

**Taxonomic position of the genus *Puto* Signoret (Homoptera: Coccinea: Pseudococcidae) and separation of higher taxa in Coccinea**  
**Таксономическое положение рода *Puto* Signoret (Homoptera: Coccinea: Pseudococcidae) и разделение высших таксонов Coccinea**

I.A. GAVRILOV-ZIMIN & E.M. DANZIG

И.А. ГАВРИЛОВ-ЗИМИН, Е.М. ДАНЦИГ

I.A. Gavrilov-Zimin & E.M. Danzig, Zoological Institute, Russian Academy of Sciences, 1 Universitetskaya Emb., St Petersburg, 199034, Russia. E-mail: coccids@gmail.com

Taxonomic characters of the families Pseudococcidae Cockerell, 1898, Putoidae Beadsley, 1969, Pennygullaniidae Koteja et Azar, 2008 and two superfamilies of Coccinea are discussed in view of phylogenetic meaning of these characters. It is shown that Putoidae Beadsley, 1969 is an unavailable name (**nomen nudum**); moreover, Putoidae sensu Williams et al., 2011 as a separate family considered in the superfamily Orthezioidea (= an informal group of “archeococcids”), is a taxonomic paradox that lies outside of both cladistic and evolutionary concepts in taxonomy and ignores the majority of well-known and carefully proven facts. There is not a single unique apomorphic character in the monotypic family Putoidae; all characters of the genus *Puto* Signoret, 1875 are plesiomorphies of all scale insects or synapomorphies with other mealybugs or with the closely related *Ceroputo* Šulc, 1898. *Ceroputo* is accepted here as a subgenus of *Puto*. The monotypic fossil family Pennygullaniidae is considered by us a **new subjective synonym** of Pseudococcidae. The taxonomic and nomenclatural problems connected with the higher taxa of scale insects and other groups of Homoptera are briefly discussed.

Таксономические признаки семейств Pseudococcidae Cockerell, 1898, Putoidae Beadsley, 1969, Pennygullaniidae Koteja et Azar, 2008 и двух надсемейств подотряда Coccinea обсуждаются в свете филогенетического значения этих признаков. Показано, что Putoidae Beadsley, 1969 является непригодным названием (**nomen nudum**). Более того, Putoidae sensu Williams et al., 2011, принимаемое как отдельное семейство внутри надсемейства Orthezioidea (= неформальная группа “архекокциды”), представляет собой таксономический парадокс, лежащий за рамками как кладистической, так и эволюционной концепций в современной систематике и противоречащий большинству хорошо известных и тщательно изученных фактов. Монотипное семейство Putoidae не имеет ни одной уникальной апоморфной черты; все изученные признаки рода *Puto* Signoret, 1875 являются либо общекокцидными плезиоморфиями, либо синапоморфиями с другими мучнистыми червецами и близкородственным *Ceroputo* Šulc, 1898. Таксон *Ceroputo* принимается здесь как подрод *Puto*. Монотипное вымершее семейство Pennygullaniidae рассматривается нами как **новый субъективный синоним** семейства Pseudococcidae. Кратко обсуждаются также таксономические и номенклатурные проблемы, связанные с названиями высших таксонов кокцид и родственных групп Homoptera.

**Key words:** mealybugs, scale insects, Hemiptera, Homoptera, Coccoidea, Orthezioidea

**Ключевые слова:** мучнистые червецы, кокциды, Hemiptera, Homoptera, Coccoidea, Orthezioidea

## INTRODUCTION

According to the paper of Williams et al. (2011), recently published in *Zootaxa*, two similar nominal genera of mealybugs, *Puto* Signoret, 1875 and *Ceroputo* Šulc, 1898, which have been considered for many years as subjective synonyms, must not only be distinguished as two separate genera but must be placed in two different families and even in two different superfamilies of Coccinea. Unfortunately, we cannot accept the opinion of the cited authors; below, we discuss all the known taxonomic characters of *Puto* in comparison with other scale insects and in view of evolutionary significance of these characters.

Before further discussion, we need to clarify our concept of the taxonomic position of scale insects as a whole and related groups, because: 1) it is not possible to consider the questions of higher classification within Coccinea without consideration of relationships of scale insects with other proboscidian insects; 2) many different classifications have been proposed for hemipteroid insects, especially in the last years [see, for example, the reviews of Brožek et al. (2003), Forero (2008), Kluge (2010a, b)]; 3) there are some nomenclatural problems connected with names of higher taxa of scale insects and other hemipteroids; 4) two principally different approaches to higher classification of hemipteroid insects (cladistic and evolutionary) are present in the literature.

It seems that the oldest non-typified name for all scale insects is Gallinsecta De Geer, 1776 (Kluge, 2000, 2010a, b). But, instead of this name (and several other non-typified old names), during the entire history of coccidology different typified names have been preferred by coccidologists: Coccidae, Coccoptera, Coccoidea, Cocomorpha, Coccinea, Coccina, etc. We recognize the scale insects and other homopterans as suborders of the order Homoptera, and use the special ending “-nea” for all typified suborder names in Homoptera [following Pesson (1951) and internal coccidological

practice (see works of E. Danzig, J. Koteja, E. Podsiadlo, R. Jashenko, I. Gavrilov and others)]: Aphidinea, Coccinea, Aleyrodinea, Psyllinea, Cicadinea. The International Code of Zoological Nomenclature (below: the Code) does not regulate now the taxonomic names higher than family-group names. We follow the principle introduced by Rohdendorf (1977) and consider the suborder names as the family-group ones with their own coordination.

Probably, it will be better to accept standardized typified names for all animal higher taxa as it is done now for botanical names or was accepted for insects by paleontologists (History of Insects, 2002). In this case all proboscidian insects will be covered by the name Cimicidea Laicharting, 1781. However, in view of numerous disputes about the future of the Code we avoid accepting typified names for taxa higher than suborders.

The name Hemiptera Linnaeus, 1758, frequently used (often under pressure from editors of journals) in coccidological literature as an order name for all the groups of proboscidian insects, is not accepted by us in this sense, because: 1) this name was used by C. Linnaeus for proboscidians + thrips (Fig. 1); therefore it is an older synonym for Condylgnatha Börner, 1904; 2) for many years until now, this name has been used by numerous authors for true bugs (Heteroptera) only; 3) there are at least two separate orders (Heteroptera and Homoptera) within the “order Hemiptera” accepted by different modern authors. A similar taxonomic situation exists with the well-known and widely used name Rhynchota Burmeister, 1835, which originally covered not only proboscidians but also Siphunculata. Moreover, this name is preoccupied by Rhynchota Billberg, 1820 (= Aphaniptera Kirby et Spence, 1815) (Kluge, 2010a). The oldest name which covers all the recently accepted proboscidian insects (and only them) is Arthroidignatha Spinola, 1850 (Kluge, 2000, 2010a, b). Although this name has not been used in entomological literature for many years, in the modern difficult taxo-

## INSECTA.

343

## II. HEMIPTERA.

195. CICADA *Rostrum inflexum*. *Pedes postici saltatorii*.  
 196. NOTONECTA *Rostrum inflexum*. *Pedes postici natatorii*  
 (ciliati.)  
 197. NEPA *Rostrum inflexum*. *Pedes antici capitis cheliferi*.  
 198. CIMEX *Rostrum inflexum*. *Pedes cursorii*.  
 199. APHIS *Rostrum inflexum*. *Abdomen bicornis*.  
 200. CHERMES *Rostrum pectorale*. *Pedes postici saltatorii*.  
 201. COCCUS *Rostrum pectorale*. *Abdomen postice setosum maribus*.  
 202. THRIPS *Rostrum obsoletum*. *Ala incumbentes abdomini reflexi*

Fig. 1. Copy of p. 343 from "Systema Naturae" by C. Linnaeus (1758).

nomical and nomenclatural situation with the names Hemiptera and Rhynchota we prefer to use Arthropoda for all proboscidian insects.

