

Ground pearls: a generic revision of the Margarodidae *sensu stricto* (Hemiptera: Sternorrhyncha: Coccoidea)

Imre FOLDI

Muséum national d'Histoire naturelle, Département Systématique et Evolution,
CP 50 Entomologie, 45 rue Buffon, F-75005-Paris.

Abstract. The ground pearls comprise the scale insect family Margarodidae *s. str.*, and are subterranean plant sucking parasites on roots of a wide variety of plants. Some ground pearls are serious destructive pests of grape vines, sugar cane, oil palms, cotton or lawn grass around the world. Both female and male development is characterised by an apodous, feeding 2nd-instar nymph, called a cyst. The cyst is primarily circular and often colourful, shiny, metallic or pearl-like, from which the common name "ground pearls" is derived. Other unique features are the strongly developed prothoracic legs for digging, the construction of a protective test from their own liquid excreta in which the cyst is enclosed and a behavioral adaptation by modification of their life-cycle to survive in adverse environmental conditions.

The 10 genera, currently include 105 species, form a monophyletic group with a worldwide distribution. First-instar nymphs and cysts are feeding instars; however, adults male and females lack mouthparts and do not feed. Species of ground pearls reproduce either bisexually or parthenogenetically, parthenogenesis is facultative in *Eurhizococcus brasiliensis*. Females undergo three, four or five developmental stages, while males have five. During the cyst stage, one, two or three molts may occur. Most species have a single generation each year, although development in *Margarodes vitis* requires three years including three instars of cysts. This revision redescribes and illustrates the type species of each genus, including *Margarodes vitis* (Philippi) and provides a key to the genera based on the morphology of adult females. Lectotypes of *Dimargarodes mediterraneus* (Silvestri), *Heteromargarodes americanus Jakubski*, *Promargarodes sinensis* Silvestri and *Termitococcus carrotai* Silvestri are designated. A nomenclatural change is proposed, the genus *Sphaeraspis* Giard, 1894 is considered to be a synonym of *Margarodes* Guilding, 1829. This work also provides information on the history of the group of Archaeococcoids; on the biology, economic importance and distribution of the margarodids.

Résumé. Les Perles de terre : une révision générique des Margarodidae *sensu stricto* (Hemiptera : Sternorrhyncha : Coccoidea). Les Perles de terre, Cochenilles Margarodidae *s. str.*, souterraines sur les racines d'une grande variété de plantes, sont d'importants ravageurs des plantes cultivées : Vigne, Canne à sucre, Palmier à huile, Coton ou gazon. Le développement des femelles et des mâles est caractérisé par un 2^e stade larvaire apode, appelé kyste, inclus dans un test. Ce kyste, plutôt globulaire, souvent d'une couleur brillante et métallique, ressemble à une perle, d'où leur nom de « Perles de terre ». D'autres caractères originaux sont la présence de puissantes pattes prothoraciques fousseuses, la construction d'un test de protection à partir de leurs propres excreta liquide et l'adaptation comportementale par une capacité de modifier leur cycle de vie en réponse aux facteurs environnementaux. Seul les immatures s'alimentent, les adultes sont dépourvus des pièces buccales. La reproduction est bisexuée ou parthénogénétique (parthénogenèse facultative chez *E. brasiliensis*). Le développement comporte chez les mâles 5 stades, chez les femelles 3, 4 ou 5 stades suivant que le kyste lui-même subit une, deux ou trois mues. Il y a en principe une génération par an, mais chez *Margarodes vitis* une génération se développe sur trois ans, incluant 3 stades de kyste.

De distribution mondiale, les 10 genres hypogés renferment 105 espèces qui forment un groupe monophylétique et une famille distincte. Chaque espèce type des genres est redécrite et illustrée incluant *Margarodes vitis* (Philippi). Une clef des genres basée sur la morphologie des adultes femelles est proposée. Les lectotypes de *Dimargarodes mediterraneus* (Silvestri), *Heteromargarodes americanus Jakubski*, *Promargarodes sinensis* Silvestri et *Termitococcus carrotai* Silvestri sont désignés. Un changement nomenclatural est proposé, le genre *Sphaeraspis* Giard, 1894 est considéré comme un nouveau synonyme de *Margarodes* Guilding 1829. Des informations sont apportées sur l'historique du groupe des Archaeococcoides ; sur la biologie, l'importance économique et la distribution géographique des Margarodidae.

Scale insects are morphologically so specialized that their external appearance does not resemble that of typical insects. Their bodies are usually covered by secretions giving a bizarre external appearance, sometimes resembling stars, mussels, bowls or an outgrowth on plants. In addition, extreme sexual dimorphism occurs in scale insects; females are apterous and males are small and usually winged. These differences are so marked that the male and female of a species seem to belong to two different species.

Scale insects constitute an integral part of our daily lives, being present on trees in city streets, public gardens, fruit orchards and forests. They are nearly invisible except to the trained eye because they are small or live in cryptic habitats on the host plants - Only some indications betray their presence, such as a small white spots due to white secretions on their host, small viscous droplets on the leaves due to honeydew excretion, or small yellow marks or yellowing on leaves. They occur in nearly all ecological habitats, excepting the poles, and colonize all plant parts including the roots, bark, stems, leaves and fruits of most of the world's existing vascular plants. They are, nearly 8000 species, distributed worldwide, and the international trade of plants facilitates their further dispersal around the world.

Among scale insects, the ground pearls are subterranean (hypogean), with immature stages feeding on roots, especially in sandy soil. Both adult female and male functions only for reproduction and does not feed. Unless the species is parthenogenetic, the adult female goes up to the surface of soil to mate, and then goes underground again on the roots and to lay her eggs in an ovisac. Development, in both females and males, ground pearls is characterised by an apodous, feeding 2nd-instar nymph with reduced antennae, and enclosed in a protective test, constructed by the insect from its liquid excreta. This liquid represents the waste from the metabolism process, which may be mixed by secreted substances emitted from some internal glands and produce a final product to construct the test. The means of constructing this protective test from the liquid excreta of hypogean species has been described recently by Foldi (1997) and is completed in this work

The term « ground pearls » derives from the shiny, colorful, often metallic, iridescent external appearance of the tests of some *Margarodes* spp. The test may be thick and hard as in *Margarodes* spp. thin and soft as in *Dimargarodes* spp. and *Porphyrophora* spp.

Scale insects are serious plant-feeding pests because they remove plant sap. The excessive sap loss reduces plant vigour and may provoke plant death. Ground

pearls are significant pests of grape vines, sugar cane, oil palms, cotton or lawn grass.

Ground pearls, are distributed throughout all biogeographical regions (Fig. 1). In Mediterranean countries, they are represented by about 20 species belonging to four subterranean genera: *Dimargarodes* Silvestri, *Promargarodes* Silvestri, *Neomargarodes* Green and *Porphyrophora* Brandt.

Taxonomically, species and genera of ground pearls are challenging to identify; the first major revision was published nearly 80 years ago in Morrison's (1928) monograph (tribe Margarodini) and the last one, Margarodidae and Termitococcidae by Jakubski (1965).

In this revision, the Margarodidae *sensu stricto* include the ground pearl genera only and the main goal is to revise their taxonomy by redescribing the type species of each genus, including the adult female, cyst and first-instar nymph, using current standards in scale insect taxonomy.

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); Dipartimento di Entomologia e Zoologia Agraria (DEZA), Università degli Studi di Napoli "Federico II", Portici, Italy; Departamento de Entomologia, Museu de Zoologia, Universidade de São Paulo, São Paulo and Universidade de Curitiba, Zoologia, Curitiba, Brazil.

The specimens were examined using a Leica DMR microscope. For the SEM study, 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.

Porphyrophora crithmi (Goux) was reared on *Crithmum maritimum* (Umbelliferae), whereas *Eurhizococcus brasiliensis* (Wille) was reared on *Solonum tuberosum* and *Cucurbita maxima*. The observation of the development of different instars of male and female and the mating of males and females were conducted under laboratory conditions. In addition, I collected numerous females and cysts in the field in Brazil with my colleague Dr S. J. Soria and, found adult females free in soil and also cysts with enclosed females inside containing both eggs and crawlers.

Abbreviations used on Fig. 13

aed = aedeagus	pa = mesopostnotal apophysis
al = alar lobe	plr = pleural ridge
as = abdominal spiracle	pn = mesopostnotum
ce = compound eye	pra = prealare
cd = claw digitule	prn = pronotum
cl = claw	ps = penial sheath
cv = cervical sclerite	psc = prescutum
cx = coxa	pte = post-tergite
e = endophallus	sc = scape
eps 1, 2, 3 = pro-, mes-, and metepisternum	scu = scutum
f = furca	sl = scutellum
fe = femur	ste = sternite
fs = fleshy seta	t = tegula
ha = hamuli	ta = tarsus
hh = hamulohaltere	ter = tergite
lpl = lateropleurite	ti = tibia
me = median	tcp = tubular pores cluster
p = pedicel	tr = trochanter
pcr = precoxal ridge	ts = thoracic spiracle
pcr1, 2 = meso, meta precoxal ridges	vcr = ventral midcranial ridge

History of the group of Archaeococcoids and their current higher classification.

The division of scale insects into two higher groups, Palaeococcoidea and Neococcoidea was used for the first time by Borchsenius (1950: 14), followed by Bodenheimer (1952: 317) with the terms Archaeococcidea and Neococcidea. Later, Borchsenius (1958) introduced the term Archaeococcoidea to include 3 families, (Ortheziidae, Phenacoleachiidae and Margarodidae) based on characters such as the presence of abdominal spiracles, chaetotaxy and wax producing glands in the females, and presence of compound eyes in males and Neococcoidea lacking abdominal spiracles, with a highly developed wax gland system in females, and males without compound eyes. Since Archaeococcoidea and Neococcoidea were not based on nominal genera, the classification of scale insect in the suborder of Coccinea consisting 2 superfamilies, the Orthezioidea Amyot and Serville, 1843 (Archaeococcoids) and Coccoidea Fallén, 1814 (Neococcoids) as suggested by Koteja (1974) and Danzig (1980). However, most coccidologists continue to use the superfamily Coccoidea to include all scale insects dividing them, based on the presence or absence of characters interpreted as ancestral, into two major informal groups (Archaeococcoids and Neococcoids) (Lambdin, 2002).

The archaeococcoids currently are defined having abdominal spiracles in females and males, compound eyes in males and XX-XO chromosome system present. The neococcoids are defined by absence of abdominal spiracles, compound eyes absent in males and with a paternal genome elimination (PGE), (Gullan & Cook

2002; Cook *et al.* 2002). A pair of campaniform sensilla on the apical part of labium may be a probable synapomorphy for archaeococcoids (Koteja 1996). Archaeococcoids comprise two large families, Margarodidae *sensu* Morrison (1928) with about 460 species (Foldi 2001), the Ortheziidae with about 200 species (Kozár 2004), and several small groups: Carayonemidae, Phenacoleachiidae, Pityococcidae and Putoidae. Relationships among many archaeococcoids groups are not well known even the monophyly is uncertain resulting in there being no stable higher level classification.

The phylogenetic placement of the Ortheziidae is consistently arises from one of the basal nodes in relation to most other Coccoidea and near margarodids (Foldi 1997; Gullan & Sjaarda 2001; Cook *et al.* 2002). The recent revision of ortheziids is by Kozár (2004) in describing 10 new genera 94 new species. Recent phylogenetical informations (Cook *et al.* 2002) support the family status of Phenacoleachiidae and Gullan & Cook (2002) suggest the early origin of *Phenacoleachia* (Phenacoleachiidae) in scale insect evolution based on the occurrence of plesiomorphic features such as XX-XO sex determination, a four-segmented labium, abdominal spiracles, a pair of apical organs in the labium and cicatrices, which also characterize numerous other archaeococcoids. They pointed out the importance of *Phenacoleachia*, which either may be sister to the rest of the scale insects taxa or belong to the archaeococcoid lineage as suggested by Koteja (1984) and Danzig (1980), but in any case its phylogenetic relationship is fundamental to understanding early Coccoidea evolution. The phylogenetic placement of *Puto* remains unresolved but the recent results (Cook *et al.* 2002) place it outside of the main neococcoid clades and Koteja (1990, 1996) believed that *Puto* was ancestor of all neococcoids and among neococcoids putoid-like fossils are the oldest. The Carayonemidae forms a small Neotropical group with 4 monotypic genera living in leaf litter humide or semi aquatic environment; one characteristic remarkable is the dorsal spines with considerably enlarged apical part as an umbrella allowing to float on the water (Kozár & Konczné-Benedicty 2002; Kozár & Foldi 2002); his phylogenetic placement is near of margarodids (Foldi 1997). Pityococcidae show affinities with coelostomidids and the Steingeliidae with Xylococcidae (Gullan & Sjaarda 2001). The structure of ovary suggest that Steingeliidae, (*Steingelia* based on external morphology is an aberrant controversial genus), are closely related to the Ortheziidae, Xylococcidae and Matsucoccidae (Koteja *et al.* 2003).

Among the extant scale insects, some archaeococcoids are among the earliest described. Linnaeus (1758)

in his *Systema Naturae* described *Coccus polonicus* L. (= *Porphyrophora polonica* (L.)) (Margarodidae) and *Aphis urticae* L. (= *Orthezia urticae* (L.)) (Ortheziidae). Other old species include *Coccus fabae* Fabricius (= *Gueriniella serratulae* (Fabricius)) (Margarodidae) described in 1775, some ortheziids, such as *Pediculus cataphracta* Olafsen (= *Arctorthezia cataphracta* (Olafsen 1772)), *Coccus floccosa* De Geer (= *Newsteadia floccosa* (De Geer 1778)), *Margarodes formicarum* Guilding 1829, and *Porphyrophora hamelii* Brandt 1835. For a long period, all described scale insects were included in the family group Coccides Fallen 1814, corresponding to the Coccoidea of current usage.

The first tentative classification of scale insects was introduced by Targioni-Tozzetti (1868). He discussed scale insect characters and divided them into four “tribes” which formed the basis of the current major groups of Coccoidea: 1) Orthezites including *Orthezia* and 14 species of margarodids belonging to four genera (*Callipappus* Guérin-Ménéville, *Porphyrophora* Brandt, *Monophlebus* Guérin-Ménéville and *Guerinia* Targione Tozzetti (= *Gueriniella* Fernald, 1903); plus the genus *Margarodes* Guilding he considered as questionable; 2) Coccites including principally the mealybugs; 3) Lecanites comprising mainly the soft scales and a variety of scale insects such as Kermesidae, *Physokermes* Targione Tozzetti, *Pollinia* Targioni Tozzetti and the Asterolecaniidae; 4) Diaspidites which are the Diaspididae of today. This work also provided a list of 117 species belonging to 28 genera.

Signoret's (1869) classification mainly corresponds to that of Targioni Tozzetti. He also divided the Coccides into four main « sections » without using the name Orthezites and he discussed 25 genera. The sections are: 1) Diaspides; 2) Brachyscélides, now corresponding to the subfamily Apiomorphinae; 3) Lécanides; 4) Coccides which included margarodids belonging to five genera (*Monophlebus*, *Callipappus*, *Tessarobelus* Montrouzier, *Margarodes*, *Porphyrophora*), the genera *Coccus* and *Orthezia* (Ortheziidae). He described *Putonia antennata* in 1875 now *Puto antennata* (Signoret) corresponding to type-genus of Putoidae (Beardsley 1969). Later Signoret (1876: 346 (1875)) created the group name *Monophlébites* and *Porphyrophorites* and discussed 27 species belonging 11 margarodid genera (*Icerya* Signoret, *Drosicha* Walker, *Guerinia*, *Leachia* Signoret (= *Palaeococcus* Cockerell), *Monophlebus*, *Ortonia* Signoret (= *Ecuadoronia* (Signoret), *Llaveia* Signoret, *Callipappus*, *Porphyrophora*, *Margarodes* and *Walkeriana* Signoret).

From this era, several systems of classification were successively proposed that are of historical interest. Comstock (1881) included the genera *Icerya* and *Orthezia* in the subfamily Coccinae; Maskell (1887)

placed the genera *Icerya*, *Coelostoma*, *Monophlebus*, *Leachia*, *Ortonia*, *Callipappus* and *Walkeriana* in the Monophlebidae (Subdivision IV), and the genera *Porphyrophora* and *Margarodes* in the Porphyrophoridae (Subdivision V); Cockerell 1896, Fernald 1903, Green 1922) recognized two subfamilies, the Monophlebinae and Porphyrophorinae and MacGillivray (1921) placed all margarodid species in five subfamilies: Callipappinae, Kuwaniinae, Margarodinae, Monophlebinae and Xylococcinae.

The number of species described belonging to the Margarodidae *s.l.* increased considerably during the last century. The catalogue of Fernald (1903) listed 89 species belonging to 16 genera, whereas Foldi (2001) listed 439 species in 76 genera. The latter lists all taxa in alphabetical order, without indication of classification (subfamilies, tribes), because the relationships within this assemblage of heterogenous groups has not been resolved and there exist no current reliable phylogeny.

The genus *Margarodes*, named after a Greek word meaning pearl-like, was erected by Guilding (1829) to accommodate a subterranean (hypogean) species and became the type genus of the family Margarodidae (Williams & Foldi 2005). The subfamily name of Margarodinae was introduced by Cockerell (1899) to include the genus *Margarodes* and subgenus *Sphaeraspis* Giard. The family name Margarodidae was first used in the literature by Enderlein in Brohmer (1914). However, the family was established definitively by Morrison (1927, 1928) in his remarkable monography, where he published a detailed classification based principally on the females, but also included nymphal and adult male characters recognizing 5 subfamilies and 15 tribes, which represents the currently used higher classification of Margarodidae *s.l.*

Morrison's (1928) classification of Margarodidae *s.l.*

Subfamily **Xylococcinae** Pergande 1898. 3 Tribes:
Matsucoccini Morrison, Stigmacoccini Morrison,
Xylococcini Cockerell.

Subfamily **Steingeliinae** Morrison 1927. 1 Tribe:
Steingeliini Morrison.

Subfamily **Margarodinae** Cockerell 1899. 3 Tribes:
Kuwaniini Handlirsch, Margarodini Cockerell,
Callipappini MacGillivray.

Subfamily **Coelostomidiinae** Morrison 1927. 3 Tribes:
Coelostomidiini Morrison, Marchalinini Morrison,
Platycoelostomini Morrison.

Subfamily **Monophlebinae** Signoret 1875. 5 Tribes:
Drosichini Morrison, Iceryini Cockerell, Llaveiini
Morrison, Monophlebini Cockerell, Monophlebulini
Morrison.

Morrison (1928) included in the Margarodidae all scale insect species possessing abdominal spiracles, lacking a setiferous anal ring in the female and possessing compound eyes in the male.

Among subsequent authors, Koteja (1974) proposed the deepest modifications in subunits (subfamilies and tribes) for the margarodids. In his work on the classification based on the mouthparts, recognized within Margarodidae *s.l.* (6 families plus the *Neosteingelia* group) and in subsequent works (1996, 2000), he created others new families summarised below. All subfamilies and a few of the tribes of Margarodidae *sensu* Morrison (1928) have been elevated to family status.

Koteja's (1974, 1996, 1998, 2000) classification of Margarodidae *s.l.*

Callipappidae MacGillivray, **Coelostomidiidae** Morrison, **Kuwaniidae** MacGillivray, **Margarodidae** Cockerell, **Marchalinidae** Morrison, **Matsucoccidae** Morrison, **Monophlebidae** Signoret, **Pityococcidae** McKenzie, **Steingeliidae** Morrison, **Xylococcidae** Pergande (in Hubbard & Pergande).

The family Termitococcidae Jakubski 1965 is here considered as synonym of Margarodidae Jakubski 1965.

Recently, fossil data compiled by Koteja (1998 1999, 2000 a,b, 2001, 2002) suggest that Margarodidae *s.l.* represent the relics of an ancient radiation. Although it would be difficult to identify even the best preserved fossils to species level based on keys to the recent fauna, Koteja gave a new dimension to scale insects studies by linking the study of fossils and extant species, providing important data for classifications, creating several new families based on fossils, and by proposing pertinent hypotheses on the evolution and radiation of scale insects.

The oldest scale insect impression fossils are known from the Upper Jurassic, about 140 millions years old, represented by three specimens of winged males that have not been named and described (Jan Koteja pers. comm.). Numerous fossil scale insects have been described from Lower Cretaceous (Lebanon, Alaska) amber and Upper Cretaceous (New Jersey, Canada, Taymyria, Burmese) amber. Koteja (2001) suggested that an extensive scale insect radiation must have occurred in pre-Cretaceous times. In Lower Cretaceous Lebanese amber, estimated to be about 125 millions years old, and in Siberian and European impressions, scale insects appear as a diverse, abundant and specialized group. Although neococcoids appear among those fossils, the archeococcoids, dominate throughout the Mesozoic, and even into the Eocene period about 40 mill. years ago, constituting the majority of scale insect fossils. Representatives of the main archeococcoid

branches (Matsucoccidae, Monophlebidae, Xylococcidae, Pityococcidae, Steingeliidae) are recognizable in various deposits, and sometimes they appear similar to the extant forms (e.g. *Matsucoccus*). However, most fossils represent extinct, highly specialized groups (Koteja 2000 a,b). To date, no species of the ground prarls have been found in fossil records.

Fossil taxa

Coelostomidiidae: *Cancerococcus apterus* Koteja 1988.

Matsucoccidae: *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; *Eomatsucoccus popovi* Koteja 1988. Lower Cretaceous (Berriasian-Valanginian); male from Siberian deposits (Baissa). *Eomatsucoccus sukachevae* Koteja 1988. Lower Cretaceous (Neocomian) about 125 Million years.

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.

Monophlebidae: *Monophlebus irregularis* Germar & Berendt 1856; *M. simplex* Scudder 1890.

Steingeliidae: *Steingelia cretacea* Koteja 2000

Fossil Archaeococcoids

Electrococcidae Koteja 2000. *Electrococcus canadensis* Beardsley 1969.

Turonicoccus Koteja 2000. *Turonicoccus beardsleyi* Koteja 2000; *T. grimaldii* Koteja 2000.

Jersicoccidae Koteja 2000. *Jersicoccus kurthi*, Koteja 2000.

Grimaldiellidae Koteja 2000. *Grimaldiella gregaria* Koteja 2000, *G. resinophila* Koteja 2000.

Kukaspidae Koteja & Poinar 2001. *Kukaspis usingeri* Koteja & Poinar 2001.

Obenberger (1957) recognized 5 of Morrison's subfamilies, and 2 subfamilies, (Kuwaniinae and Callipappinae), established by MacGillivray (1921) that were treated as tribes by Morrison. Zahradnik (1972) used three famil-

ial categories: Xylococcidae, Margarodidae and Monophlebidae. Beardsley (1968) elevating the tribe Matsucoccini to subfamilial rank based on the characters of male of *Matsucoccus bisetous* and in 1969, described a fossil *Pityococcus* species and raised McKenzie's (1942) margarodid tribe Pityococcini to subfamily rank. Jakubski (1965) elevated the tribe Margarodini of Morrison to familial rank (Margarodidae) with four subfamilies: Porphyrophorinae, Eumargarodinae, Neomargarodinae, and Margarodinae. He also created a new family Termitococcidae with 1 subfamily (Termitococcinae), to include two genera, *Termitococcus* Silvestri and *Eurhizococcus* Silvestri. Danzig (1980) regarded Margarodidae *s.l.* as a single family and recognized three subfamilies, Monophlebinae with five tribes, Coelostomidiinae with three tribes and Margarodinae with five tribes and two subtribes. Miller (1984), based on a preliminary cladistic analysis, considered the Margarodidae *s.l.* as a monophyletic group, except for *Pityococcus* that was separated from the Margarodidae leaving the cyst forming fossorial margarodids as a well-defined, natural group. Kosztarab & Kozár (1988) retained the broad Morrison's concept (1928) of Margarodidae. Morales (1991) followed Morrison's classification and assigned all native margarodids of New Zealand to the subfamily Coelostomidiinae. Tang & Hao (1995) assigned all Margarodidae *s.l.* of China into two families, the Margarodidae with three subfamilies, Margarodinae, Xylococcinae and Kuwaniinae, and the Monophlebidae, with two subfamilies, Coelostomidinae and Monophlebinae. Foldi (1997) concluded the Margarodidae *s.l.* to be paraphyletic based on a cladistic analysis of one representative genus for each family and three margarodid genera. Gullan & Sjaarda (2001), in their morphological cladistic analysis, proposed that the most traditional tribal groupings within Margarodidae are monophyletic, but that the relationships among the subfamilies Coelostomidiinae, Margarodinae and Xylococcinae are not resolved and these three subfamilies may be either paraphyletic or polyphyletic. Only Monophlebinae and Steingeliinae were well supported by morphological characters. Their analysis suggests that Marchalini and Monophlebinae are derived with respect to other margarodids and thus, development by legless cysts may be plesiomorphic within margarodids. They suggested that a probable morphological synapomorphy for archaeococcoids is the presence of an anal tube, however, in some species this is weakly developed or lacking. Recently, Gullan & Cook (2002) suggested the early origin of *Phenacoleachia* (Phenacoleachiidae) in scale insect evolution based on the occurrence of plesiomorphic features such as XX-XO sex determination, a four-segmented labium, abdominal spiracles, a pair of apical

organs in the labium and cicatrices, which also characterize numerous other archaeococcoids. They pointed out the importance of *Phenacoleachia*, which either may be a sister group to the rest of the scale insects taxa or belong to the archaeococcoids. In any case, its phylogenetic relationship is fundamental to understanding early Coccoidea evolution.

Cook *et al.* (2002) proposed a preliminary phylogeny of the scale insects based on nuclear small-subunit ribosomal DNA. The monophyly of the archaeococcoids was equivocal, whereas the monophyly of the neococcoids was supported. The molecular differentiation among margarodid lineages favors Koteja's (1974) hypothesis that all subfamilies of Margarodidae *sensu* Morrison should be elevated to family status. Their analyses indicate the Pseudococcidae appear to be a sister taxa to the rest of neococcoids while the genus *Puto* status remains unresolved and possibly outside the neococcoids.

The history of the names used in suprageneric categories of Margarodidae *s.l.* apparently began with *Coccionella* (Gmelin 1766) as a uninominal to designate the cochineal insect, which we presume currently to be *Dactylopius cacti*. According to Morrison & Morrison (1966) "this usage does not give the name generic standing in the Coccoidea". Hahnemanns (1793) used *Coccionella* as a generic name in combination with "polonicus" as *Coccionella polonicus* (L.) (= *Coccus polonicus* L. 1758), currently known as *Porphyrophora polonica* (L.), by writing the name in italics; unfortunately, he also used *Coccionella* as a uninominal name in the same alphabetical sequence to refer to cochineal insect which he referred to under the name *Coccus cacti* L. was written in Roman type. Lindinger (1954: 614) concluded Hahnemanns' writing about *Coccionella* to be apparently a binominal, favored the use of this name for the coccid, and presented a case for its acceptance as a replacement for *Margarodes* Guilding 1829. Morrison & Morrison (1966), after reviewing the original Hahnemanns lecture presentations, stated that it is possible to interpret this name presented in italics as a binominal scientific name, but they do not agree with Lindinger's use of *Coccionella* as total replacement for *Margarodes* Guilding 1829, and if *Coccionella* was accepted, it could replace only *Porphyrophora* Brandt 1833. However, in this work, I support Jakubski (1965: 5) concept that the name of *Coccionella* is a *nomen oblitum* and synonym of *Porphyrophora*.

