

ACTA ZOOLOGICA  
CRACOVENSIA

Tom XIX

Kraków, 15. X. 1974

Nr 14

Jan KOTEJA

On the phylogeny and classification of the scale insects (*Homoptera*, *Coccinea*)  
(discussion based on the morphology of the mouthparts)

[Pp. 267—326, 5 text-figs.]

Filogeneza czerwców (*Homoptera*, *Coccinea*) w świetle budowy narządów gębowych

Филогенез кокцид (*Homoptera*, *Coccoidea*) с точки зрения строения ротового аппарата

Abstract. The phylogeny and classification of the scale insects are discussed on the basis of the morphology of the mouth-parts (clypeolabral shield, sucking pump, labium). Four categories higher than the family have been recognized — subordo, superfamily, section and family group. The scale insects are considered as a monophyletic group — subordo *Coccinea*, which presumably evolved into two major branches — the superfamilies *Orthezioidea* and *Coccoidea*.

CONTENTS

Introduction . . . . .	267
General remarks on the classification of the <i>Coccinea</i> . . . . .	268
Taxonomic categories . . . . .	272
The phylogeny and classification of the <i>Coccinea</i> . . . . .	279
Final notes . . . . .	314
References . . . . .	316
Streszczenie . . . . .	323
Резюме. . . . .	324

INTRODUCTION

The present publication has been originally planned as a part of a larger work on the mouthparts in the *Coccinea* which has been divided for technical reasons into following papers: 1. "Comparative studies on the labium in the

*Coccinea*" (KOTEJA, 1974). This study contains (a) a general introduction to the question, (b) a review of the literature records, (c) an introduction to the methods, (d) a list of examined species including some collecting data, (e) a general characteristic of the labium (shape, size, segmentation, setae, location), (f) a discussion on the variability, correlation and taxonomic significance of some labial characters, (g) observations on postembrional changes of the labium, (h) a discussion on the general trends in the evolution of the labium, (i) descriptions of the labium in families and finally (j) a key to higher taxa on the basis of labial characteristics; 2. "The sucking pump in the taxonomy of the *Coccinea*" (KOTEJA, M. S.); 3. "The clypeolabral shield in the taxonomy of the *Coccinea*" (KOTEJA and LINIOWSKA, M. S.). In this paper as well as in the former one the investigations are concentrated mainly on the taxonomic value of the mouthparts. 4. The present study which presents a discussion on the phylogeny and classification of the *Coccinea* based on the morphology of the mouthparts.

From the origin of these papers it is clear that they constitute one unit and that the factual material presented in the three former papers cannot be repeated in all details in this one. On the other hand, the division and arrangement of the taxa and other questions in the former papers are fully understandable only in the light of the present discussion.

Each of the three former papers presents a classification of the *Coccinea* based on that mouth part which is an object of morphological examination. In the present paper the results of all these investigations are taken into consideration. When studying these papers, the reader is requested to bear in mind the mentioned points. The evolutionary trends in the phylogenic development of the labium, clypeolabral shield and sucking pump are presented in Figs. 1—4.

The author would like to express his gratitude, once more, to all the persons who made material available and helped in completing this study in any other way.

#### GENERAL REMARKS ON THE CLASSIFICATION OF THE *COCCINEA*

The classification of the *Coccinea* is based almost entirely on the characters of the adult females and particularly on these which can be noticed on the slide-mounted preparations made of the cuticle. The reasons responsible for this situation are generally known and there is no need to discuss this question once more. The high degree of specialization, the secondary reduction of many morphological structures, the neotenia of the females, the ecological polymorphism and numerous convergencies between the closely related as well as distant groups made sometimes the classificatory systems proposed by various students extremely different.

Thus, attempts were made to solve the problem of the phylogeny and classification of the scale insects otherwise. BROWN, HUGHES-SCHRADER, SCHRADER and their collaborators (for records see MORRISON and RENK, 1957; MORRISON



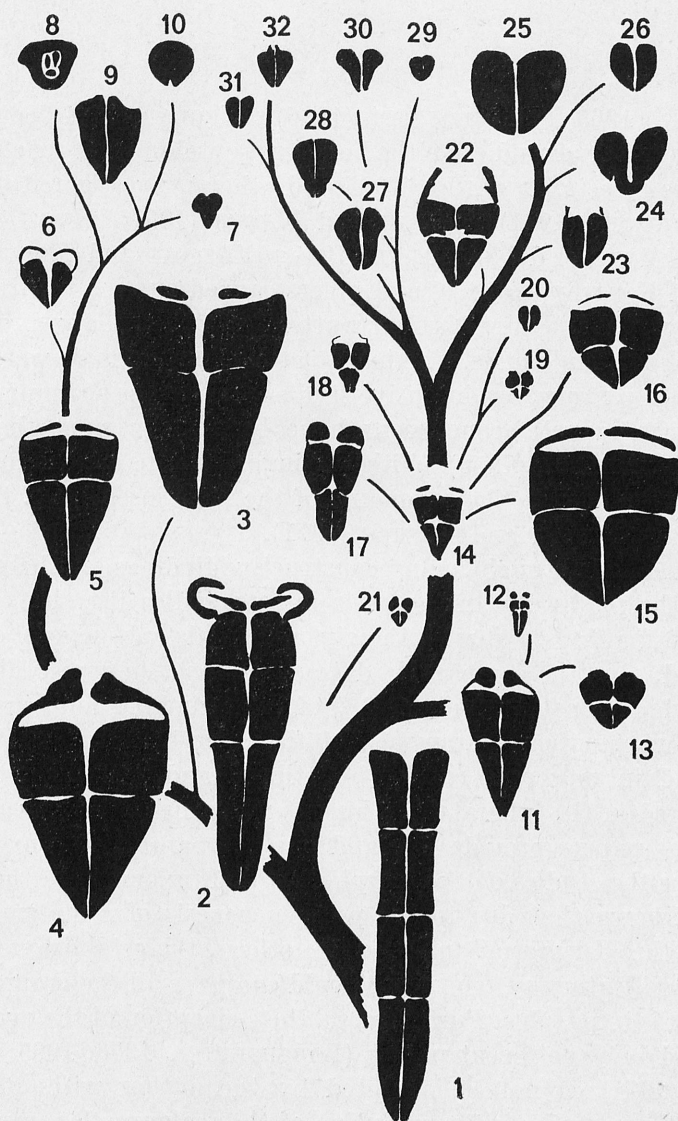


Fig. 1. Evolutionary trends of the labium in the *Coccinea* presented in a form of a phylogenetic tree. The figures represent the largest labia in given groups. (After KOTEJA, 1974)

1. Primitive ancestors of the *Coccinea*, 2. *Phenacoleachia* COCKERELL (*Phenacoleachiidae*), 3. *Arctorthesia* COCKERELL (*Orthesiidae*), 4. *Drosicha* WALKER (*Monophlebitidae*), 5. *Coelostomidia* COCKERELL (*Coelostomidiidae*), 6. *Neosteingelia* MORRISON (*Neosteingelia* group), 7. *Kuwanina* COCKERELL (*Kuwaninae*), 8. *Porphyrophora* BRANDT (*Porphyrophoridae*), 9. *Xylococcus* LÖW (*Xylococcidae*), 10. *Matsucoccus* COCKERELL (*Matsucoccidae*), 11. *Macrocerococcus* LEONARDI (*Pseudococcidae* — *Trabutinae*), 12. *Rhizococcus* HÜNCKEL D'HERCULAIS (*Pseudococcidae* — *Rhizococcinae*), 13. *Antonina* SIGNORET (*Pseudococcidae* — *Sphaerococcinae*), 14. *Phloeococcus* HOY (*Acanthococcidae*), 15. *Dactylopius* O. G. COSTA (*Dactylopiidae*), 16. *Apiomorpha* RÜBSAAMEN (*Apiomorphidae*), 17. *Kermes* BOITARD (*Kermesidae*), 18. *Cerococcus* COMSTOCK (*Cerococcidae*), 19. *Cryptococcus* DOUGLAS (*Cryptococcidae*), 20. *Kuwanina* COCKERELL (*Kuwanina* group), 21. *Conchaspis* COCKERELL (*Conchaspidae*), 22. *Stictococcus* COCKERELL (*Stictococcidae*), 23. *Kerria* TARGIONI TOZZETTI (*Kerriidae*), 24. *Opisthoscelis* SCHRADER (*Opisthoscelis* group), 25. *Eulecanium* COCKERELL (*Coccidae*), 26. *Lachnodius* MASKELL (*Lachnodius* group), 27. *Callococcus* FERRIS (*Callococcus* group), 28. *Trichococcus* KANDA (*Beesoniidae*), 29. *Asterodiaspis* SIGNORET (*Asterolecaniidae*), 30. *Halimococcus* COCKERELL (*Halimococcidae*), 31. *Phoenicococcus* COCKERELL (*Phoenicococcidae*), 32. *Quadraspidotus* MCGILLIVRAY (*Diaspididae*)

and MORRISON, 1965), DROZDOVSKIJ (1966), WĘGLARSKA (1966) and others carried out a number of studies on the histology, cytology and genetics in various groups of scale insects. BUCHNER (1965 and others) investigated the endosymbionts. BORATYNSKI (1961), TAKAGI and KAWAI (1967), KOSZTARAB and his collaborators (YANG and KOSZTARAB, 1967; D'ASCOLI and KOSZTARAB, 1969; WILLIAMS and KOSZTARAB, 1970) and others carried out comparative investigations on the nymphal instars. Particular attention has been given recently to the morphology of the adult male. The investigations on the male were initiated as early as the 19th century, but intensive studies and serious attempts to construct independent phylogenetic conclusions have been made since the publication of the paper by THERON (1958). With the investigations on the males a "new" method was introduced to the taxonomy of the scale insects, i.e. the numerical techniques (BORATYNSKI and DAVIES, 1971).

All these methods brought many constructive findings and helped to understand better the phylogeny of the scale insects, indicating also the directions of further investigations, but with the given methods only several dozen species were examined, e.g., the comparable data concerning the males slightly exceed 100 species, which constitutes about 2% of the estimated number of described species. Another significant drawback of these methods is that thousands of slides collected in museums cannot be utilized and new materials must be collected or bred in the laboratory. This extends considerably every study and the subsequent papers provide less and less comparable information.

As concerns the studies on the morphology and taxonomy of the adult male, it is already known that due to the parthenogenesis of some species and the occurrence of the "larviform" males in the others, the establishment of a comprehensive classificatory system which could comprise all the groups and species of scale insects is impossible. Furthermore, the conception of the evolution of the male expressed in some recent papers (BORCHSENIUS, 1956, 1965; BORATYNSKI and DAVIES, 1971) cannot be accepted by the author without reservation. According to these students the evolution of the male was less rapid than that of the female and followed the changes which first occurred in the latter, being mainly concerned with characters connected with fertilization. The males, moreover, devoid of the mouthparts, are not under the stress of the adaptative processes bound with the feeding. Thus, this sex may have preserved more features of the "normal" insects than the female, and owing to this, it may constitute a better object for the investigations on phylogeny and for classification of scale insects than the latter. But the point is, what we know about the morphological changes of structures not connected with fertilization or nutrition, what are their trends, and what has brought them about. In some species we can observe reduction processes which lead to polymorphism of the males, represented by the "normal", brachypterous, apterous, and larval forms (SCHMUTTERER, 1952; DZIEDZICKA, 1961; AFIFI, 1968). Analogically the normal males could decay in some groups of scale insects. But we know nothing about the progressive processes which could follow particularly at the "beginning" of the evolution of

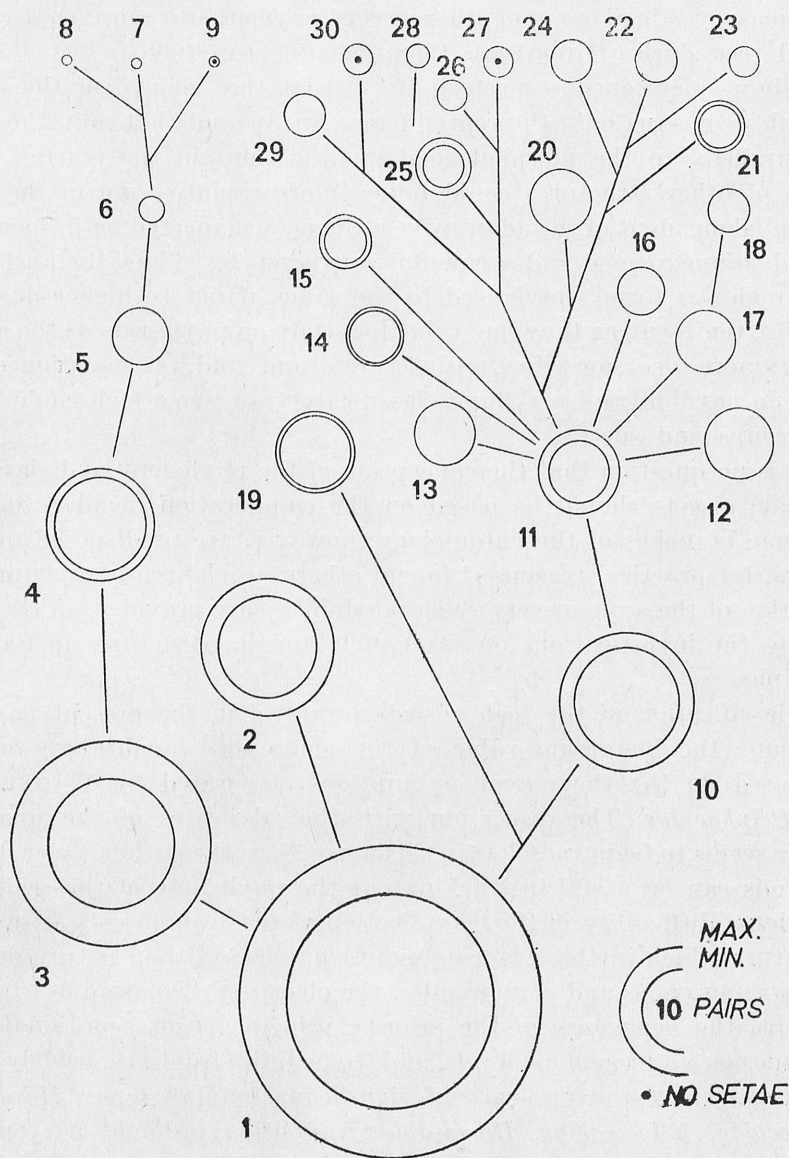


Fig. 2. Reduction of the setae on the labium in the *Coccinea*. The diameter of the circles represents the number of setae. (After KOTEJA, 1974)

1. *Phenacoleachiidae*, 2. *Ortheziidae*, 3. *Monophlebidae*, 5. *Neosteingelia* group, 6. *Kuwaniidae*, 7. *Xylococcidae*, 8. *Matsucoccidae*, 9. *Porphyrophoridae*, 10. *Pseudococcidae*, 11. *Acanthococcidae*, 12. *Dactylopiidae*, 13. *Apiomorphidae*, 14. *Kermesidae*, 15. *Cerococcidae*, 16. *Calyeicoccidae*, 17. *Cryptococcidae*, 18. *Kuwanina* group, 19. *Conchaspidiidae*, 20. *Stictococcidae*, 21. *Kerriidae*, 22. *Coccidae*, 23. *Lachnodi* group, 24. *Opisthoscelis* group, 25. *Callococcus* group, 26. *Beesoniidae*, 27. *Asterolecaniidae*, 28. *Halimococcidae*, 29. *Phoenicococcidae*, 30. *Diaspididae*



scale insects as a group. The interpretation of the homology of some structures in the male is difficult and we often hesitate whether a given structure should be considered as a vestigial organ of other insects, or whether it represents a new one, developed secondarily (GILIOMEY, 1968; BEARDSLEY, 1968).

The above mentioned respects indicate that the "delay" of the evolution of the males concerns only the reproductive organs and that only these organs evolve parallelly to the morphological modifications in the females, but the evolution of other structures could follow more rapidly than in the females, and being independent of the adaptative influences connected with the nutrition, could lead to unexpected and accidental convergencies. Thus, the author considers the males as forms specialized to the same, if not to higher degree than the females, representing the same value for study on phylogeny as the latter but providing more occasions for misinterpretation, and, as mentioned above, offering no possibility of making a classificatory system which could comprise all the groups and species.

There is no question that the conception of the phylogeny and classification of the scale insects should be based on the co-operation in all entomological fields. Some branches of the entomology, however, are predisposed more than the others, for practical reasons if for no others, to elaborate a comprehensive classification of the scale insects. Such possibilities are provided, in the author's opinion by the investigations on the cuticle and its structures in the females and nymphs.

The classification of the scale insects proposed in the present paper takes into account the hierarchic value of the characters (qualitative taxonomy) and is based on the theoretical assumptions elaborated by WAGNER (1962) for the *Delphacidae*. The discussion with the advocates of the quantitative taxonomy seems to be purposeless in this paper. It is the author's view that both the methods can be useful in tracking out the phylogeny of the scale insects.

Additional difficulties in the classification of the scale insects arise from the nomenclature which in this group is more complicated than in any other. The numerous synonymies and homonymies, the obscure designation of type species and genera, the negligence of the priority principle, cause continual changes of the names on all taxonomic levels, and, to be quite frank, the widely accepted and used names of the majority of significant families (e.g., *Margarodidae*, *Pseudococcidae*, *Eriococcidae*, *Diaspididae* and others) should be rejected for various reasons and substituted by other names. The attempt of solving the nomenclatorial problems made recently by MORRISON and MORRISON (1966) and WILLIAMS (1969) was very helpful in the present study.

#### TAXONOMIC CATEGORIES

The scale insects are regarded as being the most specialized group among the *Homoptera*. The earlier authors supposed their affinities with the *Aleyrodinea* (OSBORN, KIRKALDY, TILLYARD, SPOONER) or *Psyllinea* (HANDLIRSCH, WEBER).

Recently, the opinion on the close relationship of *Coccinea* with *Aphidinea* has been widely accepted (THERON, 1958; BORATYNSKI and DAVIES, 1971).

The information on the mouthparts is more complete in the *Aphidinea*, *Psyllinea* and *Aleyrodinea* than in the *Coccinea*, but these groups also lack in comprehensive investigations based on large material. With this in view, the author will not discuss the relationship between scale insects and other *Sternorrhyncha* because the comparison of scattered data actually available does not seem to lead to reliable conclusions.

Some authors (OBENBERGER, 1957) suggested that groups which constitute the *Sternorrhyncha* should form distinct orders, the others, on the contrary (LINDINGER, 1957), determined the level of scale insects as no higher than a family. WILLIAMS (1969), commenting upon the investigations on the males wrote: "If adult male characters had been used (as basis for classification) from the beginning instead (the female ones), then probably no category higher than a family would have been recognized for the whole group".

In the present paper the scale insects are regarded as a suborder — *Coccinea*, as in the publications by OBENBERGER (1957), DANZIG (1964), PESSON (1951) and others. This category seems to harmonize with the classification within the *Homoptera* as well as within the scale insects.

In the literature of scale insects different systems of classification can be found. MACGILLIVRAY (1921), SILVESTRI (1939), BODENHEIMER (1952), BORCHSENIUS (1950) and others divided the scale insects into two major groups — the *Paleococcoidea* (*Archaeococcoidea*, *Paleococcomorpha* and other names) and *Neococcoidea* (*Neococcidae*, *Neococcomorpha* and others); the former group containing the *Ortheziidae*, *Margarodidae* (s.l.) and occasionally the *Phenacoleachiidae*, i.e. all the insects in which the abdominal spiracles are present, the latter comprising the remaining families with the abdominal spiracles absent. The first group was considered to be more primitive and the second more specialized.

In the second type of classification, represented by the system of BALACHOWSKY (1942, 1948), adopted also by other workers (OBENBERGER, 1957), the scale insects are divided into three major groups ("phylla") — the *Margaroidae*, *Lecanoidae* and *Diaspidoidae*. This classification, based on the morphology of the male, was supported by many investigations in the recent years.

The third type is presented by MAMET (1954a) and BALACHOWSKY (1956). The latter divided the scale insects into four families — the *Margarodidae*, *Lecaniidae*, *Conchaspidae* and *Diaspididae* (cited after SCHMUTTERER, KLOFT and LÜDICKE, 1957). The fourth type represents the classification by FERRIS (1957). This author divided the scale insects into six major groups ("rami") — the *Margarodi*, *Eriococci*, *Cocci*, *Lacciferi*, *Beesoni* and *Diaspidi*.

