Boll. Zool. agr. Bachic.
Ser. II, 33 (3): 139-150

C. F. STUMPF, P. L. LAMBDIN

Distribution and phylogenetic relationships of native and introduced pit scales (Hemiptera: Coccoidea: Asterolecaniidae) in North and South America

Abstract - The pit scales or Asterolecaniidae represent a diverse group found in all major biogeographic regions of the world on a variety of host plants. Specimens representing both known and unknown species were obtained from institutions in North and South America for study. Species were described and illustrated based on morphological characters of the adult females. This study assessed the morphological characters for 48 of the 64 species of pit scales found in North and South America representing the genera *Asterodiaspis*, *Asterolecanium*, *Bambusaspis*, *Neoasterodiaspis*, *Palmaspis*, *Planchonia*, and *Russellaspis*. Because of the presence of recent descriptions, eight species of *Grammococcus* and *Palmaspis* were not described, but were included in a systematic key in addition to 11 new species (two species of *Asterolecanium*, five species of *Bambusaspis*, and four species of *Palmaspis*). Also, three species in the genus *Bambusaspis* were synonymized and the genus *Grammococcus* was included in the subfamily Asterolecaniinae. Computer-generated phylogenetic trees were developed and tested for robustness. The phylogenetic relationships of 38 species in the subfamily Asterolecaniinae were evaluated based on 43 morphological characters of the adult females. A complete consensus tree of the 40 most parsimonious trees was developed. This study suggests that most genera may be monophyletic, while the genera *Asterolecanium* and *Palmaspis* appear to be paraphyletic. Pit scale biodiversity has not been adequately investigated, and many additional discoveries of new species are expected from tropical regions.

Key words: pit scales, *Asterolecanium*, phylogenetic analysis, scale insects.

INTRODUCTION

The family Asterolecaniidae is a large group of scale insects with a worldwide distribution in all major zoogeographic regions. However, most species are found in the tropical and subtropical regions of the world. The taxon includes an estimated 400 species (Scalenet - http://www.sel.barc.usda.gov/scalenet/scalenet.htm) in 22 genera elevating the Asterolecaniidae to the 5th largest family of Coccoidea after the Diaspididae, Pseudococcidae, Coccidae, and Eriococcidae. The objectives of the this study were to assess the distribution of species within the subfamily Asterolecaniinae in North and South America, and elucidate species affinities.

MATERIALS AND METHODS

Specimens were borrowed from several institutions and government agencies as slide mounted specimens, in alcohol, or as dry material. A cladistic analysis was performed on morphological characters of adult females to test the monophyly of the New World pit scale genera. All characters were treated as unordered. The lack of good characters due to the general tendency of character reduction in the pit scales limited the analysis to 38 species and the two outgroups, *Cerococcus* and *Lecanodiaspis*. The outgroups were scored by comparing the data of several species in the two genera from the literature (Howell & Kosztarab, 1972; Lambdin & Kosztarab, 1973, 1977) and from specimens available at the University of Tennessee Insect Museum, to create a generalized type for both genera. A parsimony analysis was performed with the computer program, PAUP (Swofford, 1993), the resulting complete consensus tree was analyzed with MacClade (Maddison & Maddison, 1992) and TreeView (Page, 1996).

RESULTS AND DISCUSSION

Some 37 species were redescribed and illustrated, three species were merged into one, and 11 species new to science were described and illustrated. In the New World, 56 species of pit scales in the subfamily Asterolecaniinae are present in eight genera. A description of characters and character states for the phylogenetic analysis is presented in Table 1. Table 2 presents the distribution of character states for all included species. In addition to the 37 known species of Asterolecaniinae in the genera *Asterodiaspis* (*As.*), *Asterolecanium* (*Al.*), *Bambusaspis* (*Ba.*), *Neoasterodiaspis* (*Ne.*), *Palmaspis* (*Pa.*), *Planchonia* (*Pl.*), and *Russellaspis* (*Ru.*), the species *Grammococcus* (*Gr.*) *adetocorymbus* was also included in the analysis. Based on the morphological characters examined, the Asterolecaniinae may have more in common with the genera *Cerococcus* and *Lecanodiaspis* than with several genera currently included in the family Asterolecaniidae. Similarities of such characters as the anal plates and the arched plate in the anal area, and the arrangement of dermal ducts and pores justify the use of *Cerococcus* and *Lecanodiaspis* as outgroups for phylogenetic analysis.

