A re-evaluation of the genus *Colonomyia* Colless (Diptera, Sciaroidea), with the description of two new species

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The genus *Colonomyia* Colless contains six species in the Australasian and Neotropical Regions. Several recognized synapomorphies leave no doubt that *Colonomyia* is a monophyletic group, with the Australasian species more closely related to one another than to the Neotropical species. On arguments derived from the wing venation, *Colonomyia* is hypothesized to be the sister-group of the genus *Ohakunea* Edwards, both together representing a lineage distinct from the family-level taxa currently recognized in the Sciaroidea. *Colonomyia borea* sp. n. from Costa Rica and *C. rakelae* sp. n. from Papua New Guinea are described. Recognition of these new species extends the distribution of the genus *Colonomyia* into the tropical zone and the northern hemisphere.

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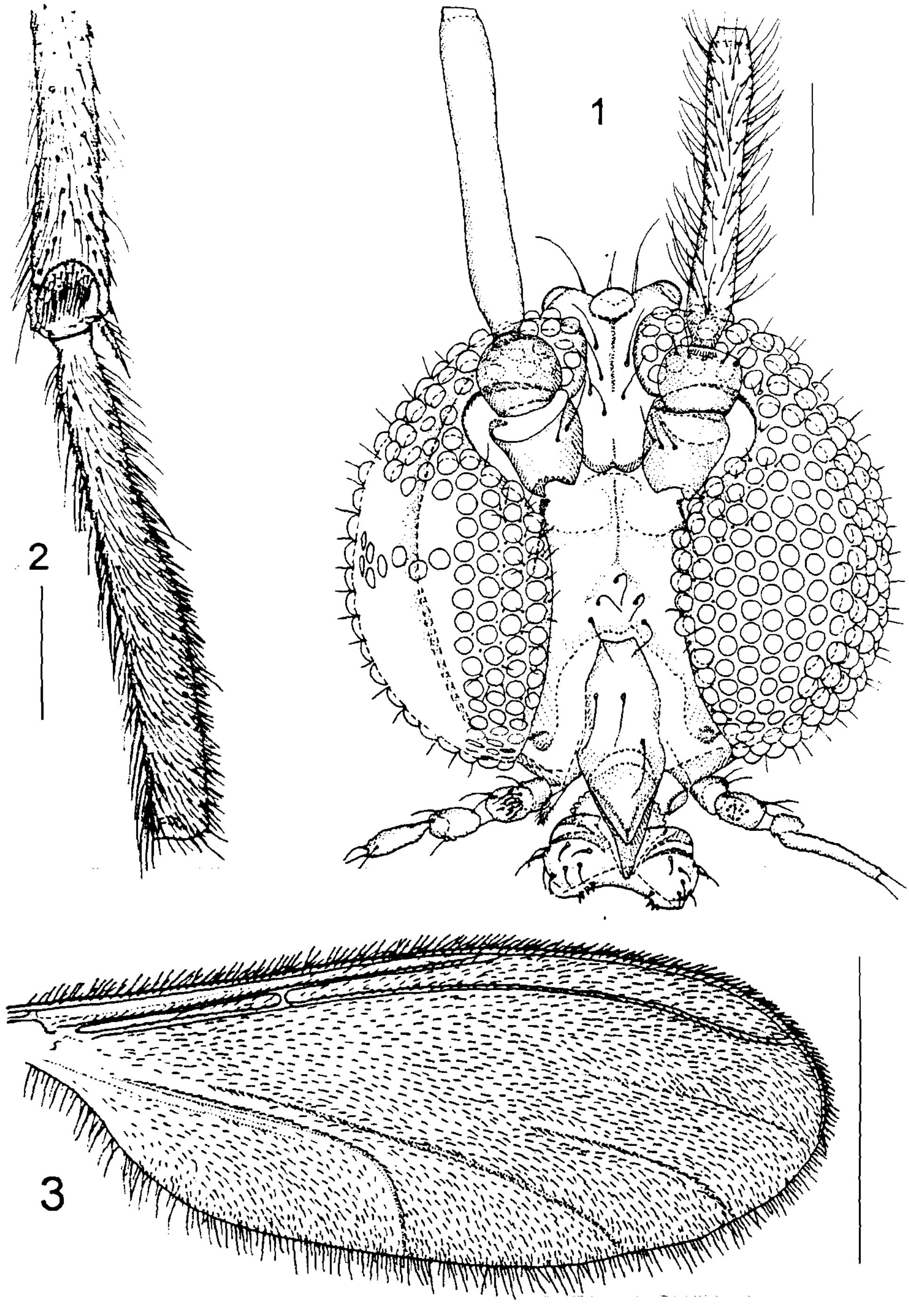
Introduction

Among the unplaced sciaroids within the currently recognized familial classification of the Bibionomorpha, species of the genus *Colonomyia* Colless, 1963 are among the least known. Described from Australia as long ago as 1963, the genus was not mentioned for more than thirty years – until three more species were described from the southern Neotropics (Matile & Duret 1994). These additional findings made it clear that *Colonomyia* was not endemic to Australia but was rather an extant Gondwanan element. In this paper, we describe two more *Colonomyia* species from Costa Rica and Papua New Guinea, which extend the known distribution of this genus into the tropical zone and the northern hemisphere.

Colless (1963) originally suggested that there is a close phylogenetic relationship between *Colonomyia* and *Ohakunea* Edwards and classified both genera in the Sciaridae, although he emphasized that there are differences mainly in the terminalia that make such an assignment only provisional. Based on the narrow thoraco-abdominal insertion, Matile (1990) and Matile & Duret (1994) concluded that both *Colonomyia* and *Ohakunea* should be excluded from the Sciaridae and placed in the *Heterotricha* Loew group – at that time a loosely delineated catch-all pool for enigmatic, 'unplaceable' Sciaroidea. Chandler (2002) has recently sharpened the concept of the *Heterotricha* group by excluding *Colonomyia*, *Ohakunea* and the genus *Pterogymnus* Freeman, 1951. However, the phylogenetic relationships of all these lineages with each other and with sciaroid families such as the Sciaridae and Mycetophilidae *s.str.* remain unresolved. In the light of the new material we have available for study, we review the genus *Colonomyia* and provide arguments for its monophyly as well as for its sister-group relationship with *Ohakunea*.

Material and methods

Specimens of the described species were borrowed from the Australian National Insect Collection, Canberra (*C. albicaulis*), or came from the collec-



Figs 1-3: *Colonomyia albicaulis* Colless, 1963; - 1: head of male, frontal view (scale 1.0 mm); - 2: front tibia and basitarsus 1 of female, prolateral view (scale 0.10 mm); - 3: wing of male, dorsal view (scale 1.0 mm). 1 and 3: specimen from Monga; 2: specimen from Brown Mountain.

tions at our disposal (*C. magellanica*, *C. obtusistyla*). Specimens of the new species were collected during an expedition to Papua New Guinea in 1999 led by one of us (H. H.) (*C. rakelae*), or were found in unsorted Malaise trap samples belonging to the Instituto Nacional de Biodiversidad (INBio), Santo Domingo, Costa Rica (*C. borea*). Pinned museum specimens were soaked in water, cleared by treatment with KOH, dehydrated in ethanol and eventually mounted on microscope slides in Canada balsam or Euparal. Specimens stored in ethanol were also slide-mounted. Types of the newly described species are deposited in the Swedish Museum of Natural History, Stockholm, in INBio, and in the Zoological Institute and Museum, Greifswald, Germany. The morphological terminology follows that of Söli (1997) for Mycetophilidae. Drawings were made using a camera lucida attached to a Leitz Laborlux S compound microscope.

The genus *Colonomyia* Colless, 1963

Type species.- Colonomyia albicaulis Colless, 1963: 305 ff., Fig. 2.

Description.- **Habitus.** Slender, hump-backed sciaroids, 2-3 mm in size, with moderately long antennae, legs and wings, rather narrow waist, slightly downcurved abdomen and distinctive wing venation. Colour brownish in ethanol-preserved specimens.

Head. Head capsule higher than long, covered with setae of various lengths. Postfrons bilobed, setose or non-setose; frontal tubercle clearly to slightly two-pointed. Face larger than clypeus, setose or non-setose. Clypeus setose, clearly separated from face along its upper margin. Antenna shorter than body, longer in males than in females, inserted slightly above mid-height of head. Scape somewhat conical, slightly larger than subglobular pedicel, both setose. Antennal flagellum with 14 flagellomeres gradually decreasing in length, terminal flagellomere longer than penultimate; each flagellomere cylindrical with very short conical neck and node several times as long as wide, neck and node with smooth transition. Flagellum without microtrichia except a few basally on flagellomere 1. Each flagellomere usually with an even covering of setae arising from membraneous rings and occurring in two lengths: fine ones shorter than diameter of node, and stronger ones slightly longer than diameter of node; setae interspersed with numerous sensory spines; first flagellomere usually with 1 (rarely 2 or more) seta(e) arising from socket(s); terminal flagellomere above with 3-4 sensory spines and, in some species, with a seta arising from a socket. At vertex with 3 ocelli arranged in triangle immediately behind compound eyes. Eyes reniform, separated at vertex for a distance usually smaller than width of ocellar triangle, with numerous, comparatively strong interommatidial setulae. Mouthparts well developed, with short proboscis. Labrum sclerotized, elongate triangular, setose or non-setose. Maxilla with lacinia well developed, the latter style-like and fringed. Maxillary palpus basically with 5 segments; with first segment ("presegment") smaller than second, smooth and non-setose; segments 2-5 setose with some setae spine-like; segment 3 with hyaline sensory hairs; segment 2 and/or 3 thickest and 5 longest. Labium with prementum (including premental apodemes) strongly developed, non-setose; labial palpus 2-segmented; labellum 1 smooth, small and non-setose; labellum 2 large, with numerous spine-like setae.

