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Classification and phylogeny of the Buprestoidea (Insecta: Coleoptera)

JIŘÍ KOLIBÁČ
Moravian Museum, Department of Entomology, Hviezdoslavova 29a, 627 00 Brno, Czech Republic;
e-mail: ento.kol@volny.cz

KOLIBÁČ J. 2000: Classification and phylogeny of the Buprestoidea (Insecta: Coleoptera). *Acta Musei Moraviae, Scientiae biologicae* (Brno) **85:** 113–184. – Selected species of 19 buprestid genera were studied in holomorphological fashion. The genera represent all the subfamilies described within the Buprestidae LEACH: Schizopodinae LECONTE (*Schizopus* LECONTE), Julodinae LACORDAIRE (*Julodis* SOLIER), Thrincopyginae LECONTE (*Thrincopyge* LECONTE), Acmaeoderinae KERREMANS (*Acmaeoderella* COBOS), Polycestinae LACORDAIRE (*Ptosima* SOLIER, *Polycesta* SOLIER, *Sponsor* LAPORTE & GORY, *Paratrachys* SAUNDERS), Buprestinae LEACH (*Buprestis* LINNAEUS, *Melanophila* ESCHSCHOLTZ), Chrysobothrinae LAPORTE & GORY (*Chrysobothris* ESCHSCHOLTZ), Chalcophorinae LACORDAIRE (*Chalcophora* SOLIER), Sphenopterinae LACORDAIRE (*Sphenoptera* SOLIER), Mastogeniinae LECONTE & HORN (*Mastogenius* SOLIER), Galbellinae REITTER (*Galbella* WESTWOOD), Agrilinae LAPORTE & GORY (*Coraebus* LAPORTE & GORY, *Agrilus* CURTIS), Trachyinae GORY & LAPORTE (*Trachys* FABRICIUS) a Cylindromorphinae PORTEVIN (*Cylindromorphus* THÉRY). Some of the body parts studied were figured. Eighty seven characters of larvae and adults were used in a character state matrix. The matrix was mostly based on the material studied, although, literature data were also used (especially for larval and anatomical characters). The families Derodontidae, Bostrichidae, Dermestidae, Dascillidae, Byrrhidae, Elateridae, and Dryopidae were used as outgroups. The Hennig86 program (commands *mhennig*bb**, *successive weighting*) was used for computing the matrix. Only one tree is a result of the matrix and that shows high congruence of matrix data. The resulting tree is congruent with a general opinion on a higher taxonomy for Buprestoidea. Family rank is confirmed for Schizopodidae. Such a classification, i.e. two respective sister families Schizopodidae and Buprestidae, is strongly supported by morphological evidence. A comparison of character states of some the studied taxa as well as of the tree shows paraphyly of several subfamilies of Buprestidae. Therefore, the subfamilies Acmaeoderinae and Thrincopyginae are synonymized with Polycestinae, the subfamilies Chrysobothrinae and Chalcophorinae are synonymized with Buprestinae, the subfamily Mastogeniinae is synonymized with Galbellinae, and the subfamily Cylindromorphinae is synonymized with Agrilinae. A part of the former polyphyletic subfamily Trachyinae (the tribes Aphanisticini JACQUELIN DU VAL incl. *Anthaxomorphus* DEYROLLE, Germaricini COBOS, Cylindromorphoidini COBOS, and Trachyini LAPORTE DE CASTELNAU) is synonymized with Agrilinae and the second part of the former Trachyinae (the tribes Pachyschelini BÖVING & CRAIGHEAD and Brachyini COBOS incl. *Leiopleura* DEYROLLE) is shifted to Galbellinae.

Key words: Phylogeny, morphology, classification, character analysis, Coleoptera, Buprestoidea

Introduction

A history of examination of the taxonomy of the Buprestidae appears in, for example, COBOS (1980, 1986), BELLAMY (1985) and HOŁYNSKI (1993). In recent times, two approaches to the higher classification of the family may be identified. In the first, the scientific approach is associated with the name Antonio Cobos, who established 13 subfamilies (COBOS 1980) based on morphological characters. Several years later, this author re-erected the 14th subfamily Galbellinae (COBOS 1986). Although Cobos's higher taxa are not established according to the principles of phylogenetic taxonomy, they are strictly based on observed character states so his system can be used as a basis for further examination. This system was followed by BELLAMY (1985), who compiled the all recent literature and wrote an invaluable list of the higher taxa of the Buprestidae from subfamilies to subgenera. The system adopted in that list underliesthe present communication.

The second approach is represented by Roman Hołynski who writes articles often based on intuition, rather than characters. His communication on a higher classification of Buprestidae (HOŁYNSKI 1993) is particularly incongruent with basic principles of scientific work and his system should be omitted by the entomological taxonomists' community. No arguments for the suggested classification are offered in that article and the attached key can be used only for basic differentiation of taxa. Lack of any evidence precludes any reasoning on the concepts emplyed. Unfortunately, the system from that article has been recently followed in a review of the Coleoptera higher taxa (LAWRENCE & NEWTON 1995) as well as by C. Bellamy in his prepared world catalogue of Buprestidae (see the internet page *http://www-tm.up.ac.za/coleop/bupclass.htm* where a proposal for a higher system of Buprestidae has recently been presented.)

Several papers dealing with the comparative morphology of adult Buprestidae have been published to date. For example, the wing venation was studied by GOOD (1925), the genitalia of both sexes by KALASHIAN (1983, 1986), the ventral body sides were figured by COBOS (1980, 1986), and valuable information on buprestid morphology and anatomy features in an excellent paper by GARDNER (1989). Three important papers are being prepared at present: a comparative morphology of antennae (VOLKOVITSH in litt.), abdominal segments (JENDEK in litt.), and a reclassification of Coraebini based on a detailed study of a morphology (KUBÁŇ, MAJER & KOLIBÁČ in press).

Oddly enough, very professional papers on the buprestid morphology can be found among literature on larvae rather than that on adults. Excellent older papers dealing with larval morphology are, for example, those by BRUCH (1917a, b) and BÖVING & CRAIGHEAD (1931). Also, relatively speaking, numerous modern papers deal with a descriptive morphology of larvae (e.g. BENOIT 1964, 1965, 1966; BÍLÝ 1972a, b, 1975a, b, 1983, 1986, 1989, 1993, 1996, 1998; COSTA et al. 1988; KOGAN 1963, 1964a, b, c; MATEU 1972; VOLKOVITSH 1975, 1979; VOLKOVITSH & HAWKESWOOD 1987, 1990, 1993, 1994, 1999). The most recent paper on larvae is a monograph on the Central European species (BÍLÝ 1999).

Material examined

Figured species

[taxa are named and ordered according to BELLAMY (1985)]

Julodinae LAC.
Julodis andreae OL.
Polycestinae LAC.
Polycesta porcata F.
Ptosima flavoguttata ILL.
Acmaeoderinae KERR.
Acmaeoderella discoidea F.
Schizopodinae LECONTE
Schizopus laetus LECONTE
Thrincopyginae LECONTE
Thrincopyge alacris LECONTE
Mastogeniinae LECONTE & HORN
Mastogenius parallelus SOL.
Chalcophorinae LAC.
Chalcophora marianna L.
Sphenopterinae LAC.
Sphenoptera lapidaria BRULLÉ
Buprestinae LEACH
Buprestis octoguttata L.
Melanophila acuminata DEGEER
Chrysobothrinae LAP. & GORY
Chrysobothris affinis F.
Chrysobothris chrysostigma L.
Agrilinae LAP. & GORY
Agrilus biguttatus F.
Agrilus viridis L.
Coraebus undatus F.
Cylindromorphinae PORTEVIN
Cylindromorphus filum GYLL.
Trachyinae GORY & LAP.
Trachys minutus L.
Galbellinae REITTER
Galbella felix MARS.

About 40 mostly surface character states of two other Polycestinae representatives (*Sponsor* GORY & LAP. sp. and *Paratrachys nigricans* KERR.) were added to the matrix. These characters were not figured.

Excepting the species listed above, numerous species of the following genera were studied (in alphabetical order):

Aaata Sem., *Acmaeodera* Esch., *Acmaeoderella* Cobos (sg. *Euacmaeoderella* Volkov.), *Acmaeoderoides* Van Dyke, *Actenodes* Dej., *Afrobothris* Théry, *Agaeocera* Waterh., *Agelia* Lap. & Gory, *Agrilodia* Obenb., *Agriloides* Kerr., *Agrilomorpha* Théry, *Agrilus* Curtis (sg. *Anambus* C. G. Thoms.), *Acherusia* Lap. & Gory, *Alcinous* Deyr., *Alissoderus* Deyr., *Amblysterna* Thoms., *Amorphosoma* Lap., *Amorphosternus* Deyr., *Anadora* Kerr., *Ancylotela* Waterh., *Anilara* Thoms., *Anthaxia* Esch., *Anthaxomorphus* Deyr., *Aphanisticus* Latr., *Aristosoma* Thoms., *Asemochrysus* Deyr., *Astraeus* Lap. & Gory, *Asymades* Kerr., *Autarcontes* Waterh., *Baudonisia* Cobos, *Beerellus* Nelson, *Belgaumia* Kerr., *Belionota* Esch., *Bergidora* Kerr., *Brachelytrium* Obenb., *Brachycoraebus* Kerr., *Brachys* Dej., *Bubastes* Lap. & Gory, *Bulis* Lap. & Gory, *Buprestis* L., *Callimicra* Deyr., *Callipyndax* Waterh., *Callopistus* Deyr., *Calodema* Gory & Lap., *Cantonius* Théry, *Capnodis* Esch., *Cardiaspis* Saund., *Castaliella* Cobos, *Catoxantha* Dej., *Chalcogenia* Thoms., *Chalcophlocteis* Obenb., *Chalcophora* Serv. in Dej., *Chalcophorella* Kerr., *Chalcophoropsis* Thoms., *Chalcoplia* Thoms., *Chalcopoecila* Thoms., *Chlorophorella* Desc., *Chrysaspina* Théry, *Chrysesthes* Serv. in Dej., *Chrysobothris* Esch., *Chrysodema* Lap. & Gory, *Chrysophana* LeConte, *Chrysopistus* Théry, *Cinyra* Lap. & Gory, *Cisseicoraebus* Kerr., *Cisseis* Lap. & Gory, *Clema* Sem., *Cochinchinula* Volkov., *Colobogaster* Sol., *Conognatha* Esch., *Coomaniella* Bourg., *Coroebina* Obenb., *Coraebosoma* Obenb., *Coraebus* Gory & Lap., *Cryptodactylus* Deyr., *Cupriscobina* Bell., *Curis* Gory & Lap., *Cyalithus* Thoms., *Cylindromorphus* Kiesw., *Cyphogastra* Deyr., *Cyphonota* Dej., *Cyphothorax* Waterh., *Cyria* Serv. in Dej., *Dactylozodes* Chevr., *Demostis* Kerr., *Dessumia* Desc. & Vill., *Deyrollius* Obenb., *Diadoxus* Thoms., *Dicerca* Esch., *Dicercomorpha* Deyr., *Dinocephalia* Obenb., *Dinocoraebus* Obenb., *Discoderes* Chevr., *Discoderoides* Théry, *Dismorpha* Gistel, *Dystaxiella* Knull, *Ectinogonia* Spin., *Endelus* Deyr., *Entomogaster* Saund., *Epidelus* Deyr., *Epimacha* Kerr., *Epistomentis* Sol., *Ethon* Gory & Lap., *Eudiadora* Obenb., *Euchroaria* Obenb., *Euchroma* Serv. in Dej., *Euplectalecia* Obenb., *Eupristocerus* Deyr., *Euryspilus* Lac., *Eurythyrea* Serv. in Dej., *Evides* Thoms., *Evimantius* Kerr., *Fahraeusia* Obenb., *Galbella* Westw., *Genestia* Théry, *Geralius* Harold, *Germarica* Blackb., *Glyptoscelimorpha* Horn, *Habroloma* C. G. Thoms., *Halecia* Lap. & Gory, *Haplostethus* LeConte, *Haplotrinchus* Kerr., *Helferella* Cobos, *Heromorphus* Obenb., *Hilarotes* Thoms., *Hiperantha* Gistel, *Hippomelas* Lap. & Gory, *Hylaeogena* Obenb., *Hypocisseis* Thoms., *Hypoprasis* Fairm. & Germ., *Icarina* Alluaud, *Iridotaenia* Deyr., *Julodella* Sem., *Julodimorpha* Thoms., *Julodis* Esch., *Kamosia* Kerr., *Kerremansia* Péring., *Kisanthobia* Mars., *Lamprocheila* Obenb., *Lampropepla* Fairm., *Latipalpis* Sol., *Leiopleura* Deyr., *Lepidoclema* Bell., *Lius* Deyr., *Maoraxia* Obenb., *Mastogenius* Sol., *Megactenodes* Kerr., *Megaloxantha* Kerr., *Melanophila* Esch., *Meliboeus* Deyr., *Melobasis* Lap. & Gory, *Merimna* Thoms., *Metasambus* Kerr., *Metaxymorpha* Parry, *Microacmaeodera* Cobos, *Microcastalia* Heller, *Micropistus* Théry, *Mixochlorus* Waterh., *Mundaria* Kerr., *Nalanda* Théry, *Nanularia* Casey, *Nascio* Lap. & Gory, *Nascioides* Kerr., *Nastella* Kerr., *Neobuprestis* Kerr., *Neocuris* Fairm., *Neojulodis* Kerr., *Neotoxoscelus* Fisher, *Neotrachys* Obenb., *Nickerleola* Obenb., *Nipponobuprestis* Obenb., *Nothomorpha* Thoms., *Notographus* Thoms., *Obenbergula* Strand, *Odettea* Baudon, *Oedisterna* Lac., *Omochyseus* Waterh., *Ovalisia* Kerr., *Pachyschelus* Sol., *Palmar* Schaef., *Paracephala* Thoms., *Paracupta* Deyr., *Paracylindromorphus* Théry, *Parademostis* Obenb., *Paragrilus* Saund., *Parakamosia* Obenb., *Paraphrixia* Saund., *Parasambus* Desc. & Vill., *Parataenia* Kerr., *Paratassa* Mars., *Paratrachys* Saund., *Paraxenopsis* Cobos, *Pelecopselaphus* Sol., *Perotis* Megerle in Dejean, *Perucola* Théry, *Phaenops* Meg. in Dej., *Philanthaxia* Deyr., *Philocteanus* Deyr., *Phlocteis* Kerr., *Planidia* Kerr., *Poecilonota* Esch., *Polycesta* Serv. in Dej., *Polyctesis* Mars., *Polyonychus* Chevr., *Promeliboeus* Obenb., *Prospheres* Thoms., *Pseudagrilus* Lap., *Pseudacherusia* Kerr., *Pseudocallopistus* Obenb., *Pseudocastalia* Kraatz, *Pseudoclema* Théry, *Pseudokamosia* Théry, *Pseudokerremansia* Bell. & Horn, *Pseudoperotis* Obenb., *Pseudotaenia* Kerr., *Psiloptera* Serv. in Dej., *Pterobothris* Fairm. & Germ., *Ptosima* Serv. in Dej., *Pygicera* Kerr., *Rhaeboscelis* Chevr., *Sambomorpha* OBENB., *Sambus* DEYR., *Saundersina* COBOS, *Scaptelytra* KERR., *Scintillatrix* OBENB., *Shimogia* OBENB., *Schizopus* LECONTE, *Siamastogenius* TOYAMA, *Sjoestedtius* THÉRY, *Speophora* THÉRY, *Sphenoptera* DEJ. (sgg. *Hoplistura* JAK., *Chilostheta* JAK.), *Sponsor* GORY & LAP., *Steraspis* DEJ., *Sternocera* ESCH., *Stigmodera* ESCH., *Strigoptera* DEJ., *Strigopteroides* COBOS, *Strigulia* KERR., *Synechocera* DEYR., *Taphrocerus* SOL., *Tetragonoschema* THOMS., *Texania* CASEY, *Therybuprestis* STRAND, *Thomassetia* THÉRY, *Thrincopyge* LECONTE, *Thurntaxisia* SCHATZM., *Thymedes* WATERH., *Tonkinula* OBENB., *Torresita* GEMM. & HAR., *Touzalinia* THÉRY, *Toxoscelus* DEYR., *Trachykele* MARS., *Trachys* F., *Trigonogenium* GEMM. & HAR., *Trypantius* WATERH., *Tylauchenia* BURM., *Tyndaris* THOMS., *Vanroonia* OBENB., *Velutia* KERR., *Xantheremia* VOLKOV., *Xenorhipis* LECONTE, *Xyroscelis* THOMS., *Yamina* KERR. (All studied material is in collections of V. Kubáň and National Museum Prague on deposit.)

Methods

The first selection of the taxa studied follows the system adopted in the list of BELLAMY (1985) (see the section "Figured taxa" in the previous chapter). All body parts were dissected under the stereomicroscope and studied and figured using the compound microscope (50–1000 ×). After study of these taxa, representatives of other buprestid genera were studied and some of them added to a matrix. Altogether, species of 263 buprestid genera were studied.

The character states matrix is mostly based on the studied material; however, literature data were also used (especially in larval and anatomical characters). Representatives of the families Derodontidae (*Derodontus macularis* FUSS), Bostrichidae (*Bostrichus capucinus* L.), Dermestidae (*Attagenus pellio* L.), Dascillidae (*Dascillus cervinus* L.), Byrrhidae (*Byrrhus pilula* L.), Elateridae (*Agrypnus murinus* L.), and Dryopidae (*Dryops lutulentus* ERICHS.) were used as outgroups. The series Bostrichiformia (Derodontidae, Bostrichidae, Dermestidae) is generally considered a primitive group among the polyphagan beetles. The other families mentioned are classified together with Buprestoidea within the series Elateriformia (see e.g. LAWRENCE & BRITTON 1994, LAWRENCE & NEWTON 1995). Another reason for this particular selection of outgroups selection is an unpublished analysis of sequences in three genes (cytochrome oxidase I, 18S ribosomal RNA, and 28S ribosomal RNA), which were downloaded from the Internet gene bank (*http://www3.ncbi.nlm.nih.gov*). The analysis shows Bostrichiformia as a sister group of Elateriformia (KOVALOVSKÝ 1999, unpublished bachelor theses, Faculty of Biological Sciences, University of South Bohemia in České Budějovice, Czechia).

The Hennig86 computer program (commands *mhennig*bb**, *successive weighting*) in connection with TreeGardener 1.0 were used for an analysis of the character states matrix. Autapomorphies were mostly removed excepting the characters 11, 26, and 64. They are being prepared for the addition of further taxa into the matrix but switched off during computing.

Abbreviations

Terminology used for the wing venation follows that in the paper by KUKALOVÁ-PECK & LAWRENCE (1993).

Head

ad . . . . . apical dens
asp . . . . . antennal sensorial field
bs . . . . . basistipes
cd . . . . . cardo
lac . . . . . larval lacinia (BÍLÝ 1989)
m . . . . . mentum
md . . . . . medial dens
mic . . . . . mandibular internal canal
ms . . . . . mental sclerite
mt . . . . . mediostipes
pf . . . . . palpifer
pms . . . . . premental sclerite
prs . . . . . larval prostheca

Thorax

cl . . . . . claw
dil . . . . . discriminal line
em . . . . . empodium
hme . . . . . hypomeron
le . . . . . lateral edge
msm . . . . . mesepimeron
msn . . . . . mesepisternum
mtl . . . . . metasternal transversal line
pip . . . . . prosternal intercoxal process
pre . . . . . prepectus

Abdomen

as1 . . . . . abdominal sternite 1
bc . . . . . bursa copulatrix
mo . . . . . median oviduct
mt9 . . . . . male abdominal tergite 9
mt10 . . . . . male abdominal tergite 10
ps . . . . . parasternite
pt1 . . . . . paratergite 1
pt2 . . . . . paratergite 2
s . . . . . spiracle
sc . . . . . spermatheca
sg . . . . . spermathecal gland
si . . . . . sternal incision
sp . . . . . sternal pore
tp . . . . . tergal pore

A proposed system for the Buprestoidea

Family Schizopodidae LECONTE

Synapomorphies: Apex of prosternal process dilated, male terminalia dissymmetric, unique premental sclerites and larval body, development in soil (similarly as in *Julodis*).

S y m p l e s i o m o r p h i e s : Prementum conspicuous (fused with mentum, see GARDNER 1989), antennal sensillae dispersed, eyes elevated, primitive wing venation, paratergite 1 absent.

Remarks. For other character states see Tree 2 and Tab. 2. The family was re-evaluated by NELSON & BELLAMY (1991) who also described the taxonomic history of this group. However, this opinion has not been generally accepted and most authors have classified the group as the subfamily Schizopodinae since 1991. As LAWRENCE & NEWTON (1995) rightly stated, although Schizopodidae is considered a sister group to Buprestidae, this does not necessarily elevate it to family rank. However, I found the Schizopodidae studied much more "distant" from the other buprestid subfamilies than from one another from the morphological and biological points of view. Therefore, the rank of the Schizopodidae should be higher than subfamily. I consider such a classification more suitable to a well-balanced system.

Family Buprestidae LEACH

S y n a p o m o r p h i e s : Prosternal process acuminate or wide (parallel-sided), premental sclerites simple or galbelline, larval body buprestine (with dilated thorax), julodine or trachyine.

S y m p l e s i o m o r p h i e s : Male terminalia symmetric, development mostly in wood.

Remarks. For other character states see Tree 2 and Tab. 2. Buprestidae is generally the more advanced group with regard to Schizopodidae. However, primitive taxa (or, better, primitive character states) can be found in all its major lineages (polycestine, buprestine, and agriline ones). All the above-mentioned apomorphies are multistate characters. It is frequently the case in as rich a group as the Buprestidae that truly inclusive apomorphies are absent. Many morphological and biological homoplasies occur in the studied taxa, as is shown in the character state matrix (Tab. 2). An interesting phenomenon is parallelism in bionomics. The ancestral bionomics is probably that of the primitive buprestines, especially of the subfamily Polycestinae: larval development in dead wood (*Strigoptera*). The similar life histories developed independently in unrelated genera of several subfamilies: (1) development in fresh wood or under bark, for example in Polycestinae (*Ptosima*), Buprestinae (*Anthaxia*), Sphenopterinae (*Sphenoptera*, especially sg. *Hoplistura*), Galbellinae (*Galbella*), and Agrilinae (*Agrilus*, especially sg. *Anambus*); (2) development in stems or roots of herbaceous plants, for example in Polycestinae (*Acmaeoderella*, especially sg. *Euacmaeoderella*) Julodinae (all genera probably live externally in soil and feed on roots), Buprestinae (*Cyphosoma*), Sphenopterinae (*Sphenoptera*, especially sg. *Chilostheta*) and Agrilinae (*Cylindromophus*); (3) leaf miners in Polycestinae (*Paratrachys*), Agrilinae (*Trachys*), and Galbellinae (*Pachyschelus*).

Polycestine lineage

Subfamily Polycestinae LAC.

[= Polycestinae LAC. + Thrincopyginae LECONTE + Acmaeoderinae KERR. (*sensu* COBOS 1986)]

Synapomorphies: Mandible with absent medial dentes, prosternal process wide, paratergite 2 inconspicuous, parameral portion of tegmen very weakly ciliate, some taxa with dense erect dorsal pubescence or denticulate pronotal base, larval urogomphi absent.

Symplesiomorphies: Paratergite 1 absent, mesepimeron as large as mesepisternum, larva with simple pronotal groove and separated galea and lacinia.

Remarks. For other character states see Tree 2 and Tab. 2. The apomorphies of Polycestinae are also not inclusive, excepting weakly ciliate parameral portion of the tegmen. COBOS (1980, 1986) claimed that the pubescence is quite missing but this is not so: a sparse fine ciliation is visible under the compound microscope. Homologization of the membranous appendage called the lacinia in larvae is not quite clear. I follow the terminology of BÍLÝ (1989) here. Polycestinae are relatively the most primitive subfamily within Buprestidae with relations to the buprestine lineage rather than the agriline. This relationship can be demonstrated, for example, in the following larval characters: (1) prostheca absent (present in the agrilines), (2) spiracles uniforous or multiforous ["agriloid" in the agrilines, see BÍLÝ (1999) for figures], (3) proventriculus present (absent in the agrilines). Hypothetical primitiveness of the polycestines is, except for the morphological evidence, also based on their bionomics: most of species (especially morphologically primitive ones) develop in dead wood. The bionomics of leaf miners (*Paratrachys*) is clearly advanced as well as their morphology.

Buprestine lineage

Subfamily Julodinae LAC.

Synapomorphies: Pubescence grows during life of adults, labrum without distinct tormal processes, Malpighian tubules distally grouped (GARDNER 1989), pronotum extended to elytral suture (mesonotum inconspicuous), larval pronotal groove and body shape unique.

Symplesiomorphies: Abdomen without sternal pores, antennal sensillae dispersed, eyes elevated.

Remarks. For other character states see Tree 2 and Tab. 2. Julodinae seem to be derived from the buprestine lineage. Key characters are its life history and antennal sensorial fields. According to an outgroup comparison, the julodine way of life is considered advanced with regard to development in wood. This hypothesis is supported by morphological evidence in some primitive Polycestinae wherein plesiomorphies are correlated with development in dead wood. On the other hand, relatively advanced Sphenopterinae develop in both wood and the roots of herbaceous plants. The later larval habitat can be considered the first step to the julodine life history. The outgroup criterion was also strictly used for determination of the polarity of the antennal sensillae state (as well as the elevation of the eyes). Therefore, the dispersed sensillae at the dorsal side of the antennal segments are considered primitive in the character state matrix (Tab. 2). On the other hand, these character states may be a consequence of adaptation to the julodine way of life. Moreover, the character is probably correlated with presence of the sensorial fields. The latter character does not occur in the studied outgroups, which is why the old hennigian criterion of frequency of occurrence was used. Lack of the fields in the julodines is therefore considered a secondary reduction. The Australian genus *Julodimorpha* shows some external character states in common with the julodines. All its other external character states are ancestral with regard to *Julodis* (if the hypothesis on the secondary reduction of the sensorial fields is accepted), so that *Julodimorpha* can be considered ancestral to Julodinae and classified within this subfamily. The labral tormal processes of *Julodimorpha* should be studied to test the hypothesis supporting a buprestine origin for the Julodinae.

Some of the character states mentioned, as well as some others, are common to Julodinae and Schizopodidae (Tab. 2). This fact can be probably explained by an adaptation to similar way of life.

Subfamily Buprestinae Leach

[= Buprestinae Leach + Chrysobothrinae Lap. & Gory + Chalcophorinae Lac. (*sensu* Cobos 1986)]

Synapomorphies: Mesothorax with arcuate suture between mesepimeron and mesepisternum, six or four paratergites 1 present, larva with Y-shaped pronotal groove, urogomphi absent.

Symplesiomorphies: Paratergites 2 absent, antennal sensorial fields conspicuous, frons mostly flat, 2nd cubito-anal cell (“wedge” cell) present.

Remarks. For other character states see Tree 2 and Tab. 2. The Buprestinae constitute a very large group, so most of the above-mentioned apomorphies are multistate characters and representatives with plesiomorphic character states can be found. One of the most important characters for recognition of the buprestines is the arcuate suture between the mesepimeron and the mesepisternum; however, probably not even this state is inclusive. Former Chrysobothrinae can be relatively simply incorporated into Buprestinae, as is shown in the character state matrix (Tab. 2). The former Chalcophorinae are a very rich group in which some genera differing from the nominotypical one are classified at present (especially in the tribe Psilopterini). Hołynski (1993) pointed out a connection between the tribes Dicercini (formerly classified within Buprestinae) and Psilopterini. However, this statement, although probably right, needs to be confirmed by due study of taxonomic characters.

Agriline lineage

Subfamily Sphenopterinae Lac.

Synapomorphies: Scutellum cordate, sternal pores absent, larva with Y-shaped pronotal groove, development in wood or inside roots (under soil surface).

S y m p l e s i o m o r p h i e s : Mesepimeron approximately as large as mesepisternum, with suture oblique; prosternal process rounded, narrow; phallus as long as tegmen.

Remarks. For other character states see Tree 2 and Tab. 2. The apomorphies of Sphenopterinae are also not inclusive, excepting inverted Y-shaped pronotal groove in larvae. According to a character analysis, a sister group of the subfamily is the cluster Galbellinae – Agrilinae. The distinguishing synapomorphies for the three Buprestinae subfamilies mentioned are as follows: (1) lyriform male sternite 9, (2) five paratergites 1 present, (3) sternal incision more or less conspicuous, (4) mandibular medial dentes absent, (5) mesepimeron small, suture between it and mesepisternum oblique (not arcuate), sometimes suture imperfect, (6) tibiae sometimes with spines, (7) scutellum relatively large. Another character state (not included in the character data matrix) is the very similar shape of the mental sclerites: these conspicuously robust sclerites occur in most of the Agrilinae studied (KUBÁŇ, MAJER & KOLIBÁČ in press). On the other hand, there are also apomorphies that Sphenopterinae share with Buprestinae: (1) adult and larval body shapes in some groups, (2) shape of metasternal transversal line in some groups, (3) radial cell elongate, (4) larval mandible without prostheca, (5) urogomphi absent. Some modern authors prefer to believe in a phylogenetic relationship of the sphenopterines with the buprestine lineage (VOLKOVITSH, pers. comm.). However, according to the method of comparative morphology, the sphenopterines are more closely related with the agriline lineage because of a higher number of shared apomorphies. Oddly, Sphenopterinae are classified near to Agrilinae in older systems as well(incl. COBOS 1986). Further study is needed to resolve this problem.

Subfamily Galbellinae REITTER

[= Galbellinae COBOS + Mastogeniinae LECONTE & HORN + Trachyinae GORY & LAP. part (*sensu* COBOS 1986)]

S y n a p o m o r p h i e s : Unique shaped premental sclerites, tendency to coalescence of maxillar sclerites (basistipes, mediostipes, palpifer), antenna with inconspicuous sensorial fields (probably secondary reduction), metasternal transversal line absent, phallus short.

S y m p l e s i o m o r p h i e s : wing veins ScP+RA (subcosta and radius) not prolonged behind radial cell in *Galbella* and *Mastogenius* (but prolonged in *Pachyschelus* and *Brachys*).

Remarks. For other character states see Tree 2 and Tab. 2. Classification of the former Mastogeniinae within the Galbellinae may be surprising for some entomologists; nevertheless, there is morphological evidence for such a result in the character analysis. There is another apomorphy of the mastogeniines which could be derived from a character state of *Galbella*: their distinct hypomeral keel is perhaps not homological with that in e.g. *Thrincopyge* (see Tab. 2) but it can be derived from the galbelline furrow for antennae (secondary closing of furrow). This hypothesis is of course very speculative.

There are some symplesiomorphies (e.g. "buprestoid" larval spiracles; VOLKOVITSH, unpublished observation on *Galbella acaciae* DESC. & MATEU), which both *Galbella* and *Mastogenius* share with the polycestine and buprestine lineages (Tab. 2) Therefore, some authors (probably mistakenly) speculate about phylogenetic relations between these groups. The only true synapomorphies shared by *Galbella* and the cited lineages are absence of the larval prostheca and retracted sensory appendage (VOLKOVITSH, unpublished observation on *Galbella acaciae*). However, such reductions are possible in the agriline lineage as well. Unfortunately, the larva of the former Mastogeniinae remains, to date, unknown.

On the other hand, Galbellinae show important synapomorphies shared with Agrilinae (plus synapomorphies shared also with Sphenopterinae; see above): (1) male tergite 9 (paraproct) not separated from tergite 10, (2) abdominal sternite 1 absent, (3) larval proventriculus absent (VOLKOVITSH, unpublished observation on *Galbella acaciae*), (4) mesepimeron small with suture (between it and mesepisternum) oblique or imperfect.

