Museum Victoria Science Reports 31: 1–19 (2025)
ISSN 1833-0290
https://museumsvictoria.com.au/collections-research/journals/museum-victoria-science-reports/
DOI https://doi.org/10.24199/j.mvsr.2025.31

How to find and describe egg masses of aquatic insects

Jill Lancaster

School of Geography, Earth and Atmospheric Science, University of Melbourne, Melbourne, Victoria 3010, Australia.

JillL@unimelb.edu.au

https://orcid.org/0000-0003-4249-7951

Abstract

The morphological characters of the egg masses of some aquatic insects are presented, with particular emphasis on the Trichoptera. Diagnostic features that can separate taxa are described in detail for two categories of egg mass shape: two-dimensional plaques attached to hard substrates and egg balls. Where egg masses occur and how they may be found are also discussed.

Lancaster, J. 2025. How to find and describe egg masses of aquatic insects. Museum Victoria Science Reports 31: 1–19. https://doi.org/10.24199/j.mvsr.2025.31

Keywords Insecta, caddisfly, egg ball, egg plaque, oviposition





Figure 1. The author in the field (A) examining the underside of an emergent rock and (B) using a hand lens to examine small features of an egg mass. Image locations – Central Victoria, Australia; UK.

Contents

Introduction	2
When, where and how to find egg masses	3
Options to identify egg masses taxonomically	3
General morphological characters	4
Egg mass shape	6
A predominantly 2-dimensional plaque	6
A loop or wreath of eggs	6
An approximately spherical ball of eggs	6
An elongate string of eggs	6
An irregularly shaped mass	6
Terrestrial	6
Egg mass size and number of eggs	7
Egg size, shape and colour	7
Single vs many egg masses	8
Diagnostic characters – 2D plaques	9
Amount and texture of jelly covering eggs	ç
Shape of egg mass	ç
Arrangement of eggs within a plaque	10
Diagnostic characters - egg loops and balls	1 4
Arrangement of eggs within an egg ball	14
Egg ball surface	16
Acknowledgements	17
References	17
Appendix - Non-insect aquatic egg masses	19

Introduction

This is a guide to the characters that may be useful in describing the morphology of aquatic insect egg masses in the field and at low magnification. It is not a key for taxonomic identification, which is not yet possible based solely on the morphological characteristics that can be observed at low magnification. The objective is to provide tools that will help field investigators describe and characterise egg masses into morphotypes that may be associated with a particular taxonomic group. Descriptions of insect eggs and egg masses began over a century ago (e.g. Eaton, 1883), but such descriptions are often restricted to a few taxa and seldom provide guidance on the diversity of forms or how to distinguish between them, especially in the field (but see Reich, 2004). Only some groups of aquatic insect produce egg masses; in others, eggs may be broadcast, laid singly, laid endophytically, inserted into soft sediment, etc. (Lancaster & Downes, 2013).

This guide will focus on some egg masses that occur in, or very close to water. Coverage is biased toward the egg masses of Trichoptera that inhabit the UK or Australia, simply because my research has focussed on those taxa and locations. The aim, however, is to propose characters that are general and may be applied to many taxa and geographic regions. This is not an exhaustive or comprehensive list of all egg mass morphologies, or even all the egg masses that I have observed, and there may be more to discover.

Egg mass morphology is related to the morphology of female genitalia, particularly egg-laying structures (Smith & Storey, 2018), and genitalia may be morphologically similar among related taxa. The classification of taxa within the Trichoptera generally mirrors variations in egg mass morphology and oviposition habits, but variations are numerous. Egg mass morphology is probably conserved to some extent within genera, although this requires testing with data. Within genera, species-level identification may be impossible, or

at least difficult, using morphological characters only. There are exceptions of course and, for example, congeners may be separated in systems where there are few species. Egg masses of genera in the same family may have similar morphological characteristics, or they could be completely different. Likewise, egg masses of different families may share some morphological characteristics – the number of ways to produce an egg mass is much smaller than the number of taxa.

Why describe morphotypes? Assuming that distinct morphotypes are separate taxa, ecological information can be collected in the field about egg mass abundances and distribution patterns, and also oviposition behaviour – even if the taxonomic identity is uncertain in the short term. Taxonomic names can be added later. Being able to quantify insect egg masses in the field is central to testing diverse hypotheses about insect behaviour, population and community dynamics (e.g. Encalada & Peckarsky, 2012; Lancaster *et al.*, 2010a, 2020, 2021; Peckarsky *et al.*, 2000), and also addressing applied problems related to habitat management and degradation (e.g. Dilworth & Taylor, 2024; Miller *et al.*, 2020; Wahjudi *et al.*, 2024).

When, where and how to find egg masses

Knowing where particular egg mass morphotypes occur may help to distinguish between taxa and provide insight into species' autoecologies. For example, certain egg masses may occur always on particular substrates (wood, bark, roots, rocks, plants), in particular places (submerged vs emergent objects, pools vs riffles, river banks, macrophytes, riparian vegetation), at select times of year, or in particular microenvironments, characterised perhaps by water velocity or depth. Thus, noting where and when where particular egg masses occur may be informative. Collecting such information in a systematic manner is relatively simple, although potentially labour-intensive, and welldesigned surveys or experiments can be carried out with minimal experience. (For examples, see Lancaster et al., 2010a,b, 2020, 2021; Macqueen & Downes, 2015; Reich & Downes, 2003; Reich et al., 2011).

Most aquatic insects lay eggs during the warm season in temperate, high latitude or high elevation regions, although egg-laying periods of some species can last several months, even in temperate regions (Lancaster *et al.*, 2010a, 2021; Peckarsky *et al.*, 2000). At low latitude and low elevation, oviposition could occur at any time. Egg-laying periods may be short for species with highly synchronised cohorts, but much longer for species with over-lapping generations and

weakly synchronised cohorts.

Many egg masses are attached to hard substrates (rocks, wood, shopping trolleys, etc.); they occur most frequently on the sides or undersides of objects, and less frequently on the top. The easiest way to find egg masses is by examining potential substrates, e.g. turning over rocks, examining pieces of wood, macrophytes stems and leaves, and looking carefully. Many egg masses have a covering of jelly so globules of jelly are worthy of investigation. Some aquatic insects lay egg masses attached to riparian vegetation above and close to the water surface, so a search of plant leaves that overhang water may be rewarding. In rivers, begin with emergent rocks (rocks that protrude above the water surface), because they are less numerous than submerged rocks and more likely to have egg masses attached (Figure 1A). Some species oviposit exclusively on emergent rocks or objects; species that can oviposit on submerged substrates may also exploit emergent objects (Lancaster et al., 2010b; Reich, 2004). Return substrates to their original position after inspection to avoiding damaging any egg masses or the epilithic flora and fauna. Most egg masses are small (typically <15 mm) so a hand lens (commonly used by botanists and geologists) can be useful to see small features, especially if you have poor eyesight (Figure 1B).