On the basis of the structure of the mouthparts at least two higher categories can be recognized — i.e. the superfamily category and the family group category. The superfamilies are represented by the *Orthezioidea* which correspond with the *Paleococcoidea*, and the *Coccoidea* corresponding with the *Neococcoidea*. The two



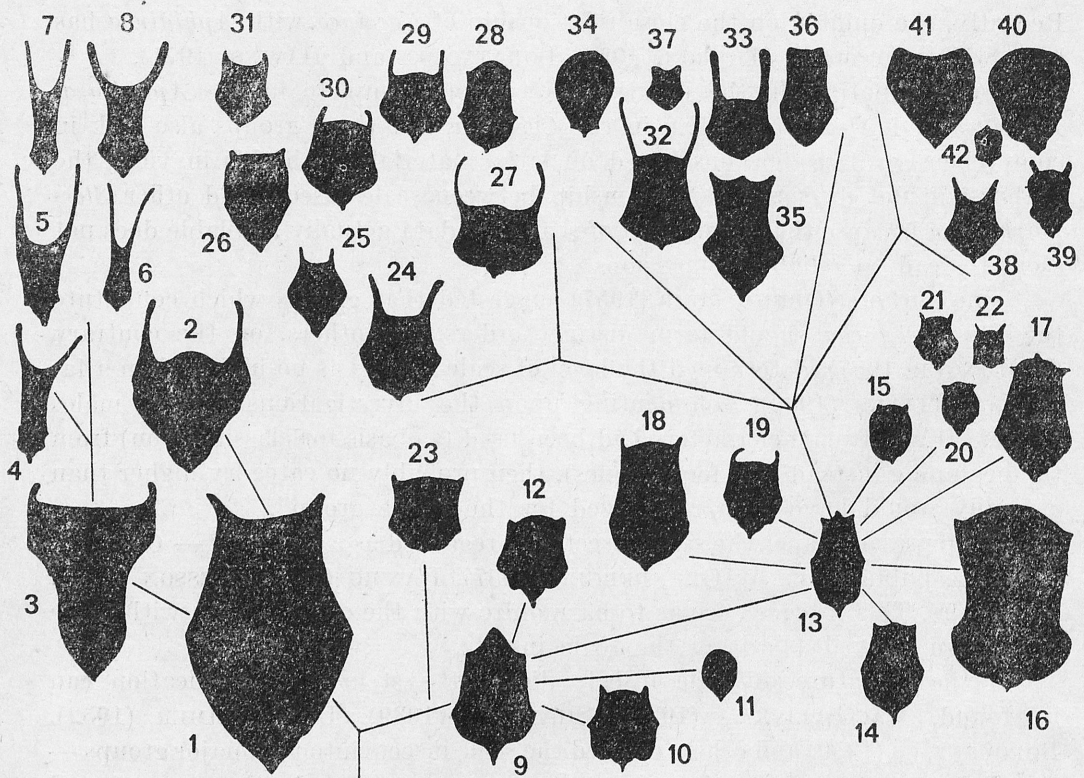


Fig. 3. Evolutionary trends of the clypeolabral shield in the *Coccinea*

1. *Phenacoleachia* COCKERELL (*Phenacoleachiidae*), 2. *Orthezia* BOSC D'ANTIC (*Ortheziidae*), 3. *Gueriniella* FERNALD (*Monophlebidae*), 4. *Coelostomidia* COCKERELL (*Coelostomidiidae*), 5. *Neosteingelia* MORRISON (*Neosteingelia* group), 6. *Kuwanina* COCKERELL (*Kuwaninae*), 7. *Xylococcus* LÖW (*Xylococcidae*), 8. *Porphyrophora* BRANDT (*Porphyrophoridae*), 9. *Phenacoccus* COCKERELL (*Pseudococcidae* — *Trabutinae*), 10. *Antonina* SIGNORET (*Pseudococcidae* — *Sphaerococcinae*), 11. *Rhizococcus* KÜNCKEL D'HERCULAIS (*Pseudococcidae* — *Rhizococcinae*), 12. *Pseudococcus* WESTWOOD (*Pseudococcidae* — *Pseudococcinae*), 13. *Phloeococcus* HOY (*Acanthococcidae* — *Phloeococcus* group), 14. *Gossyparia* SIGNORET (*Acanthococcidae* — *Acanthococcini*), 15. *Ovaticoccus* KLOET (*Acanthococcidae* — *Ovaticoccus* group), 16. *Dactylopius* O. G. COSTA (*Dactylopiidae*), 17. *Apiomorpha* RÜBSAAMEN (*Apiomorphidae*), 18. *Kermes* BOITARD (*Kermesidae*), 19. *Cerococcus* COMSTOCK (*Cerococcidae*), 20. *Calycicoccus* BRAIN (*Calycicoccidae*), 21. *Pseudochermes* NITSCHKE (*Cryptococcidae*), 22. *Kuwanina* COCKERELL (*Kuwanina* group), 23. *Conchaspis* COCKERELL (*Conchaspidae*), 24. *Stictococcus* COCKERELL (*Stictococcidae*), 25. *Kerria* TARGIONI TOZZETTI (*Kerriidae*), 26. *Austrotachardia* CHAMBERLIN (*Kerriidae*), 27. *Eulecanium* COCKERELL (*Coccidae* — *Ctenochitini*), 28. *Psilococcus* BORCHSENIUS (*Coccidae* — *Eriopeltini*), 29. *Ceroplastes* GRAY (*Coccidae* — *Coccini*), 30. *Prosopophora* DOUGLAS (*Lecanodiaspididae*), 31. *Nipponaclerda* MCCONNELL (*Acleridae*), 32. *Callococcus* FERRIS (*Callococcus* group), 33. *Capulinia* SIGNORET (*Asterolecaniidae* family group), 34. *Asterodiaspis* SIGNORET (*Asterolecaniidae*), 35. *Trichococcus* KANDA (*Beesoniidae*), 36. *Halimococcus* COCKERELL (*Halimococcidae*), 37. *Thysanococcus* STICKNEY (*Asterolecaniidae* family group), 38. *Phoenicococcus* COCKERELL (*Phoenicococcidae*), 39. *Lepidosaphes* SHIMER (*Diaspididae*), 40. *Howardia* BERLESE et LEONARDI (*Diaspididae*), 41. *Limacoccus* BONDAR (*Diaspididae* family group), 42. *Xanthophthalma* COCKERELL et PARROTT (*Diaspididae* family group)



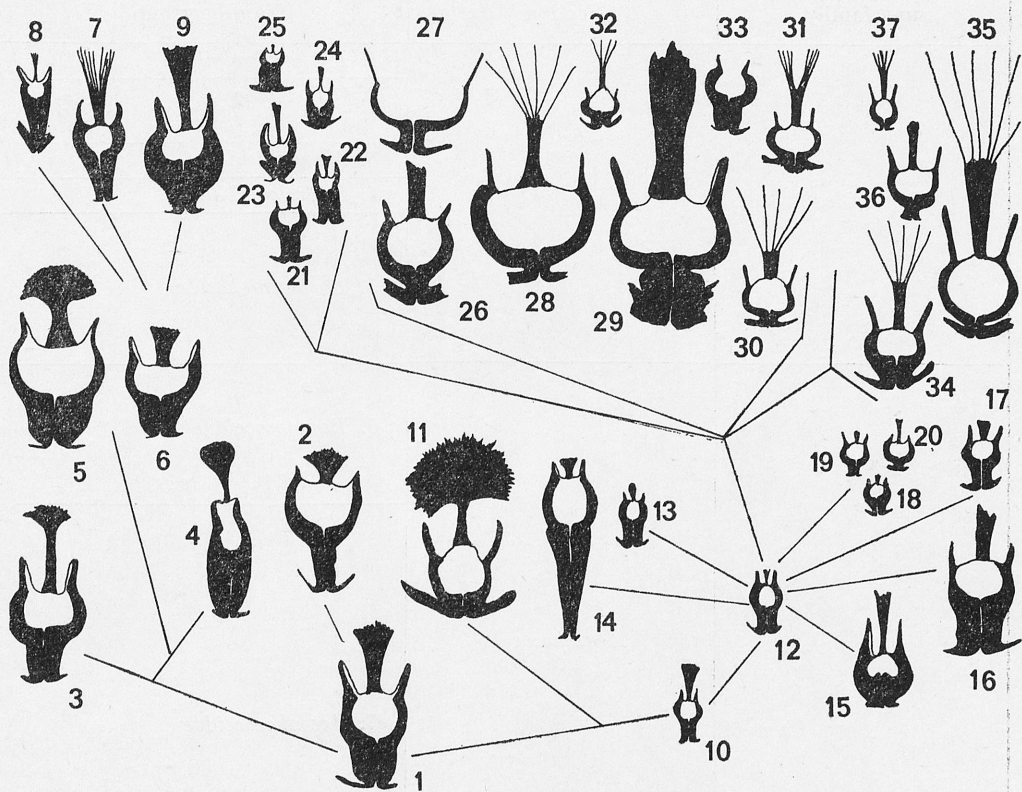


Fig. 4. Evolutionary trends of the sucking pump in the Coccinea

1. *Phenacoleachia* COCKERELL (*Phenacoleachiidae*), 2. *Arctorthesia* COCKERELL (*Orthezidae*), 3. *Icerya* SIGNORET (*Monophlebidae*), 4. *Coelostomidia* COCKERELL (*Coelostomidiidae*), 5. *Neosteingelia* MORRISON (*Neosteingelia* group), 6. *Kuwania* COCKERELL (*Kuwaniidae*), 7. *Matsucoccus* COCKERELL (*Matsucoccidae*), 8. *Xylococcus* LÖW (*Xylococcidae*), 9. *Dimargarodes* SILVESTRI (*Porphyrophoridae*), 10. *Phenacoccus* COCKERELL (*Pseudococcidae*), 11. *Conchaspis* COCKERELL (*Conchaspidae*), 12. *Acanthococcus* SIGNORET (*Acanthococcidae*), 13. *Cerococcus* COMSTOCK (*Cerococcidae*), 14. *Kermes* BOITARD (*Kermesidae*), 15. *Xerococcus* FERRIS (*Acanthococcidae* family group), 16. *Dactylopius* O. G. COSTA (*Dactylopiidae*), 17. *Apiomorpha* RÜBSAAMEN (*Apiomorphidae*), 18. *Cryptococcus* DOUGLAS (*Cryptococcidae*), 19. *Calyciococcus* BRAIN (*Calyciococcidae*), 20. *Kuwanina* COCKERELL (*Kuwanina* group), 21. *Stictococcus* COCKERELL (*Stictococcidae*), 22. *Kerria* TARGIONI TOZZETTI (*Kerriidae*), 23. *Lecanodiaspis* TARGIONI TOZZETTI (*Lecanodiaspididae*), 24. *Lecanopsis* TARGIONI TOZZETTI (*Coccidae*), 25. *Aclerda* SIGNORET (*Aclerdiidae*), 26. *Lachnodius* MASKELL (*Lachnodius* group), 27. *Capulinia* SIGNORET (*Asterolecaniidae* family group), 28. *Opisthoscelis* SCHRADER (*Opisthoscelis* group), 29. *Callococcus* FERRIS (*Callococcus* group), 30. *Asterodiaspis* SIGNORET (*Asterolecaniidae*), 31. *Trichococcus* KANDA (*Beesonidae*), 32. *Thysanococcus* STICKNEY (*Asterolecaniidae* family group), 33. *Halimococcus* COCKERELL (*Halimococcidae*), 34. *Phoenicococcus* COCKERELL (*Phoenicococcidae*), 35. *Maskellia* FULLER (*Diaspididae*), 36. *Limacoccus* BONDAR (*Diaspididae* family group), 37. *Xanthophthalma* COCKERELL (*Diaspididae* family group)

Classification of the

Superfamily	Section	Family group
<i>Orthezoidea</i>		1. <i>Phenacoleachiidae</i>
		2. <i>Ortheziidae</i>
		3. <i>Monophlebidae</i>
		4. <i>Coelostomidiidae</i>
		5. <i>Porphyrophoridae</i>
<i>Coccoidea</i>		6. <i>Pseudococcidae</i>
		7. <i>Acanthococcidae</i>
	<i>Acanthococci</i>	8. <i>Onchaspidae</i>
		9. <i>Coccidae</i>
		10. <i>Asterolecaniidae</i>
	<i>Cocci</i>	11. <i>Diaspididae</i>

Table I

suborder *Coccinea*

Family	Subfamily	Tribe
1. <i>Phenacoleachiidae</i>		
2. <i>Ortheziidae</i>	<i>Orthezia</i> group <i>Newsteadia</i> group	
3. <i>Monophlebidae</i>		
4. <i>Coclostomidiidae</i>		
5. <i>Neosteingelia</i> group		
6. <i>Kuwaniidae</i>		
7. <i>Matsucoccidae</i>		
8. <i>Xylococcidae</i>		
9. <i>Porphyrphoridae</i>		
10. <i>Pseudococcidae</i>	<i>Trabutinae</i> <i>Pseudococcinae</i> <i>Rhizoecinae</i> <i>Sphaerococcinae</i>	
11. <i>Acanthococcidae</i>	<i>Acanthococcinae</i>	<i>Phloeococcus</i> group <i>Acanthococcini</i> <i>Rhizococcus</i> group <i>Ovaticoccus</i> group
	<i>Eriococcinae</i>	
12. <i>Dactylopiidae</i>		
13. <i>Apiomorphidae</i>		
14. <i>Kermesidae</i>		
15. <i>Cerococcidae</i>		
16. <i>Calycicoccidae</i>		
17. <i>Cryptococcidae</i>		
18. <i>Kuwanina</i> group Genera unplaced: <i>Xerococcus</i>		
19. <i>Conchaspididae</i>		
20. <i>Stictococcidae</i>		
21. <i>Kerriidae</i>		
22. <i>Coccidae</i>	<i>Ctenochitinae</i> <i>Eriopeltinae</i> <i>Coccinae</i>	
23. <i>Lecanodiaspididae</i>		
24. <i>Aclerididae</i>		
25. <i>Cissococcidae</i>		
26. <i>Micrococcidae</i>		
27. <i>Lachnoidius</i> group		
28. <i>Opisthoscelis</i> group		
29. <i>Callococcus</i> group		
30. <i>Beesoniidae</i>		
31. <i>Asterolecaniidae</i>		
32. <i>Halimococcidae</i> Genera unplaced: <i>Capulinia</i> , <i>Thysanococcus</i> , <i>Colobopyga</i>		
33. <i>Phoenicococcidae</i>		
34. <i>Diaspididae</i> Genera unplaced: <i>Xanthophtalma</i> , <i>Limacoccus</i>		



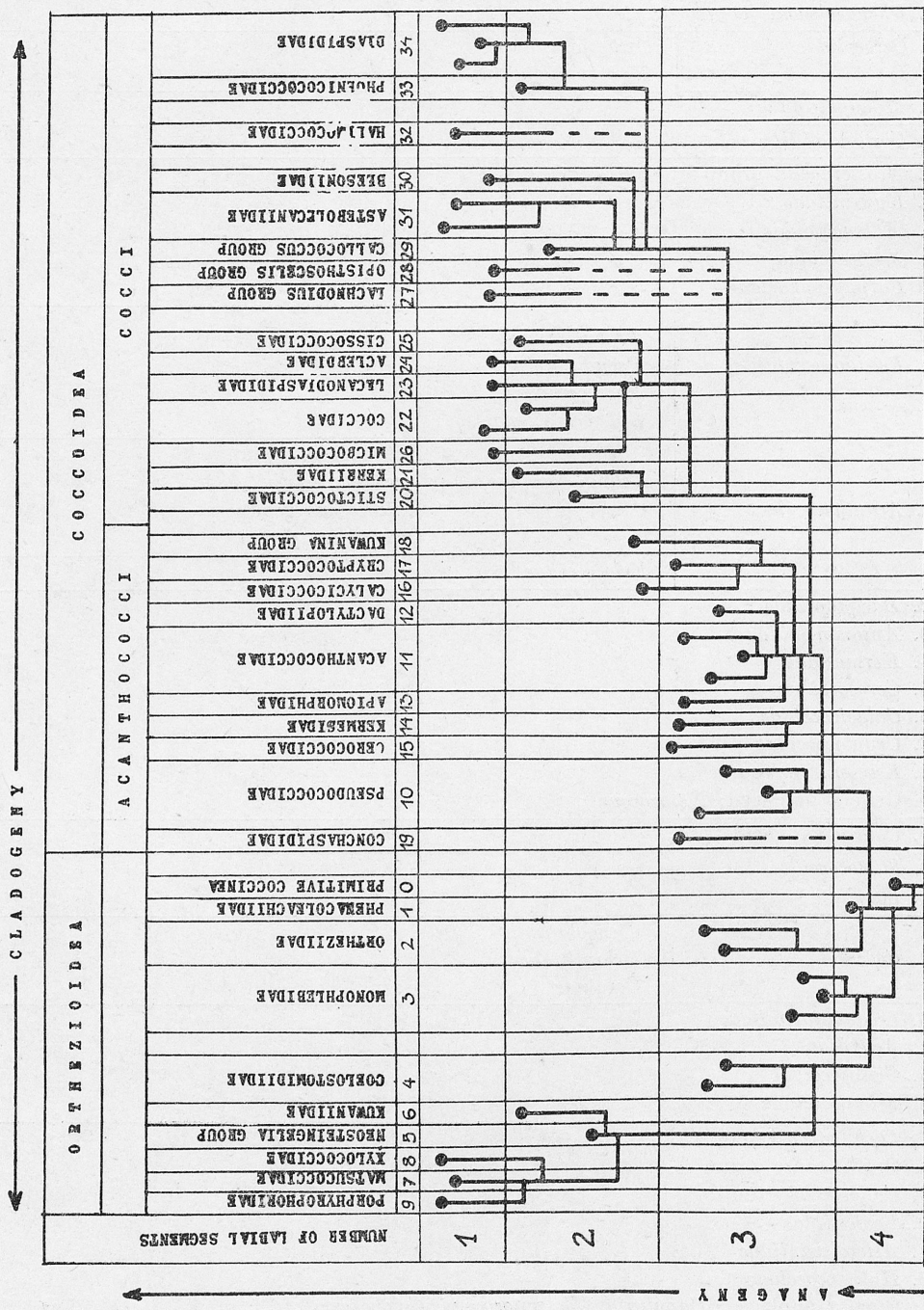


Fig. 5. Probable relationships of families of the *Coccinea*, as indicated by the characters of the mouthparts (labium, clypeolabral shield, sucking pump). The infrafamily branches figured in some families do not represent real groups

superfamilies are distinguished by the presence or absence of the apical setae and apical organ on the labium.

The family groups comprise families which represent different forms of radiation within the same branch. The family groups resemble approximately the "rami" of FERRIS. The most abundant family group is the *Acanthococcidae* family group (= *Eriococcidae* s.l.) which associates as many as 8 families.

The family groups can be further grouped into sections or "floors" which represent great stages of evolution. In the *Orthezioidea* which are represented in the recent fauna only by a small number of forms, the sections are practically identical with the family groups. In the *Coccoidea* two sections can be recognized — the first section containing the *Pseudococcidae*, *Acanthococcidae* and *Conchaspidae* family groups and the second section which comprises the *Coccidae*, *Asterolecaniidae* and *Diaspididae* family groups. It may be noticed incidentally that METCALF (1950) recognized in the *Auchenorrhyncha* six categories higher than the family and lower than the suborder.

Particular attention has been given to the definition of the family category, because it was also the basis for establishing all higher and lower categories. Taking into account the whole of the examined material the author proposes to define the family as the highest category which can be considered on the basis of the mouthparts as a homogeneous and monophyletic group. On the basis of this definition all the aberrant groups and genera should be removed from the actual families, and, if necessary, new families should be established. It appears, furthermore, from this definition that the lower categories are not needed to be natural groups, e.g., the species grouped in the family *Pseudococcidae* derived without doubt from common ancestors, but, taking into account the characters of the mouthparts, the author does not know whether the subfamily *Trabutinae* is a homogeneous group or not.

In the present paper 34 groups of the family category have been recognized. This number includes 29 previously established families or subfamilies and 5 groups of genera which are supposed to represent a family level. Six genera remained unplaced.

In the majority of families the mouth apparatus showed such an uniform structure that its characteristics could be utilized in the infrafamily classification only in a few groups and other features must have been taken into consideration to distinguish subfamilies and tribes.

## THE PHYLOGENY AND CLASSIFICATION OF THE COCCINEA

### Suborder *Coccinea*

*Coccides* FALLÉN, 1814: 23.

The scale insects are widely accepted as a monophyletic group and the present investigations seem to support this view, but on the other hand it is true

that the characters uniting these insects are all specialized features which could originate due to the convergency.

The author recognizes in the phylogeny of the *Coccinea* two major branches — the *Orthezioidea* and the *Coccoidea*, which evolved probably from a common stock (Fig. 5, Tab. I). The genus *Phenacoleachia* is considered to be a relict member of the primitive ancestors. The *Orthezioidea* contain at least two development lines — one leading to the *Ortheziidae*, the other to the remaining groups. Among these, *Monophlebidae* represent the most primitive group, the *Coelostomidiidae* being more specialized and the members of the *Porphyrophoridae* family group, the most specialized. Among the *Coccoidea*, the *Pseudococcidae* should be regarded as an ancestral group for all other families. From the *Pseudococcidae* had derived at an earlier time the *Acanthococcidae* and the *Acanthococcidae* gave rise to the three specialized groups of families centered around the *Coccidae*, *Asterolecaniidae* and *Diaspididae*.

### Superfamily *Orthezioidea*

*Orthezides* AMYOT and SERVILE, 1843: 619;  
*Orthezioidea* AMYOT and SERVILE; CHOU, 1963: 592;  
*Margaroidae* COCKERELL; BALACHOWSKY, 1942: 37;  
*Margarodi* COCKERELL; FERRIS, 1957: 67;  
*Paleococcoidea* BORCHSENIUS, 1950: 14 (not *Palaeococcinae* HEYMONS, 1915);  
*Archaeococcidea* BODENHEIMER, 1952: 317;  
 Generalized *Coccidae* MACGILLIVRAY, 1921: 45.

The *Orthezioidea* introduced by CHOU (1963) as a superfamily name, has priority over names based on the nominal genera *Margarodes*, *Monophlebus*, *Porphyrophora* and *Palaeococcus*.

To the superfamily *Orthezioidea* there are assigned the families *Phenacoleachiidae*, *Ortheziidae* and the groups associated usually with the *Margarodidae* s.l. Since the publication of the principal work by MORRISON (1928) the family status of the *Margarodidae* has been widely accepted, but from time to time students (e.g., GILIOME, 1965, 1967a) expressed the opinion that the groups associated in this "family" represent distinct families. Thus, ZAHRADNIK (1959) elevated the *Xylococcini* to full family rank, JAKUBSKI (1965) limited the name *Margarodidae* to *Margarodes* and closely related genera and established a new family — the *Termitococcidae*. BEARDSLEY (1968) on the basis of male characters elevated the *Matsucoccini* to *Matsucoccinae* and later (1969), the *Pityococcini* to *Pityococcinae*. These actions resulted in a disturbance of MORRISON's classification, but the name *Margarodidae* s.l. was still in use.

The *Orthezioidea* were regarded as a primitive group until the investigations on the male (THERON, 1958, 1962) indicated that also this group contains highly specialized forms.

The characters of the mouthparts well define the *Orthezioidea* and the groups associated in this superfamily. Furthermore, from the structure of the mouthparts it appears clearly that the *Orthezioidea* should not be considered as opposite to the



*Coccoidea* on the ground of specialization, but the two groups should be rather regarded as different phylogenetic branches, both of which contain primitive as well as specialized forms.

The characters of the mouthparts as well as these of the male indicate that the *Orthezioidae* are a relict group comprising various and supposedly heterogeneous forms.

The author assigned to this superfamily the following families *Phenacoleachiidae*, *Ortheziidae*, *Monophlebidae*, *Coelostomidiidae*, *Kuwaniidae*, *Matsucoccidae*, *Xylococcidae*, *Porphyrophoridae* and the unplaced genus *Neosteingelia* which may represent a distinct group.

### ***Phenacoleachiidae* family group**

#### ***Phenacoleachiidae* COCKERELL**

*Phenacoleachiinae* COCKERELL, 1902: 260.

The taxonomic status and the relationships of the genus *Phenacoleachia* have been a problem since it was described. For illustration of the various and contradictory opinions concerning this question a review of some papers in the chronological order is presented below<sup>1</sup>:

MASKELL, 1891, described *Leachia zealandica* and placed it in his *Ortheziinae*, regarding it as a primitive coccid;

COCKERELL, 1896, placed the species *zealandica* in *Palaeococcus* in his *Monophlebinae*;

COCKERELL, 1899a, established for *zealandica* a new genus — *Phenacoleachia* and placed it in his *Ortheziinae* with the comment that it also had some "dactylopine" features;

COCKERELL, 1902<sup>2</sup> recognized the subfamily *Phenacoleachiinae* and placed it in his scheme after the *Margarodinae*;

FERNALD, 1903, placed *Phenacoleachiinae* between *Ortheziinae* and *Conchaspidinae*;

FERRIS, 1921, on the basis of male characters indicated some similarities between *Phenacoleachia* and pseudococcid scale insects, e.g., *Puto*;

MACGILLIVRAY, 1921, placed the *Phenacoleachiinae* between *Ortheziinae* and *Eriococcinae* in the "Specialized Coccidae";

MORRISON and MORRISON, 1922, redescribed *Phenacoleachia zealandica* and stated its uncertain relationships;

BRUES and MELANDER, 1932, elevated the subfamily *Phenacoleachiinae* to full family rank;

PFLUGFELDER, 1939, included *Phenacoleachia* in the *Coccinae*;

BALACHOWSKY, 1942, placed it as a distinct family in his "*Lecanoidae*", indicating that it may link the "*Margaroidae*" with the "*Lecanoidae*";

<sup>1</sup> The author rejected in this statement all the unsuitable spellings of the family name *Phenacoleachiidae*.

