Ametamorphic Direct Development in *Dendrodoris behrensi* (Nudibranchia: Dendrodorididae), with a Review of Developmental Mode in the Family

Jeffrey H. R. Goddard

Marine Science Institute, University of California, Santa Barbara,
California 93106, USA; Email: goddard@lifesci.ucsb.edu

***Dendrodoris behrensi* Millen and Bertsch, 2005 has ametamorphic direct development. The embryos passed through a vestigial veliger stage lacking a shell, operculum, larval retractor muscle and pedal sensory cilia. After an embryonic period of 38 days (16–19°C) they hatched as juveniles averaging 512 μm in dorsum length. Newly hatched juveniles possessed eyespots and a lattice of spicules on the ventral surface of the dorsum, and after an additional four days, they possessed rudimentary rhinophores. Only three other examples of direct development have been noted from nudibranchs from the northeast Pacific Ocean, all from the Family Dendrodorididae.**

Based on a survey of the literature, mode of development was determined for 26 species and forms of dendrodoridids worldwide. Fifty-four percent of these taxa have planktotrophic development, 4% lecithotrophic development, and 42% direct development. Direct development is significantly more prevalent in the Dendrodorididae than reported for opisthobranchs worldwide by Hadfield and Miller (1987). Three hypotheses are presented to explain this: (1) direct development is adaptive in overcoming size constraints on post-metamorphic juveniles stemming from their lack of a radula and suctorial mode of feeding on sponges. (2) Direct development is prevalent because small adult size, which is generally correlated with direct development in marine invertebrates, has been selected for in many dendrodoridids. (3) Direct development is an adaptation against high larval mortality in some regions. Limited evidence tends to support hypotheses 2 and 3, but with some interesting developmental exceptions, not hypothesis 1.

KEY WORDS: Ametamorphic, direct development, dorid nudibranch, northeast Pacific Ocean, porostome

Direct development, in which juveniles, rather than larvae, hatch from egg coverings, is rare in shallow-water, benthic opisthobranchs from the northeast Pacific Ocean (Goddard 2005). Among the nudibranchs, the porostome dorids *Dendrodoris nigromaculata* (Cockerell in Cockerell and Eliot, 1905) and *Doriopsilla spaldingi* Valdes and Behrens, 1998 have been noted to hatch from their egg masses as juveniles (Lance 1982; Behrens 1998; Valdés and Behrens 1998). Additionally, direct development has been reported for a yellow-gilled porostome from Bahía de los Ángeles in the Gulf of California (Mulliner 1972; J. Lance, pers. commun., 2005). As presently understood, this form is considered *Doriopsilla gemela* Gosliner et al., 1999, which was described from Bahía de los Ángeles, the west coast of Baja California and California (S. Millen, pers. commun., 2005). However, *Doriopsilla gemela* produces free-swimming larvae (Gosliner et al., 1999; pers. observ.; J. Lance, pers. commun., 2005). Given the rarity of variable developmental mode, or poecilogony (Bouchet 1989; Chia et al. 1996), the form referred to by Mulliner (1972)

may be an undescribed, cryptic species. All three of the above taxa with direct development occur south of Point Conception, the boundary between the Oregonian and Californian biogeographic provinces, although *Doriopsilla spaldingi* has also been collected from 64 m depth in central California (Behrens 2004). Development has not been described in detail for any of them. The present paper describes ametamorphic direct development in *Dendrodoris behrensi* Millen and Bertsch, 2005, a porostome known from central Baja California to Monterey, California (Millen and Bertsch 2005). This is the first detailed account of direct development in a nudibranch from the northeast Pacific Ocean.

Methods

Four specimens of *Dendrodoris behrensi*, 12 to 22 mm long, were collected on 27 May 2001 from the interstices of a low intertidal oyster reef on the east shore of Bahía Falsa near San Quintín, Baja California, Mexico. These were transported back to the laboratory and held in a 100 ml jar of coarsely filtered seawater on a flow-through seawater table at 16–19°C until they laid egg masses. Three newly laid egg masses were examined using an Olympus compound microscope equipped with an ocular micrometer and 35-mm camera, and the diameters of a random sample of ten zygotes were measured from two of these. Each egg mass was then transferred to a separate vial. The water in all of these vials was changed at least once daily, and the egg masses examined every few days until the juveniles hatched. The live juveniles were then examined, measured and photographed using the compound microscope. Juveniles were not reared more than eight days after hatching. After obtaining the above egg masses, the adult slugs were relaxed in 7.5% MgCl$_2$ and then fixed in 70% ethanol. These adults were subsequently deposited as paratypes of this newly described species in the California Academy of Sciences (CASIZ 171659, 171660) (Millen and Bertsch 2005).

