9

Mollusca: Gastropoda

Jeffrey H. R. Goddard

Gastropods include the snails and slugs and the less familiar free-swimming pteropods ("sea butterflies") and heteropods. They are the most speciose class in the second-largest phylum of animals. Approximately 400 species are known from the Pacific Northwest or have distributions encompassing the Pacific Northwest (Goddard, 1984, 1990, 1997; Austin, 1985). Type of development is known for a significant number of these species, but illustrations and specific descriptions of their larvae, especially at later stages of development, are lacking for the vast majority. Identification of larvae is therefore usually possible only to higher taxonomic levels.

Gastropods are now divided into two, rather than the traditional three, subclasses, the Prosobranchia and Heterobranchia (Table 1). The prosobranchs include most of the familiar limpets, abalone, snails, and slipper shells. The heterobranchs include the opisthobranchs (sea slugs and allies, including the pteropods), pulmonates (land and freshwater snails and slugs), the small, ectoparasitic pyramidellid snails, the pulmonate-like gymnomorphs, and some lesser known families not known from local waters and formerly allied with the Prosobranchia (see Bieler, 1992; Gosliner, 1996; Ponder and Lindberg, 1997, for recent reviews of gastropod higher classification).

The prosobranchs include more species than the heterobranchs, but repeated evolutionary loss of the shell in the latter subclass has resulted in greater morphological and ecological diversity. Of the local gastropods, 63% (255 species) are prosobranchs; the remainder are heterobranchs, mostly opisthobranchs. Families and genera of local gastropods are listed in Table 2.

Morphology

Gastropods have a distinct head with sensory tentacles and eyespots, and they crawl, burrow, or swim by means of a broad muscular foot. The foot supports and carries an overlying visceral mass that is covered, in turn, by a layer of tissue called the mantle and a calcified, protective shell secreted by the mantle. The foot of most species also carries an operculum, a shield-like structure used for closing off the shell aperture after

Table 1. Higher classification of gastropods known from the Pacific Northwest.

Phylum Mollusca
- **Class Gastropoda**
  - **Subclass Prosobranchia**
    - Order Patellogastropoda (= Archaeogastropoda, in part; includes most limpets)
    - Vetigastropoda (= Archaeogastropoda, in part; keyhole limpets, abalone, turban snails, etc.)
    - Caenogastropoda (= Meso- and Neogastropoda; periwinkles, whelks, drills, moon snails)
  - **Subclass Heterobranchia**
    - Superorder Pyramidellidacea (pyramidellid snails)
    - Opisthobranchia (sea slugs, bubble snails, pteropods)
    - Gymnomorpha (gymnomorph slugs)
    - Pulmonata (lunged snails)

Table 2. Families and genera of the class Gastropoda known from the Pacific Northwest (from Austin, 1985; Behrens, 1990; Kozloff, 1996)[1]

Patellogastropoda
Acmaeidae: *Acmaea*
Lottidae: *Discurria, Lottia, Tectura*
Lepetidae: *Cryptobranchia, Iothia, Lepeta*

Vetigastropoda
Fissurellidae: *Arginula, Craniopsis, Diodora, Fissurellidea, Puncturella*
Haliotidae: *Haliotis*
Scissurellidae: *Anatoma*
Trochidae: *Bathybembix, Calliostoma, Halistylus, Lirularia, *Margarites, Solariella, Tegula, Tricolia*

Caenogastropoda
Lacunidae: *Lacuna*
Littorinidae: **Littorina*
Rissoidae: *Alvania, Onoba*
Barleeidae: *Barleeia*
Assimineidae: **Assiminea*
Turritellidae: *Tachyrynchus, Turritellopsis*
Vermetidae: *Dendropoma, Vermetus*
Caecidae: *Fartulum, Micranellum*
Cerithiidae: **Bittium*
Potamididae: *Batillaria* (introduced)
Cerithiopsidae: *Cerithiopsis*
Hipponicidae: **Hipponix*
Calyptraeidae: **Crepidula, Crepipatella*
Trichotropididae: **Trichotropis*
Naticidae: *Calinaticina, Natica, Neverita, Polinices*
Marseniidae: *Lamellaria, Marsenina, Marseniopsis*
Velutinidae: *Velutina*
Cymatiidae: *Fusitriton*
Epitoniidae: *Nitidiscala* (=*Epitonium*), *Opalia*
Janthinidae: *Janthina* (pelagic)
Eulimidae: *Balcis, Eulima*
Entoconchidae: *Enteroxenos, Thyonicola*
Muricidae: **Ceratostoma, *Ocenebra, *Trophonopsis,*
Nucellidae: **Acanthina, *Nucella*
Buccinidae: **Buccinium, *Searlesia*
Neptunidae: *Ancistrolepis, *Beringius, *Colus, Exilioidea, *Neptunea, *Plicifusus*
Columbellidae: *Alia, *Amphissa, Mitrella*
Nassariidae: **Nassarius*
Fusinidae: **Fusinus*
Olividae: **Olivella*
Marginellidae: *Granulina*
Cancellariidae: *Cancellaria*
Turridae: *Ophiodermella, Pseudomelatoma, Taranis, Clathromangelia, Kurtzia, Kurtziella, Oenopota, Cymakra, Antiplanes*

Heteropoda
Carinariidae: *Carinaria*
Atlantidae: *Atlantia*
Pterotracheidae: *Pterotrachea*

Pyramidellacea
Pyramidellidae: *Iselica, Odostomia, Turbonilla*

Opisthobranchia, Cephalaspidea
Acteonidae: *Rictaxis, Microglyphis*
Haminoeidae: *Haminaea*
Retusidae: *Volvulella*
Diaphanidae: *Diaphana*
Philinidae: *Philine*
Aglajidae: *Aglaja*
Gastropteridae: *Gastropteron*
Cyclichnidae: *Cylichna, Acteocina*
Runcinidae: **Runcina*

[1]Genera with representatives in Oregon known (or suspected, based on the development of congeners from other regions) to have direct development and therefore lack a larval stage are preceded by an asterisk (*). See the above sources for lists of species known from the Pacific Northwest.

Table continues

Table 2. Families and genera of the class Gastropoda known from the Pacific Northwest (continued)

Opisthobranchia, Anaspidea
Aplysiidae: *Aplysia*, **Phyllaplysia*

Opisthobranchia, Notaspidea
Pleurobranchidae: *Berthella*, *Pleurobranchia*

Opisthobranchia, Sacoglossa
Stiligeridae: *Placida*, *Stiliger*
Elysidae: *Elysia*
Hermaeidae: *Alderia*, *Hermaea*

Opisthobranchia, Nudibranchia, Doridacea
Corambidae: *Corambe*, *Doridella*
Goniodorididae: *Ancula*, *Hopkinsia*
Onchidorididae: *Acanthodoris*, *Onchidoris*, *Adalaria*, *Diaphorodoris*
Notodorididae: *Aegires*
Polyceratidae: *Crimora*, *Laila*, *Polycera*, *Triopha*
Chromodorididae: *Cadlina*
Actinocyclidae: *Hallaxa*
Aldisidae: *Aldisa*
Rostangidae: *Rostanga*
Archidorididae: *Archidoris*
Discodorididae: *Anisodoris*, *Diaulula*, *Geitodoris*

Opisthobranchia, Nudibranchia, Dendronotacea
Tritoniidae: *Tochuina*, *Tritonia*
Dendronotidae: *Dendronotus*
Dotoidea: *Doto*
Tethyidae: *Melibe*

Opisthobranchia, Nudibranchia, Arminacea
Arminidae: *Armina*
Dironidae: *Dirona*
Zephyrinidae: *Janolus*

Opisthobranchia, Nudibranchia, Aeolidacea
Flabellinidae: *Chamylla*, *Flabellina*
Cumanotidae: *Cumanotus*
Eubranchidae: *Eubranchus*
Tergipedidae: *Catriona*, *Cuthona*, *Tenellia*
Fionidae: *Fiona*
Facelinidae: *Hermissenda*
Aeolidiidae: *Aeolidia*, *Cerberilla*

Opisthobranchia, Thecosomata, Euthecosomata
Limacinidae: *Limacina*
Cavoliniidae: *Cavolinia*, *Clio*, *Creseis*, *Diacria*, *Styliola*, *Cuvierina*

Opisthobranchia, Thecosomata, Pseudothecosomata
Cymbuliidae: *Corolla*

Opisthobranchia, Gymnosomata
Clionidae: *Cliona*
Pneumodermatidae: *Pneumoderma*, *Pneumodermopsis*
Cliopsidae: *Cliopsis*

Gymnomorpha
Onchidiidae: **Onchidella*

Pulmonata
Melampidae: **Mysotella* (= *Ovatella*)
Siphonariidae: **Siphonaria*, *Williamia*
Trimusculidae: *Trimusculus*

withdrawl of the body. Adult shells vary from the spiraling coils of whelks and periwinkles, to the cap-shaped shells of limpets and abalone, to the sessile, calcareous tubes secreted by the wormlike vermetid snails. The shell and operculum are reduced or lost altogether in postlarval slugs and free-swimming forms.

All gastropods are characterized by an unusual developmental phenomenon called torsion, a 180º twisting of the viscera, mantle, and shell relative to the head and foot. Torsion results in a forward placement of the gill, anus, and reproductive openings, all of which are housed in a cavity formed by the overhanging mantle and shell. Gastropods lacking shells generally lack a mantle cavity and also show varying degrees of detorsion. The latter is manifested externally by the position of the anus, gill, and reproductive openings on the right side or posterior end of the organism and can impart a superficial bilateral symmetry to the body.

Adult gastropods exhibit a wide range of feeding modes, ranging from generalist, grazing herbivory, to specialized carnivory, to suspension feeding with mucus nets. Except for some highly specialized ectoparasites, suctorial predators, and suspension-feeders, all use a tooth-studded, ribbon-like radula in feeding. The radula is unique to the Mollusca, and in different groups of gastropods its teeth are variously modified for rasping, grasping, pulling, piercing, or harpooning prey. Acting in concert with secretions from the foot, the radula is also used by members of some taxa for drilling through the shells and skeletons of their prey.

Individuals of most prosobranchs are either male or female, whereas most heterobranchs are hermaphroditic. Fertilization can be external or internal, and eggs are freely spawned into the water column or deposited in a wide variety of benthic or even pelagic egg masses and capsules. Individuals of some species brood their egg capsules, especially in the mantle cavity or under the foot. Reproduction and development of many Pacific Northwest species are summarized by Strathmann (1987), and comparative data on the development of most opisthobranchs known from the Pacific Northwest are presented in Appendix A (pages 118-22).