The family name Margarodidae *sensu* Morrison is junior to three other suprageneric names: Porphyrophorites Signoret 1876: 349 (1875), Monophlébites Signoret 1876: 350 (1875) and Xylococcinae Pergande, in Hubbard & Pergande 1898: 26 (Williams 1969).

However, the family name of Margarodidae *sensu stricto* (Jakubski 1965) has been in use for 41 years; therefore, we should to preserve Margarodidae in favor of nomenclatural stability. I follow the classification proposed by Koteja (1974) in which all subfamilies and some tribes of Morrison (1928) are elevated to family status since molecular differentiation among margarodid lineages favors his hypothesis (Cook *et al.* 2002) and our preliminary phylogeny based on the adult males suggests that the hypogaecic margarodids should be considered as a separate family (Hodgson & Foldi 2005). Therefore, in this revision, the Margarodidae *sensu stricto* include only the ground pearl genera.

Family Margarodidae Cockerell *sensu stricto*
Common name: ground pearls, margarodids.

Margarodinae Cockerell 1899; Morrison 1928.

Margarodidae Cockerell; Enderlein 1914; Jakubski 1965.

Termitococcidae Jakubski 1965: 167. New synonymy of Margarodidae *s. str.*

The family Margarodidae *s. str.*, in this work, includes 10 hypogaecial genera with 105 species belonging to 8 tribes included in six subfamilies. This family is based on the concept of Jakubski (1965) with the addition of a new subfamily Margarodesiinae with a new tribe Margarodesiini Foldi and with the omission of Termitococcidae, which is considered as synonym of Margarodidae *s. str.*

1. Subfamily: **Margarodinae** Cockerell 1899. Tribe: Dimargarodini Jakubski 1965: *Dimargarodes* Silvestri; 1938; *Heteromargarodes* Jakubski 1965. Tribe: Margarodini Cockerell 1899: *Margarodes* Guilding 1828; *Promargarodes* Silvestri 1938.
2. Subfamily **Margarodesiinae** new subfamily. Tribe: Margarodesiini new tribe: *Margarodesia* Foldi 1981.
3. Subfamily: **Eumargarodinae** Jakubski 1965. Tribe: Eumargarodini Jakubski 1965: *Eumargarodes* Jakubski 1950.
4. Subfamily: **Neomargarodinae** Jakubski 1965. Tribe: Neomargarodini Jakubski 1965: *Neomargarodes* Green 1914.
5. Subfamily: **Porphyrophorinae** Signoret 1876. Tribe: Porphyrophorini Jakubski 1965: *Porphyrophora* Brandt 1833.
6. Subfamily: **Termitococcinae** Jakubski 1965: Tribe: Termitococcini Jakubski 1965: *Termitococcus* Silvestri 1901. Tribe: Eurhizococcini Jakubski 1965: *Eurhizococcus* Silvestri 1938.

There are two monotypic genera, *Heteromargarodes* Jakubski, *Margarodesia* Foldi; there are three numerically important genera: *Margarodes* with 26 species,

Neomargarodes with 16 species and particularly *Porphyrophora* with 47 species (Foldi 2001).

Diagnostic characters of adult females

An adult female ground pearl can be recognized by the following major characters: (i) all species live underground (hypogaecial) on roots or crown; (ii) presence of powerful, fossorial prothoracic legs; (iii) development via an apodous, feeding 2nd-instar nymph, the cyst; (iv) presence of 2-8 pairs abdominal spiracles, but apparently absent in a few *Porphyrophora* species; (v) presence of multilocular disc-pores throughout body except *Termitococcus* spp.; (vi) thoracic and abdominal spiracles with pores in atrium; (vii) perispiracular sensilla present near of peritreme margin of thoracic spiracles; (viii) mouthparts absent but some genera with an invaginated tube-like membranous area; (ix) presence of spines, except *Heteromargarodes*, *Neomargarodes* and *Porphyrophora*; (x) presence of long, medium and short setae; (xi) apical segment of antennae with flagellate setae and fleshy setae; (xii) presence of an anal tube, with or without pores, rarely atrophied or absent.

Morphology of adult females

Apterous, sac-like, without a well defined dorsal tagmosis dividing the head, thorax and abdomen. Body length usually 4-8 mm. Body shape oval, broadly oval or sub-circular. Body color ranging from yellow, yellow-brown, bright violet to reddish. Derm mostly membranous, soft, flexible with segmentation visible, often densely covered by long hair-like setae, medium and small setae and disc-pores. Antennae from 5-segmented (*Termitococcus carotai* Silvestri) to 18 segmented (*Porphyrophora hisutissima* Hall), but usually 6-11 segmented bearing flagellate, hair-like, short and fleshy setae; basal segments always widest. Eyespots positioned postero-lateral of antennae. Mouthparts absent. Legs well developed, each usually with five segments; prothoracic legs of fossorial type with highly developed femur and strongly sclerotized claw, adapted for digging. Abdominal spiracles varying between 2-8, apparently absent in some *Porphyrophora* spp. Wax gland system well developed, except *Termitococcus* spp; these species have no disc-pores on body surface, only in the atrium. Wax, filamentous or cottony, emitted by a large variety of pore structures, and sometimes by setae and spines. Disc-pores often very abundant, distributed throughout dorsal and ventral sides of body; simple to multilocular pore type, with loculi number up to 40. Tubular ducts absent. Anus a simple opening. Anal tube present, sometimes weakly developed or absent; pores, when present, only internal.

Cyst

The term cyst refers to the feeding, apodous second-instar nymph including its test and can be diagnosed as follows. Body shape globular, broadly oval, body size without test about 2-5 mm in diameter, or elongate, 5-8 mm long, 2.5-4 mm wide. Dorsally lacking morphological structures; ventrally lacking eyespots, setae or spines, and legs. Antennae represented by only a deep pit with 1-4 or more fleshy setae. Mouthparts present, labium apparently 1-2 segmented. Microcicatrices absent or present near of labium. Thoracic spiracles with apodemes strongly developed; each spiracle with cylindrical atrium with strongly sclerotised base containing multilocular disc-pores; each spiracle with a group of perispiracular sensilla on derm at posterior side of each peritreme. Perispiracular pores often numerous, for example in *Porphyrophora* spp. can have about 120 pores producing an amorphous secretion. (Foldi, 1981). Abdominal spiracles in 2-8 pairs rarely absent; spiracular atrium with disc-pores. Anal opening circular, subapical on venter, with or without anal plate, with 0 to 24 cicatrices on derm near anal opening. A transverse line (genital scare) anterior to anal opening present or absent.

First-instar nymph

The first-instar nymphs are usually elongate, but may be circular as in *Eurhizococcus* or *Termitococcus*, and small, 0.7-1.4 mm long, 0.2-0.6 mm wide. They are characterised as follows: dorsum with only few short setae; venter similar to dorsum but with a pair of stout short setae and a pair of long setae on last abdominal segment, sometimes long setae along margins of the body. Antennae 1-4-segmented, segments I-III with few hair-like setae; terminal segment broad, globular with hair-like setae and fleshy setae. Legs well developed with very few setae; trochanter with 2 sensilla on each side. Anal opening circular, sub-apical, with a thin sclerotized ring. Perispiracular sensilla usually present.

Diagnostic characters of adult males

Adult males of ground pearls are characterised by the following diagnostic features: (i) body stout, compact with well developed wings and hamylohalteres with 1 halamus; (ii) presence of large compound eyes; (iii) prothoracic legs fossorial; (iv) a group of long tubular pores in a cluster dorso-medially on segments VI and VII; each pore secretes long white waxy filaments which forms the characteristic long, white tail tuft on posterior end of abdomen; (v) antennae normally 10-segmented; 7-segmented in *Neomargarodes erythrocephalus*; (vi) loculate pores present rarely absent; (vii) abdominal spiracles number varying between 2-7, often very difficult to detect them; (viii) scutum without

membranous area; (ix) scutellum without lateral membranous area; (x) endophallus densely covered by spines; (xi) absence of collared setae.

Morphology of adult males

Adult males resemble small flies with one pair of mesothoracic wings and one pair of vestigial metathoracic wings or hamulohalteres; they have a well developed and distinct head, thorax and abdomen. They possess compound eyes, but lack mouthparts and do not feed. The apical segment of the antennae has capitate setae. Possess a group of tubular pores in a cluster dorso-medially on segments VI and VII; each pores secrete long white waxy filament which together form a whole unit as a long, dorsal waxy tail tuft. Prothoracic legs fossorial and quite different from posterior pairs; profemur usually rather setose with bifurcated setae; tibia and tarsus fused or tibio-tarsal segmentation distinct but with no articulation; claw broadly fused to base of tarsus. The eversible endophallus is densely covered by strongly sclerotized sharply pointed spines along all surfaces; each spines directed in direction of the proximal base of endophallus. This appears to be a major morphological adaptation to enhance successful mating since females are quite mobile during copulation. As such, the spines prevent the accidental or early exit of the endophallus from the female's vagina. The shape, size of spines and their distribution along endophallus is diversified in such a manner as to be a useful complementary character.

Biology

Ground pearls prefer habitats with dryland conditions and sandy soil, often develop large infestations and first-instar nymphs and the cysts live and feed in dense aggregations on the roots of their host-plants. Development in females may consist of three, four or occasionally five stages. The additional stages occur during the cyst stage where one, two or three molts occur. *Margarodes vitis* can stay and survive multiple years in the cyst stage. First-instar nymphs (crawlers) are mobile seeking out potential hosts on which to settle and feed. Also, crawlers of *Eurhizococcus brasiliensis* may be transported by ants (*Iridomirmex*, *Nylanderia* spp., and *Linemithopa humile* (Mayr) reported by Hickel (1994) to the roots of *Vitis* sp. located within their tunnels (Soria & Gallotti 1986). The remaining developmental stages are the second-instar nymph or cyst, and, depending on species, third instar nymph or cyst while the adults constitute the fourth stage. Males exhibit an unusual but complete metamorphosis with development differing somewhat from that in females having additional prepupal and pupal stages consisting of a mobile first-instar nymph,

an immobile second-instar nymph (cyst), a mobile third-instar nymph or prepupa that constructs a waxy test in which the pupa and adult male develop. Upon ecdysis, the reproductive females and males are devoid of functional mouthparts and do not feed. As a result, males live only a few days, but females may live for several weeks or some even several months.

Development is summarized here for the ground pearls based on observations on *Porphyrophora crithmi* (Goux) (unpublished data), *Eurhizococcus brasiliensis* (Wille) (Foldi 1990), and *Margarodes capensis* Giard and *M. vredendalensis* De Klerk described by DeKlerk (1980, 1980a).

The life cycle of both sexes is represented in Figure 1. The crawlers settle on the roots and begin to feed. Shortly afterwards, the wax glands located at the base of atrium of each thoracic spiracle begins secretion of a broad, long filament comprised of entangled fibrils. Simultaneously, droplets of liquid excreta appear representing the first step in the construction of the protective test. The body continues to enlarge becoming slightly circular to globular. After the first molt, the second-instar nymph or cyst lose their legs and antennae, and continues to feed and grow enclosed within

the test. During the cyst stage, one or two molts may occur, three molts in *Margarodes vitis*. Most species of South African *Margarodes* cysts were generally found at depths of 46-60 cm although some specimens were found at depths of 1.2 m (DeKlerk 1980a). Upon molting, adult females and males migrate from their subterranean feeding sites to the soil surface to mate. Females position themselves at the highest point available on the vegetation or on the soil and emit a sex pheromone to attract males (Foldi 1986). After mating, the females move back into the soil to depths varying from 5 to 30 cm and settle on the roots where they immediately begin to produce large quantities of white, waxy filaments for construction of an ovisac that will cover and protect their body and laid eggs. Oviposited egg numbers normally varied between 150 to 500, with some specimens rarely producing 900 depending on size of the female, over a period of 10 days to several months.

After the last molt, some females of *E. brasiliensis* remain within the cyst and lay their eggs within the thick exuviae surrounded by the test. With the progressive increase in the number of eggs produced, the posterior end of female's abdomen is pushed toward the inside



Figure 1
Distribution of the ground pearls species in the world.

of the body forming an invaginated cavity terminating at the thorax resembling a large marsupial pouch. The most plausible hypothesis for reproduction in encysted females is parthenogenetic. For bisexual reproduction to occur in females enclosed within the thick cyst, males would need to be able to project their long endophallus through the sclerotised anal tube of the cyst to reach the vulva and penetrate the vagina. Such a condition exists in others species, i.e., *Ultracoelostoma assimile* (Maskell) (Coelostomidiidae), a bisexual species where all female instars reside within the hard test, develop from the eggs laid inside the test, and only the crawlers emerge using the anal tube as the exit hole. Although most species of ground pearls have one generation per year, the duration of the development of one genera-

tion is extended in a few species such as *Margarodes vitis* for up to three years (Gonzalez 1983). The number of generations for species of *Margarodes* (DeKlerk 1980), *Eurhizococcus brasiliensis* (Soria & Foldi 1989; Foldi 1990) and *Porphyrophora crithmi* is one per year.

Bisexual reproduction is currently known to occur in *Dimargarodes tanganyicus*, *Heteromargarodes americanus*, *Margarodes prieskaensis*, *Neomargarodes erythrocephalus* *Porphyrophora crithmi*, *P. hamelii*, *P. polonica* and others; however, males have not been observed in many species. Reproduction is parthenogenetic in *Margarodes capensis* and *M. vredendalensis* (DeKlerk 1980, 1980a), with the rare apparition of males in the population in *Margarodes vitis*, and the apparent facultative parthenogenes in *E. brasiliensis*.

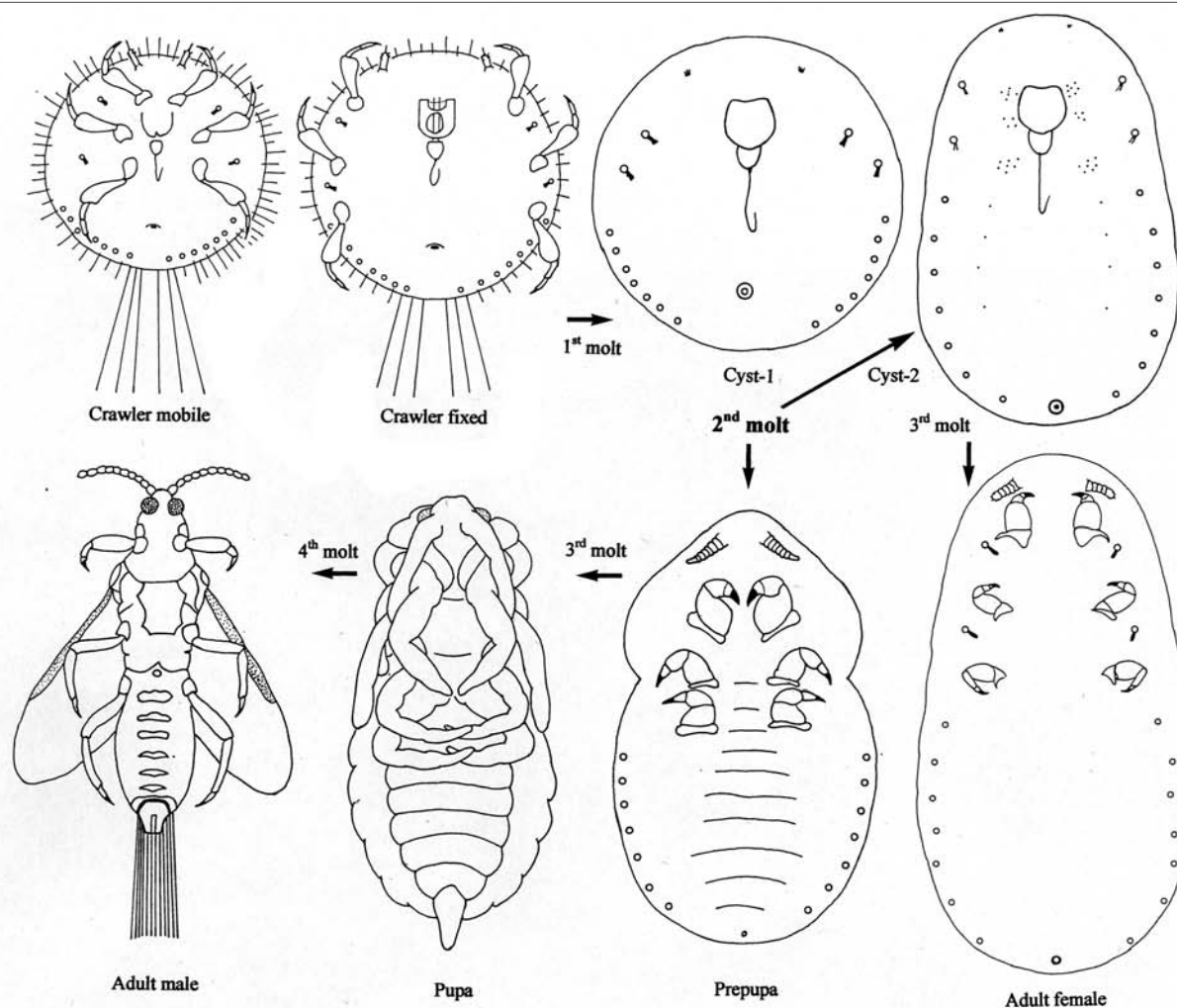


Figure 2
Diagram of the general life history of the bisexual ground pearls.

Test formation

The second-instar nymph or cyst in ground pearls is encased within a separate test constructed by the excreted fluids (Foldi 1997). The designation of “cyst” is also used for all legless 2nd-instar in groups other than ground pearls, but the protective structures are different. In some cyst formers of non subterranean species the cyst protection is assumed from the presence of a strongly sclerotised integument that serves the function of a test (*Kuwania*, *Matsucoccus*), by lateral waxy secretions that originate from spiracular wax glands (*Matsucoccus*); the test may be a complete covering of a glassy secretion (*Xylococcus*, *Xylococcus*) or a thick, hard waxy-resinous mixture (*Cryptokermes*, *Ultracoelostoma*) (Foldi 1977).

The first-instar and the cyst feed on the roots and the extracted nutrients are obtained from vascular tissues or parenchyma cells by the modified mouthparts adapted for piercing and sucking. Mandibles and maxillae are modified into thread-like stylets which interlock into a single tight bundle to form a food canal and a salivary canal. Ground pearls may be monophagous, oligophagous or polyphagous (*Eurhizococcus*, *Margarodes*). The ingested sap is rich in carbohydrates, poor in amino acids and nitrogenous compounds, which are furnished by the endosymbionts housed in the mycetomes. The filter chamber, in which the anterior and posterior part of intestine connects by a modified epithelium, directs the excess sugar and water in the food more directly into the rectum. This excreted waste product is a fluid excreta serves to construct his protective test.

In hypogean species, the test differs in texture and thickness among genera. Surface of these tests are quite-variable; it is rough in specimens of *Margarodes vitis* (Philippi) and *Margarodesia desmieri* Foldi, and smooth as in *Margarodes formicarum* Guilding; the color may be yellow, white yellow, dark brown. The test walls may be very thin as in *Dimargarodes* spp., or *Porphyrophora* spp., or thick and very hard as in *Margarodes* spp., which assures good protection against adverse environmental conditions. Ferris (1919) reported that an adult female of *M. vitis* emerged after 17 years of cyst dormancy.

The modes of construction of this protective test in hypogean species recently was described by Foldi (1997) and is summarised here for *Porphyrophora crithmi* and *P. polonica*. The first instar nymph settles on the host with its head downward and anus upward. After feeding is initiated, droplets of liquid excreta are expelled through the anus in rapid succession and slowly flows around the posterior end of body and becomes solidify. The liquid excreta continues to be regularly extruded and progressively covers its body. The second-instar nymph continues to form more and more new layers originating below the old ones, between the integument

and the older test layers. The layers are sometimes ruptured due to the growth of the nymph and droplets are then fused out onto the external surface. The body gradually becomes covered with about 5-30 layers, each new layer resulting from numerous droplets and each layer composed of an amorphous structure of equal or varying thickness, ranging from 5 to 100 µm. The material used for the test construction emitted by anus, clearly visible under microscope, corresponding a liquid excreta, a slightly viscous substance. The liquid excreta is also used in other scale insect taxa such as the diaspidids, to cement or glue together the waxy filaments of their scale cover (Foldi 1982, 1990).

SYSTEMATICS

Subfamily **Margarodinae** Cockerell 1899

Tribe **Dimargarodini** Jakubski 1965

Genus *Dimargarodes* Silvestri

Dimargarodes Silvestri 1938: 22.

Type species. *Margarodes mediterraneus* Silvestri 1908: 140, by original designation and monotypy.

Generic characters. Adult female broadly oval, sometimes sub-circular, with pleural triangular shaped body extensions bearing setae, spines and pores characteristic of this genus. Antennae 7-8 segmented; segment-I wide, segments-III-VII with basally enlarged setae and fleshy setae mostly in 2 whorls; apical segment globular, smaller. Mouthparts absent; only an invaginated membranous tube present. Each thoracic sternite with apodemes. Prothoracic legs fossorial with a strongly developed femur and a heavily sclerotized strong claw. A group of campaniform sensilla ventro-laterally on trochanter and dorsally on tarsus. Thoracic spiracles with pores in atrium and with a group of perispiracular sensilla around peritreme. Abdominal spiracles in 6 pairs with pores in atrium. Multilocular disc-pores with 2 central loculi of variable size on venter and dorsum. Body and legs sparsely covered with basally swollen setae. Abdominal sternites bearing spines, setae and pores together in distinct groups. Vulva as a simple transverse, narrow fissure. Anus a simple opening; anal tube weakly developed. Immature development occurs underground; first instar-nymph possess only prothoracic legs and with antennae 3-segmented.

Dimargarodes mediterraneus (Silvestri)

Adult female (Fig. 3)

Common name: mediterranean pearl scale,
perle de terre méditerranéenne

Margarodes mediterraneus Silvestri 1908: 140.

Dimargarodes mediterraneus; Silvestri 1938: 22.

Coccinonella mediterraneus; Lindinger 1954: 615.

Dimargarodes mediterraneus; Jakubski 1965: 91.

Material examined. Lectotype of adult female and 2 Paralectotypes designated here from material of Silvestri bearing inscription of "type". Italy: Bevagna (Umbria), on roots of *Cynodon*, IX-1906, Lectotype depository: Dipartimento di Entomologia e Zoologia Agraria (DEZA), Università di Napoli Federico II, Portici, Italy.

France: Saint Guilhem le Désert (Hérault), on roots of *Asphodelus microcarpae*; July 1996, I. Foldi rec.; Port-Cros Island (îles d'Hyères) on roots of *Cynodon dactylon*, August 1997, I. Foldi rec. MNHN.

Live appearance. Body broadly oval, clear yellow color.

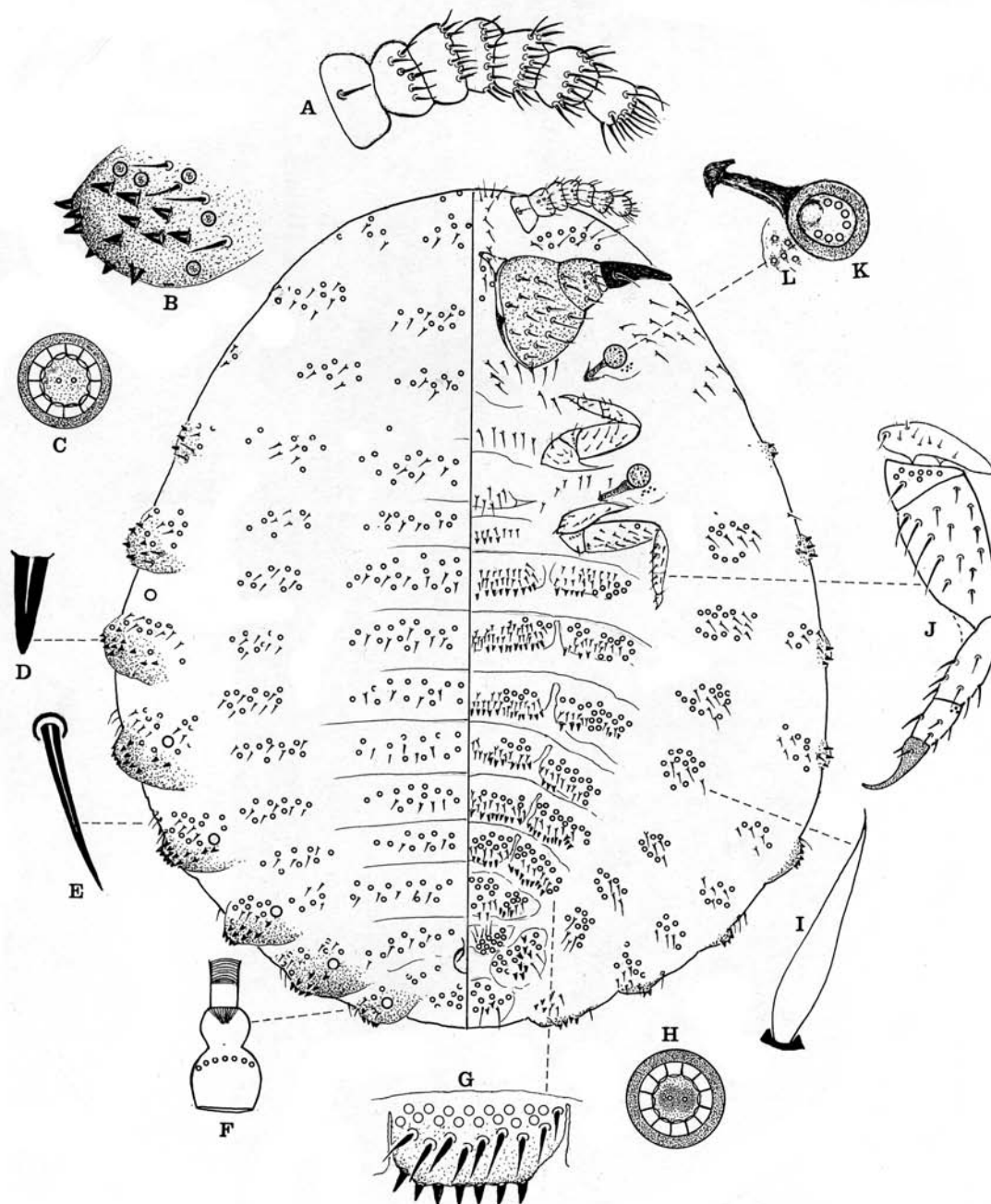


Figure 3

Adult female of *Dimargarodes mediterraneus* (Silvestri). A, antenna. B, detail of a pleural extension. C, dorsal multilocular disc pores. D, spine. E, dorsal seta. F, abdominal spiracle. G, detail of a ventral sternite bearing multilocular disc-pores, spines and flagellate setae in distinct groups. H, ventral multilocular disc-pore. I, basally swollen flagellate seta with concave socket. J, metathoracic leg. K, thoracic spiracle. L, perispiracular sensilla.

