**Conochironomus** Freeman: an Afro-Australian Chironomini genus revised (Diptera: Chironomidae)

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**Abstract.** The chironomid genus *Conochironomus* is revised, with diagnoses provided for both sexes of adults and, for the first time, the immature stages. The Afrotropical genotype *Cacutistilus* Freeman and the newly described Australian species *C.australiensis* (for misidentified *acutistilus* in Australia), *C.cygnus* and *C.kakadu* are described in all stages. *Cavica* Freeman is redescribed from the male, and *C.deemingi* is described as new from the male alone, both from the Afrotropical Region. The Australian species *C.cervus* is described as new, based on the pupa alone. Comments are made on the ecology and distribution. A previously little-recognized 'tropical' Gondwanan biogeographic explanation for *Conochironomus* distribution is postulated.

**Introduction**

The immature stages of insects are rarely as well known taxonomically as the adults, excepting some few medically significant taxa. The Chironomidae (Diptera) are exceptional in this regard because a historical adult-based classification has been reconciled with larval taxonomy as driven by the identification requirements of field aquatic biologists. Synthetic studies reconciling larval taxonomy as driven by the identification requirements of field aquatic biologists. Synthetic studies (Wiederholm, 1983, 1986, 1989) demonstrate that most Holarctic chironomid genera are known in larval, pupal and adult stages. Many Holarctic genera occur also in the southern hemisphere, and northern-based keys and diagnoses generally remain valid. However, several non-Holarctic genera have been named, and increasingly more are being recognized, for which published descriptions of the immature stages do not exist. These lacunae limit our ability to determine the status and evolutionary relationships of certain southern hemisphere genera and represent barriers to understanding the aquatic systems in which they live.

Species of a genus distributed in the Afrotropical and Australian regions, *Conochironomus*, described as adults by Freeman (1961), are common in some southern hemisphere lotic and lentic ecosystems. The putative association of larvae with adults already has enabled the use of the generic names in aquatic faunal studies in Australia (e.g. Smith & Cranston, 1995) and Africa (Hare & Carter, 1986, 1987). Furthermore, in the Australian 'grey literature', *Conochironomus* is keyed as a larva by Martin (1975), and the larva and pupa are illustrated and keyed together with brief distribution notes by Cranston (1991, 1994).

Representatives of *Conochironomus* have been reared from West Africa and Australia. In this paper formal descriptions and redescriptions are provided for the genus, five new species are described, and details of the distribution, ecology and phylogenetic relationships are provided.

**Species concepts**

The pupal life-history stage has proved valuable in species segregation in Chironomidae (e.g. Langton & Cranston, 1991). However, in this study our original recognition of segregates in *Conochironomus*, which we term species, was based upon non-overlapping features of the male genitalia. Subsequent testing of the concepts came from morphometrics of the male imago, including some non-overlapping differences between African populations of *C.acutistilus* and putative Australian conspecifics. These segregates coincided with those we recognized subsequently, based upon features of the female genitalia particularly the diagnostic shape of the ventrolateral lobes of gonapophysis VIII. However, as Porter & Shapiro (1990) observe, the use of differences in genitalia in insect taxonomy can lead to circular reasoning, with populations differentiated by the genitalia being treated as species, and species being considered as 'things differentiated by genitalia'. In this case the validity of these segregates based on genitalia appears confirmed by other features of the adults, notably morphometrics, and certain features of the larvae and pupae. Unusually in the Chironomidae, the pupae appear rather homogenous and even with reared and reliably associated specimens, discriminatory features between some taxa are few.

**Methods and Materials**

West African material was collected using a 15 x 15 x 15 cm Ekman grab. Immature insects were separated from sediment by sieving through a 250 μm mesh. Larvae from Australian and African sites were reared individually in cotton-wool-stoppered 12 x 50 mm tubes in small volumes of water from the collecting sites, and maintained at close to ambient temperatures of 21–33°C.

Microscope slide preparation for Australian material involved clearing where necessary with 10% KOH, neutralization...
and initiation of dehydration with glacial acetic acid, then mounting from propan-2-ol (isopropanol) into Euparal. African material was prepared in the same manner then mounted in Canada balsam.

Morphological terminology follows Sether (1980), except where we adopt Langton's (1994) suggested use of taenia (adjective taeniate) for 'filamentous' or 'lamelliform' setae.

Australian locality data are cited in a clockwise sequence, thus: Northern Territory, Queensland, listed north to south followed by Western Australia, listed south to north. All Australian data are entered into the ANIC database.

Abbreviations used in the text and tables are as follows (all measurements in mm unless otherwise stated*): A.L., anal lobe setal number (pupa); ANIC, Australian National Insect Collection, CSIRO, Canberra, Australia; Atr 1–6, length of antennal segments 1–6 (larva); A.R., antennal ratio = (adult) length of ultimate; flagellomere, combined lengths of flagellomeres 1–12; (larva) length of larva; BMNH, British Museum (Natural History) (now the Natural History Museum); B.V., combined length Fe + Ta + Ti; combined lengths ta2–4; Ck, creek; Clyp, clypeus (setal count); CNC, Canadian National Collection, Agriculture Canada, Ottawa, Canada; Dc, dorsocentral setae (pupa); E, East; FCu, cubital fork; Fe, femur; Fl (1–14) Flagellomeres (1st–14th); F.L., frontal seta length (pupa); Gcx, gonocoxite length; Gst, gonostylus length; H.I, head capsule length, measured dorso-medially from anterior labrum to posterior margin (larva); H.r., number of hooks in hook row, tergite II (pupa); H.r.r., hook row ratio = width of hook row: width of segment II; HV, hypopygium value = body length: gonostylus length × 10; HS, homestead; L, larva; L.aps., lateral antenneapostals (setal count); Le, larval exuviae; Le/Pe/δ(9), reared adult male (female), with larval and pupal exuviae; L.R., leg ratio: tarsomere 1 length: tibia length; M.w. mentum width (compressed larval head capsule); Md.l., mandible length (larva); N, North; P, pupa; P1–3, legs (1, fore; 2, mid; 3, hind); Pa, prealar setae; Pe, pupal exuviae; Pö (5), pharate male (female) within pupa; Pmnd., premandible length; R., river; R. a., R. a., wing veins R. a. and R. a., respectively (setal count); RM, radius to media crossvein; R. ap., antennal segment 1–6 (larva); R. ap., antennal segment 1–6 (larva); R. a., R. a., R. a., wing veins R. a., R. a., and R. a., respectively (setal count); RM, radius to media crossvein; R. ap., antennal segment 1–6 (larva); R. ap., antennal segment 1–6 (larva); R. a., R. a., R. a., wing veins R. a., R. a., and R. a., respectively (setal count); RM, radius to media crossvein; S, South; S.Chr, sensilla chaetica, tarsomere 1; Ssq, squama (setal count); St. I., antennal style length (larva); S.V., ratio of length of Cu,:length of M; S.V., ratio of length of Cu,:length of M; S.V., ratio of length of Cu,:length of M;sq, length of M; W, West; W.I., wing length (arcus to apex) in mm; ZMB, Zoologische Museum, Bergen, Norway; ZSM, Zoologische Staatsammlung München, Germany.