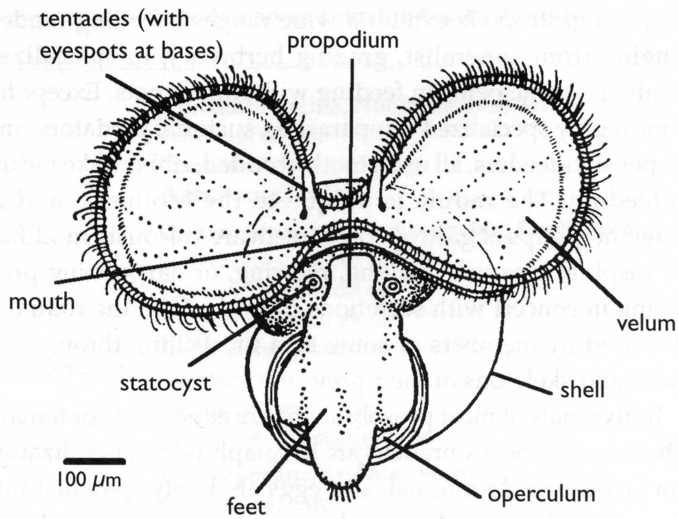
Larval Forms

Most gastropods hatch from their egg coverings as one of two types of larval forms, veligers and trochophores. A minority (although this can include entire clades) bypass a planktonic larval stage in their life cycles and hatch as crawl-away juveniles (e.g., species of *Nucella*). Though not strictly planktonic, hatchlings of many of these "directly developing" species are capable of significant dispersal via drifting in the water column and may be caught in plankton tows near adult habitat (Martel and Chia, 1991). The same can also apply to post-larval stages of species with planktonic development. Identification of post-larval and juvenile stages is better accomplished using adult characters and is beyond the scope of this chapter. Keen and Coan (1974) and Kozloff (1996) provide keys to adult gastropods known from the Pacific Northwest.

Veliger Larvae

Most gastropods hatch from benthic or pelagic egg capsules or egg masses as veliger larvae (Figs. 1, 2). Gastropod veligers are distinguished by their univalve, usually coiled shells and an anterior, round to multilobed velum, the primary organ of

Fig. 1. External morphology of a veliger larva, ventral view. (Modified from Fretter and Graham, 1962, Fig. 237A)



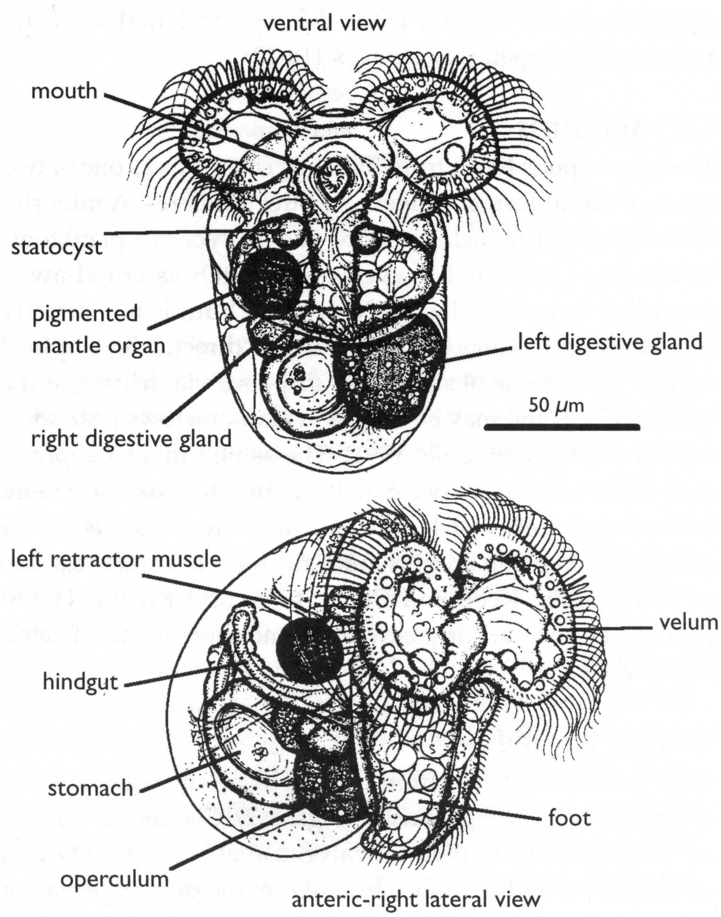


Fig. 2. Internal anatomy of a veliger larva. (Modified from Rasmussen, 1951, Fig. 14)

propulsion and food particle capture. The velar lobes of planktotrophic species especially are delicate, extensible, and edged with two powerful circlets of cilia that bound a ciliated food groove (Hyman, 1967). Most veliger larvae also have an operculum, carried on the back of the foot, which is used to close the shell aperture after withdrawal of the body into the shell. Except for the velum, the body plan of most gastropod veligers resembles that of a typical adult prosobranch with a coiled shell. Although there is not a close correspondence between larval and adult appearance which might allow specific identification of one based solely on knowledge of the other (Fretter and Pilkington, 1970), larval shells do persist as "protoconchs" at the apex of the shells of many adult gastropods. Thus, larval shells can be identified by comparison with the protoconch of an identified juvenile or adult specimen (Thorson, 1946; Robertson, 1971; Thiriot-Quiévreux, 1980).

The veliger stage can last from days to months, depending on larval feeding mode (i.e., lecithotrophic vs. planktotrophic), taxon (especially at the species level), and environmental factors such as food supply and presence of settlement cues. Larval life ends with settlement and metamorphosis into a post-larva or juvenile, a process often triggered by specific environmental cues. In the absence of these cues, metamorphosis can be delayed for long periods. The larvae of holoplanktonic species obviously do not settle to the bottom like those of benthic species, and metamorphosis for many of these is a more gradual process.

A major component of metamorphosis in both holoplanktonic and meroplanktonic species is the irreversible loss or absorption of the velum. After metamorphosis the foot takes over as the organ of propulsion, and its development, especially of the propodium, is one of the best indicators of metamorphic competence.

Trochophore Larvae

Some of the more primitive prosobranchs hatch from their egg coverings as trochophores (Fig. 3), a developmental stage shared with other coelomate protostomes (e.g., polychaete annelids) and one that most gastropods pass through as encapsulated embryos. Gastropod trochophores do not feed on particulate matter (they may take up dissolved organic matter) and swim by means of the prototroch, a band of ciliated cells encircling the body (see Fig. 3). Prosobranchs hatching as trochophore larvae include all of the Patellogastropoda (except those hatching as crawl-away juveniles) and some of the Vetigastropoda (e.g., haliotids and some of the trochids). The

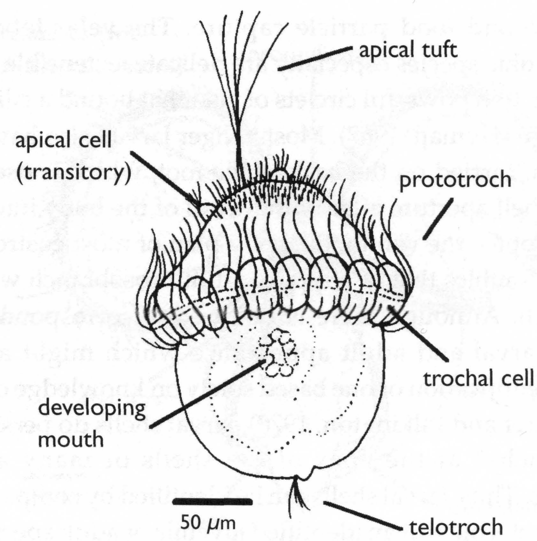


Fig. 3. Gastropod trochophore larva, ventral view. (Modified from Kessel, 1964, Fig. 6)

trochophore stage is short in gastropods, lasting only a few hours, and grades into the veliger stage as shell secretion and development of the foot and velum progress.

Polytrochous Larvae

Veliger larvae of gymnosomatous pteropods, the shell-less "sea-butterflies," develop into fusiform, polytrochous larvae before metamorphosing into juveniles. Polytrochous larvae (see 11 in the key) lack both shell and velum and rely on three ciliary rings for propulsion. This stage grades into the juvenile stage as the swimming wings (specialized lobes of the foot) enlarge and replace the ciliary rings as the primary means of propulsion.

Identification of Local Taxa

The key in this chapter is largely pictorial and based on gross morphological features such as shell shape and sculpture, shape of the velum, and, to a lesser degree, color pattern. Identification is best accomplished using live material, but many diagnostic characters are apparent in specimens relaxed in 7.5% magnesium chloride and fixed in 4% formalin buffered with borax (see Strathmann, 1987, Chap. 1, pp. 228–29). Most of the illustrations used in the key were obtained from the primary literature; sources of these are listed in Appendix B (page 123).

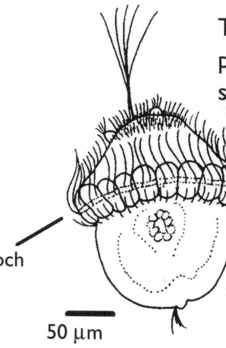
For many taxa identification of larvae is not possible beyond the level of family or even order, either because the larvae of most local species have not been described, or because the larvae of closely related species are not sufficiently differentiated to permit identification based on qualitative morphological features (the latter applies especially to young larvae). In many cases, diagnoses are based on descriptions of close relatives from other parts of the world. Many of these descriptions give more detail than could be included in this chapter, and workers are encouraged to examine the primary literature. The most useful references, especially for the larvae of the prosobranchs, include Thorson (1946), Fretter and Pilkington (1970), Richter and Thorson (1975), Pilkington (1976), and the works of M. Lebour and C. Thiriot-Quiévreux.

If a larva keys to a group of opisthobranchs, the comparative data provided in Appendix A (especially data on type and size of the shell) may help to narrow the choices.

Nomenclature used in the keys generally follows Austin (1985), Kozloff (1996), and Behrens (1990), and these sources should be consulted for lists of gastropod species found in the region.

