NOTES ON NYCTERIBIIDAE, WITH DESCRIPTIONS OF TWO NEW GENERA.

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(With Plate XXIV.)

This paper is written primarily with the intention of publishing descriptions of two new genera of Nycteribiidae, together with some notes relating to certain already known forms of that family. But it also includes an account of some recent work (not my own), which for the first time gives us a detailed insight into the habits of these bizarre creatures. This latter side of the subject will be considered first.

A. BIOLOGICAL SECTION.

The summary of recent biological observations may be prefaced with some more general remarks.

Nycteribiidae are a family of highly modified and quite wingless Diptera, classed in the probably polyphyletic group "Diptera Pupipara." The components of this differ widely *inter se*, but all possess in common the characteristic of retaining the young within the body of the parent till larval life is practically completed, and of then giving birth to the matured larva, which almost immediately commences its transition into the pupal stage. Nycteribiidae, as well as another family of Pupipara, the Streblidae, are external parasites found exclusively on bats.

Geographical Distribution. Only a brief allusion will be made to this subject. Speiser tabulated the distribution of all known forms (1901, pp. 62–3[1]), and discussed the question further in two interesting later papers (1907, 1908[1]). His statements have necessarily been somewhat modified by subsequent findings, and our knowledge needs sum-

[1] References thus given are to the list at the end of the paper.

marising afresh before detailed conclusions are drawn. But some broad facts seem fairly established. As remarked by Speiser (1908, p. 423) the geographical headquarters of Nycteribiidae appear to be in the Old World, the lands bordering the Indian Ocean being particularly rich in species. By comparison, the family seems but poorly represented in America. The Streblidae, on the other hand, are much better represented in the New World, while possessing also a second centre in certain of the lands adjacent to the Indian Ocean.

Many Nycteribiidae have a very wide geographical range, which, as previously remarked (Scott, 1913, p. 93), is not surprising in view of their hosts' powers of distribution, and of the insects' power of attaching themselves to several different species of hosts (see below). The paper just referred to shows that certain species known from many parts of Europe and from N. Africa have been found also in Formosa, and may occur across all the intervening part of the Palaearctic Region; while other forms are widely distributed in the Oriental Region. *Eucampsipodia hyrtli* is known from Egypt, West and South Africa, Comoro Islands, Burma, Ceylon and Sumatra. *Tripselia fryeri* (discussed in this paper) was described from Assumption Island, to the North of Madagascar, and from Labuan; it has now been found in the Belgian Congo.

RELATION OF PARASITE TO HOST. (i) A single species of Nycteribiid may infest several species of bats. (ii) Conversely, a single species of bat—even a single individual—may harbour several species of Nycteribiidae.

(i) Speiser's enumeration of species (1901, pp. 49–56), and subsequent work, show that it is quite frequent for a single species of Nycteribiid to have several species of hosts. In such cases the hosts may be several bats of the same genus, or may represent two or more genera, or may even belong to more than one family, though the last condition is probably rare. There do appear, however, to be some broad restrictions, *e.g.* the same species of Nycteribiid is not usually found on both fruit-eating and insect-eating bats. Thus, the genus *Cyclopodia* (*s. str.*) seems to be confined to frugivorous forms (Pteropidae; cf. Speiser, 1907, p. 23), and I am not aware that the large Eastern species, such as *C. sykesi* and *C. albertisi*, have been found on any host but the big "flying-foxes" (*Pteropus* spp.). Other forms of *Cyclopodia*, which, as shown below, should be placed on account of structural characters in distinct subgenera, break this rule. Thus *Cyclopodia roylei* has been recorded from two genera and several species

of the small insect-eating Vespertilionidae, and also from the Nycterid bat *Megaderma lyra*, which eats small Vertebrates. This last is one of the cases in which the hosts belong to more than one family. It is shown in a table which I drew up for some Ceylonese Nycteribiidae (1914*a*, p. 212). The same table includes another such case, that of the wide-spread *Eucampsipodia hyrtli*, which has been recorded from several species of the fruit-eating genus *Rousettus* (evidently its normal hosts), and also in a solitary instance from the Vespertilionid *Tylonycteris pachypus*. *Penicillidia dufouri* is known from both Rhinolophidae and Vespertilionidae (Speiser, 1901, p. 50), both of which families, however, belong to the insectivorous category. The insects' powers of selection of hosts seem fairly elastic.

(ii) Conversely, as stated above, one species of bat may harbour several kinds of Nycteribiidae. At least 9 species have been recorded from *Miniopterus schreibersi* in various parts of its wide range. Attention has previously been called to the fact that examples of several species and genera of Nycteribiids may be found *on the same individual bat* (Scott, *Nycteribiidae from Formosa*, 1908, p. 359, and 1913, p. 93). In this connection the habits of the bats must be taken into consideration. So far as known, the insects leave the bats only rarely and for short intervals (see below), therefore their chances of infesting several species of bats must depend on the extent to which these come in contact with one another. The big flying-foxes of the genus *Pteropus*, which eat fruit, rest, as far as I know, not in caves or buildings, but hanging from branches of trees, and consort in great numbers in particular places (called "camps" in Seychelles). Such bats are not likely to come into contact with bats of other families and genera: as far as I am aware, no Nycteribiidae have been found on them except certain large species of *Cyclopodia*, which, conversely, have not been taken from bats of any other genus. On the other hand the vast majority of the Formosan Nycteribiids referred to above were obtained from large numbers of *Miniopterus schreibersi* congregated in an old temple. Isolated individuals of two other bats, a *Myotis* and a *Pipistrellus*, hung among the *Miniopterus*; the parasites could easily wander from one species to another, and some specimens were collected from *Myotis* and *Pipistrellus*, though the collector (Hans Sauter) stated that when these latter were captured alone, they were usually quite free from Nycteribiids. Perhaps some kinds of bats are constitutionally less liable than others to become infested, even though they may be equally accessible to the parasites. Somewhat in contrast to the Formosan case is that of 5 species of Nycteribiidae collected

from 3 species of bats in a large cave at Hammam Meskoutine in Eastern Algeria (P. A. Buxton, *Ent. Record*, Vol. XXVI, 1914, p. 68). One species of bat, *Myotis oxygnathus*, harboured 3 species of Nycteribiids; the other two, *Rhinolophus euryale* and *Miniopterus schreibersi*, were infested by only one species apiece. Also, none of the 5 species of parasites was taken from more than one species of bat. But the *Rhinolophus* and *Miniopterus* were found almost solitarily, in parts of the cave removed from one another and from the *Myotis*, great numbers of which were congregated in one place; and it is precisely this last species which harboured 3 kinds of Nycteribiids. If this was the normal disposition of the bats when at rest, it helps to explain the distribution of the insects, on the assumption that the latter do not wander any distance from their hosts.

