

Larval leg structure of *Nannochorista* Tillyard, 1917 and characteristics of Mecoptera

Строение ног личинки *Nannochorista* Tillyard, 1917 и характеристика Mecoptera

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КЛЮЧЕВЫЕ СЛОВА: Panzygothoraca, Mecopteroidea, Mecopteria, Hymenoptera, Panmecoptera, Mecoptera, Nannomecoptera, *Nannochorista*, личинка, строение ног.

ABSTRACT. Larva of a South American representative of Nannomecoptera is reported for the first time. Examination of its leg structure allows to make a new interpretation of nannomecopteran larval legs: they are vestigial, consisting of coxa, trochanter and vestigial femur only, with secondary apical hooks instead of true claws. This fact allows to suggest corrections to diagnoses of higher taxa — Nannomecoptera, Mecoptera, Panzygothoraca taxon nov. (Panmecoptera + Hymenoptera) and Oligoneoptera.

РЕЗЮМЕ. Приведено первое указание личинки южноамериканского представителя Nannomecoptera. Изучение этой личинки позволяет по-новому интерпретировать строение личиночных ног у Nannomecoptera: они рудиментарные, состоят только из тазика, вертлуга и рудимента бедра с вторичными апикальными крючками вместо настоящих коготков. Это позволяет внести исправления в диагнозы высших таксонов — Nannomecoptera, Mecoptera, Panzygothoraca taxon nov. (Panmecoptera + Hymenoptera) и Oligoneoptera.

Introduction

Mecoptera in general, and particularly Nannomecoptera, are regarded to have a great phylogenetic importance. Handlirsch [1903] united Mecoptera (his Panorpata), Trichoptera (his Phryganoidea), Lepidoptera, Diptera and Aphaniptera (Suctoria, or Siphonaptera), to a taxon which he called Panorpoidea (the name unusable for this taxon, according to the recently accepted ICZN); since that time, this huge and quite diverse taxon is widely accepted under other names (Mecopteroidea auct., Papilionidea of Rohdendorf, 1977, or Panmecoptera Wille, 1960), in spite of the fact

that good apomorphies which could prove its holophyly, are unknown. Mecoptera are often regarded to be the most primitive taxon among Panmecoptera, ancestral for some or even all others [Novokshonov, 2002]. This lends a special interest to Mecoptera; however, this taxon remains to be poorly investigated: larvae are described for a few species only.

A special interest among Mecoptera excites a small taxon Nannomecoptera. According to some of phylogenetic hypotheses, Nannomecoptera represent a sister-group for all other Mecoptera [Willmann, 1987]. Some authors regarded Nannomecoptera to appear in Permian — i.e., to be one of the oldest taxa among Oligoneoptera; according to other data, true Nannomecoptera appeared in Mesozoic only, but were very widely distributed at that time [Novokshonov, 1997, 2002]. Till now, knowledge about larval Nannomecoptera was based on a single species; nannomecopteran larvae were regarded to be most primitive among Mecoptera, retaining two-segmented tarsus and a claw [Pilgrim, 1972], or even two claws [Novokshonov, 2002]. As it will be shown below, this interpretation of nannomecopteran larval leg is wrong, and actually this leg is not so primitive.

The taxon Nannomecoptera Hinton, 1981 includes 8 leaving species only and has Amphitropic distribution, being represented in Australia, New Zealand and South America. It is used to unite all these species to a single family Nannochoristidae Tillyard, 1917, where initially two genera were established — a plesion *Nannochorista* Tillyard, 1917 (type species — Australian *N. dipteroides* Tillyard, 1917) and a monospecific genus *Microchorista* Byers, 1974 (objective synonym: *Choristella* Tillyard, 1917, non Bush, 1897; type species — New Zealand *Ch. philpotti* Tillyard, 1917). As such classification has no phylogenetic significance, Kristensen

[1989] suggests to regard all Nannomecoptera as a single genus *Nannochorista*. In the hierarchical nomenclature [Kluge, 1999a, 1999b, 2000] both the family Nannochoristidae and the genus *Nannochorista* of Kristensen have a single name *Nannochorista* fg1. All species of Nannomecoptera are known as imagoes, while larva was described by Pilgrim [1972] for a single species *philpotti* [*Choristella*].

