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Morphology, phylogeny and classification of the family Erotylidae based on adult characters (Coleoptera: Cucujoidea)

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Abstract. Morphology of 25 geneera of Erotylidae – the type-genera of all higher taxa (subfamilies and tribes) distinguished in the family, as well as representatives of morphologically distinctive groups is described and discussed. 85 adult morphological characters have been used. The results of phylogenetic analysis show that Erotylidae and Languriidae must be combined into single family Erotylidae. Erotylidae are divided into two subfamilies: Xenoscelinae (including Cryptophilinae **n. syn.**, Toraminae **n. syn.** and Setariolinae **n. syn.**). and Erotylinae (including former Languriinae **n. syn.**). Erotylinae is divided into five tribes: Dacnini, Languriini, Erotylini, Tritomini, Encaustini (= Megalodacninae **n. syn.**).

Key words: entomology, taxonomy, morphology, Cucujoidea, Coleoptera, Erotylidae

INTRODUCTION

The superfamily Cucujoidea (Clavicornia) contains *ca.* 30 beetle families of extraordinarily variable anatomy and bionomy. One of the richest in terms of both genera and species is Erotylidae, known to entomologists (or at least: documented in literature) already since middle of XVIII century: contrasting, bright colouration as well as usually large size attracted scientists of that time. Despite rather great number of known taxa (currently – including Languriidae – *ca.* 3200 species in more than 280 genera) the supraspecific classification of this group – based largely on Lacordaire's (1842) and Crotch's (1876) systems! – is still not stable, and until now no comprehensive comparison of morphological characters (neither in adults nor in preimaginal stages) throughout the family has been attempted: all studies were restricted to a single geographical area, to few subgroups, or to particular character.

HISTORY OF STUDIES ON THE EROTYLIDAE

First species currently included in the Erotylidae were described by LINNAEUS in tenth edition of *Systema Naturae* (1758). He ranged them among the then widely interpreted genera *Coccinella* and *Chrysomela*. Few years later FABRICIUS (1775) described the first two genera of this family – *Erotylus* and *Tritoma* – and until the end of XVII century further two had been erected: *Triplax* HERBST (1793) and *Dacne* LATREILLE (1796). In 1802 LATREILLE separated Erotylidae as a family. With the discoveries of new lands and acquisition of more extensive collections the list of known species rapidly grew: to its augmentation – besided four above-mentioned authors – contributed C. P. THUNBERG, J. G.SCHALLER, F. W. HERBST, O. F. OLIVIER, G. W. F. PANZER, G. PAYKULL, T. SAY, P. A. J. DUPONCHEL, J.STURM, F. E. GUÉRIN-MENÉVILLE, L. A. A. CHEVROLAT and many others. In 1825 DUPONCHEL published a monograph of then very widely understood genus *Erotylus* (containing practically all the subfamily Erotylinae as presently interpreted). Catalogue of Napoleon's general and addict collectioner of beetles, baron DEJEAN (1837) included the first proposals of generic classification of the family; the names introduced by him were then accepted also by later authors. The – for that time enormous – collection of DEJEAN enabled Théodore LACORDAIRE, professor of natural history on the Liége University, to write (1842) the only comprehensive monograph of the World Erotylidae ever produced. This work, containing detailed descriptions of 570 species classified in 28 genera, provided the base of study on the Erotylidae – especially of the Neotropical Region – for many generations of entomologists. LACORDAIRE divided Erotylidae into two groups: Erotyliens engidiformes (Erotylini engidiformes) and Erotyliens vrais (Erotylini genuini). The concepts of genera remained until now or have been only marginally modified. In 1876 posthumously appeared, unfortunately far from perfect, revision – in fact a catalogue of all species known by that time, with descriptions of new taxa – by CROTCH; despite "unpolished" state it was a milestone in erotylid studies. Since then nobody ventured to work out the entire family, though the number of known genera and species increased at a bewildering pace. In 1876, in the series "Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus", appeared

XX century, and especially its first half, was a period of many descriptions of new genera and species. To the most productive authors of that time belong (in chronological sequence): T. KUHNT, S. SCHENKLING, G. J. ARROW, L. MADER and K. DELKESKAMP, while among the most important publications having then appeared are the respective volumes of Genera Insectorum (1909) and Coleopterorum Catalogus (1911) (both by KUHNT), as well as ARROW's (1925) review of the fauna of British India and MADER's (1942, 1951) of Peru. Between mid-thirties and late seventies Kurt DELKESKAMP worked intensively on African Erotylidae, having published a series of comprehensive revisions (DELKESKAMP 1936, 1954, 1957, 1962, 1965), a monograph of Madagascan fauna by his disciple (PHILLIPP 1965), and a summary of the knowledge on that continent's fauna in Coleopterorum Catalogus Supplementum (DELKESKESKAMP 1981). Also the North-American (BOYLE 1956) and Japanese (CHŰJÔ 1969) erotylids have been monographed, and recently appeared also catalogues of South and Middle America (ALVARENGA 1994) and the Old World (excluding Africa and Madagascar) (CHŰJÔ and CHŰJÔ 1988, 1989, 1990).

HISTORY OF CLASSIFICATION OF THE FAMILY AND THE PROBLEM OF "LANGURIIDAE"

Although the Erotylidae had already been recognized in early XIX century, some genera were placed in other, often distant families, and only LACORDAIRE (1842) grouped them (still without *Dacne* or "Languriidae") together. He was also the first to attempt the comprehensive generic classification of the family, having divided it into Erotyliens engidiformes (Erotylini engidiformes), containing the subfamilies Megalodacninae, Encaustinae and Tritominae, and Erotyliens vrais (Erotylini genuini) with the subfamily Erotylinae and genus *Aulacochilus* (Encaustinae). BEDEL (1869), in his very accurate comprehensive study of European, North African and West Asian Erotylidae, was the first to include the genus *Dacne* to to this family, divided by him into two sections (subfamilies): Enginae (as Engides) (= Dacninae) and Triplacinae (as Triplacines).

The publication based on the World fauna was that of CROTCH (1876); unfortunately the author died young before having finished it, and therefore while some groups have been worked out in detail, other parts of the text remained as simple uncritical list of species. Despite its incompleteness, this work was an important contribution to the classification of the family. CROTCH described several new genera and several tens of new species, having also included Languriidae and Helotidae (as subfamilies) to Erotylidae. CROTCH's system has been accepted by most students – including CHAPUIS (1876), LECONTE and HORN (1883) – and remains with minor modifications until now.

An original hypothesis was set forth by GANGLBAUER (1899). His work, formally concerning the coleopterofauna of Middle Europe, often listed all known European species, while the author worked out the general classification of beetles. GANGLBAUER divided the Erotylidae into three subfamilies: Erotylinae [with tribes: Erotylini, Triplacini, Dacnini, Xenoscelini, Diphyllini (= Biphyllidae, but including the genus *Cryptophilus*)], Cryptophaginae (comprising almost all small representatives of the Languriidae, classified until 1971 in the family Cryptophagidae) and Atomariinae (now a subfamily of the Cryptophagidae). The adequacy of such system may be questioned, but the Austrian scientist deserves the credit for drawing attention to the phylogenetic affinity between Erotylidae, (at least part of) Languriidae, Biphyllidae and Cryptophagidae. KUHNT (1909, 1911), in two catalogues including all species of the Erotylidae [except most Languriidae, elaborated by SCHENKLING (1923, 1928) and FOWLER (1908)], retained GANGLBAUER's system almost unchanged, dividing Erotylidae into the following tribes: Erotylini (Erotylinae + *Aulacochilus*), Encaustini, Triplacini, Dacnini, Diphyllini (now family Biphyllidae) and Xenoscelini.

ARROW (1925) based his revision of the Erotylidae of British India on Lacordaire's concept, unfortunately applying it only to the Old World fauna. He placed *Aulacochilus*, *Micrencaustes* and *Encaustes* in one group, treating Languriidae as a separate family. Arrow's system includes the following subdivisions: subfamily Dacninae, subfamily Tritominae [tribes: Encaustini, Tritomini, Erotylini (ARROW does not mention this New World group, but the morphological characters used by him placed it here)] and Euxestinae [now included in the family Cerylonidae (SEN GUPTA and CROWSON 1973)].

The classification proposed in 1969 by famous Japanese entomologist CHŰJÔ was a synthesis of earlier views. A novelty was the inclusion of Cryptophilinae (previously placed either in Cryptophagidae or in Biphyllidae), as a subfamily, into Erotylidae. In his publication, concerning South-East Asian fauna, CHŰJÔ divided Erotylidae into Dacninae, Triplacinae {with tribes Encaustini and Triplacini [the latter further divided into subtribes Triplacina and Cyrtotriplacina (= Tritomina)]}, Erotylinae and Cryptophilinae.

SEN GUPTA (1969) distinguished three (two of them new) tribes in the subfamily Dacninae; unfortunately this work is full of ambiguities or even evident errors, including many dubious or simply false characters. The family is divided into two subfamilies: Dacninae (with tribes: Megalodacnini, Cryptodacnini and Dacnini) and Erotylinae (with Erotylini and Triplacini).

In all catalogues (DELKESKAMP 1981, CHŰJÔ and CHŰJÔ 1988, 1989, 1990, ALVARENGA 1994), including practically all species of Erotylidae, traditional division into 3-4 subfamilies (Dacninae, Triplacinae, Encaustinae and Erotylinae) was applied.

Close affinity between the Erotylidae and Languriidae is beyond doubt, but still remains the question how close it is? The first author to consider them as relatives was CROTCH, who – in his monograph – merged them into one family. His opinion was shared by (among others) CHAPUIS (1876), GORHAM (1887-1889, 1898) and FOWLER (1908), but they remained a minority: more frequently [e.g.. GEMMINGER and HAROLD (1876), KUHNT (1910), ARROW (1925), SCHENKLING (1928), CROWSON (1955), SEN GUPTA and CROWSON (1971)] the two groups were treated as separate. The uncertainty mainly concerned rather large, slender, colourful beetles of the old subfamily Languriinae; only in 1971 SEN GUPTA and CROWSON showed that tropical genera formerly classified as Cryptophagidae mostly belong in fact to Languriidae, having created a muddled, highly diversified in terms of morphology and bionomy, conglomerate of obscure evolutionary relationships. With lack of reliable phylogenetic analysis including both the Erotylidae and Languriidae no unambiguous hypothesis of their affinities could hitherto have been proposed (LESCHEN and WĘGRZYNOWICZ 1998).

MATERIAL AND METHODS

The source of the material, on which as well the descriptions and drawings as the cladistic analysis have been based, were more than ten thousand specimens from dry and alcoholic museum collections, representing all the described (and many yet undescribed) erotylid/languriid genera and the majority (including ca. 80% types) of species; various other groups of Cucujoidea have also been examined. The study of the types and identified specimens was performed during my visits in the major zoological institutions: Muséum National d'Histoire Naturelle in Paris (collections of DEJEAN, DUPONCHEL, LACORDAIRE, CHEVROLAT and others), The Natural History Museum in London (GORHAM and ARROW), Zoological Museum of Cambridge University in Cambridge (CROTCH), Deutsches Entomologisches Institut w Eberswalde (SCHENKLING), Museum für Naturkunde der Humboldt Universität in Berlin (KUHNT and DELKESKAMP), Staatliches Museum für Tierkunde in Dresden (HELLER). Indetermined specimens came from various public and private collections from almost all-over the world, but mainly from USA, Canada and Europe, including the rich (especially in South-American species) material of the Museum and Institute of Zoology in Warsaw – where all the voucher-examples (including glycerine preparations) of the present study are preserved.

Morphological characters were checked on dry material as well as on cleared preparations. For clearing the specimen was boiled for few minutes in water, and then placed in cold 10% solution of KOH; if the melanin had not been effectively removed within a week or so, stronger oxidant (H_2O_2) was used. Cleared specimen was washed in distilled water and stained (for – according to the size of the object – 5 to 10 minutes) in a mixture of glycerine and chlorazol black to enhance the visibility of most morphological structures (especially intersegmental membranes). Then the beetle was again washed in water and transferred into a drop of glycerine on object-glass where it remained as long as needed. Large specimens were cut into separately prepared pieces. This procedure enables the observation from any desired angle at any time without dissolving the medium as in the case of durable preparations; the only inconvenience – the necessity to keep the object-glasses horizontally in tightly closed drawers – may be at least partly avoided by placing the preparation (or its fragment) in plastic microvial stuck (through the cork) on entomological pin.

For hind wing preparation the method proposed by KUKALOVA-PECK and LAWRENCE (1993) was used. After softening of the beetle in water, but before maceration in KOH, left wing was removed and placed on object-glass and carefully spread with pair of entomological pins; when the water has been drained off the drying wing adheres firmly to the glass – only very large and strongly sclerotized ones must have been fixed with a bit of glue.

Morphological terminology follows Lawrence and BRITON (1991), MCHUGH et al. (1997), and (for wing structures) KUKALOVA-PECK and LAWRENCE (1993).

Drawings were done under stereomicroscope Olympus SZH10 or compound microscope Olympus BX50, in both cases with use of “camera lucida”-type drawing device. The morphological structures to be drawn were so chosen as to illustrate all the character-states used in phylogenetic analysis. The criteria for selection of genera and characters to, as well as the procedure of, cladistic analysis have been discussed in the respective chapter.

PALAEONTOLOGICAL DATA

Palaeontological data concerning the family Erotylidae are very scanty: only few fossil species have been known, and their appartenance to this group is – in my opinion – often doubtful. From the Florissant (USA) schists two species assigned to the genus *Tritoma* – *T. submersa* and *T. materna* – have been described (WICKHAM 1912, 1914, 1916). A very well preserved specimen, representing a new species (*Dacne brodzinskyi*) closely related to recent representatives of a recent genus, has been found in Dominican amber (SKELLEY 1997). Besides, the literature mentions some inclusions tentatively determined at the generic level: *Cryptophilus*, *Dacne*, *Tritoma* (Baltic amber) and *Erotylus* (copal) (SPAHR 1981a, b), and *Dacne* (Baltic amber) and Erotylidae (Dominican amber) (POINAR 1992). As too scanty and mostly irreliable, the palaeontological data were omitted from the discussion of the phylogeny of the Erotylidae.

BIONOMY

The natural history of the Erotylidae remains practically unknown: we have no data on the life and habits of overwhelming majority of species, generalizations and conclusions are usually drawn *per analogiam* to few somewhat better studied common species.

The bionomy of the Erotylidae is bound up with large fructifications of the basidiomycetous fungi, usually growing on weakened trees od dead wood. These frutifications provide the only food for both larvae and adults – no proven exceptions have been known, though in tropical countries imagines are frequently found on leaves or trunks of living trees. Some misunderstandings resulted from inexact or simply false observations: e. g. the reports of larvae of some species belonging to the genus *Lybanodes* (Middle America) feeding on flat Ascomycetes proved wrong: in closer examination they turned out to be resupinates of basidiomycetous *Polyporales* (Skelley et al. 1997).

The beetles copulate on or near the host-fungus. Fertilized female lay eggs into the hymenophore or directly on the fructification, less frequently [e. g. Japanese *Megalodacne bellula* - CHŰJÔ (1969)]. Larvae feed on or inside the fungus, devouring all its available parts. Of two morphoecological groups one includes larvae which feed drilling galleries inside of the fructification; theit body is more or less elongated, round in cross-section, virtually naked, with prognathic head, short antennae, and variously developed hooked urogomphi on IX tergite. Here belong representatives of the subfamily Dacninae, as well as parts of Megalodacninae and Tritominae. The second group consists of species feeding on the surface of frutifications, gnawing out irregular, wide, relatively shallow depressions – these larvae are rather broad and dorsoventrally flattened, of hypognathous head, as a rule longer antennae, IX tergite adorned with usually very long straight urogomphi, and the cuticle of dorsal side very strongly sclerotized, with branched outgrowths. This group is composed of the subfamily Erotylinae and the remaining parts of Megalodacninae and Tritominae.

Aggregation and common feeding of larvae is a frequent phenomenon. Also pre-social behaviour have been observed: female of the South-American genus *Pselaphacus* protects the larvae – at least in the first instar – sheltering them with her own body (LESCHEN 1994).

Larva undergoes three moults before pupation; that occurs in, on, or near (on the wood or under the bark) the host-fungus, but usually in the soil directly under the feeding-place (CHŰJÔ 1969, LAWRENCE 1991, original observations). In the regions of distinctly seasonal climate Erotylidae pass through a resting-stage during the adverse period; in Poland they winter as imago or – less frequently – pupae under bark and within fungi (personal observations).

Adults have finely facetted eyes, are very often brightly coloured and active in full sunshine; that activity is so high, their reactions so rapid, that sometimes it is difficult to capture them. On the other hand, the night-active species show coarsely facetted eyes, duller colouration, and much slower motions: when disturbed they try to fall on the ground drawing up their legs and antennae rather than actively escape; spending the daytime hidden under bark, in its crevices, or in other dark places, they may be easily found in the night walking on trunks among fungi. Some tropical species, e.g. of the genera *Aulacochilus* or *Megalodacne*, come to light (original observations). Larvae are probably not very mobile, finding around them all what is needed to survive – supposedly they undertake short-distance travels only in case of shortage of food or some accidents (e.g being thrusted or washed down from the fungus). In Colombia some larvae (porbably belonging to the genus *Homoeotelus*) were observed walking on tree-trunk despite lack of any fungi in their proximity (original observations).

Almost all erotylids show small holes (pores) on the body-surface, interpreted (though no exact study has been undertaken) as scent-glands attracting individuals of own species or deterring enemies. Conspicuously bright, contrasting colouration might also serve as aposematic signal informing a predator of poisonous properties of the potential prey. Individuals of *Callischyrus cyanopterus* ERICHSON, captured by me in Ecuador, excreted from their knee-joints droplets of orange-coloured haemolymph of acrid smell (and probably also taste) like that of ladybirds (Coccinellidae) or leaf-beetles (Chrysomelidae).

Much more differentiated – but also poorly known – is the bionomy of the related family Languriidae. Many species feeding on moulding plant debris are found in forest litter, on rotten wood or under bark; some of them, e.g. those of the genera *Cryptophilus* and *Leucohimatium*, have been spread all-over the world with mildewy store-products (AITKEN 1975). Interesting group are specialists living on flowers of cycads (Cycadaceae), distributed in those areas where these plants occur (SEN GUPTA and CROWSON 1971, LAWRENCE 1991, LESCHEN and WĘGRZYNOWICZ 1998, WĘGRZYNOWICZ 2000). Two species of *Loberopsyllus* (Mexico) live as commensals of a particular rodent, attached to its fur feed on peeled epidermis and other organic matter (BARRERA 1969, LESCHEN and WĘGRZYNOWICZ 1998). Larvae of the subfamily Languriinae develop in stems of herbaceous angiosperms, while adults can be foung on leaves (nothing more being known about their life-history – VAURIE 1948, LESCHEN and WĘGRZYNOWICZ 1998).

ADULT MORPHOLOGY

The morphological description has been made based on all groups actually classified in the Erotylidae, i.e. including Languriidae. The beetles belonging here show an extraordinary variability in size and outlook (figs 126-139) from very small (length of body 1.5 mm.) to rather large (up to 30 mm.) and from elongate (almost cylindrical or somewhat flattened dorsoventrally) to nearly circular in outline (then dorsal side most often strongly convex). Some species of *Erotylus* have elytra markedly widened, making them similar to chrysomelids of the subfamily Cassidinae, while representatives of the tribe Languriini display conspicuously elongated body. In the variable, usually bright colouration dominate mutually contrasting black background and pale (yellow to red) elytral patches (very often four: two humeral and two apical); if yellowish-red colours prevail, then either all the body is such (some Xenoscelinae, Languriini and Tritomini), or elytra are yellow (e.g. *Erotylus*, *Cypherotylus*) or all the body except (black or metallic) elytra (Languriini). Colours different from black and yellowish-red – green or greenish-blue (usually on strongly lustrous body-surface) – occur rarely: genera *Coptengis*, *Callischyrus*, *Aulacochilus*, *Erotylus*, and tribe Languriini.

Almost all species of Erotylidae show glabrous body – the exceptions are the genera *Episcapha*, *Trichulus*, *Hirsotriplax*, *Trichotritoma*, as well as numerous representatives of Xenoscelinae. If developed, the pubescence is short and recumbent, but often some smaller parts of the body (tibiae, tarsi, antennae, abdomen) may be more or less densely pubescent.

Sculpture – besides most apparent primary punctures secondary punctulation and microsculpture – is also variable. Primary punctures are most often moderately large and deep, rather sparsely distributed; only in some groups (several species of *Episcaphula*, most of Ischyrus, some representatives of the subfamily Xenoscelinae) the sculpture is very coarse and dense or – to the contrary – strikingly obliterated (*Coptengis*, *Encaustes*, *Scaphidomorphus*, and numerous species of the Languriini). Secondary punctulation occurs typically as more or less distinct pricks and may also be strongly reduced. Microsculpture – most frequently in form of fine reticulation – is sometimes (e.g. in the genus *Ischyrus*) very conspicuous, but in other cases (e.g. *Coptengis*, some species of *Episcaphula* and *Aulacochilus*, many representatives of the tribe Languriini) totally disappears (or at least is not visible under 100× magnification); obsolete primary puncturation is usually correlated with disappearance of microsculpture.

Head (figs 1-73)

Head prognathous, always well visible from above, retracted into prothorax up to hind margins of eyes, usually symmetrical (only several representatives of the tribe Languriini – e.g. females in the genus *Doubledaya* – show marked asymmetry including mouthparts). Head-capsule variable in size but usually not very large; anterior part often prolonged into short, broad rostrum (*Erotylus*, *Homoeotelus*) (figs 1-3); fronto-clypeal suture distinct throughout (usually straight at middle and strongly bent anterad on sides) (figs 1, 3, 8, 10, 13) or (most frequently) medially interrupted (figs 4, 6, 16), or totally reduced. Clypeus (figs 1, 3) broad, though only exceptionally wider than the interocular space; anterior margin typically straight but may be shallowly (in extremal cases – genus *Pselaphacus* – deeply - figs 6, 7) arcuately emarginated (figs 16-18), or (in some species of the genus *Anadastus* of the Languriini) very narrow with sharp denticle at middle. Lateral margins of clypeus, sides of head, and inner edges of eyes may or may not (independently from each other) be more or less (from fine and shallow to deep) distinctly bordered with striae or sulci (figs 1, 4, 6, 8, 10, 12, 13, 15-17).

