A comparative study of the abdomen in the family Buprestidae (Coleoptera)

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JENDEK E. 2001: A comparative study of the abdomen in the family Buprestidae (Coleoptera). *Acta Musei Moraviae, Scientiae biologicae* (Brno) **85:** 1–41. – A survey is made of the major features of the abdominal arrangement within Buprestidae, as well as comparison with representatives from families Byrrhidae, Dryopidae, Elateridae, Eucnemidae and Heteroceridae. Evolutionary trends in development of particular abdominal parts are reviewed and the polarities are indicated. The systematic position and phylogenetic relationships of taxa are discussed. All significant structures and evolutionary schemes are illustrated.

Key words: Buprestidae, abdomen, comparative morphology, evolution, phylogeny

Introduction [1]

The systematic position of Buprestidae within Coleoptera (CROWSON 1982; FORBES 1942; KASAP & CROWSON 1975; LAWRENCE 1988; LAWRENCE & NEWTON 1995), as well as its higher classification within Buprestidae (BELLAMY 1985, 1986; COBOS 1980, 1986; HOLYNSKI 1988, 1993; NELSON & BELLAMY 1991) is controversial and still under discussion. One reason for this situation is a lack of data on the comparative morphology and evolution of particular body parts, evaluated over a wide spectrum of taxa. Only a few such works exist in the buprestid literature, e.g. GOOD (1925) on wing venation; the comprehensive study of GARDNER (1989) on Stigmoderini; and the work of KASAP & CROWSON (1975), in which buprestids were examined along with families from the Elateriformia and Dascilloidea.

This work does not claim to be exhaustive; its main intent is to provide further data on the evolutionary morphology of buprestids as a contribution to considerations of phylogeny.

Material and methods

Dissecting techniques

Dry-preserved specimens were minimally relaxed for 12 hours in Okena [2]. After relaxation, the abdomen was separated and cut along one pleural portion to divide tergal and ventral portions and for internal cleaning.

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[1] This paper is an extended version of a lecture presented to the First International Symposium on Buprestidae (Visegrad, Hungary, 18–23 September 1995) and prepared for publication in the Proceedings of the Symposium (Crystal, Publications of the Natural Science Foundation at Göd, Series Zoologica). For this reason, the formal structure of chapters and sections in the manuscript does not correspond to customary practice in *Acta Musei Moraviae*. The manuscript was originally submitted in 1998 and does not include references to papers published after 31 December 1998.

Strongly sclerotised and pigmented specimens were first softened in 10% NaOH and then cleared in a mixture of 1:1 concentrated lactic acid and hydrogen peroxide. All dissected specimens were preserved and examined in glycerol. Part of the material was examined dry-preserved, after removing elytra and wings. Such species are marked herein by an asterisk. Material was mounted in glycerol on slides and examined with a stereoscopic microscope with direct lighting or with a transmitted light microscope. Micrographs were provided by a Hitachi S-800 scanning electron microscope (SEM) from gold sputter-coated specimens.

Terminology and abbreviations

The following terms and abbreviations are used in the text or illustrations. The terms follow the work of LAWRENCE & BRITTON (1994). The proposed new terms are marked "(new term)".

CT	cuticularium (new term)
IP	intercoxal process
LS	laterosternite (LAWRENCE & BRITTON 1994)
LSP	lateral sternal projection (new term)
LSS	laterosternal sulcus (new term)
LT	laterotergite (LAWRENCE & BRITTON 1994)
OS	ostium (new term)
PS	parasternite (LAWRENCE & BRITTON 1994)
S	sternum
SC	sternal carina
SG	sternal groove (new term)
SI	sternal inflexion (new term)
SP	spiracle
T	tergum

Arabic numerals indicate the sequence of skeletal segments, Roman numerals are for genital segments; ABD9, ABD8, ABD8–7, ABD7 designate the types of abdominal arrangement, where numbers indicate the count of visible terga.

Character analysis

To evaluate trends in the evolution of particular characters it was necessary to assign presumed plesiomorphic extremes as starting points for reconstruction of transformation series. Though outgroup analysis is widely accepted in the determination of character state polarity, the basic presumption is that comparison with the proven sister group shows the closest affinities. The relationship of Buprestidae to the closest outgroup remains, however, uncertain and is still being discussed (see Introduction). Determination of polarity was therefore performed employing presumptions about the tendencies with which evolution is often associated (increase in organisation or complexity, elaboration or differentiation of structures, numerical reduction by loss or fusion, etc).

I am aware that efforts to artificially compress the evolutionary continuum into particular character states, as well as the capacity to establish maximum level of nuance,

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[2]) A water-free mixture of various alcohols, sold in Slovakia as window cleaner.

are very subjective and cannot always correspond to the observations and interpretations of various authors. Furthermore, most of the characters examined represent, in fact, several subjectively correlated characters and, because of the limited number of specimens examined, various states of different characters may appear in a larger range of combinations than that given in this work. In order to facilitate clarity of understanding, I have supported my observations and interpretations with the maximum number of illustrations.

List of taxa examined

For purely practical reasons, the higher classification adopted in this work follows that of BELLAMY (1985)) with the following modifications: taxa of former subfamily Chalcophorinae are included under the subfamily Buprestinae as suggested by TOYAMA (1987); the subfamily Stigmoderinae is downgraded to tribal level (BELLAMY 1986, GARDNER 1989); the genera *Paratrachys* and *Sponsor* are placed in a separate tribe, the Paratrachyini (TOYAMA 1987), but in the subfamily Polycestinae, not in Trachyinae; the Galbellinae are treated as a separate subfamily (COBOS 1986). A total of 94 species belonging to 80 genera were examined for this project. A list of taxa examined for the distribution of abdominal receptors (cuticularia) is given in Table 2.

Genera examined:

Acmaedoderella COBOS, *Acmaeodera* ESCHSCHOLTZ, *Actenodes* DEJEAN, *Agrilodia* OBENBERGER, *Agrilus* CURTIS, *Alissoderus* DEYROLLE, *Amorphosternus* DEYROLLE, *Anthaxia* ESCHSCHOLTZ, *Aphanisticus* LATREILLE, *Astraeus* LAPORTE & GORY, *Aurigena* LAPORTE & GORY, *Belionota* ESCHSCHOLTZ, *Brachys* SOLIER, *Buprestis* LINNAEUS, *Capnodis* ESCHSCHOLTZ, *Chalcophora* SOLIER, *Chrysobothris* ESCHSCHOLTZ, *Chrysochroa* SOLIER, *Cisseis* LAPORTE & GORY, *Clema* SEMENOV, *Coomaniella* BOURGOIN, *Coraebus* LAPORTE & GORY, *Curis* LAPORTE & GORY, *Cylindromorphus* KIESENWETTER, *Cyphogastra* DEYROLLE, *Cyphosoma* MANNERHEIM, *Dactylozodes* CHEVROLAT, *Dicerca* ESCHSCHOLTZ, *Ectinogonia* SPINOLA, *Endelus* DEYROLLE, *Ethon* LAPORTE & GORY, *Euchroma* SOLIER, *Eupristocerus* DEYROLLE, *Eurythyrea* LACORDAIRE, *Galbella* WESTWOOD, *Glyptoscelimorpha* HORN, *Habroloma* THOMSON, *Haplostethus* LECONTE, *Iridotaenia* DEYROLLE, *Julodis* ESCHSCHOLTZ, *Kisanthobia* MARSEUL, *Lamprocheila* OBENBERGER, *Melanophila* ESCHSCHOLTZ, *Meliboeus* DEYROLLE, *Mundaria* KERREMANS, *Omochyseus* WATERHOUSE, *Pachyschelus* SOLIER, *Paracylindromorphus* THÉRY, *Paragrilus* SAUNDERS, *Paratrachys* SAUNDERS, *Phaenops* DEJEAN, *Poecilonota* ESCHSCHOLTZ, *Polycesta* SOLIER, *Polyctesis* MARSEUL, *Polyonychus* CHEVROLAT, *Pseudocastalia* KRAATZ, *Psiloptera* SOLIER, *Ptosima* SOLIER, *Ptychomus* MARSEUL, *Sambus* DEYROLLE, *Schizopus* LECONTE, *Scintillatrix* OBENBERGER, *Sphenoptera* SOLIER, *Sponsor* LAPORTE & GORY, *Steraspis* SOLIER, *Sternocera* ESCHSCHOLTZ, *Stigmodera* ESCHSCHOLTZ, *Strigoptera* DEJEAN, *Thrincopyge* LECONTE, *Tonkinula* OBENBERGER, *Toxoscelus* DEYROLLE, *Trachys* FABRICUS, *Tylauchenia* BURMEISTER, *Tyndaris* THOMSON, *Vanroonia* OBENBERGER, *Xantheremia* VOLKOVITSH, *Xyroscelis* THOMSON.

Species examined:

Schizopodinae: *Glyptoscelimorpha marmorata* HORN, *Schizopus laetus* LE CONTE, **Julodinae**: *Julodis onopordi* (FABRICIUS), *Sternocera pulchra* (WATERHOUSE), **Polycestinae**: *Polycesta porcata* (FABRICIUS), *Pseudocastalia aegyptiaca* (LINNÉ), *Ptosima flavoguttata* (ILLIGER), *Strigoptera obsoleta* (CHEVROLAT), *Tylauchenia crassicollis* (LAPORTE & GORY), *Astraeus sp.*, *Polyctesis rhois* MARSEUL, *Tyndaris planata* (LAPORTE & GORY), *Xyroscelis sp.*, Paratrachyini: *Paratrachys sp.*, *Sponsor sp.*, **Acmaeoderinae**: *Acmaeodera brevipes* KIESENWETTER, **Acmaeodera impluviata* MANNERHEIM, *Acmaeoderella flavofasciata* (PILLER), **Acmaeoderella glasunovi* (SEMENOV), **Xantheremia koenigi* (GANGLBAUER), *Ptychomus sp.*, **Thrincopyginae**: *Thrincopyge ambiens* (LE CONTE), **Mastogeniinae**: *Mastogenius parallelus* SOLIER, *Haplostethus subcyaneus* LE CONTE, **Buprestinae**: Catoxanthini: **Chrysochroa fulminans* (FABRICIUS),

Steraspis sp., Chalcophorini: *Chalcophora mariana* (LINNÉ), *Cyphogastra foveicollis* (BOISDUVAL), *Euchroma gigantea* (LINNÉ), *Lamprocheila maillei* (LAPORTE & GORY), Iridotaenini: *Iridotaenia chrysostoma* DEYROLLE, Psilopterini: *Aurigena lugubris* (FABRICIUS), *Capnodis tenebrionis* (LINNÉ), *Cyphosoma* sp., *Ectinogonia buqueti* SPINOLA, *Psiloptera mimosae* KLUG, Dicercini: *Dicerca alni* (FISCHER), *Dicerca furcata* (THOMSON), *Poecilonota variolosa* (PAYKULL), *Scintillatrix tschitscherini* (SEMENOV), Buprestini: *Buprestis octoguttata* LINNÉ, *Buprestis haemorrhoidalis* HERBST, *Eurythyrea austriaca* (LINNÉ), Coomaniellini: *Coomaniella* sp., Kisanthobiini: *Kisanthobia ariasi* (ROBERT), **Melanophilini**: *Melanophila picta* PALLAS, *Melanophila acuminata* (DE GEER), *Phaenops cyanea* (FABRICIUS), Anthaxiini: *Anthaxia podolica* (MANNERHEIM), *Anthaxia scorzonerae* (FRIVALDSZKY), *Curis yalgoensis* CARTER, Stigmoderini: *Dactylozodes rousseli* SOLIER, *Stigmodera auricollis* THOMSON, *Stigmodera vittata* SAUNDERS, **Sphenopterinae**: *Sphenoptera substriata* KRYNICKY, *Sphenoptera manderstjernai* JAKOVLEV, **Chrysobothrinae**: *Actenodes aurolineatus* (LAPORTE & GORY), *Chrysobothris affinis* (FABRICIUS), *Chrysobothris chrysostigma* (LINNÉ), *Belionota prasina* (THUNBERG), **Agrilinae**: Coraebini: *Coraebus rubi* (LINNÉ), *Coraebus denticollis* SAUNDERS, *Meliboeus robustus* (KÜSTER), *Ethon fissiceps* (KIRBY), *Eupristocerus* sp., *Sambus* sp., *Amorphosternus bruchi* KERREMANS, *Alissoderus superciliosus* (WIEDEMANN), *Cisseis regalis* THOMSON, *Polyonychus tricolor* (SAUNDERS), *Tonkinula aurofasciata* (SAUNDERS), *Clema deserti* SEMENOV, *Mundaria typica* KERREMANS, *Toxoscelus auriceps* SAUNDERS, *Vanroonia coomani* DESCARPENTRIES & VILLIERS, **Agrilini**: *Agrilus biguttatus* (FABRICIUS), *Agrilus viridis* (LINNÉ), *Agrilus cyaneoniger* (SAUNDERS), *Dismorpha linearis* (LINNÉ), *Agrilodia paraguayensis* OBENBERGER, *Omochyseus terminalis* WATERHOUSE, *Paragrilus rugatulus* THOMSON, **Trachyinae**: *Trachys minutus* (LINNÉ), *Habroloma geranii* (SILFVERBERG), *Brachys floccosus* (MANNERHEIM), *Pachyschelus secendens* WATERHOUSE, Aphanisticini: *Aphanisticus pygmaeus* LUCAS, *Endelus* sp., **Cylindromorphinae**: *Paracylindromorphus subuliformis* (MANNERHEIM), *Paracylindromorphus transversicollis* (REITTER), *Cylindromorphus pubescens* SEMENOV, *Cylindromorphus filum* GYLLENHAL, **Galbellinae**: *Galbella felix* (MARSEUL).

Comparative morphology within Buprestidae

General morphology (Figs 1, 2)

Abdominal segments in buprestids can be divided morphologically, functionally and by position into skeletal segments, and genital segments that create a capsule either partially or fully retracted into the abdomen. The lateral sternal projections extend to the anterior margin of T1; the basal part of the abdomen along with S3 extends from T1 to T3; segmentation of S4–S6 articulates with T4–T6; and S7 corresponds to T7 proximally, distally to T7, TVIII or TIX.

KASAP & CROWSON (1975) studied the abdominal structure in Elateriformia and Dascilloidea and they distinguished several structures in relation to the pleural membrane: those ventral were termed parasternites and laterosternites, while those dorsal either pleurites or paratergites.

Laterosternites are in fact dorsally inflexed sides of sterna, delimited by simple inflexion, carina or groove. Parasternites develop outwards from, and in parallel to, the corresponding laterosternites and are usually separated from tergal parts by the pleural membrane (Figs 35, 44, 52, 53).

Pleurites, according to KASAP & CROWSON (1975), should never coexist with parasternites and differ from them in having a position not necessarily parallel to the corresponding laterosternites and in being separated from laterosternites by a broad pleural membrane. I failed to find pleurites within Buprestidae; I consider those referred to in *Trachys* by KASAP & CROWSON (1975) to be parasternites.

KASAP & CROWSON (1975) termed "paratergites" the lateral parts of the terga delimited by a membrane and bearing the insertion of the tergosternal muscles. I use the term "laterotergites" for these structures, after LAWRENCE & BRITTON (1994).

Spiracles are developed in eight pairs on T1–T7 and TVIII. The first, and largest, pair is located on the structurally different anterior angles of T1 or even on separate sclerites, sometimes solidly fused with postnotum. Pairs 2–7 are located in the pleural membrane or in the anterior, sometimes membranous angles of T2–T7. The last, obscured and atrophied, 8th pair is situated on the anterior angles of TVIII, retracted under T7. The morphology of spiracles is not studied in this work.

The genital segments (TVIII, TIX [3], SVIII, SIX) create the genital capsule (Fig. 4), surrounding the aedeagus in the male. In the female, SXI is replaced by the ovipositor. The pair TVIII–SVIII creates the outer tube of the genital capsule, TIX–SIX the inner one. Each pair is proximally connected by muscles and membranes. The foreparts of the genital segments can project beyond S7 or T7.

CROWSON (1955, 1985) and KASAP & CROWSON (1975) reported the presence of small, paired, transparent, pore-like areas on the sterna and terga in both sexes. These pores, termed cuticularia in this work, are present in maximum development on T2–T6 dorsally, in metacoxal cavities, and on S4–S6 ventrally (Figs 1, 12).

Primary abdominal arrangement (Figs 3, 4)

According to the degree of insertion of the tergal genital segments into the abdomen, two principal morphotypes of the buprestoid abdomen can be distinguished [4]: 1) abdomen with exposed genital terga and 2) abdomen with fully overlapped genital terga. The main difference between them is in the number of visible terga. In first type of arrangement, the distal parts of TVIII, and sometimes TIX, are exposed below T7. At ABD7, both TVIII and TIX are obscure, fully overlapped by T7.

