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Curious Caddis Couture: Form and function among cases of Australian Hydroptilidae

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Abstract

Trichoptera larvae that construct portable cases occur worldwide, in some groups building highly distinctive cases. Fifth instar larvae of several genera in the micro-caddisfly family Hydroptilidae always build cases of the same form, thus affording ready identification of their larvae and pupae to genus level. Examples are *Oxyethira* and *Orthotrichia*: the former have transparent flask-shaped silk (secretion) cases, the latter 'wheat seed'-shaped silk cases that are generally dark brown to black in colour. Additionally, in the fauna of mainland Australia, cases of the endemic genus *Orphninotrichia* are unmistakable in form; enigmatically, however, quite different forms are seen in two of the four locally endemic species on the small, off-shore, oceanic island of Lord Howe. The larval cases of some other Australian genera also vary considerably, some in materials (e.g., *Hydroptila*) and others in both materials and shape (e.g., *Hellyethira* and an Australian endemic genus, *Maydenoptila*). Known larvae of microcaddisfly species in the Australian fauna are examined in search of patterns in the three most obviously variable attributes of cases: mode of construction, shape, and materials. Possible relationships between form and function are postulated for some of the cases.

INTRODUCTION

The micro-caddisflies, family Hydroptilidae, are often grouped with Rhyacophilidae, Hydrobiosidae and Glossosomatidae as cocoon-makers (Spicipalpia) (Wiggins 2004). However, more recent combined molecular-morphological-based phylogenetic analyses place them closer to the portable tube-case makers, the Integripalpia (Holzenthal *et al.* 2007). The group has always presented a puzzle with their curious hypermetamorphosis in which, for the first four brief, free-living instars, the larvae scarcely feed; and only the final (i.e., the fifth) instar larvae develop a protective case that they increase in size as they feed and grow.

Many of the hydroptilid larvae develop portable cases, most of which are 'bi-valved' purse- or envelope-shaped—few are of the 'tube' case shape seen in many of the other families of portable case makers. In some groups the larval case is fixed to the substrate and the larva feeds by grazing around the fixed case; the case is attached to the substrate and sealed prior to pupation. This paper takes a look at the nature of cases among hydroptilid genera in Australia, particularly at three attributes of the cases: their mode of construction, materials, and shapes. Questions asked are as follows: In what way do their forms reflect adaptations to the niches occupied by the species? Did some of the variations arise simply as 'frivolous' consequence of the plasticity of the genotype [i.e., phenotypic variation exposed to unusual environmental conditions and subsequently fixed (Moczek *et al.* 2011)]? To what extent is form in some groups 'hard-wired'?

ATTRIBUTES OF CASES

Mode of construction of cases

Among Trichoptera in general, most portable larval cases are initiated with a short tube or other shape, starting at what usually becomes the distal end, and lengthening as the larva grows, often with an increase in internal diameter. In some groups, such as some leptocerid and calamoceratid genera, the growing larva replaces its case with progressively larger ones. In some species, as the larva matures it clips off the narrower end. Hy-

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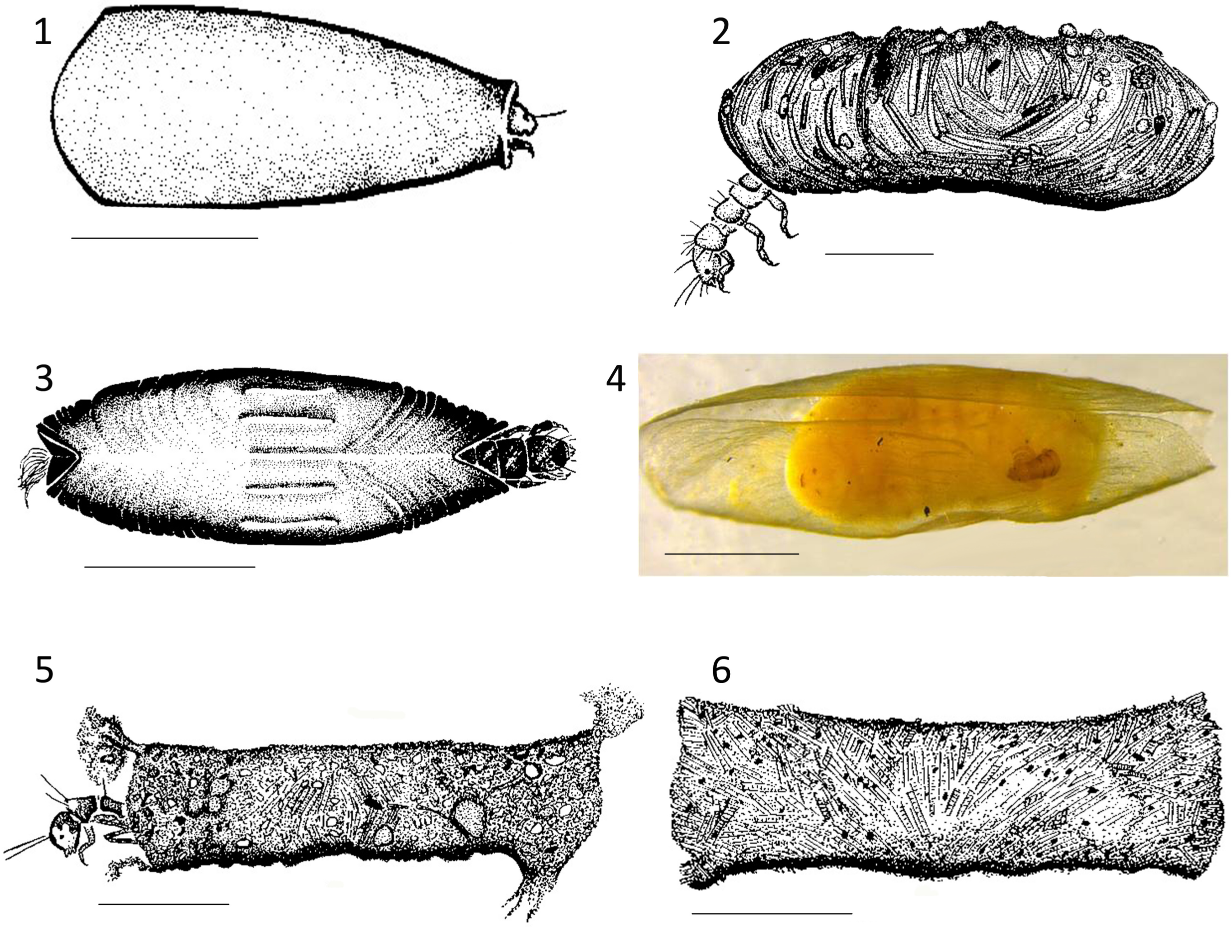
droptilids appear always to enlarge the capacity of the case, rarely to discard the case and build a new one; discarding of a case would expose the larva to risk of predation.

