The Matsucoccidae in the Mediterranean basin with a world list of species (Hemiptera: Sternorrhyncha: Coccoidea)

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Résumé – **Les Matsucoccidae du bassin Méditerranéen avec une liste mondiale des espèces (Hemiptera: Sternorrhyncha: Coccoidea)** – Les Cochenilles matsucoccides, dont certaines sont très nuisibles, vivent dans l'hémisphère Nord, où elles sont phytophages, s'alimentant exclusivement sur *Pinus* spp. La révision taxonomique des espèces méditerranéennes a permis de confirmer leur statut d'espèces valides, malgré les variations importantes de certains caractères morphologiques dépendant des facteurs environnementaux. Pour la redescription et l'illustration du genre, *Matsucoccus matsumurae* Kuwana, l'espèce type du genre, du Japon a été utilisée. Les espèces Méditerranéennes, *M. feytaudi, M. pini* et *M. josephi* sont redécrites et illustrées. Une clef pour leur identification est proposée en utilisant des caractères morphologiques et des données quantifiées. Chez *M. feytaudi*, tous les stades du développement, mâle et femelle, sont examinés et illustrés. Les lectotypes de *M. feytaudi* et *M. pini* sont désignés. Des informations sur la biologie, les plantes-hôtes, l'importance économique, les ennemis naturels et la distribution de toutes les espèces méditerranéennes étudiées sont données. Une liste mondiale des espèces actuelles et fossiles de Matsucoccidae avec quelques informations (plante-hôte, microhabitat, distribution) est présentée.

Abstract – The matsucoccid scale insects inhabit the northern hemisphere, feed exclusively on *Pinus* spp., and some are very serious pests. This taxonomic revision of the Mediterranean species supports their status as valid species, despite the wide variation of certain morphological characters caused by environmental factors. For the genus redescription and illustrations, *Matsucoccus matsumurae* Kuwana, the type species of the genus, from Japan is used. The Mediterranean species, *M. feytaudi*, *M. pini* and *M. josephi* are redescribed and illustrated. A key for their identification is provided using morphological characters and quantitative features. In *M. feytaudi*, all stages of development of both the male and female are described and illustrated. Lectotypes of *M. feytaudi* and *M. pini* are designated. Some information on the biology, host plants, economic importance, natural enemies and distribution of all species is given. A world list of extant and fossil species of Matsucoccidae is provided along with some pertinent (host plant, feeding site, distribution) information.

The genus name *Matsucoccus* was erected in 1909 by Cockerell for the species *Xylococcus matsumurae*, described by Kuwana (1905, 1907) from Tokyo, Japan. During the earthquake in 1923, the type was destroyed (pers. com. of Dr Takagi), but fortunately some syntypes were sent by Kuwana to Herbert (USA) allowing a redescription by both Herbert (1921) and Morrison (1928). However, the authors based their redescription on "mixed" material, i.e. material originating from both Japan and the eastern United States. Indeed, Boratynski (1952) and Tang et *al*. (1997) questioned whether this "mixed described species" actually corresponded to the true *M. matsumurae*. Morrison, (1927) created the tribe Matsucoccini within the subfamily Xylococcinae, family Margarodidae. Beardsley (1968), on the basis of the male morphology of *Matsucoccus bisetosus* Morrison, considered that *Matsucoccus* was the least specialized group within the Margarodidae, sharing characters with *Orthezia* and *Aphis*, and proposed elevating the tribe Matsucoccini to subfamilial rank. However Koteja (1974) pointed out that their derived characteristics, such as the structure of the labium which had evolved from more primitive mouthparts, and suggested that matsucoccus was

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one of the most specialized genera among the Archaeococcoids, and raised it to family status, the Matsucoccidae. Koteja (1984, 1990), following his studies on amber fossils, stated that the Matsucoccidae were among the earliest archaeococcids. *Matsucoccus* species are sister to the remaining taxa in Miller (1984), Foldi (1997); *Araucaricoccus* + *Matsucoccus* and *Steingelia* + *Stomacoccus* are sister to the rest of the margarodids in Gullan & Sjaarda (2001) in their phylegenetic history of margarodids. The results of a phylogenetic study of the Margarodidae *s. l.* based on adult male morphology suggest that the Marsucoccidae are sister to all other families (Hodgson & Foldi in print).

The Matsucoccidae currently include the oldest known scale insect fossils. The first and oldest *Matsucoccus* fossil species was described in 1856 by Germar and Berendt as *Monophlebus pinnatus* from a Baltic amber inclusion, in Tertiary-Eocene Baltic amber, about 40 millions years old. However Ferris (1941) transferred it to *Matsucoccus.* Koteja (1984, 1986) described four further species from this deposit, i.e. *Matsucoccus apterus, M. electrinus, M. larssoni* and *M. saxonicus*. He also created a new genus, *Eomatsucoccus* about 125 millions years old, characterized by very broad wings, currently including four species from Cretaceous deposits in Siberia (Russia), southern England and eastern USA (Koteja 1988, 2000, 2000a). Currently, the Matsucoccidae constitute more than 50% of all coccid fossils, represented mainly by adult males. The males of only three species have been studied previously: *Matsucoccus bisetosus* Morrison (Beardsley 1968), *M. mugo* Siewniak (Siewniak 1970), and *M. pini* (Green) (Rieux 1976, Siewniak 1976. Other males of Margarodidae *s.l.* were studied by Theron (1958), Morales (1991) and Foldi (1990, 1999), although Hodgson & Foldi (in prep.) are describing males representing most higher taxa within the Margarodidae sensu Morrison.

All matsucoccids inhabit the northern hemisphere in Neartic and Palaeartic zones, feed exclusively on *Pinus* spp., and some are very serious pests of natural pine forests and plantations, particularly in the USA, China and the Mediterranean basin. Major pests are the Japanese pine bast scale, *M. matsumurae* (Kuwana)*;* the pinyon needle scale, *M. acalyptus* Herbert, the ponderosa pine twig scales, *M. bisetosus* Morrison and *M. vexillorum* Morrison. In the Mediterranean area (Algeria, France, Israel, Italy, Morocco, Portugal, Spain), *M. feytaudi*, *M. josephi* and, to some extent, *M. pini* may cause considerable injury to pine forests. High populations provoke serious outbreaks, resulting in needle drop, shortened needles, weakened crowns, chlorosis in mature trees, and the deformation or death in young trees (Gill 1993).

This research is part of a broad revision and higher classification of the Margarodidae and related taxa belonging to the informal group, the Archaeococcoids, defined by the plesiomorphic characters as the presence of abdominal spiracles, an XX-X0 chromosome system and in males presence of compound eyes and a long dorsal waxy tail tuft on the posterior end of abdomen, excepted two groups, the Monophlebinae and Coelostomiidinae. Koteja (1974, 1996) pointed out that the presence of a paired apical organ on the labium may be a probable synapomorphy for archaeococcoids and recently its presence was clearly demonstrated in *Phenacoleachia* Cockerell (Phenacoleachiidae) by Gullan & Cook (2001a).

The aims of this work were to redescribe the genus *Matsucoccus*, to revise the taxonomy of the species of *Matsucoccus* found in countries around the Mediterranean and to redescribe them, using current standards in scale insect taxonomy. Data on host plants, biology, ecology, and economic importance are also included.

Materials and methods

The examined slide mounted specimens are deposited in the following institutions: Muséum national d'Histoire naturelle, Paris, France (MNHN); The Natural History Museum, London, United Kingdom (BMNH); US National Museum of Natural History, Washington, D.C., USA (USNM); Department of Entomology, The Volcani Centre, Bet Dagan, Israel (ICV).

The specimens were examined using a Leica DMR microscope; all measurements of scale insect morphology were made on several specimens and are expressed as a range; the drawing of each female or male represents a synthesis of all specimens used for the description.

For the SEM study, a small slit was made on the margin of each specimen and the whole insects were treated in KOH (10%), washed in water and in a series of alcohol, 30%, 70% to absolute alcohol, cleaned in a ultrasonic cleaner and critical point-dried.

Abbreviations used on fig. 7

aed = aedeagus
al = alary lobe
as = abdominal spiracle
ax1, ax2, ax3 = axillary sclerites
ce = compound eye
cd = claw digitule
cl = claw
cs = capitate seta
cv = cervical sclerite
cx1, cx2, cx3 = pro,-meso-, metathoacic coxa

dep = dorsomedial epicranium
der = dorsal midcranial ridge
eps 1, 2, 3 = pro-, mes-, and metepisternum
fe = femur
fs = fleshy seta
fu = furca
ha = hamuli
hh = hamulohaltere
me = median
mphr = mesoprephragma
mts = metatergal setae
oc = ocellus
ocs = ocular sclerite
pa = postalare
pcr = precoxal ridge
p = pedicel
plr = pleural ridge
pn2 = mesopostnotum
pos = postoccipital suture
pra = prealare
prs = prescutum
ps = penial sheath
pt = post-tergite
ptcr = postcoxal ridge
pwp = pleural wing process
r = radial
sct = subcostal
scp = scape
scu = scutum
scut = scutellum
stn1 = prosternum
stn2 = basisternum
stn3 = metasternum
t = tegula
ter = tergite
ti = tibia
tcp = tubular pores cluster
tr = trochanter
ts = thoracic spiracle
vcr = ventral midcranial ridge

SYSTEMATICS

Matsucoccidae Morrison

Tribe Matsucoccini Morrison, 1927: 101.
Sub-family Matsucoccinae Morrison, 1927; Beardsley, 1968: 1458.
Family Matsucoccidae Morrison, 1927, Koteja, 1974: 288.

The matsucoccids inhabit the Northern Hemisphere in Holartic region, morphologically very homogenous group, oligophagous, feed exclusively on *Pinus* spp., and some are very serious pest of pine forests.

A matsucoccid female can be recognized easily by the following major characters: large simple pores or cicatrices dorsally in rows on abdomen; presence of bilocular tubular duct and multilocular disc-pores; unique structure of thoracic and abdominal spiracles, each with a globular and elongated atrium; 2-segmented tarsus; claw with two knobbed digitules longer than claw; mouthparts absent, and reticulated pattern on legs and antennal segments.

A matsucoccid male can be recognized easily by their so characteristic surface (pinnate sculpture) of their mesothoracic wings. In addition, they have compound eyes and a dorsal waxy tail tuft, these characters shared by many margarodid males.

The family Matsucoccidae currently includes 2 genera with 43 species; the genus *Matsucoccus* with 33 extant and 6 fossil species and the fossil genus *Eomatsucoccus* with 4 species (Foldi 2001, and see Appendix-1). Ray & Williams (1984, 1991) described four new species and provided a key to species in North America while Gill (1993) reported 17 species occurring in North America.

GENUS **MATSUCOCCUS** Cockerell

Matsucoccus Cockerell, 1909: 56.
Type species. *Xylococcus matsumurae* Kuwana, 1905, by original designation and monotypy.
Americoccus MacGillivray, 1921: 78. Type species: *Matsucoccus fasciculensis* Herbert, 1919; junior synonym by Morrison, 1928: 48.
Sonsaucoccus Young 1980. Type species: *Matsucoccus sinensis* Chen, 1937; junior synonym by Tang & Wu and Li 1997: 17.
Acreagris Koch & Berendt, 1854. Type species *Acreagris crenata*. Synonymised by Ben-Dov & Koteja, 2002: 379.

Generic characters – All the known species live concealed beneath bark, or in bark crevices, cracks in the trunk or branches, in twig axils or at the base of needle bundles of *Pinus spp.* (Pinaceae).

Adult female elongate oval usually broadest across posterior part of abdomen, with rounded ends; body sometimes distorted by pressure of bark; length 2-6 mm, 1-2 mm wide. Derm membranous throughout. Antennae close together on anterior margin of head, usually 9-segmented, 6 or 7 on *M. subdegeneratus* Morrison, and only 3-segmented on *M. degeneratus* Morrison; segment I obviously longer and wider than others and usually with a group of short setae dorsally; most antennal segments with a sclerotized, reticulated surface, made of elongate polygonal patterns, resembling fish scales, appearing to slightly overlap; most subapical segments with short hair-like setae and, in addition, segments V or VI to IX each with two fleshy setae. Legs similar in structure; trochanter with a group of sensilla (pores) and usually with 1 long or 2 subequally long setae; tarsus 2-segmented with a short basal segment; claws on pro-,meso- and metathoracic legs small, equal in size, curved, with pair of knobbed digitules, each digitule longer than claw. Mouthparts absent, represented by a weakly sclerotized folded area. Spiracle structure unique to *Matsucoccus* species: thoracic spiracles composed of two morphologically distinct parts: a wide globular atrium followed by a narrower elongate atrium or atrial tube whose distal end expands, becoming an attachment point for a tuft of tracheae; proximal part of atrial tube bearing a network of small, oval or irregular cuticular structures (pores),

which appear on slide mounted specimens as a reticulated surface; with 7 pairs abdominal spiracles nearly similar in similar structure to the thoracic ones, except for the absence of reticulated surfaces. Setae hair-like with a flat socket. Bilocular tubular ducts present on both dorsum and venter. In dorsal view, each bilocular tubular duct consisting of double ovoid pores with a strongly sclerotised rim and one very tiny, often invisible pore leading to a central narrow ductule. In lateral view, this wax gland appears to have two distally joined short ducts and a narrow ductule medially between ducts; sclerotised rim deeply invaginate, forming a characteristically circular, broad, sac-like structure, opening at distal end like a cup, enclosing major part of gland. Multilocular disc pores localized on venter at posterior end of abdomen; each multilocular disc pore composed of two parts: a central bilocular tubular duct similar in structure to bilocular ducts described above but externally with numerous loculi placed in an outer ring; this sclerotised rim also deeply invaginated and forming a sac-like structure as on bilocular tubular ducts.

Large simple pores or cicatrices in transverse rows on dorsum of abdomen. Anus apparently absent.

Second instar or cyst oval to almost round without antennae and legs; fully developed cysts elongate with hard integument; with waxy secretion laterally around abdomen produced by spiracular glands; tentorium without corpotentorium (this represents a plesiomorphy in matsucoccids). First-instar nymph (crawler) small, elongate, body without pores, wax secretion only at base of atrium of spiracles and with very few short setae, with 2 long setae on posterior end of abdomen.

