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OF AUSTRALASIA (DIPTERA: BOMBYLIIDAE)

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ISSN 0893-1348

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REVIEW AND PHYLOGENETICS OF THE ANTONIINAE OF AUSTRALASIA (DIPTERA: BOMBYLIIDAE)

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ABSTRACT. The bombyliid subfamily Antoniinae of the Australasian Region is reviewed taxonomically and analyzed cladistically. *Antoniaustralia*, previously treated as a junior synonym of *Antonia*, is shown to be a good genus and *A. arida*, **n. sp.**, is described and illustrated. *Cyx*, **n. gen.**, is described to include *Cyx rieki*, **n. comb.**, *C. roddi*, **n. comb.**, *C. decorata*, **n. comb.**, and the new species *Cyx papuana*, **n. sp.** The eggs of *Cyx* possess an unusual apically-flared pedicel with papillae. This pedicel suggests that the female oviposits directly onto a substrate rather than while hovering in the air as in other Bombyliidae.

INTRODUCTION

Becker (1913) proposed the new genus *Antoniaustralia* for his new species *hermanni* from northern Australia and separated the genus from its closest relative, *Antonia* Loew, by the placement of the r-m crossvein, the shape of the first posterior cell, the segmentation of the abdomen, and the shape of the third antennal segment. Hardy (1922) and Bezzi (1924) followed in treating *Antoniaustralia* as a separate genus. However, Paramonov (1929) elected to reduce *Antoniaustralia* to subgeneric status under *Antonia*. Paramonov (1939) returned it to generic status, but subsequent works treated *Antoniaustralia* as a junior synonym of *Antonia* (e.g., Paramonov 1950, Hull 1973).

Bowden (1978), in examining the zoogeographical implications of the distribution of *Antonia* in the Old World, preferred to exclude discussion of the Australian species "being unconvinced that they are correctly placed [in *Antonia*]". Evenhuis (1989), in his catalog of the Australasian Bombyliidae, returned *Antoniaustralia* to generic status and subsequently followed this treatment in his world classification of the Bombyliidae (Evenhuis 1991). Yeates (1990), however, treated the Australian species as *Antonia*. The present study gives characters to support the treatment of *Antoniaustralia* as separate from *Antonia* and describes a new genus allied to *Antoniaustralia*, into which all the previously described Australian species except *hermanni* are transferred.

MATERIALS AND METHODS

Specimens examined in this study derived from the following institutions and collections: Australian Museum, Sydney (AMS), Australian National Insect Collection, CSIRO, Canberra (ANIC), Biological Resources Division, Agriculture Canada, Ottawa (CNCI), Bishop Museum, Honolulu (BPBM), California Academy of Sciences, San Francisco (CAS), N. L. Evenhuis Collection (NLE), J. C. Hall Collection, now housed at the University of California, Riverside (UCR), Illinois Natural History Survey,

Champaign (INHS), National Museum of Natural History, Washington, D.C. (USNM), The Natural History Museum, London (BMNH), South African Museum, Cape Town (SAMC), and the Zoologische Sammlung des Bayerischen Staats, Munich (ZSMC).

Morphological terminology follows McAlpine (1981) with modifications to female genitalia terminology following Hall & Evenhuis (1980). Eggs of *Cyx*, used for scanning electron microscopic analysis, were fixed using a 0.16 M Sorensen's phosphate buffered solution of 3.5 % glutaraldehyde, postfixed with osmium tetroxide, critical-point dried, sputter-coated with gold-palladium, and photographed on a Hitachi S-800 scanning electron microscope. Label data for specimens examined are given verbatim. Inferred data or data taken from other sources are placed in square brackets.

SYSTEMATICS

Subfamily Antoniinae

Loew's (1856) description of *Antonia* was without subfamilial placement. Schiner (1868) was the first to treat *Antonia* within a subfamily and put it in the Lomatiinae, which included *Cyllenia* Latreille, *Acrophthalmyda* Bigot, *Apatomyza* Wiedemann, *Amictus* Wiedemann, *Tomomyza* Wiedemann, *Ogcodocera* Macquart, *Plesiocera* Macquart, *Lomatia* Meigen, *Anisotamia* Macquart, *Comptosia* Macquart, and *Neuria* Newman.

This placement of *Antonia* within the Lomatiinae stood until Becker (1913) proposed the subfamily Tomomyzinae, in which he placed *Antonia* and *Antoniaustralia* along with *Tomomyza* and *Plesiocera*. Becker characterized the members of this subfamily by their produced, snoutlike face. Becker's placement of *Antonia* within the Tomomyzinae was followed by Hesse (1956), Zaitzev (1966), Greathead (1967), and Hennig (1973) while other workers retained the genus within the Lomatiinae (e.g., Bezzi 1924, Paramonov 1939, Hall 1976, Evenhuis 1982, Theodor 1983, Zaitzev 1989).

Hesse (1956) recognized the peculiarity of members of the *Antonia*-group in southern Africa and stated that the group probably warranted separate subfamilial status. However, before this opinion was echoed by Bowden (1978) and Theodor (1983), Hull (1973) had already placed *Antonia* (including the Australasian species) into its own family-group category when he proposed his new tribe Antoniini within the Lomatiinae. Bowden (1980 [17 July]) and Greathead (1980 [15 August]) subsequently raised this tribe to subfamilial status in their respective works. This treatment has been followed by Evenhuis (1989, 1991) and Yeates (1990) and is continued here with further support from cladistic analysis.

Morphology of the terminal abdominal segments of female Antoniinae

Considerable confusion has existed regarding the terminology, structural homologies, and sexual differences of the terminal abdominal segments of genera of Antoniinae. Sexes have been mistaken as a direct result of this confusion (i.e., females appear like males). The focus of this difficulty is the unusual modification of the last visible female tergite (tergite 9+10) into paired lamellate projections (which apparently have been mistaken by some previous authors as gonostyli of male genitalia). Zaitzev (1966) considered these lamellate projections as a portion of tergite 9; however, I follow McAlpine (1981) in treating these as a single fused tergite 9+10.

The purpose of these modified structures is unknown (see discussion on oviposition below for more details), but they may well be homologous to the acanthophorites found in other genera of Bombyliidae. Modifications of acanthophorites (which usually possess

spines or thickened bristles in many asilomorph genera) are known in other bombyliid genera, for example, *Lordotus* Loew, where the acanthophorites have been enlarged and strengthened by heavy sclerotization, presumably for oviposition in the soil. The terminal female abdominal morphology for the genera of Antoniinae is illustrated in Figs. 12–14 and described below.

Tergite 9 fused indistinguishably with tergite 10; this tergite (9+10) enlarged laterally into paired lamellate projections bearing sensillae along apical margin and at tip; lamellate projections of varying lengths and thickness; basal portion of tergite 9+10 extending toward sternite 8 and hypoproct as paired, thin, sclerotized rods in *Antonia* and *Antoniaustralia*, these sclerotized basal rods absent in *Cyx*; cerci paired, fused ventrally by thick, sclerotized structure (penial guide); penial guide barbed along its length in *Antonia*, smooth or with small patch of hairs in *Antoniaustralia* and *Cyx*, not barbed; cerci with strong, thick bristles apicoventrally (these bristles on prominent projection in *Cyx* and some species of *Antonia*), remainder of ventral margin of cerci with long to short hairs; cerci connected basally to sclerotized sternal plate (hypoproct); area between hypoproct and sternite 8 defines genital opening.

KEY TO THE WORLD GENERA OF ANTONIINAE

1. Female with 3 spermathecae; proboscis thick with fleshy labellum; lateral margin of oral cavity of female thin, ridgelike, bare or hairs present only sparsely (except in *deco-rata*); disc of squama of wing bare in females; male genitalia with stout spines on produced apicomeral portion of gonocoxite; aedeagal apodeme not cruciate in cross-section . . . (Australasian Region) 2
- Female with 1 spermatheca; proboscis thin with pointed labellum; lateral margin of oral cavity of females thick, curved inward medially, with distinct patch of hairs; disc of squama hairy in females; male genitalia without spines on gonostylus or apicomeral portion of gonocoxite; aedeagal apodeme cruciate in cross-section . . . (Africa and south western Asia) *Antonia*
2. Wing with 3 submarginal cells; cerci of female without mesal projection with dense patch of bristles; male genitalia not rotated; egg without pedicel *Antoniaustralia*
- Wing with 2 submarginal cells; cerci of female with mesal projection with dense patch of bristles; male genitalia rotated 45°; egg with pedicel *Cyx*, new genus

Genus *Antoniaustralia* Becker

Antoniaustralia Becker, 1912: 422. *Nomen nudum*.

