The immature stages and phylogenetic position of Nilodosis Kieffer, an Afrotropical genus of Chironomini (Diptera: Chironominae)

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The immature stages of Nilodosis fusca Kieffer, the type species of the Afrotropical genus Nilodosis Kieffer, are recorded for the first time and complete diagnoses are provided. The larva, pupa and female of N. fusca are described and illustrated, and the male hypopygia are redescribed. The second known species, N. grisea Freeman, is redescribed and illustrated from the male adult, the only known stage, and its congenercity is discussed. A phylogenetic position for Nilodosis close to the South American/Australian Fissimentum Cranston & Nolte is postulated, and the consequences for recognition and differentiation are discussed. This study provisionally associates Nilodosis with previously reported but unallocated larvae, providing some inference to their ecology.

Key words: Diptera, Chironomidae, Nilodosis, immature stages, Africa.

INTRODUCTION

Recognition of the importance of Chironomidae in aquatic biology, including biological monitoring of water quality, has increased with our understanding of the identity of the immature stages. This family of primarily aquatic Diptera is encountered by all freshwater biologists and identifications can be made for taxa of the Holarctic Region, using identification guides that include most taxa at generic level (Wiederholm 1983, 1986, 1989). Many of these genera also occur in the Southern Hemisphere, and the keys and diagnoses generally remain valid. However, several non-Holarctic genera have been described for which there are no published descriptions of immature stages. This limits our ability to determine the status and evolutionary relationships of some important Southern Hemisphere taxa and restricts our understanding of the aquatic systems they inhabit. Among the adult-based genera with undescribed immature stages is Nilodosis Kieffer, 1921, described from Sudan and subsequently also recognized from Central and West Africa by Freeman (1957b) who provided a recent means of identification for Kieffer’s genus. Although Dejoux (1973, 1984) extended the distribution to Cameroon and Guinea and reported N. fusca adults as being common throughout sahelo-soudanian Africa, his specimens have not been traced.

Nilodosis keys to Endochironomus Kieffer in the publication on Holarctic adult male Chironominae (Cranston et al. 1989), confirming the assessment of resemblance made by Freeman (1957b). Freeman observed that the absence of pulvilli and presence of a strong anterior tibial spur in Nilodosis provided a distinction from Endochironomus, and such features are indeed considered to be significant indicators of relationships among Chironomini (e.g. Sæther 1977). However, as he mentioned, Freeman’s (1957b) concept of the genus Endochironomus in the Afrotropical Region differed from the diagnosis that was based on Northern Hemisphere taxa at that time. Developing knowledge of the immature stages of the species that Freeman (1957b) included in Endochironomus has already led to placement of some taxa in Conochironomus Freeman and Kieferulus Goetgheme, but others in which the immature stages are unknown are of uncertain affinity.

In his putative phylogeny of the Chironominae, Sæther (1977) included Nilodosis in brackets and postulated that it, together with Henrardia Goetgheme, was closely related to Endochironomus and Tribelos Townes in ‘an old and relatively plesiomorphic group’. In revisiting Henrardia, Amakye & Sæther (1993) suggested a close relationship, even potential senior synonymy with Tribelos and, furthermore, that Nilodosis appeared to be a senior synonym to both names.

At this stage all estimations of relationships were based upon the adult and, in the case of Nilodosis, derived solely from Freeman’s work. Several
recent assessments show that reconstructions of phylogeny based on adults only and perhaps especially males only, might be misleading (Cranston & Edward 1998). Not only can incorporation of information from the immature stages provide a more robust estimation of the phylogeny, but can assist in assessing and recognizing which adult characters are homoplasic (converge) (Cranston 1994).

By coincidence, two two possible rearings of *Nilodosis* have become available to the author. Although one rearing took place in Nigeria over 20 years ago, and a provisional identification as *Nilodosis* based on the adult female was made at that time (Hare & Carter 1987), confirmation of the identity and a formal description was not provided. The second rearing from Ghana was more recent, but was doubtfully identified as *Nilodosis*. This taxon, which fails to match any described genus in all life history stages, is closest to *Poly pedilum* Kieffer and will be described elsewhere.

Since our knowledge of the phylogeny of Southern Hemisphere Chironomini has advanced, it is now appropriate to: (a) describe the larva and pupa, (b) analyse relationships including morphology from all life history stages, (c) include other austral genera previously unavailable for analysis and, (d) assess the hypothesized relationships with *Tribelos* and *Endochironomus*.