Photographs and notes of where egg masses were found are essential. Ideally, photos should include a scale (Figures 7, 13F). Good options include a steel ruler with mm lines etched into the metal (plastic rulers get worn, "printed" lines get scratched and wear off) or some flexible, fibreglass tape measures that will not shrink or stretch. The ability of modern cameras and mobile phones to take close-up photos is incredible. There are also some excellent compact waterproof cameras, with features for macrophotography (e.g. image stacking) and that are very robust. Some of my best images were acquired using an Olympus ToughTM. Black cameras are best; coloured cameras can result in unwanted colour reflections in wet egg masses.

Options to identify egg masses taxonomically

As yet, it is not possible to identify many egg masses taxonomically using only the morphological characters that can be observed in the field and at low magnification. It is possible, with some effort, to characterise the variety of egg masses at a location based on their morphological characters, and use other techniques to associate morphotypes with taxonomic identity. In-

formation on the local species composition (e.g. from surveys of aquatic juveniles or winged adults) may be useful to limit the list of possible taxa, regardless of the identification procedure. There are three main ways to identify egg masses taxonomically. (1) Catch an adult female in the act of egg laying and identify the female, if possible (Figure 2). Gravid females enclosed in aquaria may also oviposit in captivity, if suitable substrates and microenvironments are present (Reich, 2004).

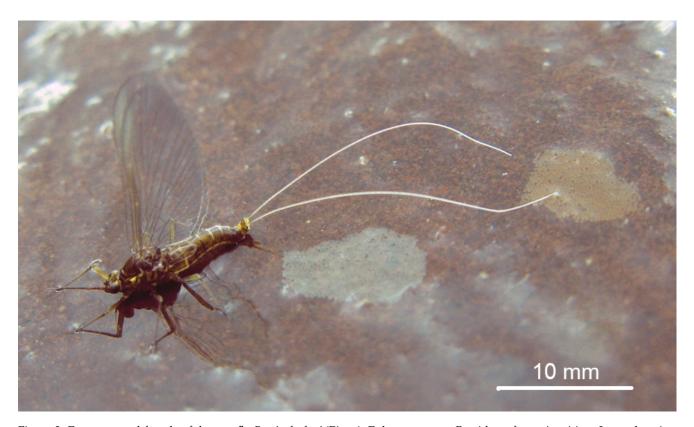


Figure 2. Egg mass and female of the mayfly *Baetis rhodani* (Pictet), Ephemeroptera: Baetidae, after ovipositing. Image location – SE Scotland, UK.

(2) Collect eggs and keep them in the laboratory (or similar) until they hatch, and raise larvae until they are large enough to identify (Lancaster & Glaister, 2019; Reich, 2004). In the field, egg masses may be easily removed from substrates with a pen knife or sharp blade. Keeping larvae alive long enough for them to develop the characters required for species-level identification may involve a significant investment of time and resources, and there is no guarantee of success because mortality can be high. Nevertheless, a lot can be learnt from examining the early instars, such as identifying the insect order or family, or determining whether it is even an insect. Other aquatic invertebrates also produce egg masses, including some gastropods and water mites, and their egg masses may appear morphologically similar to those of insects (see Appendix Figure 17).

(3) Use DNA barcoding of eggs https://

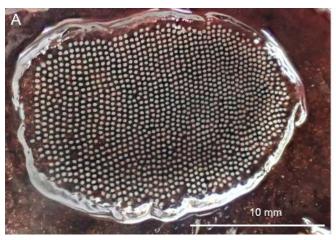
boldsystems.org/, as used in some studies on egg masses (Lancaster & Glaister, 2019; Storey *et al.*, 2017). This can be successful, if DNA libraries include your species, although costly. Ideally, avoid very fresh eggs because the amount of DNA may be small and difficult to amplify (my experience). Eggs that are in the later stages of development may be more suitable for DNA techniques.

General morphological characters

Useful morphological characters to describe any egg mass include the overall egg mass shape; egg mass size and number of eggs; arrangement and orientation of eggs within the mass; egg size, shape and colour; and whether egg masses occur singly or in aggregations.



Figure 3. Contrasting examples of different kinds of egg masses based on overall shape: (A) plaque-shaped egg mass, (B) loop of eggs, (C) attached ball of eggs and (D) unattached ball of eggs. Eggs arranged in strings attached (E) at one end or (F) along the string length. (A) *Ethochorema turbidum* (Neboiss), Trichoptera: Hydrobiosidae, (B) *Potamophylax latipennis* (Curtisty, Trichoptera: Limnephilidae, (C) Undet., Trichoptera, (D) *Triplectides proximus* Neboiss, Trichoptera: Leptoceridae, (E) Undet. Diptera and (F) Undet. Diptera: Chironomidae. Image locations – (A) and (D): Central Victoria, Australia; (B,) (C), (E) and (F): SE Scotland, UK.



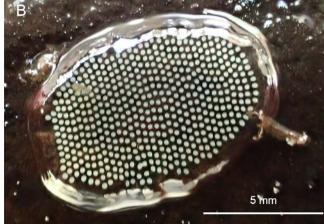


Figure 4. Egg mass size and number of eggs per mass can vary with female body size, even among closely related taxa. (A) *Ethochorema turbidum* (Neboiss), Trichoptera: Hydrobiosidae. Wing length = 14.9 mm; mean fecundity = 1173 and (B) *Taschorema evansi* (Mosely), Trichoptera: Hydrobiosidae. Wing length = 7.8 mm; mean fecundity = 460. All image locations – Central Victoria, Australia.

Egg mass shape

A predominantly 2-dimensional plaque

A predominantly 2-dimensional plaque, comprised of a single layer of eggs, and attached to a hard surface underwater (Figure 3A). They may be attached to fully submerged or partially emergent objects (e.g. rocks, wood, bark, roots), although these plaques invariably occur underwater. Females walk or swim underwater in order to oviposit.

Occurrence Many Trichoptera, some Ephemeroptera, Plecoptera and Diptera, but also some Mollusca and Hydracarina.

