2. Glossary of Morphological Terms

John F. Lawrence, Rolf G. Beutel, Richard A. B. Leschen and Adam Ślipiński

Although a brief overview of beetle morphology may be found in Crowson (1955, 1981), Lawrence (1991), Lawrence & Britton (1991), Lawrence et al. (1999 a, b) and Beutel & Lawrence (2005), the following set of definitions and discussions represents a preliminary attempt to standardize nomenclature within the order, especially with respect to terminology introduced in relatively recent publications and not included in general textbooks or dictionaries. This is not meant to be a complete glossary, and a detailed treatment of beetle morphology will be included in a later volume of this series. The terms discussed below are, in general, those which turn up regularly in adult and larval descriptions of the beetle families included in this volume, and commonly used words found in general insect morphology texts are included only when their use within the order Coleoptera requires some explanation or elaboration. Terms or topics are arranged alphabetically under each of eight subheadings: head, prothorax, pterothorax, hind wing and abdomen for adults and head, thorax and abdomen for larvae.

Adult Head

Antennae: Clavate. Antennomeres gradually broader towards the apex; synonymous with incrassate.

Antennae: Capitate. One or more apical antennomeres are abruptly broader than and/or distinctly longer than those preceding them.

Antennal Fossa. Saucer-like concavity surrounding the countersunk antennal insertion (not to be confused with the antennal insertion or socket).

Antennal Insertion. Point of attachment of the antenna. Antennal insertions are considered to be exposed when at least some portion of each antennal socket is visible from above the long axis of the head (without regard to head orientation with respect to the body).

Cervical Sclerite. Compound sclerite in Polyphaga joining the ventrolateral edge of the occipital foramen with the lateral portion of the prosternum on each side. Each sclerite is usually divided into an anterior and posterior section separated by membrane.

Corpotentorium. Transverse bridge (tentorial bridge) connecting the posterior tentorial arms,

often arched and occasionally bearing an anteriorly projecting median process (Stickney 1923).

Corporotentorium (see Corpotentorium).

Epistomal Suture (or Sulcus) (**see** Frontoclypeal Suture).

Frontoclypeal Suture. Transverse suture representing an invagination between the frons and clypeus to form the epistomal ridge beneath with the anterior tentorial pits at either end.

Laminatentoria. Mesal expansions of the anterior tentorial arms, which may meet at the midline to form a secondary bridge anterior to the corpotentorium, if present (Stickney 1923).

Median Occipital Endocarina. Internal longitudinal ridge extending anteriorly from the dorsal edge of the occipital foramen.

Subantennal Groove. Groove or concavity lying below the antennal insertion and housing the base of the antenna. Placed between the eye (if present) and the mandibular articulation, and sometimes extends below or behind the eye.

Transverse Occipital Ridge. Any transverse line, carina or elevated ridge extending across the occipital region between the eyes and the occipital foramen. Usually indicates the extent to which the head is retracted into the prothorax; an elevated ridge may abut the anterior edge of the pronotum.

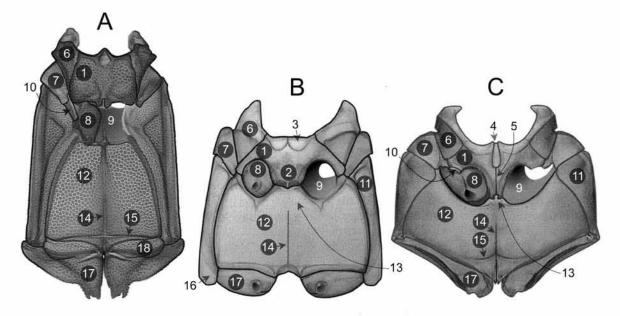
Vertexal Line (see Transverse Occipital Ridge).

Adult Prothorax

Cryptopleuron (see Endopleuron).

Endopleuron. Portion of the propleuron beneath the pronotum; not visible externally. In Archostemata, Adephaga and some Myxophaga this is a relatively minor part of the pleuron, but in almost all Polyphaga the pleuron is entirely internalized.

Hypomeron. Ventral portion of pronotum below the lateral pronotal carinae when these are present. In many Polyphaga, the two hypomera extend mesally behind the coxae partly or completely closing the procoxal cavities externally (**see** Postcoxal Process).



- Mesoventrite
- Mesoventral Process
- 3. Procoxal Rest
- Mesoventral Cavity
- 5. Mesothoracic Discrimen
- Mesanepisternum
- 7. Mesepimeron
- 8. Mesocoxa
- 9. Mesocoxal Cavity
- 10. Mesotrochantin
- 11. Metanepisternum
- 12. Metaventrite
- 13. Metaventral Process
- 14. Metathoracic Discrimen
- 15. Metakatepisternal Suture
- 16. Metepimeron
- 17. Metacoxa
- 18. Metatrochantin

Fig. 2.1. Coleopteran pterothoraces, ventral: A, *Distocupes varians* (Lea) (Archostemata: Cupedidae); B, *Episcaphula australis* (Boisduval) (Polyphaga: Cucujoidea: Erotylidae); C, *Sclerocyphon* sp. (Polyphaga: Byrrhoidea: Psephenidae). (© CSIRO Australia).

Lateral Pronotal Carina. Distinct edge separating the pronotal disc from the pronotal hypomeron on each side. Equivalent to the lateral edge of the prothorax (but not the pronotum, which terminates only at the notopleural or notosternal suture). The lateral carina may be raised to form a margin or bead, but that is not always the case.

