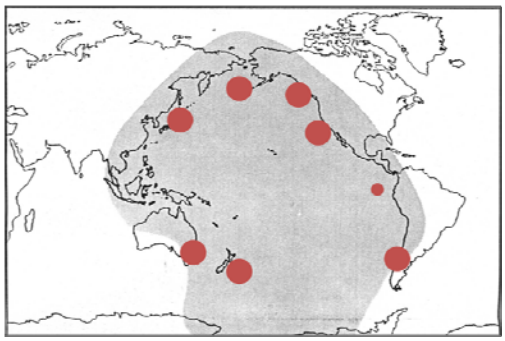
# Interactions Among Clades in Macroevolution

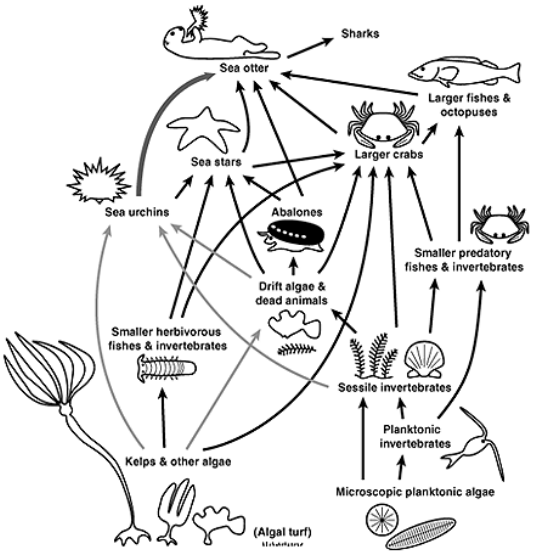
## Kelp Forests:

Nearshore kelp communities are predominate around the shores of the Pacific Rim.

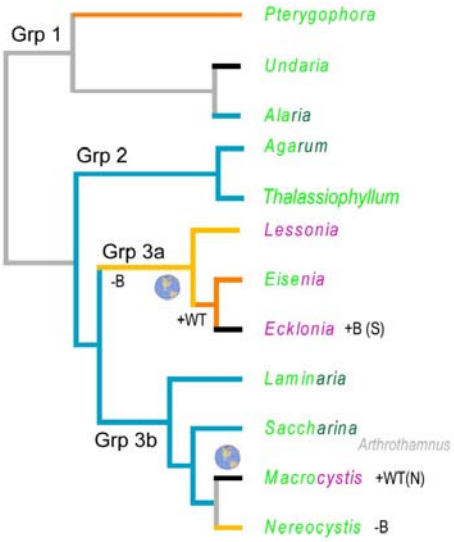


They have been well studied and the trophic interactions that occur within them are well known. Kelp beds dynamics are thought to represent a classic trophic cascade including primary producers (the kelps), primary consumers (typically sea urchins) and predators (sea otters, fish). Experimental and observational data has confirmed these similar interactions and outcomes throughout North America, South America, Australia and New Zealand.

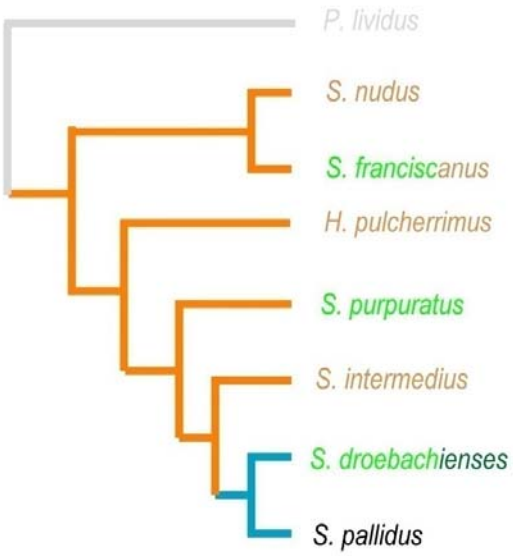
However, while the use of these terms (kelp, sea urchin, fish, otter) to describe the interacting members of these communities may provide and important and vivid description of the trophic interactions in these communities, might they also obscure other levels of information and complexity – for example, the history of the kelp communities and their interacting components?




