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Larval/pupal leg transformation and a new diagnosis for the taxon Metabola Burmeister, 1832 = Oligoneoptera Martynov, 1923

Трансформация ног при превращении личинки в куколку и новый диагноз таксона Metabola Burmeister, 1832 = Oligoneoptera Martynov, 1923

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КЛЮЧЕВЫЕ СЛОВА: Metabola, Oligoneoptera, Holometabola, Trichoptera, *Rhycophila nubila*, Coleoptera, *Tenebrio molitor*, *Leptinotarsa decemlineata*, Neuroptera, Birostrata, *Chrysoperla carnea*, *Chrysotropia ciliata*, *Myrmeleon bore*, Rhaphidioptera, *Raphidia*, Meganeuroptera, *Sialis sordida*, *Acanthocorydalis*, Lepidoptera, Glossolepidoptera nom.n., Neolepidoptera, Diptera, Tipulidae, Cyclorapha, Hymenoptera, Apocrita, метаморфоз, голометаморфоз, личинка, предкуколка, пронимфа, трансформация ног, антирост, онтогенетическая гомология, антенна, скапус, протоптерон, Endopterygota, имагинальный диск, базигенный карман, акрогенный карман, куколка, pupa obtecta, pupa conglutinata, pupa larvodectica, pupa neodectica.

ABSTRACT. There is described a process of leg transformation when larva moults to pupa in *Rhyacophila nubila*, *Tenebrio molitor*, *Leptinotarsa decemlineata*, *Myrmeleon bore*, *Chrysoperla carnea*, *Sialis sordida* and some other insect species from various orders. In all Metabola, when larva transforms to pupa, each leg gets an immobile knee bent; in all Metabola except for Meganeuroptera, the leg loses all its musculature; in species with relatively long larval legs, the living part of leg under detached cuticle at first strongly diminishes, and only than grows up to the pupal size. This process of diminishing is unusually variable – from even or uneven anti-growth to breaking of distal part; ontogenetic homology of leg segments can be kept or not. The presence of phase of diminishing before leg growth and the diversity of this phase testifies in favour of the theory, that among Metabola a short-legged (eruciform) larval type is the primary one, and elongation of larval legs occurred secondarily. Only in Meganeuroptera diminishing of the living part of leg is insignificant, and some leg muscles pass from larva to pupa and than to imago. While Meganeuroptera have no anatomical reasons for existing resting phases, they have the same resting phases (pronymph and pupa) as other Metabola, that testifies about secondary simplification of their metamorphosis. The special method of leg transformation at the penultimate (larval/pupal) moult, which invariably leads to appearing of immobile knee bent in pupal stage, is an autapomorphy of Metabola and that conservative feature, which appearing in the common ancestor of Metabola determined the main tendentions in evolution of Metabola – the extending differences between larva and imago the inactivity of pupa. Other autapomorphies of Metabola are discussed, among them – absence of scapus in larval antenna and peculiarity of its transformation to pupal and imaginal antenna; ventral direction of pupal protoptera (external wing buds) and peculiarity of pupal pose. Probably, endopterygotism (presence of internal protopteron buds in larva) is not an autapomorphy of Metabola. So called “leg imaginal discs” of Diptera-Cyclorapha are not special embryonic germs of future imaginal legs, but sensory larval organs, which initially exist in Diptera and represent modified vestiges of larval legs.

РЕЗЮМЕ. Описан процесс трансформации ног при линьке личинки на куколку у *Rhyacophila nubila*, *Tenebrio molitor*, *Leptinotarsa decemlineata*, *Myrme-*

leon bore, *Chrysoperla carnea*, *Sialis sordida* и некоторых других видов насекомых их разных отрядов. У всех Metabola нога при трансформации из личиночной в куколочную приобретает неподвижный коленный сгиб; при этом у всех Metabola кроме Meganeuroptera нога утрачивает всю мускулатуру; у видов с относительно длинными личиночными ногами живая часть ноги под отслоившейся личиночной кутикулой сначала сильно уменьшается, а только потом растет до куколочных размеров. Этот процесс уменьшения необычайно разнообразен – от равномерного или неравномерного антироста до отбрасывания дистальной части; онтогенетическая гомология члеников ноги может соблюдаться или нарушаться. Наличие фазы уменьшения перед ростом ноги и разнообразие этой фазы свидетельствует в пользу теории о первичности у Metabola коротконогих личинок эруковидного типа и вторичности удлинения личиночных ног. Только у Meganeuroptera уменьшение живой части ноги незначительное, и лишь некоторые ножные мышцы утрачиваются, а некоторые ножные мышцы переходят от личинки к куколке и далее к имаго. Хотя в анатомии Meganeuroptera нет причин для существования фазы покоя, у них имеются такие же покоящиеся состояния (пронимфа и куколка), как у других Metabola, что говорит о вторичном упрощении их метаморфоза. Уникальный способ трансформации ног на предпоследней (личиночно-куколочной) линьке, всегда приводящий к появлению неподвижного коленного сгиба у куколки, является аутапоморфией Metabola и той ключевой особенностью, которая, возникнув и консервировавшись у общего предка Metabola, предопределила основные тенденции в эволюции Metabola — углубление различий между личинкой и имаго и неактивность куколки. Обсуждаются другие аутапоморфии Metabola, среди них — отсутствие у личиночной антенны скапуса и особенности ее трансформации в куколочную и имагинальную; вентрально направленные куколочные протоптероны (наружные крыловые зачатки) и особенности позы куколки. Вероятно, эндоптериготность (наличие у личинки внутренних зачатков протоптеронов) не является аутапоморфией Metabola. Так называемые “ножные имагиналные диски” у Diptera-Cyclorapha представляют собой не специальные эмбриональные зачатки будущих имагинальных ног, а сенсорные личиночные органы, которые исходно свойственны Diptera и являются преобразованными вестигиями личиночных ног.

Contents:

1. General remarks

1.1. Insect system and nomenclature

The general classification of insects recently accepted by the author is given in the Table 1. In modern literature, often for the same taxa different names are used. To bring in order non-typified names, the strict rules of circumscriptional (= volumetric) nomenclature were elaborated [Kluge, 1991a; 1991b; 2000; 2004a]. Now status of certain names of arthropods can be learned from the electronic catalogue “Nomina Circumscribentia Insectorum” [http://www.bio.bu.ru/win/entomol/KLUGE/nom/~Cont.htm]. In this paper all names are used according to the rules of circumscriptional nomenclature, with the only exception for Coleoptera: it is proposed to suppress the name Coleoptera Linnaeus 1758 and conserve the name **Coleoptera** De Geer 1774, regarding **Eleuterata** Fabricius 1775 to be its junior circumscriptional synonym. Names of taxa in Neu-

Table 1. Systematic position of accepted taxa mentioned in the text
Таблица 1. Систематическое положение принятых таксонов, упоминаемых в тексте

1 **Polygnatha** Latreille 1821 = **Mandibulata** Snodgrass 1935 (= **Scarabaeus/fg1**)
1.1 **Eucrustacea** Kingsley 1894 (= **Cancer/fg1**)
1.2 **Atelocerata** Heymons 1901 (= **Scarabaeus/fg2**)
1.2.1 **Myriapoda** Latreille 1802 (= **Scolopendra/fg1**)
1.2.2 **Hexapoda** Blainville 1816 (= **Scarabaeus/fg3**)
1.2.2.1 **Entognatha** Stummer-Traunfels 1891 (= **Podura/fg1**)
1.2.2.2 **Amyocerata** Remington 1955 (= **Scarabaeus/fg4**)
1.2.2.2.1 **Triplura** Ewing 1942 (= **Lepisma/fg1**)
1.2.2.2.2 **Pterygota** Gegenbaur1878 (= **Scarabaeus/fg5**)
1.2.2.2.2.1 **Ephemeroptera** Hyatt & Arms 1891 (= **Ephemera/fg1**)
1.2.2.2.2.2 **Metapterygota** Borner 1909 (= **Scarabaeus/fg6**)
1.2.2.2.2.2.1 **Odonata** Fabricius 1793 (= **Libellula/fg1**)
1.2.2.2.2.2.2 **Neoptera** Martynov 1923 (= **Scarabaeus/fg7**)
1.2.2.2.2.2.2.1 **Polyneoptera** Martynov 1923 (= **Gryllus/f1=Forficula/g1**)
1.2.2.2.2.2.2.2 **Paraneoptera** Martynov 1923 (= **Cimex/f1=Cicada/g1**)
1.2.2.2.2.2.2.2.1 **Zoraptera** Silvestri 1913 (= **Zorotypus/fg1**)
1.2.2.2.2.2.2.2.2 **Acercaria** Borner 1904 (= **Cimex/f2=Cicada/g2**)
1.2.2.2.2.2.2.2.2.1 **Panpsocoptera** Crampton 1938 (= **Psocus/f1=Pediculus/g1**)
1.2.2.2.2.2.2.2.2.2 **Condylognatha** Borner 1904 (= **Cimex/f3=Cicada/g3**)
1.2.2.2.2.2.2.2.2.2.1 **Thysanoptera** Haliday 1836 (= **Thrips/fg1**)
1.2.2.2.2.2.2.2.2.2.2 **Arthroidignatha** Spinola 1850 (= **Cimex/f4=Cicada/g4**)
1.2.2.2.2.2.2.2.2.2.2.1 **Hemelytrata** Fallen 1829 (= **Cimex/f5=Cicada/g5**)
1.2.2.2.2.2.2.2.2.2.2.2 **Phytadelga** Dumeril 1806 = **Sternorhynchi** Amyot & Serville 1843 (= **Aphis/fg1**)
1.2.2.2.2.2.2.2.2.2.2.2.1 **Gynaptera** Laporte 1834 (= **Aphis/fg2**)
1.2.2.2.2.2.2.2.2.2.2.2.2 **Gallinsecta** De Geer 1776 (= **Coccus/fg1**)
1.2.2.2.2.2.2.2.2.2.2.2.3 **Scytinelytra** Amyot & Serville 1843 (= **Aleyrodes/fg1**)
1.2.2.2.2.2.2.2.2.2.2.2.4 **Saltipedes** Amyot & Serville 1843 (= **Psylla/fg1**)
1.2.2.2.2.2.2.3 **Metabola** Burmeister 1832 = **Oligoneoptera** Martynov 1923 (= **Scarabaeus/fg8**)
1.2.2.2.2.2.2.3.1 **Neuropteroidea** Handlirsch 1903 (= **Myrmeleon/f1=Hemerobius/g1**)
1.2.2.2.2.2.2.3.1.1 **Birostrata** Kluge, **in press** (= **Myrmeleon/f2=Hemerobius/g2**)
1.2.2.2.2.2.2.3.1.2 **Rhaphidioptera** Navas 1916 (= **Raphidia/fg1**)
1.2.2.2.2.2.2.3.1.3 **Meganeuroptera** Crampton 1916 (= **Corydalus/f1=Chauliodes/g1**)
1.2.2.2.2.2.2.3.1.3.1 **Sialis/fg1**
1.2.2.2.2.2.2.3.1.3.2 **Eumegaloptera** Riek 1974 (= **Corydalus/f2=Chauliodes/g2**)
1.2.2.2.2.2.2.3.2 **Elytrophora** Packard 1883 (= **Scarabaeus/fg9**)
1.2.2.2.2.2.2.3.2.1 **Coleoptera** De Geer 1774 (if suppress Coleoptera Linnaeus 1758) (= **Scarabaeus/fg10**)
1.2.2.2.2.2.2.3.2.1.1 Plesiomorphon **Protadephaga** Kolbe 1903 = **Archostemata** Kolbe 1908
1.2.2.2.2.2.2.3.2.1.2 **Pantophaga** Klausnitzer 1975
1.2.2.2.2.2.2.3.2.1.2.1 **Adephagi** Clairville 1798
1.2.2.2.2.2.2.3.2.1.2.2 **Polyphaga** Emery 1886 **(s.l.)**
1.2.2.2.2.2.2.3.2.2 **Strepsiptera** Kirby 1813 (= **Stylops/f1=Xenos/g1**)
1.2.2.2.2.2.2.3.3 **Panzygothoraca** Kluge 2004 (= **Papilio/fg1**)
1.2.2.2.2.2.2.3.3.1 **Hymenoptera** Linnaeus 1758 (= **Vespa/f1=Cynips/g1**)
1.2.2.2.2.2.2.3.3.1.1 Plesiomorphon **Ventrosessiles** Latreille 1802 = **Symphyta** Gerstaecker 1867 (= **Tenthredo/fg1**)
1.2.2.2.2.2.2.3.3.1.2 **Apocrita** Gerstaecker 1867 (= **Vespa/f2=Cynips/g2**)
1.2.2.2.2.2.2.3.3.2 **Mecaptera** Packard 1886 (= **Panorpa/fg1**)
1.2.2.2.2.2.2.3.3.2.1 **Scorpiomusci** Kluge 2004 (= **Panorpa/fg2**)
1.2.2.2.2.2.2.3.3.2.2 **Nannomecoptera** Hinton 1981 (= **Nannochorista/fg1**)
1.2.2.2.2.2.2.3.3.2.3 **Metamecoptera** Crampton 1930 (= **Bittacus/fg1**)
1.2.2.2.2.2.2.3.3.2.4 **Raphioptera** MacLeay 1821 (= **Boreus/fg1**)
1.2.2.2.2.2.2.3.3.3 **Aphaniptera** Kirby & Spense 1815 (= **Pulex/fg1**)
1.2.2.2.2.2.2.3.3.4 **Diptera** Linnaeus 1758 (= **Musca/f1=Oestrus/g1**)
1.2.2.2.2.2.2.3.3.4.1 Plesiomorphon **Nemocera** Latreille 1817 (= **Tipula/fg1**)
1.2.2.2.2.2.2.3.3.4.2 **Brachocera** Macquart 1834 (= **Musca/f2=Oestrus/g2**)
1.2.2.2.2.2.2.3.3.4.2.1 Plesiomorphon **Mesodiptera** Crampton 1916 (= **Bombylius/f1=Tabanus/g1**)
1.2.2.2.2.2.2.3.3.4.2.2 **Cyclorapha** Brauer 1863 (= **Musca/f3=Oestrus/g3**)
1.2.2.2.2.2.2.3.3.5 **Sorbentia** Haeckel 1896 = **Amphiesmenoptera** Kiriakoff 1948 (= **Papilio/fg2**)
1.2.2.2.2.2.2.3.3.5.1 **Trichoptera** Kirby 1813 (= **Phryganea/fg1**)
1.2.2.2.2.2.2.3.3.5.2 **Lepidoptera** Linnaeus 1758 = **Glossata** Fabricius 1775 (= **Papilio/fg3**)
1.2.2.2.2.2.2.3.3.5.2.1 Plesiomorphon **Protolepidoptera** Packard 1895 (= **Micropterix/fg1**)
1.2.2.2.2.2.2.3.3.5.2.2 **Glossolepidoptera** Kluge, **nom.nov.** (= **Papilio/fg4**)
= Lepidoptera haustellata Packard 1895, non Haustellata Clairville 1798
= Lepidoptera glossata Packard 1895, non Glossata Fabicius 1775
1.2.2.2.2.2.2.3.3.5.2.2.1 Plesiomorphon **Palaeolepidoptera** Packard 1895 (= **Eriocrania/fg1**)
1.2.2.2.2.2.2.3.3.5.2.2.2 **Neolepidoptera** Packard 1895 (= **Papilio/fg4**)

ropteroidea are discussed in the paper on mouthparts development [Kluge, in press].

1.2. Phylogenetic and ontogenetic homology

To indicate that an organ develops from the homologous organ of previous developmental stage, a term "**sequentially homologous**" was suggested [Svacha, 1992]. However, sequences can be different — ontogenetic, phylogenetic, or spatial (when serially homologous organs are repeated in one organism). Thus, instead of "sequential homology" here is used a term "**ontogenetic homology**". Usually that organs or segments which are phylogenetically homologous, are at the same time ontogenetically homologous. This allows to discover phylogenetic homology by direct examination of ontogenetic homology [Kluge, 2002; Kluge, in press]. However, in some cases phylogenetically homologous segments are not ontogenetically homologous. For example, this takes place in well known cases of regeneration occurring in many (or in all) insects, when after extirpation distal segments of a limb develop from the remaining proximal segment of this limb. As a result of normal larval/pupal leg transformation, in some insects all phylogenetically homologous segments appear to be ontogenetically homologous, but in some others some phylogenetically homologous leg segments are not ontogenetically homologous (see below, 3.6 and Figs 56–58).

1.3. Processes connected with moult

It is usually regarded that at moulting process, after detaching of hypoderm from cuticle, the hypoderm enlarges — either evenly grows (when the moult leads to larval growth), or forms outgrowths (when the moult leads to appearing of new external outgrowths — see 1.4), becoming pressed or crumpled under the old cuticle. Actually, besides enlargement, moult can lead to diminishing or disappearing of some external body parts. In these cases hypoderm of certain body part after its detaching, diminishes. During the larval/pupal moult in Metabola with long-legged larvae, an unusual process takes place, when leg hypoderm temporarily diminishes, while finally it strongly enlarges (see below, 3.3). Unlike enlargement of hypoderm, which can be served only by its growth, diminishing of hypoderm can be served by various methods — either by anti-growth, or by breaking.

Anti-growth. This is diminishing of size of living tissues by decreasing of number and/or size of cells. It resembles growth in opposite succession: the organ gradually and proportionally diminishes, at the same time simplifying in its structure. In some arthropods, during a moult certain body parts become smaller or disappear thanks to the anti-growth of hypoderm and other living tissues, which occurs under cuticle at the pre-moulting period. For example, in all mayflies (Ephemeroptera) larva has mouth apparatus, while subimago and imago have not it; disappearance or diminishing of the mouth appendages is always reached by the anti-growth, independently of their structure and independently in which stage (subimago or imago) and at which degree they degenerate. In some Metabola, when larval leg transforms to pupal leg, at first occurs the anti-growth, and than growth. Among species described below, nearly even anti-growth occurs in *Rhyacophila nubila*, *Tenebrio molitor* and *Leptinotarsa decemlineata*; sharply uneven anti-growth occurs in *Myrmeleon bore*.

Breaking without wastes. This is diminishing of size of living tissues thanks to a process when a part of tissues degenerates and appears out of the living part of appendage, between its epithelium and cuticle; later this degenerated part is completely dissolved and utilized, thus at the ecdysis only the old clean cuticle is shed, without remainders of any tissues. In some Metabola, when larval leg transforms to pupal leg, distal part of the larval leg breaks without wastes; in this case phylogenetically homologous leg segments are not ontogenetically homologous. Among species described below, waste-less breaking occurs in *Chrysoperla carnea* and *Chrysotropia ciliata*.

Breaking with wastes. A part of tissues is detached and appears out of the living part of appendage, between its epithelium and cuticle; the detached part is dissolved and utilized only partly, thus at the ecdysis together with the old cuticle remainders of tissues are shed. For example, in all mayflies (Ephemeroptera) larva has tergalii, while subimago and imago have not them; when larva moults to subimago, tergalii are shed together with their internal tissues, thus consistence of tergalii allows to distinguish exuviae shed at larval/subimaginal moult from exuviae shed at larval/larval moult (when only cuticle is shed from tergalii). In many mayflies, belonging to various non-related taxa, larva has a long, multi-segmented paracercus, while subimaginal and imaginal paracercus is vestigial [Kluge, 2004a]; in all these cases at larval/subimaginal moult the superfluous part of paracercus is detached becoming an empty sack, and at the ecdysis sheds together with the larval cuticular paracercus, remaining inside it. Such way of diminishing of paracercus occurs not only in mayfly species with long larval paracercus, but even in those species whose larval paracercus is only slightly longer than the subimaginal-imaginal one.

It is interesting to note, that the way of diminishing (anti-growth or breaking) of a certain appendage can be very conservative — even more conservative than the initial and/or the final structure of this appendage. The above-given examples with Ephemeroptera concern all mayfly species; in the same individual at the same time (during moult from larva to subimago) mouth parts degenerate by anti-growth, while paracercus degenerates by breaking with waste. Situation with legs of Metabola is opposite: transformation of homologous appendages (legs) in different taxa of Metabola occurs by principally different ways.

1.4. Forms of hypodermal buds

Outgrowth of hypoderm which appears under cuticle and after a moult gives rise to external appendage, by different English-language authors is called “bud”, “anlage” (“Anlage”), “rudiment”, “primordium”, “germ” (“germen”), or “fundament”; in Russian it is called “zachatok” (“зачаток”). Some authors use the term “imaginal disc”, which should be avoided (see 1.5). To discuss peculiarities of metamorphosis, it is necessary to distinguish the following forms of hypodermal buds. **Simple bud without pocket** — a bud which is covered only by old cuticle; such bud exists only in the instar preceding that in which the bud becomes an external organ. These buds exist in life cycles of all arthropods; for example, the simple bud of protopteron exists in the last larval instar of all Metabola (Figs 4–7, 13b, 20, 33–36, 42, 53) and in one of early larval instars of other Pterygota (Fig. 59). **Bud in a pocket** — a bud which is separated from the old cuticle by a hypodermal fold forming a pocket (protopteron buds in Figs 2, 12, 60; leg bud in Figs 52–55). The bud in a pocket either exists only in the instar preceding appearing of the external organ (like a bud without pocket), or appears earlier and passes from instar to instar; in the last case it represents an **internal bud**. According to their form, pockets can be basigenous and acrogenous. In a **basigenous pocket** the bud arises from the bottom of the pocket, and apex of the bud is directed toward (or projects from) the mouth of the pocket (protopteron bud in Fig. 12; leg buds of Diptera — see 3.5.1 and Figs 52–55). In an **acrogenous pocket** the bud is sinked into the pocket by its apex (protopteron bud in Figs 2 and 60; leg buds of Apocrita — see 3.5.2). Besides distinctly basigenous and distinctly acrogenous pockets, there are pockets of various intermediate and combined forms, when both base and apex of the bud are sinked into a pocket; these pockets can be called **basigenous-acrogenous** or **acrogenous-basigenous**.

When we speak about buds existing in larva of Metabola, epithet “imaginal” is wrong, because actually these are buds of pupal organs; buds of imaginal organs appear at the pupal stage.

1.5. Confusion provoked by the term “imaginal discs”

The term “**imaginal discs**” (in German — “Imaginascheiben”) was introduced by Weismann [1864] for a couple of peculiar bodies inside the thorax of larval Diptera-Cyclorapha (= **Discota** Weismann 1866); each “disc” is an invagined portion of ectodermal epithelium in a form of stalked, closed, ovoid sack with an epithelial projection inside; stalks of these “disks” are so slender, that first investigators [Weismann, 1864; Ganin, 1877] overlooked them. “Imaginal discs” open only at larval/pupal transformation and give rise to pupal hypoderm of head and thorax, antennae, proboscis, legs, stenothoracic stigmal horns and protoptera. Here the epithet “imaginal” is wrong, because imaginal parts develop only at the next, pupal/imaginal moult, and stenothoracic stigmal horns in imago are absent at all. In his next publication Weismann [1866] stated that other Metabola (at least *Chaoborus* Lichtenstein 1800 [= *Corethra* Meigen 1800]) have no imaginal discs, and united them in a division **Adiscota** Weismann 1866.

However, some authors [Pratt, 1899 and others] used the term “imaginal discs” not only for internal closed hypodermal formations, but for any portions of any tissues, which do not undergo lysis and take part in formation of imaginal tissues. In this case they say that larvae of Cyclorapha have hypodermal “imaginal discs” not only in the thorax, but in the abdomen as well. Under the “abdominal imaginal discs” they understand portions of external larval hypoderm (which produce normal larval cuticle and later produce normal pupal cuticle), which during the pupal/imaginal transformation grow out and substitute other portions of abdominal hypoderm. Probably, this term was useful in the discussion which in the 19th century flared up around a Weisman’s concept of “histolysis” and his opinion that some of imaginal cells appear from non-cellular products of the “histolysis”. His opponents used the term “imaginal disc” for all cells which do not undergo lysis, to say that all imaginal tissues (but not only head and thorax hypoderm) appear from the “imaginal discs”, but not from products of lysis. In this sense “imaginal discs” are present in every multicellular animal, in other case the animal would not live.

Many authors used the term “imaginal discs” simultaneously in three quite different senses:

(1) In the original sense, for the disc-like internal organs, which represent an autapomorphy of Cyclorapha. Different “imaginal discs” of Cyclorapha have different origin, and their true nature can be understood only if compare them with homologous formations in related taxa (see below, 3.5.1).

(2) In a secondary sense, for any tissues which are retained when other tissues are dissolved. In this sense “imaginal discs” were described as a peculiarity of Cyclorapha, but actually are present in any animal, and represent a general character of Metazoa.

(3) In another secondary sense, for any hypodermal bud which grows under cuticle before a moult, at which this bud will become an external appendage (independently, if other parts of hypoderm will be dissolved, or not). In this sense, it was stated that *Chaoborus* (which is the type of Adiscota) also has “imaginal discs”. Such “imaginal discs” obligatory exist in any moulting animal, thus represent a character of Gnathopoda (= Arthropoda s.l.).

Mixed usage of the term “imaginal discs” leads to confusion. Somebody regard that “imaginal discs” in some sense are peculiar for Metabola; this is wrong in all respects.

2. Metabola and holometamorphosis

Peculiarities of insects with complete metamorphosis (**holometamorphosis**, or **holometaboly**) were already known to Aristotle, who distinguished in ontogenesis of Lepidoptera, Hymenoptera, Diptera and Coleoptera three stages — the feeding worm, the non-feeding nymph and the adult. However, a taxon uniting all holometamorphic insects, was not generally accepted up to the 20th century. In our days this taxon is accepted probably by all investigators; its circumscriptional names are **Metabola** Burmeister 1832 = **Heteromorpha** Westwood 1839 (non Heteromorphes Blainville 1816) = **Heterognatha** Borner 1920 (non Heterognatha Saussure & Humbert 1872) = **Oligoneoptera** Martynov 1923 = **Euneoptera** Martynov 1924 = **Endopterygotida** Boudreaux 1979 = **Endoneoptera** Kukalova-Peck & Brauckmann 1992; it is known also under wrong names — Holometabola auct. (non Burmeister 1835) and Endopterygota auct. (non Sharp 1898).

Theories which explain existence of holometamorphosis, can be divided into two groups — polyphyletic and monophyletic ones.

2.1. Hypotheses about polyphyly of holometamorphosis

In the past, there were expressed opinions about polyphyly of the taxon Metabola [Lowne, 1890; Haeckel, 1896; Schwanwich, 1946]. These opinions were connected with an assumption that the holometamorphosis appeared repeatedly thanks to some universal reasons — either thanks to its advantage at the natural selection, or thanks to some universal mechanism, such as desembryonization or necessity of a mould.

