

Cerataphis lataniæ, a peculiar Aphid. By ALICE L. EMBLETON, B.Sc.; 1851 Exhibition Science Research Scholar. (Communicated by Prof. G. B. HOWES, D.Sc., LL.D., F.R.S., Sec.L.S.)

[Read 19th February, 1903.]

(PLATE 12.)

IN the autumn of 1901, Mr. Lamb, of Cambridge, noticed this insect on various orchids in one of the tropical houses at the University Botanic Garden. Through the kindness of Dr. D. Sharp it was brought to my notice, and this paper is the result of some investigations carried out with his assistance. I wish here to express my sincere thanks to him for all the valuable help he has given me.

The chief interest in this creature centres round its life-history, which exhibits some remarkable biological features, very little understood up to the present. Many notes have been written on the insect, but its extraordinary resemblance to *Coccidæ* and *Aleurodidæ* has given rise to great confusion. It has been described as belonging to three distinct families of Rhynchota, and even in a recent number of the 'Gardeners' Chronicle' it is still referred to the family *Coccidæ*, to which it certainly does not belong. At present in entomological literature it stands in three different genera, belonging to two different classes of insects. Seeing that so much confusion surrounds the nomenclature and taxonomy, it will perhaps be well, before discussing the points of biological interest, to give a brief historical account of the literature.

HISTORY.

This insect was first described by Boisduval in 1867*, under the provisional name of *Coccus ? lataniæ*. He found it in Paris on various palms belonging to the genus *Latania*; but as it is only to be found in hothouses, he concludes it must be of exotic origin, for it is killed by putting the host-plants into the open air. He is uncertain as to what family of insects it belongs, but suggests that when the male is known it will probably become the type of a new genus; provisionally he places it in his genus

* Ent. Horticle, p. 355, figs. 49, 50.

Coccus. He describes the colour and form of the several stages through which it passes, and states that it has been reported as doing damage to the young shoots of *Latania borbonica*, and as occurring in all its stages on the leaves of *L. rubra*. He sent it to M. Signoret, who concluded that it belonged to the 'Pentatomides,' "mais ayant remis cette année au mois d'avril à sa disposition des individus plus développés, il est revenu sur cette opinion; aujourd'hui il ne serait pas éloigné de le regarder comme le premier état d'un genre nouveau voisin des *Aleurodes*. D'autant plus qu'un autre insecte analogue trouvé en Provence, sur le laurier-tin et que, tous les deux, nous avons pris pour une Coccide, lui a produit une *Aleurode* voisine de celle que l'on rencontre sur le chélidoine."

The next year Signoret* described it at length in his monograph of *Aleurodidæ*, where he named it *Boisduvalia lataniæ*, though he had doubts as to its systematic position, being uncertain whether it belonged to the *Aphidæ* or *Coccidæ*. The male being unknown, Signoret suggested that it may be winged, and that its life may be short like that of the males of *Dorthesia* and of *Coccidæ*. His specimens came from the Isle of Bourbon, where they were living on *Latania*.

Four years later Signoret† again refers to this insect, in a letter from Venice, in which he says that he can now settle the vexed question as to its affinities. "En effet, M. Targioni-Tozzetti vient de démontrer que c'est un état particulier d'un Aphidien attaqué par des Grégaires; il y a arrêt de développement et formation d'un état tout particulier. M. Targioni a eu la bonne fortune de suivre le développement normal de cet *Aphis* qui vit sur les *Lataniæ*, et il en donnera la description détaillée dans le Bulletin de la Société entomologique italienne." We may suppose that this idea was abandoned, for no record appears in the Bull. Soc. Ent. Ital. from 1872-1888 of any publications by Targioni-Tozzetti, or any other writer, on the subject.

An insect like this was described by Westwood‡ in 1879 under the name of *Asterolecanium orchidearum*, "a new species of scale insect." He calls it the fimbriated or star-scale, and places it in the genus *Asterolecanium*, which had been erected by

* Ann. Soc. Ent. France, (4) viii. 1868, p. 400, pl. x. figs. 2, 2 a.

† Bull. Soc. Ent. France, (5) ii. 1872, p. xxx.

‡ 'Gardeners' Chronicle,' ser. 2, xii. 1879, p. 796, fig. 131.