The analysis with PAUP was performed as a heuristic search with one tree held at each step during stepwise addition using tree-bisection-reconnection (TBR) branch-swapping. The 40 shortest trees found were retained with a length of 129 steps. Tree 1 (Fig. 1) as well as the strict consensus tree (Fig.2) are shown as cladograms. The first analytical procedure included two bootstrap analyses in PAUP resulting in the same tree topology (100 bootstrap replicates and 10 random addition replicates

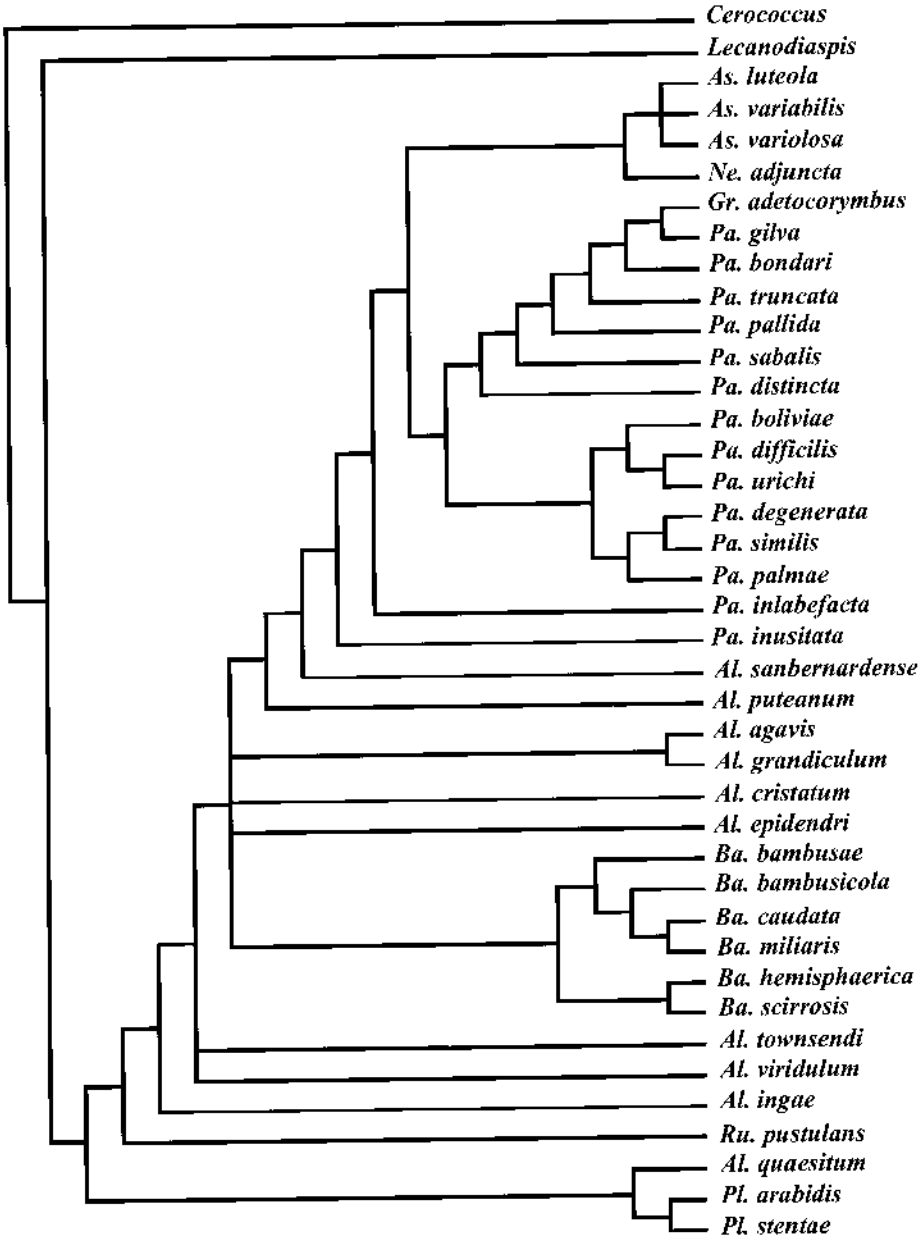

Fig. 1 - Tree 1 of 40 most parsimonious trees. Tree length = 129, CI = 0.43, HI = 0.57, CI excluding uninformative characters = 0.42, HI excluding uninformative characters = 0.58, RI = 0.77, RC = 0.33. *Cerococcus* and *Lecanodiaspis* are used as outgroups.

for each bootstrap replicate, 1,000 bootstrap replicates without random addition replicates). Bootstrap numbers are shown in the strict consensus tree (Fig. 2) above the horizontal line indicating each clade of the ingroup. Only bootstrap values equal to or greater than 50% are presented. The second analytical procedure was a decay analysis performed with TreeView and PAUP. Decay indices of the ingroup are presented below the horizontal line indicating each clade in the strict consensus tree (Fig. 2).