Males *Matsucoccus* characterized by some unique structures: surface of wings with paralell fine folds (lines), forming a "pinnate" sculpture, unique in Coccoidea; alar setae absent; sensillae localized at wing base; body narrow in dorsal view; mesothorax deep and unusually narrow; basisternum very long, extending anteriorly below prescutum; mesopostnotum broad apparently narrow in dorsal view but lying vertically and resembling that on the Aphididae (Beardsley 1968). Compound eyes present and a waxy tail tuft dorso-medially on abdominal segment VII.

Biology – The general life history of matsucoccids was established by earlier workers such as Herbert (1921), Morrison (1939), McKenzie (1942, 1943) and Boratynski (1952).

Female development usually involves 3 instars: first-instar nymphs (crawlers) which emerge from ovisac, apparently similar in structure in both sexes. This instar is dispersal stage and select host-plant and feeding site, often a crevice or under bark on trunk, branches or, in a few species, at base of needles. Second-instar nymph or cysts also a feeding stage but lacking legs and antennae. Honeydew not observed, therefore probable feeding site parenchima. Fully developed cyst with hard integument and often represents an overwintering stage; last molt produces an active female which emits a pheromone and, after mating, lays several hundred eggs in a white ovisac which also encloses tip of abdomen. Rarely, development can involve 4 instars, as in *M. vexillorum* Morrison. Thus development, from first-instar nymph to cyst stage consists of radically changing body shape and size, accompanied by a displacement of legs and antennae to periphery of body, giving insect a strange appearance (fig. 3a,b). Most *Matsucoccus* species are bisexual, except *M. pini* Green which is apparantly peculiar to England, and *M. macrocicatrices* Richard in Canada which are both parthenogenetic. Species may be univoltine, bivoltine or have many generations, with, for example, 5 or 6 in *M. josephi* Bodenheimer & Harpaz.

Male development involves 5 instars: an initially mobile 1st instar, but which later becomes fixed; a 2nd immobile instar or apodous cyst; a mobile 3rd instar or prepupa and which may be resemble to female but lacks a vulva and has a shorter abdomen; followed by a sessile 4th instar or pupa which occurs in a waxy test and has with wing pads; the final molt produces an active, winged adult male (Figs. 7, 10). Life history stages of female and male of *M. feytaudi* are illustrated in Fig. 8.

Genus **EOMATSUCOCCUS** Koteja

Eomatsucoccus Koteja, 1988: 143.

Type species – *Eomatsucoccus sukachevae* Koteja, 1988, adult male from Lower Cretaceous (Neocomian) deposits in Siberia (Transbaikalia). Represents oldest currently known scale insect impressions of about 125 millions years old. Major morphological characters are: prescutum about twice as broad as long; scutellum transversaly rectangular; head strongly sclerotised, and wings broad.

Description of the Mediterranean *Matsucoccus* species

Matsucoccus feytaudi Ducasse, 1942
Maritime pine bast scale,
La Cochenille du Pin maritime

Matsucoccus feytaudi Ducasse, 1942: 217.

Lectotype – here designated: adult female, MNHN: 5760/-1; France: Landes; on *Pinus maritimus*, 29.IX.1938; G. Ducasse rec.; 7 paralectotypes, MNHN: 5760/2 – 5; 5760/8, 10-11 with same data.

Other material examined – France: Island of Porquerolles, road of Sémaphore in front of vineyard, under bark of trunk of *Pinus pinaster*, 15.III.1996, Foldi rec. Vendée: Notre Dame de Monts; Gironde: Commune de Cestas et de Marcheprime; Haute Corse:

Commune de Ponte Leccia. INRA coll.; Avignon, VI.1969. P. Carle rec.: Forêt du Dom des Bormes (Var), 10.IV.1964. P. Teocchi rec.; Cap Ferret (Gironde), IV. 1965. F. Hascoet rec.

Adult female (fig. 1, 9, 18), described from 30 specimens.
Live appearance. Body elongate, derm membranous throughout, greyish-black. Mated female with white cottony ovisac on tip of abdomen. Found in bark crevices of trunk.

Mounted specimens. Body elongate oval, broadest across posterior end of abdomen, with rounded ends, tapering gradually towards head; 2.5 -5.3 mm long, 1.5-2 mm wide, with few setae; body segmentation distinct. Derm with dense network of small, globular projections over entire body.

Venter. Antennae 9-segmented, each 800-950 µm long; placed close together ventrally on head margin; segments conical; segment I obviously longer and wider than others and with a group of small setae dorsally; segment II with 1 or 2 sensilla, segments III-IX sclerotized each with elongate polygonal pattern, and distal margins with short hair-like setae; segments V to IX with two fleshy setae; membranous intersegmental zone with granular surface on segments III-VIII; segment III bearing intersegmental sensilla; apical segment narrower and shorter. Antennal segment lengths and setal data: segment I: 160-180 µm long, 140-150 µm wide, dorso-basally with 15-16 short setae, each 10 µm long, plus 16 setae medially, each 20 µm long; II: 70 µm long, 90 µm wide, with 18 setae, each 20-40 µm long but one seta 60 µm long; III: 90 µm long, 60 µm wide, with 8 setae, each 30-40 µm long; IV: 100 µm long, 60 µm wide, with 7-8 setae, each 30-40 µm long; V: 90 µm long, 55 µm wide, with 6-7 setae, each 30 µm long, plus 2 fleshy setae, each 20-25 µm long; VI: 70 µm long, 65 µm wide, with 6 setae, each 30 µm long, plus 2 fleshy setae, each 30 µm long; VII: 70 µm long, 60 µm wide, with 4 setae, each 30 µm long plus 2 fleshy setae 20 µm long; VIII; 70 µm long, 45 µm wide, with 3-4 setae each 30 µm long plus 2 fleshy setae 20 µm long and segment IX: 70 µm long, 30 µm wide, with 4-5 hair-like setae plus 2 stout fleshy setae, each 30 µm long. Eyespots located on margin just posterior to antennae. Mouthparts absent but with an invaginated membranous area.

Femur, tibia and tarsus reticulated as on antennal segments. Metathoracic legs measurements: coxa about 270 µm long, 150 µm wide with about 12-14 short setae, 1each 0 µm long; trochanter + femur 240 µm long; trochanter with 6-8 sensilla on each side, and with 1 or 2 unbequal setae, one about 90 µm long, other 40-50 µm long; occasionally one seta 20 µm long; femur 280 µm long, 100 µm wide, with few setae; tibia 280 µm long, 55 µm wide, with about 20 short setae; tarsus 2-segmented, t1 + t2 160 µm long, 50 µm wide; basal segment short without reticulated surface; longer distal segment with about 10 setae ventro-laterally plus a pair of thin tarsal digitules; claw short, 30 µm long, thick and strongly curved, strongly enlarged basally, without a denticle, with 2 knobbed digitules, each longer than claw. Thoracic spiracles wider than abdominal spiracles. Thoracic spiracles each with peritreme about 15 µm wide, a globular atrium 25-30 µm in diameter, followed by a narrower elongate atrium or atrial tube, 40-45 µm long and 10-12 µm in diameter; proximal part of atrial tube with a reticulated surface (pores) whose distal end expands, from which a tuft of 18-30 small tracheae arise; one of these tracheae always wider than others (Fig.17). Abdominal spiracles in 7 pairs, similar in structure to thoracic spiracles, except absence of reticulated surface; each spiracle with unsclerotised peritreme, with an globular atrium 15-20 µm in diameter, followed by an atrial tube 35-45 µm long from which a tuft of tracheae arise from expanded distal end (Fig. 16). Hair-like setae, each 40-50 µm long: with about 2-4 setae on median and submedian area of each abdominal segment, and with 4 or 5 setae near of each coxae; shorter setae, each about 15-25 µm long, distributed in transverse bands 1-2 wide over venter, most abundant on posterior abdomen.

Bilocular tubular ducts, 9-11 µm long, about 5-6 µm wide, scattered on head, but arranged segmentally on thorax and abdomen in rows 1 pore wide associated with short setae. In dorsal view, each bilocular tubular duct consists of a double ovoid pore with a strongly sclerotised rim and one very tiny, often invisible, pore leading to a central narrow ductule. In lateral view, this wax gland appears to have two short ducts joined distally plus a narrow ductule medially between ducts; sclerotised rim deeply invaginate, forming a characteristic circular, broad, sac-like structure, opening at distal end cup-like, enclosing major part of gland. Vulva: a ventral longitudinal opening on posterior abdominal segment, surrounded by a cluster of 80-100 multilocular disc pores; each pore measuring about 10 µm in diameter, each with 9-14 loculi in an outer ring, a bilocular tubular duct centrally and a narrow ductule medially; sclerotized rim invaginated as described above for bilocular ducts.

Dorsum. Large circular pores or cicatrices, each 7-10 µm in diameter and usually with a smooth surface, often with numerous, obvious fine micro-openings; cicatrices arranged in transverse rows 1-4 wide on abdominal segments IV to VII. Cicatrices number varying from 172 to 277, number per segment variable, range as follows: segment IV: 11-38, V: 72-110, VI: 53-84, VII: 21-45 corresponding to a mean of 224. Bilocular tubular ducts, 8-10 µm long, 4-5 µm wide, scattered on head but in transverse rows about 1 pore wide on thorax and abdomen, associated with short hair-like setae, each about 30 µm long. Anal opening not visible.

Biology. Found in crevices and under the bark of *Pinus pinaster;* bisexual; populations of *M. feytaudi* in France and in Italy have univoltine development (Riom & Gerbinot 1977; Covassi & Binazzi 1992). however, Branco et *al.* (2001), reported univoltine and bivoltine populations in Portugal. The biology of *M. feytaudi* in France was reviewed by Riom (1994). The female has 3 instars and the male 5. In maritime pine stands of the Maure and Esterel forests, adult males and females appear in February-March. After mating, the females settle in crevices in the bark and lay about 250-350 eggs in a white ovisac, which also encloses the tip of the abdomen. The newly hatched first-instars appear about

30-35 days later in April or May, disperse and than settle and feed under the bark; this instar has a long development. The apodous, feeding second instar or cyst appears until September, is the overwintering stage for the female and the cyst or prepupa for the male. The integument of the cyst is thick and hard.

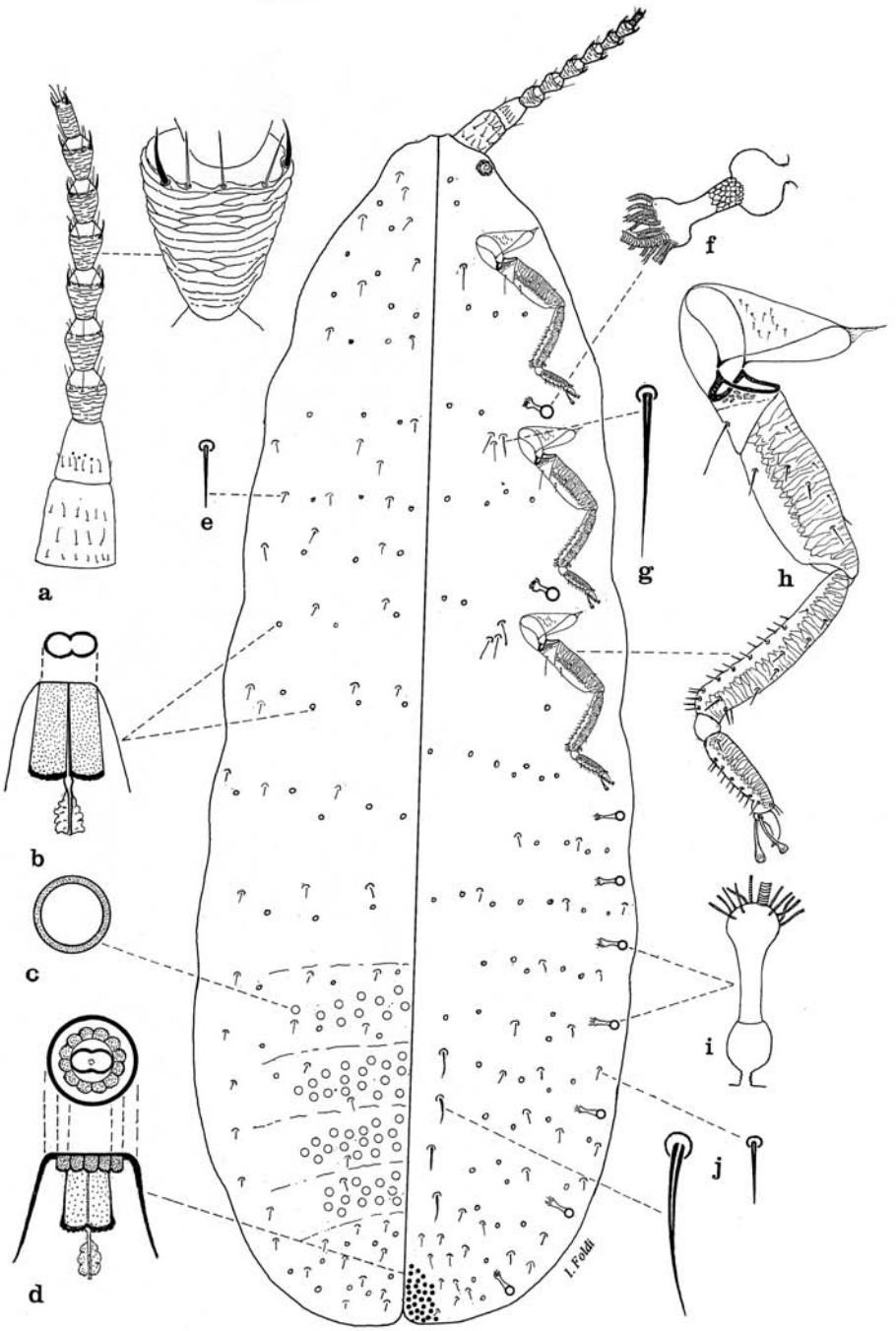


Figure 1
Adult female of *Matsucoccus feytaudi* Ducass. – a. antenna; b. bilocular tubular duct; c. cicatrice; d. multilocular disc-pore; e. dorsal seta; f. thoracic spiracle; g. setae near coxae; h. metathoracic leg; i. abdominal spiracle; j. ventral setae.

