter model by the analytical tools on BOLD (the Barcode of Life Datasystems – www.boldsystems.org). Our results demonstrate species level resolution of the COI sequences in most taxa. The barcoding provides only additional data for scientific discussions on Zygaenidae systematics. However, our DNA results coincide on the whole with the contemporary system of the family.

A new subfamily of Zygaenidae

In 1999 K. A. Efetov described the genus *Inouela* Efetov, 1999, and included the two species *Inouela formosensis* Efetov, 1999 (type-species of the genus) and *I. exiguitata* (Inoue, 1976) (described as *Clelea* in Procrinae). He placed this new genus in the subfamily Chalcosiinae as both species have a double uncus which is not typical for Procrinae. Yen (2003) and Yen et al. (2005) found that this genus cannot be placed in Chalcosiinae based on a number of characters. However, *Inouela* agrees with the main characters of Zygaenidae. Nevertheless, it can neither be placed in Procrinae, nor in Chalcosiinae, nor for that matter in the two other subfamilies Callizygaeninae or Zygaeninae. To accommodate this isolated taxon it is therefore necessary to describe a new subfamily **Inouelinae subfam. nov.**

Historical note

The history of this group began in 1910 when H. Sauter collected two male zygaenid specimens in 'Formosa, Taihorin' (Taiwan). These specimens are deposited in the Museum für Naturkunde in Berlin (Germany). The late Dr Burchard Alberti dissected one of these two specimens and intended to describe a new genus and species that he wanted to name 'Taihorina

formosensis'. This is discernible from the handwritten pin-labels by Alberti under both specimens (Efetov 1999: 93, figs. 2–4). However, Alberti never described these taxa.

In 1976 Prof. Hiroshi Inoue described the nominal taxon *Clelea exiguitata* Inoue, 1976 (Zygaenidae: Procrinae) from Japan (9 male specimens from the three localities: Mikyo, Island of Tokunoshima (leg. H. Inoue), Yuwandake, Amami-oshima, and Sumiyoson, Amami-oshima (leg. T. Okada). The genus *Clelea* Walker, 1854, belongs to the subfamily Procrinae (Alberti 1954; Efetov & Tarmann 1995; 2012). However, the genitalia structures of '*Clelea*' *exiguitata* have nothing to do with the genitalia structures of *Clelea* Walker, 1854, but they are close to those of the dissected male from Taihorin examined by Alberti.

After reinvestigation of the material in Berlin with the additional dissection of the second male specimen from Taihorin and one paratype of *Clelea exiguitata* from the type locality in Japan (now deposited in the Natural History Museum in London) Efetov (1999) described *Inouela* Efetov, 1999, with the two species *Inouela formosensis* Efetov, 1999, and *Inouela exiguitata* (Inoue 1976).

Xue & Han (2003: 255) included *Inouela formosensis* in the check-list of Zygaenidae from China in Chalcosiinae. Also Horie (2013: 329) included *Inouela exiguitata* in Chalcosiinae. Yen (2003: 293) writes that the monophyly of the subfamily Chalcosiinae is doubtful when the genera *Inouela* Efetov, 1999, *Chalcosiopsis* Swinhoe, 1894, *Cleoda* Tremewan, 1973, and *Heteropan* Walker, 1854, are included. Yen et al. (2005) underline the necessity of these exclusions and suggest to place *Inouela* into 'Procrinae s. l.' However, as the characters of *Inouela* do not agree with the main autapomorphies of Procrinae (without *Inouela* this subfamily is monophyletic) we see no other possibility as to describe a new subfamily to accommodate this isolated group: **Inouelinae subfam. nov.**

Inouelinae subfam. nov.

Type genus *Inouela* Efetov, 1999 (here designated)

Diagnosis

Small Zygaenidae (length of forewing 4–7 mm) with unicolorous greyish brown wings and body (Fig. 82). Male and female similar in habitus. Head of male and female without sexual dimorphism. Male and female antenna tapered towards apex, with dorsoventrally compressed shaft and very long, large distances between pectinations, length of pectinations only slightly shorter in female, sensory setae of rami long. Proboscis reduced, developed as two short, only slightly

downward-curved lobes, labial palps very short (note that the mouthparts are not completely reduced, as mentioned by Yen et al. 2005: 183, 184). No sexual dimorphism in size of compound eyes (present in Chalcosiinae and Procridinae). Ocelli and chaetosemata present. Chaetosema situated dorso-laterally on an almost vertical part of head between (slightly posterad) compound eye and the small ocellus, with characteristic structure with upright scales in the centre and a group of sensillae trichodea at the anterior margin (Fig. 83) (Yen et al. 2005: fig. 15C). Inouelinae are not able to release protective fluid from the membrane between patagia and parapatagia (present in Chalcosiinae) (Yen et al. 2005: 188). Foreleg with long tibial epiphysis, hindtibia without spurs.

Wing venation with full number of veins in forewing, M_1 absent in hindwing; veins almost evenly spaced; in *I. formosensis* all veins free from cell, in *I. exiguitata* R_4+R_5 stalked; medial stem in both wings present as a vein but only distally; hindwing with a short cross vein between Sc and anterior margin of cell. Frenulum developed as one spine in male and female, retinaculum in male developed as a small fold at base of Sc, in female as a long row of filiform scales at base of CuP.

Androconial hairbrush in male hindwing and invagination of pleural membrane absent (present in Chalcosiinae).

Male genitalia (description based on the two species: *I. formosensis* and *I. exiguitata*) (Figs. 84, 85). Uncus broad, with two lobes. Valva with very weakly sclerotized, rounded distal part; sacculus with sclerotized process; transtilla dorsally with sclerotized bifurcated process (not true gnathos). Aedeagus not spiny or hooked; vesica with two cornuti, at least one of them serrate (see also additional comments below).

Female genitalia (description based on additional material from Taiwan collected by W. Mey and G. Ebert and deposited in Museum für Naturkunde, Berlin). Ovipositor absent (present in Chalcosiinae). Ductus bursae tubular, corpus bursae translucent, not double-lobed, without signa. Pseudobursa absent (present in Chalcosiinae) (see also additional comments below).

Differential diagnosis when compared to Procridinae and Chalcosiinae.

The description of Inouelinae has to be based on only a few existing specimens. However, the characters are clear. The fact that there is no sexual dimorphism in the head capsule in Inouelinae (breadth of frons and size of compound eyes are equal in male and female) separates this subfamily from the Procridinae and Chalcosiinae. Moreover, the chaetosema in the Inouelinae is a unique

character in the Zygaenidae and is considered to represent a good autapomorphy of this newly described subfamily. It differs from the chaetosemata of Procridinae and Chalcosiinae. The procridine chaetosema and the chalcosiine chaetosema are considered to represent autapomorphies for each of these two subfamilies. The antenna of Inouelinae is also unique within Zygaenidae. The shaft is dorsoventrally compressed and the long and slender pectinations are arranged with large spaces between them, reminiscent of similar antennae in some Psychidae. The wing venation of the Inouelinae shows an ancestral character combination with the full number of veins present in forewing and all veins arising evenly spaced from the cell. This character is shared with the more primitive groups in Procridinae but is in contrast to this character situation in Chalcosiinae (with several radial veins stalked together).

Additional comments.

Some important characters could not be sufficiently studied owing to lack of material. It would be especially interesting to know how the receptaculum seminis is constructed in the female. We also studied additional specimens from the Philippines (deposited in the Museum für Naturkunde, Berlin) with the external habitus of Inouelinae and strong similarities in the characters of the head and wing venation. However, these specimens have very different genitalic structures from those of the two species *I. formosensis* and *I. exiguitata*.

Nevertheless, these specimens may belong to Inouelinae and represent a separate group in this subfamily. Extreme variation in genitalic morphology (for example in the American genus *Neoprocris* Jordan, 1915 (Tarmann 1984)) is known in the Procridinae. The same situation can be present also in the Inouelinae. In future more species could be included in this subfamily.

So far this new subfamily is only known from South East Asia. The biology of Inouelinae species is unknown.

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FIGURES

Black and white figures on following pages are in numerical order. However, figures 23, 32, 33, 35, 36, 37, 41, 52, 53, 54, 55, 56, 57, 58 and 82 are color images included in separate color plates at the end of the paper.

Photos taken by Konstantin A. Efetov – (KAE), by Gerhard M. Tarmann – (GMT).

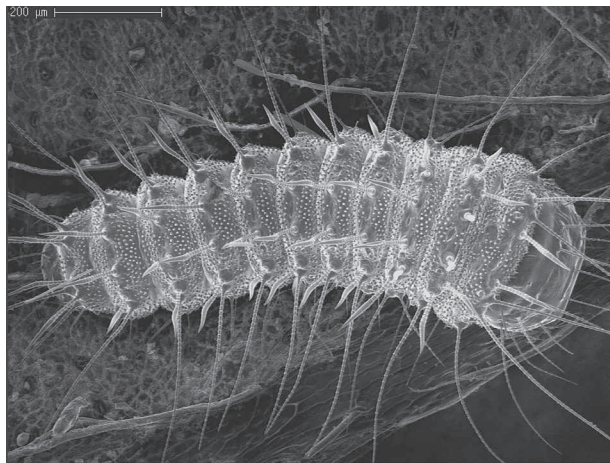


Fig. 1. First instar larva of *Pollanisus subdolosus clara* Tarmann, 2004 (Procridinae, Artonini), Australia, New South Wales. (Photo A. Zwick). (after Tarmann 2004)

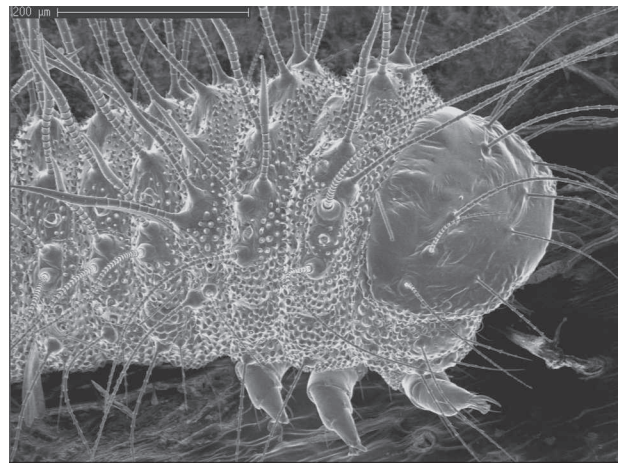


Fig. 2. Idem, head and thorax in higher magnification. (Photo A. Zwick). (after Tarmann 2004).



Fig. 3. Head hidden (retracted) below the thoracic shield in first instar larva of *Pollanisus subdolosus clara* (same larva as figs 1, 2). (Photo A. Zwick).

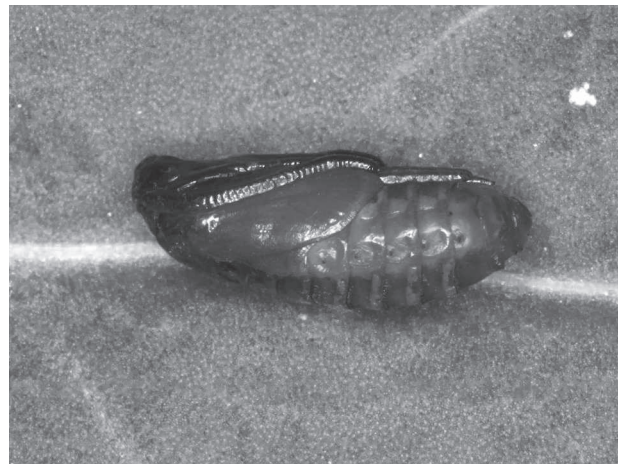


Fig. 4. Pupa of *Adscita mannii* (Lederer, 1853) (Procridinae, Procridini), lateral view. The second spiracle is covered by the wing. (GMT).