Postcoxal Process. Mesal extension of the posterior part of the propleuron (Archostemata and Adephaga) or hypomeron (Myxophaga and Polyphaga) behind the procoxa, which may meet the prosternal process or the opposing postcoxsal process, thus closing the procoxal cavitiy externally.

Pronotal Disc. Dorsal portion of the pronotum, lying above the lateral pronotal carinae when these are present.

Procoxal Cavity. Countersunk prothoracic housing into which the procoxa fits. Formed in part by the prosternum (but see Prosternum) and in part by the propleuron (Archostemata, Adephaga and Myxophaga) or pronotal hypomeron (Polyphaga). This is an autapomorphy of the order Coleoptera but is secondarily reduced in a number of soft-bodied beetles.

Procoxal Cavities: External Closure. Externally closed when the postcoxal processes of the hypomera meet the prosternal process or meet one another.

Procoxal Cavities: Internal Closure. Internally closed when a narrow or broad bridge connects a portion of the internal lining of the cavity (usually in the vicinity of the sternal apophysis) with the internal wall of the postcoxal process.

Prosternal Process. Posterior projection of the mesal portion of the prosternum which extends between the procoxae and may overlap the mesoventrite or fit into the mesoventral cavity. The term "spinasternum" has been used by those studying Curculionoidea for the posterior end of the prosternal process, when the central portion of that process has been obliterated to accommodate the enlarged and contiguous procoxae.

Prosternum. Used for the entire ventral plate lying in front of and between the procoxae and between the notosternal or pleurosternal sutures, although it is likely that this sclerite has a complex origin, like comparable structures in the mesothorax and metathorax (**see** Mesoventrite and Metaventrite).

Spinasternum (see Prosternal Process).

Sublateral Pronotal Carina. Applied to various longitudinal carinae lying mesad of the lateral carinae. These may extend the length of the pronotal disc, as in Laemophloeidae, or be restricted to the posterior angles, as in many Elateridae.

Adult Pterothorax

Elytral Sutural Flange: Deflection. Deflected when the apical portion of the flange is expanded and thus visible when the elytra are in the closed position. Characteristic of certain families of Cucujoidea (Leschen *et al.* 2005) but may occur elsewhere.

Lateral Closure of Mesocoxal Cavity. Laterally open when the lateral wall is formed partly by one or more pleural sclerites and laterally closed when the lateral wall is formed entirely by the meeting of the mesoventrite and metaventrite.

Mesanepisternum. Anterior pleural sclerite of the mesothorax.

Mesendosternite. A pair of internal apodemes formed by invaginations within the mesocoxal cavities and representing the original furca.

Mesepimeron. Posterior pleural sclerite of the mesothorax.

Mesocoxal Cavity. Countersunk pterothoracic housing into which the mesocoxa fits. Formed by portions of the mesoventrite and metaventrite, often with the addition of mesopleural sclerites and less commonly the metanepisternum. This autapomorphy of the order Coleoptera is secondarily reduced in a number of soft-bodied beetles.

Mesofurca (see Mesendosternite).

Mesometathoracic Joint. Joint between mesothorax and metathorax which is visible only within the mesocoxal cavities; membranous in Archostemata and Adephaga and some families of Polyphaga, but either consists of a solid joint or is completely absent in Myxophaga and most Polyphaga.

Mesometaventral Joint (see Mesometaventral Junction).

Mesometaventral Junction. Meeting of the mesoventrite and metaventrite between the mesocoxal cavities. The junction may involve the abutment of the two sclerites, the overlapping of one by the other, or a complex, monocondylic or dicondylic joint. In some instances the two sclerites are fused together with or without a visible joint.

Mesosternal Cavity (see Mesoventral cavity).

Mesosternum (see Mesoventrite).

Mesothoracic Discrimen. Median line on the mesoventrite representing the invagination of the true mesosternum. This line is rarely complete and often absent in the mesothorax, where the single invagination or furca is replaced by well separated endosternal apodemes.

Mesoventral Cavity. Cavity on the mesoventrite into which the prosternal process fits.

Mesoventral Process. Mesal lobe at the posterior edge of the mesoventrite which usually extends between the mesocoxal cavities and meets the metaventral process (**see** Mesometaventral Junction).

Mesoventrite. Applies to the ventral plate lying in front of and between the mesocoxal cavities; delimited laterally by the mesothoracic pleurosternal sutures. Although called the mesosternum in most earlier works on Coleoptera, this sclerite is equivalent to the paired mesothoracic preepisterna and paired mesokatepisterna, the true mesosternum having been largely invaginated and represented only by the area in the immediately vicinity of the bases of the mesendosternites). The transverse suture separating the katepisterna from the preepisterna is never complete in the mesothorax of beetles (indicated by an internal transverse ridge in a few Archostemata) and the discrimen, representing the invagination of the original mesosternum, is present in most Archostemata, Gyrinidae, most Scirtoidea, most Buprestidae, a number of byrrhoid families and the elateroid family Artematopodidae.

Metacoxal Cavity. Countersunk abdominal housing into which the metacoxa fits. Usually formed by abdominal sternites II and III combined with the posterior wall of the metaventrite. This autapomorphy of the order Coleoptera is secondarily reduced in a number of soft-bodied beetles.