Front usually normal, but in males of some genera densely pubescent and adorned with peculiar lobate outgrowths on sides (*Zythonia*) (figs 16-18) or short but sharp tubercles and foveae at middle (*Cytorea*). Like other parts of the body, also head is usually provided with some pores – secretory glands probably producing deterring substances; if present (rather large group of species does not show any) these pores are placed before the eyes, near antennal cavities (figs 1, 3, 4, 8, 10, 12, 13, 15), and on subgenal braces (figs 5, 9, 14). These are usually well developed and distinctly protruding, either horizontal or vertical (in the latter case conspicuously extended downwards, sheltering the mouth-parts) (figs 12, 15). Sometimes – besides pores – hair-tufts (often extending over large surfaces) may be found on subgenal braces.

Submentum (fig. 2) separated from the rest of head with (only exceptionally – e.g. in *Cryptodacne* and *Pharaxonotha* – entirely obliterated) suture or deep furrow. Between mouth-parts and eyes more or less distinct cavities for reception of antenna. Here at the posterior margin of the head may double or (very rarely) single stridulatory organs (dense rows of lamellae) be found (fig. 17). Gular suturae usually rather short.

Compound eyes (figs 22-25) placed laterally (figs 12, 15), of mostly moderate size, seldom very small or strikingly large, more or less convex, usually protruding, sometimes extending far onto vertex. Shape of eyes vary between (most frequent) rounded and vertically ovate; anterior (rarely posterior) margins may be emarginated (figs 24, 25). Facetting very fine to coarse (figs 26, 27). Antennal bases visible from above (fig. 2) or placed under head margin (fig. 4).

Antennae (figs 28-38) always 11-jointed, of variable length (usually rather short, never very long), with distinct though sometimes poorly distinguished, mostly 3-jointed (4- to 6-jointed often in Languriini, 2-jointed in *Pharaxonotha*), more or less flattened and usually symmetrical, often with surface-increasing depressions (where probably sensory organs are concentrated) (fig. 29). Flagellar joints vary from strongly elongated to short, globular. Third joint in most cases (but nt always) distinctly elongated, much longer than second. Antennal pubescence usually scanty, only on club-joints often dense (short and recumbent).

Mouth-parts (figs 19-21, 39-73) of gnawing type, very well developed. Labrum (fig. 70) free (not fused to clypeus), sometimes with inconspicuous denticle at middle of anterior margin. Mandibles (figs 39-49) powerful, short and broad, nearly triangular; dorsal side (distal part) with distinct depression usually containing several punctures and setae; apex double (with two dents), rarely simple, sharp (e.g. *Toramus* i *Cryptophilus*), or simple and scapular (adapted to scrape food – *Scaphidomorphus*) (figs 48, 49). Mandibular base almost always (with but rare exceptions like genera *Homoeotelus* and *Languria*) emarginated; the right one usually with additional outgrowth above mola (fig. 41) (in few genera missing). Mola (figs 50-53) well developed, variable (ovate, triangular, rectangular or horseshoe-shaped), naked, usually distinctly costate; typically above mola there is (only in *Toramus* missing) soft and pubescent (only in *Cryptophilus* and *Setariola* glabrous) prostheca with additional tuft of hairs (reduced in few genera, e.g. in *Coccimorphus*, and *Languria*).

Maxillae (figs 54-63): cardo subtriangular, stipes – articulated to cardo – elongated, articulated to the latter are galea, lacinia and maxillary palp. Galea shorter but wider than lacinia, somewhat widened towards apex and there densely pubescent. Lacinia much longer and narrower, apically covered with dense pubescence, with strongly sclerotized double hooks (figs 55, 56); sometimes these hooks are weak and slender (almost indistinguishable from the surrounding pilosity), totally absent, or transformed into flattened, bent, scapular structures (*Scaphidomorphus*) (figs 57, 58). Maxillary palpi 4-jointed, first joint elongated, following two shorter, last one the largest (fusiform to subtriangular, symmetrical or not, in some cases many times wider than long (figs 59-63).

Labium (figs 64-69, 71-73) consists of mentum (figs 64, 71-73), paraglossae, glossae and 3-jointed labial palps. The last joint of labial palps may be fusiform, ovate, club- or axe-shaped (asymmetrical) (figs 65-69); as a rule it is shorter than the respective joint of maxillary palp, but exceptions (e.g. genera *Megalodacne*, *Linodesmus* and *Toramus*, where it is narrowly fusidorm in maxillary but securiform (axe-shaped) in labial palps) do exist. Mentum (figs 71-73) not large, usually transverse, most often with one or more depressions and setae at middle; shape variable: from transverse (some Languriini) without denticles at anterior margin, through triangular and pentagonal, to definitely tridentate; at middle and on sides more or less distinct lamellae may occur; in some species a pair of secretory (probably scent) glands can also be found.

Thorax (figs 74-101)

Prothorax. Like in other beetles, it is the best developed part of thorax. Placed between head and mesothorax, prothorax is variable in proportions from definitely transverse to elongated, moderately convex (seldom – e.g. in some genera of Languriini – almost globular). Pronotum (figs 74-81) is deprived of any special structures like lamellae or tubercles, only longitudinal or transverse depressions, foveae, or groups of coarse punctures may occur near base. Anterior angles usually protruding anterad (sometimes sharp), rarely absent or inconspicuous (Languriini); posterior angles sharp or obliterated. Sides typically more or less rounded, but sometimes nearly straight or arcuately emarginated before base (often in Languriini). Lateral margins smooth (without distinct denticles), almost always (the sole exception are some genera of the Languriini) with distinct sharp carina and border (of variable width). Also anterior and posterior margins may be bordered or not, the border being sometimes interrupted at middle. Secretory pores – very characteristic of the Erotylidae and lacking only in few representatives of the family (e.g. *Dacne*, *Cryptodacne*, Xenoscelinae, Languriini) are distributed on sides of pronotum (most often one by one in anterior and posterior angles, rarely more of them are dispersed all-along the lateral margin). Prosternum (figs 82-84) convex, sometimes with more or less conspicuous carina along midline; anterior margin smooth and densely ciliate or (rarely – e.g. in *Cryptophilus*) finely denticulate. Notosternal suturae distinct, entire or (e.g. in *Megalodacne*, *Linodesmus*, *Ischyrus*, and *Erotylus*) interrupted at middle. Procoxal cavities rounded or ovate, internally open (usually) or closed (Xenoscelinae, Languriini), externally open in most Xenoscelinae and Languriini, closed in Erotylinae except Languriini and in *Cryptophilus*. Prosternal process usually wide (wider or slightly narrower than coxae). Femoral lines – shorter or longer, bent inwards or nearly straight – frequently occur. Sometimes a pair of secretory pores may be found between procoxae.

Meso- and metathorax (figs 85-101). In Erotylidae firmly fused to one another. Scutellum (figs 95, 96) always visible, variously shaped (most frequently pentagonal or triangular); otherwise both meso- and metanotum (figs 95, 96, 99-101) entirely hidden beneath elytra, and – consequeltly – poorly (except few elements) sclerotized, semitranslucent, almost depigmented. In wingless forms metanotum underwent marked reduction: it is membraneous, with totally absent lateral phragmae. Outer margin of metascutellum, except in representatives of the tribe Erotylini, touches posterior margin of metascutum.

Mesosternum is in the Erotylidae distinctly reduced and much shorter than metasternum, both being very strongly sclerotized and firmly coalescent.

Metasternal process (figs 87-89), inserted into the respective cavity of mesosternum, may be single or double (in the latter case both elements are sometimes close to each other, sometimes widely separated). Mesocoxal cavities, placed at the border between meso- and metasternum, are rounded in outline. Sometimes (e.g. in *Dacne*, *Setariola* and *Pharaxonotha*) a fragment of mesepimeron squeezes between meso- and metasternum, otherwise both parts touch one another. Intercoxal part of mesosternum usually narrower than mesocoxae. Suture between mesepisternite and mesepimeron lies far anterad of, or at equal level with, meso-metasternal suture in coxal cavity. Metasternum is typically the longest section of thorax. Near the coxal cavities shorter or longer femoral lines can often be found. Suture between metepisternite and metepimeron almost always at the level of posterior margin of metasternum, only in few genera displaced much behind it. Along midline of metasternum runs median suture (usually not reaching anterior margin, rarely – genus *Erotylus* – entire). Main element of internal skeleton of metasternum is metendosternite (figs 97, 98) – a sclerite fixed at apical margin and providing a firm base for attachment of muscles (also those operating wings); in the *Erotylidae* it is a branched structure composed of median plate (of variable shape, often short and wide), paired arms (usually more or less curved), lateral plates (placed at ends of arms, sometimes reduced), and tendons (typically long and slender outgrowths). Reduction of metendosternite (with all elements strikingly short and thin) occurs in functionally (wings rudimental) or entirely wingless species.

Abdomen (fig. 106)

Abdomen typically elongated (only in few species definitely short and wide), always with five visible, not fused sternites. On the first – longer than others – sternite sometimes femoral lines are seen, and in females of some species also densely punctured and pubescent field at middle. Last sternite usually rounded, often bordered and/or pubescent, some additional swellings and other structures may also occur (some genera of Languriini). All six tergites are membraneous, poorly sclerotized. Six pairs of spiracles.

Elytra

Elytra strongly sclerotized; usually elongated and moderately convex, but in some cases almost circular in outline and gibbose or even sharply pointed. Epipleura in some genera of Languriini not developed, otherwise well demarcated and extending almost all-over the elytral length. Puncturation usually distinct, sometimes (*Erotylus*, *Cypherotylus*) placed in conspicuous foveae, arranged into five (most often regular, but sometimes more or less confused) rows. No other major elements of sculpture can be found, except long, sharp spine at middle of elytra, pointing obliquely backwards, in males of *Homoeotelus spinifer* THOMSON. Humeral protuberances typically conspicuous. Elytral base in most species bordered, shape of the border most often fits the surface of hind margin of pronotum. Apical margins of elytra mostly smooth, less frequently denticulated or armed with single long spines Elytra entirely cover the abdomen, or but a fragment of last tergite is exposed.

Hind wings (figs 102-105)

Most Erotylidae are good flyers, but in some groups reduction of wings has (probably independently) occurred (fig. 104). Wings are rather short and wide, veins usually sclerotized and clearly visible, membrane translucent or (less frequently) brownish. Apical part typically elongated and rounded. Medial fleck always present, usually well developed, transversely ovate. Cross-vein in media present; radial cell conspicuous, single, only in few genera lacking; anal cell placed, in basal portion of thw wing, occurs in almost all Erotylidae (with the only exception of some representatives of former Languriidae). Vein MP3+4 simple or (rarely) forked at end; cross-vein r3 in most cases normally developed, simple or (only in *Scaphodacne*) forked, seldom markedly shortened or totally reduced (*Dacne*, *Toramus*, *Setariola*, and *Cryptophilus*). Branching from radial cell cross-veins r3 and r4 mmay be widely removed from, close to, or contiguous with, one another.

Legs (figs 107-114)

Legs of variable length, from rather short to markedly elongated. Pro- and mesocoxae almost globular, metacoxae transverse, cigar-shaped. Femora elongated, smooth, without spines or other outgrowths. Tibiae long, usually nearly straight, somewhat widened distally, sometimes more distinctly curved; on inner surface may occur small denticles that rarely attain larger size – in extreme cases tibiae assume the shape of isosceles triangle. Outer surface of tibiae smooth, sometimes longitudinally sulcate and carinulate, less frequently denticulate; inner surface often densely pubescent at distal end. Apex of tibiae (figs 111-114) with a crown of wide flat setulae (only very rarely, e.g. in *Coccimorphus*, reduced) and two spurs of which sometimes one (*Encaustes*) or both (*Aulacochilus*) may disappear; spurs may be placed close to one another or widely removed (in which case they are separated by small outgrowth of tibia).

Tarsi (figs 108-110) always 5-jointed, apical joint the longest and armed with pair of strongly curved but simple claws. In most primitive forms basal four joints are cylindrical, of similar thickness, all densely pubescent below (genus *Dacne*); that pubescence may be reduced to pair of setae on fourth tarsomere (e.g. in *Pharaxonotha*). The remaining Erotylidae underwent gradual reduction of fourth joint, concealed in emargination of third, while basal theree become wider.

Male genitalia (figs 115-121)

Penis (fig. 115) closed, more or less elongated and markedly flattened laterally. Apex mostly pointed, sometimes beak-shaped. Apophyses double, firmly fused, usually long or very long (several times longer than penis). Internal sac with well developed flagellum (fig. 116), which is composed of two parts: head and virga and may be robust, subulate to very long, filiform. Penis is surrounded by rather strongly sclerotized tegmen (figs 117, 118), whose elongated, fused arms may be adorned with peculiar tubercles. Parameres movably connected to tegmen (only in *Setariola* fused), reduced to short but strongly sclerotized, densely pubescent outgrowths; their shape vary from narrow to markedly dilated and from apically pointed to blunt. Position in repose may be different (lateral, dorsal), but unambiguous determination is difficult because of post-mortem changes in musculature. Penis and tegmen are surrounded by 9. tergite (together with reduced 10. – proctiger) and 9. sternite (figs 119-121).

Female genitalia (figs 122-125)

Eighth sternite is always armed with long outgrowth: spiculum gastrale (fig. 125). On genital segments sometimes two rows of very conspicuous denticulate lamellae are found (genus *Dacne*) (fig. 123). Ovipositor (figs 122, 123) of complex structure, dependent upon the substrate to which eggs are laid. In species laying into soft substrate ovipositor (except coxites and styli) is rather poorly sclerotized and usually conspicuously pubescent; it is composed of valvifers and coxites divided into basal (poorly sclerotized, wide) and apical (more sclerotized, of width equal to length) parts – small movable outgrowth (styli) are situated at coxite apices (fig. 122). In groups ovipositing into hard substrate (*Dacne* and *Languria*) coxites are undivided, pointed, not or but sparsely pubescent, and strongly reduced (often spiniform) styli are placed in small depression on outer side of coxite (fig. 123).

Spermatheca (fig. 124) typically rather small, strongly sclerotized, its capsule of ovate or rounded outline. Spermathecal duct usually long, tightly coiled; its base of often also strongly sclerotized, elongated, frequently S-shaped, making the entire spermatheca resembling a duck or swan. Spermathecal gland usually small but always present.

PHYLOGENETICAL ANALYSIS

Selection of taxa and characters

25 genera of Erotylidae – the type-genera of all higher taxa (subfamilies and tribes) distinguished in the family, as well as representatives of morphologically distinctive groups – have been included in the analysis. Except for *Aulacochilus* and *Apolybas* – whose respective types (*Auliacochilus javanus* and *Apolybas normalis*) had not been available for dissection and were replaced by *Aulacochilus quadrisignatus* and *Apolybas bicolor* of similar morphology – each genus was represented by its type-species. Because the systematic position of the Languriidae in relation to Erotylidae was controversial, to avoid in principle abortive analysis of incomplete paraphyletic group one representative of each subfamily (according

to the classification of LESCHEN and WĘGRZYNOWICZ 1998) of the former has also been included, so increasing the number of analysed taxa by five (four of them were type-genera of subfamilies represented by their type-species, but the genus *Xenoscelis* remained unavailable and thence the subfamily Xenoscelinae was represented by the type-species (*P. kirschii* REITTER) of closely related genus *Pharaxonotha* REITTER. All the above-mentioned taxa were treated as in-groups, while for out-groups four genera representing four families of the Cucujoidea: *Nitidula* (Nitidulidae), *Helota* (Helotidae), *Cryptophagus* (Cryptophagidae) and *Biphyllus* (Biphyllidae); the former two are considered (LAWRENCE 1982, LAWRENCE and NEWTON 1995) as the most primitive in the superfamily, whereas the latter two as closely related to the Erotylidae (SEN GUPTA and CROWSON 1971, LESCHEN 1996, LESCHEN and WĘGRZYNOWICZ 1998).

Initially 103 adult morphological characters of the Erotylidae had been taken into consideration, yet some of them were later excluded from the analysis as difficult to define or individually variable, so that at last 85 imaginal – external as well as anatomical – have been used. In the matrix the states of each character has been coded numerically, starting from 0; usually two states were distinguished, rarely three or more. Unknown character-stateswere coded as "?" All characters and character-states have been discussed (according to the respective body-parts – in the section "Characters chosen to analysis and their states" and presented in the matrix (Tab. 1).

Methods

In this work the principles of cladistic (phylogenetic) taxonomy – based on monophyletic groups characterized by common derived characters (apomorphies) – were applied. Polarization was established by the out-group method (WATROUS and WHEELER 1981). Because of unclear origin of some characters or difficulties in reliable determination of the direction of transformation, all states were treated as unordered. Analysis was performed using the computer-program Hennig86 (FARRIS 1988).

CHECK LIST OF TAXONS USED IN ANALYSIS

Outgrups:
Nitidulidae: *Nitidula bipunctata* (LINNAEUS, 1758)
Helotidae: *Helota vigorsii* MACLEAY, 1825
Cryptophagidae: *Cryptophagus* sp.
Biphyllidae: *Biphyllus lunatus* FABRICIUS, 1787

Ingroups:
Languriidae – division into subfamilies based on LESCHEN and WĘGRZYNOWICZ (1998).
Languriinae: *Languria* Latreille, 1802 (*L. bicolor* Fabricius, 1798)

Cryptophilinae: *Cryptophilus* Casey, 1900 [*C. integer* (Heer, 1841)]
Toraminae: *Toramus* Grouvelle, 1916 [*T. pulchellus* (LeConte, 1863)]
Setariolinae: *Setariola* Jakobson, 1915 [*S. sericea* (Mulsant et Rey, 1863)]
Xenoscelinae: *Pharaxonotha* Reitter, 1875 (*P. kirschii* Reitter, 1875)

Erotylidae – division into subfamilies based on Chűjô and Chűjô (1988, 1989, 1990), and Lawrence and Newton (1995)
Dacninae:
Dacne Latreille, 1796 [*D. bipustulata* (Thunberg, 1781)]
Combocerus Bedel, 1867 [*C. glabrus* (Schaller, 1783)]
Cryptodacne Sharp, 1878 (*C. synthetica* Sharp, 1878)
Megalodacninae:
Megalodacne Crotch, 1873 [*M. fasciata* (Fabricius, 1777)]
Coptengis Crotch, 1876 [*C. scheppardi* Pascoe, 1860)]
Episcapha Dejean, 1837 [*E. quadrimacula* (Wiedemann, 1823)]
Linodesmus Bedel, 1882 [*L. coecus* (Fabricius, 1777)]
Scaphodacne Heller, 1918 [*S. rectesignata* (Crotch, 1876)]
Encaustinae:
Encaustes Lacordaire, 1842 [*E. verticalis* MacLeay, 1825]
Aulacochilus Lacordaire, 1842 [*A. quadrisignatus* (Guérin-Méneville, 1841)]
Tritominae: Tritomini:
Tritoma Fabricius, 1775 (*T. bipustulata* Fabricius, 1775)
Megischyrus Crotch, 1873 [*M. undatus* (Olivier, 1792)]
Amblyopus Lacordaire, 1842 [*A. vittatus* (Olivier, 1807)]
Triplacini:
Triplacidea Gorham, 1901 [*T. motschulskyi* (Bedel, 1872)]
Triplax Herbst, 1793 [*T. russica* (Linnaeus, 1758)]
Pselaphacus Percheron, 1835 (*P. nigropunctatus* Percheron, 1835)
Ischyrus Crotch, 1873 [*I. quadripunctatus* (Olivier, 1792)]
Mycotretus Chevrolat in Dejean, 1837 [*M. ornatus* (Duponchel, 1825)]
Apolybas Alvarenga, 1965 [*A. bicolor* (Guérin-Méneville, 1841)]
Amblyscelis Gorham, 1888 (*A. kelleni* Gorham, 1888)
Zythonia Westwood, 1874 (*Z. fulva* Westwood, 1874)
Erotylinae:
Coccimorphus Hope, 1841 [*C. unicolor* (Olivier, 1807)]
Erotylus Fabricius, 1775 [*E. giganteus* (Linnaeus, 1758)]
Scaphidomorphus Hope, 1841 [*S. quinquepunctatus* (Fabricius, 1775)]
Homoeotelus Hope, 1841 [*H. testaceus* (Fabricius, 1775)]

CHARACTERS CHOSEN TO ANALYSIS AND THEIR STATES

#0. Head. Clypeus and anterior part of head at the level of antennal bases contracted, forming a kind of rostrum. 0. Absent; 1. Present.

Table 1. Character data matrix

Taxon/character	1 2 3 4 5 6 7 8
	012345678901234567890123456789012345678901234567890123456789012345678901234567890123
Nitidula	0002101021010022001211000000001100310020000110001000000001011000001??010210002000011
Dacne	001001011100100101111000010000011021002000000100101000010000001011101110001012111011
Coptengis	00021120010010100012100001000110011010001000101011011110000111101??0?111110012110100
Combocerus	000201001100100001001000011003111021022001000100101000010100000101200111110012110100
Cryptodacne	00100102210010200000100001100011112101110000100001011111000001101??01111111012110100
Episcapha	00021002210010110002100010000110021000101000101101000011100110101200?111110012110100
Megalodacne	000211222100101101111000010001010021030102001101101000011000100101200111110012110100
Linodesmus	000111100000101201121000011000110011030102001101011000011100100101200111110012110100
Scaphodacne	000111121100101201111000011001110021010102000101101000011000100101201011111012110100
Encaustes	000011121101101101111100011001111121011102000101011000000001001012000112210012110100
Aulacochilus	000011122101101200111100011001111121010102001001010000010001001012000113211012110100
Pselaphacus	000111110001102011111000110000111310311010001010010000110001001011000110211012110100
Megischyrus	000111121110100201121100010001010221120101000100101000100001001011001110210012110100
Ischyrus	000111122110110201111000100010111211101010011000110000110001001011001110211012110100
Mycotretus	000111012010110201111100011001011121012201000100011000011000001011001110211012110100
Apolybas	000111012010100200111100011001011111002010001000110011100110101011001111211012110100
Triplacidea	011211012010110201111100011001011231012201000101111000011000001012001110211012110100
Tritoma	011111010010000201111100011001010131001201000101111000111000001011000110210012110100
Amblyopus	011211022110110201111100011000010111021201000101101000101000001011001110211012110100
Amblyscelis	001111022110110201111100011001011121011201000101111000111000001011001110211012110100
Zythonia	011111000010111201111100011001011111022201000100101000101000001012001110211012110100
Triplax	001111012010100200011100011000011121022101000100001000010000001012000110211012110100
Coccimorphus	000111011010101100011100011011111210312020010101110010100011011112000100210112110100
Erotylus	100011110010110000111100011001111110302020011010011001100101001012000111210112110100
Scaphidomorphus	100011110101100001111020110021121110302020001010011001100000001011000111210012110100
Homoeotelus	100010101010110000111100111002111110312010001010111001000001101011001111210012110100
Languria	000011001011110000121001100101110000220000000100110000100001001012000110210012110011
Toramus	0001010121000001011010010102000100110320000000100110001100000010001??110111012110100
Setariola	0001010221000001011000000101111103101000000010011000100000011010021??110110012100100
Pharaxonotha	000100011100002001003000011000110011002100000010001000010000001001000110010012110100
Cryptophilus	0002000221010001011010010101000100110220000000011000110000011010001??110111012110100
Helota	000200121010002211111010100013000001021000110001000110200100000020000100000001100100
Cryptophagus	0002000121000020011020010100111031012013002110011000010000001000101??010000000010100
Biphillus	000100012101002101011000010000010021032010110000010000000000000012000110111001000100

This character defines three South-American genera (*Erotylus*, *Scaphidomorphus* and *Homoeotelus*) (fig. 3). Function of the rostrum is unknown.

