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Phenacoleachia Cockerell (Hemiptera: Coccoidea: Phenacoleachiidae) re-visited

Abstract - The small and enigmatic family Phenacoleachiidae is of phylogenetic interest due to its combination of derived and ancestral features and its very restricted distribution in the southern hemisphere. Previous studies have placed it with the archaeococcoids (Margarodidae *sensu lato* and Ortheziidae) or near the mealybugs (Pseudococcidae). This study re-describes and illustrates the first-instar nymph of *Phenacoleachia zealandica* (Maskell) and re-considers the relationships of *Phenacoleachia* as indicated by morphology and molecular data. Phylogenetic analysis of nuclear small-subunit ribosomal DNA suggests that *Phenacoleachia* is not closely related to the Pseudococcidae. The features that *Phenacoleachia* shares uniquely with Pseudococcidae either may be plesiomorphies that have been lost in more derived groups or may be convergent structures.

Key words: *Phenacoleachia*, Phenacoleachiidae, Pseudococcidae, mealybugs.

INTRODUCTION

Phenacoleachia Cockerell contains two described species, *P. zealandica* (Maskell) and *P. australis* Beardsley, restricted to New Zealand and two subantarctic islands, respectively (Miller & Gimpel, 2001). This genus is usually placed in its own family because, although it shares some features with mealybugs (Pseudococcidae), it also possesses a number of unique features plus many plesiomorphies. The relationships of the Phenacoleachiidae were reviewed by Cox (1984), who concluded that the Phenacoleachiidae and Pseudococcidae may be sister groups based on apparent synapomorphies of the adult females, namely the presence of trilocular pores of a characteristic swirled form, lateral wax filaments and dorsal ostioles (*Puto* Signoret was treated as part of Pseudococcidae). *Phenacoleachia* also was postulated as the sister group of the pseudococcids plus *Puto* in a cladistic analysis of morphological data from adult females, adult males and first-instar nymphs in an analysis also including eriococcids, kermesids and margarodids (Miller & Miller, 1993a). In contrast, Borchsenius (1958), Koteja (1974a,b; 1996) and Danzig (1980) have placed *Phenacoleachia* among the archaeococcoids because of its plesiomorphic morphology (see last section of this paper). Koteja (1974a) reviewed the widely diverse suggestions for the affinities of *Phenacoleachia* and, based on his study of scale insect mouthparts, concluded that the genus represented a relict member of an archaic group of scale insects.

The type species *P. zealandica* was described by Maskell (1891) based on adult females, adult males and one poorly-cleared, slide-mounted first-instar nymph; subsequently, the species was redescribed by Morrison & Morrison (1922) using the same Maskell slides and thus their description of the first-instar nymph is very brief. Beardsley (1964) described the second species, *P. australis*, based on adult females, penultimate instar females and adult males from Auckland and Campbell Islands, but first-instar nymphs were not mentioned. The relationships of *Phenacoleachia* are revisited here because additional data are available following the collection of live adult females and crawlers of *P. zealandica* for molecular and further morphological study. The first-instar nymph is redescribed and unusual features of the mouthparts and tracheal system are reported. Other features of the crawler and adult female are discussed.

MATERIALS AND METHODS

The terms used follow Beardsley (1964) and Gullan and Sjaarda (2001) for general morphology and Koteja (1980) for the antennal sensilla. Specimens were identified as *P. zealandica* by reference to Maskell's syntypes in the New Zealand Arthropod Collection (NZAC), Landcare Research, Auckland. Although adult females from all localities appeared identical, some first-instar nymphs from near Springs Junction and the one nymph from the W.M. Maskell collection in NZAC had a slightly shorter apical segment to the labium than nymphs from Lake Rotoiti (120-145 µm vs 145-160 µm). The following specimens were studied: NEW ZEALAND, South Island: 1 adult female, 1 first-instar nymph, Maskell syntypes, from Reefton district (NZAC); 2 adult females, 13 first-instar nymphs, BR, Lake Rotoiti, St Arnaud, 41°48'S, 172°52'E, 31 Jan. 2000; 1 adult female, 5 first-instar nymphs, BR, *c.* 4 km N of Springs Junction, 42°18'S, 172°11'E, 30 Jan. 2000; 2 adult females, BR, *c.* 7 km SW of Reefton, 42°09'S, 171°48'E, 2 Feb. 2000; 1 adult female, NN, Harwood Hole, 40°57'S, 172°53'E, 3 Feb. 2000, PJG. Other than the Maskell types, all collections were made by P.J. Gullan on the trunks of *Nothofagus fusca* (Hook. F.) Oerst., mostly under loose bark. Slides were prepared by P.J. Gullan and are housed in the Bohart Museum of Entomology, University of California, Davis, USA.

