A REVIEW OF THE MESOAMERICAN AND SOUTH AMERICAN BLACK FLIES OF THE TRIBE PROSIMULIINI (SIMULIINAE, SIMULIIDAE)

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THE BLACK FLY FAUNA of cool and cold temperate South America is composed of a comparatively small number of species of *Simulium* (Simuliinae, Simuliini) and several genera and species of the Prosimuliini. This survey of Neotropical Prosimuliini, which also includes Guatemalan and Mexican highland forms, is a taxonomic treatment mainly on the generic level accompanied by notes on biology and geographical distribution.

The following genera, as arranged by their geographical areas, are dealt with: Mayacnephia, new genus (type: Simulium pachecolunai De Leon) and Tlalocomyia Wygodzinsky and Díaz Nájera [Mesoamerican highlands]; Gigantodax Enderlein [western South America and Mesoamerican highlands]; Araucnephia, new genus (type: Simulium montanum Philippi) and Araucnephioides, new genus (type: Araucnephioides schlingeri, new species) [Mediterranean climate area of Central Chile]; Cnesia Enderlein, Cnesiamima, new genus (type: Simulium atroparvum Edwards) and Paraustrosimulium Wygodzinsky and Coscarón [Valdivian and Magellanic areas of southern Chile, and western Patagonia]; and Lutzsimulium d'Andretta and d'Andretta [coastal ranges of southern Brazil]. Species are also described, redescribed, or discussed as well as illustrated, except for the large genus Gigantodax which is planned to be monographed later. Cnesia ornata and Cnesia pusilla [western Patagonia] are new species; Cnesia gynandrum is synonymized with Cnesia dissimilis.

None of the genera listed is found in America north of Mexico, or on other continents. It has not been possible to trace the origin and routes of dispersal of the Latin American prosimuliine genera, but some intergeneric affinities, especially among sympatric genera, are postulated.

INTRODUCTION

A survey of the black fly fauna of the cool and cold temperate regions of South America shows that although the genus Simulium is represented in these areas by several subgenera and species groups, it is in most cases neither the dominant nor the only genus of black flies. This is in marked contrast to conditions in the warmer areas of South America where only Simulium is found. The additional black fly genera occurring in cool and cold temperate South America belong to the tribe Prosimuliini, as redefined by Crosskey (1969). The present paper is a survey of these genera except for the large genus Gigantodax which is the subject of a separate study. We are including the Prosimuliini of Mexico and Guatemala, not only for completeness, but also because they have hitherto not been well understood.

None of the prosimuliine genera found in Latin America occur in America north of Mexico, or, as much as we have been able to ascertain, on any other continent. It had been our desire when we began research for this survey to work out in detail the phyletic and possibly the zoogeographic relationships of the genera concerned, be it among each other or between them and genera from other parts of the world. As our work progressed it became more and more obvious that it was beyond our ken to integrate these genera into the world system of the Simuliidae, at least at this time. Much progress has been made lately toward the creation of a satisfactory system of the Simuliidae as set forth in the extremely important papers by Davies (1965) and Crosskey (1969), but until further data on such highly critical forms as the South African "Cnephia" turneri and the Australian "Cnephia" and even on some North American species become available, no rational world-wide system can be attempted.

We believe that a strictly phyletic analysis of the world fauna of the family Simuliidae will show that a clear-cut tribal division of the subfamily Simuliinae into Prosimuliini and Simuliini cannot be maintained. Although most genera of the Prosimuliini sensu Crosskey (1969) can be well characterized by autapomorphic characters, the tribe as defined by Crosskey, and before him by others in less detail, seems to be based on symplesiomorphic characters; it is therefore probably not tenable as a cladistic group, at least as understood now.

The conditio sine qua non for research into the dispersal and evolutionary history of the family

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Simuliidae is the establishment of a comprehensive cladistic system. We hope that the data contained in our work will contribute elements to such a system. Our main purpose is an analysis of structure to show differences and thus to permit identification. Future research will have to emphasize and weigh similarities, leading to the discovery of cladistic relationships.

ACKNOWLEDGMENTS

Although we have collected and studied Patagonian and Andean black flies since 1949, the real impetus for intensive collecting and laboratory work came with the generous assistance from the National Science Foundation (grants GB-5852 and GB-8783), beginning in 1967. We are deeply grateful for this support. The second author is also obliged to several Argentinian institutions for their support of his field and laboratory work connected with the preparation of this paper, namely, the National Council for Scientific Research, the National Institute of Microbiology, and the Schools of Natural Sciences of the National Universities of Buenos Aires and of La Plata. The authors' wives, Betty Wygodzinsky and Carmen Coscarón, greatly assisted us in the field, as did numerous other persons.

We have had the privilege of examining material from various collections as listed below. This list also contains the names of the colleagues who graciously lent the specimens or otherwise aided us, together with the abbreviations used for the respective depositories mentioned in the text.

AMNH, The American Museum of Natural History MLP, Museo de La Plata, Argentina

CAS

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Most illustrations, including the photographs, were made by the authors. Miss Elvira Buono contributed some drawings, which bear her signature.

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STRUCTURAL CHARACTERS AND DESCRIPTIVE METHODS

WE ASSUME that the reader is acquainted with the terminology generally in use for descriptions of black flies. Consequently, the following discussion is limited to especially relevant points.

The adults of most Mesoamerican and South American Prosimuliini show a great degree of uniformity in external appearance, with the prevailing overall color being black, although some species show an overall brownish, reddish, or orange color. Complex color patterns of the thorax or abdomen, as found in many of the Simuliini, are never encountered in our Prosimuliini. The general morphology of the adults is equally quite uniform, but this is amply compensated for by an amazing diversity in the structure of the genitalia of both sexes. In the female, the structure of the spermatheca distinguishes most genera; characters taken into consideration are the microsculpture of the inner and outer surfaces of the spermatheca, the presence or absence of spicules on the inner surface, the size of the membranous area of the spermatheca on which the spermathecal duct inserts, and the extension, in some cases, of the sclerotization of the spermatheca onto the duct. The structure of the genital fork is also taken into consideration; the proportional length of the stem and the arms and their degree of widening as well as the absence or presence of long apodemes on the arms are important. The gonapophyses are of uniform structure and, except in *Tlalocomyia*, the cerci and paraprocts are equally similar among the different genera.

The morphology of the male genitalia (fig. 1) is as varied as that of the female, at least in regard to some of their parts. The structure of the parameres is rather uniform, with only slight differences in the shape and relative size of the distimeres; there are invariably several apical spines. The ventral plate is also comparatively uniform in the various insects examined, varying from subtriangular to subpentagonal or rhomboid, when seen in full view; the shape of its basal arms differs in some cases from one genus to the other. The main differences are found in the median sclerite, which in some of the South American genera (*Cnesia, Gigantodax, Araucnephia, Araucnephioides, Cnesiamima* and *Paraustrosimulium*) shows probably more complex shapes than in other simuliids. The great variation of this sclerite among the genera mentioned constitutes an evolutionary trend typical of and to our knowledge restricted to South America. The endoparameral organ also provides excellent differential characters: it may either be indiscernible, the basal and apical portions may both be well developed, or either may be obsolescent or completely absent.

We have prepared special keys to the adults based on genitalic characters alone, but we have also found it necessary to make some use of genitalic characters even in the keys to adults based mainly on external characters because these characters are of such a limited range.

Finally, we call special attention to a very useful term introduced by Knoz (1965), the "vertical frons angle"; we suggest the shorter term "frontal angle." This angle is determined in dichoptic specimens as shown in figure 2, and makes the comparison of the frontal width of different specimens meaningful, irrespective of their size. The frontal angle is constant in each species and generally similar in closely related species; we believe this index will be found useful in the definition of supraspecific taxa.

As uniform as the external aspect of the imagos of Latin American prosimuliine black flies may be, their pupae and larvae show considerable variety.

The cocoon of the pupa is generally loosely constructed and lacks a distinct shape and may even be obsolescent, but tightly woven cocoons of definite shape occur in Paraustrosimulium and some Gigantodax. The basic type of pupal gill is arborescent, but there are many of highly modified structures, such as in Paraustrosimulium, Mayacnephia, and Tlalocomyia; Gigantodax contains by far the greatest variety of shapes of pupal respiratory organ found in any known simuliid genus. The presence or absence and number of trichomes on the cephalic sclerite, and the shape of the thoracic trichomes vary in different groups, providing very useful taxonomic data. The onchotaxy of the abdomen, viz., the number and distribution of the spines and hooks found on the different segments, the shape



FIG. 1. Male genitalia of some Prosimuliini. A. Cnesia sp., parameres, ventral plate, median sclerite, and endoparameral organ. B. Araucnephioides schlingeri, idem. C, D. Stegopterna mutata. C. Ventral plate and median sclerite. D. Endoparameral organ. E. Paraustrosimulium anthracinum, paramere, aedeagus, ventral plate, median sclerite, and endoparameral organ. F. Araucnephia montana; parts as labeled. G. Araucnephioides schlingeri, ventral plate and median sclerite.

of the setae of the eighth and ninth segments, and the degree and kind of development of the terminal spines are equally extremely varied.

Larval characters of the black flies studied here have proved of exceptional value for defining groups. The length of the antennae as compared to that of the stem of the mouth fans, and length ratios of antennal segments have been used extensively. The toothing of the mandibles is of special importance. We mention the different number of outer teeth found in different groups, the various size ratios of the preapical teeth, the number of rows of inner teeth, the diversity in the number of mandibular serrations, and even the existence of supernumerary mandibular serrations in one species.

The hypostomial teeth are either arranged in three prominent groups, each containing one very large and several smaller teeth (fig. 4E) or they are less diverse in size and arranged in a row in which none is strikingly prominent (fig. 4F, G). The former condition, found among our genera in Mayacnephia, Tlalocomyia, Araucnephia, Araucnephioides, and Gigantodax, is probably plesiomorphic because a comparable arrangement occurs in Prosimulium and other comparatively primitive genera. The second condition, as observed in Cnesia, Paraustrosimulium, and Lutzsimulium, is probably apomorphic, and is commonly found in Simulium; however, the simplified structure of the hypostomium in the last three genera is not identical in all details, and may have evolved more than once.

In regard to toothing of the hypostomium, it seems to be customary (for example, Stone, 1964, and Crosskey, 1969) to designate all teeth



FIG. 2. Portion of head of female black fly in front view, to show measurement of frontal angle.

laterad of the corner teeth as "lateral serrations," especially in the hypostomium of the apomorphic type. A comparison with a hypostomium of the plesiomorphic type (fig. 4E, F) shows, however, the presence of several teeth laterad of the corner teeth, clearly different from the lateral serrations. These "lateral teeth," as they are designated in this paper, are situated on the main body of the toothed plate, while the lateral serrations are found on the margins of the main body of the hypostomium. There invariably are one median tooth, 3+3 intermediate, and 1+1corner teeth. The number of lateral teeth varies although it is constant for each genus; this number is indicated in our generic descriptions. In most Simulium there are not more than 2+2lateral teeth (fig. 4F), or they may be completely absent (fig. 4G).

The interpretation of the shape and size of the cervical sclerites of the larvae as to their significance for the taxonomy of the forms considered is difficult. Apparently, closely related species such as, for example, *Mayacnephia grenieri* and *M. aquirrei* (figs. 9G, 10G) or *Lutzsimulium hirticosta* and *L. pernigrum* (figs. 42M, 43S), may possess completely different types of cervical sclerites.



FIG. 3. Pupa of black fly, schematic side view, to show measurement of cephalopterothecal length.

We can only conclude that the evolution from large, transverse cervical sclerites connected to the upper ends of the postocciput (characteristic for many of the Prosimuliini) to small and free sclerites (found in all the Simuliini) must have occurred more than once. This hypothesis does not diminish the usefulness of these structures for defining certain taxa but cautions us to ponder their value when searching for possible cladistic relationships. A similar situation may obtain for other characters, expressed apomorphically in Simulium sensu lato, probably the most highly evolved genus, and plesiomorphically in most of the Prosimuliini but which also make scattered appearances in certain prosimuliines otherwise quite typical for their tribe (for example, see discussion under Lutzsimulium).

A final set of important larval characters which we and others before us have used widely is found in the structure of the anal sclerite, which becomes ring-shaped in *Gigantodax* (fig. 21F) and shows auxiliary strutlike components in *Gigantodax* and *Paraustrosimulium* (fig. 41G).

Measurements. The shrinkage or distortion of the abdomen of preserved black flies in their different stages make measurements of the total length of a specimen comparatively unreliable. It has been customary to express the size of the adult through the measurement of its wing length, a system we follow in our work. The indication of the total length of the larva is customarily supplemented by the indication of the width of the cephalic capsule (head width), a more reliable measurement. It will be found that the head width usually equals slightly less than one-tenth of the total body length of the living or well-preserved larva; this fact allows a calculation of the minimum total body length from the head capsule alone. Measurements of the pupal length also suffer imprecision due to the variable degree of abdominal contraction; these measurements are almost impossible to carry out for empty pupal skins. We here introduce a measurement which we name the "cephalopterothecal length," viz., the distance from the level of the anterior border of the pupal head to the level of the apex of the pterothecae (fig. 3). This portion of the pupal skin is strongly sclerotized and not subject to contraction, and its measurement is indicative of the actual size of the pupa when alive or well preserved.

Although the prosimuliine genera treated in this paper share a certain number of characters,



FIG. 4. A-E. Stegopterna mutata. A. Some short basal setae of mandible of larva. B. Facial trichomes of pupa, high magnification. C. Frontoclypeus of pupa. D. Apex of mandible of larva, with terminology as used in present paper. E. Anterior border of hypostomium of larva, with terminology as used in present paper. F. Simulium (Psilopelmia) escomeli, anterior border of hypostomium of larva. G. Simulium (Hemicnetha) mexicanum, anterior border of hypostomium of larva. H. Simulium (Psilopelmia) escomeli, apical portion of mandible of larva. I. Simulium (Pternaspatha) barbatipes, idem. J. Simulium (Hemicnetha) mexicanum, idem. K. Stegopterna mutata, cervical region of head, dorsal.

these characters are not necessarily found in all known prosimuliines; they are here enumerated and generally not mentioned again in the generic and specific descriptions. Adult. Fronto-ocular triangle of female well developed. Cibarium of female unarmed. Costa invariably with spinelike setae interspersed among simple hairs. Length of basal section of R about one-third of distance from base of $R_{\rm s}$ to wing tip, or more. Fore tarsus of legs slender. Pedisulcus absent. Macrochaetae of scutellum minutely plumose.

Pupa. Abdominal sterna VI and VII with striate semimembranous area longitudinally

along middle. All hooks on terga VI-VIII simple.

Larva. Head of normal shape. Cephalic fans present. Maxillae with dark hairtuft near base of palp. Anal gills with three simple lobes.

DISTRIBUTION AND RELATIONSHIPS

THE GENERAL DISTRIBUTION of the Latin American Prosimuliini is illustrated in figure 5. There are five areas: The Mexican and Guatemalan highlands, the coastal ranges of southern Brazil, the Mediterranean climate area of central Chile, the Valdivian and Magellanic area of southern Chile and Patagonia, and the Andean area in the broad sense. It is not known if the Prosimuliini occur in the cool area comprising the high mountains of Guyana and western Venezuela.

This distribution pattern is rather similar to that of the cool-adapted grypopterygid Plecoptera (Illies, 1969). These distribution patterns are comparable because in both groups the mechanisms of dispersal are limited to drift by larvae that are aquatic, and to very shortdistance flight of adults; either stage, in both groups, is probably quite incapable of tolerating temperatures higher than those prevailing at their normal habitats.

We have no information about the origin and dispersal of the Latin American prosimuliine genera, but a few facts are apparent. Mayacnephia and Tlalocomyia are closely related, and so are, in our opinion, Araucnephia and Araucnephioides. Lutzsimulium contains two species that are quite different from each other in many important respects, and a different subgenus for each could be considered. Gigantodax and Cnesia, which share a part of their geographic area, have in all probability a relatively recent common ancestor that may also be shared by Paraustrosimulium. The relationships of Cnesiamima are not clear.

Although intergeneric relationships exist within each of the four smaller areas considered, there does not seem to be any such affinity among allopatric genera. This may indicate dissimilar histories of the genera or subgeneric pairs of each area as compared with those of any other. At least in some cases, ecological differences between areas point to distinct ecological requirements of their groups of genera. This becomes quite obvious when the distribution of the Chilean-Patagonian genera is analyzed: although the Mediterranean climate areas of central Chile and the Valdivian and Magellanic area of southern Chile are adjacent, four among the six genera found (Araucnephia and Araucnephioides, and Cnesiamima and Paraustrosimulium) are precinctive to their respective areas. Gigantodax has a very wide ecological spectrum, and its range encompasses both areas mentioned; Cnesia extends over the whole Valdivian-Magellanic zone but intrudes into the southern portion of the Mediterranean climate area of central Chile.

One conspicuous fact shown by figure 5 is the very small number of species contained in most genera, as opposed to the very large number of species making up one single genus, *Gigantodax*. We plan to offer an explanation for this and correlated phenomena in a future paper summarizing our knowledge of the Simuliidae of cool and cold temperate South America.



FIG. 5. Distribution scheme of the Prosimuliini of Mesoamerica and South America; see explanation in text.

Key to the Genera of Mesoamerican and South American Simuliidae

ADULTS

- 4. Antennae 10-segmented (fig. 40C); arms of furcasternum with conspicuous projections (fig. 40K); male genitalia with median sclerite geniculate, composed of slender basal Y-shaped portion and two subparallel elon-gate apical arms (figs. 1E; 40R); apical portion of endoparameres with numerous elon-gate denticles (figs. 1E; 40R, S); genital fork of female almost entirely unpigmented, its stem very stout, not longer than arms (fig. 40M) Paraustrosimulium
 - Antennae 11-segmented (fig. 22C); arms of furcasternum lacking conspicuous projections (fig. 22K) (except *Lutzsimulium* [fig. 42D]); median sclerite of male not as above, or apical portion of endoparameres obsolescent, lacking denticles; genital fork of female distinctly pigmented, with stem not as above (figs. 22 O; 42F). 5
- 5. R₁ with hairlike and spiniform setae (fig. 221); if spiniform setae not very distinct (fig. 22J), then basal tooth of claw of female small (fig. 22N) 6 R₁ only with hairlike setae, spiniform setae not
 - developed (fig. 38Q); basal tooth of claw of female large (fig. 38U) *Cnesiamima*
- Basal cell absent; Cu₂ in some specimens with small branch near middle; mandible of female toothed only on internal margin (similar to fig. 13C); claws of female with one very small sub-basal tooth (figs. 42C; 43B); arms

of furcasternum with conspicuous projections (fig. 42C); male genitalia with endoparameral organ not perceptible *Lutzsimulium*

- Median sclerite in shape of transversal flange with narrowly bifid, deeply incised perpendicular central portion; endoparameres lacking denticles (similar to fig. 11H, I) . Mayacnephia Median sclerite of complex geniculate shape, with distal half divided into two wide but short arms (figs. 1B, F; 24I, J, L, N; 34J, T,
- U); endoparameres with numerous denticles (figs. 1B, F; 24K; 34W) 10 10. Sclerotized areas of abdominal sterna small,
 - transverse (fig. 23H); sclerotized areas of abdominal terga increasing in size toward posterior segments (fig. 23L); genitalia with ventral plate subtriangular; its basal arms narrow, straight (figs. 1F; 23K); arms of median sclerite parallel (fig. 24I, J); endoparameral organ with basal portion large and denticles of apical portion well developed (figs. 1F; 24K) Arauenephia
 - Sclerotized areas of abdominal sterna larger, subquadrate (fig. 34Q); sclerotized areas of abdominal terga of subequal size on all segments (fig. 34D); genitalia with ventral plate subrectangular, its basal arms stout, rounded at apex and recurved (figs. 1B; 34I, O); arms

of median sclerite sharply diverging apically (fig. 34J); endoparameral organ with basal portion small and denticles of apical portion obsolescent (figs. 1B; 34W). *Araucnephioides* Basal tooth of claws narrowly hooklike (fig. 33L)

- Frons very narrow (fig. 7A), frontal angle approximately 50°; inner surface of spermatheca without spicules (Mesoamerica) . Mayacnephia Frons wider (fig. 22A), frontal angle approximately 85°; inner surface of spermatheca with scattered spicules (similar to fig. 33S) (southern South America) Araucnephia

FEMALES, BASED ON GENITALIA

- 4. Area of insertion of spermathecal duct on spermatheca with peculiar network-like structure extending to base of duct (figs. 421; 43F) Lutzsimulium

MALES, BASED ON GENITALIA

1. Endoparameral organ not perceptible; median sclerite comparatively simple, in shape of basally

widened, elongate lamella, apically divided into two short arms connected by membrane (fig. 43H) Lutzsimulium At least some portion of endoparameral organ dis-

- - Basal portion of endoparameral organ distinct, platelike; denticles of distal portion, varying from absent to well developed, but not arranged as described above 4

