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THE ORIENTAL GENUS *SHANGOMYIA* SÆTHER & WANG (CHIRONOMIDAE: DIPTERA): IMMATURE STAGES, BIOLOGY, PUTATIVE RELATIONSHIPS AND THE EVOLUTION OF WOOD MINING IN CHIRONOMID LARVAE

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ABSTRACT. **–** The enigmatic chironomid (Diptera: Chironomidae) genus *Shangomyia* Sæther & Wang, previously known from the adult alone, is associated newly with its pupa and larva. The distribution of the pupal exuviae, previously unassociated but described as 'Taxon 1' by Coffman and colleagues, provides evidence for a rather widespread distribution of a single species, *Shangomyia impectinata* Sæther & Wang, throughout oriental Asia. The larva, which mines in allochthonous aquatic immersed wood, has a ventromental plate with spines and creases, as seen elsewhere in *Stenochironomus* Kieffer and *Harrisius* Freeman (subfamily Chironominae). Support for a relationship to these genera comes from phylogenetic analyses of morphological data from all life history stages. Thus this taxon, whose classification has been under debate for the adult and especially the pupa, evidently lies in the tribe Chironomini of the subfamily Chironominae, in a clade with mining larvae. Morphological modifications of the wood-mining Chironomidae are reviewed briefly in the light of this finding. Two alternative hypotheses for the origin of wood mining habit early in the cladogenesis of Chironomidae are examined.

KEY WORDS. **–** *Shangomyia*, Chironomidae, phylogeny, evolution, wood-mining, immature stages.

INTRODUCTION

Much demand for identification of aquatic insects comes from aquatic biologists, who inevitably encounter the larval stages. Interest in the pupa and adult stages are, in contrast, modest. However, many taxonomists typically study adults alone, and classifications continue to be based on this stage. The history of study of Chironomidae (Diptera) in the second half of the 20th century has involved reconciliation of variably disparate adult and immature stage systematizations, such that in the Holarctic region, few genera are known solely from the adult. Since few suspects exist amongst either larvae and pupae, these remainign unassociated taxa may have non-aquatic immature stages. Elsewhere this situation is less satisfactory, because isolated (unreared) adult-based taxa continue to be described often lacking knowledge of immature stages. This may be because less emphasis has been devoted to water quality and/or aquatic ecological-driven study to associate larvae and pupae. Although identification tools for the immature stages associated with Holarctic genera can be used for taxa shared outside the region, and many can be identified, regional endemics may be unidentifiable. This causes practical problems in ongoing biomonitoring efforts, and may prevent accurate estimation of phylogenetic relationships at higher levels.

Recent publications on the chironomid fauna of the Oriental region allow us to understand the diversity and levels of generic endemism within the family. However, in comparison with studies from the Holarctic region, larval stage descriptions have lagged. Amongst the descriptions of enigmatic adults endemic to the Oriental region, are three new taxa including *Shangomyia* described by Sæther & Wang (1993) as a new genus. They proposed a position close to the base of the subfamily Chironominae, and perhaps belonging to an as-yet-undescribed higher ranked taxon. Recently, associated material collected by the author in Brunei shows that *Shangomyia* belongs with a curious pupal exuviae described previously by Coffman et al. (1988) from southern India as pupal 'Taxon 1', whose affinities were unknown to the extent of being unable to be placed in a known subfamily. More recently still, amongst a collection made by Cathy Yule from Kelian River, Kalimantan, a pharate male of *Shangomyia* was found with cast larval exuviae attached, allowing recognition of the complete life history. Comparison of these materials leads to recognition that there is but one species, albeit with a very wide distribution, from South India (Coffman et al., 1988) to Burma and Hainan (oriental China) (Sæther & Wang, 1993), and Thailand and Borneo (this paper).

In this paper, the previously unknown larva is described and illustrated, its biology discussed briefly, and a phylogenetic position postulated based on cladistic parsimony analysis of a large data morphological matrix for the genera of the subfamily Chironominae.

MATERIALS AND METHODS

Larvae were sought by prising apart immersed wood (Cranston, Sungai Belalong) or by kicking benthos into a 500 µm mesh net (Yule, Kelian River). Individual rearing was impractical, and life-history associations were obtained from interception of drifting pupae and their exuviae (cast skins) by exposing one or more drift nets with a 300 µm mesh to intersect a flowing water surface.

Microscope slide preparation involved clearing where necessary with 10% KOH, neutralisation and initiation of dehydration with glacial acetic acid, then mounting from propan-2-ol (isopropanol) into Euparal. Pupal exuviae were displayed by dissecting the cephalothorax from the abdomen.