Antoniaustralia Becker, 1913: 458. Type species: *Antoniaustralia hermanni* Becker, 1913, by original designation.

Antoniaustralia is separated from *Antonia* by the thick proboscis and labellum, the presence of 3 spermathecae, and the lack of hairs on the disc of the squama in females. In *Antonia*, the proboscis is thin with a rather pointed labellum, females possess only 1 spermatheca, and the squama in females has hairs on the disc.

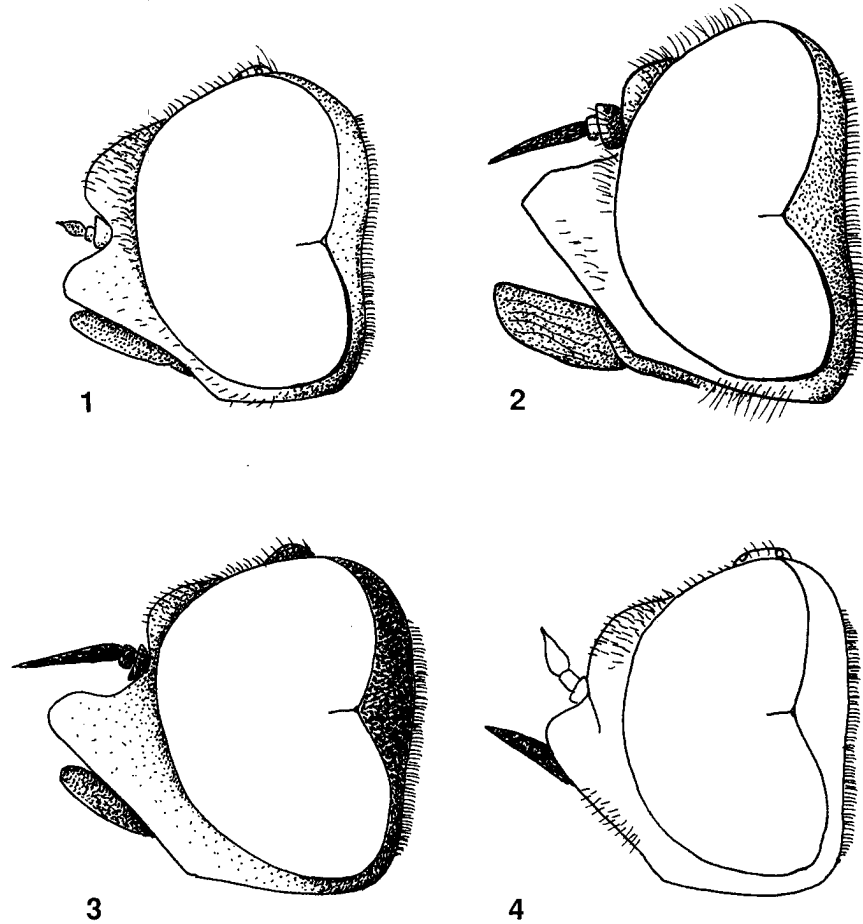
Antoniaustralia arida Evenhuis, new species

Figs. 1–3

This species is only known from 3 females; however, I do not hesitate in describing it as new based on comparisons with the other known species of *Antoniaustralia* and *Cyx*, n. gen. It is easily separated from the only other species of *Antoniaustralia*, *A. hermanni*, by the short 3rd antennal segment and the different abdominal pattern (Fig. 8).

Female. *Lengths.* Body: 7.5–8.0 mm; wing: 6.5–7.0 mm. *Head* (Fig. 1). Eyes dichoptic; touching lateral edges of ocellar tubercle, separation of eyes narrowing anterior to ocellar tubercle but still separated by width of anterior ocellus; ocellar tubercle brown, with pale yellow hairs; vertex brown to gray in ground color, front gray to yellow, overlaid by silvery gray pollinosity continuing

to bulbous frontal protuberance; yellowish gray ground color of face continuing laterally between oral margin and inner eye margin as thin strip to postgena; front and vertex with erect short yellow hairs, bulbous frontal projection and face with thick yellow scalelike hairs, scales continuing laterally to just below level of antennae; occiput brown to yellowish gray with yellow to silvery pollinosity; occiput with dense short white hairs surrounding occipital foramen, slight amount of white recumbent hairs on upper occiput between occipital fringe and hind eye margin; oral margin developed, but much reduced, blunt, thick at tip, produced forward only to level of 1st antennal segment, subshining white to postgena, with pale yellow hairs along lateral margin of oral cavity and ventrolaterally. Antennal segment I obconical, about 2 times wider than long, concave apically, yellow-white with yellowish orange to yellow hairs laterally and ventrally, white hairs mesally; segment II small, cylindrical, less than 1/2 size of segment I, yellow with yellowish orange hairs laterally and ventrally, short sparse brown hairs mesally; segment III conical basally, tapering to long thin neck (much the same as in *Villa*-group genera), bare, length subequal to length of segments I and II combined, with tiny apical brown stylar segment. Proboscis yellowish brown, slightly shorter than oral



Figs. 1-4. Heads of Antoniinae. 1, *Antoniaustralia arida* Evenhuis, n. sp.; 2, *Antoniaustralia hermanni* Becker; 3, *Cyx papuana* Evenhuis, n. sp.; 4, *Antonia* sp. (Kenya).

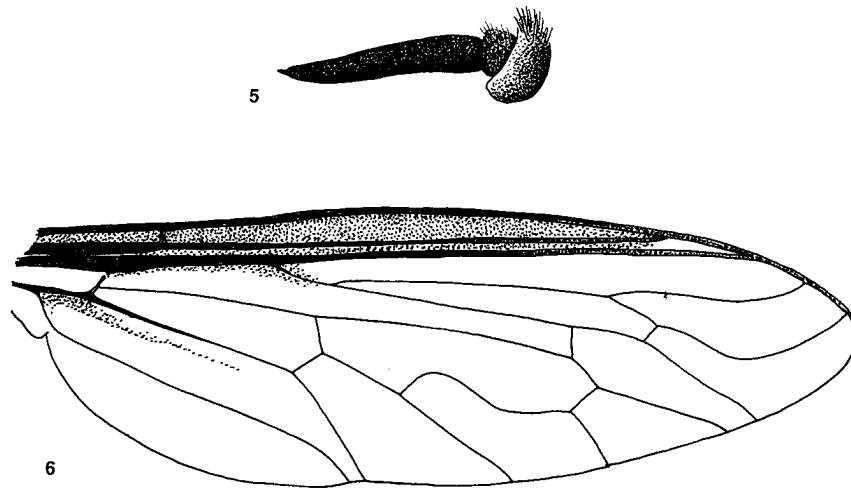


Fig. 5, *Cyx papuana* Evenhuis, n. sp., antennal, lateral view. Fig. 6, *Antoniaustralia hermanni* Becker, wing of holotype.

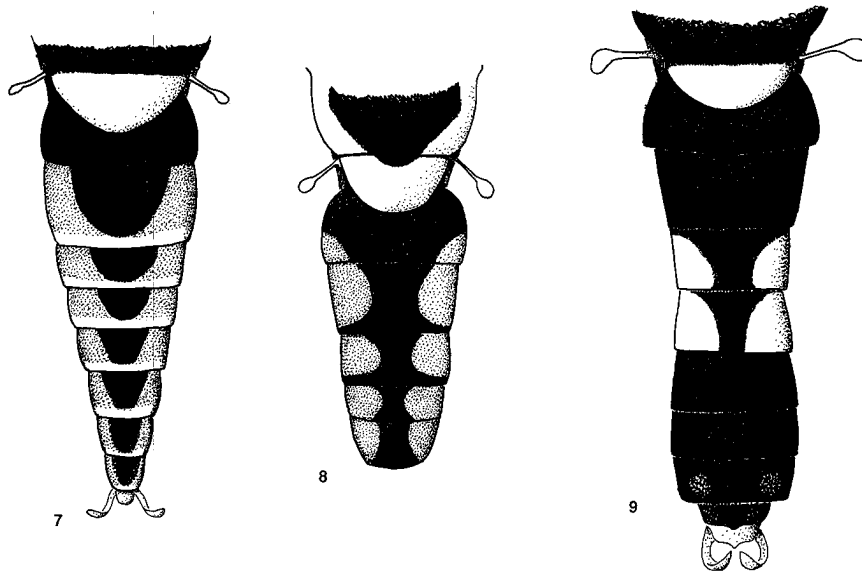
cavity; labellum very large, thick, about 4/5 length of entire proboscis; maxillary palpus short, thin, yellowish, not curled, with sparse white hairs, length 1/5 length of proboscis.