#1. Head. Clypeus, anterior bordering. 0. Absent; 1. Present.

Anterior bordering of clypeus is rare in these beetles: it has been found only in representatives of four genera.

#2. Head. Clypeus, lateral bordering. 0. Absent; 1. Present.

This character occurs more frequently than, and is not correlated with, the previous one.

#3. Head. Fronto-clypeal suture. 0. Entire (figs 1, 3, 8, 10, 13); 1. Interrupted at middle (figs 4, 6, 16, 17); 2. Absent.

Presence or absence of fronto-clypeal suture is very important diagnostic character in many families of the Cucujoidea (e.g. Coccinellidae and Endomychidae), but in Erotylidae is less significant. Among the representatives of this family all character-states from conspicuous entire suture through interrupted at middle to total lack may be observed; in out-groups the suture is usually missing.

#4. Head. Periocular pores. 0. Absent (figs 6, 16, 17); 1. Present (figs 1, 3, 8, 10, 13).

The body of adult Erotylidae usually show many pores – probably outlets of scent-glands. They occur in both sexes, what may exclude sexual function. Only few genera lack these pores.

#5. Head. Eyes, bordering. 0. Absent (figs 6, 8); 1. Present (figs 1, 4, 10, 13).

Only few genera (*Episcapha*, *Homoeotelus*, *Pharaxonotha*, *Cryptophilus* and outgroups) have eyes without bordering.

#6. Head. Eyes, shape. 0. Rounded (fig. 22); 1. Ovate (fig. 23); 2. Reniform (figs 24, 25).

In most genera eyes are rounded, somewhat less frequently they are elongately ovate, while reniform – with distinct emargination for posterior margin; for antennal base – occur but sporadically.

#7. Head. Eyes, size. 0. Small; 1. Medium-sized; 2. Very large.

Size of eyes is difficult to interpret, because among the Erotylidae species of either entirely reduced or decidedly enlarged (like in some predatory forms) do not occur. According to standards applied herein, large denote eyes occupying entire or almost entire sides of head, medium-sized – about half of the head-height, and small – about a quarter of this height. Most common are eyes small and medium-sized, large are much less frequent.

#8. Head. Eyes, convexity. 0. Slightly convex, following the outline of head; 1. Moderately convex, protruding; 2. Strikingly convex, strongly protruding.

Eyes of Erotylidae usually strongly protrude, albeit a sensible correlation with other characters is not easy to find.

#9. Head. Eyes, coarseness of facetting. 0. Fine (fig. 26); 1. Coarse (fig. 27).

Most Erotylidae show fine facetiing, only in few genera facets are coarse (and consequently less numerous). Coarseness of facets is explained as adaptation to nocturnal activity.

#10. Head. Subgenal braces. 0. Elongated (figs 5, 7, 11, 18); 1. Shortened (figs 2, 9, 14).

In the majority of Erotylidae (consecutively from *Dacne* to *Pselaphacus*, and then from *Toramus* to *Cryptophilus*) the subgenal braces are normally developed (elongated); reduction (shortening) has occurred in most genera of Tritominae and Erotylinae, as well as Languriini.

#11. Head. Subgenal braces. 0. Horizontal (figs 2, 5, 7, 9, 14, 15, 18, 19, 20); 1. Vertical (rys. 11, 12, 21).

Vertical position may be observed in *Encaustes* and *Aulacochilus* (grouped for this reason into the subfamily Encaustinae) as well as *Languria* and *Cryptophilus*.

#12. Head. Pores on subgenal braces. 0. Absent; 1. Present (figs 5, 9, 19-21).

Pores on subgenal braces occur singly – their absence is rare in Erotylidae. They probably mark the outlets of scent-glands.

#13. Head. Hair-tuft on subgenal braces. 0. Absent; 1. Present (figs 5, 9, 14, 19).

Beetles feeding on fungi have frequently structures enabling transfer of spores or fragments of spawn. Such a structure in some Erotylidae are undoubtedly tufts or brushes of stiff hairs on subgenal braces. Interesting is the presence of such tufts in supposedly herbivorous *Languria* – perhaps adults feed on fungi living on the surface of plants, but no suporting observations are known. On the other hand this may suggest close affinity to the Erotylidae, herbivory being a secondary phenomenon.

#14. Head. Submentum, separation from rest of head. 0. Suture (fig. 19); 1. Sulcus (figs 20, 21); 2. None.

In almost all examined beetles mentum was distinctly separated by suture or sulcus, only in *Cryptodacne* i *Pharaxonotha* lack any of them.

#15. Head. Sulcus between mouth-parts and eyes for reception of antennal flagellum. 0. Not developed; 1. Inconspicuous, short; 2. Well developed, long.

This sulcus is present (albeit sometimes short) in almost all studied beetles, only few genera lack it.

#16. Head. Sulcus on underside of head for reception of antennal flagellum. 0. Not developed; 1. Developed.

The sulcus mentioned in #15 is prolonged to ventral side of head (almost to its base) only in the outgroup genus *Helota*.

#17. Antennae. Bases. 0. Visible from above (figs 1, 13); 1. Not visible from above, hidden under head margins (figs 4, 6, 8, 16).

In majority of genera antennal bases are concealed from above with head margins, but in some they are at least partly visible.

#18. Antennae. Length of 3. joint. 0. Equal to or but slightly longer than others (fig. 33); 1. Definitely longer than others (figs 28, 30-32, 34-38).

This character has since long been used for distinguishing genera in the Erotylidae. The proportion of the length of third antennomere to length of 2. is not significantly dependent upon their shape (thickness). State (0) is much less frequently encountered than (1).

#19. Antennae. Flattening of club. 0. Not flattened; 1. Moderately lattened. 2. Strongly flattened.

Antennal club in the Erotylidae is as a rule conspicuously (in several genera – *Coptengis*, *Episcapha*, *Linodesmus* and *Megischyrus* – to exceptional degree) flattened, but sometimes (in *Combocerus*, *Cryptodacne*, *Toramus*, *Setariola*, *Pharaxonotha* and *Cryptophilus*) it is not or but indistinctly flattened (interestingly, these taxa group usually small species of cryptic way of life – but this is not always so). Among out-groups only in *Nitidula* the club is markedly flattened.

#20. Antennae. Number of joints in club. 0. 2; 1. 3 (figs 28-38). 2. More than 3.

Among in-groups dominate beetles with clearly defined 3-jointed club, only exceptionally greater (e.g. in *Languria* and some related genera) or lesser (2 joints, e.g. *Pharaxonotha*) number of antennomeres is involved.

#21. Antennae. Depressions on club. 0. Absent; 1. Present (fig. 29).

Depressions on club-joints occur in the majority of studied representatives of the Erotylidae; they are absent in subfamilies Dacninae and Megalodacninae, in genera *Toramus*, *Setariola*, *Pharaxonotha* and *Cryptophilus*, as well as in outgroups except *Nitidula*. Function of these depressions is not clear, probably they hold sense- (taste-? scent-?) receptors. This character has not been hitherto mentioned in the literature on the Erotylidae, and consequently has not been used in studies of their relationships.

#22. Mouth-parts. Labrum, fusion to epistome. 0. Not fused; 1. Fused.

Only in *Helota* (outgroup) labrum is fused to epistome, in all remaining taxa it is free. Fusion of these mouth-parts is generally rare phenomenon in beetles.

#23. Mouth-parts. Mandibles, apical part. 0. Double (figs 39, 40, 41-47); 1.Single; 2. Single, bluntly truncated (figs 48, 49).

Many beetles show double apex of mandibles, and so do almost all examined genera (both Erotylidae and outgroups), with the exception of *Toramus* and *Cryptophilus* (with simple apex) and *Scaphidomorphus* (apex single and spathulate). While in the former case reduction of one denticle has probably been a consequence of small body-size, the mandible of *Scaphidomorphus* is – like hooks of lacinia, transformed into scapular structures (cf. character #32) – adapted to scraping and rakijng up the food (fructification? spores?). Hitherto these characters have been neglected in studies of the Erotylidae.

#24. Mouth-parts. Mandibles, incision at base. 0. Present (figs 39, 40, 44-49); 1. Absent (figs 42, 43).

Lack of the incision has been observed only in genera *Homoeotelus* and *Languria*, as well as in outgroups: *Helota* and *Cryptophagus*.

#25. Mouth-parts. Mandibles, distal part with depression and pubescence. 0. No; 1. Yes (rys. 40).

All examined erotylids display a pubescent fovea on diatal part of mandible; in outgroups it is present (*Biphyllus*) or not (*Nitidula*, *Helota* and *Cryptophagus*). Such structure serves to transfer spores of the fungi on which representatives of this family feed.

#26. Mouth-parts. Mandibles, additional outgrowth above mola on right mandible. 0. Absent (figs 46, 47); 1. Present (figs 39-43, 46-49).

Additional outgrowth above mola on right mandible is characteristic of most Erotylidae, lacking only in *Dacne*, *Coptengis*, *Episcapha*, *Megalodacne*, *Megischyrus*, *Ischyrus*, and genera attributed to the Languriidae except *Pharaxonotha*. As to the outgroups, it is absent in *Nitidula*, *Helota* and *Biphyllus* but present in *Cryptophagus*.

#27. Mouth-parts. Mandibles, prostheca. 0. Pubescent (figs 39-49); 1. Glabrous; 2. Absent.

Prostheca is lacking only in *Toramus*, otherwise it is developed and mostly (except *Cryptophilus* i *Setariola*) pubescent.

#28. Mouth-parts. Mandibles, prostheca. 0. With hair-tuft (figs 39, 40, 42, 43, 46-49); 1. Without hair-tuft (figs 44, 45).

Hair-tuft above prostheca occurs universally in the studied groups, lacking only in *Coccimorphus*, *Languria* and *Toramus*, and among out-groups only in *Helota*. Heretofore this character has not been used in systematics of the Erotylidae.

#29. Mouth-parts. Mandibles, shape of mola. 0. Triangular (fig. 53); 1. Horseshoe-shaped (fig. 50); 2. Rectangular (fig. 52); 3. Ovate (fig. 51).

In the studied beetles mola may assume various shapes, which may be grouped as triangular, horseshoe-shaped, rectangular and ovate. This and the next character have not been hitherto applied in erotylid classification.

#30. Mouth-parts. Mandibles, carinulation on mola. 0. Present (figs 51, 53); 1. Absent (figs 50, 52).

Mola is carinulate in about half of the studied genera of the Erotylidae, and in similar proportion of out-groups. It enhances the effectiveness of chewing hard food.

#31. Mouth-parts. Mandibles, pubescence of mola. 0. Present; 1. Absent.

Pubescent mola occurs only in one of the out-groups: *Helota*. It is an adaptation to the food – fermenting sap of wounded trees – of these beetles.

#32. Mouth-parts. Maxillae, hooks on lacinia. 0. Absent; 1. Present (figs 54-56); 2. Present, spathulate (figs 57, 58).

In many erotylids apical part of lacinia is armed with strongly sclerotized hooks; in some they are thin, weak, hardly distinguishable from the surrounding dense pubescence, while in others have been entirely reduced. It should be mentioned that this character has since long been used to separate many supergeneric taxa in the Erotylidae. Interesting, not noted previously and unique in this family form of these outgrowths show the representatives of the genus *Scaphidomorphus*, where they are flattened and bent, spatular. Together with widened and bluntly truncated mandibular apices such laciniae make an excellent tool to scrape fructifications or spores of fungi – unfortunately no concrete observations supporting this interpretation have been available (cf. remarks to the character #23).

#33. Mouth-parts. Maxillae, shape of apical joint of maxillary palpi. 0. Fusiform (figs 59, 60); 1. Symmetrically triangular (figs 54, 62); 2. Asymmetrically triangular (figs 61, 63).

Shape of the last segment of maxillary palpi has been commonly used to distinguish taxa of various rank (from species- to subfamily-level) in the Erotylidae. It is assumed that the plesiomorphous state is not widened, fusiform shape. The degree of widening vary considerably. In outgroups have fusiform apical joints. It should be mentioned that this joints holds sensillae, whose number is directly proportional to the degree of dilatation. See also remarks on the character #37.

#34. Mouth-parts. Mentum, shape. 0. Widened, rectangular, without anterior denticles; 1. Triangular (figs 64, 71); 2. Pentagonal (fig. 72); 3. Tridentate (fig. 73).

The simplest – transversely rectangular without denticles – form occurs only in *Helota* (outgroup) and *Languria* (ingroup); the remaining states occur in almost equal proportions and show no apparent correlation with other characters.

#35. Mouth-parts. Mentum, lateral dents. 0. Absent; 1. Present (figs 64, 71-73).

Lateral dents occur in all taxa except *Helota* (outgroup) and *Languria* (ingroup).

#36. Mouth-parts. Mentum, pores. 0. Absent; 1. Present.

Pores (always a pair, placed symmetrically on sides of mentum) mark the outlets of secretory (probably scent-) glands (though no special study has been performed). These pores rarely occur in the group under study, and even where they do (genera *Megischyrus*, *Ischyrus* and *Apolybas*), their occurrence is not stable (e.g. some representatives of *Ischyrus* lack them) (Skelley, 1998).

#37. Mouth-parts. Labium, shape of apical joint of labial palps. 0. Fusiform (fig. 65); 1. Ovate (fig. 64); 2. Clavate (fig. 66); 3. Securiform, asymmetric (figs 67-69).

Last joint of labial palps is in the examined taxa usually both shorter and thinner than its counterpart in maxillary palps, but exceptions do occur: in *Megalodacne*, *Linodesmus*, *Toramus* and *Biphyllus* it is narrowly fusiform in maxillar but securiform in labial palps. See also remarks under #33.

#38. Prothorax. Bordering of pronotal base. 0. None (figs 77, 79, 81); 1. Partial (present only at hind angles in lateral third) (figs 74, 78); 2. Entire (figs 75, 76, 80).

All three states occur in studied Erotylidae with almost equal frequency. This character does not seem correlated to others. In outgroups the border is either entire or totally absent.

#39. Prothorax. Bordering of anterior margin of pronotum. 0. None (figs 76, 79, 81); 1. Partial (present only at apical angles in lateral third) (ryss 75, 77); 2. Entire (figs 74, 78, 80).

The distribution of this character is similar to that of the previous one, but genera without border are somewhat less numerous.

#40. Prothorax. Lateral margins of pronotum. 0. Smooth (fig. 74); 1. Denticulate.

In the majority of examined taxa lateral margins are smooth; denticulation is characteristic only of three outgroups: *Helota*, *Cryptophagus* and *Biphyllus*.

#41. Prothorax. Pores on pronotal sides. 0. None (fig. 75); 1. One by one in each angle (figs 79, 80); 2. Numerous all-along the lateral margins (figs 74, 77, 78, 81); 3. Only in anterior angles.

Secreting pores on pronotal sides are very characteristic of the Erotylidae, only few genera lack them (*Dacne*, *Cryptodacne*, those belonging to the Languriidae). Usally they are placed singly in anterior and posterior angles, less frequently dispersed throughout the lateral margins. In the outgroups the pores are lacking or (in *Cryptophagus*) one is seen in each anterior angle.

#42. Prothorax. Pronotum. 0. No sharp carinae; 1. Two sharp carinae.

Two sharp carinae on pronotal surface characterize the genus *Biphyllus* and do not occur in other examined beetles.

#43. Prothorax. Anterior margin of prosternum. 0. Smooth (figs 82-84) or very finely denticulate; 1. Conspicuously denticulate.

Denticulation is characteristic of genera *Cryptophilus* (but here the denticles are very fine and hardly appreciable) and *Biphyllus* (very conspicuous, of truncated apices); in other studied taxa anterior prosternal margin is smooth.

#44. Prothorax. Notosternal sutures on prosternum. 0. Entire (figs 82-84); 1. Interrupted at middle; 2. Absent.

Almost all examined representatives of in-groups had entire, conspicuous notosternal sutures, only in *Megalodacne*, *Linodesmus*, *Ischyrus* and *Erotylus* they are interrupted at middle; in outgroups notosternal sutures are either interrupted or (*Cryptophagus*) not discernible at all. This character has not been hitherto used in classification of the Erotylidae.

#45. Prothorax. Procoxal cavities internally. 0. Closed; 1. Open.

Procoxal cavities are almost always internally opened, only in genus *Biphyllus* and those classified in the Languriidae they are closed. This character, not discernible without dissection, has frequently been neglected by coleopterologists. It is not directly correlated with the next one, i.e. there a beetle may have the cavities opened externally but closed internally or the reverse, as well as closed from both sides. See also remarks under #46.

#46. Prothorax. Procoxal cavities externally. 0. Closed (figs 82-84); 1. Open.

Externally open cavities are characteristic only of *Languria*, *Toramus*, *Setariola*, *Pharaxonotha* (ingroups) and *Cryptophagus* (outgroup). Externally closed or open procoxal cavities have been commonly used to distinguish taxa of various (usually suprageneric) rank, among others in case of Erotylidae (closed) vs. Languriidae (open). This character is so distinct that coleopterologists had no serious doubts as to its reliability, and as a consequence numerous similarities between both groups were left out of consideration. Besides, some of the genera classified in the Languriidae, e.g. *Cryptophilus*, have also the cavities externally closed, but because of small body-size this fact was overlooked. Cf. remarks to the character #45.

#47. Prothorax. Pores between procoxae. 0. Absent; 1. Present (figs 82-84).

Prosternal pores, like those on head and pronotum, are outlets of secretory glands, but their role in unknown. They occur in most genera of the Erotylidae, lacking only in *Dacne*, *Combocerus*, *Cryptodacne*, *Aulacochilus*, *Megischyrus*, *Ischyrus*, *Mycotretus*, *Apolybas*, *Zythonia* and *Triplax*, as well as all included formerly in the Languriidae and outgroups.

#48. Prothorax. Femoral lines. 0. Absent (figs 82, 84); 1. Present (fig. 83).

Presence, length and shape of femoral lines (as well on pro- as on metasternum and 1. sternite) have been universally used in the classification of the Erotylidae and Languriidae on both generic and specific level. About half of erotylid genera have them on prosternum, while Languriidae and outgroups have not.

#49. Mesothorax. Mesepisterno-mesepimeral suture. 0. Far before meso-metasternal suture in mesocoxal cavities (figs 85, 91, 92, 93); 1. At the level of meso-metasternal suture in mesocoxal cavities (figs 90, 94).

In almost half of studied genera of the Erotylidae (including *Pharaxonotha*) the suture between mesepisternum and mesepimeron advanced much anterad in relation to that between meso- and metasternum in coxal cavities; in the remaining ones (as well as in outgroups) both are situated at the same level. This character hes not been used hitherto in erotylid classification.

#50. Mesothorax. Mesoepimeron. 0. Builds the mesocoxal cavities together with meso- and metasternum; 1. Does not build the mesocoxal cavities together with meso- and metasternum, but deeply enters between them; 2. Neither builds the mesocoxal cavities together with meso- and metasternum, nor enters between them (figs 85, 90-94).

In three outgroups (*Nitidula*, *Biphyllus* and *Helota*) mesoepimeron, together with meso- and metasternum, makes the mesocoxal cavities. The first step towards removal of mesepimeron from coxal cavity may be observed in *Dacne* (primitive Erotylidae) and two genera classified among the Languriidae (*Setariola* i *Pharaxonotha*): all have it deeply inserted between meso- and metasternum, but separated from the cavity. Other genera are characterized by contiguity of the two parts of sternum, with epimeron not entering between them. This character has not been used in erotylid classification hitherto.

#51. Metathorax. Outer margin of metascutellum. 0. Touching posterior margin of metascutum (figs 100, 101); 1. Not touching posterior margin of metascutum (fig. 99).

Outer margin of metascutellum not touching hind margin of metascutum seems to be a strong synapomorphy of a large group of New World *Erotylidae*, the naturalness of which – though evident – remained hitherto unsupported. The group is now flourishing (more than 500 described species) and vigorously speciating. Among the studied genera here belong *Coccimorphus*, *Erotylus*, *Scaphidomorphus* and *Homoeotelus*.

#52. Metathorax. Metanotum. 0. Normal (figs 99, 100); 1. Markedly shortened (fig. 101).

Striking shortening of metanotum is characteristic of all taxa with reduced wings (*Coptengis*, *Cryptodacne*). Reduction of wing (and of flying ability) causes partial or total atrophy of respective muscles, and consequently reduction and poor sclerotization of metanotal exo- and endoskeleton.

#53. Metathorax. Lateral phragmae of metanotum. 0. Normally developed (figs 99, 100); 1. Entirely reduced (fig. 101).

The remarks on the preceding character (#52) are in force also here.

#54. Metathorax. Metendosternite, lateral plates. 0. Present (fig. 97). 1. Absent (fig. 98).

Metendosternite is an internal sclerite (fixed to the hind margin of prosternum) to which muscles (also those operating wings) are attached. Therefore in wingless and poorly flying forms metendosternite is atrophied (its particular elements are shortened). Not directly related to loss of flying ability is reduction of lateral plates, occurring frequently in examined beetles and apparently correlated with other characters. Structure of metendosternite has not been taken into consideration in studies on erotylid classification.

#55. Metathorax. Metasternum, attachment to mesosternum. 0. Simple (fig. 87); 1. Double (fig. 88, 89).

In beetles metasternum is firmly connected to mesosternum; metasternal process, inserted into respective cavity in mesosternum, may – in case of the Erotylidae – be simple or double (both parts of double one may be close to or distant from one another, but in view of inermediate forms, these states have not been distinguished in the analysis). In outgroups the connection is simple. The role of the process consists in additional mechanical consolidation of attachment between meso- and metasternum. This character was applied in classification of Cryptophagidae (Leschen 1996) and Languriidae (SenGupta and Crowson 1971), but not Erotylidae.

