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Thirty years of Hydroptilid Studies – 1979 to 2009[1]

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A b s t r a c t : A review of studies on microcaddisflies over the thirty years since publication by Jane Marshall of her detailed world review reveals the considerable involvement of Dr. Hans Malicky in taxonomy of the group. It also highlights some of the fascinating aspects of biology discovered for some species, and suggests that future emphasis on life history studies is likely to be rewarding.

K e y w o r d s : Trichoptera, Hydroptilidae.

In the 30 years since publication of Jane Marshall's review of the genera of the Trichoptera family Hydroptilidae considerable interest has been generated in the family. Now, far from the 46 valid genera and 616 species noted by Marshall, the extant world fauna as listed by Morse in 2009 numbers some 73 valid genera and around 2000 species. However, we still know little about the biology of many groups. This note reviews briefly knowledge of the group, and highlights some of the fascinating features of hydroptilid biology.

Hydroptilidae were grouped by MARSHALL (1979) with Rhyacophilidae and Glossosomatidae in the superfamily Rhyacophiloidea. More recently, the term Spicipalpia has been applied to the set of trichopteran families that make closed pupal cocoons, namely the three families above and the Hydrobiosidae, although it is apparent from molecular- and morphology-based phylogenetic analyses that this is a grouping of convenience rather than a monophyletic group (WIGGINS 2004; HOLZENTHAL et al. 2007). Marshall recognised two hydroptilid subfamilies, the Ptilocolepinae and Hydroptilinae, subsequently elevated by MALICKY (2001, 2005) and MORSE (2009) to full family status, with the Hydroptilinae tribes as subfamilies, and these are the arrangements followed in the online *Trichoptera World Checklist* (MORSE (2009). However, subfamily status was accepted by WIGGINS (2004) and more recently by HOLZENTHAL et al. (2007a) who based their decision on analyses of combined morphological and molecular data, and by HOLZENTHAL et al. (2007b) based on molecular data alone, both of which studies support monophyly of Ptilocolepinae+Hydroptilinae. Nonetheless, Xin Zhou (pers comm. 2010) advises that a study using COI sequences found considerable differences between 'Ptilocolepidae' and other Hydroptilidae, but Holzenthal (pers comm. 2010) notes that COI sequence data are inappropriate for asking questions about deep divergences. Thus, the controversy over the status of Ptilocolepinae is not yet settled.

MARSHALL (1979) was unable to assign six extant genera to subfamily. Among these, *Nothotrichia* FLINT, *Maydenoptila* NEBOISS and *Caledonotrichia* SYKORA were considered by HARRIS & ARMITAGE (1997) to belong to '…tribe Ochrotrichiinae'. However, *Nothotrichia* was grouped with *Ithytrichia* EATON and *Orthotrichia* EATON in Orthotrichiini by

[1] This paper is dedicated to Prof. Dr. Hans Malicky on the occasion of his 75th birthday.

HOLZENTHAL et al. (2007) who left *Caledonotrichia*, *Maydenoptila*, *Dibusa* ROSS and *Orphninotrichia* MOSELY unplaced to tribe, together with *Dicaminus* MUELLER and *Macrostactobia* SCHMID. Undoubtedly *Orphninotrichia*, an Australian endemic, is a member of the Hydroptilinae (WELLS 1987). As noted by HOLZENTHAL et al. (2007), a new review of relationships within the Hydroptilidae is apposite.

Numerous workers have contributed to our recent knowledge of species diversity in the Hydroptilidae. Major contributors, either alone or with colleagues: working primarily on the fauna of South-East Asia – Hans Malicky, Porntip Chantaramarangkol, Wolfram Mey, Jolanda Huisman and Alice Wells; on the Palaearctic fauna, Hans Malicky, Lazare Botosaneanu and Füsun Sipahiler; on the South and Central American fauna – Oliver Flint, Steve Harris and Ralph Holzenthal; on the African fauna – Marjorie Scott (deceased), François-Marie Gibon, Jostein Kjaerendsen, Trond Andersen and Alice Wells; and on the Australasian fauna – Alice Wells, Robert Kelley and John Ward. This work has certainly demonstrated that the family is richly diverse. Many of the species are described from one or few specimens, suggesting that often they are uncommon in the water bodies, and experience from Australia demonstrates that repeated collecting in the same areas still leads to discovery of further new species. But while species numbers are of interest, particularly for faunistic and biogeographic studies and for natural resource management, some of the very interesting studies are those on aspects of life history of hydroptilids.

