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[With 4 Tables and 17 Text-figures]

Abstract. The *Matsucoccidae* from the Baltic amber, their host, life history and taxonomy are discussed. Three new species — *Matsucoccus larssoni*, *M. electrinus* and *M. apterus* are established; *M. pinnatus* (GERMAR et BERENDT) **comb. n.** is redescribed. The status of *Acreagris crenata* KOCH et BERENDT and *Monophlebus irregularis* GERMAR et BERENDT, as well as some paleontological questions concerning the scale insects are discussed.

CONTENTS

I. INTRODUCTION

Needless to say that the amber, a fossil resin, with its inclusions of animals and plant parts represents an extraordinary phenomenon and a very rich source of information on the Tertiary fossils, particularly the terrestrial arthropods. Hundreds of publications deal with various aspects of the amber, and especially with the flora and fauna of the Baltic amber period (Larsson, 1978).

It is therefore surprising that coccidologists had paid no, but little attention to the amber. Through one hundred years, since 1845–1856, when the fossil scale insects have first been mentioned, until the redescription of *Acreagris* by Ferris, 1941, the coccid literature — with the exception of some remarks in general handbooks of entomology and paleontology (Handlirsch) — was practically devoid of any information on the Baltic amber fossils. But since the paper by Ferris there have been another 40 years with only one publication and one new scale insect described by Beardsley (1969) from the Canadian amber.

There are certainly several reasons responsible for this ignorance, but one seems to play a major role. Let us see what Ferris (1941) says:

"The present writer has previously entirely ignored the fossil forms, simply because of feeling that conclusions concerning them would be merely guesses and unworthy of serious consideration".

After the examination of the amber inclusions Ferris changed his opinion: "Of the females at hand, one is a beautifully preserved specimen which can be examined with the higher powers of compound microscope and is actually as suitable for study as were most of the preparations with which students of the *Coccoidea* were content up to scarcely more than twenty-five years ago".

However, Ferris did not describe any new species because "... we would almost certainly not be able to differentiate among such species on the basis of specimens preserved in amber".

The above quotations from Ferris' publication certainly reflect the feeling of all coccidologists who have ever directly contacted with amber scale insect inclusions.

The present paper is an attempt to overcome, once again, the barrier between the knowlegde on the recent and fossil scale insect faunas: thus it has been planned as an introduction to the Baltic amber scale insects; further, the paper refers the results of the studies on the fossil *Matsucoccidae*, a group represented by about half of the known amber material, and which was certainly connected with the mother plant of the Baltic amber.

Since the paper is the first, more comprehensive, study on fossil scale insects, there were some troubles with the displacement of information, particularly it was difficult to decide whether and how to repeat the information in the following paragraphs to make the reading easy.

General information on the Baltic amber coccid collections, distinctive features of scale insect inclusions and methods of their treatment, as well as a review of literature records have been presented in Chapters II and III.

Chapter IV deals with two forms – *Acreagris crenata* KOCH et BERENDT and *Monophlebus irregularis* GERMAR et BERENDT – which were previously affiliated with the *Matsucoccidae*, but now are excluded from this group.

The following Chapters V–VII refer to the studies on the fossil *Matsucoccidae*. The supposed host, development, reproduction etc. of the Baltic amber matsuccocids are discussed in chapter V on the background of the knowledge of the recent species. Characters available for study on amber inclusions are analysed in Chapter VI; it also contains a general morphological description of the group and a discussion on the species conception of fossil *Matsucoccus*. Chapter VII includes keys, diagnoses and descriptions of species.

Results of studies on remaining groups, as well as conclusions concerning the Baltic amber scale insect fauna will be presented in following papers.

Materials for this study have been made available by dr B. ŻAK-OGAZA (Academy of Agriculture, Cracow), dr Sv. G. LARSSON and dr N. MØLLER ANDERSEN (Zoological Museum, Copenhagen), Prof. W. HENNING (Staatliches Museum für Naturkunde, Ludwigsburg), dr H. JAEGER and dr E. PIETRZENIUK (Museum für Naturkunde der Humboldt-Universität, Berlin), dr L. A. MOUND and Mrs L. HUDDLESTONE (British Museum, Natural History, London) and dr E. M. DANZIG (Zoological Institute, Academy of Sciences, Leningrad) who also provided information on fossil coccid collections. I am very grateful for their kind assistance. I am also indebted to Miss Irena KOTEJA for technical assistance.

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II. REVIEW OF LITERATURE

Although the present paper deals with the Baltic amber scale insects, publications concerning fossils of other origin are also included to the review to form a more broad basis for the studies.

KOCH and BERENDT (1845: 873, 1845a: 56) mentioned *Acreagris* (uninominal, nom. nud.) from the Baltic amber, which has then been described and illustrated in the monograph by Berendt (1854: 123) as *A. crenata* Koch et Berendt among "Aptera, Poduride". "M". (presumably Menge, footnote in the above paper, p. 123) identified *A. crenata* with a coccid — adult female of "*Monophlebus*" — and mentioned on existence of 10 specimens in his collection.

Germar and Berendt (1856: 2–4) described and illustrated among the "*Coccina*" *Monophlebus pinnatus*, *M. trivenosus* and *M. irregularis*, all alate specimens. It is somewhat surprising to note that Koch and Berendt did not recognize these specimens as males, but as coccids which may be males or females as well. We read in the description of *M. trivenosus*: "Die Fühler haben nicht ganz die Länge des Körpers und sind lang behaart; sie erscheinen zehngliedrig, aber das dritte, vierte, fünfte und sechste Glied sind dreiknotig, das siebente, achte und neunte zweiknotig, so dass die Fühler als zwanziggliedrig angenomen werden können, nur dass mehrere Glieder miteinander varwachsen, und es wäre möglich, dass man Individuen mit weniger verwachsenen Gliedern fände, oder dies beim Männchen statt fände".

Menge (1856: 17–18) collected 24 amber fossils supposed to be scale insects and described *Coccus avitus* (♂), *Coccus termitinus* (♂), *Ochyrocoris electrina* (♀, suggests relation to *Orthezia*) and *Aleurodes aculeatus* as new species, and *Polyclona* (uninominal) as a new genus; he further mentioned *Coccus* sp. (supposed female), *Dorthezia* (♀), *Monophlebus pinnatus* Germar et Berendt (2 ♂), *M. irregularis* Germar et Berendt (♂) and *Acreagris* Koch et Berendt (16 apterous specimens), and repeated his opinion that the latter may be females of "*Monophlebus*".

Menge's record contains the most abundant information of amber coccids up to now, unfortunately without any drawings.

Scudder (1890: 241–242) described *Monophlebus simplex* (♂) from Oligocene freshwater clay (Florissant, Colorado) and mentioned 9 already known fossil scale insects in 6 genera.

Cockerell commented the status of *Ochyrocoris* (1896), *Polyclona* (1906) and *Monophlebus trivenosus* (1909a).

Pampaloni (1902: 253) mentioned a Miocene fossil (Melilli, Sicily) which he suggested to be a species related to *Aspidiotus*.

Zeuner (1938: 141) described 23 specimens on a *Lauraceae* leaf (Tertiary Mainzer Hydrobienkalk). The insects are supposed to be various development stages of a species similar to larva of *Parlatoria zizyphi*.

Ferris (1941) rediscovered the amber scale insects for the coccidologists, redescribed male *Monophlebus pinnatus* and female *Acreagris crenata* and suggested the inclusion of both in one species within the recent genus *Matsucoccus* (detailied discussion on following pages).

Becker-Migdisova (1959) described *Mesococcus asiatica* from Upper Triassic deposit from Kirgizia. Coccidologists (Beardsley 1969) hesitate whether this wingless specimen, in poor condition (antennae and mouth parts not preserved), has correctly been assigned to the scale insects.

Larsson (1962, 1965, 1978) informed of the existence of amber scale insects in the Copenhagen Collection and discussed the Baltic amber fauna, however without description of species.

Morrison and Morrison (1966) listed *Acreagris*, *Ochyrocoris* and *Mesococcus* among the genera of scale insects and briefly discussed their status.

Bearsley (1968) mentioned *Acreagris crenata* Koch et Berendt (sensu Ferris 1941) in connection with the description of male *Matsucoccus bisetosus* Morrison, a recent species, and discussion on the phylogenic position of *Matsucoccus*. Later (1969) he established a new genus and species — *Electrococcus canadensis* — for a fossil male from Canada amber (Cedar Lake, Manitoba) which is supposed to be of the Upper Cretaceous age.

Miller and Kosztarab (1979) recapitulated briefly the information on fossil scale insects and presented the opinion of Evans (1963) and Szelęgiewicz (1971) on *Thekardoella thekardoensis* (Lower Permian) and *Permaphidaspis sojanensis* (Upper Permian) supposed to be the oldest known scale insects, but without mention of the Baltic amber inclusions.

The sparse data on the fossil scale insects have further been mentioned and repeated in textbooks of entomology and paleontology, and in connection with discussion on phylogeny of *Coccinea*, however without any new contribution.

III. MATERIAL AND METHODS

The Baltic amber scale insect collections

The oldest (half of the ninetheenth century) collections of the Baltic amber scale insect inclusions were those of Berendt (Koenigsberg, Kaliningrad) and Menge (Gdańsk). The former contained at least 17 pieces, but only 5 have been mentioned in the original papers; 12 pieces are now preserved in the musea of Berlin and Stuttgart; however, type specimens are not among them. Menge's collection consisted of 24 pieces (Menge 1856); it is unknown where (if) this material may exist.

The Staatliches Museum für Naturkunde, Stuttgart, loc. Ludwigsburg contains 11 inclusions, all from the Koenigsberg Collection. Six pieces are polished to thin plates and embedded in Canada balsam. The remaining ones are excellently polished but unmounted (Tab. I).

The Institut für Paläontologie und Museum at the Humboldt University, Berlin, preserves 9 scale insect inclusions: 1 of Berendt, 1 of Simon and 7 of Kuenow collections. All are very well polished and, except the piece of Berendt, embedded in Canada balsam.

In the British Museum, Natural History, London, only one large piece mounted in Canada balsam is preserved. According to the label, it has been collected on Samland.

Table I. Baltic amber scale insect inclusions available for the present study

	Family — stage																								
	Matsucoccidae			*Ortheziidae*			other *Ortheziidea*			*Pseudococcidae*			*Eriococcidae*			*Coccidae*			*Diaspididae*			Undetermined			
Depository	1	♀	♂	1	♀	♂	1	♀	♂	1	♀	♂	1	♀	♂	1	♀	♂	1	♀	♂	1	♀	♂	total
ZMC-MMC		15	39[a]			1	1		2	10[d]		2[f]	4		1[e]	5		1			1	1		2	85
PMHU	2		2						1			1	1		1			1							9
SMNS		2	4			1	1	2		(5)[b]	1														11
PIM					1				3	4[c]			1												9
BMNH					1																				1
MZW										1		1													2
total	2	17	45		2	2	2	2	6	15	1	4	6		2	5		2			1	1		2	117

[a] three specimes apterous, [b] these first stage larvae are embedded together with a female, [c] amber pieces have been considered, in some of them several larvae are present, [d] one piece contains 13 larvae, [e] apterous, [f] one specimen apterous

In the Paleontological Institute of the Academy of Sciences, Moscow, 9 amber inclusions are preserved. The pieces, except one, were unpolished when received for study, and 3 specimens (adult males) were greatly damaged because the pieces had been broken across the inclusions.

Two polished pieces have been found in the Museum of Earth (Muzeum Ziemi), Warsaw.

The largest material (85 polished pieces) for the present study has been provided by the Copenhagen Amber Collection, arranged at the Zoological Museum, Copenhagen, which also preserves amber inclusions owned by the Mineral Museum. This young collection, founded in the fifties, has grown very rapidly. In 1962 LARSSON mentioned 190 pieces with *Homoptera* inclusions; in 1965 the collection contained 212 homopteran pieces including 42 of scale insects, and in 1978 LARSSON recorded 439 *Homoptera*, among them 111 *Coccinea*. For further information concerning this collection see HEIE (1967) and LARSSON (1978).

Twenty one Baltic amber pieces of scale insect inclusions are preserved in the Museum of Comparative Zoology at the Harvard University. This collection has not been included to the present study.

Scale insect inclusions

The scale insect inclusions originated in the same way as those of other arthropods and underwent the same preservation and damage processes during embedding and petrification, but there seem to be some particular, or more often occurring, features and phenomena affecting amber fossils of this insect group.

The small weight and relatively large surface of winged males cause that they do not sink at once in the resin, but remain on the surface, with part of the body (usually the dorsal one) exposed to the air. Owing to the movement of the insect or some other reasons the surface of the resin hardens into numerous subcircular ripples and is further polluted with some substances of the insect and foreign particles until a new layer of resin entirely covers the specimen. The great majority of winged males are preserved in this condition and body parts situated directly within the ripples and lines are practically unavailable for examination.

Concerning the relation between body and resin, three conditions are possible. The resin may adhere immediately to the cuticle without entering the insect body (this condition offers the best results of study), or may be isolated by a thin layer of air; the body surface glitters then silverish, and the setae, enclosed within air-sheaths are distinct and look much thicker than they are in fact. Sometimes the air layer is thick and surrounds the appendages together with the setae in one strong sheath, making the examination of details impossible. Rarely the resin impregnates the body and then respective parts (particularly wings and setae) become more or less hyaline. This may bring to light some further details, but may also obscure many cuticular structures. Similar effects may secondarily occur when paraffin or other oil penetrates the insect body through fissures within the amber (see further remarks in "Methods").

The body is mostly significantly shrivelled and constricted, thus deformed in the resin. On the other hand, specimens not shrivelled are to a lesser or greater degree surrounded with milky (containing minute bubbles) resin. Sometimes the specimens seem to be swollen or filled with air, presumably for putrefaction processes which occurred before petrification.

As a rule, each of the amber pieces contains only one scale insect specimen, sometimes accompanied by other insects or mites. However, occasionally more specimens may be embedded within the same piece. Mostly they are first stage larvae (up to 13 specimens observed) which might have fallen to the resin with the ovisac. In one instance adult female with first stage larvae has been found, and in another one four females with one male. Such inclusions are of great taxonomic value.

Material studied

A total of 64 inclusions classified as *Matsucoccidae* have been selected from 117 available amber pieces; 54 belong to the Copenhagen Collection, 4 to the Humboldt University, Berlin, and 6 to the Staatliches Museum für Naturkunde, Stuttgart (Tab. I). All the amber pieces were well polished and did not require any further treatment, except that some were removed from the Canada balsam in which they had been embedded (pieces from Berlin and Stuttgart), when photographed and examined.

Some of the materials, when received for study, were not labelled (e. g. from the collection of Moscow) on some others the date when arrived in the collection, the finding locality and name of the collector are given (Copenhagen Collection); some inclusions have several numbers and marks of various origin. For this reason it seemed reasonable to give each of the examined pieces its own number preceded by the abbreviation "Cocc" (*Coccinea*) independent of to which collection it belongs, and mark the specimens originally closed within the same piece (even when later separated) with "a", "b", "c" etc. This procedure will made it possible to find easily the material again. Furthermore, it is hoped that this way, if consequently followed, a basis will be formed for a world catalogue of fossil scale insects. With the above number, followed then by the abbreviation of the depository and other collection and catalogue data starts the description of each inclusion. Similar method has been adopted to the amber aphids of the Copenhagen Collection (Heie 1967) with the difference that not amber pieces, but specimens have been numbered separately, and that, in case of the scale insects, the pieces were numbered incidentally, or according to dates (Copenhagen Collection) irrespective of to which species they have then been assigned.

Methods

The inclusions have been examined with an ordinary Zeiss microscope at magnification 60 × to 300 ×. Changeable transparent and direct lights have been applied, mostly both simultaneously. Sometimes the pieces have been lowered in mineral oil or covered with oil and coverglass to get a plane surface. The examination of amber pieces lowered in liquid paraffin or equivalent substances is a practice adopted by many students (applied to aphid inclusions by Heie 1967). The suitable refraction of the oils makes the examination of pieces with curved or rough surfaces much more succesful. However, in one or two instances the oil penetrated through fissures the amber piece and impregnated the inclusion, and eventually some cuticular structures dissapeared irrevocably. Thus students are warned of this method in some cases.

Measurements have been made with occular-micrometer and stated in μm. Since the scale insects shrivel significantly in the resin, measurements of the body refer to given inclusions and not to living specimens; usually they have been omitted for giving no reliable information. It has been tried to place the measured appendages, or their parts in a position paralled to the microscopic table; oblique objects have not been measured. But the dimensions of semi-parallel details are also affected with a fault, e.g. the same wing measured from dorsum and venter appeared to have different dimensions. It happens for the amber itself acts as a lens. Thus the error of the measurements must be evaluated as about 10%, and sometimes perhaps more.

For almost all drawings a prism occular has been employed. The few free-hand drawings are indicated in the explanations of figures. Specimens, or the same details of various specimens, although assigned to the same species, have been drawn because all they form a basis for an imagination of the living insects. It has not been tried to draw reconstructions because the specimens seemed to be much deformed and particularly, because the species as understood in the present study, are artificial units.

Respective figures are all drawn in the same scale, except that females of *Matsucoccus larssoni*, being much smaller than other species, have been drawn in a somewhat larger scale. Body parts obscured by milky resin are marked with sparse dots; dense dots indicate sclerotized parts of cuticle (technique adopted in scale insects) or simply the convexity of various body parts.

The terminology, abbreviations (see list below) as well as description scheme of adult male is greatly adopted from Beardsley (1968).