As for the widely known and frequently discussed order name Homoptera Latreille, 1810, we do not see serious reasons to reject it. It originally covered all proboscidian insects without true bugs but with the addition of thrips. However, all other authors used this name in its modern composition, i.e. without thrips. The notion about paraphyletic content of Homoptera auct. [for review, see for example, von Dohlen & Moran (1995) or Gullan (1999)] is merely a hypothesis that considers some facts and ignores others. According to the cladistic point of view, the problem boils down to considering synapomorphies of the Hemelytrata Fallen, 1829 (Cicadinea+Coleorrhyncha+Heteroptera) in contrast to synapomorphies of Homoptera. Some authors (for example, Gullan, 1999) even affirm that Homoptera is characterized by plesiomorphic characters only. Of course, it is not so easy to find reliable synapomorphies for all, very diverse groups of Homoptera. However, such features as large loral sutures defining the mandibular plate, the characters of structure of wing-coupling apparatus, the presence of wax glands and

filter chamber of the digestive tract as well as ability to produce honeydew can be considered as synapomorphies of Homoptera (Hamilton, 1981; Lambdin, 2001; D'Urso, 2002; present paper). We do not see any reason to ignore these characters and prefer the probable morphological synapomorphies of Hemelytrata (see, for example, Emeljanov, 1987) or believe the untestable data of molecular cladograms based on a small number of studied taxa (Campbell et al., 1995; von Dohlen & Moran, 1995; and others; see also our comments below, in the section "The data of DNA sequencing"). A detailed historical revision of different phylogenetic reconstructions of proboscidian insects was given by Brožek et al. (2003) and by Forero (2008) and will not be repeated here. *In any case, whether further investigations support the hypothesis about the paraphyly of the Homoptera or not, it cannot be a reason to reject the taxon Homoptera.*

The cladistic dogma about rejecting paraphyletic taxa is not based on any scientific arguments; it is only based on voluntary decision. There is not a single scientific reason to suppose that species in paraphyletic taxa should be less related to each other than the species in holophyletic taxa. This main conceptual contradiction

between cladistic taxonomy (in its original W. Hennig's sense) and evolutionary taxonomy was discussed in many special papers and books [see, for example, Simpson (1961), Mayr (1974), Mayr & Ashlock (1991), Gorochov (2001), Kerzhner & Danzig (2001), Hołyński (2005), Rasnitsyn (2010), and others] and well phrased by R.B. Hołyński (2005): "...paraphyletic taxa do not exist; why not? – because what is paraphyletic is not a taxon; why? – of course because no taxon can be ancestor of another taxon... Maybe it is good philosophy, but good biology it is certainly not...". Moreover, paraphyly of any taxon is closely connected with our subjective view of the borders of the taxon. For example, if we include the fossil ancestor groups of Arthro-dignatha (in particular, Archescytinoidea) in Homoptera, the latter will evidently be paraphyletic; on the other hand, if we include Archescytinoidea in Hemelytrata, the latter will be paraphyletic. The factual paleontological data on the appearance of different Arthro-dignatha groups are provided in the recent scheme of D.E. Shcherbakov and Yu.A. Popov (History of Insects, 2002).

As for the frequently used name *Sterno(r)rhynch(i)(a)* (= Coccinea + Aphidinea + Aleyrodinea + Psillinea), we are not sure of the commonly discussed syn-

apomorphies of this group. For example, according to the scheme of D.E. Shcherbakov and Yu.A. Popov (History of Insects, 2002), *Sternorhynchi* seems to be polyphyletic. Moreover, we believe this taxon to be superfluous in practical classification, because it needs to add and use one more rank between order and suborder for this group. In addition, *Sternorhynchi* Amyot et Serville, 1843 is a junior synonym of *Plantisuga* Dumeril, 1805 (Kluge, 2010a).

As for names of superfamilies within the Coccinea, they are regulated by the Code and are well known. However, in the modern coccidological literature, some authors [including those of the discussed paper of Williams et al. (2011)] use informal and non-typified names "archaeococcids" and "neococcids" for the same family-groups that were placed in the superfamilies *Orthezioidea* and *Coccoidea* many years ago. This strange preference of informal names is probably the result of the consistent use of cladistic dogmata, because *Coccoidea* evidently originated from the *Orthezioidea* and the latter taxon is paraphyletic [see, for example, the phylogenetic reconstruction of Danzig (1980) or the phylogeny of Koteja (1989) based on paleontological data].

As a result, we use the following classification in the present paper:

**Phylogenetic line Paraneoptera Martynov, 1923** (including Zoraptera, Copeognatha, Parasita, Thysanoptera, Homoptera, Coleorrhyncha, Heteroptera)

**Cohors Hemiptera Linnaeus, 1758** (= *Condylgnatha* Börner, 1904, non Hemiptera auct.)

**Superordo Thysanoptera Haliday, 1836**

**Superordo Arthro-dignatha Spinola, 1850** (= Hemiptera auct. non Linnaeus, 1758; = *Rhynchota* auct. non Burmeister, 1835)

**Ordo Coleorrhyncha Meyers et China, 1929**

**Ordo Heteroptera Latreille, 1810** (= Hemiptera auct. non Linnaeus, 1758)

**Ordo Homoptera auct. non Latreille, 1810**

**Subordo Cicadinea Batsch, 1789**

**Subordo Psillinea Latreille, 1807**

**Subordo Aleyrodinea Newman, 1834**

**Subordo Aphidinea Latreille, 1802**

**Subordo Coccinea Fallén, 1814** (= *Coccoidea* auct., *Gallinsecta* De Geer, 1776)

**Superfamilia Orthezioidea Amyot et Serville, 1843** (= *Paleococcoidea* Borchsenius, 1950; = *Archeococcoidea* Bodenheimer, 1952)

**Superfamilia Coccoidea Fallén, 1814** = *Neococcoidea* Borchsenius, 1950; = *Neococcoidea* Bodenheimer, 1952)

## MATERIAL

The paper is based on the scale insect collection of Zoological Institute, Russian Academy of Sciences, St Petersburg (ZIN), including species from all the scale insect groups noted or discussed in this paper; in particular, sixteen species of *Puto* and four of *Ceroputo*.

