

Phenacoleachia, *Steingelia*, *Pityococcus* and *Puto* – Neococcoids or Archaeococcoids? An Intuitive Phylogenetic Discussion Based on Adult Male Characters

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Abstract: The superfamily Coccoidea is divided into two informal groups, the archaeococcoids (essentially the more “primitive” families) and the neococcoids, including all of the more “advanced” or derived families. The former are mainly diagnosed by the possession of an XX-XO chromosome system and the presence of abdominal spiracles, whereas the latter have a Paternal Genome Elimination chromosome system and lack abdominal spiracles. Traditionally, the families Phenacoleachiidae, Steingeliidae, Pityococcidae and sometimes the Putoidae have been considered to belong to the archaeococcoids (*Phenacoleachia*, *Steingelia* and *Puto* have an XX-XO chromosome system). However, a recent phylogenetic study of all coccoid families based on the morphology of macropterous males has suggested that these four families form a monophyletic group with the neococcoids rather than within the archaeococcoids. The present paper discusses the phylogenetic relationships of these four families based on adult male characters, with particular emphasis on the structure of the wax-tail secreting organs which are significantly different in these four archaeococcoid families + the neococcoids (all of which have glandular pouches) compared with the remaining archaeococcoids (which lack glandular pouches but have tubular ducts). It is argued that these four families + neococcoids could have arisen as a separate lineage arising from ancestors close to the Ortheziidae + Matsucoccidae.

Key words: archaeococcoid, neococcoid, *Phenacoleachia*, *Steingelia*, *Pityococcus*, *Puto*, phylogenetic relationships

Introduction and basic phylogenetic relationships

The superfamily Coccoidea contains about 8000 species in some 33 extant families and 16 extinct families and these have been divided traditionally into two informal groups, the archaeococcoids and the neococcoids (GULLAN, COOK 2007). The latter form a monophyletic group supported by both morphological and genetic data, but the archaeococcoids, which currently include 15 extant families, appear to be non-monophyletic and almost all characters that define them are plesiomorphies and, so far, molecular and morphological studies have failed to support their monophyly.

A recent phylogenetic study (HODGSON, HARDY, 2013), based on the morphology of the fully-winged (macropterous) adult males, produced a well-resolved estimate of the phylogenetic relationships, particularly within the archaeococcoids. The current paper only considers the relationships of four of these families to the rest of the Coccoidea, namely Phenacoleachiidae, Steingeliidae, Pityococcidae and Putoidae (here referred to as the *Phenacoleachia*-group (note that the term ‘group’ in this essay is not intended to imply monophyly – the *Phenacoleachia*-group is only monophyletic in the context of the

neococcoids + these four families)). Traditionally, these four families (but with the possible exception of Putoidae) have generally been included in the archaeococcoids because of (i) the presence of abdominal spiracles in at least the adult female, and (ii) the possession of an XX-XO chromosome system. The classification and relationships of the members of the *Phenacoleachia*-group have been reviewed by HODGSON, FOLDI (2006) and GULLAN, COOK (2007).

As indicated above, the neococcoids are considered to be monophyletic and this is also clear based on adult male morphology as they have a number of significant synapomorphies that are absent on archaeococcoid males minus the *Phenacoleachia*-group. Among them are: (i) 1 or more pairs of simple eyes; (ii) presence of microtrichia (small setae-like structures) on the wings; (iii) presence of a pair of triangular plates laterad to the scutum, (iv) absence of abdominal spiracles, and (v) secretion of waxy tail filaments by one pair of lateral glandular pouches (on abdominal segment VIII) or two pairs (on segments VII and VIII). On the adult males of most archaeococcoids (i.e. without the above four families and here referred to as the margarodoid-group), the equivalent character states are: (i) compound eyes present; (ii) microtrichia absent; (iii) triangular plates absent, (iv) abdominal spiracles present, and (v) secretion of waxy tail filaments by groups of tubular ducts medially on the dorsum of the abdominal segments VI or VI and VII (with the exception of the Monophlebidae and Coelostomidiidae). So, what are the character states found on the adult males of the *Phenacoleachia*-group? In this group: (i) the compound eyes have been replaced by a band or line of 5-8 pairs of simple eyes on a large ocular sclerite; (ii) microtrichia are present; (iii) triangular plates are present, (iv) if abdominal spiracles are present (possibly in *Phenacoleachia* and *Steingelia*), then they are minute, and (v) the wax tail-extruding organs are pairs of glandular pouches posteriorly on the abdominal segment VIII (absent on Pityococcidae). This combination of structures on the latter four families strongly suggests that they share more character-states with the neococcoids than with the archaeococcoids and accounts for the relationships found in HODGSON, HARDY (2013).