Morphological terminology follows Sæther (1980) and Cranston (1994a) and all measurements, unless otherwise stated, are in µm. Abbreviations for repositories: ANIC - Australian National Insect Collection, CSIRO Entomology, Australia; BMNH - British Museum (Natural History) = (Natural History Museum, London), Cromwell Road, London, UK; ZRC - Zoological Reference Collection of the Raffles Museum of Biodiversity Research, Singapore; ZSM - Zoologische Staatsammlung München, München, Germany.

TAXONOMY

Shangomyia Sæther & Wang, 1993

Shangomyia Sæther & Wang, 1993: 188.
Taxon 1 – Coffman et al., 1988: 159.

***Diagnosis.* –** Larva with dorsal surface of head (Fig. 1f) with S3 on sclerotized anterior margin of frontoclypeal apotome, deeply divided by apparently flexible area from separate anterior sclerites. Antenna (Fig. 1a) 5-segmented, with 3 short apical segments, 3rd subequal to 5th, both shorter than 4th; basal segment with basal Ring organ, strong seta arising from mid-segment; style slightly longer than Lauterborn organs, which are subequal to length of 3rd segment; blade extending far beyond antennal apex.

Labrum (Fig. 1e, in semilateral view) narrowed and tapering anteriorly. SI simple, stout, SII and SIII simple, long and thin, SIVa, b quite well developed. No evidence of labral lamellae. Pecten epipharyngis of 3 broad rounded scales, 3 chaetulae laterales, weakly serrate apically. Premandible with one apical tooth and fine, stubble brush.

Mentum (Fig. 1b) with prominent extended saggitate median tooth, with four pairs of retracted lateral teeth, with outermost teeth fused basally, separated by notch, ventromental plate (Fig. 1c) small and short, without beard, with bifid seta submentum.

Mandible (Fig. 1d) without dorsal tooth, with apical tooth and four inner teeth, decreasing in size from outer to inner, with 4th (innermost) larger, bulging from swollen mola with narrow seta subdentalis curving around its margin; mola bearing 4 strong spines; seta interna absent.

Abdomen. Body setae short. Procercus strong, darkened, 4-6 times as long as wide, with 2 strong lateral setae and 6 relatively short apical setae. Anterior parapods apparently scarcely separated, crowned with simple yellow claws. Posterior parapods claws large curved, simple, dark yellow. Anal papillae undeterminable.

Pupa (as in Coffman et al., 1988, ‘Taxon 1’) lacking frontal setae and thoracic horn, leg sheaths all recurved beneath wing sheaths. Abdomen (Fig. 2a) with tergites II-V each with anterior transverse band of uniserial spines, medially interrupted on II, complete on III-V (Fig. 2b), lying posterior to area of dense shagreen, TII and III each with uniserial row of hooklets, TIV with medio-posterior patch of strong, anteriorly-directed dark spines, TVI with anteromedian semicircular area of tubercular blunt spines (Fig. 2c), pedes spurii B on III, posterolateral corner of VIII without comb, with cluster of spinules; anal lobe without fringe, with hair-like dorsal and ventral seta.

Adult (as Sæther & Wang, 1993) with 13 flagellomeres, eye with no dorsomedial extension, front tibia with long spur, mid and hind legs with long curved and simple spurs - all spurs denticulate and arising from apical scale; Hypopygium (Fig. 2d) with flexible gonocoxite/gonostylus, gonostylus with apical tooth.

The larva and pupa can be distinguished from other regional Chironomidae using the keys provided by Cranston (in press).

Shangomyia impectinata Sæther & Wang, 1993

Shangomyia impectinata Sæther & Wang, 1993: 190.

Material examined (all slide mounted in Euparal)**. –** 2L, Le, 22Pe, Pe/m, m, BRUNEI: Temburong District, Kuala Belalong Field Study Centre, Sungai Belalong, 4°33’N 115°09’E, coll. Cranston, Aug.1995 (BMNH, 17Pe ANIC); Le, Pm, INDONESIA: Kalimantan, Kelian River, coll. Yule, no date (ZRC); 1 male, 1 female, THAILAND, Doi Inthanon, coll. Malicky, 13-20 Mar.1990 (ZSM); 1 male, 1 female, Fluss [R.] Ping, 15 km s[üdlich], Chiang Dao, coll. Malicky, 30.Dec.1989 (ZSM); 8Pe, 3m, THAILAND/ LAOS border, Loei Province, nr Na Haew N.P., Huang River, International Falls, 17°34’N 100°59’E, coll. Cranston, 9-10 Mar.2002 (ANIC).