## RESULTS AND DISCUSSION

There is no need to provide here the general morphological description of *Puto* or Pseudococcidae, or Coccinea. This has been done many times in special coccidological literature as well as in the discussed paper of Williams et al. (2011). In the same paper the history of taxonomic conceptions of *Puto* was also provided. It is interesting that Williams et al. (2011), as well as some other authors (for example, Hodgson & Foldi, 2006), consider *Puto* in a separate family "Putoidae" with the authorship of Beardsley, 1969. However, any description or diagnosis of "Putoidae" are absent in the paper of Beardsley, 1969. The cited author simply mentioned "Putoidae" once in the paper during consideration of phylogenetic relationships of *Puto* and other genera of scale insects. So, according to Article 13 of the Code, the name "Putoidae Beardsley, 1969" must be considered an unavailable name (**nomen nudum**). It seems that Tang (1992) was the first to provide diagnosis of a family group taxon with a name based on the genus *Puto*; he considered this taxon as a tribe Putoini within Pseudococcidae and in addition to *Puto*, Tang also included in the tribe the following genera: *Ceroputo*; *Artemicoccus* Balachowsky, 1953; *Coccidohystrix* Lindinger, 1943; *Rastrococcus* Ferris, 1954; *Berendracoccus* Ali, 1975 synonymised with *Phenacoccus* Cockerell, 1893 by Williams (2004).

Below, we will discuss the characters used by Williams et al. (2011) for substantiation of the placement of *Puto* in a separate family outside of Pseudococcidae and in the

superfamily Orthezioidea, and try to clearly interpret the characters as plesiomorphic, apomorphic, and synapomorphic for higher taxa of scale insects. In general, we will either use well known morphological characters studied in detail, which were already involved many times in phylogenetic studies [for example, in the monograph of Danzig (1986) or in the special paper of Miller & Miller (1993)], or provide the consideration of some less studied characters, such as, for example, eyes in males, sensory pores, etc.

### Symplesiomorphic characters of *Puto* and all scale insects (Coccinea)

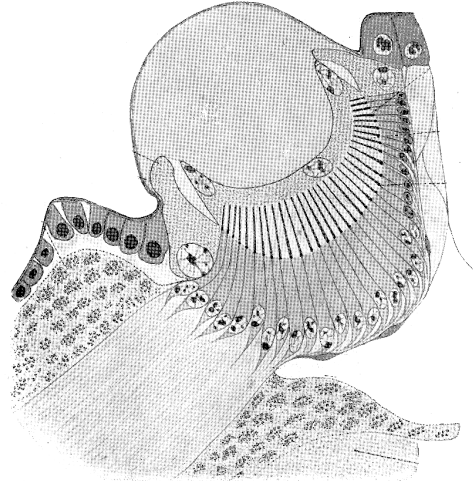
*Genetic system.* The genetic system XX-X0 is an ancient character of Paraneoptera (Blackman, 1995), present in all suborders of Homoptera. However, it can evolve from its original condition to more complicated genetic systems. So, in the studied Orthezioidea this system evolves also to XX-X0 with multiple sex chromosomes, diplo-diploid ( $2n-2n$ ) and hermaphroditism (Hughes-Schrader, 1948; Nur, 1980; Normark, 2003; Gavrilov, 2007). In the studied Coccoidea, the XX-X0 system is demonstrated by *Puto* only; the other groups show systems with paternal genome elimination (Lecanoid, Comstockioid, and Diaspidoid) or diplo-diploidy (in Stictococcidae and in *Lachnodi* Maskell, 1898 from Eriococcidae) (Hughes-Schrader, 1948; Nur, 1980; Normark, 2003; Gavrilov, 2007).

Hitherto, only five American and one Palaearctic species of the genus *Puto* have been studied cytogenetically (Hughes-Schrader, 1944; Brown & Cleveland, 1968; Gavrilov-Zimin, 2011) and no species have been studied in *Ceroputo*. In general only about 6% of Coccoidea species have been studied cytogenetically till now (for review see Gavrilov, 2007) and so, unfortunately, we cannot say if the ancient system XX-X0 remains in *Puto* only or it will be found in the future in other mealybugs or in other still unstudied groups from numerous families of Coccoidea. So, the XX-X0 system as a taxonomic

character cannot be used for the separation of Putoidae, not only because it is a plesiomorphy of all Paraneoptera, but also because the distribution of this character is not clear within the superfamily Coccoidea. A similar situation takes place now with Thysanoptera. As it was shown recently (Brito et al., 2010), these insects preserve plesiomorphic monocentric chromosomes in contrast to all the other Paraneoptera groups which have holocentric chromosomes. However, as we know, nobody excludes Thysanoptera from Paraneoptera, but all specialists consider them as a sister group to Arthrotrichoptera (= Hemiptera s. str.).

**Eyes of males.** Some morphological terms related to the eyes of scale insects probably need to be clarified. In the modern coccidological literature two terms are usually used: *compound eyes* (consisting of numerous ommatidia located close to each other) and *ocelli* (simple eyes). It is well known that the compound eyes and ocelli are innervated from different (lateral and medial, correspondingly) parts of the cerebrum and that the number of ocelli is not greater than three in all insects. In scale insects the ocelli are fully absent (Emeljanov, 1987). However single unicorneal eyes [accessory and primary (larval) eyes, in the terminology of old authors], being elements of compound eyes, are also often referred to as “ocelli” by coccidologists; it leads to the mixing of terms and misunderstanding. Unfortunately, we do not know any comparative anatomical studies of eyes in scale insect males in addition to the old work of Kreckler (1909), but it seems that the compound eyes of scale insects differ from the usual compound eyes of other insects, because single unicorneal elements of scale insect compound eyes lay not close to each other but with clear gaps and have a tendency to be reduced in number (down to only one unicorneal eye on each side of the head of imago).

The same reduction is also known in Myriapoda, Entognatha and in larvae of different groups of Ectognatha (Kluge, 2000), and such reduced unicorneal eyes are desig-



**Fig. 2.** Structure of stemma in the male of *Planococcus citri*, microtomal dissection [reproduced from Kreckler (1909)].

nated by a special term “stemmata” (Weber, 1933; Torre-Bueno, 1989). The structure of the eye of the male of *Planococcus citri* (Risso, 1813) illustrated by Kreckler (1909) (Fig. 2) is rather similar to, for example, larval stemma of *Cicindela* Linnaeus, 1758 (Coleoptera) (Weber, 1933: fig. 304): a group of retinal cells covered by a single cornea. In the collection of ZIN we have found a series of microtome slides prepared many years ago by T.N. Bustshik from the males of *Lichtheimia viburni* Signoret, 1873. The internal structure of the eyes of this species appears similar to that of *P. citri*. Moreover, Kreckler (1909) revealed that nerves from all eyes of *P. citri* are connected with “lateral lobes of the supraoesophageal ganglion”, which unambiguously supports the presumption of absence of ocelli in scale insects. This character can be considered as an apomorphy of the Coccinea. The reduction of the number of unicorneal eyes in imago and larvae seems to be the general character of Coccinea+Aphidinea+Aleyrodinea.

For many years it has been traditionally accepted that two superfamilies of scale insects, Orthezioidea and Coccoidea, differ correspondingly in the presence or absence

of compound eyes. However, at present, when significant additional data on scale insects male morphology have been published (Hodgson & Foldi, 2006), it is difficult to distinguish true compound eyes from stemmata, because the number of unicorneal eyes varies very significantly (from 0 to 150 for Coccinea as a whole) between the genera of Orthezioidea as well as within Coccoidea, but Orthezioidea usually have a greater number of the eyes. On the other hand, males of such genera as *Stigmacoccus* Hempel, 1900, *Phenacoleachia* Cockerell, 1899, *Steingelia* Nasonov, 1908, *Pitycoccus* McKenzie, 1942, and *Stomacoccus* Ferris, 1917 [all these genera are traditionally included in the Orthezioidea; see, for example, Morrison (1928) and Danzig (1986)] retain only 36, 16, 14, 10, and 2 stemmata, respectively (Hodgson & Foldi, 2006).