Table II. Structures and features accessible
Head numerals

Structures and features	*Matsucoccus larssoni*								*Matsucoccus*								
	15a	37	56	60	67	70	71	100	4	13	18	19	28	29	32	33	36
Head — at least from one side	+				+	+	+	+	+								
Antenna — at least length of flagellar segments	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Setae on pedicel								+									
Setae on 1st flagellar segment	+		+	+	+	+		+	+	+				+	+		+
Mesothorax from dorsum	+						+						+			+	
venter																	
side						+		+		+							
Wing — at least length	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+
sensilla and/or sclerites															+		
Hamulohaltere — setae	+	+		+		+		+		+	+	+	+		+	+	+
Legs — at least one tibia	+	+	+	+	+	+	+	+	+	+		+	+		+	+	+
Anterior and posterior tibia and femur	+	+			+	+		+									
Abdomen — at least seminatural shape	+					+		+					+			+	
Penial sheath from dorsum		+															+
venter	+												+				
side						+		+								+	
Length of wing, antenna and tibia	+	+	+	+	+	+	+	+		+		+	+		+	+	+
As above and number of hamuli	+	+		+		+		+		+		+	+		+	+	+

The information on included species is displaced in the following order:

— the basic, mainly quantitative information, obtained from all or numerous specimens is presented in Tables III and IV;

— brief descriptions and diagnoses of genus and species based on characteristics which have been stated in at least some of the examined specimens are given in Chapter VII. Features occurring in recent species, and certainly in the fossil ones, but not found in any of the studied inclusions, have been omitted from these descriptions;

— comprehensive description and discussion of taxonomic characteristics of the group are presented in Chapter VI.

for study in alate male
refer to inclusions

pinnatus										*Matsucoccus electrinus*										*Matsucoccus* sp.					no	%%
38	52	55	66	68	69	82	85	98	99	5	21	27	31	39	47	58	65	72	97	23	30	46	59	61		
+	+	+			+	+	+		+	+			+		+	+	+	+	+	+					21	50
+	+	+	+	+	+		+		+	+	+		+	+	+	+	+	+	+				+		35	85
	+	+					+			+	+				+			+		+					9	22
+	+	+	+				+			+	+			+	+	+		+	+	+	+				25	60
+	+	+					+										+								9	22
+	+						+																		3	7
					+							+				+		+	+						8	20
+	+	+	+	+	+	+	+	+	+		+	+		+	+		+	+	+			+			34	82
							+												+						3	7
+	+	+	+	+	+	+		+		+	+	+			+	+		+	+						27	65
+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+		+		37	89
+	+	+		+	+		+			+			+	+	+	+	+	+	+						19	46
+	+	+			+							+			+	+	+	+	+						15	36
+											+														4	10
	+									+															4	10
+		+	+	+	+							+		+	+	+		+							13	31
+	+	+	+	+	+		+		+		+			+	+		+	+							27	65
+	+	+	+	+	+						+				+			+							20	48

Abbreviations

ABBREVIATIONS OF DEPOSITORY NAMES

BMNH — British Museum, Natural History, London
MMC — Mineral Museum, Copenhagen
MZW — Muzeum Ziemi, Warsaw
PIM — Paleontological Institute, Moscow
PMHU — Institut für Paläontologie und Museum der Humboldt Universität, Berlin
SMNS — Staatliches Museum für Naturkunde, Stuttgart loc. Ludwigsburg
ZMC — Zoological Museum, Copenhagen

species		body		head	eye	antenna length of flagellar segments									setae on first	wing	
	Cocc	l	w	w	ø	total	I	II	III	IV	V	VI	VII	VIII	no	l	w
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Matsucoccus pinnatus	4			370	130	1200	130	150	160	140	150	140	140	130	16	1560	670
	13			300	130	1150	170	140	120	120	140	140	130	130	8	1680	650
	18	1200			150	1650										2040	890
	19				120	1300	170	160	170	170	180	150	120	115		1650	550
	28	1300	370	330	130	1300	180	150	150	160	140	150	140	130	10	1880	770
	29					1470	240	220	200	190	180	140	130	130	15	2040	
	32			300	120	1500	210	170	180	180	180	170	160	140	17	1820	770
	33	1300	450	370	150	1500	200	200	200	200	180	180	180	160		1850	770
	36				150	1470	180	170	180	180	180	180	170	160	15	2000	790
	38	1400	370		150	1500	220	180	180	190	200	180	170	180	19	1680	720
	52	1170	430	310	130	1500	220	190	200	200	190	170	160	150	12	1680	700
	55			360	150	1300	180	180	170	180	160	150	150	150	10	1920	860
	66				130	1300	150	180	150	150	150	150	140	140	9–11	1680	
	68	1125			150	1420	190	180	160	170	170	170	140	140		1680	720
	69	1270				1650	220	230	210	220	180	160	160	140		2040	820
	82	1170		300	150	1300										1800	720
	85	1200	330	290	150	1300	190			160	170	150	140	150	21	1820	770
	98					1500										2040	790
	99	1050				1150	140	140	120	140	140	120	120	110		1630	650
	min	1050	330	290	120	1150	130								8	1560	550
	max	1400	450	370	150	1650	240								21	2040	890
M. larssoni	15a			280	150	970	160	120	120	120	110	100	80	90	8–10	1420	600
	37				150	980	130	120	120	120	120	120	90	90		1150	530
	56	980		300	120	1050	130	130	120	130	130	110	110	110	11	1440	610
	60				110	900	150	120	120	120	120				9	1400	550
	67			370	130	950	170	140	130	120	120	110	100	100	23	1320	600
	70	970		300	120	900	110	100						90	10	1130	470
	71	1200	330	340	120	950	150	140					100	90		1300	600
	100	1000			120	900									16–18	1400	550
	min	970		280	110	900	110								8	1130	470
	max	1200		370	150	1050	170								23	1440	610
M. electrinus	5	1350	370	390	150	1870	270	250	230	250	250	260	190	170	16		
	21			340	160	1700	260	230	240	240	230	210	200	170	18	1990	
	27				160	1600										2040	840
	31			400	160	1900	260	240	250	250	230	220	190	160		2150	960
	39			370	150	1870	270			270	270			240	14	2600	1130
	47	1500		390	180	1800	250	230	230	240	240	220	170	190	15	2400	1030
	58			370	150	1870	250	200	200	230	220	210	190	200	14		1000
	65			400	160	1870	260	260	260	260						2100	930
	72	1450			160	1650	240	230	220	230	200	180	160	140	13	2300	1080
	97	1650	400	400	190	1810	270	240	240	220	220	220	200	210	10	2090	960
	min	1350	370	340	150	1600	240								10	1990	840
	max	1650	400	400	190	1900	270								18	2600	1130
M. apterus	35	1050	250	330	120											—	—
	54			190	100	750										—	—
	57	1400	300	340	130	1300	180	140	160	160	160	140	140	150	0	—	—

of male (dimensions in μm)

haltere		ant. leg			middle leg			post. leg			wing	ratios 1: ant.: wing	ti_3: ti_1	ti_1: ant.	ti_1: wing
l	no	fe	ti	ta	fe	ti	ta	fe	ti	ta	w : l	1 : 1	1 : 1	1 : 1	1 : 1
19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
			370	130							2.3	1.3		3.2	4.2
	4	340	450	130		400	120		370	120	2.6	1,5	1.2	2.5	3.7
190	4		550			550			550		2.3	1.2	1.0	3.0	3.7
	3	300	450	120		360	100		390	100	2.8	1.2	1.1	2.9	3.4
220	?4	390	540	150		570	150		450	150	2.4	1.4	1.0	2.4	3.6
		340	450									1.4		3.3	4.3
190	4		450	130					450	150	2.4	1.2	1.0	3.3	4.0
190	?4	370	490						490	150	2.5	1.2	1.0	3.1	3.7
180	5		520						450		2.5	1.4	1.1	2.8	3.8
160	4–5	370	550	150				280	450	130	2.3	1.1	1.2	2.7	3.0
130	4–5	360	450	120		370	120	300	450	120	2.4	1.1	1.2	3.3	3.7
130	?4	340	450	120	330	390	110	340	390	110	2.2	1.5	1.1	2.9	4.3
150	?3	300	450	120					380	120		1.2	1.2	2.9	3.6
	4	310	450	130		360		300	390	120	2.3	1.2	1.1	3.1	3.7
	5		550	160	330	450		360	510		2.4	1.2	1.1	3.0	3.7
150	4	300	430	130		340	120		390	110	2.5	1.4	1.1	3.0	4.2
		300	490	130	300	380	130		400		2.4	1.4	1.2	2.6	3.7
210	4		510	130		450	120		510		2.6	1.4	1.0	2.9	4.0
		270	370						330		2.5	1.4	1.1	3.1	4.4
130	3	270	370	120	300	340	100	280	330	100	2.2	1.1	1.0	2.5	3.0
220	5	390	550	160	330	570	150	360	540	150	2.8	1.5	1.2	3.3	4.4
120	3	220	250	100	220		100	220	280		2.4	1.5	0.9	3.0	5.7
150	3	210	270	100	250	300	100	210	270	100	2.2	1.2	1.0	3.1	4.3
150		270	300	100					270		2.5	1.4	1.1	3.5	4.8
110	2–3								270		2.5	1.5			
		270	330	100				220	330	100	2.2	1.4	1.0	2.9	4.0
150	1	250	300	100	220	300	100	240	300	100	2.4	1.2	1.1	3.0	3.8
150		220	300	120							2.2	1.4		3.2	4.3
130	3	250	330	110	240	330	100	240	300	100	2.5	1.5	1.1	2.7	4.2
110	1	210	250	100	220	300	100	210	270	100	2.2	1.2	0.9	2.7	3.8
150	3	270	330	120	250	330	100	240	330	110	2.5	1.5	1.1	3.5	5.7
210	7	450	690	180	400	600	180	390	600	180			1.1	2.7	
180	6	480										1.1			
190	7		570	150							2.3	1.3		2.8	3.6
		480	750	180					600	140	2.2	1.1		2.4	2.9
		510	710	180	510	600	180	510	710	180	2.3	1.4	1.0	2.6	3.7
210	4	450	640	180	430	600	150	450	570	140	2.3	1.3	1.1	2.8	3.7
190	7		670	150		550	130	390	570	130			1.2	2.8	
		450	600	180					520	180	2.3	1.1	1.1	3.1	3.5
190	6–7	480	670	150	370	570	140	400	600	150	2.1	1.4	1.1	3.4	3.4
220	7	490	670	150		550	150	460	640	150	2.2	1.1	1.1	2.7	3.1
180	4	450	570	150	370	550	130	390	520	130	2.1	1.1	1.0	2.4	2.9
220	7	510	750	180	510	600	180	510	710	180	2.3	1.4	1.2	3.4	3.7
—	—										—	—			—
—	—										—	—			—
—	—	340	420	130		420	150		450		—	—	0.9	3.0	—

Table IV. Quantitative characters of female (dimensions in μm)

	Cocc	body		antenna – length										width					leg	fe		ti		ta	
		l	w	I	II	III	IV	V	VI	VII	VIII	IX	tot.	I	II	III	VIII	IX		l	w	l	w	l	w
M. larssoni	15b	720	360	30	24	30	30	30	30	30	30	30	264	36	30	24	24	18	III	72		72		48	
	15c	936	408	42	24	30	30	30	30	30	30	30	276	48	42	30	30	24	I			72		42	
	15d	720	384																III			72		48	
	15e	1032	432	72	36	30	30	30	36	36	36	36	362	84	60	42	42	30	I	120	48	100	36	66	24
	11	600	288																III	132	36	90	24	72	20
Matsucoccus pinnatus	17	1296	480	102	60	30	42	42	42	48	36	48	450	90	66	54	42	36	I	180		120		72	
	22	960	648	108	54	42	42	48	48	54	48	66	510	90	72	48	42	36	I	192	60	150	35	102	24
	50	1056	624																I			120		96	
	73	1200	648	102	60	42	42	42	36	42	42	48	456	90	80	60	40	36	II	180		144		90	
	74	1632	720	90	60	48	48	48	48	54	48	60	504	108	90	60	48	36	I			150	36	102	24
	75	1440	770										540						I					108	
	77	1392	720	102	54	48	42	42	42	42	42	48	462	108	102	90	54	36	II	192		120		84	
	81	1128	600										384						I			132		77	
	94	1560	480	90	60	30	36	36	42	42	42	48	426	90	60	42	36	30	I	156		132		78	
	95	1248	576	114	60	42	42	42	48	48	42	48	486	90	64	50	50	42	II	192	60	168	42	90	30
M. electrinus	14	2160	1320	120	72	48	60	60	60	60	60	60	600	90	72	48	36	30	II			180		120	
	26	2040	1080										600						I	240		210		120	

ABBREVIATIONS IN TABLES AND FIGURES

a — anus
ab — antennal bristles
aed — aedeagus
af — anal fold
as — abdomial segment
asc — auxiliary wing sclerite
ast — abdominal sternite
at — abdominal tergite
ax — axillary wing sclerite
ba — basalare
ccx — costal complex
ce — compound eye
cs — capitate setae
cv — cervical sclerite
cxa — coxa
dms — dorsomedial sclerite
eps — episternum
fe — trochanter + femur
hh — hamulohaltere
l — length
la — labium
m — media vein
mcr — midcranial ridge
mem — membranous derm
mo — mouth opening
mr — marginal ridge
mt — metathorax
oc — ocellus
ocs — ocular sclerite
ols — ommatidium-like structure
pa — postalare
pcr — precoxal ridge
pdc — pedicel
plr — pleural ridge
pn_2 — mesopostnotum
pock — pocket
pra — prealare
pres — prescutum
ps — penial sheath
pt — prothorax
pwp — pleural wing process
r — radius
scp — scape
sct — subcostal thickening
scu — scutum
scut — scutellum
ser — subepisternal ridge
sens — sensilla
$sh\pm$ — stellate hairs, present or absent
spb — sperm bundle
$stap_2$ — mesosternal apophysis
$stap_3$ — metasternal apophysis
stn_2 — mesosternum
stn_3 — metasternum
t — tegula
$ta_{1\text{-}2}$ — tarsal joints
tdc — tubular duct cluster
ti — tibia
vms — ventromedial sclerite
vp — ventral plate
w — width
wf — wax filaments

IV. THE STATUS OF *ACREAGRIS CRENATA* AND *MONOPHLEBUS IRREGULARIS*

Acreagris crenata Koch et Berendt and *Monophlebus irregularis* Germar et Berendt have been affiliated with the *Matsucoccidae*. According to the present investigations this opinion is not quite justified, thus it is necessary to discuss the question once again.

Acreagris Koch et Berendt in Berendt 1854 (first bionominal presentation and description of species) has been established as a monotypic genus among the "Aptera" within the family *Poduridae*. However, in the paper there is a footnote signed by "M". (supposedly Menge):

"Meine Sammlung enthält... von *Acreagris* 10 Exemplare...; nur will ich mir noch zu bemerken erlauben, dass ich *Acreagris* für nichts anderes als das *Monophlebus* Weibchen halte". Menge's "*Monophlebus*" refers here to male amber coccids described by Germar and Berendt two years later (1856), but which were known to him.

Menge repeated this opinion in his own paper on the Baltic amber fossils which was published simultaneously with the monography by Germar and Berendt (1856). He says:

"Mit diesen thiere... (Ochyrocoris)... stehen in naher verwandschaft die gattung dorthesia... und monophlebus, dessen weibchen Koch unter dem namen acreagris als besondere apteren gattung beschrieben hat".

Ferris (1941) redescribed briefly the forgotten scale insects, on the basis of amber pieces preserved at the Harvard University, illustrated some morphological details and presented the following suggestions:

1. *Acreagris crenata* ♀ Koch et Berendt 1854 is a senior synonym of *Monophlebus pinnatus* ♂ Germar et Berendt 1856,

2. *Monophlebus irregularis* ♂ Germar et Berendt 1856 is a junior synonym of *Monophlebus pinnatus* ♂ Germar et Beredt 1856 (page priority),

3. *Acreagris* Koch et Berendt 1854, is a senior synonym of *Matsucoccus* Cockerell 1909,

4. *Monophlebus trivenosus* ♂ Germar et Berendt 1856 is not a member of *Margarodidae*, but rather belongs to *Pseudococcidae*.

Eventually, Ferris formally proposed only the first conclusion which continues the idea by Menge, and has also been accepted by other coccidologists (Beardsley 1968, Morrison and Morrison 1966).

Ferris rejected the suggestion no 2 "because of absence of autentic specimens", and not for "four or five species... may be found upon the same pine", as he wrote on the same page. Conclusion no 3 has been rejected because "*Matsucoccus* is now a well-known genus..." and "the name should, if at all possible, be preserved", and because "... there are still various features of *Acreagris crenata* which are not known".

However, there is also no reliable basis for conclusion no 1. In fact, the general appearance of Koch's drawing may certainly fit for specimens examined by Ferris and identified with *Matsucoccus*; this is also my personal impression. Further, the fact that the definite majority of known fossil females are similar to *Acreagris crenata* may justify Ferris' opinion, but the original description mentions no one matsucoccid feature, neither they can be found on the drawing. Prepupa and adult female have a two-joined tarsus and are devoid of mouth-parts, while the tarsus in *Acreagris crenata* (figure) is one-joined, and the absence of mouth-parts is not mentioned in the description.

As mentioned above, Ferris followed the opinion of Menge that *Acreagris crenata* is a female of "*Monophlebus*" (*Matsucoccus* according to Ferris), but Menge (1856) says:

"Von monophlebus pinnatus Germ. hat meine sammlung zwei geflüglte thiere, von m. irregularis 1 st; auserdem... 16 ungeflügelte weibchen, deren zugehörigheit schwer anzugeben ist. An zwei exemplaren der letzteren (*acreagris* Koch) is der saugrüssel deutlich, und daher nich zu bezweifeln, das sie hier ihre richtige stellung haben. In einem stück befinden sich drei exemplare, ein beweis ihres geseltigen lebens".

It is clear from this citate that MENGE's problem was not the question whether the wingless females were *Acreagris*, but whether these insects, described two years earlier in the "Aptera" may correctly be placed within the scale insects. MENGE believed that they all had beak-like mouthparts, although not always visible in the fossil specimens. Furthermore, he treated them (females), at least the specimens provided with mouthparts, as belonging to the "species" in question (i. e. *Acreagris crenata*). "Species" is taken within quotation-mark because MENGE distinguishes quite well species within "*Monophlebus*" (each of the three mentioned species is a member of a different family according to the present investigations), and on the other hand considers *Acreagris crenata* as females of *Monophlebus* without indicating any species.

Among fossils examined during the present course there were specimens externally quite similar to *Acreagris*, but provided with mouthparts and with a one-joined tarsus, thus definitely not related with *Matsucoccus*. Therefore, it seems to be reasonable to consider *Acreagris crenata* as nomen dubium until the type specimen will be recovered, and refer *Monophlebus pinnatus*, as well as specimens (♀and ♂) described by FERRIS (1941) to the recent genus *Matsucoccus*.

It is evident from this discussion that MENGE did not recognize within the larviform females members of different species or groups, thus his opinion that *Acreagris* are females of *Monophlebus* is devoid of any value.

As mentioned above, FERRIS considered *Monophlebus pinnatus* as a male of *Acreagris crenata*, while *M. irregularis* as a junior synonym of *M. pinnatus* and all as members of the genus *Matsucoccus*, but refused to propose a formal conclusion because of lack of autentic material. However, there are several characteristics in the original description of *M. irregularis* which indicate that this species does not belong to *Matsucoccus*. The antennae have 18 joints "in der Mitte kugelartig aufgetrieben", which simply means that there are supposedly 10 joints, but the flagellar joints being distinctly binodose (scape, pedicel $+ 2 \times 8$), a feature never met in *Matsucoccus*. The original description mentions "Anhänge oder Raife... auf den Ecken des Aftersegments" which correspond with the "Fleischwarzen... bei anderen lebenden Arten". These structures are certainly abdominal lobes or "fleshy tassels" occurring in *Monophlebidae*, but not in *Matsucoccidae*. The structure of the wing with the very regular fine foldes is unique in *Matsucoccus*, while in *M. irregularis* these folds are irregular in the middle of the wing. At last, GERMAR and BERENDT emphasized that the structure of the wing in *M. irregularis* resembled that of *M. trivenosus* (considered by FERRIS to be a pseudococcid) and not *M. pinnatus*, as we might expect, if FERRIS' conception would be right.

The discussion may be concluded as follows:

1. *Monophlebus pinnatus* ♂ GERMAR et BERENDT is a matsucoccid and will be dealed with on the following pages,
2. *Monophlebus trivenosus* ♂ GERMAR et BERENDT may be a pseudococcid as suggested by FERRIS (and earlier by COCKERELL 1909a) while *M. irregularis* ♂ GERMAR et BERENDT a monophlebid,

3. *Acreagris crenata* ♀ Koch et Berendt may be a matsucoccid, but none of the listed characters nor the figure indicate that it actually belongs to this group; thus it is not included in the present paper.

V. HOST AND LIFE HISTORY OF THE FOSSIL *MATSUCOCCUS*

The present day *Matsucoccus* lives exclusively on *Pinus* and most species feed on trunk and larger branches. The first stage crawlers wander about under the bark scales; here they grow and moult into the second apodous stage. From the female second stage, called preadult or intermediate female, emerge mature, mobile, but unfeeding specimens, while the male second larva moults into the third stage (prepupa) which is also mobile and resembles morphologically the adult female. The pupa (male forth stage) and adult male (fift stage) correspond with those of other scale insects. After mating (some species are considered to be parthenogenetic) females lay eggs within loose ovisacs. The dates of hatching, oviposition, duration of diapause and other phenological data vary from species to species, even when occupying the same area or the same tree. There may also be one or more generation per year.

Although serious investigations have been carried out on the life history and ecology of *Matsucoccus* for damages which it causes to the forests, there are many obscure points of the development, reproduction and behaviour of this coccid, and the records contain contradictory and misleading information.

From the point of view of the present investigations it is important to note that *Matsucoccus* is confined to the genus *Pinus*. Botanists believe that the Baltic amber originated from resin produced mainly or exclusively by a pine — *Pinus* (or *Pinites*) *succinifera*. However, various investigations on chemical and physical features of amber indicate that it could be produced by various trees, perhaps mainly angiospermous, but that the mother plant of the Baltic amber cannot be closely related with any of the recent *Pinaceae*, since the compounds and characteristics of amber are quite well distinct from resin produced by the present day pines (Larsson 1978).