Thorax. Mesonotum subshining black, humeral and anterior 1/2 of post alar callus white, posterior 1/2 of post alar callus gray, yellowish pile anteriorly and anterolaterally, remainder of mesonotum with dense recumbent golden tomentum; scutellum white with thin black strip anteriorly, black color extending to small anterolateral black patch, long sparse pale yellow pilose; macrochaetae pale yellow to white in supra alar area and on post alar callus. Pleura reddish gray, anepisternum with dense patch of pale yellow hairs; katepisternum with patch of yellow hairs on ventral portion and longer yellow hairs on dorsal portion, bare medially; proepimeron bare; proepisternum yellow pilose; anepimeron and katepimeron bare; katatergite with patch of yellow hairs; metepimeron subshining gray-brownish black, bare; halter stem yellow, knob yellow with tinge of brown along anterodorsal border. **Legs:** reddish yellow; coxae long pale yellow pilose; femora short recumbent yellow pilose, tibiae short yellowish white pilose with small sparse orange spicules along apical portion of anterior surface; tarsi brown only on segments IV–V; claws brown, tips black; pulvilli yellowish brown, almost as long as claws.

Wing. Hyaline, veins brown except vein Sc, basicosta, and base of radial vein yellowish brown; cell sc slightly translucent yellowish gray; 3 submarginal cells; crossvein r-m at apical 3/4 of discal cell, placed obliquely in relation to radial and medial veins; anal lobe narrow; alula vestigial.

Abdomen. Tapered to almost pointed apex; patterned with black medial spots, lateral orange ground color, and yellow color along apical margins of tergites as in Fig. 8; sternites all yellow, with dense recumbent golden yellow hairs; tergum yellow pilose on segment 1, recumbent yellow pilose on segments 2–8, short brown hairs dorsally and medially on segments 3–8; lamellae of tergite 9+10 (Fig. 13) long, thin, brown; cercus brownish orange, without mesal projection, strong setae evenly distributed along mesal margin.

Genitalia (Fig. 15) with vaginal apodeme (furca) as in illustration; 3 spermathecae; spermathecal reservoir cap-shaped, darkly sclerotized; apical spermathecal duct long, thin, membranous, leading to membranous common duct, sperm pump not evident, common duct short, thick, membranous.



Figs. 7–9. Abdomens of Antoniinae. 7, *Cyx rieki* (Paramonov); 8, *Antoniaustralia arida* Evenhuis, n. sp.; 9, *Antoniaustralia hermanni* Becker.

Egg (Fig. 18). Length: 0.7 mm. Length about 2–3 times greatest width, ovate-ellipsoid, smooth, white, without apparent chorionic texture, operculum, or collar.

Male. Unknown.

HOLOTYPE ♀ and 1 paratype ♀ from: AUSTRALIA: Northern Territory: Alice Springs: 12 km WSW Roe Creek, 10.x.1978, D.H. Colless, Malaise trap (both in ANIC). **PARATYPE**. 1 ♀, Australia: Northern Territory: 82 km W. Alice Springs, Ellery Creek, Gorge N.P., creek with pools, 1.x.1983, E.I. Schlinger & M.E. Irwin (INHS).

Etymology. The name derives from the Latin *aridus* = dry, referring to the general aridity of the type locality.

***Antoniaustralia hermanni* Becker**

Figs. 2, 6, 9

Antoniaustralia hermanni Becker, 1912: 422. *Nomen nudum*.

Antoniaustralia hermanni Becker, 1913: 458. Hardy, 1922: 62. Bezzi, 1924: 6. Hall, 1976: 5. Evenhuis, 1989: 369; 1991: 19.

Antonia (*Antoniaustralia*) *hermanni* (Becker). Paramonov, 1929: 15.

Antonia hermanni (Becker). Paramonov, 1950: 529; 1953: 204. Hull, 1973: 321. Evenhuis, 1983: 474.

I have examined the unique holotype male of *hermanni*, which is deposited in ZSMC. The description given by Becker suffices to distinguish this species. The dorsal abdominal pattern is illustrated in Fig. 9. As Paramonov (1953: 204 [footnote]) noticed,

Becker's (1913) illustration of the eye of *hermanni* is incorrect in that it lacks the posterior indentation and bisection line. The head of the holotype is redrawn in Fig. 2. Because the holotype is unique, the male genitalia were not dissected; however, the apicomeral projection of the gonocoxites and the gonostyli are easily visible from a caudal view and both structures possess strong black sclerotized spines.

The holotype is in fair condition. The right wing has been mounted on a slide for illustration (Fig. 6). The left wing is shriveled. The head is glued to the thorax. Apparently this was done before Becker (1913) illustrated it because the present orientation of the head is exactly as it is figured by Becker.

The exact type locality is ambiguously referred to on the specimen labels. One of the labels of the type specimen is printed "Palmerston, N. Australien, xi.1908", while a large green square label below it is handwritten with "Queensland". Palmerston is the old name for Darwin in Northern Territory; but there is a Cape Palmerston in Queensland. It is possible that Cape Palmerston could be considered "N. Australien" though it is more commonly referred to as eastern coast; while Darwin is truly a northern Australian locality. Until further specimens of this species are collected from one or the other locality, its true type locality will have to remain unresolved.

Genus *Cyx* Evenhuis, new genus

Type species: *Antonia rieki* Paramonov, 1953, by present designation.

Cyx is distinguished from other Australasian Antoniinae by the presence of 3 submarginal cells in the wing (there are only 2 in *Antoniaustralia*), the dense concentration of bristles on a mesal projection of the cerci of the female (in *Antoniaustralia* these bristles more evenly concentrated along the mesal margin, which is without a projection), the 45° rotation of the male genitalia (not rotated in *Antoniaustralia*), and by the egg possessing a pedicel (see Figs. 19–20). The presence of a large, thick labellum of the proboscis, the 45° rotated male genitalia, and the 3 spermathecae in the females will serve to separate species of *Cyx* from *Antonia*. There is no apparent sexual dimorphism in thoracic or abdominal pattern in *Cyx*, which makes possible association of male and female specimens collected separately.

Etymology. The genus-group name is an arbitrary combination of letters. Gender is feminine.

Cyx decorata (Paramonov), 1950, new combination

Fig. 10

Antonia decorata Paramonov, 1950: 532. Liepa, 1969: 14. Hull, 1973: 321. Evenhuis, 1983: 469.

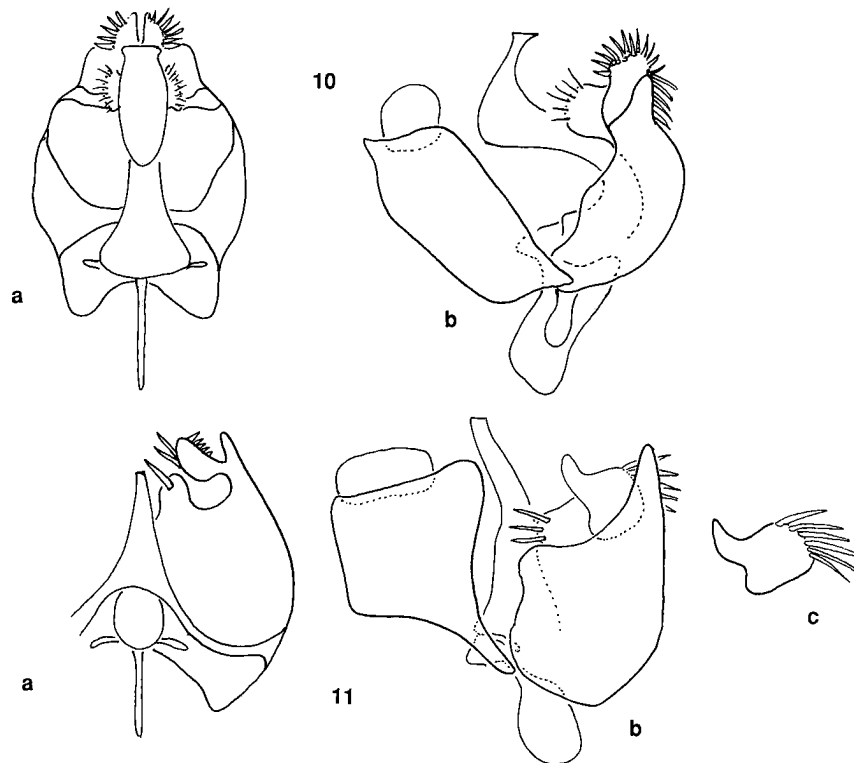
Antoniaustralia decorata (Paramonov). Evenhuis, 1989: 369.

