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A REDESCRIPTION OF PUTO ANTENNATUS SIGN. (HOMOPTERA, COCCOIDEA)

WITH NOTES ON *CEROPUTO PILOSELLAE* ŠULC AND *MACROCEROCOCCUS SUPERBUS* LEON.

by

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In the taxonomy of Coccoidea or scale insects much confusion is due to an insufficient knowledge of the type species of several genera. Especially our knowledge of some of the older genera is very incomplete, as the descriptions of their type species are extremely short and superficial from the modern point of view. The type specimens, on which the original descriptions of the genera were based, are distributed over several museums in all parts of the world; in some cases type material is no longer in existence, and as far as available it is seldom lent to persons in foreign countries. In consequence of this we have often to rely on the original description, as the type material is not available for examination.

Signoret (Essai sur les Cochenilles, 1868-1876) was one of the first to describe the microscopical details of the genera and species which he introduced. He boiled his specimens in a solution of caustic potash to make microscopical preparations of the chitinous parts and did not hesitate to prepare even unique specimens ("que nous n'avons pas hésité à sacrifier dans l'intérêt de la science, tout en conservant les préparations bonnes à consulter, pensant qu'elles seraient ainsi plus utiles qu'une masse informe attachée à un épingle et qui ne peut présenter aucun caractère que l'on puisse énumérer"). In many cases, however, his descriptions are not detailed enough for the needs of present taxonomy. As the number of described species has increased greatly since Signoret's time, it has become necessary to pay attention to several minute details which were formerly of no importance to separate the species then known.

In consequence of the superficial descriptions by earlier authors the concepts of several genera are rather vague. Ferris has emphasized that in order to obtain a sound foundation for the classification of scale insects it is more important to re-examine the species already named, especially the generic types, than to describe continuously new species by which the confusion in the nomenclature is only increased. Ferris himself has published detailed figures of the type species of more than 200 (of ca. 275) genera that have been named in the family Diaspididae (Microentomology, 1936-1941).

The Morrisons (1922) had already described the generic types in Maskell's collection; their paper was followed by others (1923, 1927) describing the species of Monophlebinae, Margarodidae, and Asterolecaniinae which had been named by Maskell in the years 1879-1898. In his monograph of the Margarodidae Morrison (1928) has paid special attention to the type species of the genera.

Steinweden (1929) studied 32 important genera of the 60 or more described in the family Coccidae (former subfamily Lecaniinae) by examination of their type species and (or) other species available to him.

Very little of such work has been done in Europe. Green (1899, 1934) has examined Signoret's types of *Aspidiotus lataniae* and *Antonina purpurea* (type species of the genus *Antonina),* and also Walker's type of *Monophlebus contrahens* (Green, 1923). Šulc (1943, 1944, 1945) published an elaborate description of all instars of *Phenacoccus aceris* (Sign.), *Phenacoccus piceae* (Loew) and *Pseudococcus nipae* (Maskell). The first species is the type of the genus *Phenacoccus* Ckll., the two last named species were chosen as types of Šulc's new genera *Peukinococcus* and *Nipaecoccus.* Sachtleben (1944) examined some original specimens of Bouché's collection, e.g., *Aspidiotus nerii* Bouché, 1833 (= *Chermes hederae* Vallot, 1829), the type species of the genus *Aspidiotus* Bouché.

The present writer has recently described Signoret's specimens of *Ripersia corynephori* Sign., the generic type of *Ripersia* (Reyne, 1951). After publication of this paper Dr. Harold Morrison called his attention to the confusion in the genera *Puto* Signoret, 1875, *Ceroputo* Šulc, 1897, and *Macrocerococcus* Leonardi, 1907, and suggested to redescribe also *Puto antennatus* Sign., type of the genus *Puto,* if the original material could be obtained from the Vienna Museum of Natural History. I am greatly indebted to Dr. Max Beier of the Vienna Museum for sending me on loan Signoret's specimens of *Puto antennatus,* viz., one male and two females (mounted dry), and one microscopical preparation of a female, made in 1934 from Signoret's specimens by E.E.G. (apparently E. E. Green). I also express my sincere thanks to Dr. H. Schmutterer of Munich, who in July 1951

discovered *Puto antennatus* in the Bavarian Alps, and provided me with three females and three males which were preserved in alcohol. In July 1952 he visited the same place again, and collected more material, including larvae of all stages and male cocoons; further he made observations on the behaviour of these insects in their natural environment, which he kindly put at my disposal. I am obliged to Dr. Morrison for his suggestion, for a translation of the Czech and Russian papers of Šulc (1897) and Borchsenius (1948), and for the loan of preparations of some American species of *Puto* (*P. yuccae* Coq. ♀, and ♂, *P. ulter* Ferris ♀), and of *Ceroputo pilosellae* Šulc. He also took the trouble to read my manuscript, and to make some remarks on it. By the courtesy of Dr. G. Remaudière at Paris I could examine preparations of some specimens of *Puto antennatus* (♀ and ♂), which had been collected by Dr. P. Vayssière in September 1932 at Pesey (Savoy), as mentioned by Balachowsky (1932).

The following description of *Puto antennatus* [1]) is based on Signoret's specimens, as far as this was possible. For the male, and the larval stages, it has been supplemented by details found in the slides of Schmutterer's specimens from Bavaria. The males and females, collected by Vayssière on *Abies pectinata* in French Savoy (Sept. 1932), belong certainly to the same species as those collected by Schmutterer on *Pinus cembra* in Bavaria (July, 1951). Signoret's old dry specimens (2 ♀ ♀ and 1 ♂) were shrivelled and shrunk. In the male, which was pasted on a pinned strip of cardboard, the principal details of the eyes, antennae, legs, wings, genital armature, and caudal filaments were still visible with a binocular microscope (60 ×); as far as could be ascertained this male agrees with the specimens collected in Bavaria. The two available females, preserved dry in a small vial, were without legs and antennae, but two legs (only femur, tibia, and tarsus) could be recovered from the vial and were mounted on a slide for microscopical examination. In the microscopical preparation of E. E. G. the legs are also missing; only the coxae, and in one leg also the trochanter, are left; the segments I-VIII of one antenna are present, but the apical segment is lacking and the basal ones are ruptured. I have made a second preparation of one of Signoret's females, but this is still less complete, as the antennae are wholly lacking. Though these preparations of Signoret's females are very defective, I have been able to trace in them all the characters shown by the

1) The original name was *Putonia antennata,* but afterwards Signoret changed the generic name *Putonia* (already used for a genus of the Pentatomidae) into *Puto* which is usually taken as a masculine noun. Crabro, bufo, pavo, leo, unio, struthio, vespertilio (with genitive -onis) are masculine, but hirudo and hirundo (with genitive -inis) are feminine in Latin.

fresh specimens from Bavaria, except those of the last antennal segment. In Vayssière's specimens from France the last antennal segment is quite similar to that of the Bavarian specimens; this applies also to the sensory hairs on the 3 last segments.

Šulc (1897) has also examined Signoret's specimens of *Puto antennatus* in connection with his description of *Ceroputo pilosellae*. He has briefly described the differences between *Puto* Sign. and his new genus *Ceroputo*; his figures 18-22 represent the antennae, legs, claw, anal ring, and trilocular pores of *Puto* Sign. Due consideration has been given to Šulc's description and figures, which agree with my own observations, as Signoret's material must have been in a much better condition in 1897 than it is at present. Šulc prepared two of Signoret's female specimens for microscopical study; they were boiled in a solution of caustic potash and mounted in glycerine; three other females were also treated with KOH and examined in toto in glycerine. It seems that the microscopical preparations are no longer available, and that only the three last mentioned specimens have been returned to the Vienna Museum; two of these specimens have afterwards been used by E. E. G. and myself for microscopical mounts.

Puto antennatus Sign., *Ceroputo pilosellae* Šulc, and *Macrocerococcus superbus* Leon., which are the type species of their genera, have been compared with each other. I have examined specimens of *Macrocerococcus superbus* from Italy (♀ ♀, larvae I) and Bavaria (♀ ♀, ♂ ♂, larvae III). With reference to *Ceroputo pilosellae* Šulc I had to rely on a slide with 2 specimens (♀ ad. and larva 1), borrowed from Dr. Morrison; these specimens had been intercepted by the Plant Quarantine Service in New York. Further I have consulted for this species the descriptions and figures of Šulc (1897) and Borchsenius (1949).

Puto antennatus is at present known from the French, Swiss, and Bavarian Alps. Signoret's females were collected about 1875 on *Pinus cembra* L. at Briançon (Hautes Alpes), his males on the "sapin ordinaire" (= *Abies pectinata* D.C. = *A. alba* Mill.) at Chambéry (Savoy). Vayssière's males and females were taken on *Abies pectinata* at Pesey (Savoy) in Sept. 1932. The occurrence in Switzerland is reported by Lindinger (1912) and Keller (1921). Dr. Schmutterer found this species in July 1951 in the Bavarian Alps near the Funtensee, a small lake about 20 km S.S.W. of Berchtesgaden; the specimens (♀ and ♂) were collected under bark scales of twigs and slender stems of *Pinus cembra*. In July 1952 he found the species again on *Pinus cembra* near the Funtensee and the Schwarzsee, but also on *Picea excelsa* near the Grünsee and on the Gotzenalm, east of the Königsee. All these localities are from 1600 to 1900 m above sea-level, and located south

