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ABERRANT HEAD-STRUCTURE IN LARVAL SIMULIIDAE (Diptera)

By L. J. Dumbleton

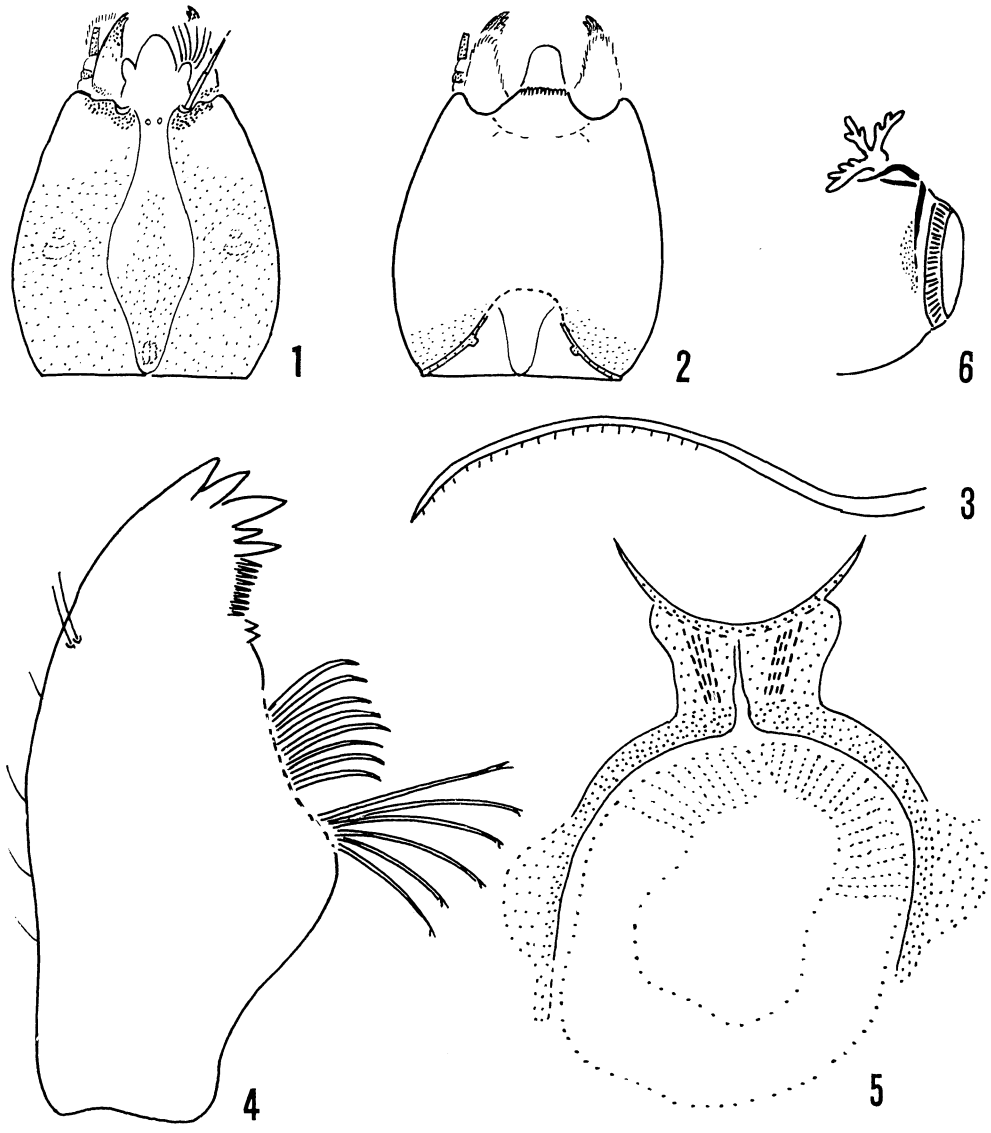
ENTOMOLOGY DIVISION, D.S.I.R., CHRISTCHURCH, NEW ZEALAND

The anomalous features in the morphology of the head of the larvae of *Simulium oviceps* Edwards were reported by Edwards (1935). Those of the second species, *Cnephia crozetense* Womersley (1937) were recognised in the course of an examination of the type material. Descriptions of the larvae of both species, and a redescription of the male of *C. crozetense*, are presented below as a basis for the discussion.