A feature considered to be a defining attribute of hydroptilids is their larval hypermetamorphosis. Hydroptilinae larvae in their first four instars are very different from the final instar larvae, being free-living (caseless), tiny and often spidery in appearance; the fifth (final) instar larva does most of the feeding, accumulating reserves for pupation, adult life and egg production. Only the fifth instar larva builds a case, usually following the moult, and the mature larval case is modified subsequently when the pupal cocoon is developed.

In 1979 MARSHALL commented that it was not known if a hypermetamorphosis occurs in Ptilocolepinae. This has been clarified in biological studies of Ptilocolepinae published during the last 30 years by a number of workers, most notably Tomiko Ito, in Japan, and colleagues, describing early instar ptilocolepines as ‘campodeiform’, noting that final instar larvae are suberuciform, and describing how case building is initiated following the moult to the final larval instar. Thus, Ptilocolepinae undergo hypermetamorphosis, although the changes are not as pronounced as in some Hydroptilinae.

Studies on hydroptilid life histories reveal an extraordinary range in feeding and case-building behaviour, probably greater than in any other Trichoptera family.

Ptilocolepines are herbivorous, having close associations with particular liverwort species. Ito and colleagues have published detailed studies on the life histories of several ptilocolepine species. In Japan *Palaeagapetus ovatus* ITO & HATTORI feeds exclusively on a leafy liverwort, *Chiloscyphus polyanthos*, and builds its case using portions of the liverwort leaves (ITO 1997). Similarly in Belgium, *Ptilocolepus granulatus* (PICTET) was found to feed on this and another leafy liverwort species, *Scaptania undulata* (ITO & HIGLER 1992), and *Ptilocolepus extensus* MCLACHLAN in the Iberian Peninsula is reported to make ‘…dorsoventrally flattened, elongate-oval cases of leaf pieces from several moss and liverwort species’ (GONZÁLEZ et al. 2000). Furthermore, *Palaeagapetus fukuiensis* ITO and *P. finisorientis* ITO & VSHIVKOVA were observed to use *Chiloscyphus polyanthos* as food and building material. ITO & VSHIVKOVA (1999) reported that early instar larvae also feed on the liverwort.

Patterns in feeding behaviour are seldom evident among Hydroptilinae. Some genera appear to show specificities for food and case material. For example, feeding on filamentous green algae is common, but many species are scrapers, others predatory, several filter-feeding species are known and one group are parasitoids. Videofilm provided by KEIPER (2009) illustrates an early larva of *Ochrotrichia wojcickyi* BLICKLE feeding on epiphytic diatoms, a mode of feeding that also occurs in early larvae of species of *Hellyethira* and may occur commonly among early instar hydroptiline larvae.

Members of Hydroptilini genera such as *Agraylea, Hydroptila, Oxyethira, Paroxyethira* and *Hellyethira* are generally considered to be filamentous green alga feeders, feeding on species of *Spirogyra*, *Zygnema*, *Cladophora* and other genera; no clear evidence is available on specificities for particular algae. The cells of the alga are pierced and the contents sucked out. Some species of *Hydroptila* construct their cases from the algal filaments, generally arranged to lie neatly alongside each other, almost in concentric rings as the valves of the case are increased in size.

Scrapers are rare among Hydroptilini, but larvae of the Australian endemic genus *Orphninotrichia* scrape diatoms and other fine epilithic material as they move across the rock surface in the splash zone of waterfalls (WELLS 2002) or on rocks in riffles.