2.1.1. **Hypothesis about desembryonization.** Some authors [Lowne, 1890, et al.] assumed the following way of appearing of holometamorphosis: Metabola chose such a strategy of propagation, when parents produce more eggs at the expense of their viability; their eggs became smaller, with less quantity of yolk. Because of this, embryo does not reach the final phase of initial embryonic development, but hatches from the egg at some of earlier phases. Because of this, larva is similar to early embryo and strongly differs from imago. According to this theory, larvae of various Metabola hatch from eggs at various phases — either "cyclopiform" (= "protopod"), or "eruciform" (= "polypod"), or "vermiform", or "campodeiform" (= "oligopod"), while other insects hatch at the "campodeiform" phase [Lowne, 1890] or at a similar phase "Prosopon" [Berlese, 1913]. This classification of embryonic phases and larval types demonstrates diversity among Metabola, but not difference between Metabola and other insects (about "eruciform" and "campodeiform" larval types see below, 3.8).

Actually, in various insect taxa eggs have size from 0.05 mm to several millimeters, both among Metabola and among other insects. There is no any correlation between egg size and larval structure (or type of metamorphosis) — independently, if take into account egg size in relation to adult size, or absolute volume of eggs, or quantity of yolk. In many species of Metabola each egg is large enough to allow parasitic Hymenoptera to develop up to imaginal stage.

2.1.2. **Hypothesis about mould.** Some authors [Poyarkoff, 1914; Hinton, 1948; Lower, 1954; Du Porte, 1958; Ivanova-Kazas, 1961] regarded that two and only two moults (larval/pupal and pupal/imaginal ones) are necessary to that insects, whose imaginal shape strongly differs from larval shape, in order to create at one moult the imaginal shape (as a "mould"), and at the next moult — the imaginal musculature connected with the imaginal cuticle.

This is surely wrong, because other insects can get such or even greater differences in body shape and musculature during a single moult: in mayflies (Ephemeroptera) active larva and flying subimago (which are separated by one moult) can differ in body shape and musculature not less than larva and imago of such Metabola as Neuropteroidea; in whiteflies (Scytinelytra) larva and imago differ in shape, segmentation and musculature much more than larvae and imagoes of any Metabola, but larva transforms to imago at one moult. At the same time, in thrips (Thysanoptera) between larva (which is similar to imago) and imago there are 2 or 3 pupa-like inactive stages. In some Metabola (especially in Meganeuroptera), during transformation from larva to imago most part of muscles of trunk and mouth appendages, and even a part of leg muscles, do not change, retain contact with cuticle and are able to act at all phases of development.

In arthropods any change of body shape and size can appear in course of one moult, and no "intermediate forms" or "moulds" like pupa, are needed. If during the moult some body part has to change its shape and/or size so strongly, that can not find enough space under the old cuticle, it is pushed out into a neighbouring part of the body and develops under its cuticle up to the ecdysis. For example, in some Lepidoptera during moult from one larval instar to another, head capsule increases so strongly that before ecdysis is shifted into the thorax; this makes impossible feeding at the pre-moulting period, but does not cause appearing of a special non-feeding instar [Packard, 1898: 609].

2.2.3. **General failure of hypotheses about polyphyly of holometamorphosis.** If the holometamorphosis would appear thanks to its advantage at natural selection or some other universal reasons (see 2.2.1 and 2.2.2), it would either exist in all insects, or appear in that insect species whose mode of life provokes its appearing. Hypotheses of such kind could exist in the 18th–19th centuries, when there were accepted such artificial taxa as an order Neuroptera Linnaeus 1758, which united both holometamorphic and hemimetamorphic insect species. However, recent knowledge about insect phylogeny allows to state, that each taxon, whose holophyly is proven by good autapomorphies, has either all species holometamorphic, or all species non-holometamorphic, independently of their mode of life. This means, that existence of the holometamorphosis is determined not by mode of life, but by origin only. Now we do not know any reliable apomorphies which could prove any hypothesis about polyphyletic origin of holometamorphosis (and polyphyly of Metabola); as shown below, there are enough apomorphies proving its monophyletic origin.

2.2. Monophyletic origin of holometamorphosis

The idea about monophyletic origin of the taxon Metabola means that holometamorphosis is not caused by some reasons which could be explained, but was inherited by each holometamorphic species from the single common ancestor, which got this mode of metamorphosis as a result of a unique, casual, evolutionary event.

Recently most investigators accept Metabola as a holophyletic taxon. Nevertheless, autapomorphies of Metabola remain to be formulated as indistinctly as in the 19th century, and not much better than by Aristotle. The aim of this paper is to formulate exactly the autapomorphies of Metabola initial for this gigantic taxon as a whole, and to clarify which features of Metabola, being initial ones, caused appearing of other peculiarities of their ontogenesis.

The only reliable known autapomorphy of Metabola is the holometamorphosis. It is evident that such definitions of holometamorphosis as "great difference between larva and imago", "slight mobility of pupa" and "aphagy of pupa", while being correct, are not enough to argue monophyly of Metabola or to explain features of these insects. Those authors who limited themselves by such definitions of the holometamorphosis, regarded to be holometamorphic not only Metabola, but also some Condylognatha, namely Thysanoptera and Gallinsecta, and, thus, accepted polyphyly of this type of metamorphosis. Speaking about differences between larva and imago, it is necessary to determine exactly, which are these differences, because some difference exists between any instars of any arthropods. The statement about limited mobility of pupae also needs in a more precise definition, because within Metabola pupae vary from absolutely immovable to able for very active locomotion.

One of autapomorphies of Metabola is **pupal aphagy**: all Metabola are unable to eat during all pupal stage. It is not a unique feature: aphagy at these or that stages of development is widely spread among insects. Many Metabola lack not only pupal, but imaginal nutrition as well. The pupal aphagy is not connected with any known common morphological or anatomical feature of pupae. In many Metabola, during the larval/pupal moult, many or all mouth appendages strongly change their structure, lose muscles, and in pupa appear to be immovable. However, in such Metabola as Rhaphidioptera and Meganeuroptera, this does not occur [Kluge, in press]; in Birostrata, whose mandibular musculature is completely changed at pronymphal phase, young pupa already has new mandibular muscles and is able to bite. During the larval/pupal moult most part of intestine epithelium can be changed; however, in some caterpillars the same change of intestine epithelium takes place at moult from one larval instar to another, but this does not prevent to feed at these instars [Henson, 1946].

Such well-known features of the holometamorphosis as change of larval eyes to imaginal ones (see 5) and absence of external larval wing buds (see 6.2) are good autapomorphies of Metabola; but they could not be reasons for that sharp differences between larva, pupa and imago, which are so characteristic for most representatives of this taxon.

My special attention was attracted by transformation of legs, because it can determine other peculiarities of Metabola: as during the transformation from larva to imago the insect obligatory loses ability to use its legs, in its developmental cycle could appear the characteristic inactive pupal stage. In the beginning of investigation, I believed that the most primitive forms of Metabola could be found among species with long-legged larvae, as they seem to be most similar to other insects; however, as will be shown below, ways of larval/pupal leg transformation in Metabola with long-legged larvae are surprisingly variable, that leads to conclusion about secondary nature of this form.

3. Legs

3.1. Leg structure

While insect leg segmentation is described in numerous entomological text-books, for a long time taxonomic status of its characters remained to be unclear. Presence of coxa, trochanter, femur, tibia, tarsus and pretarsus were regarded to be characteristic for "insects" in various senses — from Euarthropoda to Pterygota. Some authors regarded this type of segmentation to be a character of Euarthropoda or Atelocerata; they saw that in some arthropods it is different, and concluded that it can also differ among Hexapoda. Because of this, for some Hexapoda (including some larvae of Metabola) there were suggested various homologizations of leg segments, sometimes quite fantastic. Recently it is shown that this leg segmentation represents a unique autapomorphy of Hexapoda [Kluge, 2000].

Typical leg of Hexapoda has the following structure (Fig. 1). Muscles going from trunk to leg, in the trunk are attached in limits of that half of that thoracic segment, to which the leg belongs; in the leg they are attached to coxa and trochanter only. Coxa is articulated dorsally (sometimes also ventrally) and moved by muscles attached in the thorax. Trochanter is movably articulated with the coxa by two condyles, moved by levator(s) attached in the coxa and depressors attached in the coxa and the thorax. Femur is attached to the trochanter usually without distinct condyles, moved by muscle(s) attached in the trochanter only. Tibia is composed of immovably fused patella and telotibia (suture separating them is retained in Odonata and Ephemeroptera only); the tibia is movably articulated to femur by two condyles (some authors wrongly regarded Entognatha to have one condylus only); it is moved by extensor(s) attached in the femur and flexor(s) attached in the femur and the trochanter. Tarsus is articulated with tibia by one condylus and moved by muscle(s) attached in the tibia (in patella and/or telotibia). Tarsus never has more than 5 segments; 5-segmented tarsus is initial either for Amyocerata, or for Hexapoda in general. Pretarsus bears a single long apodeme (unguitractor) which is moved by muscles attached in the femur and the tibia (both in the patella and the telotibia), but not in the tarsus (this is an autapomorphy of Atelocerata in general). Pretarsus bears two side claws; in Pterygota primary pretarsal claw is reduced, and dorsally two side claws are directly articulated with apex of the tarsus.

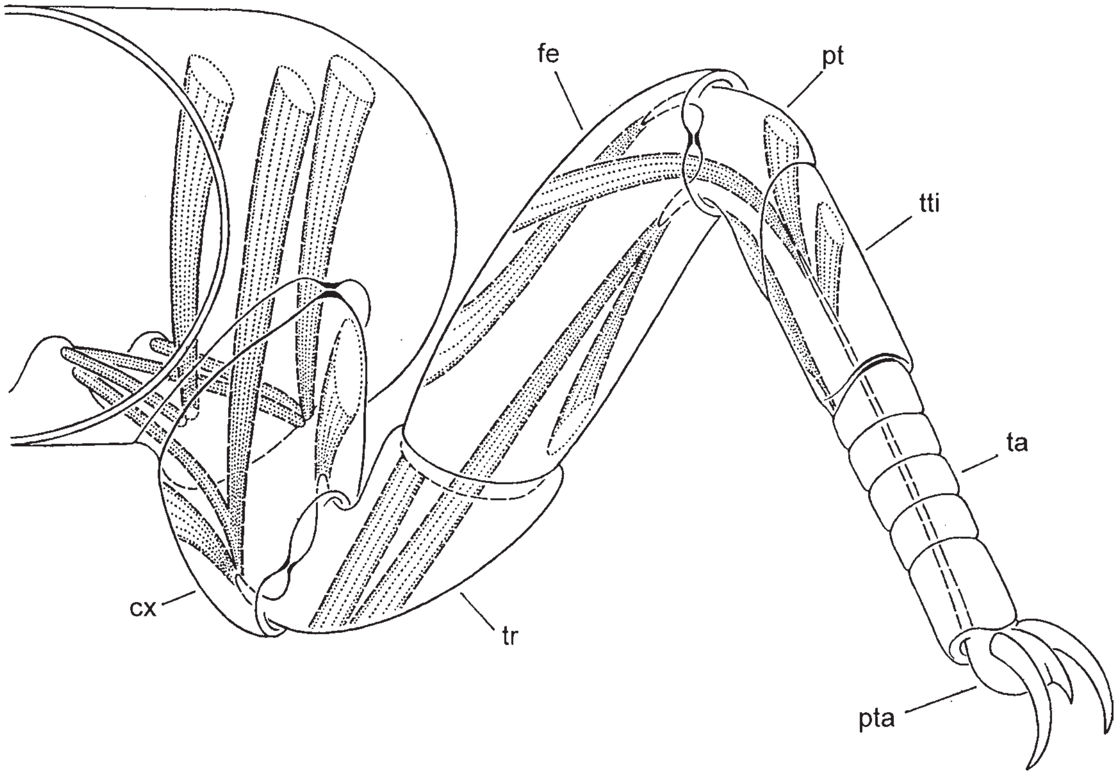


Fig. 1. General scheme of segmentation and musculature of leg of Hexapoda. Abbreviations: cx — coxa; fe — femur; pt — vestige of patella; pta — pretarsus; ta — tarsus; tr — trochanter; tti — telotibia.

Рис. 1. Общая схема расчленения и мускулатуры ноги Hexapoda. Сокращения: cx — тазик; fe — бедро; pt — вестигий пателлы; pta — претарсус; ta — лапка; tr — вертлуг; tti — телотибия.

In some Hexapoda this structure can be modified — some segments can be fused, or some muscles can be lost, or, vice versa, some additional muscles can appear as a result of division of the initial ones. But each leg segment of Hexapoda has so unique initial structure, that nearly always can be easily recognized, even in a strongly modified leg. Only five tarsal segments are initially similar, so when their number is less than five, it can be unclear which of them are lost or fused.

Articulation and musculature allow to establish undoubted phylogenetic homology of coxa, trochanter, femur, tibia, tarsus and pretarsus in all adult and larval Metabola discussed below, in spite of the fact that phylogenetically homologous segments are not obligatory ontogenetically homologous (see 3.6).

In all Metabola larval leg has no tarsal segmentation, while pupal-imaginal leg has tarsus usually 5-segmented. The formerly published information about two-segmented larval tarsus in Nannomecoptera appeared to be wrong [Kluge, 2004b]. In other respects larval leg of Metabola can have all structural details initially peculiar for the leg of Hexapoda.

In all Metabola larval leg differs from pupal-imaginal not only by the absence of tarsal segmentation, but also by all taxonomic characters more particular than the general characters of Hexapoda and Pterygota. This is due not only to shape of legs, but also to chaetotaxy (which is determined by arrangement of sensory neurons in hypoderm). Unlike legs, some other parts of the body can have features common for larvae, pupae and/or imago of the same taxon (for example, head structure in Rhaphidioptera, maxillary chaetotaxy in *Sialis* [Kluge, in press], structure of head and prothorax in Eumegaloptera [Kelsey, 1954], larval-pupal urogomphs in Coleoptera).

3.2. Problem of leg transformation

In all Metabola the process of transformation from larva to pupa is accompanied by a period of immobility, when insect can not locomote at least by help of legs; this period covers a final part of the last larval instar (this part of larval stage is named **pronymph**, or **prepupa**) and at least the most part of pupal stage (often the whole pupal stage). In many Culex/fg1 (incl. *Chironomus*) and some other Diptera, larvae and pupae can actively locomote during all development, but this is connected with the fact that larvae have no legs, and larvae and pupae locomote without help of legs. The obligatory presence of the resting period can not be explained by great difference in structure and size between larval and imaginal legs. In some Metabola (such as Trichoptera and most Neuropteroidea) difference between larval and imaginal legs in not greater than in such insects as Ephemeroptera and others, which develop without resting period and are able to walk actively by their legs during all development. There must be some other explanation, why in Metabola transformation from larval to imaginal legs is always accompanied by temporary loss of walking ability.

Birket-Smith [1984] assumed that larval legs (which he called "prolegs") are non-homologous to the true legs of pupa and imago, and because of this in the process of metamorphosis they have to disappear and to be substituted by the true legs. He grounded this theory only by data about musculature and innervation of limbs in larvae, pupae and imagoes, not tracing transformation from one stage to another. Against the Birket-Smith's theory testify following facts: (1) in all Metabola larval and imaginal legs have the plan of Hexapoda leg, which is not found in other limbs and in other groups of arthropods (see 3.1); (2) in all Metabola epithelium of the pupal-imaginal leg is completely or at least partly retained from the larval leg (see 3.3–5); (3) in *Sialis* not only all epithelium, but partly musculature of the pupal-imaginal leg is retained from the larval leg (see 3.3.2).

Tichomirova [1976, 1983, 1991] suggested an opposite idea, that in Metabola the larval leg directly transforms to the pupal leg, and the taxon Metabola has no any peculiarities of larval/pupal leg transformation. This conclusion was based on her interpretation of indirect experiments on leg transformation in a single species *Tenebrio molitor*. As will be shown below (3.3.2), her interpretation is erroneous and contradicts the direct observation of leg transformation in this species.

3.3. Leg transformation in Metabola with long-legged larvae

Relatively long larval legs (see 3.8) are present in most Neuropteroidea (all Rhaphidioptera, all Meganeuroptera and most Birostrata), in some Coleoptera, in Trichoptera and in a few representatives of Lepidoptera. Till now, leg transformation of these insects was not described. Below, there are given descriptions of leg transformation in several species belonging to Trichoptera, Coleoptera and Neuropteroidea.

During the larval/pupal transformation, larval legs, being immovable, retain that poses which they got when the larva was active and could move its legs. These poses can be different in different specimens and different legs of the same specimen: legs can be variously directed, can be either straight, or in this or that degree bent in coxotrochanteral or/and femorotibial articulations. Pose of larval leg does not influence on process which takes place inside it. In this paper, in Figs 13–20 and 25–29 legs are shown in their natural position; in Figs 2–7, 8–9, 21–24 and 32–36 legs are shown as if they had the same pose.

Larval legs can be long only relatively to legs of other larva of Metabola, but they are much shorter than pupal and imaginal legs of the same individual (compare Figs 9 and 10; 36 and 37; 45 and 46). Thus, one can think that during larval/pupal transformation the leg hypoderm under the old larval cuticle should grow. But actually in all long-legged species examined, except for *Sialis*, leg hypoderm at first strongly diminishes, and only after this starts to grow. During this diminishing, the leg loses its musculature and changes its shape from larval to pupal. As shown below, methods of leg diminishing are unusually diverse: there can be nearly even anti-growth (see *Rhyacophila nubila*, *Tenebrio molitor*, *Leptinotarsa decemlineata*), or sharply uneven anti-growth (see *Myrmeleon bore*), or waste-less breaking (see *Chrysoperla carnea* and *Chrysotropia ciliata*). Ontogenetic homology of leg segments can be either kept (see *Rhyacophila nubila*, *Myrmeleon bore*, *Sialis sordida*), or not (see *Tenebrio molitor*, *Leptinotarsa decemlineata*, *Chrysoperla carnea* and *Chrysotropia ciliata*).

3.3.1. **Trichoptera: *Rhyacophila nubila*** (Figs 2–11). Cocoons of *Rhyacophila nubila* Zetterstedt 1840, containing pronymphs and pupae at various phases of development, were collected 11 June 1992 in Peterhoff Canal (Saint Petersburg, Russia). There were examined more than 50 pronymphs. Living parts of legs are seen through cuticle of intact specimens fixed in alcohol; because of this, only 16 pronymphs were dissected and mounted on slides in Canadian balsam fore closer examination.

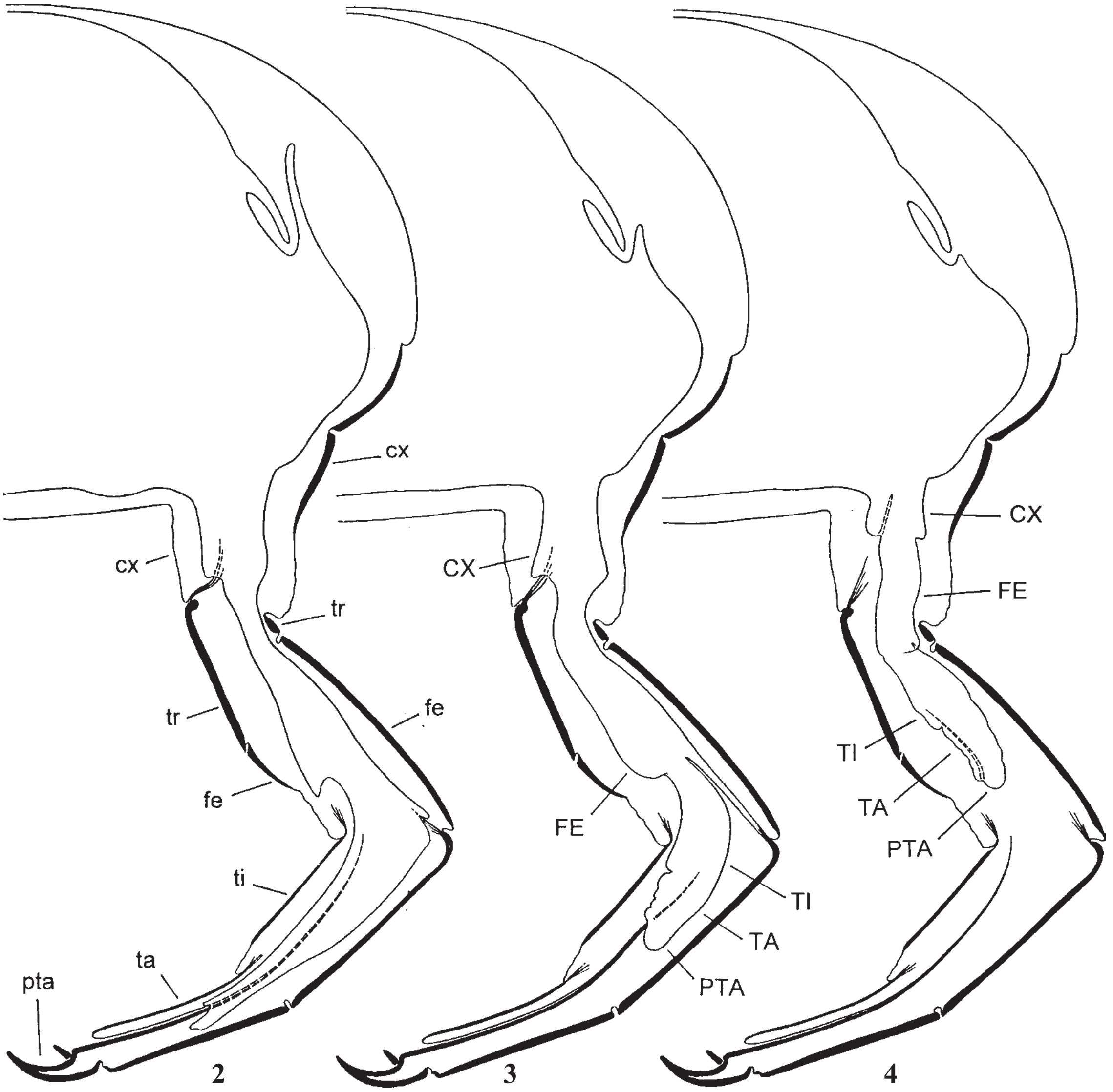
Larval legs are dissimilar: fore legs are shorter and stouter than middle and hind legs. In pronymph the fore legs are directed forward, and middle and hind legs are directed backward (Figs 8, 9). The larval/pupal leg transformation starts with degeneration of musculature and diminishing of hypoderm. At the beginning of this process, fore legs retain their musculature for a longer time, than middle and hind legs do; especially this is due to coxal musculature.

After building a silk cocoon, larva loses ability to leg movements (i.e. becomes a pronymph). Leg hypoderm detaches from the larval cuticle, and leg musculature degenerates. Than (after formation of a hard brown cocoon) the living part of leg undergoes intensive anti-growth and, as a result of it, becomes so small, that terminates inside the larval cuticular femur. Remaining to have the same small size, the living part of leg gets a pupal-imaginal structure. Only after this it starts to grow. The process of leg transformation can be arbitrarily divided into the following phases:

1st phase (3 specimens examined). *In all legs* hypoderm is partly detached from cuticle; in tibia and tarsus it undergoes some anti-growth. *In fore leg* either all muscles (located in coxa, femur and tibia) are retained, or some muscles undergo degeneration. *In middle and hind legs* (Fig. 2) either all muscles are completely lost, or non-functional vestiges of some muscles are retained.

2nd phase (1 specimen examined). *In fore leg* the living tibia and tarsus become so small, that completely locate in the larval cuticular tibia; coxa and femur retain larval structure and muscles. *In middle and hind legs* (lacking muscles) hypoderm of all segments undergoes such anti-growth, that apex of the living part of leg is shifted into the middle of the larval cuticular tibia (Fig. 3).

3rd phase (1 specimen examined). *In fore leg* femur undergoes anti-growth, its muscles lost connection with knee and partly degenerate (while in coxa most muscles are retained); apex of the living part remains to locate in the larval cuticular tibia. *In middle and hind legs* (lacking muscles) apex of the living part is shifted into the larval cuticular femur; the living part gets a dorsal knee



Figs 2–4. *Rhyacophila nubila*, pronymphs of successive phases of development (arbitrary 1st, 2nd and 4th — see the text), cross section of right half of metathorax. Setae not drawn. Larval cuticular leg shown as optic section; living part of leg shown from behind. Abbreviations: CX — future pupal coxa; cx — larval cuticular coxa; FE — future pupal femur; fe — larval cuticular femur; PTA — future pupal pretarsus; pta — larval cuticular pretarsus; TA — future pupal tarsus; ta — larval cuticular tarsus; TI — future pupal tibia; ti — larval cuticular tibia. tr — larval cuticular trochanter.

Рис. 2–4. *Rhyacophila nubila*, пронимфы последовательных фаз развития (условных 1-й, 2-й и 4-й — см. текст), поперечный срез правой половины заднегруди. Щетинки не нарисованы. Личиночная кутикулярная нога показана как оптический срез; живая часть ноги показана сзади. Сокращения: CX — будущий куколочный тазик; cx — личиночный кутикулярный тазик; FE — будущее куколочное бедро; fe — личиночное кутикулярное бедро; PTA — будущий куколочный претарсус; pta — личиночный кутикулярный претарсус; TA — будущая куколочная лапка; ta — личиночная кутикулярная лапка; TI — будущая куколочная голень; ti — личиночная кутикулярная голень. tr — личиночный кутикулярный вертлуг.