Simulium oviceps Edwards. The Tahitian species. Figs. 1–6.

Simulium oviceps Edwards, 1935, Bishop Mus. Bull. **113**: 35–8.—Grenier & Rageau, 1960, Bull. Soc. Path. Exot. **53**: 734–6.

Larva. Length 3.3 mm. Markedly smaller than that of *S. tahitiense* Edw. Head (Figs. 1, 2): not strongly pigmented or patterned, surface bearing scattered small spinules; mandibular phragma black and unusually stout, as in *C. crozetense*; sides convex, strongly narrowed anteriorly; frontal sclerite narrow, not constricted posteriorly before reaching posterior margin of head, very narrow anteriorly between antennal bases where it bears a pair of prominent pores; post-frontal epicranial lobes nearly meeting caudad of frons but not forming a coronal suture. Labrum without a strong pair of apical bristles. Mouth brushes present, basal piece bearing a few short setae but no strong apical setae, brush rather weakly organized composed of about 12 short slender rays (Fig. 3) which are fringed with very fine hairs on the distal 1/2. Antenna four-segmented, weakly or not pigmented, segments 1 and 2 sub-equal in length, 3 longer than 2 but not as long as 1 plus 2. Mandible (Fig. 4) of nearly normal simuliid form, but without strongly developed sub-apical external hair brushes and without the strong internal sub-apical brush of *C. crozetense*, with 5 apical teeth, a comb of 8–10 pale bristle-like teeth and 2 conical internal sub-apical teeth not recessed behind as in *C. crozetense*; long basal internal hairs forked at tips and those immediately distad of them (? sub-apical internal) stout and somewhat falcate apically. Labium and maxillae normal. Sub-mentum with about 13 teeth of even length and identical shape, rounded apically and sub-parallel-sided. Occipital foramen not as oblique in plane as in *C. crozetense*; lobes projecting into it mesad of the posterior tentorial pits; throat cleft shallow and rounded. Breathing-organ (dissected from gill-spot of type larva): common trunk bearing 3 primary branches, dorsal (DP), lateral (LP), and ventral (VP); VP and LP bifurcate once, giving 2 secondary filaments on each; first bifurcation of DP giving 2 dorsal secondary branches, each bifurcates again giving 2 tertiary filaments; a total of 8 filaments. VP and LP long, sub-equal in length: DP difficult to discern in the mount,



Figs. 1–6. *Simulium oviceps*, larva. 1, head, dorsal; 2, head, ventral; 3, ray of mouth-brush; 4, mandible; 5, anal sclerite, caudal; 6, anal sclerite, lateral.

appears to be more than 1/2 as long as LP and VP. Thoracic proleg normal. Anal sclerite (Fig. 5) X-shaped, posterior arms reaching slightly more than half way round crotchet ring and expanded cephalad in the pleural region; backward struts between anterior and posterior arms present, most evident in lateral view (Fig. 6). Ventral tubercles absent. Anal gills with 2 or 3 short secondary lobes on each of the 3 primary lobes. Posterior body-form of normal type, not abruptly narrowed posteriorly on venter.

DISTRIBUTION: Tahiti.

Holotype: gill-spot larva (BISHOP), Papara R., Tahiti. Coll. Adamson & Mumford, undated.

