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# Egg masses of some stream-dwelling caddisflies (Hydrobiosidae, Trichoptera) from Victoria, Australia

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**Running Title**
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## Abstract

Eggs are a largely neglected life stage in most ecological studies of aquatic insects, despite the importance of oviposition behaviour and fecundity estimates for many research questions. Incorporating egg stages into ecological research requires that ecologists can identify and quantify eggs, but descriptions of eggs and egg masses are scarce for many groups and particularly for Australian taxa. This paper focusses on stream-dwelling caddisflies in the family Hydrobiosidae and provides species-level identifications, morphological descriptions and images of egg masses of some species that commonly occur in south-eastern Australia. All the species we identified laid plaque-shaped egg masses attached to the underside of river rocks that protrude above the water surface. These egg masses can be identified in the field with the naked eye or the aid of a low-magnification hand lens. Interspecific variations in egg mass morphology were primarily thickness and firmness of the spumaline layer, egg mass size and arrangement of eggs within the mass. We also provide some ecological information on clutch sizes and the physical characteristics of oviposition sites, and we discuss various ways in which these taxa could be exploited as model systems for ecological research.

**Key words**
aquatic insect, clutch size, ecology, oviposition

## INTRODUCTION

An important challenge in modern ecology is to understand the processes that influence patterns of dispersal and recruitment, within and between populations and communities. This can be particularly challenging for species with complex life cycles, such as aquatic insects, where different life stages occupy different habitats. Traditionally, freshwater ecological research has focussed on the aquatic juvenile stages and predominantly late instar larvae, but estimating the factors that drive population dynamics requires examination of multiple life stages, including the often-neglected stages of eggs, pupae and adults. For example, terrestrial adults of aquatic insects are important vectors for the colonisation of new habitats and for maintaining connectivity of populations in different locations (Hughes *et al.* 2008; Hughes *et al.* 2009), yet there is very little information on even the most basic life history traits for adults of most aquatic insect species. Pupae are rarely considered by freshwater ecologists but high, density-dependent mortality of pupae can regulate some populations (Marchant & Hehir 1999). Eggs are also a largely neglected life stage, but a growing number of ecological studies in running waters is integrating information on the eggs and oviposition characteristics of aquatic insects into research on population dynamics (Willis & Hendricks 1992; Peckarsky *et al.* 2000; Hildrew *et al.* 2004; Lancaster *et al.* 2010a; Encalada & Peckarsky 2011; Lancaster *et al.* 2011; Encalada & Peckarsky 2012). The success of such studies, however, depends on understanding the environmental factors that influence oviposition behaviours, and hence the spatial and temporal distribution of eggs within water bodies (Hoffmann & Resh 2003; Lancaster *et al.* 2003; Reich & Downes 2003a, 2003b; Encalada & Peckarsky 2007; Lancaster *et al.* 2010b; Reich *et al.* 2011; Storey *et al.* 2016), and on understanding the factors that can influence successful hatching of eggs and recruitment of juveniles into the population (Siva-Jothy *et al.* 1995; Purcell *et al.* 2008; Bovill *et al.* 2013; Bovill *et al.* 2015; Smith & Reid 2016). Even more fundamentally, such studies require that ecologists can identify and quantify eggs, either in the field or in laboratory-processed samples.

Information on egg characteristics and oviposition behaviour is clearly important to many aspects of insect ecology, but there is a paucity of such information for aquatic insects, especially in the southern hemisphere (Reich 2004; Smith & Storey 2018). Although the eggs of aquatic insects have been described for some taxa and occasionally egg morphology has been included in taxonomic studies of some groups (e.g. Eaton 1888), these descriptions are often restricted to certain groups (e.g. nuisance Diptera: Kalpage & Brust 1968; Matsuo *et al.* 1974), largely anecdotal, or associated with taxonomic descriptions of individual species. Furthermore, the geographic coverage in these studies is uneven and descriptions of eggs for lotic insects in Australia remain relatively scarce (e.g. Hynes 1974; Towns 1983; Yule & Jardel 1985; Reich 2004). Not all taxa are ideal for ecological investigations that include the egg stage, such as groups where taxon-specific egg identification requires imaging by electron microscope or where taxa broadcast their eggs, which makes quantitative sampling difficult (but see Watanabe & Ohkita 2000). Many taxa, however, oviposit their eggs in discrete masses that are large enough to see in the field with the naked eye (or with a low magnification hand lens) and that have distinctive morphological features that can facilitate relatively detailed taxonomic identification.

The egg masses of Trichoptera vary in form and oviposition can occur in a variety of places (Holzenthal *et al.* 2015). For example, females of some taxa oviposit terrestrially, typically in moist places adjacent to water (Berté & Prichard 1983; Towns 1983; St Clair 1993; Enders & Wagner 1996), some release eggs at the water's edge or on the open water surface (Hanna 1961), some attach eggs to objects at or just above the water line (Jones 1976; Hoffmann & Resh 2003), some taxa swim underwater and oviposit on hard substrates (Badcock 1953; Deutsch 1984), whereas others walk underwater and oviposit on hard substrates (Hanna 1961; Gunn 1985; Reich 2004). A very few species of Trichoptera are viviparous (Wood-Mason 1890; Morse & Neboiss 1982) and some lay eggs singly (e.g. Spänhoff *et al.* 2003), but most species probably lay eggs in masses, which are held together and/or adhered to objects with a gelatinous material (spumaline) produced by the colleterial glands (Hinton 1981; Lancaster & Downes 2013). The most common shapes of caddisfly egg masses are gelatinous spheres, strings and loops, and plaques, which are flattened or slightly raised patches of eggs attached to hard surfaces (Lancaster & Downes 2013). It is common for species within a family to lay egg masses of the same shape (e.g. spheres or plaques, but not both), although there may be exceptions (Hanna 1961). Within each general shape, we can identify different morphotypes that correspond to different species. Potentially useful characteristics to distinguish between morphotypes include, egg mass dimensions, the amount of spumaline, number and arrangement of eggs within the mass, as well as the colour, shape and size of individual eggs.

The aim of this paper is to provide descriptions and images of the egg masses of some caddisflies in the family Hydrobiosidae that commonly occur in south-eastern Australia.