RECENT BIOLOGICAL OBSERVATIONS. Apart from the broad facts of their larviparism and parasitism, the biology of Nycteribiidae has been hitherto very little known. Recently, however, a very interesting paper by Rodhain and Bequaert (1916) has been published, describing in detail the behaviour of one species, *Cyclopodia greeffi* Karsch (= *rubiginosa* Bigot[1]), in the Belgian Congo. These writers commence by summarising the earlier contributions of Westwood, Osten-Sacken, etc., but they do not appear to have noticed some valuable particulars *à propos* of certain Oriental forms contained in a paper by Muir (1912). It is intended here to give a *résumé* of Rodhain's and Bequaert's work, referring also to that of Muir for purposes of comparison.

Rodhain and Bequaert procured at Leopoldville a number of living fruit-eating bats, *Cynonycteris straminea* E. Geoffr., which almost always harboured abundant specimens of *Cyclopodia greeffi*, to which species alone do their statements refer. The bats proved easy to keep alive in cages of wire-gauze. During almost the whole day they hung motionless, head downwards, from wooden perches, but at night they climbed actively about. They were fed almost entirely on bananas. In one case the roof of the cage was glazed, so that the movements of the parasites on the bodies of their hosts could be watched. [Muir was less fortunate, since the forms observed by him lived on an insect-eating bat, *Miniopterus schreibersi*: many specimens of this were placed

[1] The insects were determined as *C. greeffi* from Karsch's description, published in 1884. Specimens, submitted to me later, proved to be identical with the type of *C. rubiginosa* Bigot (1891), with which I compared them. It is extremely probable that the two names are synonyms; *C. greeffi* was originally discovered on the same species of bat as Rodhain's and Bequaert's material.

in cages, but they refused to eat the insects given to them and died within 48 hours (1912, p. 352).]

The *Cyclopodiae* often remain motionless for hours together, buried in the host's fur, the head and thorax quite hidden and only the hind end of the abdomen visible. They do not seem to cause the bats very great discomfort, though after a bite from one of the insects a bat will often scratch itself with the hooks of its wings or the claws of its feet. The parasites do not pry into their hosts' heads, and when pursued they escape with surprising agility and hide in the long hair of the neck or under the wings. [The agility of living Nycteribiids has been noticed before, *e.g.* as mentioned in the case of *Tripselia fryeri* (Scott), 1914*b*, p. 163: and Mr F. M. Howlett tells me that he has remarked the extreme agility of *Cyclopodia sykesi*, in India.] They do not normally leave their hosts without very good reason: females do so for short periods in order to give birth to larvae; males were never seen to leave the host-bats, though they may pass from one bat to another in search of females [especially when the bats are almost or quite in contact.]

As a result of more than 50 dissections, *fresh blood was always found in the dilated part of the middle intestine*, which would seem to indicate that they feed very frequently. Neither intestinal nor coelomic parasites of the *Cyclopodia* were ever found in the course of these dissections.

Insects removed from the bats survived but a very short time, and could not be induced to feed. In a glass tube they rarely lived more than 12 hours, and males under these conditions fought and killed one another very quickly. [Howlett found that specimens of *C. sykesi* survive only a very short time when removed from their hosts, whether they be placed in glass tubes or confined in gauze cages.] Nevertheless, specimens newly emerged from their puparia have greater powers of resistance, which is important for them, as in this stage they must find and invade their hosts. But if they cannot do this within 48 hours, they perish. They belong to that narrow category of ectoparasites which are closely adapted to their hosts and scarcely able to survive without the latter.

It is not rare to observe the coitus of the *Cyclopodia* on the bats: the male climbs on to the female and curves the extremity of the abdomen under the anal segment of the female, holding on to the latter by means of his powerful claspers. The coitus lasts at least 10 minutes.

Gravid females are distinguishable by the distension of the abdomen, which in a non-gravid condition is bluish-black, but when distended by

the larva becomes whitish. Then the insect leaves its host and runs rapidly about on the wooden perches to which the bats cling, and on the walls of the cage. From time to time it stops and raises its abdomen, which it brushes with its hind legs. Having at length discovered a suitable place in which to deposit its larva, the female stops, and, keeping the thorax still, moves the abdomen several times from left to right: at the same time it rapidly expels the larva, which by constriction and stretching passes through the narrow genital orifice and then almost instantaneously resumes its normal shape.

The larva does not move about after birth, but immediately adheres to the substratum on which it is laid. The female also immediately moves backwards, places itself over its progeny, and by alternately raising and lowering itself presses the ventral surface of its thorax closely against the larva. By this means the latter is, as it were, gummed to the substratum, from which it can only with difficulty be detached undamaged. The female repeats this pressing movement three or four times, then stays a moment uplifted on its legs, after which it runs quickly back to its host.

Puparia were never found on the bodies or in the excrement of the hosts: the numerous examples were all laid close to the bats, in most cases on the lower surface of the wooden perches from which the latter hung, sometimes on the wire-gauze or glass walls of the cages. Smooth and dry surfaces seem to be preferred for the deposition of the larvae. In a natural state the bats sleep suspended from branches, particularly those of *Dracaena*, on the smooth branches and trunks (perhaps also leaves) of which the larvae are probably laid.

