ON THE RELATIONSHIPS AND ZOOGEOGRAPHICAL SIG-NIFICANCE OF AUSTROSIMULIUM ANTHRACINUM (Bigot), A BLACKFLY FROM SOUTHERN SOUTH AMERICA

(Diptera: Simuliidae)

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The extreme austral portion of South America is of special interest to the student of blackflies as there exist, in addition to a peculiar group of *Simulium* s. str., several supraspecific taxa either limited to, or concentrated in, said region.

Among these insects, Austrosimulium anthracinum (Bigot, 1888), the single South American representative of the genus, is of special significance. The bulk of the species of Austrosimulium is found in Australia, Tasmania and New Zealand; in New Zealand, no other blackfly genus occurs. Three species groups are customarily recognized for the Old World, viz. the bancrofti, furiosum and mirabile groups (see Mackerras & Mackerras, 1948, 1955), but at least one additional group is found in New Zealand, and to judge from data pertaining to the pupal chaetotaxy, the bancrofti group contains heterogeneous elements. Available evidence seems to support monophyletic origin of all Australasian Austrosimulium, though the species around mirabile and those from New Zealand possess a specialized character in the circular chitinous ring which completely surrounds the body just before the posterior circlet of hooks, and which is lacking in the remaining species. A tendency towards a pronounced elongation of the second and a correlated shortening of the apical section of the first segment of the larval antenna is strongly expressed in the mirabile and New Zealand group, but is also at least hinted at in furiosum.

The relationships of the South American species described as *Simulium anthracinum* Bigot, 1888 (syn. *Simulium moorei* Silva Figueroa, 1917), placed by Edwards (1931) and later authors in *Austrosimulium*, have recently been discussed by Wygodzinsky (1953) and Dumbleton (1960). Wygodzinsky (1953), in addition to describing the pupa for the first time, redescribed and figured the female. The larva was first described by Dumbleton (1960). Wygodzinsky is inclined to confirm the position of *anthracinum* within the genus *Austrosimulium* but Dumbleton thinks that the species "has no close affinities with *Austrosimulium* from which it is so widely separated, geographically, but may finally be placed in a subgenus of *Gigantodax*, or a new genus intermediate between *Simulium* (*Hearlea*) and *Gigantodax*."

Material of *anthracinum* recently collected by us in Tierra del Fuego enables us to complete the descriptions of the instars already known and to describe the male. In the light of this additional knowledge, the systematic position of the species will be re-examin-

ed here.

It must be determined if *anthracinum* is more nearly related to the Australasian *Austrosimulium* or to any other known simuliid. The only valid criterion for proving phylogenetic relationship between two or more taxa is the common possession of derived characters indicating that the respective groups share a common ancestor (viz. the possession of synapomorphic characters [Hennig, 1953]). The sharing of plesiomorphic (not derived, primitive) features does not prove relationship, just as the presence of autapomorphic traits lacks significance from a phylogenetic point of view. It will thus be convenient to examine the characters found in the present complex, and to judge their significance in the light of the above considerations.

The ten (or rarely nine) segmented antenna of the adult, so typical of Austrosimulium, are also found in other clearly plesiomorphic genera, such as Gymnopais Stone, Twinnia Stone & Jamnback, Greniera Doby & David, and even in occasional species of Prosimulium Roubaud and Simulium Latreille, thus they seem to be plesiomorphic and do not prove the common origin of anthracinum and typical Austrosimulium. The same holds true for the presence of a basal cell (also found in the presiomorphic Gymnopais, Twinnia, Greniera, Prosimulium and Cnephia¹, and the presence of bristles on the lower and also a considerable extension of the upper surface of Rs (a condition equally prevalent in Gymnopais, Prosimulium, Gigantodax, Cnesia, but not in Simulium sensu latu).

The male genitalia, now known for *anthracinum* (fig. 2A-J) as well as for the Australasian group, are of special significance. The rather generalized structure of the adminiculum and the parameres does not furnish evidence for either associating or separating the species involved. The median plate of the phallus of *anthracinum* is well developed and thus contrasts with the condition found in the Australasian species where this sclerite is exceedingly feeble; this latter condition is here interpreted as derived, and is quite unique in the family. On the other hand, the forwardly directed arms that arise posteriorly on the median plate of *anthracinum* resemble those found in species of *Gigantodax* and *Cnesia*; the presence of these arms is considered as apomorphic in relation to other simuliid genera, but as plesiomorphic whithin the *Austrosimulium-Gigantodax-Cnesia* complex.

