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Additions to the system of neopterous insects (Neoptera)

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Дополнения к системе новокрылых насекомых (Neoptera)

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Abstract. The taxon Rhipineoptera Kluge, 2012 is divided into two subordinated taxa – Plecoptera Burmeister, 1839 and Tegminoptera, **taxon n.**; autapomorphies of the taxon Tegminoptera are described. The taxon Tegminoptera comprises Pandictyoptera Crampton, 1917, Dermatoptera Burmeister, 1838, Orchesopia Rafinesque, 1815 (= Saltatoria Latreille, 1817, **syn. n.**) and Spectra Latreille, 1802; Mantophasmatodea is a subordinated taxon within Spectra. Instead of the preoccupied name Pleuroptera Kluge, 2010, a new name Calyptroptera **nom. n.** is suggested for the taxon uniting boreids (Raphioptera MacLeay, 1821) and fleas (Aphaniptera Kirby et Spence, 1815, or Siphonaptera Latreille, 1825). Autapomorphies of Calyptroptera in pterothorax structure are described.

Key words. Insects, systematics, new taxa, Rhipineoptera, Tegminoptera, Pleuroptera, Calyptroptera, boreids, fleas.

Резюме. Таксон Rhipineoptera Kluge, 2012 делится на два подчиненных таксона – Plecoptera Burmeister, 1839 и Tegminoptera, **taxon n.**; описаны аутапоморфии таксона Tegminoptera. В состав Tegminoptera входят Pandictyoptera Crampton, 1917, Dermatoptera Burmeister, 1838, Orchesopia Rafinesque, 1815 (= Saltatoria Latreille, 1817, **syn. n.**) и Spectra Latreille, 1802; таксон Mantophasmatodea является подчиненным в составе Spectra. Для таксона, объединяющего бореид (Raphioptera MacLeay, 1821) и блох (Aphaniptera Kirby et Spence, 1815 или Siphonaptera Latreille, 1825) предложено новое название Calyptroptera **nom. n.** взамен преоккупированного Pleuroptera Kluge, 2010. Описаны аутапоморфии Calyptroptera в строении птероторакса.

Ключевые слова. Насекомые, систематика, новые таксоны, Rhipineoptera, Tegminoptera, Pleuroptera, Calyptroptera, бореиды, блохи.

Introduction

Thanks to cladoendesis, which is a constructive approach to phylogeny analysis, it became possible to determine status and give new diagnoses for high level insect taxa and to make certain changes in the general system of insects (Kluge, 2012a, 2012b). In the present paper, two additions to this system are given: 1) a new taxon Tegminoptera **taxon n.** is established within Rhipineoptera Kluge, 2012 (Pterygota: Metapterygota: Neoptera); 2) autapomorphies of the taxon Calyptroptera **nom. n.** belonging to Enteracantha Kluge, 2010 are described (Neoptera: Metabola: Panzygothoraca).

Results

1. Additions to the system of Rhipineoptera

In the previous paper (Kluge, 2012b) I suggested to reject the artificial taxon Polyneoptera Martynov, 1923 and to accept two independent taxa – Idioprothoraca Kluge, 2013 and Rhipineoptera Kluge, 2012. The taxon Idioprothoraca comprises web-spinners (Embioptera Lameere, 1900) and grylloblattids (Notoptera Crampton, 1915), while to Rhipineoptera belong all other insects formerly attributed to Polyneoptera. Among Rhipineoptera, stoneflies (Plecoptera Burmeister, 1839) occupy a separate position and can be opposed to all other Rhipineoptera, for which I suggest a new taxon Tegminoptera **taxon n.** Below, a new classification of neopterous insects is given. Here and below, the abbreviation «**nom. typ.**» means a typified name in basic format, i.e. the base for correct formation of typified hierarchical and rank-based names (Kluge, 2010).