Metafurca (see Metendosternite).

Metakatepisternal Suture. Transverse suture on the metaventrite which separates the paired metathoracic preepisterna from the paired metakatepisterna. Although a complete suture, extending from the discrimen to the lateral edges of the mesoventrite on each side, is part of the groundplan of Coleoptera, it is often shortened so that it extends for only a short distance on either side of the discrimen.

Metanepisternum. Anterior pleural sclerite of the metathorax, which in Coleoptera is laterad of the metaventrite and mesoventrad of the metepimeron. Because the lateral (dorsal) portion of the metanepisternum is often concealed beneath the elytral epipleura, its shape in descriptions is based on the visible portion only. Metathoracic Discrimen. Median line extending forward from the posterior edge of the metaventrite, internally corresponding with a more or less high median ridge representing the invagination of the true metasternum. The ridge is usually connected with the metendosternite. The discrimen is often relatively long and may extend anteriorly to or beyond the base of the metaventral process, but it is reduced or absent in a number of groups.

Metaventral Process. Mesal lobe at the anterior end of the metaventrite which often extends forward between the mesocoxae and meets the mesoventral process (see Mesometaventral junction).

Metaventrite. Ventral plate lying behind and between the mesocoxal cavities and delimited laterally by the metanepisterna. Although called the metasternum in most earlier works on Coleoptera, this sclerite is equivalent to the paired metapreepisterna and paired metakatepisterna, the true metasternum having been invaginated along the midline. The transverse suture separating the katepisterna from the preepisterna is often complete, but may be shortened (extending for a short distance on either side of the discrimen) or absent, and the discrimen, representing the invagination of the original metasternum, is often very long, sometimes completely dividing the metaventrite into halves, but may be shortened or absent in various taxa. [Ferris 1940; Campau 1940; Matsuda 1960; Lawrence 1999; Lawrence et al. 1999 b; Beutel & Haas 2000.]

Metendosternite. Complex internal apodeme equivalent to the metafurca. Arises at or near the posterior edge of the metaventrite usually at the junction of the discrimen and the metakatepisternal suture and projecting anterodorsally. It usually consists of a median stalk, two short to long lateral arms and an anterior process from which a pair of tendons arise; however a lamina may be associated with each of the lateral arms and a pair of anteroventral processes may arise from the point where the lateral arms meet the stalk. In some taxa the stalk may be short or absent and the anterior tendons often arise on the arms. [Crowson 1938, 1944, 1955.]

Metepimeron. Posterior pleural sclerite of the metathorax, which in Coleoptera is located laterad of and above the metanepisternum and mostly concealed by the elytral epimeron. In most beetle groups a small portion of this sclerite is visible near the lateral edge of the metacoxa.

Prepectus. Anterior portion of mesoventrite and combined mesanepisterna, especially when set off from remainder of ventrite.

Pretarsus. The terminal segment of the leg, consisting of a pair of claws in most adults or rarely a single claw.

Postcoxal Lines of Metaventrite. Slightly raised ridges or abrupt edges of impressions at the anterior edge of the metaventrite. Sometimes these lines delimit crural impressions, but this is not always the case.

Procoxal Rests of Mesoventrite. Pair of impressions at the anterior edge of the mesoventrite into which the procoxae fit; these impressions may be almost horizontal in lateral view, but more often they are distinctly inclined or occasionally almost vertical. The procoxal rests sometimes extend laterally beyond the mesoventrite and onto the mesanepisterna.

Prosternal Rest of Mesoventrite. Median elevation at the anterior edge of the mesoventrite which fits against the underside of the prosternal process; in those elateroid taxa utilizing the clicking maneuver this process blocks the prosternal process from sliding into the mesoventral cavity until sufficient pressure is built up to overcome the inertia. In some other taxa the process may be flattened and abut the underside of the prosternal process.

Prothoracic Rest of Mesoventrite. Refers to a condition in which the entire anterior edge of the mesoventrite and flanking mesanepisterna form a peduncle over which the prothorax fits; this is usually correlated with a broad external closure of the procoxal cavities.

Scutellar Shield. Exposed portion of the mesoscutellum which lies between the bases of the elytra.

Scutellum. Posterior portion of mesotergum. Often referring only to that portion of the scutellum which is visible between the bases of the elytra (**see** Scutellar Shield).

Transverse Metasternal Suture (see Metakatepisternal Suture).

Transverse Metaventral Suture (see Metakatepisternal Suture).

Trochantin. Precoxal remnant articulating with the coxa, sternum and pleuron.

Trochantin (**Prothorax**). Used in Myxophaga and Polyphaga for the exposed portion of the trochantinopleuron.

Trochantinopleuron. Fusion product of the prothoracic trochantin with the propleuron.