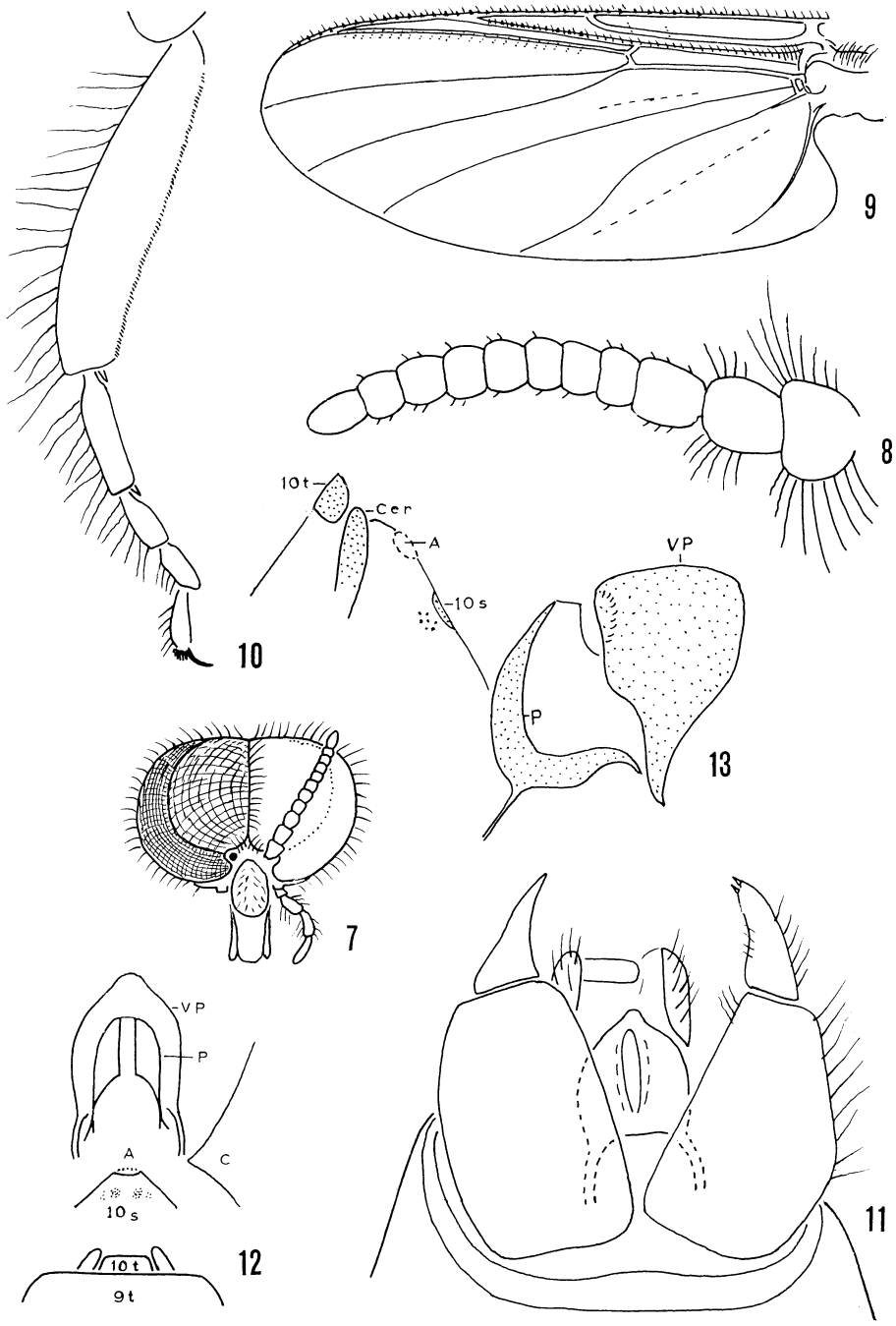
Larvae, pupae and females collected by Adamson and Mumford are in the British Museum. Specimens collected by the author were on dead leaves among rocks in the Fautaua R., 13–IX–1954.

Edwards was unable to distinguish the female from that of *S. tahitiense* Edw., and until the publication of the study of Tahitian Simuliidae by Grenier and Rageau (1960) the correctness of the correlation of the three stages remained uncertain. They considered that the three species present in Tahiti were closely related, that all belonged to *Simulium* Latreille, and that on the characters of the adult they could be placed in the subgenus *Eusimulium* Roubaud as defined by Edwards.