[At this point it is important to compare the observations of Muir (1912, pp. 357–8), which show that at any rate some forms of Nycteribiidae fasten their larvae to their hosts. His observations are concerned with the kind described below as *Eremoctenia progressa*, referred to by him as *Penicillidia progressa*, and may be cited as follows: "The full-grown larva, when passing out of the uterus, becomes greatly flattened, especially on the ventral surface, and is held by its anterior end for a short time between the external flaps of the vagina, its ventral surface being pressed against the skin of its host; generally near the junction of the wing-membrane with the body or limb. The chitinous exudation...first appears along the edges of the flattened ventral surface and fastens it to its host..."] Kolenati attributed to a Nycteribiid certain puparia which he found attached to the hairs of a *Vespertilio*, but proof is required that these were not puparia of a Streblid. As

stated by Rodhain and Bequaert, the puparia of *Lipoptena* and *Melophagus* adhere to the hairs of their hosts.

As far as can be judged from several experiments, the first larvae of the *Cyclopodia* are born from 8 to 11 days after the emergence of the ♀ from the puparium, and succeeding births are separated only by intervals of 2–6 days. The conditions under which the bats are living at any particular time seem to affect the fecundity of the parasites.

Immediately after birth the larva assumes a shape identical with that of the puparium. It is a soft, transparent, milky-white body, half ellipsoidal, with elliptic contour, with dorsal surface convex and ventral surface flat, the two surfaces separated by an angular margin. Although stuck to the substratum, it undergoes active internal movements in relation with the process of nymphosis. It seems to be born at a less advanced stage than the larvae of *Hippobosca* and *Melophagus*, which at birth are already much more like puparia. There are two pairs of spiracles only, both postero-dorsal in situation, one pair being about one-third the length of the body from the hind end, the other pair closer to the hind end.

In transforming to a puparium, the hardening and darkening of the convex dorsal surface is completed in 20 to 30 minutes after birth. On the flattened ventral surface the process seems to be slower, and internal movements can be seen through this surface for more than 48 hours after birth. The puparium is shown in profile in Rodhain's and Bequaert's paper, Fig. 4, p. 258, with convex dorsal and flattened ventral surface and narrow explanate margin. The curved suture in the antero-dorsal part, along which the operculum is detached at the emergence of the imago, is more distinct than the divisions of the segments.

[Here again Muir's words (*l.c.*) regarding *Eremoctenia progressa* may be cited for comparison: "the chitinous exudation that covers the soft larval skin, to form the puparium, first appears along the edges of the flattened ventral surface and fastens it to its host, then covers the dorsal surface, but does not appear on the ventral side [apart from the edges], that side remaining a soft membrane through which, if carefully detached from the host, the pupa can be seen developing. The larval spiracles remain distinct and stand up above the surface. No anterior pupal spiracles or 'horns' appear, but the pupal thoracic tracheae are attached to two spots on the inner surface of the operculum, and can be faintly discerned externally. The operculum is large, the posterior edge curving across the dorsal surface near the middle, slightly in front

of the anterior spiracles, and continuing along the sides to the front; no line of dehiscence runs towards the ventral surface. The position of the head of the pupa would prevent the use of a ptilinum, as the legs are folded over the head and thorax, the femorotibial joints meeting in the middle line (see Muir's figure 10, plate II). A movement of the legs would force off the operculum."]

The pupal stage of *Cyclopodia greeffi* was found to last from 12 to 16 days. At emergence the imago is pale and feebly chitinised, but otherwise this phase is outwardly precisely similar to the fully matured form. The ♂ and ♀ internal genital organs of the adult are described and figured. The two ovaries were always found in an unequal state of development, indicating that their functions do not correspond chronologically, though whether there is a regular alternation in the production of ova is not known.

B. SYSTEMATIC SECTION.

Genus **EREMOCTENIA**, gen. nov. (Pl. XXIV, figs. 1–5).

Diagnostic Characters. *Thoracic ctenidium* entirely absent in both sexes. *Abdominal ctenidium* also entirely absent in both sexes, its place taken by a few ordinary bristles. *Eyes* quite absent. *Tibiae* not ringed, not broad and flattened. *Metatarsi* long, approximately $\frac{2}{3}$ the length of the tibiae.

Description. The form on which this genus is founded has at first sight somewhat the aspect of a *Penicillidia*, from which genus it is however clearly separated by the absence of ctenidia and eyes. The *head-capsule* is of characteristic shape, swollen and bulbous behind, narrowed in front. I am convinced of the absence of *eyes* in both sexes after a careful examination with the compound microscope: when these organs consist of single facets and have no dark pigment beneath them they are very easy to overlook, but in the present case diligent search has quite failed to reveal them. *Thorax:* Fig. 5 is specially drawn to demonstrate the complete absence of *ctenidia*, the front and middle legs being held aside to show the space where the ctenidia normally lie: the only visible structures which could possibly represent them consist of a small series of fine and minute bristles on the lateral margin immediately in front of the base of the middle coxa, but these hardly seem to be in the normal position for a ctenidium. Further particulars as to the thorax are included in the specific description below. *Halteres*

flattened and scale-like. *Anterior coxae* not elongated. *Middle coxae* each with a small blackish area at the outer distal angle (see Fig. 5). *Femora* of average form, only moderately robust. *Tibiae* rather slender, not ringed, with about 6 obliquely transverse series of bristles on the distal half of the lower surface, in the proximal series fine and short, in each successive series towards the apex becoming longer and more robust, in the apical series long, stout, and curved (there is *not* a marked predominance of three or four bushy series of long, stout bristles, as in some *Penicillidiae*). *Metatarsi* of all the legs, as stated above, long and slender. *Abdomen* described below, under the species.

Larva and pupa, see below, in the specific description.

TYPE of the genus: *Eremoctenia progressa* (Muir).