RESULTS AND DISCUSSION

First-instar nymph (Fig. 1; structures drawn ventromarginally may be marginal in the live nymph).

Mounted material. Body elongate-oval, sides usually parallel, 1.33-1.48 mm long, 0.50-0.58 mm wide, cuticle of abdomen with microtrichia medially on venter and dorsum.

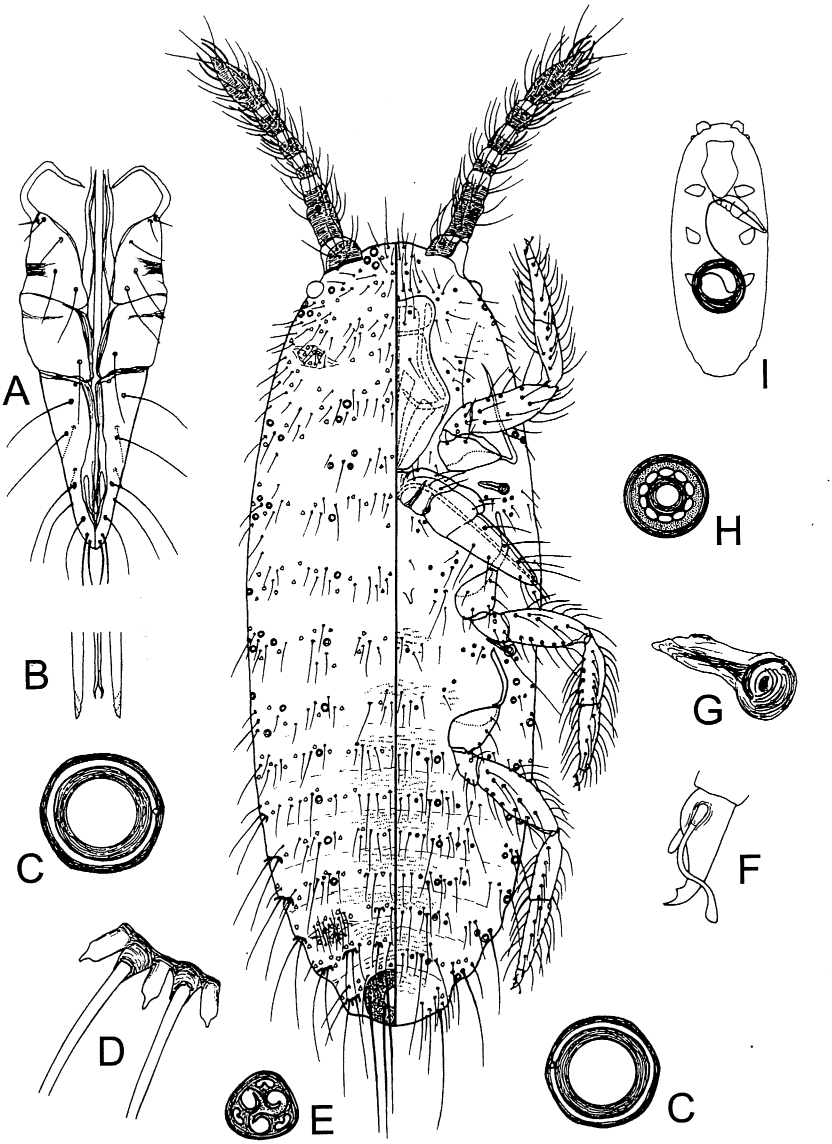
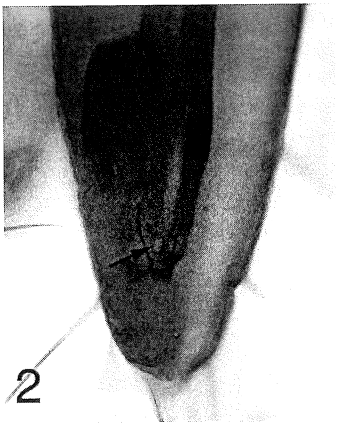
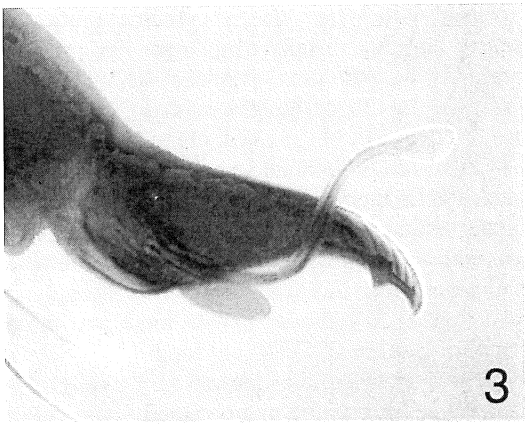