Key to Marine Gastropod Larvae of Oregon

1



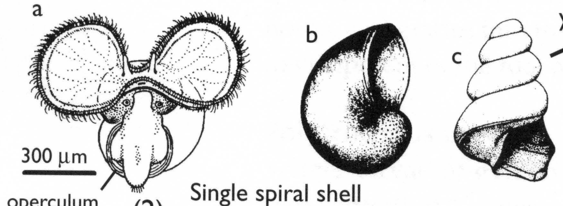
Top-shaped, with prototroch, but no shell or velum — yes → Most Patellogastropoda and some Vetigastropoda. Go to 1-1 (page 98)

Trochophore larvae

no ↓

Veliger larvae

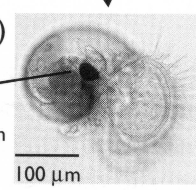
2



Single spiral shell — yes → Shield-like **operculum** present on back of foot (see Figs. 2a, 3b)

- yes → Most Gastropoda. Go to 2-1 (p. 99)
- no ↓

(2A)

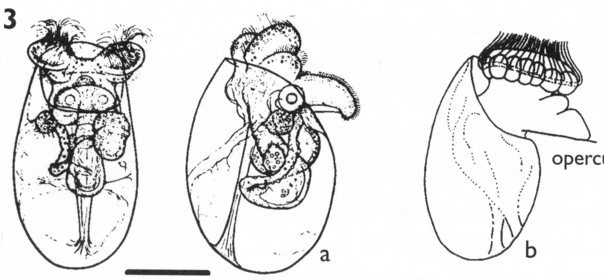


Darkly **pigmented mantle organ** (PMO) on the right side of the body near the anus

- no → Early veliger of doridacean multibranch *Aegires albopunctatus* (see Goddard 2001). For late veliger see Fig. 9
- yes → Early veliger of notaspidean opisthobranchs *Pleurobranchae californica* (pictured in Fig 2A) or *Berthella californica*. For later veligers of these species, see Figs. 8a, 8b (p. 96)

Single spiral shell — no ↓

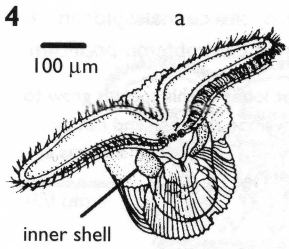
3

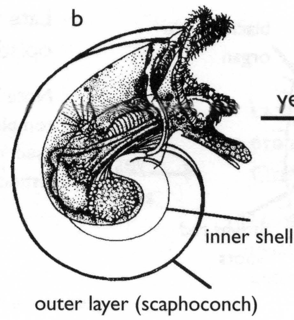


Egg-shaped, inflated shell, truncated more or less by shell aperture; coiling hardly discernable

- no → 4 (next page)
- yes → Most Patellogastorpoda and some Nudibranchia. Go to 3-1 (p. 112)

4



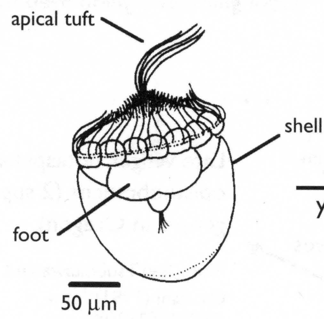


Double spiral shell

yes → Echinospira larvae of marseniid and velutinid prosobranchs. Go to 4-1 (p. 113)

↓ no

5

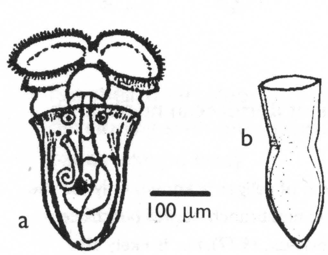


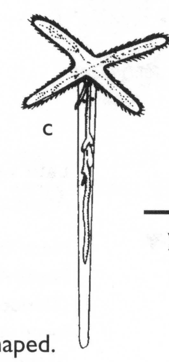
Cap- to bowl-shaped shell; velum round to oval, not bilobed

yes → Early veliger of patellogastropods and those vetigastropods hatching as trochophores. The former possess an apical tuft of non-motile cilia; the latter do not. This stage is brief in both groups and rapidly develops into a fully developed veliger (for later veligers of these two groups, see 3-1 and 2-4.1 to 4-2)

↓ no

6





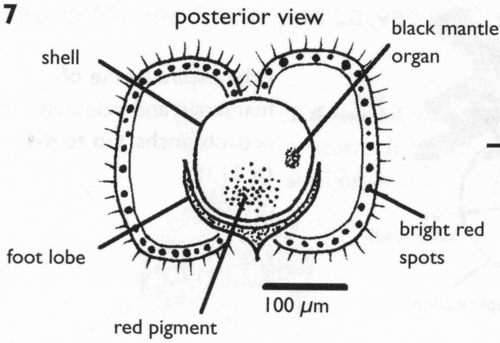
Shell-, thimble-, cone-, or vase-shaped. Bi- to multi-lobed velum

yes → Cavoliniid thecosomatous pteropods and gymnosomatous pteropods. Go to 6-1 (p. 114)

↓ no

7 (next page)

7



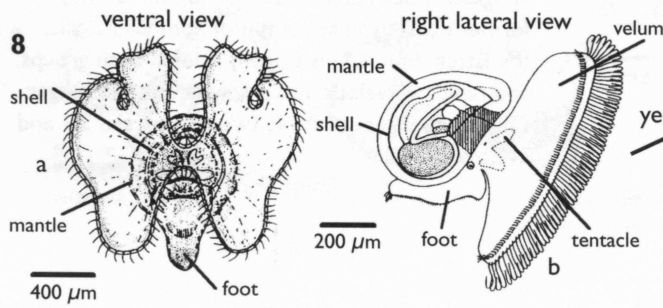
Coiled shell present but covered or obscured by lateral lobes of the **foot**. Bright red spots around edge of velum

yes → Late veliger of the cephalaspidean opisthobranch *Gastropteron pacificum*

Note: The foot lobes of this species grow to completely envelope the shell and can be used for swimming. This species also has a distinctive shell (see Fig. 2-12)

no ↓

8



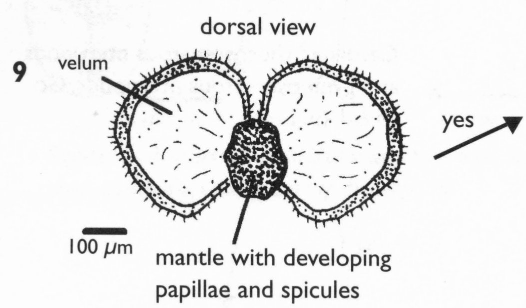
Coiled shell present but mostly or completely covered by the **mantle**; no operculum

yes → Late veliger, notaspidean opisthobranchs (2 spp. in 2 genera in Oregon)

Note: See Tsubokawa and Okutani (1991) for a description of mantle growth in these larvae; except for their lack of an operculum, the early larvae are similar to those of other opisthobranchs with paucispiral shells and pigmented mantle organs (PMOs) (see Figs. 2-8b, 2-15, 2-9-8)

no ↓

9



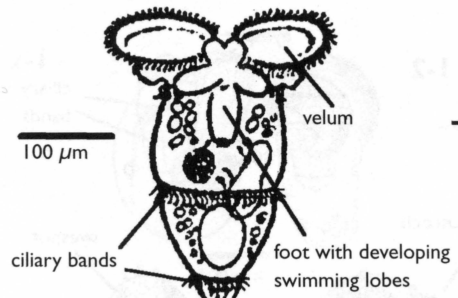
yes → Late veliger of doridacean nudibranch *Aegires*.

Note: This type of veliger is known only for the North Atlantic nudibranch *Aegires punctilucens* (Thiriot-Quiévreux, 1977), but is likely also found in the northeastern Pacific *A. albopunctatus* (Goddard, 2001)

no ↓

10 (next page)

10



No shell or operculum. Velum present. Ciliary bands around fusiform body; foot with developing swimming lobes

yes → Late veliger of gymnosomatous pteropods (4 species in 4 genera off Oregon)

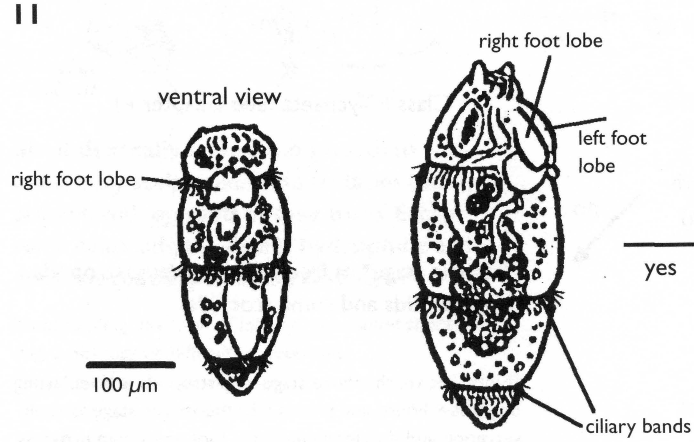
Note: *Clione limacina,* pictured at left, is the most abundant gymnosome nearshore and is occasionally found in Oregon bays

Veliger larvae

no ↓

Polytrochus larvae

11



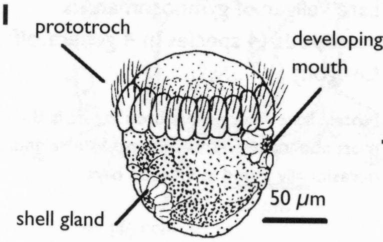
No shell, operculum, or velum. Small foot with developing swimming lobes or "wings"; three ciliary bands around body

yes → Polytrochous larvae. Last larval stage of gymnosomatous pteropods (4 species in 4 genera off Oregon)

Note: *Clione limacina,* pictured at different stages of development at left, is the most abundant gymnosome nearshore and is occasionally found in Oregon bays

From 1 (top-shaped, with prototroch, but no shell or velum)

1-1

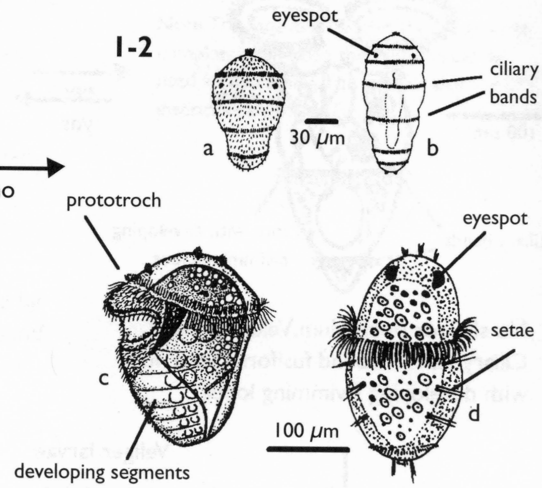


Top-shaped, with large trochal cells and shell gland

yes → 1-3

no → 1-2

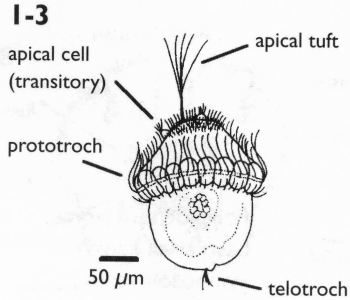
1-2



Small trochal cells and some combination of eyespots, setae (bristles), and segmentation

yes → Class Polychaeta (see Chapter 6)

1-3



Apical tuft (of non-motile cilia) and telotroch

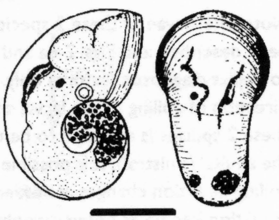
yes → Hatching stage* of most Patellogastropoda

no → Hatching stage* of free-spawning Vetigastropoda (e.g., haliotids and some trochids)

*Note: The trochophore stage of gastropods is brief, lasting only a few hours, and grades into the veliger stage as shell secretion and development of the foot and velum progress

From 2 (single spiral shell)

2-1

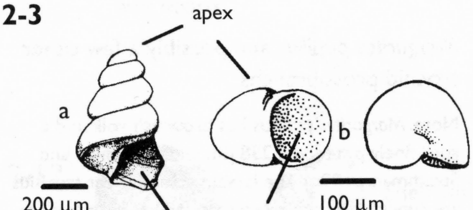


Shell planispiral (coiling in one plane) or nearly so

yes → Go to 2-2 (p. 103)

no ↓

2-3



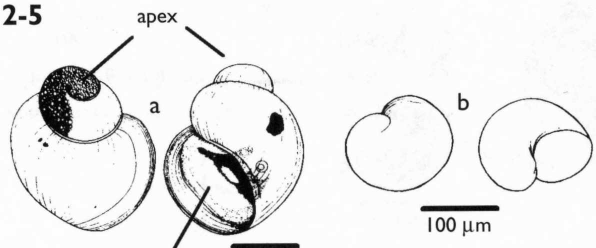
Shell dextrally coiled and smooth to elaborately sculptured. Head tentacles usually present, with eyespots at their bases. Except some epitoniids, the shell is **hydrophilic** and does not get trapped at the air-water interface

