AQUATIC WOOD — AN INSECT PERSPECTIVE

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Abstract—Immersed wood provides refugia and substrate for a diverse array of macroinvertebrates, and food for a more restricted genuinely xylophagous fauna. Worldwide, xylophages are found across aquatic insect orders, including Coleoptera, Diptera, Trichoptera and Plecoptera. Xylophages often are specialised, feeding on the wood surface or mining deep within. Many feed preferentially on wood of particular species or of a particular decay class. Some of the most specialised genuine wood miners occur among the Chironomidae, and the fauna is particularly rich in Australia. Recent discoveries of unusual midges in Australia and south-east Asia allow speculation about the evolution of immersed-wood mining by Chironomidae. Subfamily Orthocladiinae contains many unrelated taxa with larval mouthpart modifications associated with gouging wood. Wood-mining chironomines, in fewer groups, mostly lack morphological differentiation. However, several early-branching clades of both subfamilies show radiation (diversity), and the condition can be inferred as ancestral, potentially associated with differential historical survival from cataclysmic extinction events.

INTRODUCTION

Coarse woody debris (CWD) in aquatic habitats fulfills many important functions, including structuring of stream channels (Bilby 1984, Gippel 1995, Gippel and others 1996), enhancement of organic matter retention (Bilby and Likens 1980) and provision of substrate for life history activities of aquatic macroinvertebrates including attachment, feeding and oviposition (Anderson and others 1984, Andrus and others 1988, Harmon and others 1986, O'Connor 1991). Wood also provides an abundant but refractory source of carbon which worldwide is fed on by an array of specialized insects, including elmid coleopterans like *Lara avara* LeConte (North America) and *Notriolus* spp. and *Simsonia* spp. (Australia), the burrowing ephemeropteran *Povilla adjusta* Navas (Polymitarcidae, Africa), the trichopterans *Lype* (Psychomyiidae, Europe) and *Triplectides* (Leptoceridae, Australia), species of the dipteran *Lipsothrix* (Tipulidae, Holarctic) and the plecopteran, *Acruroperla* (Austroperildae, Australia). However, inventories of macroinvertebrates associated with CWD tend to be dominated by species belonging to non-gouging functional groups that may use the wood substrate stochastically (e.g., McKie and Cranston 2001). Indeed, as a generalization, larval insect taxa living internally within immersed wood are underestimated. Nevertheless, a summary of the stenophagous (narrowly restricted) xylophagous mining taxa in major groupings in well-studied regions can be presented (table 1).

Few of these taxa have been studied in detail, but it is apparent that many exhibit significant ecological specialisation. Preferences for different wood species and/or decay classes can reflect both palatability and complexity of surface sculpturing of the host wood (McKie and Cranston 1998, 2001). For example, conifer woods have notably high carbon/nitrogen ratios and large quantities of secondary chemical compounds,

Table 1—Species of stenophagous xylophagous mining insects known from USA, New Zealand, and Australia

	Central Europe[a]	Oregon[b]	USA[c]	New Zealand[d]	Australia[e]
Ephemeroptera	0	3	3	0	2
Plecoptera	2	3	3	1	4
Trichoptera	4	5	5	2	3+
Col: Elmidae	1	2	2	0	> 8
Col: Ptilodactylidae	0	1	1	0	1+
Dipt: Chironominae	1	1	2	1	6+
Dipt: Orthocladiinae	3	3	5	1	7+
Dipt: Tipulidae[f]	17	Yes	Yes	Yes	Yes

Col = Coleoptera; Dipt = Diptera: Chironomidae.

[a] Hoffmann and Hering (2000) (NB. taxa listed as "probably xylophageous").

[b, c] Anderson and others 1984, Cranston and Oliver 1988.

[d] Anderson 1982.

[e] McKie and Cranston 1998, 2001.

[f] Probably multiple species in all regions, though many may be semiaquatic.