A most unusual example of fine particle feeding in a Hydroptilini genus, was described by MALICKY (1999) and LAUDEE (2008). Final instar larvae of the Giant Microcaddisfly, *Ugandatrichia maliwan* MALICKY & CHANTARAMONKOL, construct remarkable net-like domiciles on rocks on the face of waterfalls. These nets filter fine particulate matter from the water, and the larvae reach out to clear the material from the net. Another unusual feature reported for this genus is that the free living earlier instar larvae have been found to feed together with the fifth instar larvae in their nets, in an apparent obligate commensalism (MALICKY 1999: 201).

Scraper/grazers are the norm among Stactobiini, Leucotrichiini and Ochrotrichiini, although some of the latter group apparently feed on filamentous green algae. Many Stactobiini are found on rocks and cobbles in streams, in the splash zones on water falls, and in seepages and soaks; some Stactobiini and Leucotrichiini species fix their dome-shaped cases to the substratum and graze out around the case. Diatoms and other micro algae are probably their main food. However, at least several *Scelotrichia* species specialise on aquatic mosses, and in this respect resemble Ptilocolepinae. *Scelotrichia willcairnsi* CAIRNS & WELLS in north-eastern Australia feeds on, and constructs its cases from, the aquatic moss *Platyhypnidium muelleri*, and several other species in New Guinea make their cases of aquatic moss (WELLS 1990), and probably also feed on the moss.

In the tribe Orthotrichiini, members of the genus *Orthotrichia* exhibit a variety of feeding behaviours. Traditionally *Orthotrichia* is described as an algae-feeding group, and certainly it is known to feed on filamentous green algae (KEIPER 2002) and also on diatoms. *Orthotrichia* larvae were reported to feed on *Simulium* larvae by BURTON & MCRAE (1972) and DISNEY (1973), and unidentified *Orthotrichia* larvae have been observed to feed on eggs of other insects (WELLS 1985). At least two, and probably all, members of a distinctive group of *Orthotrichia* species, designated the '*aberrans*-group' are parasitoid on other Trichoptera species (WELLS 1992, 2005). Their strangely physogastric mature final instar larvae and the earlier dorso-ventrally flattened larva and case puzzled workers for many years. This group has what appears to be an additional larval stage following the final larval moult. Larvae at this stage can be collected with fine mesh kick nets and are encased between a pair of tiny, unequal-sized, almost flat valves. The larvae are next found inside the pupal cases of hydropsychids. WELLS (1992) suggested that the small very strongly dorso-ventrally flattened larva becomes entrapped in the feeding net of the hydropsychid larva, and somehow becomes incorporated in its pupal case. At this stage, the flat valves are either discarded, or incorporated into a thin tubular silk case more closely resembling the normal *Orthotrichia* case. In this, the moribund larva expands as it grows to extraordinary proportions, feeding on its pupal host.

Members of two of the Hydroptilinae genera that are unplaced to tribe specialise on red algae. A detailed account, published by RESH & HOUP (1986) on the North American *Dibusa angata* ROSS, describes how that species makes its cases from and feeds on only two species of the freshwater red alga *Lemanea* (Rhodophyta: Batrachospermales). Similar behaviour was described for final instar larvae of the Australian endemic, *Maydenoptila cuneola* NEBOISS, which feeds and makes its cases from another species red alga in the same order, *Batrachospermum*. Could this be in some way indicative of a relationship between *Dibusa* and *Maydenoptila*? Another species in *Maydenoptila* feeds on a filamentous diatom, *Melosira* sp., and has a univoltine life cycle (WELLS 1985) very similar to that of *Dibusa angata*.

Much is yet to be discovered about larval behaviour in Hydroptilidae. So, too, much is unknown about behaviour of adults in this family, probably due to their small size and often very low numbers. Experience of the author in South-east Asia, New Guinea and north-eastern Australia is that many Stactobiini species are diurnal. During sunshine, often a number of these tiny black caddisflies are seen running about frenetically on the dry exposed surface of one or a few rocks in a stretch of stream; they generally run back and forth, fly off, then return to run around again (Wells unpublished observations). This behaviour can sometimes be observed, too, on particular riparian shrubs. Adults swept or collected by 'dabbing' with a finger tip wetted by alcohol from these gatherings usually are mostly males. Thus, it is likely that the males are displaying lek behaviour. Similar behaviour has been observed in species of *Orphninotrichia*, a Hydroptilini genus (WELLS 2002).