Economic importance. The maritime pine bast scale is a serious pest of *Pinus pinaster* and causes damage by ingesting sap, perforating the phloem, inhibiting the growth of tissues, and injecting toxic saliva. The most conspicious sign of the early stages of scale insect infestation are cottony white ovisacs within the bark crevices. External signs of infestations consist of loss of tree vigor, dieback of branches, chlorosis and death of needles, and resin exudates. Trees weakened by this scale are susceptible to other pests such as the xylophagous insects *Pissodes notatus* (Curculionidae) and *Blastophagus destruens* (Scolytidae) and some Cerambycidae and Buprestridae. Attack by successive pests results in the death of the trees in maritime forests. Western populations of *M. feytaudi* are supposed to be endemic to the area (Landes, South-West France) and, surprisingly, in this area, *M. feytaudi* does not cause significant injury to maritime pine. In contrast, after it was accidentally introduced into southeastern France (Maures, Esterel) it was implicated in the decline of 120 000 ha of maritime pine between 1960-70 (Joly 1963, Schvester 1967, Carle 1973, Riom 1994). The difference in the level of damage is assumed to be caused by differences in environmental conditions, different secondary pests, and variability in the susceptibility of host trees (Riom & Gerbinot 1977). In Landes climatic factors keep pest populations at low levels, primarily because of high mortality of the crawlers. In addition, the bark of maritime pine is more fissured in Maures, thus offering more settling sites for the crawlers. Recent research reinforces the assumption that the genetic resistance structure of the host has an important influence on *M. feytaudi* populations and therefore distribution (Burban et *al*. 1999). The species was recently discovered in Corsica, where an outbreak initiated decline of maritme pine and an epidemic of the pest is feared (Jactel et *al*. 1996, 1998). Researchers at INRA are attempting to slow its spread with the use of a synthetic pheromone for monitoring range expansion and for mass trapping of males. Other strategies include the removal of highly suseptible trees.

M. feytaudi is also a serious pest in North Italy (Liguria) and causes damage on maritime pine forests (Covassi & Binazzi 1992) and also in Portugal and Spain.

Natural enemies. Only predator are associated with *M. feytaudi*, no attacked by parasitoids. About 15-20 insect species feed on *M. feytaudi*, belonging to the families Coccinellidae, Rhaphidiidae, Chrysopidae, Hemerobiidae and Anthocoridae The bug, *Elatophilus nigricornis* Zetterstedt (Heteroptera, Anthocoridae) is a specialist predator of *M. feytaudi*, feeding on all stages (Fabre et *al*. 2000). A close relationship between the predator of *Hemerobius stigma* Stephens (Neuroptera: Hemerobiidae) and *M. feytaudi* was signaled by Branco *et al.* (2001).

In Italy, *Rhyzobius chrysomeloides* (Coccinellidae), is a remarkable predator of *M. feytaudi* (Toccafondi, Covassi & Pennacchio 1991). Other predators: Heteroptera, Anthocoridae: *Elatophilus nigricornis, E. pini, E. crassicornis and Dufouriellus ater;* Neuroptera*, Hemerobiidae: H. simulans, H. stigma;* Inocellidae: *Inocellia bicolor;* Coleoptera, Coccinellidae: *Rhyzobius chrysomeloides, Scymnus suturalis, S. interruptus, Oenopia conglobata, O. lyncea.* (Toccafondi, Covassi & Pennacchio 1991).

Host plants. *Pinus pinaster*.

Distribution. Algeria, France, Italy, Morocco, Portugal, Spain, Tunisia (Riom 1984, Burban *et al*. 1999). In France, *M. feytaudi* is present throughout most of the western part of the natural range of maritime pine, as determined by direct observation and by pheromone trapping by INRA researchers (Bordeaux). In southeast France, Bormes les Mimosa (Var), it was first observed in 1961 by M. Donskoff (Joly 1963). It has been reported from Brittany, Cévennes, Charentes, Gard, Gironde, Pays de Loire, Vendée, Aquitaine, Maures and Esterel (Burban et *al*. 1999), from Corsica (Jactel et *al*. 1996, Foldi 2003), and from the island of Porquerolles (Foldi 2000).

In Italy, introduced from France, it was signaled by Fabre (1980); subsequent surveys discovered it from Liguria, and Tuscany and, are presently spreading in the north-west of Italy (Arzone & Vidano 1981, Binazzi & Covassi 1989, Covassi, Binazzi, Toccafondi 1991, Covassi & Binazzi 1992). In Portugal it was reported from Galicia, Apostiça, Sintra, Península de Setúbal, Marinha Grande, Lousã (Branco et *al*. 2001). In Spain from Castilla, Granada, Malaga and Punta cires (Burban et *al*. 1999). In Maroc from Middle Atlas.

First-instar nymph (described from 6 specimens)
Structure of mobile phase (fig. 2).

Newly hatched first instar 420-460 µm long, 170-200 µm wide with very few short setae on antennae, legs and body; without wax secreting pores, with wax secretion only from base of atrium of spiracles. Antennae 6 segmented. Abdominal spiracles in 7 pairs. Mouthparts well developed. With 2 long setae on posterior end of abdomen.

Venter. Antennae 6 segmented, total length 110 µm; scape about 20 µm long, 20 µm wide with one short seta; segment II with 2 short setae and one longer seta about 40 µm long; segment III with a wide sensilla on each side, and no setae; segment IV with a curved fleshy seta; segment V without setae; apical segment about 30 µm long with an constricted apex 10 µm long; segment VI with 4 fine setae, each about 8-12 µm long,

2 fleshy setae, each 12-14 µm long, and a pair of coeloconic sensory organs (co), about 8 µm long. Eyespots postero-lateral of antennae.

Meso- and metathoracic spiracles very small, each peritreme about 2-3 µm wide; abdominal spiracles in 7 pairs located submarginally on venter, each with peritreme 6-7 µm wide; trachea opening centrally in strongly sclerotised base of atrium, which also has a network of small unequal and irregular pores of stigmatic wax glands.

Legs relatively short, subequal in size, lengths L-1: 95; L-2: 105; L-3: 120 µm long; distances separating coxae of pro- and mesothoracic legs, about 100 µm, greater than between meso- and metathoracic legs, about 50 µm long.

Hind leg measurements: coxa 16-18 µm long, 30 µm wide, with 8-10 short setae; trochanter + femur 45 µm long; each trochanter with a long seta, 95-110 µm long; femur with only one short seta; tibia 30 µm long without setae; tarsus 20 µm long, with a short seta ventrally and 2 setae-like tarsal digitules; claw 12 µm long, slightly curved at distal end and with a pointed projection at its base ventrally; with a pair of knobbed digitules surpassing end of claw. With two short setae between antennae and also between prothoracic legs. Posterior segment with a pair of setae, each 40 µm long. Anal opening circular, about 3 µm in diameter, invaginated, with a short, faint anal tube.

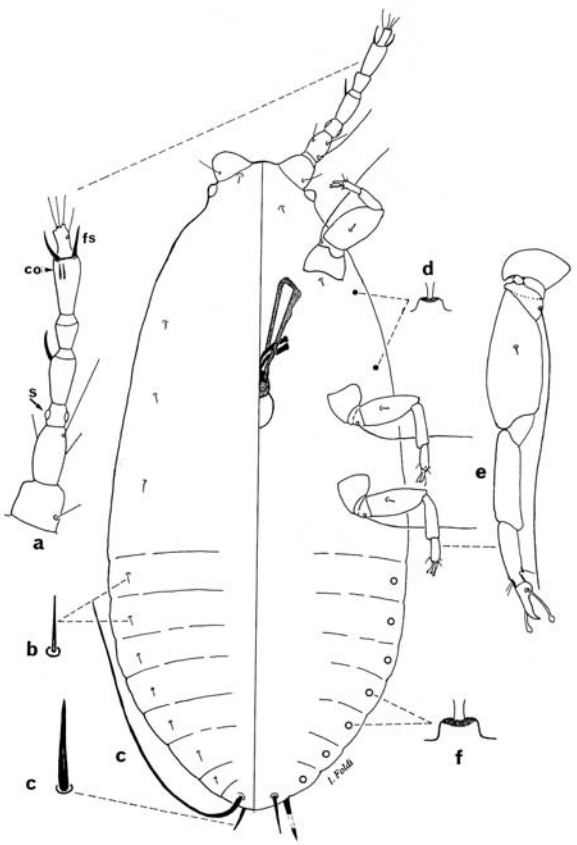
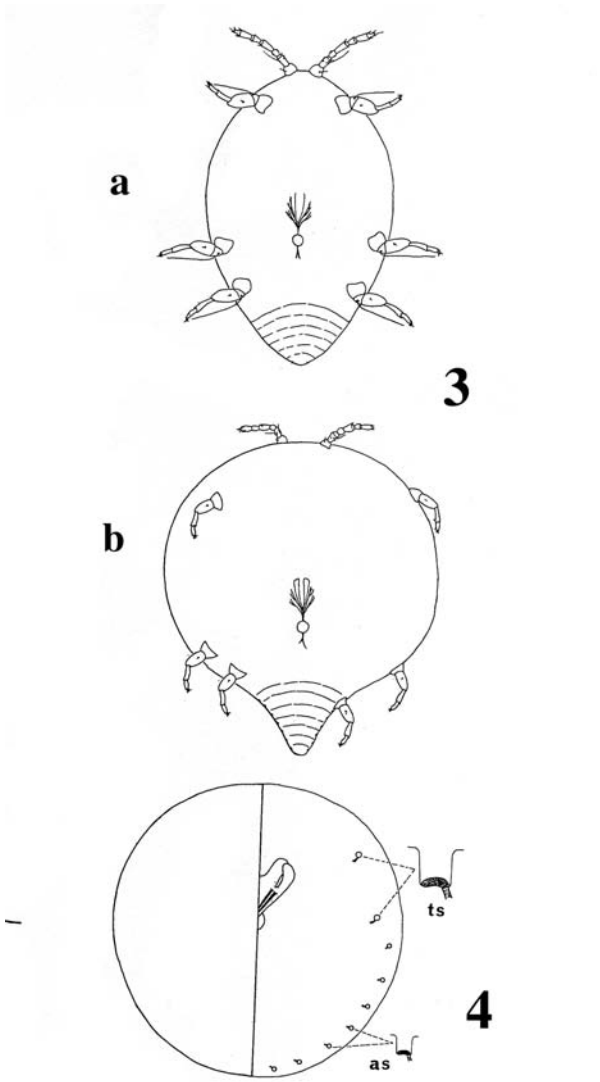


Figure 2
First-instar nymph, mobile phase. – a. antenna; co = coeloconic sensilla; fs = fleshy seta; s = sensilla; b. dorsal seta; c. caudal setae; d. thoracic spiracle; e. metathoracic leg; d. abdominal spiracle.



Figures 3-4
3, First-instar nymph, fixed phase; this stage undergoes a series of external morphological changes as it feeds and grows. – a. early phase, b. late phase. – 4, Second instar or cyst of *Matsucoccus feytaudi* Ducass. – ts = thoracic spiracle; as = abdominal spiracles.

Dorsum. A minute seta present near base of each antenna, one seta on each side of each thoracic segment, each about 10-15 µm long; plus a short submarginal seta on each of 8 abdominal segments. Posterior segment with 2 long setae, each about 210-230 µm long.

Physical changes during the fixed phase of first-instar (fig. 3). Once the crawler has settled, it begins feeding and than undergoes a series of external morphological changes. The body progres-

sively changes considerably in size and shape, particularly the head and thorax, becoming broadly rounded. Fully developed first-instar nymphs become pyriform, increasing in size to about 800-950 µm long, and about 700-800 µm wide. With this increase in size, the legs become progressively displaced to the periphery, plus prothoracic legs moving anteriorly, mouthparts move posteriorly, meso- and metathoracic legs becoming located more posteriorly on the body. As a result, the fully-developed first instar possesses strongly displaced legs; grouped on the posterior end of the body; rarely, the antennae, always together, never separated but found at the middle-lateral part of body. In addition, because this expansion takes place within a crevice or under bark the body can become distorted and asymetrical. The body color changes from yellow to grey. Also, after feeding has begun, each abdominal spiracle starts secreting waxy filaments laterally from the wax glands across the modified cuticle located at the base of the spiracles.

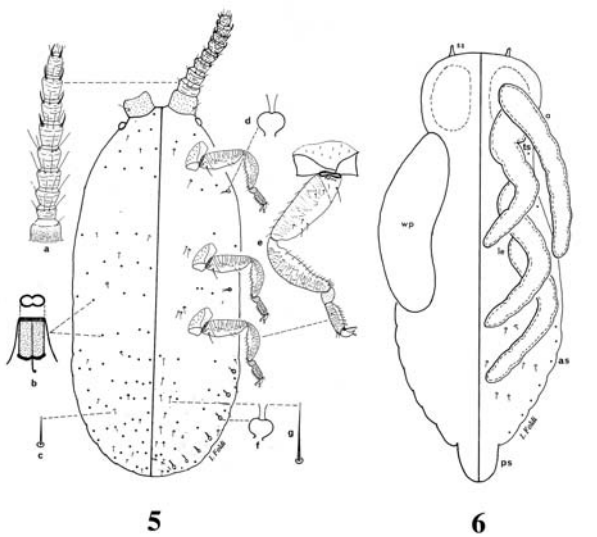
Structures of second instar or cyst (fig. 4).
Cyst brown and with sclerotised integument, without antennae, legs or derm pores. Body shape rather sub-circular, depending upon bark pressures; about 800 µm at widest part, becoming progressively elongate and wider with growth, so that fully developed cysts may be 2-2.5 mm long and 1.7-1.9 mm wide. Mouthpart well developed, tentorium without corpotentorium. Thoracic spiracles (ts) each with peritreme 20-30 µm wide; base of atrium strongly sclerotised and cuticle deeply modified (mc), allowing passage of secretions from spiracular glands to atrium (Foldi 1991). These irregular fibrils waxy secretions are molds by the atrium into a filament; 1-2 cm or more long. From base of each atrium, a single, broad tracheal tube extends laterally. Abdominal spiracles (as) in 7 pairs, each peritreme 20-25 µm wide; base of atrium similar in structure to thoracic spiracles, secreting waxy filaments. Cysts of males usually smaller and more elongate than those of females.

Comment: The wax secreted from the spiracular wax glands forms irregular waxy fibrils which are moulded by the atrium into a filament, 1-2 cm or more.