Mounted specimens. Body broadly oval, subcircular, 3.5 mm long, 2.5-3.3 mm wide. Margin with characteristic pleural body extensions. Abdominal spiracles numbering 6 pairs. Few setae, flagellate setae basally swollen with a constricted base and with a broad concave socket on body and legs; spines, setae and disc-pores together with distinct groups on abdominal sternites. Multilocular disc-pores with about 12 peripheral loculi and 2 central circular loculi.

Venter. Antennae 7-segmented, 500 μm long, antennal segments more and less equal in length, slightly tapering toward apex. Segment-I about 200 μm wide with only one basally swollen seta; segment-II with few setae and 6 sensilla; segments III-VI with basally swollen flagellate setae more and less in two whorls; apical segment globular, 70 μm long, 70 μm wide with a group of 12-15 mostly blunt flagellate setae, 30 μm long, and some basally swollen setae 70 μm long. Eyespots absent. Mouthparts absent, only a membranous mouth tube present. Legs small in comparison to body size, sparsely covered with basally swollen setae. Prothoracic legs strongly developed. Coxa with a few short setae. Trochanter+femur 700 μm long, 600 μm wide, each trochanter with 7 campaniform sensilla plus some short setae on each side; each femur laterally with numerous setae, 10-70 μm long. Tibia 200 μm long, 240 μm wide with numerous setae 50 μm long, dorsally fused with tarsus. Tarsus 50 μm long, 180 μm wide, fused with claw, dorsally with 5-6 campaniform sensilla in 2 rows. Claw 400 μm long, with one pair of short digitules. Meso and metathoracic legs same shape and size. Trochanter with 5-7 campaniform sensilla and 4 setae, 60 μm long and 10-12 short setae, 20 μm long. Femur 250 μm long, 150 μm wide ventrally with a group of about 4 setae, 70 μm long and laterally with 4-5 short setae, 40 μm long. Tibia 150 μm long, 60 μm wide with 3 setae laterally, 50-60 μm long. Tarsus 140 μm long, 50 μm wide, with 2 setae, 50 μm long on each side, dorsally with 6 campaniform sensilla. Claw curved, longer than tarsus, 220 μm long, 40 μm wide at its base, with a pair of short digitules, 30 μm long.

Thoracic spiracles peritreme with thick rim 70 μm wide, each spiracle with 7-8 multilocular disc-pores with 2 central loculi in atrium. A group of 5 perispiracular sensilla near of peritreme. Each thoracic sternite with a median intersegmental apodemes. Abdominal spiracles numbering 6 pairs, with peritreme 25 μm wide with about 11 multilocular disc-pores with 2 central loculi in atrium.

Flagellate setae basally swollen with a constricted base and with a broad concave socket on body and legs, each about 70-100 μm long; some shorter setae on coxae. Spines on abdomen, absent on thorax.

Weakly sclerotized sternal plates on abdominal segments in median and submedian area; mostly three plates in a row with median longer than lateral plates. Each plate has distinctly divided groups: 1 row of spines, each about 40 μm long, 1-2 rows of strong setae, each 70 μm long, and several rows of multilocular pores. Multilocular disc-pores, each about 10 μm in diameter, with a well sclerotized outer rim, with 12 peripheral loculi and 2 central circular loculi. These disc-pores distributed also in small groups, associated with setae, in submedian and submarginal horizontal lines on abdomen.

Margin. Margin with characteristic pleural extensions, dimensions varying between 100-250 μm long and about 100-350 μm wide, localized on metathorax and abdomen. Each extension bears strong spines, setae, and multilocular pores, all same type as described on Venter -

Dorsum. Flagellate setae basally swollen with a concave socket, 70 μm long, associated with same type of pores as venter, distributed in medial and submedial horizontal lines on body. Anus sub apical, anal tube faintly developed without pores.

Biology. Crawlers and cysts on roots of grass or asphodeles (Liliaceae). Reproduction apparently parthenogenetic, males were never observed. Females emerge in South of France on June to August and secrete long waxy filaments, producing an ovisac which includes both the female and eggs.

Host plants. *Asphodeles microcarpae*, *Cynodon* spp., *Cynodon dactylon*.

Distribution. Palaearctic: France, Greece, Italy, Spain, Turkmenistan and Ukraine.

First instar nymph

Material examined. Italy: Bevagna (Umbria), on roots of *Cynodon*, IX-1906, Silvestri rec.

Mounted specimen. Newly hatched first instar characterised by absence of meso and metathoracic legs which is a major character of taxonomic significance. Body slender, elongate, 680 μm long, 180 μm wide; derm without pores and setae.

Antennae 3-segmented, total length about 80 μm : scape naked; segment II with 2 short, stout setae; terminal segment well developed, obviously longest than others, turned obliquely outwards, about 45-50 μm long, 25 μm wide with 2 fleshy setae, 20-25 μm long, with 3 short setae, and with about 4-6 stouter setae, 40 μm long. Labium not discernable. Thoracic spiracles with peritreme 5-6 μm wide; each spiracle with one perispiracular sensilla near of peritreme. Abdominal spiracles in 6 pairs with peritreme 5-6 μm wide. Both thoracic and abdominal spiracles with sclerotised base of atrium including a network of microopenings emitting waxy secretions. Prothoracic legs measurements: coxa 35 μm long, 30 μm wide; trochanter + femur 40 μm long, 30 μm wide; ventrally with 2 short setae; tibia 6 μm long; tarsus 6 μm long; claw broad at its base, 12 μm long, and with 2 short acute digitules about 5 μm long. A short tube anal on posterior end of abdomen.

Genus *Heteromargarodes* Jakubski

Heteromargarodes Jakubski 1965.

Type species. *Heteromargarodes americanus* Jakubski 1965: 85, by monotypy.

Heteromargarodes americanus Jakubski.

Deuteromargarodes americanus Jakubski 1965: 88. *Nomen nudum* by Jakubski 1965: 88.

Material examined. Lectotype adult female designated here. USA: Wyoming, Powell, 24 September 1949, H.S. Beaudoin rec, host plant unknown. Type depository: USNM, 49 1727, USNM n°: 2008921.

Adult female (Fig. 4)

Mounted material. Body broadly oval, 8 mm long, 7 mm wide; derm covered by long flagellate setae, dorsum and venter with broad naked intersegmental zones.

Venter. Antennae 8 segmented, total length 645 μm ; segment-I longer and wider than others, 200 μm long, 250 μm

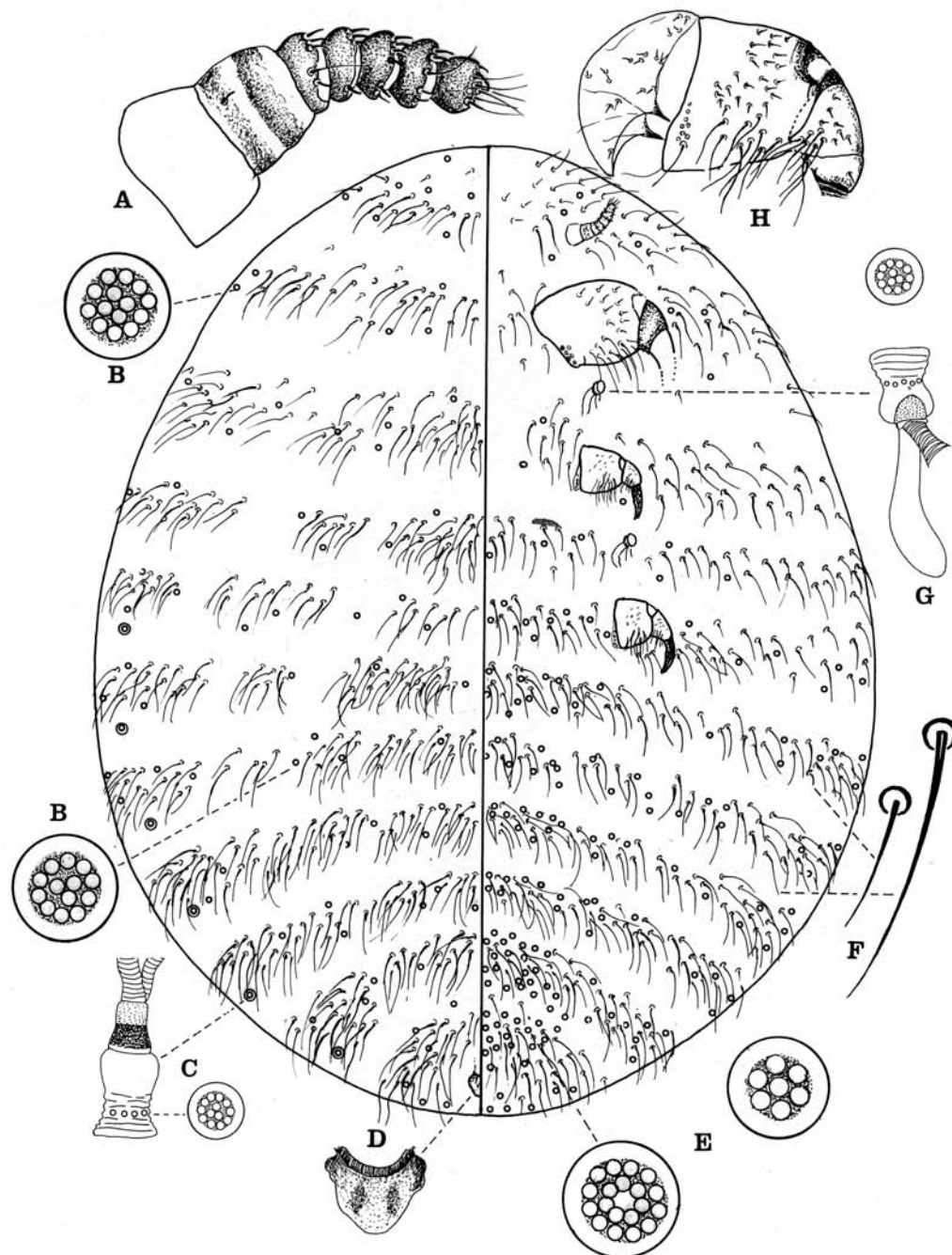


Figure 4

Adult female of *Heteromargarodes americanus* Jakubski. A, antenna. B, dorsal multilocular disc-pores. C, abdominal spiracle. D, anal opening with an strongly sclerotised structure. E, ventral multilocular disc-pores. F, ventral flagellate setae. G, thoracic spiracle. H, prothoracic leg with claw cut off.

wide, naked; segment-II 70 µm long, 185 µm wide, with one short seta 10 µm long; segment-III 60 µm long, 130 µm wide, with 4 fleshy setae, 35 µm long, and one long seta, 125 µm; segments IV-VII 60 µm long, 120 µm, each with fleshy setae, 35 µm long, plus one long seta, 140 µm long on segment VII; terminal segment 75 µm long, 100 µm wide, with 6 fleshy setae, 30-35 µm long and 6 hair-like setae, 100-110 µm long.

Eyespots absent. Mouthparts absent. Prothoracic legs fossorial; lectotype's claw cut off on slide; coxa with a strong apodeme 590 µm long, 220 µm wide; trochanter narrow with 3-5 sensilla; femur 950 µm long, 800 µm wide, dorsally with about 16 short setae, 20-25 µm long, laterally with few setae, 30 µm long, ventrally with about 6-8 setae 200-270 µm long, articulating with tibia by 2 strongly sclerotised process; tibia fused with tarsus, both strongly sclerotised; tibia, short, 150 µm long, 370 µm wide ventrally with a group of hair-like setae, 350 µm long; tarsus, 125 µm long, 300 µm wide, with a group of hair-like setae. Metathoracic legs measurement: coxa 500 µm wide with about 14-16 short setae, 20-30 µm long; trochanter narrow with about 8-9 sensilla and 1 or 2 short setae; femur 270 µm long, 360 µm wide, dorsally with about 16-18 short setae, 20 µm long, laterally with a few setae, 25-30 µm long and, ventrally with a group of 8-10 setae, 150-210 µm long; tibia fused with tarsus, both strongly sclerotised tibia 210 µm long, 90 µm wide, dorsally with about 10 short setae, 20 µm long and, ventrally with a group of 4 setae, µm long; tarsus 180 µm long, 150 µm wide, dorsally with 4 sensilla, ventrally with 4 setae, 50 µm long; claw 290 µm long with 2 setae-like tarsal digitules.

Thoracic spiracles, with unsclerotised peritreme, atrium 100 µm long, 70 µm in diameter, with a strongly sclerotised dome-shaped structure basally and, with a circularly folded, reduced diameter medially; atrium with about 20-22 circular or oval multilocular pores placed in 2 rows distally, each pore with about 18 loculi in outer ring and 2-4 in inner ring, with a strong apodeme, 230 µm long.

Multilocular disc-pores, 10-12 µm in diameter, with a thin rim and, with about 7-19 loculi of same size or 8-12 loculi in a outer ring and 2-4 wider loculi in inner ring; pores very sparsely distributed on head and thorax, denser toward posterior V-VIII abdominal segments.

Flagellate setae, 280-500 µm long on head, thorax, denser on abdomen, rather 400-550 µm long in transvers rows, 4-5 setae wide: short setae, 25-30 µm long, scattered on whole ventral surface.

Dorsum. Abdominal spiracles in 6 pairs, each atrium with about 50 µm in diameter, except last one, 40 µm; atrium medially with reduced diameter, circularly folded, with a row of 6-8 multilocular pores; atrium basally strongly sclerotised, followed by a short atrial tube 20 µm wide, 25-30 µm long, and finally a trachea. Multilocular disc-pores, flagellate setae and short setae same types than described on Venter - Anal tube simple with lateral apodemes; derm with raised bare patches.

Host plant. Unknown.

Distribution. Nearctic: USA: Wyoming, Powell.

Tribe MARGARODINI Cockerell 1899

Genus *Margarodes* Guilding 1829

Margarodes Guilding 1829: 118.

Type species. *Margarodes formicarum* Guilding 1829: 119 by original designation.

Margarodes (Sphaeraspis) Giard 1894: 712. Type species: *Margarodes vitium* Giard. (syn. in Morrison & Morrison 1966: 186).

Margarodes (Sphaeraspis) capensis Giard 1897: 685.

Sphaeraspis Fernald 1903: 28.

Sphaeraspis vitis (Philippi): Jakubski 1965: 111. New synonymy.

Based on the current morphological observations and redescription of *Sphaeraspis vitis* (Philippi), the genus *Sphaeraspis* is considered a new junior synonym of *Margarodes*.

Generic characters. Adult females broadly oval, size varying length 2.5-8 mm, 4-5 mm wide; derm membranous, flexible. Antennae 7 or 8 segmented, most segments wider than long with basally swollen setae and fleshy setae, usually distally in one whorl; segment I obviously wider; segment II short; terminal segment longer and narrower with long flagellate setae and fleshy setae. Presence of most spines bluntly pointed, longer on anterior end and shorter on posterior end of body, a major character of taxonomic significance; short setae among long hair-like setae, more numerous on abdomen; flagellate setae basally swollen, with a concave socket on body and legs. Prothoracic legs fossorial with a strongly developed femur and with a heavily sclerotized strong claw, adapted for digging and much larger than meso- and metathoracic legs; a group of campaniform sensilla on trochanter; tarsus and claw fused, not flexible; claw without denticle and with 1 or 2 pairs of basally swollen digitules. Abdominal spiracles in 7 pairs. Thoracic spiracles with circular peritreme, and an obviously long straight apodeme. Both, thoracic and abdominal spiracles with pores in atrium. A group of perispiracular sensilla near of peritreme. Thoracic sternites with poorly developed apodeme. Mouthparts absent, only an infolded membranous area present. Multilocular disc-pores of two type; - one circular with 2 rings of loculi, each outer ring with numerous small loculi, each inner ring with less number of large loculi, and without a central loculus, only with a bright zone; other oval, each outer ring with numerous small loculi and with two large bilocular centre. Vulva as a transverse fissure. Anal opening postero-dorsal.

Cyst or second-instar nymph apodous feeding instar on roots enclosed in a test hard, shiny, slightly iridescent.

First instar nymph with antennae 4-segmented, terminal segment globular near as long than other segments together and 3 terminal segments set strongly obliquely.

Margarodes formicarum Guilding 1829

Common names: ground pearl, perle de terre

Adult female (Fig. 5)

Margarodes formicarum Guilding 1829: 119.

Porphyrophora margarodes Burmeister 1835: 79.

Coccionella formicarum Lindinger 1954: 615.

Margarodes formicarum: Jakubski 1965: 153.

Material examined. Bermuda: Paget Parish, on roots of *Acalypha* sp., 4 July 1965, I.W. Hughes rec., USNM 65-14333. Antigua, BM 1987-176; West Indies. Montserrat, BM, 1940 / 80. Puerto Rico: Manati, on pineapple, 15-V-1987, A. Pantoja rec., USNM 87 4822; 25-87, 28-87. Chile: 1914, Girard det. MNHN:7805/1.

Mounted specimens. Body broadly oval, 6 mm long, 5 mm wide; body with segmentation well visible. Setae sparsely distributed on dorsum, spines on margin, particularly on abdominal sternites. Abdominal spiracles in 7 pairs.

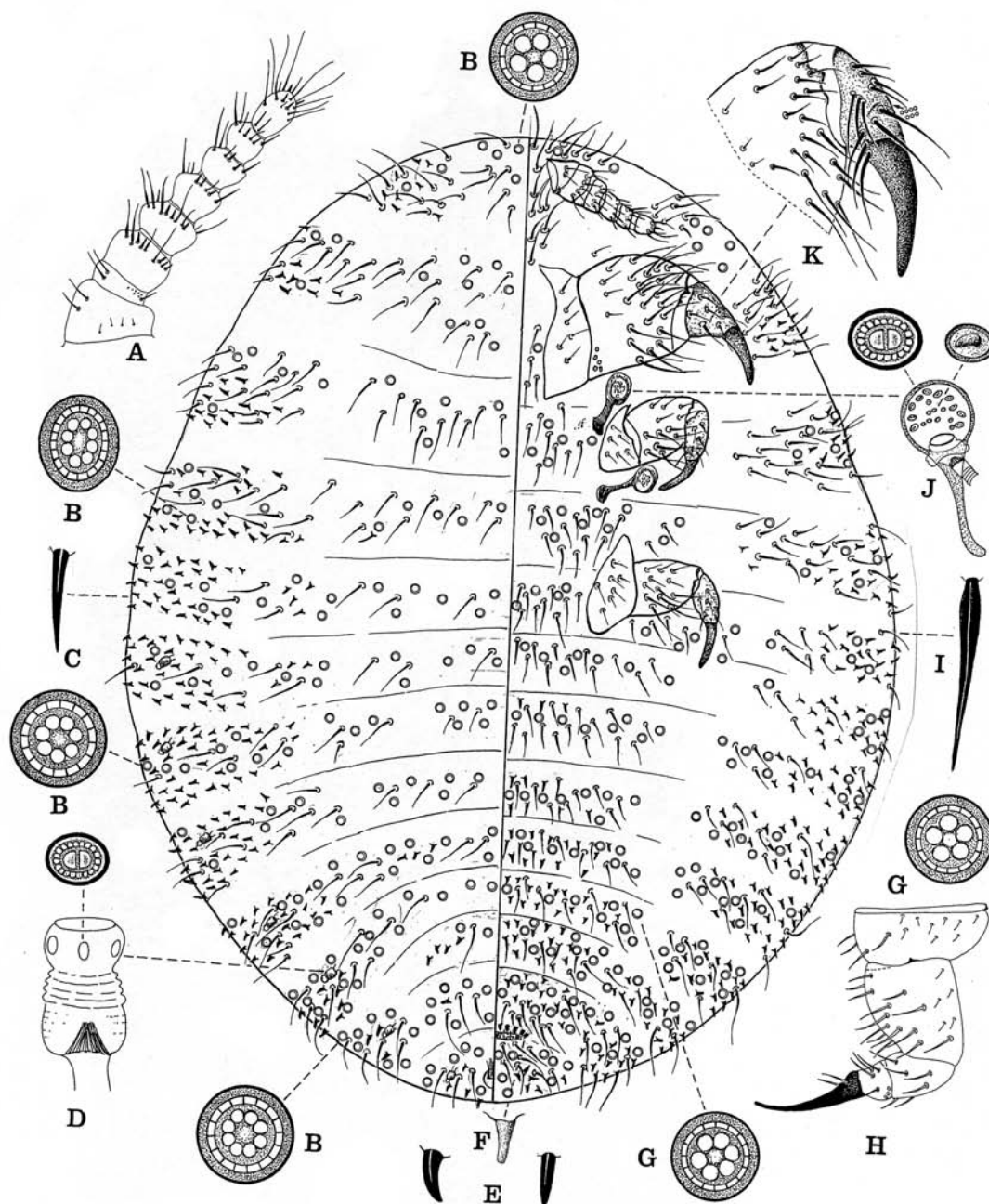


Figure 5

Adult female of *Margarodes formicarum* Guilding. A, antenna. B, multilocular disc-pores with bright central zone. C, dorsal seta. D, abdominal spiracle, spiracular atrium with multilocular disc-pores with 2 large central loculi. E, dorsal spine. F, finger-like structures before vulva in a semicircular pattern. G, ventral multilocular disc-pores. H, metathoracic leg. I, ventral seta. J, thoracic spiracle with same disc-pores in atrium than abdominal ones plus small pore-like structures. K, prothoracic leg fossorial with strongly developed femur and claw.

Venter. Antennae 7-8-segmented, 700-850 μm long; antennal segments short, wider than long, stout, gradually tapering toward apical segment; segment I well developed, greatest length 150 μm , 190 μm wide, with 2 setae, much broader than remaining segments; segment II poorly developed obviously shorter, 50 μm long, and 130 μm wide, with 2 setae, and with 6-8 small sensilla; segments III to VII with an whorl of setae constituted by basally swollen flagellate setae, 70-90 μm long, and fleshy setae 20-30 μm long; terminal segment with rounded apex, 90-110 μm long, 75-80 μm wide with 8-12 basally swollen flagellate setae, 80-150 μm long, 6-8 stout fleshy setae, 25-35 μm long and 2-4 short setae 20 μm long. Eyespots absent. Mouthpart absent, only a membranous infolded area present.

Thoracic spiracles, with perimetre 100-110 μm wide with about 7-11 multilocular disc-pores with bilocular centre, plus about 6-9 unilocular pores in atrium, and with a well developed, straight apodeme 170-200 μm long; each spiracle with two small perispiracular sensilla, rarely only one, on a weakly sclerotized plate on the posterior side of peritreme. Thoracic sternites apodeme poorly developed. Prothoracic legs fossorial with a strongly developed femur and with a heavily sclerotized strong claw. Prothoracic legs measurements with setal and pore data: coxa μm long, μm wide, trochanter+femur 650-700 μm long, 650-800 μm wide, dorsally and dorso-laterally with about 12-14 setae 40-100 μm long, and ventrally with about 15-20 flagellate basally swollen setae 160-250 μm long, with a constricted base, and with a concave socket; presence of about 5-7 campaniform sensilla signaling trochanter and delimiting it from femur; tibia 150-180 μm long, 180 μm wide, with about 8-12 flagellate basally swollen setae about 100-140 μm long; tarsus and claw fused; tarsus with about 6 same type of setae as tibia and with 4-6 sensilla dorsally; claw strongly developed, 370-420 μm long, 100-130 μm at base, tapering gradually to a 30-35 μm wide point, with 2-3 pairs of basally swollen digitules, about 200-240 μm long.

Metathoracic leg measurements with setal and pore data: coxa 500 μm wide, with 4-5 setae basally, 90-100 μm long and numerous setae apically 20-45 μm long; trochanter+femur 340-400 μm long, 300 μm wide; trochanter with about 7 sensilla ventro-laterally and with a few setae 40-100 μm long; femur with about 6-9 basally swollen setae, 100-130 μm long, and with shorter setae 25-40 μm long dorso-laterally; tibia 170-200 μm long, 100-120 μm wide with basally swollen setae 60-90 μm long; tarsus 80 μm long fused with claw, dorsally with 4 sensilla and 4-6 basally swollen setae, 80-100 μm long; claw 240-270 μm long with a pair of digitules about 120-130 μm long.

Long flagellate basally swollen setae 100-120 μm long in transverse row medially on abdomen, 1-2 setae wide, sparsely on head and margin. Spines buntly pointed 30-35 μm long, 12-13 μm wide at base, in transverse rows medially on abdomen associated with pores and setae, progressively denser to posterior extremity, 3-4 setae wide per segment, and, becomes shorter, about 25 μm long, towards posterior extremity; spines also distributed on margin, and submargin throughout of body.

Multilocular disc-pores, about 13-15 μm in diameter, with a wide sclerotized rim, each pore with 2 rings of loculi, each outer ring with about 16-28 small loculi, and each inner ring with 5-8 large loculi, lacks a central loculus only with a bright

zone central; these pores, distributed on margin, particularly medially on abdominal sternites, denser towards genital area. Vulva, about 360 μm wide, as a transverse fissure surrounded by a group of setae, 80-100 μm long. Before vulva, in a semicircular pattern, a group of 15-17 finger-like structure with flattened apex, 35-40 μm long, and 10-13 μm wide, present.

Dorsum. Abdominal spiracles in 7 pairs, much smaller than thoracic ones, with perimetre 30 μm wide, and with 5-6 multilocular oval pores with bilocular centre in atrium. Multilocular disc-pores same type than venter, sparsely distributed in an uneven row, 1-2 pore wide per segment. Dorsum moderately setose with long hair-like setae on head (110-160 μm) and extremity of abdomen (180-230 μm); hair-like setae 90-110 μm long, in a sparse, uneven row 1-2 setae wide per each segment. Spines, 25-35 μm long, on margin from anterior to posterior end of dorsum, absent medially and submedially. Anal opening postero-apicale with a weakly developed internal tube.

Biology. Immatures feeding on roots of plants growing of preference for sandy or loose soil. *M. formicarum* probably parthenogenetic species, males never found.

Host plants. *Acalphia* roots, *Citrus*, *Saccharum officinarum*.

Distribution. Neotropical: Chile, Antigua, Bahamas, Barbados, Grenadines, Montserrat, Puerto-Rico, Virgin Islands: Santa Cruz, Leeward Island; Redonda, Saint Kitts, Windward Islands.