As far as the scale insects are concerned, the present findings do not concur with the above presented opinion, but strongly favour the view of the orthodox paleobotany: about 55% of the currently known Baltic amber inclusions belong to *Matsucoccidae*, while as many as 77%, when adult females are compared; not considering other groups which also may infest the pines (Tab. I).

The assumption that *Pinus* was the actual mother tree of the Baltic amber is further supported by the larva — female — male proportion. Among the examined material there were 2 first stage larvae, 17 adult females and 45 males of *Matsucoccidae*, while 29 pieces with first or young stage larvae, 5 adult females and 19 males of all other groups. It means that in the matsucoccids the first stage larvae (passive disperssion) and adult males (active movement) constitute about 73 % while in the others about 90 % of the inclusions.

Similar conditions have been observed in the Baltic amber aphids. Heie (1967) examined 138 specimens in 39 species, but as many as 53 (about 38%) were representatives of *Germaraphis dryoides* (Germar et Berendt). The situation in this case is somewhat complicated by the fact that *G. dryoides* is known only from fossils and its relationships are not quite evident, thus Heie concluded: "If *dryoides* is related to *Phloemysus*, *Populus* is a conceivable host; if it is related to *Stegophylla*, *Quercus* is a probable host, and if it is related to *Mindarus*, *Coniferae* are probable hosts".

Heie discusses further the peculiar deformations of parenchyma often occurring in amber. According to some authors *Germaraphis* should be responsible for their origin, but Heie does not concur with this assumption: "The tissue in question rarely occurs in the early springwood, more frequently between the spring and the summer-wood or in the summer-wood. Neither Conwentz nor others have found *dryoides* or other aphids on such branches, however, and no proof of the connection suggested is available". But these deformations fit very well with those caused by at least some recent species of *Matsucoccus* which represent serious forest pests (McKenzie 1943, Siewniak 1969, and others).

The amber tree is eventually classified within the genus *Pinus*, as *P. succinifera* Conventz 1890, but no closer relationship of this pine to any of the now-living species could be found. Summarizing the dendrological studies of Schubert, Larsson (1978) stated: "... he too was unable to find any recent *Pinus* which could reasonably be considered a descendant of the amber tree".

It seems to be very likely from the above discussion that the speciation and radiation of *Pinus* and *Matsucoccus* have followed simultaneously and analogically, and that studying the taxonomy and evolution of *Matsucoccus*, we will have the same troubles as in the case of *Pinus*.

Another important question is the way and circumstances of the origin of the matsucoccids inclusions. All the mobile stages (adult male and female, male third stage, and first stage crawlers) could have fallen into the resin like other active arthropods, but since living on the tree which exudates resin, one could expect that the insects should also be overflown with the resin in situ. In this case feedingfirst stage and second stage larvae as well as pupae and egg-laying females with ovisacs should occur in the amber, but this has not been stated, except that in one or two instances there were small bubbles near the female bodies which could originate from air of the ovisac. The lack of immobile stages and dead females with eggs may be explained by the supposed habitat of the insects (they might have lived on small twigs), or simply by the circumstance that they have not been recognized as scale insects (or insects at all) during the preliminary selection of amber inclusions. This particularly concerns the globular apodous second stage exuvia which remain in enormuos numbers under bark scales through years, but which remind rahter egg-shells of some athropods, or products of a plant origin.

It is characteristic of *Matsucoccidae* and some related groups that the integument of the adult females seems to be "too large" in comparison with the body content, thus they are worm-like. This effect is further marked by the membraneous cuticle. In result, the females may significantly shrivel and contract even when alive, and in the amber most of the specimens look like females after oviposition. On the other hand, some specimens (more often the males than females) might have dried out before being covered with next layers of resin, or had fallen to the resin being dead. However, some of them are not shrivelled, and in these instances the body is all in milky resin, caused surely by water or gas from the insect.

The males live only a short time. According to Beardsley (1968) *Matsucoccus bisetosus* males died the same day when emerged from the puparia in laboratory conditions. When stressed, they very easily ejaculate sperm. This certainly occurs often, but have rarely been observed. In the amber about half of the specimens have been found with the sperm ejaculated into the resin. It seem be quite obvious that the males had fallen into the resin when looking for the females.

There is a close morphological similarity between adult female and male third stage (prepupa). Practically, the size of the body and appendages are the only criteria which allow the recognition of these forms in amber pieces, but there are certainly species adult females of which are as small as are large the male third stage of other ones. Among the examined material there were one alate male and four specimens which could be regarded as adult females or male third stage in one piece of amber (later dissected into five pieces). These specimens were definitely smaller than others, considered to be adult females, thus initially they have been determined as male third stage. However, further studies on adult males revealed that their size may vary within 100%, and the male embedded together with the specimens in question was actually one of the smallest; thus eventually they have been identified as adult females, the more so that it seemed reasonable to expect the male associated with adult females rather than with the prepupae (pupae have not been found).

Another, and perhaps the most difficult problem in studies on fossil coccids arises from the extreme sexual dimorphism of these insects. It is not possible to identify the males and females as one species on the basis of the same external criteria. For various, mainly practical reasons, the females are easier to be studied, and the taxonomy of lower taxa is based exclusively on adult females. In the case of fossil material preserved in amber the situations is quite reverse — males dominate among the inclusions and provide more information for taxonomic studies. Thus, the taxonomy of fossil *Matsucoccus* has been based on adult males, while the females have been "ascribed" to the males. It is not quite sure now whether this procedure may be applied to all amber material. Another solution is to establish separate species for males and females, or wait for an incident that male and female will be found in the same amber piece which has actually once happened (see above).

Beside sexual dimorphism, polymorphism of males may occur in some recent species. The differences between various forms concern mainly the wing apparatus, i. e., the wings (and consequently the structure of mesothorax, sense organs etc.) may be reduced to various degree, from full winged to apterous and larval forms; however, in some species, may be it is the rule, only one form is known. Among the *Orthezioidea* (= *Margarodidae* s. l. including *Ortheziidae* and *Phenacoleachiidae*) very few species are known in which the male is larviform, but in these cases it has simple eyes or ocelli only.

Within the amber inclusions several males have been found which are assumed to be matsucoccids, but which are devoid of wings, while having compound eyes. Apterous males have not been met among the recent *Matsucoccidae*.

Further difficulties in studies on fossil matsucoccids arise from the fact that at least some species are considered to be parthenogenetic (Boratyński, 1952). If among the fossil material are parthenogenetic species, then any attempts of combining females with males are devoid if sense.

Information on the time (season) may be provided by the coincident occurrence of other fossils in amber pieces with matsucoccids inclusions. Among them the so called stellate hairs play the most important role. These structures, being products of some trees, mainly the oaks, occur in enormous numbers in the spring, so that they may be found even in small amber pieces. Their presence (or absence) in given amber pieces could be then an additional argument for the relation of specimens, since species differ, among others, by their seasonal histories. However, in species with more than one generation per year, the generations may also differ morphologically. As shown recently by Ben-Dov (1981), *Matsucoccus josephi* Bodenheimer et Harpaz females exhibited, in addition to much greater variability than it has been expected, considerable differences between the spring and autumn generations. Thus, concerning the amber material, specimens distinct morphologically and with stellate hairs present or absent, may belong to the same species.

In the examined material stellate hairs have been found in about ⅓ of amber pieces, but no correlation between the presence of hairs and morphological characters has been stated, thus eventually individuals accompanied with stellate hairs have been classified within all species recognized among the amber inclusions.

VI. ANALYSIS OF TAXONOMIC CHARACTERISTICS

The main purpose of the present discussion is to answer the question how many species represent the Baltic amber inclusions recognized as *Matsucoccidae*. Little help can be expected from the knowlegde of the recent species because (a) the characteristics and diagnoses of female are based on structures which can be studied on amber inclusions only to some extend, or not at all; (b) the over twenty species numbering *Matsucoccus* is very little known — there is no key, nor revision covering the whole group; (c) the male is described in three or four species, but even the most detailed study of *M. bisetosus* MORRISON by BEARDSLEY (1968) lacks information the knowledge of which appeared important in the analysis of the fossil material; (d) the variability of adult males has not been studied in any species — the monographs by GHAURI (1962), GILIOMEE (1967) and AFIFI (1968) are based on an analysis of about 10, certainly brother, specimens of each species, and like in the female, numerous characters cannot be examined in the fossil material.

It is evident to the cocidologists that given characters can be examined only in a portion of the prepared specimens; but the student usually knows, before examination, that the sample to be studied forms one biological unit, and that features, although not observed in that or another individual for various reasons, "certainly" exist in all of them. Furthermore, it is usually possible to prepare further specimens to get an exact answer to a given question. None of these conditions occur in studies on amber material. Thus it seems reasonable to inform the reader which features and characteristics can be examined and in how many specimens (Tab. II). For instance, the length of wings and antennal segments could be measured in about 85% of specimens, setae on hamulohalteres in 65%, sclerites of mesothorax (at least from dorsum) could be examined only in 22%, and several structures, as setae on head, sensilla on wing base, have been observed only in one or two specimens; the gland cluster could not been seen exactly in any alate specimen. The more so limited is the possility of simultaneous comparison of several characters. The length of wing, antenna and posterior tibia — characters available for examination in most specimens — could be measured only in 65% of specimens, and if the number of hamuli is added to the above combination, then the possibility of comparison becomes lowered to about 48%.

The description of adult male follows the scheme proposed in the classical monographs (GHAURI, GILIOMEE, AFIFI, l.c.), and the fossil specimens are compared, as far as possible, with the recent species, particularly with *Matsucoccus bisetosus*, described by BEARDSLEY (1968). With respect to the female, such comparison is extremely reduced for reasons pointed out above.

Alate male

The specimens are yellowish brown to dark brown, depending on whether and how the resin has penetrated the body. The plumbish blue colour occurring in some specimens originated supposedly from pirytes, and the black or silver appearance depends on the air which surrounds various body parts, particularly the setae.

The specimens are 970–1650 μm long, 300–400 μm wide, but these numbers are apparently smaller than dimensions of living individuals because of significant shrinking of body in resin, with which not only weak, but also the hard parts, as head capsule and mesothorax are affected.

The head is transversely subtriangular, definitely shorter than broad (280–400 μm wide), with antennae inserted deep between eyes; flattened dorsoventrally – the eyes are larger than height of head. The dorsomedial sclerite is diamond-shaped, with lateral corners extending nearly to margin of compound eyes. Postoccipital ridge and sclerites have not been detected. The ventromedial sclerite is triangular, with apparent preoral ridge. The mouth opening has been noted on one specimen. Other structures of this head region are poorly preserved. Both dorsomedial and ventromedial sclerites (plates) are bisected by a well defined, longitudinal midcranial ridge. The ocular sclerites are surrounded with a distinct ridge; anteriorly entirely occupied by compound eyes, posteriorly developed in the form of conical projections with simple eyes at apices. Generally, the above description fits with the structure of head in recent species, except that the diameter of eyes is definitely greater than the height of capsule in the fossil specimens.

Two minute setae have been found on dorsal face of head in *Matsucoccus bisetosus* (Beardsley 1968) and *M. matsumurae* (Morrison 1928), while 6 setae on ventral face of the former. In the fossil material the setae are difficult to study, but in the few cases when they could be seen, they were quite large (about 35 μm in comparison with 6–13 μm given by Beardsley) and numerous (over 10, sometimes even 40–50 seemed to be present).

The compound eyes are very large (120–190 μm diameter), hemispherical, definitely circular in lateral view (broadly oval in *M. bisetosus*), composed of about 100 ommatidia. In one specimen there is a spherical tubercle on one side of the dorsomedial plate (Fig. 11: A–5) which makes an impression of an ommatidium, but may be also an artefact.

The antennae are filiform (900–1900 μm long), 10-segmented; in few instances 7–9 joints, and in one 11 ones have been counted. In all cases only one antenna was affected with such abnormalities. The scape is cylindrical, shorter than broad; it seems to be covered with numerous setae. The pedicel is broadly ovoid, with one long seta (about as long as the segment), few shorter setae and numerous minute setae. Above characteristics do not correspond with those described in *M. bisetosus*, neither they can be exactly studied in any of the fossil specimens. The flagellar segments are cylindrical or very slightly clubshaped, except for the first segment which is usually definitely expanded at apex. The apical segment is always the shortest, constituing about ⅔ or ¾ of the longest segments; then follows the subapical segment. In the majority of specimens the first flagellar segment is the largest one, rarely it is equal, or slightly shorter than the second segment. However, there is no correlation between relative lengths of first and second segments and the entire length of antenna or other characteristics. The width-length ratio of flagellar segments varies significantly from specimen to specimen but is not correlated with length of segments (Fig. 5; C). It seems be likely that the shape of flagellar segments is greatly affected with artefacts during embedding in resin. The same can be said on antennal sensilla which sometimes are excelently visible, sometimes hardly recognizable.

Beardsley (1968) recognized "slender setae", setae "with slightly expanded spatulate apices" and "thicker digitiform setae" on flagellum, of which the two latter occur only on apical segment. In males of other scale insects a greater diversity of sensilla has been stated (Ghauri 1962, Giliomee 1967, Afifi 1968). In the fossil *Matsucoccus* basiconic or coeloconic sensilla could not be detected; it was also not possible to distinguish between "fleshy" and "hair-like" setae, but the "digitiform setae" (antennal bristles) and "capitate setae" are quite distinct. The former occur on 4 terminal segments (not on one as given by Beardlsey). On apical segment the setae, 2 in number, are strongly bent to each other, forming together a closed circle; on 3 proximal segments the setae are straight and long (about half the length of segment), usually (always ?) 2 in number. The number, shape and size of these setae may possibly be important in recognizing species, but should first be studied and applied to recent material. The capitate setae may occur on all flagellar segments (on apical one only, accordings to Beardsley) and are inserted on the very apices of segments. On apical segment the setae, 4–5 in number, are definitely shorter than on the intermediate segments; on these segments the capitate setae are straight, longer than ordinary setae, but shorter than antennal bristles; their number increases from 1 or 2 on first to 4 on seventh flagellar segment, but sometimes they may be absent on proximal segments. Beside the above types 2–4 short and straight setae have been found on all flagellar segments, except perhaps the frist one. They may be homologous with the basiconic sensilla, but their proper nature must be studied on recent material. The length of the "oridinary setae" varies between the width and double width of flagellar segments. About 10–30 setae may occur on each segment, but they are difficult to count. On first antennal segment they are usually sparse, from about 8 to 23 (none in the apterous specimens). In *M. bisetosus* (Beardsley 1968) and *M. matsumurae* (Morrison 1928) only 2 and 3 setae, respectively, have been drawn on this segment. Whether these differences have any taxonomic value must be examined on larger material.

The complicated structure of thorax is very difficult to study on fossil material because of deformations and difficulties in distinguishing between ridges, scletrites and membranes recognized on the basis of stained preparations. The brief description below should only support this opinion that the material at hand is actually *Matsucoccus*.

The membranous prothorax is in all specimens completely shrievelled and constricted, so that the anterior legs seem to be inserted at the ventral face of head. In some specimens the strong cervical sclerite has been noted and in several others the tergite which looked rather like a solide, transversely subrectangular plate, while drawn by BEARDSLEY (l. c.) in the form of paired longitudinal patches (postergites). This plate is covered with numerous (over 20) minute setae with slightly knobbed apices. There is no mention of this feature in the paper by BEARDSLEY.

The mesothorax is extremely strongly compressed from sides, distinctly deeper than wide, with convex dorsal and ventral sclerites, as shown in all *Matsucoccus* species. The prescutum is oval, longer than wide; scutellum of similar shape, is smaller than prescutum; the broad prealares join prescutum and mesepisterna. The mesopostnotum is not clearly visible in any specimen, except for its anterolateral portions (postalares) viewed from side. All sclerites of the pleural region, with the characteristic, nearly circular, episternum are similar to those described in recent *Matsucoccus* (see BEARDSLEY 1968 and Figs. in the present paper). The mesosternum is large, strongly convex and sclerotized, well defined by the marginal and precoxal ridges. In one specimen the strenal apophysis may well be seen (Fig. 6; A–85).

The metathorax is largely membranous thus shrievelled and deformed in the amber. Like on pronotum, there is a large group of minute setae with knobbed apices on metanotum. The setae seem to be much more abundant than drawn in *M. bisetosus*.

The legs are comparatively well preserved in the amber, although difficult to be measured owing to oblique position of given parts. All segments are covered with characteristic reticulation. The anterior coxae are definitely longer than the remaining ones, and all with two groups of minute setae at basal ridge (resembling supposedly the "hair plates" of other insects) and numerous longer setae on all surface, except ventral one (only 2 setae have been drawn on coxa in *M. bisetosus*, BEARDSLEY, l. c.). The trochanter is constricted medially, with 2 groups of minute setae (3–4 setae in each) which supposedly represent also hair plates; the proximal part is provided with 3–4 setae, while the apical one with a long seta (and several small ones ?). In the recent species only 1 or 2 setae have been stated on trochanter. Campaniform sensilla have not been found in the fossil material. According to MORRISON (1928) 6 sensilla are present on trochanter in *M. matsumurae*.

The femur is always shorter than tibia, with numerous, thin and small needle-like setae; near apex setae are somewhat longer. The tibia is slender, almost parallelsided, with straight, spine-like setae on ventral face and somewhat weaker setae on dorsal one. In comparison with other segments, the setae on tibia are inserted definitely more perpedicular to the segment surface. The anterior tibia is usually longer than the remaining ones, rarely this joint is subequal in all legs, and only in 3 cases the posterior tibia was the longest. However, no correlation could be found between the size relation of anterior and posterior tibia and other characters, e.g., the size of legs. The tarsus is relatively short, one-segmented, with a double row of 8–10 setae on ventral margin, and 1 seta on dorsal side. The ventral setae are long, weak and curved in comparison with the small dorsal seta. In addition there are 2 minute, needle-like setae at apex of tarsus dorsally, and another 2 ventrally; the former may represent tarsal digitules. The claw is slender, slightly bent (conditions opposite to those in *M. matsumurae* and *M. bisetosus*), with strong digitules the tips of which exceeding the apex of claw.

The wings are structures the best preserved in amber, 1130–2600 μm long, 470–1130 μm wide. Among the margarodids (s. l) the wing in *Matsucoccus*, and perhaps *Steingelia*, are narrow, width: length ratio being 1 : 2.1–1 : 2.8. No correlation between this feature and the size of the wing has been stated. All the wing disc is folded in parallel ripples which radiate from the median vein at the angle of about 60° near the centre of disc. These ripples give the wing in *Matsucoccus* a characteristic pinnate nature. The number of folds per unit of wing surface is almost constant (about 5.6 on each 100 μm in the center of disc) independent of the wing size. Although the actual veins cannot be seen on the fossil material, they seem be identical with those described and illustrated by Beardsley (1968). It may only be added that what Beardsley calls "thickenings" are only (or mainly) longitudinal folds; such thickenings viewed from reverse look like grooves. The sclerites of the wing base could be seen only in 2 or 3 hyaline wings impregnated with resin (or secondarily with oil); however it cannot be said whether they have been correctly drawn and interpreted (Fig. 10: D). The pocket for holding the hamuli is identical with that described by Beardsley (l.c.). In the region of the costal complex, dorsally, there occurs a group of about 10 minute sensilla (Fig. 6: G) corresponding with the alar setae in the *Pseudococcidae* and *Eriococcidae* (Afifi 1968), but campaniform sensilla at about ⅓ the length of radius which occur in *Pseudococcidae* and other primitive groups have not been observed in the fossil *Matsucoccus*. There is no mention of both the sensilla in recent species in the papers by Beardsley (1968) and Morrison (1928).

The halteres may well be seen in numerous specimens; they are clubshaped, mostly much more slender than in *M. bisetosus* and *M. matsumurae*, with 1–7 hamuli of usual shape (Figs. 5: E, 6: H, 10: E). The number of hamuli generally corresponds with the size of anterior wing. Among species studied 2 hamuli occur in specimen redescribed by Ferris (1941) as *Acreagris pinnatus* from Baltic amber, 4 in *M. bisetosus* (Beardsley 1968), about 6 in *M. matsumurae* (Morrison 1928) and 7–8 in *M. secretus* (Beardsley l. c.).