Hind Wing

The terms for wing veins and related structures used in this volume are based primarily on that of Kukalová-Peck & Lawrence (1993, 2004). Some changes in wing vein terminology listed on p. 144

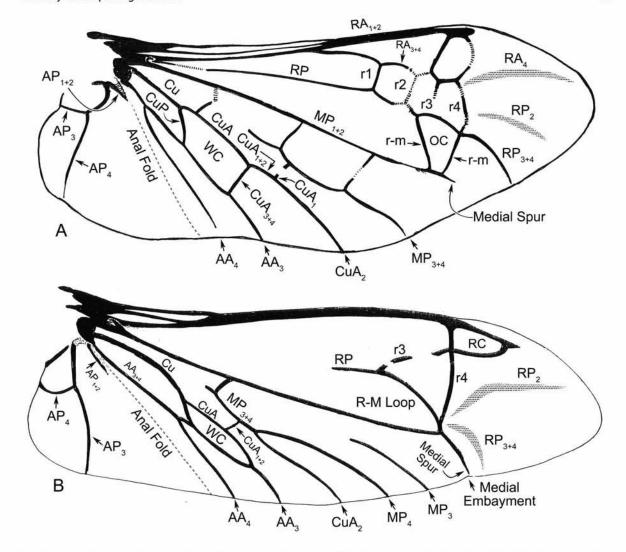


Fig. 2.2. Coleopteran hind wings: A, *Omma stanleyi* Newman (Archostemata: Ommatidae); B, *Notodascillus sublineatus* Carter (Polyphaga: Dascilloidea: Dascillidae). (Modified from Lawrence & Britton 1991; © CSIRO Australia.) RC = Radial cell; OC = Oblongum cell; WC = Wedge cell.

of the latter work and based in part on the study by Haas & Kukalová-Peck (2001) have been overlooked in some subsequent studies. The most important of these deal with venation in the medial field and will be repeated here: CuA = Cu, $CuA_{1+2} = CuA$, $CuA_{3+4} = CuP$, $CuA_2 = CuA_{3+4}$, $AA = AA_{3+4}$, $AA_{1+2} = AA_3$, $AA_{3+4} = AA_4$.

Anal Area (see Anal Lobe).

Anal Embayment. Embayment in the wing margin at the end of the anal fold which may be weak and gradual or consist of a deep notch.

Anal Field (see Anal Lobe).

Anal Fold. Fold between AA_{3+4} and AP; delimiting the anal lobe.

Anal Lobe. Portion of the wing basad of the anal fold. The anal lobe (actually homologous with the ano-jugal lobe but the jugal component is highly

reduced in beetle wings) usually contains AP_{3+4} (which may be forked to form AP_3 and AP_4) and occasionally a small AP_{1+2} may also be present. In Lawrence *et al.* (1999 b) the term "anal lobe" was used in narrower sense for those instances where the anal field was separated from the remainder of the wing by a deep notch.

Anal Notch. Deep and usually narrow anal embayment.

Ano-Jugal Lobe (see Anal Lobe).

Anterior Wing Strut (see Radial Bar).

Apical Area (see Apical Field).

Apical Extensions of RP. Branches of RP (usually RP1 and RP2) extending apicad of the R-M loop. In some taxa there may be two or three branches, in others only RP2 remains and branches

may be vaguely indicated or absent. Linear, often oblique sclerotizations in the apical field of various elateroid wings (Crowson 1961; Dolin 1975) may represent remnants of these radial extensions, but this is uncertain.

Apical Field. Portion of the wing membrane lying apicad of the radial cell (Polyphaga), cross-vein r4, the R-M loop (Polyphaga), the oblongum cell (most Archostemata, Myxophaga and Adephaga) and medial spur, and often containing terminal branches of RA and RP or the elateroid sclerites possibly derived from them.

Basal Portion of RP. Portion of RP between its origin (usually obliterated) and its junction with an R-M cross-vein forming the R-M loop or the base of the oblongum cell. Rarely complete and very short or even absent in some taxa.

Bending Zone. Area of weakness in the radial and medial bars which allows them to be curved towards one another when the bar is rotated in a certain way (by movements of the axillary sclerites). The weakness may be caused by a series of transverse impressions or by a flattening of the strut. Bending zones may be relatively broad so that bending is gradual or may be shortened to the point where they are more like a sharp hinge. Bending zones are found in only a few of the polyphagan families included in this volume.

Cross-vein r3. Subapical cross-vein between RA₃₊₄ and RP; transverse (perpendicular to long axis of wing) or strongly oblique in Archostemata, Myxophaga and Adephaga and often slightly oblique to longitudinal (parallel to long axis of wing) in Polyphaga; rarely complete and often absent. Termed the "radial recurrent vein" in some older systems of nomenclature.

Cross-vein r4. Apical cross-vein between RA₃₊₄ and RP; always more or less transverse and usually complete.

Cubito-Anal Remnant. Occasionally used when a single compound vein consisting of Cu, CuP and AA₃ remains in the medial field.

Deflexion Zone (see Bending Zone).

Free Veins. Veins not joined apically to another vein and often extending to the wing margin; in the medial field usually consisting of MP₃₊₄ (or MP₃ and MP₄), CuA₂, AA₃ and AA₄.

Medial Area (see Medial Field).

Medial Bar. Posterior wing strut, consisting entirely of MP_{1+2} .

Medial Binding Patch (see Medial Fleck).

Medial Bridge. Bridge at the base of the wing connecting RA with MP_{1+2} ; important in the folding and unfolding of the wing.

Medial Embayment. Emargination of the wing membrane at or beyond the end of the medial spur.

Medial Field. Portion of the wing membrane between medial bar (MP_{1+2}) and the anal fold and usually containing branches of MP_{3+4} , Cu and AA_{3+4} . Veins in the medial field, referred to by Crowson (1955, p. 91) as "anal veins in the main group", tend to anastomose in various ways and reduction of free veins from five to one or none is relatively common, especially in small species.