Thorax. Cervical sclerite well sclerotized. Antepronotum well developed, setose, antepronotal sclerites connected by postpronotum which forms a very narrow ridge above neck. Episternum 1 clearly separated from pronotum, setose. Epimeron 1 small, subtriangular, situated at posteroventral margin of episternum 1. Scutum with dorsal surface evenly but slightly arched, with both anterior parapsidal suture and median transverse suture weak, with lateral, dorsocentral and usually acrostichal setae of various lengths. Paratergite distinct from scutum and well sclerotized. Scutellum setose. Mediotergite in lateral profile very high, evenly but slightly arched. Laterotergite large, pronounced, its anterior margin in contact with posterior margin of preepisternum 2, setose or non-setose. Postphragma well developed, with its posterior portion usually somewhat produced into abdominal cavity. Anepisternum 2 subquadrate, much smaller than preepisternum 2, the two sclerites separated by distinct (anapleural) suture. Preepisternum 2 subtriangular to rounded ventrally. Pleural suture distinct. Pleural pit present but inconspicuous. Epimeron 2 with a cleft dorsally, indicating a subdivision into upper anepimeron and lower katepimeron, the latter short, i.e. reaching ventrally somewhat beyond anapleural suture. Internal mid-coxal fork distinct. Metanotum small, forming a narrow collar above

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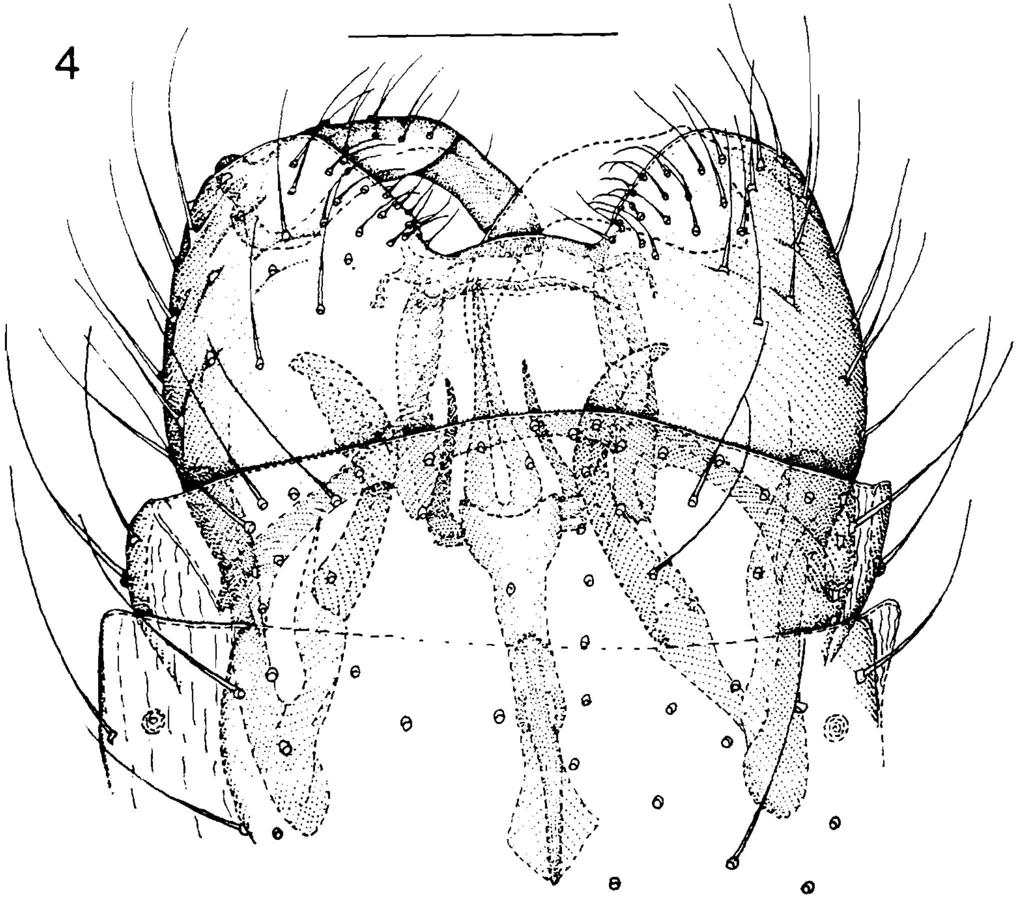
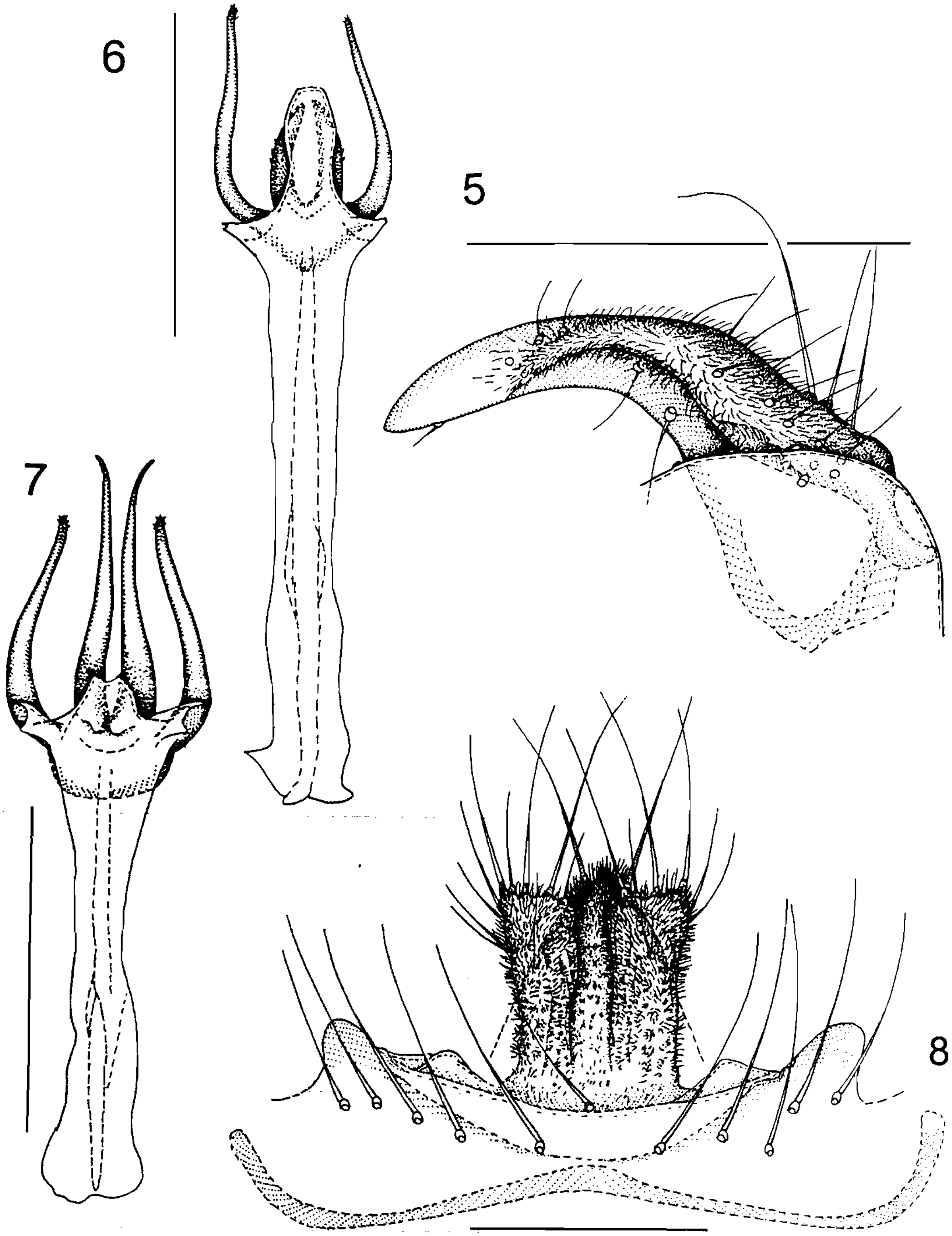


Fig. 4: *Colonomyia albicaulis* Colless, 1963; male terminalia with sternites 7 and 8, ventral view (scale 0.10 mm). Specimen from Dorrio-Coramba Road.