Little can be said on the membraneous and shrievelled abdomen, except that in several specimens numerous minute setae of the same shape as on thorax been observed on 1–7 abdominal tergites (Fig. 11). The occurence of similar setae on sternites is not quite evident, although here and there small setae have been noted. The 7th segment bears the pore cluster plate characteristic of *Matsucoccus*. The tubular glands protrude above the plate surface as in recent species (Figs. 5: D, 8: G), similar is also the shape and size of the tube (observed in one specimen impregnated with resin). Resoluting from the number of waxy treeds, 8–12 ducts occur in the amber species, i. e. definitely smaller than in the recent species. The 8th segment is normal, little shrievelled, with few minute setae on dorsum and venter.

The penial sheath is often well preserved and available for examination from various sides, but difficult to be measured because of oblique positions. Thus sometimes it lookes long and slender, sometimes short and broad. The large, strongly sclerotized, almost ringshaped 9th sternite forms the basis of the sheath. Its dorsal ends articulate with the longitudinal ridges which are hardly, or not at all separable from the margins of the 9th tergite. The latter bears the oval anus at about half its length and posteriorly tappers to a moderately sharp tip. Laterally the sheath is formed of membraneous bulges and ventrally occur the basal rods which articulate the aedeagus with the 9th sternite. The bulges bear several setae; minute setae, supposedly basiconic sensilla also occur on apex of the penial sheath (Figs. 8: D, 11: D); these sensilla have not been mentioned by Beardsley (1968). Generally, the sheath seems to be more slender, particularly in the part posterior to anus, than in *M. bisetosus*. The aedeagus is strong, almost parallelsided, curved.

Apterous male

Wingles males may occur althogether with brachypterous and alate forms within the same species, but may also represent the only form of adult male in various groups. The main differences between winged and wingless males, beside the absence of the wings, occur in the structure of mesothorax, but several other body parts may be affected with the consequences of the wing reduction.

Among the few apterous males of the Baltic amber, three specimens definitely belong to the *Matsucoccidae*. It is demonstrated by the structure of head, antennae, legs, penial sheath and pore cluster plate. However, these specimens are characterized by a feature unique in the scale insects – being apterous, they have compound eyes of the same type as the alate specimens; as it is known, the margarodid (s. l.) wingless males have a pair of ocelli like the females and larvae (*Stomacoccus*) or simple eyes (isolated ommatidia) arranged in groups or circle (*Phenacoleachia australis*).

Another somewhat peculiar feature is the presence of a well developed pore cluster plate (in apterous males these organs are greatly reduced).

Adult female

The specimens considered to be adult females offer very few characteristics for infrageneric taxonomic studies. Practically only the size of legs as well as size and shape of antennal segments may be used to separate species, although the different shapes of the antennal joints may as well be interpreted as artefacts.

In one instance some adult females have been found with an alate male in the same amber piece, thus it may be supposed that both belong to the same species, the other have been arbitrally assigned to the remaining species (see also discussion on life history and conclusions below).

First stage crawler

The available Baltic amber material contains two first stage larvae (crawlers) which definitely belong to *Matsucoccus*. It is evident from the shape of the body and legs, and particularly from the shape of the antennal segments and their sensilla which are almost identical with those described in *M. matsumurae* (Morrison 1928). The specimens have been assigned to the fossil *M. pinnatus*.

Summary and conclusions

1. There is no doubt that the 64 specimens dealt with in the present paper, including first instar larvae, adult females, alate and apterous males. are scale insects most closely related or identical with the recent *Matsucoccus*,

2. It is now not possible, and supposedly will never be possible, to include the fossil and recent forms of *Matsucoccus* into one system and recognize them on the basis of the same criteria. Thus, we may a priori reject any attempts of taxonomic studies on fossil *Matsucoccus* and retain the already established *Acreagris crenata* ♀ Koch et Berendt and *Monophlebus pinnatus* ♂ Germar et Berendt (= *Acreagris pinnata* ♀ ♂ sensu Ferris) as symbolic representatives of the fossil *Matsucoccus*, or try to deal with them in spite of the actual difficulties and "impossibilities", being quite aware of all the faults and weaknesses of the results of such taxonomy. I believe that the latter conception is a better one because it provides any information; and information gives always rise to further studies.

3. The taxonomy of scale insects is based on the female. The males are "ascribed" to species on the basis of biological data (common occurrence, mating), and studies on males provided only complementary information to the taxonomy of this group of insects. In case of the fossil material the situation is quite reverse — the males are much more numerous than the females (45 : 17) and provide more information for study — thus the taxonomy of the amber *Matsucoccidae* has been based on the male.

4. The wings, antennae and legs are best preserved in most specimens. The analysis of chacteristics of these structures revealed their great variability (quantitative characters vary within 100%) which, furthermore, is quite contiguous (normal), but there is no correlation between any characters, e. g., if the specimens are arranged according to length of the wing, then other features

become greatly disordered (Fig. 1). This phenomenon may be interpreted in the following ways:

a. All the specimens belong to one, variable, species which occurred on and through all the Baltic amber area and period.

b. The specimens represent numerous, 10 or more, species which are,

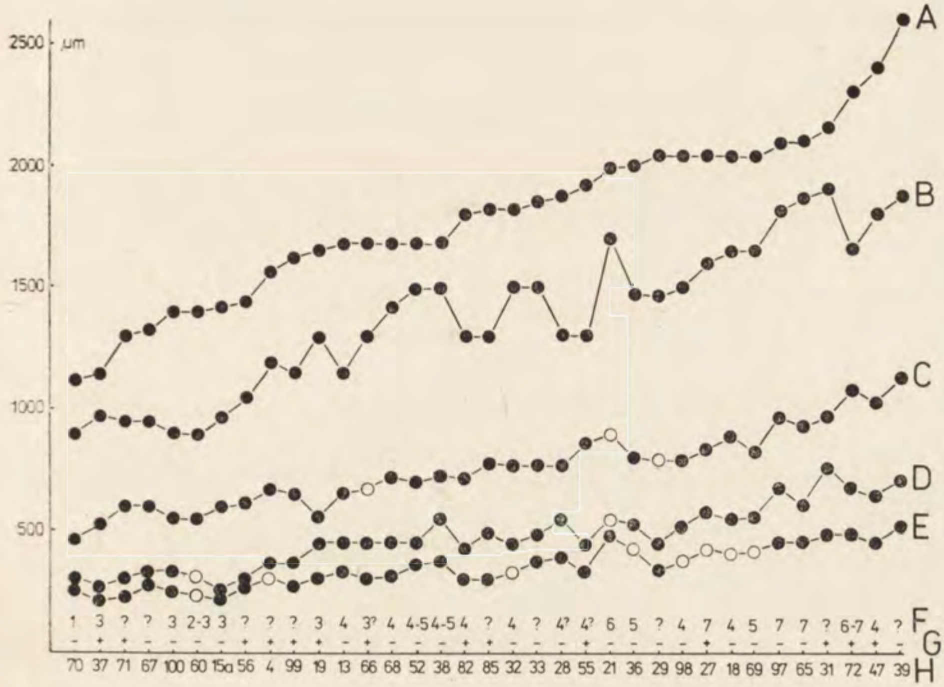

Fig. 1. Alate *Matsucoccus* males arranged according to increasing wing length; A — length of wing, B — length of antenna, C — width of wing, D — length of anterior tibia, E — length of anterior femur, F — number of hamuli, G — stellate hairs (present or absent), H — numerals of specimens.

owing to the conditions of the inclusions, not distinguishable; we may then establish several species each with its single, best preserved specimen (holotype) and remain all other unattached (undetermined), or describe each inclusion as a different species (a nonsense procedure, as indicated by Ferris 1941). In any case, the belief that numerous species occurred in the Baltic amber period is quite justified by the existence of more than 20 species in the present-day fauna.

c. We may assume that the 45 male specimens at hand represent a few species and then group them more or less arbitrarily into several units. Such classification will be evidently artificial, but for practicial reasons seems to be the best solution.

5. Since the males have been described only in very few recent species

and since the comparison of the fossil and recent material is greatly limited for technical reasons, all the fossil species, except one already described, are considered to be new taxa. At any rate, the fault of such resolution will be smaller than that of the assumption that this or another recent species occurred in the Baltic amber period, although it is quite likely.

6. Brachypterous and apterous males are known in scale insects. Sometimes these forms occur together with alate specimens in one species, sometimes only one form is known. In the general scale insects (margarodids s. l.), as I am informed, only alate or apterous males occur in one species; in the recent *Matsucoccus* only alte specimens have been described. Thus it seems reasonable to consider the fossil apterous specimens as a distinct species.

7. The alate specimens can be divided into three groups on the basis of a combination of several morphological characteristics, as shown on Fig. 2. The

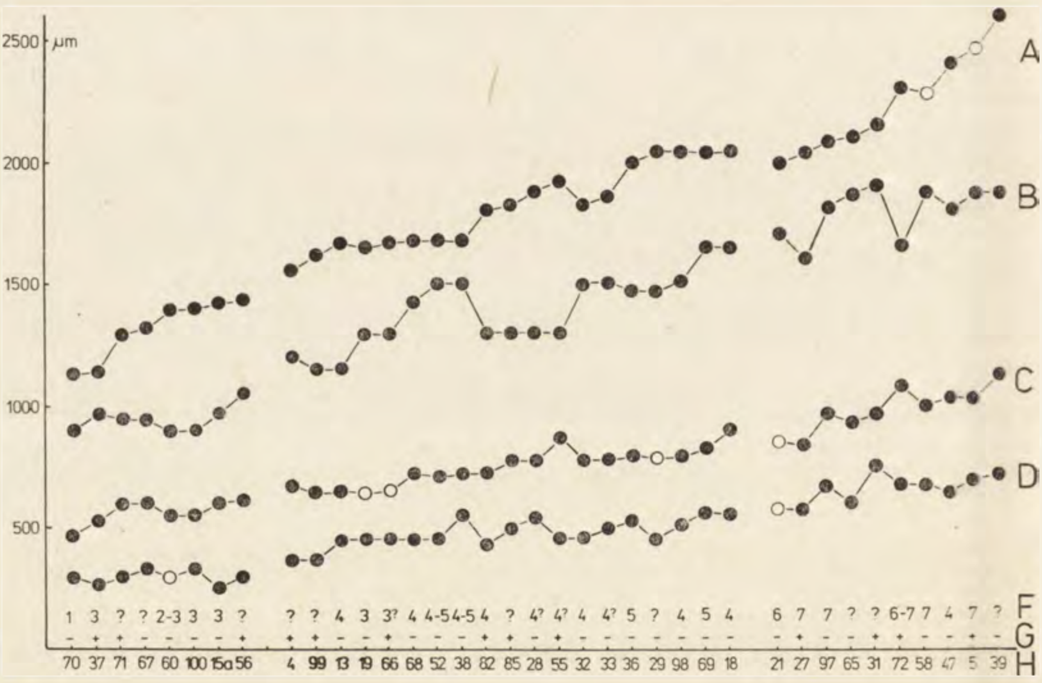

Fig. 2. Alate *Matsucoccus* males arranged in "homogeneous" groups; *M. larssoni* (*Cocc* 70 ... 56), *M. pinnatus* (*Cocc* 4 ... 18), *M. electrinus* (*Cocc* 21 ... 39). For further explanation see Fig. 1.

main criteria considered are the number of hamuli (1–3, 4–5, 6–7, however with some exceptions), length of antenna, wing and anterior tibia. The consideration of absolute numbers resulted in that each group contains specimens with narrow and broad wings, relatively long or short antennae, etc.; stellate hairs also occur in each group. For the time being this solution may be useful and further changes will be no problem, since the species name is, in fact, restricted to the holotype.

8. There is no doubt that *Monophlebus pinnatus* GERMAR et BERENDT is *Matsucoccus*, as suggested by FERRIS (1941). However, the question is which of the three recognized groups, if at all, represents the species described by these authors. Since the original description and figure are devoid of any indication (except that the antennae should be longer than the body), and the type specimen is not available, we may assume that none is *M. pinnatus* and describe all the units as new species, or that the "intermediate" group represented by numerous specimens and with a great variability may be identical with the species in question. For practical reasons the latter conception is accepted here.

9. As pointed out elsewhere in the paper, the "male third stage-adult female"—like specimens are regarded as adult females. In one instance such specimens and an alate male were enclosed within the same amber piece (both females and male are the smallest in the sample). The remaining females have been further divided into two groups — the "intermediate-sized" and "large" ones, and consequently ascribed to respective groups of males. This way each species (except *M. apterus*) is represented by female and male specimens.

10. The two first stage crawlers are assigned to *M. pinnatus* since it comprises numerous male and female specimens.

11. It should, once again, by emphasized, that most of the taxonomic decisions are arbitral, and that the taxonomy of the fossil *Matsucoccus* must then be artificial, but this procedure seemed to be the best solution in the transformation of the existing amber material into information.

VII. TAXONOMY OF THE BALTIC AMBER *MATSUCOCCIDAE*

This group has been established by MORRISON (1927) as a monotypic tribe — *Matsucoccini* — and placed together with *Xylococcini* and *Stigmacoccini* in the subfamily *Xylococcinae*, family *Margarodidae*. Studies by BEARDSLEY (1968) on adult male indicated that *Matsucoccus* should be removed from the *Xylococcinae* as a separate subfamily. Simultaneously several students emphasized that the generally accepted family *Margarodidae* represented in fact a much higher taxonomic level, and that at least all groups recognized by MORRISON (1927, 1928) as sufbamilies should be elevated to family rank. This suggestion has been supported with investigations on mouth parts by KOTEJA (1974, 1974a and others). In the present paper the classification by the above author is followed, according to which *Matsucoccus* constitutes a monotypic family within the superfamily *Orthezioidea* (= *Phenacoleachiidae* + *Ortheziidae* + *Margarodidae* s.l.).

Matsucoccus Cockerell

Type: *Xylococcus matsumurae* Kuwana 1905:91

Recognition characters based on fossil material

Alate male. Wings almost parallelsided, narrow (width:length ratio 1 : 2.1–2.8). Subcostal thickening and radius extending beyond apex of wing; single media reaching margin of wing just behind apex; anal vein delimiting a small portion of wing (anal lobe). Pocket for holding hamuli narrow, not extending beyond wing margin. All wing disc in regular folds radiating from media to margins. Hamulohalteres clubshaped, with 1–7 hamuli.

Head markedly wider than long, flattened dorsoventrally, with distinct midcranial ridge and well developed, subtriangular dorsal and ventral plates. Compound eyes hemispherical, large, with about 100 ommatidia. Antennae shorter than wings (ratio 1 : 1.1–1.5), longer than legs (ration anterior tibia: antenna 1 : 2.5–3.5), inserted deeply between eyes, filiform, 10-segmented; flagellar segments cylindrical, not nodded, with numerous hair-like, evenly scattered, setae about 2 times as long as width of segments; 1–5 capitate setae usually on all segments; antennal bristles, 2 in number, on 4 terminal segments.

Thorax significantly compressed from sides; prescutum, scutum, scutellum and mesosternum all strongly sclerotized, convex. Legs slender, with needdle-, on ventral face of tibia spine-like, setae. Anterior coxa, and usually other segments, longer than remaining. Tarsus one-segmented, tarsal digitules needle-like. Claw slender, slightly curved, without a denticle; ungual digitules spatulate extending beyond apex of claw. Anal lobes absent. Definite pore cluster plate on 7th abdominal tergite present. Penial sheath solid, elongate; aedeagus slender, long.

Body setae small, present on head, pro- and metathorax, on tergites and sternites of abdomen and lateral membranes of penial sheath. Penial sheath with minute sensilla near apex.

Apterous male. Wings entirely lacking; prescutum, scutum and scutellum distinct, but flat. Remaining characteristics correspond with those in the winged form.

Adult female. Body elongate, parallelsided, but usually shrivelled and deformed in the amber. Mouth parts wanting. Body setae and other dermal structures not recognizable. Eyes relatively large, situated on head margin near antennal bases, well preserved in most specimens. Antennae inserted close each other at body apex, but not contiguous, 9-segmented; scape large, usually longer than wide; pedicel cylindrical, slightly narrowed at apex, usually shorter than broad; 1st flagellar segment cylindrical, definitely shorter than wide, segments 2nd to 6th conical, with the base directed distally; apical segment ovoid, with truncate tip; flagellar segments reticulated, intersegmental membrane very large; antennal bristle on 3–4 terminal segments, hair-like setae sparse, on all flagellar segments, inserted apically; scape and pedicel with minute setae. Legs shorter than antennae; femur longer than tibia; tarsus about ⅔ the length of tibia, distinctly 2-segmented; claw small, without a denticle; ungual digitules conspicuously spatulate; setae on coxa and femur minute, on tibia and tarsus slightly longer than width of segments.

First stage larva. Body regularly elongate eliptical; posterior apex with a small but definite lobe and a pair of setae about 1/5 the body length. Antennae inserted almost contiguously, 6 segmented, with each segment of a characteristic shape and sensilla as shown on Fig. 16. Labium small, without setae, placed near mesothoracic legs. Femur stout, tibia and tarsus together shorter than femur, claw relatively large, ungual digitules capitate, slightly extending beyond apex of claw.

Host and life cycle. *Pinus succinifera*; life history resembling supposedly that in recent species, with several generation per year possible and/or asynchronic cycle of different species.

Deposit and distribution. Eocene-Oligocene Baltic amber deposits.

Classification. Although *Matsucoccus* represents a serious forest pest both in the Old and New World, and a number of studies have been undertaken to learn its biology, behaviour etc., there is no revision or key to the more than 20 species of this genus, and adult males have been mentioned in few species, while described in details only in one. Thus it is not possible to elaborate a classification of both fossil and recent species. The classification proposed in the present paper is based on adult male, and is apparently artificial.

Key to adult male

1. Wings entirely lacking . . . . *M. apterus* sp. n.
—. Anterior wings and halteres present 2
2. Halteres with 1–3 hamuli; wings 1130–1440 μm long; antennae 900–1050 μm long, slightly shorter than body length; femur 210–270 μm, tibia 250–330 μm long . . . . *M. larssoni* sp. n.
—. Halteres with 4–7 hamuli, if 3 hamuli present, then all dimensions larger than given above; antenna equal to, or longer than body 3
3. Halteres with 4–5 (rarely 3) hamuli; wings 1560–2040 μm long; antennae 1150–1650 μm long, usually longer than body; femur 270–390 μm, tibia 330–570 μm long . . . . *M. pinnatus* (Germar et Berendt)
—. Halteres with 6–7 hamuli, if less numerous, then wings 2000–2600 μm long; antennae 1600–1900 μm, tibia 520–750 μm long . . . *M. electrinus* sp. n.

Key to adult female

1. Body 600–1000 μm, antenna 250–360 μm, femur 80–120 μm, tibia 70–100 μm, tarsus 50–70 μm long . . . . *M. larssoni* sp. n.

—. All dimensions larger than given above 2

2. Body 1000–1600 μm long; antenna 400–550 μm long, flagellar segments 2–6 stout, broader than long; femur 150–190 μm, tibia 120–150 μm, tarsus 70–100 μm long . . . . *M. pinnatus* (German et Berendt)

—. Body about 2000 μm; antenna about 600 μm long, flagellar segments slender, conspicuously longer than wide; femur about 250 μm, tibia about 200 μm, tarsus 120 μm long . . . . *M. electrinus* sp. n.

Description of species

Matsucoccus larssoni sp. n.

(Figs. 3–5, 13)

Holotype: alate male, Cocc 15a, Baltic amber inclusion, 16 V 1957, A. K. Andersen, ZMC; paratypes; 4 adult females Cocc 15b-e originally embedded with holotype in the same amber piece.