In South-east Asia and Australia, few Hydroptilini are ever taken by sweep-netting, although large numbers are often collected at lights. On one occasion in New Caledonia a swarm of *Hydroptila losida* MOSELY & KIMMINS was observed at dusk, ascending and descending beside a river. These were also mostly males, so again this could have been lek behaviour. Such behaviour in small insects could result in freak dispersal by winds, the swarm being caught up by a gust and transported in the aerial plankton. Considerable numbers of stactobiine microcaddisflies were sorted from canopy-fogging samples taken in rainforest in North Sulawesi in 1985, high in the trees some considerable distance from the nearest stream. It seemed unlikely that such small insects could have flown over the distance and into the tops of high trees. Possibly some kind of aggregation behaviour resulted in their being caught up in air currents. This may explain some of the anomalous distributions observed in the group.

HOLZENTHAL et al. (2007: 669) summarised the distributions within the family. Three major groups, Leucotrichiini, Neotrichiini and Ochrotrichiini, are restricted largely to the Neotropics. Hydroptilini are 'primarily Old World in distribution', and Orthotrichiini are cosmopolitan. Stactobiini, although worldwide, are best represented in Old World regions, and have only limited representation in the tropics in eastern Australia (two species), and are unknown further to the east in the Australian Region. With the exception of one species described from Thailand by MALICKY & CHANTARAMANGKOL (1996), and another described by SCHMID (1990) from Assam, Ptilocolepinae are known from the Holarctic.

Several of the most diverse genera are very widespread. *Oxyethira* is cosmopolitan, being found everywhere but the poles. *Hydroptila* and *Orthotrichia* are also widespread, although less so than *Oxyethira* – both are absent from New Zealand. However, at generic level most Hydroptilidae display high levels of endemism and endemism is even higher at species level.

Taking the Oriental-Australian Regions as examples, a number of species are widespread. Several species of *Oxyethira* have been found from northern Australia through New Guinea, Indonesia, the Philippines and as far as West Malaysia. *Hydroptila losida* and *H. incertula* MOSELY are similarly widely distributed; the former is also found in New Caledonia. Behaviour may be the key to their wide distributions. Often more curious than these broad ranges, are real or apparent absences, and again, the answers probably lie in behaviour of the species or group. For example, why is the hydroptilid fauna of New Zealand represented by only two genera? If, as suggested by WELLS (1995), species such as *Hydroptila losida* and *Hellyethira malleoforma* WELLS reached New Caledonia either in aerial plankton or as tramps, why are they absent from New Zealand to which some eastern Australian insects are blown from time to time (TOMLINSON 1973), including some as small as aphids?

More widely, a highly anomalous disjunct distribution is that of the genus *Jabitrichia* WELLS. This genus currently comprises four almost indistinguishable species, from three different continents. The nominate species, *J. dostinei* WELLS was described from the north of the Northern Territory of Australia (WELLS 1990), and is now known to occur also on Cape York in north-eastern Queensland. *Jabitrichia wellsae* O'CONNOR & ASHE was described from West Malaysia (O'CONNOR & ASHE 1992); *J. voltensis* KJAERENSEN & ANDERSEN was described from East Africa (KJAERENSEN & ANDERSEN 2002); and *J. flagellata* (MARLIÉR) from Angola (MARLIÉR 1965). The habitats at the type localities, known only for the first two species, appear to be very similar – large lentic systems with abundant emergent macrophytes.

In summary, we have learned much about the Hydroptilidae over the last 30 years, but they are still a group in which rich discoveries can be made, especially by exploration of life histories and behaviour.

Zusammenfassung

Die Übersicht über die Hydroptiliden-Untersuchungen der dreißig Jahre seit der Publikation von Jane Marshall zeigt eine beträchtliche Beteiligung von Hans Malicky an der Taxonomie der Gruppe. Auch einige faszinierende Aspekte der Biologie mancher Arten wurden gefunden und lassen weitere lohnende Entdeckungen auf diesem Gebiet erwarten.

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