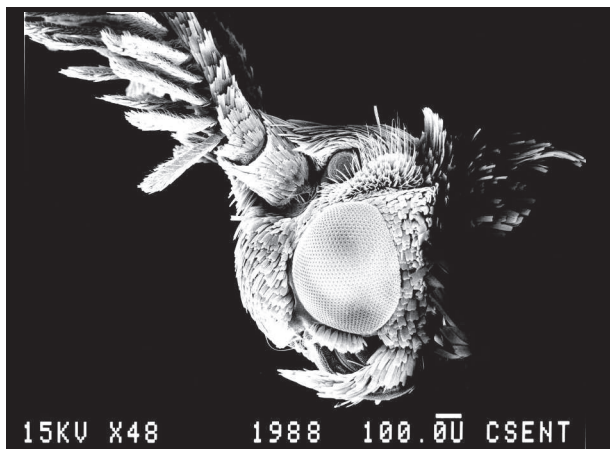


Fig. 5. Head of *Pollanisus viridipulverulenta* (Guérin-Ménéville, 1839) (Procridinae, Artonini), male, lateral view, Australia, ACT. (Photo C. Beaton). (after Tarmann 2004).

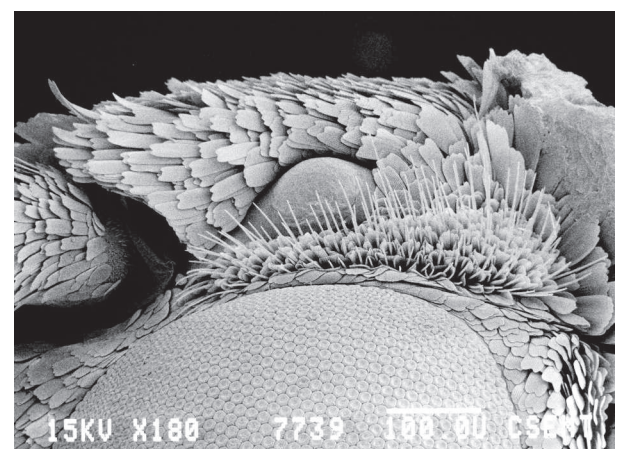


Fig. 6. Head of *Pseudoamuria uptoni* Tarmann, 2004 (Procridinae, Artonini), male, lateral view, with ocellus, chaetosema and upper half of compound eye, Australia, Queensland. (Photo E. Hines). (after Tarmann 2004).

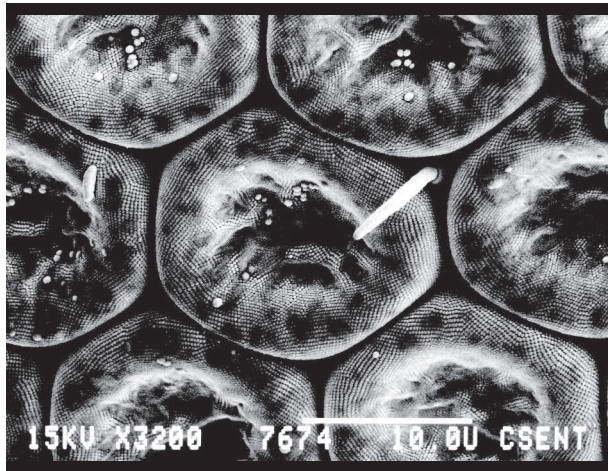


Fig. 7. Compound eye of *Homophylotis thyridota* Turner, 1904 (Procrinae, Artonini), with interommatidial seta, Australia, Queensland. (Photo E. Hines). (after Tarmann 2004).

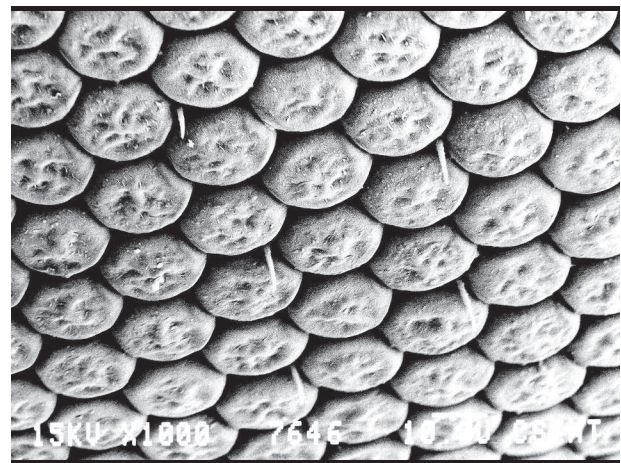


Fig. 8. Compound eye of *Adscita statice* (Linnaeus, 1758) (Procrinae, Procrini) with interommatidial setae, Austria, Tirol. (Photo E. Hines). (after Tarmann 2004).



Fig. 9. Idem, higher magnification.

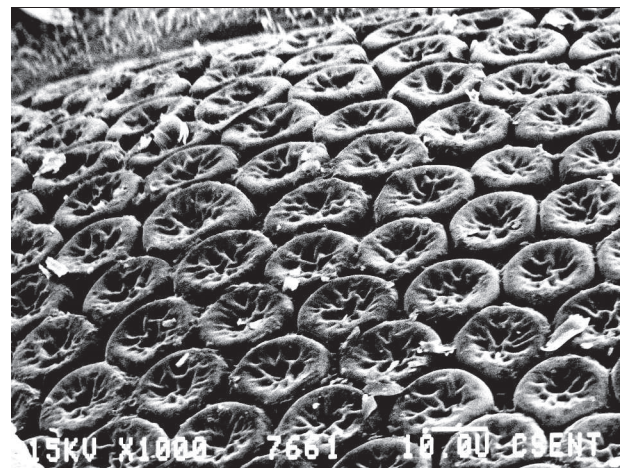


Fig. 10. Compound eye of *Illiberis (Primilliberis) pruni* Dyar, 1905 (Procrinae, Procrini), without interommatidial setae, Japan. (Photo E. Hines). (after Tarmann 2004).

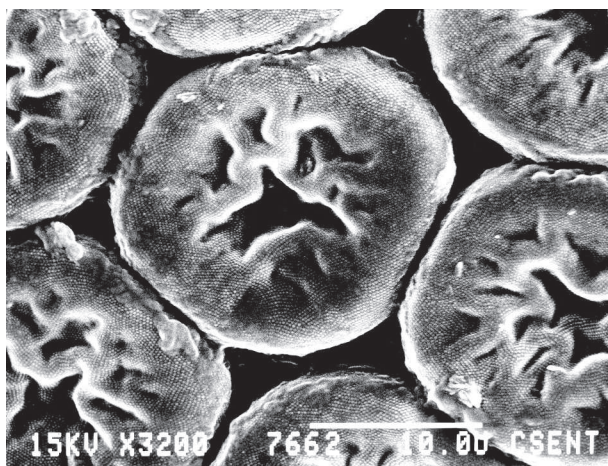


Fig. 11. Idem, high magnification.

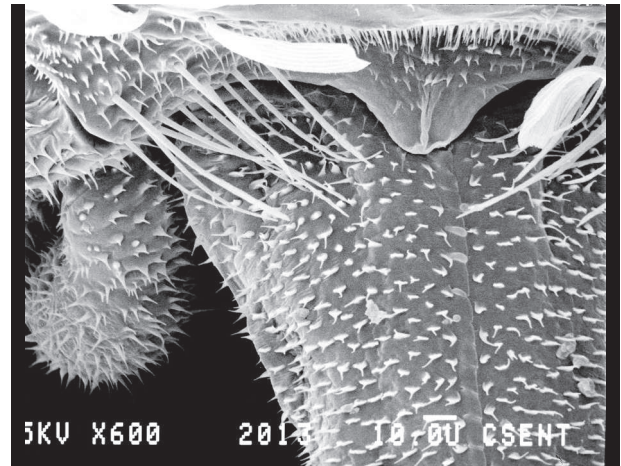


Fig. 12. Base of proboscis and maxillary palps of *Turneriprocris dolens* (Walker, 1854) (Procrinae, Artonini), male, Australia, ACT. (Photo C. Beaton). (after Tarmann 2004).

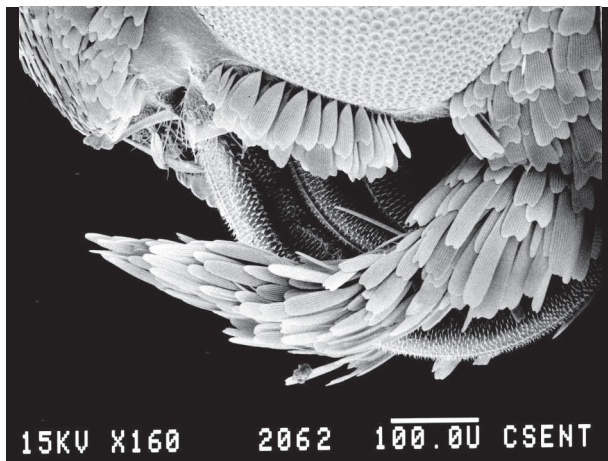


Fig. 13. Labial palp and eyelash below compound eye of *Pollanisus viridipulverulenta* (Guérin-Ménéville, 1839) (Procrinae, Artonini), male, lateral view, Australia, ACT. (Photo C. Beaton). (after Tarmann 2004).

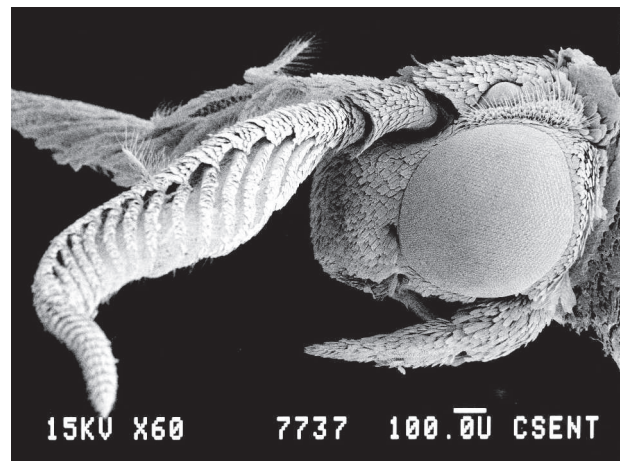


Fig. 14. Head in lateral view with labial palps of *Pseudoamuria uptoni* Tarmann, 2004 (Procrinae, Artonini), male, lateral view, Australia, Queensland. (Photo E. Hines). (after Tarmann 2004).



Fig. 15. Head in lateral view of *Adscita statices* (Linnaeus, 1758) (Procrinae, Procrini), Austria, Tirol. (Photo E. Hines). (after Tarmann 2004).

