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EGG MASSES OF CHROMODORID NUDIBRANCHS (MOLLUSCA: GASTROPODA: OPISTHOBRANCHIA)

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ABSTRACT

The egg mass characteristics of 20 species of chromodorid nudibranchs are presented, representing the genera *Chromodoris, Digidentis, Diversidoris, Glossodoris, Hypselodoris, Noumea* and *Pectenodoris*. The egg mass details for 14 of the included species appear previously unrecorded. These results combined with observations from the literature (comprising a total of 67 species from 15 genera) indicate that most genera in the Chromodorididae show only one type of egg mass. The exception to this is the genus *Chromodoris,* which includes all three egg mass types outlined in this study. Based on anatomical evidence, a group of flat-spawning *Chromodoris* species has been suggested to belong to a monophyletic clade, which indicates that egg mass structure can reflect phylogenetic signal. Genera considered to be more derived among the Chromodorididae are more likely to lay an egg mass that is outward sloping or crenulated. *Cadlinella* shows spawning traits (flat egg mass containing extra-capsular yolk) that indicate it may be ancestral to the *Chromodoris* lineage. Developmental data is presented for 11 species of *Chromodoris,* seven of which utilized extra-capsular yolk in their egg masses. The presence of extra-capsular yolk appears to correlate with upright egg masses within this genus. However, the occurrence of extra-capsular yolk appears to be restricted to Indo-Pacific and Red Sea *Chromodoris* species, while upright spawns from Caribbean species lack this feature.

Key words: nudibranch, egg mass, chromodorid, reproduction, extra-capsular yolk

INTRODUCTION

All doridinean nudibranch egg masses, including those of chromodorids, take the form of a spiral ribbon that is attached to the substratum and consists of embryos embedded in a gelatinous matrix. The shape of the egg mass has been considered to a certain extent to characterize particular groupings (Eliot, 1910; Ostergaard, 1960; Hurst, 1967; Bandel, 1976; Fernandez-Ovies, 1981; Soliman, 1987), and some authors have equated the taxonomic value of the structure of egg capsules (and associated coverings) in shelled gastropods with shell, radular and opercular characters (Andrews, 1935). In a recent cladistic analysis, Mikkelsen (1996) confirmed that the opisthobranch order Anaspidea had a particular egg mass type (string) common to all investigated members of the group.

An extensive literature exists on the anatomy and systematics of chromodorids. However, comparatively little is known about chromodorid reproduction aside from the morphology of the reproductive system itself (Rudman, 1984). In particular, very little is known about the structure of the chromodorid egg mass in species occurring in Australian waters, apart from a few brief descriptions, illustrations or unpublished theses (Kenny, 1970; Thompson, 1972; Rose, 1981, 1985; Avern, 1986; Marshall & Willan, 1999). Often descriptions of chromodorid egg masses are brief and include such ambiguous expressions as "tangled coils" or "loosely coiled" (MacGinitie & MacGinitie, 1949; Boucher, 1983; Johnson & Boucher, 1983). This gives no indication as to whether these terms pertain to the distance between the coils, the regularity of coiling, or to the actual attachment of individual whorls of the spiral mass to the substratum. Numerous papers from Japan have significantly improved our understanding of opisthobranch egg masses (Baba & Hamatani, 1961; Hamatani, 1960a, b, 1961, 1962). However, only one account described chromodorid nudibranch egg masses (Baba et al., 1956). Other studies may inadequately identify the parent species or give conflicting data, thus rendering the resulting egg mass information less useful (Bandel, 1976; Barash & Zanziper, 1980; Rose, 1985). However, many photographic nudibranch identification guides have helped highlight substantial diversity in nudibranch egg mass structure (Gosliner, 1987; Coleman, 1989; Behrens, 1991; Wells & Bryce, 1993; Debelius, 1998). More recently, websites have also contributed significantly to our knowledge of egg masses (for example, www.seaslugforum.net).

Opisthobranch egg masses were classified according to a scheme introduced by Hurst (1967). This scheme aimed to describe egg masses in a format that would facilitate comparison between taxa. As it was based on opisthobranch taxa from the cold temperate northwest coast of the USA, chromodorids were not included, although nearly all egg mass types laid by chromodorids were represented in the scheme by other dorids. Hurst's scheme consists of four categories, which show some taxonomic correlations, for example, Type C (jelly bag attached by string) common amongst cephalaspideans and Type D (sac-like structure) typical of very small aeolid nudibranchs. Doridinean spawns were only present in one category that Hurst defined as Type A:

"The egg mass is in the form of a ribbon attached along the length of one edge, capsules occurring throughout most of it. This is common amongst dorids, which whilst laying may grip the mass between foot and mantle edge tending to flatten it, as mentioned by Fretter & Graham (1964). This is probably not the sole cause of the flattened shape" (Hurst, 1967: 256).

Hurst (1967) noted differences in relative lengths of the free edge compared to the attached edge of the masses, but did not incorporate this variation in her classification. Consequently, any descriptions of doridinean spawn masses that employ Hurst's categories define the ribbon as simply being upright. This does not provide enough information to make any comparisons at or below the familial level. Bandel (1976) briefly discussed Hurst's scheme and proposed 12 of his own groupings. Many of these groupings were based on a single opisthobranch species, and all doridinean egg masses remained in one group, providing no improvement over Hurst's original scheme. Some subcategories were added to Hurst's classification by Fernandez-Ovies (1981), who recognised that the scheme did not adequately describe variation within each 'type'. While these subcategories were a significant improvement, they still did not account for all the variation caused by differences in the length of the free edge of upright egg masses and did not account for flat egg masses. In fact, Fernandez-Ovies incorrectly listed *Chromodoris orientalis* (as *Glossodoris pallescens*) laying an upright egg mass, whereas it is actually laid flat (Baba et al., 1956). MacGinitie & MacGinitie (1949) report that some dorids lay flat egg masses, but it is not until much later that this shape is formally recognised in a classification (Soliman, 1987).