In Coccoidea we also see variation of the unicorneal eye number in males, from two to ten stemmata (Giliomee, 1967; Afifi, 1968), but very few species (may be several percent of the total number) of Coccoidea are studied in terms of male morphology till now. According to the paper of Williams et al. (2011), different species of *Puto* have from 5 to 8 pairs of stemmata. So, even within *Puto* s. str. we see significant variation of the discussed character. Also, from the paper of Williams et al. (2011) it seems that there is a clear hiatus in the stemmata number between *Puto* s. str. (5–8 pairs) and *Ceroputo* + other mealybugs (1–3 pairs). However, Goux (1931) noted that males of *Heliococcus radicolica* Goux, 1931 (Pseudococcidae) had 4 pairs of unicorneal eyes. So, any hiatus in this character in Pseudococcidae s.l. is absent, and we see a whole row of variability from one to eight pairs of stemmata in the family. In general, based on all the above-mentioned facts, we can be sure that reduction of the compound eyes and the number of unicorneal eyes evolved separately many times in different groups of scale insects and that this character cannot be used as an apomorphy of Coccoidea and all the more, of *Puto*.

*Other morphological characters of males.* Unfortunately, only two male organs (eyes and aedeagus) of different *Puto* species were comparatively analyzed in the paper of Williams et al. (2011). The shape of aedeagus was noted as having two different conditions (bifid and simple) and varying within *Puto* s. str. as shown in Williams et al. (2011: table 1). As for other papers, detailed morphological descriptions have been provided till now for only one species of *Puto* (*P. yuccae* Coquillett, 1890) and one species of *Ceroputo* (*C. pilosellae* Šulc, 1898) (Afifi, 1968; Hodgson & Foldi, 2006). Moreover, it should be noted that nobody described any males of *Ceroputo* before or after Afifi (1968) and we cannot exclude that the material used by Afifi (Yugoslavia: Belgrade, on *Fragaria vesca*, 30 Sept. 1961, coll. N. Mitic-Muzina) was in reality males of *Phenacoccus* sp. inhabiting the same place as females of *Ceroputo pilosellae*. Meanwhile, Ch. Hodgson [personal communication and paper of Hodgson & Foldi (2006)] supposes that the following characters of *P. yuccae* can be used to separate it from *Ceroputo* and even from other mealybugs.

1) Special collared and satellite setae are present; mesothoracic furca is very similar to that in monophlebids; anterior position of anus is on penaeal sheath; usually four hamuli on each hamulohaltere; four or five campaniform sensilla on trochanter are present. [*These characters are clearly plesiomorphic because they are present also in different Margarodidae s. l.; the last 2 characters vary significantly between genera of Margarodidae s. l. in addition* (I.G.-Z. and E.D.)].

2) Claw denticle is exceptionally large [*the size of claw denticle varies significantly within Pseudococcidae s. str.* (I.G.-Z. and E.D.)].

3) Antennal segments show some sign of nodulations on more apical segments [*the character does not have a taxonomic significance to our mind; it varies within Margarodidae s. l. and within Pseudococcidae; see for example, figure 13 showing the anten-*

*nae of Helicococcus radicolica in the paper of Goux (1931) (I.G.-Z. and E.D.).*

4) Genae are absent (as in Margarodidae s. l.) [*the character is plesiomorphic and connected directly with the degree of reduction of ocular sclerite; in majority of Orthezioidea the ocular sclerite and compound eyes cover most part of the male head; when reduction of compound eyes takes place, the head surface not occupied with eyes looks as genae (I.G.-Z. and E.D.).*]

Thus, all these additional and very poorly studied male characters demonstrate (as do the characters of adult females) either plesiomorphic condition or intergeneric variation which obviously will increase in the course of more intensive studies of mealybug males.

*Trochanter campaniform sensilla of adult females.* These sensilla are present in numerous scale insects from different families, but in view of the absence of special histological studies it is not clear if these organs have the same origin as campaniform sensilla of other insects (Koteja, 1974; De Lotto, 1979). The number of trochanter sensilla varies in scale insects significantly between higher taxa as well as between species of the same genus (Morrison, 1928; De Lotto, 1979; Williams et al., 2011). The highest variation is known for Margarodidae s. l., from two to sixteen sensilla on each side of the trochanter (Morrison, 1928). For Ortheziidae, 3–4 pores on each side of trochanter are known (Kozár, 2004). In the Pseudococcidae s. l., the variation from one to four pores on each side of trochanter is known (De Lotto, 1979; Williams et al., 2011). The same range of variation was shown by Williams et al. (2011) for 49 species of *Puto* s. str. As for other mealybugs, it seems that they usually demonstrate two sensilla on each side of trochanter, excluding *Lenania* De Lotto, 1979 with three sensilla (Williams et al., 2011). So, the higher number of the discussed sensilla in some (but not in all) species of *Puto* s. str. is a plesiomorphic character that has an evolutionary tendency of decreasing in both scale

insect superfamilies and even within the genus *Puto* s. str., and sometimes even within a population [types of *Puto (Ceroputo) graminis* Danzig, 1972].

*The number of antennal segments in first-instar larva.* This number is seven for most studied species of *Puto* (Williams et al., 2011). However, not all species of the genus were studied till now because of the absence of first-instar larvae in the available collections. It was also noted by Williams et al. (2011) that “in all mealybugs (Pseudococcidae), the number of antennal segments in first-instar nymphs is six at most (Miller, 1991)”. This statement seems to be rather strange, because many (maybe most) morphological descriptions of mealybug species (and Coccinea in general) do not include information about immature stages. So, we cannot say about mealybugs in general. Moreover, the number of antennal segments in scale insects is one of the most variable morphological characters; it often varies even individually within the same population. For example, Williams et al., 2011 noted that first-instar larva of *Ceroputo pilosellae* Šulc, 1898 (type species of *Ceroputo*) had 6-segmented antennae, but Reyne (1954: p. 319) wrote about 7-segmented antennae in the same species. So, this character cannot be used for any taxonomic decisions in higher taxa.

#### **Synapomorphic characters of *Puto* with all Coccoidea (= Neococcoidea)**

*Abdominal spiracles.* They are not detected in *Puto* as in all Coccoidea (Danzig, 1986; Hodgson & Foldi, 2006). Among Orthezioidea, only *Phenacoleachia* spp. have lost abdominal spiracles in the females, but these spiracles are present in the males with perfectly visible tracheae branched to the abdominal margins (Theron, 1962; Hodgson & Foldi, 2006).