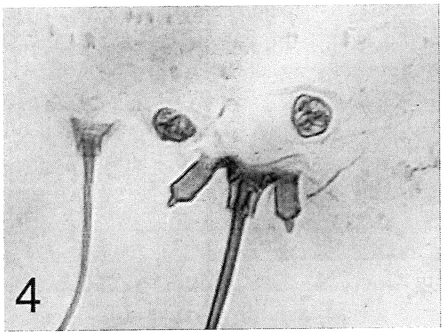
Fig. 1 - First-instar nymph of *Phenacoleachia zealandica* (Maskell); dorsum on left, venter on right. Enlargements (not drawn to scale): A. Ventral view of labium; B. Apex of splayed stylets; C. Cicatrix; D. Bases of two dorsal setae with evaginated cylindrical tubes; E. Trilocular pore; F. Claw with digitules; G. Metathoracic spiracle. H. Multilocular disc pore. I. Outline of body showing position of coiled stylets in relation to other mouthparts and to leg bases in slide-mounted nymph.

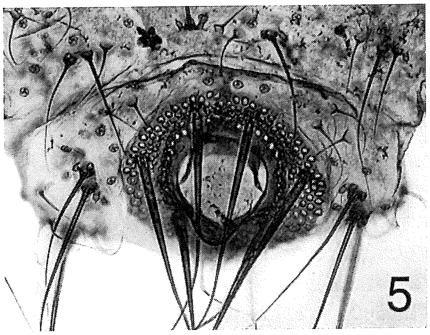
Venter. Antenna robust, 7-segmented; apical segment longest, 130-140 µm long, 45-50 µm wide; basal segment broadest, 50-65 µm long, 75-90 µm wide; sclerotized parts of segments covered with hair-like setae (trichoid sensilla) 40-90 µm long; 1 hair-like seta 65-75 µm long at antennal apex; apical segments with thin-walled pegs (also called antennal bristles or fleshy setae) as follows: 1 peg 40-50 µm long on each of segments V and VI, 4 pegs 50-65 µm long near apex of VII; membranous lateral half of segment I and apical/intersegmental parts of segments III-VI devoid of setae except for 2 intersegmental sensilla 10-12 µm long on lateral membrane distally on segment IV; a campaniform sensillum dorsally on segment II. Eyespot, 30-42 µm across greatest width, marginal, just posterolateral to antennal base. Labium large, conical-elongate, 280-340 µm long, 100-130 µm wide, 4-segmented, basal segment narrow, apical segment longest (120-160 µm), with 2 pairs of blunt-tipped sensory pegs, 38-43 µm long, near apex; other labial setae hair-like, 45-80 µm long, mostly confined to ventral surface (only 2 pairs clearly dorsal), apical setae absent; paired apical organ well developed (Fig. 2). Stylets long and robust, coiled inside body. Clypeolabral shield only slightly longer than labium, 350-400 µm long, 200-240 µm wide. Legs well developed, stout, with many setae; trochantin well developed, 200-240 µm long on fore legs, 70-105 µm long on mid legs and 100-135 µm on hind legs; trochanter with a very long seta, 140-170 um long, on apical ventral margin and 2 circular campaniform sensilla on each face; tibia and tarsus longest on hind legs, each about 120-135 µm; tarsal digitules not developed; claw (Fig. 3) slender, 35-40 µm long, with a well-defined denticle, 1 spatulate digitule (slender, usually curved and with apical expansion) 30-45 µm long, extending to or beyond apex, and 1 short, finger-like, bluntly rounded digitule 10-20 µm long. Thoracic spiracles small, 55-75 µm long, 27-30 µm wide, with an elongate peritreme and an atrium lacking pores. Abdominal spiracles indistinct, but stigmatic tracheae apparently in 7 or perhaps 8 pairs with a fine trachea contacting marginal cuticle on each side of segments. Cicatrices irregularly circular, 8.0-12.5 µm wide, present adjacent to longest abdominal setae, 2-3 pairs per segment except absent on last segment, lining up in 1-2 marginal and 1 submedial longitudinal rows on each side of abdomen, and also a few marginally on thorax just lateral to coxae and sometimes one near eye. Trilocular pores, 5-6 µm across, each with 3 inner loculi and 3 small outer loculi, in marginal areas only. Multilocular disc pores 6-7 µm wide, in irregular row of 1-7 pores per abdominal segment and in small scattered groups on head and thorax. Setae flagellate, of 2 sizes: (i) 112-200µm long, 2 pairs per abdominal segment with setae lining up in 1 marginal and 1 submedial longitudinal row on each side of abdomen, plus some long setae on thorax and head; (ii) 35-65 µm long, in irregular transverse rows on abdomen but more scattered on head and thorax.