The steps involved in case building by representatives of five hydroptilid genera were described in considerable detail by Nielsen (1948)—for *Oxyethira, Hydroptila, Agraylea, Orthotrichia*, and *Ithytrichia*. He illustrated early stages of the cases of all five, finding that they began with a starting ring of silk developed either around a clump of detritus or around algal filaments. Wiggins (2004) postulated that basically the hydroptilid case is developed from a dome. However, even the fixed dome-shaped cases are constructed with two parts, an upper dome-shaped 'roof' and a lower base or 'floor', suggesting that a better interpretation may be that the basic case structure is of two 'valves', usually equal in size, but unequal in fixed-abode cases (see Holzenthal *et al.* 2007).

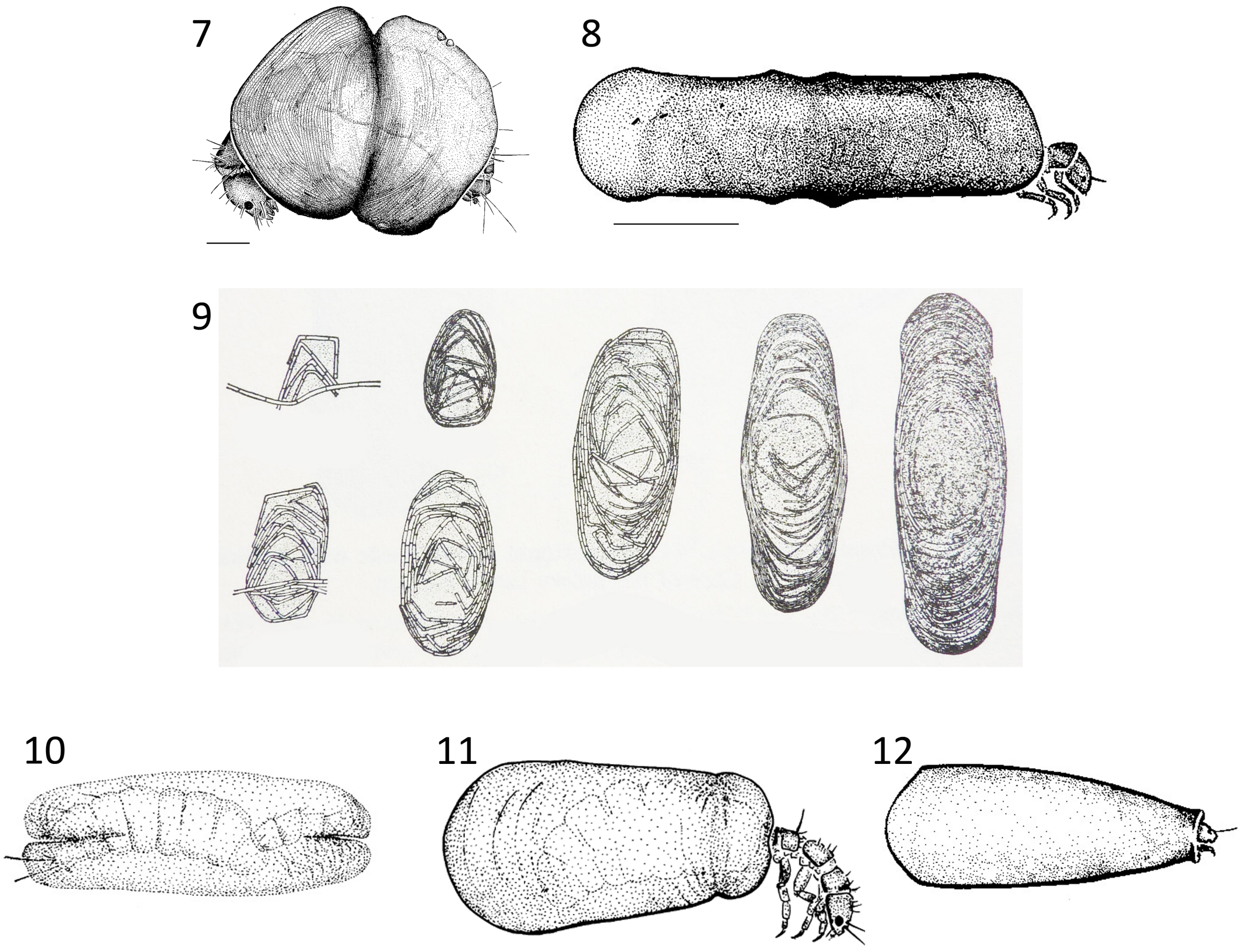
Cases of all hydroptilid genera that occur in Australia can be interpreted as a 'purse' built of two equal valves. The actual engineering involved in construction often differs between genera, rarely within genera. Within genera such as *Oxyethira*, *Hydroptila*, and *Orthotrichia* the process appears to be strongly conserved. In *Oxyethira*, starting from the 'anterior' ring of silk, the larva lengthens and widens equally each of the laterally flattened sides on the 'posterior' end only (Fig. 1); this averts the need to open the long sides, thus avoiding risky exposure of the larva. In *Hydroptila* (Fig. 2) and *Orthotrichia* (Fig. 3), growth of each valve, effected equally, involves additions made in more or less semicircular bands around a small starting 'platform' or 'plate'; this mode of construction must involve opening of one long side as seen in the rather flimsy case of *Orthotrichia muscari* Wells 1983 (a parasitic species) (Fig. 4).