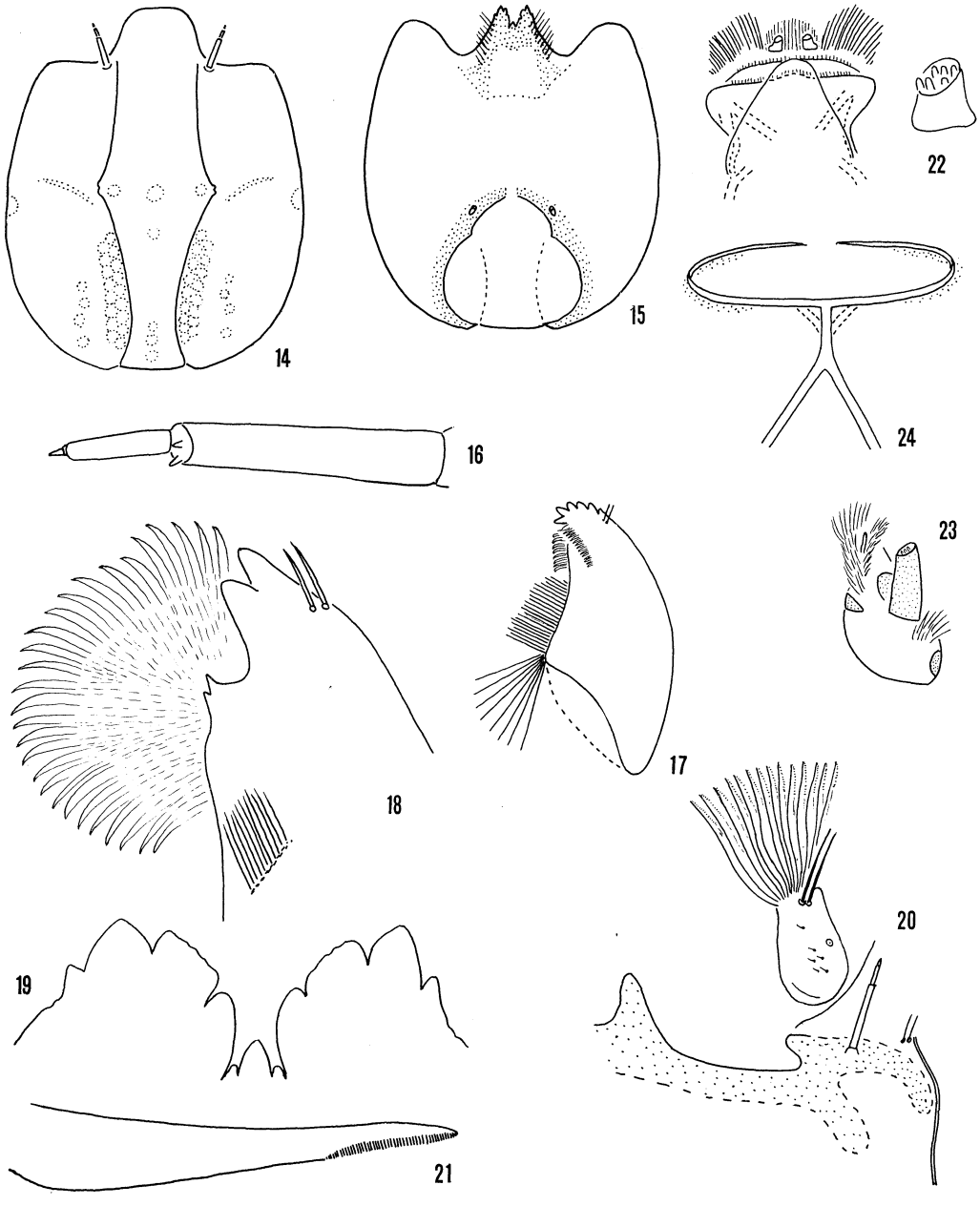
Cnephia crozetense Womersley. The Crozet Islands species. Figs. 7–24.

Cnephia crozetense Womersley, 1937, Brit. Austral., N. Zeal. Antarct. Res. Exped. **4** (3): 66–7.—Séguy, 1940, Mus. d'Hist. Nat., Mem. Paris, ser. 2, **14**: 228–30.

