

Hypothesis

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## Sexual selection on land snail shell ornamentation: a hypothesis that may explain shell diversity

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### Abstract

**Background:** Many groups of land snails show great interspecific diversity in shell ornamentation, which may include spines on the shell and flanges on the aperture. Such structures have been explained as camouflage or defence, but the possibility that they might be under sexual selection has not previously been explored.

**Presentation of the hypothesis:** The hypothesis that is presented consists of two parts. First, that shell ornamentation is the result of sexual selection. Second, that such sexual selection has caused the divergence in shell shape in different species.

**Testing the hypothesis:** The first part of the hypothesis may be tested by searching for sexual dimorphism in shell ornamentation in gonochoristic snails, by searching for increased variance in shell ornamentation relative to other shell traits, and by mate choice experiments using individuals with experimentally enhanced ornamentation. The second part of the hypothesis may be tested by comparing sister groups and correlating shell diversity with degree of polygamy.

**Implications of the hypothesis:** If the hypothesis were true, it would provide an explanation for the many cases of allopatric evolutionary radiation in snails, where shell diversity cannot be related to any niche differentiation or environmental differences.

### Background

Broadly speaking, the process of sexual selection is caused by the fact that, in sexually reproducing organisms, not all individuals will be equally successful in securing mates. In species with separate sexes (gonochorists), fertilization success is often unequally distributed among males, either because of direct male-male competition or by female choice, or both. Sexual selection by female choice happens when a female, on the basis of visual, auditory, tactile, or other stimulation, exerts a choice on which males' sperm she will use for fertilizing her eggs. The process has been clearly demonstrated in a wide variety of organisms [1,2], and is implicated in the evolution of celebrated

instances of extreme sexual dimorphism, e.g., elongated tail feathers [3] and bright coloration [4] in birds, exaggerated horns and spikes on insect genitalia, and bizarre modifications on male arthropod appendages [5].

In some species, however, types of ornamentation that are presumably sexually selected, are not sexually dimorphic. For example, in birds like grebes (Podicipitidae), both males and females carry brightly coloured feather-whiskers and crests on their heads, and there is no observable sexual dimorphism. Similarly, certain species of pheasant, like *Crossoptilon auritum*, are sexually monomorphic, with both species carrying the same exaggerated tailfeathers,

ear tufts and velvety crimson skin around the eyes [6]. In such cases, the assumed cause is either an expression in the female of traits that are sexually selected only in the male [7] or mutual sexual selection [8].

In sexually reproducing organisms without separate sexes (i.e., simultaneous hermaphrodites), opportunities for sexual selection also exist, as hermaphroditic organisms will compete for access to a finite number of ova in the population [9]. However, as pointed out by Greeff & Michiels [10], the strength of sexual selection in hermaphrodites is likely to be less, given that the male and female functions are expressed in a single set of reproductive organs in a single individual, and compromises between the demands of all functions will need to be found. Nevertheless, extreme diversification in the reproductive anatomy in several groups of simultaneous hermaphrodites is presumably the result of sexual selection (e.g., penis size and shape in flatworms and sea slugs [11,12]).

Sexual selection is considered one of the major causes for morphological diversification among species [13,14], if not for the speciation process itself [15,16]. Hence, it is justified to view sexual selection as one of the prime candidates for explaining any strong morphological differentiation that is not readily explained by ecological niche differentiation. In this paper, I aim to present sexual selection as an explanation for the diversification of shell ornamentation in both gonochoristic and hermaphroditic land snails; an explanation that, as far as I am aware, has not been offered before.

### Presentation of the hypothesis

In land snails, shell diversification is often dramatic. Related species usually differ in the settings for the major shell-developmental parameters [17], which produces a variety of shell shapes that often may be correlated with differences in key environmental factors [18]. However, in other groups, additional conchological diversification is present that may be termed ornamentation. These include ribs, spines and lamellae on the shell surface, and flaps and flanges at the aperture. In some cases such ornamentation can be shown to be a response to structural demands from the environment, including camouflage and defense against predators and parasites [[19,20]: 117–131]. However, in other cases such an ecological relation appears insufficient to explain the full range of diversity. Two examples may serve to illustrate the latter situation.