An unusual feature of egg masses that often goes unnoted is the existence of yolk reserves external to the capsule, but still contained within the egg mass. Boucher (1983) termed this "extra-capsular yolk" in a paper that reported the phenomenon in the sacoglossan genera *Elysia* Risso (Elysiidae) and *Bosellia* Trinchese (Polybranchiidae) and the chromodorid genera *Chromodoris* Alder & Hancock and *Cadlinella* Thiele (Chromodorididae). Risbec (1928) erroneously interpreted extra-capsular yolk in the egg masses of *Cadlinella ornatissima* Risbec as crustacean ova. A few brief descriptions or illustrations have highlighted the presence of extra-capsular deposits in the egg masses of opisthobranchs (Gohar & Aboul-Ela, 1957; Marcus & Burch, 1965; Gohar & Soliman, 1967a; Kay & Young, 1969), but Thompson (1972) appears to be the first author to formally recognize these bodies as being composed of "yolky material". The first and only paper to call attention to the widespread occurrence of extra-capsular yolk resulted from a taxonomic survey of opisthobranchs in the Marshall Islands (Boucher, 1983). Since that study, no other literature has specifically addressed the subject of extra-capsular yolk in nudibranch egg masses. The actual deposition of extra-capsular yolk varies between major taxa, and may take the form of granules, caps or blobs in chromodorid nudibranchs (Boucher, 1983) or yolk strings in sacoglossans (Clark et al., 1979; Clark & Jensen, 1981; Boucher, 1983). Goddard (1991) renamed the phenomenon "extrazygotic" and "extra-embryonic" instead of "extra-capsular" in order to include his observation of extra yolky polar bodies inside aeolid nudibranch capsules. It is unlikely that all of these extra yolk sources are homologous.

Although most nudibranchs spawn readily in captivity, perhaps in response to capture and handling stress (Hadfield & Switzer-Dunlap, 1984), there are few detailed descriptions of egg masses. The aims of the present study are to increase awareness of structural variation in chromodorid nudibranch egg masses, and to highlight the presence of extra-capsular yolk in certain taxa. Knowledge of egg mass types and extra-capsular yolk may provide new data to help evaluate existing phylogenies.

MATERIALS AND METHODS

Egg Mass Collection, Maintenance and Measurement

A total of 20 species were collected for this study from the east coast of Australia during 1998–2001. The austral summer is represented by the months December, January, February; autumn by March, April, May; winter by June, July, August, and spring by September, October, and November. The majority of specimens were collected using SCUBA, although some material was collected in the intertidal zone. Animals were kept in holding tanks with gentle aeration and flowing seawater. There is some evidence to suggest that egg masses produced after a prolonged period of stress can be atypical of the species, that is, when organ systems begin to deteriorate (J. Havenhand, pers. comm.). To minimize the likelihood of this effect, only egg masses that were produced in the first week after capture were used in the study. A portion of each egg mass was excised with a scalpel and preserved in either glutaraldehyde (3% prepared in 0.1M sodium phosphate buffer containing 10% w/v sucrose) or neutral-buffered formalin (10%). The remainder of each egg mass was maintained in a holding tank at a water temperature equivalent to that of the collection locality. Portions of the egg mass were observed under a compound microscope at least every second day, and more frequently closer to hatching. The developmental period was deemed to cease on the first day that hatching was observed. Uncleaved ova were measured either from black and white photographs taken using an Olympus BH-2 Nomarski contrast compound microscope fitted with an Olympus OM-2N camera attachment and Kodak T-max 100 ASA film, or from heat images generated from a National F10 CCD Video attachment to the above microscope, printed on a Sony video graphic printer UP-811. To increase the sample size for comparisons at generic levels, descriptions and photographs from the literature were included. However, any data that contained ambiguous terminology or was difficult to interpret was excluded.

Definition of Egg Mass Types

The egg masses examined in this study were classified into three types (Fig. 1) based on whether or not they are attached flat on the substratum or whether they are attached along one edge. Type A egg masses are attached to the substratum by the broad side of the ribbon, and are therefore flat. Type B egg masses had a free edge that was either shorter than the attached edge, causing the ribbon to slope toward the centre of the spiral or was equal in length to the attached edge, standing upright. Type C egg masses had a free edge that was either slightly longer than the attached edge, causing the ribbon to slope away from the centre of the spiral or much longer than the attached edge, causing undulations or waves along the ribbon in addition to an outward slope. In some egg masses, the free edge was so long that the ribbon showed tight crenulations.

Extra-Capsular Yolk Categories

Boucher (1983) recognised two categories of extra-capsular yolk in nudibranchs and these are applied here with some modifications. Boucher (1983) defined Type 1 as "cap-like bodies associated with individual capsules". In this study, caps falling into this category were further subdivided into (A) caps that were distributed equally and (B) caps that were distributed unequally (Fig. 2). Type 2, as defined by Boucher (1983), was "discrete yolk bodies strewn throughout the egg mass", and were not observed during this study, although are known to occur within the genera *Cadlinella* and *Chromodoris* (Risbec, 1928; Gohar & Aboul-Ela, 1957; Boucher, 1983).

Developmental Type Definitions

Where possible, larvae were examined by light microscope (Olympus BH-2 Nomarski contrast compound microscope) and categorized into developmental types according to the definitions proposed by Thompson (1967) and Bonar (1978). A well-developed velum and larval retractor muscle, small ova and short embryonic period identified planktotrophic larvae, whereas lecithotrophic larvae typically exhibited a less developed but recognisable velum and larval retractor muscle, prominent propodium, and large ova with

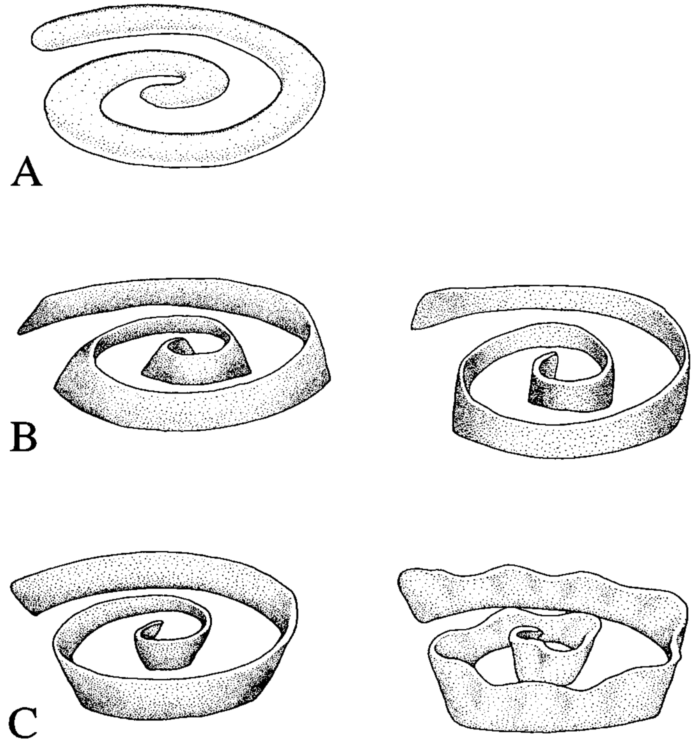

FIG. 1. Stylized drawing of the three types of chromodorid egg masses. Type A is laid flat on the substratum, Type B is laid upright and may also slope inwards, and Type C is laid upright, slopes outwards and may be crenulated.