Male. Length 4 mm. Wing length 4 mm. Colour dark brown almost black, long sub-erect hairs dark brown. Hairs of head, thorax, coxae and abdomen erect, no recumbent hairs or scales. Head (Fig. 7): very slightly narrower than thorax, wider than abdominal tergite 8; hemispherical in dorsal view with eyes occupying all except the narrow occiput which bears long erect hairs as do the cheeks and the venter of the head. Clypeus convex, subtriangular, with long hairs. Eyes holoptic, a row of long hairs along the mid frontal line; larger upper facets sharply delimited from smaller lower facets along a curved line from level with the antennal socket to the posterior margin of the eye; eye in lateral view occupies 2/3 of the depth of the head and the small-facetted ventral portion reaches the clypeus; no bulla present behind eye. Antenna (Fig. 8): eleven-segmented, the sockets separated by the width of the basal segment; segments 1 and 2 with long hairs, 3–11 with short paler hairs; length and width of segment 1 sub-equal, 2 narrower, lengths of 1 and 2 sub-equal, 3 longer than wide, 4 sub-quadrate, 5–10 wider than long, 11 longer than wide. Mouthparts short, not longer than clypeus. Maxillary palpi with segments 3 and 4 sub-equal in length, hairy, 5 longer. Thorax: scutum without pattern, with moderately long erect hairs, longer posteriorly and much longer on scutellum. Post-notum bare. Wing (Fig. 9): veins C, R and R_1 haired above for their whole length, 1 or 2 hairs below on distal 1/2 of Sc; Rs not forked, haired below on distal 3/4; spiniform setae present on C and distal 3/4 of R_1; R_1 joining C well beyond mid-length; submedian vein not discernible as more than a proximal fold between M and Cu_1; Cu_2 twice curved; 1A present only as a straight fold; 2A pigmented and curved nearly reaching wing margin; basal cell present. Halteres light in colour. Legs (Fig. 10): all segments with at least some erect hairs, additional short paler hairs on tibia and basitarsus; hind tibiae non-clavate; hind basitarsus 2/3 as long as tibia, sub-cylindrical, slightly flattened, calcipala absent; 2nd tarsal segment 1/3 as long as basitarsus, 2× as long as segment 3, pedisulcus absent; claws of normal male type not toothed. Abdomen: basal fringe with longer hairs; tergite 1 longer than 2; tergites 2–8 subequal in length and width, dark brown with sparse hairs; sternites 3–8 sub-rectangular, haired, decreasing in size posteriorly. Genitalia (Figs. 11–



Figs. 7–13. *Cnephia crozetense*, ♂. 7, head; 8, antenna; 9, wing; 10, hind tarsus; 11, genitalia, ventral; 12, genitalia, dorsal (parts separated) (A, anus; C, coxite; P, paramere; VP, ventral plate; 10s, 10th sternite; 9t, 9th tergite; 10t, 10th tergite); 13, genitalia, lateral (Cer, cercus).



Figs. 14–24. *Cnephia crozetense*, larva. 14, head, dorsal; 15, head, ventral; 16, antenna; 17, mandible; 18, tip of mandible; 19, sub-mentum; 20, mandibular phragma, antenna and mouth-brush; 21, ray of mouth-brush; 22, labium and (enlarged) palp; 23, maxilla; 24, anal sclerite.

13): basistyle as long as tergite 8, massive, sub-trapezoidal, short haired; dististyle 1/2 as long as basistyle, sub-triangular, slightly curved, with 2 teeth apically; tergite 9 continued in complete ring ventrally; 10 small, transverse, rectangular; cerci haired; adeagus without dorsal sclerite or median (sternal) sclerite; parameres nearly meeting in the mid-dorsal line, with posterior arms to the coxite and to the arms of the ventral plate, without hooks or spines apically; ventral plate slightly concave dorsally, sub-circular and strongly keeled in caudal view giving a T-shaped aspect; sternite 10 between adeagus and anus with 2 small circular para-median sclerotized areas with sclerotized points laterad of each.