1. Neoptera Martynov, 1923 (nom. typ.: Scarabaeus/fg)
1.1. Idioprothoraca Kluge, 2012 (nom. typ.: Embia/fg)
1.1.1. Embioptera Lameere, 1900 (nom. typ.: Embia/fg)
1.1.2. Notoptera Crampton, 1915 (nom. typ.: Grylloblatta/fg)
1.2. Rhipineoptera Kluge, 2012 (nom. typ.: Gryllus/f=Forficula/g)
1.2.1. Plecoptera Burmeister, 1839 (nom. typ.: Perla/fg)
1.2.2. Tegminoptera **taxon n.** (nom. typ.: Gryllus/f=Forficula/g)
1.2.2.1. Pandictyoptera Crampton, 1917 (nom. typ.: Blatta/fg)
1.2.2.2. Dermatoptera Burmeister, 1838 (nom. typ.: Forficula/fg)
1.2.2.3. Orchesopia Rafinesque, 1815, or Saltatoria Latreille, 1817 (nom. typ.: Gryllus/fg)
1.2.2.4. Spectra Latreille, 1802 (nom. typ.: Phasma/fg)
1.3. Eumetabola Hennig, 1953 (nom. typ.: Scarabaeus/fg)
1.3.1. Parametabola Crampton, 1838 (nom. typ.: Cimex/f=Cicada/g)
1.3.2. Metabola Burmeister, 1832 (nom. typ.: Scarabaeus/fg)

Assumed autapomorphies of Tegminoptera

1). Wings lack integral marginal vein. Fore margin of the wing can bear a costal vein; sometimes the costal vein continues on outer and partly on hind margin of the wing, but does not border the whole wing margin; the anal fan of hind wing [see 3)] is never bordered by a vein. In this respect Tegminoptera differ from Plecoptera, whose wings of the both pairs have the costal vein continued as a marginal vein, which borders the whole wing margin, including the anal fan of hind wing. Probably, loss of the marginal vein is an autapomorphy of Tegminoptera. Marginal vein is developed in palaeopterous insects (in all Odonata and majority of Ephemeroptera) and in many neopterous insects, but it is absent in many taxa independent one from another.

2). Fore wings have membrane more or less thickened and sclerotized, thus they represent tegmina and serve for protection of hind wings in a folded condition. In some representatives of Tegminoptera, the thickening of fore wings is poorly expressed or completely lost.

3). On hind wing, the anal fan (peculiar for Rhipineoptera as a whole) has the following structure: it includes many straight vannal veins, which diverge fan-like and basally movably connected one with another; between each two convex vannal veins, a concave intercalary vein or a fold is situated; no one fold crosses any vein. The anal fold (i.e. the fold which separates the non-overturned and the overturned parts of the hind wing) entirely passes in front of the vannal vein V_1 – either between Pcu and V_1, or along the convex vein Pcu, not crossing V_1. The vannal veins reach hind margin of the wing, which is not bordered by a marginal vein [see 1)]. Thus, the anal fan of Tegminoptera differs from the anal fan of Plecoptera, whose number of longitudinal veins and folds do not coincide, the anal fold crosses the vein V_1, and all vannal veins fall into a marginal vein. In some Tegminoptera, secondary reduction of the anal fan takes place: in primitive termites (Isoptera-Hemiclidoptera) and in some cockroaches the fan-like folds are lost; in majority of termites (Isoptera-Cryptoclidoptera) the anal fan is completely lost.

Status of the new name Tegminoptera

The suggestion to unite Pandictyoptera, Dermatoptera, Saltatoria and Spectra basing of the presence of tegmina and true anal fan had been expressed many times. However, the taxon whose circumscription fits Tegminoptera, never had been established.