FIGURES 1–6. Larval cases of Australian species of Hydroptilidae. 1, *Oxyethira columba* (Neboiss 1977), silken, flask-shaped, bivalved case; 2, *Hydroptila robusta* Wells 1979a, purse-shaped and composed of algal filaments; 3, *Orthotrichia bishopi* Wells 1979c, comprises two silken valves, dorso-ventrally flattened; 4, *Orthotrichia muscari* Wells 1983, a parasitoid species with thin, transparent bivalved case, open along ventral seam; 5–6, *Hellyethira ramosa* Wells 1983 and *H. vernoni* Wells 1983, bivalved cases incorporating sand grains and diatoms. Scale bars = 1 mm. [Figs 1–3, 5–6, after Wells 1985]

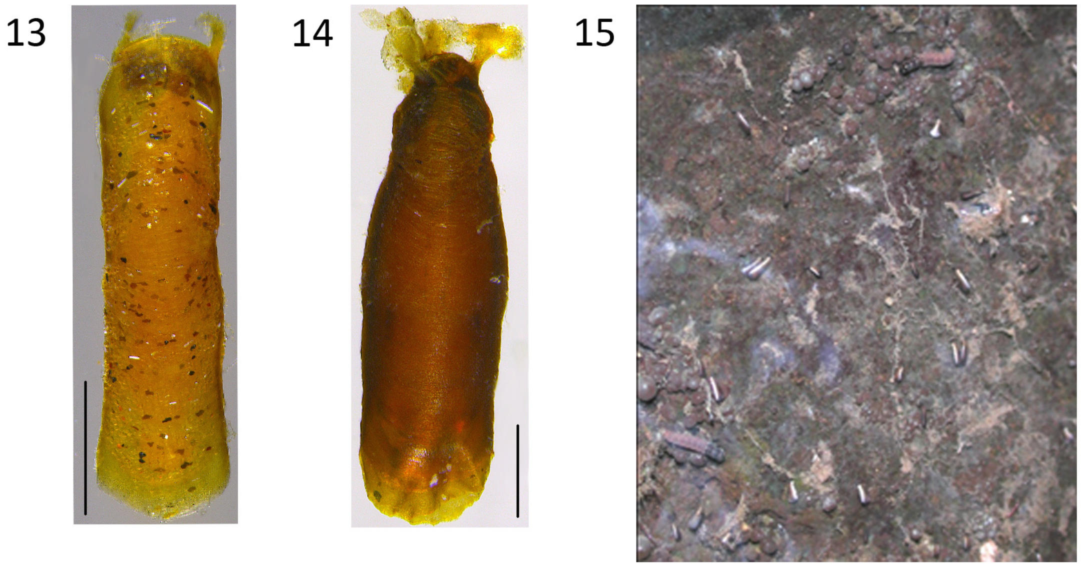
In other genera, for example, *Hellyethira*, the basic mode of case building is probably similarly conserved (Figs 5–6), the cases being developed developed from a pair of small starting plates and built out from them. However, in the cases of at least some species of *Hellyethira*, the lines of interwoven sand or diatoms appear to radiate from the starting plates (Fig. 6), rather than being added in semicircular bands.

In contrast, in larval cases of the 16 mainland species of *Orphninotrichia*, an Australian endemic genus, each valve is consistently developed symmetrically as apparent in Figs 7–8, from an early maximum width. Species of *Agraylea*, as illustrated by Nielsen (1948), show similarity to those of mainland *Orphninotrichia* in that symmetry is maintained throughout development of the case, but the two differ. In *Agraylea* (Fig. 9), as the larva matures, it increases case width as well as length. Prior to pupation, cases of *Orphninotrichia* are usually attached at each corner of one end, or at both ends (Fig. 13); they can sometimes be seen hanging downward on a rocky cascade or waterfall.