The genera *Leiopleura*, *Pachyschelus*, *Brachys* and their relatives [probably genera in three nominal subtribes *sensu* HOŁYNSKI (1993): Leiopleurina, Pachyschelina and Brachydina] formerly classified with Trachyinae, should also be classified within Galbellinae. The species *Pachyschelus mandarinus* THÉRY and *Brachys aerosa* MELSH. were studied in detail, and members of *Leiopleura* are similar to these species in external character states. The following important apomorphic character states of the both species are, among others, common with *Galbella*: (1) furrow for antennae present, (2) mediostipes strongly widened, palpifer large, rounded (3) general structure of maxilla galbelline, excepting strong pigmentation of central sclerite, (4) inner side of mandible concave, 2 or 3 apical dentes present, (5) all sternites with incision in *P. mandarinus*, *B. aerosa* with inconspicuous incision at apex of the last visible sternite. One very important symplesiomorphy occurs in the studied species: their mandibles are without the internal canal (this is present in *Trachys* and other Agrilinae).

The newly defined Galbellinae show some transformation series of both morphological and biological character states that are independent of similar transformations in Agrilinae (e.g. larval development in wood towards leaf miners). That is why these subfamilies are treated as separate and Galbellinae are not included into Agrilinae.

Subfamily Agrilinae LAP. & GORY

[= Agrilinae LAP. & GORY + Cylindromorphinae PORTEVIN + Trachyinae GORY & LAP. part (*sensu* COBOS 1986)]

Synapomorphies: Mandible with internal canal, maxilla with conspicuously straight and elongate cardo, midgut caeca reduced, reduced number of tubules per testis (<10) (the both later states according to GARDNER 1989), larva with "agriloid" spiracles, development in "living" wood.

S y m p l e s i o m o r p h i e s : Larval mandible with prostheca, urogomphi present, sensory appendage ejected (also in Polycestinae: *Paratrachys*), pronotal groove simple or weakly V-shaped.

Remarks. For other character states see Tree 2 and Tab. 2. Agrilinae are very well defined by synapomorphies, although, considering richness of the subfamily, some of the characters can be multistate. The mentioned larval plesiomorphies are unique among buprestine genera (excepting the simple pronotal groove occurring also in the polycestines and *Galbella*). That is why Agrilinae are not a group derived from some other buprestide subfamily and the proposed system is strictly monophyletic. On the other hand, Agrilinae can be considered the most advanced group among Buprestidae (Trees 1 and 2).

A position of *Agrilus* and *Coraebus* should be probably reversed in the Trees 1 and 2 as KUBÁŇ, MAJER & KOLIBÁČ (in press) suggest in their detailed study. The former subfamilies Agrilinae and Cylindromorphinae, and the formerly trachyine tribes Aphanisticini, Germaricini, Cylindromorphoidini, and Trachyini (all groups *sensu* BELLAMY 1985) should be included in the newly defined subfamily Agrilinae [i.e. Agrilinae minus the subtribes Brachydina, Leiopleurina, Galbellina, and Pachyschelina; all groups *sensu* HOŁYNSKI (1993)].

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Appendices 1 and 2

Tab. 1. Numbers and descriptions of the characters and character states. 0 = plesiomorphy, 1–6 = apomorphies.

1. **Abdomen** – male sternite 9:
   0, coniform (*Melanophila*-like); 1, lyriform (*Trachys*-like); 2, dissymmetric
2. **Abdomen** – male tergites 9, 10:
   0, T9 (paraproct) distinct; 1, T9 fused with T10 or reduced
3. **Abdomen** – parasternites:
   0, present; 1, inconspicuous; 2, absent
4. **Abdomen** – paratergite 1:
   0, absent; 1, seven present; 2, six present; 3, five present; 4, four present
5. **Abdomen** – paratergite 2:
   0, absent 1, inconspicuous; 2, conspicuous
6. **Abdomen** – sternal incision:
   0, absent; 1, in sternites 4–7; 2, in sternite 7
7. **Abdomen** – sternal pores:
   0, absent; 1, four pairs; 2, three pairs; 3, two pairs; 4, one pair (sternite 4); 5, one pair (sternite 6)
8. **Abdomen** – sternite 1:
   0, present; 1, absent
9. **Abdomen** – suture between sternite 3 and 4:
   0, perfect; 1, perfect but sternites inmovable; 2, inconspicuous; 3, nearly invisible
10. **Abdomen** – tergal pores:
    0, absent; 1, five pair; 2, four pairs; 3, three pairs; 4, one pair (tergite 2); 5, one pair (tergite 4)
11. **Antenna** – number of segments:
    0, eleven; 1, segments 10 and 11 coalescent
12. **Antenna** – sensillae dorsally:
    0, dispersed; 1, in central field; 2, laterally situated, bordered; 3, absent; 4, dispersed and bordered; 5, as in 4 but with field; 6, several fields dorsally
13. **Antenna** – sensorial fields (ventral):
    0, absent; 1, single field; 2, two fields; 3, three and more fields
14. **Antenna** – sensorial fields:
    0, conspicuous; 1, inconspicuous
15. **Antenna** – serrate from joint:
    0, 4th; 1, 5th; 2, 6th; 3, 7th
16. **Antenna** – the last segment:
    0, conical, rounded; 1, truncate; 2, truncate with jag

17. Body shape:
0, elytra wider than pronotum; 1, scaphoid (e.g. *Sphenoptera*); 2, cylindrical; 3, triangular
18. Body shape – ratio pronotum/elytra:
0, base of elytra wider than pronotum; 1, base of elytra equal to base of pronotum
19. Claw:
0, without denticle; 1, with denticle; 2, enlarged
20. Dorsal pubescence:
0, absent; 1, coarse and conspicuously erected; 2, long, growing during life; 3, decumbent, in patterns
21. Dorsal surface:
0, bare; 1, pubescent; 2, with scales (toment)
22. Elytra:
0, with carinae or regular punctation; 1, without carinae, punctation irregular
23. Elytral apex – shape:
0, evenly rounded; 1, denticulate; 2, narrowed (*Dicerca*); 3, with spurs
24. Elytral epipleura – humeral portion:
0, normal; 1, distinctly extends to mesothorax
25. Elytral carinae:
0, present; 1, absent
26. Eyes dorsally:
0, their combined diameters not exceed half of head width; 1, exceed it
27. Eyes elevated:
0, yes; 1, no
28. Frons – shape:
0, flat; 1, concave; 2, convex; 3, with longitudinal groove; 4, concave with groove
29. Frons between eyes:
0, parallel; 1, narrowed towards vertex; 2, narrowed towards clypeus
30. Labium – mental sclerites:
0, medium; 1, small; 2, large
31. Labium – number of palpal joints:
0, three; 1, two
32. Labium – premental sclerites, size:
0, two compact sclerites; 1, two elongate sclerites
33. Labium – premental sclerites, shape:
0, Y-like (*Buprestis*); 1, simple; 2, schizopine; 3, galbelline
34. Labrum – shape:
0, rounded; 1, even; 2, emarginate
35. Labrum – tormal processes:
0, U-shaped; 1, simple; 2, absent

36. Larva – spiracles:
0, buprestoid; 1, agriloid
37. Larva – body shape:
0, agriline; 1, buprestine; 2, trachyine; 3, julodine; 4, schizopine
38. Larva – development in wood:
0, in dead wood; 1, in “living” wood; 2, under bark
39. Larva – development:
0, in wood; 1, in stems of grass; 2, in leaves; 3, in roots; 4, on roots externally
40. Larva – lacinia and galea:
0, separated; 1, not separated (mala present)
41. Larva – pronotal groove:
0, I-shaped; 1, Y-shaped; 2, V-shaped; 3, absent; 4, julodine (wide Y-shaped)
42. Larva – prostheca:
0, present; 1, absent
43. Larva – proventriculus:
0, present; 1, absent
44. Larva – sensory appendage:
0, ejected; 1, retracted
45. Larva – stemmata:
0, some present; 1, perfectly absent
46. Larva – urogomphi:
0, present; 1, absent
47. Malpighian tubules – arrangement (GARDNER 1989):
0, evenly spaced at both points of insertion; 1, grouped proximally;
2, grouped distally; 3, grouped at both ends
48. Mandible – apical dens:
0, double; 1, simple
49. Mandible – apical dens:
0, sharp; 1, blunt
50. Mandible – internal canal:
0, absent; 1, present
51. Mandible – medial dentes:
0, present; 1, absent
52. Maxilla – basistipes, mediostipes, palpifer:
0, conspicuous; 1, tendency to coalescence
53. Maxilla – cardo relatively straight and elongate:
0, no; 1, yes
54. Maxilla – lacinia:
0, separated of mediostipes; 1, coalescent with mediostipes (tendency)
55. Maxilla – palpifer:
0, triangular; 1, oval or small
56. Mesothorax – mesepimeron:

0, ca as large as mesepisternum, suture oblique (e.g. *Julodis*); 1, dtto, suture partially vertical (e.g. *Buprestis*); 2, mesepimeron small, suture oblique (e.g. *Agrilus*); 3, mesepimeron small, suture imperfect and horizontal (e.g. *Cylindromorphus*); 4, mesepimeron reduced; 5, suture absent (sclerites coalescent)

57. Mesothorax – mesosternum:
0, not divided by prosternal process; 1, imperfectly divided; 2, perfectly divided (process touches metasternum)

58. Metasternum – shape of transversal line:
0, evenly rounded; 1, with two tops; 2, absent; 3, acuminate

59. Middle coxae:
0, encircled about to 1/2 by mesosternum; 1, encircled less than to 1/3

60. Middle tarsus – 1st tarsomere:
0, as long as 2nd or shorter; 1, weakly longer; 2, distincly longer

61. Midgut caeca (GARDNER 1989):
0, long (>0.1× length of midgut); 1, reduced (<0.1× length of midgut)

62. Number of tubules per testis (GARDNER 1989):
0, low (10–20); 1, high (20–50); 2, very high (50+); 3, reduced (<10)

63. Phallus:
0, as long as tegmen; 1, weakly shorter; 2, <3/4 of tegmen

64. Pronotum extended to elytral suture:
0, no; 1, yes

65. Pronotum – shape (sides):
0, rounded (*Castalia*); 1, oblong (*Psiloptera*); 2, conical (*Buprestis*)

66. Prosternal process – shape:
0, rounded, moderately narrow; 1, acuminate; 2, acuminate with lateral jag; 3, dilated at apex; 4, very wide along whole length

67. Prosternum:
0, without keel; 1, with keel

68. Prothorax – base:
0, arcuate; 1, straight

69. Prothorax – denticulate base:
0, absent; 1, conspicuous; 2, inconspicuous

70. Prothorax – hypomeral keel:
0, absent; 1, present; 2, in apical portion (inconspicuous)

71. Prothorax – lateral edge:
0, present; 1, partially reduced (about 1/2); 2, strongly reduced (<1/4)

72. Prothorax:
0, without posterior interlocking mechanism; 1, with this mechanism

73. Scutellum – shape:
0, triangular; 1, cordate; 2, oval; 3, absent; 4, prolonged; 5, secondarily triangular

74. Scutellum – size:

0, medium sized; 1, small; 2, large; 3, absent

75. Tarsi flattened from above:
0, no; 1, yes

76. Tarsus – 4th tarsomere shortened:
0, no; 1, yes

77. Tarsus – 5th tarsomere:
0, longer than 3rd and 4th together; 1, as long as 3rd and 4th together; 2, shorter

78. Tarsus – pulvilli:
0, equal (medium sized) in all tarsomeres; 1, more/less reduced in tarsomeres 1 or 2; 2, enlarged in all tarsomeres

79. Tegmen – pubescence at apex:
0, conspicuous; 1, more/less reduced (inconspicuous)

80. Tibiae – spines along sides:
0, absent; 1, present

81. Wing – MP3+4 connected with MP1+2:
0, yes; 1, no

82. Wing – ScP+RA prolonged (reaches behind radial cell):
0, no; 1, yes

83. Wing – number of veins in medial field:
0, 6 veins; 1, 5 veins; 2, 4 veins; 3, 3 veins; 4, 2 veins; 5, 1 vein

84. Wing – radial cell:
0, rhomboid (*Coraebus*-like); 1, elongate (*Buprestis*-like); 2, reduced (*Ptosima*-like); 3, reduced (*Mastogenius*-like)