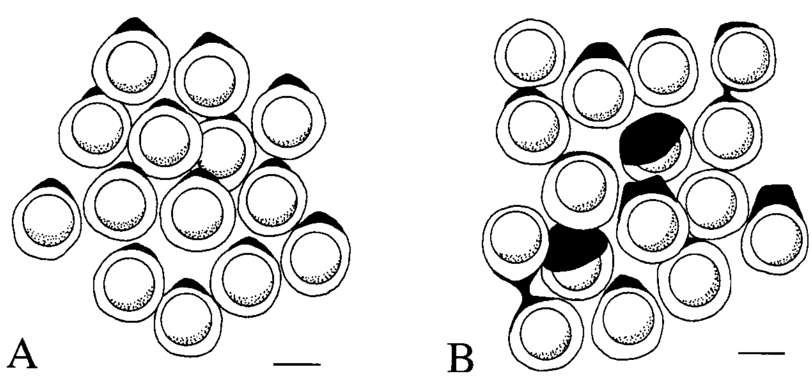

FIG. 2. Extra-capsular yolk. A, equally distributed. B, unequally distributed. Scale bar = 100 μm.

a longer embryonic period (Thompson, 1967). Intracapsular development was determined to be either metamorphic (undergoing capslar metamorphosis) or ametamorphic (not undergoing a typical veliger stage) (Bonar, 1978).

RESULTS

The developmental characteristics of twenty chromodorid species are described below and summarized in Table 1.

TABLE 1. Developmental characteristics of some chromodorid nudibranchs

Species	Egg mass type	Colour	Ova size (μm)	Extra-capsular yolk type	No. ova per capsule	Developmental type	Embryonic period in days (no. egg masses)	Temperature (°C)
Chromodoris collingwoodi	B	yellow	—	1A	1	planktonic	6 (1)	23
Chromodoris daphne	B	cream	128 ± 5 (n = 8)	1A	1	planktotrophic	6 (1)	25–26
Chromodoris elisabethina	A	cream	93 ± 5 (n = 15)	no	1	planktonic	5 (1), 8–10 (3)	27, 21–22
Chromodoris geometrica	B	orange-cream	82 ± 7 (n = 8)	1B	1	planktonic	10 (1)	21–22
Chromodoris kuiteri	A	cream	—	no	1	planktonic	6 (1), 6 (1)	27, 23–28
Chromodoris kuniei	B	orange-cream	109 ± 2 (n = 7)	1B	2	planktonic	15 (1)	20–22
Chromodoris leopardus	B	orange-cream	104 ± 3 (n = 10)	1B	1 or 2	planktonic	14 (1)	20–22
Chromodoris lochi	A	cream	—	no	1	planktotrophic	9 (1)	25
Chromodoris roboi	B	orange-cream	101 ± 8 (n = 10)	1B	2–4	planktonic	11 (1)	20–22
Chromodoris strigata	A	cream	80 ± 2 (n = 11)	no	1	planktonic	8 (1)	24
Chromodoris tinctoria	B	orange	—	1A	2–3	—	—	—
Digidentis cf arbutus	B	orange	491 ± 12 (n = 7)	no	1	—	—	—
Diversidoris aurantionodulosa	B	white	—	no	1	lecithotrophic	8 (1)	25
Glossodoris vespa	B	cream	300 ± 19 (n = 10)	no	1	ametamorphic	56 (1)	17–22
Hypselodoris bullocki	C	yellow	—	no	1	—	—	—
Hypselodoris obscura	C	white	104 ± 5 (n = 11)	no	1	planktonic	9–10 (2), 4 (1)	22, 25–26
Hypselodoris sp.	C	orange	146 ± 4 (n = 10)	no	1	lecithotrophic	9–11 (2)	20–22
Hypselodoris zephyra	C	white	—	no	—	planktonic	5 (1)	27
Noumea norba	B	cream	83 ± 3 (n = 12)	no	1	planktonic	12–14 (2)	21–22
Pectenodoris trilineata	B	pink	205 ± 11 (n = 8)	no	1	—	—	—

Chromodorididae

Chromodoris Alder & Hancock

Chromodoris collingwoodi Rudman, 1987

A single egg mass was observed in March from an animal collected at North Stradbroke Island, Queensland. The egg mass was upright, consisting of two whorls slightly sloping inward to centre of spiral. Ova were yellow, and associated with extracapsular yolk of Type 1A. Each capsule contained a single embryo. The embryonic period was six days at 23°C. Larvae were planktonic, although the exact developmental type was not determined.

Chromodoris daphne (Angas, 1864)

A single egg mass was observed in November from an animal collected at Wellington Point, Moreton Bay, Queensland. The egg mass was upright, with the broad side of ribbon constricted slightly toward centre of spiral, giving it a slightly "hour-glass" shape. Two whorls were present, containing cream ova arranged linearly within the spawn mass. Uncleaved ova were 128 ± 5 μm in diameter (n = 8). Extra-capsular yolk of Type 1A was present, and each capsule contained a single embryo. The embryonic period lasted six days at 25-26°C, and the veligers that were released were planktotrophic.

Chromodoris elisabethina Bergh, 1877

Four egg masses observed from three individuals. The adult nudibranchs were all collected from the Gneering Shoals, Mooloolaba, Queensland, and the egg masses laid in January and May. All egg masses were laid flat, and while all were spiral in shape, they often ended askew. The egg masses ranged from three to five whorls. Ova were cream and there was no extra-capsular yolk observed. The rate of deposition of the egg mass for one individual was measured at 1.58 mm/min. Uncleaved ova were 93 ± 5 μm in diameter (n = 15). Each capsule contained a single embryo. The embryonic period lasted 5-6 days at approximately 27°C (n = 1) and 8-10 days at 20.5-22°C (n = 3). Larvae were planktonic, although the exact developmental type was not determined.