The Monophlebidae + Coelostomidiidae (hereafter referred to as the M + C clade) differ from the remaining families in the margarodoid-group in

lacking tail-filaments (which appear to have been replaced by long caudal extensions from at least abdominal VIII in the Monophlebidae and longer penial sheaths in the Coelostomidiidae) and in having a membranous area medially on the scutum. Nonetheless, for the purposes of this paper, they are here included in the (polyphyletic) margarodoid-group. HODGSON, HARDY (2013) found the M + C clade as sister to the *Phenacoleachia* group + the neococcoids. This relationship was well supported (posterior probability 1.0). However, whilst there are many synapomorphies/symplesiomorphies that support the families within the margarodoid-group, and there are several synapomorphies which support the *Phenacoleachia*-group + neococcoids (as described above) (Fig. 1), there are few that support a sister relationship between the M + C clade and the neococcoids + *Phenacoleachia*-group (Fig. 1). The possible significance of this will be discussed later.

Conclusions. A. Based on the characters of the macropterous males, the families of the *Phenacoleachia*-group share a number of significant features with the neococcoids rather than the remainder of the archaeococcoids (margarodoid-group as defined here).

B. Despite the strong support for a sister relationship between the (*Phenacoleachia*-group + the neococcoids) and the M + C clade in HODGSON, HARDY (2013), there appear to be few synapomorphies supporting this relationship (Fig. 1).

Tail-filament secreting organs

Most adult male archaeococcoids and neococcoids secrete waxy filaments from the posterior end of their abdomen. It has been suggested that these filaments evolved in relation to dipterisation (KOTEJA, 1996, p.66) and may assist in their aerodynamics during flight, although there are species in both groups which lack them but are believed to fly well and so this may not be the whole story. However, the structure and distribution of the filament-secreting organs in the margarodoid-group and in the *Phenacoleachia*-group + neococcoids are significantly different and it is here considered that the importance of these differences has been overlooked.

In most of the margarodoid families (i.e. excluding the Monophlebidae and Coelostomidiidae), the tail filaments are stiff and glassy and are extruded from non-paired groups of ducts medially on abdominal tergites VI and VII (or just VII on Matsucoccidae