Larva. Length 12 mm. Head (Figs. 14, 15): colour mahogany-brown, mouth frame and margin of foramen black; sides strongly convex, widest at mid-length, as wide in front as posteriorly; in lateral view flat ventrally but strongly convex on posterior dorsum; occipital foramen not at right angles to long axis of head but occupying part of ventral surface of head in ventral view; the sides commencing from slightly laterad of frontal suture are concave with a pointed prominence at mid-length anterior to which is the posterior tentorial pit. Throat cleft shallow and rounded with a poorly pigmented narrow median area anteriorly. Surface of head capsule with many fine spinules and fine transverse wrinkles anteriorly on both dorsal and ventral surfaces; no colour pattern evident, muscle insertions visible on frons at mid-length and posteriorly, but most strongly developed in a longitudinal band on the epicranium adjoining the frontal sutures posteriorly. Eye spots at mid-length laterally, slightly anterior to each is a pale oblique line. Frons narrow, frontal sutures diverging posteriorly in anterior 1/3, thereafter converging to just after 2/3 length, then diverging to posterior margin of head. Epicranial halves not meeting in a median coronal suture caudad of the frons. Antenna (Fig. 16): short, dark brown, three-segmented; 1st segment 3× as long as 2nd. Mandible (Figs. 17, 18): massive, heavily sclerotized and pigmented, with 6 rather rounded teeth apically, a comb of about 20 paler teeth ventrally; sub-apical internal brush prominent, composed of dense, broad, rather falcate hairs; 2 strong sub-apical setae dorsally on outer face; no well-developed sub-apical external brush of hairs; a bifid tooth dorsally on an internal ridge running basad from near apical tooth 1. Sub-mentum (Fig. 19): median tooth deeply recessed and flanked by smaller teeth on each side; laterally with 4 teeth, 2nd broad, 3rd longest, 4th on lateral margin; about 18 setae postero-laterally on each side. Mouth-brush (Fig. 20): basal piece short, bearing 5 or 6 short setae on dorsal surface, and 2 long stout setae apically; brush with about 25 rays, blade of ray (Fig. 21) strong and deep and with a comb of strong teeth on distal 1/3, ray teeth uniordinal; ray nearly 2× as long as antenna, not as long as mandible. Labium (Fig. 22) and maxilla (Fig. 23) normal. Thoracic proleg without sclerites or processes. Anal gills of 3 simple lobes. Ventral tubercles absent. Anal sclerite (Fig. 24): dorsal arms Y-shaped, ventral arms forming a ring, incomplete only in mid-ventral line, and expanded cephalad in pleural region; short backward struts running from ventral surface of stem of Y to ventral arms. Crotchet ring normal. Body form not recorded and not ascertainable from existing larvae. The intestine contained several masses of a filamentous alga.

DISTRIBUTION: Possession Island, Crozet Islands.

Holotype; male (SAM, Adelaide), American Bay, Possession I. 3–XI–1929, T. H. Johnston & J. W. Marr. Paratype; male, same data. Morphotypes; 2 larvae on slide mounts, same data.

Johnston (1937) states that he and J. W. Marr were responsible for the collections on shore and he remarks of this station, "beach and adjacent peaty flats and a rivulet..... were examined." The reference in the original description to "waterhole" presumably means a pool in a running stream, and "wet vegetation" on which the larvae were taken may mean leaves which were trailing in running water. The stream is likely to have been slow-flowing and peaty. Womersley, presumably quoting the collectors' record, states that the adults were "found over waterhole in main valley and appeared to have affinity for water." As the adults were not reared their relationship with the larva is presumptive.

Womersley (1937) figured the mandible, sub-mentum, maxillary palp and antenna. His figure 7b is the maxillary and not the labial palp, and figure 7c, described as the maxilla, is another view of the tip of the mandible. No comment was made on the general form of the head or the structure of the anal sclerite.

Séguy (1940) described the male and female of a *Cnephia* from Navire Bay, Possession Island, which he identified as *C. crozetense.* The description and figure of the distinctive dististyle, which is swollen or flanged on the basal two-thirds, suggests that a second species may be present. If this is so then the correlation of the larva described by Womersley and the female described by Séguy with *C. crozetense* remains uncertain.

Discussion. Most simuliid larvae possess mouth brushes with which they sieve the food particles from the passing water, and mandibular hair brushes which sweep the food from the rays of the mouth brush into the mouth. The larvae of the subfamily Gymnopaidinae (genera *Gymnopais* and *Twinnia*) have neither and Rubtzov (1956) points out that they feed by a browsing action of the mandibles with the epipharyngeal hair brushes acting as auxiliaries. Movement of water is not essential to the feeding process and these larvae may be in slower water or under stones.

The larvae of *Cnephia crozetense* and *Simulium oviceps* both possess mouth brushes but these are much reduced in *oviceps* and the short stout rays in *crozetense* are toothed only at the apices. The only other species in which comparable ray teeth have been noted by me is *Cnephia aurantiacum* (Tonnoir) but in this species the rays are long and the teeth occupy a greater length of the ray. The rays in *oviceps* are too few, short, and slender to form an efficient filter, while in *crozetense* though strongly developed they appear to be specialized, possibly for the collection of food from the substratum since the intestine was noted to contain plugs of a filamentous alga. The mandibles of both species lack any well-developed external hair brushes. That of *oviceps* is, with this exception, fairly normal in form, but that of *crozetense* is more modified and has a strong internal sub-apical hair brush not seen in this position in any other species. The form of the mandible contrasts with that of larvae of *Gymnopais* and *Twinnia* and neither *oviceps* or *crozetense* has the processes which are present on the sub-apical buccal face in Gymnopaidine species.