Statistical analyses (see section on developmental mode in the Dendrodorididae) were conducted using JMP 4.0.4 (SAS Institute).

Results

Dendrodoris behrensi laid white egg ribbons, up to 1.9 mm high, in a loose, open spiral of one turn. The mean diameter of the uncleaved eggs was 181.4 µm (SD = 9.82 µm, n = 10) in one egg mass and 187.5 µm (SD = 6.75 µm, n = 10) in another. Each egg mass contained approximately 100 white eggs, deposited one, or rarely two, per capsule. The walls of the egg capsules were 10-20 µm thick, and in some capsules, up to 30 µm thick (Fig. 1a). The jelly matrix surrounding the egg capsules was slightly milky in appearance and tougher than that typically observed in the egg masses of nudibranchs from the northeastern Pacific (pers. observ.).

The embryos were observed at irregular intervals until late in development, and therefore an exact chronology of the major stages of embryonic development cannot be presented. However, certain stages and events were noted on the following dates: blastulae 3 days after egg mass deposition (Fig. 1a); gastrulation in process on days 6 and 7; clear anal cells and the rudimentary lobes of the metapodium and velum on day 12. On day 18 the embryonic veligers had small cilia on the velum and were moving slightly; these also had very early eyespots. By day 24 the embryos had well-developed eyespots with lenses and were rotating slowly in their capsules (Fig. 1b). After 28 days, the mantle was semi-transparent and contained refractile glands, which presumably serve a defensive function after hatching. On day 31, the velum on most of the embryos was in the process of being resorbed, and this was complete by day 33. By this time the body had a more juvenile
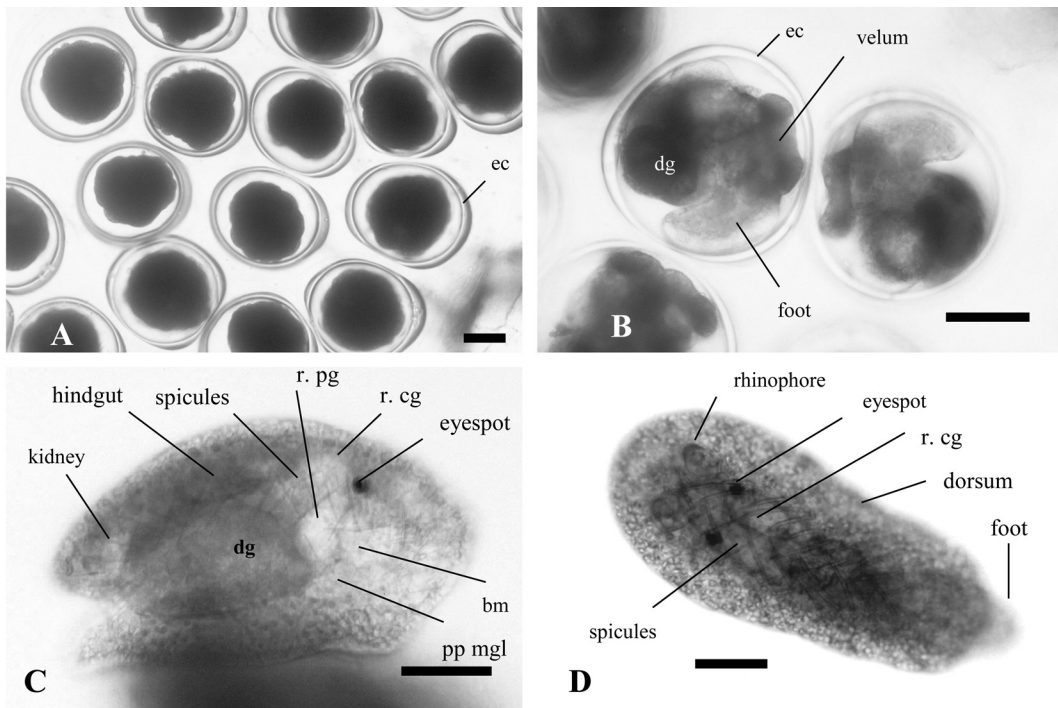
FIGURE 1. Stages in the development of *Dendrodoris behrensi*. (A) Blastulae, three days after oviposition. (B) Embryonic veligers, right lateral views, day 24. (C) Day 38, hatching juvenile, right lateral view. (D) Juvenile four days after hatching, dorsal view. All images are bright field photomicrographs of live specimens; scale bars = 100 μm. Abbreviations used in figure: bm, buccal mass; ec, egg capsule; dg, digestive gland; pp mgl, propodial mucus gland; r. cg, right cerebral ganglion; r. pg, right pedal ganglion.