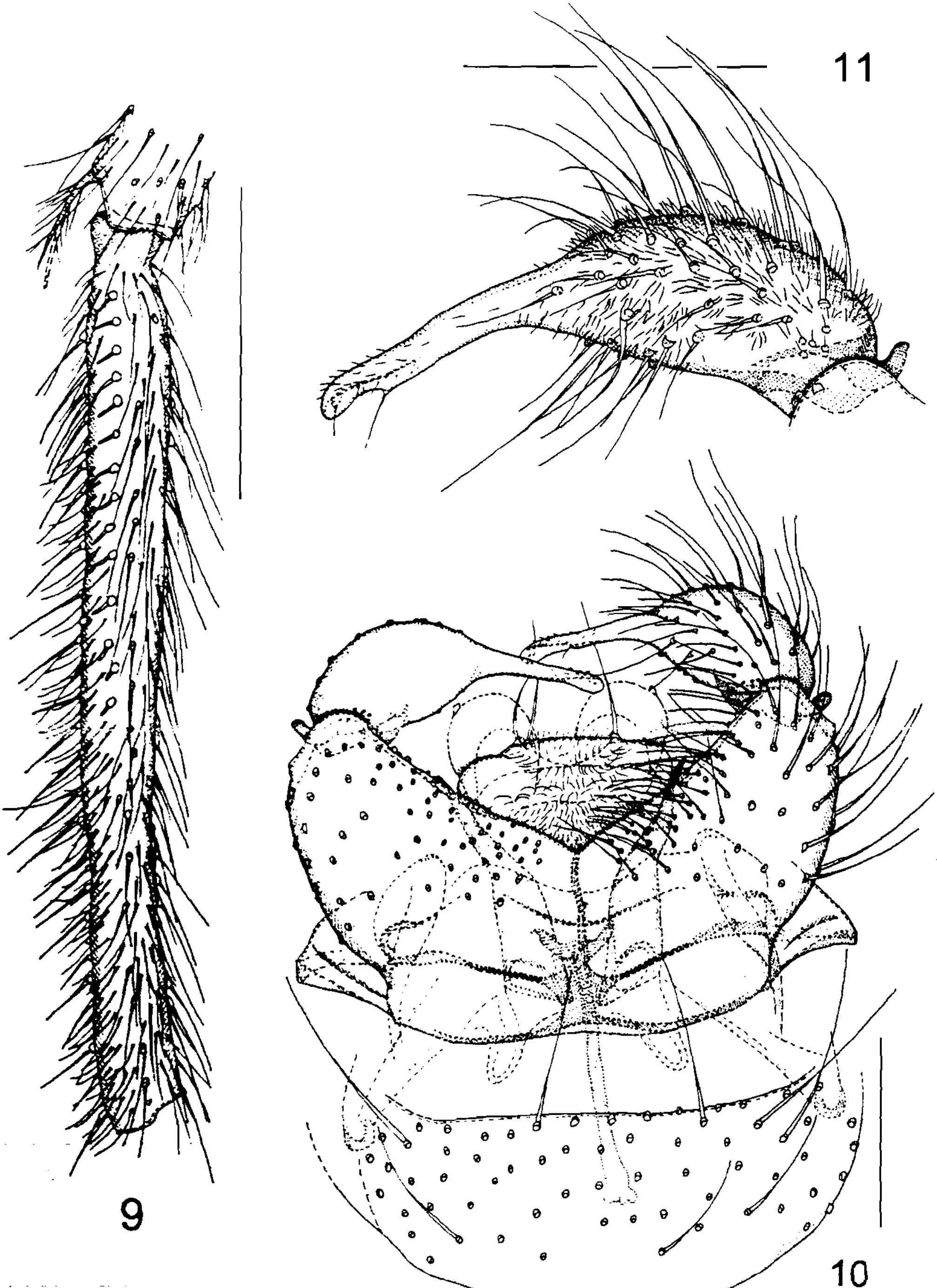
mediotergite. Episternum 3 subquadrate, with subdivision into small anepisternum and larger, subquadrate preepisternum. Epimeron 3 very narrow. Openings of thoracic spiracles without striking features.

Legs. Long, i.e. about 1.3 (fore legs) to 1.5 (hind legs) times the length of body. Coxae moderately short, i.e. 0.7 (fore coxa) to 0.5 (hind coxa) times the height of thorax. Femora slightly shorter than tibiae; on fore leg tibia clearly shorter than tarsus, on mid leg tibia barely shorter than tarsus, and on hind leg tibia and tarsus subequal in length. Tarsomeres 1-4 gradually decreasing in length, basitarsi very long, tarsomeres 5 slightly longer than 4. Coxae flattened, with long setae largely confined to anterior margins (fore and mid coxae) or distolateral portions (hind coxa). Femora barely flattened, with longest setae (i.e. those along hind margins) a little longer than width of femur. Tibiae with a dense covering of comparatively short setae interspersed with large trichia, the latter half to two-thirds as long as setae. Tibial spurs 1:2:2, small, subequal in size. Fore tibia with a distinct anteroapical depression, usually delineated by a sharp, semicircular rim and bearing numerous setae in irregular and/or comb-like arrangement. Vestiture on tarsi mainly as on tibiae but somewhat shorter and including strong, spine-like setae beneath. Tarsal claws deeply split into two branches equal in size. Empodia narrow, with their hairs about as long as claws. Pulvilli present but small.

Wing. Long, i.e. about as long as body or some-



Figs 5-8: *Colonomyia albicaulis* Colless, 1963, male; - 5: gonostylus, ventral view (scale 0.10 mm); - 6: ejaculatory apodeme, ventral view (scale 0.10 mm); - 7: ditto; - 8: tergite 9, cerci and hypoproct, dorsal view (scale 0.10 mm). 5: specimen from Dorrio-Coramba Road; 6 and 8: specimen from Bonang Highway; 7: specimen from Coff's Harbour.



Figs 9-11: *Colonomyia borea* sp. n., male; - 9: hind basitarsus showing a row of pale, blunt setae (scale 0.10 mm); - 10: terminalia with sternite 8, ventral view (scale 0.10 mm); - 11: gonostylus, ventral view (scale 0.10 mm). 9: from Honduras; 11: paratype; 10: holotype.

what shorter, about 2.5 times as long as wide, widest near midpoint. No distinct alular or calypterous areas, anal area moderately developed. Membrane transparent, with brownish tinge, densely and evenly covered with microtrichia and setae on both sides, in some species setation partially or completely reduced. Venation: C extending to apex of wing; Sc pale, almost entering C, or abbreviated and ending free; h present, oblique; Rs present but hardly visible, situated unusually close to wing base, with oblique inclination; R (i.e. vein portion between arculus and Rs) very short; R1 (i.e. vein portion between Rs and junction point with anterior wing margin) excessively long, usually joining C near or slightly beyond midpoint of wing; R4 present as a short, transverse vein between R1 and R5, situated in proximal half of wing; R5 (i.e. vein portion between diverging point of M1+2 and junction point with C, which is before wing apex) excessively long, its distalmost portion slightly sinuous and upcurved; frm (i.e. vein portion between Rs and diverging point of M1+2) present but short; ta absent; tb present but short and faint, with horizontal inclination; mcu absent; M1+2 furcate with its stem and proximal portions of fork often obliterated, with point where M1+2 diverges from R5 very far basally and situated beyond Rs, fork slightly longer than stem in cases where M1+2 is distinct throughout; CuA1 and CuA2 originating from one and the same point, i.e. forming fork without common stem; CuA1 often obliterated proximally, almost straight throughout; CuA2 more distinct, strongly curved inwards distally; CuP faint, running close to and reaching about 2/3 the length of CuA2; A1 faint, sometimes reaching beyond half length of CuA2 but usually shorter; A2 absent or indistinct and short, just detectable in large specimens. With setae present along wing margin and on all veins dorsally except R4, A and sometimes Sc. With the number of sensory pores somewhat variable but usually 6-8 on R1, and 2 distally and 2 proximally on R5, apart from numerous pores on Sc, stem vein and CuA2 proximally. Haltere club-shaped, long and slender, with very sparse setation on both stem and knob.