Some Hydrobiosidae and their egg masses have already featured as model systems to test ecological ideas in Australia (references below) and New Zealand (Smith & Reid 2016; Storey *et al.* 2016), and there is scope for further useful research using this system. There are over 15 genera and over 60 species of Australian Hydrobiosidae, occurring primarily in eastern Australia, with the highest species richness in south-eastern Australia and Tasmania (Dean 1997). Ovipositing females of many hydrobiosids first land on a rock that protrudes above the water surface (i.e. an 'emergent rock'), climb down the side of the rock and lay their eggs in a single, plaque-shaped mass covered in spumaline and attached to the underside of the rock. Perhaps the first detailed studies of hydrobiosid egg masses in Australia were descriptions of the egg masses of three genera and the physical characteristics of rocks selected for oviposition by each genus (Reich & Downes 2003a, 2003b; Reich 2004). Subsequent ecological research on these same genera has provided further insight into the consequences of oviposition behaviour for the spatial arrangement of egg masses (Lancaster *et al.* 2003; Reich *et al.* 2011), and into the effects of flow and egg predation on hatching success (Bovill *et al.* 2013; Bovill *et al.* 2015). This paper builds on those initial, genus-level descriptions and, for seven species that commonly co-occur in Victoria, we provide species-level identifications and morphological descriptions of egg masses that allow identification in the field. We also provide some ecological information on each species, including estimates of clutch sizes (a direct measure of adult fecundity) and the physical characteristics of oviposition sites.

## MATERIALS AND METHODS

Specimens were collected primarily from two rivers in Victoria, Australia: the Little River and Steavenson River, both within the Acheron River catchment on the north west side of the Yarra Ranges. These rivers drain into the Acheron River and subsequently into the Goulburn River. In the collection areas (Little River: S 37.345, E 145.751 280 m ASL; Steavenson River: S 37.488, E 145.752, 374 m ASL), the rivers had rocky substrates, gentle gradients (slopes: 1.3% and 1.0 % for Little and Steavenson Rivers, respectively), cool water temperatures (Fig. 1) and largely intact and diverse riparian vegetation characterised by species of *Eucalyptus, Acacia, Pomaderris* and *Dicksonia*. During the summer months of 2016-18, egg masses were collected, photographed and categorised into morphologically distinct types. All photographs were taken in the field with a compact digital camera (Olympus Stylus TG-4 Tough). Rocks were rolled over so that egg masses were photographed exposed to air. For each species, clutch size was measured by counting the number of eggs in each of 20 egg masses. In order to test for relationships between female body size and clutch size, adults were also collected from the same locations using light traps on an ad hoc basis. Wing measurements were made on ten females of each species. Wings were removed, dry mounted on microscope slides, photographed and forewing length measured on digital images.

Egg masses were identified by rearing and identifications also confirmed by genetic analyses. For rearing, egg masses were scraped from rocks during summer months and kept in well-aerated river water in a constant temperature room at 15˚C (mean temperature of these rivers in summers, Fig. 1) and on a 16:8 hour day:night light cycle. Once embryogenesis was complete (approx. 2 weeks for newly laid eggs), the predaceous larvae were fed early-instar chironomid larvae and various microfauna from the same rivers, and *Chironomus* larvae from a lab culture. Larvae were reared until sufficiently well developed for unambiguous identification, usually in the third instar or later. Genetic analyses were carried out at the Canadian Centre for DNA Barcoding using freshly collected egg masses, preserved in >95% ethanol. Total genomic DNA was extracted using a spin column DNA extraction protocol. The target genetic marker (barcode region of the mitochondrial DNA) was amplified using PCR (Polymerase Chain Reaction), followed by cycle sequencing. Sequencing reactions were analysed by high-voltage capillary electrophoresis. DNA sequences recovered from the specimens were compared against the species sequence reference library in the Barcode of Life Data System (BOLD) at http:/www.boldsystems.org.

Environmental characteristics of emergent rocks used as oviposition sites were based on very extensive surveys of the Steavenson River, Little River and nearby Snobs Creek (S 37.274, E 145.877, 280 m ASL). Briefly, in summer 2017, all emergent rocks in five to seven riffles on each river were mapped (X-Y-Z coordinates), characterised according to several environmental parameters (rock size, water depth, water velocity, height of emergent portion of rock) and egg masses of all Trichoptera identified and counted. Over 4000 emergent rocks were examined during that survey, of which >1000 had egg masses of at least one species of Hydrobiosidae. Full analyses of those data are the subject of a future publication; here we report some summary statistics for the environmental characteristics of oviposition sites used by species of Hydrobiosidae.

## RESULTS

Egg masses were identified for seven species of Hydrobiosidae that are common in the study area (Table 1) and these species dominated the hydrobiosids in light trap samples from the same stretches of river (unpublished data). A single egg mass for each of two less common species of *Ulmerochorema* Mosely were also identified (see text below). Egg masses of the seven common species were present simultaneously on most sampling trips over many months. The females of all species, for which we were able to identify egg masses, laid eggs in plaque-shaped masses in a transparent spumaline attached to the underside of partially emergent rocks. One exception, *Psyllobetina locula* Neboiss, was common in light trap samples but we failed to identify any eggs of this species.

The egg masses were grouped into three general morphotypes based on the thickness of the spumaline (Fig. 2) (see also Bovill *et al.* 2015). A-type masses were domed to nearly hemispherical in cross section, approx. 5–8 mm tall at the highest point, and the layer of spumaline was quite soft or fluid. U-type masses were raised approx. 2 mm but typically flattened or slightly depressed on top, with very firm spumaline. E-type masses were very flat with only a thin layer of spumaline ≤1 mm. Note, the tag names for egg mass morphotypes (A-, E-, U-type) simply reflect the genus of the first species we identified in each type. The eggs themselves had a thin and largely transparent/translucent chorion, which appears to provide minimal protection to the developing embryo. Most protection from environmental factors and oophagous predators appears to come from the overlying spumaline.

## Egg mass descriptions

Two species of *Apsilochorema* Ulmer, *A. gisbum* (Mosely) and *A. obliquum* (Mosely), had A-type egg masses with round white eggs, widely spaced and arranged in rows, with a wide margin of egg-free spumaline around the array of eggs (Fig. 3). The distance between eggs within and between rows was much greater than the maximum dimension of an egg. Masses of *A. obliquum* were typically elongate or oval in shape (Fig. 3a), whereas those of *A. gisbum* were more circular (Fig. 3b). Egg mass size varied somewhat with clutch size (number of eggs, Table 1); the largest masses were approx. 30 × 20 mm and 25 × 25 mm, for *A. obliquum* and *A. gisbum*, respectively. Once hatched, neonates remained in the egg mass for a short time, as the spumaline gradually lost its integrity, perhaps abetted by the neonates moving around (Fig. 3c). In this advanced stage it was difficult to determine which species had originally laid the eggs.