shape, with a distinct dorsum and large foot. Slightly curved, spindle shaped spicules were observed in the dorsum on day 36, and 2 days later, on day 38, the embryos hatched as juvenile slugs. A shell, operculum and larval retractor muscle were not observed at any stage of development, and the velar cilia remained small compared to the locomotive cilia found on the velum of embryos hatching as swimming veliger larvae. The foot of the embryos also never developed the long, stiff sensory cilia observed on developing planktotrophic veligers (Thompson 1967; pers. observ.).

At hatching, the juveniles measured 465–550 μm along the dorsum (mean = 512 μm, n = 3) and had distinct eyespots, rhinophore rudiments and a small protruding tail (Fig. 1c). The ventral surface of the dorsum had a lattice of spicules 5 μm in diameter. Outside the hepatic region the dorsum was studded with defensive glands up to 12 μm in diameter. Anteriorly, the end of the dorsum was not fully differentiated and lacked a distinct edge. The buccal mass, cerebral and pedal ganglia, and propodial mucus gland were visible through the body wall. Posteriorly, the digestive gland and a posterior, refractile, translucent yellow organ (presumably a kidney) were also visible through both the dorsum and the lateral body wall (Fig.1c).

Four days after hatching, the juveniles were 570 μm long, and the dorsum was oval-shaped, slightly wider anteriorly and generally more adult-like in appearance (Fig. 1d). Rhinophores, 35-40 μm high, had developed, and the foot and dorsum measured up to 100 and 230 μm wide, respectively. Eight days after hatching, the juveniles were about 600 μm long.

Discussion

Dendrodoris behrensi has ametamorphic development, as described by Bonar (1978). Veliger structures such as the shell, operculum, larval retractor muscle, and pedal sensory cilia are all lacking, and the velum and its locomotive cilia are vestigial. Its development is similar to that described by Thompson (1967) for *Cadlina laevis* (Linnaeus, 1767). No shell was detected in the development of *D. behrensi*, however, and the development of the spicules in the dorsum was accelerated compared to those in *C. laevis*, which develop after hatching.

Although none of the other examples of direct development in nudibranchs from the northeast Pacific Ocean (see Introduction) has been described in detail, enough information exists to categorize further the development of two of them. Mulliner (1972) noted the lack of a shell in the embryonic development of the yellow porostome from Bahía de los Ángeles, indicating that this form has ametamorphic direct development. The illustration by Lance (1982), although not specifically labeled, clearly depicts a post-metamorphic *Dendrodoris nigromaculata* hatching at a length of 500 μm with notal spicules and a distinct eyespot. An empty egg capsule, with no sign of a veliger shell, is also shown, suggesting that this species also has ametamorphic development. Not enough information is available on the development of *Doriopsilla spaldingi* to categorize its development as ametamorphic or capsular metamorphic (Goddard 2005, Table 1).

The hatching juveniles of *Dendrodoris behrensi* are similar to those of *D. miniata* (Alder and Hancock 1864) in their possession of a spiculate dorsum (Thompson 1975), but their embryonic development differs in that the latter develops a coiled shell (Thompson 1975; Rose 1985).

All known examples of direct development in nudibranchs from the northeast Pacific Ocean are from the family Dendrodorididae, and of the species of *Dendrodoris* from this region for which mode of development is known, both have ametamorphic development (Goddard 2005). These findings suggest that the non-feeding modes of development, especially direct development, might be more prevalent in the Dendrodorididae than in other Opisthobranchia, an estimated two-thirds of which produce planktotrophic larvae (Hadfield and Miller 1987). Patterns of developmental mode in the family are therefore examined below.