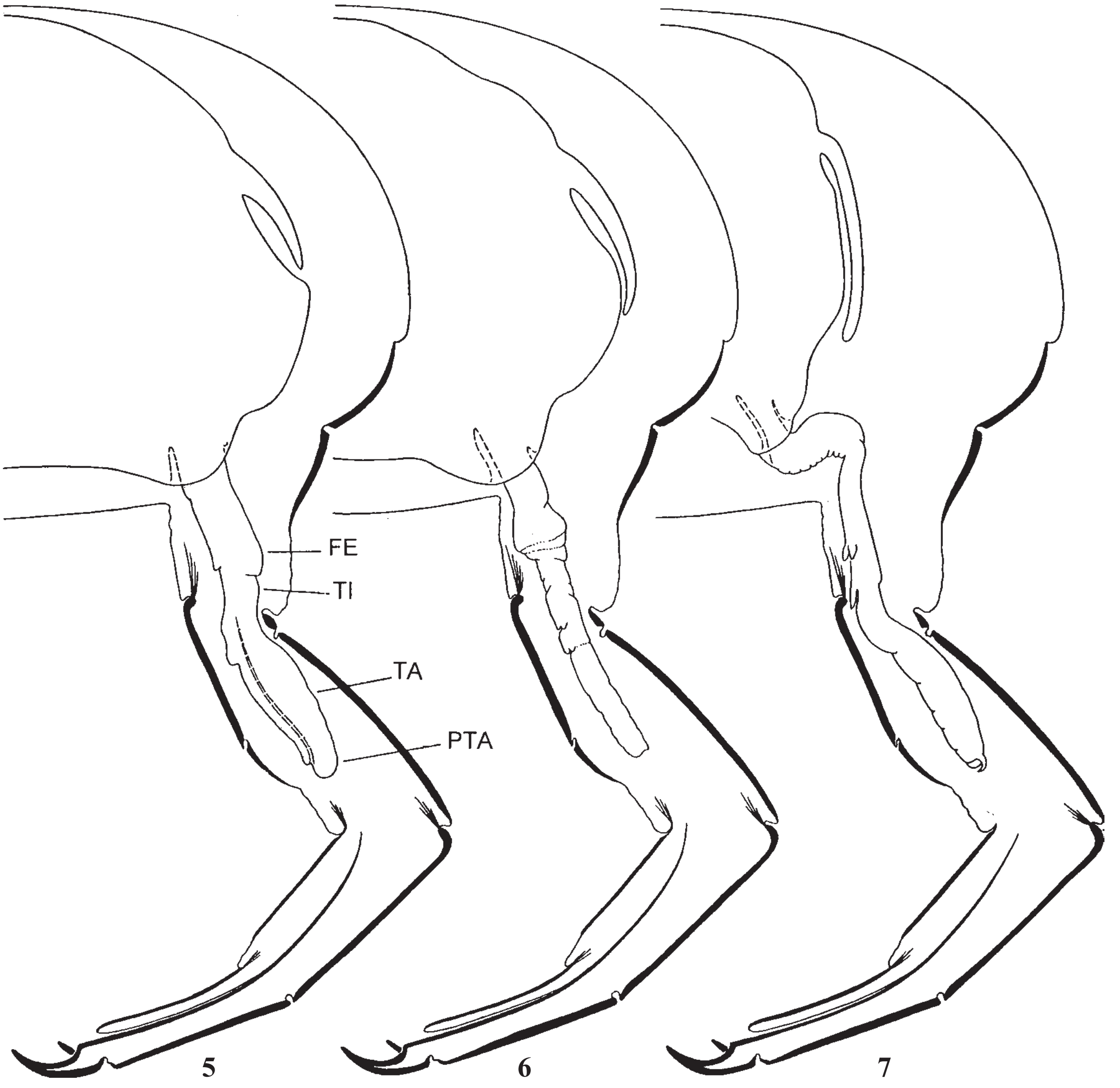
fold shifted into the larval cuticular trochanter (as in Fig. 4) and buds of pupal-imaginal details — bilobed pretarsus and four protuberances corresponding to tibial spoors (as in Figs 4–5).

4th phase (1 specimens examined). *In fore leg* apex of the living part is shifted into the larval cuticular femur; coxal muscles are partly retained. *Middle and hind legs* are as at the 3rd phase (Fig. 4).

5th phase (1 specimens examined). *Fore leg* as at the 4th phase. *In middle and hind legs* (Fig. 5) the living coxa and femur undergo anti-growth, thus the dorsal knee fold (which appeared at the 3rd phase) is shifted into the larval cuticular coxa.

6th phase (2 specimens examined). *In fore leg* all muscles disappear. *In middle and hind legs* (Fig. 6) living part (terminated in the larval cuticular femur and bearing buds of spoors and claws) gets a distinct thickening at apex of femur. Now in all legs living part is muscle-less and terminates in the larval cuticular femur.

7th phase (3 specimens examined). *In all legs* (Fig. 7) the living part gets a knee bent; as a result of this, its femur and a part of tibia are shifted into the space



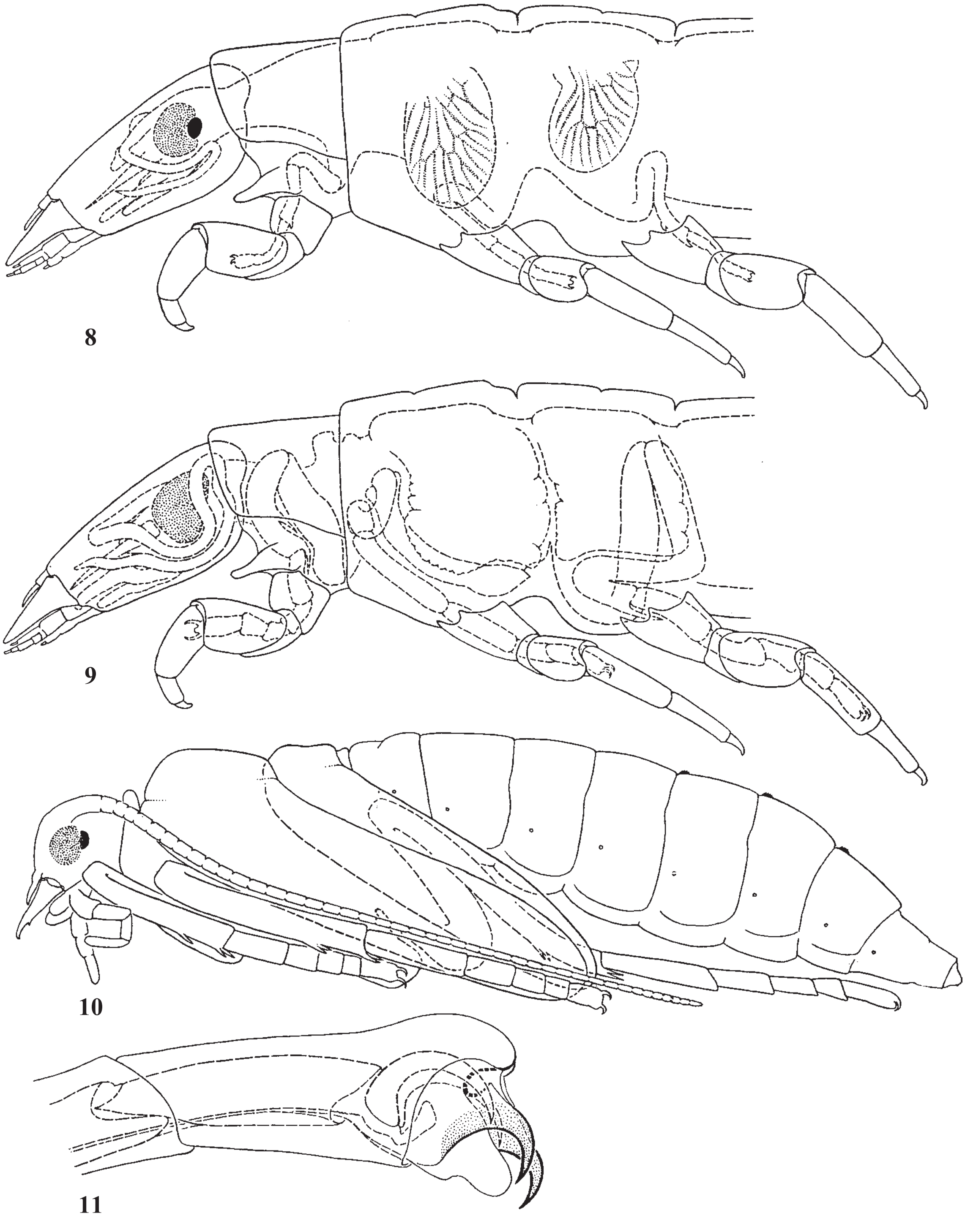
Figs 5–7. *Rhyacophila nubila*, pronymphs at successive phases of development (arbitrary 5th, 6th and 7th — see the text), cross section of right half of metathorax. Comments and abbreviations as in Figs 2–4.

Рис. 5–7. *Rhyacophila nubila*, пронимфы последовательных фаз развития (условных 5-й, 6-й и 7-й — см. текст), поперечный срез правой половины заднегруди. Комментарии и сокращения как на рис. 2–4.

between the trunk hypoderm and the larval trunk cuticle. Pupal claws become distinct on all legs.

Phase of growth (4 specimens examined). After the shortening, the living part of leg starts to grow. Thanks to the knee bent, femur and most part of tibia elongate, locating under the larval trunk cuticle (Fig. 8). During subsequent growth, the femur and tibia, appearing in a cramped space between the larval trunk cuticle and the growing trunk tissues, bent at several places (Fig. 9). After the larval/pupal moult, the pupal legs spread in such a manner, that all bends caused by the cram, become spread, and knee bends which were formed initially, are retained (Fig. 10). During the leg growth, muscles do not appear, and after the larval/pupal moult legs remain to be muscle-less. Leg musculature appears later, when under the pupal cuticle appears imaginal integument (Fig. 11).

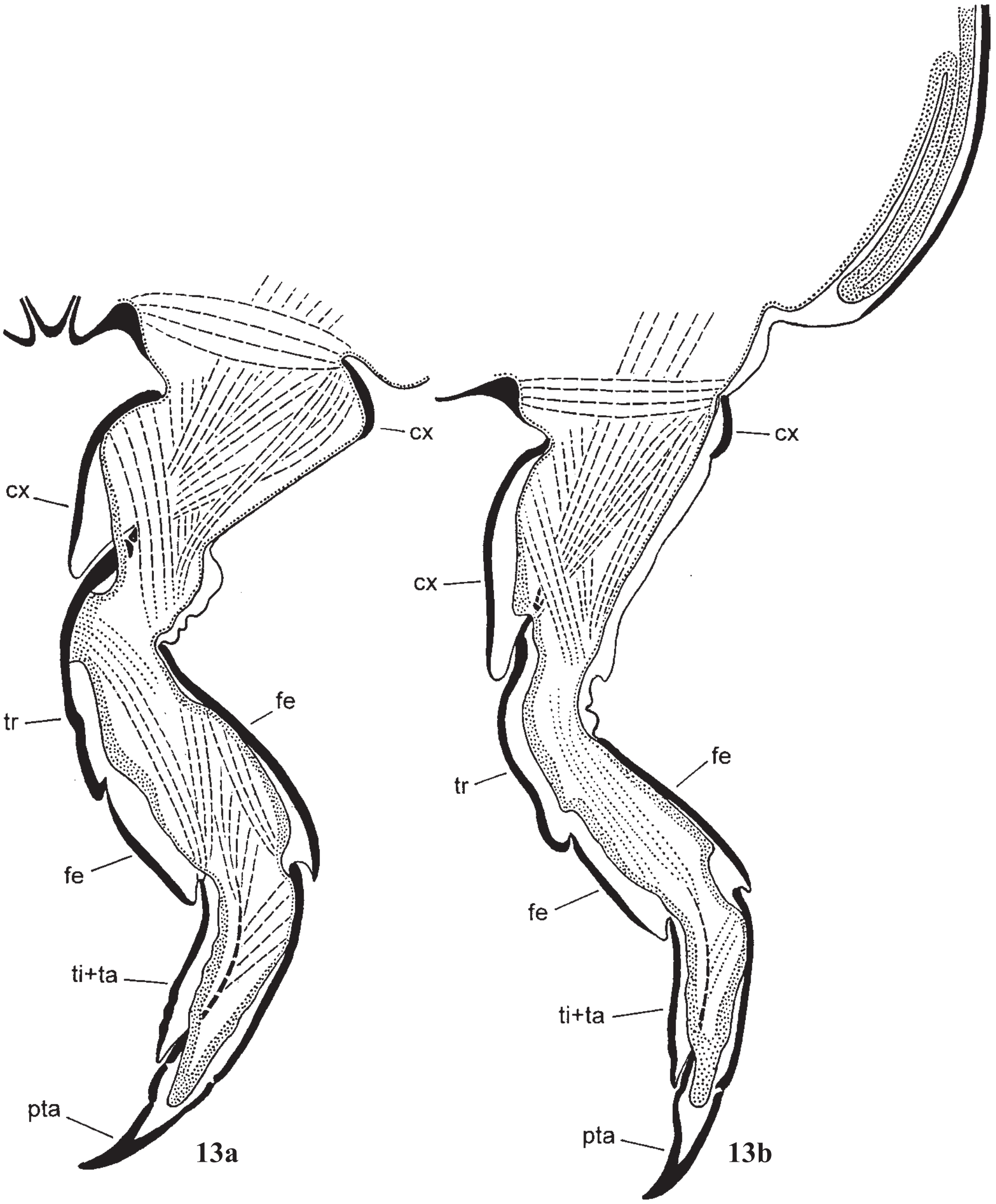
At least coxa, femur and tibia of pupal-imaginal leg are ontogenetically homologous to the phylogenetically homologous larval leg segments. This can be traced if compare the living part of leg in specimens at different phases of leg anti-growth. When (at the 2nd phase) the hypoderm still retains a bridge connecting it with apodeme of tibial extensor, living part distad of this place already has a ventral incision between tibia and tarsus and thickenings corresponding to pupal apical tibial spurs (Fig. 3). The living tibia and tarsus retain the same shape being shifted into the larval cuticular femur, when (at the 3rd phase) appears a dorsal knee fold separating the future pupal femur from the future pupal tibia (Fig. 4). This shifting takes place because of anti-growth of the living coxa and femur. Thanks to further anti-growth of the living



Figs 8–11. *Rhyacophila nubila*: 8–9 — head and thorax of pronymphs, lateral view (living part shown by interrupted line): 8 — at beginning of phase of leg growth; 9 — just before ecdysis (pharate pupa); 10 — young pupa, lateral view (hidden parts shown by interrupted line); 11 — pharate imago, apex of fore leg (imaginal cuticle shown by interrupted line). Setae not drawn. Larval eye black, bud of imaginal eye dotted.

Рис. 8–11. *Rhyacophila nubila*: 8–9 — голова и грудь пронимф, латерально (живая часть показана прерывистой линией): 8 — в начале фазы роста ног); 9 — перед самым экдизисом (фаратная куколка); 10 — молодая куколка, латерально (скрытые части показаны прерывистой линией); 11 — фаратное имаго, вершина передней ноги (имагинальная кутикула показана прерывистой линией). Щетинки не нарисованы. Личиночный глаз показан черным, имагинальный глаз пунктирован.

12



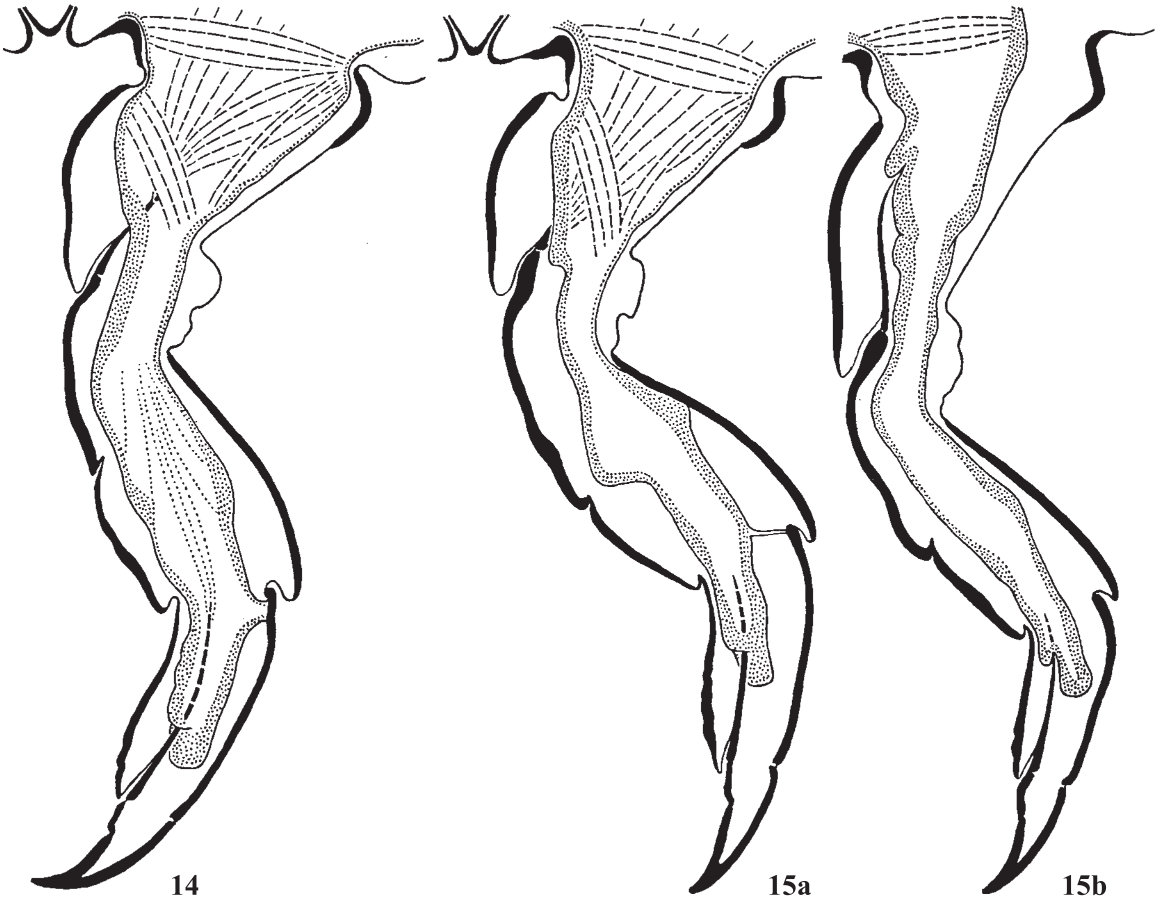
Figs 12–13. *Tenebrio molitor*. 12 — active larva of last instar, cross section of lateral part of mesothorax with bud of protopteron. 13 — early pronymph able to crawl (arbitrary 1st phase): 13a — fore leg; 13b — middle leg and cross section of protopteron bud. Setae not drawn. Trunk cuticle shown as section, larval cuticular leg shown as optic section. Other comments and abbreviations as in Fig. 16.

Рис. 12–13. *Tenebrio molitor*. 12 — активная личинка последнего возраста, поперечный срез латеральной части среднегруди с зачатком протоптерона. 13 — ранняя пронимфа, способная ползать (условная 1-я фаза): 13a — передняя нога; 13b — средняя нога и поперечное сечение зачатка протоптерона. Щетинки не нарисованы. Кутикула туловища показана в разрезе, личиночная кутикулярная нога показана как оптический срез. Прочие комментарии и сокращения как на рис. 16.

coxa, the future pupal knee shifts into the larval cuticular coxa (Fig. 5); at this phase shape of the living part is comparable with previous phases (Figs 3–4), but position and length of segments are already the same as in small bud of pupal leg which has buds of all four tibial spurs and two apical pretarsal claws (Fig. 6).

3.3.2. **Coleoptera: *Tenebrio molitor*** (Figs 13–20). Larvae of *Tenebrio molitor* Linnaeus 1758 were taken from a laboratory culture; 30 pronymphs were fixed at various phases of transformation, dissected and mounted on slides in Canadian balsam.

As in all Polyphaga, larval leg has an integral tibiotarsus and a single claw on pretarsus. Homology of these segments is undoubted, because pretarsus has a single large apodeme — unguitractor, from which muscles go into tibia and femur (Fig. 13a), as in all other Hexapoda (see 3.1 and Fig. 1). Some authors suggested for larval legs of Polyphaga other homologizations, which are not grounded (see review by Tichomirova [1983]).



14 **15a** **15b**

Figs 14–15. *Tenebrio molitor*, two pronymphs able to crawl by help of fore legs only (arbitrary 2nd phase), optic section of legs: 14 and 15a — fore leg; 15b — middle leg. Comments as in Fig. 16.

Рис. 14–15. *Tenebrio molitor*, две пронимфы, способные ползать только с помощью передних ног (условная 2-я фаза), оптический срез ног: 14 и 15a — передняя нога; 15b — средняя нога. Комментарии как на рис. 16.

Larval legs of *T. molitor* are dissimilar: fore legs are stronger than others and are used for burrowing. The larval/pupal leg transformation starts with degeneration of musculature and diminishing of hypoderm. At the beginning of this process, fore legs retain their musculature for a longer time, than middle and hind legs do; especially this is due to coxal musculature (Figs 13a–b, 15a–b, 16a–c, 17a–c). Thus, during some period, larva is able to move forward and burrow, using fore legs only; this period is very short (no more than one day), and, hence, can not have adaptive significance.

At first, hypoderm detaches from cuticle, and the living part of leg undergoes anti-growth, thus its apex shifts at first into the larval cuticular tibiotarsus, and than into the larval cuticular femur. After the anti-growth starts, leg muscles begin to disappear: at first in middle and hind legs, later in fore legs; at first in tibiotarsus and femur, later in coxa. The process of leg transformation can be arbitrarily divided into the following phases:

1st phase (1 specimen examined) (Figs 13a–b). Hypoderm starts to detach from cuticle and undergoes some anti-growth. *In fore leg* (Fig. 13a) nearly all muscles remain to be functional. *In middle and hind legs* (Fig. 13b) muscles of femur and tibiotarsus lost cross-striation; muscles of coxa remain to be functional.

2nd phase (8 specimens examined) (Figs 14, 15a–b, 16a–c, 17a–c). Hypoderm is completely or nearly completely detached from cuticle. *In all legs* at least portion distad of coxa lost muscles. *In fore leg* (Figs 14, 15a, 16a, 17a) coxa retains large larval size and functional muscles (depressors and levators of trochanter). *In middle and hind legs* (Figs 15b, 16b–c, 17b–c) living coxa undergoes strong anti-growth and lost muscles. In spite of difference in size of the living coxae, in all legs apex of the living part of leg locates at the same level — in proximal part of the larval cuticular tibiotarsus.

3rd phase (3 specimens examined). *In fore leg* living coxa undergoes strong anti-growth and lost muscles; apex of the living part of leg locates in proximal part of the larval cuticular tibiotarsus (thus, fore leg at the 3rd phase resembles middle and hind legs at the 2nd phase). *Middle and hind legs* either remain to be as in the 2nd phase, or have apex of the living part of leg shifted into the larval cuticular femur.

4th phase (8 specimens examined) (Fig. 18). The living parts of all legs become similar. Future pupal

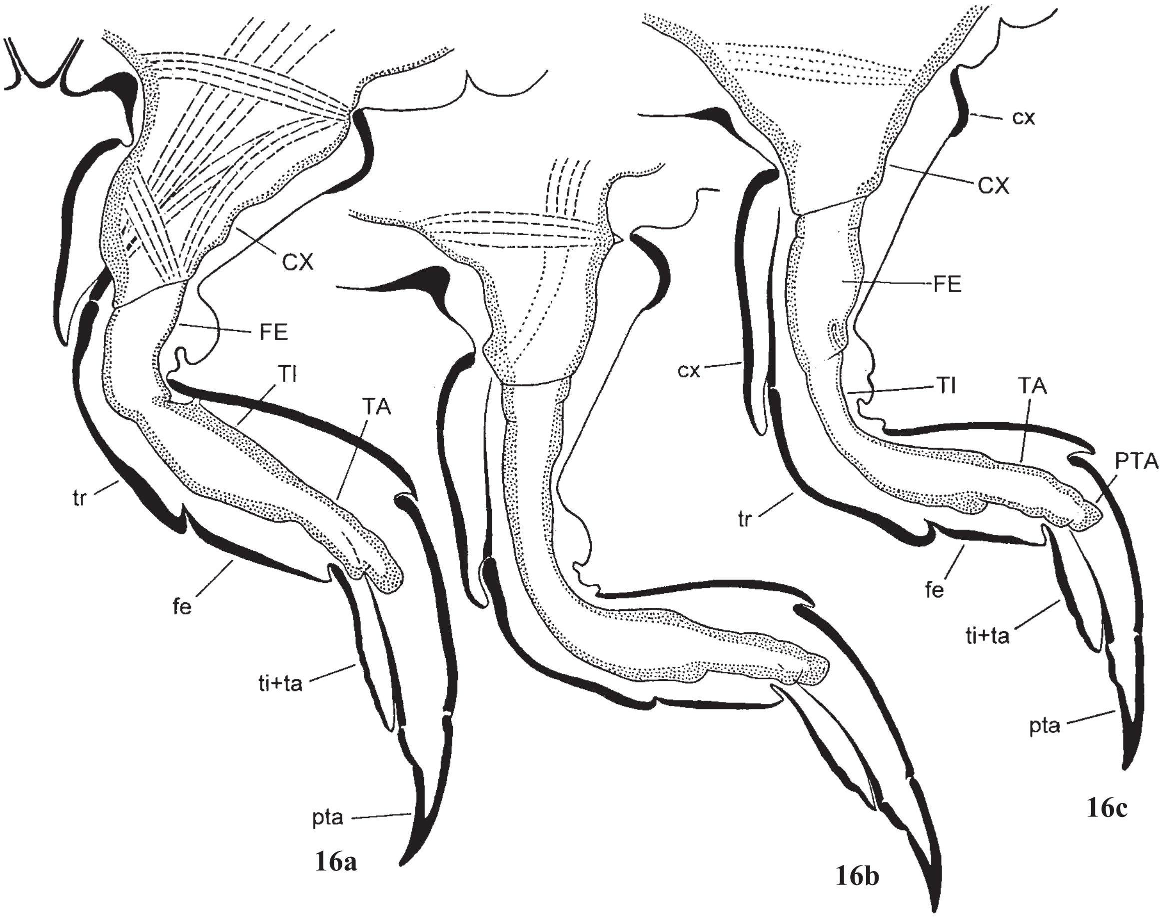


Fig. 16. *Tenebrio molitor*, pronymph able to crawl by help of fore legs only (arbitrary 2nd phase): a — fore leg; b — middle leg; c — hind leg. Setae not drawn. Larval cuticle shown as optic section by black. Living part of leg shown from behind, but thickness of hypoderm shown as optic section by dots. Functional cross-striated muscles shown by interrupted lines, non-striated muscular vestiges shown by dotted lines. Abbreviations: CX — future pupal coxa; cx — larval cuticular coxa; FE — future pupal femur; fe — larval cuticular femur; PTA — future pupal pretarsus; pta — larval cuticular pretarsus; TA — future pupal tarsus (former larval tibiotarsus); ti+ta — larval cuticular tibiotarsus; TI — future pupal tibia (former larval femur); tr — larval cuticular trochanter.

Рис. 16. *Tenebrio molitor*, пронимфа, способная ползать только с помощью передних ног (условная 2-я фаза): a — передняя нога; b — средняя нога; c — задняя нога. Щетинки не нарисованы. Личиночная кутикула показана черным как оптический срез. Живая часть ноги показана сзади, но толщина гиподермы показана пунктировкой как оптический срез. Функционирующие поперечно-полосатые мышцы показаны прерывистыми линиями, гладкие остатки мышц показаны точечными линиями. Сокращения: CX — будущий куколочный тазик; cx — личиночный кутикулярный тазик; FE — будущее куколочное бедро; fe — личиночное кутикулярное бедро; PTA — будущий куколочный претарсус; pta — личиночный кутикулярный претарсус; TA — будущая куколочная лапка (бывший личиночный тибиотарсус); ti+ta — личиночный кутикулярный тибиотарсус; TI — будущая куколочная голень (бывшее личиночное бедро); tr — личиночный кутикулярный вертлуг.

femur becomes thick and short, a slightly expressed knee bend appears. Apex of the living part locates in the larval cuticular femur.

