Host specificity and phylogenetic relationships among Atlantic Ovulidae (Mollusca: Gastropoda)

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Abstract
Ovulid gastropods and their octocoral hosts were collected along the leeward coast of Curaçao, Netherlands Antilles. New molecular data of Caribbean and a single Atlantic species were combined with comparable data of Indo-Pacific Ovulidae and a single East-Pacific species from GenBank. Based on two DNA markers, viz. CO-I and 16S, the phylogenetic relationships among all ovulid species of which these data are available are reconstructed. The provisional results suggest a dichotomy between the Atlantic and the Indo-Pacific taxa. Fully grown Simnia lena uniplicata closely resembles juvenile Cyphoma gibbosum conchologically. Cymbovula acicularis and C. bahamaensis might be synonyms. The assignments of Caribbean host species for Cyphoma gibbosum, C. signatum, Cymbovula acicularis and Simnia lena uniplicata are revised.

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Introduction
Ovulid snails are obligate associates of Cnidaria. As far as known, most occur associated with octocorals (Anthozoa: Octocorallia: Alcyonacea), but in both the Caribbean and the Indo-Pacific some ovulid species feed on antipatharians (Anthozoa: Hexacorallia: Antipatharia) (Tazioni et al., 2007). The species of Pedicularia Swainson, 1840, that have been classified with the Ovulidae for a long time (Goud and Hoeksema, 2001), live on stylasterid corals (Hydrozoa: Athecatae: Filefera). Pedicularia differs from the undisputed ovulids in radula morphology (Simone, 2004); it is now classified in the separate family Pediculariidae (Fehse, 2007; Lorenz and Fehse, 2009).

Thirty-seven species of Ovulidae Fleming, 1822, are known from the Caribbean and Atlantic area (Lorenz and Fehse, 2009). The dominant genus in the Caribbean is Cyphoma Röding, 1798, with 14 species of which Cyphoma gibbosum (Linnaeus, 1758) is the most common. Due to the low number of ovulid species in the Caribbean and the well-known diversity of Octocorallia (Bayer, 1961) parasite/host relationships are most easily studied here.

It has been hypothesized that colour patterns and texture of ovulid mantles may either mislead potential predators by mimicking its host’s branches and polyps, or that its colour acts as a warning of unpalatability (aposmatic species) (Rosenberg, 1992; Schiaparelli et al., 2005). Snails closely resembling coral branches and polyps of their host may be camouflaged in such a way that they are almost undetectable for predators, such as shown by the Caribbean Cymbovula acicularis (Lamarck, 1810), which uses its mantle colour and protrusions to mimic the branches and polyps of its gorgonian host (Fig. 1d).

As a first step to a better understanding of the associations between alcyonaceans and ovulids, Yamamoto (1972) and Schiaparelli et al. (2005) studied the snails and their hosts in the Indo-Pacific. In the present paper we primarily deal with the Ovulidae and their octocoral hosts of the Caribbean island of Curaçao. Our new data on species associations are used to investigate whether the gastropod species should be considered generalists or specialists. Based on the molecular data from this study and GenBank, a provisional molecular phylogeny reconstruction of Ovulidae is presented.
Material and methods

In April - June 2005, both ovulid snails and their octocoral hosts were sampled using SCUBA diving at 32 localities off the leeward western coast of Curaçao, Netherlands Antilles. Observations on the windward eastern shore were hampered by exposure to the open sea. All snails and hosts were photographed in situ and collected by hand, and subsequently stored as vouchers in the collection of NCB Naturalis. Three species of the Atlantic ovulid Simnia patula (Pennant, 1777), dredged from the Dutch North Sea bottom by fishermen, were added as additional samples for the phylogeny reconstruction.

For the Ovulidae the nomenclature accepted by the ‘Checklist of European Marine Mollusca’ (CLEM-AM, 2008) and Cate (1973) was followed, except for Neosimnia aequalis sensu stricto (not Sowerby II, 1832), which is referred to as N. arcuata (Reeve, 1865), in accordance with Lorenz and Fehse (2009). The status of the former nominal taxon will remain uncertain as long as no valid lectotype selection has taken place, but this cannot affect the use of the latter name.

Molecular analyses

For molecular phylogeny reconstructions, tissue samples from the foot of the snails were used to extract DNA with the E.Z.N.A. Mollusc DNA Kit (Omega BioTek). The primer sets published by Meyer (2003) and Schiaparelli et al. (2005) were used to amplify the mtDNA markers CO-I and 16S marker, respectively. The PCR reaction mixtures were composed after Gittenberger et al. (2006). For 16S, 0.005 ml MilliQ was replaced by an equal volume of Qsolution (Qiagen). The annealing temperature used for 16S was set at 52°C, whereas for CO-I a ramp was used, starting at 40°C and ending at 44°C, increasing with 0.1°C s⁻¹.