The taxon Dermaptera De Geer, 1773 (= Ulonata Fabricius, 1775; = Hemiptera Retzius, 1783; = Deratoptera Clairville, 1798; = Orthopteria Rafinesque, 1815) in its composition was nearly identical to Tegminoptera, but in contrast to Tegminoptera did not include termites (De Geer, 1773; Fabricius, 1775; Retzius, 1783; Clairville, 1798; Rafinesque, 1815). This was caused by the fact, that termites (Isoptera Brulle, 1832) have lost the most characteristic features of Tegminoptera – tegminization of fore wings and anal fan of hind wings. Recently, we know apomorphies which prove close relationship between termites and cockroaches, that makes us to place termites into Pandictyoptera and include them into Tegminoptera.

The taxon Orthopteromorpha Hennig, 1969 in its composition is also close to Tegminoptera, but, in contrast to Tegminoptera, includes grylloblattids (Hennig, 1969, 1981). This is caused by the fact, that in all grylloblattids (Notoptera Crampton, 1915) wings are lost, so their initial structure is unknown. As the result of revealing synapomorphies of Notoptera and Embioptera, it became clear, that these two taxa can't be attributed to two different higher taxa (Kluge, 2012b).

According to the principles of circumscriptional nomenclature (Kluge, 2010), the taxon which includes termites, but does not include grylloblattids, web-spinners and stoneflies, should get a new name. Some zoologists are against such strict usage of the circumscriptional principle in nomenclature and prefer to use the oldest name, even if its original circumscription does not fully fit the taxon under consideration. If accept this position in this case, the taxon characterized here should be named "Dermaptera DeGeer, 1773", that evidently contradicts to the existent tradition.

Classification of Tegminoptera

The taxon Tegminoptera includes four subordinated taxa, each of which is clearly outlined at least in recent fauna, these are: 1) Pandictyoptera Crampton, 1917 (cockroaches, preying mantids and termites), 2) Dermatoptera Burmeister, 1838 (earwigs), 3) Orchesopia Rafinesque, 1815 (= Saltatoria Latreille, 1817, **syn. nov.**) (leaping orthopterans), 4) Spectra Latreille, 1802 (stick-insects). Phylogenetic relations of these fore groups remain to be unclear; no one of hypotheses suggested so far is based on unique apomorphies.

For the taxon known under the name Saltatoria Latreille, 1817, an older circumscriptional synonym is revealed – Orchesopia Rafinesque, 1815. Originally, the both names, Orchesopia and Saltatoria, have been given to a taxon in a family rank (Rafinesque, 1815; Latreille, 1817). An argument in favor of usage the name Saltatoria is the fact, that this name is regularly used (as well as the evidently wrong name "Orthoptera"), while the name Orchesopia had been forgotten. An argument in favor of restoring the senior name Orchesopia is the fact, that the name Saltatoria is preoccupied, as the same name Saltatoria Retzius, 1783 had been earlier given for fleas (Kluge, 2010).

Last decades a taxon Mantophasmatodea has been established (Klass et al., 2002), which is either regarded to be a separate order, or is united with Notoptera. Uniting of Mantophasmatodea and Notoptera is evidently wrong (Kluge, 2012b). Judging by everything, Mantophasmatodea represents an aberrant group of stick-insects – Spectra Latreille, 1802. A unique autapomorphy of Spectra, which is present in all its representatives including Mantophasmatodea, is that male genital apparatus contains a peculiar formation – vomer. Vomer represents a movable sclerotized ventral process on the anterior part of tenth (the last) abdominal segment. Vomer has a narrow, usually asymmetric apex and a wide base by which it is movably attached to the abdomen in such a way that has one degree of freedom: it is able to turn out, rotating ventrally, and to press itself to the ventral side of tenth abdomere, rotating caudally. At copulation, vomer of the male serves for fixation of subgenital plate of the female, which is formed by VII abdominal sternum. The authors who deny relationship of mantophasmatids with true stick-insects, name vomer of mantophasmatids "vomeroid" and explain its difference from vomer as the following: "while in *Mantophasma* the morphologically posterior rim of the sclerite articulates with tergum X, in phasmids this is true for the anterior rim of the vomer sclerite" (Klass et al., 2002). Actually, vomer is not a sclerite, but a sclerotized process, whose sclerotized part of surface can be either connected or not connected with

tergum. Besides other recent and extinct species, to the order Mantophasmatodea was attributed *Ensiferophasma velociraptor* Zompro, 2005 from Baltic amber. Judging by the photo (Zompro, 2005, Fig. 4), this is a young larva belonging to an extinct taxon Oedischioidea within Orchesopia, or Saltatoria.