First-instar nymph (Fig. 6)

Mounted material. Elongate, parallel sides, rounded anteriorly 680-730 μm long, 200-210 μm wide, dorsum and venter with few small setae, dermal pores absent.

Venter. Antennae 4-segmented, 80-85 μm long; 3 terminal segments set strongly obliquely to the first. Segment-I about 20-22 μm long, 20-22 μm wide, segments II and III smaller; terminal segment globular, 42 μm long, 32 μm wide and bearing a group of setae: 4 short setae, 25-30 μm long, 5 longest setae 40-45 μm , 3 stout fleshy setae, 15-20 μm long, 1-2 longest truncated, stout setae and, 2 coeloconic sensilla. Eyespot absent. Mouthparts present, labium with 6 or more setae. Thoracic spiracles with a peritreme about 8-10 μm , and with a cylindrical corrugated atrium, about 20-25 μm long; its base strongly sclerotised with numerous pores and cuticular papillae; one perispiracular sensilla present. Prothoracic legs about 130-140 μm long with very few setae. Prothoracic legs measurements: trochanter + femur 45 μm long, 30 μm wide; trochanter with 2 sensilla on each face plus 2 setae; femur broader than in meso and metathoracic legs; tibia 30 μm long, 10 μm wide with 2 setae; tarsus 22 μm long, 8-10 μm wide, dorsally with a single, round sensilla, and with one seta; claw almost straight, sharply pointed, 10-12 μm long apparently with a pair of minute digitules. Mesometathoracic legs slender and with very few setae, femur+tibia each with 2 setae, tarsus with only one seta, and with a sensilla; claw long, about 20 μm , straight apparently without digitules. Head and thorax with few small setae, 10-15 μm long, abdomen

with 2-4 setae similar; posterior segment with a pair of long, about 230-250 μm , caudal setae. A median finger-like structure, about 20 μm long, on last abdominal segment. Anal opening with a small anal tube posteriorly.

Dorsum. Abdominal spiracles in 7 pairs varying in size; first spiracles about 15 μm long, and 2-3 μm wide, following spiracles about 10 μm long. Head and thorax with few setae, 10-12 μm long, plus a pair of 50 μm long setae between antennae and on prothorax; abdominal segments also with 2 setae about 20-25 μm long in a transverse row, and 4 setae on VII and VIII abdominal segments, last segment with a pair of stouter and longest, about 30 μm long setae.

Second-instar or Cyst (Fig. 7)

Apodous second-instar feeding on roots, included into a hard, thick test constituted by several overlapping layers of hardened exuded liquide excreta. The test with shape and size variable, 6-8 mm long, 3-4 mm wide, shiny, golden yellow, iridescent, bronze tint, always with a brilliant metallic lustre, with about

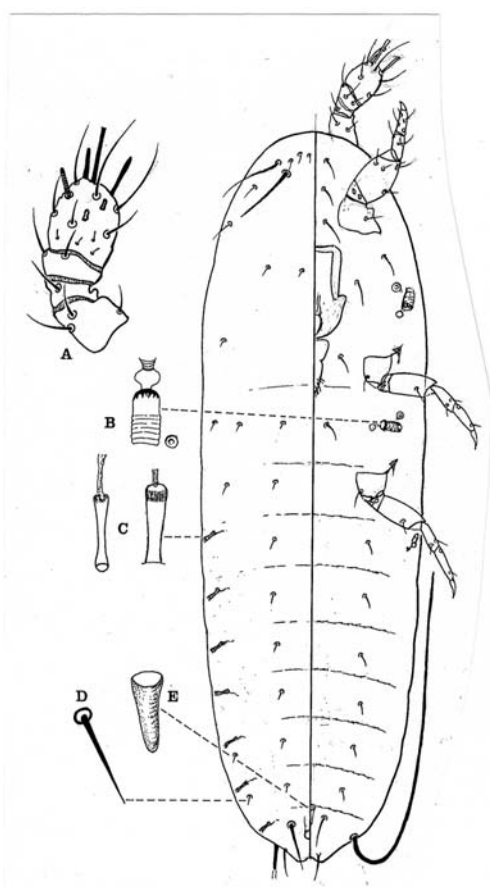


Figure 6
First-instar nymph of *Margarodes formicarum* Guilding. A, antenna. B, thoracic spiracle. C, abdominal spiracle. D, dorsal seta. E, a single ventro-medial finger-like structure.

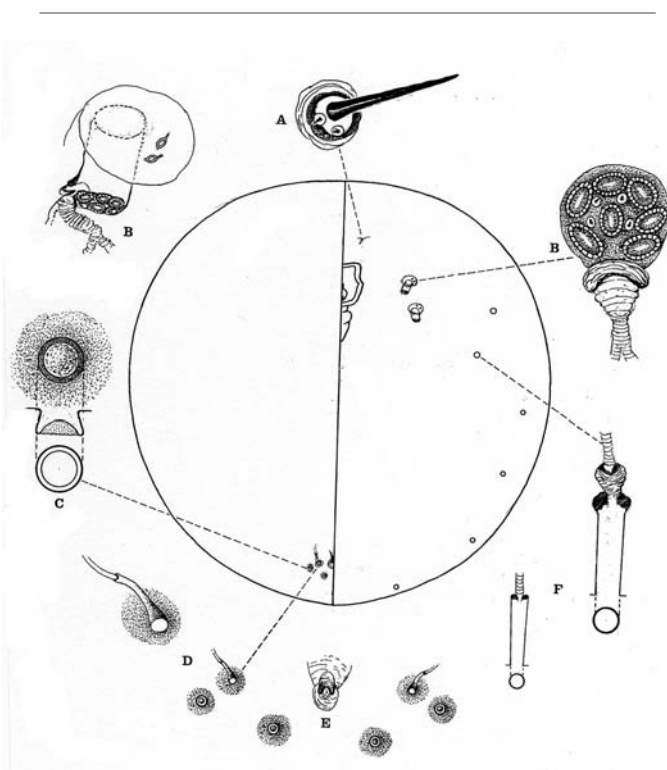


Figure 7
Cyst of *Margarodes formicarum* Guilding. A, antenna. B, thoracic spiracle with disc-pores in base of atrium and with 2 perispiracular sensilla near of perimetre. C, cicatrice. D, last abdominal spiracle, perimetre on a sclerotised zone. E, anal region with cicatrices, abdominal spiracle and anal opening. F, abdominal spiracle.

6 distinct protrusions. Cysts removed from tests almost globular, 5-6 μm in diameter, oval or irregular shape with few morphological structures.

Venter. Antennae consist of a small protrusion with a deep pit with emerging a single fleshy seta, sometimes slightly bifurcated at apex. Labium well developed, conical. Thoracic spiracles well developed, with a peritreme 35-40 μm wide, open within a sclerotized, large, rather circular well visible cupola-like structure; with 2 perispiracular sensilla near of peritreme; atrium cylindrical, 65-75 μm long, with 5-9, usually 7 at base, oval multilocular pores with numerous, 18-20, small loculi in a single outer ring and biloculate center; 6 of these oval pores arranged in a outer ring, and with 4 unicular pores bearing a small structures at center, and again one oval multilocular pore at center. Abdominal spiracles in 7 pairs varying in size; spiracles I and II with perimetre about 20 μm wide, and with about 6 pores in atrium, spiracles III to VII with perimetre about 7-8 μm wide and without pores; first spiracle site positioned dorsad, last spiracle opens in a circular sclerotized area.

Dorsum. Anal opening, heavily sclerotized, about 20 μm wide on a conical structure; anal area with 3 or 4 cicatrices, about 10-12 μm in diameter, located in deep cavities; cicatrices surrounded by circular sclerotized area.

Margarodes vitis (Philippi)
 Common name: grape ground pearl,
 margarodes de la Vid

Heterodera vitis Philippi 1884: 226. Described as a Nematoda.
Margarodes vitium Giard 1894: 126. Giard recognized that it was a scale
 insect. (syn. in Jakubski 1965: 111).

Margarodes trilobitum Reed 1895: 86 (syn. in Morrison, 1928: 227).
Margarodes (Sphaeraspis) vitium Giard 1894: 712.
Sphaeraspis vitis (Philippi) Jakubski 1965: 111.
Margarodes vitis (Philippi), Gonzalez et al. 1969: 93.
Margarodes vitis (Philippi), Gonzalez 1983: 27.

Adult female (Fig. 8)

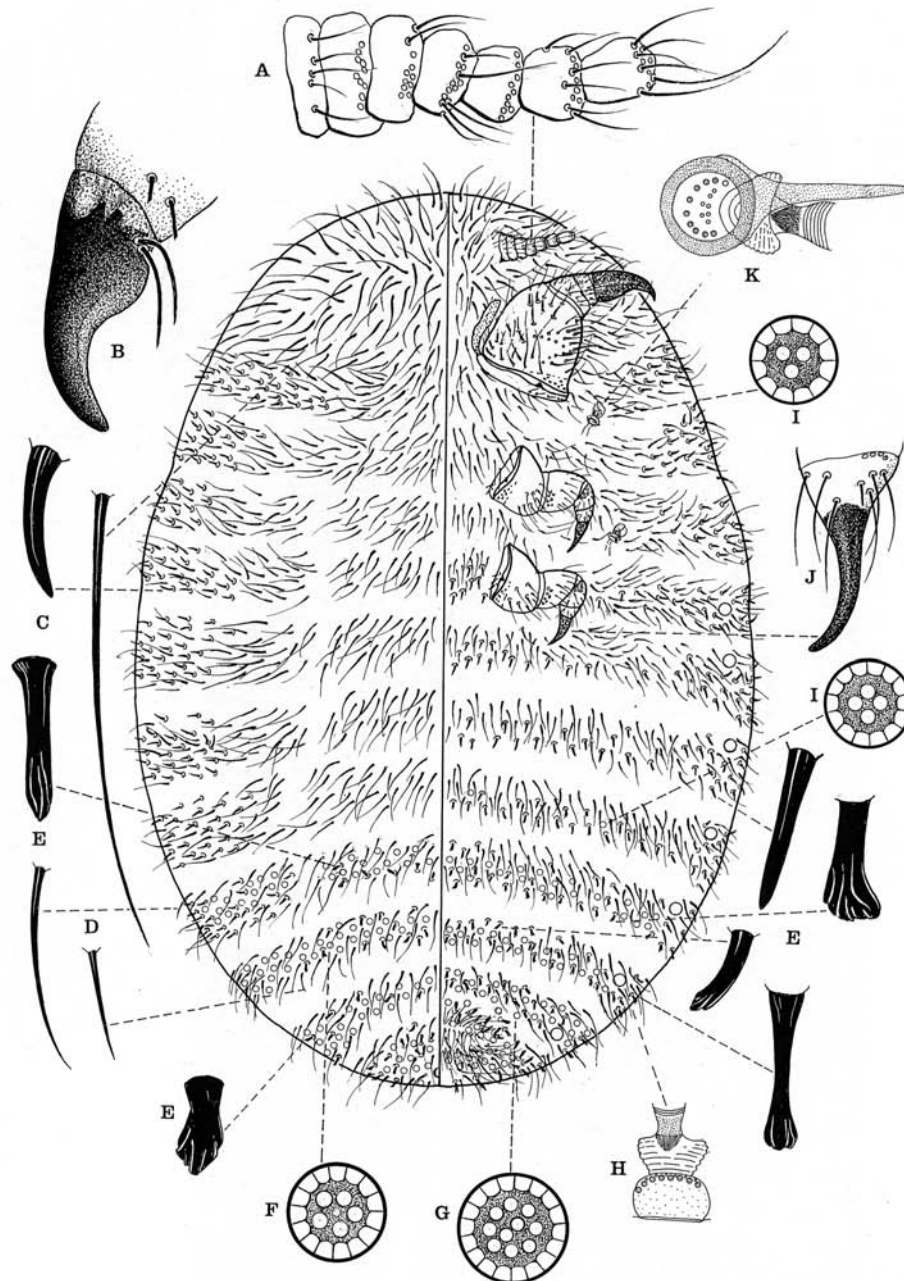


Figure 8

Adult female of *Margarodes vitis* (Philippi). A, antenna. – B, claw of prothoracic leg. C, dorsal and ventral spines. D, dorsal and ventral setae. E, apically and irregularly enlarged spines on both surface. F, dorsal multilocular disc-pores. G, multilocular disc-pore on posterior abdominal segments. H, abdominal spiracle. I, multilocular disc-pore on venter. J, tarsus and claw of metathoracic leg. K, thoracic spiracle.

Material examined. Chile: near Santiago, locality Buin, on roots of grapevine; 1893; Immatures from Chile sent by Lateste to Giard. The adult female was obtained from the cyst stage, processed and mounted on slides by I. Foldi in 1975.

Chile: Santiago, Metropolitan region, on *Vitis vinifera*, 14 March, 1980, Barria rec.; 1 slide from the collection of Lateste (1919) sent by Ferris.

Live specimen. Female white-yellow color, densely covered by hair-like setae.

Mounted specimen. Body broadly oval, 6-8 mm long, 3-5 mm wide.

Venter. Antennae 8 segmented, total length 750-800 μm long, antennal segment ring shaped, wider than long with setae located apically in a single whorl, terminal segment with 4 long setae and numerous fleshy setae. Eyes and mouthparts absent. Thoracic spiracles with peritreme 100 μm wide, with a curved short apodeme, with about 15-20 multilocular disc-pores in atrium; each disc-pores with about 12 loculi in outer ring and 3 loculi in inner ring. About 2 perispiracular sensilla on a small plate. Abdominal spiracles in 8 pairs identical, with peritreme 20 μm wide and with about 8-10 multilocular disc-pores in atrium. Legs short and robust. Prothoracic legs fossorial; coxa with 6-8 long seta, trochanter 3-5 sensilla on each side femur 500 μm long, 500 μm wide with long setae, about 200 μm long; tibia 150 μm long, 100 μm wide with very few setae; tarsus short dorsally fused with tibia but not ventrally; claw strongly sclerotised, curved, 250 μm long with 2 pairs of digitules. Setae long, about 240-260 μm long on head, prothorax and along margin of body. Setae shorter, about 100-150 μm long throughout of venter. Spines numerous, straight and enlarged apically on metathorax and abdomen, distribution progressively denser toward end of abdomen. Multilocular disc-pores, 10-12 μm wide, with 14-16 loculi in outer ring and 4-7 (5) larger loculi in inner ring from on segment III and increasing in number toward the posterior end of abdomen. Larger multilocular pores, 14-16 μm in diameter, with 18 loculi in outer ring, 8 larger loculi in intermediate ring and 2 large loculi in inner ring.

Dorsum. Setae long, about 300-330 μm long, on head and prothorax, and throughout on median and sub-median regions. Shorter setae, 150 and 250 μm long on the along margin. Spines absent on head, numerous and multiple types on dorsum: curved, straight or apically irregularly enlarged (clavate) denser to last segments abdominal. Multilocular disc-pores same then on venter in transversal band, 3-4 pores wide, on last four abdominal segments.

Host plants. *Coletia spinosissima*, *Opuntia*, *Vitis vinifera*.

Distribution. Neotropical: Argentina; Brazil: Rio Grande do Sul, Santa Catarina; Chile; Paraguay; Uruguay; Venezuela.

Economic importance. A serious pest of grapevine in South America, particularly in Chile (Gonzalez 1983).

Genus *Promargarodes* Silvestri 1938

Promargarodes Silvestri 1938.

Type species. *Promargarodes sinensis* Silvestri 1938: 22.

Generic characters. Body broadly oval. Prothoracic legs fossorial, claw with 1-2 protrusions at its base which is a significant taxonomic character. Each trochanter and tarsus with a group of sensilla. Antennae 8-segmented, each segment with basally swollen setae and fleshy setae located rather in two whorls. Mouthparts absent. Body and legs sparsely covered with basally swollen flagellate setae, each seta with wide basal concave socket. Presence of spines or spine-like setae on body. Multilocular disc-pores 2 types: disc-pores usually with numerous loculi in outer ring and few and larger loculi in inner ring; disc-pores with numerous small loculi in outer ring and 2, 3 or 4 very large loculi in inner ring. Thoracic atrium with multilocular disc-pores with a bilocular center and simple pores; a small group of perispiracular sensilla and a small seta near of peritreme. Abdominal spiracles in 6 pairs.

Promargarodes sinensis Silvestri 1938

Adult female (Fig. 9)

Material examined. Lectotype and 2 paralectotypes designated here from material of Silvestri labelled "Typus". China: Peitao, Foochow, Fukien, Peikuan, host plant no reported, 1924-1925, Silvestri rec. Lectotype depository: Dipartimento di Entomologia e Zoologia Agraria (DEZA), Università di Napoli Federico II, Portici, Italy.

Mounted specimen. Body broadly oval, 2.2-2.5 mm long, 1.1-1.3 mm wide, derm membranous with dense alveolar surface, weakly sclerotised pleural plates along margin and sternal plates on abdominal segments bearing spines, setae and pores, with naked broad intersegmental area; antennae 8-segmented; prothoracic claw with a characteristic protrusion at base; with 6 abdominal spiracles.

Venter. Antennae 8-segmented, total length 320-340 μm ; segment I very large, 65 μm long, 120 μm wide, with 1 seta and about 7 fleshy setae; segment II narrow, 10-20 μm long, 70 μm wide; segment II-VIII with basally swollen setae, short setae and fleshy setae; segment VII 30 μm long, 55 μm wide, with 2-3 hair-like setae, 40-50 μm long and 2-3 fleshy setae, 30-45 μm long 3 short setae; terminal segment globular, 50-55 μm long, 50 μm wide, with 3-4 setae 60-70 μm long, 5-6 fleshy setae 30 μm long and a short seta about 15 μm long. Eyespot absent. Mouthparts absent. Thoracic spiracle with peritreme 60 μm wide, atrium with 2-4 multilocular disc-pore with large bilocular center plus 6 pores simple and apparently one seta; 1-2 perispiracular sensilla posteriorly. Abdominal spiracles in 6 pairs, with unsclerotised peritreme; atrium about 15 μm wide, with 2-3 pores. Prothoracic legs measurement with data on setae and pores: coxa much wider than long, with a large dorsal apodeme; trochanter+femur 190 μm long; trochanter with about 6 sensilla on each side; femur as broad as long, greatest 200 μm width, dorsally with setae 15-20 μm long, laterally with some setae 30-40 μm long and ventrally

with basally swollen setae with concave socket, 70-100 μm long, articulate freely with slender tibia; tibia+tarsus+claw sclerotised and fused but show segmentation; tibia 50 μm long, 100 μm wide, laterally with 3 setae, 30 μm long; bare dorsally, and ventrally 1 pair setae; tarsus 30 μm long, 70 μm wide, dorsally with 4-5 sensilla, laterally with 3 setae, 60 μm long; claw strong,

160 μm long, slightly curved, with a characteristic protrusion at base, apparently with 2 pairs of claw digitules, 100 μm long. Metathoracic legs measurement with data on setae and pores: coxa 180 μm long, ventrally with about 6 short setae, 15-20 μm long and with 2 setae, 60 μm long, coxa with an apodeme, 120 μm long; trochanter+femur 120-130 μm long, greatest width

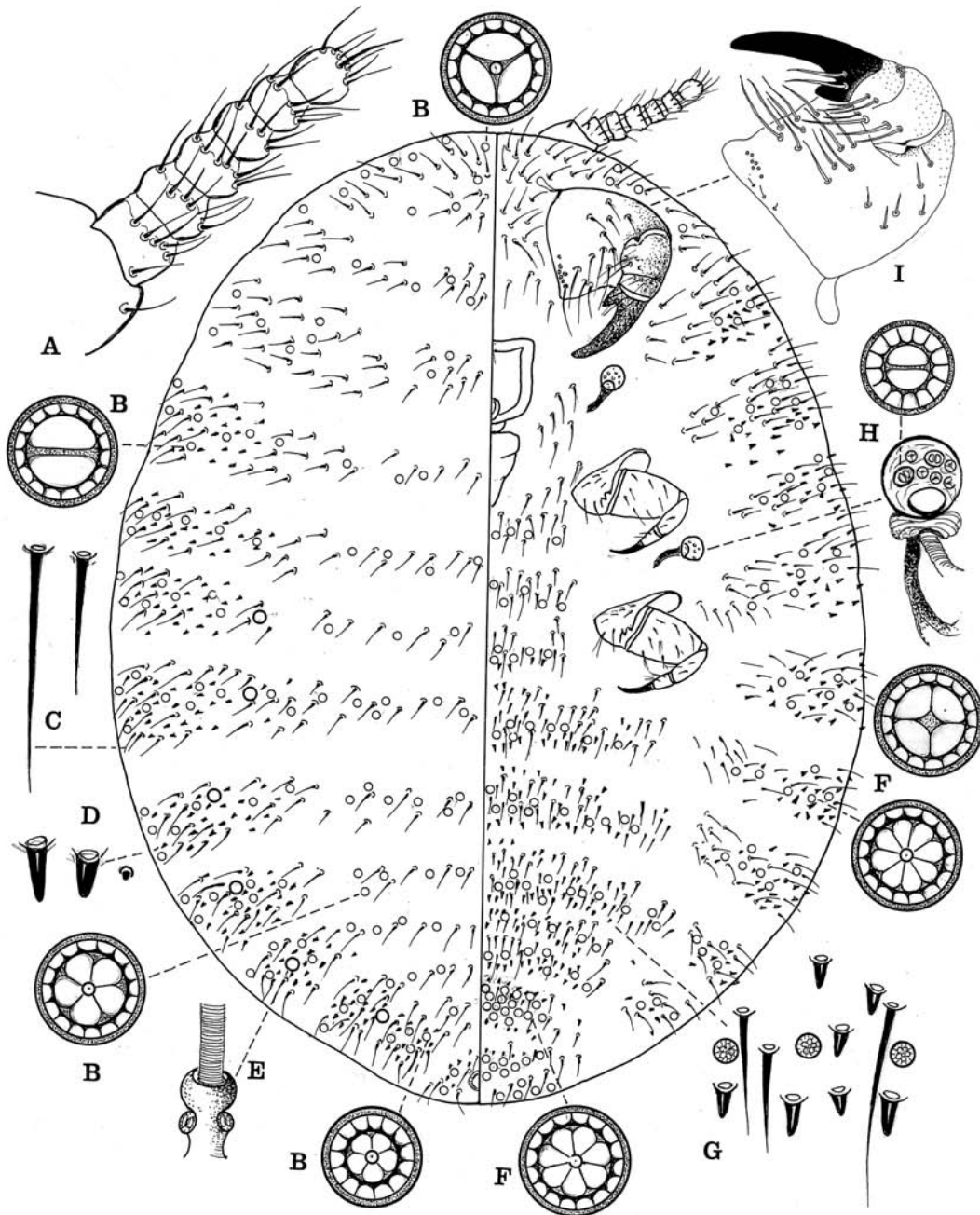


Figure 9

Adult female of *Promargarodes sinensis* Silvestri. A, antenna. B, multilocular disc-pores on dorsum. C, dorsal setae. D, dorsal spines. E, abdominal spiracle. F, multilocular disc-pores on venter. G, detail of a medial part of venter with setae, spines and multilocular disc-pores. H, thoracic spiracle with multilocular disc-pores and simple pores in atrium; I, prothoracic leg, claw with 1 or 2 obvious protrusions at its base representing a unique character.

about 100 µm, laterally 3 setae, 20-30 µm long, ventrally 6-7 setae, 60-80 µm long; tibia 70 µm long, 40 µm wide; tarsus 35 µm long, 30 µm wide, dorsally with 4-5 sensilla, ventrally with 2 setae, 30 µm long; claw 80-90 µm long with 2 digitule acutes.

Multilocular disc-pores, spines and setae on weakly sclerotized sternal plates of abdominal segments and on pleurites together in distinct groups. Multilocular disc-pores 11-12 µm in diameter, with 12-14 loculi in an outer ring but varying in shape (semi circular, oval or triangular) and size (large or small), with 2 to 8 loculi in inner ring; disc-pores distributed particularly medially on abdomen; denser around of vulva, and on margin.

Flagellate setae, 80-120 µm long on anterior end and 80-190 µm long on posterior end of body; thorax and abdomen with setae, 70-80 µm long medially; spines with a sharp point, length about 20 µm long absent medially on head and thorax, present on all abdominal segments and on margin. Weakly sclerotized sternal plates of abdominal segments with distinct groups of spines, setae and, multilocular disc-pores together in transverse rows. Pleural area with large and dense group with equally of these setae, spines and multilocular pores.

Vulva as a transverse fissure, 200 µm wide, radially folded, located intersegmentally between segment VIII and IX surrounded by numerous disc-pores.

Dorsum. Flagellate setae, 60-150 µm long, few on head and thorax, sparsely distributed medially, 1 seta wide, on abdominal segments; posterior segment with some setae 180-190 µm long. Lateral areas with dense group of setae, spines and disc-pores as on ventral margin. Anal opening sclerotised, situated on apex, 25-30 µm wide, surrounded by a naked area.

Host plant. Gramineae (Tang & Hao 1995).

Distribution. Oriental: China (Fukien), Hubei (Tang & Hao 1995).

Subfamily MARGARODESIINAE n. subfam.
Tribe MARGARODESIINI n. tribe

Genus *Margarodesia* Foldi 1981

Margarodesia Foldi 1981: 331.

Type species. *Margarodesia desmieri* Foldi 1981: 332, by monotypy and original designation.

Generic characters. Adult female broadly oval. Entire body surface densely covered in medium long basally swollen setae. Antennae 8-segmented; most antennal segments with fleshy setae and basally swollen setae. Prothoracic legs fossorial. Mouthparts absent. Spines medially, medio-laterally densely on venter of abdomen. Multilocular disc-pores unique in structure with unusual considerably elongated loculi in inner ring distributed on dorsum and Venter-Thoracic spiracles with multilocular pores and with simple pores in atrium; a group of perispiracular pores near of peritreme present. With 2 pairs of abdominal spiracles; anterior pair of spiracles located more dorsally and wider than those of posterior pair; each spiracles with multilocular pores within atrium. Well sclerotized anal tube present.

Second instar or cyst round, apodous; antennae represented by a long seta surrounded by a few shorter setae. Thoracic spiracles with pores in atrium; perispiracular sensilla present. With 2 pairs of abdominal spiracles; anterior spiracles with pores in atrium same structure than thoracic ones. A group of cicatrices usually about 15-18 around anal opening.

Margarodesia desmieri Foldi 1981

Adult female (Fig. 10)

Common name: palm ground pearl

Material examined. Holotype adult female, Ivory Coast: Dabou, on roots of *Elaeis guineensis*, February 1981, R. Desmier de Chenon rec., Type depository: MNHN. Paratypes: 5 females and cysts, MNHN.

Live specimen. Body broadly oval, red-orange, densely covered by setae.

Mounted specimen. Body broadly oval, with segmentation well visible, 2-4 mm long, 1.5-3 mm wide.

