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The Cypraeidae of the Southeast Atlantic Vema Seamount (Mollusca: Gastropoda: Cypraeidae)

John D. "Duffy" Daughenbaugh
203 North Wilton Place, Los Angeles, CA. 90004
shoduffy@ca.rr.com

ABSTRACT The Vema Seamount, discovered in 1957, is located in the southeast Atlantic Ocean, 480 km west off the Namibian coast and 1,000 km west northwest of Cape Town, South Africa. To say this is an unusual location and habitat for Indo-Pacific Cypraeidae species is an obvious understatement. Yet, in the late 1980s and early 1990s, at least two species and possibly a third were reported from that location. Are these migrants or from a population at the seamount? The acquisition of one such species from Werner Massier, a prominent Namibian dealer and author, prompted the research which led to this article.

INTRODUCTION

In their seminal first edition of a Guide to Worldwide Cowries (Guide) published in 1993, Lorenz & Hubert provided the following information under the "Discussion" of three species of Cypraeidae found or reported at Vema Seamount (Vema). The same notations were included in the second edition of the Guide published in 2000. Under *Ovitipsa chinensis violace*a (Rous 1905), they wrote (p. 140): "A strange, elongate specimen of *violacea* with a bright orange base and a white frame separating the dorsum from the margins was collected by a diver at Mount Vema, off the Atlantic coast of South Africa. This is the third record of an Indo-Pacific cowry at this particular spot in the Atlantic (see *Erosaria cernica*, *Erronea* [subsequently reclassified by Meyer (2004) as *Contradusta*] *barclayi*). Whether the single *chinensis* was a stray specimen or whether there is really a population of *chinensis* in the Atlantic needs confirmation."

NOTE: The status of the genus *Erosaria* is unsettled at present. Meyer (2004) reclassified *Naria irrorata* (Gray, 1828) as *E. irrorata*, although it was poorly supported as sister to a strongly supported clade including *E. albuginosa* and *E. poraria*. Some authors have reclassified the Genus *Erosaria* as *Naria* as the latter was introduced 26 years prior to *Erosaria*. As the matter needs to be resolved, for the purposes of this paper, *Erosaria* is retained for all species presently classified in that genus. This is also in accordance with the World Register of Marine Species (WoRMS) (Moretzsohn, 2013).

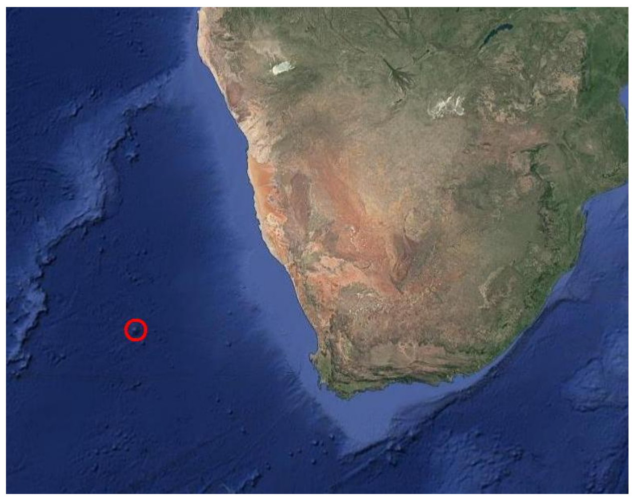

Figure 1. Location of Vema Seamount (located inside the red circle) in relation to the southern portion of the African continent; approximately 600 km west of South Africa.

Under the Discussion of *Erosaria cernica cernica* (Sowerby, 1870), they wrote (Guide, p. 195): “Its occurrence in the Atlantic at Mount Vema was verified by several divers.” They illustrate a specimen on Plate 87, numbers 17 & 20 with the caption “Mount Vema, a submerged volcanic peak off southwest Africa, in the Atlantic (taken by diver at 55 m). 23.9 mm.” Separately, Lorenz wrote in a 2003 internet article: “a single shell [*cernica*] was collected at 45 m on the submerged volcanic rock called Mount Vema, 600 km offshore the South African coast, in the Atlantic”. (*See* Figure 1)

