Paradoxical molting process in *Orthezia urticae* and other coccids (Arthroidignatha: Gallinsecta) with notes on systematic position of scale insects

Парадоксальный процесс линьки у *Orthezia urticae* и других кокцид (Arthroidignatha: Gallinsecta) с замечаниями о систематическом положении кокцид

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Process of transformation in legs and antennae, which takes place in *Orthezia urticae* (Linnaeus, 1758) in course of molt from one instar to another, disagrees with modes of life of these instars. Each molt from one actively feeding instar to another (these are two first instars of male and all instars of female) is accompanied with deep degeneration, dedifferentiation, new differentiation and subsequent growth of each appendage; proximal segment of each appendage newly grows in an unusual inverted condition and everts only during ecdysis. Unlike this, quiescent instars of male molt like most other insects, so that molting processes do not cause immobility of their appendages. Examination of some other coccid species allows to assume that this alternation of molt modes is usual for Gallinsecta. Possibly, this character is initial for Gallinsecta and is connected with existence of leg-less feeding instars in non-related representatives. To describe processes which take place at metamorphosis, new terms for preimaginal instars of Pterygota are introduced. New taxa names Psyllaleyroda **taxon nov.** and Aphidococca **taxon nov.** are suggested.

Процесс трансформации ног и антенн, происходящий у *Orthezia urticae* (Linnaeus, 1758) в ходе линьки с одного возраста на другой, не согласуется с образами жизни этих возрастов. Каждая линька с одного активно питающегося возраста на другой (это два первых возраста у самца и все возраста у самки) сопровождается глубокой дегенерацией, дедифференциацией, новой дифференциацией и последующим ростом каждого придатка; проксимальный членик каждого придатка заново растет в необычном ввернутом состоянии и выворачивается только во время экдизиса. В отличие от этого, неподвижные возраста самца линяют как большинство других насекомых, так что линочные процессы не вызывают неподвижности их придатков. Изучение некоторых других видов кокцид позволяет предположить, что это чередование форм линьки обычно для Gallinsecta. Возможно, этот признак является исходным для Gallinsecta и связан с наличием безногих питающихся возрастов у неродственных представителей. Для описания процессов, происходящих при метаморфозе, введены универсальные термины для обозначения преимагинальных возрастов у Pterygota. Предложены новые названия таксонов — Psyllaleyroda **taxon nov.** и Aphidococca **taxon nov.**

Key words: metamorphosis, morphogenesis, molt, instar, larva, nymph, primolarva, primonympha, secundolarva, secundonympha, tertiolarva, tertionympha, penultimolarva, penultimonympha, ultimolarva, ultimonympha, antennae, legs, Psyllaleyroda **taxon nov.**, Aphidococca **taxon nov.**, Gallinsecta, Ortheziidae, Monophlebidae, Pseudococcidae, Coccidae, Diaspididae, *Orthezia urticae, Icerya* sp.*, Coccus hesperidum, Pseudococcus viburni.*

Ключевые слова: метаморфоз, морфогенез, линька, возраст, личинка, нимфа, антенны, ноги, примоларва, примонимфа, секундоларва, секундонимфа, тертиоларва, тертионимфа, пенультиморва, пенультимонимфа, ультиморва, ультимонимфа, Psyllaleyroda **taxon nov.**, Aphidococca **taxon nov.**, Gallinsecta, Ortheziidae, Monophlebidae, Pseudococcidae, Coccidae, Diaspididae, *Orthezia urticae, Icerya* sp.*, Coccus hesperidum, Pseudococcus viburni.*

INTRODUCTION

Nomenclature notes. For various higher insect taxa, there are traditionally used either non-typified, or typified names. According to the principles of dual nomenclature system, non-typified names should be used according to the rules of circumscriptional nomenclature, and typified names — according to the rules for family-group names in the International Code of Zoological Nomenclature; typified names can be written either in traditional manner, with suffixes and endings corresponding their ranks, or as hierarchical names, or in the basic format (or "universal form") (Kluge, 1999, 2000, 2005, 2009). The basic format is a non-italicised genus-group name followed by slash and the letter(s) "f" (where a family-group name derived from that generic name is available) and "g" (to indicate availability as a genus-group name). According to the insect classification recently accepted by me, the species discussed here belong to the following taxa (Kluge, 2010):

1. Eumetabola Hennig, 1953 [typified name in basic format: Scarabaeus/fg (incl. Cimex/f=Cicada/g)]. Eumetabola are divided into Metabola and Parametabola.

1.1. Metabola Burmeister, 1832 [typified name in basic format: Scarabaeus/fg (sine Cimex/f=Cicada/g; incl. Hemerobius/fg, Papilio/fg)]; circumscriptional synonym: Oligoneoptera Martynov, 1923. This generally accepted taxon is widely known under names "Holometabola" and "Endopterygota", whose original circumscriptions do not fit circumscription of this taxon (Kluge, 2000).

2.1. Parametabola Crampton, 1938 [typified name in basic format: Cimex/f=Cicada/g (incl. Zorotypus/fg)]. This taxon is widely known under the name Paraneoptera Martynov, 1923. However, the name Paraneoptera is a junior monosemantic circumscriptional synonym of Panhomoptera Crampton, 1919, being at the same time a non-monosemantic circumscriptional synonym of Parametabola and a non-monose-

mantic circumscriptional synonym of Acercaria. In other words, when we use the name Paraneoptera, we do not clarify if this taxon includes Zoraptera, or not. Unlike it, the name Parametabola clearly indicates that Zoraptera are included here. For the taxon excluding Zoraptera, the oldest correct name is Acercaria. In the classification accepted here, Parametabola are divided into Zoraptera Silvestri, 1913 [typified name in basic format: Zorotypus/fg] and Acercaria.

2.1.1. Acercaria Börner, 1904 [typified name in basic format: Cimex/f=Cicada/g (sine Zorotypus/fg; incl. Psocus/f=Pediculus/g)]. This generally accepted taxon is divided into Panpsocoptera Crampton, 1938 [typified name in basic format: Psocus/f=Pediculus/g] and Condylognatha.

2.1.1.1. Condylognatha Börner, 1904 [typified name in basic format: Cimex/f=Cicada/g (sine Psocus/f=Pediculus/g; incl. Thrips/fg)]. This generally accepted taxon is divided into Thysanoptera Haliday, 1836 [typified name in basic format: Thrips/fg] and Arthroidignatha.

2.1.1.1.1. Arthroidignatha Spinola, 1850 [typified name in basic format: Cimex/f=Cicada/g (sine Thrips/fg; incl. Aphis/fg)]. This taxon is widely known under wrong names "Hemiptera" and "Rhynchota". The name Hemiptera is used in quite variable senses; if ascribe its authorship to Linnaeus, 1758 (according to the starting point of zoological nomenclature), the name Hemiptera Linnaeus, 1758 appears to be an older circumscriptional synonym of Acercaria. The name Rhynchota Burmeister, 1835 was originally given to a taxon, which, besides others, included sucking lice (Siphunculata). Arthroidignatha are divided into Hemelytrata Fallen, 1829 [typified name in basic format: Cimex/f=Cicada/g (sine Aphis/fg)] and Plantisuga. The taxon Hemelytrata, in its turn, is divided into Auchenorrhyncha Dumeril, 1806 [typified name in basic format: Cicada/fg] and Heteropteroidea Schlee, 1969 [typified name in basic format: Cimex/fg (incl. Peloridium/fg)]. The plesiomorphon, widely known un-

der the wrong name "Homoptera" and comprising Auchenorrhyncha with Plantisuga, is not accepted here.

2.1.1.1.1.1. PLANTISUGA Dumeril, 1806 [typified name in basic format: Aphis/fg (incl. Psylla/fg)]; circumscriptional synonyms: PHYTADELGES Dumeril, 1806; PENDULIROSTRES Spinola, 1839; STERNORHYNCHI Amyot & Serville, 1843; STERNORHYNCHA Fieber, 1851; APHIDOPTERA Haeckel, 1896; STERNORRHYNCHA Meyers & China, 1929. Platisuga are divided into Psyllaleyroda and Aphidococca.

2.1.1.1.1.1.1. PSYLLALEYRODA **taxon nov.** [typified name in basic format: Psylla/fg (incl. Aleyrodes/fg)]. This taxon is known under typified names Psyllina, Psylliformes and Psyllomorpha. As the same typified names are used also for Saltipedes, here I suggest a new non-typified circumscriptional name Psyllaleyroda. Psyllaleyroda are divided into Saltipedes and Scytinelytra.

2.1.1.1.1.1.1.1. SALTIPEDES Amyot & Serville, 1843 [typified name in basic format: Psylla/fg (sine Aleyrodes/fg)]; circumscriptional synonyms: MESOHOMOPTERA Crampton, 1916; PSYLLOPTERA Krausse & Wolff, 1919.

2.1.1.1.1.1.1.2. SCYTINELYTRA Amyot & Serville, 1843 [typified name in basic format: Aleyrodes/fg]; circumscriptional synonyms: CONIOHOMOPTERA Crampton, 1916; ALEYROPTERA Krausse & Wolff, 1919.

2.1.1.1.1.1.2. APHIDOCOCCA **taxon nov.** [typified name in basic format: Aphis/fg (sine Psylla/fg; incl. Coccus/fg)]. This taxon is known under typified names Aphidina, Aphidioidea, Aphidiformes and Aphidomorpha. As the same typified names are used also for Gynaptera, here I suggest a new non-typified circumscriptional name Aphidococca. Aphidococca are divided into Gynaptera and Gallinsecta.

2.1.1.1.1.1.2.1. GYNAPTERA Laporte, 1834 [typified name in basic format: Aphis/fg (sine Coccus/fg; incl. Adelges/fg)]; circumscriptional synonyms: GRADIPEDES Amyot & Serville, 1843; CLINOHOMOPTERA Crampton, 1916; APHIDIOPTERA Krausse & Wolff, 1919.

2.1.1.1.1.1.2.2. GALLINSECTA De Geer, 1776 [typified name in basic format: Coccus/fg (incl. Orthezia/fg)]; circumscriptional synonyms: PHAULOPTERA Laporte, 1834; MONOMERA Westwood, 1839–1840; PSEUDOPTERA Amyot, 1848; HYPEREPIMORPHA Heymons, 1909; MICROHOMOPTERA Crampton, 1916; COCCOPTERA Krausse & Wolff, 1919.

2.1.1.1.1.1.2.2.1. Plesiomorphon PALEOCOCCOIDEA Borchsenius, 1950 [typified name in basic format: Orthezia/fg]; circumscriptional synonyms: ARCHAEOCOCCIDEA Bodenheimer, 1952; PALEOCOCCOMORPHA Borchsenius, 1965.

2.1.1.1.1.1.2.2.2. NEOCOCCOIDEA Borchsenius, 1950 [typified name in basic format: Coccus/fg (sine Orthezia/fg)] circumscriptional synonyms: NEOCOCCIDEA Bodenheimer, 1952; NEOCOCCOMORPHA Borchsenius, 1965.

Ontogenesis of Gallinsecta. Ontogenesis of Gallinsecta is often compared with complete metamorphosis peculiar for Metabola. It is used to regard that male coccids undergo metamorphosis similar to the complete metamorphosis: their first two feeding instars are regarded to be similar with larva of Metabola, and the next two inactive instars are regarded to be similar with pupa of Metabola. It is regarded that female coccids do not pass through metamorphosis, because in puberty stage they retain larval structure. Really, two instars of coccid males do not feed and locate in shelters, like pupae of Metabola; last of them has antennae immovably turned backward, that gives it some similarity with pupa of Metabola. Some authors (e.g., Sikes, 1928: 270) characterised ontogenesis of Gallinsecta as intermediate between incomplete and complete metamorphosis. Taking into account, that complete metamorphosis is an autapomorphy of Metabola, and Gallinsecta belong to subsequently subordinated holophyletic taxa Aphidococca, Plantisuga, Arthroidignatha, Condylognatha, Acercaria and Parametabola, such interpretation cannot be correct.