The term kelp refers to algae that belong to the clade Laminariales. Of the more than 50 described 'species' that compose this clade, 12 are recognized as forming the base of the kelp forest.




In contrast to the kelps, the sea urchins that comprise the primary consumers in the Pacific Rim kelp forests represent at least 3 major clades in the echinoids. Only in the Northern hemisphere is there evidence for an *in situ* radiation of urchins in a kelp forest communities. In all other instances, the taxa appear to be derived from adjacent tropical or subtropical faunas.





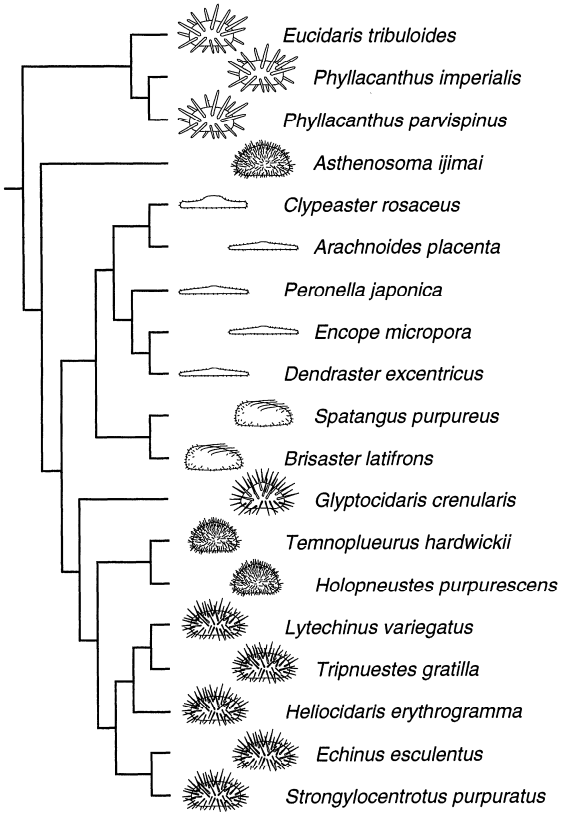
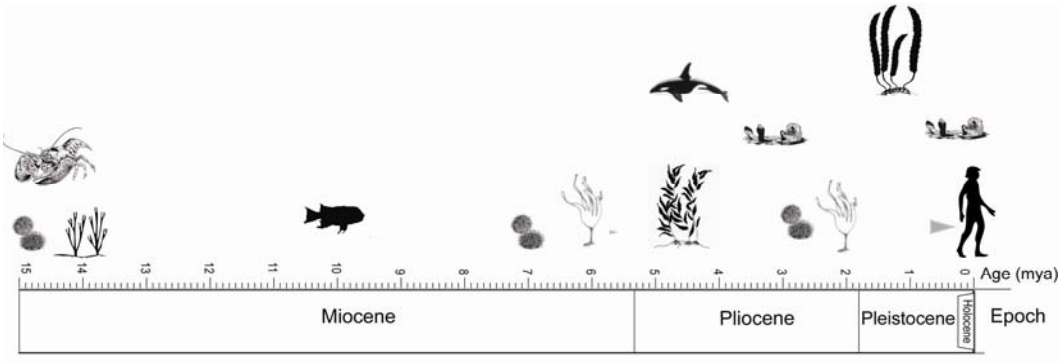
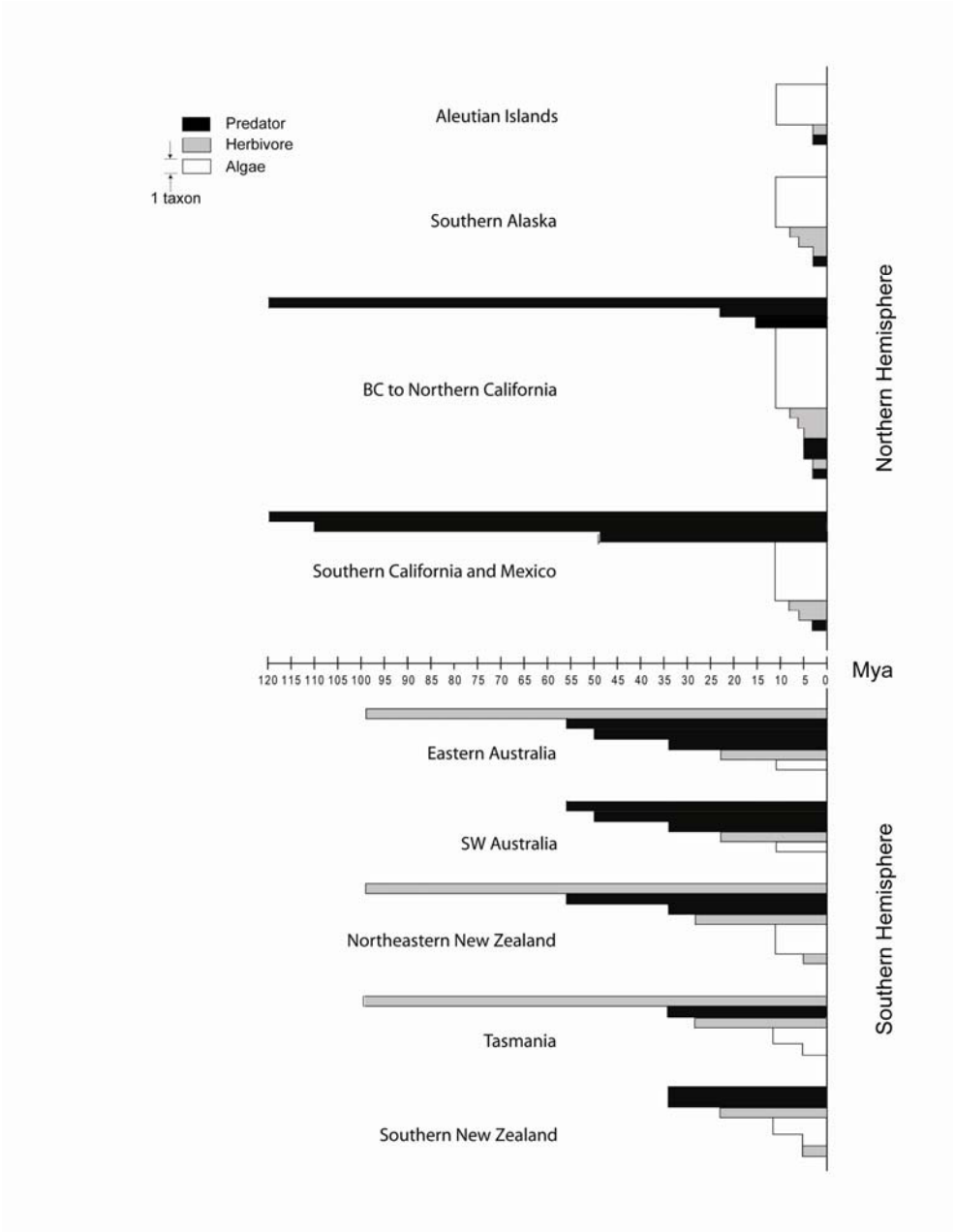