Note: Coiling direction of inflated, paucispiral shells (Fig. 2-3b) may be difficult to determine

yes → Most prosobranch gastropods. Go to 2-4 (p. 106)

no ↓

2-5



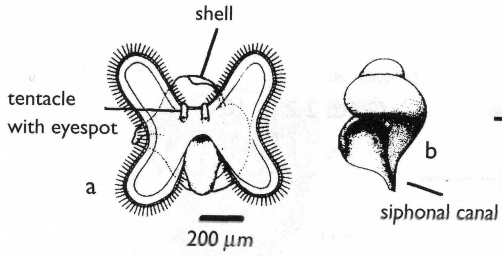
Shell sinistrally (counter clockwise) coiled and generally unsculptured. Head tentacles usually lacking, but if present they are usually separate from and anterior to the eyespots. Velum usually bilobed. Most heterobranchs (starting on section 2-8) and a few prosobranchs (next 2 sections, 2-6, 2-7). The former have hydrophobic shells, the latter hydrophilic ones

Note: Coiling direction of inflated, paucispiral shells (Fig. 2-5b) may be difficult to determine

yes ↓

2-6 (next page)

2-6



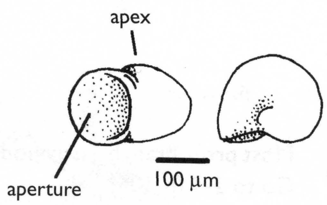
Tentacles with eyespots; shell multiwhorled, with well-developed siphonal canal

→ yes: Turrid prosobranchs *Antiplanes voyi* and *A. perversa*.

Note: The larvae of these 2 species have not been described and Figs. 2-6a and b are used to depict diagnostic features only. In addition, direction of coiling of the larval shells of these 2 species is assumed to be the same as the adults' (sinistral); it is possible that their coiling direction changes at settlement, a condition known as heterostrophy (see Hadfield and Strathmann, 1990; and Box 1, p. 102)

↓ no

2-7



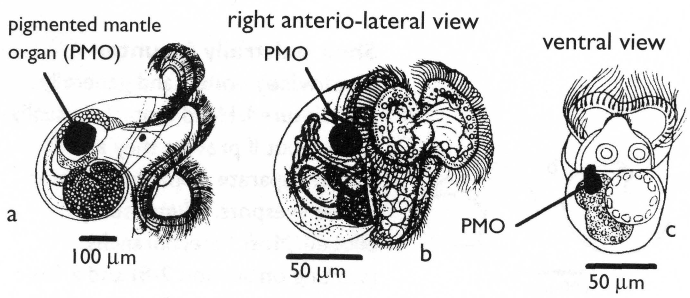
Velum round to only slightly bilobed. Inflated, paucispiral shell of about one whorl. Larvae semiopaque, owing to brown to greenish yolk reserves, and develop head and foot tentacles at metamorphosis. Shell coiling changes direction at metamorphosis, becoming dextral (see Box 1, p. 102)

→ yes: *Margarites pupillus* and possibly a few other trochid prosobranchs

Note: *Margarites pupillus* has brownish yolk and a shell finely pitted and 238 μm wide (Hadfield and Strathmann, 1990). The larval shells of most trochids are superficially similar to that of *M. pupillus* but are dextrally coiled (see section 2-4). Most trochids have non-feeding, pelagic, lecithotrophic development and settle after about a week in the plankton (Hickman, 1992)

↓ no (most heterobranchs)

2-8



Body with **pigmented mantle organs** (PMOs) located on the right side, near the anus

→ no: Go to 2-9 (p. 104)

↓ yes

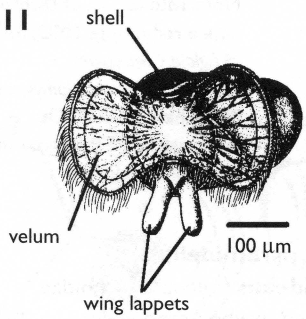
2-10 (next page)

2-10 Black pigment on visceral mass → yes → Late veliger, aglajid opisthobranch *Melanochlamys diomedea* and possibly some sacoglossan opisthobranchs.

Note: Hatching *Melanochlamys* has a nearly black PMO and an inflated, paucispiral shell. PMOs are not known in the larvae of the few local species of sacoglossans that have been examined

↓ no

2-11

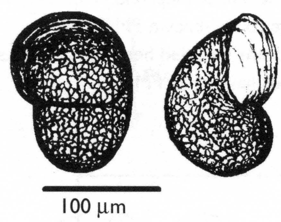


Foot with wing lappets (developing swimming wings). Shell with purple tinge, low spire, and high aperture → yes → Late veliger, euthecosome pteropod *Limacina helicina*

Note: Presence of a PMO in the late larvae is inferred from Paranjape's (1968) description of the hatching larvae of this species

↓ no

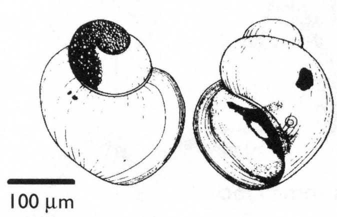
2-12



Shell with netlike sculpture of slightly raised ridges → yes → Early veliger, cephalaspidean opisthobranch *Gastropteron pacificum*

Note: *Gastropteron pacificum* larvae have a black PMO and develop lobes (parapodia) on the foot and bright red spots on the edge of the velum (for later stage larvae see section 7)

↓ no



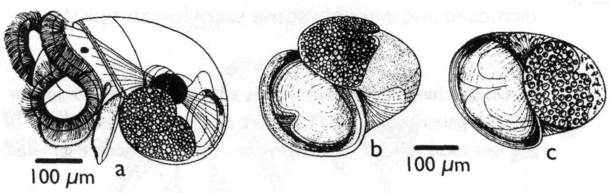
Shell with 2–2.5 whorls, medium high spire, large body whorl, and rounded apex → yes → Late veligers, **pyramidellid heterbranchs** (17 species in 3 genera; in need of taxonomic revision)

Note: PMOs variably colored. Larvae of some species may develop head tentacles prior to metamorphosis. Heterostrophic shell growth (see Box 1, p. 102)

↓ no

2-14 (next page)

2-14



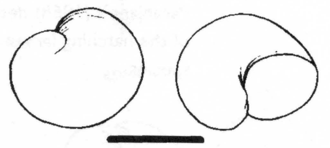
Shell 1.5–2.25 whorls, low spire, rounded apex, and large aperture

yes → Late veliger, **cephalaspidean opisthobranchs** (except families Cylichnidae, Retusidae, and maybe Acteonidae, which lack PMOs)

Note: Late Larvae of *Diaphana* have a red-orange PMO; those of *Aglaja, Gastroperon, Haminaea, Melanochlamys,* and *Philine* have black PMOs. Heterostrophic shell growth (see Box 1, below)

no ↓

2-15

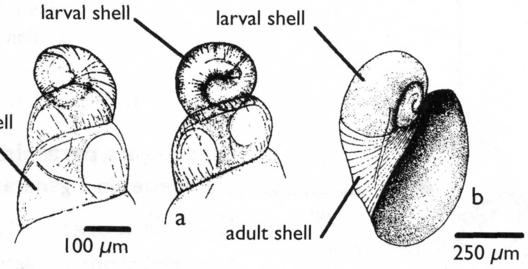


Inflated, paucispiral shell of less than 1.5 whorls; bilobed velum; with or without eyespots

yes → Early veliger, **pyramidellids, cephalaspideans** (minus Cylichnidae, Retusidae, and maybe Acteonidae), **notaspidean heterobranchs,** and pteropod *Limacina helicina*

Note: Early larvae of *Diaphana, Haminaea,* and *Aglaja* have orange to red-brown PMOs; other cephalaspideans included here and at least some pyramidellids have black PMOs

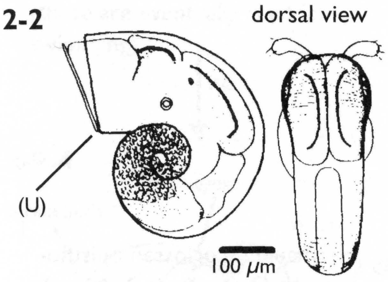
Box 1. Heterostrophic shell growth



In most heterobranchs shelled as adults and some trochid prosobranchs, the direction of shell coiling changes at metamorphosis, a condition known as heterostrophy. The shells of (a) pyramidellids become dextral and conical in shape; those of (b) the cephalaspideans dextral and cylindrical or bulloid, with an aperture nearly as long as the entire shell

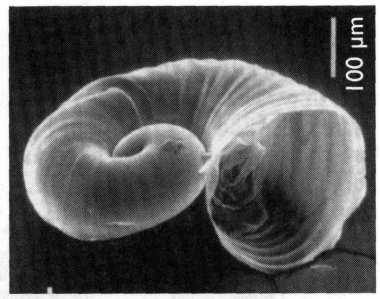
From 2-1 (shell planispiral, or nearly so). Also see double spiral shells, section 4-2

2-2



Outer whorl starting to uncoil (U)

yes → **2-2-1**



Shell thin, with accordion-like transverse folds, especially on the outer whorl. Velum with 4 lobes

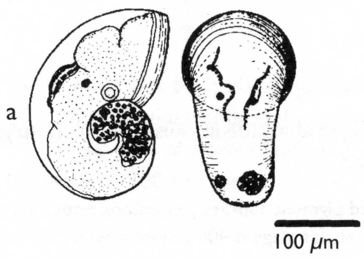
yes → Late veliger of pterotracheid heteropod prosobranch *Pterotrachea coronata*

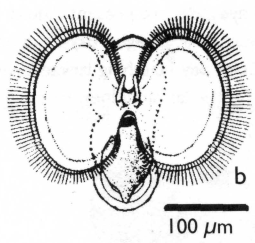
Note: Heteropods are visual predators and in the larval stage develop complex eyes with a lens and retina (see Thiriot-Quiévreux, 1973)

no → Late veliger of **caecid prosobranchs** (2 species in 2 genera in Oregon)

Note: Velum of caecids is bilobed (see Fig. 2-2-2b) and the shell is smooth

no ↓





Sides of shell relatively straight (not inflated or rounded)

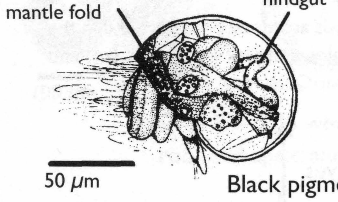
yes → Early veliger, **caecid prosobranchs** (2 species in 2 genera)

no → Early veliger, **Calyptraeidae** (slipper shells; 5 species in 2 genera; some of these, as known for *Crepidula adunca*, may lack a planktonic phase and hatch as crawl-away juveniles) or **pterotracheid heteropods** (2 species in one genus)

