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THE MORPHOLOGY, METAMORPHOSIS, AND LIFE-CYCLE OF THE SCALE INSECT QUADRASPIDIOTUS GIGAS (THIEM ET GERNECK) (HOMOPTERA, COCCOIDEA, DIASPIDIDAE)

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1. Introduction

There are many papers in the Czechoslovak as well as foreign literature investigating the scale insects (Coccoidea) especially their females. The oldest work are limited to descriptions of new species, re-described many times and, as a rule, inaccurately. Too little attention is paid to the Coccoid biology, their relations to host plants, their development cycles, individual developing stages, etc. This applies also to the family Diaspididae. It was Ferris (1937—1942) who investigated the North-American species of Diaspididae on a modern scale in his "Atlas of the Scale Insect of North America"; Balachowsky (1948—1954) published a monograph of palearctic species.

In our country it was Sulc (1894—1952) who studied the Coccoids for many years, and who was one of the pioneers in the research of these insects in Central Europe. Sulc considered it important to study in detail every individual species living in our country, to pay attention to the morphology of all developing stages, their biology, their relation to host plants, parasitation, geographical distribution, etc. In this way he elaborated the descriptions of a number of species. His followers, Zahradník, (1952) made a monograph of the families Diaspididae and Pseudococcidae, and Řeháček, (1960) investigated the family Coccidae.

Papers on male morphology are rare in literature as compared with the number of works on the female scale insects. On rare occasions only the males of some species are mentioned. It was Šulc, (1931, 1943, 1944, 1945, 1953), Jancke, (1955), and Buščik, (1958) who investigated them in greater detail.

The following study on *Quadraspidiotus gigas* is a continuation of the classical work of Šulc.

It is only recently *Q. gigas* has been described, (1934), and up to now, it has been little known although in warmer parts of the palearctic region it belongs to the most frequent species of scale insects living on poplars and willows. Likewise, it has a considerable importance in forestry. In our country, it lives most often on poplars which are now being planted in great numbers as fast growing and easily cultivated woody plants. With

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the problem of cultivating these woody plants a need arose to carry out detailed studies of diseases and parasites living on poplars.

In literature *Q. gigas* has been described as a little known species (Balachowsky, 1948, Bachmann, 1952; Zahradník, 1952; Kosztarab, 1955). Only the morphology of the female, and the IInd female larva are given by Buščik, (1958).

I feel particularly indebted to Dr. J. Zahradník for his valuable advice, and help in my work, for lending me literature otherwise inaccessible, and some material. Further, I thank Ing. R. Leontovyč for rich materials from Slovakia, to Dr. A. Hoffer for preliminary determination of some scale-insect parasites, and to the graduate biologist P. Štys for determination of bugs. It is a pleasant duty to me to thank, likewise, workers from abroad such as Dr. F. Bachmann and Dr. M. Kosztarab for sending some materials, and for valuable remarks on the occurrence of *Q. gigas* in Switzerland, Yugoslavia and Hungary. To Professor Dr. E. Bartoš, and Dr. M. Kunst I give my thanks for their interest and help during my work.

2. Material and Methods

The material of the scale insect $Quadraspidiotus\ gigas$ Thiem & Gerneck was sampled from various places in Czechoslovakia, from October 1952 till 1959. The samplings were carried out regularly every fortnight, occasionally even every week during the spring and summer months in years 1953—1956, in the village Jiřina near Čelákovice near the ferry, on the river Elbe (Čelákovice a), on $Populus\ canadensis$ Moench., and on $Populus\ nigra\ L$. (Čelákovice b). The same intervals were kept in sampling at Sedlčánky near the ferry on $Populus\ alba\ L$. In later years, materials were sampled from these localities during the vegetation period once-amonth.

During the years 1955-1959 samplings were carried out in Prague at Žižkov near goods station (Praha d) on Populus canescens, and in the vicinity of National Museum, Washington Street, on American poplar hybrids (Praha a), regularly once-a-month, in summer every fortnight, or even every week. During the vegetation period of 1959, samplings were carried out in Prague-Podolí, near the Yellow Baths (Praha b) on American poplar hybrids.

For comparison, materials were used from Slovakia, Germany (Dresden, Leipzig, own samplings), from Hungary (lgt. M. Kosztarab), from Yugoslavia (lgt. J. Zahradník, F. Bachmann), from Switzerland (lgt. F. Bachmann).

The material was fixed by the usual method, i. e. in 75—80% alcohol with a few drops of glycerine. Part of material with pieces of bark was put into dry glass tubes closed with cotton-wool stoppers. In these tubes I managed to follow the hatching of males, and parasitic Hymenopters.

Q. gigas was cultivated also in the laboratory on poplar branches placed in water or Knapp nutrient solution, or on rooted willow twigs (in flower pots). The Ist larvae which were transferred to these willow

branches always settled well on the host plant, and changed into the IInd larvae. However, the willow branches were mass-attacked by Tetranychid mites in the autumn, and dried-off.

Further, I tried to transfer the poplar scale *Q. gigas* from poplars to other host plants, and from climatically convenient places to places less convenient so that I could prove my hypothesis that it is a warm-loving species not able to withstand inconvenient climatic conditions. I transferred the Ist larvae, or adult females shortly before egg-laying.

Pieces of bark provided with the desired stages of the insects were either tied by means of a thread to the trunk and stronger branches of the host plant, or fixed with fine nails. So, e.g. the *Q. gigas* from poplars in Čelákovice was replanted to *Tilia cordata* Mill., *Ulmus scabra* Mill., *Fraxinus excelsior* L., *Salix* sp. in the courtyard of the Faculty of Natural Science, in Prague. In all cases, the scale insects settled to their new host plants, and underwent the whole developing cycle. Only from *Ulmus*, it disappeared in 1961. On *Fraxinus* its occurrence was negligible after two years, *Chionaspis salicis* prevailing; in 1961, *Q. gigas* multiplied very much, again, and *Chionaspis salicis* is now in a minority. Not much experience could be gained concerning willows as these were felled after two years.

Individuals from Prague and Central Elbe regions were transferred to Blatná, to the environment of the hydrobiological station, to *Populus tremula* L., at the Žoldánka pond and to a *Populus tremula* L. on the Smyslov pond embankment, to four trees. In all cases, the animals settled on the poplars, developed into the IInd larvae but died during winter.

At Blatná, in an open down country, the climatic conditions are rougher than in Prague. 1)

This experiment, and the fact that neither myself nor Zahradník succeeded in finding *Q. gigas* in colder parts of Czechoslovakia confirm its being a warm-loving species.

I also attempted to transfer *Q. gigas* to different ornamental indoorplants cultivated in the laboratory. Only the Ist larvae formed scales on Ficus carica, the IInd larvae did not develop at all, on Sansivierii or Chlorophyll they did not settle at all. Similar observations were carried out by Vasseur and Schvester, (1957), with *Q. perniciosus* Comst., in France.

Microscopic specimens were mounted into Swann liquid, glycerine, or glycerine-gelatine (Dušková, 1953). A successful attempt was made with a clearing mixture of polyvinyl alcohol, according to an advice by Dr. Kramář. Staining with basic fuchsine, and covering in Canada balsam provides the best preparation of specimens, (Zahradník and Mikula, 1962). For a quick orientation, however, and for inspecting such extensive material, this procedure was too slow, therefore, most of the investigated material was mounted in Swann liquid.

¹⁾ In Prague (Klementinum), the average yearly temperature varied in 1955—1959 from 8,2—10,2 Centigrades, the five-year average being 9,4 Centigrades; in Elbe region (Lysá nad Labem) the yearly averages within the years of 1953—1956 were 7,2 to 9,2 Centrigrade, the four-year average being 8,1 Centigrade; in Blatná region (Vráž u Písku) the yearly averages within the years 1955—1959 counted 6,1—8,0 Centigrade, the five-year average being 7,0 Centigrade.

All drawings of Q. qiqas are originals; they were drawn by means of the Abbé drawing device using a phase contrast microscope.

3. Host plants

The scale insect Q. gigas prefers host plants of the Salix (willow) family. It occurs frequently on poplars in warm protected places in parks, alleys, woods, etc., often in thick layers, and forming whole crusts. It occupies, particularly, the trunks with smooth bark, and thicker branches less often thin twigs. Only exceptionally, it occupies the leaf petioles. In that case, it dies when the leaves fall off.

I myself found this insect mostly on poplars: Populus alba L., P. canescens SM., P. canadensis Moench., P. pyramidalis Rozier, P. nigra L., P. tremula L., Populus sp. and on all sorts of American popular hybrids. Recently, I received a consignment from Slovakia of the scale insect Q. gigas from P. deltoides Marsh., cv. monilifera and P. euramericana (Dodet) Guinier, cv. robusta (lgt. R. Leontovyč).

On willows, I found Q. qiqas only at Přerov on the Elbe, near Karasí tůně and in Sedlčánky, near the stream Vejmola. These individuals were,

however, heavily infested with parasites.

In literature, it is reported from willows (Thiem & Gerneck, 1934b, Balachowsky, 1948; Bachmann, 1952-53, Tereznikova, 1957 on Salix sp., S. acutifolia Wild., S. daphnoides Vill., S. fragilis L., S. pedicellata, S. viminalis L., S. alba L., on a lime-tree (Tilia) Čorbadžijev, on Tilia parvifolia Ehr.), and on a birch-tree (Tereznikova — Betula sp.). See the Survey of Host Plants!

The Survey of Host Plants

Host plant:

Salicaceae: Populus alba L.

P. canescens Sm. P. pyramidalis Rozier

P. canadensis Moench.

P. tremula L.

P. italica (Duroi) Moench.

P. nigra L.

P. nigra var. italica (Münch) Koehne

P. trichocarpa Torrez e Graz

P. berolinensis Dipp.

P. euramericana (Dodet) Guinier cv. robusta

P. deltoides Marsh. cv. monilifera

Populus sp.

the hybrids of American poplars Salix acutifolia Wild. S. daphnoides Vill.

The authors according to whom Q. gigas has been gathered on these plants:

Balachowsky (1948)*, Zahradník (1952)*, Kosztarab (1955)*, Tereznikova (1957)*, Lelláková

Lelláková

Balachowsky (1948)*, Bachmann (1952-1953)*, Tereznikova (1957)*, Lelláková

Lelláková

Zahradník (1952)*, Bachmann (l. c.)*,

Tereznikova (1959 a, b)*, Lelláková Balachowsky (1948)*, Kosztarab (1955)*

Kosztarab, Lelláková

Kosztarab Kosztarab

Kosztarab

Leontovyč Leontovyč

Balachowsky (l. c.)*, Borchsenius (1935, 1950)*, Zahradník, Tereznikova (1959)*, Lelláková

Lelláková

Thiem et Gerneck (1934b)*

Thiem et Gerneck (1934b)*

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S. fragilis L.
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Tiliaceae: Tilia parvifolia Ehr.

Betulaceae: Betula sp.

Thiem et Gerneck (l. c.)*, Tereznikova [1957]*

Balachowsky (l. c.)*

Bachmann et Geier [1950]*

Kosztarab

Thiem et Gerneck (l. c.)*, Bachmann et Geier (1950)*, Kosztarab, Tereznikova

(1959)*, Lelláková Balachowsky (l. c.)*

Tereznikova (1957)*

Names * marked are according to references given in literature; the other data are according to my own samplings or packets of material.

