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Essay on the prehistory of the scale insects (*Homoptera, Coccinea*)

Abstract. Coccids remained in the primary habitat — the forest litter — and retained the primary, semiparasitic feeding behaviour much longer than any other *Homoptera*. Specialization to this habitat caused modifications of leg (one claw), wing shedding and larvalization in female, dipterism, polymorphism and degeneration of male, and origin of resting stages in male ontogeny. Main radiation occurred also in this time. With the appearance of angiosperms, coccids became true parasites. Apterism in female directed their evolution towards sedentary life behaviour and development of protective systems. Fragility of male brought about diverse and elaborated chromosome systems. The combination of adaptation to soil habitat with specialization to parasitic life behaviour made the scale insects peculiar with respect to morphology and biology. The appearance of main radiations before acquisition of parasitic life habit resulted in morphological diversity, heterogenity of endosymbiotic systems and convergency of protecting devices. Various aspects of this hypothesis are discussed in the paper.

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> I have not any concrete arguments
> to support this hypothesis,
> except logic and facts.
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> Z. Mlynař

INTRODUCTION

"Scale insects are some of the most fascinating and unusual organisms in the *Insecta*" (MILLER, KOSZTARAB 1979). "This family in some respects is one of the most anomalous of all *Insecta*" (IMMS 1948). "For more than a hundred years curious scientists have been intrigued, and often deceived, by coccids, because of the fascinating and unorthodox structures, life histories, and genetics exhibited by these insects" (ROBINSON 1977). This idea, expressed in various words, may be found in dozens of publications and handbooks of entomology.

What is the reason for this peculiarity? There exists only one answer to this question: It is the "extreme specialization to parasitic behaviour on flowering plants", or "unconventional approach to the plant parasitic regime" (MILLER, KOSZTARAB l.c.) responsible for the unusual features and phenomena in the scale insects. By means of this clue the morphology, development, evolution and phylogeny of scale insects are also interpreted.

PESSON (1951) discussing the evolution and adaptation of the scale insects wrote: "Les divers faits biologiques et anatomiques exposés ci-dessus montrent que les Coccides, en même temps qu'elles deviennent des parasites sédentaires ou fixés, subissent une régression morphologique souvent considérable". And then: "Cette simplification organique peut donc n'être pas directement liée au parasitisme, mais dépendre d'une évolution générale du groupe". But he concluded: "On relèverait ainsi un assez grand nombre d'exceptions à ce qui, dans l'ensemble du groupe nous semble correspondre à une adaptation parasitaire. Cela ne suffit cependant pas pour en nier la réalité".

Among many authors I studied, PESSON was perhaps the only one who was aware of the "relatively large number of exceptions" which might indicate that adaptation to parasitism on flowering plants was not the exclusive trend

of the coccid evolution. Unfortunately, PESSON disregarded these "abnormalities" according to the proverb "The exceptions prove the rule".

However, as we will see, it is not the problem of exceptions, but of the very nucleus of the conception. Many questions cannot be answered by means of this key, or the explanation and interpretation appear to be unsatisfactory; for instance, "when did the scale insects originate", "why have they only one claw", "are the females actually neotenic", "what is the source of the endosymbiosis heterogenity", etc. The only solution to this problem is "to forget" that the scale insects are specialized plant parasites, and try to answer question by question using other keys.

And since the discussion of each question leads us back to the Paleozoic and Mesozoic times, when the appearance of the flowering plants was still expected, this study is entitled "The prehistory of the scale insects".

The names "scale insects" = "coccids" (like aphids, psyllids, etc). refer to the suborder *Coccinea*; "archaic coccids" = "archaeococcids" = "*Archaeococcoidea*" refer to the superfamily *Orthezioidea* (= *Margarodidae* s.l. + *Ortheziidae* + *Phenacoleachiidae*); respectively "advanced coccids" = "neococcids" = "*Neococcoidea*" refer to the "*Coccoidea*". For proper families scientific names are used. In quotations original names are retained.

II. THE TIME OF ORIGIN OF SCALE INSECTS

Coccidologists generally ignore the fossils. There is only one fossil species described by BEARDSLEY (1969) and another one redescribed by FERRIS (1941). The few other forms have been established by non-coccidologists. The status of the Permian and Triassic fossils, supposed to be related to scale insects, is controversial, but the amber fossils from Cretaceous[1] and Tertiary are evidently scale insects and, moreover, represent almost all main groups of the recent fauna (FERRIS 1957, KOTEJA 1984).

Little attention has also been paid to the early stages of coccid evolution and phylogeny and to the conclusions provided by paleontologists. As a result, the coccidologists think about the scale insects in terms and figures of the present-day fauna, with some little changes which "certainly" occurred during their more than 200 million-year-old evolution; and the paleontologists, on the other hand, discuss the phylogeny and evolution of an object which they to not know.

Most entomologists (MARTYNOV, JEANNEL, OBENBERGER, BECKER-MIGDISOVA, EVANS) place the origin of the *Hemiptera* and the divergences *Homoptera-Heteroptera*, *Auchenorrhyncha-Sternorrhyncha* in Carboniferous, while the

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[1]KÉLER (1956) mentions 4 species of the Cretaceous age, but without giving names; I mean *Electrococcus canadensis* described by BEARDSLEY (1969)

radiation of *Sternorrhyncha* (*Psyllinea-Aleyrodinea-Aphidinea-Coccinea*) in Permian. Some students even believe that groups corresponding with the present-day superfamilies split in Lower Permian.

Only few entomologists assume the scale insects to be very young. For instance, KÉLER (1956) says: "Es ist wohl phylogenetisch eine der jüngsten Insektengruppen, die sich anscheinend erst in der zweiten Hälfte des Mesozoicums, im Zusammenhang mit der Entfaltung der Blüttenpflanzen, differenziert hat".

Since the main, if not the only, Paleozoic and Mesozoic object of studies is the structure of the wing, which in the recent coccids is extremely simple, and on the other hand, very little known, only a limited number of paleontologists have dealt with the fossil scale insects.

BECKER-MIGDISOVA (1962) assumes the *Protopsyllidiidae* to be the ancestors of the scale insects and includes them to the "Infraordo *Coccaria*". This group consists of small *Homoptera* (wing 2–6 mm long) known from Permian and Jurassic. All these forms are represented by wings only or wings and some body parts (e.g. *Propatrix psilloides* BECKER-MIGDISOVA). Another fossil, without proper placement, *Mesococcus asiaticus* BECKER-MIGDISOVA from upper Triassic is a wingless, elongate-oval, scale-like but with distinct segmentation (ventral face) insect, 1–2 mm long, with short legs, which makes an impression of a *Coccidae*, *Pseudococcidae* or *Monophlebidae*. However, mouthparts and antennae are not preserved[1]. BECKER-MIGDISOVA interpreted this form as an adult female or larva of scale insects.

The above conceptions are accepted by TEREZNIKOVA (1975), but other hemipterologists disagree with the assumption that the *Protopsillidiidae* may be related to the scale insects; particularly SZELĘGIEWICZ (1971) protests strongly against this conception and believes this group to be ancestors of the *Psyllinea*. As concerns *Mesococcus asiaticus*, BEARDSLEY (1969), DANZIG (1980) and SCHLEE (in HENNIG 1980) hesitate whether this form may be associated with scale insects.

A detailed discussion of the early (Permian) scale insects is presented by SZELĘGIEWICZ (1971). His reasoning is based on apomorphic wing features and the HENNIG's sister-group conception. According to SZELĘGIEWICZ the *Sternorrhyncha* are monophyletic and branched off from the Homopteran stock in Carboniferous. At the end of this period, but at least at the transition to Permian, they branched into the *Psylliformes* (*Psyllinea* + *Aleyrodinea*) and *Aphidiformes* (*Aphidinea* + *Coccinea*). The former radiated during the Lower Permian into numerous groups of which most died out in the Permian and Triassic, except *Psyllinea* and *Aleyrodinea*. The latter (*Aphidiformes*) much less abundant, gave rise to *Aphidinea* and *Coccinea*. The splitting of *Aphidinea* into *Aphidoidea* and *Phylloxeroidea* must have taken place in about the middle

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[1] In some recent reproductions (HENNIG 1980) antennae are drawn!

of Lower Permian, because at that time already existed forms (*Kaltanaphis*) which SZELĘGIEWICZ considers to be actual ancestors of the *Phylloxeroidea*.

Concerning the scale insects SZELĘGIEWICZ assumes *Tshekardaella tshekardaensis* BECKER-MIGDISOVA from Lower Permian to be a putative member of the coccid ancestors (this form has a long, distinctly 3-segmented tarsus), while *Permaphidopsis sojanensis* BECKER-MIGDISOVA from Upper Permian almost certainly as a member of such a group. *Mesococcus asiaticus* from Upper Triassic is also tentatively included among the ancestors of coccids.

The factual basis of SZELĘGIEWICZ conception is rather poor. The interpretation of the wing structure by PATCH (1909) and SCHLEE (1969) on which the reasoning is based must be taken with reservations; for instance, SCHLEE recognized in *Sphaeraspis priaskaensis* as many as 10 veins in the wing (see also comments by MORRISON 1928), and SZELĘGIEWICZ himself believes that scale insects have only one bristle on posterior wing, etc.

In a recent paper SZELĘGIEWICZ and POPOV (1978) assigned *Permaphidopsis* to the *Protopsyllidiidae* (ancestral group of *Psyllinea*), while *Tshekardaella* to the extinct *Archescytinidae*. Thus, the conception of the coccid ancestors has radically been changed.

HENNIG (1980) reviewed the Paleozoic and Mesozoic fossils and their interpretations. It seems likely from his discussion that all possible relationship combinations of the homopteran fossils have already been proved, with all possible conclusions.

In spite of the differences in understanding various fossils from the Permian and Mesozoic, and any reservations that coccidologists may have concerning the interpertation of these forms, it is evident that the coccids or their ancestors, coexisted with psyllids, aleyrodids and aphids at least in the Permian.

At the end of this part of discussion let us see how aphidologists imagine the phylogeny of the sister group of scale insects. HEIE (1967) in his comprehensive study on fossil aphids presented the following reconstruction of the aphid phylogeny (only some conclusions are quoted):

— "The evolution of the aphids begins in the Carboniferous or during transition from the Carboniferous to the Permian".

— "*Adelgidae* and *Phylloxeridae* separated at an early time (Permian) and adapted themselves to *Coniferae* and other gymnosperms, respectively, among the latter the primeval forms of Apetalae"[1].

— "Heterogony may be older, but it is probable that the fixed cycle, at least in *Adelgidae*, has developed at a time around the glacial period in Lower Permian, with seasonal changes".

— "Some features characteristic of the aphids arose in connection with a reduction of the body size".

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[1]HENNIG (1980) believes that the splitting of these groups occurred in the Cretaceous!

— "*Hormaphididae* and *Pemphigidae* separated presumably in the Permian, the Triassic, or the Jurassic".

— "The remaining families… are developed… in the Cretaceous and early Tertiary in connection with the triumphal progress of the angiosperms".

— "The angiosperms partly 'inherit' aphids from their gymnosperm ancestors, partly receive polyphagous mutants from elsewhere".

— "*Aphididae* is a young family, whose evolution can probably be connected with that of *Rosales* in the Early Tertiary".

It should be added that HEIE based these conclusions, as far as paleontological material is concerned, on the following Mesozoic fossils: *Triassoaphis cubitus* (Upper Triassic), *Genaphis valdensis* (Jurassic) and *Canadaphis carpenteri* (Cretaceous).

The only comprehensive conception of the phylogeny of scale insects that accounts time, presented by a coccidologist, is that of BORCHSENIUS (1956, 1958). He considered the scale insects to be very old and dated their origin as early as the late Devonian, with primary radiation (divergence of archaeococcids and neococcids) and origin of main families in the Carboniferous, Permian and Triassic. The youngest group, according to BORCHSENIUS, the *Kermesidae*, split off from the *Eriococcidae* in Cretaceous.

BORCHSENIUS based his view on the following statements:

(1) The scale insects are extremely specialized and differentiated with respect to morphology, biology, ecology, cytogenetics, etc.

(2) Both primitive and specialized groups, and even particular genera, are distributed all over the world, thus they must have appeared when the continents were still united, i.e., before the Jurassic.

(3) The bulk of scale insects is represented in the tropics of the New and Old Worlds.