<sup>2</sup> This date is given by WILLIAMS (1969). According to THERON (1962) the family-group name was erected in 1900, and according to BALACHOWSKY (1948), in 1899.

- BALACHOWSKY, 1948, lowered its rank, together with other groups, to subfamily category;
- FERRIS, 1957, left it among the "Unplaced Genera" with the remark: "The author would prefer to see them left unattached rather than assume a position that indicates an understanding which we do not possess";
- IMMS, 1957, placed the family *Phenacoleachiidae* between *Asterolecaniidae* and *Stictococcidae*;
- OBENBERGER, 1957, placed it in the "*Lecanioidea*" between *Lacciferidae* and *Asterolecaniidae*, indicating that it has some characters in common with the *Margarodidae*;
- BORCHSENIUS, 1958, assigned *Phenacoleachiidae* in the *Archaeococcoidea* and stated that they represent the most primitive and the oldest group of scale insects;
- THERON, 1962, on the basis of male characters, stated: "*Phenacoleachia* ostensibly belongs to the margaroid group, but is apparently not closely related to any member of it, except perhaps to the European genus *Steingelia*" and "... it should presumably be regarded as an annectant genus, linking the primitive *Margarodidae* with the more specialized *Lecanoidae*";
- KAWECKI, 1964, indicated that the number of bristles on the hamulohalters in *Phenacoleachia* is more reduced than in some species of the family *Lecaniidae* (= *Coccidae*);
- BEARDSLEY, 1964, described a second species of *Phenacoleachia* — *Ph. australis* and discussed the position of this genus; his conclusion was that "*Phenacoleachia* might well be regarded as constituting a primitive subfamily of the family *Pseudococcidae*";
- GILIOMEE, 1967, indicated (on the basis of male characters) that *Phenacoleachia* is more similar to *Pseudococcidae* than to *Coccidae*, and *Steingelia* vice versa more similar to *Coccidae* than to *Pseudococcidae*, but he added: "At this stage of research it is difficult to determine, however, whether the similarities have any phylogenetic significance or whether they are merely due to the convergency";
- AFIFI, 1968, followed the idea of GILIOMEE and, using simple numerical methods, came to the conclusion that "there appeared to be at least two links between the primitive margaroids and the more specialized lecanoids" — one represented by *Steingelia* (*Margarodidae* — *Coccidae*) and the second by *Phenacoleachia* (*Margarodidae* — *Pseudococcidae*);
- WILLIAMS, 1969, on ground of the investigations by THERON (1962) and BEARDSLEY (1964) proposed the association of the genera *Steingelia*, *Phenacoleachia* and possibly *Puto* into one group;
- BORATYNSKI, 1970, agreed with the authors who regarded the "*Lecanoidae*" as a polyphyletic group, with *Phenacoleachia* and *Steingelia* as annectant genera, and later;
- BORATYNSKI and DAVIES, 1971, presented this conception in the form of a phylogenetic tree.

From this statement a conclusion could be drawn which appears somewhat paradoxical, namely that *Phenacoleachia* is closely related with nearly all families, and that it is primitive and specialized at the same time. When the characters of the labium are taken into consideration there is no doubt where to place this genus and what a specialization level it represents. The labium in *Phenacoleachia* is not comparable with that of any other group or genus, and represents an extremely primitive condition. It is very long and slender, four-segmented, with numerous setae variable in number. Labia of such a structure are to be found among the primitive *Aphidinea*.

*Phenacoleachia* is not related to *Steingelia*<sup>1</sup>. The mouthparts in these two genera show a basically different structure. The opinion on the relation between them is based on the male characters, but with the increasing accumulation of the information it becomes obvious that the evolution of the males follows parallelly in all groups of *Coccinea*, and that we can never decide whether a given structure represents a primitive or specialized condition. Thus, e.g., the presence of a large number of radially arranged, similar, unicorneal eyes usually marked as a character shared by *Phenacoleachia* and *Steingelia*, has been stated also in *Pityococcus* and *Electrococcus* (both *Margarodidae* s.l., BEARDSLEY, 1969), *Puto* (BEARDSLEY, 1962), *Kermes* (BORCHSENIUS, 1960) and some *Coccidae* (GILIOMEE, 1967). For the same reasons *Phenacoleachia* cannot be included in the *Coccoidea* (= "lecanoid" coccids). Mention should be made here, moreover, that THERON (1962) and BEARDSLEY (1964) found abdominal spiracles in both males *Phenacoleachia zealandica* and *Ph. australis*.

The author protests strongly against the conception according to which *Phenacoleachia* and *Steingelia*, as highly specialized representatives of the *Margarodidae* (s.l.), may be regarded, each separately, as annectant genera between the margaroid and lecanoid coccids. *Phenacoleachiidae* can be regarded as a group from which the *Coccoidea* derived not due to their specialization but that they represent in fact the most primitive features known in the *Coccinea*. In this respect *Phenacoleachiidae* can be considered as well as an ancestral group for the *Orthezioidea*. As mentioned elsewhere in this paper, the males achieved specialized conditions independently in many groups. The mouthparts in *Steingelia*, however, represent a high level of specialization, which is in this case in accordance with that of the male, and therefore this genus should be rejected as a link between *Margarodidae* (s.l.) and *Coccidae* (for further discussion see "*Kuwaniidae*").

As concerns the relationship between *Phenacoleachiidae* and *Pseudococcidae*, it can be said on the basis of the structure of the mouthparts that these two groups share really more common characters in comparison with other combinations, e.g., *Phenacoleachiidae* — *Acanthococcidae*, or *Coccidae*, but this is rather

<sup>1</sup> The author's names of genera and species, with some necessary exceptions, are omitted in this paper. For full list of generic and specific author names of taxa under discussion see the earlier paper (KOTEJA, 1974).



clear if we take into consideration that *Pseudococcidae* are the most primitive group among the *Coccoidea*.

In the opinion of the author, based on the characters of the mouthparts, *Phenacoleachia* represents a relict member of an archaic group of scale insects which was probably widely distributed and now limited to New Zealand and some Pacific islands. In the independent evolutionary processes some members of this group achieved a high level of specialization, and on the other hand, from this group derived the other, at least two, major groups of modern *Coccinea* — the *Orthezioidea* and *Coccoidea*. This conception is close to the suggestions expressed by the earliest authors and later by BORCHSENIUS (1958).

### *Ortheziidae* family group *Ortheziidae* AMYOT and SERVILE

*Orthezides* AMYOT and SERVILE, 1843: 619.

The *Ortheziidae* have been widely accepted as a well defined and isolated group, sometimes associated with the *Margarodidae* (s.l.) in a higher taxon, the *Margaroidae* (BALACHOWSKY, 1942) or *Archaeococcidea* (BORCHSENIUS, 1950). These opinions are supported by the present investigations.

The characters of the mouthparts indicate that the *Ortheziidae* represent a level of specialization which can be compared with that in the *Coelostomidiidae* and in the primitive groups of *Coccoidea*, but acquired in a quite different way. The *Ortheziidae* have derived from the primitive ancestors supposedly as a separate branch.

On the basis of the labial characters the *Ortheziidae*<sup>1</sup> could be further divided into two groups — the *Orthezia* group (*Orthezia* and *Arctorthezia*) and the *Newsteadia* group (*Newsteadia* and *Ortheziola*). This groupment displays some common points with the classification by MORRISON (1952), but due to the scarcity of the examined material it is difficult to ascribe any definite taxonomic status to these groups.

### *Monophlebidae* family group *Monophlebidae* SIGNORET

*Monophlebites* SIGNORET, 1875: 350;

*Palaeococcinae* HEYMONS, 1915: 183.

The *Menophlebidae* have been regarded for a long time as a subfamily in the family *Margarodidae*. In the recent years some authors (ZAHRADNIK, 1959) elevated this group to full family rank.

There is no doubt that the *Monophlebidae* represent one of the most primitive groups in the whole suborder, although, as far as the structure of the mouthparts

---

<sup>1</sup> The genera and species assigned to this and other families, discussed in the present paper are listed in the earlier publication dealing with the morphology of the labium (KOTEJA, 1974).

is concerned, they contain also forms which show a high degree of specialization (*Icerya*).

The *Monophlebidae* possess an exclusive character — the presence of a special kind of setae on the labium — the "sensory setae", which was not found in any other group, and there is a basical question whether this group represents a separate branch on the phylogenetic tree of the *Orthezioidea* or whether it can be regarded as an ancestral group from which the other orthezioids have derived. The structure of the clypeolabral complex seems to support this latter conception.

MORRISON (1928) recognized in the *Monophlebidae* (subfamily according to this author) several lower taxa. Although the characters of the mouthparts well define the genera assigned to this group, a classification was rather not possible because only a few species were examined. It can be only said that *Drosicha* represents the most primitive and *Icerya* the most specialized members of this family.

### ***Coelostomidiidae* family group**

#### ***Coelostomidiidae* MORRISON**

*Coelostomidiinae* MORRISON, 1927: 102.

MORRISON assigned the subfamily *Coelostomidiinae*, with the tribes *Marchalini*, *Platycoelostomini* and *Coelostomidiini* to the family *Margarodidae*. MCKENZIE (1942) recognized the tribe *Pityococcini* and included it in this subfamily. BEARDSLEY (1969) elevated this tribe to subfamily rank.

The characters of the mouthparts well define this small group, which is more specialized than the *Monophlebidae* but evidently more primitive than the remaining groups of the *Orthezioidea*, excluding *Phenacoleachia*. It is worth noticing that the structure of the labium (but not that of the clypeolabral complex and sucking pump) in this group is very similar to that in the *Pseudococcidae*.

If the author is right in regarding the *Monophlebidae* as a group from which the other *Orthezioidea* derived, the *Coelostomidiidae* could be considered as a link between the former and the members of the *Porphyrophoridae* family group.

### ***Porphyrophoridae* family group**

This family group contains some genera which with respect to the structure of the mouthparts should be considered as highly specialized scale insects. Similar conclusions can be drawn if other features are taken into account, e.g., the morphology of the male in *Steingelia*, the morphology and biology of the *Porphyrophoridae* and *Xylococcidae*, and others.

The author could not accept the classification of the insects assigned here given by MORRISON (1928), but on the other hand, due to the scarcity of the examined materials, he also could not offer another, satisfactory conception. The genera associated in this group on the basis of the similar structure of the

clypeolabral complex, seem to represent a heterogenous assemblage and the family group name indicates in this particular case the high specialization level of the included taxa, rather than the phylogenetic relations.

The author assigned to the *Porphyrophoridae* family group, tentatively, the following genera and families: *Neosteingelia*, *Kuwaniidae*, *Matsucoccidae*, *Xylococcidae* and *Porphyrophoridae*. *Neosteingelia* and *Kuwaniidae* probably represent a natural group, but the relations and origin of the other families remain obscure.

### *Neosteingelia* group

*Neosteingelia* MORRISON, 1927: 101.

MORRISON (1928) placed this genus in the tribe *Kuwaniini* together with *KUWANIA* (subfamily *Margarodinae*, family *Margarodidae* after the classification by MORRISON). The author had the opportunity to examine *Neosteingelia* as well as *Dimargarodes* and *Porphyrophora*, the members of another tribe — the *Margarodini*, and came to a different conclusion than MORRISON. On the basis of the labial characters *Neosteingelia* cannot be associated with the *Margarodes* group (in this respect the author agrees with JAKUBSKI, 1965), and its relation with *Kuwanina* cannot be regarded as very close, either. On the other hand, *Kuwanina* is close to *Steingelia*. In this situation the author left the genus under discussion unattached, but with an indication that it could be regarded as a link between the *Coelostomidiidae* and *Kuwaniidae*.

The labium, and particularly the clypeolabral shield and sucking pump in *Neosteingelia* represent a comparatively high degree of specialization.

### *Kuwaniidae* MACGILLIVRAY

*Kuwaniinae* MACGILLIVRAY, 1921: 45;

*Steingeliinae* MORRISON, 1927: 101.

COCKERELL (1909) included *Kuwanina* in a table of genera allied to *Xylococcus* (*Margarodinae*, *Xylococcini*); MORRISON (1928) placed it with *Neosteingelia* in the *Kuwaniini* (*Margarodinae*); MACGILLIVRAY (1921) assigned *Kuwanina* together with *Matsucoccus*, *Paragreenia*, *Americococcus*, *Stomacoccus* and *Steingelia* in his *Kuwaniinae*.

The genus *Steingelia* has been placed by its describer (NASSONOV, 1908) close to *Xylococcus*; MORRISON (1928) assigned it with *Stomacoccus* to the subfamily *Steingeliinae* and it would probably remain as an ordinary member of the *Margarodidae* (s.l.) had it not been for the male which caused a discussion persisting to this day. First GREEN (1917) noticed the unusual form of the male and suggested the removal of this genus from the *Margarodidae*. In a later



work (1920) he supposed that the male characters of *Steingelia* may constitute a connecting link between the *Margarodidae* and *Pseudococcidae*. MORRISON (1928) was so surprised by the unusual structure of the male that he supposed the specimens were erroneously determined and may belong to another coccid. THERON (1958) studied the male in detail and stated that this species, showing affinities with *Margarodidae*, is also close to *Eulecanium* and *Pseudococcus*. He agreed with GREEN that *Steingelia* should be removed from the *Margarodidae*, and that it constituted a link between *Margarodidae* and *Pseudococcidae*. Later, THERON (1962) studied another unusual genus — *Phenacoleachia*, and came to the conclusion that the two genera "seem to be fairly closely related and their inclusion to the same family is perhaps not unlikely". GILLOMEE (1967), on the basis of male characters stated that all the compared characters (7) which differentiate *Steingelia* and *Phenacoleachia* are shared between the latter and the *Pseudococcidae*, and on the other hand, 6 of them (opposite conditions) are found in *Steingelia* and *Coccidae*. AFIFI (1968) established that *Steingelia* shares 73% of the compared male characters with *Margarodidae* and 77% with *Coccidae* (12 characters were compared), whereas *Phenacoleachia* shares 73% with *Margarodidae* and 88% with *Pseudococcidae*. For completion it can be added that *Steingelia* and *Phenacoleachia* share 62% characters, and *Coccidae* with *Pseudococcidae* have only as few as 42% characters in common.

On the basis of these data, WILLIAMS (1969) and BORATYNSKI and DAVIES (1971) expressed some, rather contradictory, general suggestions. WILLIAMS proposed the including of *Steingelia* and *Phenacoleachia* (and *Puto*) into one family. BORATYNSKI and DAVIES suggested that the two genera represent, each, a different phylogenetic branch — *Phenacoleachia* linking the *Margarodidae* with *Pseudococcidae* (and *Eriococcidae* and *Dactylopiidae*), *Steingelia* — the *Margarodidae* with the *Coccidae* and all other lecanoid and diaspidoid coccids.

The present investigations show that *Steingelia* cannot be associated with *Phenacoleachia* (see above "*Phenacoleachiidae*"), and much less with the *Coccidae*. *Steingelia* is a definite member of the *Orthezioidea* (= *Margarodidae* s.l.) in all its respects. The similarities between the male of this genus and that of the *Coccidae* indicate only the similar specialization level. The labium, for instance, is two-segmented in the two groups, but this does not mean that they may be closely related. For the same reasons the idea that *Steingelia* may form a link between *Margarodidae* and *Coccidae* must be rejected. This genus, being highly specialized with respect to both male and female, cannot be regarded as an annectant form between any groups. It is generally known that the phylogenetic links are usually represented by primitive forms.

On the basis of the characters of the mouthparts it can be said that *Steingelia* belongs to the superfamily *Orthezioidea*, being closely related to *Kuwania* and, to a lesser degree, to *Neosteingelia*. This group represents a comparatively high level of specialization in the superfamily. The author supposes that *Kuwaniidae* may represent a separate branch which derived from the *Coelostomidiidae*.

*Matsucoccidae* MORRISON

*Matsucoccini* MORRISON, 1927: 101;

*Matsucoccinae* MORRISON; BEARDSLEY, 1968: 1458.

This group represents another case of a striking incongruity between the opinions based on the male morphology and the results of the present investigations. MORRISON (1928) included the tribe *Matsucoccini* to the subfamily *Xylococcinae*, family *Margarodidae*. BEARDSLEY (1968) examined the male of *Matsucoccus bisetosus* and came to the conclusion that *Matsucoccus* was one of the most primitive genera among the *Margarodidae* (s.l.), not particularly closely related to *Margarodes*, *Xylococcus* or *Monophlebus*, but rather showing similarities with *Orthezia* and *Aphis*, and he advised that it should form a separate group, if the classification by MORRISON was accepted, of a subfamily rank.

Contrarily to the opinion presented above, the characters of the mouthparts indicate that *Matsucoccus* is one of the most specialized genera among the superfamily *Orthezioidea*. Its relation to *Xylococcus* or *Margarodes* cannot be precluded, but it seems most unlikely that *Matsucoccus* could have some affinities with the *Ortheziidae*. The author can say nothing more to support his view-point than he has already said on the other pages of this paper.

*Xylococcidae* PERGANDE

*Xylococcinae* PERGANDE (in HABBART and PERGANDE), 1898: 26;

*Xylococcidae* PERGANDE; ZAHRADNIK, 1959: 527.

In the earlier classificatory system the *Xylococcinae* have been regarded as a separate group equal in rank to *Margarodinae*, *Monophlebinae* and others. MORRISON (1928) included this group in the family *Margarodidae* which action was widely accepted. ZAHRADNIK (1959) removed it from the *Margarodidae* as a distinct family, containing the genera *Matsucoccus* and *Xylococcus*. BEARDSLEY (1968) suggested the exclusion of the former one from this group (see *Matsucoccidae*).

As far as the structure of the mouthparts is concerned, the *Xylococcidae* should be considered as a separate, highly specialized branch of the *Porphyrophoridae* family group. At present only *Xylococcus* and *Xylococcus* are included in it.

*Porphyrophoridae* SIGNORET

*Porphyrophorites* SIGNORET, 1875: 346;

*Margarodinae* COCKERELL, 1899: 390.

The group under discussion formed the tribe *Margarodini* in the subfamily *Margarodinae* according to the classification by MORRISON (1928). JAKUBSKI (1965) elevated it to full family rank without taking into consideration the large number of other taxa already recognized under the family *Margarodidae* and established a new family — the *Termitococcidae*.



As *Porphyrophorites* SIGNORET has priority over *Margarodinae* COCKERELL, the former name should be used for stability. However, it should be borne in mind that the name *Margarodidae* has been in use for a long time in the systematic as well as in the applied entomology, but the retaining of this name requires a formal action (see MORRISON and MORRISON, 1966; WILLIAMS, 1969).

In the examined species assigned to the family *Porphyrophoridae* the mouthparts show the highest level of specialization among the *Orthezioidea* as well as in the whole *Coccinea*. The labium in the first stage nymph of *Neomargarodes trabuti* figured by MORRISON (1928) is, however, much more primitive, among others it possesses several setae. The point is, whether this genus belongs to another group, or whether the labium in the *Porphyrophoridae* shows a considerable degree of variability.

The *Porphyrophoridae* seem to form the fourth branch, beside *Kuwaniidae*, *Matsucoccidae* and *Xylococcidae*, in which the more specialized *Orthezioidea* have developed.

### Superfamily *Coccoidea* FALLÉN

*Coccides* FALLÉN, 1814: 23;

*Lecanoidae* + *Diaspidoidae* BALACHOWSKY, 1942: 37;

*Neococcoidea* BORCHSENIUS, 1950: 14;

*Neococcidea* BODENHEIMER, 1952: 317;

*Neococomorpha* BORCHSENIUS, 1965: 362;

Specialized *Coccidae* MACGILLIVRAY, 1921: 45.

The scale insects assigned to this superfamily possess the apical setae on the labium, but the apical organ, compound eyes, and abdominal spiracles are lacking. In some members of the *Asterolecaniidae* family group in which the labium shows the highest level of specialization the apical setae as well as any other setae have not been observed.

This superfamily contains the majority of families of the scale insects, from *Pseudococcidae*, the most primitive group, to *Asterolecaniidae* and *Diaspididae*, the most specialized ones. Some authors (BALACHOWSKY, 1942; OBENBERGER, 1957, and others) included in this assemblage also the family *Phenacoleachiidae* or even *Ortheziidae* (MACGILLIVRAY, 1921). BALACHOWSKY (1942, 1948), BORCHSENIUS (1965) and other authors regarded the *Diaspididae* as a group which should be classified separately as a distinct superfamily or similar category. BORATYNSKI and DAVIES (1971) suggested that the scale insects under discussion represent two heterogeneous groups — one, more primitive, containing the *Pseudococcidae*, *Eriococcidae* and *Dactylopiidae*, derived from ancestors similar to *Phenacoleachia*, the other, containing all the remaining families, may be derived from the *Steingelia*-like ancestors.

On the basis of the mouthparts the author comes to the conclusion that the *Coccoidea* are a monophyletic group which derived from ancestors close to *Phenacoleachia*. The most primitive *Coccoidea* are the *Pseudococcidae*, represented by the genus *Puto* and its relatives. From the *Pseudococcidae* probably two



branches derived — the *Conchaspididae* and the *Acanthococcidae*. This latter group ramified into a number of small branches (*Dactylopiidae*, *Apiomorphidae*, *Kermesidae*, *Cerococcidae*, *Cryptococcidae* and others), simultaneously giving origin to three major branches which form in the present classification three family groups — the *Coccidae*, *Asterolecaniidae* and *Diaspididae* family groups. The *Coccidae* and *Diaspididae* family groups seem to be natural groups, but little can be said on the relationship between the families associated in the *Asterolecaniidae* family group. It contains rather genera which do not show definite coccid or diaspidid characters.

The *Pseudococcidae*, *Acanthococcidae* and *Conchaspididae* family groups represent the "first floor" of the *Coccoidea* (*Acanthococciidae* section); the remaining three family groups, being more specialized, the "second floor" (*Coccidae* section).

### *Pseudococcidae* family group

#### *Pseudococcidae* COCKERELL

*Pseudococcini* COCKERELL, 1905: 193;

*Dactylopiinae* SIGNORET; auct.;

*Phenacoccinae* ŠULC, 1944: 152.