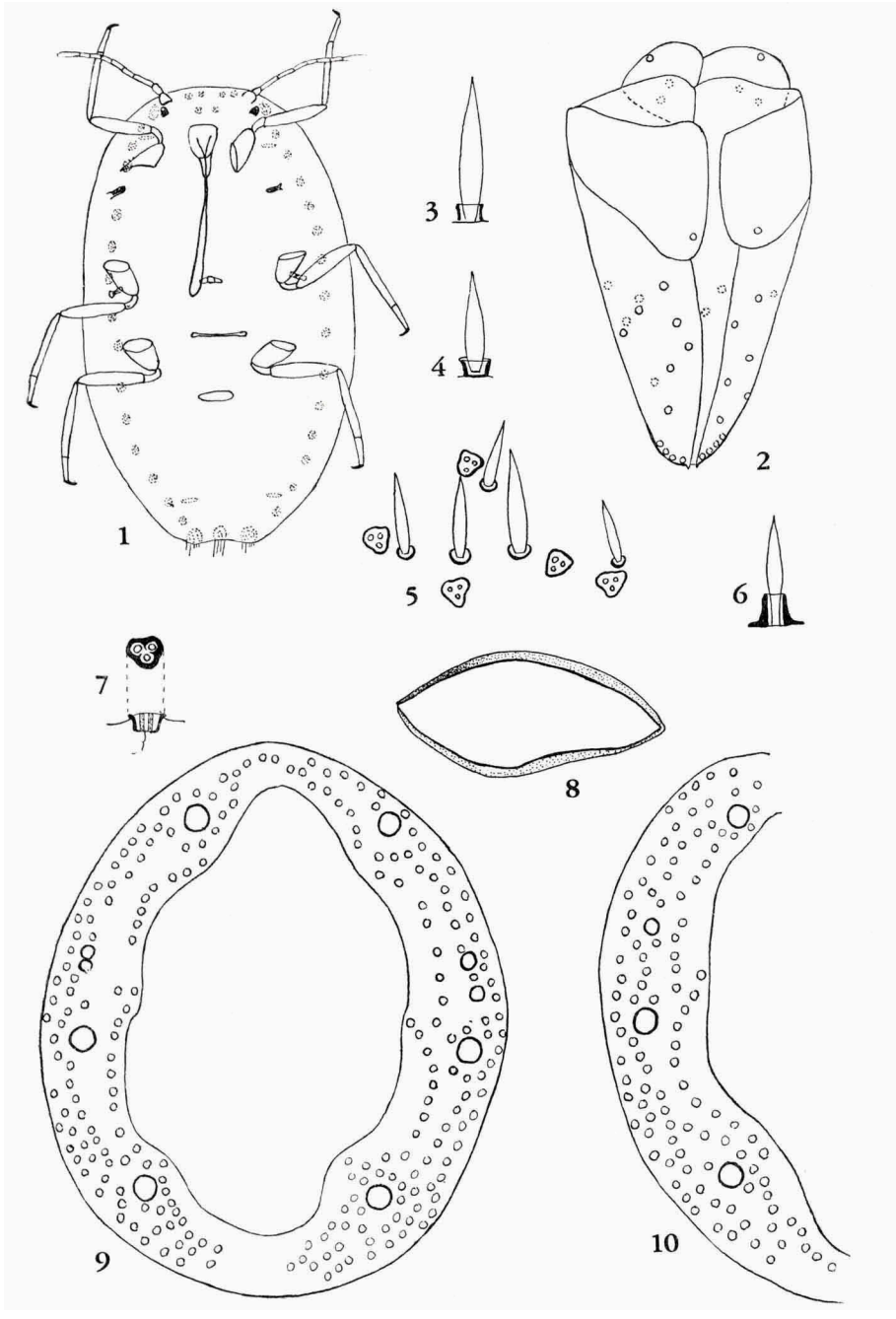
of Berchtesgaden. On *Abies pectinata,* which is common there but not found above 1200 m, Dr. Schmutterer has searched in vain for *Puto antennatus.* He called my attention to Dingler's short description of *Pseudococcus tirolensis,* found on *Picea excelsa* in the Karwendel mountains of Tirol, which seems to refer to *Puto antennatus* (cf. Zeitschr. f. angew. Entomologie, 1924, vol. 10, p. 387). *Puto kônoi* Tak., found on the stem of *Abies mariesii* in the southern part of the island of Sakhalin, is probably different from *P. antennatus* Sign. (cf. Takahashi, R., 1941. Insecta Matsumurana, vol. 15, pp. 164-166).

Adult female (figs. 1-29)

Dimensions 3.0-4.0 × 2.0-2.5 mm in the Bavarian specimens, and 3.7-4.0 × 2.5 mm in two French specimens of Signoret (measured on the slide). Dimensions of the two dry specimens of Signoret only 2.5 × 1.8 mm and 2.3 × 1.5 mm; after preparing, the latter specimen measured 3.7 × 2.5 mm on the slide. Dimensions according to Signoret (1875) 3.5 × 2.5 mm.

Šulc (1897) states that Signoret's specimens were of a dark grey colour, that he failed to find any trace of wax secretions (though wax glands of the same type as in *Ceroputo* were present), and that it would be interesting to know the form of these secretions. The two dry specimens of Signoret at my disposal were brown grey and without visible secretions of wax. It is likely that Šulc has treated these specimens with caustic potash as was mentioned above. Signoret (1875) says nothing about wax secretion in the female.

The three females which were collected in Bavaria, and preserved in alcohol, showed almost no wax covering; hairs and spines were clearly visible at the circumference. Dorsum and venter were smooth and white, with some brown spots on the dorsal surface. Dr. Schmutterer informed me that the living specimens had only a slight covering of wax, similar to that of a *Phenacoccus,* but usually less dense. Lindinger (1912, p. 258), however, describes the wax secretions as well developed ("mit mehr oder weniger dichter, fädig-flockiger, etwa dick eiförmiger oder mehr oder weniger kugeliger, hüllenartiger Wachsbedeckung"). Further observations by Dr. Schmutterer in 1952 showed that the adult females are covered by powdery wax on the dorsal surface, sometimes shaped into small processes, especially along the margin. The females often hide in the empty cocoons of the males; it seems that Lindinger (1912) has taken these cocoons for secretions of the females. On two bark samples of *Picea excelsa,* received from Dr. Schmutterer, I have found in the empty male cocoons three living female larvae of the third stage. They had powdery wax on the dorsal surface and 17 pairs of



Figs. 1-10. *Puto antennatus* Sign., adult female, figs. 2-5, 8-10 from Signoret's type specimens.

wax processes along the sides of the body which apparently corresponded to the number of cerarii along the margin. These processes were composed of short wax spirals (produced by the trilocular pores), and at the ends of the body supported by some straight wax filaments (produced by the tubular glands).

Antennae dark brown, 9-segmented (fig. 24). Average length of six antennae in the specimens from Bavaria 0.92 mm (variation 0.90-0.96 mm). The third and ninth segments are the longest, the other segments are about equal in length.

Length of antennal segments (μ)

Antennal segment	I	II	III	IV	V	VI	VII	VIII	IX	Total
Bavarian specimens (average of 6 antennae)	100	97	147	80	83	76	84	100	154	921 μ
Signoret's specimen (slide of E.E.G.)	83	83	137	77	73	73	70	80	—	—
Signoret's specimen according to Šulc (1897)	96	96	144	77	96	77	88	96	144	914 μ

In the slide of E.E.G. only the sclerotized parts of the segments have been measured, as the membranous parts were not visible in the balsam mount; the total length of segments I-VIII on the slide was ca. 0.73 mm. The antenna of Signoret's specimen is well represented in Šulc's fig. 22; according to his description there are 4 hairs on the basal segment and on each of the other segments 4-5 rows of 3-4 hairs.

The number of hairs counted on the different segments of 6 antennae in the specimens from Bavaria was as follows: I 4, II 8-11, III 13-16, IV 11-

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Fig. 1. Ventral view. On the ventral surface the appendages, mouth parts, eyes, spiracles, thoracical apophyses, and circulus are visible, on the dorsal surface (dotted) the cerarian plates, ostioles, and anus. Drawn from a microscopical mount.

Fig. 2. Labium, ventral view. Position of hairs indicated (those at the under surface by a dotted line).

Fig. 3. Spine of posterior cerarian plate.

Fig. 4. Spine of ocular cerarian plate (cer. 3).

Fig. 5. Part of a transversal row of spines on one of the abdominal terga.

Fig. 6. Spine from the side of the thorax.

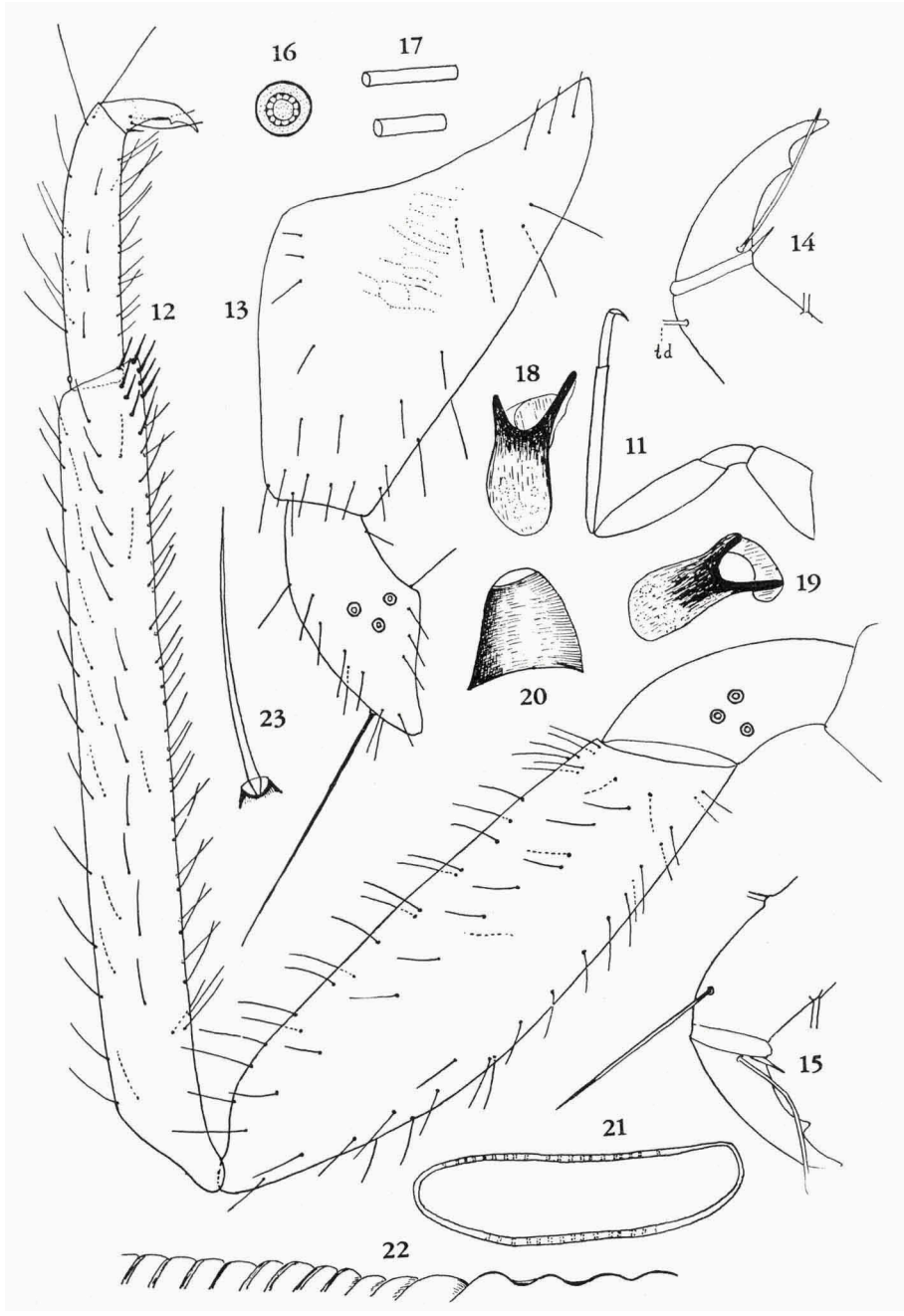
Fig. 7. Trilocular pore from the dorsal side of the head; surface and lateral view. Only a slight twist is seen in these pores when focussing at different levels; the upper figure shows the pore as seen when focussing deeply.

Fig. 8. Posterior ostiole, with sclerotized rim.

Fig. 9. Anal ring. Position of pores and anal hairs indicated; at both sides a double accessory hair.

Fig. 10. Anal ring with only one accessory hair on one side, and two on the other side (this side omitted as it was almost in a vertical position).

Fig. 1, × 20; 2, 8, × 200; 3, 4, 5, 6, 7, × 630; 9, 10, × 425.



Figs. 11-23. *Puto antennatus* Sign., adult female, figs. 15, 17-19, 21-23 from Signoret's type specimens.

16, V 14-18, VI 10-14, VII 11-14, VIII 14-16, IX 25-27. On the slide with Signoret's specimen the numbers were, as far as could be ascertained: I 4, II 5(?), III 16, IV 9, V 13, VI 11, VII 8 and VIII 12. The antennal hairs are rather irregularly arranged, more or less in longitudinal rows, but not in whorls. The so-called sensory hairs are not included in the numbers mentioned above. There is a conspicuous sensory hair near the top of the eighth segment; it is also visible in Signoret's specimen on the slide but the hair has been broken off near its base. In the upper part of the apical segment there are three other sensory hairs; further a very inconspicuous one is found near the top of the seventh segment, just below that on the eighth segment. In addition to the 3 sensory hairs there are 2 minute sensoria on the last segment of the antenna (fig. 24); for further particulars see description of the male.