*Parasitism of Hymenoptera wasps.* There are numerous genera and species of parasitic Hymenoptera more or less strongly associated with respective host species of Coccoidea.



coidea. On the other hand, parasitic wasps are almost not known for Orthezioidea (Rosen & DeBach, 1977; Trjapitzin, 1989). Rosen & DeBach (1977) wrote: “although large gap in our knowledge exists, it appears as though the association of parasitic Hymenoptera and scale insects has evolved only after the Neococcoidea was completely separated from the Archeococcoidea”. At present, two species of Encyrtidae from two different genera are known as parasites of *P. yuccae* (see in Scalenet, 2012) that was considered by Williams et al. (2011) as a real *Puto*. These two species are *Aenasius maplei* Compere, 1937 and *Anagyrus yuccae* (Coquillett, 1890). All the species of the large genera *Aenasius* Walker, 1846 (42 species) and *Anagyrus* Howard, 1896 (270 species) are parasites of different mealybugs including *Puto* and do not live in other scale insects, with very rare exceptions of Eriococcidae and Stictococcidae species, and never in Orthezioidea (Universal Chalcidoidea Database, 2012). Thus, parasitic wasps of these genera do not “see” any difference between *Puto* and other mealybugs but “see” the difference between Pseudococcidae s. l. and other scale insects.

#### **Synapomorphic characters of *Puto* with Pseudococcidae (Coccoidea) and Phenacoleachiidae (Orthezioidea)**

*Trilocular pores and ostioles.* Presence of these well-studied structures only in these families probably testify to the origin of Pseudococcidae directly from Phenacoleachidae or the origin of both families from a common Orthezioidea ancestor (Danzig, 1986; Cox, 1983). Moreover, *Phenacoleachia zealandica* (Maskell, 1891) demonstrates ovoviviparity as do *Puto*, *Ceroputo* and numerous other genera of Pseudococcidae (see below).

#### **Synapomorphic characters of *Puto* with Pseudococcidae**

*Cerarii.* The presence of cerarii is a unique apomorphic character of all mealy-

bugs (Pseudococcidae s. l.). All species of *Puto* have a number (at least 18 pairs) of very well developed cerarii.

*Simple tubular ducts.* These ducts, present in mealybugs including *Puto*, differ significantly in their structure from other types of ducts that are present in some Orthezioidea and in different families of Coccoidea.

*Unpaired ventral mycetome.* The presence of this structure is a unique synapomorphy discovered by P. Buchner (1965). The reasoning of some authors (Downie & Gullan, 2004; Hardy et al., 2008) concerning the presence of different symbiotic bacteria in *Puto* and in other mealybugs is not actual for the present discussion, because new, more comprehensive studies (Gruwell et al., 2010) have appeared. It is clear now that all morphologically different groups of mealybugs have different symbiotic bacteria. Moreover, the same bacteria can be found in very phylogenetically distant organisms, as for example, *Spiroplasma* spp. in *Puto* and in *Drosophila* Fallén, 1823 (Diptera).

#### **Synapomorphic characters of *Puto* with *Ceroputo***

*Morphological characters.* Dorsal and ventral trilocular pores are different in size. Eye height is as great as length of the first antennal segment. All cerarii are with numerous conical setae.

*Ovoviviparity.* Ovoviviparity is widely distributed within Coccoidea and very rarely, in several species only (*Phenacoleachia zealandica*, in particular), present in Orthezioidea (Gavrilov & Trapeznikova, unpublished). All species of *Puto* and *Ceroputo*, as well as all or most species of similar genera of Phenacoccini mealybugs, such as *Heliococcus* Šulc, 1912, *Coccura* Šulc, 1908, *Fonscolombia* Lichtenstein, 1877, and *Phenacoccus* are characterized by obligate ovoviviparity (Trapeznikova & Gavrilov, 2008; Trapeznikova, 2011; Gavrilov & Trapeznikova, unpublished).

### Character of unclear phylogenetic significance

*Claw basal spurs.* These spurs are present in most (but not in all) species of *Puto* and in *Ceroputo mimicus* (McKenzie, 1967) and *C. nulliporus* (McKenzie, 1960) (Williams et al., 2011). If we consider the genus *Puto* in the traditional sense, we can see that this character has geographic variation: all the New World species have the spurs, but in the Palearctic species the spurs can be present or absent. There is no special study of this character in other Coccinea, but a somewhat similar structure is present, for example, in *Macropulvinaria* Hodgson, 1968 [C.H. Hodgson, pers. comm., cit. after Williams et al. (2011)].

### The data of DNA sequencing

The data of DNA sequencing for analysis of relationships between organisms are widely used now in different fields of biology and medicine. It is not possible to discuss here all the particular advantages and disadvantages of this approach; they are considered in numerous special papers [see, for example, Lukhtanov (2010)]. In general, the construction of molecular cladograms is mainly based on the so-called “molecular clock” hypothesis, which assumes that nucleotide sequences of analyzed genes in different organisms evolve with the same speed due to random mutations. This “clock” works more or less correctly when recently diverged groups are compared, for example, groups of individuals, populations or related species within the same genus. In these cases all or most members of the analyzed group can be representatively involved in the same study and, in combination with analysis of other taxonomic characters, the DNA sequencing seems to provide good results, as shown for many genera of plants and animals. In scale insects, such a combined taxonomic approach was used recently by Unruh & Gullan (2007) for the genus *Icerya* Signoret, 1876 and related

groups, and by Gullan et al. (2010) for the genus *Ferrisia* Fullaway, 1923.

Unfortunately, the use of DNA sequencing to reveal relationships between higher taxa now seems to be rather far from the reconstruction of real phylogenies [see, for insects in general, the paper of Rasnitsyn (2010), for example]. For us personally, the main practical problems of this method of phylogenetic reconstructions of higher taxa are the following.

1) The molecular cladograms are not easily testable in practice; we can only believe or not believe their data (in contrast to cladograms based on concrete phenotypic characters).

2) When higher taxa are considered, the molecular cladograms, in fact, extrapolate the data of one or several species from a particular genus to this genus as a whole. This is probably an acceptable admission for small, morphologically homogeneous genera but, to our mind, this is not acceptable for large, taxonomically difficult genera like *Puto*, *Phenacoccus* or *Trionymus* Berg, 1899.

3) DNA sequencing does not operate with huge numbers of species or genera of higher taxa, because it requires fresh and adequately fixed material for sequencing, meanwhile the majority of described species of Coccinea were collected during the last 100 and more years and preserved in numerous museums as specially prepared Canada-balsam slides.

These problems, in combination with the methodological problems of computer statistical analysis itself [see discussion in Lukhtanov (2010)], often lead to the appearance of absolutely bizarre clades which contradict to all other scientific data on studied taxa. A good example of such bizarre cladograms we can see, for example, on page 49 of the paper of Cook et al. (2002). The cladogram presented includes only 19 species of scale insects from different families and suggests that *Eriococcus aceris* Signoret, 1875 (Eriococcidae) is more “related” to *Aonidiella aurantii* (Maskell, 1879) (Diaspididae) than to *Eriococcus buxi* (Fonscol-

ombe, 1834); that *Othezia urticae* (Linnaeus, 1758) (Ortheziidae) and *Puto yuccae* are in the same clade, and that *Phenacoleachia zealandica* is not placed within Coccinea but occupies the “outgroup” position, like *Phylloxera notabilis* Pergande, 1904 (Aphidinea). In any traditional phylogenetic study this cladogram would be considered a mere artefact, but in the discussed paper it was provided as one of the scientific results. The second cladogram presented in the same paper (fig. 1 on p. 48), includes 39 species of scale insects and seems to be slightly more realistic, but as for *Puto*, the authors have deduced (on p. 50): “The phylogenetic placement of *Puto* remains unresolved”. However, in a subsequent paper on molecular sequencing of scale insects, Downie & Gullan (2004) state, with reference to Cook et al. (2002) and Hodgson (2002), that “*Puto* is clearly a separate family” (p. 251), even though the position of *Puto* on the new cladogram in the paper of Downie & Gullan (2004) is the same as in the older cladogram of Cook et al. (2002), i.e., unresolved. The genus is not placed there in the same clade with other studied species of mealybugs, nor in the clade with any other scale insect family. The data of Hodgson (2002) on the morphological characters were discussed above.