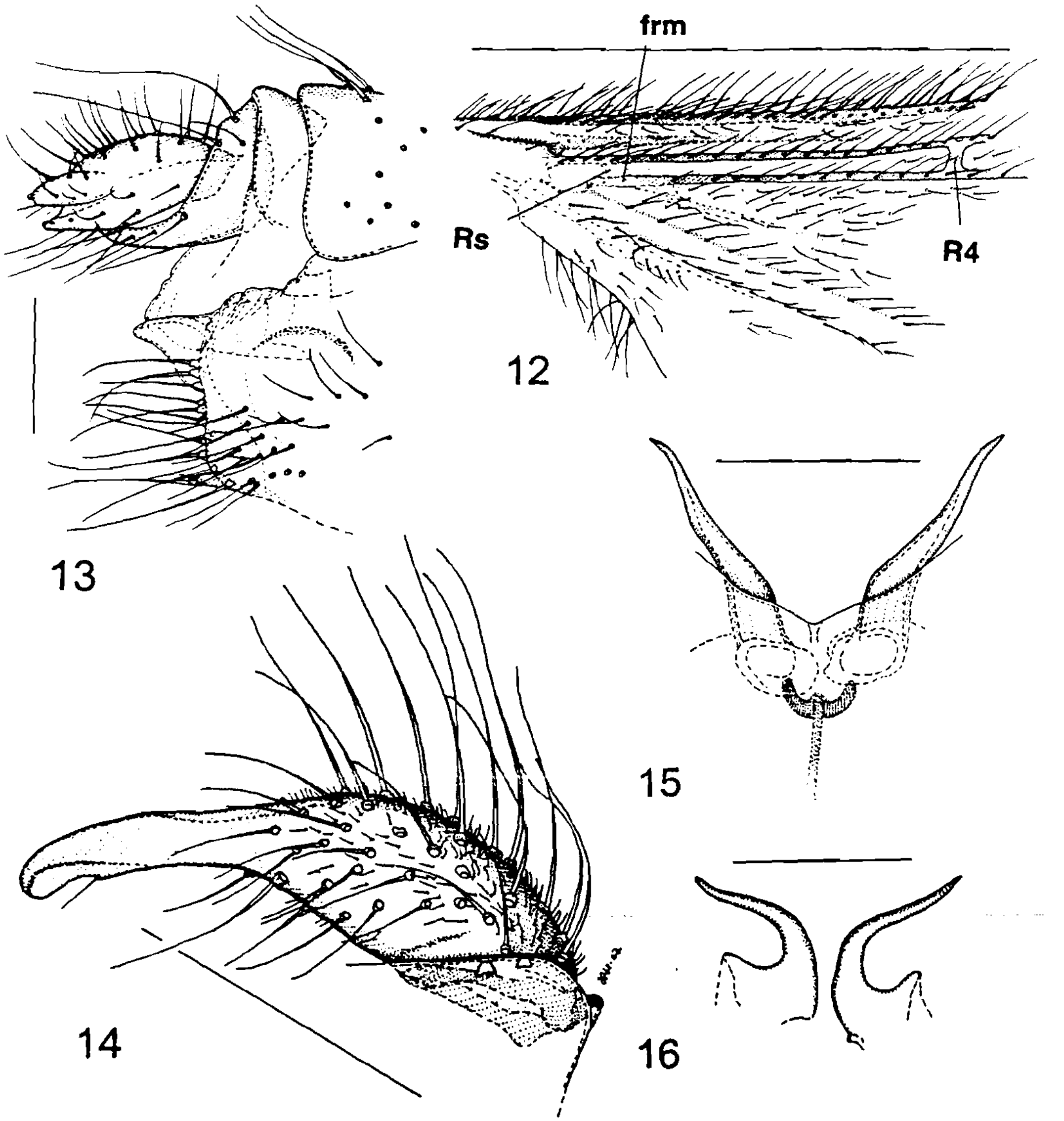
Abdomen. With segments 1 and 8 shorter than other segments. Sternite 1 always bare. With six pairs of spiracles, one each on segments 2-7. Tergal plaques small and inconspicuous, situated in a lateral position on each of the sclerites, with their pattern, where recognizable, 0/2/2/1/1/1/1/0.

Terminalia. Male. Sternite 9 absent as a distinct sclerite. Gonocoxites without lobes, with strongly sclerotized transverse and longitudinal ribs interiorly; gonocoxal apodemes long, extending far beyond ventral gonocoxal margin, with inwardly-directed processes that provide the base for parameres. Gonostyli simple (i.e. not lobed), slender or stout, with basolateral apophysis large, with apical tooth-like structure. Ejaculatory apodeme long, strongly sclerotized, usually with head-like extension terminally and sometimes with widened basal portion. Parameres fully separated, i.e. not forming a tegmen, consisting of one pair of tusk-like processes (in one species, a second pair of parameral structures may be indicated). Tergite 9 present as a short, weakly sclerotized plate usually following laterally the convexity of, and being connected to, the gonocoxites. Tergite 10 absent. Cerci with numerous setae of various lengths distally and dorsally. Hypoproct smooth, consisting of one or two lobes, densely pubescent and with 2 strong setae or pairs of setae at distal margin. Female (basic pattern: consult species descriptions for deviating characters). Tergite 8 large, sclerotized, setose. Gonocoxites 8 comparatively broad and short, i.e. extending maximally up to proximal cercus, truncate terminally, with less than 10 strong setae ventrodistally and finer, shorter setae elsewhere; gonapophyses 8 distinct, weakly sclerotized; tergite 9 short, non-setose; gonapophysis 9 present as sclerotized internal ribs that merge anteriorly; tergite 10 well-developed, setose, with a long posterior extension in which the proximal cercus is embedded; sternite 10 largely hidden behind tergite 10 but distinct, merged posteriorly, setose; cerci two-segmented and bearing numerous strong, straight setae, proximal cercus large and elongate, truncate posteriorly, distal cercus much smaller, elongate and narrow, embedded in depression of proximal cercus. Without sclerotized spermathecae.

Immature stages. Unknown.

Monophyly and phylogenetic relationships of *Colonomyia*

In addition to the *Heterotricha* group sensu Chandler (2002), Rangomaramidae (Jaschhof & Didham 2002) and *Ohakunea* (Jaschhof & Hippa 2003), *Colonomyia* is another group of sciaroids with some resemblance in its habitus to the Sciaridae. However, as soon as one begins to con-



Figs 12-16: *Colonomyia borea* sp. n.: - 12: wing base of female, dorsal view (paratype) (scale 1.0 mm); - 13: female terminalia, lateral view (paratype) (scale 0.10 mm); - 14: gonostylus, ventral view (from Honduras) (scale 0.10 mm); 15: parameres, ventral view (paratype) (scale 0.10 mm); 16: ditto (from Honduras).

sider structural details, it becomes obvious that *Colonomyia* is a monophyletic group distinct from the lineages referred to above and apparently most closely related to *Ohakunea*.

The monophyly of *Colonomyia* is based on the following synapomorphies (Colless 1963, Matile & Duret 1994, this study): (1) the epimeron 2 is shortened, which is accompanied by the strong development ventrally of the laterotergite; (2) the mediotergite is very high and in a subvertical position; (3) the basitarsi bear a longitudinal row of pale, blunt-ended and projecting setae; (4) the tarsal claws are deeply split into two branches; (5) M1+2 is mainly obliterated except for its most proximal and distal portions; (6) in the male terminalia the gonocoxal apodemes are exceedingly long and bear inwardly-directed processes that provide the base for the parameral tusks; (7) the gonocoxites bear interiorly sclerotized ribs; (8) in the female terminalia the distal cercus segments are much reduced in size and are characteristically embedded in the proximal segments.

Arguments for the sister-group relationship between *Colonomyia* and *Ohakunea* are derived from the wing venation, which is very peculiar in these two genera. As explained previously for *Ohakunea* (Jaschhof & Hippa 2003), these pecularities are the strong basalization of Rs and the presence of R4. As regards plesiomorphous features in *Colonomyia*, it is noteworthy that the maxillary palpi are basically five-segmented and the male terminalia have the parameres separated. In these two points *Colonomyia* agrees with *Ohakunea*, but contrasts with the Sciaridae where the palpi never exceed four segments and the parameres are fused to form a tegmen.

There is now common agreement that the clade *Colonomyia*+*Ohakunea* (*C*+*O*) is distinct from the Sciaridae and should not be classified in this family (Matile 1990, Matile & Duret 1994, Chandler 2002, Jaschhof & Hippa 2003); however, the relationship between *C*+*O* and the Sciaridae is less clear. It is obvious that this latter issue must also take into consideration the *Heterotricha* group (which may not be monophyletic, see Chandler 2002), the Rangomaramidae or Rangomaramidae +Cecidomyiidae (Jaschhof & Didham 2002), and possibly even the Diadocidiidae. One of the main obstacles to the further resolution of these phylogenies appears to be the lack of any information on the preimaginal stages of the enigmatic groups referred to above. Chandler (2002: 132) points to the difficulties arising from comparative studies that depend exclusively on sciaroid adults. His argumentation scheme on sciaroid interrelationships (Chandler 2002: 142, Fig. 103) reflects these difficulties, and these may become even worse when new taxa are added to his analysis (Jaschhof *in press*).

Distribution and phenology

Five of the six species of *Colonomyia* are distributed in the southern hemisphere; only *C. borea* occurs north of the equator. Even though two species, *C. borea* and *C. rakelae*, are found in tropical latitudes, their occurrence appears to be confined to high elevations, where the climatic conditions are certainly comparable to those in the cool-temperate regions where the other four species live. As regards the Australian *C. albicaulis*, Colless (1963) describes it as occurring by preference in "the colder, more mountainous areas" of southeastern Australia. Cool-temperate regions of the southern Neotropics (Argentina, Chile) provide the habitats for the three species *C. acutistyla*, *C. magellanica* and *C. obtusistyla*. As the sciaroid fauna in all these regions is poorly studied, and *Colonomyia* individuals appear to be uncommon or even rare, one may assume that further congeneric species remain to be discovered. As regards other Gondwanan landmasses, the presence of *Colonomyia* in New Zealand is very unlikely as this sciaroid fauna has recently been intensively studied (Jaschhof *unpubl.*). *Colonomyia* is clearly a group of silvicolous flies. Individuals have been obtained by Malaise traps and sweep nets, with males captured more abundantly than females (sex ratio males:females = 2.4:1). In total, only some 90 *Colonomyia* specimens have been mentioned in the sciaroid literature (including this article). The immature stages and larval biology of *Colonomyia* species are unknown.