A loop or wreath of eggs

A loop or wreath of eggs, attached at a single point to a submerged object (rock, wood, macrophytes, etc) (Figure 3B). These egg masses are typically neutrally buoyant and may float above, or adjacent to the substrate surface when underwater. Females walk or swim underwater to oviposit.

Occurrence Many Trichoptera.

An approximately spherical ball of eggs

An approximately spherical ball of eggs – that has been oviposited underwater (Figures 3C, 3D). Egg balls may be attached to a submerged object (rock, wood, macrophytes, etc) or loose on the benthos. Females release such egg balls into the water, often at the water's edge or when resting on the water surface. Whether egg balls are attached may not be a reliable character in all cases because some may be attached only weakly (e.g. if the egg mass has a sticky surface) and may be easily dislodged. Loose balls may be moved by

currents and accumulate in depositional areas or in crevices between substrate particles. They can also be seen attached to the tip of a female's abdomen if the egg ball has not yet been released. The appearance of an egg ball can change markedly after oviposition: a sticky surface may accumulate fine detritus; many egg balls absorb water, swell and change shape. Note, many Ephemeroptera and Plecoptera also produce egg balls that are often seen attached to the tip of a female's abdomen. However, these balls are typically held together with a material that "explodes" upon contact with water and scatters the eggs, which may subsequently attach singly to a hard object underwater (Lancaster & Downes, 2013).

Occurrence Many Trichoptera.

An elongate string of eggs

An elongate string of eggs. Strings may be attached at one end (Figure 3E), often just below the waterline, or attached along the string length (Figure 3F).

Occurrence Many Diptera. Not discussed further.

An irregularly shaped mass

An irregularly shaped mass that may comprise multiple layers of eggs, often found on trailing vegetation along stream margins. (For images, see: dos Santos-Neto *et al.*, 2015; Zahar, 1951)

Occurrence Simuliidae (Diptera). Not discussed further.

Terrestrial

Some aquatic insects lay eggs terrestrially, e.g. on the leaves of riparian vegetation overhanging water (Crichton, 1987; Otto, 1987). The egg masses of some Megaloptera that oviposit on leaves resemble those of some terrestrial insects.

Occurrence Some Trichoptera, Megaloptera. Not discussed further.

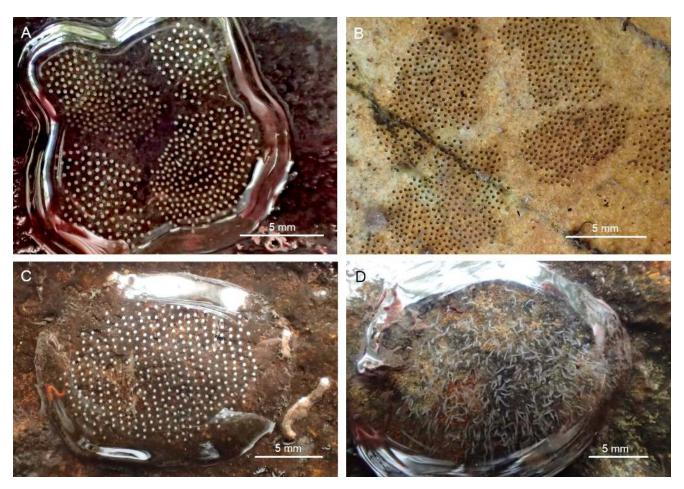


Figure 5. Within-species variations in egg colour and shape. (A) Newly-laid, pale eggs and (B) darker, late-stage eggs of *Ulmerochorema rubiconum* Neboiss, Trichoptera: Hydrobiosidae. (C) Newly-laid eggs and (D) neonates that have hatched but remain in the egg mass of *Apsilochorema obliquum* (Mosely), Trichoptera: Hydrobiosidae. All image locations – Central Victoria, Australia.

Egg mass size and number of eggs

The overall size of an egg mass and/or number of eggs in a mass can be useful diagnostic characters, especially for species where females produce a single egg mass per life time. In general, large-bodied species (Figure 4A) produce larger egg masses with more eggs (higher fecundity) than smaller-bodied species (Figure 4B) (Lancaster, 2025; Lancaster & Glaister, 2019).

Egg size, shape and colour

Among taxa, individual eggs can vary in size and colour, and common shapes range from round to

elongate. For identification, however, these characters should be used with caution because they can change during embryogenesis, especially for eggs that lack a hard chorion (Figures 5A, 5B). In addition, eggs may hatch and neonates emerge while still in the egg mass, and the marked change in shape is visible in the field (Figures 5C, 5D) (Berté & Pritchard, 1982). Occasionally, a few eggs within a mass may appear discoloured, unusually pale or opaque, indicating eggs that are infertile or non-viable for some reason. If all the eggs in a mass have hatched recently, a "ghost" egg mass may be apparent, with a distinct egg mass outline and visible remains of individual egg chorions.

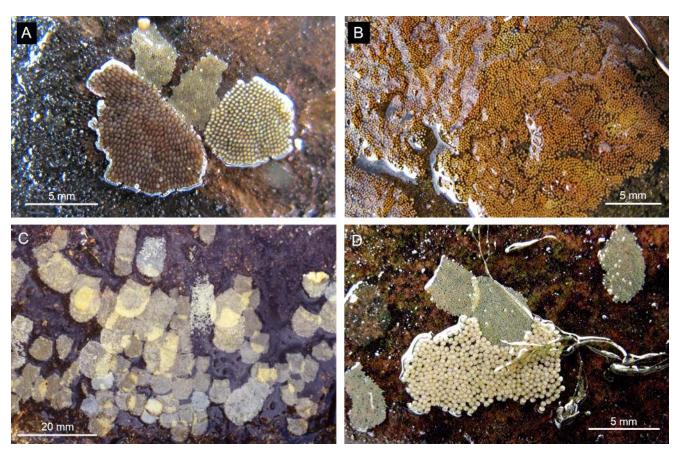


Figure 6. Egg masses may have (A) discrete boundaries or (B) and (C) indistinct boundaries when they occur in aggregations of many egg masses that can abut or overlap one another. Multiple species may oviposit close together (A) and (D). (A) Left: *Hydropsyche siltalai* Doehler, Trichoptera: Hydropsychidae; right: *Polycentropus flavomaculatus* (Pictet), Trichoptera: Polycentropodidae; middle top: two egg masses of *Baeitis rhodani* (Pictet), Ephemeroptera: Baetidae, (B) Undet. Trichoptera, (C) *Baetis rhodani* (Pictet), Ephemeroptera: Baetidae and (D) below: one large egg mass of *Rhyacophila dorsalis* (Curtis), Trichoptera: Rhyacophilidae; above, far left, far right: four egg masses of *Baetis rhodani*, Ephemeroptera: Baetidae. All image locations – SE Scotland, UK.