*The larval antennal ratio is calculated from summed lengths of individual segments, rather than, as conventionally, from total length. The latter measure significantly varies depending on intersegmental membrane extension and contraction.

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**Genus Conochironomus Freeman**

**Conochironomus Freeman, 1961: 701.** Type species: *Endochironomus acutistillus* (as *acutistillus*) Freeman, 1955, orig. descr.

**Generic description**

**Adult**

Medium-sized species, with body length to 8 mm, wing length to 3.5 mm. Wing unpatterned; thorax brown with darker vittae and postnotum; legs dark brown with some yellower sections but not banded.

Antenna. Male with 13 flagellomeres, antennal ratio 2.0–3.0. Female with 6 flagellomeres (Fig. 4a), antennal ratio c. 0.6.

Head. Eye bare, with strong dorsomedial parallel-sided extension about 8 ommatidia long; in both sexes eyes separated medially by about width of 4–5 ommatidia. Temporal setae of uniserial postorbitals becoming multiserial verticals anteromedially; clypeals present. Frontal tubercles absent. Palp 5 segmented, segment 2 subcylindrical, segments 3–5 increasingly elongate; segment 3 apparently lacking sensilla.

Thorax (Fig. 1b–d). Antepenultimate lobes scarcely tapered dorsally, medially fused, without indication of median notch. Scutum not overreaching antepenultimate; profile of scutum gently rounded anterior to distinct median tubercle. Acrostichals absent, dorsocentrales, prealars and scutellars uniserial.

Wing (Fig. 1a). Membrane without setae, with fine to moderate punctuation. Anal lobe rounded. Costa ending abruptly at apex of R2+3, somewhat proximal to wing apex: R2+3, ending at proximal 1/3 between R1 and R2+3. FCu slightly distal to RM, ventral ratio 1.0–1.1. R and R1 setose in both sexes, R2+3 setose in males of some species and all females. Squama setose.

Leg. Apex of fore tibia with low flat scale, without spur (Fig. 1e). Mid and hind tibiae apically with two conical combs occupying two-thirds circumference and slightly separated, both combs with short, straight spur (Fig. 1f). Fore leg ratio c. 1.5. Pulvilli quite well developed, about half length of claw. Mid and hind tarsomeres 1 with multiserial sensilla chaetica on apical half, denser on mid-leg, sparser in male. Legs densely setose but without beard.


Hypopygium (Figs 2a–f, 3a–f). Anal tergite bands weak, medially separated to form incomplete V-shape, with or without median anal tergite setae, few short apical anal tergite setae on posterior margin of tergite. Anal point arising from elevated tergal ridge, narrow with bluntly tapered apex. Inferior volsella (Fig. 3e, f) diagnostically variable, often narrow basally, variably swollen medially and often with sinuous digitiform apicomedial extension, without microtrichia, with or without 2–3 medially directed setae near inner margin. Median volsella either present and well developed, reduced to tubercle with 1–3 long setae or absent. Superior volsella basally appressed to mid-gonocoxite, short, somewhat bulbous apically, extending no further than apex of anal point; microtrichiose with medially and dorsomedially...
Conochironomus Freeman

Fig. 1. Conochironomus adult. a, Wing of C. cygnus; b–d, thoracic profiles of females; b, C. acutistilus; c, C. kakadu; d, C. cygnus; legs of C. acutistilus, e, fore-tibial apex; f, one (of two) spurs on apex of mid-tibia.

directed, simple setae, without any differentiated posteriorly directed strong seta. Gonostylus squat to arrow cylindrical, inwardly curved, ending bluntly or with quite acute point, with creased medio-dorsal surface (Fig. 3a–d). Sternapodeme bluntly rounded anteriorly, without oral projections. Phallapodeme elongate, narrow.

Female genitalia (Fig. 4d–i). Notum long and thin, with short thin rami. Gonocoaxapodeme almost straight, not fused medially. Coxosternapodeme IX weakly sclerotized and gently curved. Gonapophysis VIII divided into elongate dorsomesal lobe, continuous with inner contour of vagina, microtrichiose except hyaline apico-medially, and distinct, darkened, rectangular, ventrolateral lobe as large as dorsomesal lobe, lying lateral to, and not covering, dorsomesal lobe, microtrichiose basally, with pointed scales medio-apically; apodeme lobe more or less rectangular, darkly sclerotized, lying dorsal to dorsomesal lobe. Labia hyaline without microtrichia. Gonocoxite IX small, not laterally extended, with 1–2 setae. Tergite IX large, undivided. Postgenital plate large, microtrichiose. Seminal capsules oval darkened near very short neck; seminal ducts straight and ending separately. Cerci relatively small, elongate-quadrate.

Pupa

Medium-sized to large, up to 11 mm long. Thorax, cephalic area and anterior abdominal segments golden brown, posterior abdomen pale brown, apophyses weakly darkened, anterior pleural conjunctives may be dark brown.

Cephalothorax. Frontal setae present, on cephalic tubercles (Fig. 5a, b) except in australiensis. Frontal apotome wrinkled, without frontal warts. Pedicel sheath with 1 or more tubercles on median surface.