Two species had the E-type morphology, *Ethochorema turbidum* (Neboiss) and *Taschorema evansi* Mosely (Fig. 4). Egg masses were flat (closely adhered to the rock surface) and covered in a thin layer of spumaline. Eggs were round, pale coloured (white – yellow) and tightly packed in neat, straight rows (distance between eggs within and between rows was equal to or slightly less than the maximum dimension of an egg). Egg masses of the two species differed primarily in size of the mass and number of eggs. Egg masses of *Ethochorema turbidum* (Fig. 4a) were large (max. dimension 15–25 mm), typically elongate and approximately rectangular (although occasionally nearly circular) and had very many eggs (mean clutch size > 1000, Table 1). Egg masses of *Taschorema evansi* (Fig. 4b) were also elongate with rounded corners, but smaller (max. dimension 8–12 mm) and included roughly half the number of eggs (Table 1). Egg masses of both species often had ragged edges where eggs on the periphery had been eaten by oophagous late instar larvae of the hydroptilid caddisfly, *Orthotrichia armata* Wells (Bovill *et al.* 2015) (Fig. 4c).

Common representatives of the U-type morphology were *Koetonga clivicola* Neboiss and two species of *Ulmerochorema*, *U. rubiconum* Neboiss and *U. seona* (Mosely) (Fig. 5). All had egg masses with a thick layer of spumaline and round white eggs arranged somewhat irregularly within the mass. The elongate and somewhat rectangular egg masses of *K. clivicola* (Fig. 5a) were the largest in this group (max. dimension ≈20 mm) with the thickest jelly and the largest numbers of eggs (Table 1). Masses were flat on top or with a slight depression in the centre and had a noticeably egg-free margin of spumaline. Egg masses of *U. rubiconum* and *U. seona* were smaller (max. dimension 8–10 and 5 mm, respectively) and often occurred in large aggregations with 10 to > 100 egg masses per rock (see also Lancaster *et al.* 2003; Reich & Downes 2003a; Reich *et al.* 2011). Egg masses of *U. rubiconum* had a noticeable egg-free margin of spumaline, whereas eggs of *U. seona* usually extended right to the edge of the mass (Figs 5b, c). Corresponding to the larger egg mass dimensions, clutch size was larger for *U. rubiconum* than *U. seona* (Table 1). Masses of *U. rubiconum* were typically flat on top, whereas those of *U. seona* often appeared dome-shape, perhaps because the spumaline is quite thick relative to the egg mass length and width. Eggs of both these species of *Ulmerochorema* were initially white, but became brown near the end of embryogenesis, as eye spots became visible and sclerites of the head and pronotum became hardened and tanned.

Several other species of *Ulmerochorema* appeared in light trap samples at these locations in very low numbers, *U. membrum* Neboiss, *U. stigmum* (Ulmer) and *U. onychion* Neboiss. We have identified one egg mass of each of two of these species, both of which fit the U-type morphology and were similar to *U. rubiconum*, with similar egg mass dimensions and an egg-free margin of spumaline (Fig. 6). Unlike, *U. rubiconum* and *U. seona*, these egg masses occurred singly not in aggregations. A possible distinctive feature of the egg mass of *U. stigmum* was the arrangement of eggs in loose rows (Fig. 6a). We could not distinguish the egg mass of *U. onychion* (Fig. 6b) from *U. rubiconum* based on morphology alone so this requires further work and more specimens.

### Clutch size and environmental characteristics of oviposition sites

Clutch size varied markedly between species and was correlated with female wing length, a surrogate measure of body size (Fig. 7). We note that clutch size for these species could vary spatially and temporally, especially with seasons and in rivers with different temperature regimes.

All seven species selected emergent rocks for oviposition that were large (min. b-axis 18 cm, Gordon *et al.* 2004), in water deeper than 8 cm and that protruded well above the water surface (min. 7 cm vertical height exposed). The species differed, however, in whether oviposition sites occurred in fast or slow velocity (Table 1). *Apsilochorema* spp. and *Taschorema evansi* were most likely to occur in slowly flowing water, whereas *Ulmerochorema* spp., *Ethochorema turbidum* and *Koetonga clivicola* typically occurred in fast flows.

## DISCUSSION

This paper provides detailed descriptions and identification of the plaque-shaped egg masses of seven species of Hydrobiosidae that co-occur in some rocky, cool-water streams of Victoria, Australia. These egg masses can be identified in the field with the naked eye or with a low magnification hand lens. Our identifications of egg masses, via rearing and genetic analyses, are consistent with the outcomes of a previous rearing study for three genera or species groups: *Ulmerochorema*, *Apsilochorema* and *Taschorema*-complex (Reich 2004). We have built on that earlier work and provide species-level descriptions of egg masses for two species in each of three of those relatively coarse taxonomic groups (*Ulmerochorema rubiconum* and *U. seona*; *Apsilochorema obliquum* and *A. gisbum*; *Ethochorema turbidum* and *Taschorema evansi*) plus another species (*Koetonga clivicola*). Two additional species of *Ulmerochorema* were represented by a single identified egg mass each (*U. stigmum*, *U. onychion*). The seven common species were also abundant in light trap samples at the same locations and comprised virtually all the Hydrobiosidae in those samples.

Another species of Hydrobiosidae, *Psyllobetina locula*, was abundant in light trap samples but we have no information about their oviposition habits or characteristics of the eggs. It is possible that the adult *P. locula* we trapped were itinerants that commonly occurred as adults at these sites but did not oviposit (Lancaster & Downes 2017). This seems unlikely, however, because larvae of *Psyllobetina* do occur in benthic samples from these rivers (Downes *et al.* 1998; Downes unpublished data). Alternatively, it is possible that *P. locula* has a different oviposition behaviour. This species has an elongate, up-turned oviscapt (a type I ovipositor of Scudder 1971), in contrast to the more truncate genitalia of the other seven species. Roughly 80% of the described species of Australian Hydrobiosidae in Neboiss (1986) have truncate genitalia, suggesting that plaque-shaped egg masses may be common in this family. An oviscapt appears to be characteristic of females in three Australian genera of Hydrobiosidae: *Psyllobetina* Banks, *Allochorema* Mosely and *Moruya* Neboiss (Neboiss 1986), and these genera often cluster together in phylogenetic trees (Ward *et al.* 2004). Some Trichoptera with short oviscapts can lay eggs as encrusting masses on solid substrata, such as *Tinodes waeneri* (L.), Psychomiidae (Jones 1976), whereas another psychomiid with a longer oviscapt, *Lype phaeopa* (Stephens), lays eggs in cracks and crevices (Spänhoff *et al.* 2003). Many New Zealand Hydrobiosidae with truncate genitalia also oviposit spumaline-covered, plaque-shaped egg mass on emergent rocks (Smith & Storey 2018). One New Zealand genus, *Tiphobiosis*, has an oviscapt and its egg mass type is unknown.