These sensory hairs are usually somewhat curved, bluntly pointed, and slightly granulated; at their base they are stouter than the ordinary hairs and their socket (alveolus) is larger. Pseudococcidae with 8-segmented antennae have 4 sensory hairs on the apical segment of which three are found in the upper part and one in the middle of the segment; just below the latter there is another sensory hair near the top of the preceding segment. In Pseudococcidae with 9-segmented antennae, like *Phenacoccus,* there are 3 sensory hairs on the ninth, one near the top of the eighth, and one near the top of the seventh segment. In *Puto antennatus* (and also in *Macrocerococcus superbus* Leon.) the last mentioned hair is small, inconspicuous, and hardly distinguishable from the ordinary hairs. A connection of these sensory hairs with nerve fibres has still to be demonstrated; this applies also to the sensoria on the second antennal segment, the trochanter and the tarsus.

Legs dark brown, provided with many hairs as figured by Šulc (1897,

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Fig. 11. Hind leg.

Figs. 12-13. The same leg with all observable hairs.

Fig. 14. Claw of the same leg (*td*, base of tarsal digitule).

Fig. 15. Claw.

Fig. 16. Multilocular pore (near base of hind leg).

Fig. 17. Tubular glands. Upper figure, a tubule near the antennae. Lower figure, a tubule near the posterior cerarian plate.

Fig. 18. Anterior spiracle.

Fig. 19. Posterior spiracle.

Fig. 20. Eye.

Fig. 21. Circulus with wrinkled rim.

Fig. 22. Wrinkled rim of circulus, lying almost flat at the left side, and seen in a vertical position at the right side.

Fig. 23. Hair on the ventral surface of the abdomen.

Fig. 11, × 40; 12, 13, 18, 19, 20, 21, × 180; 14, 15, × 400; 16, × 850; 17, 22, 23, × 570.

fig. 19). These hairs are arranged in six longitudinal rows on the tarsus, tibia, and femur. In the two legs of Signoret's specimens at my disposal (see fig. 26) I have counted 27 hairs on the tarsus, 63-69 on the tibia, and 55-56 on the femur. The leg of Signoret's specimen figured by Šulc (1897, fig. 19) had probably about 30 hairs on the tarsus, 60 on the tibia, and 60 on the femur. The average for 6 hind legs in the specimens from Bavaria was 30 (25-33), 80 (69-93), and 55 (53-55), for 6 fore legs 30 (28-32), 76 (71-81), and 59 (50-65). A hind leg with all hairs observed is shown in figs. 12-13, the outline of fore, middle, and hind legs in figs. 27-29. The tibia is 2.5-3.0 times as long as the tarsus, and only slightly longer than the femur.

Claw slender, with a conspicuous denticle on the inner side and two small, hyaline, spine-like outgrowths at the base (figs. 15 and 55, both drawn from Signoret's specimens). The claw digitules are slightly longer than the claw and bluntly pointed or only very faintly knobbed. The tarsal digitules are also unknobbed. The same condition is found in the specimens collected in Bavaria (fig. 14).

A lens-shaped sensorium, similar to those found on the second antennal segment and the trochanter, is observed on the exterior side of the basal end of the tarsus. It seems that this sensorium is generally present in the Pseudococcidae (examined in several species of *Pseudococcus, Trionymus, Phenacoccus* and *Ripersia*). In the adult female of *P. antennatus* it is only clearly visible, if the tarsus is seen from the exterior (or interior) side; in the larva and in the adult male it can be easily observed (figs. 36 and 42), as the base of the tarsus is less sclerotized.

The trochanter has three sensoria on each side in Signoret's specimens; they are visible in both slides at my disposal and are also represented in Šulc's fig. 19. According to Šulc there are 2-3; in the Bavarian specimens I have found three sensoria on each side, rarely two. These lens-shaped sensoria on the tarsus, trochanter, and second antennal segment are presumably "tension receptors", as is suggested by their position near the joints.

Labium (fig. 2) elongate, bipartite, of the usual Pseudococcid type, with 4 pairs of short hairs at the tip, 20 longer hairs on the apical, and 2 on the basal segment. At the base of the labium there are 2 small sclerites, each with 3 hairs. Rostral loop reaching the middle legs, when the mouth setae are withdrawn.

Eyes (fig. 20) sclerotized, protruding; height 60-80 μ. Distance between the eyes 0.6-0.8 mm (measured on the slide).

Thorax with two apodemes between middle and hind legs (fig. 1).

Anal lobes obsolete. On the top of these lobes, on the posterior cerarian plate, there are 2 long hairs (about 180 and 120 μ) and 4 shorter

ones (70-75 μ). In the slides with Signoret's specimens the same condition was found, but the hairs were broken (2 large hairs and 4 smaller ones, of which one entire, measuring 75 μ). Šulc says that in *Puto* there are besides the 2 large setae more hairs on the anal lobe than in *Ceroputo,* viz., 6-7; probably he has also included 2-3 hairs which are not inserted on the posterior cerarian plate.

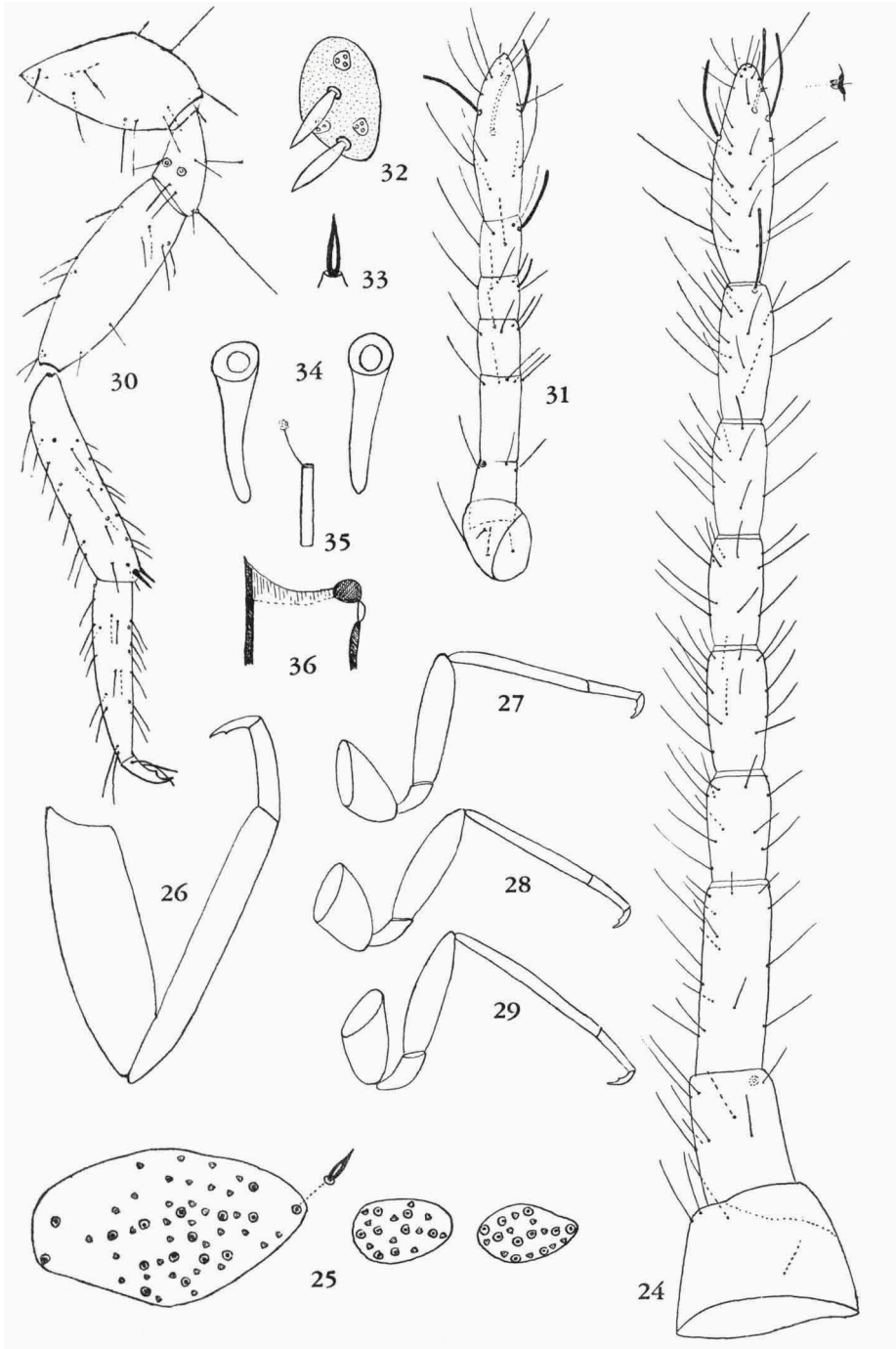
Dorsal surface provided with lanceolate spines (fig. 5) and trilocular pores (fig. 7). The spines on the abdomen are arranged in transversal rows (or narrow bands near the apex); the trilocular pores are principally found in or near these rows (fig. 5).

Ostioles, two pairs, with a narrow sclerotized rim (fig. 8), in Signoret's specimens as well as in those from Bavaria.

Anal ring. Signoret's fig. 4b shows the anal ring with 8 hairs which are about equal in length. Šulc's fig. 21 of Signoret's specimen shows the anal ring also with 8 hairs, but those of the second pair are $^1/_3$ shorter than the other hairs and seem to be accessory ones. In Signoret's specimen, prepared by E.E.G., these accessory hairs are doubled (fig. 9), and much shorter than the other hairs. In another specimen of Signoret, prepared by myself, there are 2 accessory hairs on one side and only one on the other side (fig. 10); the same condition was observed in 2 of Vayssière's specimens. In 3 specimens from Bavaria only one accessory hair is present, one specimen has an accessory hair on both sides, and in the fifth specimen such hairs are wholly absent. In all cases observed these accessory hairs are inserted behind the anterior pair of anal hairs. They are much shorter and more slender than the regular anal hairs which have a length of 220-270 μ. The anal ring (figs. 9 and 10) is broad and provided with 3-4 rows of pores.

The cerarii along the sides of the body are replaced by sclerotized plates (figs. 1 and 25) with trilocular pores and lanceolate spines of the same type as found on the dorsum (figs. 3 and 4). The posterior cerarian plate and one near the eye (the ocular plate) are the largest in size, and have more spines than the other plates; the mesal side of the posterior one bears no spines (fig. 25). Between the ocular plates are found 4 small marginal plates in front of the body, and one accessory pair on the dorsum, about in the line of the eyes. Dorsal rows of accessory plates as found in *Macrocerococcus superbus* Leon. are absent.

In Signoret's specimens on slide the following numbers of spines and trilocular pores were counted. Ocular plate 15-18 spines, 7-10 pores. Posterior plate 12-16 spines, 26-33 pores. Penultimate plate 8-9 spines, 10-18 pores. Antepenultimate plate 9-10 spines, 9-10 pores. The other cerarian plates have with few exceptions 8-12 spines, and about an equal number of



Figs. 24-36. *Puto antennatus* Sign., adult female (figs. 24-29) and first stage larva (figs. 30-36), 25 and 26 from Signoret's type specimens.

trilocular pores. On the small frontal plates 6-7 spines and 4-6 pores were found. With regard to the cerarian plates the specimens from Bavaria agree with those of Signoret.

