

Intraspecific aggression in the nudibranch *Chromodoris annae* Bergh, 1877: novel 'fighting' behaviour for the Chromodorididae (Gastropoda, Opisthobranchia)

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This paper documents a bout of very aggressive behaviour between two individuals of *Chromodoris annae* witnessed by the author subtidally in Timor-Leste in August 2010. Pugnacious behaviour has been observed and recorded previously in two other families of anthobranch (= dorid) nudibranchs, viz. Polyceridae (one genus only) and Gymnodorididae (two genera at least), both phanerobranch families where cannibalism of conspecifics is an extension of predation on other anthobranch dorids. Pugnacious behaviour has apparently never previously been recorded in the Chromodorididae, the largest family of cryptobranch dorids. Although the observed aggression was certainly not cannibalistic, it is uncertain whether it was related to mating or feeding, or had some other purpose.

Key words: Gastropoda, Opisthobranchia, Anthobranchia, Doridina, Chromodorididae, *Chromodoris*, in situ observations, conspecific-directed aggression.

INTRODUCTION

With over 400 described species, the Chromodorididae is numerically the largest family of cryptobranch nudibranchs (i.e., nudibranchs capable of retracting the gills into a pocket

beneath the mantle). Morphologically the Chromodorididae are characterised by the thin body wall (except for *Ceratosoma*), lack of spicular elements in the integument (except for *Cadlinella*; see Chang et al., 2010) resulting in a very soft and deformable body, possession of repugnatorial glands in the mantle margin, lack of a medial indentation (philtrum) in the upper lip of the foot, and origin of the receptaculum seminis directly off the distal section of the duct to the bursa copulatrix. The glands in the mantle store toxins derived from sponge prey and these toxins are liberated when individuals are irritated. Production of toxins underlies the most visually distinctive external characteristics to the family – those of vivid colour and bold patterns, characteristics traditionally interpreted as aposomatic by most nudibranch workers, but disputed by some (e.g., Thompson, 1976: 52).

Unquestionably the family Chromodorididae, and particularly its largest genus *Chromodoris*, attains maximum global diversity in the tropical waters of the Coral Triangle (Willan & P. Poppe, 2010). Here species are extremely diverse, and coexistence of sibling species and mimetic relationships between species (and even between other phyla of invertebrates with chromodorids) are rife.

Chromodorids are usually encountered singly on coral reefs during the day. They are always considered docile both

in the wild and in captivity and up to now, they have never been seen to be hostile to conspecifics or to other species of nudibranchs under any circumstances. On the contrary however, nudibranchs belonging to two other groups of phaneorobranchs (i.e., nudibranchs not capable of retracting the gills into a pocket beneath the mantle) that are closely related to each other, have regularly been recorded as aggressive; they are Gymnodorididae and Polyceridae. The Gymnodorididae are all notoriously aggressive towards other dorid nudibranchs both in the wild and in captivity; that aggression relates to the fact that they are unselective carnivores eating other opisthobranchs, including conspecifics. Indeed, some gymnodorids apparently feed exclusively on members of their own genus (Behrens, 2005). Gymnodorids eat their prey whole or suck out the viscera to leave only a bag of skin remaining (pers. obs.). One species of gymnodorid has switched its diet to feed on the fins of sand-dwelling gobioid fishes (Osumi & Yamasu, 1994). The Polyceridae contain one genus, *Roboastra*, that specialises in selectively eating whole other members of the same family (Kerstitch, 1989; Miller, 1999; Behrens, 2005; Willan, 2003: 104 shows a photo by Diane Armstrong), particularly species of *Tambja*, tracking prey by following their mucous trails and this behaviour occurs both in the wild and in captivity. Species of *Roboastra* certainly do cannibalise their own species.