(4) Numerous groups (according to BORCHSENIUS) are associated with gymnosperms.

Paleontological evidence has not been taken into consideration by BORCHSENIUS because Paleozoic and Mesozoic fossils of scale insects were not known at that time, or they were not recognized as potential relatives of the coccids.

Following the idea of the early origin of the coccids BORCHSENIUS suggested that their primary hosts had been gymnosperms and that both coccids and those plants had evolved parallel. After the angiosperms had appeared, most coccids changed the host and a few new groups originated (e.g. *Kermesidae*), but first of all, the appearance of the flowering plants brought about radiations mainly at generic and species levels.

The above conception has been accepted and supported with some paleontological data by TEREZNIKOVA (1975), while BUCHNER (1965) provided arguments of endosymbiotic studies, but most coccidologists rejected such an early date of origin of the scale insects, as did some paleontologists (HENNIG 1980).

HOY (1962) says: "The time of origin of the scale insects does not appear

to have appreciably antedated that of the angiosperms, which is generally considered to be mid Cretaceous. If the *Coccoidea* did originate earlier than the angiosperms, there is, today, no evidence of exclusive association with gymnosperm hosts at family level in the *Coccoidea*, and exclusive association even at generic level occurs in relatively few genera".

Although HOY recognizes "large" families, the species, genera and few small groups associated today exclusively with gymnosperms may actually be quite well considered as secondary parasites of these plants. This point has been strongly emphasized by DANZIG (1980). (For further discussion see Chapter XV).

HOY further notes: "BORCHSENIUS (1958) placed the origin of the family *Apiomorphidae* (...) in the Jurassic. The genus *Apiomorpha* is restricted to the plant genus *Eucalyptus* and is confined to Australia. PIKE (1956) after examining fossil pollens could not confirm the presence of *Eucalyptus* even in the Oligocene". The dating of the origin of *Apiomorpha* is then evidently erroneous, as is the association of this group with *Stictococcidae* suggested by BORCHSENIUS. There are certainly other unlikely suggestions and interpretations in the conception of BORCHSENIUS, but HOY and DANZIG who associate the origin of scale insects with angiosperms are also not consequent and logical in their views.

Discussing the age of *Eriococcidae*, HOY says: "The ancestral stock of the New Zealand *Eriococcidae* appear to have been in this country for a very long period, possibly from the late Cretaceous time". He further suggests Antarctica as the center of origin of this family. This leads to an unlikely conclusion that the origin of scale insects, their divergence and radiation into numerous specialized groups, and dispersion all over the world by means of intercontinental bridges and wind took place between the mid and late Cretaceous. (Some aspects of dispersion and distribution of scale insects have been recently discussed by WILLIAMS 1983.)

DANZIG (1980), like HOY, associates the origin of the scale insects with angiosperms and the Cretaceous age, but says: "...even if the coccids had actually existed prior to the appearance of angiosperms, then these archaic forms did not survive", and "there is no one evidence that the coccids existed before the Cretaceous". However, whether the scale insects existed prior to the angiosperms, is one question, whether they survived, is another one, and whether there is paleontological evidence for their early origin is the third question; but one cannot discuss the evolution and phylogeny of any living creature without considering the time. Besides, DANZIG, as a coccidologist, may question the fossils of the coccids, but not those of the aphids or psyllids, and paleontologists are definitely certain that those groups existed throughout all Mesozoic, and in the Cretaceous were much specialized; from which group might the scale insects have evolved, then?

Once again we must quote HOY's resolution because it reflects the very

nucleus of the question under discussion. He says: "Placing the origin of most of the families of the *Coccoidea* in the Carboniferous would allow the wide dispersion of the ancestral stock of families at a period when the world's vegetional and climatic patterns were much more uniform than they are now. If this had been the case, the present distribution of the *Coccoidea* has largely been the result of extinction of certain families and genera in some geographic areas and isolation and radiation of genera and species". All those arguments are logical and fairly well supported by facts, but Hoy says: "The writer cannot agree with such conclusions, involving a very long period of stability at family level, a wide range of similar generic and species radiation, and similar host-range adaptations in several geographically isolated areas".

Concerning the stability at family level, paleontologists know even genera which morphologically were stabile through millions of years, and the *Phylloxeridae* and *Adelgidae* (aphids) are supposed to exist through all Mesozoic, for which may be paleontological evidence. Besides, "stability at family level" may be understood as genetic isolation or genealogical continuity, and not necessarily as morphological stability. This point has strongly been emphasized by Hennig (1980): "It is important to distinguish between the origin of a group and the origin of the discrete morphological-functional structural type which now represents it". Furthermore, convergence is one of the most evident and striking features of the coccid evolution, and this means exactly the same as "similar generic and species radiation" and "similar host-range adaptation".

Miller and Kosztarab (1979) represent an "intermediate" opinion concerning the age of scale insects; they note: "Although useful fossil evidence is scarce, it seems likely that the *Coccoidea* diverged from the aphidoid sister group sometimes in Early to Middle Permian. The high degree of specialization of *Electrococcus* (Cretaceous) and the apparent small amount of divergence since Oligocene and Miocene times suggest that primary radiation occurred before the end of the Mesozoic".

It seems likely from the above discussion that the scale insects derived from the homopteran stock in the Carboniferous, and that the primary radiation occurred in the Permian and Triassic, but that the host, habitat, life behaviour and phylogeny remained concealed until the evolution of flowering plants when they (coccids) appeared "suddenly" in numerous and diverse groups. It is also certain that the clue of resolving their early history lies in the question of their habitat and feeding behaviour.

III. THE PRIMARY HOST AND HABITAT OF COCCIDS

There is an opinion that angiosperms are main hosts of the coccids and that the relatively few associations with gymnosperms might have originated secondarily. On the other hand, many facts indicate that the scale insects must

have existed long before the origin of angiosperms. Thus, we may assume that all ancestral forms associated with gymnosperms died out for some reason, which is very unlikely, or that they were not plant parasites in the proper sense, which, at first sight, is even more unlikely.

For the coccidologists the scale insects are so evidently plant parasites which suck only living tissues (parenchyma or phloem) that they do not imagine these insects could have ever had a different feeding behaviour. However, *Heteroptera* try to suck anything; to some extent also *Homoptera* may do it, and BUCHNER (1965), on the basis of symbiotic studies, arrived at a hypothesis that the ancestral *Hemiptera* might have been carnivorous.

Furthermore, one should remember that the hemipteran piercing stylets are provided with two canals — the salivary and sucking ducts — and that by means of this device not only liquids directly from the surface, but also solid food can be taken up (like in the *Arachnida*). This idea draws our attention to the possible primary habitat of the scale insects. Let us see what WIGGLES-WORTH (1972) says:

"The ancestral insects may have lived chiefly in the moist litter of the forest floor" ... "we should regard them as being originally "saprophytic" animals, feeding in the dead and decaying remains of plants, and particularly on the fungi and bacteria that are responsible for that decay".

Continuing this reasoning we may assume that the adaptation and specialization to "true" parasitism on higher plants might have developed unevenly in various groups of the *Homoptera*. Some of them might have remained in the primary habitat, and adhered to the primitive feeding behaviour much longer than others, and undergone further specializations to this habitat. If this was the case with the scale insects, they should exhibit much more numerous and striking features of soil inhabitants than the other *Homoptera*. This hypothesis will be proved in the following paragraphs.

IV. THE COCCID LEG IS PRINCIPALLY A DIGGING ORGAN

It is so obvious to us that there is only one claw on the coccid tarsus that we have never asked about the reason for this curious phenomenon.

In the *Insecta* one claw occurs in the *Protura* and *Collembola* which apparently is a primary condition, and in a few species, genera and small groups of various orders as a result of secondary reduction. Exclusively all *Anoplura* and a large proportion of *Mallophaga* have only one claw. Among the *Sternorrhyncha* one claw has been noted in a fossil aphid (HEIE 1967).

In most cases, particularly in the *Anoplura*, *Mallophaga*, the water inhabiting *Heteroptera* and others, the modifications of the leg structure which involve reduction of one or both claws on some or all legs, are clear when viewed from the point of function. In the scale insects the reasons for the claw reduction

are obscure. Moreover, the habitat, life conditions and behaviour of sexes, development stages and groups of scale insects, that we know now, are so different that we feel quite certain there cannot exist a common reason (function) by means of which we could understand the loss of one claw both in the digging *Margarodidae* and sessile *Diaspididae*, in larva and adult, etc. On the other hand, it is evident that there must have been only one reason for which the ancestors of scale insects lost one claw, or that the stimulus for claw reduction was strong enough to force all the coccid groups, with no exception, to shed one claw. The assumptions that the loss of the claw is the first step in leg reduction, as a result of passing from a mobile to sedentary life behaviour in connection with parasitism, or that all coccids "incidentally" lost the claw, are an absurdity.

The coccid leg is further devoid of arolium, empodium, pulvillae and any other similar structures except digitules. The tarsus is one-segmented and the tibio-tarsal articulation is reinforced by some means or other. There may be articular sclerosis, the tibio-tarsal joint may be immobilized, or the two segments may be fused without any traces of articulation. Supposedly in most or all instances these segments operate as one article — the tibiotarsus. As a further result of this process both articles become subequal in length with the widest part in the middle. Eventually, the coccid leg is short in comparison with the body size, even if we take into consideration the hypertrophy of the body which certainly occurs to various extent in different groups.

Taking into account the above-described structure of the coccid leg it is evident that such an organ is ineffective in climbing perpendicular and smooth objects and the walking back-down would not be possible at all. But the coccid leg fits very well the crawling directly on the ground, among and under soil particles, plant parts, humus, detritus etc. This kind of moving, being a combination of swimming and digging (or "swimming" among solid particles) does not require any adhesive organs and a double claw to fix the position of the tarsus. The leg is fixed by means of sticking the apex of tarsus into the soil, thus it should be short, sharp and tapered. All this indicates that the forest litter was presumably the primary habitat of the scale insects, in which, furthermore, they remained much longer than any other *Homoptera*, in any case long enough to bring about basic changes in the leg structure in all members of this group.

In this context the characteristic coccid tarsal and ungual digitules may be understood as adhesive, and not sensory, organs which developed when the scale insects started to climb plants, to replace the missing claw and substitute any other adhesive primary pretarsal structures, if they existed at all.

Spatulate or capitate setae (digitules) as clinging and sensory organs have developed independently in many terrestrial arthropods and occur in various groups of all *Sternorrhyncha*. In the scale insects they originated in all likelihood after the main radiation, i.e. convergently in various groups. As a rule there

is a pair of digitules inserted on the base of claw (ungual digitules) and the other one on tarsus (tarsal digitules), but there may be more than one pair on claw (*Cryptokermes*, *Ultracoelostoma*, *Stomacoccus*, *Steingelia*), and capitate clinging setae may also develop on the apex of tibia (*Kuwania*). In primitive groups the digitules are acute and small, developed only on claw or tarsus, and in specialized groups they may secondarily disappear (in specialized diggers). In the *Coccidae* and similar groups both tarsal and ungual digitules are very strong, with large apical knobs, and the leg contacts with the ground only by means of the pretarsus in five points (4 digitules and apex of claw).

RICHARD (1971) reported three digitules on claw and one on tarsus in the *Stictococcidae*, and emphasized this phenomenon as unique in the scale insects. Although this condition is actually unique, it has been misinterpreted by RICHARD. In fact, there are two ungual digitules of which one is normally strong, the other significantly atrophied and functionally (!) replaced by one of the tarsal digitules which was translocated at the very apex of the tarsus and became morphologically close to the ungual digitule. At the same time the other tarsal digitule took an asymmetrical position. Thus, the conditions in *Stictococcidae* represent an extreme form of asymmetry of digitules which occurs in many coccids.

For discussing the primary habitat and life behaviour of the archaic scale insects it is of no importance what structure the single claw actually represents. It is a general view (SNODGRASS 1935, WEBER 1968) that scale insects had originally two claws ("lateral claws") like other *Pterygota*, and that one of them atrophied, while the other became hypertrophied.

The conditions in *Phenacoleachia* may support the above supposition. In this genus (in both known species and both sexes) the claw is provided with one typical coccid digitule and a structure which definitely makes an impression of the other claw reduced to some extent (tarsal digitules are lacking). The occurrence of this condition in *Phenacoleachia*, a genus considered to be primitive also with respect to some other features, is of particular importance.