In spite of the fact, that Metabola is generally accepted as a holophyletic taxon, whose single known autapomorphy is the complete metamorphosis, nature of this metamorphosis had not been studied till the last years. My investigations on processes which take place in course of molt from larva to pupa in some representatives of Metabola allowed to formulate concrete autapomorphies of Metabola (Kluge, 2005).

In this context, it was interesting to compare processes which take place in metamorphosis of Gallinsecta with those of Metabola. Among coccids, the widely distributed species *Orthezia urticae* (Linnaeus, 1758 [*Aphis*]) seems to be one of the most "primitive", saving a lot of plesiomorphic characters, such as complete set of abdominal spiracles, well developed legs and antennae, primitive wax secreting structures, compound eyes in males, etc. The result of investigation of this species appears to be surprising: process of transformation in legs and antennae, which takes place in *O. urticae* at each molt from one actively feeding instar to another, is accompanied with such deep degeneration, which is comparable with degeneration taking place at larval/pupal molt of Metabola; it has also a unique feature — inverting of proximal part of appendage, which is not found neither in Metabola, nor in any other insects. Unlike this, quiescent instars of male *O. urticae* molt like most other insects, so that molting processes do not cause immobility of their appendages. In this respect pupa-like instars of *O. urticae* principally differ from pupa of Metabola, whose immobility is determined by peculiar processes taking place at larval/pupal molt.

Observation of occasional specimens belonging to some other coccid species indicates that the features found in *O. urticae* are common for Gallinsecta.

MATERIAL AND METHODS

Orthezia urticae was collected by me near village Staroe (Russia, Tver' Prov., Ves'egonsk Distr.) 21–31 Aug. 2010, in bushes at the boundary between forest and flood-lands of river Zvana. Numerous larvae and female adults formed colonies on nettle and other plants. Number of males was many times less. Quiescent male nymphs and their exuviae were collected in crumpled dry dead leaves of nettle (*Urtica dioica*). Exuviae found in the same wax nest with male nymph or male imago evidently belong to the same individual; each such set of insect(s) and exuviae was placed into a separate tube. There were collected: 89 larvae of the 1st instar (among them 18 larvae at various phases of pre-molting process); 2 larvae molted from 1st to 2nd instar; 328 larvae of 2nd instar (among them 110 larvae at various phases of pre-molting process); 20 female larvae molted from 2nd to 3rd instar; 122 female larvae of 3rd instar (among them 8 larvae at various phases of pre-molting process); 7 female larvae molted from 3rd instar to imago; many female imagoes; 2 male nymphs of 3rd instar with their exuviae of 2nd instar (among them 1 nymph at pre-molting process); 23 male nymphs of 4th instar, most with their exuviae of 2nd and 3rd instars (many of them at various phases of pre-molting process); 14 male imagoes, most with their exuviae of 2nd, 3rd and 4th instars; exuviae of male nymphs of more than 30 individuals; 6 male imagoes collected out of shelters.

Internal parts (cuticle of next instar, hypoderm and musculature) were examined on thick translucent permanent slides in Canadian balsam. To prepare such slide, insect was dissected by hands into 5 parts: (1) dorsal part of head with antennae; (2) prothorax and ventral part of head with fore legs and mouthparts; (3) mesothorax with middle legs; (4) metathorax with hind legs; (5) abdomen. Head of some individuals was also dissected longitudinally; some individuals were dissected longitudinally into two halves. Fine cuticular details were also examines on specimens treated by alkali on temporary slides in glycerin.

TERMINOLOGY

The term '**ontogenetic homology**' was introduced by me (Kluge, 2005) to indicate that an organ develops from the homologous organ of previous developmental stage or instar. The term '**protopteron**' (plural '**protoptera**') was introduced in the same paper (Kluge, 2005) for an outgrowth of nymphal notum, from which imaginal wing develops.

For preimaginal stages of Pterygota, the terms 'larva' and 'nymph' are used. Traditionally, the term 'larva' is used either for all preimaginal instars, or only for instars which have no protoptera, and the term 'nymph' is used either for all preimaginal instars or only for instars which have protoptera. As many insects have intermediate instars with very small protoptera, there is no agreement which instars should be named 'larva' and which 'nymph', if distinguish these stages. Only for Metabola there are generally accepted terms: the term 'larva' is always applied for all instars up to penultimate preimaginal one, the term 'pupa' is used for the last preimaginal instar, and the term 'nymph' is not used. As the terms 'larva' and 'nymph' are very old and traditionally are used polysemantically, it is impossible to restrict them now. Individual instars are usually numerated from the earliest to the oldest ones and are termed 'first instar larva', 'second instar larva' etc., or 'first instar nymph', 'second instar nymph', etc. These terms are correct, but in some cases inconvenient, being too long. Sometimes there are used abbreviations 'L$_1$', 'L$_2$', etc. instead of 'first instar larva', 'second instar larva' etc. or 'N$_1$', 'N$_2$', etc. instead of 'first instar nymph', 'second instar nymph' etc. Such abbreviations are convenient in a scheme supplied with a legend (see p. 254), but not in a text. Here I suggest to use Latin (but not latinised Greek) terms for instars as the following: '**primolarva**' or '**primonympha**' for larva or nymph of first instar; '**secundolarva**' or '**secundonympha**' for larva or nymph of second instar; '**tertiolarva**' or '**tertionympha**' for larva or nymph

of third instar, and so on. In some cases it is convenient to count instars beginning not from the earliest, but from the oldest one. In this case penultimate preimaginal instar can be termed '**penultimolarva**' or '**penultimonympha**', and the last preimaginal instar can be termed '**ultimolarva**' or '**ultimonympha**'. Numeration of all instars should be through and universal for all taxa: in the cases when larval and nymphal stages are distinguished, nymphal instars should have numbers following after numbers of larval instars; for example, in male coccids tertionympha follows after secundolarva. In application for Metabola, the term 'penultimolarva' should be used for the last larval instar, after which pupa follows, while the term 'ultimonympha' should be not used, because it is substituted by the generally accepted term 'pupa'. In aleyrodids, which have no protoptera at any instar, the last immovable instar (which is often wrongly called 'pupa') can be termed either 'ultimolarva', or 'quatrolarva'. In male coccids preimaginal instars can be termed: (1) primolarva (= primonympha); (2) secundolarva (= secundonympha); (3) penultimonympha (= penultimolarva = tertionympha = tertiolarva); (4) ultimonympha (= ultimolarva = quatronympha = quatrolarva). In female coccids preimaginal instars can be termed: (1) primolarva (= primonympha); (2) secundolarva (= secundonympha); (3) tertiolarva (= tertionympha = ultimolarva = ultimonympha).

RESULTS

Ontogenesis of *Orthezia urticae*

Life history and external morphology of all stages are well described by E.K. Sikes (1928). Male has 2 feeding instars (primolarva and secundolarva), 2 inactive instars (penultimonympha and ultimonympha) and winged imago. Female has 4 feeding instars: primolarva, secundolarva, tertiolarva and wingless imago. Primolarva and secundolarva have the same external structure in male and female.

Primolarva and secundolarva (Figs 1–2). Body is oval; abdominal segments VII–X are fused to a single anal segment, which bears two pairs of spiracles and anal opening. Cuticle apart of antennae, eyes, mouthparts, legs, pleural ridges and spiracles, has even consistence and covered by numerous stout glandular setae; this cuticle is non-sclerotised, but rather thick, so that after molt keeps shape of the larva. Eyes are single-lens; each eye represents a prominent protuberance, whose cuticle is well-sclerotised, but colourless. Antennae are heavily sclerotised, brown. Antenna consists of 6 segments: scapus, pedicellus and 4-segmented flagellum (see below). In primolarva segments 1–5 have subequal length (Fig. 16); in secundolarva 3rd segment (i.e., 1st segment of flagellum) is twice longer than neighboring ones (Fig. 17). Mouth apparatus is well developed, consists of sclerotised non-segmented external proboscis (labium), internal proboscis (formed by mandibles and maxillary laciniae) and apodemes. Legs are heavily sclerotised, brown. Leg consists of coxa, trochanter+femur, tibia, non-segmented tarsus and claw; trochanter and femur are synsclerotised, without suture between them.

Primolarva and secundolarva are very similar, can be distinguished by proportion of antennal segments.

Female tertiolarva. Similar to primolarva and secundolarva, but antenna has one segment more: it is 7-segmented, i.e. has 5-segmented flagellum (Fig. 18).

Female imago. Similar to primolarva, secundolarva, and tertiolarva, but antenna has one segment more than in tertiolarva: it is 8-segmented, i.e. has 6-segmented flagellum (Fig. 19).

Male penultimonympha (Fig. 3). Body shape is intermediate between larval and adult; mesonotum is somewhat enlarged, with fore protoptera; metanotum bears very small flaps, corresponding to hind protoptera; abdominal segments VII, VIII and IX+X are separated by sinusoid grooves; genitals are indicated as two small protuber-

ances. Cuticle apart of antennae, eyes, legs, pleural ridges and spiracles, is very thin and soft, without glandular setae, so that after molt it crumples and does not keep shape of the larva. Besides single-lese eyes (which are the same as in primolarva and secundolarva), there is a pair of compound eyes, whose cuticle is as soft, as that of other body. Antennae are sclerotised, brownish. Antenna consists of 8 segments: shortened scapus, well-articulated pedicellus and 6-segmented flagellum. Antennae are always directed anteriorly-laterally. Mouth apparatus is absent: on the place of external proboscis there is a non-sclerotised colourless protuberance; internal proboscis and apodemes are completely absent. Legs are sclerotised, brownish; their structure is similar to that of primolarva and secundolarva.

Male ultimonympha (Figs 4, 30, 31). Body shape approximates to that of adult; mesonotum is divided into scutum and scutellum; fore protoptera are large; hind protoptera are well-expressed; abdominal segments VII, VIII and IX+X get shape similar to that of adult, penis and penial sheath are expressed as immovable projections. Cuticle as in penultimonympha. Eyes as in penultimonympha. Antennae are sclerotised, brownish. Antenna is markedly longer than in penultimonympha and consists of 9 segments: scapus, pedicellus and 7-segmented flagellum. Antennae are always bent down and directed backward. Mouth apparatus is completely absent. Legs are sclerotised, brownish; they are similar to that of primolarva, secundolarva and penultimonympha, but longer; suture separating trochanter from femur is traced.

Male imago (Figs 5, 29). In detail structure of male imago is described by J. Koteja (1986). Antenna has the same number of segments as in ultimonympha, but all segment of flagellum are much longer. Legs are very long; trochanter is separated from femur by suture.