Prepupa (fig. 5).
Body 1200-1400 µm long, 650-750 µm wide, characteristically with a shortened abdomen. Other major features: absence of multilocular pores and cicatrices; presence of bilocular tubular ducts; short setae few (but these of variable length); legs stout. Derm of body and membranous intersegmental zones of antennae with globular projections, similar to those on adult female. Antennae 9 segmented, placed close together ventrally on head margin, each about 550-650 µm long; sclerotized parts of segments III-IX with a reticulated pattern as on adult female. Scape 100 µm wide, with a dark rim basally and numerous short setae dorsally; also with one seta 50 µm long plus a short seta about 20 µm long and with one circular sensilla; segments from VI to VIII each with 2 fleshy setae about 25-30 µm long plus 2-4 setae about 40-45 µm long; apical segment 70 µm long, 40 µm wide, with 2 fleshy setae each about 25-30 µm long plus 4 or 5 setae each about 30 µm long. Mouthparts absent. Legs well developed, stout with reticulated surfaces. Metathoracic leg measurements: coxa triangular, about 130 µm wide at base, with 6-10 short setae; trochanter + femur 270 µm long; trochanter with 5 sensilla on each face, with one seta 80 µm long plus 3-5 setae, each 30 µm long; femur 200 µm long, 60 µm wide, with about 28-32 setae, each 15-30 µm long; tibia 250 µm long, 50-60 µm wide, with about 26-30 setae each 20-35 µm long; tarsus 2-segmented, proximal segment short, 30 µm long, 45 µm wide, without setae; distal segment 130 µm long, 40 µm wide ventrally, with 9-12 setae, each 25-30 µm long, and with a pair of tarsal digitules, each 30 µm long; claw stout, curved, 30 µm long, with a pair of knobbed digitules, each 35 µm long. Thoracic spiracles with a peritreme 15 µm wide; atrium globular, 30 µm wide, basal part deeply modified allowing passage of secretions from spiracular glands to atrium. Abdominal spiracles in 7 pairs, each peritreme 8-9 µm wide, with a globular atrium, 16 µm wide, and with a single tracheal tube extending medially. Bilocular tubular ducts about 4-5 µm wide, 10 µm long, each with a oval rim, sparsely scattered on head and thorax, and in transverse line, one pore wide, on abdomen. Ventrally with about 4-6 setae, each 20-30 µm long, in a single transverse lines medially on abdomen and near of each coxa; also with a few short setae, each 10-15 µm long, sparsely scattered over whole body and on submargin; dorsally with short setae sparse, each about 10-15 µm long.

Comment: prepupa secrete long white waxy filaments through their bilocular tubular ducts and these filament are used to construct the cocoon within which it moults to the pupal stage.

Pupa (Fig. 6).
Body elongate, oval, with penial sheath (ps) 1800-1900 µm long, 700-750 µm wide; abdomen with a few short setae; pores appar-



Figures 5-6
5, Prepupa of *Matsucoccus feytaudi* Ducass. – a. antenna; b. bilocular tubular duct; c. dorsal seta; d. thoracic spiracle; e. metathoracic leg; f. abdominal spiracle; g. ventral seta. – 6, Pupa of *Matsucoccus feytaudi* Ducass. – a. antenna in a sheath; as. abdominal spiracle; le. leg in a sheath; ps. penial sheath; ss. short structures; wp. wing pad.

ently absent. Head broad, 400-450 µm wide, fused with thorax, bearing a pair of antennae (a), each 900 µm long, included in a sheath. Wing pads (wp) 850 µm long, 270 µm wide. Legs (le) with indistinct segmentation, included in a sheath 900 µm long. Thoracic spiracles (ts), each peritreme 30 µm wide; abdominal spiracles (as) in 7 pairs, each peritreme 10 µm wide. Also with two short structures (ss), each about 40 µm long, apically on head margin.

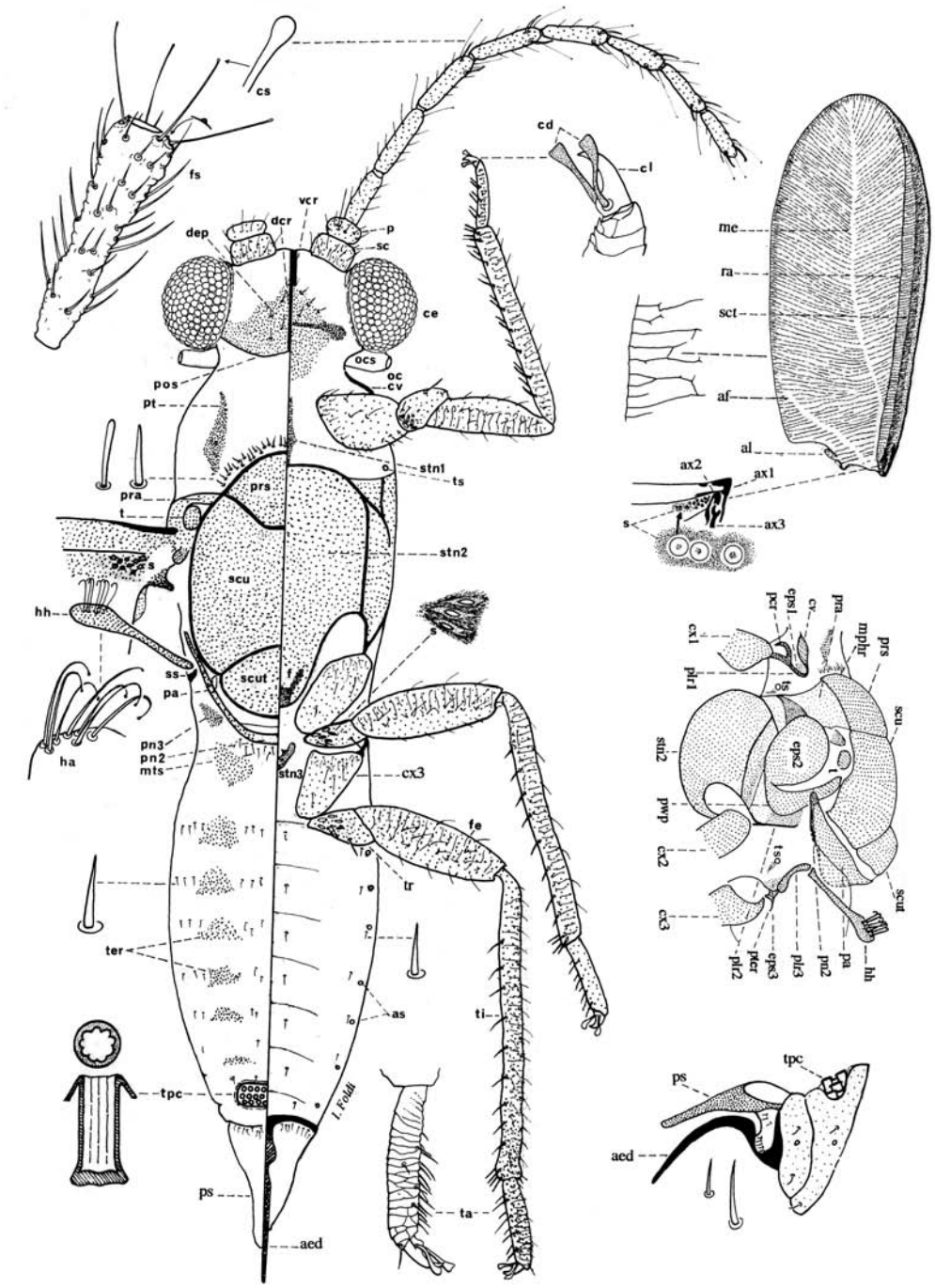


Figure 7
Adult male of *Matsucoccus feytaudi* Ducass.

Adult male (figs. 7, 10), described from 12 specimens.
Mounted material. Males small, with narrow body, 380-420 µm wide across prealar and 1800-2000 µm long. Morphological features characterizing *M. feytaudi* are: body with few short setae and without loculate pores; head very wide in dorsal view, with a pair of large of compound eyes laterally; antennae long; setae on flagellar segments without satellite setae; mesothorax unusually deep dorso-ventrally; basisternum elongate and narrow, obviously longer than on other margarodid males; legs well developed, setose and reticulated; tarsus one segmented; tergite of abdominal segment VII with a group of tubular pores; surface of wings « pinnately » sculptured; penial sheath short, with a narrow aedeagus and without an endophallus.

Head. Very wide, 400-430 µm across compound eyes and 190-210 µm long. Head with a pair of compound eyes (ce) laterally, each about 150-170 µm wide and with about 210-230 ommatidia; each eye with an ocular sclerite (ocs) along posterior margin, and with a single ocellus (oc) laterally. A posterior projection extends medially from each ocular sclerite, articulating with cervical sclerite (cv). Ventrally, epicranium membranous anteriorly and laterally, but with a large sclerotized area medially with a strongly sclerotized ventral extension of midcranial ridge (vcr). Ventromedial part of epicranium with 4-5 short setae on each side. Dorsomedial part of epicranium (dep) with 4 or 5 short setae on both sides, sclerotised on posterior half, with a postoccipital suture (pos) extending between compound eyes; postocciput, cranial apophysis and preocular ridge absent. Dorsal midcranial ridge (dcr) extending from anterior part of epicranium to postoccipital suture (pos).

Antennae. Antennae 10 segmented, total length 1350-1400 µm; most antennal segments with fleshy setae, hair-like setae, capitate setae (cs) and antennal bristles; satellite setae absent. Scape (sc) 50-60 µm long, 75-80 µm wide, with a sclerotized articulatory ring with head; with a group of 8 or 9 very short setae, each about 3-5 µm long and 1-3 longer setae, about 8 µm long. Pedicel (p) 50 µm long, 65 µm wide, with 4 or 5 short setae, plus one much longer seta, about 50 µm long, and 3 campaniform sensilla on dorsal surface. Length of other segments varying between 130-190 µm. Segments III with about 18-20 fleshy setae (fs), each about 20-30 µm long; segments IV-VIII with fleshy setae (fs), hair-like setae, capitate setae, and antennal bristles; segments VII-VIII also with 1 coeloconic sensilla; apical segment 120-130 µm long and 20 µm wide proximally, widening slightly to 30 µm distally with about 17-21 fleshy setae throughout segment; also with 2 antennal bristles and 5 capitate setae on its distal end.

Prothorax. Membranous, separated from head by a broad neck. Pronotal ridge and pronotal sclerites absent; pronotal setae in a line of 35-45, immediatly anterior to prescutum. Post-tergites (pt) longitudinal, elongate, weakly sclerotized, each about 100 µm long.Ventrally with a pair of cervical sclerites (cv). Pleural ridge (plr1) long, extending from articulation with coxa and fusing with cervical sclerite (cv) posteriorly. Proepisternum (eps1) present between cervical sclerite (cv) and pleural ridge (plr1). Precoxal ridge (pcr) well developed, long, curving anteriorly and extending ventrally. Prosternum (stn1) weakly sclerotised with a median ridge about 250 µm long; with a single apophysis medially. Setae absent ventrally.

Mesothorax. Narrow, strongly developed, distinctly deeper than other Coccoidea, 600-750 µm long and 380-420 µm wide, with tergum and sternum strongly convex. Prescutum (prs) without setae, strongly curved, anterior part extending beneath prothorax and forming a mesophragma (mphr); prescutal ridges and prescutal sclerites present. Prealar (pra) elongate extending ventrally to mesepisternum (eps2). Scutum (scut) very narrow, without a median membranous area and without setae. Anterior notal wing process well developed (pwp). Scutellum (scu) without membranous areas laterally; setae and pores absent; posterior margin curving ventrally; scutellum separated from scutum by distinct scutoscutellar ridges. Membranous area between scutellum and mesopostnotum (pn2) and extending anteriorly laterad to scutum and bordered laterally by a postalare (pa), which extends beneath wing sclerites. Mesopostnotum (pn2) almost vertical extending below metatergite and forming a deep mesopostphragma. Laterally, a large sclerotised tegula (t) present posterior to each prealare, without tegular setae. Basisternum (stn2) very long (340-360 µm) and narrow, extending to anterior margin of prealare, without setae; bounded anteriorly by marginal ridge (mr), which extends posteriorly along lateral margin, and posteriorly by well-developed precoxal ridges (pcr2); median ridge and setae absent. Furca (f) narrow, with rather short arms which diverge strongly. Mesopleural ridge (plr2) well developed, extending vertically from mesocoxal articulation. Spiracles (ts) small each peritreme 17-25 µm wide. Wing sclerites: costal complex of wing veins with two articular processes: dorsal process articulating with anterior axillary sclerite (ax1), ventral process articulating with median axillary sclerite (ax2); third axillary sclerite (ax3) with outer edge sclerotised.

Metathorax. Membranous. Dorsally, metapostnotum (pn3) represented by two sclerotised lateral areas. Medially a group of metatergal (mts) setae. Pleural ridge (plr3) extending from metepimeron (epm3) to base of hamulohalteres near to suspensorial slerites (ss). Precoxal ridge well developed widely extending ventrally. Postcoxal ridge (ptcr) extending dorso-posteriorly around metacoxae. Pleural apophysis well developed, located at point where pleural and precoxal ridges meet. Metepisternum (eps3) weakly sclerotised. Metasternum (stn3) with a medial circular metasternal apophysis; metasternal setae absent. Spiracles (ts) similar to mesothoracic spiracles.

Wings. Well developed, each 1900-2000 µm long and 770-800 µm wide. Surface of wings is unique in Coccoidea; i.e. surface of wings with a dense, fine, evenly spaced parallel folds (Fig. 11) which, on microscopic slides appear as a series of lines or ridges forming a pinnate sculpture. With a well developed subcostal (sc) and radial (r) vein; median (m) vein represented by a clear fold, arising from posterior apex of axillary sclerite (ax2) and terminating at distal margin of wing; with a short clear anal fold (af) arising from posterior apex of axillary sclerite extending to inferior margin; alary lobe (al) represented by a short, narrow structure. Base of subcostal ridge with a group of 7-9 circular sensoria (s); other alar pores and setae absent. Hamulohalteres (hh) sclerotised, 240-260 µm long, 40-45 µm wide, broadening distally, with 6-9 hamuli (ha) along anterior margin at distal end, each hamulus (ha) about 80-120 µm long, curved distally and with a swollen apex.