Chromodoris geometrica Risbec, 1928

Two incomplete egg masses were observed in May from two individuals collected at the Gneering Shoals, Mooloolaba, Queensland. Egg masses were upright and consisted of only a partial whorl (animals tried to lay their spawn on the air-water interface, which could not sustain the weight of more than a partial egg mass). Ova were cream and extra-capsular yolk Type 1B was present in the egg mass. The ova were 82 ± 7 μm (n = 8) in diameter. Each capsule contained a single embryo. The embryonic period of one of the pieces lasted 10 days at 20.5-22°C. Larvae were planktonic, although the exact developmental type was not determined.

Chromodoris kuiteri Rudman, 1982

Three egg masses were observed from individuals from Cook Island, New South Wales (n = 1), and Heron Island, Great Barrier Reef, Queensland (n = 2). These were laid in December and March respectively. Egg masses were laid flat, and consisted of 2-5 whorls. The regularity of the coiling varied greatly between egg masses laid by different individuals. The ova were pale orange in colour, arranged linearly, and no extra-capsular yolk was observed. Each capsule contained a single embryo. The embryonic period lasted six days at 27°C, and also six days at a variable temperature range of 23-28°C. Larvae were planktonic, although the exact developmental type was not determined.

Chromodoris kuniei Pruvot-Fol, 1930

A single egg mass was observed in August from an individual collected from Heron Island, Great Barrier Reef, Queensland. The egg mass was upright, consisting of two whorls. The ova were orange and were associated with extra-capsular yolk Type 1B. The uncleaved ova were 109 ± 2 μm (n = 7) in diameter. Each capsule contained two embryos. The embryonic period was 15 days at 20-22°C. Larvae were planktonic, although the exact developmental type remains undetermined.

Chromodoris leopardus Rudman, 1987

A single egg mass was observed in September from an individual collected in the Gneering Shoals, Mooloolaba, Queensland. The egg mass was upright, consisting of two whorls. The ova were orange and were associated with extra-capsular yolk Type 1B. The uncleaved ova were 104 ± 3 μm in diameter (n = 10). Each capsule contained one or two embryos. The embryonic period lasted 14 days at 20–22°C. Larvae were planktonic, although the exact developmental type was not determined.

Chromodoris lochi Rudman, 1982

A single egg mass was observed in April from a specimen collected at Ribbon Reef Number 10, Great Barrier Reef, Queensland. The egg mass was laid flat and consisted of three whorls. The ova were cream in colour, and no extra-capsular yolk was present. Each capsule contained a single embryo. The embryonic period lasted nine days at 25°C, and larvae showed a planktotrophic developmental pattern.

Chromodoris roboi Gosliner & Behrens, 1998

Two egg masses have been observed from two individuals collected from Heron Island, and another egg mass was observed from the Whitsunday Islands, Great Barrier Reef, Queensland. The egg masses from Heron Island were laid in March and September, and were upright and consisted of two whorls. The ova were orange and were associated with extra-capsular yolk of Type 1B. The ova were 101 ± 8 μm in diameter (n = 10). Many capsules contained multiple embryos; typically they contained two, but up to four were observed. The embryonic period of one egg mass lasted 11 days at 20–22°C. Larvae were planktonic, although the exact developmental type remains undetermined. The egg mass observed in the Whitsundays was laid in August and consisted of one whorl. This egg mass was upright but laid in an irregular spiral, so that the whorl consisted of short, straight sections with a distinct kink that joined to another short, straight section. Thus, the egg mass appeared to be crenulated, but both the free edge and attached edge were equal in length.

Chromodoris strigata Rudman, 1982

A single egg mass was observed in October from an animal collected on Heron Island, Great Barrier Reef, Queensland. The egg mass was flat, and consisted of five whorls. The ova were pale orange and no extra-capsular yolk was observed. The ova measured 80 ± 2 μm in diameter (n = 11). Each capsule contained a single embryo. The embryonic period lasted eight days at 24°C. Larvae were planktonic, although the exact developmental type remains undetermined.

Chromodoris tinctoria
(Rüppell & Leuckart, 1828)

A single egg mass was observed in March from North Stradbroke Island, Queensland. The egg mass was upright and consisted of three whorls. The orange ova were arranged linearly within the egg mass and were associated with extra-capsular yolk of Type 1A. Each capsule contained two to three embryos. The embryos died after 11 days at 22–24°C, and no further details of development could be ascertained.

Digidentis Rudman
Digidentis cf. *arbutus* (Burn, 1961)

A single egg mass was observed in February from Pt Puer, Tasmania. The animal was disturbed while laying, so the egg mass was incomplete. However, the spawn was upright and quite firm. The ova were orange and no extra-capsular yolk was observed. The ova measured 491 ± 12 μm (n = 7) in diameter and each capsule contained a single embryo. The developmental type could not be determined, although the large size of the ova potentially indicates direct development.

Diversidoris Rudman
Diversidoris aurantionodulosa
Rudman, 1987

Four egg masses were observed in April from Pt. Cartwright, Mooloolaba, Queensland. The egg masses were upright and consisted of one to two whorls each. Two egg masses laid in the laboratory sloped inwards very slightly while those laid in the field appeared typically upright. The ova were cream-white in colour, no extra-capsular yolk was observed and each capsule contained a single embryo. The embryonic period lasted 8 days at 25°C, with the larvae showing a lecithotrophic developmental pattern.

Glossodoris Ehrenberg
Glossodoris vespa Rudman, 1990

A single egg mass was observed in May from an individual collected in the Gneering Shoals, Mooloolaba, Queensland. The egg mass was upright, very firm and consisted of two whorls. The cream ova measured 300 ± 19 μm (n = 10) and no extra-capsular yolk was observed. The embryonic period lasted for 56 days at 17–22°C, and the development pattern was ametamorphic direct.

Hypselodoris Stimpson
Hypselodoris bullocki (Collingwood, 1881)

Two egg masses were observed from two individuals during November on Orpheus Island, Great Barrier Reef, Queensland. They were upright but with the free edge of the egg mass sloping away from the centre of the spiral. Ova were yellow and no extra-capsular yolk was observed. Each capsule contained a single embryo, but the developmental type remains unknown.