85. Wing – r4 cross vein:
0, present; 1, absent

86. Wing – r3 and RP connected:
0, no; 1, yes

87. Wing – 2nd cubito-anal cell (“wedge” cell):
0, present; 1, absent

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              1         2         3         4         5         6         7         8
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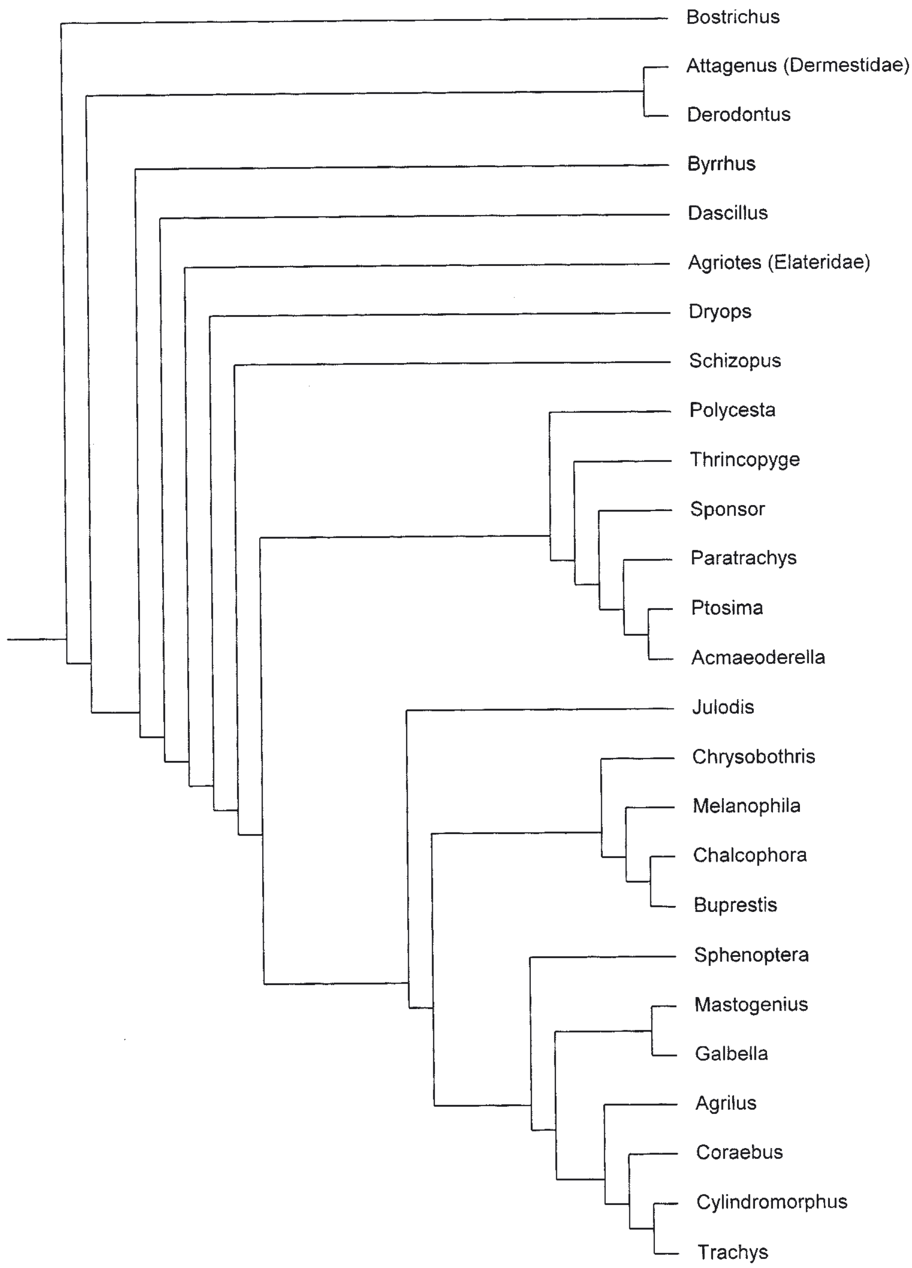
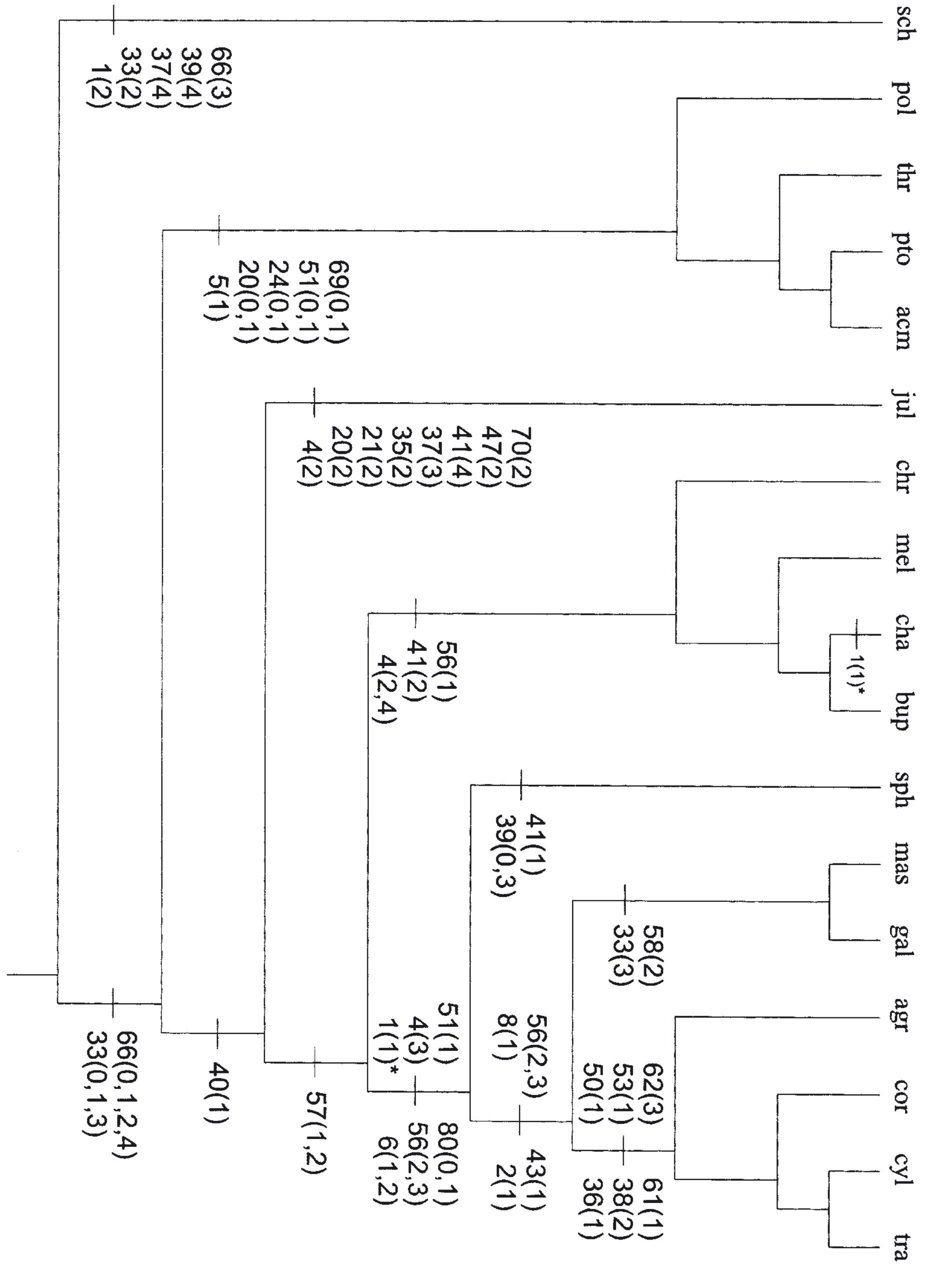
der  00202001000?????000??000?00??001?01??????0??00?0001000000??0??0?????0000??000?0?105??01
bos  00200000000?????010??100?00??000?00??????0??01?1100000000??0??0?????0020??011?0?0020000
byr  00000001000??????00??000?0???100?11??????1???1?0001000000??1??0?????0000??000?1?0020001
das  00200001000?????000??100?00??200?01??????1??11?0001000000??0??1????00001??00100?0010000
dry  ??000001100?????010??000?00??001?21??????1??01?0001000001??0??2????00001??000?0?001?000
ela  00000001000???0?010??100?00??200?11????????????0001000001??2??0????00001??000?0?0010001
jul  0002000011000100010220000000010102203?4141?111211001000010000?0120000221331020100101111
pol  000010401401310000000001000101????2?0100001?111111?????01000???004000011200101100101111
pto  0010103014010101211110111012000102001100010111?0101000001311??2004011001200101100112101
acm  000010203203010021111010101200111200110001010130100000041311001004011011330001101122111
sch  20101031210001000010010010001201221?4?4?3??001000000000001100???003000021000100100010000
thr  00101030120121102100000110100101120010000??111?1001000001110??1004000101000020100111101
mas  11030011330101002100010010121111300???0????????0001100022212??2024012101200101101013001
cha  100400211102300011000010001311010110110121011101000000011101??0011000001210110000111100
sph  10030140110100011100000001010020111001?31110111?1101000002101??002000000112101001010 1001
bup  0012005011010000110000301010020101101101210111010000001121020?1021000001000021000111000
mel  0002002014010000110000301010120110101101210111?0000000012302??1022000001000011000111000
chr  00120020110100000000001001101201100011012101011100000001210 2??1012000001000101000101100
agr  110321313311000021130110101202011001020100101011011011122302130001000101520000000100001
cor  1103213122010001211311101011020110010201001010111110101223 11?3100100000152010001 0100101
cyl  1103124115010020210001101011011110010?11301010?1011011131011??100010000150010110104 2101
tra  1103212121010030311311001011021102112?21301011310111111323111310211000015200011 01030101
gal  11031201200101013110010010121201311001010111 11?1101100132211??2024010001520002010000101
par  ?????0????0???213111110110100???????1?2001?011???????????010??2024011?0100000210?0?0???
spo  ?????0????0???001120010110120????????????????????????????000??2024111?0101000210?1?1???
```

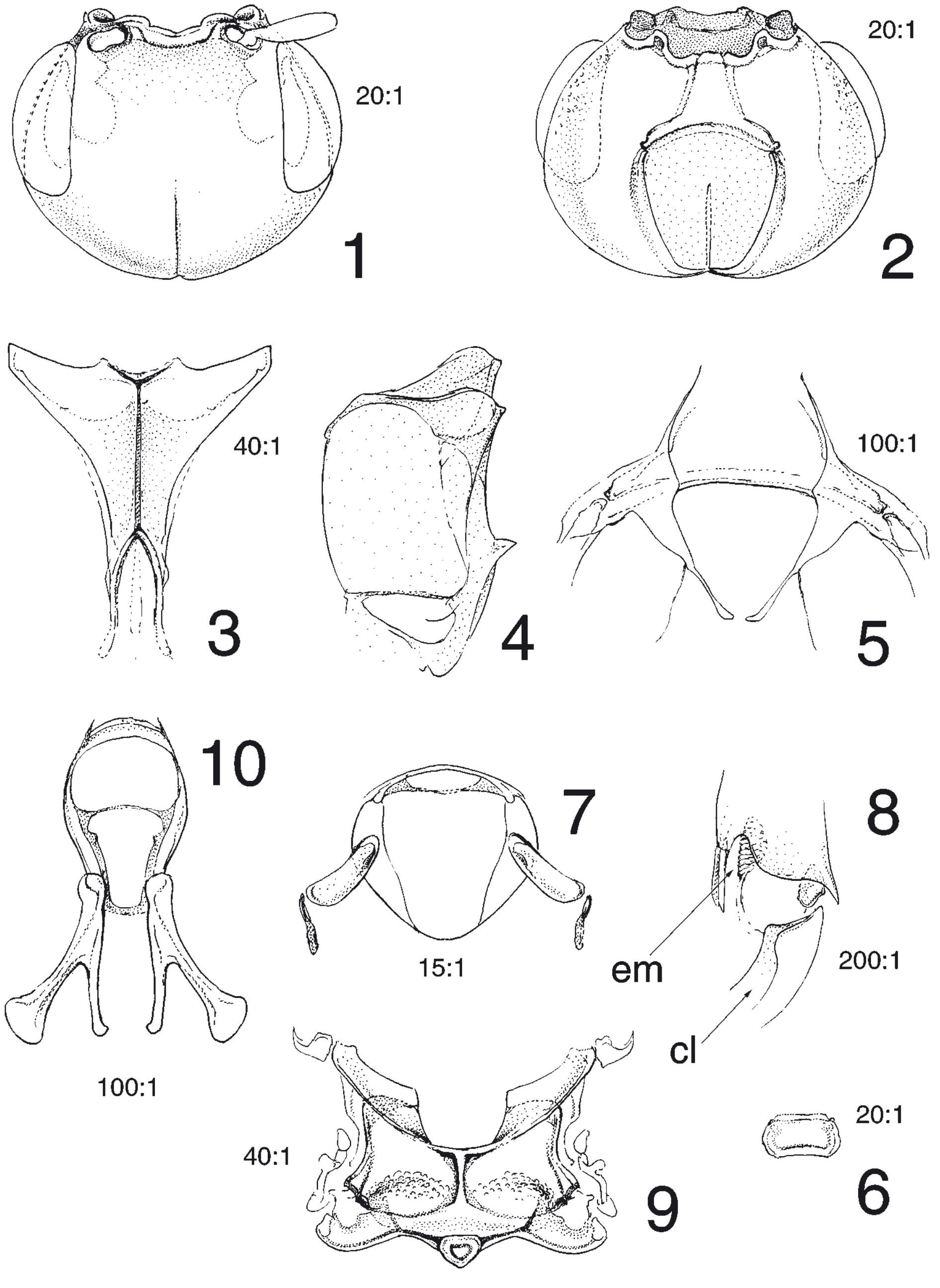