2. The taxon uniting boreids and fleas

In the previous paper (Kluge, 2010) I have suggested to unite the paraphyletic taxon Mecaptera Packard, 1886 (or Mecoptera Hyatt et Arms, 1890) and fleas (Aphaniptera Kirby et Spence, 1815, or Siphonaptera Latreille, 1825) to a holophyletic taxon Enteracantha Kluge, 2010, which is divided into holophyletic taxa Scorpiomusci Kluge, 2004, Metamecoptera Crampton, 1930, Nannomecoptera Hinton, 1981, and Pleuroptera Kluge, 2010; the last one unites fleas and boreids (Raphioptera MacLeay, 1821, or Neomecoptera Crampton, 1930).

The name Pleuroptera seems to be unsuccessful, because the identical name, formed as plural from the generic name *Pleuropterus* Burnett, 1829 (junior synonym of *Cynocephalus* Boddaert, 1768) sometimes is used for colugos (Porter, 1913). Because of this, for the taxon uniting boreids and fleas, I suggest a new name Calyptroptera **nom. n.** (from Greek words καλυπτρα – hood, and πτερον – wing); this name is connected with the fact that base of wing vestige has a form of hood, putted on the pleural column.

Besides this, the name Scorpiomusci Kluge, 2004 should be changed to a grammatically more justified Scorpiomuscae **nom. n.** The corrected classification is the following.

