

Convergent or related? Considerations on certain Conidae (Gastropoda: Toxoglossa) from South Africa, Arabia and Australia

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Abstract

This paper reports a research project on the taxonomy and phylogeny of Conidae, focusing on the radiation and relationship of South African endemics.

Introduction

The generic subdivision of the gastropod family Conidae is one of the challenges of modern molluscan taxonomy. To try to get a reasonable order among the vast number of species, various methods have been suggested, but few have delivered satisfactory results (PEILE, 1939; ENDEAN & RUDKIN, 1965; LIM, 1969; DA MOTTA, 1991; ROLAN & RAYBAUDI MASSILIA, 1994a, b; RÖCKEL *et al.*, 1995; KOHN *et al.*, 1999; NISHI & KOHN, 1999). In order to study taxonomic questions concerning the generic relationship between populations, species and species groups, we have begun research on Conidae at the Institute of Zoology, University of Giessen, Germany. This short essay reports the details of our project.

In order to find mechanisms and methods to subdivide a large group of species such as the Conidae, it makes sense to pick out a manageable unit first. We have chosen the radiation of South African endemic species, as these present a group of fewer than twenty species within a relatively small geographic region. To the West, the border of distribution is the Atlantic coast just above Cape Town; to the East, the coast of central Natal forms the limit. During the Pleistocene, the meeting of the Indian and the Atlantic Oceans was farther westward along the Atlantic than today. That is why several South African species, like those of *Cypraeovula* still occur, just around the Cape of Good Hope in the present Atlantic.

We exclude some deepwater species (e.g. *C. patens* Sowerby III, 1903, and *C. gradatulus* Weinkauff, 1875), as morphologically these belong to groups that have close conchological relatives in the Indian Ocean and do not resemble the radiation that is genuinely South African (e.g. *C. teramachii* Kuroda, 1956, and similar taxa). The species we deal with include *algoensis* Sowerby 1834, *mozambicus* and *tinianus* (both Hwass, 1792), *infrenatus* and *pictus* (both Reeve, 1843) and allied species. The questions we deal with are:

- 1) where do these species have their origin,
- 2) which species from other places are their closest relatives,
- 3) how are they related to each other?

In the following, we will try to show our preliminary observations and results.

Question No. 1): Where do the South African endemic species have their origin?

The earliest *bona fide* fossils of *Conus* appear in the Lower Eocene (50-55 million years ago) of England and France (KOHN, 1990), but there are several other reports of *Conus* fossils. For example, the oldest fossils described as *Conus* are from the Lias (lower Jurassic 175-190 million years ago), and another *Conus* is described from the middle Jurassic (155-175 million years ago). In all these cases, it is not certain that these taxa are really members of the genus *Conus* (Kohn, 1990). It seems that the members of the genus *Conus* originated from an area around England and France, where in the lower Eocene was a warm temperate climate.

The radiation of the family might have taken place in various independent steps (KOHN, 1990; RÖCKEL *et al.*, 1995). On account of the great similarities of the South African and Australian endemics we expect that the groups discussed

earlier may have already reached their habitats some 60 million years ago. At that time the distances between the landmasses (South America, Australia, South Africa, Antarctic and India) were not as great as at present. This could also be case for ophiid fishes of the genus *Xiphiurus*. One species, *X. blacodes*, occurs on both sides of South America, New Zealand and Australia. *X. capensis*, a related species, is found in southern Africa (BRIGGS, 1974).

Which methods can be applied to characterize the degree of relationship between all those groups, and how can we use these data to establish a system to subdivide the family? Our project aims at the South African species first. We will try to analyze genetic features as well as morphological and toxicological data chiefly, gathering all information we can extract from a shell and its preserved animal.

Question No. 2) Which species from other places are their closest relatives?

In the discussion of *Conus ardisiaceus* Kiener, 1845, a distinctive species from the Gulf of Oman, RÖCKEL *et al.* (1995) mention *Conus anemone* Lamarck, 1810; *C. peronianus* Iredale, 1931; and *C. papilliferus* Sowerby I, 1834, all Australian endemics, and *C. tinianus*, a species endemic to South Africa. Other species from Australia, *C. klemae* Cotton, 1953; *C. wallangra* Garrard, 1961; *C. angasi* Tyron, 1883; *C. gabelishi* Da Motta & Niomiya, 1982; and *C. rutilus* Menke, 1843, show considerable resemblance to South African species, but to no other species distributed in the Indo-Pacific. Likewise, another strange and distinctive Arabian endemic, namely *C. cuvieri* Crosse, 1858, bears a great resemblance to both *C. tinianus* and *C. anemone*. Looking to the other side of the African continent, there is a large radiation of species that show only superficial resemblance to the South

African radiation. On the African west coast, a few species exist that are similar to *C. mozambicus* and *C. tinianus*. These species may be assigned to a group of *Conus bulbus*-like species.