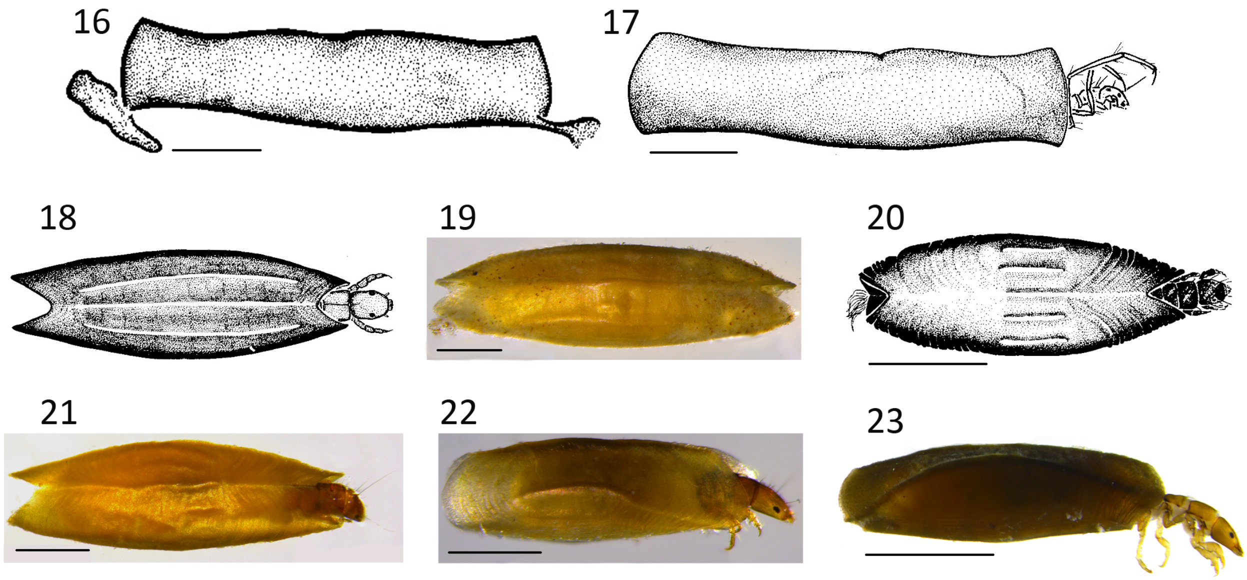


FIGURES 7–12. Larval cases of Australian species of Hydroptilidae. 7–9, stages in case construction: 7–8, early and mature larval cases of mainland Australian *Orphninotrichia*; 9, progression from several woven algal threads to mature case in an *Agraylea* species. 10–11, atypical case forms of species of *Orphninotrichia* from Lord Howe Island: 10, *O. squamosa* Wells 1999; 11, *O. rugosa* Wells 1999. 12, *Oxyethira* case (*Oxyethira* cases show close similarities to those of *Orphninotrichia rugosa*, but *O. rugosa* cases are extended for short distance at the anterior end). Scale bars: Fig. 7 = 0.2 mm; Fig. 8 = 1 mm. [Figs 1, 8, 12 after Wells (1985); Fig. 9, after Nielsen (1948); Figs 10, 11, after Wells (1999)]