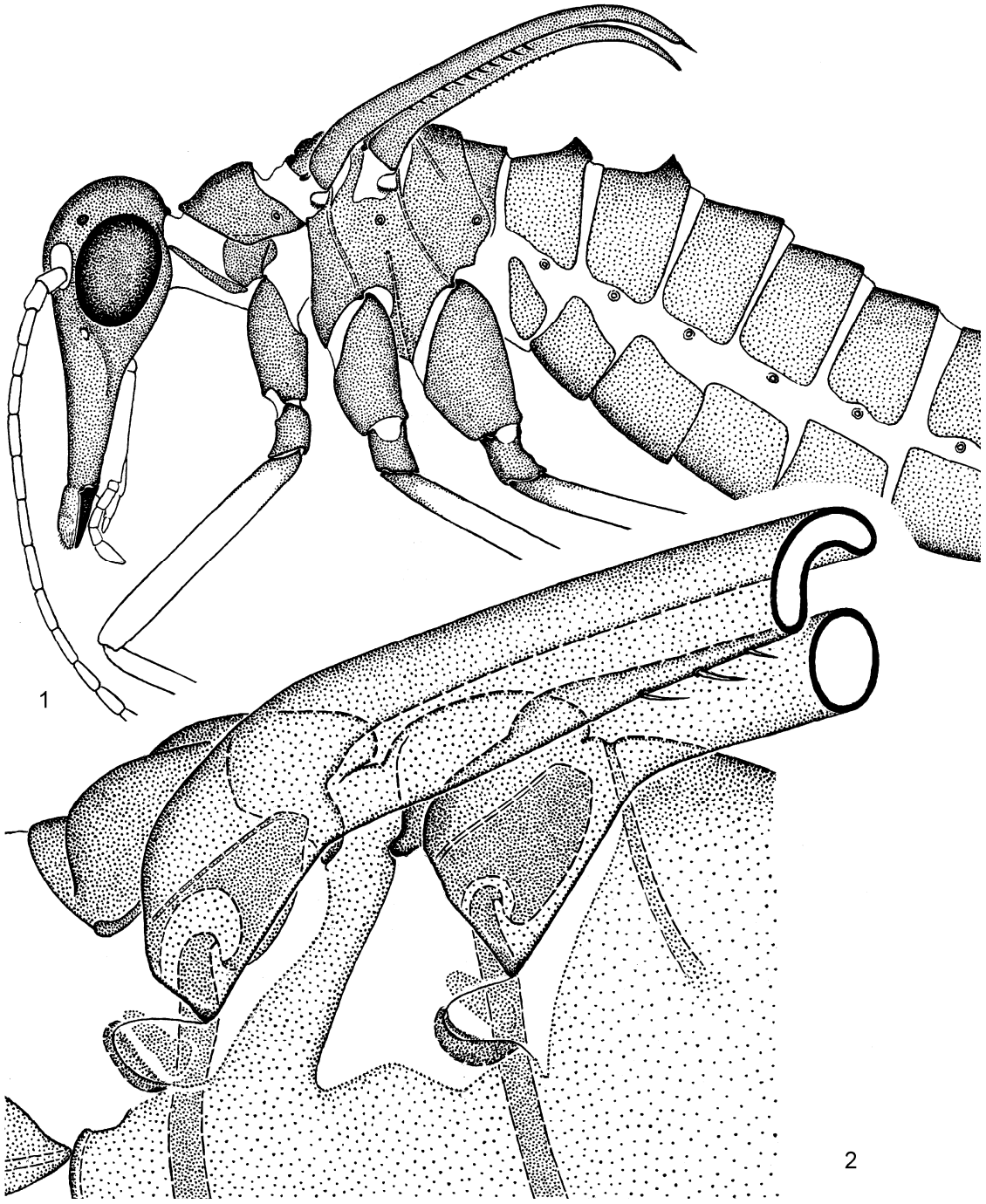
1. Metabola Burmeister, 1832 (nom. typ.: Scarabaeus/fg)
1.1. Elytrophora Packard, 1883 (nom. typ.: Scarabaeus/fg)
1.2. Neuropteroidea Handlirsch, 1903 (nom. typ.: Myrmeleon/f=Hemerobius/g)
1.3. Panzygothoraca Kluge, 2004 (nom. typ.: Papilio/fg)
1.3.1. Hymenoptera Linnaeus, 1758 (nom. typ.: Vespa/f=Cynips/g)
1.3.2. Amphiesmenoptera Kiriakoff, 1948 (nom. typ.: Papilio/fg)
1.3.3. Diptera Linnaeus, 1758 (nom. typ.: Musca/f=Oestrus/g)
1.3.4. Enteracantha Kluge, 2010 (nom. typ.: Panorpa/fg)
1.3.4.1. Scorpiomuscae **nom. n.** (= Scorpiomusci Kluge, 2004) (nom. typ.: Panorpa/fg)
1.3.4.2. Metamecoptera Crampton, 1930 (nom. typ.: Bittacus/fg)
1.3.4.3. Nannomecoptera Hinton, 1981 (nom. typ.: Nannochorista/fg)
1.3.4.4. Calyptroptera **nom. n.** (= Pleuroptera Kluge, 2010) (nom. typ.: Pulex/fg)
1.3.4.4.1. Raphioptera MacLeay, 1821 (nom. typ.: Boreus/fg)
1.3.4.4.2. Aphaniptera Kirby et Spence, 1815 (nom. typ.: Pulex/fg)

The idea about relationship of boreids and fleas have been expressed in many publications (e.g., Bilinski et al., 1998; Grimaldi, Engel, 2005; Zrzavy, 2008). However, among synapomorphies of boreids and fleas, mentioned in literature, the most part is either found in some other insects, or is referred to such details of structure, which in other insects are poorly investigated. Boreids and fleas have unique synapomorphies in the thorax structure, but till recently these characters had not been correctly described; their description is given below.