- Median sclerite consisting of transversal basal flange and deeply incised median portion perpendicular to flange (figs. 7Q; 9F; 10A; 11I); endoparameral organ reduced to basal platelike portion, denticles absent (figs. 7R; 10A; 11H) Mayacnephia, Tlalocomyia
 - Median sclerite different; endoparameral organ with or without denticles 5
- Median sclerite strongly geniculate in side view (figs. 29J; 40S), roughly M-shaped when seen in full view (figs. 39R; 40R), with inner arms of M partly fused and connected to basal flange . 6 Median sclerite not as above, in shape of complex structure occupying three different planes . . 7
- 6. Endoparameral organ in shape of free platelike basal portion and numerous elongate subparallel apical denticles not connected to basal portion (fig. 40R, S) *Paraustrosimulium*
- Ventral plate subtriangular, its basal arms in shape of elongate slender rods (figs. 1F; 24G); arms of median sclerite parallel (fig. 24I, J); endoparameral organ with denticles of distal portion conspicuous (fig. 24H, K) . Araucnephia
 - Ventral plate subrectangular, its basal arms stout, apically knobbed (fig. 1B); arms of median sclerite diverging apically (fig. 34J); endoparameral organ with denticles of distal portion obsolescent (fig. 34W) Araucnephioides

PUPAE

1. Abdominal sterna VI and VII divided longitudinally along middle by membranous, striate area (figs. 6L; 12C; 26); hooks of terga VI- VIII invariably simple (fig. 26); abdominal segments VIII and IX in many cases with strongly curved, twisted, looped or grapnel-like strong setae (figs. 6Q; 43L) 2 Abdominal sterna VI and VII entire; in many cases, some hooks on terga VI-VIII bifid or trifid; abdominal terga VIII and IX without

- - Q), covering whole body of pupa except gills, latter (fig. 40 O, Q) in shape of twisted pseudosegmented lamella; abdomen less strongly sclerotized than thorax; abdomen without supernumerary hooks, and with short terminal processes (fig. 40T) . . . Paraustrosimulium
- 4. Abdominal terga with spine-combs (fig. 26); tergum VIII without large hooks 5 Abdominal terga without spine-combs; tergum VIII with four large hooks (fig. 15B) . . Cnesia
- 5. Facial trichomes, thoracic trichomes, and setae of eighth and ninth abdominal segments tightly looped apically (figs. 42J; 43L, M). Lutzsimulium At least facial and thoracic trichomes not looped apically 6
- Head sclerite (fig. 25F) with frontal, facial, epicranial, lateral, and genal trichomes; facial trichomes hairlike (fig. 25B) Araucnephia Head sclerite not with all the trichomes mentioned; facial trichomes hairlike or spinelike. 7
- Cephalic sclerite with 2+2 or 3+3 frontal trichomes (fig. 8C); branches of gills more or less tubular (figs. 6H; 8A; 9A; 10B) . Mayacnephia Cephalic sclerite without frontal trichomes; gill branches varied in shape Gigantodax

LARVAE

1. Anal sclerite with an accessory sclerite forming

- 2. Teeth of hypostomium arranged in three conspicuous groups (figs. 6S; 12E; 27M; 37E, J); mandibular serrations numerous, more than five (figs. 6M; 12F; 27J; 37M) 3
 - Teeth of hypostomium more evenly distributed, not arranged in conspicuous groups (figs. 16H, J; 41C, F; 42N, Q); mandibular serrations less numerous, not more than five, generally only two (figs. 16G; 41E; 42P; 43R) 6
- Antennae approximately as long as stem of cephalic fan (fig. 37C); hypostomium with either 13 (fig. 12E) or 17 (fig. 37J) teeth.
 Antennae much shorter than stem of cephalic fan
- 4. Cervical sclerites very small, isolated in neck membrane (fig. 37N); mandibles (fig. 37M, O, P) with accessory serrations at level of inner teeth, with second preapical tooth minute, and with short basal setae slender, only faintly dentate (fig. 37H); hypostomium with 17 teeth (fig. 37J) Araucnephioides
 - Cervical sclerites small (fig. 10G) or transverse and isolated in neck membrane (figs. 6R; 8D), or transverse and fused with upper ends of postocciput (figs. 9G; 12H); mandibles without accessory serrations, with second preapical tooth as long as first (fig. 12F) or only slightly shorter (fig. 6M), and with short basal setae bearing conspicuous elongated denticles (fig. 6O); hypostomium with 13 teeth (figs. 6S; 12E) . 5
- 5. First antennal segment more than half as long as second (fig. 6N).
 Mayacnephia First antennal segment at most half as long as second (fig. 12J)
- 7. Gular cleft well developed (figs. 42Q; 43Q); hypostomium with at most 13 teeth (fig. 42N), the 2+2 lateral ones, when perceptible, somewhat similar to lateral serrations; mandible with two outer teeth (figs. 42P; 43R)....8 Gular cleft very shallow (fig. 16A); hypostomium

with 17 teeth, the 4+4 lateral ones similar to remaining teeth (fig. 16J); mandibles with four outer teeth (fig. 16G, I) $\ldots \ldots \ldots$ Cnesia

- 9. Preapical teeth of mandible subequal in size (fig. 4I, J), or decreasing in size from first to third (fig. 4H).
 Preapical teeth of mandible with second much smaller than either first or third (fig. 43R).
 Lutzsimulium (part)

MAYACNEPHIA, NEW GENUS

DIAGNOSIS: Differs from other prosimuliine black flies by a combination of characters found in larvae, pupae, females, and males, indicated in the generic keys.

DESCRIPTION: Adult. Antennae with 11 segments. Male holoptic. Female with frons narrow, frontal angle 50 degrees. Mandibles and maxillae of female normally developed, mandibles with teeth on both margins. Apical segment of maxillary palp in both sexes less than twice as long as penultimate. Mesepisternal sulcus wide, shallow, evanescent anteriorly. Katepisternum glabrous, in profile about as long as high. Pleural membrane glabrous. Arms of furcasternum lacking projections. Metanotum glabrous. Wings with basal cell present. R_1 with hairs and spinelike setae. Basal section of a R hairy; R_s hairy below and hairy above on its apical half, beginning at level of junction of R_1 on C. R_s not forked. M appearing duplicated. Cu2 conspicuously curved. A₂ ending well before wing margin. Calcipala present, bluntly rounded apically. Hind basitarsus of male strongly widened. Claws of female with large, bluntly subtriangular, basal tooth. Female with spermatheca normally sclerotized, not reticulate and without spicules internally, with small circular membranous area at insertion of spermathecal duct, the latter not sclerotized. Gonapophyses large, subtriangular, apices rounded, medial borders approximated, surface with numerous microtrichia and a few setae. Branches of genital fork without backwardly directed apodemes. Stem slender, at least as long as arms. Male with distimere about as long as basimere, conical, with two apical spines. Ventral plate somewhat wider than long, subsemicircular, setose. Median sclerite with transversal basal flange and deeply incised elongate median portion perpendicular to flange. Endoparameral organ reduced to platelike sclerite; denticles absent.

Pupa. Cocoon irregularly shaped, covering part or all of body. Body of pupa sclerotized throughout. Head, thorax with pterothecae, and abdominal segments, tuberculate. Gills consisting of several thickened, tubular, occasionally divided (or basally fused) branches arising from a short common base, all with superficial but mostly conspicuous transverse annulations. Head with 2+2 or 3+3 frontal and 1+1 facial trichomes; all hairlike. Thorax with approximately five simple trichomes. Abdomen pointed posteriorly. Distinct pleural plates absent. Abdominal segments without perceptible transversal ridges. Terga III and IV with 4+4 or 5+5 hooks posteriorly, in some cases 5+5 hooks also on tergum II, and 1+1 hooks on V. Terga V-IX, or VI-IX, with continuous spine-combs anteriorly; faint spine-combs also perceptible on III and IV. Sternum IV with l+l strong setae or hooks; sternum V with from 2+2 to 4+4hooks; sternal plates VI and VII either each with 1+1 hooks accompanied by no or 1+1hooks in pleural membrane, or sternal plates VI with 3+3 and sternal plates VII with 2+2hooks, accompanied by 1+1, 2+2 or 3+3hooks in pleural membrane; all hooks simple. Terminal hooks well developed, relatively stout, not sinuous. Posterior segments with a few irregularly formed hook or grapnel-shaped setae.

Larva. Head spots positive. Cephalic apotome broadest well before hind margin. Cervical sclerites transverse, small or large, either free or fused to upper ends of postocciput. Postgenal cleft very shallow. Antennae as long as stem of cephalic fans; third segment slightly darker than remaining. First antennal segment over half as long as second. Cephalic fans normal. Mandibles with two outer and one apical tooth; third preapical tooth the largest, but not so large as apical tooth. Inner teeth arranged in a single row. Mandibular serrations very numerous (15-22). Short basal setae stout, with conspicuous denticles along almost their entire length. Hypostomium with 13 teeth arranged in three conspicuous groups, with median tooth and corner teeth by far the largest; the 2+2 lateral teeth situated only slightly below level of remaining teeth. Lateral sclerites of proleg well developed, about as long as wide, subrectangular, their lower border subparallel to longitudinal axis of proleg. Setae of lateral sclerites less than half as long as sclerite, arranged in an irregular double row, this row extending slightly beyond sclerite below. Larval cuticle bare, except simple setae at base of anal sclerite, and a few perianal scales. Anal sclerite normal, X-shaped. Ventral papillae absent or present.

TYPE-SPECIES: Simulium pachecolunai Leon, 1944.

ETYMOLOGY: The Mayas, a people of Mesoamerica, and *Cnephia*, a genus of black flies.

DISTRIBUTION: Highlands of Mexico and Guatemala.

DISCUSSION: Mayacnephia is most closely related to Tlalocomyia Wygodzinsky and Díaz Nájera; the two genera form a monophyletic group, Tlalocomyia being the more apomorphic component. The similarities and differences between Tlalocomyia and the species now included in Mayacnephia were enumerated by Wygodzinsky and Díaz Nájera (1970); they are recapitulated in this paper under the heading of Tlalocomyia.

We have compared Mayacnephia and Tlalocomyia with all genus-group assemblages of the Prosimuliini (sensu Crosskey, 1969) known to us. Only the following share with our genera the



FIG. 6. Mayacnephia pachecolunai. A, B. Antennae. A. Male. B. Female. C. Maxillary palp of female. D. Paramere. E. Calcipala of female. F. Gonapophyses of female, microtrichia not shown. G. Claw of female. H. Pupal gills. I, J. Larva. I. Labral sclerite. J. Lateral sclerite of proleg. K, L. Onchotaxy of abdomen of pupa. K. Terga II and III. L. Sterna. M-O. Larva. M. Apex of mandible. N. Antenna. O. Some short basal setae of mandible. P. Terminal hook of pupa. Q. Setae of apical segments of pupal abdomen. R, S. Larva. R. Cervical region of head. S. Portion of hypostomium.

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combination of the presence of a basal cell, spiniform setae on the anterior wing veins, presence of calcipala and absence of pedisulcus, and a larval hypostomium with the teeth arranged in three compact groups: *Stegopterna* Enderlein (Holarctic) (fig. 4E), *Greniera* Doby and David (Palearctic), *Paracnephia* Rubtsow (Ethiopian), and an unnamed group containing *Cnephia stewarti* Coleman (western Nearctic). The last group mentioned is of special interest as its typical Cordilleran distribution in North America (Shewell *in litt.*) suggests the possibility that it might also occur in Mexico. We do not know if it does or not, but the species here included in *Mayacnephia* and *Tlalocomyia* do not resemble *stewarti*; the latter is characterized by such features as an apically forked R_s , a heavily sculptured spermatheca, a very specialized pupal onchotaxy, and a different larval hypostomium, viz., of the type found in many *Prosimulium*, with the outermost tooth of each outer group longer than any other of this group.

The Mesoamerican genera differ from *Stegopterna* and *Greniera* by peculiarities of the male genitalia with the deeply incised median sclerite (figs. 7Q, 111) (divided only apically in *Stegopterna* [fig. 1C] and *Greniera*), the absence of endoparameral spines or hooks, present in the other



FIG. 7. Mayacnephia roblesi. A–I. Female. A. Frons. B. Basitarsus and second tarsal segment of hind leg. C. Claw. D. Maxillary palp. E. Sensory vesicle. F. Genital fork. G. Portion of eighth abdominal sternum, schematic; microtrichiae not shown. H. Cercus and paraproct. I. Spermatheca; pigment not shown. J–S. Male. J. Sensory vesicle of maxillary palp. K. Hind leg. L. Maxillary palp. M. Apex of posterior basitarsus, with second tarsal segment. N. Wing. O. Furcasternum. P. Paramere. Q. Ventral plate and median sclerite. R. Ventral plate, with endoparameral organ at left. S. Ventral plate in lateral view with median sclerite.

two genera (fig. 1D), the more or less tubular respiratory organs of the pupae (filiformarborescent in Stegopterna and Greniera), and the antennae of the larvae which are not longer than the stalk of the cephalic fan. Other characters of Greniera, which do not agree with those of Mayacnephia and Tlalocomyia, are the tensegmented antennae of the adult, a small bifurcation at the apex of R_s, and the small number of serrations on the mandible of the larva. The Mexican genera can be distinguished further from the geographically much closer Stegopterna by the large basal tooth of the claw of the female (figs. 6G, 9B, 11F) (very small or absent in Stegopterna), and the presence of several pairs of frontal trichomes in the pupae (fig. 8C), which are absent in Stegopterna (fig. 4C). It is possible to consider comparatively recent common ancestry for Stegopterna and Mayacnephia.

Crosskey (1969) divided Paracnephia into three species groups, the brincki, muspratti, and turneri groups; muspratti is the type of the genus. The members of the brincki and muspratti groups differ from Mayacnephia and Tlalocomyia in such essential characters as the absence of spinelike setae on R_1 , the Stegopterna-like median sclerite, the presence of endoparameral denticles and of more than two apical spines on the distimeres of the male genitalia, the much smaller gonapophyses of the females, the unbranched setae on the abdominal apex of the pupae, and the enormously enlarged third comb-tooth of the mandible of the larva. The trend toward, in some cases, highly modified tubular branches of the gills of the pupa of the Mexican genera also differentiates the Mexican species from the *brincki* and *muspratti* groups of *Paracnephia*. These differences justify, in our opinion, a generic separation of the taxa involved.

The relationships between *Mayacnephia* and *Tlalocomyia* and the monotypic *turneri*-group of *Paracnephia* are more difficult to judge. The presence of spinelike setae on R_1 , the more rounded calcipala, and the much larger gonapophyses distinguish *turneri* from the remaining *Paracnephia* and approach it to *Mayacnephia*. As *turneri* is known only from a single not too well preserved female, a final decision on its possible affinities with *Mayacnephia* will have to await the discovery and analysis of the male, larva, and pupa of the African species.

We include in *Mayacnephia* all six Mexican and Guatemalan species formerly placed in *Cnephia*, even though only four of them have been adequately described; the two remaining are listed as *species inquirendae*.

The four well-described species can be divided into two groups, according to the onchotaxy of the abdomen of the pupa. In the type-species, *pachecolunai* (fig. 6L), and in *roblesi* (fig. 8B) the



FIG. 8. Mayacnephia roblesi. A. Gills of pupa. B. Onchotaxy of abdomen of pupa, from third sternum on. C. Frontoclypeus of male pupa. D. Cervical region of larva.

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sternum V has 2+2 spines or hooks, the sternal plates VI and VII have one spine each, and there is not more than one spine on the pleural membrane of segment VI or VII; all this adds up to a seemingly plesiomorphic condition. In the other two species, grenieri (fig. 9D) and aguirrei (fig. 10E), the number of spines on the sternal sclerites is larger; there are 3+3 or 4+4spines on sternum V, the sternal plates VI have three and sternal plates VII two spines each; there may be two or three spines per segment on the pleural membrane of the posterior segments: all this suggests an apomorphic condition. There is another character set possibly correlated with the above. In the first group mentioned, the gills of the pupa are either relatively simple (fig. 6H), with numerous still rather slender branches, or its branches, still comparatively numerous, are partly fused and thickened at their bases (fig. 8A). In the second group, there is a progressive consolidation of the branches (figs. 9A, 10B) which are reduced in number and have lost their filamentous portion.



FIG. 9. Mayacnephia grenieri. A. Gills of pupa. B. Claw of female. C. Onchotaxy of abdomen of pupa, dorsal surface. D. Onchotaxy of abdomen of pupa, ventral surface, from fourth sternum on. E. Calcipala of female. F. Median sclerite of male genitalia. G. Cervical region of larva.

We refrain from giving these two groups any formal rank, even that of "species group," because we have been unable to find features either in the adult or the larvae that would reinforce the characterization of the groups. It was especially disconcerting to us that the structure of the cervical sclerites of the larvae does not at all fit the scheme suggested by the pupal structures described above. The probably most apomorphic condition (cervical sclerites small and free) is found in aguirrei (fig. 10G), a member of the apomorphic group, but the probably most plesiomorphic condition (cervical sclerites large and fused to upper ends of postocciput) is found in grenieri (fig. 9G), also a member of the apomorphic group. On the other hand, both members of the plesiomorphic group, pachecolunai and roblesi, have cervical sclerites of an intermediate type (large and free), as shown in figures 6R and 8D.

Díaz Nájera (1962) gave a key for the determination of the larvae of *Mayacnephia* (as *Cnephia*).

Mayacnephia pachecolunai (León), new combination

Figure 6

Simulium pacheco-lunai León, 1945, p. 67.

Cnephia pacheco-lunai: DALMAT, 1951, p. 48; VARGAS AND DÍAZ NÁJERA, 1954, p. 67; DALMAT, 1955, p. 93; DÍAZ NÁJERA, 1962, p. 273.

Although this species has been abundantly figured, we offer some drawings of our own, not only to illustrate features mentioned in our discussion of the genus but also to make this survey of the Latin American Prosimuliini more complete.

DISTRIBUTION: Guatemala; Mexico (Chiapas). BIOLOGY: The following data are extracted from Dalmat (1955). One adult was found to bite man, but the real host of this species is not known. Normally M. pachecolunai occurs only above 2100 meters. It breeds in cold streams of not more than 17°C., although the concentration of specimens is largest at water temperatures below 11°C. The breeding grounds were "almost . . . entirely minute trickles of water that pass over a swampy area supporting large quantities of vegetation. Such rivulets usually dried up during the months of November through March." These rivulets were most frequently less than 15 cm. wide, and 13 cm., or less, deep. The current was generally very slow, less than

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38 cm. per second. About half of the pupae collected were attached to rocks, and the remainder to leaves or some few to branches or twigs.

Mayacnephia roblesi (León), new combination

Figures 7, 8

Simulium roblesi León, 1943, p. 97; 1945, p. 67. Cnephia roblesi: Dalmat, 1951, p. 48; Vargas and Díaz Nájera, 1954, p. 64; Dalmat, 1955, p. 97.

This species is herein illustrated in some detail, although many figures have been published before. Our illustrations of *roblesi* together with those of other species of the genus are hoped to provide the reader with a fair view of the overall



FIG. 10. Mayacnephia aguirrei. A. Ventral plate and median sclerite; endoparameral organ shown at left. B. Gills of pupa. C. Labral sclerite of larva. D. Onchotaxy of abdomen of pupa, dorsal surface. E. Onchotaxy of abdomen of pupa, sterna IV to VII. F. Spine of apex of abdomen. G. Cervical region of larva.

morphology of the members of this genus, in reference to characters of taxonomic importance.

DISTRIBUTION: Highlands of Guatemala. BIOLOGY: Dalmat (1955) provided our only

information on the biology of this species. The food habits of the adult are not known. This is a highland species breeding at altitudes above 2100 meters. The aquatic instars were found in streams with a water temperature below 13°C., not infrequently between 10 and 11°C. *Mayacnephia roblesi* breeds in the same types of small rivulets in swampy areas as *pachecolunai* (see above), and is restricted to rivulets of less than 6 inches wide, with depths of generally less than 1 inch; the current is slow, with speeds of 25 cm. per second, or less. Contrary to *pachecolunai*, the pupae of *roblesi* are never found on rocks or stones; they are in most cases attached to leaves, with only a few found on branches or twigs.

Mayacnephia grenieri (Vargas and Díaz Nájera), new combination

Figure 9

Cnephia grenieri VARGAS AND DÍAZ NÁJERA, 1948, p. 325; 1957, p. 270; DÍAZ NÁJERA, 1962, p. 273.

This species has been well illustrated. Our drawings illustrate features mentioned in the discussion of the genus.

DISTRIBUTION: Mexico (Veracruz).

BIOLOGY: The aquatic instars of this species were found at an altitude of 1500 meters, in a small clear stream 60 cm. below its origin from a spring.

Mayacnephia aguirrei (Dalmat), new combination

Figure 10

Simulium aguirrei DALMAT, 1949, p. 544.

Cnephia aguirrei: DALMAT, 1951, p. 48; VARGAS AND DÍAZ NÁJERA, 1952, p. 53; DALMAT, 1955, p. 89; VARGAS AND DÍAZ NÁJERA, 1957, p. 268; DÍAZ NÁJERA, 1962, p. 273.

This species has been abundantly illustrated by various authors; our figures show aspects of the male genitalia and the onchotaxy of the abdomen of the pupa.

DISTRIBUTION: Highlands of Guatemala; Mexico (Chiapas).