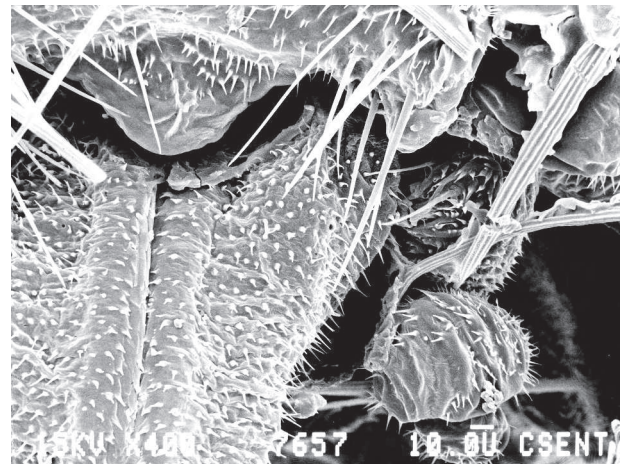


Fig. 16. Base of proboscis with clypeus and mandible lobe in *Illiberis (Primilliberis) pruni* Dyar, 1905 (Procrinae, Procrini), Japan. (Photo E. Hines). (after Tarmann 2004).

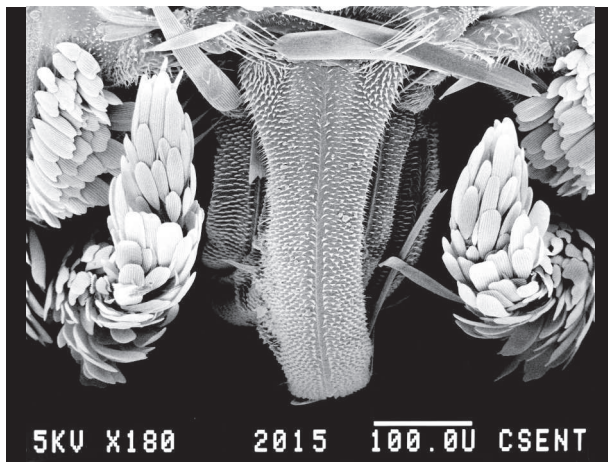


Fig. 17. Proboscis of *Pollanisus viridipulverulenta* (Guérin-Ménéville, 1839) (Procrinae, Artonini), male, frontal view, Australia, ACT. (Photo C. Beaton). (after Tarmann 2004).

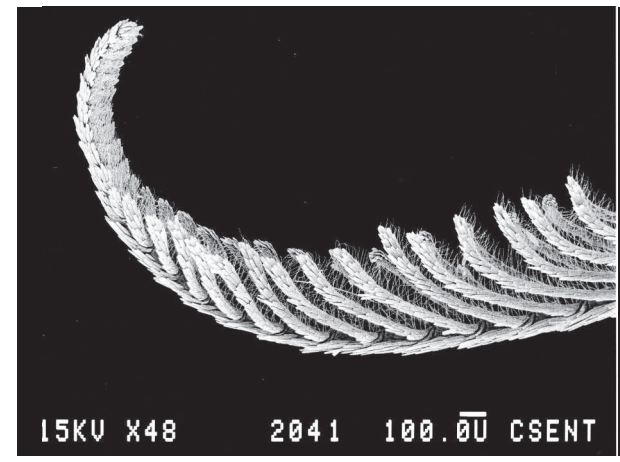


Fig. 18. Male antenna of *Australartona mirabilis* Tarmann, 2004 (Procrinae, Artonini), Australia, NSW. (Photo C. Beaton). (after Tarmann 2004).



Fig. 19. Distal part of male antenna of *Adscita statipes* (Linnaeus, 1758) (Procrinae, Procrini), Austria, Tirol. (Photo E. Hines). (after Tarmann 2004).

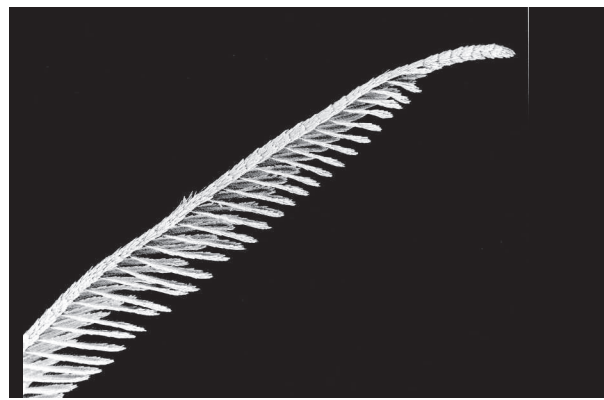


Fig. 20. Male antenna of *Pollanisus viridipulverulenta* (Guérin-Ménéville, 1839) (Procrinae, Artonini), Australia, ACT. (Photo C. Beaton). (after Tarmann 2004).

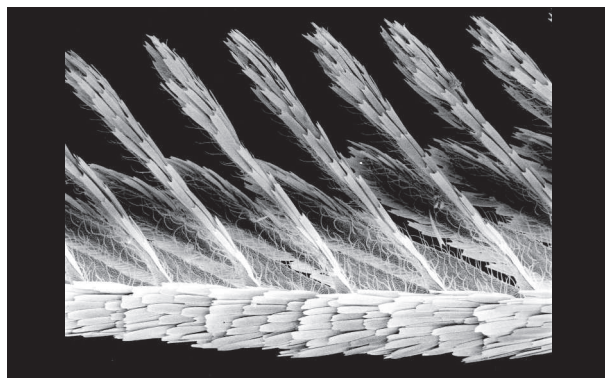


Fig. 21. Pectination of male antenna of *Pollanisus viridipulverulenta* (Guérin-Ménéville, 1839) (Procrinae, Artonini), Australia, ACT. (Photo C. Beaton). (after Tarmann 2004).

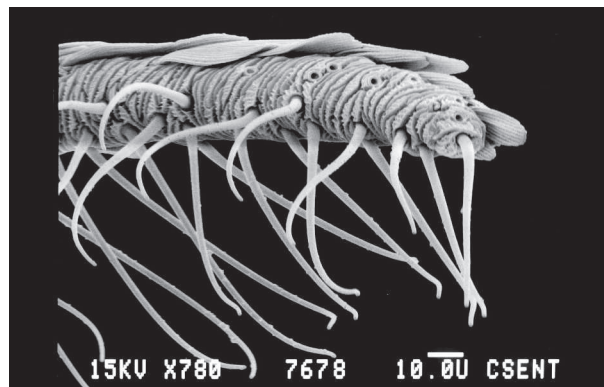


Fig. 22. Distal end of pectination of male antenna of *Homophylotis thyridota* Turner, 1904 (Procrinae, Artonini), Australia, Queensland. (Photo E. Hines). (after Tarmann 2004).

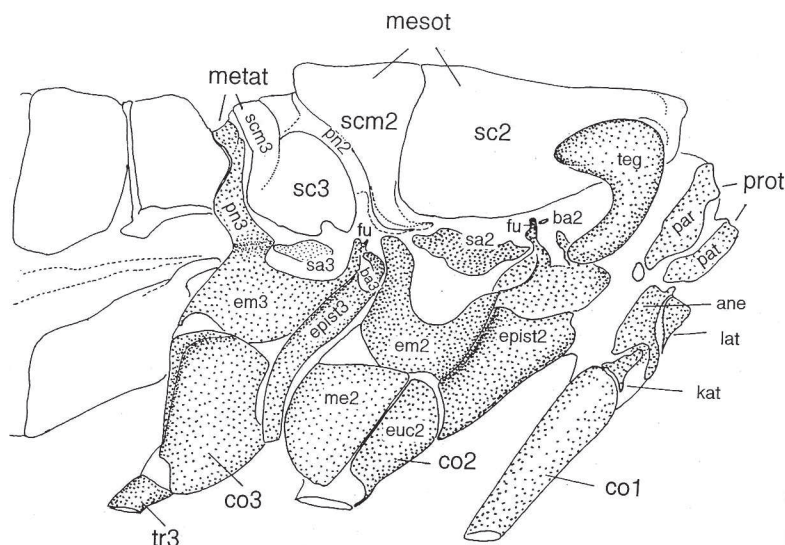


Fig. 24. Lateral view of thoracic segments of adult of *Zygaena trifolii* (Esper, 1783). **ane**: anepisternum; **ba**: basalare; **co**: coxa; **em**: epimeron; **epist**: episternum; **euc**: eucoxa; **fu**: fulcrum; **kat**: katepisternum; **lat**: laterocervicale (anterior arm omitted); **me**: meron; **mesot**: mesothorax; **metat**: metathorax; **par**: paraptagium; **pat**: patagia; **pn**: postnotum; **priot**: prothorax; **sa**: subalare; **sc**: scutum; **scm**: scutellum; **teg**: tegula; **tr**: trochanter; figures 1, 2, and 3 depict the pro- (1), meso- (2) and metathorax (3). (after Naumann et al. 1999).

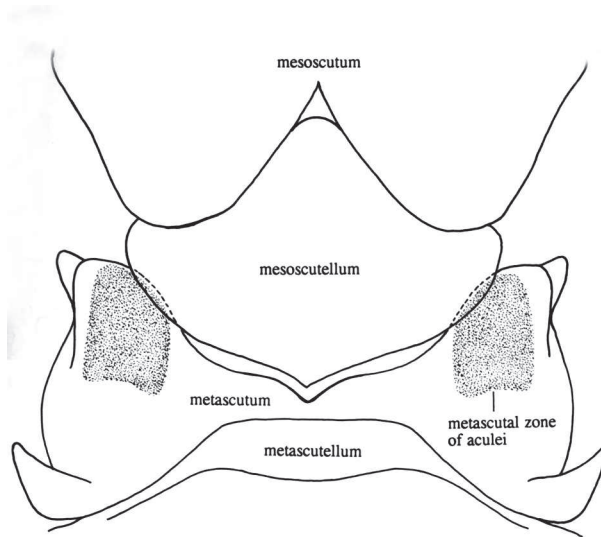


Fig. 25. Metathorax with wing-thorax-coupling mechanism, as in most ditrysian Lepidoptera. (after Scoble 1992).

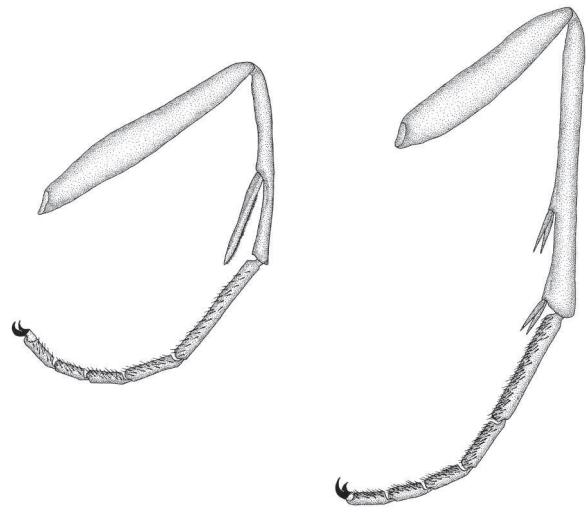


Fig. 26. Right foreleg of *Zygaena (Zygaena) filipendulae* (Linnaeus, 1758). (after Efetov 2001c).

Fig. 27. Right hindleg of *Zygaena (Zygaena) filipendulae* (Linnaeus, 1758). (after Efetov 2001c).