Patterns of developmental mode in the Dendrodorididae

Data on mode of development of the Dendrodorididae, gathered from the literature, are summarized in Table 1. Of the 28 species and forms listed, mode of development could be determined or inferred for 26. The egg diameters reported by Valdés et al. (1996) and Marcus and Marcus (1967) for *Dendrodoris warta* and *Doriopsilla janaina*, respectively, are enough above the 105 μm minimum diameter known for nudibranch species with either lecithotrophic or direct development (see Hadfield and Miller 1987) that developmental mode can not be reliably inferred for them based on egg size alone.

Two species in Table 1, *Dendrodoris krebsii* and *Doriopsilla areolata*, appear to have more than one type of development, suggesting that each may actually represent a complex of cryptic species, or that the taxonomy of the forms studied is simply problematic. As noted by Millen and Bertsch (2005), the latter appears to be the case for at least the specimens from the eastern Pacific previously referred to as *Dendrodoris krebsii*. According to Millen and Bertsch (2005) some of these specimens may actually be *Dendrodoris arborescens*, a possibility consistent with the determinations of developmental mode in Table 1. With regard to *Doriopsilla areolata*, three subspecies were recognized by Valdés and Ortea (1997), two of which have large egg diameters and direct development (Table 1). Valdés and Ortea (1997) did not specify the subspecies from which they observed relatively small eggs (and for which planktotrophic development is inferred in Table 1).

Based on the geographic distributions in Valdés and Ortea (1997, Figure 5) it presumably was *Doriopsilla areolata areolata*. However, according to Ballesteros and Ortea (1980) this subspecies has large eggs. If this discrepancy in egg diameters is accurate, then *Doriopsilla areolata areolata* as presently understood may actually consist of at least two cryptic taxa.

Doriopsilla gemela was originally reported as having lecithotrophic larval development, from eggs 240 μm in diameter (range: 120 to 300 μm), based on observations of larvae from flat egg masses laid by adults collected 7 km north of the tip of Point Loma, San Diego (Schaefer 1997; Gosliner et al. 1999:207). However, the larva pictured in Figure 5 of Schaefer (1997) appears to have a small foot lacking a propodium, and based on the egg mass measurements reported by Gosliner et al. (1999:207), the eggs/embryos in their Figure 4B measure approximately 100 μm in diameter. This egg size, and especially the lack of a propodium, indicate planktotrophic develop-ment (Bonar 1978; Hadfield and Miller 1987). Moreover, the 180 μm range in egg diameter, if accurate, is much larger than any known from a NE Pacific opisthobranch (Goddard 2005) and could only indicate poecilogony, which is extremely rare, or a species complex. For these reasons, the egg sizes and lecithotrophic development reported by Gosliner et al. (1999) require confirma-tion, and I here classify its development as planktotrophic, based on my own recent observations and the older observations of J. Lance, both from flat egg masses laid by adults collected at Point Loma (see Table 1).

Of the 26 species and forms in Table 1 for which mode of development was determined, 11, or 42% have direct development, 4% are lecithotrophic, and 54% are planktotrophic (Table 2). Direct development is significantly more prevalent in the Dendrodorididae than in opisthobranchs worldwide (Table 2; 2×2 contingency table analysis, log-likelihood ratio $\chi^2 = 8.937$, $p = 0.003$, lumping lecithotrophic and planktotrophic modes together as "indirect" development with a free-living larval stage). Moreover, at least five of the 11 taxa with direct development have ametamor-phic development (Table 1), presumably the most evolutionarily derived mode of development (Hadfield and Miller 1987).

Three hypotheses, not mutually exclusive, might explain the high prevalence of direct devel-opment in the Dendrodorididae. These are presented below, each followed by a brief discussion of the pertinent evidence.

(*Hypothesis 1*) Direct development has been selected for in the Dendrodorididae as a means of overcoming size constraints on post-metamorphic juveniles stemming from their lack of a radu-la and suctorial mode of feeding on sponges. It may be difficult to commence this mode of feed-ing, at least on some prey species, at the post-metamorphic sizes (typically well under 500 μm) characteristic of many indirectly developing opisthobranchs. Hadfield and Miller (1987, Figure 13) found that direct development, especially ametamorphic development, can result in post-metamor-phic sizes double that of planktotrophy and lecithotrophy. They concluded that the presence of a larval shell sets a maximum size limit of about 500 μm in newly metamorphosed opisthobranch juveniles. Based on the hatching sizes of the directly developing species in Table 1 (which range from 300 to 800 μm, with a mean of 474 μm), this hypothesis does not appear to be supported. However, the sample size (n = 6) is small, and to reject this hypothesis, the hatching sizes of the directly developing species should really be compared to the post-metamorphic sizes of their planktotrophic and lecithotrophic congeners. To my knowledge, these data do not exist.