BIOLOGY: Dalmat (1955) reported that this species was found between 900 and 1825 meters, most frequently above 1525 meters. The aquatic instars occurred in streams the temperature of which ranged between 14 and 23°C., with most specimens at 19°C. and below. None of the streams where this species bred was wider than 1.50 meters, and almost all were not deeper than 30 cm. The preferred current was between 2.5 and 25 cm. per second, and never over 50 cm. per second. Pupae preferred stones or rocks as a substrate; less than 10 percent were found on leaves and twigs.

Species Inquirendae

The following two species, described by Díaz Nájera (1962), are based upon larvae and pharate pupae. They were placed by their author in close relationship with other species of Mexican black flies here included in *Mayacnephia*, with which they seem to agree in many characters; at this time, we accept the Mexican author's point of view, and therefore place the species in *Mayacnephia*. We do believe, however, that a more detailed study, based on a more complete life history, is necessary before the generic position of these species can be settled definitely.

Mayacnephia atzompensis (Díaz Nájera), new combination

Cnephia atzompensis Díaz Nájera, 1962, p. 273.

The gill of the pupa of *atzompensis* is composed of 11 basically very wide branches, as illustrated by Díaz Nájera (1962). DISTRIBUTION: Mexico (Morelos).

BIOLOGY: This species was collected in a cold, very small stream.

Mayacnephia mixensis (Díaz Nájera), new combination

Cnephia mixensis Díaz Nájera, 1962, p. 274.

The gill of the pupa of this species has only three branches, according to the original description.

DISTRIBUTION: Mexico (Oaxaca).

TLALOCOMYIA WYGODZINSKY AND DÍAZ NÁJERA

Tlalocomyia Wygodzinsky and Díaz Nájera, 1970, p. 83.

This genus, named for the Aztec rain god Tlaloc, is closely related and in many respects similar to *Mayacnephia*, described in the present paper. In order to define *Tlalocomyia* here, an enumeration of the characters distinguishing it from *Mayacnephia* is deemed sufficient.

DEFINITION: Adult. Female with frons very narrow; frontal angle 30 degrees. Apical segment of maxillary palp more than twice as long as penultimate. Pleural membrane hairy on upper third. Spermatheca reticulate on outer, and not spiculate on inner surface; spermatheca sclerotized throughout, without membranous area at insertion of spermathecal duct, the latter



FIG. 11. *Tlalocomyia revelata*. A. Female, maxillary palp. B. Male, maxillary palp. C. Thorax, lateral view. D. Male, hind leg. E, F. Female. E. Sensory organ of maxillary palp. F. Claw. G–I. Male. G. Sensory organ of maxillary palp. H. Aedcagus and endoparameral organs. I. Median sclerite. J–L. Female. J. Spermatheca. K. Genital fork. L. Cercus and paraproct.

sclerotized at base, this sclerotization terminating abruptly.

Pupa. Cocoon obsolescent, composed of closely woven basal cushion and irregular threads loosely covering, at most, posterior half of abdomen of pupa. Body of pupa very heavily sclerotized throughout. Gills composed of elongate, basally thickened trunk from which arise sequentially a few threadlike filaments. Facial trichomes spinelike. Abdomen rounded-truncate posteriorly. Spine-combs of abdominal terga absent. Terminal hooks not developed. Abdominal terga and sterna each with median transverse ridge. Ridges on terga II-VIII and sterna III–V each with one row of very numerous simple spines or hooks. Sternal plates of segments VI and VII with several irregularly arranged hooks. Pleural membranes of posterior segments with 4-5 additional spines or hooks per segment. All hooks simple.

Larva. Cervical sclerites large, transverse, fused to upper ends of postocciput. First antennal segment not longer than half of length of second.

TYPE-SPECIES: *Tlalocomyia revelata* Wygodzinsky and Díaz Nájera.

DISTRIBUTION: The genus and species is known from a single locality in the Transversal Volcanic range of Mexico.

BIOLOGY: The single species included in Tlalocomyia has been found only during the rainy season in a single small, fast-flowing, cold (10°C.), probably temporary, stream at about 3000 meters altitude. Larvae and pupae were restricted to a stretch between 50 and 150 meters below the spring where the stream originated. Larvae and pupae were found in most cases on the under surface of large stones and on trailing vegetation, but some were found on the hardened clay bottom of the stream, freely exposed to the strong current. It is remarkable that the rudimentary cocoon is sufficient to keep these pupae in place. The population was found to be protandric, and the females observed were judged to be anautogenous, because their mouthparts were well developed, and the ovarian development was minimal upon hatching.

DISCUSSION: The type-species differs from all species of *Mayacnephia*, in addition to the generic characters, also by its accentuated sexual dimorphism, viz., the considerable size difference of the sensory organ of the maxillary palp in both sexes (fig. 11E, G) and the color of the

scutum, black in the male and bright orangeyellow in the female. Both are specialized features, as are those enumerated above, but we are not certain that they are indicative of generic differences.

Tlalocomyia shares with Mayacnephia a combination of so many characters that the close affinity of the two genera is beyond doubt, for example, the deeply incised median sclerite of the male genitalia, a synapomorphic character shared by these two genera and no other.

Tlalocomyia revelata Wygodzinsky and Díaz Nájera

Figures 11, 12

Tlalocomyia revelata Wygodzinsky and Díaz Nájera, 1970, p. 88.

The original description of this species is very detailed. For easy reference, a few diagnostic characters are illustrated here again. The short basal setae of the larval mandible, not formerly examined, are very similar to those found in *Mayacnephia* (fig. 6O), but the denticles are slightly shorter and less numerous.

CNESIA ENDERLEIN

Cnesia Enderlein, 1934, p. 273. Stone, 1963, p. 4.

DESCRIPTION: Adult. Antennae with 11 segments. Male holoptic. Female with frons medium wide; frontal angle 50-67 degrees. Mandibles with well-developed teeth only on internal margin, external border weakly serrated. Apical segment of maxillary palp in both sexes less than twice as long as penultimate segment. Mesepisternal sulcus shallow, evanescent anteriorly. Katepisternum glabrous, in profile slightly longer than high. Pleural membrane glabrous. Metanotum with hairs in some but not all species. Arms of furcasternum lacking conspicuous projections. Wings with basal cell present. R1 with hairs and spinelike setae, the latter not more delicate on R1 than on C. Sc and basal section of R with hairs arranged in several irregular series. R_s entirely hairy below, hairy above only on apical half. R_s not forked apically. M not appearing double. Cu₂ only weakly curved in both sexes. A2 almost attaining wing margin. Calcipala present, large, bluntly rounded apically. Claws of female with large subtriangular basal tooth. Spermatheca of normal size, normally sclerotized, oval; internal surface



FIG. 12. *Tlalocomyia revelata*. A. Pupae on leaf. B. Onchotaxy of pupal abdomen, dorsal. C. *Idem*, ventral. D. Gill of pupa, outlines. E. Portion of hypostomium of larva. F. Apex of mandible of larva. G. Apex of abdomen of pupa, lateral view; sterna to left. H–J. Larva. H. Cervical region. I. Anal sclerite. J. Antenna.

minutely wrinkled and with small irregularly scattered spicules; area of insertion of spermathecal duct membranous, distinctly larger than diameter of duct; duct not sclerotized. Gonapophyses subtriangular, transverse, their medial borders narrowly pigmented, approximated, their surface with microtrichia and a few setae. Posterior arms of genital fork wide, with small but distinct forwardly directed apodemes. Male with distimere distinctly shorter than basimere, narrowly conical, with two apical spines; medial surface of distimere smooth, limited by two carinae. Ventral plate subpentagonal, about as long as wide, setose, with very low median longitudinal keel. Median sclerite with flaring base, then narrowed, apically widened again and with two winglike pointed subapical flanges. Endoparameral organs with basal portion strongly reduced, apical portion composed of a group of one or two large and several oppositely directed medium-sized denticles.

Pupa. Cocoon large, shapeless, covering pupa to base of respiratory organs. Body of pupa well sclerotized throughout. Head and thorax with or without platelets. Gills bushy, much shorter than pupa proper, composed of 35-40 slender filaments arising from about 12 primary branches very close to their base. Head with 1+1 prefrontal, 1+1 or 2+2 frontal, 1+1facial, and occasionally 1+1 labial trichomes. Prefrontal and single or anterior frontal trichomes spinelike; posterior frontal, facial and labial trichomes hairlike. Disc of thorax with approximately 5+5 trichomes, the two or three dorsalmost ones in shape of strong spines, the others hairlike. Abdomen pointed posteriorly. Distinct pleural areas not developed. Terga with numerous small platelets or tubercles, those near anterior margins of sclerites arranged in very conspicuous transversal ridges. Onchotaxy of abdomen as follows. Terga III and IV with 4+4 short hooks posteriorly; tergum VIII with 2+2 very elongate spines posteriorly; terga without spine-combs. Sterna IV and V with 3+3 hooks posteriorly, those of IV arranged in one median and 1+1 submedian groups of two spines each, those on V arranged in 1+1 closely approximated groups of three spines each. Sternal plates VI with 2+2, VII with 1+1hooks; 1+1 hooks each also in pleural membrane of segments VI and VII. Terminal spines well developed, stout, not sinuous. Posterior segments with several strong S-shaped setae, often apically curved, looped or spiraled, occasionally branched near base or apex.

Larva. Head spots positive. Cephalic apotome broadest well before hind margin. Cervical sclerites very small, isolated in neck membrane. Postgenal cleft very shallow, broadly U-shaped. Antennae about as long as stem of cephalic fans. Second antennal segment distinctly more than half as long as first; third segment darker than remaining. Mandibles with four outer teeth in addition to apical tooth; third preapical tooth longer and more strongly sclerotized than other preapical teeth, as long as apical tooth; first inner tooth as long and stout as third preapical tooth; inner teeth arranged in three or more series; two large mandibular serrations followed by two or three small ones. Short basal setae of mandible slender, glabrous. Hypostomium slightly bi-emarginate anteriorly, with 17 teeth, not arranged in conspicuous groups; median tooth and corner teeth somewhat larger than remaining; the 4+4 lateral teeth inserted almost at same level as other teeth. Lateral sclerites of proleg well developed, rather narrow for most of their length but abruptly flaring toward below

and above at anterior margin. Setae conspicuously decreasing in size from dorsal to ventral portion of anterior border of sclerite; lowermost setae barbed, some of the others once or twice branched on their apical half. Setae arranged in one or two irregular rows, not arranged in groups and not inserted upon distinct tubercles. Larval cuticle bare, except perianal scales. Anal sclerite normal, X-shaped. Ventral papillae absent.

TYPE-SPECIES: Simulium (Cnephia) dissimile Edwards, 1931 (as Simulium (Cnephia) gynandrum Edwards, 1931).

DISTRIBUTION: Valdivian and Magellanic areas of southern Chile and western Patagonia, with slight intrusion into Mediterranean climate area of central Chile.

DISCUSSION: Edwards (1931) considered that dissimilis (and some other Chilean-Patagonian species) belonged to the "Stegopterna group." Enderlein created the genus Cnesia for gynandrum (=dissimilis); this genus was accepted by various subsequent workers. Stone (1963) finally considered Cnesia to be a synonym of Cnephia (Cnephia).

Our evidence suggests that Cnesia should be maintained as a good genus. It differs from Stegopterna and Cnephia sensu strictu as well as from all other boreal Prosimuliini bearing spinelike setae on the anterior wing veins by such important characters as the anteriorly directed apodemes of the genital fork of the female, by the complex median sclerite of the male genitalia, by the onchotaxy of the pupa, viz., the absence of spine-combs and the presence on tergum VIII of four strong, elongate spines, and by the multiplication of the apical and inner teeth of the mandibles of the larva. Cnesia differs from Cnephia also by the much smaller spermatheca that is unusually large in Cnephia, from Stegopterna by the simplified hypostomial teeth of the larva, and from both genera by the large basal tooth to the claw of the female.

Among the Latin American Prosimuliini there are two others in which the teeth of the hypostomium of the larva are not arranged in three prominent groups: *Lutzsimulium* and *Paraustrosimulium*. The differences between adult and aquatic stages of *Cnesia* and of the genera mentioned are so many and so obvious that they need not be enumerated here; most are expressed in the generic keys found in this paper.

Cnesia shares with Gigantodax the apomorphic

structure of the genitalia in both sexes, and on this basis alone the two genera are indistinguishable. *Cnesia* and *Gigantodax* do differ considerably



FIG. 13. Cnesia dissimilis, female. A. Maxillary palp. B. Sensory vesicle of maxillary palp. C. Apex of mandible. D. Apex of maxilla. E. Wing. F. Apex of hind basitarsus, with second and base of third tarsal segment. G. Spermatheca. H. Claw. I. Furcasternum. J. Portion of eighth abdominal sternum, with gonapophyses. K. Genital fork of gynandrum, specimen studied by Vargas and Díaz Nájera (1951). L. Genital fork of paratype of gynandrum. M. Genital fork of lightcolored specimen. in other ways (wing venation, onchotaxy of the abdomen of the pupa, several characters of the larvae), but their synapomorphic genitalia suggest common ancestry not shared by any other known genus.

Upon comparison of Cnesia with the Ethiopian Prosimuliini, the genus will key out to Paracnephia Rubzow, but there is no evidence that would indicate identity with, or close relationship to, Paracnephia. The main characters separating Cnesia from the Ethiopian insects are found in the male genitalia with its complex median sclerite and peculiar endoparameral organ, the structure of the genital fork of the female, the peculiar onchotaxy of the pupa, and, in the larva, the free postcervical sclerites, the hypostomial teeth not arranged in three prominent groups, the multiplication of the apical and inner teeth of the mandibles, and the reduced number of mandibular serrations. Cnesia differs further from the brincki and muspratti groups of Paracnephia by the presence of well-developed spiniform setae on R₁. Cnesia does share this character with the turneri group of Paracnephia, but because this group is known only from a single not too well-described female no useful comparisons can be made at this time.

Edwards (1931) stated that [Cnesia] dissimile "is more closely related to the Australian and Tasmanian S[imulium] aurantiacum Tonn. than to any other Simulium. . . ." However, a comparison between aurantiacum based on the available descriptions and dissimilis shows so many differences in the genitalia of both sexes, the onchotaxy of the pupa and characters of the larva, such as the completely different hypostomium, that even phenetic affinities between Cnesia and "Cnephia" aurantiacum cannot be advocated. No other Prosimuliini described from Australia show any similarity to Cnesia.

KEYS TO THE SPECIES OF Cnesia

FEMALES

- Scutum pale reddish brown, dark brown on disc in some specimens; wing length more than 3 mm.
 Scutum black; wing length 3 mm. or less . pusilla

¹The fully developed female of *ornata* is not known; the character given to include it in the key is found in the male, and almost certainly shared by the female.

MALES

- 1. Scutum varying from dark brown to black; metanotum with short hairs posteriorly . . . 2 Scutum bright reddish brown; metanotum glabrous ornata
- Wing length more than 3 mm.; scutum varying from dark reddish brown to black . . dissimilis Wing length 3 mm. or less; scutum black . pusilla PUPAE
- Head and thorax with numerous platelets, those on thorax generally arranged in circles (figs. 19A; 20F) ornata Head and thorax without platelets 2
- Cephalopterothecal length approximately 2.5 mm.
 Cephalopterothecal length approximately 2.0 mm.
 Cephalopterothecal length approximately 2.0 mm.

The larvae of the species of *Cnesia* are so similar that we have been unable to find any differential characters, but larvae of *pusilla* from Argentina can be distinguished from those of the two other species by their smaller head width.

Cnesia dissimilis (Edwards)

Figures 13, 14A, C, E-M, 15, 16, 17E, F

- Simulium (Cnephia) dissimile EDWARDS, 1931, p. 145.
- Cnephia dissimile: SMART, 1945, p. 498.
- Cnesia dissimile: VARGAS AND DÍAZ NÁJERA, 1951, p. 166. COSCARÓN AND WYGODZINSKY, 1962, p. 310. COSCARÓN, 1968, p. 66.
- Stegopterna dissimilis: ENDERLEIN, 1934, p. 274.
- Simulium (Cnephia) gynandrum Edwards, 1931, p. 147 (new synonym).
- Cnephia gynandrum: SMART, 1945, p. 498.

Cnesia gynandra: ENDERLEIN, 1934, p. 273.

Cnesia gynandrum: VARGAS AND DÍAZ NÁJERA, 1951, p. 166.

Cnesia (Stegopterna) gynandrum: RUBZOW, 1940, p. 132. Simulium gynandrum VARGAS, 1945, p. 142.

This species was redescribed and illustrated in detail by Coscarón and Wygodzinsky (1962). Some of their figures are reproduced here to illustrate structures mentioned in the present paper. New figures have also been included either when we thought there was need for



FIG. 14. A. Cnesia dissimilis, male, portion of forewing, showing C, R_1 , and R_8 . B. Cnesia sp., El Radal, Linares, posterior basitarsus of male. C. Cnesia dissimilis, basitarsus and second tarsal segment of hind leg of male. D. Cnesia sp., male, El Radal, portion of wing. E–M. Cnesia dissimilis, male. E. Sensory organ of maxillary palp, in scale with identical organ of female, figure 13B. F. Ventral plate. G, H. Aedeagus, endoparameral organ and median sclerite, different views. I. Ventral plate, different aspect. J, K. Median sclerite, sublateral aspect. L. Median sclerite inserted on ventral plate. M. Median sclerite.

better illustrations of certain structures, or where features formerly not studied in detail needed to be shown. Most of the characters newly illustrated for this species are mentioned either in the generic redescription or in the key; some are discussed below.

Female. The sensory organ of the maxillary palp (fig. 13B) is shown in detail; it is slightly larger than that of the male (fig. 14E).

Male. Different views of the median sclerite are illustrated to help comprehension of its structure (fig. 14J-M).

Pupa. The abdominal onchotaxy is shown

schematically (fig. 15A, B). An enlarged section of the posterior area of tergum II (fig. 15D) shows the minute tubercles making up the posterior ridge of this sclerite, together with some of the tiny rodlike setae found here.

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Larva. Several structures not taken into account formerly are here illustrated, such as the cervical sclerites (fig. 16K), details of the dentition of the mandible (fig. 16G, I), the lateral sclerite of the proleg (fig. 16C), and the gill histoblast (fig. 16N).

MATERIAL EXAMINED: Chile: Magallanes: Punta Arenas, Chorillo Tres Puentes, Dec. 3,



FIG. 15. Cnesia dissimilis, pupa. A. Onchotaxy of abdomen, ventral. B. Onchotaxy of abdomen, dorsal. C. Frontoclypeus of female, pupa. D. Enlarged section of posterior area of abdominal tergum II. E. Gill, dorsal portion to the left. F. Apex of abdomen, ventral.

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female; San José de Maipo, 1000 m., Nov. 3, 1963 (G. F. Edmunds; CNC), larvae; El Canelo, 880 m., Nov. 3, 1963 (G. F. Edmunds; CNC), larvae; Cajon del Río Maipo, El Canelo, Nov. 1, 1967 (S. Coscarón; AMNH), one pupa and larvae; Cuesta La Dormida, March 1, 1966 (E. I. Schlinger; CIS), one female. Valparaiso:

Río Marga-Marga, Oct. 13, 1966 (M. E. Irwin; CIS), one male, reared, pupae and larvae. Argentina: Chubut: Lago Fontana, Jan. 3, 1961 (S. Coscarón; MLP), larvae; Lago Futalaufquen, Puerto Limonao, Jan. 14, 1962 (S. Coscarón; MLP), pupae; Lago Futalaufquen, Arroyo Las Plumas, Jan. 14, 1962 (S. Coscarón; MLP), five females, reared, pupae and larvae. Río Negro: Arroyo Los Repollos, 20 km. N of El Bolson, on Route 258, Jan. 12, 1962 (S. Coscarón; MLP), one pupa; Cerro Catedral, Arroyo La Cascada near hostelry, 1600 m., Jan. 9, 1962 (S. Coscarón; MLP), pupae and larvae; Arroyo Casa de Piedra, 15 km. SW of Bariloche, Feb. 14, 1967 (S. Coscarón; AMNH), pupae and larvae; stream, 5 km. S of Bariloche, Oct. 23, 1970 (S. Coscarón; AMNH), pupae and larvae; Lago Guillelmo, Jan. 12, 1962 (S. Coscarón; MLP), one pupa; 10 km. SW of Bariloche, stream on road to El Bolson, 1 km. W of Arroyo de la Virgen, Jan. 23, 1971 (S. Coscarón; AMNH), larvae; Bariloche, Sept. 28, 1957 (J. Illies; AMNH), pupae and larvae. Neuquen: Arroyo Chacabuco, 6 km. NW of Nahuel Huapi, on route f, Feb. 16, 1967 (S. Coscarón; AMNH and MLP), pupae and larvae; 30 km. NE of Bariloche, Oct. 22, 1970 (S. Coscarón; AMNH), one pupa and larvae; Río Huemul, north fork, on route f, Jan. 18, 1968 (S. Coscarón; MLP), pupae; Arroyo Carbón, Valle Encantado, Jan. 27, 1971 (S. Coscarón; MLP), one pupa; 2 km. SE of Casa de Piedra, Oct. 22, 1970 (S. Coscarón; AMNH), one male, reared, pupae; Arroyo del Pino, 3 km. NW of Casa de Piedra, Oct. 22, 1970 (S. Coscarón; AMNH), larvae; Pichi Traful, Río Pichi Traful, on route j, Feb. 17, 1967 (S. Coscarón; AMNH), one female, reared, pupae and larvae; tributary of Río Limay, 30 km. N of Confluencia, on Route 40, Oct. 24, 1970 (S. Coscarón; AMNH), pupae and larvae; Río Limay, 30 km. N of Confluencia, Oct. 24, 1970 (S. Coscarón; AMNH), one female, reared, pupae and larvae; Arroyo Limay Chico, 5 km. S of Estancia Chacabuco, 600 m., Oct. 24, 1970 (S. Coscarón; AMNH), three males, reared, pupae and larvae; stream 40 km.