Sequencing was performed on a MegaBace 1000, 96 capillary sequencer at Leiden University, and on an Automatic Sequencer 3730xl by Macrogen, Korea. The raw sequence data were assembled and edited using Sequencher 4.2 (Gene Codes Corporation®) and aligned with ClustalX. The sequences in the CO-I dataset were all checked for stop codons. All sequences were referenced against GenBank (National Center for Biotechnology Information, NCBI) to ensure that non-targeted DNA had not been sequenced. For the
phylogeny reconstruction, 17 GenBank sequences for both 16S and CO-I (Table 1), representing the same species, were combined with sequences of the Atlantic species. For the single individual of *Cyphoma signatum*, CO-I could not be amplified. Therefore, this species was excluded from the dataset. The final alignment consisted of 28 sequences containing 961 base pairs. Newly sequenced species are deposited in GenBank under accession numbers GU363427 – GU363450.

Within 16S highly variable regions exist, formed by either insertions or deletions. Aligning this region proved to be very difficult and the unalignable region, consisting of 75 base pairs in length (position 166 till 241), was deleted. To check whether both datasets could be combined, an incongruence length difference test (ILD-test) was performed. This test resulted in a P-value (P = 1.00) allowing the data combination. To determine the optimal evolutionary models the combined molecular dataset was subjected to Modeltest (Posada and Crandall, 1998). This resulted in the Generalised Time Reversible evolutionary model + invariable sites + gamma (GTR + I+G). The obtained parameters were used to run a maximum likelihood search in PAUP* 4.0b (Swofford, 2003). No fewer than a 100 bootstrap replicates were used to evaluate the robustness of the nodes. The search was carried out with tree bisection-reconnection (TBR). Gaps were in all cases treated as missing character and not as a fifth character state. The selected outgroup sequence was that of the cypraeid *Cypraea tigris* (Linnaeus, 1758).

### Results

#### Species and associations

A total of 104 samples of ovulids was collected, representing *viz. Cyphoma gibbosum* (Linnaeus, 1758), *Cyphoma signatum* Pilsbry and McGinty, 1939, *Simnia uniplicata* (Sowerby II, 1848) and *Cymbovula acicularis* (Lamarck, 1810) (Fig. 2, including specimen resembling the so-called *C. bahamaensis*). The 72
snails of *Cyphoma gibbosum* that could be studied were found with 21 alcyonacean species, representing nine genera. The 27 individuals of *Cymbovula acicularis* were found in association with five gorgoniid species, belonging to two genera. *Simnialena uniplicata* occurred with two congeneric host species, but since only four individual snails were found, it would be premature to derive any conclusions about host specificity. Unfortunately, only a single specimen of *Cyphoma signatum* could be studied, which was associated with *Plexaurella dichotoma* (Esper, 1791). This gorgonian species was also mentioned by Botero (1990), who additionally reported the congeneric *P. nutans* as a host for *C. signatum*. Due to the poverty of its records, the host preferences of this ovulid remain largely unknown.

From a total of 46 octocoral species recorded at Curaçao, 26 (57%) were found to be occasionally parasitized by one or more ovulid species (Table 2). Not all encountered Octocorallia species were found associated with ovulids. Additionally, a list was composed (Table 3) of encountered Octocorallia without associated ovulids.

### Phylogeny reconstruction

*Cyphoma gibbosum* is a common Caribbean species that is easily recognized by its colour pattern and morphology. To exclude possible sibling species occurring on, for example, different hosts or at other localities at Curaçao, several individuals from different Octocorallia species and from different localities along the coast were sequenced. Based on the molecular data no sibling species occurrence was detected. In Fig. 3 the results of the combined dataset subjected to a maximum likelihood analysis (ML) with bootstrap values is presented.

The phylogeny reconstruction indicates that there is a separation between the Atlantic and the Indo-Pacific clade (moderately supported, bootstrap value 70), although the East-Pacific species *Neosimnia arcuata* clusters with the Atlantic clade (poorly supported, bootstrap value 51). *Simnialena uniplicata* (Fig. 2f-g), *Neosimnia arcuata* and *Cymbovula acicularis* (Fig. 2a-d) are characterized conchologically by long and slender shells, but in the cladogram *S. uniplicata* does not appear as sister species to either *N. arcuata*.
or C. acicularis. Instead, it forms a highly supported (bootstrap value 100) clade with the Cyphoma group. The individual sequence of the ovulid specimen resembling Cymbovula bahamaensis (Fig. 2c) forms a highly supported clade (bootstrap value 100) with the included C. acicularis species.

Discussion

Associations

Reported host preferences of Cyphoma gibbosum (Bertsch, 1984; Lasker et al., 1988; Botero, 1990; Nowlis, 1993; Chiaponne et al., 2003) are partly confirmed and supplemented with new observations of associations of this species, showing once more that C. gibbosum is a generalist parasite (Table 2). Cymbovula acicularis turned out to be another generalist.

It remains unclear why 43% of the encountered alcynoacean species did not appear as hosts for ovulids at the time of our fieldwork (Table 3). It is known that Octocorallia may produce secondary metabolites as
protection against predation (Ciereszko and Schneider, 1987; Chiaponne et al., 2003), but the effect of this defence strategy on ovulids is still largely unexplored. Other factors, such as the nutritional value of the corals (O’Neal and Pawlik, 2002) and the unpalatability of sclerites (Alstyne and Paul, 1992), may also influence host choices.