Venter. Antennae 8-segmented, total length 550-650 µm; scape obviously wider than others, 95 µm wide, 70 µm long, with 3 setae 20-30 µm long, basally with 6 short setae, 5-7 µm long, pedicel with 3-4 setae, 25-30 µm long and with 2 sensilla; all other segments with fleshy setae and basally swollen short setae, 25-40 µm long; fleshy setae about 20-30 µm long particularly numerous on segments III-IV and V; all setae on distal parts of segments; terminal segment 90 µm long, 50 µm wide, with about 8-12 hair-like setae, 30-50 µm long, 4-5 fleshy setae, about 20 µm long and one longer fleshy seta about 32 µm long. Eyespots absent. Mouthparts absent. Apophyse sternal between metathoracic legs well developed.

Prothoracic legs fossorial, obviously larger than meso- and metathoracic leg, measurements with setal and pores data; coxa narrow, 350 µm wide with a strong apodeme dorsally, with few setae ventrally; trochanter narrow with 4 sensilla on each side and with short setae; femur strongly developed, 330 µm long, 320 µm wide, with a few setae dorsally 20 µm long, latero-ventrally with numerous setae, each 100-120 µm long swollen towards base and with a constricted base; tibia short, 60 µm long, 140-160 µm wide with 4-6 setae, 120-130 µm long; tarsus dorsally with 4 sensilla, fused with claw; claw powerful, 280-310 µm long, slightly curving and narrowing gradually to a blunt apex, proximal part with 2 claw digitules, 90-100 µm long, on each side. Metathoracic legs measurements: coxa 250 µm long, 100 µm wide, with about 12 setae; trochanter with 3-5 sensilla on each side; femur 200 µm long, 140 µm wide, ventrally with a few setae, 50 µm long, dorsally with setae, 15-30 µm long; tibia 80 µm long, 50 µm wide, with few setae, about 30-40 µm long; tarsus dorsally with 3-4 sensilla, ventrally with a few basally swollen setae, 30-40 µm long and with 2 acute tarsal digitules; claw 110-120 µm long with 2 short digitules.

Thoracic spiracles each with wide, well sclerotized peritreme 90-100 µm in diameter, outer atrium with 1-3 multilocular-pores, each pore with 10-14 small loculi in outer ring and, 2-3 obviously wider loculi within inner ring along with a group of 8-12 pores simple: outer atrium opens into an inner atrium

with membranous folded walls; base of inner atrium opens into a sclerotised cone-like structure into a membranous tube which followed by a trachae with an apodeme straight 120 μm long. A group of 4-11 perispiracular sensilla near of peritreme.

Abdominal spiracles in 2 pairs in obvious different size; anterior spiracles with peritreme 55-65 μm wide, with 3-4 multiloc-

ular pores plus a group of 10-12 pore simples; each spiracle constituted as thoracic spiracles with an outer and an inner atrium; posterior spiracles with peritreme only 15-20 μm wide, with 3 multilocular pores and without simple pores. Spines 10-15 μm long, located medially, medio-laterally on abdomen, 3-10 spines wide in transversal band, less frequent on segments

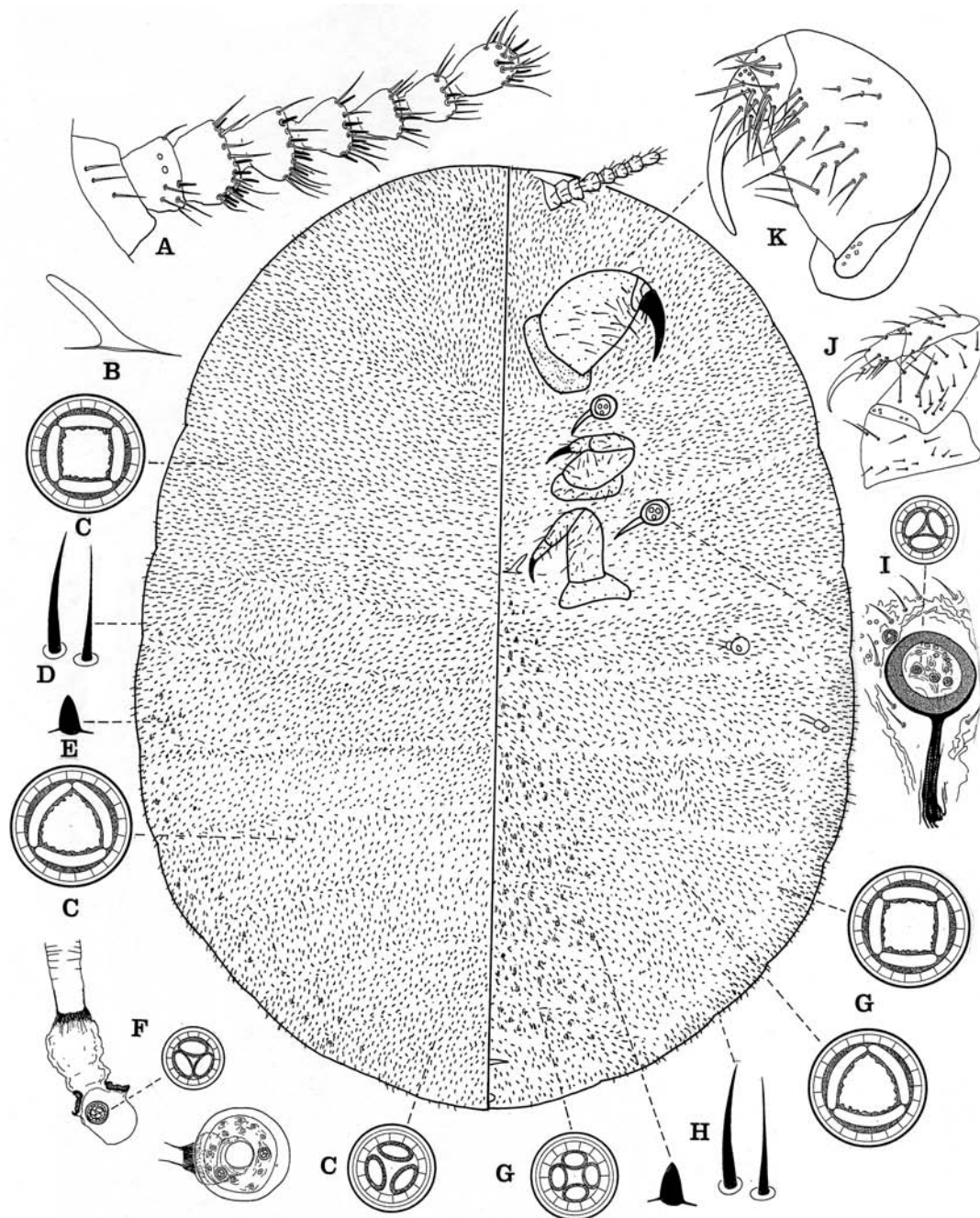


Figure 10

Adult female of *Margarodesia desmieri* Foldi. A, antenna. B, metathoracic apophyse sternal. C, dorsal multilocular disc-pores with large triangular or quadrate central zone. D, dorsal setae. E, dorsal spine; F, abdominal spiracle; G, multilocular disc-pores on venter. H, ventral setae and spine. I, thoracic spiracle with multilocular disc-pores with 3 large loculi in inner ring and pore simples. J, metathoracic leg. K, prothoracic leg with basally swollen setae.

I-II-III, progressively denser towards posterior end, most abundant on segments IV to VIII, accompanied by rare setae, 30-45 μm long and broad multilocular disc-pores.

Entire venter surface densely covered in medium short setae, about 30-45 μm long, sharply pointed as flagellate setae; each seta broadening progressively towards base. Slightly longer setae, about 50 μm , sparsely distributed on thorax and submargin. Multilocular disc-pore of broad size, each about 16-17 μm in diameter, unique in structure; each pores with 18-20 small loculi in outer ring but with 3 or 4 particularly elongated loculi in inner ring, each elongated loculi, about 8-9 μm long, and their number, 3 or 4 elongated loculi determine the shape, triangular or quadrate, of a broad central zone. These disc-pores distributed in transverse rows, 1-4 pores wide, on abdominal segments; each row with about 20-32 pores; their total number on dorsum varying between 230-260. Smaller multilocular disc-pores about 10-12 μm in diameter, each with 12-14 small loculi in outer

ring and, with 3-4 wider loculi in inner ring distributed on posterior abdominal segments.

Dorsum. As on venter, thick setae 30-45 μm long, usually sharply pointed broadening progressively towards base, in dense covering throughout dorsum; with a few similar setae slightly longer about 50 μm scattered over derm. Spines absent. Broad multilocular pores, 16-18 μm wide, similar than on venter, distributed in 2-4 pores wide in transversal lines; smaller multilocular pores, 10-12 μm wide, similar than on venter on posterior abdominal segments. Anal opening, 20 μm in diameter, on posterior end of body surrounded by a small area without setae; anal tube well sclerotised 50 μm long.

Cyst (Fig. 11)

Live material. External aspect strongly rough, white-yellow, spherical shape, 2-4 mm in diameter. Live nymph shiny white.

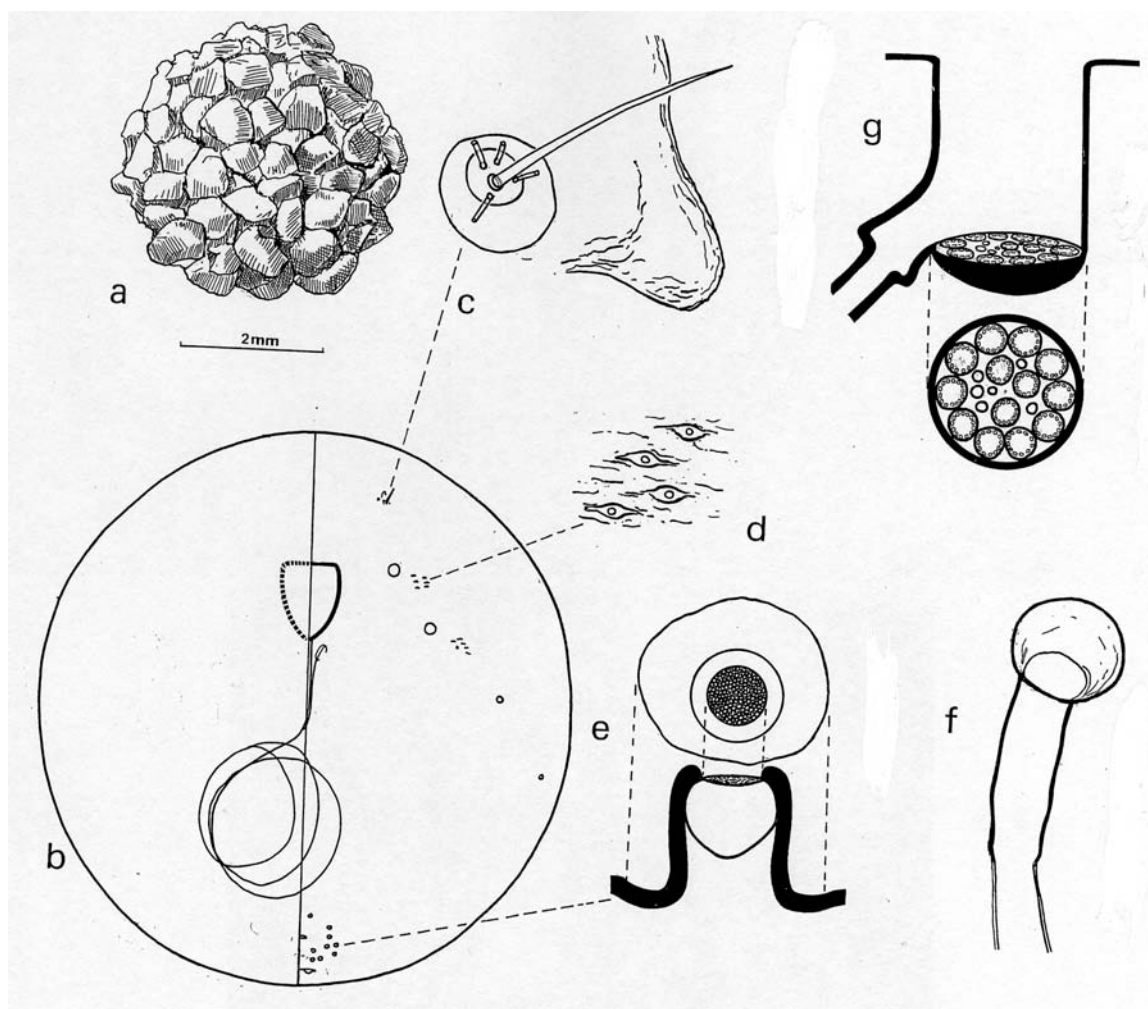


Figure 11

Cyst of *Margarodesia desmieri* Foldi. A, external aspect of cyst. B, cyst without test. C, antenna near of a dermal protuberance. D, perispiracular sensilla. E, cicatrice. F, abdominal spiracle. G, thoracic spiracle.

Mounted specimen. Body circular, 1.5-3 mm in diameter.

Venter. Eyespots, legs, setae and spines absent. Antennae located near a derm protuberance represented just by a seta, 50 μm long, and surrounded by with 2-4 short setae about 5 μm long. Labium without setae and no pores near labium; stylets twice as longer as body. Thoracic spiracles with perimetre 40 μm

wide; base of atrium with 10-15 multilocular pores; each with about 14-20 loculi in a single outer ring plus 4-6 simple pores; a group of 4-5 small perispiracular sensilla latero-posteriorly of peritreme. Abdominal spiracles in 2 pairs; anterior spiracles with perimetre 40 μm wide, with same pore type as on thorax; posterior spiracles smaller with perimetre 10-12 μm wide, and atrium

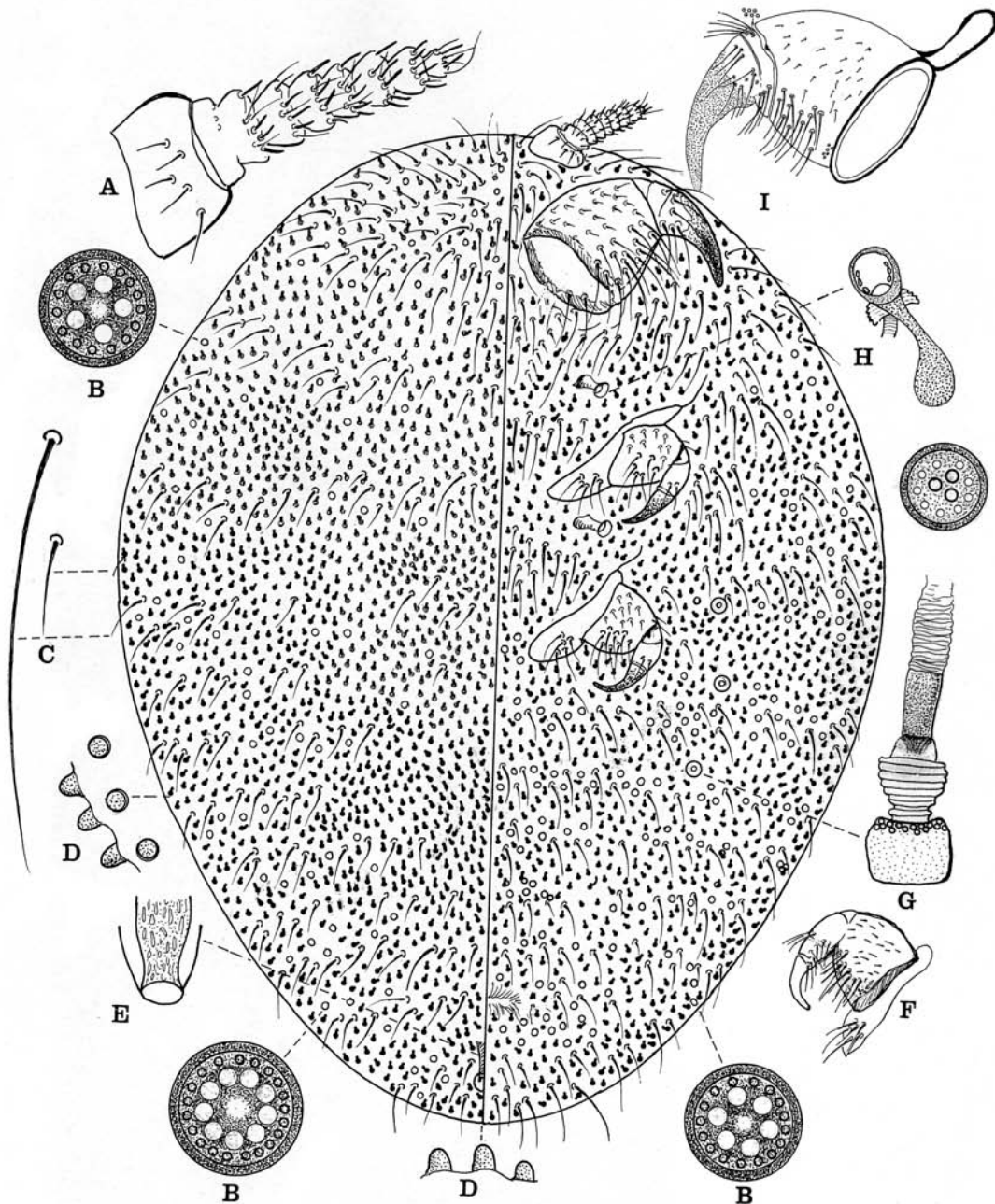


Figure 12

Adult female of *Eumargarodes laingi* Jakubski. A, antenna. B, multilocular disc-pores on dorsum and venter. C, dorsal and ventral setae. D, derm on dorsum and venter densely covered with small papillae. E, anal tube. F, metathoracic leg. G, abdominal spiracle. H, thoracic spiracle with multilocular disc-pores in atrium. I, prothoracic leg.

without pores. A group of cicatrices (8-24, usually 15-18) around anal opening; each cicatrice with about 10 µm in diameter and, 12-15 µm high.

Dorsum. No morphological structures visible.

Host plant. *Elaeis guineensis* (Palmae), the cysts were recorded on roots of oil-Palm.

Distribution. Afrotropical: Ivory Coast.

Economic importance. The important aggregation of cysts on roots remove plant sap resulting in sap loss reduces plant vigor, inhibits the growth of the Palm trees, and may transmit the divers elements pathogenic.

Subfamily EUMARGARODINAE Jakubski 1965
Tribe EUMARGARODINI Jakubski 1965

Genus *Eumargarodes* Jakubski 1950

Eumargarodes Jakubski, 1950.

Type species. *Eumargarodes laingi* Jakubski 1950: 397.
Eumargarodes laingi Jakubski 1950.

Adult female (Fig. 12)

Material examined. Holotype adult female, Australia, Queensland, Bundaberg, on roots of sugarcane (*Saccharum officinalis*), 26 November 1938, R.W. Mungomery rec. Type depository: BMNH, n° I.B.E. 8735.

USA: South Carolina, Myrtle Beach, on centipede lawn, 24 May 1985, Brown rec., n° 85-6384, USNM; Alabama, Auburn, on grass, 14 July 1975, n° 75-10423, USNM; Florida, near Orlando, on centipede grass roots, 16 May 1991, I. Foldi rec., MNHN.

Mounted specimen. Body of adult female broadly oval, about mm long, mm wide. Entire dorsal and ventral surface covered in a dense covering of dermal ornamentale papillae but with few flagellate setae and pores.

Venter. Derm membranous, densely covered with small usually circular papillae, 7-8 µm long and 5-6 µm wide, each distributed about 6-10 µm of distance of others. Antennae 9-segmented, total length 750 µm; segment I µm long, µm wide with 4-5 setae along middle area; segment II narrow with 3 setae, µm long; segments III-VIII tapering gradually to terminal segment varying from 130 µm to 90 µm width and 50, 55, 60 and 60 µm length, each with 0-3 setae, 80-90 µm long 4-6 fleshy setae, each 30-45 µm long; terminal segment 40 µm long, 45-50 µm wide, with 3-4 setae, 90 µm long and 4 curved fleshy setae, 30-40 µm long. Eyespot apparently absent. Mouthparts absent.

Thoracic spiracles with peritreme 60 µm wide, atrium with 5-6 multilocular pores varying in shape, in size and in number of loculi; usually with 7-9 small loculi in a irregular outer ring and 2-4 larger irregularly placed loculi in inner ring; each spiracle with a strongly sclerotised apodeme, 150 µm long. Abdominal spiracles in 3 pairs, with peritreme 35 µm wide,

atrium without pores. Pro-, meso- and metathoracic sternal apodemes submedially.

Legs well developed, prothoracic legs very large. Prothoracic legs measurement with data on setae and pores: coxa triangular, 400-500 µm long, with 4 long setae; trochanter fused with femur without any indication of segmentation, with 5-6 sensilla and 5-6 setae; femur strongly developed, greatest length 550-650 µm, 500 µm wide at its base, with a small group of short setae, 20-25 µm long, 4 setae 180-190 µm long dorso-laterally and ventrally with numerous setae, 150-250 µm long; tibia 130 µm wide, 220 µm wide, with two setae, 80-90 µm long on each side, articulating with femur; tibia, tarsus and claw fused, showing segmentation but no articulation; tarsus 100 µm long, 200 µm wide, with 4 long setae, 70-80 µm long, dorsally with 4-5 sensilla in 2 rows, claw about 320 µm long, 130 µm wide at base, curving and narrowing gradually to a blunt apex. Metathoracic legs data: coxa elongate with about 350 µm wide, with 4-5 setae; trochanter fused with femur with a group of 4-5 sensilla in line; femur, greatest length 350 µm, greatest width 280 µm, dorsally with short setae, 25-30 µm long and ventrally a group of 5-7 setae, 140-180 µm long; tibia 150 µm long, 90-100 µm wide, tarsus 70 µm long dorsally with 4-5 sensilla in 2 rows and, 2 setae 65-70 µm long on each side; claw about 200 µm long, 55 µm wide at base, almost strighth or slightly curving, sharply pointed, with 2 setae 90-100 µm long.

Multilocular disc-pores, with about 10 µm in diameter, with well sclerotised rim, with 5-9 large loculi in a simple outer ring and usually with a central white spot same size than loculi, rares on head and thorax, in transvers rows, 1-2 pores wide on abdominal segments, denser towards posterior abdomen.

Long flagellate setae along margin, 240-260 µm long; setae 80-220 µm long and smaller setae 25-35 µm long few in number, weakly scattered, denser on anterior end of body; these setae in transversal rows, 1 setae wide, on abdominal segments; all setae with flat sockets.

Dorsum. Derm densely covered with small papillae as on Venter. Long fagellate setae similar to those on venter; setae 80-240 µm long and short setae 25-35 µm long scattered on head and thorax, in transvers row, 1 setae wide, on abdominal segments. Multilocular disc-pores similar to those on venter, distributed sparsely throughout. Anal opening situated at posterior end of abdomen, sclerotised, 25 µm in diameter, supported by 2 lateral apodemes, 50 µm long, followed by an anal tube 70 µm long.

Host plant. *Saccharum officinalis*

Distribution. Australian: Australia: Queensland, New South Wales. Nearctic. USA: Florida, South Carolina.

Subfamily NEOMARGARODINAE Jakubski 1965
Tribe NEOMARGARODINI Jakubski 1965

Genus *Neomargarodes* Green 1914

Neomargarodes Green 1914.

Margarodiella Jakubski 1965: 81 In combination with *Margarodiella pilosa* Brain. Nomen nudum.

Type species. *Neomargarodes erythrocephalus* Green 1914: 263 by monotypy and original designation.

Generic characters of adult male. Antennae basically 7-segmented but with unique structure for scale insects characterized by “branched antennae”, i.e. segments IV to VI with lateral extensions; antennal segments IV to VII and lateral branches densely covered by short fleshy setae. Compound eyes bright red very large which almost meet ventrally; ocelli absent. Body robust, with broad, fine, transparent wings with large alar setae and with anterior margin serrated along distal half. Body moderately setose, with long setae with rather shallow basal sockets. Prothoracic legs with fused tibia, tarsus and claw; femur with numerous bifurcated setae. Dorsal waxy tail tuft on the abdominal segments VI and VII. Scutum and scutellum without lateral membranous areas. Furca without lateral arms. Tergites and sternites presents. Hamulohaltere with only a single and short hamulus. Abdominal spiracles difficult to detect, probably 4-5 pairs present. Penial sheath tubular; aedeagus membranous, endophallus present. Cyst in soil on roots of grass.

Generic characters of adult female. It is based on *Neomargarodes festucae* Archangelskaya. Prothoracic claw with a prominent heel represents a character unique to this genus. Profemur with long and thin setae. Body with very long and fine setae; spines absent. Antennae 6-segmented; antennal segments short and stout, wide at base, with very long hair-like setae and fleshy setae. Mouthparts absent. Legs short and stout. Abdominal spiracles in 8 pairs. Thoracic and abdominal spiracles with multilocular disc-pores and simple pores in atrium. Thoracic spiracles with a long, narrow, stright apodeme. Genital opening radially folded.

Neomargarodes erythrocephalus Green 1914

Adult male (Fig. 13)

Neomargarodes erythrocephalus Green 1914: 263.

Material examined. Lectotype male designated by Foldi 1999: 323. Type depository: BMNH. Algeria: Sahara, El Meksa, South of El Golea, April, 2 1913, light trapped by J.O. Hartert. Soudan: 68 km after Gao toward Hombori, January, 30 1935, light trapped by Breteuil (MNHN).

Live appearance. Greyish–clear brownish color, eyes bright red, with long wings, fine, and transparent; and with a dorsal waxy tail tuft, on the segments abdominal VI and VII, about twice longer than the body.

Mounted specimens. Adult male with robust body, 3-3.5 mm in length including penial sheath, and 0.8-1 mm wide across mesothorax. Body with long setae and without loculate pores except a group of tubular pores medially on abdominal segments VI and VII. Antennae 7-segmented but with 3 segments branched. Compound eyes bright red, ocelli absent. Prothoracic legs fossorial, tibia and tarsus fused, femur with numerous bifurcated setae. Scutum and scutellum without lateral membranous areas. Furca without lateral arms. Tergites and sternites presents. Hamulohaltere with only a single and short hamulus. Abdominal

spiracles present, probably 4 pairs. Penial sheath tubular; aedeagus short and membranous, endophallus present.

Head: triangular in dorsal view, 300-360 μm long, 550-570 μm width across compound eyes, compound bright red eyes covering the major part of the cephalic capsule, almost in contact on posterior margin ventrally; each compound eye with about 31-40 large ommatidia and with sclerotised ridges along all margins; ocular sclerite and ocelli absent. Dorsally: postoccipital sutures, postocciput and midcranial ridge absents; a lightly sclerotised median crest (mc) present on medial part of epicranium with 6-9 setae, 60-70 μm long on each side. Ventrally: a short midcranial ridge (vmcr) with 8-12 long setae on each side between eyes. Ventral plate (vp) represented by a small median sclerotization on posterior margin of head just before mouth. Cranial apophysis and tentorial arms absents. Mouth opening visible.

