System of generic groups in mealybugs (Homoptera: Coccinea: Pseudococcidae)

Система групп родов мучнистых червецов (Homoptera: Coccinea: Pseudococcidae)

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The paper provides a brief conspectus of the system of morphological generic groups, elaborated earlier by the author basing on the total taxonomic revision of Palaearctic mealybugs. Here the system is complemented by the analysis of all 249 genera of the world fauna. Borders of two generic groups are reconsidered and two else groups (with mainly Oriental and Australasian genera) are included in the system. Main taxonomic characters of generic rank are discussed and illustrated.

Статья представляет собой краткий конспект системы морфологических групп родов мучнистых червецов, предложенной автором ранее на основе тотальной ревизии палеарктической фауны. В настоящей работе эта система дополнена обзором всех 249 родов мировой фауны псевдококцид. Объем двух родовых групп пересмотрен; еще две группы, включающие преимущественно рода ориентальной и австралазийской фаун добавлены в систему. Рассмотрены и проиллюстрированы основные таксономические признаки родового уровня.

Key words: scale insects, mealybugs, systematics, morphology, ovoviviparity

Ключевые слова: кокциды, мучнистые червецы, систематика, морфология, яйцеживорождение

INTRODUCTION

The Pseudococcidae or mealybugs are one of two largest scale insect families and comprises more than 2000 species in world fauna. Unfortunately, general classification and phylogeny reconstruction for the family have been poorly elaborated till now in view of the numerous problems with the correct, unequivocal evolutional interpretation of the mealybug morphological (and some other) characters as plesiomorphic, apomorphic, convergent or parallel (homoplasy). In our recent total review of Palaearctic mealybugs (Danzig & Gavrilov-Zimin, 2014; 2015) we have provided comparative analysis of the basic morphological characters of mealybugs, discussed in detail all main modern contradictions in the higher classification of the family and introduced a system of 19 morphological generic groups, most of which seem to be monophyletic (holophyletic or paraphyletic) and will be probably considered in future as taxa of the formal nomenclatural rank (for example, tribes). Some other morphological groups are perhaps polyphyletic and combine genera which demonstrate convergent similarity only; however, the decision of this problem is impossible basing on the present basis of our knowledge.

Here I am providing a synopsis of the elaborated system, a discussion of some additions to the system, basing on analysis of non-Palaearctic genera and a conspectus of all mealybug genera of the world fauna with preliminary grouping of them according to the system. Two generic groups used in the revision of Palaearctic fauna (Danzig & Gavrilov-Zimin, 2014, 2015), g/g *Trabutina* and g/g *Planococcus*, are included here correspondingly to g/g *Nipaecoccus* and g/g *Trionymus* (see below). On the other hand, two other groups, which combine mainly Oriental and Australasian genera, g/g *Pedronia* and g/g *Allomyrmococcus* are added to the system.

The analysis and discussion below are based on the study of the type species of 249 genera, most of which are represented (as type and non-type specimens) in the collections of Zoological Institute, Russian Academy of Sciences (St Petersburg) and Muséum National d'Histoire Naturelle (Paris). Some material was also loaned by me from the collection of the British Museum of Natural History (London) and Plant Protection Institute of Hungarian Academy of Sciences (Budapest). In addition to the study of the materal I used for the analysis the morphological descriptions and illustrations published in the comprehensive faunistic reviews by following authors for the main non-Palaearctic zoogeographical regions of the world: for Nearctic (Ferris, 1950, 1953; McKenzie, 1967), for Neotropical (Williams & Granara de Willink, 1992), for Oriental (Williams, 2004) and for Australasian (Ferris, 1948; Beardsley, 1964, 1966, 1971; Williams, 1985; Cox, 1987; Williams & Watson, 1988). The Afrotropical region has not been covered by the general taxonomic revision till now, but the following basic publications help to understand the main morphological trends in the evolution of the mealybugs of the region: Mamet, 1940, 1951, 1954, 1962, 1967; De Lotto, 1957, 1958, 1964, 1967, 1969, 1977; Millar, 2002).

DISCUSSION

The main taxonomic characters used in the analysis of the genera (Fig. 1)

[authorship of the generic names see below in the system of generic groups]

Wax glands (Table). The structure and distribution of wax glands are the main diagnostic characters in the systematics of mealybugs and all scale insects. Cuticular sclerotized parts of these glands are clearly visible because they absorb stain during preparation of scale insects and can be subdivided into 3 main groups: discoidal glands, cylindrical glands and glands connected with conical setae ("spines" in non-English literature). {In the English coccidological tradition the term "wax glands" is usually not used, probably because the soft parts of the glands are lost during preparation and only "ducts" and "pores" are visible on specimens mounted in Canada-balsam. In Russian and other old European coccidological schools the term "glands" is widely used, because there are no special terms to indicate the soft parts of the wax glands.}

Discoidal glands produce powdery wax and can be subdivided in the following subtypes.

1) Simple discoidal pores; have a single opening (loculus). Such pores are often scattered in more or less quantity on both body surfaces of mealybugs and/or present in groups with other wax glands or associated with different types of setae. Monotypic genus *Hopefoldia* is characterized by very peculiar compact groups of discoidal pores, so-called "poraria" located on sclerotized plates on both body sides.

2) Trilocular (3-locular) pores have 3 excretory openings and approximately triangular in form. These pores are one of the synapomorphic characters of mealybugs and the monotypic family Phenacoleachiidae and can be found in majority of mealybugs on all body surface. Only some mealybug genera, such as from g/g *Heterococcus*, g/g *Boreococcus*, g/g *Neotrionymus*, g/g *Metad-*

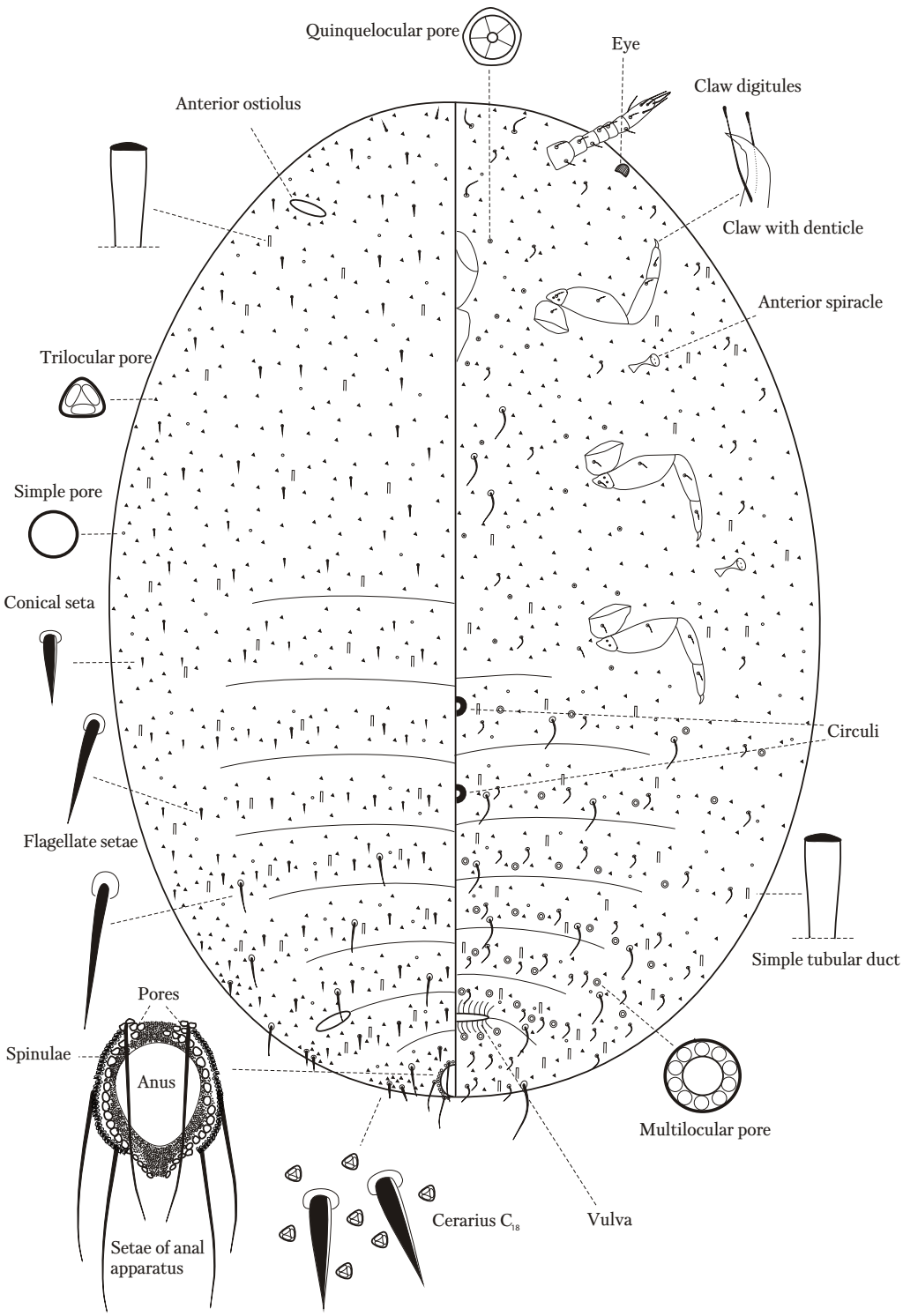


Fig. 1. Main taxonomic characters of mealybug females (*Fonscolombia tomlinii* (Newstead, 1892), Russia: Voronezh Prov.).

enopus, and also some genera from other groups demonstrate reduction in the number of trilocular pores or their secondary total absence. Sometimes trilocular pores are scattered on body very irregularly; thus, they can be absent or very few in medial zone of the thoracic and anterior abdominal sternites (as, for example, in some species of the species-rich genus *Phenacoccus*) or form dense marginal or medial bands (as in *Trimerococcus* and *Kiritshenkella*, respectively). The size of the trilocular pores is usually equal throughout the body. However, in the species of g/g *Puto*, dorsal trilocular pores (and especially cerarian ones) are larger than ventral pores. Trilocular pores of peculiar structure are known in some species and genera, for example, in *Cucullococcus arrabidensis* (Neves, 1954) (pores without fringe) and in the species of *Iberococcus* (pores are strongly convex and located in a deep cup).

3) Quinquelocular (5-locular) pores have one central loculus and 5 peripheral loculi; sometimes central loculus absent. These pores are present mainly in the species of the subfamily Phenacoccinae (in Pseudococcinae they are known mainly in g/g *Metadenopus*) and usually scattered on the ventral surface of body, especially around mouthparts and near spiracles. In some cases (for example, in g/g *Heterococcus* and g/g *Metadenopus*) 5-locular pores are numerous on both body sides and replace partly or totally reduced trilocular pores.

4) Multilocular pores usually have one central loculus and 8–10 peripheral loculi and form transverse rows on abdominal sternites. More rarely multilocular pores present on other surface of body and/or show a peculiar distribution, structure and size. For example, in *Mirococcus sphaeroides* Danzig, 1975 some of multilocular pores have several central loculi; species of the genera *Pelionella* and *Rosebankia* show 2 different types of multilocular pores in the same female. In g/g *Neotrionymus*, multilocular pores replace partly or totally reduced trilocular pores.

Cylindrical glands (Table 1) produce wax filaments. There is a great diversity of these glands, probably, exceeding the diversity of such glands in other scale insects all together.