Medial Fleck. Binding patch located in the medial field. In Polyphaga this is located in front of MP_{3+4} . In some Adephaga a non-homologous fleck is located behind MP_{3+4} , and usually containing MP_{3+4} , Cu and AA_{3+4} and their branches.

Medial Spur. Apical extension of MP₁₊₂ beyond the R-M loop or oblongum cell. Very short and straight or absent in Archostemata, Myxophaga and Adephaga and usually longer and posteriorly curved in Polyphaga.

Median Area. Error in Lawrence et al. (1999 b) (see Medial Field).

Median Bar. Error in Lawrence et al. (1999 b) (see Medial Bar).

Medio-Cubital Brace. Reinforced cross-vein joining MP_{1+2} and Cu near their bases, but usually broken in the middle by a fold.

 MP_{3+4} : Cross-vein and Basal Spur. Sub-basal cross-vein joining MP_{3+4} to MP_{1+2} and often accompanied by a basal spur, which is a remnant of the true base of the vein. When the spur is absent, the cross-vein may appear to be the base of MP_{3+4} , but in a more apical position.

Oblongum Cell. Cell in most Archostemata, Adephaga and Myxophaga formed between two R-M cross-veins.

Posterior wing strut (see Medial Bar).

Radial Bar. Anterior wing strut consisting of an alignment and fusion of ScP and RA.

Radial Cell. Forking of RA into RA_{1+2} and RA_{3+4} and a subsequent rejoining of these two branches near the anterior wing margin in Polyphaga. Not homologous with cells formed by cross-veins between RA_{1+2} and RA_3 or RA_{3+4} in Archostemata, Myxophaga and Adephaga.

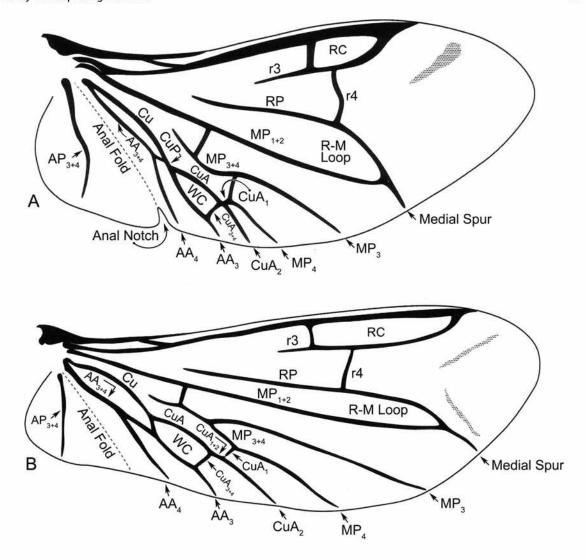


Fig. 2.3. Coleopteran hind wings: A, Osslimus freyi (Cobos) (Polyphaga: Elateroidea: Elateridae); B, Stichotomus sp. (Polyphaga: Elateroidea: Elateridae). (Modified from Calder 1996; © CSIRO Australia.)

Radio-Medial Loop (see R-M Loop).

R-M Loop. Apically arched R-M cross-vein joining the basal portion of RP and MP_{1+2} . Homologous to the apical side of the oblongum cell. Often forming a continuous curve between RP and MA, but sometimes narrowed so that an acute angle is formed.

Second Cubito-Anal Cell (see Wedge Cell).

Subcubital Fleck (see Medial Fleck).

Transverse Folds. More or less obliquely transverse folds; involved in the shortening of the wing length.

Wedge Cell. Cell formed by CuA anteriorly, CuP basally, AA₃ posteriorly, and CuA₃₊₄ apically and usually giving rise apically or subapically to one or more branches of Cu and to the terminal portion of AA₃. This cell is also referred to as the 2nd cubito-anal cell,

the first being formed at the wing base between Cu and AA_{3+4} , with CuP at its apex.

Adult Abdomen

Accessory Lobes. Paired lobes articulated with the apicale in the aedeagus of various Tenebrionoidea.

Aedeagus. Combined structure consisting of phallobase, parameres and penis.

Apicale. Formed by the fusion of the two parameres.

Baculum. Sclerotized bar or strut which serves to support a membranous ovipositor. Paired longitudinal baculi are often present on the proctiger and paraprocts, and a transverse baculum often occurs at the base of the coxite.

Basal Piece (see Phallobase).

Basale (see Phallobase).

Bursa. Enlargement of the female genital tract, which is often a blind sac at the anterior end of the tract (anterior bursa), but may be an enlarged section of the tract in the vicinity of the common oviduct (vaginal bursa).

Connate Ventrites. Visible sternites which are not freely movable. This is not always easy to determine in lightly sclerotized abdomens, and there tends to be a continuum from sclerites which are capable of some limited movement to those which are solidly fused together. In rare cases the sutures between connate ventrites may be partly to almost entirely effaced.

Coxite (see Gonocoxite).

Cucujiform Aedeagus. That type of aedeagus in which the phallobase forms a sheath or ring partly or entirely enclosing the penis.

Double Tegmen. Referring to a type of cucujiform aedeagus found in a number of Cleroidea plus the cucujoid families Biphyllidae and Byturidae in which the tegmen bears a pair of anterior struts and an opposing median anterior strut.

Endophallus. Inverted membranous tube within the penis and sometimes armed with a variety of sclerotized structures.