#56. Metathorax. Metasternum, femoral lines. 0. Absent (figs 85, 91, 94); 1. Present (figs 90, 92, 93).

See remarks under #48.

#57. Metathorax. Metasternum. Metepisterno-metepimeral suture. 0. At the level of posterior margin of metasternum (figs 85, 90-92, 94); 1. Distinctly removed backwards (fig. 93); 2. Absent, both sclerites fused without suture.

In overwhelming majority of studied taxa the suture between metepisternite and metepimeron is situated at the end of metasternum, only in some genera (*Combocerus*, *Cryptodacne*, *Episcapha*, *Linodesmus* and one outgroup: *Nitidula*) it is displaced far backwards, while in *Helota* episternite is (probably in connection with considerable general stiffening of the body) totally coalescent with epimeron so, that even on cleared preparation suture is not discernible. This character has hitherto not been taken into account in classifying the Erotylidae.

#58. Metathorax. Metasternum, median suture. 0. Shortened (figs 90-94); 1. Entire (fig. 85).

Median suture of metasternum in the group under study almost never reaches anterior margin, only in *Erotylus* it is entire. This character have not been hitherto used in the classification of the Erotylidae.

#59. Elytra. Length of elytra. 0. Elytra extend to abdominal apex; 1. Elytra abbreviated, leave pygidium exposed.

Marked shortening of elytra is characteristic of *Nitidula* (outgroup); in the remaining taxa elytra cover the abdomen entirely or at most the last tergite slightly protrudes (but even in such cases pygidium is not developed).

#60. Elytra. Bordering of base. 0. Present; 1. Absent.

Border on elytral base (if present) is usually tight-fitted to the respective surface of posterior margin of pronotum; such attachment stiffens the pronoto-elytral connection (and consequently the body in general). In majority of studied taxa elytral base is not bordered, and among the outgroups some (*Cryptophagus*, *Biphyllus*) have it, others (*Nitidula* and *Helota*) do not.

#61. Elytra. Punctures. 0. Arranged in regular rows; 1. Dispersed irregularly.

In overwhelming majority of Erotylidae elytral punctures are arranged in regular rows, and this character should be accepted as most primitive. In few genera rows are strongly confused or are not discernible at all; those showing irregular puncturation are: *Coptengis*, *Episcapha*, *Apolybas* (sculpture almost totally obliterated, hardly appreciable), *Coccimorphus*, *Homoeotelus* and members of the former Languriidae – *Setariola* i *Cryptophilus*, while among outgroups only *Cryptophagus*.

#62. Wings. 0. Present; 1. Reduced (fig. 104).

Erotylidae are as a rule good flyers (as is usuall among mecetophages, which must be able to find such irregularly occurring food as fungi), only few species have lost the flying ability by atrophy of wings. Among the studied genera reduced wings characterize only *Coptengis* and *Cryptodacne*, which show also – at least partial – fusion of elytra along suture.

#63. Wings. Attachment of medial vein. 0. Absent. 1. Present.

All ingroups have attached media, all outgroups show no attachment.

#64. Wings. Vein MP3+4. 0. Simple; 1. Forked at end.

Forked MP3+4 appears only in the genus *Coccimorphus*.

#65. Wings. Radial cell. 0. Absent; 1. Present.

Anal cell, situated in basal part of wing, is developed in almost all studied beetles except outgroups *Helota* and *Nitidula* and ingroups *Toramus*, *Setariola*, *Pharaxonotha* and *Cryptophilus*. Its presence may be considered secondary, because in supposedly more primitive *Helota* and *Nitidula* it is lacking. Its absence may be an aspect of simplification of wing-venation in consequence of decrease in, but in some small erotylids (*Dacne*, *Combocerus* and others) it is well developed.

#66. Wings. Radial cell. 0. Lacking; 1. Triangular (figs 102, 105, 106); 2. Rectangular or elongate (figs 103, 107-109).

Simple radial cell is a characteristic element in the family Erotylidae – only representatives of two genera, *Toramus* and *Cryptophilus*, show wing-venation reduced (see comments under #65) to the extent of disappearance of this cell (wingless genera *Coptengis* and *Cryptodacne* naturally also lack it). Radial cell in erotylids may assume two main forms: triangular and (somewhat more frequent) rectangular (angles are sometimes poorly distinguishable, then the cell could be termed “elongate”). In outgroups radial cell is well developed (*Helota*, *Biphyllus*), or entirely lacking (*Nitidula* and *Cryptophagus* – again the reduction is perhaps connected to small body-size).

#67. Wings. Cross-vein r3. 0. Normally developed; 1. Markedly or totally reduced.

Vein r3 is in the Erotylidae usually well developed, but some exceptions – *Dacne*, *Toramus*, *Setariola* and *Cryptophilus*, where it is strikingly shortened or entirely absent – do occur. In outgroups it may (*Helota* and *Biphyllus*) or may not (*Nitidula* and *Cryptophagus*) be present.

#68. Wings. Cross-vein r3. 0. Simple; 1. Forked at end.

Vein r3 is forked only in *Scaphodacne*, otherwise always simple.

#69. Wings. Cross-veins r3 i r4. 0. Far removed (figs 103, 106-109); 1. Closely approaching or touching each other (figs 102, 105).

In the Erotylidae both states are represented by equal number of genera.

#70. Wings. Medial fleck. 0. Absent; 1. Present.

All in-groups and the genus *Biphyllus* show developed medial fleck, all the remaining outgroups lack it.

#71. Legs. Crown of flattened setulae at end of tibia. 0. Absent; 1. Present.

Only in *Coccimorphus* the crown of flat setules is lacking – a derived character (apomorphy), never used in erotylid systematics.

#72. Legs. Tibial spurs. 0. Two, approached; 1. Two, wide apart; 2. Single; 3. Absent.

A pair of spurs at tibial apex occur in almost all studied beetles. Two states are distinguishable: the spur bases are either very close to (often touching) one another, or they are placed at considerable distance (sometimes separated with small outgrowth of tibia); very rarely one (in *Encaustes*) or both (in *Aulacochilus*) spurs disappear. Outgroups show two approximate spurs.

#73. Legs. Tarsi. 0. Basal four joints cylindrical, similar in length and thickness (rys. 109); 1. Basal four joints cylindrical, 3. slightly emarginated, 4. much shorter than 1.-3. (fig. 108); 2. Three basal joints widely triangular, fourth minute, deeply hidden in emargination of 3 (fig. 110).

Tarsal structure has since long time been used in classification of the Erotylidae. It is supposed (probably with reason), that primitive is the pattern of four cylindrical joints of similar size; evolution then proceeded in the direction of widening of third tarsomere with simultaneous marked reduction of (both size and pubescence of) the fourth. Primitive type has been retained only in *Dacne* and *Pharaxonotha* (in the latter case with atrophy of pubescence of 4. joint). The next step is represented by the subfamilies Dacninae (except *Dacne*) and Megalodacninae, as well as genera *Toramus*, *Setariola* and *Cryptophilus* of the Languriidae and *Biphyllus* from among outgroups. Evolution proceeded further, and in the majority of erotylids the tiny 4. joint is hardly visible in the emargination of widened third – such tarsal structure assures better adherence to substratum (fungi, leaves, &c.). Among outgroups state (0) is characteristic of *Helota* and *Cryptophagus*, (1) of *Biphyllus*, (2) of *Nitidula*.

#74. Legs. Tarsi, undersurface of 4. joint. 0. Pubescent (fig. 109); 1. Glabrous, with but 2 bristles (fig. 107).

Reduction in size of fourth tarsomere was accompanied with reduction of pubescence on its underside. Densely pubescent it is only in *Dacne* (Erotylidae) and outgroups *Helota* and *Cryptophagus*. Hitherto this character has not been taken into account.

#75. Abdomen. Femoral lines. 0. Absent; 1. Present.

Femoral lines on abdomen are rather frequent among the Erotylidae, characterizing mostly species of small body-size. See also remarks to characters #48 i 56.

#76. Abdomen. Tuft of hairs on 1. sternite in male. 0. Absent; 1. Present (fig. 106).

Besides the Erotylidae, tuft of hairs on first sternite occurs in of some other families, e.g. Buprestidae, Dermestidae and Ciidae. Function – perhaps secretory – of this structure remains unknown. Among the genera under study it has been found in *Coccimorphus* and *Erotylus*.

#77. Male genitalia. Penis. 0. Open; 1. Closed (fig. 115).

Close, bilaterally flattened penis occurs in almost all ingroups with sole exception of *Cryptophilus*, which – like all outgroups – shows open penis.

#78. Male genitalia. Penis, apophyses. 0. Absent; 1. Present, not fused; 2 Present, fused (fig. 115).

Characteristic feature of the Erotylidae are long, fused apophyses of penis; among outgroups fused apophyses occur only in *Nitidula*, while in *Helota* and *Biphyllus* they are free, and in *Cryptophagus* lacking at all.

#79. Male genitalia. Penis, flagellum. 0. Absent; 1. Present (fig. 116).

Flagellum in the internal sac of penis penisa is very characteristic of the Erotylidae. Its shape vary, but usually two interconnected elements can be distinguished: head and virga. In *Helota* (outgroup) flagellum is also present, but of different structure.

#80. Male genitalia. Tegmen, attachment of parameres. 0. Fused to tegmen; 1. Articulated (figs 117, 118).

Parameres of the Erotylidae are – with the only exception of *Setariola* – robust and movably articulated to tegmens.

#81. Female genitalia. Genital segments, rows of denticulate plates. 0. Absent; 1. Present (fig. 123).

Rows of denticulate plates on genital segments occur only in *Dacne*.

#82. Female genitalia. Coxites. 0. Single, glabrous (fig. 123); 1. Double, pubescent (fig. 122).

Single glabrous coxites characterize only females of *Dacne* and *Languria*. Such structure is an adaptation to hard substratum (bracket-fungi *Polyporaceae* in case of *Dacne*, leaf tissues of higher plants in that of *Languria*) in which females lay eggs: to be effective, ovipositor must be stiff and smooth. This type occurs also in *Nitidula* (outgroup), while all the remaining taxa show double, pubescent coxites.

#83. Female genitalia. Coxites. 0. Bluntly truncated at apex (fig. 122); 1. Pointed (fig. 123).

This character is directly correlated with the previous one: pointedness of coxites enables penetration of tissues of fungi or plants.

#84. Female genitalia. Styli, placement on coxites. 0. Apical (fig. 122); 1. Lateral (fig. 123).

This also is functionally connected to the character #82: lateral position of (reduced in size) styli allows to thrust ovipositor into the tissues of fungus or plant.

RESULTS

Characters

85 morphological characters have been coded for 4 outgroups and 30 ingroups (including 5 species of Languriidae – one of each subfamily – and 25 species of Erotylidae, representative of its morphological variability. Characters and character-states of all studied genera have been presented in the character-matrix (Tab. 1).

Coded unweighed characters have been cladistically analysed with a computer-program „Hennig86", applying the algorithm "mhennig*" under the assumption that the main outgroup is the genus *Nitidula*. As the result 2 shortest (most parsimonous) trees have benn obtained, with L = 394, Ci = 0,29, Ri = 0,54 (where L – length of cladogram, Ci – consistency index, Ri – retention index (figs 140-141). Both cladograms showed almost identical topology (differences between trees were slight and concerned the genus *Mycotretus*) and identical position of out-groups. Further considerations and classification are based on the cladogram #1 (fig. 140).

In order to check the stability of cladograms successive weighing has been performed, applying the algorithm "mhen* bb* xsteps w cc", until stable, above-mentioned parameters have been arrived at. The result of successive weighing were 27 cladograms of L = 498, Ci = 0, 64, Ri = 0,78. They have much greater length and higher values of indexes, but otherwise stability of cladograms did not increase. Topology of all cladograms was similar, with minor differences.

Maximum congruence (nelsen) cladograms (figs 142, 143) have also been constructed, using the algorithm "n" (L = 396, Ci = 0,29, Ri = 0,53) for cladograms of the "mhennig" algorithm (fig. 142) and those of successive weighing (L = 415, Ci = 0,27, Ri = 0,50) (fig. 143).

CONCLUSIONS, DISCUSSION AND TAXONOMIC DECISIONS

The results of phylogenetic analysis support the earlier supposition, that the Erotylidae as conceived hitherto are not a monophyletic group, and cannot be treated as independent taxon (here: family). As previously (SEN GUPTA and CROWSON 1971, LESCHEN and WĘGRZYNOWICZ 1998) suggested, and now confirmed by the topology of the "mhennig" cladogram, the traditionally separated Erotylidae and Languriidae are in fact a single natural unit with following synapomorphies:

- hind-wing with joint medial vein (#63-1);
- penis closed and laterally flattened (#77-1) (fig. 115);
- very peculiar flagellum in the of penis (#79-1) (fig. 115);

Thus, Erotylidae and Languriidae must be combined into single family under the senior name - Erotylidae.

Neither do both units make monophyletic groups separately: the genus *Languria* is located on cladograms deeply inside the traditional Erotylidae, what makes the simple division of the Erotylidae into two - Erotylinae and Languriinae – subfamilies (as suggested by LESCHEN and WĘGRZYNOWICZ, 1998), unwarranted.The results confirm the sister-group affinity between the families Biphyllidae and Erotylidae. This was already postulated by SEN GUPTA and CROWSON (1971) who, however, did not present clear and unambiguous evidence to support their thesis. In analysis close relationship between both families is indicated by the following synapomorphies:

- notosternal sutures on prosternum usually entire (rarely broken at middle) (#44-0, 1);
- presence of medial fleck (#70-1);
- frontoclypeal suture very frequently incomplete (broken at middle) (#3-1);
- mandibulae depressed and pubescent on distal surface (#25-1).

Full reconstruction of the phylogeny of Erotylidae would demand inclusion of more genera in the analysis, but even now several groups of genera can be distinguished.

Clade #1 (*Pharaxonotha*, *Toramus*, *Setariola* and *Cryptophilus*) contains representatives of four (out of five hitherto accepted) subfamilies of the Languriidae (Xenoscelinae, Toraminae, Setariolinae and Cryptophilinae).

These subfamilies had been classified in the Cryptophagidae, until SEN GUPTA and CROWSON (1971) noticed the close affinity between them and the Languriidae and transferred them accordingly. The clade is defined by the following characters:

- lack of anal cenn in the hind-wing (#65-0) (a unique feature of this clade – all the remaining Erotylidae show very conspicuous anal cell);
- no pore on the subgenal braces (#12-0) (among other genera only *Tritoma* lacks this pore);
- antennal club not flattened (#19-0) (this state occurs also in the next clade, but there it is probably a reversal);
- procoxal cavities externally opened (only in *Cryptophilus* closed) (#46-1) (this character has been heretofore used to distinguish Languriidae from Erotylidae, but in my opinion closing and opening of procoxal cavities occurred in this group several times and is not very significant phylogenetically).

In the present study only one representative of each hitherto distinguished subfamily of the Languriidae has been examined, thence further research – better considering the internal diversity and including more genera – would be very important and needed.

Clade #2 (*Coccimorphus*, *Homoeotelus*, *Erotylus* and *Scaphidomorphus*) groups the genera traditionally included into Erotylinae (KUHNT 1909, 1911, ALVARENGA

1994). This subfamily was hitherto distinguished rather intuitively according to large body-size, brightly variegated colouration, and distribution (tropical regions of the New World).

The diagnostic (unique for the included genera) synapomorphy of this clade is separation of outer margin of metascutellum from hind margin of metascutum (#51-1).

Clade #3 (*Amblyopus*, *Triplacidea*, *Zythonia*, *Tritoma* and *Amblyscelis*) – includes five genera placed in the subfamily Tritominae (Delkeskamp 1981, Chűjô and Chűjô 1990), which (except *Amblyscelis*), show a character never occurring in other Erotylidae: anteriorly bordered epistome (#1-1).

Clade #4 (*Encaustes* and *Aulacohilus*) – very distinctive by its reduced (at least one) tibial spur (#72-2, 3) and vertical placement of cheek-process (#11-1) (this character is present – but never so well developed – in few other genera of Erotylidae). The analysis supports the hitherto accepted position of these genera as a natural group (Chűjô 1969, Delkeskamp 1981, Chűjô and Chűjô 1989).

Clade #5 (*Scaphodacne-Linodesmus*) – here belong the genera of the former subfamily Megalodacninae (Sen Gupta 1969). All these taxa are very close to one another, but the clade is not supported by any strong synapomorphy. Its distinguishing characters are the following:

- lack of depressions on antennal club (#21-0) (character occurring in but few Erotylidae);
- lacinia without hooks (#32-0);
- last joint of maxillary palpi fusiform (#33-0);
- proximal four tarsomeres cylindrical, but three of them of similar length and thickness, third slightly emarginated, and fourth markedly shorter (#73-1).

Clade #6 (clades ##4 and 5). Both above-mentioned groups share the following characters:

- overy large eyes (#7-2);
- lack of tuft of setae on subgenal braces (#13-0);
- submentum separated from rest of the head with sulcus (#14-1) (in other groups this character is very rarely observed).

Moreover, the majority of species of both clades is similarly (black with red pattern) coloured – what may represent a convergence – and both occur in the same zoogeographical ares: Middle and South America, Africa, South-East Asia, Australia (Chűjô and Chűjô 1989, 1990, Alvarenga 1994). The clade #4 contains decidedly less genera and species, and is morphologically less diversified, than the Clade #5. According to the present state of knowledge clades ##4 and 5 are considered sister-groups.

Clade #7 (klady ##2 and 6). Following characters show that the clade #6 is the sister-group of #2:

- lack of ribbing on mandibular mola (#30-1);
- pores on pronotal margin numerous (#41-2) (this is a strong synapomorphy, diagnostic of this group);
- radial cell quadrangular or elongated (#66-2);
- lack of femoral lines on 1. abdominal sternite (75-0).

Clade # 8 (*Dacne*, *Combocerus* and *Cryptodacne*). These three genera were hitherto combined in the subfamily Dacninae, or *Cryptodacne* was separated into a subfamily of its own. All of them show simple structure of tarsi (tarsomeres not dilated) and more or less fusiform distal joints of maxillary palpi. On the cladogram this group is characterized by two synapomorphies:

- mesothoracic episternites fused to mesepimera far before the meso-metathoracic suture in coxal cavities (#49-0);
- cross-veins r3 and r4 approach or touch one another(#69-1).

Clade #9 (*Lybas*, *Megischyrus* and *Ischyrus*). Three South-American genera characterized by lack of pores on mentum (cecha #36-1).

The cladograms resulting from the phylogenetic analysis show that the hitherto distinguished subfamily Tritominae is polyphyletic. However, the affinities of the respective genera is debatable and demands further studies, including also other related taxa.

PROPOSED SUPRAGENERIC CLASSIFICATION OF THE FAMILY EROTYLIDAE

The phylogenetic analysis presented above has provided the basis for a modified – even if still preliminary and demanding further research – classification of the Erotylidae.

The Erotylidae have been divided into two subfamilies - Xenoscelinae and Erotylinae (the name Xenoscelinae has priority over the synonymized subfamily-names Cryptophilinae, Toraminae and Setariolinae).

The Xenoscelinae is equivalent to the above-mentioned Clade #1; its further subdivision into tribes is not possible until the analysis including more genera has been done.

To the Erotylinae belong all the remaining Erotylidae (including the former Languriinae).

The tribe Dacnini contains beetles characterized by: four proximal tarsomeres cylindrical; fourth tarsomere either densely pubescent below or with but two setae; last joint of maxillary palpi cylindrical; mesothoracal episternites meeting mesepimera far anterad of meso-metathoracal suture in coxal cavity; cross-veins *r*3 and *r*4 close to, or touching, one another; and small body-size. Majority of species included here inhabits the temperate zones of both northern and southern hemisphere, but some occur also in the tropics (Africa, Ceylon).

The tribe Languriini groups usually strongly elongated beetles of bright metallic colouration and phytophagous larvae (VILLIERS 1943). They are distributed in hot and humid regions: especially numerous in South-East Asia and Africa, less numerous in Americas and Australia, absent in Europe, Northern Asia and New Zealand (LESCHEN and WĘGRZYNOWICZ 1998).

To the Erotylini belong the genera of the clade #2; it is a monophyletic group of strong synapomorphy: outer margin of metascutellum not touching hind margin of metascutum (#51-1). Representatives of this tribe are usually large and brightly coloured. The distribution area extends over South America and reaches southern states of USA.

The Tritomini appear as an artificial, composite group not supported with synapomorphies, defined by a set of characters occurring also in other taxa: last joint of maxillary palpi symmetrically (#33-1) or asymmetrically (#33-2) triangular; tibiae with two spurs (#72-0, 1); proximal three tarsomeres broadly triangular, the fourth tiny, deeply included in the emagination of the third (#73-2). Further studies on this group are indispensable. The analysis has proven beyond doubt, that hitherto accepted subtribes Tritomina and Triplacina (CHŰJÔ 1969, CHŰJÔ and CHŰJÔ 1990), based on presence or absence of hooks on lacinia (character #32-0, 1), is artificial: this feature appears – probably independently – several times in the Erotylidae.

The tribe Encaustini combines the clades ##4 and 5 (former Encaustini and Megalodacninae). The apomorphies characteristic of this taxon are: submentum separated with sulcus from the rest of the head (#14-1) (the character occurring very rarely in other groups); lack of ribbing on mola (#30-1), pores numerous over all the length of pronotum (#41-2) (otherwise this feature occurs only in some Erotylidae); radial cell quadrangular or elongated (#66-2) (in the remaining Erotylidae very rarely so). Representatives of the Encaustini inhabit mainly the hot areas of the Old World, being rather scarce in the Americas; both clades show similar distribution, but #5 incomparably more speciose than #4 (CHŰJÔ and CHŰJÔ 1989, 1990).

The classification proposed above is basically different from those advocated by other coleopterologists (CROWSON 1955, CHŰJÔ 1969, SEN GUPTA 1969, SEN GUPTA and CROWSON 1971, CHŰJÔ and CHŰJÔ 1988, 1989, 1990) – the main differences are the division of the Erotylidae into two subfamilies and downgrading of the Languriinae to the status of tribe within the Erotylinae.