It is difficult to ascertain the original number of cerarian plates, as those on the thorax have a tendency to split. In one case, e.g., 4 small plates (with 5, 4, 1, and 1 spines) were found between 2 normal plates with 10 and 9 spines, so that the intermediate plate had apparently been divided into 3-4 smaller parts. If 2 or 3 adjacent plates split, it becomes difficult to establish the original number. Among 7 adult females examined (2 specimens of Signoret, and 5 from Bavaria) one young specimen from Bavaria (length 2.5 mm) had 14 cerarian plates behind the ocular plate. In the 6 other specimens, where the number was uncertain, all plates with their number of spines were counted. By combining the smaller plates it was found that as a rule there were 15 plates behind the ocular plate. If the 4 marginal plates between the eyes are taken into account, we find 18 pairs of marginal cerarian plates in the latter case, and 17 pairs in the first mentioned case.

The original number of cerarian plates is probably 17 pairs as may be deduced from the first stage larva (q.v.), where the plates show no tendency to disintegration The 2 accessory dorsal plates (in the line of the eyes) are absent in larva I, but already represented in larvae II and III, where the thoracical plates have a tendency to split, especially in larva III (q.v.). The American species of *Puto* figured by Ferris (1950) have 17 pairs of marginal plates, and sometimes a pair of accessory plates behind the first pair (*P. ambigua, calcitectus, ulter,* and *yuccae*); in 2 species the accessory plates seem to be fused with the first marginal pair (*P. barberi* and *P. lasiorum*).

Fig. 24. Antenna with all observable hairs. A separate figure shows the structure of the two sensoria on the apical segment (the sensory hairs in figs. 24, 31, 38, and 39 are drawn too thick, to bring them out clearly).

Fig. 25. Cerarian plates of the posterior cerarius (left figure), the penultimate cerarius (middle figure), and the antepenultimate cerarius (right figure). See also figs. 3 and 4.

Fig. 26. Part of a leg (hairs omitted; numbers mentioned in the text; claw of the same leg in fig. 15).

Figs. 27-29. Fore-, middle-, and hind leg of a specimen from Bavaria (see also figs. 11-13).

Fig. 30. Fore leg.

Fig. 31. Antenna.

Fig. 32. Cerarian plate from an abdominal segment.

Fig. 33. Dorsal spine.

Fig. 34. Anterior spiracle (left figure), and posterior spiracle (right figure).

Fig. 35. Tubular gland near antenna.

Fig. 36. Base of tarsus with lens-shaped sensorium.

Fig. 24, × 180 and 570; 25, 30, 31, × 180; 26, × 80; 27, 28, 29, × 40; 32, 33, 35, 36, × 570; 34, × 400.

The ventral surface is provided with hairs (fig. 23), multilocular, trilocular, and tubular gland pores. A large circulus with a peculiar wrinkled rim (figs. 21 and 22) is present at the posterior side of the second abdominal segment; dimensions about 230 × 60 μ.

The multilocular pores (fig. 16) are sparingly scattered over the whole mesoventral surface, and intermingled with trilocular pores. They are most numerous around the vulva, and have a diameter of 8-10 μ. The number of loculi is usually 12; pores with 10 loculi are common; even pores with 8

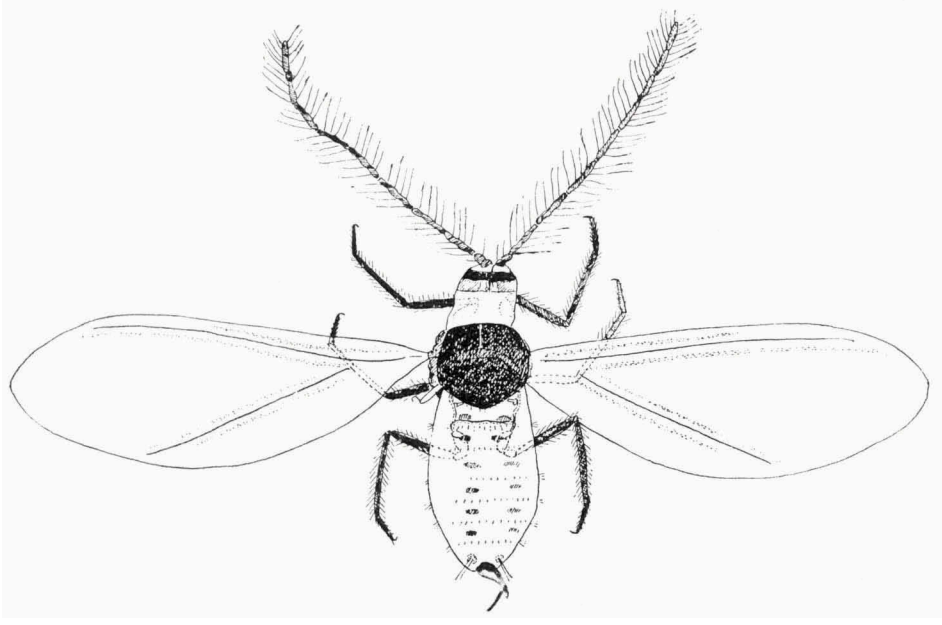


Fig. 37. *Puto antennatus* Sign., adult male, drawn from a microscopical preparation. × 16.5.

loculi are occasionally seen. These loculi are rather difficult to observe, and were apparently overlooked by Šulc (1897).

Tubular glands are very scarce, and are principally found at the ends of the body; dimensions 18-20 × 3-5 μ (the slender type only near the antennae). On the abdomen these glands are usually confined to the sides of the last 3 or 4 segments, and are always present near the posterior cerarian plate (fig. 17). Occasionally some tubular glands are found along the margin of the thorax and single ones near the base of the legs. Not more than 20 tubules have been counted on the abdomen, and not more than 10 between the antennae and the mouthparts (examined in 7 specimens).

The trilocular pores are similar to those on the dorsal surface. Quinquelocular pores are absent.

The spiracles of Signoret's specimens are shown in figs. 18 and 19.

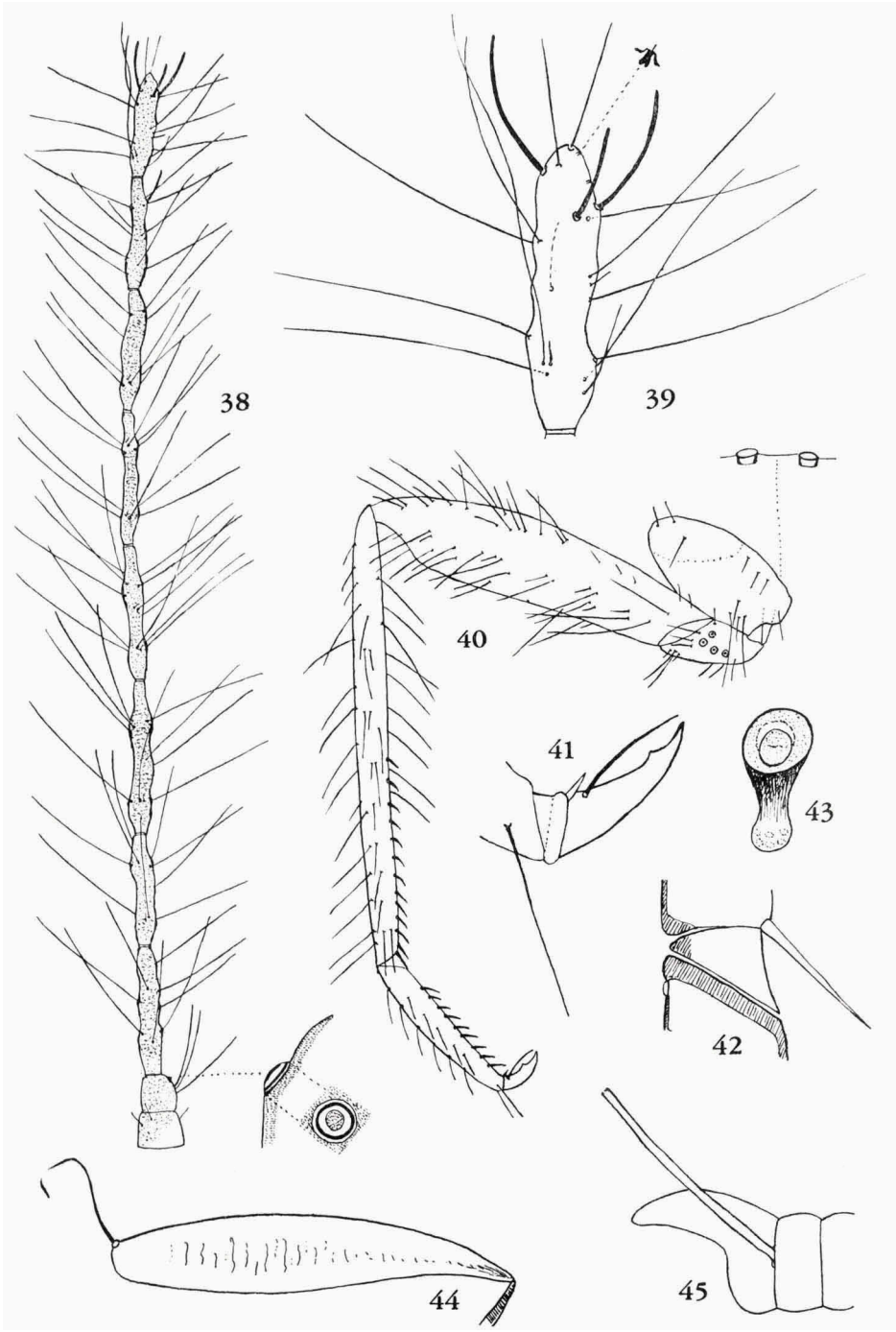
No essential differences have been observed between the female specimens of Signoret and those collected in Bavaria; this applies also to the French specimens which were collected in Savoy by Vayssière in 1932.

The adult male (figs. 37-48, 51-53, and 58).

Signoret's male specimens belong certainly to the same species as his female *Puto antennatus*. This is proved by the male specimens which Dr. Schmutterer has collected in the Bavarian Alps together with female specimens. The males and females of *Puto antennatus,* collected by Vayssière in French Savoy on *Abies pectinata,* offer another proof that Signoret was not mistaken. Šulc (1897) was sceptical about Signoret's combination of male and female, as the specimens had been found in different localities and by different collectors. Apparently he has changed his opinion afterwards, as one of the labels of Signoret's male in the Vienna Museum reads: "*Puto antennata* det. Šulc."

Length of body in Signoret's specimen (mounted dry; body shrivelled) only 2 mm; length according to Signoret 3 mm. The abdomen is covered by wax powder, especially at the sides. Mesothorax and head are dark brown and without wax. Near the tip of the abdomen, on the dorsal side there arise 2 long wax filaments (fig. 45) which are longer than 4 mm; one of the filaments is split at the top. The length of the Bavarian specimens (mounted on slide) is 2.4-2.8 mm, the width of the thorax ca. 0.75 mm. The wax covering of these specimens could not be examined, as they were preserved in alcohol. Dr. Schmutterer informed me that the males are slightly dusted with wax powder, especially on the abdomen; the caudal filaments are about $1^1/_2$ times as long as the body, sometimes 5 mm.