This species was originally described from a single female in the National Museum of Victoria, Abbotsford, Australia without locality or collector data. I have before me the first male of the species from which the following redescription originates. This species is easily separated from the congeners by the thoracic and wing patterns, as well as other characters given in the key to species below.

Male. *Lengths.* Body: 12.0 mm; wing: 11.0 mm. *Head.* Eyes dichoptic; separated at vertex from lateral edges of ocellar tubercle by slightly more than width of 2 ommatidia, narrowing in front of ocellar tubercle, but still separated by width of anterior ocellus; ocellar tubercle dark brown, with brown hairs; front and vertex both black in ground color overlaid by silvery gray pollinosity continuing to bulbous frontal protuberance; grayish black ground color and silvery gray pollinosity of

face continuing laterally between oral margin and inner eye margin as thin strip, connecting ventrally to grayish black color and pollinosity of postgena; front and vertex with erect short brown hairs, bulbous frontal projection with small patch of brown hairs on upper 1/3; face, gena, and ventrolateral portion of frontal protuberance with thick, scalelike yellow to yellowish orange hairs; occiput black with silvery gray pollinosity laterally, pollinosity continuing ventrally to posterior margin of oral cavity; occiput with dense short white hairs surrounding occipital foramen, slight amount of white recumbent hairs on upper occiput between occipital fringe and hind eye margin; oral margin developed, but relatively short, produced forward to level of antennal segment II, yellow to yellowish orange to just posterior to oral cavity, tip of oral margin produced as swollen "lip", with short yellow to golden yellow hairs along oral margin, ventrolaterally, and at tip. Antennal segment I obconical, well produced mesally, about 2 times wider than long, concave apically, yellow, with orange hairs laterally; segment II small, cylindrical, less than 1/3 size of segment I, yellow with brown and orange hairs intermixed dorsally and laterally; segment III lanceolate-ovate, black, bare, length about subequal to length of segments I and II combined, with tiny apical brown stylar segment. Proboscis yellowish brown, slightly shorter than oral cup; labellum large, thick, about 1/3 length of entire proboscis; maxillary palpus thin, orange, curled, with long, sparse, white hairs, length (uncurled) slightly more than 1/3 length of proboscis.

Thorax. Mesonotum subshining black, humeral callus, anterior 1/2 of post alar callus, and triangular supra alar mark bright yellow, posterior 1/2 of post alar callus brown; dense white pile anter-



Figs. 10–11. *Cyx* male genitalia. **10.** *C. decorata* (Paramonov); **a,** ventral view; **b,** lateral view. **11.** *C. rieki* (Paramonov); **a,** ventral view, gonostyli removed; **b,** lateral view; **c,** detail of gonostylus.

iorly, dense golden yellow to yellow pile anterolaterally and anterodorsally, becoming sparser toward scutellum; scutellum bright yellow with black only as thin strip anteriorly, black color extending to small anterolateral black patch, long sparse yellow pilose. Pleura black with gray pollinosity; anepisternum with dense patch of golden yellow hairs; katepisternum with small patch of short yellow to golden hairs on extreme ventral and dorsal portions, bare medially; proepimeron brown, bare; proepisternum brown, dense white pilose; anepimeron and katepimeron bare; katatergite with dense patch of long golden yellow pile; metepimeron subshining brownish black, bare; halter stem yellow, knob yellow with tinge of brown along anterodorsal border. *Legs*: Coxae orange-yellow, long white to golden yellow pilose; fore and mid legs orange-yellow, tarsal segment becoming brown toward apicalmost segments, femora yellow pilose, tibiae short yellowish pilose with small sparse orange spicules; hind femur yellow on basal 4/5, dark brown on apical 1/5, swollen on apical 1/3, with short hairs concolorous with ground color, becoming denser apically, with 5 subapical brown bristles dorsally, tibia and tarsi brown, with usual hairs and spicules; claws all black; pulvilli brown, almost as long as claws.

Wing. Smoky hyaline, with brownish infuscation along fore border, infuscation extending to 1/2 of 1st submarginal, and bases of 1st posterior and discal cells, veins brown, vein Sc yellowish brown; cell sc infuscated yellowish orange; 2 submarginal cells; crossvein r-m at apical 3/4 of discal cell, placed obliquely in relation to radial and medial veins; anal lobe narrow; alula vestigial.

Abdomen. Patterned with black and yellow color, ventral curled portion of tergites (not visible from above) black laterally; sternites all yellow, with sparse, short, yellow hairs; tergum dense white pilose on segment 1, sparse white pilose laterally on segment 2, segments 3–7 with brown hairs lat-

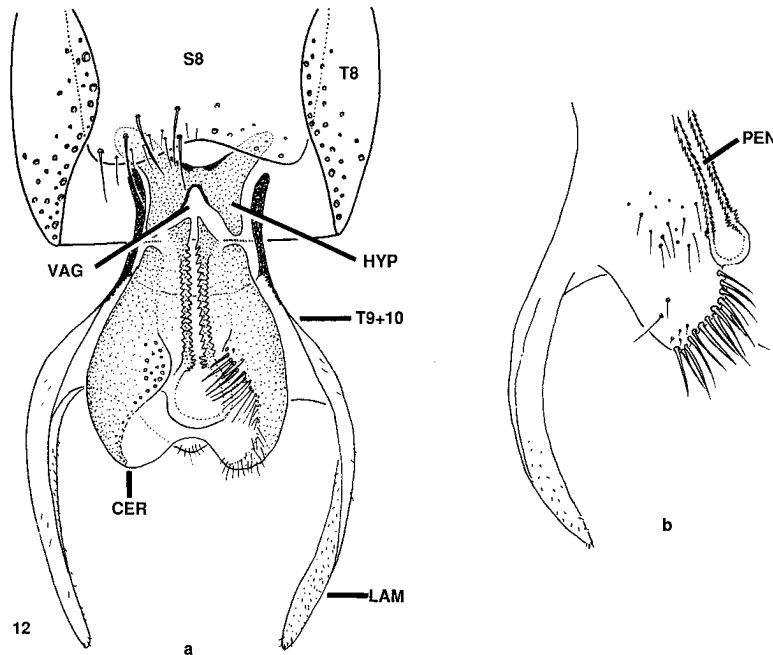


Fig. 12a. Female postabdomen of *Antonia* sp. (Kenya), ventral view; setae removed from left cercus for clarity. **Fig. 12b.** detail of tergite 9+10 and cercus. Abbreviations: CER = cercus; HYP = hypoproct; LAM = lamella; PEN = penial guide; S8 = sternite 8; T8 = tergite 8; T9+10 = tergite 9 + 10; VAG = vaginal orifice.

erally, segment 8 bare, yellow tomentum dorsally and dorsolaterally on segments 2 and 3 (sparser on 3 than on 2).

Genitalia (Fig. 10) in lateral view with gonocoxites higher than wide, slightly sinuous in shape, lateroapical projection rounded, with numerous thick bristles; gonostyli placed subapically within gonocoxites, with thick bristles caudally; parameres forming complete sheath of aedeagus, strongly sinuous and tapering to narrow truncate and slightly flared apex, widest at apical 1/3; sperm pump (aedeagal bulb) rather small, rounded; basal aedeagal apodeme large, subrectangular; lateral rami small, linear-foliate; epandrium subrectangular, higher than wide, with small posterodorsal projection connected to gonocoxites by membrane; cercus rounded, well exerted.

Female. As described in Paramonov (1950). Genitalia not dissected.

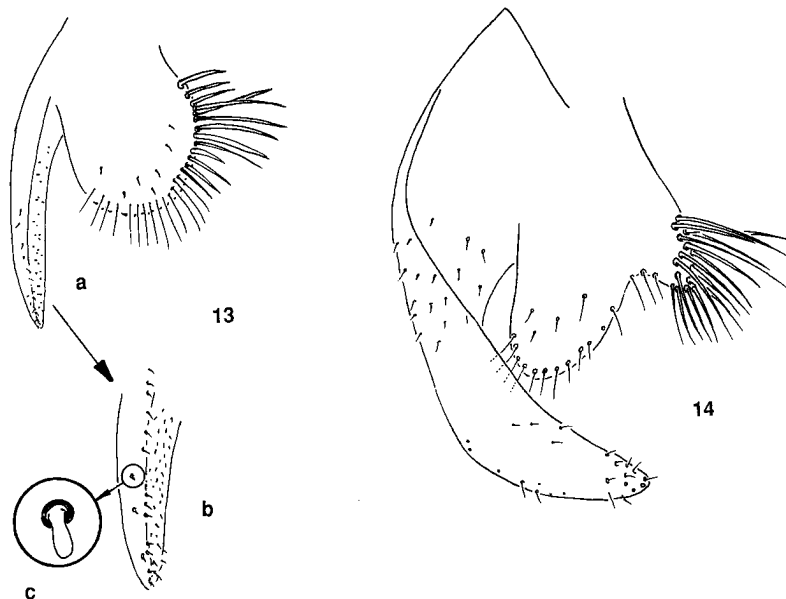
Material examined. AUSTRALIA: 1 ♂ [Queensland]: Bruce Highway, 20.x.1963, C.F. Ashby (ANIC).