Legs. Well developed, with reticulated surfaces; prothoracic legs longest. Metathoracic leg mesurements: coxa (cx): 175-190 µm long, 100 µm wide; each with a group of 10-12 very short setae, about 3-5 µm long, near base and hair-like setae distally; trochanter (tr) + femur (f) 360-380 µm long; trochanter with one seta 45-50 µm long, with 2-3 short hair-like setae and with a group of 5-6 oval campaniform sensillae on each side; femur 90 µm wide, with about 10-12 hair-like setae; tibia (ti) obviously longest than femur, 500 µm long, ventrally each with 25-30 setae, 20-25 µm long; tarsus (ta) one segmented, 160 µm long, with 16-20 setae, each 20-25 µm long, along ventro-lateral margin; tarsal digitules short, each 11-15 µm long; claw (cl) broad, 30-35 µm long, with a minute, fine lamella at its base; each claw with 2 strong, knobbed digitules (cd), each 40 µm long, longer than claw, arising very close to base of tarsus.

Abdomen. Membranous. Each abdominal segment with a pair of tergites mediolaterally, which become smaller posteriorly; sternites and pleurites absent. Dorsal setae short, each 5-8 µm long, in two groups medially; segment I with about 12-22 setae, number reducing progressively towards posterior end. Pleural setae with about 2-3 on segments IV-VIII. Ventral setae, each 8-15 µm long, as follow: 0 on segments I; 2 on segment-II; 4 on segment IIII-VIII. Segment VII with a group of 20-37 tubular pores in a cluster (tpc), each about 20-24 µm long and 5-6 µm wide with a conical opening; each with about 8 longitudinal internal ridges; these tubular pores secrete long, white caudal filaments. Abdominal spiracles (as) unsclerotised, with a pairs on segments II-VIII, on venter. Anus apparently present on segment IX, positioned dorsomedially over penial sheath consisting a sclerotised ring, about 3 µm in diameter.

Genital organs. Formed from segment IX positioned ventrally. Genital organs consisting of a strongly sclerotised penial sheath (ps) and an aedeagus (aed). Penial sheath about 280-300 µm long, 180-200 µm wide at broadest point anteriorly, narrowing to a short, blunt apex posteriorly; rather triangular in shape; ventrally with a group of 20-23 small setae, each 15-25 µm long, located medially just anterior to base of aedaegus; distally with a group of small sensoria. Aedeagus (aed)

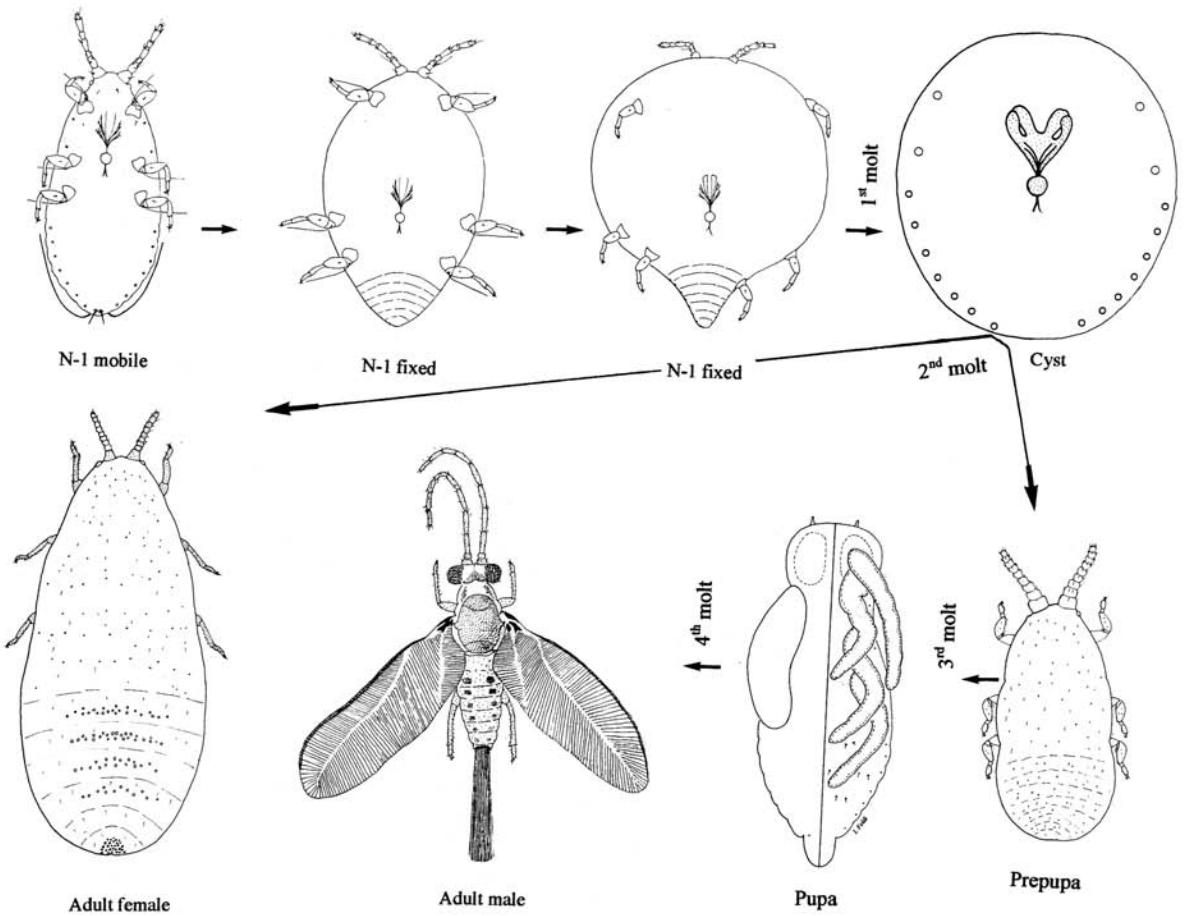
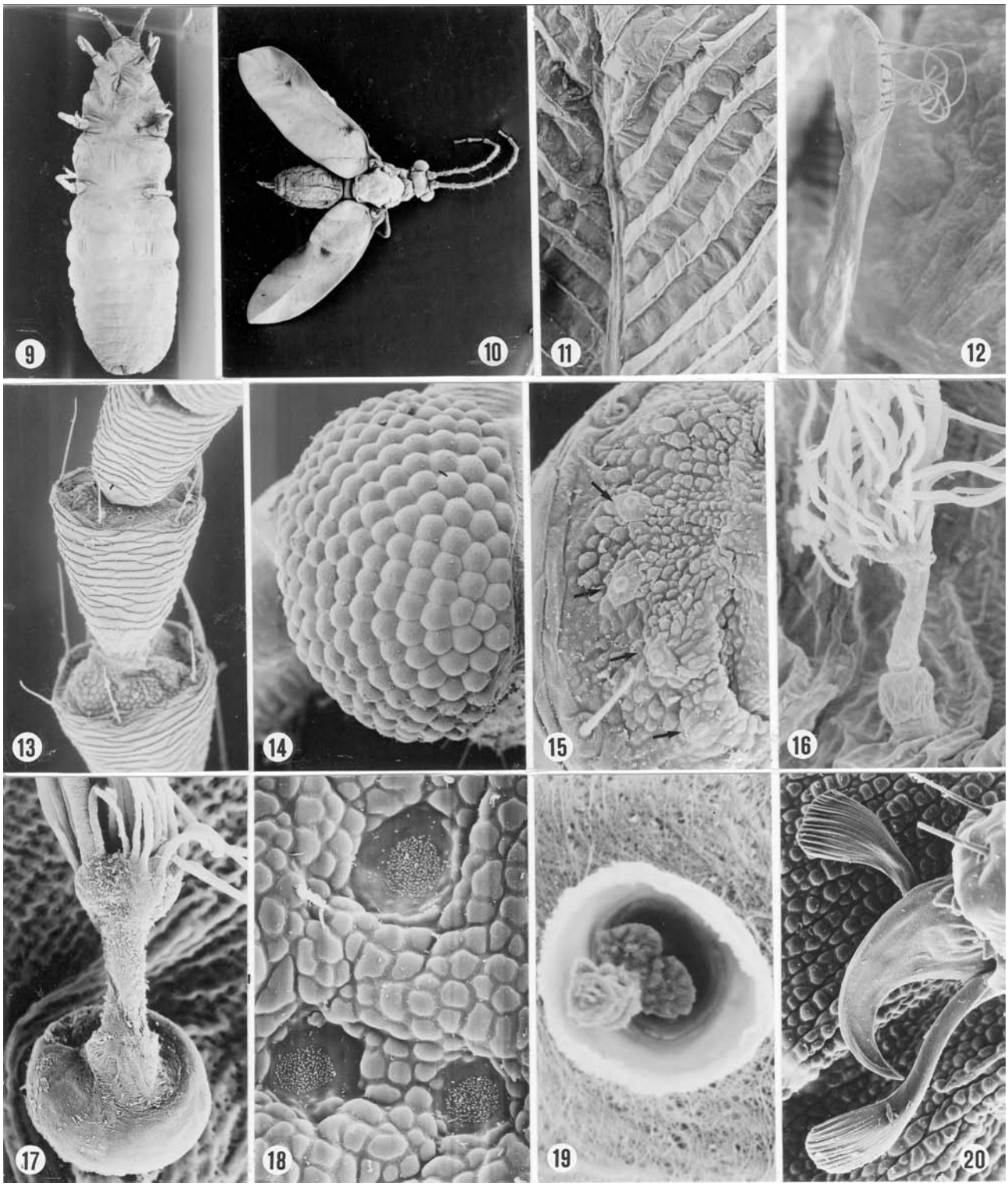


Figure 8
Diagram of the general life history of *M. feytaudi*.



Figures 9-20
Micrographs of *Matsucoccus feytaudi* Ducasse. – 9, Adult female, ventral aspect. x 20. – 10, Newly hatched adult male still without waxy tail tuft, dorsal aspect. x 16. – 11, Adult male: note the surface of each wing with a series of evenly placed, fine parallel folds, forming a pinnate pattern. x 700. – 12, Hamulohaltere, distally with 7 hamuli, each curved with a swollen apex. x 450. – 13, Antennal segments of female with reticulated surface. x 500. – 14, Compound eye of adult male with about 220-240 ommatidia. x 400. – 15, Adult female: membranous intersegmental area of 3rd antennal segment; note the 4 sensilla present (indicated by arrows). x 2500. – 16, Adult female, internal structure of an abdominal spiracle. x 1000. – 17, Adult female, internal structure of a thoracic spiracle; note the presence of a globular and an elongated atrium. x 1200. – 18, Adult female, details of dorsal cicatrices (pores) emitting very fine secretions; note the very dense network of small, globular projections on the derm surface over the entire body. x 2200. – 19, Adult female, internal structure of a bilocular tubular duct. x 8000. – 20, Adult female, metathoracic claw with knobbed digitules longer than claw. x 1100.

sclerotised, bent ventrally, approximately 340-400 µm long and 40-50 µm in diameter at proximal end and 15-20 µm in diameter at distal end; with a short basal rod at its anterior end; eversible endophallus absent.

Material examined. France: Island of Porquerolles, road of Sémaphore in front of vineyard, under bark of trunk of *Pinus pinaster*, 15.III.1996, Foldi rec.; Haute Corse: Commune de Ponte Leccia. INRA coll.; Avignon, VI.1969. P. Carle rec.; Forêt du Dom des Bormes (Var), 10.IV.1964. P. Teocchi rec.; Cap Ferret (Gironde), IV. 1965, F. Hascoet rec.

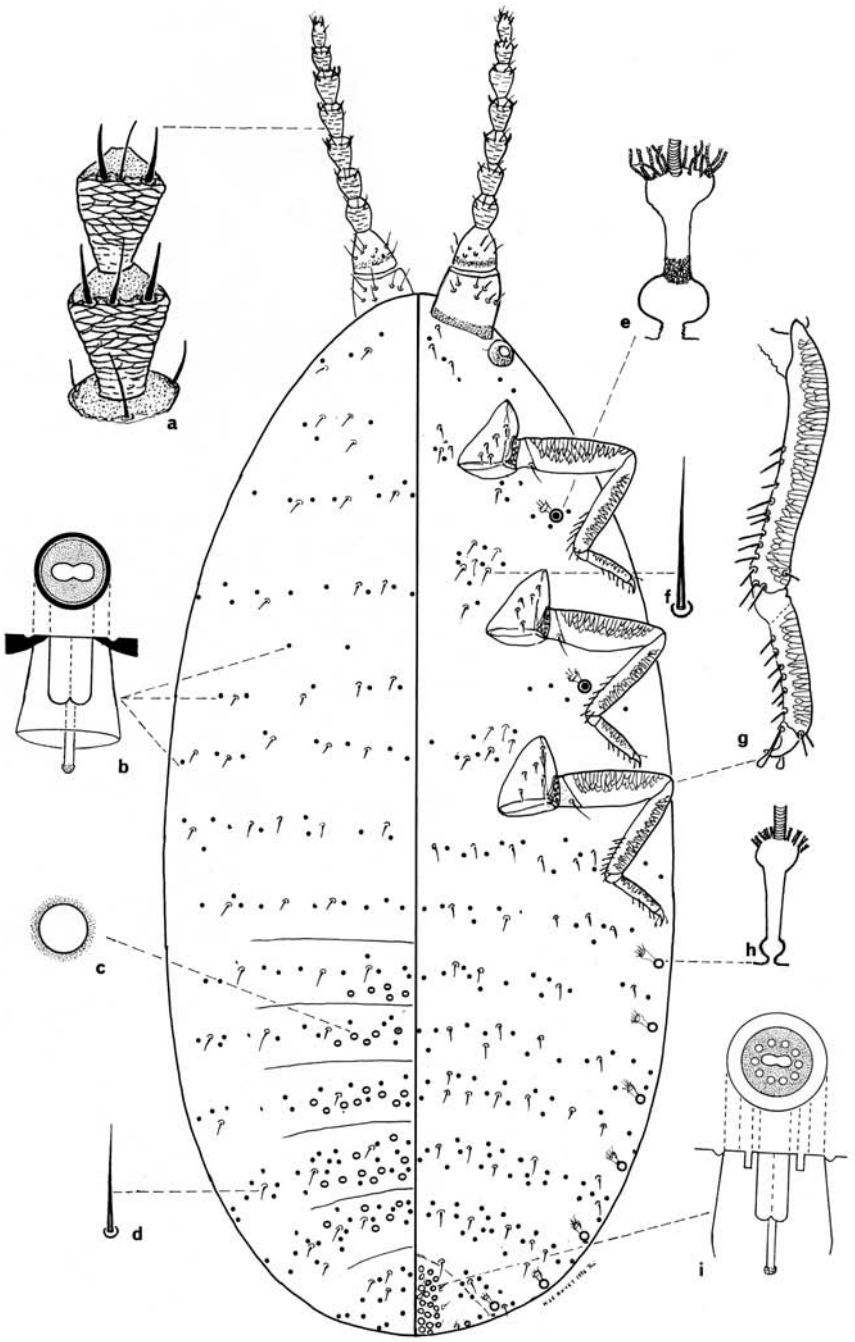


Figure 21
Adult female of *Matsucoccus josephi* Bodenheimer & Harpaz. – a. detail of antennal segments; b. bilocular tubular duct; c. cicatrice; d. dorsal abdominal seta; e. thoracic spiracle; f. group of hair-like setae near meso-coxa; g. detail of metathoracic leg; h. abdominal spiracle; i. multilocular disc-pore.