In South America 3 species of Nannomecoptera are known as imagoes — *edwardsi* Kimmins, 1929 [*Nannochorista*], *neotropica* Navas, 1929 [*N.*] and *andina* Byers, 1989 [*N.*]; each of them is reported from various localities in Chile and Argentina [Byers, 1989]; till now, larvae were unknown for any of these species. Recently M. Mercado (Institute de Zoologia, Universidad Austral de Chile) collected two specimens of larvae similar to *philpotti* [*Ch.*]; we regard these larvae belonging to some of these South American nannomecopteran species, while it is unclear to which species concretely.

Material

Larvae of following mecopteran species were examined:

(1) *Nannochorista* sp.: Chile: Valdivia, Curinanco, Cordillera de la Costa, small cool stream surrounded by native forest, depth about 15 sm, 7.II.2002 (coll. M. Mercado) — 1 immature larva; Osorno, Damas River, I.1988 (coll. S. Elliot) — 1 larva.

(2) *Panorpa communis* Linnaeus, 1758: Russia, Leningradskaya Oblast' (= Leningrad Province), Lodeynopolskiy Region, Zaostrov'e, VII.2001 (coll. N. Kluge) — many larvae of instars I–III fixed in various stages of moulting cycle, reared from eggs layed by imagoes.

(3) *Boreus* sp.: Russia, Saint-Petersburg, Piskarevskiy Forest-Park, 25.V.2000 (coll. V. Ivanov, S. Grigorenko) — 5 larvae.

All larvae were preserved in alcohol; for examination of leg structure total legs were mounted on slides in Canadian balsam.

Larval leg of Neotropical *Nannochorista* sp.

While larvae described by Pilgrim [1972] and larvae examined by us belong to different species and have some differences in leg structure, their legs seem to have the same ground plan; comparison of Neotropical *Nannochorista* sp. with the Pilgrim's description of New Zealand *philpotti* [*Choristella*] allows to make following interpretation (Figs 1, 2).

Leg is vestigial and consists of coxa, trochanter and vestige of femur only, while knee articulation, tibia, tarsus and pretarsus are absent.

The leg is attached to a prominent paired thoracic protuberance bearing a few long setae. In the description of *philpotti* [*Ch.*], this protuberance was taken for a proximal leg segment — coxa; in contrast to true leg segment, this protuberance has no muscles attaching to its base.

Coxa is rather large and in most part non-sclerotized; it bears one longest seta and 5 stout lanceolate setae (three of them are shown in Fig. 1, two others are located on median side and are invisible in lateral view). In the description of *philpotti* [*Ch.*], this leg segment (also having 5 lanceolate setae) was taken for a femur. In

contrast to true femur, it has muscles arising from tergal part of corresponding thoracic segment, and no muscles arising from previous leg segments.