AFFINITIES. All other described genera of Nycteribiidae have both thoracic and abdominal ctenidia, with the exception of *Archinycteribia* Speiser (1901), which has no abdominal ctenidium. *Archinycteribia* has however no other special points of resemblance to *Eremoctenia*, for it possesses thoracic ctenidia and single-faceted eyes, and has all its metatarsi very short. Its single species, *A. actena* Speiser, also differs widely in specific characters from *Eremoctenia progressa*. In having no eyes and in the form of the legs the genus resembles the subgenus *Acrocholidia* of *Nycteribia*, but I doubt if there is really any close affinity between them. On the whole I should be inclined to place *Eremoctenia* nearer to *Penicillidia*, in spite of the absence of eyes and ctenidia. In specific characters certain forms of *Penicillidia* are not altogether unlike *Eremoctenia progressa*: *e.g.* Kolenati's figures (1863, Pls. X, XI) of *Penicillidia conspicua* Speiser (= *westwoodi* Kol. nec Guér.-Mén.) show certain resemblances to *E. progressa* in the abdomen of both sexes. But in the present state of our knowledge *Eremoctenia* must stand fairly wide apart from any known form, its diagnostic characters being, as will be seen above, largely negative, that is, consisting in the absence of structures which other genera possess.

Eremoctenia progressa (Muir).

Penicillidia progressa Speiser, MS.; Muir, *Bull. Mus. Zool. Harvard*, LIV, no. 11, 1912, pp. 351–2, 356–8; Pl. II, figs. 8, 10 (larva, pupa, etc., but no description of the adult).

Length of body, not including head or legs, about 2·25 mm.

Head: the remarkable shape of the capsule has been mentioned; front part of vertex rather densely clothed with stoutish bristles, which

extend also down the margins of the cheeks; palpi bearing very long stout bristles at the apex.

Thorax. Absence of ctenidia dealt with above. The chitinous part of the thorax just in front of the halter bears an irregular group of 9 or 10 bristles, not a regular series as in some forms. *Halteres* large, flattened, scale-like, with surface minutely pollinose (they recall those of *Cyclopodia sykesi*). *Ventral surface of thorax* (Fig. 2) very strongly convex from back to front, much broader than long, the exact proportions being difficult to gauge owing to the convexity: median longitudinal line marked by a fairly broad streak of darker pigment, and strongly impressed, especially at the posterior extremity: the obliquely transverse lines present in other Nycteribiidae are only discernible here with difficulty (represented in Fig. 2 by faint dotted lines), the parts being very firmly consolidated: surface-bristles very fine and short, hind margin bearing a few longer ones at the angles; surface also with two other impressions, one on either side near the lateral margin, just in front of the transverse line.

♂ ABDOMEN: dorsally (Fig. 1) this is very bristly indeed. *5 tergites* are visible in addition to the anal segment, but the basal one has its basal portion pale, soft, and bare; the remainder of its surface, and the entire surfaces of tergites 2 and 3, are densely covered with short, fine, sub-erect bristles: these surface-bristles are present also on tergites 4 and 5, but only near the hind-margins, the basal parts being bare. All 5 tergites have their hind-margins set with longer and shorter bristles, the long ones of tergites 2–5 being very long and stout. *Anal segment* rather short, broad at the apex, its dorsal surface bare, hind margin and sides bearing moderately long bristles, and one very long one near each hind angle.

Ventrally (Fig. 2), the *basal sternite*, though bare at its base, is otherwise rather closely covered with short bristles, those at the sides being rather longer and directed outwards: the hind margin bears no trace of a ctenidium, but only a few bristles of varying lengths, set at rather wide and irregular intervals. *Sternites 2 and 3* have their surfaces bare except for a few bristles near the hind angles: their hind margins bear bristles of varying lengths, set rather wide apart, two or more short bristles between each two long ones, the long ones near the outer angles being very long. *Sternite 4* obtusely produced in the middle behind, the apical part of the hind margin bearing a group of short, stout, blackish thorn-bristles; there is a submarginal series of short sub-erect bristles, and on either side of the thorn-bristles the margin bears bristles

of varying lengths, set rather wide apart (as on the preceding sternites), there being one very long bristle on either side near the angle; the surface of the sternite behind the submarginal series is bare. The parts of the *anal segment* visible ventrally on either side of the claspers are bare at the base, but distally have numerous erect bristles directed outwards: the *claspers* lie very wide apart, and are curved inwards and slightly dorsalwards at the apex; each bears one very long bristle near its base, and a number of short bristles, but the apical portion is bare.

♀ Abdomen (Fig. 3). *Basal tergite* of remarkable form, produced backwards with rounded margin in the middle: on the surface this middle part is bounded on either side by a line of dark brownish pigment, so that the tergite appears to consist of a nearly round median, and of two separate lateral, portions: the basal part of the median portion is soft and whitish, and bears some extremely minute rudiments of bristles, otherwise the surface is bare: the margin also is bare except in the rounded middle part, which has a series of about 14 long bristles, the median ones of which are slightly longer than the outer. *Tergite 2* sinuate and slightly produced in the middle: surface bare, except for a small median area, which bears very minute short bristles: margin furnished with a series of bristles of varying length, those in the middle close together (and the 4 nearest the middle line very long), those towards the sides wide apart. Behind tergite 2 is an expanse of bare whitish *connexivum*, posterior to which, and immediately in front of the anal segment, is a widely and bluntly triangular *chitinous area*, with a marginal series of long bristles, of which the median are longer than the lateral, and with a number of short submarginal bristles on the surface. *Anal segment* tapering considerably, its mid-dorsal portion bare (even including the hind margin), its lateral parts densely covered with moderately long erect bristles, and bearing several very long bristles near each hind angle.

Ventrally (Fig. 4), the *basal sternite* differs decidedly from that of the ♂, a difference which is exceptional among Nycteribiidae[1]: it is proportionately longer, its hind margin is more curved, the bristles of the surface are sparser, and appear to be absent in the submarginal as well as the extreme basal portion: there is no trace of ctenidium, and only a few bristles very wide apart on the median part of the margin. Posterior to this is an area of soft whitish *connexivum*, bearing a curved series of 8 very long bristles, the convexity of the curve being directed

[1] An extreme case is provided by *Cyclopodia roylei* (Westwood); see Scott, 1914*a*, p. 225.

forwards: within and behind this series the connexivum bears several irregular transverse rows of moderately long bristles, while outside the curved series the lateral portions bear extremely minute rudimentary bristles. Posterior to this connexivum are two roughly oval, convex, *chitinous areas* (cf. *Penicillidia jenynsi*); each has a dense group of bristles at its outer angle, some of which are very long, otherwise the surface of each area is almost bare, but the hind margin of each bears inwardly (*i.e.* towards the middle line of the body) 4 or 5 bristles, rather wide apart. Behind these two chitinous areas is a transverse series of bristles, rising from two slight chitinous ridges which almost meet in the middle line, and on either side of the body is a blunt protuberance bearing a group of bristles, one of which is very long: [these two bristle-bearing ridges and protuberances may possibly represent rudiments of a second pair of chitinous areas similar to those immediately in front]. *Subgenital plate* slightly bi-lobed, the apex of each lobe bearing a group of bristles, one of which is very long; the median part of the surface also bears a number of shorter and longer bristles.