Thoracic horn with 6 subequal-lengthed, plump, smooth, branches; basal ring (Fig. 6a, b) well developed, oval, with 1 roundish to elongate-oval tracheal bundle. Median suture strongly rugose, with moderately developed rugose tubercle (Fig. 6c). Prealar tubercle absent.
Fig. 2. *Conochironomus* male genitalia, left side dorsal, right side ventral, stylized, cut-away. a. *Cavicula*; b. *C.deemingi*; c. *C.auctus*; d. *C.australiensis*; e. *C.kokadie*. f. *C.pygmaeus*.
Conochironomus Freeman 25

Fig. 3. Conochironomus male genitalia, scanning electron micrographs: a, c, e, C. kakadu; b, d, f, C. australiensis; a, b, gonostyli; c, d, gonostylar 'creases'; e, f, superior volsellae.

One median, 2 lateral antepronal setae; 2 fine precorneals; dorsocentral (dc), close to dc,, separated from approximated dc, and dc,, all subequal and fine.

Abdomen (Fig. 5c, d). Tergite I bare, II–III bare or II with sparse spinules, III–V with variable-sized subquadrate spinule area, VI–VIII with antero-lateral fine spinule area. Anal segment densely spinose. Tergite II hook row continuous, 30–50% tergite width, comprising 50–100 hooks. Conjunctives bare, heavily pigmented laterally on I/II–III/IV. Sternites VII–VIII with extensive quadrate spinule pattern, others bare. Pedes spurii A absent; pedes spurii B moderately to strongly developed on segment II (Fig. 5e, f). Posterolateral corner of segment VIII with few small pale teeth (Fig. 6d–g). Apophyses moderately developed.

Setation. Segment I with 3D, IV and without L setae; II–VII with 5D, 2–3V; 3L on II–VI, VII with 4L setae, L, taeniate; VIII with 1D, 2V, 5 taeniate L setae. 1 pair of 0 setae on sternites II–VIII.

Anal lobe semilunar, with fringe of 150+ multiserially inserted, taeniate setae, extending to apex and sometimes around inner apical margin. Dorsal surface with 1 taeniate seta. Genital sac of male not quite reaching apex of anal lobes, female genital sac much shorter than anal lobes.
Fig. 4. *Conochironomus* females: a, antenna, *C. australiensis*; b, c, second palp segment of b, *C. cygnus*, c, *C. australiensis*; d–i, genitalia, d, ventral, e, lateral, d, e, *C. acutipennis*; f–i, ventrolateral lobes (to same scale), f, *C. acutipennis*; g, *C. australiensis*; h, *C. kokoda*; i, *C. cygnus*.

Fig. 5. *Conochironomus* pupae: a, frontal setae, *C. australiensis*; b, cephalic tubercles, *C. cervus*, c, tergites, d, sternites, of *C. australiensis*; e, f, pedes spurii B of e, *C. australiensis*, f, *C. cygnus*. 
Larva (fourth instar)

Medium sized to large, red coloured, up to 11 mm long, with ventral head length up to 530 μm. Head capsule evenly golden coloured to brown with darker brown gula, mentum and apical mandibular tooth. Occipital margin darkened.

Dorsal surface of head (Fig. 7h). Frontoclypeal apotome broad, without frontal pit; 1 labral sclerite.

Antenna (Fig. 7e) with 6 segments, segments 2, 5 and 6 short, 3 and 4 subequal, with 4 often characteristically curved; Lauterborn organs moderately developed, one apical on segment 2, the other placed on opposite apex of third segment. Ring organ in middle of segment 1, seta absent. Blade extending to near apex of antenna.

Labrum (Fig. 7g). SI plumose; SII densely plumose, arising from prominent tubercle; SIII simple, short; SIVa and b moderately developed. 10 plumose subequal long chaetae. Seta praemandibularis strong and simple. Labral lamellae broad, without indication of median division. Pecten epipharyngis of three narrow scales, perhaps apically notched, but not deeply toothed. 10–12 apically plumose chaetulae laterales, 2 apically branched chaetulae basales. Premandible with 3–4 teeth and strong brush.

Mandible (Fig. 7f). Weak, pale, dorsal tooth present; strong apical tooth and 2 inner teeth. Pecten mandibularis not extending to apical mandibular tooth. Seta subdentalis (Fig. 7f) inserted on ventral surface, somewhat sickle-shaped and extending to inner mandibular teeth. Mola and inner margin smooth. Seta interna inserted on dorsal surface, strongly plumose, 4-branched.

Mentum (Fig. 7a–d). With clearly demarcated ventromental component of four subequal teeth, and dorsomentum of six teeth on each side, with the first smaller, the second taller, then evenly decreasing in size laterally; all teeth similarly medium brown, without any paler median teeth. Ventromental plates separated mediadly by width of ventromentum plus 1–2 lateral teeth. Ventromental plate elongate fan-shaped, with curved, smooth or wavy margin; striae of mid and posterior plate present as variable-lengthed ridges running into a subapical band of regularly spaced lappets (Fig. 7b). The scanning electron microscope reveals a double series of spines between and anterior of the lappets (C. J. Webb, unpubl.). Setae submenti simple.

Abdomen. Lateral and ventral tubules absent. Anterior parapods with dense, fine, simple claws; posterior parapod claws simple. Procercus weakly pigmented, small, wider than high, bearing 7 subequal anal setae.

Generic recognition

Conochironomus larvae are diagnosed by the six-segmented antenna with Lauterborn organs alternate on the apices of the second and third segments, a unicoloured brown mentum with delimited four subequal median ventromental teeth. Conochironomus fails to key beyond couplet 17 in the Chironominae key of Wiederholm (1983), since a pale dorsal mandibular tooth is present and the four median subequal-sized mental teeth protrude anterior to the remaining dorsomental teeth. Disregarding the pigmentation of the dorsal mandibular tooth and mentum, the median mental teeth pattern and length of antennal flagellum resembles that of Paratendipes but this genus differs in the pecten epipharyngis structure. Otherwise similar Stictochironomus larvae have small paired median mental teeth in the Holarctic region (Wiederholm, 1983), though Australian
S. fluviatilis (Skuse) and S. illawara Freeman fail to conform to the Holarctic diagnosis (Cranston, unpubl.). Separation of larval Conochironomus from the larvae of these Australian 'Stictochironomus', Australian Imparipennis Freeman and Afro-Australian Skusella Freeman is the subject of ongoing study (Cranston, in prep.).