Matsucoccus josephi Bodenheimer & Harpaz, 1955
The Israeli Pine Bast Scale

Adult female (fig. 21) (described from 4 specimens)
Matsucoccus josephi Bodenheimer & Harpaz, 1955: 12.

Material examined. Israel. Bet Dagan, on *Pinus halepensis*, 25 May, 2002, Y. Ben-Dov rec., MNHN.

Mounted specimens. Body oval, 1.6-4.2 mm long, 1.1-3 mm wide. Derm with a dense network of globular projections over the entire body.

Venter. Antennae 9-segmented, 800-850 µm long; all segments with setae always located on sclerotized areas; scape located on ventral surface, each 150-170 µm long, pedicel each 110 µm long. Scape and pedicel both with a basal dark rim, and each with about 12 short setae, and about 12 longer hair-like setae. Pedicel with 3 or 4 sensilla. Segments III-VIII conical, each 50-75 µm and made of two parts, a long basal sclerotized part, with small polygonal reticulations and a shorter, apical part, corresponding to the membranous intersegmental area. Segments V-IX, each with 2 fleshy setae and about 2-4 hair-like setae; apical segment, completly sclerotized and reticulated. Eyespots posterior to antennae, located ventrally. Mouthparts absent. Thoracic spiracles each with peritreme 20-25 µm wide, and with a globular atrium, 40 µm in diameter, followed by a narrower atrial tube, 40-45 µm long; proximal part with a reticulated surfaces, whilst distal end expands with a tuft of tracheae, one wider than rest. Abdominal spiracles in 7 pairs, each with unsclerotised peritreme; with a small globular atrium followed by a long narrower atrium without reticulated pattern. Legs well developed, femur, tibia and tarsus with a reticulated surface similar to that on antennal segments. Metathoracic leg measurements: trochanter + femur 400 µm long; trochanter 110 µm long, with 6-8 sensilla on each side and one seta, 80 µm long; femur 290 µm long, with about 12 short setae, and 2 or 3 long setae; tibia 300 µm long with about 20 ? ? stout spine-like setae along inner margin, and about 10 hair-like setae. Tarsus 2-segmented, total length 180-200 µm, basal segment without reticulated pattern, distal part reticulatedwith about 8-12 stout spine-like setae along inner margin; tarsal digitules 2 short, acute setae; claw about 40 µm long; denticle absent; with 2 knobbed digitules, each longer than claw. Vulva surrounded by a cluster of multilocular pores; number of pores rather variable considerably, ranging from 52 to 163 (Ben-Dov 1981), each pore about 10 µm in diameter, with 9 loculi in outer ring, with a bilocular tubular duct centrally and with a narrow ductule medially. Bilocular tubular ducts, according to Ben-Dov (1981) with two ductules; scattered on head, but in transverse rows on thorax and abdomen associated with short setae.

Dorsum. Bilocular tubular ducts, similar in structure to those on venter, present on head, thorax and abdomen. Cicatrices circular, varying from 10 to 12 µm in diameter, distributed in transverse bands on abdominal segments III-VII. Number of cicatrices varying considerably, with 61-161 in spring generation and 46-92 in autumn generation; number also varying depending on host (*Pinus halepensis, P. brutia*) (Ben-Dov, 1981). Short hair-like setae often placed together with bilocular tubular ducts. Anal opening not discernable.

Biology – Mated females are found on the lower stems at the base of needle-bundles and underneath the outer bark layers of *Pinus brutia* and *P. halepensis*. *M. josephi* is a bisexual species, polyvoltine, apparently with five or six generations per year (Bodenheimer & Neumark 1955). The females develop in 3 instars and the males in 5. The adult females settle for oviposition on the lower stems at the base of needle-bunches on inflorescences and underneath the outer layers of bark. In late February, the newly hatched first-instar nymphs choose feeding sites both on and beneath the bark and the adult females emerge about mid-May; the second and third generations take 46 days, with the third generation ovipositing in early June; the fourth generation oviposits on about 20th August, with development takes about 50 days, the new adults appearing early October, possibly overlapping with the ovipositing females of the fifth generation. The sixth generation starts in early December and development takes about 90 days, the adult females appearing in February. Ben-Dov (1981) reported seasonal differences in morphology, such as in the number and size of pores and cicatrices.

Economic importance. The Israel pine *Matsucoccus* is a serious pest in pine forests in Israel, particularly causing severe damage to young Aleppo pine, *Pinus halepensis*. Mendel (1998) reported that the presence of *M. josephi*, at densities similar in natural stands or plantations of *P. brutia brutia* and *P. halepensis*, caused severe injury to *P. halepensis* even though the damage was pratically nil on *P. brutia brutia*, which has high resistance to this scale. Indeed, it is the host resistance rather than the natural enemies which is the key factor in the population dynamics of *M. josephi*, and this resistance has probably been acquired through a long coevolution between *P. brutia brutia* and *M. josephi* (Mendel 1998).

Natural enemies. A specific predator of *M. josephi* is *Elatophilus hebraicus* Pericart (Hemiptera, Anthocoridae), occurs in brutia pine and Aleppo pine forest of the East Mediterranean (Mendel et *al.* 1991).

Host plants. *Pinus brutia* ssp. *brutia* (brutia pine) and *Pinus halepensis* (Aleppo pine). Ben-Dov (1981) cite *P. elderica*.

Distribution. In Israel, it has been reported from Bet Dagan, Biriya, Mt. Carmel, Galilee: Biriyya Forest, Hanita Forest; Hamasrek, Hazore'a, Horeshim, Ilanot, Jerusalem, Kedoshim, Samaria, Segev, Sha'ar haGai,Tarom, Tarqumiye, Zikhron (Ben-Dov 1981, Mendel et *al.* 1994, Mendel 1998).

Mediterranean area: Crete: Prasas, Anapolis; Cyprus; Israel; Jordan: Ajlun, Jerash, Dibbin, Suweilih, Es Salt;

Lebanon, in southeastern area: Ed Damur, Mazraat Chouf, Sidon, Jezzin, Aichiye, Hasbaya; Turkey (southern Anatolia) (Mendel et *al*. 1994, Mendel 1998).

Note. All stages of *M. josephi*, bar the pupa and adult male, were redescribed by Ben-Dov in 1981, who also did an SEM study of the wax produced by the various stages.

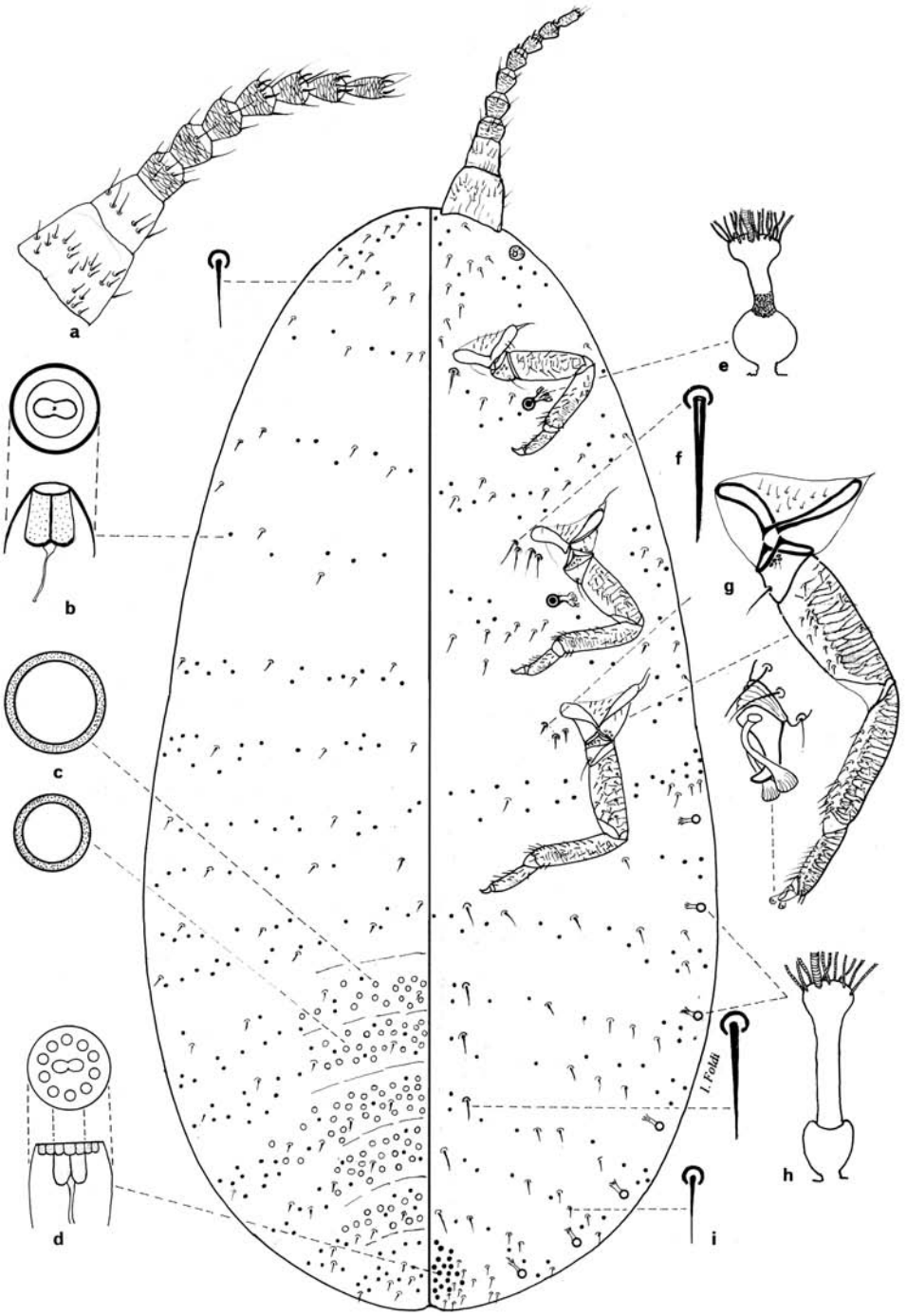


Figure 22
Adult female of *Matsucoccus matsumurae* (Kuwana). – a. antenna; b. bilocular tubular duct; c. cicatrices; d. multilocular disc-pore; e. thoracic spiracle; f. group of setae near coxae; g. metathoracic leg; h. abdominal spiracle; i. ventral abdominal seta.

Matsucoccus matsumurae (Kuwana, 1905)
The Japanese Pine Bast Scale

Xylococcus matsumurae Kuwana, 1905: 91.
Matsucoccus matsumurae (Kuwana, 1905), Cockerell, 1909: 55.

Material examined. Adult female, Japan, Shinano Prov., on *Pinus koraiensis*, Sept. 13. 1914, E.H. Wilson coll., USNM, n°: 7521. 2 slides of adult females from Japan, Kyoto, April 28 or 29, 1970, A. Takoya coll., USNM.

Adult female (Fig. 22) (described from 3 specimens)

Live appearance. Adult female brownish red; mated females with white ovisac on tip of abdomen; lives in bark crevices.

Mounted specimens. Body elongate, widest across abdomen, with posterior rounded, body 2.5-4.5 mm long, 1.2-2.5 mm wide.

Venter. Antennae close together at base on anterior margin of head; 9-segmented, each 800-900 µm long; scape and pedicel obviously longer and wider than more distal segments; all flagellar segments with a reticulated surface; segments VI-IX each with 2 fleshy setae; segments III-VIII each with 0-2 intersegmental and coeloconic sensilla.

Antennal segments and setae measurements: scape: 180 µm long, 200 µm wide, with about 20-26 short setae, 8-12 µm long; pedicel: about 130 µm long, 145 µm wide, with 10-14 setae, 40 µm long, and with 4-6 campaniform sensilla; III 70 µm long, 80 µm wide, with 10-12 setae, 15-40 µm long; IV 70 µm long, 80 µm wide, with 7-8 setae, 15-30 µm long; V 75 µm long, 75 µm wide, with 4 setae, 15-30 µm long; VI 80 µm long, 80 µm wide, with 3-4 setae, 15-30 µm long; VII: 80 µm long, 65 µm wide, with 3-4 setae, 15-30 µm long; VIII: 70 µm long, 60 µm wide, with 2 setae, 20-30 µm long; apical segment: 80 µm long, 40 µm wide, with 4-5 short hair-like setae, 15-30 µm long and 2 slightly curved fleshy setae, 20-25 µm long.