Although informal, the name *Pseudococcidae* is now widely accepted for the mealybugs (MORRISON and MORRISON, 1966; WILLIAMS, 1969). In the past, the *Pseudococcidae* were associated with various groups of scale insects, usually with *Acanthococcidae* (= *Eriococcidae*) and sometimes also with the genus *Kermes* as *Dactylopiinae* (FERNALD, 1903); *Eriococcidae* (BALACHOWSKY, 1942), *Pseudococcidae* (with *Eriococcinae*, BORCHSENIUS, 1949) or *Kerminae* (BALACHOWSKY, 1948; SCHMETTERER, 1952).

The *Pseudococcidae* are usually considered as being a primitive group; only few scholars (OBENBERGER, 1957) place it after the *Asterolecaniidae* and *Coccidae*. The characters of the mouthparts adequately define this family and place it on the lowest level among the *Coccoidea*. The *Pseudococcidae* probably link this superfamily with the primitive scale insects, showing some common characters with the *Phenacoleachiidae*.

The *Pseudococcidae* contain numerous and various forms and some subcategories were recognized by the earlier workers within this family, but no serious attempt has been made to classify the whole group.

SILVESTRI (1939) recognized the subtribe *Trabutina* (tribe *Pseudococcini*). BODENHEIMER (1949) elevated this group to subfamily rank and placed it in the *Eriococcidae*, regarding it as equal in level to the *Pseudococcinae*. FERRIS (1950a) associated *Trabutina* with the genera *Nipaecoccus*, *Naiacoccus* and *Anomostherium*.

COCKERELL (1899) recognized the tribe *Sphaerococcini*, SHINJI (1935) the subfamily *Serrolecaniinae*, BORCHSENIUS (1948a) the tribe *Coccurini* and later (1949) the tribe *Antoninini* (BODENHEIMER, 1952, elevated this group to sub-

family rank), EZZAT and McCONNEL (1956) the tribe *Planococcini*, WILLIAMS (1969) the tribe *Rhizoecini*. In many papers the name "*Phenacoccus* group" is used to contain *Phenacoccus* and related genera. BEARDSLEY (1969) proposed the family *Putoidae* as a group distinct from the *Pseudococcidae*.

The most comprehensive classification of the family *Pseudococcidae* was presented by AFIFI (1968). This author, on the basis of male characters (13 genera examined by himself and 2 genera by BEARDSLEY, 1962) recognized among the *Pseudococcidae* 8 groups of genera: the *Puto*, *Ceroputo*, *Nairobiia*, *Planococcus*, *Pseudococcus*, *Saccharicoccus*, *Octococcus* and *Rhizoecus* groups. He proposed, furthermore, to divide these groups into 4 sections (which may be regarded as subfamilies): the first section containing the genus *Rhizoecus*, the second section with *Ceroputo* and *Nairobiia* groups, the third section for the *Ceroputo* — *Octococcus* groups and the fourth for *Puto*. Numerical methods applied to the same material by BORATYNSKI (1970), confirmed in general outline the conception presented by AFIFI. A comparatively small number of examined species and the absence in this classification of such important genera as *Phenacoccus*, *Heterococcus*, *Ripersia*, *Rhodania* and others, diminishes somewhat its significance.

The uniform structure of the mouthparts (particularly that of the sucking pump) and the convergencies in various groups and different taxonomic levels present the *Pseudococcidae* as a homogenous and compact group. Thus, the author utilized also other characters in dividing this family into lower taxa.

The examined species can be placed, although not always without hesitation, in four subfamilies — the *Trabutininae*, *Pseudococcinae*, *Rhizoecinae* and *Sphaerococcinae*. The proposed classification has many common points with that of AFIFI. The differences concern the following questions:

In AFIFI'S classification the genera *Ceroputo* + *Nairobiia* and *Puto* are placed in two distinct sections. In the present classification *Puto* and *Ceroputo* are placed in the same subfamily (see *Trabutininae*).

AFIFI did not discuss the relations between *Puto* section and the *Ceroputo* — *Nairobiia*, and *Planococcus* — *Octococcus* sections. The arrangement of the sections seems to indicate that AFIFI regarded *Puto* closer to *Planococcus* — *Octococcus* than to the *Ceroputo* — *Nairobiia* section. As mentioned above, the author sees *Puto* close to *Ceroputo*.

AFIFI placed the genus *Nipaecoccus* among *Planococcus*, *Trionymus* and other genera in the *Planococcus* group. The shape of the clypeus is also similar to that in this group, but other characters make them close to the members of the *Ceroputo* — *Nairobiia* section (*Trabutininae* in the present classification). The separation of this genus from the *Planococcus* — *Octococcus* group was also indicated by some numerical methods (BORATYNSKI, 1970).

AFIFI recognized the *Ceroputo* — *Nairobiia* section as a more specialized group than the *Planococcus* — *Pseudococcus* — *Saccharicoccus* — *Octococcus* section. In contrast with this view, the author supposes that *Ceroputo* (and *Centroccoccus*, *Phenacoccus*, *Ripersia* and other members of the subfamily *Trabutininae*) represents a group, which as a whole, is more primitive than that



represented by *Planococcus* (and *Pseudococcus*, *Trionymus* and other members of the subfamily *Pseudococcinae*), although in some species the males can represent a high level of specialization.

### *Trabutininae* SILVESTRI

*Trabutini* SILVESTRI, 1939: 60;

*Phenacoccinae* ŠULC, 1944: 152, partim;

*Phenacoccus* group, auct.;

*Coccurini* BORCHSENIUS, 1948a: 954;

*Ceroputo* + *Nairobiia* section AFIFI, 1968: 69;

*Putoidae* BEARDSLEY, 1969: 278.

There is a nomenclatorial question because the genus *Trabutina* is not particularly characteristic of this subfamily, but as it was placed in this group, the name *Trabutininae* had priority over all other names.

The scale insects placed in this subfamily are defined by the following, or at least one of the following characters:

- On the posterior surface of the apical segment of the labium there occur 3 pairs of setae.
- Anterior margin of the clypeus is arched.
- Dorsal setae are spineform.
- The plantar surface of the claw is provided with a denticle.
- Quinquelocular pores are present.
- The colour of living specimens is yellowish, pinkish, greenish, rarely brownish.

In the opinion of the author this subfamily, although comprising various and sometimes highly specialized forms, represents the most primitive *Pseudococcidae*. In the radiation processes the various groups within this subfamily originated, and on the other hand, it gave rise to other *Pseudococcidae*. The most primitive forms (*Puto*, *Macrocerococcus*, *Ceroputo*, *Phenacoccus*, *Paroudablis*, *Spinococcus* and others) possess all the above mentioned characters. Due to the reductive processes various groups of genera originate, e.g., *Mirococcus* (reduction of dorsal spines and quinquelocular pores in some members), *Heterococcus* (reduction of trilocular pores), *Euripersiā* (partial reduction of denticle on claw), *Rhodania* and *Metadenopus* (reduction of trilocular pores, denticle, spineform setae on dorsum, partial reduction of posterior setae on labium). Owing to the progressive processes originate other groups, e.g., *Helicoccus* (development of a special kind of tubular ducts), *Peliococcus* (special arrangement of multilocular pores). Other aberrations of not clear nature are represented by the genera *Lacombia*, *Trabutina* and *Nipaecoccus* (KOTEJA, 1974; KOTEJA, manuscript; KOTEJA and LINIOWSKA, manuscript).

Of particular interest is the genus *Puto*. LINDINGER (1912) and LEONARDI (1920) regarded the genera *Macrocerococcus* and *Ceroputo* as synonyms. BORCHSENIUS (1949) recognized *Puto*, *Ceroputo* and *Macrocerococcus* as distinct genera, FERRIS (1950) and BALACHOWSKY (1953) united the three taxa in one genus and REYNE (1954) once again dissociated them into three distinct genera.



This author noted furthermore, that the American and European species of *Puto* (*Puto yuccae* and *P. antennatus*, respectively) represent different lines of development. BEARDSLEY (1962), on the basis of male characters, expressed the opinion that *Puto*, being the most primitive among the *Pseudococcidae* shows some similarities with *Stomacoccus* and *Steingelia*, genera of the *Orthezioidea* (= *Margarodidae* s.l.). Later (1969), this author erected the family *Putoidae*. The view on the extreme position of the genus under discussion has also been supported by the cytological studies (HUGHES-SCHRADER, 1944; BROWN and CLEVELAND, 1968). WILLIAMS (1969) supposed that *Puto* could be placed in one group with *Steingelia* and *Phenacoleachia* (family *Phenacoleachiidae*), and MILLER and MCKENZIE (1973) noticed that "a remarkable amount of similarity exists between *Puto* and *Phenacoccus*".

The present investigations show that *Macrocerococcus superbus*, *Puto caucasicus* and *Ceroputo pilosellae* (species examined by the author) are definite members of the family *Pseudococcidae*. Among these three species, *Macrocerococcus superbus* is the most primitive and *Ceroputo pilosellae* the most specialized species, but it is another question whether *Puto caucasicus*, the single species of this genus examined by the author, is congeneric with *P. antennatus* and *P. yuccae*. The author does not believe that *Puto* should form a separate family, but there is no doubt that the groups associated in the subfamily *Trabutininæ* represent various forms and that further investigations may divide this subfamily into more taxa, one of which formed by the genus *Puto* with its relatives.

### *Pseudococcinae* COCKEREL

*Pseudococcini* COCKERELL, 1905: 193;

*Pseudococcus* group, auct.;

*Planococcini* EZZAT and McCONNELL, 1956: 3;

*Planococcus*, *Pseudococcus*, *Saccharicoccus* and *Octococcus* sections AFIFI, 1968: 69.

The *Pseudococcinae* are characterized by the presence of only 2 pairs of setae on the posterior surface of the labium, the anterior margin of the clypeus not arched, presence of hair-like (not spine-like) setae on the dorsum, absence of the denticle on the claw, the brownish colour of the body. The *Pseudococcinae* represent a much more homogeneous group than the *Trabutininæ*, and, as a whole, are more specialized than the latter. Among the genera assigned to this group *Ferrisia* represents the most primitive, and *Saccharicoccus penium* the most specialized forms.

### *Rhizoecinae* WILLIAMS

*Rhizoecini* WILLIAMS, 1969: 335.

The genus *Rhizoecus* and its relatives were for a long time considered as an unusual group among the *Pseudococcidae*. This opinion was formally accepted by WILLIAMS (1969) who established the tribe *Rhizoecinae*. BEARDSLEY (1962), on the basis of male characters considered the genus *Rhizoecus* as the most

specialized pseudococcid, and AFIFI (1968) proposed a separate section to contain it (see discussion under *Pseudococcidae*).

The basical characters of the mouthparts in this group are similar to those in the subfamily *Pseudococcinae*. The shape of the labium, however, represents primitive conditions. From both male and female morphology it appears that the position of *Rhizoecinae* among the *Pseudococcidae* is not clear and requires further studies.

### *Sphaerococcinae* COCKERELL

*Sphaerococcini* COCKERELL, 1899;

*Antoninini* BORCHSENIUS, 1949: 44.

As pointed out by many authors (HOY, 1963; AFIFI and KOSZTARAB, 1967; KOSZTARAB, 1968) the genus *Sphaerococcus* contained a heterogeneous assemblage of species, some of which seem to represent new genera assignable to the *Acanthococcidae* family group (= *Eriococcidae* s.l.), e.g., *Sphaerococcus tomentosus*. The type species, *S. casuarinae*, examined by the author, exhibits definite pseudococcid characters and seems to be related to the genera *Antonina* and *Chaetococcus*. The genus *Serrolecanium* (not examined by the author) may belong, according to WILLIAMS (1969) also to this group.

AFIFI (1968) basing on the description of the male *Antonina crawi* given by BEARDSLEY (1965) considered this species as close to his *Planococcus* group. AFIFI and KOSZTARAB (1967) examined 5 species of *Antonina* and indicated that this genus shares more common characters with the *Saccharicoccus* group.

On the basis of the structure of the mouthparts it is difficult to infer about the relationship of this group. In any case, it shows general characters typical of the subfamily *Pseudococcinae*. On the other hand, it is not unlikely that this group contains highly specialized, heterogeneous forms which became similar due to the convergency.

### *Acanthococcidae* family group<sup>1</sup>

The labium in this family group is three-segmented (with the exception of *Kuwania* and possibly *Calycicoccus*) but with one subapical seta only, and it is therefore easy to distinguish it from the *Pseudococcidae*.

In comparison with the *Pseudococcidae*, the mouthparts in the families associated in this group are more specialized, although some characters, e.g. the size of the labium, are in some groups more primitive than in certain *Pseudococcidae*.

In the earlier classificatory systems the *Acanthococcidae* (= *Eriococcidae*) were insufficiently defined and had very wide limits, containing many aberrant forms. Especially HOY (1963) placed in this family all the genera which did not show definite characters of other groups.

<sup>1</sup> If the position of the genus *Kermes* in this group is accepted, the name *Kermesites* SIGNORET, 1875: 15, has priority over *Acanthococcites* SIGNORET, 1875: 16, as a family group name.

The proposed *Acanthococcidae* family group contains the following distinct families: *Acanthococcidae*, *Apiomorphidae*, *Dactylopiidae*, *Kermesidae*, *Cerococcidae*, *Cryptococcidae*, *Calycicoccidae*, the *Kuwanina* group (presumed family status) and the unplaced genus *Xerococcus*. Most of these families were placed by FERRIS (1957a) and HOY (1963) as lower categories (usually genera) in the family *Acanthococcidae* (= *Eriococcidae*). The genera *Cissococcus* and *Opisthoscelis*, associated sometimes with *Acanthococcus* (= *Eriococcus* auct.) were removed to other groups, and the genera *Cerococcus* (associated usually with *Asterolecanium*) and *Kuwanina* (grouped with *Pseudococcidae*) are placed here as distinct families.

#### *Acanthococcidae* SIGNORET

*Acanthococcites* SIGNORET, 1975: 16;  
*Kerminae* SIGNORET; BALACHOWSKY, 1948: 253, partim;  
*Dactylopiidae* SIGNORET; FERRIS, 1955, partim;  
*Eriococcini* COCKERELL, 1899: 389.

The taxonomic status, limits and the name of this group have been changed many times and will not be discussed in this paper. In the recent catalogue of this group, HOY (1963) placed in the *Acanthococcidae* (= *Eriococcidae*) 57 genera, and among others *Apiomorpha*, *Calycicoccus*, *Capulinia*, *Cryptococcus*, *Dactylopius*, *Kermes*, *Micrococcus* and *Pseudochermes*. In the present classification the family *Acanthococcidae* is limited to *Acanthococcus* and closely related genera. This conception is in accordance with the opinion of BORCHSENIUS (1948), AFIFI (1968) and other workers who excluded from this family many genera and transferred them to other families or established new ones.

The author agrees with the opinion of BORCHSENIUS (1948) that the genera *Acanthococcus* and *Eriococcus* are distinct. In this situation, "*Acanthococcidae*" should be used instead of "*Eriococcidae*" as a family name because the former has priority.

Two subfamilies are assigned to the *Acanthococcidae* — the *Acanthococcinae* and *Eriococcinae*.

#### *Acanthococcinae* SIGNORET

*Acanthococcites* SIGNORET, 1875: 16;  
*Eriococcidae* COCKERELL, auct.

The labium in this group is characterized by the presence of two pairs of basal setae and seems to be most primitive in the family.

The subfamily contains tentatively 4 tribes: *Phloeococcus* group, *Acanthococcini*, *Rhizococcus* group and *Ovaticoccus* group.

#### *Phloeococcus* group (tribe status)

The genus *Phloeococcus* HOY (1962) was erected for two new species from New Zealand. The describer considered this genus to be primitive. The present investigations are in complete accord with this view. The labium shows primitive



characters, among others, on its posterior surface occur three pairs of setae which condition has not been observed in any member of the *Acanthococcidae* family group.

### *Acanthococcini* SIGNORET

*Acanthococcites* SIGNORET, 1975: 16.

The genus *Acanthococcus* SIGNORET (not KIRIČENKO, 1936) has been widely accepted as a synonym of *Eriococcus* TARGIONI TOZZETTI. It was so considered by FERRIS (1957a) and HOY (1963). BORCHSENIUS (1948) recognized both the genera as distinct and transferred most species from *Eriococcus* to *Acanthococcus*. This action was accepted by DANZIG (1964), BORATYNSKI (1962) and some other workers.

BORCHSENIUS (1948) emphasized the special type of tubular ducts present in *Eriococcus* as a character which clearly distinguishes the two genera. The present investigations show that they differ also in the structure of the labium. In *Eriococcus* there occur one pair of basal setae and 7 pairs on apical segment, in *Acanthococcus* on basal segment there are 2 pairs and on apical one 6 pairs.

Although the apical segment of the labium in *Acanthococcus* bears only 6 pairs of setae (1 pair of the anterior setae is reduced), all other characters of the mouthparts indicate that it is more primitive than those in other members of this family, excluding *Phloeococcus*.

Following species are assigned to the *Acanthococcini*: *Gossyparia spuria*, *Acanthococcus aceris*, A. sp., "*Eriococcus*" *quercus* and "*Eriococcus*" *coriaceus*<sup>1</sup>. All these species live on trees and bushes. For further discussion see *Rhizococcus* group.

### *Rhizococcus* group (tribe status)

SIGNORET (1875) presented this genus, with the type species *Rhizococcus gnidii* SIGNORET (1875), as very close to *Eriococcus* and *Acanthococcus*, but having a distinct habitat. Later this genus was considered as a synonym of *Nidularia* (LINDINGER, 1933) or *Eriococcus* (FERRIS, 1955, 1957a). This latter action was widely accepted by coccid workers. BORCHSENIUS (1948) revalidated *Rhizococcus* and transferred to it a number of species formerly assigned to *Eriococcus*, and DANZIG (1962, 1964) concurred. HOY (1962) once again placed *Rhizococcus* with the synonyms of *Eriococcus*.

The present investigations show that *Acanthococcus*, *Eriococcus* and *Rhizococcus* are distinct, but they indicate different limits between the genera than those defined by BORCHSENIUS and DANZIG. These authors placed in *Acanthococcus* all the species with dorsal setae as long as the marginal ones, and in *Rhizococcus*

<sup>1</sup> The specific names were taken from the specimen labels. In the case when the author transferred a species to another genus, its generic name was not changed but only put in quotation-marks. For details see first part of these investigations (KOTEJA, 1974).

the species with dorsal setae shorter than the marginal ones. Some authors (HOY, 1962; DZIEDZICKA and KOTEJA, 1971) noticed that the length of the dorsal spines vary sometimes within a species, thus this character could not be taken into consideration as a distinguishing feature. The materials examined by the author can be divided into two groups, one comprising the genera *Gossyparia*, *Acanthococcus aceris* and 4 other species determined on the labels as *Acanthococcus* or *Eriococcus*, being characterized by long apical setae and presence of 6 pairs of setae on the apical segment of the labium, and the second group characterized by comparatively short apical setae and 7 pairs of setae on apical segment, containing the genera *Greenisca*, Genus D, and a number of species determined as belonging to *Acanthococcus*, *Eriococcus* and *Rhizococcus*. Unfortunately the author has not seen the type species of *Rhizococcus* — *Rh. gnidii*, and it is not sure whether this species belongs to this group. AFIFI (1968) investigated several acanthococcid (= eriococcid) males but it seems there were no members of the *Rhizococcus* group among the examined species. It is the author's opinion that the two groups — the *Acanthococcus* group and the group provisionally called *Rhizococcus* group, represent distinct taxa, but further study, based on more information is needed to confirm this view.

Genus D includes two species — "*Greenisca*" *glyceriae* and "*G.*" *rubra*. On the basis of the structure of the mouthparts and some other characters these species seem to be distinct from *Greenisca brachypodii* and *G. gouxii* (type species). In the revision of this genus, BORCHSENIUS and DANZIG (1966) placed these species in different groups. *Greenisca brachypodii* and *G. gouxii* are close to the species assigned here to the genus *Rhizococcus*.

### ***Ovaticoccus* group (tribe status)**

*Ovaticoccini* group MILLER and MCKENZIE, 1967: 472.

*Ovaticoccus* KLOET 1944 (= *Gymnococcus* DOUGLAS, 1888, preoccupied in *Porozota*) is widely accepted as a member of the *Acanthococcidae* (= *Eriococcidae*). MILLER and MCKENZIE (1967) redescribed and revised this genus and three other related genera and stated that they may constitute a tribe or some other suprageneric category. The results of the present investigations concur with this opinion.

### ***Eriococcinae* COCKERELL**

*Eriococcini* COCKERELL, 1899: 389.

The name *Eriococcidae* has been recently used with respect to a wide group of scale insects. The author limits this group to *Eriococcus* TARGIONI TOZZETTI (s. str.) as done by BORCHSENIUS (1948).

The mouthparts in this group show acanthococcid characters but the labium seems to be more specialized than in other groups.

The subfamily status proposed for *Eriococcus* is only a provisional action. Further studies may place it in the subfamily *Acanthococcinae* as a lower category.

The relations and other taxonomic questions concerning the genus *Eriococcus* are discussed above.

### *Apiomorphidae* MACGILLIVRAY

*Apiomorphinae* MACGILLIVRAY, 1921: 45.

*Apiomorpha* is a specialized and isolated genus, although some other gall-making insects were associated with it, e.g., *Ascelis*, *Opisthoscelis* and sometimes even *Frenchia* and *Kerria*. FERRIS (1957) placed this genus in the *Acanthococcidae* (= *Eriococcidae*), but *Opisthoscelis* among the "Genera Unplaced" indicating a possible relationship of the latter to the *Coccidae*. HOY (1963) assigned *Apiomorpha* to *Acanthococcidae*. THERON (1968) investigated the males of some *Apiomorpha* and *Opisthoscelis* species and discussed the taxonomic and nomenclatorial problems concerning this group, in detail. He expressed the opinion that the two genera may be closely related and may have some affinities with the *Acanthococcidae* (= *Eriococcidae*).

The structure of the mouthparts indicates following conclusions:

- *Apiomorpha* belongs definitely to the *Acanthococcidae* family group.
- It should be regarded as a distinct family in this group.
- *Apiomorpha* and *Opisthoscelis* are not related, the latter genus, as supposed by FERRIS (1957) showed no acanthococcid characters.

The labium in *Apiomorpha*, with its large base, with a narrow but strongly sclerotized basal segment and a reduced number of setae may be considered as a specialized form.

### *Dactylopiidae* SIGNORET

*Dactylopites* SIGNORET, 1875: 305;

*Coccinae* FALLÉN; MACGILLIVRAY, 1921: 45.