These species of Hydrobiosidae are well suited for ecological studies that require empirical information on oviposition or recruitment for several reasons. Most importantly, the egg masses are morphologically distinct, can be identified readily and enumerated. Oviposition substrates are discrete objects (emergent rocks), which can be sampled quantitatively and, for example, facilitate empirical estimates of recruitment for studies on population dynamics. Tests of hypotheses involving ecologically similar species (e.g. species coexistence mechanisms, community assembly) are possible because multiple species of Hydrobiosidae often co-occur in the same river. Oviposition by all the species we observed occurred simultaneously over many months (Lancaster unpublished data), suggesting that these species do not have tight cohorts and may be multivoltine. Species differed somewhat in the physical characteristics of emergent rocks selected for oviposition, particularly with respect to water velocity; the patterns we observed were consistent with previous studies (Lancaster *et al.* 2003; Reich & Downes 2003a, 2003b). These flow preferences are related, in part, to egg mass morphology and the ability of the spumaline to resist the forces of hydraulic shear stress (Bovill *et al.* 2013). Species also differed in the degree to which they aggregated egg masses. Strong aggregative behaviour was shown by *U. rubiconum* and *U. seona* resulting in many egg masses on individual rocks (Lancaster *et al.* 2003; Reich *et al.* 2011). Egg mortality of these Hydrobiosidae appears to be low, apart from some predation by other aquatic insects (Reich 2004; Bovill *et al.* 2015; Lancaster pers. obs.), although high mortality from oophagous predators has been documented for some other caddisflies (Wisseman & Anderson 1984; Purcell *et al.* 2008).

The main elements of fecundity, often used in studies of population dynamics and life history trade-offs, include egg size, clutch size and number of clutches per female, of which clutch size is probably the most variable in invertebrates. In these Hydrobiosidae, each female appears to lay a single egg mass and variation in egg size is small (Reich 2004), and counting the number of eggs in a single mass (clutch size) is straightforward. Thus, clutch size provides a direct estimate of actual adult fecundity for individuals that have oviposited and avoids the assumptions involved with recruitment estimates based on counting eggs inside the abdomens of adult females (e.g. Werneke & Zwick 1992). Although there was considerable inter-individual variation in clutch size for each species in our study, there were clear between-species differences and clutch size was positively correlated with body size. A positive relationship between body size and fecundity is generally expected *within* insect species (Honěk 1993), and positive correlations *between* spiders with similar foraging modes has also been recorded (Enders 1976; Simpson 1995). Ecological correlates of variations in clutch size *between* species are central to some questions in evolutionary ecology (e.g. fecundity selection) for diverse groups including spiders (Simpson 1995; Prenter *et al.* 1999), birds (Martin *et al.* 2006) and reptiles (Huey & Pianka 1981; Seigel & Fitch 1984). Trichoptera may also be ideal systems for such hypothesis tests.

The hydrobiosid fauna of Australia is diverse and we have provided descriptions for only approximately 10% of the species described to date. Clearly it would be worthwhile to increase the number of descriptions to include more species, from more genera and over a wider geographical range. This increases the opportunities to test ecologically interesting questions and there is scope to test for associations between the functional morphology of female genitalia and the morphology of egg masses (e.g. Smith & Storey 2018).

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Table 1: Some characteristics of the egg masses of seven species of hydrobiosid caddisfly grouped by morphotype and including, approximate thickness of the spumaline, the arrangement of eggs within each egg mass and a summary of the maximum dimension of the largest egg mass observed. See text for comprehensive descriptions. Mean clutch size (number of eggs per mass), standard deviation and range based on N = 20 for each species. Median velocity (and interquartile range) was measured immediately upstream of emergent rocks with egg masses. Note: too few *K. clivicola* were encountered in the survey of 2017 to estimate interquartile velocity with confidence.

| | | Spumaline thickness | Egg arrangement | Max. dimension of egg mass | Clutch size | | Velocity |
|---|---|---|---|---|---|---|---|
| Type | Species | (mm) | | (mm) | mean | SD (range) | (cm/s) |
| A-type | *Apsilochorema gisbum* (Mosely) | 5–8 | widely spaced rows | 25 | 210 | 55 (126–322) | 16 (8 – 31) |
| | *Apsilochorema obliquum* (Mosely) | 5–8 | widely spaced rows | 30 | 400 | 92 (248–543) | 14 (7 – 29) |
| E-type | *Ethochorema turbidum* (Neboiss) | ≤1 | tightly packed rows | 25 | 1173 | 155 (975–1563) | 43 (19 – 57) |
| | *Taschorema evansi* Mosely | ≤1 | tightly packed rows | 12 | 460 | 138 (217–628) | 13 (4 – 24) |
| U-type | *Keotonga clivicola* Neboiss | 2 | irregular | 20 | 353 | 59 (264–461) | 25 |
| | *Ulmerochorema rubiconum* Neboiss | 2 | irregular | 10 | 194 | 54 (72–305) | 36 (18 – 50) |
| | *Ulmerochorema seona* (Mosely) | 2 | irregular | 5 | 103 | 36 (57–153) | 40 (24 – 51) |

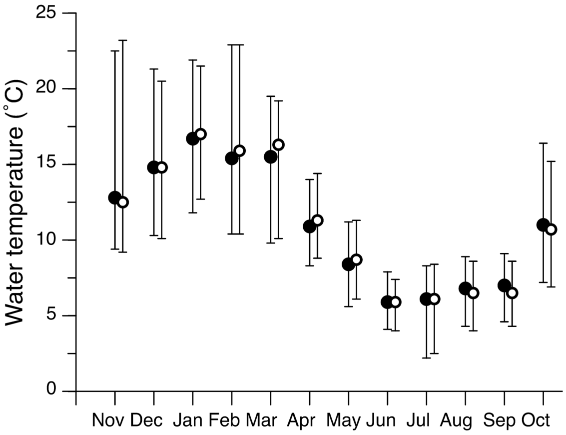


Figure 1 Monthly mean, maximum and minimum water temperature in Steavenson River (closed symbols) and the Little River (open symbols), 1 Nov 2016 to 31 Oct 2017. Temperature was recorded at 30 minute intervals using a Mini-Diver water level recorder (van Essen Instruments).

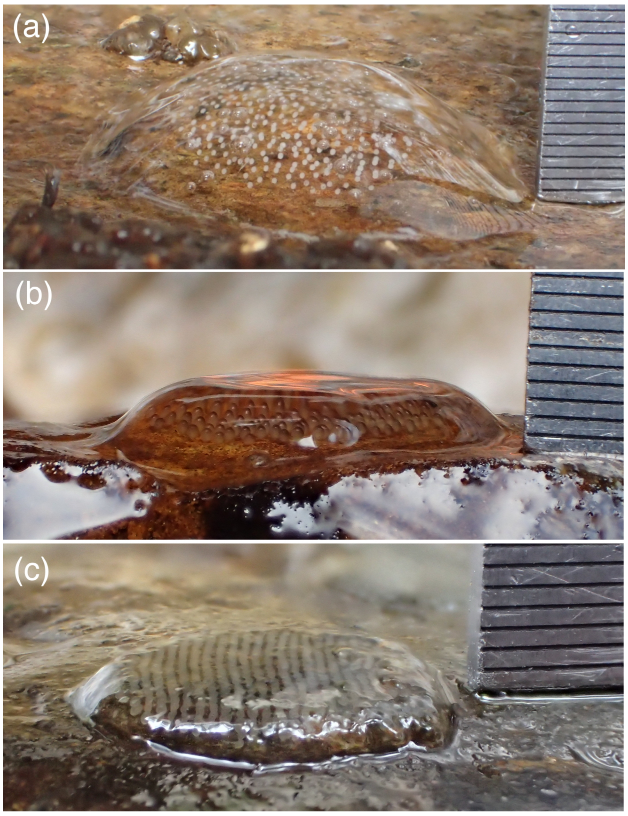


Figure 2 Examples of egg masses of hydrobiosid caddisflies belonging to three morphotypes based on the thickness of the spumaline covering the eggs (a) A-type, (b) U-type and (c) E-type. See text for further description. On the right of each image is a steel ruler with 0.5 mm divisions.