***Cyx papuana* Evenhuis, new species**

Figs. 3, 5, 14, 16, 19

This species is easily identified by its infumate wings, predominantly black body, and large size. It is the only species of this genus known outside of Australia.

Female. *Lengths.* Body: 13.0 mm; wing: 11.0–12.5 mm. **Head** (Fig. 3). Eyes dichoptic; separated at vertex from lateral edges of ocellar tubercle by slightly more than width of lateral ocellus; ocellar tubercle black, with dark brown hairs; front and vertex dark brown in ground color, front overlaid by silvery gray pollinosity except for yellowish orange bulbous frontal protuberance; face, gena, and oral margin yellow; front and vertex with dark brown hairs, bulbous frontal projection



Figs. 13–14. Tergites 9+10 of Antoniinae. **13.** *Antoniaustralia arida* Evenhuis, n. sp.; a, lamella and cercus; b, detail of apex of lamella; c, detail of sensillum on apex of lamella. **14.** *Cyx papuana* Evenhuis, n. sp.

with brown hairs on upper one-third; occiput velvety black with brown pollinosity laterally at level of eye indentation on hind margin, pollinosity continuing to postgena; occiput with dense short white hairs surrounding occipital foramen, slight amount of short dark hairs on upper occiput between occipital fringe and hind eye margin; oral margin well developed, produced forward to level of middle of third antennal segment, slightly pollinose along lateral margin, with sparse, short orange hairs laterally. Antennae (Fig. 5) with segment I obconical, about 2 times wider than long, concave apically, brown color basally fading to yellow apically, with brown hairs laterally; segment II small, obconical, less than 1/2 size of segment I, black with black hairs laterally; segment III linear-lanceolate, black, bare, length about 2.0 times length of segments I and II combined, with tiny apical brown styler segment. Proboscis yellowish brown, shorter than oral cup; labellum large, thick, about 1/2 length of entire proboscis; maxillary palpus thin, yellowish brown, curled, with long, sparse, white hairs, length (uncurled) slightly more than 1/2 length of proboscis.

Thorax. Mesonotum velvety black, humeral and post alar calli and notopleural stripe yellow to yellowish orange; yellow pile anteriorly and anterolaterally, a few short, erect brown hairs on center of mesonotal disc; scutellum orange-yellow with black only as thin strip anteriorly, black color extending to small anterolateral black patch, long sparse black pilose. Anepisternum black on anterior 2/3, yellowish orange on posterior 1/3, with dense patch of yellow hairs; katepisternum black on ventral 2/3, yellowish orange on dorsal 1/3, with sparse short yellow hairs on ventral and dorsal portions, bare medially; proepimeron and proepisternum yellowish orange, yellow pilose; anepimeron yellow, bare; katepimeron black on posterior 1/2, yellow dorsally and on anterior 1/2, bare; katatergite yellowish orange, with patch of yellow pile; metepimeron yellow, bare; halter stem yellow with brown along lateral border, knob yellow dorsally, brown ventrally. *Legs:* coxae orange-yellow, yellow pilose; fore and mid legs yellowish orange, tarsal segment becoming brown on apicalmost segments, femora short yellow pilose, tibiae short yellowish pilose with small sparse orange spicules along apical portion of anterior surface; hind femur yellow only on extreme base, otherwise brown, swollen on apical 1/3, with short hairs concolorous with ground color, becoming denser apically, with 3–5 subapical brown bristles dorsally, tibiae and tarsi brown, with usual hairs and spicules; claws brown, tips black; pulvilli yellowish orange, almost as long as claws.

Wing. Entirely smoky gray-brown, veins brown, base of radial vein orangish; 2 submarginal cells; crossvein r-m at apical 3/4 of discal cell, placed obliquely in relation to radial and medial veins; anal lobe narrow; alula vestigial.

Abdomen. Patterned with black and yellow color, dark tergal color on 1–4 black, on 5–8 dark brown with dark reddish brown laterally; sternites 1–2 yellowish, with yellowish hairs; sternites 3–7 orange-brown, 2–5 with dense yellow recumbent hairs, 5–8 with brown hairs; tergum yellow pilose on segment 1, sparse white pilose laterally on 2–4, segments 5–8 with recumbent brown hairs laterally, brown tomentum dorsally and dorsolaterally on segments V–VIII; lamellae of tergite 9+10 brown dorsally, yellow apically and ventrally.

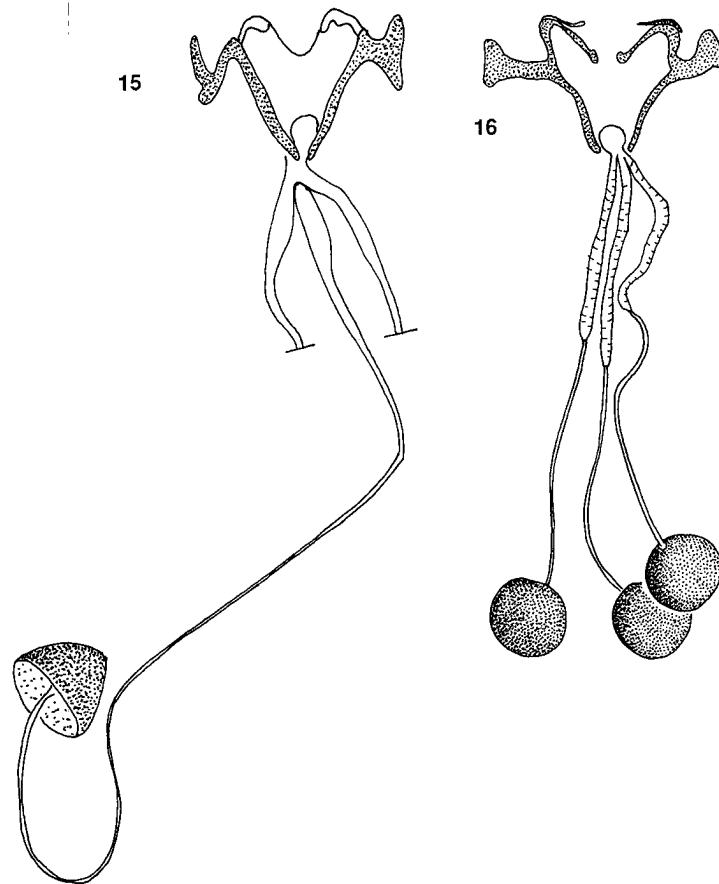
Genitalia (Fig. 16) with vaginal apodeme as in illustration; 3 spermathecae; spermathecal reservoir spheroid, darkly sclerotized; apical spermathecal duct long, thin, membranous, subequal in length to basal duct (sperm pump?); basal duct membranous, thicker than apical duct, leading to extremely small common duct.

Egg (Fig. 19). Length (without pedicel): 0.5 mm; pedicel: 0.1 mm. Ovate-ellipsoid, length about 3 times greatest width, sclerotized brown, with operculum; with short basal pedicel, pedicel flared apically with micropapillae along margin.

Male. Unknown.

HOLOTYPE ♀ (BPBM 15,072) from: [PAPUA] NEW GUINEA: [East Sepik Prov:] Maprik: Mal[aria] Cont[rol] Sect., iv.1953 [no further data]. One ♀ paratype from [INDONESIA: Irian Jaya]: Genjam, 40 km W of Hollandia, 100–200 m, 1–10.iii.1960, T.C. Maa. Both specimens are deposited in BPBM. The holotype is in fair condition with the right mid leg and both hind legs beyond the coxae broken off and missing (except one hind leg, which is glued to the locality label).

Etymology. The name derives from the type locality in Papua New Guinea.