The strict consensus tree was transferred into Mac-Clade. Characters supporting each individual clade are presented in a phylogram depicting branch lengths (Fig. 3). The numbers for each branch correspond to the list of characters in Table 1. The picture emerging from a close inspection of the ingroup Asterolecaniinae supports Russell's (1941) suspicion over splitting the genus *Asterolecanium*. She introduced 12 groups based on morphological and host plant characters without giving them official status. Borchsenius (1950, 1960, 1961) and Bodenheimer (1951) then elevated these groups to the generic level. The cladistic analysis of adult females (Figs. 1, 2, 3) clearly indicates the genus *Asterolecanium* to be paraphyletic. The basic split into the clades *quaesitum-arabidis-stentae* and the rest of the Asterolecaniinae is well supported (Fig. 2, bootstrap value = 94, decay index = 3). The position of *Al. quaesitum* and of both species of *Planchonia* in the cladogram also shows a high level of bootstrap and decay index support (Fig. 2, bootstrap values = 85 and 90, decay indices = 2 and 3, respectively).

However, most other clades do not depict bootstrap support and only have a decay value of one. The genera *Russellaspis* and *Bambusaspis* appear to be part of a basal group of species within *Asterolecanium*. *Bambusaspis* is divided into two groups, from which the clade *bambusae-bambusicola-caudata-miliaris* is relatively well supported (Fig. 2, bootstrap value = 80, decay index = 1). The agave-feeding species *Al. agavis* and *Al. grandiculum*, both ranging from California to Texas and Mexico, fall together as sister species on the tree (Fig. 1). The clade *Asterodiaspis-Grammococcus-Palmaspis* is clearly delineated by 7 characters (Fig. 3). However, no bootstrap support is available for this clade, and the decay index is just 1 (Fig. 2). *Palmaspis* is paraphyletic in regard to both *Grammococcus* and *Asterodiaspis*, but with low support values (Fig. 2). Only the relationship between *Pa. degenerata* and *Pa. similis* shows at least some support with a bootstrap value of 65 and a decay index of 2 (Fig. 2). The genus *Grammococcus* clusters well inside *Palmaspis* with both genera exclusively feeding on palms. Monophyly of the pit scales on oak represented by the genera *Asterodiaspis* and *Neoasterodiaspis* is well supported with bootstrap values of 60 for the whole clade and 89 for *Asterodiaspis*, and decay indices of 1 and 2, respectively (Fig. 2). However, this clade also originates within *Palmaspis*.

CONCLUSIONS

The statistics (Figs. 1, 2) show that more data are needed (both morphological as