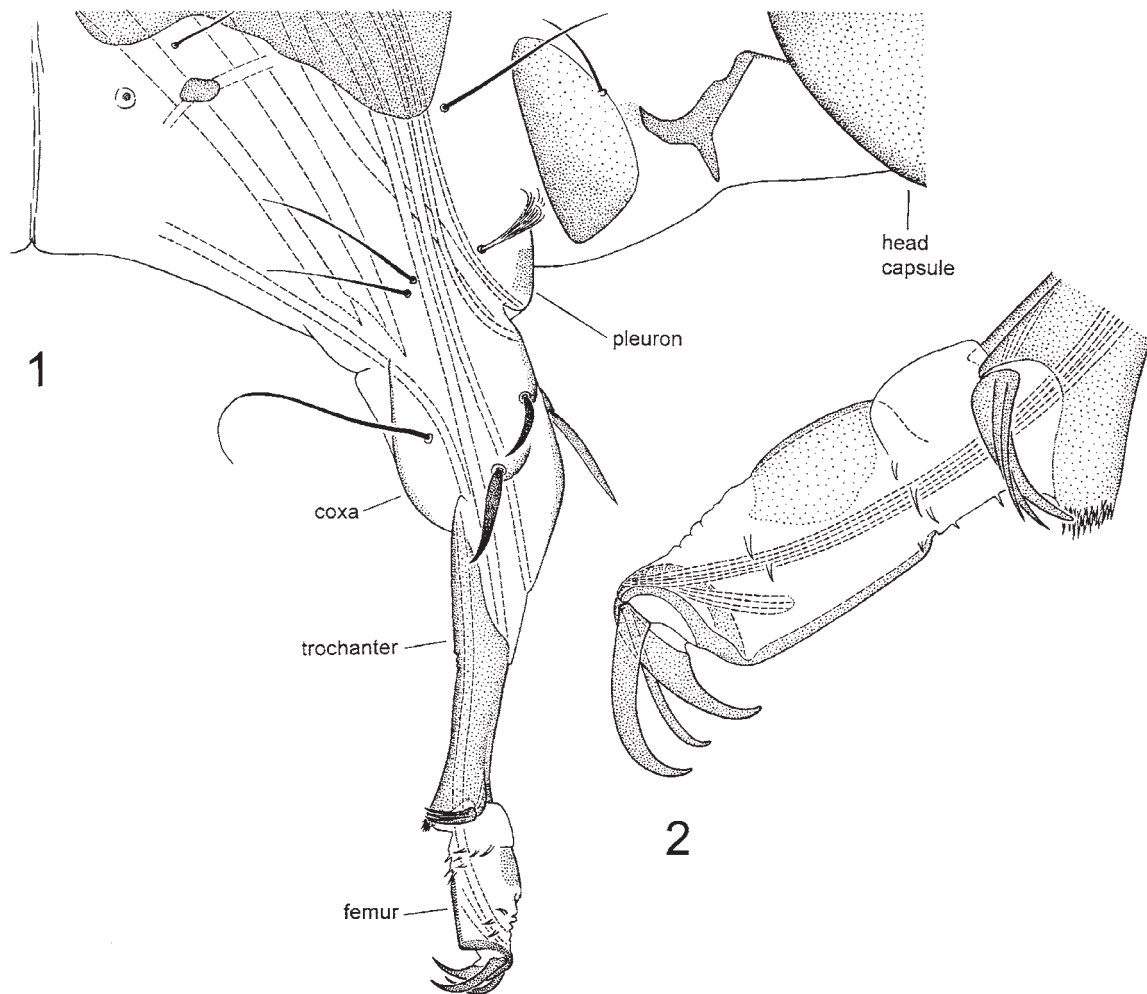
Trochanter is unusually long and slender; this is the only normally sclerotized leg segment; it lacks setae, apically-posteriorly bears a bunch of small spines of non-setal origin, and apically-laterally bears a sclerotized claw-like hook; on fore leg this hook is 3-pointed (Figs 1, 2), on middle leg — 2-pointed, on hind leg — 1-pointed; a small muscle seems to attach to the base of the hook. In the description of *philpotti* [*Ch.*], this leg segment was taken for a tibia; in contrast to true tibia, muscles attaching to its base arise from tergum and sternum of corresponding thoracic segment, but not from previous leg segment.

Femur is a terminal leg segment; it is thicker than trochanter, in most part non-sclerotized, with indistinctly outlined sclerites. Its anterior (dorsal) side has a fold incompletely dividing the femur to two portions which can be interpreted as secondary segments. The femur lacks setae and bears hooked spines of non-setal origin; the spines on lateral, median and posterior surfaces are small, colourless and irregular, and three spines on apex represent large sclerotized claw-like hooks. These apical hooks are movably articulated to a sclerite which arnes femoral apex and continues on its posterior (ventral) side. In the description of *philpotti* [*Ch.*], the femur was taken for a 2-segmented tarsus, and its largest mid-apical hook was taken for a pretarsus (claw). In contrast to true pretarsus, apical hook has no unguitactor and muscles-flexors, but has muscles-extensors arising from femur and base of trochanter. This hook has secondary origin, like the hooks on apex of trochanter and the paired hook on apex of 10th abdominal segment (which is present both in *philpotti* [*Ch.*] and the Neotropical species described here).

All Hexapoda have a common leg structure with true coxa, trochanter, femur, tibia, tarsus and pretarsus (Fig. 4), that differs from leg structure in any other group of arthropods [Kluge, 2000]. Particularly, in Hexapoda, as well as in other Atelocerata, pretarsus has a single apodeme — unguitactor, which arises from ventral (posterior) side of pretarsal base and serves for attachment of muscles arising from femur and tibia; no other muscles go to pretarsus, thus pretarsus never has muscles-extensors, and tarsus never has any muscle insertions inside. The hexapodan leg structure is retained not only in insects with well developed legs, but in many insects with vestigial legs, including larvae of Oligoneoptera. Presence of another musculature moving apical hooks of *Nannochorista* testifies that these hooks can not belong to pretarsus.