Species of *Colonomyia*

Six species of *Colonomyia* are currently known:

C. acutistyla Matile & Duret, 1994 (Neotropical: Chile)

C. albicaulis Colless, 1963 (Australasian: Australia)

C. borea sp. n. (Neotropical: Costa Rica, possibly also Honduras and Venezuela)

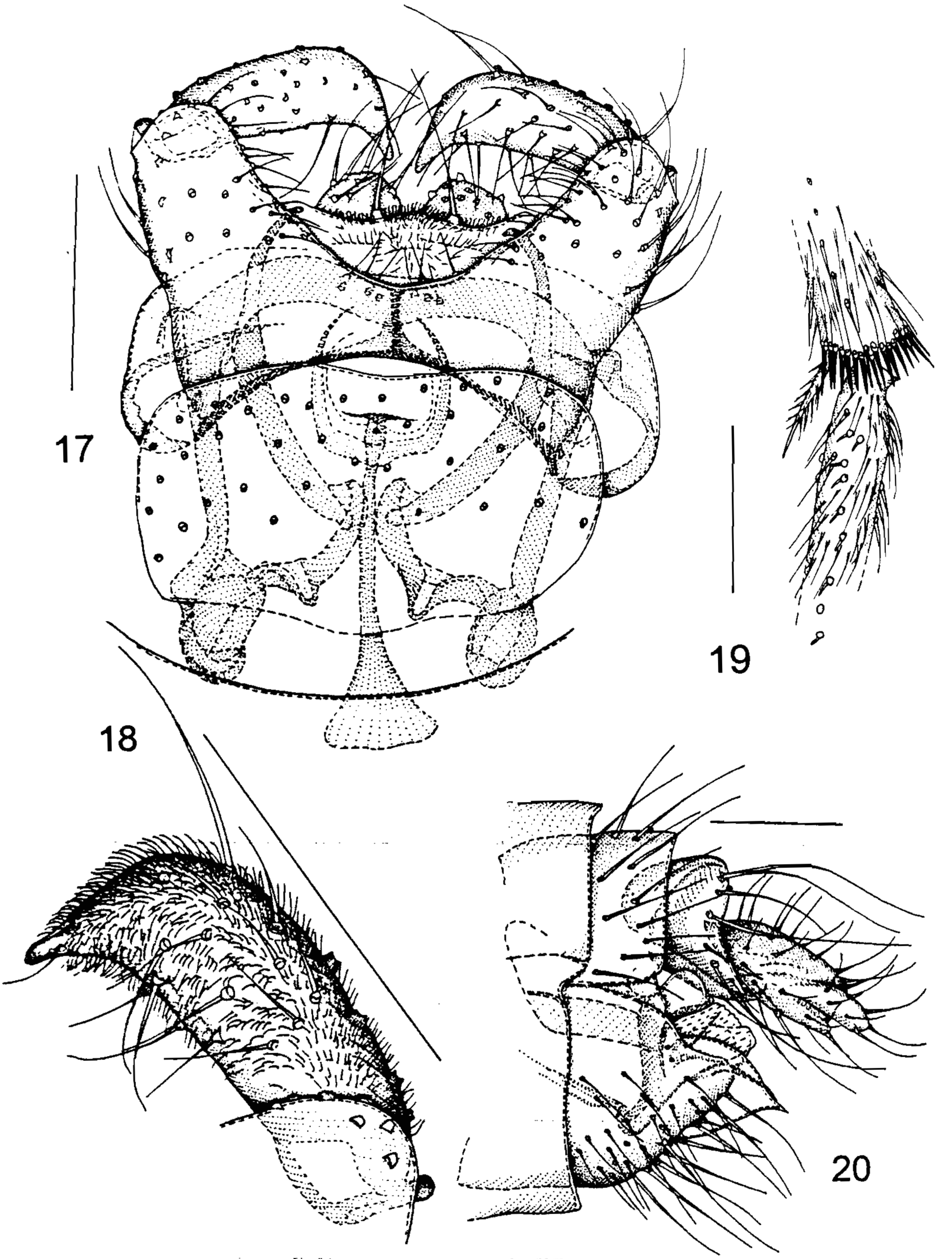
C. magellanica Matile & Duret, 1994 (Neotropical: Argentina, Chile)

C. rakelae sp. n. (Australasian: Papua New Guinea)

C. obtusistyla Matile & Duret, 1994 (Neotropical: Argentina, Chile).

Key to species (males)

1 Wing membrane without setae .... ***C. obtusistyla* Matile & Duret**
– Wing membrane covered with setae **2**
2 Male genitalia with gonocoxites deeply emarginated ventrally, i.e. emargination extending clearly beyond half-length of gonocoxites............. **3**
– Male genitalia with gonocoxites shallowly



Figs 17-20: *Colonomyia magellanica* Matile & Duret, 1994; - 17: male terminalia, ventral view (scale 0.10 mm); - 18: gonostylus, ventral view (scale 0.10 mm); 19: apical portion of mid tibia and proximal portion of basitarsus of female (scale 0.10 mm); - 20: female terminalia, lateral view (scale 0.10 mm). 17: specimen from Talca; 18-20: specimens from Malleco.

emarginated ventrally, i.e. emargination not reaching up to half-length of gonocoxites 4
3 Gonostyli crossing each other due to their considerable length, strongly tapering to tip.......... .... *C. acutistyla* **Matile & Duret**
– Gonostyli shorter, not crossing, largely parallel-sided with hook-like tip .... *C. magellanica* **Matile & Duret**
4 Labrum setose; laterotergite setose... *C. borea* **sp. n.**
– Labrum non-setose; laterotergite non-setose 5
5 Gonocoxites with a sclerotized rib longitudinally along midline; ejaculatory apodeme without pairs of slender processes apically...... .... *C. rakelae* **sp. n.**
– Gonocoxites without a sclerotized rib along midline; ejaculatory apodeme with 2 pairs of slender processes apically........... *albicaulis* **Colless**

Colonomyia albicaulis Colless, 1963

(Figs 1-8)

Supplement to the original description.- **Male. Head** (Fig. 1). Postfrons and face setose. Clypeus narrow, i.e. longer than wide. Fourth antennal flagellomere 5.5 times as long as wide. Terminal flagellomere with top-seta arising from a socket. Eyes at vertex more approximated than in congeneric species. Labrum non-setose. Lacinia rather short. Maxillary palpus with first segment absent, thus second of four segments bearing hyaline sensory hairs (contrary to original description).

Thorax. Scutum with setation rather sparse but some setae very long. Laterotergite non-setose.

Legs. Fore tibia with anteroapical depression bearing numerous setae, the distalmost of which form an irregular comb. Mid and hind tibiae apically with a comb of 8-10 spine-like setae. Basitarsi beneath with numerous spine-like setae which are much fewer in number and are concentrated apically on tarsomeres 2-5, also with longitudinal row of 3-4 pale, blunt-ended, projecting setae proximally. Tarsal claws, contrary to original description, deeply split into two branches as in congeneric species.

Wing (Fig. 3). Venation: Sc long, almost reaching C.

Terminalia. Gonocoxites (Fig. 4) with setae of various lengths, ventroproximally with a broad, non-setose connection, interiorly with strongly sclerotized ribs both running along ventroproximal margin and framing the non-setose portion; with gonocoxal apodemes long and wide. Gonostyli (Figs 4, 5) elongate, crossing each other due to their considerable length, with a broad, densely setose basal portion extending into a long, narrow, curved process, the latter densely hairy and bearing a few short, fine setae and with its apical portion bare except for 1 setula. Ejaculatory apodeme (Figs 6, 7) consisting of a long sclerotized rod and head-like extension, the latter with two pairs of slender processes, inner pair usually shorter than outer pair (Fig. 6) but longer in two of the specimens studied (Fig. 7, see Discussion). Parameres (Fig. 4) tusk-like, arising from obliquely-inclined processes of gonocoxal apodemes. Tergite 9 (Fig. 8) with a very narrow central portion and lobe-like, subtriangular lateral portions, the latter setose and with bare apices. Cerci (Fig. 8) terminally rounded and with long, strong setae. Hypoproct (Fig. 8) one-lobed, elongate triangular, bearing dense pubescence and 2 long, strong top-setae.