Note: The calyptreids have a bilobed velum and develop simple eyespots; the pterotracheids develop a 4-lobed velum and complex eyespots with a lens and retina

From 2-8 (without pigmented mantle organs)

2-9 left lateral view



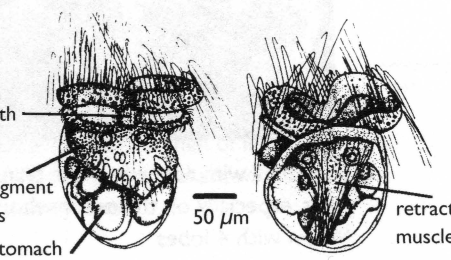
Black pigment on mantle fold at edge of shell

yes → Early veliger, hermaeid sacoglossan opisthobranch *Aplysiopsis enteromorphae*

Note: This species can be abundant on the green alga *Chaetomorpha* sp. in Coos Bay

↓ no

2-9-1



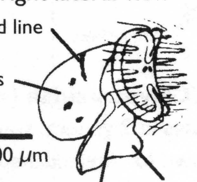
Black pigment scattered on body

yes → Hermaeid sacoglossan opisthobranchs (3 species in 2 genera)

Note: Early larvae of *Alderia modesta* are pictured at left. This species can be abundant on the green alga *Vaucheria* sp. in Coos Bay (Goddard, 1984)

↓ no

2-9-2 right lateral view



4 to 6 red spots on perivisceral membrane, and a red line on the edge of the mantle

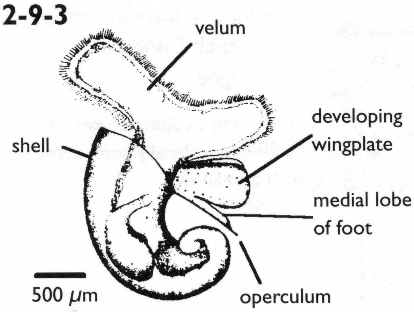
yes → Late veliger, anaspidean opisthobranch *Aplysia californica*

Note: Red pigment appears just before settlement The shell at this stage is 400 μm long, with 2.25 whorls, and propodium and eyespots are present. Adults of this species occur infrequently in Oregon bays, and have not been found in Coos Bay. Hatching larvae have opaque white grains in the larval kidney, an apparently unique trait

↓ no

2-9-3 (next page)

2-9-3



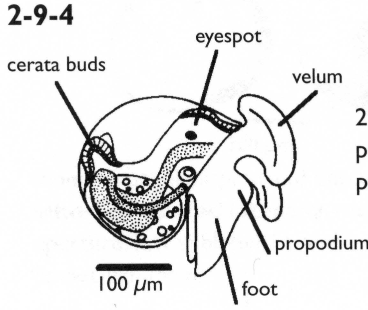
Foot with developing wingplates (these are eventually used for swimming)

yes → Late veliger, pseudothecosome pteropod *Corolla spectabilis* (family Cymbuliidae)

Note: The cymbuliid *Gleba* sp. is pictured at left; the larvae of *Corolla spectabilis* are unknown. Late larvae of *Cymbulia peroni*, a cymbuliid from another region, have a 6-lobed velum

no ↓

2-9-4



2 cerata buds present on posterior of body

yes → Late veliger, dentronotacean nudibranch *Melibe leonina*

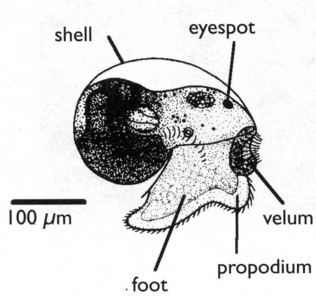
no ↓

2-9-5 Rhinophore buds visible just anterior to eyes, and rudiments of dorsal papillae preset on dorsal part of body. Paucispiral shell of 1.5 whorls, 300 μm long

yes → Late veliger, doridacean nudibranch *Rostanga pulchra*

no ↓

2-9-6



Small velum, large foot with well-developed propodium, and no mantle fold at edge of shell. Paucispiral shell ca. 240 μm long and less than one whorl

yes → Dendronotacea nudibranch *Doto amyra*

Note: Only native nudibranch in Oregon known to have lecithotrophic development

no ↓

2-9-7 (next page)

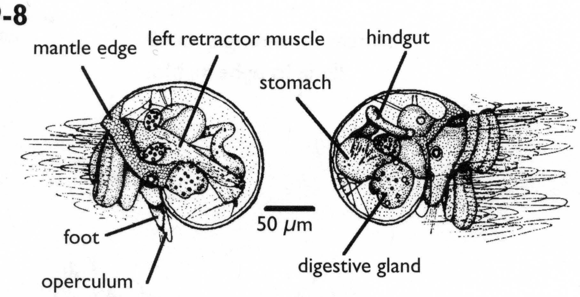
2-9-7 Eyespots and propodium present, mantle withdrawn from edge of shell, all at a shell size of 168 μm

yes → Late veliger, doridacean nudibranch *Doridella steinbergae*

Note: Only nudibranch known to be metamorphically competent at such a small size

no ↓

2-9-8



left lateral view   right ventro-lateral view

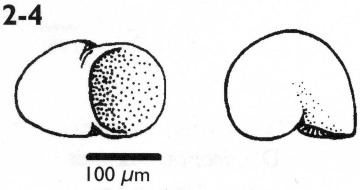
Clear, generally smooth, paucispiral shell. Bilobed velum. Viscera relatively transparent owing to lack of yolk reserves

yes ↓

Early veliger, most nudibranchs (ca. 45 species in Oregon; all but *Doto amyra* have planktotrophic development) and the cephalaspideans of the families Cylichnidae, Retusidae, and possibly Acteonidae (8 species in 4 genera in Oregon)

From 2-3 (shell dextrally coiled)

2-4



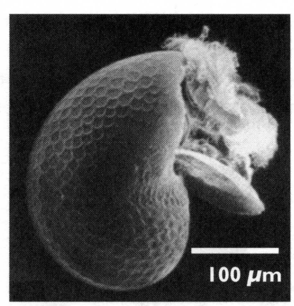
Shell **inflated paucispiral** of 1.25–1.5 whorls. **Round to only slightly bilobed velum.** Body semiopaque owing to yellow, green, or brown yolk reserves

yes →

no ↓

2-4-3 (next page)

2-4-1

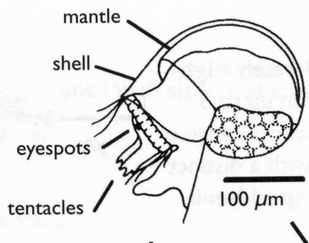


yes ↑ *Calliostoma* (5 species in Oregon)

no ↓

2-4-2 (next page)

2-4-2

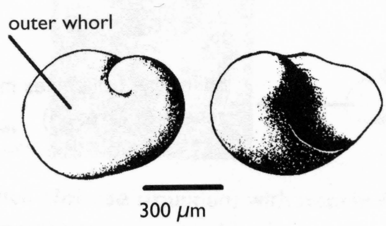


With head tentacles that become branched just before settlement and metamorphosis

yes → *Haliotis* (4 species in Oregon)

no → Most Vetigastropoda

2-4-3

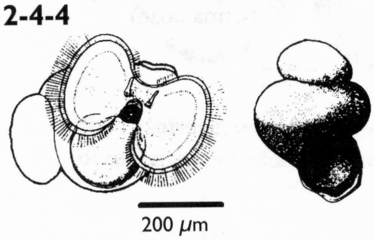


Inner whorl planispiral and unsculptured; **outer whorl expanded laterally**, resulting in large aperture, low shell height, and beginning of limpet-like form

yes → Late veliger, Calyptraeidae (slipper shells; 5 species in 2 genera in Oregon [*Crepidula adunca* has direct development])

no ↓

2-4-4

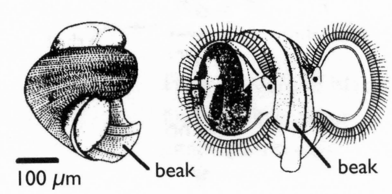


Up to 2.5 **strongly inflated shell whorls**; apex roundly blunted

yes → 2-4-5

no → 2-4-6 (next page)

2-4-5

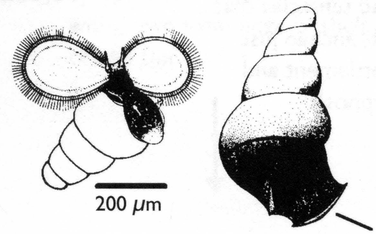


Body whorl with distinct **tongue-shaped beak**

yes → Cerithiidae (5 species of *Bittium*)

no → Turritellidae (3 species in 2 genera)

2-4-6

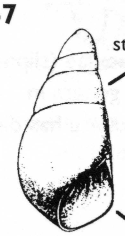


Shell moderately **high-spired**, with up to 5 rounded whorls; edge of aperture with a distinct **chisel-shaped beak**

yes → Certhiopsidae (2 species in Oregon)

no ↓

2-4-7

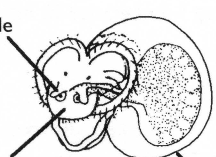


Shell **transparent, shiny,** and relatively **straight-sided**; aperture distinctly angulated

yes → Eulimidae (6 species in 2 genera in Oregon)

no ↓

2-4-8

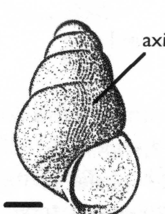


Head with tentacles and a ciliated, snout-like **oral lobe**

yes → Hatching veiger of *Fusitriton oregonensis* (Ctmatiidae)

no ↓

2-4-9



Body with *blue-purple* pigmented mantle organ (PMO; see section 2.8). Shell turbinate, with rounded apex, up to 5 whorls, and fine axial sculpture

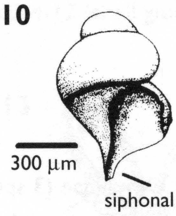
yes → Epitoniidae and Janthinidae (*10 species in 3 genera*)

Note: Hatching larvae of *Nitidiscala tincta* have eyespots, small head tentacles, a black pigmented mantle organ, and a dextral, hydrophobic shell of about 1.3 turns (Collin, 2000)

no ↓

2-4-10 (next page)

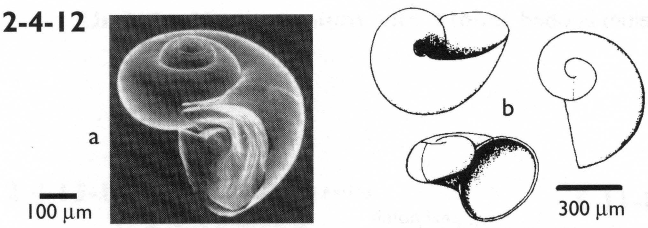
2-4-10



Shell with **siphonal canal** → yes → Go to 2-4-11 (p. 110)