Family Erotylidae LATREILLE, 1802

= Languriidae CROTCH, 1873 **n. syn.**

Subfamily Xenoscelinae GANGELBAUER, 1899

= Cryptophilinae, CASEY, 1900 **n. syn.**,

= Toraminae SEN GUPTA, 1967 **n. syn.**,

= Setariolinae Crowson, 1952 **n. syn.**

Subfamily Erotylinae LATREILLE, 1802

- Tribe Dacnini GISTEL, 1856
- Tribe Languriini CROTCH, 1873
- Tribe Erotylini LATREILLE, 1802
- Tribe Tritomini CURTIS, 1834
- Tribe Encaustini CROTCH, 1876
  - = Megalodacninae SEN GUPTA, 1969 **n. syn.**

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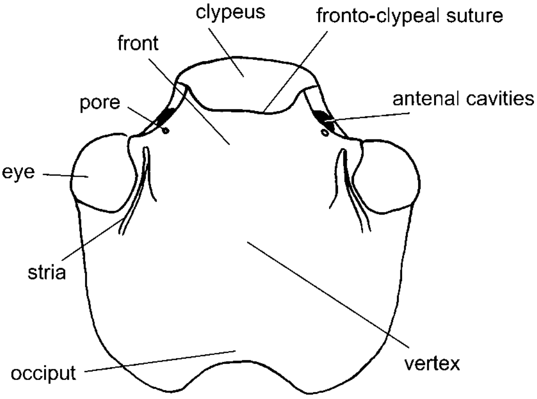

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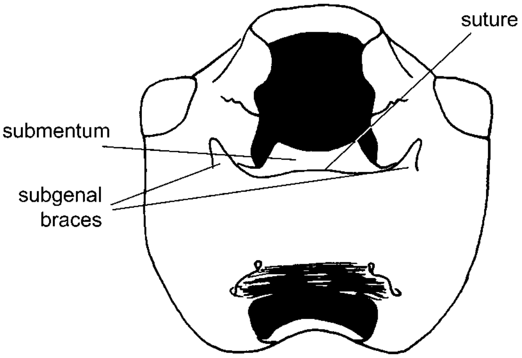

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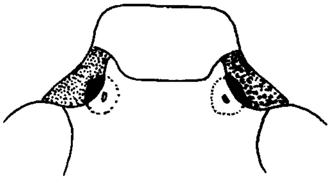

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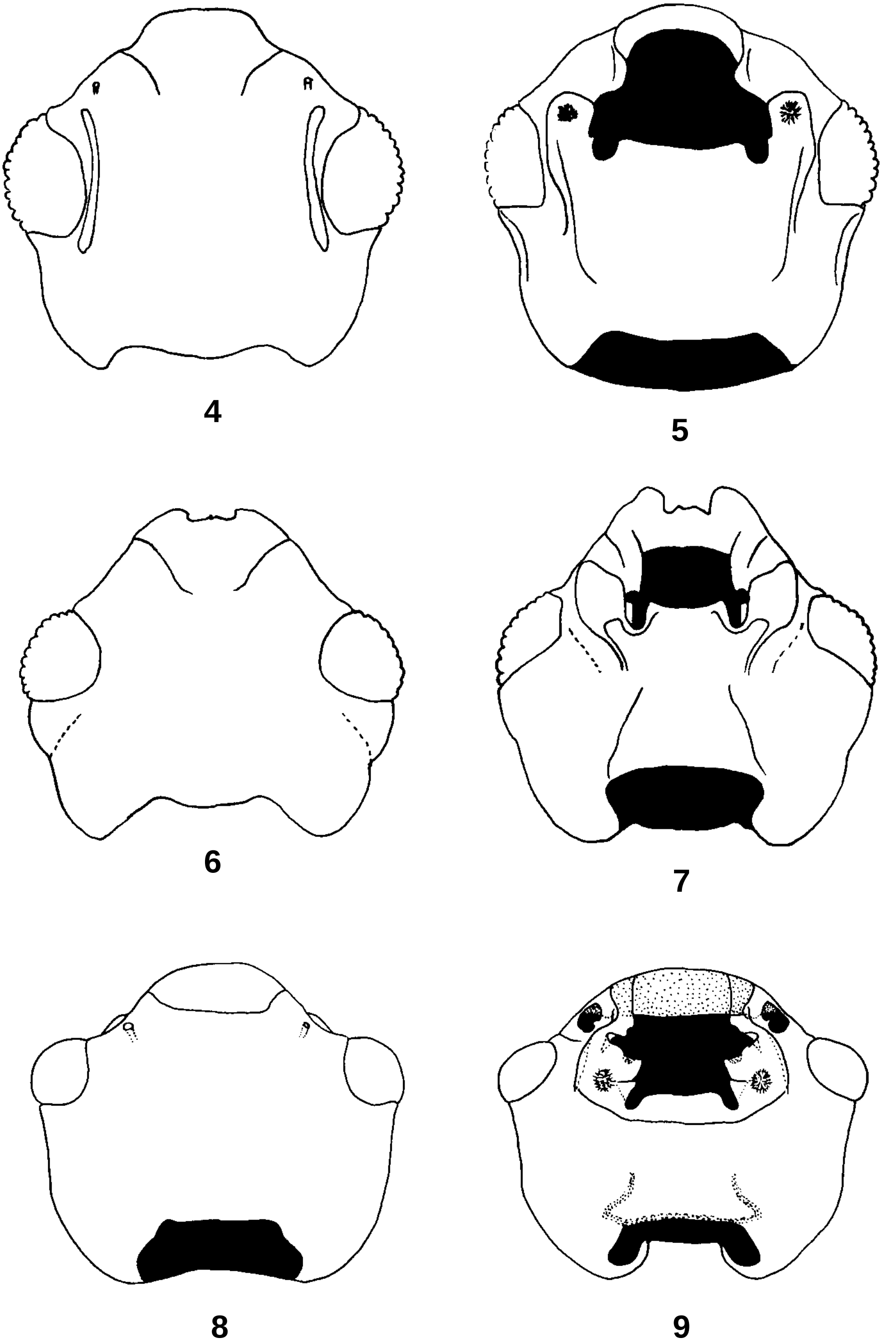
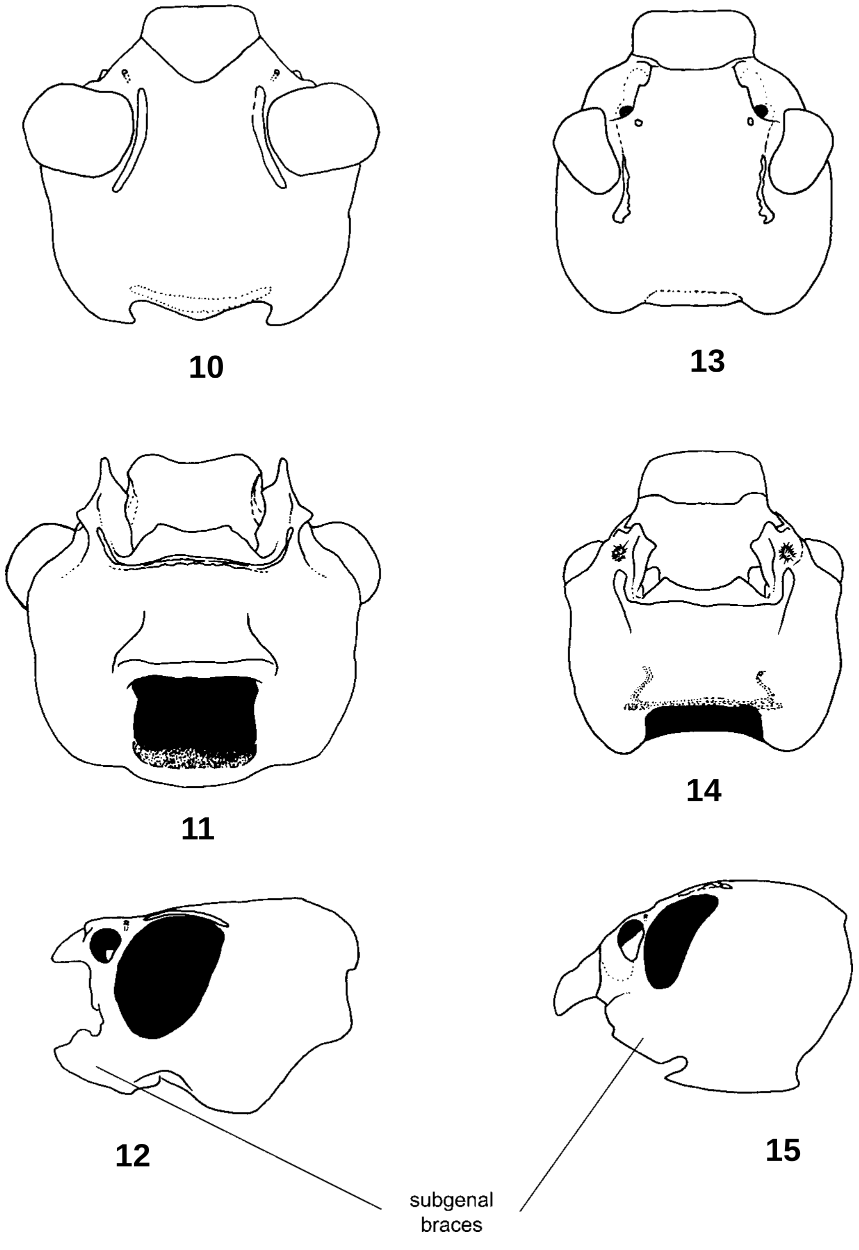
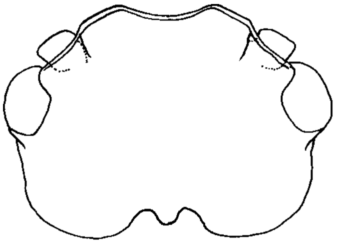
1-3. *Erotylus giganteus* - head: 1 - dorsal view, 2 - ventral view, 3 - rostrum, dorsal view



4-9. Head (4, 6, 8 - dorsal view, 5, 7, 9 - ventral view): 4, 5 - *Scaphodacne rectesignata*; 6, 7 - *Pselaphacus nigropunctatus*; 8, 9 - *Coccimorphus unicolor*



10-15. Head (10, 13 - dorsal view, 11, 14 - ventral view, 12, 15 - lateral view): 10-12 - *Encaustes verticalis*; 13-15 - *Scaphidomorphus quinquepunctatus*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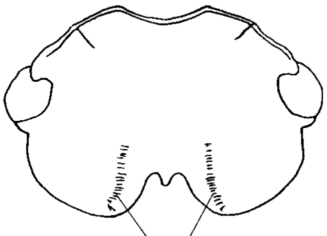

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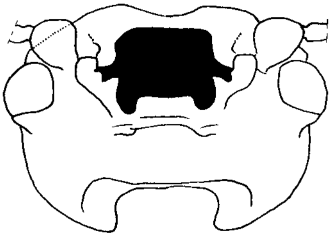
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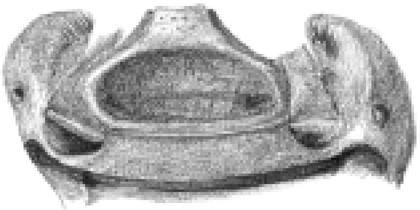
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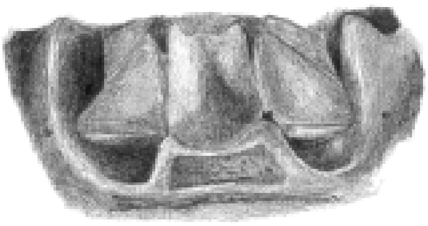
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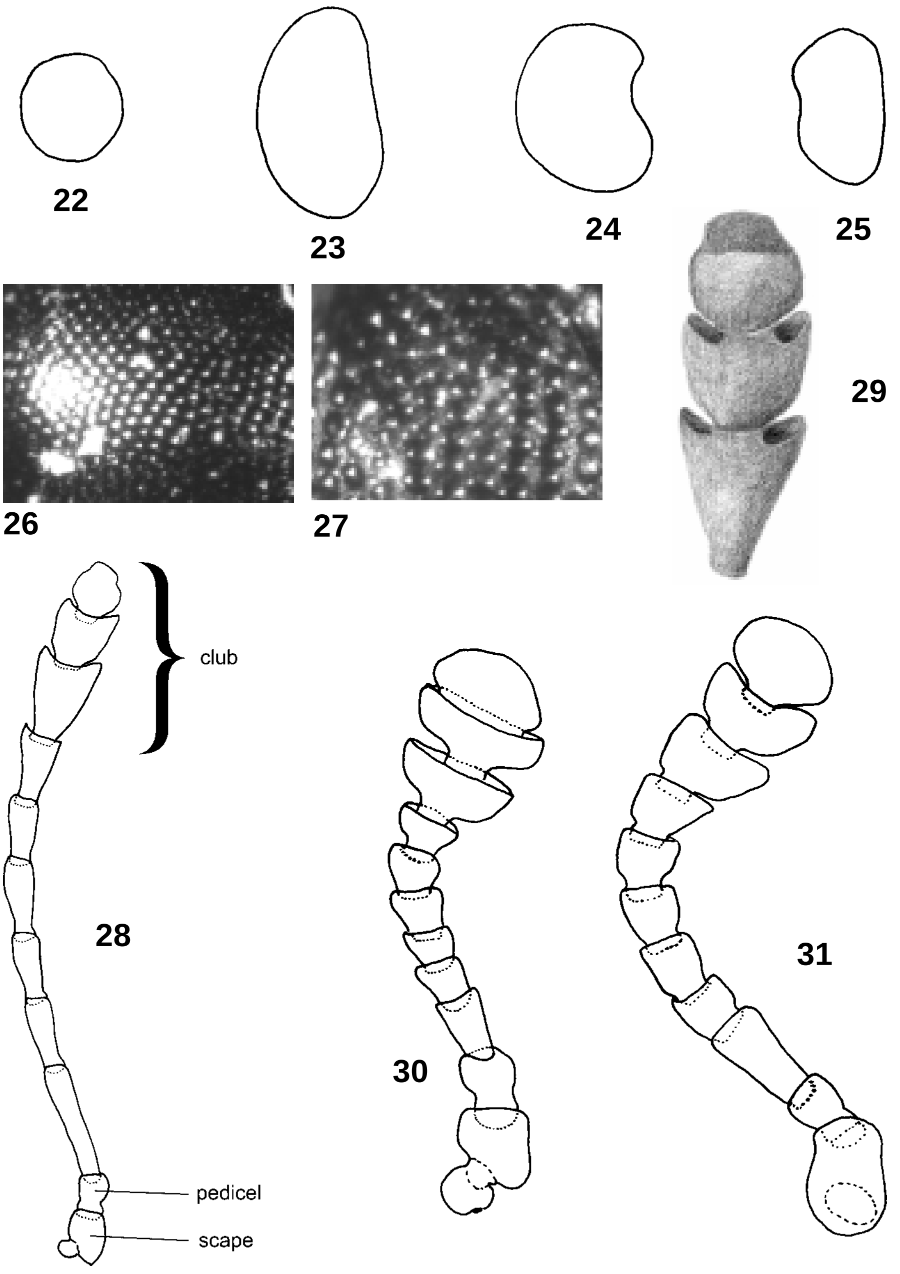
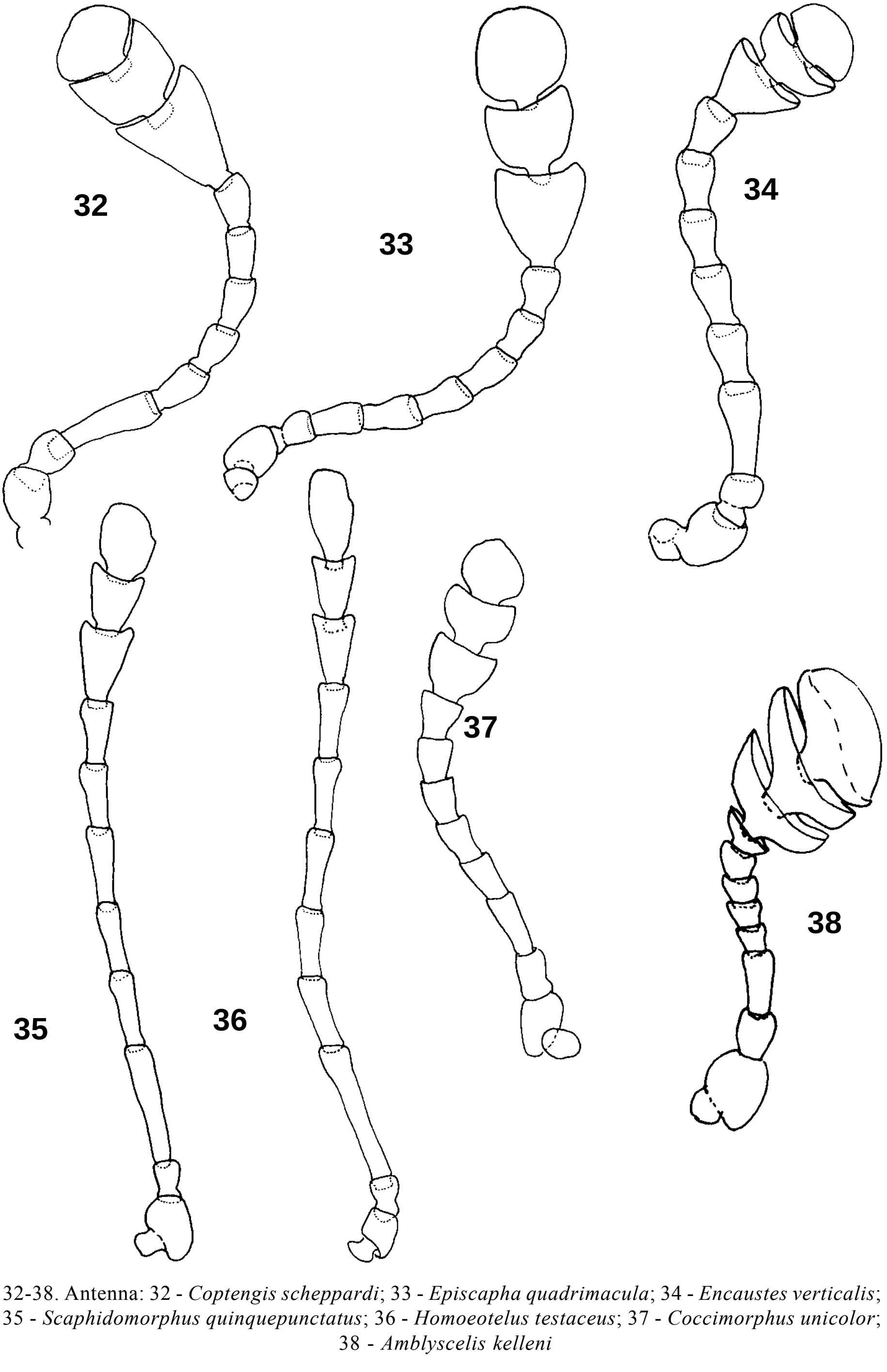
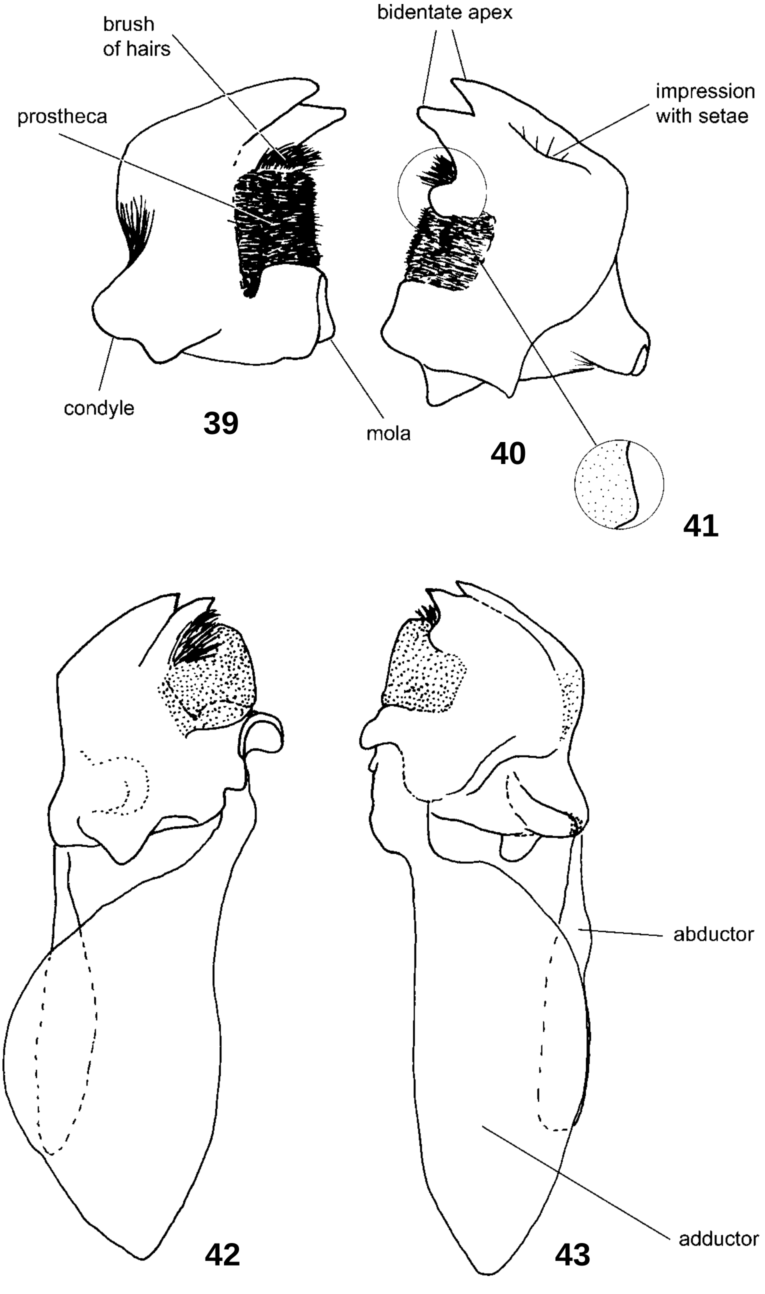
16-18. *Zythonia fulva*, head (16 (female), 17 (male) - dorsal view, 18 (male) - ventral view). 19-21. Mouth-parts - ventral view: 19 - *Erotylus giganteus*; 20 - *Megalodacne fasciata*; 21 - *Pselaphacus nigropunctatus*