1) Simple tubular ducts. They have one simple excretory duct. The opening of this duct usually lies on the surface of the cuticle or more rarely it is slightly raised or slightly invaginated from the surrounded cuticle area. Most genera of subfamily Phenacoccinae have only this type of cylindrical glands. The deviation of this type is so-called "bottle-shaped" ducts in the species of g/g *Coccidohystrix*: distal (distant from the excretory opening) part of such duct is enlarged in the form of a bottle.

2) Collar tubular ducts. In these glands the duct is surrounded by collars of different sizes and forms. The greatest diversity of collar ducts takes place in the subfamily Pseudococcinae, whereas among more primitive Phenacoccinae these ducts are known in several genera only, for example in *Heliococcus*, *Seyneria*, *Ehrhornia*. There are at least the following main variants of collar ducts.

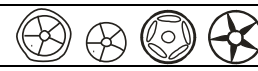
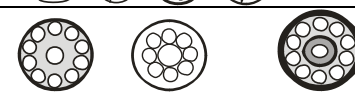
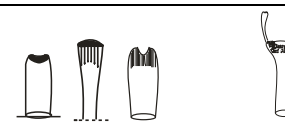
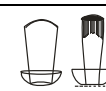
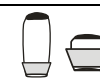
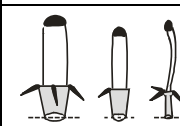
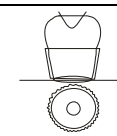
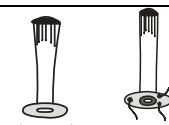
a) Fungiform ducts. The collar of these ducts is very wide and similar to a cap of fungus. Most of species with fungiform ducts are members of g/g *Pseudococcus* and only some species with such ducts are known in other genera, for example, in the genera *Mirococcopsis* and *Humococcus*.

b) Oral collar ducts, with narrow collar which surrounds the excretory opening and part or all tube of the duct. Such ducts are most common and known in most genera of the subfamily Pseudococcinae. The length of the collar can be rather different, from very small to longer than the length of the duct itself.

c) Middle collar ducts, with collar located in the middle part of the duct (for example, in *Volvicoccus volvifer* Goux, 1945, *Metadenopus caudatus* (Borchsenius, 1958), etc.).

d) Double collar ducts. Proximal part of such collar is always more sclerotized than

Table 1. Wax glands in Pseudococcidae.

Discoidal wax glands		
Simple discoidal pores	 *Nudicauda nigra*	
Trilocular pores	 *Cucullococcus* *Iberococcus*	
Quinquelocular pores		
Multilocular pores	 *Pelionella*	
Cylindrical wax glands		
Simple tubular ducts	 *Coccidohystrix*	
Collar tubular ducts	Fungiform ducts	
	Oral collar ducts	
	Middle collar ducts	
	Double collar ducts	
	Crateriform ducts *Heliococcus*	
	Mitral ducts *Ehrhornia, Discococcus*	
Bitubular /tritubular ducts (in g/g *Rhizoecus*)		
Peculiar types	 *Nudicauda* *Ferrisia*	

the distal part (for example, in some *Trionymus*, *Paraputo*, etc.).

f) Crateriform ducts. The collar of such ducts bears one or several conical setae. These are known in the genus *Heliococcus* only.

g) Mitral ducts; resemble a headwear ("mitre") of orthodox religious superiors. These ducts are known, for example, in the genera *Ehrhornia, Discococcus*, *Paradiscococcus*.

3) Bitubular and tritubular ducts are structures, consisted of 2 or 3 crossed ducts, with or without general collar; these are present in many (but not in all!) species of g/g *Rhizoecus*.

4) Peculiar types of tubular ducts are known in different genera. For example, in the species of the genus *Nudicauda*, and in the monotypic genus *Malekoccus*, the duct opening is encircled by a flat sclerotized ring; in the species of pantropical genus *Ferrisia*, the opening is encircled by a sclerotized zone of the cuticle with several associated flagellate setae.

In addition to these rather large ducts which are well visible under usual translucent microscope, many mealybugs have numerous poorly visible minute microtubular ducts, which can be located on different parts of the body and sometimes on the hind coxae. Fine structure and function of these microducts are unknown till now.

Conical setae have different forms and sizes (Fig. 2) and produce consistent wax. Especially large and numerous conical setae are known in the species of g/g *Puto*, g/g *Coccidohystrix* and g/g *Pedronia*. In contrast, in some desert mealybugs, conical setae are totally lost and the body is covered by flagellate and/or hair-like setae only.

In most of mealybugs the conical setae have pointed or slightly roundish apex and only in the genera *Rastrococcus* and *Stemmatomerinx* the conical setae are sharply truncated (see Fig. 2). The conical setae with associated discoidal glands (usually with trilocular pores, more rarely with 5-locular pores) form multiple binate structures along body margin, cerarii, which is one of unique apomorphic characters of Pseudococcidae. Structure and number of cerarii are important taxonomic characters which are used in the classification and identification at the species level and at higher taxa level. The number of cerarii usually ranges from 1 to 18 pairs (first pair on head and the last pair on last abdominal tergite) and their exact number is usually stable inside of the species. More rarely there are small individual variations of this number. An extraordinary variability of the number is currently known in some species only. For example, *Dysmicoccus angustifrons* (Hall, 1926) has from 2 to 10 pairs of cerarii, *Atrococcus alhagii* (Hall, 1926) – from 2 to 15 pairs. Evolutional and individual reduction in the number of cerarii always occurs in the following succession: thoracic and anterior abdominal cerarii become absent initially; followed by the cerarii on head, and at the end the anal pair (C_{18}) is reduced.

In some mealybugs the normal cerarii are totally absent or in the place of the last cerarian pair there are one or several flagellate setae, accompanied by group of trilocular pores. We consider such structures as **pseudocerarii**. Numerous pseudocerarii, distributed along all body margin are a very rare character which is known in monotypic *Madagasia* and *Telocorys* and in *Dysmicoccus trispinosus* (Hall, 1923), which is probably must be transferred to *Telocorys*.

In g/g *Puto* and g/g *Paraputo*, the marginal cerarii are more numerous, up to 26 pairs. Moreover, additional (non-marginal) cerarii can present in the in medial zone of dorsum. In the monotypic genera *Trimerococcus* and *Eastia* and in many species of g/g *Paraputo* the marginal cerarii are fused in a solid marginal band.

In some species of *Coccidohystrix*, normal cerarii are replaced by groups of large conical setae on cuticular tubercles, without trilocular or 5-locular pores – **mamelons**.

Flagellate and hair-like setae of different size are more or less numerous on ventral body side of all species. Dorsal flagellate

and/or hair-like setae are present mainly in the species of subfam. Pseudococcinae. Amongst Phenacoccinae these setae (usually together with conical setae) are present, for example, in Palaearctic genera *Fonscolombia* and *Perystrix*.

Ostioles represented by slit-like openings, located symmetrically as one or 2 pairs on dorsal (rarely on margin of ventral) surface of body. These structures are one of the unique synapomorphic characters of mealybugs (including "Putoidae" of some authors) and the monotypic family Phenacoleachiidae. The position of the ostioles is constant; anterior pair always located on anterior part of cephalothorax and the posterior pair – on VI or VII abdominal tergites or between them. Margins (lips) of ostioles usually slightly raised above surrounded cuticle and bearing the same cuticular structures, i.e., different setae and pores. In the Oriental mealybugs of g/g *Allomyrmococcus*, the ostioles are highly convex and strongly sclerotized. In very rare cases, the ostioles are secondary absent though they are known in related species and genera or even in the larvae of the same species.

Anal apparatus of a compound structure: flat sclerotized ring around anus, one inner row of round or oval pores, one outer row of spinulae and 6 setae, which are usually slightly longer than the diameter of anal ring. Such most common type of anal apparatus we name as complete apparatus (Fig. 3). In some species the number of spinulae is more numerous – 2–4 rows; such type of anal apparatus we consider as complicated. On the contrary, in some species, especially in deserts, anal apparatus is strongly simplified, with reduced number of pores and spinulae or even with their total absence. Additionally, many species have more or less developed anal tube, invaginated inside of anal segment of body. In most species of g/g *Rhizoecus*, pores and spinulae of anal apparatus are enlarged and irregular-shaped. In the genera *Rhodania* and *Pararhodania*, anal ring strongly enlarged and sclerotized. Different types of anal apparatus are shown on Fig. 3. The compound structure of the anal apparatus is connected with the mode of mealybug nourishment. Constant sucking of sweet sap from the plant floem leads to problems with eliminating the surplus of water and sugar (honeydew) from the organism. The honeydew would easily cover the anal segment and occlude the anus if lacking special morphological structures that envelop the honeydew drop with wax in order to discard it from the body. Secondary simplification of the anal apparatus can be connected with the feeding of sap directly from the plant cells or by obligate symbiosis with ants which feed on the excreted honeydew.

Legs usually small in comparison with body; in the species of g/g *Antonina* legs significantly reduced or totally absent. Tarsus 1-segmented, with 2 thin setae at the apex, so-called "tarsal digitules". Claw with or without a denticle; this is important taxonomic character that is traditionally used for the separation of two subfamilies of Pseudococcidae. Claw digitules are usually slightly longer than claw and have a clavate apex; very rarely they are short and/or pointed. In the species of g/g *Allomyrmococcus* claw digitules are widely expanded. All legs more or less equal in size, but in Mongolian endemic, *Mirococcus fossor* Danzig, 1983, anterior legs of burrowing type: femur, tibia and tarsus strongly enlarged and claw elongated, with 2 denticles; claws of other legs of this species are also elongated, but without denticles. Claws with 2 denticles are also known in some other mealybugs, for example, in *Perystrix ulmaria* Gavrilov, 2004; the second denticle is always smaller than the first one. Unusually enlarged legs are known in the species of Australian *Pseudoripesia* and South African *Diversicrus*. Hind coxae (more rarely hind femurs and tibiae) of many species, mainly from the subfamily Pseudococcinae, bearing so-called "translucent pores" or, more rarely, very small microtubular ducts. In the species of g/g *Antonina* numerous and closely spaced translucent pores or microtubular ducts form two compact groups

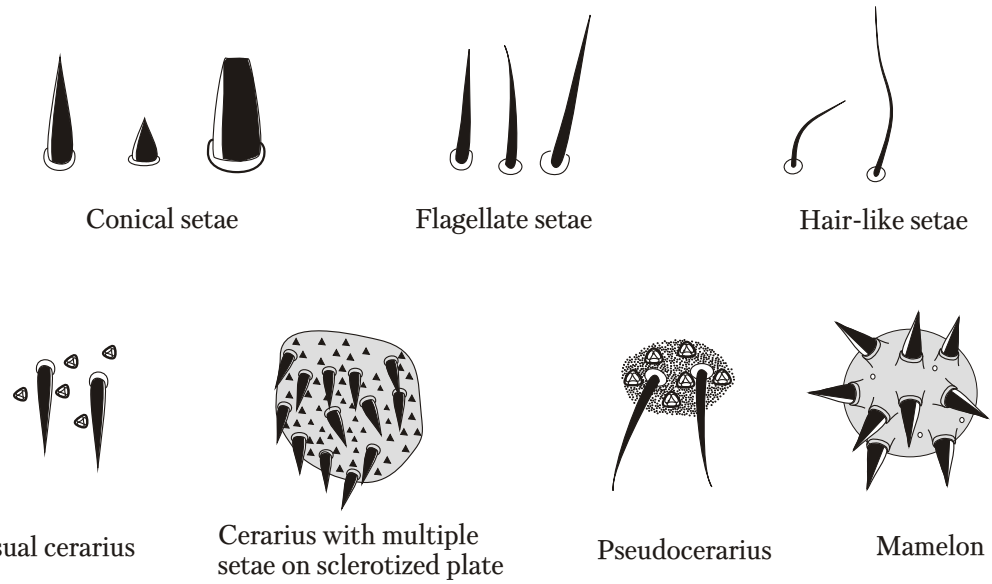


Fig. 2. Setae, cerarii and cerarius-like structures.

on metathorax and anterior abdominal sternites instead of lacked hind legs.