The pupa of Conochironomus, with six subequal branched thoracic horn and continuous hook row on tergite II, keys in Wiederholm (1986) to couplet 28. Amongst the small number of Holarctic genera with such few (6–8) branches to the thoracic horn, Conochironomus differs from Sergentia and Phaenopsectra in lacking apically spinose cephalic tubules and in having no differentiated transverse band of tergal spines. The absence of pedes spurii A, thoracic horn structure and distribution of taeniate lateral setae allow separation from Paratendipes and Stelechomyia. The otherwise similar pupa of Harrisius Freeman...
has taeniate lateral setae on segments V and VI (fine in _Conochironomus_), and the single posterolateral spur on sternite VIII contrasts with the multiple small teeth of the _Conochironomus_ comb.

Adult _Conochironomus_, in which the male has 13 flagellomeres, the anterior tibial apex lacks a spur, and acrostichal setae are absent, can be distinguished from other genera with these character states by the conical shape of the tibial spurs. The unusual structure of the tapering, microtrichose anal point is shared only with _Omisus_ and _Zavrelia_ (O. A. Sæther, pers. comm.). Species possessing median volsellae key in Wiederholm (1989) to _Paratendipes_; those in which it is lacking key to _Stictochironomus_. The female of _Conochironomus_ is keyed in Sæther (1977), in which the rounded anterior tibial apical scale, conical tibial combs each with a spur, six flagellomeres, lack of acrostichals, and gonapophysis VIII divided into a ventrolateral lobe subequal in size to the dorsolateral lobe form a diagnostic combination.

**Keys to Conochironomus**

*Males (C. cervus unknown)*

1. Setose median volsella present (Fig. 2a, b). Wing vein R, setose ................................................................. 2
   - Median volsella absent, at most weak tubercle with 1–2 fine setae (Fig. 2c–f). Wing vein R, bare, or with few subapical setae............. 3
2. Superior volsella bifid, with short basal digitus, narrow base (Fig. 2a) ................................................................. avicula Freeman
   - Superior volsella without digitus, broad at base (Fig. 2b) ................................................................. deemingi sp.nov.
3. Superior volsella rectangular; digitus arises from mediadorsal surface, directed caudally (Fig. 2c, d) .................................. 4
   - Superior volsella globular; digitus arises mediobasally, and curved caudally, then dorsally (Fig. 2e, f) ......................... 5
4. Medio-dorsal surface of gonostylus microtrichose and setose, with weak creases (Fig. 2c) ................................................. acutistilus Freeman
   - Medio-dorsal surface of gonostylus bare, with prominent creases (Figs 2d, 3a, c) ........................................................... australiensis sp.nov.
5. Anal tergite with 3–4 median setae; inner margin of gonostylus angled; digitus without seta (Figs 2e, 3c). Antennal ratio <2.2 ............................................................................................................... kakadu sp.nov.
   - Anal tergite without median setae; inner margin of gonostylus straight; digitus with 1–2 setae medially (Fig. 2f). Antennal ratio >2.5 ............................................................................................................... cygnus sp.nov.

*Females (C. deemingi and C. cervus unknown)*

1. Dorsocentral setae row uninterrupted, commencing at one third of thorax (Fig. 1b). Antennal ratio >0.5 (Fig. 4a) ........................................ 2
   - Dorsocentral setae with disjunct group of 3–4 setae on anterior third of thorax, anterior to medio-posterior row (Fig. 1c, d). Antennal ratio <0.5 ............................................................................................................... 4
2. Wing length >3.5 mm. Setal count R + R, >70 ...... avicula Freeman
   - Wing length <3.5 mm. Setal count R + R, <60 ............................................................................................................... 3
3. Ventrolateral lobe with narrow microtrichia-free band lateral to inner margin (Fig. 4f) ................................................................. acutistilus Freeman
   - Ventrolateral lobe completely microtrichiose (Fig. 4g) ............................................................................................................... australiensis sp.nov.
4. Ventrolateral lobe robust, with few macrotrichia (Fig. 4h). Second palp segment distally bulbous (Fig. 4i) ................................................................. cygnus sp.nov.
   - Ventrolateral lobe squat, with denser macrotrichia (Fig. 4i). Second palp segment distally bulbous (Fig. 4b) ................. kakadu sp.nov.

**Pupa (C. avicula, C. deemingi unknown)**

1. Tergite III bare ................................................................. 2
   - Tergite III with spinules ................................................................. 3
2. Frontal tubercles absent ....................................................... acutistilus Freeman
   - Frontal tubercles grossly developed, over 150 μm long, apically bifid (Fig. 3b) ................................................................. cervus sp.nov.
3. Anal lobe unicolourous, pale yellow. Tracheal bundle elongate-oval, greater than 50 μm in longest dimension, length:width ratio >2.0 (Fig. 6a). Hook row on tergite II with >95 hooks and occupying about 50% of tergite width (Fig. 5c). Pedes spurii A weakly developed (Fig. 5e) ............................................................................................................... australiensis sp.nov.
   - Anal lobe pale apically, brown terminally. Tracheal bundle rounded-oval, less than 50 μm in longest dimension, length:width ratio <2.0 (Fig. 6b). Hook row on tergite II with <75 hooks and occupying less than 50% of tergite width. Pedes spurii B strongly developed (Fig. 5f) ............................................................................................................... 4
4. Combs on posterolateral corners of VIII of small tubercles (Fig. 6g) ................................................................. kakadu sp.nov.
   - Combs on posterolateral corners of VIII of small curved hooklets (Fig. 6i) ................................................................. cygnus sp.nov.

**Larva (C. avicula, C. deemingi, C. cervus unknown)**

(applies only to fourth instar, recognized by mandible length >140 μm.)

1. Gula/submentum brown, occipital margin dark brown .................. 2
   - Gula/submentum pale, occipital margin light brown .................. 3
2. Basal antennal segment >80 μm; antennal ratio >1.0 (Fig. 7e) ............................................................................................................... australiensis sp.nov.
   - Basal antennal segment <70 μm; antennal ratio 1.0 or less .... 4
   - Anterior margin of ventromental plate smooth (Fig. 7c) .... 5
   - Anterior margin of ventromental plate wavy (Fig. 7d) ............................................................................................................... kakadu sp.nov.
   - Anterior margin of ventromental plate smooth (Fig. 7c) ........ cygnus sp.nov.