To agree with the above conception, one should also accept the heterogeneous origin of the ungual digitules: one being a modified claw, the other a secondary, new structure. The occurrence of several digitules on claw (*Steingelia*) provides arguments against this hypothesis. In this case we should assume a complete atrophy of one claw and an independent origin of ungual digitules.

In *Collembola*, which have only one claw, the "ungual spur" sometimes may be strongly developed and play a role of the second claw (BOUDREAUX 1979). Viewed at this angle, we may also consider the condition in *Phenacoleachia* as an "attempt" to reconstruct the missing claw by means of a modification of the true ungual digitule.

Eventually, there should be mentioned the third, basically different, and rather unlikely hypothesis, that the unpaired coccid claw represents the "me-

dian claw" like that in *Thysanura* (SNODGRASS 1935) or some other unpaired structure, for instance, paronychium in the *Aleyrodinea* (OBENBERGER 1957), while the lateral claws are modified into digitules.

Closing this chapter I would like to emphasize that the term "digging organ" has been applied to the coccid leg in a general sense. It only means that among various functions that the hemipteran leg may perform, digging seems to correspond most closely with the structure of the coccid leg, but it does not mean that the leg represents a specialized digging organ. Even in te "true" diggers (*Margarodidae*) the digging legs are primitive, i.e., they are only thicker and stronger than other legs, but their structure is the same. This feature is particularly striking when compared with the deep structural modifications of the digging legs in the Cicadoidea larvae. The same concerns also the digging behaviour and hypogeic mode of life which are primitive in coccids while extremely sophisticated in cicadas. The reason responsible for these differences is the starting point of the modifications: in *Cicadoidea* it was a "normal" walking leg to be modified, in scale insects a leg already significantly simplified. Similarly the "hypogeic" habitat with respect to the ancestral coccids should be understood as litter of the forest floor, and not in a narrow and strict sense applied, for instance, to the habitat of the larvae of some *Cicadoidea*.

V. WHY THE COCCID FEMALE LOST THE WINGS

The biological reasons for wing reduction in coccid females and the way in which this process followed are two different questions and will be discussed separately.

Wing reduction occurs in all insect orders, but only in *Mallophaga*, *Anoplura*, *Aphaniptera* and the female of *Coccinea* it is complete, without exceptions, with no transiting forms, rudimentary organs or atavism. Among the reasons for wing reduction two play a major role: the parasitic life behaviour and hypogeic habitat.

As far as the scale insects are concerned, only the first reason has ever been taken into consideration. There is a generally accepted opinion (WEBER 1968, TEREZNIKOVA 1975, MILLER, KOSZTARAB 1979, DANZIG 1980) that the loss of wings in coccid female is an adaptation to parasitic life habit and an expression of the very high level of parasitic specialization, or "unconventional approach to the plant parasitic regime". DANZIG (1980) says: "The females and larvae of scale insects feed on sap taken up from the sieve-tubes of perennial plants. The permanent source of food and the lack of necessity of searching for it directed the evolution of coccid females towards the wing reduction".

The above reasoning is much generalized because not parasitism as such, i.e., parasitic food uptake, but circumstances in which it takes place — the habitat of the parasite — is responsible for wing reduction. *Anoplura* and other parasites lost the wings because they lived among hairs, i.e., in conditions in which the wings are uncomfortable, making the movement difficult and being

exposed to damage. It means that the main reason for wing reduction in parasitic and hypogeic forms is exactly the same. As a matter of fact, complete wing reduction is for a plant parasite a fatal adventure because it greatly limits not only active dispersion but also host finding and changing. Among the *Homoptera* actually only very few species shed the wings completely.

However, there is a much stronger argument against the hypothesis that wing reduction in coccid female might have been a result of parasitic life behaviour. Since there is no exception to the rule, one should assume that the loss of wings occurred only once, at the very beginning of the coccid evolution, it is, when the ancestors of scale insects were represented by a single species, in the Carboniferous or Permian (!). It would be very difficult to call this form "extremely specialized plant parasite".

To accept the alternative hypothesis we must assume that the coccid females shed the wings convergently in all groups, in the specialized and actually sessile *Coccidae, Asterolecaniidae, Diaspididae*, as well as in the primitive *Ortheziidae, Phenacoleachiidae, Monophlebidae*, etc., without exception (!).

We can see from this discussion that it is not possible to associate in any logical way the wing reduction in coccid female with parasitic life behaviour.

If not the feeding behaviour, then only the habitat of the ancestral coccids might have brought about the wing reduction in the female. This leads us again to the litter of the forest floor, i.e., to the habitat of the *Myriapoda, Apterygota, Psocoptera*, larvae and wingless adults of many insect orders. In contrast with the hypothesis that parasitism is responsible for the wing reduction, the present conception does not require the scale insects to lose the wings only once. In case of parasitism the possession of wings may be useful for the perasite, at least in some circumstances. For the inhabitants of the forest floor (except perhaps the social insects) the wings are always uncomfortable and "superfluous". It means that the pressure of the soil habitat towards wing reduction is much stronger than that of parasitic life behaviour, thus the wing shedding in scale insects could have occurred simultaneously with the primary radiation or even after then, in any case, before the scale insects left the forest litter.

It is clear that the above hypothesis radically changes the reason-result sequence, and the interpretation of the coccid phylogeny. Instead of a straight-lined evolution with one stimulus (parasitism) and the sequence —
parasitism on flowering plants ———➤ sedentary life behaviour ———➤
———➤ wing reduction ———➤ development of protecting systems, there we have a curve-lined evolution, with two independent trends and two causal sequences —

(a) soil habitat ———➤ wing reduction

(b) apterism + parasitism ———➤ sedentary life behaviour ———➤
———➤ development of protecting systems

In other words: The loss of wings (caused by the soil habitat) at the beginning of the "true" parasitic career on flowering plants directed the evolution of scale insects towards sedentary life behaviour (reduction of legs) and stimulated the development of a diversity of highly specialized, and evidently convergent, protecting systems which, furthermore, involved significant modifications of the female body, and in some instances also of the larva. And there was no other possibility: the wings once lost can never be rebuilt.

VI. COCCID MALE AND CHROMOSOME SYSTEMS

"Some of the most interesting features of coccid biology are the wide variety of sex-determination mechanisms and of chromosome behaviour (both referred to as "chromosome systems")...; in coccids, the chromosome systems are more diverse than in any other animal group of comparable size". (NUR 1980). What are the reasons for this phenomenon?

NUR says: "The various coccid families tend to differ in their mode of adaptation, and thus may be considered to occupy different adaptative zones (as suggested by MILLER and KOSZTARAB 1979)... However, ...several of the families analysed cytologically in some detail possess more than one chromosome system, while several others possess the same system. Thus, the origin of new families apparently was not triggered by the origin of new chromosome systems. This point was emphasized by BROWN (...) in relation to the origin of the specialization associated with the lecanoid and diaspidoid groups of families. The realization that the evolution of chromosome systems was not closely associated with morphological evolution, however, does not rule out the possibility that some of the new chromosome systems may have conferred a selective advantage, either when they first arose, or after they were further refined. For example, male coccids do not feed during the third (prepupal), fourth (pupal) and adult stages, while the female may feed throughout her life. Thus, males may be more likely to die of dessication than the females. Moreover, while adult males survive at most for a few days, uninseminated females may survive for several weeks. It is likely, therefore, that under certain circumstances these differences between the sexes may lead to a shortage of males. Thus, the evolution of such chromosome systems, as thelytoky and hermaphroditism may have been adaptative because they dispensed with the males. Moreover, ...the fragility of the males may also have played a role in either the evolution or the success of some of the other chromosome systems".

Two points are important in the above citation: (a) that the evolution of chromosome systems is not strictly correlated with adaptation to different ecological zones, neither with morphological evolution, and (b) that the origin and/or success of the chromosome systems and their variety are associated with the fragility of the male.

The former conclusion will be discussed later; now I would like to emphasize the logical sequence of the latter one (fragility of male ⟶ peculiarity

of chromosome systems) because at some point of reasoning we might have been inclined to explain the degeneration of the male by means of elaborated chromosome systems.

From the studies by NUR we now know why the coccid chromosome systems are complicated and diverse, but we do not know why the male is gnat-like and why it undergoes a peculiar metamorphosis. As concerns the fragility, there is currently no other explanation than the suggestion that size-decrease a general evolutionary trend in plant parasites, e.g., the diminution of the body size is considered to be the main tendency of the evolution in the *Aphidinea* (HEIE 1967).

The same is suggested to the female of *Coccinea* (PESSON 1951, DANZIG 1980). However, this suggestion is evidently not correct. The tendency to body decrease supposedly first occurred when the scale insects were still inhabiting the forest litter, which we now may see in the *Ortheziidae*: the more advanced forms (*Newsteadia, Ortheziola*) are smaller than the primitive ones (*Orthezia, Arctorthezia*). When the scale insects became parasites of flowering plants some groups tended to be dwarf-like, the other gigantic. The divergence of these trends may best be seen in the eriococcids (s.l.). The primitive forms are medium-sized (*Eriococcus* and relatives), the specialized ones became dwarf-like (*Pseudochermes, Cryptococcus, Kuwanina* etc.), or large-sized (*Kermes, Dactylopius, Apiomorpha*). Similar conditions occur in the *Pseudococcidae*.

It seems likely that parasitism, associated with sedentary life behaviour, and the mode of reproduction stimulate the female body rather to grow. In the viviparous aphids the differences in food abundance result in the number of larvae born. In the egg-laying coccids, which as a rule stop feeding before oviposition, the whole material for progeny production must be accumulated within the female body. Thus, the food abundance causes automatically body increase (HABIB 1957, and others).

The hypothesis of a general tendency of body-decrease in plant parasites cannot be applied either to the coccid male. HEIE (1967) says: "As they (aphids) are parasites on plants there is a very narrow limit of their body size, and they use air currents as a means of spreading". However, although the coccid males are small enough to be dispersed by means of wind, at the same time they do not feed and, irrespective of size, live very short. It would be difficult to imagine that coccid males look for the females using air currents! It is clear that there must have been another reason for which the coccid males have become dwarf-like.

As concerns the unusual metamorphosis, i.e., the occurrence of two resting stages (unfeeding larva and pupa in *Orthezioidea*, prepupa and pupa in *Coccoidea*) it is assumed that the pupal stages have been introduced to the male development to overcome the deep structural differences between larva and imago (per analogy with the *Holometabola*), or because of different specialization between larva and imago. DANZIG (1980) says: "And so, the transition (adaptation) of coccids to a sedentary life behaviour resulted in a modification of the development cycle. The females became neotenic, with only 2–3 larval instars

in place of 5 in the generalized *Homoptera*. In the males the different specializa-
tion of larva and imago gave rise to the complete development and origin of
a particular type of metamorphosis — the hyperepimorphosis". However, on
the same page she writes: "The need of synchronizing (closing within the same
period of time) the complete morphogenesis of male with the simplified mor-
phogenesis of female brought about the origin of resting stages in the develop-
ment of the male".

It is difficult to understand this way of reasoning. First, it is nuclear how
adaptation of coccids to a sessile life behaviour may change the "specialization"
of larva and male. Feeding in larva and mating in male are the only speciali-
zations in all circumstances. Second, the resting stages are present in all groups
of scale insects, even in the most primitive ones being evidently not sedentary
(for instance the *Ortheziidae*), which means that the resting stages had originated
much earlier than the scale insects became sessile, and prior to the main radia-
tion. Third, the term "simplification of morphogenesis" is somewhat obscure;
once it may be understood as a reduction in the number of larval stages, once
as shortening of the time of development, once as "larvalization" or neoteny,
but these phenomena are not correlated. The synchronization of development
might have been quite well achieved by simultaneous reduction in male instars,
as it actually occurs in some groups (*Stictococcidae*, *Polystomophora*). However,
as a matter of fact, it would be more logical to expect an introduction of resting
stages in male development in the case of prolongation of the female develop-
ment.