4. Geographical distribution

Q. qiqas is a warm-loving species occurring in warm, protected places of the palearctic region. It lives on poplars and willows growing on sandy ground and along the rivers and streams in insolated biotopes with a favourable temperature and humidity.

Bohemia: Prague and environs; Beroun, Populus alba L.; Pilsen, Populus sp.; Poděbrady, Populus tremula L. (Zahradník, 1952), the whole Elbe region; Čelákovice, Sedlčánky, Byšičky, Lysá nad Labem, Přerov nad Labem, on different species of poplars (Populus alba L., P. canescens SM., P. pyramidalis Rozier, P. canadensis Moench., P. tremula L., P. nigra L., Populus sp.); Nehvizdy, P. alba L.; Řečany nad Labem, Populus sp.; Selmice near Kladruby, P. canescens SM.; Kladruby, Populus sp.

Moravia: Břeclav (lgt. Zahradník), Populus sp.

Slovakia: Bratislava and environs on Populus alba L., P. canescens SM., Salix sp. (lgt. Huba); Štúrovo (lgt. Zahradník); Komárno, at the bridge across the river Váh (lgt. Leontovyč), Populus euramericana (Dodet) Guinier cv. robusta, P. deltoides Marsh. cv. monilifera.

Germany: Dresden, Leipzig (lgt. Lelláková), Populus sp.; Naumburg a. d. Saale, Berlin [Thiem et Gerneck (1934b)], Salix sp., S. acutifolia, S. daphnoides, S. fragilis; Erlangen and environments, München, Nord and Südbayern, Hessen, Thüringen (Schmutterer 1959).

Holland: (Schmutterer 1959).

Switzerland: Zurich, Salix sp., Adliswil (Zurich), Populus sp.; Loco (Tessin), Salix sp.; Châteauneuf (Wallis), Salix sp. (viminalis?) (Bachmann et Geier 1950).

France: Quemmigny (Côte d'Or), Populus pyramidalis (Balachowsky 1948).

Italy: Chiavari (Genes), Populus alba; Fiorne, P. (Chermotheca) italica (Balachowsky l. c.).

Yugoslavia: Palič near Subotica, Salix sp., Populus sp.; Bajmok near Subotica, P. sp. (Bachmann 1952—1953); Vipolže, Salix sp., Skoplje, Bitolj (lgt. Zahradník).

Bulgaria: Sofia, Tilia parvifolia (Balachowsky l. c.).

Hungary: all the country except the highlands (Kosztarab).

Soviet Union: USSR; Kanivski-reservation, Populus alba L., P. pyramidalis Rozier, Betula sp., Salix fragilis L. (Tereznikova 1957); Caucasus, Populus sp. (Borchsenius 1950). Turkey: Anatolia, Populus sp. (Balachowsky l. c.).

Algeria: Arba (Mitidja), Salix pedicellata (Balachowsky l. c.).

5. The economic importance

In cases of strong infestations Q. gigas forms thick crusts on poplar barks and causes weakening, drying of parts, or of whole plants, especially of young trees. It forms special hollows in the infested places (see photo. no. 4) the same as e. g. Epidiaspis betulae, various species of genus Astero-

S. pedicellata

S. viminalis L.

S. alba L. Salix sp.

lecanium and others, and thus, it makes the wood worthless for industry. Baudyš (1951) who recorded similar formations on oaks and hawkweeds caused by different species of the genus *Asterolecanium*, scale-insects, etc. indicates them as galls—(Gallen)—coccoideocecidia (zoocecidia).

Q. gigas spread particularly strongly on weakened trees (insufficient moisture, heavy frosts, unsuitable stand, infestation by plant or animal destructive organisms such as mycoid necroses—Dothichiza populnea Sacc., Cytospora chrysosperma Fr., various beetles, caterpillars of some Lepidoptera, etc.). Together with these factors, it causes degeneration, and subsequent death of the trees. In particular young trees die-off, especially at the nursery stage. An 11 year old poplar stand of the species Populus deltoides Marsh. and P. euramericana Dodet in Southern Slovakia (Komárno, near a bridge crossing the river Váh) was attacked in 1961. A vast area of about 6 ha. was destroyed there. Balachowsky, (1948) states that Q. gigas infested and destroyed in Southern France stands of young poplars in the wind-breaks. Also Kosztarab stated in Hungary many young poplars were destroyed owing to strong infestations.

From the economic point of view poplars are very important as one of the fastest growing woods (poplar, willow, alder, birch). It is necessary to renew as fast as possible quickly growing trees plundered during the second world war. Therefore trees are now being planted which produce already in 20 to 30 years felling timber of considerable dimensions. A vast cultivation of poplars in avenues, woods, plantations and wind-breaks is being introduced which can be carried out in lowlands as well as in higher parts up to 400 to 500 m. above sea level.

6. Morphology

The Scale of the Female

The scale of the adult female (Fig 1 A) is roughly round, sometimes slightly oval, comparatively flat. As a rule, it is light to dark grey, dull. However, on some American poplar hybrids very light scales can be found, buff to light brown. The colour depends also on the foundation and the age of the scale. The lightest part is the scale margin. The scale carries 2 orange-yellow larval exuvia placed slightly eccentrically, especially where $Q.\ gigas$ forms thick crusts on the bark. Provided the females are present in small numbers on host plants, isolated from each another, the scales may be round and the exuvia placed centrally.

The first larval exuvia is round or mildly pear-shaped, convex, of about 580 μ in diameter. The second pear-shaped larval exuvia is placed underneath it. Its average length is 1200 μ , the width approximately 1100 μ . The scale is highest in the place of the Ist larval exuvia. The scales contain concentrically alternating thicker and thinner layers. The whole scale becomes gradually lower towards the margin which is entirely flat.

The average size of the female scale from the 11 investigated localities varies from 2—2.6 mm. (min. 1.8 mm., max. 2.8 mm.). In individuals from Yugoslavia (Skoplje, 12. 8. 1958) on *Populus* sp., (lgt. Zahradník), the female scale reaches a size of as much as 2.9 mm.

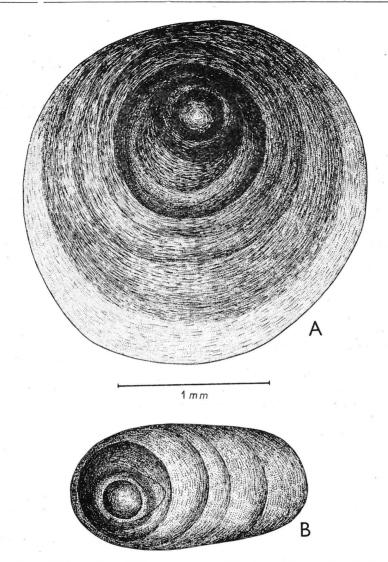


Fig. 1: Quadraspidiotus gigas (Thiem et Gerneck): A — The Scale of the Female; B — The Scale of the Male

The ventral scale is greyish white, thin, foil-shaped, after shedding the dorsal scale it remains sticking to the host plant.

The Scale of the Male

is prolonged, with parallel lateral margins at front and rear, it is rounded (Fig. 1B), 1.8—2 mm. long in diameter. It contains but one orange-yellow larval exuvia of pear or round shape, placed usually accross

the scale. Similarly like in other Diaspidids, the IInd male larval exuvia is pushed back under the scale after molting, and it is not further used for building the scale. The scale colour is light to dark grey. Across the scale and around the larval exuvia thicker and thinner layers are concentrically placed increasing gradually towards the lower margin. The ventral scale is greyish white and, likewise, it remains on the foundation after the shedding of the dorsal scale.

The Female

The female (Fig. 2 A) is pear-shaped with a wide head and, especially, the thoracic part, where it reaches the maximum width. Backwards, it becomes narrower, the narrowest part being the pygidium. The body is heavily dorso-ventrally flattened, the dorsal part is mildly convex.

In *Q. gigas* a very wide individual variability was ascertained according to which the females may be classed into three main groups. There are intermediate types among them. There is a striking difference especially in the shapes of the first and third lobes, in the numbers of perivulvar discs, the total size, the numbers of macropores, etc. This variability will be further mentioned in a special paragraph on morphology.

The length and width of the females from various localities varies considerably. The average length ranges from 1.1 mm. to 1.6 mm., the average width from 0.96 mm. to 1.4 mm. The largest females in my material were from Yugoslavia (lgt. Bachmann, Zahradník); they reached a maximum length of 2.1 mm., a maximum width of 1.7 mm. The smallest females were from Prague, of a maximum length of 1.3 mm. and a maximum width of 1.1 mm. The ratio of length and width is approximately 1:1 to 1:1.2 in all individuals.

The female is greenish yellow or lemon yellow, in some localities (Prague b, Čelákovice a), yellow to yellowish-orange, the pygidium being darker. At the time of egg-lying the ventral part of the pygidium is covered with a white waxy powder, an excretion of the perivulvar glands.

The antenna (Fig. 2B) is cone-shaped with three higher and one lower protuberance. From the lower protuberance a long, mildly curved seta grows.

Piercing and sucking mouth parts are the same as in other Diaspidids.

Pro-, meso- and metathorax are firmly fused and separated only by shallow sutures. The pro- and mesothorax are each provided with a pair of spiracles (Fig. 2 C).

The metathorax is followed by three praepygidial segments, and a sharply separated pygidium formed by the fusing of five abdominal segments.

The pygidium (Fig. 3, 4) bears the following distinguishing characters: the lobes (L_1 , L_2 , L_3), plates (p_1 , p_2 , p_3), perivulvar discs, macropores, micropores, etc. On the ventral part at both sides of the vulva there are 2 strong chitinous stripes—the paravulvar apophyses. The micropores are also placed on the ventral side. They start usually at the third pygidial

segment between the 2nd and 3rd seta, however, in solitary cases they can be found also on the praepygidium, and on the thorax.

The distribution of spines on the ventral part of the pygidium: one

each in the centre of the base, and on the upper ends of the chitinous wing

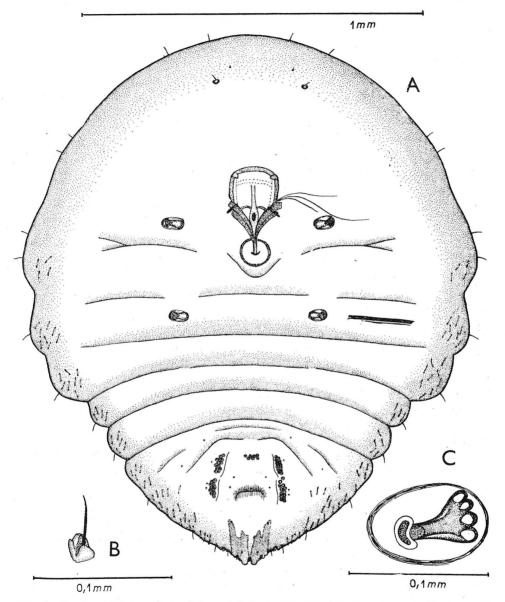


Fig. 2: Quadraspidiotus gigas (Thiem et Gerneck), the female: A — ventral aspect; B — antenna; C — the anterior spiracle

processes between the 2nd and 3rd marginal seta, and above the 3rd marginal seta; two each—laterally above the vulva, on the outer side of the lower groups of the perivulvar discs; one each—at the upper groups of perivulvar discs, on the 4th pygidial segment, between the 4th and 5th segment of the pygidium. Approximately through the centre of the dorsal part of the pygidium runs a dorsopygidial apophysis—a heavily sclerotized part which corresponds to the paravulvar apophysis of the ventral part. The anal opening is placed approximately 53—62 μ from the caudal margin of the pygidium, of the dorsal part.