The antennae (fig. 38) are dark brown, 10-segmented, and closely set together; distance less than the width of the basal segments (figs. 46 and 58). Length in the Bavarian specimens (mounted on slide) 2.3-2.5 mm, i.e., about as long as the body. Two specimens, examined while submerged in alcohol, had antennae of 3 mm, wings of 3.3 mm, and bodies of only 2.5-2.6 mm. Signoret's measurements are: body 3 mm, antennae 3.5 mm. The antenna with its nodulose segments and their long hairs is well represented by Signoret's fig. 4a. Several of the antennal hairs have 1-2 small hairs near their insertion. Segments I and II are shorter and stouter than the other segments, of which segments III-VII are the longest (also in Signoret's fig. 4a). There are 3 sensory hairs on the apical segment (fig. 39), one near



Figs. 38-45. *Puto antennatus* Sign., adult male (fig. 45 from a dried specimen of Signoret).

the top of segment VIII, and an inconspicuous one near the top of segment VII, as found in the adult female. Two peculiar minute structures (fig. 39), which are probably the chitinous part of a sensorium, are found near the apex of the last segment. They are also present in the adult female and the larvae of *Puto antennatus*, and seem to be present in several other Pseudococcidae. Šulc (1943) calls this structure "sensillum clavuliforme".

The legs (fig. 40) are dark brown and very slender. They are provided with several long hairs which, like those of the antennae, are often accompanied by 1-2 minute hairs near their insertion. The hairs on the inner side of the tibia (distal half) and tarsus are short and stout. The tibia is about 1.5 times as long as the femur, and 2.5 times as long as the tarsus.

The tarsal claw (fig. 41) has the same peculiar structure as in the female. This was Signoret's chief argument for combining male and female into one species, though they had been collected in different localities. A lens-shaped sensorium is present at the basal end of the tarsus on the exterior side (fig. 42). Between tibia and tarsus there is a small hairless sclerite as was already observed by Signoret (fig. 42).

The trochanter shows 4-5 sensoria on both sides (fig. 40). They seem to have the same structure as the sensorium on the tarsus and the second antennal segment.

These details of the legs are described from the Bavarian specimens. In the French specimen of Signoret one fore leg could be measured; the tibia was $2^1/_2$ times as long as the tarsus.

Wings (fig. 37) slightly longer than the body, about 3 mm in the Bavarian specimens, and also in Signoret's specimen from France. According to Signoret their spread is at least 7 mm; it is about 6.5 mm in the Bavarian specimens on slide. The wings are densely covered by very minute hairs, and provided with 2 veins which are accompanied on both sides by a narrow dark band running parallel with them.

Halteres (fig. 44) with 1-2 hook-shaped setae at the top. In Signoret's

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Fig. 38. Antenna. Separate figure, sensorium on the second antennal segment, lateral and surface view.

Fig. 39. Apical segment of the antenna. Separate figure, one of the two sensoria.

Fig. 40. Hind leg; only the hairs on the upper side are shown. Separate figure, lateral view of the sensoria on the trochanter.

Fig. 41. Claw.

Fig. 42. Base of tarsus with lens-shaped sensorium, and accessory sclerite.

Fig. 43. Posterior spiracle.

Fig. 44. Haltere.

Fig. 45. Posterior end of abdomen with base of caudal filaments.

Fig. 38, × 65 and 630; 39, × 200 and 630; 40, × 90 and 630; 41, 42, × 425; 43, 44, × 200; 45, × ca. 50.

specimen one of the halteres was clearly visible and provided with only one seta; Signoret himself observed 2 setae. Two Bavarian specimens have 2 setae on one side and only one on the other side; the third specimen has 2 setae on both sides. Among 9 males, collected in 1952, one specimen had 3 hook-shaped setae on the left haltere and 4 on the right; in a second specimen the numbers were 1 and 3.

The external genitalia of the male (figs. 51 and 52) consist of a conical sheath, with the point bent downward, and a slit on the ventral side through which the penis is protruded. In the Bavarian specimens the penis has the shape of a curved rod. In the American *Puto yuccae* (Coquillet) the tip of the penis is bifid and serrated (fig. 59). According to Dr. Morrison the intromittent organ in other American *Putos* is similar to that of *P. yuccae*. Considering the difference in the number of eyes (as mentioned below), and in the structure of the penis, it seems that the American *Putos* represent a special line of development.

The head is surrounded by a row of 12 eyes which are about equally spaced (fig. 46). These eyes appear as light-coloured round spots when seen from above, and as dark hemispheres if viewed from the side (fig. 47). Their sizes are about equal, but they appear larger if seen from the side. Signoret's description ("presque aussi gros, placés en couronne autour de la tête, qui présente une teinte plus foncée, surtout autour des yeux") is more correct than his fig. 4. The 12 eyes were clearly visible in Signoret's dry specimen; the same condition was found in the male specimens from Bavaria.

Dr. Morrison called my attention to 2 small accessory eyes which he had found in a male *Puto antennatus*, received from Dr. Schmutterer. These eyes are very small (diameter about $^1/_4$ of the usual type), and located behind the line of regular eyes. The slide with this male was kindly sent to me for examination; as the accessory eyes are in a favourable position their bulging corneas can be clearly seen (fig. 58). In another preparation Dr. Morrison found only a tiny round clear spot that might represent this structure. I have examined 15 males from Bavaria but only in 3 or 4 of them the accessory eyes could be recognized in the position shown by fig. 58. In 2 specimens, whose position was favourable, they were certainly absent. My present conclusion is therefore that in some cases 2 minute accessory eyespots are present in *Puto antennatus* behind the row of regular eyes. Dr. Morrison informed me that all male American *Putos*, as far as examined, have 14 eyes (instead of 12, as found in *Puto antennatus*), and also the 2 accessory eyes mentioned above, which in this case are conspicuous [1]). This condition is

1) Afterwards Dr. Morrison received through quarantine collection an adult *Puto*-male from Monstera which has only 12 eyes. The accessory eyes and penis, however, are like those found in other American *Puto*-males (in litt., 19-I-'53).

even found in the wingless male of *P. ambigua* Fullaway. A slide with a male of *P. yuccae* (Coquillet) was sent to me for examination. The 2 accessory eyes in this specimen are as large as the 14 regular eyes (fig. 57). Their position is about the same as in *Puto antennatus*.

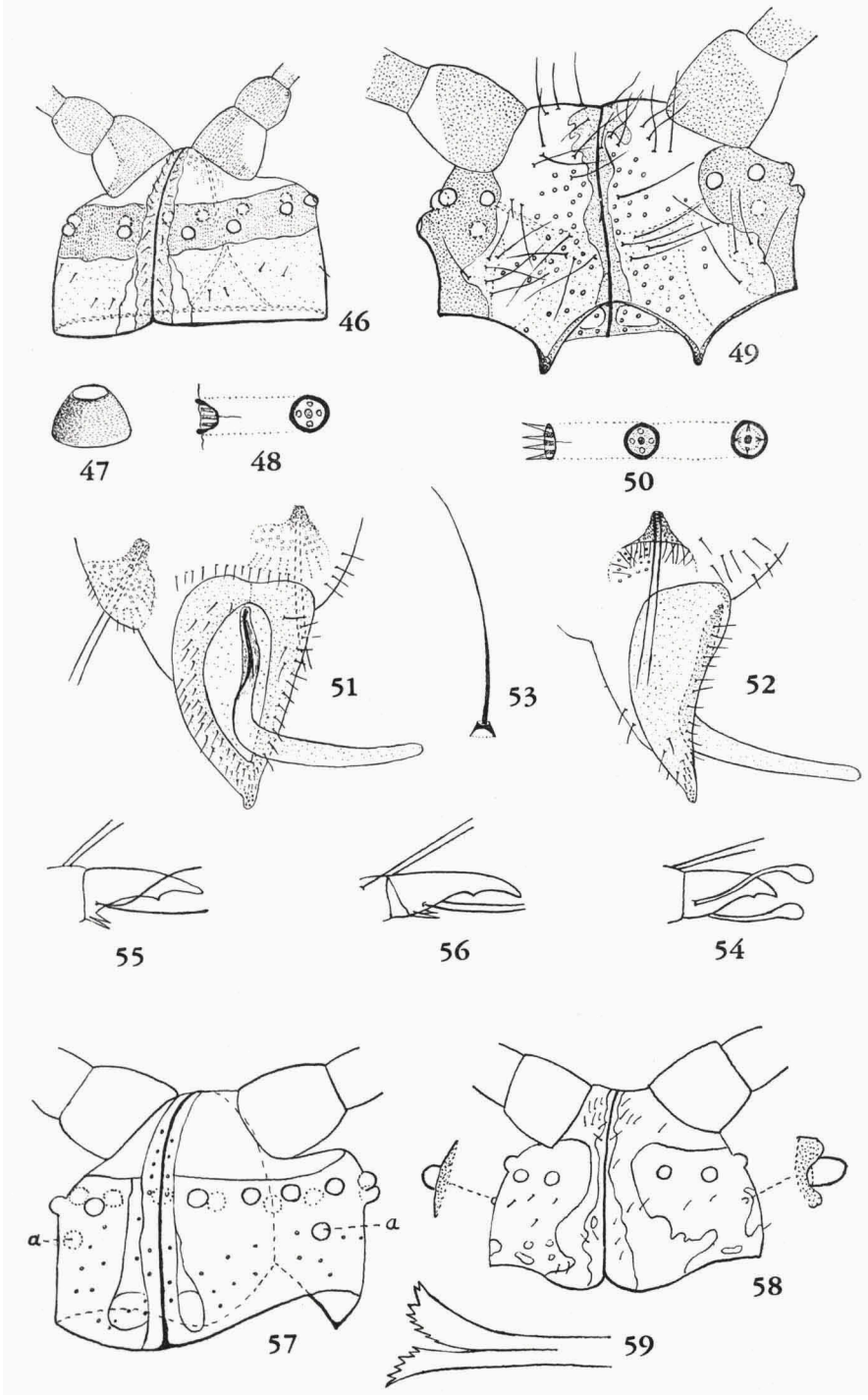
The head of *P. antennatus* is supported by a frame work of sclerotic strands (e.g., in the dorsal and ventral middle line), and also by flat sclerotized parts of the cuticle which alternate with membranous parts. In consequence of this uneven sclerotization the different parts of the head are easily dislocated in microscopical preparations by pressure of the cover glass. The same applies to the mesothorax, in which the sclerotization is very complicated. The head is provided with a few short hairs and very few gland pores; only 5 or 6 of the latter were observed near the antennae (fig. 46). The head, mesothorax, and appendages are darkly coloured; the other parts are almost colourless (fig. 37).

The dorsal surface of the body is covered by hairs (fig. 53); lanceolate spines are absent in the male. The dorsal gland pores are similar to those found at the base of the caudal filaments (fig. 48). They have usually 4 loculi, sometimes 3 or 5; at the base of the caudal filaments there are also pores with 6-7 loculi. These caudal filaments arise from 2 dorsal pockets (figs. 51-52) with closely set gland pores which are especially crowded at the base of the filaments. The wax filaments are supported by 2 (sometimes 3) long setae (about 260 μ); several smaller hairs are present on the walls of the pockets.

The ventral surface of the body shows the same type of hairs and gland pores as found on the dorsum. These gland pores are very sparingly distributed. On the abdominal segments about 5-6 pores are observed on the dorsal and 1-3 on the ventral surface. Along the margin of the segments small groups of hairs are present with 6-10 of these pores. Trilocular pores and tubular glands are nowhere found in the adult male; only one type of gland pore is present, as described above.

