RAFFLES BULLETIN OF ZOOLOGY **67**: 684–693
Date of publication: 4 December 2019
DOI: 10.26107/RBZ-2019-0049
http://zoobank.org/urn:lsid:zoobank.org:pub:18A31A71-0288-4D0A-8F44-B71099C14EB9

A new tribe in the Chironominae (Diptera: Chironomidae) validated by first immature stages of *Xiaomyia* Sæther & Wang and a phylogenetic review

Hongqu Tang[1] & Peter S. Cranston[2*]

Abstract. The newly discovered larva and previously unassociated pupa of *Xiaomyia* Sæther & Wang, a distinctive outlier in the subfamily Chironomidae, allows description, illustration and comparison with its proposed closest relative, *Shangomyia* Sæther & Wang. A previously described bizarre pupal exuviae, 'Taxon 2' sensu Coffman et al. (1988) from south India belongs to *Xiaomyia*. Molecular data from other sources allows review of the phylogeny and an estimate of the evolutionary tempo. As proposed for the pupa, and independently from adult male morphology, molecular data locate the two genera in a clade that is the sister group to the three other named tribes combined, warranting tribal status within the subfamily Chironominae. Expanded and revised diagnoses for larva, pupa, and adults of Xiaomyiini new tribe are provided. A novel ribbed and spinulose plate-like lobe associated with the ventral larval maxilla in *Shangomyia* and *Xiaomyia* is a major synapomorphy for the tribe.

Key words. Chironomidae, aquatic insects, phylogeny, new tribe, *Xiaomyia*, larva, Oriental

INTRODUCTION

Typically, in systematic studies of the Chironomidae, complete life-history data are desired for description and in estimating relationships. Understanding the immature stages provides data of great importance to aquatic biological monitoring. In the Holarctic region, at least at the generic level, nearly all genera with aquatic immature stages are documented (see Wiederholm, 1983, 1986, 1989; Ferrington, 2008). Elsewhere there remain distinctive taxa in one or more life stages, but many are not formally described for all immature stages. From a survey of pupal exuviae collected from the Nilgiri Hills of south India, Coffman et al. (1988) reported two unusual exuviae, 'Taxon 1' and 'Taxon 2', representing two distinct new exuvial types. Almost simultaneously, two very distinctive adult males were collected by X.H. Wang in oriental China (Guangdong) and described subsequently by Sæther & Wang (1993) as new genera *Xiaomyia* Sæther & Wang, 1993 and *Shangomyia* Sæther & Wang, 1993. In both publications, the authors argued that their taxa deserved high rank as tribe or conceivably subfamily despite incomplete life histories. Discovery of the immature stages of *Shangomyia* in Brunei (Cranston, 2003) and of a pharate *Xiaomyia* male from Fujian (China) by Hongqu Tang (pers. obs., reported in litteris to Cranston, de la Rosa & Spies, 2014), revealed Coffman and colleagues' mystery pupal types were the life stages of Sæther and Wang's adult genera. However, the larva of *Xiaomyia* remained unknown.

Analyses of molecular data derived from adults have shown that *Xiaomyia* and *Shangomyia* are maximally supported as sister groups (Cranston et al., 2011), as predicted by Coffman et al. (1998) from the pupae and Sæther & Wang (1993) from the adult males.

Here we formally associate the pupa of *Xiaomyia* to 'Taxon 2' sensu Coffman et al. (1988) and describe the larva and the female of *Xiaomyia* for the first time. A diagnosis for the new tribe Xiaomyiini is provided.

MATERIAL & METHODS

Material. We followed standard and special techniques to seek the immature stages. Searching immerse wood of various states of decay failed. Kick netting and drift netting were useful for exuviae and eventually the larva of *Xiaomyia* was found in the final-instar with developing abdominal pupal spinulation visible within, supplemented by larval exuviae sorted from drift samples. Slides were made following standard procedures (Epler et al., 2013). We sought pupal material of Coffman et al. (1988) without success.

Abbreviations. Slides are deposited in the following institutions: Australian National Insect Collection CSIRO, Canberra, Australia (ANIC); The Natural History Museum, London, U.K. (BMNH); The Institute of Groundwater and

---

[1] Institute of Groundwater and Earth Science, Jinan University, Guangzhou, 510632, China; Email: towninngt@gmail.com

[2] Evolution & Ecology, Australian National University, Canberra, ACT 0200, Australia; Email: pscranston@gmail.com (*corresponding author)

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

Earth Science, Jinan University, Guangzhou, China (EJNU); Zoological Reference Collection of the Lee Kong Chian Natural History Museum, Singapore (ZRC); Zoologische Staatssammlung München, Munich, Germany (ZSM). Distributional information is provided for all material seen (abbreviations: C., city; Co., county, Ctr., country; m asl, metres elevation above sea level; Mun., municipality; NNR, national nature reserve; NP, national park; Pr., province; R., river; T., town; Vill., village).

Map. The distribution map (Fig. 5) was made using ArcGisTM software, with all GPS locations implanted into a vector of World Map (http://www.vectorworldmap.com). Location data follows that of slide labels: for older specimens lacking precise location details including published records that we have not seen (Δ, Fig. 5), estimates were made from available detail (e.g., city/country).

Terminology. Morphological terminology largely follows Sæther (1980) excepting some new terminology for the adult hypopygium and larval head derived from Cranston (2019).

Imaging. Phase and Nomarski optics were used to view hyaline structures. Although photography can illustrate many taxonomic features, we also used ink on tracing film to produce 'synthetic' line art to illustrate, for example, pupal abdomens, and the fine detail of larvae and male genitalia. Ink drawings were substantially made by hand, using a drawing tube, or from photographic images scanned for editing. Photographs were taken with an Olympus CX41 compound microscope with phase-contrast optics and images were manipulated with MshOt™ (MSX2) to allow automated retention of focused parts of exposures at different depths. Image manipulations were made in Adobe® Photoshop™.

Molecular materials. Molecular materials were prepared according to Krosch & Cranston (2012), with subsequent extraction, sequencing, alignment and analyses described in Cranston et al. (2011) and Krosch et al. (in press).

TAXONOMY

Xiaomyia Sæther & Wang, 1993

(Figs. 1–4)

Type species. *Xiaomyia aequipedes* Sæther & Wang, 1993, by original designation.

Material examined. Pe/♂, THAILAND, Phang Nga, Sri Phang Nga NP, 8°59′N 98°27′E, 16.vi.2004, Cranston, MV 'XIAO' (molecular voucher) (ANIC). ♂, Tam Nam Lod, 23.12.1989, LF [light trap], H. Malicky (ZSM); ♂, Sob Pong, 23.12.1989, H. Malicky (ZSM).