The number and distribution of the marginal seta is the same as in other species of the genus Quadraspidiotus, i. e. on the dorsal part circumference there are 32 setae, and on the ventral one there are two less.

Lobes and Plates (Fig. 5, 6, 7).

Three pairs of lobes are distinctly developed. The largest ones are L_1 ; L_2 are smaller; the smallest size attain L_3 .

The plates are tooth or finger-like branched. 2 plates grow out between L_1 (p_1), between L_1 and L_2 there are 2 plates at each side (p_2), and between L_2 and L_3 there are 2—3 plates (p_3). The lobe shape varies considerably in Q. gigas. 3 types of lobes may be distinguished with a number of intermediates.

In my material typical L_1 are developed, lobes large and wide, slightly separating, widely rounded at the front, with a deep notch at the rear. On the inner side they are always without notch. Some females have L_1 not separating. The inner margins being parallel, wide, rounded, without any outer deep notch. Sometimes, this notch is weakly marked. Often, individuals can be found with one L_1 lobe without notch, and the other one notched, even if not very deeply. Extreme cases are females where L_1 is strongly separated with the outer notch shallow, wide and protruding. It is interesting that in most cases, on the inner side of L_1 a notch is indicated even if comparatively small.

Between L_1 2 strong spiny plates are developed. Sometimes, they form 2 shallow teeth at the end. The plates are short, they reach to $\frac{1}{2}$ — $\frac{2}{3}$ of L_1 .

 L_2 stet shifted upwards, so that stet reaches approximately to one half of L_1 . Stet more or less rounded, on stet outer side being provided with a notch which is usually considerably deep. If shallow, there are two of them. Between L_1 and L_2 2 plates are developed as a rule. The inner one is usually much narrower than the outer one, and in most cases, it is spine-shaped. In a few cases it branches terminally into 2 teeth. The outer plate is always stouter, wider and terminally, (sometimes even slightly laterally) it forms 2-3 sharp teeth. The length of the plates stightly exceeds the top of the lobes L_2 and reaches to the outer notch L_1 . Sometimes, only the outer plate is developed, in which case it is wider and stouter by the width of the inner plate. Two long chitinous wing processes protrude from the first and second lobes towards the centre.

 L_3 vary a great deal. They are the smallest ones but they are always distinctly developed. In the basic shape they protrude into a sharp process in the centre. In females which have their L_1 unnotched on the outer side, L_3 are usually just widely rounded. If a process is developed in the centre, then it is very obtuse or wide, and in that case, an inner notch is formed on the inner side; the outer part is larger, and the whole lobe possesses a two-lobed appearance. In females with separating L_1 , L_3 protrudes into a small sharp process but the whole lobe is smaller and flatter than in the basic type, and it runs off sidewards.

Between L_2 and L_3 3 plates are usually developed. The inner plate is always the smallest, shortest and, as a rule, it is only spine-shaped and, in extreme cases, it can branch into two teeth. Sometimes it is not at all developed. The central plate branches terminally into two teeth only; provided the inner plate is not developed the central one is stouter and more branched. Sometimes, there is a tendency to a lateral branching. The outer plate is the largest and stoutest, wide at the base, narrowing towards the apex, and branching into 3—5 (3—6) teeth. Rather often it branches in a finger-like fashion, and laterally. The width of all plates varies. Outwards from L_3 the plates are not usually developed; only wing extentions of the macroducts occur there in the number of 3—4 (2—6).

All lobes are separated from each other by intersegmental crypts bordered by marginal paraphyses.

The notch width between L_1 varies strongly. The notch between L_1 and L_2 is equal in its width to approximately half of the L_1 width; the notch between L_2 and L_3 is the widest one, and is approximately as wide as the width of L_1 .

Macroducts

The macroducts of the pygidium are arranged in four groups (I-IV). Between L_1 opens 1, exceptionately 2, macroducts. Thiem & Gerneck (1934a) consider the position and height of pores between L_1 regarding the anus as constant. That statement I could not confirm, for the position of the glands is different not only in females from various localities but also in females from the same place. Macroducts open either at the lower margin in the centre or at the upper margin of the anus.

A group of macroducts of an average number of 6—7 open into the intersegmental crypt between L_1 and L_2 and above it. The slightest variability was found in the specimens from Poděbrady, 5—8 macroducts, the highest from Dresden, 4—11 macroducts. Beside the Ist group of macroducts there is sometimes one, rarely two macroducts. Exceptionately, there can be more of them but in that case there is a smaller number of macroducts in the IInd group. Thus, it is evident, they arose from being split from the IInd row.

The IInd row of 11-16 macroducts open into the further intersegmental crypt between L_2 and L_3 and above it. While the number of macroducts in the first group is comparatively even, in the IInd group it varies

much more. On the average, it was the lowest in females from Poděbrady 11 (7-14), the highest in females from Prague 16 (7-25).

On the third pygidial segment the IIIrd row of macroducts is placed, the most numerous one. The average values range between 14-20 macroducts.

On the second pygidial segment the IVth group of macroducts is placed half of which possess pores already above the dorsopygidial apophysis. The average number of macroducts ranges between 10 and 16. The number of macroducts in this group represents a very important determination factor by which Q. gigas is distinguished from Q. ostreaeformis (Curtis) which, in this row possesses only 3—5 macroducts.

Besides these 4 main groups of macroducts, sometimes there are 1 or 2 macroducts between the 1st and IInd group, 2-3 (1-6) between the IInd and IIIrd group, and between the IIIrd and IVth row 5-7 (2-13) macroducts. Behind the IVth group there are, on the average 5-7 macroducts.

The total number of macroducts on the female pygidium varies between 92 and 135.

Regarding the measurements carried out by Thiem & Gerneck (1934) they show the same average data and the variation range in individual groups of macroducts in Dresden females. From other localities the number of macroducts in the individual groups indicates a greater variation range.

Perivulvar discs.

Five groups of perivulvar discs are distributed in an arch around the vulva. The total number of perivulvar discs in all five, as well as in individual groups, indicates, again, in females from various localities but also in females from the same locality a considerable variation range. (Fig. 4, 5).

Bachmann (1953) states that there is only a small variation in the number of the central perivulvar pores in Quadraspidiotus piri and Q. schneideri [mařani], and that this group is fairly stable. In the species Q. qigas, however, this group indicates approximately the same variation range as the other four groups. The average total number of all 5 groups is 76 (54-98), in the central group 10 (5-15), in the upper left 18 (10-25), in the lower left 14 (10-20), in the upper right almost 19 (12-25), in the lower right 15 (9-24), The greatest variation range is shown by the females from Dresden (25-108). The smallest number of perivulvar discs is in females from Poděbrady and Čelákovice, i. e. a total of 49 (37—59). In the central group there are 2.6 (0—8), in the upper left group 11 (8—18), in the upper right group 11 (10—14), in the lower left 11 (9-13), and in the lower right group not quite 11 (0-13).

The two upper groups show practically the same averages and variation range in females from individual localites. However, the females from various localities differ. Similar are the conditions in the two lower groups as far as the same localities are concerned. The average values, however,

are somewhat lower.

Compared with the data by Thiem & Gerneck (l. c.) my material shows a wider variation range. These authors state the lowest values of the total number of perivulvar discs, 61 discs, the highest one 100. In my material the lowest limit is 36 discs. The absolutely highest number of discs, 108, was found in females from Dresden, while their lower limit was 52 discs.

It is interesting to note that in the material from M. Kosztarab from Hungary I ascertained an average number of perivulvar discs in females from *Salix alba* 2—3 discs more than in females from Populus italica. The same is true of the number of macroducts where the average total number of macroducts on the pygidium of adult females from *Salix alba* counts 15 discs more than in females from *Populus italica*.

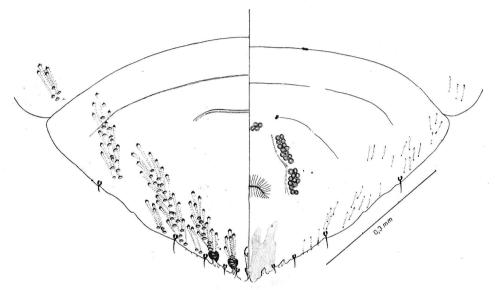


Fig. 3: Quadraspidiotus gigas (Thiem et Gerneck), the female: pygidium — left ventral surface, right dorsal surface (Prague a)

The distance of the anus and vulva from the pygidium margin

It was Thiem & Gerneck (1934) who first pointed out the systematic importance of the distance of anus and vulva from the pygidium margin. These measurements, however, can only be carried out on young females not deformed by egg laying. As a base for measuring the distance of anus the distance of base p_1 from the upper anus border is taken; the distance of the vulva is measured from base p_1 to the vulva slit.

In my material the distances of anus from the bases p_1 (p_1 —A) in the Q. gigas females of various localities are very similar. The maximum average values were ascertained in scale insects from Hungary (Pécz), i. e. $62~\mu$ at a variation range of 56— $68~\mu$, the minimum values in the specimens from Bratislava, $53~\mu$ at a variation range of 46— $63~\mu$. Even these

extreme values, however, differ only 9 μ . For most of the localities also the variation range is similar, i. e. in the range of 51—66 μ .

The distance of the vulva from the pygidium margin (p_1-V) is approximately three times longer but constant in the same way. The extreme values of their averages 148—191 μ and 127—173 μ differ only 26 μ . The distance of the vulva from the base p_1 as well as the distance of vulva from the pygidium margin is thus relatively the same.

The females from individual localities differ in their total size, number of perivulvar discs, etc. although the same species are taken from host plants growing closely together, and the females sampled at the same time. It seems also that other factors are here involved such as the degree of infestation of the scale insects, genetical factors, etc.

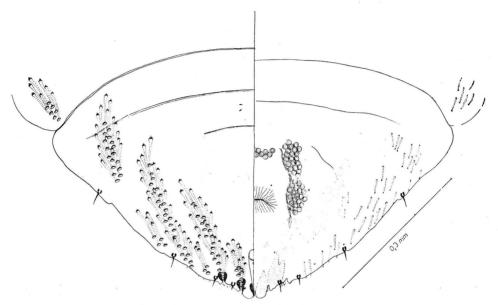


Fig. 4: Quadraspidiotus gigas (Thiem et Gerneck), the female: pygidium — left ventral surface, right dorsal surface (Prague b)

The Male

The male of the species Q. gigas (Fig. 12 D, E) is of an aspidoid type. The total length and width of the body, the stylus length etc., varies in individual specimens the same as in females.

Measurements were carried out on males from 4 localities. Although I had abundant material, it was not possible to measure all the males as they deform easily in prepared specimens, and the data thus received would not correspond to reality.