Fourth, unclear are the terms "complete or complex (složnyj) morpho-
genesis" in male, "simplified (uproščennyj) morphogenesis in female", and
"complication (složnenie) of development". If complete morphogenesis in male
means that it undergoes a metamorphosis from larva to winged male (in con-
trast with wingless female), the "problem" of male metamorphosis remains
exactly the same under all conditions and is definitely independent of the deve-
lopment of the female, and also cannot be associated with passing to sessile
life behaviour. But if "complete morphogenesis" and/or complete development
means that resting stages are involved in it, the second citation of DANZIG paper
("The need of synchronization...") is not an explanation but a tautology.

Polymorphism of male is another peculiar feature of the scale insects.
There may be winged, brachypterous and apterous forms. Brachypterous and
apterous forms may appear together with winged ones, one form may slightly
precede the other (DZIEDZICKA 1961), or various forms may be displaced among
different generations (PESSON 1951, VINIS, KOZÁR 1981). The apterous forms
may undergo a complete metamorphosis, i.e., with resting stages (it is the rule),
or without them (VINIS, KOZÁR 1981). Eventually, polymorphism may occur
in primitive groups (*Phenacoleachia*) as well as in specialized ones. The apterous
forms have, as a rule, simple eyes, but may have also compound eyes (fossil
Matsucoccus, Koteja 1984). A strong polymorphism occurs also in related aphids,

but in this group it may be understood on ground of their peculiar life cycles (heterogony, host-range, etc.). In scale insects the biological reasons for polymorphism are difficult to trace, and I do not remember whether anybody has ever attempted to do it.

It may be seen from the somewhat lengthy discussion that the current interpretation of the sexual dimorphism, polymorphism of male and particularities of postembrional ontogeny is not satisfactory, and that the clue to these questions may lie in the fragility of the male which has been pointed out by NUR (1980) when discussing the possible reasons for the unusual chromosome systems in the scale insects.

We have concluded in the preceding chapter that the supposed primeval habitat of the archaic scale insects exerted a strong pressure towards wing reduction, and that the females eventually lost the wings. The evolution of the male was directed by two stimuli: the habitat towards wing shedding, and reproduction, towards wing retaining. The coacting of these two factors resulted in the origin of four characteristic features of the coccid male:

(1) The posterior wings are reduced to halteres or completely atrophied (the dipterization of the wing apparatus in the *Coccinea* is then biologically different from that in the *Diptera*, *Strepsiptera*, *Aphidinea* and others).

(2) The anterior wings are folded flat and overlapping along the abdomen in resting position which faciliates the moving among soil particles, plant parts etc.

(3) The males are polymorphic with respect to the wings, i.e., winged, brachypterous and wingless forms have been accepted by the natural selection. During further evolution and adaptation to different ecological conditions the polymorphism has been retained or one morph has been preferred; for instance winged males in *Phenacoleachia zealandica*, apterous in *Ph. australis*; winged forms in *Steingelia*, larviform in related *Stomacoccus*; winged in the *Coccidae*, but polymorphic in related *Aclerdidae*, etc.
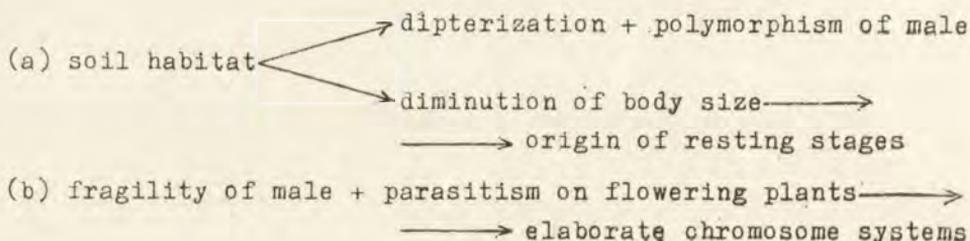
(4) The males are dwarf-like. We may hypothesize that, to reach the female elsewhere in the litter, among plant parts and soil particles, the male should be strong (to move the particles) or much smaller (to crawl among the particles) than the female. We may assume that for bioenergetic reasons the evolution preferred the latter way.

Thus, in their prehistoric times, the coccid females lost the wings and the males became fragile, polymorphic gnats. With this condition the scale insects started their career as parasites of flowering plants. To achieve a success they had to develop some particular morphological, biological and physiological adaptations; among others, it was the diverse and complicated chromosome behaviour with various hereditary types, sex determination, parthenogenesis and hermaphroditism.

The diminution of the male body could only be realized by an early stopping of feeding; however, without shortening of the time of development: the emer-

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gence of adult males and females must have been simultaneous. The only solution to this problem was the transformation of the last male larval instars into resting stages. In the *Coccoidea* the third and fourth (prepupa and pupa) instars are immobile and unfeeding, in the *Orthezioidea* the third stage is unfeeding but mobile, while the fourth instar resembles the pupa. Subsequently, the wing buds in the resting stages became enlarged, whereas in the female larvae reduced. In this way the paurometabolic metamorphosis became sexually diverse.