Ovoviviparity. We (Gavrilov-Zimin & Danzig, 2012; Danzig & Gavrilov-Zimin, 2014) consider ovoviviparity as a plesiomorphic character of all Pseudococcidae. This character was probably inherited by mealybugs from the obligate ovoviviparous ancestral family Phenacoleachiidae and is known in all primitive groups of mealybugs: g/g *Puto*, species-rich genera *Heliococcus*, *Coccura*, *Fonscolombia*, *Paraputo*, *Formicococcus* and in many other genera, for example in legless mealybugs (g/g *Antonina*), species-rich genus *Mirococcopsis*, in numerous small and monotypic genera: *Nudicauda*, *Adelosoma*, *Antoninella*, *Cucullococcus*, *Lacombia*, *Ritsemia*, *Ehrhornia*, *Paratrionymus*, *Lankacoccus*, *Stricklandina*, *Madacanthococcus*, *Mauricoccus*, *Mascarenococcus*, *Cirnecoccus*, *Pleistocerarius*, etc. To date more than 500 obligate ovoviviparous species of mealybugs from more than 60 genera have been found (Trapeznikova & Gavrilov, 2008; I. Gavrilov-Zimin, unpublished), that is about 25% of the species diversity in the global fauna. Moreover, there is no doubt that the real number of ovoviviparous species in nature is higher. Some species-rich, but morphologically heterogenous genera such as *Phenacoccus*, *Pseudococcus*, *Trionymus* include oviparous and obligate ovoviviparous species and also species with facultative ovoviviparity.

Family **Pseudococcidae** Cockerell, 1905

Putoidae Tang, 1992: 382 (as a tribe of Pseudococcidae with several genera). Williams et al., 2011: 11 (as a separate monotypic family without *Ceroputo*). Gavrilov-Zimin & Danzig, 2012: 108 (synonymy).

Rhizoecidae Williams, 1969 (as a tribe of Pseudococcidae). Hodgson, 2012: 8 (as a separate family). Gavrilov-Zimin & Danzig, 2014: 124 (synonymy).

Pennygullaniidae Koteja et Azar, 2008: 158. Gavrilov-Zimin & Danzig, 2012: 108 (synonymy).

Two subfamilies of the Pseudococcidae generally differ in the following characters. Species of the subfamily Phenacoccinae usually possess claw denticle, dorsal conical setae, 9-segmented antennae, 5-locular pores and only simple tubular ducts. Species of the subfamily Pseudococcinae without claw denticles, with flagellate dorsal setae,

6–8-segmented antennae and tubular ducts of different types (not only simple); 5-locular pores absent. However, there are numerous exclusions from this general definition. Moreover, some genera and groups of genera (for example, g/g *Metadenopus*) have a questionable phylogenetic and taxonomic position – see the scheme of estimated relationships from Danzig & Gavrilov-Zimin, 2014 with minor changes and additions (Fig. 4).

System of the morphological generic groups (g/g)

1 g/g ***Puto*** Signoret, 1876

Combination of diagnostic characters (plesiomorphic+apomorphic): claw with a denticle; most or all cerarii with multiple (more than 4) conical setae or all cerarii merged in a solid marginal band; 9-segmented antennae; both pairs of ostioles well developed; complete anal apparatus (with one inner row of pores, one outer row of spinulae and 6 long setae); tubular ducts of simple type; trilocular pores numerous and evenly scattered on all body surface.

Additional characters: marginal cerarii are usually supernumerary (more than 18 pairs) in comparison with other Phenacoccinae or even merged in the solid marginal band of conical setae and trilocular pores (as in *Trimerococcus* and in South African endemic *Eastia*).

All species of the group are highly movable insects possessing well developed antennae and legs and living openly on their host plants. Probably all species are ovoviviparous and do not construct wax ovisacs. There is no doubt that the group or at least the genus *Puto* itself are the most ancient and primitive mealybugs and neococcids (superfamily Coccoidea) as a whole. The species of g/g *Puto* demonstrate all apomorphic characters of the family Pseudococcidae, plesiomorphic characters inherited from estimated ancestral family Phenacoleachiidae and almost uninterrupted variability row of general taxonomic characters with vast g/g *Phenacoccus*.

Nominal genera (6): *Eastia* De Lotto, 1964 (Afrotropical), *Mombasinia* De Lotto, 1964 (Afrotropical), *Nairobia* De Lotto, 1964 (Afrotropical), *Puto* Signoret, 1876 (mainly Holarctic), *Rastrococcus* Ferris, 1954 (Oriental, Australasian), *Trimerococcus* Balachowsky, 1952 (Palaearctic).

Deviating genera/species. Several species of *Puto* (Palaearctic *P. borealis* Borchsenius, 1948 and Neotropical *P. paramoensis* Matile-Ferrero, 1985 + *P. lamottei* Matile-Ferrero, 1985) and monotypic genera *Mombasinia* and *Nairobia* lacked claw denticle. Moreover, *Mombasinia* lacked ostioles and demonstrates very peculiar large dorsal groups of simple tubular ducts, enclosed by multilocular pores.

All species of *Rastrococcus* have peculiar truncate conical setae.

2 g/g ***Phenacoccus*** Cockerell, 1893

Combination of diagnostic characters (plesiomorphic + apomorphic): cerarii each with 2–3 conical setae, never merged in marginal band; 9-segmented antennae; quinquelocular pores present; both pairs of ostioles present.

Additional characters (plesiomorphic): well developed dorsal conical setae (often organized in several medial cerarii), claw with a denticle; simple type of tubular ducts; well-developed legs and antennae, complete anal apparatus; trilocular pores numerous and evenly scattered on all body surface.

Nominal genera (10): *Coccura* Šulc, 1908 (Palaearctic), *Fonscolombia* Lichtenstein, 1877 (Palaearctic), *Malekoccus* Matile-Ferrero, 1988 (Palaearctic), *Mammicoccus* Balachowsky, 1959 (Neotropical), *Octococcus* Hall, 1939 (Afrotropical), *Oxyacanthus* De Lotto, 1970 (Afrotropical), *Perystrix* Gavrilov, 2004 (Palaearctic), *Phenacoccus* Cockerell, 1893 (global distribution), *Stemmatomerinx* Ferris, 1950 (Nearctic), *Synacanthococcus* Morrison, 1920 (Palaearctic and Oriental).

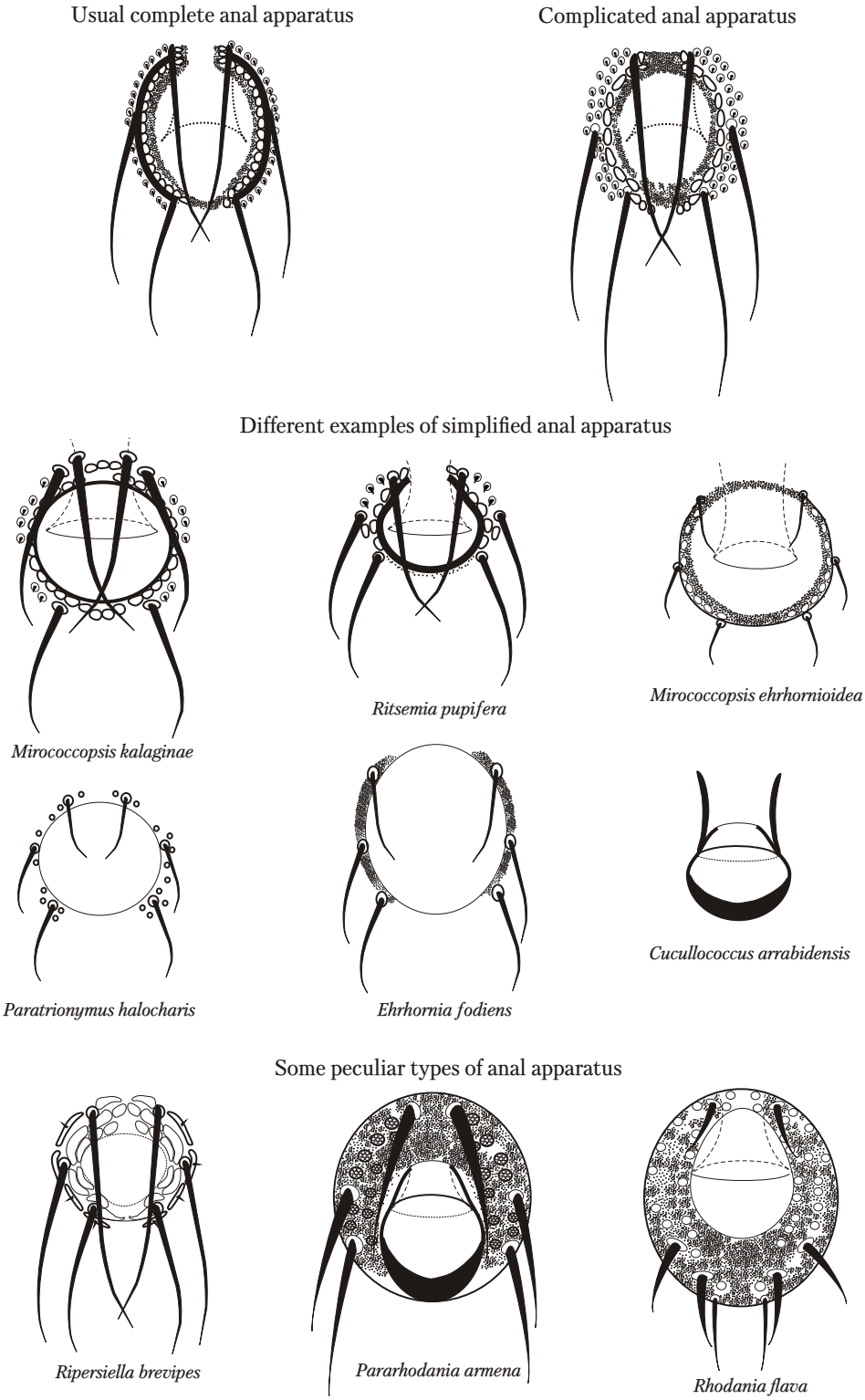


Fig. 3. Different types of anal apparatus.

Deviating genera/species. Majority of deviating species are combined in the genus *Fonscolombia*, all species of which have flagellate setae on dorsum, some species lack claw denticle or 5-locular pores or have 6–8-segmented antennae. Monotypic genus *Malekoccus,* known from Saudi Arabia, demonstrates tubular ducts with flat ring near opening and peculiar large 5-locular pores, which are of the same size as multilocular pores. The species of *Stemmatomerinx* have peculiar truncate conical setae with the base surrounded by small pores. The species of *Mammicoccus* have unusual circuli, divided into protuberances. The correct taxonomic placing of the genus *Octococcus* (4 species) is most disputable: all species have only 2 (posterior) pairs of cerarii, dorsal flagellate setae and ducts with flat ring (rim) near opening; two species (including the type one) have ducts with two rims (additional rim encircling the middle of the duct).