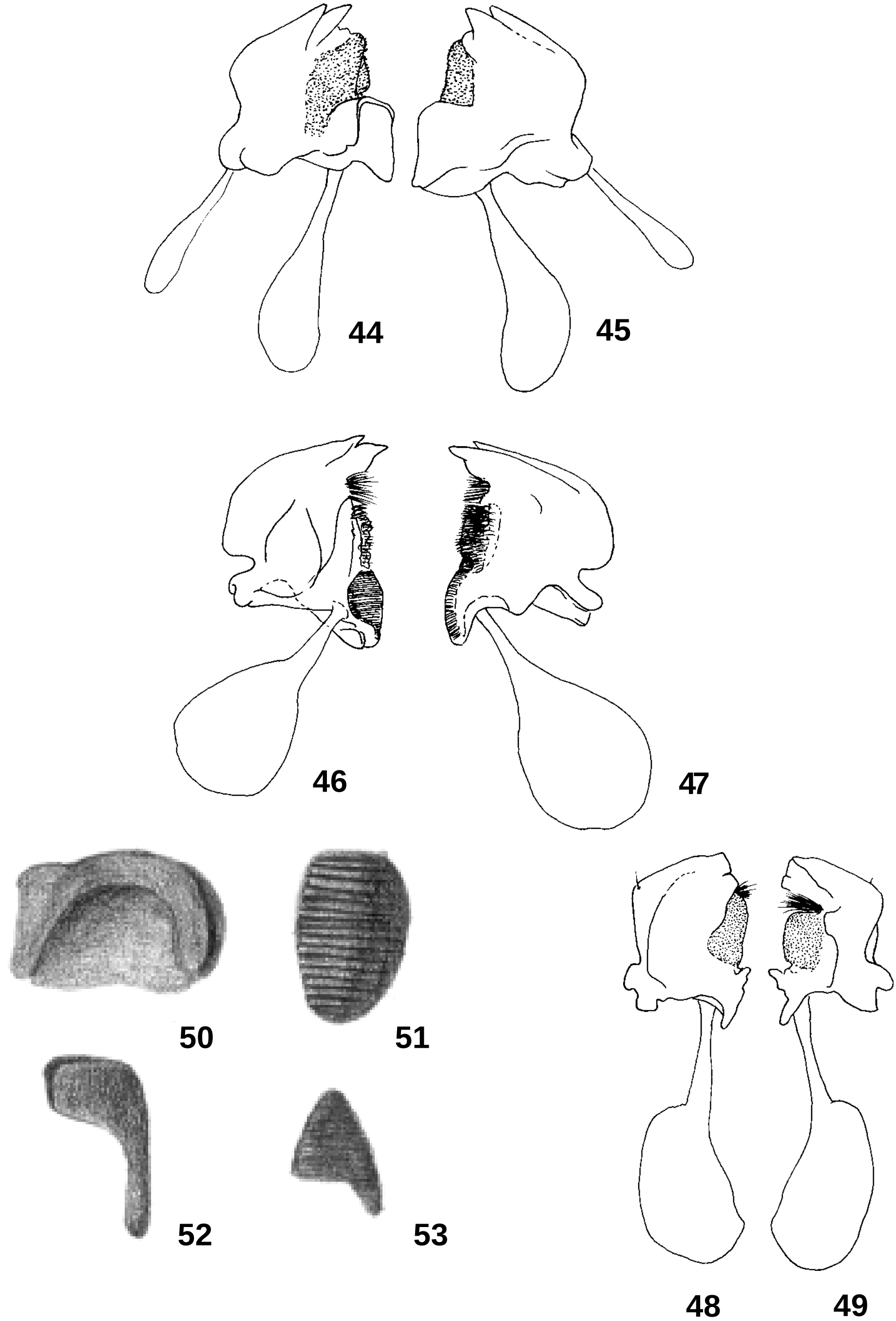
22-25. Outline of eye: 22 - *Dacne bipustulata*; 23 - *Erotylus giganteus*; 24 - *Episcapha quadrimacula*; 25 - *Coptengis scheppardi*. 26, 27. Facetting of eyes: 26 - *Erotylus giganteus*; 27 - *Ischyrus quadripunctatus*. 28. *Erotylus giganteus* - antenna. 29. *Erotylus giganteus* - antenal club. 30-31. Antenna: 30 - *Dacne bipustulata*; 31 - *Scaphodacne rectesignata*



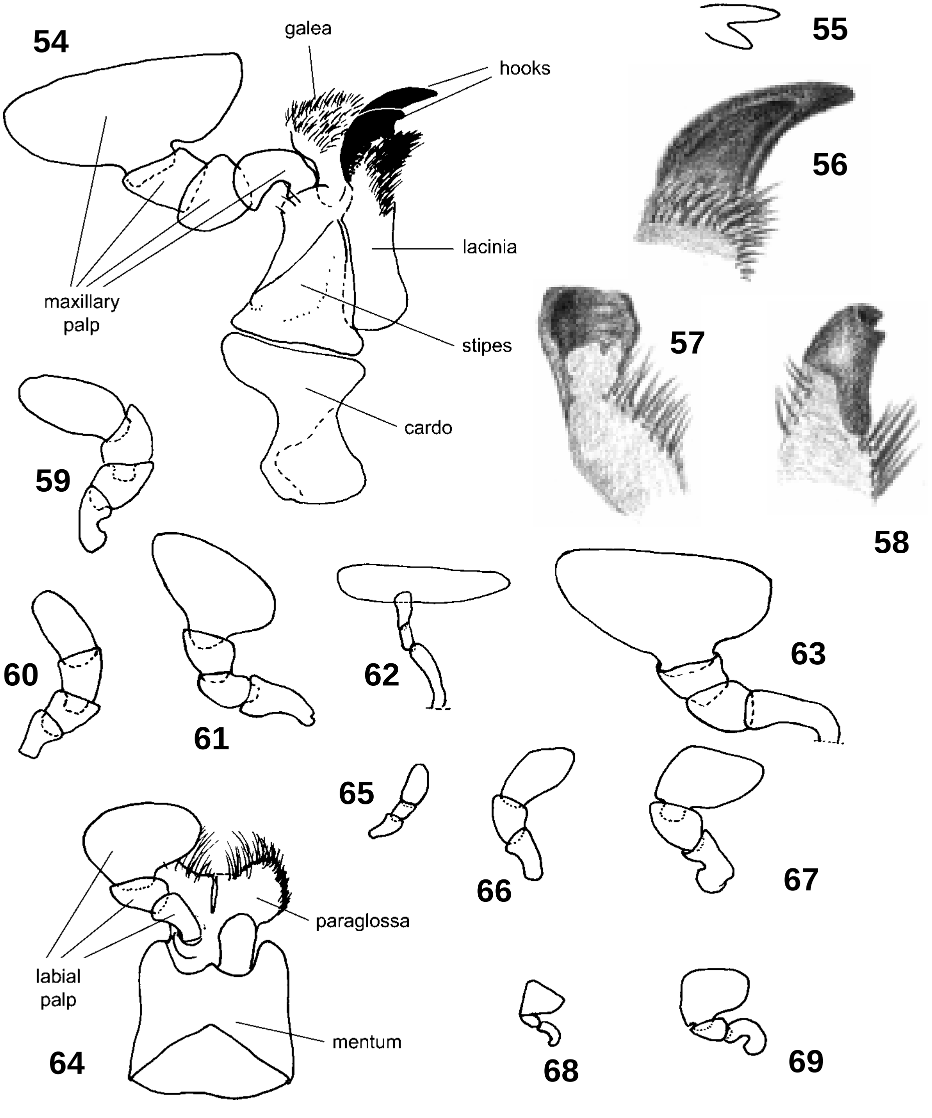
32-38. Antenna: 32 - *Coptengis scheppardi*; 33 - *Episcapha quadrimacula*; 34 - *Encaustes verticalis*; 35 - *Scaphidomorphus quinquepunctatus*; 36 - *Homoeotelus testaceus*; 37 - *Coccimorphus unicolor*; 38 - *Amblyscelis kelleni*



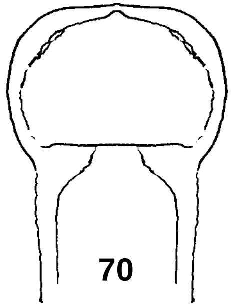
39-43. Mandibula. 39-41. *Erotylus giganteus* (39 - right mandibula, ventral view, 40 - right mandibula, dorsal view, 41 - fragment of left mandibula). 42, 43 - *Homoeotelus testaceus* (42 - ventral view, 43 - dorsal view)



44-53. Mandibula (44, 46, 48 - ventral view; 45, 47, 49 - dorsal view; 50-53 - mola): 44, 45 - *Coccimorphus unicolor*; 46, 47, 53 - *Episcapha quadrimacula*; 48, 49, 52 - *Scaphidomorphus quinquepunctatus*; 50 - *Erotylus giganteus*; 51 - *Combocerus glaber*



54-69. Mouth-parts. 54. *Erotylus giganteus* - maxilla. 55, 56 - *Erotylus giganteus* - hooks on lacinia (55 - dorsal view, 56 - lateral view). 57, 58. *Scaphidomorphus quinquepunctatus* - hooks on lacinia (57 - inner side, 58 - lateral view). 59-63. Maxillary palp: 59 - *Linodesmus coecus*; 60 - *Coptengis scheppardi*; 61 - *Megischyrus undatus*; 62 - *Triplacidea motschulskyi*; 63 - *Pselaphacus nigropunctatus*. 64 - *Erotylus giganteus* - labium (left labial palp absent). 65-69. Labial palp: 65 - *Dacne bipustulata*; 66 - *Coptengis scheppardi*; 67 - *Linodesmus coecus*; 68 - *Triplacidea motschulskyi*; 69 - *Megischyrus undatus*



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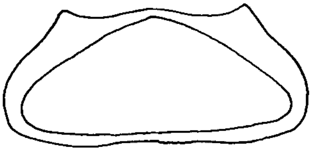

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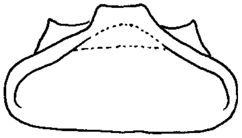

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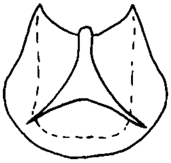

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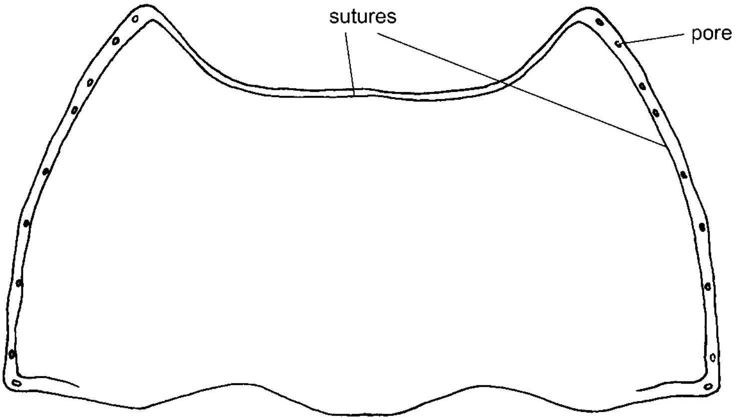

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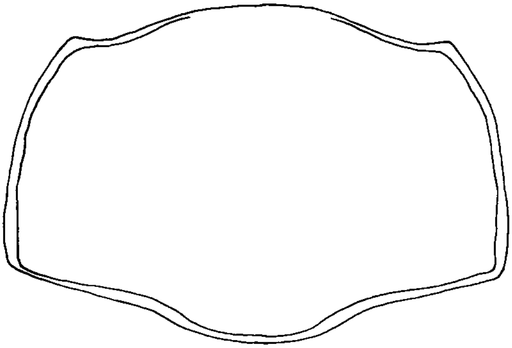
70. *Erotylus giganteus* - labrum. 71-73. Mentum: 71 - *Coptengis scheppardi*; 72 - *Episcapha quadrimacula*; 73 - *Tritoma bipustulata*. 74. *Erotylus giganteus* - pronotum



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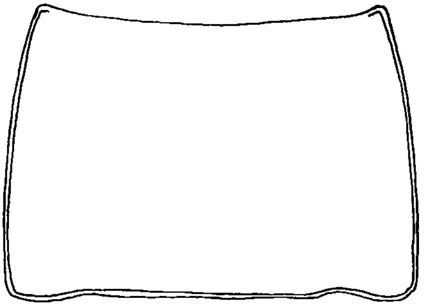

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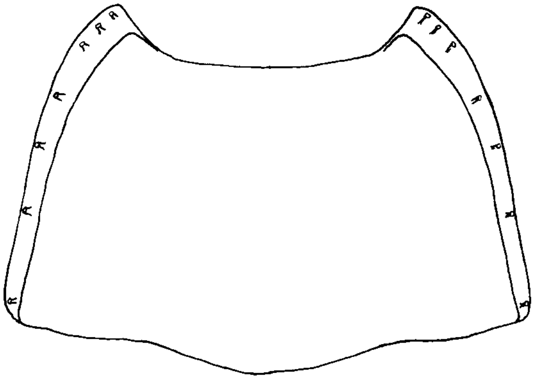

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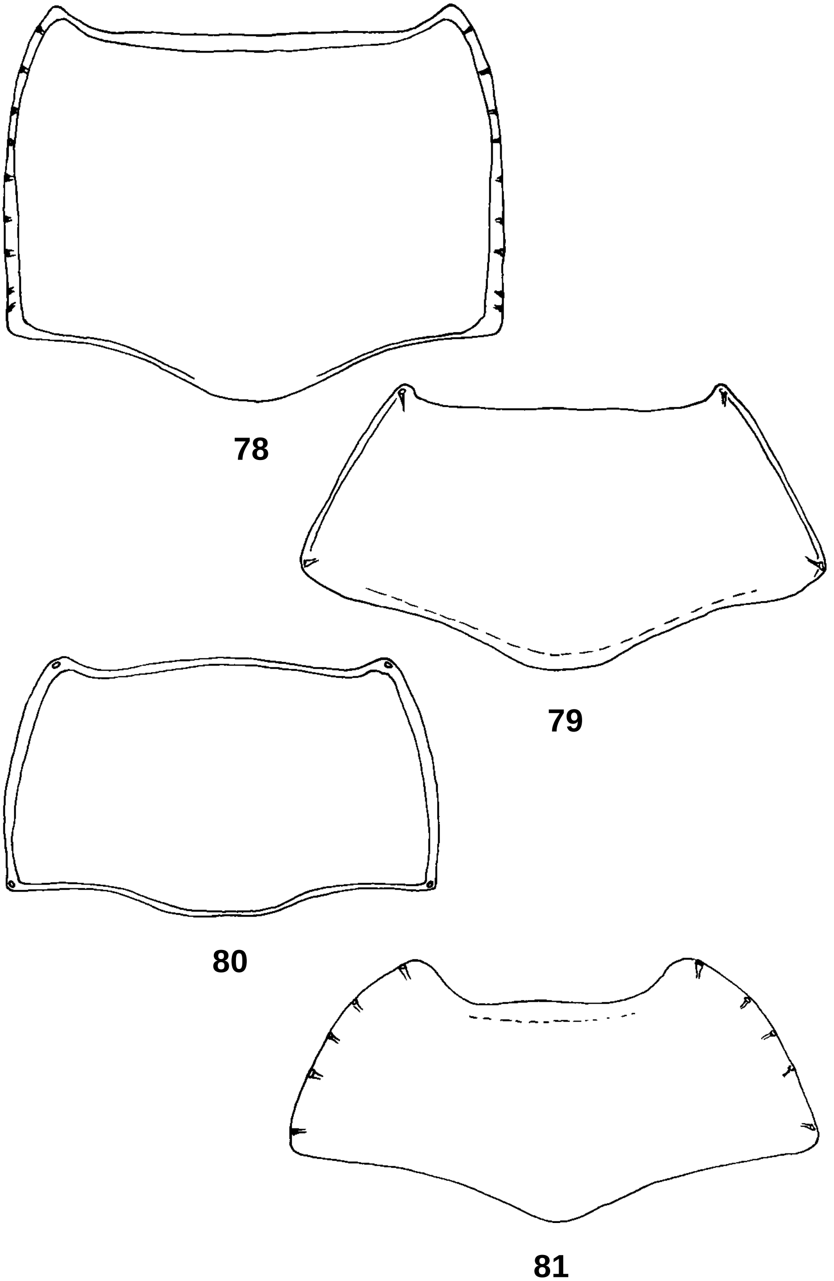
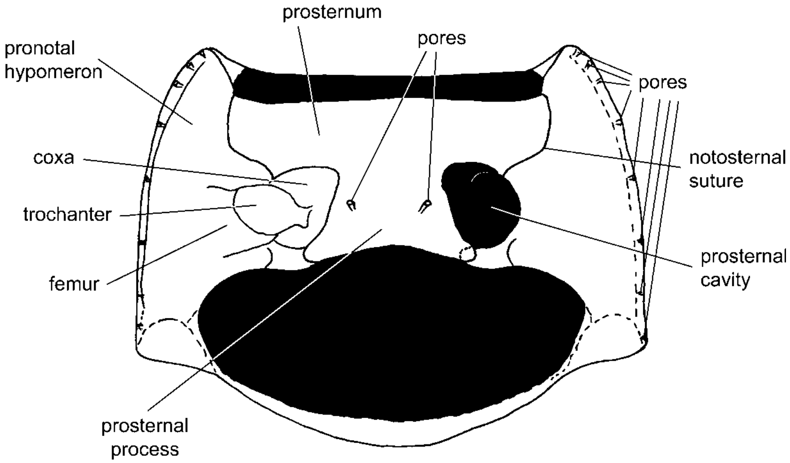
75-77. Pronotum: 75 - *Dacne bipustulata*; 76 - *Coptengis scheppardi*; 77 - *Scaphodacne rectesignata*



78-81. Pronotum: 78 - *Encaustes verticalis*; 79 - *Tritoma bipustulata*; 80 - *Triplax russica*; 81 - *Coccimorphus unicolor*



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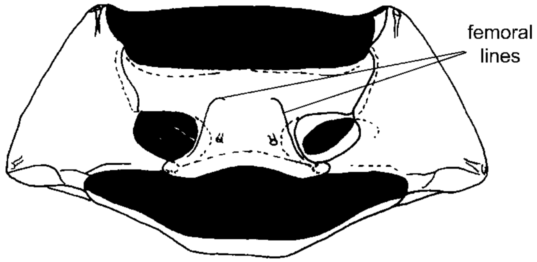

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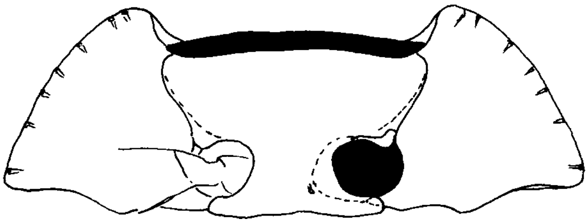

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82-84. Prosternum: 82 - *Encaustes verticalis*; 83 - *Tritoma bipustulata*; 84 - *Coccimorphus unicolor*

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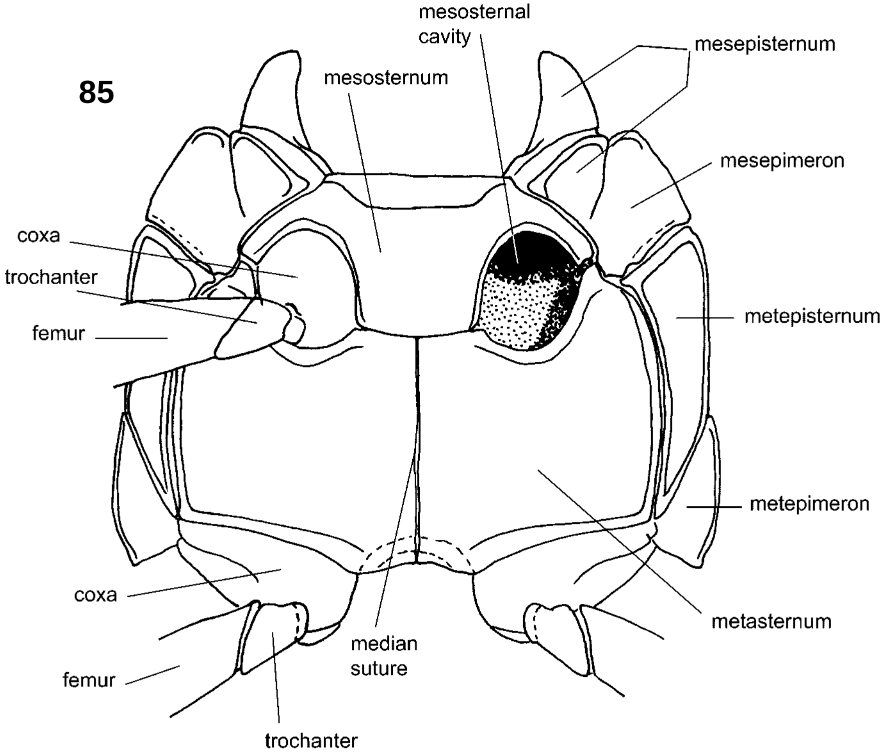

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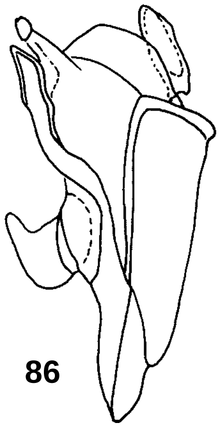

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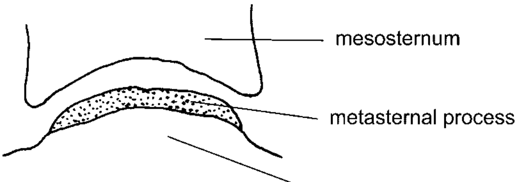

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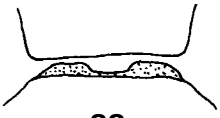