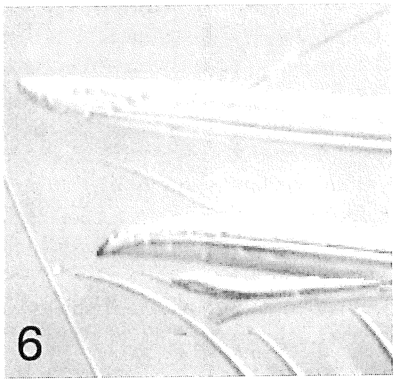
Dorsum. Two pairs of ostioles present; posterior pair more developed than anterior pair. Cicatrices similar to those of venter, 1 pair per anterior abdominal segment (absent on last 3 segments), but singly and in small groups on head and thoracic segments, with those on abdomen lining up to form a submedial longitudinal row continuous with submedial cicatrices on thorax. Trilocular pores, similar to those of venter but more numerous, in irregular rows or clusters among setae on all segments. Multilocular disc pores absent. Setae flagellate, of 2 kinds: (i) 65-155 µm long and with base

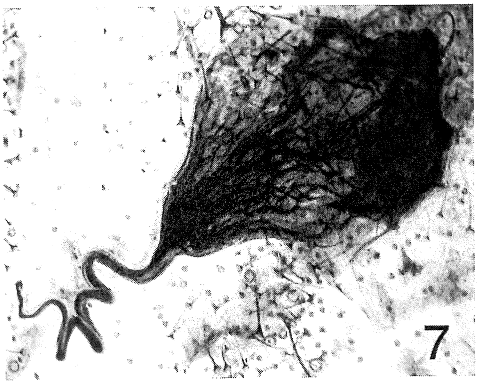












Figs 2-6 - First-instar nymph of *P. zealandica*: 2. Apex of labium showing apical organ (indicated by arrow); 3. Claw showing denticle and two kinds of digitules; 4. Trilocular pores and dorsal setae, one with associated evaginated tubular structures; 5. Anal ring; 6. Apex of stylets, separated to show serrated tips of mandibles.

7. Adult female of *P. zealandica*: structure in reproductive tract that contains sperm bundles.

associated with 1-2 evaginated cylindrical tubes, 7-10 µm long and *c.* 3 µm wide, each tapering abruptly distally to a finger-like prolongation of apex (Fig. 4), found only marginally on abdominal segments III-VIII and transversely on abdominal segments V-VII; (ii) 25-110 µm long, similar to shorter of ventral setae, in irregular transverse rows on abdomen but more scattered on head and thorax.

Apex of last abdominal segment with very weakly developed anal lobes, each with a pair of apical setae, 210-270 µm long, homologous with longest ventromarginal setae of other abdominal segments. Anal opening apical to subapical on dorsum, 43-52 µm across. Anal ring (Fig. 5) 105-120 in maximum width, sclerotized and with about 300 small pores, each 2-4 µm wide, in 5-6 irregular-packed concentric circles forming a broad ring 25-35 µm across, with inner part more sclerotized than outer part; 3 pairs of anal ring setae, 225-270 µm long.