3 g/g ***Peliococcus*** Borchsenius, 1948

Combination of diagnostic characters (apomorphic): clusters of multilocular pores and/or tubular ducts and/or with enlarged conical setae with attached trilocular pore(s) just near the base. Both these characters are present in the type species of *Peliococcus*, *P. chersonensis* (Kiritshenko, 1936), and also in several other species of *Peliococcus* and related genera. Most other species of g/g *Peliococcus* show only one of these characters: either clusters of glands or setae with pore just near the base that impedes a classification of the group and a practical identification of the taxa.

Additional characters (plesiomorphic): well developed dorsal conical setae (often organized in several medial cerarii), simple type of tubular ducts, well developed legs and antennae, complete anal apparatus; claw with a denticle; cerarii each with 2–3 conical setae, never merged in marginal band; 9-segmented antennae; quinquelocular pores; both pairs of ostioles present; trilocular pores numerous and evenly scattered on all body surface.

Nominal genera (6): *Dawa* Williams, 1985 (Australasian), *Peliococcus* Borchsenius, 1948 (global distribution), *Peliococcopsis* Borchsenius, 1948 (Palaearctic), *Erimococcus* Ezzat, 1965 (Palaearctic), *Seyneria* Goux, 1990 (Palaearctic), *Pelionella* Kaydan, 2015 (Palaearctic).

Deviating genera/species. The species of *Seyneria* have tubular ducts with collar.

4 g/g ***Heliococcus*** Šulc, 1912

Combination of diagnostic characters (unique apomorphic): crateriform tubular ducts.

Additional characters (plesiomorphic): claw with a denticle; cerarii each with 2–3 conical setae; 9-segmented antennae; quinquelocular pores; dorsal surface of body covered by conical setae; both pairs of ostioles present; trilocular pores numerous and evenly scattered on all body surface.

The g/g *Heliococcus* includes only one genus in the global fauna. This genus is probably a collateral blind branch of the phylogenetic line *Puto-Phenacoccus* (see Fig. 4). The species of *Heliococcus* show in addition to their general plesiomorphic morphology and a plesiomorphic mode of life (highly movable ovoviviparous females) one unique apomorphic character – the appearance of crateriform tubular ducts.

Deviating genera/species: some species (for example, *H. takae* (Kuwana, 1907), *H. takahashii* (Kanda, 1935) and *H. varioporus* Matesova, 1968) have cerarii with multiple conical setae.

5 g/g ***Coccidohystrix*** Lindinger, 1943

Combination of diagnostic characters (apomorphic): cerarii replaced by the groups of large conical setae without associated trilocular or quinquelocular pores (mamelons); tubular ducts of characteristic bottle-shaped form; the presence of more or less cylindrical setae on dorsum; the absence of ostioles.

Additional characters (plesiomorphic): claw with a denticle; 9-segmented antennae;

quinquelocular pores present ; tendency to decreasing of the number of trilocular pores.

Nominal genera (3): *Coccidohystrix* Lindinger, 1943 (Palaearctic + Oriental), *Lantanacoccus* Williams et Granara de Willink, 1992 (Neotropical), *Eriocorys* De Lotto, 1967 (Afrotropical).

Deviating genera/species. Some of *Coccidohystrix* species demonstrate significant decreasing of the number of trilocular pores, up to their presence near spiracles only. This feature in combination with the absence of ostioles and scattering of enlarged dorsal conical setae denote similarity and probably relationship of *Coccidohystrix* g/g with the family Eriococcidae (felt scales) and it seems that *Coccidohystrix* can be considered as an ancestor group for the felt scales. In particular, two recently described North-African species, *C. maghribiensis* and *C. monicae* (Gavrilov-Zimin & Matile-Ferrero, 2014) differ, in fact, from the species of the largest (and probably most primitive) genus of felt scales, *Acanthococcus* Signoret, 1875, only in the presence of small number of trilocular pores near spiracles.

Lantanacoccus lacked claw denticle and has 6-segmented antennae.

Coccidohystrix insolita (Green, 1908) and monotypic genus *Eriocorys* save one (posterior) pair of ostioles.

6 g/g ***Heterococcus*** Ferris, 1918

Combination of diagnostic characters (apomorphic): trilocular pores totally lacked or very few and present near spiracles and in the cerarii only; quinquelocular pores numerous and scattered on all body surface.

Additional characters (plesiomorphic): claw with a denticle; cerarii each with 2–3 conical setae; dorsal setae usually conical; 9-segmented antennae.

Nominal genera (4): *Brevennia* Goux, 1940, *Heterococcus* Ferris, 1918, *Paramococcus* Foldi et Cox, 1989 (Neotropical), *Laingiococcus* Morrison, 1945 (Australasian),

Deviating genera/species. Some species of *Brevennia* lack anterior ostioles and have dorsal flagellate setae. Monotypic genus *Paramococcus* lacks both pairs of ostioles. Some species of *Heterococcus* lack cerarii and have dorsal flagellate setae. *Brevennia dasiforae* (Danzig, 1977) and *B. rehi* (Lindinger, 1943) lack claw denticle.

7 g/g ***Boreococcus*** Danzig, 1960

Combination of diagnostic characters (unique apomorphic): trilocular pores lacked and replaced by multilocular pores of two types: usual type and asteroid multilocular pores.

Additional characters (plesiomorphic): claw with a denticle; cerarii each with 2–3 conical setae; 9-segmented antennae; both pairs of ostioles present.

Nominal genera (2): *Annulococcus* James, 1936 (Afrotropical), *Boreococcus* Danzig, 1960 (Palaearctic).

Deviating genera/species. Both species of *Annulococcus* have collar tubular ducts and numerous long flagellate setae on dorsum.

8 g/g ***Mirococcus*** Borchsenius, 1947

Combination of diagnostic characters (apomorphic): cerarii totally lacked.

Additional characters (plesiomorphic + apomorphic): claw with a denticle; quinquelocular pores usually present; anal apparatus often simplified; tendency to decreasing of the number of trilocular pores.

I include in this group different mealybugs with features of simplification and reduction of main morphological characters, such as cerarii, ostioles, anal apparatus, wax glands, etc. These mealybugs are placed in different small and monotypic genera and perhaps form not monophyletic group. This group is probably originated from different ancestors similar with modern species of *Fonscolombia* or/and *Brevennia* (subfamily Phenacoccinae), that confirmed by the presence of claw denticle, often presence of quinquelocular pores, total or partial replacement of trilocular pores by quinquelocular ones, 8–9 (rarely 7)-segmented an-

tennae and simple tubular ducts. The genus *Mirococcus* seems to be the most primitive in considered group, because it saves usual for most mealybugs high number of evenly distributed trilocular pores, more or less complete anal apparatus and thick setae, accompanied by a group of trilocular pores in place of last (18-th) pair of cerarii (pseudocerarii).

Nominal genera (8): *Cucullococcus* Ferris, 1941 (Holarctic), *Discococcus* Ferris, 1953 (Nearctic and Neotropical), *Ehrhornia* Ferris, 1918 (Holarctic), *Mollicoccus* Williams, 1960 (Australasian), *Neosimmondsia* Laing, 1930 (Australasian), *Scaptococcus* McKenzie, 1964 (Nearctic), *Sinococcus* Wu et Zheng, 2000 (Palaearctic), *Stipacoccus* Tang, 1992 (Palaearctic).

Deviating genera/species. Three oligotypic genera, *Cucullococcus*, *Discococcus*, *Ritsemia* and *Sinococcus* are characterized by very peculiar morphological characters and perhaps related to each other. All these genera demonstrate sclerotization of the cuticle on whole body or on some parts of body in adult females, significant reduction of the number of trilocular pores, absence of ostioles and presence of numerous circuli (4–6 in number). All species of *Discococcus* lack claw denticle.

9 g/g ***Paraputo*** Laing, 1929

Combination of diagnostic characters (plesiomorphic + apomorphic): cerarii with multiple conical setae, which are often merged in entire marginal band; dorsal surface of body usually covered by conical setae, more rarely – by thick flagellate setae; quinquelocular pores absent, claw without a denticle.

Additional characters (plesiomorphic + apomorphic): tubular ducts with collar; both pairs of ostioles well developed; 6–8-segmented antennae; trilocular pores numerous and evenly scattered on all body surface.

The group is undoubtedly most primitive in subfamily Pseudococcinae and shares many characters with *Puto*, but lacked claw denticle, decreasing of the number of antennae segments, appearing of collar tubular ducts and flagellate setae on dorsum.

A row of nominal monotypic and oligotypic genera, described mainly from southern hemisphere do not have any clear differences from the oldest genera *Paraputo* or *Formicococcus* and the names of such genera must be probably synonymised in future; this supposed synonymy is noting below.

Nominal genera (29): *Anisococcus* Ferris, 1950 (Nearctic, Neotropical), *Brasiliputo* Williams et Granara de Willink, 1992 (Neotropical, ?=*Paraputo*), *Chileputo* Williams et Granara de Willink, 1992 (Neotropical, ?=*Paraputo*), *Crenicoccus* Williams, 2004 (Oriental, ?=*Formicococcus*), *Criniticoccus* Williams, 1960 (Australasian), *Cyperia* De Lotto, 1964 (Afrotropical), *Delococcus* Ferris, 1955 (Afrotropical), *Eucalyptococcus* Williams, 1985 (Australasian, ?=*Paraputo*), *Exallomochlus* Williams, 2004 (Oriental), *Exilipedronia* Williams, 1960 (Oriental), *Farinococcus* Morrisson, 1922 (Neotropical, ?=*Paraputo*), *Formicococcus* Takahashi, 1928 (Palaearctic, Oriental), *Hopefoldia* Foldi, 1988 (Neotropical), *Lachnodiella* Hempel, 1910 (Neotropical, ?=*Formicococcus*), *Laminicoccus* Williams, 1960 (Australasian, ?=*Paraputo*), *Lanceacoccus* Williams, 2004 (Oriental), *Lankacoccus* Williams, 2004 (Oriental), *Mascarenococcus* Mamet, 1940 (Afrotropical), *Moystonia* Williams, 1985 (Australasian, Oriental), *Mutabilicoccus* Williams, 1960 (Australasian), *Odacoccus* Williams et Watson, 1988 (Australasian), *Paraputo* Laing, 1929 (Palaearctic, Oriental), *Circaputo* McKenzie, 1962 (Nearctic), *Palmicultor* Williams, 1960 (pantropical), *Pleistocerarius* Matile-Ferrero, 1970 (Afrotropical), *Stricklandina* Matile-Ferrero, 1998 (Afrotropical, Oriental), *Sarococcus* Williams et de Boer, 1973 (Australasian), *Tomentocera* Beardsley, 1964 (Australasian: Hawaii), *Yudnapinna* Williams, 1985 (Australasian).

Deviating genera/species. The species of *Formicococcus* and *Lachnodiella* have numerous (more than 6–8) setae of anal ring. Monotypic *Lankacoccus* demonstrates

9-segmented antennae and numerous 5-locular pores on venter. The species of *Moystonia* and *Tomentocera* have small fungiform ducts. Monotypic genus *Circaputo* demonstrates minute claw denticle.