Tab. 2. Character state matrix. All the multistate characters (1, 3, 4, 5, 6, 7, 9, 10, 12, 13, 15, 16, 17, 19, 20, 21, 23, 28, 29, 30, 33, 34, 35, 37, 38, 39, 41, 47, 56, 57, 58, 60, 62, 63, 65, 66, 69, 70, 71, 73, 74, 77, 78, 83, 84) were treated as unordered ("non-additive" in TreeGardener 1.0). The autapomorphies 11, 26, and 64 were switched off for computing. Abbreviations: Char = characters, Out = Outgroup, att = *Attagenus* (Dermestidae), der = *Derodontus*, bos = *Bostrichus*, byr = *Byrrhus*, das = *Dascillus*, dry = *Dryops*, ela = *Agriotes* (Elateridae), jul = *Julodis*, pol = *Polycesta*, pto = *Ptosima*, acm = *Acmaeoderella*, sch = *Schizopus*, thr = *Thrincopyge*, mas = *Mastogenius*, cha = *Chalcophora*, sph = *Sphenoptera*, bup = *Buprestis*, mel = *Melanophila*, chr = *Chrysobothris*, agr = *Agrilus*, cor = *Coraebus*, cyl = *Cylindromorphus*, tra = *Trachys*, gal = *Galbella*, par = *Paratrachys*, spo = *Sponsor*.



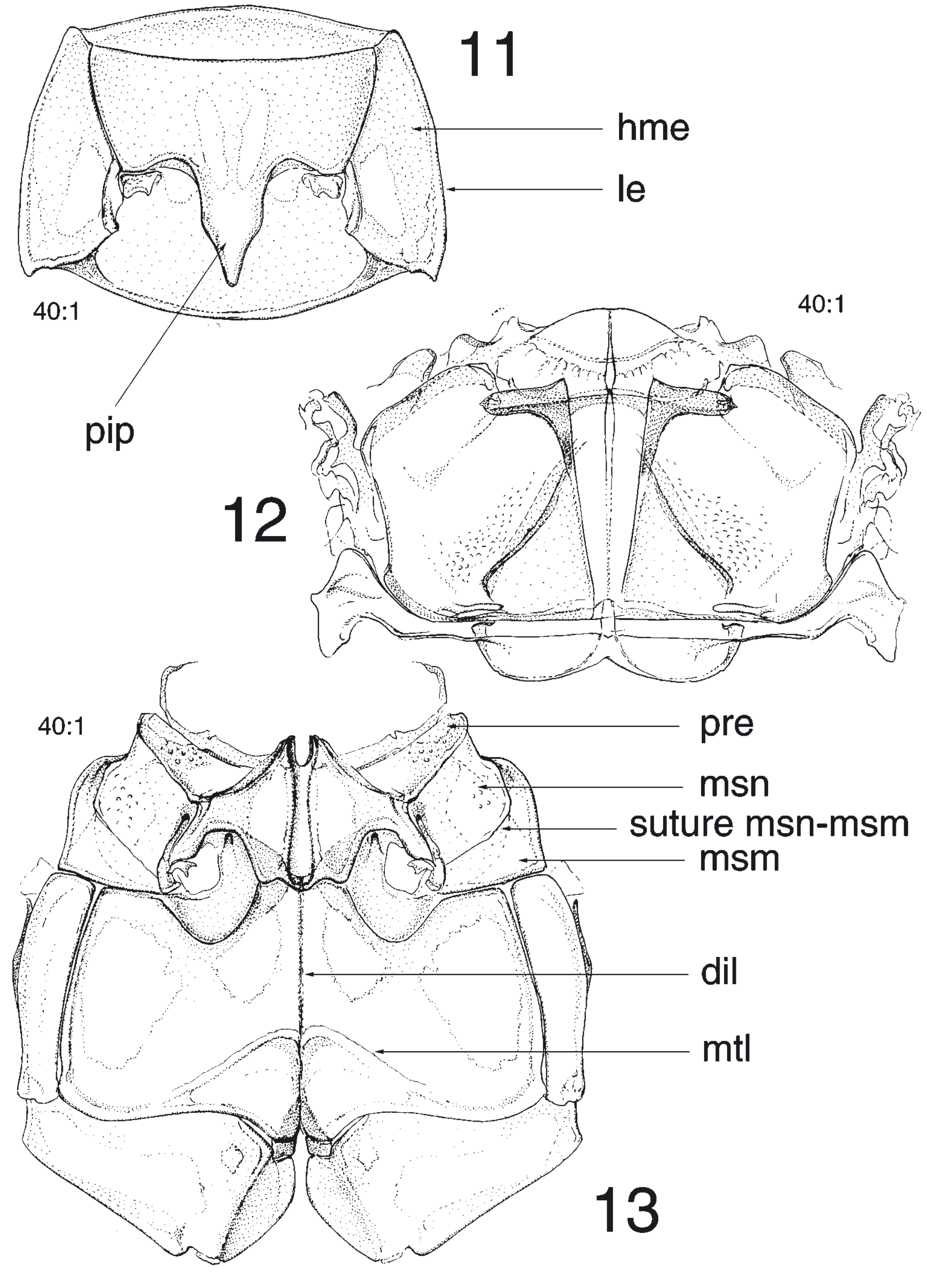
Tree 1. Cladogram computed from the character states matrix (Tab. 2) using the commands *mhennig*bb**, *successive weighting*. The single tree was a result of the analysis (length = 675, ci = 62, ri = 78).



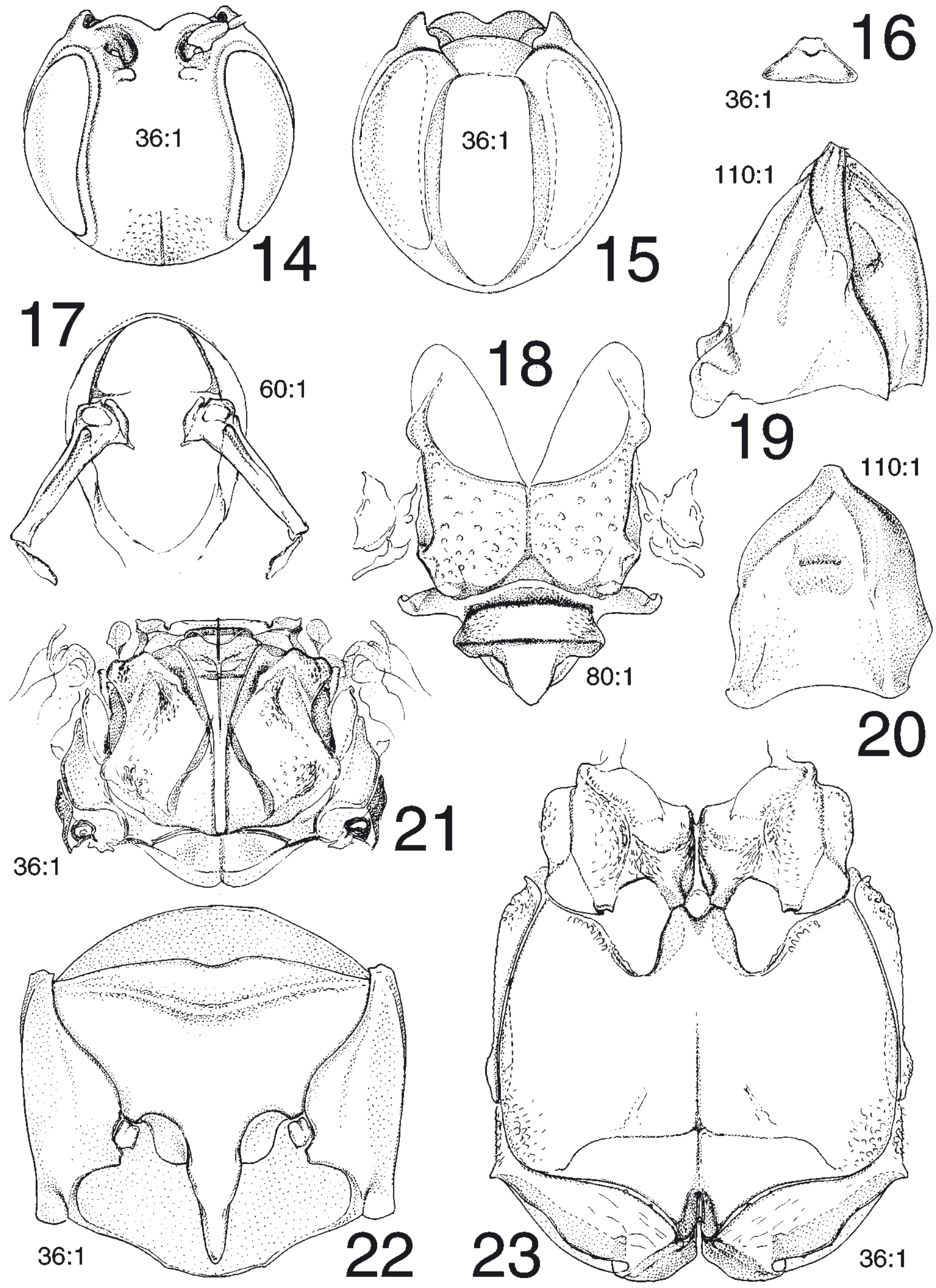
Tree 2. Simplified Tree 1 (outgroups, *Paratrachys* and *Sponsor* removed) with selected character states that support monophyly of respective groups. Homoplasies were excluded with exception of 1(1)*.



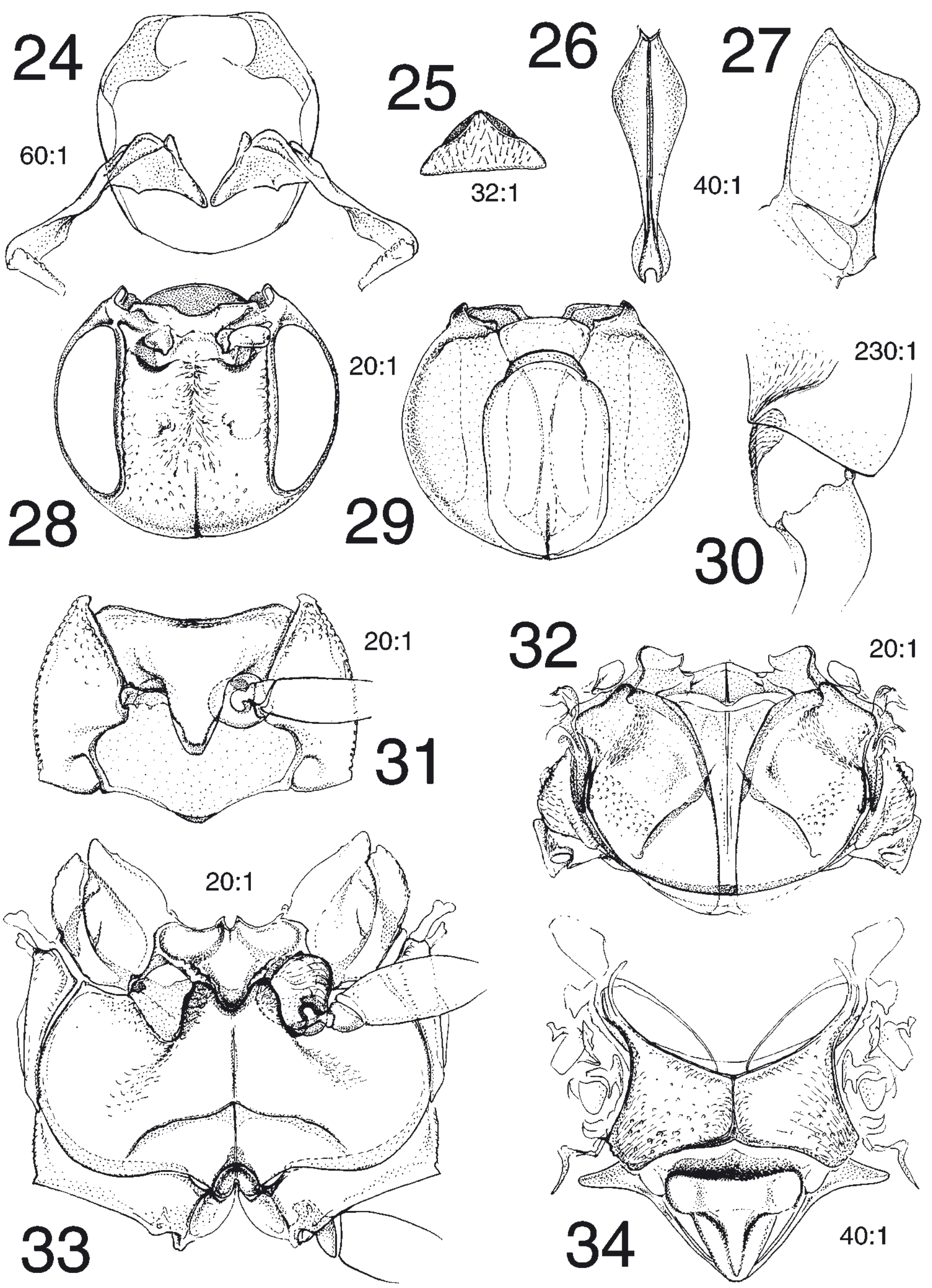
Figs 1–10. *Buprestis octoguttata*: 1, cranium dorsally; 2, cranium ventrally; 3, metendosternite ventrally; 4, metendosternite laterally; 5, tentorium; 6, mentum; 7, cranium posteriorly, with cervical sclerites; 8, 5th tarsomere, detail of apex; 9, mesonotum. *Mastogenius parallelus*: 10, cranium posteriorly, with cervical sclerites.



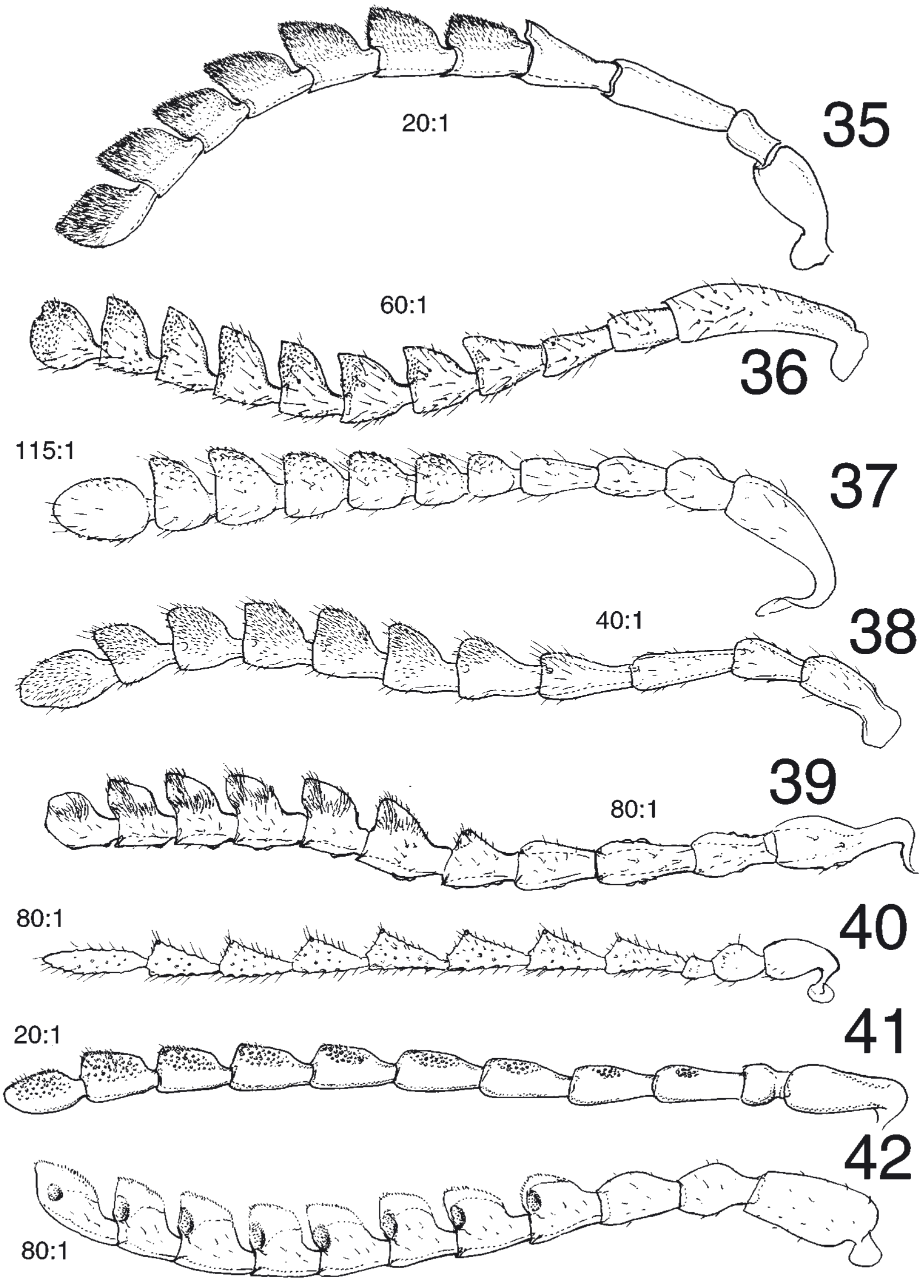
Figs 11–13. *Buprestis octoguttata*: 11, prothorax ventrally; 12, metanotum; 13, meso- and metathorax ventrally.



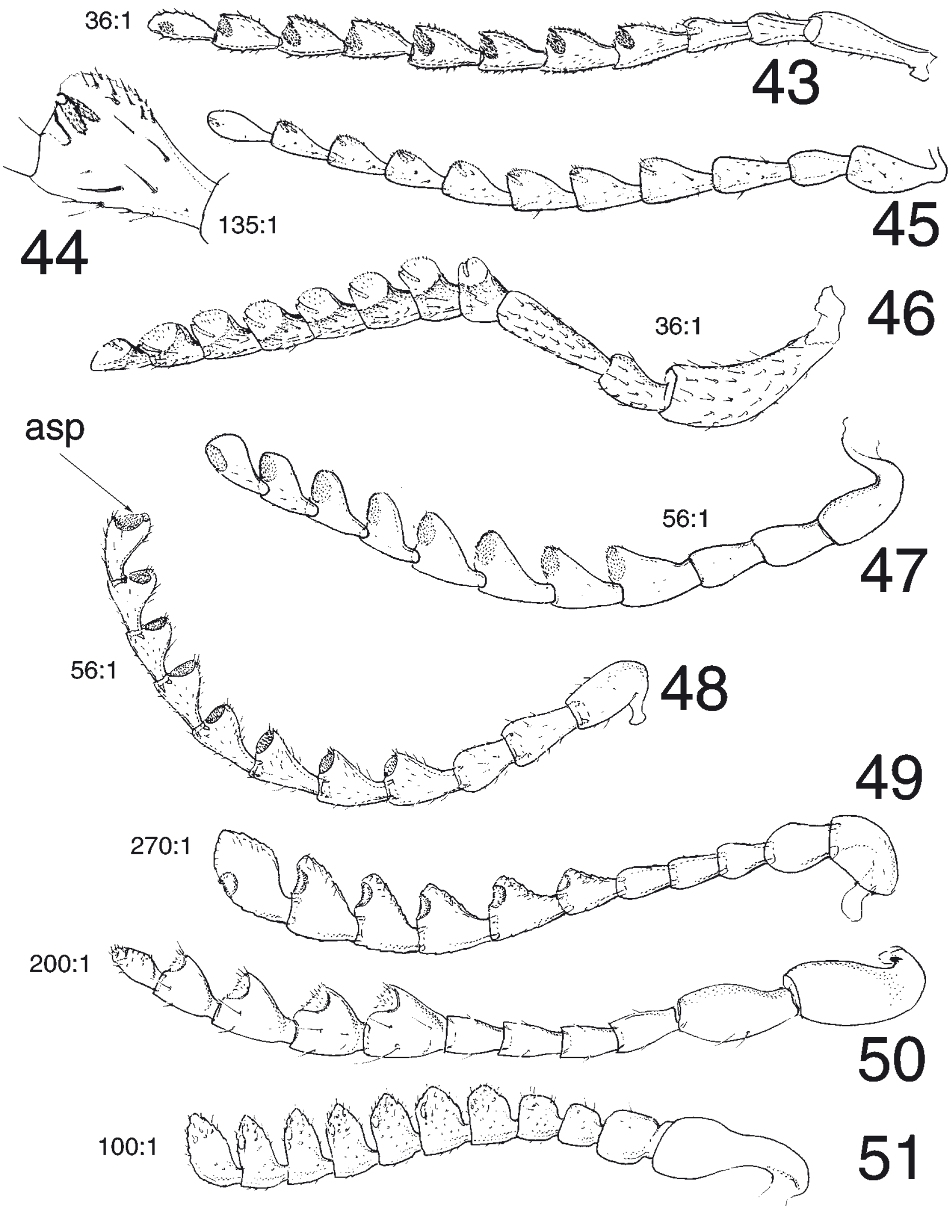
Figs 14–23. *Agrilus viridis*: 14, cranium dorsally; 15, cranium ventrally; 16, mentum; 17, cranium posteriorly, with cervical sclerites; 18, mesonotum; 19, mandible ventrally; 20, mandible innerside; 21, metanotum; 22, prothorax ventrally; 23, meso- and metathorax ventrally.



Figs 24–34. *Coraebus undatus*: 24, cranium posteriorly, with cervical sclerites; 25, mentum; 26, metendosternite ventrally; 27, metendosternite laterally; 28, cranium dorsally; 29, cranium ventrally; 30, 5th tarsomere, detail of apex; 31, prothorax ventrally; 32, metanotum; 33, meso- and metathorax ventrally; 34, mesonotum.



Figs 35–42. Antennae dorsally: 35, *Julodis andreae*; 36, *Ptosima flavoguttata*; 37, *Acmaeoderella discoidea*; 38, *Schizopus laetus*; 39, *Thrincopyge alacris*; 40, *Mastogenius parallelus*; 41, *Chalcophora marianna*; 42, *Sphenoptera lapidaria*.



Figs 43–51. Antennae dorsally: 43, *Buprestis octoguttata*; 44, *Melanophila acuminata*, detail of antennomere; 45, *Melanophila acuminata*; 46, *Chrysobothris affinis*; 47, *Agrilus biguttatus*; 48, *Coraebus undatus*; 49, *Cylindromorphus filum*; 50, *Trachys minuta*; 51, *Galbella felix*.

52

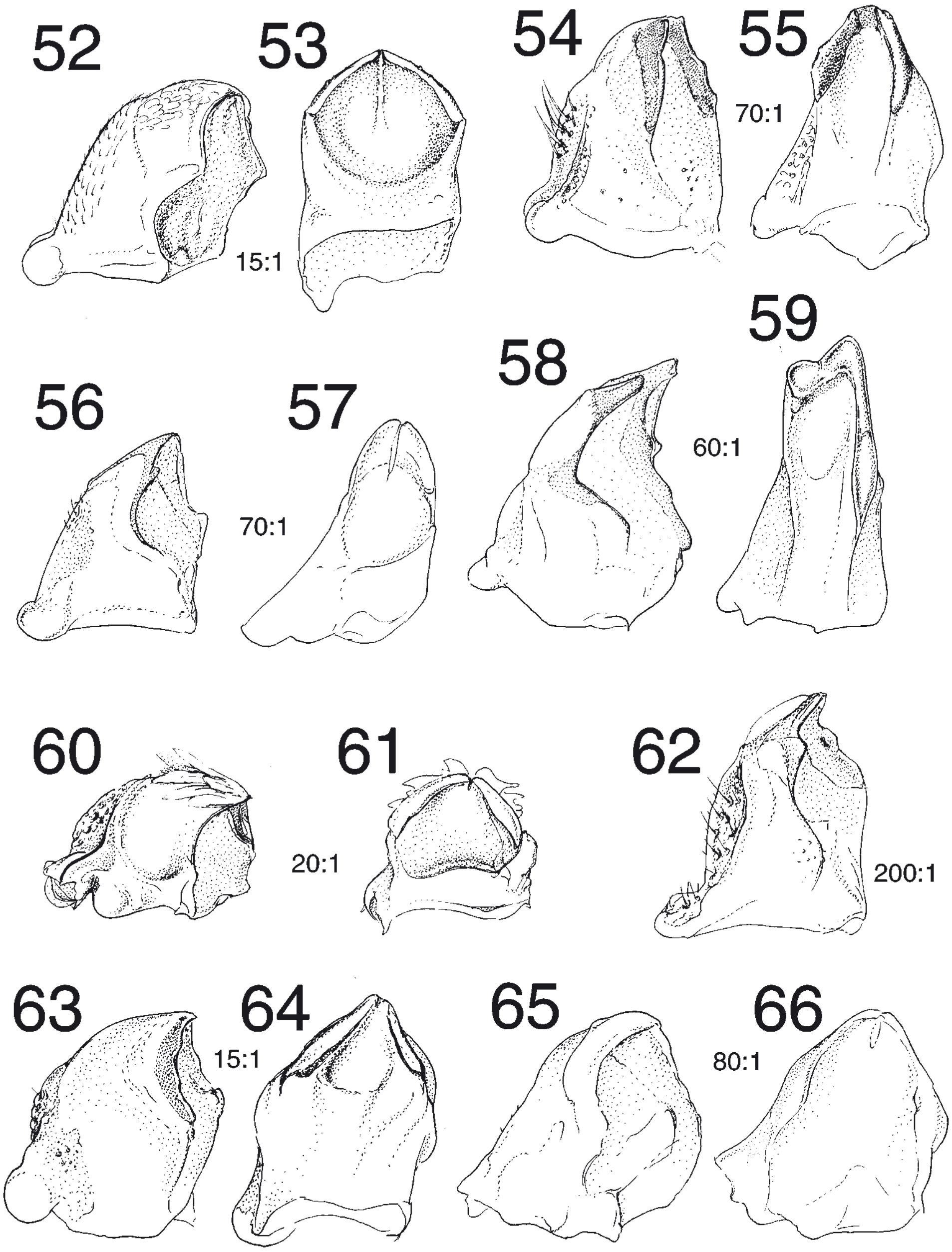
53

15:1