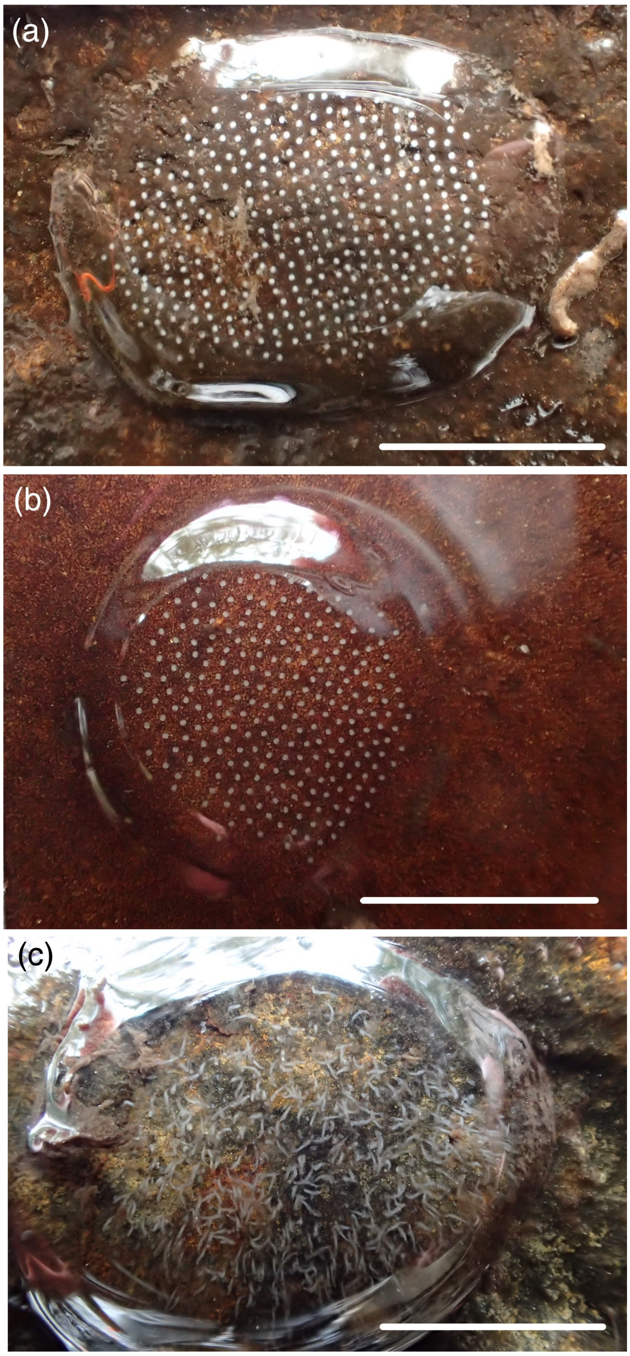


Figure 3 Egg masses of (a) *Apsilochorema obliquum* and (b) *Apsilochorema gisbum*. (c) Egg mass of *Apsilochorema* sp. with neonates still inside the spumaline. Scale bars are approx. 10 mm.

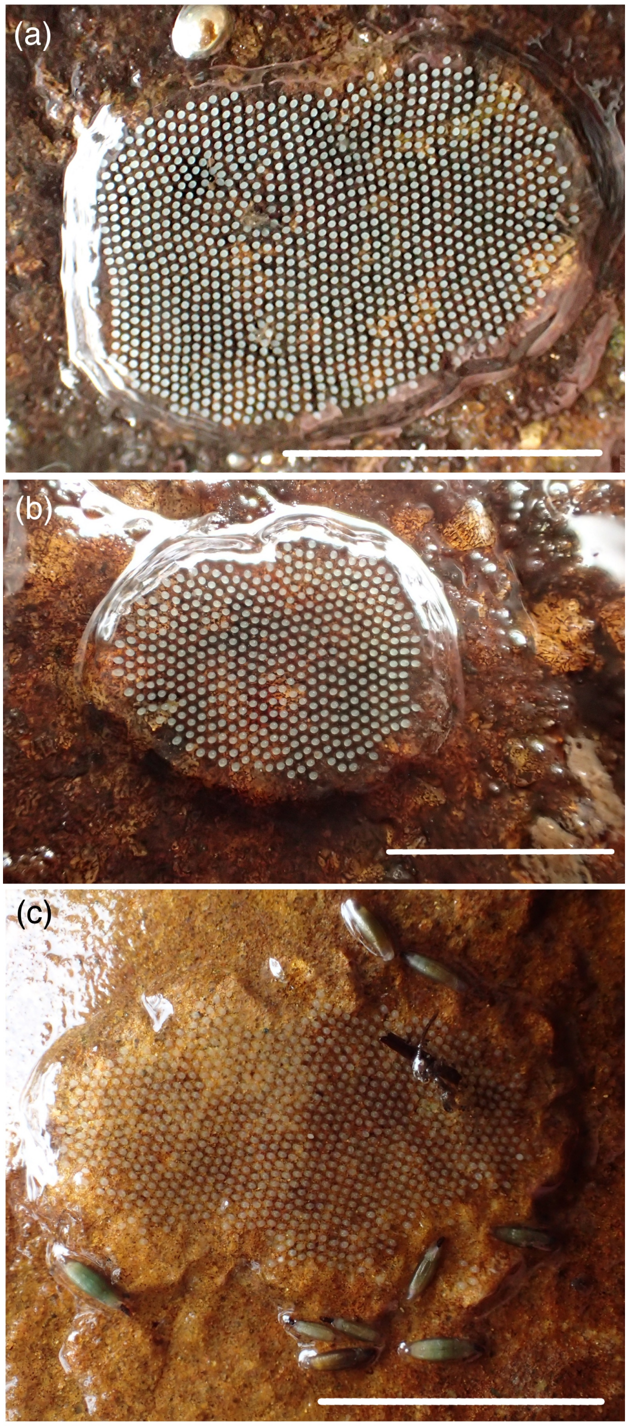


Figure 4 E-type egg masses of (a) *Ethochorema turbidum* and (b) *Taschorema evansi*. (c) Ragged-edged, egg mass of *E. turbidum* surrounded by oophagous late instar larvae of *Orthotrichia armata* (Hydroptilidae) on the periphery. Scale bars in (a) and (c) are approx. 10 mm, in (b) approx. 5 mm.