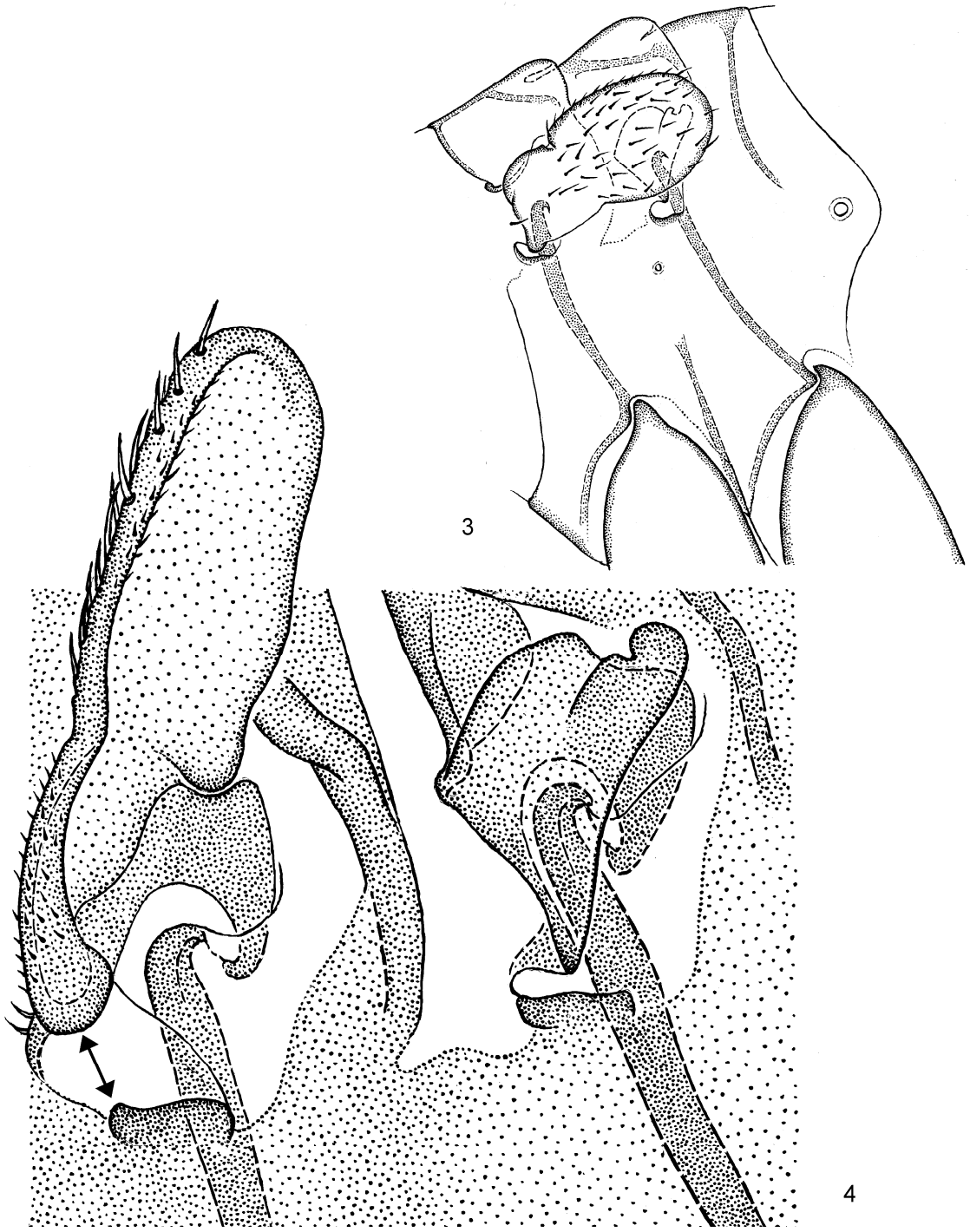
Autapomorphies of Calyptroptera in thorax structure