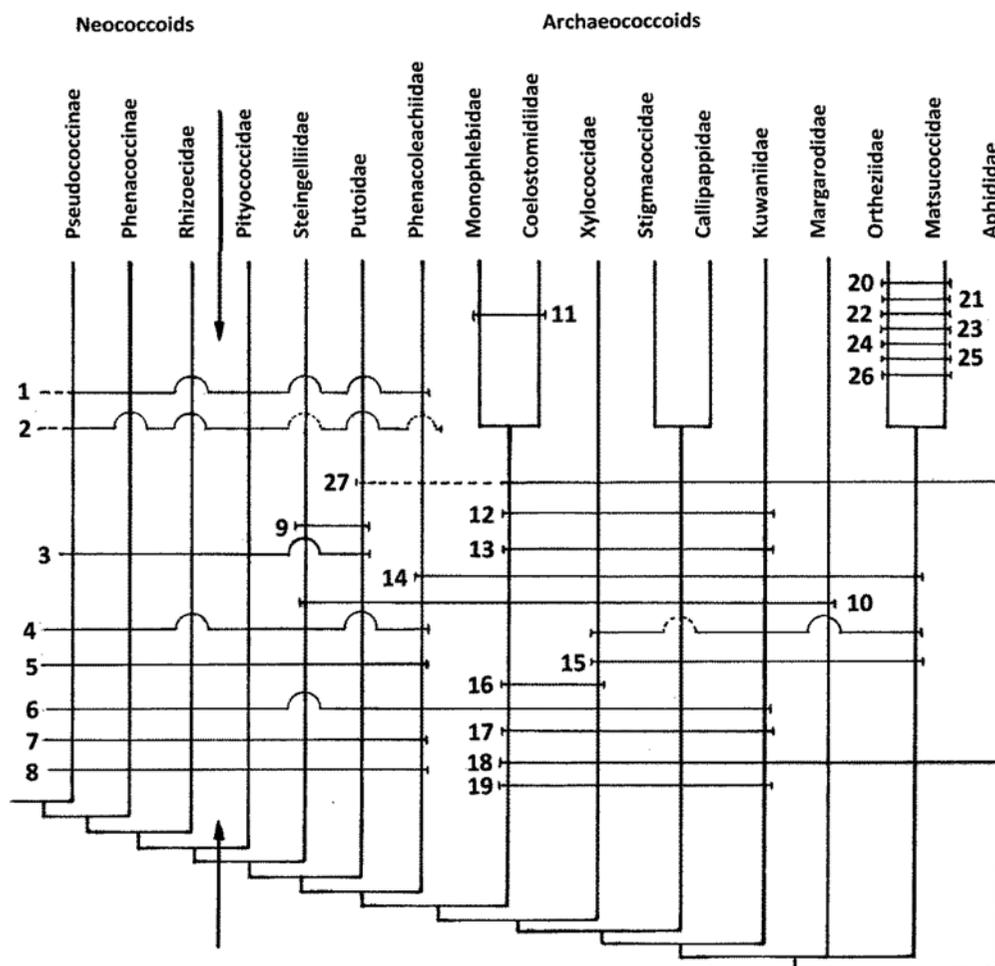


Fig. 1. A section of the tree from HODGSON, HARDY (2013) modified to show synapomorphies and symplesiomorphies for macropterous adult male characters. Where: 1 = presence of ostioles; 2 = presence of capitate setae on antennae; 3 = presence of prescutal apodeme; 4 = presence of glandular pouches; 5 = presence of microtrichia on the wings; 6 = tarsi two segmented; 7 = presence of triangular plate; 8 = presence of simple eyes; 9 = presence of abdominal sternite I; 10 = presence of endophallus; 11 = presence of membranous area on scutum; 12 = scutellum triangular; 13 = presence of membranous areas on scutellum; 14 = presence of postmesoprecoxal ridge setae; 15 = presence of tubular ducts medially on tergites VI and VII or just VI; 16 = presence of hairs; 17 = post-tergite long, extending longitudinally; 18 = presence of compound eyes; 19 = ridges ventrally on head forming 5-armed star; 20 = presence of abdominal sternite I; 21 = narrow mesopostnotum; 22 = trochanter campaniform pores in a line; 23 = narrow hamuli; 24 = presence of capitate setae on antennae; 25 = ventral head ridges represented by post-ocular and post-occipital ridges only, and 26 = tail extruding tubular ducts on tergite VII only

and Ortheziidae). Each duct is a large, cylindrical tubular duct, often with inner longitudinal ridges (Fig. 2), but without an inner ductule. These ducts occur in a group or band across the middle of the relevant tergite and each duct usually extends above the surface of the derm, rather like a short chimney. Whilst each group of ducts usually does have some associated setae, these are short and not thought to have any particular function with regard to the tail filaments, the stiffness of which is due to the glassy nature of the extruded wax. In the Monophlebidae and Coelostomidiidae, these filaments appear to have been replaced by either a rather elongate abdomen + penial sheath (Coelostomidiidae) or by one or more

pairs of finger-like extensions from the margins of the abdomen (Monophlebidae).

In the *Phenacoleachia*-group and the neococcoids, on the other hand, the tail filaments are extruded by one or two pairs of more or less invaginated glandular pouches, each of which has a large group of loculate pores and several associated long setae (Fig. 3). These glandular pouches are restricted to either side of segment VIII (or VII and VIII in the mealybug subfamily Phenacocccinae and many fossils). In the *Phenacoleachia*-group, these “pouches” tend to be broad and flat or very shallow, with several long setae. In the more derived families, such as the Coccidae, these pouches are