Antennae: unique in structure for scale insects named “branched antennae” characterized by existence of lateral extensions on segments IV-V-VI. Basically 7-segmented, 1.1-1.2 mm long. Scape (sc) about 100-130 μm long, 100-140 μm wide, with 5-7 long fleshy setae and 8-12 short hair-like setae. Pedicel (p) about 90-100 μm long, 90-120 μm wide, with about 15-20 long flagellate setae, with a few short hair-like setae and ventrolaterally 8-10 small basiconic sensilla; apical part of pedicel, near area articulating with segment III with numerous sensilla placed in a single line. Segment-III 50 μm long, 100 μm wide with 10-15 long flagellate setae and 7-10 short hair-like setae. Segments IV-VII and each lateral extensions of segment IV-VI bear numerous, uniform and densely distributed, robust fleshy setae, each parallel-sided with a blunt apex, generally 15 μm long, and a few shorter setae, 5-6 μm long. Segment and lateral branch length: IV:100-130 μm , lateral branch 220-280 μm ; V 120-140 μm , lateral branch 360-380 μm ; VI 150-170 μm , lateral branch 370-390 μm ; terminal segment 440-460 μm long. Satellite setae absent.

Prothorax: membranous separated from head by a broad neck. Dorsally with a median weakly sclerotised pronotum (pr) anterior to prescutum with 7-8 long pronotal setae. Two large, lightly sclerotised post-tergites (pt), each with about 12 long post-tergital setae. A group of lateral prothoracic long flagellate setae, setae, on each side. Ventrally with a pair of cervical sclerites (cv) which do not articulate with head structure but fusing posteriorly with pleural ridge (plr1). Prosternum (stn1) membranous without sternite or apophysis.

Mesothorax: sclerotised, well developed, convex dorsally and flat ventrally with about 16-20 long setae. Dorsally, prescutum (psc) oval without prescutal setae, anteriorly extending below prothorax forming a large mesoprephragma; prescutal ridge mesad to each prealare (pra) extending anteriorly to mesoprephragma; prescutal sclerites separating prescutum from scutum. Prealare (pra) elongate, extending latero-ventrally to mesepisternum (eps2). Scutum (scu) sclerotised, without membranous area bearing about 12-20 long setae; laterally with a small anterior notal wing process (anp). Scutellum (sl) median, triangular, with a strong ridge along posterior margin, without membranous area and without scutellar setae, separated from scutum by a scutoscutellar ridges. Immediately posterior to scutellum, a large membranous area present bordered posteriorly by mesopostnotum (pn), latter overlapped posteriorly by meta-

thorax; with mesopostnotal apophysis (pa) on each side; lateral margins this membranous area bordered by a postalare which extends antero-ventrally below wing sclerites. A membranous area present laterally, between each prealare (pra) and scutum (sc); each with a large sclerotised tegula (t) bearing a group of 10-16 tegular setae. Mesopleural ridge with a pleural apophysis.

Episternum (eps2) large, weakly reticulated. Ventrally, basisternum (stn2) (mesosternum) sclerotised, bearing about 30-40 short, hair-like setae; basisternum anteriorly without a obvious marginal ridge, laterally a marginal suture separate from lateropleurite (lpl) and posteriorly with well developed precoxal ridges (pcr2); median ridge absent; lateropleurite (lpl) large, each with

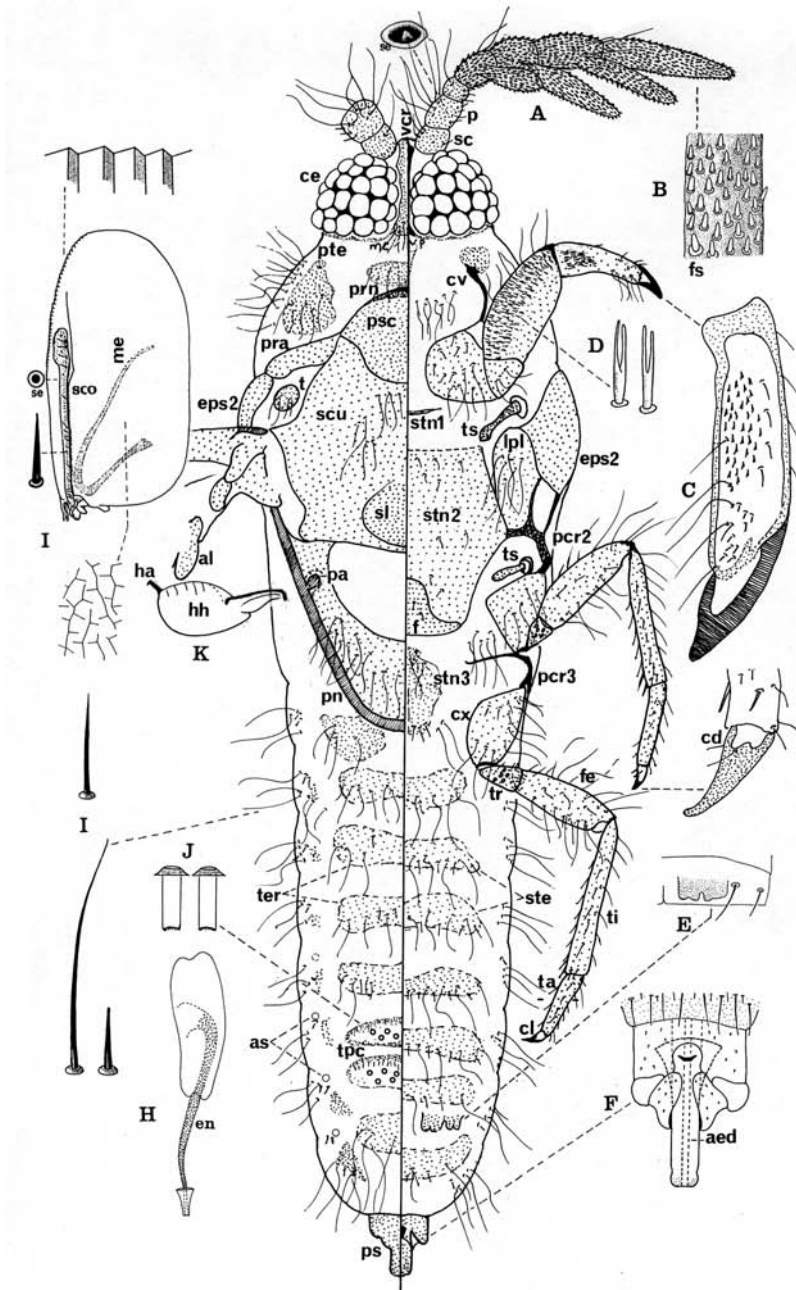


Figure 13

Adult male of *Neomargarodes erythrocephalus* Green. A, antenna, unique in structure for scale insects characterised by lateral extension on segments IV-V-VI densely covered by fleshy setae. B, detail of a lateral extension. C, prothoracic leg with tibia and tarsus fused. D, profemur densely covered by bifid setae. E, sclerotised dermal plate only on abdominal segment VII, view by SEM. F, ventral view of genital segment. H, endophallus. I, dorsal and ventral setae. J, tubular pores on segments VI-VII. K, hamulohaltere. I, mesothoracic wing. For detail see abbreviations.

10-16 flagellate and hair-like setae, bounded posteriorly by precoxal ridge and laterally by a strong projection of subepisternal ridge; furca broad basally, about 210-250 μm long, 180-200 wide, narrowing to apex, without lateral arms. Mesothoracic spiracles with peritreme 90-110 μm wide. Axillary wing sclerite and additional sclerite present.

Metathorax: mainly membranous. Dorsally, metapostnotum (pn3) represented by a pair of large sclerites which fuse medially, and fused with tergite of first abdominal segment; with 6-8 metatergal setae medially and 10-15 flagellate setae. Pleural ridge extending from metacoxae to base of hamulohalteres; precoxal ridge (pcr3) extending about 250 μm long ventrally. Ventrally; metepisternum present as a sclerotisation on either side of precoxal ridge; metepimeron present as a posterior ridge. Metasternum (stn3) sclerotised with lateral apophysis and with various numbers of metasternal setae, about 10-30, mainly long flagellate setae, distributed medially or laterally. Spiracles with peritremes 80-100 μm wide.

Wings: forewings very broad, transparent, about 4 mm long and 2 mm wide. Wing surface membranous with faint cuticular reticulations; anterior margin serrated along distal half. Subcostal vein (sc) well developed and sclerotised; wing anterior to subcostal (sc) sclerotised; alar setae present, subcostal setae in a line along sub costal vein, each 40-60 μm long and small circular sensilla, about 2 μm in diameter, on its distal part; radial vein represented by a light sclerotisations, arising from posterior apex of axillary sclerite extending in diagonal line and terminating at near of half distal margin of wing; a short clear anal fold arising from posterior apex of axillary sclerite extending to inferior margin Anal lobe (al) well developed. Hamulohalteres (hh) broad, 400-500 μm long, 130-200 μm wide, with a strong vein along anterior margin, representing costal complex of Koteja (2001), with 1 blunt, apically bent hamulus about 45-50 μm long. Koteja (2001) observed a double function of margarodid halteres: a role that they play in flight and also in reposing the wings.

Legs: prothoracic leg deeply modified, fossorial type; tibia, tarsus and claw fused, distinctly different from meso- and metathoracic legs. Prothoracic leg measurements with setal and pore data: coxae (cx) 280-300 μm long; each coxa with a strong internal ridge; coxae + trochanters with hair-like setae, bifid setae and long flagellate setae; trochanter (tr) + femur (f) 450-500 μm long; each trochanter with 8-12 campaniform sensilla; femur densely covered by strong bifid setae, with about 15-20 flagellate setae, 100-150 μm long, and a few short hair-like setae; tibia (t) + tarsus (ta) + claw (cl) fused 320-370 μm long with 4-5 flagellate setae an numerous shorter setae; tibial and tarsal spurs absent; claw broadly fused with tarsus, without claw digitules.

Metathoracic leg length measurements and setal distribution: coxae (cx) 280-320 μm long, with about 20-25 short hair-like setae and 20-30 long flagellate setae; trochanter + femur 450-550 μm long; trochanter with about 10-15 short hair-like setae, with 2 long flagellate setae, and with about a group of 6-9 campaniform sensilla on each side; femur with about 20 flagellate setae, with 10-12 hair-like setae, and one strong bifid seta; tibia 480-550 μm long, with about 18-20 stout spine-like setae along ventral margin, with 4-6 long flagellate setae, and 4 ibial spurs distally; bifid setae absent; tarsus 1 segmented, 210-220 μm long, with 1 campaniform sensilla dorso-proxi-

mally and 15-25 hair-like setae; without bifid setae; tarsal digitules short, 20 μm long; claw strong and broad basally, pointed at apex, 75-80 μm long, with short, fine digitules, each about 15-20 μm long, and without denticle.

Abdomen. Membranous, abdominal segments tapering progressively to the end of the body. Dorsally large, elongate tergites medially on all segments; each tergite with about 6-16 long flagellate setae and with about 10-20 short hair-like setae. Segments VI and VII with a median group of 7-8 and 9-10 of sclerotised tubular pores, each about 60-70 μm long, 15-17 μm wide, each with slightly spiral longitudinal ridges; emitting long, white waxy filaments forming waxy tails; each group of pores with a line of minute setae, 3-5 μm long, along anterior margin. Pleural setae about 6-12 on each segment. Ventrally, large, elongate sternites present on all segments; each sternite with about 10-15 flagellate setae and 12-15 short hair-like setae; sternite VIII with an narrow sclerotisation laterally extending from outer margin of penial sheath; sternite VI with a plate; abdominal spiracles numbering perhaps 4 or 5 on posterior segments because opening are indistinct anteriorly. Anal opening on dorsum near anterior margin of penial sheath.

Genital organs. Formed from segment IX positioned ventrally and consisting of a strongly sclerotised penial sheath (ps) and an aedeagus (aed). Penial sheath tubular, 220-260 μm long, 270-300 μm wide, with opening for aedeagus at posterior end, with short hair-like setae and small sensillae near posterior margins; aedeagus membranous, about 250-270 μm long, 80 μm wide, with an endophallus densely covered by short spines, about 6-8 μm long and with a sclerotised structure at base of aedeagus.

Distribution. Afrotropical: Sudan, Yemen. Palaearctic: Algeria.

Neomargarodes festucae Archangelskaya 1935

Common name: grass pearl scale

Adult female (Fig. 14)

Neomargarodes festucae Archangelskaya 1935: 21.

Neomargarodes borhsenii Hadzibejli 1959: 61. (syn. in Jashenko 1999: 43).

Material examined. France: Marseille, Goudes, on roots of *Festuca ovina*, 12 June, 1976, I. Foldi rec.

Mounted specimens. Body broadly oval, almost circular, (3.5-6 mm long, 2.5-4.5 mm wide).

Venter. Antennae 6-segmented. Antennal segments short and stout, width at base gradually narrowing towards apex. Segments I obviously wider than others, with one seta μm long; segments II-VI with long flagellate setae, μm long and fleshy setae about μm long; terminal segment smaller, μm long, μm wide with 3 flagellate setae and 3-4 fleshy setae. Eyespots absent. Mouthparts absent, with an invaginated membranous tube-like area. Thoracic spiracles rather with a small peritreme, with 5-7 multilocular pores in atrium; thoracic spiracular apodeme narrow, stright. Prothoracic legs considerably developed, powerful, fossorial; meso and meta thoracic legs short and stout. Prothoracic legs: coxa wide; femur strongly developed, greatest wider at distal part, laterally with 6-9 long setae; tibia + tarsus + claw fused together, short

and strongly sclerotized; tarsus large dorsally with numerous sensilla; claw short, with a basal prominent heel. Metathoracic legs: coxa obviously wider than long; trochanter fused with femur; trochanter with two campaniform sensilla and a long seta; femur with 2-3 long and 2-3 short setae; tibia with about four setae; tarsus with 2 sensilla and with 2 tarsal digitules; claw long and

without digitules. Spines absent. Long slender hair-like setae of two length, 500-650 μm and 350-400 μm covering derm, latest more numerous on head and last segments abdominal. Multilocular disc-pores with 8 peripheral loculi in transverse rows on abdomen, on segments I-II-III interrupted. Vulva in radial folds.

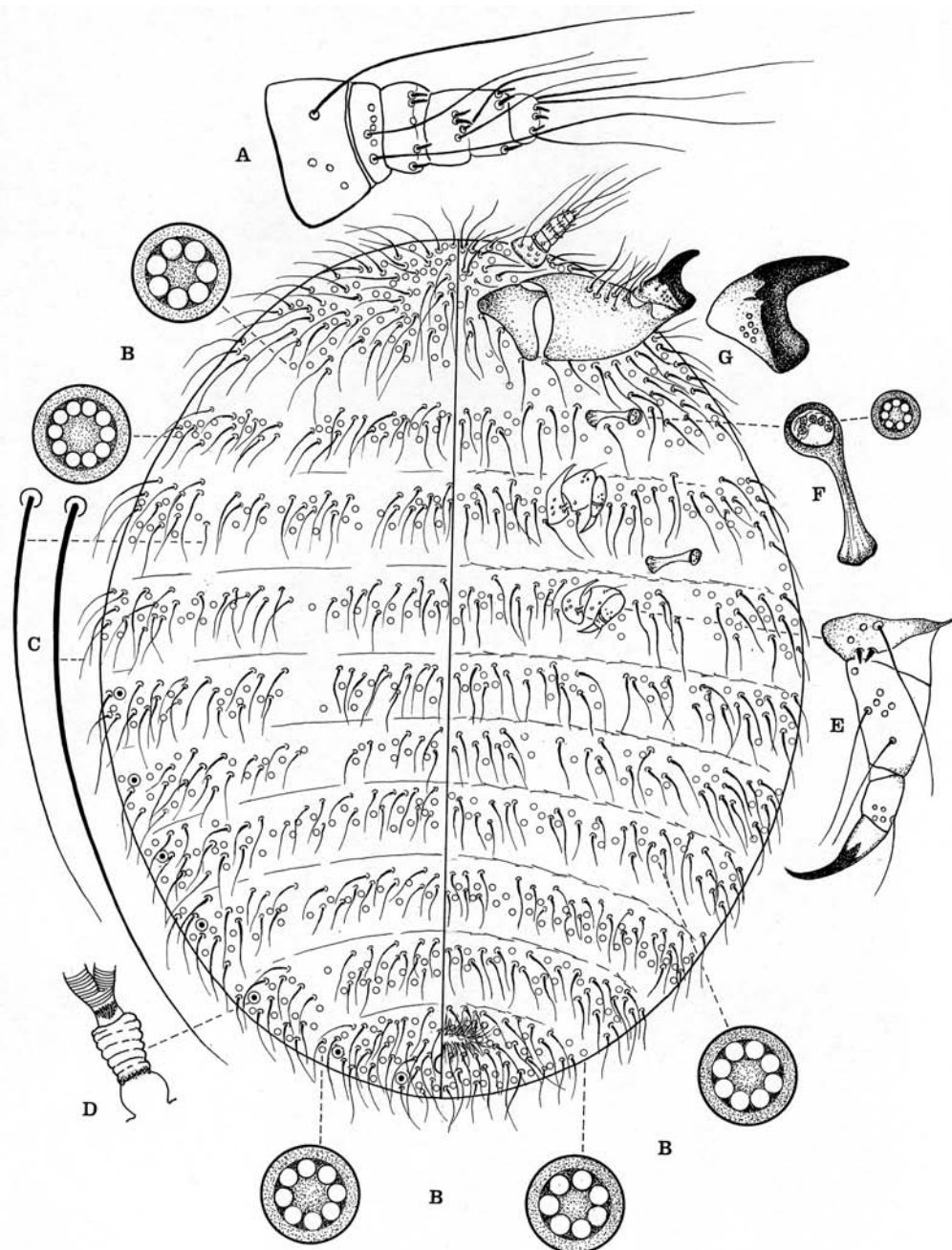


Figure 14

Adult female of *Neomargarodes festucae* Archangelskaya. A, antenna. B, dorsal and ventral multilocular disc-pores. C, long dorsal and ventral setae giving a hirsute appearance. D, abdominal spiracle. E, metathoracic leg. F, thoracic spiracle. G, prothoracic leg, claw with a prominent heel representing a unique character.

Dorsum. Abdominal spiracles numbering 8 pairs, with simple and multilocular pores in atrium. Multilocular disc-pores with 7, 8 and 10 peripheral loculi scattered, more numerous on head and extremity of abdomen. Setae same than on Venter - Anal opening semicircular, apical; anal tube present.

Host plant. *Agropyrum cristatum*, *Dactylis*, *Festuca ovina*, *F. sulcata*, *F. vaginata*, *Koeleria vallesiana*, *Stipa capillata*.

Distribution. Palaearctic: Czech Republic, France, Georgia, Hungary, Italy, Poland, Ukraine.

Subfamily PORPHYROPHORINAE Signoret 1876
Tribe PORPHYROPHORINI Jakubski 1965

Genus *Porphyrophora* Brandt

Porphyrophora Brandt, in: Brandt & Ratzeburg 1833.

Type species. *Porphyrophora frischii* Brandt in Brandt & Ratzeburg 1833: 356 (= *Coccus polonicus* L., 1758: 456). Subsequently designated by Kirkaldy 1906: 254).

Coccionella Hahnemann, 1793: 193. Type species: *Coccus polonicus* L., 1758. Jakubski (1965: 5) considered *Coccionella* as a *nomen oblitum* and synonym of *Porphyrophora*.

Generic characters. Adult female broadly oval, pear-shaped, size varying considerably from 1.5 mm to 12 mm, derm soft and flexible, derm relief with a dense network of small integumentary protuberances irregularly shaped; body always covered by long hair-like setae in variable density and small setae on both side throughout of body giving more and less hirsute appearance; spines absent. Antennae with 7 to 18 segments, usually segments VIII-X wider than long except apical segment; subapical segments mainly with sclerotized ring along of each segments. Usually antennal segment IV with a sensilla placodeum consisting of a small area with group of sensilla and some setae. Each apical segment with a group of setae, including very long flagellate setae, some up to 500 µm long, straight or curved fleshy setae mainly 20-35 µm long, short setae (=basiconic sensilla) 15-20 µm long, and often a various number of coeloconic sensilla. Membranous base of scape with usually 0-4 small setae. Mouthparts absents. Prothoracic legs strongly developed fossorial type with wide femur and enlarged, pointed claws. Thoracic spiracles with multilocular pores in atrium and with a group of perispiracular sensilla around of peritreme. Abdominal spiracles only 2 anteriors pairs present or lacking. Multilocular pores usually with numerous and approximately same size and shape of loculi, their number may up to 36 loculi. Anus in a naked area which surrounded by numerous setae. Vulva represented by a small opening surrounded by radial folds of derm, in some species with a cavity on either side of vulva; area around vulva mostly naked. Mated females produces white cottony ovisac including both eggs and body. Cysts living on roots or rarely may be found on plant near of the soil.

Remarks. *Porphyrophora* is a large and uniforme genus including currently 47 species particularly distributed

in the Palaearctic region (Foldi 2001). Several morphological characters of adult females show large variations within species particularly in the number of antennal segments and asociated structures (setae, sensilla), the number of setae and sensilla on the placodeum or presence or absence of the abdominal spiracles results in the need of a combination of characters for species identification.

Porphyrophora polonica (Linnaeus 1758)

Common name: polish cochineal scale

Coccus polonicus L. 1758: 456.

Coccus radicum Beckmann 1790: 3.

Coccionella polonica; Hahnemanns 1793: 1090.

Porphyrophora frischii, Brandt in Brandt & Ratzeburg 1833: 356.

Porphyrophora polonica; Burmeister 1835: 78.

Margarodes (Porphyrophora) polonicus; Cockerell 1902: 258.

Margarodes polonicus; Fernald 1903: 29.

Porphyrophora polonica polonica; Goux 1948: 185.

Porphyrophora polonica (L. 1758); Jakubski 1965: 18.

Adult female (Fig. 15)

Material examined. Adult female, Poland: Klucze Plusz. Bledowska, Wyzyna Slaska, on *Scleranthus perennis*, 12 July, 1997, T. Szklarzewicz rec., det. J. Koteja. Type material lost, D.J. Williams pers. comm.

Live appearance. Adult female oval, red-brown to violet color, becoming coated with a white waxy secretion after mating occurs. Derm soft, flexible and hairy.

Mounted specimens. Adult female broadly ovale, varying size from 3 mm to 7.5 mm, mostly 4-5 mm. Body covered by long hair-like setae and disc pores.

Venter. Antennae 7-8 segmented, 300-350 µm long; segments more and less conicals. Segment-I about 180 µm and apical 100 µm wide. Segments naked, except segment IV and apical one, occasionally segment V with a long seta. Segment IV with a sensilla placodeum (see arrow) with about 5-8 sensilla, occasionally one small seta about 20 µm long, and 1 or 2 of 130 µm long setae may also observed. Apical segment longest 100 µm long, 100 µm wide, with 4-7 flagellate setae about 150-200 µm long, plus a group of thick, curved fleshy setae numbering 10-14 about 30 µm long, and some small, 3-4, circular sensilla. Membranous base of scape with one small seta. Eyespots circular, 110 µm in diameter, situated on a sclerotized plate in postero-lateral position of antennae. Mouthparts absent. Prothoracic legs strongly developed, fossorial. Measurements: trochanter + femur 550-600 µm long and 600 µm wide; each trochanter fused with femur, laterally with 14 sensilla and about 10 setae on each side; each femur bearing ventrally a group of 25-30 flagellate setae, about 140 µm long, and dorso-laterally 4-6 short setae, each about µm long; tibia short, about 120-130 µm long, with a few setae of 130 µm long and 4-6 small setae; tarsus, 100 µm long, µm wide, fused with a strong and curved claw, dorsally with of 9-11 campaniform sensilla in 2 rows, with 2 hair-like tarsal digitules of 120 µm long and plus some few short setae dorso-laterally; each claw about 260-300 µm long, without a denticle. Metathoracic leg measurements: coxa

400 μm long, with about 8 setae, 220 μm long and 6-8 short setae; trochanter + femur 300 μm long, as long as broad; each trochanter laterally with 11 sensilla on each side; each femur with a touff 6-8 seta, 230 μm long, and some short setae; tibia 180-210 μm long, 150 μm wide, with 4-6 short setae and 2 fleshy setae on eachside; tarsus, 110-150 μm long, 100 μm wide,

dorsally with 4-5 campaniform sensilla and 1-2 fleshy tarsal digitules about 80 μm long, and with some small setae; claw fine and about 190-240 μm long with a pair of acute digitules, 60 μm long. Thoracic spiracles with peritreme 110 μm in diameter, with 5-9 multilocular pores with numerous loculi from 30 to up 50 loculi in atrium. A group of 3 perispiracular sensilla near

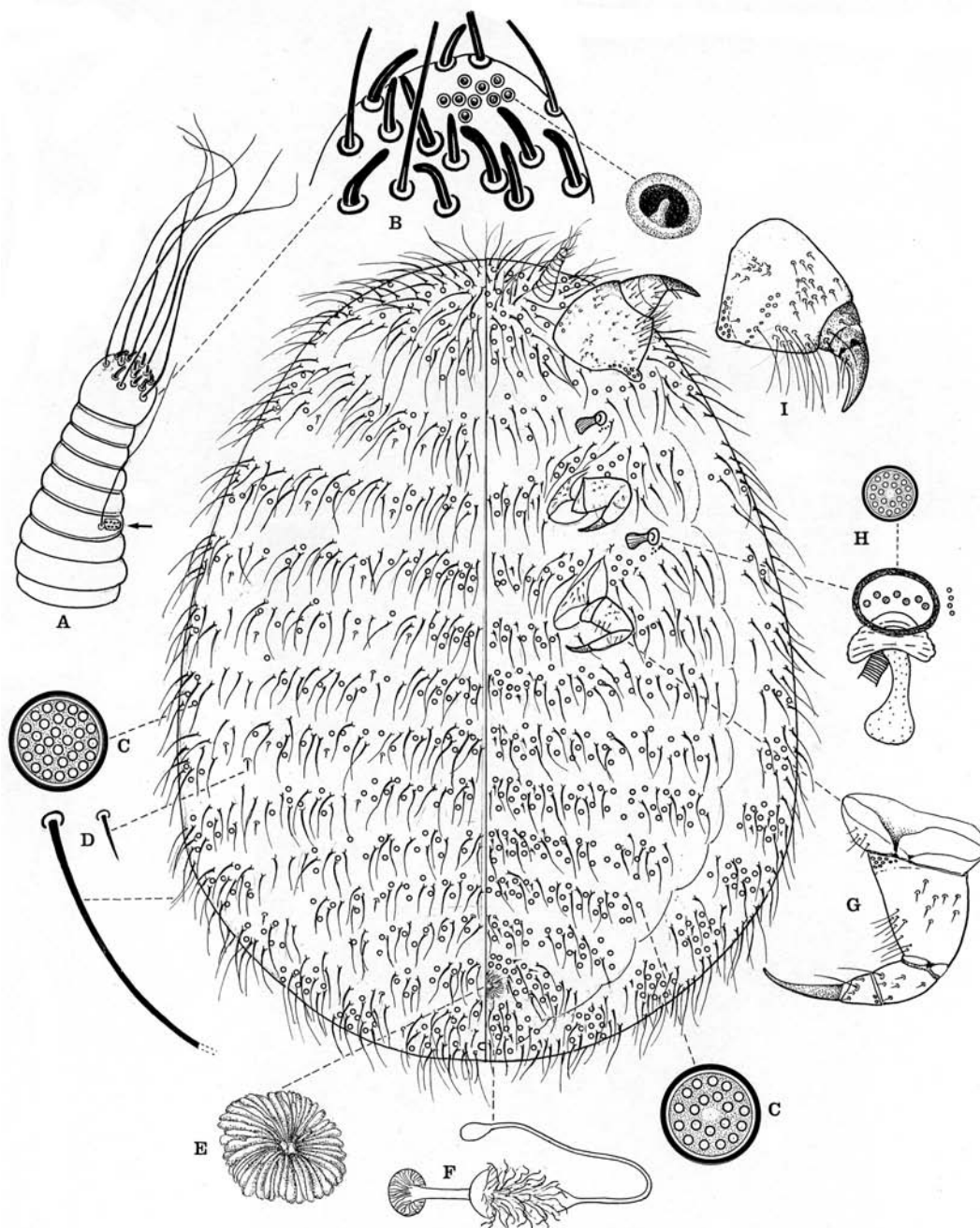


Figure 15

Adult female of *Porphyrophora polonica* (Linnaeus). A, antenna, segment IV with a sensilla placodeum (arrow). B, apical segment with flagellate setae, fleshy setae and sensilla. C, dorsal and ventral multilocular disc-pores. D, long and short setae on dorsum and venter. E, circular vulva radially folded. F, genitalia. G, metathoracic leg. H, thoracic spiracle. I, prothoracic leg.

of peritreme. Abdominal spiracles numbering 2 pairs present on first two abdominal segments, faintly developed, peritreme 25 µm in diameter, without pores. Hair-like setae with range of 250–400 µm long, distributed in transversal rows, each row 2–3 wide per segment on abdominal segments, more numerous on head and thorax; small setae 10–15 µm long throughout of body. Multilocular pores, about 10–16 µm in diameter, with a large variation of loculi ranging from 14 to 36 in 1, 2, or 3 rings, distributed in whole body in a band 2–3 pores wide on each segment. Disc-pores, on head and thorax with 14 to 19 loculi primarily ranged in one ring. Most numerous on last abdominal segments and around of vulva, these pores 14–16 µm in diameter with 20–36 loculi in 3 rings, outer ring: 13–19, middle ring: 10–11 and inner ring: 4–5 loculi. Vulva membranous, radially folded area.