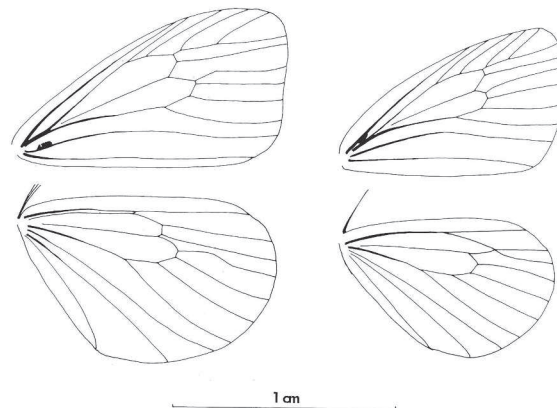


Fig. 28. Frenulum and retinaculum of female and male of two Chalcosiinae: *Pseudarbudas ochrea* (Elwes, 1890), female (left), *Heteropanula flavimacula* (Hampson, 1892), male (right). (after Tarmann 1992).

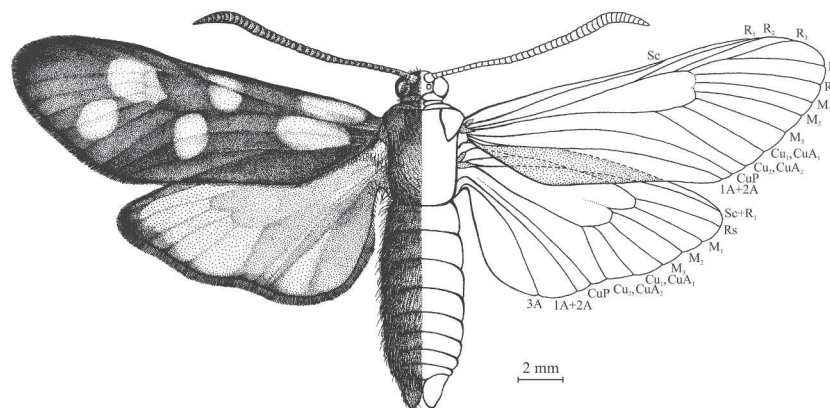
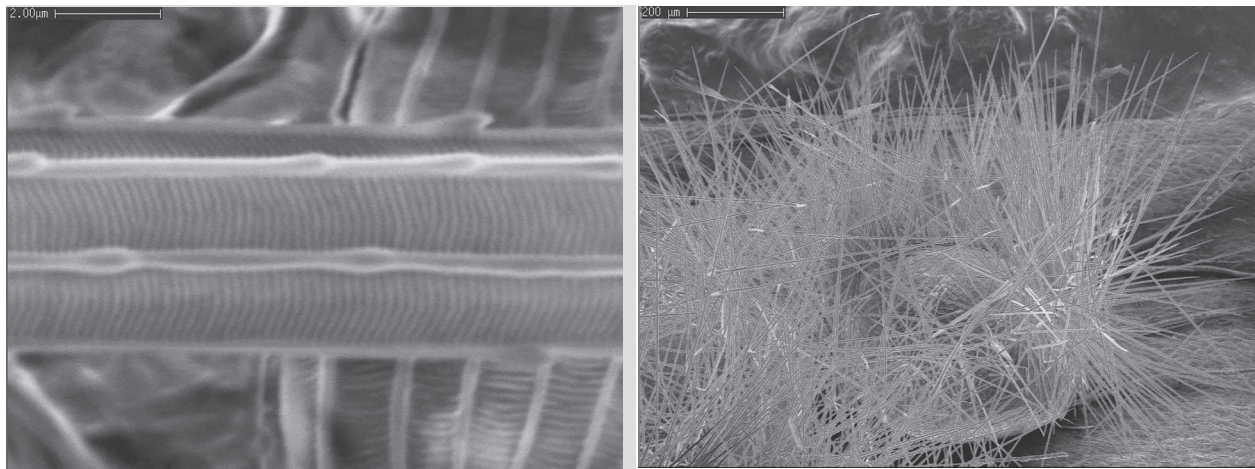


Fig. 29. *Zygaena (Zygaena) filipendulae* (Linnaeus, 1758). Male. Wing venation. (after Efetov 2005b).



Figs 30a, b. Scales with longitudinal ribs and transverse striae from the abdominal hairtuft of *Pollanisus subdolosus clara* Tarmann, 2004 (Procridae, Artonini), protecting the egg, Australia, New South Wales. (Photo A. Zwick). (after Tarmann 2004).

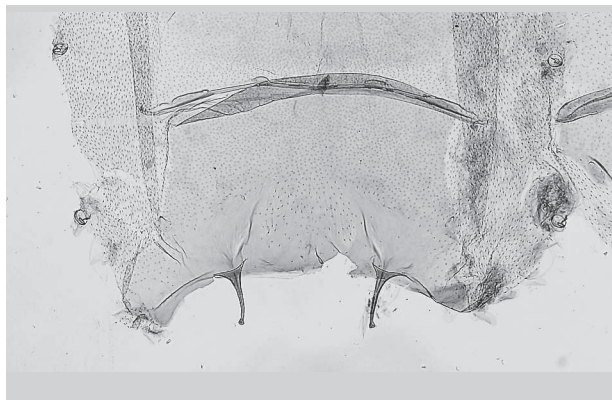


Fig. 31. Tortricoid apodemes on first abdominal segment of abdomen of *Pseudoamuria uptoni* Tarmann, 2004 (Procridae, Artonini), Australia, Queensland. (after Tarmann 2004).

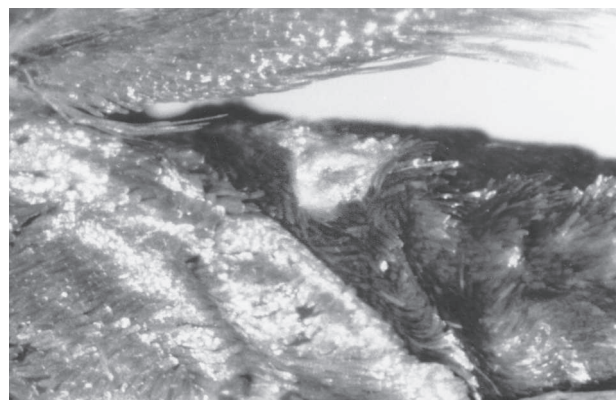


Fig. 34. Lateral gland on second abdominal segment of male of *Australartona mirabilis* Tarmann, 2004 (Procridae, Artonini), Australia, NSW. (Photo J. Green). (after Tarmann 2004).

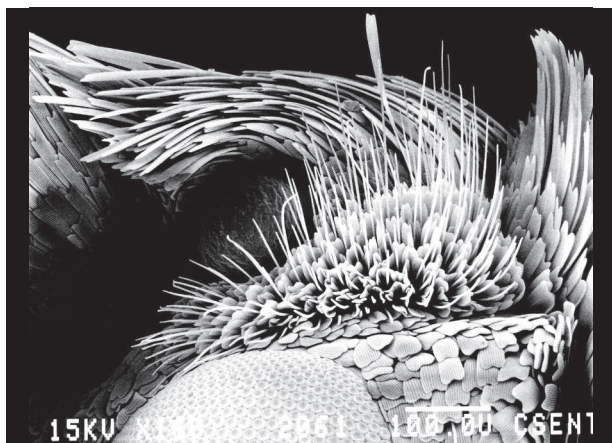


Fig. 38. Chaetosema of *Pollanisus viridipulverulenta* (Guérin-Méneville, 1839) (Procridae, Artonini), male, Australia, ACT. (Photo C. Beaton). (after Tarmann 2004).

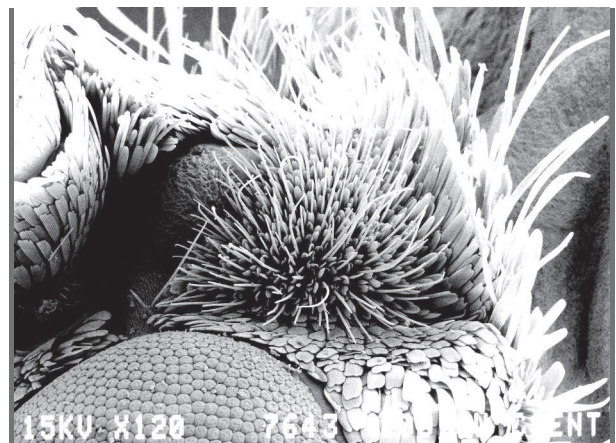


Fig. 39. Chaetosema of *Adscita statices* (Linnaeus, 1758) (Procridae, Procradini), Austria, Tirol. (Photo E. Hines). (after Tarmann 2004).

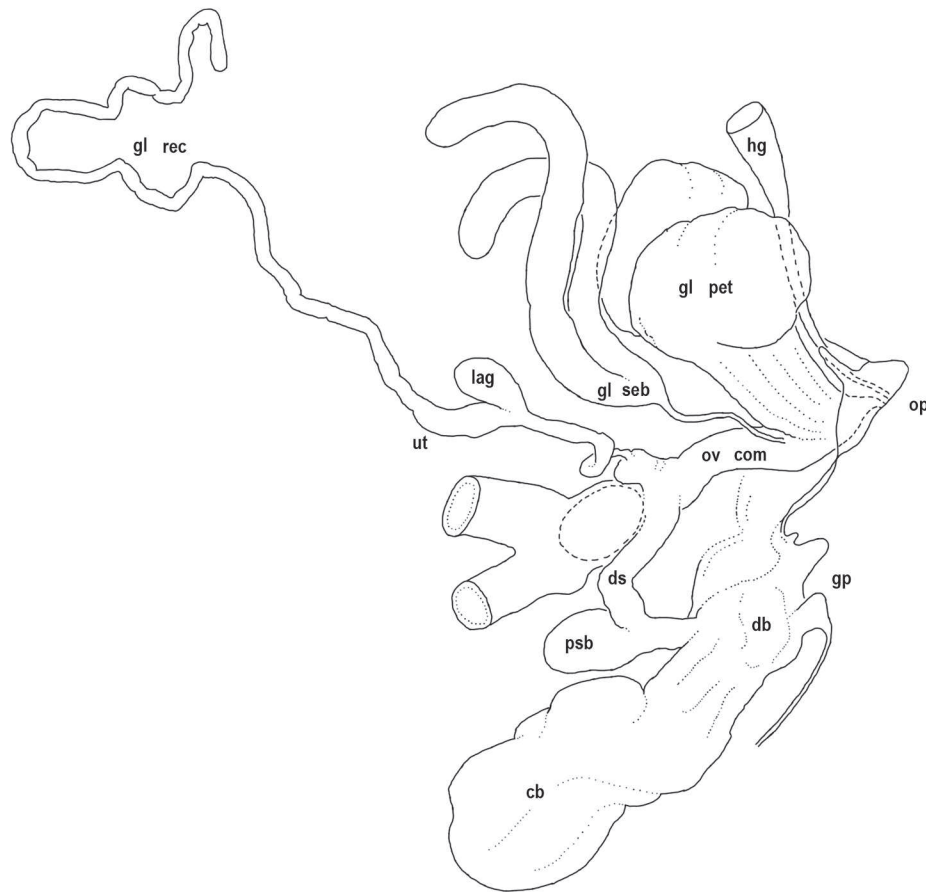


Fig. 40. Internal female genitalia of *Zygaena (Zygaena) trifolii* (Esper, 1783). **cb**: corpus bursae; **db**: ductus bursae; **ds**: ductus seminalis; **gl pet**: Petersen's gland; **gl rec**: glandula receptaculi; **gl seb**: sebaceous gland; **gp**: gonoporus; **hg**: hind gut; **lag**: lagena; **op**: ooporus; **ov com**: oviductus communis; **psb**: pseudobursa; **ut**: utriculus. (after Naumann et al. 1999).