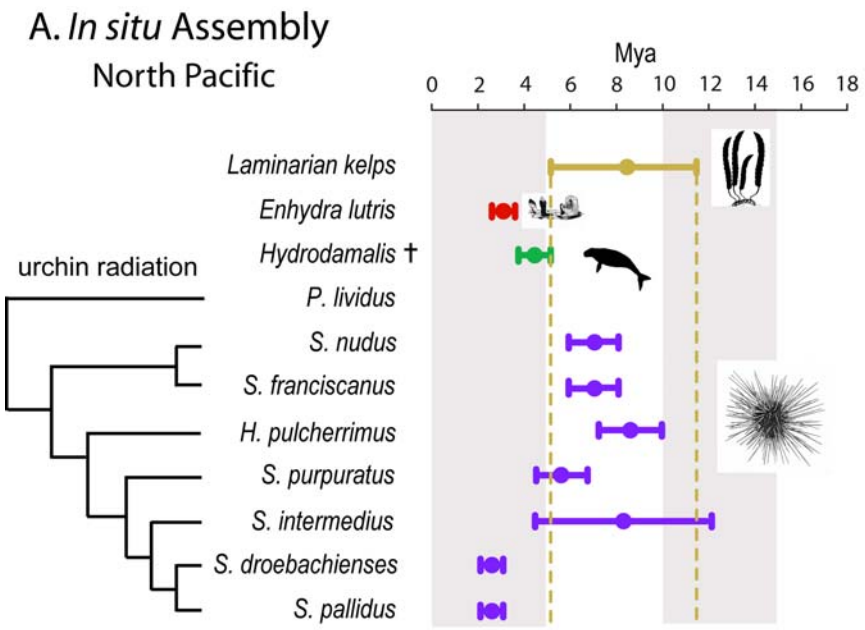

FIGURE 2. Echinoid phylogeny. The phylogenetic framework for the present analysis is based on the total evidence analyses of Littlewood and Smith (1995) and Smith et al. (1995), with relationships among clypeasteroids based on an analysis of adult morphology (Mooi, 1990). Species not included in either of these studies are assumed to belong to the orders or suborders to which they are traditionally assigned. Importantly for the present analysis, the eight study species with derived developmental modes almost certainly represent seven independent transformations that have occurred in seven different families in six different orders (Raff, 1987; Emlet, 1990; Hart, 1996). Beyond this assumption of seven independent transformations, the precise topology of the tree does not significantly affect the analyses described here.

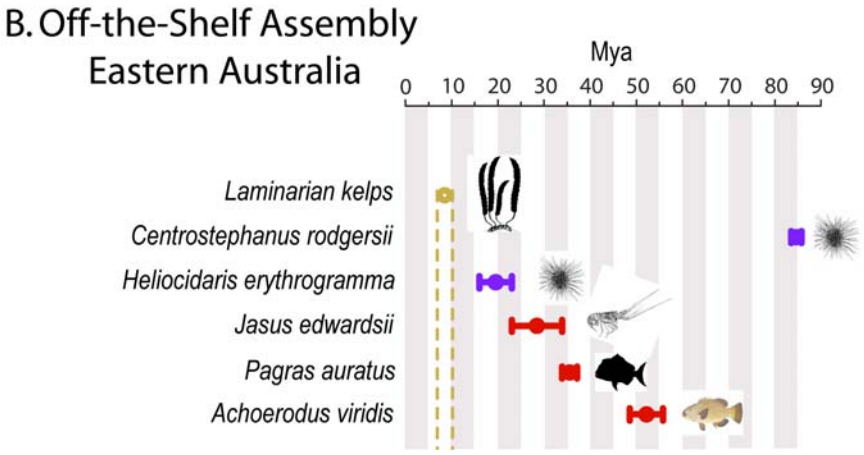
Lastly, the predators, like the primary consumers, represent a diverse array of clades with the single exception of the sea otter in the North Pacific.

'Kelp' communities in the temperate regions appear more diverse in than those in the more poleward regions. They also contain more contributions from the tropical and subtropical faunas and appear more resistant to abiotic and biotic perturbations.


15 14 13 12 11 10 9 8 7 6 5 4 3 2 1 0
Age (mya)
Miocene
Pliocene
Pleistocene
Holocene
Epoch

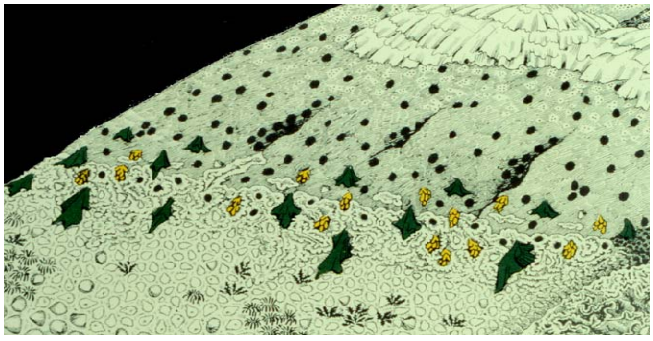

Predator
Herbivore
Algae
1 taxon
Aleutian Islands
Southern Alaska
BC to Northern California
Southern California and Mexico
Northern Hemisphere
120 115 110 105 100 95 90 85 80 75 70 65 60 55 50 45 40 35 30 25 20 15 10 5 0
Mya
Eastern Australia
SW Australia
Northeastern New Zealand
Tasmania
Southern New Zealand
Southern Hemisphere