Larval description (n=1-2)**. –** Head capsule yellow, with dark mentum. Antenna (Fig. 1a) segment lengths: 54-60; 16-17; 3-4; 4-5; 3; blade 68-78; subsidiary 4-5um; style 7-8. A.R.

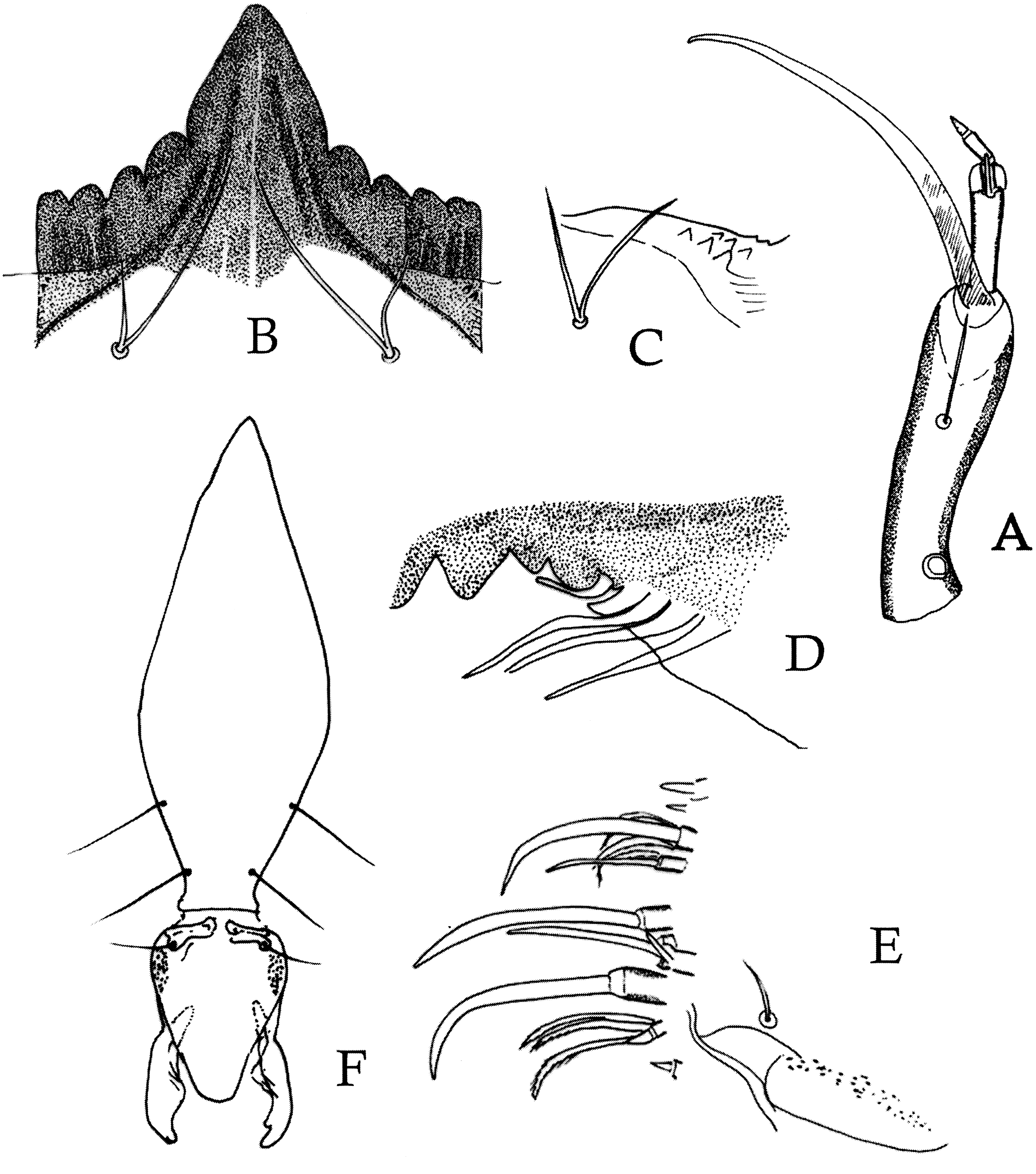

Fig. 1. *Shangomyia impectinata* Sæther & Wang, 1993, Larva; A. Antenna; B. Mentum, ventral; C, Ventromental plate (x1000 magnification); D. Mandible, inner teeth and mola; E. Labrum, semi-lateral view of rotated labrum; F. Dorsal head.