The males reach an average length of about 1000 μ (929—1032 μ). The width of the abdomen varies on the average between 217—306 μ , the stylus length ranges around 300 μ (305—332 μ).

The body is divided into head, thorax and abdomen. The antennae have 10 segments (Fig. 12 A). The average length of an antenna is somewhat over 600μ ($609-643 \mu$). The lengths and widths of individual segments vary slightly. The average lengths of individual segments in μ : 1st (basic) segment 29-33, bears no setae; 2nd segment 20.4-22, bears 3-4 setae; 3rd segment 66-71.6, bears 9-12 setae; 4th segment 69-83,

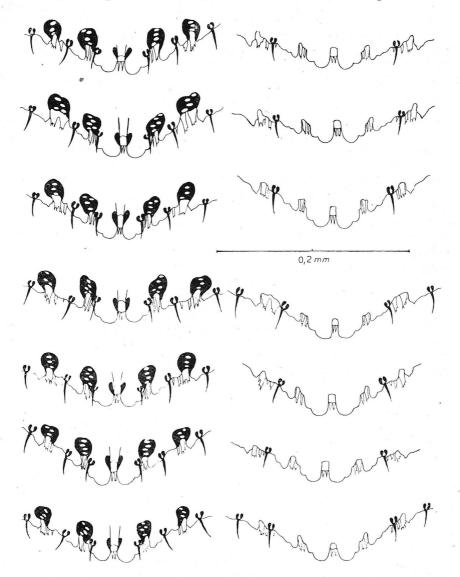


Fig. 5: Quadraspidiotus gigas (Thiem et Gerneck), the female: variability in the form of the lobes and plates of pygidium (Poděbrady)

^{40 –} Sborník entomologický

bears 9—11 setae; 5th segment 74—88, bears 9—11 setae; 6th segment 75—87, bears 12—14 setae; 7th segment 76.5—84, bears 13—15 setae (this segment is always the one most covered with setae); 8th segment 62.5—68, bears 11—13 setae; 9th segment 60—71.4, bears 9—12 setae; 10th segment 61—62, bears 11—13 setae; of these 2 seate in the centre of the segment are approximately twice as long as the other setae, thinner, and club-shaped at the apex (sensory function). The segment is terminates with a strong seta, somewhat longer than other setae (but shorter than the 2 above mentioned ones), also with a club-shaped end. The setae of the antenna exceed slightly in length the width of the segments. The most frequent of the first segment is 30.6; of the 2nd segment 20.4, 3rd segment 71.4, 5th and 6th segment 86.7 (not so significant), 9th segment 61.2 μ .

The width of the 2nd antennal segment is most often 30.6 μ , 3rd segment 25.5, or 30.6 μ . The ratio of the width and length of the 3rd segment is 1:2—3.5. In literature, the ratio of the length and width of the 2nd segment is never given. I ascertained, however, that all values of the 2nd segment are more stable than those of the 3rd segment. The ratio of the width and length of the 2nd segment is 1:1.3—1.7, (most frequently 1:1.5). The second segment forms also a typical structure unlike the other segments. (Fig. 12 B). In the upper half of the segment there are 4 ribs, joined together by anastomoses, so that this part has a roughly meshed appearance. Similar structures on this segment can be found in males of other families.

Apart from the first two, the antennal segments are prolonged, stout, the eighth and ninth segments possess more convex margins, the tenth segment is spindle shaped, prolonged terminally into a short process.

Two pairs of eyes are developed. The first pair is placed in front at both sides of the dorsal part of the head, the second pair is in the middle on the ventral side of the head, near each other. The diameter of the lower eyes is most often 29.9 μ . Two pairs of long setae form an arch over the ventral eyes. They are roughly as long or slightly longer than the diameter of these eyes. The ratio of the eye diameter to the length of setae is 1:1-1.3.

On the ventral side of the head the eye apophysis is placed reaching to 1/2 to 2/3 of the ventral eyes, sometimes right to the upper border. The side arches of the eye apophysis extend, on the outer side to 2/3 of the ventral eyes and are closely connected to them.

The inter-antennal band (Fig. $13\,\mathrm{C}$) is comparatively narrow and bears usually 4-5 setae, the lower one of which is slightly longer than the upper ones.

On the dorsal part in the middle of the head there is a sclerotic area; its basal part is shallowly convex, towards the upper head border (Fig. 13 A, B), sometimes it forms 2 protuberances. The fork branches are well distinguishable on the whole and are, in their basal parts on the outer side, hemisphere shaped. Their upper ends reach to the upper part of the inner border of the dorsal eyes, eventually right to the basal antennal

segment. Each of the sclerotic area branches bear on their inner side one seta, the upper head margin between the antennae, at the sides of the apex seta of the interantennal band, carry one seta on each side.

The thorax, especially its central part—the mesothorax, is very strongly developed. Prothorax is weak, flat, and on its ventral part, under the lateral sclerites, there is the first pair of legs.

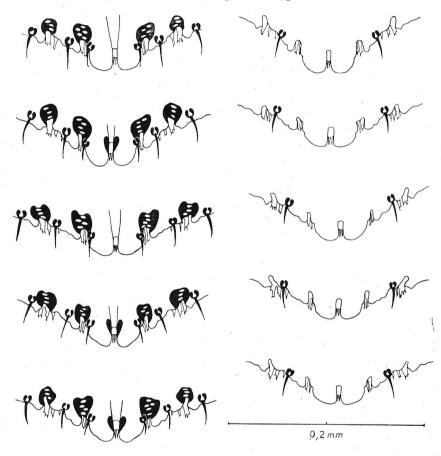


Fig. 6: Quadraspidiotus gigas (Thiem et Gerneck), the female: variability in the form of the lobes and plates of pygidium (Prague b)

On the dorsal part of the mesothorax (Fig. 13 G), there is an archlike cephalad curved praescutum to which a scutum is attached forming with the praescutum a closed oval formation. Laterally of the scutum the frontal phragma curve downwards protruding at the ends into praealar wing processes. A prolonged sclerotized axis of the sternal region (the median sclerite of the basisternum) runs from the apex of the praescutum towards the mesonotum centre.

Laterally, the mesonotum is limited by pleural sclerites of the mesothorax protruding on the inner side into a pleural apophysis. At the inner side of the pleural sclerite a pleural bridge ruuns, reaching right to the praealar wing processes.

The postnotum is limited at the bottom by a rear phragma which, again, is archlike curved but with an apex at the bottom, and is connected to the pleural sclerites of the mesothorax. On its inner sides it protrudes into two processes.

In the centre of the mesonotum there is a disc shaped scutellum mildly curved frontwise, the most strongly chitinized part of the whole body. In its centre there is a membraneous oval area to which the mesothoracal muscles are joined (the membraneous scutellum area). The scutellum is approximately 159—191 μ long, on the average, and 32—38 μ wide. The flat mesosternum is provided on its ventral part with the second pair of legs and the first pair of spiracles.

The metathorax is bordered by a pleural sclerite on each side; above the coxae of the third pair of legs the metathoracal bridge protrudes from both sides almost right to the centre.

The mesothorax bears the first pair of wings (Fig. 13 D) which are normally developed. The vein network is reduced to the same extent as in other Diaspides, to a short subcosta, radius running to $^2/_3$ of the wing parallel with the upper margin, and the media, which separates from radius in about $^1/_3$, and runs parallel with the lower wing margin, approx. as far as radius (slightly shorter). At the root, an alar lobe is developed. The wing is approximately 812 μ long (774—855 μ), and 388 μ wide (335—421 μ). On the metathorax the second pair of wings is placed in the form of vestigial halteres (Fig. 13 F). These are club-shaped protuberances each ending with a long terminally curved seta which is pushed into the alar lobe of the 1st pair of wings during flight (Fig. 13 E). The metathorax bears the third pair of legs and the second pair of spiracles.

All three pairs of legs have the same composition differing only in their size. The 1st pair is the shortest, the 3rd pair the largest (Fig. 12 C). The leg consists of a hemispherical coxa provided with 2—3 setae, coneshaped trochanter with one seta; at the proximal end of the trochanter there are 4 prolonged slit-like shapes (sensory function), 2 on the upper, and 2 on the lower side. The trochanter is followed by a cylindrical femur narrowing towards tibia; it is provided with 7—8 setae. The tibia is slim, prolonged, provided with 14 setae. The one-segmented long tarsus is covered by 16—17 setae. Two setae at the distal end are longer and are ended with club-shaped extentions (sensory function). The claw is simple, mildly archlike curved. The digitals are also provided with club-shaped extentions at their ends.

The width of the hind leg tibia (at the apex) ranges between $27-31\,\mu$. The setae on the inner side of the hind tibia apex are roughly the same as the tibiae width at the apex, or somewhat longer. The average length is $29-53\,\mu$; the ratio of the tibia length to the length of the apex seta is 1-1.2:1-1.3.

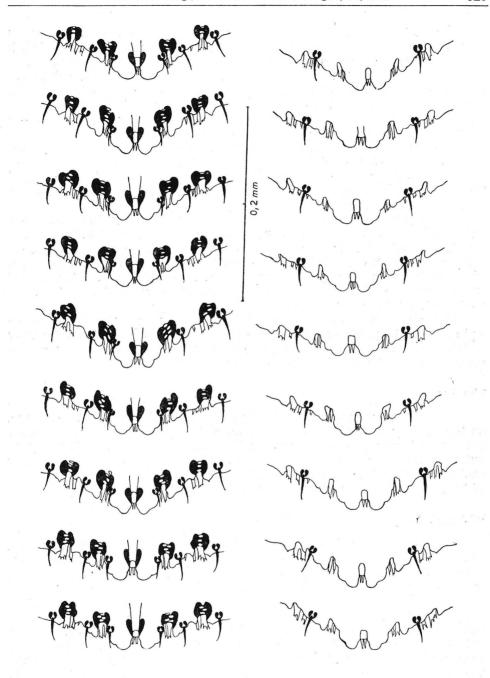


Fig. 7: $Quadraspidiotus\ gigas$ (Thiem et Gerneck), the female: variability in the form of the lobes and plates of pygidium (Prague d)

The abdomen consists of nine segments, it is wide, and narrows conically caudad. The last segment is prolonged into a genital sheath (stylus), in which the penis is placed (Fig. 14 A). The stylus is provided with 5 pairs of wartlike swellings (Fig. 14 B). At the border of the abdomen from the 1st to 3rd segment there is one pair of marginal setae on each segment, and from the 4th to the 8th segment there are two pairs of setae on every segment. On the abdominal side there is the following formation of setae shifted rather more towards centre: -1; 1 (2); 2; 2; 1 (2); 2 (3); 2 (3); 3 (4), or 4 (4). The eighth segment bears on the dorsal and ventral sides two pairs each of slightly longer setae than on other segments.

The eighth abdominal segment bears also a special longitudinal fibrous structure (special engraving) which reaches to the middle, or

over the whole segment (Fig. 14 F, G).

At the penis base on the ventral side (Fig. 14, C, D) there are 2—3 pairs of setae, and one pair of setae on the base of the genital sheath. On the dorsal side, somewhat lower, there is one more pair of setae, a little shorter one. The setae at the penis base can be divided into upper ones reaching the length of 23—39 μ , middle ones, 11.5—18.4 μ long, and the lower ones 32.2—46 μ long. The pair of setae at the base of the genital sheath is rather long—over 40 μ .