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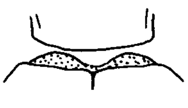
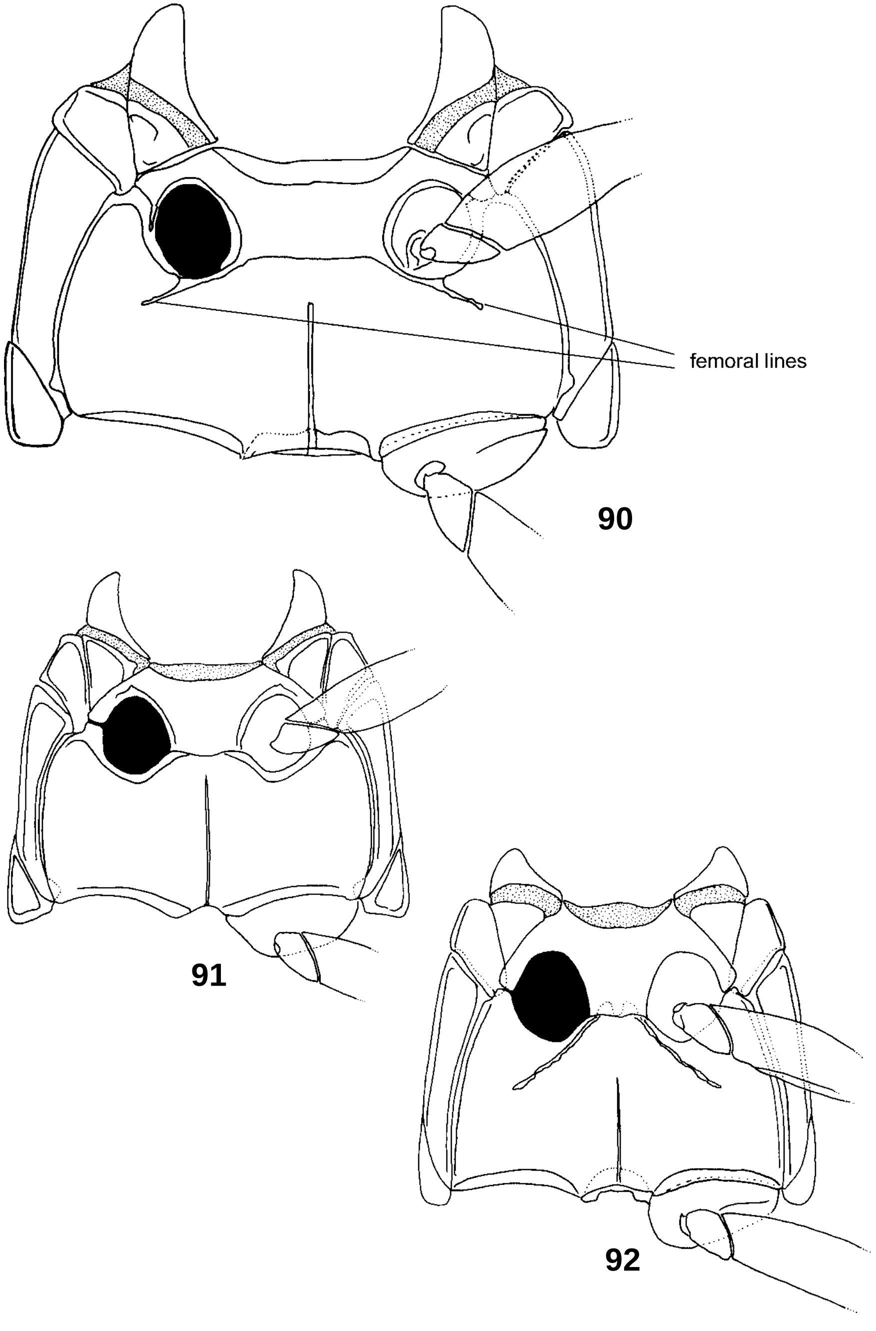
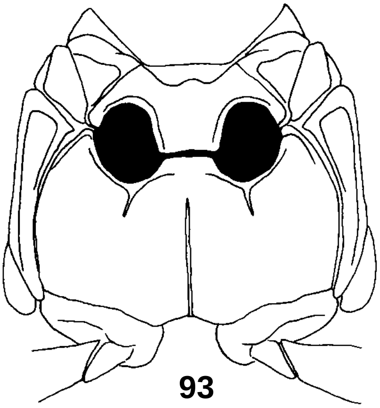


85. *Erotylus giganteus* - meso- and metasternum. 86. *Erotylus giganteus* - metepisternit, lateral view; 87-89. Meso-metasternal connection: 87 - *Encaustes verticalis*; 88 - *Episcapha quadrimacula*; 89 - *Erotylus giganteus*



90-92. Meso- and metasternum: 90 - *Tritoma bipustulata*; 91 - *Megischyrus undatus*; 92 - *Scaphodacne rectesignata*



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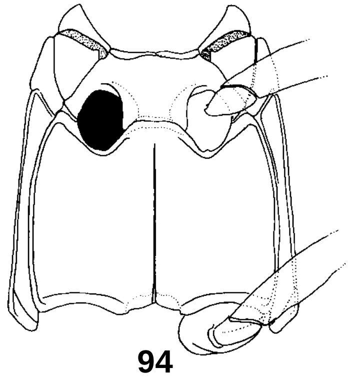

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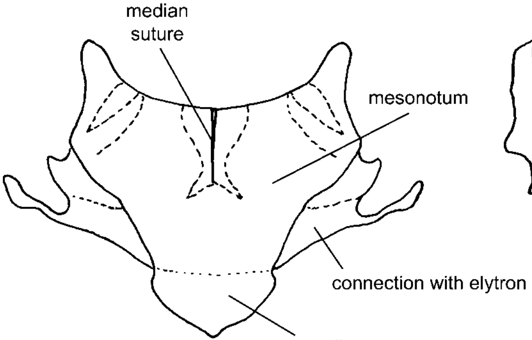

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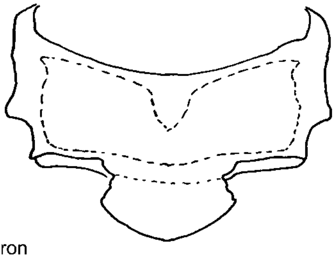

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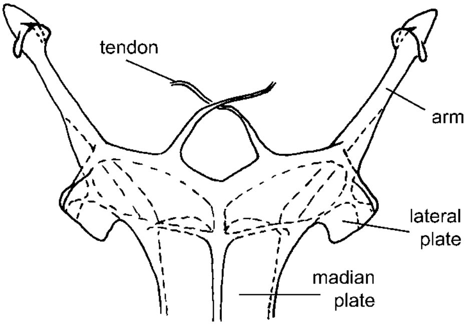

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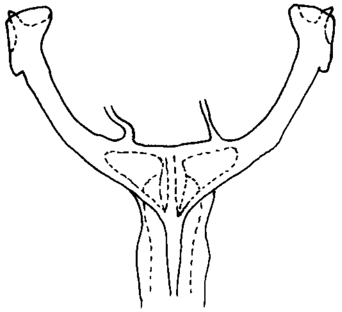

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93, 94. Meso- and metasternum: 93 - *Episcapha quadrimacula*; 94 - *Encaustes verticalis*. 95, 96. Mesonotum: 95 - *Erotylus giganteus*; 96 - *Coptengis scheppardi*. 97, 98. Metendosternit: 97 - *Episcapha quadrimacula*; 98 - *Homoeotelus testaceus*

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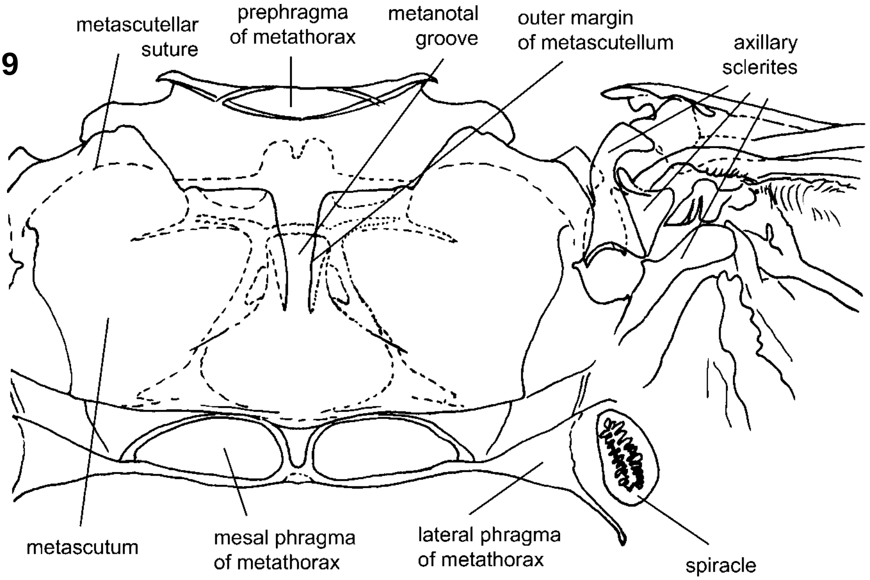

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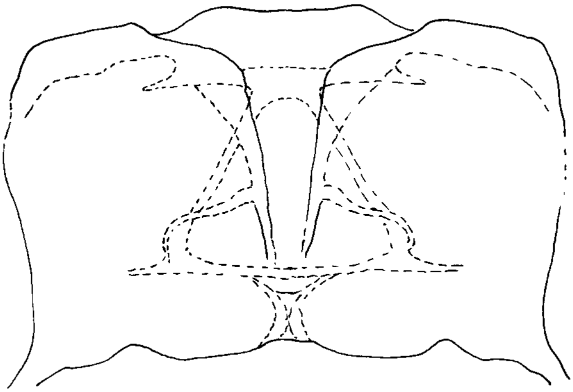

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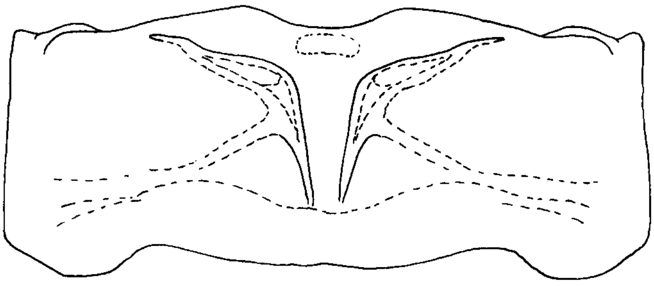

99. *Erotylus giganteus* - metanotum with basal part of wing. 100, 101. Metanotum: 100 - *Episcapha quadrimacula*; 101 - *Coptengis scheppardi*

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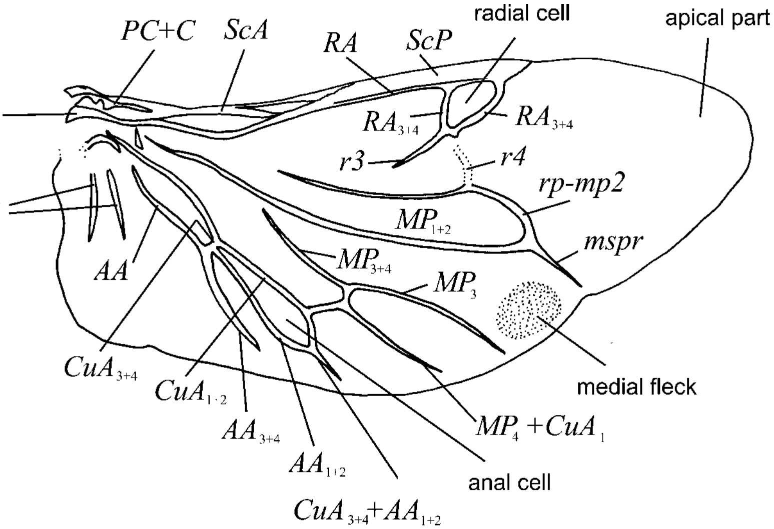

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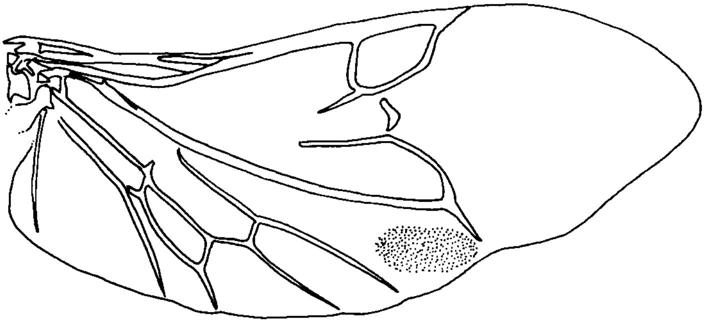

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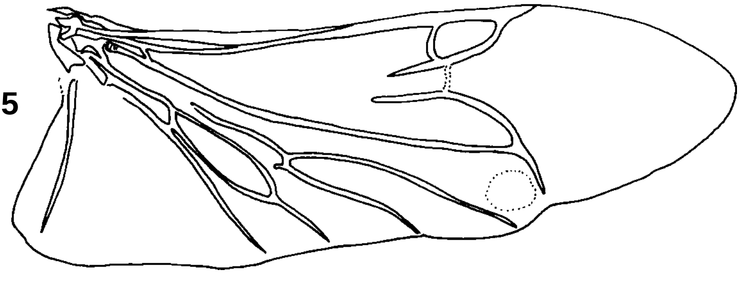
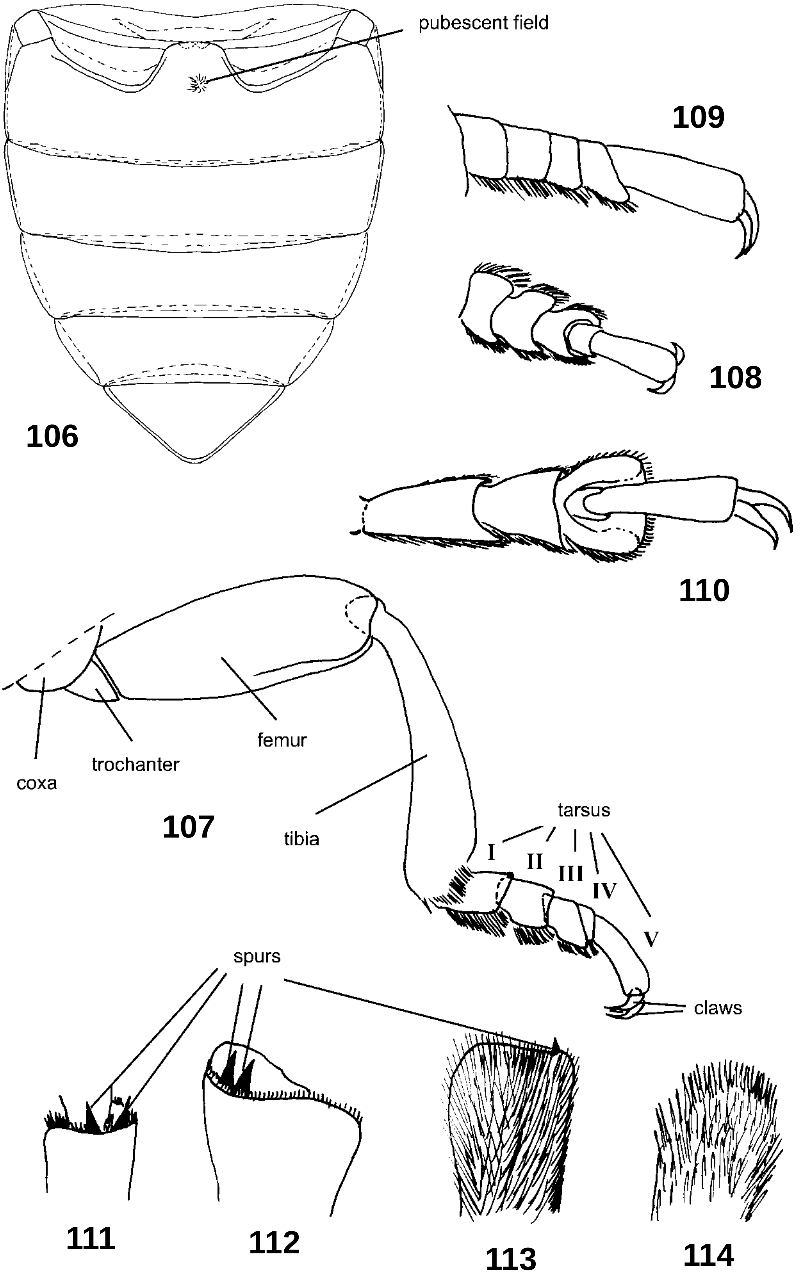
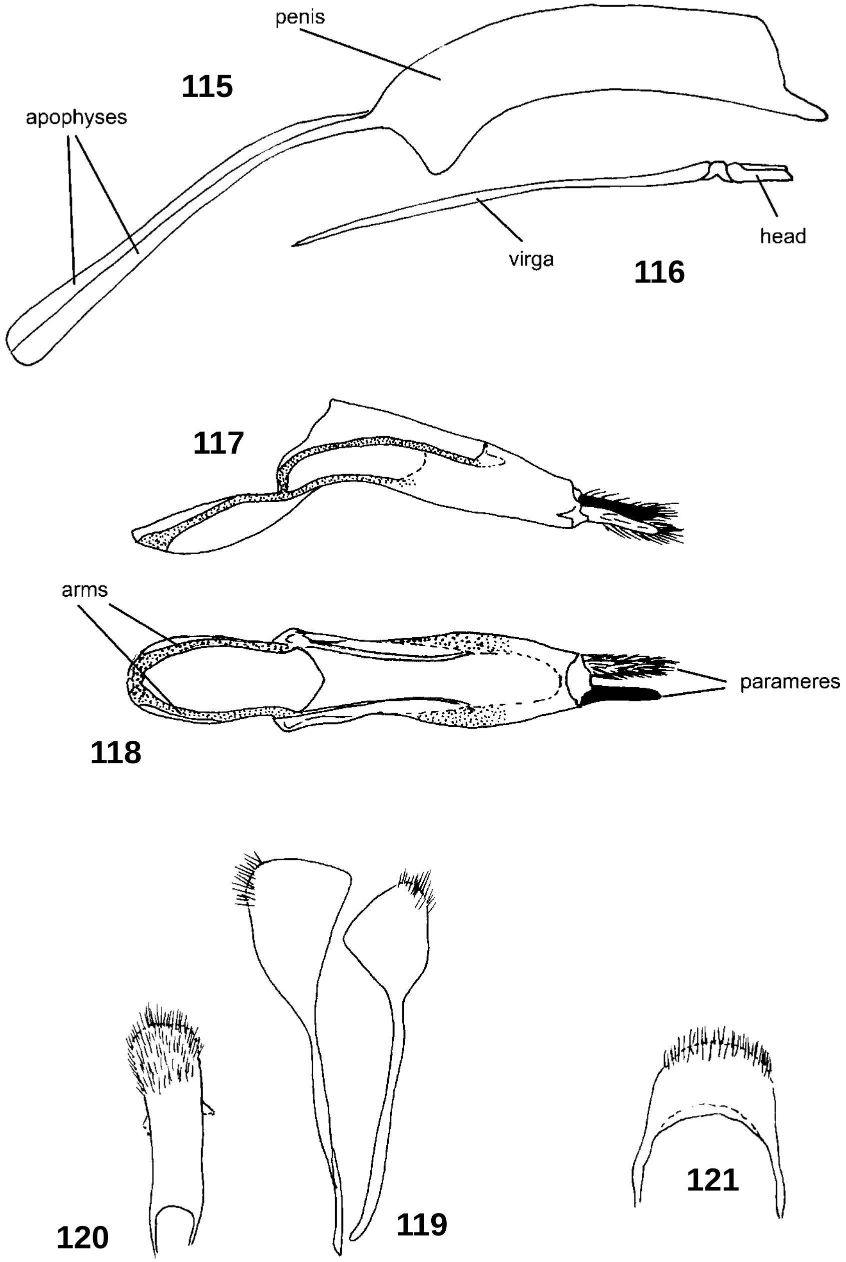


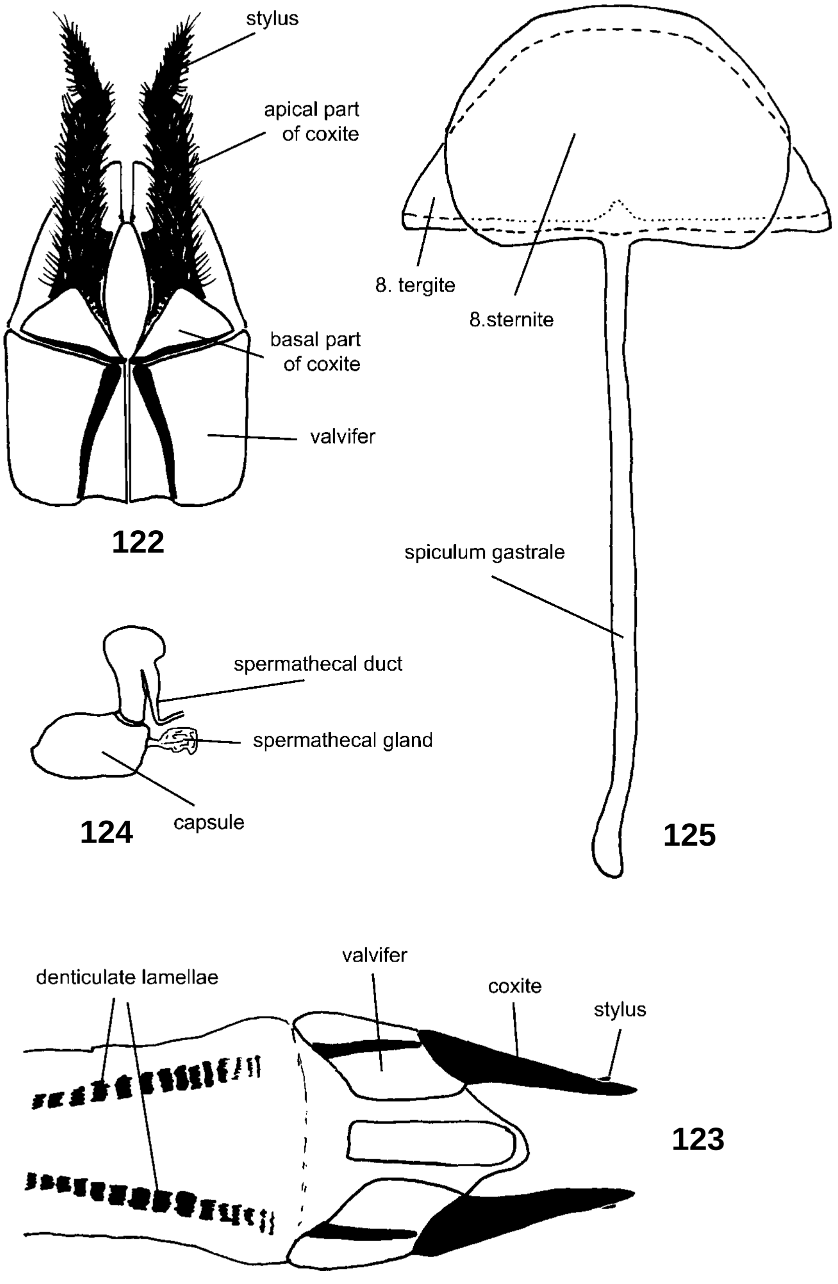
102-105. Wing: 102 - *Tritoma bipustulata*; 103 - *Aulacochilus quadrisignatus*; 104 - *Coptengis scheppardi*; 105 - *Encaustes verticalis*. Ax - axillary veins; AA, AA1+2, AA3+4 - anal veins; BSc - base of subcosta; CuA1, CuA1+2, CuA3+4 - cubitus anterior; MP3, MP4, MP3+4 - media posterior; PC+C - costa; RA, RA3+4 - radius anterior; rp-mp2 - connection radius posterior to media posterior; ScA - subcosta anterior; ScP - subcosta posterior