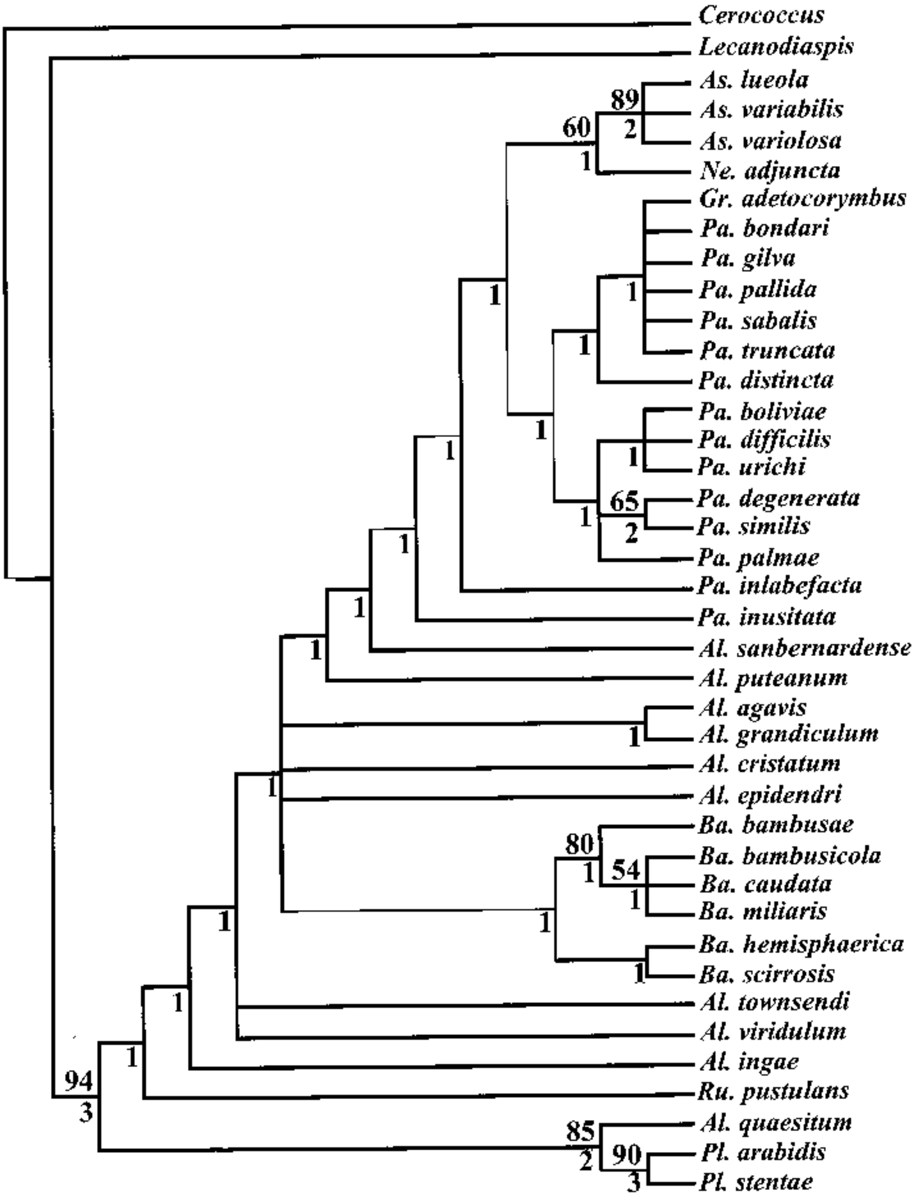

Fig. 2 - Strict consensus tree of 40 most parsimonious trees (cladogram). Numbers above branches indicate bootstrap support, numbers below branches show decay values. Only bootstrap values 50% or greater are presented. *Cerococcus* and *Lecanodiaspis* are used as outgroups.