Targioni-Tozzetti. "One such species," he says, "was lately described in this work under the name of *Coccus stellifer*, and we are now enabled to figure another species, for a knowledge of which we are indebted to Mr. F. W. Burbidge, of the Botanical Garden of Trinity College, Dublin, by whom it was found in the Orchid-house, especially affecting the Ladyslippers (*Cypripediums*), but also occurring sparingly on *Sobralias*, *Cattleyas*, and *Dendrobiums*. Our engraving (fig. 131) represents two small leaves of a *Cypripedium*, showing that it is chiefly the plain underside, and not the spotted upper side of the leaves, that the insects attack, forming small groups. The natural size of the full-grown insects is shown upon the leaves (figs. 1, 2), and the magnified insect is seen at fig. 3, with a small portion of the waxy marginal scales at fig. 4. It will be seen from fig. 3 that all traces of articulation in the body are lost, and that the fimbriated margin is more or less incomplete in parts, and not so continuous as shown in fig. 4 Fig. 5 represents the underside of a young specimen of one of the insects, copied from Dr. Signoret's plates, showing the articulation of the body, and the three pairs of jointed legs, which are gradually absorbed and lost after the insect has become affixed as a scale upon the surface of the leaf. The species may be termed *Asterolecanium orchidearum*, J. O. W. It closely resembles *A. bambusæ*, Sign.*, which is parasitic on the bamboo, but the scaly fimbriation is longer than in that species, the habitat also indicating it as distinct. The males of none of the species of the genus have yet been observed."

The insect under investigation was found to agree with the descriptions of *Cerataphis lataniae* (see next page); and to be quite certain that the Cambridge species was the same as the one Westwood had received from Dublin in 1879, I wrote to Mr. Burbidge at the Trinity College Botanic Garden, who very kindly sent me some specimens: these proved to be identical with the species found in Cambridge. Mr. R. Newstead, to whom specimens were submitted, confirmed the identification of the insect as *Cerataphis lataniae*. Professor Poulton has not been able to find any type of *A. orchidearum* in the Museum at Oxford.

Westwood's name of *Asterolecanium orchidearum* has never appeared in the 'Zoological Record,' or other lists, doubtless

* Ann. Soc. Ent. France, 4^e sér. x. (1870), pl. 8. fig. 3.

because he named and described it in the 'Gardeners' Chronicle,' which is not a zoological work.

In 1881 Signoret* having received the winged female of *Boisduvalia lataniæ*, realized that he had given the same name to two different genera. The name as applying to this insect he preserved on the ground of priority, for in this case it was given in 1868, while the name as applying to two *Coccidæ*, given in 1875 (*B. lauri* and *B. 4-caudata*), he changed to *Oudablis*.

The next year Lichtenstein† found the winged form, and changed the name to *Cerataphis lataniæ*, having determined that it is an Aphid. "L'insecte des *Latantias*, que Boisduval a nommé *Coccus lataniæ* et Signoret *Boisduvalia lataniæ*, est décidément un Aphidien du groupe des *Pemphigiens* et très voisin du genre *Vacuna* Heyden. J'ai enfin obtenu par élevage la forme ailée vivante. C'est un petit Puceron jaune clair à sa sortie de la nymphe, et, trois ou quatre jours après, devenant brun, à yeux noirs, qui a tout à fait l'apparence du *Phylloxera* et porte ses ailes à plat comme lui. La nervure cubitale des ailes supérieures est fourchue et les antennes ont cinq articles, caractères qui sont ceux du genre *Vacuna*. Mais la présence de deux petites cornes coniques et aiguës entre les antennes l'en distinguent et m'ont dicté le nom générique sous lequel je l'ai placé en collection; *Cerataphis lataniæ* Bois. (sub *Coccus*). Je ne puis conserver le nom de Signoret, parce qu'il a été donné sans diagnose et qu'il fait double emploi avec le genre *Boisduvalia* du même auteur, genre *Coccide* bien diagnosté." On p. xvi Lichtenstein refers the insect to his tribe Schizoneuriens, and this must at present be regarded as its scientific position. His remarks are best quoted fully for they are of signal importance:—

"Notre collègue M. Signoret a fait paraître dans le Bulletin no. 24 de 1881 une note relative à un insecte des serres, décrit pour la première fois par Boisduval dans son 'Entomologie agricole,' sous le nom de *Coccus lataniæ*, et après lui par M. Signoret sous celui de *Boisduvalia lataniæ*, dans sa Monographie des *Aleurodes*. Cet insecte n'est ni un *Coccidien* ni un *Aleurodien*, c'est un *Aphidien* fort curieux, dont je pourrai sous peu, je l'espère, présenter l'histoire complète de l'évolution.

"La forme ailée, très rare, le rapproche des *Schizoneura*, dont il

* Bull. Soc. Ent. France, 6^e sér. i. 1881, p. clvii.

† *Op. cit.* (6) ii. 1882, p. lxxiv.

a les antennes courtes et annelées. N'ayant pas pu encore le faire pondre, j'ignore si c'est une forme émigrante à petits à rostre, ou la forme pupifère à petits sexuels sans rostre, ou enfin un mâle. La forme arrondie et frangées, qui est la plus commune, me paraît très voisine de celle du genre *Acanthohermes* de Kollar, dont le pourtour est orné également d'une frange élégante.

"Je l'ai mis en collection sous le nom de *Cerataphis lataniae** en attendant de donner la diagnose de toutes les formes, ce qui me paraît indispensable pour une bonne description d'un Aphidien.