1). Wings have lost ability to flight, strongly diminished, sclerotized, permanently directed backward; wing base has a peculiar structure, supplied with immovable articulatory sclerite and, as a hood, covers the pleural column, whose apex is bent inward (Figs 1–8). Anteriad of the pleural column, the wing base is fused with lateral body wall, so that line of wing attachment is not straight, but L-shaped or C-shaped, rounding the pleural column anteriorly. Thanks to such attachment, the wing being immovably directed posteriorly covers the pleural column laterally. Apex of the pleural column is bent inward the body and ventrally; there, by means of a membrane, it is connected with an articulatory sclerite, which, in its turn, is immovably connected with wing base. Judging by the fact that the articulatory sclerite is articulated with the pleural column, it correspond to the second axillary sclerite. Unlike the second axillary sclerite of flying insects, the articulatory sclerite of Calyptroptera has no dorsal surface: one of its sides (anatomically external) is faced laterally, being partly hidden behind the pleural column and completely hidden behind the wing lamella; another its side (anatomically internal) is faced medially, into the body

cavity. Thus, in Calyptroptera wing base overlaps the pleural column from three sides: anteriorly – by its fusion with body wall; from inside (medially) – by the articulatory sclerite; from outside (laterally) – by the wing lamella. The parts of wing (wing lamella and articulatory sclerite) are fused together immovably, but they are not fused with pleural column, retaining a movable connection with it by means of membrane.



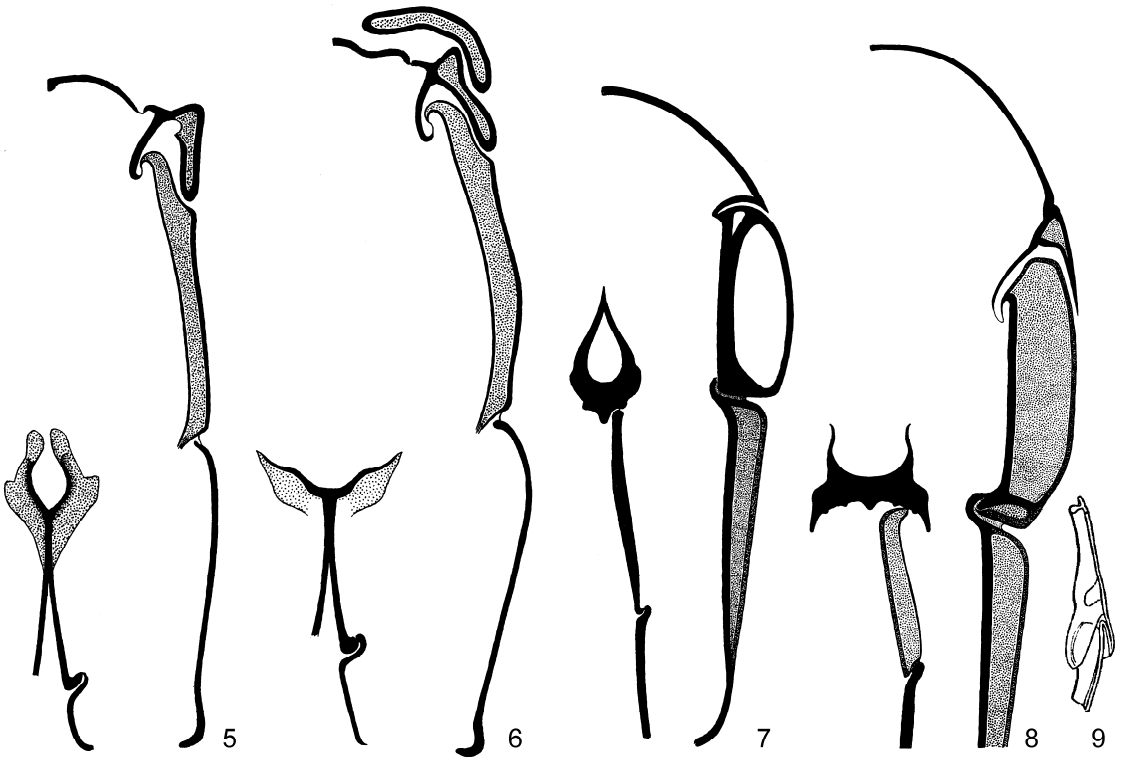
Figs 1, 2. *Boreus westwoodi* Hagen 1866 (Raphioptera), male, lateral view. 1 – anterior part of the body (setae not shown); 2 – bases of wing vestiges (hidden parts shown by interrupted lines).