Modes of life of different instars. Feeding stages — primolarva, secundolarva, female tertiolarva and female adult,
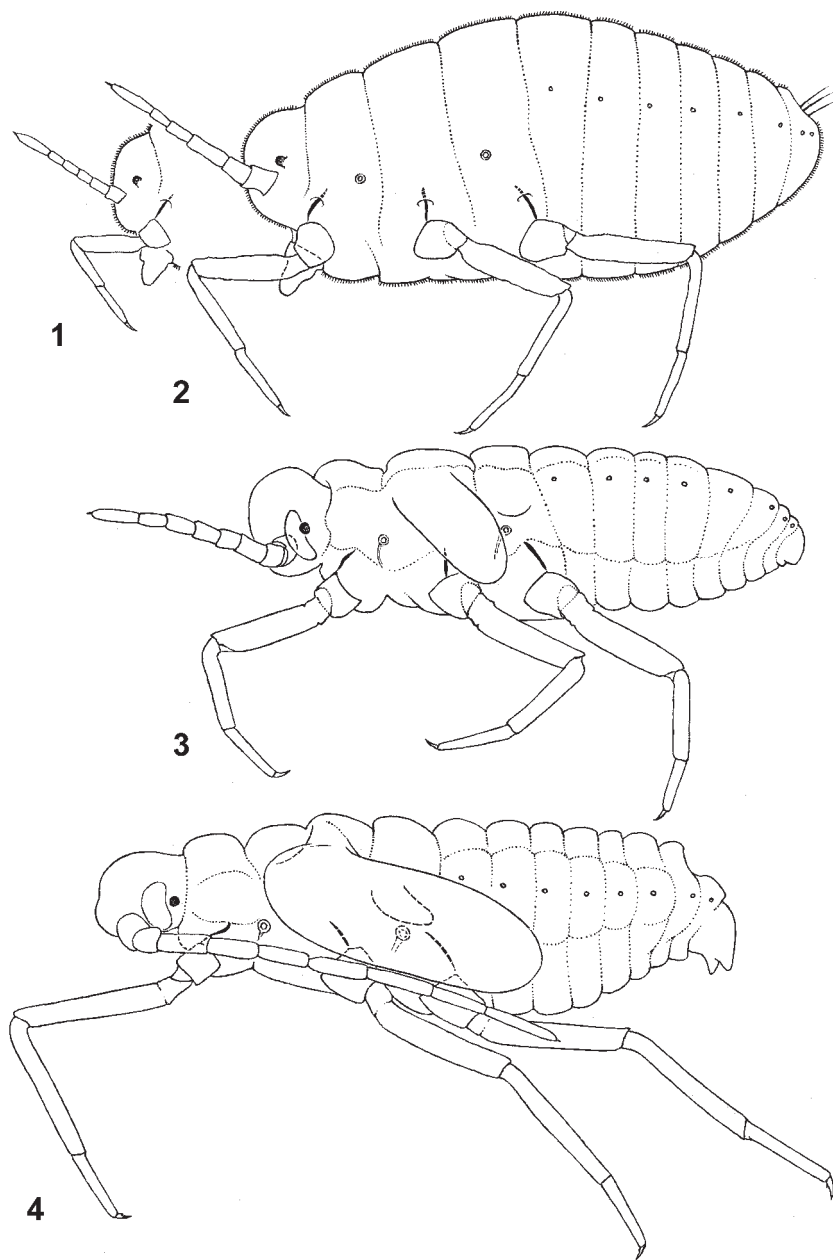
Figs 1–4. *Orthezia urticae*, male larvae, lateral view. **1**, head and fore leg of primolarva; **2**, secundolarva; **3**, penultimonympha (= tertiolarva); **4**, ultimonympha (= quatrolarva).

live openly on green parts of plants, being protected by transportable wax plates only; unlike some other coccids, they don't build immovable shelters. So, feeding larva holds on the plant only by means of its legs and internal proboscis. Some larvae and adult females were collected from dead dry parts of plants and on ground, where they could not feed. Some individuals molt in crumpled dead dry leaves, using them as natu-
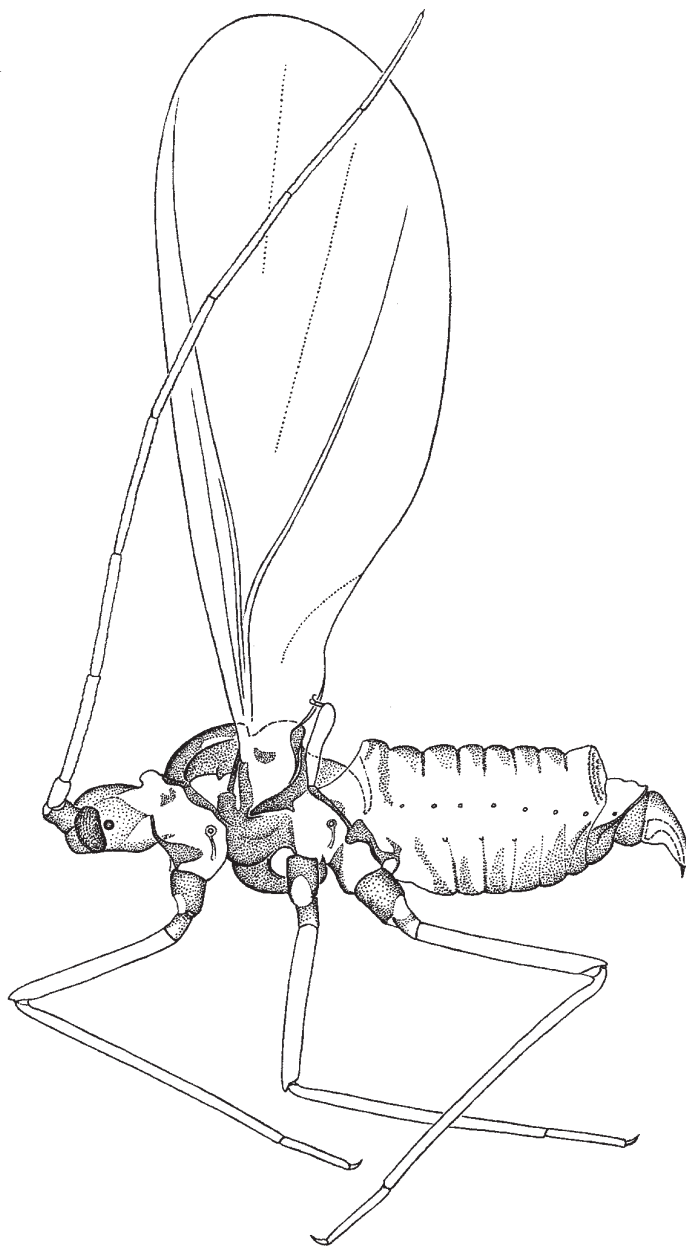
Fig. 5. *Orthezia urticae*, male imago, lateral view.

ral shelters; but other individuals were observed molting openly on the plant where they feed (Fig. 28). It seems that such mode of life should determine direct method of molt, in course of which insect should keep ability to use legs during the most part of molting cycle; but as shown below, this is not so.

Non-feeding male penultimonymphae and ultimonymphae were found in natural shelters formed by rolled and crumpled dry dead nettle leaves. Judging by exuviae

found in such shelters, secundolarva which have finished feeding, crawls into the shelter and molts there to penultimonympha; penultimonympha remains to stay near secundolarval exuviae and produces very fine wax down, which fills all space between the insect and walls of the shelter, protecting the insect against water and enemies; at the same place penultimonympha molts to ultimonympha, which remains to stay at the same place and continues to produce wax down; at the same place ultimonympha molts to imago, which remains to stay there during some period. In this case in the same wax mass or close to it, three exuviae of one individual are located (secundolarval, penultimonymphal and ultimonymphal). Sometimes two or more male individuals develop in the same wax mass; they can do it either synchronously, or asynchronously. Normally penultimonymphae and ultimonymphae do not move. But being disturbed, they can walk, using their legs (Figs 30, 31). Ultimonympha always keeps its antennae directed backward and does not move by them. However, as shown below, there is no any anatomical reason for immobility of antennae and/or legs both of penultimonympha and ultimonympha at any phase of their development.

Modes of transformation from one instar to another. In course of ontogenesis, *Orthezia urticae* demonstrates two quite diverse modes of molt and transformation from one instar to another: (1) with partial degeneration of legs and antennae and inverting of their first segments; (2) without degeneration processes and without inverting of any segments. The first mode of molt, which leads to immobility for a long time, takes place at molts of movable, openly living and actively feeding instars: from primolarva to secundolarva, from secundolarva to the next instar (i.e., tertiolarva in female and penultimonympha in male) and from tertiolarva to adult female. The second mode of molt, which exists in most insects and allows to keep mobility, in *Orthezia urticae* takes place only at molts of the im-

mobile, hidden, non-feeding instars of male: from penultimonympha to ultimonympha and from ultimonympha to male adult.

Both modes of molt in *Orthezia urticae* are presented below in a scheme where the following abbreviations are used: L_1 — primolarva; L_2 — secundolarva; L_3 — tertiolarva; N_3 — penultimonympha; N_4 — ultimonympha; Im — imago; double-line arrow indicates normal molt without degeneration and inverting; single-line arrow indicates molt with partial degeneration of legs and antennae and inverting of their first segments.

$$\text{♂} \quad L_1 \rightarrow L_2 \rightarrow N_3 \Rightarrow N_4 \Rightarrow \text{Im}$$
$$\text{♀} \quad L_1 \rightarrow L_2 \rightarrow L_3 \rightarrow \text{Im}$$