5th phase (6 specimens examined) (Fig. 19). Knee bent becomes sharp, thus future pupal femur and a part of future pupal tibia are shifted into the space between the trunk hypoderm and the larval trunk cuticle. Appear buds of pupal-imaginal details — two apical tibial spoors and two pretarsal claws.

Phase of growth (4 specimen examined) (Fig. 20). The living part of leg grows, becoming thicker and forming numerous small folds; but up to the larval/pupal moult it remains to occupy the same space as in the final (5th) phase of anti-growth, with its apex inside the larval cuticular femur and its knee under the larval trunk cuticle. During the leg growth muscles do not appear, and after the larval/pupal moult legs remain to be muscle-less.

During the 1st–3rd phases of leg transformation, shape of the living part remains to be rather constant, that allows to distinguish its areas: the area corresponding to apex of the larval femur, is widened, with thick epithelium; the area corresponding to the larval knee, is narrower, with thinner epithelium; in the area corresponding to the larval tibiotarsus, epithelium becomes thicker toward apex. Boundary between areas corresponding to the lar-

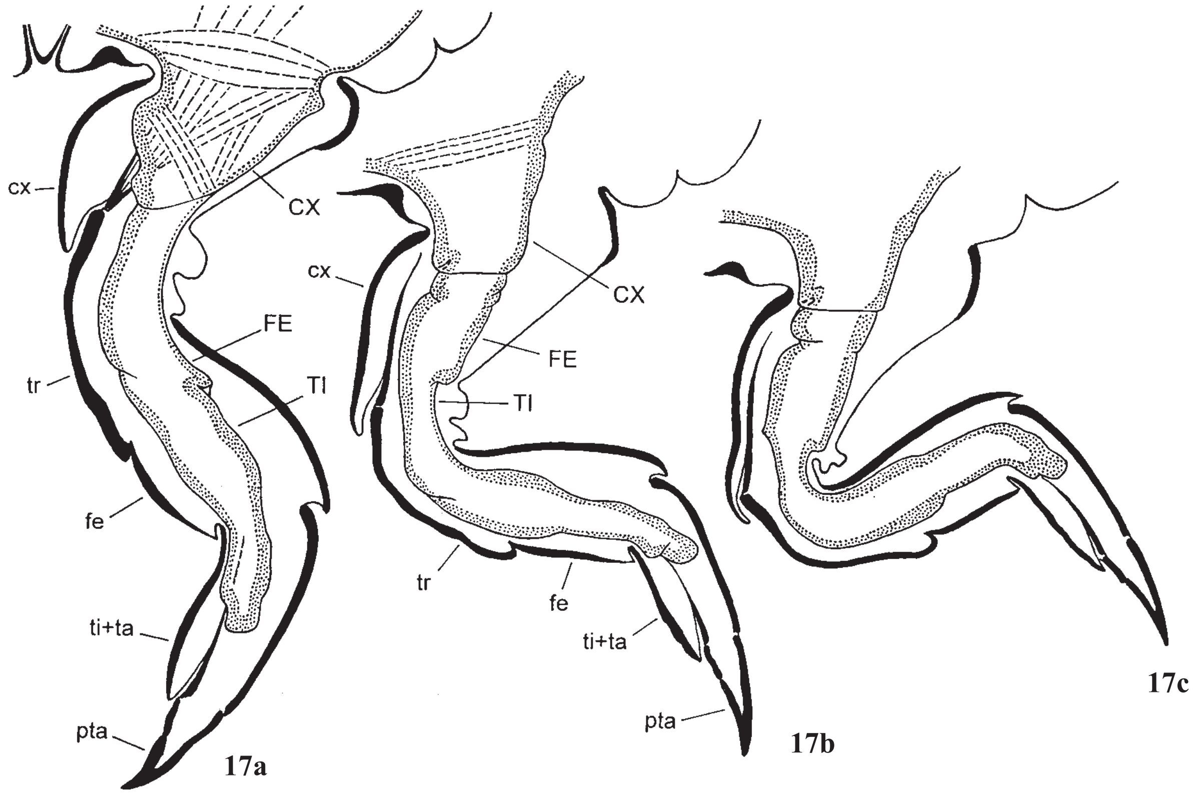


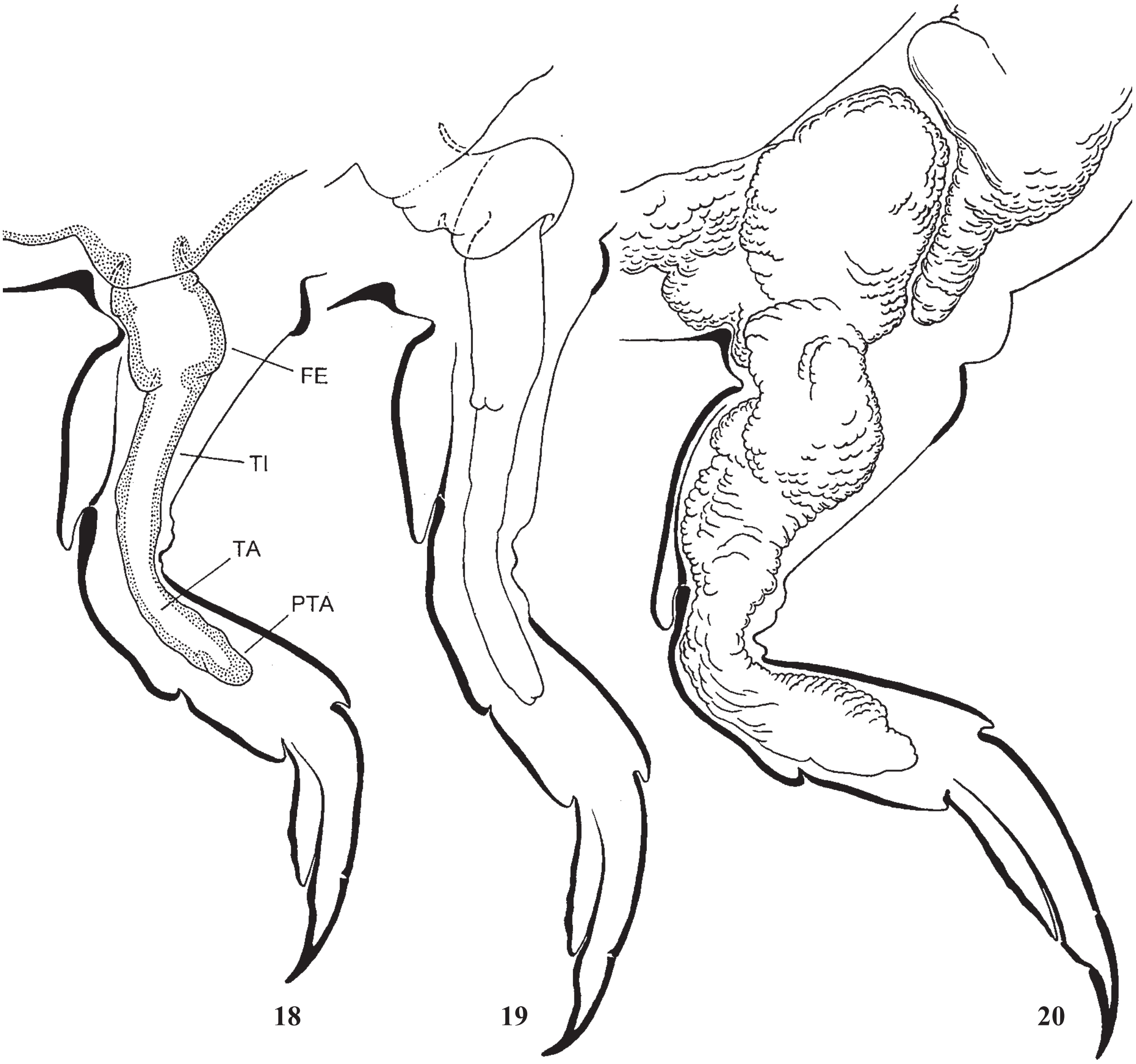
Fig. 17. *Tenebrio molitor*, pronymph able to crawl by help of fore legs only (arbitrary 2nd phase), optic section of legs: a — fore leg; b — middle leg; c — hind leg. Comments and abbreviations as in Fig. 16.

Рис. 17. *Tenebrio molitor*, пронимфа, способная ползать только с помощью передних ног (условная 2-я фаза): a — передняя нога; b — средняя нога; c — задняя нога. Комментарии и сокращения как на рис. 16.

val tarsus and pretarsus is marked by the opening of pretarsal apodeme. The area corresponding to the larval coxa, during some time retains larval coxal muscles or their remnants (Figs 13–17). Boundaries between segments of future pupal-imaginal leg appear, when shortening of the leg is not finished yet. Namely, pupal-imaginal knee articulation becomes distinguishable at the 2nd phase; it appears not at the area corresponding to the larval knee articulation, but much more proximally: on fore leg (which at this phase retains long coxa with larval coxal muscles) the pupal-imaginal knee appears at first inside the base of the larval cuticular femur (Figs 16a, 17a), and only later shifts into the larval cuticular coxa; on middle and hind legs (which at this phase have coxa shortened) the pupal-imaginal knee appears inside the larval cuticular coxa (Figs 16c, 17b–c). Thus, tissues of the larval femur give rise to the pupal-imaginal femur and tibia, and tissues of the larval tibiotarsus give rise to the pupal-imaginal tarsus only (Fig. 57).

Tichomirova [1976, 1983, 1991], in order to clarify the process of larval/pupal leg transformation in *Tenebrio molitor*, studied influence of analogues of juvenile hormone and results of extirpation of leg segments. Using these indirect methods only, she came to conclusion that (1) each larval leg segment gives rise to the homologous pupal-imaginal leg segment; (2) under larval cuticle the living part of leg only grows and differentiates; (3) at some phase (called "pronymphoid stage") the living part of leg has separate tibia and one-segmented tarsus, that was regarded to be recapitulation of leg structure characteristic for larval Adephagi. Actually, as can be seen from direct observation of pronymphal legs, all these conclusions are incorrect: (1) larval femur gives rise to pupal-imaginal tibia; (2) the living part of leg passes through diminishing and dedifferentiation, and only after this grows and differentiates; (3) there is no phase with one-segmented tarsus separated from tibia; there is only the phase when the future pupal tibia+tarsus retains separation between the former larval femur and tibiotarsus (Figs 16 and 17). Most probably, the methods used by Tichomirova, are not adequate. She believed that abnormal individuals which appear under influence of juvenile hormone analogues, have structure of the "concealed stages" intermediate between larva and pupa; but judging by her figures, this is not so. Correct interpretation of experiments with extirpation of leg segments is difficult, because in each case it is unclear at which phase of leg transformation the extirpation was made. Unlike some other insects, in *Tenebrio molitor* pronymphal legs are non-translucent in alive condition, and tissues can be well visible only after putting dehydrated leg into xylene.

3.3.3. **Coleoptera: *Leptinotarsa decemlineata*** (Figs 21–24). Pronymphs of *Leptinotarsa decemlineata* (Say 1824 [*Chrysomela*]) were got from larvae collected in

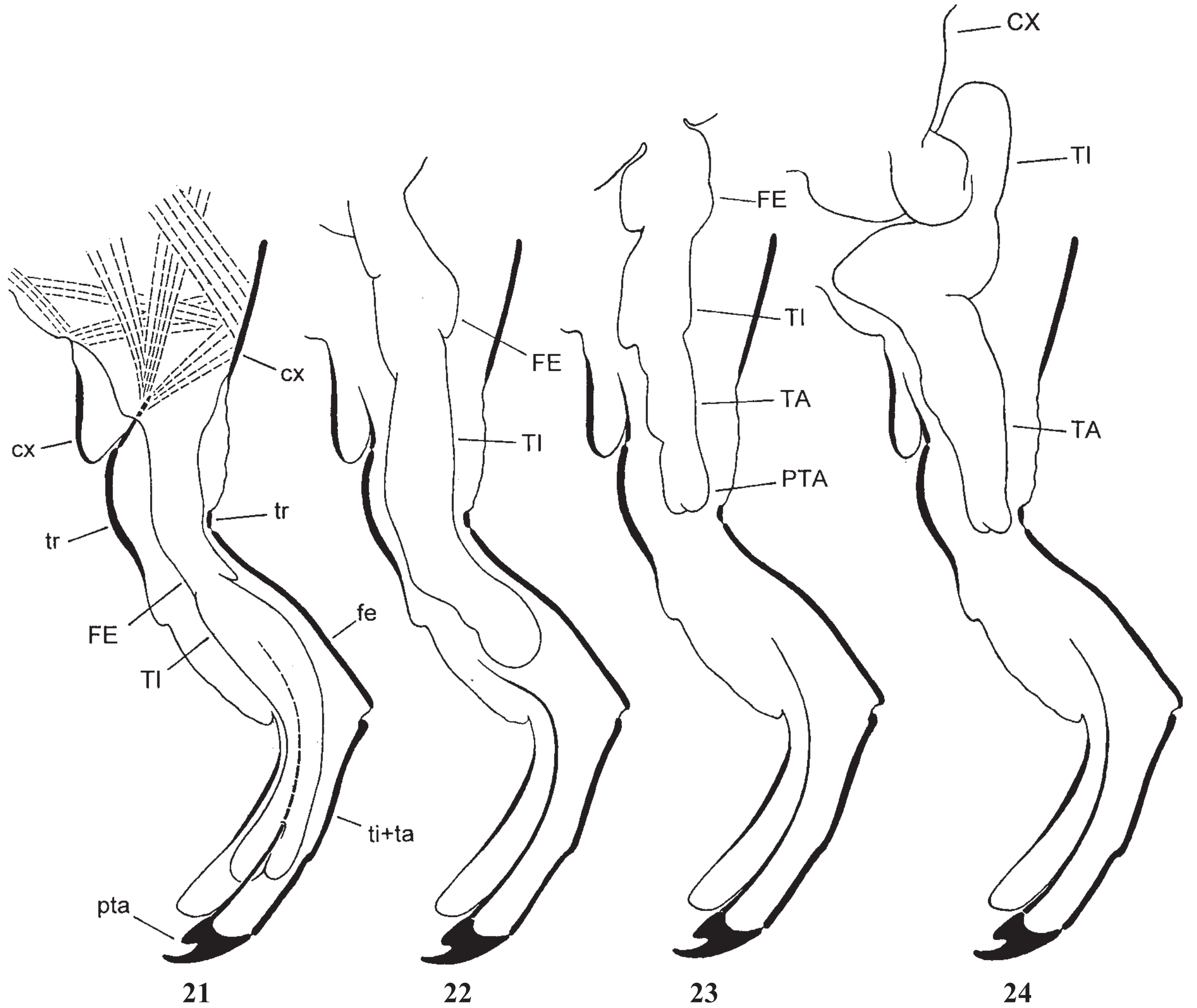


Figs 18–20. *Tenebrio molitor*, pronymphs at successive phases of development (arbitrary 4th, 5th and the last — see the text), optic section of middle leg. For Figs 18 comments and abbreviations as for Fig. 16; in Figs 19–20 cuticle shown as optic section, living part shown from behind only, thickness of hypoderm not shown.

Рис. 18–20. *Tenebrio molitor*, пронимфы последовательных фаз развития (условных 4-й, 5-й и последней — см. текст), оптический срез средней ноги. К рис. 18 комментарии и сокращения как к рис. 16; на рис. 19–20 кутикула показана как оптический срез, живая часть ноги показана только сзади, толщина гиподермы не показана.

Borisovka of Belgorod Province (Russia). There were examined numerous pronymphs. Some features of the living part of leg can be seen through cuticle of intact specimens preserved in alcohol; because of this, only 9 pronymphs were dissected and mounted on slides in Canadian balsam.

Larval legs of all three pairs have similar structure and develop simultaneously. Larva, which buries itself into the ground, looses ability to move by its legs (i.e. becomes a pronymph). In distal part of the leg hypoderm detaches from cuticle and undergoes anti-growth at that time, when coxa retains larval structure with musculature; the fold corresponding the pupal-imaginal knee articulation, appears at proximal part of femur, much more proximally than the initial larval knee articulation (Fig. 21) (the same on fore legs of *Tenebrio molitor* — Fig. 17a). Thus, tissues of larval femur give rise to pupal-imaginal femur and tibia, and tissues of larval tibiotarsus give rise to pupal-imaginal tarsus only (Fig. 57). When all leg musculature is completely lost, the living part of leg gets pupal-imaginal features — a knee bent and a heel protuberance (Fig. 22), but continues to anti-grow. Anti-growth finishes only when the living part of the leg becomes so small that completely locates inside the larval cuticular coxa, not projecting into the larval cuticular femur (Fig. 23) (unlike *Tenebrio molitor* and other species described here). Besides the knee bent (which is characteristic for Metabola in general), the living part of leg has a heel bent, which is directed medially and becomes acute when the living



Figs 21–24. *Leptinotarsa decemlineata*, pronymphs at successive phases of development, optic section of fore leg. Setae not drawn. Larval cuticle shown as optic section by black. Living part of leg shown from behind. Functional cross-striated muscles shown by interrupted lines. Abbreviations as in Fig. 16.

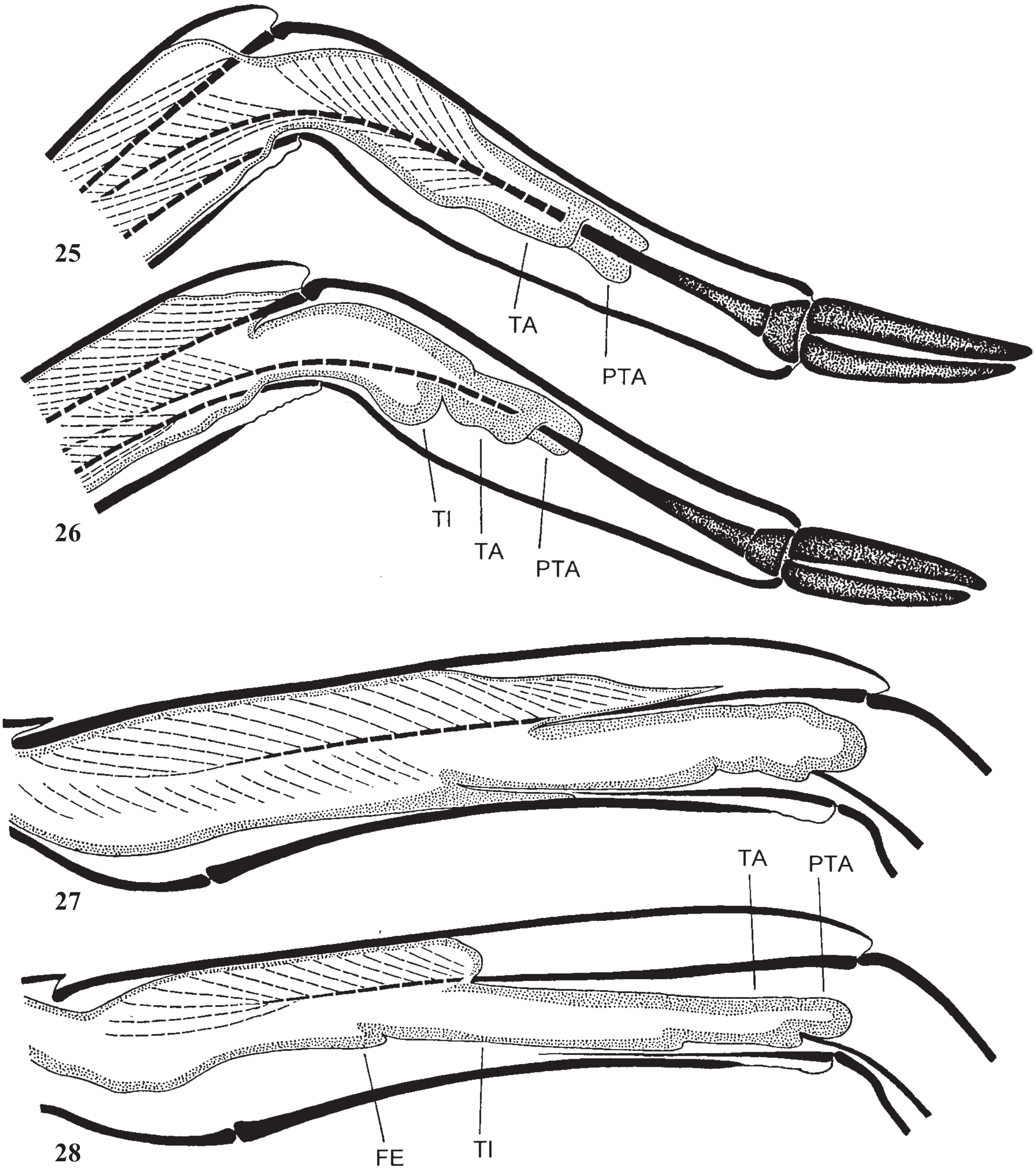
Рис. 21–24. *Leptinotarsa decemlineata*, пронимфы последовательных фаз развития, оптический срез передней ноги. Щетинки не нарисованы. Личиночная кутикула показана черным как оптический срез. Живая часть ноги показана сзади. Функционирующие поперечно-полосатые мышцы показаны прерывистыми линиями. Сокращения как на рис. 16.

part of leg starts to grow (Fig. 24). Thanks to these two bents, growing leg is folded and pressed in the space between the larval trunk cuticle and hypoderm, somewhat projecting only into the larval cuticular coxa, but never projecting into the larval cuticular femur. During the leg growth, muscles do not appear, and after the larval/pupal moult legs remain to be muscle-less.

3.3.4. **Neuroptera-Birostrata:** ***Myrmeleon bore*** (Figs 25–31). Metamorphosis of the species determined as *Myrmeleon europaeus*, was described and beautifully illustrated by Sundermeir [1940]; leg transformation was described only beginning from the phase when living part of leg becomes strongly diminished and occupies a half of the larval cuticular leg; process of its diminishing was not described.

Larvae of the last (3rd) instar of *Myrmeleon bore* (Tjeder 1941 [*Grocus*]) were collected in August 2004 on southern shore of Gulf of Finland in Izhora near Saint-Petersburg. Larvae of the 3rd instar have a winter diapause, so in laboratory they actively eat, but did not develop. In September larvae were placed into refrigerator. In November–February reactivated larvae were taken from refrigerator and placed under permanent light. After some period (about a month) of active life and feeding, larva made a cocoon, in which started to transform to pupa. 25 specimens were fixed at various pronymphal phases, dissected and mounted on slides in Canadian balsam.

Fore and middle legs of larva are very thin; the living part of leg when undergoes diminishing, is stretched in the narrow space inside the larval cuticular leg, and because of this sometimes has not enough distinct those convexities and concavities, which would allow to determine its parts. The process of diminishing of the living part of leg is better understandable if examine hind legs,

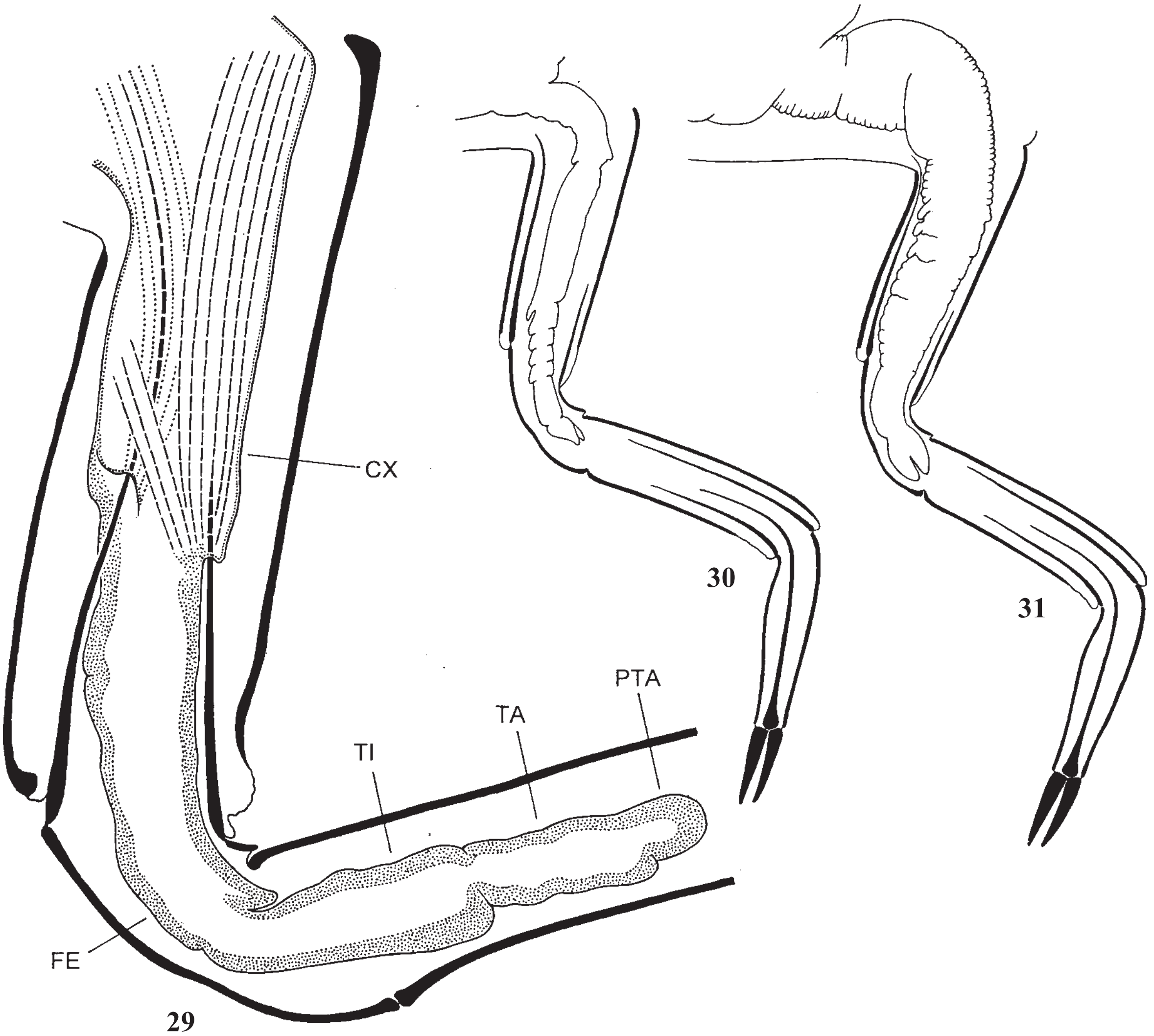


Figs 25–28. *Myrmeleon bore*, pronymphs at successive phases of development (arbitrary 2nd, 3rd and 4th — see the text), optic section of hind leg: 25–26 — tibiotarsus and apex of femur; 27–28 — femur. Setae not drawn. Larval cuticle shown as optic section by black. Living part of leg shown from behind, but thickness of hypoderm shown as optic section by dots. Functional cross-striated muscles shown by interrupted lines. Abbreviations as in Figs 2–3.