The recent cladogram of Hardy et al. (2008) analyses 33 species using DNA sequencing [in addition to the species studied by Downie & Gullan (2004)] in combination with morphological cladistic computer analysis of “adult females of 35 species, first-instar nymphs of 28 species, and adult males of 20 species”. Only 35 species were studied morphologically, whereas adult females of all 2000 species of mealybugs and 6000 species of other scale insects preserved in museums, are available for morphological analysis. The combined cladogram of Hardy et al. (2008) seems to us to be more realistic than those in the two previously discussed papers, but the position of *Puto* remains here absolutely the same, i.e., unresolved.

### Conclusion on the genus *Puto* and “family Putoidae”

The summarizing of all the above facts, including the synapomorphies of *Puto* with *Ceroputo* and the evident absence of clear diagnostic characters for separation of adult females of these taxa, leads us to accept *Ceroputo* as not higher than a subgenus of *Puto* in the tribe Putoini Tang, 1992. In this case the identification key may be the following.

- 1(2) Five or more pairs of unicorneal eyes present in adult males. First instar larvae with 7-segmented antennae. Sensilla on each side of female trochanter are usually 3–4 in number, rarely 2 (as an intraspecific variation only) ..... subgenus ***Puto***
- 2(1) Three pairs of unicorneal eyes present in adult males. First instar larvae with 6-segmented antennae (7-segmented as an intraspecific variation only). Sensilla on each side of female trochanter are 2 in number, rarely 1 or 3 [in *P. (C. graminis)*] ..... subgenus ***Ceroputo***

So, to our mind, Putoidae as a separate family placed in the superfamily Orthezioidea (= an informal group of “archeococcids”) is a taxonomic paradox that lies outside of both cladistic and evolutionary concepts in taxonomy and ignores the majority of well known and carefully proven facts. There is not a single apomorphic character in Putoidae; all characters of the genus *Puto* are plesiomorphies with all scale insects or synapomorphies with other mealybugs or with the closely related *Ceroputo*. Putoidae as a separate family is evidently a paraphyletic taxon that does not include all descendants of *Puto*, i.e., *Ceroputo* and other mealybugs. This paraphyly is not a problem for us, but it seems that it is not a problem for some cladistic authors either. Now, this is the best time to remember the splendid words of one of the co-authors of the paper by Williams et al. (2011), P.J. Gullan: “Ideally, all higher taxa should be monophyletic because natural groups provide an unambiguous representation of relationships...” and “Homoptera might not be monophyletic because all

diagnostic features used to separate it from the Heteroptera are all plesiomorphies...” (Gullan, 1999: “Why taxon Homoptera does not exist”). Due to these recommendations, we believe that in the present paper we provide the answer to the question: why the taxon Putoidae does not exist.

Finally, we present our conception of the taxonomic position of *Puto* (subordo Coccoinea: superfamilia Coccoidea: familia Pseudococcidae: subfamilia Phenacoccinae: tribe Putoini: genus *Puto*: subgenus *Puto*, subgenus *Ceroputo*).

#### **Fossil family Pennygullaniidae Koteja et Azar, 2008, syn. nov.**

The fossil species *Pennygullania electrina* Koteja et Azar, 2008, described on the basis of remains of one adult male and a probably congeneric larva in Lower Cretaceous amber, was placed in the original paper in the new monotypic genus and monotypic family Pennygullaniidae, which in the judgment of Koteja & Azar (2008) “seems to represent a special branch of neococcids”. However, any special description or differential diagnosis of the family were not provided by Koteja & Azar (2008). The differential diagnosis of the genus *Pennygullania* Koteja et Azar, 2008 was presented as follows: “slim neococcid with two pairs of simple eyes, slender appendages bearing very long setae, solid scutum, thochanter and femur fused, two pairs of strong tail setae (with two setae in each group), penial sheath of coccid s. str. type” (Koteja & Azar, 2008). Plate 17b in the discussed paper, in contrast to the text description, clearly demonstrates that the thochanter and femur of the male are not fused. Moreover, these two parts of legs in scale insects often lie close to one another, so that the border between them can be poorly visible in fossil individuals. Other characters noted in the diagnosis and in the description of a probably congeneric larva do not demonstrate, to our mind, anything different from the morphological characteristics of Pseudococcidae. In contrast to *Puto* s.

str., which really has a number of plesiomorphic characters, *Pennygullania* bears only apomorphic characters of Coccoidea and Pseudococcidae: two pairs of stemmata, two pairs of tail setae, remains of wax secretions of trilocular and multilocular pores in larva. So, we consider *Pennygullania* as one of the ancient genera within Pseudococcidae.

#### **ACKNOWLEDGEMENTS**

The authors thank all colleagues who participated in the discussion on the present paper, especially Dr Ferenc Kozár, Dr Giuseppina Pellizzari, Dr Christopher Hodgson, Dr Boda Kaydan, Dr Douglas Williams, Dr Penny Gullan, Dr Dmitry Gapon, Dr Alexander Emeljanov, Dr Dmitry Scherbakov, Dr Denian Kondo, Dr Dmitry Dmitriev, Dr Valentina Kuznetsova and others. The work of I. G.-Z. was partly supported by the Russian Foundation for Basic Research (grant no. 11-04-00734-a) and by special grants of St Petersburg government. The collection of Zoological Institute of Russian Academy of Sciences was financially supported by the Ministry of Education and Science of the Russian Federation.

#### **REFERENCES**

- Affi S.** 1968. Morphology and taxonomy of the adult males of the families Pseudococcidae and Eriococcidae (Homoptera: Coccoidea). *Bulletin of the British Museum (Natural History). Entomology. Supplement*, **13**: 3–210.
- Beardsley J.W.** 1969. A new fossil scale insect (Homoptera: Coccoidea) from Canadian amber. *Psyche*, **7**: 270–279.
- Blackman R.L.** 1995. Sex determination in insects. In: **Leather S.R. & Hardie J.** (Eds) *Insect Reproduction*. Boca Raton: CRC Press. 255 p.
- Bodenheimer F.S.** 1952. The Coccoidea of Turkey. I. *Revue de la Faculté des Sciences de l'Université d'Istanbul (Ser. B)*, **17**: 315–351.
- Borchsenius N.S.** 1950. *Koktsidy SSSR* [Scale Insects of the USSR]. Moscow–Leningrad: Akademiya Nauk SSSR, Zoological Institute. 250 p. (In Russian).
- Börner C.** 1904. Zur Systematic der Hexapoden. *Zoologischer Anzeiger*, **27**: 511–533.
- Brito R.O., Affonso P.R.A.M. & Silva Jr. J.C.** 2010. Chromosomal diversity and phyloge-