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both of which may inhibit decay and reduce suitability as a food source for macroinvertebrates (Anderson and Sedell 1979, Aumen and others 1983). More complex and/or decayed wood surfaces potentially provide more surface area for feeding and more refugia, and facilitate mining (Collier and Halliday 2000, Magoulik 1998, McKie and Cranston 1998, Spänhoff and others 2000). In subalpine Australia, dominant xylophagous taxa, (primarily Coleoptera: Elmidae), have been shown to respond to wood species, favouring native *Eucalyptus* but avoiding the alien pine, *Pinus radiata* (McKie and Cranston 1998). Similarly, the north American shredders *Lara avara* (Coleoptera: Elmidae) and *Lipsothrix* (Diptera: Tipulidae) both favour alder over coniferous wood (Anderson and others 1978, Dudley and Anderson 1987). However, while the New Zealand caddisfly *Pycnocentria funerea* (Trichoptera: Conoesucidae) varies in its feeding efficiency (assessed via faecal production) on five different wood species, it shows no aversion to introduced conifers (Collier and Halliday 2000, Collier and others 2004). Different xylophages also exploit different components of wood, some gouging at the surface (e.g., McKie and Cranston 1998) and others mining within (e.g., Cranston and Hardwick 1996), and there is evidence for differential exploitation of wood at different stages of decay (Anderson and others 1984, Collier and Halliday 2000).

In contrast to community studies, there have been few autecological studies of these obligate wood-mining insects, despite the pioneering studies by Norm Anderson's team at Oregon State University in the 1980's, including those on *Lara avara* (Steedman and Anderson 1985) and *Lipsothrix* (Dudley and Anderson 1987) are rare examples. The many chironomid miners also are poorly known and only the life history of *Xylotopus par* Coquillett has been studied in detail (Kaufmann and King 1987, Kaufmann and others 1986). Many aspects of the ecology of wood-miners remains poorly understood, not least processes of cellulose digestion.

Our studies have revealed a diverse chironomid fauna associated with immersed wood, especially in Australia (table 1). Many of these species are true wood-miners, which are difficult to sample using standard methods and consequently may be little known to most freshwater biologists. True richness of this fauna can be assessed by quantitative intercepts of their floating pupal exuviae, whose presence demonstrates completion of the life cycle in nearby wood. This contribution reviews and synthesizes research on xylophagous chironomids. We include a summary of appropriate sampling techniques, discuss what can be discerned of their phylogenetic relationships, and speculate on some less-well understood aspects of their evolutionary ecology.

METHODS USED TO STUDY AQUATIC WOOD

The most commonly employed method for studying biodiversity of macroinvertebrates, associated with immersed wood is to examine recovered sticks of various sizes and wood classes (e.g., varying in density and degree of abrasion (which depends on wood species), immersion time, water velocity, etc.). Washing sticks into a bucket with appropriate sieving allows retention of macroinvertebrates dislodged from the surface. Increasing water pressure and scrubbing with a brush removes most organisms clinging to the surfaces including those secreted in crevices. However, rigorous survey for true miners requires visual inspection of the wood while stripping off surface layers, sometimes under a dissecting microscope. Wood that shows external evidence of internal activity, such as appropriate-sized bore-holes or accumulation of frass, is worthy of such close inspection. Examination of the gut contents can confirm wood-mining habits amongst larval Chironomidae. Gut contents, visible through the body wall especially after clearance for slide preparation, consists of comminuted wood fibres and little else (Cranston 2003, Cranston and Hardwick 1996, Cranston and Oliver 1988, McKie and Cranston 2001).

Making life history associations for wood-mining taxa is difficult, because many are stenophagous and die outside their natural larval habitat. Placing immersed wood into aerated aquaria can provide some estimation of species presence (by collecting emerged adults and/or pupal exuviae at the surface), but the technique is fraught with possible mis-association and general contamination. Physical examination of large quantities of wood, though tedious and often poorly rewarded, can reveal complete life histories through fortuitous discovery of larva/pupa associations, and of pupae containing pharate adult stages.