Single vs many egg masses

In the field, egg masses may be discrete objects with well-defined boundaries and thus are simple to enumerate (Figure 6A). Females of some species avoid laying egg masses close together whereas others commonly aggregate masses (Hoffmann & Resh, 2003; Lancaster *et al.*, 2020, 2003; Reich *et al.*, 2011). If many

females oviposit simultaneously (in oviposition aggregations), then egg masses may abut or overlay one another, and defining the boundaries of individual egg masses may be difficult (Figures 6B, 6C). Egg masses of multiple species can also occur close together (Figures 6A, 6D), which may be chance or may indicate that suitable oviposition sites are in short supply (Lancaster et al., 2021).

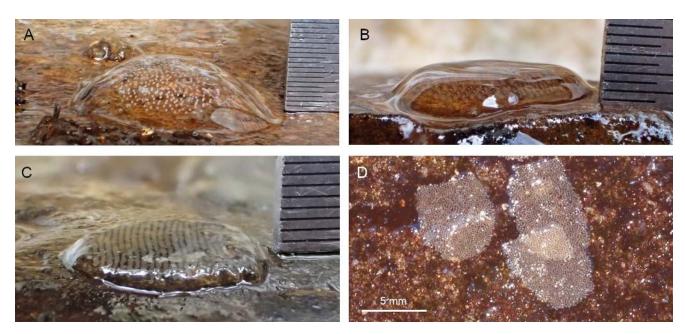


Figure 7. Variation in the thickness of jelly covering egg masses: (A) thick, soft jelly, (B) thick, firm jelly, (C) thin, firm jelly and (D) No obvious jelly. (A) *Apsilochorema* sp., Trichoptera: Hydrobiosidae, (B) *Ulmerochorema rubiconum* Neboiss, Trichoptera: Hydrobiosidae, (C) *Ethochorema turbidum* (Neboiss), Trichoptera: Hydrobiosidae and (D) *Baetis rhodani* (Pictet), Ephemeroptera: Baetidae. The finest scale lines are 0.5 mm apart in (A) – (C). Image locations – (A), (B) and (C): Central Victoria, Australia; (D): SE Scotland, UK.

Diagnostic characters – 2D plaques

Amount and texture of jelly covering eggs

When viewed in cross-section, egg mass plaques can vary in height and texture of jelly (spumaline) (Figure 7). Gently touch the egg mass to assess texture, e.g. whether jelly is present and whether the jelly is firm or soft. Egg masses with very thick jelly, relative to egg size, can appear dome-like or hemispherical and can project several mm above the substrate surface (Figure 7A). Egg masses with thinner jelly coverings typically have a flatter but distinctly raised profile, greater than the width of a single egg (Figures 7B, 7C). Egg masses

covered in jelly feel smooth to the touch; those without jelly (Figure 7D) often feel rough if individual eggs can be detected by finger tips.

Shape of egg mass

In plan view, egg mass plaques of some species have characteristic outlines or shapes, often with distinct, smooth edges (Figures 8A–8C), whereas others are more irregular in outline (Figure 8D). Caution: plaque shape can vary with substrate texture (smooth, rough, creviced) and whether a female was interrupted before completing the egg mass. Egg predators (oophages) can also alter the egg mass outline (Figure 8E) (see also: Bovill *et al.*, 2015; Purcell *et al.*, 2008).

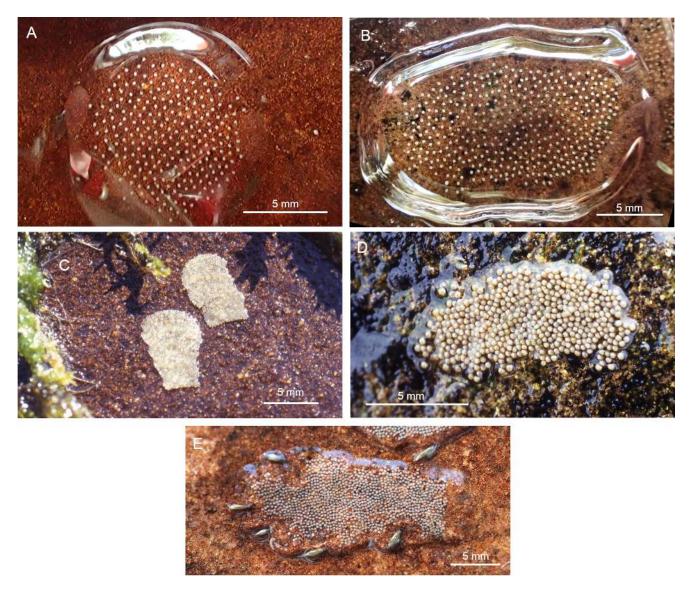


Figure 8. Some characteristic shapes of egg masses in plan view: (A) circular, (B) oval-elongate, (C) flask-shaped and (D) irregular. (E) Irregular outline caused by egg predation. (A) *Apsilochorema gisbum* (Mosely), Trichoptera: Hydrobiosidae, (B) *Koetonga clivicola*, Trichoptera: Hydrobiosidae, (C) *Baetis rhodani* (Pictet), Ephemeroptera: Baetidae, (D) *Rhyacophila dorsalis* (Curtis), Trichoptera: Rhyacophilidae and (E) larvae of *Orthotrichia armata* Wells, Trichoptera: Hydroptilidae, consuming egg mass of *Ethochorema turbidum* (Neboiss), Trichoptera: Hydrobiosidae. Image locations – (A), (B) and (E): Central Victoria, Australia; (C) and (D): SE Scotland, UK.

Arrangement of eggs within a plaque

Females oviposit eggs in characteristic patterns that are generally visible in the egg mass. Common arrangements include rows (Figure 9A) or a fan-like arrangement of concentric arcs (Figure 9B), but can also appear irregular (Figure 9C) or even quite complex or fancy patterns (Figures 9D). Patterns of egg arrangement may not be unique to particular taxonomic groups. For example, fan-like arrangements occur within at least three families of Trichoptera (Figure 10). In a further distinction, eggs may be attached

directly to the substrate (Figure 10) or embedded in jelly that is attached to the substrate (Figure 9D).