Epiproct (see Proctiger).

Genital Ring. Ring-like structure surrounding the aedeagus and consisting of segments IX and X, which may be partly or entirely fused together.

Gonangulum (see Gonocoxite).

Gonocoxite. One of two coxites associated with segment IX in female Coleoptera. The coxite is often divided into a basal and apical lobes, the first of which may have a transverse or oblique baculum which articulates with the paraproctal baculum. The apical lobe is further subdivided in some taxa. The basal coxital lobe may be homologous to the gonangulum of Scudder (1961).

Gonostylus (see Stylus).

Hemitergite IX (see Laterotergite IX, Paraproct).

Internal Sac (see Endophallus).

Lateral Lobes (see Parameres).

Laterotergite IX. Paired plates formed when tergite IX is divided into two parts in either male or female (see Paraproct).

Median Lobe (see Penis).

Ovipositor. In female Coleoptera usually referring to the combined proctiger, paraprocts, gonocoxites and styli. One or more of these elements may be absent in certain groups and in a few families there is no distinct ovipositor, but just a vulva surrounded by membrane.

Parameral Piece (see Apicale).

Parameres. Paired structures articulated with the posterior end of the phallobase in aedeagi of the trilobate type; sometimes fused to the phallobase, fused together in various ways or fused to the anterior end of the penis.

Paraproct. Referring to one of the two hemitergites or laterotergites of segment IX in most female beetles in which segment IX has become entirely divided into two parts which lie on either side of tergite X.

Penis. Major intromittent organ containing the inverted endophallus and the opening of the ejaculatory duct; enclosed by the phallobase and parameres or the tegmen.

Phallobase. Anterior or basal portion of the aedeagus to which the parameres are attached in aedeagi of the trilobate type. In aedeagi of the cucujiform type, the phallobase forms most of the sheath or ring enclosing the penis.

Postcoxal Lines of First Abdominal Ventrite. Slightly raised ridges of abrupt edges of impressions at the anterior edge of ventrite 1. Usually delimiting crural impressions.

Proctiger. Referring to tergite X in both male and female; lies immediately above the anal opening and may become membranous in some groups.

Spermatheca. Usually referring to a sac-like structure, often sclerotized; attached by a slender duct to the genital tract.

Spermathecal Gland. Gland associated with the spermatheca, usually either joined directly to it or to the spermathecal duct.

Spiculum Gastrale. Slender strut formed by an anterior extension of the subgenital plate.

Spiculum Relictum. Anterior strut on sternite VIII in the male.

Spiculum Ventrale. Anterior strut on sternite VIII in the female.

Stylus. Small lobe articulated apically or subapically to the coxite in the ovipositor of most Coleoptera.

Subgenital Plate. Ventral portion of the genital ring, formed by a fusion of sternite IX and anteroventral extensions of tergite IX or laterotergites IX.

Tegmen. Usually synonymous with the phallobase in aedeagi of the cucujiform type, in which the phallobase forms a sheath or ring partly or entirely surrounding the penis (**see** Cucujiform Aedeagus). When the parameres are fused to the end of the phallobase, the term tegmen is often used for the entire combined structure.

Tegmenite. Slender sclerite articulated with sternite IX or in the connecting membrane between the sternite IX and the phallobase.

Tergite X (see Proctiger).

Trilobate Aedeagus. Basal type of aedeagus in Coleoptera, which consists of a penis lying dorsad of a phallobase and paired, articulated parameres. In many Coleoptera, including most Archostemata, Adephaga and Myxophaga, as well as a variety of Polyphaga, the phallobase appears to be absent, having become membranous or fused to the parameres.

Vaginal Palp. Combined gonocoxite and stylus (Mikoleit 1973).

Valvifer. Used inconsistently by Tanner (1927) but in general homologous with the paraproct (see Paraproct).

Ventral Sclerite. Slender longitudial sclerite lying ventrally between the coxites and below the vulva.

Ventrite: Abdominal sternite exposed in intact specimens; not concealed by the metacoxae or enclosed within the abdominal apex. The first ventrite in most Polyphaga and in Myxophaga and Archostemata is sternite III, but it is sternite II in Adephaga and in some groups of Polyphaga.

Vulvar Sclerite (see ventral sclerite).

Larval Head

Coronal suture (see Epicranial Stem).

Ecdysial lines. Lines of weakness on the dorsal head surface where the cuticle separates during moulting.

Epicranial Stem. Median ecdysial line, which forks to form the frontal arms.

Epicranial suture (see Ecdysial Lines, Epicranial Stem, Frontal Arms).

Frontal Arms. Paired ecdysial lines either arising from the epicranial stem or independently joined to the posterior edge of the head capsule.

Frontal Sutures (see Frontal Arms).

Gula. Sclerotised region posterad of the posterior tentorial pits.

Hypopharyngeal Bracon. More or less sclerotized (but not usually pigmented) bridge joining the ventral mandibular articulation on each side with the hypopharynx.

Hypopharyngeal Sclerome. Sclerotized bar or tooth-like structure on the hypopharynx; acts in conjunction with the mandibular molae.

Hypostomal Cavity. Excavation of the ventral portion of the head capsule enclosing the retracted maxillae and labium.

Hypostomal Ridges. Sclerotized lateral edges of the hypostomal cavity.

Hypostomal Rods. Posterior continuations of the hypostomal ridges beyond the maxillary bases and onto the ventral portion of the head capsule.