Eyespots dome shaped, located postero-marginally to antennae, each 50 µm wide with circular lens 25 µm in diameter. Mouthparts absent, but a folded membranous area present. Thoracic spiracles each with peritreme 15-20 µm wide, a globular atrium about 35-40 µm in diameter, followed by a narrower atrial tube whose distal end expands, from which emerge numerous tracheae; proximal part of atrial tube bearing a network of irregular or circular cuticular structures which appear on mounted specimens as a reticulated surface. Abdominal spiracles numbering 7 pairs, each without a sclerotized peritreme, atrial tube about 50-60 µm long; structure of spiracles similar to thoracic spiracles but with no reticulated surface. Legs well developed; lengths: prothoracic 800 µm; mesothoracic 890 µm; metathoracic 950 µm long. Femur, tibia and tarsus all with a reticulated surface. Metathoracic leg measurements: coxa 110 µm long, with 15-25 short setae; trochanter + femur 360 µm long; trochanter with 1 long seta, 70-80 µm long, 1 or 2 short setae plus 4-5 sensilla on each side; femur 310 µm long, 130 µm wide, with about 20-24 hair-like setae, each 20-30 µm long; tibia 270-290 µm long, 70 µm wide, with about 22-28 setae, each 30-40 µm long; tarsus 170 µm long, 40 µm wide, 2 segmented, basal segment very short and without setae; distal segment with about 14 setae, each 30-40 µm long, and with 1 or 2 campaniform sensilla on dorsal margin; claw 40 µm long, strongly curved, with a strongly enlarged base, and with a pair of knobbed digitules, each 55 µm long, longer than claw. With a group of setae just mesad to each coxa, procoxa with about 1-3 setae, meso- and metacoxa with about 3-4 setae, each about 25-40 µm long. Abdominal segments III-VII each has a pair of longer setae medially about 30-45 µm long. Shorter setae, each about 10-12 µm long, in rows 1 seta wide, present on head, thorax and sub-median area of abdominal segments. Vulva located near apex of abdomen, surrounded by a cluster of 40-85 multilocular disc-pores; each disc-pore, 10-12 µm in diameter and with 9-13 loculi in outer ring; also with a bilocular tubular duct centrally and a narrow ductule medially. Bilocular tubular ducts each about 3-4 µm wide, 6-7 µm long, scattered on head but in rows 1 duct wide on thorax and abdomen; also with short rows of bilocular tubular ducts on margin and submargin of each abdominal segment. Anus not discernable.

Dorsum. Cicatrices, each 9-11 µm in diameter, in transverse rows 1-3 wide medially and submedially across segment III-VII; total number varying from 180 to 280. Bilocular tubular ducts each 3-4 µm wide, 6-7 µm long, in transversal rows 1 pore wide on head, thorax and abdomen; also with short rows of bilocular tubular ducts on margin and submargin; with short setae, each 10-15 µm long, in transverse rows 1 seta wide often near of bilocular tubular ducts on head, thorax, and abdomen.

Biology – Present in bark crevices; mated females with white ovisac. *M. matsumurae* is a bisexual and bivoltine species. In the USA, it has a summer generation, with the eggs being laid in May and the adults emerging in August; the overwintering generation lays its eggs in August or early September, with the adults emerging the following spring (McClure 1983). In eastern China, there are also two generations each year throughout its range (McClure et *al*. 1983a). The females develop through 3 stages and the males through 5. Females produce a sex pheromone for attracting the males. The second generation mated females settle in bark crevices about mid-August, and lay approximately 250 eggs in a white fluffy-silky, cottony ovisac at the tip of the abdomen; each female dies soon after oviposition. The eggs hatch after about two weeks, with the first-instar nymphs eventually settling in crevices and beneath flakes of bark; these overwinter in these feeding sites; in April, they moult to the second instar, or cyst and, after a further moult, the adult females emerge in the second half of May. After mating, the females of this first generation begin laying eggs, with the first instar nymphs appearing in June and July; cysts appear in mid-July, and the 2nd generation adults appear in mid-August (Bean & Godvin 1955, McClure 1983). This scale is confined to areas with a moderate temperature, and cannot

inhabit areas with winter and summer temperatures more extreme than in its native habitats (McClure 1983).

Economic importance. *M. matsumurae* is a destructive pest of pines, injecting toxins which provoke serious damage by causing foliage discoloration cracking and distortion of branches and, in cases of heavy infestations, death after a few years. In the northeastern US, *M. matsumurae* is the most important pest of red pine, *Pinus resinosa,* plantations. In China, this species is a pest throughout the east-central area, and is very destructive to two native Chinese pines, *P. tabulaeformis* and *P. massoniana*. In Japan, the scale inhabits nearly every stand of *Pinus densiflora* (Japanese Red Pine) and *P. thunbergiana* (Japanese Black Pine) but its density is rather low and the trees suffer no apparent injury (McClure 1986). In the southwestern coastal area of Korea, it causes serious damage to *Pinus thunbergiana* forests. It is also a pest of pines in Russia.

Naural enemies. No parasitoids have been reported but predators have an important role in the regulation of endemic populations of *M. matsumurae.* In Japan, *Harmonia axyridis* (Coccinellidae) killed about 97% of the scales in one heavily infested forest stand of the exotic host *P. massoniana* (McClure 1986). This Asian predator was used also to control *M. resinosae* in the US. Other efficient predators are *Elatophilus nipponensis* (Anthocoridae), *Ballia obscurosignata* (Coccinellidae) (McClure et al. 1983a); larvae of *Hemerobius stigmatus* and *Chrysopa* sp. (Hemerobiidae, Neuroptera); also *Dromius sp.* (Carabidae*)* (Siewniak, 1976), *Mulsantia picta* (Cocinellidae) and *Lestodiplosis nr. grassator* (Diptera, Cecidomyiidae) (McClure *et al.* 1983).

Host plants. *Pinus densiflora*, *P. halepensis, P. massoniana, P. mugo, P. nigra, P. pinaster, P. pinea, P. resinosa, P. rigida, P. sylvestris*, *P. tabulaeformis* and *P. thunbergiana*.

Distribution. *M. matsumurae* is distributed in Nearctic and Palearctic regions. In the USA *M. resinosae* is considered to be identical with *M. matsumurae* and is found in: Connecticut, New Jersey, New Jersey, New York, and Pennsylvania (Kosztarab 1996). In China, it occurs in the provinces of Anhui, Chekiang, Hebei, Jiangsu, Liaoning, Shandong, Shantung, and Zhejiang (Young, Hu, Ren 1976, McClure et *al.* 1983). It also occurs in Japan (in central and southern area; Shinano Prov, Kyoto), Korea (south-western coastal area), Ukraine, Russia.

Matsucoccus pini (Green, 1925)

The European pine bast scale

Kuwania pini Green, 1925: 34.
Matsucoccus pini (Green), Boratynski, 1952: 285.

Material examined. Lectotype designated here: England, Surrey, Oxshott, on *Pinus sylvestris*, 5.V.1923. Withycombe F.C. rec., BMNH.
France, Mont-Ventoux, near of Malaucène, 1100 alt., on *Pinus sylvestris*, 16.V.1988, I. Foldi rec., MNHN.

Adult female (Fig. 23) (described from 10 specimens)

Live appearance. Body elongate, anterior end tapering gradually towards bases of antennae; body clear brown; integument highly flexible. Found in bark crevices.

Mounted specimens. Body length varies considerably, on average 2.8 long, 1.1 mm wide; broadest posteriorly. Body with weak pilosity.

Venter. Antennae 9 segmented, each 700-750 µm long, placed at anterior end of body with bases close together. Scape on average 120 µm long, 165 µm wide, wrinkled longitudinally, bearing a group of 8-10 minute setae, each about 5-7 µm long, at base dorsally, and 12-20 longer setae, each about 10-15 µm long accross middle part of segment; pedicel about 90 µm long, 110 µm wide, with 8-1 of setae, 12-30 µm long. Segments III-VIII with a sclerotized and reticulated surface and with a membranous intersegmental area; only sclerotized part bearing setae, each segment with one seta 40 µm long and 2-4 short setae, each about 15 µm long, plus segments VI - IX have 2 stout, weakly curved, fleshy setae, each 25 µm long; segments V-VII with coeloconic sensilla; apical segment narrower, with a truncate apex and with all surfaces sclerotized and reticulated. Eyespots small, located postero-laterally to antennae. Mouthparts absent, just an integumentary depression present. Metathoracic leg measurements: trochanter+femur 260 µm long; trochanter with 4 oval campaniform sensilla on each side, 3 setae, each 20-30 µm long, plus one seta 70 µm long; femur 210 µm long, 100 µm wide, with about 15 setae, each 20-25 µm long; tibia 250 µm long, 60 µm wide with about 30 setae, each 10-25 µm long; tarsus 2-segmented, total length 115 µm, 40 µm wide, with few setae, each 20-25 µm long; claw short, 30 µm long, strongly curved and strongly widened at base, with a pair of knobbed digitules, both obviously longer than claw.

Thoracic spiracles each with peritreme 15 µm wide; globular atrium about 30 µm in diameter, followed by a narrow atrial tube whose distal end expands, with a tuft of 18-30 small tracheae. Abdominal spiracles on venter submargin in 7 pairs, each without a sclerotised peritreme; atrium globular, each about 12 µm in diameter and similar in structure to thoracic spiracles but smaller; atrial tube without reticulations. Small setae, each about 10-12 µm long sparsely present throughout; larger setae, each about 35-40 µm long, in cluster of 5 or 6 mesad to each pro-, meso- and metathoracic coxa, and in pairs medially on each abdominal segment. Bilocular tubular ducts, each 4-5 µm wide and 10-12 µm long, with a central ductule about 10-15 µm long; they are randomely and very sparsely distributed on head

and thorax, and in transverse rows 1 pore wide on abdomen. Vulva surrounded by 2 contigous clusters of 30-50 very close together multilocular disc-pores, each 10-12 µm in diameter and composed of two distinct parts: externally with 9-14 loculi in an outer ring and medially with a bilocular tubular duct which has a minute ductule medially.

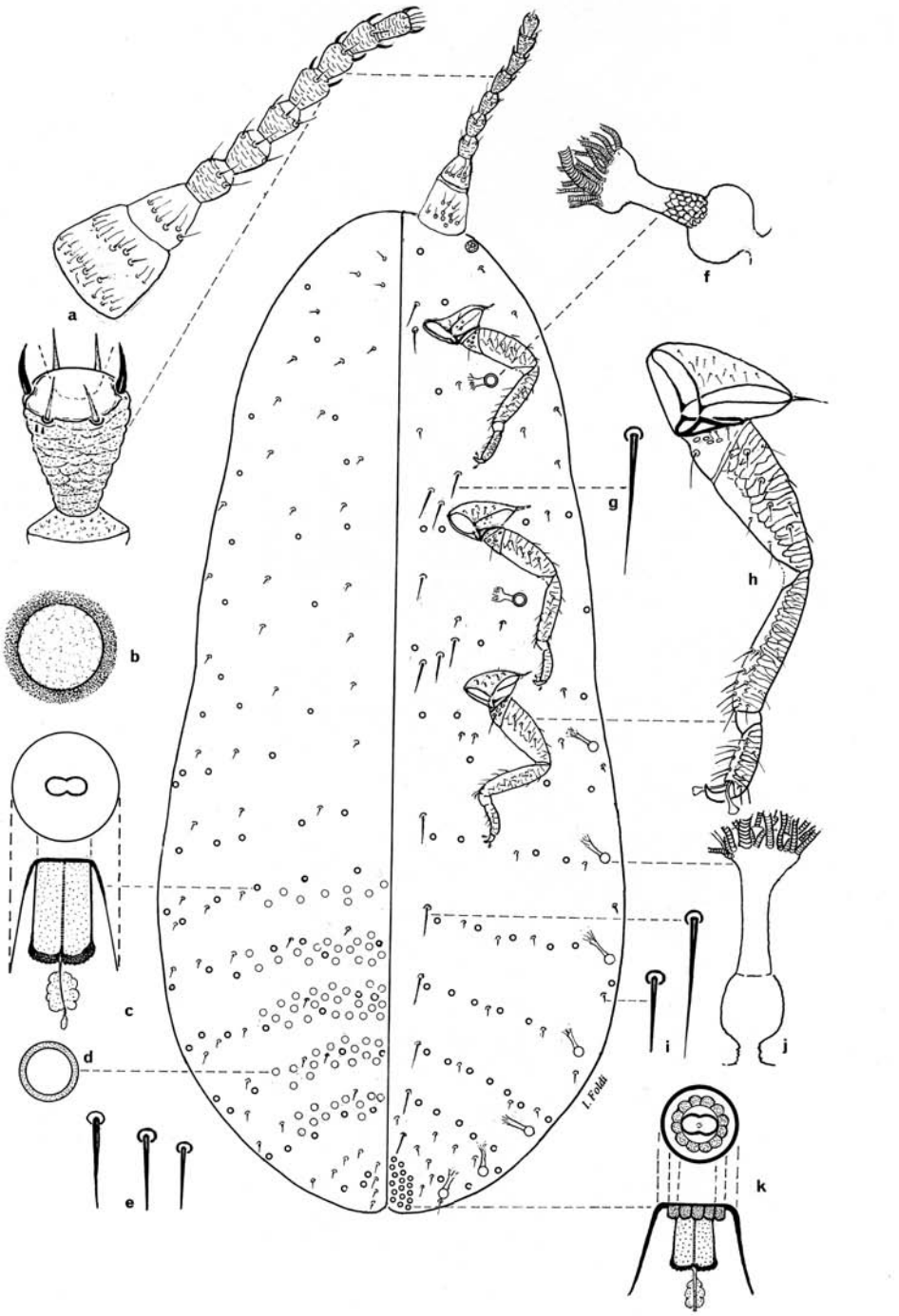


Figure 23
Adult female of *Matsucoccus pini* (Green). – a. antenna; b. cicatrice with reticulated surface; c. bilocular tubular duct; d. cicatrice with smooth surface; e. dorsal setae; f. thoracic spiracle; g. group of setae near coxae; h. metathoracic leg; i. ventral setae; j. abdominal spiracle; k. multilocular disc-pore.

Dorsum. Bilocular tubular ducts 4-5 µm wide 10-12 µm long, with a minute central ductule about 10-15 µm long; weakly scattered on head and thorax, and in transverse rows 1 pore wide on each abdominal segment. Short setae, each 10-12 µm long, with a distribution as bilocular tubular ducts. Cicatrices circular, each 9-11 µm in diameter; variable in total number from 100-250, in transverse rows across segments III-VII on abdomen; 5 cicatrices wide, on abdominal segments IV-V-VI; segments III and VII with reduced cicatrix bands and posterior segment without cicatrices. Anal opening not apparent.