Fig. 42. Abdominal fold on the second pleurite of *Arbudas submacula* (Wileman, 1910) (Chalcosiinae), Taiwan. (after Tarmann 1992).

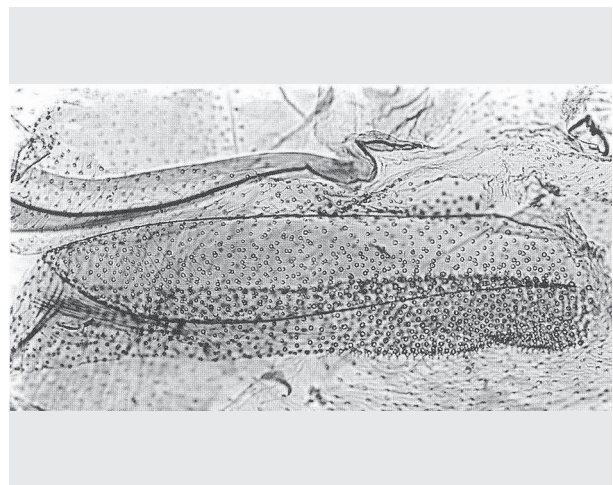


Fig. 43. Idem, higher magnification.

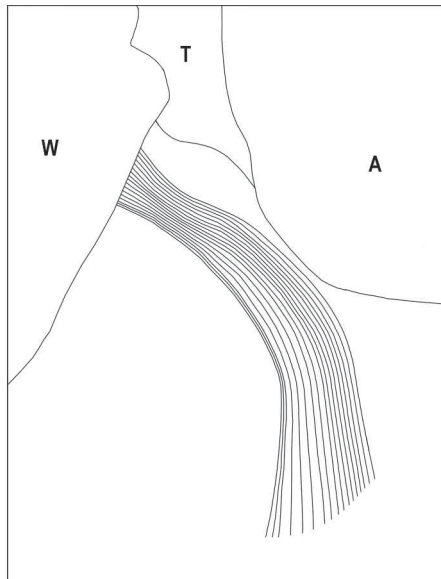


Fig. 44. Hindwing of *Arbudas submacula* (Wileman, 1910) with S-shaped bristles. **A**: abdomen; **T**: thorax; **W**: hindwing.

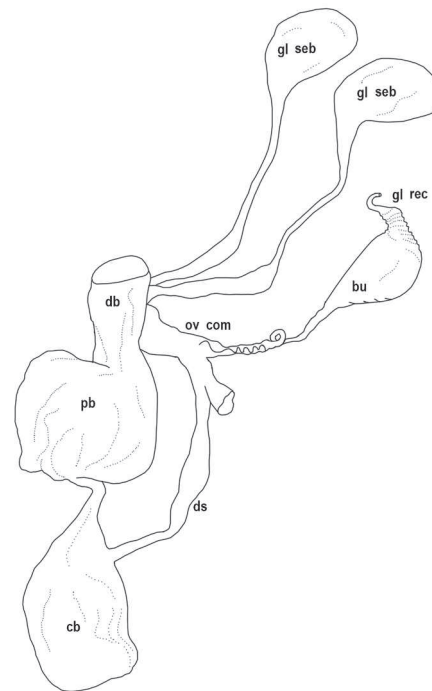


Fig. 45. Internal female genitalia of *Myrtartona coronias* (Meyrick, 1886) (Procrinae, Artonini) with bursa utricularis. **bu**: bursa utricularis; **cb**: corpus bursae; **db**: ductus bursae; **ds**: ductus seminalis; **gl rec**: glandula receptaculi; **gl seb**: sebaceous gland; **ov com**: oviductus communis; **pb**: prae bursa.



Fig. 46. Female genitalia of *Pollanisus apicalis* (Walker, 1854) (Procrinae, Artonini), with well-developed prae bursa, Australia, ACT. (after Tarmann 2004).

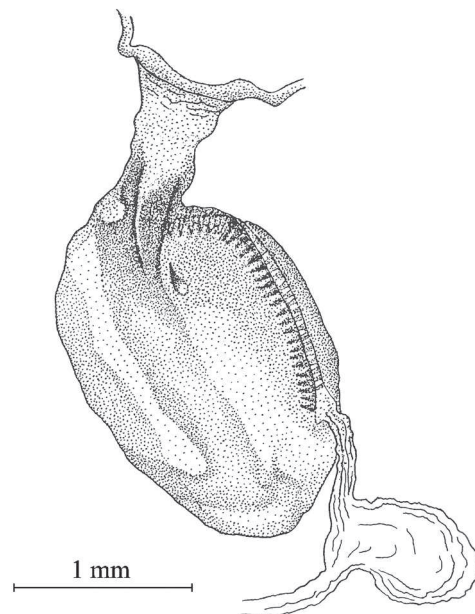


Fig. 47. Female genitalia of *Artona (Fuscartona) martini* Efetov, 1997 (Procrinae, Artonini), with well-developed prae bursa, China. (after Efetov 1997a).

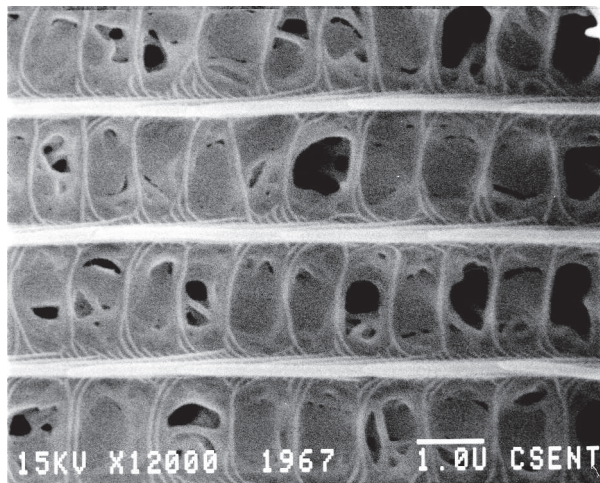


Fig. 48. Ultrastucture of forewing scale of *Turneriprocris dolens* (Walker, 1854) (Procridinae, Artonini), male, Australia, ACT. (Photo C. Beaton). (after Tarmann 2004).

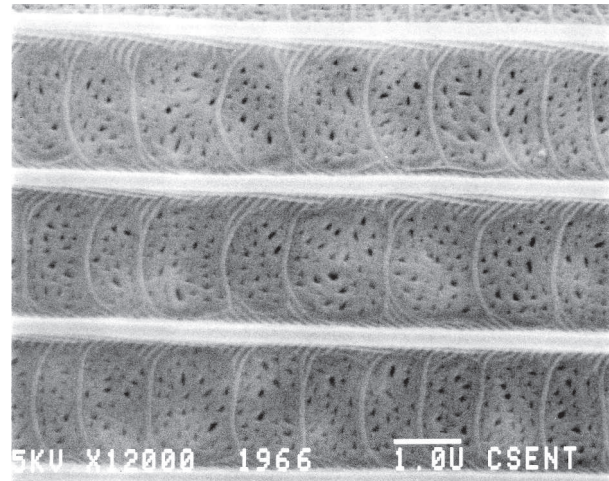


Fig. 49. Idem, shiny scale.

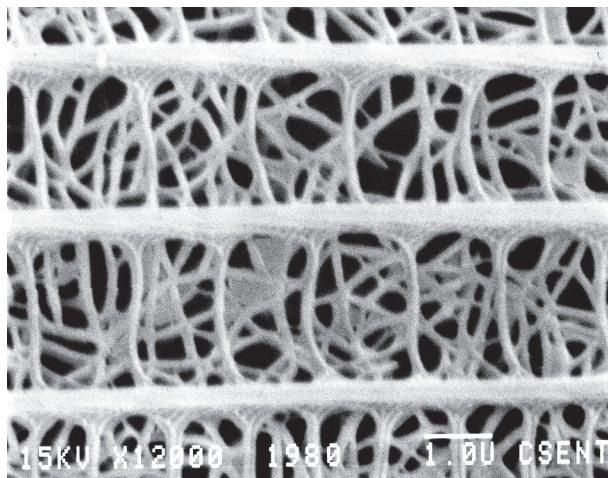


Fig. 50. Ultrastucture of forewing scale of *Myrtartona leucopleura* (Meyrick, 1886) (Procridinae, Artonini), male, Australia, NSW. (Photo C. Beaton). (after Tarmann 2004).

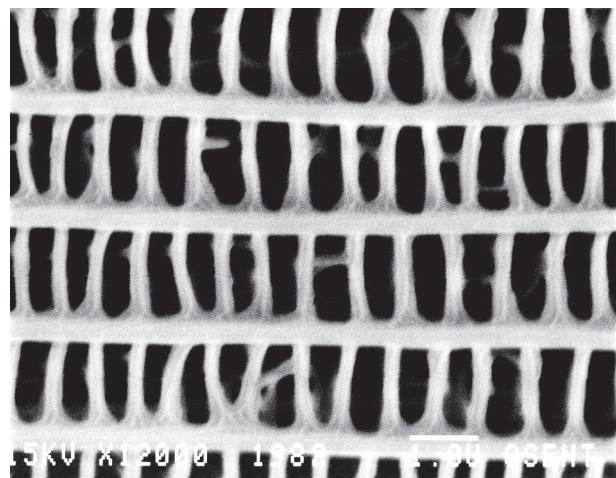


Fig. 51. Idem, hindwing scale.

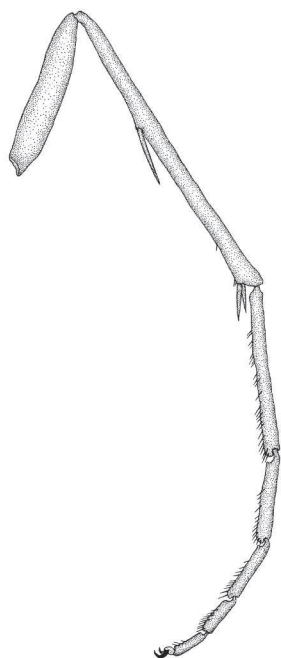


Fig. 59. Right hindleg of *Artona (Balataea) gracilis* (Walker, 1865). (after Efetov 2005a).