The stylets of the crawler are very long (10.4-10.7 mm if fully extended; or 8.3-8.6 times as long as the nymph's body) and coiled internally with the crumena rolled so that it is in the perpendicular plane of the body inside the posterior thorax and anterior abdomen. The natural orientation is not clear from balsam-mounted crawlers, but is obvious in the ethanol-preserved specimens. Long stylets coiled in a crumena occur in the New Zealand margarodid genera *Coelostomidia* Cockerell, *Platycoelostoma* Morrison and *Ultracoelostoma* Cockerell, but in these groups the crumena lies at a more oblique angle to the perpendicular and the stylets are slightly shorter and, in some species, less robust than in *Phenacoleachia*. The occurrence of such long, strong stylets in these New Zealand taxa may be an ecological convergence associated with reaching the phloem when feeding on the trunk of *Nothofagus* and other trees or woody shrubs. In a few slide-mounted crawlers of *P. zealandica*, the stylets had separated and one pair (assumed to be the mandibles) are larger and resemble cutting blades (about 8 µm in their widest dimension, 5 µm in the other dimension) with small serrations apically (Fig. 6). The shape and great length of the stylets suggest that the nymphs probe deeply into the substrate on which they feed.

The claw digitules of *P. zealandica* are unusual in that one of the pair is much reduced in length and of unique shape; in the first-instar nymph this digitule is thumb-like but in the adult female it resembles a short second claw. Koteja (1985) considered whether this unusual digitule might represent a remnant claw or a modified digitule, or even whether the paired digitules of most scale insects might be modified lateral claws and the structure that coccidologists call the claw might be a median claw, empodium or homologous structure.

A substance (probably haemolymph) that stained strongly in acid fuchsin was observed exuding from both pairs of ostioles of one crawler that had been cleared and then stained without piercing the body; the posterior ostioles had more of this substance than the smaller anterior ostioles.

The first-instar nymph has a tracheal network in the abdomen with a double longitudinal tracheal branch on each side with a finer trachea extending laterally in each segment. In one specimen, at least seven pairs were visible and the tracheae touched the cuticle marginally, although stigmatal openings were very small and difficult to visualise. The anal ring of the first-instar nymph most closely resembles that of ortheziid crawlers, although there are a greater number of pores in the anal ring of *Phenacoleachia*, and many more than the number found in mealybug crawlers, which usually have one to two rows only. Borchsenius (1958) also noted the similarity of the phenacoleachiid and ortheziid anal ring.

Adult female

Seven of eight slide-mounted adult females of *P. zealandica* that we examined had a lightly sclerotized sac-like structure (Fig. 7) in their reproductive tract; the eighth female had been dissected open and all body contents removed. Each structure was relatively large (190-350 µm maximum length, 140-240 µm maximum width) with a coiled tube at the end closest to the vulva and evidence of internal longitudinal partitions, which may have held the sperm bundles. Evidence of sperm bundles or their remnants were seen inside the structure in one female. The occurrence of this kind of genital structure (a spermatophore if male-derived or a spermatheca if female-derived) does not appear to have been reported in the coccidology literature, although the long, narrow sperm bundles of some coccoids have been relatively well studied and many have a sheath modified anteriorly into a hardened corkscrew (Robison, 1977). Apparently the retention of spermatophores (in the form of sperm bundles or sperm-bundle sheaths, often aggregated together) in female scale insects is a rather common phenomenon and spermatophores have been preserved even in impression fossils from the Lower Cretaceous (Koteja, 1998; Koteja, pers. comm.). The vulva of the adult female of *P. zealandica* is surrounded by four elongate apodemes, as in *Platycoelostoma* and *Callipappus* (Gullan & Sjaarda, 2001). These apodemes possibly serve as attachment points for muscles that control the opening of the vulva during copulation. Females appear to be ovoviviparous because fully developed embryos were present in dissected females and live females produced nymphs without laying eggs, although birth was not actually observed.

The shorter of the two claw digitules is variable in shape and length, apparently due to wear with age, because this variation occurs among females collected within a few metres of each other. The tracheal system in the abdomen is similar to that in the crawler, with fine tracheae contacting the body margin segmentally.

Possession of trilocular pores with a swirled form were interpreted as one synapomorphy of *Phenacoleachia* and Pseudococcidae (Cox, 1984), however, the trilocular pores of *P. zealandica* differ slightly in structure from those of mealybugs, as evidenced from comparison of SEM photographs (Cox & Pearce, 1983; Cox, 1984). In *Phenacoleachia* the trilocular pores have the usual three interconnected loculi centrally plus three outer, smaller loculi (as noted by Morrison & Morrison, 1922; see also Cox, 1984, Fig. 9), which have never been reported in Pseudococcids.