This principal character in the abdominal arrangement of Buprestidae has been briefly reported within the general morphology of buprestids by SCHAEFER (1936, 1949) and COBOS (1980, 1986), who applied it in a key to the subfamilies.

Abdomen with exposed genital terga (ABD9, ABD8, ABD8–7). T7 similar in length to T6, extends approximately to 1/2 length of S7. Difference in lengths between S7 and T7 creates space for distal parts of TVIII and TIX, which have similar sclerotisation, coloration and structure of surface as foregoing segments. PS7 extends to apex of T7.

ABD9 were observed only in subfamily Buprestinae, in most species of more bulky genera of Catoxanthini, Iridotaenini, Psilopterini and Dicercini; with the more bulky species and medium-sized species of Melanophilini. ABD8 is characteristic within the subfamilies Schizopodinae, Julodinae, Acmaeoderinae, Thrincopyginae, Mastogeniinae,

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[3] TIX is actually composed of two segments T9 and T10 (proctiger) as given in LAWRENCE & BRITTON (1994).

[4] While examining the number of visible terga, it is important to distinguish artificially protruding genital structures, which always extend beyond the apex of S7 and differ in their weaker sclerotisation, paler coloration, and finer structure on the surface.

Chrysobothrinae, Buprestinae (Catoxanthini pars, Chalcophorini, Psilopterini pars, Buprestini pars, Stigmoderini, Coomaniellini, Anthaxiini) and Polycestinae pars (*Xyroscelis*, *Tylauchenia*, *Astraeus*, *Polyctesis*, *Tyndaris*). There is also an intermediate arrangement (ABD8–7) with T7 longer, extending behind 1/2 of S7, but not to the apex, PS7 extends about to 2/3 of T7, TIX is obscure, TVIII is exposed or obscure, but similarly sclerotised and more pale coloured than the foregoing terga, which indicates its closer affinity to the morphotype with exposed genital terga. Such an arrangement was observed in Polycestinae pars (*Polycesta*, *Ptosima*, *Strigoptera*, *Pseudocastalia*) and Buprestinae pars (*Scintillatrix*, *Poecilonota*, *Kisanthobia*).

Abdomen with overlapped genital terga (ABD7). T7 distinctly longer than T6, extending to the apex of S7, TVIII and TIX fully inserted in abdomen, more feebly sclerotised and coloured compared to the foregoing segments. PS7 extends to 1/2 of T7. Representatives of Sphenopterinae, Agrilinae, Trachyinae, Cylindromorphinae and Galbellinae, along with Paratrachyini from Polycestinae, belong to this morphotype.

The abdominal arrangement with exposed, less specialised genital terga embodies a primitive condition in comparison with those with overlaps (Fig. 4). Within the primitive condition ABD8 is more advanced, derived from ABD9 by prolongation of TVIII. ABD7 can be derived from ABD8 by prolongation of T7, which is indeed longer than T6. Moreover, PS7 extends, due to prolongation, only to 1/2 of T7. The process of segment prolongation may also be facilitated by a parallel and progressive retraction of the whole genital capsule deeper into the abdomen.

A trend toward a decrease in the number of visible terga occurs universally within Buprestidae; the significant difference, however, lies in the degree of reorganisation and its frequency within particular higher taxa. Groups generally considered to be primitive exhibit a range of states (ABD9, ABD8, ABD8–7), while specialised ones show completion of the abdominal rearrangement (Sphenopterinae, Agrilinae, Trachyinae, Cylindromorphinae, Galbellinae and Paratrachyini). ABD9 was discovered only in the subfamily Buprestinae, while the occurrence of both primary morphotypes, exposed and overlapped, was demonstrated only in subfamily Polycestinae.

In males of *Schizopus*, *Glyptoscelimorpha*, *Euchroma* and *Steraspis*, sexual dimorphic modifications were observed in the abdominal arrangement (Figs 5, 6). Sternum S7 is distinctly emarginate, SVIII and SIX strongly sclerotised, differently exposed. Within Schizopodinae, the form of SVIII is unique, *Schizopus* possesses a long anteromedial projection; in *Glyptoscelimorpha* it is firmly fused with S7. Because this character seems to have only sexual importance (females possess ABD9 or ABD8), with a diversity of states within particular genera, it was not examined in great detail and is considered to be derived in relation to the arrangement of obscure genital sterna and developed as a sexual adaptation, e.g. limited mobility of sterna.

Tergal side (Fig. 1)

The tergal side in buprestids consists of 7 skeletal terga, a number that may apparently be increased to 8 or 9, because of the exposed genital terga (TVIII, TIX).

The first two terga (T1, T2) are always immovably fused (connate) in Buprestidae, as noted by KASAP & CROWSON (1975), but with a preserved suture. T1 and T2 are

distinctly incurved (Figs 7, 22, 28, 30, 51, 65) or even deeply emarginated. This emargination reaches almost to the suture between T1 and T2 (Acmaeoderinae, Thrincopyginae, Mastogeniinae, most of Polycestinae including Paratrachyini) (Figs 7, 16, 17, 19, 21). The incurve of the first two terga seems to be a plesiomorphy within Buprestidae, occurring in various degrees of development in all examined species; this also influences subsequent terga, especially T3, bearing sometimes acute anterior angles, embracing the sides of T2 (e.g. *Agrilus*, Figs 34, 35, 65). The emargination of T1 is considered to be the more derived state.

The last tergum (T7) exhibits a tendency to slip beneath T6. It possesses anterolateral projections inserted along with anterior margin under T6.

The consistency of the skeletal terga can be divided into three states: a) terga membranous, or feebly sclerotised, with transparent sides coinciding with pleural membrane, spiracles located in the transparent portions or closely adjoined to them; b) terga feebly sclerotised, without transparent membranous margins; c) terga heavily sclerotised[5]. Spiracles in the last two cases are not located in the pleural membrane. Sclerotisation is not necessarily correlated to pigmentation or body size; species possessing feebly sclerotised terga often have a brightly metallic tergal side. Large species (e.g. from *Julodis, Iridotaenia, Psiloptera*) have less sclerotised tergal segments than small ones (e.g. from *Agrilus, Paratrachys, Sponsor, Trachys*). To the group with transparent tergal sides belong Schizopodinae, Julodinae, Acmaeoderinae, Thrincopyginae and Mastogeniinae. The subfamilies Polycestinae and Buprestinae exhibit a graded series in tergal consistency, from membranous (*Polyctesis, Melanophila*) to strongly sclerotised (most of Polycestinae, Buprestini, Stigmoderini, Anthaxiini, *Coomaniella, Kisanthobia*). The tergal sides in the subfamilies Chrysobothrinae, Sphenopterinae, Agrilinae, Trachyinae, Cylindromorphinae, and Galbellinae are strongly sclerotised. The character state with membranous terga and spiracle location in pleural membrane is considered the most plesiomorphic.   •

This increased degree of tergal sclerotisation induces changes in the connections between terga. Originally telescopically overlapped terga capable of free movement via an inter-tergal membrane become abutted, with mobility limited by the loss of the intersegmental membrane (Polycestinae pars including *Paratrachys*, Buprestinae (Dicercini pars, Buprestini pars, Stigmoderini, *Coomaniella, Kisanthobia*, Anthaxiini), Chrysobothrinae pars, Sphenopterinae, Agrilinae, Trachyinae, Cylindromorphinae, Galbellinae). This trend is most strongly manifest in proximal terga. In *Stigmodera* and *Strigoptera*, even the first two terga are immovably fused, tending to form an integral tergal plate.

Tergal sides bearing spiracles are frequently morphologically modified and are demarcated by either a ridge, an elevation or a convexity (Polycestinae pars, Buprestinae pars, Coraebini pars, Trachyinae pars, Cylindromorphinae pars), or even by forming separate sclerites, laterotergites (Figs 1, 2, 26, 35, 44, 65), flanking tergites (most Agrilinae, several Trachyinae, Cylindromorphinae, *Kisanthobia*). KASAP & CROWSON

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[5] Sclerotised terga have a tendency to burst when compressed.

(1975) also discovered laterotergites in *Maoraxia*. Typically developed independent laterotergites are present in e.g. *Agrilus* and *Paragrilus*.

Sternal side (Fig. 1)

The sternal side is composed of 4–5 visible, heavily sclerotised ventrites, corresponding to S3–S7. Sterna S1 and S2 are fused, indicated sometimes by a suture in lateral sternal projections, forming parts of coxal cavities and intercoxal process (Fig. 24). S3 and S4 are always connate, with distinct (5 ventrites) (Fig. 27) or obliterated (4 ventrites) suture (Figs 32, 42, 48, 53, 56, 60). The fusion of S3 and S4 is universal within Buprestidae, and the suture between them is variously preserved [6]. In the most primitive state the suture is complete, later becoming obliterated medially or laterally, and in the most advanced forms completely obliterated, sometimes indicated only by different surface microstructure. Within the subfamilies Julodinae, Thrincopyginae, Buprestinae, Chrysobothrinae, Polycestinae (excluding Paratrachyini) the suture is constantly preserved and visible. In Acmaeoderinae a range of states occurs, from complete to fully obliterated; Sphenopterinae exhibit a trend towards obliteration of the medial part of the suture. Further subfamilies are characterised by more advanced sutural obliteration. While in Schizopodinae and Agrilinae intermediate forms still occur, in Trachyinae, Cylindromorphinae, Mastogeniinae and Paratrachyini the suture is completely obliterated. In Galbellinae the suture is obsolete but structurally indicated along its whole length.

Laterosternites (Figs 1, 2, 8, 9, 35, 44, 52). Laterosternites present lateral sternal parts, delimited by a simple inflexion (Figs 9a, 25), by a sternal carina (Figs 1, 9b, 31) or by a sternal groove (Figs 9c–d, 27, 36, 43, 52). Delimitation merely by simple inflexion is considered to be the most primitive condition, occurring in the subfamilies Schizopodinae, Polycestinae pars, Thrincopyginae and Buprestinae (Catoxanthini pars, Buprestini pars, Melanophilini pars, Stigmoderini). At the next stage in the development of inflexion, the sternal carina becomes more elaborate (Julodinae, Polycestinae pars including Paratrachyini, Acmaeoderinae, Mastogeniinae, Buprestinae (most species), Chrysobothrinae and Galbellinae. The sternal carina are variable in length and run along both sides of the abdomen, in maximum development extending from the lateral projection of the abdomen to the apex of S7 (Fig. 1). The genus *Mastogenius* even has twin sternal carina, resembling twin carina on the pronotal sides. The subfamilies Sphenopterinae, Agrilinae, Trachyinae and Cylindromorphinae are characterised by sternal carina partially or fully substituted by a sternal groove, extending sometimes proximally up to S3 and bordering S7 distally (Figs 8b–e, 33, 35–37, 43, 48, 53). Besides the foregoing subfamilies, the sternal groove was found only in the genera *Kisanthobia* (Fig. 27) and *Coomaniella*. In the *Coomaniella*, however, the sternal groove does not border the apex of S7, but is merged with it (Fig. 8a). In advanced forms of Agrilinae, Trachyinae and Cylindromorphinae, the sternal groove becomes obsolete or obliterated

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[6] The most exact type of examination of the preserved suture should be performed on dissected and cleared specimens.

on S3–S6, but still borders the apex of S7 (e. g. *Clema, Habroloma, Brachys*) (Figs 8d, 48). In small species (*Aphanisticus, Cylindromorphus*), the sternal groove is indicated only in the form of a shallow impression on the apex of S7 (Figs 8e, 54, 55, 60, 61). In the genus *Paracylindromorphus*, the sternal groove is preserved on the apex of S7 and along the hind sternal angles of S3–S6 in the form of 4 pairs of small openings or orifices (ostia) (Figs 8d, 56, 57, 58).

Laterosternites may be modified to interlock with the elytra. KASAP & CROWSON (1975) distinguished four basic types of adaptation within the Elateriformia and Dascilloidea, with buprestids belonging to the third of the four types. The findings from my examinations do not always agree with those of KASAP & CROWSON (1975). Only two major types of sterno-elytral fitting, simple or sulcate, depending on the presence or absence of a laterosternal sulcus, can be distinguished within Buprestidae (Fig. 9). The first, a simple fitting (Figs 9a–c, 25, 26, 31, 35), represents the primitive state, characterised by the laterosternites simply inflexed dorsally and with the elytra adjoining freely on the inflexed portion. This type is analogous to elytral fitting types I and II of KASAP & CROWSON (1975). The second, a sulcate fitting (Figs 9d–f, 42, 43, 52), is characterised by laterosternites bearing a laterosternal sulcus, which gives a tightly fitting accommodation of the elytra to the abdomen. The laterosternal sulcus is variable in size, from deep and equally developed along all laterosternites (*Ethon, Amorphosternus, Endelus, Brachys*), to shallow (*Omochyseus, Trachys, Cylindromorphus*) and distinct only on those most basal [7]. The sulcate sterno-elytral fitting corresponds to elytral fitting types III and IV sensu KASAP & CROWSON (1975). Exclusively simple sterno-elytral fitting was examined in subfamilies Schizopodinae, Julodinae, Polycestinae, Acmaeoderinae, Thrincopyginae, Mastogeniinae, Buprestinae, Chrysobothrinae, Sphenopterinae and Galbellinae; both simple and sulcate types are present in Agrilinae. Trachyinae and Cylindromorphinae possess sulcate elytral fitting, though frequently with a very fine laterosternal sulcus, persisting only on basal abdominal laterosternites.

Parasternites (Figs 1, 2, 10, 11). The utmost portions of the sterna are modified into two additional structural strips (parasternites) creating, together with the pleural membrane, a sterno-tergal interlink. Parasternites are present in all buprestids, with a maximum number of 4–5 (PS3–PS7), parallel to the corresponding sterna (S3–S7). Parasternites are contiguous with the outer margins of the laterosternites (Figs 10a, 14) (Schizopodinae, Julodinae, Polycestinae, Acmaeoderinae, Thrincopyginae, Mastogeniinae, Buprestinae pars) or they are discrete, demarcated from the laterosternites by a distinct border-line (Figs 10b, 26, 31, 35, 44, 52) (Buprestinae pars, Chrysobothrinae, Sphenopterinae, Agrilinae, Trachyinae, Cylindromorphinae, Galbella). Parasternites are separated from terga by a pleural membrane, most obvious proximally (Fig. 1). Parasternites are subrectangular (Figs 22, 23, 26, 31, 35, 44, 52), from feebly to strongly sclerotised, or subtriangular and membranous (Figs 14, 18). PS3 is present, obsolete or absent; PS4–PS7 are always developed, PS7 extends to 1/2 of T7 or to the apex of T7, depending on type of abdominal arrangement (Fig. 3).

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[7] If within particular abdominal sterna both types of sterno-elytral fitting were determined, the type was assessed as sulcate.

By reference to the consistency and number of parasternites, three major morphotypes (Fig. 11) may be distinguished within Buprestidae: 1) 4 subtriangular or subrectangular, membranous or feebly sclerotised parasternites (PS4–PS7), PS3 obscure or absent, pleural membrane obvious, (Schizopodinae, Julodinae, Polycestinae, Acmaeoderinae, Thrincopyginae, Mastogeniinae, Buprestinae pars); 2) 5 feeble sclerotised parasternites (PS3–PS7), PS3 subrectangular, pleural membrane at least proximally obvious, (Buprestinae pars, Chrysobothrinae pars); 3) 5 strongly sclerotised, discrete parasternites (PS3–PS7), PS3 subtriangular, pleural membrane vestigial or absent (Buprestinae pars, Chrysobothrinae pars, Sphenopterinae, Agrilinae, Trachyinae, Cylindromorphinae, Galbellinae).

The number of parasternites does not seem to correlate to decreased body size. Small species of Trachyinae and Cylindromorphinae have the full number (PS3–PS7) of sclerotised parasternites, unlike large species of Julodinae and Polycestinae in which the number is reduced (PS4–PS7) and feebly sclerotised.

Presuming that the parasternites differentiated continuously from sternal sides, then the most plesiomorphic state should be an arrangement with 4 membranous or feebly sclerotised parasternites, developing contiguously from the sternal portions in the form of lobes. Further development could be explained by the subsequent differentiation of PS3, sclerotisation of parasternites and obliteration of the pleural membrane. This opinion is also supported by fact that the taxa considered to be primitive, such as Schizopodinae, Julodinae, Polycestinae and the robust species of Buprestinae, possess a reduced number of parasternites.