106. *Erotylus giganteus*, abdomen, male. 107. *Scaphodacne neglecta*, leg. 108-110. Tarsus: 108 - *Scaphodacne neglecta*; 109 - *Dacne bipustulata*; 110 - *Erotylus giganteus*. 111-114. Apex of tibia: 111 - *Erotylus giganteus*; 112 - *Pselaphacus nigropunctatus*; 113 - *Encaustes verticalis*; 114 - *Aulacochilus quadrisignatus*



115-121. *Erotylus giganteus*, male genitalia. 115 - penis; 116 - flagellum; 117-118 - tegmen (117 - lateral view, 118 - dorsal view); 119 - 9th abdominal tergite; 120 - 10th abdominal tergite; 9th abdominal sternite



122-125. Female genitalia. 122-123. Ovipositor: 122 - *Erotylus giganteus*; 123 - *Dacne bipustulata*. 124 - *Erotylus giganteus*, spermatheca. 125 - *Erotylus giganteus*, genital segments

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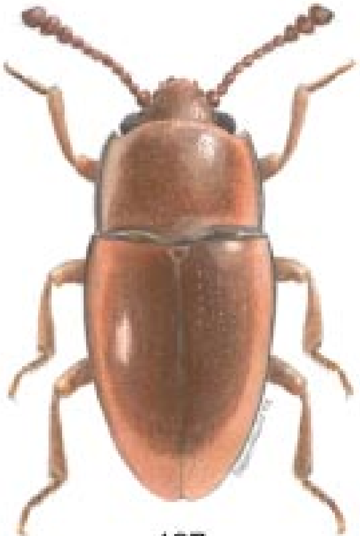

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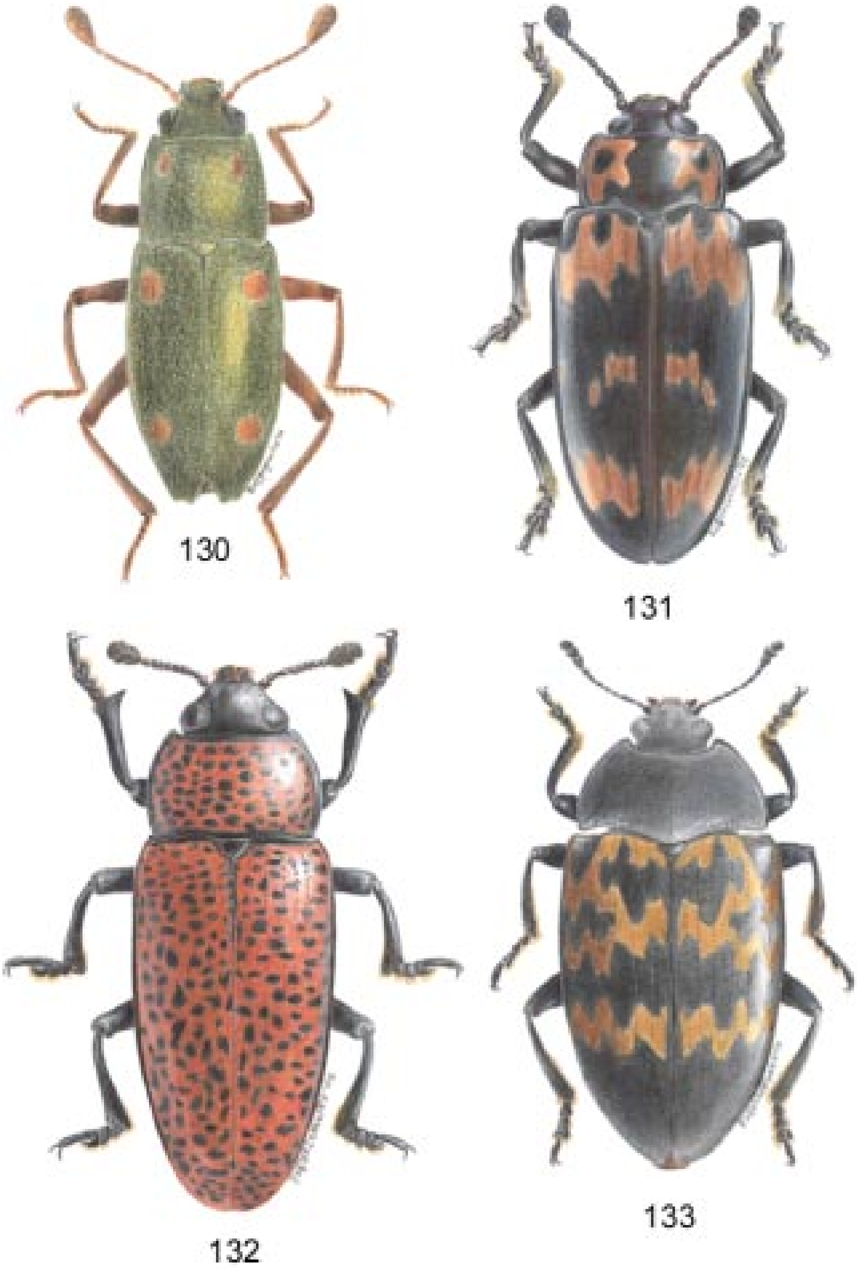
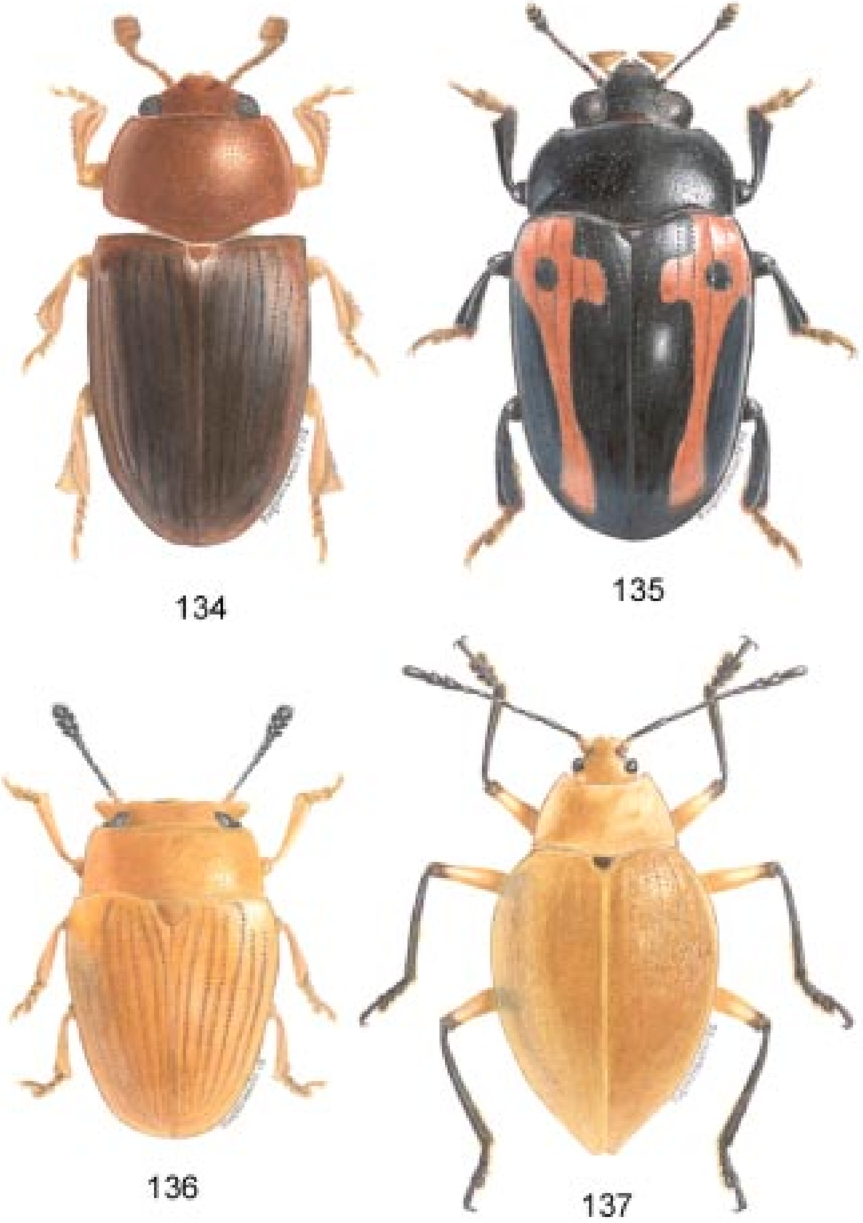
126-129. Adult. 126 - *Dacne bipustulata*; 127 - *Cryptodacne synthetica*; 128 - *Megalodacne fasciata*; 129 - *Episcapha quadrimacula*



130-133. Adult. 130 - *Coptengis scheppardi*; 131 - *Encaustes verticalis*; 132 - *Pselaphacus nigropunctatus*; 133 - *Megischyrus undatus*



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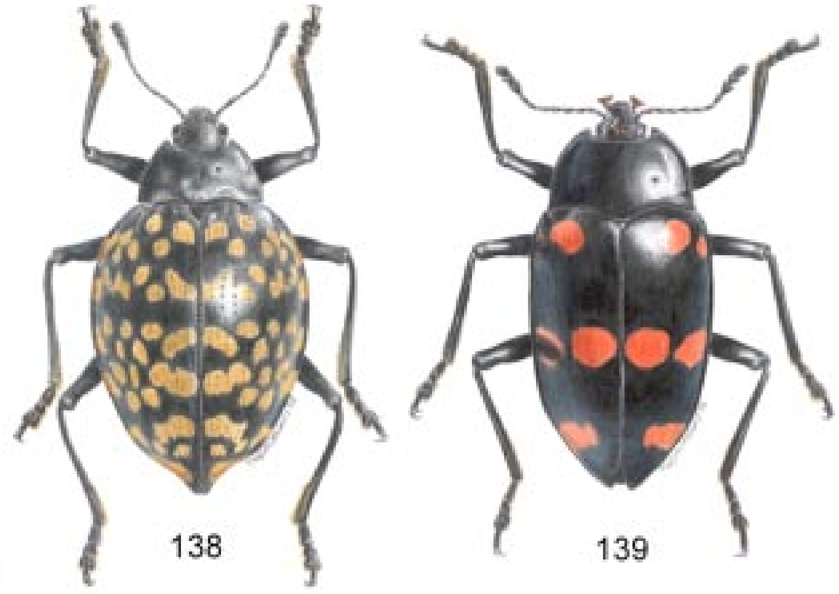
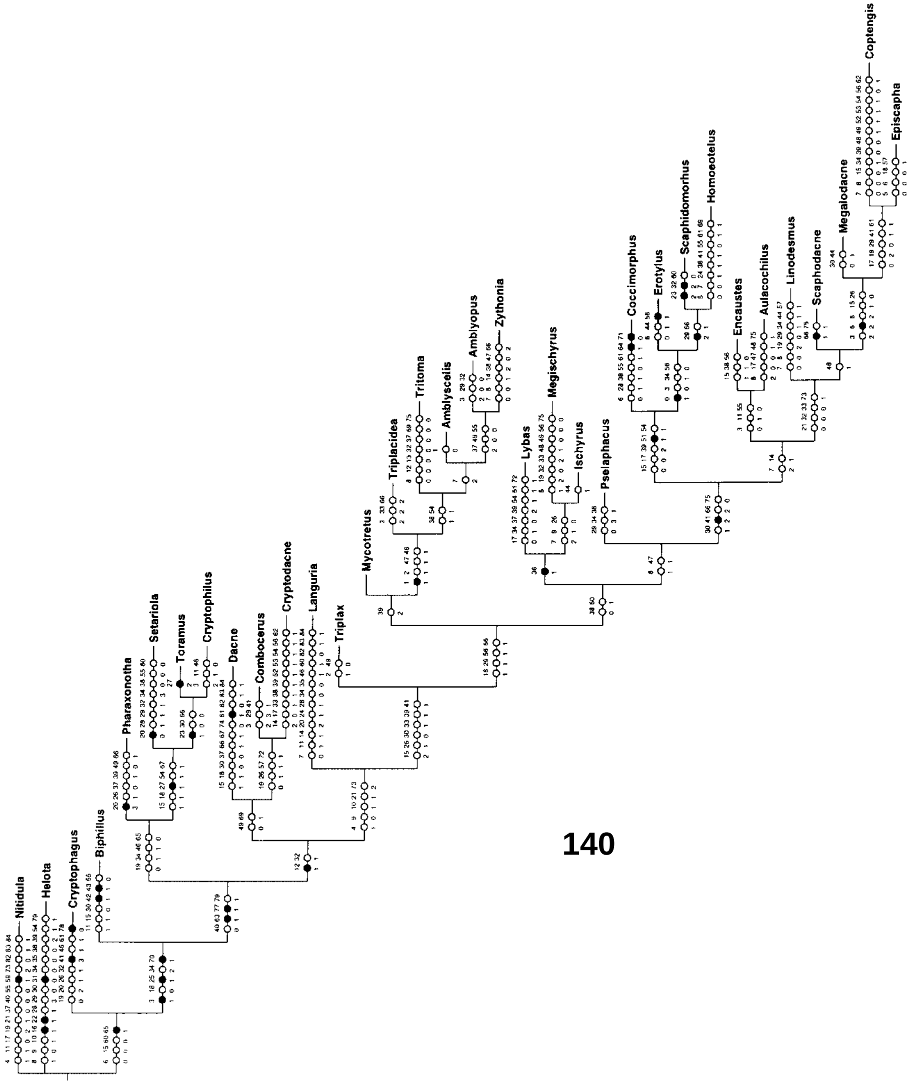
134-137. Adult. 134 - *Amblyscelis kelleni*; 135 - *Amblyopus vittatus*; 136 - *Zythonia fulva*; 137 - *Homoeotelus testaceus*



138-139. Adult. 138 - *Erotylus giganteus*; 139 - *Scaphidomorphus quinquepunctatus*



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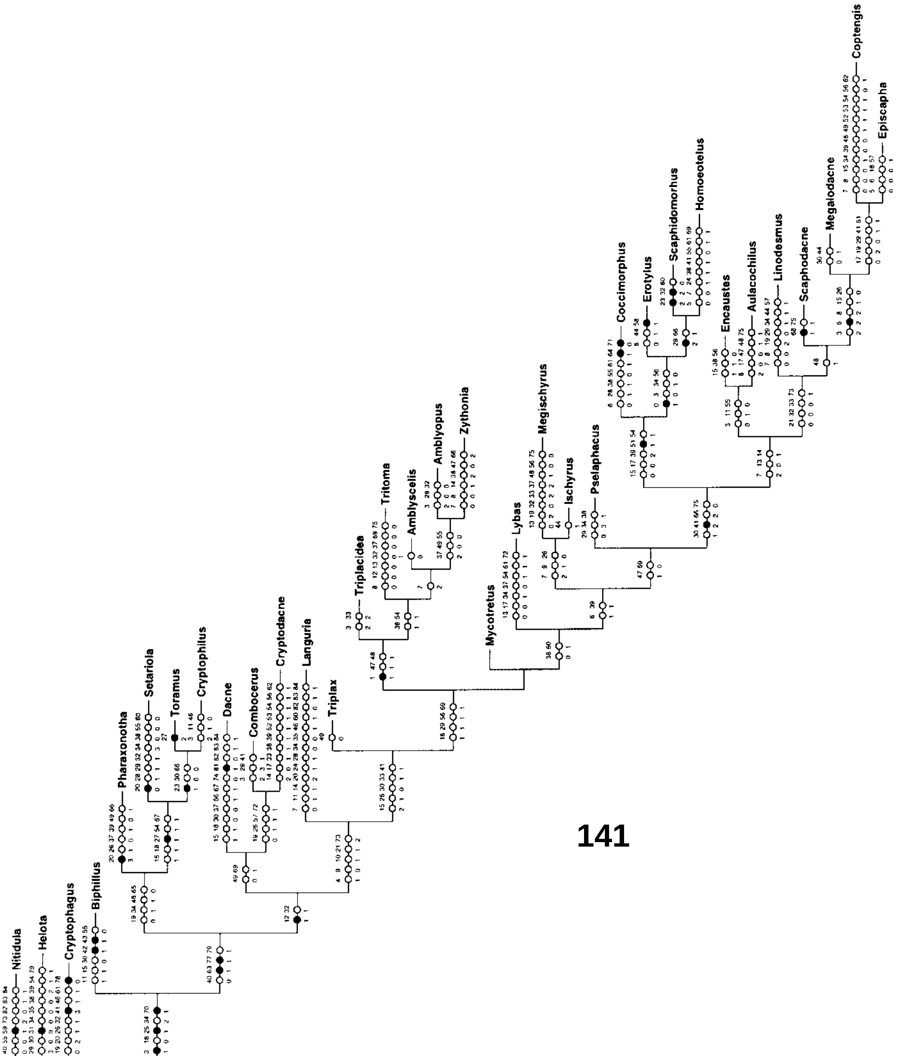
140. Cladogram "mhennig*" #1



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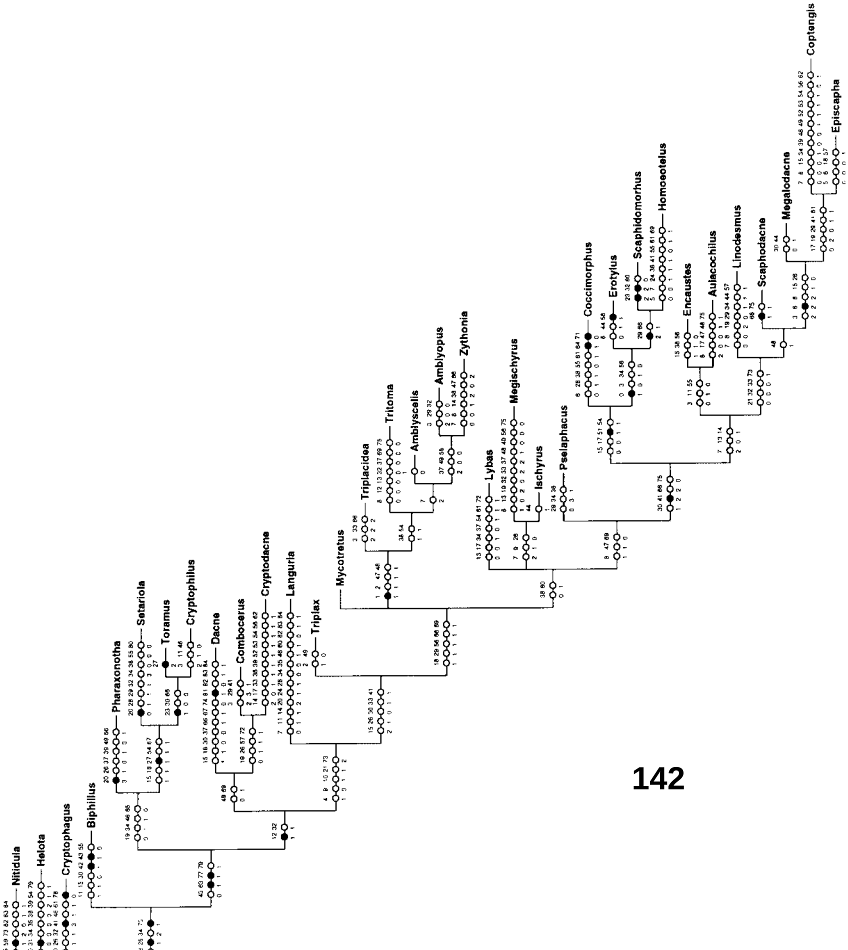
141. Cladogram "mhennig*" #2



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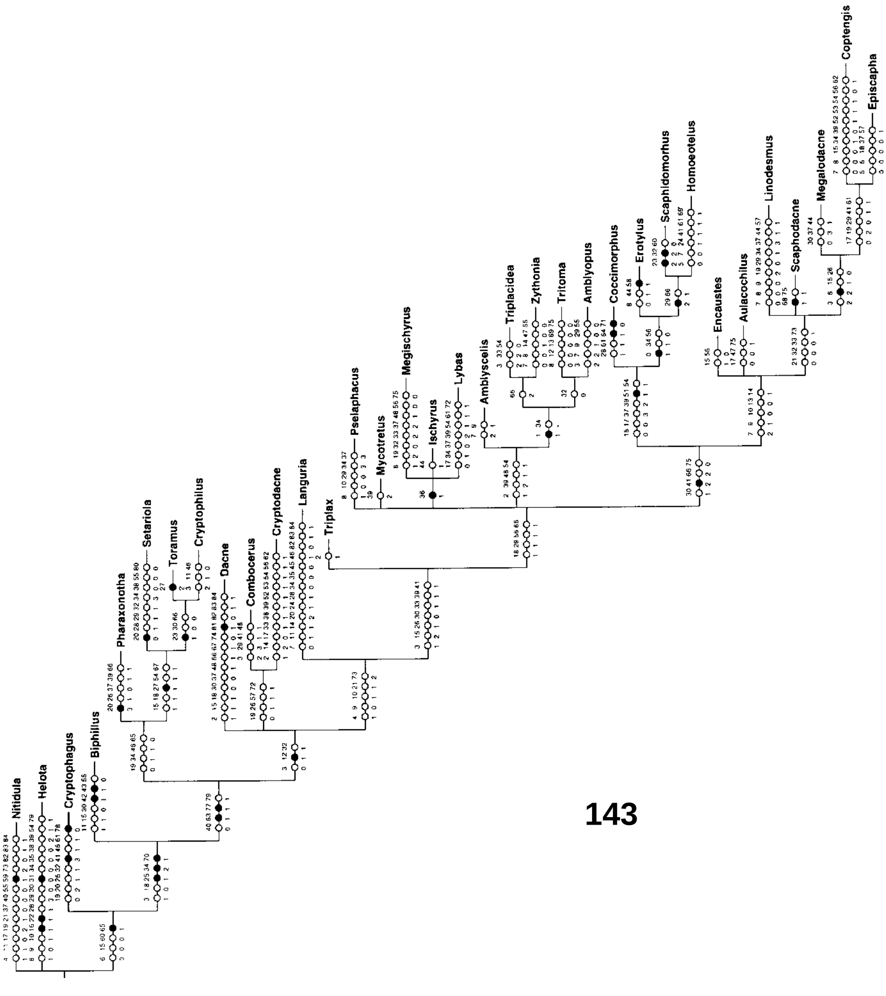
142. Maximum congruence (nelsen) cladograms of the "mhennig" algorithm



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143. Maximum congruence (nelsen) cladograms of successive weighing