Serendipitous, qualitative studies are important in documentation of the diversity of wood-mining species, and with experience preferred types (species and decay state) of wood for mining can be identified. Naturally this varies geographically. For example, alder (*Alnus*) is especially preferred in the northern hemisphere and other riparian soft woods elsewhere. Generally softer woods sustain higher densities and diversity of wood-miners than do harder woods, although *Eucalyptus* is favoured by surface-gougers in Australia. Wood of differing decay states may yield different densities and/or assemblages of xylophages, and this often may be more important than the taxonomic affinity of the wood in determining what species are found (Personal observation. McKie and Cranston, authors of this paper) (Spänhoff and others 2000). Although succession among aquatic xylophages according to wood decay has been little studied; some evidence exists for its occurrence (e.g., Collier and Halliday 2000). Transitions from surface feeding to deeper mining taxa are likely as the wood softens.

Quantitative and experimental studies can involve placement of wood of known history (species identity, age, size) into selected water bodies for controlled durations to study colonization dynamics (e.g., Spänhoff and others 2000). Appropriate hierarchical designs, similar to those used by Townsend and others (1997) and McKie and Cranston (2001), allow recognition of distinct preferences among locations and wood types.

DIVERSITY AND ECOLOGY OF CHIRONOMID WOOD MINERS

Only three of the 10 subfamilies of Chironomidae include larvae that are associated closely with immersed wood. These predominantly occur in the very diverse Orthocladiinae and Chironominae, with a sole example in the Diamesinae (*Pagastia*). The subfamily Tanypodinae is comprised mainly of predatory larvae that never mine but search the outer wood surfaces for prey. Amongst the other subfamilies for which larval behaviours are known, certain Australian Podonominae larvae utilize external wood surfaces, whereas Telmatogetoninae, Prodiamesinae and Buchonomyiinae show no special association with CWD.

In both Orthocladiinae and Chironominae wood mining appears to be distributed across the taxa such that there are many isolated examples, with just one or a few species often within some of the most speciose genera. For example, throughout much of the northern hemisphere, the appositely-named *Orthocladius* (*Symposiocladius*) *lignicola* Thienemann mines woods such as alder (Cranston 1982). Although *O. lignicola* may comprise several closely related entities, evidently there has been no radiation within *Orthocladius* and all potential relatives are non-mining algal grazers. Likewise, amongst the Chironominae, larvae of one or two species of *Polypedilum* in S.E. Asia and Australia mine in relatively soft immersed woods. Since close relatives in this large genus are collector-gatherers that do not mine, apparently this too is an apparent example of an evolutionarily facultative switch to living in wood, with no commensurate radiation within the substrate.

Despite the disparate occurrence of xylophagy amongst the Chironomidae, there is sporadic convergence in some morphological features associated with the mining habit. Thus menta are often either awl-like (e.g., fig. 1G), with the central tooth sagittate and protruding (e.g., several Orthocladiinae and the Chironominae *Shangomyia* Sæther and Wang) or more blade / plough-like (e.g., fig. 1F), with the distal edge flattened to recessed (the orthocladiine *Austrobrillia* Freeman and chironomine *Harrisius* Freeman), but other menta do not appear especially modified (e.g., fig. 1D). Similarly, there are some common but by no means universal modifications to the abdomen, including a flattened and/or flaccid form, reduced or no prolegs, and, in some undescribed orthocladiines, curious posterior body sclerotisation (McKie 1996).