**MATERIAL AND METHODS**

Larvae were collected from Lake Opi (=Ogelube Lake), Nigeria (64.05N 07.29E) by L. Hare, using a 15 x 15 x 15 cm Ekman grab, with immature insects being separated from sediment by sieving through a 250 µm mesh. Larvae were reared individually in 12 × 50 mm tubes, stoppered with cotton wool, in small volumes of water from the collecting sites, and maintained at ambient temperatures of 21–33 °C.

Microscope slide preparation involved clearing where necessary with 10 % KOH, neutralization and initiation of dehydration with glacial acetic acid, then mounting from propan-2-ol (isopropanol) into Canada Balsam. Morphological terminology follows Sæther (1980), except where Langton’s (1994) suggested use of *taenia* (adjective *taeniate*) for ‘filamentous’ or ‘lamelliform’ setae is adopted. All measurements are in µm, unless stated otherwise. Abbreviations used in the text are: BMNH, The Natural History Museum, London; INSB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium. Morphological abbreviations are standard in Chironomidae systematics and can be found in Sæther (1980) or Cranston & Edward (1998).

Phylogenetic analysis was based on data matrices comprising character states scored from all life history stages of more than 50 genera of Chironomini (available from the author). These matrices have been combined and analysed using the criterion of parsimony, undertaken with Hennig86 (Farris 1988) operating within a Microsoft Windows shell of Tree Gardener 1.0 (Ramos 1996). In initial analyses using *Brillia* (Orthocladiinae) and *Prodiamesa* (Prodiamesinae) as outgroup(s), *Riethia* Kieffer and *Pseudochironomus* Malloch (both Pseudochironomini were consecutive sister groups to the remainder of the Chironominae (including the Tanytarsini)). For all detailed analyses of the Chironomini, trees were rooted with *Riethia* (and selectively with *Pseudochironomus*).

**Genus Nilodosis Kieffer**


‘*Chironomus* sp. 125c. *Chironomus* cf. (*Crypto chironomus*) sp.’ McLachlan 1969: 283, Fig. 11 (21). No included species, larva only.

‘*Larvae inconnus de la tribu des Chironomini, species D’* Chrispeels 1959: 163.

**Diagnosis**

**Adult (only female available is N. fusca)**

**A. Male**: With 13 flagellomeres, antennal ratio (AR) 2.0–2.6. Female (Fig. 7) with 5 flagellomeres, AR 0.35–0.45.

**Head**: Eye bare, with strong dorsomedial parallel-sided extension about 7–8 ommatidia long; separated medially by about width of 5–6 ommatidia; extension less developed in female. Temporal setae comprising uniserial to biserial verticals continuous with postorbitals; dyepeals present. Frontal tubercles absent. Palp 5 segmented, segment 2 subcylindrical, segment 4 shorter than 3 or 5; not obviously reduced; segment 3 lacking sensilla.

**Thorax** (Fig. 1). Antepronotal lobes tapered basolaterally then parallel-sided in dorsal half, slightly separated medially. Scutum slightly over-
reaching antepronotum; profile of scutum curved without tubercle. All setae strong, acrostichals and dorsocentrals biserial, scutellars and prealars uniserial.

Wing (Freeman 1957b: Plate 1j) with variably intense dark patterning. Membrane without setae, with moderate punctuation. Anal lobe rounded. Costa ending abruptly at apex of R4+5, somewhat proximal to wing apex; R2+3 ending at proximal third between R3 and R4+5. FCu slightly distal to RM, Venarum Ratio 1.1–1.2. R setose in both sexes, R1 and R4+5 setose or bare. Squama setose.

Legs. Fore femora non-clubbed; apex of fore tibia with extended triangular scale and long curved spur (Fig. 2). Mid and hind tibiae apically with two triangular, separated combs occupying about half circumference, each with short straight spur, sometimes outer spur very short. Foreleg ratio c. 1.7–1.9. Pulvilli absent. Sensilla chaetica absent on mid-leg, extending uniserially full length of tarsomere 1 of hind leg.