In the female sex, the genital fork of *Austrosimulium* (fig. 11) seems to differ from that of all other simuliids by the combination of its lack of intense pigment and the very short and wide stem and arms; the complete agreement between *anthracinum* and the Old World species is significant.

The well formed cocoon of the pupa of *Austrosimulium* is clearly apomorphic as compared with the poorly developed cocoon in such plesiomorphic genera as *Gymnopais*, *Twinnia*, *Greniera*, *Gigantodax* etc. It seems probable, however, that the evolutionary step from small and shapeless to well formed cocoons has been taken more than once in the history of the family, thus would not necessarily be absolute proof for common origin in the *Austrosimulium* complex.

The absence of rows of spinulets on the posterior tergites of the pupal abdomen in the Australasian species is rather unique in the family, and interpreted here as apomorphic. This trend towards a simplification of the abdominal chaetotaxy is further expressed by the loss of all spines on the ventral surface, as observed in the *bancrofti* and *furiosum*

^{1.} Cnephia is here understood as limited to the northern hemisphere group.

group. The presence of the above mentioned rows of spinulets in *anthracinum* would thus represent a plesiomorphic character and lack significance for the problem under consideration.

The reduction of the size of the terminal hooks of the pupal abdomen, observed to a variable degree in all species of *Austrosimulium*, is found elsewhere mainly in *Simulium* sensu latu (in addition to their complete absence in one species of *Gymnopais*); in plesiomorphic genera such as *Prosimulium*, *Cnephia* (most but not all species), *Gigantodax*, *Cnesia* and *Greniera*, the terminal hooks are very large. Though this is clearly a case of convergence with *Simulium* and possibly correlated with the presence of a well formed cocoon, the reduction of the size of the terminal hooks in Australasian *Austrosimulium* and in *an-thracinum* can also be interpreted as synapomorphic.

The curious ramified, anchor-shaped or curled setae on the posterior segments of the abdomen of the pupae, found in *anthracinum* (fig. 3C) and the Australasian species (fig. 3D-F, H), are more difficult to judge as to their phylogenetic value, not only because of their somewhat varied structure in the various species but mainly because similar setae are found in some (but not all) species of *Gigantodax* (fig. 3G) and the boreal *Cnephia* and *Greniera*; they are lacking in *Cnesia, Gymnopais, Prosimulium*, at least some of the Australian "*Cnephia*" and in *Simulium*; we are unable to judge at this moment if the presence of these setae should be considered as plesiomorphic or apomorphic, and, in the latter case, if convergence can be excluded.

The backwardly directed struts of the anal sclerites of the larva (fig. 4N) are very typical of all species placed in *Austrosimulium* and represent clearly an apomorphic trait, but they are also found in *Gigantodax* and a few isolated species belonging elsewhere. Though significant for judging the relationships of the genus as a whole, this character does not furnish evidence for the main problem under discussion, viz. the position of *anthracinum*.

There is one structure in the larvae that has been described and figured both for the Australasian group and for anthracinum but the possible importance of which has not been appreciated. We refer to the broad shield-like extension projecting from the anterior margin of the submentum and covering a considerable portion of the teeth of this sclerite (fig. 4G-K). The only comparable structure in simuliid larvae is found in some species of *Cnephia*. At the same time it is well to keep in mind that the general structure of the larval submentum in *Austrosimulium* is quite different from the complex arrangement of the teeth found in most of the primitive genera, such as *Gymnopais*, *Twinnia*, *Prosimulium*, *Greniera*, *Gigantodax*, *Cnesia* and many *Cnephia*. This simplification of structure is generally found in *Simulium* sensu latu, but we think that the similar simplification found in the different components of the *Austrosimulium* complex represents an independent development.

Another larval character might be of significance. As mentioned above, in many species of the Australasian group there is a pronounced tendency towards a shortening of the apical portion of the first and a correlated elongation of the second antennal segment (Tonnoir, 1924; Mackerras & Mackerras, 1948). The antenna of the larva of *anthracinum* (fig. 4D) follows this trend, a fact that speaks for common ancestry.

To summarize: In addition to numerous symplesiomorphic characters that cannot be taken as proof of common origin, Australasian *Austrosimulium* and *anthracinum* share such features as the peculiar structure of the genital fork of the female, the presence of a well

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formed cocoon and a reduction of the terminal hooks of the pupa, a trend towards a unique modification of the proportions of the antennal segments of the larva and peculiarities of the submentum of this instar, which we consider as synapomorphic and that are not shared by any other possibly related assemblage in the group, thus being indicative of the monophyletic origin of the species involved.