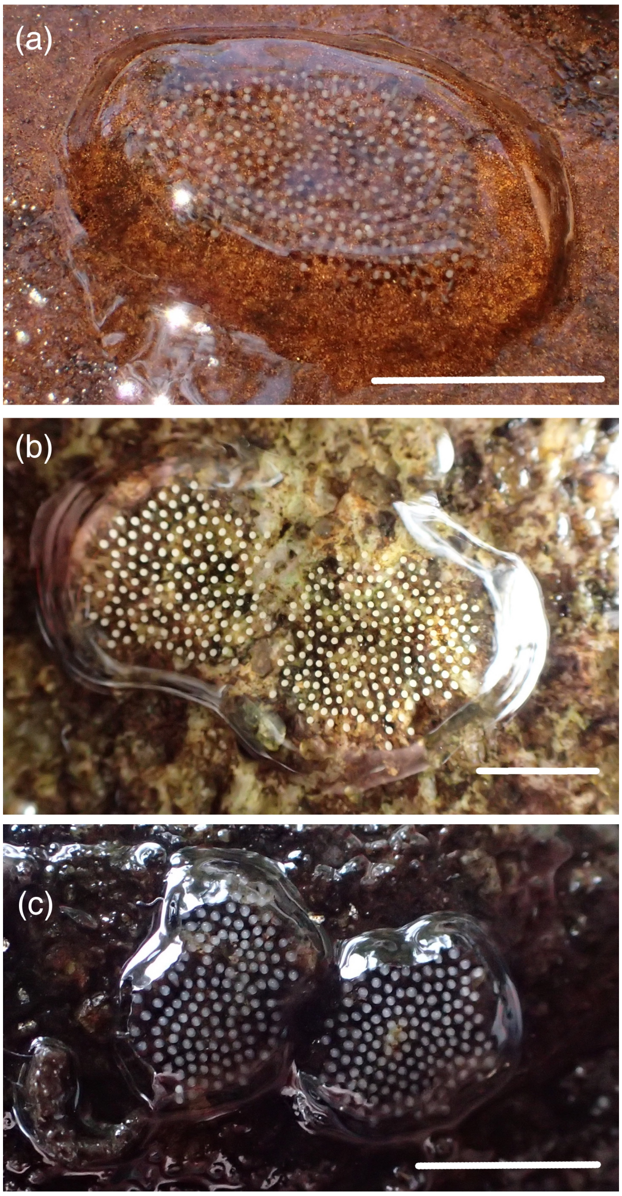


Figure 5 U-type egg masses of (a) *Koetonga clivicola,* (b) *Ulmerochorema rubiconum,* and (c) *Ulmerochorema seona*. Note two egg masses adjacent to one another are shown in (b) and (c). Scale bar in (a) is approx. 10 mm, in (b) and (c) approx. 5 mm.

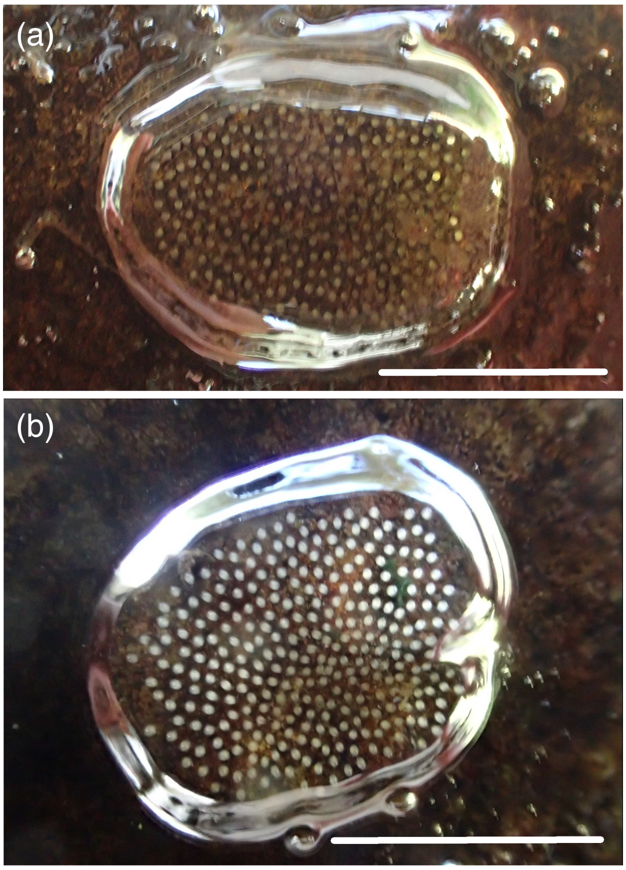


Figure 6 Egg masses of (a) *Ulmerochorema stigmum* (clutch size = 258) and (b) *Ulmerochorema onychion* (clutch size = 297). Scale bars are approx. 5 mm.

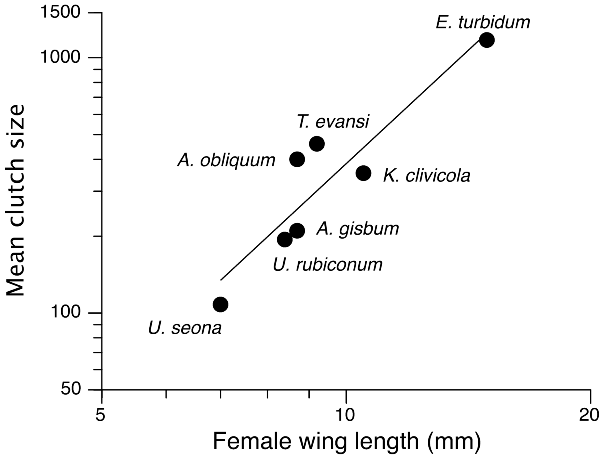
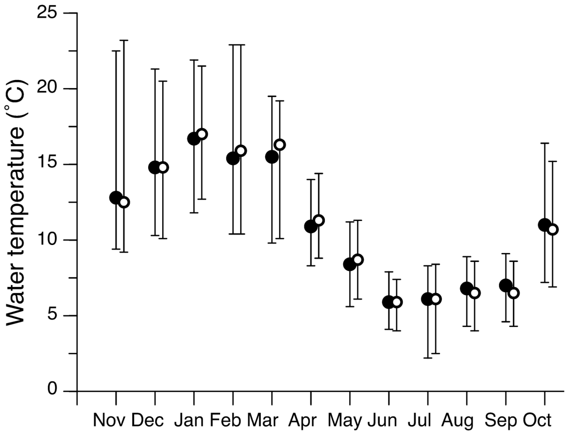