↓ no

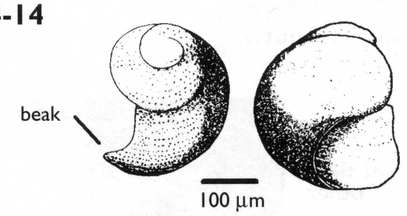
2-4-12



Shell **globose** (rounded) with **nearly flat spire** and **large aperture**; no apertural beak or siphonal canal → yes → Go to 2-4-13 (p. 111)

↓ no

2-4-14

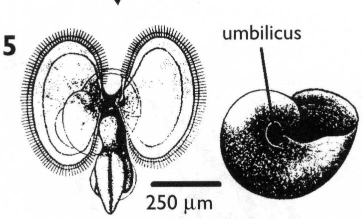


Shell **globose, with beak** on outer lip of aperture and bilobed velum → yes → **Umbilicus** (opening on bottom of shell; see Fig. 2-4-15) present

- no → Rissoidae and Barleeidae (9 species)
- yes → Early veligers of Nassariidae and possibly other caenogastropods

↓ no

2-4-15

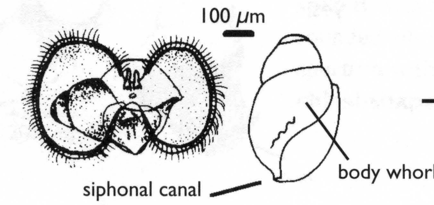


Globose shell with **umbilicus** but **no beak**; velum bilobed → yes → Lacunidae and Littorinidae

Note: At hatching lacunid larvae have a beak on the outer lip of the aperture; it gradually disappears during development. Lacunids develop red pigment on the velum, littorinids purple/black

From 2-4-10 (shell with siphonal canal)

2-4-11

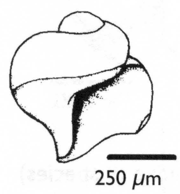


Shell **ovoid** (oval in shape), with **large body whorl and oval shaped aperture**; velum bilobed

yes → Late veligers of Olivellidae (3 species)

no ↓

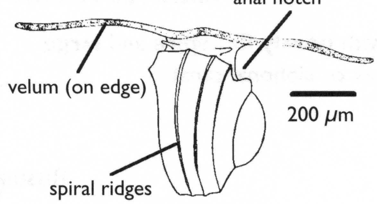
2-4-11-1



Shell globose (roughly spherical in outline)

yes → 2-4-11-2

2-4-11-2



Shell with **wide body whorl**, 3–4 distinct **spiral ridges**, and **anal notch**

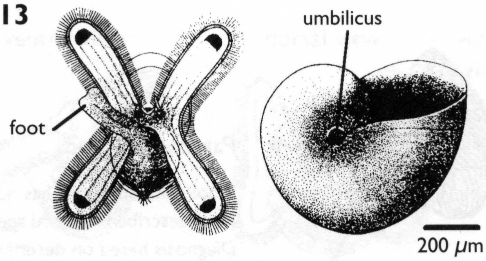
yes → *Oenopota levidensis* (Turridae)

no ↓

Late veligers of Nassariidae and other caenogastropods, including species of Columbellidae, Turridae, and possibly Cancellaridae and some of the Muricidae

From 2-4-12 (shell globose, with flattened spire; no beak or siphonal canal)

2-4-13



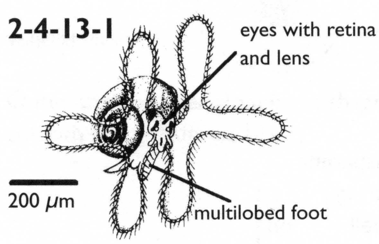
Umbilicus present; **velum with 4 lobes**

yes → Naticidae (6 species in Oregon)

Note: The giant moon snail, *Polinices lewisii*, is the most common moon snail in Oregon bays. Pedersen and Page (2000) give a detailed description of its veliger

↓ no

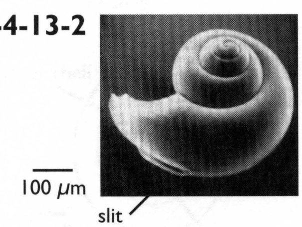
2-4-13-1



Umbilicus absent (?); **velum with 6 lobes; complex eyes** with retina and lens; **multilobed foot**

↓ yes

2-4-13-2

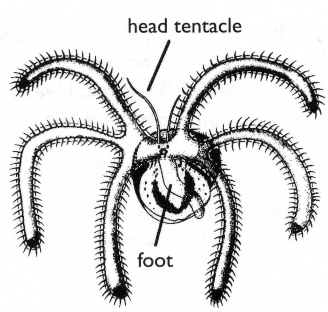


Slit in center of shell lip

yes → Atlantid heteropod *Atlanta peroni*

↓ no

2-4-13-3

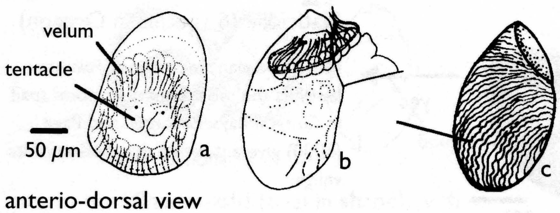


Long head tentacles

yes → Carinariid heteropods (3 species)

From 3 (egg-shaped, inflated shells, coiling hardly discernable)

3-1



anterio-dorsal view

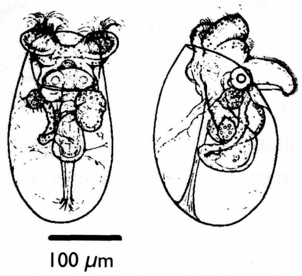
Velum round to oval, with large trochal cells. Tentacles or tentacle buds with eyespots at bases. Shell with granulated or wavy surface sculpture (marked in figure c above)

→ yes: **Patellogastropoda**

Note: Shell sculpture has not been described for local species. Diagnosis based on descriptions of NW Pacific congeners in Amio (1963)

↓ no

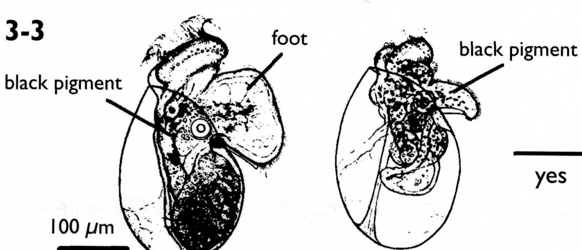
3-2



Shell smooth and transparent and does not grow during larval development. Shell **hydrophobic** (repels water) and is prone to getting trapped in the air-water interface. Velum bilobed. No head tentacles

↓ yes

3-3



a (lecitho.) b (plankto.)

Epidermal black pigment

→ yes: Introduced aeolid nudibranch *Tenellia adspersa*. Shell 195–228 µm long

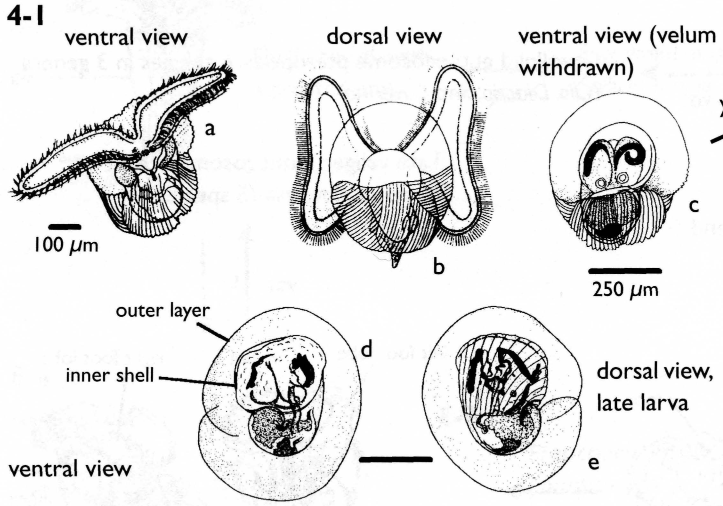
Note: This estuarine species can produce both lecithotropic and planktotrophic larvae. Both types have epidermal black pigment; both are illustrated at left

↓ no

Nudibranchs of the families Dendronotidae, Tergipididae, Eubranchidae, and Fionidae (18 species in 5 genera)

From 4 (double spiral shell). Outer shell (scaphoconch) thin, transparent, not calcified. Inner shell calcified

4-1



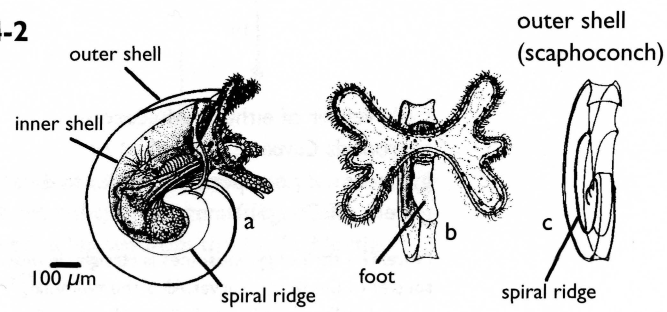
Outer shell or layer globular in shape, with spiral striations early; smooth and gelatinous late

yes → *Velutina velutina* and *V. plicatilis*

Note: The inner shell of late veliger acquires spiral ridges and eventually becomes thick, white, and opaque. Hatching larvae of *Velutina plicatilis* described and depicted by Strathmann (1987) (Fig. 4-1a at left) are virtually identical to young larvae of *V. velutina* described by Thorson (1946) (Fig. 4-1c at left). One, possibly 2, additional species of *Velutina* occur in Oregon; their larvae are unknown

↓ no

4-2



Outer shell flat-sided planispiral

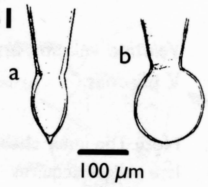
↓ yes

Marseniid prosobranchs (4 species in 3 genera)

Note: Diagnosis based on descriptions of congeners from other parts of the world (e.g., Fretter and Pilkington, 1970; Pilkington, 1976)

From 6 (shells thimble-, cone-, or vase-shaped)

6-1

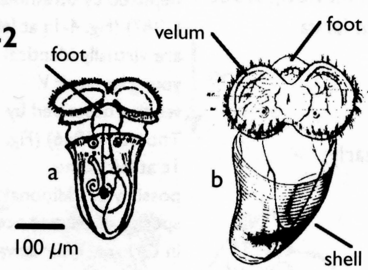


Shell conical with a swollen end

→ yes: Cavoliniid euthecosome pteropods. 6 species in 3 genera (*Clio, Diacria,* and *Cuverina*)