Correct taxonomic placing of monotypic *Hopefoldia* is very questionable; this genus is characterized by very unusual sclerotized plates with pores, so-called "poraria", scattered on both body sides.

10 g/g ***Pedronia*** Green, 1922

Combination of diagnostic characters (apomorphic): dorsal enlarged conical setae located on sclerotized tubercles and/or on prominent lobes.

Additional characters (plesiomorphic): claw without a denticle; quinquelocular pores absent; antennae 6–8-segmented.

Nominal genera (9): *Acrochordonus* Cox, 1987 (Australasian: New Zealand), *Agastococcus* Cox, 1987 (Australasian: New Zealand), *Clavicoccus* Ferris, 1948 (Australasian: Hawaii), *Extanticoccus* Williams, 2004 (Oriental), *Neoclavicoccus* Cohic, 1959 (Australasian: New Caledonia), *Nesopedronia* Beardsley, 1971 (Australasian: Hawaii), *Pedrococcus* Mamet, 1942 (Afrotropical, Oriental), *Pedronia* Green, 1922 (Oriental), *Tylococcus* Newstead, 1897 (Afrotropical, Oriental).

Deviating genera/species. Two endemic New Zealand genera, *Acrochordonus* are *Agastococcus* as well as Afrotropical *Tylococcus* are characterized by peculiar very prominent lateral lobes on posterior abdominal segments or along all body margin; these lobes bear multiple conical setae; similar, but smaller lobes are present in Oriental monotypic *Extanticoccus*. Type species of Hawaiian endemic genus *Clavicoccus* also have numerous extremely long dorsal prominences with multiple conical setae; the second species of the genus have prominences of moderate size, but also with multiple conical setae. Probably, these genera occupy intermediate position between g/g *Paraputo* and g/g *Pedronia*.

11 g/g ***Nipaecoccus*** Šulc, 1945

Combination of diagnostic characters (apomorphic): conical setae (in addition or instead of cerarian setae) numerous along all body margin or/and throughout on dorsum.

Additional characters (plesiomorphic): claw without a denticle; quinquelocular pores absent; antennae 6–8-segmented; cerarii (if present) each with 2–3 conical setae; trilocular pores numerous and evenly scattered on all body surface.

The g/g *Nipaecoccus* is similar with g/g *Paraputo* in the presence of numerous dorsal conical setae in addition to conical setae of cerarii.

The type species of the genera *Hypogeococcus* and *Nipaecoccus*, namely *H. barbarae* Rau, 1938 and *N. nipae* (Maskell, 1893) are very similar morphologically and the characters of other nominal species of both genera are totally overlapped.

In the review of Palaearctic fauna (Danzig & Gavrilov-Zimin, 2014, 2015) we considered the genera *Adelosoma* and *Trabutina* in the separate g/g *Trabutina*, but basing on the present analysis of the world fauna we do not see morphological hiatus between it and g/g *Nipaecoccus*.

Nominal genera (22): *Adelosoma* Borchsenius, 1948 (Palaearctic), *Amonostherium* Morrison et Morrison, 1922 (Nearctic), *Australicoccus* Williams, 1985 (Australasian), *Conulicoccus* Williams, 1985 (Australasian), *Cyphonococcus* Cox, 1987 (Australasian), *Erioides* Green, 1922 (Oriental), *Epicoccus* Cockerell, 1982 (Australasian), *Fijicoccus* Williams et Watson, 1988 (Australasian), *Grewiacoccus* Brain, 1918 (Afrotropical), *Hordeolicoccus* Williams, 2004 (Oriental), *Hypogeococcus* Rau, 1938 (Nearctic, Neotropical, Afrotropical, Australasian), *Kenmorea* Williams, 1985 (Australasian), *Lanceacoccus* Williams, 2004 (Oriental), *Madangiacoccus* Williams, 1985 (Australasian), *Melanococcus* Williams, 1985 (Australasian), *Nipaecoccus* Šulc, 1945 (global distribution), *Paramonostherium* Williams, 1985 (Australasian), *Porococcus* Cockerell,

1898 (Neotropical), *Pseudoripersia* Cockerell, 1899 (Australasian), *Strombococcus* Williams, 1985 (Australasian), *Trabutina* Marchal, 1904 (Palaearctic), *Ventrispina* Williams, 1985 (Australasian).

Deviating genera/species.

The taxonomic position of the genus *Amonostherium* is disputable; its type species has a claw denticle and lack ostioles. The species of *Cyphonococcus* have numerous fungiform ducts.

12 g/g ***Trionymus*** Berg, 1899

Combination of diagnostic characters (apomorphic): cerarii with 2–3 conical setae; conical setae present in cerarii only; both body sides covered by flagellate or hair-like setae.

Additional characters (plesiomorphic): claw without a denticle; antennae 6–8-segmented; trilocular pores numerous and evenly scattered on all body surface.

A row of nominal monotypic and oligotypic genera, described mainly from southern hemisphere do not have any clear differences from the older genus *Trionymus* and the names of such genera must be probably synonymised in future; this supposed synonymy is noting below.

In the review of Palaearctic fauna (Danzig & Gavrilov-Zimin, 2014, 2015) we considered the genera *Planococcus* and *Crisicoccus* in the separate g/g *Planococcus*. This group included species which are very similar morphologically with the species from large genera *Trionymus* Berg, 1899 and *Dysmicoccus* Ferris, 1950, but demonstrate so-called "anal bar" – sclerotized stripe on ventral surface of anal lobe. Such character is very subjective, because it is often difficult to differ anal bar from other variants of cuticular sclerotization on anal lobes. Also, examples of individual variation of the character, i.e. presence/absence of the anal bar in females of the same population, are known, for example, in the type series of *Atrococcus expressus* (Borchsenius, 1949) and *A. pacificus* (Borchsenius, 1949) (see g/g Pseudococcus). In view of these facts we consider all g/g *Planococcus*, genera inside of it and also the tribe Planococcini Ezzat et McConnell, 1956 as unnatural.

Nominal genera (45): *Anthelococcus* McKenzie, 1964 (Nearctic), *Asaphococcus* Cox, 1987 (Australasian), *Asteliacoccus* Williams, 1985 (Australasian), *Boninococcus* Kawai, 1973 (Australasian: Bonin Islands, ?=*Trionymus*), *Callitricoccus* Williams, 1985 (Australasian), *Chaetotrionymus* Williams, 1985 (Australasian, ?= *Trionymus*), *Chlorococcus* Beardsley, 1971 (Australasian: Hawaii), *Chnaurococcus* Ferris, 1950 (Nearctic, ?=*Trionymus*), *Cirnecoccus* Mamet, 1967 (Afrotropical), *Crisicoccus* Ferris, 1950 (global distribution), *Crocydococcus* Cox, 1987 (Australasian), *Delottococcus* Cox et Ben-Dov, 1986 (Afrotropical), *Dysmicoccus* Ferris, 1950 (global distribution), *Erium* Cockerell, 1897 (Australasian), *Eurycoccus* Ferris, 1950 (global distribution, ?=*Trionymus*), *Ferrisia* Fullaway, 1923 (global distribution), *Ityococcus* Williams, 1985 (Australasian), *Leptococcus* Reyne, 1961 (Oriental), *Macrocepicoccus* Morrison, 1919 (Neotropical), *Maculicoccus* Williams, 1960 (Australasian), *Madagasia* Mamet,1962 (Afrotropical), *Marendellea* De Lotto, 1967 (Afrotropical), *Mauricoccus* Mamet, 1967 (Afrotropical), *Nesococcus* Ehrhorn, 1916 (Australasian), *Ohiacoccus* Beardsley, 1971 (Australasian), *Oracella* Ferris, 1950 (Nearctic), *Orococcus* De Lotto, 1964 (Afrotropical), *Orstomicoccus* Mamet, 1962 (Afrotropical), *Paradoxococcus* McKenzie, 1962 (Nearctic), *Paraferrisia* Williams et de Boyer, 1973 (Australasian), *Phyllococcus* Ehrhorn, 1916 (Australasian: Hawaii), *Planococcus* Ferris, 1950 (global distribution), *Poecilococcus* Brookes, 1981 (Australasian), *Pseudoferrisia* Kaydan et Gullan, 2012 (Nearctic), *Pseudotrionymus* Beardsley, 1971 (Australasian: Hawaii), *Renicaula* Cox, 1987 (Australasian), *Spartinacoccus* Kosztarab, 1996 (Nearctic), *Strandanna* De Lotto, 1969 (Afrotropical), *Tasmanicoccus* Williams, 1985 (Australasian), *Telocorys* De Lotto,

1967 (Afrotropical), *Trionymus* Berg, 1899 (global distribution), *Trochiscococcus* Williams et Pellizzari, 1997 (Afrotropical), *Turbinococcus* Beardsley, 1966 (Australasian), *Tympanococcus* Williams, 1967 (Oriental), *Villosicoccus* Williams, 1985 (Australasian).

Deviating genera/species. Monotypic *Anthelococcus* has dorsal conical setae (together with flagellate ones) and 5-locular pores on venter. Four monotypic and oligotypic genera, *Maculicoccus*, *Pseudotrionymus, Spartinacoccus*, *Trochiscococcus* save only several cerarian pairs, but these cerarii with multiple conical setae, the character which these genera share with g/g *Paraputo*.

Monotypic *Cirnecoccus* demonstrates unusually prominent and sclerotized anal lobes and replacing of most cerarii (excluding only C_{18}) by long flagellate setae. Similar in size, but not sclerotized anal lobes is known only in monotypic *Poecilococcus*.

Monotypic *Marendellea* has peculiar clusters of multilocular pores+tubulars ducts, the same as in g/g *Peliococcus*, but share most of other characters with the genus *Trionymus*.

Ferrisia and very similar monotypic genus *Pseudoferrisia,* have unique tubular ducts with sclerotized rim, bearing several pores and flagellate setae. Monotypic *Paraferrisia* has tubular ducts with similar sclerotized rim, but without pores or setae on it.

Monotypic *Londiania* has 6 pairs of with multiple very thin (almost flagellate) setae.

Monotypic *Madagasia* and *Telocorys* possess 17–19 pairs of pseudocerarii, each with 2–3 long flagellate setae.

The species of *Renicaula* have very small antennae and legs and enlarged hind coxae with numerous translucent pores.

The species of *Chlorococcus* Beardsley, 1971 (Australasian: Hawaii), *Leptococcus* Reyne, 1961 (Oriental), *Macrocepicoccus* have unusually long, slender antennae and legs with long pointed claws.

The taxonomic position of monotypic genus *Phyllococcus*, endemic of Hawaii, is questionable; the type species produces peculiar galls (very rare example in g/g *Trionymus*!) and has heavily sclerotized lobate posterior end of body (two posterior segments); the other abdominal segments significantly narrowed in comparison with cephalothorax.

13 g/g ***Pseudococcus*** Westwood, 1840

Combination of diagnostic characters (apomorphic): fungiform ducts

Additional characters (plesiomorphic): claw without a denticle; cerarii with 2–3 conical setae; antennae 6–8-segmented; trilocular pores numerous and evenly scattered on all body surface.