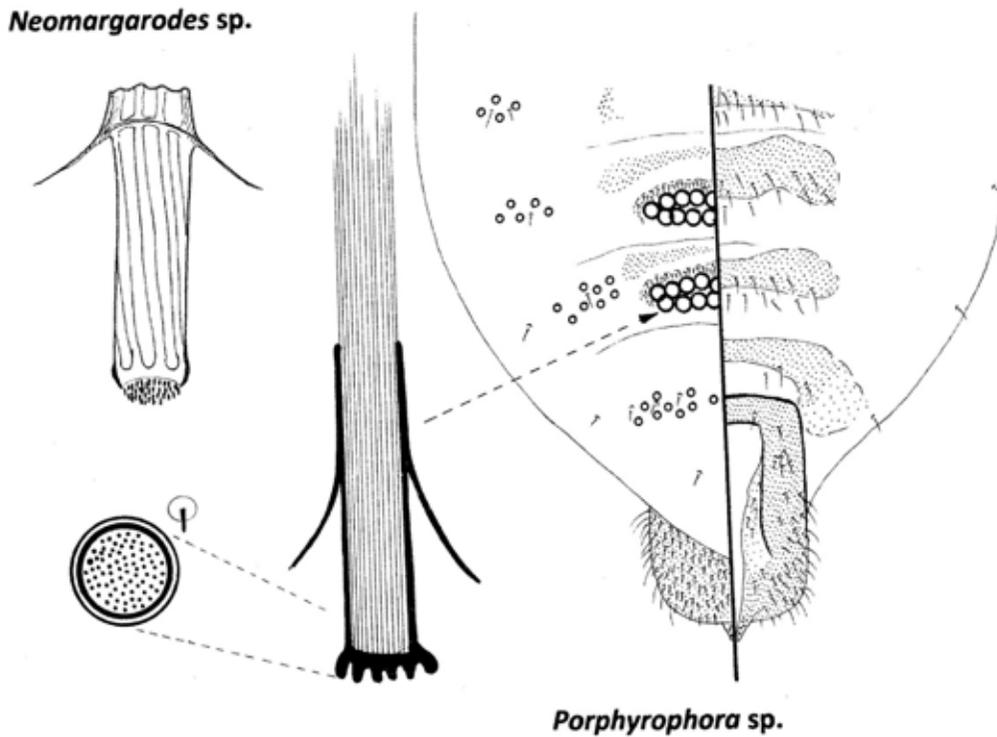


Fig. 2. Tail-filament extruding tubular ducts on tergites VI and VII in two genera of ground pearls (Margarodidae), as exemplars of the condition in most archaococcoid families

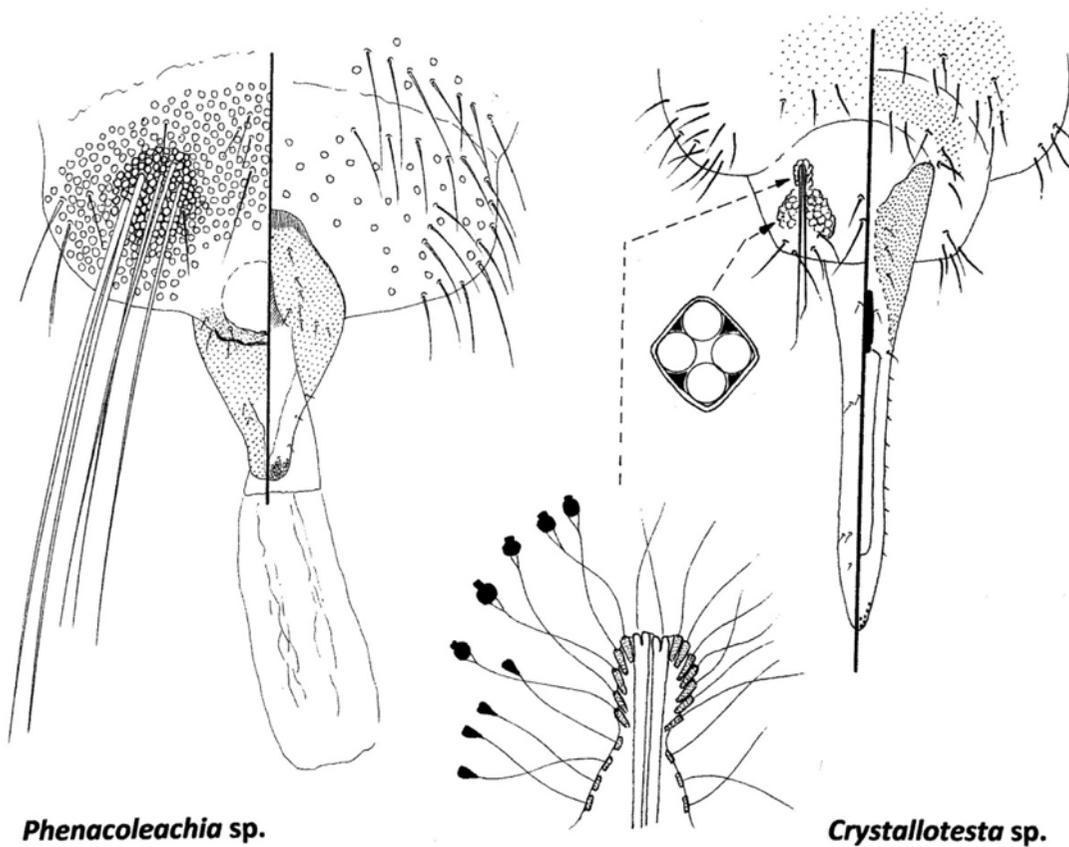


Fig. 3. Tail-filament extruding glandular pouches on segment VIII of *Phenacoleachia* sp. (Phenacoleachiidae) (from HODGSON, FOLDI (2006)) and *Crystallotesta* sp. (Coccidae) (HODGSON, HENDERSON, 2004) as exemplars of the condition in many neococcoids