The clausiliid (hermaphrodite) genus *Albinaria* is common and widespread throughout Greece and Asia Minor [21]. Almost 100 species are known, most of which have narrow, non-overlapping ranges, and usually only a single species occurs in a locality, where it normally occupies the

niche of microflora-grazer on limestone rocks. Shell diversification is considerable, and although differences may be present in a large number of conchological characters (e.g., spire shape, riblet density, and the form and position of apertural folds and lamellae), the largest and clearest diversification is in the external shape of the cervix, the last half whorl of the shell. The cervix may be smooth or ribbed. Cervical ribs may be narrow or broad, high or low, parallel or intertwined. In addition, cervical keels may be present, which can take a variety of forms as well. Figure 1 gives examples of cervical morphologies in a few species.

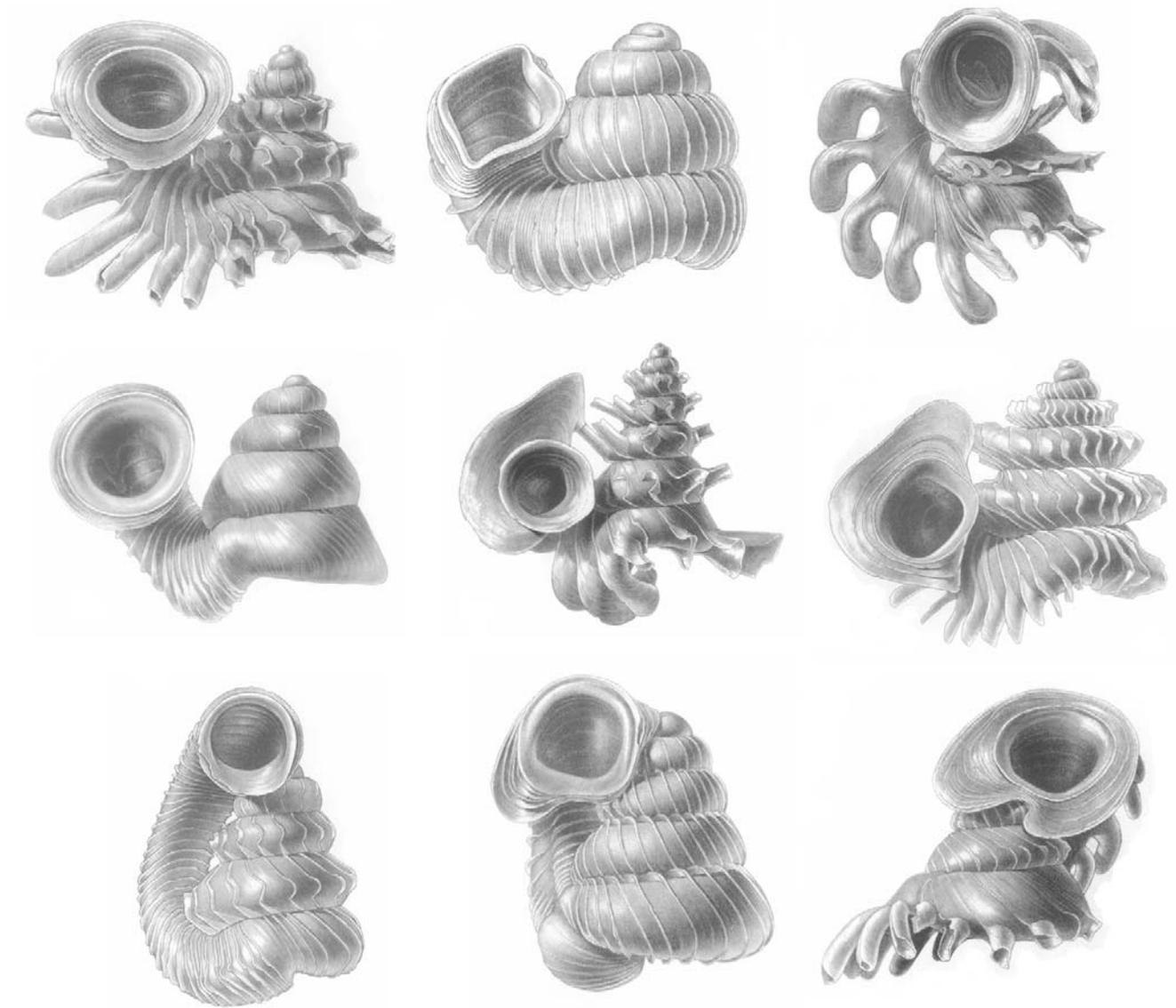
The second example is the diplommatinid (gonochoristic) subgenus *Plectostoma* in Borneo. These snails feed on moss growing on shaded limestone. In Borneo, limestone occurs as isolated outcrops, each on average less than a kilometer in diameter, but often separated from each other by tens or hundreds of kilometers of acidic soils, where *Plectostoma* does not live [22]. In Malaysian Borneo, almost 300 such hills are known, and most of the ones that have been studied support a dense population of one or two *Plectostoma* species. Each of the circa 50 known species and subspecies, however, has only a narrow distribution range, being confined to a few outcrops in each other's vicinity, or often just to a single outcrop [23]. Shell diversification in *Plectostoma* is extreme, with varying degrees and kinds of ornamentation, involving ribs (that often have developed into hollow spines) and apertural flanges (see figure 2 for examples).