I believe a more decisive factor for determining males is the shape and setae of the pygidium than measurements of various parts of the body which, as is evident from the above remarks, vary greatly (e.g. the

measurements of the 3rd antennal segment).

The Egg

Q.~gigas is ovoviviparous. The eggs are of a prolonged eliptical shape, on the average 168 μ (158—178 μ) long and 92 μ (82—117 μ) wide. They are covered with a waxy powder on the surface, a secretion of the perivulvar glands. They fill the whole inside of the female, being closely packed together. They are arranged concentrically, and point to the centre of the female body with their longer axis.

Ist Larva

No sexual dimorphism was ascertained in the Ist larvae. (Morstatt, 1908) states some different morphological signs of the Ist larvae of some scale insects). The shape of some larvae some of which are rounded, other prolonged, reminds one, of the sexual dimorphism of the IInd larvae.

The larva of the Ist instar (Fig. 8 A) is flat, oval, approximately 260—270 μ long and 160—170 μ wide. Towards the end of this instar its length increases by approx. 100 μ . The head grows together at its whole width with the thorax, the abdomen passes into a pygidium gradually and is not separated as in the IInd larva and the female. On the ventral side of the head there are 5 segmented antennae (Fig. 8 B), placed under the body when resting, during activity they point forward. The antenna length ranges around 70 μ .

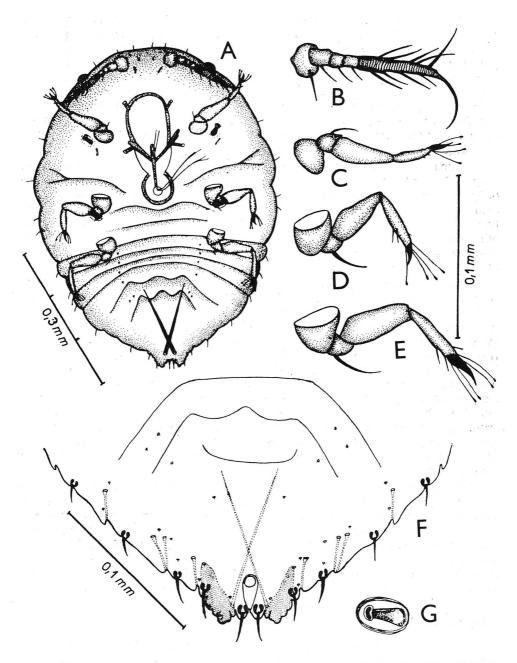


Fig. 8: Quadraspidiotus gigas (Thiem et Gerneck), Ist Larva: A — ventral surface; B — antenna; C, D, E — legs of I., II., III. pair; F — pygidium of the dorsal surface (spotted in the ventral view); G — the anterior spiracle

The basic segment is wide, hemispherical [13 μ], the 2nd segment somewhat over 11 μ long and 9.5 μ wide, the 3rd segment wider than long, 5.7 μ long, and 7.6 μ wide, the 4th segment similar but somewhat shorter—the length being 4.7 μ , the width 6.6 μ ; all 4 segments bear one seta each. The 5th segment is the longest, typically ringed. It is approximately 34 μ long, 4.7 μ wide and bears approximately 10 setae. At the end of this segment a long, strong, usually curved seta grows out (21—28.5 μ). Two simple eyes are set at the sides of the head. The mouth organ is placed on the ventral part of the head. The piercing spines are packed together in young larvae, and form a typical loop.

There is one pair of legs each on the pro-, meso- and metathorax (Fig. 8 C, D, E). They are of similar composition differring slightly in size only. The leg of the 1st pair is approximately 95 μ long, of the 2nd pair 96.9 μ , and the 3rd pair 98.8 μ . The legs are ended with one-segmented tarsi, out of which 2 long, and 2 somewhat shorter setae grow (digituli) with club-shaped extentions at the ends, serving as fastenings. At the same time they have a tactile function. These setae reach approximately $^2/_3$ of the tibia length.

The pygidium, approximately 160 μ wide and 99 μ long terminates with 2 great lobes (width 12 μ , height 13 μ). These lobes have on the top of their outer side one great notch, towards the lobe apex two shallower notches, stepwise following (Fig. 8 F). On the inner side there is one more shallow and one deep oblique notch, at each side. In the middle between the two great lobes there are 2 smaller rounded lobes. Each one of them is provided with a laterally pointing strong spiny seta. May (1899) designates them in some Ist scale-insect larvae as plates and, according to their shapes, he determinates some species. The first larva of Q. gigas, however, could not be distinguished, on the ground of this sign only, for example, from the Ist larva of Q. ostreaeformis and Q. piri where there are similar spiny plates. It is, however, necessary to consider also the shape of the great and smaller central lobes and then, these larvae can be fairly well distinguished.

There are 4 deep notches on the pygidium, before each of which one seta is placed. On the dorsal side 1-2 macropores open into these notches. On the ventral side 2, approximately $70~\mu$ long trailing setae are placed. When at rest, they are crossed underneath the body, when moving the larva trails them behind itself. On this side of the body, especially on the pygidium, small micropores open, to a total number of approximately 20. The distribution of the spines is evident from Fig. 8 F. The anus on the dorsal side is approximately $36~\mu$ distant from the pygidium margin.

IInd Female Larva

After molting, the Ist larva changes into the immobile IInd larva which considerably differs from the first instar. A number of organs are reduced. It entirely loses eyes and legs, the antennae are reduced to small three-lobed protuberances provided with one sensory seta (Fig. 9 G).

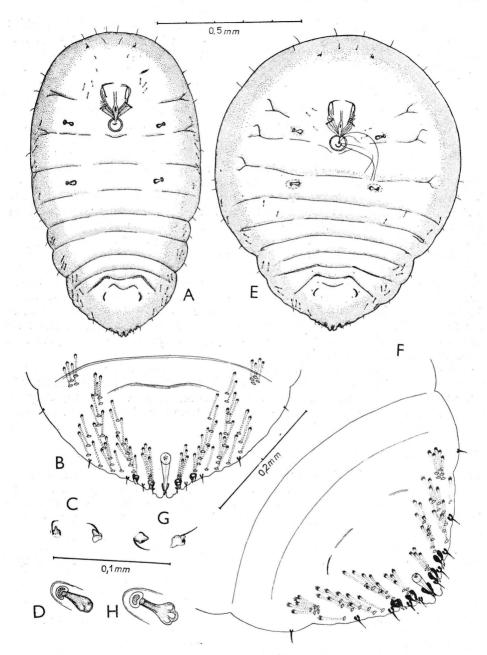


Fig. 9: Quadraspidiotus gigas (Thiem et Gerneck), IInd male larva: A — ventral surface; B — pygidium of the dorsal surface; C — antenna; D — the posterior spiracle IInd female larva: E — ventral surface; F — pygidium of the dorsal surface; G — antenna; H — the posterior spiracle

The average length of the IInd female larva (of the 7th October, 1956) is 389 μ (300—479 μ), the average width being 310 μ (250—393 μ). The ratio of the length to the width is 1.2:1. By its appearance, it resembles an adult female (Fig. 9 E). It differs by the build of the pygidium, size, number of glands, and the absence of the vulva.

On the pygidium (Fig. 9 G) all 3 pairs of lobes are already developed. The shape of the lobes of the IInd female and male larvae varies only very little in relation to adult females. L_1 are large, wide (width equals length), with a deep notch on the outer side. L_2 are of a similar shape to those of a female but smaller, L_3 are pointed, however, they form no sharp processes on their tops. Between L_1 there are 2 narrow, spiny plates reaching approximately to the height of the outer notches. Between L_1 and L_2 there are, as a rule, 2 plates (sometimes only one), between L_2 and L_3 2 (3) plates. The plates are narrow with terminal small teeth. They are always narrower and less toothed than in females (Fig. 10 D, E, F). On the average, 50-65 macroducts open at the pygidium.

The distribution of the macroducts on the pygidium: between L_1 opens 1, into the first intersegmental crypt, and above it, 4; into the second crypt and above it, 6—12, then 1—2. Further, there is a row of 8—13 macroducts, behind it, there are 1—2, on the 4th segment open 3—5 macroducts. Borchsenius (1939) states, on the average 13—21 macroducts more (1; from each side, 7—8; 11—12; 1—3; 11—13; 1—2; 3—5). In the first group of glands there are, in my material, always 3—4 macroducts less than in that of Borchsenius.

Neither vulva, nor perivulvar discs are developed. On the ventral side, there are 30—40 microducts. Their distribution is evident in Fig. 9 E. On each segment, there are 2 marginal setae, they are missing only on the ventral side besides the first lobes. The distance of anus from the base p_1 is $40-45~\mu$.

IInd Male Larva

differs from the IInd female larva at the first sight by the shape of its body. (Fig. 9A). It is of a prolonged egg-shape, the ratio of length to width being 1.4—1.5: 1. The average length (7. 10. 1956) is 458 μ (387—520 μ), the average width 319 μ (270—362 μ). Before molting, the larva is approximately 100 μ longer.

Morphologically the IInd male larva resembles a great deal the IInd female larva. The antennae, however, are composed only of a simple process each bearing a long sensory seta (Fig. 9C). The pygidium is higher and slimmer, there are, on the average 10—15 macroducts more than in the IInd female larva. (The number of macroducts corresponds to the number given by Borchsenius [1939] for the IInd female larva.)

Pronymph (Praepuppa)

After moulting, the IInd larva changes into the male pronymph (Fig. 11 A). The larval exuvia is no longer used for building the scale but is pushed into the rear part of the scale. The further development is

carried out under this scale right up to the emergence of the male. The yellow coloured pronymph (20. 5. 1956) is approximately 480 μ long (440—516 μ), and 260 μ (223—275 μ) wide.

The pronymph is not so strongly dorsoventrally flattened as the larva and its total shape reminds one of the nymphal stage. The foundation of legs, wings and antennae are already developed. On the head, the rudiments of eyes already shine through. The mouth organ is reduced. Between

the antennae bases 3 pairs of unevenly long spines are placed.

The pygidium margin is rounded, the lobes are not developed (Fig. 11 B). Laterally, on the ventral part of the last pygidial segment, two long, very strong, approximately 25 μ long spines are placed. There are two setae at each inner side of the spines, in the centre at the lower pygidium margin there are two further setae. The pygidium shape, the size, the number and distribution of setae is a determinating sign (e.g., in *Q. piri* there is a different arrangement (Dušková, 1953). No gland pores are developed. There are two marginal setae at each pygidial segment.

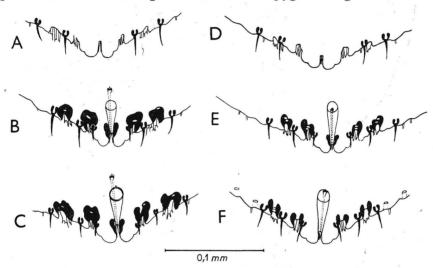


Fig. 10: Quadraspidiotus gigas (Thiem et Gerneck), left: pygidium-margin of the IInd male larva: A — ventral surface: B, C — dorsal surface right: pygidium-margin of the IInd female larva: D — ventral surface; E, F — dorsal surface

The Nymph (Male-puppa)

The nymph (Fig. 11 C) is, on the average approximately 600 μ (550—654 μ) long, and 280 μ (275—292) wide (30. 4. 1956). The ratio of length and width is roughly 2:1. It is yellow.