Dalcahue, Feb. 7, 1967 (S. Coscarón; AMNH), one pupa and larvae; Castro, stream close to town, Feb. 6, 1967 (S. Coscarón; AMNH), four females, three males, all reared; small stream 12 km. N of Castro, Feb. 6, 1967 (S. Coscarón; AMNH), pupae and larvae. Llanquihue: Río Pescado, 10 km. SW of Ensenada, Feb. 8, 1967 (S. Coscarón; AMNH), one pupa. Osorno: Río Gol-Gol, March 13-19, 1955 (L. Peña: CNC), one female; ibid., Feb. 8-11, 1967 (L. Peña; CNC), one female; Lago Puvehue, stream crossing road to Termas Puyehue, Feb. 4, 1967 (S. Coscarón; AMNH), four females, one male, all reared: Termas Puvehue, Feb. 4, 1967 (S. Coscarón; AMNH), three females, reared; Puyehue Park, Feb. 4, 1967 (S. Coscarón; AMNH), one pupa and larvae; 30 km. E of Puyehue, Jan. 25, 1951 (E. Ross and A. E. Michelbacher; CAS), two females. Valdivia: Cudicó, 40 m., Nov. 10-11, 1966 (M. E. Irwin and E. I. Schlinger; CIS), six males; Corral, Arroyo La Marina, Feb. 3, 1967 (S. Coscarón; AMNH), one female, reared, one pupa. Cautin: Lago Villarrica, stream crossing road between Pucon and Villarrica, Feb. 2, 1967 (S. Coscarón, AMNH), pupae and larvae; stream 2 km. E of Pucon, Feb. 1, 1967 (S. Coscarón; AMNH), pupae and larvae; Termas de Palguin, Feb. 2, 1967 (S. Coscarón; AMNH), pupae and larvae; Fork of Río Minetué, 2 km. N of Termas de Palguin, Feb. 2, 1967 (S. Coscarón; AMNH), pupae and larvae. Malleco: Curacautín, Río Blanco, 1100 m., Feb. 1964 (L. Peña; CNC), two females. Bio-Bio: Río Bio-Bio, near Marimenuco, Dec. 11, 1963 (G. F. Edmunds; CNC), three females, one pupa, larvae. Nuble: 40 km. E of San Carlos, Dec. 23-24, 1950 (E. Ross and A. E. Michelbacher; CAS), one female, one male. Linares: Las Cruces, Oct. 1958 (L. Peña; CNC), one female; Río Ancoa, Oct. 12, 1951 (O. Barros; AMNH), three males. Talca: Cajon del Río Claro, on Los Quenes road, 1000-1200 m., Oct. 9, 1966 (E. I. Schlinger), three females, seven males; El Radal, 1100 m., Nov. 27, 1957 (L. Peña; CAS), one female. Curicó: El Coigal, Jan. 20–24, 1964 (L. Peña; CNC), one female; Estero La Jaula, Jan. 1964 (L. Peña; CNC), 24 females, one male. O'Higgins: Near Río Pangal, Oct. 9, 1967 (S. Coscarón; AMNH) pupae and larvae; La Leonera, Oct. 5, 1967 (S. Coscarón; AMNH), larvae. Santiago; Canello, Nov. 13, 1957 (G. Kuschel; AMNH), one

1961 (T. Cekalovič; CNC), one pupa. Chiloë:



FIG. 16. *Cnesia dissimilis*, larva. A. Head capsule, seen from below. B. Gular cleft, as seen on slide mount. C. Lateral sclerite of proleg. D, E. Antennae, pigment not shown in E. F. Teeth of ray of mouth brush. G. Apex of mandible. H. Hypostomium. I. Apex of different mandible. J. Teeth of anterior margin of hypostomium. K. Posterior portion of head, with cervical sclerites. L. Rays of short basal setae of mandible. M. Anal sclerite. N. Gill histoblast. O. Labral sclerite.

S of San Martín de Los Andes, Feb. 17, 1967 (S. Coscarón; AMNH), pupae and larvae; Lago Falkner, stream flowing into lake at route j, Jan. 19, 1968 (S. Coscarón; MLP), pupae and larvae; Río Pucará, Lanin National Park, Feb. 20, 1967 (S. Coscarón; AMNH), pupae and larvae; Río Pucará, Pucará, Lanin National Park, in stream on Chusquea culeou Desvaux and on wire, Oct. 20, 1970 (S. Coscarón; AMNH), pupae and larvae; Pucará, Lanin National Park, stream W of tree nursery, Oct. 22, 1970 (S. Coscarón; AMNH), larvae; Río Chachil, Lanin National Park, Jan. 16, 1968 (S. Coscarón; MLP), one pupa; Río Quilquihué, Oct. 20, 1970 (S. Coscarón; AMNH), pupae and larvae; Arroyo Pil-Pil, 1100 m., Oct. 22, 1970 (S. Coscarón; AMNH), larvae; Chapelco Chico, Oct. 20, 1970 (S. Coscarón; AMNH), pupae and larvae.

DISTRIBUTION: This is one of the most wideranging species of the South American Prosimuliini. It extends through all the Valdivian and Magellanic area of southern Chile and penetrates into the Mediterranean climate area of central Chile north to the province of Valparaiso; it is also very common east of the Andes in Argentina, at least from Chubut to southern Neuquen.

BIOLOGY: The aquatic stages of this species are restricted to clear, large streams and rivers with considerable current; they are never found in trickles, small streams, irrigation ditches or any slow-flowing watercourse. The preferred water temperature varies from 10° to 12°C. Larvae are generally found attached to branches, stems, and roots of terrestrial plants trailing in the streams; the plant involved is frequently a bamboo, *Chusquea culeou* Desvaux. Pupae are found where larvae occur, but occasionally also on the under surface of large stones or rocks resting on the river bottom. Larvae and pupae generally occur in large aggregations, with cocoons often forming irregularly multilayered masses, as in certain *Prosimulium* in the Northern Hemisphere.

Cnesia dissimilis is a spring species, with abundant larvae and pupae found as early as October; in January, larvae become very rare, and most pupae encountered are empty.

Dissection of freshly hatched females shows the species to be anautogenous. The feeding habits are unknown, but to judge from the structure of the claws of the female with their large basal process, *Cnesia dissimilis* is probably ornithophilous.

Edwards (1931) described gynandromorphic females (=intersexes) occurring together with normal specimens of gynandrum; Vargas and Días Nájera (1951) studied the genitalia of some of these specimens; we have seen no intersexes of *Cnesia*.

DISCUSSION: Although this widespread species is surprisingly uniform, some variation was observed. The wing length fluctuates between 3.2 and 4.3 mm.; most specimens have wings close to 4 mm. Females with wing length close to 3 mm. were observed occasionally in Chilean material; none of the Argentinian females examined had wings shorter than 3.5 mm.

These variations are paralleled by variations in the measurements of pupae and larvae. The cephalopterothecal length of Argentinian pupae remains very close to 2.5 mm., but fluctuates in a Chilean population from Cautín between 2.25 and 2.50. Likewise, the head width of last instar larvae of Argentinian material varies from 0.70 to 0.75 mm., with 0.75 mm. being the most frequent, but in the Chilean population mentioned it extends from 0.65 to 0.75 mm., with most specimens ranging between 0.65 and 0.70.

Some variation was also observed in the color of the thorax of the adults. In males, the scutum varies from dark brown to black. The scutum of the females, normally dull orange brown, may become dark brown in some specimens, especially at the center of the disc, but it is never black.

We have synonymized Simulium (Cnephia) gynandrum with Cnesia dissimilis, which has page precedence, because of the following reasoning:

Edwards (1931) described gynandrum as having a wing length of 3 mm., as opposed to an average wing length close to 4 mm., for dissimilis (our observations). The holotype of gynandrum (Crosskey in litt.) has wings at least 4 mm. long, and two paratypes examined by us have a wing length of 3.8 mm.; thus a possible differential character is eliminated. The thorax of the female of gynandrum (the only sex known) was described by Edwards (loc. cit.) as "very largely blackish" and as "dull brownish orange" in dissimilis. However, Crosskey (in litt.) describes the color of the scutum of the holotype of gynandrum as "orange-reddish around the edges but darkened to dark reddish-brown over much of the surface." The same coloring is found in two paratypes of gynandrum examined by us, and also in dark specimens of dissimilis reared from the same batch of pupae as light-colored females. In some of our specimens the degree of darkening depends on the angle of incidence of the source of illumination used. We conclude that the color differences mentioned are individual variations, due to state of preservation and possibly to food ingestion, and cannot be used to differentiate species.

As to possible morphological differences between the two supposed species, Vargas and Díaz Nájera (1951) described and illustrated the female genitalia of specimens identified as dissimile and gynandrum. According to these authors, the main differential characters are said to be in the shape of the genital fork. The arms of the genital fork are described to be as wide apically as basally in dissimile, but of uniform width in gynandrum. Furthermore, the apices of the arms of gynandrum are supposed to be turned farther outward than in dissimilis, and the apodemes of the arms are said to be shorter in gynandrum than in the other species. We illustrate the genital forks of the specimen of gynandrum examined by Vargas and Díaz Nájera (their fig. 62, our fig. 13K) and of one of the paratypes of gynandrum examined by us (fig. 13L) and of two specimens with bright orange scutum clearly identical with dissimilis (fig. 13M). A perusal of these drawings shows the basic similarity of the structure of all these genital forks.

Cnesia pusilla, new species

Figure 17A-D, G-K

DIAGNOSIS: This species differs from the related *dissimilis* mainly by the black scutum of the female, and by its smaller size.



FIG. 17. A-D. Cnesia pusilla. A. Basitarsus and second tarsal segment of hind leg, female. B. Idem, male. C. Frontoclypeus, pupa. D. Cercus and paraproct. E, F. Cnesia dissimilis. E. Area of insertion of spermathecal duct on spermatheca. F. Spermatheca. G-K. Cnesia pusilla. G. Area of insertion of spermathecal duct on spermatheca. H. Spermatheca. I. Genital fork. J. Antenna of larva. K. Dorsal portion of thorax of pupa.

DESCRIPTION: This species is so close to *Cnesia* dissimilis that an enumeration of the differential characters will be sufficient to define it.

Female. Length of wing, 2.9 mm. Overall color of head and its appendanges black; scapus and pedicellus brownish; pilosity silver or brasscolored. Thorax with lateral portion brownish, with grayish pruinescence; pleural membrane gray. Scutum matte black; shoulders tinged with yellow; decumbent pilosity as on head. Scutellum yellowish; metanotum piceous. Wings and legs colored as in *dissimilis*. Abdomen silver gray; hairs of basal fringe as on head and thorax.

Frontal angle narrow, 50 degrees; mouthparts as in *dissimilis*. Structure of wings and legs as in *dissimilis*; hind basitarsus (fig. 17A) seven times as long as wide. Eighth sternum and gonapophyses as in *dissimilis*. Paraprocts and cerci (fig. 17D) much as in *dissimilis*. Genital fork as shown in figure 17I; terminal plates with conspicuous areas of pigment difference. Spermatheca (fig. 17G, H) with membranous area at insertion of duct comparatively small as compared with that of *dissimilis* (fig. 17E, F).

Male. Length of wing, 3.0 mm. Overall color of head and its appendages as in female. Lateral portion of thorax colored as in female. Scutum velvet black; shoulders silver gray. Scutellum, metanotum, wings, and legs as in female. Abdomen gray; tergal plates velvet black. Basal fringe silver gray.

Structure of head with appendages as in *dissimilis*. Wings and legs much as in *dissimilis*; hind basitarsus (fig. 17B) 3.2 times as long as wide. Genitalia as in *dissimilis*.

Pupa. Cephalopterothecal length 1.8–2.1 mm., in most specimens between 1.9 and 2.0 mm. Structure and onchotaxy as in *dissimilis*; frontoclypeus (fig. 17C) and chaetotaxy of thorax (fig. 17K) as illustrated.

Larva. General structure as in *dissimilis*, but specimens smaller; head width only 0.65–0.70 mm.; antennae as shown in figure 17].

ETYMOLOGY: The specific name is from the Latin *pusillus*, very small.

MATERIAL EXAMINED: Argentina: Río Negro: Bariloche, Río del Medio, 3 km. W of Bariloche airport, Oct. 24, 1970 (S. Coscarón; MLP), one female, reared, holotype; *ibid*. (S. Coscarón; AMNH), one male, allotype, one female, one male, paratypes, all reared, pupae and larvae. Neuquen: Arroyo Mulahuanca, 15 km. N of Confluencia, at Route 40, Oct. 24, 1967 (S. Coscarón; AMNH), pupae and larvae.

BIOLOGY: The larvae of this species were found in large numbers on the surface of rocks, but no pupae could at first be located. They were finally discovered on the under surface of large rocks resting on the stream bottom, a situation in which *dissimilis* is found only rarely.

DISCUSSION: Cnesia pusilla seems to be very close to C. dissimilis, and may not always be easy

to recognize; it differs from *dissimilis* mainly in being smaller in size in all stages, the black scutum of the female, and morphologically by the comparatively small membranous area at the insertion of the spermathecal duct on the spermatheca. *Cnesia pusilla* can be distinguished from *C. ornata*, described below, by its smaller overall size, the presence of small hairs on the metanotum of the adults, the black scutum of the male, and the absence of platelets in the pupa.

Cnesia ornata, new species

Figures 18-20

DIAGNOSIS: Differs from the other two species of the genus mainly in the bright reddish brown scutum of the male, the absence of setae on the metanotum, and the presence of platelets and capitate trichomes on the head and thorax of the pupa.

DESCRIPTION: Pharate female. Color unknown. Characters of head, eyes, antennae, mouthparts, and legs with claws as in *dissimilis*, as far as discernible. Thorax and abdomen not examined.

Male. Length of wing, 4 mm.

Head and its appendages light brown. Antenna shortly pubescent; scapus and pedicellus with long golden hairs, these also present between eyes, on clypeus and on basal segments of maxillary palp.

Scutum bright reddish brown with golden decumbent hairs. Scutellum pale yellow brown with long golden hairs. Metanotum light reddish brown, with golden pruinescence. Pleura light brown; katepisternum slightly darker. Wings with veins pale and hairs golden brown, including basal tuft. Stem of halteres whitish, capitulum pale brown. Legs light yellowish brown, their hairs from golden to brown; coxae, bases and apices of femora and tibiae, and all tarsi, darkened. Pigment pattern of hind legs as shown in figure 18A. Abdomen grayish brown, except posterior border of terga and pleural regions, which are grayish. Hairs of abdomen, including those of basal fringe, brass-colored.

Shape and proportions of antennal segments as shown in figure 18B. Last segment of maxillary palp less than twice as long as penultimate; sensory vesicle slightly smaller than one-third of diameter of third segment; structure of sensory vesicle much as in *dissimilis*. Shape and proportions of hind leg segments as shown in figure



FIG. 18. Cnesia ornata, male. A. Hind leg; setae not shown. B. Antenna. C. Apex of basitarsus and second tarsal segment of hind leg. D. Denticles of endoparameral organ. E. Ventral plate. F. Median sclerite. G. Ventral plate, different view. H. Median sclerite, different aspect. I. Ventral plate, side view. J. Median sclerite, seen from side and somewhat from above.

18A; hind basitarsus 3.8 times as long as wide. Genitalia (fig. 18E-J) much as in *dissimilis*.

Pupa. Cocoon light brown, covering pupa almost completely, exposing only respiratory organs and part of dorsal surface of thorax. Cocoon with filaments of varying diameter, easily perceptible; cocoon often covered with foreign organic matter. Length of cocoon dorsally along middle, 3.5 mm.; length along base, 4.5 mm.

Length of body of pupa, 3.5–4.0 mm.; cephalopterothecal length 2.4–2.5 mm. Maximum length of respiratory organ, 1.5 mm., viz., approximately one-third of length of pupa proper. Head and thorax of pupa light brown.

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FIG. 19. Cnesia ornata, integument of pupa. A. Platelets of thorax. B, C. Platelets of abdominal terga.

Gills (fig. 20F) very similar to those of *dissimilis*. Number of filaments about 35, arising from about 12 primary branches inserted on very short common trunk; some of primary branches divided twice, thus giving origin to three filaments. Surface of filaments minutely granulose; their apex rounded. Chaetotaxy of head much as in *dissimilis*, but prefrontal and

frontal trichomes capitate (fig. 20C). Frontoclypeus with platelets arranged as in figure 20C. Chaetotaxy of thorax as in *dissimilis*, but strong trichomes capitate (fig. 20G). Exposed dorsal surface of thorax with numerous smooth platelets arranged in circles (figs. 19A, 20G). Abdomen with general onchotaxy as in *dissimilis*. Stout setae of tergum II blunt apically (fig. 20D). Platelets or tubercles of terga (figs. 19B, 20D) more numerous than in *dissimilis*. Setae of apex of abdomen as shown in figure 20H.

ETYMOLOGY: The specific name is from the Latin ornatus, decorated.

MATERIAL EXAMINED: Argentina: Río Negro: Bariloche, small stream flowing into Lake Trebol, Nov. 23, 1950 (P. Wygodzinsky; AMNH), one male, holotype, two males, paratypes, all reared, one pharate female; Puerto Blest, near Los Cantaros Falls, Jan. 11, 1962 (S. Coscarón; MLP), pupae.

Several cocoons contained anal portions of larval skins, which could not be distinguished from those of *dissimilis*. One live larva found with the pupae at Los Cantaros Falls had no pupal elements developed, and can therefore not be assigned with certainty to *ornata*. A few of its structures are illustrated herein (fig. 20A, B, E, I-M), but we have found no elements to distinguish this larva from those of *dissimilis*.

Cnesia sp.

Figure 14B, D

MATERIAL EXAMINED: Chile: Linares: El Radal, 1100 m., Nov. 23-30, 1957 (L. Peña; CNC), 10 males.

DISCUSSION: The above males all have a velvety black scutum, and their wing length varies from 2.7 to 3.5 mm.; they could belong either to *C. dissimilis* or to *C. pusilla* or represent both species.

GIGANTODAX ENDERLEIN

Gigantodax Enderlein, 1925, p. 205.

DESCRIPTION: Adult. Antennae with 11 segments. Male holoptic, rarely dichoptic. Apical article of maxillary palp from less than twice to about twice as long as penultimate. Mesepisternal sulcus shallow, evanescent anteriorly. Katepisternum glabrous, in profile very slightly longer than high. Pleural membrane glabrous.


FIG. 20. Cnesia ornata. A, B. Antennae of larva; pigment not shown in B. C. Frontoclypeus of pupa. D. Detail of cuticular structure at limit between terga II and III of pupal abdomen. E. Larva, side view. F. Gill. G. Detail of dorsal surface of thorax of pupa. H. Detail of apex of abdomen of pupa, sublateral aspect. I–M. Larva. I. Apex of mandible. J. Larva, dorsal. K. Anterior portion of hypostomium. L. Labral sclerite. M. Under surface of head, as seen in slide mount.

Metanotum glabrous. Arms of furcasternum without projections. Wings with basal cell not developed. R_1 with, rarely without, spinelike setae. Sc with hairs in one row, basal portion of

R with hairs arranged in several irregular series. R_s entirely hairy below, setose above on apical portion. R_s not forked apically. M not appearing double. Cu₂ and A₁ straight; A₂ attaining

wing margin. Calcipala well developed, unusually wide, bluntly rounded apically. Claws of female with large basal tooth of varied shape. Spermatheca fully sclerotized, its internal surface with spicules; spermathecal duct inserted in very small circular membranous area hardly larger than diameter of duct. Gonapophyses with microtrichia and a few small setae. Genital fork distinctly pigmented; stem narrow, longer than arms, the latter with 1+1 forwardly directed well-developed apodemes. Male with distimere from slightly to considerably shorter than basimere, conical, with two or three apical spines. Ventral plate subpentagonal or rhomboid in shape, indented or emarginate apically; basal arms long, connected by wide membrane. Median sclerite of complex and somewhat varied structure, not unlike that of Cnesia. Endoparameres with basal portion not discernible or small; apical portion composed of a group of one or two large, conspicuous, and several oppositely directed medium-sized denticles.

Pupa. Cocoon generally large, covering most



FIG. 21. Gigantodax. A. G. rufescens, wing venation. B. G. fulvescens, genital fork. C. G. rufescens, ventral plate and endoparameral organ. D. G. igniculum, labral sclerite of larva. E. G. fulvescens, apical portion of mandible. F. G. rufescens, anal sclerite of larva.

of body of pupa, only rarely reduced; cocoon generally shapeless, but in some species of definite shape. Body of pupa well sclerotized throughout. Head and thorax with or without platelets. Gills of extremely varied structure, from filamentous to arborescent, tubular or globular. Number of branches or filaments extremely varied, from four to more than 100. Head sclerite without frontal, but with 1+1facial and often with 1+1 labral trichomes. Disc of thorax with from 5+5 to 8+8 trichomes, some of which spinelike. Abdomen pointed posteriorly. Distinct pleural areas not developed. Onchotaxy: Terga III and IV with 4+4 short, simple hooks posteriorly; terga VI-IX with continuous spine-combs anteriorly. Sternum V with 2+2 or 3+3 hooks posteriorly; sternal plates VI and VII with at least 1+1hooks each, hooks also in pleural membrane of segments VI and VII. Terminal spines well developed. Posterior segments with specialized setae, variously bent and curved, rarely grapnelshaped.