It was at first considered, because of the chironomid-like heads and the apparently relict type of distribution, that these two larvae were primitive. Both species however occur on isolated oceanic volcanic islands of reputed late Tertiary age and the Crozet Islands were in addition subjected to Pleistocene glaciation. To regard these species as primitive requires the acceptance of the improbable coincidence that two such species reached their present locations by chance dispersal of adults over the sea, though there are no comparable larval forms recorded from adjoining continental areas. The presumed male of *crozetense* is not distinctively primitive and its characters do not preclude its retention in *Cnephia*

(s. l.). The adult of *S. oviceps* is a typical *Simulium*. The character of the anal sclerites of the larvae, with the exception of the development of an accessory strut, is broadly consistent with the genera in which the species have been placed, and is quite distinct from that of the Gymnopaidinae. Gibbins (1934) has recorded the presence of backward struts in two African species of *Simulium* and the multiple anal gills are known only in *Simulium* (s. l.).

Dr. J. Smart, in criticism of the view that these characters are primitive, has pointed out that if the mouth brushes of Simuliidae are homologous with the premandibular organs or messores of some Chironomidae and with the labral brushes of Culicidae—as Cook (1949) accepts—then the primitive Simuliidae possessed mouth brushes in some form and these may be lost in the larvae of the Gymnopaidinae. The evidence for such loss has still to be adduced however. On the other hand Davies (1960) interprets the morphological characters shared by fourth instar larvae of *Gymnopais* and *Twinnia*, first instar larvae of *Prosimulium* sp., and some chironomid larvae, as primitive rather than as secondary specializations. The phylogenetic status of the Gymnopaidinae is however a separate problem, though the subfamily may stem from a deviant line of *Prosimulium* stock originating by the same mechanism as produced *S. oviceps*. The two species under discussion present clearer evidence of reduction or specialization in the mouth brushes.

On this hypothesis the presence of these two species on widely separated isolated islands presents fewer inconsistencies. Neither the adult nor the larva of either species is distinctively primitive in whole or even in part. The most easily credible explanation of their morphological modifications is that they arose after the normal parent species reached, or was isolated in, the island. It is not clear however how the change, from the normal parallel-sided head capsule and a frons which is widest posteriorly, to the convex-sided head and narrow frons, is related to these reductions. The massive mandibles of *crozetense* may require both increase and rearrangement of musculature but the mandible of *oviceps* is small and almost normal in form. The Gymnopaidinae, which have no mouth brush and a very different anal sclerite, are the only other simuliid larvae known to possess the same type of head structure in the fourth instar. The larva of *Cnephia ? umbratorum* (Tonnoir) (Mackerras & Mackerras, 1952) has an unusual parallel-sided frons but it is otherwise normal, except for the weak anal sclerite and the more ventral position of the crotchet ring.

It is to be remarked that *oviceps* is not only an unusually small species but is relatively rare and not so well adapted as to be numerically dominant over its associate *S. tahitiense*. *C. crozetense* is a large robust species but there is no field evidence as to its abundance or the successfulness of its adaptation.

The phenomenon of a high incidence of apterism in subantarctic islands appears to differ in that apterism may be considered to confer an advantage under conditions of high frequency and high velocity of winds. The development of the terrestrial habit in the larva of the damselfly *Megalagrion oahuaense* (Blackburn) on Oahu, Hawaiian Islands (Williams, 1936) would seem to be more nearly comparable with what has occurred in these two species of Simuliidae.

No simuliid species has so far been maintained in culture, or used in controlled breeding experiments, and apart from further field studies perhaps only a study of the chromosomes of *S. oviceps* and the closely related *S. tahitiense* can throw some light on the mecha-

nism by which these aberrant forms arose.

If the reputed late Tertiary age of the islands is conceded then the method of colonization was by drift or flight over the ocean, with a probability that the colonizing population was small. The faunas of these islands are disharmonic and this may be expected to result in reduced selection pressures in at least some niches. The meagre faunas characteristic of fresh water streams in the southeast Pacific, for example, imply reduced competition and predation.

All that can be said at the moment is that these conditions may be significant in connection with the origin and fixation of variations, some of which, as in the case of *S. oviceps*, appear to confer little or no adaptational advantage. One can only speculate as to whether such phenomena are really more frequent under insular conditions or merely more apparent in the smaller faunas.

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