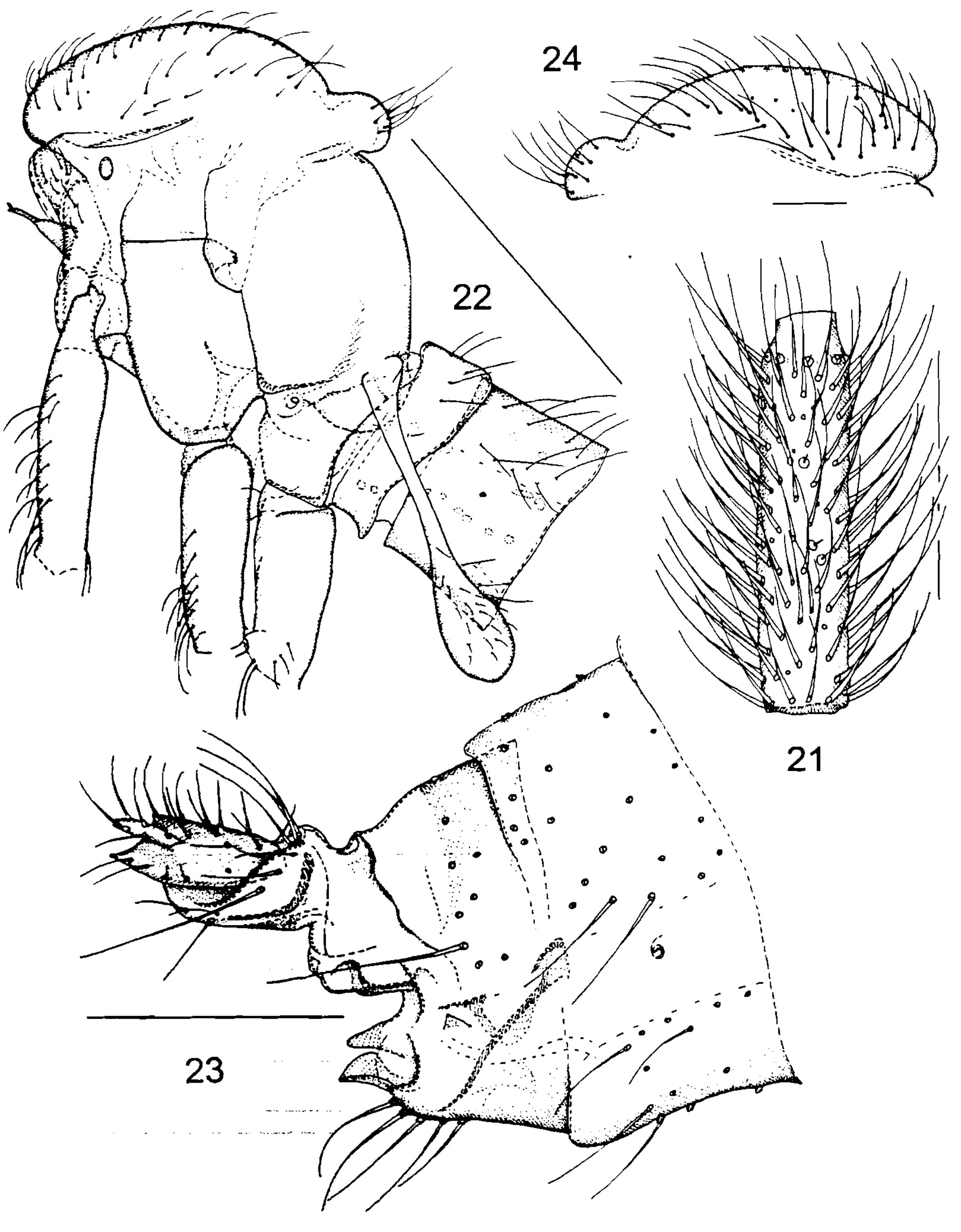
Female. Head. Fourth antennal flagellomere a little shorter than in males.

Legs. Mainly as in males (for details of fore leg, see Fig. 2). Basitarsi with a row of pale, blunt-ended setae up to 5 setae long.

Terminalia. The terminalia differ from the basic pattern outlined in the genus description by having an extensive, complicated sclerotized armature interiorly that involves tergite 9, gonapophyses 9 and possibly further structures. On the basis of the few specimens available for study, we are unable to resolve this type of structure in detail.

Discussion.- Two of the males studied (from Coff's Harbour and Dorrio-Coramba Road) differ from the remaining males in the outline of the ejaculatory apodeme (Fig. 6 vs 7) but otherwise show no further differences. We assume that the inner pair of distal processes of the apodeme is contractile and its length thus variable – consequently we consider all the specimens studied to be conspecific.

Material studied.- Australia: New South Wales: Brown Mountain, Rutherford Creek, 11 Nov. and 19 Jan. 1961, D.H. Colless, 1 male paratype and 1 female paratype; Macquarie Falls, 14 Nov. 1960, D.H. Colless, 1 male; 33 miles Dorrio-Coramba Road, 18 April 1970, D.H. Colless, 1 male; Coff's Harbour, Bruxner Park, 11 Oct. 1962, D.H. Colless, 1 male and 1 female; Monga, 19 July 1962, D.H. Colless, 1 male and 1 female; Victoria: Cumberland Creek, 24 Nov. 1964, N. Dobrotworsky, 1 male; Mount Dom-Dom, 22 Oct. 1961, D.H. Colless, 1 male; Cement Creek, 27 Oct. 1961, D.H. Colless, 1 male; Bonang Highway, Bendoc Road junction, 10 km S Bonang, 9 Nov. 1976, D.H. Colless & Z. Liepa, 1 male and 1 female; Tasmania: Mount Wellington, 12 Feb. 1963, D.H. Colless, 1 male (all in Canberra).



Figs 21-24: *Colonomyia rakelae* sp. n. (Figs. 21-23) and *C. borea* sp. n. (Fig. 24); - 21: male antennal flagellomere 4 (scale 0.10 mm); - 22: thorax of male, lateral view (scale 0.50 mm); - 23: female terminalia, lateral view (scale 0.10 mm); 24: scutum and scutellum of male, lateral view (scale 0.10 mm). All paratypes.

Colonomyia borea sp. n.

(Figs 9-16, 24)

Description.- **Measurements.** Body length in males 2.2-2.8 mm, in females 2.0-2.8 mm. Wing length in males 2.1-2.5 mm, in females 1.9-2.8 mm.

Male. Head. Postfrons and face setose. Fourth antennal flagellomere 4-4.5 times as long as wide. Terminal flagellomere rarely with top-seta arising from a socket. Labrum setose.

Thorax. Scutum with some of lateral setae very strong and long. Laterotergite with 1-3, rarely more setae.

Legs. Fore tibia with an anteroapical depression bearing numerous setae, the distalmost of which form an irregular comb. Mid tibia apically with a sparse comb of 5-6 spine-like setae. Hind tibia with apical portion bearing numerous spine-like setae. Basitarsi beneath with numerous spine-like setae which are much fewer in number on tarsomeres 2-5, also with a longitudinal row of 8-14 pale, blunt-ended, projecting setae proximally (Fig. 9). Inner branches of tarsal claws with a small side tooth.

Wing. Venation: Sc long, almost reaching C; M1+2 complete but extremely pale in most specimens studied.

Terminalia. Gonocoxites (Fig. 10) short and wide, ventrally with a wide, V-shaped emargination not extending to half length of gonocoxites, with setae of various lengths except in ventroproximal half, interiorly with three strongly sclerotized transverse ribs: one along ventroproximal gonocoxal margin and two parallel to it but running more distally, with another rib running longitudinally along midline; gonocoxal apodemes long, characteristically angled. Gonostyli (Figs 10, 14) crossing each other due to their considerable length, with heavy, densely setose basal portion extending into a long, slender process, the latter bare except for 2 weak, subterminal setulae and numerous trichiae. Ejaculatory apodeme (Fig. 10) present as a long sclerotized rod with a short, three-pointed fork terminally. Parameres (Fig. 10, 15 and 16) tusk-like, arising from obliquely-inclined, strikingly looped processes of gonocoxal apodemes. Tergite 9 subtrapezoid, with straight to slightly emarginate distal margin, with numerous setae of various lengths. Cerci (Fig. 10) large, broadly rounded terminally, setose. Hypoproct (Fig. 10) apparently consisting of two lobes located one behind the other, both lobes large with almost straight to broadly rounded distal margin, densely pubescent, dorsal lobe bearing 2-4 strong setae.

Female. Head. Fourth antennal flagellomere 3.5 times as long as wide.

Wing. Venation as in males but in some specimens M1+2 more distinctive due to the large size of individuals (for details of wing base, see Fig. 12).