Description

Adult male: Alate; body small (970–1200 μm long). Head 280–370 μm wide, with several setae 15–20 μm long recognizable on both dorsum and venter in some specimens. Eye 110–150 μm in diameter. Antenna slightly shorter than body, 900–1050 μm long; apical segment 90–110 μm long; first flagellar segment longer than others, subequal to them in *Cocc* 56, with 8–10 setae, but about 18 in *Cocc* 100, and as many as 23 in *Cocc* 67. Thorax accessible for examination from dorsum in *Cocc* 71, from sides in *Cocc* 70 and 100. Prescutum and scutellum in *Cocc* 71 definitely shorter than wide, but this seems to be an effect of deformation. Mesepisternum nearly circular, about 100 μm in diameter; mesosternum 280 μm long (both measurements taken from *Cocc* 100). Dorsal setae on pro- and metathorax recognized in some specimens; setae bent, with minute knobs at apices, about 15 μm long. Wing 1130–1440 μm long, 470–610 μm wide, width : length ratio 1 : 2.2–2.5; longer than antenna, length ratio 1 : 1.2–1.5. Halteres 110–150 μm long, with 3 setae, but 2–3 in *Cocc* 60, and only 1 in *Cocc* 70. Legs short, relatively robust; trochanter + femur 210–270 μm long, tibia 270–330 μm, but only 250 μm long in holotype; tarsus about 100 μm long; anterior tibia equal to, shorter or longer than posterior one, about 3 times shorter than antenna, and 4–4.5 times than wing, except holotype in which it is nearly 6 times shorter than wing. Abdomen with dorsal and ventral setae similar to those on thorax, but apical knob indistinct; 8th segment supposedly only with one pair of setae dorsally and ventrally. Pore cluster plate relatively large (Figs. 3, 4); about 8–10 pore tubes may be present, tubes about 25 μm long, 9 μm in diameter (Fig. 5: G). Penial sheath 180 μm long, 100 μm high in *Cocc* 70, 190 μm and 120 μm, respectively, in *Cocc* 100. Lateral membranes with several setae similar to those on abdomen.

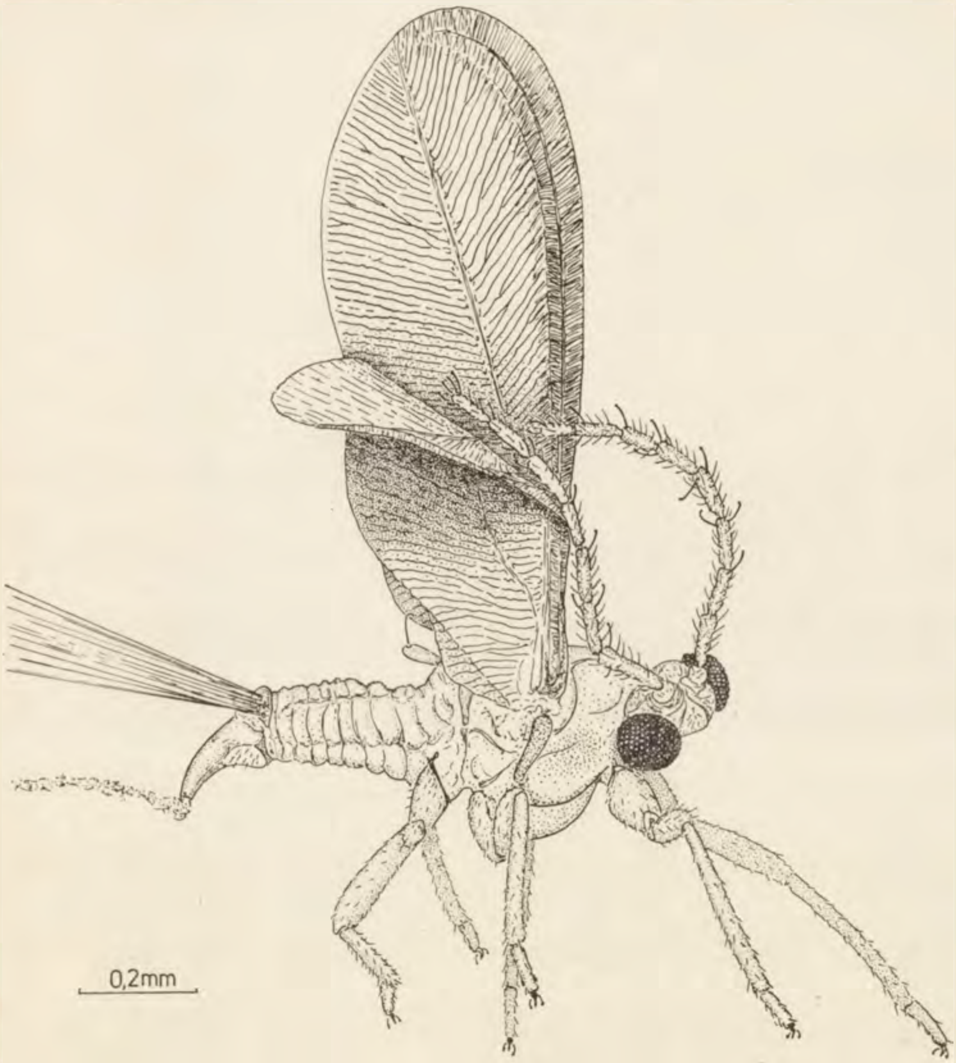

Fig. 3. *Matsucoccus larssoni* sp. n., ♂, *Cocc* 70.

Adult female: Body much shrivelled, supposedly 800–1100 μm long, about 400 μm wide. Antenna 260–360 μm long, with all segments, but apical, at least as wide as long, usually wider than long; antennal bristles noted only

Fig. 4. *Matsucoccus larssoni* sp. n. ♂, *Cocc* 100.

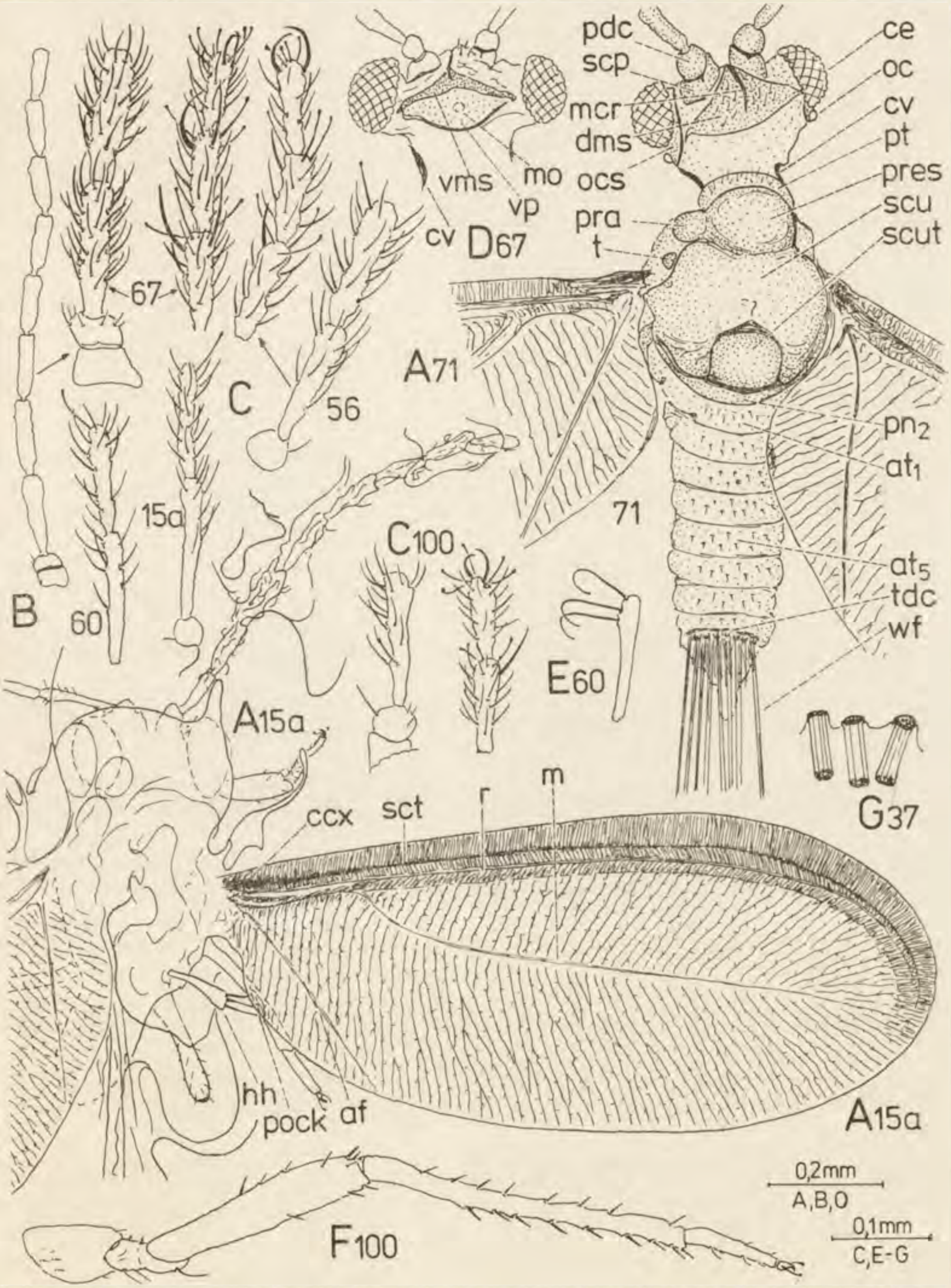

Fig. 5. *Matsucoccus larssoni* sp. n., ♂, A – dorsal view of body, B – antenna, C – scape, pedicel, first, and two terminal segments of flagellum, D – ventral view of head, E – hamulohaltere, F – anterior leg, G – tubular ducts of glandular plate (free hand).

on 3 terminal segments. Trochanter+femur 70–120 μm, tibia 70–100 μm, tarsus 40–60 μm long.

Stellate hairs present in 3 pieces with adult males.

Note. The description of species has been based on all 8 included males and 5 females. The holotype Cocc 15a is rather in a poor condition and only few structures can be seen exactly, further its legs are extremely short. It has been selected as type because of having been found together with 4 specimens, considered to be adult females, in one amber piece. The male Cocc 67 is somewhat aberrant in having very numerous setae on antennae, and male Cocc 70 with only 1 hamulus.

The male redescribed and figured by Ferris (1941) belongs supposedly to this species since it has only 2 hamuli and the wings are small, even smaller (750 μm) than in any of the examined specimens. As far as the female is considered, it is difficult to infer whether the specimens described by Ferris may be placed in this species.

Material examined

Adult male. *Cocc* 15a. ZMC, 16 V 1957, A. K. Andersen. Holotype. Originally with four females (*Cocc* 15b–d). Embedded between two layers of resin; lines and "floods" of brown resin from dorsum make examination impossible; median parts of venter in milky clouds; legs and antennae seem to be impregnated with resin and filled with air. Sh-.

Cocc 37. ZMC, 27 V 1963, C. V. Henningsen. Amber clear; specimen shirivelled; part of body removed during polishing process from one side, obscured by milky clouds from the other; legs and hamulohalteres well visible, penial sheath exposed; body impregnated with resin, or secondarily with some oil, owing to this internal parts of pore tubes accessible for examination. Sh+.

Cocc 56. ZMC, 1 XII 1966, C. V. Henningsen. Amber clear; specimen situated among "floods" of brown resin and a split which strongly reflects the light; all venter in milky clouds; appendages accessible for examination. Sh+.

Cocc 60. ZMC, 1 V 1967, C. V. Henningsen. Amber clear; specimen trapped into a cobweb and supposedly shrunken before embedded in resin; only part of antennae and legs available for examination. Sh—.

Cocc 67. ZMC, 28 III 1968, A. K. Andersen. All dorsum obscured by numerous lines and cracks; thorax and abdomen ventrally covered with strongly reflecting split; apex of one wing removed; head from venter and appendages may be examined. Sh—.

Cocc 70. ZMC, 28 III 1968, A. K. Andersen. Amber clear but in "dust" which makes the examination somewhat difficult; many details may be studied. Sh—.

Cocc 71. ZMC, 28 III 1968, A. K. Andersen. Specimen situated within lines, ruptures and impurities, examination from venter impossible; apices of one wing and antenna removed; antennae shrivelled, legs beneath wings; all dorsum available for examination. Sh+.

Cocc 100. SMNS, z4889, from the Koenigsberg Baltic Amber Collection. Amber clear; specimen embedded within a fissure; this and a large bubble make the observation difficult; specimen may be examined from side; setae on thorax and abdomen distinct. Sh—.

Adult female. *Cocc* 11. ZMC, 26 II 1955, C. V. Henningsen. Specimen embedded within lines and fissures; antennae obscured; dorsal face veiled with milky clouds. Sh—.

Cocc 15b. ZMC, 16 V 1957, A. K. Andersen. Originally embedded with three other females (Cocc 15c–e) and adult male (Cocc 15a) in one amber piece. A large fissure with numerous particles makes the examination somewhat difficult; setae not visible. Sh—.

Cocc 15c. Abdomen partly hidden under milky and granulate clouds, a leaf scale (or something like that) on metathorax ventrally; setae on antennae distinct. Sh—. For further data see *Cocc* 15b.

Cocc. 15d. Body dark, impregnated with resin (?) and filled with air, very difficult to study. Sh—. For further details see *Cocc* 15b.

Cocc 15e. A well preserved specimen, but a comparatively thick layer of air makes the examination somewhat difficult; some setae on legs visible, on antennae indistinct. Sh—. For further data see *Cocc* 15b.

Matsucoccus pinnatus (Germar et Berendt), comb. n.

(Figs. 6–8, 14–16)

Monophlebus pinnatus Germar et Berendt, 1856: 3, Pl. I, Fig. 1; Menge, 1856: 18; Scudder, 1890: 242;

Acreagris crenata Koch et Berendt; Ferris, 1941: 6 (misinterpretation); Beardsley, 1968: 1457 (misinterpretation).

Type material: not seen, its fate is unknown.

Original description

"Monophlebus antennarum articulis filiformibus, alarum striolis numerosis subtilissimo e nervo medio pinnatim exeuntibus, ano aculeato.

Das vorliegende Exemplar zeigt das Thier von der Seite zusammengedrückt, und fast alle Theile noch in ihrer natürlichen Lage und vollständig, nur der, kaum eine Linie lange Körper, ist mit einem Ueberzug von undurchsichtigen Bernstein hier und da bedeckt.

Der Kopf is verhältnissmässig klein und nicht genau erkennbar. Die Fühler sind beträchtlich länger als der Körper, borstenförmig, fein behaart, das erste Glied erscheint als ein stumpfer Kopfhöcker, die folgenden sind alle gleichlang untereinander, langgestreckt, dünn, fast stielrund, nur an der Spitze etwas verdickt. Es lassen sich nur acht Glieder beobachten, da die Endglieder beiden Fühlern fehlen. Der Mittelleib, den man im Profil sieht, ist vorn gewölbt, die Brust stark erhaben der Hinterrücken abschüssig. Der Hinterleib hat hinten einen Vorsprung auf welchem an jeder Ecke eine kleine Fleischwarze gesessen zu haben scheint, unter diesem Vorsprunge befindet sich ein kegelförmiges, am Ende abgestutztes Glied, an welches das herabgebogene kegelförmige in einen gekrümten Stachel sich endigende Afterglied anschliesst. Die Vorderflügel sind gross, eirund, der starke Randnerv läuft mit dem Rande parallel bis in die Krümmung des Hinterrandes. Von ihm weg gehen fast rechtwinkeling zahlreiche feine Striche nach dem Aussenrande. Eine feine Längsader läuft ziemlich durch die Mitte des Flügels und von ihr weg gehen auf beiden Seiten fast rechtwinkeling federförmig zahlreiche feine Striche durch, welche dem ganzen Flügel das Ansehen einer feinen federförmigen Streifung geben. Die Schwingkölbchen sind bei dem prachtvollen Exemplar, das mit vorwärts gebogenen Flügeln liegt, ganz deutlich zu erkennen. Die Beine sind mässig lang, dünn, die Krallen einfach".

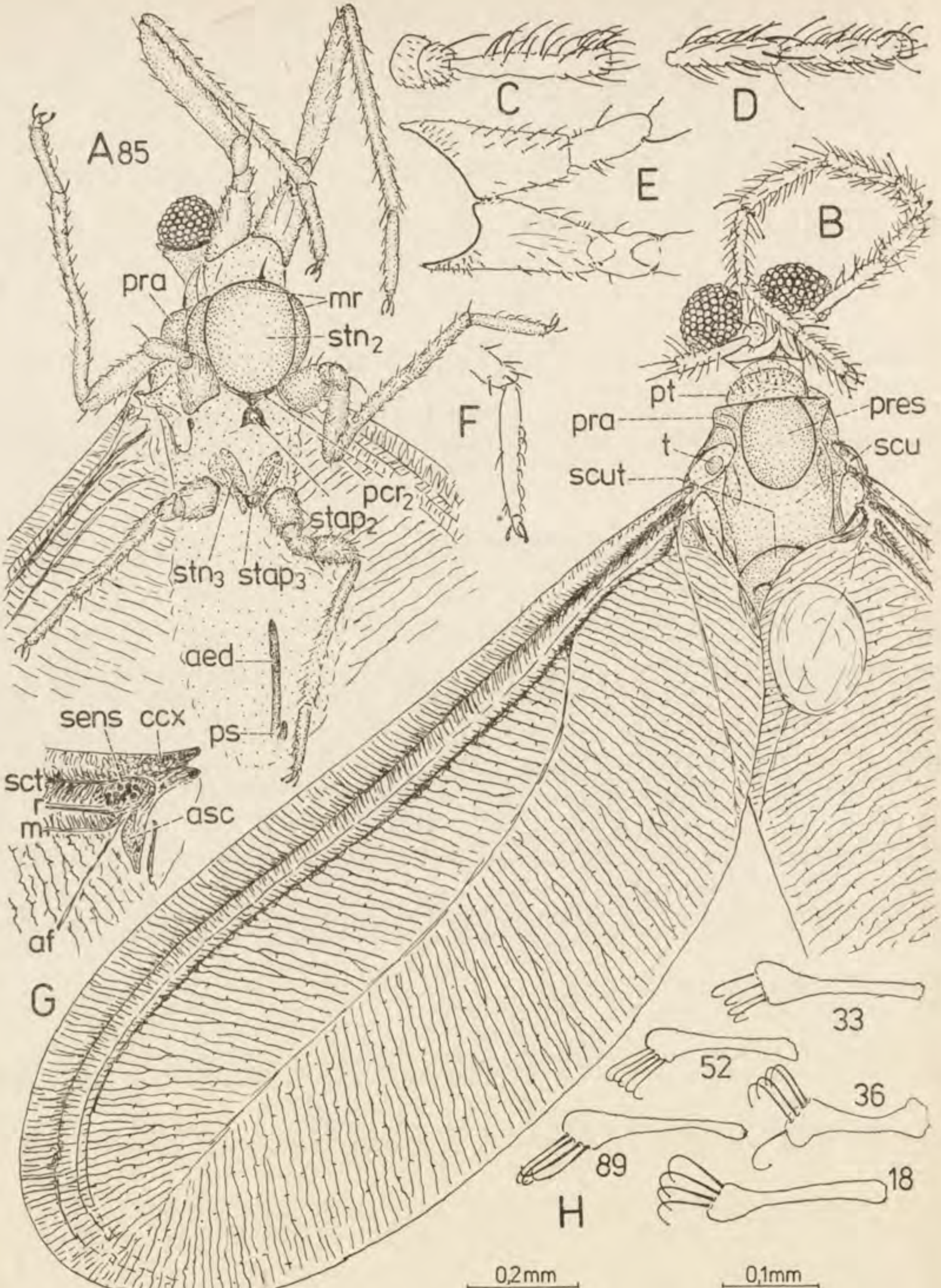

Fig. 6. *Matsucoccus pinnatus* (GERMAR et BERENDT), ♂, A – ventral view, B – dorsal view, C – scape, pedicel and first flagellar segment, D – apical segment, E – anterior coxae and trochanteres, F – tarsus, G – basal portion of wing (dorsal view), H – hamulohaltere, Figures A–G refer to *Cocc* 85.