Hypselodoris obscura (Stimpson, 1855)

Four egg masses were observed in total from three individuals. Three egg masses were observed from a pair of nudibranchs collected in April from Amity Point, North Stradbroke Island, Queensland, and one egg mass was observed in November from an individual collected from Wellington Point, Moreton Bay, Queensland. The egg masses consisted of 2–5 whorls. All egg masses were upright but ranged from being slightly outward sloping to having a crenulated free edge. The ova were white, arranged linearly in the egg mass and no extra-capsular yolk was observed. The ova from one egg mass measured 104 ± 5 μm (n = 11). Each capsule contained a single embryo. The embryonic period lasted 9–10 days at 22°C (n = 2) and 4–5 days at 25–26°C (n = 1). Veligers were planktonic, but the exact development type remains undetermined.

Hypselodoris sp. Chromodoris geometrica
Coleman, 1981: 32. Misidentified

Four egg masses were observed in total from three individuals, all from the Gneering Shoals, Mooloolaba, Queensland. Three egg masses were laid in September and one in January. The egg masses ranged from 1–3 whorls and were upright with the free edge crenulated. Ova were dark orange and no extra-capsular yolk was observed. Ova were 146 ± 4 μm in diameter (n = 10). Each capsule contained a single embryo. The embryonic period took 9–11 days at 20–22°C (n = 2), and the resulting veligers were lecithotrophic.

Hypselodoris zephyra
Gosliner & Johnson, 1999

Two egg masses were observed from a single animal in December from Cook Island, New South Wales. The egg masses ranged from 2–3 whorls and were upright with the free edge crenulated. Ova were white and the embryonic period took five days at 27°C. Veligers were planktonic, although exact developmental type was not determined.

Noumea Risbec
Noumea norba Marcus & Marcus, 1970

Four egg masses were observed from two individuals in May, from the Gneering Shoals, Mooloolaba, Queensland. The egg masses ranged from 2–3 whorls and ranged from upright to having the free edge sloping toward the centre of the spiral. Ova were cream, arranged linearly and measured 83 ± 3 μm in diameter (n = 12). Each capsule contained a single embryo. The embryonic period was 12–14 days at 20.5–22°C (n = 2). Veligers were planktonic, although the exact developmental type was not determined.

Pectenodoris Rudman
Pectenodoris trilineata
(Adams & Reeve, 1850)

One egg mass was observed in August on Heron Island, Great Barrier Reef, Queensland. The egg mass was firm, and consisted of one whorl. The ova were pale pink in colour and measured 205 ± 11 μm (n = 8). Each capsule contained a single embryo. Developmental details were not recorded.

DISCUSSION

Although only a small fraction of the spawning details of chromodorid species is known, there is some evidence to suggest that egg mass morphology is consistent within genera and even groups of genera (Table 2). The obvious exception to this is the presence of multiple egg mass types within *Chromodoris*, the

TABLE 2. Egg mass types of chromodorid species

Species	Egg Mass Type A	B	C	Source
Cadlina luteomarginata		•		Dehnel & Kong, 1979
Cadlina modesta		•		Behrens, 1991
Cadlina pellucida		?		Fernandez-Ovies, 1981
Cadlinella ornatissima	•			Boucher, 1983
Cadlinella sp.	•			Debelius, 1998
Tyrinna nobilis			•	Muniain et al., 1996
Chromodoris aspersa	•			Gohar & Soliman, 1967b, as *C. inornata* Pease
Chromodoris africana	•			Gohar & Aboul-Ela, 1957, as *C. quadricolor* (Rüppell & Leuckart)
Chromodoris annulata		•		Gohar & Aboul-Ela, 1957
Chromodoris aureopurpurea		•		Baba et al., 1956, as *Glossodoris*
Chromodoris binza		•		Ortea et al., 1994
Chromodoris coi		•	?	Taylor, 2001
Chromodoris collingwoodi		•		present study
Chromodoris clenchi		•		Ortea et al., 1994
Chromodoris daphne		•		present study
Chromodoris elisabethina	•			Johnson & Boucher, 1983; present study
Chromodoris geometrica		•		Johnson & Boucher, 1983; Chuk, 2001; present study
Chromodoris geometrica			•	Rose, 1981; Fraser, 2001a
Chromodoris kuniei		•	?	present study; Adams, 2001; Warren, 2001
Chromodoris kuiteri	•			present study
Chromodoris leopardus		•		present study
Chromodoris lineolata	•			Kenny, 1970
Chromodoris lochi	•			present study
Chromodoris magnifica			•	Klussman-Kolb & Wägele, 2001
Chromodoris orientalis	•			Baba et al., 1956, as *Glossodoris pallescens* Bergh
Chromodoris perola		?	?	Bandel, 1976
Chromodoris roboi		•	?	present study
Chromodoris strigata	•			present study
Chromodoris tinctoria		•		present study
Chromodoris willani	•			Gill, 2001
Chromodoris woodwardae		•		Rudman, 1998a
Glossodoris cincta		•		Gohar & Soliman, 1967c, as *C. obseleta* (Rüppell & Leuckart)
Glossodoris pallida		•		Soliman, 1987
Glossodoris plumbea		•		Gohar & Aboul-Ela, 1959, as *G. atromarginata* Cuvier
Glossodoris sibogae		•		Baba et al., 1956
Glossodoris sp.		•		Fraser, 2001b
Glossodoris sp.		•		Ostergaard, 1960
Glossodoris vespa		•		present study
Noumea decussata		•		Johnson, 2001a
Noumea haliclona		•		Avern, 1986; present study
Noumea norba		•		present study
Noumea simplex		•		Johnson, 2001b
Verconia verconis		•		Debelius, 1998
Pectenodoris trilineata		•		present study
Digidentis cf arbutus		•		present study
Diversidoris aurantionodulosa		•		present study
Ceratosoma amoena			•	Coleman, 2001
Ceratosoma brevicaudatum			•	Smith et al., 1989
Ceratosoma magnifica			•	Jamieson, 1999, as *Miamira*
Mexichromis cf multituberculata			•	Miller, 2001a
Thorunna australis			•	S. Johnson, pers. comm.
Thorunna daniellae			•	Miller, 2001b
Thorunna florens			•	Coleman, 2001
Thorunna montrouzieri			•	Rudman, 1998b
Hypselodoris bullocki			•	present study
Hypselodoris emma			•	Marshall & Willan, 1999

(continues)