"Comme tout le monde, et notre savant collègue lui-même, avait oublié qu'il y avait un genre *Boisduvalia* dans les *Aleurodes*, et que le même auteur l'a remis dans les *Coccides*, où il renferme trois espèces (*lauri* Boisd., *4-caudata* Sign., *parietariae* Licht.), ne vaudrait-il pas mieux considérer comme non avenue la description de cet *Aphidien* parmi les *Aleurodes*, où M. Signoret ne l'ajoute qu'à regret, et laisser *Boisduvalia* comme genre de *Coccides*, en attendant ma description, ou celle d'un collègue plus avancé que moi dans l'étude de l'insecte, pour mettre le *Cerataphis lataniae* à la place qu'il devra occuper un jour entre les *Pamphigiens* et les *Phylloxériens*?"

In a note in the same volume (p. xxxv) Signoret refers the species to the family *Aphidæ* without remarking on the changed position, merely stating that this species of Aphid is found on an orchid (*Cælia albiflora*) and on many other plants.

The insect is next (1883) noticed by Buckton † in an Appendix to his 'British Aphides,' where he expresses himself doubtful as to its position. He has found no male, and says only three specimens of the winged female have been recorded, and those were not taken in England.

Yet another synonym now exists, for in 1901, Hempel ‡ placed it in the genus *Ceratovacuna* as a n. sp. *brasiliensis*; it is met with on various species of palm at S. Paulo in Brazil, on a species of *Epidendron*, and also on *Cattleya harrisonia*. Though he found winged and apterous females, he obtained no males.

The most recent reference to it is Jan. 15th, 1902, in the

* "*Cerataphis* à cause de deux petites cornes sur la tête chez toutes les formes que je connais jusqu'à présent; mais M. Signoret a vu aussi des Embryons sans cornes."

† British Aphides: Ray Society, 1883, p. 197.

‡ Ann. & Mag. Nat. Hist. ser. 7, viii. p. 384.

'Gardeners' Chronicle,' where Westwood's figures are reproduced still under the name of *Asterolecanium orchidearum*. Mr. Lynch, of the Cambridge Botanic Garden, who is interested in the insect as being an inhabitant of the orchid-house, brought to my notice this article, which led to my finding Westwood's original description.

Thus it is seen that the creature has appeared under the names of *Coccus? lataniæ*, Boisd., *Boisduvalia lataniæ*, Sign., *Asterolecanium orchidearum*, Westw., *Cerataphis lataniæ*, Licht., *Ceratovacuna brasiliensis*, Hemp. Of these the name of *Cerataphis lataniæ* must stand.

Synonymy of CERATAPHIS LATANIÆ.

Cerataphis, Lichtenstein (1882): [Rhynchota, Fam. *Aphididæ*, Tribe *Schizoneuriens*].

Boisduvalia, Signoret (1868); [nec *Boisduvalia*, Desv. 1830; nec *Boisduvalia*, Montre. 1855; nec *Boisduvalia*, Sign. 1875].

lataniæ (*Coccus?*), Boisduval, 1867, Ent. Horticole, p. 355, figs. 49, 50 (ascribed to *Coccidæ*).

lataniæ (*Boisduvalia*), Signoret, 1868, Ann. Soc. Ent. France, (4) viii. p. 400, pl. x. figs. 2, 2 A [young] (ascribed to *Aleurodidæ*). *orchidearum* (*Asterolecanium*), Westwood, 1879, Gardeners' Chronicle, ser. 2, xii. p. 796, fig. 131 (ascribed to *Coccidæ*); new synonym.

lataniæ (*Cerataphis*), Lichtenstein, 1882, Bull. Soc. Ent. France, (6) ii. pp. xvi & lxxiv (ascribed to *Aphidæ*, tribe *Schizoneuriens*).

lataniæ (*Cerataphis*), Buckton, 1883, Ray Society, Mon. Brit. Aphides, iv. p. 198, pl. 134 (ascribed to *Aphidæ*).

brasiliensis (*Ceratovacuna*), Hempel, 1901, Ann. & Mag. Nat. Hist. ser. 7, viii. p. 384 (ascribed to *Aphidæ*); new synonym.

orchidearum (*Asterolecanium*), Gardeners' Chronicle, ser. 3, xxxi. Jan. 25th, 1902, p. 57 (ascribed to *Coccidæ*).

BIOLOGY.

In turning to the natural history of this interesting species it is, perhaps, not out of place to briefly summarize the facts that are known at present. The species occurs frequently in orchid-houses in Britain, as the apterous parthenogenetic form; and for

one or more years about 1879, Mr. G. S. Saunders noticed the winged adult female in an orchid-house at Bristol; he has kindly given me a note on the subject, which will be found on p. 105, at the end of this memoir. In Brazil the winged female form is apparently not uncommon (cf. *Ceratovacuna brasiliensis*, Hempel, and is met with as a very rare occurrence on the continent of Europe—so far only three specimens have been recorded. No male has been discovered anywhere. On the Continent the apterous female is well known in hothouses, living on various species of palms and orchids. With us it always occurs on orchids, and has been reported from several localities—I have received it from Dublin, where it has been known for many years; and also from Cambridge. At Kew it is, I find, recognized as an orchid parasite, but I could get no specimens from the houses there.