Under the discussion of *Erronea* [*Contradusta*] *barclayi* (Reeve, 1857) they wrote (Guide, p. 131): “The occurrence of *barclayi* on Mount Vema, a submerged volcanic peak west of the South African coast in the Atlantic Ocean, needs confirmation.” Subsequent to the publication of the 1993 edition of the Guide, Raybaudi, in World Shells Nr. 15 of December, 1995, p. 57, wrote: “And today I am happy to announce to you the finding in the Atlantic of a *barclayi*, a species considered endemic to a zone from the Natal to Chagos. This very rare species was *supposedly* [emphasis added] found live in a crayfish trap at a depth of 200 meters at Sea Mount Vema, 300 miles off Port Nolloth.” The latter is on the Namibian coast. The specimen illustrated by Raybaudi appears to be a normal *barclayi*, albeit somewhat light in its dorsal coloration. No further information was provided regarding the source of the shell. Lastly, Liltved, in his Cowries and Their Relatives of South Africa of 2000, does not include Vema in the distribution range of *C. barclayi* while, in the same publication, included *Trivia vemacola* Liltved 1987.

The author is not aware of any other published reports of these or other Cypraeidae species from Vema subsequent to the reports above. These reports support the presence of *O. c. violacea* and *E. c. cernica* at Vema while the presence of *C. barclayi* still needs to be confirmed. None the less, while a definitive answer to the question of the status of the species at Vema (emigrants or viable populations) is not possible, there is enough information to address the possibilities.

Subsequently

The data associated with the specimens from Vema as conveyed to Lorenz has been clarified. The data for *E. c. cernica* was supplied by Arie Jooste with the shell when it was sold by him to Lorenz in 1989. The data stated that it was collected by diver at 150 ft. (45 m) in 1988. It appeared fresh at that time. A pair of *O. c. violacea*, matching the Guide description, also passed through at that time. (Lorenz, personal communication).

In May, 2016, the author acquired a specimen of *O. c. violacea* which had been taken from a rock lobster, *Jasus tristani* (Holthuis, 1963), trap at 150 m at Vema in June, 1991 (*see* Figure 4). The shell was acquired from Werner Massier, a well known shell dealer and author, who was living in South Africa at the time. Massier acquired the shell in Cape Town from Arie Jooste who had connections with the South African boats working in the area. The shell’s features match those described by Lorenz in the Guide. Similar specimens inhabit the Natal Bight and are collected by trawl or ex-pisces at depths of 100-150 m. They also match the features of the Vema specimens, except some have the white frame separating the dorsum from the margins and some do not.

The Vema Cypraeidae

Erosaria cernica cernica is a wide ranging Indo-Pacific species while *O. c. violacea* is a regional subspecies of the Indo-Pacific *O. c.*

chinensis (Gmelin, 1791). Both are known from the Southwest Indian Ocean generally and from both diveable and trawled depths off the Natal coast of South Africa. The populations of these species off the Kwazulu-Natal coast between Richards Bay and Durban, South Africa (Natal Bight) are of particular interest to this study as they form the closest populations of these species to Vema and represent a potential source of the shells found at Vema.

Regarding *C. barclayi*, it is a deeper water species collected either ex-pisces or by trawl. However, without additional supporting evidence of its presence at Vema, either in the initial report or subsequently, its presence there is considered doubtful.

Vema Seamount

Vema Seamount was discovered in 1957 by the Lamont Geological Observatory research vessel Vema. In 1959, R.V. Vema returned and made additional traverses of the seamount. In November 1964, a detailed survey of the peak was undertaken, using the diamond prospecting tug, Emerson K. (*See* Figure 2) Further expeditions were conducted in 1966 and 1978. The peak was established to have a position at 31° 37.8' S, 8° 18.7' E, which is 1,000 km west northwest of Cape Town, South Africa. It lies near the center of the Cape Basin, about midway between the Walvis Ridge and the Namibian and South African coasts. The Walvis Ridge is an oceanic ridge which extends more than 3,000 km from near Tristan da Cunha at 37° S to the African coast near Senegal at 18° S.