CHINA (all collected H.Q. Tang, deposited EJNU unless stated otherwise): Southeast, 5♂, 34Pe, Anhui Pr., Huangshan C., Tangkou T., Fu stream, 30°04′N 118°09′E, 05.viii.2014; 3Pe, Zhejiang Pr., Yongjia C., Shangtang T., 28°12′N 120°40′E, alt. 150 m asl., 04.v.2019; 2♀, 4Pe, Fujian Pr., Nanping C., Wuyishan NNR, Tongmu Ctr., 27°45′N 117°40′E, 09.viii.2014; 8♂, 3♀, 1Pe/♂, 12Pe, Fujian Pr., Zhangzhou C., Nanjing Co., Huboliao NNR, 24°31′N 117°14′E, 20.xi.2012; 2Pe, Taiwan Pr., Pingdong Co., Mudan T., 22°09′N 120°49′E, 19.iii.2013, 233 m asl.

South, 10♂, 2Pe/♂, 5P/♀, 26Pe, 3Le, 2L/ Pe, Guangdong Pr., Guangzhou C., Zengcheng Distr., Shuimei Vill., Lan Stream, 23°21′N 113°58′E, 20.i.2017 (2♂, 2♀, 2Pe, 2Le, ZRC); 3Le, L/P, as previous, except 13.xii.2018; Le, L, as previous, except 2.xi.2017 (ANIC); 3Pe, Guangdong Pr., Fengkai Co., Heishiding NNR, 23°28′N 111°54′E, 320 m asl, 26.viii.2011; 2Pe, Guangdong Pr., Yangchun C., Ehuangzhang NNR, 21°50′N 111°29′E, 60 m asl, 14.xi.2013, Y.D. Lei; 2Pe, Guangxi Pr., Guilin C., Gongcheng Co., Longhu Ctr., 25°05′N 110°57′E, 195 m asl, 28.vii.2013, Y.D. Lei; 4Pe, Guangxi Pr., Guilin C., Lipu Co., Magangqiao Ctr., 24°40′N 110°20′E, 171 m asl, 29.vii.2013, Y.D. Lei; Pe, Guangxi Pr., Guilin C., Lipu Co., Balu Ctr., 24°26′N 110°28′E, 182 m asl, 30.vii.2013, Y.D. Lei; 20Pe, Guangxi Pr., Hezhou C., Gupo Mt. NNR., 24°36′N 111°34′E, 473 m asl, 25.viii.2011; Pe, Guangxi Pr.., Hezhou C., Fuchuan Co, Xiling Mt., 24°57′N 111°06′E, 527 m asl, 28.vii.2013, Y.D. Lei; Pe, Guangxi Pr., Laibin C., Jinxiu Co., Lahe, 23°58′N 110°07′E, 466 m asl, 30.xi.2013, Y.D. Lei; 3Pe, Guangxi Pr., Laibin C., Jinxiu Co., Dishui Ctr., 24°01′N 110°07′E, 370 m asl, 31.vii.2017, Y.D. Lei; 4Pe, Guangxi Pr., Baise C., Napo Co., Nazhen Ctr., 23°00′N 105°53′E, 463 m asl, 23.ii.2012, W. Xia & C.B. Duan; 6Pe, Hainan Pr., Changjiang Co., Bawangling NNR, 19°05′N 109°08′E, 30.xi.2011; 4Pe, Hainan Pr., Lingshui Co., Diaoluo T., Diaoluo Mt. NNR., 18°40′N 109°56′E, 31.viii.2013; 2Pe, Hainan Pr., Wuzhishan C., Wuzhi Mt. NNR., site 1, 18°45′N 109°36′E, 03.xii.2011.

Southwest, Pe, Yunnan Pr., Xishuangbanna Pref., Jinghong C., Menglun T., Luosuo R., 21°55′N 101°16′E, 18.ii.2019; Pe, Yunnan, 7 km E. Mung Lun, 28.v.1980, E.J. Fittkau [Label 1, added in red ink 'cold water, upper part of Mekong' and in pencil '?Telmatogetoninae'. Label 2 in pencil "? *Xiaomyia*, see email Cranston of 15.iv.2014"] (ZSM); Pe, Guizhou Pr., Chishui C., Lushi T., 28°29′N 105°56′E, 270 m asl, 13.viii.2018, W. Han & T.G. Gou; 3♂, 2♀, 4 Pe, Chongqing Mun., Wuxi Co, Chengxiang T., Daning R., 31°24′N 109°37′E, 1002 m asl, 03.ix.2018, W. Han & T.G. Gou; 2Pe, Chongqing Mun., Chengkou Co., Gaoguan T., Re R., 31°5′N 108°55′E, 860 m asl, 06.ix.2018, W. Han; 4Pe, Hubei Pr., Enshi Pref., Xianfeng Co., Erxianyan, 29°43′N 108°47′E, 1620 m asl, C.M. Zhang.

Diagnosis. Male (Fig. 1A–C). Wing smoky dark except distal margins (Fig. 1A). Proctiger present (Fig. 1B), shallowly concave in the middle; pseudovolsella well-developed, extending clearly beyond a weak inferior volsella (basal lobe); depressed oval area (possibly remnant of pars ventralis or virga) present on ventral side of hypopygium (Fig. 1C).

Female (Fig. 1D). Gonocoxapodeme straight, weakly sclerotised. Dorsomesal lobe well-developed, with clear outer crystalline 'ribs' and inner microtrichiose part. Ventrolateral lobe spherical, with microtrichia covered whole surface,