An overview of natural products produced by West Indian gorgonian octocorals reveals that many types of secondary metabolites are found. The largest class of metabolites encountered in Caribbean alcyonaceans are diterpenoids, followed by the sesquiterpenes (Rodriguez, 1995). For some of these compounds that are obtained from alcyonaceans, such as *Erythropodium caribeorum*, feeding experiments were performed, resulting in the observation that coral extracts are deterrent to fish. Also, crude extracts from the gorgonian *Gorgonia ventalina*, containing terpenoids, were used in feeding experiments with *C. gibbosum*. As a result, *C. gibbosum* consumed only 49% of an artificial diet containing terpenoids (Alstyne and Paul, 1992).

The sclerites of the gorgonian species that we found as hosts for *Simnia uniplicata* and *Cymbovula acicularis* turned out to be relatively small. The sclerites of *Gorgonia* spp. and *Pseudopterogorgia* spp. have average sizes of 0.10 mm and 0.10-0.15 mm, respectively, whereas 0.30-1.00 mm is common for other Octocorallia species, like *Eunicella* and *Pseudo-
plexaura species (Bayer, 1961). For Cyphoma gibbosum, however, the sclerites’ size seems to be irrelevant for host selection, since this species is found on corals containing either small or large sclerites. By analysing faecal pellets which all contained sclerites, we conclude that C. gibbosum at least ingests sclerites instead of eating around them.

Paedomorphosis

In the phylogeny reconstruction, Simnia patula is the sister group of the combined Simnialena uniplicata and Cyphoma species group. This is surprising because, at first sight, fully grown individuals of Cyphoma species clearly differ from S. uniplicata in shell morphology. However, when shells of S. uniplicata are compared to a series of shells of C. gibbosum in various growth-stages (Fig. 4), it turns out that S. uniplicata closely resembles juvenile C. gibbosum (as well as juvenile ovulids in general). Both species lack a clear funiculum (narrow ridge of callus at the ventral side of the shell close to the aperture) and have rounded, tapering ends, character states that are absent in fully grown C. gibbosum. Identification of juvenile ovulid shells is difficult, if not impossible, due to a lack of diagnostic shell characters. However, some specimens that were collected alive showed a mantle colour pattern diagnostic for C. gibbosum, viz. bright

Fig. 4. Shells in dorsal and ventral view. Simnialena uniplicata (d) compared to a series of shells of Cyphoma gibbosum (a-c, e-k) in different developmental stages. Scale bar 1 cm.
orange spots, encircled with a black line at a whish background (Fig. 1). Cymbovula acicularis had a nearly transparent mantle, sometimes with white protubercences. In Simnialena uniplicata the mantle is entirely black, whereas in Cyphoma signatum it had a distinct yellow/black fingerprint pattern. This leads to the conclusion that the mantle colour and pattern may be diagnostic in Ovulidae (Mase, 1989) and that this character can be used to distinguish fully grown Simnialena uniplicata from juvenile C. gibbsom. Therefore, we hypothesize that S. uniplicata exemplifies paedomorphism.

Systematics, biogeography and nomenclature

According to the principles of phylogenetic systematics, the species referred to as Simnialena uniplicata should be called Cyphoma uniplicata (Fig. 3). Meanwhile, the status of the nominal genus Simnialena Cate, 1973, with its insufficiently known type species Simnialena marferula Cate, 1973, remains unclear. According to Lorenz and Fehse (2009: 105), ‘S. marferula is a close relative of S. uniplicata’. This conclusion, on which we cannot elaborate here, is based on similarities in shell morphology.

The DNA sequences of specimens belonging to Cymbovula acicularis and specimens that agree with the description of C. bahamaensis (Figs 2c-d) are almost identical. As a consequence, these nominal taxa should most probably be considered synonyms, as has also been suggested by Lorenz and Fehse (2009) based on morphological data.

There is a moderately strong supported dichotomy between the Atlantic and the Indo-Pacific taxa, with Neosimnia arcuata from the East-Pacific having an aberrant, but poorly supported, position in the cladogram, where it clusters with the Atlantic taxa. Together, these species represent the Simnialae Schilder, 1927. Furthermore, two undisputed clades were found among the Indo-Pacific taxa, supporting the occurrence of the subfamilies Prionovolvinae Fehse, 2007, and Ovulininae Fleming, 1822, respectively.

In order to get a better understanding of the phylogeny and parasite/host associations of the Atlantic Ovulidae, additional shells and DNA material are needed. DNA obtained from other ovulids occurring in the Atlantic area (e.g. Cyphoma macumba Petuch, 1979; C. versicolar Fehse, 2003; C. mcgintyi Pilsbry, 1939) may elucidate the taxonomical position of the genus Cyphoma as a monophyletic group. However, several ovulid species are rare and generally only their shells are found, which hampers further investigations.

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