This group name with various endings has been given in the past to a wide range of scale insects. It was caused in part by the discordance of the opinions concerning the type species of this genus (see MORRISON and MORRISON, 1966). FERRIS (1955) used the name *Dactylopiidae* to include all the acanthococcids (= eriococcids), and later (1957) for the genus *Dactylopius* alone. BALACHOWSKY (1942), OBENBERGER (1957), BORCHSENIUS (1958) recognized the *Dactylopiidae* as being distinct from the *Acanthococcidae* and HOY (1963) once again united the two groups.

Most workers regard *Dactylopiidae* as a group close to *Acanthococcidae*. BORCHSENIUS (1958) affiliated it with *Stictococcidae* and *Apiomorphidae*. LOBUSTER (1966) and BORATYNSKI and DAVIES (1971) supposed this group may have derived from the *Pseudococcidae* as a separate branch, beside the *Acanthococcidae*. MACGILLIVRAY (1921) placed this group among his "Generalized *Coccidae*" (*Orthezioidea* in the present classification).



The mouthparts in *Dactylopiidae* show an acanthococcid nature. The labium is distinctly three-segmented, with 9 pairs of setae as in the primitive *Acanthococcidae*, but it is much larger and particularly much wider at the base, though the setae remain normal-sized. The author supposes that the enlargement of the labium in this group is a type of specialization.

The *Dactylopiidae* are at present recognized as a monotypic family containing the Mexican cochineal scale insect. The genus *Epicoccus* placed in this family by OBENBERGER (1957) belongs definitely to the family *Pseudococcidae*.

### *Kermesidae* SIGNORET

*Kermesites* SIGNORET, 1875: 15;

*Kermococcinae* BALACHOWSKY, 1930: 313.

The genus *Kermes* was included by the majority of workers with the genus *Eriococcus* (s.l.) into one family or subfamily which name was derived either from the genera *Kermes* (or *Kermococcus*) or *Eriococcus*. Some authors included in this group also the genus *Dactylopius*. BALACHOWSKY (1942), SCHMUTTERER (1952) and OBENBERGER (1957) affiliated it with the *Pseudococcidae*. MACGILLIVRAY (1921) and BORCHSENIUS (1950, 1960) recognized a distinct, monotypical family to contain the genus *Kermes*.

GILMEE (1967, 1968) and BORATYNSKI and DAVIES (1971), on the basis of male characters suggested a close relationship between *Kermesidae* and *Coccidae*. The detailed description of the male *Kermes quercus* showed (KOTEJA and ŽAK-OGAZA, 1972), however, that the similarity between *Kermes* and *Coccidae* was based principally on the specialized features, whereas the primitive characters indicated a relationship between *Kermes*, *Acanthococcidae* and *Pseudococcidae*. The morphological accordance between *Kermes* and *Coccidae* should be, therefore, regarded as a convergency and not a relationship.

The characters of the mouthparts indicate without doubt that *Kermes* should be placed among the *Acanthococcidae* family group. The structure of the labium and particularly that of the sucking pump indicate, moreover, that it should form a distinct family which represents another branch of the radiation of the scale insects associated in the *Acanthococcidae* family group.

On the basis of the morphology of the mouthparts (labium comparatively long and slender, with the setae reduced to 6—7 pairs) it can be inferred that the *Kermesidae* represent approximately the same specialization level as the *Apiomorphidae* and *Cerococcidae* but acquired on a quite different way.

### *Cerococcidae* BALACHOWSKY

*Cerococcinae* BALACHOWSKY, 1942: 44.

The genus *Cerococcus* has long been associated with the genus *Asterolecanium* and/or *Lecanodiaspis* in the family *Asterolecaniidae*. BALACHOWSKY (1948) and

OEBENBERGER (1957) regarded the genera *Asterolecanium* and *Lecanodiaspis* as more closely related, forming the subfamily (or tribe) *Asterolecaniinae*, while *Cerococcus* — the subfamily (or tribe) *Cerococcinae* in the *Asterolecaniidae*. BORCHSENIUS (1960) removed from this family the genus *Lecanodiaspis* and its relatives and erected a new family — the *Lecanodiaspididae* (= *Lecaniodiaspididae*), but left the genus *Cerococcus* in the family *Asterolecaniidae* as a subfamily *Cerococcinae*. Prof. Dr. M. KOSZTARAB in a letter to the author (7. 6. 1972) expressed the opinion that *Cerococcus* shows close relationship with *Lecanodiaspis*. Quite a different suggestion was presented by WILLIAMS (1969) — on the basis of male characters he supposed that *Cerococcus* may be related to *Acanthococcidae* (= *Eriococcidae*).

The structure of the mouthparts indicates undoubtedly that *Cerococcus* can be affiliated neither with *Asterolecaniidae* nor with *Lecanodiaspididae*. The three-segmented labium with sharp pointed apex shows typical acanthococcid characters. Thus, the author places *Cerococcus* as a distinct family into the *Acanthococcidae* family group. This action agrees with the above presented suggestion of WILLIAMS (1969).

Some characters of the labium (segmentation, shape) show primitive conditions, while the others (reduction of setae to 4—6 pairs) specialized ones.

BORCHSENIUS (1960) divided his *Cerococcinae* into two tribes — the *Polliniini* and *Cerococcini*. On the basis of the mouthparts which are uniform in the examined genera (*Cerococcus*, *Cercococcus*, *Asterococcus*, *Pollinia*) the distinguishing of lower taxa is impossible in the family under discussion.

The genera *Callococcus*, *Frenchia* and *Mycetococcus* included tentatively in this group by BORCHSENIUS (1960) are transferred to the *Asterolecaniidae* family group.

### *Cryptococcidae* KOSZTARAB

*Cryptococcidae* KOSZTARAB, 1968: 12.

The genus *Cryptococcus* has been widely accepted as a member of the family *Acanthococcidae* (= *Eriococcidae* s. str.). BODENHEIMER (1953) basing on the sedentary behaviour of this genus, included it in the subfamily *Antoniniinae* of the family *Pseudococcidae*. KOSZTARAB (1968) rejected this action and established a new family — the *Cryptococcidae* which contains the genera *Cryptococcus* and *Kuwanina*. This author stated, furthermore, that *Cryptococcidae* should be incorporated as a group between *Acanthococcidae* (= *Eriococcidae* s. str.) and *Kermesidae*.

The present investigations support KOSZTARAB's opinion and *Cryptococcidae* are regarded here as a distinct family among the *Acanthococcidae* family group.

The labium in this group shows a high degree of specialization and this condition is in accordance with that of other characters.

The family *Cryptococcidae* contains at present two genera: *Cryptococcus* and *Pseudochermes*. The genus *Kuwanina* assigned to this family by KOSZTARAB is discussed separately.

### *Calycicoccidae* BRAIN

*Calycicoccinae* BRAIN, 1918: 111.

BRAIN assigned this group to the *Coccidae* of FERNALD (1903). FERRIS (1957) placed the genus *Calycicoccus* in the *Acanthococcidae* (= *Eriococcidae*), and suggested a relationship to *Aculeococcus* and *Macracanthopyga*. This suggestion was confirmed by HOY (1963).

The specimens of *Calycicoccus merwei* which the author has had an opportunity to examine, were in a bad condition and the mouthparts could not have been described in detail. The labium seems to be only two-segmented, but with the typical number of setae on the medial and apical segments.

This group is assigned to the *Acanthococcidae* family group as a distinct family, but further investigations may lower its rank.

### *Kuwanina* group (presumed family status)

The genus *Kuwanina* represents a small, highly specialized group with the rather obscure relationships. The majority of workers (FERRIS, 1918, 1941; MAMET, 1954; TAKAHASI, 1958) associated this genus with the *Pseudococcidae*, close to such genera as *Ehrhornia*, *Rhodania*, *Paludicoccus*, *Paulianodes*. YANK and KOSZTARAB (1967) studied the nymphs of this genus in connection with the genera *Antonina* and *Chaetococcus*. LINDINGER (1937) recognized *Kuwanina* as a synonym of the genus *Cryptococcus*. HOY (1963) assigned it as a valid genus to the *Acanthococcidae* (= *Eriococcidae*). KOSZTARAB (1968) included it in his family *Cryptococcidae*. Both HOY and KOSZTARAB noticed that the genera *Kuwanina*, *Antonina* and *Sphaerococcus* included forms which are not congeneric and that the relationships of these genera should be discussed on the basis of type species. They supposed that *Kuwanina parva* (type species) may be related to *Acanthococcidae* while *Antonina* and *Sphaerococcus* represent aberrant genera of the *Pseudococcidae*.

The sucking pump in *Kuwanina* is typical of the *Acanthococcidae* family group. The labium is small, conical, indistinctly two-segmented, with strong basal ring and 5 pairs of setae. It displays, therefore, some coccid and asterolecaniid characters. The relationship of this group with the *Pseudococcidae* seems to be most unlikely. On the other hand, the similarities with *Coccidae* and *Asterolecaniidae* seem to be of secondary nature, owing to the high specialization and convergency. It is the author's opinion that *Kuwanina* represents a member of the *Acanthococcidae* family group (as indicated by HOY) and may be closely related to *Cryptococcus* (as supposed by KOSZTARAB). The author believes, however, that this group may form a distinct family.



## Genera unplaced

### *Xerococcus* FERRIS

FERRIS (1921a) placed *Xerococcus* in the *Acanthococcidae* (= *Dactylopiidae* = *Eriococcidae*) and noticed the divergence of this genus from the eriococcid type. HOY (1963) shared FERRIS's opinion.

The structure of the labium is close to that in other *Acanthococcidae*, particularly to the *Ovaticoccus* group, but the sucking pump is quite different. Thus, the author leaves this genus unplaced among the *Acanthococcidae* family group. It is not unlikely that *Xerococcus* represents a distinct branch in this group, similar in rank to *Kermes*, *Cerococcus* and others.

## *Conchaspididae* family group

### *Conchaspididae* GREEN

*Conchaspinae* GREEN 1896: 17.

*Conchaspididae* are a well defined and isolated group. Its systematic status has been permanently discussed since it was established. NEWSTEAD (1903), FERRIS (1957) and BORSCHENIUS (1958) suggested that *Conchaspididae* are closely related to *Diaspididae* and may be a link between primitive *Coccoidea* and the latter group. GREEN (1896) indicated a possible relationship of this group to *Coccidae*. COCKERELL (1896) placed the genus *Conchaspis* in the family *Coccidae* (s. str.). FERNALD (1903) listed *Conchaspinae* between *Phenacoleachiinae* and *Dactylopiinae*. BALACHOWSKY (1942, 1948) assigned *Conchaspididae* to his *Lecanoidae* on the basis of the adult male, and BROWN (1959) found a lecanoid type of chromosome system in this group. MAMAT (1954a) suggested a fourth type of males — the conchaspidoid (beside margaroid, lecanoid and diaspidoid) which was close to the diaspidoid one. AFIFI (1969) agreed with this opinion and regarded this type as a link between the lecanoid and diaspidoid ones, but which was more closely related to the lecanoid than to the diaspidoid type. BORATYNSKI and DAVIES (1971) in their schematic presentation of the phylogenetic relationships of scale insects linked *Conchaspididae* with *Coccidae* (s. str.). BODENHEIMER (1944, 1952) and BALACHOWSKY (1948) wrote about three pairs of spiracles in this group (the preserved first pair of abdominal spiracles according to BODENHEIMER, or three pairs of thoracic spiracles according to BALACHOWSKY). D'ASCOLI and KOSZTARAB (1969) found only two pairs of spiracles, regarding the "third pair" as thoracic invaginations which are not homologous with spiracles.

From the morphology of the mouthparts following conclusions can be drawn:  
— The family *Conchaspididae* represents an isolated group among the *Coccoidea*.  
— The labium shows a comparatively low degree of specialization (three-segmented, with 9 pairs of setae) which is about the same as in the *Acantho-*

*coccidae*. The sucking pump, in contrast, shows a very high level of specialization, being similar to that in some members of the *Asterolecaniidae* family group. The estimation of other features lead also to divergent conclusions.

— The relationship between *Conchaspidae* and *Diaspididae* cannot be precluded but seems to be very unlikely.

— The ancestors of this group are to be found among the primitive *Coccoidea*, possibly related to the *Pseudococcidae*.

The genus *Fagisuga*, placed by BALACHOWSKY (1948) in the *Phoenicococcinae* is assigned to this family.

### *Coccidae* family group

The *Coccidae* family group comprises various forms and is therefore difficult to define. In the primitive groups the labium is distinctly two-segmented, in the more specialized ones indistinctly two-segmented or definitely one-segmented; hemispherical or (in the primitive groups) conical; usually with a rounded apex. The basal ring is weak, not connected anteriorly with the clypeolabral shield; in some groups lateral, band-shaped sclerotizations are present which join the labium to the clypeolabral shield. Setae are not numerous, usually 5, rarely 4—7 pairs. The sucking pump is comparatively small, similar to that in the *Pseudococcidae* and *Acanthococcidae*. The anal ring is always present in this group, usually accompanied by anal plates. The claw (if legs are developed) is comparatively robust and strongly curved. A special type of pores — "dark-rimmed" ventral pores (BORATYNSKI and WILLIAMS, 1964) of various modifications and different names, is present here. The male puparia are formed of waxy shields.

The *Coccidae*, *Asterolecaniidae* and *Diaspididae* family groups represent a higher stage in the evolution of the *Coccoidea* in comparison with the *Pseudococcidae*, *Acanthococcidae* and *Conchaspidae* family groups. They seem to be derived from the *Acanthococcidae* ancestors. The question is whether these groups are monophyletic or have been evolved separately. It is not easy to solve this problem because the very conception of three branches in the higher *Coccoidea* is not sufficiently demonstrated. It is possible that the families here associated have common ancestors, but represent numerous, separate branches.

The author assigned to the *Coccidae* family group 7 families: *Stictococcidae*, *Kerriidae*, *Coccidae*, *Lecanodiaspididae*, *Acleridae*, *Micrococcidae* and *Cissococcidae*.

### *Stictococcidae* LINDINGER

*Stictococcinae* LINDINGER, 1913: 63.

The genus *Stictococcus* is well defined by the characters of the mouthparts and some other characters. NEWSTEAD (1908) placed it tentatively in the *Margarodidae* (s.l.), near *Xylococcus*; COCKERELL (1903) associated it with *Coccidae*.

LINDINGER (1913) and BALACHOWSKY (1942) regarded it as a distinct subfamily related to the *Coccinae*. MACGILLIVRAY (1921) assigned it to the *Monophlebidae*. OBENBERGER (1957) placed this family near *Kerriidae* while BORCHSENIUS (1958) suggested its relationship with *Dactylopiidae* and *Apiomorphidae*. FERRIS (1957) is uncertain where to place this family. RICHARD (1971) found a lecanoid type of the male in *Stictococcus*.

The characters of the mouthparts indicate a relationship of this family with *Coccidae* and *Kerriidae*.

The labium in the *Stictococcidae* represents the most primitive type among the *Coccidae* family group — it is distinctly two-segmented, conical, comparatively large, bearing numerous setae. Some other characters (great number and various types of dermal pores, well developed legs) show also primitive conditions. On the other hand, the modified setae and the translocation of the anal opening are specialized characters.

### *Kerriidae* LINDINGER

*Kerriidae* LINDINGER, 1937: 187;

*Lacciferidae* COCKERELL 1924: 47; nominal genus invalidated;

*Tachardiinae* GREEN, 1896: 17; nominal genus — *Tachardia* BLANCHARD, 1886, synonymized with *Laccifer*, OKEN, 1815.

The *Kerriidae* represent a well defined and specialized group. Most coccid workers regard it as a separate branch which may have some affinities with the *Coccidae* (BALACHOWSKY, 1942; FERRIS, 1957; OBENBERGER, 1957; BORCHSENIUS, 1958).

The mouthparts are typical of the *Coccidae* family group, but the labium has lateral sclerotizations like those in the *Stictococcidae*. It shows various degrees of specialization in different members of this family, being primitive in *Austrotachardia* and specialized in *Tachardiella*.

CHAMBERLIN (1923, 1925) and BALACHOWSKY (1950) recognized in this family some lower taxa, but due to the scarcity of the examined material the results of the present investigations cannot be compared with the classification of these authors.

### *Coccidae* FALLÉN

*Coccidae* FALLÉN, 1814: 23;

*Lecanites* TARGIONI TOZZETTI, 1868: 713.

The *Coccidae* are one of the greater families within the suborder; well defined by the female and, not so distinctly, however, by the male characters. The coccid workers associate it with *Asterolecaniidae* and *Lecanodiaspididae* (FERRIS, 1957), adding to this group also *Aclerdidae* (BALACHOWSKY, 1942; BORCHSENIUS, 1958) and *Micrococcidae* (BALACHOWSKY, 1936, 1942), and in the recent years also *Kermesidae* (GILIOME, 1967, 1968; BORATYNSKI and DAVIES, 1971).



The family *Coccidae* is supposed to be derived from the pseudococcid or acanthococcid ancestors. The opinion of some authors based on male morphology (GILMEE, 1967; AFIFI, 1968; BORATYNSKI and DAVIES, 1971) that *Coccidae* derived from the *Margarodidae* (s.l.) independently as a second branch (beside the *Pseudococcidae*) through a form close to *Steingelia* seems to be unlikely (see discussion under *Phenacoleachiidae* and *Kuwaniidae*).

The family *Coccidae* is characterized by the hemispherical, one-, or indistinctly two-segmented labium with 5 pairs of setae and the presence of anal plates. The labium represents a comparatively high degree of specialization but which is undoubtedly lower than that in some *Asterolecaniidae* and *Diaspididae*.

BALACHOWSKY (1942, 1948) divided the *Coccidae* (= *Lecaniinae*) into three groups — *Coccini* (= *Lecaniini*), *Micrococcini* and *Aclerdini*. BORCHSENIUS (1957) distinguished among the *Coccidae* three subfamilies, the *Filippinae*, *Coccinae* (with the tribes *Pulvinariini* and *Coccini*) and *Ceroplastinae*. GILMEE (1957), on the basis of male characters recognized four groups of genera — the *Eulecanium* group, the *Eriopeltis* group, the *Inglisia* group and the *Coccus* group, but the generic components of these groups are basically different from those of BORCHSENIUS. Beside the above named groups some other taxa were erected in this family: *Eriopeltini* (ŠULC, 1941), *Ctenochitini* (COCKERELL, 1899b), *Paralecaniini* (WILLIAMS, 1969).

On the basis of the uniform structure of the mouthparts, the author associated in a recent scheme (KOTEJA, 1974) the *Coccidae*, *Lecanodiaspididae*, *Acleridae* and *Cissococcidae* into one family with these groups as subfamilies. The investigations on the campaniform sensillum on tarsus (KOTEJA, 1974a) revealed, however, that this sense organ, being present in the *Lecanodiaspididae* (and in the majority of scale insects) was absent in both female and male *Coccidae*. Thus the author recognizes the *Lecanodiaspididae*, and consequently the *Acleridae* and *Cissococcidae* as being distinct from the *Coccidae*.

The simple and uniform nature of the mouthparts in the *Coccidae* makes the classification based on these organs impossible. Thus, the classification proposed by GILMEE (1967) is adopted here in general outline.

The family *Coccidae* contains tentatively three tribes (or subfamilies): the *Ctenochitini*, *Eriopeltini* and *Coccini*.

### *Ctenochitini* COCKERELL

*Ctenochitini* COCKERELL, 1899b: 16;

*Filippinae* BODENHEIMER, 1952: 317;

*Filippinae* BODENHEIMER; BORCHSENIUS, 1957: 88 (partim);

*Eulecanium* group GILMEE, 1967: 37.

The labium in the *Ctenochitini* is comparatively large, with the anterior basal part enlarged and the sclerite of medial segment indistinct.

At present following genera are assigned to this tribe: *Eulecanium*, *Lecanopsis*, *Cryptes*, *Stotzia*, *Sphaerolecanium*, *Filippia*, *Phyllostroma*, *Parafairmairia*, *Nemolecanium*, *Physokermes*, *Rhodococcus*, *Palaeolecanium* and *Dicyphococcus*.

As mentioned by GILIOME (1967) on the basis of male morphology, this group does not seem to be homogeneous and further studies could provide reasons to divide it into more taxa.

### *Eriopeltini* ŠULC

*Eriopeltini* ŠULC, 1941: 3;

*Filippinae* BODENHEIMER; BORCHSENIUS, 1957: 88 (partim);

*Eriopeltis* group GILIOME, 1967: 77.

The labium in this group is comparatively small; the sclerite of the media segment is usually indistinct.

This homogenous group contains following genera: *Eriopeltis*, *Scythia*, *Luzulaspis*, *Exaeretopus*, *Psillococcus* and *Vittacoccus*.

### *Coccini* FALLÉN

*Coccides* FALLÉN, 1914: 23;

*Coccinae* FALLÉN; BORCHSENIUS, 1957: 199 (partim);

*Coccus* group GILIOME, 1967: 92;

*Ceroplastinae* MASKELL; BORCHSENIUS, 1957: 447;

*Pulvinariini* TARGIONI TOZZETTI; BORCHSENIUS, 1957: 202;

*Paralecaniini* WILLIAMS, 1969: 333.

The labium in this group is comparatively small, with distinct and narrow medial sclerite.

The following genera are assigned to this tribe: *Pulvinaria*, *Ceroplastes*, *Rhizopulvinaria*, *Parthenolecanium*, *Chloropulvinaria*, *Protopulvinaria*, *Saissetia*, *Eucalymnatus*, Genus E, *Coccus*, *Paralecanium*. On the basis of modifications connected with various habitats, this group can be easily divided into some lower taxa.

### *Lecanodiaspididae* TARGIONI TOZZETTI

*Lecanodiaspites* TARGIONI TOZZETTI, 1969: 260.

This group has been for a long time associated with the *Asterolecaniidae*. BORCHSENIUS (1959, 1960) regarded it as a distinct family, closer to the *Coccidae* than the *Asterolecaniidae*. The investigations on the male (GILIOME, 1967a, 1968; AFIFI and KOSZTARAB, 1969) and on the endosymbionts (BUCHNER, 1965) confirmed this opinion.

The present investigation showed identical structure of the mouthparts in *Lecanodiaspididae* and *Coccidae*. In a recent paper (KOTEJA, 1974) dealing with the labium, the group under discussion is placed as a subfamily in the *Coccidae*.

### *Aclerdidae* COCKERELL

*Aclerdini* COCKERELL, 1905: 197.

The *Aclerdidae* represent a small and well defined group. FERRIS (1957) placed it as a distinct family in his "*Eriococci*" together with the *Pseudococcidae* and *Eriococcidae*. BORCHSENIUS (1958, 1960) and other authors affiliated it usually with *Coccidae* and *Asterolecaniidae*. BALACHOWSKY (1942, 1948) placed it into his *Lecaniidae* (or *Lecaniinae*) as a subfamily (or tribe, respectively).