If the hypothesis linking direct development to feeding-related constraints on juvenile body size is eventually borne out, then: (a) it obviously does not apply to all members of the family, depending perhaps on dietary composition. (b) We might expect to find a similarly high prevalence of direct development in the Phyllidiidae, a closely related family also characterized by the evolu-tionary loss of the radula and suctorial feeding on sponges (Valdés 2003). (c) We might expect

TABLE 1. Comparative data on embryonic development in the Dendrodorididae.

Species	Egg diameter (µm)	Embryonic period (days)	Temp. (°C)	Shell or juvenile length at hatching (µm)	Mode of development	Max adult size (mm)[a]	Reference
Dendrodoris angolensis Valdés & Ortea, 1996	64	-	-	-	(P)	45+	Valdés et al. 1996
D. arborescens (Collingwood, 1881)	121-159	6-9.2	22-27	144-153	P	78	Rose 1985b; Brodie et al. 1997; Brodie and Calado *in press*
D. behrensi Millen & Bertsch, 2005	181-187	38	16-19	512	AM	22	This study
D. coronata Kay & Young, 1969	55	6	27-29	-	(P)	40	Johnson and Boucher 1983
D. form 1[b]	105	6-7	22-26	150	P	138	Rose 1985; Orr 1981
D. form 2[c]	186	18-19	22-23	440	AM	-	Rose 1985
D. elongata Baba, 1936	165	-	-	-	(L)[d]	75	Johnson and Boucher 1983
D. fumata (Rüppell & Leuckart, 1831)							Gohar & Soliman. 1967; Soliman 1991; Brodie et al. 1997; Brodie & Calado (in press)
Gray form	100-151	5.5-17	16-30	157-220	P	97	
Orange/red form	85-129	-	-	-	(P)	38	Brodie et al. 1997
D. grandiflora (Rapp, 1827)	80	-	-	-	(P)	32+	Valdés et al. 1996
D. krebsii (Mörch, 1863)							
From Florida and Caribbean coast of Panama	146-205	21-23	10	410-460	CM	70[e]	Clark & Goetzfried 1978; DeFreese & Clark 1983; Gonsalves-Jackson 2004
From Caribbean Sea, Brazil and Pacific coast of Panama	66-114	9-10	10	210	(P)	70	Bandel 1976; Valdés et al. 1996; Gonsalves-Jackson 2004
D. limbata (Cuvier, 1804)	270-300	>17	-	-	CM[f]	53+	Tchang-Si 1931; Bonar 1978; Valdes et al. 1996
D. nigra (Stimpson, 1855)	60-93	4-9.6	22-29	114-135	P	64	Ostergaard 1950; Kay & Young 1969; Johnson & Boucher 1983; Rose 1985b; Brodie et al. 1997; Brodie & Calado *in press*
D. nigromaculata (Cockerell in Cockerell and Eliot 1905)	-	-	-	500	(AM)	10	Lance 1982
D. rubra (Kelaart, 1858) var. *nigromaculata* (Eliot, 1913)	30[g]	7	-	165	(P)	70	Baba 1949; Amio 1963
D. senegalensis Bouchet, 1975	< 110[h]	-	-	-	(P)	44+	Valdés et al. 1996
D. warta Marcus & Gallagher, 1976	120	-	-	-	-	71+	Marcus & Gallagher 1976
Doriopsilla albopunctata (Cooper, 1863)	108	18-19[i]	14-15	195	P	60	Goddard 2005; personal observations
D. areolata Bergh, 1880	106	-	-	-	(P)	37+	Valdés & Ortea 1997
D. areolata areolata Bergh, 1880	209-266	-	-	-	(D)	38+	Ballesteros & Ortea 1980; Valdés & Ortea 1997
D. areolata nigrolineata Meyer, 1977	195	>35	10	-	(D)	30	Gonsalves-Jackson 2004
D. gemela Gosliner, Schaefer & Millen, 1999							
From Point Loma	80	-	-	162	P	-	J. Lance, pers. commun. 2005
From Point Loma[j]	111	8.5	15-21	173-184	P	-	Personal observations
From 7 km N of Point Loma	240	31	14	-	L[k]	40	Shaefer 1997; Gosliner et al. 1999
D. janaina Marcus & Marcus, 1967	97-140	>22	10	-	-	25	Marcus & Marcus, 1967; Gonsalves-Jackson 2004
D. miniata (Alder & Hancock, 1864)	215-228	16-17	22-23	360	AM	28	Thompson 1975; Rose 1985
D. pharpa Marcus, 1961[l]	203-234	14-16	23-25	300	CM	19	Clark and Goetzfried 1978; Eyster & Stancyk 1981; DeFreese & Clark 1983
D. spaldingi Valdés & Behrens, 1998	-	-	-	-	D	85	Valdés and Behrens 1998; Behrens 1998
Yellow porostome from Bahía de los Ángeles, Baja California[m]	~260	-	-	800	(AM)	35	J. Lance, pers. commun., 2005; Mulliner 1972