more invaginated and can have a more complex structure (Fig. 3), consisting of two parts, an outer, more or less tubular or funnel-shaped section lined with loculate pores, and an inner chamber lined with more elongate pores. Both the loculate pores and the inner, more elongate pores have long, fine, rather distinctive inner ductules with small glandular apices. The extruded wax appears to be soft and rather woolly and the purpose of the long glandular pouch setae appears to be to support the waxy filament as it is extruded.

Thus, both the structure of the actual wax of which the filaments are composed and the structure of the organs which extrude them are quite different in the neococcoid + *Phenacoleachia*-group compared with those in the margarodoid-group. It is here considered that the structure and distribution of these two types of tail-filament secreting organs are likely to have evolved separately, i.e. once in the ancestor of the margarodoid-group and once in the ancestor to the non-margarodoid families. In other words, it is considered very unlikely that the paired glandular pouches found in most non-margarodoid families (including the *Phenacoleachia*-group) evolved from the non-paired structures found in the margarodoid families (or vice versa) because, not only are the abdominal segments on which they occur not the same, the actual structure of the organs is significantly different. Thus, although the relationships suggested by HODGSON, HARDY'S (2013) study indicate that the tail-forming structures found in the *Phenacoleachia*-group + neococcoids evolved from a common ancestor with the M + C clade, this is here considered very unlikely. Although no fossils of either Phenacoleachiidae or putative members of the M + C clade have been described to date, there are no known fossils that show intermediate stages between these two tail-forming structures and it is difficult to see what form such intermediates might take.

Conclusion. The structure and distribution of the tail-extruding organs found in the margarodoid-group and in the *Phenacoleachia*-group + neococcoids are very different, as is the actual wax produced. It is here considered that it is highly unlikely that either of these groups could have evolved from the other, suggesting that the two groups evolved separately at an early stage in the evolution of the Coccoidea.

Two (or more) separate scale insect lineages?

JAN KOTEJA (1974) found that adult female *Phenacoleachia zealandica* (Maskell) have a four-segmented labium and GULLAN, COOK (2001) found the same in the first-instar nymph. This is the only species of Coccoidea in which this state is known (all other taxa have 3 or fewer labial segments, including *Phenacoleachia australis* (BEARDSLEY, 1964)) but four-segmented labia are typical of most other Sternorrhyncha. KOTEJA (1974) considered that *Phenacolechia* must be ancient and sister to the rest of the extant coccoids because of the plesiomorphic condition of its labium. In addition, KOTEJA *et al.* (2003) studied the structure of the ovary of *Steingelia gorodetskia* Nasonov and concluded that it was "primitive" and suggested a close relationship with Ortheziidae, Xylococcidae and Matsucoccidae and with other non-coccoid Sternorrhyncha. Thus, both of these studies suggest that some members of the *Phenacoleachia*-group possess plesiomorphies that are either otherwise unknown in the rest of the Coccoidea (but typical of other Sternorrhyncha) or apparently restricted to some of the taxa arising from the basal nodes in HODGSON, HARDY'S (2013) study, i.e. the Margarodidae *sens. str.*, Matsucoccidae and Ortheziidae. The most recent molecular study (GULLAN, COOK, 2007) recovered all included archaeococcoid families (including *Phenacoleachia*, *Steingelia*, *Pityococcus* and *Puto*) in a single polytomy. Thus, to date, molecular studies have offered little insight into the close relatives of the *Phenacoleachia*-group other than that they do not fall within the neococcoids (*sens. str.*).