C. aemulus Reeve, 1844; *C. albuquerquei* Trovão, 1978; and *C. bruguieri* Kiener, 1845, for example, resemble *C. tinianus* and *C. mozambicus* in shape and often even in coloration. *C. decoratus* Röckel, Rolán & Monteiro, 1980, can be compared with *C. algoensis agulhasi* Coomans, Moolenbeek & Wils, 1980; it differs only in the width, whereas size, spiral shape and pattern are almost identical.

The East African coast. Although many Indo-Pacific species are still found as far south as Northern Transkei, no living or fossil species occur in the southwestern Indian Ocean that can be compared to the South African endemics. Along the east coast of Africa a strong southward stream, the Mozambique Current, parallels the coast. When this stream enters the coastal area below 30°S latitude, it is joined by additional flow from around Madagascar, and then becomes a well-defined, swift narrow stream called the Agulhas Current. The Agulhas Current parallels the coast westward, where it approaches the Cape of Good Hope region. Although at times some Agulhas water rounds the Cape to become mixed TALBOT & PENRITH, 1962), the greater volume bends sharply to the south and then toward the east and returns to the Indian Ocean. The Agulhas Current is one reason why a warm-temperate fauna can persist on the African south coast (BRIGGS, 1974).

Apparently, we have to focus our attention on the West African coast, Arabia and Australia.

West Africa. The Benguela Current comes from the Atlantic and goes northward. Since the Paleocene, the sea currents circulate in such a manner that an eastward migration of taxa from the Atlantic into the Indian Ocean appears im-

Sud Africa	Arabia	Australia
<i>tinianus, mozambicus</i>	<i>ardisiaceus</i>	<i>anemone, peronianus, papilliferus</i>
<i>bairstowi</i>	<i>cuvieri</i>	<i>angasi</i>
<i>infrenatus</i>		<i>gabelishi</i>
<i>visagenus</i>		<i>rutilus</i>
<i>algoensis, pictus</i>		<i>klemae</i>

Table 1: The conchological groups of South African endemics and close resemblances from Arabia and Australia.

South Africa



Arabia



Australia



possible (BRIGGS, 1974). The similarities between the West African and the South African Conidae are most probably not the result of close generic relationship, and possibly the result of a convergent evolution.

Arabia. In theory the Indian plate could have carried some Conidae (suspected ancestor of *C. cuvieri*, *C. ardisiaceus*, see above) on its way northward. Another possibility is that the ancestors of the Conidae had a wide distribution in the ancient Ocean between these landmasses. Then the Arabian species are not ancestors, but descendants of our South African group.

Australia. Despite the great distance between the continents, there are many biological similarities between Australia and South Africa. The South African *C. typhon* Kilburn, 1975, is not a member of the group we are investigating, but it gives a good example of this phenomenon.

This taxon shows its closest resemblance to *C. nielsenae* Marsh, 1962, and is indeed considered a subspecies by some authors (RÖCKEL *et al.*, 1995). *C. nielsenae* inhabits the coast of north-west (*C. n. reductaspiralis* Walls, 1979) and northeast Australia (*C. n. nielsenae*), *C. typhon* on the other hand inhabits the coast of eastern South Africa. The deepwater species *C. visagenus* Kilburn, 1974, from Natal and Northern Transkei shows little similarity to other African species, but to *C. rutilus* from southern Australia.

The Australian genus *Notocypraea* Schilder, 1927 (Cypraeidae) seems to be the closest relative of the South African genus *Cypraeovula* Gray, 1824. The recently described *Cypraeovula immelmani* Liltved, 2001, resembles the Australian *Notoluponia* Schilder, 1935 (Lorenz, pers. comm.). This genus is understood as the closest relative of *Notocypraea* (LORENZ & HUBERT, 2000). *Bernaya teulerei* Cazenavette, 1846, from Oman shows similarities to *Barycypraea fultoni fultoni* Sowerby III, 1903, of South Africa and the Australian endemic genus *Zoila* Jousseume, 1884. The cretaceous *Afrocypaea chubbi* Rennie, 1930, from South Africa is thought to share a common ancestor with *Zoila* or to be the ancestor of this genus (LORENZ, 2001). But other faunistic examples may also be quoted: two frog families, Myobatrachidae and Heleophrynidae. These are considered sister taxons (HAY *et al.*, 1995). Whereas the Myobatrachidae are endemic in Australia, the Heleophrynidae occur only at