The investigations on the mouthparts demonstrate a close relationship between *Aclerdidae* and *Coccidae*. In a recent paper this group has been placed by the author (KOTEJA, 1974) as a subfamily in the *Coccidae*. MCCONNELL (1954) redescribed and revised this group.

### *Cissococcidae* BRAIN

*Cissococcinae* BRAIN, 1918: 107.

COCKERELL (1902) placed the genus *Cissococcus* in the *Eriococcini*. BRAIN (1918) established the *Cissococcinae* for it. FERRIS (1920) and STEINWEDEN (1929) assigned it to the *Coccidae*. This view was supported by WILLIAMS (1969).

The structure of the mouthparts indicates a close relationship between *Cissococcidae* and *Coccidae*. The question is whether this group should be placed as a lower category in the latter family.

### *Micrococcidae* SILVESTRI

*Micrococci* SILVESTRI, 1939: 702.

LEONARDI (1907) described the genus *Micrococcus* in the *Pseudococcidae*; FERRIS (1921) assigned it to one group with *Eriococcus*; BALACHOWSKY (1936) suggested a relationship with *Antonina* (*Pseudococcidae*); SILVESTRI (1939) erected the subtribe *Micrococci* in the tribe *Pseudococcini*; in 1942, BALACHOWSKY changed his mind and placed *Micrococcinae* in the family *Lecaniidae* (= *Coccidae*); FERRIS (1957, 1957a) once again transferred *Micrococcus* to the *Acanthococcidae* (= *Eriococcidae*) and HOY (1963) concurred.

The author has not seen the specimens of *Micrococcus*, but the comparison of the materials labelled as "*Ixeidococcus graminis*" (for details see KOTEJA, 1974) with the description and drawing of *Micrococcus rungsi* given by BALACHOWSKY (1936: 160, Fig. 2) and of *M. silvestrii* given by FERRIS (1957: 64, Fig. 38) indicated without doubt that "*Ixeidococcus graminis*" belongs to the group under discussion and probably may be congeneric with *Micrococcus silvestrii*.

The author agrees with the morphological interpretation of *Micrococcus* given by BALACHOWSKY and with his opinion on the relationships of this genus and places it, tentatively as a distinct family, in the *Coccidae* family group.



### *Asterolecaniidae* family group

The labium in this group is comparatively small, conical or heart-shaped, with a distinct and well sclerotized basal ring, one-, in the primitive groups two-segmented, with 0—7 pairs of setae; the clypeolabral complex is large and the sucking pump extremely large; anal cleft and anal plates are absent, 8-shaped pores are present.

The mouthparts show a high degree of specialization and this is in accordance with the specialization of other structures in the male and female, as well as in the biological phenomena.

The *Asterolecaniidae* family group contains various, usually small and monotypic families and genera, and it is rather problematical whether it is a homogeneous and monophyletic group. At present, 3 previously established families (*Asterolecaniidae*, *Beesoniidae*, *Halimococcidae*), 3 groups of genera which are assumed to represent family categories (the *Lachnodi*us, *Opisthoscelis* and *Callococcus* groups) and 3 genera unplaced (*Capulinia*, *Colobopyga*, *Thysanococcus*) are included in this family group.

#### *Lachnodi*us group (presumed family status)

The genus *Lachnodi*us was placed in the *Pseudococcidae* (BALACHOWSKY, 1948; BORCHSENIUS, 1949). MORRISON and MORRISON (1922) expressed the opinion that it is not particularly closely related to the *Pseudococcus* group. FERRIS (1955a) also commented on the uncertainty of its position in the *Pseudococcidae*. HOY (1963) placed it tentatively in the family *Acanthococcidae* (= *Eriococcidae*).

The characters of the mouthparts (labium hemispherical, one-segmented, with 4 pairs of setae) as well as the nature of the legs and antennae, the types of the dermal pores demonstrate clearly that *Lachnodi*us has no connection either with the *Pseudococcidae* or with the *Acanthococcidae*. In connection with the study on the labium (KOTEJA, 1974) *Lachnodi*us was placed in the *Coccidae* family group. The structure of the sucking pump, however, showed no coccid characters, but was rather close to that in *Opisthoscelis* and *Callococcus*. The author sees the genus *Lachnodi*us as a distinct taxon on the family level placed tentatively in the *Asterolecaniidae* family group.

#### *Opisthoscelis* group (presumed family status)

The genus *Opisthoscelis* was usually associated with the genera *Apiomorpha* and *Ascelis*. This group was regarded as a distinct family or united with the *Acanthococcidae* (= *Eriococcidae*). FULLER (1897) and FERRIS (1957) indicated that *Apiomorpha* and *Opisthoscelis* cannot be associated in the same group. FERRIS placed *Apiomorpha* in the *Acanthococcidae* and *Opisthoscelis* among the "Genera Unplaced", but noticed that this genus may be related to the *Coccidae*. HOY (1963) placed both *Apiomorpha* and *Opisthoscelis* in the *Acanthococcidae*.

THERON (1968) redescribed the males of some species of the genera in question and discussed their taxonomic status and nomenclatorial problems. His study, however, did not answer the question whether the two genera are related or not, or where to place this group if it represents a distinct family. Some structures of the head and abdomen indicated relationships with *Acanthococcidae*.

The structure of the labium, which is membranous, one-segmented, with 5 pairs of setae, indicates that *Opisthoscelis* is neither related to *Apiomorpha* nor to *Acanthococcidae*. In this respect it shows some similarities with the *Coccidae*. The sucking pump and the tentorial frame make it close to the insects associated in the *Asterolecaniidae* family group. It is the author's opinion that the *Opisthoscelis* group represents a high taxonomic category, for which calls particularly the morphology of the first stage nymph.

### *Callococcus* group (presumed family status)

The genus *Callococcus* was assigned to the *Asterolecaniidae* (FERRIS, 1918). MORRISON and MORRISON (1927) redescribed 3 included species and agreed with FERRIS's opinion. BORCHSENIUS (1960) suggested the inclusion of this genus to his *Polliniini* (*Cerococcinae*, *Asterolecaniidae*). The present investigations show that *Callococcus* cannot be associated with *Pollinia* — a genus close to *Cerococcus* and placed now in the *Cerococcidae* — *Acanthococcidae* family group.

The comparatively large, conical, two-segmented labium with many setae (about 5 pairs) and the presence of many types and numerous dermal pores indicate that *Callococcus* is a primitive member of the *Asterolecaniidae* family group. On the other hand, some characters — reduction of antennae and legs, the enormous sucking pump show a high degree of specialization.

The distinct characters of the mouthparts and other features of this genus induced the author to ascribe to it a family status.

### *Beesoniidae* FERRIS

*Beesoniidae* FERRIS, 1950a: 5.

This group of unusual insects is well defined and isolated. FERRIS (1957) placed it in the *Beesonii*, a separate ramus between the *Kerriidae* (= *Lacciferidae*) and *Diaspididae*. BORCHSENIUS (1958) did not indicate the relationships of this group but placed it near the *Kerriidae*. HOY (1963) assigned *Beesonia* tentatively to the *Acanthococcidae* (= *Eriococcidae*). WILLIAMS (1969) on the basis of adult males and pupillarial females supposed its close affinities with the family *Diaspididae*. The characters of the mouthparts indicate relationships of *Beesoniidae* with families of the *Asterolecaniidae* family group and particularly with *Callococcus*, but some characters of the first, and male second instars show resemblances to *Acanthococcidae* and *Diaspididae*.

Two genera — *Beesonia* GREEN and *Trichococcus* KANDA, 1941 not BORCHSENIUS, 1948, are assigned to this family. *Trichococcus* KANDA (type species *Xyllococcus napiformis* KUWANA, 1914) was placed by its described close to



*Xylococcus* Low, which is an obvious error. *Beesonina* and *Trichococcus* are close relatives and supposedly may be synonymous (Suggestion of Dr. Sadao TAKAGI, letter of 17. 3. 1972). The redescription and figures of *Xylococcus napiformis* KUWANA given recently by DANZIG (1971) do not refer to *Trichococcus napiformis* (KUWANA) but to a species of *Xylococcus*. *Trichococcus* BORCHSENIUS (type species *Trichococcus filifer* BORCHSENIUS, 1948) belongs to the *Acanthococcidae*.

### *Asterolecaniidae* COCKERELL

*Asterolecaniinae* COCKERELL, 1896: 327.

This group is now widely accepted as a distinct family but its limits undergo some changes from time to time. BORCHSENIUS (1959, 1960) removed *Lecanodiaspis* with related genera from the *Asterolecaniidae* and established a new family — the *Lecanodiaspididae*. In the present paper *Cerococcus* with related genera, and *Callococcus* are transferred to other groups. The author is not sure either, whether the genera *Mycetococcus*, *Frenchia* and *Eremococcus*, tentatively left in the group under discussion, are relatives of the *Asterolecaniidae*.

In the classification by BORCHSENIUS (1960), *Mycetococcus* belongs to the subfamily *Cerococcinae* which is now regarded as a distinct family among the insects of the *Acanthococcidae* family group. On the other hand, the investigations by BROWN and MCKENZIE (1962) showed a cytological relationship of *Mycetococcus ehrhorni* to *Diaspididae*. The characters of the mouthparts indicate no relationship to *Cerococcidae* or to *Diaspididae*, being rather closer to the *Asterolecaniidae*.

The genus *Frenchia* was associated by BORCHSENIUS (1960) with the genus *Pollinia*. The present investigations show close relationship between *Pollinia* and *Cerococcus* but not between *Frenchia* and *Pollinia* or *Cerococcus*, and as the characters of the mouthparts agree in general outline with those of the *Asterolecaniidae*, *Frenchia* is assigned to this family.

*Eremococcus* was supposed to be related with *Asterolecanium* (MORRISON and MORRISON, 1922). BORCHSENIUS (1960) erected for it a new subfamily — *Eremococcinae*, the third one among the *Asterolecaniinae* and *Cerococcinae* (*Asterolecaniidae*). The mouthparts demonstrate that *Eremococcus* is closer to *Asterolecaniidae* than to other *Coccoidea* but its proper relationships and taxonomic category require further studies.

The *Asterolecaniidae* are regarded as highly specialized *Coccoidea*. This view was confirmed by the investigations on the male (GILIOME, 1968) and by the present studies.

### *Halimococcidae* BROWN and MCKENZIE

*Halimococcidae* BROWN and MCKENZIE, 1962: 168.

STICKNEY (1934) assigned this genus to his *Phoenicococcinae* and so did BALACHOWSKY (1948) and BORCHSENIUS (1966). BROWN and MCKENZIE (1962), on the basis of cytological and morphological studies suggested that a new



family was needed to contain the pupillarial insects in the *Phoenicococcidae*. WILLIAMS (1969) regarded this suggestion as a formal establishment of the family *Halimococcidae*.

BROWN and MCKENZIE supposed that this family was close to the *Diaspididae*. The characters of the mouthparts and some others (first instar nymph) are quite different in these two groups. A close relationship between *Halimococcidae* and *Asterolecaniidae* or another member of this family group must be also precluded.

### Genera unplaced (among the *Asterolecaniidae* family group)

#### *Capulina* SIGNORET

*Signoret* (1875) assigned this genus to his *Acanthococcites*; COCKERELL (1899a) and HOY (1963) referred it with the *Acanthococcidae* (= *Eriococcidae*); MACGILLIVRAY (1921) and BALACHOWSKY (1948) assigned it to the *Cylindrococcinae*; according to FERRIS (1957) *Capulinia* cannot be placed comfortably in any of the accepted families, but he suggested a possible relationship to *Opisthoscelis*.

The specimens which the author has the opportunity to examine were in a bad condition and the mouthparts could not be described in detail. The labium seems to be one-segmented, with 4—5 pairs of setae, the sucking pump is very large, as in some members of the *Asterolecaniidae* family group. Thus, the author accepts the opinion of FERRIS and places the genus *Capulinia* in the *Asterolecaniidae* family group, near *Opisthoscelis* and *Callococcus*.

#### *Thysanococcus* STICKNEY

STICKNEY (1934) placed this genus in his *Phoenicococcinae* (*Diaspididae*). BORCHSENIUS (1966) concurred with this opinion.

The materials (*Thysanococcus pandani*) which the author examined were in a bad condition and little can be said on the relationships of this genus. The labium seems not to be of a diaspidid type.

#### *Colobopyga* BRÉTHES

*Colobopyga* BRÉTHES, 1912: 279;  
*Palmaricoccus* STICKNEY, 1934: 49.

STICKNEY (1934), FERRIS (1952) and BORCHSENIUS (1966) placed this genus close to *Phoenicococcus*.

The author examined some poor specimens of *Colobopyga* (= *Palmaricoccus*) *attaleae*. The mouthparts show no diaspidid characters.

### *Diaspididae* family group

The most characteristic feature of the labium in the insects associated in the *Diaspididae* family group are the modified apical and subapical setae which represent a sort of small, membranous tubercles. The other characters of the mouthparts, being rather uniform, are similar to those in the *Asterolecaniidae* family group.

The mouthparts in the *Diaspididae* family group show a high degree of specialization, and only some members of the *Porphyrophoridae* and *Asterolecaniidae* family groups are more specialized.

The origin of this group and its relationships to other *Coccinea* constitute the most difficult questions in the taxonomy of the scale insects. The coccidologists agree that *Diaspididae* represent a distinct, isolated and highly specialized group. BALACHOWSKY (1942) and BORCHSENIUS (1966) elevated it to a superfamily category. NEWSTEAD (1903), BODENHEIMER (1944) and BORCHSENIUS (1958) suggested close relationships between *Diaspididae* and *Conchaspidae*, regarding the latter as an annectant group between primitive *Coccoidea* and *Diaspididae*. BALACHOWSKY (1942, 1948) explained the similarities between these two groups simply as a result of convergency. BROWN and MCKENZIE (1962) and BORATYNSKI and DAVIES (1971) followed the conception suggested by NEWSTEAD but regarding the *Conchaspidae* as link between the highly specialized *Coccoidea* (e.g. the *Asterolecaniidae*) and the *Diaspididae*. On the other hand, GILIOME (1961, 1968) and AFIFI (1968) noticed that males *Asterolecaniidae* are in many respects more specialized than the males *Diaspididae* which have retained some primitive characters found in the *Pseudococcidae* and *Acanthococcidae*, and that it appeared to be most unlikely that *Diaspididae* could have been derived from the asterolecaniid ancestors. GILIOME (1968) emphasized, moreover, that *Mycetococcus ehrhorni*, the species on which BROWN and MCKENZIE based their conclusions is not particularly closely related to *Asterolecanium* (see *Asterolecaniidae*).

From the studies on the mouthparts following conclusions can be drawn:

- The characters of the mouthparts do not indicate a particular group of *Coccinea* from which the *Diaspididae* could be derived.
- The modified setae, characteristic of a diaspidid labium have not been found in any other group and therefore it seems to be unlikely that the *Diaspididae* originate from a primitive group separately.
- The one-segmented labium with a few setae indicates that the *Diaspididae*, *Asterolecaniidae* and *Coccidae* family groups derived from primitive *Acanthococcidae* ancestors, probably as one branch which later ramified into various groups. This view is in agreement with WILLIAMS'S suggestion (1969) that *Phoenicococcus*, *Xanthophtalma* and *Limacoccus* (= *Canceraspis*), associated usually with *Diaspididae*, have many affinities with the *Acanthococcidae*.
- In contrast with BALACHOWSKY (1942) and BORCHSENIUS (1966) the author does not see any reasons for which *Diaspididae* should be considered in a higher category (superfamily) than other groups here recognized as family groups.

As the classification on the basis of labial characters appeared impossible in the *Diaspididae* family group, the conception of BORCHSENIUS (1966) was accepted here in general outline. Thus the *Diaspididae* family group contains two families — the *Phoenicococcidae* and *Diaspididae*. The genera *Limacoccus* (= *Canceraspis*) and *Xanthophtalma* placed by BORCHSENIUS in the *Phoenicococcidae* and *Diaspididae*, respectively, are assigned to the "Genera unplaced".

### *Phoenicococcidae* STICKNEY

*Phoenicococcinae* STICKNEY, 1934: 26;

*Phoenicococcidae* STICKNEY; BALACHOWSKY, 1942: 39.

COCKERELL (1899c) associated *Phoenicococcus* with pseudococcid genera. STICKNEY (1934) erected for it and some other unusual genera the subfamily *Phoenicococcinae* in the family *Diaspididae*. BALACHOWSKY (1942), FERRIS (1957) and BORCHSENIUS (1958, 1966) regarded this group as a distinct family close to the *Diaspididae*. BROWN and MCKENZIE (1962) on the basis of cytological studies dissociated *Phoenicococcus* from other pupillarial genera (see *Halimococcidae*). Some workers (FERRIS, 1957; OBENBERGER, 1957; BORATYNSKI and DAVIES, 1971) considered the *Phoenicococcidae* as a more specialized group than the *Diaspididae*, the others (BALACHOWSKY, 1942; BORCHSENIUS, 1958, 1966) as a rather primitive one, from which the *Diaspididae* could have derived. WILLIAMS (1969) believes that *Phoenicococcus* and perhaps *Xanthophtalma* should be studied further in connection with the *Acanthococcidae*. As far as the characters of the mouthparts are concerned, *Phoenicococcus* represents a more primitive group than the *Diaspididae*.

BORCHSENIUS (1966), rejecting the actions made by earlier authors, assigned to the *Phoenicococcidae* the genera *Phoenicococcus*, *Colobopyga* (= *Palmariococcus*), *Platycoccus*, *Halimococcus*, *Thysanococcus*, *Madhalimococcus* and *Canceraspis*. The genus *Xanthophtalma* is placed by him in the subfamily *Xanthophtalminae*, family *Diaspididae*. The author examined six of the above mentioned genera: *Halimococcus* is assigned to the family *Halimococcidae* (*Asterolecaniidae* family group), *Colobopyga* and *Thysanococcus* are placed tentatively in the *Asterolecaniidae* family group, *Limacoccus* (= *Canceraspis*) and *Xanthophtalma* are discussed in the "Genera unplaced" in the *Diaspididae* family group, and *Phoenicococcus* is left in the family *Phoenicococcidae*.

The genus *Fagisuga* placed by BALACHOWSKY (1948) in this group is assigned to the family *Conchaspidae*.

### *Diaspididae* TARGIONI TOZZETTI

*Diaspites* TARGIONI TOZZETTI, 1868: 713;

*Lepidosaphidae* SHIMER, 1868: 372.

The mouthparts in the *Diaspididae* represent an uniform type. Some insignificant differences in the structure of the labium, clypeolabral shield and sucking



pump do not offer a possibility of constructing a comprehensive classification comparable with these of other authors (FERRIS, 1937; BALACHOWSKY, 1948; GHOURI, 1962; BORCHSENIUS, 1965).

### Genera unplaced (among the *Diaspididae* family group)

#### *Xanthophtalma* COCKERELL

Ferris (1937), BALACHOWSKY (1942, 1948) and BORCHSENIUS (1965, 1966) placed this genus as a tribe or subfamily in the family *Diaspididae*. BROWN and MCKENZIE (1962) stated that it had some relationship with the genus *Phoenicococcus*. WILLIAMS (1969) suggested this group may have affinities with the *Acanthococcidae* (= *Eriococcidae*).

The mouthparts in the available specimens of *Xanthophtalma concinnum* were difficult to examine. They seem to be of diaspidid type.

#### *Limacoccus* BONDAR

*Limacoccus* BONDAR, 1929;  
*Canceraspis* HEMPEL, 1934;  
*Canceraspidinae* HEMPEL, 1934.

BONDAR (1929) described this genus in the *Pseudococcinae*, HEMPEL (1934) placed *Canceraspis* and its nominate group near *Diaspididae*. LEPAGE (1938) synonymized *Canceraspis* with *Limacoccus* and placed this genus in the *Phoenicococcidae*. BORCHSENIUS (1966) considered *Limacoccus brasiliensis* GOMEZ COSTA and REDAELI as a synonym of *Canceraspis brasiliensis* HEMPEL, and the subfamily *Canceraspidinae* as a synonym of *Phoenicococcidae*. WILLIAMS (1969), on the basis of the first instar nymph characters, suggested that *Limacoccus* (= *Canceraspis*) may belong to the *Acanthococcidae* (= *Eriococcidae*).

The mouthparts, somewhat destroyed on the slides which the author examined, showed characters of the diaspidid type. The genus is therefore assigned to the "Genera unplaced" of the *Diaspididae* family group.

### FINAL NOTES

From the study on the mouthparts certain conclusions of general significance for the investigations on scale insects can be drawn. Some of them are discussed below.

In the morphology and taxonomy of scale insects not all characters under examination were given similar attention. The reasons for giving preference to some characters seem to be sometimes of a subjective and incidental nature. The study on the mouthparts indicates that the significance of this or that

character for understanding the phylogeny of a given group can be evaluated after detailed and comparative investigations on large material.

As far as the *Coccinea* are concerned no investigations on the relations between various morphological structures were carried out. The present study on the relation between labium, clypeus, sucking pump, body and legs shows that such investigations are interesting and useful.

The present study demonstrates that even the recent investigations in which the modern microscopic techniques are used, are not sufficiently accurate. The antennae, for instance, were examined and described in hundreds of species, but in fact, we cannot answer what is the exact number of setae in given groups and whether it is constant or variable, and we know nothing on the structure, number and distribution of the sensilla on the antennae in the *Coccinea* as a group.

As already mentioned, the mouthparts have been neglected in the taxonomy of the scale insects because of the presumed variability of their characters. The present investigations revealed that the essential characters of the mouthparts were more constant than any others, and that the "variability" resulted in this case from the deformations during the preparation.

The present investigations deal with single and comparatively simple structures but the species under study represent almost all groups of *Coccinea*. There is no question that the further investigations will add new details to the knowledge on the mouthparts and that some obscure questions, e.g., the nature of the apical organ on labium, will be elucidated; the conclusions based on the morphology of the mouthparts will be changed or rejected. But the study seems to constitute a general framework of investigations on the mouthparts and seems to suggest the future results to be obtained in this field.

The case of the mouthparts calls for comparative investigations on other structures. First of all there is need for investigations on dermal structures, representing principal characters in the taxonomy of the scale insects. The 8-shaped pores, for instance, are present in the *Cerococcidae*, *Asterolecaniidae*, *Lecanodiaspididae* and other groups, but there is a question whether these pores represent homologous structures or whether they originated due to the convergency.

The topic of this study has been discussed with some coccid workers. Most of them questioned the advisability of building a family level classification based solely on a single structure. "A classification and phylogenetic conclusions based exclusively on labial characters are subjective and much risky" they said. There seems to be some misunderstanding in connection with this opinion. The author would like to emphasize that the basing of a classification and of phylogenetic conclusions on a single structure does not mean a rejection of other taxonomic criteria. The purpose of the present investigations was the evaluation of the characters of the mouthparts in the taxonomy, but to be able to answer the question whether or not they can be useful, an attempt of classification must have been made. Besides, it is known that taxa on high level are usually distin-

guished by a small number of characters. In the scale insects the females of the *Orthezioidea* (= *Margarodidae* s.l.) were separated from other groups solely after the abdominal spiracles.