In the first case (when the degeneration and the inverting take place) the molting process is the following. After apolysis, tissues of legs and antennae undergo degeneration, so that muscles inside legs and antennae disappear completely (Fig. 6); in the distal part of leg all tissues are dissolved (Fig. 15); later all tissues are dissolved in the distal part of antenna (Fig. 7). In course of this degeneration, remainders of leg and antennal tissues, represented by hypoderm and non-differentiated mesoderm, lose segmentation. After the process of shortening, tissues of legs and antennae start to grow and get a new segmentation. All new segments of the appendage originate from the proximal part of appendage of the previous instar, so each new segment originates not from the old one; thus, segments of legs and antennae of different instars, being phylogenetically homologous, are not ontogenetically homologous (Figs 16–19). In course of their growing, tissues of legs and antennae do not penetrate back into the empty distal parts of cuticular legs and antennae; the first segment of appendage (i.e., coxa of leg and scapus of antenna) grows in inverted condition, being inserted into the body together with base of the next segment (Figs 7, 15). When growing tissues become longer than the space where they locate, they crumple, forming numerous folds (Fig. 8) (in the
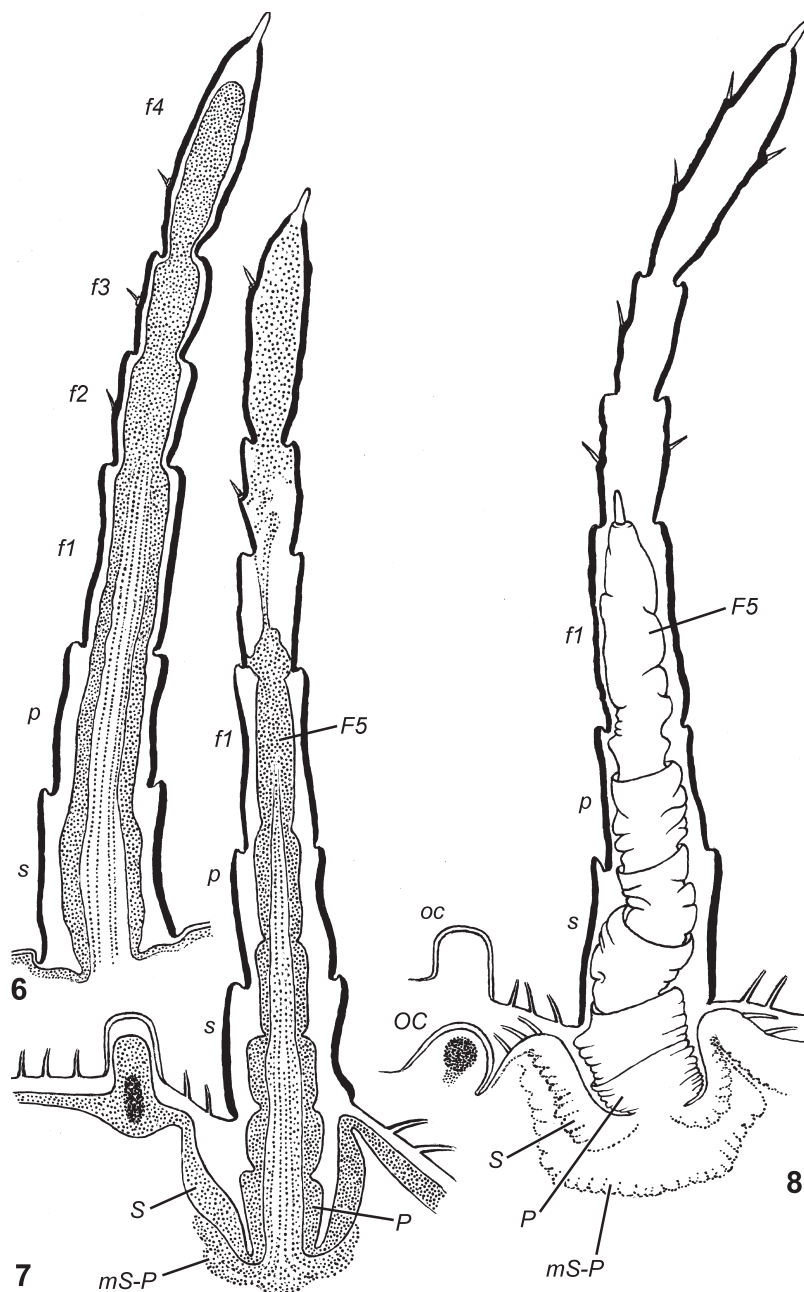
Figs 6–8. *Orthezia urticae*, longitudinal optic sections through antennae of female secundolarva before molt to tertiolarva, demonstrating subsequent phases of transformation. Optic sections of old secundolarval cuticle shown by black. In Figs 6 and 7 optic sections of hypoderm dotted and outlined, mesoderm shown by dotted lines and not outlined. In Fig. 8 crumpled tertiolarval pedicellus and flagellum, covered with new cuticle, shown as if viewed from outside, but inverted tertiolarval scapus shown in longitudinal section. *f1, f2, f3, f4* – 1st–4th flagellomeres of old secundolarval antenna, *F5* – 5th flagellomere of new tertiolarval antenna, *mS-P* – everted scapo-pedicellar muscles of new tertiolarval antenna, *oc* – secundolarval cuticle of oculus, *OC* – oculus, *p* – old secundolarval pedicellus, *P* – new tertiolarval pedicellus, *s* – old secundolarval scapus, *S* – inverted new tertiolarval scapus.

same manner as it takes place at usual pre-molting growths of other insects). Muscles newly develop inside crumpled legs and antennae, so that before ecdysis each append-age has a complete set of muscles. Muscles of the first segment (i.e., all coxo-trochanteral muscles of the leg and all scapo-pedicellar muscles of the antenna) develop in inverted condition, being located around hypoderm of their segment (Figs 7, 15). This unusu-al inverted condition of the first segment, with integument inside and musculature outside, retains up to ecdysis, so that just before ecdysis new cuticle lines hypoderm of the first segment from inside. In course of ecdysis, the old cuticle breaks dorsally (as in most insects), and the insect moves out of its old cuticle, spreading its crumpled legs and antennae (Fig. 28); only at this time inverted coxae of legs and scapes of anten-nae evert and get normal form with muscles inside and integument outside.

In the second case (when molt takes place without degeneration and inverting) the molting process is similar to that of most arthropods. After apolysis, tissues of legs and antennae do not undergo degeneration, but start to grow and get size and shape characteristic for the next instar. Tissues of each segment grow and crumple, remaining in limits of the old cuticle of this segment. Thanks to this, all articulations of the grow-ing tissues locate inside articulations of the old cuticle, and muscles (which remain to be functional) locate inside their segments (Fig. 21). Growing appendages are only crumpled, but never inverted. In course of this molt, each segment originates directly from the corresponding segment of the pre-vious instar; thus, segments of legs and an-tennae of different instars, are homologous both phylogenetically and ontogenetically. Such mode of molt can allow insect to move its legs and antennae during the whole pre-ecdysial period.

This is a paradoxical situation, because the feeding stages of *Orthezia urticae* (un-like some other coccids) actively walk using their legs and hold on plants mainly by help of legs; but thanks to their unusual mode of molt, they lose ability to move legs for a long time. The processes of drastic degen-eration and subsequent regeneration of legs and antennae is not connected with any marked morphological changes, because the feeding instars, which molt by such method, are very similar one to another. Female ima-go, being very similar to larva, in course of its ontogenesis three times undergoes this process of degeneration, regeneration and inverting. In contrast to the feeding instars, the quiescent instars of male do not need to move by legs and antennae; in course of their molts they get marked morphological changes; but in contrast to the feeding in-stars, they molt by the usual method, which allows to keep mobility.

Marked changes of body structure take place in course three molts of male (Figs 2–5): (1) from secundolarva to penulti-monympha (mouthparts disappear, pro-toptera appear, body cuticle changes con-sistence); (2) from penultimonympha to ultimonympha (antennae change shape, protoptera enlarge, mesonotum and last ab-dominal segments get imaginal shape); (3) from ultimonympha to imago (antennae and legs change shape, protoptera trans-form to wings, penis becomes movable, all cuticle changes consistence). One of these three molts (the molt from secundolarva to penultimonympha) is accompanied by the degeneration and inverting, while two other molts (from penultimonympha to ultimonympha and from ultimonympha to imago) pass without degeneration and inverting. All other molts (i.e., molt from primolarva to secundolarva and all molts of female) are not connected with morpho-logical changes, but cause only proportional enlargement of all parts of the body.

Structure and transformation of antennae in *Orthezia urticae*

General characters of antennae. In all instars of both sexes antennae of *Orth-ezia urticae* have structure characteristic

for Amyocerata: scapus (the first segment) includes muscles which go from its base to the base of pedicellus (the second segment); pedicellus and flagellum (all other segments) lack muscles. In all instars of both sexes there are muscles, which go from the base of scapus in ventral direction and attach to ventral side of head anteriad of anterior tentorial pits; in larvae and female adult they are attached near anterior tentorial pits, on anterior margin of the sclerotised clypeolabral shield [which in Ortheziidae has a form of apodeme inserted into the head (Koteja & Liniowska, 1976)]; in male imago they are attached far anteriad of anterior tentorial pits, on a sclerotised ventral head wall, which is homologous to clypeus. In all instars of both sexes flagellum has determined number of segments. The last segment bears a sclerotised but non-pigmented terminal spine (characteristic for Ortheziidae); structure of this spine is the same in all instars of both sexes.

Antennae of feeding instars. Antennae of primolarva, secundolarva of both sexes, tertiolarva and imago of female have similar structure. Besides the characters common for all instars, they have the following ones (Figs 1,2, 6–8, 9–14, 16–19): antennae are not long; cuticle is thick, heavily sclerotised, brown; a few spine-like setae are located irregularly, some of them having more or less constant position. Scapus usually has two such setae: one locates on distal part of medial side, another on proximal part of dorsolateral side (Fig. 9); in selected individuals one or both of them can be absent (Figs 10–13). Sikes (1928) gave concrete numbers of setae for each segment in each instar; these numbers can be true for selected individual only, being variable (compare Figs 9–13).

Transformation of antennae of feeding instars. In course of molt from each feeding instar (primolarva, secundolarva and female tertiolarva) to the next instar, antenna undergoes resorption of its distal part, degeneration of musculature, dedifferentiation of all segments and inverting of scapus. Just after apolysis, muscles inside scapus (scapo-pedicellar muscles) and muscles attaching to scapus base (clypeo-antennal muscles) disappear (Fig. 6). Tissues of the distal part of antenna are dissolved, so that apex of new antenna appears located in the middle or in the proximal part of the old cuticular antenna (Fig. 7). In course of this degeneration, remainders of antennal tissues lose segmentation. After the process of resorption and dedifferentiation, tissues of antenna start to grow and get a new segmentation (Fig. 7). In course of growing, tissues of new antenna do not penetrate back into the empty distal part of cuticular flagellum. Scapus of new antenna grows in an unusual inverted condition, so that forms a pouch inserted into the body, and the rest of antenna (pedicellus and flagellum) arises from the bottom of this pouch (Fig. 7). New muscles which should be located inside scapus (i.e., scapo-pedicellar muscles) develop in inverted condition, being located around hypoderm of the inverted scapus. When growing new antenna becomes longer than the space where it locates, it crumples, forming numerous folds (Fig. 8). This inverted condition of the scapus, with integument inside and musculature outside, is retained up to ecdysis, so that just before ecdysis new cuticle lines hypoderm of scapus from inside. In course of ecdysis, when the insect moves out of its old cuticle, crumpled new antennae are spread; only at this time inverted scapus everts and gets its normal form with muscles inside and integument outside.

All segments of the new antenna originate from the proximal part of antenna of the previous instar, so each segment of the new antenna originates not from the homologous segment of the old antenna (Figs 16–19). This means that all antennal sensilla, including spine-like setae, must newly appear at each molt. As a result of this, sensilla on the same antenna at subsequent instars vary in number and position; this variability is comparable with variability between left and right antennae of the same individual (Figs 9–14) or between antennae of different individuals.
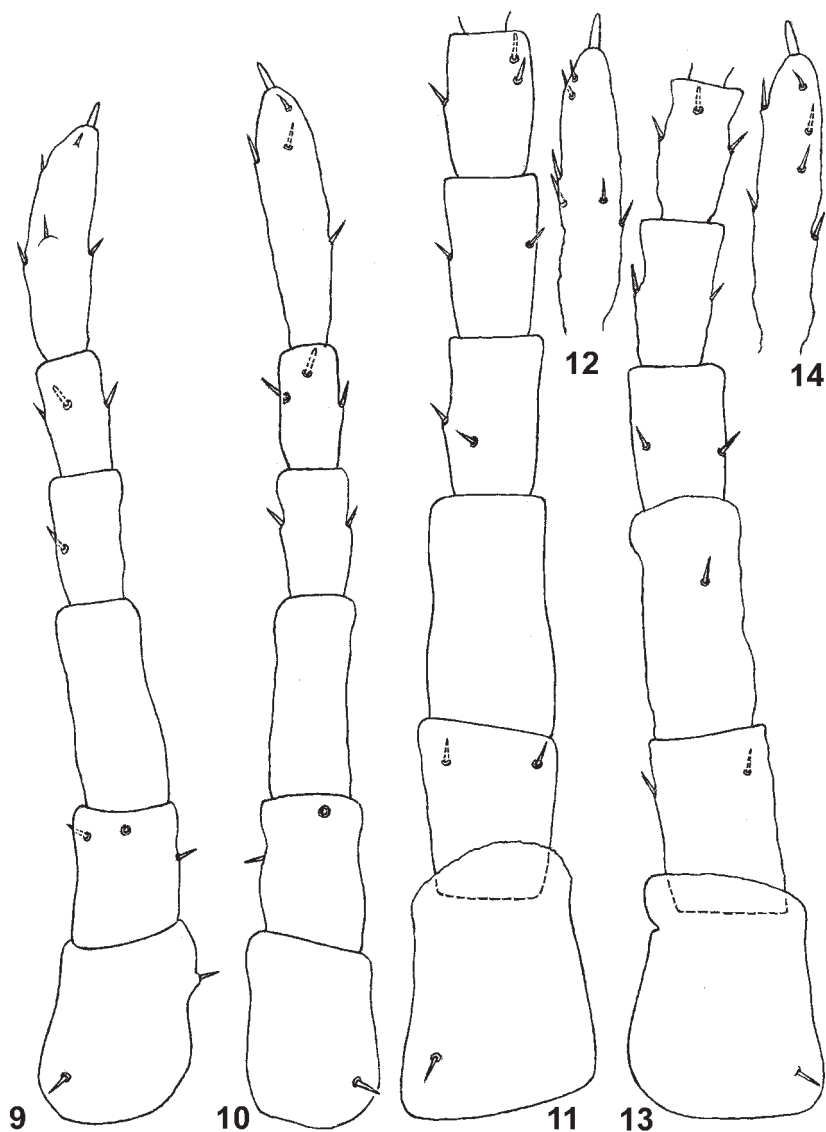
Figs 9–14. *Orthezia urticae*, secundolarval (9, 10) and tertiolarval (11–14) antennae of the same female individual, dorsal view.