Up to the present (and apart from the recently recorded Brazilian form which we know only by description), only three individuals of the winged form have ever been obtained, and they are all females. Buckton*, in 1883, says the imago of this viviparous winged female is apparently very rare, “for only three mutilated specimens are at present known. It has not yet been taken in England.”

As regards this Brazilian form, which Hempel† described last year under the name of *Ceratovacuna brasiliensis*, n. sp., it is, as already stated, another synonym for *Cerataphis lataniæ*, an opinion confirmed by Mr. R. Newstead. Hempel has found no males, but describes, not only the adult apterous female, but also the larval and adult winged female. This is important evidence as showing that in its native countries this species does not permanently remain in the form in which it is found with us, and as shown in Plate 12. It forms conspicuous groups or colonies on leaves and flower-stems of *Cypripedium* and other orchids, and can be procured all the year round. The colonies consist of individuals of all ages, from the small pale yellow young which actively wander about, to the round black immotile adults with their characteristic halo of white wax. The youngest forms, measuring about 5 mm. (or less) in length, are free from this fringe of wax; the pair of dark eyes, situated anteriorly near the

* British Aphides, Ray Society, 1883.

† Ann. & Mag. Nat. Hist. ser. 7, viii. (1901) p. 384.

edge of the body, are easily seen because the general colour of the creature is pale yellow. In this condition they move about freely on the plant, but their wanderings are not very extensive, and, in a state of nature, the species could scarcely rely on these young forms as the sole means of dissemination. In their native countries this probably is effected by the winged forms. Later on the early form becomes covered with a powdery white secretion, but still there is no definite ring round the margin of the body such as marks the older stages.

In the active or locomotive early form the antennæ are rather stout and blunt; they are composed of a basal joint and four segments, of which the last is the longest (Pl. 12. fig. 4); at its tip it carries several setæ and a hook or claw, and there are, in addition, one or two setæ on each of the other segments. The last three joints of the antennæ are ringed (Pl. 12. figs. 3, 5). Between the antennæ, on the front of the head, are two small horns in all the specimens I have seen, and in all forms according to Hempel and Lichtenstein; but Signoret* states that in some young there are no traces of these horns, and suggests that this may be a sexual difference†. In this early condition the body is elongated and the dorsum is but slightly convex; the head and thorax make up almost one-half of the length of the body, being clearly marked off from the abdomen by a groove; the articulation of the body is very obvious at this stage. The legs are not yet hidden by the marginal waxy secretion, which makes its appearance later. The tarsi are two-jointed, and are armed with setæ, and end with two strong recurved bristles or claws; all the segments bear scattered setæ, and in all respects are formed normally as in *Aphis*. The rostrum is proportionately longer in this stage than it is in the adult, for it reaches beyond the posterior coxæ; the basal section is bulbous, and the third and terminal joint is pointed; each of the first two parts bears a pair of setæ, while the third, or last, is provided with two pairs.

This form is succeeded by one of an ochreous green colour, larger in size, and in which the body has developed, round the margin, the ring of tubercles from which, later, the fringe of

* Ann. Soc. Ent. France, 4^e sér. viii. (1868) p. 400.

† See footnote, p. 94.

wax is secreted. The eyes are still conspicuous as dark red-brown spots. The body, still powdered over with a fine white dust which soon disappears, is broader than in the preceding stage and is less flattened. The antennæ and legs are unchanged; the head is less pointed, and the rostrum ends between the second and third legs.

As the adult condition is approached the activity becomes less, while the colour deepens and the body becomes more round in outline and more arched dorsally. The adult insect (Pl. 12. fig. 2), like a Coccid, is fixed by the suctorial proboscis to the host plant, and appears as a dark, almost black, rounded excrescence, surrounded by a conspicuous fringe of white wax; it is about 1.50 mm. in length and 1.25 mm. in width: the antennæ are about .23 mm. in length, but are usually hidden by the border of wax. Across the dorsal surface, about halfway back, is a deep furrow, caused by the articulation becoming more marked in these two segments, separating the thorax from the abdomen, and so the insect has the appearance of being, to some extent, divided across the middle. Dorsally, in the posterior region of the body, are two cornicles as shown in figs. 7-9. The eyes are now inconspicuous.