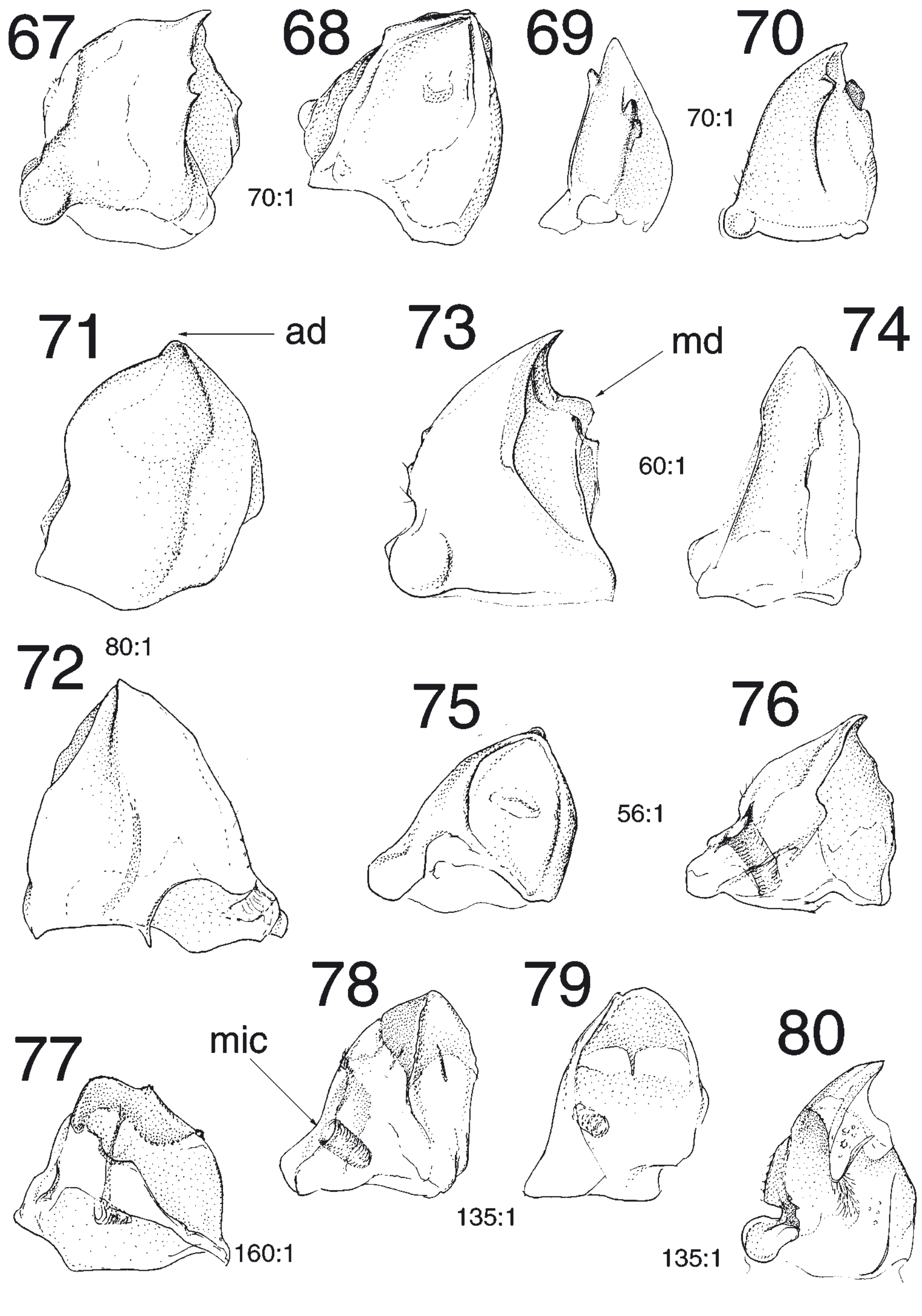
54

55

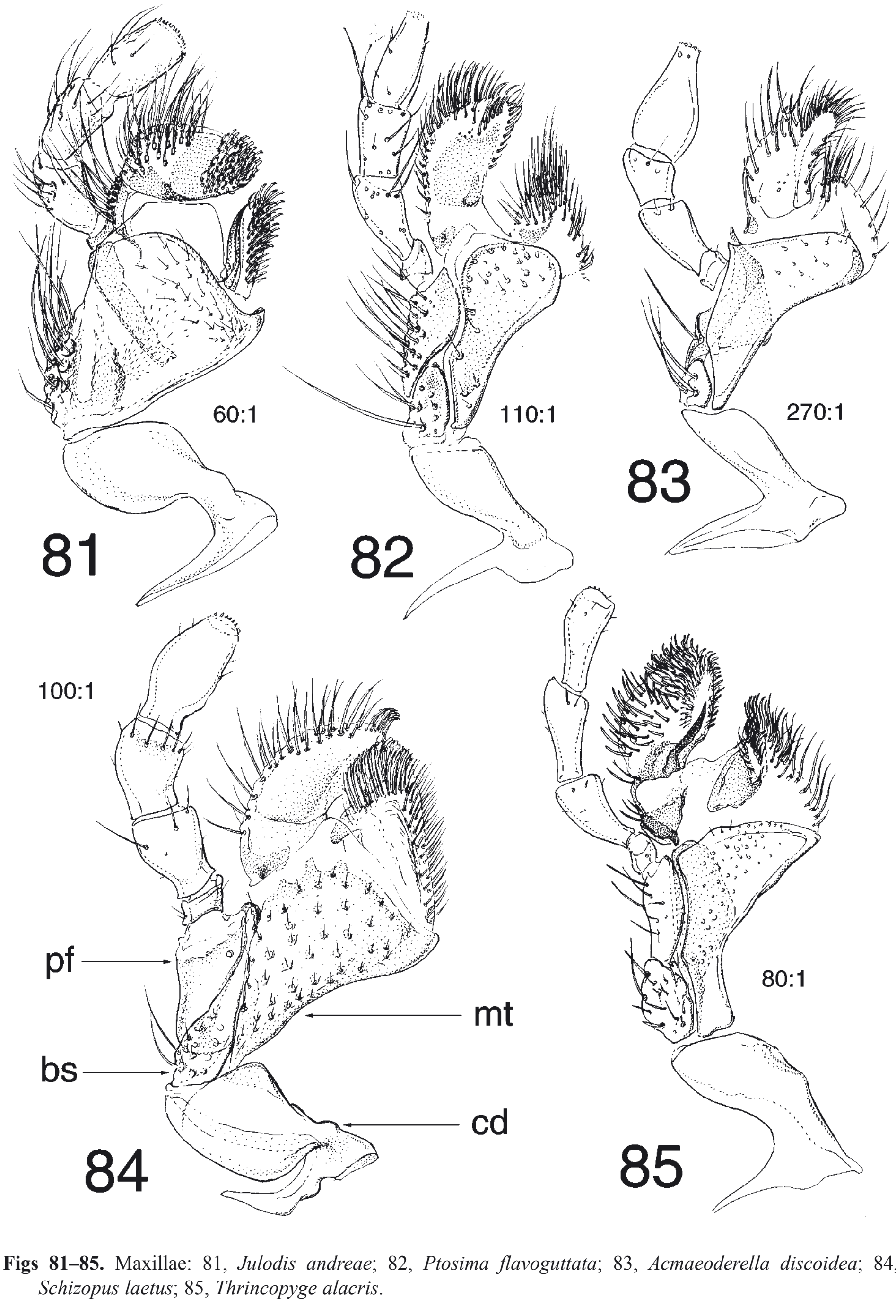
70:1



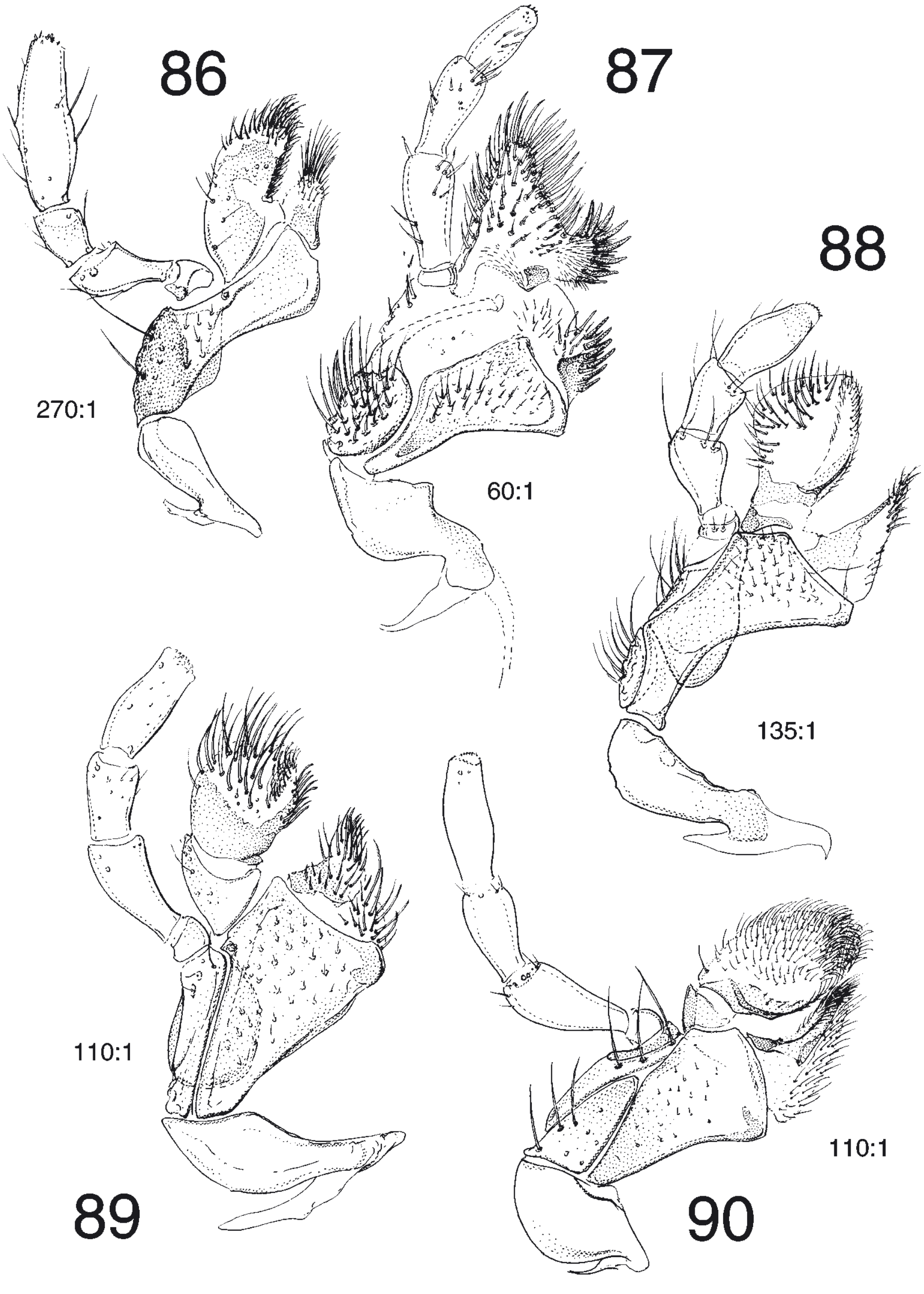
Figs 52–66. Mandibles ventrally, innerside: 52, 53, *Julodis andreae*; 54, 55, *Ptosima flavoguttata*; 56, 57, *Acmaeoderella discoidea*; 58, 59, *Schizopus laetus*; 60, 61, *Thrincopyge alacris*; 62, *Mastogenius parallelus*; 63, 64, *Chalcophora marianna*; 65, 66, *Sphenoptera lapidaria*.



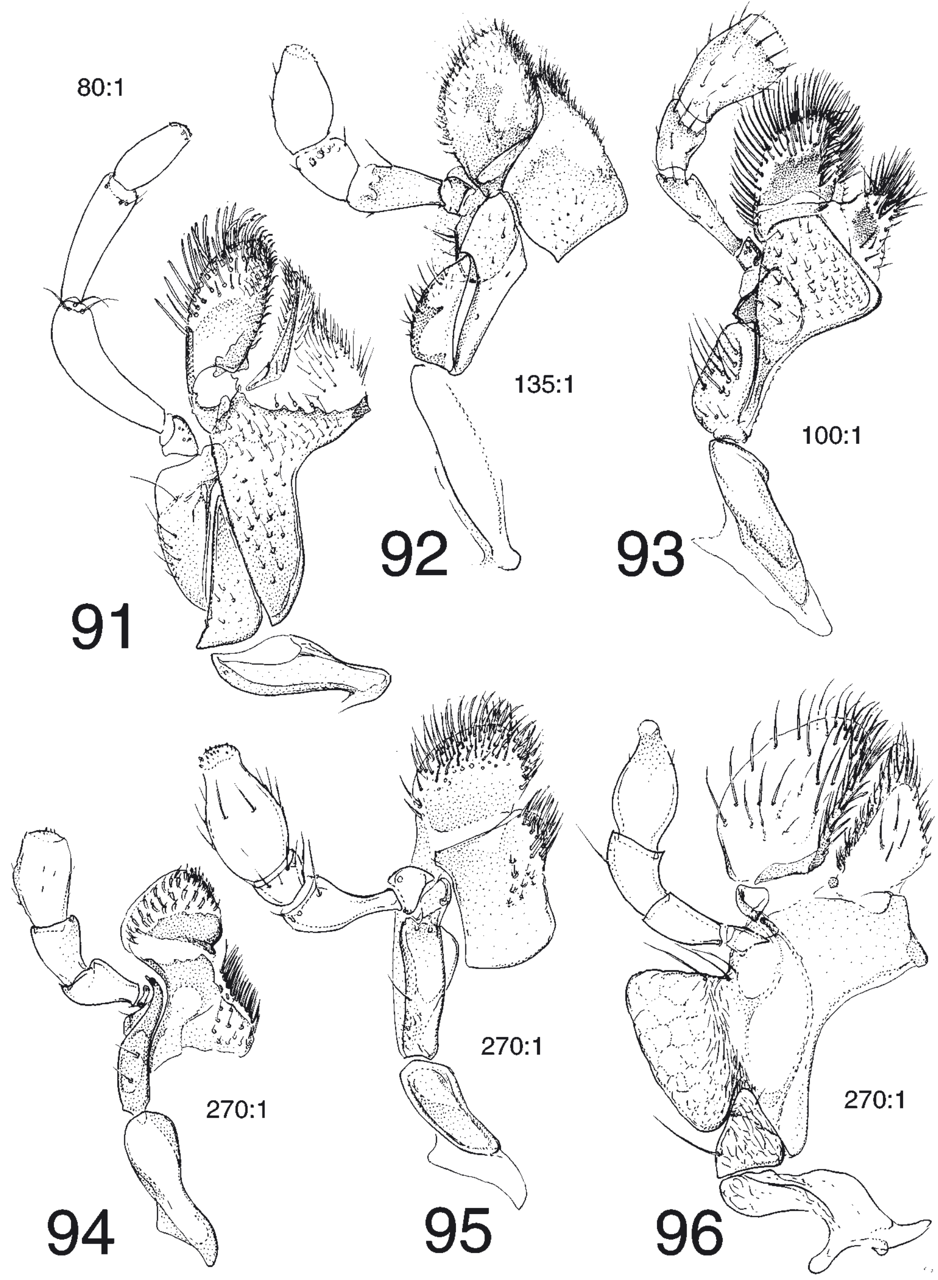
Figs 67–80. Mandibles ventrally, innerside: 67, 68, *Buprestis octoguttata*; 69, 70, *Melanophila acuminata*; 71, 72, *Agrilus viridis*; 73, 74, *Chrysobothris affinis*; 75, 76, *Coraebus undatus*; 77, 78, *Trachys minuta*; 79, 80, *Galbella felix*.



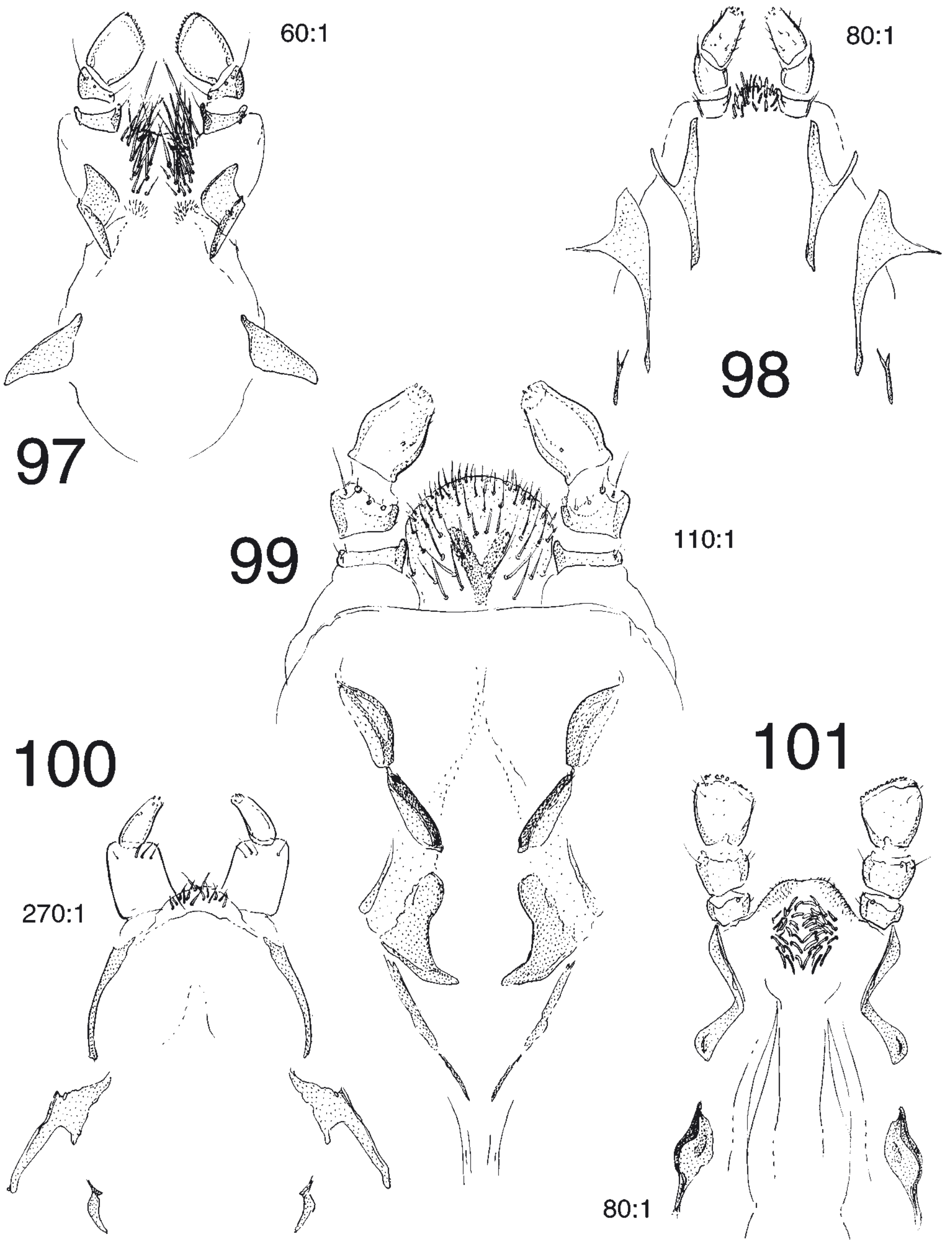
Figs 81–85. Maxillae: 81, *Julodis andreae*; 82, *Ptosima flavoguttata*; 83, *Acmaeoderella discoidea*; 84, *Schizopus laetus*; 85, *Thrincopyge alacris*.



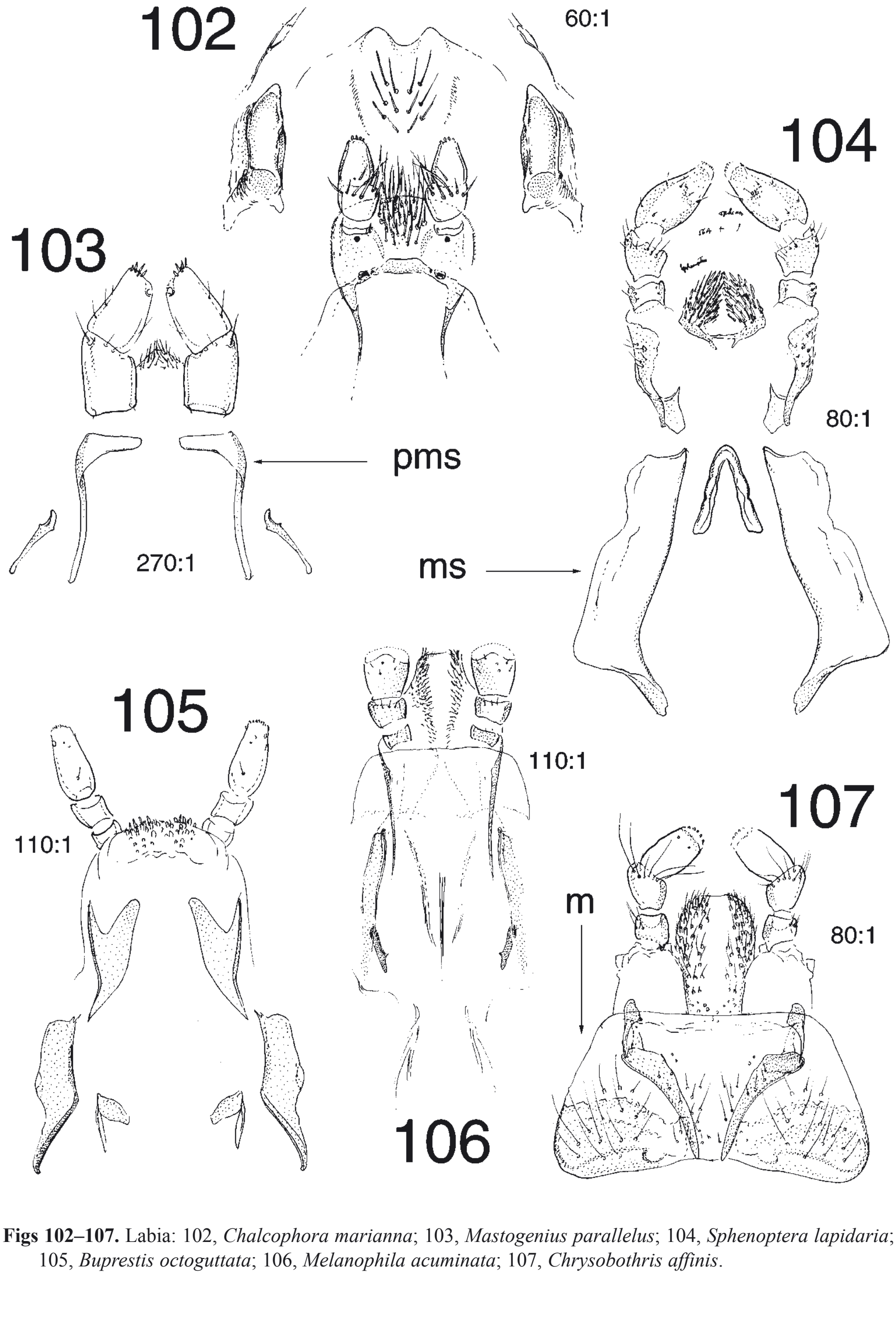
Figs 86–90. Maxillae: 86, *Mastogenius parallelus*; 87, *Chalcophora marianna*; 88, *Sphenoptera lapidaria*; 89, *Buprestis octoguttata*; 90, *Melanophila acuminata*.



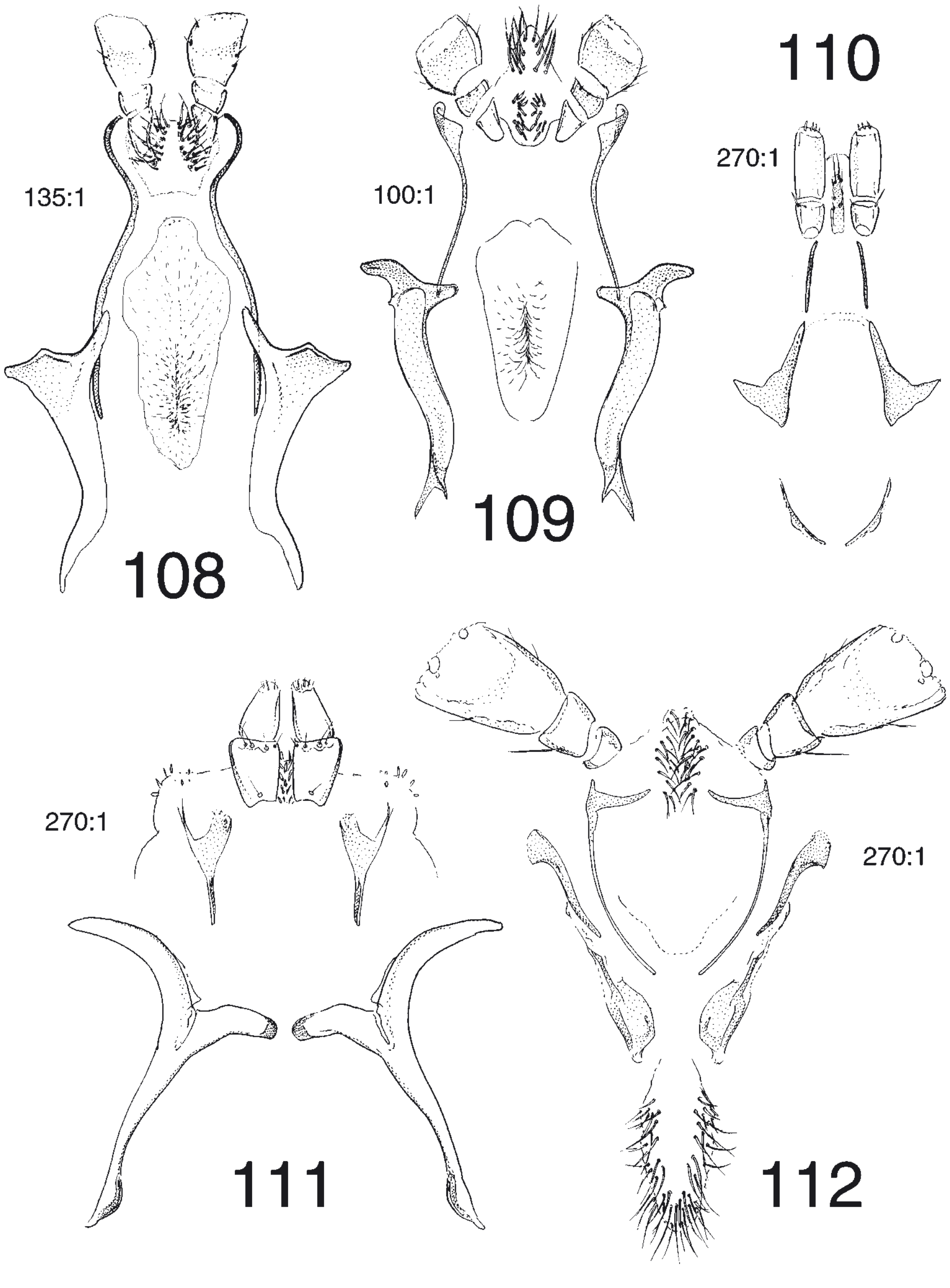
Figs 91–96. Maxillae: 91, *Chrysobothris affinis*; 92, *Agrilus biguttatus*; 93, *Coraebus undatus*; 94, *Cylindromorphus filum*; 95, *Trachys minutus*; 96, *Galbella felix*.



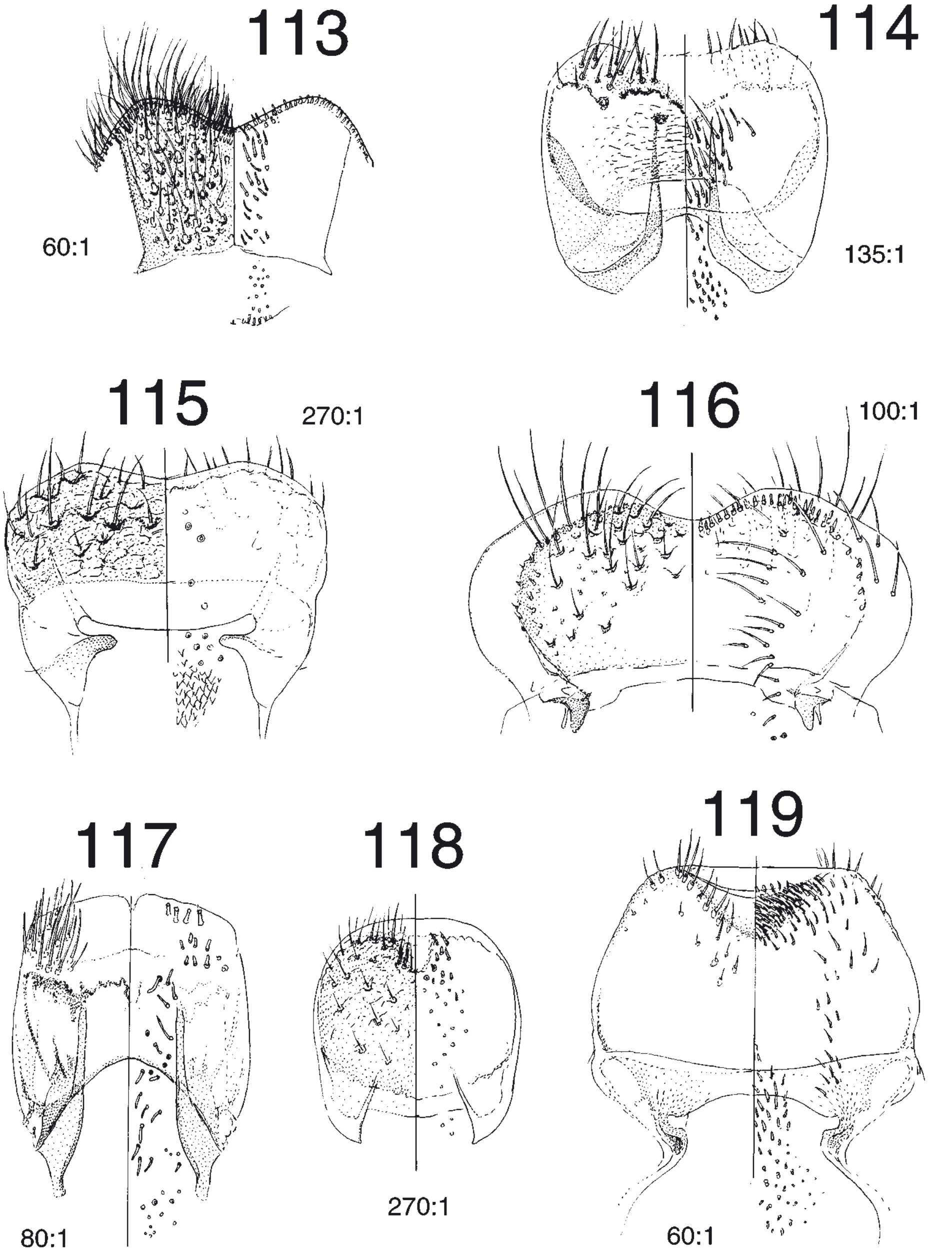
Figs 97–101. Labia: 97, *Julodis andreae*; 98, *Ptosima flavoguttata*; 99, *Schizopus laetus*; 100, *Acmaeoderella discoidea*; 101, *Thrincopyge alacris*.



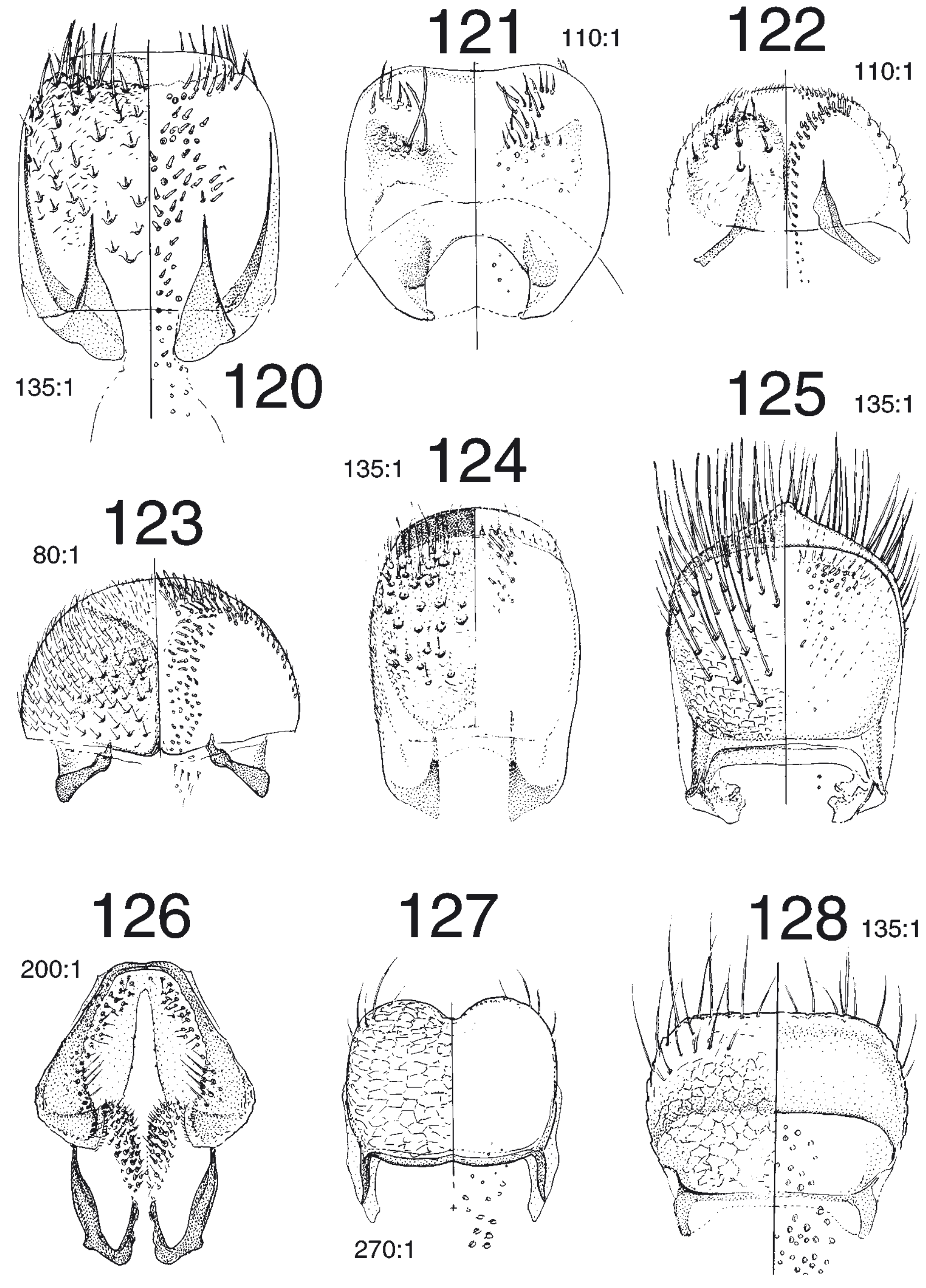
Figs 102–107. Labia: 102, *Chalcophora marianna*; 103, *Mastogenius parallelus*; 104, *Sphenoptera lapidaria*; 105, *Buprestis octoguttata*; 106, *Melanophila acuminata*; 107, *Chrysobothris affinis*.



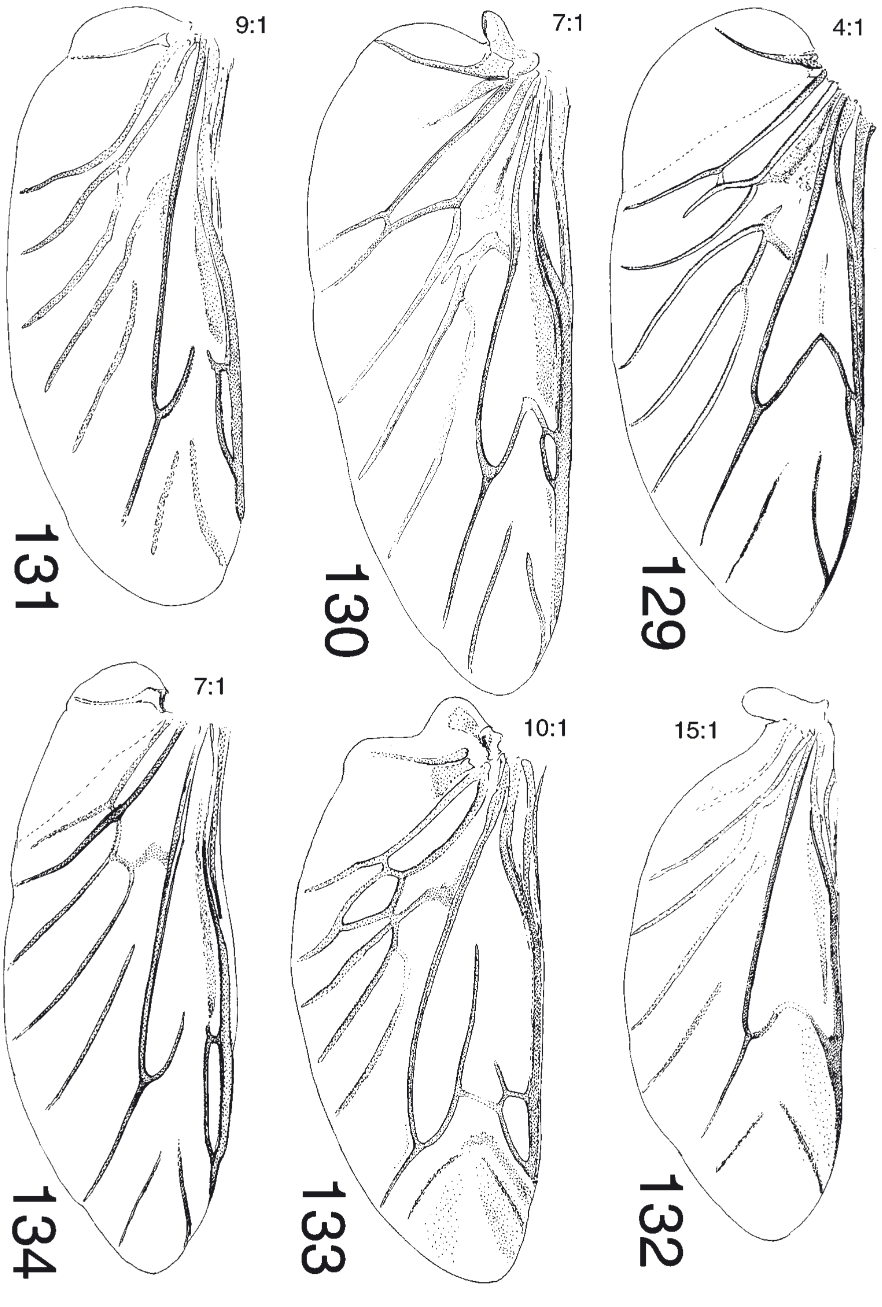
Figs 108–112. Labia: 108, *Agrilus biguttatus*; 109, *Coraebus undatus*; 110, *Cylindromorphus filum*; 111, *Trachys minutus*; 112, *Galbella felix*.



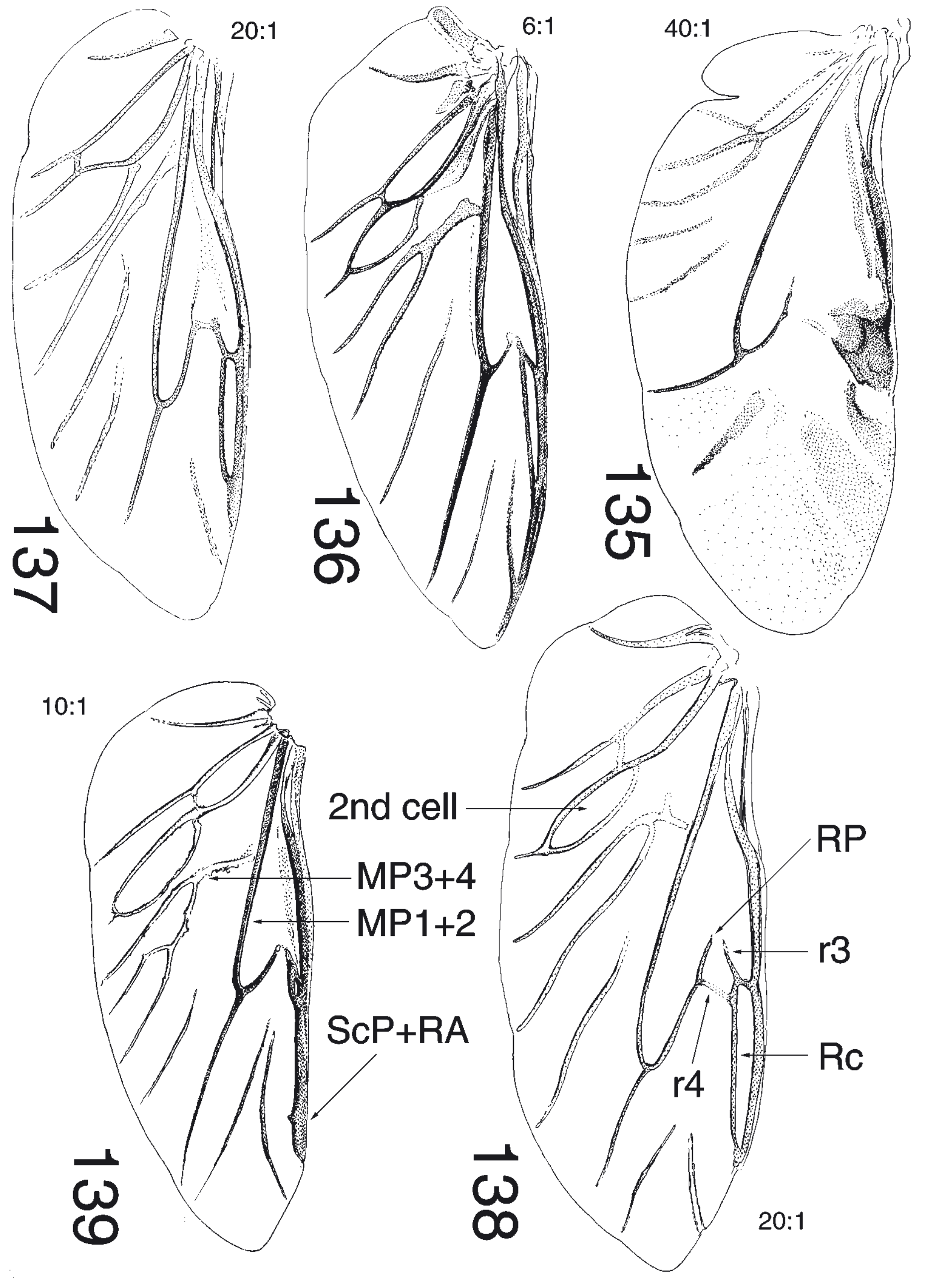
Figs 113–119. Labra, left dorsally, right ventrally (epipharynx): 113, *Julodis andreae*; 114, *Ptosima flavoguttata*; 115, *Acmaeoderella discoidea*; 116, *Schizopus laetus*; 117, *Thrincopyge alacris*; 118, *Mastogenius parallelus*; 119, *Chalcophora marianna*.



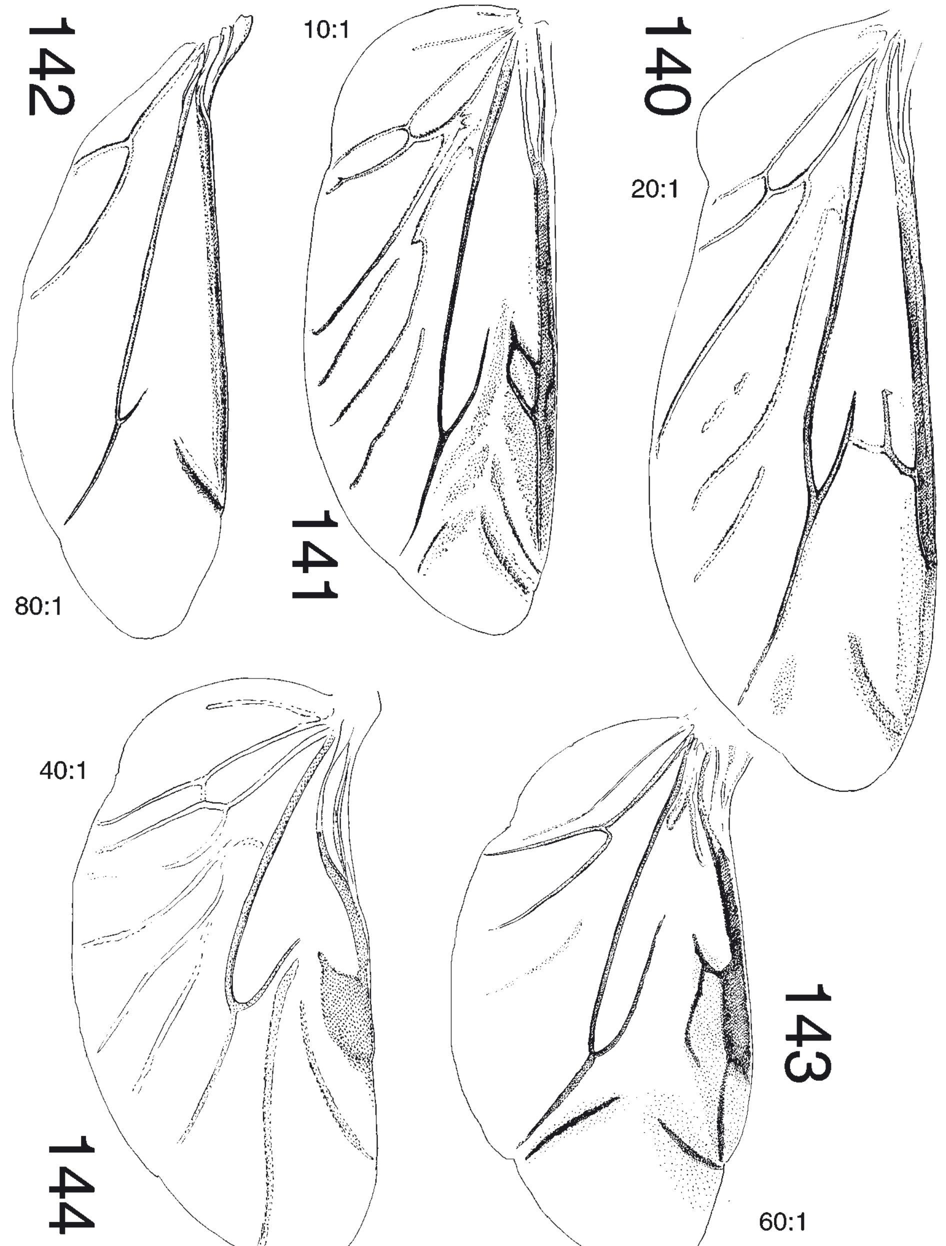
Figs 120–128. Labra, left dorsally, right ventrally (epipharynx): 120, *Sphenoptera lapidaria*; 121, *Buprestis octoguttata*; 122, *Melanophila acuminata*; 123, *Chrysobothris affinis*; 124, *Agrilus viridis*; 125, *Coraebus undatus*; 126, *Cylindromorphus filum*; 127, *Trachys minutus*; 128, *Galbella felix*.



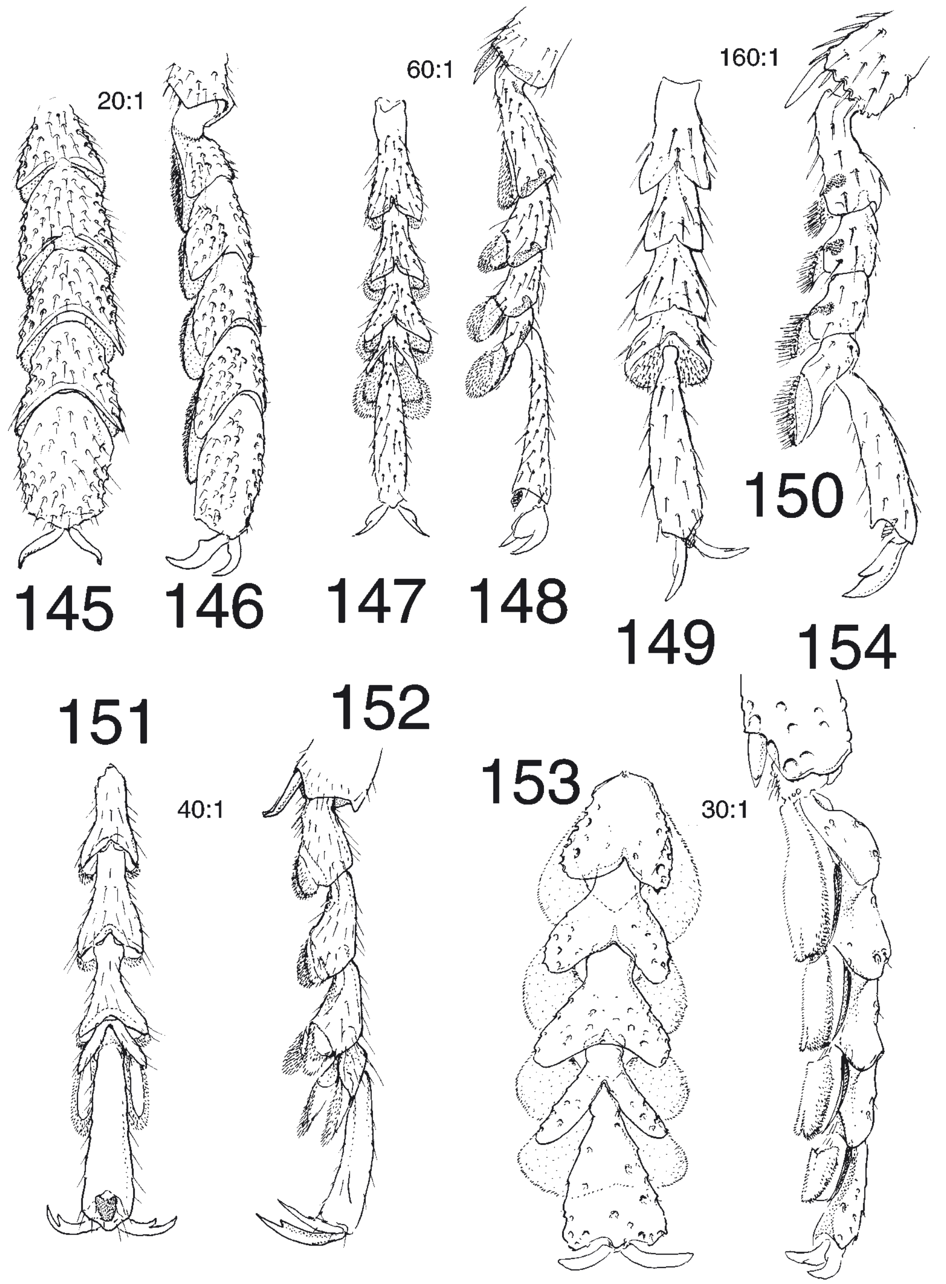
Figs 129–134. Wings: 129, *Julodis andreae*; 130, *Polycesta porcata*; 131, *Ptosima flavoguttata*; 132, *Acmaeoderella discoidea*; 133, *Schizopus laetus*; 134, *Thrincopyge alacris*.



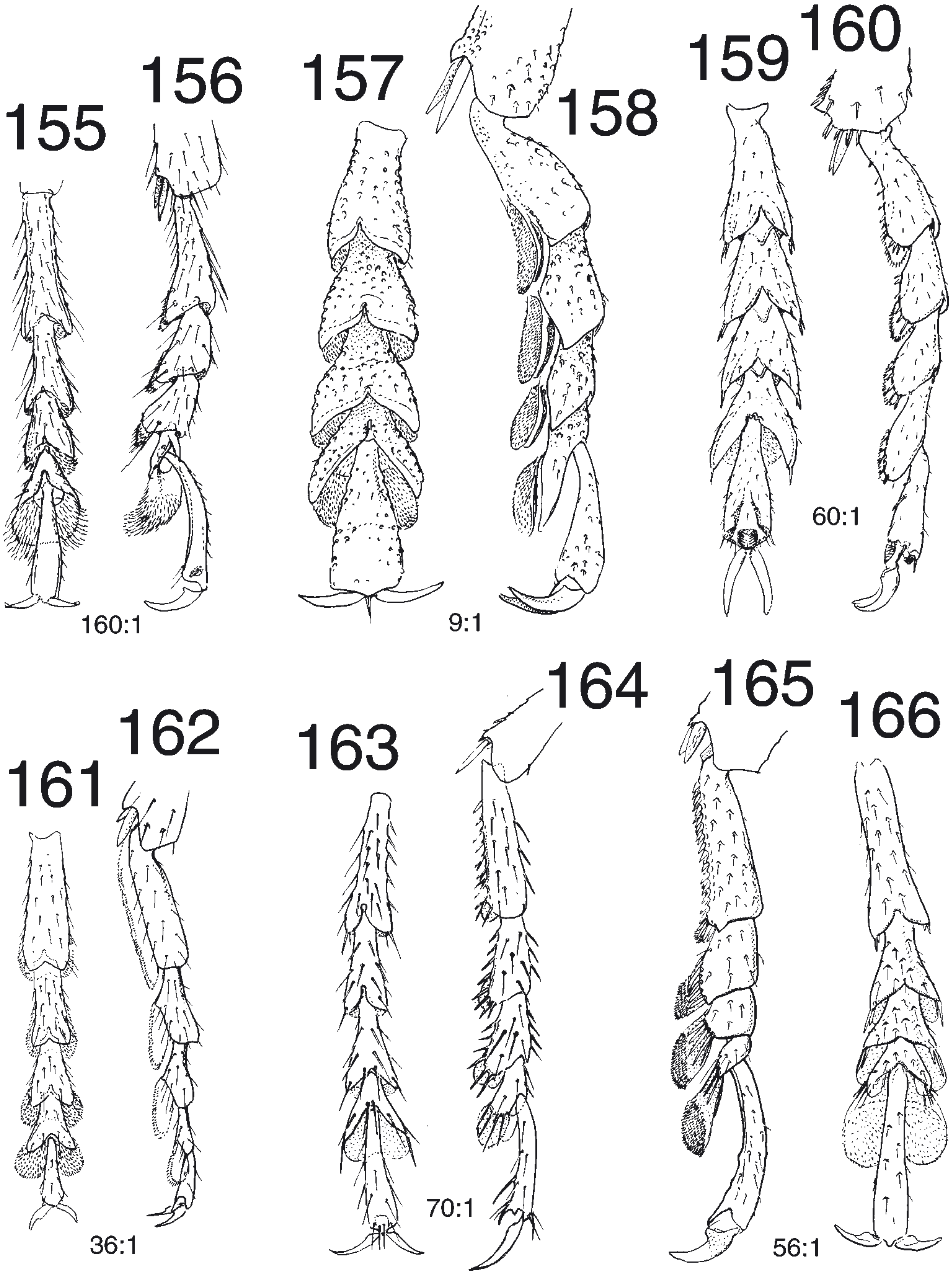
Figs 135–139. Wings: 135, *Mastogenius parallelus*; 136, *Chalcophora marianna*; 137, *Sphenoptera lapidaria*; 138, *Buprestis octoguttata*; 139, *Chrysobothris chrysostigma*.