Characteristics of higher taxa

Oligoneoptera Martynov, 1923 [circumscriptional synonyms: Euneoptera Martynov, 1924, Endopterygota Boudreaux, 1979, Endoneoptera Kukalova-Peck et Brauckmann, 1992; in circumscription also matches:



Figs 1–2. *Nannochorista* sp. from Chile, immature larva: 1 — right fore leg, lateral view; 2 — apex of left fore leg, lateral view. Muscles are shown by interrupted lines.

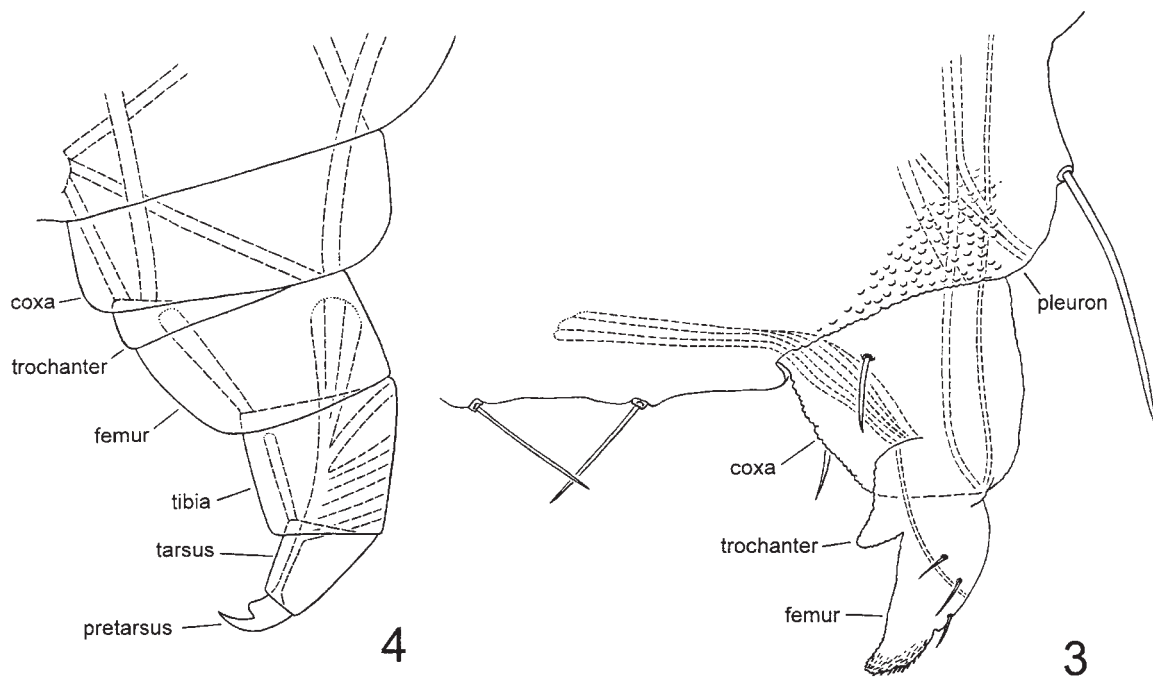
Рис. 1–2 — *Nannochorista* sp. из Чили, незрелая личинка: 1 — правая передняя нога, латерально; 2 — вершина левой передней ноги, латерально. Мышцы показаны прерывистыми линиями.

Metabola Burmeister, 1832 (non *Metabolia* Leach, 1815); *Holometabola* auct. (non Burmeister, 1835); *Endopterygota* auct. (non Sharp, 1899); hierarchical name: *Scarabaeus/fg8* (¹in *Araneus/fg*; ²sine *Cancer*; ³sine *Scolopendra*; ⁴sine *Podura*; ⁵sine *Lepisma*; ⁶sine *Ephemera*; ⁷sine *Libellula*; ⁸sine *Forficula & Cicada*). Besides other autapomorphies, Oligoneoptera have the following:

The whole leg structure, including its segmentation, obligatory changes during transformation from larva to pupa (about this testifies presence of immobile prepupa in all oligoneopterans which larvae actively move by legs). Larval leg structure differs from the pupal/imaginal one; particularly, larval tarsus is always non-segmented, while pupal/imaginal tarsus is usually five-segmented [that is probably initial either for *Amyocerata*, or for *Hexapoda*]; larval tibia never has spurs, while pupal/imaginal tibia often has two apical (and

sometimes other) spurs [that is probably initial for *Neoptera*]. Except for the tarsal segmentation, larval leg can have all features of normal hexapodan leg (coxa, trochanter, femur, tibia, tarsus and two-clawed pretarsus with normal hexapodan articulations and musculature), but never has peculiar features of imaginal leg of the same insect; sometimes larval leg undergone further reduction.