Larva: described and figured by Muir (1912, p. 356, Pl. II, fig. 8). According to him, it is about 1·6 mm. by 1·2 mm., ovoid, broader behind, of the same general form as the other Nycteribiid larvae which are known, with two pairs of spiracles, the anterior being dorso-lateral and slightly behind the middle line, and the posterior pair being postero-dorsal, quite close to the hind end of the body. At the anterior end is a small constriction bearing the mouth-opening: but Muir's description is made from full-grown larvae taken from the uteri of their parents, and as he himself states, the larvae change their shape somewhat on passing out of the uterus. Probably, therefore, this anterior constriction would disappear after the birth of the larva. No such constriction is described by Rodhain and Bequaert in the already born larvae of *Cyclopodia greeffi* (see above, p. 599). In 1908 the present writer described and figured a larva of *Penicillidia jenynsi* with a much more marked constriction near the anterior end: but in this case, as justly remarked by Rodhain and Bequaert (1915, p. 257), the constriction was doubtless due to pressure of the sides of the genital orifice of the parent, which had been killed at the moment when the larva was passing through, or being held protruding from, that orifice. The normal form of a Nycteribiid larva after birth is probably that described by Rodhain and Bequaert for *Cyclopodia greeffi*, with elliptic or ovoid contour, the anterior end being the more pointed, but not constricted. Muir's figure also shows the anterior spiracles of the larva of *Eremoctenia progressa*

as considerably further forward than are those of *Cyclopodia greeffi* or *Penicillidia jenynsi*. This may be a constant difference, or may be partly due to the slightly earlier stage of development of the larvae examined by Muir.

PUPARIUM AND PUPA: these are described, and the latter is figured, by Muir (1912, pp. 357–8, Pl. II, fig. 10). His remarks have already been cited (above, p. 599) for comparison with the corresponding facts in *Cyclopodia greeffi*.

LOCALITY. Amboyna (Dutch East Indies).

TYPES, ♂ and ♀, in British Museum.

The material was obtained by Mr Frederick Muir in 1908, about 30 specimens being collected from a number of individuals of *Miniopterus schreibersi*. They were submitted to Dr P. Speiser, who gave them the manuscript-name of *Penicillidia progressa*, under which name they are referred to by Muir in his paper (1912). Speiser no doubt intended to publish a description, but appears never to have done so. Meanwhile 1 ♂ and 1 ♀ (in good condition, preserved in alcohol) were given by Muir to the British Museum, where the present writer drew up a description and made figures of them. Muir (1912) published descriptions of the larva and pupa, but not of the adult, neither did he give any diagnosis for identification of the species, since he anticipated an early publication on the matter by Speiser. Therefore, since the form is a highly remarkable one, the present writer has thought it best, after re-examination of the British Museum specimens, to publish his description above. Speiser's manuscript-name "*progressa*," used by Muir in print, must be the specific name, while a new genus is erected for reasons already stated.

Genus **PENICILLIDIA**, Kolenati.

Penicillidia fletcheri Scott, *Ann. Mag. Nat. Hist.*, ser. 8, XIV, p. 214, Pl. X, figs. 1–4, 1914.

This species was described from Coimbatore, Madras, on *Pipistrellus dormeri*. It can now be recorded also from Bangalore, Mysore, collected by Rev. Father Assmuth, name of host not stated; Dr Bequaert has sent me a ♂ received from that locality, and the specimen closely agrees with the type ♂. A var. *majuscula* of this species has also been described by F. W. Edwards from West Sumatra, where it was found in numbers on "*Vespertilio* sp." (Robinson and Kloss coll.): I am informed that the description will appear in *Journ. Fed. Malay States Museums*, vol. VII.

Penicillidia fletcheri var. **pumila** Scott, *op. cit.* p. 217, Pl. X, fig. 5.

Described from Peradeniya, Ceylon, on *Pipistrellus abramus*. It can now be recorded from Khandala, Bombay Presidency; Rev. Father Assmuth coll., name of host not stated. Dr Bequaert has sent me two ♀ received from that place, which agree with the type in all particulars, except that they both have the two groups of bristles on the small basal tergite much longer. In his letter Dr Bequaert remarks that he is inclined to give var. *pumila* rank as a separate species, since the differences between it and typical *fletcheri* seem marked and constant. Since it has now been found in India, it cannot be an exclusively Ceylonese race of *fletcheri*.

Genus **CYCLOPODIA.**

DIVISION INTO SUBGENERA AND ERECTION OF A NEW GENUS.

In describing *Cyclopodia roylei* (Westwood) I stated (1914*a*, p. 225, footnote) that it differs in some ways from all other *Cyclopodiae* known to me. Its separation in a distinct subgenus, *Paracyclopodia*, is proposed below. A distinct new genus, *Tripselia*, is also proposed for one or more species described some time since.