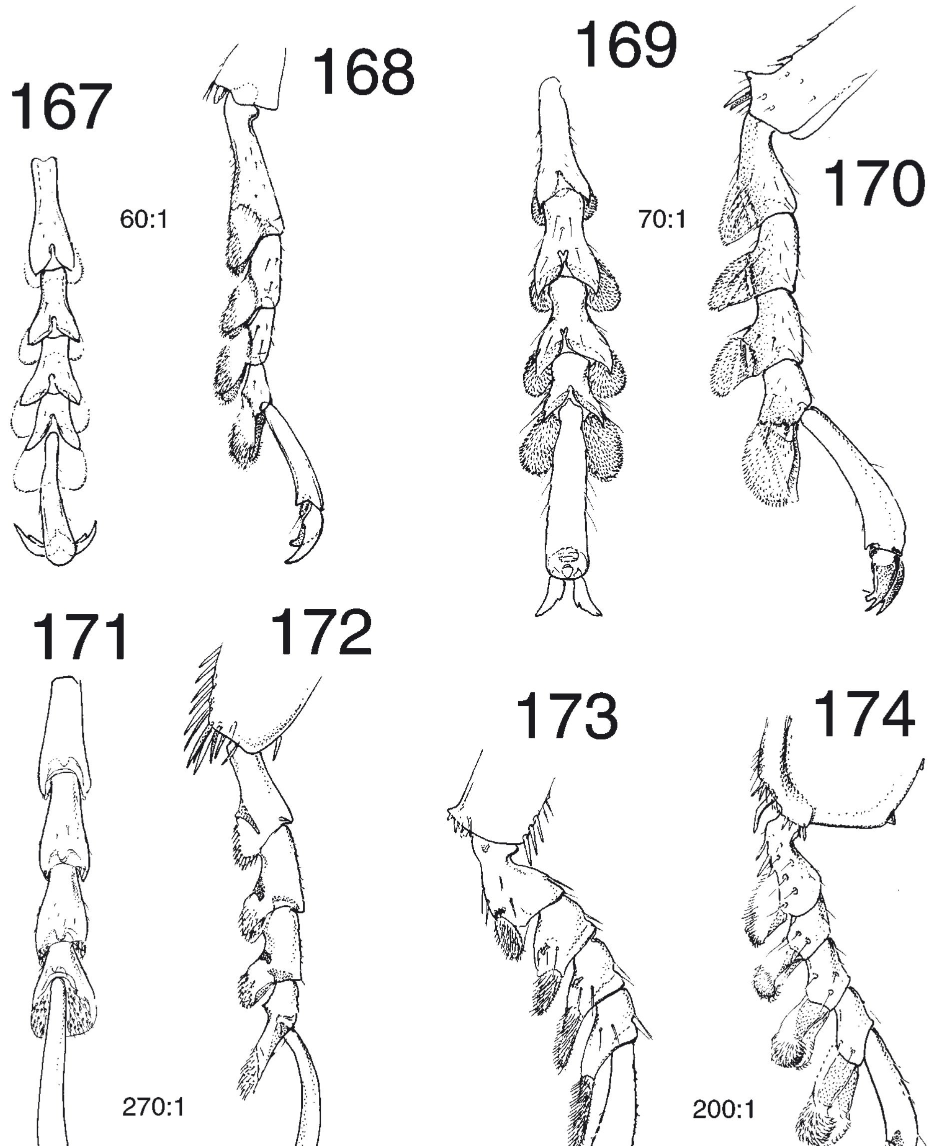
Figs 140–144. Wings: 140, *Agrilus viridis*; 141, *Coraebus undatus*; 142, *Cylindromorphus filum*; 143, *Trachys minutus*; 144, *Galbella felix*.



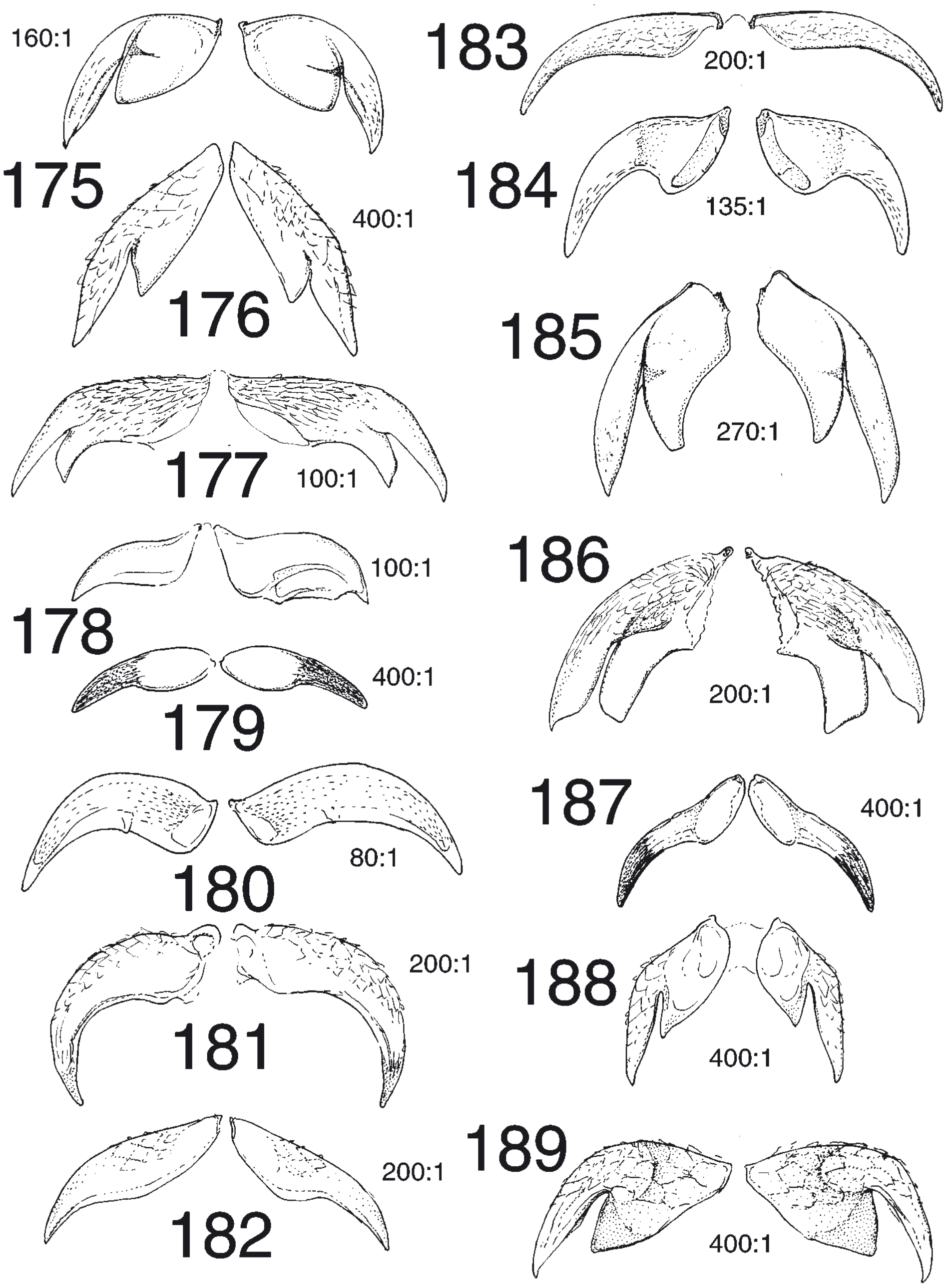
Figs 145–154. Middle tarsi dorsally and laterally: 145, 146, *Julodis andreae*; 147, 148, *Ptosima flavoguttata*; 149, 150, *Acmaeoderella discoidea*; 151, 152, *Schizopus laetus*; 153, 154, *Thrincopyge alacris*.



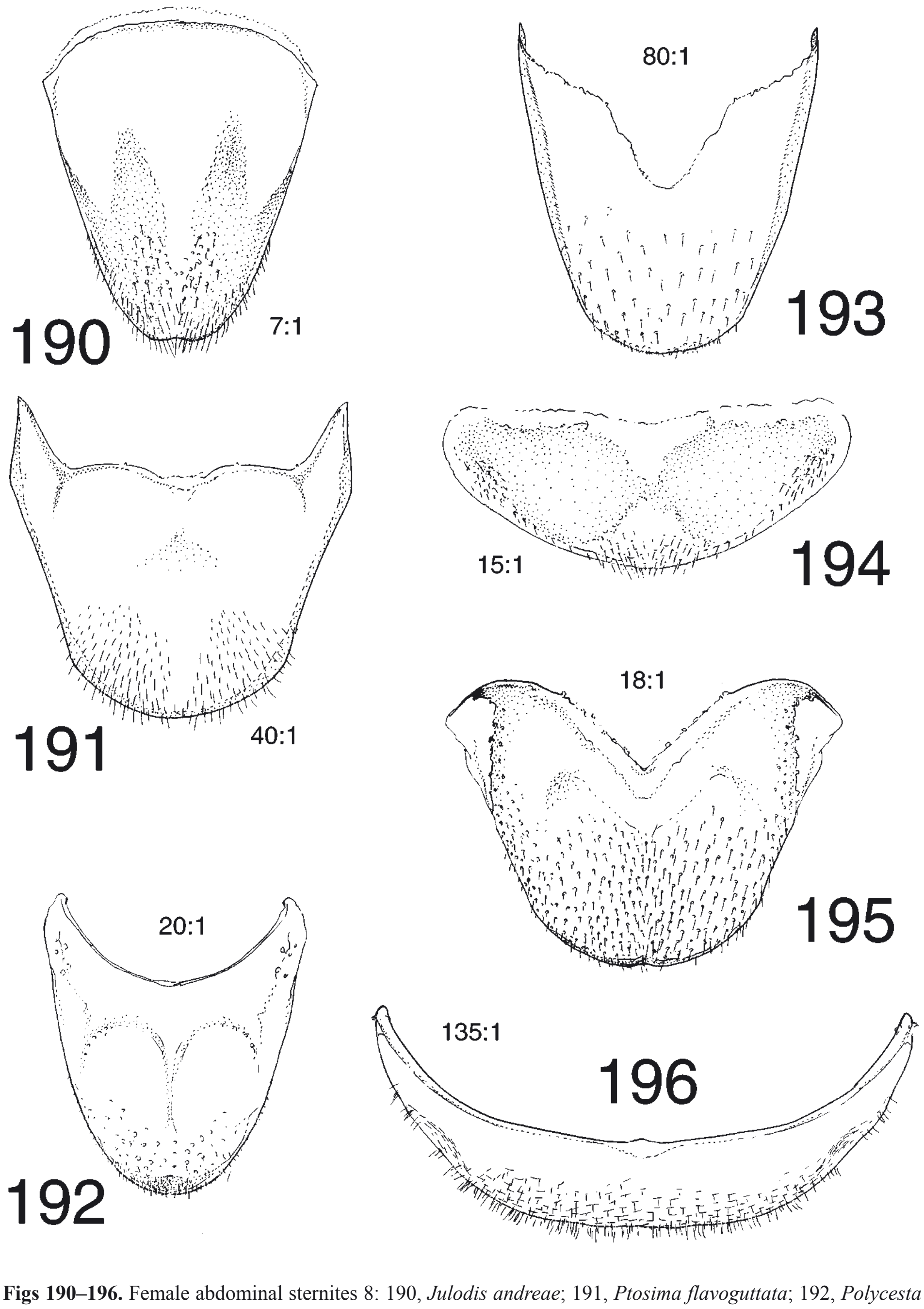
Figs 155–166. Middle tarsi dorsally and laterally: 155, 156, *Mastogenius parallelus*; 157, 158, *Chalcophora marianna*; 159, 160, *Sphenoptera lapidaria*; 161, 162, *Buprestis octoguttata*; 163, 164, *Melanophila acuminata*; 165, 166, *Chrysobothris affinis*.



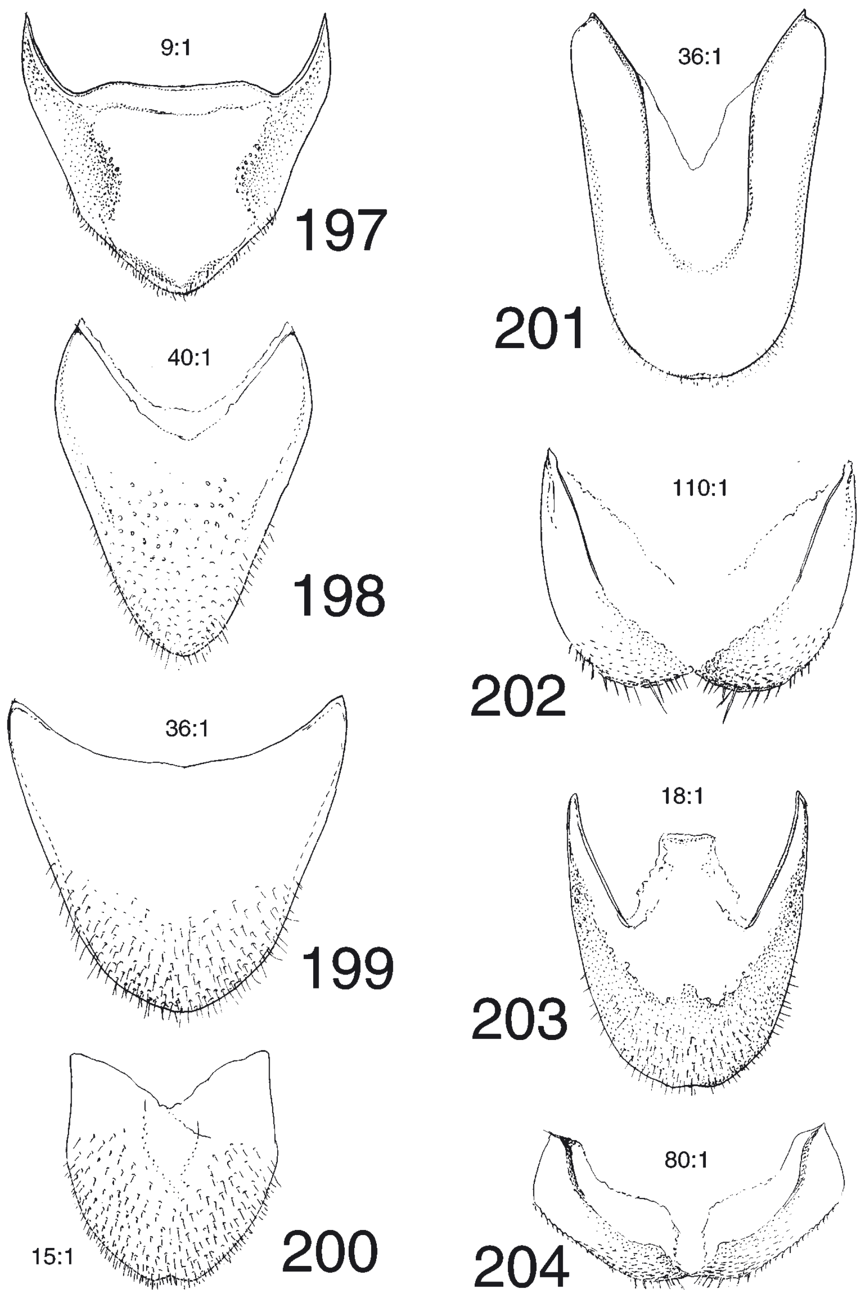
Figs 167–174. Middle tarsi dorsally and laterally: 167, 168, *Agrilus biguttatus*; 169, 170, *Coraebus undatus*; 171, 172, *Cylindromorphus filum*; 173, *Trachys minutus*; 174, *Galbella felix*.



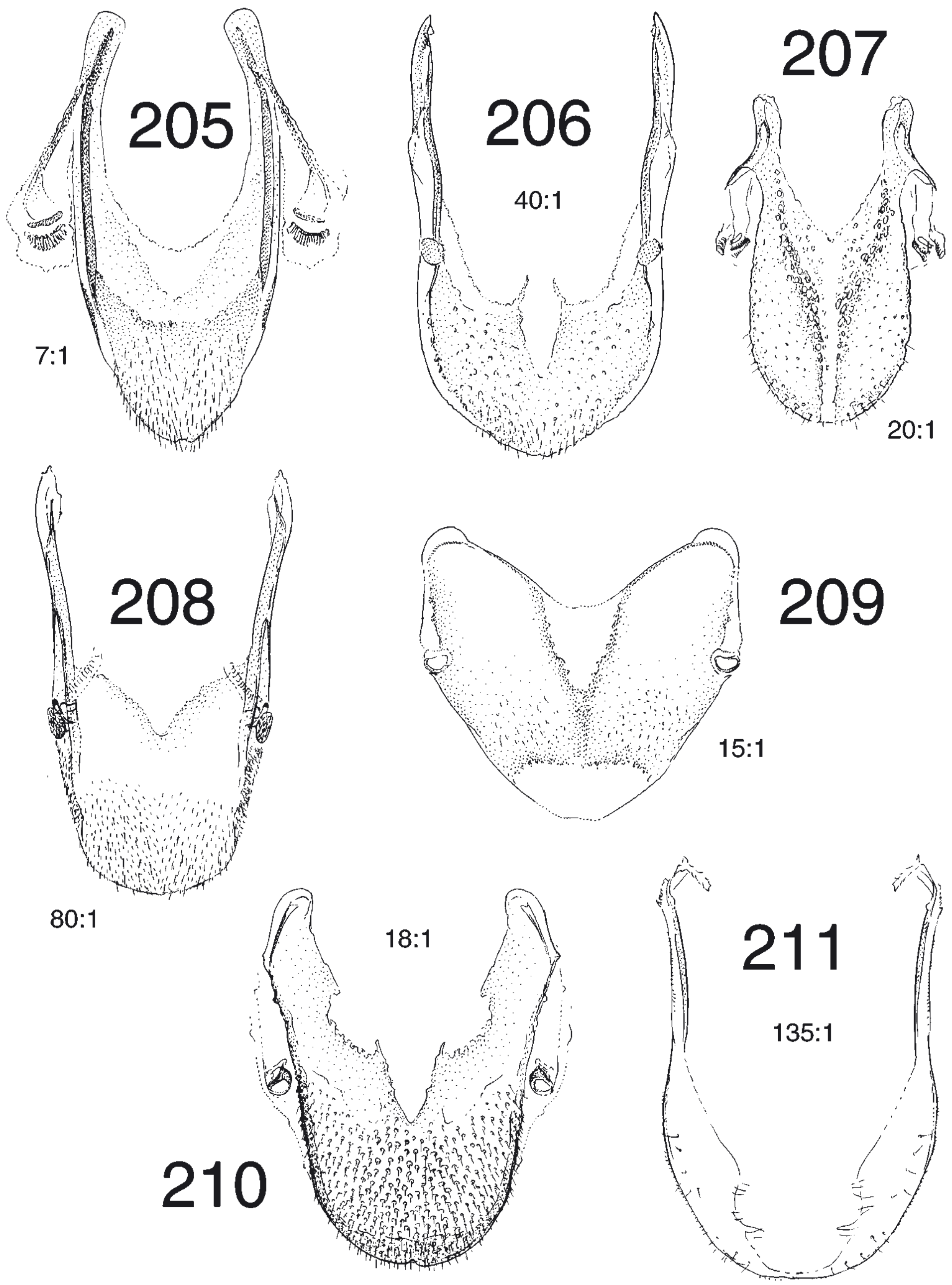
Figs 175–189. Middle claws: 175, *Ptosima flavoguttata*; 176, *Acmaeoderella discoidea*; 177, *Schizopus laetus*; 178, *Thrincopyge alacris*; 179, *Mastogenius parallelus*; 180, *Chalcophora marianna*; 181, *Sphenoptera lapidaria*; 182, *Buprestis octoguttata*; 183, *Melanophila acuminata*; 184, *Chrysobothris affinis*; 185, *Agrilus biguttatus*; 186, *Coraebus undatus*; 187, *Cylindromorphus filum*; 188, *Trachys minutus*; 189, *Galbella felix*.



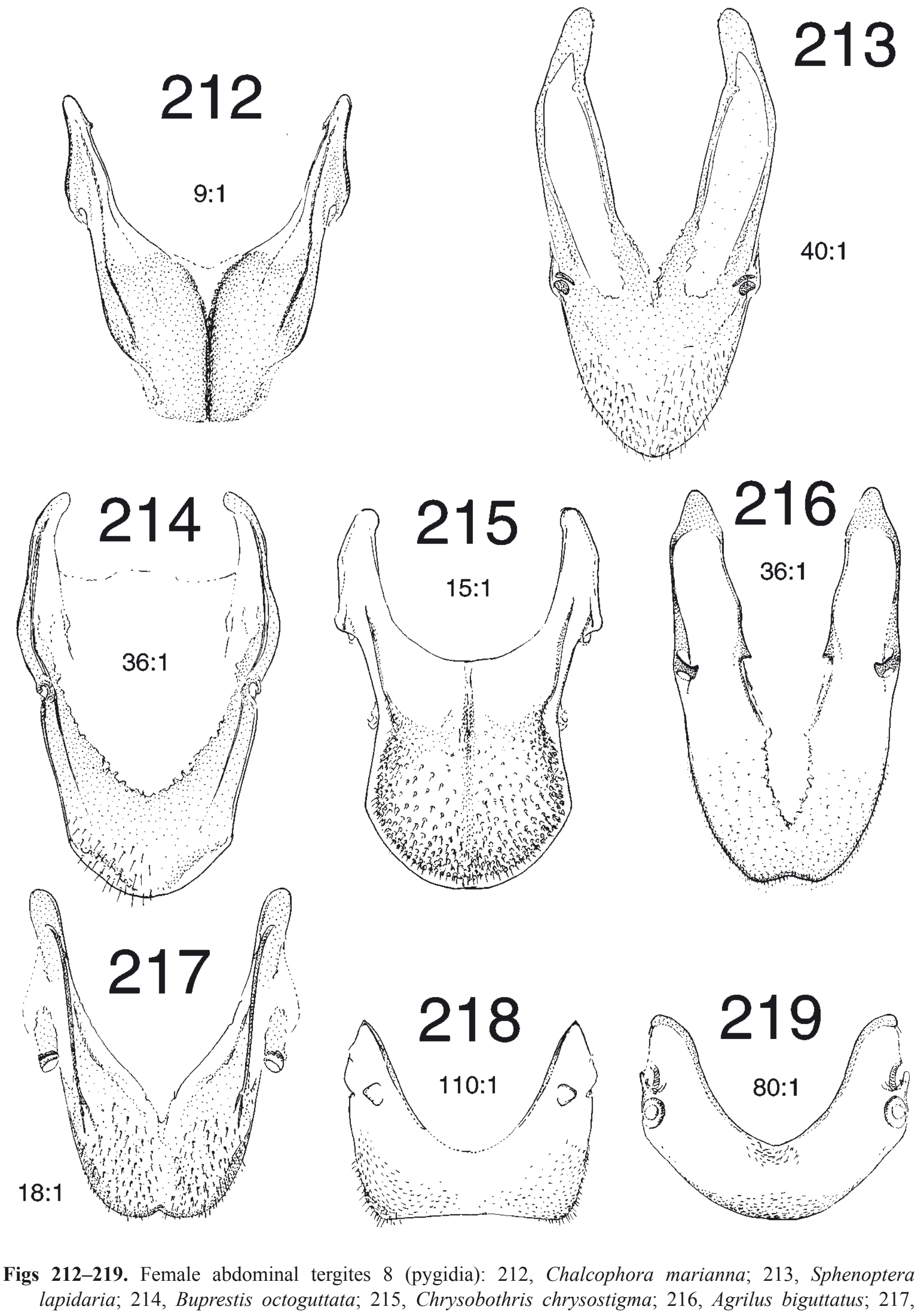
Figs 190–196. Female abdominal sternites 8: 190, *Julodis andreae*; 191, *Ptosima flavoguttata*; 192, *Polycesta porcata*; 193, *Acmaeoderella discoidea*; 194, *Schizopus laetus*; 195, *Thrincopyge alacris*; 196, *Mastogenius parallelus*.



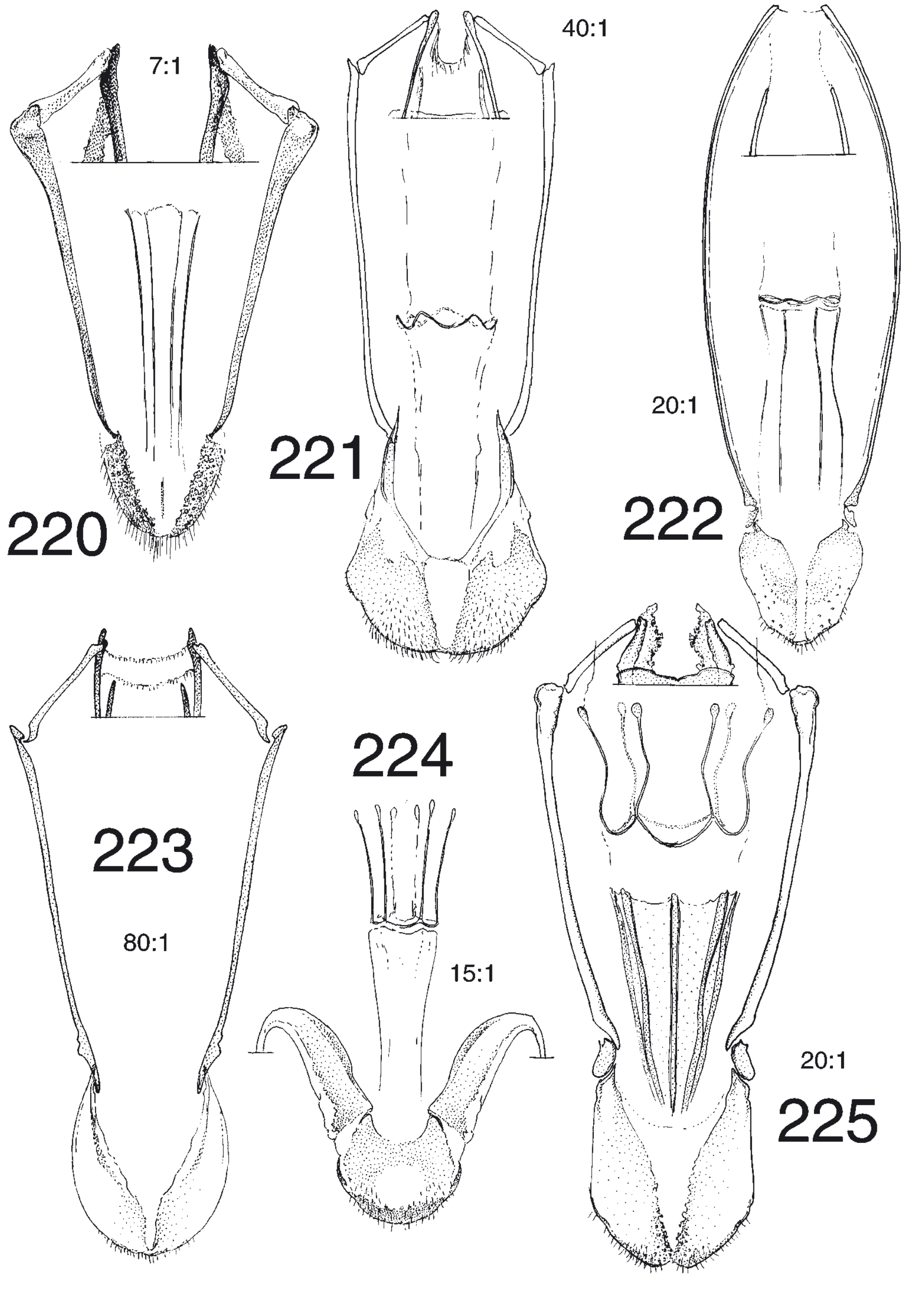
Figs 197–204. Female abdominal sternites 8: 197, *Chalcophora marianna*; 198, *Sphenoptera lapidaria*; 199, *Buprestis octoguttata*; 200, *Coraebus undatus*; 201, *Agrilus biguttatus*; 202, *Cylindromorphus filum*; 203, *Chrysobothris chrysostigma*; 204, *Trachys minutus*.



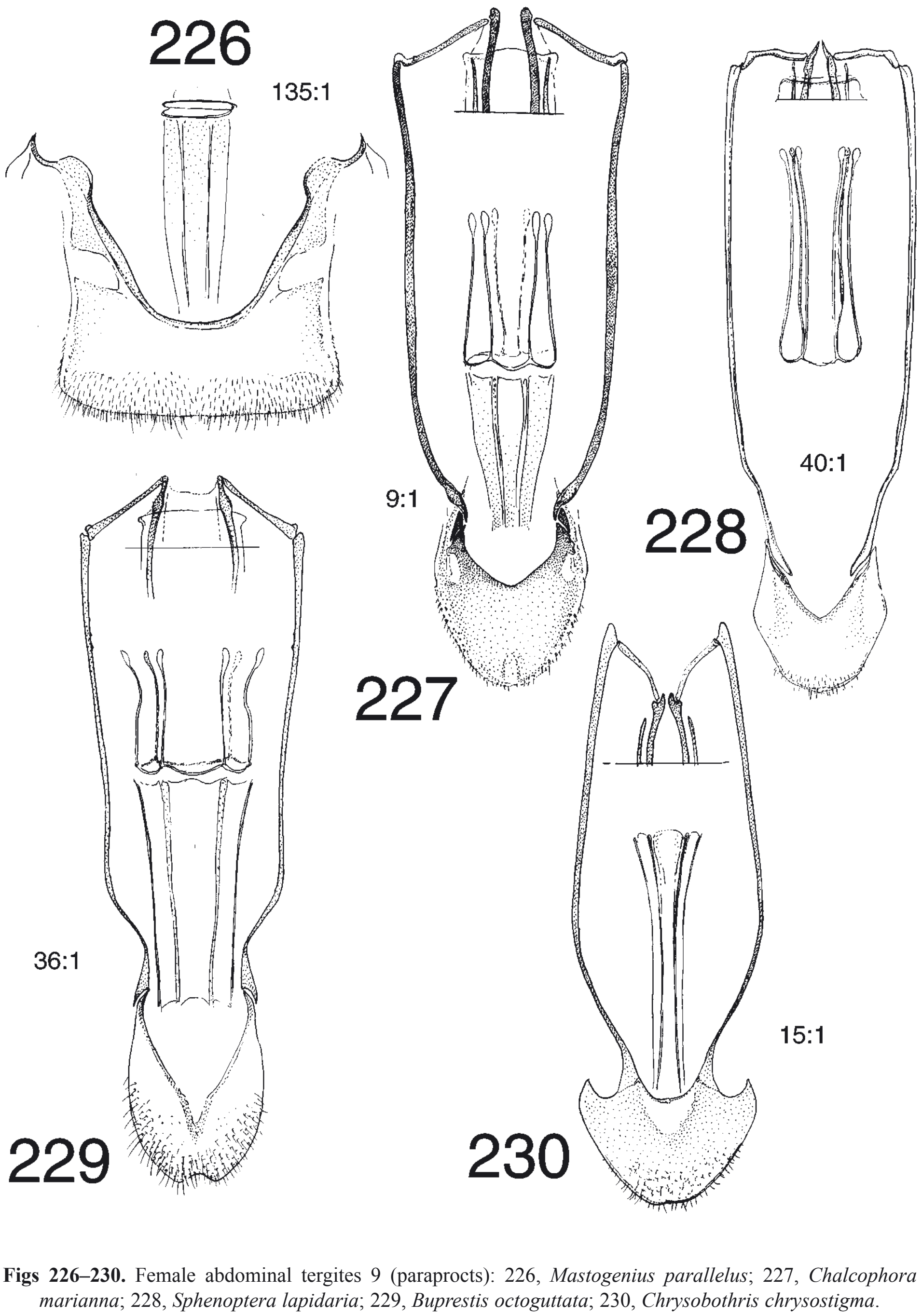
Figs 205–211. Female abdominal tergites 8 (pygidia): 205, *Julodis andreae*; 206, *Ptosima flavoguttata*; 207, *Polycesta porcata*; 208, *Acmaeoderella discoidea*; 209, *Schizopus laetus*; 210, *Thrincopyge alacris*; 211, *Mastogenius parallelus*.



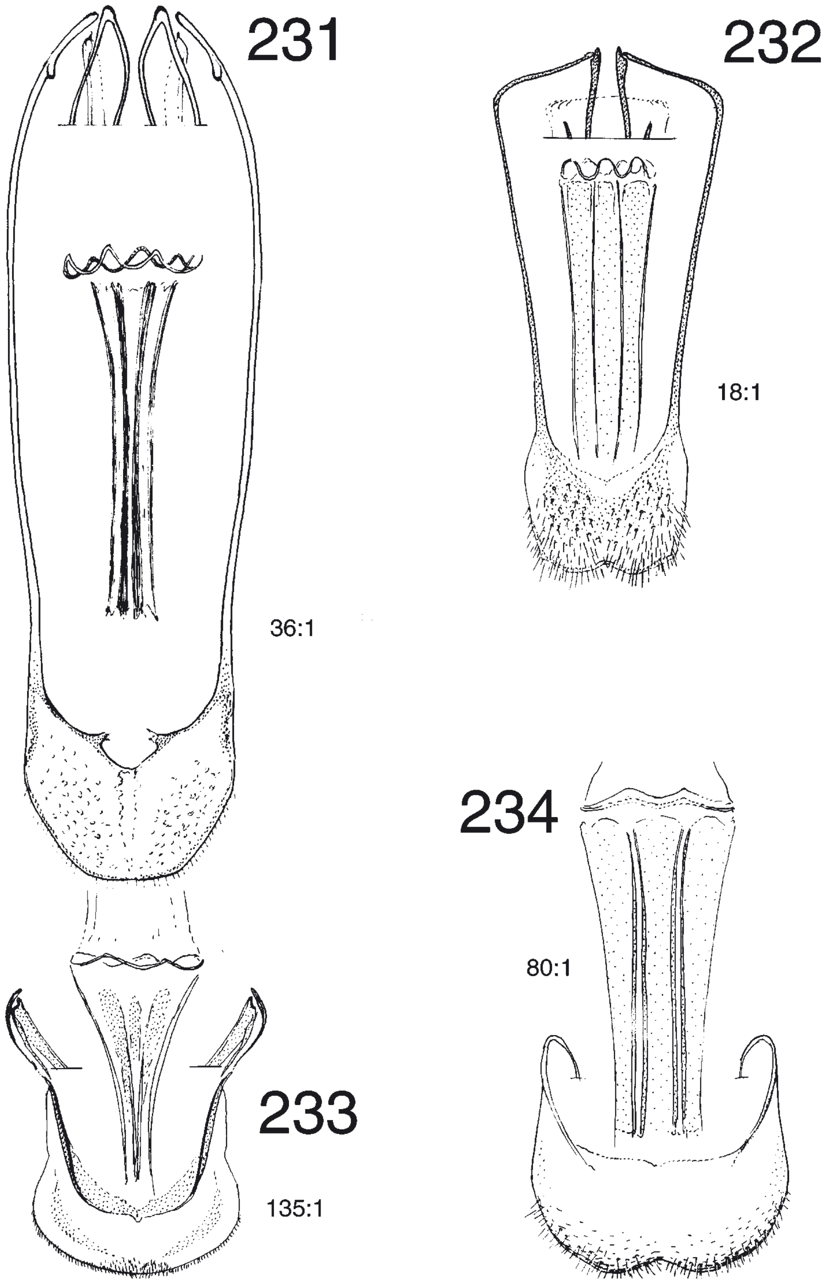
Figs 212–219. Female abdominal tergites 8 (pygidia): 212, *Chalcophora marianna*; 213, *Sphenoptera lapidaria*; 214, *Buprestis octoguttata*; 215, *Chrysobothris chrysostigma*; 216, *Agrilus biguttatus*; 217, *Coraebus undatus*; 218, *Cylindromorphus filum*; 219, *Trachys minutus*.



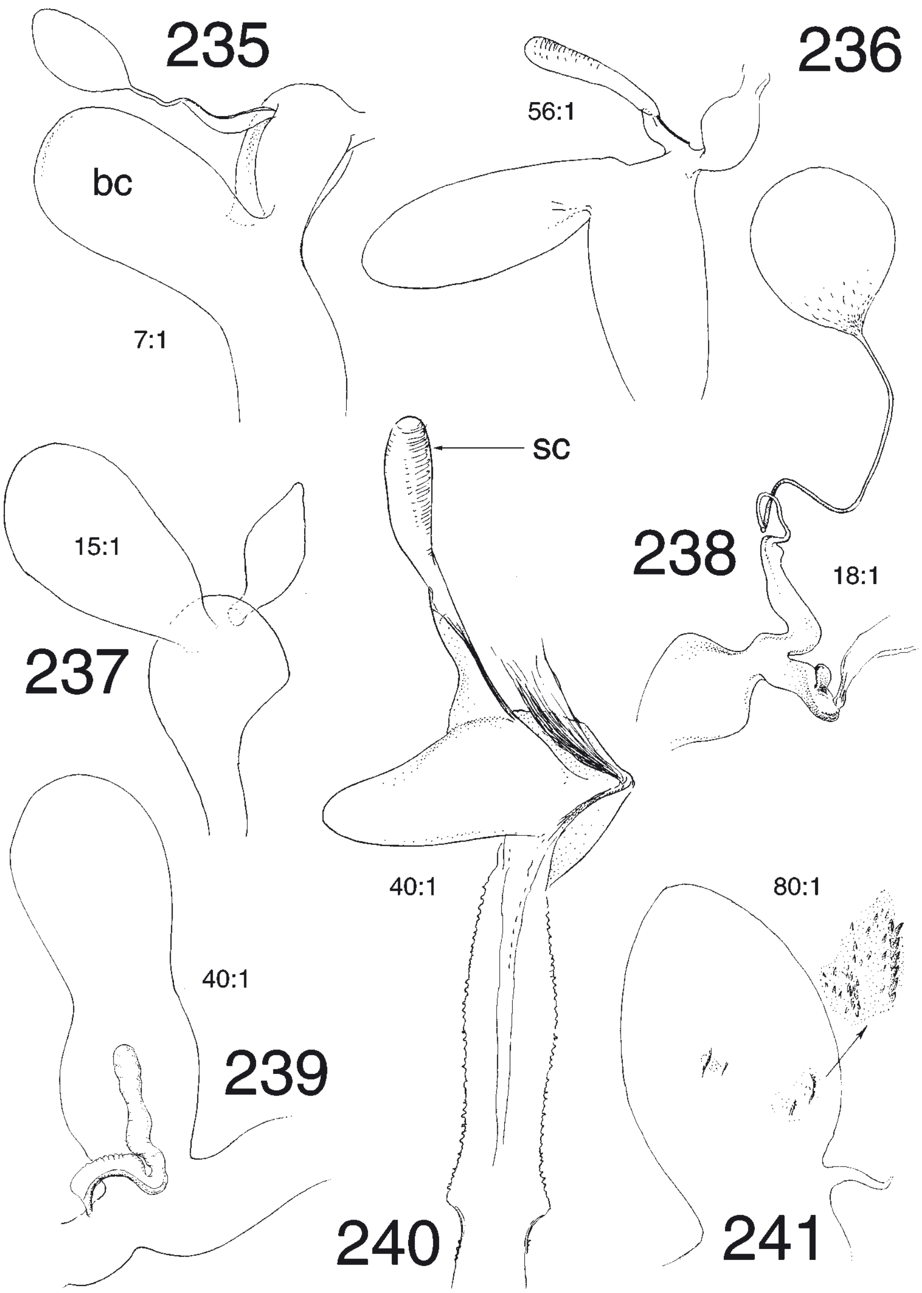
Figs 220–225. Female abdominal tergites 9 (paraprocts): 220, *Julodis andreae*; 221, *Ptosima flavoguttata*; 222, *Polycesta porcata*; 223, *Acmaeoderella discoidea*; 224, *Schizopus laetus*; 225, *Thrincopyge alacris*.