It is presently difficult to assess the ecological significance of such morphological variation, as the ecology of xylophagous chironomids is generally poorly known, though there is certainly species-specific variation in stenophagy and patterns of resource utilisation. The evolution of wood-mining and leaf-shredding appears somewhat related among Chironomidae (thus the genera *Stenochironomus* Kieffer and *Brillia* Kieffer include both feeding modes), and there are some xylophagous species that feed on both leaves and wood (e.g., the Australian species of *Austrobrillia* and *Harrisius*). Such larvae evidently are "coarse detritus specialists" rather than obligate xylophages. Other species appear genuinely stenophagous, being found only mining within logs and failing to rear to emergence away from wood. Surveys of the wood-inhabiting fauna of south-east Australian streams revealed differential utilisation of wood by chironomid xylophages. Several taxa, including *Austrobrillia, Harrisius* and some novel orthocladiine species, were associated with the surface layers of mid-sized (diameter 2 — 5 cm) sticks (McKie 1996). In contrast, *Stenochironomus* sp. never was found associated with the wood-surface, and its presence was confirmed only after adults emerged from extremely well-decayed wood that had been kept in laboratory aquaria for several months, indicating a very deep mining habit (also see Cranston and Hardwick 1996). All such xylophages were associated most with more decayed wood from native forested streams (McKie 1996), with no species utilising fresh wood. Notably, negligible colonisation of fresh wood by xylophagous chironomids in an experimental study contrasted strongly with observations for surface gouging elmid beetles (McKie and Cranston 2001). Further details of the autecology of xylophagous chironomids generally are lacking, with only the north American lotic *Xylotopus par* Coquillett studied in detail — in Michigan, USA, it colonises wood of various decay classes, apparently has an annual life cycle, and bears a band of bacteria in its midgut that may be involved in wood digestion (Kaufmann and King 1987, Kaufmann and others 1986).

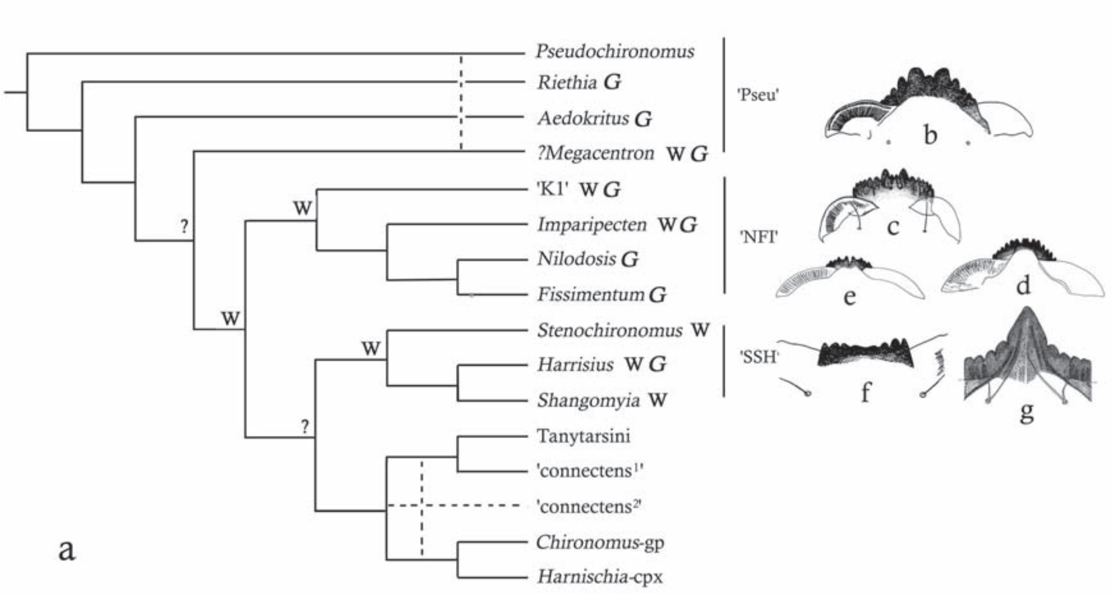

Figure 1—(A) Postulated early-nodes of subfamily Chironominae phylogeny (after Cranston 2004), broken lines represent ambiguous relationships; W = wood-mining taxa and reconstructed nodes, *G* = Gondwanan in distribution, ? — uncertain reconstruction. Menta of (B) ?*Megacentron* Freeman, (C) Australian genus 'K1', (D) *Imparipecten* Freeman, (E) *Nilodosis* Kieffer, (F) *Harrisius* Freeman, (G) *Shangomyia* Sæther and Wang.