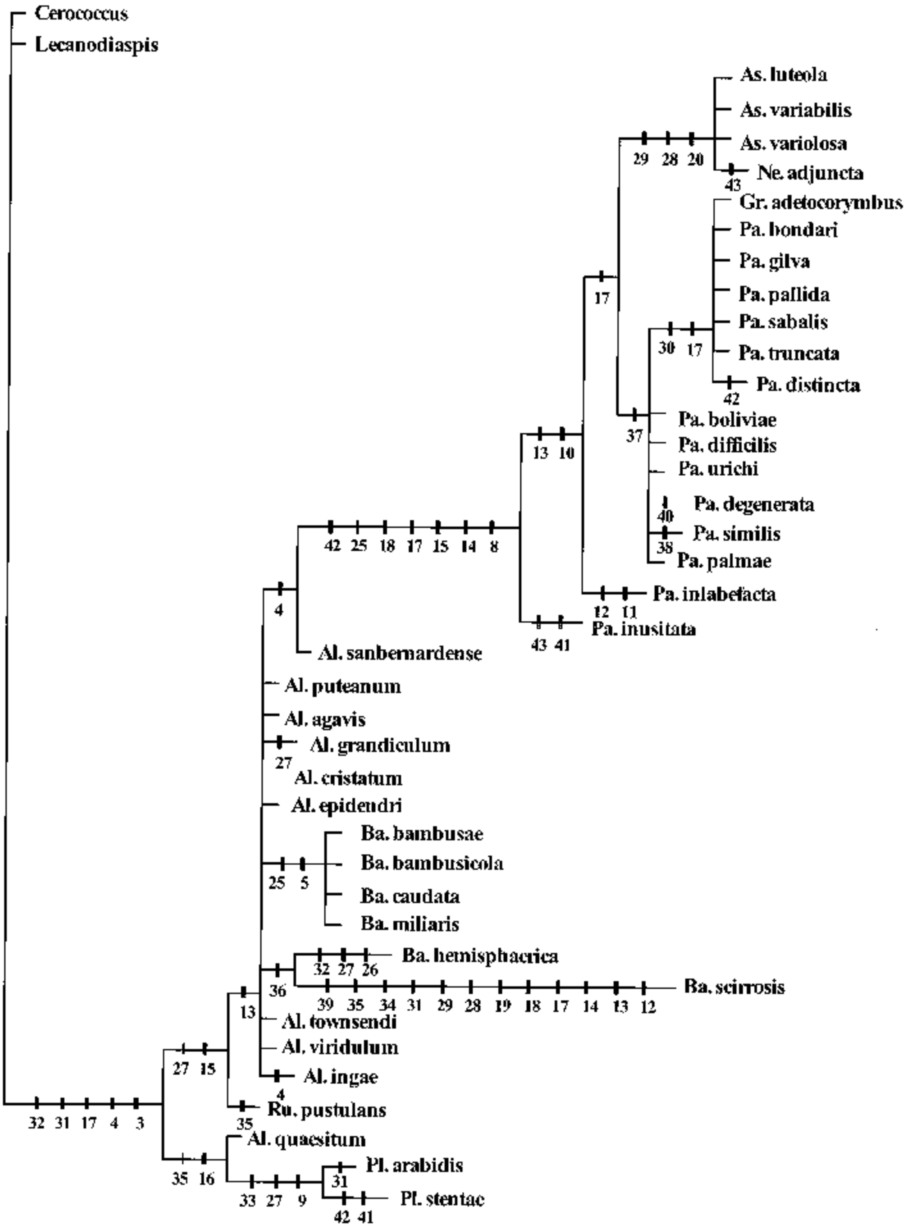

Fig. 3 - Strict consensus tree of 40 most parsimonious trees (phylogram). Branch lengths indicate the number of characters supporting each clade. Numbers shown on each branch depict the characters contributing to branch support (numbers correspond to Table 1 and Table 2). *Cerococcus* and *Lecanodiaspis* are used as outgroups.

Table 1 - Characters and character states.

Character	Character name	Character states
1	Caudal tube	0 = absent; 1 = present
2	Antenna	0 = several segments; 1 = 1 segment
3	Antenna indented	0 = no; 1 = yes
4	Clypeolabral shield with additional tentorial arm	0 = no; 1 = yes
5	Additional tentorial arm arch-shaped	0 = no; 1 = yes
6	Lateral clypeal sulcus	0 = present; 1 = absent
7	Labial setae	0 = present; 1 = absent
8	Spiracles long and slender, *Palmaspis* type	0 = no; 1 = yes
9	Spiracles completely enveloped in dorsal folds, *Planchonia* type	0 = no; 1 = yes
10	Anal dorsal setae	0 = present; 1 = absent
11	Position of apical setae	0 = apical or slightly dorsal; 1 = ventral
12	Subapical setae	0 = present; 1 = absent
13	Anal ventral setae	0 = 3 pairs; 1 = 2 pairs; 2 = 1 pair; 3 = 0 pairs
14	Arched plate	0 = present; 1 = absent
15	Anal plates	0 = fused; 1 = separated; 2 = absent
16	Anal plates fused, anvil-shaped	0 = no; 1 = yes
17	Anal ring setae	0 = 8 setae; 1 = 6 setae; 2 = 4 setae; 3 = 2 setae; 4 = setae absent; 5 = anal ring absent
18	Anal ring circular, *Asterolecanium* type	0 = yes; 1 = no
19	Anal ring circular, plate-like	0 = no; 1 = yes
20	Anal ring triangular, *Asterodiaspis* type	0 = no; 1 = yes
21	Anal ring plate-like	0 = no; 1 = yes
22	Anal ring in 2 connected plates	0 = no; 1 = yes
23	Anal ring in 2 separated plates	0 = no; 1 = yes
24	Anal ring absent	0 = no; 1 = yes
25	Anal lobes sclerotized ventrally	0 = yes; 1 = no
26	Large dorsal 8-shaped pores	0 = present; 1 = absent
27	Marginal 8-shaped pores	0 = band on dorsum and venter; 1 = dorsal band; 2 = dorsal row; 3 = absent
28	Large dorsal 8-shaped pores bent	0 = yes; 1 = no
29	Marginal 8-shaped pores flat, *Asterodiaspis* type	0 = no; 1 = yes
30	Marginal 8-shaped pores long and thin, *Palmaspis* type	0 = no; 1 = yes
31	Simple disk pores	0 = on venter and dorsum; 1 = in submarginal row; 2 = on dorsum only

(Table 1. continued)

Character	Character name	Character states
32	Submarginal row of simple disk pores on venter only	0 = no; 1 = yes
33	Simple disk pores in ventral and dorsal submarginal rows	0 = no; 1 = yes
34	Tubular ducts in longitudinal bands	0 = no; 1 = yes
35	Ventral submarginal bilocular pores	0 = band; 1 = extension of transverse bands; 2 = row
36	Marginal quinquelocular or trilocular pores	0 = absent; 1 = strongly reduced row; 2 = row; 3 = band
37	Marginal pores	0 = mainly quinquelocular; 1 = mainly trilocular
38	Pores in spiracular furrows	0 = mainly quinquelocular; 1 = mainly trilocular
39	Segmental multilocular pores	0 = present; 1 = absent
40	Segmental multilocular pore loculi	0 = 5-12 loculi; 1 = only 5 loculi
41	No. of multilocular pore bands	0 = 5 or more bands; 1 = 4 or fewer bands
42	No. of multilocular pores	0 = more than 74; 1 = fewer than 60
43	Row of ventral submarginal setae	0 = complete; 1 = incomplete

well as molecular) for an improved estimate of the phylogenetic relationships within the pit scales. However, most species are only known from slide mounted adult females, therefore limiting future phylogenetic research. Because of the strong reduction of morphological characters in pit scales, only 43 characters were available for this analysis.