A spiracle of the male is shown in fig. 43.

Fossil *Puto*-males have been reported from Baltic amber (Lower Oligocene). Cockerell (The Entomologist, vol. 42, p. 100) states that *Monophlebus trinervosus* Germar & Berendt (Org. Reste, II, 1856) is a male *Puto*, congeneric with the male of *P. calcitectus* (Ckll.). After examining the description and figure of this insect I have come to the conclusion that it is not possible to decide whether this coccid male belongs to the Pseudococcidae or to the Monophlebinae. The structure of the head was obscure in the specimen examined by Germar & Berendt, the eyes were not visible. *Monophlebus irregularis*, which is described by Germar & Berendt in the same paper, in certainly not a *Puto*-male, since it has conspicuous compound eyes.



Figs. 46-48, 51-53, 55, 58. *Puto antennatus* Sign. (fig. 55 from one of Signoret's type specimens).

Ferris (1941) found *Puto*-males in a piece of Baltic amber from the Museum of Comparative Zoölogy at Cambridge (U.S.A.) but did not describe them. To my regret I had no opportunity to examine these specimens.

First stage larva (larva I).

Length of 10 available specimens 1.1-1.2 mm. One specimen of 1.2 mm was on the point of moulting to the second stage. Newly emerged larvae and eggs were not observed; the embryos in a mature female had a length of 0.85 mm.

Antennae 7-segmented (fig. 31); average length of 6 antennae 385 μ. The antennae of this stage show a more primitive condition than in the adult female, as the segments III-VI have only 5 hairs which are arranged in a whorl near their distal end; occasionally one hair has shifted a little from the alignment of the whorl. Segment VI has a sensory hair near its top; 3 others are found in the upper part of segment VII. There is also a small sensory hair near the top of segment V, but it is inconspicuous and scarcely distinguishable from an ordinary hair.

Fig. 46. Head of ♂, dorsal surface; sclerotized areas dotted.

Fig. 47. One of the (12) eyes.

Fig. 48. Gland pore. Lateral and surface view (deeply focussed).

Fig. 51. External genitalia of ♂, ventral surface; the dorsal pockets of the caudal filaments are also shown in this figure.

Fig. 52. The same, seen from the side; with pocket of caudal filament.

Fig. 53. Hair from the side of the body.

Fig. 55. Claw of ♀. Copy from Šulc (1897, fig. 20).

Fig. 58. Head of ♂ from Bavaria; dorsal surface. Two minute accessory eyes are present behind the row of regular eyes; separate figures show them more enlarged. It seems that in this specimen the cuticle was better spread than in the one of fig. 46. Due to uneven sclerotization of the head it is difficult to make perfect preparations. In 15 males examined the medio-dorsal sclerotized strip is usually touching or almost touching the adjacent sclerotized parts, in which outline and holes are somewhat variable. The frontal hairs between the antennae are in my slides on the ventral surface.

Figs. 49, 50, 56. *Macrocerococcus superbus* Leon.

Fig. 49. Head of ♂, dorsal surface.

Fig. 50. Gland pore of the same. At left lateral view; the middle figure shows the inner, and the right figure the outer side in surface view.

Fig. 56. Claw of ♀.

Fig. 54. *Ceroputo pilosellae* Šulc. Claw of ♀. Copy from Šulc (1897, fig. 17).

Figs. 57, 59. *Puto yuccae* (Coq.).

Fig. 57. Head of ♂ from California; dorsal surface. A row of 14 eyes surrounds the head. Behind this row 2 accessory eyes (*a*) are visible which are as large as the other eyes. Position of hairs indicated by circlets. The specimen of this balsam mount was collected by Coquillet at Los Angeles in 1893.

Fig. 59. ♂; the same specimen as in fig. 57. Bifid, serrated top of penis.

Figs. 46, 49, 51, 52, 57, × 90; 47, × 200; 48, 50, × 630; 53, 59, × 425; 56, × 240; 58, × 90 and 425.

Legs (fig. 30) with the tibia (165-180 μ) slightly larger than the tarsus (130-145 μ), when the claw is left out of consideration; ratio tarsus to tibia in the hind legs 1 : 1.2-1.3. The basal end of the tarsus is provided with a lens-shaped sensorium on the exterior side (fig. 36). Tarsal and claw digitules are unknobbed. The claw has a distinct denticle on the inner side, but the spine-like outgrowths at its base (as found in the adults) are not yet developed. The trochanter shows 2 sensoria on both sides.

Dorsal surface of body with trilocular pores and lanceolate spines (fig. 33). On the abdomen 4 longitudinal rows of spines are observed; the spines and pores are arranged in a regular transversal series on each abdominal segment. Eyes sclerotized and protruding as in the adult female. Both pairs of ostioles are present, but the rims are not yet sclerotized as in the following stages. There are 17 pairs of cerarian plates along the margin of the body. The third plate, which lies quite close to the eye, has 4-6 spines. The other cerarian plates, including the posterior one, have only 2 spines (fig. 32). Occasionally some plates near the ocular plate have 3 (rarely 4) spines. The ocular plate and the posterior one are of a larger size than the others. Two pairs of plates are found between the ocular plates, and 14 pairs behind them. Accessory dorsal plates, behind the first cerarii, as found in the following stages, are absent. Anal ring with 2 rows of pores, and 6 anal hairs (100-130 μ). The posterior cerarian plates on the anal lobes are provided with 2 prominent hairs (ca. 90 and 50 μ) besides the 2 lanceolate spines.

The ventral surface of the body is sparingly provided with rather long hairs; those on the abdomen are arranged in 6 longitudinal series. Further a number of multilocular pores, with 12 loculi and a diameter of about 8μ, are distributed over the whole ventral surface. A few trilocular pores are present on the abdomen, the head, and the sides of the body. Four slender tubular glands (of ca. 18 $\times$ 3 μ) are found near the antennae (fig. 35); tubular glands on the abdomen and thorax, as found in the following stages, are absent. A circulus of about 50 $\times$ 30 μ is present near the posterior side of the second abdominal segment. The rostral loop extends to the line of the posterior spiracles. The spiracles are rod-shaped (fig. 34). Labium elongate; length about 1.5 $\times$ width at base.

Second stage larva of the female (larva II ♀).

Length of 5 available specimens 1.6-1.8 mm. As the length of a moulting larva I is 1.2 mm, and that of a larva III just moulted 1.8 mm, it is likely that these lengths are about the limits in larva II ♀.

Antennae 7-segmented, as in larva I, but somewhat larger; average

length of 10 antennae 500 μ. The regular position of the hairs on segments III-VI is already disturbed, as one or more hairs are found outside the top whorl. From 7-12 hairs were counted on segment III, and 24-31 on the segments III-VI together.

Legs like those of larva I, but larger. Average length of tarsus and tibia in the hind legs 170 and 285 μ; ratio 1 : 1.6-1.8 (as against 1 : 1.2-1.3 in larva I).

Dorsal surface of the body as in larva I but spines and trilocular pores more abundant.

In addition to the 17 pairs of marginal cerarian plates 2 accessory dorsal plates are present, as mentioned in the description of the adult female. The thoracical plates have already a tendency to split. In 3 cases 15 plates (instead of 14) were counted behind the ocular plate, but only on one side of the body. The number of spines is 7-8 in the ocular plate, 5-6 in the posterior one, and 4-6 (usually 4) in the other plates. Larvae I and II, which have both 7-segmented antennae, can be easily separated by counting the number of spines on the cerarian plates; the posterior plate has only 2 spines in larva I, but at least 5 in larva II.

Anal hairs 150-170 μ; hairs on the posterior cerarian plate ca. 110 and 70 μ. The number of anal hairs is 6, but in one specimen an accessory hair was already noticed. Both pairs of ostioles with brown sclerotized rim.

Ventral surface of the body. The multilocular pores (with 12 loculi; diameter ca. 8 μ) are confined to the mesoventral area. Trilocular pores are found outside this area, and sometimes also in the middle of the abdomen. From 6-9 tubular glands were observed near the antennae. The marginal series of tubular glands on thorax and abdomen is already developed; one tubule is found opposite each cerarian plate, but due to gaps not more than 7-8 were counted on each side. One single tubular gland is also found near the base of each leg. The circulus measures about 70 × 40 μ.

Second stage larva of the male (larva II ♂).

Examined 4 specimens; length 1.3-1.5 mm; one specimen of 1.3 mm had just moulted. Three of these specimens were found alive on bark samples of *Picea excelsa* with male cocoons, sent by Dr. Schmutterer. The colour of these larvae was greenish. Their dorsal side was dusted with wax powder; 17 pairs of more or less confluent wax processes were seen along the sides of the body.

The structure is similar to that of larva II ♀. The main difference is the presence of a large number of tubular glands which are distributed over

the whole surface of the body, including the dorsal surface; about 25 tubules were counted between the antennae and the mouthparts. Apparently these tubular glands serve to make the male cocoon, which consists of densely interwoven wax filaments (produced by the tubular glands), intermingled with short pieces of wax spirals from the trilocular pores. The male cocoons are snowwhite. They measure about 3 × 1.5 mm, and were found densely accumulated in the bark fissures of *Pinus cembra* and *Picea excelsa*. Occasionally some cocoons are found on the leaves and on lichens. Pupal stages were scarce, but the adult males numerous, when Dr. Schmutterer collected his material (23-24 July, 1952). No pupal stages are available for description.

In the first larval stage the sex could not be recognized.

Third larval stage of the female (larva III ♀).

This stage can be easily recognized by its 8-segmented antennae. Examined were 6 specimens. Length of body 1.8-2.4 mm; 2 specimens just moulted (top of antennae still membranous) are 1.8 mm, and 3 specimens ready to moult to adults 2.4 mm.

Antennae 8-segmented; average length of 9 antennae 740 μ. The position of the antennal hairs, which have increased in number, is more irregular than in larva II; about 40 hairs were counted on segments III-VI, i. e., twice as much as in larva I.

Legs larger than in larva II; average length of tarsus and tibia in the hind legs 200 and 410 μ (ratio 1:2). The number of hairs has largely increased in comparison with the preceding stages; those on the tibia and tarsus are distinctly arranged in 6 longitudinal rows as in the adult female.

Dorsal surface of body with lanceolate spines and trilocular pores. Ostioles with sclerotized rim. Anal ring with 3 rows of pores. Anal hairs 175-220 μ; among 6 specimens examined 3 had already an accessory pair of anal hairs behind the first pair. Hairs on posterior cerarian plate ca. 145 and 100 μ; besides these large hairs 1-3 smaller hairs are inserted on the plate.

The number of cerarian plates is difficult to ascertain due to a tendency of the thoracical plates to split. In one case, e. g., 19 plates were counted behind the ocular plate with the following number of spines: 9, (1, 3, 2), 9, 10, (2, 8), (5, 2), 7, 8, 8, 8, 7, 9, 10, 6, 11; the figures between brackets probably refer to divided plates. In 3 specimens there were 14 cerarian plates behind the ocular plate, but in 3 other specimens the number remained uncertain. The ocular plate has 11-14 spines, the posterior plate 9-12, and the other plates usually about 8.

The ventral surface of the body shows about the same con-

dition as larva II with regard to the distribution of multilocular and trilocular pores, but some of the latter are already represented in the middle area, though the multilocular pores are still prevailing. These have 9-12 loculi and a diameter of about 8μ. From 11-12 tubular glands were observed behind the antennae, from 8-13 along the sides of the body, and single ones near the base of each leg. Circulus about 170 × 50 μ; rim wrinkled as in the adult female (in some cases already observed in larvae II ♀).