These two examples show a situation that is often found in land snails: a largely allo- or parapatrically distributed group of species, which show a great diversification in shell ornamentation that is not obviously paralleled by niche-differentiation. Patterns similar to the one exemplified by *Albinaria* and *Plectostoma* occur in other groups of land snails, such as southeast-Asian Vertiginidae [24], and Cuban Annulariidae [25]. Here, I propose the hypothesis that such shell diversification may result from sexual selection on shell ornaments.

One condition for this hypothesis to be true is that mating partners can sense each other's shell ornamentation. This is not inconceivable, as many land snails have been reported to reciprocally mount each other's shell before achieving copulation [26,27]. In some cases, a snail will crawl in a complicated but stereotyped itinerary over the surface of its mate's shell [28]. In ornamented shells, the type and development of ornamentation may be sensed by the receptors in the foot tissue. In *Albinaria*, for example, copulation takes place with one snail sitting on the part of the cervix that carries the cervical ornamentation (figure 3), and similar behaviour has been observed in *Plectostoma* (Schilthuizen, unpublished data).

**Figure 1**

Diversity of shell ornamentation in the genus *Albinaria* (Clausiliidae) from Greece. Top row, from left to right: *A. rebeli*, *A. teres*, *A. drakakisi*. Middle row, from left to right: *A. praeclara*, *A. moreletiana*. Bottom row, from left to right: *A. eburnea*, *A. coerulea*, *A. spratti*. Most diversity is present in the ornamentation of the cervix (the dorsal part of the last whorl), which is also the place most in contact with the partner's foot before and during copulation (see figure 3). All photos were taken by A. 't Hooft, Leiden.



**Figure 2**

Diversity of shell ornamentation in Bornean species of the subgenus *Plectostoma* of the genus *Opisthostoma*. Top row, from left to right: *O. everettii*, *O. goniostoma*, *O. grandispinosum*. Middle row, from left to right: *O. hosei*, *O. mirabile*, *O. pulchellum*. Bottom row, from left to right: *O. lituus*, *O. shelfordi*, *O. stellasubis*. All drawings by J.J. Vermeulen.