Dorsum. Hair-like setae with average length 350 µm long, distributed in transversal row mostly in 3–4 setae wide per segment, more dense on head and prothorax. Small setae, 10–15 µm long, in a sparse uneven row 2 setae wide per segment, throughout body. Anus postero-dorsal with a weakly developed tube anal. Apparently some very small filamentous structure, difficult to discern, on margin of VI–VII and VIII segments of abdomen. Multilocular pores same structure but less numerous than those on Venter.

Host plants. *Agropyron*, *Alkanna*, *Caragana kirshinski*, *C. microphylla* *Cerastium*, *Dianthus*, *Herniaria*, *Festuca ovina*, *Fragaria*, *Koeleria cristata*, *Medicago*, *Melampyrum*, *Potentillaacaulis*, *P. bifurcata*, *P. impolita*, *P. recta*, *Scleranthus perrenis*, *Spergularia*.

Distribution. Palaearctic: China, Czech Republic, France, Germany, Hungary, Kazakhstan, Lithuania, Netherlands, Poland, Sweden, Switzerland.

Ethnoentomology. *Porphyrophora polonica* (L.), has played an important role for several centuries by providing dyes used in the textile industries and art paintings (Donkin 1977; Cardon 2003).

Subfamily TERMITOCOCCINAE Jakubski 1965

Tribe TERMITOCOCCINI Jakubski 1965

Genus *Termitococcus* Silvestri 1901

Termitococcus Silvestri 1901.

Type species. *Termitococcus aster* Silvestri 1901: 4, by original designation based on first-instar nymph and cyst.

Termitococcus carratoi Silvestri 1938: 33, adult female was made the type species of the family Termitococcidae by Jakubski (1965).

Termitococcus aster Silvestri

First-instar nymph

Material examined. Paraguay: Tacuru Pucu, from nest of termites, *Leucotermis tenuis*. Deposited at the Dipartimento di Entomologia e Zoologia Agraria (DEZA), Università degli Studi di Napoli “Federico II”, Portici, Italy.

Mounted material. Body almost globular, 1.2 mm long, 1 mm wide; derm throughout covered by setae.

Venter. Antennae 3-segmented; segment I–II short, without setae; apical segment very long, with about 4 setae and 2 long fleshy setae. Margin and submargin with long setae, medial and submedial area with setae about 25 to 150 µm long. Thoracic spiracles with small peritreme; base of atrium with numerous disc-pores. Mouthpart well developed. Legs similar shape and size, Metathoracic leg measurement with setal data: coxa; trochanter with 2 sensilla and 2–3 setae; femur long, distal part considerably enlarged; tibia with about 3 setae, fused with tarsus but with segmentation indicated by a distinct line; tarsus with a pair of short tarsal digitules dorsally; claw curving slightly, without digitules. Four long caudal setae, on posterior end of body.

Dorsum. Abdominal spiracles in 7 pairs.

Distribution. Neotropical: Paraguay.

Generic characters. Based on adult female of *Termitococcus carratoi* Silvestri.

Body elongate. Antennae probably 5-segmented. Abdominal spiracles in 8 pairs. Multilocular disc-pores absent, apart from those in the thoracic spiracular atrium. Long and fine flagellate setae densely covering dorsum and venter; on dorsum medially and submedially setae organising into characteristic groups in transverse (thorax) or oval (abdomen) area, each group with setae more or less pointing inwards and swirled; setae absent from five small areas medially between abdominal segments; surface of each of these area of a different structure to rest of derm. Spines present, with a broad base narrowing to a sharp point. Anal opening U-shaped and heavily sclerotised, posterior end of body, surrounded by a wide naked area. Anal tube present.

Termitococcus carratoi Silvestri 1936

Termitococcus carratoi Silvestri 1936: 34.

Termitococcus carratoi Silvestri, Jakubski 1965: 170.

Adult female (Fig. 16)

Material examined. Lectotype adult female designated here from material of Silvestri, labelled “Typus”. Brazil: Tres Lagoas, Mato Grosso district, on grass roots. Lectotype depository: Dipartimento di Entomologia e Zoologia Agraria (DEZA), Università degli Studi di Napoli “Federico II”, Portici, Italy.

Mounted material. Body elongate, segmentation clearly visible, approximately 10 mm long and 4–5 mm wide. Prothoracic legs modified for digging. Antennae probably 5 segmented, terminal segment long and oval in shape, all segments with long setae. Almost entire body surface covered in very long, fine, flagellate setae, each 650–950 µm long (650–700 µm); each with almost parallel sides and with a very small, narrow socket,

narrower than width of seta: long setae tending to be in indistinct groups, particularly on Dorsum - Medially on venter of abdomen, long setae shorter and more spin-like, some as short as 200 μm ; however, these shorter setae as broad basally as long setae, with a similar basal socket. Small fine setose setae absent apart from immediately anterior to opening of vulva. Spines present, each with a rather broad base (12-16 μm wide), abruptly

to a sharp point, length about 45 μm ; with a hint of a basal socket: present medially on venter of all abdominal segments and with a few laterally posterior to most abdominal spiracles. Multilocular disc-pores absent except within spiracular atrium. Derm quite thick but unsclerotised. With 8 pairs of abdominal spiracles, those on segment I displaced somewhat dorsad onto Dorsum.

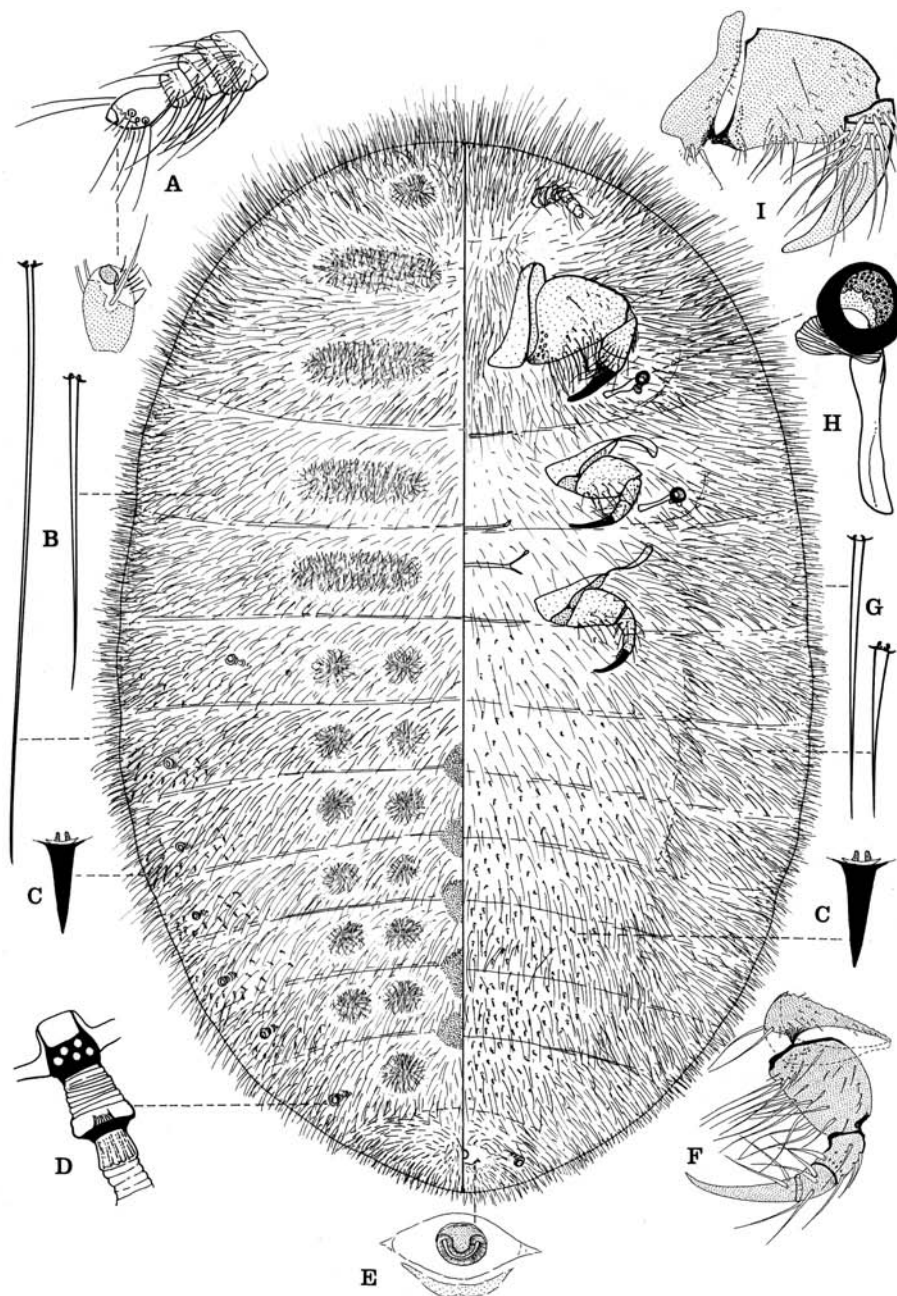


Figure 16

Adult female of *Termitococcus carratoi* Silvestri. A, antenna. B, dorsal setae. C, dorsal and ventral spines. D, abdominal spiracle. E, anal opening surrounded by a wide naked are and microductules. F, metathoracic leg. G, setae on venter. H, thoracic spiracle; prothoracic leg.

Venter. Sternal area of segment I present between metathoracic legs. As with dorsum, venter covered in a dense covering of long setae, but these rather sparse medially on abdominal segments I-VIII, where replaced by spines and shorter long setae. Spines most abundant on segment VIII, just anterior to opening of vulva, becoming less frequent anteriorly, where replaced by medium to short long setae, particularly medio-laterally. Microductules and other pores apparently absent.

Antennae apparently 5-segmented, total length 580-650 μm , but with a narrow, incomplete sclerotised basal ring which might represent segment I, latter without setae or pores; also, structure of basal segment possibly indicates two fused segments (thus antennae might be 7 segmented!); total length 620 μm (580 μm), including basal ring. Basal four segments all sclerotised and ring-like, each with 6-8 long setae, each 230-460 μm long and not narrowing near socket, plus spinose or fleshy setae, with 11 on basal segment and 4 on segment IV, plus 1 round sensilla; basal part of basal segment rather broad, possibly representing a rudimentary 2nd segment, with a band of pale areas which might be pores. Terminal segment (V) about 1/3rd total length of antenna (210 μm long), swollen, narrow basally, heavily sclerotised on basal 2/3rds; apical 1/3rd unsclerotised, with six (possibly eight) long setae, similar to those on lower segments, plus about 18 blunt spinose or fleshy setae (each about 30-55 μm long), and about five small sensilla. Eyespots apparently absent.

Thoracic spiracles: peritreme opening round, 100-112 μm wide, probably with a shallow raised rim; sclerotised margin of peritreme slightly oval and 150-165 x 130-140 μm wide; outer atrium of peritreme sclerotised towards outer rim, with 11-15 disc-pores plus some smaller spots; inner part of atrium membranous; with a membranous bow-tie shaped area mesad of peritreme, probably an inner atrium; inner apodeme more or less straight, broadest near peritreme and 260-330 μm long. Each spiracle with 2 small perispiracular sensilla near posterior margin.

Prothoracic legs very large, measurements with data on setae and pores for anterior surface only; all medium to long setae rather swollen towards base. Coxa ring-like, about 990 μm wide and 270 μm long, much wider than trochanter, with a strong articular scleritis; with 16 short (numerous) and 3 (4) long setae. Trochanter and femur fused and without any indication of segmentation; heavily sclerotised throughout; greatest length 1100 μm , width 760 μm ; distal end slightly narrower than proximal end; trochanter with about 19 campaniform pores in a broad transverse band near articulation with coxa, plus 10 setae of intermediate length along ventral surface. Femur with about 35 short setae (each 30-80 μm long) plus about 10 long setae, each perhaps 230-360 μm (500 μm) long. Tibia articulating strongly with femur; tibia + tarsus + claw, showing segmentation but no articulation; tibia about 260 μm long and 300 μm wide, with 1 long seta, plus 5 setae of medium length plus 3 minute setae; tarsus 115-120 μm long and 260 μm wide, with 6 medium to long setae but no campaniform pore located. Claw about 430 μm long, slightly curving and narrowing gradually to a blunt apex; with 4 long setae.

Meso- and metathoracic legs: basically similar to prothoracic legs but significantly smaller; data on setae and pores for anterior surface only; all medium to long setae rather swollen towards base. Coxa ring-like, about 754 μm wide and 230 μm long,

much wider than trochanter, with a strong articular scleritis; with about 18 very short setae (20-65 μm long) plus 2 long setae (265 μm long). Trochanter and femur fused but with segmentation indicated by a distinct line; heavily sclerotised throughout; greatest length 465 μm , width 360 μm ; distal end slightly narrower than proximal end; trochanter with about 12-14 campaniform pores in a broad transverse band near articulation with coxa, plus 5 (3) long and 4 shorter setae laterally and on ventral surface. Femur with about 10 short setae plus 5 long setae, each perhaps 220-365 μm long. Tibia articulating strongly with femur; tibia + tarsus + claw, showing segmentation but no articulation; tibia about 260 μm long and 150 μm wide, with 5 setae of medium length plus 6 minute setae; tarsus 185 μm long and 130 μm wide, with 4 setae of medium length setae and 4-6 campaniform pores. Claw about 370 μm long, slightly curving and narrowing gradually to a sharp apex; with 2 long digitules, each 195 μm long.

Pleural area of each segment with a large, dense group of long setae; those on abdominal segments I-V also with sparse groups of spines posterior to each abdominal spiracle, plus an occasional spine on segment VI, similar to those on Venter - Abdominal spiracles: eight pairs; pair on segment I much more dorsal than on more posterior segments; pair on segment VIII laterad to anal opening and therefore appearing ventral on Mounted material - Each spiracle with a circular outer opening with a distinct raised rim, 70 μm wide, which opens into an outer atrium, whose sclerotised walls appear to have a ring of disc-pores, structure of which could not be determined; outer atrium opens into an inner atrium with membranous, folded walls; a sclerotised cone-like inner opening present at base of inner atrium, which opens into a membranous tube, which is slightly balloon-like initially but gives way to membranous trachea. Perispiracular pores absent.

Vulva located intersegmentally between segments VIII and IX and covered by a dense group of long setae. Outer part broad, short and tubular, with parallel sides, 780 μm wide and 220 μm long; inner vagina radially folded and narrowing. Outer vulvar opening with numerous setae, some along margin of vulva thin and setose.

Dorsum. Long flagellate setae covering almost entire segment, but absent from a narrow band along each intersegmental membrane; also absent from a broad area around anus, and from five diamond-shaped areas medially, between abdominal segments II-III; III-IV; IV-V; V-VI, and VI-VII; surface of each of these area of a different structure to rest of derm. Long setae on head and thoracic segments in two large, transverse, oval areas, one on each side of mid-line. On abdomen, each segment apparently with four oval groups of setae, each medial group much larger than those more laterally; each group with setae more or less pointing inwards and swirled. Anal opening considered to be on 9th segment, which forms posterior end of body, but on mounted specimen appears ventral; surrounded by a wide area without setae. Anal opening sclerotised, 90 μm wide and 70 μm long, at base of cone-shaped indentation, latter about 260 μm wide and 170 μm long. Actual anal opening u-shaped and heavily sclerotised. Anal cone-shaped indentation with a pair of membranous areas along dorsal margin similar in structure to those intersegmentally on dorsum. Microductules very

long, perhaps 65 μm long, outer pore each about 2-3 μm wide, narrowing slowly to a long filamentous apex: extremely sparse, but perhaps most abundant laterad and dorsad to anal opening.

Host plant. Graminae.

Distribution. Neotropical: Brazil.

Cyst (Fig. 17)

Mounted material. Body oval, 5-6 mm long, 3.5-4 mm wide.

Venter. Antennae a simple circular structure, about 55 μm in diameter, including 8-9 fleshy setae. Thoracic spiracles with a long and tubular outer atrium with numerous disc-pores at its base and connected centrally to an inner atrium. Mouthparts present. Legs absent. Cicatrices in few number on abdomen, in a dense group medially on metathorax area. Setae scattered, denser on posterior end of abdomen.

Dorsum. Abdominal spiracles in 8 pairs with peritreme well apparente, slightly projecting from derm; each spiracles with disc-pores in atrium. Cicatrices few in number and arranged in a transvers row, one cicatrice wide on abdomen, scattered on head and thorax. Setae scattered, denser on head and posterior end of abdomen. Anal plate structure complex; an u-shaped anal opening surrounded by a circular sclerotised rim which is located in a larger oval area including a few number of pores surrounded by a large sclerotised rim.

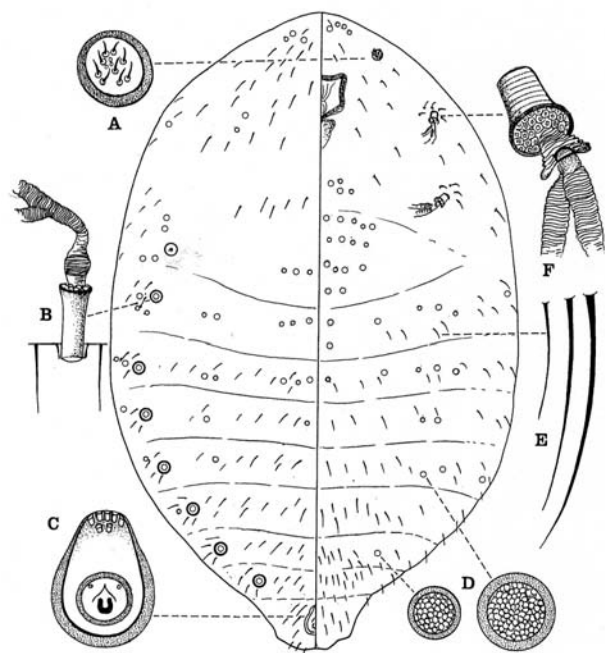


Figure 17

Cyst of *Termitococcus carratoi* Silvestri. A, antenna. B, abdominal spiracle with peritreme apparente, slightly projecting from derm. C, anal plate structure. D, dorsal and ventral cicatrices in different size; E, setae on both surface. F, thoracic spiracle.

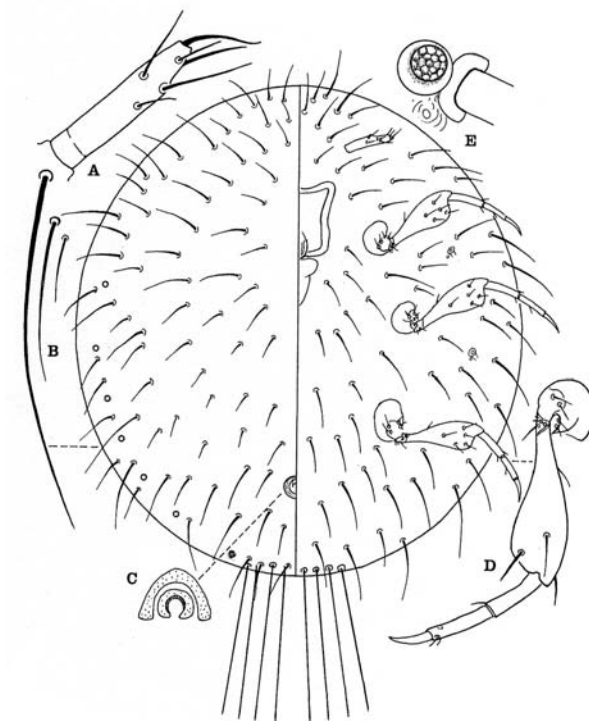


Figure 18

First-instar nymph of *Termitococcus carratoi* Silvestri. A, antenna. B, setae on margin and submargin. C, anal region. D, metathoracic leg. E, thoracic spiracle.

First-instar nymph (Fig. 18)

Mounted material. Body nearly circular, about 1-1.2 mm in diameter, with setae throughout on body.

Venter. Antennae 3-segmented, total length about 200-220 μm ; segment I-II very short without setae; apical segment about long, about 170-190 μm , with 6-7 setae and with one central apical stout seta, about 80-90 μm long. Mouthparts well developed. Thoracic spiracles with disc-pores in atrium. Legs well developed and identical. Coxa globular with 2 setae and one shorter; trochanter+femur 480-500 μm long; trochanter with 2 short setae, with 2 sensilla on each side; femur as long than tibia and tarsus+claw together, with 3-4 setae, distal end characteristic as in *Eurhizococcus* strongly enlarged; tibia with one ventral seta; tarsus with a short pair of tarsal digitules and with a ventral sensilla; claw long without digitules. Long setae, about 200-230 μm long, around body margin; setae, 120-140 μm long throughout on venter, shorter setae 25-50 μm , rare medially. Cicatrices absent.

Dorsum. Long setae as on venter around dorsal margin and submargin; median area with short setae, 30-50 μm long, scattered. Anal opening u-shaped surrounded by a half strongly sclerotised rim. Abdominal spiracles 7 in number. 4 pairs of caudal setae, about 500 μm long, on posterior end margin.

Tribe EURHIZOCOCCINI Jakubski 1965
Genus *Eurhizococcus* Silvestri 1936

Eurhizococcus Silvestri 1936: 39.

Type species. *Margarodes brasiliensis* Wille 1922: 84.

Generic characters. Body elongate. Prothoracic legs fossorial; tibia + tarsus of all legs with long basally swollen setae; trochanter with sensilla on each side and with some setae. Antennae 5-segmented, antennal segments short and stout; segments II-V with numerous long setae, short setae and fleshy setae. Meso and metathoracic sternite with an intersegmental apodemes. Thoracic and abdominal atrium with multilocular disc-pores and simple pores. Abdominal spiracles in 7 pairs, subequal in size. Long and thin hair-like setae and shorter setae both with a flat socket densely covering whole body. Spines present, particularly medially on venter and on margin and submargin dorsally. Multilocular disc-pores with 2 rings of loculi. Vulva a transverse fissure. Anal tube well developed.

Eurhizococcus brasiliensis (Wille 1922)

Common name: brasilian ground pearl

Margarodes brasiliensis Wille 1922: 84.

Margarodes brasiliensis Hempel, Costa Lima 1924: 136.

Eurhizococcus brasiliensis (Hempel), Silvestri 1936: 39.

Eurhizococcus brasiliensis (Hempel), Jakubski 1965: 174.

Margarodes soriai Foldi 1987. Syn. in Foldi 1989: 320.

Eurhizococcus brasiliensis (Wille), Foldi. Correct citation of author. Adolph Hempel has been cited over the past 80 years as author of *Margarodes brasiliensis*, but in reality he only suggested this name to J. Wille who described and published this species in 1922.

Material examined. Four slides bearing the following indications: *Margarodes brasiliensis*, 8-1921, J. Will, Hempel, Santa Maria, Rio Grando do Sul, deposited in the Departamento de Entomologia, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil, MZSP.

Other materials examined. Brazil: Rio Grando do Sul, on *Vitis vinifera*, in the following localities: Bento Gonçalves, 18 November 1985; Veranópolis, 20 November 1985; Anne Rech, Faizenda Souza, 21 November 1985, Flores de Cunha, 22 November 1985 on *Vitis riparia*, Soria and Foldi rec.

Adult female (Fig. 19)

Live material. Body elongate, derm flexible, yellow, covered by long, thin setae.

Mounted specimen. Body elongate, 5-8 mm long, 3-5 mm wide, with body segmentation clearly visible. Body with long flagellate setae, medium and short setae; all setae with thin base; presence of spines. Multilocular disc-pores with 2 rings of loculi. Tibia and tarsus with long and thin hair-like setae. Abdominal spiracles in 7 pairs.

Venter. Antennae apparently 5-segmented, total length 500-600 μ m, but an incomplete basal ring may represent two fused segments, thus antennae might be 7 segmented; all segment short and wide, each with long setae, except segment I; segment II-IV with about 8-12 long setae, plus 8-12 fleshy setae; terminal

segment longest and oval in shape with 6-8 setae, plus about 20-26 fleshy setae. Eyespot absent.