The body is more convex than that of the pronymph, especially in the thoracal part attaining the shape of the imago. The foundations of wings, legs, and especially of antennae, are longer as compared with the preceding stage. The segmentation of the extremities is already marked.

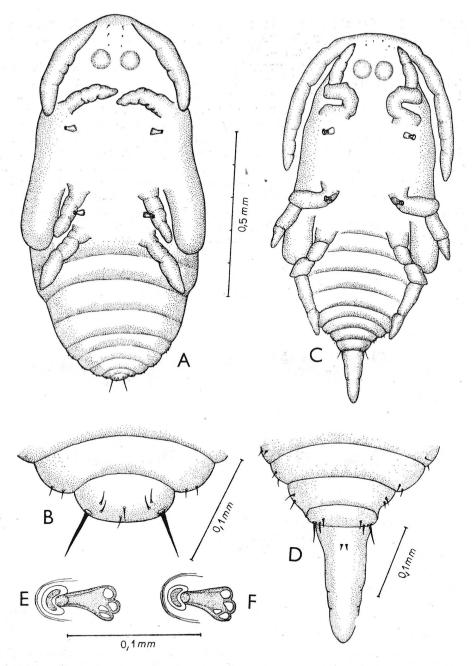


Fig. 11: Quadraspidiotus gigas (Thiem et Gerneck), Pronymph: A — ventral surface; B — pygidium of the dorsal surface; E — the anterior spiracle Nymph: C —ventral surface; D — pygidium of the dorsal surface; F — the anterior spiracle

On the head, the eyes are becoming evident. 2 pairs of spines are placed between the antennae foundations.

The abdomen is clearly segmented, the last segment protruding into a foundation of the genital sheath. The setal distribution is characteristic of the two last abdominal segments (Fig. 11 D). Laterad of the penultimate one (eighth segment) one seta is placed at each side. Cephalad of them, on the dorsal side, there are 2 shorter setae at each side lying one behind the other. In the centre of the last segment, on its dorsal side, there is 1 pair of short, strong spines. The individual pygidial segments, except the last two, bear one pair of marginal setae each.

7. Biology

The development cycle of *Quadraspidiotus gigas* is an annual one. The time data on the occurrence of individual stages vary arer a range of 2—3 weeks according to climatic conditions, the place of settling, etc. It is important, even, on which side of the host plants the scale insects are settled. So, e. g., on the northern side of the same tree the development of the individuals against those from the southern side is retarded by a week to a fortnight.

The scale insect *Q. gigas* hibernates in the stage of the IInd larva. Schmutterer (1959) noticed that it can hibernate in the stage of the Ist larva. In such a case, however, it is not capable of further development, and dies. I noticed that also in our country (Czechoslovakia) it can hibernate at this stage. However, it is always the case of a small number of the Ist larvae which were not hatched until October.

Up to March the IInd male and female larvae occur. In some years, they occur also in April; e. g. 22. 4. 1954, in Prague (d) (Žižkov) IInd male larvae were changing into pronymphs. Under normal circumstances, this happens during the first half of April (to 10th April), in a warm spring even at the beginning of May the nymphs are beginning to appear (3. 4. 1960, 6. 5. 1959, 11. 5. 1956). Beginning the end of April, to the end of May, until the beginning of June, males are hatching. At the same time, the females are maturing. Schmutterer (l. c.) states that males and ripe females appear in April, and copulation takes place. In our climate, most of the males hatch during May when copulation occurs. Copulation occurs in the same way as described by Bachmann (1953) in Quadraspidiotus piri and Q. schneideri (mařani). Bachmann described also potent and impotent males. I noticed the same phenomenon in Q. gigas. Some males are not even strong enough to creep out from under their scale and die underneath it.

However, I cannot confirm the observations of some authors carried out on various Coccids — Suter, (1932), Geier, (1949), Van Dinther, (1950), Bachmann, (1953) that the males die one hour after hatching. On the contrary, some males from my material lived as long as 39 hours. The strongest activity was manifested approximately 2 hours after hatching, they lost it, however, 4—6 hours after hatching. Then, they remained

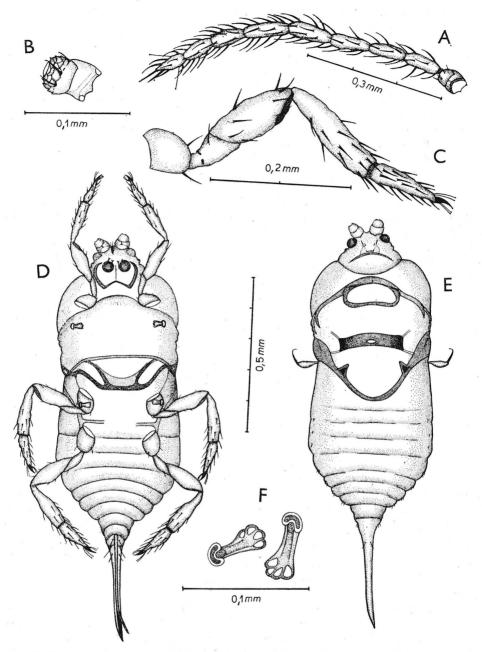


Fig. 12: Quadraspidiotus gigas (Thiem et Gerneck), the male (Prague a): A — antenna; B — 1. and 2. segment of antenna; C — the metathoracic leg; D — ventral surface: E — dorsal surface; F — the anterior spiracle

quiescent. When touched, however, they moved, although they were not so agile as before.

The *Q. gigas* males usually only creep along the host plant. When examining the twigs, I noticed that, from time to time, a male flew up and settled on the window pane (my working table is near the window). A longer flight was never noticed. In breeding vessels they did not fly at all although the cultivated parasitic wasps even in those spaces flew about very actively.

Fertilized females lay eggs from June until September, the highest number of eggs being, however, laid in July and August. Even on 25. 10. 1952, in Sedlčánky near Čelákovice ovipositing females were found. Under normal conditions, however, most of the females finish their laying in August and die.

A female lays during its lifetime an average of 140—150 eggs. The laying lasts a little less than two months; during the first month it lays approximately 100 eggs, the rest during the second month. When laying, the female lifts its abdomen, and moves it slowly up and down. According to my observations on females cultivated in the laboratory Q. gigas females lay six eggs daily, at most. It depends on a number of factors, in the first place, on temperature. The average temperature ranged, during my observations, from 18—25 Centrigrade, at 8 a.m. 18—19 Centigrade at 2 p. m. 20—25 Centigrade, at 8. p. m. 18—22 Centigrade).

The first larvae hatch 48—56 hours after the eggs are laid. For a short time, they remain laying stiffly but in a few minutes they begin to move. They run around the plant, and look for a convenient place to settle. In two days, at most, they fasten themselves by means of their proboscis to the host plant, and immediately, they begin to form the protective round scale which is white at first, gradually however, it grows darker. The Ist larval instar lasts approximately for 50 days. Towards the end of October, most of the larvae are in the IInd stage in which they hibernate.

8. Natural enemies

Q. gigas is very strongly attacked by parasitic wasps of the family Encyrtidae (50—90% infestation). In my cultures I cultivated many of these Hymenoptera. The material was given to Dr. A. Hoffer for determination but it has not yet been carried out. According to a preliminary examination, Aphytis mytilaspidis (Le Baron), and Pteroprix dimidiatus (Westw.) (det. A. Hoffer) occur in it, besides other species. These parasites are stated also by Schmutterer (1953) from Germany, and Kosztarab (1956) from Hungary. Aphytis mytilaspidis is one of the most frequent parasites of the Coccids. It is considerably polyphagous with a wide distribution (Europe, Asia, North America). Also Pteroptrix dimidiatus, the endophage of various parasites, is fairly widely spread (Italy, France, Austria, Hungary, North Africa, Ceylon, Jawa, North America) (Schmutterer l. c.).

Kosztarab (l. c.) cultivated from individuals of *Q. gigas* sampled on Populus italica also *Azotus matritensis* Merc. (Aphelinidae), and from

the individuals on *Populus alba* a polyphagous cosmopolitan species *Aspidiotiphagus citrinus* Crawf., and *Pteroptrix maritima* Nik. (Aphelinidae).

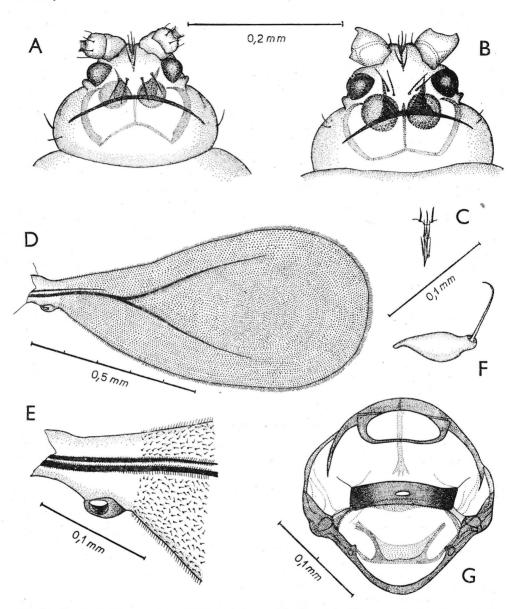


Fig. 13: Quadraspidiotus gigas (Thiem et Gerneck), the male (Prague a): A+B-head (spotted in the ventral view); C-head interantennal band; D-head first wing; E-head of the first wing; E-head in the ventral view)

A considerable importance in the destruction of the poplar scale *Q. gigas* is possessed by the imagines and larvae of the ladybirds *Chilocorus bipustulatus* L., and *Coccinella bipunctata* L., which occur in great numbers on infested trees. On old laid-out females quantities of all sorts of mites were found. However, these have no practical importance in the control of these insects for they do not attack living individuals. This applies also to various species of Nematodes and moulds which also do not spread on living females.

In the Elbe region, at Čelákovice and Sedlčánky, the predatory bugs Loricula pselaphiformis Curt., and L. elengatula Baerensprung of the family Microphysidae and Ectemnus nigriceps E. Wagner and Temnostethus longirostris (Horv.) of the family Anthocoridae (determined by P. Štys) were found, especially in June, on poplars attacked by Q. gigas. These bugs devour particularly the individuals of the family Psocidae

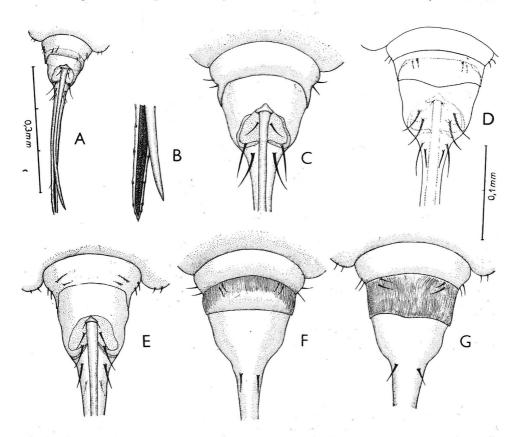


Fig. 14: Quadraspidiotus gigas (Thiem et Gerneck), the male (Prague a): A — abdomen with genital armature (ventral aspect); B — ventral aspect of the penis tip; C, E — abdomen (ventral surface); F, G — abdomen (dorsal aspect); D — reconstruction of the dorsal and ventral surface

^{41 –} Sborník entomologický

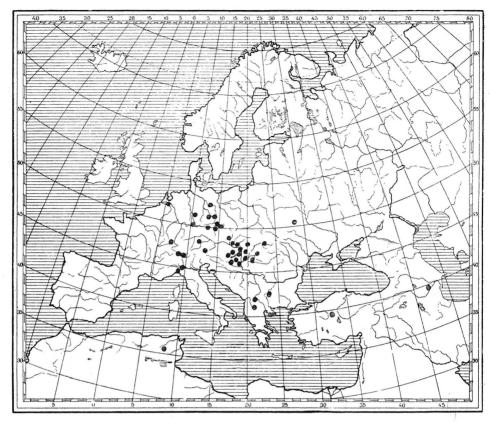


Fig. 15: Geographical distribution of Quadraspidiotus gigas (Thiem et Gerneck)

which occur abundantly among the colonies of *Q. gigas*. I noticed, however, some of the bugs piercing Coccids and sucking them out.