Рис. 25–28. *Myrmeleon bore*, пронимфы последовательных фаз развития (условных 2-й, 3-й и 4-й — см. текст), оптический срез задней ноги: 25–26 — тибиотарсус и вершина бедра; 27–28 — бедро. Щетинки не нарисованы. Личиночная кутикула показана черным как оптический срез. Живая часть ноги показана сзади, но толщина гиподермы показана пунктировкой как оптический срез. Функционирующие поперечно-полосатые мышцы показаны прерывистой линией. Сокращения как на рис. 2–3.

which being specialized as burrowing, are thickened. Unlike fore and middle legs, which retain articulation between tibia and tarsus, the larval hind leg has tibia and tarsus fused in an integral tibiotarsus. Processes of hypoderm diminishing and muscle degeneration in hind legs pass slower than in middle and fore legs.

After building a spherical silk-and-sand underground cocoon, larva loses ability to walk (i.e. becomes a pronymph). The larval/pupal leg transformation starts with degeneration. This degeneration is so asynchronous, that resembles burning of a candle: all its processes — detaching of hypoderm from cuticle, dissolving of



Figs 29–31. *Myrmeleon bore*, pronymphs at successive phases of development (arbitrary 5th, 7th and the last — see the text), optic section of hind leg: 29 — coxa, trochanter and base of femur; 30–31 — whole leg. Setae not drawn. Larval cuticle shown as optic section by black. Living part of leg shown from behind, but thickness of hypoderm shown as optic section by dots. Active cross-striated muscles shown by interrupted lines. Abbreviations as in Figs 2–3.

Рис. 29–31. *Myrmeleon bore*, пронимфы последовательных фаз развития (условных 5-й, 7-й и последней — см. текст), оптический срез задней ноги: 29 — тазик, вертлуг и основание бедра; 30–31 — нога целиком. Щетинки не нарисованы. Личиночная кутикула показана черным как оптический срез. Живая часть ноги показана сзади, но на рис. 29 толщина гиподермы показана пунктировкой как оптический срез. Функционирующие поперечно-полосатые мышцы показаны прерывистой линией. Сокращения как на рис. 2–3.

muscles, anti-growth of hypoderm — occur nearly synchronously in a short area of the leg; proximad of this "burning" area nothing changes, larval hypoderm retains its attachment to cuticle, larval muscles are attached to cuticle and can move the leg. The "burning area" moves from apex of the leg to proximal direction, until the whole living part of leg is transformed to a small muscle-less bud of pupal leg. Thanks to such mode of leg degeneration, legs retain ability to some movements during this process. This has no practical significance for the insect, because all this process occurs inside the cocoon, where legs can not be used; being taken out of the cocoon, the pronymph can make only useless leg movements, but is unable to walk or burrow. Process of leg transformation can be arbitrarily divided into the following phases:

1st phase (1 specimen examined). *In fore and middle legs* tibial muscles disappear, and tarsus undergoes anti-growth; femoral and coxal muscles remain to be functional. *In hind leg* tarsal hypoderm (in distal part of the tibiotarsus) only starts to detach from cuticle, while all muscles remain to be functional.

2nd phase (1 specimen examined). *In fore and middle legs* femoral muscles disappear; tibial hypoderm (lacking muscles) undergoes such anti-growth, that apex of the living part of leg is shifted into the larval cuticular tibia; coxal muscles remain to be functional. *In hind leg* (Fig. 25) only tarsus undergoes anti-growth, and tibial hypoderm is partly detached from cuticle; nearly all tibial, all femoral and all coxal muscles remain to be functional.

3rd phase (7 specimens examined). *In fore and middle legs* femoral hypoderm (lacking muscles or with vestigial muscles) undergoes such anti-growth, that apex of the living part of leg is shifted into the larval cuticular femur; coxal muscles remain to be functional; in fore legs coxal hypoderm distally stars to detach from cuticle and anti-grows. *In hind leg* (Fig. 26) tibial muscles disappear, and tibial hypoderm undergoes anti-growth; the living parts of tibia and tarsus become well separated (unlike the integral larval tibiotarsus) and get a characteristic shape; on ventral side of femur hypoderm detaches from cuticle, but on dorsal side of femur remains to be attached to cuticle; part of femoral and all coxal muscles remain to be functional.

4th phase (5 specimens examined). *In fore and middle legs* (whose living part terminates in the larval cuticular femur) coxal hypoderm continues or starts to detach from cuticle and anti-grow; coxal muscles remain to be functional. *In hid leg* (Figs 27–28) femoral hypoderm undergoes such anti-growth, that apex of the living part of leg is shifted into the apex of larval cuticular femur. The anti-growth of femur can take place when its hypoderm still remains to be attached to cuticle, and muscles have not degenerated; in this case the living part of tibia, tarsus and pretarsus appear to be inserted between living muscular portions of the femur (Fig. 27).

5th phase (3 specimen examined). *In all legs* (Fig. 29) the living part of leg lacks femoral and tibial muscles, and terminates in the larval cuticular femur. Coxal hypoderm detaches from cuticle and undergoes anti-growth (which in middle legs was started at the 4th phase, and in fore legs — at the 3rd phase). As a result of coxal anti-growth, most part of the living femur shifts into the larval cuticular coxa, and the whole living part of leg terminates in proximal half of the larval cuticular femur. Coxal muscles in fore legs disappear, but in middle and hind legs remain to be functional; levators of trochanter are retained longer that depressors of trochanter.

6th phase (2 specimens examined). In all legs all muscles completely disappear; coxal hypoderm undergoes such anti-growth that the living femur and tibia are shifted into the larval cuticular coxa.

7th phase (1 specimen examined) (Fig. 30). The living part of leg (completely lacking muscles) is transformed to a small bud of pupal leg and gets a knee bent. Its base is shifted medially; coxa is strongly shortened and becomes hardly distinguishable; most part of femur is shifted into the space under trunk cuticle between the new leg base and the larval base of coxa; tibia locates in the larval cuticular coxa. This position of pupal leg bud is the same as in *Chrysoperla carnea* (see below), and possibly is characteristic for Birostrata. Tibia gets apical spoors, and tarsus gets segmentation.

Phase of growth (5 specimens examined) (Fig. 31). After the process of diminishing, the living part of leg grows; all its segments remain the same length and location as at the final phase of their diminishing; they become only thicker and get numerous transverse folds. During the leg growth, muscles do not appear, and after the larval/pupal moult legs remain to be muscle-less.

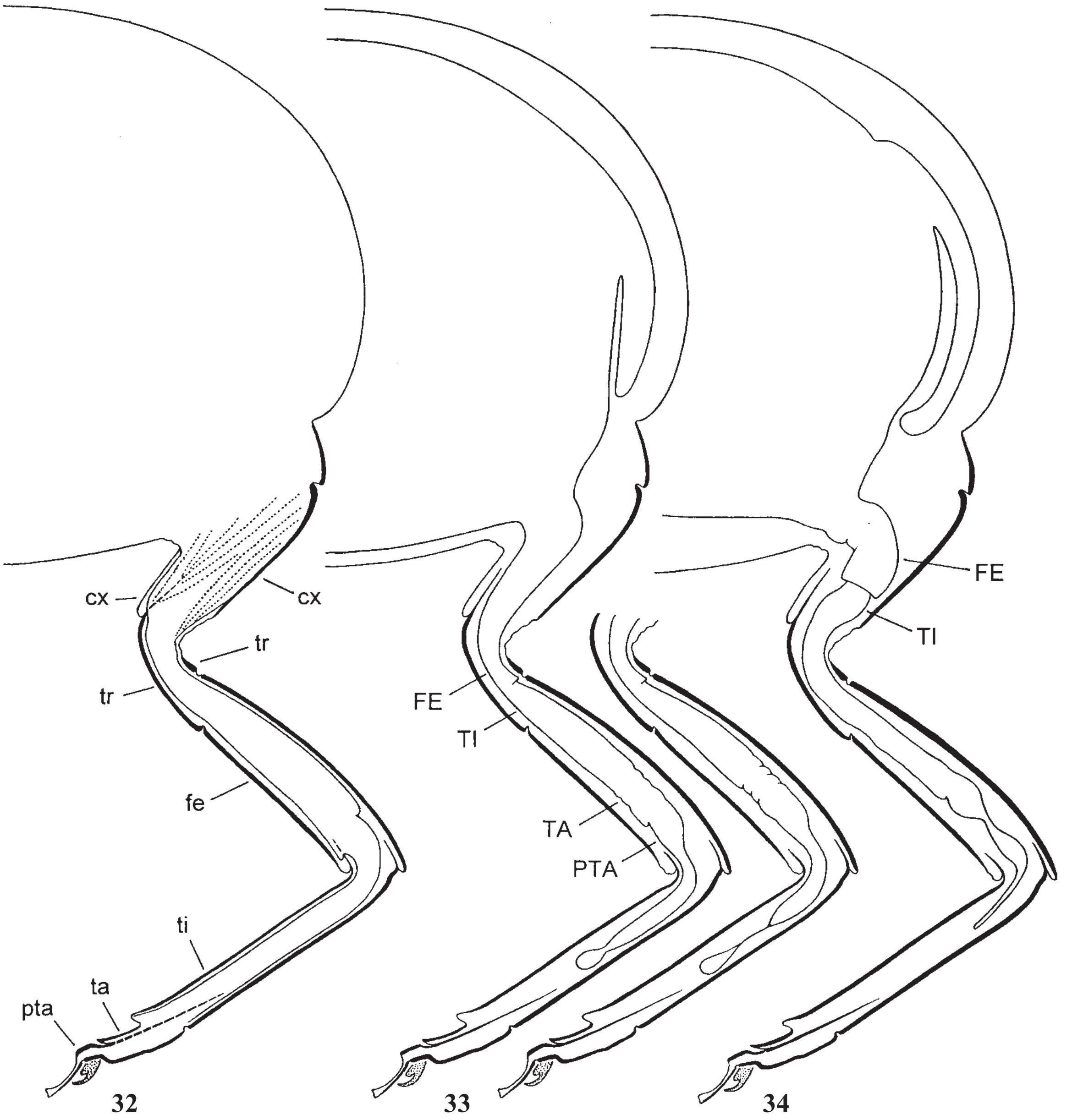
If the process of leg transformation passes normally (as in Figs. 25–31), each imaginal leg segment appears to be ontogenetically homologous to the phylogenetically homologous larval leg segment: hypoderm of each leg segment, after separating from larval cuticle, at first undergoes anti-growth and changes its shape, at the next phases shifts into more proximal segment(s) of the larval cuticular leg, and finally transforms to hypoderm of the phylogenetically homologous pupal leg segment. However, in selected legs of some specimens, during the leg degeneration, besides the regular anti-growth of hypoderm and dissolving of muscles, in the living part of leg appear irregular, ovoid, hollow bubbles. Probably, these bubbles appear inside the living part of leg, and later can open, forming concavities. The bobbles can be nearly as wide as the leg; because of them, some segments have anomalous shape and lack most part of their hypoderm. Possibly, in some of such cases, future pupal-imaginal hypoderm develops from hypoderm of neighbouring segments (as in the case of regeneration), and ontogenetic homology of larval and pupal-imaginal segments can be lost.

3.3.5. **Neuroptera-Birostrata: *Chrysoperla carnea*** (Figs 32–40). Larvae of *Chrysoperla carnea* (Stephens 1836 [*Chrysopa*]) were collected in July 2004 in Borisovka of Belgorod Province (Russia), and kept in cages. 8 pronymphs taken from cocoons were fixed at various phases of development, dissected and mounted on slides in Canadian balsam.

Larval legs of all three pairs have similar structure and develop simultaneously. After building a silk cocoon, larva loses ability to move by legs (i.e. becomes a pronymph). Leg transformation starts with its degeneration: the whole distal half of the leg (including apex of femur, all tibia, tarsus and pretarsus) dissolves, so living tissues are retained only in proximal half of the leg and give rise to the whole pupal-imaginal leg. Before the larval cuticle is shed, all remainders of larval tissus of tibia, tarsus and pretarsus completely disappear, thus at the ecdysis, from legs is shed an empty clean cuticle, without remainders of tissues inside (as well as in other insects discussed here). Process of leg transformation can be arbitrarily divided into the following phases:

1st phase (1 specimen examined) (Fig. 32). Muscles of tibia and femur disappear completely; muscles of coxa are partly dissolved. Hypoderm detaches from cuticle, but does not undergo marked anti-growth.

2nd phase (3 specimens examined) (Figs 33a–b, 38). All muscles disappear. Tissues in distal half of the leg (including apex of femur, all tibia, tarsus and pretarsus) are transformed to a slender process made of thin hypoderm. The living part of leg, which locates inside the larval cuticular femur, starts to develop pupal-imaginal segmentation: there appears a boundary between pretarsus and tarsus (with the canal of unguitractor) and a boundary between femur and tibia (as a fold on dorsal side) (Fig. 38). At this phase the leg hypoderm is divid-



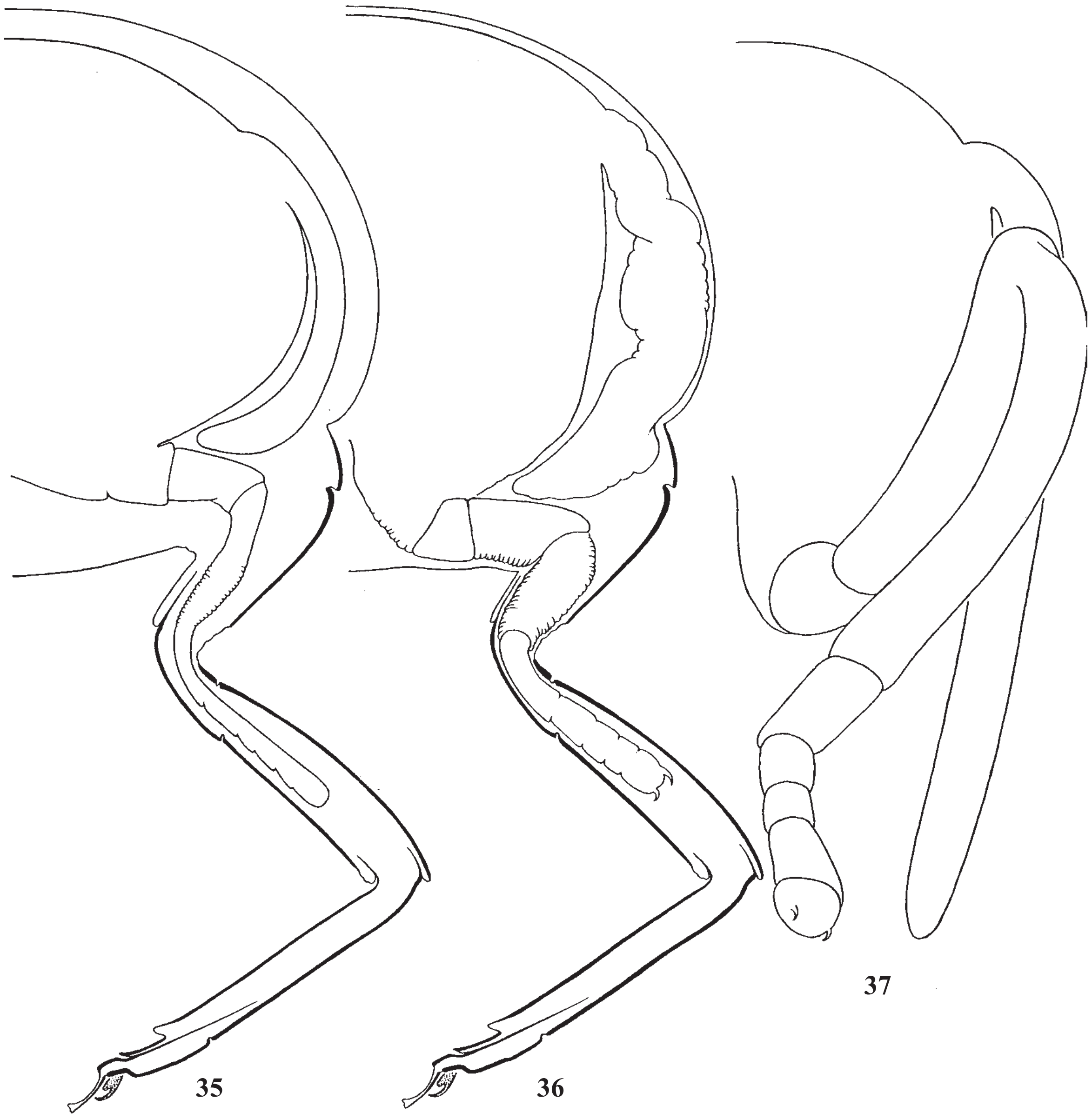
Figs 32–34. *Chrysoperla carnea*, pronymphs at successive phases of development (arbitrary 1st, 2nd and 3rd — see the text), cross section of right half of metathorax. Setae not drawn. Larval cuticular leg shown by black as optic section; living part of leg shown from behind; vestiges of muscles shown by dotted lines. Abbreviations as in Figs 2–4.

Рис. 32–34. *Chrysoperla carnea*, пронимфы последовательных фаз развития (условных 1-й, 2-й и 3-й — см. текст), поперечный срез правой половины заднегруди. Щетинки не нарисованы. Личиночная кутикула показана черным как оптический срез; живая часть ноги показана сзади; остатки мышц показаны точечными линиями. Сокращения как на рис. 2–4.

ed into segments, which paradoxically change place: the developing (i.e. future pupal) pretarsus distally continues as the degenerating (i.e. former larval) tibia.

3rd phase (1 specimen examined) (Fig. 34). The knee articulation of living part of leg is shifted from the larval cuticular femur (where it appeared at the 2nd phase) into the larval cuticular coxa. Future pupal pretarsus still continues by a process consisting of larval tibial tissues.

4th phase. (1 specimen examined) (Fig. 35). The process distad of the future pupal pretarsus disappears, thus living part of leg now consists of a pupal leg bud only. Base of the pupal leg bud is shifted medially (in Birostrata, as well as in most Metabola, pupal-imaginal coxa are brought together, while larval coxae are widely separated). Thanks to this, between base of the living coxa and base of the larval cuticular coxa appears a space, into which the living femur is shifted; the living tibia is shifted into the larval cuticular coxa, and only the living tarsus remains to locate in the larval cuticular femur. Because of its position under the larval cuticle, the living part of leg appears to be bent in knee articula-



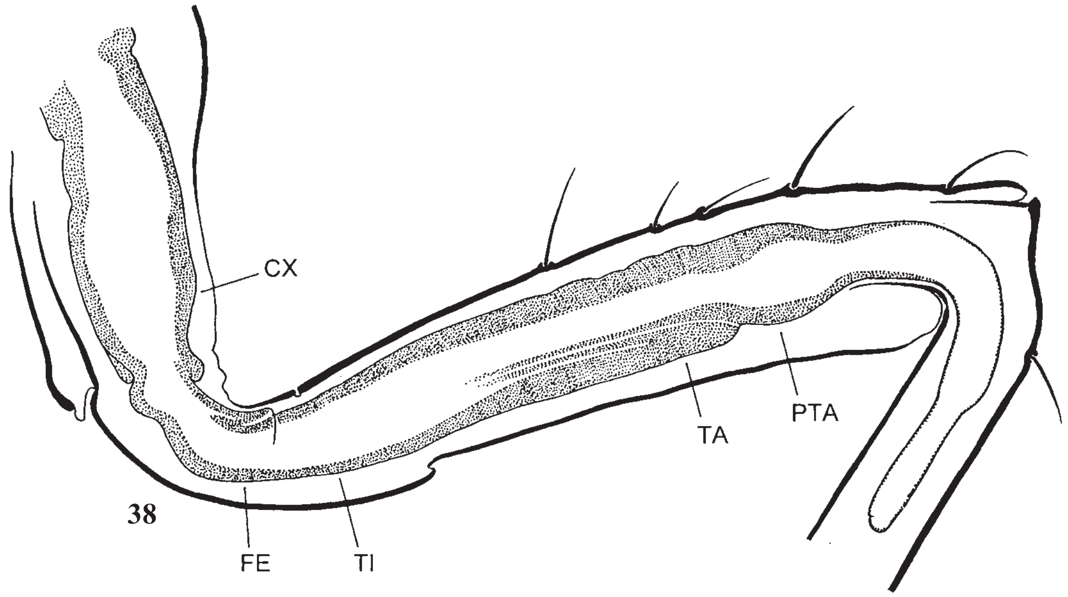
Figs 35–37. *Chrysoperla carnea*: 35–36 — pronymphs at successive phases of development (arbitrary 4th and later), cross section of right half of metathorax (larval cuticular leg shown as optic section; living part of leg shown from behind). 37 — young pupa, right half of metathorax from behind, the same scale. Setae not drawn.

Рис. 35–37. *Chrysoperla carnea*: 35–36 — пронимфы последовательных фаз развития (условной 4-й и более поздней — см. текст) (личиночная кутикула показана черным как оптический срез; живая часть ноги показана сзади). 37 — молодая куколка, правая половина заднегруди сзади, в том же масштабе. Щетинки не нарисованы.

tion: its femur is directed laterally, toward the base of the larval cuticular coxa, and its tibia is directed ventrally, together with the larval cuticular coxa, inside which it locates. Unlike Trichoptera and Coleoptera (see above), this initial knee bend is not free, but forced, i.e. determined by the shape of space in which the leg develops.

Phase of growth (2 specimens examined) (Fig. 36). In course of subsequent growth, up to the ecdysis, the pupal leg occupies the same space as at the 4th phase; increasing of length of femur and tibia is reached only by means of appearing numerous transverse folds. During the leg growth, muscles do not appear, and after the larval/pupal moult legs remain to be muscleless (Fig. 37). Leg musculature appears later, when under the pupal cuticle appear imaginal integument (Figs 39–40).

As a result of this larval/pupal leg transformation, phylogenetically homologous segments of the larval and the pupal-imaginal legs are not ontogenetically homologous: hypoderm of the pupal-imaginal tibia, tarsus and pretarsus originate from hypoderm of the larval femur, while larval tissues distad of the femur are completely dissolved (Fig. 58).



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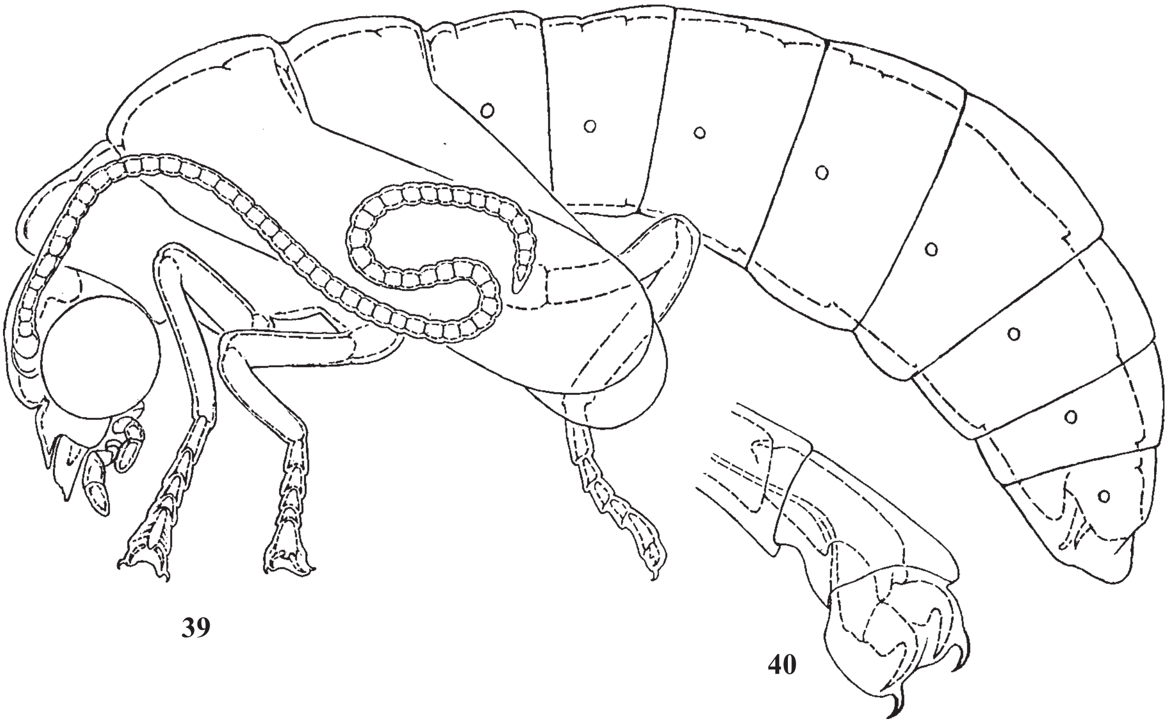

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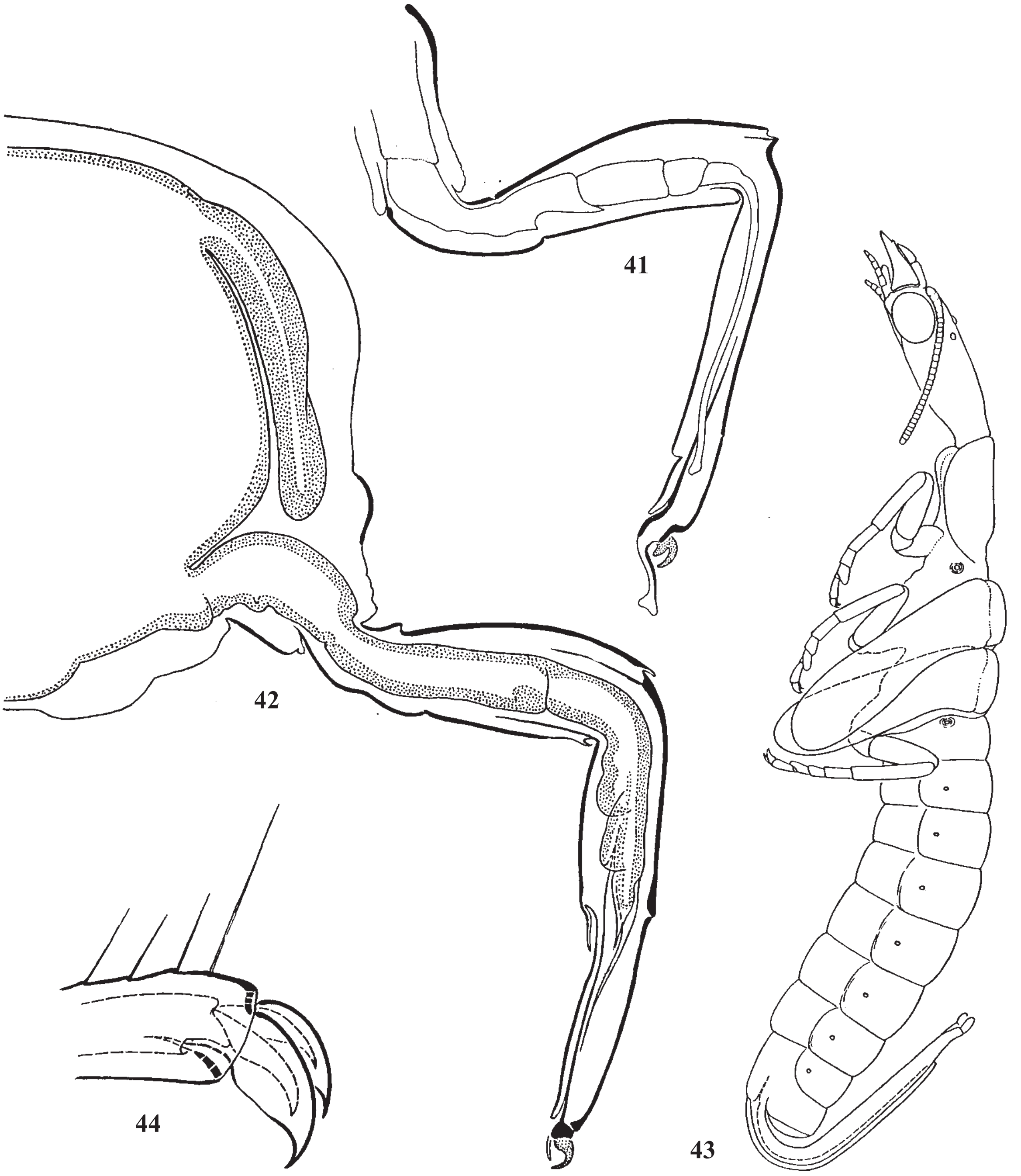
Figs 38–40. *Chrysoperla carnea*: 38 — pronymph (arbitrary 2nd phase), optic section of part of hind leg (cuticle shown by black, hypoderm dotted). 39–40 — late pupa (pharate imago) which left cocoon (imaginal cuticle shown by interrupted line, setae not drawn): 39 — lateral view; 40 — apex of tarsus. Abbreviations as in Figs 2–4.