Ligular Sclerome. Sclerotized wedge-like sclerite formed from the ligula. Not equivalent to the hypopharyngeal sclerome, which is located well posterad of this on the surface of the hypopharynx.

Maxillolabial Complex. The combination of maxillae and labium when these are closely associated and mainly or exclusively moved in a nearly vertical direction (without an intervening maxillary articulating area).

Medial Endocarina. Dorsal internal ridge on the head usually lying beneath the epicranial stem, when present, and often extending forward between the frontal arms. May also be present when ecdysial lines are absent.

Mola. Usually basal and armed with asperities, tubercles or transverse ridges. In some groups somewhat reduced and sub-basal.

Paired Endocarinae. Pair of dorsal internal ridges on the head, usually lying beneath the bases of the frontal arms.

Prostheca. Located distad of the basal mola and either membranous, sclerotized but hyaline, or consisting of hair-like structures of various kinds. Similar structures in the absence of a mola are not referred to as prosthecae.

Sensorium. Usually refers to a large sensillum located on the preapical antennomere. Although it is usually conical or palpiform, it may be dome-like

or occasionally multiple or complex (consisting of several dome-like sections). Occasionally located on the apical palpomere or very rarely (some Phalacridae) on the basal one.

Sensory Appendage (see Sensorium).

Ventral Epicranial Ridges. Pair of ridges extending posteriorly from the ventral mandibular articulations; located laterad and ventrad of the hypostomal ridges and more or less supporting the maxillolabial complex.

Ventral Mouthparts. Refers to the maxillae plus the labium or the maxillolabial complex when these structures form a single unit.

Ventral Mouthparts: Retraction. The retraction of the ventral mouthparts is the distance between the ventral mandibular condyles and the basal attachments of the cardines or the depth of the hypostomal cavity. In larvae with protracted ventral mouthparts, this distance or depth is minimal or zero, and the mandibles and maxillae are attached approximately at the same level.

Larval Thorax

Basisternum. Anterior part of the larval sternum, anterad of the sternal pits.

Cervicosternum. Small anteromesal sclerite, separate from the presternum.

Laterotergite. One of the sclerotized plates lying between the inflected part of the tergum and the pleural sclerites (precoxale and postcoxale); one of the mesothoracic laterotergites may contain the spiracle.

Precoxale. Pleural (episternal) sclerotised area anterolaterad of the coxal articulation.

Postcoxale. Pleural (epimeral) sclerotised area posterolaterad of the lateral part of the coxal articulation.

Presternum. Separate anteromedian sclerite anterad of the basisternum; sometimes large and more or less triangular, but often vaguely defined or absent.

Pretarsus. The terminal segment of the larval leg, consisting of a pair of claws in most Adephaga and a few Archostemata or a single claw in some Adephaga, most Archostemata and all Myxophaga and Polyphaga.

Tarsungulus. The terminal of claw segment of the larval leg in Polyphaga as used by those who maintain that this segment represents a fusion of the tarsus and pretarsus (**see** Pretarsus and Tibiotarsus).

Tibiotarsus. Formed by the fusion of the tibia and tarsus in larvae of Myxophaga and Polyphaga.

Larval Abdomen

Interurogomphal Pit. Pit or one of a pair of pits lying between the urogomphi.

Laterosternite. Sclerotized plate lying between the main sternal plate and the tergosternal fold.

Laterotergite. Sclerotized plate lying between the inflected part of the tergum and the tergosternal fold. One of the laterotergites usually contains the spiracle.

Pygopods. Paired projections on segment X which may or may not bear hooks and usually assist in locomotion.

Tergosternal Fold. Fold or membrane connecting the abdominal terga and sterna.

Urogomphi. General term used for a number of non-homologous, doubtfully homologous or rarely clearly homologous paired cuticular outgrowths arising from the posterior end of tergum IX. The basally articulated urogomphi occurring in some Adephaga and Staphyliniformia were formerly homologized with cerci, which occur on segment X or XI in some other orders, but these, like the fixed urogomphi, have clearly evolved on several occasions within Coleoptera.

Larval Spiracles

Spiracular Closing Apparatus. Apodeme attached to the trachea at or near the base of the spiracular atrium. It is involved in the closure of the trachea.

Annular-biforous Spiracle. Type of spiracle with the main spiracular opening accompanied by a pair of accessory openings. In some families (e.g., Histeridae, Nitidulidae), these accessory openings are much longer than the main opening, so that they resemble the biforous type of spiracles; however the spiracular scar is always absent.

Annular-multiforous Spiracle. Type of spiracle with a number of accessory openings around the perimeter of the main opening.

Annular-uniforous Spiracle. Type of spiracle with the main spiracular opening accompanied by a single accessory opening.

Bicameral Spiracle (see Annular-biforous Spiracle).

Biforus Spiracle. Spiracular opening entirely blocked by a medium septum with a narrow, slit-like opening on either side. Biforous spiracles have evolved in connection with the elateroid ecdysial process (Hinton 1947) and are always associated with a spiracular scar.

Bilabiate Spiracle (see Biforous Spiracle).

Cribriform Spiracle. Spiracular opening entirely or partly blocked by a sieve plate. Three or four types of cribriform spiracles have evolved in connection with the elateroid ecdysial process (Hinton 1947) and are associated with a spiracular scar, and another two or three in which normal ecdysis occurs and the spiracular scar is absent.