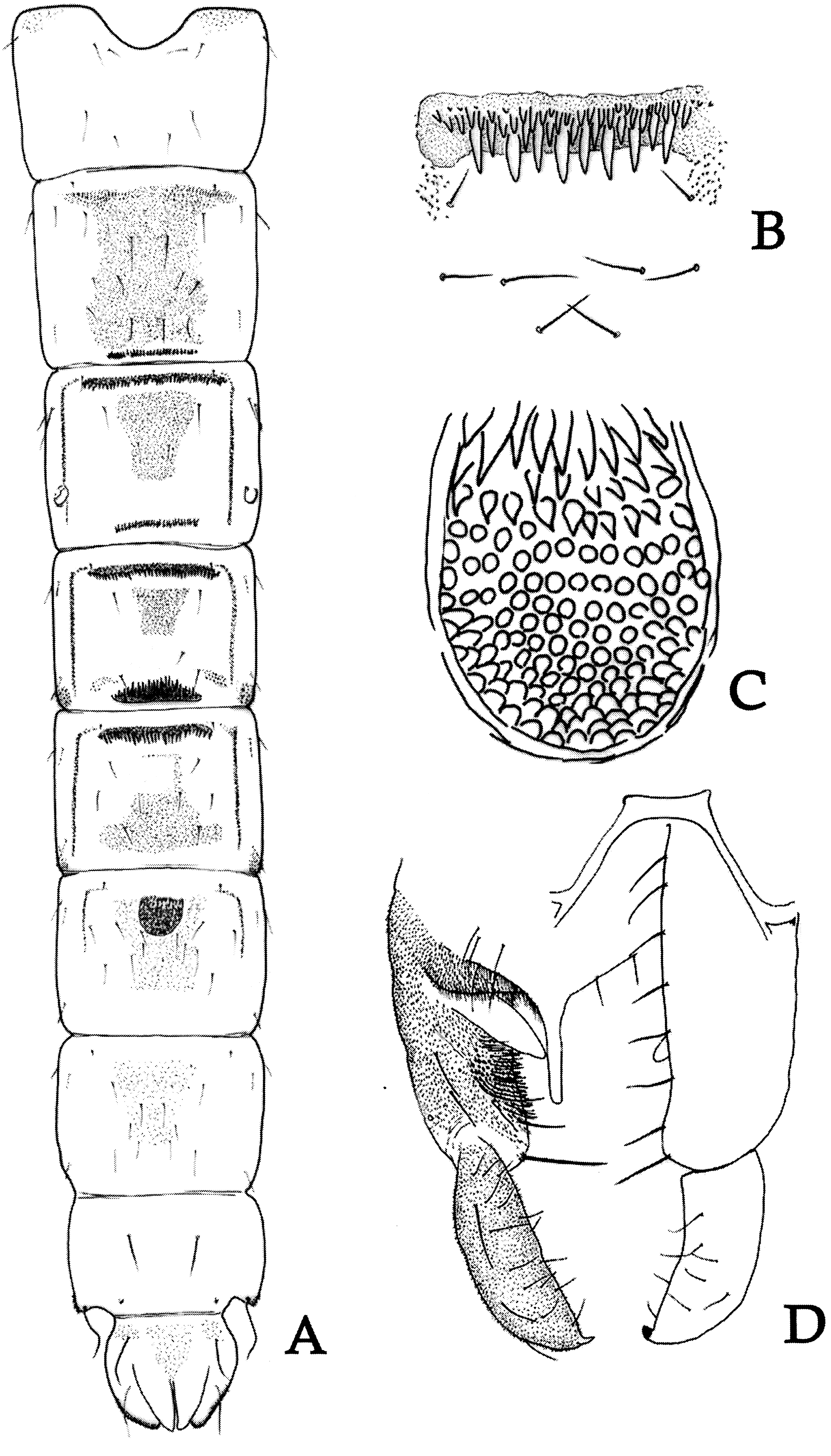

Fig. 2. *Shangomyia impectinata* Sæther & Wang, 1993, Pupa, male hypopygium; A. Tergites, dorsal; B. anterior tergite IV; C. posterior tergite VI. D. Male hypopygium, left side dorsal, right side ventral/ stylised internal.

1.9-2.2. Lauterborn organs 4-5um. Ring organ basal. Very strong (but pale) seta on 1st antennal segment, 18-21 long, arising from mid-segment and extending near to apex of segment 1. Mentum (Fig. 1b) width 110 -113, ventromental plate (Fig. 1c) triangular with 4-5 creases and 3-7 thorn spines antero-laterally on dorsal surface. Mandible (Fig. 1d) 120-132. Premandible 200, apical tooth blunt, brush Chironominae-like.