This part of discussion may be summarized with the following causal sequences (corresponding with those presented for the wing reduction in female, p. 473):

```
                            dipterization + polymorphism of male
(a) soil habitat
                            diminution of body size--------->
                    --------> origin of resting stages
(b) fragility of male + parasitism on flowering plants-------->
                    --------> elaborate chromosome systems
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VII. HOW THE COCCID FEMALE LOST THE WINGS

In the preceding chapters the ecological and biological reasons for wing reduction in female and origin of some particular features of male have been discussed. It is obvious that these phenomena have been realized by means of modifications of the postembrional development. However, the ontogeny of the coccids is such a vast and difficult problem that it must be discussed at another opportunity. In this paper the following may by suggested:

(1) The scale insects are now considered to be almost certainly a sister-group of the aphids. Although the ontogeny of coccids is fairly distinct from that of aphids, it can easily be deduced from the latter which is undoubtedly plesiomorphic.

(2) In comparison with the aphids, in male coccids the development of wings is retarded (only one or two preimaginal instars have wing-buds), a phenomenon occurring convergently also in other *Heterometabola*; the two preimaginal instars (as well as the imago) do not feed, and both, or only the last instar, do not move.

(3) The reduction of wings in the male of recent species shows that this process involves a very deep regressive transformation of the cephalothorax, antennae, legs, sense organs, etc., so that the appearance of some wingless males is exactly the same as that of the larva. We may quite rightly assume that the reduction of wings, associated with the larviform body structure, had once happened in this manner also in the female.

(4) The simplification of male connected with wing reduction is realized in two ways: with retaining of resting stages (it is the rule), or with elimination of these instars, i.e., with lowering of the number of instars from five to four (*Stictococcidae*) or three (*Polystomophora ostiaplurima*). The former process may be understood as "larvalization", the latter as "neoteny".

(5) As concerns the female, supposedly we will never learn in which of the two possible ways it has become larviform. First, we must remember that, according to the present conception, the resting stages, like those in the male, have never existed in the female development, thus one cannot speak about elimination of "particular (resting) instars", but only about "reduction of the number of any developmental instars". On the other hand, it is evident that the reduction of larval instars is a general tendency in all insects. In the scale insects various numbers of larval stages occur in well defined and homogeneous groups, for instance in the *Coccidae*. Thus, we may quite safely assume that the structural simplification (larvalization) of the female, as a result of wing reduction, and the lowering of larval instars, also followed independently.

In this context the consideration of the coccid female as a neotenic larva (a widely accepted opinion) is somewhat problematic because, if we take the lowering of the number of larval instars (in comparison with the ancestors?) and/or morphological simplification of imagines as criteria of neoteny, then perhaps most of the insects should be termed neotenic. An argument to support the hypothesis that the coccid female is a neotenic larva might be the circumstance that it grows after the last moult. However, the increase in body volume may be enormous in some groups, slight in others, while apparently absent in species in which the females do not feed. Thus, it is most likely that the significant growth of the last instar has appeared just recently in connection with parasitism, while structural modifications of the female body originated much earlier.

VIII. THE COCCID ANTENNA IS PRIMITIVE

Disregarding the evidently secondary, convergent and radical reductions of the antennae to stubs or plates in numerous groups of scale insects, it must be stated that the basic structure is more primitive than in any other group of the *Homoptera*, with respect to the shape, segmentation and sensilla.

In the *Auchenorrhyncha* the antenna is short, with flagellum represented by one article of unique shape, provided with specialized chemoreceptors. In the *Psyllinea*, the flagellum, although composed of 6–8 segments, is clearly separated from pedicel and provided with special chemoreceptors (rhinaria) and 2 particular bristles at apex. A similar structure of antenna occurs in the *Aleyrodinea*, except that there are only 5 flagellar segments and 1 apical bristle, but rhinaria also are present. In the *Aphidinea* the flagellum is 1–4 segmented

with extremely specialized primary and secondary rhinaria, and tactile hairs are greatly reduced in winged forms. In the scale insects the flagellum consists of 1 to 13 (up to 23 according to Imms 1948), normally 6–8 articles, with primitive chemoreceptors (thin-walled pegs) and numerous trichoid sensilla; specialized, rhinarium-like sensilla are entirely lacking.

Chemoreceptors are important in finding the host and sexual partner. The level of their specialization depends on the distance possible to be covered by flying or only by walking. The antenna in the scale insects is basically a tactile organ and chemoreceptors represent primarily primitive conditions, both being characteristic of insects which make use of wings to a very limited extent or not at all.

One could argue that the lack of specialized chemoreceptors is a result of secondary reduction associated with passing to a sedentary life condition. Had this been the case, we should have found some vestiges or traces of such specialized organs, at least in the most primitive groups, but we did not; in all coccids only peg-like chemoreceptors are developed (Koteja, unpublished). The reversion of rhinaria into peg-like sensilla seems even theoretically impossible.

The discussion on the coccid antenna may be summarized as follows:

(1) The ancestral coccids lived for a long time in forest litter; the sense organs retained a primitive condition and the antenna served mainly as tactile organ.

(2) The long-lasting pressure of the habitat towards wing reduction eventually brought about the wing shedding in female and polymorphism in male. In that time other *Homoptera* were already plant parasites.

(3) With the appearance of flowering plants the scale insects also became parasites of those hosts, but being already deprived of wings and doomed to a passive dispersion and host finding, they retained primitive chemoreceptors, both in male and female.

(4) A more and more sedentary life behaviour and development of protective systems caused a secondary reduction of antenna, together with the sensilla, to complete atrophy in some groups.

Thus, the primitive structure of the antenna and their sense organs provide strong arguments against the hypothesis that the scale insects had started their parasitic career as flying insects, and then, because of parasitic life behaviour, became sedentary and lost the wings.

IX. THE EVOLUTIONARY PATTERNS OF THE LABIUM AND PIERCING STYLETS ARE EVIDENTLY DIFFERENT

Hennig (1980) says: "The female labium (in coccids) has been reduced to 1–2 segments, but the stylets are very long..." This statement is not correct. The coccid labium is 1–3, or even 4-segmented, but is very short, with few exceptions (*Phenacoleachia*), and sometimes overgrown by the integument, thus

invisible from exterior, or entirely atrophied together with other mouthparts (KOTEJA 1974), while the piercing stylets are extremely diversiform in length (and other features), and definitely independent of the size of labium, and, which may be surprising, independent of the habitat, feeding behaviour and systematic position of species. It is a complex question and has not yet been studied in detail, thus I may give only some "examples" to support the above suggestion.

In *Parthenolecanium corni* the stylets are medium-sized, in *Sphaerolecanium* very long; both are *Coccidae* and in adult stage feed on twigs and branches of trees; the labium is of similar size. In *Kaweckia glyceriae*, a grass infesting eriococcid, the stylets are long, in *Greenisca brachypodii* which also feed on grass, the stylets are very short; until recently both the species have been considered as congeneric. In female *Lecanopsis formicarum*, as in other members (larvae and adults) of the *Eriopeltini*, the stylets are very short, but in the larva long. The stylets may be long and short in primitive as well as in specialized groups. The same species may feed on soft leaves, on twigs, branches and stems, etc. The stylets may be twisted within the body like spirals, or may form single, double or multiple loops. Thus, with the piercing stylets we may observe the same diversity and "heterogenity" as in the chromosome systems and endosymbiotic devices.

As concerns the labium, it has been shown (KOTEJA 1974) that its reduction (length, number of segments, sensilla, etc.) follows in all scale insects and is independent of the feeding behaviour, but shows a correlation with the "level of specialization" of given groups. Thus, we may conclude, following PESSON (1951), that reduction is a general tendency of coccid evolution. However, this may be a conclusion, but not a causal explanation of facts.

It is necessary to distinguish between morphological reduction that results from reduction of function, and structural simplification associated with modification of the function. The purpose of the latter is specialization and precision. The reduction of labium cannot be discussed in terms of functional reduction (except for the male, pupal stages and females of some groups) but only in the context of specialization.

In some aphids the labium exceeds twice the body length. HEIE (1967) interprets this phenomenon by means of feeding habits: those aphids insert the long labium within bark crevices to reach the living tissues. This problem has been solved in the scale insects in quite a different way. In the most specialized forms like *Xylococcus*, *Matsucoccus*, *Beesonia*, etc. the minute first stage larvae enters the narrow splits of bark and then, growing, enlarge the chamber which they inhabit and/or the plant tissues overgrow the larvae which do not leave the pseudogalls until maturity, or do not leave them at all.

Now a question of the sequence of events arises. In the forms mentioned above the labium is very short, but the piercing stylets may be very long. We may assume that the reduction of the labium occurred because of the new feeding

behaviour, or reversely, the new feeding habit was adopted because the labium was too short and there was no other possibility to reach the plant tissue within the bark cracks.

As has been stated earlier, significantly reduced labia also occur in primitive groups which life behaviour is slightly, or not at all, sedentary. Thus, it seems likely that the process of reduction of the labium had been initiated before the scale insects became sessile, and brought about by some other reasons. One may only guess that the short and broad labium was by some means associated with uptaking the food from decaying plant parts, fungi or the like.

There arises a further conclusion from the phenomena described above. It is very likely that at least some groups acquired new ecological niches by means of the first stage larva. This assumption corresponds with the present-day dispersion which occurs mainly, if not exclusively, by means of this instar. Eventually, it should be noted that the diversity of the piercing stylets indicates the possibility that part of the coccid radiation occurred before the adaptation to "true" parasitism. Similar conclusions arise from the study of the salivary pump (KOTEJA 1976), but not of the labium which is much more "monophyletic".

X. THE MARSUPIUM BEARS WITNESS OF THE PRIMARY COCCID LIFE BEHAVIOUR

There is another peculiar and unique (among the *Sternorrhyncha*) phenomenon in scale insects that should be kept in mind. In the most primitive groups — the *Ortheziidae* and some *Monophlebidae* — the female carries the eggs in a marsupium. It means that neither the wing reduction can be taken as final result of parasitic life behaviour, nor the sedentary life habit as the only result of the wing shedding.

The misinterpretation of the coccid evolution lies in the ambiguous understanding of "immobility". The lack of wings means only that the insect does not fly, but it may and can walk and run about. As we can see in numerous instances, the wing shedding resulted in an increase of activity by means of walking and running. The development of marsupium in primitive scale insects indicates that wing reduction primarily was associated with increased walking activity in the forest litter and that the sedentary life behaviour, in a proper sense, is a secondary acquisition connected with parasitism on plants, when the attachment of eggs to anything "stabile" was possible at all.

The complex, elaborated and diverse structure of the marsupium (BIELENIN 1978) comparable, with respect to level of specialization, with the protectiong systems of the most advanced neococcids, demonstrates that the "running about" in forest litter with the eggs carried in the marsupium, has a very long history. We may assume that carrying eggs in the marsupium and attaching

of ovisacs and/or the female herself to plants have developed independently and parallelly, or that the former behaviour preceded the latter. The evidence that egg-carrying occurs in groups, which for various other reasons must be considered primitive, indicates that attaching of egg layers is a derived behaviour. In this context the overall presence of perivulvar pores in the neococcids could be considered as a remnant of the marsupial device. On the other hand, the circumstance that the most primitive neococcids show no traces of marsupium may support the view of independent development of marsupial devices only in the archeococcids.

XI. ENDOSYMBIOSIS AND FEEDING BEHAVIOUR

The endosymbiosis of animals with plant organisms is an important source of information on their evolution and phylogeny. However, with scale insects the information is controversial, thus it is difficult to draw any reliable conclusions.

BUCHNER (1965) associated the origin of endosymbiosis in coccids (and other *Homoptera*) with transition from cell-sucking to phloem-sucking; consequently, groups which live symbiont-free are primitive ("adhere to the old way of feeding"), or advanced because of secondary loss of symbionts associated with return to cell-sucking or for some other reasons (TREMBLAY 1977). Thus, according to BUCHNER (1969), *Steingelia, Matsucoccus, Xylococcus* and *Kuwania* are primarily asymbiotic which coincides with the classification of MORRISON (1928), but not with others (KOTEJA 1974a, DANZIG 1980, MILLER 1983).

The *Apiomorphidae* are considered to be close to the *Eriococcidae* (sometimes united within one family); they live in galls and change the feeding behaviour during their lives (GULLAN 1983). BUCHNER did not find any rudiments of symbiotic devices in these coccids; but other gall-producers have symbionts.

Orthesia insignis artificially devoid of symbionts may live and reproduce for years, while *Planococcus citri* cannot; but in the same time the latter is given as an instance of parenchyma-sucker (BUCHNER 1965, p. 796 and 798, respectively). According to BANKS (1977) the coccid pigments are of endosymbiotic origin; in fact, some pigment-producers (*Porphyrophora*) have endosymbionts, while others (*Kermes, Dactylopius*) have not. The symbionts in the *Diaspididae* are yeast-like according to BUCHNER (1965), but bacteroid according to TREMBLAY (1977), etc., etc.

The most important incongruity concerns the primordial conditions of the feeding behaviour. BUCHNER (1965) assumes that "all the *Hemiptera* were carnivorous originally and only gradually turned to sucking plant juices exclusively" which "manifestly requires symbionts". With scale insects he agrees that "the present feeding habit was preceded by one that required no symbionts, namely, puncturing and sucking out cells of the plant host". However, STRÜMPEL