Рис. 38–40. *Chrysoperla carnea*: 38 — пронимфа (условная 2-я фаза), оптический срез части задней ноги (кутикула показана черным, гиподерма пунктирована). 39–40 — поздняя куколка (фаратное имаго), покинувшая кокон (имагинальная кутикула показана прерывистой линией, щетинки не нарисованы); 39 — общий вид, латерально; 40 — вершина лапки. Сокращения как на рис. 2–4.

3.3.6. **Neuroptera-Birostrata: *Chrysotropia ciliata*** (Fig. 41). One pronymph of *Chrysotropia ciliata* (Wesmael 1841 [*Chrysopa*]) was got from larva collected in August 2004 in Saint Petersburg (Russia).

In this species the living part of leg already gets sharp boundaries between some tarsal segment at that time, when the dissolving distal part of leg is yet retained all along the larval tibia in a form of an integral slender cord (Fig. 41) (unlike *C. carnea*, whose tarsal segment boundaries are yet not so sharp when the dissolving part is already markedly shortened — Fig. 33).



Figs 41–44. 41 — *Chrysotropia ciliata*, pronymph, optic section of fore leg. 42 — *Raphidia xanthostigma*, pronymph, optic section of right half of metathorax (cuticle shown by black, hypoderm dotted). 43–44 — *Raphidia* sp.: 43 — pupa, lateral view (setae not drawn); 44 — pharate imago, apex of fore leg (imaginal cuticle shown by interrupted line).

Рис. 41–44. 41 — *Chrysotropia ciliata*, пронимфа, оптический срез передней ноги. 42 — *Raphidia xanthostigma*, пронимфа, оптический срез правой половины заднегруди (кутикула показана черным, гиподерма пунктирована). 43–44 — *Raphidia* sp.: 43 — куколка, латерально (щетинки не нарисованы); 44 — фаратное имаго, вершина передней ноги (имагинальная кутикула показана прерывистой линией).

3.3.7. **Rhaphidioptera** (Figs. 42–44). I was unable to study metamorphosis of Rhaphidioptera, but examined only some specimens, mainly from collection of the Zoological Institute of Russian Academy of Sciences. Among them — one pronymph of *Raphidia xanthostigma* Schummel 1832 (from S.-Petersburg, Udelnaya, 24 IV 1919, collected by A.N. Reichardt) and one pronymph of *Raphidia* sp. gr. *ophiopsis* (from Voronezh Province, Kamennaya Step', 1935, collected by Berezina). Pronymphs of *R. xanthostigma* and *R.* gr. *ophiopsis* are well-distinguishable by venation of the hypodermal buds of pupal protoptera.

During larval/pupal leg transformation, leg muscles completely disappear (in contrast to *Sialis* — see below). The living part of leg diminishes so that its claws are located in the end of the larval cuticular tibia (but not in the femur, unlike the species described above). At a certain phase each claw has a distal slender continuation which locates inside the larval cuticular tarsus (Fig. 42). Possibly, these continuations are remnants of larval tarsal tissues; this allows to conclude that the shortening of living part of leg is reached here not by anti-growth, but by breaking, similarly to *Chrysoperla carnea* and *Chrysotropia ciliata* (see above).

3.3.8. **Meganeuroptera: *Sialis sordida*** (Figs 45–50). Metamorphosis of *Sialis* was briefly described by Geigy [1937], but details of larval/pupal leg transformation remained to be unknown. Larvae of *Sialis sordida* Klingstedt 1932 ready to pupation (i.e. pronymphs) were collected 11 May 2004 at the bank of Peterhoff Canal (Saint Petersburg, Russia) in the upper layer of ground and in rotten wood. Their development continued in laboratory. 12 specimens were fixed at, or near, the moment of larval/pupal ecdysis — 5 larvae ready to moult, 4 moulting specimens and 3 pupae just after moult. They were dissected and mounted on slides in Canadian balsam.

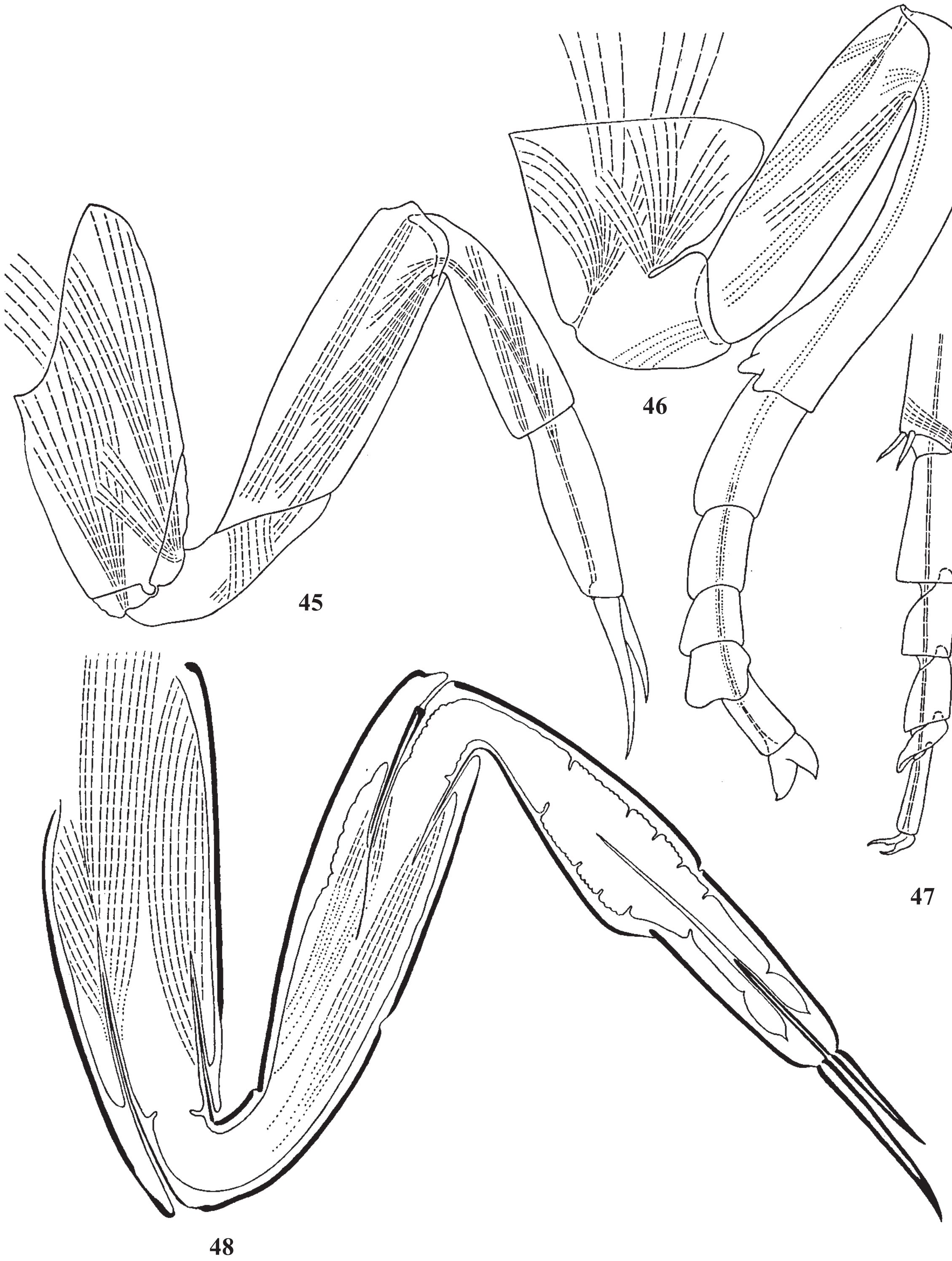
Pronymph immovably lies in a chamber made inside substrate, in a ring-like pose. Being taken out of its chamber, pronymph of *Sialis* some time continues to lie immovably, like pronymphs of other Metabola, whose legs lost mobility because of the transformations inside them (see above). However, unlike other Metabola, disturbed pronymph of *Sialis*, after some period of immovable lying, stands on its legs, runs away and bury itself into the ground. This means that its immobility is not connected with any physical reasons. Only at the last day before larval/pupal moult, pronymph loses ability for normal running: it retains ability to move actively by coxae and femora, but tibiae are able only to weak movements.

During the whole pronymphal development, the living part of leg retains its initial position in the larval cuticular leg — i.e. the living tissues of coxa, trochanter, femur, tibia and tarsus are located, correspondingly, inside the larval cuticular coxa, trochanter, femur, tibia and tarsus (Figs 48, 50). All larval cuticular apodemes (the unguitractor, the apodemes of tibial flexor and extensor and the apodemes of trochanteral levator and depressor) are inserted into the corresponding future pupal apodemes (Fig. 48), thus muscles attached to the future pupal apodemes are able to move the larval cuticular leg. Just before larval/pupal moult, the future pupal tarsus and pretarsus are somewhat shifted proximally, thus the future pupal claws locate inside the larval cuticular tarsus, and the future pupal tarsus is partly shifted into the larval cuticular tibia (the same occurs also in some insects with direct development of legs [Kluge, 2004a: Figs 98A–B]). Unlike insects with direct development, in *Sialis* the future pupal knee articulation is shifted into the larval cuticular femur; however, this does not prevent active mobility of the knee articulation, because the apodeme of knee extensor in *Sialis* is large, composite (Fig. 48) and able to serve connection of femoral muscles with larval articulation even it such position.

Most part of muscles in trunk, head and mouth appendages are retained during the whole development; muscles moving leg coxae and trochanters are also retained and are able to work during the whole development. At the moment of larval/pupal ecdysis, leg musculature is the following. Muscles, which fill the coxae, are retained — these are the trunk-coxal muscles, the coxal levators and depressors of trochanter and the depressors of trochanter attached in the trunk. Either all these coxal muscles retain normal shape and cross-striation, or (in some individuals) they are partly deformed or/and lack cross-striation. Muscles located inside trochanter (the trochanteral-femoral muscle and the trochanteral-tibial flexor), are often absent or lack cross-striation. Muscles located inside femur, are partly retained: the femoral-tibial flexor often retains its shape and cross-striation, but sometimes has no proximal part, sometimes has no cross-striation; the femoral-tibial extensor is non-functional and usually has no cross-striation. The femoral and tibial muscles of unguitractor and the tibial-tarsal muscle are always completely absent, thus there are no muscles distad of the knee articulation.

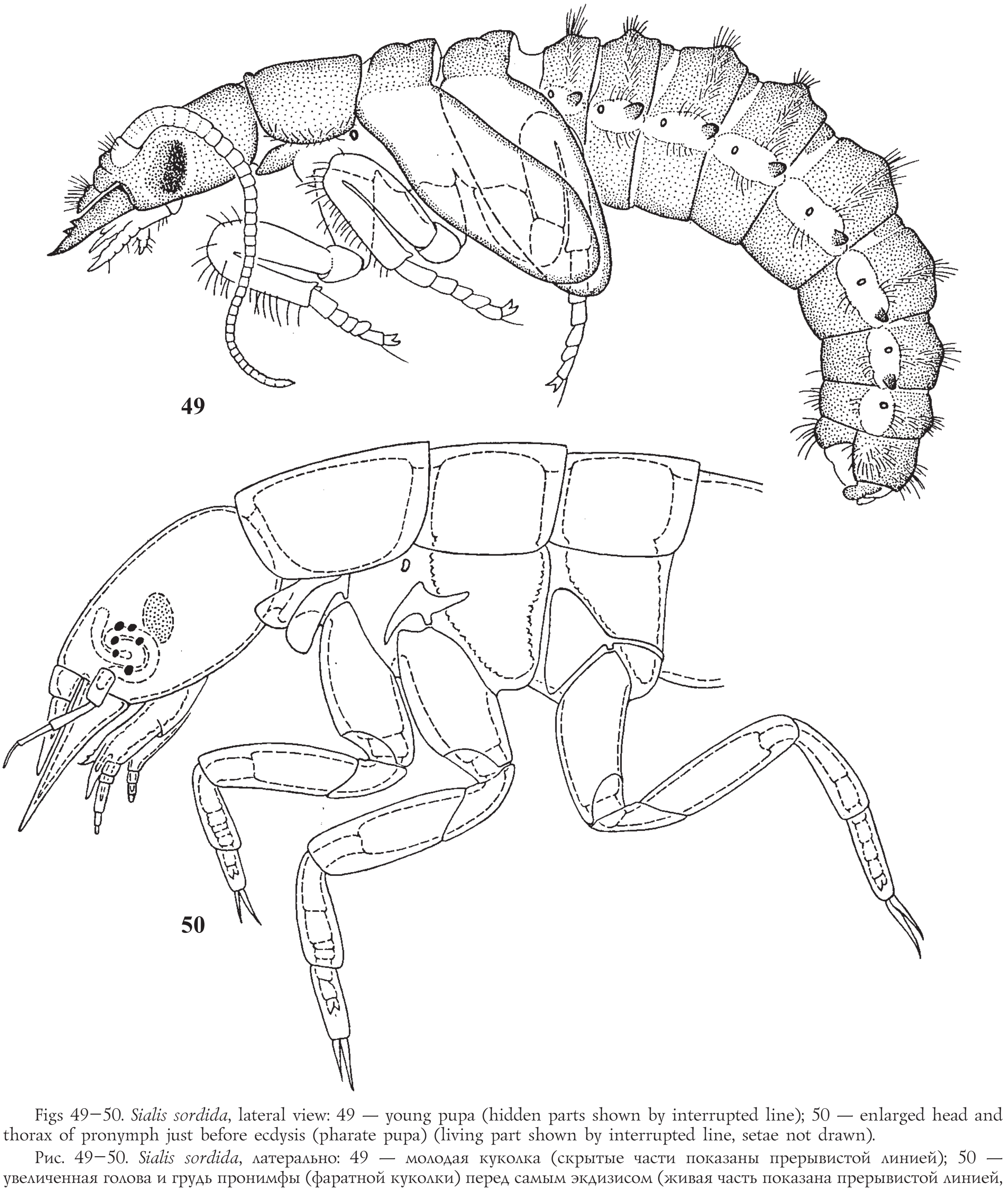
While both larva and imago have the same general plan of leg musculature peculiar for Hexapoda (see 3.1 and Fig. 1), shape of their muscles is different. Larval femoral-tibial extensor is parallel-sided, attached near base of the femur (Fig. 45); unlike, imaginal femoral-tibial extensor is pectinate, attached along most part of outer side of femur. Pronymph and young pupa have vestigial femoral-tibial muscle of the larval type (Fig. 48). In two pupae examined, this muscle, being non-striated, has a separate non-striated branch, attached to distal part of outer side of femur (Fig. 46); probably this is a beginning of transformation from the larval to the imaginal condition. Larval tibial-tarsal muscle is long, attached at base of tibia (Fig. 45); unlike, imaginal tibial-tarsal muscle is very short, nearly transverse, attached at apex of tibia (Fig. 47). This muscle, as well as the unguitractoral muscles, completely disappears in pronymph, and than appears anew in pupa. Thus, among larval leg muscles, imago retains in unchanged condition only muscles located in the coxa, and possibly sometimes also the femoral-tibial flexor or its part.

In pupal stage legs are bent in knees so that tibia is pressed to femur (Figs 46, 49); leg muscles retain the same condition, as in larva before ecdysis (i.e. there are well-developed coxal muscles and non-functional vestiges of larval femoral muscles). During the whole its development, pupa retains ability to move actively by legs in trunk-coxal and coxal-trochanteral articulations, thus can make various strong movements by femora, but can not unbend knees. In such manner pupa, if it is taken out of its chamber, is able to crawl clumsily and tries to bury itself, working by fore legs. Knee articulation always remains immobile, in bent condition. This per-



Figs 45–48. *Sialis sordida*: 45–47 — hind leg at the same scale: 45 — of active larva; 46 — of pupa; 47 — of imago (tarsus and apex of tibia). 48 — enlarged schematic section of hind leg of pronymph just before ecdysis (pharate pupa). Functional cross-striated muscles shown by interrupted lines, non-striated muscular vestiges and anlages shown by dotted lines.

Рис. 45–48. *Sialis sordida*: 45–47 — задняя нога в одном и том же масштабе: 45 — у активной личинки; 46 — у куколки; 47 — у имаго (лапка и вершина голени). 48 — увеличенный схематичный разрез задней ноги пронимфы (фаратной куколки) перед самым экдизисом. Функционирующие поперечно-полосатые мышцы показаны прерывистыми линиями, гладкие мышечные остатки и зачатки показаны точечными линиями.



Figs 49–50. *Sialis sordida*, lateral view: 49 — young pupa (hidden parts shown by interrupted line); 50 — enlarged head and thorax of pronymph just before ecdysis (pharate pupa) (living part shown by interrupted line, setae not drawn).

Рис. 49–50. *Sialis sordida*, латерально: 49 — молодая куколка (скрытые части показаны прерывистой линией); 50 — увеличенная голова и грудь пронимфы (фаратной куколки) перед самым экдизисом (живая часть показана прерывистой линией, щетинки не нарисованы).

manent knee bend is not connected with resiliency of the pupal cuticle: after the pupal/imaginal moult the knee articulations of empty pupal skin do not retain the knee bends, but, vice verse, are obligatory unbent.

3.3.9. **Meganeuroptera:** ***Acanthocorydalis*** **sp.** I was unable to study metamorphosis of Eumegaloptera, but examined only some specimens from collection of the Zoological Institute of Russian Academy of Sciences. Among them — pupa and imago of *Acanthocorydalis* sp. collected by D. Panfilov in China, Yunnan, Jindung, 10–15 III 1957.

Pupa, whose leg hypoderm is already separated from pupal cuticle and has imaginal structure, but has no imaginal cuticle yet, has muscles arranged as in imago (namely, femoral-tibial extensor is pectinate, and tibial-tarsal muscle is short). Muscles, located in coxa, have both cross-striated and smooth fibrils; trochanteral-femoral muscle is also cross-striated; muscles, located in femur and tibia, have smooth fibrils only. This allow to conclude, that the coxal and trochanteral muscles were inherited from larva, and continued to function in pupa, while the femoral and tibial muscles appeared in pupa anew and do not function at early period of pupal stage. This is similar to *Sialis* (see above), whose coxal (but not trochanteral) muscles also directly pass from larva to imago.

3.4. Leg transformation in Metabola with short-legged larvae

Short larval legs are characteristic for most Lepidoptera, Hymenoptera-Symphyta and some other taxa. These insects have no phase of leg shortening, unlike the insects with longer larval legs described above.

3.4.1. **Lepidoptera** (Fig. 51). Leg transformation in Lepidoptera is described for *Lithocolletis populifoliella* [Ganin, 1877], *Pieris brassicae* [Gonin, 1894; Packard, 1898; Kim, 1959], *Galleria mellonella* [Kuske, Penner & Pierno, 1961] and *Anterea pernyi* [Kuske, 1963]. In these papers is shown that during the whole pronymphal development the living part of leg fills the whole larval cuticular leg up to its apex. Leg muscles completely disappear, and epithelium grows unevenly. The area of most early intensive epithelial growth ("differentiation center" by Kim [1959]) occupies an outer side of knee articulation, thus at earliest stage of growth there appears a knee bent which projects proximally from the larval cuticular leg and locates under the larval trunk cuticle. During subsequent growth, the most part of the pharate pupal leg is forced out from the larval cuticular leg and crumples under the larval trunk cuticle; distal part of pharate pupal leg, being also crumpled, fills the larval cuticular leg. The same was observed by me in some other species (Fig. 51).

3.4.2. **Hymenoptera-Symphyta.** Leg transformation in Hymenoptera was described only by Ivanova-Kazas & Ivanova [1964] for *Pontania capreae*. These authors stated that "No any degenerative transformations occur in leg hypoderm".

3.5. Leg transformation in Metabola with leg-less larvae

Larval legs are lost in Diptera, Aphaniptera, Hymenoptera-Apocrita, some other Hymenoptera, several taxa within Coleoptera, some Lepidoptera and some Birostrata. In some leg-less larvae, in fact legs are not completely lost, but retained as sensory vestiges, which are not projected above the trunk surface, but bear own setae; this is described for Coleoptera-Rhynchophori [Pérez, 1911; Keilin, 1915] and Diptera (see below).

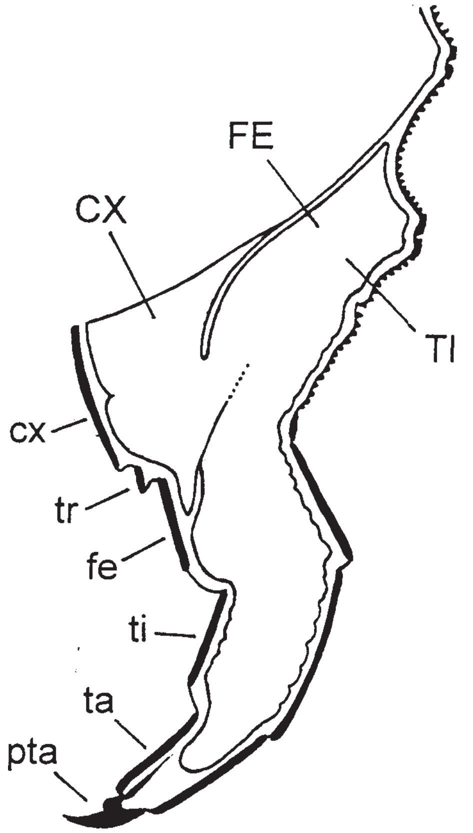
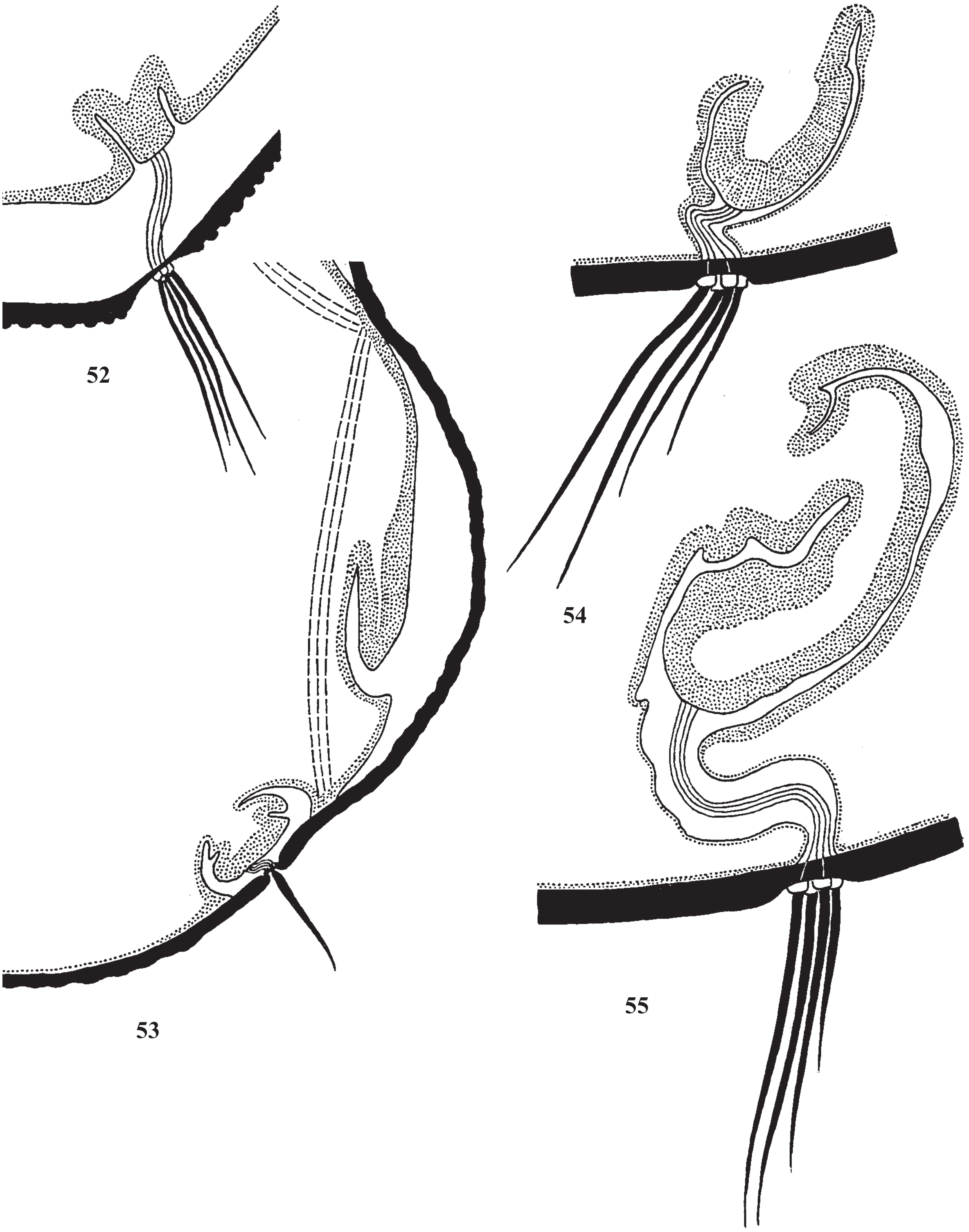


Fig. 51. *Araschnia levana* (Linnaeus 1758 [*Papilio*]), pronymph, transverse section of a part of prothorax with fore leg. Abbreviations as in Figs 2–4.