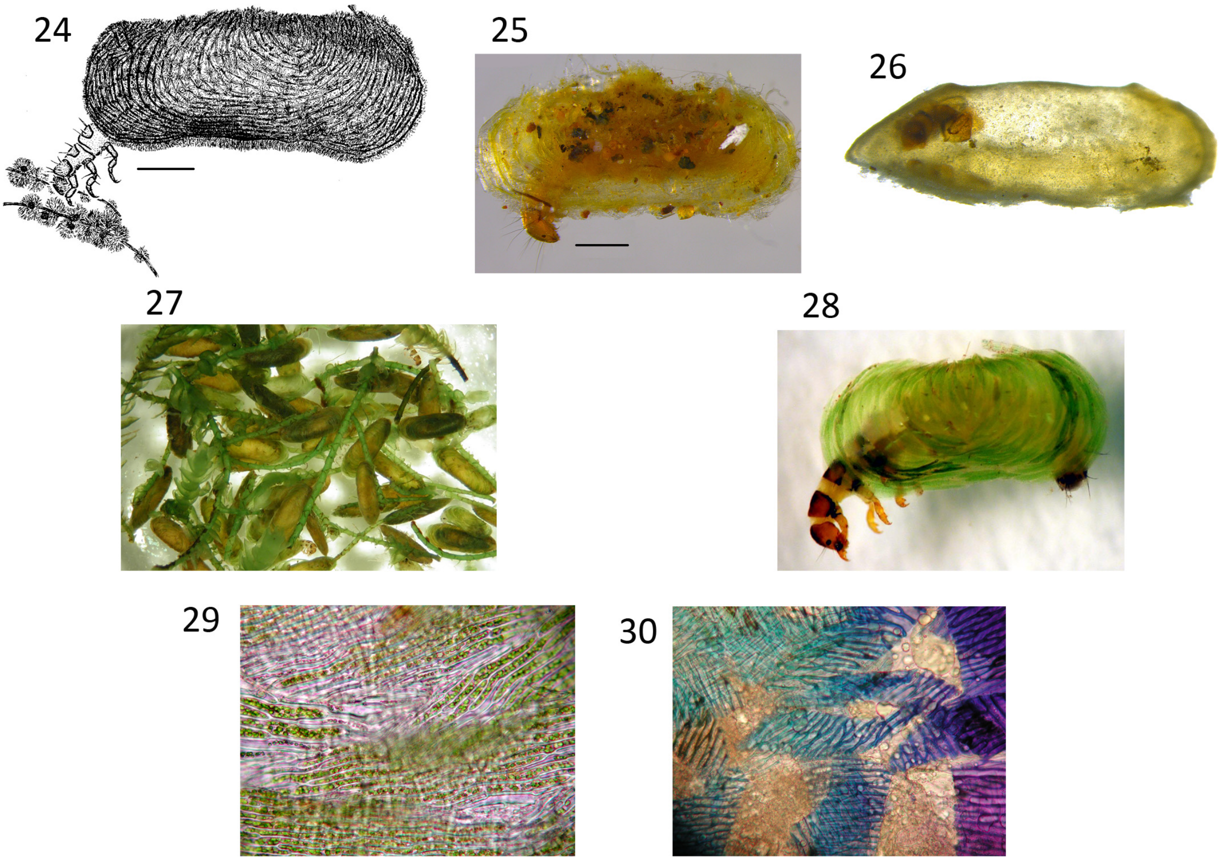
In addition to the mainland species, *Orphninotrichia* species are found in the streams of the tiny off-shore island of Lord Howe (area about 16 km^2), a rocky remnant of the wall of a volcanic crater about 600 km off the Australian mainland. The three small, very short, permanent streams that occur on the island support at least eight endemic Trichoptera species (Wells 2011), among them four hydroptilid species, all in *Orphninotrichia* (Wells 1999). Two of these species have highly aberrant cases: One resembles a tatting (lace-making) shuttle, being elongate-ovoid with a median slit at each end of each valve (Fig. 10), while the other (Fig. 11) is closely similar to the case of *Oxyethira* species (Fig. 12). However, in contrast to the cases of *Oxyethira* species, this *Orphninotrichia* case (Figs 14–15) is built with a small extension at the ‘anterior’ end of the case and the opening is not so tightly constricted as in *Oxyethira*; mostly the case is increased in length and width posteriorly. Prior to pupation, the case is attached to the substrate at the anterior end (Fig. 14), usually to hang downward on the sloping rocky face of the stream base (Fig. 15).



FIGURES 13–15. Pupal and larval cases of Australian species of *Orphninotrichia* (Hydroptilidae). 13–14, pupal cases of *Orphninotrichia* species: 13, *O. maculata* Mosely 1934; 14, *O. rugosa* Wells 1999. 15, larvae of *O. rugosa* grazing on epilithos on the face of a short fall on Erskine Creek, Lord Howe Island. Scale bars = 1 mm. [Fig. 15 after Wells 2011]



FIGURES 16–23. Silk cases of larvae and pupae of Australian species of *Hellyethira* and *Orthotrichia* (Hydroptilidae). 16–17, *Hellyethira* species: 16, pupal case of *H. litua* Wells 1979b; 17, larval case of *H. malleoforma* Wells 1979b. 18–23, larval cases of *Orthotrichia* spp.: 18, *O. bishopi* Wells 1979c; 19, *O. alata* Wells 1990a; 20 *O. tortuosa* Wells 1979c; 21, *O. amnica* Wells 1990a; 22–23, *Orthotrichia* unidentified species.



FIGURES 24–30. Cases and case materials of larvae and pupae of Australian species of Hydroptilidae. 24–26, Larval cases of *Maydenoptila* species: 24, *M. cuneola* Neboiss 1977 (built with strands of the red alga *Batrachospermum*); 25, *M. baynesi* Wells 1983 (built with threads of chain diatoms); 26, *M. pseudorupina* Wells 1980 (built of silk only). 27–30, Cases and case materials of *Pseudoxyethira willcairnsi* (Cairns & Wells 2008): 27, larval and pupal cases (among the aquatic moss of which they construct their cases and on which the larvae feed); 28, larval case (built of segments of moss microphylls); 29, portion of wall of case showing alignment of microphyll cells; 30, gut contents showing transverse cuts on moss microphylls.

Lord Howe Island is estimated to have erupted about 6.9 Mya (McDougall *et al.* 1981), so it seems most probable that the streams were colonised by dispersal from mainland Australia, or possibly New Zealand (but the genus is not recorded from the latter). Why the distinctive cases? Presumably they evolved after the coloniser arrived on the island. Given the paucity of flowing freshwater on the island and the proximity of the small streams, could they have evolved in sympatry? All four of the island's *Orphninotrichia* species were collected at the same site in one short stream on Mt Gower at approximately 270 m (the summit of Mt Gower reaches the highest point on the island at 875 m); and one of the species was collected from this site only.

Lord Howe Island supports some 242 plant species and these exhibit a very high level of endemism—90 plant species are endemic to the island. In a study on a subset of these, selected as groups for which at least one pair of endemic sister species could be identified on the island, Papadopulos *et al.* (2011) analysed phylogenetic, karyological, and ecological data. They demonstrated 11 possible examples of species that have radiated with gene flow on the island. For these they postulated that speciation occurred in sympatry.