Abdomen (n=1). Body setae quite strong, on thorax 50 - 120 long. Anterior parapods apparently scarcely separated, crowned with simple yellow claws. Procercus light brown pigmented, 125 long by 33 wide, bearing 2 lateral setae 100 and 50 long, 6 apical setae of length 325. Posterior parapod claws large curved, simple, dark yellow.

PHYLOGENETICS

Coffman et al. (1988) could not allocate their pupal Taxon 1, or a presumptively related pupal Taxon 2, to subfamily, suggesting that the unusual morphology represented perhaps a new higher taxon, perhaps even subfamily. A resemblance of thoracic setation to Orthocladiinae, and abdominal features to (Chironominae) genus *Pseudochironomus* Malloch was recognised, but Coffman et al. (1988) concluded that clarification of the taxonomy and phylogeny would have to await discovery of larvae and adults.

In describing *Shangomyia* from adults of both sexes, but unaware of the association with Coffman et al.'s pupa, Sæther & Wang suggested a possible high-ranked taxon to include also *Ziaomyia* Sæther & Wang, known from the adult alone and clearly synapomorphous in many features with *Shangomyia*. Although showing many symplesiomorphies and some autapomorphies in the male, the 'conventional' female genitalia and some male features implied to Sæther & Wang possible membership of the *Harnischia* complex of genera in the subfamily Chironominae. The authors doubted this placement and instead suggested a 'plesiomorphic' position in Chironomini, perhaps of high rank, and hoped that the immature stages, when eventually found, would solve the dilemma.