A genus *Basilia* was described by A. de Miranda Ribeiro (*Arch. Mus. Rio Janeiro*, XII, pp. 175–9, Pl. I, 1903) for a South American Nycteribiid[1] characterised by the presence of eyes composed of more than one facet, as in *Cyclopodia*, but also by the *absence* of tibial rings. The same writer later described a second genus[2], *Pseudelytromyia*, which however is regarded by Speiser (1908, p. 437) as a synonym of *Basilia*. Speiser has recognised *Basilia* as distinct, and has also referred to it certain Old-World species. But Brèthes, in describing a new *Cyclopodia* from Chili (*Boletin del Museo Nacional de Chile*, pp. 1–4 and Figs., 1913), considers *Basilia* to be a synonym of *Cyclopodia*. Presumably he imagines that the tibial rings are present, but have been overlooked. This is possible, as the rings are not always easy to see, especially if the specimens are not very mature and the chitin consequently is pale. I have seen no representative of *Basilia*, and shall assume for the present that it is distinct. *Cyclopodia*, *Tripselia*, and *Basilia* may then be separated as follows:

(A) Eyes present, composed of more than one facet. Tibiae 3-ringed...*Cyclopodia*.

[1] *Basilia ferruginea*, on *Vespertilio aurantius*.

[2] On *Atalapha frantzii* Peters. (Vespertilionidae): *Pseudelytromyia* was described *op. cit.* XIV, pp. 233–5, Pl. XXIII–IV, 1907.

(B) Eyes absent. Tibiae 3-ringed...*Tripselia.*

(C) Eyes present, composed of more than one facet. Tibiae not ringed...*Basilia.*

One may proceed to a more complete diagnosis of the two former.

Genus **CYCLOPODIA**, Kolenati.

Tibiae 3-ringed. *Eyes* composed of more than one facet on a dark pigmented ground.

Subgenus **CYCLOPODIA**, s. str.

Head broad, somewhat compressed in the horizontal, but not at all in the vertical, plane, its dorsal surface between the eyes only slightly arched. *Anterior coxae* much elongated. *Hosts*, so far as known, all frugivorous (Pteropidae).

Type of subgenus: *Cyclopodia sykesi* (Westwood).

Other species actually examined by me which conform to the above diagnosis are: *C. horsfieldi* de Meij., *C. albertisi* Rondani, *C. greeffi* Karsch (= *rubiginosa* Bigot[1]), *C. oxycephala* Bigot, *C. ferrarii* Rondani. In all these each *eye* appears to consist of two facets, and this number may be constant for the whole subgenus (or even for the genus). In all the above-named species except *C. ferrarii* the *tibiae* are nearly cylindrical in section, but in *C. ferrarii* they are rather flattened laterally, as in *C.* (*Paracyclopodia*) *roylei*, but *not* broadened as in subgenus *Listropodia* of *Nycteribia*. In most, if not all, of the above-named members of the subgenus *Cyclopodia*, the hollow containing the ♂ intromittent organ in the ventral side of the anal segment, over the claspers, does not extend as far forward as the apex of the claspers; while in *C.* (*Paracyclopodia*) *roylei*, and in certain other genera, it does extend so far forward. The *halteres* differ: in a number of the large species (*e.g. C. sykesi*, *C. oxycephala*) they are large, flattened and scale-like, and minutely pollinose: but in *C. ferrarii* and *C. greeffi* they are very small, with slender pedicel and knobbed apex.

Cyclopodia horsfieldi de Meijere, *Tijdschr. v. Ent.* XLII, 1899, p. 153.

A hitherto unpublished record for this species is that of a number of ♂ and ♀ from the Philippine Islands: La Carlota, Occidental Negros, taken from *Pteropus philippinensis*, 8–9, IX, 1911: sent by Dr H. B.

[1] See footnote, p. 596.

Mitzmain to the Quick Laboratory, Cambridge: the material is now at Cambridge and in Brit. Mus.[1]

The species has previously been recorded from Java, Sumatra, and Engano, without record of host; and (by Speiser, 1903) from the Malay Peninsula, from *Pteropus vampyrus* (Linn.).

Subgenus **PARACYCLOPODIA**, nov.

Head very narrow, strongly compressed in the vertical plane, strongly arched dorsally between the eyes; its form is like that found in *Nycteribia* and other genera. *Anterior coxae* not much elongated. *Hosts*, so far as known, insectivorous and carnivorous (species of Vespertilionidae and Nycteridae).

Type of subgenus: *Cyclopodia* (*Paracyclopodia*) *roylei* (Westwood); Scott, 1908, p. 368, 1914*a*, p. 224 (= *Nycteribia chlamydophora* Speiser, 1903).

I am not acquainted with any other species of the subgenus. In *C. roylei* the *tibiae* are somewhat flattened laterally, but not broadened, resembling in form those of *C.* (*s. str.*) *ferrarii*, referred to above. The *eyes* are dark-pigmented, and consist each of at least two facets, as in *Cyclopodia* s. str. The front *coxae* are not elongated like those of *Cyclopodia* s. str., but are no more elongated than in some species of other genera. The hollow above the ♂ claspers extends as far forward as the apex of the claspers; contrast *Cyclopodia* s. str. *Halteres* small and erect, with slender pedicel and knobbed apex.

C. roylei appears to be not uncommon and widely distributed in India, Ceylon, and the Malay Peninsula. For a list of localities and hosts, see my paper (1914*a*); an additional record is: 1 ♂, 2 ♀, pale and small, from *Scotophilus wroughtoni*, at Helwak, near Satara, Western Ghâts, India, 4, v, 1900: N. C. Rothschild don.

Genus **TRIPSELIA**, gen. nov.

(*Tripselia*, Speiser MS., in litt. 1908, from ψέλιον, an armlet,)

Tibiae 3-ringed, as in *Cyclopodia*. *Eyes* quite absent. *Head* narrow, laterally compressed. *Anterior coxae* not much elongated.

Type of genus: *Tripselia fryeri* (Scott); described as *Nycteribia* (*Acrocholidia*) *fryeri* Scott, *Trans. Linn. Soc. London*, ser. 2, *Zool.*, XVII, p. 163, 1914.

[1] Since the above was printed I have received through Dr Bequaert 2 ♂ and 1 ♀ of *C. horsfieldi* from another island of the Philippines: Porto Galera, Mindoro, on large fruit-bats.

The *head* resembles in form that of *Cyclopodia* (*Paracyclopodia*) *roylei* and of many species of *Nycteribia*, etc. The *legs* are long and very slender, the tibiae not appreciably flattened. The *front coxae* are no more elongated than in many species of *Penicillidia*, etc. The hollow above the ♂ claspers extends as far forward as the apex of the claspers. *Halteres* small and erect, with knobbed apex and slender pedicel.