Figure 7 Relationships between mean clutch size and forewing length of females for seven species. Error bars associated with means along both X- and Y-axes are sufficiently small that they are included in the symbol. Note logarithmic scales on both axes. There is a significant correlation between wing length and clutch size (Pearson's correlation coefficient, one-tailed test: $r_5 = 0.919$, $P = 0.003$). If the largest species, *E. turbidum*, is removed from the analysis, the correlation is still significant ($r_4 = 0.803$, $P = 0.027$)



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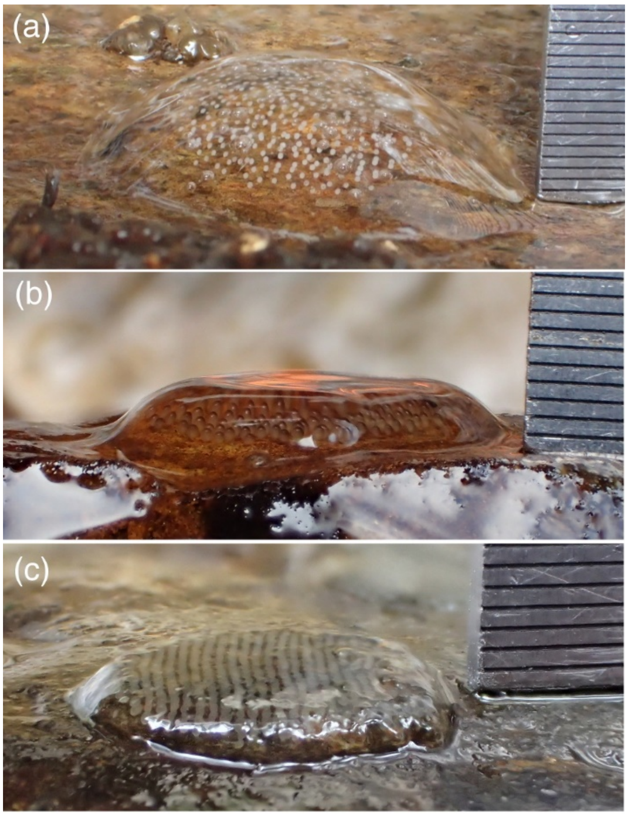

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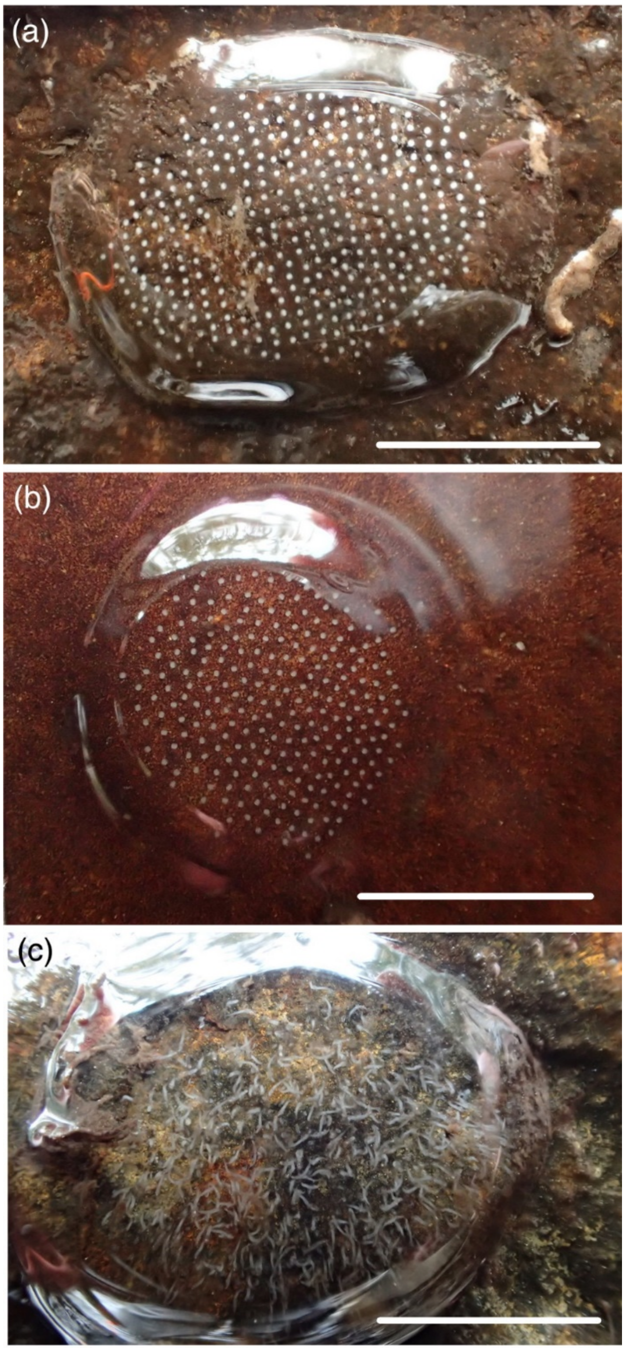