Many eggs appear quite round and not oriented in any obvious direction (Figure 11A). Eggs that are ovoid or elongated can vary in their orientation with the long axis parallel to the substrate (Figures 11B, 11C) or perpendicular (Figure 11D). How closely eggs are packed together in a plaque can also vary among species. Eggs may be tightly packed or partially overlapped, with no or minute spaces between eggs (Figure 12A), widely and evenly spaced (Figure 12B), or more closely spaced (Figure 12C).

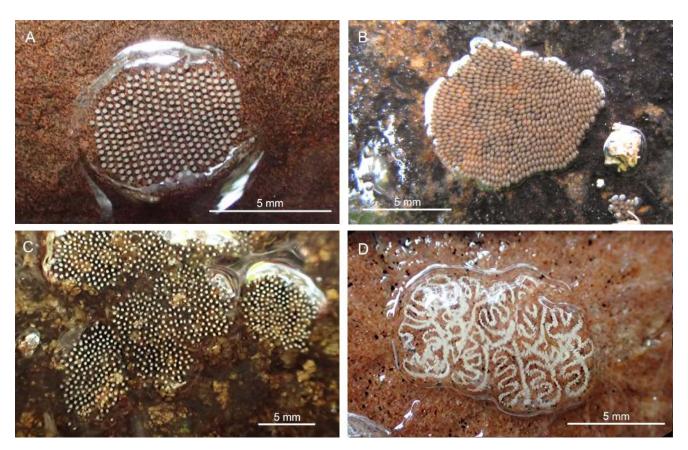


Figure 9. Different arrangements of eggs within plaque-shaped egg masses: (A) rows, (B) fan-like, (C) irregular, (D) fancy! (A) *Taschorema evansi* Mosely, Trichoptera: Hydrobiosidae, (B) *Hydropsyche siltalai* Dohler, Trichoptera: Hydropsychidae, (C) *Ulmerochorema seonum* (Mosely), Trichoptera: Hydrobiosidse and (D) Undet. Diptera: Chironomidae. Image locations – (A), (C) and (D): Central Victoria, Australia; (B): SE Scotland, UK.

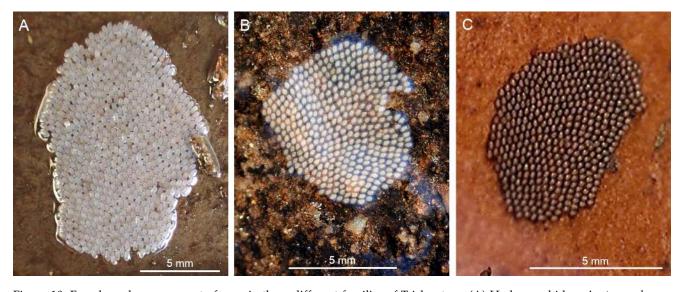


Figure 10. Fan-shaped arrangement of eggs in three different families of Trichoptera: (A) Hydropsychidae: *Austropsyche* sp., (B) Polycentropodidae: *Polycentropus flavomaculatus* (Pictet) and (C) Ecnomidae: *Ecnomus* sp. Image locations – (A) and (C): Central Victoria, Australia; (B): SE Scotland, UK.

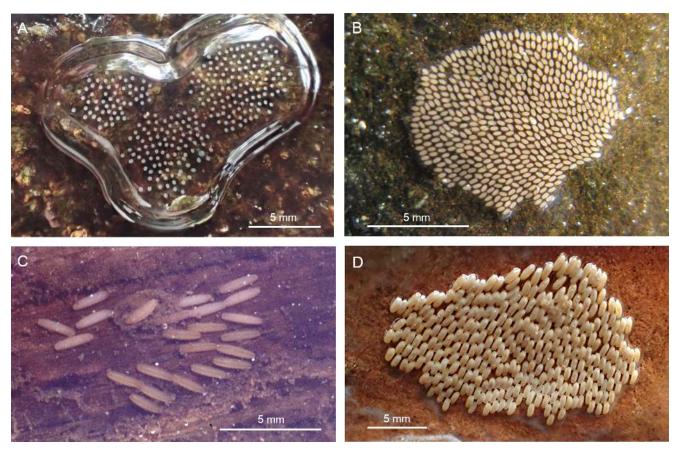


Figure 11. Egg shape and orientation: (A) round eggs, (B) ovoid, (C) and (D) elongate or rod-shaped. (A) *Ulmerochorema seonum* (Mosely), Trichoptera: Hydrobiosidae, (B) *Hydropsyche siltalai* Dohler, Trichoptera: Hydropsychidae, (C) and (D) Undet. Hemiptera: Gerridae. Image locations – (A), (C) and (D): Central Victoria, Australia; (B): SE Scotland, UK.

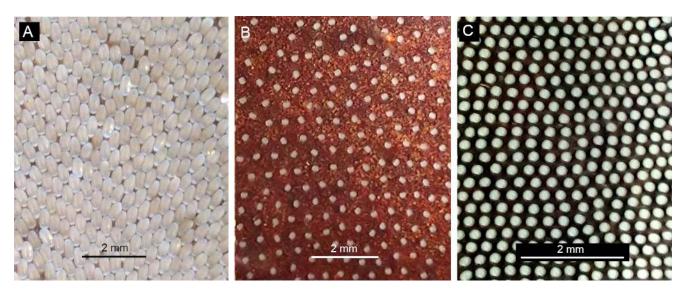


Figure 12. Egg packing within egg masses: (A) packed tightly with eggs touching one another, (B) widely-spaced within and between rows, e.g. spaces between eggs greater than egg width, and (C) narrowly spaced, e.g. spaces between eggs less than or equal to egg width. (A) *Austropsyche* sp., Trichoptera: Hydropsychidae, (B) *Apsilochorema* sp., Trichoptera: Hydrobiosidae and (C) *Taschorema evansi* (Mosely), Trichoptera: Hydrobiosidae. All image locations – Central Victoria, Australia.

Diagnostic characters – egg loops and balls

In strongly 3-dimensional masses, eggs may be arranged in a short, wide string of soft jelly, with both ends attached at the same point, thus forming a loop or wreath (Figure 13A). As for plaque-shaped egg

masses, egg loops can occur in dense aggregations (Figure 13B). Such loops lie flat when removed from the water, but may float upright when submerged, e.g. see images in Purcell *et al.* (2008). The arrangement of eggs within these masses may be difficult to discern, but there is likely to be a regular structure. I have limited information on these kinds of egg masses and further investigation would be beneficial.