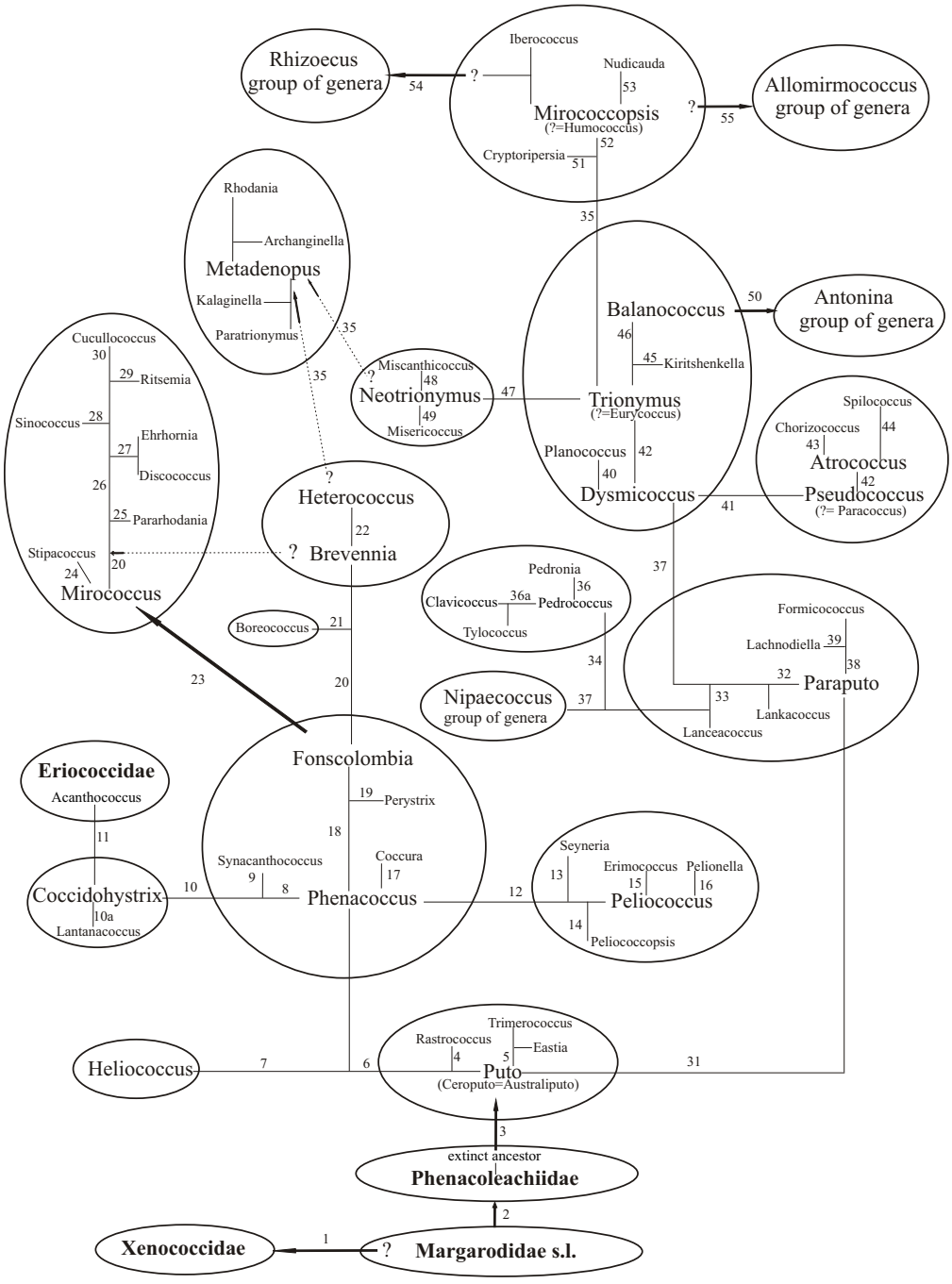
Nominal genera (13): *Apodastococcus* Williams, 1985 (Australasian), *Atrococcus* Goux, 1941 (Holarctic), *Atriplicicoccus* Williams et Granara de Willink, 1992 (Neotropical), *Chorizococcus* McKenzie, 1960 (Nearctic), *Chryseococcus* Cox, 1987 (Australasian), *Colombiacoccus* Williams et Granara de Willink, 1992 (Neotropical), *Cormiococcus* Williams, 1989 (Afrotropical), *Distichlicoccus* Ferris, 1950 (Nearctic, Neotropical), *Gallulacoccus* Beardsley, 1971 (Australasian), *Maconellicoccus* Ezzat, 1958 (pantropical), *Papuacoccus* Williams et Watson, 1988 (Australasian), *Paracoccus* Ezzat et McConell, 1956 (pantropical), *Spilococcus* Ferris, 1950 (Nearctic).

Deviating genera/species. The species of *Chorizococcus* have claw denticle. The species of *Maconellicoccus* possess 9-segmented antennae. Monotypic *Cormiococcus* has very numerous multilocular pores, scattered on all body surface and even inside of spiracular peritremae.

14 g/g ***Neotrionymus*** Borchsenius, 1948

Combination of diagnostic characters (apomorphic): total or partial replacement of trilocular pores by multilocular ones in combination with a presence of one several normally developed cerarian pairs.

Additional characters (plesiomorphic): claw without a denticle; cerarii with 2–3 conical setae; antennae 6–8-segmented.


Rhizoecus group of genera
54
?
Iberococcus
Nudicauda
53
Mirococcopsis
(?=Humococcus)
52
Cryptoripersia
51
?
55
Allomirmococcus group of genera
35
Rhodania
Archanginella
Metadenopus
Kalaginella
Paratrionymus
35
35
Balanococcus
50
Antonina group of genera
46
45
Kiritshenkella
Miscanthicoccus
48
?
Neotrionymus
47
Trionymus
(?=Eurycoccus)
49
Misericoccus
Spilococcus
Chorizococcus
44
43
Atrococcus
42
Planococcus
42
40
Dysmicoccus
41
Pseudococcus
(?= Paracoccus)
Cucullococcus
30
29
Ritsemia
Sinococcus
28
Ehrhornia
27
Discococcus
26
25
Pararhodania
Stipacoccus
24
20
Mirococcus
?
Heterococcus
22
? Brevennia
37
Pedronia
36
Clavicoccus
36a
Pedrococcus
Tylococcus
Formicococcus
Lachnodiella
39
38
32
Paraputo
33
Lankacoccus
Lanceacoccus
Boreococcus
21
34
23
20
Nipaecoccus group of genera
37
Eriococcidae
Acanthococcus
Fonscolombia
19
Perystrix
18
11
Synacanthococcus
9
Coccura
17
Seyneria
13
Erimococcus
15
Pelionella
16
Coccidohystrix
10
10a
Lantanacoccus
8
Phenacoccus
12
Peliococcus
14
Peliococcopsis
Trimerococcus
Rastrococcus
4
5
Eastia
Heliococcus
7
6
Puto
(Ceroputo=Australiputo)
31
3
extinct ancestor
Phenacoleachiidae
2
Xenococcidae
1
?
Margarodidae s.l.

Nominal genera (6): *Coorongia* Williams, 1985 (Australasian), *Miscanthicoccus* Takahashi, 1957 (Holarctic), *Neoripersia* Kanda, 1943 (Palaearctic, Australasian: Bonin Islands), *Neotrionymus* Borchsenius, 1948 (Palaearctic), *Pandanicola* Beardsley, 1966 (Australasia), *Rosebankia* De Lotto, 1967 (Afrotropical).

Deviating genera/species. Monotypic *Miscanthicoccus* possesses peculiar campaniform spiracles. Both *Miscanthicoccus* and *Neoripersia* have zones of shagreen cuticle. Monotypic *Rosebankia* demonstrates multilocular pores of two sizes on both body sides.

15 g/g ***Metadenopus*** Šulc, 1933

Combination of diagnostic characters (apomorphic): total replacement of trilocular pores by multilocular/quinquelocular ones in combination with the absence of cerarii.

Additional characters (plesiomorphic): claw without a denticle; antennae 6-8-segmented.

According to these characters the group occupies intermediate position between g/g *Neotrionymus* and g/g *Mirococcopsis*. Among 8 genera considered below, five, *Cypericoc-*

Fig. 4. Scheme of estimated relationships between main generic groups of Pseudococcidae and related families. Ovals designate borders of families and generic groups. Species-rich and/or phylogentically important genera are written in larger font.

Evolutional changes of characters:

1 – lack of compound discoidal wax glands, primarily absence of ostioles and tubular ducts, primarily presence of female pupal larva; 2 – appearance of ostioles and swirled trilocular pores; 3 – lack of abdominal spiracles, appearance of cerarii and tubular ducts; 4 – truncate conical setae; 5 – solid marginal band of conical setae and trilocular pores; 6 – standardization of the number of cerarian setae (up to 2 per cerarius) and of the size of trilocular pores (equal on all body); 7 – crateriform ducts; 8 – enlarging of conical setae; 9 – tubular ducts with associated simple pores just near the excretory opening;10 – lacking of ostioles and normal cerarii, appearance of mamelons and "bottle-shaped" tubular ducts, decreasing of the number of trilocular pores; 10a – lacking of claw denticle; 11 – total lacking of trilocular pores; 12 – clusters of multilocular pores and/or tubular ducts;13 – tubular ducts with collar;14 – dorsal 5-locular pores;15 – dorsal clusters include tubular ducts only;16 – multilocular pores of 2 different types; 17 – tubular ducts forming marginal band and produce acetabuliform ovisac;18 – decreasing of the number of cerarii and appearance of dorsal flagellate setae; 19 – pseudocerarii along body margin;20 – decreasing of the number of 3-locular pores and their partial replacement by other discoidal glands; 21 – trilocular pores replaced by multilocular pores, tubular ducts with collar; 22 – total lacking of trilocular pores; 23 – total lacking of cerarii and simplification of anal apparatus; 24 – dorsal setae conical, lacking 5-locular pores; 25 – enlargement of anal ring and appearance of unusual pores on it; 26 – multiple circuli with double fringe, cuticle sclerotized; 27 – mitral ducts, lacking of 5-locular pores; 28 – conical setae on dorsum; 29 – lacking of tubular ducts; 30 – reduction of legs, trilocular pores without fringe; 31 – lacking of claw denticle; 32 – decreasing of the number of cerarii; 33 – enlarging of dorsal conical setae; 34 – dorsal conical setae located on sclerotized tubercles; 35 – lacking of cerarii; 36 – decreasing of the number of 3-locular pores; 36a – prominent lateral lobes of body; 37 – decreasing and standardization of the number of conical setae in cerarii; 38 – anal apparatus with numerous (more than 8) setae; 39 – tubular ducts of simple type only; 40 – anal lobe bar present; 41 – fungiform ducts; 42 – lacking of auxiliary flagellate setae in cerarii and decreasing of the number of cerarii; 43 – secondary appearance of claw denticle; 44 – fungiform ducts of different sizes; 45 – grouping of 3-locular pores in medial zone of body; 46 – multilocular pores form non-interrupted marginal band; 47 – replacement of trilocular pores by multilocular pore; 48 – campaniform spiracles; 49 – conical setae on dorsum; 50 – reducing of legs and sclerotization of cuticle; 51 – complete anal apparatus; 52 – simplification of anal apparatus; 53 – tubular duct opening encircled by a flat sclerotized ring; 54 – simplification of anal apparatus together with enlarging of scanty pores and spinulae, appearance of bitubular and tritubular ducts; 55 – enlargement of ostioles, legs and antennae, lacking of tubular ducts.

cus, *Metadenopus*, *Misericoccus*, *Paratrionymus* and *Syrmococcus* show replacement of trilocular pores by multilocular ones. Two else genera, *Rhodania* and monotypic *Archanginella*, lack multilocular pores as well as trilocular ones, but have numerous quinquelocular pores on both body sides. The fifth genus, monotypic *Kalaginella*, has only quinquelocular pores, which similar in size with multilocular pores of other mealybugs. Furthermore, large discoidal pores of complicated structure are demonstrated by *Rhodania aeluropi* Williams et Moghaddam, 2007 which differs in this and in some other characters from its cogeneres and from all other species of g/g *Metadenopus*.