Рис. 51. *Araschnia levana* (Linnaeus 1758 [*Papilio*]), пронимфа, поперечный срез части переднегруди с передней ногой. Сокращения как на рис. 2–4.

3.5.1. **Diptera** (Figs 52–55). Larvae of Diptera are not completely leg-less, but have external leg vestiges: initially each larval leg is represented only by its tip, which forms a portion of thorax wall and bears a quadrate-like group of 4 setae ("sensory organ *d*" by Keilin [1915]); these setae can be either distinct (Figs 52, 54, 55), or fused together retaining four bases, or modified in other manner; sometimes there are less than four setae, or all these setae are lost. Cuticle of the larval leg vestige is either non-distinguishable from the trunk cuticle, or differs from it (Fig. 52). Sometimes hypoderm of the larval leg vestige is thicker than hypoderm of the trunk itself; sometimes this hypodermal thickening is separated from the trunk hypoderm by a ring-like groove, so the leg vestige is located in an opened basigenous pocket (Fig. 52). Hypoderm faced inside this groove, does not produce cuticle and does not participate in moulting processes, thus it can pass from instar to instar as a completely internal formation. In larva of the last instar, which starts to transform to pupa, pupal leg buds develop from the hypoderm of external leg vestige together with the hypoderm of internal ring-groove. Thus, at first, pupal leg bud is short and sinked by its base into a pocket (Fig. 53). Than this leg bud elongates, lies in plan parallel to the larval cuticle and curves, forming knee bent and other curvations of characteristic shape; for some time its tip retains sensory cilia connected with setae of the external larval leg vestige. Leg bud sinked into the opened basigenous pocket and connected by four cilia with setal bases, was observed by me in various representatives of the plesiomorphons Nemocera and Mesodiptera; among them,



Figs 52–55. Larvae of Diptera, partial transverse section of thoracic segment with right leg vestige: 52 — *Phalacrocera replicata* (Linnaeus 1758 [*Tipula*]), immature larva; 53 — Asilidae gen. sp., early pronymph (muscles shown by interrupted lines); 54 — *Nephrotoma* sp., immature larva; 55 — *Tipula (Pterelachisus) irrorata* Macquart 1823, early pronymph. Cuticle shown by black, hypoderm dotted; all 4 setae are drawn, while only two of them fall to the section.

Рис. 52–55. Личинки Diptera, частичный поперечный срез грудного сегмента с правым вестигием ноги: 52 — *Phalacrocera replicata* (Linnaeus 1758 [*Tipula*]), незрелая личинка; 53 — Asilidae gen. sp., ранняя пронимфа (мышцы показаны прерывистыми линиями); 54 — *Nephrotoma* sp., незрелая личинка; 55 — *Tipula (Pterelachisus) irrorata* Macquart 1823, ранняя пронимфа. Кутикула показана черным, гиподерма пунктирована; все 4 щетинки нарисованы, хотя только две из них попадают на срез.

Tabanus sp., *Xylophagus* sp., *Stratiomys* sp., *Odontomyia* sp. and *Phalacrocera replicata* (Linnaeus 1758 [*Tipula*]) have four cilia connected with four separate setae (Fig. 52); *Atherix ibis* (Fabricius 1798 [*Rhagio*]), Therevidae gen.sp. and Asilidae gen.sp. have four cilia connected with a composite quadrate base, from which arises a single seta (Fig. 53).

In some taxa the larval leg vestige has hypoderm non-thickened; in these cases leg vestige is non-distinguishable until the last larval instar, when its hypoderm starts to transform to a bud of pupal leg. For example, this is due to *Chaoborus* [Weismann, 1866], while in related taxa — Culex/fg5 (= Culicidae s.str.) and *Dixa* — each leg vestige has a distinctly thickened hypoderm, which passes from instar to instar.

In Tipulidae (Figs 54–55) the hypodermal basigenous pocket of the larval leg vestige is very deep and stalked; hypoderm of the leg vestige is completely sinked into this pocket and lost connection with cuticle; thus, externally the larval leg is represented only by the setae which cilia arise from sensilla in the hidden leg hypoderm (Fig. 54). This stalked hypodermal pocket with hypodermal leg vestige passes from instar to instar and resembles the leg disc of Cyclorapha (see below). When the hypodermal leg vestige starts to transform to a bud of pupal leg, at first it grows and forms a knee bent, retaining inside its pocket (Fig. 55). Such internal leg vestige with external setae is found in examined species of *Tipula*, *Nephrotoma*, *Prionocera* and *Tanyptera*. Unlike Tipulidae, in related *Phalacrocera replicata* larval leg has the usual structure and retains not only the external seta, but also the external surface (Fig. 52).

In Diptera-Cyclorapha the hypodermal pockets with leg vestiges are modified as **discs** (so-called "imaginal" discs, in the original meaning of this term — see 1.5): they are closed and can be inserted deeply into the body, so that each disc represents a compact, ovoid, internal organ, connected with the external integument by means of a slender stalk. Unlike Tipulidae, tip of the hypodermal leg vestige is directed not to the mouth, but to a side wall of the pocket, so the whole formation has a disc-like shape. Probably, the disc can retain sensory function initial for the dipteran larval leg vestiges: it is always connected with nervous system and can contain sensory cilia [Poodry & Schneidermann, 1970]; the group of setae can exist at its mouth [Keilin, 1915]. Being closed, the discs can be retained in the body during all larval instars. Remaining inside the disc, hypodermal leg vestige grows, transforming to pupal leg bud, divides to segments and forms a knee bent [Ganin, 1877: Figs 7–8]. Later mouth of the disc opens, and the leg bud and outer wall of the disc become components of hypoderm, which lies directly under the puparium wall (modified larval cuticle). Most probably, presence of such discs is an autapomorphy of Cyclorapha: they are present both in various Cyclorapha-Atriata Meijere 1900 and in *Lonchoptera* [Meijere, 1900].

The hypodermal thickenings located inside the discs of Cyclorapha, as well as other internal hypodermal thickenings, which exist in active larvae of Diptera, and finally give rise to the pupal legs, are usually interpreted as pupal leg buds, which appear in ontogenesis earlier than in other insects. However, if they would be leg buds, they should be non-functional and have a more simple structure than the definite legs. The formations under consideration bear peculiar setae, which are absent in pupa; these setae can serve special sensory and/or mechanical functions. The hypodermal thickening contains sensory and enveloping cells which serve development and function of these setae. Thus, this hypodermal thickening is not a special embryonic anlage of pupal-imaginal leg, but a component of a larval sensory *d*-organ, which in its turn is a derivative of the larval leg [Pérez, 1911; Keilin, 1915]. Origin of other "imaginal discs", which exist in larval thorax of Cyclorapha, is different.

3.5.2. **Hymenoptera-Apocrita.** Loss of larval legs is either an autapomorphy of Apocrita, or a synapomorphy of Apocrita and some taxon within a plesiomorphon Ventrosessiles (= Symphyta).

When the pupal leg bud develops in the larva of last instar, from very beginning of its development it is directed by its apex posteriorly, thus its apex is sinked into an acrogenous pocket which is formed behind it. Subsequently, outer wall of the pocket disappears, thus leg bud lies between trunk hypoderm and cuticle. During all development, leg buds are directed by apices posteriorly or posteriorly-medially; at first, they are short and straight; than, becoming longer, form knee bents and sometimes other curvations. Such development is described for *Lasius flavus* [Karawaiew, 1898] and observed by me for *Myrmica* sp., *Eurytoma* sp. and some other species of Apocrita.

3.6. General remarks about leg transformation

Different authors assumed that in course of metamorphosis the pupal-imaginal legs either appear anew and substitute the larval legs, or develop directly from the larval legs (see above, 3.2).

As shown above, methods of larval/pupal leg transformation are diverse, but all of them in some respect can be interpreted both as a substitution of the larval leg by the pupal-imaginal leg and as a direct development of the pupal-imaginal leg from the larval leg.

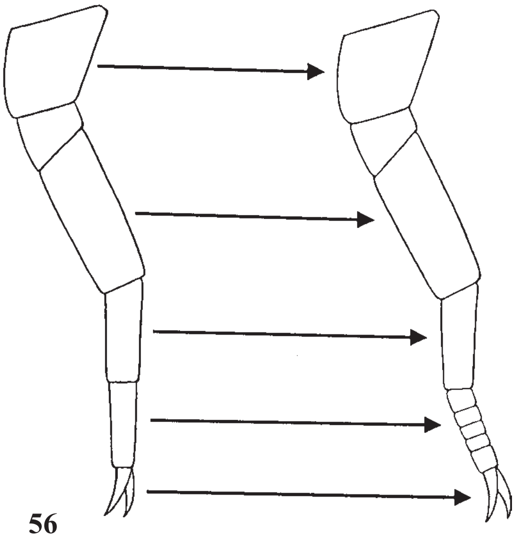
In all cases the pupal-imaginal leg as a whole is ontogenetically homologous to the larval leg: at least its hypoderm develops only from hypoderm of the larval leg. In this respect leg transformation should be regarded as a direct development, but not a substitution.

In all cases the larval/pupal leg transformation is accompanied by loss of musculature and mobility (in Meganeuroptera — partly, in others — completely), and the pupal/imaginal leg transformation is accompanied by restoration of muscles. This process takes place obligatory, independently if larval and imaginal leg muscles are different (as tibial-tarsal muscle in *Sialis sordida*) or similar (as pretarsal flexors of the same species). In this respect leg transformation can be regarded as a substitution.

The loss of musculature during the larval/pupal leg transformation in Metabola is not directly caused by differences between larval and imaginal leg structure or size. In some other insects (for example, in all Ephemeroptera) legs strongly change their structure and size during one moult without loss of musculature. In Scytinelytra imaginal leg develops from an extremely short immovable larval leg, and before larval/imaginal moult is strongly crumpled inside the trunk, but when imago emerges from larva, it has well-developed leg muscles and is able to walk. In Metabola body parts other than legs, during the same larval/pupal transformation can either lose muscles or not. For example, pronymph of *Myrmeleon* loses both mandibular and leg musculature, but before larval/pupal ecdysis a new mandibular musculature appears, and newly hatched pupa is able to move mandibles (but at the same time has absolutely immovable muscle-less legs — see above). Pronymph of *Raphidia* has well-developed mandibular musculature (which probably never disappears) when its legs are completely muscle-less.

Unlike the leg as a whole, which always keeps ontogenetic homology in all stages, selected leg segments in various taxa of Metabola either keep ontogenetic homology, or not. In such insects as *Rhyacophila nubila*, *Myrmeleon bore*, or *Sialis sordida* pupal-imaginal leg segments are ontogenetically homologous to the corresponding larval leg segments (Fig. 56), and this can be regarded as retaining of leg segmentation during larval/pupal transformation; in *Sialis sordida* leg is well-segmented during all transformation, but in *Rhyacophila nubila* and *Myrmeleon bore* segment boundaries become indistinct and than restore at the same places. Unlike them, in such insects as *Tenebrio molitor*, *Leptinotarsa decemlineata*, *Chrysoperla carnea* and *Chrysotropia ciliata* these or that pupal-imaginal leg segments are not ontogenetically homologous to the corresponding larval segments (Figs 57, 58). In these cases during larval/pupal transformation leg segmentation is partly lost and than appears anew.

Pose and position of the living part of leg, which it gets under the larval cuticle during larval/pupal transformation, varies from taxon to taxon. This is due both for long-legged larvae (compare Figs 9, 24, 36) and for leg-less larvae. Probably, further investigation of pronymphs would allow to discover important characters of some taxa. Similar characters — pose of subimaginal genital buds under larval cuticle — are used in systematics of Ephemeroptera-Turbanoculata [Kluge, 2004a].



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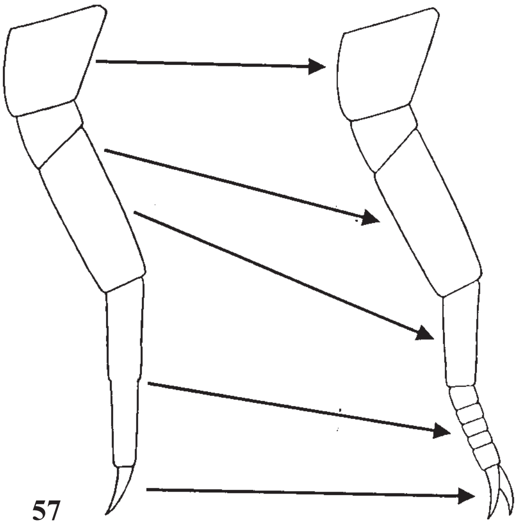

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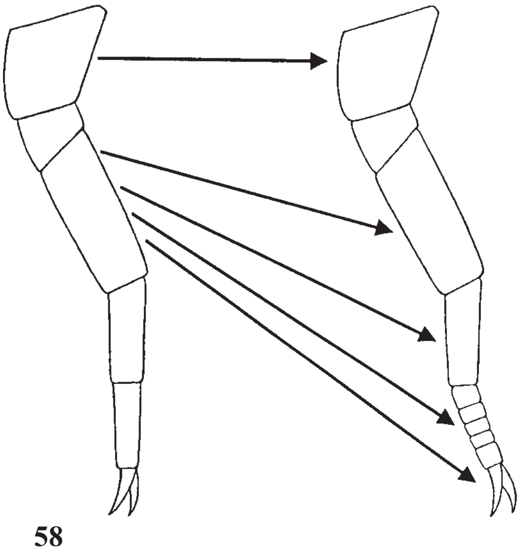

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Figs 56–58. Ontogenetic correspondence between larval and pupal-imaginal leg segments: 56 — *Rhyacophila nubila*, *Myrmeleon bore* and *Sialis sordida*; 57 — *Tenebrio molitor* and *Leptinotarsa decemlineata*; 58 — *Chrysoperla carnea* and *Chrysotropia ciliata*.

Рис. 56–58. Онтогенетическое соответствие между личиночными и куколочно-имагинальными члениками ног: 56 — *Rhyacophila nubila*, *Myrmeleon bore* и *Sialis sordida*; 57 — *Tenebrio molitor* и *Leptinotarsa decemlineata*; 58 — *Chrysoperla carnea* и *Chrysotropia ciliata*.

3.7. Pupal knee bent

In all Metabola pupal legs of all three pairs are bent in knee articulation (Figs 10, 37, 44, 46, 49), independently if this articulation is expressed or not (see also 7.1). Some pupae have leg structure similar to imaginal, and it seems that the insect simply bent its knees (Fig. 44). In other pupae leg cuticle has a form of immobile bent tube lacking distinct articulations; the bend can be located not at the knee itself, but at a proximal part of tibia. In all cases the tibia appears to be pressed to the femur.

In some cases the knee bend is served by resiliency of cuticle, and in pupae conglutinatae of Neolepidoptera, Diptera et al. (see 7.2) — also by the fact that the legs are immovably adhered to trunk and protoptera. But in pupae of such insects as Neuropteroidea, resiliency of cuticle, vice versa, is directed to unbent knee. The knee bend can not be served by muscles, because in early pupa femoral muscles are either weak (in *Sialis*), or absent at all. In course of development in the pronymphal phase, the knee bend differently appears in different insects. In Trichoptera, Lepidoptera, Coleoptera and others, it appears independently of the space in which the pupal leg develops (Figs 7–8, 18–20, 24, 51). In Birostrata it corresponds to the sterno-coxal bend of larva (Figs 35–36). In pronymph of *Sialis* the pupal knee articulation, being located inside the larval cuticular femur, is forcedly unbent (Figs 48, 50), and bents only when the larval cuticle is shed (Figs 46, 49). In all cases the knee bend appears thanks to more intensive growth of hypoderm at the area of outer side of knee articulation (including distal part of femur and proximal part of tibia). At early phase on this place can appear a characteristic fold (Figs 17a, 21, 29, 38).

In many Metabola all pupal legs remain to be permanently bent in knees up to the pupal/imaginal moult. But in some cases just before this moult pupal legs, under whose cuticle imaginal legs are developed, get ability to move actively and unbent knees (Fig. 39) (these are all legs in Birostrata and Rhaphidioptera, fore and middle legs in Trichoptera — see 7.2).

3.8. Evolution of larval legs in Metabola

Traditionally, larvae were divided into campodeiform and eruciform ones.

The term “**campodeiform**” (or “*Campodea*-form”) was introduced by the authors of the 19th century [Brauer, 1869; Packard, 1898; et al.], who regarded *Campodea* to be ancestral for other insects and believed the “biogenetic law”. To the campodeiform type were attributed larvae of all hemimetamorphic and some holometamorphic insects, which have six well-developed legs, independently if their other features resemble *Campodea* or not. In order to avoid confusion, here is used the term “**long-legged**” for that larva of Metabola whose legs are long enough to walk or crawl; most of these larvae when walking, use besides legs, also a pygopod (or a pair of pygopods) on the tip of abdomen (see below).

The term “**eruciform**” was originally introduced in a wide sense, including both short-legged and leg-less larvae. In restricted sense it can be attributed to larva of Neolepidoptera (caterpillar, or eruca) and similar larvae of other taxa. But here similarity can be understood differently: some authors pay most attention to size of thoracic legs, others — to presence and origin of abdominal false legs. In order to avoid confusion, here is used the term “**short-legged**” for larvae whose legs are so short that in order to locomote the larva has to use its middle abdominal segments (independently if they bear or not false legs of this or that origin).

The traditional point of view is that among Metabola the log-legged larvae are the most primitive. Initially this opinion was based on errors popular in the 19th century — the “biogenetic law” and the opinion about primitiveness of *Campodea* with its entognathous head structure [Brauer, 1869; et al.]. If reject these theories, it still seems that the idea about primitiveness of long-legged larvae is reliable, because the presence of long larval legs looks as a symplesiomorphy with hemimetamorphic insects. According to this point of view, it is regarded that the short-legged larval form appeared from long-legged independently in various taxa.

An alternative point of view is that among Metabola the most primitive are the short-legged larvae [Rasnitsyn, 2002]. This idea is supported by two well-known facts: (1) presence of pygopod and (2) repeated loss of legs; now this opinion is supported by one fact more — (3) diminishing of leg during larval/pupal transformation in long-legged larvae.

(1) Presence of pygopod. In spite of the fact that larval legs of Metabola can be as large and composite as full-value legs of some other insects, they are initially not full-value organs of locomotion, but are supplemented by a pygopod, whose presence is initial for Metabola. **Pygopod** locates at the extreme tip of the last (tenth)[1] abdominal segment and surrounds the anal opening; when larva moves, the pygopod is used as a seventh bearing, in addition to the six legs. Structure of the pygopod is variable — it can be a soft sucker (in Rhaphidioptera, many Birostrata, Coleoptera, Mecaptera), or a pair of false legs (in Neolepidoptera and others), or a pair of hooks (in Eumegaloptera, Trichoptera, Nannomecoptera, some Coleoptera). Presence of the larval pygopod is an autapomorphy of Metabola not found in other taxa. In larvae of some Metabola the pygopod is secondarily lost either in connection with a special mode of larval movement (for example in larvae of *Sialis*, whose paraprocts are transformed to a swimming tail), or in connection with immobility of larva. In addition or instead the pygopod, some larvae of Metabola have abdominal false legs (pseudopodia, or prolegs), which also serve as additions for the legs, but appeared independently in various taxa [Hinton, 1955]. Presence of pygopod testifies that larva of the common ancestor of Metabola could not move by its legs only, and used abdomen as a locomotory organ.

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[1] Abdomen of Hexapoda is initially 10-segmented, but not 11-segmented as it was proposed by Snodgrass and some other authors [Kluge, 2000, 2004a].

(2) Loss of legs. In many Metabola larval legs have this or that simplified structure or are lost at all. If regard the reduction and loss of legs as apomorphies, we have to admit that these apomorphies repeatedly appeared in various non-related taxa belonging to Metabola. In many Metabola this loss of larval legs is not connected with immobile mode of life; many legless larvae find their food actively searching it in nature, many of them are predators and hunt active pray. At the same time, among other insects loss of legs occurs very rare; even absolutely immovable representatives of Phytadelga (larvae and females of many Gallinsecta, wingless forms of some Gynaptera, larvae of Scytinelytra) retain small non-functional legs; legs are lost only in a few ones among immovable forms of Gallinsecta and Gynaptera. From this, we can make a conclusion that the loss of larval legs as a regular tendency, which exists in all Metabola and is absent in other insects. Presence of such tendency should be explained by some autapomorphy of Metabola. This autapomorphy can be the initial shortening of legs and using of abdomen for locomotion.

If assume that the loss of larval legs is not a tendency, but an autapomorphy itself (i.e. once occurred in the common ancestor of Metabola), and that in many Metabola larval legs were independently secondarily restored, it will be difficult to explain the fact that larval legs always have specific larval structure, always without tarsal segmentation. If larvae would got legs secondarily, by means of shifting of the imaginal legs to the larval stage (as it happened, for example, with faceted eyes in Culex/fg4 — see below), the larval legs would have these or that features of imaginal structure characteristic for the given taxa; however, this is not so.

(3) Diminishing of leg during transformation. The features of larval/pupal leg transformation described above, also testify in favour of the theory about plesiomorphy of the short-legged larval type and secondary origin of long-legged larvae. If assume an opposite idea, that long larval legs are symplesiomorphic, it would be difficult to understand, why they transform to pupal legs (which are similar in these taxa) by so different ways — anti-growth, breaking or direct development.

Probably, initially for Metabola larval legs are short. Besides this, the common ancestor of Metabola got such a method of larval/pupal leg transformation, when all leg muscles degenerate, and a sharp immobile knee bend appears. In various taxa of Metabola larval legs were secondarily elongated, but retained the ancestral method of larval/pupal transformation. This method obligatory demands, that the leg transformation should start from a short condition. Because of this, each taxon, whose larval leg was secondarily elongated, got its own method of leg shortening. This can explain why in various taxa with long-legged larvae ways of leg shortening are so diverse (see 3.3). In short-legged larvae the phase of leg shortening is absent (see 3.4), and this is the primitive condition. The phase of leg elongation is similar in short-legged and all long-legged larvae, being inherited from the common ancestor: in all cases it is an uneven growth, which leads to formation of the knee bend. Growing legs are variously packed under larval cuticle, but these differences are caused not by the method of growth, but by a shape of space in which they appear as a result of the forgoing diminishing. The loss of leg muscles during larval/pupal transformation in the ancestral Metabola was not directly caused by the shortening of leg, but the both features are independent autapomorphies (see 3.6).

Among Metabola, only in Meganeuroptera larval legs, besides secondary elongation, secondarily got also a more direct method of larval/pupal transformation. Here is partly reduced that phase, when leg hypoderm shortens and muscles degenerate, thus leg transformation becomes similar to that of hemimetamorphic insects. Secondary nature of this feature is indicated by the fact that like other Metabola, Meganeuroptera retain such mode of life, at which pronymph and pupa do not use their leg muscles.

The assumption about primitiveness of short-legged larvae does not contradict the Dollo's principle of non-reversibility and non-repeatability of evolution, because under the short-legged larvae should be understood such larvae, whose legs retain the leg structure typical for Hexapoda, with all its muscles and segments, where only tarsal segmentation is lost. Legs of the long-legged larvae differ from the ancestral short larval legs only by proportions of these or that segments. Such change of proportions could appear independently in non-related taxa.

Among recent insects, short larval legs most similar to the ancestral one, are retained in Lepidoptera-Neolepidoptera and some Hymenoptera-Symphyta (while they differ from the ancestral larval leg by a single-clawed pretarsus — an autapomorphy of Panzygothoraca). Possibly, the primitively short larval legs are retained in some Coleoptera, such as Archostemata. Larval legs of Mecaptera, while also being very short, are far not primitive, because their tibia, tarsus and pretarsus are lost [Kluge, 2004b].

4. Antennae

In all Metabola larval antenna has no scapus (which in Amyocerata is the single segment containing muscles). Thus, larval antenna can move only by muscles which come to its base from tentorium or from head capsule (sometimes these muscles are also lost, and antenna is immovable). Some authors wrongly described for larval Metabola a scape with muscles; for example, Kelsey [1954] reported for larva of *Corydalus cornutus* two muscles in the first antennal segment, which he called "scape" — these are muscles called him "7 — the levator of the flagellum" and "8 — the depressor of the flagellum" [Kelsey, 1954: Fig. 16]. Actually, these are not muscles, but nerve tissues (possibly chordotonal organs). In connection with the initial absence of scape, larval antenna often undergoes reduction, thus in many larval Metabola antennae are small or vestigial. Probably, the longest larval antennae are present in Coleoptera-Scirtes/f=Elodes/g; externally their antennae resemble setiform antennae primitive for Amyocerata (which consist of a thick scapus, a movably articulated pedicellus and a long multisegmented flagellum, whose segments become narrower and longer toward antennal apex); but there are no muscles in the first segment, which externally resembles scapus.

Even when larval and pupal-imaginal heads are similar, they have different places of antennae attachment: usually larval antennae (Fig. 50) are attached nearer to mandibles, than pupal-imaginal antennae (Fig. 49).

Antenna of pupa resembles the imaginal antenna, but has no movable articulations between head, scapus, pedicellus and flagellum. At the beginning of pupal development, muscles of scapus are absent; they appear later, when pharate imaginal antenna develops under cuticle of the pupal antenna. During the whole pupal development, antennae remain to be immovable; this is true for all Metabola, including those whose pupae at some phase have movable legs and mandibles (Figs 10, 39, 44, 49).

In course of larval/pupal transformation, at least scapus appears as a new segment from epithelium at the boundary between larval antenna and head capsule [Svacha, 1992]. When the future pupal antenna grows, it is shifter from the larval cuticular antenna into the head, and often forms characteristic loops under the cuticle of larval head (Figs 9, 50).

Only in Diptera-Nymphomyia/fg1 pupal antenna sharply differs from the imaginal antenna and retains similarity with the larval antenna [Courtney, 1994], thus the transformation of antennae takes place not at the larval/pupal moult, but at the next, pupal/imaginal moult.