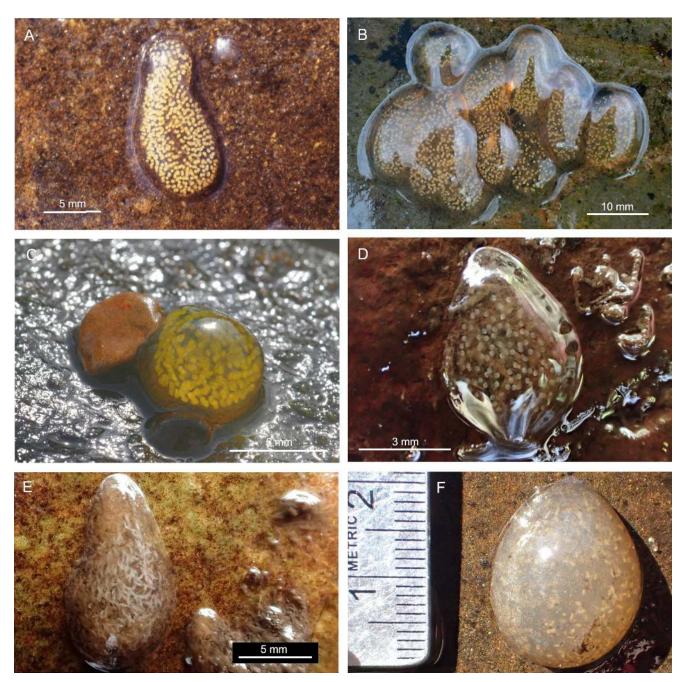


Figure 13. Overall shape of egg loops and balls attached at a single point to an hard surface underwater: (A) an egg loop, (B) an aggregation of egg loops, (C) an egg ball of firm jelly, (D) an egg ball of soft jelly hanging from the attachment point, (E) and (F) neonates within egg balls that have become enlarged. (A) and (B) *Potamophylax latipennis* (Curtis), Trichoptera: Limnephilidae, (C) Undet.,Trichoptera, (D) and (E) *Tasimia* sp., Trichoptera: Tasimiidae and (F) *Anisocentropus* sp., Trichoptera: Calamatoceratidae. Image locations – (A), (B) and (C): SE Scotland, UK; (D), (E), and (F): Central Victoria, Australia.

Egg masses may also consist of a ball of jelly (spumaline) with eggs embedded within. If the jelly is firm, the egg ball largely retains its spherical shape when removed from the water (Figure 13C), whereas a ball of soft jelly lies flat in a teardrop-shape when removed from the water (Figure 13D). The distinction between firm and soft jelly may not be entirely reliable because texture can change with age of the egg ball, and firm jelly can become soft (Berté & Pritchard, 1983). As with plaque-shaped egg masses, neonates may be visible within the egg balls and loops, which

gradually lose their integrity as neonates move around before leaving the mass (Figures 13E, 13F). For example, the late stage egg mass of *Anisocentropus* sp. in Figure 13F is large (max. dimension 20 mm), in contrast to the description of Reich (2004), who collected egg masses in the same area, that this genus produces an egg ball of 5 mm diameter.

Useful morphological characters to describe egg balls associated with different taxa include the arrangement of eggs within the ball, and surface texture of the ball.



Figure 14. Ventral view of a female caddisfly (in alcohol) with the egg ball still attached to the abdomen. *Triplectides proximus* Neboiss, Trichoptera: Leptoceridae. Image location – Central Victoria, Australia.

Diagnostic characters - egg loops and balls

Arrangement of eggs within an egg ball

Among caddisflies that produce egg balls, a gravid female that is ready to oviposit extrudes eggs in a string, which is wound into a ball and on a bowl-like surface in the female's genital cavity. Initially, the string of eggs appears to be folded back-and-forth into rows to form an elongate sheet or short ribbon, and it is this ribbon that is then rolled into a ball. Rows within a ball are typically aligned perpendicular to the body before oviposition (Figure 14). In external appearance, there appear to be at least three distinctive kinds of egg ball, which are best described in terms of how the rows of eggs may be arranged within the ribbon

(Figure 15). First, the egg ball may resemble an old fashioned bird cage, especially if the jelly is transparent (Figures 3D), or a rolled-up mattress, e.g. a ball flattened on opposite sides (Figure 15A), if the rows of eggs within the ribbon are of equal length (Figure 15B). Second, the egg ball may resemble a snowball in which long rows appear to overlap shorter rows (Figure 15C), if the rows of eggs within the ribbon gradually increase in length (Figures 15D). Third, the egg ball may resemble a ball of yarn in which sets of rows appear to be at right angles to one another (Figure 15E). This pattern could arise if rows are arranged in sets and each set has rows that increase in length (Figure 15F). Whether rows of eggs are actually arranged in ribbons in these different ways remains to be tested, but they provide plausible mechanisms for how different appearances could arise.

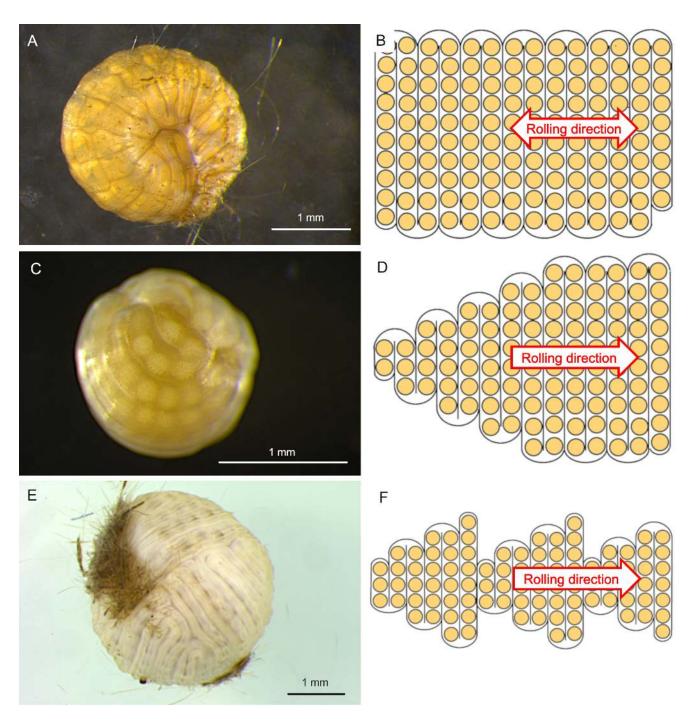


Figure 15. Three kinds of egg ball and hypothetical diagrams illustrating how the different appearances could arise when rolling up a ribbon in which rows of eggs are arranged in various ways. A ball may have the appearance of (A) a rolled up mattress if (B) rows of eggs are of equal length, (C) a snowball if (D) rows increase in length and (E) a ball of yarn if (F) rows are arranged in sets that increase in length. In (A), the ribbon can be rolled in either direction. In (D) and (F), the ribbons are rolled starting on the left and ending on the right. (A) *Tamasia acuta* Neboiss, Trichoptera: Calocidae, (C) *Hampa* sp., Trichoptera: Conoesucidae and (E) *Kosrheithrus tillyardi* Mosely, Trichoptera: Philorheithridae. All image locations – Central Victoria, Australia.