It is now necessary to establish the degree of relationships within the genus, viz. to determine if *anthracinum* is a vicariant of the Old World group as a whole, or of a section of the latter, or even if it can be shown to be subordinate to such a section. The significance of the answer for zoogeographical considerations is obvious (Hennig, 1960). If it can be shown that *anthracinum* is subordinate to a part of the Australasian *Austrosimulium*, the possibility cannot be excluded that it has reached South America via the Antarctic or at least the southern Pacific; if no such relationship can be established, viz. if *anthracinum* shares a common ancestor with the Old World group only as a whole, or with a clearly monophyletic section of the latter, no support for a biogeographical connection between Australia—New Zealand and southern South America can be obtained. This complex of problems has recently been exposed very clearly by Hennig (1960) who has also called attention to the special significance of *Austrosimulium* in this respect.

As has been mentioned before, autapomorphic characters cannot furnish information about phylogenetic relationship; thus the presence of spinulets on the apical portion of R_1 in *anthracinum* (lacking in the remaining species), the very peculiar branchiae of the pupa, or the longitudinal subdivision of the posterior abdominal sternites in this stage (equally lacking in the Old World species) are not necessarily evidence against a possible more intimate relationship with some species group among the Australasian forms. The same, of course, is true for all plesiomorphic characters, in the present case the well developed median plate of the phallus and the presence of transverse rows of spinulets on the posterior tergites of the pupal abdomen of *anthracinum*; the respective conditions in the Old World forms have been discussed above.

It is unfortunate that those characters of *anthracinum* that are shared with some but not all species groups of the remainder of the genus are clearly plesiomorphic in nature and thus not pertinent, viz. the lack of a circular sclerite surrounding the larval abdomen anterior to its end (this sclerite, a specialized structure, exists in the *mirabile* and New Zealand group, but is lacking in the remaining species) and the presence of well developed ventral spines on the posterior segments of the pupal abdomen, present also in the *mirabile* group and, though somewhat modified and reduced, in *pestilens*, but lacking in the majority of the species belonging to the *bancrofti* and *furiosum* group.

The situation is tabulated here to facilitate understanding. Three sections are accepted in the genus *Austrosimulium*, each characterized by autapomorphic features : A by the loss of the ventral spines on the pupal abdomen, B by the presence of the distal ring-like sclerite of the larva, and C mainly by the structure of the respiratory organs of the pupa. A and B are united by synapomorphic characters, viz. the differently specialized respiratory organs and the loss of the rows of spinulets on the posterior tergites of the pupa, and the strong reduction of the median plate of the phallus of the male. The table shows that though C is related to A+B as a whole, it is not subordinate to either A or B. It is true that the modification in the proportions of the larval antennal segments, an apomorphic character, is not shared by all Australasian species, but though it has not been found in the *bancrofti* group, it is present in at least one species (*furiosum*) of the *furiosum* group

Taxonomic units				aland	шп	ax	
Characters	<i>bancrofii</i> group	<i>furiosum</i> - group	<i>mirabile-</i> group	New Zes group	anthracin	Gigantod	
Adult. Spinulets present at apex of R ₁ .					×		
Adult &. Median sclerite of aedeagus strongly reduced.	×	×	×	×			
Adult \Leftrightarrow . Specialized structure of genital fork (A).	×	×	×	×	×		
Adult \Leftrightarrow . Specialized structure of genital fork (B).						×	
Pupa. Specialized respiratory organ (A).					×		
Pupa. Specialized respiratory organ (B).	×	×	×	×			
Pupa. Reduction of size of terminal hooks of abdomen. Cocoon well developed.	×	×	×	×	×		
Pupa. Abdominal sternites VII and VIII divided longitudinally along middle.					×	×	
Pupa. Transverse rows of spinulets on posterior tergites lost.	×	×	×	×			
Pupa. Loss of spines on ventral surface of abdomen.	×	×					
Larva. Modification of proportions of antenna.		×	·×	×	×		
Larva. Teeth arrangement of submentum simpli- fied; plate-like extension underlying teeth.	×	×	×	×	×		
Larva. Posterior ring-like sclerite surrounding body of larva.			×	×		×	
Larva. Backwardly directed struts underlying main body of X-shaped anal sclerite.	×	×	×	×	×	×	
	Α		В		С		

Distribution of apomorphic characters in Austrosimulium and Gigantodax.

which belongs to the same section as the *bancrofti* group, thus indicating a trend of the whole assemblage rather than of parts of it only.