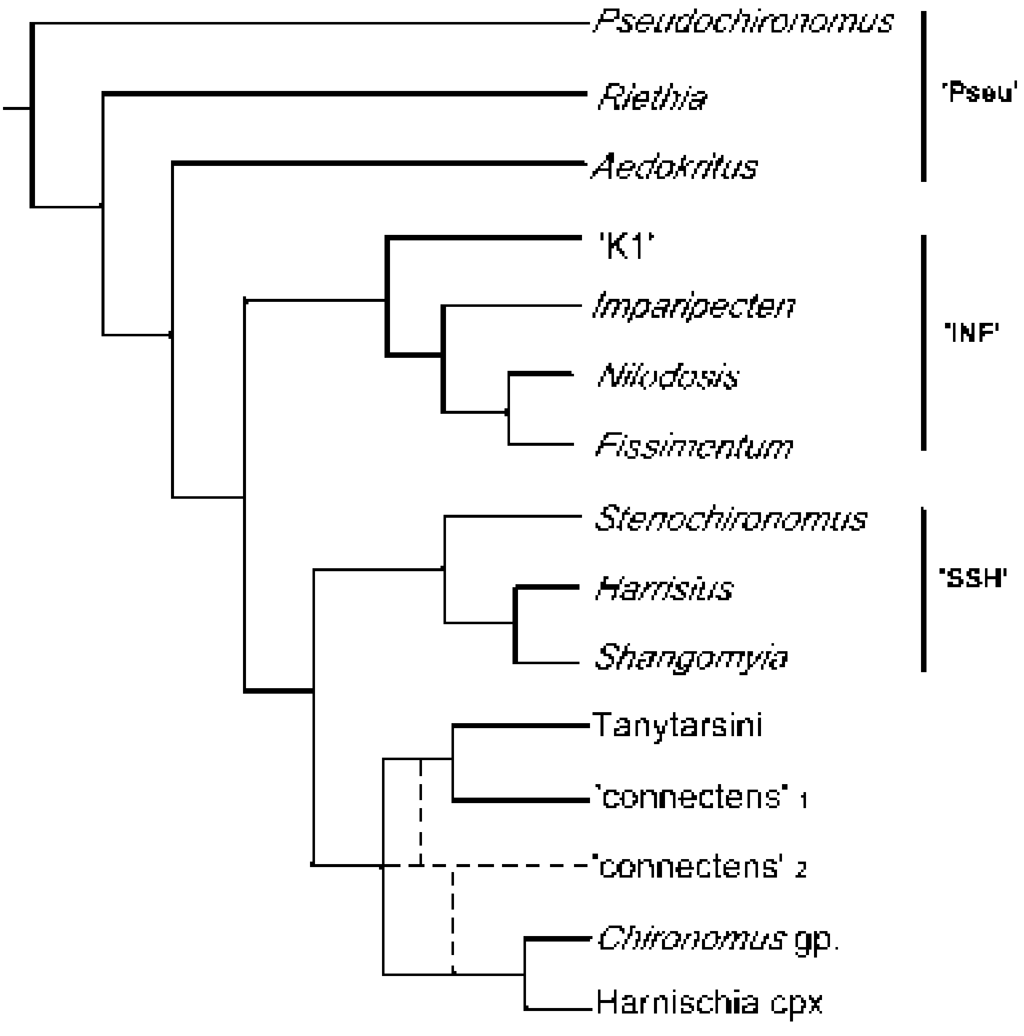

Fig. 3. Reduced phylogeny for Chironominae, strict consensus, all characters unordered. Abbreviations – 'Pseu' – 'Pseudochironomini', a paraphyletic grade on these data; 'INF' – monophyletic clade, 'K1', *Imparipecten*, *Nilodosis*, *Fissimentum*; SSH – monophyletic clade, *Stenochironomus*, *Shangomyia*, *Harrisius*. 'connectens' 1 and 2 – an informal grouping, possibly monophyletic but unresolved in this analysis, comprising 1. *Polypedilum*, *Pagastiella* and relatives, and 2 *Stictochironomus* and relatives with 6-segmented larval antenna and alternate Lauterborn organs.

To assess if the now-known larva, and newly-associated pupa could assist in reconstructing the phylogeny, *Shangomyia* was scored for 119 characters in a pre-existing data matrix for 62 Chironominae genera for which minimally pupa plus adult, preferably all life stages, were known. The matrix is available from http://entomology.ucdavis.edu/chiropage/chironominaematrix.pdf or electronically from the author on application. Analysis used Hennig 86 (Farris, 1988) operating within a Microsoft Windows shell of Tree Gardener 1.0 (Ramos, 1996) employing the heuristic search options mhennig* followed by bb*, or PAUP* 4.0b10 (Swofford, 2002) for Macintosh. Trees were rooted with *Brillia* Kieffer, an early-branching Orthocladiinae genus. In analyses all characters were treated as additive (ordered). Assessment of confidence in certain phylogenetic results from the analyses were made using permutation tests, which compare the length of minimal-length trees against the lengths obtained by similar searches of the data matrix in which within character randomisation has destroyed phylogenetically informative covariation (Faith & Cranston, 1991) using topology-dependent permutation tests (T-PTP) (Faith, 1991) as implemented in PAUP 4.0b10 with 100 random addition sequences of 100 randomisations of the data matrix.

The result (Fig. 3) shows *Shangomyia* as sister to *Harrisius* Freeman in a clade with *Stenochironomus* Kieffer (‘SSH’ clade), sometimes included *Nandeva* Wiedenbrug, Reiss & Fittkau. *Nandeva* is unknown as a larva, unstable in position, and subject to doubt concerning an adult wing character (angle of the wing crossvein RM) and thus was excluded from analyses run for statistical testing.. Tree statistics (derived from Hennig86 and PAUP) are as follows: all character states unordered, > 100 trees of length 922, consistency index (c.i.) .17, retention index (r.i.) .53. T-PTP tests showed the clade *Stenochironomus* (*Shangomyia* + *Harrisius*) has a probability of p=0.01, and the reverse p =1.0, providing robust support for the clade. Surprisingly, bootstrap values for the clade were >80% and Bremer support 6 steps, unusually high values for morphological data.

The relationship between *Stenochironomus* and *Harrisius* has been unchallenged since recognised first by Borkent (1984); both taxa have wood-mining larvae with very limited ventromental plate sculpturing, only modest resemblance in pupa, but more resemblance in the adult. *Shangomyia* bears no resemblance in the highly autapomorphic pupa, little resemblance in adult, but derives most similarity from the larva. In all taxa the ventromental plate is triangular, extending from the mentum to the gula with the anterior margin almost exactly transverse, with evidence for microstructure visible only at highest magnifications. In all 3 genera lamellate striae are lacking, but anterolaterally the dorsal (inner) surface of the plate has few to several creases (which could represent striae) and some unaligned submarginal triangular spines. Possibly the ventromental features are convergent (as independent reductions from broad and fully striate) or symplesiomorphic (as pre-Chironominae non-striate type) but both are rendered unlikely by two factors. Undoubtedly *Pseudochirornomus*, *Riethia* and *Aedokritus* (“Pseudochironomini’, almost certainly a paraphyletic grade) form a pectination at the base of the subfamily phylogeny with respect to an austral *Imparipecten/Nilodosis/Fissimentum* clade, *SSH* clade and undoubtedly monophyletic Tanytarsini. Thus the non-striate ventromental plate condition of *SSH* should be considered apomorph reduction, rather than representing the plesiomorph condition. Furthermore larval *Stenochironomus* and *Harrisius* are unusual in the tribe Chironomini in possessing a strong basal antennal seta, a condition found in *Shangomyia* (Fig. 1a), otherwise in all Tanytarsini but absent in all putative outgroups, thus suggesting a synapomorphy for the SSH clade. Although few adult character states can be found to support the relationship proposed here, the female genitalia of *Shangomyia* appears quite concordant with that of *Stenochironomus*, although the condition is very generalised.