PHYLOGENETIC RELATIONS AMONGST WOOD-MINING CHIRONOMIDAE

In the Orthocladiinae, the wood-mining habit appears clustered within a grouping of genera with no formal name, but to which the sobriquet '*Brillia* group' sensu Sæther and Wang 1992, can be applied (Cranston 2000). It includes the genera *Austrobrillia* Freeman, *Brillia* Kieffer, *Eurycnemus* v.d. Wulp, *Euryhapsis* Oliver, *Plhudsonia* Sæther*, Neobrillia* Kawaii and *Xylotopus* Oliver and *Irisobrillia* Oliver and *Tokyobrillia* Kobayashi & Sasa probably should be included also despite their immature stages remaining unknown. Although detailed phylogenetic relationships in this most diverse subfamily remain unclear, poorly resolved or contradictory, morphological analyses are converging on the view that the '*Brillia* group' may either be sister group to the remainder of the subfamily (as 'the most basal group'; Sæther and Wang 1992, Cranston 2000) or forms a paraphyletic grade at the base of the subfamily tree.

Wood-mining also appears to be concentrated in early branching ('basal') clades of Chironominae. As with the Orthocladiinae, ideas on the phylogeny and even the monophyly of some high ranking groups of the Chironominae, remain uncertain. However, the recently elucidated life history of an unusual Oriental wood-mining taxon, *Shangomyia* Sæther and Wang, provoked a reconsideration of some of the earliest branching events, based on morphology (Cranston, 2003), as depicted in figure 1A. Thus in the likely grade (paraphyletic) 'Pseudochironomini' ('Pseu', fig. 1A) the putative larva of *Megacentron* Freeman (fig. 1B) is found in soft wood (Cranston 1996). The next postulated branch comprises an undescribed Australian genus 'K1' (fig. 1C) (Cranston 1996), *Imparipecten* Freeman (fig. 1D), *Nilodosis* Kieffer and *Fissimentum* Cranston & Nolte in the clade ('NFI' (fig. 1). Larvae of *Imparipecten* mine in immersed wood in eastern Australia (Cranston and Hardwick 1996); those of 'K1' mine wood in monsoonal tropical streams of Northern Territory. The curious cleft menta of *Nilodosis* (fig. 1E) and *Fissimentum* seems to preclude mining, but their feeding mode is poorly understood.

The next node on the tree involves a clade that clearly constitutes a radiation of mining larvae: the long-understood sister-species pair of wood- and leaf-mining genera *Stenochironomus* Kieffer and *Harrisius* Freeman (Borkent 1984) is robust. Reviewing xylophagous chironomids, Cranston and Oliver (1988) observed that mining Chironominae (such as *Stenochironomus* and *Harrisius*) (fig. 1F) lacked 'adaptive' wood-mining modifications of the mentum that appeared restricted to a convergent suite of Orthocladiinae with protruding median mental teeth. This seemed to have generality even after revelation of diverse Australian woodminers (e.g., Cranston 2000, Cranston and Hardwick 1996, McKie 1996). However, the recently-discovered wood-mining larva of the Oriental chironomine genus *Shangomyia* has the sagittate protruding median mentum (fig. 1G) of a type associated previously only with Orthocladiinae miners (Cranston 2003). Never-the-less, phylogenetic analyses place *Shangomyia* unequivocally within the *Stenochironomus* / *Harrisius* clade (Cranston 2003), although superficially they differ in many aspects of their morphology in each life history stage.