T. fryeri was described from Assumption Island (N. of Madagascar) and from Labuan. Dr Bequaert has since collected 4 ♀ in the Belgian Congo, at Medje, and has called my attention to the presence of the tibial rings, the overlooking of which caused me to place the species in a wrong genus. I have examined one of his ♀ side by side with the series from Assumption, and am convinced of their identity, and he states that the other 3 examples also agree closely with my description.

Possibly *Cyclopodia amiculata* Speiser (*Rec. Ind. Mus.* I, 1907, p. 296), which I have not seen, is also a *Tripselia*. Though Speiser placed it in *Cyclopodia* on account of its 3-ringed tibiae, he wrote to me in 1908 that on re-examination it proved to have either no eyes at all, or only a single unpigmented lens on either side of the head—probably the former. In either case he considered it could not remain in *Cyclopodia*, and proposed the generic name *Tripselia*, which I now adopt. If *amiculata* has no eyes at all, it is certainly a *Tripselia* (*sensu meo*). But if it has single unpigmented lenses like those of *Penicillidia* and *Eucampsipodia*, it may necessitate the erection of yet another genus. Furthermore, if *amiculata* is a *Tripselia*, it is possible that my *T. fryeri* is identical with it. With his letter Speiser sent rough sketches of the abdomen of ♂ *amiculata*, not unlike the abdomen of *fryeri* ♂. His published description of the ♀ was very short and only intended as preliminary, but it mentions characters which make me suspect the identity of *fryeri* with *amiculata*.

[Since the above was written I have received through Dr Bequaert 1 ♂ and 1 ♀ from Sumatra, belonging to a form which very closely resembles *T. fryeri* except in the following particulars: size smaller; legs noticeably shorter, especially femora, and both femora and tibiae stouter; ventral hind margin of thorax in both sexes fringed with long bristles (absent in typical *fryeri*), three on each side of the middle line, with shorter ones between them. Detailed consideration of this form, stated to be from *Pipistrellus* sp., must be deferred.]

Hosts of *Tripselia fryeri* are: *Taphozous mauritianus* (Emballonuridae), Assumption Island; *Saccolaimus* (= *Taphozous*) *saccolaimus*, Labuan; *Saccolaimus* (= *Taphozous*) *peli*, Belgian Congo.

Speiser's *amiculata* was described from Calcutta, from *Taphozous longimanus*.

Genus **EUCAMPSIPODIA**, Kolenati.

Eucampsipodia hyrtli (Kolenati), *Horae Soc. ent. Ross.* II, 1863, p. 78, Pl. XII, figs. 26 *d*, *e* (♀), Pl. XIV, figs. 26 *a–c* (♂); Scott, *Ann. Mag. Nat. Hist.* ser. 8, XIV, pp. 213, 228–230, Pl. XII, figs. 18, 19, 1914.

A correction. In my paper (*l.c.*) I twice stated that Kolenati only figured the ♂ sex of this species. This was erroneous, for he also figured the ♀. I was misled by the fact that his figures of the two sexes are on two different plates between which a third plate intervenes.

REFERENCES.

KOLENATI, F. A. (1863). Beiträge zur Kenntniss der Pthirio-myiarien. *Horae Soc. ent. Ross.*, II, 11–109, pl. i–xv.

MUIR, F. (1912). Two new species of Ascodipteron. *Bull. Mus. Zool. Harvard*, LIV, 351–366, pl. i–iii.

RODHAIN, J. et BEQUAERT, J. (1916). Observations sur la biologie de *Cyclopodia greeffi* Karsch (Dipt.), Nyctéribiide, parasite d'une chauve-souris congolaise. *Bull. Soc. Zool. France*, XL, 248–262.

SCOTT, H. (1908). On certain Nycteribiidae, with descriptions of two new species from Formosa. *Trans. Ent. Soc. London*, 1908, 359–370, pl. xviii.

SCOTT, H. (1913). H. Sauter's Formosa-Ausbeute: Nycteribiidae. *Arch. Naturg.*, 79, A, 1913, 92–103 (published Feb. 1914).

SCOTT, H. (1914*a*). On some Oriental Nycteribiidae. *Ann. Mag. Nat. Hist.*, ser. 8, XIV, 209–235, pl. x–xii.

SCOTT, H. (1914*b*). Mallophaga, Aphaniptera, and Diptera Pupipara [of the W. Indian Ocean; Percy Sladen Trust Exp.]. *Trans. Linn. Soc. London*, ser. 2, *Zool.*, XVII, 161–7.

SPEISER, P. (1901). Ueber die Nycteribiiden. *Arch. Naturg.*, 67, I, 11–78, pl. iii.

SPEISER, P. (1903). Diptera Pupipara [Malay Peninsula]. *Fascic. Malay., Zool.*, I, 121–126.

SPEISER, P. (1907). Die Fledermäuse und ihre Schmarotzer. *Ber. Westpreuss. Bot.-Zool. Ver.*, XXIX, 15–24.

SPEISER, P. (1908). Die geographische Verbreitung der Diptera pupipara und ihre Phylogenie. *Zeitschr. wiss. Insektenbiol.*, IV (1 Folge, Bd xiii), Heft 7, pp. 241–6; 8, pp. 301–5; 11, pp. 420–7; 12, pp. 437–447.

EXPLANATION OF PLATE XXIV.

Eremoctenia progressa (Muir).

Fig. 1. ♂, dorsal view, × circa 27.

Fig. 2. ♂, ventral view of thorax and abdomen.