Biology – *M. pini* is parthenogenetic or bisexual, mono or bivoltine species. Information about its biology varies between countries. Rieux (1976) noted intraspecific morphological variations in the European populations. The species is reported as parthenogenetic and bivoltine in England, with the adult females of the first and second generations having quantitative morphological differences, with more cicatrices on the overwintering generation than on the summer/fall generation (Boratynski 1952). In France, *M. pini* is bisexual and, depending on the altitude, has one or two generations a year, associated with morphological variation on the females. Thus, at 1350-1450 m *M. pini* is univoltine but is bivoltine at 200-400 m. Rieux (1976) also observed that the number of cicatrices and multilocular pores decreased progressively with increasing altitude, with a mean of 54 multilocular disc-pores and 276 cicatrices at 500 m and about 37 multilocular disc-pores and 137 cicatrices) at 1700 m. It is also bisexual in Germany and Poland (Siewniak 1976) but the situation is more complex in Spain, where *M. pini* is bivoltine, with the autumn-winter generation bisexual and the spring-summer generation parthenogenetic (Cadahia 1971). The life cycle of *M. pini* at low altitude is as follows: in May, the females settle in bark crevices and lay about 150 eggs in a white cottony ovisac, dying soon afterwars. The first-instar nymphs appear after about 2 weeks and the 2nd-instar in July. From about mid-August, the adult females and males of the 2nd generation are present, laying eggs from about mid-August to the end of September. The newly-hatched first-instar nymphs cease development, overwintering in bark crevices until March. Adults of the spring generation appear again about April-May.

Economic importance. Occasionally a pest on pine trees.

Natural enemies. Predators only have been observed. The anthocorids *Acampocoris pygmaeus* and *Elatophilus nigricornis* feed on eggs and nymphs under bark. The lacewing, *Hemerobius pini* (Hemerobiidae), is thought to feed on the 1st- and 2nd - instar nymphs, prepupa and adults. Nymphs of Cecidomyiidae, Cleridae, and Raphidiidea are also egg predators.

Host plants. *M. pini* is host specific in England, confined to Scots Pine, *Pinus sylvestris*, often occurs with *Pineus pini* (Adelgidae). In France, it was reported by Rieux (1975) from *Pinus mugo*, *P. nigra, P. pumilio, P. sylvestris,* and *P. uncinata*.

Distribution. In England, it was reported from the following localities: Berks: Silwood Park; Hants: Hordle, New Milton; Surrey: Bagshot, Lower Barnes, Oxshott, Pyrford, Richmond, Wimbledon; Sussex: Highwood and Ashburn Park, near Bexhill-on-Sea (Boratynski 1952).

In France: it was first observed in 1963, at Mimet (Bouches-du-Rhône) by P. Teocchi. Subsequent surveys have found it in the Alpes de Haute Provence, Ardèche, Drôme, Haute-Loire, Lozère, Seine-et-Marne and at Vaucluse on Mont-Ventoux up to 1.400 m.

In Italy, it has been reported from Friuli-Venezia Giulia (from the alpes to the sea), Marche, Abruzzo by Tranfaglia et *al*. (1985) and Veneto (pers. com. of Prof. G. Pellizzari).

In Mediterranean area: France, Italy, Morocco, Spain, Turquey.

Palaearctic: Austria, Bulgaria, Croatia, Czech Republic, England, Germany, Hungary, Netherland, Poland, Romania and Russia.

Remarks. Some authors believe it is synonym of *M. matsumurae* (e.g., Morrison 1928, Kosztarab & Kozár 1988, Kosztarab 1996).

Key to the adult females of *Matsucoccus* species in the Mediterranean basin.

1. Antennal segments V-IX with two fleshy setae; scape longer than wide 2
– Antennal segments VI-IX with two fleshy setae; scape wider than long 3
2. Dorsal cicatrices fewer than 165, in bands across abdominal segments III-VII . . . . . *josephi*
– Dorsal cicatrices greater in number than 165, in bands across abdominal segments IV-VII . . . . . *feytaudi*
3. Bilocular tubular ducts each 6-7 µm long; multilocular disc-pores in a cluster of 40-85 (62) at apex of abdomen . . . . . *matsumurae*
– Bilocular tubular ducts each 10-12 µm long; multilocular disc-pores in a cluster of 30 to 50 (39) at apex of abdomen . . . . . *pini*

Remarks – The family Matsucoccidae is an homogeneous group, with both females and males having easily recognizable morphological characters which quickly distinguish them from other taxa. On the other hand,

within the family, the adult females are mostly morphologically very similar and their identity is supported only by small differences. Quantitative data of taxonomically important structures, such as pores and cicatrices, are used also for species separation, although both quantitative and qualitative data differ widely on which generation is being studied and on differences related to locality, altitude, and host plant (Boratynsky 1952, Rieux 1976, Ben-Dov 1981, McClure et *al*. 1983a, Miller & Park 1987).

It was observed by McClure et *al*. (1983) in the Chinese population of *M. matsumurae* that the overwintering generation had more multilocular pores and larger cicatrices than the summer generation. McClure et *al*. also found that *M. matsumurae* shoed an inability to adapt to geographic areas with moderate temperatures, and also was an unable to exploit apparently suitable hosts in region where the winter and summer temperatures were more extreme than in its native habitats (McClure 1983). As already suggested by Miller & Park (1987), a detailed intraspecific taxonomic analysis of *M. matsumurae* is needed from a world viewpoint, using material from each generation separately. Seasonal differences in the numbers and measurements of pores and cicatrices have been reported on *M. josephi* in Israel (Ben-Dov 1981). On this species, the cicatrices are bigger and the multilocular disc-pores more numerous on females of the spring generation than those of the autumn generation.

M. pini is another enigmatic species, showing remarkable variation in both morphology and biology. Information about its biology varies between different countries (France, Germany, Poland, Spain, United Kingdom). According to Rieux (1976), *M. pini* should be defined as a widespread species belonging to a species complex living on pines of section *sylvestris* and showing large geographic variation. McClure et *al*. (1976, 1983) and Young et *al*. (1984) suggested also that *M. resinosae* is probably a junior synonym of *M. matsumurae*, since female sex pheromone experiments on *M. matsumurae* had a strong attraction to the males of both *M. matsumurae* and *M. resinosae*. In addition, the convergence of male morphology between of *M. resinosae* and *M. pini*, the morphology and life history of female *M. pini* are apparently very similar to those of *M. matsumurae*, suggesting that *M. pini* could also be conspecific with *M. matsumurae.* However, *M. matsumurae* is bivoltine, whereas *M. pini* may be uni or bivoltine.

The present work, based on the morphology female supports the validity of the Mediterranean species. They form two clearly separate groups: *M. feytaudi and M. josephi* with two fleshy setae on antennal segments V to IX, *M. matsumurae* and *M. pini* only from VI to IX. In addition, *M. feytaudi* can be separated from *M. josephi* by the greater number of dorsal cicatrices on 4 abdominal segments, whilst in *M. josephi* fewer cicatrices but they are present on 5-6 segments. On *M. pini* the bilocular tubular ducts are distinctly longer than on *M. matsumurae* and fewer multilocular pores than in *M. matsumurae*.

However, the wide variation in the quantitative and qualitative data strongly suggest that the true status of these species will only be clarified by a molecular phylogenetic study. *M. matsumurae* along with *M. pini* and *M. resinosae* may be a single species with a high capacity to exploit available hosts in variety of climatic areas or a widespread complex of sibling species.

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Appendix 1

Extant *Matsucoccus* species

Matsucoccus acalyptus Herbert, 1921. Crawlers occur on exposed needle surfaces and adult females under bark of *Pinus monophylla*, *P. edulis and P. balfouriana.* USA: Arizona, California, Colorado, Idaho, Nevada, New Mexico and Utah.

Matsucoccus alabamae Morrison, 1939. In crevices of the heavy bark of trunk of *Pinus* sp. USA: Alabama.

Matsucoccus apachecae Ray & Williams, 1984. Under bark of *Pinus engelmanii and P. ponderosa.* USA: Arizona

Matsucoccus banksianae Ray & Williams, 1991. On *Pinus banksiana*. USA: Minnesota.

Matsucoccus bisetosus Morrison,1939. Adult female occurs in cracks of bark on small twigs, and in twig axils of *Pinus ponderosa, P. jeffreyi*, *P. radiata, P. scopulorum.* USA: Arizona, California, Colorado and Oregon.

Matsucoccus boratynskii Bodenheimer & Neumark, 1955. In bark of trunk of *Pinus sylvestris*. Russia.

Matsucoccus californicus Morrison, 1939. In crevices on trunks of *Pinus ponderosa* and *Pinus jeffreyi.* USA: California.

Matsucoccus dahuriensis Hu & Hu, 1981. On *Pinus sylvestris* var. *mongolica.* China: Mountain Dahinganling in Heilongjiang Province.

Matsucoccus degeneratus Morrison, 1939. Occuring between sheath and needles at base of needle bundles of *Pinus ponderosa.* USA: Arizona. Mexico.

Matsucoccus eduli Morrison, 1939. In the axils of small branches of *Pinus edulis.* USA: Arizona.

Matsucoccus fasciculensis Herbert, 1919. Cyst usually occuring between needles of *Pinus ponderosa and P. jeffreyi.* USA: California, Idaho, Oregon.

Matsucoccus feytaudi Ducasse, 1942. In crevices and under bark of trunk of *Pinus pinaster*. Algeria, France, Italy, Morocco, Portugal, Spain, Tunisia.

Matsucoccus gallicolus Morrison, 1939. Nymphal stages in galls; adult females migrate to the trunk or branches of *Pinus rigida*, *P. echinata, P. ponderosa, P. resinosa, P. virginiana, P. taeda, P. glabra*. USA: wide distribution through pine areas of Eastern States.

Matsucoccus josephi Bodenheimer & Harpaz, 1955. On lower stems at base of needle-bundles and underneath outer bark layers of *Pinus brutia and P. halepensis.* Crete, Cyprus, Israel, Jordan, Lebanon and Turkey.

Matsucoccus koraiensis Young & Hu, 1976. On *Pinus koraiensis*. China: Mountain Xiaohinganling in Heilongjiang Province.

Matsucoccus liaoningensis Tang, 1978. On twigs of *Pinus tubulaeformis.* China: Fengcheng in Liaoning Province.

*Matsucoccus leiophylla*e Ray & Williams, 1984. On stems and trunks of *Pinus leiophylla.* USA: Arizona. On *Pinus* sp. Mexico.

Matsucoccus macrocicatrices Richards, 1960. On trunks of *Pinus strobus.* Canada: Lynedoch, Ontario. USA: Massachusetts.

Matsucoccus massonianae Young & Hu, 1976. On *Pinus massoniana, P. thunbergiana.* China: Zhejiang Province.

Matsucoccus matsumurae (Kuwana, 1905). In bark crevices on *Pinus densiflora*, *P. halepensis, P. massoniana, P. nigra, P. pinaster, P. pinea, P. resinosa, P. rigida, P. sylvestris*, *P. tabulaeformis* and *P. thunbergiana*. China, Japan, Korea, Russia, USA.

Matsucoccus monophyllae McKenzie, 1941. Cyst occurs on bark at bases of needle bundles, in twig axils and in bark cracks of *Pinus monophylla and P. edulis.* USA: California.

Matsucoccus mugo Siewniak, 1970. On *Pinus mugo* var *pumilo* . Germany.

Matsucoccus oocarpae Ray & Williams, 1991. On *Pinus ooccarpa*. Guatemala.

Matsucoccus paucicicatrices Morrison, 1939. Cyst occurs in bark cracks, in twig axils and on bark at bases of needle bundles of *Pinus flexilis, P. lambertiana, P. monticola.* USA: California, Montana, Oregon, Wyoming.

Matsucoccus pini (Green, 1925). In bark crevices of *Pinus sylvestris;* known also from *Pinus mugo* and *P. nigra.*

Matsucoccus secretus Morrison, 1939. Occuring within bundle sheath at base of needles of *Pinus ponderosa*. USA: Arizona, California, Colorado, Nevada, New Mexico, widely distributed through pine areas of western part of US; Mexico.

Matsucoccus shennongjiaensis Young & Lu, 1986. On *Pinus armandi*. China: Shennongjia Hubei Province; Lu Chang-ren and Zhan zhong-cai.

Matsucoccus sinensis Chen, 1937. On exposed needle surfaces of *Pinus massoniana* and *P. tubulaeformis.* China: Chekiang and Shaanxi Provinces.

Matsucoccus subdegeneratus Morrison, 1939. In sheath around base of needles of *Pinus occidentalis.* Dominican Republic: Monte Cristi Prov.

Matsucoccus thunbergianae Miller & Park, 1987. On *Pinus thunbergiana.* Korea: Chollanam-do.

Matsucoccus vexillorum Morrison, 1939. Feedings on twigs, particularly in angle formed by twig and needle bundle of *Pinus ponderosa.* USA: Arizona, Colorado, New Mexico.

Matsucoccus yunnanensis Ferris, 1950. Beneath bark of *Pinus yunnanensis.* China: Kunming City of Yunnan Province.

Matsucoccus yunnansonsaus Young & Hu, 1980. On *Pinus yunnanensis*. China: Yunnan Province.

Fossil Matsucoccidae species

Genus Matsucoccus

Matsucoccus pinnatus (Germar et Berendt, 1856). Tertiary-Eocene, about 40 Millions years; male, female, larva from Baltic and Bitterfeld amber.

Matsucoccus apterus Koteja, 1984. Tertiary – Eocene; male from Baltic amber.

Matsucoccus crenata (Koch et Berendt, 1845). Eocene; Baltic; perhaps not a *Matsucoccus* sp.

Matsucoccus electrinus Koteja, 1984. Tertiary-Eocene; male and female from Baltic amber.

Matsucoccus larssoni Koteja, 1984. Tertiary-Eocene; male and female from Baltic amber.

Matsucoccus saxonicus Koteja, 1986. Tertiary-Eocene; male from Bitterfeld amber.

Genus Eomatsucoccus

Eomatsucoccus sukachevae Koteja, 1988. Lower Cretaceous (Neocomian) about 125 Million years.

Eomatsucoccus popovi Koteja, 1988. Lower Cretaceous (Berriasian-Valanginian); male from Siberian deposits (Baisa).

Eomatsucoccus andrewi Koteja, 1999. Lower Cretaceous (Hauterivian); male from southern England (Wealden).

Eomatsucoccus casei Koteja, 2000. Upper Cretaceous (Turonian) about 95 Million years; male from New Jersey amber.

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