↓ no

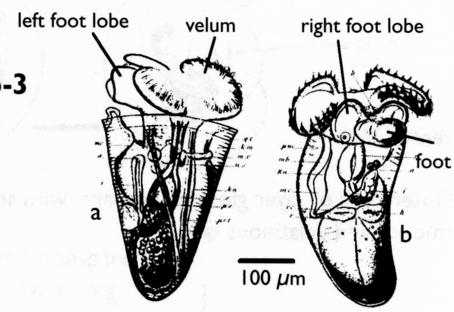
6-2



Shell thimble- to cone-shaped with a rounded end

→ yes

6-3



Foot with 2 developing swimming lobes (wings); these expand as the velum shrinks

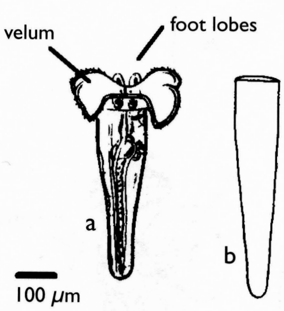
↑ yes: Late veliger, euthecosome pteropods of genus *Cavolinia* (5 species)

↓ no: Early veliger of either euthecosome pteropods *Cavolinia* (5 species) or gymnosome pteropods (4 species in 4 genera off Oregon)

Note: The shell of gymnosomes is straight; in most species of *Cavolinia* it curves. Also, the swimming wings develop early in cavoliniids and not until after shell loss in gymnosomes

(from 6-2) ↓ no

6-4



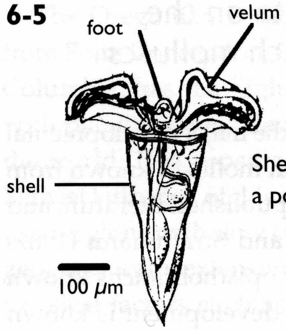
Shell a straight narrow cone with a rounded end

↘ yes: Cavoliniid euthecosome pteropod *Creseis virgula*

↓ no

6-5 (next page)

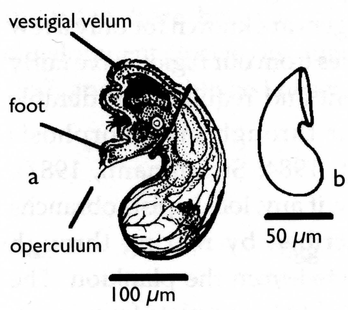
6-5



Shell conical, with a pointed end → yes → Cavoliniid euthecosome pteropod *Styliola subula*

↓ no

6-6



Shell with sinuous branching ridges → yes → Entoconchid prosobranch *Enteroxenos parastichopoli*

Note: Entoconchids are endoparasites of holothuroids (sea cucumbers). They have not been reported from Oregon waters but are likely present, given their occurrence in Washington and the occurrence of their hosts in Oregon. The larvae apparently do not swim (see Lützen, 1979) and are therefore unlikely to be taken in plankton samples

↓ no

Entoconchid prosobranchs (see note above right) of the genus Thyonicola (2 species known from the Pacific Northwest)

Note: The shells of members of this genus are unsculptured (Lützen, 1979)

Appendix A. Comparative data on the development of opisthobranch molluscs reported from Oregon

This appendix provides a summary of the major developmental features of the larvae of opisthobranch molluscs known from Oregon. It is based on a survey of the published literature and my own observations. Hurst (1967) and Strathmann (1987) provide data on additional species of opisthobranchs known from the Pacific Northwest. Mode of development is known for many species and can be determined by morphological examination of hatching veligers or inferred from data on egg size and embryonic period (see table note 2). A glance at the data table will, however, show that both the duration of the larval period and specific morphological characteristics of metamorphically competent veligers are known for only a few species. This is because most species from our region have fairly long planktotrophic development and require considerable skill, care and facilities to rear through metamorphosis (Hadfield and Switzer-Dunlap, 1984; Strathmann, 1987). Moreover, the larval stages of few, if any, local opisthobranchs have been identified and described by rearing through metamorphosis specimens collected from the plankton. The following data, therefore, comprise an incomplete framework for identifying the larvae of these diverse and morphologically flamboyant organisms.

The type or mode of development of most of the opisthobranchs known from Oregon is given in the table. Almost all hatch as free-swimming planktotrophic veliger larvae with a paucispiral shell, operculum, no eyespots, and a small foot lacking a propodium (see Fig. 2). These larvae feed and grow in the plankton for weeks or months and become competent to settle and metamorphose only after they have acquired eyespots, a propodium and sufficient tissue mass and lipid reserves to fuel the transformation into a functional juvenile. Settlement and metamorphosis in many species is triggered by chemical cues emanating from the prey of the adult slugs (Thompson, 1976; Hadfield and Switzer-Dunlap, 1984).

Two species (*Doto amyra* and the introduced *Tenellia adspersa*) hatch from larger eggs as lecithotrophic veligers competent to metamorphose within a few days of hatching, and one or two more (*Phyllaplysia taylori* and probably *Runcina macfarlandi*) lack a larval stage entirely and hatch as crawl-away juveniles. *Tenellia adspersa* (and possibly also the sacoglossan *Alderia modesta*; see table note 6) has variable developmental mode (known as poecilogony) and also hatches as planktotrophic larvae.

The Oregonian biogeographic province, which stretches from Point Conception, California, to Vancouver Island, British Columbia, has the highest proportion (97%) of nudibranchs with planktotrophic development known from any region in the world. This appears to reflect the suitability, at all but the highest latitudes, of this mode of development for nudibranchs from regions with slow currents, high primary production, and geographically extensive adult habitat with weak gradients in physical factors such as temperature and salinity (Goddard, 1992).

Values given for each species are in most cases means (or ranges in means) derived from at least one source. An additional 22 species of opisthobranchs (17 benthic species and five pelagic) have been recorded from Oregon but are not included here because of lack of information on their development. Species list compiled from Goddard (1984, 1990, 1997, and unpublished observations).

Taxa	Egg diameter (µm)	Shell size at hatching (µm)	Shell type[1]	Eyes at hatching	Dev. type[2]	Min. larval period (days)[3]	Shell size at meta-morph. (µm)	Refs.[4]
Cephalaspidea								
Diaphana californica	73	123	I	no	P	–	–	33
Gastropteron pacificum	95	158	I	no	P	–	–	6, 37
Philine auriformis	–	125	I	no	P	–	–	42
Melanochlamys diomedea	98	180	I	no	P	>40	–	6, 37
Rictaxis punctocaelatus	–	137	I	no	P	–	–	44
Runcina macfarlandi	–	–	–	–	D[5]	none[5]	–	–
Anaspidea								
Aplysia californica	81	125-135	I	no	P	34	400	18, 22, 44
Phyllaplysia taylori	144-157	250-300	I	yes	D	none	250-280	19, 44, 47
Notaspidea								
Berthella californica	93	153	I	yes	P	–	–	33
Pleurobranchaea californica	–	150-215	I	no	P	–	–	44, 45
Sacoglossa								
Alderia modesta	62-80	90-130	I	no	P[6]	35	300-340	3, 5, 8, 37, 48
Aplysiopsis enteromorphae	66-70	109-113	I	no	P	–	–	33, 37
Elysia hedgpethi	68	100-105	I	no	P	–	–	9, 37, 44
Hermaea vancouverensis	63	114	I	no	P	–	–	44
Placida dendritica	47-72	82-127	I	no	P	–	–	9, 20, 37, 44
Stiliger fuscovittatus	95	150	I	no	P	–	–	37

table continues

Taxa	Egg diameter (µm)	Shell size at hatching (µm)	Shell type[1]	Eyes at hatching	Dev. type[2]	Min. larval period (days)[3]	Shell size at meta-morph. (µm)	Refs.[4]
Thecosomata								
Limacina helicina	75[7]	~75	1	no	P	>30	300	10, 24
Gymnosomata								
Clione limacina	85, 110	120-160	3	no	P	14[8]	280-360	1, 17, 39
Nudibranchia: Doridacea								
Acanthodoris brunnea	80	130-150	1	no	P	–	–	37
Acanthodoris hudsoni	67-70	127	1	no	P	–	–	36, 37
Acanthodoris nanaimoensis	–	133	1	no	P	–	–	6
Acanthodoris rhodoceras	–	112	1	no	P	–	–	44
Adalaria sp.	83	140	1	no	P	–	–	33
Aegires albopunctatus	98-120	154	1	yes	P	–	–	37, 46
Aldisa cooperi	110	–	1	–	P	–	–	35
Aldisa sanguinea	90-100	163	1	no	P	–	–	35, 41
Ancula pacifica	59	104	1	no	P	–	–	33
Anisodoris lentiginosa	90	154	1	no	P	36	241	30
Anisodoris nobilis	83	153	1	no	P	–	–	33
Archidoris montereyensis	81-90	154-169	1	no	P	–	–	4, 6, 41
Archidoris odhneri	96	186-189	1	no	P	–	–	6, 41
Cadlina flavomaculata	85	140	1	no	P	–	–	44
Cadlina luteomarginata	90-94	–	–	–	P	–	–	27, 41
Cadlina modesta	92	157	1	no	P	–	–	33
Crimora coneja	73	116-119	1	no	P	–	–	33, 41
Diaphorodoris lirulatocauda	63	115	1	no	P	–	–	33
Diaulula sandiegensis	83	130-153	1	no	P	–	–	6, 37, 41
Doridella steinbergae	75-85	142	1	no	P	25	168	26
Geitodoris heathi	73-79	102, 144	1	no	P	–	–	33, 37, 41
Hallaxa chani	81-83	131-152	1	no	P	–	–	33, 41
Hopkinsia rosacea	81-82	141	1	no	P	–	–	44
Laila cockerelli	95	142	1	no	P	–	–	33
Onchidoris bilamellata	100	147-165	1	no	P	38	320	6, 37, 38
Onchidoris muricata	76-80	117-137[9]	1	no	P	>49	–	33, 34, 41
Palio zosterae	65-70	101, 150	1	no	P	–	–	37, 41
Polycera atra	68-71	122	1	no	P	–	–	44
Rostanga pulchra	73-80	148-161	1	no	P	35	300	6, 12, 23
Triopha catalinae	75-87	131-134	1	no	P	–	–	6, 33, 37, 41
Triopha maculata	–	–	1	no	P	–	–	15
Nudibranchia: Dendronotacea								
Dendronotus albopunctatus	108	–	2	–	P	–	–	16
Dendronotus diversicolor	96	–	–	–	P	–	–	11, 37
Dendronotus frondosus	85-90	230-245	2	no	P	–	230-245	37, 41
Dendronotus iris	110	268-280	2	no	P	–	268-280	6, 37
Dendronotus subramosus	–	–	–	–	P	–	–	41
Doto amyra	152	239	1	yes	L	1	239	33, 43
Doto kya	78	133	1	no	P	–	–	43
Doto form B	70	122	1	no	P	–	–	43
Melibe leonina	86-90	140-152	1	no	P	30	250	6, 32, 37, 41
Tritonia diomedea	87	145	1	no	P	34	329	6,21,37
Tritonia festiva	79	131	1	variable	P	—	-	41