The confusion that has grown up in the literature relating to this insect has been due, as I have already stated, to the fact that it closely resembles many *Coccidæ* and *Aleurodidæ*. The three great families of these insects—*Coccidæ*, *Aleurodidæ*, *Aphidæ*—have, so far as outward appearance goes, much in common, and systematically the members of these families are distinguished from one another by such minor points as differences in the number of joints in the feet and antennæ. But the real distinctions are biological, occurring in the life-histories—the *Coccidæ* going through a complex metamorphosis which is totally different in the two sexes, resulting in the production of imagoes where the two sexes differ completely. The *Aleurodidæ*, though they show a remarkable series of metamorphoses, are identical in the two sexes, and these are constantly produced in each generation, the development resulting in the production of the normal Hemipterous form, alike for male and female. The *Aphidæ*, on the other hand, exhibit a very different and striking series of changes, the unique feature of which is that the development is, so to speak, spread over a number of successive

generations, resulting in the production of a winged sexual form in cases where winged individuals have previously occurred in the cycle of generations. The life-history of *Cerataphis lataniæ* is very different from that of the *Coccidæ*.

This insect has now been under observation for more than a year in Cambridge, and though the investigation has been of a somewhat desultory nature, owing to the lack of a special laboratory in which to pursue such work, yet nothing has been found to suggest in any way that the conditions of form and development mentioned above have been departed from by any individuals. Specimens have been collected from time to time by Miss M. A. Sharp and myself, and submitted to examination with a view to ascertaining whether any diversity, other than that of age, could be detected among them, but we have failed to find any indication of such diversity. Moreover, all figures and records that exist of the insects in this country exhibit it in this form only. Westwood's figures of the specimens obtained from Dublin in 1879 show the young and adult forms as we have them now at Cambridge. Buckton's figures and remarks give evidence of the same uniformity.

All the observations, then, that have been made in this country lead to the belief that the species exhibits here only one form which reproduces parthenogenetically in an uninterrupted manner. Parthenogenesis extending over a variable number of generations is, of course, a very common occurrence among *Aphidæ*; and it is probable that even in climates (such as the Isle of Bourbon, Brazil, &c.) where the winged females of this species are produced not infrequently, that it is still an important, if not an exclusive, mode of perpetuating the species. No males have yet been discovered anywhere. Remarkable as this fact is, it is not without parallel, but it is extremely unusual for this mode of reproduction to be the concomitant of a metamorphic ontogeny repeated uninterruptedly from generation to generation. It is possible that the parthenogenetic reproduction of *Aphidæ* can be carried on for a great number of generations; indeed, such continuity has been shown to exist, though its limits have not yet been determined.

Cerataphis lataniæ in this country appears to be entirely deprived of the complex life-history found in its allies (on which I shall subsequently enlarge). In the Cambridge Natural

History * Dr. Sharp says :—" The simple form of Aphid life may be described as follows :—Eggs are laid in the autumn and hatch in the spring, giving rise to females of an imperfect character having no wings ; these produce living young parthenogenetically, and this process may be repeated for a few or for many generations, and there may be in these generations a greater or less number of winged individuals, and perhaps a few males. After a time when temperature falls, or when the supply of food is less in quantity, or after a period of deliberate abstention from food, sexual individuals are produced, and fertilized eggs are laid which hatch in the spring, and the phenomena are repeated. In other cases these phenomena are added to or rendered more complicated by the intercalated parthenogenetic generations exhibiting well-marked metamorphosis, of kinds such as occur in apterous or winged insects ; while again the habits of successive generations may differ greatly, the individuals of some generations dwelling in galls, while those of other generations live underground on roots."

It being taken for granted that *Cerataphis lataniæ* as found in Britain is an Aphid, although it departs biologically very widely from that group of Insects, inasmuch as it appears to be totally deprived of those successional metamorphoses that are so characteristic of *Aphidæ*, it becomes interesting to inquire how this arises. In order to make my ideas on this point comprehensible it is advisable briefly to summarize Pergande's † recent remarkable discoveries as to the life-histories of migratory Aphides. Although the results are only lately published, he has been prosecuting this inquiry for more than 20 years. The simplest form of Aphid-life is that described by Dr. Sharp, and quoted above, while the most complex is that described by Pergande. He shows that these migratory Aphides exhibit the most complex form, not merely of ontogenesis, but also of the cycles of generations that are so marvellous in this family. He has discovered that these creatures possess, in their ontogeny, an "aleurodiform" stage, to which our hothouse inhabitant bears a most striking resemblance. The allied forms which Pergande studied are *Hormaphis hamamelidis*, Fitch, and *Hamamelistes*

* Insects, part ii. p. 582.

† U.S. Dep. Agric., Ent. 1901, no. 9. "The Life-history of two Species of Plant-lice, inhabiting both the Witch-hazel and Birch."

spinosus, Shimer, Aphids that make galls on the leaves of the witch-hazel (*Hamamelis virginiana*) in North America. The individuals in the gall pass through a metamorphosis, appearing in a different form after each ecdysis. The individuals of this generation are not winged, but remain on the host plant, and produce a second generation within the walls of the gall. The individuals of this generation also undergo their development and metamorphosis inside the gall, but they differ essentially from those of the first generation inasmuch as they develop wings and all ultimately leave the shelter of the gall.