Cuticularia (Figs 1, 12, 20, 29, 38–41, 44–46, 49–50, 62–65, Table 2)

A characteristic feature occurring universally within Buprestidae is the presence of small, paired, pore-like areas located dorsally on T2–T6 to a maximum of 5 pairs, ventrally on S4–S6, to a maximum of 4 pairs (Figs 1, 65) and inside metacoxal cavities as a single pair. An individual tergal or sternal segment bears, at most, one pair of cuticularia. The cuticularia are located in small impressions, often connected with intersegmental spaces by a siphon (Fig. 64).

CROWSON (1955) suggested that cuticularia are glandular openings KASAP & CROWSON (1975) reported a lack of any glandular structure associated with cuticularia, and they considered them some kind of heat receptor with similarities to the metathoracic infrared sensory organs of *Melanophila acuminata* DE GEER described by EVANS (1966a, 1966b, 1971, 1975) and EVANS & KUSTER (1980).

Under a transmission light microscope, cuticularia appear as semi-transparent honeycomb-like structures (Figs 62–63); under SEM they exhibit a morular structure (Figs 20, 39, 50, 64), with distinct micropores (Fig. 46). If a glandular function is confirmed, then cuticularia might prove to bear some relation to the sensory organs located on buprestid antennae. Cuticularia and antennal sense organs are present in buprestids of both sexes.

The distinctiveness of cuticularia varies within genera, and also in particular segments, from the obvious to the scarcely visible and rudimentary. To determine their

presence with certainty is sometimes possible only on dissected specimens under SEM examination. Cuticularia are most frequently developed dorsally on T3–T5, ventrally on S4–S5. Within the dorsal and ventral segments are pairs of cuticularia developed serially, never discontinuously. Cuticularia are located close to the fore margins of segments or directly adjoining to them. The first tergal and sternal pair may even lie in the sutural region between two fused T1–T2 and S3–S4. The size of cuticularia is often similar to, or larger than, that of corresponding spiracles (*Brachys*, *Chrysobothris*, *Galbella*) (Figs 12, 29). The form of cuticularia varies from circular to spindle-shaped; tergal ones are more extended than the sternal, which are mostly circular. Towards the spiracles, tergal cuticularia are always located at a distance from the lateral margin and never lie on laterosternites.

The occurrence of cuticularia in buprestids is a unique character among the Coleoptera, probably occurring solely within this family, although KASAP & CROWSON (1975) mentioned similar structures found between the junctions of connate sterna in *Psephenus* and *Artematopus*. Examination of sternal and tergal portions in members of the families Byrrhidae, Dryopidae, Elateridae, Eucnemidae, Heteroceridae and Eulichadidae (see below) failed to reveal similar structures. The universal presence of cuticularia within Buprestidae (Table 2) and their occurrence in full numbers across almost all subfamilies suggests that a buprestoid ancestor possessed a minimum of 5 tergal pairs and 3 sternal pairs, along with 1 pair of metacoxal cuticularia. A reduction in the number of cuticularia frequently occurs in Buprestidae and is probably associated with a general reorganisation of the abdomen, rather then decreasing body size. The full number of tergal and sternal cuticularia is preserved in Chrysobothrinae and most of Buprestinae, but also occurs in Julodinae, Polycestinae, Agrilinae and Trachyinae. A reduced number was demonstrated exclusively in Schizopodinae, Acmaeoderinae, Thrincopyginae, Mastogeniinae, Sphenopterinae, Cylindromorphinae and Galbellinae. Tergal cuticularia absent from both proximal (T2) and distal (T6) terga are characteristic of Agrilinae, Trachyinae, Cylindromorphinae, *Paratrachys* and *Sponsor*. Throughout the Acmaeoderinae, they were seen to be only proximally obliterated. Distally obliterated cuticularia occur in Schizopodinae, Julodinae, Mastogeniinae, Buprestinae and Sphenopterinae. Sternal cuticularia vanish only from the distal end (S6). Generally, the trend towards numerical reduction is exhibited firstly on tergal cuticularia. A full number of sternal cuticularia combined with a reduced number of tergal ones was found only in Acmaeoderinae. Sternal cuticularia were entirely absent only in *Galbella*; in all other buprestids examined there was at least one pair on S4. Tergal cuticularia occur on a minimum of two segments, only in *Schizopus* and *Glyptoscelimorpha* are they obscure, due to a membranous terga.

Tergal or sternal cuticularia are sometimes overlapped by the hind margin of the previous segment (*Julodis*, *Polycesta*, *Stigmodera*) and visible only in dissected specimens. This might be the reason for the absence of sternal and/or tergal cuticularia in *Julodis*, *Dystaxia* and *Buprestis* reported by KASAP & CROWSON (1975). Metacoxal cuticularia are visible only after separating the abdomen from the other body parts.

Comparison with representatives from other families

Based upon the preceding examination, the abdomen of the hypothetical buprestoid ancestor should exhibit the following organisation.

◆Abdomen with exposed genital segments, type ABD9 (Figs 1, 3, 4,);

◆Terga membranous, with transparent margins coinciding with obvious pleural membrane bearing spiracles;

◆Terga entire, not separated into tergites and laterotergites;

◆T1 and T2 fused, T1–T3 incurved (Fig. 7), T3–T7 telescopically overlapped and freely movable;

◆Sternites S3–S4 fused, with complete suture;

◆Laterosternites delimited by simple inflexion, sterno-elytral fitting simple (Fig. 9a);

◆Parasternites 4 merous (PS3–PS7), membranous (Fig. 11a), contiguously growing out from laterosternites (Fig. 10a);

◆Cuticularia: 5 tergal pairs (T2–T6), 3 sternal pairs (S4–S6), 1 pair in metacoxal cavities (Fig. 1).

Representatives of six families were examined and compared with the generalised buprestoid ancestor (Fig. 13).

Byrrhus pustulatus (FORSTER, 1771), Byrrhidae. ABD9; terga feebly sclerotised, with semi-transparent spiracle-bearing margins coinciding with the pleural membrane; lateral sternal projections extending only to anterior margin of T2; sterna flanked with sternal carina; S3–S7 connate; sterno-elytral fitting simple; parasternites 5 merous (PS3–PS7), sclerotised, well demarcated from the laterosternites; PS3 very long, extending to anterior margin of T2.

Dryops auriculatus (GEOFFROY, 1875), Dryopidae. ABD8; terga feebly sclerotised; spiracles located in semitransparent sides of terga, coinciding with pleural membrane. Lateral sternal projections extending only to the anterior margin of T2; S3–S4 connate; sterno-elytral fitting sulcate, sulcus not bordering apex of S7; parasternites absent.

Agrypnus murinus (LINNAEUS, 1758), Elateridae. ABD8; terga feebly sclerotised, with semi-transparent lateral margins bearing spiracles; lateral sternal projections extending only to the anterior margin of T2; S3–S6 connate; sterno-elytral fitting sulcate, sulcus bordering apex of S7; parasternites as *Byrrhus* LINNAEUS.

Melasis buprestoides (LINNAEUS, 1761), Eucnemidae. ABD7; terga sclerotised, laterally membranous, membranous portions coincide with pleural membrane; spiracle locations similar to previous; T1 immovably fused with postnotum; lateral sternal projections extending only to anterior margin of T3, T2 and T3 anteriorly with deep medial emargination; sterno-elytral fitting simple, sternal carina present; S3–S7 immovable fused together, suture between them complete; parasternites 5 merous (PS3–PS7), feebly sclerotised and coloured.

Heterocerus fenestratus (THUNBERG, 1784), Heteroceridae. ABD7; terga weak, laterally broadly membranous, bearing spiracles. Lateral sternal projections extending to anterior margin of T1; sterno-elytral fitting sulcate, sulcus not bordering apex of S7;

S3–S7 connate, basal sternal part including S3 corresponds to T1 and T2. Parasternites absent.

Eulichas sp. Eulichadidae. ABD9; terga feebly sclerotised, well demarcated from pleural membrane; spiracles located in pleural membrane; lateral sternal projections extending only to anterior margin of T2; T1 and T2 unfused; sterno-elytral fitting sulcate, sulcus not bordering apex of T7; S3–S5 connate; parasternites only indicated in pleural membrane by darker subtriangular pigmentation.

A trend towards obscuring the genital segments probably occurs generally in Coleoptera. The species examined exhibit whole a wide range of abdominal arrangement from ABD9 (*Byrrhus* LINNAEUS, *Eulichas* JACOBSON) via ABD8 (*Dryops* OLIVIER, *Agrypnus* ESCHSCHOLTZ) to ABD7 (*Melasis* OLIVIER, *Heterocerus* FABRICIUS). The main difference in comparison with the buprestoid morphotype is in the diverse organisation of the basal abdominal parts. The basal terga (T1, T2) in Buprestidae never extend beyond the basal margin of the sternal side of the abdomen because of the long lateral sternal projections (Fig. 1), such as those that occur in *Byrrhus*, *Dryops* and *Agrypnus* (T1) or *Melasis* (T1, T2) (Fig. 13). Although the organisation of basal parts in *Heterocerus* is similar to the buprestoid, the suture at S3–S4 corresponds dorsally to T2–T3 and not to T3–T4 as in buprestids.

Due to the feeble sclerotisation of the terga, the fusion of T1 and T2 was revealed only in *Melasis* and *Eulichas*. In *Melasis* T1 is fused with the postnotum and T2 is deeply emarginate; in *Eulichas* T1 and T2 are unfused. Different degrees of connation of S3 and S4 were observed in all examined species; in *Byrrhus*, *Agrypnus*, *Melasis*, *Heterocerus* and *Eulichas* there exists a trend towards connation of subsequent sterna. The suture between S3 and S4 is always complete, unlike in Buprestidae, where in advanced forms it is incomplete or obliterated.

The simple type of sterno-elytral fitting in *Byrrhus* and *Melasis* is similar to that in buprestids. The sulcate sterno-elytral fitting in *Dryops*, *Agrypnus*, *Heterocerus* and *Eulichas* has no analogy in Buprestidae, where it is always accompanied by a sternal groove, although often rudimentary and preserved only on the apex of S7. The parasternites in *Byrrhus* and *Agrypnus* are contiguous with the laterosternites, similar to those in primitive Buprestidae. PS3 in *Byrrhus* and *Agrypnus*, compared to that in buprestids, is oblong and very long, extending to the base of abdomen. Generally, the abdominal arrangement of these two genera resembles that in *Rhinorhipus* as figured by LAWRENCE (1988).

Cuticularia were not observed in these specimens.

Discussion

The evolutionary trends investigated can be divided into: 1) trends occurring universally throughout Coleoptera; 2) trends specific to Buprestidae, but occurring in parallel in different groups and; 3) trends specific to particular groups within Buprestidae. To distinguish the latter two cases sufficiently is possible only with a complete set of information on the detailed morphology of whole body parts. Nevertheless, I will try to outline several implications.

As already stated by KASAP & CROWSON (1975), definite fusion of the first two tergal (T1+T2) and sternal (S3+S4) segments, with the interface possibly indicated only by a suture, is common to all Buprestidae. The suture between S3 and S4 may be incomplete or absent in many cases. Other characteristics are a tendency to sclerotisation along with metallic coloration of abdominal segments and presence of unique paired pore-like areas (here named cuticularia) on dorsal and ventral sides. Typical for buprestids is also the arrangement of the basal abdominal part, which possesses long lateral sternal projections extending up to the anterior margin of T1. In all representatives from other families examined, lateral sternal projections extend to anterior margin of T2 at the maximum (see previous section). Compare Figs 1, 24 for Buprestidae and Fig. 13 for other families examined. The incurve of T1–T3 seems also to be a specific feature of the buprestoid abdomen.

The occurrence of the character states examined within higher taxa of Buprestidae is given in Table 1. In Buprestidae, a whole range of states (from ABD9 to ABD7) occurs in primary abdominal arrangement. Nevertheless, this character alone is probably of little taxonomic value and expresses only the same level of reorganisation achieved in parallel by the most advanced taxa. Both the principal morphotypes – abdomen with exposed genital terga along with abdomen with overlapped genital terga – were found only within Polycestinae. According the level of abdominal organisation achieved, the two groups can be distinguished in buprestids as follows:

Buprestoid group (Schizopodinae, Julodinae, Polycestinae, Acmaeoderinae, Thrincopyginae, Mastogeniinae, Buprestinae, Chrysobothrinae, ?Galbellinae).	**Agriloid group** (Sphenopterinae, Agrilinae, Trachyinae, Cylindromorphinae)
ABD9, ABD8, ABD8–7, exceptionally ABD7	ABD7
Terga from membranous to heavily sclerotised	Terga heavily sclerotised
Terga overlapped or abutted	Terga abutted
Parasternites contiguous with outer margin of laterosternites or discrete, demarcated from laterosternites by distinct border-line	Parasternites demarcated from laterosternites by distinct border-line
Parasternites from membranous to sclerotised	Parasternites sclerotised
PS3 absent or developed	PS3 developed
Pleural membrane obvious, rarely vestigial	Pleural membrane vestigial or absent
Laterosternites delimited by sternal inflexion, sternal carina, exceptionally by sternal groove	Laterosternites delimited by sternal groove, persisting sometimes only on apex of S7 as shallow impression
Suture between S3 and S4 complete, rarely partly or fully obliterated	Suture between S3 and S4 partly or fully obliterated, exceptionally complete

The Buprestoid group is characterised by plesiomorphic arrangement with prevailing ABD8. Type ABD9 occurs only in Buprestinae in large species of

Catoxanthini, Iridotaenini, Psilopterini, Dicercini and Melanophilini. Intermediate arrangement ABD8–7 was found intermittently in Polycestinae (*Polycesta, Ptosima, Strigoptera, Pseudocastalia*) and Buprestinae (*Scintillatrix, Poecilonota, Kisanthobia*). A most advanced ABD7 was revealed solely in Paratrachyini (*Paratrachys, Sponsor*) and Galbellinae. The position of Galbellinae is indefinite but, although it has an abdominal arrangement of type ABD7 and an advanced organisation of particular abdominal parts, it probably bears no affinity to the Agriloid group due to a lack of a sternal groove delimiting the laterosternites.

The Agriloid group has completed abdominal reorganisation, with fully overlapped genital terga (ABD7). An advanced primary abdominal arrangement in this group is also universally associated with an advanced organisation of particular abdominal parts (see table above), contrary to the Buprestoid group with its high occurrence of primitive character states.

The emargination of T1 (Fig. 7), seems to be a character of serious taxonomic value, probably relating to a reorganisation of the notal part and to the sutural weld of the elytra, known e.g. in Acmaeoderinae. An emarginate T1 was demonstrated in Acmaeoderinae (Figs 15, 16), Thrincopyginae, Mastogeniinae and most of Polycestinae including Paratrachyini (Figs 17, 19, 21), which may indicate its relationship. An affinity of Mastogeniinae to this group is also supported by a crenulate hind margin of the pronotum (visible after removal of elytra), characteristic for Acmaeoderinae and several Polycestinae (*Ptosima, Sponsor, Paratrachys*). Despite small body size, the primary abdominal arrangement of Mastogeniinae is primitive (ABD8) and the tergal side is feebly sclerotised, contrary to similarly-sized *Sponsor* and *Paratrachys* with ABD7 and heavily sclerotised terga. Besides the emargination of T1, the most obvious apomorphy which Mastogeniinae shares with *Sponsor* and *Paratrachys* is the obliteration of the suture between S3 and S4. Paratrachyini exhibit, within the Polycestinae, the most advanced organisation, with no affinity to agriloid groups (absence of sternal groove, simple sterno-elytral fitting).

Schizopodinae and Julodinae exhibit the most primitive constitution of the abdomen (along with several large taxa from Buprestinae), except for the trend towards the obliteration of suture between S3 and S4 in Schizopodinae and the presence of sternal carina in Julodinae.

Representatives of the subfamily Buprestinae are characterised by the broadest range of extremes in abdominal organisation, from the most primitive to very derived. Generally, the highest quantity of plesiomorphic characters were found in Buprestini, Catoxanthini, Iridotaenini, Dicercini and Psilopterini, where most of the features were revealed at plesiomorphic extremes, but often accompanied by several advanced character states, though of little importance, such as more sclerotised terga and presence of sternal carina. Advanced forms within Buprestinae, together with Chrysobothrinae, are characterised mainly by an increased sclerotisation of the terga and parasternites, sometimes accompanied by a trend towards abdominal reorganisation from ABD8 to ABD7. The suture between S3 and S4 is, however, still complete. Very interesting is the presence of a sternal groove in *Coomaniella* and *Kisanthobia* (Fig. 27), which resembles

that in Sphenopterinae, Agrilinae, Trachyinae and Cylindromorphinae. Moreover, the separation of terga into tergites and laterotergites in *Kisanthobia* is similar to that in Agrilinae, Trachyinae and Cylindromorphinae.