Oligoneoptera can be divided into the following taxa: (1) *Euneuropteroidea* Krausse et Wolff, 1919 [hierarchical name: *Myrmeleon/fl=Hemerobius/g1*]; (2) *Raphidioptera* Handlirsch, 1908 [hierarchical name: *Raphidia/fg1*]; (3) *Meganeuroptera* Crampton, 1916 [circumscriptional synonym: *Eumegalopteroidea* Krausse et Wolff, 1919; in circumscription matches: *Megaloptera sensu* Latreille, 1807 (non Latreille, 1802, nec Burmeister, 1839); hierarchical name: *Corydalus/fl=Chauliodes/g1* (incl. *Sialis*)]; (4) *Elytrophora* Pack-



Figs 3–4. 3 — *Panorpa communis*, larva of 3rd instar, musculature of right hind leg, view from behind; 4 — scheme of musculature of vestigial insect leg retaining all segments, based on right hind leg of larval *Pieris brassicae* (numerous setae and setae-bearing protuberances not shown). Muscles are shown by interrupted lines.

Рис. 3–4. 3 — *Panorpa communis*, личинка 3-го возраста, мускулатура правой задней ноги, вид сзади; 4 — схема мускулатуры рудиментарной ноги насекомого, сохраняющей все сегменты, основанная на правой задней ноге личинки *Pieris brassicae* (многочисленные щетинки и щетинконосные бугорки не показаны). Мышцы показаны прерывистыми линиями.

ard, 1883 [circumscriptional synonyms: Coleopteroidea Handlirsch, 1903, Pancoleoptera = Coleopteria Crampton, 1938, Coleopterida Boudreaux, 1979; hierarchical name: Scarabaeus/fg9 (incl. *Xenos*)] and (5) Panzygothoraca (see below).

Panzygothoraca, taxon nov. (hierarchical name: Papilio/fg1). In its circumscription matches: Mecopteroidea *sensu* Bey-Bienko, 1964 (non Bey-Bienko, 1962 et al.); Mecopteria *sensu* Mickoleit, 1969 (non Hennig, 1953); Hymenopterida *sensu* Weaver, 1984 (non Boudreaux, 1979).

This taxon unites Mecoptera (see below), Aphaniptera Kirby et Spense, 1815 (circumscriptional synonym: Siphonaptera Latreille, 1925), Diptera Linnaeus, 1758, Sorbentia Haeckel, 1896 (circumscriptional synonym: Amphiesmenoptera Kiriakoff, 1948) and Hymenoptera Linnaeus, 1758. The name Panzygothoraca is formed from the name of an old polyphyletic taxon Zygothoraca Schoch, 1884, which united Diptera, Lepidoptera and Hymenoptera, but did not include Mecoptera and Trichoptera. Panzygothoraca are characterized by following autapomorphies:

(1) Both larval and imaginal head has tendency to form a hypostomal bridge: margins of head capsule are often (but not always) more or less brought together, or contiguous, or fused ventrally separating base of labium from posterior tentorial pits, while the posterior tentorial

pits retain their position close to occipital foramen (in contrast to Coleoptera, Raphidioptera, Meganeuroptera and some other taxa, which have externally similar bridge separating posterior tentorial pits from the occipital foramen). Being separated from the occipital foramen, labium and maxillae often form an integral labio-maxillary complex.

(2) Larval labial glands are modified as silk glands. Non-unique apomorphy: the same in Copeognatha.

(3) Larval pretarsus is reduced to a single claw (Fig. 4) (instead of two claws initial for Hexapoda, which are retained in larvae of Raphidioptera, Meganeuroptera, many Euneuropteroidea and some Coleoptera). Non-unique apomorphy. Sometimes pretarsus or the whole leg is reduced.

Mecoptera Hyatt et Arms, 1891 (older circumscriptional synonym: Mecaptera Packard, 1886; younger circumscriptional synonyms: Eumecoptera Tillyard, 1919, Mecopteroidea Boudreaux, 1979; hierarchical name: Panorpa/fg1).