TABLE 2. (*Continued*)

Species	Egg Mass Type A	B	C	Source
Hypselodoris festiva			•	Baba et al., 1956, as *Glossodoris*
Hypselodoris kanga			•	Rudman, 1999
Hypselodoris maculosa			•	Johnson, 2000
Hypselodoris obscura			•	present study
Hypselodoris sp.			•	present study
Hypselodoris whitei			•	Johnson & Boucher, 1983, as *H. mouaci* (Risbec)
Hypselodoris zebra		•		Geiger, 1999
Hypselodoris zephyra			•	present study
Risbecia ghardaqana			•	Gohar & Aboul-Ela, 1957
Risbecia pulchella			•	Gohar & Aboul-Ela, 1957
Risbecia tryoni			•	Johnson & Boucher, 1983, as *Chromodoris*

largest genus in the Chromodorididae. Currently, it is estimated that *Chromodoris* contains approximately 200 species (Gosliner & Draheim, 1996), whereas most other chromodorid genera are considerably less speciose and some are monotypic (eg., *Diversidoris, Verconia*). Although the total percentage of *Chromodoris* species sampled within the present study is very low, all three types of egg mass structure were detected (Table 2).

The nine *Chromodoris* species that are known to exhibit flat egg masses (Type A) occur in two colour groups. Rudman (1977, 1982, 1983) described these groups in order to facilitate identification of similarly coloured species. The first of these groups, the *Chromodoris quadricolor* colour group, contains all but two of these flat-spawning species. Based on the distribution of mantle glands and on reproductive characters, it has been suggested that this colour group may represent a discrete clade within the genus *Chromodoris* (Gosliner & Behrens, 1998). This provides further evidence that egg masses can potentially reflect phylogenetic influence. The remaining species that lay a flat egg mass, *Chromodoris aspersa* (Gould) and *C. orientalis* Rudman, both belong to the *C. aspersa* colour group (Rudman, 1983). These species have long been confused, although external colouration can be used to reliably separate them (Rudman, 1983). The notal spots in *C. orientalis* are black, whereas in *C. aspersa* they are deep purple. The precise nature of the relationship between the two colour groups remains to be investigated, but it is interesting to note that most recorded Type A spawners in *Chromodoris* share a band of orange around the mantle. They also typically possess translucent orange gills and/or rhinophores, and all but *C. aspersa* share the presence of black pigment (present as stripes or background colour in the *C. quadricolor* colour group and as spots in *C. orientalis*).

Upright egg masses (Type B) were present in at least 13 of the 24 species of *Chromodoris* species listed in Table 2. There was some difficulty in classifying the egg masses of *Chromodoris coi, C. kuniei* and *C. roboi.* These species all lay ribbons that in most cases are upright, but are often attached in short kinks that cause them to appear outward sloping. These egg masses may also have grooves on the broad side of the ribbon running parallel to attachment, although the significance of this is unclear. The two reports of a clearly crenulated egg mass (Type C) occurring in *Chromodoris* warrant further attention. *Chromodoris magnifica* falls into the *C. quadricolor* colour group of Rudman and would thus be predicted to lay a flat egg mass similar to all other known members of the group. However, Klussmann-Kolb & Wägele (2001) report *C. magnifica* laying an upright and crenulated egg mass, although further observations are desirable to confirm the report. Similarly, conflicting reports occur regarding the egg mass of *Chromodoris geometrica.* Boucher (1983) recorded *C. geometrica* in the Marshall Islands with an upright, orange egg mass containing extra-capsular yolk. This study confirmed that report for specimens from subtropical eastern Australia, and an upright orange ribbon was also reported from Papua New Guinea (Chuk, 2001). However, Rose (1985) recorded some spawning details of *C. geometrica* from temperate eastern Australia and reported an absence of extra-capsular yolk. It is only in his unpublished thesis (1981) that he describes the egg mass as being fluted. Although it is quite possible that the single specimen that Rose collected was misidentified, Fraser (2001a) also shows an egg mass of *C. geometrica* that is clearly crenulated. This latter observation from South Africa also differs from all previous accounts in that the colour of the egg mass is white. It is likely that this egg mass lacked extra-capsular yolk as well, as the resulting orange hue is usually visible to the naked eye. As both Rose (1981) and Fraser (2001a) made their observations at similar latitudes in the Pacific and Indian oceans respectively (approximately the southermost limits for *C. geometrica*), it is possible that the production of extra-capsular yolk reserves is related to temperature.

An upright egg mass structure (Type B) was found in all species of *Glossodoris, Noumea, Verconia, Pectenodoris, Digidentis* and *Diversidoris* represented in Table 2. According to the first phylogeny proposed for the Chromodorididae (Rudman, 1984), all these genera are typically considered in the "mid region" of evolution within the family, neither basal nor highly derived (Fig. 3). Gosliner & Johnson's (1999) cladistic analysis found no resolution between the lineage containing *Chromodoris, Ceratosoma* and *Glossodoris* and the one containing *Noumea, Pectenodoris, Verconia, Thorunna* and *Digidentis* (Fig. 4). However, both phylogenies agree that the crown group within one lineage consists of *Risbecia + Hypselodoris.* This crown group (with the exception of *Hypselodoris zebra*) all show egg masses that are either outwardly sloping or crenulated. This indi-