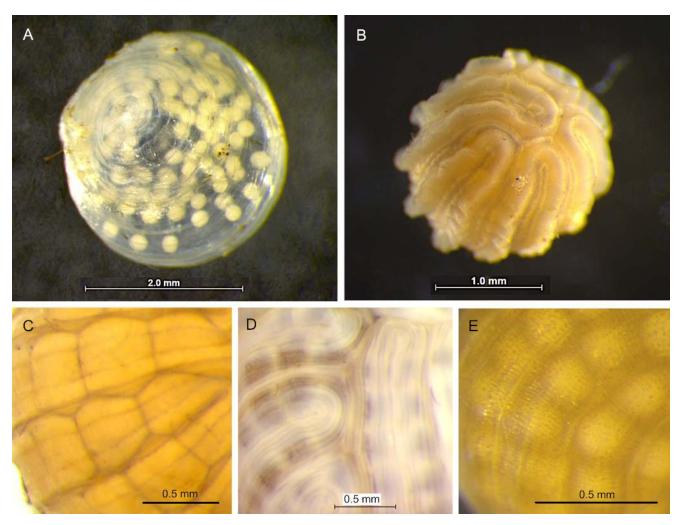


Figure 16. Appearance of the surface skin of egg balls: (A) smooth and transparent and (B) frilly and opaque. Rows of eggs visible below the ball surface may be associated with surface features in the form of (C) geometric shapes, (C) and (D) strings and (E) striations. (A) *Triaenodes fuscinula* Neboiss & Wells, Trichoptera: Leptoceridae, (B) *Caloca* sp., Trichoptera: Calocidae, (C) *Tamasia acuta* Neboiss, Trichoptera: Calocidae, (D) *Kosrheithrus tillyardi* Mosely, Trichoptera: Philorheithridae and (E) *Hampa* sp., Trichoptera: Conoesucidae. All image locations – Central Victoria, Australia.

Egg ball surface

The surface of an egg ball typically has a skin which provides some protection for the eggs within. The texture and features of this outer skin can vary among taxa and may be useful diagnostic characters. The skin may, of course, change as the ball expands with the egg development and moisture levels, so caution is required. Balls can also shrink and the skin become quite leathery if dehydrated; this process can be reversed by rehydration and enables some taxa to survive in ephemeral systems (Berté & Pritchard, 1983; Otto, 1987). Preserving egg balls in ethanol can also result in a hard skin.

The egg ball surface may be transparent and eggs

clearly visible inside (Figures 3C, 3D, 13C, 16A); eggs may remain partially visible if the surface is translucent (Figure 15B), but obscured if the surface is opaque (Figure 15E, 16B). Most egg balls have a more or less smooth surface, but some very fresh egg balls appear frilly, owing to a raised fold that runs parallel to the egg rows (Figure 16B). These folds allow the ball to expand as it absorbs water, swells and develops a smoother surface. The ball surface above rows of eggs often has longitudinal stripes (Figure 16C, 16D) or geometric shapes that correspond approximately to individual eggs (Figure 16C). Striations oriented perpendicular to the row characterise the surface of some other egg balls (Figure 16E).

Acknowledgements

My thanks to Wim Bovill, Barb Downes, Sam Dilworth and Ros St. Clair for helpful comments on an earlier version of this guide. I am eternally grateful to the various people who helped me collect and identify egg masses over the years, and especially: Amanada Arnold, Wim Bovill, Barb Downes and Alena Glaister.

This work benefitted from the support of various research grants including, the Natural Environment Research Council, UK (NE/E004946/1) and the Australian Research Council Discovery Project grants (DP0772845, DP120103145, DP160102262, DP210101887).

References

- Berté, S.B. & Pritchard, G. (1982). The phenomenon of egg mass liquefaction in *Nemotaulius hostilis* (Hagen) (Trichoptera:Limnephilidae). *Freshwater Invertebrate Biology*, 1, 49–51. https://doi.org/10.2307/1467142.
- Berté, S.B. & Pritchard, G. (1983). The structure and hydration dynamics of trichopteran (Insecta) egg masses. *Canadian Journal of Zoology*, 61, 378–384. https://doi.org/10.1139/z83-050.
- Bovill, W.D., Downes, B.J. & Lancaster, J. (2015). Caddisfly egg mass morphology mediates egg predation: Potential costs to individuals and populations. *Freshwater Biology*, 60, 360–372. https://doi.org/10.1111/fwb.12497.
- Crichton, M. (1987). A study of egg masses of *Glyphotaelius pellucidus* (Retzius), (Trichoptera: Limnephilidae). In: *Proceedings of the Fifth International Symposium on Trichoptera*. Springer, pp. 165–169.
- Dilworth, S. & Taylor, B.W. (2024). Facilitating the recovery of insect communities in restored streams by increasing oviposition habitat. *Ecological Applications*, 34, e2939. https://doi.org/10.1002/eap.2939.
- dos Santos-Neto, C.R., Hamada, N. & Couceiro, S.R.M. (2015). Bionomics of the black fly *Simulium guianense* (Diptera: Simuliidae) in Northeast Brazil. *Florida Entomologist*, 98, 446–450. https://doi.org/10.1653/024.098.0209.
- Eaton, A.E. (1883). A revisional monograph of recent Ephemeridae or mayflies.- Part I. *Transactions of the Linnean Society of London. 2nd Series: Zoology*, 3, 1–77. https://doi.org/10.1111/j.1096-3642.1883.tb01550a.x.