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Larva. Head spots positive. Cephalic apotome widest well before hind margin. Cervical sclerites variously developed, generally transverse and connected to upper ends of postocciput. Postgenal cleft not perceptible. Antennae with ratios of segments varied; third segment darker than preceding. Rays of cephalic fan normal. Mandibles with three external (one long and two short) and one apical tooth; first and second preapical teeth very small, second shorter than first; third preapical tooth large, spinelike, as long as but distinctly stouter than inner teeth, the latter apparently arranged in a single row; one or two large mandibular serrations followed by a varied number of often very irregular minute ones. Short basal setae of mandibles stout, very faintly dentate. Hypostomium with 17 teeth arranged in three conspicuous groups, with median tooth and corner teeth by far the largest; arrangement of the 4+4 lateral teeth varied. Lateral sclerites of proleg comparatively narrow and elongate, setae much shorter than sclerite, arranged in one or two irregular rows, inserted individually on barely perceptible tubercles. Larval cuticle bare except generally very well-developed perianal scales. Anal sclerite X-shaped, with posterior arms prolongated to form complete ring around body. 1+1 backwardly directed struts underlying main body of sclerite.

TYPE-SPECIES: Gigantodax bolivianum Enderlein.

DISTRIBUTION: Cool and cold temperate western South America; highlands of Meso-america.

DISCUSSION: Gigantodax can be distinguished from all other Prosimuliini by the combination of the straight Cu_2 and A_1 , the structure of the larval mandibles, the complete ring formed by the posterior arms of the anal sclerite, and the backwardly directed struts underlying the Xshaped portion. The most important diagnostic characters of the genus are illustrated in figure 21. As mentioned in the discussion of *Cnesia*, we believe that *Gigantodax* and *Cnesia* are more closely related to each other than to any other black fly genus.

A list of the species named until now can be found in Vulcano (1967). We have before us a considerable number of additional species, which we plan to describe in another paper. The morphological analysis of these species and those already known will lead to a better definition of the genus, and possibly to its subdivision.

ARAUCNEPHIA, NEW GENUS

DIAGNOSIS: The most important differential characters of this genus are shown in the keys.

DESCRIPTION: Adult. Antennae with 11 segments. Male holoptic. Female with frons comparatively wide; frontal angle, 85 to 100 degrees. Mandibles denticulate on both margins. Apical segment of maxillary palp of both sexes less than twice as long as penultimate. Mesepisternal sulcus shallow, evanescent anteriorly. Katepisternum glabrous, in profile higher than wide. Pleural membrane glabrous. Metanotum glabrous. Arms of furcasternum without projections. Wings with basal cell present. R_1 with spinelike setae, more delicate than those of C. Sc setose. Basal section of R with hairs arranged in several irregular rows. Rs entirely hairy below, hairy above only on apical half. Rs generally simple, very rarely faintly forked apically. M appearing duplicated for most of its length. Cu₂ conspicuously curved in both sexes. A2 ending well before wing margin. Calcipala present although comparatively small, bluntly rounded. Claws of female with medium-sized pointed subtriangular tooth. Male with sclerotized areas of abdominal terga increasing in size toward posterior segments; sclerotized areas of abdominal sterna

small, transverse. Spermatheca of normal size, well sclerotized, with circular membranous area at insertion of spermathecal duct, the latter not sclerotized at base. Surface of spermatheca not sculptured; internal surface smooth, with scattered spicules. Gonapophyses short, subtriangular, apex rounded, their median borders narrowly pigmented, approximated; surface of gonapophyses with microtrichia and a few setae. Genital fork without forwardly directed apodemes; arms narrow. Male with distimere slightly shorter than basimere, broadly conical, with two apical spines; median surface of distimere smooth, glabrous, limited by two carinae. Ventral plate transverse, subtriangular, its basal arms in shape of elongate parallel-sided sclerotized rods. Median sclerite in shape of complex geniculate plate; basal half entire, fitting into concavity of ventral plate, distal half arising at sharp angle with basal half, divided into two straight parallel arms narrowed toward their apex. Endoparameral organ with large platelike basal portion connected to numerous denticles forming apical portion.

Pupa. Cocoon large, shapeless, covering entire pupa except respiratory organs. Body of pupa well sclerotized throughout. Head and thorax with or without platelets. Gills arborescent, divided very close to base into primary and secondary branches; general structure of branches filamentous. Head sclerite with 1+1 frontal and facial, and 2+2 epicranial, labral and genal trichomes, all hairlike. Thorax with 6-8+6-8 simple hairlike trichomes. Abdomen pointed posteriorly. Distinct pleural areas not developed. Onchotaxy of abdomen as follows. Terga III and IV with 4+4 hooks posteriorly; terga VI-IX with continuous spine-combs anteriorly. Sternum V, or IV and V, with 2+2 hooks posteriorly; sternal plates VI and VII with 1+1hooks, l+1 hooks each also in pleural membranes of segments VI and VII. Terminal spines well developed, from stout to slightly sinuous. Posterior segments with several strong S-shaped or apically curved or looped setae, only very rarely branched.

Larva. Head spots positive. Cephalic apotome broadest well before hind margin. Cervical sclerites wide, fused with upper ends of postocciput. Postgenal cleft shallow but distinct, inverted U-shaped. Length of hypostomium approximately equal to length of postgenal bridge. Antennae much shorter than stem of



FIG. 22. Araucnephia montana, females, Quebrada de La Plata. A. Frons. B. Maxillary palp. C. Antenna. D. Third segment of maxillary palp, with outlines of sensory vesicle. E. Apical portion of mandible. F. Apex of basitarsus, second and base of third tarsal segment of hind leg. G. Wing. H. Sensory vesicle of maxillary palp. I. Portion of wing, showing part of C and R₁. J. Portion of wing, different specimen, showing portion of C, R₁, and R_s. K. Furcasternum. L. Portion of abdominal sternum VIII, with gonapophyses and spermatheca; microtrichia not shown. M. Cercus and paraproct. N. Claw. O. Genital fork.

cephalic fan; first segment of antennae very short, less than half as long as second; third segment distinctly darker than remainder. Cephalic fans with rays unusually stout and heavily sclerotized; teeth of most rays almost uniform in size. Mandibles with two outer teeth and one apical tooth; third preapical tooth larger than remaining teeth, but shorter than apical tooth; first and second preapical teeth subequal in size. Inner teeth arranged in several rows; one large mandibular serration followed by numerous (10–15) very unequal smaller ones. Short basal setae of mandibles very stout, with conspicuous barbules. Hypostomium with 15 teeth arranged in three conspicuous groups, with median tooth and corner teeth by far the largest; the 3+3 lateral teeth descending below level of remaining teeth. Lateral sclerites of proleg about as long as wide, subtriangular, narrow at base, strongly widened apically. Setae of lateral sclerites less than half as long as sclerite, inserted on distinct individual tubercles, arranged in an irregular double row, this row extending slightly beyond sclerite below. Larval cuticle bare, except for perianal scales. Anal sclerite normal, X-shaped. Ventral papillae absent.

TYPE-SPECIES: Simulium montanum Philippi. ETYMOLOGY: The Araucans, an Indian people of central Chile, and Cnephia, a genus of black flies.



FIG. 23. Araucnephia montana, male. A. Antenna. B. Maxillary palp. C. Sensory organ of third segment of maxillary palp. D. Foreleg. E. Hind leg. F. Detail of venation of wing, showing short bifurcation of R_s as observed in some specimens. G. Sensory vesicle of maxillary palp, different specimen, same scale as figure 22H. H. Sclerotization pattern of abdominal sterna; sternum VII at bottom. I. Mid leg. J. Apex of basitarsus, with second tarsal segment, hind leg. K. Genitalia, general aspect. L. Sclerotization pattern of abdominal terga; tergum II on top.

DISTRIBUTION: Mediterranean climate area of central Chile.

DISCUSSION: Araucnephia montana, the type of the genus, was already thought by Edwards (1931), who knew only the female, to be quite different from the remaining Chilean-Patagonian species of "Simulium (Cnephia)." While Edwards considered the other species as belonging to the "Stegopterna group," he stated that montana "is evidently closely related to the North American S. invenustum. . . . "

A comparison of *montana* with *Ectemnia invenusta* shows the differences between the two species to be so great as to exclude their belonging to the same genus; we mention only the absence of a calcipala in *invenusta*, the very different genitalia in both sexes, the stalked cocoon of the pupa in *Ectemnia*, and, in its larva, the minute teeth of the hypostomium and the apparent absence of an anal sclerite.

The structure of the hypostomium of the larva distinguishes Araucnephia also from certain of the other Prosimuliini with spines on their anterior wing veins, i.e., the boreal Cnephia and the South American Cnesia, Paraustrosimulium and Lutzsimulium. Araucnephia differs from all these genera also by other characters, the most important ones being mentioned in our generic keys.

We have compared *Araucnephia* with those other prosimuliine genus-group taxa with which

it shares the presence of spines at least on the costa and which have a similar hypostomium.

Araucnephia differs from both the holarctic Stegopterna and the palearctic Greniera by the large and complex median sclerite of the male genitalia, by the somewhat different structure of the gill of the pupa, and, in the larva, by the antennae that are much shorter than the stem of the cephalic fan. Araucnephia can be further distinguished from Stegopterna by the large basal tooth of the claw of the female, by the spermatheca, which is not sculptured but bears spicules on its inner surface, by the pupa with hairlike facial trichomes and often curved or loosely looped but only very rarely branched setae at the end of the abdomen, and by the very short first antennal segment of the larva. Greniera differs from Araucnephia also in the smaller number of antennal segments in the adult, the single spine on the distimere, and the small number of mandibular serrations in the larva.

Araucnephia differs from the Mexican Mayacnephia and Tlalocomyia again by the specialized median sclerite of the male genitalia and also by the presence of distinct endoparameral spines, by the spicules of the spermatheca, by the single pair of frontal trichomes, and by the rarity of branched setae at the end of the abdomen of the pupa; in the larva, the first segment of the antennae is not more than half as long as the second, as it is in Mayacnephia and Tlalocomyia.

There are only two South American genera with comparable hypostomial characters, *Gigantodax* and *Araucnephioides*. *Gigantodax* is easily distinguished from *Araucnephia* by the absence of a basal cell and its specialized wing venation, the quite different genitalia of both sexes, and the accessory sclerite forming a complete ring at the posterior end of the body of the larvae; the pupae are less easy to distinguish, but those of *Gigantodax* do not have the full complement of cephalic trichomes as described for *Araucnephia*. *Araucnephia* is possibly closest to *Araucnephioides*; this is discussed under the heading of the latter genus.

The last South American genus to be considered is *Cnesiamima*, known only from adults. These differ from *Araucnephia* in the absence of spinelike setae on R_1 and specialized genitalic features, such as the structure of the median sclerite in the male and that of the spermatheca in the female.

We have also compared Araucnephia with

Paracnephia. Araucnephia differs from the brincki and muspratti groups of the African genus by the presence of spinelike setae on R_1 , the very complex median sclerite and the two spines on the dististyle of the male, and by the third preapical tooth of the mandible of the larva, which is distinctly smaller than the apical tooth. Araucnephia shares with the single known species of the turneri group of Paracnephia the presence of spinelike setae on R_1 , but as the African species is so poorly known, no useful comparison can be made at this time.

We have personally examined material of two Australian species of "Cnephia," viz., strenua Mackerras and Mackerras, and tonnoiri (Drummond) and have carefully analyzed the available descriptions of the remaining species of Australian Prosimuliini. We have not discovered any data that would indicate that any of the Australian species could possibly be congeneric with Araucnephia.

Araucnephia montana (Philippi), new combination

Figures 22-32

Simulium montanum PHILIPPI, 1865, p. 633. Simulium (Cnephia) montanum: EDWARDS, 1931, p. 149.

Cnephia montanum: SMART, 1945, p. 498.

DESCRIPTION: Female. Length of wing, 3.3– 4.3 mm., generally close to 4 mm. (type, 3.9 mm.). Head black; occiput, frons, and clypeus gray pruinose; antennae, palpi, and labrum brownish black. Pilosity of antenna very short, that of palpi, clypeus, frons, and occiput somewhat longer, its color from silvery gray to black.

Thorax dull black, with silvery gray pollinosity; metapleura and wing base brownish. Hairs of thorax silvery gray. Wings hyaline; veins light brown, hairs and spines blackish; tufts at wing base from silvery to brownish yellow. Halteres light brown. Legs from light brown with darkened apices of femora, tibiae and tarsi, to entirely dark brown or black; most specimens with legs dark, concolorous. Hairs of legs from silvery gray to black. Exact proportions and relative intensity of pigmented areas of legs as in male (fig. 23D, E, I).

Abdomen from dark grayish brown to dull black; dorsal surface always darkest. Hairs of abdomen from silvery gray to black.

Frons as shown in figure 22A; frontal angle 85–90 degrees. Fronto-ocular triangle (fig. 22A)



FIG. 24. Araucnephia montana, male. A, B. Parameres, different views. C. Ventral plate, full view. D. Ventral plate, side view. E. Distimere, showing membranous inner surface. F. Ventral plate with median sclerite, side view. G. Paramere with ventral plate and median sclerite. H. Aedeagus, with endoparameral organ, apical free portion of median sclerite, and ventral plate. I, J. Median sclerite, different aspects. K. Endoparameral organ. L–N. Median sclerite, various views.

approximately as long as wide. Antennal segments as shown in figure 22C. Mandible with about 75 teeth (fig. 22E). Last segment of maxillary palp (fig. 22B) slightly less than twice as long as penultimate. Diameter of sensory vesicle smaller than half the diameter of third segment (fig. 22D); shape of sensory vesicle as shown in figure 22H. Maxillae with 30–35 teeth. Wings as in generic description and figure 22G. Spinelike setae of R_1 often distinctly more slender than those of C (fig. 22I, J). Calcipala subtriangular (fig. 22F). Hind basitarsus 6.1– 6.9 times as long as wide. Claws as in generic description and figure 22N. Eighth abdominal



FIG. 25. Araucnephia montana, pupa. A. Gill; dorsal branch at left. B. Frontoclypeus, female pupa. C. Pupa in cocoon, dorsal; drawn by Elvira Buono. D. Portion of surface structure of gill filament. E. Base of different gill; dorsal branch at left. F. Portion of head sclerite of pupa, with trichomes. G. Portion of thorax of pupa, with trichomes.

sternum as shown in figure 22L; pigmentation variable, from only central area darkened to entire sternum dark. Gonapophyses with abundant microtrichia and 10–14 short setae. Cerci and paraprocts as illustrated in figure 22M. Cerci much wider than high; paraprocts short, their free extremity somewhat truncate. Genital fork as in generic description and figure 22 O. Stem and apical portion of arms well pigmented. Spermatheca as in generic description and figure 22L.

Male. Length of wing, 3.5-3.6 mm.

Head black; clypeus dark gray pollinose; antennae, palpi, and proboscis brownish black. Antennae shortly pubescent; setae of basal segments longer than remaining. Occiput, line between eyes, clypeus and basal segments of maxillary palps with several long hairs.

Thorax velvet black. Pleura with silvery gray pollinosity. Scutum with decumbent hairs from light silvery to light brass-colored. Distal portion of scutum as well as scutellum and metanotum with black, erect setae. Color of wings, halteres and legs as in female. Abdomen blackish, dark dorsally, grayish laterally and below. Hairs of abdomen colored as on thorax.

Shape and proportion of antennal segments as shown in figure 23A. Distal segment of maxillary palp (fig. 23B) almost twice as long as penultimate; diameter of sensory vesicle smaller than half the diameter of third segment; structure of sensory vesicle as shown in figure 23C, G.

Chaetotaxy of wings as in female, but fewer setae on S_c . Spiniform setae of R_1 distinctly smaller than those of C. In some specimens, R_s shortly bifurcated apically (fig. 23F). Shape and proportion of leg segments as shown in figure 23D, E, I. Hind basitarsus 3.9–4.6 times as long as wide. Calcipala narrowly rounded apically (fig. 23J).

Genitalia as in generic description and figures 23K, 24. Ventral plate with arms and basal margin distinctly sclerotized, disc uniformly pigmented.

Pupa. Cocoon covering pupa completely or almost so (fig. 25C), in some cases also including part or all of gills. Cocoon closely woven, threads not perceptible under medium magnification; color light grayish brown. Length of cocoon along dorsum, 7-8.3 mm. Total length of pupa, 4-4.5 mm.; cephalopterothecal length, 3 mm. Gill about half as long as pupa, or slightly less, normally with 14 filaments, in some cases one or two more or fewer. Gill composed of six short primary branches arising from extremely short common trunk (fig. 25A, E. G). The first two of the three dorsal primary branches generally several times as long as wide, the third much shorter than others; all giving rise to two filaments. Two median branches giving origin to three filaments each, filaments arising at variable relative position. Ventral primary branch very short, with two filaments. Surface of filaments delicately pitted



FIG. 26. Araucnephia montana. Abdomen of pupa; dorsal surface to the left, ventral surface to the right; many setae and denticles shown separately with higher magnification.

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(fig. 25D). Head and thorax of pupa light brown. Trichomes of head as in generic description and figure 25B, F; epicranial, lateral and genal trichomes in pairs, the others single; all trichomes simple. Head sclerite lacking platelets, faint pattern elements as shown in figure 25B; platelets absent.

Thorax as in generic description and figures 25G, 30A, without platelets and with not more than eight trichomes on each side on disc. Abdominal segments distinctly sclerotized although somewhat less so than thorax, intensity

of sclerotization diminishing toward posterior segments. Onchotaxy and accessory hairs and setae of abdomen as in generic description and figure 26; platelets on abdomen absent or few in number (fig. 30C).

Larva: Maximum length, 11 mm.; maximum width of head capsule, 1.2 mm. General body shape as shown in figure 27B. Color of larva light grayish brown; head often very dark. Cephalic apotome (fig. 27F) yellowish brown, darker along middle, along hind border, and with one or two sublateral spots on each side.



FIG. 27. Araucnephia montana, larva. A–C. Specimen from Quebrada de La Plata. A. Portion of head, dorsal. B. Habitus, side view. C. Antenna. D. Antenna of specimen from Olmué. E–Q. Specimen from Quebrada de La Plata. E. Central portion of under surface of head, as seen in slide mount. F. Pattern of cephalic apotome. G, H. Detail of teeth of rays of mouth fan. I. Apex of ray of mouth fan. J. Apex of mandible. K. Lateral sclerite of proleg. L. Posterior region of head, dorsal, with cervical area. M. Anterior portion of hypostomium. N. Maxillary palp. O. Anal sclerites, with perianal scales shown in detail. P. Labral sclerite. Q. Some of short basal setae of mandible.

Antennae as in generic description and figure 27C. Ratio of length of segments I-III: 1/2.75-3.0/2.75-3.2. Cephalic fan with 23-26 rays; teeth of rays as shown in figure 27G, H. Mandibles as in generic description and figure 27J, with 13-20 inner teeth and 7-15 marginal

serrations irregularly decreasing in size. Short basal setae of mandible with strong denticles (fig. 27G). Maxillary palp as shown in figure 27N. Labral sclerite as shown in figure 27P. Hypostomium as shown in figure 27E, its anterior border strongly pigmented; teeth as in



FIG. 28. Araucnephia montana, intersex. A–I. Adult. A. Fronto-ocular triangle. B. Antenna. C. Maxillary palp. D. Sensory vesicle of maxillary palp. E. Frons. F. Foreleg. G. Hind leg. H. Apex of basitarsus, with second and base of third tarsal segment of hind leg. I. Portion of eighth abdominal sternum, with gonapophyses. J. Gill of pupa. K, L. Adult. K. Genital fork. L. Cercus and paraproct. M–O. Pupa. M. Pupa in cocoon, dorsal view. Elvira Buono del. N. Gill of other specimen. O. Frontoclypeus.

generic description and figure 27M. Lateral border of hypostomium with 3–8 distinct serrations. Hypostomial setae arranged in one, rarely in two irregular series, with 5–7 setae in each group. Disc of hypostomium with a few scattered short hairs. Postgenal cleft about half as long as postgenal bridge (fig. 27E). Lateral sclerites of proleg as in generic description and figure 27K. Anal sclerite as shown in figure 27Q. Perianal scales numerous, two to five-pronged. Crochet ring with 80–100 rows with 18–22 hooks each.