Observations on the biology of *Puto antennatus*.

On bark samples of *Picea excelsa*, collected on 23-VII-'52 and sent by Dr. Schmutterer, 3 larvae III ♀ and 3 larvae II ♂ were found alive. Colour and wax covering were the same in both cases; see description of larva II ♂ and adult ♀. The green colour is probably caused by chlorophyll; it is especially concentrated in the axis of the body, due to the green contents of the alimentary canal. According to observations of Dr. Schmutterer the young larvae feed on the leaves of the conifers. Apparently they migrate afterwards to bark fissures to complete their development. The above mentioned larvae III ♀ and II ♂ were still alive, though deprived of food, one month after the bark samples were collected. Schmutterer did not find any specimens which were attached to the bark by their mouth setae. He states that the insects are certainly not able to feed on the living tissues by piercing the bark, as the bark of old stems is too thick. I am of the same opinion. The bark of *Picea excelsa* and *Pinus cembra* in the samples is 10-15 mm thick, while the reach of the mouth setae (according to measurements in the adult female) is at most 2 mm.

Dr. Schmutterer made the following observations. Males as well as females complete their development in bark fissures of the stem or older branches. Copulation takes place on the bark. Numerous males were seen gathering around the bark crevices where the young females were hiding. The males were crawling rather slowly and not seen on the wing. He observed an old spruce fir (*Picea excelsa*) with a stem of 40 cm diameter, which was severely infested with *Puto antennatus* up to a height of about 2 metres. Dense accumulations of male cocoons were found in fissures of the bark. Numerous males were seen crawling in these fissures and on the bark scales in search of females; observations made during the last week of July at 7-8 a.m. (temperature 10° C), and at 3 p.m. (temperature 18° C). Copulation was several times observed. The females, of which the majority was not yet mature, were hiding in the fissures and under the bark scales; several larvae had taken refuge in the empty cocoons of the males.

As was already mentioned, *Puto antennatus* has been found in the Bavarian Alps on *Pinus cembra* and *Picea excelsa* at an altitude of 1600-1900 m, and in the French Alps on *Pinus cembra* and *Abies pectinata* (altitude not stated). Dr. Schmutterer found the insects especially on the east- and south-east sides of the stems; he failed to find *Puto* on *Abies pectinata* which, though common, did not occur above 1200 m in his collecting grounds.

It is not yet known where the eggs are deposited. Eggs, newly born larvae, and ovipositing females were not observed in the last week of July 1952, when Schmutterer made his observations. The majority of the females on the bark were young specimens; older ones with eggs and embryos were very scarce. Some embryos in an old female (of 4 mm length) had the legs and antennae fully developed, but the mouth setae were not yet visible. We do not know whether the fertilised female migrates back to the leaves or younger twigs to feed, neither how the insects hibernate. In view of the climatic conditions in the Bavarian Alps at an altitude of 1600-1900 m [1]), it is likely that the season of growth and reproduction is very short, and that of the resting stage very long. A few parasitized specimens were observed by Dr. Schmutterer, but the parasites have not yet been examined.

Prof. Dr. P. Buchner, who examined the mycetomes of *Puto antennatus* and *Macrocerococcus superbus,* informed me that these species show some characteristics of the Pseudococcidae, but also a number of peculiar features ("Die Untersuchung von *Puto* und *Macrocerococcus* hat zwar einige Pseudococcinen-Züge ergeben, aber doch auch eine Reihe sehr eigenwilliger Züge, die sie symbiontisch stark abrücken").

Summary and conclusions.

Puto antennatus Sign., the type of the genus *Puto,* is redescribed from Signoret's specimens which were collected about 1875 in the French Alps.

1) There is no meteorological station at an altitude of 1600-1900 m in the localities where Dr. Schmutterer collected his material. I am indebted to the "Koninklijk Nederlands Meteorologisch Instituut" at De Bilt (Holland) for the following data. The nearest station for comparison at that altitude is Wendelstein (alt. 1727 m), about 80 km west of Berchtesgaden (alt. 603 m). The mean monthly temperatures (centigrade scale) for these stations are:

	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Wendelstein (alt. 1727 m)	-4.7	-5.1	-3.1	-0.1	5.0	7.4	9.8	9.9	7.4	3.0	-0.8	-4.0
Berchtesgaden (alt. 603 m)	-2.8	-1.1	2.5	6.8	11.6	14.5	16.1	15.2	12.1	7.3	2.2	-1.7

From these figures it appears that the mean monthly temperature in Dr. Schmutterer's collecting grounds is probably during 6 months (Nov.-April) below or quite near the freezing point.

One male and two females (mounted dry), and one microscopical preparation (made from a third female by E. E. Green in 1934) were received on loan from Signoret's collection in the Vienna Museum of Natural History. Moreover several females, males, and larvae of all stages were received from Dr. H. Schmutterer who had discovered this insect in 1951 in the Bavarian Alps. The adult specimens from Bavaria agree in every respect with those of Signoret; the same applies to the specimens which were collected in 1932 by Dr. Vayssière in French Savoy. Šulc's description (1897) and figures, showing the difference between the above mentioned specimens of Signoret and his new genus *Ceroputo*, were consulted; his description and figures of the female *Puto antennatus* agree with my own observations.

The principal characters of *Puto antennatus* Sign. are as follows:

Adult female. Body scantily covered with wax at the dorsal side, sometimes shaped into short processes, especially at the sides. Dimensions (on slide) 3-4 × 2-2½ mm. Antennae 9-segmented; segments III-VIII with 10-15 hairs each (fig. 24); length 0.90-0.96 mm. Legs (figs. 12-13) with many hairs, arranged in 6 longitudinal rows on tarsus, tibia, and femur, tarsal digitules unknobbed. Claw with a conspicuous denticle on the inner side, and 2 small spine-like outgrowths at its base; claw digitules blunt, at most very faintly knobbed, slightly longer than the claw (figs. 14-15). Trochanter with 3 sensoria on each side. Eyes protruding, sclerotized. Labium elongate (fig. 2).

Dorsum with lanceolate spines and trilocular pores; spines on abdomen arranged in transversal series. Ostioles 2 pairs; rim sclerotized. Cerarii represented by sclerotized plates with trilocular pores and lanceolate spines. Number of cerarii 17-18 pairs, difficult to ascertain due to splitting of the plates on the thorax. The third plate which lies close to the eye, and the posterior plate are the largest in size. Number of spines on the plates usually 8-12, but more on the posterior and ocular plates. Accessory cerarian plates on the dorsal surface (as found in *Macrocerococcus* Leon.) are absent, except one small pair behind the first cerarii. Anal ring with 3-4 rows of pores; 6 anal hairs and usually 1-2 smaller accessory hairs; sometimes 2 double accessory hairs, and sometimes wholly absent (figs. 9-10).

Venter, with hairs, trilocular, multilocular, and tubuliferous pores. Trilocular and multilocular pores distributed over the whole ventral surface. Tubular glands very scarce, but a few always present on the last abdominal segments (especially near the posterior cerarian plate), and near the antennae. A circulus with a peculiar wrinkled rim (figs. 21-22) is found on the posterior side of the second abdominal segment.

Adult male. Length (without antennae) 2.4-3.0 mm. Slightly dusted

with wax powder, especially on the abdomen. Two long wax filaments (4-5 mm) at the posterior end of the body, arising from 2 dorsal pockets with crowded disc pores. These pockets are provided with 2 long setae at the bottom, and several smaller ones on the walls. Antennae about as long as the body, 10-segmented (fig. 38), closely set together, distance less than width of the first segment. Legs with claws of the same structure as found in the female, and 4-5 sensoria on both sides of the trochanter. Head surrounded by a row of 12 eyes, about equally spaced (fig. 46). Sclerotization of the head complicated; few hairs and very few gland pores present. Mesothorax darkly coloured, with complicated sclerotization; wings slightly longer than the body (fig. 37). Halteres with 1-2 hook-like setae. Gland pores very sparingly scattered on both sides of the body. These pores are disc pores (fig. 48) with 3-5, usually 4 loculi; in the caudal pockets, where the pores are crowded, 6-7 loculi may be found. Trilocular, multilocular, and tubular gland pores are absent. Genital armature well developed (figs. 51-52).

L a r v a I. Largest specimens (on the point of moulting) 1.2 mm. Antennae 7-segmented; a single whorl of 5 hairs on segments III-VI (fig. 31). Legs with the tibia slightly larger than the tarsus (fig. 30). Claw with a distinct denticle and unknobbed digitules. Dorsum with trilocular pores and lanceolate spines. Anal ring with 2 rows of pores and 6 anal hairs; accessory anal hairs absent. Two hairs on the anal lobe of which the largest is shorter than (or at most as long as) the anal hairs. Two pairs of ostioles; rim not sclerotized. Seventeen pairs of cerarian plates along the margin of the body; the third plate (near the eye) and the posterior plate are the largest in size. Ocular plate with 4-5 spines; other plates with 2 spines (fig. 32). Venter with hairs, trilocular, and multilocular pores; 4 tubular glands near the antennae; a small circulus on the second abdominal segment.

L a r v a II ♀. Largest specimens 1.8 mm. Antennae 7-segmented. Legs as in larva I, but tibia 1.6-1.8 times as long as the tarsus. All cerarian plates with at least 4 spines (ocular plate 7-8, posterior plate 5-6); 17 pairs of marginal plates (sometimes 18), and one accessory dorsal pair in the line of the eyes. Venter as in larva I, but with 6-9 tubular glands near the antennae, and also a few along the margin of thorax and abdomen. Ostioles with brown sclerotized rim.

L a r v a II ♂. Like larva II ♀, but with numerous tubular glands, distributed over the whole surface of the body, including the dorsal surface. In living specimens dorsum dusted with wax powder; along the margin of the body 17 pairs of more or less confluent wax processes, corresponding with the cerarian plates.

L a r v a III ♀. Length 1.8-2.4 mm. Wax covering as in larva II ♂.

Antennae 8-segmented. Legs with tibia about twice as long as the tarsus. Cerarian plates usually with 6-8 spines (ocular plate 11-14, posterior plate 9-12). Number of marginal plates 17-18; often uncertain due to splitting of the plates on the thorax. Venter as in larva II ♀ ; about 12 tubular glands near the antennae.

The 3 larval stages can be easily distinguished by the number of antennal segments (8 in larva III, 7 in larva I and II), and the number of spines on the posterior cerarian plate (2 in larva I, 5-6 in larva II).

Biology. The larvae feed on the leaves. Afterwards they migrate to the stem (where they do not feed) to complete their development in fissures and under scales of the bark. The male larvae produce densely woven white cocoons, which are crowded together in bark fissures. Copulation takes place on the bark. Oviposition and hibernation have not yet been observed. Found on *Pinus cembra* and *Abies pectinata* (= *A. alba*) in the French Alps, and on *Pinus cembra* and *Picea excelsa* in the Bavarian Alps at an altitude of 1600-1900 m.

Puto Signoret (1875), *Ceroputo* Šulc (1897), and *Macrocerococcus* Leonardi (1907) are allied to the large genus *Phenacoccus* Cockerell (1893). Less than 20 species are known of the 2 first mentioned genera together, only 6 of *Macrocerococcus,* but more than 100 of *Phenacoccus.* In comparing the type species of these genera (*Puto antennatus* Sign., *Ceroputo pilosellae* Šulc, *Macrocerococcus superbus* Leon., and *Phenacoccus aceris* Sign.) we find that they have in common the 9-segmented antennae, the lanceolate spines on the dorsum, and a denticle on the claw.