Description of examined material

Adult male: Alate specimen; body 1050–1400 μm long, 330–450 μm wide. Head about 300–370 μm wide; middorsal and midventral plates with numerous, small setae, difficult to measure and count, however, they seem to be large and sparse in *Cocc* 85. Eye 120–150 μm in diameter. Antenna 1150–1650 μm long,

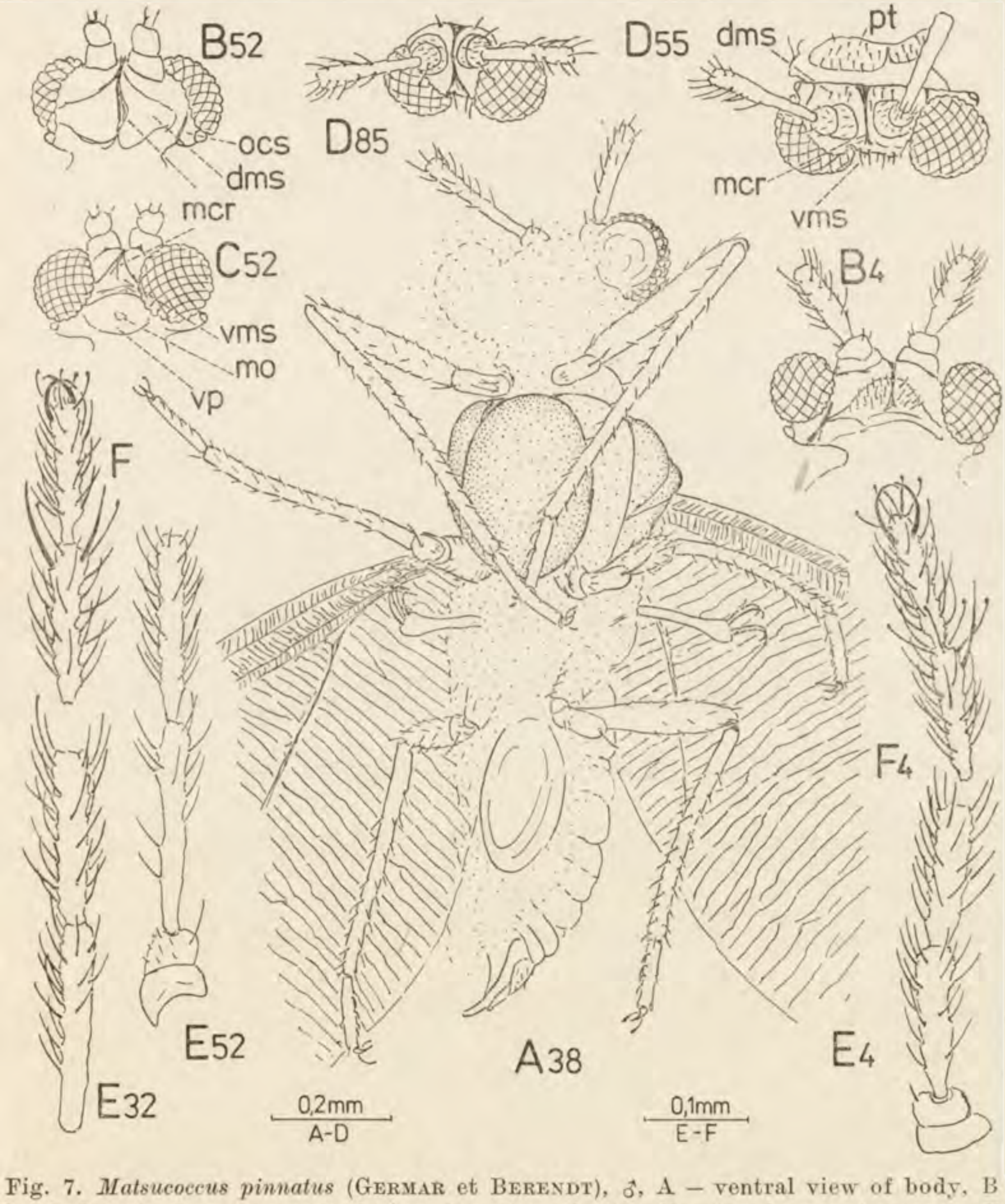

Fig. 7. *Matsucoccus pinnatus* (GERMAR et BERENDT), ♂, A – ventral view of body, B – head, dorsal view, C – ventral view, D – frontal view, E – basal part of antenna, F – apical part of antenna.

longer than body; apical segment 110–180 μm long; first flagellar segment usually the longest, rarely shorter or subequal to the second, with 8–21 setae. Prothorax with numerous dorsal setae. Prescutum oval, 150–190 μm long, 100–120 μm wide, scutum 12–140 μm long, scutellum 120 μm long, 95 μm wide (measurements taken from *Cocc* 38 and 85), episternum oval, respective diameters about 120 μm and 150 μm (in *Cocc* 69), mesosternum about 230 μm long, 150 μm wide (in *Cocc* 85). Wing 1560–2040 μm long, 550–890 μm wide (width: length ratio 1 : 2.2–2.8), longer than antenna (length ratio 1 : 1.1–1.5). Wing sclerites may be seen in *Cocc* 69, sensilla in *Cocc* 85. Haletere 130–220 μm long, with 4–5 hamuli, but supposedly only 3 in *Cocc* 19 and 66. Legs slender; trochanter + femur

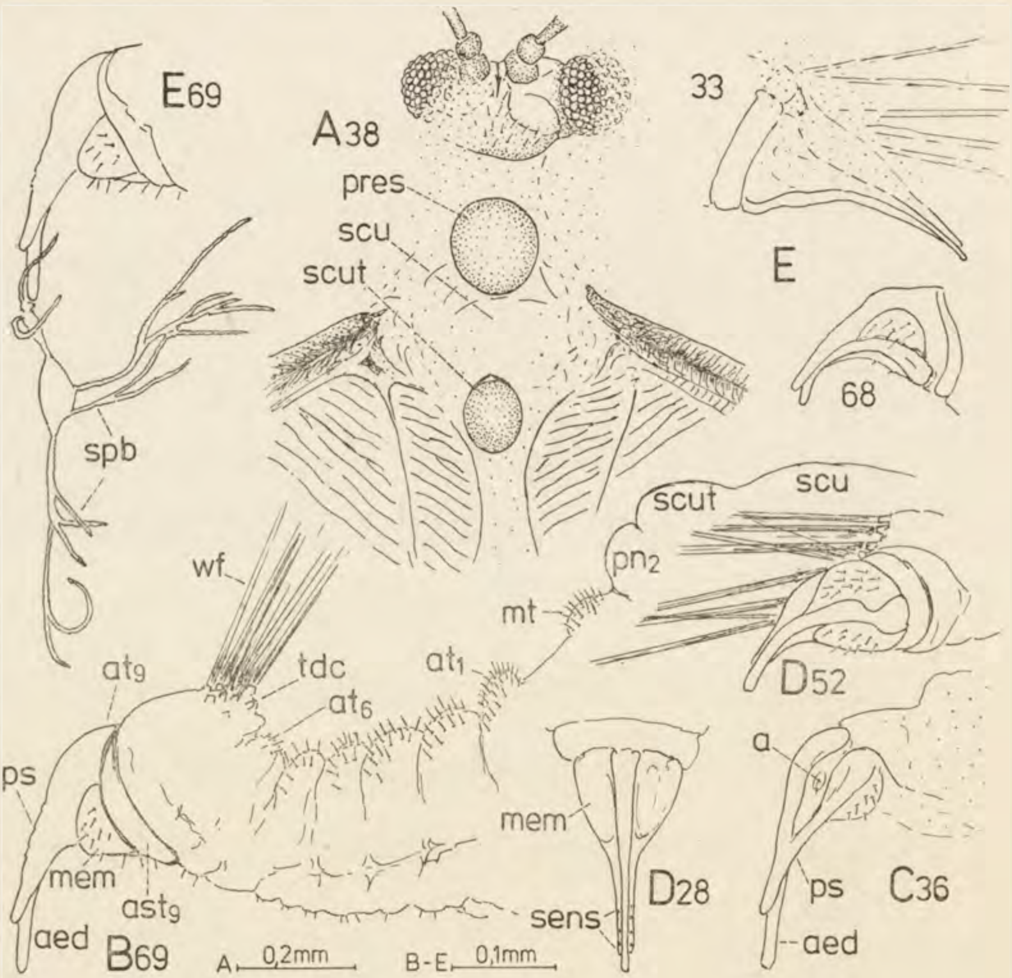

Fig. 8. *Matsucoccus pinnatus* (Germar et Berendt), ♂, A — dorsal view of body, B — lateral view of abdomen, C — penial sheath, dorsal view, D — ventral view, E — lateral view.

270–390 μm long, tibia 330–550 μm, tarsus 100–150 μm long; anterior tibia usually longer, rarely equal to posterior one, 2.5–3.4 times shorter than antenna, and 3–4 times shorter than wing. Setae on abdomen numerous with minute knobs at apices. Pore cluster plate not seen exactly in any specimen, supposedly with 8–12 pores. Penial sheath about 200 μm long, 100 μm wide and 100 μm high (measurements taken from *Cocc* 28 and 69); lateral membranes with several setae; minute sensilla on distal part of penial sheath could be seen in some specimens.

Adult female: Body 1000–1600 μm long, 600–700 μm wide; segmentation distinct in some specimens; setae, pores etc. not observed. Antenna 400–540 μm long, stout. Scape cylindrical, very large, with several small setae noted in some specimens; pedicel cylindrical, but somewhat swallen in the middle, slightly longer than half length of scape, usually broader than long; first flagellar segment subcylindrical, narrowed at apex, length always smaller than width; flagellar segments 2–8 broadening towards tip; apical segment ovoid, with truncate apex; flagellar segments each with 1 thick antennal bristle, apical segment with 4 or 5 bristles of different length; thin setae, presumably 4 in number, on each of flagellar segments. Trochanter + femur 150–190 μm, tibia 120–160 μm, tarsus 70–100 μm long; setae needlelike, shorter than width of segments, sparse, about 6 setae on tarsus.

First stage larva: see description of genus.

Stellate hairs present in 6 pieces with adult males, and in 1 with adult female (*Cocc* 81).

Note. There is no doubt that the specimen described by GERMAR and BERENDT (1856 as *Monophlebus pinnatus* is a matsucoccid, except that the sentence "Der Hinterleib hat hinten einen Vorsprung, auf welchem an jeder Ecke eine kleine Fleischwarze gesessen zu haben scheint ..." does not fit with the conditions in living *Matsucoccus* male. However, in the shrievelled specimens the pore cluster plate may imitate a projection (Vorsprung), like the tubes may protrude from the plate in the form of papillae (Fig. 4). Another question in whether the 19 alate males identified as *M. pinnatus* are actually this species because the original description is devoid of any specific characteristics. Further the designation of adult females and first stage larvae to *M. pinnatus* may also be questioned (see discussion in Chapter VI). In any case, it may be hoped that at least some of the specimens are correctly identified.

Within the male assemblage, there are two specimens (*Cocc* 19 and 66) which have supposedly only 3 hamuli as in *M. larssoni*, but in *Cocc* 66 the antennae are definitely longer than in this species, while in *Cocc* 19 the antennae as well as the legs are much greater than in *M. larssoni*.

Among the recent species with male known, *M. pini* seems to be similar to *M. pinnatus*.

Stellate hairs accompany only males with antennae shorter than 1400 μm, however, they occur again in *M. electrinus* (antennae longer than 1600 μm). Similar conditions have been noted among the females. This may indicate that *M. pinnatus*, as understood here, represent two species, or two generations of somewhat different morphology.

Material examined

Adult male. *Cocc* 4. ZMC–MMC, 569–1891, V. S. Nielsen. Amber clear, but specimen located in fissures, examination from dorsum impossible; body much shirvelled and obscured with milky resin, head and antennae available for study; wings strongly bent. Sh+.

Cocc 13. ZMC, 16 V 1957, A. K. Andersen. Amber clear; specimen embedded within lines and cracks; body shrivelled, mostly hidden in milky resin; appendages and one side of thorax available for examination. Sh–.

Cocc 18. ZMC, 19 XI 1958, C. V. Henningsen. Amber in numerous cracks; little can be seen. Sh–.

Cocc 19. ZMC, 19 XI 1958, C. V. Henningsen. Specimen embedded at the very edge of amber piece within a fissure; difficult to study. Sh–.

Cocc 28. ZMC, 16 I 1961, Th. Hansen. Specimen embedded between two layers of resin; all dorsum except scutum, prescutum and scutellum in fissures and cracks; head and thorax from venter in milky clouds; abdomen presumably little shrivelled, penial sheath distinct; appendages covered with minute particles. Sh–.

Cocc 29. ZMC, 21 III 1961, B. Mortensen. Specimen embedded within ripples and cracks; body twisted, one antenna removed; nothing except one antenna can be seen exactly. Sh–.

Cocc 32. ZMC. 25 III 1961, C. V. Henningsen. Body completely shrunken, covered with a milky cloud from venter; wings and antennae distinct. Sh–.

Cocc 33. ZMC, 31 V 1961, C. V. Henningsen. Numerous ripples, cracks and bubbles make the examination from dorsum impossible. Sh–.

Cocc 36. 15 X 1962, C. V. Henningsen. Curved surface of amber deformes the specimen from dorsum; ventral face in milky resin; specimen crumpled in unnatural position; antennal setae very distinct. Sh–.

Cocc 38. ZMC, 14 V 1963, J. Flauensgaard. All dorsum obscured by ripples, lines and cracks, except middle parts of thorax; ventral face largeley in milky clouds; body little shrivelled; seate on legs distinct, on antennae obscure; left antenna broken at first flagellar segment. Sh–.

Cocc. 52. 1 VII 1966, C. V. Henningsen. Specimen somewhat shrivelled, deformed from dorsum by curved surface of amber; apex of wing removed; venter of thorax with a large bubble; setae on appendages distinct, but difficult to count. Sh–.

Cocc 55. ZMC, 1 XII 1966, C. V. Henningsen. Amber clear, upper surface curved causing optical deformation; body little shrivelled; thorax largely covered with wings; setae on appendages mostly distinct. Sh+.

Cocc 66. ZMC, 28 III 1968, A. K. Andersen. Amber clear; specimen shrunken and crumpled; head and thorax in milky resin, few structures can be examined. Sh+.

Cocc 68. ZMC, 28 III 1968, A. K. Andersen. Amber clear, but curved surfaces of piece cause deformations; specimen within ripples; one body side with a large bubble and milky clouds; one wing removed. Sh–.

Cocc 69. ZMC. 29 II 1968, A. k. Andersen. Numerous ripples and bubbles obscure head and thorax, abdomen available for examination from sides. Sh–.

Cocc 82. PMHU, from Berendt collection. Amber clear but very dark; specimen embedded within numerous ripples and cracks, from dorsum unavailable for study; body shrunken and crumpled, partly in milky resin, difficult to study. Sh+.

Cocc 85. PMHU, 394, Kuenow collection. A thin plate of clear amber embedded in Canada balsam; ripples and black particles round the insect do not obscure morphological deitals; head twisted, thorax largely covered with wings and shrunken, abdomen in milky resin; in spite of these artefacts this specimen is one of the best preserved inclusions. Sh+.

Cocc 98. SMNS, z5198, from the Koenigsberg Baltic Amber Collection. Amber very clear, but body completely crumpled and obscured with milky resin; legs, wings and hamulohalteres may be examined. Sh –.

Cocc. 99. SMNS, z4731, from the Koenigsberg Baltic Amber Collection. Amber clear, specimen within numerous lines and cracks; all body in milky clouds; wings accessible for examination. Sh +.

Adult female *Cocc* 17. 19 XI 1958, C. V. HENNINGSEN. Resin split in numerous, subcircular fissures arranged radially round insect; splitting planes milky, causing deformations; abdomen with a large bubble. Sh –.

Cocc 22. ZMC, 21 XI 1960, C. V. HENNINGSEN. Resin round specimen split in horizontal and prependicular cracks, the latter imitate setae, but actual setae distinct. Sh –.

Cocc 50. ZMC, 1 VII 1966, C. V. HENNINGSEN. Specimen embedded within ruptures; a large bubble on dorsum; body shrivelled, antennae much deformed. Sh –.

Cocc 73. ZMC, 28 III 1968, A. K. ANDERSEN. Specimen situated between two layers of resin, dorsal face clear, ventral one obscured with numerous bubbles; antennal setae and sculpture of joints distinct. Sh –.

Cocc 74. ZMC, 28 III 1968, A. K. ANDERSEN. Except distal parts of some legs and one antenna, all body in milky resin and small bubbles. Sh –.

Cocc 75. ZMC, 28 III 1968, J. FLAUENSGAARD. Ventral face in numerous lamines, dorsal one in milky clouds, bubbles and impurities; antennae and legs free, but setae indistinct.

Cocc 77. ZMC, 1 II 1969, C. V. HENNINGSEN. Dorsal surface with numerous lamines and impurities, ventral one with a small milky cloud on thorax; abdomen constricted to about 1/4 body length; setae indistinct. Sh –.

Cocc 81. ZMC. All body except antennae and distal parts of legs in a milky cloud. Sh +.

Cocc 94. SMNS, III B 86, from the Koenigsberg Baltic Amber Collection. Fine amber piece embedded in Canada balsam (removed from balsam in 1967, once again embedded in 1983); specimen well preserved, many details can be studied. Sh –.

Cocc 95. SMNS, B 257, from the Koenigsberg Baltic Amber Collection. Like *Cocc* 94, easy to study, setae on appendages distinct. Sh –.

First stage larva (crawler) *Cocc* 87. PMHU, 446, KUENOW collection. Thin plate of amber embedded in Canada balsam; specimen well preserved; setae on body and appendages difficult to see. Sh –.

Cocc 89. PMHU, 448, KUENOW collection. Like Cocc 87, antennae in air sheaths. Sh –.

Matsucoccus electrinus sp. n.

(Figs. 9–11, 17)

Holotype: alate male, *Cocc* 72, Baltic amber inclusion, 28 III 1968, C. V. HENNINGSEN, ZMC.

Description

Adult male: Alate; body 1300–1600 μm long, about 400 μm wide. Head 370–400 μm wide; dorsomedial plate with numerous setae, ventral plate not seen exactly in any specimen. Eye 150–190 μm in diameter. Antenna 1600–1900 μm long, i.e. longer than body; apical segment 140–240 μm long; first flagellar segment longer than others, about as long as the second in Cocc 65, with 13–18

Fig. 9. *Matsucoccus electrinus* sp. n., ♂, *Cocc* 72.