Figs 3, 4. *Boreus westwoodi* Hagen 1866 (Raphioptera), pterothorax of female, lateral view. 3 – pterothorax in natural position; 4 – fore wing bent outward; two-pointed arrow shows place of attachment of its anterior-ventral margin with pleuron.

The proximal parts of wings have the same structure in all Calyptroptera, while distal parts of wings differ in boreids (Raphioptera) and fleas (Aphaniptera). In male boreids, distal part of wing is long, arched, spine-like, immovably arising from the proximal part of wing (Figs 1, 2 and 5, 6). In females of most boreids, fore wing has a small articulated distal lobe, pressed upon lateral side of the body and usu-

ally covering hind wing (Figs 3, 4). In fleas, distal parts of wings are absent, and their proximal parts are immovably fused with notum (Figs 7, 8); hind wing has proximal part well expressed and retaining membranous connection with pleural column (Fig. 8); fore wing is reduced and immovably fused not only with notum, but with pleuron as well (Fig. 7).



Figs 5–9. Transverse sections of thoracic segments at level of pleural column and furca: 5, 6 – *Boreus westwoodi* Hagen, 1866 (Raphioptera), male: 5 – mesothorax; 6– metathorax. 7, 8 – *Hystrichopsylla talpae* (Curtis, 1826) (Aphaniptera): 7 – mesothorax; 8 – metathorax. 9 – wrong figure from Snodgrass (1946: Pl.9: J), showing transverse section of connection of pleural and notal sutures in *Pulex irritans* Linnaeus, 1758.

Reduction of wings occurs in many other insects, particularly in some other Enteracantha (*Anomalobittacus* Kimmins, 1928, *Apterobittacus* McLachlan, 1893, *Apteropanorpa* Carpenter, 1940, female of *Panorpodes* McLachlan, 1875 and *Brachypanorpa* Carpenter, 1931). The unique autapomorphy of Calyptroptera, not found in other insects, is the presence of an immovable articulatory sclerite and the apical curvation of pleural column.

Snodgrass showing transverse section of the tergum/pleural connection in flea metathorax made an error: in his drawing (Snodgrass, 1946: Pl. 9: J) the wing vestige ("notal flange") is figured as connected directly with apex of pleuron, while the plate mediad of the pleuron is figured as a tergal apodeme, i.e. invagination of cuticle into the body cavity (Fig. 9). This error is repeated by other authors, who regard that in fleas and boreids, the plate mediad of the pleuron is a tergal apodeme. Actually, this is not an internal apodeme, but a portion of integument separating internal and external mediums. In contrast to other insects, in Calyptroptera ventral wall of the wing is not connected with apex of pleural column, but is freely putted on it as a hood.

2). In mesothorax, furcal arms are converging by their apices (Fig. 5); in all Aphaniptera their apices are fused (Fig. 7) (Snodgrass, 1946). In other thoracic segments furcal arms have usual shape, with apices diverging (Figs 6, 8).

3). Spiracles of the first abdominal segment are shifted anteriad and opened on epimera of metathorax (Fig. 1; Snodgrass, 1946: Pl. 8: K, M, N, O).

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