MATERIAL EXAMINED: Chile: Curicó: Cajon del Río Claro, SE of Los Quenes, 1000-1200 m., Oct. 9, 1966 (E. I. Schlinger; CIS), two females. Santiago: El Arbol, quebrada W of Aculeo, Oct. 11, 1969 (J. Rozen and L. Peña; AMNH), six females; Los Maitenes, 1100 m., Nov. 3, 1963 (G. F. Edmunds; CNC), two larvae; Cuesta La Dormida, Nothofagus forest, Nov. 1, 1966 (E. I. Schlinger; CIS), three females; Quebrada de la Plata, Hacienda La Rinconada, Maipu, 510 m., in very small temporary stream on rocks, Oct. 4 and 16, 1967 (S. Coscarón; AMNH), five intersexes, reared, pupae and larvae; ibid., flying or in Malaise trap, August to October (M. E. Irwin; CIS and AMNH), Aug. 29, one intersex; Sept. 10, one intersex; Sept. 19,

three females, one intersex; Sept. 21 and 22, 27 females, three males, six intersexes; Sept. 27, nine females, one male, three intersexes; Sept. 29, three females, one male; Sept. 30, 30 females, four males, two intersexes; Oct. 3, one female; Oct. 6, five females; Oct. 12, four females; Oct. 14, two females; Cerro El Roble, Dec. 28-31, 1963 (L. Peña; CNC), one female. Valparaiso: Base of Cuesta de Colliguay, Sept. 20, 1969 (J. Solervicens; MLP), one female; Colliguay, near La Retuca, Nov. 5, 1963 (G. F. Edmunds; CNC), two females; La Cumbre, F. C. Valparaiso, Oct. 22, 1961 (L. Peña; CNC), one female; Cuesta Pucalán, east side, Sept. 19, 1966 (E. I. Schlinger; CIS), two females; Olmué, foot of Cerro La Campana, near Limache, on rocks in small stream, Oct. 19, 1967 (S. Coscarón; AMNH), three females, reared, one pharate female, pupae and larvae; Catemu (Museo Nacional de Historia Natural, Santiago) one female, the type; Tiltil, Jan. 1, 1897 (Reiche; Museo Nacional de Historia Natural, Santiago). Aconcagua: Piscicultura, 1600 m., Nov. 11, 1963 (L. Peña; CNC), two females. Coquimbo: Illapel, Hacienda Illapel, El Calabazo, 1800 m., in small stream, Oct. 22, 1967 (S. Coscarón; AMNH), one pharate female,



FIG. 29. Araucnephia montana, specimens from Illapel. A-F. Female. A. Frons. B. Antenna. C. Apex of basitarsus, with second tarsal segment and base of third, hind leg. D. Fronto-ocular triangle. E. Sensory organ of maxillary palp. F. Claw. G-K. Male. G. Apex of basitarsus, with second and base of third tarsal segments, hind leg. H. Ventral plate, side view. I. Median sclerite. J, K. Ventral plate, different views.

pupae and larvae; Río Illapel, Caren, Hacienda Illapel, 800 m., Nov. 14, 1963 (G. F. Edmunds; CNC), five females, pupae and larvae.

DISTRIBUTION: This species, the only one of its genus, is limited to the Mediterranean climate area of central Chile.

BIOLOGY: We have collected the aquatic stages of *Araucnephia montana* on the surface of stones and rocks exclusively in small, clear, temporary streams, toward the end of the wet season. This is apparently a species that completes its cycle in late winter or very early spring (September or very early October).

A large percentage of larvae and pupae, which the second author collected at the Quebrada de La Plata and Edmunds in the Río Illapel, were parasitized by mermithid worms. Probably related to this high degree of parasitism is the large number of intersexes we have found in adults of this species; that these intersexes are capable of flight is demonstrated by their capture in Malaise traps.

The intersexes resemble females in their dull black scutum and general aspect, but can easily be distinguished from that sex by the possession of claws of the male type. Mandibles, antennae (fig. 28B) and palps (fig. 28C, D) are as in females. The frons is in some specimens as in the female, but narrower (frontal angle, 65 degrees) in others (fig. 28E); the fronto-ocular triangle is strongly reduced in all specimens (fig. 28A). The color pattern of the legs is as in the female, but the length/width ratio of the hind basitarsus (5.3-5.4) is intermediate between that of male and female. The spermatheca and external genitalia (figs. 28I, L) are as in the female, but the genital fork (fig. 28K) has a shorter stem, and the apical portion of the arms is wider than in normal females. We have found some specimens which in addition to more or less distinct

A

B

C

FIG. 30. Araucnephia montana, details of integument of pupae. A. Specimen from Quebrada de La Plata, portion of thorax. B. Specimen from Illapel, portion of thorax. C. Specimen from Quebrada de La Plata, portion of abdominal tergum II. D. Specimen from Illapel, portion of abdominal tergum II.

female genitalia also showed a slightly reduced ventral plate, as found in males.

Pupae that give rise to intersexes are in at least some observed cases different from normal pupae in that the filaments of their gills (fig. 28J, N) are shorter, stouter, and darker than in normal specimens, giving the pupae quite a distinctive aspect (fig. 28M).

DISCUSSION: We have examined a female specimen from the collections of the Museo de Historia Natural, Santiago, which we accept as the type of this species. It bears a red "typus" label, and an obviously old handwritten label "Simul. montanum Ph." "Catemu dept." The species was described by Philippi from Catemu [and Chacabuco]. This type agrees well with the specimens we are identifying as *montana*.

Our description applies to specimens collected in the Quebrada de La Plata; these are characterized by the complete or almost complete absence



FIG. 31. Araucnephia montana, specimens from Illapel. A-C. Pupa. A. Pupa in cocoon, side view. Elvira Buono del. B. Basal portion of gill. C. Entire gill, different specimen. D-I. Larva. D. Labral sclerite. E. Cephalic apotome, with pigment pattern. F. Central portion of under surface of head, as seen on slide mount. G. Maxillary palp; pigment not shown. H. Apical portion of mandible. I. Anterior portion of hypostomium.

of platelets on the thorax of the pupa. Among pupae collected at El Calabozo, Hacienda Illapel, and at Caren, Río Illapel, there were numerous specimens differing from those of the Quebrada de La Plata by the paler color of the gills and their greater length, but mainly by the presence of platelets on the thorax (fig. 30B). The number and distinctiveness of these platelets varied greatly. In many specimens, most of the dorsal surface of the thorax was covered by platelets, but in others the platelets tended to concentrate in the areas adjacent to the dorsal suture of the thoracic sclerites; in still others, platelets were very scarce or not clearly recognizable. The degree of development of thoracic platelets was found to be correlated with the degree of development of platelets on the abdomen (fig. 30D). The lot of specimens collected by Edmunds in the Río Illapel at 800 meters contains some pupae with and others without



FIG. 32. Araucnephia montana, from Olmué. A-E. Female. A. Frons. B. Cercus and paraproct. C. Frontoocular triangle. D. Antenna. E. Genital fork. F. Pattern of cephalic apotome of larva. G, H. Female. G. Hind leg; setae not shown. H. Portion of eighth abdominal sternum, with gonapophyses. I. Gill of pupa; dorsal branch at left. J, K. Larva. J. Anterior portion of hypostomium. K. Antenna; pigment not shown. L. Gill of different pupa; dorsal branch at left.

platelets. We have not been able to find characters of adults or of larvae correlated with the absence or presence of platelets on the thorax of the pupa. We illustrate features of the tuberculate pupae mentioned herein as well as those of larvae and adults securely associated with such pupae, in order to make future comparisons possible (figs. 29, 30B, D, 31).

The larvae collected at Olmué differ in all cases from those described above by certain meristic characters, such as the third antennal segment which is slightly but distinctly longer than the second (fig. 32K), the mandibles with fewer inner teeth (10-11), the smaller number of rows of the crochet ring (77-82) and the smaller number of hooks (13-14) in these rows. We have not found any character to distinguish the pupae and adults of this lot from those described above. Figure 32 illustrates various features of the Olmué specimens, in the hope that these illustrations may prove useful in the future.

Additional research based on a statistical analysis of more samples obtained throughout the range of the species or species complex is



FIG. 33. Araucnephioides schlingeri, female. A. Antenna. B. Frons. C. Fronto-ocular triangle. D. Sensory organ of maxillary palp. E. Maxillary palp. F. Wing. G. Apex of basitarsus with second and base of third tarsal segments of hind leg. H. Cibarium. I. Foreleg. J. Mid leg. K. Hind leg. L. Claw. M. Cercus and paraproct. N. Furcasternum. O. Genital fork. P. Genital area. Q. Spermatheca. R. Eighth abdominal sternum, with gonapophyses. S. Microstructure of inner surface of spermatheca.

needed to evaluate the status of the various populations we have discussed. At this time, we believe that we do not have evidence to segregate any unit from *montana* as understood here and name it.

ARAUCNEPHIOIDES, NEW GENUS

DIAGNOSIS: The keys show the most important differential characters of this genus.

DESCRIPTION: Adult. Antennae with 11 segments. Male holoptic. Female with frons medium wide; frontal angle 60-70 degrees. Mandibles of female denticulate on both margins. Apical segment of maxillary palp of both sexes less than twice as long as penultimate. Mesepisternal sulcus shallow, evanescent anteriorly; katepisternum glabrous, in profile higher than wide. Pleural membrane bare. Metanotum glabrous. Arms of furcasternum without projections. Wings with basal cell present. R_1 with spinelike setae, more delicate than those of C. Sc setose. Basal section of R with hairs arranged in several irregular rows. R_s entirely hairy below, hairy above only on apical half. R_s not forked apically. M appearing duplicated for most of its length. Cu₂ conspicuously curved in both sexes. A₂ ending well before wing margin. Calcipala small, narrowly subtriangular. Claws of female with medium-sized, pointed, and curved hooklike basal tooth.

Male with sclerotized areas of abdominal terga of subequal size on all segments; sclerotized areas of abdominal sterna subquadrate. Spermatheca globular, of normal size, well sclerotized, with circular membranous area at insertion of spermathecal duct, the latter not sclerotized at base. Surface of spermatheca not sculptured; internal surface irregularly rugose and with scattered spicules. Gonapophyses short, subtriangular, their apex rounded, their median borders pigmented, approximated; surface of gonapophyses with microtrichia and setae. Genital fork without forwardly directed apodemes; posterior arms wide. Male with distimere shorter than basimere, broadly conical, with two or three apical spines; medial surface of distimere smooth, glabrous, limited by two carinae. Ventral plate subquadrate, its anterior border truncate or slightly emarginate, its basal arms with terminal knobbed sclerotization. Median sclerite in shape of complex geniculate plate; basal half entire, transverse, fitting into

concavity of ventral plate; distal half arising at sharp angle with basal half, divided into two apically outwardly bent strong arms. Endoparameral organ with narrow platelike basal portion tapering into very narrow obsolescent apical portion; denticles weakly developed.

Pupa. Cocoon large but shapeless, covering entire pupa except gills. Head and thorax with numerous tubercles (in single species examined). Body of pupa well sclerotized throughout. Gills arborescent, consisting of several primary branches and not very numerous (approximately 10) narrow filaments arranged in two more or less distinct groups. Head sclerite without or with 1-2+1-2 very short frontal and with 1+1 hairlike well-developed facial trichomes. Thorax with 6-8+6-8 simple hairlike trichomes. Abdomen pointed posteriorly; its structure and onchotaxy as in *Araucnephia*.

Larva. Head spots positive, distinct. Cervical sclerites small, isolated in neck membrane. Postgenal cleft shallow but distinct, biarctate. Hypostomium shorter than length of postgenal bridge. Antennae almost as long as stem of cephalic fan. First antennal segment very short, less than half as long as second; third segment only very slightly darker than remaining. Cephalic fans with rays normal, slender, not heavily sclerotized; teeth of all rays distinctly of two sizes. Mandibles with two external teeth and one apical tooth; third preapical tooth larger than the two others, but shorter than apical tooth; second preapical tooth minute. Inner teeth arranged in several rows; one large basal mandibular serration followed by numerous smaller ones (10-15); accessory mandibular serrations situated on border of mandible at level of internal teeth. Short setae of mandible slender. only very faintly dentate or not at all. Hypostomium with 17 teeth arranged in three conspicuous groups, with median tooth and corner teeth by far the largest; the 4+4 lateral teeth descending below level of remaining teeth. Lateral sclerites of proleg as in Araucnephia. Larval cuticle bare, except for perianal scales. Anal sclerite normal, X-shaped. Ventral papillae absent.

TYPE-SPECIES: Araucnephioides schlingeri, new species.

ETYMOLOGY: Araucnephia, a genus of black flies described in this paper.

DISTRIBUTION: Mediterranean climate area of central Chile.



FIG. 34. Araucnephioides schlingeri, male. A. Antenna. B. Maxillary palp. C. Sensory vesicle of third segment of maxillary palp. D. Sclerotization pattern of abdominal terga; tergum II on top. E-G. Legs; setae not shown. E. Foreleg. F. Mid leg. G. Hind leg. H. Apex of basitarsus, with second and base of third tarsal segments of hind leg. I. Ventral plate, full view. J. Median sclerite. K. Paramere, side view. L. Ventral plate, side view. M. Ventral plate with median sclerite, side view. N. Distimere, showing smooth area. O. Ventral plate, with other genital structures visible through it. P. Paramere, full view. Q. Sclerotization pattern of abdominal sterna, distal sternum below. R. Ventral plate, with median sclerite and endoparameral organ at left. S. Spines at apex of distimere. T, U. Median sclerite, different views. V. Ventral plate, median sclerite and endoparameral organ. W. Endoparameral organ.

DISCUSSION: The discussion of the similarities and dissimilarities between *Araucnephia* and other genera of Prosimuliini can be applied, with a few unimportant exceptions, to *Araucnephioides*. An additional character to distinguish the present genus from the remainder is the presence of accessory mandibular serrations of the larva.

The closest relative of Araucnephioides may be Araucnephia. Both genera are sympatric, and individuals are often difficult to distinguish; we therefore present a detailed enumeration of differential characters to help to identify specimens.

Female: Basal tooth of claws subtriangular (fig. 22N); calcipala broadly rounded (fig. 22F); arms of genital fork comparatively narrow (fig. 22 O); inner surface of spermatheca not rugose. Male: Sclerotized areas of abdominal sterna small, transverse (fig. 23H); sclerotized areas of abdominal terga increasing in size toward posterior segments (fig. 23L); genitalia (figs. 1F; 23K; 24) with ventral plate subtriangular, its basal arms narrow, straight; arms of median sclerite parallel; endoparameral organ with basal portion well developed. platelike, and denticles of distal portion conspicuous. Pupa: Gills with 14-17 filaments (fig. 25A); head sclerite (fig. 25F) with full complement of trichomes; frontal, facial, epicranial, ocular, and genal. Larva: Antennae much shorter than stem of cephalic fan (fig. 27A); cervical sclerites transverse, fused with upper end of postocciput (fig. 27L); rays of cephalic fan very heavily sclerotized; mandibles



FIG. 35. Araucnephioides schlingeri. A. Arrangement of platelets on exposed portion of thorax. B. Arrangement of platelets on second abdominal tergum.

with first and second preapical teeth subequal (fig. 27J); no accessory mandibular serrations at level of inner teeth; short basal setae of mandibles very stout, with conspicuous barbules (fig. 27Q); length of hypostomium approximately equal to length of postgenal bridge (fig. 27E); postgenal cleft inverted U-shaped (fig. 27E) Araucnephia

Female: Basal tooth of claws narrowly hooklike (fig. 33L); calcipala subtriangular (fig. 33G); arms of genital fork comparatively wide (fig. 33 O); inner surface of spermatheca rugose (fig. 33S). Male: Sclerotized areas of abdominal sterna larger, subquadrate (fig. 34Q); sclerotized areas of abdominal terga not conspicuously decreasing in size posteriorly (fig. 34D); genitalia (figs. 1B; 34I-P, R-W) with ventral plate subrectangular, its basal arms stout, rounded at apex and recurved; arms of median sclerite sharply diverging apically; endoparameral organ with basal portion small and denticles of apical portion faint. Pupa: Gills (fig. 36B, E-H) with 10-13 filaments; head sclerite without or with poorly developed frontal trichomes (fig. 36C, D). Larva: Antenna almost as long as stem of cephalic fan (fig. 37C); cervical sclerites very small, isolated in neck membrane (fig. 37N); sclerotization of rays of cephalic fan normal; mandibles with second preapical tooth minute (fig. 37M, O, P); accessory mandibular serrations situated at level of inner teeth (fig. 37M, O, P); short basal setae of mandible comparatively long and slender, very faintly dentate, or glabrous (fig. 37H); hypostomium shorter than postgenal bridge (fig. 37E); postgenal cleft biarctate (fig. 37E) Araucnephioides

Araucnephioides schlingeri, new species Figures 1B, G; 33–37

DESCRIPTION: Female. Length of wing, 3.2– 4.0 mm., in most specimens more than 3.5 mm. Head blackish, eyes dark piceous. Occiput, frons and clypeus grayish brown pollinose; antennae and palpi dark brown, labrum light grayish brown. Pilosity of antennae very short, except on two basal segments, that of palpi, clypeus, frons, and occiput somewhat longer; hairs from brass-colored to black.

Scutum dull black, with gray pollinosity and decumbent hairs of same color as those of occiput. Pleura brownish, with silvery gray pollinosity; base of wings light brown. Scutellum piceous, hairs semi-erect, from light gray to dark brown. Metanotum and katepisternum brown to black, with silvery pollinosity. Color of wings and veins as in *Araucnephia montana*. Halteres piceous. Legs in most specimens dark



FIG. 36. Araucnephioides schlingeri, pupa. A. Pupa in cocoon, dorsal view. B. Gill; dorsal branch to right. A and B drawn by Elvira Buono. C. Frontoclypeus of female pupa. D. Frontoclypeus of male pupa; platelets not shown. E–H. Bases of gills; dorsal branches at right. I. Some of the setae at apex of abdomen. J. Detail of surface structure of base of gill filaments. K. Distribution of sclerotized platelike structures. L. Arrangement of platelets on thorax.

brown, with apices of femora, tibiae, and tarsi piceous; in some specimens legs lighter with dark apical regions of leg segments more conspicuous. Hairs from silver gray to blackish. Exact proportions and relative intensity of pigmented areas as shown in figure 33I-K. Color of abdomen as in *Araucnephia montana*.

Frons as shown in figure 33B; frontal angle 60-70 degrees. Fronto-ocular triangle (fig. 33C) slightly wider than high. Shape and proportions of antennal segments as shown in figure 33A. Mandible with 36-40 teeth. Last segment of maxillary palp (fig. 33E) distinctly less than twice as long as penultimate. Diameter of sensory vesicle (fig. 33D, E) less than half the diameter of third segment. Maxillae with about

30 teeth. Wings (fig. 33F) much as in *A. montana*. Shape and proportion of leg segments as shown in figure 33I-K. Calcipala as in generic description and figure 33G, about as long as wide at base. Claws as in generic description and figure 33L. Hind basitarsus 6.3-7.6 times as long as wide. Eighth abdominal sternum as shown in figure 33R. Gonapophyses each with 10-14 medium-sized hairs and with numerous microtrichia. Cerci, paraprocts, genital fork, and spermatheca as in generic description and figure 33M, O-Q.

Male. Length of wing, 2.9–3.3 mm. Color of head, body and appendages much as in *Arau-cnephia montana*.

Shape and proportion of antennal segments as



FIG. 37. Araucnephioides schlingeri, larva. A. Larva, dorsal. B. Idem, lateral. C. Scheme of head, dorsal. D. Antenna. E. Center of under surface of head, as seen from below. F. Color pattern of apotome. G. Teeth of center of rays of mouth fan. H. Some of short basal setae of mandible. I. Apical portion of ray of mouth fan. J. Anterior portion of hypostomium. K. Labral sclerite. L. Maxillary palp. M. Apical portion of mandible. N. Posterior portion of head capsule, with cervical region. O, P. Preapical teeth and mandibular serrations, mandibles of two different specimens. Q. Apex of abdomen with gills, dorsal view. R. Anal sclerite.

shown in figure 34A. Last segment of maxillary palp (fig. 34B) less than twice as long as penultimate. Diameter of sensory vesicle smaller than half the diameter of third segment; structure of vesicle as shown in figure 33C. Structure of wings as in female; R_s never bifurcate apically. Shape and proportion of leg segments as shown in figure 34E–G. Hind basitarsus 3.7–4.6 times as long as wide. Calcipala subtriangular (fig. 34H).

Genitalia as in generic description and figure 34I-P, R-W.

Pupa. Cocoon (fig. 36A) covering entire pupa, in some cases including gills and often also containing larval exuvia. Color of cocoon very light brown, loosely woven with body of pupa discernible; threads visible under medium magnification. Length of cocoon along dorsum, 4–6 mm. Total length of body of pupa 3.5–4.3 mm., cephalopterothecal length 2.05–2.1 mm. Gills (fig. 36A, B, E–H) about half as long as body of pupa, or slightly longer, with 10–12, rarely 13, filaments. Two primary branches arising from very short common trunk. Dorsal primary branch with a very short secondary branch immediately beyond base, divided into two branches; secondary branch in some cases arising directly from base, thus constituting third primary branch. Dorsal primary branch with four or five, rarely six, additional filaments. Ventral primary branch generally giving origin to four, rarely five filaments, two originating very close to base, the others slightly above. Surface of filaments delicately pitted, and with irregularly shaped and distributed minute platelike sclerotized structures basally (fig. 34I, K, L). Head and thorax of pupalight brown. Chaetotaxy of head and thorax as in generic description and figure 36C, D. Frontoclypeus with numerous platelets (fig. 36C). Thorax with numerous platelets, arranged in roughly circular groups (fig. 35A), composed of five to eight platelets each.