It was noted above that the synapomorphies that linked the *Phenacoleachia*-group + neococcoid clade to the margarodid-group (Fig. 1) were few and that none linked just the M & C clade with either just *Phenacoleachia* or with the *Phenacoleachia*-group. Those that occurred in both *Phenacoleachia* and the M + C clade were also found in most of the other margarodoid families (Fig. 1). In other words, these synapomorphies would apply even if the *Phenacoleachia*-group + neococcoids arose as a separate branch from a node much lower down in HODGSON, HARDY'S cladogram. What happens if one considers the *Phenacoleachia*-group + neococcoids to be a completely separate lineage to the remaining archaeococcoids (i.e. separate from the (paraphyletic) margarodoid-group)? This is what

is suggested by the two types of wax-tail secreting organs evolving as separate lineages, arising from a common (unknown) ancestor. Indeed, KOTEJA (1996), in his “Day after” paper, also considered that both tail-secreting organs were already present on “the day after”. The scenario suggested here fits with *P. zealandica* having a four-segmented labium and with *S. gorodetskia* having a “primitive” ovary, similar to that in other Sternorrhyncha. Studies on the chromosome systems have shown an XX-XO chromosome system in *Phenacoleachia* (BROWN & CLEVELAND, 1968), *S. gorodetskia* (NUR, 1980) and in *Puto* (HUGHES-SCHRADER, 1944), as in the margarodoid-group. Thus, under the two lineage scenario, the ancestor to both lineages (the *Phenacoleachia*-group + neococcoid lineage and the margarodoid-group lineage) would have had an XX-XO chromosome system. The neococcoids, therefore, must have evolved their paternal genome elimination system as they evolved from a common ancestor with the *Phenacoleachia*-group. In addition, with the removal of the *Phenacoleachia*-group from the archaeococcoids, it could be argued that the remaining archaeococcoid families (i.e. what is here referred to as the margarodoid-group – including the ortheziid and matsucoccid clade, the Margarodidae *s.s.* and the remaining archaeococcoids) are monophyletic, with all sharing at least one significant synapomorphy, the structure of the wax-extruding organs on the posterior abdomen. Admittedly, the M + C clade lacks filament-extruding organs but the cladogram of HODGSON, HARDY (2013) suggests the rest of the margarodoid-group as sister to the M + C clade, i.e. that, with the removal of the *Phenacoleachia*-group + neococcoids, the M + C clade falls within the margarodoid-group.

What is being suggested, therefore, is that the *Phenacoleachia*-group + neococcoids arose as a separate lineage from early ancestors of the Coccoidea. This is very close to the cladograms in MILLER (1984) and in DANZIG (1986). In MILLER’s early preliminary cladistics study based on a range of characters including morphology, life history traits and symbionts, etc., *Phenacoleachia*, *Pityococcus*, *Puto* + the neococcoids formed a clade arising from a common ancestor with the Ortheziidae – and with the archaeococcoid families forming a separate clade. However, MILLER had *Steingelia* + *Stomacoccus* sister to *Matsucoccus* + Margarodidae *s.s.* in the latter clade.

DANZIG (1986, fig. 18), in her intuitive study, also had the Margarodidae *s.l.* as sister to a clade formed from Ortheziidae + *Phenacoleachia* + neococcoids but she did not discuss *Pityococcus* and *Steingelia* (*Puto* was included in the Pseudococcidae).

If the *Phenacoleachia* group + neococcoids do form a separate lineage, to which taxon was their ancestor most close? In the cladistic analyses for HODGSON, HARDY’S (2013) study, the basal node was a polytomy with three branches, the Margarodidae (*sensu stricto*), an Ortheziidae + Matsucoccidae clade, and the remainder of the Coccoidea. With regard to the present discussion, there are quite a few synapomorphies shared by the members of the *Phenacoleachia*-group + neococcoids and either Ortheziidae or Matsucoccidae or both (Fig. 4). Of the latter, those for the adult males are: (i) antennal capitate setae – within the margarodoid-group, capitate setae on the antennae are only known in the Ortheziidae (VEA, on an undescribed male, pers. com.) and Matsucoccidae but are an important feature of all neococcoid families (with the possible exception of the Rhizoecidae) and are also found in *Pityococcus* and *Stomacoccus* (and possibly *Steingelia*); (ii) capitate claw digitules are only known in Matsucoccidae and Coelostomidiidae in the margarodoid-group but are typical of many neococcoids and are also found on *Phenacoleachia* and *Steingelia*; (iii) post tergites – all members of the margarodoid-group have extremely large post-tergites which extend longitudinally along the prothorax, but these are much less well developed in species of *Orthezia* and *Newsteadia* and are generally small and more nearly transverse (or even absent) in the *Phenacoleachia*-group and neococcoids; (iv) trochanterofemur articulation – in the Ortheziidae, this is almost at right angles to the leg, as in *Phenacoleachia* but not in other taxa; (v) the campaniform sensilla on each side of the trochanter of ortheziids and *Matsucoccus* are more or less in a straight line, quite unlike the scattered arrangement found in the rest of the margarodoid-group but similar to the arrangement in *Steingelia* and *Pityococcus* and, although not the arrangement in the Rhizoecidae, Pseudococcidae and many “eriococcids”, this is the arrangement in the remaining neococcoids; and (vi) genital segments – although the basic structure of the penial sheath in all Coccoidea is similar (consisting of two lateral sclerotizations joined dorsally and ventrally by mem-