The investigations revealed that it was very difficult or even impossible to classify species and genera within a family exclusively on the basis of labial characters, but the families and higher taxa could be well defined and separated by means of these characters.

The basing of the classification on the mouthparts did not introduce, in fact, new phylogenetic conceptions concerning particular groups as well as the *Coccinea* as a whole. It offered only new arguments for the one or the other previously expressed opinion based on other features. And these arguments were of particular value because they could be applied to all groups and all (high) taxonomic levels. One example, at least, should be quoted here — the genus *Cerococcus* and its relatives were widely accepted as belonging to the *Asterolecaniidae*. The characters of the mouthparts exhibited close relationship between *Cerococcus* and *Acanthococcidae*, but it appeared that a similar suggestion was expressed by WILLIAMS (1969) on the basis of male characters.

Academy of Agriculture  
Institute of Applied Zoology  
Al. Mickiewicza 24/28  
30-059 Kraków, Poland

#### REFERENCES<sup>1</sup>

- AFIFI S. A. 1968. Morphology and taxonomy of the adult males of the families *Pseudococcidae* and *Eriococcidae* (Homoptera: Coccoidea). Bull. Brit. Mus. (Nat. Hist.), Entomology, London, Suppl. 13: 1—210.
- AFIFI S. A. 1969. Systematic studies of the family *Conchaspidae* based on the male of *Conchaspis lata* HEMPEL (Homoptera: Coccoidea). Bull. Virginia Polytechnic Inst., Blacksburg, 36: 25—37.
- AFIFI S. A., KOSZTARAB M. 1967. Studies on the morphology and taxonomy of the males of *Antonina* and one related genus (Homoptera: Coccoidea: *Pseudococcidae*). Bull. Virginia Polytechnic Inst., Blacksburg, 15: 1—43.
- AFIFI S. A., KOSZTARAB M. 1969. Morphological and systematic studies on the adult males of some species of *Lecanodiaspis* (Homoptera: Coccoidea: *Lecanodiaspididae*). Bull. Virginia Polytechnic Inst., Blacksburg, 36: 1—23.
- \*AMYOT C. J. B., SERVILLE A. 1843. Histoire naturelle des insectes. Hémiptères. Paris, pp. I—LXXVI, 1—677, 1—6.
- BALACHOWSKY A. 1936. Contribution à l'étude des coccides du nord africain (15me note) Bull. Soc. Ent. France, Paris, 41: 157—165.

<sup>1</sup> Items marked by an asterisk are known to the author only from reports.



- BALACHOWSKY A. 1942. Essai sur la classification des cochenilles (*Homoptera* — *Coccoidea*). Ann. Grignon Ecole Nat. d'Agr., Grignon, (ser. 3), 3: 34—48.
- BALACHOWSKY A. 1948. Les cochenilles de France... IV. Monografie des *Coccoidea*. Classification — *Diaspidinae* (Première partie). Actualités Sci. et Indus., Ent. Appl., Paris, 1054: 243—394.
- BALACHOWSKY A. 1950. Sur deux *Tachardina* CKLL. (*Coccoidea* — *Lacciferinae*) nouveaux du Sahara Central. Eos, Madrid, 26: 7—17.
- BALACHOWSKY A. 1953. Sur le statut des genres *Puto* SIGNORET, *Ceroputo* ŠULC, et *Macrocerococcus* LEONARDI. Mitt. Schweiz. Ent. Gesell., Schaffhausen, 26: 301—304.
- \*BALACHOWSKY A. 1956. Les cochenilles du Continent Africain Noir. 1. Ann. Mus. Roy. Congo Belg., Tervuren, 3.
- BEARDSLEY J. W. 1962. Descriptions and notes on male mealybugs (*Homoptera: Pseudococcidae*). Proc. Hawaiian Ent. Soc. Honolulu, 18: 81—91.
- BEARDSLEY J. W. 1964. Insects of Campbell Island. *Homoptera: Coccoidea*. Pacific Insects Monogr., Honolulu, 7: 238—252.
- BEARDSLEY J. W. 1965. The male of *Antonina crawi* COCKERELL (*Homoptera: Pseudococcidae*). Proc. Hawaiian Ent. Soc., Honolulu, 19: 47—49.
- BEARDSLEY J. W. 1968. External morphology of the adult male of *Matsucoccus bisetosus*. Ann. Ent. Soc. America, Columbia, Miss., 61: 1449—1459.
- BEARDSLEY J. W. 1969. A new fossil scale insect (*Homoptera: Coccoidea*) from Canadian amber. Psyche, Cambridge, Mass, 3: 270—279.
- \*BODENHEIMER F. S. 1944. A conchaspidid from Kurdistan and its importance in the phylogeny of the *Diaspididae* (*Hemiptera*). Proc. Roy. Ent. Soc., London, ser. B. Taxonomy, 13: 4—5.
- \*BODENHEIMER F. S. 1952. The *Coccoidea* of Turkey. I. Univ. Facult. Sci. Rev., Istanbul, ser. B., 17: 315—351.
- \*BODENHEIMER F. S. 1953. The *Coccoidea* of Turkey. III. Univ. Facult. Sci. Rev., Istanbul, ser. B., 18: 91—164.
- \*BONDAR G. 1929. Um novo genro e nova especie de pulgoes da Bahia. (*Homoptera, Coccidae, Pseudococcinae*). Bol. Biol., Bahia, Salvador, 16: 59—64.
- BORATYNSKI K. 1961. A note on the genus *Asterolecanium* TARGIONI TOZZETTI (*Homoptera, Coccoidea, Asterolecaniidae*) on oak in Britain. Proc. Roy. Ent. Soc., London, (B), 30: 4—14.
- BORATYNSKI K. 1962. A new species of *Acanthococcus* SIGNORET 1875 (*Eriococcidae, Coccoidea, Homoptera*) from Britain. Proc. Roy. Ent. Soc., London, (B), 31: 55—60.
- BORATYNSKI K. 1970. Advances in our knowledge of *Coccoidea* (*Homoptera*) with reference to the studies of the males and the application of some numerical methods of classification. Polish Congress of Contemporary Science and Culture in Exile, London, 1970, 1: 585—595.
- BORATYNSKI K., DAVIES R. G. 1971. The taxonomic value of male *Coccoidea* (*Homoptera*) with an evaluation of some numerical techniques. Biological Journal of Linnean Society, London, New York, 3: 57—102.
- BORATYNSKI K., WILLIAMS D. J. 1964. A note on some British *Coccoidea* with new additions to the British fauna. Proc. Roy. Ent. Soc., London, (B), 33: 103—110.
- \*BORCHSENIUS N. S. 1948. Борхсениус. Н. С. 1948. К ревизии рода *Eriococcus* SIGN. (*Insecta, Homoptera, Coccoidea*). Докл. Акад. Наук СССР, Ленинград—Москва, 60: 501—503.
- \*BORCHSENIUS N. S. 1948 a. Борхсениус. Н. С. 1948 a. К ревизии рода *Phenacoccus* SKLL. (*Insecta, Homoptera, Coccoidea*). Докл. Акад. Наук СССР, Ленинград—Москва, 61: 953—956.
- BORCHSENIUS N. S. 1949. Борхсениус. Н. С. 1949. Фауна СССР. Насекомые хоботые. VII. Подотр. червецы и щитовки, *Coccoidea* сем. мучнистые червецы (*Pseudococcidae*). Москва—Ленинград, 383 pp.
- BORCHSENIUS N. S. 1950. Борхсениус. Н. С. 1950. Червецы и щитовки СССР, (*Coccoidea*). Определители по фауне СССР. Москва—Ленинград, 32: 1—250.
- BORCHSENIUS N. S. 1956. Борхсениус. Н. С. 1956. К вопросу о путях эволюции *Coccoidea* (*Insecta, Homoptera*). Зоол. Журн., Москва, 35: 546—553.

- BORCHSENIUS N. S. 1957. Борхсениус Н. С. 1957. Фауна СССР. Насекомые хоботные. IX. Подотр. червецы *Coccoidea* сем. подушечницы и ложнощитовки (*Coccidae*). Москва—Ленинград, 493 pp.
- BORCHSENIUS N. S. 1958. Борхсениус Н. С. 1958. Об эволюции и филогенетических связях *Coccoidea* (*Insecta, Homoptera*). Зоол. Журн., Москва, 37: 765—780.
- BORCHSENIUS N. S. 1959. Борхсениус Н. С. 1959. Материалы по фауне кокцид Китая. VII. Новое семейство кокцид — *Lecanodiaspididae* fam. nov. (*Homoptera, Coccoidea*). Энт. Обзор., Ленинград, 38: 840—846.
- BORCHSENIUS N. S. 1960. Борхсениус Н. С. 1960. Фауна СССР. Насекомые хоботные. VIII. Подотр. червецы и щитовки *Coccoidea* сем. *Kermococcidae*, *Asterolecaniidae*, *Lecaniodaspididae*, *Acleridae*. Москва—Ленинград, 284 pp.
- BORCHSENIUS N. S. 1965. Борхсениус Н. С. 1965. Основы классификации Щитовок (*Homoptera, Coccoidea, Diaspididae*). Энт. Обзор., Ленинград, 44: 362—376.
- BORCHSENIUS N. S. 1966. Борхсениус Н. С. 1966. Каталог щитовок мировой фауны. Москва—Ленинград, 449 pp.
- BORCHSENIUS N. S., DANZIG E. M. 1966. Борхсениус Н. С., Данциг Е. М. 1966. Новый вид войлочника *Greenisca* BORCHS. (*Homoptera, Coccoidea, Eriococcidae*) фауны СССР. Тр. Зоол. Инст. Акад. Наук СССР, Москва—Ленинград, 37: 41—44.
- \*BRAIN C. K. 1918. The *Coccidae* of South Africa. II. Bull. Ent. Res., London, 9: 107—139.
- \*BRÉTHES J. 1912. Description de un nuevo genero y especie de cochinilla de la Republica Argentina. Ann. Buenos Aires Mus. Nac. Hist. Nat., Buenos Aires, 23: 279—281.
- \*BROWN S. W. 1959. Lecanoid chromosome behaviour in three more families of the *Coccoidea* (*Homoptera*). Chromosoma, Berlin, 10: 278—300.
- \*BROWN S. W., CLEVELAND C. 1968. Meiosis in the male of *Puto albicans* (*Coccoidea, Homoptera*). Chromosoma, Berlin, 24: 210—232.
- \*BROWN S. W., MCKENZIE H. L. 1962. Evolutionary patterns in the armoured scale insects and their allies (*Homoptera: Coccoidea: Diaspididae, Phoenicococcidae* and *Asterolecaniidae*). Hilgardia, Berkeley, Ca., 33: 141—170.
- \*BRUES C. T., MELANDER A. L. 1932. Classification of insects. Bull. Mus. Comp. Zool., Cambridge, Mass., 73: 127—134.
- BUCHNER P. 1965. Endosymbiosis of animals with plant microorganisms. Interse. Publs, New York, London, Sydney, 909 pp.
- \*CHAMBERLIN J. C. 1923. A systematic monograph of the *Tachardiinae* or lac insects (*Coccidae*). Bull. Ent. Res., London, 14: 147—212.
- \*CHAMBERLIN J. C. 1925. Supplement to a monograph of the *Lacciferinae* (*Tachardiinae*) or lac insects. Bull. Ent. Res., London, 16: 31—41.
- \*CHOU I. 1963. Some viewpoints about insect taxonomy. Acta Ent. Sin., Peking, 12: 586—596.
- \*COCKERELL T. D. A. 1896. A check list of the *Coccidae*. Bull. Illinois State Lab. Nat. Hist., Champaign, Ill., 4: 318—339.
- \*COCKERELL T. D. A. 1899. First supplement to the check-list of the *Coccidae*. Bull. Illinois State Lab. Nat. Hist., Champaign, Ill., 5: 389—389.
- \*COCKERELL T. D. A. 1899a. Tables for the determination of the genera of *Coccidae*. Canadian Ent., Toronto, 31: 273—279, 330—333.
- \*COCKERELL T. D. A. 1899b. *Aleurodidae* and *Coccidae*. Biol. Centr. America, 2. pt. 2: 1—37.
- \*COCKERELL T. D. A. 1899c. Some notes on *Coccidae*. Proc. Acad. Nat. Sci., Philadelphia, 1899: 259—275.
- COCKERELL T. D. A. 1902. New genera and species of *Coccidae*, with notes on known species. Ann. Mag. Nat. Hist., London, (ser. 7), 9: 20—26.
- \*COCKERELL T. D. A. 1902a. A contribution to the classification of the *Coccidae*. Entomologist, London, 35: 232—233, 257—260.
- \*COCKERELL T. D. A. 1903. Two remarkable new *Coccidae*. Canadian Ent., Toronto, 35: 64—66.
- \*COCKERELL T. D. A. 1905. Tables for the identification of Rocky Mountain *Coccidae* (scale insects and mealybugs). Colorado Univ. Studies, 2: 189—203.

- \*COCKERELL T. D. A. 1909. The Japanese *Coccidae*. Canadian Ent., Toronto, **41**: 55—56.
- \*COCKERELL T. D. A. 1924. The name of the lac insects. Psyche, Cambridge, Mass., **31**: 47—48.
- DANZIG E. M. 1962. Данциг Е. М. 1962. Ревизия рода *Rhizococcus* SIGNORET (*Homoptera*, *Coccoidea*) фауны СССР. Энт. Обзор., Ленинград, **41**: 839—860.
- DANZIG E. M. 1964. Данциг Е. М. 1964. Подотряд *Coccinea* — кокциды или червецы и щитовки, in: Бей-Биенко Г. Я., Определитель насекомых европейской части СССР. Москва—Ленинград, **1**: 616—654.
- DANZIG E. M. 1964. Данциг Е. М. 1971. Новые и малоизвестные виды кокцид (*Homoptera*, *Coccoidea*) из Сибири и Дальнего Востока СССР. Known to the author only from reprint.
- D'ASCOLI A., KOSZTARAB M. 1969. Morphological studies on the three nymphal instars of *Conchaspis lata* HEMPEL (*Homoptera*, *Coccoidea*, *Conchaspidae*). Bull. Virginia Polytechnic Inst., Blacksburg, Va., **36**: 39—51.
- \*DOUGLAS J. W. 1888. Notes on some British and exotic *Coccidae* (No. 12). Ent. Monthly Mag., London, **25**: 150—153.
- DROZDOVSKIY E. M. 1966. Дроздовский Е. М. 1966. О хромосомных наборах у некоторых кокцид (*Homoptera*, *Coccoidea*). Энт. Обзор., Ленинград, **45**: 712—714.
- DZIEDZICKA A. 1961. Studia nad morfologią i biologią lysika, *Gossyparia spuria* (MOD.) (*Homoptera*, *Coccoidea*). Fragm. Faun., Warszawa, **9**: 203—219.
- DZIEDZICKA A., KOTEJA J. 1971. A revision of the species of the genus *Rhizococcus* SIGNORET (*Homoptera*, *Coccoidea*) occurring in Poland. Acta Zool. Cracov., Kraków, **16**: 557—579.
- EZZAT Y. M., MCCONNEL H. S. 1956. A classification of the mealybug tribe *Planococcini* (*Pseudococcidae*, *Homoptera*). Bull. Maryland Agr. Exp. Sta., College Park, Md., A. **84**, 108 pp.
- \*FALLÉN C. F. 1814. Specimen novam *Hemiptera* disponendi methodum exhibens. Lundae.
- FERNALD M. E. 1903. A catalogue of the *Coccidae* of the world. Mass. Agr. Exp. Sta., Amherst, Mass., Spec. Bull. **88**, 360 pp.
- \*FERRIS G. F. 1918. Notes on *Coccidae*. II. (*Hemiptera*). Canad. Ent., Toronto, **50**: 221—225.
- \*FERRIS G. F. 1920. Notes on *Coccidae*. VI. (*Hemiptera*). Canad. Ent., Toronto, **52**: 61—65.
- \*FERRIS G. F. 1921. Notes on *Coccidae*. VII. (*Hemiptera*). Canad. Ent. Toronto, **53**: 57—61.
- FERRIS G. F. 1921a. Report upon a collection of *Coccidae* from lower California. Stanford Univ. Publs. Biol. Sci., Palo Alto, Ca., **1**: 59—132.
- \*FERRIS G. F. 1937. Atlas of scale insects of North America. I. Palo Alto, Ca., 136 pp.
- FERRIS G. F. 1941. Contributions to the knowledge of the *Coccoidae* (*Hemiptera*). X. Microentomology, Palo Alto, Ca., **6**: 11—24.
- FERRIS G. F. 1950. Atlas of the scale insects of North America, V. *Pseudococcidae* (Part I), Palo Alto, Ca., VII + 278 pp.
- FERRIS G. F. 1950a. Report upon scale insects collected in China, (*Homoptera*, *Coccoidea*). Part I. Microentomology, Palo Alto, Ca., **15**: 1—34.
- \*FERRIS G. F. 1952. Some miscellaneous *Coccoidea* (*Insecta: Homoptera*). Microentomology, Palo Alto, Ca., **17**: 2—5.
- FERRIS G. F. 1955. Atlas of the scale insects of North America, VII. The families *Aclerdidae*, *Asterolecaniidae*, *Conchaspidae*, *Dactylopiidae* and *Lacciferidae*, Palo Alto, Ca., III + 233 pp.
- \*FERRIS G. F. 1955a. On some genera of the *Pseudococcidae* (*Homoptera*, *Coccoidea*). Microentomology, Palo Alto, Ca., **20**: 1—19.
- FERRIS G. F. 1957. Notes on some little known genera of the *Coccoidea* (*Homoptera*). Microentomology, Palo Alto, Ca., **22**: 59—79.
- FERRIS G. F. 1957a. A review of the family *Eriococcidae* (*Insecta: Coccoidea*). Microentomology, Palo Alto, Ca., **22**: 81—89.
- \*FULLER C. 1897. Coccid literature. West Austral. Bur. Agr. Journ., **4**: 1342—1343.
- GHAURI M. S. K. 1962. The morphology and taxonomy of male scale insects (*Homoptera: Coccoidea*). London, 221 pp.
- GILIOME J. H. 1961. Morphological and taxonomic studies on the males of three species of the genus *Pseudococcus* (*Hemiptera: Coccoidea*). Ann. Univ. Stellenbosch, **36**: 241—296.



- GILIOMEE J. H. 1965. Some advances in the taxonomy of the *Coccoidea* (Homoptera). Proc. XII Int. Congr. Ent. (1964), London, p. 118.
- GILIOMEE J. H. 1967. Morphology and taxonomy of adult males of the family *Coccidae* (Homoptera: *Coccoidea*). Bull. Brit. Mus. (Nat. Hist.), Entomology, London, Suppl. 7: 1—168.
- GILIOMEE J. H. 1967a. The morphology and relationships of the male of *Lecaniodiaspis ely-tropapii* MUNTING and GILIOMEE (Homoptera: *Coccoidea*). Jour. Ent. Soc. Sth Africa, Pretoria, **30**: 185—197.
- GILIOMEE J. H. 1968. Morphology and relationships of the male of an *Asterolecanium* species (Homoptera: *Asterolecaniidae*). Jour. Ent. Soc. Sth Africa, Pretoria, **31**: 297—308.
- \*GREEN E. E. 1896. The *Coccidae* of Ceylon. Part I. London, XI + 103 pp.
- GREEN E. E. 1917. Observations on British *Coccidae*, with descriptions of new species. No. IV. Ent. Monthly Mag., London, **53**: 260—269.
- GREEN E. E. 1920. Observations on British *Coccidae*. No. V. Ent. Monthly Mag., London, **56**: 114—130.
- \*HEMPEL A. 1934. Descrição de tres especies novas, tres generos novas e una subfamilia nova de coccideos (Hemiptera, Homoptera). Rev. Ent., Sao Paulo, **4**: 139—147.
- \*HEYMONS R. 1915. Vierfüßler, Insecten und Spinnenkerfe. in: BREHM, Tierleben, Leipzig, 4 Aufl.
- HOY J. M. 1962. *Eriococcidae* (Homoptera: *Coccoidea*) of New Zealand. Bull. New Zealand Dept. Sci. Indust. Res., Wellington, **146**: 1—219.
- HOY J. M. 1963. A catalogue of the *Eriococcidae* (Homoptera: *Coccoidea*) of the world. Bull. New Zealand Dept. Sci. Indust. Res., Wellington, **150**: 1—260.
- \*HUGHES-SCHRADER S. 1944. A primitive coccid chromosome cycle in *Puto* sp. Biol. Bull., **87**: 167—176.
- \*IMMS D. A. 1957. A textbook of Entomology, London, 9th ed.
- JAKUBSKI A. W. 1965. A critical revision of the families *Margarodidae* and *Termitococcidae* (Hemiptera, *Coccoidea*), London, 187 pp.
- \*KANDA S. 1941. Insect world, **44**: 4—8 (68—67), (in jap.).
- KAWECKI Z. 1964. The importance of the degree of the reduction in male wing apparatus for studies on the phylogeny of scale insects (Homoptera, *Coccoidea*). Zoologia Poloniae, Wrocław, **14**: 205—211.
- KOSZTARAB M. 1968. *Cryptococcidae*, a new family of the *Coccoidea* (Homoptera). Virginia Journ. Sci., Blacksburg, Va., **19**: 12.
- KOTEJA J. 1974. Comparative studies on the labium in the *Coccinea* (Homoptera). Zesz. Nauk. Akad. Rol., Kraków, ser. Rozprawy, **27**, 162 pp.
- KOTEJA J. 1974a. The occurrence of a campaniform sensillum on tarsus in the *Coccinea* (Homoptera). Pol. Pismo Ent., Wrocław, **44**: 243—252.
- KOTEJA J. The sucking pump in the taxonomy of the *Coccinea* (Homoptera) (manuscript).
- KOTEJA J., ŻAK-OGAŻA B. 1972. Morphology and taxonomy of the male *Kermes quercus* (L.) (Homoptera, *Coccioidea*). Acta Zool. Cracov., Kraków, **22**: 193—215.
- KOTEJA J., LINIOWSKA E. The clypeolabral shield in the taxonomy of the *Coccinea* (Homoptera) (manuscript).
- KUWANA I. 1914. *Coccidae* of Japan. V. Journ. Ent. Zool., Claremont, Ca., **6**: 1—11.
- \*LEONARDI G. 1907. Contribuzione alla conoscenza delle cocciniglie italiane. Portici R. Scuola Super. Agr. Lab. Zool. Gen. Agr. Bol., Portici, **1**: 135—169.
- \*LEONARDI G. 1920. Monografia delle cocciniglie italiane. Portici, Della Torre, 555 pp.
- \*LEPAGE H. S. 1938. Catalogo dos coccideos do Brasil. Rev. Mus. Paulista, São Paulo, **23**: 327—491.
- LINDINGER L. 1912. Die Schildläuse (*Coccidae*). Stuttgart, 388 pp.
- \*LINDINGER L. 1913. Afrikanische Schildläuse. V. Jahrb. Hamburg. Wiss. Anst., Hamburg, **30** (R. 3): 59—95.
- \*LINDINGER L. 1933. Beiträge zur Kenntnis des Schildläuse (Hemipt. — Homopt., Coccid.). Ent. Anz., Wien, **13**: 77—78, 107—108, 116—117, 143, 159—160, 165—166.