Traits such as wood-mining can be reconstructed onto nodes (branching points) from such phylogenic hypotheses Several competing optimisation schemes exist, but even with fully-sampled and robust phylogenies, quantitative ancestral node reconstructions remain controversial, perhaps little better than those derived from qualitative parsimonious reasoning. Accepting this, it is reasonable to postulate that the early radiation of the subfamily Orthocladiinae may have been associated with substantial wood mining, as argued by Cranston (2000). Similar rationale can be applied to the Chironominae with the more recently elucidated early nodes in the phylogeny (Cranston 2003). Since Orthocladiinae and Chironominae are likely sister taxa, wood-mining may be a plesiotypic behaviour prior to the diversification of the two sister subfamilies.

DATING THE EVOLUTIONARY EVENTS

Lack of a molecular phylogeny, with its ever-improving capacity to provide dates for branching events, need not exclude speculation on the timing and locations of the events postulated from the phylogenies discussed above. From the earliest days biologists accepted the notion of drifting continents (plate tectonics), and especially following the formalisations of Hennig (1960) and Brundin (1966), the modern-day distribution of organisms and postulated earth history events have been used in dating evolutionary events. The rationale, discussed for Chironomidae by Brundin (1966), Cranston (1994) and Cranston and Hare (1995) and for Diptera more widely (Cranston 2005), assumes that sister taxa that occupy separated, but once united as Gondwana, southern landmasses speciated in allopatry prior to tectonic-induced separation. This provides minimum dates for vicariance according to the geological timetable (see Sanmartín and Ronquist 2004). Several taxa in early (including postulated wood-associated) radiations include austral distributed groups, such as *Riethia* and *Megacentron,* 'K1', *Imparipecten* and *Harrisius* in Chironominae (labelled '*G'* fig. 1A), and *Austrobrillia* amongst the Orthocladiinae (Cranston 2000). The occurence of such taxa with specialised immature biology in both South America and Australia add weight to arguments that the radiation of Chironomidae at the taxonomic level of still extant monophyletic clades (genera) predates major fragmentation of Gondwana. While the early-departing African continent rarely is included, many distributions involve Australia (with its remarkably diverse xylophagous chironomid fauna — table 1) and South America, which were contiguous through Antarctica some 38 million years ago. Furthermore, the current more global distribution of the '*Brillia* group' and *Stenochironomus* and relatives suggests an even more ancient origin perhaps in Pangaea. Reconciliation of biogeographic evidence of great age with palaeodiversity demonstrated by Cretaceous (Brundin 1976, Kalugina 1980) and earlier (Evenhuis 1994) fossils suggests the evolutionary history of the Chironomidae already was well in place in the Mesozoic.

According to this scenario, wood mining may not have been a plesiotypic (ancestral) behaviour for Orthocladiinae + Chironominae as inferred above. Thus a wide spectrum of larval behaviours, from dwelling in the hygropetric zone to predatory, plus gouging of wood and shredding of leaves, was established by the dramatic end of the Cretaceous. A pre-existing wood-mining habit would have been an exaptation to a late Cretaceous / early Tertiary (K-T) world of 'greenhouse' climate — essentially allowing survival through the K-T event in an environmentally-buffered refugial habitat, namely immersed wood in streams and lakes. Furthermore, the severity of the environmental changes may have been distributed unevenly across the globe, with the southern hemisphere, and Australia in particular, serving as a refugial area, less impacted by the Chicxulub bolide collision (O'Keefe and Aherns 1989) and/or Deccan traps vulcanism (Caldeira and Ramino 1990). Such a model for such geographically-differentiated survival can be inferred from recent phylogenies of avian evolution by Cracraft (2001) and Barker and others (2004). Adding an ecological scenario of differential resistance to extinction between habitats to 'geographic resistance' provides a scenario to explain present-day patterns that appear worthy of further study.

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