- Encalada, A.C. & Peckarsky, B.L. (2012). Large-scale manipulation of mayfly recruitment affects population size. *Oecologia*, 168, 967–976. https://doi.org/10.1007/s00442-011-2147-1.
- Hoffmann, A. & Resh, V. (2003). Oviposition in three species of limnephiloid caddisflies (Trichoptera): Hierarchical influences on site selection. *Freshwater Biology*, 48, 1064–1077. https://doi.org/10.1046/j.1365-2427.2003.01074.x.
- Lancaster, J. (2025). Diet alters interspecific fecunditysize relationships in capital breeding insects. *Oikos*, 2025, e10992. https://doi.org/10.1111/oik.10992.
- Lancaster, J. & Downes, B. (2013). *Aquatic Entomology*. Oxford University Press, United Kingdom.
- Lancaster, J., Downes, B.J. & Arnold, A. (2010a). Environmental constraints on oviposition limit egg supply of a stream insect at multiple scales. *Oecologia*, 163, 373–384. https://doi.org/10.1007/s00442-010-1565-9.
- Lancaster, J., Downes, B.J. & Arnold, A. (2010b). Oviposition site selectivity of some stream-dwelling caddisflies. *Hydrobiologia*, 652, 165–178. https://doi.org/10.1007/s10750-010-0328-2.
- Lancaster, J., Downes, B.J., Lester, R.E. & Rice, S.P. (2020). Avoidance and aggregation create consistent egg distribution patterns of congeneric caddisflies across spatially variable oviposition landscapes. *Oecologia*, 192, 375–389. https://doi.org/10.1007/s00442-019-04587-7.
- Lancaster, J., Downes, B.J. & Reich, P. (2003). Linking landscape patterns of resource distribution with models of aggregation in ovipositing stream insects. *Journal of Animal Ecology*, 72, 969–978. https://doi.org/10.1046/j.1365-2656.2003.00764.x.
- Lancaster, J. & Glaister, A. (2019). Egg masses of some stream-dwelling caddisflies (Trichoptera: Hydrobiosidae) from Victoria, Australia. *Austral Entomology*, 58, 561–568. https://doi.org/10.1111/aen.12360.
- Lancaster, J., Rice, S.P., Slater, L., Lester, R.E. & Downes, B.J. (2021). Hydrological controls on oviposition habitat are associated with egg-laying phenology of some caddisflies. *Freshwater Biology*, 66, 1311–1327. https://doi.org/10.1111/fwb.13718.
- Macqueen, A. & Downes, B.J. (2015). Large-scale manipulation of oviposition substrata affects egg supply to populations of some stream-dwelling caddisflies. *Freshwater Biology*, 60, 802–812. https://doi.org/10.1111/fwb.12535.

- Miller, S.W., Schroer, M., Fleri, J.R. & Kennedy, T.A. (2020). Macroinvertebrate oviposition habitat selectivity and egg-mass desiccation tolerances: Implications for population dynamics in large regulated rivers. *Freshwater Science*, 39, 584–599. https://doi.org/10.1086/710237.
- Otto, C. (1987). Adaptive egg laying behaviour in two species of caddisflies. In: *Proceedings of the Fifth International Symposium on Trichoptera*. Springer, pp. 171–174.
- Peckarsky, B.L., Taylor, B.W. & Caudill, C.C. (2000). Hydrologic and behavioral constraints on oviposition of stream insects: Implications for adult dispersal. *Oecologia*, 125, 186–200. https://doi.org/10.1007/s004420000446.
- Purcell, A.H., Hoffmann, A. & Resh, V.H. (2008). Life history of a dipteran predator (Scathophagidae: *Acanthocnema*) of insect egg masses in a northern California stream. *Freshwater Biology*, 53, 2426–2437. https://doi.org/10.1111/j. 1365-2427.2008.02060.x.
- Reich, P. (2004). Patterns of composition and abundance in macroinvertebrate egg masses from temperate Australian streams. *Marine and Freshwater Research*, 55, 39. https://doi.org/10.1071/MF03129.
- Reich, P. & Downes, B.J. (2003). The distribution of aquatic invertebrate egg masses in relation to physical characteristics of oviposition sites at two Victorian upland streams. *Freshwater Biol-*

- ogy, 48, 1497-1513. https://doi.org/10.1046/j. 1365-2427.2003.01101.x.
- Reich, P., Hale, R., Downes, B.J. & Lancaster, J. (2011). Environmental cues or conspecific attraction as causes for egg mass aggregation in hydrobiosid caddisflies. *Hydrobiologia*, 661, 351–362. https://doi.org/10.1007/s10750-010-0543-x.
- Smith, B.J. & Storey, R.G. (2018). Egg characteristics and oviposition behaviour of the aquatic insect orders Ephemeroptera, Plecoptera and Trichoptera in New Zealand: A review. *New Zealand Journal of Zoology*, 45, 287–325. https://doi.org/10.1080/03014223.2018.1443473.
- Storey, R.G., Reid, D.R. & Smith, B.J. (2017). Oviposition site selectivity of some New Zealand aquatic macroinvertebrate taxa and implications for stream restoration. *New Zealand Journal of Marine and Freshwater Research*, 51, 165–181. https://doi.org/10.1080/00288330.2016.1269351.
- Wahjudi, H., Bovill, W.D., Brooks, A.J. & Downes, B.J. (2024). Seasonal differences in amounts of oviposition habitat and egg-laying by caddisflies in rivers with regulated versus unregulated flows. *Freshwater Biology*, 69, 645–659. https://doi.org/10.1111/fwb.14236.
- Zahar, A.R. (1951). The ecology and distribution of black-flies (Simuliidae) in South-East Scotland. *The Journal of Animal Ecology*, 20, 33. https://doi.org/10.2307/1643.

Manuscript submitted: 1 August 2025. Manuscript accepted: 1 October 2025.

Editor: Robin Wilson.

Appendix - Non-insect aquatic egg masses

Some aquatic invertebrates produce egg mass that may superficially resemble those of aquatic insects (Figure 17). As yet, there is no systematic way to separate these different groups in the field.

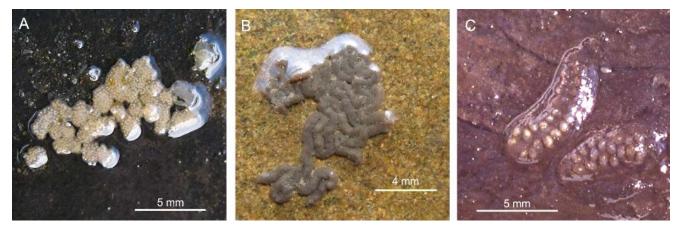


Figure 17. Some egg masses of non-insect aquatic invertebrates. (A) Hydracarina, Arthropoda: Arachnida (B) Undet. possibly Nematomorpha and (C) Gastropoda, Mollucsa. Image locations – (A) and (B): SE Scotland, UK; (C): Central Victoria, Australia..