The name of American genus *Misericoccus* is probably junior synonym of *Paratrionymus*.

Nominal genera (8): *Archanginella* Danzig et Gavrilov-Zimin, 2013 (Palaearctic), *Cypericoccus* Williams, 1985 (Australasian), *Kalaginella* Danzig et Gavrilov-Zimin, 2013 (Palaearctic), *Metadenopus* Šulc, 1933 (Palaearctic), *Misericoccus* Ferris, 1953 (Nearctic), *Paratrionymus* Borchsenius, 1948 (Palaearctic), *Rhodania* Goux, 1935 (Palaearctic), *Syrmococcus* Ferris, 1953 (Nearctic).

Deviating genera/species. The type species of both *Misericoccus* and *Paratrionymus* have occasional conical setae on last abdominal tergite.

16 g/g ***Mirococcopsis*** Borchsenius, 1948

Combination of diagnostic characters (apomorphic): cerarii and any conical setae absent.

Additional characters (plesiomorphic): claw without a denticle; legs normally developed; antennae 6–8-segmented; trilocular pores numerous and evenly distributed; anal apparatus often simplified.

Nominal genera (24): *Acaciacoccus* Williams et Matile-Ferrero, 1994 (Afrotropical), *Antoninella* Kiritshenko, 1937 (Palaearctic), *Gomezmenoricoccus* Kozár et Walter, 1985 (Palaearctic), *Bimillenia* Matile-Ferrero et Ben-Dov, 1999 (Palaearctic), *Coleococcus* Borchsenius, 1962 (Palaearctic), *Cryptoripersia* Cockerell, 1899 (Nearctic, Afrotropical, Australasian), *Diversicrus* De Lotto, 1970 (Afrotropical), *Glycycnyza* Danzig, 1974 (Palaearctic), *Hadrococcus* Williams, 1985 (Australasian), *Humococcus* Ferris, 1953 (Neactic, Neotropical, Australasian), *Iberococcus* Gómez-Menor Ortega, 1928 (Palaearctic), *Inopicoccus* Danzig, 1971 (Palaearctic), *Lacombia* Goux, 1940 (Palaearctic), *Lenania* De Lotto, 1964 (Afrotropical), *Madeurycoccus* Mamet, 1959 (Afrotropical), *Mirococcopsis* Borchsenius, 1948 (Palaearctic), *Mizococcus* Takahashi, 1928 (Oriental), *Natalensia* Brain, 1915 (Afrotropical), *Nudicauda* Gavrilov, 2006 (Palaearctic), *Palaucoccus* Beardsley, 1966 (Australasian), *Paradiscococcus* Williams, 1985 (Australasian), *Pilococcus* Takahashi, 1928 (Oriental), *Prorsococcus* Williams, 1985 (Australasian), *Tridiscus* Ferris, 1950 (USA), *Volvicoccus* Goux, 1945 (Palaearctic).

Deviating genera/species. Monotypic *Diversicrus* possesses unusual enlarged hind legs.

17 g/g ***Rhizoecus*** Künkel d'Herculais, 1878

Combination of diagnostic characters (apomorphic): special type of anal apparatus with enlarged pores and spinulae; bases of antennae located closely to each other; cephalic sclerotized plate and bi-/tritubular ducts usually present; antennae 5–6-segmented.

Additional characters (plesiomorphic): claw without a denticle; trilocular pores numerous and evenly distributed; anal apparatus often simplified; cerarii absent (with the only exclusion in *Prorhizoecus*).

The g/g *Rhizoecus* is one of the most specialized and aberrant groups in the family Pseudococcidae, but the group shares with other mealybugs obvious unique synapomorphic characters of Pseudococcidae: presence of ostioles and trilocular pores and also non-unique synapomorphies: similar structure of tubular ducts and multilocular pores and similar structure of anal apparatus.

Nominal genera (15): *Benedictycoccina* Kozár et Foldi, 2004 (Neotropical, Afrotropical), *Brevicoccus* Hambleton, 1946 (Neotropical), *Capitisetella* Hambleton, 1977 (Neotropical), *Coccidella* Hambleton, 1946 (Neotropical), *Geococcus* Green, 1902 (global distribution), *Hambletonrhizoecus* Kozár et Konczné Benedicty, 2005 (Neotropical), *Kissrhizoecus* Kozár et Konczné Benedicty, 2005 (Palaearctic), *Leptorhizoecus* Williams, 1998 (Oriental), *Marottarhizoecus* Kozár et Konczné Benedicty, 2002 (Afrotropical), *Pseudorhizoecus* Green, 1933 (Neotropical), *Pygmaeococcus* McKenzie, 1960 (USA), *Prorhizoecus* Miller et McKenzie, 1971 (Nearctic), *Rhizoecus* Kunckel d'Herculais 1878 (global distribution), *Ripersiella* Tinsley, 1899 (global distribution), *Williamsrhizoecus* Kozár et Konczné Benedicty, 2007 (Neotropical, Afrotropical).

Deviating genera/species. The species of *Geococcus* have prominent sclerotized anal lobes, each with stout conical seta at apex. Monotypic *Kissrhizoecus* has numerous quinquelocular pores on both body sides (unique example in g/g *Rhizoecus*). Monotypic *Pseudorhizoecus* possesses simplified anal apparatus, without any pores and spinulae.

Monotypic *Prorhizoecus* is probably most primitive member of the group; it saves usual type anal apparatus (with small pores and spinular) and normally developed C_{18}, but has antennae similar with that in other species of the group and peculiar bulbous ducts like in some other genera of the group, for example, in *Pygmaeococcus*.

18 g/g ***Antonina*** Signoret, 1872

Combination of diagnostic characters (apomorphic): legs strongly reduced or absent at all; hind coxae enlarged, often modified to sclerotized bag-like structures, coved by microtubular ducts or translucent pores.

Additional characters (plesiomorphic): claw without a denticle; trilocular pores numerous and evenly distributed (with only several exclusions); anal apparatus often simplified; cerarii usually absent.

The world fauna of mealybugs includes at least 26 genera, which is characterized by strong reduction or loss of legs. Eight of these genera are considered by most modern specialists to be closely related and placed in separate tribe Serrolecaniini Shinji, 1935. The diagnostic characters of this tribe are caudally directed vulva and groups of microtubular ducts located on ventral cuticle in place of reduced legs or on the surface of peculiar bag-like structures (probably modified hind coxae). The tribe includes 8 genera, seven of which are mainly Palaearctic: *Paraserrolecanium*, *Idiococcus*, *Porisaccus*, *Paraporisaccus*, *Serrolecanium*, *Chaetococcus*, *Tangicoccus* and one monotypic genus *Kermicus* has Oriental areal. Other genera of "legless" mealybugs perhaps not closely related to each other and to Serrolecaniini and demonstrate convergent similarity only (see more detail discussion in Hendricks & Kosztarab, 1999).

Nominal genera (26): *Albertinia* De Lotto, 1970 (Afrotropical), *Aemulantonina* Williams, 2004 (Oriental), *Acinicoccus* Williams, 1985 (Australasian), *Antonina* Signoret, 1872 (global distribution), *Antoninoides* Ferris, 1953 (Nearctic), *Chaetococcus* Maskell, 1893 (mainly Nearctic), *Chloeoon* Anderson, 1788 (Oriental), *Conicosoma* De Lotto, 1970 (Afrotropical), *Cypericoccus* Williams, 1985 (Australasian), *Idiococcus* Takahashi et Kanda, 1939 (Palaearctic), *Kermicus* Newstead, 1897 (Oriental), *Miconicoccus* Williams et Miller, 1999 (Neotropical), *Nesticoccus* Tang, 1977 (Palaearctic), *Paludicoccus* Ferris, 1918 (Nearctic), *Parapaludicoccus* Mamet, 1962 (Afrotropical), *Paraporisaccus* Lu et Wu, 2011 (Palaearctic), *Paraserrolecanium* Wu, 2010 (Palaearctic), *Paulianodes* Mamet, 1953 (Afrotropical), *Peridiococcus* Williams, 1985 (Australasian), *Porisaccus* Hendricks et Kosztarab, 1999 (Palaearctic), *Pseudantonina* Green, 1922 (Oriental, Nearctic, Neotropical), *Serrolecanium* Shinji, 1935 (Palaearctic), *Sphaerococcus* Maskell, 1892

(Australasian, Afrotropical), *Tangicoccus* Kozár et Walter, 1985 (Palaearctic), *Quadrigallicoccus* Williams et Miller, 1999 (Neotropical), *Wapoacoccus* Ben-Dov, 2007 (Australasian).

Deviating genera/species. Monotypic *Albertinia*, *Antoninoides*, *Conicosoma*, *Paraserrolecanium* as well as oligotypic *Pseudantonina* save very small degenerate legs with partly fused segments. Monotypic genera *Aemulantonina* and *Albertinia* possess 1–2 pairs of cerarii. Monotypic *Miconicoccus* and *Quadrigallicoccus* produce galls.

19 g/g ***Allomyrmococcus*** Takahashi, 1941
= tribe **Allomyrmococcini** Williams, 1978

Combination of diagnostic characters (apomorphic): both pairs of ostioles strongly developed, with sclerotized lips; unusually long, slender antennae and legs with long pointed claws and widely expanded digitules; anal apparatus simplified, without pores and spinulae; very long dorsal and ventral setae; cerarii and any conical setae absent; anal apparatus simplified, without pores and spinulae.

Additional characters (plesiomorphic): claw without a denticle; trilocular pores numerous and evenly distributed.

All genera of the group are endemic to Oriental region, mainly to Greater Sunda Islands of Malay archipelago.

Nominal genera (11): *Allomyrmococcus* Takahashi, 1941, *Archeomyrmococcus* Williams, 2002, *Bolbococcus* Williams, 2002, *Borneococcus* Williams, 2002, *Dicranococcus* Williams, 2002, *Doryphorococcus* Williams, 2002, *Hippeococcus* Reyne, 1954, *Malaicoccus* Takahashi, 1950, *Paramyrmococcus* Takahashi, 1941, *Promyrmococcus* Williams, 2002, *Thaimyrmococcus* Williams, 2002.