These island *Orphninotrichia* species share several attributes of the groups of plant species, having relatives on mainland Australia (or for a few of the plant species, Norfolk Island or New Zealand) and having poor dispersal ability. Hence it seems very likely that, following colonisation from mainland Australia, the species did diverge sympatrically. Studies by Pfennig *et al.* (2010) and Moczek *et al.* (2011) explored mechanisms by which phenotypic variations can become fixed in sympatric populations (populations with gene flow), eventually leading to speciation. This has been shown to be the evolutionary pathway for the two species of the endemic palm genus *Howea*, brought about by differences in flowering times on acidic and basic soils at low and higher altitudes (Savolainen *et al.* 2006; Dunning *et al.* 2016).

Case materials

The core of all hydroptilid cases is silk secretion, extruded in strands by the larva. Some cases are constructed of nothing but silk, in others the silk secretion is interwoven with organic or inorganic materials, the silk holding them in place. Among Australian species, 'silk-only' cases include those of *Tricholeiochiton* species—slim, rectangular, strongly laterally flattened 'envelopes' (Fig. 16) that could be expected to slip easily between algal filaments and could also be drawn easily among the macrophytes of lakes and slow waters.

Cases of some of the species of *Hellyethira* are almost identical with those of *Tricholeiochiton* [e.g., *H. malleoforma* Wells 1979b (Fig. 17), *H. litua* Wells 1979b (Fig. 16), and *H. simplex* (Mosely 1934) (Fig. 32)]. Other 'silk-only' cases of some species of *Hellyethira* differ in shape (see next section).

Cases of *Orthotrichia* species are always constructed of silk only, often brown to black in colour (Figs 18–23). In Australia, larvae and pupae of *Orthotrichia* are almost always found beneath rocks and cobbles, occasionally in crevices or other irregularities on the surface of rocks.

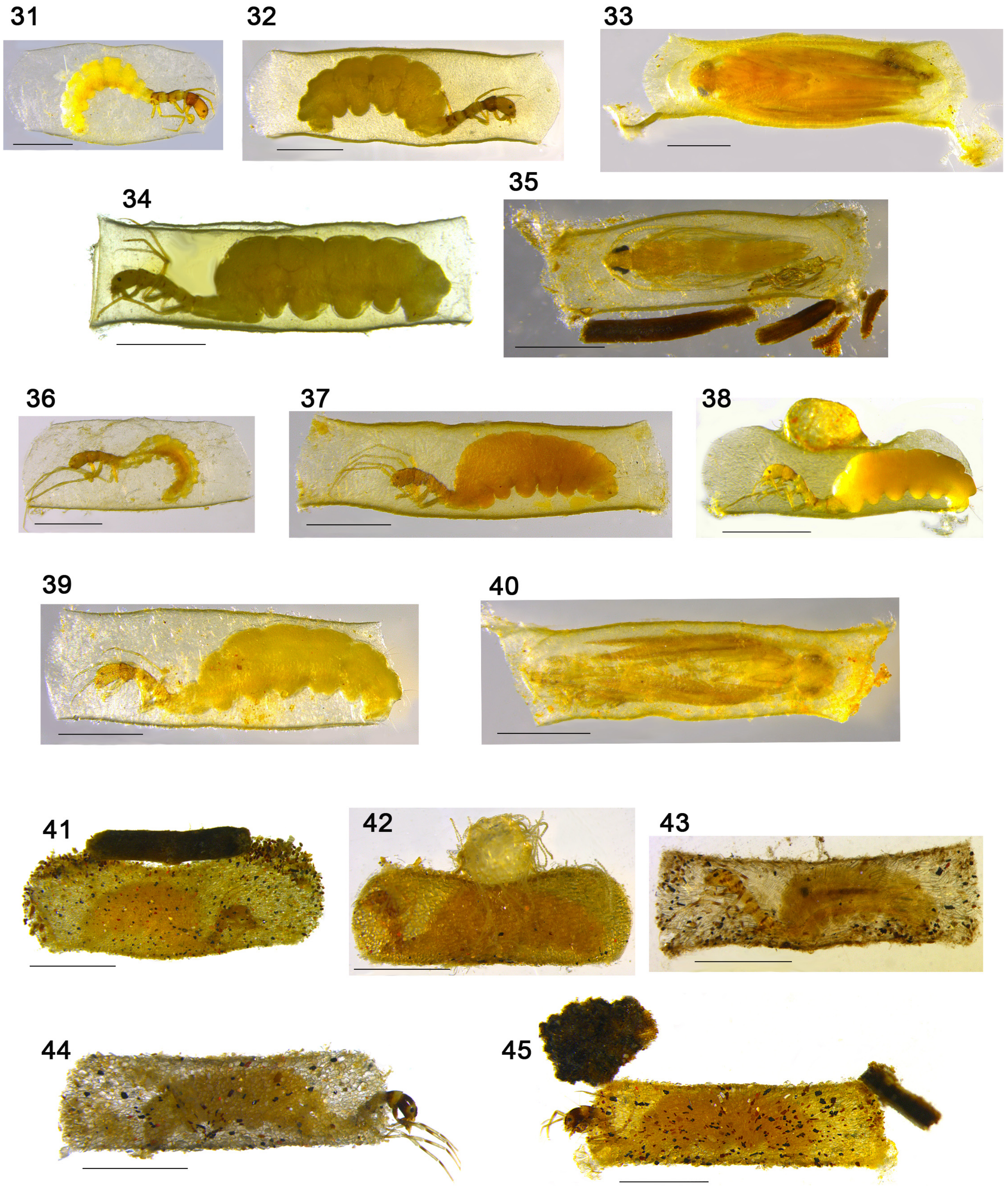
The very dark-coloured *Orthotrichia* cases are difficult to open and are much tougher than the paler, sometimes thinner, more transparent cases seen in some other congeners, including some of the parasitoid *Orthotrichia* species that build their thin, smooth bivalved cases (Fig. 4) when the final instar larva is inside the case of its host pupa (another caddisfly species).