(1983 and records cited herein) distinguishes "Systembibitoren" that suck out phloem and xylem, and "Lokalbibitoren" which take the food from cells, and considers the former (!) as primordial, while the latter as their derivatives. It is clear that phylogenic conclusions based on such assumptions must be fundamentally different.

The following evidence may be important in discussing the peculiarity of endosymbiosis in scale insects:

(1) The *Aleyrodinea* and *Psyllinea* are phloem-suckers; among the *Aphidinea* and *Auchenorrhyncha* about 95% of species take food from conducting tissues, the rest from cells, but in the *Coccinea* as many as 40% of species suck cells (STRÜMPEL l.c.).

(2) The endosymbioses in scale insects, particularly in comparison with aleyrodids and psyllids, are diversiform with respect to symbionts, their housing and embrional devices; they include primitive as well as extremely elaborated forms (BUCHNER 1965, 1969).

(3) "The change in feeding habit brought about by the symbionts ...occurred very early in aphids, psyllids and aleyrodids, but in coccids... the symbionts were acquired only after the splitting had reached essentially its present stage... thus all indications which would allow, (as with other *Homoptera*), the exposure of a monophyletic tree (of symbiosis) are thoroughly lacking" (BUCHNER 1965). TREMBLAY recognized about 20 endosymbiotic types in the coccids.

(4) The asymbiosis is "surprisingly frequent" among the coccids and occurs in both *Orthezioidea* and *Coccoidea*; sometimes it is evidently a secondary loss of symbionts (*Hippeococcus*), but possibly may also be of primary nature (BUCHNER l.c.).

(5) In coccids the "inclination to admit additional symbionts is in general moderately developed and often occurs sporadically" (BUCHNER l.c.); there are only few species with 2–3 symbionts, while in *Auchenorrhyncha* as many as 6 may occur.

Based on this evidence and some other data the origin of the peculiar endosymbiosis in scale insects may be interpreted as follows:

The ancestral *Homoptera* did live with endosymbionts from their "very beginning", although not necessarily in a manner that we may now see in the cockroaches. The host-symbiont interactions might have been at low level, the symbionts not so "indispensable" and frequently exchanged. This assumption may be supported by the facts that (a) the transmission of the symbionts is now exclusively transovarial in all *Homoptera*, (b) mycetomes represent the main type of housing symbionts, (c) some of the bacteroid symbionts are extremely specialized (among others, they cannot be cultivated on artificial diets), and in all likelihood have undergone a large proportion of their evolution in endosymbiosis (maybe, they are derivatives of one or only few forms), (e) the most primitive *Homoptera* (*Peloridiidae*) have symbionts in mycetomes.

Homoptera changed the feeding behaviour according to the sequence —

semisaprophagic mixed diet — puncturing any tissues of vascular plants — puncturing conducting tissues (systembibitoring) — return of some groups to cell-sucking (localbibitoring) — peculiar feeding behaviours (e.g. association with ants) connected with loss of symbionts.

The transition from a generalized symbiosis to an advanced and indispensable was bound with passing from cell-puncturing to phloem-sucking. i.e., elaborated endosymbioses opened for the *Homoptera* an abundant source of food. This and the former paragraphs join the contradictory views of BUCHNER (1965) and STRÜMPEL (1983) concerning the primordial feeding behaviour of the *Homoptera*.

The splitting off from the homopteran trunk and leaving the primary habitat and feeding behaviour as well as further divergence of particular groups and evolution of their endosymbioses followed independently to some extent and brought about the following result:

— The *Auchenorrhyncha* first branched off from the ancestral *Homoptera* and at the same time changed the feeding behaviour, thus their endosymbiosis is monophyletic, multisymbiotic, extremely complicated, with numerous new acquisitions and substitutions.

— Next derived the *Aleyrodinea* and *Psyllinea*. They soon changed the feeding habit, but retained a narrow specialization; their symbioses are monophyletic, with few new acquisitions.

— The *Aphidinea* changed the feeding habit after they diverged at least into the main groups — *Phylloxeroidea* and *Aphidoidea* — thus the endosymbioses of these groups and their future evolution is different. Only very few new acquisitions of yeasts are known.

The *Coccinea* remained for a long time in the primary habitat and each of the already diverged groups changed individually and in different time the feeding behaviour and endosymbiosis. Therefore, the systems seem to be polyphyletic, diversiform with respect to type and specialization level, with few symbiont species in one host, few new acquisitions, although mainly of yeasts, but with numerous asymbioses associated with some progressive modifications of feeding behaviour which, however, are little known.

The conditions within the scale insects correspond with the above hypothesis. The *Ortheziidae* live in the primary habitat and continue the primitive feeding behaviour. They are generalized morphologically (particularly the male), have primitive bacteroid symbionts, but can live symbiont-free. The *Diaspididae* are narrowly specialized, but supposedly an old group, with homogeneous morphology and monotonous symbiosis with bacteroids. The *Pseudococcidae* are an old but diverse and progressive group; they join various types of endosymbiosis, including acquisition of yeasts and secondary asymbiosis. The *Eriococcidae* s. l. are the most diverse representatives of the scale insects, with numerous asymbiosis (*Kermes, Apiomorpha, Dactylopius, Ovaticoccus*). The advanced groups — *Stictococcidae, Tachardiidae, Coccidae, Lecanodiaspididae*,

Aclerdidae — acquired yeasts, but most lost the bacteroid symbionts. The complicated and obscure phylogenic relationships of the *Orthezioidea* are well expressed by the conditions of the endosymbiosis (BUCHNER 1969).

Of particular interest are the cases of asymbiosis. If the asymbiosis in the above mentioned groups is primordial, we must assume that the acquisition of symbionts in the remaining groups (morphologically apparently more primitive) of eriococcids (s.l.), i.e., their transition to phloem-puncturing, is a very young phenomenon, which is very unlikely. More likely is the assumption that these groups lost secondarily the endosymbiosis, retained by the generalized eriococcids. Possible, the same interpretation could be applied to the symbiont-free members of the *Orthezioidea*, although BUCHNER (1969) strongly emphasized the primary nature of their asymbiosis.

As a matter of fact, the endosymbiosis of scale insects is very little known; maybe, further studies will reveal that it is not at all polyphyletic, but represents a complicated type of monophyly, as in the *Auchenorrhyncha*.

XII. COCCID WASP PARASITES

The *Coccoidea* (*Neococcoidea*) are abundantly parasitized by *Hymenoptera*, while the *Orthezioidae* (*Archaeococcoidae*) are not. According to ROSEN and DEBACH (1977) "there seem to be very few reliable, authentical records of primary parasitic *Hymenoptera* attacking the *Archaeococcoidea*". The authors further state: "Although large gaps in our knowledge admittedly exist, it appers as though the association of parasitic *Hymenoptera* and scale insects has evolved only after the *Neococcoidea* completely separated from the *Archaeococcoidea*".

The suggestion that the association of parasitic wasps with the scale insects originated after they had ramified into the main branches does not explain why this association occurred only in one, more advanced group.

It is not possible to answer this question by means of zoogeographical factors, since the distribution of the *Orthezioidea* and *Coccoidea* is the same and has, very likely, the same history. To explain the particular association of *Chalcidoidea* with the *Coccoidea* on geographical basis we should assume that this association originated and evolved in a zone in which the *Orthezioidea* were absent, or were extinct, which is unlikely and not supported by any facts.

The question is the more so difficult that the *Chalcidoidea* parasitize a very wide spectrum of hosts, including various insect orders and *Arachnoidea*, and some are also phytophagous. Members of one coccid family may be attacked by parasites of several chalcidoid groups, and reversely, parasites of one family may develop in various groups of scale insects. It seems likely from this evidence that the host-parasite associations originated many times, and at different taxonomic levels.

One of the possible solution of the dilemma lies in the ecological field. ROSEN and DEBACH (1977 and references quoted herein) recognize five distinct steps in the process of "finding" the host by a parasite, and state: "Habitat selection is the first, and sometimes most important, step. Before actually searching for its host, a parasite seeks a certain environment, a certain microhabitat. Certain scale insect parasites, for instance, have been shown to be differentially attracted to various plant species. Sometimes this is as far as the selection process goes. Many *Ichneumonidae* are known to be habitat-specific, attacking a wide range of hosts occurring in their preferred microhabitat. The *Chalcidoidea*, on the other hand, usually also exhibit marked host-specifity". The following steps are the "host finding", "host acceptance" (or "psychological selection"), "host suitability" (or "physiological selection") and "host regulation".

Although the above remarks refer to the behaviour of an individual, present-day parasite, it is clear that the host-parasite associations phylogenetically evolved in the same pattern. And it is also evident that the first step, emphasized by ROSEN and DEBACH as very important in the present conditions, was, the more so, significant in the origin of the host-parasite associations. This simply means that the potential parasite looked for its potential host in its own microhabitat.

The *Hymenoptera* are well-flying insects and their expansion was connected with the flourish of the angiosperms. They certainly looked for their victims in the crowns of the flowering plants. If the assumption that the ancient scale insects lived for a long time in the forest litter, and that the evolution of the *Coccoidea* (neococcids) was connected with the transition to the new ecological niches — the above-ground parts of flowering plants — is correct, we may also assume that this fact was the condition of the origin of the coccid–chalcidoid association. According to this conception we should also believe that the transition of some (in fact numerous) members of the ancient scale insects (*Orthezioidea*) to the above-ground habitat occurred much later, and that the *Chalcidoidea*, being already specialized parasites of the *Coccoidea*, did not recognize in them members of scale insects and potential victims. Maybe, further investigations will discover sporadical wasp parasites of the *Orthezioidea*, and the phylogenic position of the parasite will tell us whether these associations are new, or relict ones. Unfortunately, paleontological evidence of *Chalcidoidea* is very scarce and hymenopterologists rather expect some information from the coccidologists (NIKOLSKAYA 1952). Finally, it may be added that the *Orthezioidea* (apparently only eggs) are parasitized by some *Diptera* which phylogenetically are certainly much younger parasites than the *Hymenoptera*.

There are some arguments to support the above hypothesis. For instance, in the *Coccidae* both larvae and females are attacked by parasites. It may be the same parasitic species or different ones, which apparently depends on phenological factors, but in *Lecanopsis formicarum* only adult females are attacked

by two parasitic *Chalcidoidea* (BORATYŃSKI, PANCER-KOTEJA, KOTEJA 1982).
In this coccid the larvae live on underground parts of grass from July to May
next year, while females appear above ground for mating and oviposition in
May and June. Among thousands of larvae examined, only in two or so dead
parasites have been noticed, while 50–100% of adult females were parasitized.
It is quite likely that the mentioned larvae for some reasons might have deve-
loped above ground and in this way became victims of the parasites. The under-
ground habitat of *Lecanopsis* larvae is undoubtedly secondary and very young.

In numerous scale insects the entire development follows under the ground
(*Euripersia*, *Rhodania*, *Chaetococcus*, etc.), and at least in some of them both
larvae and adults are parasitized (one can never be sure about information
in this field; see remarks by ROSEN and DEBACH 1977). It is easy to assume
that the host–parasite association originated above ground, and that the secon-
dary adaptation to the subterranean habitat involved also a parallel adaptation
of the host–parasite association. In this aspect *Lecanopsis formicarum* repre-
sents a step in such succession.

No doubt biochemical and physiological aspects play the major role in
any host–parasite associations (discussed by ROSEN and DEBACH, l.c., under
"host suitability" or "physiological selection"). A rather sparse investigation
into the chemistry of coccids (reviewed by BANKS 1977) provided some useful
taxonomic information, but none indicated any basic differences between
the *Orthezioidea* and *Coccoidea*. In spite of the lack of evidence we may expect
the existence of such differences because of the supposed very long independent
evolution of these groups.

There is another important point concerning the subject under discussion.
The aphids, like coccids, are represented by two groups: the more primitive
Phylloxeroidea and advanced *Aphidoidea*. While the latter, with one possible
exception, are attacked by parasitic wasps, the former are not (HEIE 1967,
ROSEN and DEBACH 1977), thus, the conditions are exactly the same as in the
scale insects. I do not know how (and whether) this phenomenon is interpreted
in the aphids. In any case, HEIE associates the *Phylloxeroidea* with the gymno-
sperms from their very origin, and a possibility that this group could originally
have lived in forest litter has not even been mentioned.

At the end of this chapter let us see what hymenopterologists say on the
origin of the host–parasite association in the *Chalcidoidea*. TRJAPITZIN (1979)
discusses this question with respect to the *Encyrtidae* which include the major
part of coccid parasites.

Among 493 genera (2900 species) the host–parasite relations are known
in 273, i.e., in 55% of genera. Within the latter, 184 genera (70%) parasitize
Homoptera: 170 develop in coccids, 9 in psyllids and 5 in cicadas. The remaining
30% of genera are associated with 8 other insect orders and with *Acarina* and
Araneina.

According to TRJAPITZIN the primary hosts of the *Encyrtidae* were the

Homoptera and among them, to all likelihood, the scale insects. *Aleyrodinea* and *Aphidinea* are not attacked by encyrtids. The parasites of *Psyllinea* belong to a specialized and relatively young group the ancestors of which apparently parasitized the coccids, while those of the *Auchenorrhyncha* are primitive and perhaps very old. However, Trjapitzin does not discuss the question whether the *Auchenorrhyncha* acquired the encyrtids from the *Coccinea*, or reversely, neither he suggests a parallel and independent origin of these parasitic associations, although such possibility seems to be likely.

The second step of parasitic associations of the encyrtids is the parasitism on predators of scale insects, which belong to at least 10 families of different orders, and secondary parasitism, mainly on *Chalcidoidea*. The third step of adaptation includes parasitism on plants and eggs. The parasitism on predators is of particular significance in understanding the evolution of the host–parasite associations because it brings into light that the ecological relationships play a major role, in comparison with phyletic relationships, in the origin of parasitic associations. Thus, the parasitism of the *Encyrtidae* indicates, once again, that some basic ecological differences must have existed between the *Coccoidea* and *Orthezioidea* since the former are, while the latter are not parasitized by these wasps.