Notes to accompany Table 1

Mode of development: P, planktotrophic; L, lecithotrophic; CM, capsular metamorphic; AM, ametamorphic; D, direct (capsular metamorphic or ametamorphic not specified). Inferred modes of development are in parentheses and are based on morphological criteria, comparisons with congeners, and the egg size distributions reported by Hadfield and Miller (1987) for the major modes of development (see Goddard 2005). Values for egg diameter and shell or juvenile length at hatching are means or ranges in means.

[a] Values are maximum sizes of specimens examined by the authors of the references cited for each species. A plus sign (+) indicates a value for a preserved specimen.

[b] Rose (1985) used the name *Dendrodoris gemmacea* (Alder and Hancock, 1864) for this planktotrophic species. However, the *gemmacea-denisoni-gunnamatta* species complex is in need of revision, and Rose did not deposit voucher specimens or photographs by which the identity of his specimens might be confirmed (B. Rudman, T. Gosliner, pers. commun., 2005).

[c] Rose (1985) used the name *Dendrodoris denisoni* (Angas, 1864) for specimens of this directly developing form from Pilot Beach, an outer coast site in New South Wales (B. Rudman, pers. commun., 2005). The same comments in note b apply to this form.

[d] I consider lecithotrophic development most likely based on the egg size distributions reported by Hadfield and Miller (1987, Figure 1) for the major modes of development. Development in this species could actually be direct or (much less likely) planktotrophic.

[e] Marcus and Marcus (1967:96) recorded 170 mm for a specimen from Biscayne Bay, Florida.

[f] Hadfield and Switzer-Dunlap (1984) classified the development of this species as ametamorphic. As discussed by Bonar (1978) and Rose (1985), its development is intermediate between the capsular metamorphic and ametamorphic extremes of direct development, in that it possess "all of the larval structures, but in a partially reduced state" (Rose 1985).

[g] This value is probably inaccurate, as it is smaller than any other egg size known from the Opisthobranchia (see Hadfield and Miller 1987; Goddard 2005).

[h] As stated by Valdés et al. (1996), 110 mm was the mean length of the egg capsules, not the eggs.

[i] Gosliner et al. (1999) reported an anomalously long embryonic period of 31 days at 14°C.

[j] The adults that laid the egg masses from which these data were collected have been deposited in the California Academy of Sciences (CASIZ catalogue numbers 172864–172865, and 172867)

[k] Lecithotrophic development in *D. gemela* requires confirmation (see text).

[l] Clark and Goetzfried (1978) reported egg sizes and direct development in both *Doriopsilla pharpa* and *D*. sp., both from Florida. Given that the value they reported for *D*. sp. falls within the range reported for *D. pharpa*, and that the latter is the only species of *Doriopsilla* known from Florida (Valdés and Ortea 1997), I have assumed that their *D*. sp. is the same as *D. pharpa*.

[m] This form is closest to *D. gemela* (see Introduction).

TABLE 2. Percentage of developmental types in the Dendrodorididae, compared with the percentages for opisthobranchs worldwide (the latter from Hadfield and Miller 1987).

Mode of development	Percent mode of development (number of species)	
	Dendrodorididae (present study)	*Worldwide (from Hadfield and Miller 1987)**
Planktotrophic	54 (14)	68 (159)
Lecithotrophic	4 (1)	16 (37)
Direct	42 (11)	16 (37)
Total	100 (26)	100 (233)

* These proportions and numbers have been recalculated, omitting all species also listed in Table 1 of the present study.

other adaptations in the porostomes for escaping the constraints imposed by a larval shell and indirect development on post-metamorphic body size. (d) We might expect post-metamorphic juveniles of some of the indirectly developing porostomes to be at the upper size limits known for planktotrophic and lecithotrophic opisthobranchs.