Thoracic spiracles with large peritreme circular 140 μ m wide, with strongly sclerotised rim; atrium very few deep, with 1-2 multilocular disc-pores and 15-20 simples pores; with an apodeme strigth and narrow. Each spiracle with 5-9 perispiracular sensilla near peritreme.

Abdominal spiracles in 7 pairs, in margin, those on segment I-II displaced dorsad onto dorsum; pair on segment VIII laterad to anal opening, each spiracle with a peritreme 100 μ m wide which opens into an outer atrium whose sclerotised base with 1 or 2 multilocular disc-pores plus about 20 simple pores; outer atrium opens into an inner atrium with membranous, circularly folded walls; base of inner atrium with a cone-like opening which opens into a short membranous tube followed by a trachea.

Prothoracic legs fossorial very large; coxa with a strong articulatory sclerosis, with numerous short seta, and 3-4 long setae; trochanter and femur fused, heavily sclerotised throughout, greatest length 1100 μ m, width 800 μ m; trochanter with about 10-15 campaniform sensilla and some setae; femur with few short setae dorsally plus numerous long setae, each about 250-350 μ m long; tibia about 260 μ m long and 300 μ m wide, articulating strongly with femur, with several long setae, plus setae medium length; tarsus 110-120 μ m, long and 260 μ m wide, with few setae, 250 μ m long but without campaniform sensilla; claw about 430 μ m long, curving and narrowing gradually to a blunt apex, with 4 setae 150-200 μ m long on each side.

Venter, particularly margin and submargin, densely covered by long hair-like setae, 900-1100 μ m long, but these rather sparse medially on meso and metathorax and on abdominal segments I-VI where replaced by spines and shorter long setae, 300-450 μ m long; on segments VII-IX no spines located only short long setae. Vulva placed intersegmentally between segments VIII and IX, radially folded.

Multilocular disc-pores, about 12-14 μ m wide, with strongly sclerotised rim, with 15-17 loculi in outer ring and 4-8 loculi in inner ring throughout venter, denser on VIII-IX abdominal segments.

Dorsum. Setae approximately four length different: long flagellate setae, 1000-1200 μ m long, rather on margin and submargin; medium setae 400-500 μ m long and shorter setae, 130-160 μ m long, throughout on dorsum; stout seta, about 80-100 μ m long, medially on abdomen and spines, 30-50 μ m long, on margin and near of abdominal spiracles. Multilocular disc-pores same type than on venter sparse on dorsum, denser on posterior abdomen. Anus posterior, a sclerotised simple opening, associated with sclerotised plate; anal tube present.

Host plant. Jakubski (1965), Soria & Gallotti (1986), Foldi & Soria (1989) and Botton *et al.* (2000) has been reported about 70 host plants.

Amarilidaceae: *Amarilis* sp., **Compositae:** *Baccharis dracunculoides*, *Baccharis genistelloides*, *Baccharis trimera*, *Chaptalia nutans*, *Cichorium endivia*, *Cichorium intybus*, *Dahlia*, *Lactuca sativa*, *MatricariaSolidago microglossa*. **Convolvulaceae.** *Ipomoea batatas*, **Cruciferae:** *Brassica campestris*, *Brassica napus*, *Raphanus sativus*,

Sinapis nigra. **Cucurbitaceae:** *Cucurbita pepo*, *Lagenaria vulgaris*, *Sechium edule*. **Euphorbiaceae:** *Ipomoea batatas*, *Manihot palmata*, *Manihot utilissima*. **Graminae:** *Digitaria* sp., *Saccharum officinarum*. **Juglandaceae:** *Juglans regia*. **Labiatae:** *Ocimum basilicum*, *Rosmarinus officinalis*, *Salvia officinalis*, *Salvia splendens*. **Legumi-**

nosae: *Arachis hypogaea*, *Medicago sativa*. **Malvaceae:** *Hibiscus esculentus*. **Moraceae:** **Myrtaceae:** *Feijoa sellowiana*. **Onagraceae:** *Fuchsia* sp. **Oxalidačėaė:** *Oxalis articulata*, *Oxalis criorrhiza*, *Oxalis sellowiana*. **Phytolaccaceae:** *Phytolacca decandra*. **Portulacaceae:** *Talinum patens*. **Punicaceae:** *Punica granatum*. **Rosaceae:** *Cydonia*

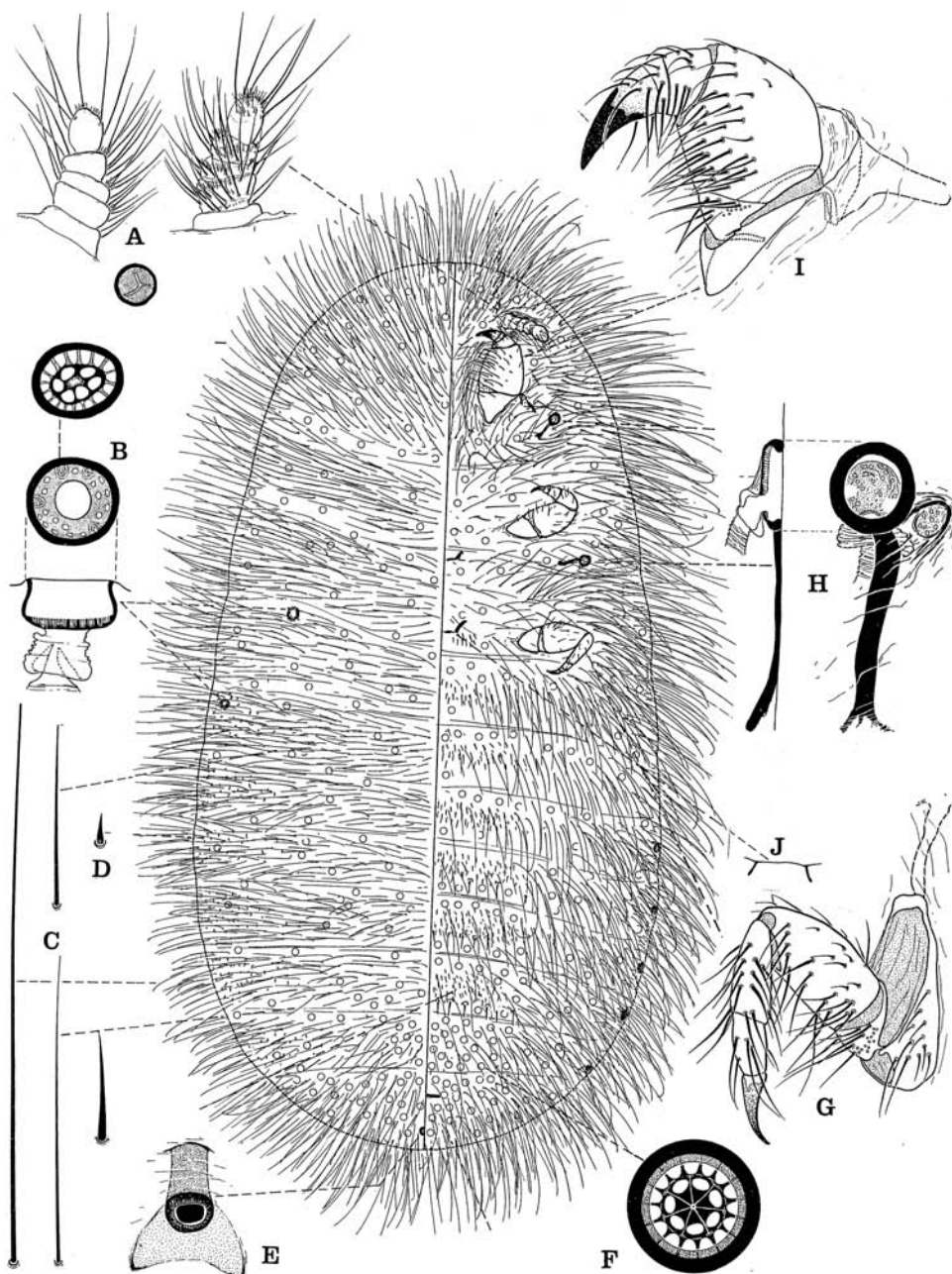


Figure 19

Adult female of *Eurhizococcus brasiliensis* (Wille). A, antenna on both side. B, thoracic spiracle with detail of pores on base of atrium. C, dorsal and ventral setae. D, dorsal and ventral spines. E, anal tube, anal opening associated with a sclerotised plate. F, multilocular disc-pores on posterior end of abdomen. G, metathoracic leg. H, thoracic spiracle. I, prothoracic leg. J, metathoracic sternal apophysis.

oblonga, *Cydonia vulgaris*, *Prunus domestica*, *Prunus persica*, *Pyrus communis*, *Pyrus malus*. **Rubiaceae:** *Gardenia* sp. **Salicaceae:** *Salix babylonica*, *Salix humboldtiana*. **Umbelliferae:** *Apium graveolens*, *Daucus carota*, *Petroselinum hortense*, *Petroselinum sativum*. **Vitaceae:** *Vitis*, *Vitis vinifera*, *V. riparia*.

Distribution. Neotropical: Brazil, Parana, Rio Grande do Sul: Anne Rech, Faizenda Souza, Antonio Prado, Bento Gonçalves, Caxias do Sul, Flores da Cunha, Veranópolis; Videira; Santa Catarina; São Paulo.

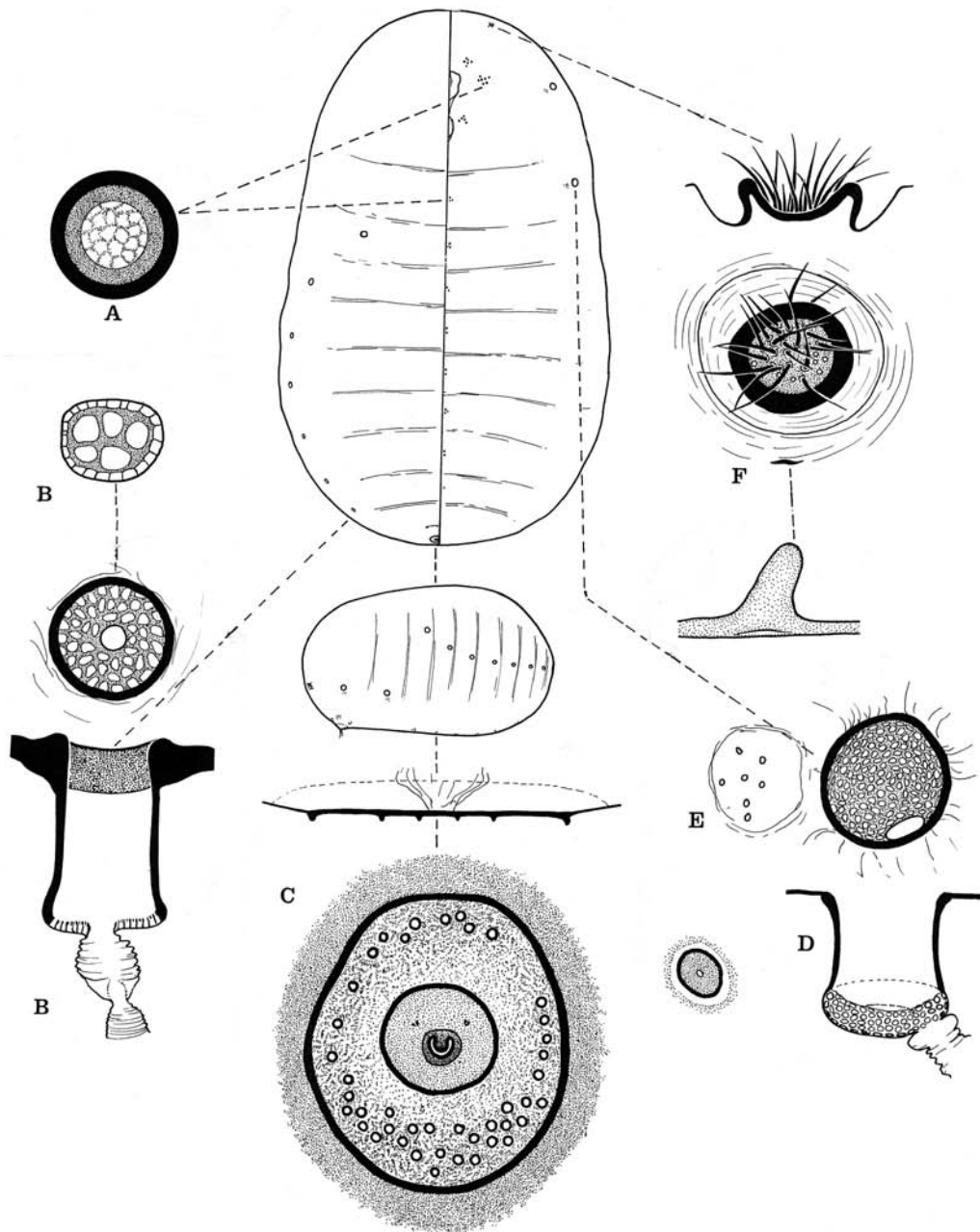


Figure 20

Cyst of *Eurhizococcus brasiliensis* (Wille). A, several group of cicatrices surrounding mouthparts. B, abdominal spiracle with detail of pores on its base. C, anal plate structure. D, thoracic spiracle showing pores at its base. E, perispiracular sensilla. F, antenna with fleshy setae and with a dermal protuberance.

Economic importance. This species is the major pest of the grapevine in Southern Brazil which is a traditional viticulture region. In the state of Rio Grande do Sul several hundred ha of vineyards were infested resulting in vines dying in patches which gradually become

larger and the whole vineyard decline in vitality and finally destroyed (Foldi & Soria 1989). The Diptera *Prolepsis lucifer* (Asilidae) was found in field in the population of *E. brasiliensis* and reveal as a potential biological control agent as a predator within a integrated pest

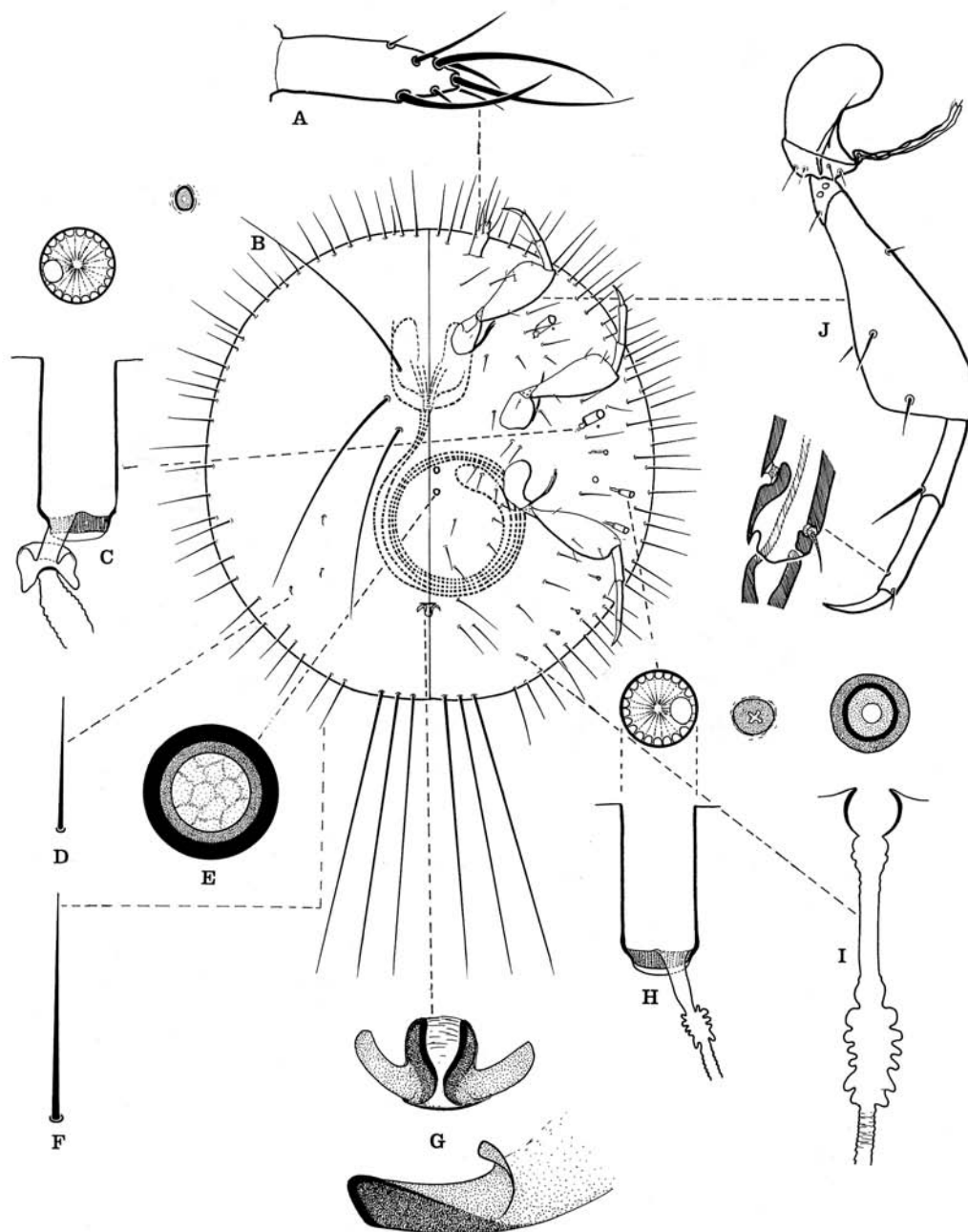


Figure 21

First-instar nymph of *Eurbizococcus brasiliensis* (Wille). A, antenna. B, three pairs of long setae medially on thorax. C, thoracic spiracle. D, dorsal setae. E, two pairs of ventral cicatrices medially on thorax. F, setae on margin. G, anal structure. H, second abdominal spiracle. I, last abdominal spiracle. J, prothoracic leg, femur with characteristic enlarged distal part.

management (Soria *et al.* 2004). *E. brasiliensis* has been recorded as a pest of *Medicago sativa* in Santa Catarina, Brazil (Kalvelage 1987).

Cyst (Fig. 20)

Test greyish, elongate, 4-7 mm long, 3-4 wide with very thin wall. Live nymph shining yellow with thick derm.

Venter. Antennae a small circular, 80 µm in diameter, protrusion with a deep pit where emerging about 15-20 soies, 50 µm long. Near of antennae a small excrescence of derm observed. Thoracic spiracles with perimetre 160 µm wide and with numerous multilocular disc-pores in atrium. Anterior spiracles with 12-18, posterior spiracles with 7-8 pores simples (sensilla). Each side of mouthparts with 2 or 3 groups of small cicatrices, number varying between 16-37. Thorax and abdomen medially with several groups of cicatrices, each group with about 2-9 cicatrices. Anal plate broadly oval, 260 µm on 240 µm, bearing U-shaped anus surrounded by about 42 cicatrices.

Dorsum. Abdominal spiracles in 7 pairs; each spiracles with perimetre 60 µm wide and atrium with numerous disc-pores indential of those thoracic spiracles. No other morphological structures visible.

First-instar nymph (Fig. 21)

Live first-instar nymph yellow, body circular about 800-850 µm in diameter, margin densely surrounded by long setae.

Venter. Antennae 1 or 2 segmented, total length 75 µm bearing about 7-8 setae in various length. Margin aroun of body with setae 120-150 µm long. Shorter setae in submargin region. Mouthparts well developed, labium with 4-5 pairs of setae. Thoracic spiracles with peritrem 15 µm wide, atrium long about 40 µm, at its base about 20 pores in a peripheral circle; each spiracle with a singl sensilla placed posteriorly. Abdominal spiracles in 7 pairs. Second and third spiracles larger than others. Atrium long its base as toracic ones. Legs strongly developed, with shape and size identical. Trochanter with 2 sensilla on each side; femur about 100 µm long, with 4-5 short setae, strongly enlarged near of tibia as in *Termitococcus* crawlers; tibia short, about 40 µm long, with a single long spinose seta; tarsus 55 µm long with a pair short tarsal digitules; claw curved, about 40-50 µm long, without claw digitules. A cruciform pore between 1st and 2nd abdominal spiracles. Two pairs of cicatrices medially on metathorax. 3 pairs of caudal setae, each about 500 µm long.

Dorsum. 3 pairs of long setae, about 400 µm long, on thorax medially, 6-8 short setae on abdomen. Anal ring with a strongly sclerotised structure.

Key to the type species of the genera based on the adult females

Note. This key is based only on the type species of each genus and the characters selected may not entirely reflect all that are exhibited by species of the genus.

1. With 8 pairs of abdominal spiracles 2

- With fewer than 8 pair abdominal spiracles 3
- 2. Multilocular disc-pores absent on body . . . *Termitococcus*
- Multilocular disc-pores present on body; prothoracic claw with an obvious basal heel *Neomargarodes*
- 3. With 7 pair abdominal spiracles; dense long hair-like, 900-1100 µm, on body; anal opening associated with a large sclerotised plate *Eurbizococcus*
- Dense long hair-like, 900-1100 µm, absent on body; anal opening not associated with a large sclerotised plate 4
- 4. Multilocular disc-pores without central loculus only with a central circular zone; finger-like structures before vulva in a semicircular pattern *Margarodes*
- Finger-like structures before vulva absent, with 6 pairs of abdominal spiracles 5
- 5. Body margin with pleural extensions bearings spines, setae and disc-pores; spines, setae and disc-pores in distinct groups on abdominal sternites . . . *Dimargarodes*
- Body margin without pleural extensions; spines, setae and disc-pores not in distinct groups on abdominal sternites 6
- 6. Derm with raised bare patches *Heteromargarodes*
- Derm without raised bare patches 7
- 7. Prothoracic claw with 1-2 obvious protrusions at its base *Promargarodes*
- With 3 pairs of abdominal spiracles; prothoracic claw without protrusions at its base 8
- 8. Body densely covered with dermal papillae *Eumargarodes*
- Body without dermal papillae, with 2 pairs of abdominal spiracles 9
- 9. Anterior pairs of abdominal spiracles obviously larger than posterior; multilocular disc-pores with loculi strongly different in size and shape with exceptionelly very large triangular or quadrate zone central *Margarodesia*
- With 0-2 pairs weakly developed abdominal spiracles; multilocular disc-pores with loculi same size and shape without very large triangular or quadrate zone central; antennal segments naked, except apical segment; spines absent on body 10
- 10. Antennal segment IV with a sensilla placodeum *Porphyrophora*

Remarks

Archaeococcoids are defined by plesiomorphic features, particularly the presence of abdominal spiracles in both sexes, the presence of compound eyes in males, an XX-XO chromosome system and, the probable generalized presence of a pair of sensilla on the apical part of labium. Study of archaeococcoid relationships forms a dynamic and controversial topic in determination of the evolutionary history of scale insects and thus higher classification.

The archaeococcoids comprise some small families and two large important groups, the Ortheziidae and the Margarodidae. In phylogenetic trees of Coccoidea, the margarodids arises from one of the basal nodes near the Ortheziidae (Foldi 1997; Gullan & Sjaarda 2001;

Cook *et al.* 2002). The family concept for Margarodidae by Morrison (1928), although a remarkable synthesis on this difficult group, resulted in a diversified morphological and biological assemblage which lacked definitive characters to define the whole family. Also, relationships among subfamilies, tribes and genera, as well the monophyly of some groups are not well yet established. However, the current view on Morrison's higher classification is that all subfamilies and some tribes of should be elevated to family rank (Koteja 1974). Subsequent studies on the phylogenetic history of margarodids (Gullan & Sjaarda 2001) and on the molecular differentiation among margarodid lineages (Cook *et al.* 2002) supports Koteja's hypothesis. Morrison's tribe Margarodini comprises the subterranean, cyst-forming species and forms a well-defined natural group (Miller 1984). A phylogenetic analysis of the Margarodidae sensu Morrison based on adult male morphology pointed out that these hypogeal margarodids constitute a distinct monophyletic group (Hodgson & Foldi 2005).

The ground pearls form a fascinating group due to their biology, behaviour and morphological traits. The features that characterize these taxa are unique, such as having a subterranean development with an apodous feeding nymphal instar referred to as a cyst, a defense strategy of constructing a separate protective test around their body from their own liquid excreta, the behavioral adaptation to modify their life-cycle to survive in adverse environmental conditions, and having modified prothoracic fossorial legs, and clearly separate ground pearls from others taxa.

Koteja (1985) postulated that scale insects may have evolved in forest litter during the Permian to Jurassic and that some groups acquired adaptations to subterranean (hypogeal) life. At present, no ground pearls fossils have been found and thus there are no indications about their antiquity. However, the earliest radiation involved the archaeococcoids and Gullan & Sjaarda (2001) proposed that the presence of the cyst in the ground pearls may be plesiomorphic in the evolution of the archaeococcoids.

The ground pearls with 105 species occur worldwide, often in high abundance and species richness. The genera of *Neomargarodes* Green with 16 species and *Porphyrophora* Brandt with 47 species are predominantly

Palearctic and, species of *Porphyrophora* has a wide-range of host preferences. According to Jakubski (1965) and Jashenko (1990), *Porphyrophora polonica* (L.) has been reported from 29 host-plant species in Europe and, from 60 plant species belonging to 20 genera from 15 families in Palearctic area. The genus *Margarodes* with 26 species is represented in all biogeographical regions, with high species richness in Afrotropical region, with at least 10 species in South Africa, and with about 7 species in Nearctic region.

A large number of ground pearls are associated with cultivated plants, may develop large infestations in dense aggregations on the roots of their host-plants and are significant pests of agriculture. These include *Eurhizococcus brasiliensis* (Wille) (Foldi & Soria 1997) and *Margarodes vitis* (Philippi) in vineyards in South America (Gonzalez *et al.* 1969; Gonzalez 1983); five endemic species of *Margarodes* (*M. capensis* Giard, *M. greeni* Brain, *M. prieskaensis* (Jakubski), *M. trimeni* Giard and *M. vredendalensis* De Klerk) infesting vineyards in South Africa (DeKlerk *et al.* 1982; De Klerk 1982); *Margarodes meridionalis* Morrison infesting roots of Bermudagrass in the southern US damaging lawns and golf courses and in California where this species is a pest on grapevines (Kouskolekas & Self 1973; Barnes *et al.* 1954; McDaniel 1965), *Eurhizococcus colombianus* Jakubski and *Margarodes carvalhoi* Costa Lima affecting sugarcane in South America (Costa Lima, 1949, Jakubski, 1965). In the Mediterranean area, *Porphyrophora tritici* (Bodenheimer) is reported to be injurious to wheat (Duran 1971; Vahedi 1999).

Some ground pearls are beneficial to people, for example, *Porphyrophora polonica* (L.), *P. hamelii* Brandt has played an important role in the human societies in the Orient, Europe, and the Mediterranean basin for several centuries by providing dyes used in the textile industries, art paintings and other activities (Donkin 1977; Lambdin *et al.* 2002; Cardon 2003).

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