The silk used in caddisfly larval cases is believed to be homologous with that of moth larvae. Lepidoptera silk comprises molecules of fibroin and a 'glue', serinin, occurring in varying arrangements and affording the silk cocoons of moths differing combinations of mechanical strength and gas permeability (Chen *et al.* 2012); these can be correlated with environmental conditions. A similar situation probably holds for the cases of *Orthotrichia*—the silk of the tough dark cases probably containing higher proportions of serinin. Such cases occur in species that live in fast-flowing waters—cases that may be subjected to abrasion or compression from dislodged stones or abraded by mobile sediments. *Orthotrichia* prepupae usually extend one end of the larval case, then attach it to a firm substrate (usually rock); sometimes the case is also attached at the other end.

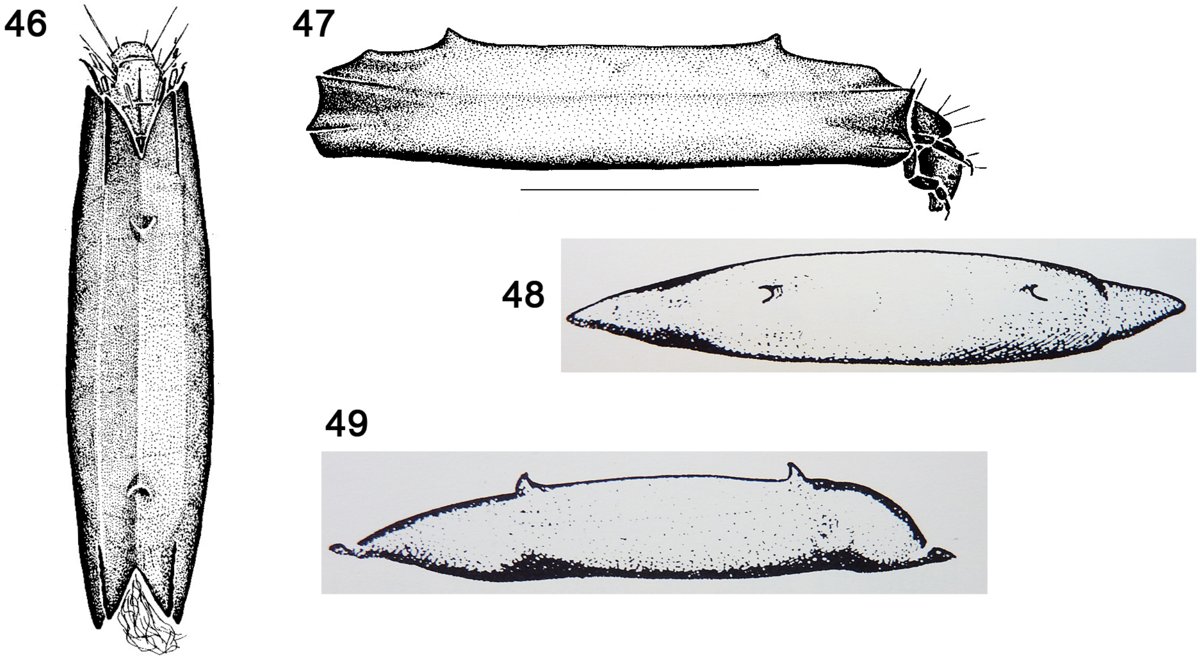
While, as mentioned above, many species of *Hellyethira* construct envelopes of silk only (Figs 31–40), others accrete sand grains, diatoms and fragments of detritus to their cases (see Figs 41–45). This could provide ballast and/or camouflage, making it less likely that the cased larvae will be dislodged or detected by a predator. The cases of *Hydroptila* species, are always built of silk plus some other material such as sand grains, sometimes with particles of detritus, again possibly affording protection or ballast—the sand grain cases are found in species that live in faster-flowing waters, living on or among the sandy sediment. Cases of some other *Hydroptila* species incorporate filamentous green algae or diatoms and are usually found in species living in slower or lentic waters among filamentous green algae—they probably also feed on the algae.

A close association between larval food and case material can be seen in several species in the Australian endemic genus *Maydenoptila*, but other *Maydenoptila* species have sand grain cases and one is known that has a 'silk-only' case. *Maydenoptila cuneola* Neboiss 1977 (Fig. 24) lives among, feeds on, and constructs its case of strands of a freshwater red alga (genus *Batrachospermum*), and another (*Maydenoptila baynesi* Wells 1983) incorporates in its case some strands of the chain diatoms on which it feeds (Fig. 25). *Maydenoptila pseudorupina* Wells 1980 has an unadorned silk case (Fig. 26)—one wonders what it feeds on!