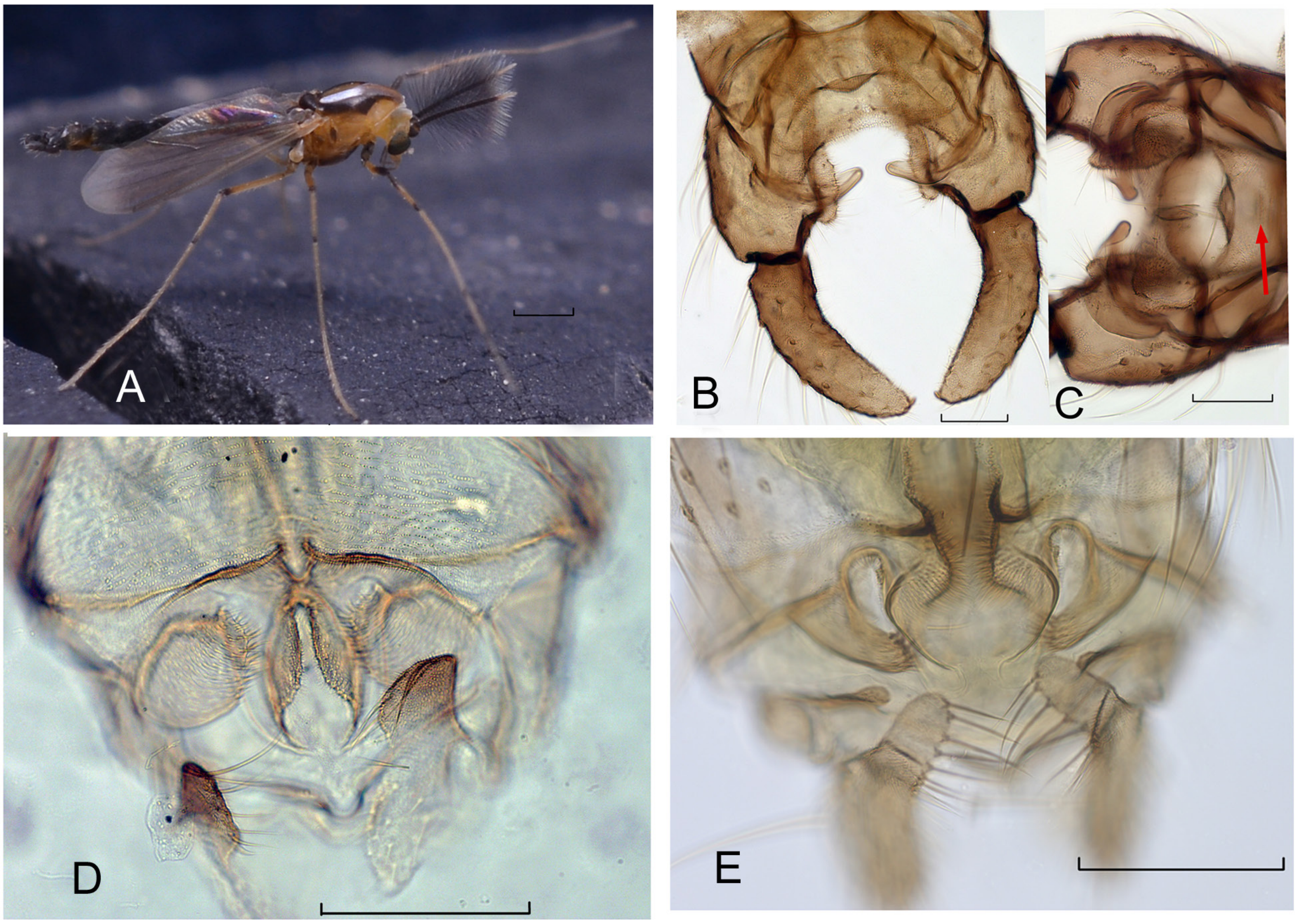

Fig. 1. Adult. A, habitus of male *Xiaomyia* Sæther & Wang, 1993 (Anhui); B, hypopygium dorsal view *Xiaomyia* (Anhui); C, hypopygium, ventral view, *Xiaomyia*; arrow indicates remnant of virga (Fujian); D, female genitalia, ventral, *Xiaomyia* (Chongqing); E, female genitalia, ventral, *Shangomyia* (Yunnan). Scale bars = 400 µm (A); 50 µm (B, C); 100 µm (D, E).

with some elongate setae occurring on only inner margin. Apodeme lobe indistinct. Vagina modest, semi-enclosed apically by fused coxosternapodemes. Spermatheca two, pale, oval, with thickened wall near a distinct neck, spermathecal ducts sclerotised in apical 1/4, relative straight, without loop, connected with each other just before the common opening. Labium small, with weak microtrichia apically. Cerci with well-developed, and usually dark sclerotised inner lobe, bearing 8–12 long setae.

Pupa (Fig. 2). T IV with posterior transverse band consisting of solitary spine (Fig. 2A, B), one pair (Fig. 2C–E) or two pairs (Fig. 2F); T V with anterior transverse toothed band contiguous (Fig. 2A–C) or interrupted medially (Fig. 2D–F). Number of hooks on T VI ranging from one to three pairs (Fig. 2B).

Larva (Figs. 3, 4). Medium-sized, ca. 3–4 mm, body purple in life, blue when preserved. Head capsule ventrally with dark sclerotised mentum and submentum, separated medially by triangular membranous area (Figs. 3A, 4A, D). Occipital margin dark brown, broadest mediolaterally, weaker mid-dorsally. Eye-spots separate, larger dorsal above smaller ventral.

Dorsal surface of head (Figs. 3B, 4F). Frons and clypeus separate; S3 located on flexible membranous area, with clypeus comprising of three separate, small sclerites, the middle clypeal sclerite 'tear'-shaped; labral sclerite divided into two small fragments (Fig. 4F).

Antenna (Fig. 3C). Five-segmented, with three short apical segments; basal segment with basal ring organ; style distinctly longer than the minute Lauterborn organs, which are subequal to length of 3rd segment; blade extending far beyond antennal apex, more than three times as long as the flagellum.

Labrum (Fig. 3D). SI bifid, SII and SIII simple, thin, and SIVa, b conventionally developed. Labral lamellae absent. Pecten epipharyngis comprising three broad rounded scales, with three chaetulae laterales, weakly serrate apically. Premandible with apical tooth, broadened near midpoint but without additional tooth, lacking a brush.

Mandible (Fig. 3E). Without dorsal tooth, with apical tooth and three conventional inner teeth, decreasing in size from outer to inner, then 'diastema' (gap) distal to broad flat innermost lobe/tooth; inner surface with evidence of one or two additional 'teeth'; seta subdentalis strong, curved, blade-like, extending to 2nd/3rd inner tooth. Inner margin of mola with a series of 4–5 setae, some or all partially