Although Coffman et al.’s pupal ‘Taxon 1’ was known (but not its association with *Shangomyia*), it is unlikely that details of the pupa would have assisted Sæther & Wang’s deliberations because it is so highly autapomorphic. It is interesting to speculate on how the larva, if known, would have affected phylogenetic reasoning based on emphasis on the adult alone. The results of this study do not assist in the placement of the postulated associated taxa *Ziaomyia* Sæther & Wang or Coffman et al.’s pupal ‘Taxon 2’. However, it might be extrapolated that the features that the original authors believed to associate them with *Shangomyia* or ‘Taxon 1’, respectively, may predict association with the SSH clade. A search for larvae in immersed wood is clearly indicated.

The proposed relationship argued above refutes earlier suggestions of a high-ranked taxon for *Shangomyia*. Since the proposed relationship is likely to be controversial, with support coming only from larval features, material should be collected for molecular sequence determination to determine molecular and total evidence relationships between higher ranked Chironomidae.

BIOLOGY:
THE SIGNIFICANCE OF WOOD MINING

Only one complete larva of *Shangomyia* has been collected, from a fast-flowing, essentially pristine river in northern Borneo (Temburong, Brunei) exposed by fragmenting immersed wood from a major log jam. The wood quality was unrecorded since many pieces of variable decomposition were harvested and assessed for mining taxa; however, the larva was distinctively red coloured and active when its tunnel was exposed. The gut contents comprises fragmented wood fibres typical of wood-mining chironomids examined from elsewhere (e.g., Cranston, 1983; Cranston & Oliver, 1988; Cranston & Hardwick, 1996; McKie & Cranston, 2001). A larval exuviae was collected from drift in the same river, and a third larva also was collected as an exuviae, associated with (attached to) a drifting pupa, from the Kelian River in Kalimantan (Indonesian Borneo), at a site where both mine and human disturbance were evident, but downstream of a semi-pristine section. All other evidence pertaining to habitat preference comes from interception of drifting pupal exuviae, from a wide geographical range of running waters from south India to Thailand. Thai sites appear representative of the wider range: flowing waters in unregulated rivers, with riffles and pools, naturally wooded riparian zones, and flowing sometimes at elevations up to 1,000m asl, with temperature regimes less than extremes of air temperature. Water temperatures in Sungai Belalong in August 1995 varied little from 25°C, with air temperatures ranging from 23 to 31°C.

Cranston & Oliver (1988) in a review of xylophagous (wood-mining) chironomids, observed that 'adaptive' modifications of the mentum were restricted to a convergent suite of Orthocladiinae larval miners with protruding median teeth, with mining Chironominae morphologically unmodified. This observation seemed to have generality outside the Holarctic when diverse Australian woodminers were examined (e.g., Cranston, 2000; Cranston & Hardwick, 1996; McKie & Cranston, 1998, 2001). However, as is evident from Fig. 1a, *Shangomyia* has the sagittate and protruding median mentum associated previously only with Orthocladiinae miners.

As alluded to already, Orthocladiinae larval mining taxa show high convergence in their morphology, since the habit has been adopted many times in the evolution of the subfamily. Perhaps only in the *Brillia* group has there been a radiation amongst plesiotypic miners using aquatic allochthonous vegetation (dead leaves and wood) (Cranston, 2000). The situation is somewhat different in the Chironominae in which adoption of allochthonous mining is less frequent, and it is essentially absent in Tanytarsini and the derived clades (*Harnischia* complex, *Chironomus* grouping). Wood mining appears to be concentrated in basal clades (perhaps analogous to the *Brillia* situation): thus in the grade 'Pseudochironomini' the putative larva of *Megacentron* Freeman is found in soft wood (Cranston, 1996), in the *NFI* clade *Imparipecten* mines, and the next most distal clade certainly constitutes a radiation of mining larvae: *Shangomyia*, *Stenochironomus* and *Harrisius*. From this phylogeny, one can postulate that the early radiation of the subfamily Chironominae may have involved substantial wood mining, as argued for Orthocladiinae (Cranston, 2000) and therefore perhaps a plesiotypic behaviour prior to the diversification of the two sister subfamilies. Interestingly, the habit is unknown in any other subfamily of Chironomidae.