**Partitioning intertidal resources:**

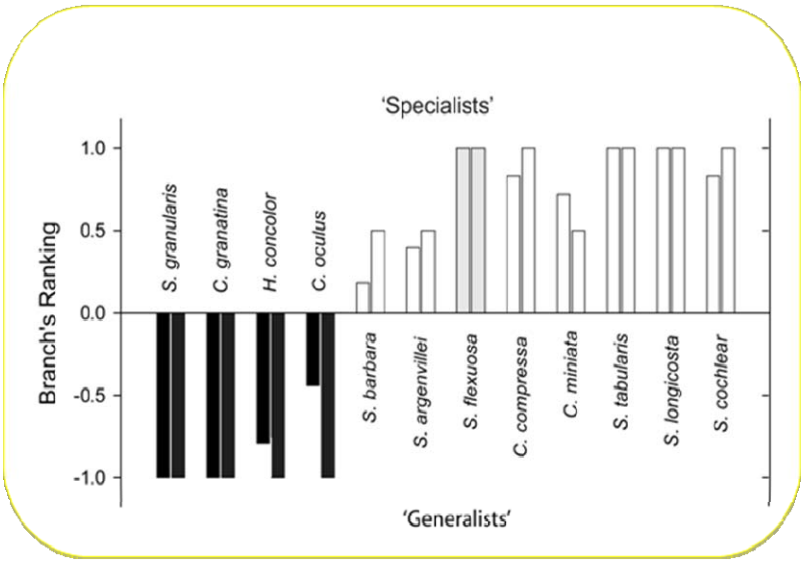
Patellogastropod limpets (or 'true' limpets) have long been studied in a broad array of biological disciplines. Because of their intertidal occurrence, they were some of the first and remain one of the commonest taxa manipulated in ecological studies They have served as physiological 'guinea pigs' in studies of desiccation and growth They also have a long and illustrious record as model organisms in life history