Regarding prediction (b), to my knowledge, information on development has been reported for only three phyllidids, one of which is known to be planktotrophic (Ros 1981; Johnson and Boucher 1983; Soliman 1991). More data are therefore needed to characterize mode of development in the Phyllididae and evaluate this prediction.

Regarding prediction (c), the planktotrophic veliger larvae of *Dendrodoris arborescens*, unlike most other nudibranchs, hatch without an operculum and have a large cephalopedal region which can not be withdrawn into the shell (Rose 1985b; Brodie and Calado 2005). Moreover, the shell is cast early in the pelagic phase (Brodie and Calado 2005). This larval morphology and development is strikingly similar to that of the aegirid dorids *Aegires punctilucens* (D'Orbigney, 1837) and *A. albopunctata* MacFarland, 1905 (Thiriot-Quiévreux 1977; Goddard 2001). After casting their shells larval *A. punctilucens* grow and develop a juvenile-like body with rhinophores, large foot and a highly spiculate dorsum (Thiriot-Quiévreux 1977). After settlement and loss of the velum, post-metamorphic juveniles are about 575 µm long (Thiriot-Quiévreux 1977, Figure 1e), a size comparable to that attained by many ametamorphically developing opisthobranchs (Hadfield and Miller 1987). This two-stage metamorphosis, in which the larval shell is cast long before the loss of the velum, therefore may represent another adaptation for escaping the constraints on juvenile size imposed by a larval shell, and it appears to have evolved independently in *Dendrodoris arborescens*.

Data to evaluate prediction (d) are lacking, but it is noteworthy that the shell size of the hatching planktotrophic veligers of the gray form of *Dendrodoris fumata*, *Dendrodoris kresbsii* from the eastern Pacific and *Doriopsilla albopunctata* range from 195 to 220 µm (Table 1), which is greater than the hatching shell size of most planktotrophic nudibranchs (Hadfield and Miller, Figures 1A and 8; Goddard 2005, Figures 2 and 3). Prediction (d) would be supported if the newly settled juveniles of these species were found to be large compared to the juveniles of other planktotrophic opisthobranchs.

(**Hypothesis 2**) Direct development is prevalent because small adult size, which is correlated with brooding and direct development in marine invertebrates (Strathmann and Strathmann 1982), has been selected for in many dendrodoridids. Species of dendrodoridids with direct development have a mean maximum adult size of 39.0 mm (n = 10), and are significantly smaller than the 15 species with indirect development, which have a mean maximum adult size of 61.9 mm of (Table 1, Wilcoxon two-sample test, normal approximation, $Z = -2.277$, $p = 0.023$), and this result is even more pronounced comparing the adult sizes of only those species with ametamorphic development to those with indirect development (Mean = 23.75 mm, n = 4 vs. 61.9 mm, n = 15, Wilcoxon two-sample test, normal approximation, $Z = -2.852$, $p = 0.004$). This hypothesis is, therefore, supported, but says nothing about the factors selecting for small adult size in the first place.

(**Hypothesis 3**) Direct development has been selected for in some dendrodoridids as an adaptation against high larval mortality (from low or poor quality food, predation, or transport away from favorable settlement sites) (see Goddard 2005). Most of the species listed in Table 1 occur in tropical to warm temperate waters, which, depending on the influence of the subtropical oceanic gyres, are often oligotrophic, less productive, and have a different phytoplankton composition compared to colder waters (Berger 1989; Mann and Lazier 1991). This hypothesis should, therefore, be investigated further, but it requires a biogeographic analysis, which is beyond the scope of this paper.

Regardless of the selective pressures that may have driven the evolution of direct development in the Dendrodorididae, once lost, larval feeding structures are not often regained (Strathmann 1978, 1993) and lineages constrained to non-feeding modes of development may then speciate or go extinct at geographic and temporal scales different from those for lineages with a larval stage or other potential for long range dispersal (e.g., Jablonski and Lutz 1983; Jablonski 1986; Palumbi 1994; Wares and Cummingham 2001). Given the prevalence of direct development in the Dendrodorididae, phylogenetic and phylogeographic analyses of this family should therefore strive to include species with this mode of development.

Acknowledgments

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