- netic inferences concerning thrips (Insecta, Thysanoptera) in a semi-arid region of Brasil. *Genetics and Molecular Research*, **9**(4): 2230–2238.
- Brożek J., Szwedło J., Gaj D. & Pilarczyk S.** 2003. Former and current views on the classification of the bugs (Insecta, Hemiptera). *Genus. Supplement*: 85–100.
- Brown S.W. & Cleveland C.** 1968. Meiosis in the male of *Puto albicans* (Coccoidea–Homoptera). *Chromosoma* (Berlin), **24**: 210–232.
- Buchner P.** 1965. *Endosymbiosis of animals with plant-like microorganisms*. New-York: John Wiley & Sons. 909 p.
- Campbell B.C., Steffen-Campbell J.D., Sorensen J.T, Gill R.J.** 1995. Paraphyly of Homoptera and Auchenorrhyncha inferred from 18 S rDNA nucleotide sequences. *Systematic Entomology*, **20**: 175–194.
- Cook L.G., Gullan P.J. & Trueman H.E.** 2002. A preliminary phylogeny of the scale insects (Hemiptera: Sternorrhyncha: Coccoidea) based on nuclear small-subunit ribosomal DNA. *Molecular Phylogenetics and Evolution*, **25**(1): 43–52.
- Cox J.M.** 1984. Relationships of the Phenacoleachiidae (Homoptera: Coccoidea). Proceedings of the 10th International Symposium of Central European Entomofaunistics, Budapest, 15–20 August 1983: 339–341. Bupadest.
- Danzig E.M.** 1986. *Coccids of the Far-Eastern USSR (Homoptera: Coccinea)*. *Phylogenetic analysis of coccids in the world fauna*. New Delhi: Amerind Publishing Co. 450 p.
- D’Urso V.** 2002. The wing-coupling apparatus of Hemiptera Auchenorrhyncha: structure, function, and systematic value. *Denisia*, **4**: 401–410.
- De Lotto G.** 1979. On two podal features in mealybugs (Homoptera: Coccinea). *Journal of the Entomological Society of Southern Africa*, **42**(1): 11–15.
- Downie D.A. & Gullan P.J.** 2004. Phylogenetic analysis of mealybugs (Hemiptera: Coccoidea: Pseudococcidae) based on DNA sequences from three nuclear genes, and a review of the higher classification. *Systematic Entomology*, **29**(2): 238–259.
- Emeljanov A.F.** 1987. Phylogeny of cicadas (Homoptera, Cicadina) based on comparative morphological studies. *Trudy Vsesoyuznogo Entomologicheskogo Obschestva* [Proceedings of the Entomological Society of USSR], **69**: 19–109. (In Russian).
- Forero D.** 2008. The systematics of the Hemiptera. *Revista Colombiana de Entomologia*, **34**(1): 1–21.
- Gavrilov I.A.** 2007. A catalogue of chromosome numbers and genetic systems of scale insects (Homoptera: Coccinea) of the world. *Israel Journal of Entomology*, **37**: 1–45.
- Gavrilov-Zimin I.A.** 2011. New cytogenetic data for some Palaearctic species of scale insects (Homoptera: Coccinea) with karyo-systematic notes. *Comparative Cytogenetics*, **5**(5): 375–390.
- Gilomee J.H.** 1967. Morphology and taxonomy of adult males of the family Coccidae (Homoptera: Coccoidea). *Bulletin of the British Museum (Natural History)*. *Entomology. Supplement*, **7**: 1–168.
- Gorochov A.V.** 2001. On some theoretical aspects of taxonomy (remarks by the practical taxonomist). *Acta Geologica Leopoldensia*, **24**(52/53): 57–71.
- Goux L.** 1931. Notes sur les coccides [Hem.] de la France (3e note). Description d’une espèce nouvelle. *Bulletin de la Société Entomologique de France*, **8**: 113–118.
- Gruwell M.E., Hardy N.B., Gullan P.J., Dittmar K.** 2010. Evolutionary relationships among primary endosymbionts of the mealybug subfamily Phenacoccinae (Hemiptera: Coccoidea, Pseudococcidae). *Applied and Environmental Microbiology*, **76**(22): 7521–7525.
- Gullan P.J.** 1999. Why the taxon Homoptera does not exist. *Entomologica* (Bari), **33**: 101–104.
- Gullan P.J., Kaydan M.B. & Hardy N.B.** 2010. Molecular phylogeny and species recognition in the mealybug genus *Ferrisia* Fullaway (Hemiptera: Pseudococcidae). *Systematic Entomology*, **35**: 329–339.
- Hardy N.B., Gullan P.J. & Hodgson C.J.** 2008. A subfamily-level classification of mealybugs (Hemiptera: Pseudococcidae) based on integrated molecular and morphological data. *Systematic Entomology*, **33**: 51–71.
- Hamilton K.G.A.** 1981. Morphology and evolution of the rhynchotan head (Insecta: Hemiptera, Homoptera). *The Canadian Entomologist*, **113**(11): 953–974.
- History of Insects.** 2002. A.P. Rasnitsyn & D.L.J. Quicke (Eds). New York, Boston, Dordrecht, London, Moscow: Kluwer Academic Publishers. 517 p.
- Hodgson C.J.** 2002. Preliminary phylogeny of some non-margarodid Coccoidea (Hemip-