Transformation of antennae from primolarva to secundolarva. Antenna of primolarva is always 6-segmented, i.e., has 4 flagellomeres; the proximal three flagellomeres have subequal length (Figs 1, 16). In course of molt from primolarva to secundolarva, after apolysis, muscles disappear and tissues of antenna are dissolved in the distal part, so that the tip of secundolarval antenna locates either in pedicellus, or in the first flagellar segment of the primolarval cuticle. Among 34 antennae examined (belonging to 17 primolarvae before molt) in 21 cases the tip of secundolarval antenna locates in pedicellus (the 2nd antennal segment); in 12 cases it locates in the 1st flagellomere (the 3rd antennal segment); in one case it locates in the distal part of 2nd

flagellomere (the 4th antennal segment). All segments of the secundolarval antenna (scapus, pedicellus and four flagellomeres) newly differentiate from the non-segmented tissues of proximal part of the primolarval antenna; scapus of the secundolarval antenna develops in inverted condition and everts during ecdysis.

Transformation of antennae from secundolarva to female tertiolarva or male penultimonympha. Antenna of secundolarva is always 6-segmented, i.e., has 4 flagellomeres; its proximal flagellomere is always much longer than the next two ones (Figs 3, 6–8, 9–10, 17). In course of molt from secundolarva to the next instar (independently, if it will be tertiolarva of female or penultimonympha of male), after apolysis, muscles disappear and tissues of antenna are dissolved in the distal part, so that the tip of the new antenna locates in the proximal part of flagellum of the secundolarval cuticle (Figs 7–8). Among 88 antennae examined (belonging to 44 secundolarvae before molt) in 82 cases the tip of new antenna locates in the 1st flagellomere (the 3rd antennal segment); in 6 cases it locates in the proximal part of 2nd flagellomere (the 4th antennal segment). All segments of the tertiolarval or penultimonymphal antenna (scapus, pedicellus and 5 flagellomeres of female or 6 flagellomeres in male) newly differentiate from the non-segmented tissues of proximal part of the secundolarval antenna; scapus of the tertiolarval or penultimonymphal antenna develops in inverted condition (Figs 7–8) and everts during ecdysis.

Transformation of antennae from female tertiolarva to imago. Antenna of female tertiolarva is always 7-segmented, i.e., has 5 flagellomeres; its proximal flagellomere is either subequal or longer than the next three ones (Figs 11, 13, 18). In course of molt from tertiolarva to female imago, after apolysis, muscles disappear and tissues of antenna are dissolved in the distal part, so that the tip of the new antenna locates in the proximal part of flagellum of the tertiolarval cuticle. Among 12 antennae examined

(belonging to 6 tertiolarvae before molt) in 10 cases the tip of new antenna locates in the 1st flagellomere (the 3rd antennal segment); in 2 antennae of one individual it locates in the middle part of 2nd flagellomere (4th antennal segment). All segments of the imaginal antenna (scapus, pedicellus and 6 flagellomeres) newly differentiate from the non-segmented tissues of proximal part of the tertiolarval antenna; scapus of the imaginal antenna develops in inverted condition and everts during ecdysis. Antenna of female imago is normally 8-segmented, i.e., has 6 flagellomeres (Fig. 19); rarely it is 7-segmented, i.e., has 5 flagellomeres, as in tertiolarva.

Transformation of antennae from male penultimonympha to ultimonympha. Antenna of male penultimonympha is always 8-segmented, i.e., has 6 flagellomeres. Its scapus and pedicellus are shorter than in the feeding instars, and lateral articulatory condylus between them is especially prominent; the 1st flagellomere is longer than the next ones (Figs 3, 20). Antennae are normally directed anteriorly-laterally (Fig. 3). Like in all other instars, scapus includes muscles going from the base of scapus to the base of pedicellus (one of them is shown in Fig. 20), and there are muscles going from the base of scapus to the vestige of clypeolabral shield on ventral side of head (one of them is shown in Fig. 20), so antennae are able to make various movements. As the whole penultimonymphal instar passes in a shelter, its antennae do not need to move. In course of molt from penultimonympha to ultimonympha all muscles are retained and do not pass through degeneration. Each segment of ultimonymphal antenna (scapus, pedicellus and 7 flagellomeres) develops from the corresponding segment of penultimonymphal antenna; exception is made by the 1st and the 2nd ultimonymphal flagellomeres, which probably originate from the single elongate 1st penultimonymphal flagellomere. In course of elongation, antennal segments of ultimonympha shift their bases proximally. In the single
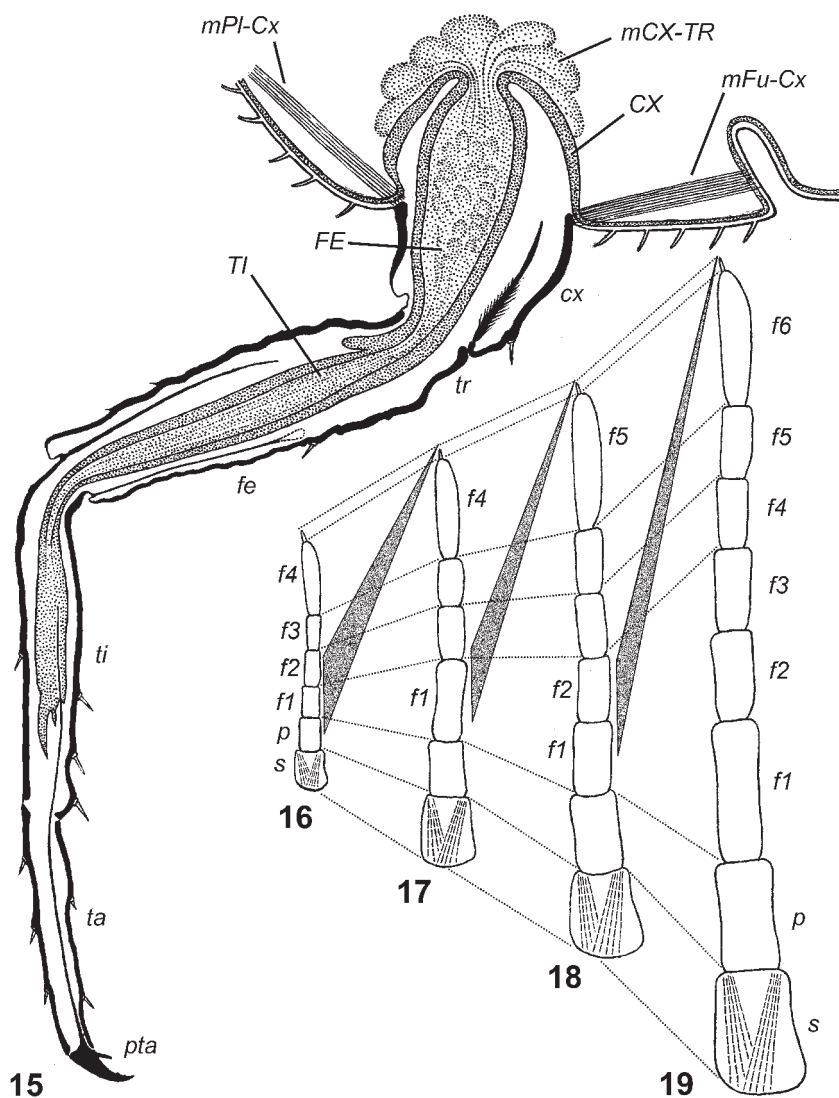
Figs 15–19. *Orthezia urticae.* **15**, optic section through middle leg of female secundolarva before molt to tertiolarva; old secundolarval cuticle shown by black, hypoderm dotted and outlined, mesoderm dotted and not outlined, functional muscles shown by longitudinal striation. **16–19**, antennae of female primolarva, secundolarva, tertiolarva and imago; dotted lines show phylogenetic homology of antennal segments; dark triangles show range of their ontogenetic homology. *cx* – old secundolarval coxa, *CX* – inverted new tertiolarval coxa, *f1, f2, f3, f4, f5, f6* – 1st–6th flagellomeres, *fe* – old secundolarval femur, *FE* – new tertiolarval femur, *mCX-TR* – everted coxo-trochanteral muscles of new tertiolarval leg, *mFu-Cx* – functional furco-coxal muscle, *mPl-Cx* – functional pleuro-coxal muscle, *p* – pedicellus, *pta* – old secundolarval pretarsus, *s* – scapus, *ta* – old secundolarval tarsus, *ti* – old secundolarval tibia, *TI* – new tertiolarval tibia, *tr* – old secundolarval trochanter fused with femur.

specimen examined, in both antennae base of each of five distalmost ultimonymphal flagellomeres is shifted to the middle of the previous cuticular flagellomere of penultimonympha; two proximal ultimonymphal flagellomeres (which probably originate from the first penultimonymphal flagellomere) occupy proximal half of the first cuticular flagellomere and the whole cuticular pedicellus of penultimonympha; crumpled ultimonymphal pedicellus and scapus locate in the cuticular scapus of penultimonympha (Fig. 20). Apical spine of ultimonymphal antenna is pushed out from the cuticular apical spine of penultimonymphal antenna, so that locates just proximad of it (Fig. 20).

Transformation of antennae from male ultimonympha to imago. Antenna of male ultimonympha is always 9-segmented, i.e., has 7 flagellomeres. Its scapus is bent ventrally, so that antenna is always bent down and directed backward (Fig. 4). Like in all other instars, scapus includes muscles going from the base of scapus to the base of pedicellus, and there are muscles going from base of scapus to the vestige of clypeolabral shield on ventral side of head. In course of molt from ultimonympha to imago all muscles are retained and do not pass through degeneration. Each segment of imaginal antenna (scapus, pedicellus and 7 flagellomeres) develops from the corresponding segment of ultimonymphal antenna. In course of elongation, each segment of imaginal antenna crumples, remaining inside its cuticular segment of ultimonymphal antenna. Apical spine of imaginal antenna is usually pushed out from the cuticular apical spine of ultimonymphal antenna and locates just proximad of it (as in Fig. 20); rarely imaginal apical spine remains to be partly inserted into the cuticular ultimonymphal apical spine.