Thus, though we agree with *Dumbleton* (1960) in that *anthracinum* has no "close" affinities with the Old World *Austrosimulium*, we still consider, based on the preceding considerations, that affinities do exist, and that *anthracinum* is more closely related to Australasian *Austrosimulium* than to any other simuliid. *A. anthracinum* is a vicariant taxonom-

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Fig. 1. Austrosimulium (Paraustrosimulium) anthracinum. A-H, \Diamond , I, \Diamond . A, antenna; B, maxillary palp; C, apical portion of pilose seta of scutellum; D, sensory pits of M; E, fore leg; F, leg of second pair; G, posterior leg; H, second and apex of first tarsal segment of hind leg; I, genital fork.—Wygodzinsky del.

ically as well as geographically, of the whole of the Old World group. These two groups, so unequal in size, share a common ancestor, which is not also the ancestor of a third group; they cannot be derived from each other. This situation makes the genus *Austrosimulium* unavailable as a biological proof for a trans-antarctic or circum-antarctic connection or relation.

Dumbleton's alternative suggestions must be discussed briefly.

The possibility that anthracinum "may finally be placed in a subgenus of Gigantodax" does not seem plausible. The only significant apomorphic feature shared by anthracinum and Gigantodax, viz. the backwardly directed struts of the X-shaped sclerite of the abdominal apex of the larvae, is found not only in anthracinum, but in all Austrosimulium. Furthermore, another synapomorphic character, the posterior ring-like sclerite surrounding the body of the larva, is shared by Gigantodax and certain Old World Austrosimulium, but not by anthracinum.

We equally cannot agree with Dumbleton's suggestion that *anthracinum* might be placed "in a new genus intermediate between *Simulium* (*Hearlea*) and *Gigantodax*." The two genera mentioned are customarily included in two different tribes; even though a future re-evaluation of the higher categories within the family might possibly change the actual system it does not seem probable that the genera mentioned will be approximated much more than they are now. The resemblance between the respiratory apparatus of the pupa of *anthracinum* and that of the species of *Simulium* (*Hearlea*) is due to convergence, but not to actual relationship.

In order to express the affinities of the South American and Australasian species of *Austrosimulium* as interpreted by us, we propose the creation of a new subgenus for *anthracinum*, to be defined as follows:

Adult: Apical portion of R_1 with spinulets in addition to hairs. Median plate of phallus of \mathcal{J} well developed (fig. 2A). *Pupa*: Respiratory organ in shape of a twisted pseudosegmented lamella (fig. 3A). Posterior abdominal tergites with a basal



Fig. 2. Austrosimulium (Paraustrosimulium) anthracinum, \Im genitalia. A, paramere and aedeagus, dorsal view; B, same, ventral view; C, aedeagus, dorsal view; D, same, antero-dorsal aspect; E, ventral plate and aedeagus, antero-ventral view; F, apical hooks of aedeagus; G, penis, lateral aspect, with ventral plate (position inverted); H, I, J, different aspects of paramere.—Wygodzinsky del.

transversal row composed of numerous spinulets. Abdominal sternites VII and VIII divided longitudinally along center..... Austrosimulium (Paraustrosimulium)

Adult: Apical portion of R_1 lacking spinulets, only hairs present. Median plate of phallus of ∂ very weakly developed. *Pupa*: Respiratory organ stalk-like, with few to generally very numerous slender filaments. Abdominal tergites lacking basal transversal row of spinulets. Abdominal sternites VII and VIII entire.....



Fig. 3. A, B, Austrosimulium (Paraustrosimulium) anthracinum, pupa, dorsal and lateral aspect; C, same, apex of abdomen, postero-lateral view. D, Austrosimulium bancrofti, portion of pupal abdomen. E, Same, Austrosimulium pestilens. F, same, Austrosimulium furiosum. G, modified setae of apical portion of pupal abdomen, Gigantodax sp. (Tierra del Fuego); H, same, Austrosimulium mirabile.-Wygodzinsky del.

...... Austrosimulium (Austrosimulium)

Austrosimulium (Paraustrosimulium) contains a single species; the following data complete the former descriptions.

Austrosimulium (Paraustrosimulium) anthracinum (Bigot, 1888) Figs. 1-4.