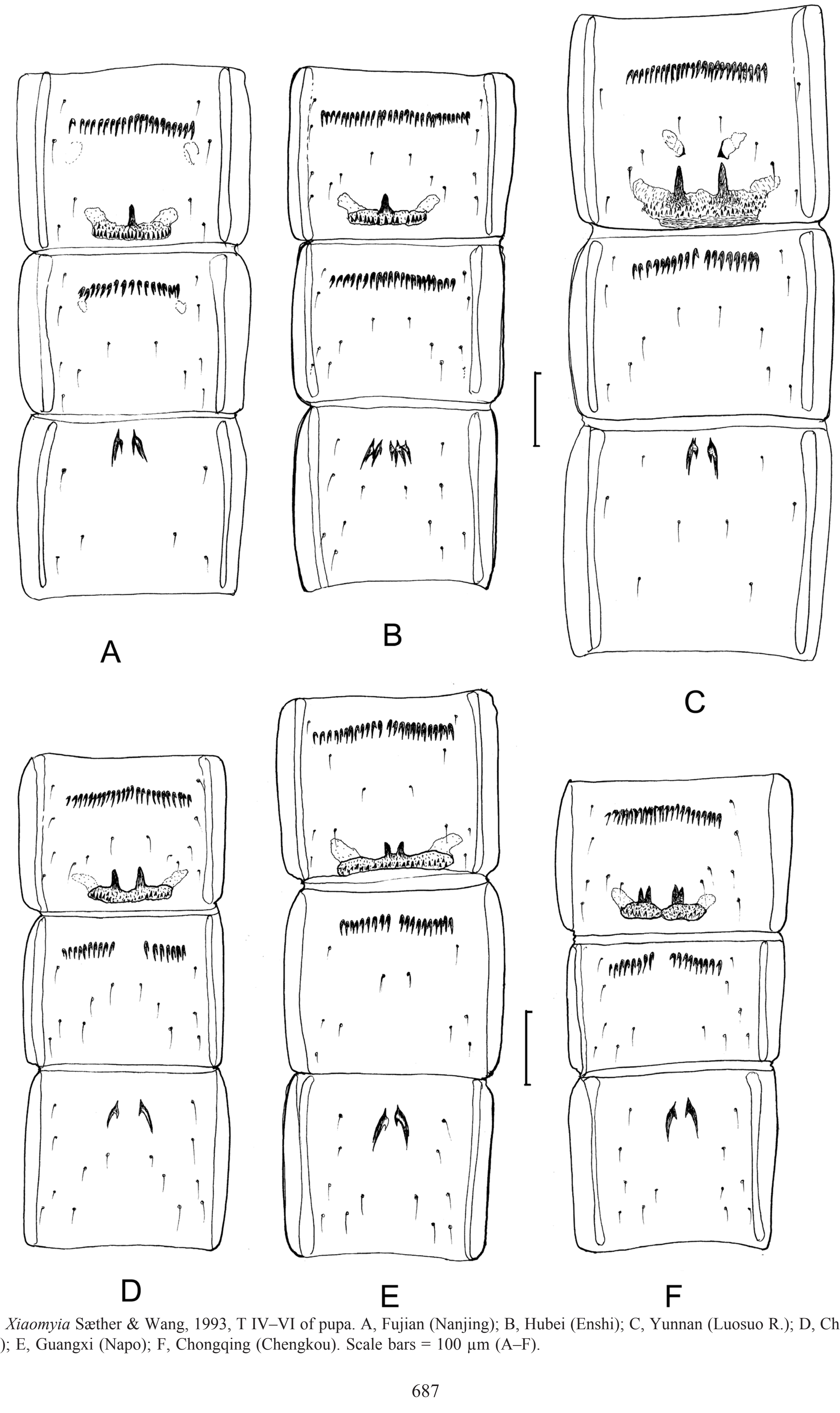

Fig. 2. *Xiaomyia* Sæther & Wang, 1993, T IV–VI of pupa. A, Fujian (Nanjing); B, Hubei (Enshi); C, Yunnan (Luosuo R.); D, Chongqing (Wuxi); E, Guangxi (Napo); F, Chongqing (Chengkou). Scale bars = 100 µm (A–F).

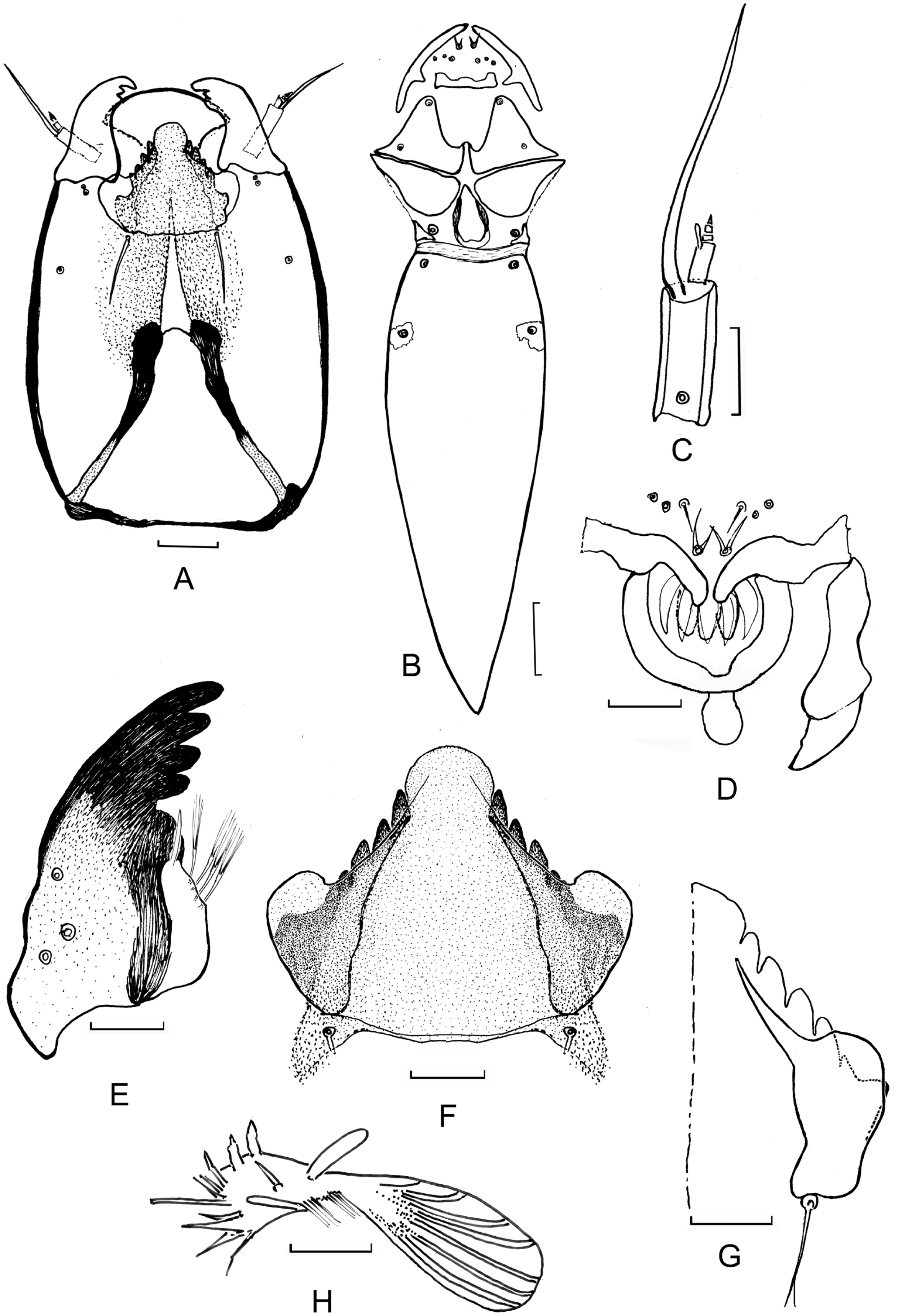

Fig. 3. *Xiaomyia* Sæther & Wang, 1993, larva. A, head capsule, ventral view; B, dorsal surface of head; C, antenna; D, labrum; E, mandible; F, mentum, ventral view; G, ventromentum, detail, indicating variation of lateral teeth; H, ribbed lobe. Scale bars = 50 µm (A, B); 25 µm (C–H).

feathered/branched, almost aligned and contiguous with seta subdentalis (Fig. 3E).