The most important taxonomic characters in the abdomen of Buprestidae seem to be the form of delimitation of the laterosternites and the type of sterno-elytral fitting. The correlation of these two characters and their occurrence in subfamilies is displayed in Table 3. The presence of a sternal groove variable in length, but always bordering apex of S7, is specific for subfamilies Agrilinae, Trachyinae, Cylindromorphinae and Sphenopterinae (Figs 33, 35–37, 42, 43, 48, 53). However, in some Trachyinae and all Cylindromorphinae, the sternal groove is already rudimentary and preserved in form of pairs of ostia (*Paracylindromorphus* Figs 56–58) or as a groove or an impression on the apical part of S7 (*Cylindromorphus* Figs 60, 61, *Aphanisticus* Figs 54, 55). Also Interesting are great differences in the degree of preservation of the sternal groove between the closely related genera *Paracylindromorphus* (Figs 8c, 56–58) and *Cylindromorphus* (Figs 8e, 60–61), as well as between *Aphanisticus* (Figs 8e, 54, 55) and *Endelus* (Figs 8b, 53). In the remaining subfamilies, the sternal groove was found solely in *Kisanthobia* (Figs 8b, 27) and *Coomaniella*. In the *Coomaniella*, however, the sternal groove does not border the apex of S7 (Fig. 8a). A close affinity among Agrilinae, Trachyinae, Cylindromorphinae is generally accepted, but the number of characters they share with Sphenopterinae is surprising. As well as the presence of a sternal groove, there is the ABD7 arrangement, the heavily sclerotised, abutted terga, sclerotised, well-demarcated five parasternites with obliterated pleural membrane, and a tendency to the obliteration of the suture between S3 and S4. In contrast to the Agrilinae, Trachyinae and Cylindromorphinae, in Sphenopterinae the sulcate sterno-elytral fitting was not found, nor was the presence of laterotergites established. Affinity of Sphenopterinae to the agriloid line is uncertain and should be supported by additional evidence. A close affinity of Agrilinae, Trachyinae and Cylindromorphinae also confirms the sulcate sterno-elytral fitting (Figs 9d–f) found solely in these subfamilies, although in several small forms (*Aphanisticus*, *Cylindromorphus*) (Fig. 9f) it is vestigial and indicates only basally; further there is a trend towards obliteration of the cuticularia (Table 2), tergal ones from an apical and basal direction, sternal ones apically.

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SCHAEFER L. 1949: Les Buprestides de France. Tableaux analytiques des Coléoptères de la faune franco-rhénane. France, Rhénane, Belgique, Hollande, Valais, Corse. Famille LVI. *Miscellanea Entomologica*, Supplément: 511 pp.

TOYAMA M. 1986: The buprestid genus Chalcophorella Kerremans and its related genera (Coleoptera, Buprestidae). Entomological Papers presented to Y. Kurosawa on the occasion of his retirement, March 20, 1986, p. 188–193.

TOYAMA M. 1987: The systematic positions of some buprestid genera (Coleoptera, Buprestidae). *Elytra* **15(1–2):** 1–11.
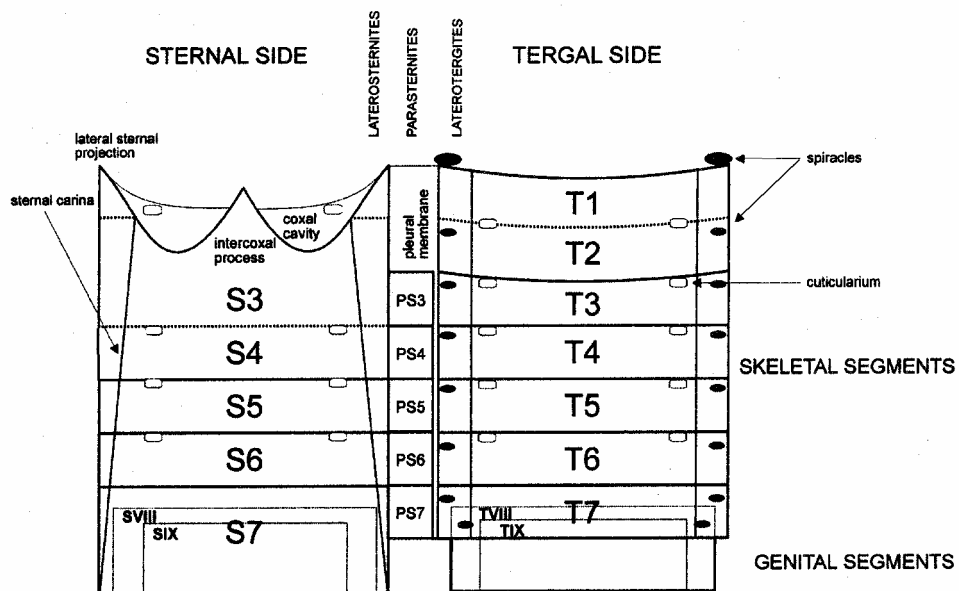
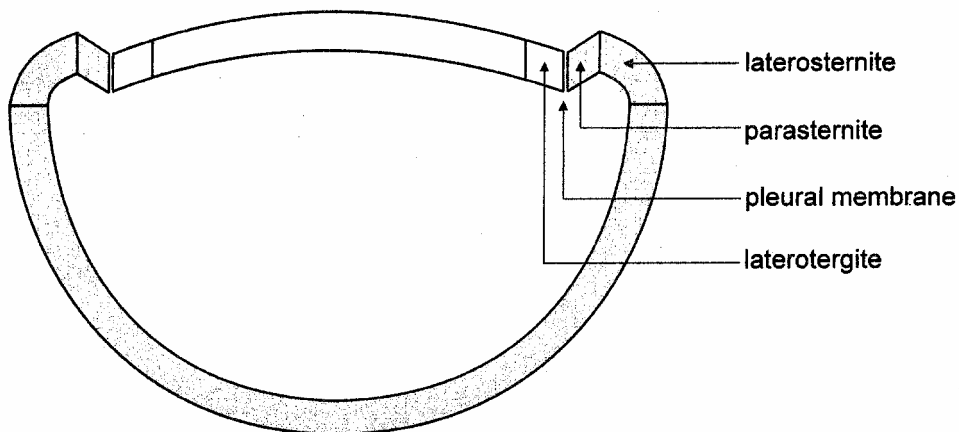**Fig. 1.** Generalised diagram of buprestoid abdomen. Abdomen arranged "open-book"-fashion.

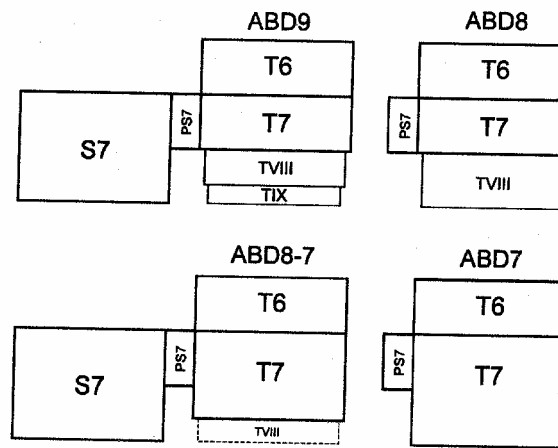**Fig. 2.** Generalised diagram of buprestoid abdomen (cross section).
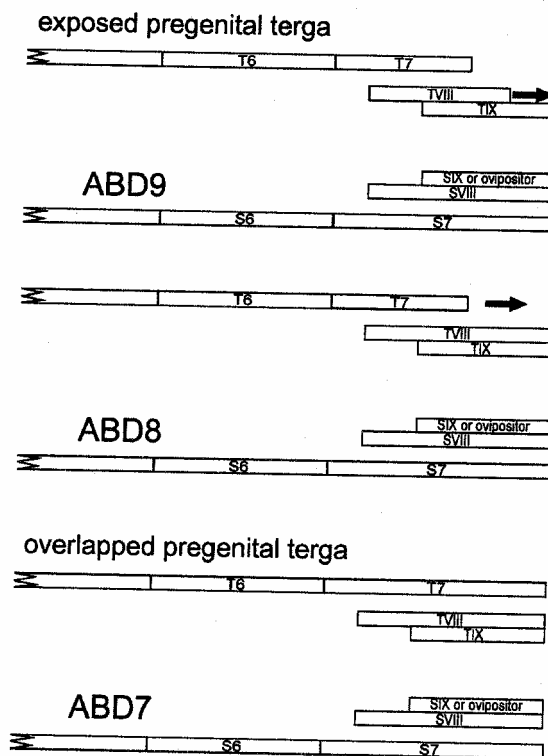
Fig. 3. Arrangement of genital terga.

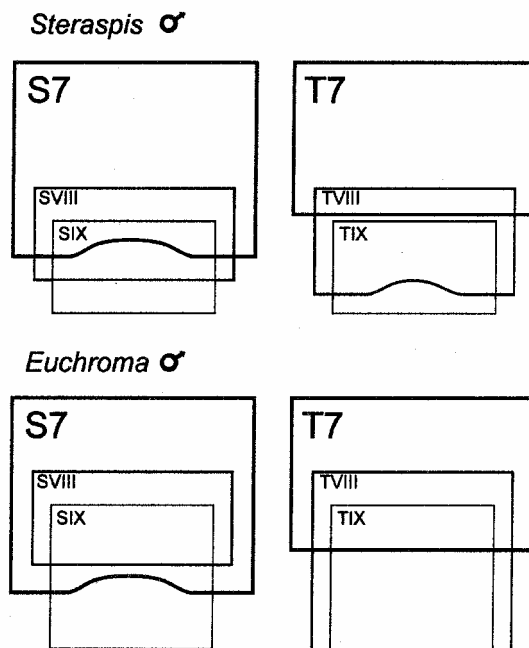**Fig. 4.** Postulated scheme of evolution of the buprestoid abdomen.

Steraspis ♂

S7   T7

SVIII   TVIII

SIX   TIX

Euchroma ♂

S7   T7

SVIII   TVIII

SIX   TIX

Fig. 5. Sexual modifications in abdominal arrangement of genital segments.

Schizopus ♂

S7

SVIII   SIX

Glyptoscelimorpha ♂

S7 + SVIII   SIX

Fig. 6. Sexual modifications in abdominal arrangement of genital segments.

T1 incurved

T1 emarginate

pterothorax

postnotum

T1+T2

T3

T4

spiracle
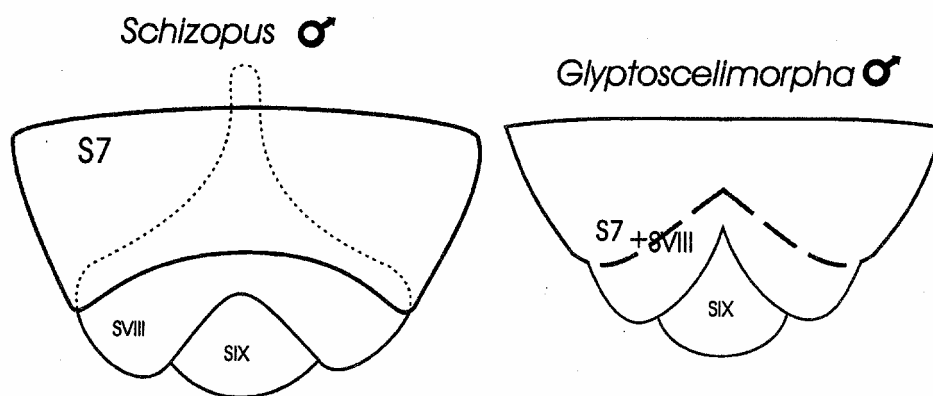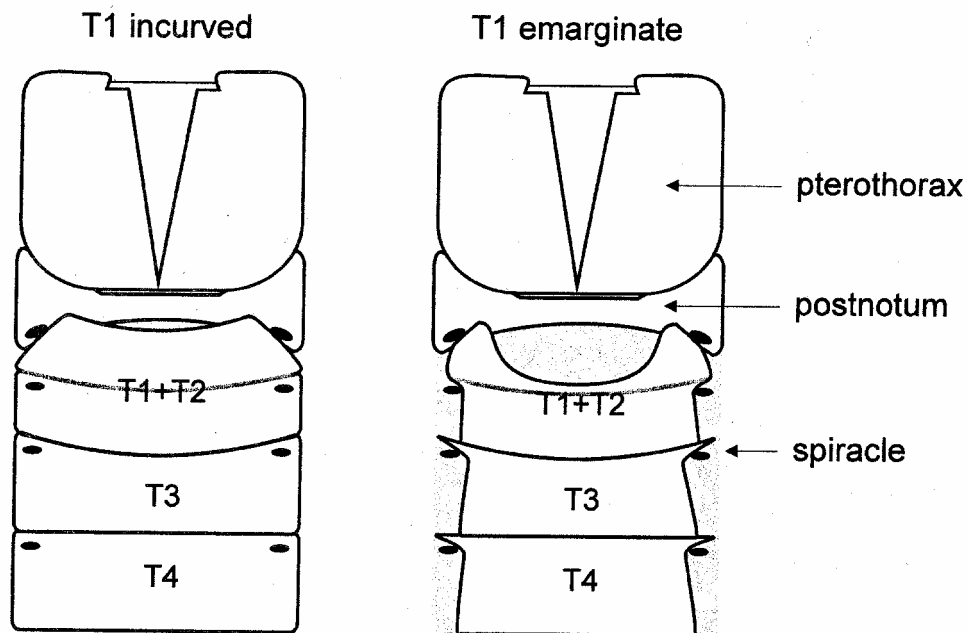
Fig. 7. Form of first two fused terga.

sternal groove

not bordering S7

bordering S7

a)   b)   c)   d)   e)
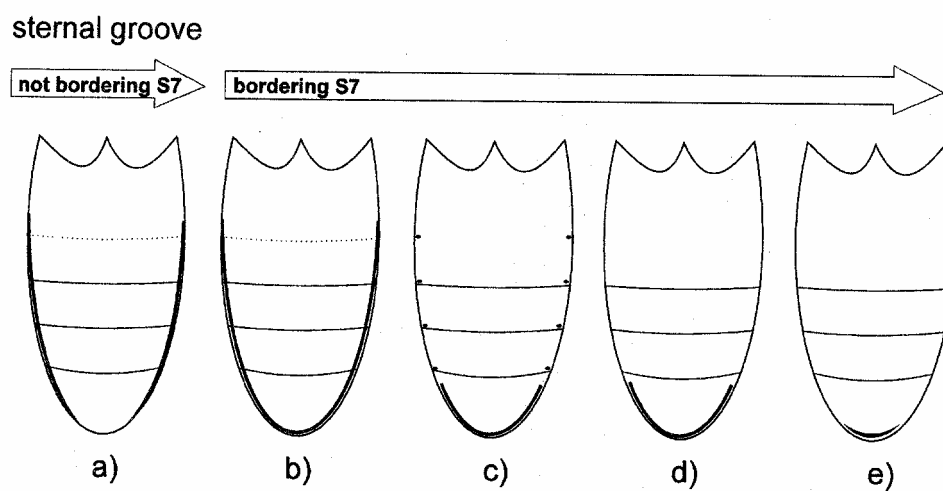
Fig. 8. Form of sternal groove: a) not bordering apex of S7; b) bordering apex of S7, in maximum development extending proximally up to suture between S3 and S4; c) bordering apex of S7, in proximal part preserved in form of ostia; d) bordering apex of S7, proximally obliterated; e) bordering apex of S7, preserved in form of impression on apex of S7.