branes, probably having evolved from partial fusion of the two claspers in the Aphidoidea), the structure of the penial sheath of Matsucoccidae, *Steingelia* and Putoidae is remarkably similar (and this was also remarked on by BEARDSLEY (1968, p. 1458)). A possible problem with this two lineage scenario is the presence of a cyst stage in the life cycle of Steingeliidae. However, Matsucoccidae also have a cyst stage, suggesting a possible connection between *Steingelia* and the Ortheziidae + Matsucoccidae clade in HODGSON, HARDY (2013) and as suggested in the cladogram of MILLER (1974). Thus, although the phylogenetic relationships of members of the *Phenacoleachia*-group have been uncertain (even as early as MORRISON, 1928, p.8), most recent studies (e.g., GULLAN, COOK, 2007), have found members of this group to be sister to one or other of the Ortheziidae, Matsucoccidae or Margarodidae.

With regard to the adult females, Ortheziidae have well-developed mouthparts and a well-developed anal ring with setae and pores, quite unlike that of any other margarodoid archaeococcoid but very similar to the anal ring of adult females of *Phenacoleachia*, Putoidae and the neococcoids, all of which normally have setae and pores. (Adult females of *Matsucoccus* have no mouthparts and do not feed and may even lack an anus (MORRISON, 1928; FOLDI, 2004). However, *Steingelia* and *Pityococcus* differ as both have short anal tubes without setae or pores, even though the adult female of *Steingelia* lacks mouthparts. The possible importance of the structure of the anal ring and its significance with regard to Coccoidea evolution has been emphasised by MILLER (1984), DANZIG (1986) and GULLAN (pers. comm.).

How does this theory fit with the fossil record? As KOTEJA (2001) pointed out, almost all the earliest fossils are adult males and are clearly already members of this superfamily and many can even be placed in families recognisable today. Thus, the earliest fossil coccoids are from rock compression impressions and are a little over 125 my old (*Eomatsucoccus*, Matsucoccidae). However, most fossil scale insect specimens have been found in amber and these have provided the best fossil records for insects for the last 120 my (GRIMALDI, ENGEL, 2005; VEA, in prep.). Currently, the earliest amber specimens are from Lebanese amber (Table 1), about 125 my old. Until recently, these had included only

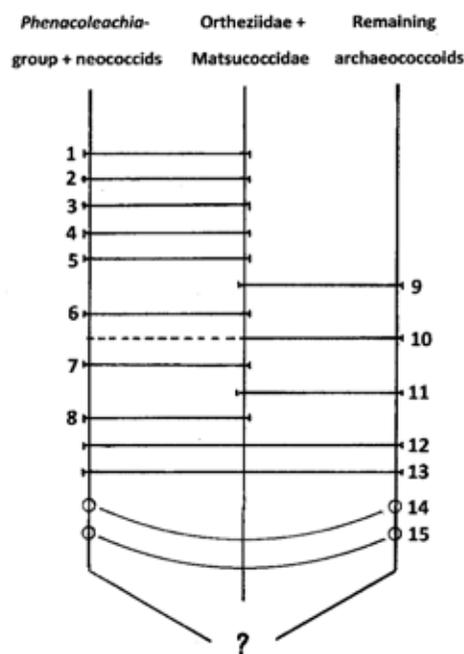


Fig. 4. Hypothetical tree with three lineages, showing synapomorphies and symplesiomorphies for macropterous adult male characters for at least one member of the *Phenacoleachia*-group and the other lineages. Dotted line: presence of abdominal spiracles in *Phenacoleachia*-group uncertain; curved lines show synapomorphies for the *Phenacoleachia*-group and remaining archaeococcoids only. Where 1 = ridges on ventral surface of head not forming a 5-armed cross; 2 = articulation between trochanter and femur at right angles in *Phenacoleachia*; 3 = penial sheath with strong, narrow lateral ridges and wide membranous areas; 4 = trochanter campaniform pores more or less in a line; 5 = claw digitules capitate; 6 = post-tergite small and not extending longitudinally; 7 = presence of capitate setae on antennae; 8 = presence of abdominal sternite I; 9 = presence of compound eyes; 10 = presence of abdominal spiracles; 11 = presence of tubular ducts on at least abdominal tergite VII [bar the M + C clade]; 12 = presence of a cyst stage in the life cycle; 13 = presence of postmesoprecoxal ridge setae; 14 = presence of an endophallus, and 15 = presence of satellite setae