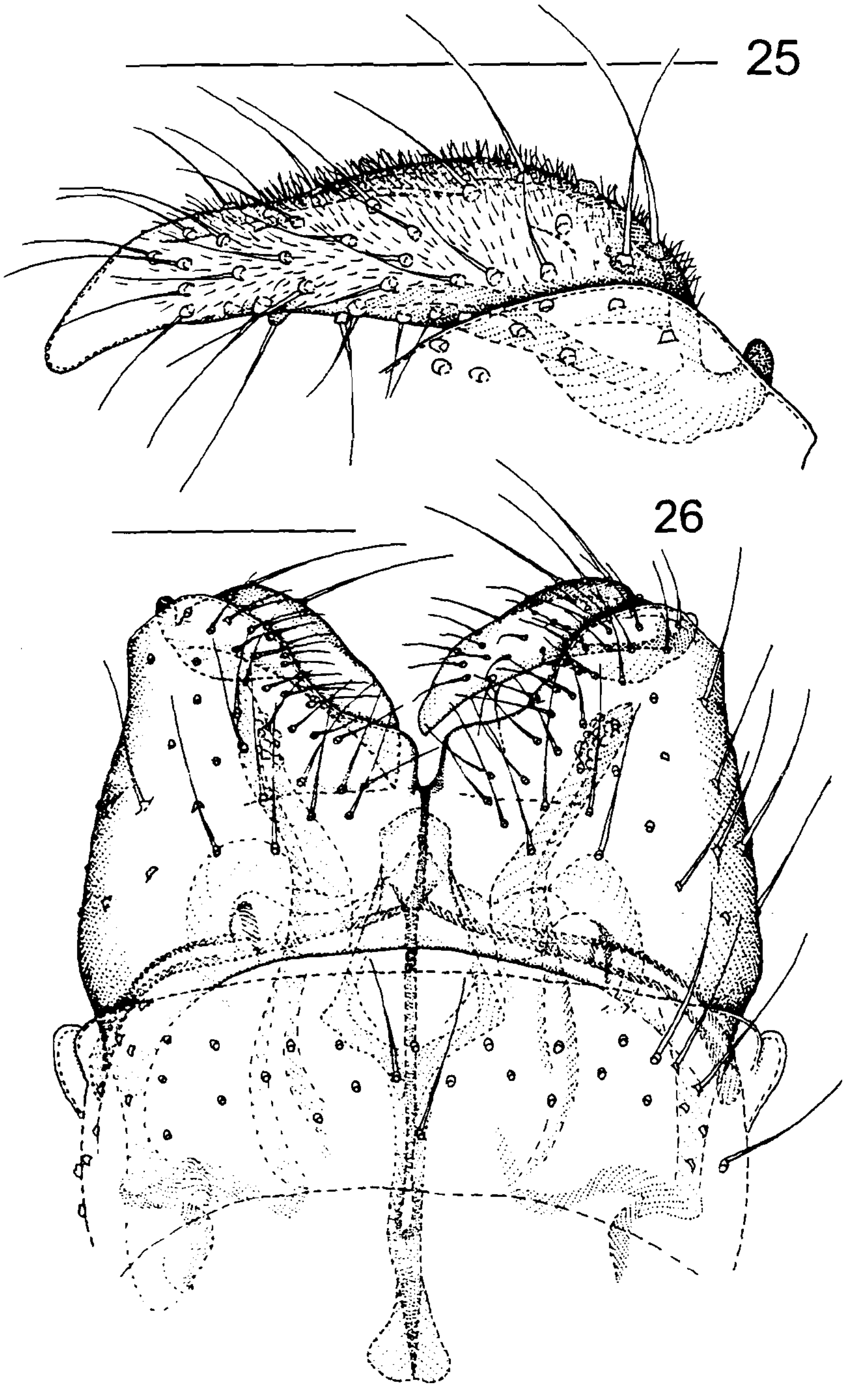
Terminalia (Fig. 13). Gonapophyses 9 present as weakly sclerotized plates, not ribs, that are not merged anteriorly.

Discussion.- The study of the 13 males from the type locality enabled us to recognize some variation in the outline of the male genitalic structures, such as the gonostyli (for instance, length of the apical process) and the parameres (for instance, length and orientation of the tusks). We are unable to decide, however, whether this variation is a natural phenomenon or a preparation artefact, or perhaps both. In addition to the type material of *C. borea*, we studied two males from Honduras and one male and one female from Venezuela which may belong to the same species, or to one or two species very similar to it. The males from Honduras (Fig. 14) have the gonostyli somewhat stouter than in Costa Rican males and the parameral tusks (Fig. 16) are directed sidewards; the male from Venezuela has the gonostyli with a strikingly short apical process and the parameral tusks are also short. On the basis of the limited material available for study, we refrain from making a definite decision but point to the possibility that there might exist a '*borea* group' of species in the mountain regions of the northern Neotropics.

Etymology.- The name is Latin meaning 'northern', referring to the distribution of this species in the northern hemisphere.

Types.- Holotype: male, Costa Rica, Prov. Cartago, Finca los Lagos, Madreselva, 2600 m, in rain forest, June 1994, by Malaise trap, M.M. Chavarria & A. Solano (in Santo Domingo). Paratypes: 12 males, 10 females, same locality as the holotype but various dates between 28 June 1993 and May 1995 (in Santo Domingo, Stockholm and Greifswald).

Additional material.- Honduras: La Tigra National Park, Francisco Morazan, 14.22'N, 87.12' W, 21 April 1995, Malaise trap, R. Cordero, 2 males (in Greifswald). Venezuela: Aragua, Henry Pittier Nat. Park, Pico Guacamaya, 1830 m, Malaise trap, 15. – 30.11.1997, T. Pape, 1 male and 1 female (in Stockholm).



Figs 25-26: ***Colonomyia rakelae*** sp. n., male: - 25: gonostylus, ventral view (scale 0.10 mm); - 26: terminalia and sternite 8, ventral view (scale 0.10 mm). Holotype.

Colonomyia magellanica Matile & Duret, 1994

(Figs 17-20)

Supplement to the original description.- **Measurements.** Body length in males 1.9-2.0 mm. Wing length in males 2.0-2.2 mm.

Male. Head. Postfrons and face setose. Fourth antennal flagellomere 3.5 times as long as wide. Labrum setose.

Thorax. Vestiture of scutum rather sparse, with some of lateral setae very strong and long. Laterotergite with 1-2 setae.

Legs. Fore tibia with an anteroapical depression bearing a comb of about 14 setae. Mid and hind tibiae apically with a comb of 7-10 spine-like setae. Basitarsi beneath with numerous spine-like setae which are much fewer in number on tarsomeres 2-5, also with a longitudinal row of 7-11 pale, blunt-ended, projecting setae proximally. Inner branches of tarsal claws with a small side tooth.

Wing. Membrane with setation sparser than in congeneric species, in particular towards wing base. Venation: R1 entering C in proximal half of wing.

Terminalia. Gonocoxites (Fig. 17) narrow, ventrally with a short connection basally and a deep, widely U-shaped emargination, with setae of various lengths except on proximal portions, interiorly with transverse sclerotized ribs: one along ventroproximal margin and another located more distally, the latter very broad and bearing a few setae on both sides of its midpoint, with another rib running longitudinally along midline; gonocoxal apodemes very long, straight and with ovoid extension anteriorly. Gonostyli (Figs 17, 18) heavy, almost cylindrical and straight, with apex curved inwards, tapering and terminating in a very short, apparently fingernail-like tooth, with setae of various lengths elsewhere. Ejaculatory apodeme (Fig. 17) consisting of a long sclerotized rod with a heavy, subtriangular extension basally and large, subrectangular head apically. Parameres (Fig. 17) tusk-like, very long, arising from obliquely-inclined, strikingly looped processes of gonocoxal apodemes. Tergite 9, cerci and hypoproct as in *C. borea*.

Female. Thorax. Laterotergite in one large specimen studied with 4 setae.

Terminalia (Fig. 20). With sclerotized armature interiorly that includes gonapophyses 9 and possibly further structures.

Material studied.- Chile: Malleco, 11.4 km E Manzanar (38°28´S, 71°30´W), 1425 m, 18 Nov.-2 Dec. 1994, by flight interception trap, R. Leschen & C. Carlton, 1 male and 1 female (in Greifswald); Talca, 66.5 km E San Clemente (35°43´S, 70°50´W), 625 m, 20 Nov.-3 Dec. 1994, by flight interception trap, R. Leschen & C. Carlton, 3 males (in Greifswald and Stockholm).

Colonomyia rakelae sp. n.

(Figs 21-26)

Description. - **Measurements.** Body length in males 2.1-2.7 mm, in females 2.9 mm. Wing length in males 2.1-2.5 mm, in females 2.4 mm.

Male. Head. Postfrons and face setose. Fourth antennal flagellomere (Fig. 21) almost 5 times as long as wide. Labrum non-setose.

Thorax (Fig. 22). Setation of scutum rather short and sparse. Laterotergite non-setose.