Alphabetic index of generic names

Acaciacoccus – g/g *Mirococcopsis*
Acinicoccus – g/g *Antonina*
Acrochordonus – g/g *Pedronia*
Adelosoma – g/g *Nipaecoccus*
Aemulantonina – g/g *Antonina*
Agastococcus – g/g *Pedronia*
Albertinia – g/g *Antonina*
Allomyrmococcus – g/g *Allomyrmococcus*
Amonostherium – g/g *Nipaecoccus*
Anisococcus – g/g *Paraputo*
Annulococcus – g/g *Boreococcus*
Anthelococcus – g/g *Trionymus*
Antonina – g/g *Antonina*
Antoninella – g/g *Mirococcopsis*
Antoninoides – g/g *Antonina*
Apodastococcus – g/g *Pseudococcus*
Archanginella – g/g *Metadenopus*
Archeomyrmococcus – g/g *Allomyrmococcus*
Asaphococcus – g/g *Trionymus*
Asteliacoccus – g/g *Trionymus*
Atriplicicoccus – g/g *Pseudococcus*
Atrococcus – g/g *Pseudococcus*
Australicoccus – g/g *Nipaecoccus*
Benedictycoccina – g/g *Rhizoecus*
Bimillenia – g/g *Mirococcopsis*
Bolbococcus – g/g *Allomyrmococcus*
Boninococcus – g/g *Trionymus*
Boreococcus – g/g *Boreococcus*
Borneococcus – g/g *Allomyrmococcus*
Brasiliputo – g/g *Paraputo*
Brevennia – g/g *Heterococcus*
Brevicoccus – g/g *Rhizoecus*
Callitricoccus – g/g *Trionymus*
Capitisetella – g/g *Rhizoecus*
Chaetococcus – g/g *Antonina*
Chaetotrionymus – g/g *Trionymus*
Chileputo – g/g *Paraputo*
Chloeoon – g/g *Antonina*
Chlorococcus – g/g *Trionymus*
Chnaurococcus – g/g *Trionymus*
Chorizococcus – g/g *Pseudococcus*
Chryseococcus – g/g *Pseudococcus*
Circaputo – g/g *Paraputo*
Cirnecoccus – g/g *Trionymus*
Clavicoccus – g/g *Pedronia*
Coccidella – g/g *Rhizoecus*
Coccidohystrix – g/g *Coccidohystrix*
Coccura – g/g *Phenacoccus*
Coleococcus – g/g *Mirococcopsis*
Colombiacoccus – g/g *Pseudococcus*
Conicosoma – g/g *Antonina*
Conulicoccus – g/g *Nipaecoccus*
Coorongia – g/g *Neotrionymus*
Cormiococcus – g/g *Pseudococcus*
Crenicoccus – g/g *Paraputo*
Criniticoccus – g/g *Paraputo*
Crisicoccus – g/g *Trionymus*
Crocydococcus – g/g *Trionymus*
Cryptoripersia – g/g *Mirococcopsis*

Cucullococcus – g/g *Mirococcus*
Cyperia – g/g *Paraputo*
Cypericoccus – g/g *Antonina*
Cypericoccus – g/g *Metadenopus*
Cyphonococcus – g/g *Nipaecoccus*
Dawa – g/g *Peliococcus*
Delococcus – g/g *Paraputo*
Delottococcus – g/g *Trionymus*
Dicranococcus – g/g *Allomyrmococcus*
Discococcus – g/g *Mirococcus*
Distichlicoccus – g/g *Pseudococcus*
Diversicrus – g/g *Mirococcopsis*
Doryphorococcus – g/g *Allomyrmococcus*
Dysmicoccus – g/g *Trionymus*
Eastia – g/g *Puto*
Ehrhornia – g/g *Mirococcus*
Epicoccus – g/g *Nipaecoccus*
Erimococcus – g/g *Peliococcus*
Eriocorys – g/g *Coccidohystrix*
Erioides – g/g *Nipaecoccus*
Erium – g/g *Trionymus*
Eucalyptococcus – g/g *Paraputo*
Eurycoccus – g/g *Trionymus*
Exallomochlus – g/g *Paraputo*
Exilipedronia – g/g *Paraputo*
Extanticoccus – g/g *Pedronia*
Farinococcus – g/g *Paraputo*
Ferrisia – g/g *Trionymus*
Fijicoccus – g/g *Nipaecoccus*
Fonscolombia – g/g *Phenacoccus*
Formicococcus – g/g *Paraputo*
Gallulacoccus – g/g *Pseudococcus*
Geococcus – g/g *Rhizoecus*
Glycycnyza – g/g *Mirococcopsis*
Gomezmenoricoccus – g/g *Mirococcopsis*
Grewiacoccus – g/g *Nipaecoccus*
Hadrococcus – g/g *Mirococcopsis*
Hambletonrhizoecus – g/g *Rhizoecus*
Heliococcus – g/g *Heliococcus*
Heterococcus – g/g *Heterococcus*
Hippeococcus – g/g *Allomyrmococcus*
Hopefoldia – g/g *Paraputo*
Hordeolicoccus – g/g *Nipaecoccus*
Humococcus – g/g *Mirococcopsis*
Hypogeococcus – g/g *Nipaecoccus*
Iberococcus – g/g *Mirococcopsis*
Idiococcus – g/g *Antonina*
Inopicoccus – g/g *Mirococcopsis*
Ityococcus – g/g *Trionymus*
Kalaginella – g/g *Metadenopus*
Kenmorea – g/g *Nipaecoccus*
Kermicus – g/g *Antonina*
Kissrhizoecus – g/g *Rhizoecus*
Lachnodiella – g/g *Paraputo*
Lacombia – g/g *Mirococcopsis*
Laingiococcus – g/g *Heterococcus*
Laminicoccus – g/g *Paraputo*
Lanceacoccus – g/g *Nipaecoccus*
Lanceacoccus – g/g *Paraputo*
Lankacoccus – g/g *Paraputo*
Lantanacoccus – g/g *Coccidohystrix*
Lenania – g/g *Mirococcopsis*
Leptococcus – g/g *Trionymus*
Leptorhizoecus – g/g *Rhizoecus*
Maconellicoccus – g/g *Pseudococcus*
Macrocepicoccus – g/g *Trionymus*
Maculicoccus – g/g *Trionymus*
Madagasia – g/g *Trionymus*
Madangiacoccus – g/g *Nipaecoccus*
Madeurycoccus – g/g *Mirococcopsis*
Malaicoccus – g/g *Allomyrmococcus*
Malekoccus – g/g *Phenacoccus*
Mammicoccus – g/g *Phenacoccus*
Marendellea – g/g *Trionymus*
Marottarhizoecus – g/g *Rhizoecus*
Mascarenococcus – g/g *Paraputo*
Mauricoccus – g/g *Trionymus*
Melanococcus – g/g *Nipaecoccus*
Metadenopus – g/g *Metadenopus*
Miconicoccus – g/g *Antonina*
Mirococcopsis – g/g *Mirococcopsis*
Miscanthicoccus – g/g *Neotrionymus*
Misericoccus – g/g *Metadenopus*
Mizococcus – g/g *Mirococcopsis*
Mollicoccus – g/g *Mirococcus*
Mombasinia – g/g *Puto*
Moystonia – g/g *Paraputo*
Mutabilicoccus – g/g *Paraputo*
Nairobia – g/g *Puto*
Natalensia – g/g *Mirococcopsis*
Neoclavicoccus – g/g *Pedronia*
Neoripersia – g/g *Neotrionymus*
Neosimmondsia – g/g *Mirococcus*
Neotrionymus – g/g *Neotrionymus*
Nesococcus – g/g *Trionymus*
Nesopedronia – g/g *Pedronia*
Nesticoccus – g/g *Antonina*
Nipaecoccus – g/g *Nipaecoccus*
Nudicauda – g/g *Mirococcopsis*
Octococcus – g/g *Phenacoccus*
Odacoccus – g/g *Paraputo*
Ohiacoccus – g/g *Trionymus*
Oracella – g/g *Trionymus*
Orococcus – g/g *Trionymus*
Orstomicoccus – g/g *Trionymus*
Oxyacanthus – g/g *Phenacoccus*
Palaucoccus – g/g *Mirococcopsis*
Palmicultor – g/g *Paraputo*

Paludicoccus – g/g *Antonina*
Pandanicola – g/g *Neotrionymus*
Papuacoccus – g/g *Pseudococcus*
Paracoccus – g/g *Pseudococcus*
Paradiscococcus – g/g *Mirococcopsis*
Paradoxococcus – g/g *Trionymus*
Paraferrisia – g/g *Trionymus*
Paramococcus – g/g *Heterococcus*
Paramonostherium – g/g *Nipaecoccus*
Paramyrmococcus – g/g *Allomyrmococcus*
Parapaludicoccus – g/g *Antonina*
Paraporisaccus – g/g *Antonina*
Paraputo – g/g *Paraputo*
Paraserrolecanium – g/g *Antonina*
Paratrionymus – g/g *Metadenopus*
Paulianodes – g/g *Antonina*
Pedrococcus – g/g *Pedronia*
Pedronia – g/g *Pedronia*
Peliococcopsis – g/g *Peliococcus*
Peliococcus – g/g *Peliococcus*
Pelionella – g/g *Peliococcus*
Peridiococcus – g/g *Antonina*
Perystrix – g/g *Phenacoccus*
Phenacoccus – g/g *Phenacoccus*
Phyllococcus – g/g *Trionymus*
Pilococcus – *g/g Mirococcopsis*
Planococcus – g/g *Trionymus*
Pleistocerarius – g/g *Paraputo*
Poecilococcus – g/g *Trionymus*
Porisaccus – g/g *Antonina*
Porococcus – g/g *Nipaecoccus*
Promyrmococcus – g/g *Allomyrmococcus*
Prorhizoecus – g/g *Rhizoecus*
Prorsococcus – g/g *Mirococcopsis*
Pseudantonina – g/g *Antonina*
Pseudoferrisia – g/g *Trionymus*
Pseudorhizoecus – g/g *Rhizoecus*
Pseudoripersia – g/g *Nipaecoccus*
Pseudotrionymus – g/g *Trionymus*
Puto – g/g *Puto*
Pygmaeococcus – g/g *Rhizoecus*
Quadrigallicoccus – g/g *Antonina*
Rastrococcus – g/g *Puto*
Renicaula – g/g *Trionymus*
Rhizoecus – g/g *Rhizoecus*
Rhodania – g/g *Metadenopus*
Ripersiella – g/g *Rhizoecus*
Rosebankia – g/g *Neotrionymus*
Sarococcus – g/g *Paraputo*
Scaptococcus – g/g *Mirococcus*
Serrolecanium – g/g *Antonina*
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Sinococcus – g/g *Mirococcus*
Spartinacoccus – g/g *Trionymus*
Sphaerococcus – g/g *Antonina*
Spilococcus – g/g *Pseudococcus*
Stemmatomerinx – g/g *Phenacoccus*
Stipacoccus – g/g *Mirococcus*
Strandanna – g/g *Trionymus*
Stricklandina – g/g *Paraputo*
Strombococcus – g/g *Nipaecoccus*
Synacanthococcus – g/g *Phenacoccus*
Syrmococcus – g/g *Metadenopus*
Tangicoccus – g/g *Antonina*
Tasmanicoccus – g/g *Trionymus*
Telocorys – g/g *Trionymus*
Thaimyrmococcus – g/g *Allomyrmococcus*
Tomentocera – g/g *Paraputo*
Trabutina – g/g *Nipaecoccus*
Tridiscus – g/g *Mirococcopsis*
Trimerococcus – g/g *Puto*
Trionymus – g/g *Trionymus*
Trochiscococcus – g/g *Trionymus*
Turbinococcus – g/g *Trionymus*
Tylococcus – g/g *Pedronia*
Tympanococcus – g/g *Trionymus*
Ventrispina – g/g *Nipaecoccus*
Villosicoccus – g/g *Trionymus*
Volvicoccus – g/g *Mirococcopsis*
Wapoacoccus – g/g *Antonina*
Williamsrhizoecus – g/g *Rhizoecus*
Yudnapinna – g/g *Paraputo*

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