From the witch-hazel these winged forms migrate to the birch (*Betula nigra*), where they immediately place their young, so that the species now lives not in galls but exposed on birch-leaves. This third generation undergoes a complex metamorphosis, the successive instars being very different from one another; the last instar so closely resembles many *Aleurodidae*, that Pergande has called it the "aleurodiform" stage. In calling it "aleurodiform" it may be as well to remark here that it is the young *Aleurodes* which the *Aphis* resembles, and not the adult form.

While living on the birch, two other aleurodiform generations (*i. e.* the fourth and fifth) are passed through, but they differ only very slightly from the third.

The sixth generation is remarkably different. In this generation the insect is winged and leaves the birch to return to the hazel. It may safely be taken for granted that hitherto all the individuals produced have been females, but a seventh generation arises in which both sexes occur. Eggs are laid before the leaves appear in the spring, the young hatching from these eggs start the galls, and the life-cycle is begun once more.

From this work by Pergande it will be seen that *Cerataphis lataniæ* found on orchids corresponds to the aleurodiform stage of a migratory *Aphis*, such as he has described in the case of *Hormaphis hamamelidis* and its ally. In these insects, however, the stage is transitory, and is usually succeeded by a winged form; but in the case of *Cerataphis* in Britain, it seems that no further stage is reached. So far as the observations in Cambridge go, they lead us to believe that this aleurodiform stage is the permanent condition of the insect; in spite of the

fact that no males * have been found, yet in the colonies there are always young forms: thus the reproduction as carried on in this country must be solely parthenogenetic, and since the creature is not in the true imago condition, it is a sort of pædogenesis as well as parthenogenesis. Possibly this condition results from the fact that the creatures live in hothouses where the climatic conditions are constant and the food-supply uniform, whereas in a state of nature one or both of these factors might be varied. If these natural conditions could be imitated, we should perhaps succeed in getting other generations to follow on this aleurodiform stage. In the case of *Hormaphis hamamelidis*, the generation which leaves the gall does so on account of the food becoming used up. The *Cerataphis* on orchids in our greenhouses does not experience this, for the food-supply is fairly constant, and also the atmospheric environment: thus it seems probable there is no incentive to produce the winged form.

Our insect, therefore, is seen to exhibit the simple condition of life-cycles as described by Dr. Sharp, while its ontogenetic and morphological form is that which occurs as part of the complex series of generations so lucidly depicted by Pergande. These facts lead to the supposition that it is one of the migratory Aphides that has been deprived of the series of metamorphoses, owing to an artificial mode of life.

When Huxley studied Aphides, the remarkable phenomena that he met with so impressed him that he devoted considerable attention to their bearing on the questions of individuality and the individual in Biology. Since then, the discoveries that have been made in this group of Insects have rendered the

* Signoret's suggestion that the differences he observed in the larvæ may be sexual, is probably incorrect, if we may judge from the life-histories of the species described by Pergande. In the latter, the sexual forms are produced in a special final generation, quite distinct from the preceding generations of parthenogenetic individuals. The larvæ that Signoret thought might be males (differing from the others mainly in possessing no frontal horns) occurred indiscriminately, and not in a special sexual generation, as described by Pergande. It is probable that those Signoret states as being without horns were merely very early larvæ in which these organs were not yet fully developed; I have often found in very young individuals that the horns are almost undiscernible.

problem still more complicated and difficult. Huxley* says: "Every organized being *has* been formless and will again be formless; the individual animal or plant is the *sum* of the incessant changes which succeed one another between these two periods of rest." [the individual] "is the sum of the phenomena presented by a single life: in other words, it is all those animal forms which proceed from a single egg taken together."

Herbert Spencer, however, holds a totally different view from that which Huxley formulated. His opinion is given in the chapter on "Individuality" in the first edition of the 'Principles of Biology,' written in 1864. Admitting the many difficulties which surround the subject, he proceeds to discuss the validity of the theory that the whole product of a single fertilized germ shall be regarded as the true individual, whether such whole product be organized as one or many masses that are partially or completely separate. He thinks this is an undesirable definition, for it involves the application of the word individual to numerous separate living bodies, a meaning strikingly in conflict with the ordinary conception of the word. As an example of this he instances the case of *Aphidæ*, "where the organism is but an infinitesimal part of the germ-product; and yet has that completeness required for sexual reproduction [If the individual is constituted by the whole germ-product, whether continuously or discontinuously developed, then, not only must individuality be denied to each of the imperfect *Aphides*, but also to each of the perfect males and females; since no one of them is more than a minute fraction of the total germ-product]"†. As he cannot therefore adopt this view, he endeavours to "make the best practicable compromise," with the knowledge that there is no definition of individuality which is unobjectionable. The essential idea of the conception of individuality he takes to be union among parts of the object and separateness from other objects; it also involves the manifestation of Life, which he regards as "the definite combination of heterogeneous changes, both simultaneous and

* Scientific Memoirs of Thomas Henry Huxley, i. p. 147. London, 1898. (The date of the original paper is 1852.)