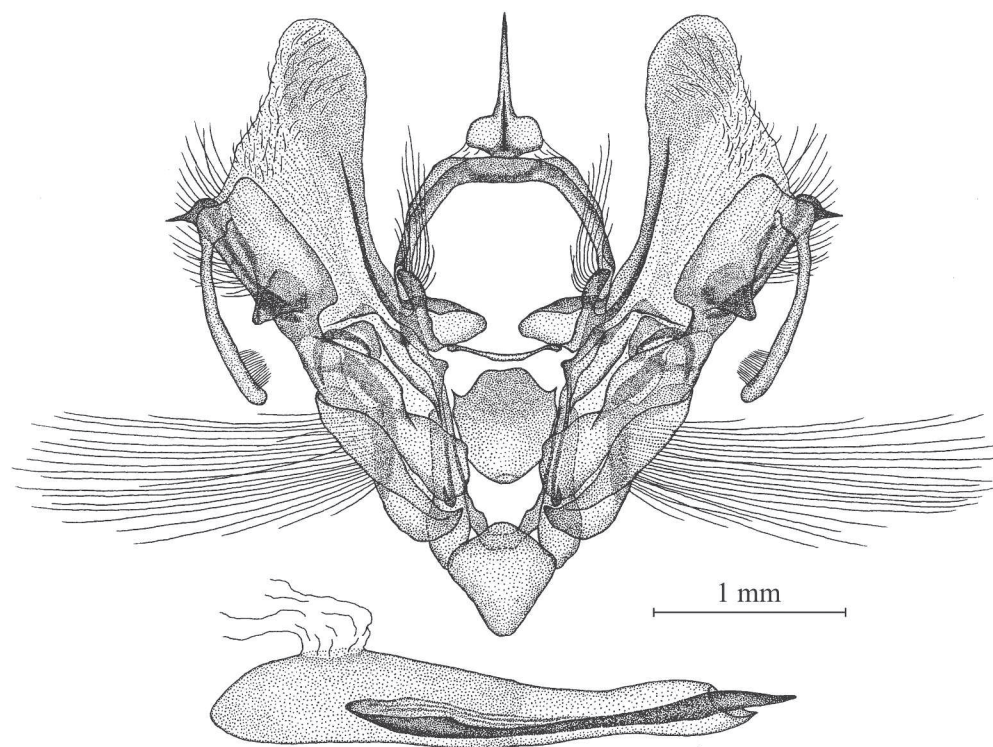
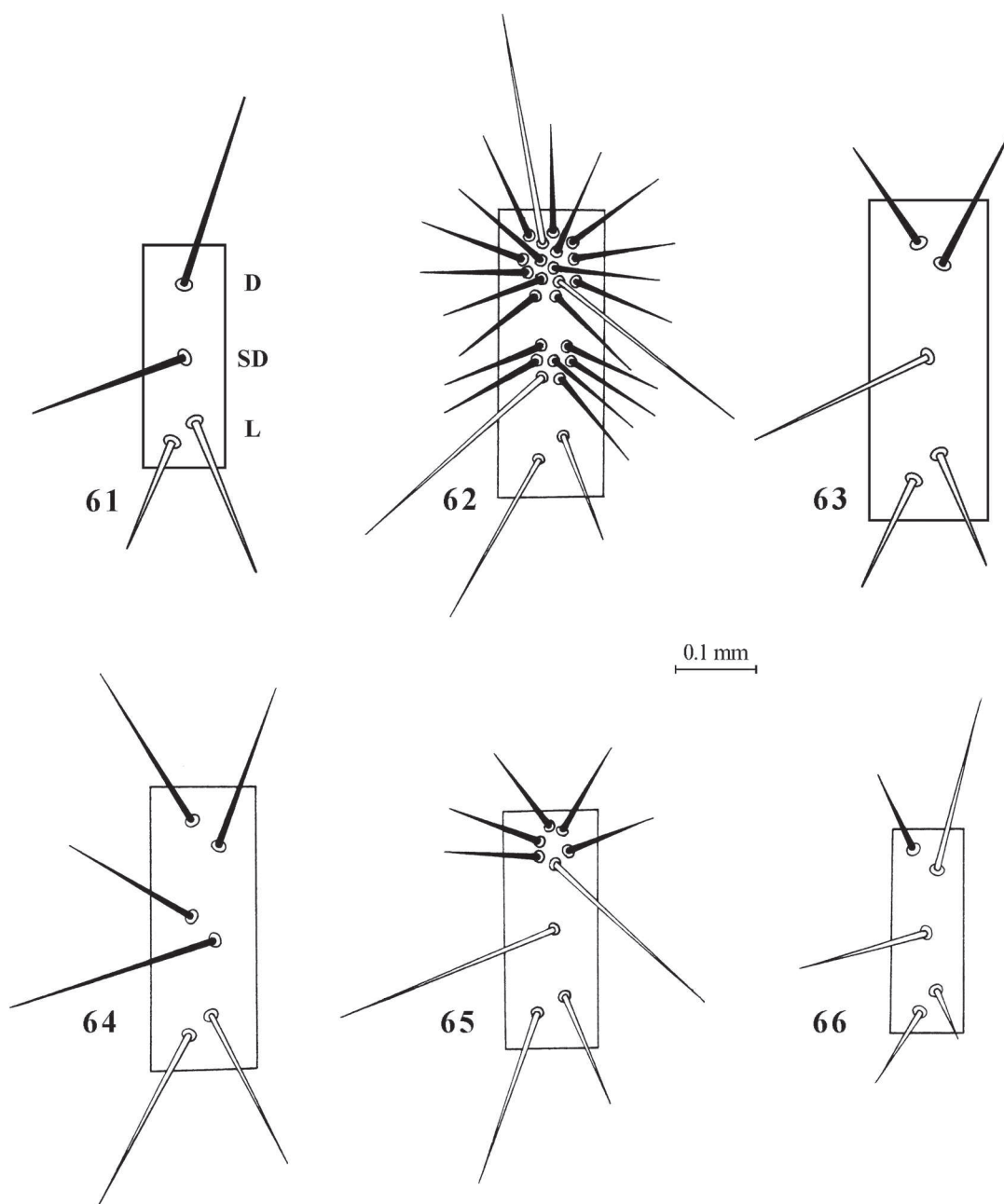


Fig. 60. Male genitalia of *Artona (Balataea) gracilis* (Walker, 1865). (after Efetov 2005b).



Figs. 61–66. Diagrams of chaetotaxy of the first abdominal segment of first instar larvae of Procridinae. Anterior end to the left. **D** – dorsal, **SD** – subdorsal, **L** – lateral setae. **61.** *Artona* (*Fuscartona*) *martini* Efetov, 1997. **62.** *Rhagades* (*Rhagades*) *pruni* ([Denis & Schiffermüller], 1775). **63.** *Adscita* (*Adscita*) *statices* (Linnaeus, 1758). **64.** *A.* (*Tarmannita*) *mannii* (Lederer, 1853). **65.** *Jordanita* (*Roccia*) *budensis* (Speyer & Speyer, 1858). **66.** *J.* (*Jordanita*) *chloros* (Hübner, 1813). (after Efetov 2001c; Efetov & Hayashi 2008).

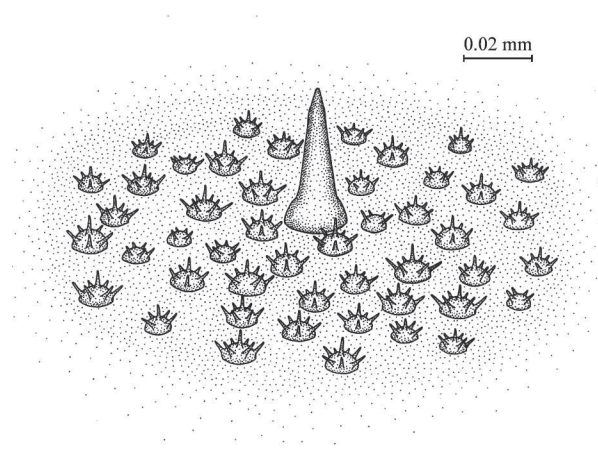


Fig. 67. Combination of the unispined macrotubercle and multispired microtubercles on the cuticle of the last instar larva of *Theresimima ampellophaga* (Bayle-Barelle, 1808). (after Efetov 2004).

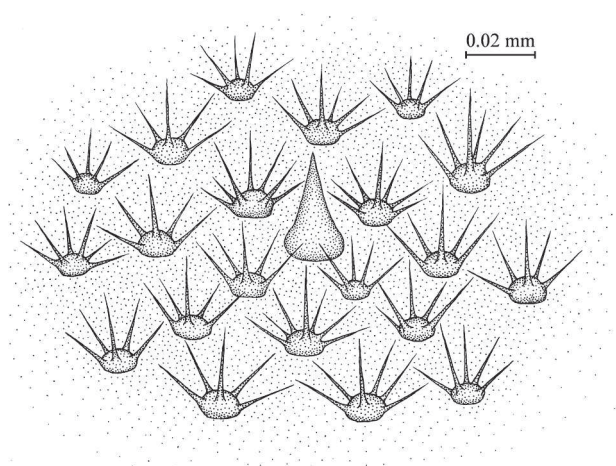


Fig. 68. Combination of the unispined macrotubercle and multispired microtubercles on the cuticle of the last instar larva of *Illiberis (Primilliberis) rotundata* Jordan, 1907. (after Efetov 2004).

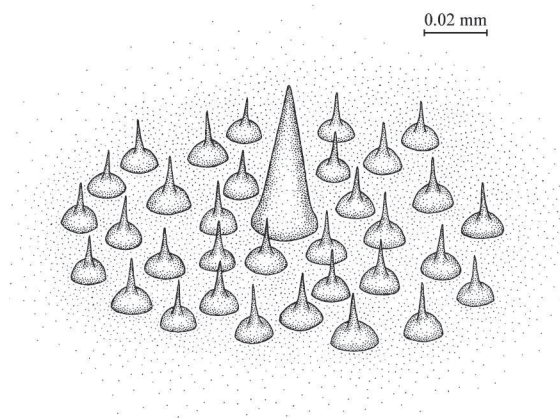


Fig. 69. Combination of the unispined macrotubercle and unispined microtubercles on the cuticle of the last instar larva of *Hedina consimilis* (Leech, 1898).