### Testing the hypothesis

This hypothesis is actually composed of two parts. The first is that shell ornamentation can evolve under sexual selection, and the second is that such evolution can result in diversification of shell ornamentation patterns. The first part of the hypothesis (that shell ornamentation can evolve under sexual selection) can be tested both indirectly and directly. Indirect evidence for it may come from

a variety of sources. First of all, sexual dimorphism in shell ornamentation would be supportive. Obviously, this can only be studied in the gonochorists among the land snails, viz. the so-called Prosobranchia. In fact, dimorphism in the general shell shape and size (not ornamentation) is known for many (mostly marine) prosobranchs, where it is usually clearly caused by different functional morphological needs (e.g., modifications in the outline of



**Figure 3**  
Two mating clausiliid snails. In clausiliids, shell-mounting is normally part of the copulation behaviour. It may allow the registration of shell ornamentation by tactile stimulation of the foot. Photo by T. Asami.

the aperture, to facilitate the laying of eggs in the female [29]) or sometimes even by phenotypic plasticity, when the male shell adapts ontogenetically to its substrate, which is sometimes different from that of the female [30,31]. For ornamented land prosobranchs (including *Plectostoma*), however, sexual dimorphism has not yet been reported, although the great majority has not yet been studied in this respect. Yet, an absence of sexual dimorphism should not be taken as evidence against sexual selection. As mentioned above, sexual selection may result in sexually monomorphic ornamentation as well.

The hypothesis also requires that shell ornamentation is variable and heritable. Therefore, a second indirect test may be an analysis of variance in shell ornaments relative to other shell traits (see for similar approaches refs. [32,33]).

Direct testing of the sexual-selection hypothesis is conceptually simple. I would propose experimental manipulation of ornamentation, and investigating the effects on mating success in a laboratory environment. For example, in species with spiny shells, the spines could be removed by breaking them off, or elongated by attaching additional chips of shell material, analogous to the experiments that have been carried out on birds [3]. Alternatively, copulating pairs could be taken from the field and measured with regards to the degree of development of their shell ornamentation. An overrepresentation of highly ornamented individuals among the mating pairs could then be taken as evidence that such snails have a higher mating success. However, there are two possible

practical obstacles to overcome. First of all, many of the shells involved may be quite small. *Plectostoma* shells, for example, are on average just 2 mm tall. Also, in many snails mating takes place only during a particular season. For instance, *Albinaria* mates only during a few days per year, at the onset of the autumn rains [34]. Another problem may be the possibility that ornaments offer other cues than tactile ones (e.g., the recently discovered chemical cues offered by helicid love darts [35]). However, this complication may be controlled for by selecting structures like spines on the top whorls of the shell, which are out of reach of the parts of the snail body that might produce such compounds.

The second part of the hypothesis (that sexual selection on shell ornamentation induces species diversity) can be tested using comparative methods. The same approach may be followed as employed in ref. [13], [36] for demonstrating the relevance of sexual selection in promoting speciation in birds and insects, respectively. This would involve comparing snail sister groups for shell diversity and degree of polygamy. The prediction under this hypothesis would be that the more polygamous groups are also the more diverse. Unfortunately, available information on reproductive strategy in land snails may at present still be too sketchy to allow for such a test to be done. Another possible problem for this test is that it may sometimes be hard to control for the effects of differences in habitat. For example, reproductive strategy may be influenced by predator abundance, and this in turn may affect defensive aspects of shell structure as well. However, one may expect that both effects act in opposite directions: high predator abundance (selecting for defensive structures) will result in low prey population density, and this in turn will reduce the number of sexual encounters, relaxing the selection pressure on sexual signalling of shell ornamentation. In any case, this complication might be controlled for by selecting sister groups with different degrees of polygamy that share the same habitat, and are experiencing similar predation pressures.

### Implications of the hypothesis

If supported, the sexual-selection explanation for shell ornamentation would add to a growing body of evidence for a strong influence of sexual selection on molluscan anatomy and morphology. It would provide a solution to the conundrum that allopatrically distributed, conchologically diverse, but ecologically similar land snail species flocks have presented to many evolutionary biologists [21,37,38]. The diversity in shell ornamentation in such allopatric species flocks suggests that each has been exposed to very different selection pressures, which are not always apparent in their respective environments. Sexual selection may provide an explanation, as it, especially when 'Fisherian' in nature, will proceed in unpre-

dictable and chaotic cycles. Hence, unconnected, allopatric populations experiencing the same environmental pressures are still expected to diverge rapidly in their ornamentations [39].

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