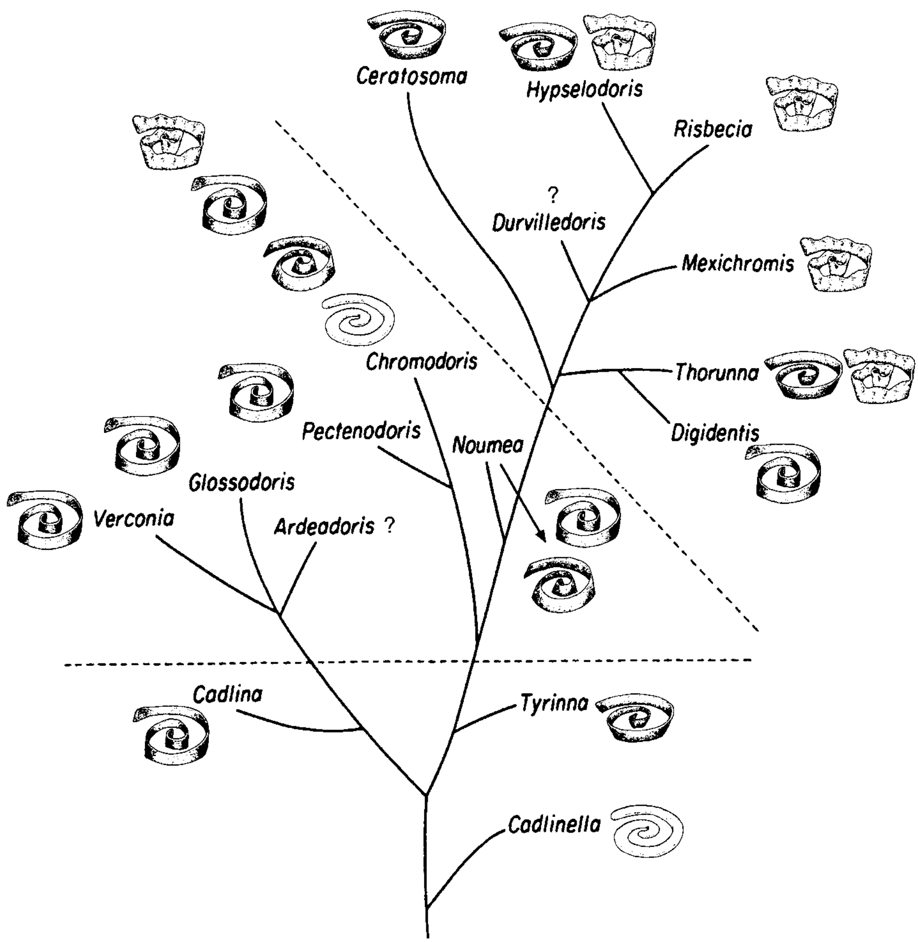

FIG. 3. Egg mass shape mapped onto hypothesized phylogeny of the Chromodorididae (from Rudman, 1984).

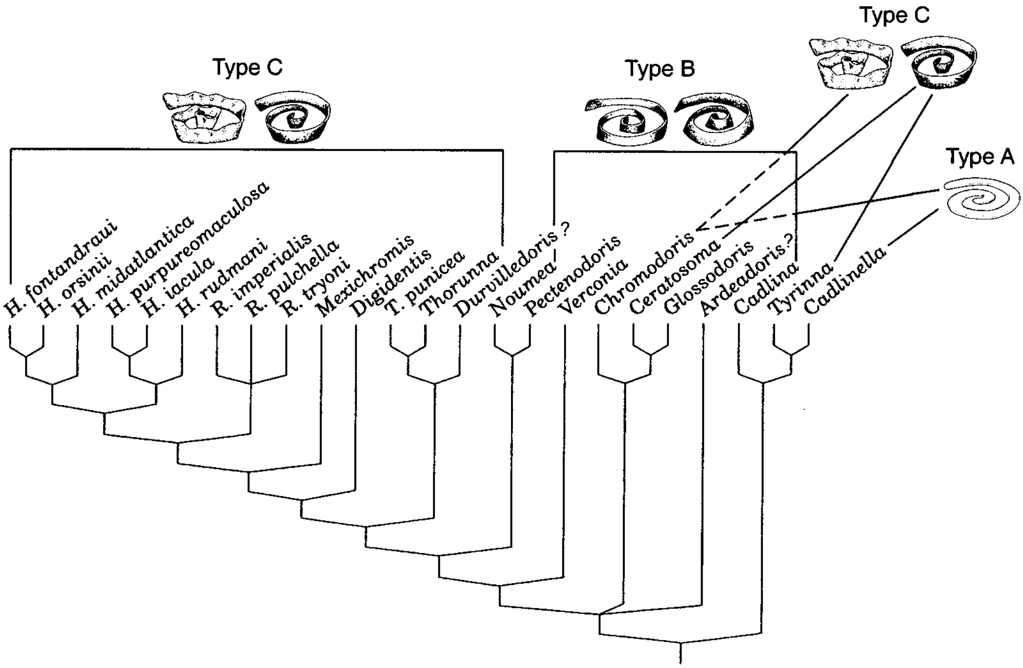

FIG. 4. Egg mass shape mapped onto hypothesized phylogeny of the Chromodorididae (from Gosliner & Johnson, 1999). Broken lines indicate that the spawn type illustrated above is also present in the genus.

cates that the most highly derived forms are more likely to lay egg masses that have the free edge of the ribbon lengthened, resulting in outward sloping or crenulated egg masses. As the structure of an egg mass is said to reflect the degree of anatomical complexity of the reproductive system (Fretter & Ko Bun, 1984), it is likely that more highly derived genera would lay more complex egg masses. The single known exception in *Hypselodoris* (*H. zebra*) shows an upright egg mass. This is the only egg mass known for a member of the Atlantic/Eastern Pacific clade of the genus. *Hypselodoris* is known to consist of two clades, the above-mentioned clade and an Indo-Pacific clade (Gosliner & Johnson, 1999), which is represented by all the other *Hypselodoris* egg masses observed in this study.

The genus *Thorunna* is considered relatively derived in both phylogenies of the Chromodorididae, and the egg mass data from Table 1 appear to sustain this. *Thorunna* has been proposed as a sister group to both *Digidentis* (Rudman, 1984) and *Durvilledoris* (Gosliner & Johnson, 1999). Observations on the egg mass of *Digidentis* offers no firm evidence in support of this relationship, and the egg mass structure of *Durvilledoris* species remains unknown.

Ceratosoma is closely allied to *Chromodoris* and *Glossodoris,* according to the phylogeny of Gosliner & Johnson (1999). This contrasts with Rudman (1984), who places it in the "hypselodorid" subgroup (also containing *Digidentis, Thorunna, Durvilledoris, Mexichromis, Risbecia* and *Hypselodoris*), considering *Ceratosoma* to have a *Chromodoris* ancestor but having diverged early in hypselodorid evolution. Here, the egg masses of three *Ceratosoma* species are reported to be outwardly sloping or crenulated, indicating a derived condition.

Extra-capsular yolk reserves have so far been recorded in only two chromodorid genera, *Cadlinella* and *Chromodoris,* with five new records in the present study (Table 3). While extra-capsular yolk is found in the flat egg masses of *Cadlinella,* the flat egg masses of *Chromodoris* never contain these reserves. It is only in the upright egg masses of Indo-Pacific *Chromodoris* species that extra-capsular yolk is present. *Chromodoris binza* and *Chromodoris clenchi,* both found in the Caribbean, lay upright egg masses but do not incorporate extra-capsular yolk reserves into the egg

TABLE 3. Chromodorids that produce extra-capsular yolk.