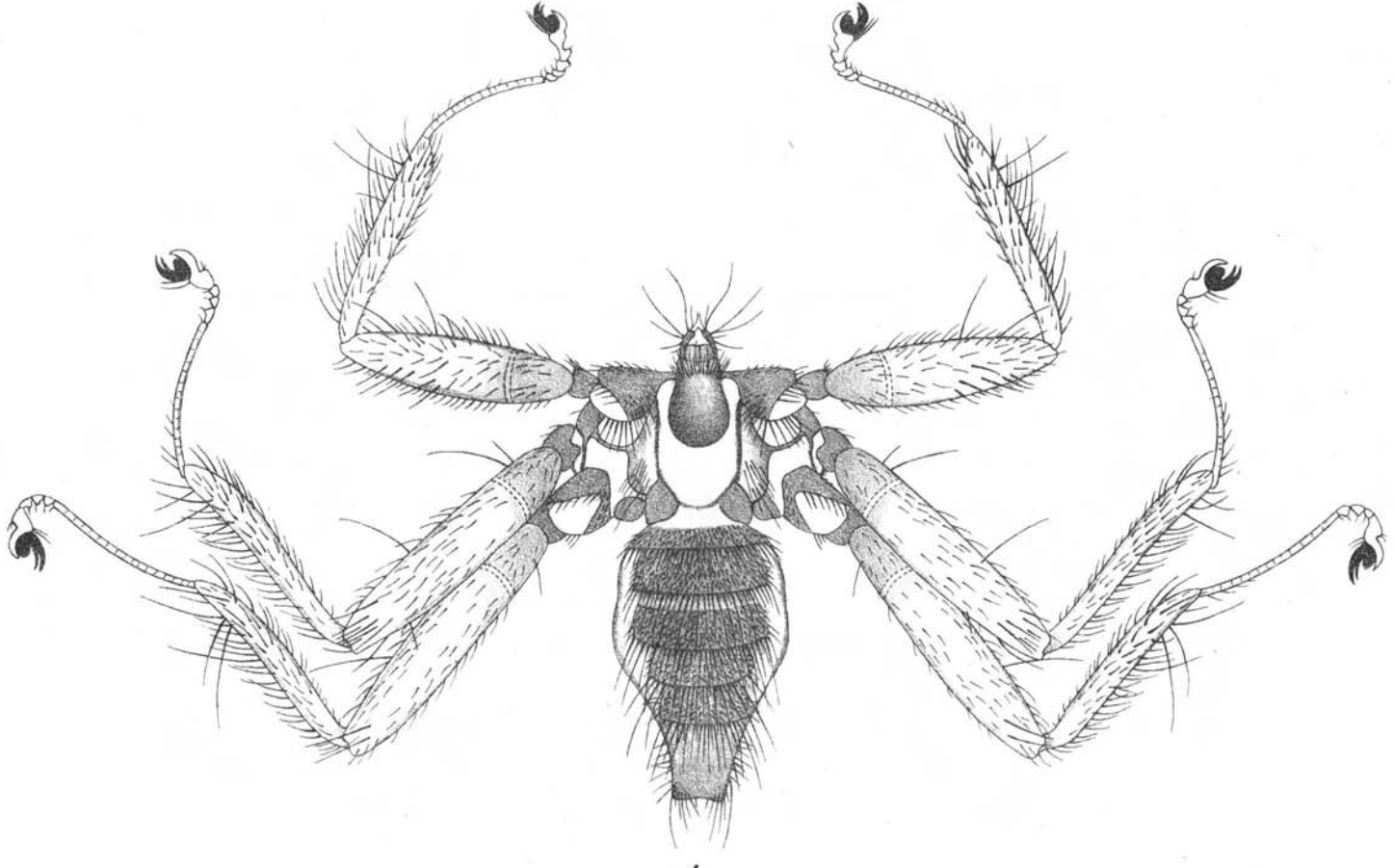
Fig. 3. ♀, dorsal view of abdomen.

Fig. 4. ♀, ventral view of abdomen.

Fig. 5. Left side of thorax and bases of legs from above, to larger scale, to show complete absence of thoracic ctenidium: *a*, outline of head; *b*, front coxa; *c*, middle coxa; *d*, middle trochanter; *e*, hind coxa; *f*, halter.

NOTE.—All the figures were made with the help of a drawing-apparatus, from specimens lying in alcohol.

NYCTERIBIIDÆ.



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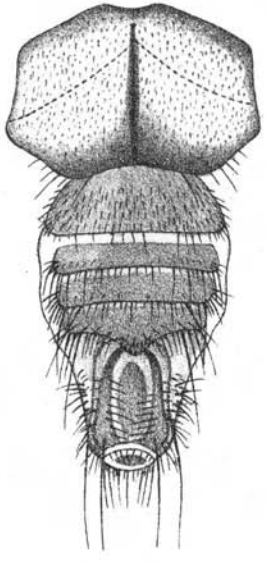

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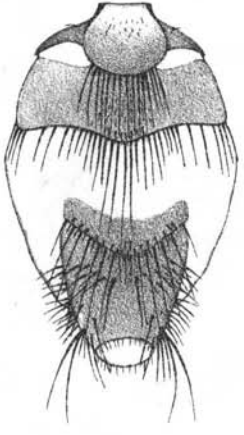

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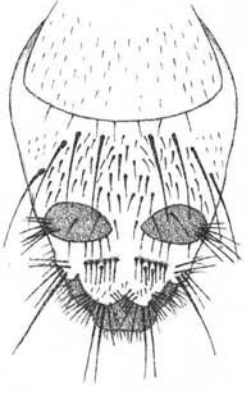

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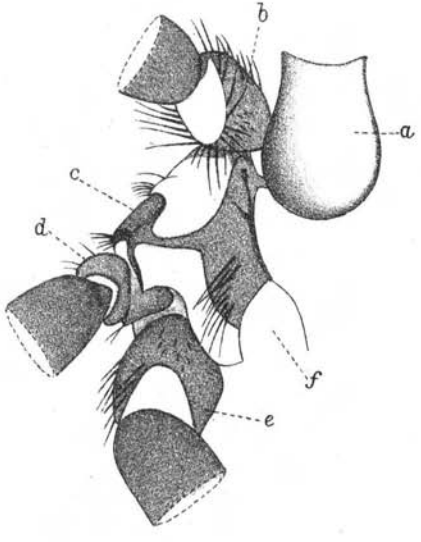

5

H. Scott del.

Eremoctenia progressa (Muir).