Boundaries between head and scapus and between scapus and pedicellus coincide in the new imaginal antenna and the old ultimonymphal cuticular antenna; this position could allow antenna to use its clypeoantennal and scapo-pedicellar muscles and to make all kinds of movement. But it seems

that ultimonympha never changes pose of its antennae: all 23 ultimonymphae, which were collected, invariably keep antennae bent backward. When ultimonympha is disturbed, it walks, moving by legs, but does not change pose of antennae (Figs 30, 31). Antenna of imago, having the same number of segments as in ultimonympha, markedly differs from antenna of ultimonympha and other instars: its flagellomeres are much longer and covered by numerous setae (which are not shown in Fig. 5).

Structure and transformation of legs in *Orthezia urticae*

General characters of legs. In all instars of both sexes each leg of *Orthezia urticae* has structure characteristic for Hexapoda (Fig. 21): it has coxa, trochanter, femur, tibia, tarsus and pretarsus. In male imago trochanter is clearly separated from femur by a suture; in all other instars trochanter is distinguishable, being narrower than femur, but not separated from it. In all instars of both sexes tarsus is one-segmented; it is separated from tibia, but slightly movable and forms one line with tibia. In all instars of both sexes pretarsus has the same species-specific structure: it usually has 2–4 very small, shallow denticles in distal part; digitules (two setae by sides near base) are spine-like, stout and pointed [however, Koteja (1986) reports one very small digitule]. As in all coccids, larval and female terga are non-sclerotised; probably, in connection with this, legs have no tergo-coxal and tergo-trochanteral muscles. This is true not only for larva and female, but also for male adult, whose terga are well-sclerotised. In other respects leg musculature is typical for Hexapoda. In all instars of both sexes leg has the following muscles: There are several extrinsic pleurocoxal and sterno-coxal muscles, which go to the coxal base from pleural suture, sternal apodeme and body wall. Coxa is filled with coxo-trochanteral muscles, which go from inner walls of coxa to two apodemes of trochanter (lateral and median ones).
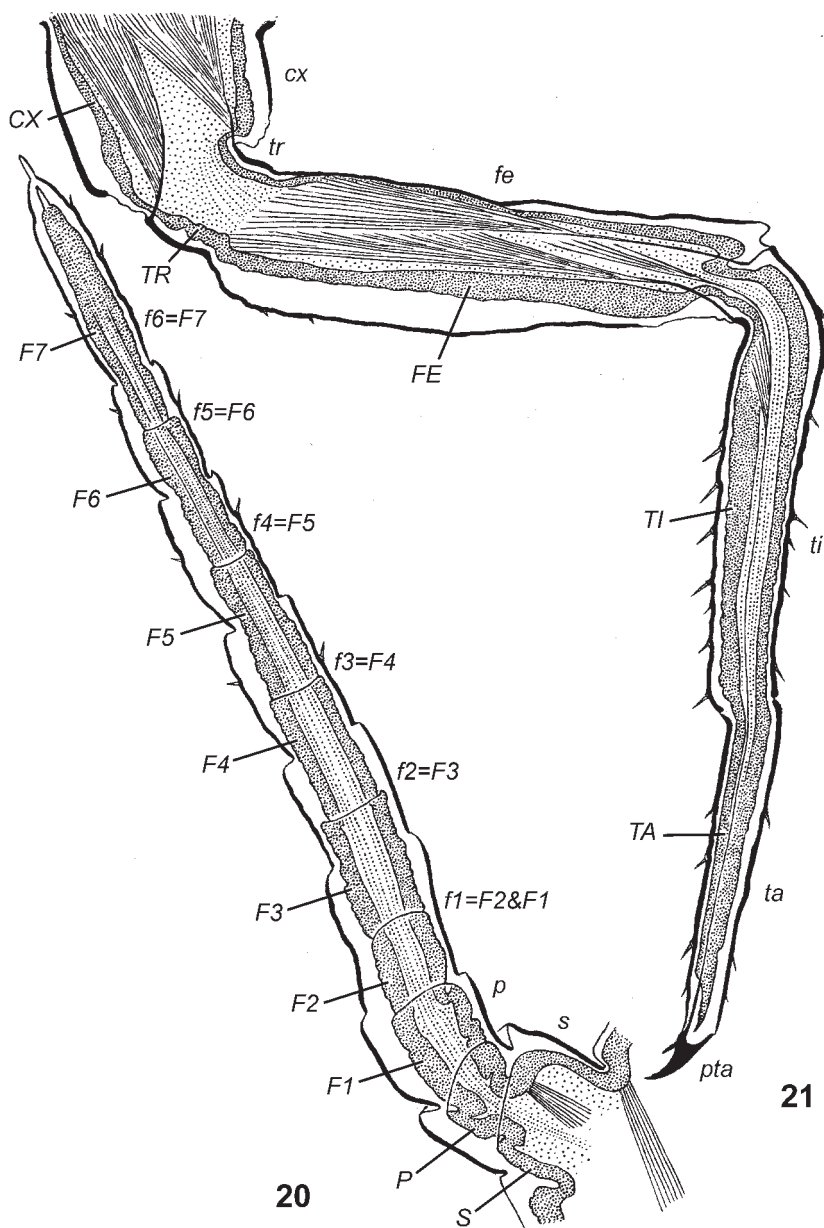
Figs 20–21. *Orthezia urticae*, optic section through antenna (20) and middle leg (21) of male penulti-monympha before molt to ultimonympha; old penultimonymphal cuticle shown by black, hypoderm dotted and outlined, mesoderm dotted and not outlined, functional muscles shown by longitudinal striation. *cx* – old penultimonymphal coxa, *CX* – new ultimonymphal coxa, *f1=F2&F1, f2=F3, f3=F4, f4=F5, f5=F6, f6=F7* – 1st–6th old penultimonymphal flagellomeres and their correspondence with 1st–7th new ultimonymphal flagellomeres, *F1, F2, F3, F4, F5, F6, F7* – 1st–7th new ultimonymphal flagellomeres, *fe* – old penultimonymphal femur, *FE* – new ultimonymphal femur, *p* – old penulti-monymphal pedicellus, *P* – new ultimonymphal pedicellus, *pta* – old penultimonymphal pretarsus, *s* – old penultimonymphal scapus, *S* – new ultimonymphal scapus, *ta* – old penultimonymphal tar-sus, *TA* – new ultimonymphal tarsus, *ti* – old penultimonymphal tibia, *TI* – new ultimonymphal tibia, *tr* – old penultimonymphal trochanter, *TR* – new ultimonymphal trochanter.

Femur is filled with longitudinal and pectinate muscles — flexor and extensor of tibia, which go from base and sides of femur to two tibial apodemes (in Fig. 21 only longitudinal muscles are shown). In femur and in proximal part of tibia, weak flexors of pretarsus are located.

Transformation of legs of feeding instars. In course of molt from each feeding instar (primolarva, secundolarva and female tertiolarva) to the next instar, each leg undergoes resorption of its distal part, degeneration of all intrinsic musculature, new differentiation of all segments and inverting of coxa. Just after apolysis, all muscles inside leg disappear, but all extrinsic muscles (pleuro-coxal and sterno-coxal ones) are retained. Tissues of tarsus are dissolved, so that apex of new leg appears located in the distal part of the old cuticular tibia (Fig. 15). Among specimens examined (26 primolarvae, 110 secundolarvae and 8 tertiolarvae) position of apex of new claw varies from distal half of old cuticular tibia to extreme base of old cuticular tarsus. In course of this degeneration, remainders of leg tissues get new boundaries of segments, so that new femoro-tibial articulation appears located in the proximal part of the old cuticular femur (Fig. 15). In course of growing, tissues of new leg do not penetrate back into the empty cuticular tarsus. Coxa of new leg grows in an unusual inverted condition, so that forms a pouch inserted into the body, and femur arises from the bottom of this pouch (Fig. 15). New coxo-trochanteral muscles, which should be located inside coxa, develop in inverted condition, being located around hypoderm of the inverted coxa. When growing new leg becomes longer than the space where it locates, it crumples, forming numerous folds. This inverted condition of coxa, with integument inside and musculature outside, is retained up to ecdysis, so that just before ecdysis new cuticle lines hypoderm of coxa from inside. During all this pre-molting period, extrinsic muscles remain to be functional and retain their attachments on the coxal base; this is possible, because base of the new inverted coxa remains to coincide with base of the old cuticular coxa (Fig. 15). In course of ecdysis, when the insect moves out of its old cuticle, crumpled new legs are spread; only at this time inverted coxa everts and gets its normal form with muscles inside and integument outside.

All segments of the new leg originate from the proximal part of leg of the previous instar, so each segment of the new leg originates not from the homologous segment of the old leg. This means that all leg sensilla must newly appear at each molt.

Unlike intrinsic leg muscles, extrinsic leg muscles do not undergo degeneration during molts and pass through the whole postembryogenesis. This fact allows feeding larvae to inhabit permanently on opened surfaces of plants and hold on these surfaces by legs: when leg loses its intrinsic muscles, and becomes unable to make active movements by the coxo-trochanteral and femoro-tibial articulations, it retains ability to move actively as a whole by help of the extrinsic muscles attached to its coxal base.

Transformation of legs from male penultimonympha to ultimonympha and from ultimonympha to imago. In course of molt from penultimonympha to ultimonympha and from ultimonympha to imago legs do not undergo any degeneration. All leg muscles are retained. Each leg segment (coxa, trochanterofemur, tibia, tarsus and pretarsus) develops from the corresponding segment of the previous instar. In course of elongation, each leg segment of the next instar crumples, remaining inside its cuticular segment of the previous instar. New claw is pushed out from the cuticular claw of the previous instar and locates just proximad of it (Fig. 21).

Boundaries between all segments of the new leg and the old cuticular leg coincide (Fig. 21); this allows insect to use its leg muscles and to make all kinds of leg movement. Normally, stages of penultimonympha and ultimonympha pass in a shelter, where insect does not need to move. The insect (ei-

ther penultimonympha, or ultimonympha) immovably stays inside its shelter on legs, which are stretched laterally-ventrally. Some ultimonymphae, being disturbed, walk, using their legs (Figs 30, 31). Small number of material did not allow me to see walking penultimonymphae; but judging by leg structure, penultimonympha also should be able to walk.

Transformation of the antennae and the legs in other coccids

Besides *Orthezia urticae*, I examined transformation of legs and antennae in a few specimens of *Icerya* sp., *Pseudococcus viburni* (Signoret, 1875) and *Coccus hesperidum* Linnaeus, 1758. Antennal development of *Diaspidiotus ostreaeformis* (Curtis, 1843) is described in literature.

Monophlebidae: *Icerya* sp. Several female larvae were collected by me in Indonesia, Lombok Isl., Senaru, 19–26 Sept. 2009. Among them, two larvae are at pre-molting period. Both are molting from one feeding instar to another feeding instar, that is proven by spirally coiled mandibular and lacinial stylets of the next instar.

One of them is at earlier phase of molting cycle: in legs and antennae hypoderm is detached from cuticle and processes of degeneration start. All tissues of coxae remain inside old cuticular coxae; coxo-trochanteral muscles are partly or completely retained. Tissues of femora are partly degenerated, muscles are partly dissolved; in some legs boundary between femur and tibia is shifted toward middle of the old cuticular femur. Tissues of tarsus are completely dissolved, so that living part of leg terminates by a blunt end in the distal part of old cuticular tibia. Tissues of antennae are narrowed, but not shortened and terminate in the last segment of old cuticular antenna; intrinsic scapo-pedicelar muscles are degenerated, but extrinsic clypeo-scapal muscles are retained.