**Conochironomus acutistilus (Freeman)**

_Endochironomus acutistilus_ Freeman, 1955: 288 (lapsus in spelling of acutistilus)_

_Conochironomus (Endochironomus) acutistilus_; Freeman, 1957: 352.

Conochironomus acutistilus; Freeman, 1961: 701; Freeman & Cranston, 1980: 188.

**Differential diagnosis**

The male of _C. acutistilus_ most closely resembles that of _australiensis_, notably in the male hypopygium which has the superior volsella somewhat rectangular with two medially directed setae and a posterodorsal bare digitus. A major difference is the presence of prominent creases on the bare medio-dorsal surface of the gonostylus in _australiensis_, in contrast to the microtrichiose, weakly creased surface of _acutistilus_. From the samples of males available, the antennal and foreleg ratios are lower in _acutistilus_ and the wing vein R and squama are more setose.

The females of _C. acutistilus_ have identical patterns of dorso-central setae as _australiensis_, lacking the anterior grouping...
seen in *cygnus* and *kakadu*. The shape of the ventrolateral lobe of the genitalia allows differentiation; however, few of the morphometric characters show distinct gaps and the sample size is small.

The lack of frontal tubercles on the pupa distinguishes this species from all other *Conochironomus*, and the fewer hooks in the hook row on segment II further distinguishes it from *australiensis*. The dark submentum of the larva is shared by *australiensis* with further larval differentiation predominantly mensural.

**Description**

*Imago male.* Morphometrics and ratios as in Table 1. Hypopygium as in Fig. 2c.

*Imago female.* Thoracic profile (Fig. 1b). Morphometrics and ratios as in Table 2. Female genitalia as in Fig. 4d, e; ventrolateral lobe of hypopygium as in Fig. 4f.

*Pupa.* Morphometrics as in Table 3. Posterolateral corner of segment VIII as in Fig. 6d.

*Larva.* Morphometrics as in Table 4.

**Distribution**

Afrotropical region: Ruanda, Sierra Leone, Uganda, Upper Volta, Zaire, Zimbabwe (Freeman & Cranston, 1980); Nigeria (Hare & Carter, 1987).

**Material examined**

Holotype, pinned male with genitalia on celluloid balsam mount, Belgian Congo [ZAIRE], Elizabethville, 7–31.xi.1932 (Seydel), BM 1933–76 (BMNH).


**Conochironomus deemingi** sp.nov.

**Differential diagnosis**

The male adult is diagnosed by the characteristic genitalia. According to Freeman (1955) the female is recognizable by the apical antennal segment being as long as the preceding three segments. However, the one remaining female paratype (of two described), slide mounted by J. Amakye, is missing most of the head and all antennae, and the remaining parts do not enable redescription. The dorsocentral setal row is uninterrupted and the mensural features used in the key to females above derive from the overall greater body size and setosity. The ventrolateral lobe of the distorted genitalia most closely resembles that of *C.cygnus* (Fig. 4i).

**Material examined**


**Conochironomus avicula** (Freeman)

Endochironomus *avicula* (Freeman, 1955: 289

*Chironomus* (Endochironomus) *avicula*; Freeman, 1957: 353.

*Conochironomus avicula*; Freeman, 1961: 701; Freeman & Cranston, 1980: 189.

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The male adult is diagnosed by the characteristic genitalia. According to Freeman (1955) the female is recognizable by the apical antennal segment being as long as the preceding three segments. However, the one remaining female paratype (of two described), slide mounted by J. Amakye, is missing most of the head and all antennae, and the remaining parts do not enable redescription. The dorsocentral setal row is uninterrupted and the mensural features used in the key to females above derive from the overall greater body size and setosity. The ventrolateral lobe of the distorted genitalia most closely resembles that of *C.cygnus* (Fig. 4i).

**Material examined**

1♀, paratype, damaged, slide mounted in Canada Balsam (Amakye), Nigeria, Onitsha, x.1932 (Anderson) (BMNH). 1♂, MADAGASCAR, Madagascar Est, Forêt d’Isaka, 225 m, dst. Fort Dauphin, 24–26.ii.1958 (Stuckenberger) (BMNH).

**Conochironomus deemingi** sp.nov.

**Differential diagnosis**

The male adult, the only known life-history stage, is diagnosed by the genitalic characters used in the key.

**Description**

*Adult male.* Morphometrics and ratios as in Table 1. Hypopygium as in Fig. 2a.

**Material examined**

Holotype ♀, slide mounted in Euparal, NIGERIA, N. Nigeria, Kaduna, 1.xi.1970 (Deeming) (BMNH).

**Etymology**

Named in honour of the collector, Josh Deeming; despite its derivation, to be treated as a noun in apposition.

**Distribution**

Afrotropical region: Nigeria.
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**Table 2.** Mensural features of *Conochironomus* females. Abbreviations as in Materials and Methods.
Table 3. Mensural features of Conochironomus pupae. Abbreviations as in Materials and Methods.

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Table 4. Mensural features of Conochironomus larvae. Abbreviations as in Materials and Methods.

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<td>Pmdn.</td>
<td>86-95</td>
<td>91-96</td>
<td>80-91</td>
<td>82-90</td>
</tr>
</tbody>
</table>

Conochironomus australiensis sp.nov.

Conochironomus acutistilus (Freeman); Freeman, 1961: 701; Cranston & Martin, 1989: 269, misident.

Differential diagnosis

In all stages C.australiensis most closely resembles C.acutistilus under which diagnostic differences are cited.

Description

Imago male. Morphometrics and ratios as in Table 1. Hypopygium as in Fig. 2d.

Imago female. Thoracic profile as in C.acutistilus (Fig. 1b). Morphometrics and ratios as in Table 2. Antenna (Fig. 4a), second palpal segment (Fig. 4c), and ventrolateral lobe of female genitalia as in Fig. 4g.

Pupa. Morphometrics and ratios as in Table 3. Cephalic area, tergites, sternites, pedes spurii B, posterolateral corner of segment VIII as in Figs 5a, c-d, c, 6e.

Larva. Morphometrics and ratios as in Table 4. Mentum, ventromental plates, antenna, mandible, dorsal and anterior head as in Fig. 7a, b, e-h.