Mentum (Figs. 3A, F, G, 4A). With somewhat paler, prominent, rounded to domed median tooth (ventromentum), with four or five pairs of retracted lateral teeth and outermost broad and protruding tooth. Ventromental plate prominent, broad, covering much of dorsomentum, without beard or striae; head setae (maxillary, frontal, clypeal and setae submenti) strong, simple (Fig. 3A) or apically bifid to finely branched (Fig. 3G).

Maxilla (Figs. 3H, 4B, C). Maxilla squat with many short sensilla and setae, lacking elongate lacinial chaeta (chaetae). Hyaline ovate lobe (plate) c. 50 µm long, ribbed on ventral surface, spinose on dorsal, arises medio-posterior to palp, lying dorsal to mentum, directed posteriorly.

Body (Fig. 4G). Body setae short. Procercus strong, darkened laterally, slightly longer than width, with two short lateral setae and six strong apical setae. Anterior parapods elongated, partially fused basally, nearly all claws pectinate. Posterior parapods reduced, with c. 14 large curved, simple, dark yellow claws. Anal papillae without constriction(s).

Remarks. We supplement the male generic diagnosis of Sæther & Wang (1993) with newly observed characters. Diagnoses for the female, pupa, and larva are given here for the first time.

Wide sampling of pupae showed variation in the tergal armament, which provides evidence for species diversity in this genus. For example, in Chongqing populations (Fig. 2D, F), in addition to the already mentioned variation, the S II has dense soft spines and associated males have a trifid superior volsella. Ongoing molecular studies indicate minimally four species occur in China (H. Tang, unpublished data). We cannot unequivocally assign our specimens to the sole described species, *X. aequipedes* Sæther & Wang and thus the generic diagnosis covers all variation without allocating to named species.

Distribution (Fig. 5). Detailed data for all records of *Xiaomyia* from across the Oriental region are presented. The genus is widespread in subtropical and tropical zones, with the most northerly records from around Mt. Qingling, China (31°23.5′N), which is the traditional boundary between the eastern Palaearctic and Oriental regions (Heiser & Schmitt, 2013). We expect that the genus extends from the South Indian first records across all suitable intervening habitat to Thailand and east Asia. The most southerly record is from southern Thailand. Although sampling further south is inadequate, we presume the genus occurs in Borneo/Indonesia but is unlikely to exceed Wallace's Line.

Sampling in China has been most intensive in mountain streams of Guangdong-Guangxi border and Hainan Island. Fewer records come from Yunnan Province, although sharing climate and altitude, and despite similar sampling effort. The distribution of *Xiaomyia* closely parallels that of its sister genus *Shangomyia* (H. Tang, pers. data, unpublished), which also has an extensive distribution in Oriental Asia, also including suspected hidden diversity.

Phylogeny, dating and ranking. Analysis of molecular data shows a monophyletic clade of *Xiaomyia* and *Shangomyia* is supported by maximum bayesian posterior probability (PP) and bootstrap (BS) values (node C1, fig. 2, Cranston et al., 2011). This pair in turn was sister (at node M, fig. 2) to all other sampled Chironominae, with maximum PP, and BS of 77%. BEAST analysis provided median ages, in Ma, and ranges (HPD, highest posterior density intervals) for a mid-Cretaceous split between *Xiaomyia* and *Shangomyia* of 88 Ma (62–111) and between this clade and the remaining Chironominae of 148 Ma (132–166) (Cranston et al., 2011; fig. 3, derived from unpublished node age data).

Recent new and existing molecular data, additional calibration fossils, and more intensive sampling of Tanytarsini and Pseudochironomini have provided another estimate of the tempo of diversification in the Chironominae (Krosch et al., in press). The analysis specifically estimated dates for a phylogeny for *Riethia* Kieffer, 1917 and lacked *Xiaomyia* but included the well-validated sister group *Shangomyia*. This dated phylogeny showed *Shangomyia* as sister to all other Chironominae and provided a nodal date of 134.5 Ma (HPD 101–197) (Krosch et al., in press).

Rank. All publications that concern at least one life stage of *Shangomyia* and/or *Xiaomyia* have commented on the need for a high rank for the clade (Coffman et al., 1988; Sæther & Wang, 1993; Cranston, 2003; Cranston et al., 2011). However, all refrained from taking formal action, in some cases due to uncertainty about the correct relationships, citing 'differences' and 'uniqueness', and in all cases, the lack of the larva. Despite robust molecular phylogenies providing strong justification, Cranston et al. (2011) cited the erratic, unstable position of *Beardius* Reiss & Sublette, 1985, that sometimes was sister to all Chironominae including *Shangomyia* + *Xiaomyia*, thus preventing facile ranking. Since then no additional *Beardius* have become available for verification of the placement based on DNA. However, the revision of *Beardius* by Pinho et al. (2013) and morphology-based phylogeny suggest that *Oukuriella* Epler, 1986 is sister group to *Beardius* in a cluster of genera identified as a '*Microtendipes* group' in Cranston et al. (2011). With *Beardius* removed from consideration in relation to *Shangomyia* + *Xiaomyia*, recognition of the clade as being of tribal or subfamily rank is justified. The question is 'what rank'? There are no hard and fast rules governing this — as stated recently: ".... taxonomic rank does not of itself confer natural comparability: Any rank above species is a function of convention and discretion as well as actual data, and as long as monophyletic groups are recognised the fact that families or tribes are not uniformly or evolutionarily equivalent does not hamper studies" (DeSalle & Goldstein, 2019: p. 2). Tribal status for *Shangomyia* + *Xiaomyia* does not impact the stability of named ranked taxa around this grouping — as sister to the three already recognised tribes in the subfamily — and does not impinge on equivalence