† This sentence is omitted in the 1898 edition.

successive, in correspondence with external co-existences and sequences." A biological individual is therefore one which possesses the power to live alone, given suitable conditions, and which is a wholly or partially independent organized mass, arising continuously or discontinuously: "we must accord the title to each separate aphis, each polype of a polypedom" There are anomalies, which he regards as inevitable, if the hypothesis of Evolution is correct, for organic forms must have arisen by insensible gradations; but he concludes the chapter by saying: "We must be content with a course which commits us to the smallest number of incongruities; and this course is, to consider as an individual, any organized mass [centre or axis]* that is capable of independently carrying on that continuous adjustment of inner to outer relations which constitutes Life."

Since the period at which Huxley and Spencer wrote, our knowledge of the cycles of generations in *Aphidæ* has become more extended, and the life-histories have been found in many cases to be extremely complex. As has been stated above, in the case of *Cerataphis lataniæ* in this country, the species is apparently maintained permanently by parthenogenetic pædogenesis of an aleurodiform instar. According to Huxley's view, we must consider all the specimens co-existent in different parts of this country, and those of all past generations that have presented the same phenomena, as a single individual.

It is well known to modern zoologists that there exists a great variety of individuals, individualities, and individual lives; and Spencer's definition is clearly more convenient practically than Huxley's, though it conveys no connotation of this variety.

The permanent, or quasi-permanent, condition of *Cerataphis lataniæ* in this country lends additional support to the view, at present accepted very widely, that in polymorphic insects the particular form attained by an individual is determined by the food. In *Hormaphis hamamelidis* the form is altered when the food becomes inadequate, and recourse is had to living on the leaves of another tree. On this the aleurodiform generations are maintained till the nutriment fails in the autumn, when winged forms are again produced. As the conditions under

* Omitted in 1898 edition.

which *Cerataphis lataniæ* lives in our hothouses are, roughly speaking, constant, especially as regards an equable supply of nutriment, we may conjecture that this is responsible for the permanence of the aleurodiform stage. Whether the form of the creature can be altered by interference with its food-supply is a very interesting subject for experiment. From this point of view it is of great importance that the converse experiments should be made on *Hormaphis*, or on some other migratory Aphis, with a view to ascertaining whether, by supplying successive generations with a constant supply of food under equable conditions of temperature, &c., the creature could be maintained for many generations, or permanently, in the aleurodiform stage.

Another factor, beyond the constant conditions of food and temperature, that may increase the tendency to the stability of this transitory form, may perhaps be found in its parthenogenetic reproduction; for it has been pointed out that parthenogenesis in Insecta is very commonly concomitant with the production of young that are all of one sex.

I am well aware of the incompleteness and inadequacy of the views expressed in this paper, but if this communication shall lead to experiments being instituted with this creature, then my object will be attained.

APPENDIX.

As stated on p. 95, when this paper was read, Mr. G. S. Saunders made some suggestions on the subject, the most important of which was that in 1879 he observed the winged female. With his permission I append his remarks:—"I was staying with an uncle of mine at Clifton near Bristol, who had a large collection of orchids, in May 1879, when I found this insect in considerable numbers on the leaves of various orchids, but most commonly on *Cypripediums*. Knowing very little at that time about insects of this nature, I took the apterous females for one of the *Coccidæ*, and I found a short account of the insect in Boisduval's 'Essai sur l'Entomologie Horticole.' One day I was surprised to find some of the larvæ had become pupæ; later on I found the females, which I then took for males, and finding that Boisduval stated that the males were unknown, I wrote to Signoret stating that I had found the males.

I forget if I sent him specimens or only described the insect: he replied that what I had found were probably females. I found these winged females were not nearly so common as the apterous ones, still at various times I must have found a hundred or so. I think I noticed this insect in its different conditions two or three years, and then my uncle got a new head-gardener and *Cerataphis* vanished, and I saw it no more."