The following differences are observed:

1) In the females and larvae of *Puto, Ceroputo,* and *Macrocerococcus* all cerarii are located on sclerotized plates, which are absent in *Phenacoccus.*

2) In *Puto* and *Macrocerococcus* larvae I have 7-segmented, and larvae III 8-segmented antennae; in *Phenacoccus* larvae I are provided with 6-segmented, and larvae III with 7-segmented antennae. Šulc (1897) describes larva I of *Ceroputo pilosellae* as possessing 6-segmented antennae, but in a preparation, received on loan from Dr. Morrison [1]), 7 antennal segments are present. A third stage larva has not been described by Šulc; the present writer has only seen larva I.

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1) The material was collected in 1936 in the port of New York on *Gentiana andrewisii* imported from England. The specimen agrees closely with the description of *Ceroputo pilosellae* by Šulc (1897) and Borchsenius (1949), though this species has never been reported from England. It is at present known from Bohemia (Czechoslovakia), Switzerland, Alsace (Germany), the Crimea, and the Caucasus (U.S.S.R.); the food plants reported are *Hieracium, Geranium, Plantago,* and *Carpinus*(?).

3) In the adult females of *Puto* and *Macrocerococcus* the vestiture of the antennae, and the structure of the claw is different from that of *Phenacoccus*; in this respect *Ceroputo* resembles *Phenacoccus*.

4) In *Puto* and *Macrocerococcus* quinquelocular pores (as found in *Phenacoccus*) are absent in all stages; on the other hand all larval stages of *Puto* and *Macrocerococcus* have multilocular pores which are absent in the larvae of *Phenacoccus*. Quinquelocular pores are present in the adult female of *Ceroputo pilosellae*, but not in larva I, as I observed in specimens lent through the kindness of Dr. Morrison. According to Borchsenius (1949) these pores are present in the adult females of *Ceroputo pilosellae* Šulc, *C. ferrisi* (Kiritshenko), and *C. pannosus* Borchs. In the original descriptions of Šulc (1897) and Kiritshenko (1935) quinquelocular pores are not mentioned; as they are only sparingly represented in the above mentioned species these pores may be easily overlooked. In the larvae of *C. pilosellae* only trilocular pores are present (Šulc's description; specimens of Dr. Morrison).

5) In the adult females of *Puto* and *Macrocerococcus* the apical hairs on the anal lobes are shorter than the anal hairs; this applies even to the first stage larvae. In *Phenacoccus* and *Ceroputo* the apical hairs are longer than the anal hairs, especially in the larvae.

6) The males of *Puto* and *Macrocerococcus* differ largely from those of *Phenacoccus* (as described by Šulc, 1943). There are differences in the number of eyes, the structure of the penis, the number of caudal filaments, and in the structure of the claw. The males of *Ceroputo* are not known.

7) The cytology of an American *Puto* sp. is different from that of two *Phenacoccus*-species which have been examined. In *Puto* sp. the number of chromosomes was 14 in the female and 13 in the male; in *Phenacoccus acericola* King and *Ph. gossypii* Towns. & Ckll. the number was 12 in both sexes. In *Pseudococcus citri* (Risso), *P. nipae* (Mask.), and *P. maritimus* (Ehrh.) 10 chromosomes were found in both sexes (Hughes-Schrader, 1948).

From what is said above it is clear that there are salient differences between *Puto, Ceroputo,* and *Macrocerococcus* on one side, and *Phenacoccus* on the other side, as is shown by the structure of the females, males, and larvae, and also by the cytology. On the whole *Ceroputo* comes nearer to *Phenacoccus* than *Puto* and *Macrocerococcus*.

Šulc (1897) has compared his new genus *Ceroputo* with the female specimens of Signoret's *Puto antennatus* in the Vienna Museum. He made 2 microscopical preparations of Signoret's specimens, and figured their antennae, legs, claw, anal ring, and trilocular pores in his figs. 18-22. Šulc's

conclusion is that *Ceroputo* is certainly different from *Puto* Sign. He mentions the difference of the legs, especially of the claw (cf. figs. 54-55 in the present paper), of the antennae (number and position of hairs), and of the anal ring (8 anal hairs in *Puto,* 6 in *Ceroputo*). There are other differences which Šulc has not mentioned. In all larval stages of *Puto antennatus* multilocular pores are present, distributed over the whole ventral surface; in the larvae of *Ceroputo pilosellae* these pores are absent. In the adult female of *C. pilosellae* the multilocular pores are confined to the ventral surface of the last 3 abdominal segments, while in *P. antennatus* they are found on the head and thorax as well as on the abdomen. Quinquelocular pores are present in *C. pilosellae,* but absent in all stages of *P. antennatus.* Tubular glands are numerous on the ventral surface of the head and thorax in *Ceroputo,* but scarce in *Puto.* In *Puto* the anal hairs are longer than the apical hairs on the anal lobes in all stages; in *Ceroputo* the reverse is the case. The lowest sensory hair on the antenna (on the third segment from the top) is vestigial in *Puto* (and *Macrocerococcus*), while it is of normal size in *Ceroputo* (and *Phenacoccus*). My own opinion is that the separation of the genera *Ceroputo* and *Puto* is fully justified.

Leonardi (1907) has described *Macrocerococcus superbus* as the type of a new genus, but afterwards (1920) he referred his new species to the genus *Ceroputo* Šulc. In my opinion Borchsenius (1948) has rightly declined Leonardi's last view, which has been adopted by several other authors. If *Macrocerococcus superbus* Leon. has to be assigned to some older genus, it should be assigned to *Puto* Sign. and not to *Ceroputo* Šulc. Leonardi as well as Borchsenius have ignored the genus *Puto* Sign., apparently because they were not acquainted with *Puto antennatus* Sign.

Macrocerococcus superbus Leon. and *Puto antennatus* Sign. resemble each other very much, and are certainly closely allied. The adult female of *M. superbus* shows the same structure of antennae and legs (including the claw), and the same distribution of gland pores as found in *P. antennatus.* Even minute details as the sclerotized rim of the ostioles, and the wrinkled rim of the circulus are alike. The larvae of *M. superbus* also resemble those of *P. antennatus;* all stages have multilocular pores on the venter, short apical hairs on the anal lobes, and the same type of legs and antennae as found in *P. antennatus.* The principal difference between the two species is that the adult female of *M. superbus* has 4-6 series of accessory cerarian plates on the dorsum, which are absent in *P. antennatus* (and *Ceroputo pilosellae*). These series of accessory dorsal plates are according to Borchsenius (1948) a special feature of the palaearctic genus *Macrocerococcus,* of which 5 new species are described in his paper. *M. superbus* is widely distributed in the

Mediterranean region, but the new species are each confined to an isolated area (Crimea, Tajikstan-Uzbekistan, Armenia, Nth Iran, and Nth Ural). Borchsenius considers these areas as the relics of a wider area of distribution in the tertiary period. He shows the differences between *Macrocerococcus* and *Ceroputo* (of which 3 species have been found in the U.S.S.R.), and states that *Ceroputo* comes closer to the genus *Phenacoccus* than the systematically isolated genus *Macrocerococcus*.

Another difference between the type species of *Puto* and *Macrocerococcus* is that in the latter no accessory anal hairs have been found. Their number is very variable in *Puto antennatus*, and sometimes they are wholly absent so that little value can be attached to this difference.

Another important difference between *Puto antennatus* and *Macrocerococcus superbus* I have found in the head of the males. In *Puto* the antennae are closely set together, at a distance less than the width of the first segment; in *Macrocerococcus* they are set rather wide apart, at a distance which is twice the width of the basal segment (fig. 49; see also Schmutterer, 1952, figs. 4-5). *Puto* has a row of 12 eyes, about equally spaced, and arranged all around the head (fig. 46). *Macrocerococcus*, however, shows a group of 5 eyes on each side of the head (fig. 49). Only few short hairs (25-40 μ) and very few gland pores are present on the head of *Puto*; in *Macrocerococcus* there are many long hairs (150-180 μ) and a large number of gland pores. On the whole gland pores are abundant in the male *Macrocerococcus*, and of another structure than in *Puto* where they are very scarce. In the male of *Macrocerococcus* the gland pores have distinct spine-like outgrowths (fig. 50), which are absent in the male of *Puto* (fig. 48). The male of *M. superbus* is wingless, the mesothorax is not sclerotized, and the gland pockets at the posterior end of the body are less developed than in *P. antennatus*. The latter features are probably due to the loss of wings. Dr. Schmutterer informed me that caudal filaments were absent in the males of *M. superbus* which he has collected in Bavaria; some of these specimens were used in the present study. The loss of wings, and other characters associated with their presence, is certainly of little importance from the taxonomic point of view.

Considering the differences between *Puto antennatus* and *Macrocerococcus superbus*, as mentioned above, I think that Borchsenius (1948) is right in re-establishing the rejected genus *Macrocerococcus* Leon. Unfortunately Borchsenius has not described the males of his five new species; any information about them is lacking. A d scription of these males is desirable for a further elucidation of the genus.

The generic types *Puto antennatus* Sign., *Ceroputo pilosellae* Šulc, and

Macrocerococcus superbus Leon. can be separated by the following characters:

1. Antennae of female 9-segmented, with whorls of about 5 hairs on the segments III-VIII. Claw stout, with a faint denticle (sometimes absent according to Borchsenius). No spines at the base of the claw. Claw digitules distinctly knobbed, considerably longer than the claw (fig. 54). Multilocular pores confined to the ventral side of the last 3 abdominal segments. Quinquelocular pores present around the rostrum. Multilocular pores absent in the larvae . . *Ceroputo pilosellae* Šulc.

—. Antennae of female 9-segmented, with at least 10 hairs (usually 10-15) on the segments III-VIII; these hairs are not arranged in whorls. Claws slender, with a conspicuous denticle, and 2 small spines at their base (figs. 55-56). Claw digitules blunt, at most very faintly knobbed, only slightly longer than the claw. Multilocular pores distributed over the whole ventral surface of the adult female, and all larval stages. Quinquelocular pores absent in all stages 2

2. Female with 4-6 longitudinal rows of accessory cerarian plates on the dorsum. Male with 10 eyes, divided in 2 groups of 5, located on the sides of the head; antennae set apart at a distance twice the width of the basal segment; gland pores with distinct spines (figs. 49-50) . . . . . *Macrocerococcus superbus* Leon.

—. Female without accessory cerarian plates on the dorsum (except a small pair behind the first cerarii). Male with a row of 12 eyes, about equally spaced, and surrounding the head; antennae closely set at a distance less than the width of the basal segment; gland pores without spines . . . . . *Puto antennatus* Sign.

Figs. 2-5, 8-10, 15, 17, 18-19, 21-23, 25-26, 45 and 55 were drawn from Signoret's type specimens. As most hairs were broken off, only the sockets (alveoli) have been indicated. The remaining figures of *Puto antennatus* were drawn from specimens collected in Bavaria by Dr. H. Schmutterer; this applies also to figs. 49, 50, and 56 which refer to *Macrocerococcus superbus* Leon. Figs. 57-59 were drawn from slides lent through the kindness of Dr. Harold Morrison from the Bureau of Entomology at Washington (U.S. Dept. of Agriculture).

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(The 3 preceding papers are written in Czech. With a short summary in German, and explanation of the figures in Latin. Each paper contains about 50 pages and 15 plates).