sterno-elytral fitting
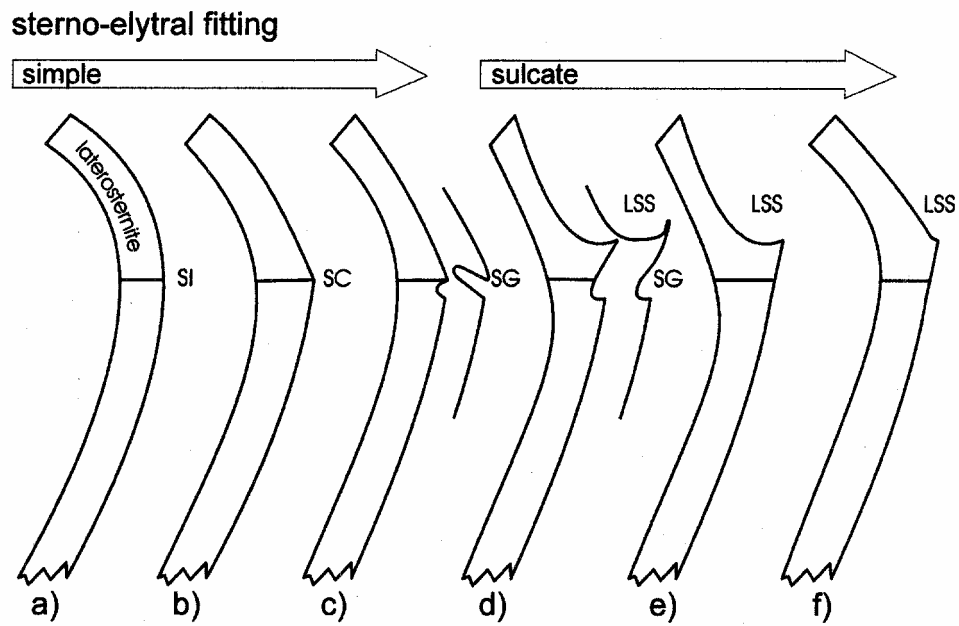
Fig. 9. Delimitation of laterosternites and forms of sterno-elytral fitting.
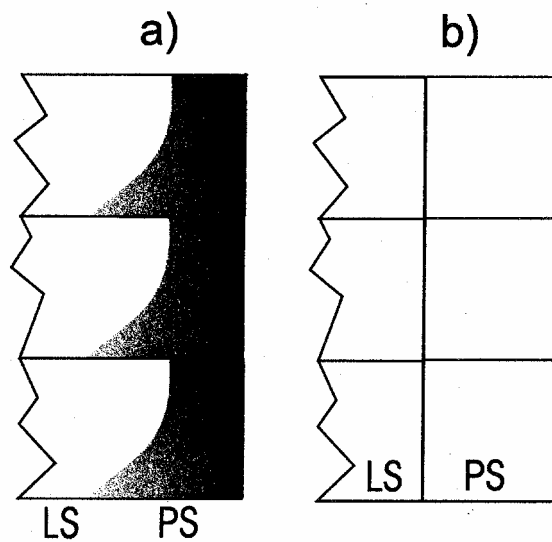
Fig. 10. Differentiation of parasternites: a) contiguous with outer margins of laterosternites, b) discrete, demarcated from outer margins of laterosternites by distinct structural borderline.
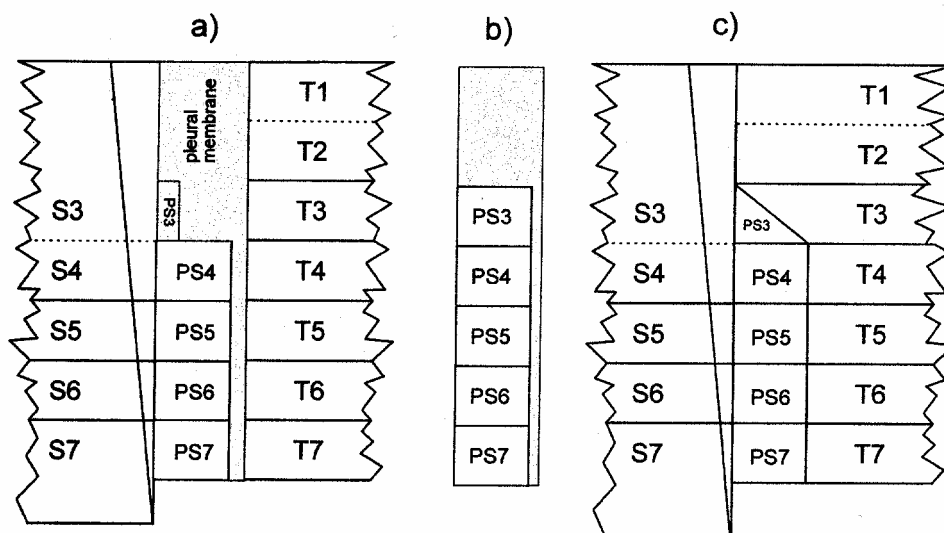
Fig. 11. Arrangement of parasternites: a) 4 subtriangular or subrectangular, membranous or feebly sclerotised parasternites (PS4–PS7), PS3 obscure or absent, pleural membrane obvious; b) 5 feebly sclerotised parasternites (PS3–PS7), PS3 subrectangular, pleural membrane at least proximally obvious; c) 5 sclerotised, discrete parasternites (PS3–PS7), PS3 subtriangular, pleural membrane vestigial or absent.
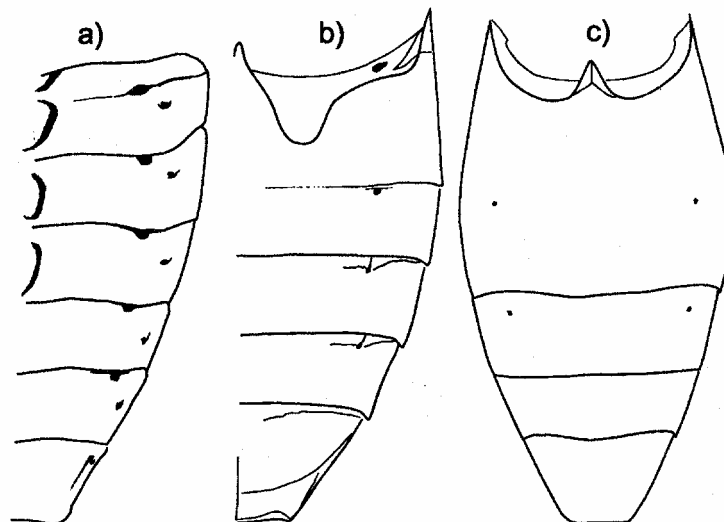
Fig. 12. Distribution of cuticularia: *Chrysobothris affinis* a) tergal side; b) sternal side; c) *Agrilus viridis* sternal side.
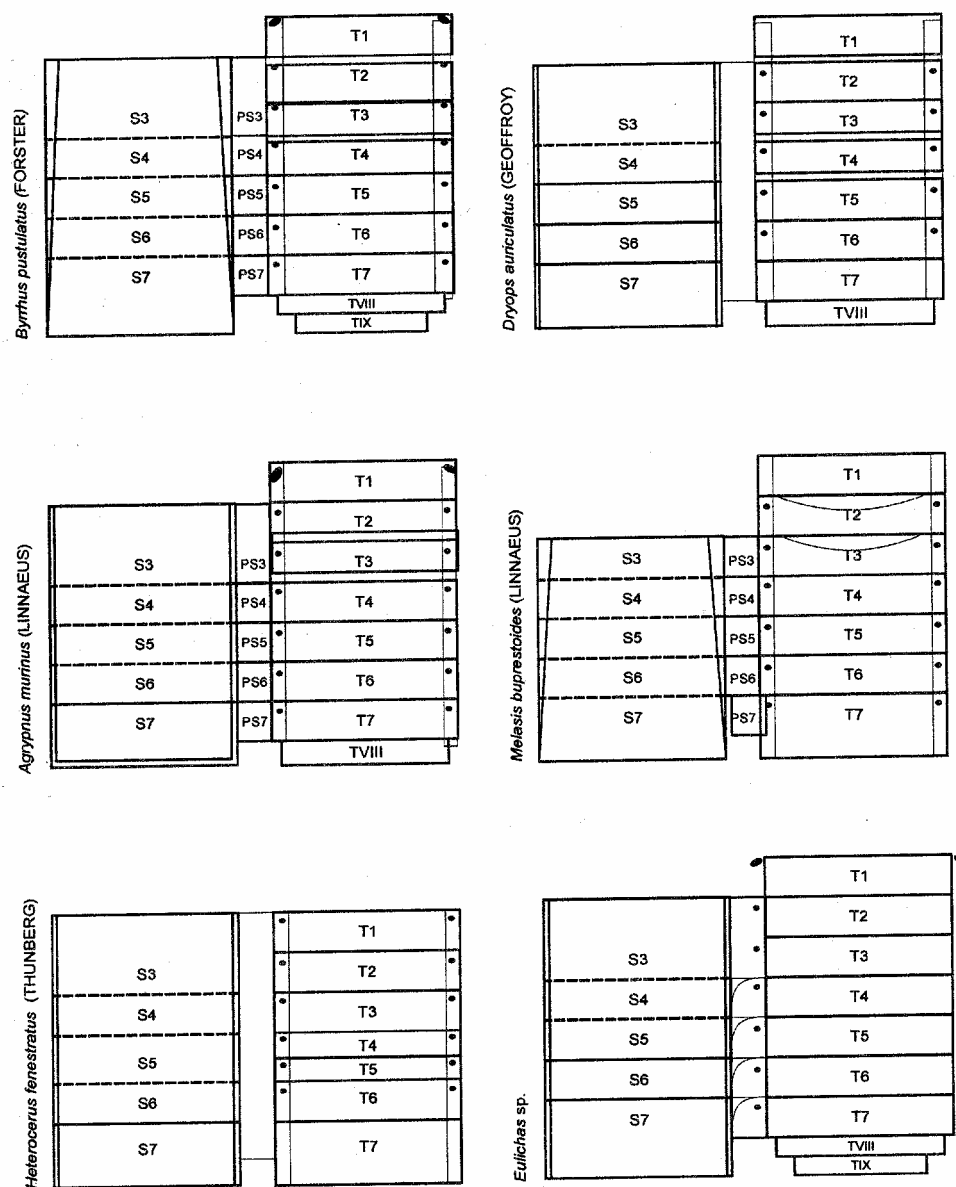
Fig. 13. Abdominal arrangement of representatives from families Byrrhidae, Dryopidae, Elateridae, Eucnemidae and Heteroceridae.
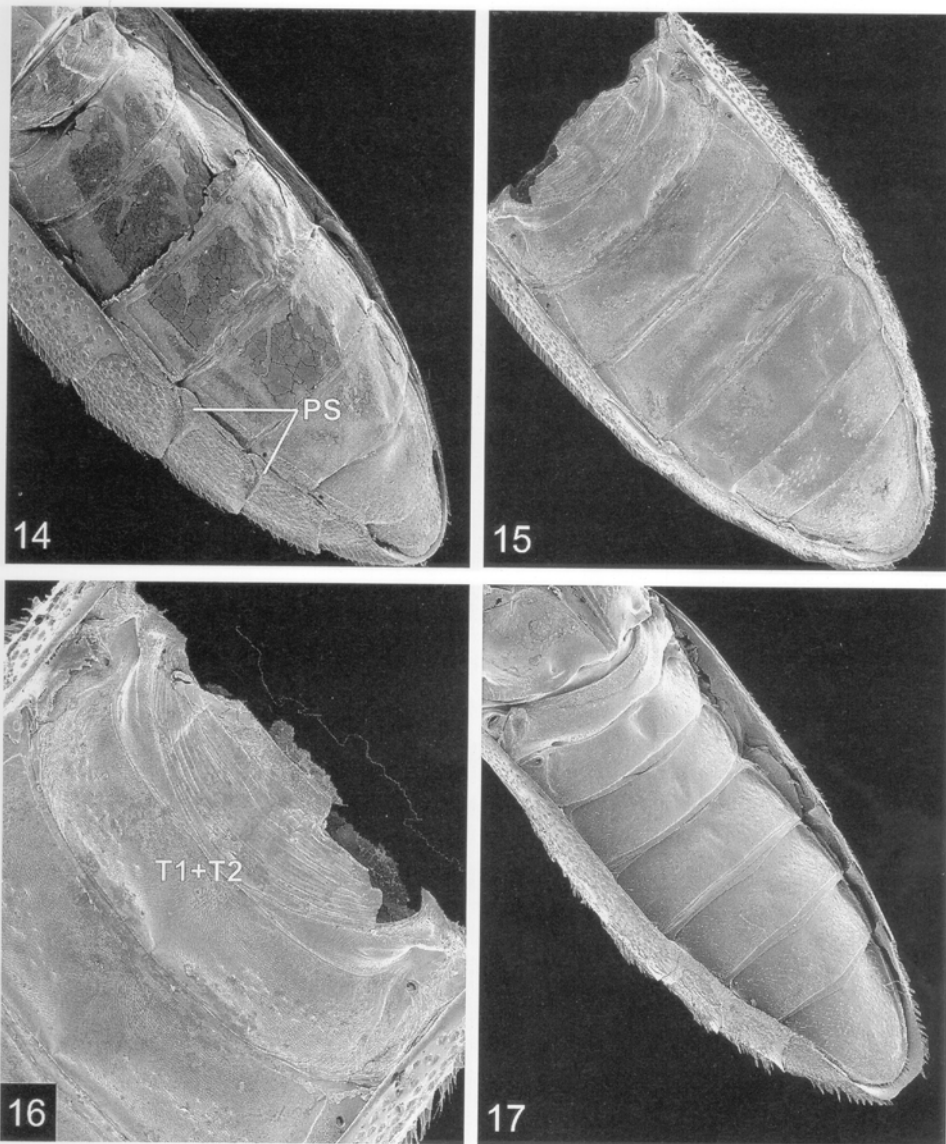
Figs 14–17. *Acmaeodera brevipes*: 14) abdomen dorso-laterally; 15) abdomen dorsally; 16) abdominal base, dorsally. *Ptosima flavoguttata*: 17) abdomen dorso-laterally.
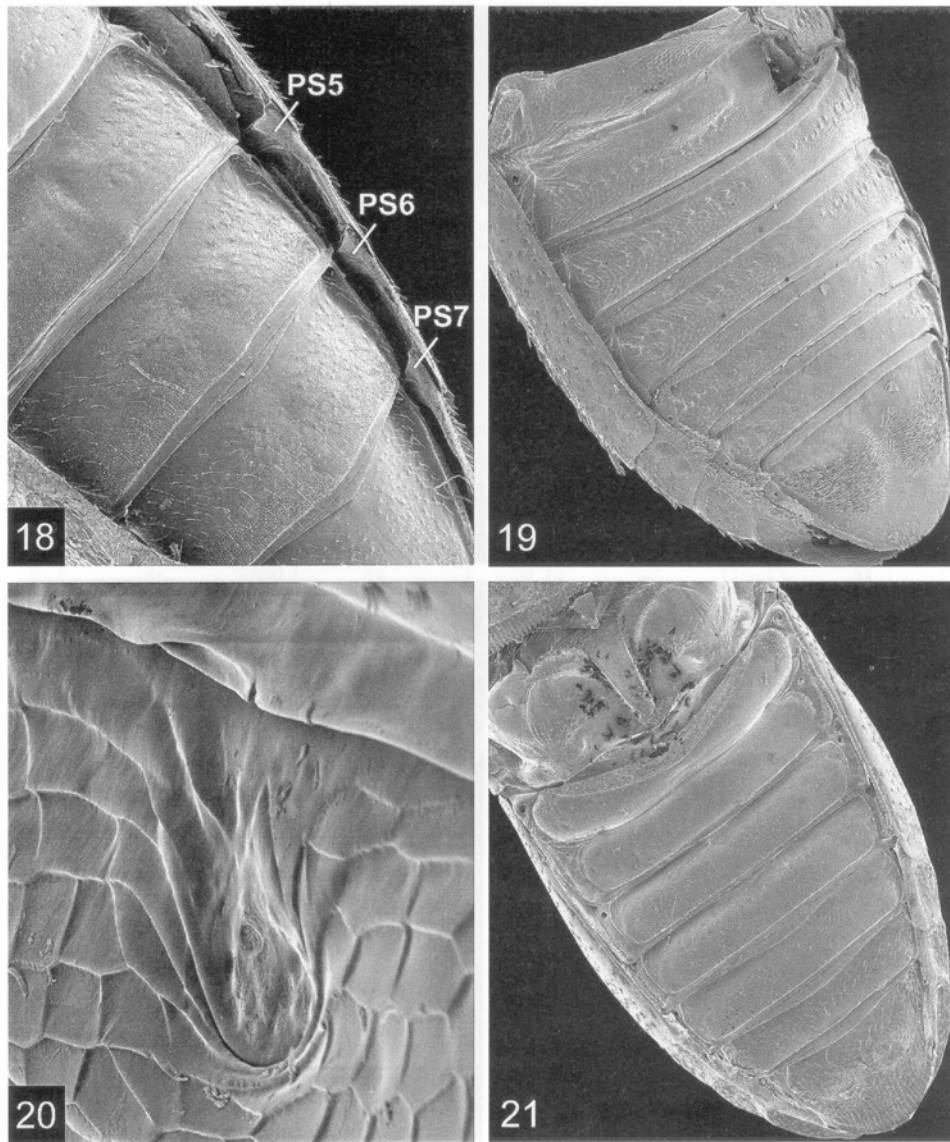
Figs 18–21. *Ptosima flavoguttata*: 18) abdomen dorso-laterally, detail. *Paratrachys* sp.: 19) abdomen dorso-laterally; 20) cuticularium on T4. *Sponsor* sp.: 21) abdomen dorsally.
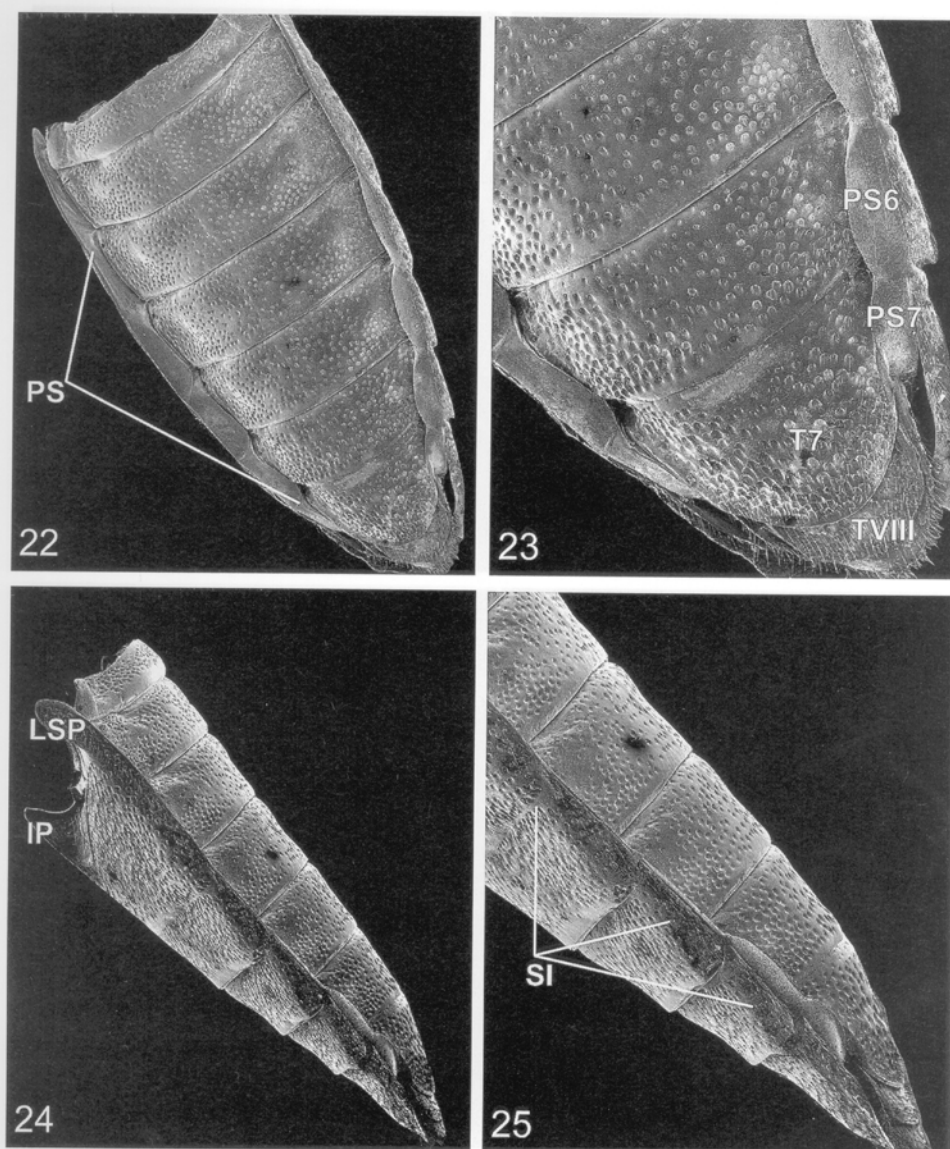
Figs 22–25. *Buprestis octoguttata*: 22) abdomen dorsally; 23) abdominal apex, dorsally; 24) abdomen laterally; 25) abdomen laterally, detail.
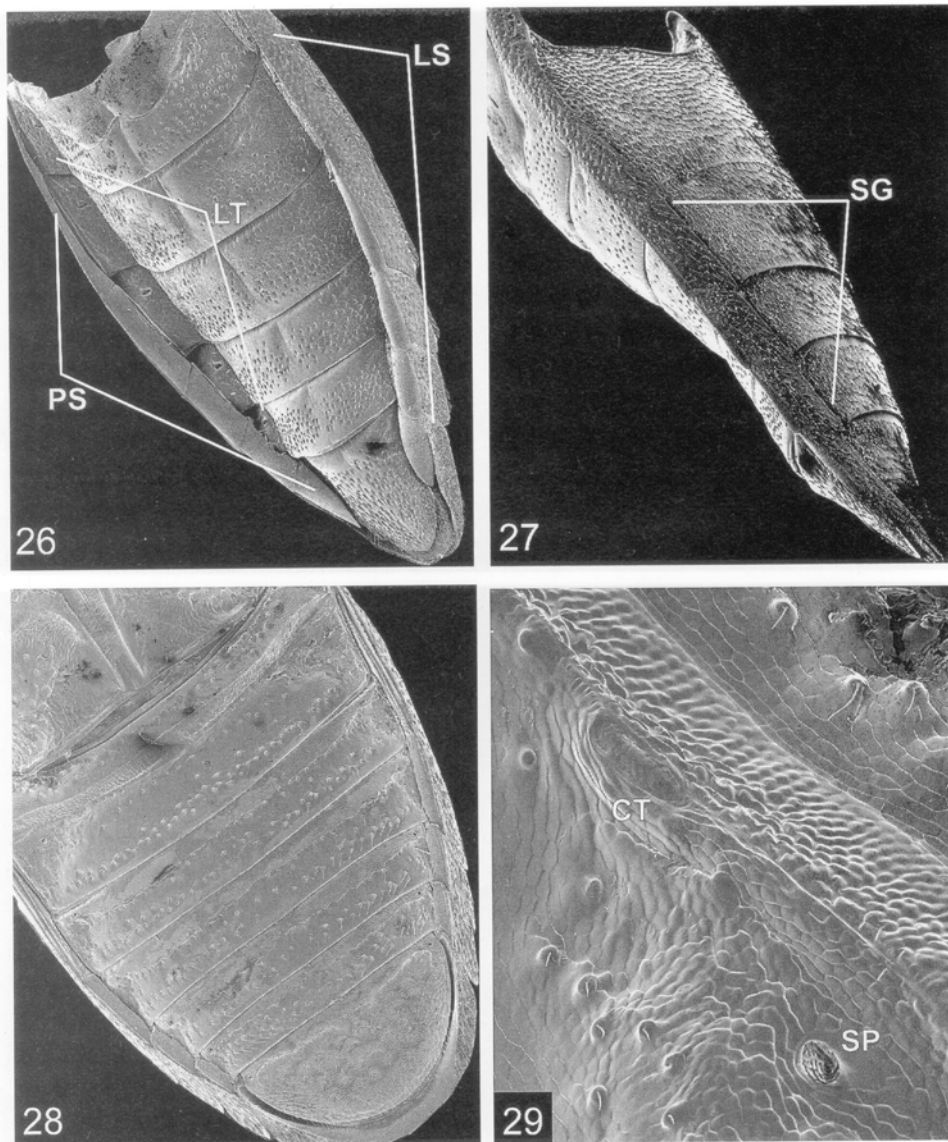
Figs 26–29. *Kisathobia ariasi*: 26) abdomen dorsally; 27) abdomen laterally. *Galbella* sp.: 28) abdomen dorsally; 29) spiracle and cuticularium on T2.
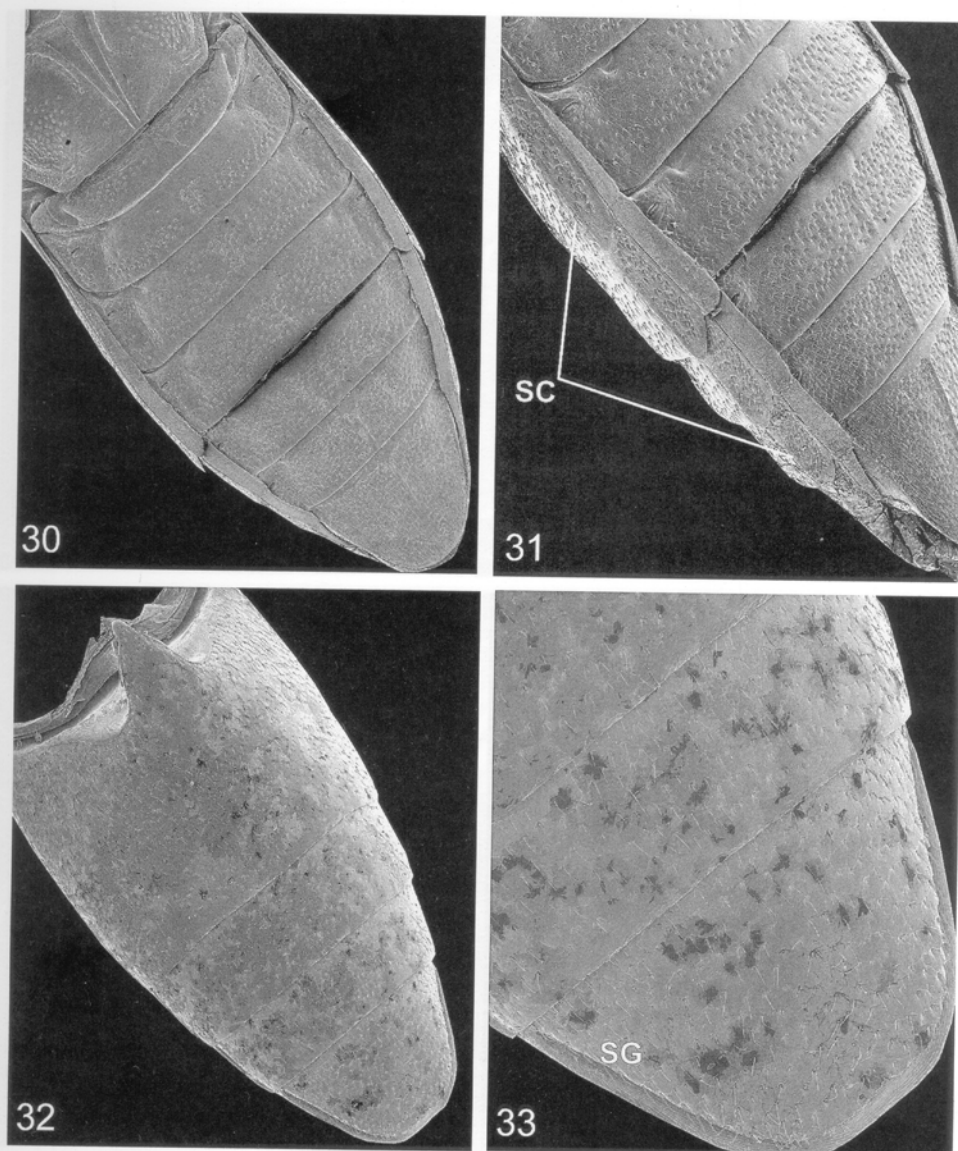