Therefore, the fortuitous observation of two individuals of *Chromodoris annae* Bergh, 1877 engaged in a protracted bout of extreme aggression in the wild puts the assumed docile behaviour of the entire family into question. To my knowledge aggressive behaviour has not been described previously for any member of the Chromodorididae, so, even though only one bout of aggressive behaviour was observed, I consider it certainly of sufficient importance to justify thorough documentation.

METHODS

The observations reported below were made during an underwater transect perpendicular to the shore to record opisthobranch diversity conducted at "Bob's Rock", west of Manatuto, approx. 40 km east of Dili, on the northern coast

of Timor-Leste (= East-Timor) (8°28.703'S, 125°54.496'E), on 14 August 2010. The transect ran from 22.2 m up to 3 m in depth. The total duration of the dive was 82 min. The water temperature was 27° C. The weather was sunny, and the water was very clear (horizontal visibility was estimated at 20 m). The particular observations on *Chromodoris annae* were made at approx. 12.15 hr on coral rubble near the top of the steep fringing reef slope at a depth of 6 m. Both individuals involved in the 'fight' (Figs 1-5) were approx. 30 mm extended crawling length. Three additional individuals of *C. annae* were also recorded nearby on the transect on similar substrates; they had similar sizes, and two of them were feeding on a clump of pale blue encrusting dictyoceratid sponge most probably belonging to the family Thorectidae (Fig. 6).

Standard SCUBA gear was used by both my diving buddy and myself. Still photos and short videos were taken with an Olympus μ 760 digital camera inside an Olympus PT-036 housing. Two of the video clips are posted as supplementary material on the Basteria website at <http://www.basteria.nl/publicaties/basteria/supplements/74/B74-Willan-1.avi> and <http://www.basteria.nl/publicaties/basteria/supplements/74/B74-Willan-2.avi>.

Figs 1-5. Photographic documentation of an aggressive encounter between two individuals of *Chromodoris annae*, at 6 m depth, "Bob's Rock", west of Manatuto, northern coast of Timor-Leste, 14 August 2010. 1, individuals in combat, note both combatants have their buccal mass fully everted; 2, one combatant withdraws its right rhinophore following an attack by the other combatant; 3, one combatant withdraws its gills following an attack by the other combatant; 4, one combatant that is upside-down rises up and directs a radular stroke vertically downward onto the other individual; 5, pieces of the mantle margin around the head (arrowed) were bitten off each combatant during the encounter. Fig. 6. Two other individuals of *C. annae* grazing amicably on a sponge (Dictyoceratida, probably Thorectidae) nearby. Feeding scars on the sponge left by these individuals are arrowed. All photos Neil Wright.



When first seen, the two *Chromodoris annae* individuals were entwined together head-to-head with one on top and the other underneath in a vigorous 'fight' in the manner of courting land slugs *Limax maximus* Linnaeus, 1758 (Janus, 1982; Rowson, 2005). However, both individuals were horizontal, always retaining some part of their foot, albeit small, attached to the substratum. Their bodies were gently wafting to and fro with the surge. Both individuals were making repeated lunges at the other (Figs 1-5). The buccal mass of each individual was protruded for about a minute at a time accompanied by rasping cycles by the radula lasting approximately two seconds. I estimate that 20 of these radular rasping cycles took place before the buccal mass was retracted. Both individuals were rasping at each other simultaneously (Fig. 1). So extreme were these rasping cycles, that I could easily make out the radular ribbon at the tip of the everted proboscis with my naked eye.

After approximately two minutes of head-to-head combat, the individuals crawled round and round each other while remaining in close contact and the attacks continued undiminished in a different orientation. At one point, one of the animals reared up above the other like a cobra, exposed its oral tube (Fig. 4), and directed a radular bite at the other individual in conjunction with a downward lunge on top of it. During the bout, radular rasping was directed at the head, the mantle margin, the rhinophores and the gills. No rasping attacks were directed towards the genital area. Clearly these attacks were painful as each individual retracted that part of the body following a bite, and the rhinophores (Fig. 2) and the gills (Fig. 3) were instantaneously retracted when they were being bitten. During the 'fight' both individuals sustained some damage to the mantle brim (Fig. 5 arrow) as the result of radular rasping.