Besides other derived characters, Mecoptera have following one: Each larval leg is vestigial and consists of coxa, trochanter and vestigial femur; its knee articulation, tibia, tarsus and pretarsus are completely lost (or, better to say, fused with the femur vestige and non-distinguishable from it) (Figs 1–3). Vestigial femur

represents the terminal leg segment; it can be directed forward, have some mobility and its posterior-ventral (initially inner) surface can increase adhesion with ground when larva crawls. Sometimes leg is more strongly reduced (in *Caurinus* Russell, 1979). Possibly such leg reduction is a synapomorphy of Mecoptera with Aphaniptera and/or Diptera, which larval legs are completely lost. Probably, initially mecopteran larvae were adopted to soil inhabitancy, crawled using ventral side of the whole trunk (as recent *Panorpa*), and in connection with this lost ability to walk on legs; only larvae of Nannomecoptera turned to inhabitancy in streams, and had to develop secondary hooks on legs (Figs 1, 2) and abdominal apex instead of the lost leg claws.

Structure of larval legs testifies that the taxon Mecoptera (or at least its crown-group outlined by recent forms and their common ancestors) can not be ancestral for Sorbentia, which retain more plesiomorphic structure of larval legs (Fig. 4). This does not exclude paraphyly of the taxon Mecoptera, as it can be ancestral for Aphaniptera and/or Diptera.

Recent Mecoptera can be divided to following subordinated taxa:

1. Raphioptera MacLeay, 1821 (circumscriptional synonym: Neomecoptera Crampton, 1930; hierarchical name: Boreus/fg1);

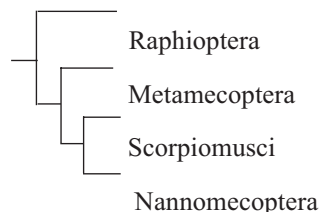
2. Metamecoptera Crampton, 1930 (circumscriptional synonym: Raptipedia Willmann, 1987; hierarchical name: Bittacus/fg1);

3. Scorpiomusci, taxon nov. (hierarchical name: *Panorpa*/fg2 (incl. *Merope*, *Notiothauma*, *Chorista*, *Panorpodes*, *Apteropanorpa*). Corresponds to parvorders Meropomorpha + Panorpomorpha of Willmann, 1987. Characterized by following unique apomorphies. (1) In male, seminal pump has a unique structure [Willmann, 1981] (while seminal pumps of various other structures are usual among insects). (2) In female, sternite of abdominal segment VIII is elongate and divided to two parts, its posterior part lies under segment IX, looks as sternite IX and can be retracted into the segment VIII together with segment IX [Mickoleit, 1975]. (3) In female, tip of abdomen has unique structure adopted as a probe for testing crevices into which eggs are lied: there are a pair of 3-segmented appendages ("cerci") fused together by their first segments dorsad of the "11th abdominal segment" [Mickoleit, 1975]. Some authors regard presence of the "11th segment" to be a plesiomorphy, that is connected with the theory about initially 11-segmented insect abdomen [Snodgrass, 1935]. Actually abdomen of Hexapoda initially has 10 segments only [Kluge, 2000], and presence of the formation called "11th segment" on female imaginal abdomen, is an autapomorphy of Mecoptera.

4. Nannomecoptera Hinton, 1981 (hierarchical name: *Nannochorista*/fg1). Being a small taxon with limited Amphitropic distribution (4 species in Australia, 3 species in South America and 1 species in New Zealand) with a uniform adult structure and larvae known for two species only, Nannomecoptera can be characterized by

many autapomorphies. Among them — aquatic larva (not found in other Mecoptera) with peculiar cylindrical body lacking dorsal and ventral abdominal processes (these processes are characteristic for *Bittacus*/fg1 and *Panorpa*/fg2 and probably are initial for Mecoptera), with a pair of anal hooks and with peculiar leg structure. As can be seen from the description above, leg structure of Nannomecoptera does not contradict to the diagnoses of Oligoneoptera (which have no more than one tarsal segment), Panzygothoraca (which have no more than one claw) and Mecoptera (which lost tibia, tarsus and claws).

While female abdomen of Nannomecoptera does not have most of modifications peculiar for Scorpiomusci, these taxa have one character in common — presence of 3-segmented appendages regarded to be "cerci" [Mickoleit, 1975]. If proceed from an assumption that these are true cerci, and that the cerci are initially segmented, this character could be regarded as a symplesiomorphy. However, it is quite probable that Oligoneoptera have no true cerci, and the appendages under discussion are socii — secondary, initially non-segmented processes. Thus, division of these appendages to 3 segments can be a synapomorphy of Nannomecoptera and Scorpiomusci, and phylogeny of Mecoptera can look as following:



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