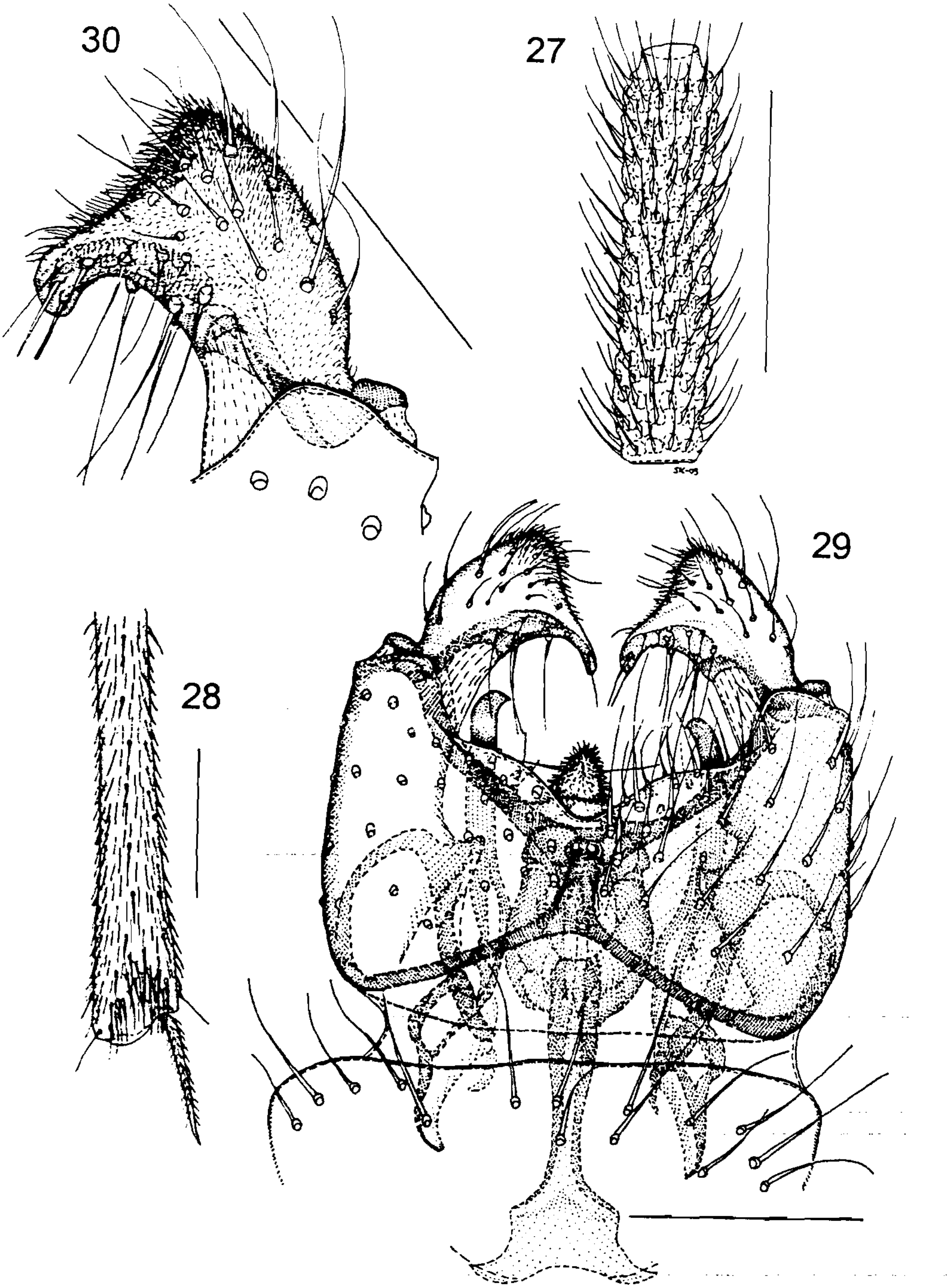
Legs. Fore tibia with an anteroapical depression bearing numerous setae, the distalmost of which forms an irregular, curved comb. Mid tibia apically with a sparse comb of 5-6 spine-like setae. Hind tibia with a comb of up to 14 spine-like setae. Basitarsi beneath with numerous spine-like setae which are much fewer in number on tarsomeres 2-5, also with a short, longitudinal row of 1-4 pale, blunt-ended, projecting setae proximally.

Wing. Venation: Sc long, almost entering C.

Terminalia. Gonocoxites (Fig. 26) massive, ventrally with an emargination that is wide at first and then strongly narrowed, interiorly with strongly sclerotized ribs both along ventroproximal margin and between that margin and emargination, with setae of various lengths except in proximal third; with gonocoxal apodemes long and wide. Gonostyli (Figs 25, 26) elongate, usually directed inwards and crossing each other, broad in basal half and much narrower in distal half, densely setose in basal three-fourths and bare in apical fourth. Ejaculatory apodeme (Fig. 26) consisting of a long sclerotized rod with broadened base and very large head-like extension distally. Parameres (Fig. 26) tusk-like, arising from the almost right-angled, inwardly-directed processes of the gonocoxal apodemes. Tergite 9 short, with very narrow central portion and subtriangular lateral portions, with numerous long setae. Cerci and hypoproct as in *C. albicaulis*.

Female. Head. Fourth antennal flagellomere 3.5 times as long as wide.

Terminalia (Fig. 23). Tergite 9 much reduced. Distal cercus very narrow.



Figs 27-30: *Colonomyia obtusistyla* Matile & Duret, 1994, male; - 27: antennal flagellomere 4 (scale 0.10 mm); - 28: fore tibia with anteroapical depression (scale 0.10 mm); - 29: terminalia, ventral view (scale 0.10 mm); - 30: gonostylus, ventral view (scale 0.10 mm). From Chile.

Types.- Holotype: male, Papua New Guinea, Morobe province, Ilauru, Mt Kolorong, 2260 m, in primary mountain forest, 30 Oct.-11 Nov. 1999, by Malaise trap, H. Hippa, R. Norberg & D. Borisch (in Stockholm). Paratypes: 1 male, same data as the holotype; 1 male, 1 female, same data as the holotype but elevation 2260 m; 1 female, same data but elevation 2200 m, 26-30 Oct. 1999 (in Stockholm and Greifswald).

Etymology.- The species epithet is devoted to Ms. Rakel Norberg, Stockholm, who assisted in collecting the material in Papua New Guinea.

Colonomyia obtusistyla Matile & Duret, 1994

(Figs 27-30)

Supplement to the original description.- **Male. Head.** Postfrons and face non-setose. Clypeus narrow, i.e. longer than wide. Antennal flagellum with a very dense covering of setae of various lengths but shorter than diameter of flagellomere, setae arising from strikingly large basal pores which produces an almost honeycomb-like pattern (Fig. 27). Fourth antennal flagellomere (Fig. 27) almost 5 times as long as wide. Eyes at vertex separated for a distance that might be longer than width of ocellar triangle (not recognizable with certainty in the one specimen available for study). Labrum non-setose. Maxillary palpus with proximal two segments reduced, i.e. with the first of three segments bearing sensory hairs.

Thorax. Scutum with some of lateral setae very long and strong. Laterotergite non-setose.

Legs. Setation strikingly short, in particular on tibiae and tarsi (Fig. 28), setation on tarsi increasingly sparse distally. Fore tibia with anteroapical depression lacking sharp border and bearing numerous irregularly arranged setae (Fig. 28). Mid and hind tibiae apically with numerous short, spine-like setae. Tarsal claws very small.

Wing. Membrane without setae. Venation: R1 entering C closer to wing apex than in congeneric species; R4 longer than in congeneric species; CuA2 not as strongly curved distally as in congeneric species.

Terminalia. Gonocoxites (Fig. 29) massive, with a wide, rather shallow emargination ventrally, with setae of various lengths except on most proximal portions, interiorly with sclerotized ribs transversally along proximal and distal margins and longitudinally along midline, distal transverse rib bearing a few setae on both sides of its midpoint. Gonostyli (Figs 29, 30) stout, with almost rectangular basal portion and hook-like apical process, the latter curved inwards, tapering and terminating in a very short, apparently fingernail-like tooth and 2 accompanying spine-like setae, with ordinary setae of various lengths elsewhere. Ejaculatory apodeme (Fig. 29) consisting of a strong sclerotized rod with a large, subtriangular extension basally and a large, horseshoe-shaped extension apically. Parameres (Fig. 29) tusk-like, long and rather slender, arising from gonocoxal apodemes. Behind ejaculatory apodeme, and between parameral tusks, with a plate-like, sclerotized structure that may also be of parameral origin (not shown in Fig. 29). Tergite 9 comparatively small, subtrapezoid, without lateral connection to gonocoxites, with sclerotized proximal margin and weak, almost straight distal margin. Cerci and hypoproct distorted in the only specimen available for study.

Female. Not studied.

Material studied.- Chile: X:e Región, Metri, 30 km S Puerto Montt, Malaise trap 20 Feb.-17 March 1995, Agneta Nilsson & Christina Halling, 1 male (in Stockholm).

Infrageneric relationships

The Neotropical species of *Colonomyia*, excluding *C. obtusistyla*, are more closely related to each other than to the Australasian species. As regards the latter, *C. albicaulis* and *rakelae* have quite a number of derived features in common, such as the narrow clypeus, the basitarsi with a short row of pale, blunt setae and the male terminalia with the hypoproct subtriangular and tergite 9 two-lobed. Among the Neotropical species, *C. magellanica* and *borea* appear to be very closely related, a fact indicated by several characters in common such as the setose labrum, setose laterotergites, the basitarsi with a long row of pale, blunt setae and the male terminalia with a two-lobed hypoproct. *Colonomyia acutistyla* should be close to both *magellanica* and *borea*, so far as can be concluded from the description by Matile and Duret (1994) which, however, does not mention many important details. In many respects, *C. obtusistyla* is peculiar. It differs from both its Neotropical and Australasian congeners in the setation of postfrons, face, antennae, wings and legs; shortened maxillary palpi; size-reduced tarsal claws; and details of the wing venation. As regards the male terminalia, however, *C. obtusistyla* appears to be a typical representative of the genus *Colonomyia*.

Unfortunately, the single specimen we had available for study is not in perfect condition, which also applies to the male genitalic structures, in particular to those behind the parameres. Despite the differences referred to above, we agree with Matile and Duret's (1994) view that a generic separation of *C. obtusistyla* would not be reasonable with present knowledge. In *Colonomyia* species, structural details of the female terminalia may provide further indications for interspecific relationships, but for this more material and in better condition than we had available is needed for study.

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