The 'fight' lasted for 12 minutes, after which time both individuals became quiescent and motionless, and moved out of contact.

At no time during the 'fight' could I observe the expulsion of any repugnatory fluid from the mantle of either individual, so I assume none was being produced.

All members of the family Chromodorididae have hitherto been considered as docile and non-aggressive by molluscan specialists and amateur divers interested in nudibranchs alike. Nowadays obvious behaviours of mantle flapping and trailing, which typify some species of chromodorids, and which I first witnessed in Vanuatu in 1972, are well known and widely reported (e.g., Behrens, 2005). However, no aggressive behaviour towards conspecifics like that undertaken by the family Gymnodorididae (i.e., opportunistic predation on other nudibranchs) or by the genus *Roboastrea* (i.e., deliberate cannibalism) has ever been reported in the Chromodorididae to my knowledge. My colleague Scott Johnson, who has been studying and observing nudibranchs subtidally in the Marshall Islands for 25 years, has never seen any aggressive behaviour by chromodorids. According to him *Chromodoris annae* is rare in the Marshall Islands.

The cause for the aggressive behaviour which I observed was not obvious. It was certainly an event involving two conspecific individuals of matched size. I can definitely eliminate the possibility that two individuals of different (i.e., sibling) species were involved. Even though a dozen species of the 'black-lined' group of *Chromodoris* species are known to occur in Indonesian waters, these two individuals were definitely both *C. annae*. I am sufficiently familiar with other very similar looking (i.e., phenetically similar) 'black-lined' species that occur in this part of southeast Asia – *C. michaeli* Gosliner & Behrens, 1998, *C. diana* Gosliner & Behrens, 1998, *C. elisabethina* Bergh, 1877, *C. magnifica* (Quoy & Gaimard, 1832), *C. cf. africana* Eliot, 1904, *C. strigata* Rudman, 1982, *C. colemani* Rudman, 1982, *C. lochi* Rudman, 1982, *C. willani* Rudman, 1982, *C. joshi* Gosliner & Behrens, 1998 and some undescribed species (Kodiat, 2010a) – to confirm that they were not involved and thus be certain the two individuals belonged to the same species.

I do not think what I observed was a courtship ritual (i.e., aggressive foreplay) because the genital aperture/organs were never protracted in either individual and the biting was never directed toward the genital region. However, both individuals would have been sexually mature and they could have mated just before this 'fight', so it could have

been rough afterplay. No spawn belonging to this species (a white flattened open coil, as figured by Behrens, 2005: 119 and by Cobb, 2009) was in the vicinity and *Chromodoris annae* does not brood its spawn, so it is unlikely one animal was defending its spawn as the aeolid nudibranch *Pteraeolidia ianthina* Angas, 1864 does (Willan, 1990).

As no nudibranch is known to be territorial [except for *Pteraeolidia ianthina* (Angas, 1864) during the incubation of its eggs; see above], it is highly improbable that the two *Chromodoris annae* were fighting over territory. However, they could have been fighting over a tiny piece of food that was invisible to me. But then a large clump of their dictyoceratid (probably family Thorectidae) sponge food was present nearby. It had already been discovered by two other individuals and it would have been producing strong pheromones, so these two individuals could have crawled over to eat it rather than fight over a tiny morsel.

Despite the inability to identify a reason for this aggressive behaviour, its existence provides an explanation for the observation that adult chromodorids, particularly members of the 'black-lined' species group, sometimes have tattered mantles (e.g., Willan, 2005: fig. 12; Willan & P. Poppe, 2010). Perhaps such damage results not from attempts at predation by fishes and/or crustaceans, but from numerous aggressive encounters with conspecifics like the one I was fortunate to have witnessed in Timor-Leste?

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