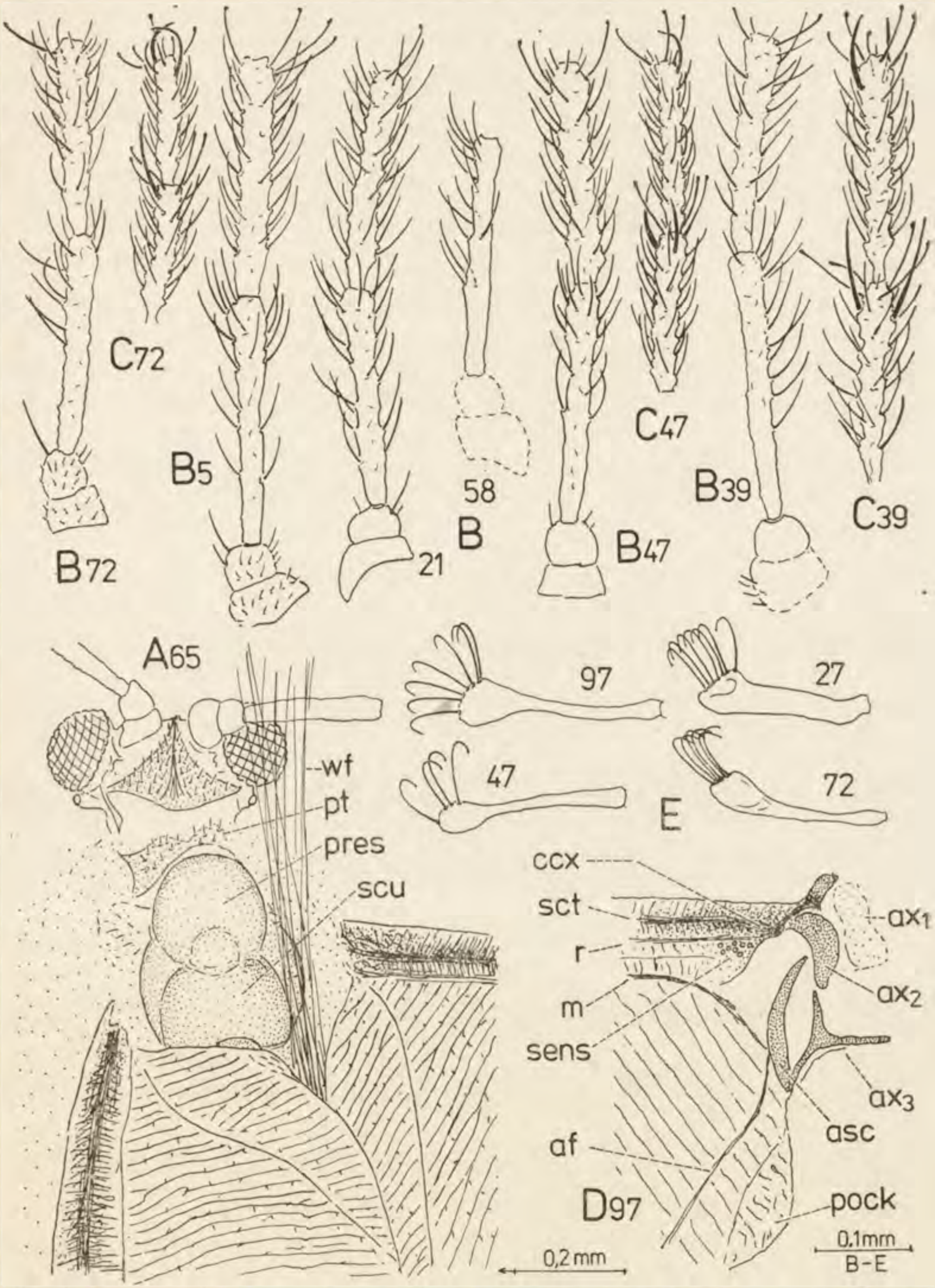

Fig. 10. *Matsucoccus electrinus* sp. n., ♂, A — dorsal view of body, B — basal part of antenna, C — apical part of antenna, D — basal part of wing, E — hamulohaltere.

setae. Thorax accessible from dorsum only in Cocc 65; prescutum about 210 μm long, 200 μm wide, scutum 160 μm long. Lateral sclerites generally resembling those in *M. bisetosus*, episternum oval, in holotype 240 μm long, 140 μm wide. Ventral face not available in any specimen; mesosternum about 380 μm long

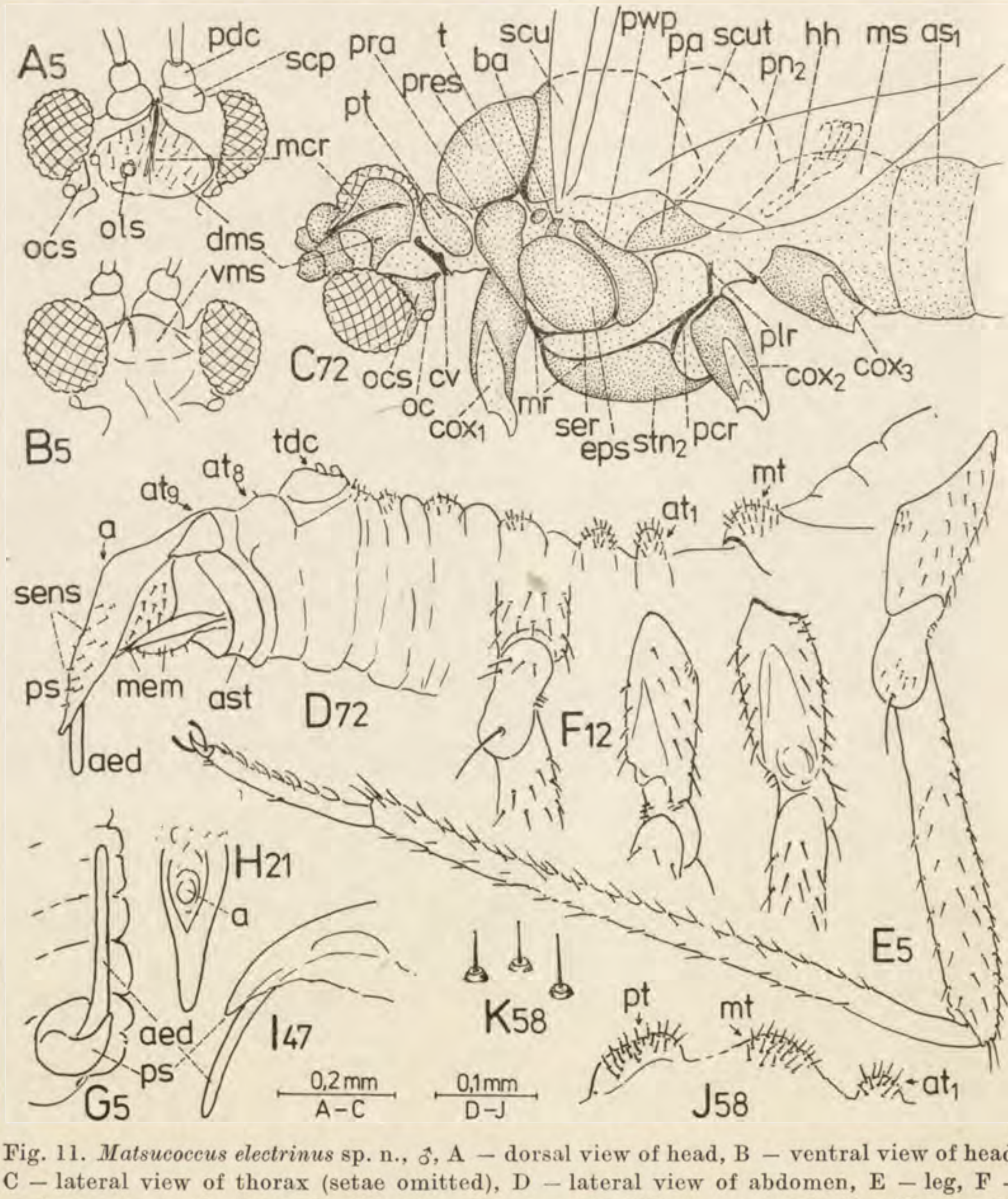

Fig. 11. *Matsucoccus electrinus* sp. n., ♂, A — dorsal view of head, B — ventral view of head, C — lateral view of thorax (setae omitted), D — lateral view of abdomen, E — leg, F — various aspects of coxa and trochanter, G — apex of abdomen, ventral view, H — penial sheath, dorsal view, I — lateral view, J — dorsal portion of prothorax, metathorax and first abdominal segment, K — dorsal setae of prothorax (free hand).

in holotype. Dorsal setae on pro- and metathorax 13–15 μm long, all with minute knobbs at apex. Wing 2000–2600 μm long, 840–1130 μm wide (width: length ratio 1 : 2.1–2.3), longer than antenna (length ratio 1 : 1.1–1.4); wing sclerites as shown on Fig. 10 D. Halteres 180–220 μm long, with 6–7, but 4 in *Cocc* 47, setae. Legs, particularly tibia, very long and slender; trochanter + femur 370–510 μm, tibia 520–750 μm, tarsus 130–180 μm long; anterior tibia longer than posterior one, subequal in Cocc 39; about 2,4–3 times shorter than antenna (about 3.5 times in holotype), and 3–3.7 times shorter than wing. Abdominal setae like those on thorax, very numerous, except 8th segment with few setae. Pore cluster plate not accessible in any specimen, about 10 waxy threads have been counted. Penial sheath difficult to measure oving oblique position, about 220 μm long, 120 μm high in holotype, 180–110 μm, respectively, in Cocc 58; dorsal face and anus visible in Cocc 21; sheath with numerous minute sensilla posterior to anus, lateral membranes with several setae smaller than those of abdomen, without spical knob.

Adult female: Body 2040–2160 μm long, 1080–1320 μm wide. Antenna about 600 μm long, slender — all flagellar segments longer than wide. Length — scape 120 μm, pedicel 72 μm, flagellar segments I — 48 μm, II–IX — 60 μm; width — scape 90 μm, pedicel 72 μm, flagellar segments I — 48 μm, VIII — 36 μm, IX — 30 μm (measurements taken from *Cocc* 14). Trochanter + femur 240 μm, tibia 210 μm, tarsus 120 μm (from *Cocc* 26). Setae on appendages have not been observed.

Stellate hairs present in 4 pieces with males and 1 piece with female.

Note. The description of male has been based on 10 specimens of which the holotype represents certainly the best conditions. The wing in *Cocc* 21, 27, 31, 65 and 97 is only slightly, or not at all, longer than in *M. pinnatus*, but in all them, except Cocc 27, the antenna is very long, nearly as long as the wing (length ratio 1: 1.1). *Cocc* 27 has been assigned to *M. electrinus* owing to the presence of 7 hamuli. On the other hand, in *Cocc* 47, a very large specimen, only 4 hamuli have been found.

In specimens included to this species several structures could be seen which are rather difficult to study in the fossil material, i.e. the wing sclerites and alar sensilla in *Cocc* 97, body setae in *Cocc* 58, anus in *Cocc* 21, sensilla on penial sheath in *Cocc* 27. Furthermore, there occur structures like ommatidia on the dorsomedial plate in *Cocc* 5 which, however, may be artefacts.

Judging from the number of hamuli, this species seem to be close to *M. secretus* Morrison.

Material examined

Alate male. *Cocc* 5. ZMC, 3 I 1956, C. V. Henningsen. Amber clear from venter, in ruptures and impurities from dorsum. Wings crumpled, partly removed; body little shrivelled but dark; difficult in study. Sh +.

Cocc 21. ZMC, 3 V 1960, C. V. Henningsen. Amber clear. Specimen crumpled and covered with milky substance. Legs partly removed. Nothing except antennae, apex of penial sheath and one hamulihaltere can be examined exactly. Sh —.

Cocc 27. ZMC, 16 I 1961. Th. Hansen. Amber clear, but from one side with curved surface which causes deformations, from the reverse side half of the specimen removed during polishing process. Sh+.

Cocc 31. ZMC, 25 III 1961, C. V. Henningsen. Specimen situated among fissures, cracks and lines; obscured further by milky clouds; both wings bent; nothing can be seen sharply. Sh+.

Cocc 39. ZMC, 11 X 1963, C. V. Henningsen. Resin round specimen in bubbles, ruptures, clouds and impurities, one wing broken; difficult to study. Sh−.

Cocc 47. ZMC, 1 I 1966, C. V. Henningsen. Amber clear. Body little shrivelled; one body side covered with wing, the other very dark, difficult for examination. Sh−.

Cocc 58. ZMC, 1 XII 1966, C. V. Henningsen. Amber clear. Specimen embedded between two layers of resin, little shrivelled, but obscured by bubbles and milky clouds. Thorax, including wing, and head absent from left side, it looks as they had been eaten before covered with next layer of resin; right wing removed to half length during polishing. Setae on various body regions very well visible. Sh−.

Cocc 65. ZMC, 28 III 1968. Specimen embedded between two layers of resin; numerous lines, fissures and bubbles veil large body parts and appendages; left wing broken. Sh−.

Cocc 72. ZMC, 28 III 1968, C. V. Henningsen. Amber clear; specimen little shrivelled; wings somewhat twisted, abdomen obscured from one side by strongly reflecting planes, from the reverse by milky clouds, but appendages, thorax and penial sheath accessible for examination. Sh+.

Cocc 97. SMNS, z5356, from the Koenigsberg Baltic Amber Collection. Amber and specimen dark; antennae in fissures and lines; body and appendages partly filled with air and resin (parafin ?); wing sclerites and sensilla may be seen. Sh−.

Adult female. *Cocc* 14. ZMC, 16 V 1957, A. K. Andersen. All body except antennae and distal parts of some legs in milky resin, bubbles and impurities; any setae visible. Sh+.

Cocc 26. ZMC, 5 I 1961 B. Mortensen. Specimen not shrivelled, left side in milky resin and minute bubbles; appendages in air sheaths, setae not recognizable. Sh−.

Matsucoccus apterus **sp. n.**

(Fig. 12)

Holotype: adult apterous male, *Cocc* 57, Baltic amber inclusion 1 XII 1966, C. V. Henningsen, ZMC.

Description

Adult male: Apterous specimen; body about 1400 μm long, 300 μm wide at thorax and 450 μm at abdomen. Head 210 μm long, 340 μm wide. Diameter of compund eyes about 130 μm. Middorsal plate heartlike, with several setae. Antenna 1300 μm long, i.e. slightly shorter than body; first flagellar segment the longest; apical segment (150 μm) slightly longer than two penultimate ones. Setae on scape and pedicel not recognized, they seem to be absent also on first flagellar segment; on further segments the setae are sparse, but capitate setae present on all, except first. Prothorax normal, with several tergal setae. Mesotergum diveded into prescutum, scutum, scutellum and mesopostnotum, but the sclerites are different from those in alate specimens. Presutum very short and wide, compressed between pronotum and scutum (artefact ?); scutum and scutellum resemble greatly the conditions in alte specimens; mesopostnotum difficult to interprete, it may be the small piece just behind scutellum; the sclerites are flat and seem to bear setae (in alate specimens setae have not been noted here). Metanotum subrectangular, well defined, with numerous setae. Legs rather stout, trochanter + femur about 350 μm, tibia 420–450 μm (anterior tibia shorter than posterior one), tarsus about 150 μm long; claw and digitules normal. Setae difficult to see, perhaps shorter than in alate specimens. Abdomen flat-

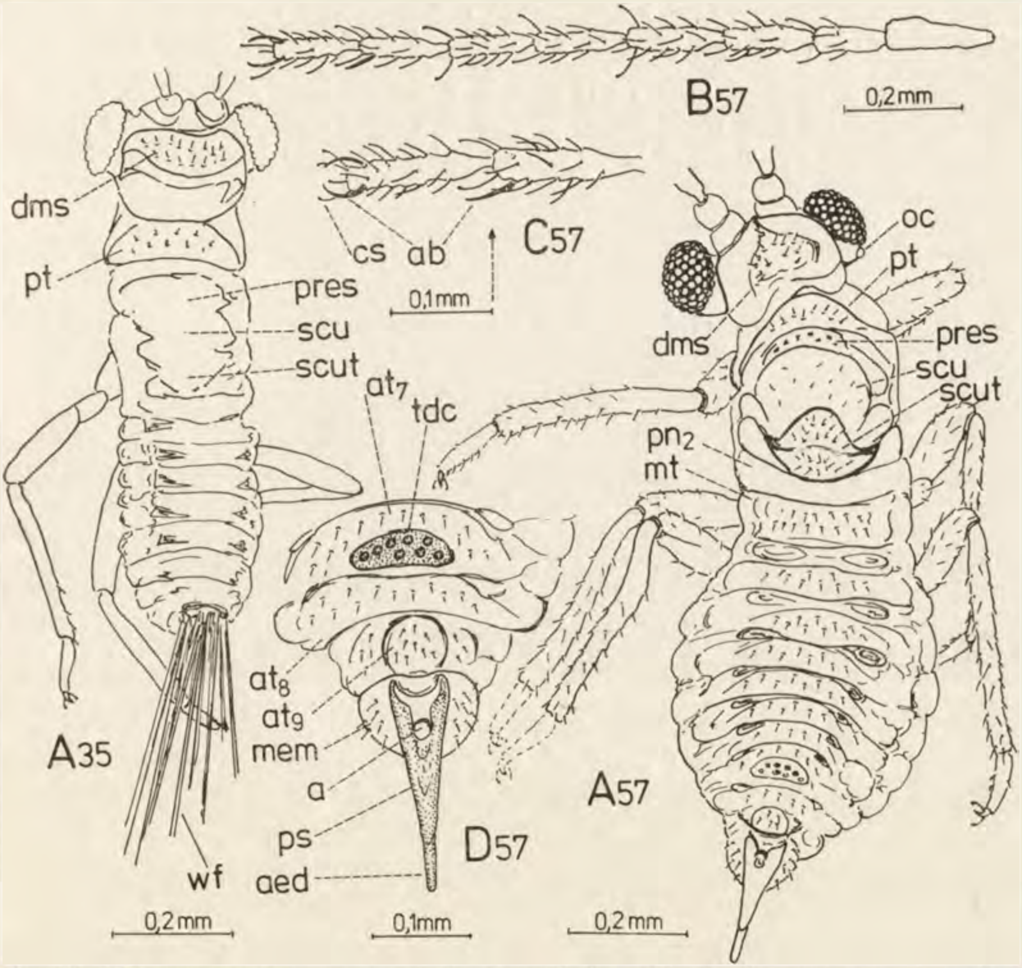

Fig. 12. *Matsucoccus apterus* sp. n., ♂, A — dorsal view of body, B — antenna, C — apical segments of antenna, D — apex of abdomen, dorsal view.

tened dorsoventrally, clearly segmented; all segments with minute setae. Pore cluster plate well defined, with 8 pores. Penial sheat normal, about 180 μm long, 110 μm wide. Ventral face of body not available for study.

Stellate hairs absent.

Note. The description of species is based only on the holotype. Two other specimens included tentatively to this species because of being apterous, are in poor condition and their description as well as identification is difficult.

For discussion of the conception of this species see Chapter VI.

Material examined

Cocc 35. Holotype, ♂, apterous, ZMC, 15 X 1962, C. V. Hennigsen. Specimen well preserved; little shrivelled; antennae partly removed when polished. Fissures and dark surface obscure some body parts, particularly from venter. Sh —.

Cocc 54. ♂, apterous, ZMC, 1 XII 1966, C. V. Henningsen. Poor specimen, crumpled and deformed; legs and antennae partly removed. Amber surfaces curved, little can be seen. Sh —.

Cocc 57. ♂, apterous, ZMC, 1 XII 1966, C. V. Henningsen. Amber clear. Specimen little shrivelled, but from venter largely covered with milky cloudiness and large bubbles, legs and antennae also obscured by air sheaths and milky resin; dorsum clear. Sh —.

Matsucoccus sp. n.

Specimens listed below, certainly matsucoccids, are in a very poor condition and their identification was not possible.

Material examined

Cocc 23. ♂, alate. ZMC, 5 I 1961, B. Mortensen. Amber clear; specimen completely shrunken and crumpled; body dark; wings, antennae and legs greatly removed; head visible from front, prescutum can be measured. Sh —.

Cocc 30. ♂, alate. ZMC, 25 III 1961, C. V. Henningsen. Specimen embedded in a fissure, at very edge of amber piece. Not available for study from any side. Sh +.

Cocc 46. ♂, alate, ZMC, 1 I 1966, C. V. Henningsen. The specimen has supposedly been dried before embedded in resin, situated within a fissure with numerous impurities. Examination not possible. Sh —.

Cocc 59. ♂, alate. ZMC, 1 V 1967, C. V. Henningsen. Amber clear, but specimen completely crumpled, embedded at very edge of piece, all details much deformed, one wing removed. Sh +.

Cocc 61. ♂, alate. ZMC, 1 V 1967, C. V. Henningsen. Specimen entirely crumpled, embedded within cracks, fissures, bubbles and milky clouds; not accessible for study.

VIII. SUMMARY

The first, and only, Baltic amber scale insects were described in 1845–56 by Koch and Berendt (*Acreagris crenata* ♀), Germar and Berendt (*Monophlebus pinnatus* ♂, *M. irregularis* ♂, *M. trivenosus* ♂) and Menge (*Coccus avitus* ♂, *C. termitinus* ♂, *C.* sp. ♀, *Ochyrocoris electrina* ♀, *Orthezia* sp. ♀). None of these inclusions were available for study; presumably they disappeared. Ferris (1941) redescribed females supposed to be *Acreagris crenata* and males believed to be *Monophlebus pinnatus*, on the basis of materials preserved at the Harvard

University. Both the forms have been considered to be male and female of the same species, close to *Matsucoccus* (Chapter I, II).