Male: Length of wing 3 mm. Eyes holoptic, reddish brown. Frons and clypeus black, with short concolorous hairs. Antennae and palps black, pilosity dark brown to silvery; hairs of antennae very short. Numerous long hairs at posterior margin of eyes. Mesonotum black, with decumbent black to golden colored pilosity. Scutellum greyish brown with long brown to black hairs. Metanotum dark, with silvery pruinescence. Pleura dark brown with silvery pruinescence and a black pleural tuft. Halters dark grey, capitate portion brown. Wing veins brownish, hairs and spinulets black. Legs dark brown;



Fig. 4. A-I, L-O, Austrosimulium (Paraustrosimulium) anthracinum, larva. A, lateral aspect; B, pattern of frontoclypeus; C, head capsule, ventral aspect; D, antenna; E, apex of inner margin of mandible; F, maxillary palp; G, submentum; H, anterior margin of submentum, high magnification, ventral aspect; I, same, different specimen, dorsal aspect; L, posterior extremity of body of larva, lateral view, with anal gills, postero-lateral portions of anal sclerite, posterior series of hooks, and ventral papillae; M, anal gills; N, anal sclerite; O, cuticular processes at base of anal sclerite, high magnification. K, Austrosimulium mirabile, apical portion of submentum, dorsal view. -Wygodzinsky del.

hairs silvery to black; pigment distributed as in \mathcal{P} , however more distinctive. Abdomen dark piceous, almost black; hairs of tergites silvery to dark grey, almost black.

Shape and relative size of antennal segments as in fig. 1A. Maxillary palp as in fig. 1B; last segment less than $2 \times$ as long as penultimate; Lutz' organ less than 1/2 length of diameter of segment. Setae of posterior portion of mesonotum and of scutellum pilose (fig. 1C). Wings as in φ ; sensory organ of M composed of 4 circlets (fig. 1D). Shape, chaetotaxy and relative measurements of legs and their articles as in figs. 1E-G. Calcipala about as long as wide (fig. 1H).

Dorsal plates of abdominal segments large, ventral plates small. Genitalia as in fig. 2A-J. Parameres not strongly pigmented, with a normal number of long setae (fig. 2A, B, I, J). Basal lobe subrectangular, shorter than wide; apical lobe subtriangular, over 1/2 as long as basal lobe, at apex with generally 4 subequal spines. Ventral plate as in fig. 2B, E, G; distinctly pigmented, its arms more strongly so; bristles numerous. Aedeagus

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as in fig. 2A, C, D, E, G; lateral sclerotization and apical hooks weakly sclerotized, the latter simple in structure (fig. 2F). Median sclerite of aedeagus distinct, Y-shaped, apically with 1+1 backwardly directed arms (fig. 2D).

Pupa: Cocoon compact, oval, opening circular. Respiratory apparatus as in fig. 3A, B. Apex of abdomen as in fig. 3C.

Larva: Maximum size 6.5 mm. Shape as in fig. 4A. Surface of body smooth. Color yellowish to grey.

Head of normal shape. Pattern of frontoclypeus as in fig. 4B. Segment 1 of antennae (fig. 4D) stout, strongly pigmented, its apical section shorter than the basal one. Segment 2 slightly longer than 1, slender, weakly pigmented only; segment 3 very short, hyaline. Structure of apical portion of mandible as in fig. 4E. Shape and pigmentation of maxillary palp as in fig. 4F. Epicranial incision very shallow (fig. 4C). Structure, pigmentation and chaetotaxy of submentum as in fig. 4C, G–I. Anal sclerite as in fig. 4N, basal portion with tiny cuticular processes (fig. 4O). Anal hooks arranged in approximately 70 rows composed each of 15–18 hooks. Anal gills consisting of 3 simple lobes (fig. 4M).

MATERIAL EXAMINED: Stream at the foot of Mt. Olivia, near Ushuaia, Tierra del Fuego, Argentina, 22–I–1960, Coscarón & Wygodzinsky (numerous larvae, pupae, and adults of both sexes obtained in the laboratory, in the collection of the authors, the Entomology Section of the National Institute of Microbiology, Buenos Aires, and the United States National Museum).

The aquatic stages of the above lot were found attached to dead branches of *Notho-fagus* sp. trailing in the water of a large stream, near the shore and just below the surface. No other blackflies were found associated with *anthracinum*. The specimens reported by Dumbleton (1960) from Navarino Is. were also collected in a large stream, but those collected by Wygodzinsky (1953) about 1,200 km farther north in the Argentinian province of Rio Negro, were obtained in small creeks.

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