the most southern tip of Africa. Lobsters of the genus *Jasus* have a warm-temperate, circumpolar distribution. There are single endemic species in South Africa, Amsterdam-St. Paul Islands, New Zealand, Juan Fernández Islands and southeastern Australia-Tasmania (HOLTHUIS, 1963). Common representatives in Australia and South Africa can also be found in the flora. Flowering plants of the family Restionaceae occur mostly in South Africa and Australia but also rarely in New Zealand, Madagascar, Indochina and Chile (WATSON & DALLWITZ, 1991). Proteacea are found only in the Cape Floristic Region of South Africa and the western coastal region of Australia (BRIGGS, 1987).

We suspect that the South African endemic *Conus* could be most closely related to the above-mentioned Australian species.

Question No. 3) how are they related to each other?

Are the South African endemics all closely related to each other (that is, one subgenus) or are they polyphyletic groups? According to the generic subdivision proposed by DA MOTTA (1991), we are looking at a vast number of different genera and subgenera: *Dendroconus* (*Ketyconus*) for *tinianus* and *natalis*, *Hermes* for *mozambicus*, *Dendroconus* (*Sciteconus*) for *pictus*, and *Conus* (*Lithoconus*) *visagenus* Kilburn, 1974. We have failed to follow the concept of his subdivision and prefer to use a grouping based on more obvious and verifiable features than shell-outline.

As well, one may arrive at a different grouping:

1) *natalis*-group (*gilchristi* Sowerby III, 1903; *C. natalis* Sowerby II, 1857; *immelmani* Korn, 1998), species with a tented pattern;

2) *tinianus*-group (*C. tinianus*; *bairstowi* Sowerby, 1889; *infrenatus*; *mozambicus*; and *C. brianhayesi* Korn, 1996), rounded shoulder and a ventricosely conical shape;

3) *pictus*-group (*C. algoensis*, *C. visagenus* and *C. pictus* Reeve, 1843), conical shells with a stepped spire.

Other interpretations may be made, such as grouping all those with regular transverse dotting against the mottled ones. That would place *bairstowi*, *pictus*, *infrenatus* and *brianhayesi* into one group, and *tinianus*, *mozambicus* and *algo-*

Listed separately by section, from top to bottom, from left to right.

South Africa:

1st row: *Conus mozambicus*, Cape of Good Hope.

2nd row: 2 x *C. tinianus*, *C. mozambicus* var. *lautus* Reeve, 1843, *C. tinianus*, all Jeffreys Bay.

3rd row: *C. brianhayesi*, Transkei, 2 x *C. tinianus*, East London, *C. bairstowi*, Jeffreys Bay,

4th row: *C. infrenatus*, 2 x *C. pictus*, all Jeffreys Bay,

5th row: 2 x *C. algoensis*, Cape of Good Hope area, 2 x *C. pictus*, Transkei.

6th row: *C. visagenus*, Transkei.

Arabia:

3 x *C. cuvieri*, Djibouti, 2 x *C. ardisiaceus*, Oman.

Australia:

1st row: *C. peronianus*, S. Australia, 3 x *C. anemone*, W. Australia.

2nd row: *C. angasi*, S. Queensland, 3 x *C. papilliferus*, New South Wales.

3rd row: 2 x *C. wallangra*, S. Queensland, *C. gabelishi*, W. Australia (after RÖCKEL *et al.*, 1995).

4th row: *C. klemae*, W. Australia.

5th row: *C. rutilus*, W. Australia.

ensis into another. We simply do not know but perhaps will find the answers in the genetic studies. We have decided to leave the tented group (*natalis*, *gilchristi* and *immelmani*) out because these have a more northeastern range than the others, and their similarities to Indian Ocean species are more apparent (e.g. *gilchristi* to *penanceus* Born, 1778, and *immelmani* to *amadis* Gmelin, 1791).

The conchological relationships between the South African and Australian Conidae as shown in Table 1 were gained from morphological comparison of the shell indices proposed by RÖCKEL *et al.*, 1995. To give additional depth to these findings, we are preparing a comprehensive genetic analysis to prove or dismiss the relationships of these geographically isolated radiations. We hope that our project may contribute to the subdivision of the whole family by using traditional conchology and molecular biological tools alike.

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