Only one species of *Pseudoxyethira* (junior synonym *Scelotrichia*) is known to occur in Australia, discovered living amongst a rare aquatic moss beneath a waterfall in north-eastern Queensland. Its use of the moss plant as habitat, food, and building material (Figs 27–30) was described and illustrated by Cairns and Wells (2008), highlighting particularly the difference in the cuts of leaf used for building and for food—fragments of microphyll ('leaf') lamina (Fig. 29) or cross-sections (Fig. 30), respectively. Other similar *Pseudoxyethira* cases are known from New Guinea (even one of entire tiny moss microphylls), but nothing is known of their larval feeding biology.



FIGURES 31–45. Larval and pupal cases of Australian species of *Hellyethira* (Hydroptilidae). 31–40, Silk larval and pupal cases: 31–33, *H. simplex* (Mosely 1934), early larval case, well-developed larval case, and pupal case; 34, *H. multilobata* Wells 1979b, larval case; 35, *H. kukensis* Wells 1991, pupal case; 36–37, *H. litua* Wells 1979b, early and well-developed larval cases; 38, *H. cubitans* Wells 1979b, larval case; 39–40, *H. malleoforma* Wells 1979b, larval and pupal cases. 41–45, sand grain larval cases: 41, *H. basilobata* Wells 1979b; 42, *H. forficata* Wells 1990a, 43, *H. dentata* Wells 1979b; 44, *H. cornuta* Wells 1979b; 45, *H. vernoni* Wells 1983.



FIGURES 46–49. Larval cases of Australian species of *Orthotrichia* (Hydroptilidae) with dorsal vents: 46–47, *O. turrita* Wells 1979c; 48–49, O. *tyleri* Wells 1979c.

Case shapes

Case shape is invariant among species in some genera. Profiles of cases of species of *Oxyethira* (Figs 1, 12) and mainland Australian *Orphninotrichia* (Fig. 8) are always recognisable. Are case attributes 'hard-wired' as in *Oxyethira*? For mainland *Orphninotrichia* species, I suggest that it is probably a developmental constraint that maintains case form, since on Lord Howe Island, the two different case forms occur (see above).

In contrast, case shape appears to be quite plastic in species of *Hellyethira* as illustrated in Figs 31–44. Similar shapes are seen among cases that comprise silk only and others with sand and/or detritus accreted. The combination of distinctive shape and materials renders some of these cases instantly identifiable to species. One can only speculate on the significance of these morphologies. The concave upper margin of several species, often with a sand grain adhered, may reflect the way in which early case development occurs in those species. Or does it reflect some close adaptation to specialised behaviour or to a niche? For example, sometimes a case with a dorsal margin excavation has a sand grain secured in the concavity (Figs 38, 42), others have a small piece of wood (Fig. 41).

Many *Orthotrichia* species build cases that are partially or more extensively ribbed dorsally (Wells 1985). These ribs, seen dorsally on many *Orthotrichia* cases (e.g., Figs 18–23), would reinforce the case, in much the way corrugations strengthen roofing iron used in house construction. A further variation seen in two species of *Orthotrichia* is a pair of unusual 'vents' on the dorsal edges of their cases (Figs 46–49). Both of these species are found in the far north of Australia where their adults can be collected beside slow-flowing to still waters of streams or macrophyte-rich billabongs. The shallow waters of the billabongs and residual pools in the streams may well have low oxygen levels much of the time, and the vents, each bracketed by a small flap, may be involved in circulation of water in the case (i.e., aid in larval respiration).

CONCLUSIONS

Wiggins entitled his review of family-level morphology of adult and larval caddisflies 'Caddisflies, the Underwater Architects' (Wiggins 2007). However, this brief discussion of case form in Australian microcaddisflies indicates that they are more than just brilliant architects, they are highly skilled 'designers' as well. The present study focuses narrowly on Australian Hydroptilidae, a fauna dominated by members of the subfamilies Hydroptilinae and Orthotrichinae, with their final stage larval cases always constructed of paired equal valves. In contrast, Stactobiinae, Leucotrichiinae, and Ochrotrichiinae (the first of these diverse in New Guinea and across south-east Asia, the other two subfamilies highly speciose in the Neotropics) sometimes exhibit greatly varied case forms within genera, some bivalved, others domed, and some 'cigar-shaped' (for Stactobiinae see Wells 1989, 1990b; Wells & Huisman 1993; Ito & Saito 2016; Ito 2017, and for Ochrotrichiinae and Leucotrichiinae see Marshall 1979; Santos *et al.* 2016). Larvae of the New Caledonian endemic genus *Caledonotrichia*, now referred together with *Maydenoptila* and several Neotropical genera previously unplaced to Ochrotrichiinae (Oláh & Johanson 2011)*,* build some remarkable cases (Wells 1995), again some having fixed dome-shaped cases, some with dorsal vents resembling those seen in the two Australian species of *Orthotrichia*.

The current study suggests that detailed studies of hydroptilid larval case form, particularly with associated ecological and molecular studies, could elucidate evolutionary pathways in the family. Such studies could usefully start with the two major radiations in Australian Hydroptilidae: *Orthotrichia*, currently with 55 and *Hellyethira* with 29 described species (ABRS 2018), or the Stactobiinae of Southeast Asia (around 100 described species), among which *Pseudoxyethira* species number some 27 (Malicky 2010) and include species with rather unusual cases.

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