Figs. 15–16. Female spermathecae of Antoniinae. **15,** *Antoniaustralia arida* Evenhuis, **n. sp.**; **16,** *Cyx papuana* Evenhuis, **n. sp.**

Remarks. The abdomen and genitalia of the paratype female have been dissected; the genitalia and some of the ovariole eggs were mounted on slides and scanning electron micrographs were taken of other ovariole eggs.

***Cyx rieki* (Paramonov), 1953, new combination**

Figs. 7, 11, 20

Antonia rieki Paramonov, 1953: 204. Liepa, 1969: 14. Hull, 1973: 321. Evenhuis, 1983: 487.

Antoniaustralia rieki (Paramonov). Evenhuis, 1989: 369.

Male. *Lengths.* Body: 7.0–9.0 mm; wing: 7.0–9.0 mm. *Head.* Eyes dichoptic; separated at vertex from lateral edges of ocellar tubercle by slightly more than width of two ommatidia; ocellar tubercle brown, with brown hairs; front and vertex (except for white to yellowish white bulbous frontal protuberance) both black in ground color overlaid by silvery gray pollinosity; grayish black

ground color of face continuing laterally between oral margin and inner eye margin as thin strip; front and vertex with erect short brown hairs, bulbous frontal projection with small patch of brown hairs on upper one-third; occiput black with silvery gray pollinosity laterally at level of eye indentation on hind margin, pollinosity continuing to postgena; occiput with dense short white hairs surrounding occipital foramen, slight amount of white recumbent hairs on upper occiput between occipital fringe and hind eye margin; oral margin well developed, produced forward to level of middle of third antennal segment, yellowish white to post gena, with brown patch of color at extreme tip, slightly pollinose along lateral margin, with short intermixed brown and white hairs along oral margin, ventrolaterally, and at tip. Antennal segment I obconical, about 2 times wider than long, concave apically, grayish black with yellow along apical margin, with brown hairs dorsolaterally, white hairs ventrolaterally; segment II small, obconical, less than 1/3 size of segment I, gray-black with brown to black hairs laterally; segment III lanceolate-ovate, brown to black, bare, length about 1.5 times length of segments I and II combined, with tiny apical brown stylar segment. Proboscis yellowish brown, as long as or shorter than oral cup; labellum large, thick, about 1/3 length of entire proboscis; maxillary palpus thin, yellowish brown, curled, with long, sparse, white hairs, length (uncurled) slightly less than 1/2 length of proboscis.

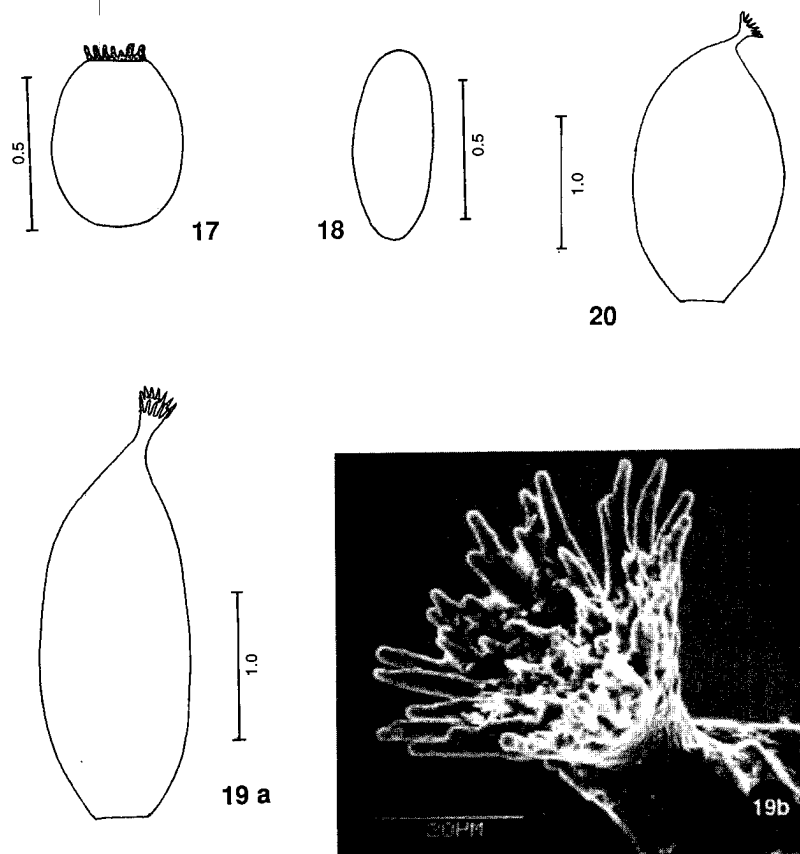
Thorax. Mesonotum subshining black, humeral and post alar calli and notopleural stripe brown to dark reddish brown; dense white pile anteriorly, anterolaterally, and anterodorsally, becoming sparser toward scutellum, a few short, erect brown hairs on center of mesonotal disc; scutellum bright yellow with black only as thin strip anteriorly, black color extending to small anterolateral black patch, long sparse white pilose; macrochaetae white in supra alar area, black on post alar callus. Anepisternum black on anterior 2/3, yellow on posterior 1/3, with dense patch of white hairs; katapisternum black on ventral 2/3, yellow on dorsal 1/3, with small patch of short white hairs on extreme ventral and dorsal portions, bare medially; proepimeron and proepisternum yellow, white pilose; anepimeron yellow, bare; katepimeron grayish black, thin yellow strip of color dorsally, bare; katatergite grayish black, with dense patch of white pile; metepimeron shining black, bare; halter stem and knob yellow with tinge of brown along anterodorsal border. *Legs:* Coxae yellow, fore coxa with brown anterobasally, short white pilose; fore and mid legs yellow, tarsal segment becoming brown toward apicalmost segments, femur short white pilose, tibiae short yellowish white pilose with small sparse orange spicules along apical portion of anterior surface; hind femur yellow on basal 1/3, brown on apical 2/3, swollen on apical 1/3, with short hairs concolorous with ground color, becoming denser apically, with 3–5 subapical brown bristles dorsally, tibiae and tarsi brown, with usual hairs and spicules; claws all black; pulvilli yellowish brown, almost as long as claws.

Wing. Subhyaline, veins brown, vein Sc yellowish brown; cell sc slightly translucent yellowish gray; 2 submarginal cells; crossvein r-m at apical 3/4 of discal cell, placed obliquely in relation to radial and medial veins; anal lobe narrow; alula vestigial.

Abdomen. Patterned with black and yellow color as in Fig. 7; sternites all yellow, with sparse, short, brown hairs; tergum dense white pilose on segment 1, sparse white pilose laterally on 2–4, segments 5–7 with recumbent brown hairs laterally, segment 8 bare, brown tomentum dorsally and dorsolaterally on segments 2, 5–7.

Genitalia (Fig. 11) in lateral view with gonocoxites large, rounded basally, tapering sharply to lateroapical pointed projection; gonostyli placed subapically within gonocoxites, shaped as in Fig. 11, with thick bristles caudally; parameres forming complete sheath of aedeagus, broad basally (in ventral view) and tapering smoothly to narrow apex; in lateral view parameral sheath long, slightly narrowing from base to tip, tip truncate; sperm pump (aedeagal bulb) rather small, rounded; basal aedeagal apodeme small, rounded, racquet-shaped; lateral rami small, linear-ellipsoid; epandrium subquadrate, with prominent posterodorsal projection connecting to gonocoxites by membrane; cercus large, subrectangular, slightly exerted.

Female. As described in male except for yellow apical abdominal lamellae of tergite 9+10. Apical lamellae and cerci illustrated as in Fig. 14. *Genitalia* with vaginal apodeme shaped as in Fig. 15; 3 spermathecae; spermathecal reservoir cap-shaped, well sclerotized; apical spermathecal duct long, thin, membranous, leading to basal duct, no apparent sperm pump, common duct thick, membranous, about 1/20 length of spermathecal duct.



Figs. 17–20. Antoniinae eggs. **17,** *Antonia* sp. (Kenya); **18,** *Antonustralia arida* Evenhuis, *n. sp.*; **19,** *Cyx papuana* Evenhuis, *n. sp.*; **a,** whole egg; **b,** detail of flared end with papillae; **20,** *Cyx rieki* (Paramonov). Scales are in mm except where indicated.

Egg (Fig. 20). Length (without pedicel): 2.0 mm; pedicel: 0.2 mm. Ovate, apparently smooth, sclerotized pale brown, with apical operculum; with short basal pedicel, pedicel flared apically with micropapillae along margin.