Figs 30–33. *Sphenoptera substriata*: 30) abdomen dorsally; 31) abdomen dorso-laterally; 32) abdomen ventrally; 33) abdominal apex, ventrally.
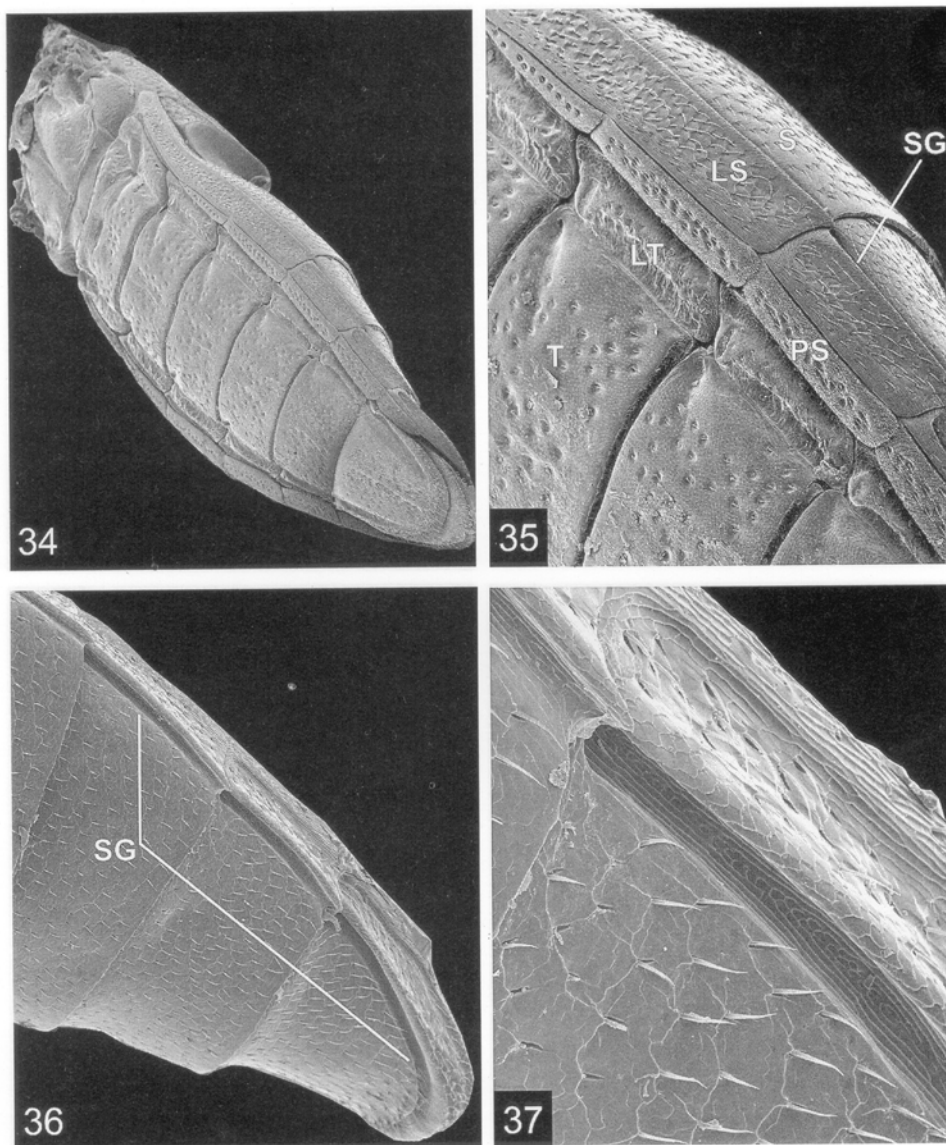
Figs 34–37. *Agrilus viridis*: 34) abdomen postero-dorso-laterally; 35) abdomen dorso-laterally, detail; 36) abdominal apex, laterally; 37) sternal groove.
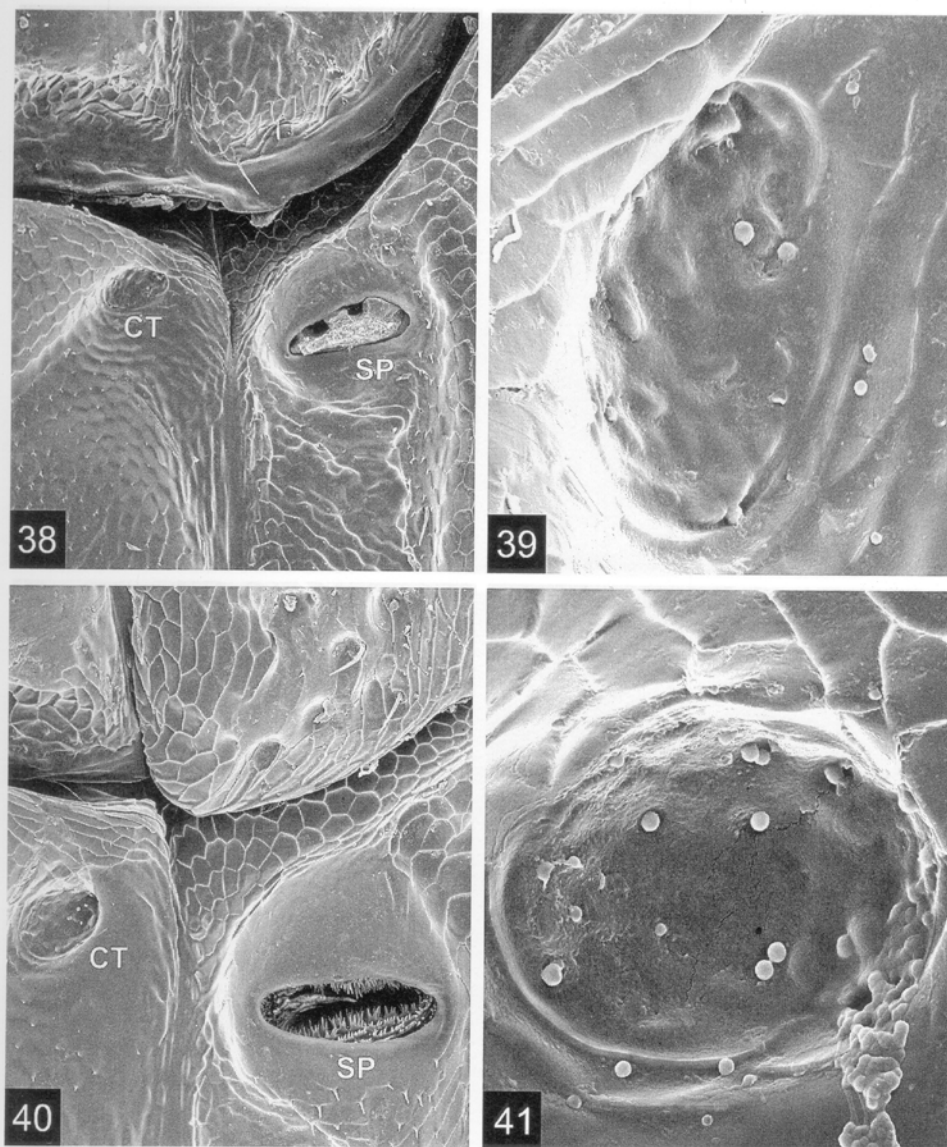
Figs 38–41. *Agrilus viridis*: 38) spiracle and cuticularium on T3; 39) cuticularium on T3; 40) spiracle and cuticularium on T4; 41) cuticularium on T5.
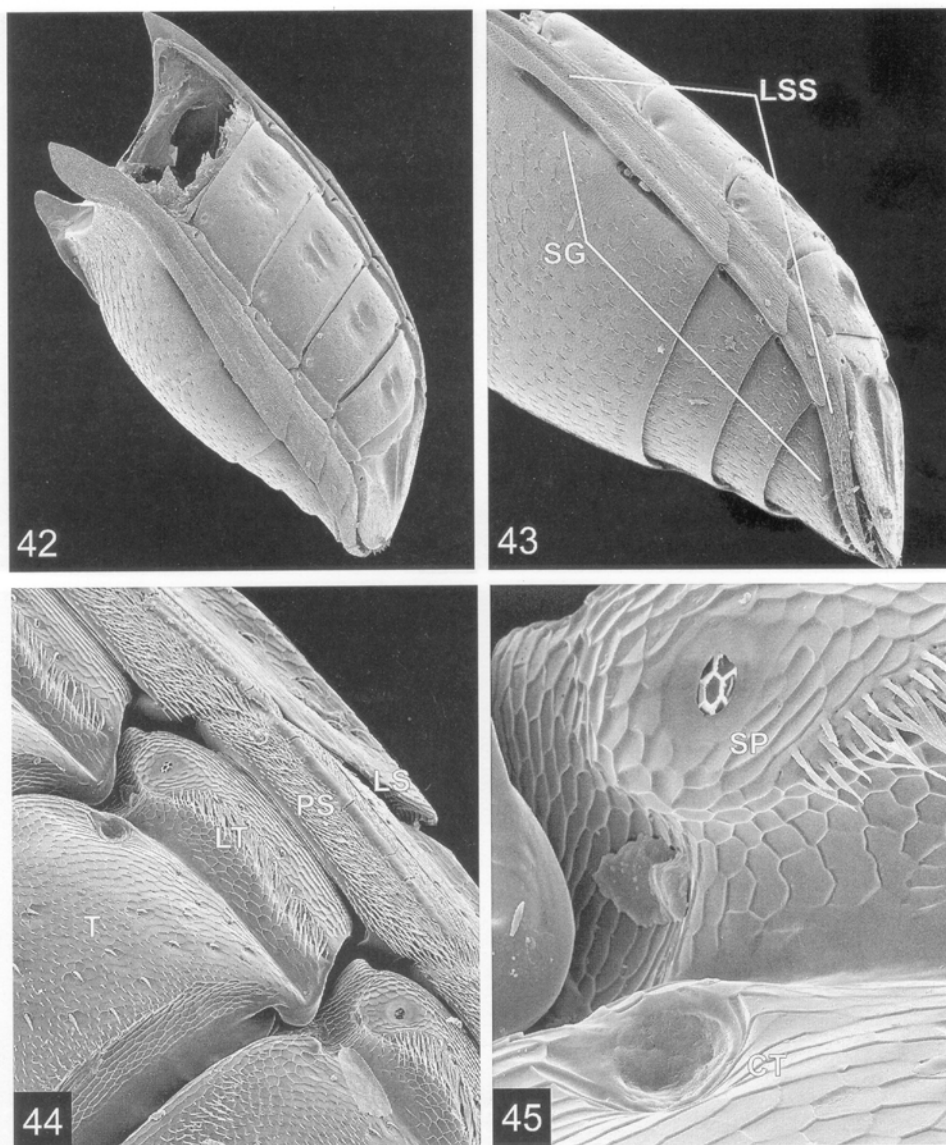
Figs 42–45. *Paragrilus rugatulus*: 42) abdomen dorso-laterally, T1 missing; 43) abdomen laterally; 44) lateral abdominal portions; 45) cuticularium and spiracle on T3.
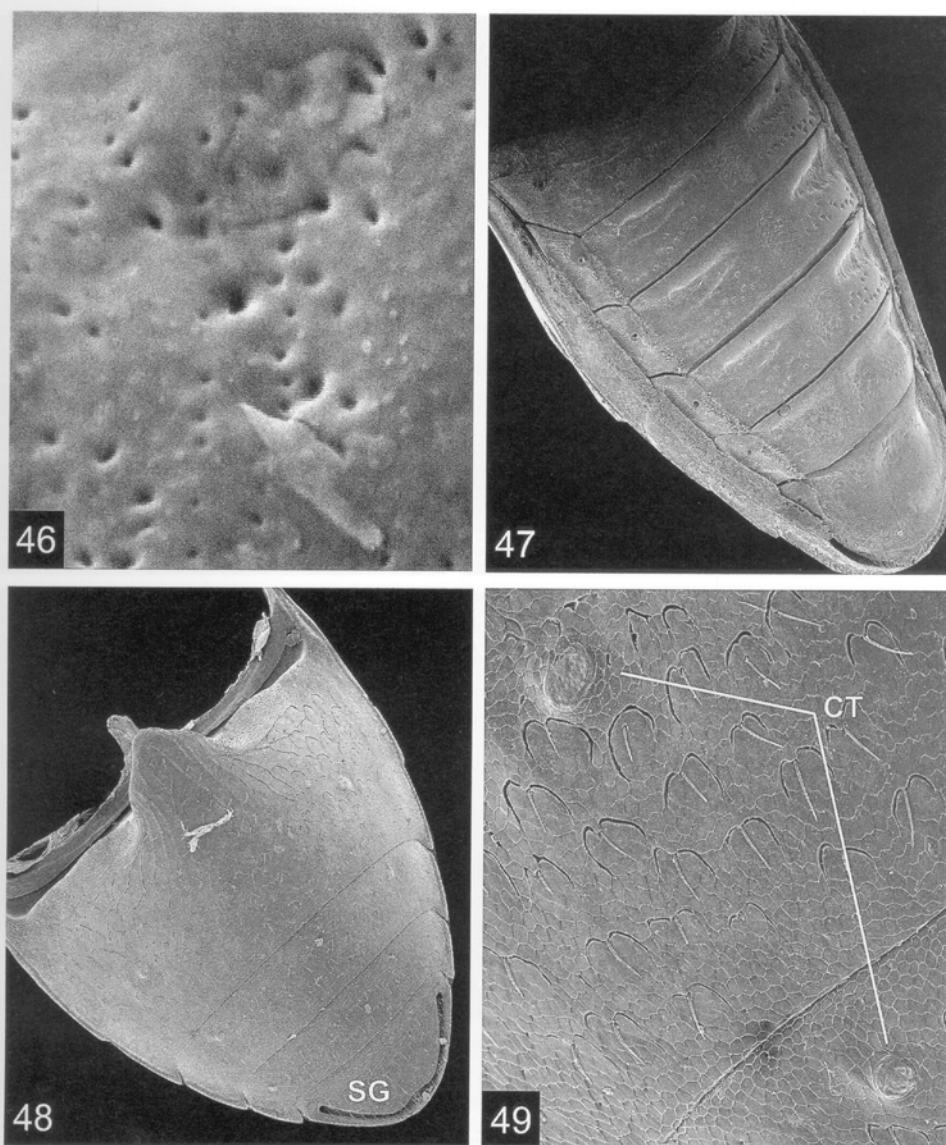
Figs 46–49. *Paragrilus rugatulus*: 46) surface detail of cuticularium on T3. *Trachys minutus*: 47) abdomen dorso-laterally. *Habroloma geranii*: 48) abdomen ventrally; 49) sternal cuticularia on S4 and S5.
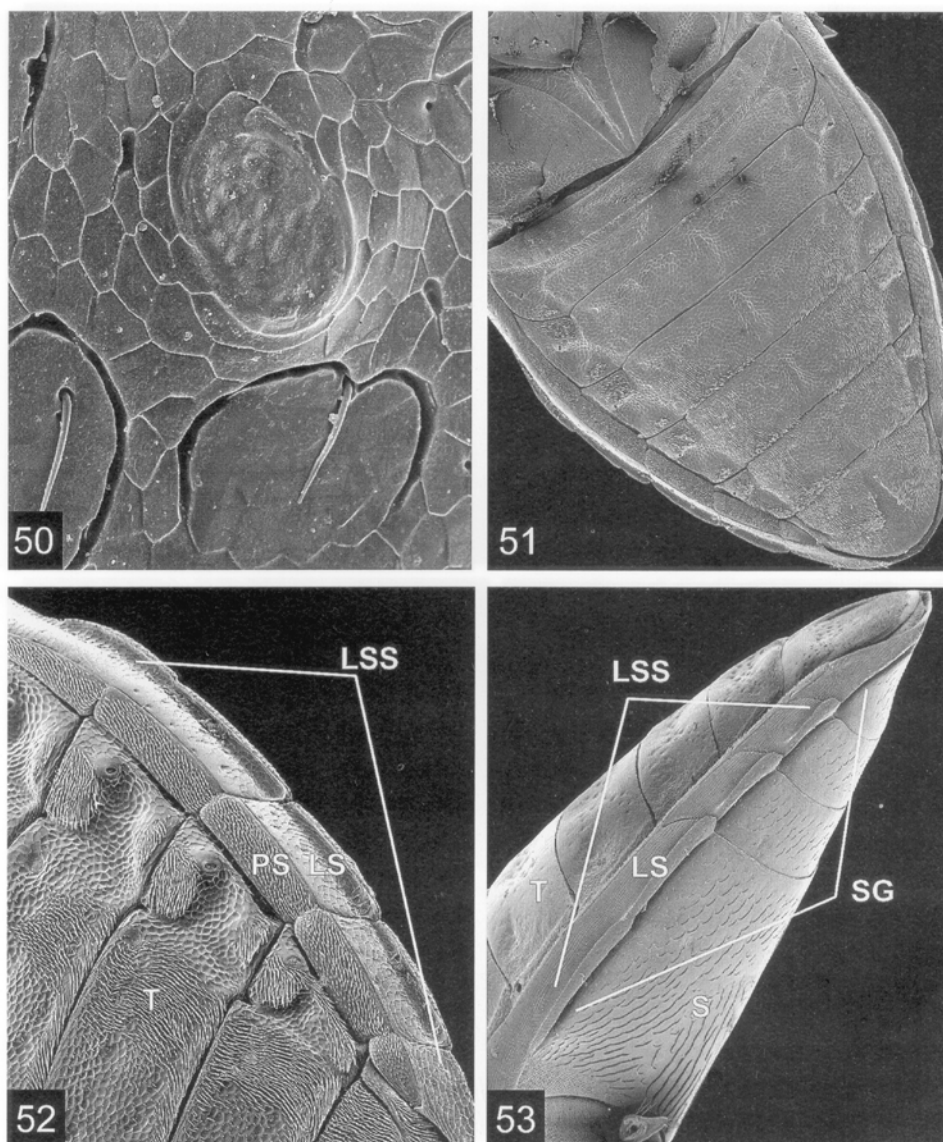
Figs 50–53. *Habroloma geranii*: 50) sternal cuticularium on S4. *Pachyschelus secendens*: 51) abdomen dorsally; 52) lateral abdominal portions. *Endelus* sp.: 53) abdomen laterally.
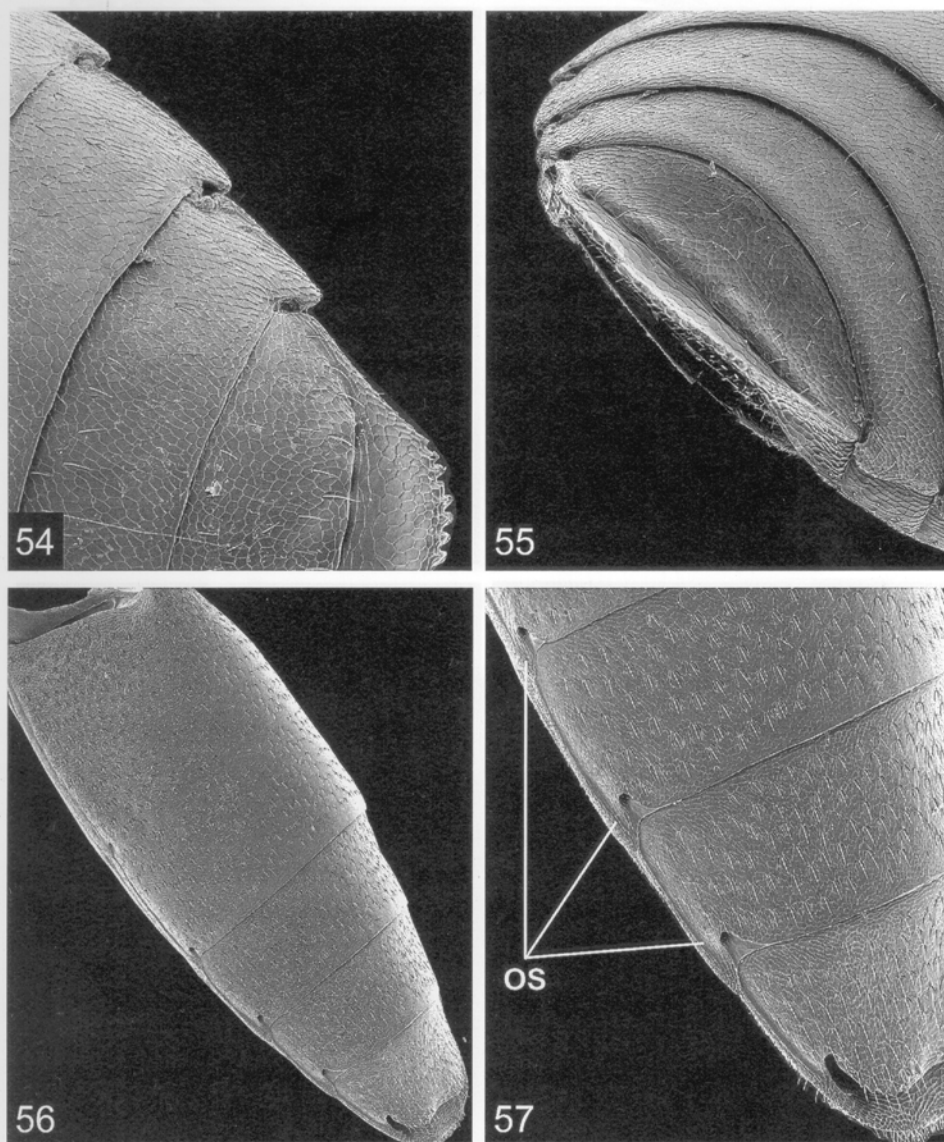
Figs 54–57. *Aphanisticus pygmaeus*: 54) abdominal apex, ventrally; 55) abdominal apex, postero-ventrally. *Paracylindromorphus subuliformis*: 56) abdomen ventro-laterally; 57) abdominal apex, ventro-laterally.
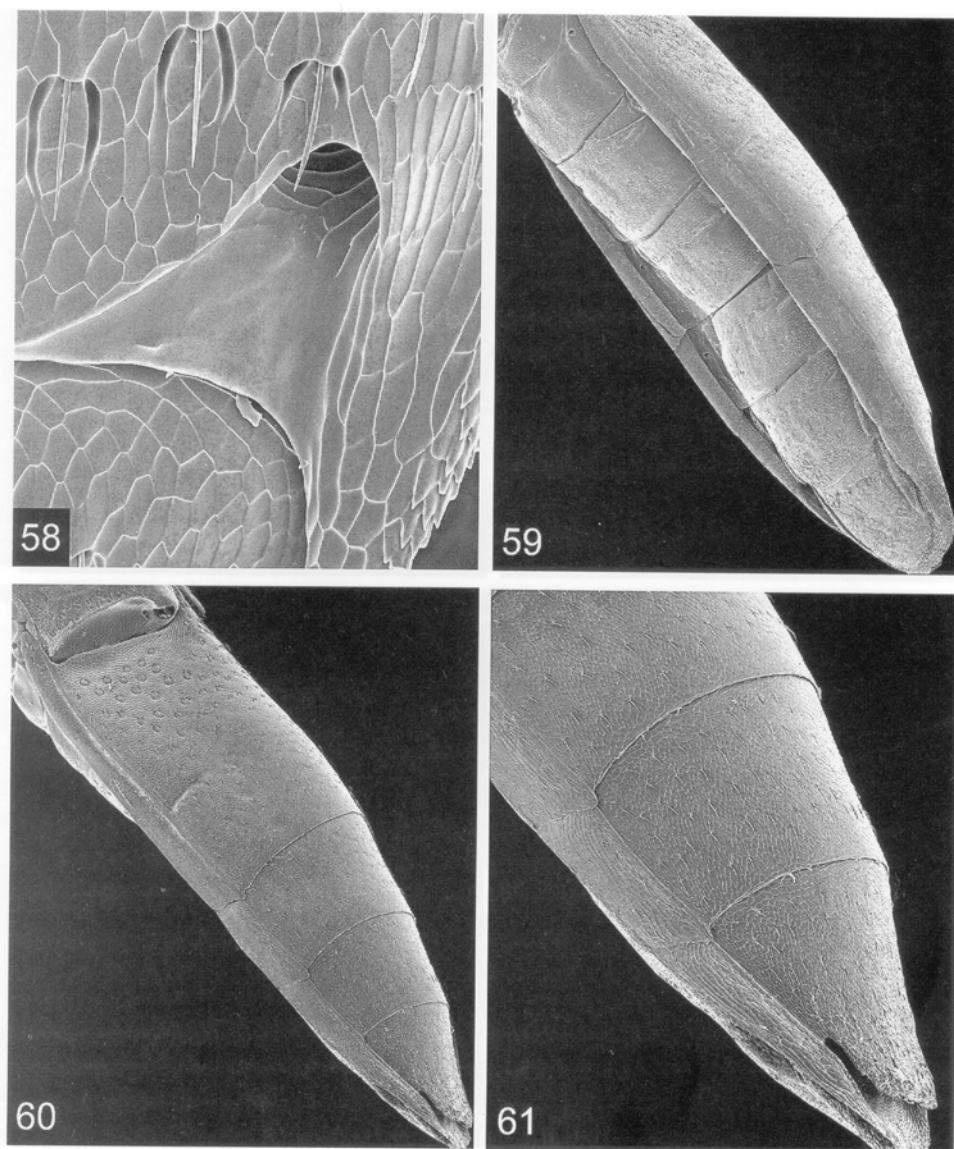
Figs 58–61. *Paracylindromorphus subuliformis*: 58) sternal ostium on S6. *Cylindromorphus fillum*: 59) abdomen dorso-laterally; 60) abdomen laterally; 61) abdominal apex, laterally.
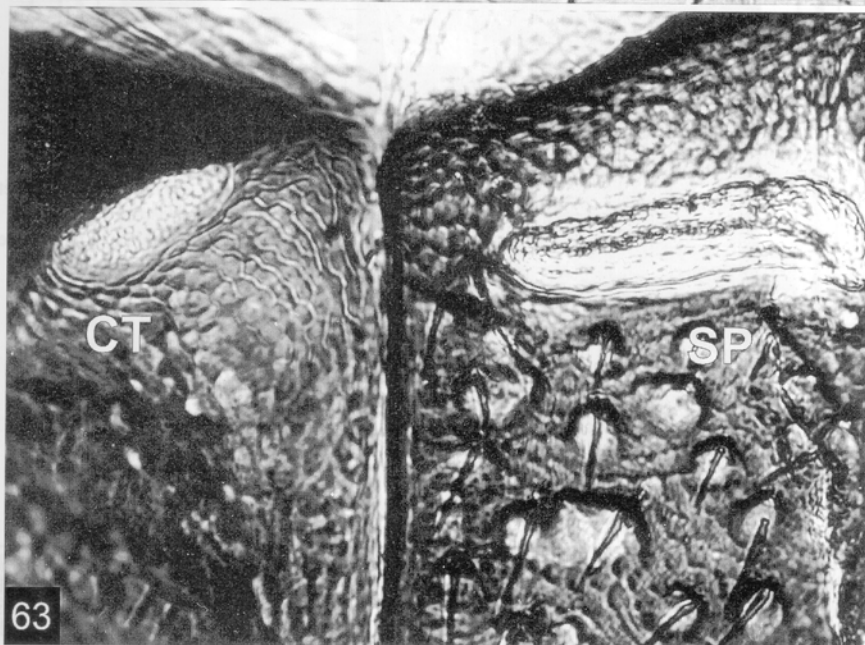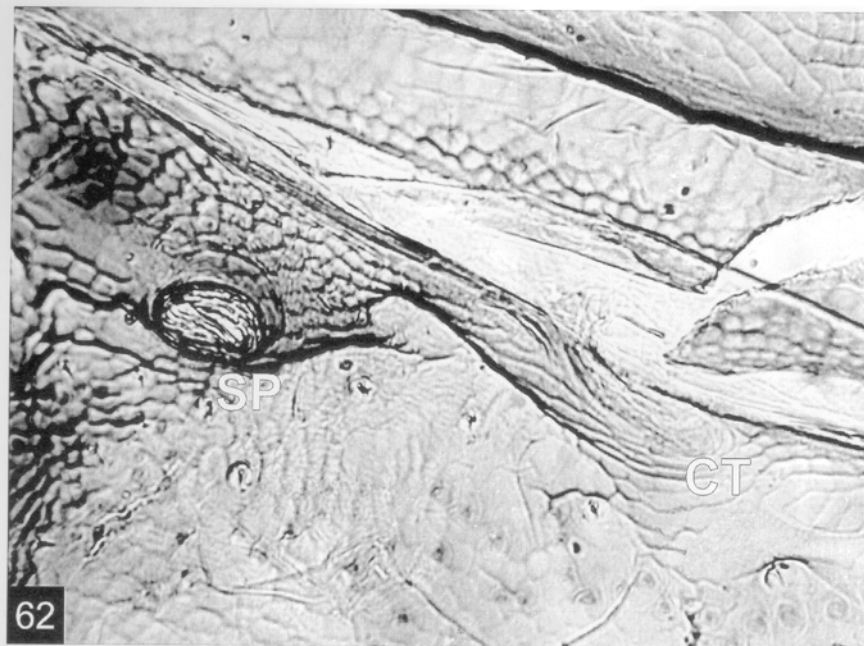
Figs 62–63. *Galbella* sp.: 62) spiracle and cuticularium on T2, (transmitted light microscope). *Agrilus viridis*: 63) spiracle and cuticularium on T3 (transmitted light microscope).
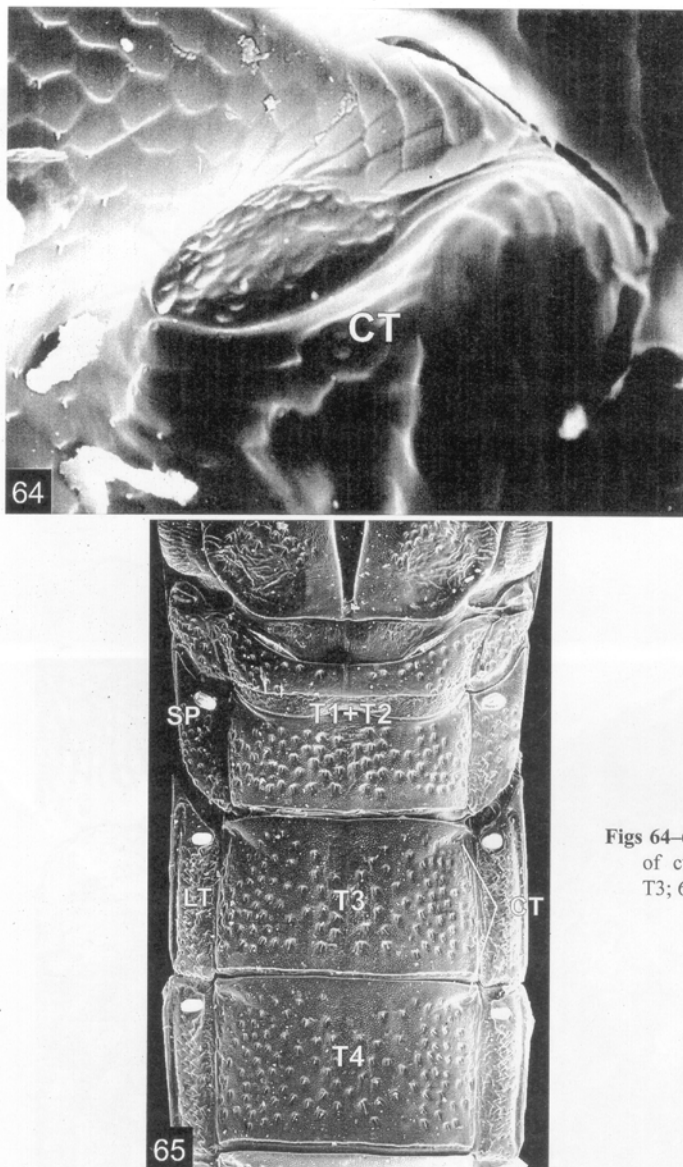
Figs 64–65. *Agrilus viridis*: 64) detail of cuticularium with siphon on T3; 65) basal part of tergal side.