Abdomen somewhat lighter than thorax. Onchotaxy much as in *Araucnephia montana* (fig. 26), but spine-combs on tergum V often absent, and composed of fewer spines (about 15) on tergum VI. All terga with numerous platelets in addition to usual hairs and spines (fig. 35B). Specialized setae of eighth and ninth segments as shown in figure 36I.

Larva. Maximum length, 8 mm.; maximum width of head capsule, 0.75 mm. Body shape as shown in figure 37A, B. Color of larva light gravish brown. Cephalic apotome yellowish brown, darker along middle, and with several spots as shown in figure 37F. Antennae as in generic description and figure 37D; ratio of length of segments I-III, 1/2.2/2.9-3. Cephalic fan with 37-42 rays; teeth of rays as shown in figure 37G, I. Mandibles as in generic description and figure 37M, O, P, their color lighter than in A. montana; with 15-17 inner teeth and 10-15 marginal serrations, including the accessory ones. Labral sclerite and maxillary palp as shown in figure 37K, L. Hypostomium as shown in figure 37E; its anterior area strongly pigmented. Teeth as in generic description and figure 37J. Lateral border of hypostomium with 6-9 serrations. Hypostomial setae arranged on each side in one irregular row composed of about four setae. Disc of hypostomium with a few scattered, short setae. Postgenal cleft as in generic description and figure 37E, shorter than half the length of postgenal bridge. Anal sclerite and perianal scales as shown in figure 37R. Crochet ring with 60-67 rows composed of 18-20 hooks each.

ETYMOLOGY: This species is named for Dr. E. I. Schlinger, whose collections of Chilean black flies was of inestimable value to our work.

MATERIAL EXAMINED: Chile: Santiago: Quebrada de La Plata, Hacienda La Rinconada, Maipu, 510 m., on rocks in very small temporary stream, Oct. 4, 1967 (S. Coscarón; AMNH), one male, holotype, five males, paratypes, all reared, pupae and larvae; ibid., Oct. 16, 1967 (S. Coscarón; AMNH), one female, allotype, one female, paratype, all reared, pupae; ibid., 510 and 775 m., flying or in Malaise trap, August to October, 1966 (M. E. Irwin; CIS and AMNH), Aug. 22, one female; Aug. 24, two females; Aug. 31, one female; Sept. 2, two females; Sept. 10, one male, nine females; Sept. 12, one male, one female; Sept. 19, 13 females; Sept. 20, one female; Sept. 21 and 22, 71 females; Sept 23, two females; Sept. 27, 45 females; Sept. 29, nine females; Sept. 30, 60 females, two males; Oct. 4, one female; Oct. 6, 15 females; Oct. 10, two females; Oct. 12, 10 females; Oct. 14, six females; all specimens collected by Irwin are paratypes. Valparaiso: Olmué, near Limache, foot of Cerro La Campana, in small, slow-flowing stream on rocks, Oct. 19, 1967 (S. Coscarón; AMNH), two females, three males, paratypes, all reared, one additional female and three males.

The great preponderance of females in Irwin's material is more apparent than real, because we have endeavored to identify but a few of the many males caught, as their distinction from those of *Araucnephia montana* is extremely laborious.

DISTRIBUTION: Same as for genus.

CNESIAMIMA, NEW GENUS

DIAGNOSIS: Differs from other genera of the Prosimuliini by a combination of characters shown in the keys.

DESCRIPTION: Adult. Antennae with 11 segments. Male holoptic. Female with frons reltively wide; frontal angle about 75 degrees. Mandibles of female with well-developed denticles on both margins. Apical segment of maxillary palp of both sexes less than twice as long as penultimate segment. Mesepisternal sulcus shallow although deeper than in *Cnesia*, somewhat evanescent anteriorly. Katepisternum glabrous, in profile slightly wider than high. Pleural membrane bare. Metanotum glabrous. Arms of 1973

furcasternum without projections. Wings with basal cell distinct. Sc with numerous hairs arranged in a single row. Basal section of R with hairs arranged in several rows. R1 with hairs only, spiniform setae absent. Rs entirely hairy below, hairy above on its apical half. Rs not forked apically. M appearing thickened on most of its length. Cu₂ rather weakly curved in female, more strongly so in male. A_2 almost attaining wing margin. Calcipala present, large, bluntly rounded apically. Claws of female with large basal tooth. Spermatheca of normal size, about as large as gonapophyses; globular, its internal surface faintly wrinkled and with a few scattered spicules; whole spermatheca and base of spermathecal duct sclerotized; sclerotized portion gradually fading into unpigmented portion. Gonapophyses widely subtriangular, somewhat transverse, their medial borders slightly pigmented, approximated, their surface with microtrichia and a few setae. Genital fork distinctly pigmented, with stem slender, longer than arms, latter wide, lacking forwardly directed apodemes. Male with distimere slightly shorter than basimere. Basimere with semicircular membranous area opposite inner basal angle of distimere, the latter with corresponding bulge at base. Distimere only slightly narrowed toward apex, with two distal spines; medial surface of distimere smooth, limited by two carinae. Ventral plate subtriangular, about as long as wide, setose, with low median longitudinal keel. Median sclerite geniculate in side view, roughly M-shaped in full view, with the inner arms of the M partly fused and connected to basal flange. Endoparameres reduced to subquadrate plates connected to arm of ventral plate; denticles not developed.

Pupae and larvae not known.

Type-Species: Simulium (Cnephia) atroparvum Edwards.

ETYMOLOGY: From Cnesia, a genus of black flies, and the Latin mimus, an imitator.

DISTRIBUTION: Valdivian and Magellanic areas of southern Chile, and western Patagonia.

DISCUSSION: Our ignorance of the aquatic stages of *Cnesiamima* makes a meaningful investigation of its affinities difficult. The adults of *Cnesiamima* are superficially very similar to *Paraustrosimulium*, as already stated by Edwards (1931). This similarity extends to the general shape of the median sclerite of the male genitalia, but the structure of the endoparameres and of the female genitalia as found in the two genera is quite different, and does not support a hypothesis of close relationship. The following enumeration summarizes the significant differences between the adults of *Cnesiamima atroparva* and *Paraustrosimulium anthracinum*:

- Antennae with 10 segments (fig. 40C); mesepisternal sulcus deep; katepisternum much wider than high (fig. 40G); R_1 with hairs and slender spinelike setae; A_2 falling distinctly short of wing margin; female with spermatheca distinctly larger than gonapophyses, fully sclerotized but with small subcircular membranous area at insertion of spermathecal duct (fig. 40J); genital fork with stem wide, not longer than arms (fig. 40M); male genitalia with endoparameres consisting of basal platelike portion and well-developed apical portion composed of long parallel denticles (fig. 40N, R, S)...

In regard to the remaining South American Prosimuliini, the adults of *Cnesiamima* can be distinguished from the Chilean-Patagonian Cnesia, Araucnephia, and Araucnephioides by, among other characters, the absence of spinelike setae on R₁, the sclerotized neck of the spermatheca, and certain features of the male genitalia, such as the bulge at the base of the distimere, the absence of denticles on the endoparameres, and the M-shaped median sclerite. Cnesiamima can be further distinguished from Araucnephia and Araucnephioides by A_2 which almost attains the wing margin, and from the latter genus also by the larger basal tooth of the claws of the female. The differences between Cnesiamima and Gigantodax are obvious and need not be discussed. Cnesiamima differs from the remaining South American Prosimuliini, Lutzsimulium, by the absence of spiniform setae on R_1 , the large tooth of the claw of the female, and by the peculiarities of the male and female genitalia.

Cnesiamima differs from Mayacnephia by the absence of spiniform setae on R_1 , the katepisternum which is wider than high, the sclerotized neck of the spermatheca, and by the quite different structure of the median sclerite of the male. *Cnesiamima* shares with *Tlalocomyia* a spermatheca with sclerotized neck, although there are differences in detail, but the apical segment of the maxillary palp of *Tlalocomyia* is very long in both sexes, the pleural membrane is hairy on its upper portion, there are spiniform setae on R_1 , and the median sclerite of the male is quite different.

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Cnesiamima does not agree with any North American genus-group assemblage in the Prosimuliini, not only because of the peculiar features of the genitalia of both sexes, but also



FIG. 38. Cnesiamima atroparva, female. A. Antenna. B. Apex of mandible. C. Frons. D. Fronto-ocular triangle. E. Furcasternum. F. Maxillary palp, schematic, specimen from Curicó. G. Maxillary palp, specimen from Bahía Inutil. H, I. Sensory vesicles of maxillary palp; drawings not to scale. H. Specimen from Curicó. I. Specimen from Bahía Inutil. J. Wing. K. Mesepisternal sulcus. L–N. Legs; setae not shown. L. Foreleg. M. Mid leg. N. Hind leg. O. Apex of hind basitarsus, with second and base of third tarsal segment. P. Genital fork. Q. Portion of wing, with C and R₁. R. Spermatheca. S. Microstructure of inner surface of spermatheca. T. Cercus and paraproct. U. Claw. V. Portion of eighth abdominal sternum, with gonapophyses and outlines of spermatheca.

because there is no form that has spiniform setae on C but not on R_1 .

In the key offered by Crosskey (1969) for Ethiopian genus-group assemblages, Cnesiamima will key out to Paracnephia Rubzow, and would fit the definition for adults of the brincki and muspratti groups (vein R_1 with hairlike setae only). There are, however, many important characters, mainly in the genitalia of the male, separating Cnesiamima and Paracnephia, viz., two versus several spines on the apex of the distimere, specialized versus nonspecialized median sclerite, and absence versus presence of parameral hooks or denticles. Furthermore, the calcipala is very large in Cnesiamima (figs. 38 O, 39H) and quite small in Paracnephia (Crosskey, 1969, figs. 23-25). We believe that no close affinities exist between Cnesiamima and Paracnephia.

Mackerras and Mackerras (1948) stated that R_1 does not bear spiniform setae in Australian species of *Cnephia*, but these setae are quite evident in at least *C. tonnoiri* (Drummond), which we have examined. The calcipala in most Australian species is as large as in *Cnesiamima*, but the known males of Australian Prosimuliini have endoparameres with spines or denticles. At this time there is no evidence to assume close affinities between Australian Prosimuliini and *Cnesiamima*.

Cnesiamima atroparva, new combination

Figures 38, 39

Simulium (Cnephia) atroparvum Edwards, 1931, p. 148. Cnephia atroparvum: SMART, 1945, p. 498.

Cnesia atroparvum: VARGAS AND DÍAZ NÁJERA, 1951, p. 165.

Simulium atroparvum: VARGAS, 1945, p. 116.

Simulium (Astega) atroparvum: Rubzow, 1940, p. 532.

DESCRIPTION: Female. Length of wing, 3.1-3.5 mm.

Color of head and its appendages, black. Eyes, antennae, palpi, labium, and occiput dark grayish brown; frons and clypeus gray pollinose. Pilosity of antennae very short, that of palpi, clypeus, frons, and occiput somewhat longer; hairs from brass-colored to black. Scapus and pedicellus slightly lighter than flagellum, and with longer hairs. Scutum dark gray, with silvery to nacreous pruinosity; shoulders reddish. Adpressed setae of scutum brass-colored. Scutellum reddish brown, its hairs from brass-colored to dark brown. Metanotum black, silvery pollinose. Wings hyaline, veins medium brown; spines and hairs from dark brown to black; hairs on wing base from yellowish to piceous. Halteres from yellowish to pale brown. Pleural tuft brasscolored. Pleura dark grayish brown, silvery pollinose. Legs rather uniform light brown to piceous, their hairs from brass-colored to black. Abdomen brownish or grayish, tergal plates darker; membranous areas light grayish brown. Hairs of abdomen, including basal fringe, brasscolored.

Frons (fig. 38C) medium wide, frontal angle 75 degrees. Fronto-ocular triangle distinctly deeper than wide (fig. 38D). Shape and proportions of antennal segments as shown in figure 38A. Maxillary palp as shown in figure 38F, G; third segment somewhat swollen. Structure of sensory vesicle as shown in figure 38H, I; its diameter about half that of third segment of palp. Maxillae with 25–28, mandibles with 37– 41 denticles (fig. 38B).

Structure of wing as in generic description and figure 38J, Q. Setae on Sc numerous, arranged in a single row. Setae on basal portion of R, on R_1 and on R_s arranged in several series. Shape and proportion of articles of legs as shown in figure 38L–N. Calcipala (fig. 38O) shorter than wide at base. Claws as shown in figure 38U.

Tergal plates of abdomen wider than long, except on terga II–IV where they are as wide as long. Ventral plates not developed. Eighth sternum (fig. 38V) with 1+1 groups of 16–20 long setae; disc of eighth sternite uniformly pigmented except darker subsemicircular band anteriorly. Gonapophyses, genital fork, paraprocts, and cerci as in generic description and figures 38P, T, V. Spermatheca (fig. 38V, R) as in generic description, microstructure of inner surface as shown in figure 38S.

Male. Length of wing, 2.9-3.2 mm.

Head black. Eyes red in live specimens, mostly black in dried material. Antennae, palpi, and clypeus black; occiput dark gray pollinose; proboscis dark grayish brown. Antennae with short silvery to black pubescence. Scapus and pedicellus, palpi, clypeus and occiput with long brown or black hairs. Scutum velvet black, scutellum dark brown, with brown to black hairs. Metanotum black, with silvery pruinosity. Color of wings and legs as in female. Halteres dark. Pleura as in female; pleural tuft from brass-colored to black. Abdomen velvet black



FIG. 39. Cnesiamima atroparva, male. A. Antenna. B. Maxillary palp. C. Sensory organ of third segment of maxillary palp. D. Portion of wing. E-G. Legs; setae not shown. E. Foreleg. F. Mid leg. G. Hind leg. H. Apex of basitarsus of hind leg, with second and base of third tarsal segments. I. Paramere, with ventral plate and associated structures. J. Ventral plate, median sclerite, and plate forming endoparameral organ, side view. K. Distimere, showing inner membranous surface. L. Paramere. M. Ventral plate with endoparameral organ. N. Basal plate, with median sclerite and endoparameral organ at right. O. Ventral plate with median sclerite and endoparameral organ at left. P, Q. Ventral plate, different aspects. R. Median sclerite.

dorsally, grayish at sides and below; hairs of abdomen from brass-colored to black.

Shape and proportion of antennal segments as shown in figure 39A. Maxillary palp and sensory vesicle as shown in figure 39B, C; third segment of palp more slender than in female; sensory vesicle only slightly smaller than in female. Wings as in female, but Cu₂ with stronger curvature (fig. 39D). Shape and proportions of articles of legs as shown in figure 39E–G. Hind basitarsus 3.5–3.9 times as long as wide. Calcipala slightly shorter than wide at base (fig. 39H). Genitalia as in generic description and figure 39I-R. Basimere subtrapezoidal, longer than wide, with membranous area apically on inner surface projecting in some cases (fig. 39K, L). Distimere elongate subcylindrical (fig. 39I, K, L). Ventral plate as shown in figure 39I, J, M, N, O, P, Q; lateral projections and basal margin conspicuously sclerotized. Median sclerite as shown in figure 39J, N, O, R. Endoparameral organ as in generic description and figure 39J, M, N, O.

MATERIAL EXAMINED: Chile: Magallanes:

Puerto Williams, Navarino Island, Nov. 22–29, 1960 (L. Peña, CNC), one female; Cameron, S of Bahia Inutil, Tierra del Fuego, Nov. 14–17, 1960 (L. Peña; CNC), one male, five females. Llanquihue: Frutillar, Sept. 20, 1954 (G. Kuschel; AMNH), two females. Curicó: Cajon del Río Claro, SE of Los Quenes, 1000–1200 m., Oct. 9, 1966 (E. I. Schlinger; CIS and AMNH), 17 females, 71 males.

DISTRIBUTION: The range of this species probably extends for the whole of the Valdivian and Magellanic areas of southern Chile, and the western portions of the Argentinian provinces of Río Negro and southern Neuquen.

BIOLOGY: We were unsuccessful in finding the aquatic stages of this species. Adults of *Cnesia*mima atroparva have been collected mostly in very early spring, and it is probable that larvae and pupae occur only in late winter or earlier in spring than we were able to carry out field work.

PARAUSTROSIMULIUM WYGODZINSKY AND COSCARÓN

Figures 1E, 40, 41

Austrosimulium (Paraustrosimulium) WYGODZINSKY AND COSCARÓN, 1962, p. 244. STONE, 1963, p. 14. Paraustrosimulium: CROSSKEY, 1969, p. 17.

DESCRIPTION: Adult. Antennae with 10 segments. Male holoptic. Female with frons relatively narrow (frontal angle about 65 degrees). Mandibles of female with well-developed denticles on both sides. Apical segment of maxillary palp of both sexes less than twice as long as penultimate. Mesepisternal sulcus deep, well defined anteriorly. Katepisternum glabrous, in profile much wider than high. Metanotum glabrous. Arms of furcasternum with conspicuous projections. Pleural membrane bare. Wings with basal cell distinct. Sc with numerous hairs arranged in a single row. Basal section of R with hairs arranged in several rows. R₁ with hairs and very slender spinelike setae arranged in one or two irregular rows. R_s entirely hairy below, hairs arranged in a single row at base and apex of vein, in several rows on central portion of vein; apical portion of R_s dorsally on apical half with one series of hairs. R_8 not forked apically. M appearing thickened on most of its length. Curvature of Cu₂ normal, somewhat more pronounced in male than in female. A₂ falling distinctly short of wing margin. Calcipala present, large, rounded apically. Claws of female with medium-sized subtriangular basal

tooth. Spermatheca larger than usual, larger than gonapophyses; its internal surface smooth, with a very small number of scattered spicules. Spermatheca fully sclerotized, except very small subcircular membranous area at insertion of spermathecal duct. Gonapophyses widely subtriangular, somewhat transverse, closely approximated, their surface with microtrichia and a few very short setae, medial border slightly pigmented. Genital fork lacking conspicuous pigment; stem very short and wide, not longer than arms, the latter also very wide; forwardly directed apodemes absent. Male with distimeres slightly shorter than basimeres, subtriangular, with two to four spines; medial surface of distimeres smooth, limited by two carinae. Ventral plate subpentagonal, with distinct median carina. Median sclerite distinct, geniculate in lateral view; basal portion narrow proximally, somewhat widened and deeply incised distally; apical portion composed of two simple divergent arms. Endoparameres composed of distinct free platelike basal portion and group of elongate parallel denticles not connected by sclerotized area to platelike portion.

Pupa. Cocoon well defined, wall-pocket shaped, viz., without anteroventral collar; under surface of cocoon reduced to a few irregular strands near base of cocoon. Body of pupa distinctly sclerotized throughout, although not strongly so. Respiratory organs in shape of twisted pseudosegmented lamella. Head sclerite with frontal and facial trichomes, all hairlike. Disc of thorax with approximately 5+5 hairlike trichomes, furthermore with 3+3 spinelike trichomes dorsally near midline. Abdomen pointed posteriorly. Distinct pleural areas not developed. Terga III and IV with 4+4 hooks posteriorly; terga V to IX with continuous spine-combs anteriorly. Sternum V with 4+4 hooks posteriorly; sternal plates VI and VII with 1+1 hooks, and 1+1 hooks each also in pleural membrane of segments VI and VII. Terminal spines in shape of short, pointed tubercle. Posterior segments with several grapnel-shaped setae.

Larva. Head spots positive. Cephalic apotome widest slightly before hind margin. Cervical sclerites composed of small subcircular sclerotized area and transverse less strongly sclerotized area, the latter not fused to upper ends of postocciput. Postgenal cleft not developed; hypostomium much shorter than postgenal bridge. Antennae slightly longer than stem of cephalic



FIG. 40. Paraustrosimulium anthracinum. A. Third segment of maxillary palp, male. B. Maxillary palp, female. C. Antenna, male. D, E. Sensory vesicle of third segment of maxillary palp. D. Male. E. Female, same scale. F. Apical portion of mandible of female. G. Mesepisternal sulcus. H. Apex of basitarsus with second tarsal segment, hind leg of male. I-M. Female. I. Spermatheca, pigment not shown. J. Central portion of eighth abdominal sternum, with gonapophyses; pilosity and pigmentation not shown. K. Furcasternum. L. Claw. M. Genital fork. N. Denticles of apical portion of endoparameral organ. O. Pupa in cocoon, side view. P. Frontoclypeus of pupa. Q. Pupa in cocoon, dorsal view. R. Aedeagus with median sclerite, endoparameral organ, and ventral plate. S. *Idem*, lateral view, ventral plate to right. T. Apex of abdomen of pupa, detail. U. Abdominal sterna V, VI, and VII of pupa. V. Gill histoblast. W. Labral sclerite of larva.

fans; their two basal segments very dark, the apical two very light-colored. Cephalic fans with rays normal. Mandibles with two external and one apical tooth; first and second preapical teeth of identical size, rather wide. Third preapical tooth larger than the others, but much smaller than apical tooth, and indistinguishable from internal teeth; the latter arranged in a single row. One large mandibular serration followed by from two to four smaller ones. Short

basal setae of mandible very slender, glabrous. Hypostomium with 13 teeth, not arranged in conspicuous groups, median tooth and corner teeth slightly larger than others; the 2+2 lateral teeth inserted almost at same level as remaining teeth. Teeth of hypostomium underlaid by lamellar extension of hypostomium. Lateral sclerites of proleg subtriangular, slightly wider than long, rounded at base, strongly widened apically. Setae of lateral sclerite shorter than sclerite, arranged in two or three irregular rows, inserted individually on barely perceptible tubercles. Abdominal cuticle bare, except for conspicuous perianal scales. Anal sclerite Xshaped; 1+1 backwardly directed struts underlying main body of sclerite.