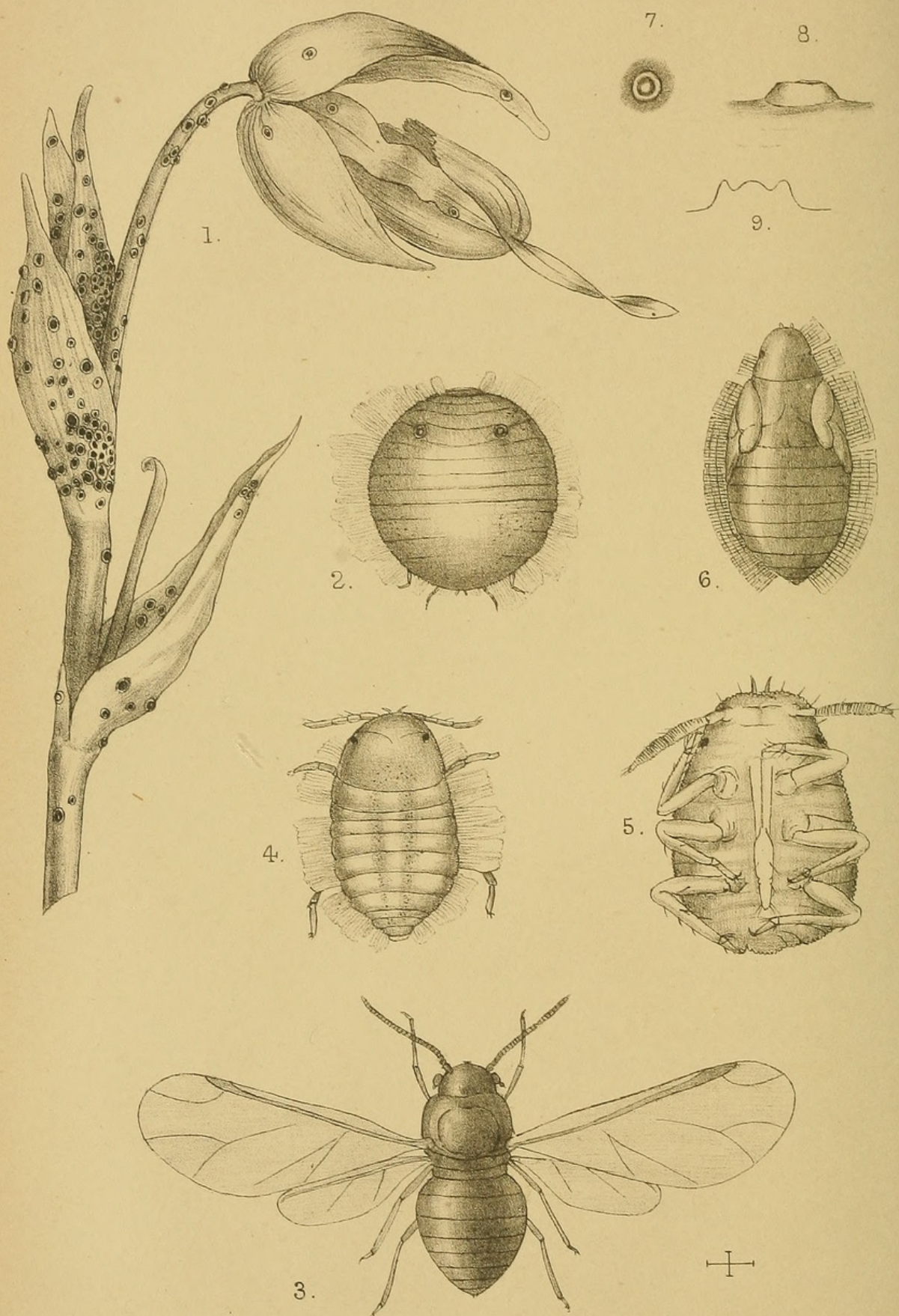
Mr. Saunders also kindly sent me some drawings made in 1879 of the winged female, and some details of structure, similar to those that have already appeared in Buckton's work: in addition there are also some figures of the nymphal condition, one of which I have added to Plate 12 (fig. 6) as no previous illustration of this instar has been published.

On March 11th, 1903, Mr. Saunders wrote to say that "On carefully examining some dried specimens of *Cerataphis lataniæ* which I had mounted on card, I noticed what I do not think had ever been discovered before, that the apterous female has cornicles; Buckton has not noticed them evidently. You do not show them in your drawing, and I certainly never saw them in the specimens I examined when fresh. I have just made a drawing under the camera lucida, which I enclose with my other drawings." I find this discovery of Mr. Saunders is correct, and I have added sketches of the cornicles as they exist in the adult (Pl. 12. figs. 7-9). Neither Mr. Saunders nor I have found them in the young larvæ; he says "they are not in the winged forms, but are present in the pupæ."

The occurrence of the winged female in England for one or more seasons twenty-four years ago is of considerable interest in connection with the peculiar life-cycle of this creature, and, on the whole, lends, it appears to me, additional support to the view I suggest, viz., that the extent of life-cycle, or the number and variety of the instars that go to make up the life-history of this creature, are determined by the conditions under which they live.

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EXPLANATION OF PLATE 12.

- Fig. 1. *Cypripedium* with *Cerataphis lataniæ* 'in situ'; natural size.
2. Dorsal view of adult, showing the cornicles. Length = 1.5 mm., width = 1.25 mm. (By an oversight, this figure is inverted.)
 3. Winged female (by G. S. Saunders).
 4. Dorsal view of larva in which the fringe of wax has developed.
 5. Enlarged view of same from the ventral surface, showing the proboscis, ringed antennæ, frontal horns, &c. Length = .55 mm., width = .4 mm., length of antennæ = .25 mm.
 6. Pupa of the winged female (by G. S. Saunders).
 - 7, 8, 9. Cornicle: (a) from above, (b) from the side, (c) in section. (By G. S. Saunders.)
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