Species of the genus *Asterolecanium* present in the New World appear to be native to the region. No conclusions can be drawn about the origin of the Asterolecaniinae. Both a New World and an Old World origin with further vicariant events are possible. However, it is interesting to see that *Asterolecanium*, *Planchonia*, and *Russellaspis* (Fig. 1), whose members occur on a variety of different host plant families, are also the most primitive ones morphologically. *R. pustulans*, the oleander pit scale, occurs on at least 46 different host plant families (Russell, 1941), and is believed to be a native of tropical Central and South America that has spread recently with the tropical plant trade.

Each of the other genera recognized in the Asterolecaniinae in North and South America can be characterized by an association with a single host plant family or a similar subgroup of a particular family, e.g., *Bambusaspis* on bamboo, *Grammococcus* and *Palmaspis* on palms, and *Asterodiaspis* and *Neoasterodiaspis* on oaks. The four genera, *Asterodiaspis*, *Neoasterodiaspis*, *Grammococcus*, and *Palmaspis*, form a monophyletic group, although this group appears as the sister taxon of *A. sanbernardense* in the analysis (Figs. 1, 2, 3). The position of the other three genera defines *Palmaspis* as paraphyletic. The oak-inhabiting genera *Asterodiaspis* and *Neoasterodiaspis* are closely related to each other (Fig. 2). Future studies, based on data presented by Liu & Shi (1990, 1993), may make it necessary to suppress the

Table 2 - Distribution of character states for the phylogenetic analysis.
Numbers of characters and character states correspond to those in Table 1.
0, 1, 2, 3, 4, 5: character states; -: character not applicable; ?: character not known.

										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4
Character	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
Cerococcus Comstock	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	-	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Lecanodiaspis Targioni Tozzetti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Asterodiaspis luteola (Russell)	0	1	1	0	0	0	0	0	0	1	1	0	2	1	2	-	3	1	0	1	0	0	0	0	1	1	2	1	1	0	2	0	0	0	2	2	0	0	0	0	0	1	0
Asterodiaspis variabilis (Russell)	0	1	1	0	0	0	0	0	0	1	1	0	2	1	2	-	3	1	0	1	0	0	0	0	1	1	2	1	1	0	2	0	0	0	2	2	0	0	0	0	0	1	0
Asterodiaspis variolosa (Ratzeburg)	0	1	1	0	0	0	0	0	0	1	1	0	2	1	2	-	3	1	0	1	0	0	0	0	1	1	2	1	1	0	2	0	0	0	0	2	0	0	0	0	0	1	0
Asterolecanium agavis Russell	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	0
Asterolecanium cristatum Ferris	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	2	2	0	0	0	0	0	0	0
Asterolecanium epidendri (Bouché)	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	2	2	0	0	0	0	0	0	0
Asterolecanium grandiculum Russell	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	0
Asterolecanium ingae Russell	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0
Asterolecanium puteanum Russell	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	2	2	0	0	0	0	0	0	0
Asterolecanium quaesitum Russell	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	3	0	0	0	0	0	0	0
Asterolecanium sanbernardense Hempel	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	2	2	0	0	0	0	0	0	0
Asterolecanium townsendi Cockerell	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0
Asterolecanium viridulum Cockerell	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0
Bambusaspis bambusae (Boisduval)	1	1	1	1	1	0	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	0	0	2	2	0	0	0	0	0	0	1
Bambusaspis bambusicola (Kuwana)	1	1	1	1	1	0	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	1	2	0	0	0	1	0	0	0	2	2	0	0	1	-	-	-	1
Bambusaspis caudata (Green)	1	1	1	1	1	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	0	0	2	0	-	0	1	-	-	-	1
Bambusaspis hemisphaerica (Kuwana)	1	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	2	3	0	0	0	0	0	0	1
Bambusaspis miliaris (Boisduval)	1	1	1	1	1	0	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	0	0	2	1	0	0	1	-	-	-	1
Bambusaspis scirrosis (Russell)	1	1	1	1	0	0	1	0	0	1	0	1	3	1	2	-	3	1	1	0	0	0	0	0	0	0	2	1	1	0	0	0	0	1	0	3	0	0	1	-	-	-	1
Grammococcus adetocorymbus Miller & Lambdin	0	1	1	0	0	0	0	0	0	1	0	0	2	1	2	-	2	1	0	0	0	1	0	0	1	1	3	-	-	-	2	0	0	1	2	0	-	1	0	0	1	1	1
Neoasterodiaspis adjuncta (Russell)	0	1	1	0	0	0	0	1	0	1	0	0	2	1	2	-	3	1	0	1	0	0	0	0	1	0	2	1	1	0	2	0	0	0	2	2	0	0	0	0	0	1	1