Hypopygium (Figs 3–6). Tergite VIII not tapered anteriorly. Anal tergite bands delimit elongate-oval area containing median anal tergite setae, with (N. fusca) or apparently without (N. grisea) anterior closure of area by bands; with few to many fine apical anal tergite setae surrounding anal point base. Anal point arising from slight ridge on tergite IX, slightly spatulate with rounded apex (N. fusca) or parallel-sided (N. grisea). Superior volsella either with expanded setose and microtrichiose basolateral pad, bearing elongate, apically hooked digitus (N. fusca) or solely a triangular setose and microtrichiose lobe, without digitus (N. grisea). Median volsella absent. Inferior volsella cylindrical, completely microtrichiose extending beyond anal point apex, setose apically but without differentiated posteriorly-directed strong seta. Gonostylus with median narrowing, ending in blunt point. Sternapodeme narrow with slight orolateral projection (N. fusca) or broad without oral projections. Phallapodeme long, narrow.

Female (N. fusca only) with distinctive genitalia (Figs 8–10). Notum narrow, moderate lengthened, short rami. Gonocoxapodeme broad, dark, curved, not fused medially. Coxosternapodeme I strongly sclerotized and sinuous. Gonapophysis VIII divided into large, rectangular, microtrichiose dorsomesal lobe, mesally continuous with inner contour of vagina; ventrolateral lobe distinct, small and lying quite lateral, microtrichiose, with apical long setae; apodeme lobe visible between dorsomesal and ventrolateral lobes. Labia non-microtrichiose. Gonocoxite IX setose, swollen, but not laterally extended. Tergite IX extremely large, undivided, extending posterior to cerci. Ventral segment X and postgenital plate microtrichiose. Seminal capsules pale, ovoid, without necks; seminal ducts short and virtually straight to apparent common opening. Cerci large, quadrate.

Pupa (female of N. fusca only)
Medium-sized, up to 8 mm long.

Cephalothorax. Frons smooth without setae, cephalic tubercles or frontal warts. Thoracic horn plumose, with large oval basal ring with one roundish to elongate-oval tracheal bundle (Fig. 11). Median suture spinose anteriorly, with slight tubercle (Fig. 12). Prealar tubercle absent. Without antepronotal seta; two fine precornicals; dorsocentrals: dc1 close to dc2, separated from approximated dc3 and dc4, all subequal and fine.

Abdomen (Fig. 13). Tergite I bare, II–VIII with fine spinule areas, subquadrate on II–VI, with anterior transverse patch on VII and posterior patches on VII and VIII. Anal segment bare. Tergite II hook row continuous, 75 % tergite width, comprising numerous small hooks. Conjunctives III and IV with narrow row of small undivided spinules. Stermites bare. Pedes spurii A of pale spines, strong on IV, weak on V, absent on VI; pedes spurii B rounded, protruding on segment II. Posterolateral corner of segment VIII with strong multi-spined mace (Fig. 14). Lateral apophyses dark, transverse apophyses not indicated.

Setation. Difficult to determine on specimens available: segment I apparently with 1D, 1V and without L setae; II–VII with 4D, 2–3V; one non-taeniate L on II–IV; V–VII with 4L setae, all taeniate; VIII with 0D, 1V, five taeniate L setae. One pair weak O setae, pale dorsally, perhaps absent ventrally. Anal lobe elongate-oval with fringe of 100+ biserially inserted, taeniate setae, extending to apex and around inner apical margin; bases rather strongly sclerotized; without dorsal taeniate setae. Female genital sac ending before apex of anal lobes.

Larva (4th instar)
Medium-sized, reddish, length unknown, with ventral head length up to 600 µm. Head
capsule golden to brown with darker brown gula, mentum and inner mandibular teeth. Occipital margin darkened, with some evidence of a double margin.

Dorsal surface of head (Fig. 15). Frontoclypeal apotome tapered posteriorly, broad anteriorly, without frontal pit; labral sclerite 1 anteriorly fragmented, labral sclerite 2 also anteriorly fragmented, labral sclerites 3-5 not developed, with S1-S3 elongate and lying lateral on labral area, S4 unusually anterior on frontal apotome, reduced to peg, and S5 in middle of frontal apotome.

Antenna (Fig. 16) with 6 segments, segments 2 and 3 subequal, 4 and 6 less than half length of 5. Lauterborn organs absent. Small style at apex of segment 3. Ring organ in middle of segment 1, seta absent. Blade extending to apex of 5th segment.