Often I found on trees with *Q. gigas*, especially in April, May and June, a common palearctic species of ant, *Lasius niger* L., (determined by H. Kholová). Occasionally, some ants held a female of *Q. gigas* in their front legs, and carried it down the trunk.

I never noticed any birds feeding on poplar scale. Newstead (1901) states *Quadraspidiotus zonatus* to be massdevoured by blue tits.

Summary

The detailed study of the poplar scale — $Quadraspidiotus\ gigas$ (Thiem et Gerneck) was inspired directly by a practical necessity as this species is an important destructor of fast growing woody plants, especially poplars and willows. Rich materials from Czechoslovakia, Hungary, Yugoslavia and Switzerland formed the basis of this work.

1) The materials for bionomic and ecological investigations were sampled from various parts of Czechoslovakia from October, 1952 until summer, 1959. The samples were taken in 4 continuously investigated localities: in Prague, at the National Museum,

in Washington Street (Prague) on American poplar hybrids, in Prague-Žižkov, goods station (Prague) on Populus canescens SM., in a village Jiřina near Čelákovice (Čelákovice a) on Populus canadensis Moench., and in a village Sedlčánky near Čelákovice (Čelákovice b) on Populus nigra L., regularly once-a-fortnight, in summer months sometimes every week. In 1959 during the vegetation period additional samplings were carried out fortnightly in Prague-Podolí (Praha b) on American poplar hybrids.

Morphological and taxonomic studies were carried out on materials from altogether 12 localities: Prague, 4 localities, Čelákovice, 2 localities, Poděbrady, Bratislava, Hungary

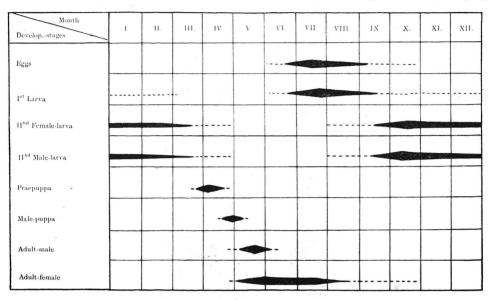


Fig. 16: Scheme of development of Quadraspidiotus gigas (Thiem et Gerneck)

(Pécs, Budapest, Tatatóvároskert), Yugoslavia (Bajmok), Switzerland (Zürich), DDR (Dresden).

2) Q. gigas was successfully experimentally cultivated in the laboratory on poplar

branches placed in Knapp nutrient solution, and on willow twigs.

3) Experiments were carried out with transferring the poplar scale from poplars to other host plants. On Tilia cordata Mill., Ulmus scabra Mill., Fraxinus excelsior L., Salix sp., it caught on well and performed the whole development cycle (for several years), on indoor ornamental plants it did not settle at all. Females shortly before laying and Ist larval stages were used for the experiment.

4) By transferring the insect from climatically convenient places (Prague, Elbe region) to places less convenient and with a higher altitude (Blatná) it was determined

that it is a warm-loving species.

5) In nature Q. gigas evidently prefers plants of the order Salicales, i. e. poplars and willows. In Czechoslovakia it lives predominantly on poplars. I found it on Populus alba L., P. canescens SM., P. canadensis Moench., P. pyramidalis Rozier, P. nigra L., P. tremula L., Populus sp., and on various hybrids of American poplars, on P. deltoides Marsh. cv. monilifera, P. euramericana (Dodet) Guinier cv. robusta, on Salix sp.

6) Q. gigas occurs in warm, protected places of the palearctic region, along rivers and streams in considerably insolated biotopes with convenient temperature and humidity. In Czechoslovakia it lives in all such parts of the country, it has been reported from Germany, Holland, Switzerland, France, Italy, Yugoslavia, Bulgaria, Hungary, USSR, Turkey, Algeria. In 1961 it caused a calamity by its enormous abundance

7) The poplar scale forms thick crusts on the poplar bark in a mass attack, and it causes special hollows (galls) to be formed on trunks and branches, weakening and drying off parts or whole trees. It is particularly dangerous to trees in weakened condition. Young trees especially are destroyed, primarily, the nursery material.

8) A detailed morphology has been given of all developing stages, female and male. For the first time, the description of the Ist larva has been made, male pronymph, male

nymph, and the description of the male has been substantially completed.

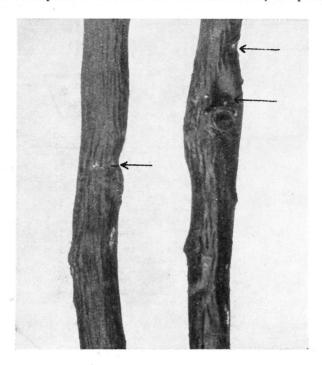


Fig. 17: The young poplars with depressions (Photo M. Kosztarab)

9) A strong variability has been ascertained in females and males of *Q. gigas*. In females, it manifests itself in the shape of the lobes and plates, in the number of macropores, and perivulvar discs, in the distance of the vulva from the pygidium margin. According to these characters they can be divided into three groups. In males the variability manifests itself in the length and width of the 2nd and 3rd antennal segment, in the build of the head (the distribution of setae on the interantennal band, the eye apophysis, and its arches, the shape of the sclerotized area and where it reaches), and in the shape and curving of the praealar wing processes, especially in the build and distribution of setae on the pygidium.

10) The biology of *Q. gigas* has been studied, the time data have been fixed for the occurrence and duration of individual stages, copulation has been observed, the

manner of male movements, etc. It hibernates in the stage of the IInd larva.

A number of parasitic Hymenoptera were cultivated in laboratory cultures, and further natural enemies of the order Coleoptera were ascertained. On colonies of the poplar scale, the Ant Lasius niger L. was observed. The greatest importance in the destruction of Q. gigas can be assigned to parasitic Hymenoptera with their 50-90~% infestation.

Acarids, Nematodes and various species of moulds attack individuals already dead.

LITERATURE

- Bachmann, F., Geier, P. W., 1950: Einige für die Schweiz neue oder wenig bekannte Cocciden aus der Unterfamilie der Diaspidinae (Homopt. Diaspidoid.). *Mitt. Schweiz. Ent. Geselsch.*, 23 (2): 117—119. Lausanne.
- Bachmann, F., 1952—1953: Beitrag zur Kenntnis der jugoslavischen Schildlausfauna. Recueil des travaux de l'Acad. Serba des Sciences, 31 (4): 175—184. Beograd.
- Bachmann, F., 1953: Untersuchungen an den gelben Obstbaumschildläusen Quadraspidiotus piri, Licht. und Quadraspidiotus schneideri n. sp. Zeit. angew. Ent., 34: 357—404. Berlin.
- Balachowsky, A. S., 1942: Essai sur la classification des Cochenilles (Homoptera, Coccoidea). Ann. Ec. Nat. Agric. Grignon, 3: 34—48.
- Balachowsky, A. S., 1948a: Sur le statut et la biologie de Quadraspidiotus pyri Licht., cochenilles nuisibles aux cultures fruitières. *Rev. Pathol. vég. Ent. Agric.* France, 27: 89—97.
- Balachowsky, A. S., 1948b: Remarques sur deux Cochenilles forestières du groupe de Quadraspidiotus ostreaeformis Curtis nouvelles pour la faune de France. Rev. de Pathol. vég. et d'Entomol. Agric. de France, 27: 14—24, Paris.
- Balachowsky, A. S., 1948c: Les Cochenilles de France, d'Europe, du Nord de l'Afrique et du Bassin méditerranéen. IV. Monographie des Coucoidea—Diaspidinae (I. partie). Paris.
- Balachowsky, A. S., 1950: Les Cochenilles de France, d'Europe, du Nord de l'Afrique et du Bassin méditerranéen. V. Monographie des Coccoidea Diaspidinae (II. partie: Aspidiotini). Paris.
- Balachowsky, A. S., 1951: Les Cochenilles de France, d'Europe, du Nord de l'Afrique et du Bassin méditerranéen. VI. Diaspidinae (III. partie: Aspidiotini). Paris.
- Baudyš, E., 1951: Československé coccoideocecidie. The coccoideocecidia of Czechoslovakia. Sbor. klubu přír. v Brně, 29: 81—89.
- Bodenheimer, F. S., 1934 (1935): Studies on the Zoogeography and Ecology of Palaearctic Coccidae. *Eos.*, Madrid, **10**: 237—271.
- Bonnemaison, L., 1936: Morphologie comparée de Pou de San José (Aonidiella perniciosa Comst.) et du l'Aspidiotus des arbres fruitières (Aspidiotus ostreaeformis Curtis). Rev. Pathol. vég. 23 (3): 230—243. Paris.
- Boratyňski, K. L., 1953: Sexual dimorphism in the second instar of some Diaspididae (Homoptera: Coccoidea). *Transact. royal Ent. Soc. London*, **104**: 451—479. London.
- Borchsenius, N. S., 1935: Pjat novych vidov ščitovok (Coccidae), morfologičeski blizkich k kalifornskoj ščitovke (Aspidiotus perniciosus Comstock). Zaščita rastěnnych, 6: 127—133. Moskva—Leningrad.
- Borchsenius, N. S., 1939: Sistematičeskije osobennosti ličinok vtorovo vozrasta ustricevidnych ščitovok (Coccidae) rasprostraněnnych v SSSR. Izdanie leningradskoj oblastnoj karantinnoj inspekcii, Leningrad.
- Borchsenius, N./S., 1948: Coccoidea Kokcidy ili červecy i ščitovki evropejskoj SSSR. Opredělitěl nasekomych evropejskoj časti SSSR, p. 226—245. Moskva-Leningrad.
- Borchsenius, N. S., 1950: Červecy i ščitovki SSSR (Diaspididae), p. 157—235. Akademija nauk SSSR, Moskva-Leningrad.
- Buščik, T. N., 1958: K sravnitělnoj morfologii samcov ščitovok (Homoptera, Coccoidea, Diaspididae). *Trudy všesajuzn. entom. obščestva,* **46**: 162—269.
- C o l v é e, P., 1882: Nuevos estudios sobre algunos insectos de la familia de los Coccidos, p. 16. Valencia.
- Curtis, L., 1942: Aspidiotus ostreaeformis (the pear-tree oysterscale). *Gard. Chron.* **46**: 805.
- Čorbadžijev, P., 1939: Kratjkj cpisjkj na ščitonosnitj vjški (Coccidae, Rhynchota) vj Bjlgarija. *Izv. na Bjlgarsk. entomol. družestvo,* **10**: 88—90. Sofija.