Table 1 (page 39). Character occurrence of states within higher taxa of Buprestidae. Explanation of character states examined. Character states are ordered from plesiomorphic to apomorphic. **Abdominal arrangement**: a) ABD9; b) ABD8; c) ABD8–7; d) ABD7. **Tergal consistency**: a) terga membranous or feebly sclerotised, with transparent sides coinciding with pleural membrane, spiracles located in transparent portions or closely adjoined to them; b) terga feebly sclerotised without transparent membranous sides, spiracles located in tergal sides; c) terga heavily sclerotised, spiracles placed in tergal sides. **Laterotergites**: a) absent; b) indicated structurally by ridge, elevation or convexity; c) present, terga flanked by independent laterotergites bearing spiracles. **Tergal interlink**: a) terga overlapped; b) abutted, connate. **T1 form**: a) incurved, with subparallel anterior and posterior margins; b) anteriorly deeply emarginate, almost divided medially. **Sterno-elytral fitting**: a) simple; b) sulcate.

Table 1 (continued). Laterosternite delimitation: a) by inflexion; b) by sternal carina; c) by sternal groove not bordering apex of S7; d) by sternal groove bordering apex of S7. **Degree of connation between S3 and S4**: a) suture complete; b) suture incomplete, obliterated medially or laterally; c) suture completely obliterated, sometimes only structurally indicated. **Parasternite arrangement**: a) 4 subtriangular or subrectangular, membranous or feebly sclerotised parasternites (PS4–PS7), PS3 obscure or absent, pleural membrane obvious; b) 5 feeble sclerotised parasternites (PS3–PS7), PS3 subrectangular, pleural membrane at least proximally obvious; c) 5 strongly sclerotised, discrete parasternites (PS3–PS7), PS3 subtriangular, pleural membrane vestigial or absent. **Parasternite differentiation**: a) contiguous with laterosternites; b) discrete, structurally well-demarcated from outer margins of laterosternites.