Labrum (Fig. 17). SI plumose on medial margin, seemingly smooth on lateral; SII simple, curved, widely separated; SIII strong, narrow, simple; SIVa well-developed bisensillum. Bases of SI contiguous on rectangular darkened plate, which bears anterolateral lobe, each bearing short fine seta of unknown homology. 6-7 plumose and simple chaetae. Seta praemandibularis short, simple. Labral lamellae broad, without indication...
of median division. Pecten epipharyngis of three scales, each with uneven row of several variable-sized short (?worn) teeth. Chaetulae laterales 4, plumose, two simple chaetulae basales displaced more anteriorly. Premandible with two narrow apical teeth and weak brush.

Mandible (Fig. 18). Lacking dorsal tooth; with very elongate apical tooth and three clumped inner teeth. Pecten mandibularis absent. Seta subdentalis inserted on ventral surface, simple, extending to inner mandibular teeth. Inner margin bare. Seta interna absent.

Mentum (Fig. 19). Medially cleft, without distinction between ventromental and dorsomentum; with eight teeth on each side, the innermost two pairs paler, outer teeth mid-brown. Ventromental plates separated medially by greater than half width of mentum. Ventromental plate elongate fan-shaped with smooth anterior margin; striae relatively uniform in length as ridges across much of plate, running into or slightly disconnected from subapical band of regularly-spaced lappets (Fig. 20). Setae submenti simple, stout.

Abdomen. Lateral and ventral tubules apparently absent. Anterior parapods with dense, fine, simple claws; posterior parapod claws simple. Procercus weakly pigmented, small, wider than high, bearing 6–7 subequal anal setae; procercal seta and possibly one taeniate apical seta laterally on squat procercus.

Figs 7–10. Nilodosis fusca, female: 7, antenna; 8–10, genitalia: 8, lateral; 9, ventral; 10, detail of gonapophysis lobes.
Nilodosis fusca Kieffer, Figs 4, 6.


Endochironomus ituriensis Goetghebuer, 1936: 461. Type male, Belgian Congo, Ituri, Mahagi-Port (not examined), Freeman 1957b: 407 (syn.).

Nilodosis fusca Kieffer: Freeman 1957b: 407, redescription and synonymy of E. ituriensis, confirmed.

Redescription

Adult male (n = 1, slide-mounted). As in generic diagnosis and Freeman, (1957b), with the following mensural features (in µm, unless stated): body length 2.3 mm. Antennal segments 1-12: 445, 13: 943, Antennal Ratio 2.1. Head setation: not measurable. Thoracic setation: antepronotals 0; 17 bi- to multiserial erect acrostichals; 37 biserial dorsocentrals extending to pre-scuteullum, 3-4 prealars: 0 supra-alar; 9 uniserial scutellars. LR₁

Figs 11–14. Nilodosis fusca pupa: 11, basal ring of thoracic horn; 12, anterior thorax (lateral); 13, tergites; 14, posterolateral spur of segment VIII.
1.9, LR2 missing, LR3 0.84, sensilla chaetica not visible, plus strong pseudospurs on basal tarsomeres of mid and hind legs. Hypopygium, as in Figs. 3, 5, gonocoxite 265, gonostylus 185, free end of anal point 120 long.


Pupa \( n = 1 \). Length 8.0 mm, cephalothorax 1.8 mm Thorax and cephalic area golden brown; abdomen pale except for brown lateral apophyses. Tergite II with 92 hooks in uniserial row occupying 70 % of posterior width of tergite (Fig. 13). Anal lobe with 77–80 triserial taeniae.

Figs 15–22. *Nilodosis fusca* larva: 15, dorsal surface of head; 16, antenna; 17, labrum and epipharynx; 18, mandible; 19, mentum; 20, ventromental plate, detail; 21, maxilla; 22, maxilla of *Fissimentum desiccatum*. 
NILODOSIS GRISEA


Redescription

Adult male (n = 1–3). As in generic diagnosis and Freeman, (1957b), with the following measurements: wing length 2.3–2.6 mm. Palp segments (2–5) 50–55, 125–135, 110–120, 175–205. Antennal segments 1–12: 400–425, 13: 960–1015, Antennal Ratio 2.4. Head setation: 12–14 uniserial temporal, 13–16 clypeals. Thoracic setation: ante-pronotals 0; cl18bi-1 to multiserial erect acrostichals; 10–13 biserial dorsocentrals extending to pre-scutellum, 4–5 prealar: 0 supra-alar; 6–9 uniserial scutellars. LR1 1.16–1.67, LR2 0.67–0.69, LR3 0.86; 2 sensilla chaetica on ta1 of P3, with strong pseudospur on basal tarsomeres of mid and hind legs. Wing vein setation: Sq 15–21, R 6–7, R1 0, R4+5 0. Hypopygium, as in Fremin 1957b, gonocoxite 260–265, gonostylus 200–215, free end of anal point 80–90 long.