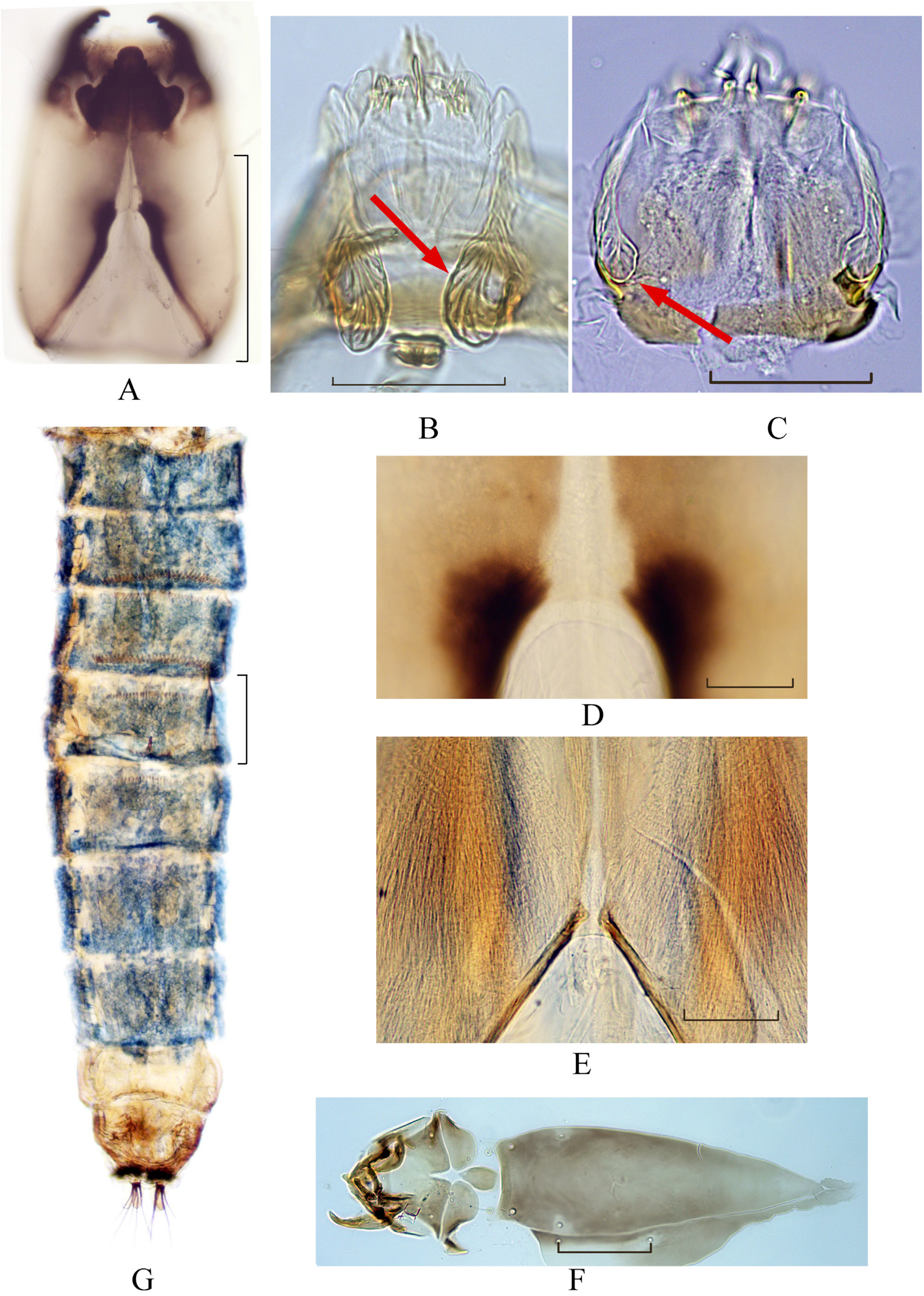

Fig. 4. Larval colour photographs, *Xiaomyia* Sæther & Wang (A, B, D, F, G) and *Shangomyia* Sæther & Wang (C, E). A, head capsule, ventral view; B, C, maxilla and premento-hypopharyngeal complex, arrows showing ribbed lobes; D, E, posterior occipital region; F, dorsal sclerite of head; G, larval abdomen, showing pupal abdominal spinulation beneath larval skin. Scale bars = 200 µm (A, G); 100 µm (F); 50 µm (B, C, D, E).

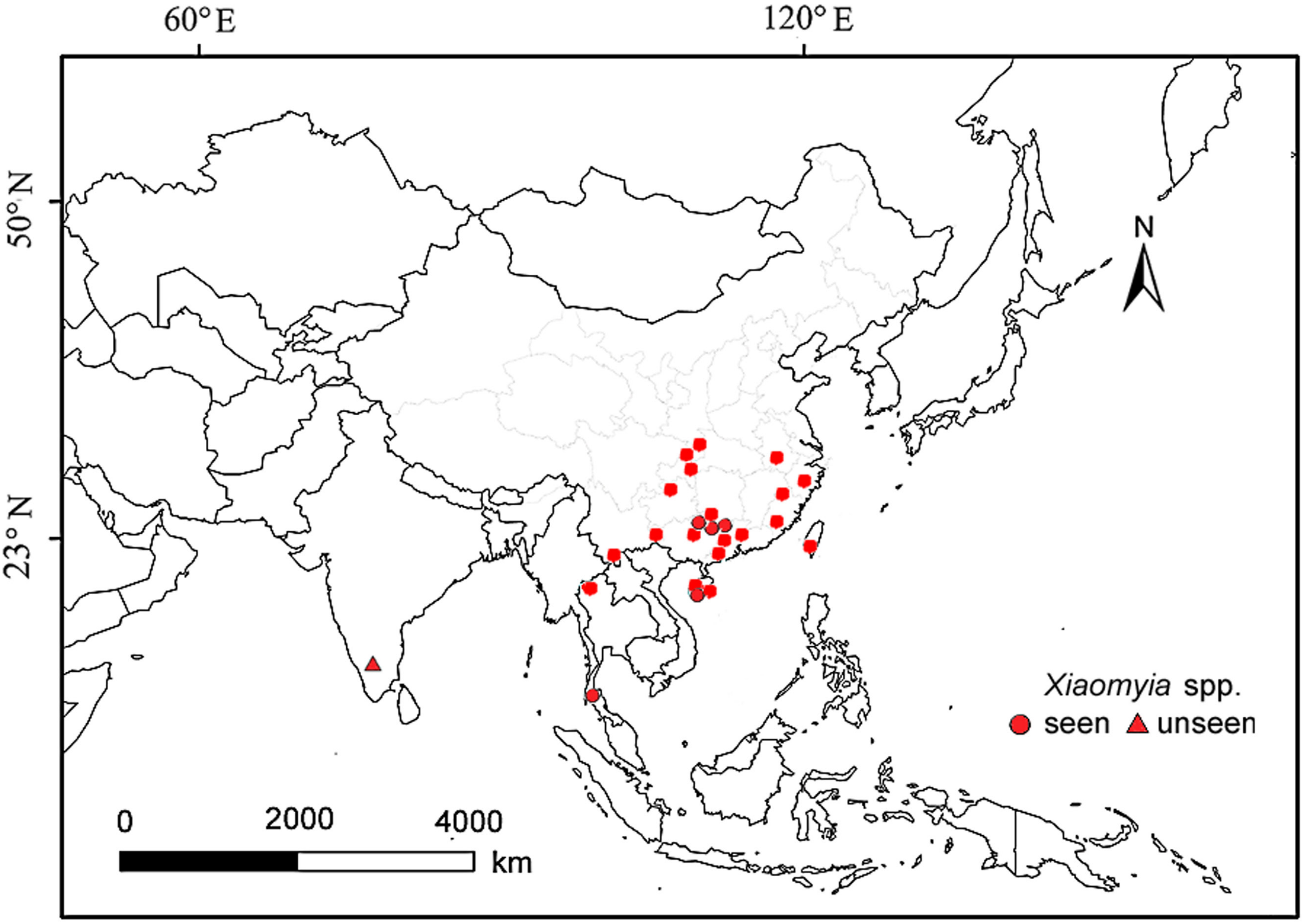

Fig. 5. Distribution of *Xiaomyia* spp. from this study.

at nodes deeper in the tree (specifically Orthocladiinae and Prodiamesinae). An alternative, expansion of taxa ranked at subfamily level, would do nothing for information content: depiction of a resolved phylogeny offers details of relationships without needing destabilisation of ranks. For this reason we support tribal rank, as Xiaomyiini, which takes our authorship according to the rules governing nomenclature, yet ought to be credited to Sæther & Wang (1993) for their explicit discussion of the taxonomic issues and recognition that their formally-named genera "eventually may deserve status as a separate tribe" (loco citato, p. 194). Regarding the pupae, Coffman et al. (1988) had suggested them to "likely represent a new higher taxon as well, perhaps a new subfamily" (opere citato, p. 164) but with reasoning based on a combination of character states that were inconsistent with any described subfamily, and without named taxa included.