Etymology

Named for its status as the commonest Australian species; despite its derivation to be treated as a noun in apposition.

Distribution

Australian region: Northern Territory, Queensland, Western Australia.

Material examined

Holotype, Le/Pe/?, slide mounted in Euparal, AUSTRALIA, Northern Territory, 12°47'S 132°10'W, W. arm of W. Alligator R., Arnhem Highway Crossing, 2.vi.1988 (Cranston) (ANIC).
Caranbirini W.H., 33 km SW of Borroloola, 3.xi.1975
Crossing, 2.vi.1988
Ck, viii.1989
Baroalba Ck, 19 km NE by E of Mt Cahill, 28.x.1972
7Pe, same data except Gorge 3; 6Pe, same data except
Gorge, 3.vii.1988
Mary Ann Dam, 23.v.1992
Western Australia, IPe, 15'543, 128'07E, E. Kimberley,
Stradbroke Island, Brown Lake, 17.i.1991
3Pe, 19'36'39'S, 134'12'27'E, Tennant Creek,
Queensland, 16, N. Queensland, McIlwraith Range, 15 km
by W of Nimbuwah Rock, 11.xi.1972
6.xi.1984
(16, 12'47'S, 132'51'E, Cooper Ck, 19 km E by
Mt Cahill, 18.xi.1972 (Colless); 16, 12'52'S, 132'51'E, Koongarra, 15 km E of Mt Cahill, 6–9.iii.1973
(Colless); 19, 12'52'E, 132'46'E, Nourlangie Ck, 6 km E of Mt Cahill, 18.xi.1972 (Colless); 2Pe, S. Alligator R., site 1,
14.vi.1988 (ARRRI 5, 64); 1Pe, Barramundie
Gorge, 3.vii.1988 (Dostine) (ARRRI 21); 2Pe, 15'18'S, 132'32'E, Graveside Gorge, 17.vii.1988 (Dostine) (ARRRI 159, 160); 2Pe, Jim Jim Gorge, 21.x.1989 (Dostine) (ARRRI);
1Pe, 12'50'S, 132'01'E, Wildman R., Arnhem Highway Crossing, 2.vi.1988 (Cranston); 3Pe, 12'18'S, 133'20'E nr
Narbalek, Cooper Ck, 27.v.1988 (Cranston); 14'18'S, 132'26'E, Katherine R., 2Pe, Katherine Gorge 1, 21.vi.1992
(Cranston) (1 to ZSM); 1Pe, same data except Gorge 2;
7Pe, same data except Gorge 3; 6Pe, same data except
14'18'S, 132'25'E, below Gorge; 1L, 16'16'S, 136'05'E,
Caranbirini W.H., 33 km SW of Borroloola, 3.xi.1975
(Upton); 3Pe, 19'36'39'S, 134'12'27'E, Tennant Creek,
Mary Ann Dam, 23.v.1992 (Cranston). Queensland, 19, 17'09'S, 125'15'E, 4 km W of King Cascade, 2.v.
1990 (Naumann); 12Pe, 27'29'S, 153'25'E, N. Stradbroke Island, Brown Lake, 17.i.1991 (Cranston).
Western Australia, 1Pe, 15'54'S, 128'07'E, E. Kimberley,
Emma Gorge, 7.v.1992 (Cranston); 2i, 15'50'12'S, 127'24.32'E, Durack R., 7.v.1992 (Cranston); 1i, 15'38'8, 125'15'E, 4 km W of King Cascade, CALM
site 28/3, 12–16.vi.1988 (Weir); 1i, 15'08'S, 126'08'E,
King Edward R., 1.vi.1988 (Naumann); 4 Pe, 14'50'S,
125'43'E, N. Kimberley, Mertens Falls, 4–5.v.1992 (Cranston); 1i, 14'49'S, 126'49'E, Carson Escarpment, Drysdale
survey site 1, 9–15.viii.1975 (Common & Upton); 1Pe,
14'29'42S, 125'47.26'E, Crystal Ck, Old Boab Camp, 3.v.1992
(Cranston).
Non-type material: 7Pe, 15'41'S, 126'47'E, Western Australia,
N. Kimberley, Drysdale R. Crossing, 1–2.v.1992 (Cranston)
[Same slide as paratype of C. cervus.]

Conochironomus kakadu sp. nov.

Differential diagnosis

C. kakadu and cygnus are distinguished in the adult by the shape
of the hypopygium with the digitus of the superior volsella arising
medially and directed dorsally. In C. kakadu tergite VIII has
several setae and the digitus of the superior volsella is bare. The
median volsella is indicated by two strong setae arising from
tubercles at the site. Mensural differences between the species
include the appreciably lower antenna ratio of kakadu. Females
are differentiated only by the shape of the ventrolateral lobe. The
paucity of immature material means that diagnostic differences
are somewhat speculative. The shape of the teeth of the postero-
lateral corner of segment VIII of the pupa and the contour of the
anterior margin of ventromental plate of the larva may prove to
be diagnostic.

Description

Imago male. Morphometrics and ratios as in Table 1. Hypopygium as in Fig. 2e.

Imago female. Thoracic profile as in Fig. 1c. Morphometrics and
ratios as in Table 2. Ventrolateral lobe of hypopygium as in Fig. 4h.

Pupa. Morphometrics and ratios as in Table 3. Postero-lateral
corner of segment VIII as in Fig. 6g.

Larva. Morphometrics and ratios as in Table 4.

Etymology

Named for its first discovery and several subsequent records
within Kakadu National Park, Northern Territory; to be treated
as a noun in apposition.

Distribution

Australia: Northern Territory, Queensland, Western Australia.

Material examined

Holotype, 1Le/Pe/δ, slide mounted in Euparal, 12°39'S, 132°53'E, AUSTRALIA: Northern Territory, Gulungul Ck,
23.v.1988 (Cranston) (ANIC).