Type-Species: Simulium anthracinum Bigot.

DISTRIBUTION: Valdivian and Magellanic areas of southern Chile, and western Patagonia.

BIOLOGY: Silva Figueroa (1917) mentioned that anthracinum (as moorei) bites man on the Taitao Peninsula of Chile, and can become very bothersome. Edwards (1931) examined a specimen that "bit, causing painful swelling of hand." We have not recorded anthropophilous behavior in this species.

The aquatic instars are found in clear, cold streams, small and large. Pupae and larvae were found attached to rocks, to leaves, to pieces of wood, and to dead branches trailing in the stream, invariably close to the surface.

DISCUSSION: Paraustrosimulium presents an array of autapomorphic characters that distinguish it from all other Western Hemisphere Prosimuliine genera, i.e., the 10-segmented antennae, the peculiar endoparameral organ and the almost unpigmented genital fork with its short and wide stem, the well-formed cocoon and the unique gills of the pupa, and, in the larva, the extremely elongate third antennal segment and the backwardly directed struts underlying the anal sclerite. The last character is also found in *Gigantodax*, but an assumption of a close relationship between the two genera is not supported by any other shared derivative character so far as we can judge at this time.

Paraustrosimulium shares with the prosimuliine Lutzsimulium and with Simulium the presence of conspicuous projections on the arms of the furcasternum, an apomorphic character within the framework of the family.

Paraustrosimulium anthracinum (Bigot)

Figures 1E, 40, 41

Simulium anthracinum BIGOT, 1888, p. 15. Simulium (Austrosimulium) anthracinum: EDWARDS, 1931, p. 143.



FIG. 41. Paraustrosimulium anthracinum, larva. A. Head from above. B. Head capsule from below. C. Hypostomium. D. Lateral sclerite of proleg. E. Apex of mandible. F. Teeth of anterior border of hypostomium. G. Anal sclerite. H. Teeth of rays of mouth brush. I. Posterior portion of head capsule, with sclerites of neck region. J. Cervical sclerite, higher magnification.

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- Austrosimulium anthracinum: SMART, 1945, p. 499. Wygodzinsky, 1953, p. 293. Dumbleton, 1960, p. 543.
- Austrosimulium (Paraustrosimulium) anthracinum: Wy-GODZINSKY AND COSCARÓN, 1962, p. 242. COSCARÓN, 1968, p. 66.

Paraustrosimulium anthracinum: CROSSKEY, 1969, p. 73.

- Simulium moorei SILVA FIGUEROA, 1917, p. 30.
- Simulium (Austrosimulium) moorei: Edwards, 1931, p. 144.

Austrosimulium moorei: SMART, 1945, p. 499.

This species has been redescribed in detail by Wygodzinsky (1953) and Wygodzinsky and Coscarón (1962). A few of the figures from those papers are published here again in order to facilitate use of the generic keys and to illustrate characters mentioned in the discussions. A few structures not described or figured before are also illustrated here. The furcasternum (fig. 40K), spermatheca of the female (fig. 40I, J), the cervical region of the larva (fig. 41I, J), the apical portion of its mandible (fig. 41E) and the lateral sclerotization of the proleg (fig. 41D) are all mentioned in the generic description. The gill histoblast of the pharate pupa (fig. 40V) is very different from that of any other South American black fly. The teeth of the rays of the large cephalic fan are shown in figure 41H; they are arranged in groups of units conspicuously decreasing in size; the larger teeth are much longer than the diameter of the portion of the ray upon which they are inserted.

MATERIAL EXAMINED: Chile: Magallanes: Isla Wellington, Puerto Eden, Sept. 23, 1969 (O. S. Flint; USNM), one male; 40 km. NW of Porvenir, Tierra del Fuego, Dec. 3, 1966 (M. E. Irwin and E. I. Schlinger; CIS), one female; 11.9 km. NW of Russfin, Tierra del Fuego, 300 m., Dec. 1, 1966 (E. I. Schlinger; CIS), three females; Laguna Amarga, Natales, E of Mt. Payne, 200 m., Dec. 14-20, 1960 (L. Peña; CNC), one female; 4 km. W of Laguna Amarga, Dec. 7 and 8, 1966 (E. I. Schlinger and M. E. Irwin; CIS), seven females. Aysen: Lago Frío, Coihaique, valley of Río Simpson, Jan. 20-23, 1961 (L. Peña; CNC), seven females; km. 50, Puerto Aysen-Coihaique road, Jan. 24, 1961 (L. Peña; CNC and AMNH), 21 females; Puerto Aysen, Jan. 24-26, 1961 (L. Peña; CNC) 13 females; Puerto Cisnes, Feb. 1-15, 1961 (L. Peña; CNC), 10 females; ibid., Feb. 16-28, 1961 (L. Peña; CNC), two females; Río Maniguales, Jan. 26-28, 1961 (L. Peña; CNC), three females. Chiloë: 6 km. NE of Huillinco, Feb. 7, 1967 (S. Coscarón; AMNH), two males and two females, reared. Llanquihue: 10 km. N of Bahía Pargua, Feb. 6, 1967 (S. Coscarón AMNH), pupae and larvae. Osorno: Río Negro, near Panamerican highway bridge, Feb. 5, 1967 (S. Coscarón; AMNH), one male, reared, one pupa. Valdivia: Río Llollehue, Itropulli, bridge between Paillaco and Manao (S. Coscarón; AMNH), one pupa. Malleco: Nahuelbuta National Park, 1300 m., Feb. 24, 1967 (M. E. Irwin; CIS), one female.

Argentina: Tierra del Fuego: Isla de los Estados, Bahía Vancouver, stream close to seashore, Nov. 21, 1967 (A. Bachmann; AMNH), three pupae. Río Negro: 3 km. SW of Pampa Linda, small roadside stream, Oct. 21, 1970 (S. Coscarón; AMNH), one female, two males, all reared, four pupae. Neuquen: 10 km. SE of San Martín de los Andes, Oct. 20, 1970 (S. Coscarón; MLP), one pupa, one larva.

DISTRIBUTION: This species is a typical element of the Valdivian and Magellanic areas of Chile, where it has been found from Tierra del Fuego north to the province of Malleco; in Argentina it extends northward to the southern part of Neuquen.

LUTZSIMULIUM D'ANDRETTA AND D'ANDRETTA

Lutzsimulium C. d'Andretta and M. A. V. d'Andretta, 1947, p. 402; 1948, p. 639. M. A. V. d'Andretta and C. d'Andretta, 1952, p. 310. Stone, 1963, p. 11.

DESCRIPTION: Adult. Antennae 11-segmented. Male holoptic. Female with frons comparatively wide; frontal angle about 90 degrees. Mandibles of female toothed only on inner margin. Apical segment of maxillary palp of both sexes only very slightly longer than penultimate. Mesepisternal sulcus rather deep, not evanescent anteriorly. Katepisternum glabrous, in profile about as high as wide. Arms of furcasternum with conspicuous projections. Metanotum glabrous. Wings without basal cell. R_1 with spinelike setae. Sc and basal section of R setose. R_8 entirely hairy below, setose above on distal half. Rs not forked apically. M appearing duplicated for most of its length. Cu₂ conspicuously curved, in some specimens with rudimentary branch submedially. A₂ ending well before wing margin. Calcipala large, widely rounded apically. Hind basitarsus of male not strongly widened. Claws

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of female with one very small, pointed, subbasal tooth. Spermatheca of normal size, fully sclerotized, not reticulate on either surface; internal surface with scattered spicules; subcircular area at insertion of spermathecal duct with peculiar network-like structure extending to base of duct, there gradually fading. Gonapophyses large, transversely subtriangular, their apex bluntly rounded; medial borders approximated, slightly pigmented. Surface of gonapophyses with microtrichia and a few short setae. Genital fork distinctly pigmented; stem slender, only slightly longer than arms, the latter wide, without apodemes. Male with distimere slightly shorter than basimere, subconical, with from two to four apical spines. Ventral plate subquadrate or subrectangular, with conspicuous keel. Median sclerite somewhat S-shaped in lateral view; in frontal view with proximal portion entire, wide basally, narrowed distally; apical portion in shape of two short, diverging arms connected by membrane; short ends of arms free, backwardly curved. Endoparameral organ not perceptible.

Pupa. Cocoon without definite shape, covering abdomen and only part of thorax of pupa. Body of pupa well sclerotized throughout. Head and thorax with or without platelets. Many of the trichomes of head and thorax, and setae of terminal abdominal segments, tightly looped apically. Gills arborescent, divided into primary and secondary branches close to base; general structure of branches filamentous. Head sclerite with l+1 facial trichomes; frontal trichomes present or absent. Thorax with 4+4 or 5+5trichomes. Abdomen pointed posteriorly. Distinct pleural areas not developed. Onchotaxy: Terga III and IV with 4+4 hooks posteriorly; terga VI-IX with continuous spine-combs anteriorly. Sternum IV without or with 1+1, V with 2+2 hooks posteriorly; sternal plates VI and VII with 1+1 hooks; 1+1 hooks each also in pleural membranes of segments VI and VII. Terminal spines well developed, long and slender, strongly curved at base. Setae of segments VIII and IX strong, looped apically, never branched.

Larva. Head spots positive. Cephalic apotome widest well before hind margin. Cervical sclerites either wide, fused to upper end of postocciput, or small and free. Gular cleft large. Antennae slightly shorter than stem of mouth fan; third segment distinctly darker than preceding. Cephalic fans normal. Mandibles with

two outer teeth in addition to apical tooth; second preapical tooth much smaller than either first or third; third smaller or larger than first, and distinctly larger than first inner tooth; inner teeth arranged in three series; mandibular serrations numbering two, first much larger than second; short basal setae slender, glabrous. Hypostomium with anterior border slightly emarginated; teeth numbering 13, subequal in size, not arranged in conspicuous groups; the 2+2 lateral teeth inserted much below level of corner teeth. Lateral sclerites of prolegs well developed, subtriangular, about as long as wide. Setae of lateral sclerites less than half as long as sclerite, arranged in an irregular row extending slightly beyond main body of sclerite below. Larval cuticle bare or conspicuously hairy; perianal scales well developed. Ventral papillae present. Anal sclerite normal, X-shaped.

TYPE-SPECIES: Simulium hirticosta Lutz (as Lutzsimulium cruzi d'Andretta and d'Andretta).

DISTRIBUTION: This genus has been found in the coastal ranges of southern Brazil, from the state of Rio de Janeiro south to Paraná, and also in Misiones (Argentina), generally at elevations of 1000 meters or above, although a few sites of lower elevation are known.

BIOLOGY: The aquatic instars have been found in fast- and slow-flowing mountain streams. Lutz (1910) collected females of L. *pernigrum* on horses.

DISCUSSION: Lutzsimulium provides an excellent example of the difficulties one encounters when attempting to divide the subfamily Simuliinae into two neatly defined tribes, viz., Prosimuliini and Simuliini, on a worldwide basis. In many respects, Lutzsimulium fits the features normally associated with the Prosimuliini, as understood by Crosskey (1969): the short apical segment of the maxillary palp of the adults, the absence of a pedisulcus, multiple apical spines on the distimere, the structure of the median sclerite of the genitalia of the male not unlike that found in Prosimulium or Stegopterna, the shapeless, loosely woven cocoon, the comparatively heavily sclerotized pupal abdomen, the membranous area dividing sterna VI and VII of the pupa along their middle, the long terminal spines of the pupal abdomen and the modified setae found on the terminal abdominal segments, and the dark third segment of the antenna of the larva. On the other hand, Lutzsimulium shows an array of apomorphic characters generally associated with the tribe Simuliini sensu Crosskey: the rather deep mesepisternal sulcus, the absence of a basal cell in the wing, the conspicuous apodemes of the arms of the furcasternum, the *Simulium*-like hypostomium of the larva, the small number of mandibular serrations, and the extremely well-developed gular cleft. It is impossible to place *Lutzsimulium*, using conventional criteria, unequivocally in one or the other tribe accepted by Crosskey (*loc. cit.*).

Stone (1963), who was acquainted only with the description of the female and pupa of Lutzsimulium hirticosta, mentioned the general agreement of Lutzsimulium with Stegopterna, but also suggested that Lutzsimulium be considered as a valid genus until further evidence became available. We can now state confidently that Lutzsimulium is indeed a valid genus and quite different from Stegopterna, which immediately becomes apparent when the larvae are compared. In Stegopterna, the teeth of the hypostomium are of very diverse size and arranged in three conspicuous groups, and there are numerous mandibular serrations; in Lutzsimulium, the teeth of the hypostomium are as in most Simulium, viz., subequal in size and not arranged in compact groups, and the mandibular serrations are reduced to two. The large gular cleft of the larva of Lutzsimulium is also an excellent differential character, as opposed to the virtual absence of a gular cleft in Stegopterna.

The combination of the peculiar autapomorphic characters of *Lutzsimulium*, such as the meshlike surface structure of part of the spermatheca, the absence of an endoparameral organ in the genitalia of the male, the apically looped trichomes of the thorax of the pupa, and the size ratios of the preapical teeth of the mandible of the larvae, are sufficient to distinguish *Lutzsimulium* from any described genusgroup in the Simuliidae.

It may be useful to compare Lutzsimulium further with those New World simuliids that share with it the general structure of the hypostomium and a strongly reduced number of mandibular serrations, viz., Cnephia, Ectemnia, Cnesia, Paraustrosimulium, and Simulium.

Lutzsimulium differs from Cnephia, in addition to its autapomorphic characters, also in the normal-sized spermatheca, the apically blunt gonapophyses, and the presence of more than one apical spine on the distimere.

The genus differs from the other boreal genus,

Ectemnia, which itself is highly apomorphic in several respects, in the wide frons and the small tooth of the claw of the female, the absence of a stalk to the pupa, the normally sized fourth antennal segment in the larva, the presence of mandibular serrations, and the normal Xshaped anal sclerite.

A comparison of *Lutzsimulium* with the South American genera mentioned above reveals even more differences. Lutzsimulium differs from Cnesia in the adult by A_1 which does not approach the wing margin, the normally curved Cu₂, the much simpler median sclerite of the male, the small tooth at the base of the claw of the female, and the absence of apodemes on the arms of the genital fork; the pupa differs in the smaller number of cephalic trichomes, the presence of spine-combs on the posterior abdominal terga, and the absence of accessory hooks on tergum VIII; the larva differs in the smaller number of outer teeth of the mandible, and the smaller number of lateral teeth of the hypostomium, which, furthermore, are not similar to the remaining teeth as they are in Cnesia.

Lutzsimulium can be distinguished from Paraustrosimulium at a glance by the number of antennal segments of the adult, the very different median sclerite of the male genitalia, the small basal tooth of the claw of the female, and the narrow stem of the genital fork; the pupa of Lutzsimulium lacks a well-defined cocoon, the gill is plesiomorphic, and the terminal spines of the abdomen are elongate; the larva is distinguished from that of Paraustrosimulium by the much shorter antennae, and the absence of backwardly directed rodlike structures underlying the anal sclerite.

Lutzsimulium can be distinguished from all species of Simulium by its autapomorphic characters, and by the combination of features mentioned in the first paragraph of this discussion as normally associated with the Prosimuliini as understood by Crosskey (1969).

Lutzsimulium is not comparable with any genus or subgenus reported from the Old World, so far as we have been able to ascertain.

We have no doubt that the two species included in *Lutzsimulium*, *hirticosta* (Lutz) and *pernigrum* (Lutz), are closely related, as demonstrated by the synapomorphic characters mentioned before; the unique structure of the spermatheca alone suffices to make recent common ancestry for the two species almost certain. On the other hand, there is also a considerable degree of morphological divergence between the two species, as shown in the following key.

KEY TO THE SPECIES OF Lutzsimulium

1. Female with scutum dark reddish brown; wing length 2.6–2.8 mm.; third segment of maxillary



FIG. 42. Lutzsimulium hirticosta. A-E. Female. A. Maxillary palp. B. Calcipala. C. Claw. D. Furcasternum. E. Genital fork. F, G. Antennae of different larvae from Boraceia. H, I. Female. H. Eighth abdominal sternum with gonapophyses and outline of spermatheca; microtrichia of gonapophyses not shown. I. Spermatheca; sclerotization shown only at insertion of spermathecal duct; insert showing spicules of inner surface. J. Apex of abdomen of pupa, lateral view. K. Labral sclerite of larva. L. Basal portion of gill of pupa. M-S. Larva. M. Cervical region, as seen on slide mount. N. Anterior portion of hypostomium. O. Spines of lateral sclerite of proleg. P. Apex of mandible. Q. Central portion of under surface of head, as seen in slide mount. R, S. Body setae of different larvae from Boraceia.

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Female with scutum piceous; wing length 2.5-3.2 mm.; third segment of maxillary palp slender, sensory organ small (fig. 43A). Pupa with gills possessing an average of 14 filaments (fig. 43T); cephalic sclerite and thorax glabrous; cephalic sclerite with hairlike frontal trichomes (fig. 43M). Larva with cervical sclerites elongate transverse, connected to upper ends of postocciput (fig. 43S); mandible with third preapical tooth larger than first (fig. 43R); gular cleft about as deep as length of postgenal bridge (fig. 43Q); abdominal cuticle glabrous .

Lutzsimulium hirticosta is clearly the more apomorphic of the two species, as shown by the loss of the frontal trichomes of the pupa, and, in the larva, the diminishing size of the third preapical tooth, the appearance of hairs on the cuticle, the very deep gular cleft, and the size reduction of the cervical sclerites. The more



FIG. 43. Lutzsimulium pernigrum. A-C. Female. A. Maxillary palp. B. Claw. C. Calcipala. D. Basitarsus and second tarsal segment, hind leg of male. E. Genital fork. F. Basal portion of spermatheca with insertion of spermathecal duct. G. Paramere. H. Basal plate with median sclerite. I, J. Antennae of different specimens. K. Cercus and paraproct. L. Apical portion of abdomen of pupa, under surface, one side only. M. Frontoclypeus of pupa. N. Lateral sclerite of proleg of larva. O. Portion of dorsal surface of thorax of pupa, with base of gill. P-S. Larva. P. Labral sclerite. Q. Center of under surface of head. R. Apex of mandible. S. Cervical region. T. Gill of pupa.

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derived condition of *hirticosta* is also shown by its tolerance of lower altitudes and, implicitly, higher water temperatures.

The descriptions of the species of Lutzsimulium given by d'Andretta and d'Andretta (1946, 1948, 1952) are reasonably detailed, but not so complete as is deemed necessary at the present time. Our figures are intended not only to supplement those given by the authors of the genus, but also to illustrate characters mentioned in our generic description and the keys.

Lutzsimulium hirticosta (Lutz)

Figure 42

Simulium hirticosta LUTZ, 1909, p. 135; 1910, p. 226.

Lutzsimulium hirticosta: VULCANO, 1967, p. 4.

Lutzsimulium cruzi D'ANDRETTA AND D'ANDRETTA, 1947, p. 402; 1948, p. 639.

We have found a surprising degree of variation in larvae identified by the d'Andrettas as belonging to this species. Specimens collected at one locality (Boraceia, São Paulo) by d'Andretta and d'Andretta and mentioned in their paper (1948) as bearing the numbers 1281, 1282, and 1283, differ by the length of the hairs of the abdominal cuticle (fig. 42R, S) and the ratios of the antennal segments (fig. 42F, G). These differences, especially those pertaining to the antennal ratios, would seem to indicate separate specific status for each of the larvae examined. The material available to us is insufficient to elucidate this question. We have examined larvae, pupae, and females all mentioned in papers by d'Andretta and d'Andretta, in addition to our own material.

MATERIAL EXAMINED: Argentina: Misiones: Route 101, 15 km. SE of Deseado, 650 m., July 20, 1972 (S. Coscarón; MLP) one male, reared, one pharate female, one pupa; Arroyo Tacuara, on route 101, Iguazú National Park, July 20, 1972 (S. Coscarón; MLP), one pupa.

DISTRIBUTION: Brazil (states of Rio de Janeiro, São Paulo, and Paraná); Argentina (Misiones).

BIOLOGY: The pupae from Misiones were collected in small, slow-flowing brooks with clear water, on aquatic plants.

Lutzsimulium pernigrum (Lutz)

Figure 43

Simulium montanum: LUTZ, 1909, p. 134 (nec Philippi). Simulium pernigrum LUTZ, 1910, p. 263.

Lutzsimulium pernigrum: d'Andretta and d'Andretta 1952, p. 312.

The illustrations are self-explanatory. Figure 43B shows the claw of the female, which has been described and illustrated by d'Andretta and d'Andretta (1952) as having two teeth; all specimens examined by us have a single tooth, as illustrated.

We have studied females, males, pupae, and larvae previously examined by d'Andretta and d'Andretta (*loc. cit.*).

DISTRIBUTION: Brazil (states of Rio de Janeiro and São Paulo).

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