There is, however, an alternative explanation for the distribution of mining amongst the Orthocladiinae and Chironominae, which can be related to the biogeographical distributions of the clades. Although the fine details of the phylogeny of each subfamily derived from morphology are poorly resolved and many clades have minimal levels of support, evidently early cladogenetic events in both subfamilies involve some clades that are near global in present day distributions, but also many others that are quite disproportionately represented in the southern hemisphere and/or south and south-east Asia. A vicariance paradigm for interpretation of such patterns infers great age for the clades, with the subfamilies present in Pangaea, and subsequent diversification associated with tectonics including Gondwanan fragmentation (for rationale and case studies see Cranston, 1994b). From this evidence of great age, increasingly substantiated by fossils from the Cretaceous period, it can be argued that wood mining may not have been plesiotypic, but the habit is associated with survival through the K-T event in a refugial habitat – immersed wood in streams. and in a refugial area, the southern hemisphere less impacted by the bolide. Such differential survival (extinction resistance) between habitats and continents provides an alternative explanation for the present-day patterns worthy of further study.

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LITERATURE CITED

Borkent, A., 1984. Systematics of the *Stenochironomus* complex. *Memoirs of the Entomological Society of Canada,* **128**: 1-269.

Coffman, W. P., L. A. Yurasits & C. de la Rosa, 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, P. S., 1983. The metamorphosis of *Symposiocladius lignicola* (Kieffer), gen. nov., comb. nov., a wood-mining Chironomidae (Diptera). *Entomologica Scandinavica,* **13**: 419-29.

Cranston, P. S., 1994a. Morphology, Chapter 2. In: Armitage, P. D., P. S. Cranston & L. C. V. Pinder (eds.), *Chironomidae: Biology and Ecology of Non-biting Midges,* Chapman and Hall, London, Glasgow, New York, Tokyo, Melbourne, Madras, pp. 11-30.

Cranston, P. S., 1994b. Biogeography, Chapter 4. In: Armitage, P. D., P. S. Cranston & L. C. V. Pinder (eds.), *Chironomidae: Biology and Ecology of Non-biting Midges.* Chapman and Hall, London, Glasgow, New York, Tokyo, Melbourne, Madras, pp. 62-84.

Cranston, P. S., 1996. *Identification Guide to the Chironomidae of New South Wales.* AWT Identification Guide Number 1. Australian Water Technologies Pty Ltd, West Ryde, NSW. pp. 376.

Cranston, P. S., 2000. *Austrobrillia* Freeman: immature stages, and a new species from the Neotropics. *Spixiana,* **23**: 101-111.

Cranston, P. S., in press. Chironomidae. In: Yule, C. M. & H. S. Yong, (eds.), *The Freshwater Invertebrates of Malaysia and Singapore*. Academy of Sciences Malaysia.

Cranston, P. S. & R. Hardwick, 1996. The immature stages and phylogeny of *Imparipecten* Freeman, an Australian endemic genus of wood-mining chironomid (Diptera). *Aquatic Insects,* **18**: 193-207.

Cranston, P. S. & D. R. Oliver, 1988. Aquatic xylophagous Orthocladiinae - systematics and ecology (Diptera, Chironomidae). *Spixiana,* Supplement **14**: 143-154.

Faith, D. P., 1991. Cladistic permutation tests for monophyly and nonmonophyly. *Systematic Zoology,* **40**: 366–375.

Faith, D. P. & P. S. Cranston, 1991. Could a cladogram this short have arisen by chance alone? On permutation tests for cladistic structure. *Cladistics,* **7**: 1–28.

Farris, J. S., 1988. *Hennig86 Reference, Version 1.* Privately published, Port Jefferson.

McKie, B. & P. S. Cranston, 1998. Keystone coleopterans? Colonisation by wood-feeding elmids of experimentally-immersed woods in south-east Australia. *Marine and Freshwater Research,* **49**: 79-88.

McKie, B. & P. S. Cranston, 2001. Colonisation of experimentally-immersed wood in south-eastern Australia: macroinvertebrate feeding groups and implications for models of longitudinal change. *Hydrobiologia,* **452**: 1-14.

Ramos, T. C., 1996. *Tree Gardener 1.0.* Privately distributed by Tiago Courrol Ramos, Museu de Zoologia, Universidade de Sao Paulo, Sao Paulo.

Sæther, O. A., 1980. A glossary of chironomid terminology (Diptera: Chironomidae). *Entomologica Scandinavica,* Supplement **14**: 1-51.

Sæther, O. A. & X. Wang, 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.

Swofford, D. L., 2002. *PAUP*. Phylogenetic analysis using parsimony (*and other methods),* ver. 4. Sinauer Associates, Sunderland, Massachusetts.