Within the *Coccoidea* about 50% of encyrtids are associated with the *Pseudococcidae* which (encyrtids) include also the most archaic forms. Answering the question of the potential parallel evolution of encyrtids and coccids Trjapitzin noted that in some groups such parallelism might have been observed, but he refused from an attempt of its outlining because of "unsufficient data on the existence of parasitic associations between encyrtids and the most archaic superfamily of coccids — the *Palaeococcoidea*" (= *Orthezioidea*).

XIII. GALLS

Endosymbiosis and parasitism show one common character — the older, the more elaborated and harmonious they are. Very little is known of the interactions between scale insects and their hosts, but what is known, indicates that the coccids are young parasites.

One of the most important aspects of parasitism is the host–parasite immunological interaction. As concerns the scale insects, Miller and Kosztarab (1979 and literature records quoted here) say: "It is not uncommon to find a heavy infestation on one of the two plants of the same species growing side by side and a light infestation on the other plant. Likewise, a plant may be susceptible to scale infestation one year and immune the next," etc., etc. (population retardation by natural enemies is not disregarded in these observations). It means that the immunological balance reached rather a low level in the host–coccid association.

The phenomena mentioned above are difficult to study, but gall-producing, one of the most striking feature of the host–parasite interaction, is easy to be observed. In spite of this, only brief notes on this subject may be found in the coccid literature. The reason is very simple: most of the coccidologists have never seen true galls produced by scale insects. Of about 120 species of the Polish coccid fauna there is one (*Acanthococcus devoniensis*) which causes slight deformation of twigs of its host (*Erica*) and 3 species of *Asterolecaniidae* which cause the generally known shallow pits on the host twigs, while numerous aphids form, often species-specific, galls. Similar conditions supposedly occur also in other geographic zones except Australia, New Zealand and South America. GULLAN (1983) recognized about 80 species (in 13 genera) of Australian coccids (about 500 species recorded) which produce galls, most of them being species-specific (pit-galls have not been considered), while HOY (1962) several gall-makers of the *Eriococcidae* from New Zealand.

Beside (a) the restricted zoogeographic area, three other phenomena are characteristic of the coccid gall-producing: (b) most of the gall-makers are eriococcids or closely related groups, (c) most of the galls are produced on *Eucalyptus* (GULLAN mentions 5 other hosts in Australia), and (d) the gall-inhabiting coccids are significantly modified morphologically.

I have no particular idea how to interpret the phenomena "a", "b" and "c", except that there is coincidence of "a" and "c" — *Eucalyptus* is restricted to the Australian Region — and that perhaps some physiological features of this plant are responsible for the gall formation. As concerns point "b" it may be noted that the eriococcids are the most expansive group among the scale insects. They radiated into numerous forms which retained basic eriococcid characters (radiations at generic level) and gave rise to the origin of a number of families which occupy various ecological niches and also geographical zones.

With respect to point "d" I may present the following interpretation. Normally, the galls serve as houses in which the insects grow and develop, but in some time and by any means they leave the galls to reproduce and/or change the host. If they reproduce within the galls, they do it only partenogenetically. In the scale insects the adult female does not leave the gall but modifies her body (elongates the abdomen) to enable the mating. Similar modification occurs in the male (GULLAN 1983). In this way not only the larvae and adult females, but also the eggs (except first instar clawlers) remain within the galls. We must assume that the principal reason for this behaviour was the lack of wings in the female of the ancestor that had to become a gall-maker. Thus, once again we come to the conclusion that the lack of wings in the coccid female is not a result, but a reason of the sessile behaviour.

In addition to true galls that are a result of physiological interaction the scale insects inhabit various pseudogalls (*Xylococcus, Kuwania, Neosteingelia, Kuwanina, Beesonia*, etc.). In this case the insects become concealed by means

of a normal growth of the host tissues. However, morphological and behavioural modifications also occur in these coccids and sometimes are even more curious and elaborated that in true gall-producers, for instance in *Beesonia* (KOTEJA, LINIOWSKA 1974).

Based on the host–parasite immunological balance, and particularly on the gall-production, which is significantly limited with respect to distribution, host plant, number of gall-makers and their taxonomic membership, as well as structural diversity, we may conclude that the scale insects are young gall-producers and certainly also young plant parasites.

Finally, it may be added that the origin of *Eucalyptus*, the main host on which galls are produced, is dated as Oligocene (HOY 1962 and records mentioned here) while HEIE (1967) dated the origin of the heterogony in *Adelgidae* as Permian. Gall-formation might have evolved in this group much later, and *Eucalyptus* might have appeared much earlier, but also in this case there is a difference of many millions of years between the origin of gall-producing in the aphids and coccids.

XIV. THE COCCID PARASITIC STRATEGY IS MAINLY DEFENSIVE

The *Homoptera*, except scale insects, are flying animals. Some groups share flying with jumping. *Psyllinea* and *Aleyrodinea* insert the eggs within living plant tissues. In both the groups the larvae are sedentary, in contrast with the adults which are active. In the latter group the last portion of the fourth stage plays the role of pupa. The *Aphidinea* developed complicated heterogony cycles associated with host change and viviparity. An aphid female may give birth to dozens of larvae, the mass of which equals the female weight every 2 or 3 days. Aphids and other *Homoptera* may give yearly numerous generations. All *Homoptera* may live on perennial as well as on annual hosts.

The coccids rarely are viviparous; the mass of progeny (eggs) never exceeds that of the female; there is one, rarely two or three generations per year; the dispersion and host finding are passive by means of the first stage crawler; host alternation or change of place of sucking to feed on a more abundant source of food (or more complete diet) are impossible or greatly limited in the scale insects; annual plants are excluded from the host list, etc; but the scale insects developed elaborate chromosome, symbiotic and protecting systems.

We may see from the review of the differences between scale insects and other *Homoptera* that most of the parasitic devices developed by the aphids, aleyrodids and psyllids have an offensive character, while those of the coccids are mainly defensive; and are brought about by the lack of wings. It is very unlikely that any insect plant parasite might have completely resigned from the advantages which arise from the flying ability.

XV. A NON-EXISTING PROBLEM

I am quite aware that any hypothesis is proved only when it fits all available evidence. However, I could not find any proper placement for the gymnosperms in the conception presented in the paper.

It would be difficult to analyse all the coccids living on gymnosperms, but HOY (1962) was perhaps not right assuming that nowadays not a single group at family level is associated exclusively with these plants; for instance, the *Matsucoccidae* and *Pityococcidae* are. One may answer that they are not families but subfamilies or so, but it does not matter. In fact, the association of the mentioned groups with gymnosperms is not of much help in understanding the evolution of scale insects.

Concerning the species level, there is a number of coccids in many genera and families associated with gymnosperms, but for the evolution of the whole group it is without any significance. To assume the gymnosperms as primary hosts of those species we should also believe that all the evolution of scale insects up to the Quaternary followed on gymnosperms, which is nonsense.

Similar conclusions arise from the analysis of the generic level. For instance, there are few genera of *Coccidae* associated exclusively with *Coniferae*. *Nemolecanium* (concerning both male and female) is close to *Eulecanium*. In *Physokermes* the male is similar to *Eulecanium*, but the female is extremely specialized (anal plates are absent in adult stage). It is unlikely that any of the two genera might have been ancestors of the *Coccidae*. Much more interesting is the genus *Toumeyella* in that most species feed on *Pinus*, but some on *Magnoliaceae*. I do not remember whether anybody has ever thought this genus to be ancestral.

Among the more generalized scale insects some feed exclusively on gymnosperms and some guesses concerning their evolution may be discussed. For instance, *Marchalina* (*Coelostomidiidae*) might have given rise to *Pityococcus* and *Desmococcus* (*Pityococcidae*) and they, in turn, to *Matsucoccus* (*Matsucoccidae*). This sequence represents a gradual simplification of the female preadult stage (McKENZIE 1942). At some points of this sequence the genera *Steingelia*, *Xylococcus*, *Neosteingelia*, *Kuwania* and their relatives might have been derived and transited on angiosperm trees. The problem is that some of these genera are supposed to be closely related with the *Margarodinae* (sensu MORRISON) which are hypogeic and infest herbaceous plants. On the other hand, MILLER (1983) dissociated all the above mentioned coccids, among others, he placed *Pityococcus*, together with *Phenacoleachia*, close to the *Pseudococcidae*. At this point we must leave the questions of primary host unanswered. However, there are some more general problems.

Coccidologists, who believe that the scale insects originated and evolved with the angiosperms, must answer why these insects have not attacked the

gymnosperms (which were present at that time) until now when these plants have become "secondary" hosts, i.e., by acquiring the coccids from the angiosperms. Those who believe that the scale insects evolved in the Permian must answer the same question — gymnosperms have been present since the Carboniferous.

As we can see it is the same problem as with the coccid–chalcidoid association: the older members of the scale insects were not attacked by the parasitic wasps. I answered the question that for some ecological reasons the archaic coccids were "not accessible" to the *Hymenoptera*. Now we may give the same answer: the gymnosperms were not accessible for some reasons to the scale insects. As suggested by LARSSON (1978) all gymnosperms have produced resin from their very origin. Possibly, this was the barrier too high to be overcome by the archaic coccids.

However, there is another solution: maybe, the problem of the "primary host" is non-existing, and such a question should never be asked. It is very likely that the impression that the scale insects form numerous, close and "apparently primary" associations with the angiosperms, whereas sporadic and at low taxonomic level, thus "apparently secondary" associations with the gymnosperms, arises simply from the absolute numbers of coccid species and groups without realizing proportions between gymnosperm and angiosperm plant species. I am unable to make such calculation for the world fauna; in Poland the relations are as follows:

There are 11 native gymnosperm species in 3 families and about 2,100 angiosperm species in about 100 families (SZAFER et al. 1953). Among the 125 native coccid species 17 infest exclusively gymnosperms, 103 angiosperms, at least 2 species both these hosts and 3 species live on decaying plant material, in litter, etc. (KAWECKI 1985). It means that each gymnosperm species is infested by 1.5 coccid species, while each angiosperm species by 0.05 coccid species! With respect to plant families, 4.3 coccid species infest one gymnosperm family, in angiosperms this relation is 1:1. Furthermore, all gymnosperms in Poland are infested by coccids, while perhaps no more than half of the angiosperms. I suppose that similar calculation for the world fauna will reveal approximate results. The figures indicate that the scale insects definitely prefer gymnopserms to angiosperms! A proper analysis may also reveal that close (exclusive) associations between coccids and their angiosperm hosts at a higher taxonomic level are relatively (!) extremely rare, in any case, not more frequent than with the gymnosperms.

Preliminary examinations of the Baltic amber coccids indicate that more than half of specimens and species were exclusively associated with gymnosperms, but it is quite possible that all lived on these hosts (KOTEJA 1984), while LARSSON (1978) records 33 gymnosperm species and 96 angiosperms in the Baltic amber flora, among which *Fagaceae* (oaks), *Lauraceae*, *Magnoliaceae*, *Myricaceae* and others were numerous and, particularly the oaks, very

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abundant. It is obvious that coccids infesting the mother plant of the amber (*Pinites succinifera*) had a better chance to be embedded in the resin, but even considering this evidence, the coccid fauna associated with gymnosperms seems to be more abundant than that infesting the angiosperms.

Aphidologists have not even the slightest doubt that the gymnosperms might not have been the primary hosts of the aphids (HEIE 1967). Let us see what the host–parasite associations are like in the Polish aphid fauna. SZELE-GIEWICZ (1969) listed 591 species, i.e., about 5 times more than in scale insects; 38 species live exclusively on gymnosperms, 549 on angiosperms and 4 share both the hosts, i.e., 6.5%, 93% and 0.5% respectively. In coccids these relations are 14%, 83% and 2% (2% living in turf and forest litter). Nine aphid genera live exclusively on gymnosperms, and also nine coccid genera show exclusive associations with these hosts (!); one aphid genus shares both gymnosperms and angiosperms, while five coccid genera do it!

Psyllids and aleyrodids are as old as, or older than, aphids and coccids, but nobody asks where they were living and feeding on before the appearance of angiosperms; it seems likely that they are now associated exclusively with angiosperms. Two conclusions arise from the above discussion: (a) the associations of coccids with gymnosperms are much closer than in any other group of *Sternorrhyncha*, and (b) our views on the evolution of scale insects with respect to the "primary host" require fundamental revision.

There is another important evidence in the host associations of coccids. Numerous specialized coccids (*Parthenolecanium corni*, *Lepidosaphes ulmi*, *Quadraspidiotus perniciosus*, *Chionaspis salicis*) infest hundreds of plant species of a variety of families, including gymnosperms. On the other hand, primitive coccid species (*Phenacoleachia*, some *Monophlebidae*, *Ortheziidae*, some primitive *Pseudococcidae*) feed on both gymnosperms and angiosperms, on monocotyledones and dicotyledones, on herbaceus and woody plants. It seems likely that the taxonomic position of the host was not of particular interest for the ancestral coccids, as it is not for some specialized forms. Furthermore, associations of coccids with particular plant species seem to be very rare, if they exist at all.

All this indicates that the scale insects, although phylogenetically an old group, are young plant parasites, and that they have transited from "anywhere" to both gymnosperms and angiosperms being already diverged into several branches. I guess the "anywhere" was the forest litter.

XVI. POSITIVE ARGUMENTS

All the arguments presented in the paper are "negative", i. e., it has been shown and emphasized what is "impossible"; for instance, that the loss of wings in coccid female cannot be a result of parasitism, etc.

To give positive arguments for the hypothesis under discussion one should demonstrate that (a) the scale insects may feed on non-living material, and that (b) at least some coccids continue the primary feeding behaviour and/or live in the primary habitat.