ortheziids (*Cretorthezia*), a possible monophlebid, some steingeliids (*Palaeosteingelia*) and putoids (*Palaeotupo*) (GRIMALDI, ENGEL, 2005; KOTEJA, AZAR, 2008). However, recently (VEA, unpublished thesis, Aug. 2013) has described two new genera of Pseudococcidae, one from Lebanese amber (ca 125 my) and the other from Burmese amber (ca 105 my). Both appear to be referable to the Phenacoccinae! Thus the Lebanese specimen is as old as most of the earliest known archaeococcoid fossils. KOTEJA'S and VEA'S studies have shown that families with bands of simple eyes (as in the *Phenacoleachia*-group) were much more common in the Cretaceous than they are today (Table 1). Indeed, of these, only the four families within the *Phenacoleachia*-group survive today

Table 1. Records of Coccoidea (mainly families) since the Jurassic, where – = absent; + = present, and +++ = abundant. Table modified after KOTEJA (2000, p. 213) but with eras and time scales modified after ANONYMOUS (2014) and with some of VEA'S (2013) unpublished records, particularly of Pseudococcidae, from the Lower Cretaceous

Family	Jurassic 201-145 my	L. Cretaceous 145-100 my	U. Cretaceous 100-66 my	Palaeocene +Cenozoic 66-2.6 my	Quaternary 2.6-0 my
<i>Mesococcus asiaticus</i>	**				
ARCHAEOCOCCOIDS (Orthezioidea)					
With compound eyes					
Ortheziidae	-	+	+	+	+
Matsucoccidae	-	+	+	+++	+
†Jerseycoccidae	-	-	+	-	-
†Arnoldidae	-	-	-	+	-
Margarodidae	-	+	-	++	++
†Lebanococcidae	-	+	-	-	-
†Hammanococcidae	-	+	-	-	-
†Burmacoccidae	-	+	+	-	-
†Grohnidae	-	-	-	+	-
†Weitschatidae	-	-	-	+	-
†Serafinidae	-	-	-	+	-
Kuwaniidae					
†Hoffeinsia	-	-	-	+	-
Xylococcidae	-	+	+/-	++	+
Monophlebidae	-	+?	+	+	+
Other families	-	-	-	-	5
Total	0	6?	5	10	10
Without compound eyes					
†Grimaldiellidae	-	-	+++	-	-
†Electrococcidae	-	-	+	-	-
†Apticoccus	-	+	--	-	-
†Turonococcus	-	-	+	-	-
†Albicoccidae	-	+	-	-	-
Steingelliidae	-	+	+	++	+
Pityococcidae	-	-	-	*	+
Putoidae	-	+	-	++	+
†Labiococcidae					
†Solicoccus	-	-	-	+	-
†Kukaspidae	-	-	+	-	-
†Pennygullaniidae	-	+	-	-	-
Phenacoleachiidae	-	-	-	-	+
Total	0	5	4	3	4
NEOCOCCOIDS (Coccoidea)					
Pseudococcidae	-	+	+	+	+++
Eriococcidae	-	-	+	++	+++
Inkaidae	-	-	+	+	-
Kermesidae	-	-	-	+	+
Coccidae	-	-	+	+	+++
Diaspididae	-	-	-	+	+++
Only recent families (about 10)	-	-	-	+	ca10
Total	0	1	4	7	15

and all except *Puto* would appear to be relicts of an earlier age.

Conclusion. Based on the data presented here, particularly regarding the two different tail-filament extruding systems, it is argued that the *Phenacoleachia*-group + neococcoids could have arisen as a separate lineage to the families here included in the margarodoid-group, each lineage having evolved its own tail-filament extruding system. This dichotomy is here considered to have evolved early on in the evolution of the Coccoidea and this appears to be increasingly supported by fossil evi-

dence. It is also argued here that there are a number of synapomorphies linking the *Phenacoleachia*-group + neococcoids and the Ortheziidae and/or Matsucoccidae and that these could have shared a close common ancestor.

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