We note that using the age of a clade as an absolute gauge for rank is simply meaningless for taxa that originated in the Cretaceous. This would imply ordinal rank for a genus of insect were it a mammal or bird. Another misunderstanding concerns the significance of 'disparity' in assessing rank. Only when disparate morphologies are placed in a robust phylogenetic framework that autapomorphies (that give rise to disparity) can interpretation be correct. In our case, the suite of unusual features of *Xiaomyia* and *Shangomyia* do indeed indicate morphological 'disparity' associated with high rank, as stated by Coffman et al. (1988) and Sæther & Wang (1993). This contrasts with past unjustified elevations in rank of apomorphic orthoclads, both terrestrial and marine intertidal in habit, such as Eretmopteridae Kellogg, 1900, Clunioninae Kieffer, 1906, and Oreadomyiinae Kevan & Cutten-Ali-Khan, 1975.

Xiaomyiini, new tribe

Diagnosis. Male. With unique spinose scale and long spur on apex of mid- and hind-tibia; eye rounded-ovoid without dorsomedial extension; strong costal extension on wing, Cu_1 ending in shallow fork near wing margin. All leg ratios (LR) greater than 1.5. Hypopygium with reduced inferior volsella; gonostylus flexible at junction with gonocoxite, with apical tooth.

Female (Fig. 1D, E). Gonocoxapodeme VIII straight. Dorsomesal lobe microtrichiose on inner surface, with outer crystalline rib. Ventrolateral lobe well-developed, with dense microtrichia and apical setae. Apodeme lobe indistinct. Seminal capsules two, ovoid, spermathecal ducts sclerotised in anterior 1/4. Labium small, with weak microtrichia apically. Cercus with extended inner lobe, sclerotised, bearing 8–10 long setae on apical 1/3.

Pupa. With heavily sclerotised cuticle. Frontal setae and thoracic horn absent. Thorax with anterior dorsocentral seta (Dc) displaced ventrally and lateral antepronotal seta (LAps) on low protuberance. Abdomen with no taeniate lateral seta and anal lobe fringe; only one (lateroventral) seta located on segment VIII; seven tergal setae present. Anal lobe disc with dorsal and ventral.

Larva. Body purple when live, patchy indigo when preserved in alcohol. Head capsule deep dark brown; posterior occipital margin dark brown laterally, weaker medio-ventrally (Fig. 4D, E), and less so dorsally. Eye-spots separate, large dorsal spot always anterolateral to (*Shangomyia*) or above (*Xiaomyia*) the ventral small spot. Labrum with SI simple or bifid, never pectinate or plumose; premandible simple, with one prominent apical tooth and one broad node, without brush. Antenna five-segmented, AR less than 1.0, blade more than three times length of flagellum. Mandible with four inner teeth, innermost tooth truncated; seta interna simple, strong, curved; inner margin of mola with feathered, bifid or simple broad setae perhaps representing displaced seta interna. Mentum with prominent median tooth, 4–5 laterals; outermost tooth squat. Ventromentum well-developed, extending margin of dorsomentum, with (*Shangomyia*) or without (*Xiaomyia*) internal (dorsal surface) spinules. All major cephalic setae simple or apically bifid/finely feathered, e.g., seta submenti simple or bifid. Maxilla with unique hyaline, ribbed and spinulose plate-like lobe, extending posteriorly from ventral maxillary surface (Fig. 4B, C), located immediately dorsal to the mentum, and ventral to salivary gland outlet on the prementum.

Anterior parapods partially fused basally; posterior parapods short, with 14 dark-brown claws. Procercus somewhat sausage-shaped, bearing six anal setae apically and one pair lateral setae basally. Anal tubules present.

Ecology. The search for the larva of *Xiaomyia* to complete the life history has been as challenging as it was for *Shangomyia*. The latter eventually was found mining in immersed wood in a shaded (i.e., cool), fast-flowing tropical river (Cranston, 2003). That larva has not been found by any routine sampling method — even where drift netting showed that pupal exuviae were frequent, as in Sungai Belalong (Brunei). Larvae remain exceedingly difficult to locate even with knowledge of the in-stream immersed wood habitat. Extrapolating this habit to the larva of *Xiaomyia* and searching in immersed wood in the rivers that provided pupal exuviae failed, but by good fortune a pupal exuviae remaining attached to a pharate male (Fujian Prov.) and subsequently many pharate adults (Guangdong Prov.) were found; what's more, two pharate larvae with developing pupal spinulation were obtained at the same locality, and is the basis for description here.

However, the larval habitat remains unknown, although pupal exuvial collections are from associated small streams (of 2nd or 3rd order), usually in open channels with water depth no more than 0.5 m, and dissolved oxygen greater than 8.0 mg/l., with exposed moss-covering cobbles. The assemblage at four sites with many pupal exuviae shows *Xiaomyia* usually co-occurs with species of *Sublettea* Roback, 1975, which may indicate a shared in-stream habitat, perhaps with an active hyporheic zone. The challenge of rearing the egg mass from the fertilised female using in-situ water fails at the transition from I–II phase, suggesting some special microhabitat or perhaps even symbiotic lifestyle. An intact larva showed gut contents comprising exclusively fine organic and mineral fragments of maximum size 10 microns, lacking complete cells of periphyton or microarthopods/crustaceans or wood fibres, suggesting that the larva had been grazing aufwuchs (biofilm).

CONCLUSIONS

A review of evidence for a high-ranked taxon for two unusual chironomid genera, *Shangomyia* and *Xiaomyia*, available now for all life stages and the publications of several authors, confirms their monophyly and their distance from the remaining subfamily Chironominae in morphology of each life stage and in estimated dating from molecular data. We argue that this rank should be tribe, thus adding Xiaomyiini to the reciprocally monophyletic existing tribes Chironomini, Tanytarsini and (likely monophyletic) Pseudochironomini in subfamily Chironomidae.