Among 117 Baltic amber inclusions of scale insects available for study, 64 are representatives of *Matsucoccidae* (Table 1), and results of investigations on this group are presented in the paper, but some particular features of scale insects inclusions and methods of their examination are also discussed (Chapter III).

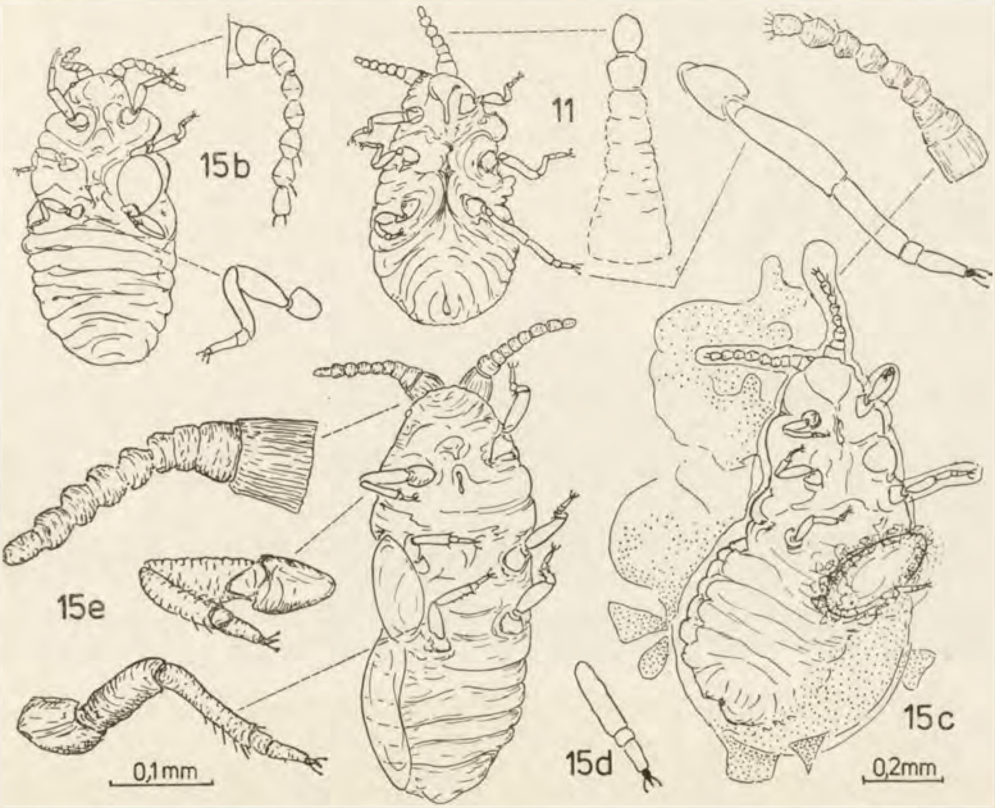

Fig. 13. *Matsucoccus larssoni* sp. n., ♀; ventral view of body, antenna and leg.

All posible information obtained from the matsucoccid inslusions has been compared with what is known about the host, life history, reproduction etc. of the present day species. *Pinus* (= *Pinites*) *succinifera*, the mother plant of the Baltic amber, is considered to be the host of the fossil matsucoccids. This belief is strongly favoured by the evidence that the recent species infest exclusively the pine, and by the proportion of inclusions of these coccids (55%), and particularly by the proportion of adult females (77% of all female inclusions) (Chapter V).

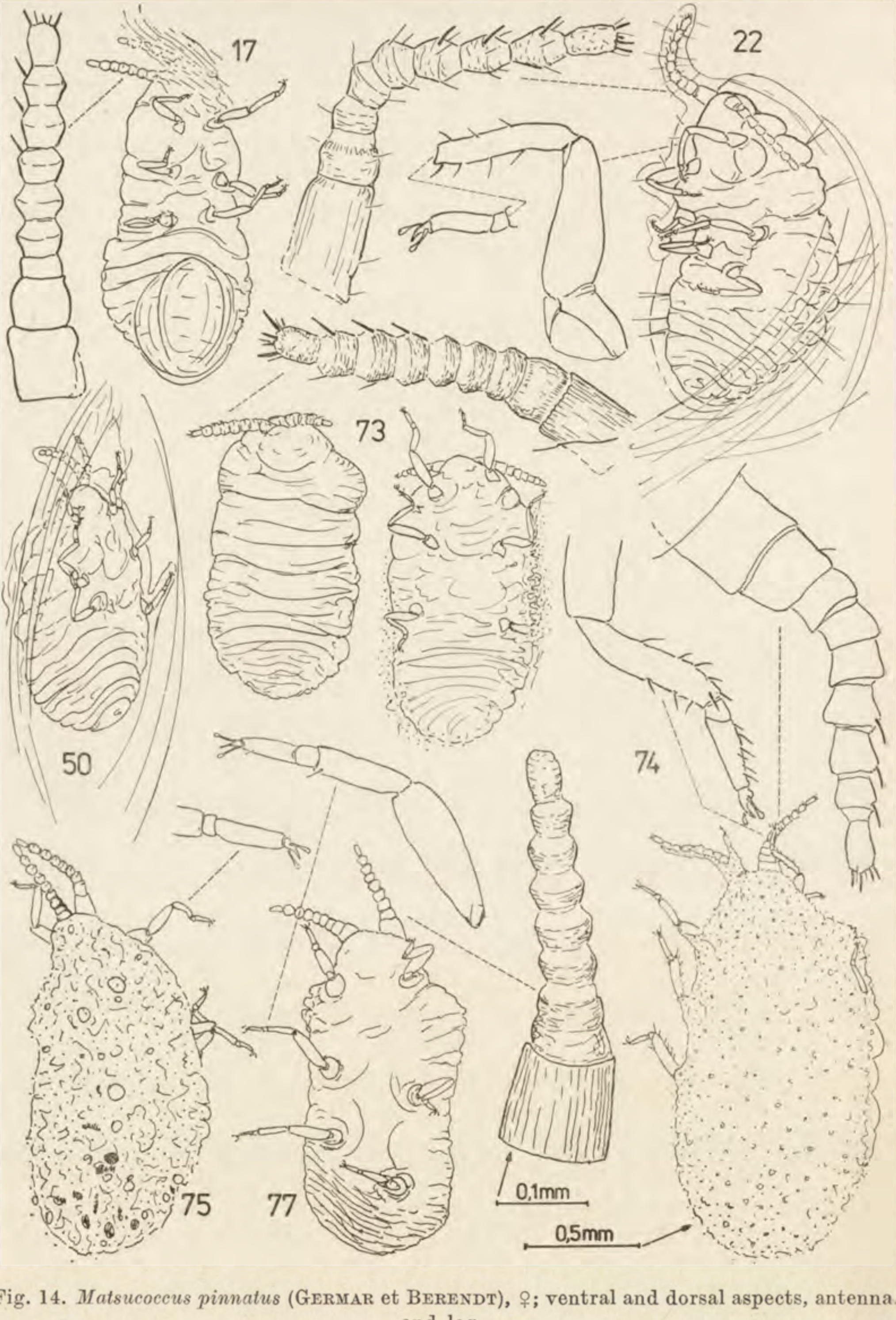

Fig. 14. *Matsucoccus pinnatus* (GERMAR et BERENDT), ♀; ventral and dorsal aspects, antenna and leg.

The taxonomic characteristics of the fossil matsucoccid alate male are broadly discussed on the background of the description of the recent *M. bisetosus* by Beardsley (1968). The wings, antennae and legs are best preserved in the amber and may be used in the taxonomy of fossil material (Table 2). Apterous male, adult female and first stage larva provide few characteristics for such purposes (Chapter VI).

Fig. 15. *Matsucoccus pinnatus* (Germar et Berendt), ♀, *Cocc* 94; dorsal and ventral aspects.

The comparison of males dealt with in the present paper with recent *Matsucoccus* justifies thier inclusion to this genus, and comparison of females and larvae concur. However, the fossil forms cannot be treated with the recent ones within one system or key because of different methods applied and sparse characteristics available in the former, thus all species recognized in the amber are considered to be new taxa, and their diagnoses and classification based mainly on few quantitative features, are apparently artificial (Chapter VI).

Alate male of *Matsucoccus pinnatus* (GERMAR et BERENDT) comb. n. has been redescribed and illustrated on the basis of 19 specimens; 10 females and

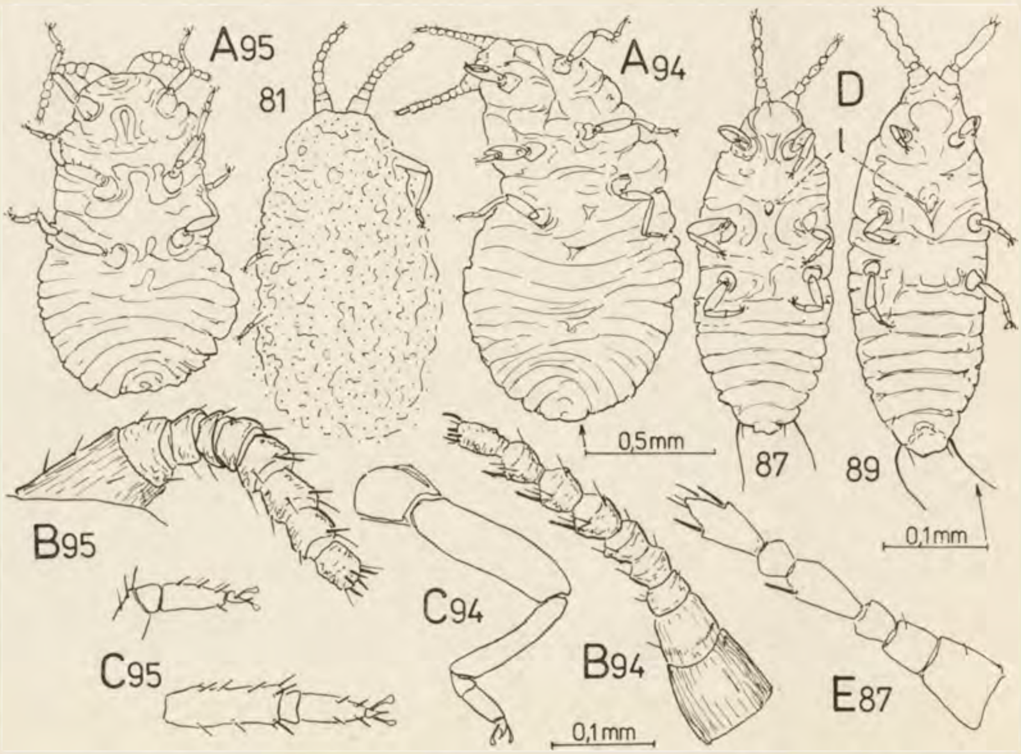

Fig. 16. *Matsucoccus pinnatus* (GERMAR et BERENDT), ♀ (A–C) and first stage larva (D, E); A — ventral aspect, B — antenna C — leg, D — ventral view, E — antenna (free hand).

2 first stage larvae have been also arbitrarily acsribed to this species. Three new species are established: *Matsucoccus larssoni* (8 ♂♂. 5♀♀). comprising the smallest forms, *M. electrinus* (10 ♂♂, 2 ♀♀) covering the largest forms, and *M. apterus* (3 ♂♂, no ♀♀). Five alate males in very poor condition remained unattached (Chapter VII).

The status of *Acreagris crenata* KOCH et BERENDT and *Monophlebus irregularis* GERMAR et BERENDT, affiliated with the *Matsucoccidae* by FERRIS (1941), is discussed. Both are excluded from this family: the former as nomen dubium because of absence of type material and very unadequate description, the latter because showing some monophlebid, but not matsucoccid features (Chapter IV).

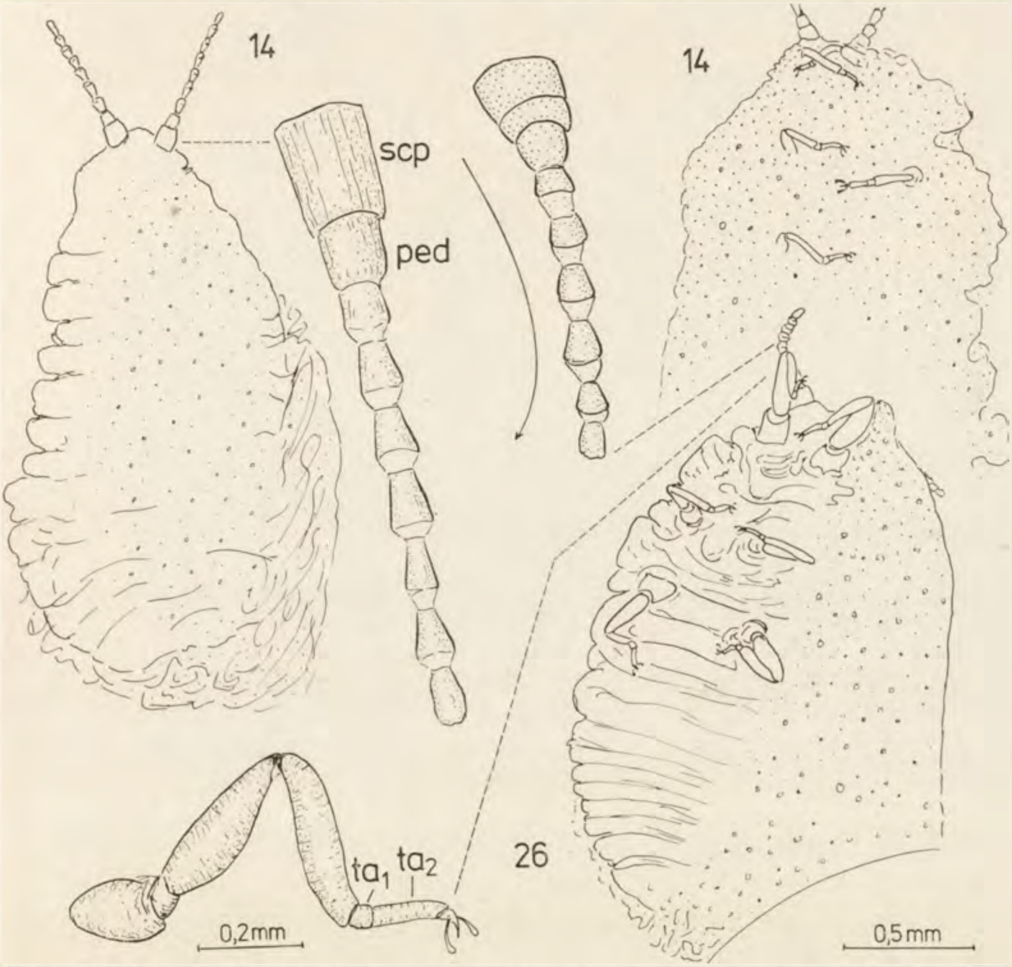

Fig. 17. *Matsucoccus electrinus* sp. n., ♀; dorsal and ventral aspects of body, antenna and leg. Antenna in *Cocc* 26 is strongly bent.

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STRESZCZENIE

[Tytuł: *Matsucoccidae* (*Homoptera*, *Coccinea*) bursztynu bałtyckiego]

Pierwsze i jedyne czerwce z bursztynu bałtyckiego zostały opisane w latach 1845–56 przez KOCHA i BERENDTA (*Acreagris crenata* ♀), GERMARA i BERENDTA (*Monophlebus pinnatus* ♂, *M. irregularis* ♂, *M. trivenosus* ♂) i MENGEGO (*Coccus avitus* ♂, *C. termitinus* ♂, *C.* sp. ♂. *Ochyrocoris electrina* ♀, *Orthezia* sp. ♀). Oryginalnych materiałów tych czerwców nie udało się zdobyć, prawdopodobnie zaginęły. FERRIS (1941) opisał na podstawie bursztynów bałtyckich z kolekcji Uniwersytetu Harwarda samicę, którą uważał za identyczną z *Acreagris crenata* i samca oznaczonego jako *Monophlebus pinnatus* (Rozdział I, II).

Spośród 117 przebadanych inkluzji czerwców w bursztynie bałtyckim 64 uznano za przedstawicieli *Matsucoccidae* (tabela I). Wyniki prac nad tą grupą przedstawiono w niniejszej publikacji. Ponadto omówiono pewne specyficzne cechy inkluzji czerwców i metody ich badania (Rozdział III).

Wszystkie informacje jakich dostarczyły inkluzje zestawiono z danymi na temat żywiciela, cyklu rozwojowego, rozmnażania itp. gatunków współczesnych. Sosna bursztynowa — *Pinus* (= *Pinites*) *succinifera* — była prawdopodobnie żywicielem kopalnych *Matsucoccidae*. Przemawia za tym duży procent (55) tych czerwców w stosunku do wszystkich pozostałych (w przypadku samych samic wynosi on aż 77%), a ponadto fakt, że współczesne gatunki żyją wyłącznie na sosnach (Rozdział V).

Obszernie opisano budowę uskrzydlonego samca na podstawie schematu współczesnego *Matsucoccus bisetosus* (BEARDSLEY 1968). Skrzydło, czułki i nogi są najlepiej zachowane w bursztynie i mogą być pomocne w taksonomii materia-

łów kopalnych. U samców bezskrzydłych, samic i larw tylko nieliczne cechy mogą być wykorzystane (Rozdział VI).

Okazy samców, którymi zajmuje się obecne opracowanie zostały włączone do rodzaju *Matsucoccus*. Również porównanie samic i larw ze współczesnymi gatunkami usprawiedliwia tę decyzję. Jednakże formy kopalne nie mogą być włączone ze współczesnymi do jednego systemu lub klucza, ponieważ metody badawcze i zakres dostępnych cech są zasadniczo różne. Z tego powodu wszystkie formy kopalne, z wyjątkiem wcześniej opisanych, uznane zostały za gatunki nowe, a ich klasyfikacja oparta na małej liczbie cech ilościowych jest w założeniu sztuczna (Rozdział VI).

Na podstawie 19 samców, 10 samic i 2 larw I stadium opisano *Matsucoccus pinnatus* (GERMAR et BERENDT) **comb. n.** Ustanowiono trzy nowe gatunki: *M. larssoni* (8 ♂♂, 5 ♀♀) obejmujący formy najmniejsze, *M. electrinus* (10 ♂♂, 2 ♀♀), do którego włączono formy największe i *M. apterus* (3 ♂♂). Pięć skrzydlatych samców, w bardzo złym stanie, nie oznaczono (Rozdział VII).

Przedyskutowano status *Acreagris crenata* KOCH et BERENDT i *Monophlebus irregularis* GERMAR et BERENDT, formy łączone z *Matsucoccidae* przez FERRISA (1941). Obydwie zostały wyłączone z tej rodziny – pierwsza jako nomen dubium, ze względu na brak materiałów typowych i bardzo ogólnikowy opis, druga ponieważ tak opis, jak i rysunek zawierają wyraźne cechy *Monophlebidae* [Rozdział IV].

РЕЗЮМЕ

[Заглавие: *Matsucoccidae* (*Homoptera*, *Coccinea*) из балтийского янтаря]

Автор исследовал 117 инклюзий червецов в балтийском янтаре, 64 из которых отнес к представителям *Matsucoccidae*. Установлены 3 новых вида — *Matsucoccus larrsoni* sp. n., *M. electrinus* sp. n. и *M. apterus* sp. n., а также описан *M. pinnatus* (GERMAR et BERENDT) comb. n. Произведена ревизия статуса *Acreagris crenata* KOCH et BERENDT и *Monophlebus irregularis* GERMAR et BERENDT и констатировано, что они не принадлежат к *Matsucoccidae*.

Проанализированы доступные для исследований таксономические признаки червецов из янтарных инклюзий. Обсуждена гипотетическая биология ископаемых *Matsucoccidae*; они жили, по-видимому на *Pinus succinifera*.

В работе приведен также обзор литературы по вопросу ископаемых червецов, обсуждено состояние исследований в этой области, существующие коллекции и методы исследований янтарных червецов.

Redaktor pracy – prof. dr J. Nast

Cena 60.—

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