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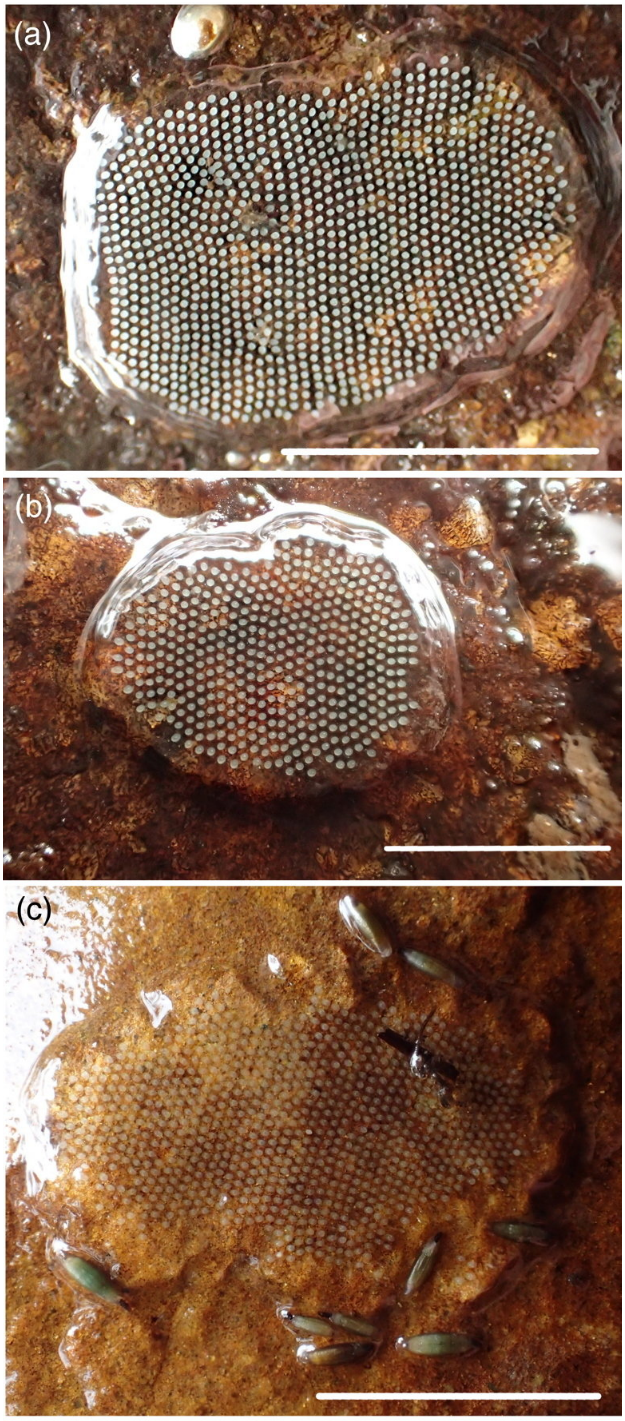

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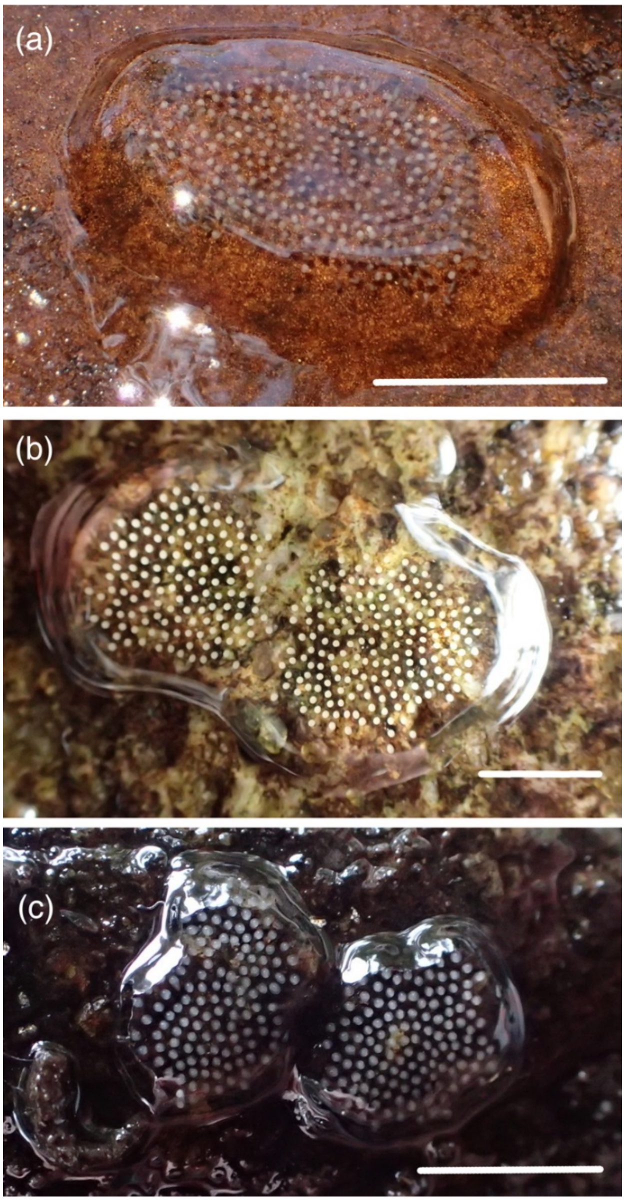

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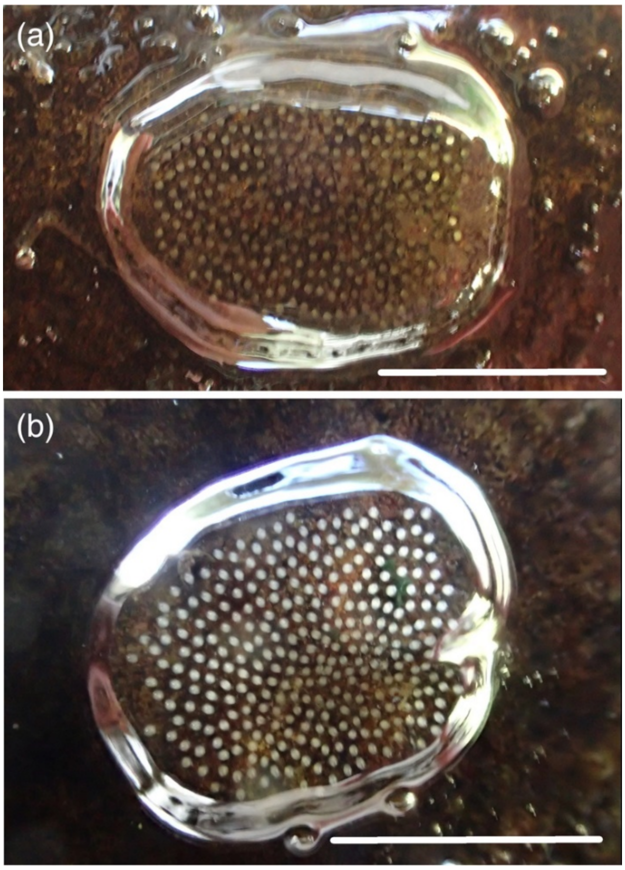

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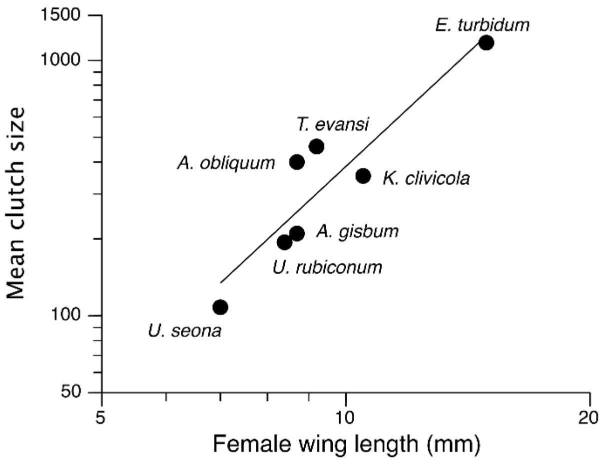

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