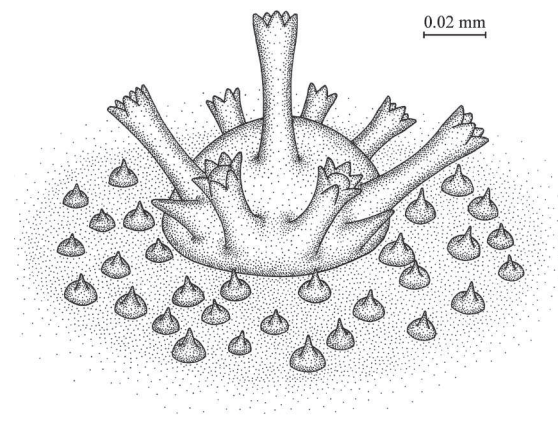
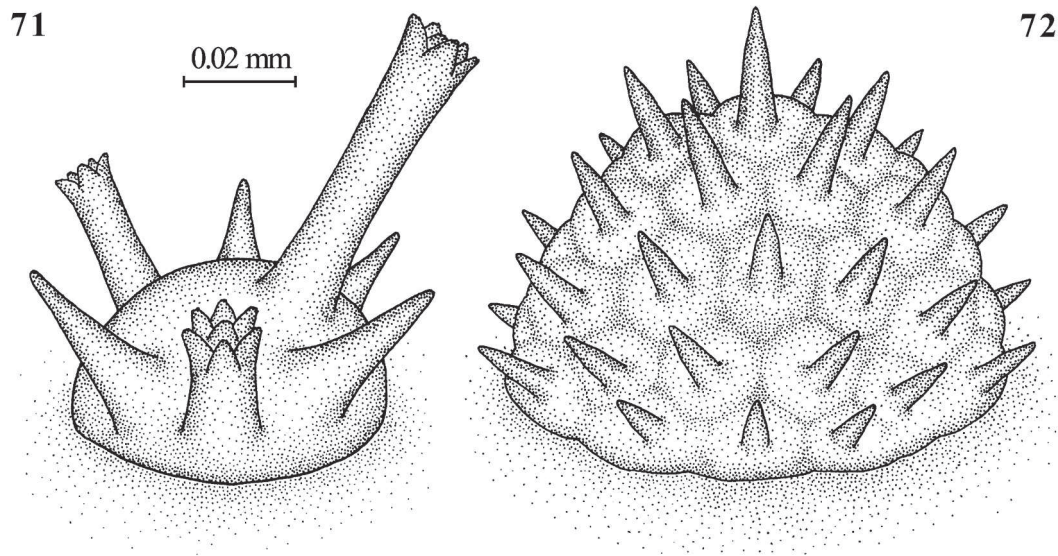
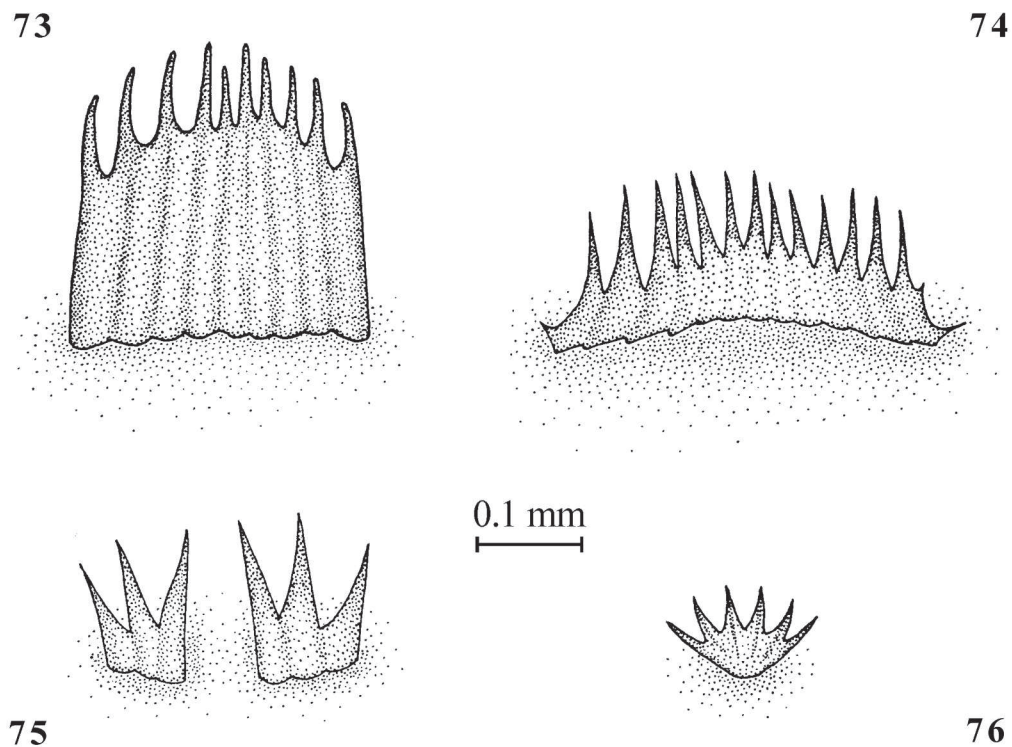


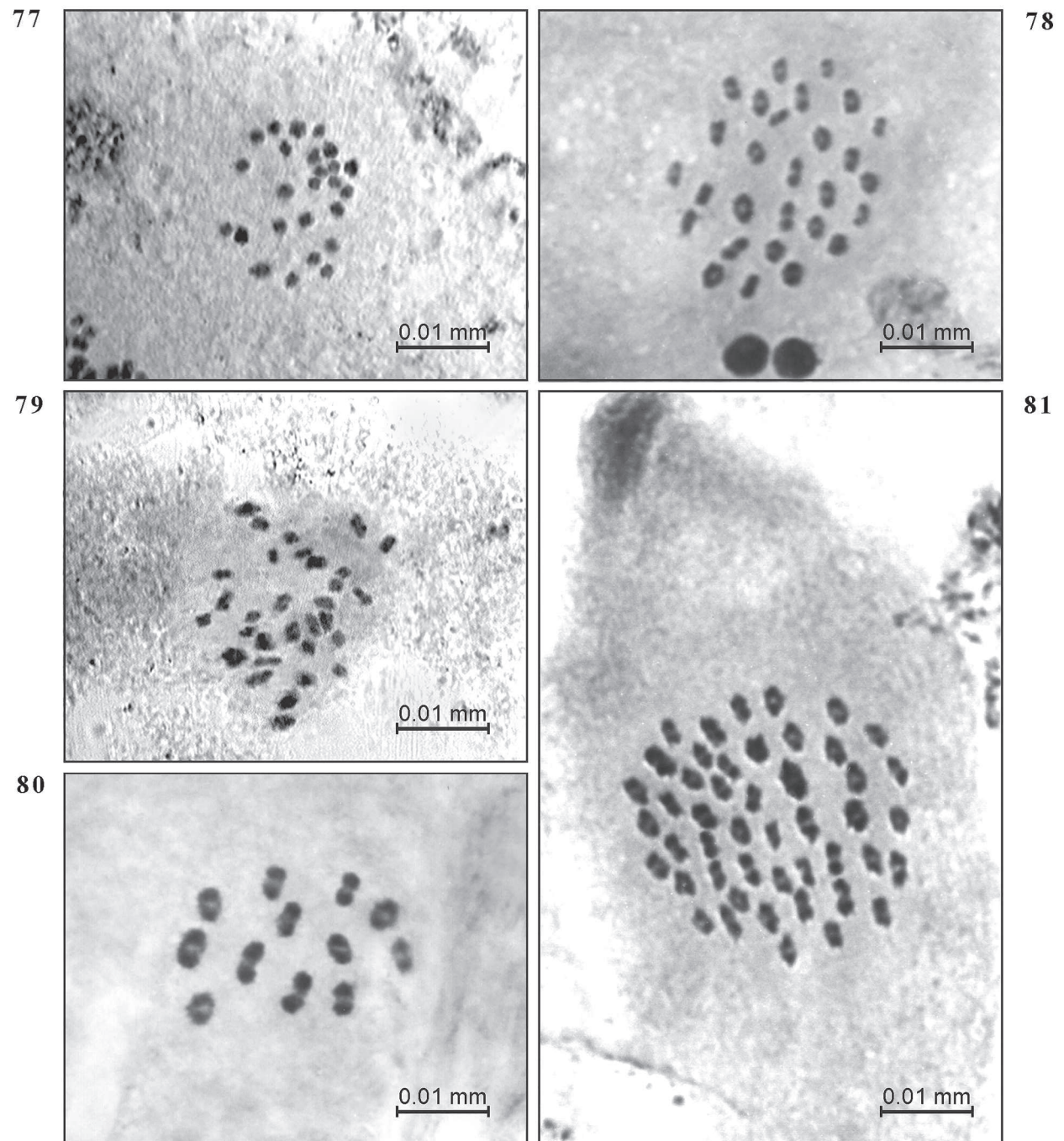
Fig. 70. Combination of the multispired macrotubercle and unispined microtubercles on the cuticle of the last instar larva of *Adscita (Adscita) geryon* (Hübner, 1813). (after Efetov 2004).



Figs. 71, 72. Macrotubercles of adult larvae. **71.** *Jordanita (Solaniterna) subsolana* (Staudinger, 1862). **72.** *J. (Rjabovia) horni* (Alberti, 1937). (after Efetov 2004).



Figs. 73–76. Anal combs of adult larvae. **73.** *Rhagades (Rhagades) pruni* ([Denis & Schiffermüller], 1775): anal comb with high base. **74.** *Adscita (Adscita) capitalis* (Staudinger, 1879): anal comb with low base. **75.** *A. (Procriterna) subtristis* (Staudinger, 1887): anal comb double. **76.** *Zygaenoprocris (Keilia) minna* (Efetov, 1991): anal comb reduced. (after Efetov 2004).



Figs. 77–81. Meiotic metaphase of spermatogenesis in some species of the Procrinae. **77.** *Illiberis* (*Primilliberis*) *rotundata* Jordan, 1907: haploid chromosome number (n) = 25. **78.** *Theresimima ampellophaga* (Bayle-Barelle, 1808): n = 28. **79.** *Rhagades* (*Naufockia*) *brandti* (Alberti, 1938): n = 31. **80.** *Rh.* (*Wiegelia*) *amasina* (Herrich-Schäffer, 1851): n = 12. **81.** *Rh.* (*Rhagades*) *pruni* ([Denis & Schiffermüller], 1775): n = 47. (KAE). (after Efetov 2004).

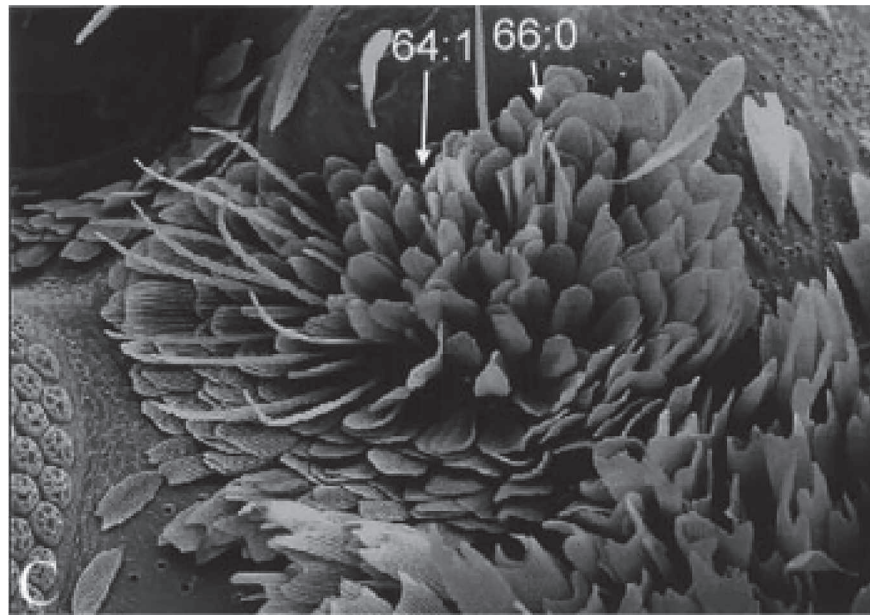


Fig. 83. Chaetosema of *Inouela formosensis* Efetov, 1999. (after Yen et al. 2005).

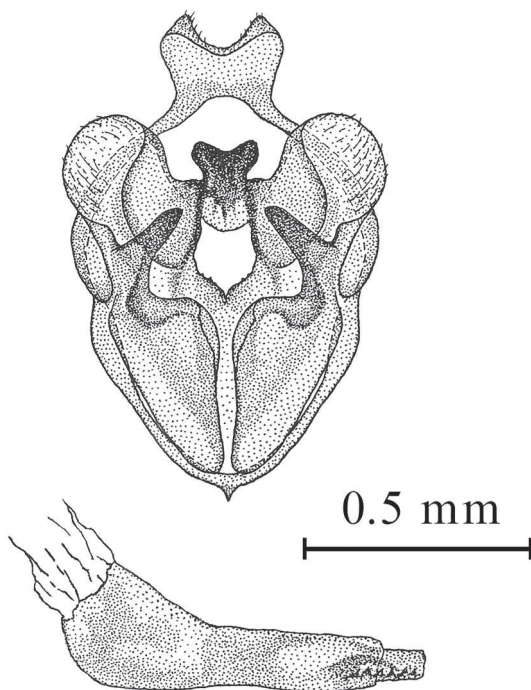


Fig. 84. Male genitalia of paratype of *Inouela formosensis* Efetov, 1999. (after Efetov 1999).