Molecular data

Phylogenetic analysis of nucleotide sequences from the nuclear small-subunit ribosomal RNA gene (SSU rRNA) derived from 39 species of 14 putative families of scale insects, including Phenacoleachiidae, using aphids as outgroups, did not resolve the phylogenetic relationships of *P. zealandica*. *Phenacoleachia* appeared as sister to the rest of the scale insects in maximum likelihood analyses and in three of the six maximum parsimony (MP) trees, and as sister to different taxa of Margarodidae *sensu lato* in the other three MP trees (Cook *et al.*, submitted). The molecular data did not support the placement of *Phenacoleachia* as sister to the Pseudococcidae.

Biogeography

Phenacoleachia is restricted to the South Island of New Zealand and at least two islands of the adjacent Campbell Plateau. The latter is a continental Gondwanan fragment that rifted from west Antarctica together with the Chatham Rise and New Zealand's South Island east of the Alpine Fault (Walley & Ross, 1991; Kroenke, 1996) and today has five island groups, including Auckland and Campbell. Parts of Campbell Plateau supported *Nothofagus* forests prior to Pliocene glaciations (Dettman *et al.*, 1990). New Zealand's subantartic islands thus represent eroded remnants of a larger landmass and in combination with their comparatively mild maritime climates provide refugia for some Gondwanan taxa (Carlton & Leschen, 2001). Identified specimens of *P. zealandica* appear to be restricted to the South Island west of the Alpine Fault, although this species may occur on the North Island, which is part of the same geological unit. *P. australis* occurs on Campbell Island (the most southerly island of the Plateau) and Auckland Island, although Beardsley (1964) noted slight differences, perhaps related to size, between the adult females from the two islands. There are a number of NZAC specimens from the extreme southern part of the South Island and adjacent Stewart Island; these have not been studied although Stewart Island appears to have undescribed species (C.J. Hodgson, pers. comm.).

Evolutionary relationships

The new morphological information on the first-instar nymph and the adult female, reported here, reinforces the view that *Phenacoleachia* is an unique taxon worthy of family status. Furthermore, the molecular data does not ally *Phenacoleachia* with the Pseudococcidae, nor with any other taxon for which nucleotide sequence data are currently available. It may be sister to the rest of the scale insects or belong among the archaeococcoid lineages. *Phenacoleachia* has a number of plesiomorphic features, such as XX-X0 sex determination (Brown & Cleveland, 1968), a four-segmented labium (in nymphs and adult females), and an abdominal tracheal system with remnant spiracles (in first-instar nymphs, adult females and adult males). It also has a well-developed apical organ in the labium (Fig. 2; Koteja, 1974b) and cicatrices (described here for the crawler and for the adult female by Morrison & Morrison (1922) who called them simple, clear pores). The latter three features occur in archaeococcoids but not neococcoids, whereas the XX-X0 system occurs in many, but not all, margarodids and ortheziids and in *Puto* (Nur, 1980) and the labium in all other scale insects has fewer than four segments (Koteja, 1974a,b). If Phenacoleachiidae is an ancient lineage, then the features of *Phenacoleachia* that are shared with *Puto* and pseudococcids (e.g., ostioles and trilocular pores) may be plesiomorphies that have been lost in more derived scale insect groups, as suggested by Danzig (1980, Fig. 18). A plesiomorphic state for ostioles would support an argument for them being homologous with the siphunculi of aphids, although they may be convergent defensive structures. Adult males of *Phenacoleachia* may be wing polymorphic because several almost apterous individuals were reported from a large collection of males of *P. zealandica* made at one time from one locality (Maskell, 1891) and apterous adult males are present among more recently collected NZAC specimens (C.J. Hodgson, pers. comm.). Adult males of *Phenacoleachia* also have complex sensilla (one long seta with 1-3 minute setae at its base) on their antennae, as do those of *Puto* and several archaeococcoids (Koteja, 1996), but not neococcoids, nor apparently other sternorrhynchans. Clearly the phylogenetic relationships of *Phenacoleachia* and also *Puto* are crucial to understanding the early evolution of the scale insects. In particular, did the ancestral scale insects most closely resemble phenacoleachiids - a scenario preferred by Koteja (1974a) and Borchsenius (1958) - in having a long, narrow, four-segmented labium and a wide anal ring bearing setae and many pores, or are margarodids closest to the prototype scale insect, as suggested by Danzig (1980)? If the former hypothesis is correct, then a complex anal ring is the ancestral condition for scale insects, and the reduction of the anal ring to a narrow sclerotised band and the diverse development of the anal tube in margarodids are derived conditions - a character polarity not supported by Danzig (1980). Only more complete molecular data and/or the discovery of older fossil scale insects provide any hope of solving these evolutionary questions.

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