Female and immature stages unknown.

Remarks. The male adult of N. grisea may be distinguished from N. fusca by the features stated by Freeman (1957a,b), namely the different shape of appendage 1 (superior volsella) of the hypopygium. Furthermore, the anal point shape differs (spatulate compared to parallel-sided), the median anal tergite setae extend towards the base of the anal point between separated anal tergite bands, rather than restricted to a median patch, the superior volsella is triangular and lacks the digitate extension, and the transverse sternapodeme is very much broader in N. grisea than in N. fusca.

In addition, the wing markings (darker clouds on pale membrane) in N. grisea can be contrasted with the dark wing with three pale spots for most N. fusca. However, fading with time, sexual dimorphism in intensity and perhaps some intraspecific variation makes use of colour of wings (and legs) in older or alcohol-preserved material somewhat unreliable. Pinned dry N. grisea certainly has a darker grey thorax, but this feature is lost on slide preparation. Mensural features derived above surely will serve to assist separation, but variation, especially in N. grisea, cannot be assessed, not least because described material of both species is missing from collections, but also because of paucity of sampling.

Type material examined. Holotype 8, badly mounted in Canada Balsam, ‘Congo-Belge, Albertville (Lac Tanganika), 25.viii.1953, J. Verbeke, KEA5026’ (Democratic Republic of the Congo) (INSB). Paratypes: 28, same data, one slide, one pinned and missing hypopygium (INSB).

COMMENTS ON IDENTIFICATION

One reason for the protracted period between the date of rearing and tentative identification of Nilodosis (Hare & Carter 1987) is that the reared specimen is a female. In Nilodosis only the female of N. fusca has previously been recognized (Freeman 1957b). The description allows recognition, but the reared specimen is appreciably smaller (see measurements above) and differs in antennal ratio (which may be allometric). Damage to the laterally-mounted female genitalia of the reared specimen precludes conclusive confirmation of identity with the immature specimen. However, the distinctive extended tergite IX, wing pattern and colour of the legs suggests the specimen is...
N. fusca, and in all non-sexually dimorphic features it evidently is congeneric with the two species already allocated to Nilodosis.

It has proved difficult or impossible to allocate all previously described larvae with a cleft mentum to Nilodosis, not least because the descriptions are brief, and the figures crude, appearing to have been drawn at low magnification. McLachlan's (1969: Fig. 11 (21) 'Chironomus sp. 125c' appears identical to the Nilodosis larva described here. In contrast, Chrispeels's (1959) cruder figures of 'Larves inconnus de la tribu des Chironomini, species D' shows a larva that resembles Nilodosis, including the distinctive maxilla (compare Fig. 21) yet the mentum has a single recessed median tooth in a uniformly dark mentum. Chrispeels's larvae were from Lake Albert, the location from which Goetghebuer (1936) described the species Endochironomus ituriensis (= N. fusca), but it is difficult to reconcile this identity with the illustration. It might thus represent the unknown larva of N. grisea or even an unknown species of Fissimemum. Evidently uncertainties remain in the allocation of larval taxa with split menta in Africa, which will be resolved only by individual rearing.

Concerns that the two species allocated to Nilodosis by Kieffer and Freeman may not be congeneric should be addressed. Freeman's (1957b) argument for a relationship based on the absence of pulvilli and presence of a strong anterior tibial spur in both species, although the male hypopygia are appreciably different. Discovery of the immature stages will verify if the resemblances noted by Freeman override the distinction of the hypopygia. For the present, the status quo is retained.