Another specimen of female larva is before molt: its legs and antennae have distal parts dissolved, newly differentiated seg-

ments crumpled in proximal part of the old cuticular appendage, and first segments are inverted. Each leg has new coxa in inverted condition; new crumpled femur with its new femoro-tibial muscles locates inside the inverted coxa, beginning from its bottom; new crumpled tibia occupies the old cuticular coxa and a proximal half of the old cuticular femur; new tarsus locates inside distal half of the old cuticular femur and proximal part of the old cuticular tibia, so that new claw terminates near middle of the old cuticular tibia (Fig. 22). Each antenna has new scapus in inverted condition; the rest part of new antenna begins from the bottom of the inverted scapus and terminates near middle of the old cuticular antenna.

Thus, mode of molt between feeding instars of *Icerya* sp. is the same as in *Orthezia urticae*.

Pseudococcidae: *Pseudococcus viburni* (Signoret, 1875 [*Dactylopius*]). Several female and male larvae were collected by me in October 2010 on *Nephrolepis exaltata* growing in the coccidological cabinet in Zoological Institute RAS (in Saint-Petersburg, Russia). Among them, 4 specimens are examined: (1) primolarva before molt to secundolarva; (2) female tertiolarva before molt to imago; (3) male penultimonympha before molt to ultimonympha; (4) ultimonympha before molt to imago. In all of them mode of molting processes in legs and antennae appears to be the same: all muscles are retained; tissues of each segment locate in limits of the corresponding old cuticular segment, so that muscles are able to function. In each leg new claw terminates in the end of the old cuticular tarsus, just proximad of the old cuticular claw. In each antenna apical segment terminates in the last segment of the old cuticular antennae, being separated from its end only by length of new apical setae.

This means, that feeding and non-feeding instars of *Pseudococcus viburni* molt without degeneration and inverting of legs and antennae. This sharply differs from *Orthezia urticae*, *Icerya* sp. and *Coccus hesperidum*,
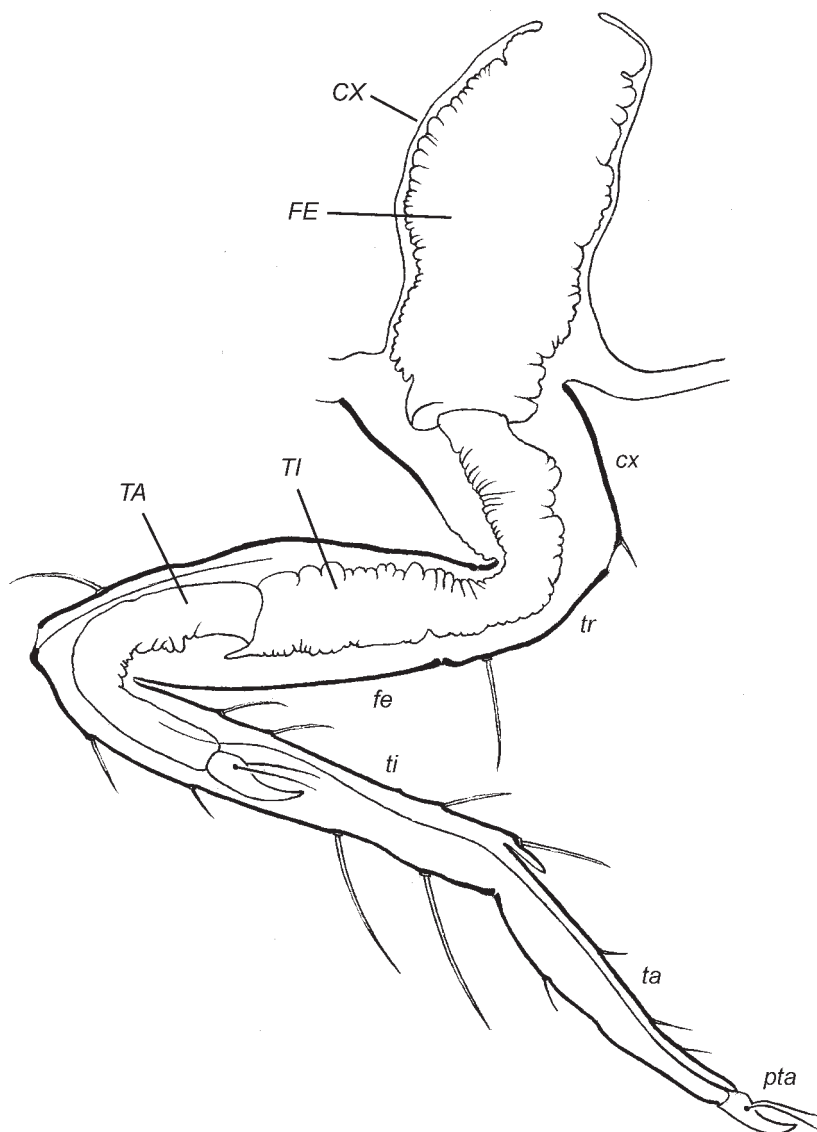
Fig. 22. *Icerya* sp., optic section through middle leg of female larva before molt to next instar; old cuticle shown by black; new femur, tibia tarsus and pretarsus, covered with new cuticle, shown as if viewed from outside, but inverted new cuticle of coxa shown in longitudinal section. *cx* – old coxa, *CX* – new inverted coxa, *fe* – old femur, *FE* – new femur, *pta* – old pretarsus, *ta* – old tarsus, *TA* – new tarsus, *ti* – old tibia, *TI* – new tibia, *tr* – old trochanter.

whose feeding instars molt with degeneration and inverting.

Coccidae: *Coccus hesperidum* Linnaeus, 1758. Series of females and larvae were collected by I.A. Gavrilov in October 2010 from the pot-growing *Zamiaculcas zamiifolia* in a private flat in St. Peters-burg, Russia. Secundolarvae and females of *Coccus hesperidum* do not use their legs, being immovably sticked to a plant. Nevertheless, they retain small legs which have well-developed intrinsic coxo-trochanteral, trochantero-femoral, femoro-tibial, femoro-unguitractoral and tibio-unguitractoral
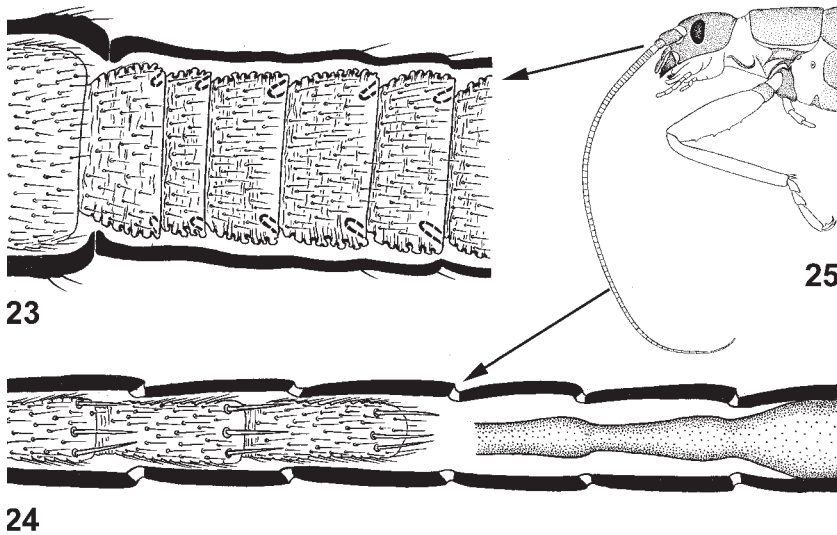
Figs 23–25. *Taeniopteryx nebulosa* (Linnaeus, 1758 [*Phryganea*]) (Plecoptera), ultimonympha before molt to imago. **23, 24**, optic sections through 1st flagellomere (23) and distal part of flagellum (24); old ultimonymphal cuticle shown by black; new imaginal cuticle with dense setae shown as if viewed from outside; remainders of dissolved tissues in distal part of antenna shown by dots. **25**, fore part of ultimonympha to show location of the optic sections.

muscles. I examined several female larvae before molt from one feeding instar to another (that can be revealed by new mandibular and maxillary stylets spirally coiled inside the body). Before molt, legs and antennae have distal parts dissolved, newly differentiated segments crumpled in proximal part of the old cuticular appendage, and first segments inverted. Each leg has new coxa in inverted condition; the rest part of leg begins from the bottom of the inverted coxa and terminates near the end of the old cuticular tibia. Each antenna has new scapus in inverted condition; the rest part of antenna begins from the bottom of the inverted scapus and terminates near middle of the old cuticular antenna.

Thus, mode of molt between feeding instars of *Coccus hesperidum* is the same as in *Orthezia urticae*.

Diaspididae: *Diaspidiotus ostreaeformis* (Curtis, 1843 [*Aspidiotus*]). Secundolarvae and females of Diaspididae have no legs, and their antennae are reduced to small non-segmented tubercles with a few sensilla. Transformations of antennae of *D. ostreaeformis* are described by Bielenin et al. (1995). According to this investigation, before molts from primolarva to secundolarva, antenal tissues degenerate to "a group of undifferentiated predetermined cells which will later produce the second generation of antennae"; before molt from secundolarva to male penultimonympha, the new penultomonymphal antenna developes with inverted proximal part (Bielenin et al., 1995: Figs 4, 5, 7). As penultomonymphal antenna lacks visible segmentation, it is unclear, if this inverted part correspond to scapus, or not. At molts from penultimonympha to ultimonumpha and from ultimonympha to imago, antenna developes without degeneration and inverting, so that the newly debveloping antenna occupies the whole length of the old cuticular antenna (Bielenin et al., 1995: Figs 8, 9, 10).

This allows to conclude, that molting processes which take place in course of on-
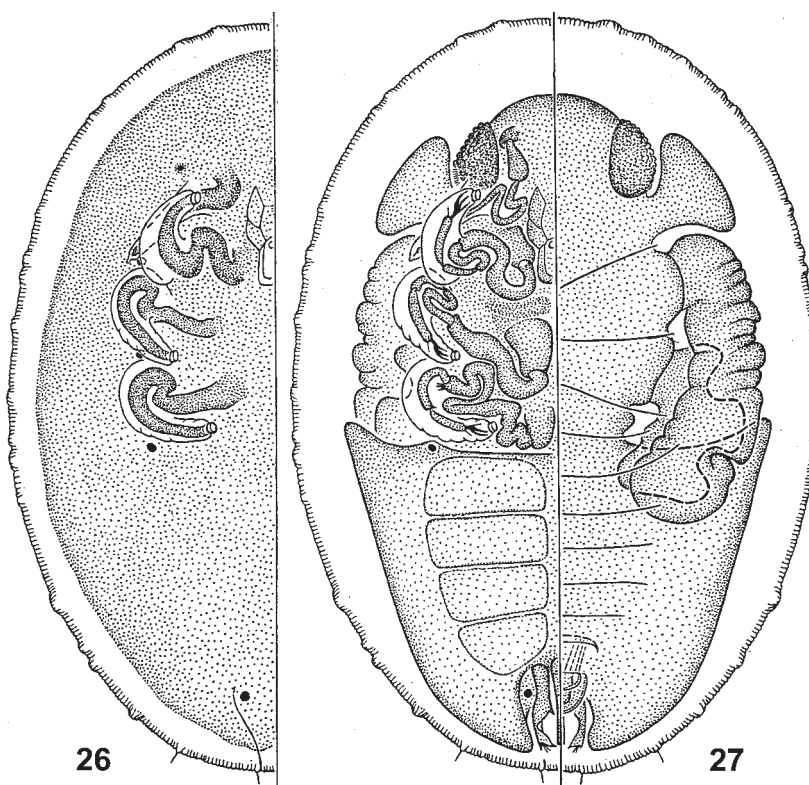
Figs 26–27. *Aleyrodes proletella* Linnaeus, 1758 [*Phalaena*], male ultimolarva before molt to imago. **26**, earlier phase, ventral view. **27**, later phase, ventral (left) and dorsal (right) view. Old ultimolarval cuticle shown by integral lines without dots; hypoderm and new imaginal cuticle shown by integral lines and dotted.

togenesis of *Diaspidiotus ostreaeformis* are basically the same as in *Orthezia urticae*.