(Table 2. continued)

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Palmaspis boliviae (Russell)	0	1	1	0	0	0	0	1	0	1	0	0	1	1	2	–	3	1	0	0	1	0	0	0	0	0	2	0	0	0	2	0	0	1	2	2	1	0	0	0	0	1	0
Palmaspis bondari (Lepage)	0	1	1	0	0	0	0	1	0	1	0	0	2	1	2	–	2	1	0	0	0	1	0	0	1	1	2	0	0	1	2	0	0	1	2	2	1	0	0	0	1	1	0
Palmaspis degenerata (Russell)	0	1	1	0	0	0	0	1	0	1	0	0	3	1	2	–	3	1	1	0	0	0	0	0	0	1	2	0	0	0	2	0	0	0	2	2	1	0	0	1	1	1	0
Palmaspis difficilis (Russell)	0	1	1	0	0	1	0	1	0	1	0	0	2	1	2	–	3	1	0	0	1	0	0	0	0	0	2	0	0	0	2	0	0	0	2	3	1	0	0	1	0	1	0
almaspis distincta (Russell)	0	1	1	0	0	1	0	1	0	1	0	0	2	1	2	–	4	1	0	0	0	0	1	0	1	0	2	0	0	1	2	0	0	0	2	2	1	0	0	0	0	0	0
Palmaspis gilva (Russell)	0	1	1	0	0	0	0	1	0	1	0	1	2	1	2	–	5	1	0	0	0	0	0	1	1	1	2	0	0	1	2	0	0	1	2	2	1	1	1	–	–	–	1
Palmaspis inlabefacta (Russell)	0	1	1	0	0	0	0	1	0	1	1	1	2	1	2	–	5	1	0	0	0	0	0	1	1	0	2	0	0	0	2	0	0	0	2	2	0	0	0	0	0	1	0
Palmaspis inusitata (Russell)	0	1	1	0	0	0	?	1	0	0	0	0	1	1	2	–	5	1	0	0	0	0	0	1	1	0	2	0	0	0	2	0	0	0	2	2	0	0	0	0	1	1	1
Palmaspis pallida (Russell)	0	1	1	0	0	1	0	1	0	1	0	0	1	1	2	–	2	1	0	0	0	1	0	0	1	1	2	0	0	1	2	0	0	0	2	2	1	0	0	0	1	1	0
Palmaspis palmae (Cockerell)	0	1	1	0	0	0	0	1	0	1	0	1	2	1	2	–	3	1	1	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	2	2	1	0	0	0	0	1	0
Palmaspis sabalis (Russell)	0	1	1	0	0	1	0	1	0	1	1	1	1	1	2	–	4	1	0	0	1	0	0	0	1	1	2	0	0	1	2	0	0	0	2	2	1	1	0	0	0	1	1
Palmaspis similis (Russell)	0	1	1	0	0	0	0	1	0	1	0	0	3	1	2	–	3	1	0	0	0	0	0	0	0	1	2	0	0	0	2	0	0	0	2	2	1	1	0	0	1	1	0
Palmaspis truncata (Russell)	0	1	1	0	0	1	0	1	0	1	1	1	2	1	2	–	2	1	0	0	0	1	0	0	1	1	2	0	0	1	2	0	0	1	2	2	1	0	0	0	0	1	0
Palmaspis urichi (Cockerell)	0	1	1	0	0	0	0	1	0	1	0	0	2	1	2	–	3	1	0	0	1	0	0	0	0	0	2	0	0	0	2	0	0	0	2	2	1	0	1	–	–	–	0
Planchonia arabidis Signoret	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	3	0	0	0	0	0	0	0
Planchonia stentae (Brain)	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	3	0	0	0	0	1	1	0
Russellaspis pustulans (Cockerell)	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	0	2	2	0	0	0	0	0	0	0

genus *Neoasterodiaspis* as a morphological variant of *Asterodiaspis*. The genus *Palmaspis* is widespread throughout the world wherever palms grow (Russell, 1941, Matile-Ferrero, 1996). A reduction in several characters is typical for *Grammococcus*, but this genus also shows some unique apomorphies, such as dorsal multilocular pores. It shares these apomorphies with the almost identical genus *Polea* (Lambdin, 1977, 1999) in the Oriental faunal region, which does not occur on palms, and should be considered as the adelphotaxon of *Grammococcus*.