- LINDINGER L. 1937. Verzeichnis der Schildlaus-Gattungen (*Homoptera* — *Coccoidea* HAN-  
DLIRSCH 1903). Ent. Jahrb., Leipzig, **36**: 178—198.
- LINDINGER L. 1954. Neue Beiträge zur Schildlaus-Nomenklatur und Anderes (*Hemiptera*:  
*Coccidae*). Beitr. Ent. Berlin, **4**: 614—620.
- \*LOBDELL G. H. 1929. Two new species of *Eriococcus* from Mississippi (*Homoptera*, *Coccoidea*).  
Ann. Soc. Ent. America, Columbia, Miss., **22**: 762—767.
- \*LOBUSTER H. J. M. 1966. A study on the morphology and taxonomy of the males of two  
*Dactylopius* species (*Hemiptera*: *Coccoidea*). M. Sci. (Agric.) thesis, University of Stellen-  
bosch.
- MACGILLIVRAY A. D. 1921. The *Coccidae*. Urbana, Ill., 502 pp.
- \*MAMET R. 1954. Notes on the *Coccoidea* of Madagascar. III. Mém. Inst. Sci. Madagascar,  
Tananarive, **4** (ser. E.): 1—86.
- \*MAMET R. 1954a. A monograph of the *Conchaspidae* GREEN (*Hemiptera*: *Coccoidea*). Trans.  
Roy. Ent. Soc., London, **105** (11): 189—239.
- \*MASKELL W. M. 1891. Further coccid notes, with descriptions of new species from New Zealand,  
Australia and Fiji. N. Zealand Trans. and Proc., Wellington, **23**: 1—36.
- MCCONNELL H. S. 1954. A classification of the coccid family *Acleridae*. Maryland Agr. Exp.  
Sta. Bull., College Park, Md., A-75, 121 pp.
- \*MCKENZIE H. L. 1942. New species of pine-infesting *Margarodidae* from California and  
southwestern United States (*Homoptera*: *Coccoidea*: *Margarodidae*). Microentomology,  
Palo Alto, Ca., **7**: 1—18.
- METCALF Z. P. 1950. Phylogeny of the *Homoptera Auchenorrhyncha*. Proc. 8th Int. Congr. Ent.,  
Stockholm, pp. 561—565.
- MILLER D. R., MCKENZIE H. L. 1967. A systematic study of *Ovaticoccus* KLOET and its relatives,  
with a key to North American genera of *Eriococcidae* (*Homoptera*: *Coccoidea*: *Eriococcidae*).  
Hilgardia, Berkeley, Ca., **38**: 471—539.
- MILLER D. R., MCKENZIE H. L. 1973. Seventh taxonomic study of North American mealybugs  
(*Homoptera*: *Coccoidea*: *Pseudococcidae*). Hilgardia, Berkeley, Ca., **41**: 489—542.
- MORRISON H. 1927. Descriptions of new genera and species belonging to the coccid family  
*Margarodidae*. Proc. Biol. Soc., Washington, D. C., **40**: 99—110.
- MORRISON H. 1928. A classification of the higher groups and genera of the coccid family *Marga-*  
*rodidae*. Techn. Bull. U. S. Dept. Agr., Washington, D. C., **52**: 1—239.
- MORRISON H. 1952. Classification of the *Ortheziidae*. Supplement to classification of scale  
insects of the subfamily *Ortheziinae*. Techn. Bull. U. S. Dept. Agr., Washington, D. C.,  
**1052**: 1—78.
- MORRISON H., MORRISON E. 1922. A redescription of the type species of the genera of *Coccoidea*  
based on species originally described by MASKELL. Proc. U. S. Nat. Mus., Washington, D. C.,  
**60**: 1—120.
- MORRISON H., MORRISON E. 1927. The MASKELL species of scale insects of the family *Asterole-*  
*caniidae*. Proc. U. S. Nat. Mus., Washington, D. C., **71**: 1—42.
- MORRISON H., MORRISON E., 1965. A selected bibliography of the *Coccoidea*. First supplement.  
Misc. Publs. U. S. Dept. Agr., Washington, D. C., **987**: 1—44.
- MORRISON H., MORRISON E. 1966. An annotated list of generic names of the scale insects  
(*Homoptera*, *Coccoidea*). Misc. Publs. U. S. Dept. Agr., Washington, D. C., **1025**:  
1—206.
- MORRISON H., RENK A. V. 1957. A selected bibliography of the *Coccoidea*. Misc. Publs. U. S. Dept.  
Agr., Washington, D. C., **734**: 222 pp.
- \*NASSONOV N. V. 1908. *Steingelia gorodetskia*, nov. gen. et nov. sp. Ann. Mus. Zool. Acad.  
Imp. Sci., St. Petersburg, **13**: 354—352.
- NEWSTEAD R. 1903. Monograph of the *Coccidae* of the British Isles. II. London, 270 pp.
- \*NEWSTEAD R. 1908. On the structural characters of three species of *Coccidae* affecting cocoa,  
rubber and other plants in western Africa. Journ. Econ. Biol., **2**: 149—157.
- OEBENBERGER J. 1957. Entomologie. III. Praha, 467 pp.

- \*PERGANDE T. 1926. in: HUBBARD H. G., PERGANDE T. A new coccid on birch. Bull. Dept. Agric. Div. Ent. (n. ser.), Washington, D. C., **18**: 13—26.
- PESSON P. 1951. Ordre de Homoptères (*Homoptera*, LEACH, 1915). in: GRASSE P. P., Traité de zoologie, anatomie, systematique, biologie. X. Insectes supérieurs et hémiptéroïdes. fasc. II, Paris, p. 1391—1656.
- \*PFLUGFELDER O. 1939. *Arthropoda, Insecta Coccina*. in: BRONN's Klassen, Leipzig, 5. Abt. 3, Bd. **8**, T. b.e. p. 1—121.
- REYNE A. 1954. A redescription of *Puto antennatus* SIGN. (*Homoptera, Coccoidea*) with note on *Ceroputo* ŠULC and *Macrocerococcus* Leon. Zool. Mededeelingen, Leiden, **32**: 291—324.
- RICHARD Cl. 1971. Contribution à l'étude morphologique et biologique des *Stictococcinae* (*Hom. Coccoidea*). Ann. Soc. Ent. France, Paris, (n. sér.), **7**: 571—609.
- SCHMUTTERER H. 1952. Die Ökologie der Cocciden (*Homoptera, Coccoidea*) Frankens. Zeitschr. angew. Ent., Berlin, Hamburg, **33**: 370—420, 544—584, **34**: 65—100.
- SCHMUTTERER H., KLOFT W., LÜDICKE M. 1957. *Coccoidea*, Schildläuse, in: SORAUER P., Handbuch der Pflanzenkrankheiten, Bd. V., *Homoptera*, T. II, Lief. 4, Berlin, Hamburg, p. 403—472.
- \*SHIMER H. 1868. Notes on the "apple bark-louse" (*Lepidosaphes conchiformis*, GMELIN) with a description of a supposed new *Acarus*. Trans. American Ent. Soc. Philadelphia, Pa. p. 361—374.
- \*SHINJI O. 1935. On a species of non-diaspine *Coccidae*, for which a new subfamily is to be erected. Jour. Japan Soc. Appl. Zool. Tōkyō, **7**: 106—108.
- SICNORET V. 1875. Essai sur les cochenilles ou gallinsects (parts 14—17). Ann. Soc. Ent. France, Paris, (ser. 5), **5**: 15—40, 305—352, 353—394.
- \*SILVESTRI F. 1939. Fam. *Coccidae*, in: Compendio di ent. appl. Parte spec., **1** (2): 618—680.
- STEINWEDEN J. B. 1929. Bases for the generic classification of the coccoid family *Coccidae*. Ann. Ent. Soc. America, Columbia, Miss., **22**: 197—245.
- STICKNEY F. S. 1934. The external anatomy of the red date scale *Phoenicococcus marlatti* COCKERELL and its allies. Techn. Bull. U. S. Dept. Agr., Washington, D. C., **404**: 1—162.
- ŠULC K. 1941. *Mohelina festucae* n. gen., n. sp. (*Lecaniidae, Eriopeltini, Coccoidea, Hemiptera*). Práce Mor. Přír. Spol., Brno, **13**: 1—17.
- ŠULC K. 1944. *Antoniella* n. gen. synonym. *Antonina sulci* GREEN 1934 (*Coccoidea, Homoptera*). Věst. České Zool. Spol. v Praze, Praha, **9**: 148—170.
- TAKAGI S., KAWAI S. 1967. The genera *Chionaspis* and *Pseudaulacaspis* with criticism on criticism on *Phenacaspis* (*Homoptera: Coccoidea*). Insecta Matsumurana, Sapporo, **30**: 29—43.
- TAKAHASHI R. 1958. Key to genera of *Pseudococcidae* in Japan, with descriptions of three new genera and two new species. Bull. Univ. Osaka Pref., Osaka, **7** (ser. B): 1—8.
- \*TARGIONI TOZZETTI A. 1868. Introduzione alla seconda memoria per glistudi sulle cocciniglie, e catalogo dei generi e delle specie della famiglia dei Coccidi. Atti. Soc. Ital. Sci. Nat., Milano, **11**: 694—738.
- \*TARGIONI TOZZETTI A. 1969. Sopra generi di cocciniglie (*Coccidae*). Bull. Soc. Ent. Ital., Firenze, Genova, **1**: 257—267.
- THERON J. G. 1958. Comparative studies on the morphology of male scale insects (*Hemiptera: Coccoidea*). Ann. Univ., Stellenbosch, **34** (sec. A): 1—71.
- THERON J. G. 1962. Structure and relationships of the male of *Phenacoleachia zealandica* (MACKELL) (*Hemiptera: Coccoidea*). Proc. Roy. Ent. Soc., London, (ser. A), **37**: 145—153.
- THERON J. G. 1968. Studies on the morphology and relationships of male *Apiomorpha* and *Opisthoscelis* (*Hemiptera: Coccoidea*). Australian Journ. Zool., Melbourne, **16**: 87—99.
- WAGNER W. 1962. Dynamische taxionomie aufgewandt auf die Delphaciden Mitteleuropas. Mitt. Hamburg. Zool. Mus. Inst., Hamburg, **60**: 111—180.
- WEGLARSKA B. 1966. Rozwój jąder i spermatogeneza u *Quadraspidiotus ostreaeformis* (CURT.) (*Homoptera, Coccoidea, Aspidiotini*). Zesz. Nauk. UJ, Kraków, **136** (pr. zool., z. 12): 59—89.



- WILLIAMS D. J. 1969. The family-group names of the scale insects (*Hemiptera: Coccoidea*). Bull. Brit. Mus. (Nat. Hist.), Entomology, London, **23**: 315—341.
- WILLIAMS M. L., KOSZTARAB M. 1970. A morphological and systematic study on the first instar nymph of the genus *Lecanodiaspis* (*Homoptera: Coccoidea: Lecanodiaspididae*). Bull. Virginia Polytechn. Inst., Blacksburg, Va., **52**: 1—96.
- YANG S. P., KOSZTARAB M., 1967. A morphological and taxonomic study on the immature stages of *Antonina* and of the related genera (*Homoptera: Coccoidea*). Bull. Virginia Polytechn. Inst., Blacksburg, Va., **3**: 1—73.
- ZAHRADNIK J. 1959. Červci — *Coccinea*, in: Kratochvíl J., Klíč zvířeny ČSR, III, Praha, p. 527—552.

## STRESZCZENIE

Praca zawiera rozważania nad filogenezą czerwców oraz próbę oparcia klasyfikacji tych owadów na cechach narządów gębowych (ryjek, pompa ślinowa, nadustek), które były przedmiotem szczegółowych badań morfologiczno-porównawczych w innych pracach (KOTEJA, 1974; KOTEJA, rękopis; KOTEJA i LINIOWSKA, rękopis).

W obrębie podrzędu *Coccinea* wyróżniono 2 nadrodziny — *Orthezioidea* i *Coccoidea*. Do *Orthezioidea* zaliczono 8 rodzin — *Phenacoleachiidae*, *Ortheziidae*, *Monophlebidae*, *Coelostomidiidae*, *Kuwaniidae*, *Matsucoccidae*, *Xylococcidae*, *Porphyrophoridae* i rodzaj *Neosteingelia* potraktowany tymczasowo jako osobna grupa, zbliżona do *Kuwaniidae*.

W obrębie *Coccoidea* wyróżniono 6 grup rodzin: *Pseudococcidae* (jedna rodzina), *Acanthococcidae* (rodziny — *Acanthococcidae*, *Dactylopiidae*, *Apio-morphidae*, *Kermesidae*, *Cerococcidae*, *Calycicoccidae*, *Cryptococcidae* i rodzaj *Kuwanina* potraktowany jako osobna grupa na szczeblu rodzinowym), *Conchaspidae* (jedna rodzina), *Coccidae* (rodziny — *Stictococcidae*, *Kerriidae*, *Coccidae*, *Lecanodiaspididae*, *Aclerdidae*, *Cissococcidae*, *Micrococcidae*), *Asterolecaniidae* (rodziny — *Beesoniidae*, *Asterolecaniidae*, *Halimococcidae* oraz rodzaje *Lachnodius*, *Opisthoscelis*, *Callococcus* potraktowane jako odrębne grupy na szczeblu rodzinowym) i *Diaspididae* (rodziny — *Phoenicococcidae*, *Diaspididae*). Rodzaje *Capulinia*, *Colobopyga*, *Thysanococcus*, *Limacoccus* i *Xanthophtalma* nie zostały zaliczone do żadnej rodziny, głównie z powodu złej jakości i małej liczby dostępnych okazów.

Na podstawie budowy narządów gębowych sądzić należy, że grupy zaliczane dotychczas do "*Margarodidae*" mają wyższą rangę niż im przypisywano — w proponowanym systemie klasyfikacyjnym otrzymały one rangę samodzielnych rodzin. Rodzaje i grupy rodzajów zaliczane przez niektórych badaczy do *Acanthococcidae* (= *Eriococcidae*) potraktowane zostały jako samodzielne rodziny w obrębie grupy *Acanthococcidae*. Do grupy tej włączono również rodzinę *Cerococcidae* zaliczaną dotychczas jako podrodzinę lub plemię w obrębie *Asterolecaniidae*, oraz rodzaj *Kuwanina* jako osobną jednostkę. Rodzaj *Kuwanina* zaliczany był do różnych grup, ostatnio do *Cryptococcidae*.

Rodziny wokół *Asterolecaniidae* stanowią prawdopodobnie zgrupowanie heterogeniczne. Włączone do tego zgrupowania rodzaje — *Lachnoidius*, zaliczany był do *Pseudococcidae*, a *Opishtoscelis* do *Acanthococcidae* lub blisko *Coccidae*.

Trzy pierwsze grupy rodzin (*Pseudococcidae*, *Acanthococcidae*, *Conchaspidiidae*) stanowią niższy, a trzy pozostałe (*Coccidae*, *Asterolecaniidae*, *Diaspididae*) wyższy stopień w ewolucji czerwców.

Koncepcja filogenezy czerwców oparta na budowie narządów gębowych różni się w kilku punktach od dotychczasowych poglądów, zwłaszcza tych, które opierają się na budowie samców. Różnice te dotyczą przede wszystkim stanowiska systematycznego i roli w filogenezie czerwców takich rodzajów jak *Phenacoleachia*, *Steingelia*, *Matsucoccus*, *Conchaspis*, *Kermes* i innych. W świetle badań nad narządami gębowymi *Phenacoleachia* jest przedstawicielem reliktowej, pierwotnej grupy czerwców, z której wywodzą się prawdopodobnie wszystkie czerwce. Cechy wspólne samców tego rodzaju z samcami *Steingelia* z jednej, a *Pseudococcidae* z drugiej strony traktować należy jako wtórne upodobnienie. Rodzaj *Steingelia* jest typowym, choć wysoko wyspecjalizowanym członkiem nadrodziny *Orthezioidea* (= *Margarodidae* s.l.). Podobieństwo samców tego rodzaju z samcami *Coccidae* traktować wypada jako konwergencję. Pogląd o polifiletycznym pochodzeniu *Coccoidea* — jedna linia prowadząca z *Margarodidae* (s.l.) poprzez *Phenacoleachia* do *Pseudococcidae*, *Eriococcidae* (s.l.) i *Dactylopiidae*, druga poprzez *Steingelia* do *Coccidae* i innych grup, jest nie do przyjęcia w świetle budowy narządów gębowych. Rodzina *Kermesidae* jest blisko spokrewniona z *Acanthococcidae*, łączenie lub wyprowadzanie jej z *Coccidae* jest z punktu widzenia cech ryjka nieuzasadnione. Stopień specjalizacji ryjka u *Conchaspidiidae* jest stosunkowo niski, porównywalny z tym, jaki spotyka się w rodzinach w obrębie grupy *Acanthococcidae*. Wyprowadzanie jej lub łączenie z *Coccidae* wydaje się nieuzasadnione. Mało prawdopodobne jest również, aby rodzina ta stanowiła grupę wyjściową dla *Diaspididae*.

#### РЕЗЮМЕ

В данной статье автор рассматривает филогенез и классификацию кокцидов с точки зрения строения их ротового аппарата (хоботка, слюнного насоса, клипеолабрума), который был подробно исследован в последних работах автора (КОТЕЖА, 1974; Koteja, рукопись; Koteja, LINIOWSKA, рукопись).

В подотряде кокцидов были выделены два надсемейства: *Orthezioidea* и *Coccoidea*. В *Orthezioidea* включены 8 семейств: *Phenacoleachiidae*, *Ortheziidae*, *Monophlebidae*, *Coelostomidiidae*, *Kuwaniidae*, *Matsucoccidae*, *Xylococcidae*, *Porphyrophoridae* и род *Neosteingelia*, представляющий собой в настоящее время особую группу, близкую к *Kuwaniidae*.

В *Coccoidea* включены 6 групп семейств: *Pseudococcidae* (одно семейство), *Acanthococcidae* (семейства: *Acanthococcidae*, *Dactylopiidae*, *Apiomorphidae*,

*Kermesidae*, *Cerococcidae*, *Calycicoccidae*, *Cryptococcidae* и род *Kuwania*, представленный автором как отдельная группа), *Conchaspidae* (одно семейство), *Coccidae* (семейства: *Stictococcidae*, *Kerriidae*, *Coccidae*, *Lecanodiaspididae*, *Acleridae*, *Cissococcidae*, *Micrococcidae*), *Asterolecaniidae* (семейства: *Beesoniidae*, *Asterolecaniidae*, *Halimococcidae* и роды *Lachnodyus*, *Opisthoscelis*, *Callococcus* представленные как самостоятельные группы) и *Diaspididae* (семейства: *Phoenicococcidae*, *Diaspididae*). Роды *Capulinia*, *Colobopyga*, *Ghysanococcus*, *Limacoccus*, *Xanthoptalma* не включены ни в какое семейство, по причине отсутствия хороших препаратов.

На основе строения ротовых аппаратов автор предполагает, что группы, включенные ранее в "*Margarodidae*" представляют собой более высокий ранг, т.е. в предлагаемой классификации они являются самостоятельными семействами. Роды и группы родов, отнесенные некоторыми авторами к *Acanthococcidae* (= *Eriococcidae*), трактуются как отдельные семейства в группе *Acanthococcidae*. В эту группу включены *Cerococcidae*, которые были ранее объединены с *Asterolecaniidae*, и род *Kuwania* как обособленная группа. Род *Kuwania* раньше включался в различные группы, последний раз — в группу *Cryptococcidae*.

Семейства из группы *Asterolecaniidae* являются гетерогенными. Род *Lachnodyus*, включенный в эту группу, ранее был отнесен к *Pseudococcidae*, а род *Opisthoscelis* — к *Acanthococcidae* или близко стоял к *Coccidae*.

Три первые группы семейств (*Pseudococcidae*, *Acanthococcidae*, *Conchaspidae*) представляют собой более низкую, а три оставшихся группы (*Coccidae*, *Asterolecaniidae*, *Diaspididae*) более высокую ступень в эволюции кокцид.

Концепция филогенеза кокцид, основанная на строении ротового аппарата, отличается в нескольких пунктах от существующих ранее взглядов, главным образом, от тех концепций, которые основывались на строении самцов. Эта разница относится особенно к систематическому положению и роли в филогенезе кокцид родов *Phenacoleachia*, *Steingelia*, *Matsucoccus*, *Conchaspis*, *Kermes* и др. Исследования ротового аппарата показали, что род *Phenacoleachia* — представитель древней, реликтовой группы кокцид, от которой берут начало все кокциды. Общие признаки самцов этого рода и самцов рода *Steingelia* с одной стороны и *Pseudococcidae* с другой стороны являются вторичным сходством. Род *Steingelia* является типичным, хотя и высокоспециализированным представителем надсемейства *Orthezioidea* (= *Margarodidae* s.l.). Сходство самцов этого рода с самцами *Coccidae* считается конвергенцией. Представление о *Coccoidea* как полифилетической группе (одна её ветвь выходит из *Margarodidae* (s.l.) через *Phenacoleachia* к *Pseudococcidae*, *Eriococcidae*, *Dactylopiidae*, а другая ветвь из *Margarodidae* через *Steingelia* к *Coccidae* и другим группам) является не правильным с точки зрения строения ротового аппарата. Семейство *Kermesidae* близко к *Acanthococcidae*; объединение или выведение этого семейства из *Coccidae* является не верным. Степень специализации хоботка у *Conchaspidae* является сравнительно низкой, сходной с семействами из группы *Acanthococcidae*. Выведение этого семейства или объединение с *Coccidae* являются не доказанными. Мало правдоподобно, что из этого семейства могут происходить *Diaspididae*.



Redaktor zeszytu: prof. dr W. Szymczakowski

PAŃSTWOWE WYDAWNICTWO NAUKOWE—ODDZIAŁ W KRAKOWIE—1974

Nakład 700+90  
Zam. 447/74

Ark. wyd. 5

Ark. druk. 3<sup>12</sup>/<sub>16</sub>

Papier ilustr. kl. III 70×100 80 g

Cena zł 20.—

DRUKARNIA UNIWERSYTETU JAGIELLOŃSKIEGO W KRAKOWIE