Paratypes, AUSTRALIA: Northern Territory, 2δ, 12°06'E,
133°04'S, Cooper Ck, 19 km E by S Mt Borradaile, 9.xi.1972
(Colless); 1δ, 12°06'5, 133°14'E, Cooper Ck, 11 km S by
W of Nimbuwah Rock, 1.xi.1972 (Colless); 1L, 12°06'E,
133°14'E, Cooper Ck, 11 km S by W of Nimbuwah Rock,
1.xi.1972 (Colless); 2L, as holotype; 1L, 12°39'S, 132°53'E,
Mudgibnerri Billabong, 12.iv.1989 (Cranston); 1L, 12°39'S,
132°53'E, Magela Ck., Stoned Billabong, 11.iv.1989 (Cranston); 1δ, 12°41'S, 132°55'E, Ranger/Magela Ck. 25.x.1982 (Sharley & Malipati) (Voucher
sp. 8); 3δ 3f, 12°52' 132°46'E, Nourlangie Ck. 6 km E of Mt
Cahill, 18.xi.1972 (Colless); 1δ, same data except 19.xi.1972;
19, same data except 14.vi.1973; 1δ, 12°47'S, 132°51'E,
Baroalba Ck, 28.x.1972 (Colless); 30 km N of Adelaide R.,
5–6.xi.1984 (Baehr) (ZSM); 1δ, 16'16'S, 136°05'E, Caranbirini
W.H., 33 km SW of Borroloola, 3.xi.1975 (Upton).

Queensland, 1δ, N. Queensland, McIlwraith Range, 15 km

Western Australia. 1δ, 16'34'S, 122°51'E, W. Kimberley, Martin's
Well, 24.iv.1977 (Colless); 1δ, 15'08'S, 126°08'E, King Edward
R., 1.vi.1988 (Naumann); 1δ, 14'49'S, 126°49'E, Carson Escarp-
ment, Drysdale survey site 1, 9–15.vii.1975 (Common & Upton).
**Conochironomus cygnus** sp. nov.

**Differential diagnosis**

Most of the diagnostic differences between the rather similar cygnus and kakadu are dealt with under kakadu. Major differences in the male genitalia include the absence of setae on tergite VIII and the presence of a median seta on the digitus of the superior volsella. There is no evidence of a median volsella in cygnus.

**Description**

*Imago male.* Morphometrics and ratios as in Table 1. Hypopygium as in Fig. 2f.

*Imago female.* Thoracic profile as in Fig. 1d. Morphometrics and ratios as in Table 2. Hypopygium as in Fig. 4i.

*Pupa.* Morphometrics as in Table 3. Pedes spurii B as in Fig. 5f; posterolateral corner of segment VIII as in Fig. 6f.

*Larva.* Morphometrics as in Table 4.

**Etymology**

Named for the fanciful resemblance of the superior volsella to the neck of a swan; to be treated as a noun in apposition.

**Distribution**

Australia: Northern Territory, Queensland, Western Australia.

**Material examined**

Holotype, 1Le/Pe/δ, slide mounted in Euparal, AUSTRALIA: Queensland, 27°32’S, 132°29’E, N. Stradbroke Island, Blue Lake, 17.i.1991 (Cranston) (ANIC).

Paratypes, AUSTRALIA: Northern Territory, 1δ, 12°06’E, 133°04’S, Cooper Ck, 19 km E by S Mt Borradaile, 2.xi.1972 (Colless); 1L, 12°18’E, 133°20’E nr Narbalek, Cooper Ck, 27.v.1988 (Cranston); 1L, 12°39’S, 132°55’E, Mudg-inberri Billabong, 12.iv.1989 (Cranston); 1δ, 12°41’S, 132°55’E, Ranger/Magela Ck, 2.iii.1983 (Sharley & Malipatil) (Voucher sp. 2); 12°46’S, 132°21’E, Flying Fox Ck, Arnhem Hwy crossing, 2.vi.1988 (Cranston); 1δ, 12°52’S, 132°51’E, Koongarra, 15 km E of Mt Cahill, 6–9.iii.1973 (Colless); 1f, same data except 12.vi.1973; 2δ, 13°32’S, 132°23’E, Kambolgie Ck, 25.v.1988, (Cranston); 1m, 13°18’S, 132°32’E, Gravelside Ck, viii.1989 (Dostine); Queensland, 1L, 27°32’S, 153°29’E, N. Stradbroke Island, Blue Lake, 17.i.1991 (Cranston); Western Australia: 1δ, Fitzroy Crossing, Fitzroy R., 18–20.xi.1984 (Baehr) (ZSM).

Non-types, Northern Territory, Litchfield National Park, 2Pe, 13°10’S, 130°41’E, Wongi Falls, 6.viii.1990 (Cranston); 2Pe, 13°07’S, 130°39’E, Petherick’s Rainforest, 6.viii.1990 (Cranston).

**Conochironomus cervus** sp.nov.

**Differential diagnosis**

Conochironomus cervus is only known from the distinctive pupal exuviae. The 'staghorn'-shaped frontal tubercles are distinctive amongst Conochironomus pupae; the bare tergite III is shared with C.acutistilus.

**Description**

*Pupa.* Morphometrics as in Table 3. Cephalic tubercles as in Fig. 5b.

**Etymology**

Named for the fanciful resemblance of the pupal frontal tubercles to the horns of a deer; to be treated as a noun in apposition.

**Distribution**

Australia: Northern Territory, Western Australia.

**Material examined**


Paratypes, AUSTRALIA, Northern Territory, 1Pe, same slide and data as holotype (Hardwick); 1Pe, 12°55’S, 132°50’E, Kakadu N.P., Hickey Creek, 29.v.1988 (Cranston); 1Pe, Magela Ck, 1992 (Dostine). Western Australia, 2Pe, 17°25’S, 124°57’E, W. Kimberley, Lennard R., Winjana Gorge, 29.v.1992 (Cranston); 3Pe, 15°41’S, 126°47’E, Drysdale R. Crossing, 1–2.v.1992 (Cranston).