		TERGA					STERNA			metacoxal cavities
		T2	T3	T4	T5	T6	S4	S5	S6	
Schizopodinae	Glyptoscelimorpha marmorata HORN	?	?	?	?	?	+	+		+
	Schizopus laetus LE CONTE	+					+	+		?
Julodinae	Julodis onopordi (F.)	+	(+)	(+)	(+)	(+)	+	(+)	(+)	-
	Sternocera pulchra (WATERH.)	+	+	+			+	(+)	(+)	?
Polycestinae	Polycesta porcata (F.)	+	(+)	(+)	(+)		+	(+)	(+)	+
	Ptosima flavoguttata (ILL.)	+	+	+	+	+	+	+	+	+
	Strigoptera obsoleta (CHEVR.)	+	+	+	+	+	+	(+)		+
	Tyndaris planata (LAP. & GORY)	+	?	?	?		+	(+)		+
	Paratrachys sp.		+	?			+	+		?
	Sponsor sp.		+				+			?
Acmaeoderinae	Acmaeodera brevipes KIESENW.		+	+	+	+	+	+	+	-
	Acmaeoderella flavofasciata (PILL.)		+	+	+	+	+	+	+	-
	Xantheremia koenigi (GANGL.)		+	+	+	+	+	+	+	-
Thrincopyginae	Thrincopyge ambiens (LE CONTE)	+	+	+	+	+	+	+		+
Mastogeninae	Haplostethus subcyaneus LE CONTE	+	+	+	+		+	+	+	
Buprestinae	Chalcophora mariana (L.)	+	+	+	+	+	+	+	+	+
	Cyphogastra foveicollis (BOISD.)	+	+	+	+	+	+	+	+	+
	Aurigena lugubris (F.)	+	+	+	+	+	+			+
	Capnodis tenebrionis (L.)	+	+	+	?	?	+			+
	Cyphosoma sp.	+	(+)	(+)	(+)	(+)	+			+
	Ectinogonia buqueti SPIN.	+	+	+			+			+
	Psiloptera mimosae KLUG.	+	+	+	+	+	+			+
	Dicerca alni (FISCH.)	+	+	+	?	?	+			+
	Buprestis octoguttata L.	+	+	+	+	+	+	+	+	+
	Eurythyrea austriaca (L.)	+	+	+	+		+	+		-
	Melanophila picta PALLAS	+	+	+	+	+	+	+	+	+
	Phaenops cyanea (F.)	+	+	+	+	+	+	+	+	+
	Anthaxia podolica (MANNH.)	+	+	+	+	+	+	+	+	+
	Dactylozodes rousseli SOL.	+	+	+	+	+	+			+
	Stigmodera vittata E.SAUND.	+	+	+	(+)	(+)	+	(+)	(+)	+
Sphenopterinae	Sphenoptera substriata KRYN.	+	+	+			+			+
Chrysobothrinae	Actenodes aurolineatus (LAP. & GORY)	+	+	+	+	+	+	+	+	+
	Chrysobothris affinis (F.)	+	+	+	+	+	+	+	+	+
	Belionota prasina (THUNB.)	+	+	+	+	+	+	+	+	+
Agrilinae	Coraebus rubi (L.)		+	+	+		+	+		+
	Meliboeus robustus (KÜSTER)		+	+	+		+	+		+
	Ethon fissiceps (KIRBY)	+	+	+	+	+	+	+	+	+
	Eupristocerus sp.		+	+	+		+	+		+
	Sambus sp.		+	+	+		+	+		+
	Alissoderus superciliosus (WIEDEM.)	+	+	+	+		+	+		+
	Cisseis regalis J.THOMS.	+	+	+	+		+	+		+
	Agrilus biguttatus (F.)		+	+	+		+	+		+
	Agrilus viridis (L.)		+	+	+		+	+		+
	Dismorpha linearis (L.)	+	+	+	+		+	+		+
	Agrilodia paraguayensis OBENB.		+	+	+		+	+		+
	Paragrilus rugatulus J.THOMS.	+	+	+	+		+	+		+
Trachyinae	Trachys minutus (L.)	+	+	+	+	+	+	+	+	+
	Habroloma geranii (SILFVER.)	+	+	+	+		+	+		+
	Brachys floccosus (MANNH.)	+	+	+	+		+	+		+
	Pachyschelus secendens WATERH.		+	+	+		+	+		-
	Endelus sp.		+	+	+		+	+		?
Cylindromorphinae	Paracylindromorphus subuliformis (MANNH.)		+	+			+			+
	Cylindromorphus filum GYLLENH.		?	+			+			?
Galbellinae	Galbella felix (MARS.)		+	+						+

Table 2. Distribution of cuticularia in Buprestidae. +, indicates presence of cuticularia; (+), indicates presence of overlapped cuticularia; ?, indicates uncertain presence or unknown data.

Table 3. Occurrence of several correlated characters in family Buprestidae.