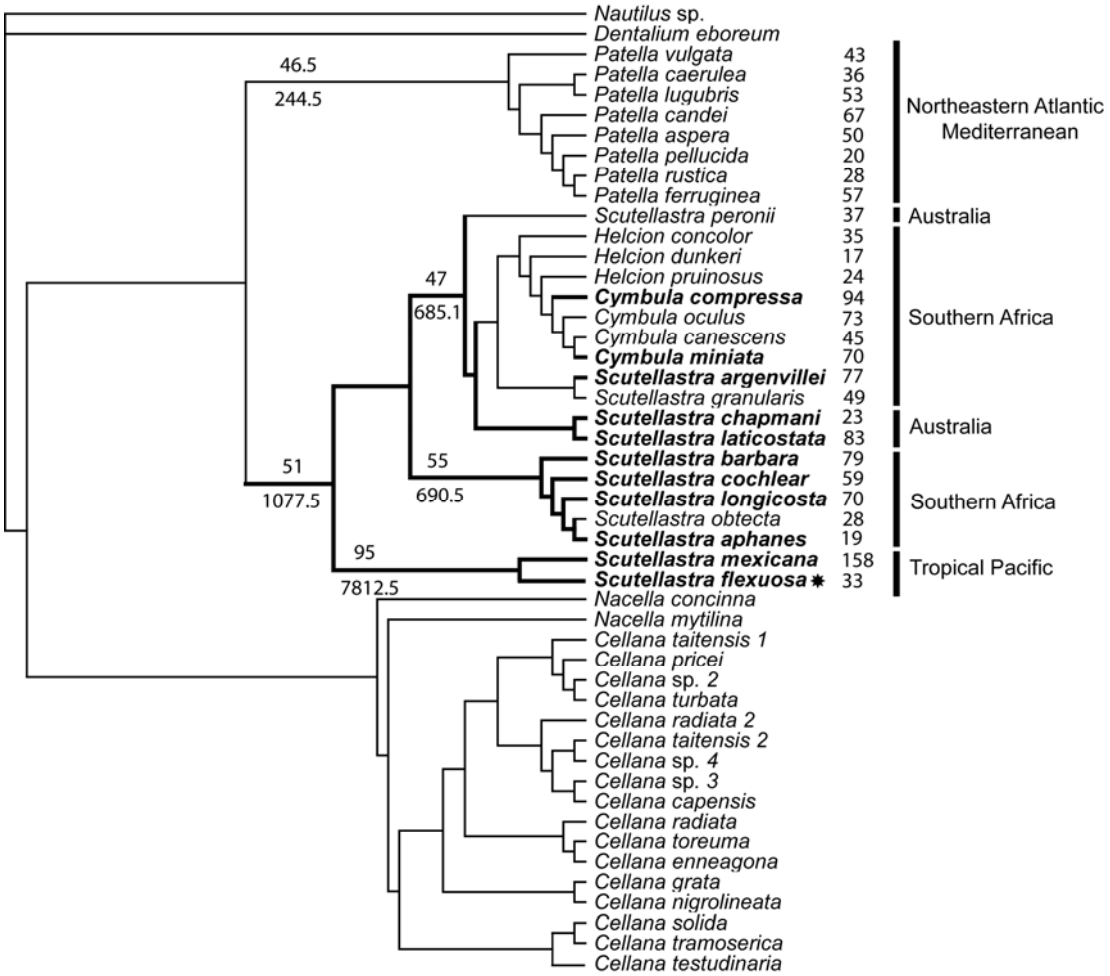


studies, especially with regard to reproductive cycles and hermaphrodism. However, the distributions of these life history characters have seldom been explored except for quick comparisons or corroborations of similarities (and differences) with 'other limpets' in another region or genus.

On Moorea *Scutellastra flexuosa* is a common member of the algal ridge community where it experiences the full intensity of reef-crest wave action**.** Unlike most other patellogastropod faunas found in high-energy environments, *S. flexuosa* is the only patellogastropod species to occur there. Therefore, it presents an opportunity to compare the roles of phyletic history and recent adaptations in shaping its ecology and life history uncomplicated by the co-occurrence of closely related taxa and interactions.

To compare the ecological and life history characteristics *S. flexuosa* with other patellid species a standardized list of ecological and life history characters was used. This list was developed by George M. Branch during his study of intraspecific competition in southern African *Patella* spp. Branch was especially interested in the role of migration, differentiation and territorial behavior and when he scored his study taxa he found that they sorted into two distinct categories with few intermediates. Branch termed these groups 'migratory' and 'non-migratory', but they also denote groupings of characters commonly associated with distinguishing generalist (migratory) and specialist (non-migratory) species. *S. flexuosa* was scored for these traits and the characters examined on a phylogenetic tree to determine character distribution and to separate shared historical characters (pleisomorphy) from new unique characters (autapomorphy) that might represent more recent and local adaptation