The positions of the other pit scale genera not belonging to the subfamily Asterolecaniinae have to be clarified by additional studies. Some of them (e.g., *Pollinia*, *Sclerosococcus*, *Mycetococcus*, and *Mycococcus*) may not belong in either Asterolecaniidae, Cerococcidae, or Lecanodiaspididae, but may cluster at the base of the pit scale tree.

REFERENCES

BODENHEIMER F.S., 1951 - Description of some new genera of Coccoidea - Entomol. Ber., 13:328-331.

BORCHSENIUS N.S., 1950 - Toward the revision of the genus *Asterolecanium* (Targ.) Sign. (Insecta, Homoptera, Coccoidea) (In Russian, Eng. transl.) - Dokl. Akad. Nauk SSSR. Leningrad (N.S.), 71: 781-783.

BORCHSENIUS N.S., 1960 - Fauna of USSR, Homoptera, Kermococcidae, Asterolecaniidae, Lecanodiaspididae, Aclerdidae (In Russian, Eng. transl.) - Akad. Nauk. SSR. Zool. Inst., 8:282pp.

BORCHSENIUS N.S., 1961 - Some data on the generic classification of Coccoidea of the family Asterolecaniidae (Homoptera, Coccoidea) - 11th Internatl. Kongr. Entomol. Wien, 1: 63-65.

HOWELL J.O., KOSZTARAB M., 1972 - Studies on the morphology and systematics of scale insects - No. 5. Morphology and systematics of the adult females of the genus *Lecanodiaspis* (Homoptera: Coccoidea: Lecanodiaspididae) - VA. Polytech. Inst. St. Univ. Res. Div. Bull., 70, 248pp.

LAMBDIN P.L., 1977 - A revision of the genus *Polea* Green (Homoptera: Coccoidea: Asterolecaniidae) - Ann. Entomol. Soc. Am., 70: 911-915.

LAMBDIN P.L., 1999 - New pit scale species of *Polea* (Hemiptera: Asterolecaniidae) - Ann. Entomol. Soc. Am., 92:188-192.

LAMBDIN P.L., KOSZTARAB M., 1973 - Studies on the morphology and systematics of scale insects - No. 5. A revision of the seven genera related to *Lecanodiaspis* (Homoptera: Coccoidea: Lecanodiaspididae) - VA. Polytech. Inst. St. Univ. Res. Div. Bull., 83, 110pp.

LAMBDIN P.L., KOSZTARAB M., 1977 - Studies on the morphology and systematics of scale insects - No. 10. Morphology and systematics of the adult females of the genus *Cerococcus* (Homoptera: Coccoidea: Cerococcidae) - VA. Polytech. Inst. St. Univ. Res. Div. Bull., 128, 252pp.

LIU Y., SHI Y., 1990 - Systematic status of *Asterodiaspis* with description of a new species (Homoptera: Asterolecaniidae) - Proc. ISSIS-VI. Krakov, 2: 85-59.

LIU Y., SHI Y., 1993 - Discussion on the systematic status of the genus *Asterodiaspis* (Homoptera: Coccinea: Asterolecaniidae) with description of a new species - Entomotax., 15:187-188.

MADDISON W.P., MADDISON D.R., 1992 - Mac-Clade: Analysis of phylogeny and character evolution. Vers. 3.0 – Sinauer, Sunderland, 398pp.

MATILE-FERRERO D., 1996 - La faune des Asterolecaniidae palmicoles de L'Amazonie Péruvienne (Homoptera: Coccoidea) - Ann. Soc. Entomol. Fr.(N.S.), 32: 251-264.

PAGE R.D., 1996 - TREEVIEW: An application to display phylogenetic trees on personal computers - Comput. Applic. Biosci., 12:357-358.

RUSSEL L.M., 1941 - A classification of the scale insect genus *Asterolecanium* - U.S. Dept. Agric. Misc. Pub., 424, 322pp.

SCALENETT - http://www.sel.barc.usda.gov/scalenet/scalenet.htm.

SWOFFORD D.L., 1993 - PAUP: Phylogenetic analysis using parsimony. Vers. 3.1.1 - Illinois Nat. Hist. Surv., Champaign, 257pp.

CHRISTOF F. STUMPF - The North Carolina State University, Dept. of Entomology, Raleigh, NC 27695, USA. E-mail: cfstumpf@unity.ncsu.edu.

PARIS L. LAMBDIN - The University of Tennessee, Dept. of Entomology and Plant Pathology, Knoxville, TN 37901. USA. E-mail: plambdin@utk.edu