Taxa	Egg diameter (µm)	Shell size at hatching (µm)	Shell type[1]	Eyes at hatching	Dev. type[2]	Min. larval period (days)[3]	Shell size at meta-morph. (µm)	Refs.[4]
Nudibranchia: Arminacea								
Armina californica	95-102	160	1	no	P	–	–	6, 37
Dirona albolineata	70	113-129	1	no	P	–	–	6, 37, 41
Dirona aurantia	–	139	1	no	P	–	–	6
Dirona picta	80[10]	–	–	–	P	–	–	7
Janolus fuscus	81	138	1	yes	P	–	–	41
Nudibranchia: Aeolidacea								
Aeolidia papillosa	74	116-138	1	no	P	–	–	6, 29, 37
Catriona columbiana	100-109	274-302[11]	2	yes	P	–	274-302	33, 44
Catriona rickettsi	98-103	291	2	yes	P	–	291	44
Cuthona abronia	95	224	2	yes	P	–	224	40
Cuthona albocrusta	97	270-281	2	yes	P	–	270-281	6, 40
Cuthona cocoachroma	95	257-277	2	variable	P	–	257-277	33, 40
Cuthona divae	107	249	2	no	P	–	249	33
Cuthona fulgens	94	252	2	yes	P	–	252	40
Cuthona lagunae	98	262	2	yes	P	–	262	40
Cumanotus fernaldi	73	119-130	1	no	P	–	–	6, 41
Eubranchus olivaceus	85	244	2	variable	P	–	244	6, 41
Eubranchus rustyus	93	240	2	yes	P	–	240	33
Fiona pinnata	100-150	280	2	no	P	–	280	14, 31, 37, 44
Flabellina fusca	–	133	1	no	P	–	–	6
Flabellina trilineata	60-65	100-110	1	no	P	–	–	13, 37, 41
Hermissenda crassicornis	65	102-119	1	no	P	34	310	6, 25, 29, 41
Tenellia adspersa	72, 103	195-228	2	yes	P or L[12]	variable[13]	195-228	2, 28, 41, 44

[1]Shell type: 1 = sinistral, pauci-spiral shells; generally 0.75 to 1 whorl. 2 = egg-shaped, inflated shells; these do not grow after hatching. 3 = thimble-shaped or hemiellipsoid shell that flares with growth after hatching.

[2]Development type: P = planktotrophic, L = lecithotrophic, D = direct (capsular metamorphic or ametamorphic). When not stated by the original author, I have assigned development type according to criteria described by Thompson (1967), Bonar (1978), Todd (1983), Hadfield and Switzer-Dunlap (1984), and Hadfield and Miller (1987). Development type was inferred for five species (*Aldisa cooperi, Dendronotus albopunctatus, D. diversicolor, D. subramosus,* and *Dirona picta*) using information on egg size, embryonic period, and comparisons with congeners (see Goddard, 1992, pp. 38–41).

[3]Duration of larval period varies with temperature and food supply. Values given are from laboratory studies (see references) using culture temperatures ranging 10–15° C (16° C for *Clione limacina*).

[4]1, Lebour (1931); 2, Rasmussen (1944); 3, Rasmussen (1951); 4, McGowan and Pratt (1954); 5, Hand and Steinberg (1955); 6, Hurst (1967); 7, Marcus and Marcus (1967); 8, Seelemann (1967); 9, Greene (1968); 10, Paranjape (1968); 11, Robilliard (1970); 12; Anderson (1971); 13, Bridges and Blake (1972); 14, Holleman (1972); 15, Mulliner (1972); 16, Robilliard (1972); 17, Lalli and Conover (1973); 18, Kriegstein et al. (1974); 19, Bridges (1975); 20, Clark (1975); 21, Kempf and Willows (1977); 22, Kriegstein (1977); 23, Chia

notes continue

and Koss (1978); 24, Lalli and Wells (1978); 25, Harrigan and Alkon (1978); 26, Bickell and Chia (1979); 27, Dehnel and Kong (1979); 28, Eyster (1979); 29, Williams (1980); 30, Millen (1982); 31, Schmekel and Portmann (1982); 32, Bickell and Kempf (1983); 33, Goddard (1984); 34, Millen (1985); 35, Millen and Gosliner (1985); 36, Goddard (1987); 37, Strathmann (1987); 38, Chia and Koss (1988); 39, Lalli and Gilmer (1989); 40, Goddard (1991); 41, Goddard (1992); 42, Gosliner (1995); 43, Goddard (1996); 44, Goddard (unpublished observations); 45, Chivers (1967); 46, Goddard (in press); 47, Bertsch and Hirshberg (1973); 48, Krug (1998).

[5]Development has not been examined for *Runcina macfarlandi*; however, direct development is considered diagnostic of the genus (Thompson and Brodie, 1988).

[6]Krug (1998) reported that a population of *Alderia modesta* in San Diego, California, produces planktotrophic larvae from eggs 68 µm diameter and lecithotrophic larvae from eggs 105 µm diameter. Hatching larvae of the latter had shells 186 µm long.

[7]Paranjape (1968, p. 323) stated that "the egg diameter was 95–100 µm in the longest dimension, while the diameter of the ovum was 75 µm." I am assuming that by "egg diameter" Paranjape meant "egg capsule."

[8]Duration of veliger larval stage only; gymnosomes have a second, "polytrochous," larval stage that undergoes a gradual metamorphosis into the adult stage.

[9]Hurst (1967) reported an anonymously high value of 186 µm.

[10]Marcus and Marcus (1967) did not specify if this value was obtained from measurements of living or preserved material.

[11]Hurst (1967) reported an anonymously low value of 230 µm.

[12]Embryos from different egg masses hatch as either planktotrophic or lecithotrophic larvae. In addition, Eyster (1979) reported capsular metamorphic development in some *Tenellia adspersa* (as *T. pallida*) from South Carolina.

[13]Hours for the lecithotrophic larvae; unknown for the planktotrophs.

Appendix B. Sources of illustrations used in the key

1a (Kessel, 1964: 6)
2a (Fretter and Graham, 1962: 237a)
2b (Rasmussen, 1951: 15)
2c (Pilkington, 1976: 2A)
2.a (personal)
3a (Rasmussen, 1944: 19)
3b (Kessel, 1964: 11)
4a (Strathmann, 1987: 11.13)
4b (Fretter and Graham, 1964: 245B)
5a (Kessel, 1964: 8)
6a (Lebour, 1931: plate 1, fig. 6)
6b (van der Spoel, 1967: 61B)
6c (Yamaji, 1977: plate 139, fig. 4c)
7 (personal)
8a (Thiriot-Quiévreux, 1967: 2A)
8b (Tsubokawa and Okutani, 1991: 7C)
9 (personal)
10 (Lebour, 1931: plate 1, fig. 9)
11 (Lebour, 1931: plate 1, figs. 10 and11)
1.1 (after Crofts, 1937: 41a)
1.2a (Chapter 9, p. X)
1.2b (Chapter 9, p. X)
1.2c (Chapter 9, p. X)
1.2d (Chapter 9, p. X)
1.3 (Kessel, 1964: 6)
2.1 (Thorson, 1946: 108A and B)
2.3a (Pilkington, 1976: 2A)
2.3b (Hadfield and Strathmann, 1990: 2B and C)
2.5a (Thorson, 1946: 117A and B)
2.5b (Rasmussen, 1944: 6)
2.6a (modified from: Pilkington, 1976: 11F)
2.6b (modified from: Pilkington, 1976: 11H)
2.7 (modified from: Hadfield and Strathmann, 1990: 2B and C)
2.8a (Thorson, 1946: 152B)
2.8b (Rasmussen, 1951: 14, lower)
2.8c (Thorson, 1946: 152A)
2.11 (Lalli and Gilmer, 1989: 35C)
2.12 (Hurst, 1967: 24.19)
2.13 (Thorson, 1946: 117A and B)
2.14a (Thorson, 1946: 152C)
2.14b (Thorson, 1946: 147B)
2.14c (Thorson, 1946: 145C)
2.15 (Rasmussen, 1944: 6)
Box 1,a (Rasmussen, 1944: 7)
Box 1, b (Thorson, 1946: 144E)
2.2 (Thorson, 1946: 108E and F)
2.2.1 (Lalli and Gilmer, 1989: 14d)
2.2.2a (Thorson, 1946: 108A and B)
2.2.2b (Fretter and Pilkington, 1970: 7b)
2.9 (Thompson, 1976: 41a)
2.9.1 (Thompson, 1976: 100)
2.9.2 (Kriegstein, 1977: 1, stage 6a)
2.9.3 (Lalli and Gilmer, 1989: 45a)
2.9.4 (Bickell and Kempf, 1983: 8C)
2.9.6 (Goddard, 1996: 3)
2.9.8 (Thompson, 1976: 41a and b)
2.4 (Hadfield and Strathmann, 1990: 2B and C)
2.4.1 (Hickman, 1992: 4)
2.4.2 (Leighton, 1974: 1.7)
2.4.3 (Fretter and Pilkington, 1970: 11a and b)
2.4.4 (Fretter and Pilkington, 1970: 32a and b)
2.4.5 (Thorson, 1946: 109E and F)
2.4.6 (Fretter and Pilkington, 1970: 9a and b)
2.4.7 (Fretter and Pilkington, 1970: 5a)
2.4.8 (Strathmann, 1987: 11.11 [top])
2.4.9 (Richter and Thorson, 1975: 43a)
2.4.10 (Pilkington, 1976: 11H)
2.4.12a (Pilkington, 1976: 7A and C)
2.4.12b (Lalli and Gilmer, 1989: 14C)
2.4.14 (Fretter and Pilkington, 1970: 3a and b)
2.4.15 (Fretter and Pilkington, 1970: 12a and c)
2.4.11 (Thiriot-Quiévreux, 1983: 1F and G)
2.4.11.1 (Pilkington, 1976: 11A)
2.4.11.2 (Shimek, 1986: 7)
2.4.13 (Fretter and Pilkington, 1970: 20b and c)
2.4.13.1 (Lalli and Gilmer, 1989: 13B)
2.4.13.2 (Lalli and Gilmer, 1989: 14B)
2.4.13.3 (Lalli and Gilmer, 1989: 13C)
3.1a (Kessel, 1964:12)
3.1b (Kessel, 1964:13)
3.1c (after Amio, 1963: 16h)
3.2a (Rasmussen, 1944: 19)
3.3a (Rasmussen, 1944: 18A)
3.3b (modified from: Rasmussen, 1944: 19)
4.1a (Strathmann, 1987: 11:13)
4.1b (Fretter and Pilkington, 1970: 33)
4.1c (Thorson, 1946: 133A)
4.1d (Thorson, 1946: 133D)
4.1e (Thorson, 1946: 133E)
4.2a (Fretter and Graham, 1962: 245B)
4.2b (Fretter and Graham, 1962: 246A)
4.2c (Fretter and Graham, 1962: 246B)
6.1a (van der Spoel, 1967: 61B)
6.1b (van der Spoel, 1967: 76C)
6.2a (Lebour, 1931: plate 1, fig. 6)
6.2b (Fol, 1875: plate III, fig. 30)
6.3a (Fol, 1875: plate III, fig. 39)
6.3b (Fol, 1875: plate III, fig. 37)
6.4a (Fol, 1875: plate VI, fig. 5)
6.4b (after van der Spoel, 1967: 37)
6.5 (Fol, 1875: plate VI, fig. 7)
6.6a (Lützen, 1979: 4A)
6.6b (Lützen, 1979: 41, lower right)
6.7 (Lützen, 1979: 4A and B)

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