Material examined. AUSTRALIA: New South Wales: 6♂, 4♀, 40 mi. E. Wilcannia, 22.xi.1949, S. J. Paramonov (ANIC, CNCI). During a visit to ANIC in 1989, the author also was able to examine the holotype male.

Remarks. Paramonov (1953) states that the bottom of the oral cavity is black. This is wrong. Examination of all the specimens in the type series shows that the oral cavity is completely yellow except for the tiny patch of brown color at the upper tip of the oral margin. The original description gives the collector as E.F. Riek, but the labels state Paramonov as the collector. Paramonov (1953: 204) also mentions that the specimens were collected off flowers of *Hakea*.

***Cyx roddi* (Paramonov), 1950, new combination**

Antonia roddi Paramonov, 1950: 530. Liepa, 1969: 14. Hull, 1973: 321. Daniels, 1978: 425. Evenhuis, 1989: 487.

Antoniaustralia roddi (Paramonov). Evenhuis, 1989: 369.

The unique holotype in the AMS was examined during a visit there by me in 1989. It is in deplorable condition with only the thorax, posterior portion of the head, right wing and left hind femur remaining. The specimen appears to have suffered considerable damage by dermestids after Paramonov's (1950) original description. Fortunately, there is enough of the specimen remaining to identify it as a member of the genus *Cyx*.

Its type locality (Lane Cove near Sydney) is a commonly frequented area, but no further specimens of this species are known to have been collected there, so one may assume that the species has either become extinct through development of the area or is hanging on in small populations elsewhere that have not yet been found by collectors. The original description is reproduced below.

"Ground color of head black; the first basal joint of antennae, which is very swollen, bright yellow, the second black (the third is broken in type); face yellow, but not bright, protruding, but only slightly (only to the apex of first antennal joint). Proboscis short, hidden in the mouth cavity, its basal part extremely short, while the labella is swollen and extremely developed, representing by itself nearly whole proboscis. Palpi yellow, extremely small. Face with parallel sides, its width a little less than the horizontal diameter of the eye. Face, first antennal joint and the area around the base of antennae with sparse, short, yellowish hairs. Lower part of frons with a golden dust, the upper part black haired. Connecting line of eyes is very narrow, but incomplete; the dividing strip is a little broader than the anterior ocellus. Ocellar triangle extremely short and low. Occiput black.

Thorax deep black, mesonotum with a bluish sheen. Humeral calli and scutellum bright yellow, the latter with a very small basal part black. Sides of mesonotum with a narrow longitudinal stripe of bright yellow hairs, bristles also yellow. Yellow hairs also on scutellum. A few golden scales are distributed on mesonotum. Sides of thorax black, grey dusted, with dense yellow and yellowish hairs. A tuft in front of the base of the halteres is very long and dense. Halteres a little brownish, but with a bright yellow knob. Legs (including the coxae) yellow, but the apical one-fifth of hind femora deep black. Spicules on legs reddish. The type has only one hind femur, other parts of legs broken.

Wings hyaline, with black veins. Subcostal cell yellowish; in area of the apex of subcostal cell there is a small spot-like (or stigma-like) dark stripe, but this spot is seen easily only under a lens. First posterior cell open about the length of r-m. Two submarginal cells; vein r_4 with a small supplementary veinlet as in *Anthrax*. Vein r-m situated close to apex of discal cell (the distance being a little larger than itself). Prefurca not reaching the base of the discal cell.

Abdomen above red, with a dark median longitudinal stripe. First tergite is quite black; second with the middle half black, the lateral fourths are red; the boundary between black and red area is distinctly concave (Excavated). Third tergite has the middle fourth part black, boundary between the red and black areas being only slightly excavated. Fourth, fifth, sixth and seventh tergites red with only a narrow black median longitudinal stripe, occupying about one-fifth to one-seventh of the tergite. Underside of abdomen yellow. Sides of first tergite with long and dense yellow hairs, other tergites with short, not dense, black hairs, which are denser at the sides. There are eight segments clearly visible."

KEY TO SPECIES OF *CYX*

1. Wing completely infumate . . . (New Guinea) *papuana*, n. sp.
- Wing mostly hyaline, infuscation only along anterior border 2
2. Anterior border of wing with definite brownish band along anterior border; mesonotum bordered laterally with yellow *decorata* Paramonov
- Anterior border of wing with only faint indication of yellow to brown along anterior border, not as definite and thick as above; mesonotum black with little if any yellow laterally 3

3. Abdomen predominantly orange to reddish orange with black median stripe *roddi* Paramonov
 - Abdomen predominantly black with yellow spots on some tergites *rieki* Paramonov

Significance of the pedicel of the egg of *Cyx*

The biology of species of Antoniinae is poorly known. Observations for *Antonia* have been recorded for only a few individuals (e.g., Hesse 1956; Greathead 1967). Greathead (1967) records a specimen of *Antonia cirrhata* Bezzi in BMNH, which was reared from a "mud nest" [Sphecidae] and mentions observing *A. suavissima* hovering near other nests of mud-daubing wasps in which subsequent examination of the nest revealed a bombyliid larva (the rearing of which was unsuccessful). The eggs of *Antonia*, however, do not have a pedicel. They are ellipsoidal and commonly have a collared end, which defines the operculum (in some species this collar is festooned with papillate structures) (Fig. 17). The operculum of eggs of *Cyx* is, interestingly, on the opposite end to the pedicel.

The presence of a pedicel in the eggs of *Cyx papuana* and *C. rieki* is significant from many standpoints. These 2 species (*rieki* and *papuana*) represent the first known bombyliids with such an egg structure (a similar structure is found in eggs of some Conopidae). The papillae at the flared end of the pedicel suggests that the egg is adhered directly to a substrate at the time of oviposition rather than being oviposited while the female is hovering in the air (as in other bombyliids such as *Bombylius* and *Anthrax*).

There are very few records of bombyliids ovipositing directly onto a substrate. Species of *Xenox* Evenhuis, which parasitize *Xylocopa* bees, have been observed by me (unpubl. data) laying eggs directly on the surface of agave stalks in close association with the nest holes of *Xylocopa*. Species of *Geron* Meigen have also been observed by me (unpubl. data) ovipositing on leaves and in and around leaf axils of some desert shrubs. I have also observed 2 specimens of a species of *Epacmus* Osten Sacken ovipositing (unpubl. data). Each female oviposited 5–7 eggs into a small pit in the sand it had made and then covered the eggs with surrounding sand with the tip of its abdomen. The eggs of *Xenox* were observed to have a sand coating (females of species of this genus possess a sand chamber used in coating the eggs with fine grains of sand presumably to help avoid desiccation). However, the eggs of the species of *Geron* and *Epacmus* observed were not coated with sand and these species do not possess such a sand chamber.

Genera of Antoniinae do not possess a sand chamber; hence, it can be assumed that their mode of oviposition would be such that the eggs would require protection from desiccation in some other fashion. The pedicel on the eggs of *Cyx* suggests that some modification of the normal mode of oviposition in bombyliids (e.g., indiscriminate oviposition while hovering in the air) has taken place in species of this genus. Adhering eggs to a substrate in close association with the potential hosts would allow the first instar to find its host quickly and thus limit an otherwise prolonged exposure to the environment.

The eggs of *Antoniaustralia* are an enigma. They neither possess a pedicel nor a collar at either end. They are simply ellipsoidal without any modifications. Because the females do not possess a sand chamber, they cannot coat the eggs with sand to prevent desiccation, so it is assumed that the mode of oviposition must be other than laying eggs while the female hovers.

Observations on the mode of oviposition in *Antonia*, *Cyx*, and *Antoniaustralia* are urgently needed to answer the question of how the eggs are protected from the environment after oviposition.

CLADISTIC ANALYSIS OF THE ANTONIINAE

The Antoniinae are a monophyletic group of the Tomophthalmae (*sensu* Bezzi 1924) as defined by the following apomorphies: a prominent bulbous frontal projection above the antennae, the enlargement of tergite 9+10 of the female into paired long thin lamellate structures with apical sensillae, the strong spines along specific portions of the ventral margin of the female cerci, and the absence of a sand chamber in the female abdomen. The subfamily Tomomyzinae was chosen as the outgroup in this analysis because it has been shown in preliminary analyses (Evenhuis unpubl.) to be the sister group to the Antoniinae.