Ecdysial Scar (see Spiracular Scar).

Stigmatic Scar (see Spiracular Scar).

Spiracular Scar. Collapsed opening of a tube through which the spiracular lining is removed at ecdysis. Occurs only in those larvae which have biforous or cribriform spiracles and which undergo the elateroid type of ecdysis.

Unicameral Spiracle (see Annular-uniforous Spiracles).

Multicameral Spiracle (see Annular-multiforous Spiracle).

Literature

- Beutel, R. G. & Haas, F. (2000): Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics* 16: 103–141.
- Beutel, R. G. & Lawrence, J. F. (2005): 4. Coleoptera, Morphology. Pp. 23–27 in Beutel, R. G. & Leschen, R. A. B. (eds.) Handbook of Zoology. Volume IV Arthropoda: Insecta. Part 38. Coleoptera. Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin, New York.
- Calder, A. A. (1996): *Click Beetles. Genera of the Australian Elateridae* (*Coleoptera*). x + 401 pp. CSIRO Publishing (Monographs on Invertebrate Taxonomy. Vol. 2), Collingwood, Victoria.
- Campau, E. J. (1940): The morphology of *Chauliognathus pennsylvanicus* (DeGeer) (Coleoptera: Cantharidae). *Microentomlogy* 5 (3): 57–85.
- Crowson, R. A. (1938): The metendosternite of Coleoptera: a comparative study. – *Transactions of the*

- Royal Entomological Society of London 87 (17): 397-416, 13 pls.
- (1944): Further studies on the metendosternite in Coleoptera. – Transactions of the Royal Entomological Society of London 94 (2): 273–310, 10 pls.
- (1955): The Natural Classification of the Families of Coleoptera. 187 pp. Nathaniel Lloyd, London.
- (1961): On some new characters of classificatory importance in adults of Elateridae (Coleoptera).
 The Entomologist's Monthly Magazine 96: 158-161.
- (1981): The Biology of Coleoptera. xii + 802 pp. Academic Press, London.
- Dolin, V. G. (1975): Wing venation in click beetles and its significance in the taxonomy of the family. *Zoologicheskii Zhurnal* 54 (11): 1618–1633 (in Russian).
- Ferris, G. F. (1940): The myth of the thoracic sternites in insects. *Microentomology* 5 (3): 87–90.
- Haas, F. & Kukalová-Peck, J. (2001): Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). – European Journal of Entomology 98: 445–509.
- Hinton, H. E. (1947): On the reduction of functional spiracles in the aquatic larvae of the Holometabola, with notes on the moulting process of spiracles.
 Transactions of the Royal Entomological Society of London 98: 449–473.
- Kukalová-Peck, J. & Lawrence, J. F. (1993): Evolution of the hind wing in Coleoptera. – Canadian Entomologist 125: 181–258.
- (2004): Use of hind wing characters in assessing relationships among coleopteran suborders and major endoneopteran lineages. – European Journal of Entomology 101 (1): 95–144.
- Lawrence, J. F. (1991): Order Coleoptera. Pp. 144–298 in Stehr, F. W. (ed.) Immature Insects, Vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- Lawrence, J. F. (1999): The Australian Ommatidae (Coleoptera: Archostemata): new species, larva and discussion of relationships. – *Invertebrate Taxonomy* 13: 369–390.
- Lawrence, J. F. & Britton, E. B. (1991): Coleoptera (Beetles). Pp. 543–683 in CSIRO Division of Entomology (ed.) *Insects of Australia: a Textbook for Students and Research Workers, Second Edition.* Vol. 2. Melbourne University Press, Carlton, Victoria.
- Lawrence, J. F., Hastings, A. M., Dallwitz, M. J., Paine, T. A. & Zurcher, E. J. (1999 a): Beetle Larvae of the World: Descriptions, Illustrations, Identification, and Information Retrieval for Families and Subfamilies. CD-ROM, Version 1.1 for MS-Windows. CSIRO Publishing, Melbourne.
- (1999 b): Beetles of the World: A Key and Information System for Families and Subfamilies. CD-ROM, Version 1.0 for MS-Windows. CSIRO Publishing, Melbourne.
- Leschen, R. A. B., Lawrence, J. F. & Ślipiński, S. A. (2005): Classification of basal Cucujoidea (Coleoptera: Polyphaga), with a cladistic analysis, descriptions of new genera and species, and keys to adults and larvae of cucujoid families. – *Invertebrate Systematics* 19: 17–73.

- Matsuda, R. (1960): Morphology of the pleurosternal region of the pterothorax in insects. *Annals of the Entomological Society of America* 53 (6): 712–731.
- Mikoleit, G. (1973): Über den Ovipositor der Neuropteroidea und Coleoptera und seine phylogenetische Bedeutung (Insecta, Holometabola). Zeitschrift für Morphologie der Tiere 74: 37–64.
- Scudder, G. G. E. (1961): The comparative morphology of the insect ovipositor. *Transactions of the Royal Entomological Society of London* 113 (2): 25–40.
- Stickney, F. S. (1923): The head-capsule of Coleoptera. *Illinois Biological Monographs* 8 (1): 104 pp., 8 pls.
- Tanner, V. M. (1927): A preliminary study of the genitalia of female Coleoptera. *Transactions of the American Entomological Society* 53: 5–50.