**Ecology and distribution of Conochironomus**

Species of Conochironomus are tropical to subtropical in distribution. In Australia, the furthest southern records are from 27°30’S on subtropical North Stradbroke Island, Queensland. The absence from more southerly areas of Australia is likely to be genuine, since very extensive pupal exuvial collections have been made in these areas over the past 8 years. On the African continent, the distribution extends from sub-Saharan Upper Volta to tropical/subtropical Transvaal (Makolo River, 24°S, Nelspruit, 25°S, A. D. Harrison, pers. comm.). Outside this distribution, the genus is not recorded in well-studied Saudi Arabia, nor does it figure in Indian publications on Chironomidae. Other areas that would link the recorded Afrotropical and Australian distributions include parts of the southern Oriental regions. Here collections are fewer, but once again have revealed no evidence of the genus. On present information, Conochironomus exhibits a vicariant tropical/subtropical Australian-Afrotropical distribution.
Conochironomus larvae live in sediments in lakes and rivers. In West Africa, Hare & Carter (1986, 1987) found larval Cacutisilus abundant in near-shore areas of less than 1 m depth in the small, dilute (conductivity c. 20 μS cm⁻¹) Lake Opi, Nigeria. Details of depth distributions, population densities and co-occurring species in Opi Lake are provided by Hare & Carter (1986). Adult emergence took place in all months of the year with the exception of August and September, the period of maximum lake depth. At the beginning of the rainy season (June 1980) the mean (±SE) abundance of larvae (total of all instars) increased with increasing water depth: 0.5 m 1030 ± 400; 1.0 m 130 ± 60; 2.0 m 25 ± 10; 2.5 m 0. The ratio of numbers of instars (4th:3rd:2nd) collected on this date was 1:2.2:2.2.

In Australia, all four species of Conochironomus have been found in lentic and seasonally lotic habitats in the northern third of the continent. During recessional flow, as rivers become a series of pools, Conochironomus can be an important faunal component. There are few Australian wet season records from smaller temporary streams (Magela Creek, Rock Hole Creek) in which no dry season above-surface water is present for up to 6 months. The mechanism for survival in such perennial streams is unknown, but dispersal from more perennial waters seems likely, since few intermittent waters of arid Australia support the larvae.

**Systematics and biogeography**

A data matrix has been compiled comprising 48 Chironominae genera scored for 131 characters, comprising 36 derived from larvae, 21 additional larval ones from ventromental plates, 34 from pupae and 40 from adults (Cranston, unpubl.). Parsimony analyses have been undertaken using the computer algorithm Hennig86 (Farris, 1988) on matrices derived from each life-history stage independently and in combination. A sister-group relationship between Conochironomus and Skusella is suggested by evidence from the larva, pupa, larva + pupa, larva + pupa + adult and all data combined: only the adult character analysis implied differing relationships. Following the rationale of Cranston (1995a), combined evidence is considered most likely to reflect relationships correctly, particularly when several partitioned sets provide similar estimates. In the combined ('total evidence') analysis, Conochironomus + Skusella forms the sister group of Omitrus (Lauerborniella + Zavrelieina). Paratendipes and Stictochironomus form consecutively more basal sister groups to (\(C + S\) (O (L + Z)). On the evidence available, all genera have a six-segmented larval antenna and alternate Lauterborn organs form a monophyletic grouping.

The monophyly of Conochironomus is proposed based on the shared derived (but not unique) adult characters of the tibial comb structure and stria tions of the inner margin of the gonostylus. Larval features are the strongest indicators of the sister-group relationship with Skusella. Estimation of relationships within Conochironomus is problematic. Firstly, many data are missing: only the adult male is known for C.deemingi, only the pupa for C.cervus and the immature stages of Cavicula remain unknown. Secondly, few characters show informative variation, and others are autapomorphic. As might be expected, a 13-character matrix scored for all Conochironomus species, with Skusella and Paratendipes as outgroups, lacks resolution. Two African species, Cavicula and C.deemingi are sisters, as are two Australian species C.kakadu and C.cygnus. Relationships between these species pairs and C.acutistilus, Caustralensis and C.cervus cannot be resolved due the high levels of homoplasy in the available data, and to the extensive missing data.

Regarding the historical biogeography of Conochironomus, the lack of a fully resolved estimate of relationships is a difficulty. However, it is clear that there are relationships between Australian and Afrotropical (including Madagascan) clades. If dispersal gave rise to the current generic distribution, Conochironomus ought to be expected in Saudi Arabia, the Indian subcontinent and south-east Asia: however, the genus appears to be absent from these intervening land masses.

In other groups of Chironomidae, notably amongst the Podonominae, Diamesinae and Aphroteniinae, present-day vicariant distributions are postulated as reflecting ancient Gondwanan ranges fragmented since the Jurassic period (Brundin, 1966; Cranston et al., 1987, Cranston & Edwards, 1992; Cranston, 1992b). These are cool-stenothermic taxa, with temperate distribution on the southern continents: a few recent tropical records, such as Aphroteniella in northern Australian Arnhemland, clearly being relictual. In contrast, Conochironomus (and similarly distributed Skusella and the tanypodine Djalmabatista, Cranston, pers. obs.) are eurythermic tropical chironomids and representing an alternative, but still Gondwanan, distribution pattern.

On geological reconstructions of Pangaea, and subsequent Gondwana (e.g. Owen, 1981), the present-day known distributions of Conochironomus can be reconstructed as contiguous only if at least southern India and part of south-east Asia were once (or still remain) part of that wider distribution. Predictions of a more extended distribution in tropical 'outer' Gondwana, such as southern India and Sri Lanka might be tested by specific collecting in appropriate larger rivers. Montane low-order streams of southern India do not support Conochironomus (Coffman, pers. comm.).

Examining the distributions of other organisms reveals that this trans-Indian Ocean track features strongly in Croizat's (1958) text, and includes angiosperm genera such as Pittosporum (Pittosporaceae). In categorizing the distributions shown by Australian leafhoppers (Cicadellidae), Evans (1959) recognized an old northern (gondwanan) track ('pre-Tertiary Indian') linking India with Africa and Australia which pre-dated the southern Gondwanan pattern with connections through Antarctica. The track is best exemplified amongst aquatic insects by the aquatic and semi-aquatic Hemiptera (Lansbury, 1981). Amongst the few examples from other aquatic insects, a traditional leptolebiid mayfly (Ephemeroptera) connection between Africa, Madagascar, Sri Lanka, India and Australasia is described by Edmunds (1975).

In conclusion, the distribution of Conochironomus provides additional evidence of a second Gondwanan-type distribution including Africa and Australia. Amongst Chironominae, this pattern is illustrated by certain other warm-stenothermic genera such as Skusella. As with the rationale for dating genera of Aphroteniinae and Archaeoelius (Podonominae) to the Jurassic (Cranston et al. 1987; Cranston & Edwards, 1992), the timing of
the fragmentation of Gondwana implies a similar minimum age for Conochironomus.

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References


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