DISTRIBUTION AND ECOLOGY

Adults of N. fusca are known from further sites in Central and West Africa, with Shambe in the Sudan the most northeastern locality, and records from across the Sahel suggesting frequent occurrence in this ecoclimatic region. The sole locality for N. grisea is Central African, and from its locality may be assumed to have come from Lake Tanganika (Freeman 1957a). Aquatic sources associated with adult localities for N. fusca include larger rivers and at least one lake (Victoria), and the single rearing is from the small, natural, highly dilute, West African Lake Opi (Hare & Carter 1984, 1987). McLachlan (1969) found the larva of Nilodosis (as Chironomus sp. 125c) to be 'rare in Lake Kariba (Zimbabwe), but specific to some habitats' but did not specify which these were. In Lake Albert, Chrispeels (1959) reported larvae of what are considered here to be a Nilodosis species (see above) from the stomach of two species of catfish (Pisces), and some from sandy benthic sediments. Nilodosis appears to occur, but is perhaps never common, in variously-sized central African and sahelian lakes, both natural and impounded, but apparently not in meso- to eutrophic situations, such as the Ethiopian crater lakes studied by Harrison. Some adult collections beside large rivers (Nile, Volta) may reflect lentic conditions that prevail seasonally, or the larvae may be genuine lotic inhabitants. With the ability to recognize pupal exuviae, it is possible to survey more widely through this life history stage that is easy to collect.

PHYLOGENY OF NILODOSIS

Analyses of a morphological data matrix of Chironominae involving all life-history stages (available from the author) postulate Nilodosis as the adelphotaxon of Fissimentum Cranston & Nolte with Imparipene Freeman, as the sister group of this pair. These genera are closely related to Conochironomus Freeman (Cranston & Hare 1995) and Skusella Freeman and more distantly to Stictochironomus Kieffer and Paratendipes Kieffer.

The monophyletic generic grouping is supported unambiguously by the larval antenna being six-segmented by postulated division of the second antennal segment. Although in all other members of the clade the Lauterborn organs are alternate on the apices of the (morphologically) second and third antennal segments, in Nilodosis these organs are absent. There are no unambiguous supportive characters from the pupa and adults, with all characters being variably, often highly homoplasious.

Since Nilodosis is scored in the matrix as a single terminal, as Fissimentum (and indeed are all taxa whether composite, multispecies or monotypic), the phylogenetic position does not identify rank. It is thus necessary to discuss the differences and similarities between Nilodosis and Fissimentum in relation to their status and rank. In the larval stage N. fusca differs from the type, F. desiccatum, Cranston and Nolte the only reared species of Fissimentum in lacking any indication of Lauterborn organs, with inner teeth of the mandi-
ble clustered, pecten epipharyngis of toothed scales, labral seta S4 reduced to a peg, and in the detailed structure of the maxilla including the presence of a cluster of chaetulae dorsal to the palpiger (Fig. 21, compare to simpler maxilla of Fissimentum, Fig. 22). However, some unreared larvae from Brazil and Australia that Cranston & Nolte (1996) tentatively referred to Fissimentum show some of these character states. For example, the mandible of Brazilian 'Fissimentum species 2' resembles that of N. fusca, except in the strength of seta subdentalis development (Cranston & Nolte, 1996: Fig. 29). On rearing it may be discovered that some or all of these actually belong to Nilodosis.

The pupa closely resembles that of Fissimentum, differing from F. desiccatum (the only reared species) principally in thoracic features including the apparent lack of antepronotal setae (no site(s) of insertion visible) and in the strongly spinose dorsothorax that includes a modest tuberide. Although the spur on segment VIII differs, this is a feature that varies inter-specifically in Chironominae.

It is in the adults that almost irreconcilable differences between the taxa occur, including the feature discerned by Freeman, the well-developed spine on the fore-tibial scale of Nilodosis, often considered to be phylogenetically significant and which is lacking in F. desiccatum. In the male genitalia of Fissimentum, the structure of tergite IX and anal point, and the fusion of the inferior volsella to the gonocoxite appear to be autapomorphic with no similarity to Nilodosis. Sather (1977) keyed female Nilodosis as if possessing pulvilli, but although this is erroneous it does not seem to have influenced the postulate of relationship with Endochironomus and Tribolus. Phylogenetic analyses suggest that this latter relationship cannot be supported on the characters used in the present study for assessing Nilodosis and its relatives.

The difference between F. desiccatum and either species of Nilodosis in the adult stage suggests an unbridgeable gap that would not allow congenericity. Although this decision is implemented in this paper, further rearing among the widespread, but seemingly rare, chironomids with cleft menta in the southern continents (e.g. genus D (Harrison, in prep)) is required to test this decision.

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