5. Eyes

A well-known peculiarity of Metabola is change of eyes during transformation from larva to imago [Gilbert, 1994]. In larvae of Metabola each eye has non-facetted structure and initially consists of 7 or 6 stemmata (Fig. 50) (secondarily eye can have less number of stemmata, or has a single lens, or is reduced); only in Mecaptera-Scorpiomusci larval eyes are secondarily facetted. During the larval/pupal transformation, facetted imaginal eyes appear anew above the larval eyes or close to them (Figs 8–10, 50); in imago, the larval eyes become internal or degenerate. An exception is made only by Culex/fg4 (^{2}sine *Chironomus*; ^{3}sine *Dixa*; ^{4}sine *Corethrella*; incl. *Chaoborus*): in this taxon facetted imaginal eyes appear not in the pupal, but in the larval stage, when the larval eyes are also functional.

Besides Metabola, the same change of eyes occurs in some Arthroidignatha: in Gynaptera and Gallinsecta larval and imaginal eyes exist simultaneously, as in larvae of Culex/fg4; in Scytinelytra simple larval eyes are substituted by facetted imaginal eyes.

6. Wings

6.1. Terms

All Pterygota, which in adult stage have wings (except for Scytinelytra), in some immature stage have immobile outgrowths, from which imaginal wings develop. These outgrowths are often called “wing rudiments” or “wing buds”. The term “rudiment” is etymologically correct, but often also used in its indirect meaning — for a secondary reduced organ, that can lead to confusion (in Russian biological tradition this term is used in this indirect meaning only). It is necessary to distinguish clearly “wing buds” as nymphal or pupal external appendages with completely developed integument (consisting of hypoderm and cuticle) from “wing buds” as hypodermal formations at some phase of moulting cycle (Fig. 59). In order not to write “larval bud of pupal wing bud”, I use here a term **protopteron** (in plural — **protoptera**) for the external appendages of immature insects. Unlike wings (which can exist in imago and subimago only), protoptera are absolutely immovable projections. Larva of Metabola can not have wing buds (as hypodermal formations), because wings are present in imago only, and in Metabola larva never moults to imago. Hypodermal formations, which can be present in larva and are ontogenetically homologous to wings, are in fact buds of pupal protoptera.

6.2. Autapomorphies in wing development

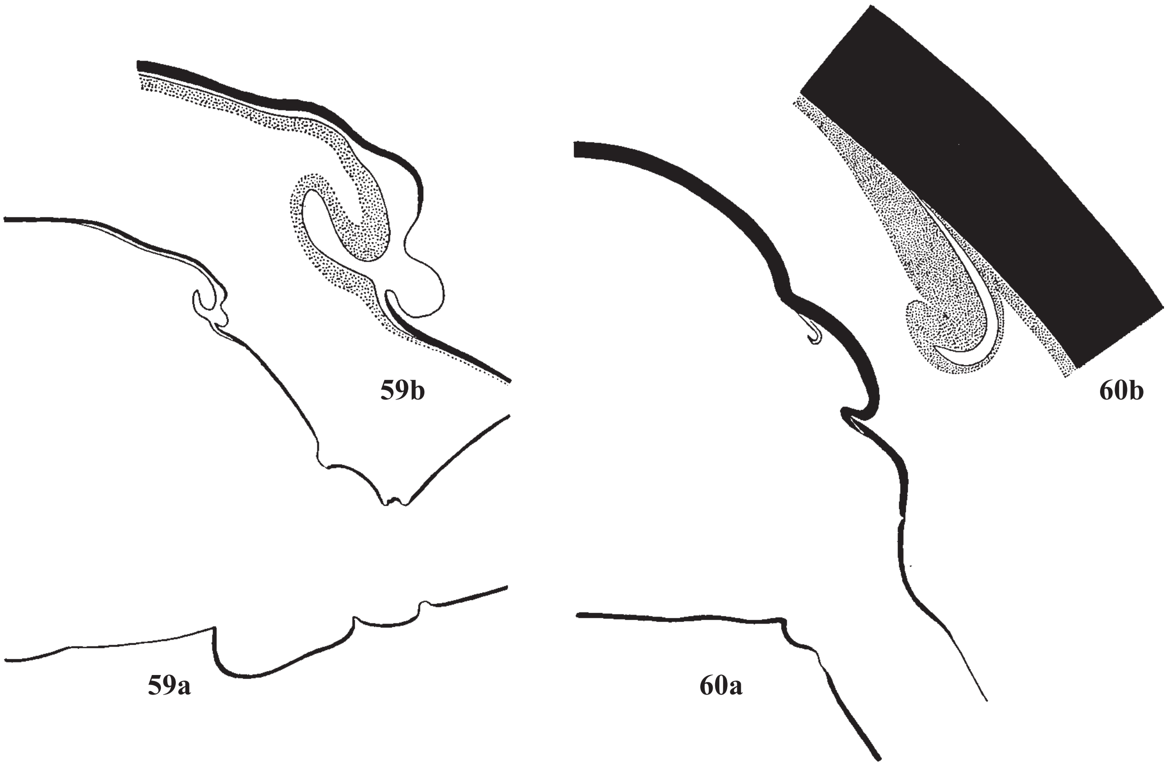
Two distinct autapomorphies of Metabola are connected with development of protoptera.

A well-known autapomorphy is absence of protoptera in larval stage. In all Metabola protoptera are absent (or at least have not form of wing-like projections) up to the last larval instar inclusively, and at the larval/pupal moult at once large pupal protoptera appear (Figs 9–10, 36–37, 49–50). Reports about presence of “atypical holometaboly” with several pupa-like instars in some Strepsiptera or Hymenoptera are wrong, as it was shown by Sehnal et al. [1996]: these reports were based on inaccurate descriptions, in which internal hypodermal formations were mixed with external protoptera, and transformations occurring under cuticle were mixed with instars separated by moults.

Another autapomorphy of Metabola is that pupal protoptera are directed by their apices ventrally-posteriorly and project beneath sterna (Figs 10, 37, 39, 44, 49). Larval buds of the pupal protoptera from very beginning of their development are usually also directed by their apices ventrally (Figs 2–9, 12, 13b, 20, 33–36, 42, 50, 53). In other Pterygota protoptera have various other positions — either directed laterally, or posteriorly, or overturned (in Odonata and Saltatoria); sometimes protoptera are directed ventrally-posteriorly (in Auchenorrhyncha), but not projecting beneath sterna (see 7.1).

6.3. Internal protopteron buds

As a characteristic feature of Metabola, some authors regarded the fact that larva can have internal “wing buds” (more correctly — buds of pupal protoptera).



Figs 59–60. Transverse section of larva. 59 — Plecoptera: *Nemoura* sp., young larva lacking protoptera (larva propre), before moult to the earliest larval (nymphal) instar possessing protoptera: 59a — right half of metathorax; 59b — enlarged bud of protopteron under cuticle of tergite; 60 — Trichoptera: *Rhyacophila nubila*, active larva of last instar: 60a — right half of metathorax; 60b — enlarged internal protopteron bud under non-sclerotized trunk cuticle. Cuticle shown by black, hypoderm dotted.

Рис. 59–60. Поперечный срез личинки. 59 — Plecoptera: *Nemoura* sp., молодая личинка, не имеющая протоптеронов (собственно личинка) перед линькой на самый ранний личиночный (нимфальный) возраст, имеющий протоптероны: 59a — правая половина заднегруди; 59b — увеличенный зачаток протоптерона под кутикулой тергита; 60 — Trichoptera: *Rhyacophila nubila*, активная личинка последнего возраста: 60a — правая половина заднегруди; 60b — увеличенный внутренний зачаток протоптерона под несклеротизованной туловищной кутикулой. Кутикула показана черным, гиподерма пунктирована.

With this is connected a wrong usage of the name Endopterygota instead Metabola (actually the circumscriptional name **Endopterygota** Sharp 1898 belongs to a paraphyletic, non-accepted taxon which does not include Aphaniptera).

As some people mix internal protopteron buds with other formations, it is necessary to give here some comments. In all arthropods external outgrowths which appear during post-embryonic development, at first grow under cuticle, and only after a moult become external; thus, every external outgrowth obligatory passes through a phase of development when it locates inside the body, so it can be called "internal". This fact never can be an autapomorphy of any taxon within Arthropoda, because directly proceeds from the autapomorphy of Gnathopoda (= Arthropoda s.l.). In Pterygota protoptera appear at some post-embryonic instar; thus, in the previous instar their buds locate under trunk cuticle, and in this respect are internal (Fig. 59); but these are not formations regarded to be internal protopteron buds, in other case we would have to attribute all Pterygota to "Endopterygota". Unlike the usual protopteron bud which develops under cuticle up to the moult, a true internal protopteron bud does not become external protopteron at the next moult, but passes from instar to instar remaining under cuticle.

Some authors regard to be an internal protopteron bud any distinguishable internal thickening of hypoderm, which passes from instar to instar and finally gives rise to the pupal protopteron [Tower, 1903: Figs 16, 26, 64]. If each epithelial cells of such thickening has a contact with external cuticle and participates in its secreting, the whole integument composed of the hypodermal thickening and its cuticle, should be regarded as belonging to a protopteron. If we regard this formation to be a protopteron, we must say, that larva has protoptera covered by external cuticle — i.e., external protoptera (but not internal ones). In this case the autapomorphy of Metabola should be formulated not as "larval protoptera are absent", but as "larval protoptera are not projected above external surface of the body", that is more exact. Unlike a simple hypodermal thickening, the true internal protopteron bud is a folded hypodermal thickening, whose hypoderm faced into the fold has no contact with external cuticle and does not participate in its secreting (Fig. 60). This hypodermal fold can be very small, so there are all gradations between distinct absence and distinct presence of the true internal protopteron buds.

In many Metabola larva has no internal protopteron buds. In some Coleoptera, some Diptera-Nemocera, Mesodiptera and others, the hypodermal bud of pupal protopteron appears in the last larval instar just under the larval cuticle and at the next moult becomes external pupal protopteron (like at the larval/nymphal moult in hemimetamorphic insects — Fig. 59). In some Metabola the hypodermal bud of pupal protopteron is sinked into a pocket formed by an impression of hypoderm (Fig. 60). In course of subsequent development the external wall of this pocket gradually shortens and disappears, thus the bud of protopteron appears outside of living tissues of the trunk, directly under the larval cuticle (Figs 2–7). In some Metabola the pocket containing protopteron bud, is closed, thus can pass from one larval instar to another not shedding cuticle, which can appear inside it [Svacha, 1992]. Such pocket with protopteron bud can occur inside the body during several larval instars; in this case it represents the true internal protopteron bud. Such internal protopteron buds are found in some Coleoptera, some Hymenoptera, some Mecaptera, some Diptera-Nemocera, Cyclorapha and Sorbentia. Various types of protopteron development are repeated in non-related taxa; for example, among Coleoptera occur all known types — from the simple development without any pocket — to pockets appearing at the last larval instar only — to internal buds in pockets which pass from instar to instar [Tower, 1903].

The question is, if the internal protopteron buds initially appeared in the common ancestor of Metabola and subsequently were repeatedly lost (i.e. constitute an autapomorphy of Metabola), or they repeatedly appeared in several taxa of Metabola [Svacha, 1992].

In favour of the first version could testify the fact, that the internal protopteron buds are found among Metabola, but not reported for other insect taxa. However, among Metabola there are found also internal leg buds (see 3.5), which sometimes are so similar to the internal protopteron buds, that are mixed with them under a common name "imaginal discs"; the internal leg buds, being connected with reduction of larval legs, could not appear in the common ancestor of Metabola; so at least some similar internal buds appeared more than once.

In favour of the assumption about repeated appearing of the internal protopteron buds, testify the diversity of forms of their pockets: like independently appeared the basigenous pocket of leg bud in Diptera (see 3.5.1) and acrogenous pocket of leg bud in Apocrita (see 3.5.2), pockets of protopteron buds also can be basigenous or acrogenous.

Some Metabola have protopteron buds in basigenous pockets ("wing fundaments of recessed type" by Tower [1903]), when the bud is sinked into a pocket by its base. Pockets of such form were observed by me in Hymenoptera (*Arge* sp. and others) and in *Tenebrio molitor*, where they appear in the last larval instar only (Fig. 12); they are also reported for Scarabaeidae, among which in *Osmoderma scabra* also appear in the last instar, but in *Lachnosterna fusca* appear in 2nd instar and represent true internal buds [Tower, 1903].

Some other taxa of Metabola have protopteron buds in acrogenous pockets ("wing fundaments of enclosed type" by Tower [1903]), when the bud is sinked into the pocket by its apex. Pockets of such form are found in some Coleoptera (in *Leptinotarsa decemlineata* [Tower, 1903: Fig. 18] and some others), in Sorbentia (Figs 2, 60), in some Diptera (for example, *Phalacrocera replicata*); Tipulidae have stalked acrogenous pockets, superficially similar to their stalked basigenous pockets of leg buds (see 3.5.1). Like the protopteron buds in basigenous pockets, the protopteron buds in acrogenous pockets can either appear in the last larval instar, or pass from instar to instar. Possibly, in different groups of Metabola similar acrogenous pockets of protopteron buds could appear independently thanks to the following reasons: (1) as in all Pterygota, in Metabola protoptera and their buds represent lateral outgrowths of tergites; (2) protoptera buds of Metabola are directed ventrally at all phases of development (see above); (3) in many Metabola larval body is more or less cylindrical, with tergites (or corresponding non-sclerotized areas) diminished, and pleural areas convex (this can be connected with initial nature of eruciform larvae — see 3.8). Because of this, when in pronymph the buds of pupal protoptera start to grow, they, being lateral outgrowths of the small tergite, at very beginning of their development turn ventrally, press upon hypoderm of the convex pleura and rumple in the pleural hypoderm a pair of pockets.

Probably, internal protopteron buds evolved from independently appeared pockets, and their presence is not an autapomorphy of Metabola.

Some authors regard that the presence of internal protopteron buds compensates the absence of protoptera: wing has to grow gradually, thus in "Exopterygota" it grows as an external protopteron, and in "Endopterygota" — inside the body. Actually, the bud of protopteron which can be located inside the pocket, is so small in comparison with the pupal protopteron (compare Figs 60 and 2–10), that for the insect there is no practical significance, if the pupal protopteron develops from an internal larval bud, or from nothing. Hinton [1948] assumed that larval protoptera became internal as an adaptation "to burrow in solids — in earth and in plants", where larvae have to "move backwards in a close-fitting burrow". Actually, if active larva of Metabola has internal protopteron buds, they are so small, that can not play any role in larva's life, independently if they would be external protoptera or internal buds (Fig. 60). Taking into account their size, internal protoptera buds of last-instar larva of Metabola can be compared with hypodermal protoptera buds, which occur in hemimetamorphic insects under cuticle of young larva before its moult to the first nymphal instar (compare Figs 59 and 60).

7. Pupa

7.1. Pupal pose

Pupae of Metabola have following non-trivial features of shape, which are autapomorphies of Metabola: (1) all legs are bent at knee articulations (see 3.7); (2) protoptera are directed ventrally (see 6.2); (3) mesothorax and metathorax differ in position of their legs and protoptera.

In various Metabola imaginal mesothorax and metathorax can be from nearly homonomous (in bimotorial insects — many Neuropteroidea et al.) to sharply heteronomous (anteromotorial and posteromotorial insects); larval mesothorax and metathorax also can be homonomous (in most larvae) or heteronomous (Fig. 50). Independently of presence or absence of differentiation of these segments in imago or larva, in pupa they are differentiated in a peculiar manner: on mesothorax the leg is directed by knee anteriorly (like the foreleg), and the protopteron is inclined posteriorly, passing the leg base from behind; on metathorax the leg is inclined by knee posteriorly, and the protopteron is inclined anteriorly, either passing the leg base from the front (Fig. 44), or overlapping it (Figs 10, 49). Thus, apex of the fore protopteron widely overlaps apex of the hind protopteron. This is true for insects which have well-developed fore and hind wings (including such as winged Hymenoptera, whose hind wings are small). Pupae of Diptera (which have smaller hind protoptera) and pupae of wingless insects (such as Aphaniptera or working ants) have knees of all legs secondarily brought together.

In pupae of all Metabola except for Neuropteroidea, tarsi of all three leg pairs are directed posteriorly, parallel one another; as the hind leg has position different from the fore and middle leg, its tarsus is bent under an angle to tibia (Fig. 10). In Neuropteroidea on all legs tarsus is directed as a continuation of tibia, thus tarsi of hind legs are not parallel to tarsi of fore and middle legs (Figs 44, 49).

Unlike pupae of Metabola, inactive pupa-like stages of Thysanoptera and Gallinsecta have another pose: their legs have no permanent knee bend, in rest fore legs are usually directed by tarsi anteriorly and middle and hind legs — by tarsi posteriorly; protoptera are directed posteriorly (not ventrally), similarly on mesothorax and metathorax.

7.2. Classifications of pupae

Linnaeus [1758] divided what he called “pupae”, or “nymphae”, into 5 groups — “pupa completa” (in arthropods other than Pterygota), “pupa semicompleta” (in Pterygota other than Metabola), “pupa incompleta” (in most Metabola), “pupa obtecta” (in Neolepidoptera) and “pupa coarcata” (which actually is not a pupa, but a puparium of Cyclorapha). The term “**pupa obtecta**” is widely used till now for a couple of pupal forms independently evolved in Neolepidoptera, Diptera and certain taxa within Coleoptera and Hymenoptera [Hinton, 1946] (while Linnaeus excluded from this group at least Diptera-Nemocera). Linnaeus defined his “pupa obtecta” as “apoda” and “thorace abdomineque distincto corticata”. Even in our days this term makes some people to think that the pupa is covered by something, and that its legs are somewhere inside. Actually the “pupa obtecta” has no any envelope which could enclose its trunk and appendages; it is covered only by cuticle, which is produced by hypoderm and, thus, covers separately each its leg, protopteron, mouth appendage, antenna and trunk. Just after the larval/pupal ecdysis, when thoracic and head appendages are spread, they are pasted to the trunk, forming a monolith. In order to avoid confusion, I suggest to substitute the term “pupa obtecta” to “**pupa conglutinata**”. Unlike the Linnaean “pupa obtecta”, the “pupa conglutinata” is present not only in Neolepidoptera, but also in Diptera (Nemocera and Mesodiptera), selected Coleoptera and Hymenoptera.

In the 19th century there were attempts to establish taxa smaller than Metabola Burmeister 1832, basing on types of pupae. A taxon **Holometabola** Burmeister 1835 united Diptera, Aphaniptera, Hymenoptera, Strepsiptera, Lepidoptera and Coleoptera (whose pupae were regarded as immovable), but did not include Neuropteroidea, Mecaptera and Trichoptera (whose pupae were regarded as movable). A taxon **Necromorpha** Newman 1834 united Hymenoptera and Coleoptera (whose pupae were regarded as immovable and free). A taxon **Amorpha** Newman 1834 united Lepidoptera, Diptera, Aphaniptera and Strepsiptera (whose pupae were regarded as immovable and either conglutinatae, or enclosed into puparium). A taxon **Subnecromorphotica** Westwood 1840 (= Planipennia Burmeister 1839) united Neuropteroidea and Mecaptera (whose pupae were regarded as movable). In our days all these taxa are rejected, being regarded to be non-holophyletic (paraphyletic and polyphyletic). Only Metabola, Cyclorapha (in Diptera), Neolepidoptera (in Lepidoptera) and a few others remain to be recognized holophyletic taxa characterized by peculiar pupal structure.

Classifications of pupae according to their mobility can be the following.

7.2.1. **Mobility of pupal mandibles.** There is a widely accepted classification of pupae (but not taxa) suggested by Hinton [1946], according to which pupae are divided into **pupa dectica** (with movable mandibles), and **pupa adectica** (with immovable mandibles or lacking mandibles). It is assumed that pupal mandibles, being always unusable for nutrition, initially for Metabola are specialized for biting pupal case, and in various taxa secondarily lost this function. According to origin of pupal mandibular mobility, the pupae decticae can be divided into two groups — pupae larvodecticae and pupae neodecticae. **Pupa larvodectica** retains larval mandibular muscles; in pronymphal phase the pharate pupal head completely locates inside the cuticular larval head, and the pharate pupal mandibles locate inside the cuticular larval mandibles (Fig. 50), thus mandibles retain mobility during the whole postembryogenesis; mandibular muscles do not disappear during ontogenesis. To this type belong pupae of Meganeuroptera and

Rhaphidioptera. **Pupa neodectica** has newly developed mandibular muscles, while larval mandibular muscles disappear; in pronymphal phase the pharate pupal mandibles are immovable and shifted into the larval cuticular head capsule (Figs 8–9). To this type belong pupae of Birostrata and Trichoptera.

Development of mandibular muscles is not correlated with development of leg muscles. In *Sialis* both mandibular and leg muscles pass from larva to imago. In *Raphidia* only mandibular muscles pass from larva to imago, but leg muscles disappear in larva and appear anew in pupa. In *Myrmeleon* both mandibular and leg muscles disappear in larva (at middle pronymphal phase); new mandibular muscles appear after this in larva (at late pronymphal phase) and are already functional in newly hatched pupa; new leg muscles appear only in pupa.

7.2.2. **Mobility of pupal legs.** If under pupal leg mobility, we understand retaining leg muscles during the larval/pupal transformation, the only mobile should be pupae of Meganeuroptera.

If under pupal leg mobility understand ability of pupa to walk before moult to imago (when any pupa has completely developed imaginal leg musculature), mobile pupae should be that of Trichoptera, Rhaphidioptera and a part of Birostrata. Pupae of Rhaphidioptera and many Birostrata, which in the beginning of development have absolutely immovable legs, before moult to imago walk and moult staying on legs (Fig. 39), like nymphs of hemimetamorphic insects. Pupae of Trichoptera have middle legs specialized as swimming; before moult to imago, pupa actively swims using middle legs, and crawls out of the water using fore and middle legs.

Probably, ability of pupa to use legs before moult to imago, is connected with structure of pupal claws and in many (or in all) cases has an adaptive significance, being not primitive. In most Metabola pupal legs are not used, and pupal claws are non-sclerotized, non-hooked, blunt. In Meganeuroptera pupal claws are also non-sclerotized and have non-hooked apex (Fig. 46), thus pupa is unable to fix itself by such claws; the pupa moults on surface of ground and does not need to hold on something. Among Birostrata, pupae of Myrmeleontidae are also unable to walk and have blunt claws; cocoons of Myrmeleontidae are underground, and pupa moults crawling out from the cocoon to the earth surface. Pupae of Chrysopidae and Hemerobiidae have on each leg an immovable hemispheric pretarsus with two small sclerotized hooks (Fig. 37), which are not similar to claws of imago or larva; cocoons of these insects are attached to plants, and pupa which escapes from the cocoon, keeps itself on the plant by its legs. The pupal claws of Chrysopidae and Hemerobiidae are so different from imaginal claws, that the imaginal claws when develop inside the pupal pretarsus, are not inserted into the pupal claws (Fig. 40), so can not serve their active mobility. In pupae of Trichoptera (which need to get out from the bottom of water reservoir to a bank) claws also can markedly differ from imaginal ones, thus the imaginal claws are inserted into them only partly (Fig. 11). In pupae of Rhaphidioptera claws are similar to imaginal ones, and the imaginal claws are located inside them serving their active mobility (Fig. 43).

8. Autapomorphies of Metabola

The most striking autapomorphy of Metabola is the method of leg transformation which takes place during the penultimate (i.e. larval/pupal) moult: the transformation starts when the leg is (or becomes) small; during the transformation, leg loses its musculature and initial shape, and gets an immobile knee bent. These features of leg transformation evolved in the common ancestor of Metabola and became conservative (as other good autapomorphies of high-level taxa), so that they were inherited by all Metabola, independently of their leg structure and independently of structure and mode of transformation of other body parts. This method of larval/pupal leg transformation is that initial autapomorphy, which caused the most evident features of Metabola — the inactivity of pupal stage and the great difference between larva and imago.

While in other insects structure of larval and imaginal legs are mutually dependent (so that during evolution they can get the same features), in the common ancestor of Metabola structure of larval and imaginal legs became completely independent, so in all phylogenetic lines of Metabola evolutionary changes of larval legs are completely independent from evolutionary changes of imaginal legs. As leg structure (and a mode of locomotion in general) markedly determines the whole mode of insect life, the obligatory difference between larval and imaginal legs caused other differences between larva and imago, which thanks to this, independently appeared in many phylogenetic lines of Metabola. Larvae of first Metabola were short-legged and used their abdomen for locomotion; because of this in course of subsequent evolution, besides secondarily long-legged larval forms, repeatedly appeared worm-like leg-less larval forms.

Thus, the ancient characteristic of Metabola as insects which have a stage of "worm" and a stage of more or less inactive nymph (pupa), now becomes supported by a concrete autapomorphy.

A formal account of recently known autapomorphies of Metabola can be the following.

- Larval eyes are substituted by imaginal eyes (see 5).
- Larval antenna lost scapus and intrinsic muscles (see 4).
- In course of larval/pupal transformation antennal segmentation changes and tentorio-antennal muscles disappear; imaginal tentorio-antennal and scape muscles appear anew only during subsequent pupal/imaginal transformation. Thus, pupa has immobile antennae with shape resembling imaginal antennae (see 4).
- Pupa is non-feeding (but Metabola have no general characters connected with structure or metamorphosis of mouthparts or digestive tract — see 2.2).

- Larval leg lost tarsal segmentation (see 3.1).
- Correlation between structure of larval and pupal-imaginal legs is lost: larval and pupal-imaginal legs of the same individual never have any characters in common other than the initial characters of Pterygota (see 3.1).
- In course of larval/pupal transformation all larval leg muscles, at least distad of coxotrochanteral articulation, disappear or at least become non-functional; imaginal muscles appear only during subsequent pupal/imaginal transformation (in all Metabola other than Meganeuroptera, all intrinsic and extrinsic leg muscles completely disappear and than appear anew) (see 3.6 and 3.8).
- In course of larva/pupal leg transformation appears an immobile knee bent which is expressed at least in pupa, at least before pharate imago develops (see 3.7 and 7.1).
- In course of larval-pupal leg transformation the living part of leg starts to grow when it is very short: if larval leg is very short or absent, its living part starts to grow beginning from this condition; if larval leg is relatively long, its living part starts to grow only after this or that process of shortening (the only exception is made by Meganeuroptera, that is probably secondary) (see 3.6 and 3.8).
- Larval protoptera are absent up to penultimate (larval/pupal) moult (see 6.2). Probably, existence of larval internal protoptera buds of is not an autapomorphy of Metabola (see 6.3).
- Protoptera in the last preimaginal (pupal) instar are directed ventrally (see 6.2 and 7.1).
- Pupal pterothoracic segments have unequal pose of appendages, so that on mesothorax legs locate in front of protoptera, and on metathorax legs locate behind or under protoptera (see 7.1).
- Larva has a pygopod (secondarily lost in many taxa) (see 3.8).

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