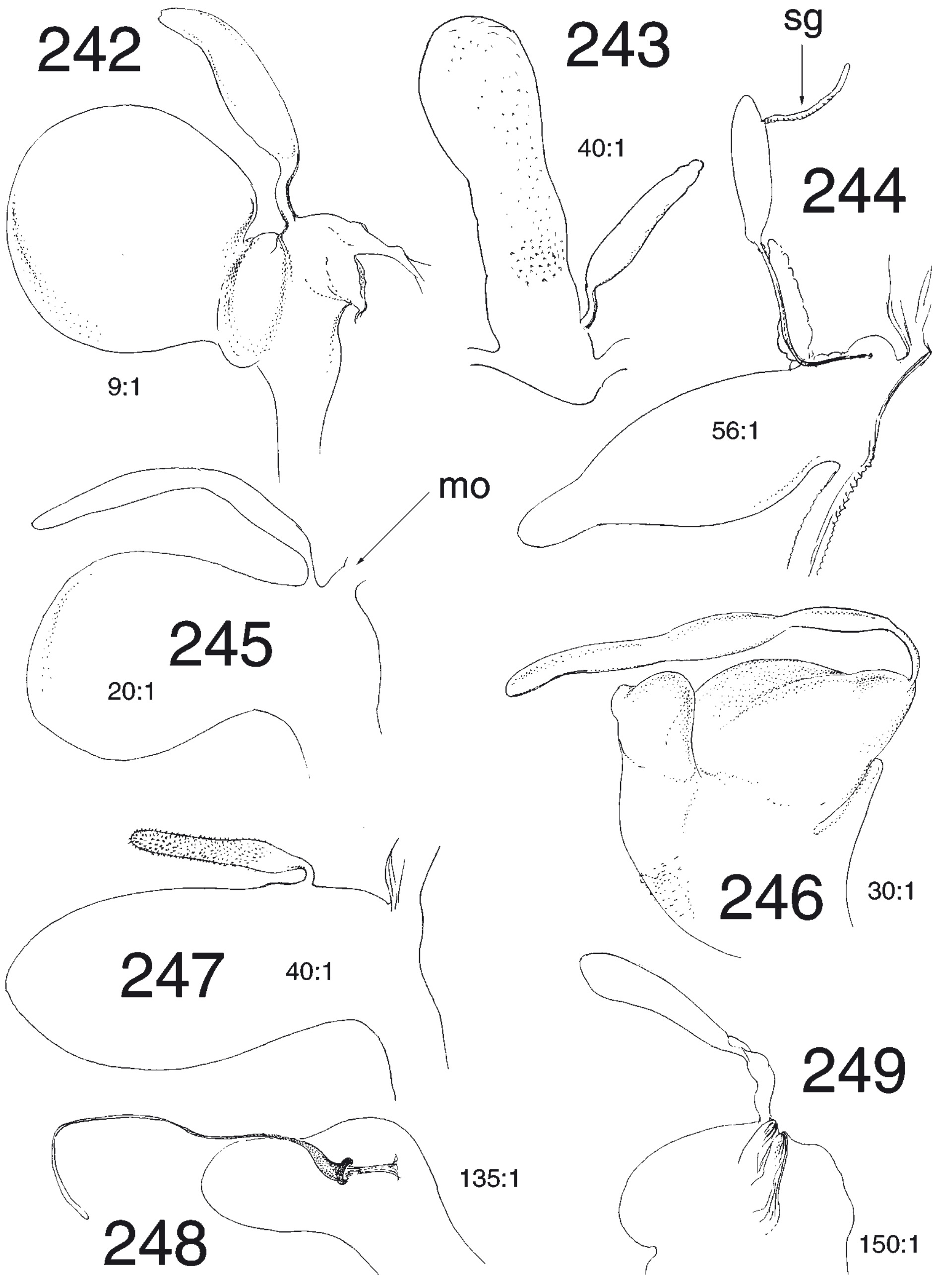
Figs 226–230. Female abdominal tergites 9 (paraprocts): 226, *Mastogenius parallelus*; 227, *Chalcophora marianna*; 228, *Sphenoptera lapidaria*; 229, *Buprestis octoguttata*; 230, *Chrysobothris chrysostigma*.



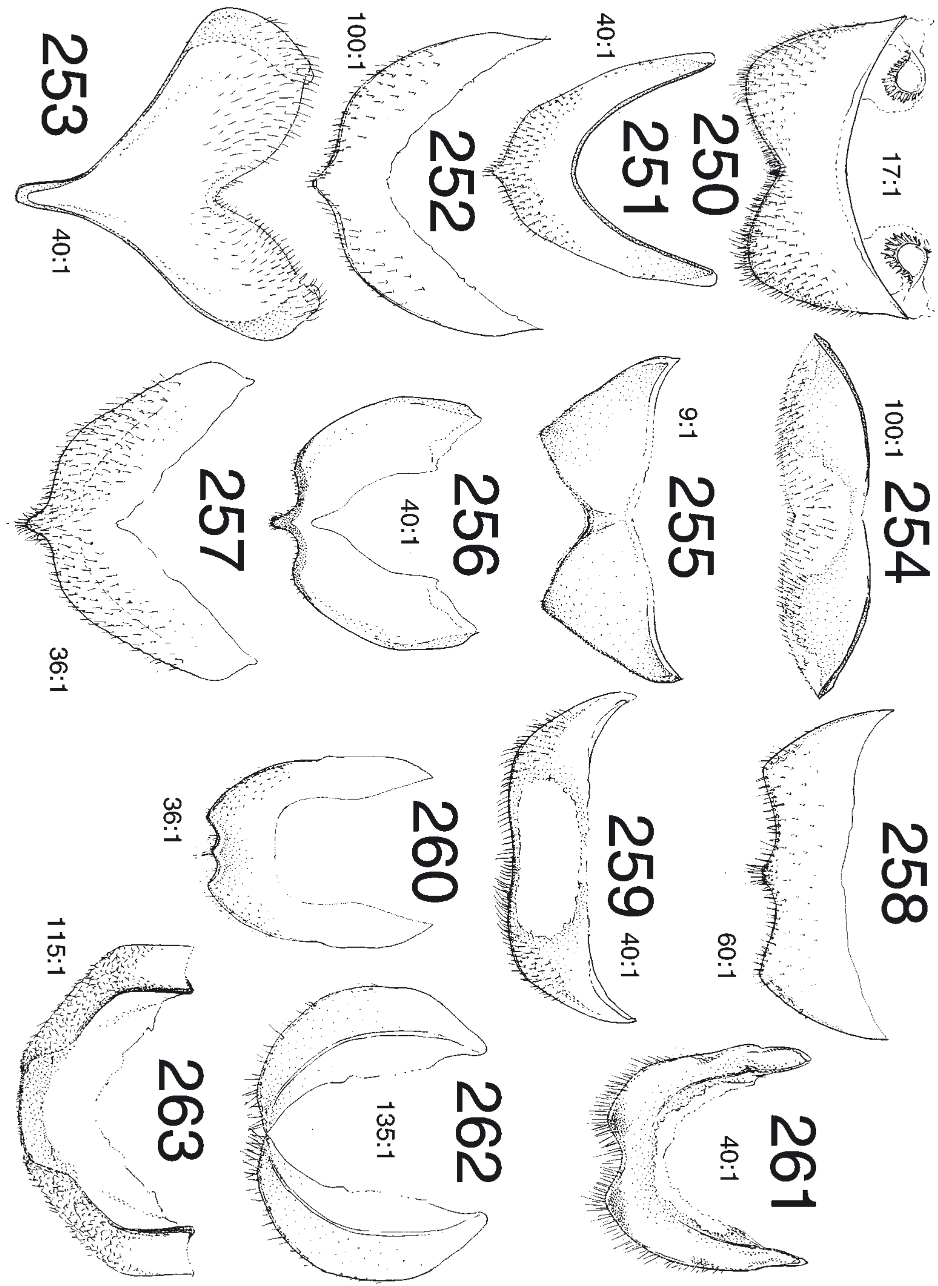
Figs 231–234. Female abdominal tergites 9 (paraprocts): 231, *Agrilus biguttatus*; 232, *Coraebus undatus*; 233, *Trachys minutus*; 234, *Cylindromorphus filum*.



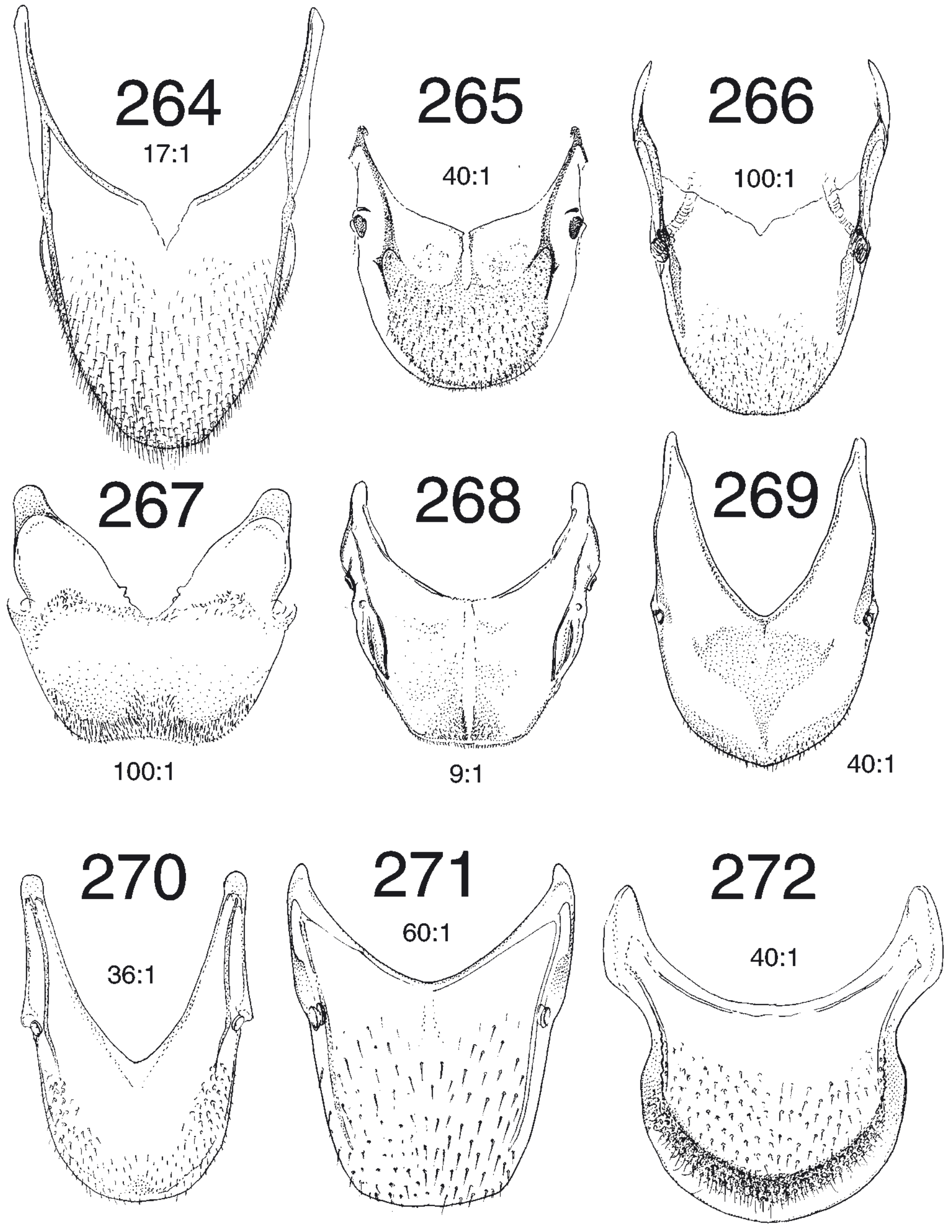
Figs 235–241. Female internal copulatory organs: 235, *Julodis andreae*; 236, *Acmaeoderella discoidea*; 237, *Ptosima flavoguttata*; 238, *Schizopus laetus*; 239, *Polycesta porcata*; 240, *Thrincopyge alacris*; 241, *Mastogenius parallelus*.



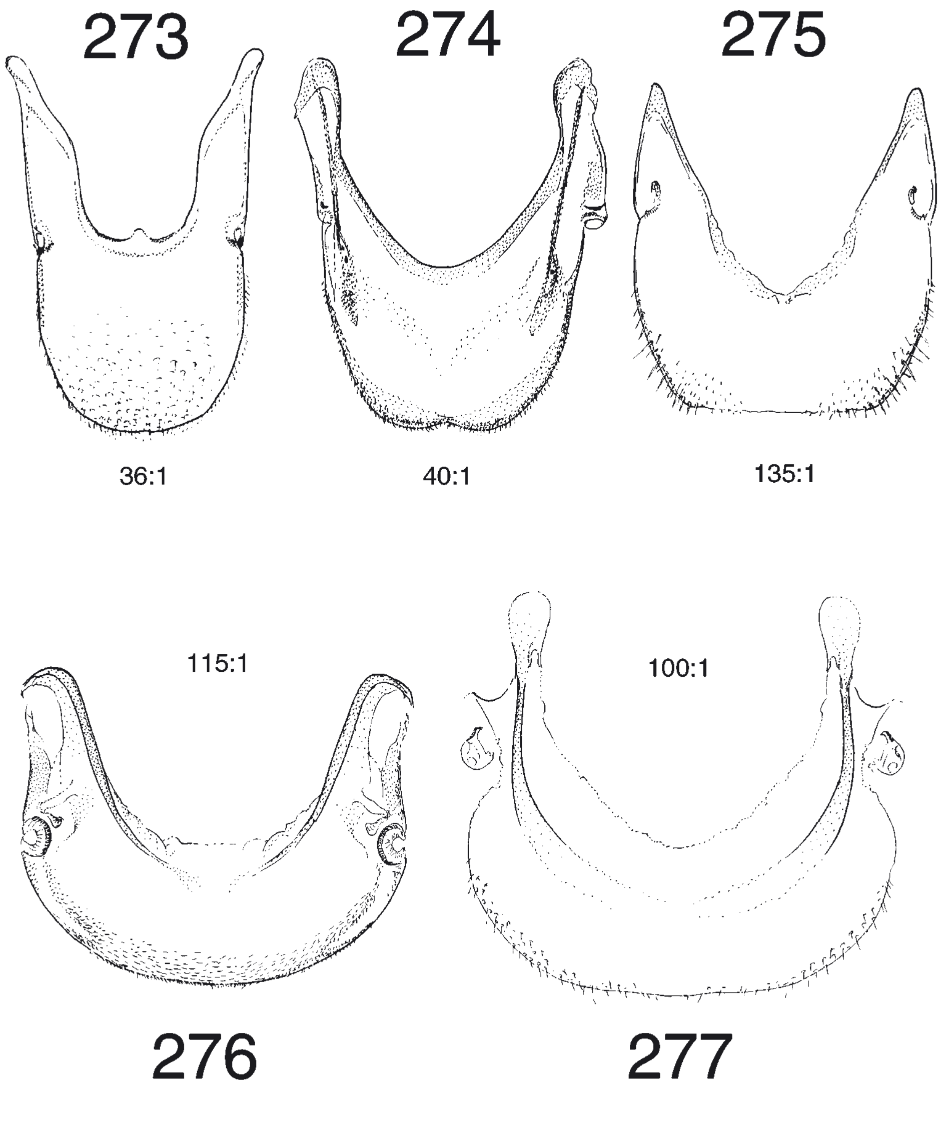
Figs 242–249. Female internal copulatory organs: 242, *Chalcophora marianna*; 243, *Sphenoptera lapidaria*; 244, *Buprestis octoguttata*; 245, *Chrysobothris chrysostigma*; 246, *Agrilus biguttatus*; 247, *Coraebus undatus*; 248, *Cylindromorphus filum*; 249, *Trachys minutus*.



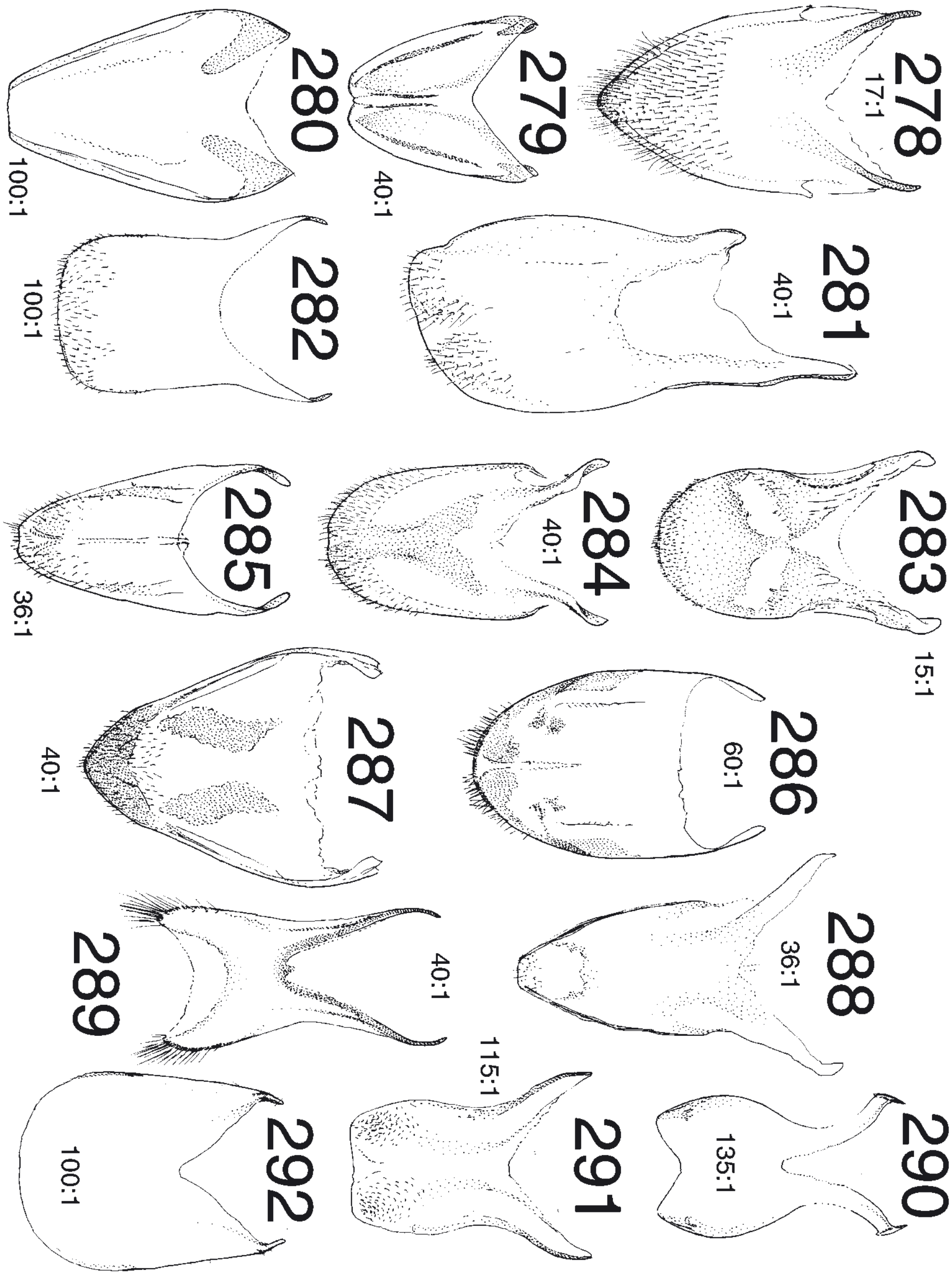
Figs 250–263. Male abdominal sternites 8: 250, *Julodis andreae*; 251, *Ptosima flavoguttata*; 252, *Acmaeoderella discoidea*; 253, *Schizopus laetus*; 254, *Mastogenius parallelus*; 255, *Chalcophora marianna*; 256, *Sphenoptera lapidaria*; 257, *Buprestis octoguttata*; 258, *Melanophila acuminata*; 259, *Chrysobothris affinis*; 260, *Agrilus biguttatus*; 261, *Coraebus undatus*; 262, *Cylindromorphus filum*; 263, *Trachys minutus*.



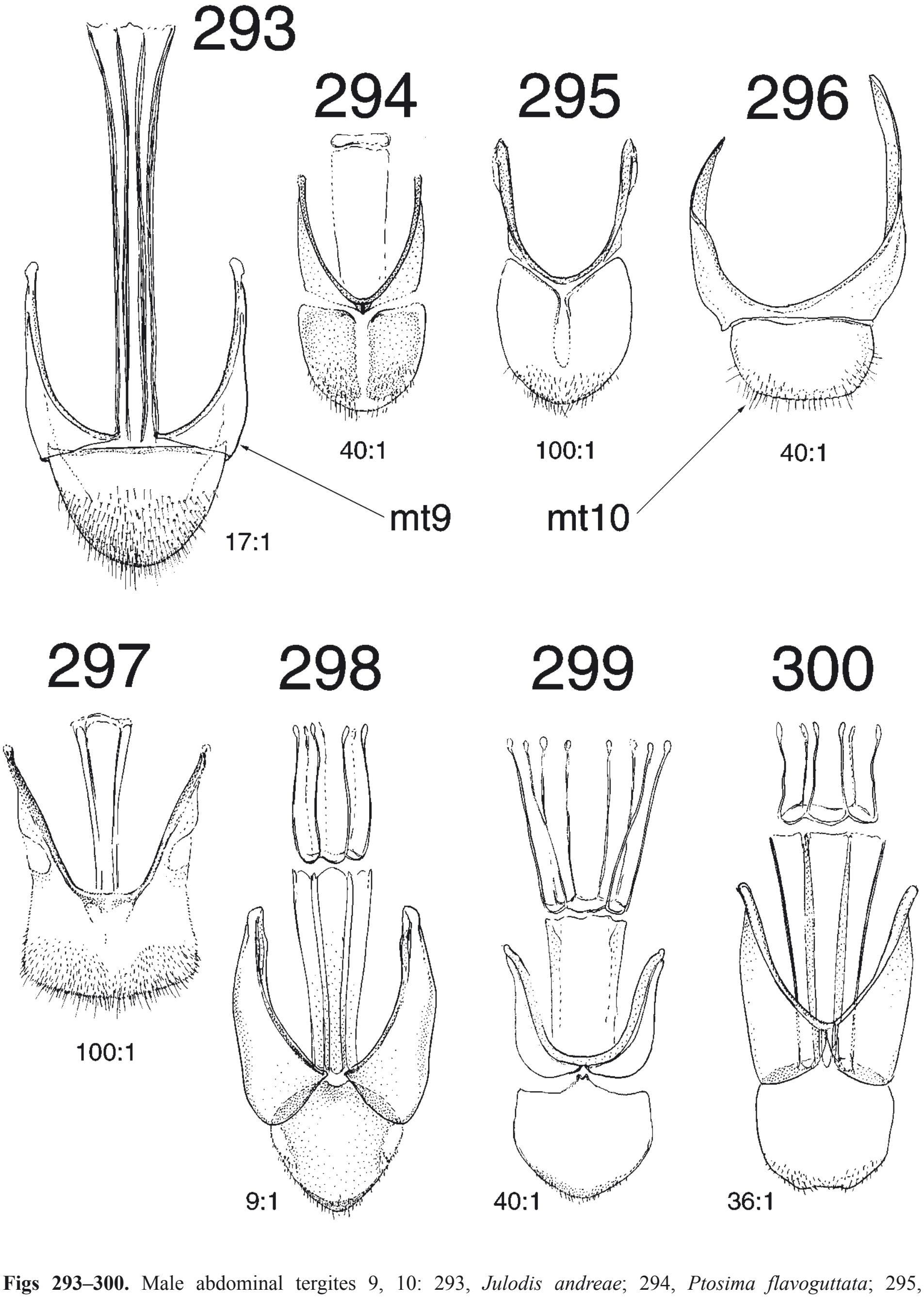
Figs 264–272. Male abdominal tergites 8 (pygidia): 264, *Julodis andreae*; 265, *Ptosima flavoguttata*; 266, *Acmaeoderella discoidea*; 267, *Mastogenius parallelus*; 268, *Chalcophora marianna*; 269, *Sphenoptera lapidaria*; 270, *Buprestis octoguttata*; 271, *Melanophila acuminata*; 272, *Chrysobothris affinis*.



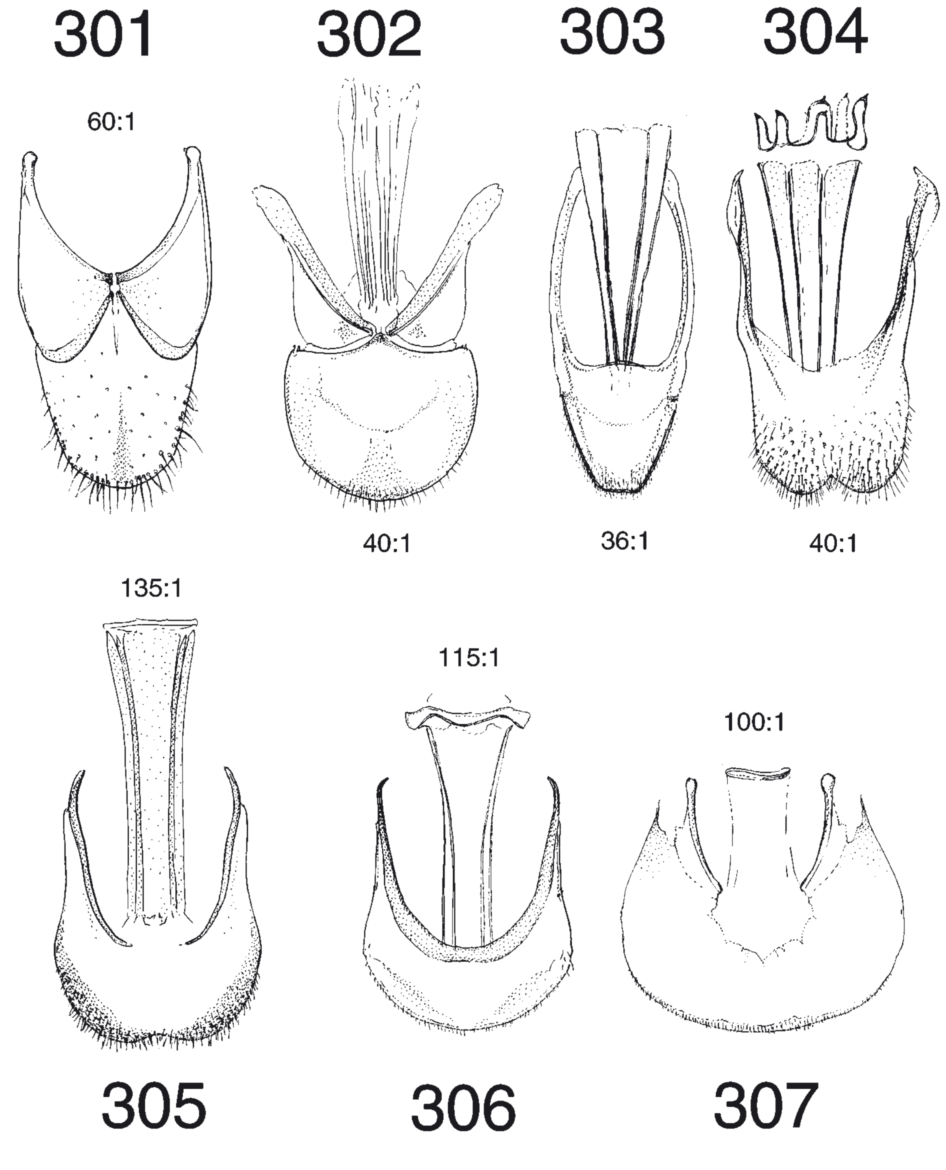
Figs 273–277. Male abdominal tergites 8 (pygidia): 273, *Agrilus biguttatus*; 274, *Coraebus undatus*; 275, *Cylindromorphus filum*; 276, *Trachys minutus*; 277, *Galbella felix*.



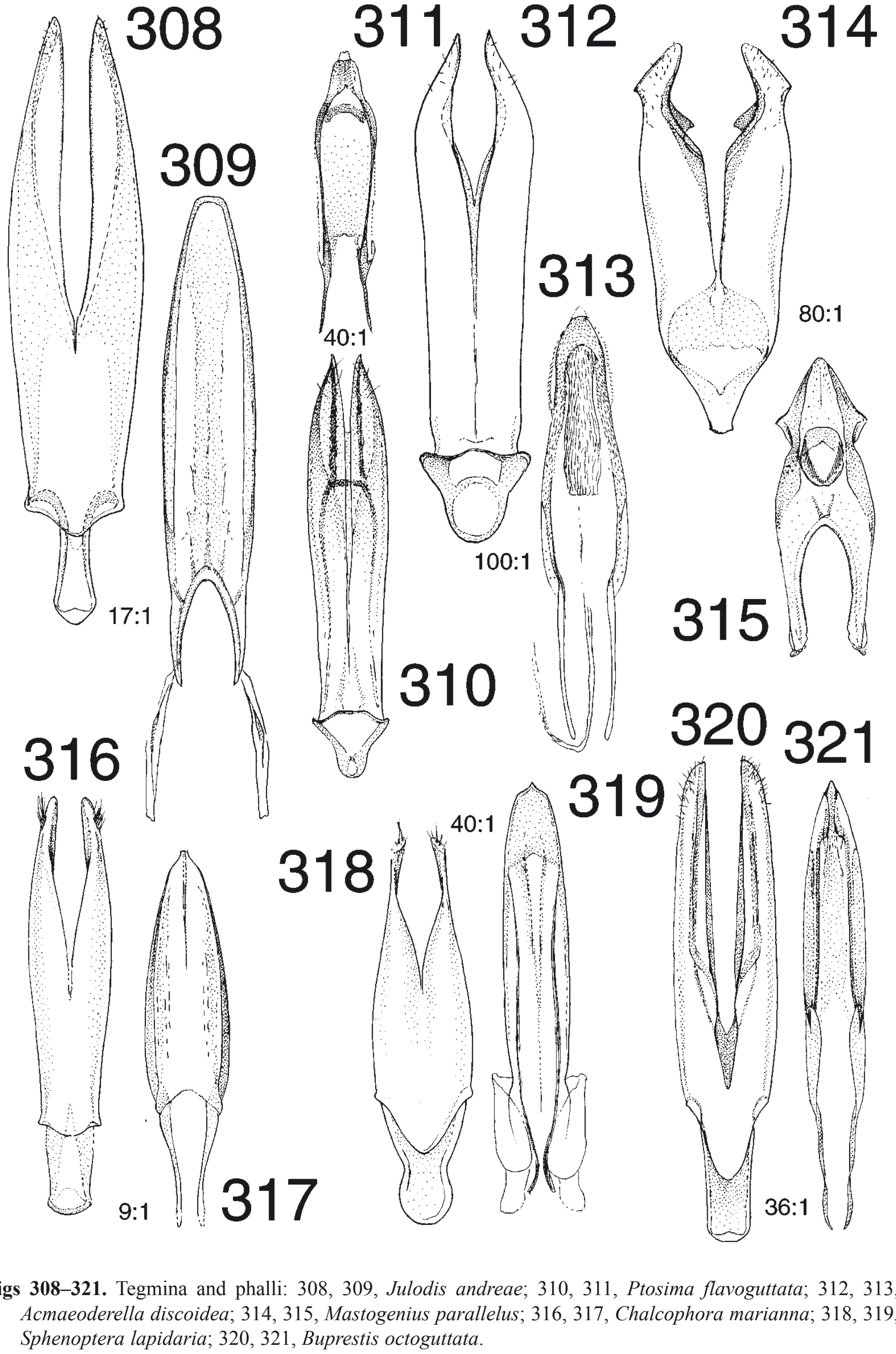
Figs 278–292. Male abdominal sternites 9: 278, *Julodis andreae*; 279, *Ptosima flavoguttata*; 280, *Acmaeoderella discoidea*; 281, *Schizopus laetus*; 282, *Mastogenius parallelus*; 283, *Chalcophora marianna*; 284, *Sphenoptera lapidaria*; 285, *Buprestis octoguttata*; 286, *Melanophila acuminata*; 287, *Chrysobothris affinis*; 288, *Agrilus biguttatus*; 289, *Coraebus undatus*; 290, *Cylindromorphus filum*; 291, *Trachys minutus*; 292, *Galbella felix*.



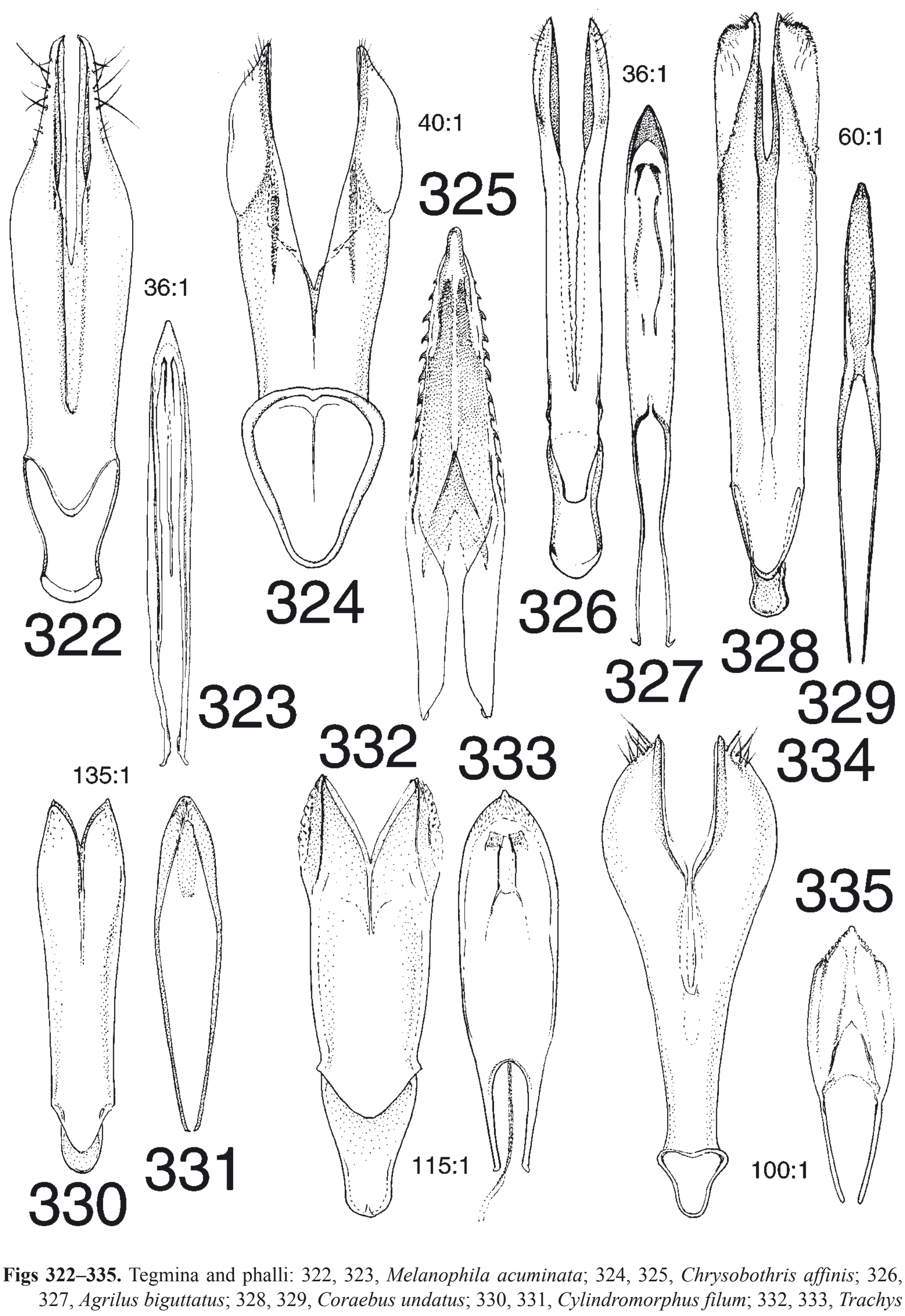
Figs 293–300. Male abdominal tergites 9, 10: 293, *Julodis andreae*; 294, *Ptosima flavoguttata*; 295, *Acmaeoderella discoidea*; 296, *Schizopus laetus*; 297, *Mastogenius parallelus*; 298, *Chalcophora marianna*; 299, *Sphenoptera lapidaria*; 300, *Buprestis octoguttata*.



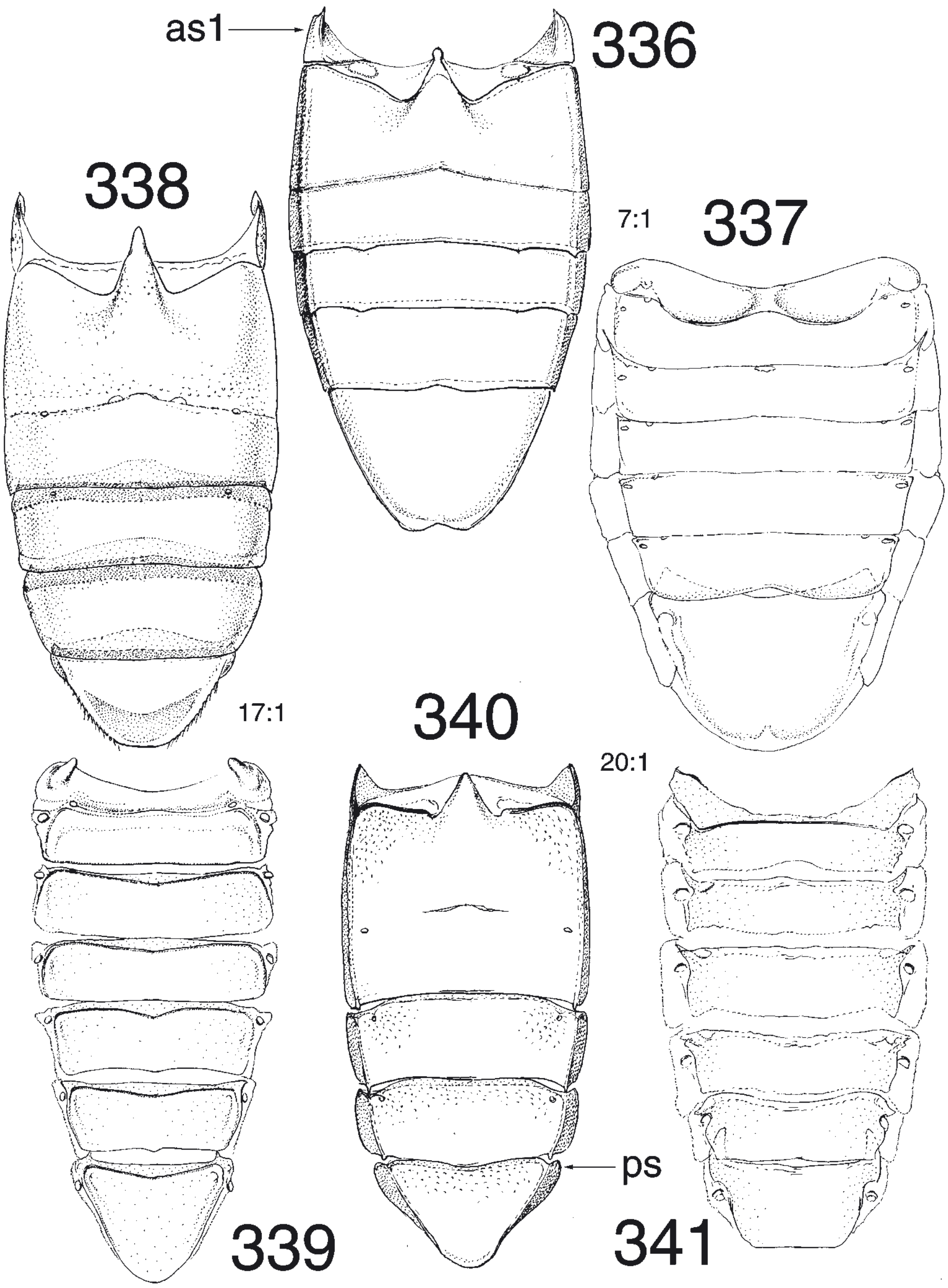