Despite much effort, the precise larval habitat of *Xiaomyia* has not been discovered. The wood-mining habit of sister group *Shangomyia* can be rejected, as can speculation that the shape of the median mentum indicates feeding on immersed wood (Cranston & Oliver, 1988). The gut content that is visible in an intact larva suggests grazing on fine particles (aufwuchs), yet routine collection has not revealed larvae in situations even where exuviae are abundant. The unexplored in-stream hyporheic zone is possibly the source and should be explored.

We note the morphological variation in pupal exuviae across the large range of the genus *Xiaomyia* — from southern India to eastern China (Fig. 5) — a linear distance of over 5,000 km. It is almost inevitable that this range will encompass discrete populations that might be considered species, as demonstrated by variation in pupal morphology (Fig. 2). However, as stated by Tang & Cranston (in press) concerning the widely distributed *Polypedilum johannseni* Sublette & Sublette, 1973, the necessary sampling, including for molecular population biological evidence across such a geopolitical range, extends beyond the scope of most studies of 'non-economic' insects.

ACKNOWLEDGEMENTS

We thank Martin Spies, Zoologische Staatssammlung München (ZSM, Munich, Germany) for discussions on these taxa over many years, and for lending material held in the ZSM. This loan was hand-carried by Marion Kotrba to Keith Bayless: we express our thanks to both. We acknowledge and thank J.X. Wei for production of the map (Fig. 5) and Jonathan Leung for transporting the material between China and Australia. Matt Krosch and Hiromi Niitsuma provided valuable insights as reviewers of an earlier draft of this manuscript.

LITERATURE CITED

Coffman WP, Yurasits LA & de la Rosa C (1988) Chironomidae of South India. 1. Generic composition, biogeographical relationships and descriptions of two unusual pupal exuviae (Diptera: Chironomidae). Spixiana, Supplement 14: 155–165.

Cranston PS (2003) The oriental genus *Shangomyia* Sæther & Wang (Chironomidae: Diptera): immature stages, biology, putative relationships and the evolution of wood mining in chironomid larvae. Raffles Bulletin of Zoology, 51(2): 179–186.

Cranston PS (2019) *Riethia* (Kieffer 1917) (Diptera: Chironomidae) revised for the Austro-Pacific region. Zootaxa, 4646(3): 461–500.

Cranston PS, Hardy NB & Morse GE (2011) [2012]. A dated molecular phylogeny for the Chironomidae (Diptera). Systematic Entomology, 37: 172–188 [VoR 20 October 2011].

Cranston PS & Oliver DR (1988) Aquatic xylophagous Orthocladiinae–systematics and ecology. Spixiana, Supplement 14: 143–154.

DeSalle R & Goldstein P (2019) Review and interpretation of trends in DNA barcoding. Frontiers in Ecology and Evolution, 7: 302.

Epler JH (1986) *Oukuriella*, a new genus of Chironomidae (Diptera) from South America. Entomologica Scandinavica, 17: 157–163.

Epler JH, Ekrem T & Cranston PS (2013) 10. The larvae of Chironominae (Diptera: Chironomidae) of the Holarctic Region. – Keys and diagnoses. In: Andersen T, Cranston PS & Epler JH (eds.) The Larvae of Chironomidae (Diptera) of the Holarctic Region – Keys and Diagnoses. Insect Systematics & Evolution, Supplement 66. Pp. 387–556.

Ferrington LC, Jr (2008) Global diversity of non-biting midges (Chironomidae, Insecta-Diptera) in freshwater. Hydrobiologia, 595: 447–455.

Heiser M & Schmitt T (2013) Tracking the boundary between the Palaearctic and the Oriental region: new insights from dragonflies and damselflies (Odonata). Journal of Biogeography, 40: 2047–2058.

Kellogg VL (1900) An extraordinary new maritime fly. Biological Bulletin, 1: 81–87.

Kevan DKM & Cutten-Ali-Khan FEA (1975) Canadian Nymphomyiidae (Diptera). Canadian Journal of Zoology, 53: 853–866.

Kieffer JJ (1906) Diptera Fam. Chironomidae. In: Wytsman P (ed.) Genera Insectorum, 42. Bruxelles, L. Desmet-Verteneuil [etc.] 1902–1970. Pp. 1–78, 4 pls.

Kieffer JJ (1917) Chironomides d'Australie conservés au Musée National Hongrois de Budapest. Annales historico-naturales Musei Nationalis Hungarici, 15: 175–228.

Krosch MN & Cranston PS (2012) Non-destructive DNA extraction, including of fragile pupal exuviae, extends analysable collections and enhances vouchering. Chironomus, 25: 22–27.

Krosch MN, Herold N, Thornhill AH & Cranston PS (in press) How ‘Gondwanan’ is *Riethia* (Diptera: Chironomidae)? Molecular phylogenetics elucidates the mode and tempo of diversification in the Austro-Pacific. Invertebrate Systematics, in press.

Pinho LC, Mendes HF & Andersen T (2013) Revision of *Beardius* Reiss et Sublette, 1985 (Diptera: Chironomidae), with the description of twenty new species. Zootaxa, 3742: 1–78. DOI: 10.11646/zootaxa.3742.1.1.

Reiss F & Sublette JE (1985) *Beardius* new genus with notes on additional Pan-American taxa (Diptera, Chironomidae). Spixiana, Supplement 11: 179–193.

Roback SS (1975) A new subgenus and species of the genus *Tanytarsus* (Chironomidae: Chironominae: Tanytarsini). Proceedings of the Academy of Natural Sciences of Philadelphia, 127: 71–80.

Sæther OA (1980) A glossary of chironomid morphology terminology (Diptera: Chironomidae). Entomologica Scandinavica, Supplement 14: 1–51.

Sæther OA & Wang XH (1993) *Xiaomyia*, new genus, *Shangomyia*, new genus and *Zhouomyia* new genus, three new and unusual genera of Chironomini from Oriental China (Diptera: Chironomidae). Entomologica Scandinavica, 24: 185–195.

Sublette JE & Sublette MS (1973) Family Chironomidae. In: Delfinado MD & Hardy DE (eds.) A Catalog of the Diptera of the Oriental Region. Volume 1. University Press of Hawaii, Honolulu, pp. 389–422.

Tang H & Cranston PS (in press) Phytophagy in a *Polypedilum* (Diptera: Chironomidae) species new to Australia and Japan: taxonomy and expanded Asian distribution. Austral Entomology, in press.

Wiederholm T (ed.) (1983) Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Pupae. Entomologica Scandinavica, Supplement 19: 1–457.

Wiederholm T (ed.) (1986) Chironomidae of the Holarctic region. Keys and diagnoses. Part 2. Larvae. Entomologica Scandinavica, Supplement 28: 1–482.

Wiederholm T (ed.) (1989) Chironomidae of the Holarctic region. Keys and diagnoses. Part 3. Adult males. Entomologica Scandinavica, Supplement 34: 1–532.