- tera) based on adult male characters. *Bollettino di Zoologia Agraria e di Bachicoltura* (Milano), **33**(3), 2001: 129–137.
- Hodgson C.J. & Foldi I.** 2006. A review of the Margarodidae sensu Morrison (Hemiptera: Coccoidea) and some related taxa based on the morphology of adult males. *Zootaxa*, 1263: 1–250.
- Holyński R.B.** 2005. Philosophy of science from taxonomist's perspective. *Genus*, **16**(4): 469–502.
- Hughes-Schrader S.** 1944. A primitive coccid chromosome cycle in *Puto* sp. *Biological Bulletin*, **87**: 167–176.
- Hughes-Schrader S.** 1948. Cytology of coccids (Coccoidea–Homoptera). *Advances in Genetics*, **2**: 127–203.
- Kerzhner I. & Danzig E.** 2001. Hemiptera, Homoptera, Sternorrhyncha. *Bollettino Di Zoologia Agraria E Di Bachicoltura (Ser. II)*, **33**(3): 217–218.
- Kluge N.J.** 2000. *Sovremennaya systematika nasekomykh* [Modern systematics of insects]. St. Petersburg: Lan'. 332 p. (In Russian).
- Kluge N.J.** 2010a. Circumscriptional names of higher taxa in Hexapoda. *Bionomina*, **1**: 15–55.
- Kluge N.J.** 2010b. Paradoxical molting process in *Orthezia urticae* and other coccids (Arthroidgnatha: Gallinsecta) with notes on systematic position of scale insects. *Zoosystematica Rossica*, **19**(2): 78–103.
- Koteja J.** 1974. The occurrence of a campaniform sensillum on the tarsus in the Coccinea (Homoptera). *Bulletin Entomologique de Pologne*, **44**: 243–252.
- Koteja J.** 1990. Paleontology, 149–163 pp. In: **Rosen D.** (Ed.) *Armored Scale Insects, their Biology, Natural Enemies and Control. Ser. World Crop Pests*, **4A**. Amsterdam: Elsevier. 384 p.
- Koteja J., Azar D.** 2008. Scale insects from Lower Cretaceous amber of Lebanon (Hemiptera: Sternorrhyncha: Coccinea). *Alavesia*, **2**: 133–167.
- Kozár F.** 2004. *Ortheziidae of the World*. Budapest: Plant Protection Institute of Hungarian Academy of Sciences. 525 p.
- Krecker F.H.** 1909. The eyes of *Dactylopius*. *Zeitschrift für Wissenschaftliche Zoologie*, **93**: 73–89.
- Lambdin P.L.** 2001. Discourse on the classification of the scale insects. *Bollettino Di Zoologia Agraria E Di Bachicoltura (Ser. II)*, **33**(3): 209–213.
- Latreille P.A.** 1810. *Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes. Avec un tableau méthodique de leurs genres, disposés en familles*. Paris: F. Schoell. 444 p.
- Linnaeus C.** 1758. *Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*. Holmiae: Laurentii Salvii. 824 p.
- Lukhtanov V.A.** 2010. From Haeckel's phylogenetics and Hennig's cladistics to the method of maximum likelihood: Advantages and limitations of modern and traditional approaches to phylogeny reconstruction. *Entomological Review*, **90**(3): 299–310.
- Mayr E., Ashlock P.D.** 1991. *Principles of systematic zoology*. New York: McGraw Hill Book Co. 475 p.
- Mayr E.** 1974. Cladistic analysis or cladistic classification? *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **12**(2): 94–128.
- Meyers J.G. & China W.E.** 1929. The systematic position of Peloridiidae as elucidated by a further study of the external anatomy of *Hemiodocus lei* China. *The Annals and Magazine of Natural History*, **105**(3): 282–294.
- Miller D.R. & Miller G.L.** 1993. A new species of *Puto* and a preliminary analysis of the phylogenetic position of the *Puto* group within the Coccoidea (Homoptera: Pseudococcidae). *Jeffersoniana*, **4**: 1–35.
- Morrison H.** 1928. A classification of the higher groups and genera of the coccid family Margarodidae. *United States Department of Agriculture Technical Bulletin*, **52**: 1–239.
- Normark B.B.** 2003. The evolution of alternative genetic systems in insects. *Annual Review of Entomology*, **48**: 397–423.
- Nur U.** 1980. Evolution of unusual chromosome systems in scale insects (Coccoidea: Homoptera). In: **Blackman R.L., Hewitt G.M. & Ashburner M.** (Eds.) *Insect Cytogenetics*: 97–117. London: Royal Entomological Society.
- Pesson P.** 1951. Ordre des Homoptères. In: **Grassé P.-P.** (Ed.) *Traite de Zoologie. X. Insectes supérieurs et Hémiptéroïdes*: 976–1948. Paris: Masson et C<sup>ie</sup> Éditeur.
- Rasnitsyn A.P.** 2010. Molecular phylogenetics, morphological cladistics and fossils. *Entomological Review*, **89**(1): 85–132.

- Reyne A.** 1954. A redescription of *Puto antennatus* Sign. (Homoptera, Coccidea). With notes on *Ceroputo pilosellae* Sulc and *Macrocrococcus superbus* Leon. *Zoologische Mededelingen Uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden*, **32**: 291–324.
- Rohdendorf B.B.** 1977. The rationalization of names of higher taxa in zoology. *Paleontological Journal*, **11**: 149–155.
- Rosen D. & DeBach P.** 1977. Use of scale-insect parasites in Coccoidea systematics. *Bulletin of the Virginia Polytechnic Institute and State University Research Division*, **127**: 5–21.
- Scalenet.** 2012. Visited 1 March 2012. Available from: <<http://www.sel.barc.usda.gov/scalenet/scalenet.htm>>
- Signoret V.** 1875. Essai sur les cochenilles ou gallinsectes (Homoptères–Coccides), 15e partie. *Annales de la Société Entomologique de France (sér. 5)*, **5**: 305–352.
- Simpson G. G.** 1961. *Principles of animal taxonomy*. New York: Columbia Univ. Press. 247 p.
- Šulc K.** 1898. Studie o coccidech. II. *Sitzungsberichte der K. Bohmisch Gesellschaft der Wissenschaften* (1897), **66**: 1–19.
- Tang F.T.** 1992. *The Pseudococcidae of China*. Shanxi. 768 p. (In Chinese with English summary).
- Theron J.G.** 1962. Structure and relationships of the male of *Phenacoleachia zealandica* (Maskell) (Homoptera: Coccoidea). *Proceedings of the Royal Entomological Society of London, Ser. A (General Entomology)*, **37**: 145–153.
- Torre-Bueno J.R. de la.** 1989. *The Torre-Bueno glossary of Entomology*. New York: New York Entomological Society. 840 p.
- Trapeznikova I.V.** 2011. *Reproduktivnye osobennosti i karyosistematika muchnistykh chervetsov (Homoptera: Coccinea)* [Reproductive features and karyosystematics of mealybugs (Homoptera: Coccinea)]. Dissertation Cand. Sci. (Biol.), Zoological Institute, Russian Academy of Sciences. St Petersburg. 232 p. (In Russian).
- Trapeznikova I.V. & Gavrilo I.A.** 2008. About ovoviviparity in mealybugs (Homoptera: Coccinea: Pseudococcidae). *Trudy Zoologicheskogo Instituta Rossiskoy Akademii Nauk* [Proceedings of the Zoological Institute, Russian Academy of Sciences], **312**(1/2): 43–53. (In Russian with English summary).
- Trjapitzin V.A.** 1989. *Paraziticheskie Hymenoptera semeistva Encyrtidae Palearktiki* [Parasitic Hymenoptera of the fam. Encyrtidae of the Palaearctic]. Leningrad: Nauka. 488 p. (In Russian).
- Universal Chalcidoidea Database.** 2012. Visited 1 March 2012. Available from: <<http://www.nhm.ac.uk/researchcuration/research/projects/chalcidoids/database/listChalcids.dsml>>
- Unruh C.M. & Gullan P.J.** 2008. Molecular data reveal convergent reproductive strategies in iceryine scale insects (Homoptera: Coccoidea: Monophlebidae), allowing the reinterpretation of morphology and a revised generic classification. *Systematic Entomology*, **33**: 8–50.
- Weber H.** 1933. *Lehrbuch der Entomologie*. Stuttgart: Gustav Fischer Verlag. iv + 726 p.
- Williams D.J.** 2004. *Mealybugs of southern Asia*. Kuala Lumpur. 896 p.
- Williams D.J., Gullan P.J., Miller D.R., Matile-Ferrero D. & Han S.I.** 2011. A study of the scale insect genera *Puto* Signoret (Homoptera: Sternorrhyncha: Coccoidea: Putoidae) and *Ceroputo* Šulc (Pseudococcidae) with a comparison to *Phenacoccus* Cockerell (Pseudococcidae). *Zootaxa*, **2802**: 1–22.
- Von Dohlen C.D. & Moran N.A.** 1995. Molecular phylogeny of the Homoptera: a paraphyletic taxon. *Journal of Molecular Evolution*, **41**: 211–223.

Received February 1, 2012 / Accepted June 1, 2012