Figs 301–307. Male abdominal tergites 9, 10: 301, *Melanophila acuminata*; 302, *Chrysobothris affinis*; 303, *Agrilus biguttatus*; 304, *Coraebus undatus*; 305, *Cylindromorphus filum*; 306, *Trachys minutus*; 307, *Galbella felix*.



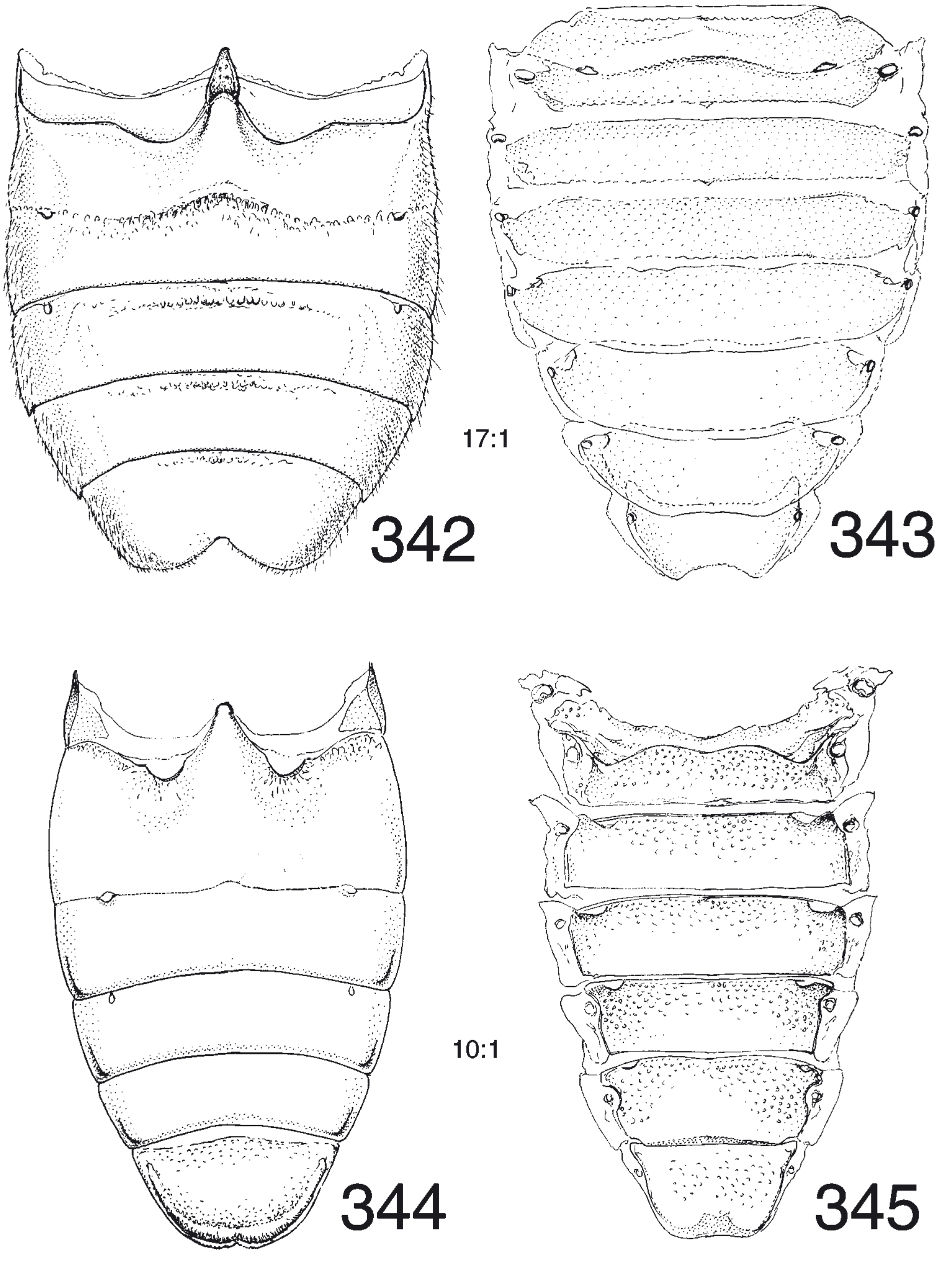
Figs 308–321. Tegmina and phalli: 308, 309, *Julodis andreae*; 310, 311, *Ptosima flavoguttata*; 312, 313, *Acmaeoderella discoidea*; 314, 315, *Mastogenius parallelus*; 316, 317, *Chalcophora marianna*; 318, 319, *Sphenoptera lapidaria*; 320, 321, *Buprestis octoguttata*.



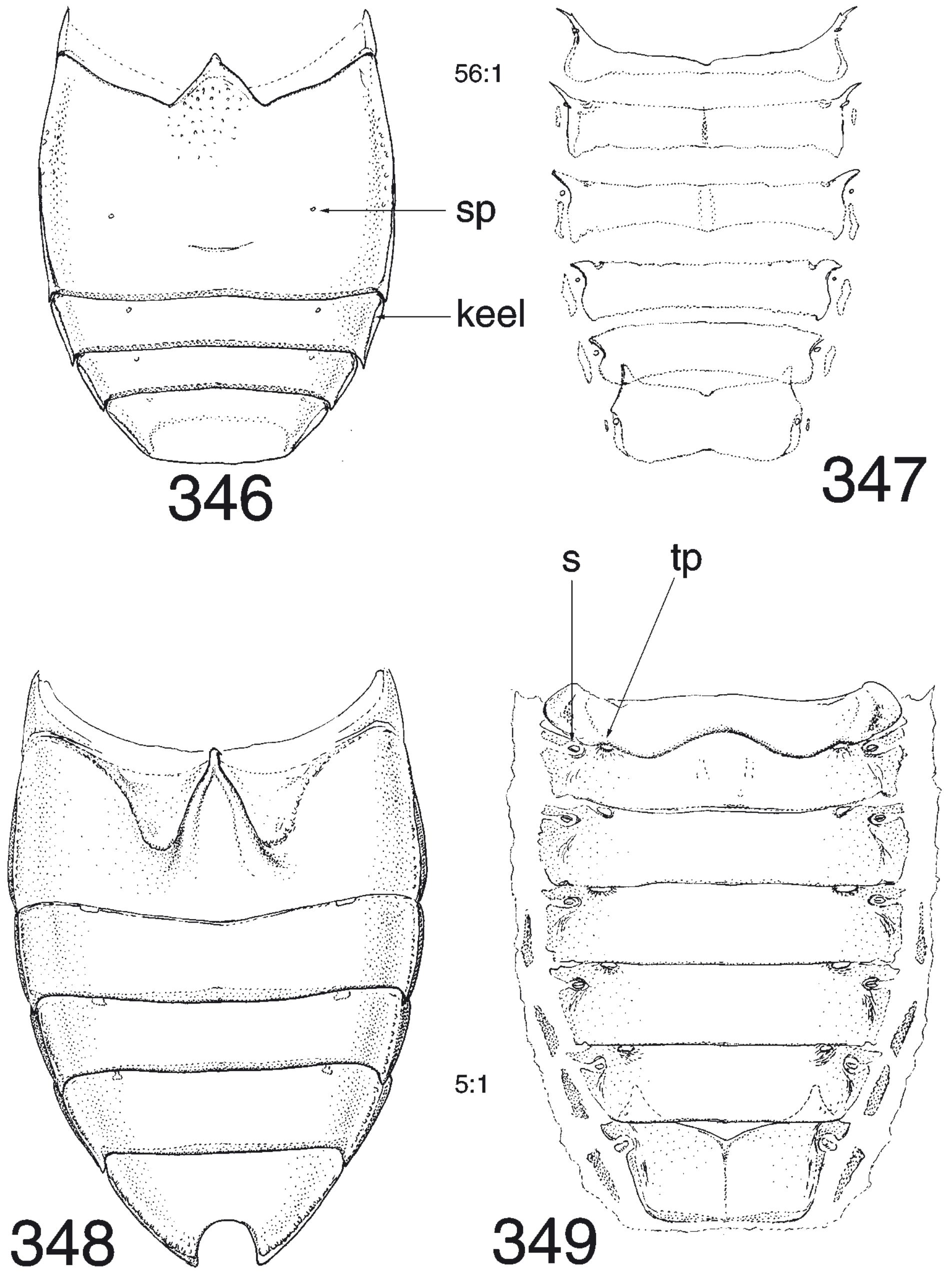
Figs 322–335. Tegmina and phalli: 322, 323, *Melanophila acuminata*; 324, 325, *Chrysobothris affinis*; 326, 327, *Agrilus biguttatus*; 328, 329, *Coraebus undatus*; 330, 331, *Cylindromorphus filum*; 332, 333, *Trachys minutus*; 334, 335, *Galbella felix*.



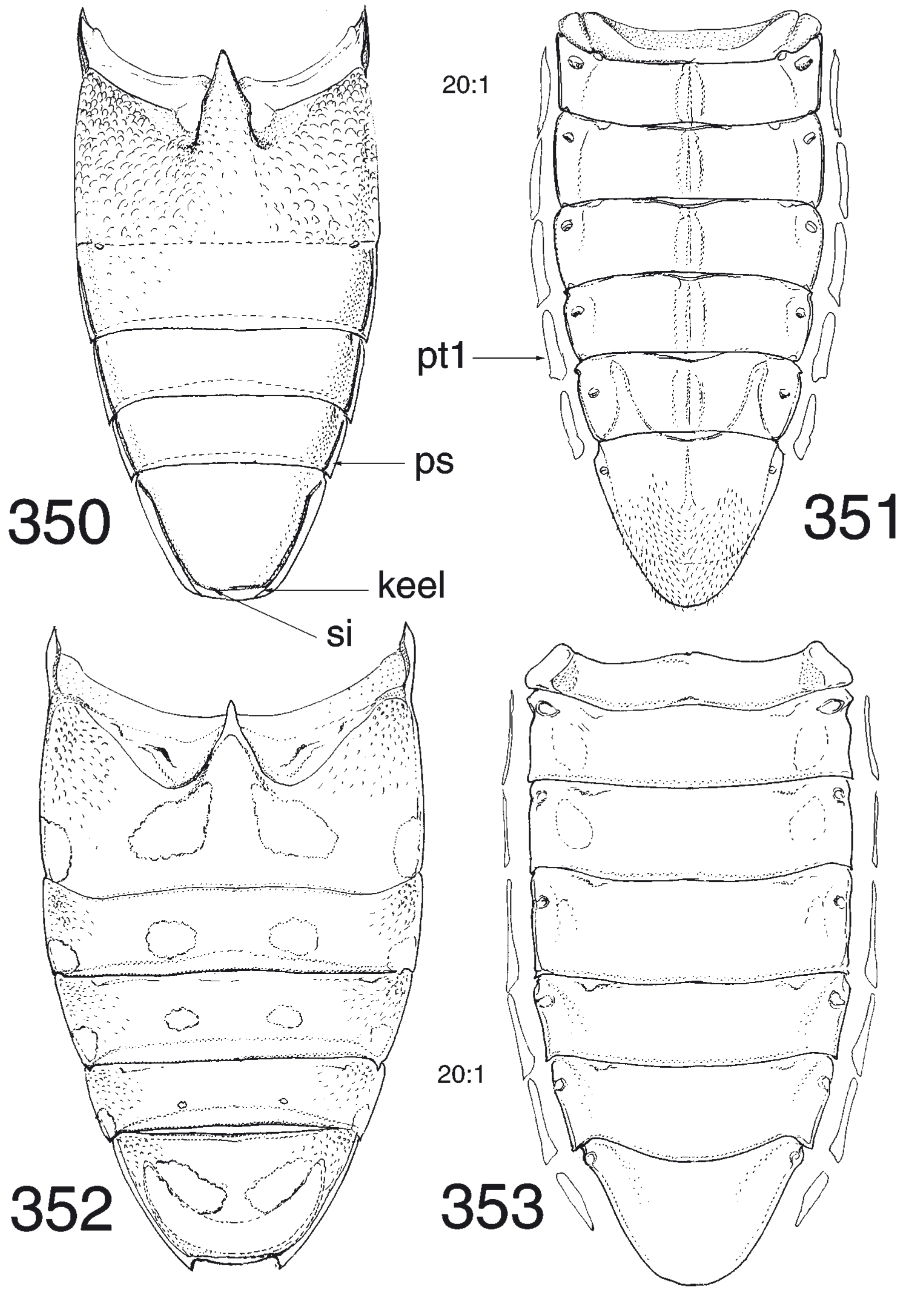
Figs 336–341. Abdomina dorsally and ventrally: 336, 337, *Julodis andreae*; 338, 339, *Ptosima flavoguttata*; 340, 341, *Acmaeoderella discoidea*.



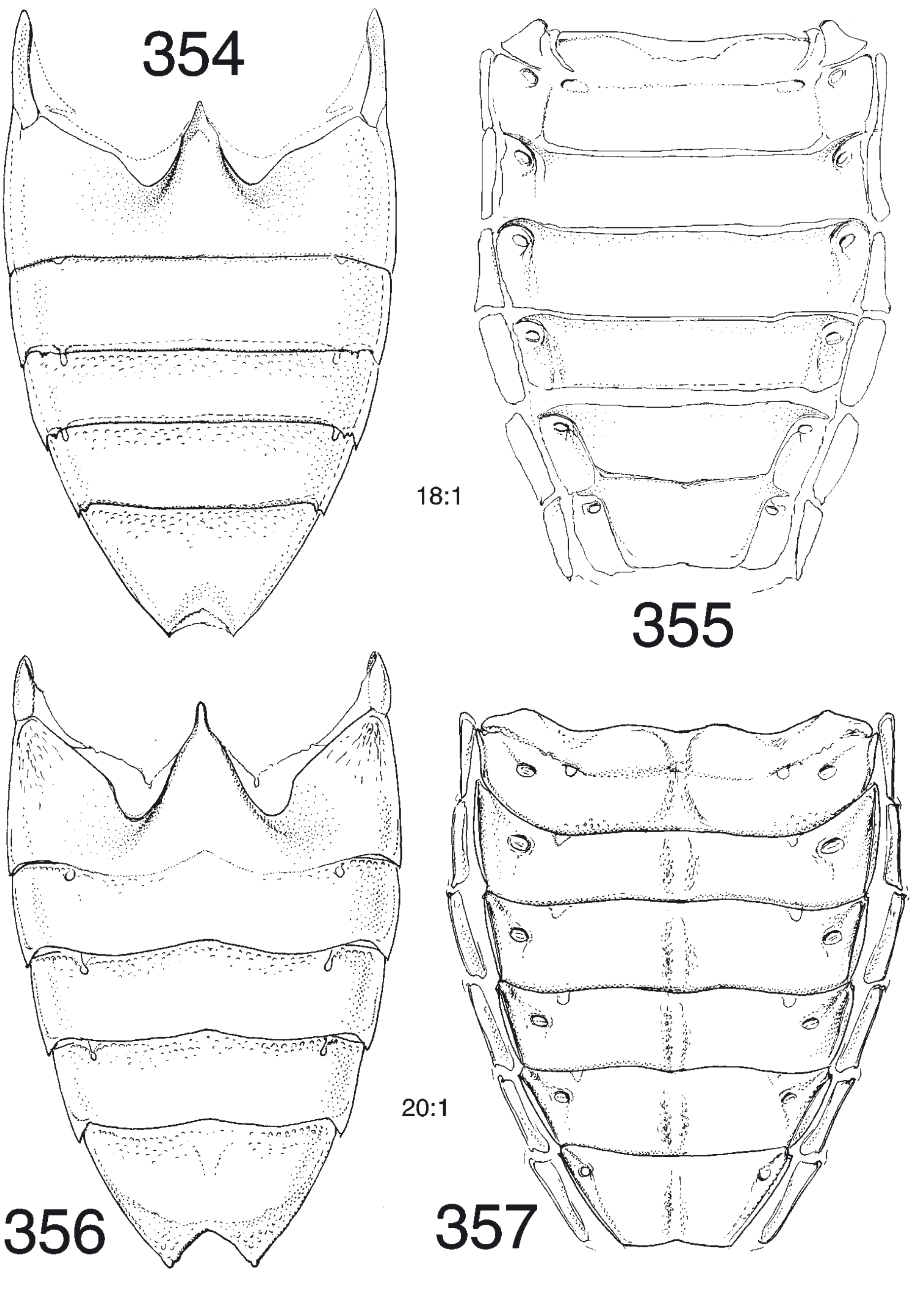
Figs 342–345. Abdomina dorsally and ventrally: 342, 343, *Schizopus laetus*; 344, 345, *Thrincopyge alacris*.



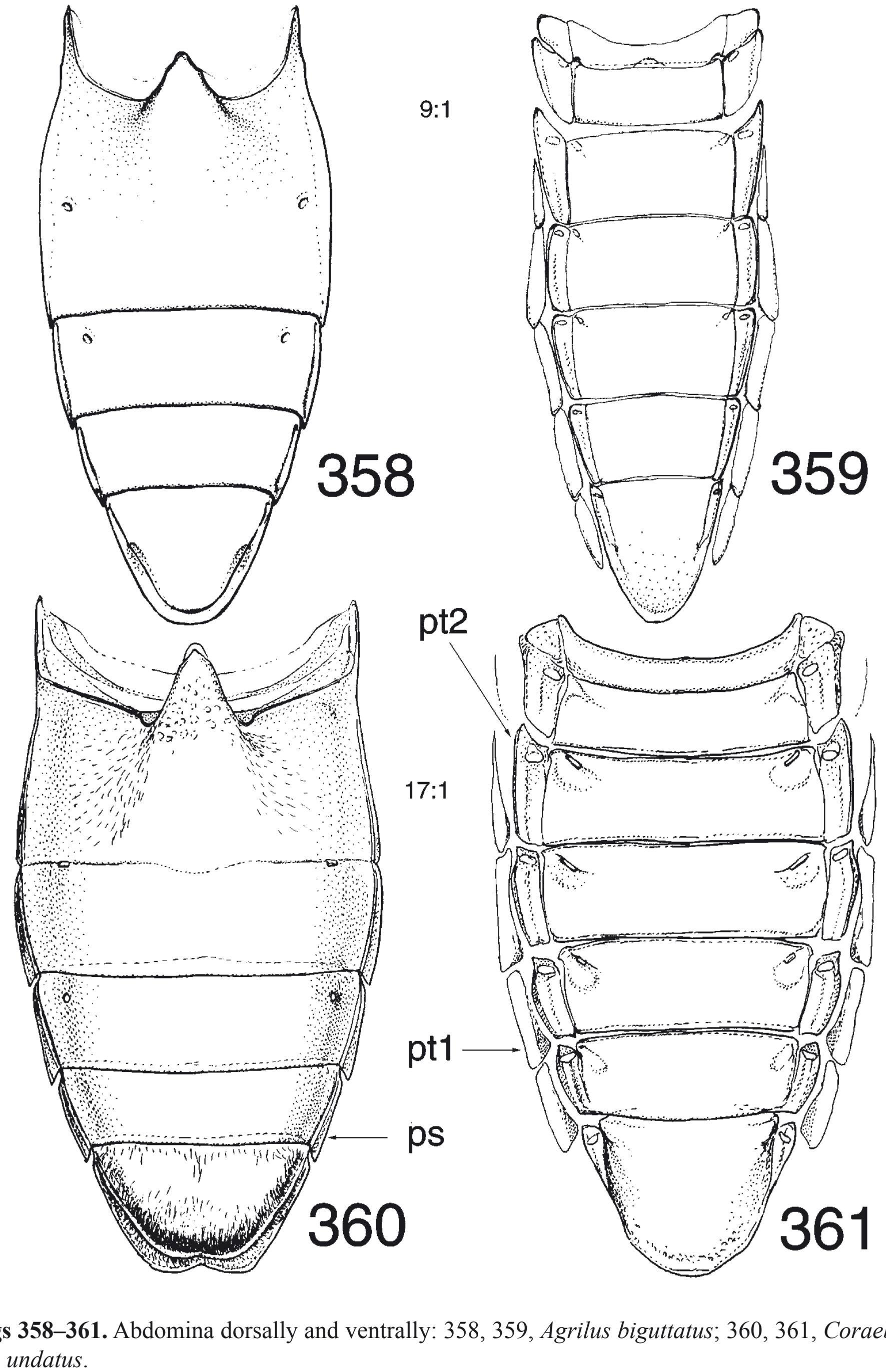
Figs 346–349. Abdomina dorsally and ventrally: 346, 347, *Mastogenius parallelus*; 348, 349, *Chalcophora marianna*.



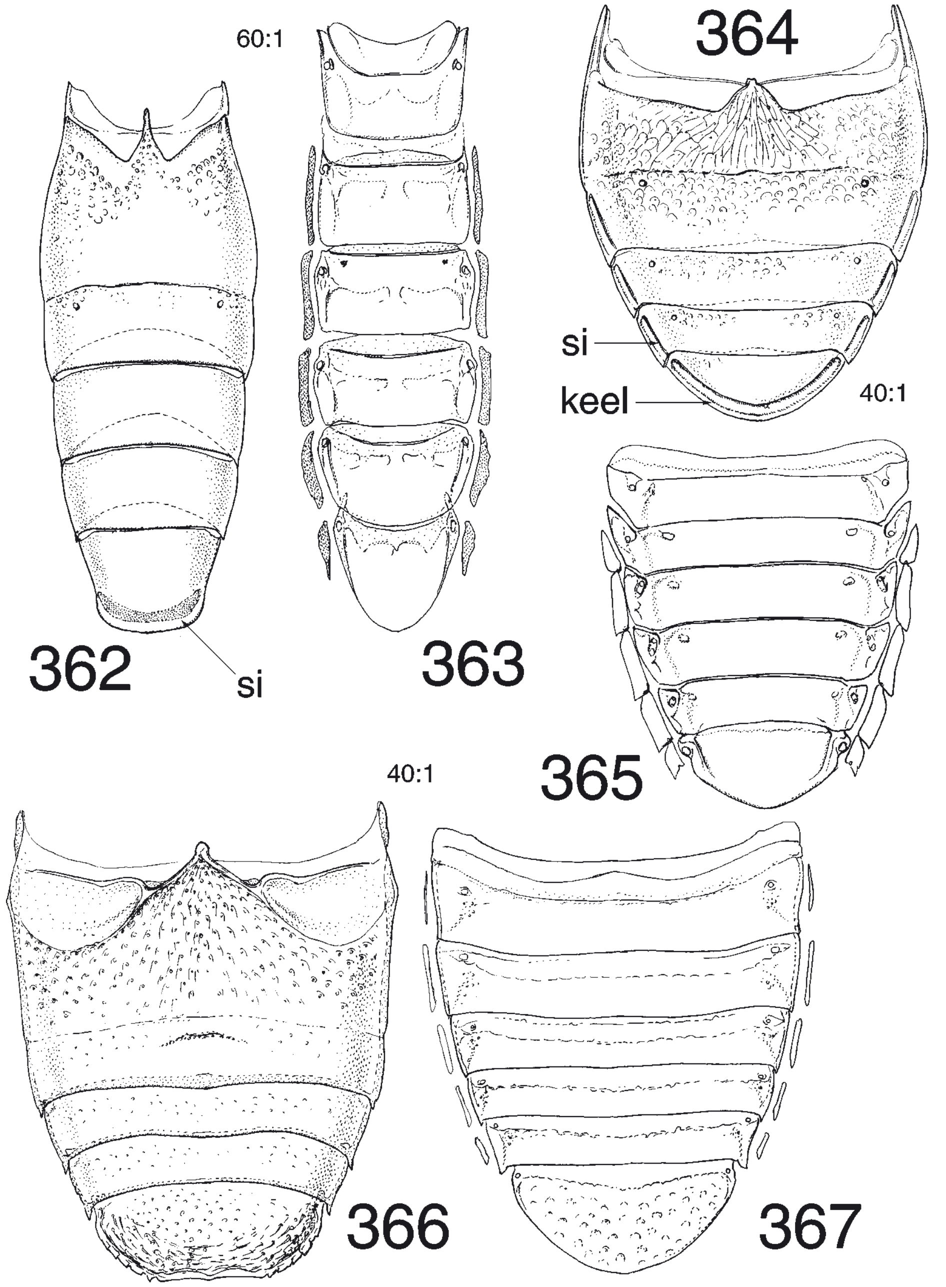
Figs 350–353. Abdomina dorsally and ventrally: 350, 351, *Sphenoptera lapidaria*; 352, 353, *Buprestis octoguttata*.



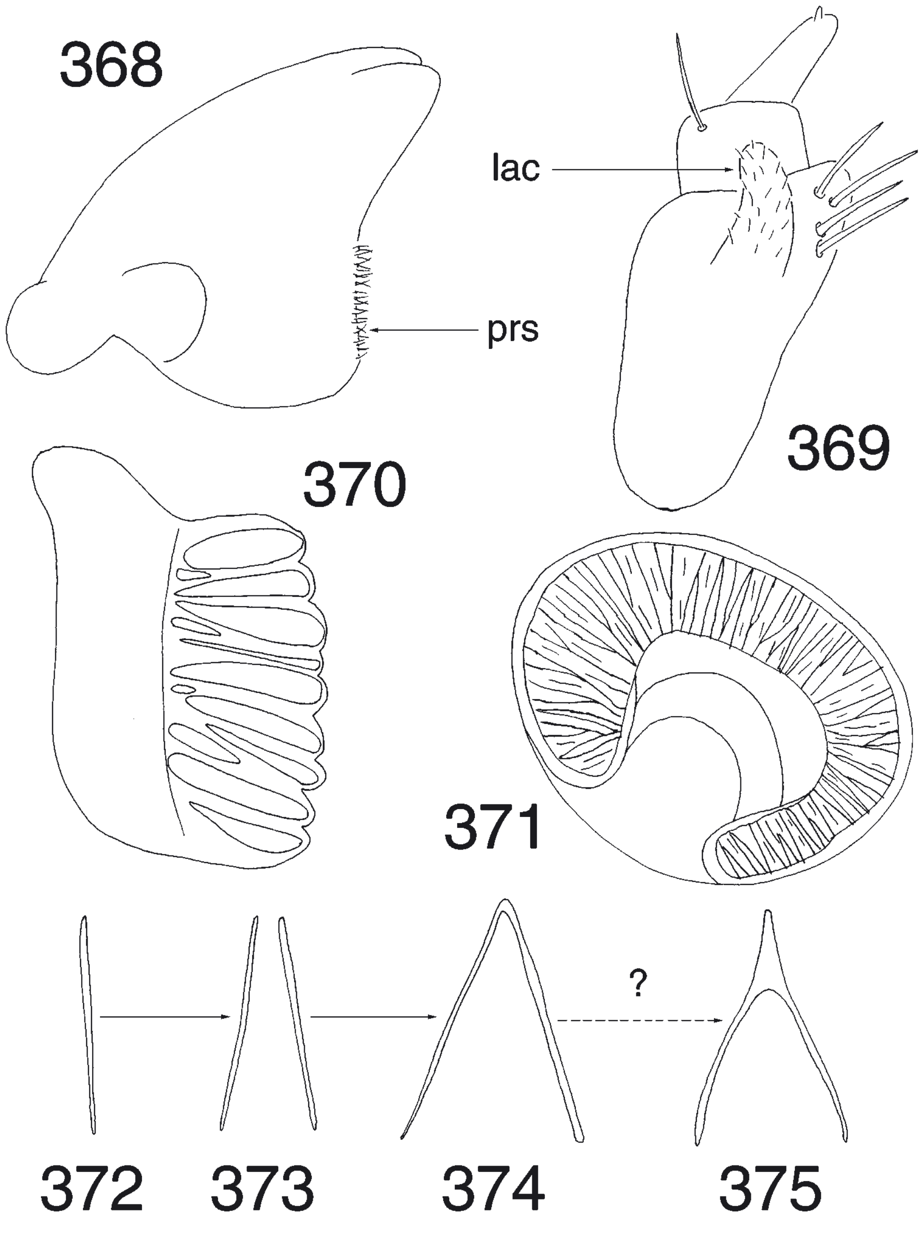
Figs 354–357. Abdomina dorsally and ventrally: 354, 355, *Melanophila acuminata*; 356, 357, *Chrysobothris affinis*.



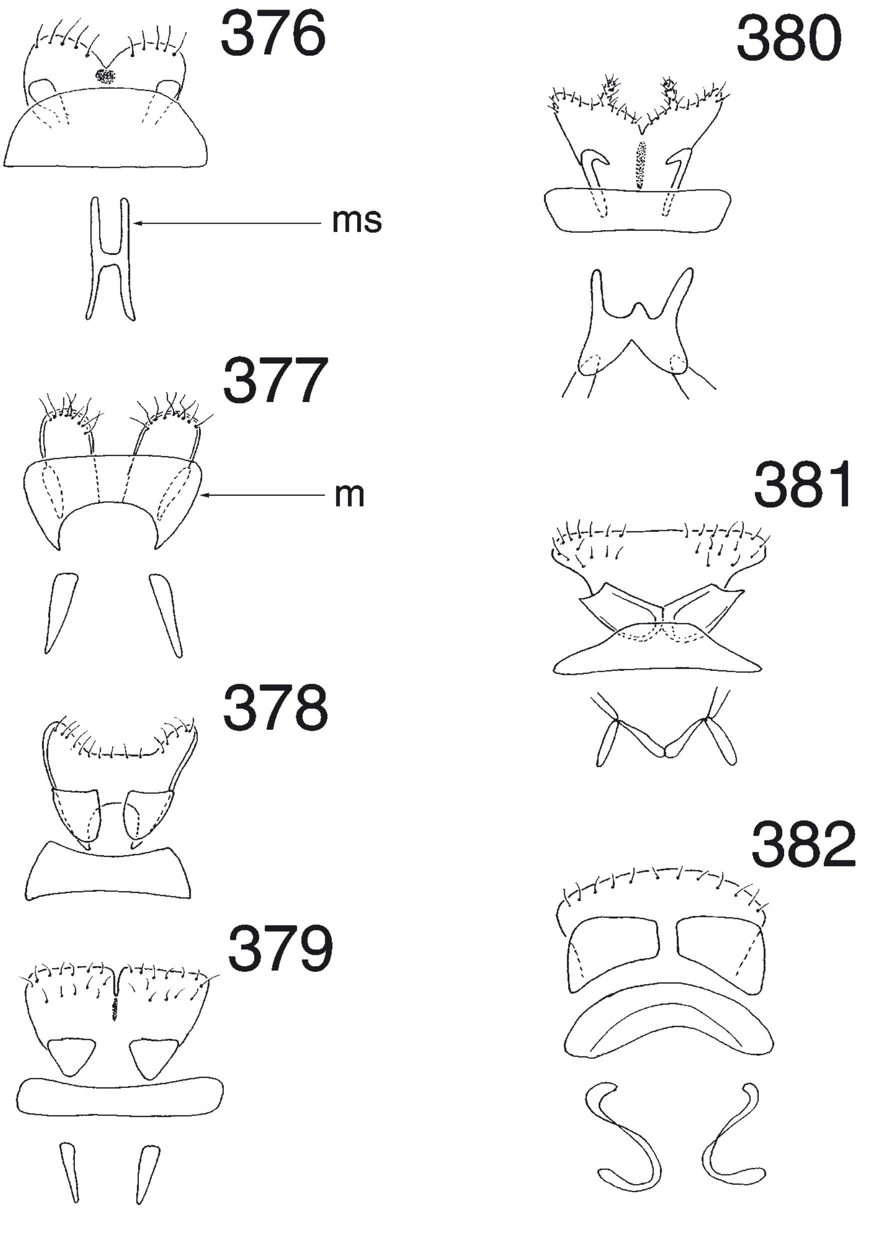
Figs 358–361. Abdomina dorsally and ventrally: 358, 359, *Agrilus biguttatus*; 360, 361, *Coraebus undatus*.



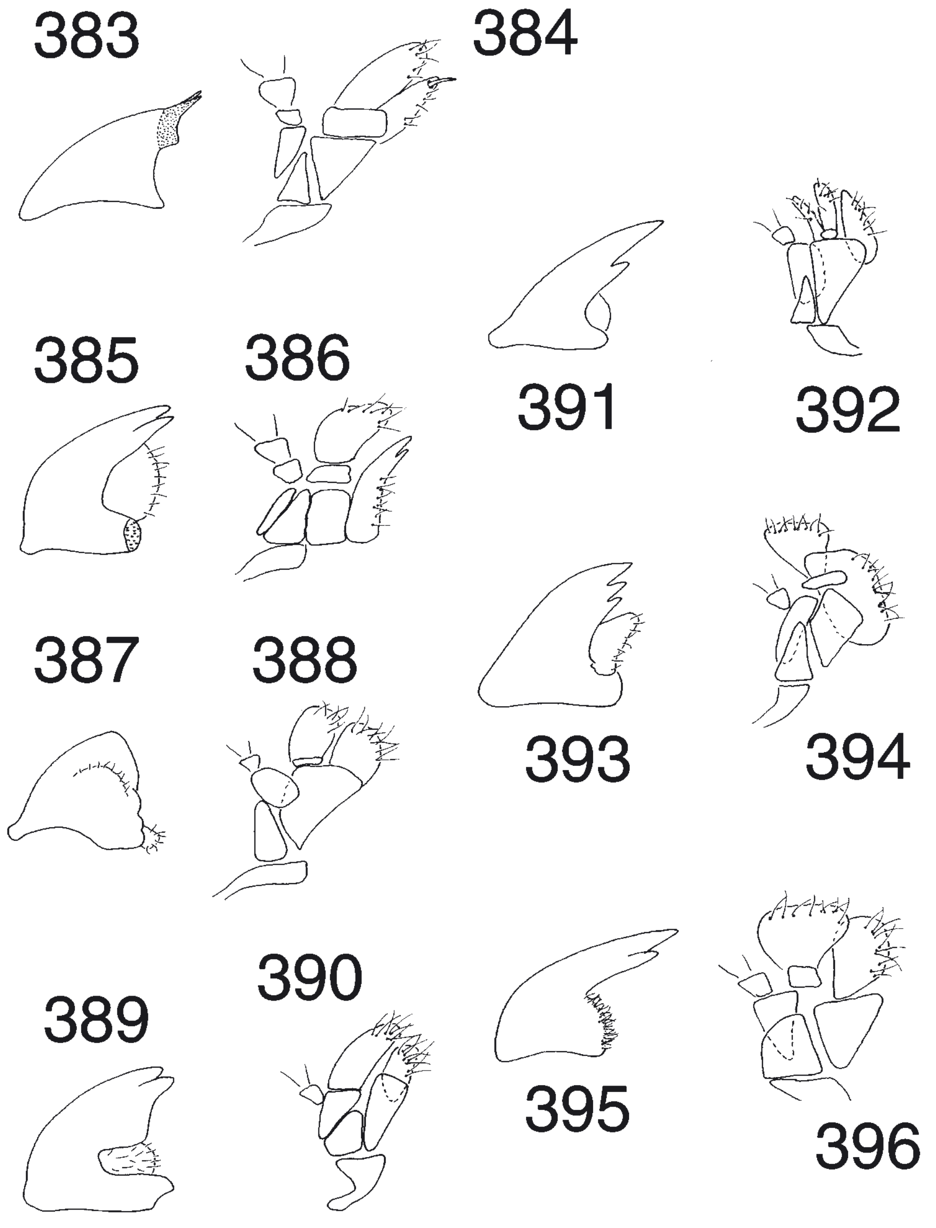
Figs 362–367. Abdomina dorsally and ventrally: 362, 363, *Cylindromorphus filum*; 364, 365, *Trachys minutus*; 366, 367, *Galbella felix*.



Figs 368–375. 368, *Coraebus undatus*, larva: mandible; 369, *Polycesta porcata*, larva: maxilla (after BÍLÝ 1989, modified); 370, *Ptosima flavoguttata*, larva: mesothoracic spiracle; 371, *Meliboeus subulatus*, larva: mesothoracic spiracle; 372 to 375, hypothetic transformation series of larval pronotal groove (polarity from 374 to 375 tentative): 372, Polycestinae, Galbellinae, Agrilinae; 373, Agrilinae; 374, Buprestinae; 375, Sphenopterinae. Figs 368, 370, 371 after BÍLÝ (1999); modified. Fig. 369 after BÍLÝ (1989); modified.



Figs 376–382. Labia of outgroups, schematic drawings: 376, *Attagenus pellio*; 377, *Derodontus macularis*; 378, *Bostrichus capucinus*; 379, *Byrrhus pilula*; 380, *Dascillus cervinus*; 381, *Dryops lutulentus*; 382, *Agrypnus murinus*.



Figs 383–396. Mandibles and maxillae of outgroups, schematic drawings: 383, 384, *Attagenus pellio*; 385, 386, *Derodontus macularis*; 387, 388, *Bostrichus capucinus*; 389, 390, *Byrrhus pilula*; 391, 392, *Dascillus cervinus*; 393, 394, *Dryops lutulentus*; 395, 396, *Agrypnus murinus*.