**Transformation of the antennae
in other insects**

In insects other than coccids, antennal scapus never inverts before molt; if antenna has scapus, pedicellus and flagellum (that takes place in all Amyocerata except for larvae of Metabola), each of these parts develops from the homologous part of the previous instar.

Comparison of antennal molt in *Orthezia* and primitive Amyocerata. Degeneration of distal segments of antenna, besides *Orthezia urticae*, is found in some Amyocerata with primitive antennal structure. Most probably, the most primitive amyoceratan

antenna has so called 'setiform' flagellum with large and undetermined number of flagellomeres, whose width decreases from the base toward the top of flagellum. Before molt some distalmost flagellomeres do not form new cuticle; in course of ecdysis, remainders of tissues of these flagellomeres are shed together with the old cuticle (Fig. 24). At the same time, one or several most proximal flagellomeres after apolysis not only grow, but also multiply in number (Fig. 23). As a total result of these two controversial processes, flagellum becomes longer and number of its flagellomeres increases. In contrast to flagellum, scapus and pedicellus do not undergo any degeneration, and each of them at each molt only increases in size. This kind of antenna has inconstant apex: after each molt apical flagellomere is
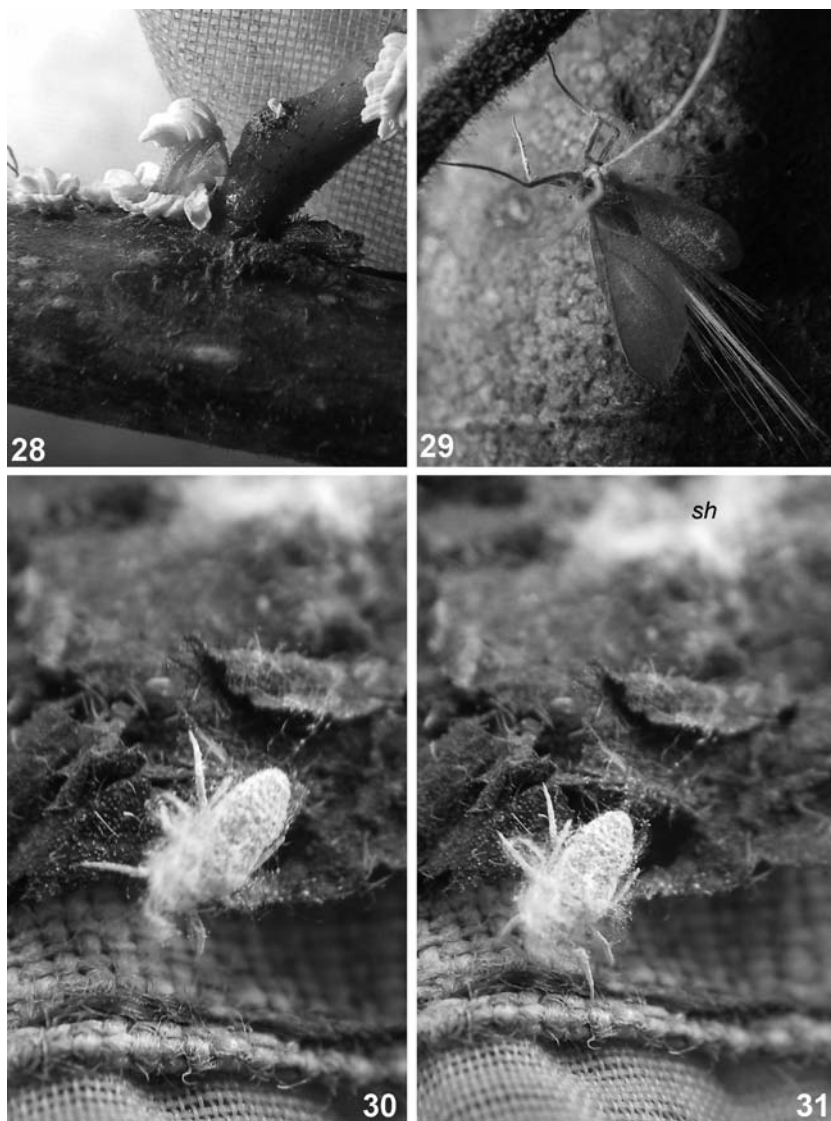
Figs 28–31. *Orthezia urticae*. **28**, female secundolarva molting to tertiolarva in natural conditions. 29, male imago. **30–31**, ultimonympha, being disturbed, walks out of its destroyed shelter. *sh* – remainders of wax down which filled the shelter.

changed to a flagellomere which in the previous instar was among middle ones. Molt of such antenna, being accompanied with degeneration of distal flagellomeres, does not include process of regeneration: apex of antenna does not regenerate, but is substituted by that flagellomere which did not undergo degeneration. As a result, antenna of such kind cannot have peculiar apical structures, and its flagellomeres cannot be differentiated.

Such antennae with undetermined number of flagellomeres and inconstant apex are found in Microcoryphia, Zygentoma, Ephemeroptera, Plecoptera (Figs 23–25), Raptoriae and some Saltatoria.

Unlike them, *Orthezia urticae* has well determined number of flagellomeres at each

instar; its apical flagellomere bears a peculiar apical spine, the same in all instars; not only distal flagellomeres degenerate, but all segments, including scapus and pedicellus, are dedifferentiated and than are newly differentiated, and the apical segment with its apical spine regenerates.

Comparison of antennal molt in *Orthezia urticae* and Metabola. Dedifferentiation and subsequent new differentiation of antennal segments takes place only at larval/pupal molt of Metabola; but in this case larval antenna has no scapus, and scapus appears only during larval/pupal molt and subsequent pupal development (Kluge, 2005). Unlike Metabola, *Orthezia urticae* in all its instars has comparable antennal segmentation with true muscle-bearing scapus, but undergoes dedifferentiation and new differentiation of all antennal segments at each molt of feeding instars.

In spite of drastic transformation, which undergo antennae of Metabola in course of the larval/pupal molt, tissues of antennae do not degenerate: the whole antenna of larva gives rise to antenna of imago, so that apical sensilla of larval antenna appear on the apex of imaginal antenna. In contrast to this, in *Orthezia urticae* distal part of antenna degenerates and is not transformed to any part of antenna of the next instar.

In Metabola dedifferentiation and subsequent differentiation of antennal segments at larval/pupal molt lead to immobility of antenna during the whole pupal stage. Even when pupa walks in phase of pharate imago (that occurs in Trichoptera and some Neuropteroidea), its antennae are immovably directed backward. This superficially resembles *Orthezia urticae*, whose ultimonympha (which is homologous to pupa) in phase of pharate imago also walks keeping antennae directed backward (Fig. 4, 30, 31). But in contrast to Metabola, in *Orthezia urticae* such pose of antennae appears not after the molt with dedifferentiation and subsequent differentiation of antennal segments, but after the molt at which all antennal segments develop directly from segments of the previ-

ous instar, and their muscles do not undergo degeneration (Fig. 20). After that molts of *Orthezia urticae*, when antennal musculature degenerates and newly develops (Figs 6–8), antennae become movable and directed forward (Fig. 3).

Transformation of the legs in other insects

In insects other than coccids, neither coxa, nor any other leg segment inverts before molt. If growing leg of the next instar is impressed into the body, this is served by a pouch, which can be either basigenous, or acrogenous (Kluge, 2005), but in all cases this pouch is formed by body wall, and never by leg segment(s). This is true even for such extraordinary pre-molting pouches as "imaginal discs" of Diptera-Cyclorrhapha and leg pouches which appear in other legless larvae before molt to pupa.

Aleyrodids (Scytinelytra), similarly to coccids, have immovable larvae with very short and functionless legs. Before molt from one instar to another, new legs locate partly in the old cuticular leg, partly in the body, and are strongly crumpled, but not inverted. Before the last molt from immovable ultimolarva (which has very short functional-less legs) to imago (which has very long functional legs) imaginal legs form numerous folds, but no one segment is inverted (Figs 26–27).

Besides coccids, partial degeneration, dedifferentiation and subsequent differentiation of leg segments take place only in Metabola and only at one molt — from penultimolarva to pupa (Kluge, 2005). In Metabola these processes lead to immobility of pupal legs and inactive mode of pupal life. In contrast to Metabola, in *Orthezia urticae* legs pass through these processes several times (2 times in male and 3 times in female) and after each molt immediately restore their function.

In all insects, other than Gallinsecta and Metabola, before that molts which do not lead to diminishing of legs, tissues of leg do not undergo degeneration.

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DISCUSSION

The alternation of molting modes, which is described here for *Orthezia urticae*, is probably characteristic for Gallinsecta in general. Among the species examined, this alternation is found, besides *Orthezia urticae* (Ortheziidae), in *Icerya* sp. (Monophlebidae), *Coccus hesperidum* (Coccidae) and *Diaspidiotus ostreaeformis* (Diaspididae), being absent only in *Pseudococcus viburni* (Pseudococcidae). If accept that Ortheziidae and Monophlebidae belong to a plesiomorphon Paleococcoidae, while Coccidae, Diaspididae and Pseudococcidae belong to a holophylum Neococcoidea, this character appears to be irregularly dispersed among Gallinsecta. In the outer group (to which belong all arthropods apart of Gallinsecta) such alternation of molting modes never occurs; the molting mode with degeneration and inverting, which occurs in feeding stages of Gallinsecta, is also unknown in the whole outer group. This fact testifies, that the alternation of molting modes with degeneration and inverting of legs and antennae before each molt of feeding stages is an autapomorphy of Gallinsecta. Probably, selected representatives of Gallinsecta, such as *Pseudococcus viburni* (or a larger taxon, to which this species belongs) secondarily lost this mode of molts and returned to the primitive molts in all instars. Such reversion is possible, because in other Gallinsecta the genetic program which determines the primitive mode of molt, did not disappear, but is realised in non-feeding instars only.

Such mode of molt, at which tissues of legs and antennae under old cuticle at first partly degenerate, and than reach their new size and shape with proximal segment inverted, looks very strange, when it occurs in *Orthezia urticae*, whose legs and antennae grow at each molt, becoming larger from instar to instar. But this mode of molt seems justified, when it occurs in male Diaspididae, whose legs and antennae at the first molt disappear and at the second molt appear, changing their structure. In this case, during the first molt legs and antennae undergo only degeneration, after which they do not grow, and, hence, do not invert. During the second molt new legs and antennae have to grow being sinked into the body, and they reach this condition by inverting of the first segment.

In all Gallinsecta primolarva and male imago (if present) have well-developed legs and antennae; in various non-related taxa secundolarva (and sometimes also female imago) has no legs and normal antennae. Two hypotheses about evolution of coccids are possible: (1) either the alternation of molting modes described here for *Orthezia urticae* is a preadaptatition, which appeared in the common coccid ancestor and caused repeated reduction of legs and antennae in various non-related phylogenetic branches of coccids; (2) or reduction of larval legs and antennae is initial for Gallinsecta, and in such representatives as *Orthezia urticae*, initially leg-less secundolarva got structure, which repeats the structure of primolarva.

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