- Dinther, J. B. M., 1950: Morphologie en biologie van de schildluis Chionaspis salicis L. *Tijdschr. Plantengilkten*, **56**: 173—252.
- Dušková, F., 1952: Vergleich der morphologischen Hauptmerkmale der Schildläuse Quadraspidiotus piri (Lichtenstein) und Quadraspidiotus mařani Zahradník (Coccoidea: Diaspididae). *Beitr. Ent.*, 2 (4/5): 452—455. Berlin.
- Dušková, F.: 1953: Morfologie Quadraspidiotus piri (Lichtenstein) (Homoptera, Coccoidea). Acta Soc. Zool. Boh., 17 (1): 8—36.
- Dušková, F., 1953: Morfologické znaky a ekologické poznámky k samicím červců Quadraspidiotus piri (Licht.), Q. mařani Zahr., Q. ostreaeformis (Curt.) a Q. perniciosus (Comst.) (Homoptera, Coccoidea). Acta Soc. Zool. Bohem., 17 (4): 229—256.
- Ezzat, Y. M., 1956: The thoracic sclerotization of coccid adult males as a promising taxonomic charakter. (Coccoidea). *Bull. Soc. Entom. Egypte*, **40**: 357—363.
- Ezzat, Y. M., 1957: Biological studies on the Olive scale, Parlatoria oleae (Colvée) (Hemiptera Homoptera: Coccoidea Diaspididae). *Bull. Soc. Ent. Egypt.*, **41**: 351—363.
- Fernald, M. E., 1903: A Catalogue of the Coccidae of the World. Amherst.
- Ferris, G. F., 1937—1942: Atlas of the Scale Insects of North Amerika. Series I—IV.
 Stanford University.
- Frank, A.B., Krüger, F., 1898: Die europäischen Verwandten der San José Schildlaus.
 Gartenflora, **47**: 393—400.
- Geier, P. W., 1949: Contribution à l'étude de la Cochenille rouge du Poirier (Epidiaspis Leperii Sign.) en Suiss. *Rev. Pathol. vég. Ent. agric. France*, **28**: 177—266.
- Goethe, R., 1898: Neuere Beobachtungen über A. ostreaeformis Curt. Geisenheimer Mitteil. 5 (13): 154.
- Gómez-Menor, O. J., 1937: Coccidos de Espana. Madrid.
- Jancke, C. D., 1955: Zur Morfologie der männlichen Cocciden. Ztschr. ang. Ent., 37 (3): 265-314.
- Kawecki, Z., 1948: Przyczynek do znajomości czerwców Polski. Some Coccidae from Poland. Polska Akad. Umietn., Kraków.
- Kosztarab, M., 1955: Revision und Ergänzung der in der "Fauna Regni Hungariae" angeführten Cocciden. Ann. Hist. Nat. Mus. Nat. Hungarici (ser. n.) 6: 371—385, Budapest.
- Kosztarab, M., 1956: Parasitologische Untersuchungen an Schildläusen. *Acta Agron. Acad. Sci. Hungaricae*, **6** (3—4): 393—410.
- Krassilstchik, L., 1893: Zur Entwicklungsgeschichte der Phitophthieres. (Über Viviparität mit geschlechtlicher Fortpflanzung bei den Cocciden). *Zool. Anz.* 16: 69—76, Leipzig.
- Lelláková-Dušková, F., 1959: Männchen der Schildläuse Diaspidiotus wünni (Lindinger) (Coccoidea, Diaspididae). *Acta Soc. Ent. Čech.* **56** (4): 338—342.
- Leonardi, G., 1897: Monograpfia del Genere Aspidiotus. Riv. Patol. veg., 5: 283—286, Portici.
- Leontovyč, R., et coll., 1959: Ochrana topolóv. Polnohospodárské aktuality, 18. sv. Vydavateľstvo PP. Bratislava.
- Lindinger, I., 1912: Die Schildläuse Europas, Nordafrikas und Vorderasiens, einschließlich der Azoren, der Kanaren und Madeiras. Stuttgart.
- Löw, F., 1882: Ungeflügelte Coccidenmännchen. Wiener ent. Zeit. 1. Wien.
- Lupo, V., 1948: Revisione delle cocciniglie italiane. VI: (Gen. Aspidiotus, Quadraspidiotus, Diaspidiotus, Rhizaspidiotus, Nuculaspis). *Boll. del Lab. di Entomol. Agr. di Portici*, 8: 137—208. Napoli.
- Mac Gillivray, A. D., 1921: The Coccidae. Tables for the identification of the subfamilies and some of the more important genera and species together with discussions of their anatomy and life history. Urbana Illinois.
- May, W., 1899: Über die Larven einigen Aspidiotus-Arten. Mitt. Naturhist. Mus. in Hamburg, 16 (2): 149—153.

- Reh, L., 1900: Über Aspidiotus ostreaeformis Curt. und verwandte Formen. Jahrb. Hamburg. Wissensch. Anst., 17: 259—271.
- Reh, L., 1903—1904: Zur Naturgeschichte mittel- und nordeuropäischer Schildläuse. Allg. Zeitschr. f. Entom. 8: 301—308, 351—356, 407—419, 457—469 (1903); 9: 12—36 (1904). Neudamm.
- Rubcov, J. A., 1952: O napravlennoj izmenčivosti v svjazi s kormovoj specializaciej u ivovoj ščitovki. *Zool. žurnal*, **31** (2): 179—182.
- Řeháček, J., 1960: Fauna puklic (Coccoidae) Slovenska. Biologické práce, ed. sekcie biol. a lék. vied slov. Akad. vied, VI/12, 88 p.
- Schmutterer, H., 1952: Die Ökologie der Cocciden (Homoptera, Coccoidea) Frankens. Zeitschr. angew. Ent. 33 (3): 369—420; 33 (4): 544—584; 34 (1): 65—100. Berlin.
- Schmutterer, H., 1953: Ergebnisse von Zehrwespenzuchten aus Schildläusen (Hymenoptera: Chalcidoidea). 1. Teil. Beitr. Ent., 3 (1, 2): 55—69. Berlin.
- Schmutterer, H., 1955: Ergebnisse von Zehrwespenzuchten aus Schildläusen (Hymenoptera, Chalcidoidea). 2. Teil. Beitr. Ent., 5: 510—521.
- Schmutterer, H., 1959: Schildläuse oder Coccoidea. I. Deckelschildläuse oder Diaspididae. Tierwelt Deutschlands, 45. Teil, 260 p., Jena.
- Stickney, F. S., 1934: The external Anatomy of the Parlatoria date Scale, Parlatoria blanchardi Targioni-Tozzetti, with studies of the head skeleton and associated parts. *Tech. Bull.*, **421**: 1—67.
- Suter, H., 1932: Untersuchungen über Körperbau, Entwicklungsgang und Rassendifferenzierung der Kommaschildlaus, Lepidosaphes ulmi L. *Mitt. Schweiz. Ent. Gesell.*, **15** (9): 347—420.
- Šulc, K., 1931: Über die männlichen Wachsschilder und die dieselben produzierenden Wachsdrüsen der mitteleuropäischen Lecaniinen. *Archiv. zoolog. ital.*, **16** (Atti dell XI Congresso Inter. di zoologia, Padova 1930).
- Šulc, K., 1943: Zevní morfologie, metamorfosa a běh života červce Phenacoccus aceris Signoret. Äußere Morphologie, Metamorphose und Lebenslauf von Phenacoccus aceris Signoret (Coccoidea). *Práce Moravské přír. spol. (Acta Soc. Sci. Nat. Moravicae*), **15**, spis 12, 52 str., Brno.
- Šulc, K., 1944: Zevní morfologie, metamorfosa a běh života červce Peukinococcus n. gn. piceae Löw 1883. Äußere Morphologie, Metamorphose und Lebenslauf von Peukinococcus n. gn. piceae Löw (Coccoidea). *Práce Moravské přír. spol. (Acta Soc. Sci. Nat. Moravicae)*, **16**, spis 11, 50 str., Brno.
- Šulc, K., 1945: Zevní morfologie, metamorfosa a běh života červce Nipaecoccus n. gn. nipae Maskell. Äußere Morphologie, Metamorphose und Lebenslauf von Nipaecoccus n. gn. nipae Maskell (Coccoidea). *Práce Moravské přír. spol. (Acta Soc. Sci. Nat. Moravicae)*, 17, spis 3, 48 str., Brno.
- Šulc, K., 1953: Zevní morfologie, metamorfosa c běh života červce Cerococcus cycliger Goux 1932. Rozpravy II. tř. České akademie, **62** [7], 18 str., Praha.
- Tereznikova, E. M., 1957: Do fauni kokcid Co cidae kanivskogo zapovidnika. *Vid. AN URSR*, Kiev, 62—64.
- Tereznikova, E. M., 1959a: Do vivčennja trotičnich zvjazkiv červeciv i ščitivok (Homoptera, Coccoidea). *Problemi entom. na Ukrajini, Vid. Ak. Nauk URSR*, Kiev, 92—93.
- Tereznikova, E. M., 1959b: Landšaftně rozmiščennja červeciv i ščitivok (Insecta, Homoptera, Coccoidea) lisiv Zakarpatskoj oblasti. *Dopovidi Akad. Nauk URSR.*, **4**: 446—450.
- Thiem, H. et Gerneck, R., 1934a: Untersuchungen an deutschen Austernschildläusen (Aspidiotini) im Vergleich mit der San-José-Schildlaus (Aspidiotus perniciosus Comstock). *Arb. über morph. u. taxon. Ent.*, 130—158, 208—238. Berlin-Dahlem.
- Thiem, H. et Gerneck, R., 1934b: Verbreitung, Entwicklung und Bestimmung der bisher in Deutschland aufgefundenen Austernschildläuse (Aspidiotini) unter Einschluß der roten Austernschildlaus (Epidiaspis betulae) und der San-José-Schildlaus (Aspidiotus perniciosus). Zeitschr. f. Pflanzenkrankh. u. Pflanzensch., 44: 529—555.

- Vasseur, R., et Schvester, D., 1957: Biologie et écologie du pou de San-José (Quadraspidiotus perniciosus Comst.) en France. *Annales des épiphyties*, **1:** 5—66. Paris.
- Zahradník, J., 1951: Revision der čechoslovakischen Arten der Schildläuse aus der Unterfamilie der Diaspidinae. Acta entomol. Musei Nat. Pragae, 27 (387): 89—200.
- Zahradník, J., 1952: Dva noví červci pro ČSR. (Rhynch. Cocc.). Čas. čs. spol. entomol., 49 (1, 2): 92-97. Praha.
- Zahradník, J., 1956: Über die geographische Verbreitung der Schildläuse (Homoptera, Coccoidea) in Mitteleuropa. Entom. Nachrichtenblatt Österr. u. Schweizer. Entomologen, 8 (3): 3-7. Wien.