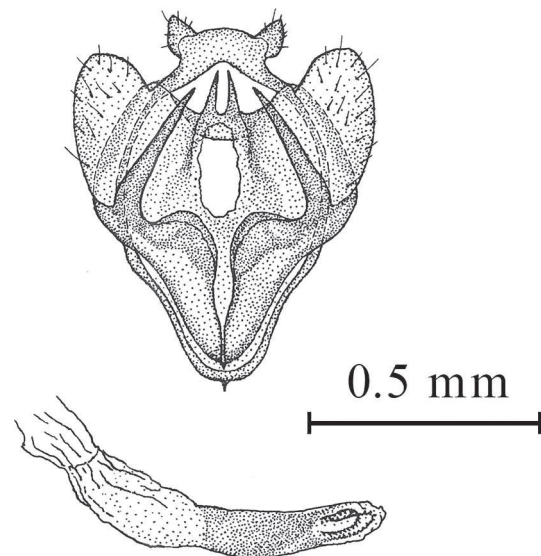


Fig. 85. Male genitalia of paratype of *Inouela exiguitata* (Inoue, 1976). (after Efetov 1999).

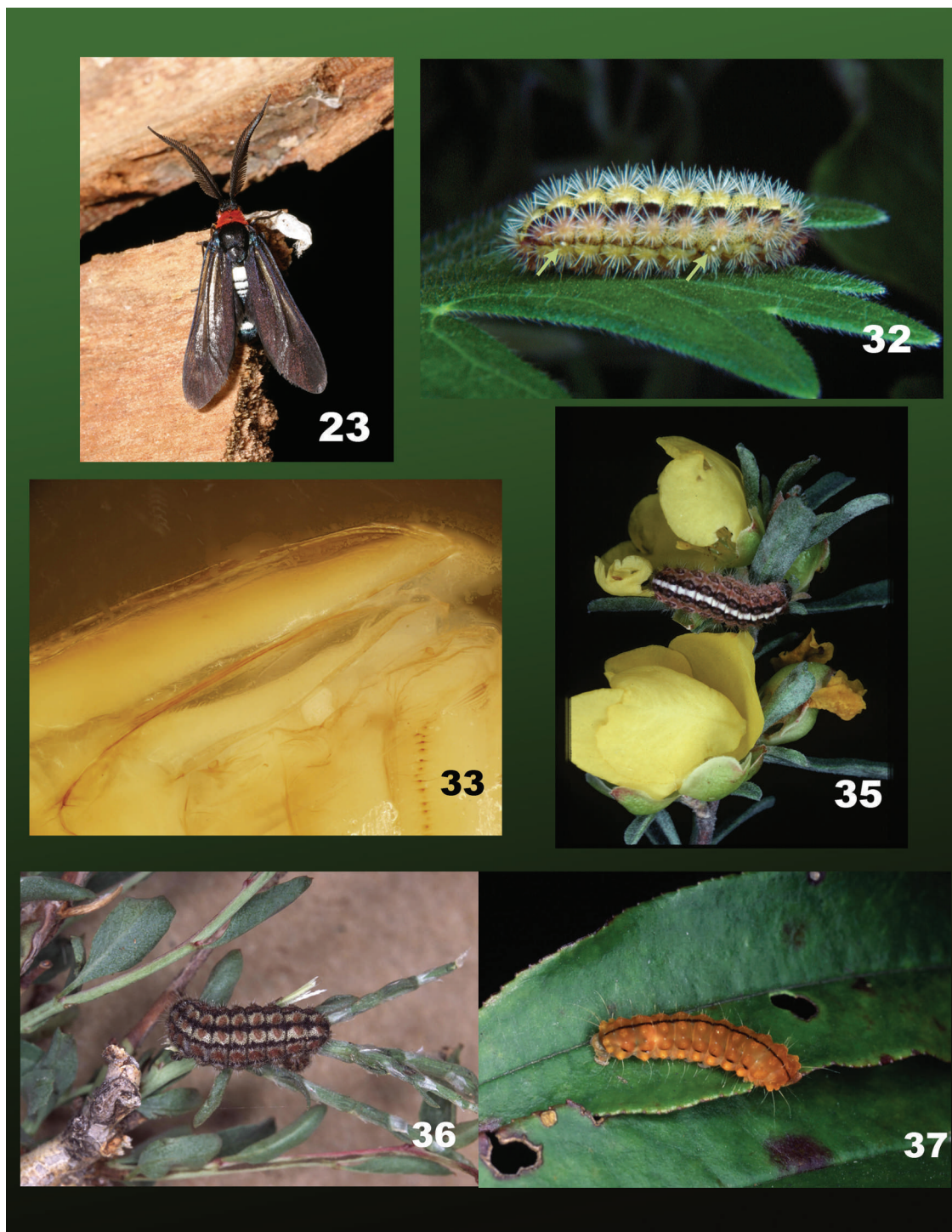


Fig. 23. Male of *Hestiochora tricolor* (Walker, 1854) (Procridinae, Artonini), with coloured patagia and parapatagia, Australia, NSW. (GMT). Fig. 32. Adult larva of *Adscita bolivari* (Agenjo, 1937) with lateral protuberances. (KAE). (after Efetov & Tarmann 2004). Fig. 33. Pupa of *Pollanisus viridipulverulenta* (Guérin-Méneville, 1839) (Procridinae, Artonini) with opened wing with the abdominal gland 2 visible. (after Tarmann 2004). Fig. 35. Adult larva of *Pollanisus apicalis* (Walker, 1854) (Procridinae, Artonini) freely feeding on *Hibbertia obtusifolia* DC. Australia, ACT. (GMT). Fig. 36. Adult larva of *Zygaenoprocris persepolis* (Alberti, 1938) (Procridinae, Procridini) freely feeding on *Polygonum spinosum* H. Gross, Iran. (GMT). Fig. 37. Adult larva of *Soritia costimacula battakorum* (Dohrn, 1906) (Chalcosiinae) freely feeding on *Eurya* sp., Indonesia, Sumatra. (GMT).

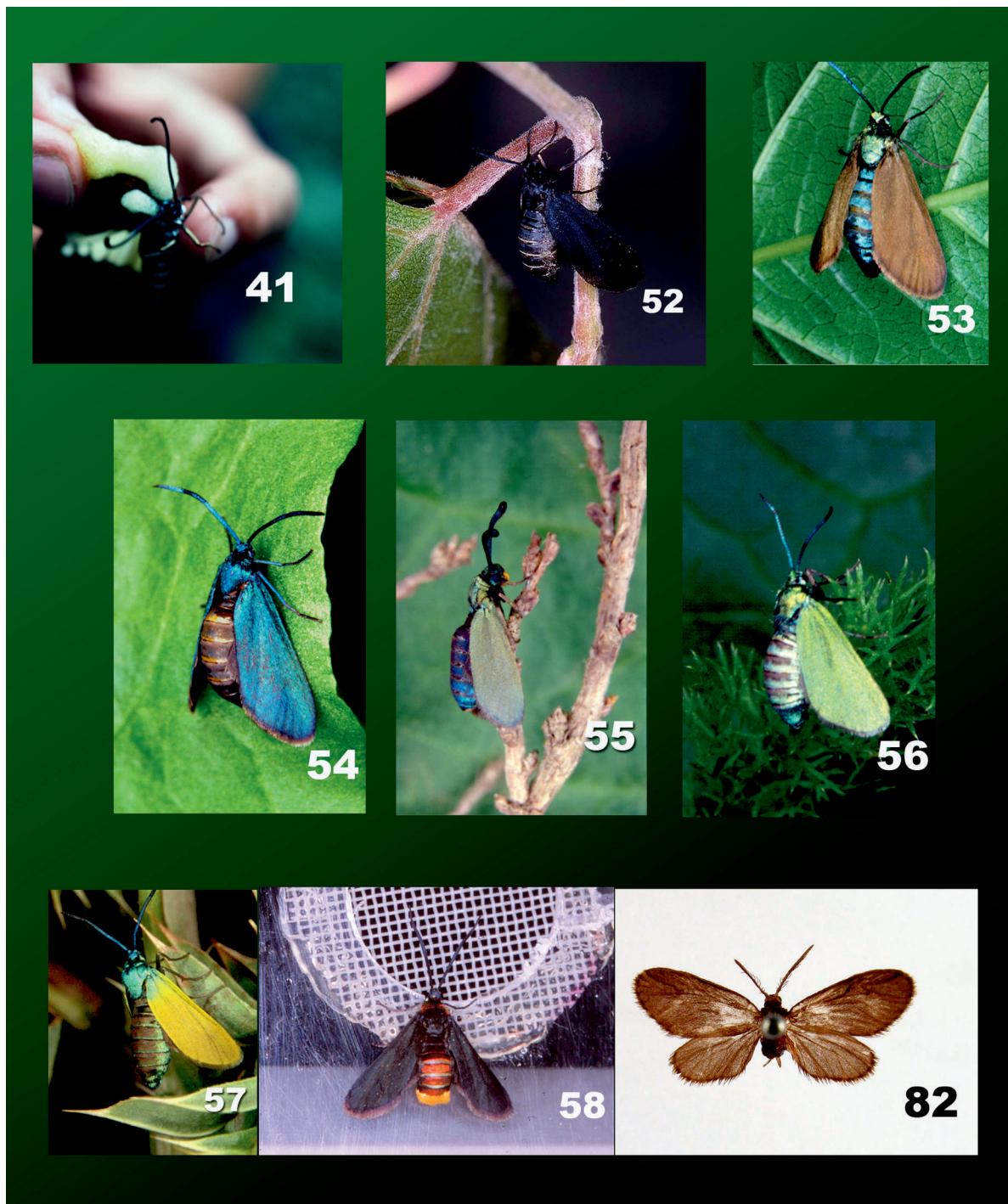


Fig. 41. Defensive foam from head of *Erasmia pulchella* Hope, 1841 (Chalcosiinae). (GMT). Fig. 52. Female of *Acolothus rectarius* Dyar, 1898 (Procridinae, Procridini) in calling position waiting for male, U.S.A., Arizona. (GMT). Fig. 53. Female of *Theresimima ampellophaga* (Bayle-Barelle, 1808) in calling position waiting for male, Crimea. (KAE). (after Efetov 2001c). Fig. 54. Female of *Rhagades (Rhagades) pruni* ([Denis & Schiffermüller], 1775) in calling position waiting for male, Crimea. (KAE). (after Efetov 2001c). Fig. 55. Female of *Zygaenoprocris (Molletia) taftana* (Alberti, 1939) in calling position waiting for male, Armenia. (KAE). (after Efetov 2001c). Fig. 56. Female of *Jordanita (Roccia) budensis* (Speyer & Speyer, 1858) in calling position waiting for male, Crimea. (KAE). (after Efetov 2001c). Fig. 57. Female of *Jordanita (Jordanita) chloros* (Hübner, 1813) in calling position waiting for male, Crimea. (KAE). (after Efetov 2001c). Fig. 58. Female of *Pollanisus communi* Tarmann, 2004, in calling position waiting for male, Australia, Queensland. (GMT). Fig. 82. *Inouela formosensis* Efetov, 1999. Holotype male (KAE).