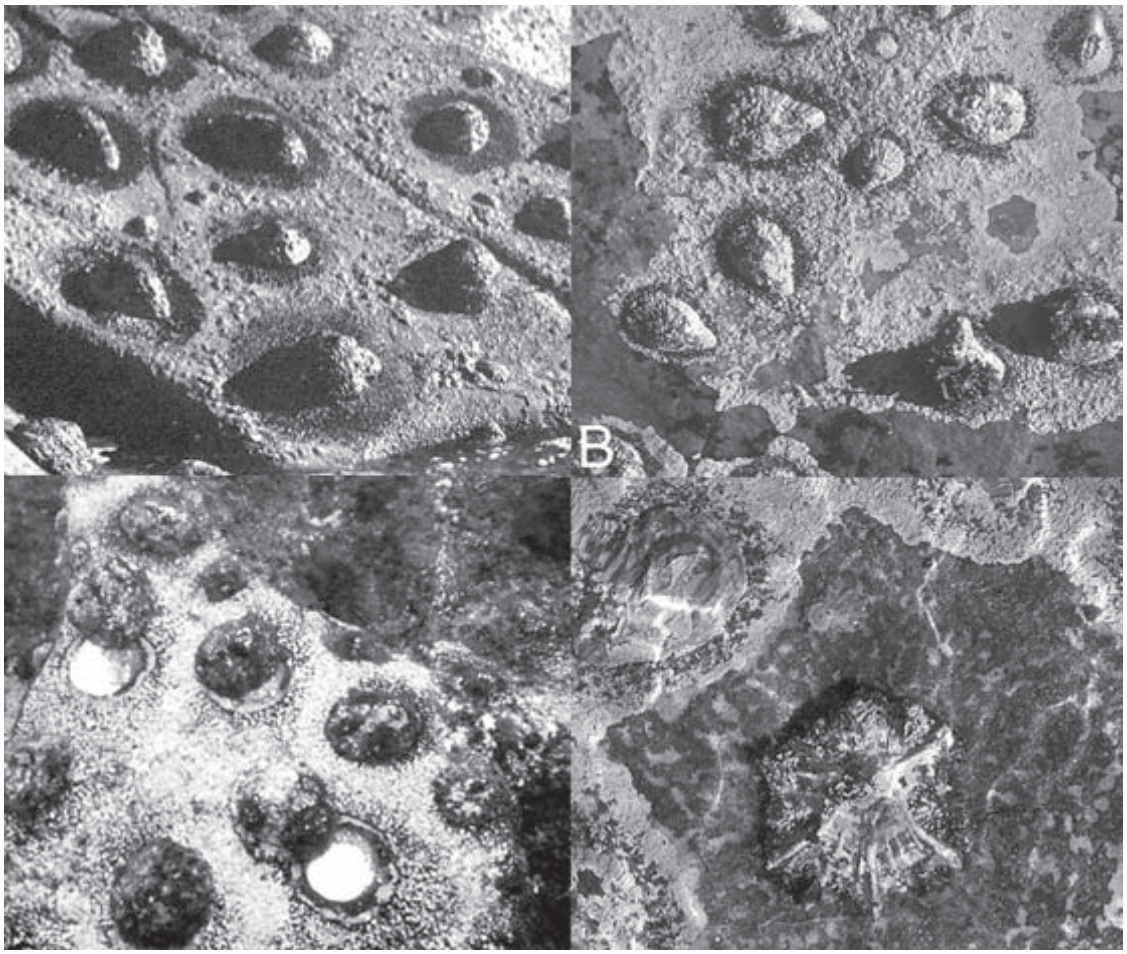





Ecological and life history traits of *S. flexuosa* most likely reflect its phylogenetic history rather than being adaptations to its current habitat and distribution. These traits include habitat restriction, algal gardening, local distribution, home site fidelity, adult/juvenile differentiation, and protandric hermaphroditism. Large body size is also correlated with these other characters, but in the case of *S. flexuosa* this trait appears reversed and autapomorphic as a result of selection for small body size reflecting the topography of the habitat.

The scutellastrid clade (*Scutellastra*, *Cymbula*, and *Helcion),* of which *S. flexuosa* is a member dates at least from the Cretaceous and may extend back to the Triassic . The basal branches of the living clade are dominated by specialized "non-migratory" species. A total of eleven of the 19 scutellastrid taxa are categorized as "non-migratory" taxa. Of these eleven species, eight are accounted for in the first 10 taxa on the tree, while in the remaining nine taxa, only three species are categorized as "non-migratory". This pattern suggests that the shared traits of the "non-migratory" species are ancestral and are present in *S. flexuosa* and the other basal members of this group because they were present in the common ancestor and are not independently

derived. This pattern also suggests that "non-migratory" traits have arisen independently in at least two taxa, *Cymbula compressa* and *C. miniata*, both of which prominently reside among "migratory" taxa




Gardening *Scutellastra* species. (A) *Scutellastra mexicana*, Tangola-Tangola, Mexico (Photograph from *Book of Bays* by William Beebe, reprinted by permission of the publisher). (B) *Scutellastra cochlear*, Dalebrook, South Africa. (C) *Scutellastra kermadecensis,* Kermadec Islands, New Zealand. Photograph courtesy of R. Creese. (D) *Scutellastra longicosta*, Dalebrook, South Africa