Table 1. Data Matrix and Taxa used in the Cladistic Analysis

<i>Taxon</i>	1	2	3	4	5	6	7	8	9	10
Tomomyza	0	0	0	0	0	0	0	0	0	0
Antonia	0	1	0	0	1	0	1	0	1	0
Antoniaustralia	1	1	0	0	1	0	0	0	1	1
Cyx	1	1	1	0	1	0	1	1	1	0

Yeates (1990), in his phylogenetic analysis of the Australian lomatiines, analyzed the placement of Australian “*Antonia*” in relation to other Australian Tomophthalmae subfamilies. Yeates’ coding of the character states for the male and female genitalia were based on Theodor (1983), who studied only Palaearctic species (true *Antonia*) and no Australasian species. The results of Yeates’ analysis showed the uniqueness of *Antonia*, which led him to conclude that the genus warranted separate subfamilial status. However, his analysis found no discrete sister group for the Antoniinae.

Character Analysis

The following characters were selected for analysis due to their relative consistency throughout members of both the Tomomyzinae and Antoniinae. The plesiomorphic state of each character is indicated by a zero (0); the apomorphic state by a one (1).

1. Labellum: 0 = pointed; 1 = thick, large, not pointed.

Tomomyza species have a larger labellum than do *Antonia* species, but it is still pointed as opposed to the even larger and more rounded labellum in *Antoniaustralia* and *Cyx*.

2. Eyes: 0 = bare; 1 = hairy.

These hairs are microscopic and are best seen from an angle under high magnification (> 75 x) as light reflects off of them. The eye hairs in *hermanni* and *arida* are much more prominent than in other species of Australasian Antoniinae. These eye hairs may be an additional apomorphy defining the Antoniinae as they have not been found in members of the Tomomyzinae or Lomatiinae examined thus far. These hairs are also known to occur in some genera of the Mythicomyiinae, though in many cases they are extremely reduced and can only be discerned through scanning electron microscopy.

3. Submarginal cells in the wing: 0 = three; 1 = two.

The type species of *Tomomyza* Wiedemann (*anthracoides* Wiedemann) possesses 3 submarginal cells and was used as the basis for coding in this analysis. There are Afrotropical species currently placed in *Tomomyza* that possess 2 submarginal cells; however, Hesse (in litt.) indicated that these are not true *Tomomyza* and should be removed to a new genus.

4. Crossvein r-m orientation to M_1 : 0 = obtuse (90°); 1 = acute (less than 90°).

The orientation of this crossvein in *Antoniaustralia arida* varies in the 2 known specimens where neither is truly at a 90° angle. The groundplan for *Antoniaustralia* is exemplified by the type species, *hermanni*, which has the crossvein at a 90° angle to vein M_1 ; the acute orientation of this

crossvein in *arida* is here considered either an aberration or independent divergence from the groundplan of the genus.

5. Disc of squama of female wing: 0 = without hairs; 1 = with hairs.

The squama of true *Tomomyza* species is extremely reduced, but is still present and without hairs on what remains of the disc.

6. Gonocoxites of male genitalia: 0 = without large rounded apicomeral projection with or without spines; 1 = with large rounded apicomeral projection with spines.

Most *Antonia* species do not have this apicomeral projection of the gonocoxites. The illustration of the male genitalia of *Antonia xanthogramma* in Hesse (1956: 137) shows a similar structure with spines, but this projection is concave whereas it is convex in Australasian species.

7. Spermathecae: 0 = three; 1 = one.

The spermathecae in the Australasian antoniines are similar to those found in other genera of Bombyliidae. However, the single spermatheca found in *Antonia* is significant in that it lacks a true spermathecal reservoir. Theodor's (1983) illustration shows that it is essentially a blind duct, which is well sclerotized along most of its length. Examination in this study of the spermatheca of an undescribed Kenyan species of *Antonia* shows that the wall of the duct is very thick throughout its length and probably serves as a large ejaculatory apparatus (sperm pump). A blind duct is also found in species of *Desmatomyia* Williston (see Hall & Evenhuis 1987), but the walls of the duct are much thinner and less differentiated along the length of the duct than they are in *Antonia*.

8. Egg pedicel: 0 = absent; 1 = present.

9. Egg operculum: 0 = absent; 1 = present.

The egg operculum is not to be confused with the collar that, of the taxa analyzed in this study, is present only in *Antonia*. The collar in *Antonia* defines the apical operculum. The operculum of *Cyx* is without a definite collar.

10. Modified female cercus: 0 = with mesal projection bearing dense patch of setae; 1 = mesal portion evenly rounded, without projection or dense patch of setae.

The modification of the female cercus into a large, rounded sensory organ in close association with the modified elongate lamellate structures on tergite 9+10 is synapomorphic for the Australasian Antoniinae. *Tomomyza* does not possess this modified cercus and was coded as "?" for this character.

Results

Data were analyzed using the exhaustive search procedure in PAUP 3.0s (Swofford 1991). Figure 21 shows the single resulting cladogram with a length of 11 steps and a consistency index (CI) of 0.909. *Antonia* is the sister group to the Australasian antoniine clade (*Antoniaustralia* + *Cyx*) with the latter clade defined by 2 apomorphies: the large, thick labellum and presence of spines on the large, rounded mesal projection of the gonocoxites.

Cyx is further defined by 3 autapomorphies (presence of a pedicel on the egg, the presence of 2 submarginal cells in the wing, and the less than 90° orientation of the r-m crossvein to vein M₁). Even if the last character is deleted because of the variation in this condition in *Antoniaustralia arida*, the integrity of tree topology is still maintained.

Only 1 autapomorphy has been identified for *Antoniaustralia* (the modified female cercus being rounded and without a mesal projection). This is primarily due to the paucity of material available for examination and dissection (4 specimens including 2 holotypes). The examination of further specimens and species should produce further autapomorphies for this genus.

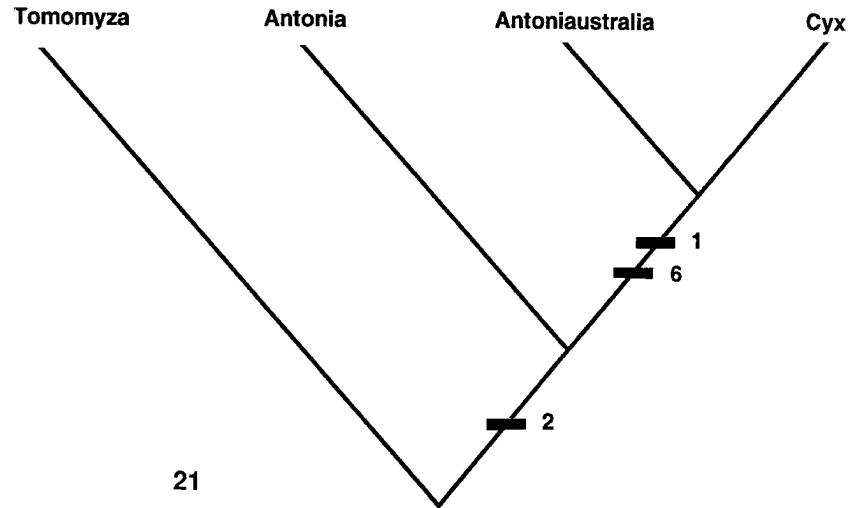


Fig. 21. Cladogram of Antoniinae. Synapomorphic characters shown on cladogram refer to character numbers in the text.

ACKNOWLEDGMENTS

Thanks are extended to the following individuals for allowing me access to specimens of Antoniinae in their collections: Paul A. Arnaud, Jr. (CAS), Daniel J. Bickel (AMS), John E. Chainey (BMNH), Margaret Cochrane (SAMC), Peter S. Cranston (ANIC), Jeffrey Cumming (CNCI), Jack C. Hall (JCH), David K. Yeates for Michael E. Irwin (INHS), and F. Reiss (ZSMC). The USNM collection of Bombyliidae, currently housed at BPBM, also provided a resource of specimens for examination. I also thank each of the above for the generous hospitality shown the author during his visits to CAS, AMS, BMNH, SAMC, ANIC, JCH, and CNCI.

Special thanks are extended to Dr. Marilyn Dunlap and Tina Carvahlo of the Pacific Biomedical Research Center, Biological EM Facility, University of Hawaii, who provided me with access to their scanning electron equipment and supplied advice and assistance where necessary. The manuscript benefitted from review and comments from Scott E. Miller, Robert Cowie, and two anonymous referees.

Thanks are also due to David K. Yeates for his discussions with me on bombyliid phylogeny. His work on the phylogeny of the Bombyliidae will undoubtedly provide a significant foundation of information and theories, which can be referred to and tested in the years to come.

A portion of my museum work in South Africa was supported by an Ernst Mayr Grant from the Museum of Comparative Zoology, Harvard University. The Bishop Museum Association provided funds in support of publication costs.

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