Species	Yolk type	Original source
Cadlinella ornatissima	2, small & pale	Risbec, 1928
Chromodoris albopunctatus	2, large & orange	Boucher, 1983
Chromodoris albopustulosa	1A	Kay & Young, 1969
Chromodoris annulata	2, large & orange	Gohar & Aboul-Ela, 1957
Chromodoris collingwoodi	1A	present study
Chromodoris daphne	1A	present study
Chromodoris decora	1A	Kay & Young, 1969
Chromodoris E-6	1A	Boucher, 1983
Chromodoris fidelis	1A	Marcus & Burch, 1965
Chromodoris galactos	1A	Boucher, 1983, as E-57
Chromodoris geometrica	1B	Boucher, 1983
Chromodoris kuniei	1B	present study
Chromodoris leopardus	1B	present study
Chromodoris marginata	1A	Boucher, 1983
Chromodoris preciosa	not determined	S. Johnson, pers. comm.
Chromodoris roboi	1B	present study
Chromodoris rubrocornuta	not determined	S. Johnson, pers. comm.
Chromodoris E-328	not determined	S. Johnson, pers. comm.
Chromodoris E-48	not determined	S. Johnson, pers. comm.
Chromodoris thompsoni	1A	Thompson, 1972, as *C. loringi*
Chromodoris tinctoria	1A	Gohar & Soliman, 1967
Chromodoris vibrata	not determined	S. Johnson, pers. comm.

mass (Ortea et al., 1994). It will be of great interest to determine whether extra-capsular yolk is restricted solely to Indo-Pacific and Red Sea *Chromodoris*. While *Cadlinella sp.* from the Red Sea does lay flat egg masses, they have not yet been examined to determine if they also contain extra-capsular yolk like *Cadlinella ornatissima.*

While *Cadlina, Tyrinna* and *Cadlinella* are all currently considered basal within the Chromodorididae, there appears to be no indication that these three genera are themselves closely related (Rudman, 1984). It is therefore no surprise that these genera exhibit different egg mass types. While varying hypotheses regarding the basal chromodorids have been proposed or supported (Rudman, 1984; Muniaín et al., 1996; Gosliner & Johnson, 1999), the most recent discussion concludes only that the phylogeny of these basal groups remains unclear (Schrödl & Millen, 2001). Given that *Cadlinella* shares a flat egg mass and extra-capsular yolk with varying *Chromodoris* species, it is likely that *Cadlinella* gave rise to the *Chromodoris* lineage.

There is some concern that egg mass structure may reflect environmental rather than phylogenetic influences (Wägele & Willan, 2000), and is therefore not suitable to be used as a character in phylogenetic analyses. Observations on spawning in the field and laboratory have shown some differences, which have been incorporated into the egg mass classification in this study. Specimens of *Noumea norba* and *Diversidoris aurantionodulosa* laid upright ribbons in the field, while the same specimens in the laboratory laid egg masses that sloped inward. Specimens of *Hypselodoris obscura* lay egg masses that range from outward sloping to crenulated. Some egg masses, particularly those that are thin and flaccid, can appear slightly fluted when laid on irregular or uneven substrata. However, it is possible to differentiate between these and egg masses that are truly outward sloping or crenulated by comparing the length of both the free and attached edges. The regularity of the coiling, that is, the space between the whorls of one egg mass, differed greatly within a species, suggesting this may be affected by environmental conditions or perhaps the reproductive history of the parent. It is not yet possible to make any correlation between egg mass type and the habitat of the parent nudibranch, since there is little information regarding movement within the latter. Many species of nudibranch are found in both intertidal and subtidal environments without showing any obvious change in egg mass structure. However, controlled experiments varying such factors as temperature, salinity and water flow are desirable to test this idea.

There are apparently conflicting reports where the colour of a egg mass has been reported to differ between localities, even when extra-capsular yolk is absent. Johnson & Boucher (1983) reported that *Hypselodoris maculosa* lays a pale pink egg mass, whereas Marshall & Willan (1999) recorded it as white. While it is possible that a change in prey items may trigger a corresponding change in ova colour, differences may also reflect subjective interpretation of colour. It is also important to know whether the animal laying the egg mass is identified correctly. *Hypselodoris maculosa* individuals are known to be variable in colour, and there is the possibility that a complex of species is currently identified as a single species. Egg masses may have the potential to help separate these complexes but need to be used in conjunction with morphological data from the parent specimens. Another factor that can influence the colour of an egg mass is the amount of time that has elapsed since it was laid. Gradual colour changes occur as the developing embryos use up the available yolk. However, while small changes in colour may be attributed to such factors, real disagreement in colour may reflect differences in the identity of the parent. *Risbecia tryoni* has been reported to lay a rose-pink egg mass with a crenulated free edge (Johnson & Boucher, 1983), whereas Marshall & Willan (1999) reported the mass as orange but do not describe its structure. Marshall & Willan (1999) also incorrectly cited Johnson & Boucher as attributing extra-capsular yolk to this species.

While the general form of the egg mass is usually characteristic of a species or genus, Rudman & Avern (1989) found both upright and crenulated egg mass types in the relatively small genus *Rostanga* (approximately 13 species). This was also the case for *Acanthodoris* (Hurst, 1967), in which both upright and crenulated egg masses were recorded. This indicates that some caution may be necessary when interpreting phylogenetic signal from egg mass structure, as it may be useful at different taxonomic levels in different groups. The absence of a fossil record means there is currently no reliable method of dating genera. It may only be in more recent genera that egg mass structure remains conservative throughout. It is possible that the trend towards crenulation of egg masses in the more derived Chromodorididae is also seen within a single "older" genus that has had more time to evolve.

Soliman (1987) recognized the potential taxonomic value of egg mass type among gastropods, but he recommended that when interpreting phylogenetic relationships, primary consideration should be given to anatomical, palaeontological or ecological evidence. Because no fossil record exists for the Nudibranchia, and accurate ecological information is still scarce for most groups, alternative characters may be found in reproductive data. Egg mass structure may help confirm or challenge phylogenetic hypotheses based solely on anatomical data, but much work is still required to understand the underlying causes of observed variation.

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