As concerns the first question it may be said that attempts have been made to keep scale insects on artificial diets (HAFEZ et al. 1971) and that some species (*Newsteadia floccosa*) may be bred on decaying leaves (SCHUMTTERER 1952, BUCHNER 1965). Another instance is provided by the curious behaviour of *Hippeococcus*. As suggested by BUCHNER (l.c.) this mealybug lives on plants, but to produce progeny it must be fed by ants. The author supposes that, like in the case of the aphid *Paracletus*, *Hippeococcus* "takes up liquids from the mouth of the ants with its snout, the tip of which is supported by the mandibles of the ants during the feeding process".

With question (b) it must be noted that there is a remarkably large proportion of species living under, on, or in some other close contacts with the soil. Of 125 native species in Poland, 5 live on roots, 7 on other underground plant parts, 5 on plant parts close to the soil, 20 in leaf sheaths of grasses just above the ground; together 41 species, i.e., one third of the fauna. The remaining species live on various above-ground plant parts, but some prefer the parts which are close to the soil (*Quadraspidiotus bavaricus*, *Spinococcus calluneti*, *Allococcus vovae*, etc.).

Some species spend all their lives in an underground habitat (*Ortheziola*, *Euripersia*, *Chnaurococcus*, etc.), others only partly. In most cases the larvae live in underground habitat, but mating and oviposition take place above the ground (*Porphyrophora*, *Steingelia*, *Lecanopsis*). Few species (*Orthezia urticae*) feed on aboveground plants, but hibernate in the soil (KÖHLER 1983).

In some instances the underground habitat is evidently of secondary origin (*Lecanopsis*, *Chnaurococcus*, etc.) but in many others the primary habitat and life behaviour might have been exactly the same as those of the recent species and the evolution as well as radiation might have followed all the time in these conditions. I do not suppose we should necessarily assume that *Steingelia*, *Margarodes* or *Rhizoecus* primarily lived on stems, twigs or leaves and then "secondarily" acquired an underground habitat.

Of particular interest are the *Ortheziidae*. Species of some genera (*Ortheziola*) constantly live in turf without "visible" association with any plants. *Newsteadia floccosa* lives in decaying plant parts in forest litter, but once I met an abundant colony on leaves and twigs of *Achillea millefolium*. *Mixorthezia* and *Nipponorthezia* live in humus, detritus, etc. (MORRISON 1982, RICHARD 1979). The same has been observed in some *Orthezia* and *Arctorthezia*. Species of this family are all their lives (except pupal instar) moving, have numerous primitive morphological features, bacteroid endosymbionts, but may live symbiont-free, have a primitive chromosome system, a world-wide distribution, etc.

BORCHSENIUS (1958) considered the *Ortheziidae* to be most primitive and

ancestral of all *Coccinea*. DANZIG (1980) regards this group as a minor side-branch which did not play any significant role in the phylogeny of the scale insects. This may be true, but the life behaviour is undoubtedly primitive and demonstrates how the ancestral scale insects might have lived in the prehistoric times.

XVII. INTERRELATIONSHIPS

All possible relationships were suggested between the *Psyllinea*, *Aleyrodinea*, *Aphidinea* and *Coccinea*, but recently aphids have been largely accepted as the sister group of the scale insects. However, the arguments for this opinion are rather poor.

SCHLEE (1969) basing on *Sphaeraspis priaskaensis*, recognized 7 synapomorphic characters of aphid and coccid wings. SZELĘGIEWICZ (1971) rejected 4 of them, but added 2 more, thus 5 remained as synapomorphic in aphids and coccids. However, 2 of them may hardly be accepted by coccidologists, while 3 others not at all. HENNIG (1980) agrees with the aphid–coccid sister group conception, but on another occasion he says: "... the venation of most recent *Sternorrhyncha* is so reduced that it can be derived from almost all other venation, even though only slightly more primitive".

THERON (1958) stated that male *Margarodes* is much closer to *Aphis* than to other *Sternorrhyncha* (wing features have not been considered). BEARDSLEY (1968) suggested a close relationship of *Matsucoccus* with *Orthezia* and *Aphis*, but not with *Margarodes*. MORRISON (1928) considered *Matsucoccus* and *Margarodes* to be primitive, but KOTEJA (1974a) as most specialized among the generalized coccids. At the same time *Aphis* is believed to be very young, thus specialized (HEIE 1967). I do not think that such comparisons will be conclusive.

With the females matters stand even worse. Irrespective of the way (neoteny or larvalization) in which the females became larviform, and acquired numerous autapomorphic characters) they must be very different from the ancestors, and it is little hope that many synapomorphies may be found in coccid females and aphids.

On the preceding pages attempts have been made to prove the conception that the sternorrhynchan primary habitat was the forest litter and that the coccids were the last to have left it. Now the question arises what was the sequence of the exodus of other *Sternorrhyncha*. Answering this question we must realize that the evolution took partly place in the primary, and partly in the secondary habitat, and that, if the conception is right, the proportions of these parts should be different in each group. Thus, the group which was the first to have left the forest litter was the one which combined the "most" primitive characters, i.e., primary features unchanged during the short stay in the original habitat, with the "most" specialized and fixed characters acquired and stabilized during the long life in the secondary habitat. And reversely,

the group which has remained very long in the primary habitat, should share divergent and fixed primitive characters with "primitive" and unstable specialized characters.

It has been shown that the latter case applies to the scale insects. They share numerous "specialized" primitive characters (one tarsal claw, one-segmented tarsus, apterism in female, dipterism in male, etc.) all being well fixed, with unstable and "primitive" specialized characters (diversity of male structure, chromosome systems, endosymbiotic devices, variable number of larval stages, low degree of immunological balance, and so on).

Based on this reasoning the following sequence may be suggested for the *Sternorrhyncha*: *Aleyrodinea*, *Psyllinea*, *Aphidinea*, *Coccinea*. This is only a suggestion which should be proved in detail, however, it is remarkable that a similar sequence of groups follows from the number of recent species: 200, 1,500, 2,000, 3,000 (according to HENNIG 1980), or 1,150, 1,250, 3,600, 5,000 (according to STRÜMPEL 1983).

XVIII. CONCLUSIONS

1. The evidence presented in the paper demonstrates that the phylogeny of the scale insects occurred within two stages clearly different concerning habitat, feeding behaviour and, consequently, evolutionary trends.

2. In the first stage, from the splitting off from the homopteran stock (Carboniferous or Permian) to the appearance of flowering plants (Jurassic), termed here "prehistoric times", the scale insects lived in the forest litter on "mixed" diet; they were sucking out various plant saps from the surface and from the living and decaying plant tissues.

3. In that time the scale insects acquired the most characteristic features which principally determined the future evolution. The leg became a digging organ (one claw, one-segmented tarsus, functional tibiotarsal joint); the females irrevocably lost the wings and became larviform; the males became unfeeding, dwarf-like, dipterous and polymorphic; the paurometaboleous development changed in that female larvae lost the wing buds, while the last male larval instars became unfeeding resting stages with enlarged wing buds. Eventually, the scale insects diverged into numerous group in that time.

4. In the second stage of evolution, from the appearance of flowering plants up to the present, the evolutionary trends radically changed: the coccids became true plant parasites. Most groups started to climb the plants. Supposedly the first to have done it were the *Coccoidea*, thus they became victims of parasitic *Hymenoptera*. Each of the group settled and elaborated its own endosymbiotic system, thus the symbiosis in coccids seems to be "polyphyletic". Ungual and tarsal digitules have been developed as clinging organs.

5. The transition from the primary to the secondary habitat and beha-

viour followed during a long period of time and independently in various groups; as a result, the level of specialization in the recent scale insects is extremely differentiated. Some groups supposedly still continue the primary mode of life.

6. The range of specialization of coccids as plant parasites was greatly limited by the absence of wings in female and the fragility of male. The specialization was directed towards a sessile life behaviour: the coccids developed a variety of protecting systems with simultaneous reduction of locomotion ability. These systems involved deep structural modifications of the female body (including diminution and hypertrophy) and development of various integumental glands and devices for honey-dew ejection. Various complicated and elaborated cytological and hereditary systems originated as a kind of replacement of the degeneration of male.

7. Among the *Homoptera* the scale insects retained for the longest time the habitat and life behaviour of the ancestors. Thus, they share primitive characters of the homopteran ancestors, many and important modifications to semi-hypogeic and semi-saprophagic life behaviours with features of extreme and sessile plant parasites. This evidence is responsible for their peculiarity. On the other hand, since the radiation occurred in various stages of evolution (before and after the transition to parasitism), the scale insects became extremely diversiform.

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STRESZCZENIE

[Tytuł: Rozważania o prehistorii czerwców (*Homoptera, Coccinea*)]

1. Budowa czerwców, ich tryb życia, rozwój, rozród, endosymbioza, determinacja płci itp. wskazują, że filogeneza tej grupy owadów dokonała się w dwóch etapach różniących się środowiskiem życia i sposobem odżywiania oraz, konsekwentnie, tendencjami ewolucyjnymi.

2. W pierwszym etapie (czasy "prehistoryczne"), od wyodrębnienia ze wspólnego pnia pluskwiaków równoskrzydłych (Karbon lub Perm) do pojawu roślin okrytozalążkowych (Jura) czerwce żyły w ściółce leśnej i odżywiały się różnymi płynami pobieranymi z powierzchni, jak i z żywych i obumarłych tkanek roślinnych.

3. W tym czasie czerwce uzyskały najbardziej charakterystyczne dla nich właściwości, które zdeterminowały również dalszą ich ewolucję. Nogi stały się organami grzebnymi (jeden pazurek, jednoczłonowa stopa, funkcjonalne połączenie stopy i goleni). Samice bezpowrotnie utraciły skrzydła, przyjmując postać larwalną. Samce skarlały, utraciły zdolność do odżywiania, stały się dwuskrzydłe i polimorficzne. Paurometaboliczne przeobrażenie uległo modyfikacji w ten sposób, że larwy żeńskie utraciły zalążki skrzydeł, a ostatnie stadia larwalne męskie przekształciły się w stadia spoczynkowe o dużych zawiązkach skrzydłowych. W tym czasie nastąpiła też pierwsza radiacja czerwców.

4. W drugim etapie ewolucji, od pojawu roślin okrytozalążkowych do dzisiaj, tendencje ewolucyjne radykalnie się zmieniły — czerwce stały się pasożytami roślin kwiatowych. Większość zaczęła się wspinać po roślinach, w związku z tym wykształciły się paluszki na stopie i pazurku jako organy zastępujące przylgi. Prawdopodobnie najpierw proces ten zaczął się u *Coccoidea*, dlatego padły one ofiarą pasożytniczych błonkówek. Każda z grup wypracowała swój własny system endosymbiotyczny, stąd symbioza u czerwców robi wrażenie polifiletycznej.

5. Przechodzenie do pasożytniczego trybu życia na roślinach kwiatowych było rozciągnięte w czasie; w rezultacie poziom specjalizacji jest bardzo różny w poszczególnych grupach czerwców, a niektóre z nich, np. *Ortheziidae*, prawdopodobnie kontynuują tryb życia przodków czerwców.

6. Zakres specjalizacji czerwców jako pasożytów roślin był poważnie ograniczony brakiem skrzydeł u samic i degeneracją samców; zostały one zmuszone do wyboru osiadłego trybu życia i w związku z tym wykształciły szereg skomplikowanych systemów obronnych. Systemy te pociągnęły za sobą daleko idącą modyfikację ciała samic, zmniejszenie wymiarów lub hypertrofię, rozwój licznych typów gruczołów skórnych i specjalnych urządzeń do wyrzucania spadzi, ale równocześnie powodowały dalszą utratę zdolności ruchowych. Degeneracja samców była bodźcem do wykształcenia wielu typów przekazywania genów i determinacji płci, z obojnactwem włącznie.

7. Nałożenie się na siebie przystosowań do życia na dnie lasu, w którym czerwce przebywały dłużej niż inne pluskwiaki równoskrzydłe, i przystosowań do pasożytnictwa na roślinach kwiatowych, zadecydowało o szczególnych cechach tej grupy owadów. Natomiast okoliczność, że znaczna część radiacji dokonała się jeszcze w pierwszym etapie ewolucji (na dnie lasu), i że poszczególne grupy przechodziły do nowego środowiska niezależnie i w różnym czasie, jest przyczyną dużej różnorodności wśród czerwców.

Powyższe stwierdzenia mają charakter hipotez, a celem pracy była próba ich potwierdzenia.

РЕЗЮМЕ

[Заглавие: Рассуждения о предистории червецов (*Homoptera, Coccinea*)]

1. Строение червецов, их образ жизни, развитие, размножение, эндосимбиоз детерминация пола и т. п. указывают на то, что филогенез этой группы насекомых прошел два этапа, отличающиеся средой обитания и способом питания, а также, последовательно, эволюционными тенденциями.

2. На первом этапе („доисторический" период) — от отделения от общего ствола рзвнокрылых хоботных (Карбон или Перм) до появления покрытосеменных растений (Юра) — червецы жили в лесной подстилке и питались различными жидкостями, поглощаемыми как с поверхности, так и из живых и мертвых растительных тканей.

3. В этот период червецы приобрели наиболее характерные для них особенности, которые предопределили также их дальнейшее эволюционное развитие. Ноги преврзтились в органы, приспособленные для разгребания (один коготок, одночленистая стопа, функциональное соединение стопы и голени). Самки безвозвратно утратили крылья, принимая вид личинки. Самцы измельчали, утратили способность питаться, сделались двукрылыми и полиморфными. Наступила модификация паурометаболии, заключающаяся в том, что женские личинки утратили зачатки крыльев, а последние мужские личиночные стадии превратились в формы в состоянии покоя, с большими зачатками крыльев. В это время произошла также первая радиация червецов.

4. На втором этапе эволюции — от появления покрытосеменных растений до настоящего времени — эволюционные тенденции изменились коренным образом — червецы превратились в паразитов цветковых растений. Большинство начало взбираться по растениям, в связи с чем сформировались пальчики на стопе и коготки как органы заменяющие присоски. По-видимому, этот процесс начался сначала у *Coccoidea*, поэтому они сделались жертвами паразитических двукрылых. Каждая группа выработала свою собственную систему эндосимбиоза. В связи с этим симбиоз у червецов производит впечатление полифилетического.

5. Переход к паразитическому образу жизни на цветковых растениях был растянут во времени; в результате этого уровень специализации весьма различен в отдельных группах червецов. А у некоторых из них, например, *Ortheziidae* образ жизни не изменился, видимо, со времени их предков.

6. Пределы специализации червецов как паразитов растений были значительно ограничены отсутствием крыльев у самок и дегенерацией самцов; они вынуждены были избрать оседлый образ жизни и в связи с этим выработать ряд сложных оборонительных систем. Системы эти повлекли за собой далеко идущие изменения в строении тела самок, уменьшение или чрезмерное увеличение размеров, развитие многочисленных типов кожных желез и специальных приспособлений для выпрыскивания пади, но одновременно вели к дальнейшей потере способности к передвижению. Дегенерация самцов стимулировала формирование многих типов передачи генов и детерминации пола, включая гермофродитизм.

7. Факт, что наложились на себе приспособления к жизни на дне леса, где червецы пребывали дольше чем иные равнокрылые хоботные, и приспособления к паразитическому образу жизни на цветковых растениях, обусловил особый характер признаков этой группы насекомых. В то время, как факт, что значительная часть радиации имела место еще на первом этапе эволюции (на дне леса) и что отдельные группы переходили в новую среду независимо друг от друга и в различное время является причиной значительного разнообразия среди червецов.

Изложенные выше тезисы имеют гипотетический характер, а целью работы была попытка их подтверждения.