Vema rose from the central abyssal region of the Cape Basin, 4,572 m below sea level, approximately 11 million years ago. The latter was determined through analysis of volcanic green phonolite rock collected near Collin's Peak, which represents the highest point of the seamount at 26 m. The roughly oval shaped base has a diameter of 58 km. The 15° upward slope ends at a T shaped plateau covering an area of 10 km². The plateau's depth averages from 55 to 75 m with a mean depth of 75 m. The plateau corresponds to a wave cut platform which probably formed during the Pleistocene epoch (2.58 million years ago to 11.7 thousand years ago) when sea levels were considerably lower during extended periods of time. At 110 m, there is another level area which was also probably caused by wave cut action.

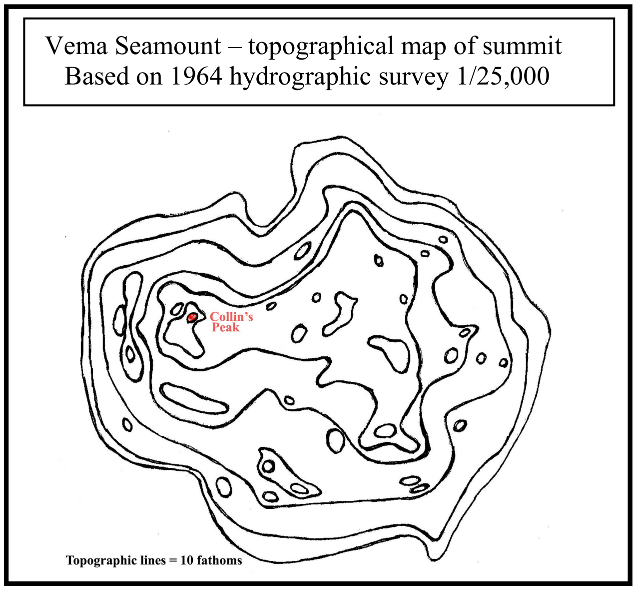

Figure 2. Diagram of the Vema Seamount. Topographic lines denote 10 fathoms. (Mallory, 1966)

During the expeditions, specimen collection was carried out via an air lift dredge and by scuba divers, with the latter diving up to 60 m. Collection of rock samples confirmed that Vema is entirely volcanic. Prolific growth of sponges, hydroids, seaweeds and kelp cover the rock substrate. Divers observed abundant populations of fish, primarily pelagic, and the rock lobster, *J. tristani*. Subsequent to the visit by the Emerson K, Vema was inundated with many unregulated visits by commercial fishing vessels, focusing primarily on the rock lobster

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population. Predictably, this resulted in a drastic decline in their population within two years. Since then, Vema has only been fished occasionally with acceptable rock lobster catches coming only from the deeper peripheral areas off the plateau.

Vema Seamount Faunal Affinities

A number of studies of the invertebrate populations at Vema have been published, including on the rock lobster population as well as other populations collected from the plateau during the 1964 and 1978 expeditions. In addition to establishing a species census, the studies focused on the affinities of the species to other regions throughout the world. The results offer some guidance regarding the origin of the two Cypraeidae species at Vema.

The earliest studies based on the rock lobster, *J. tristani*, populations at Vema demonstrated a close relationship between the Vema and the Tristan da Cunha Archipelago (Tristan) populations, 2,000 km west southwest of Vema. While a hypothetical means of recruitment of *J. tristani* larvae from Tristan to Vema was posited (Lutjeharms & Heydorn 1981), the great distance between the two locations, as well as the variability of the currents northeast from Tristan, make such recruitment highly unlikely, despite a larval life of many months. Subsequently, genetic studies have shown shallow but significant genetic separation between the Vema population and all other populations from Tristan to New Zealand. The studies also showed that these populations share a common ancestry which dates back at least one million years ago during the Pleistocene

Faunal Distribution						
Phylum	**A.** Europe and/or West Africa only	**B.** Vema Endemic	**C.** W. Africa, S. Africa (Atlantic), some Europe overlap	**D.** South Arica (Atlantic)	**E.** Cosmopolitan or scattered	**F.** Indo-Pacific
Porifera - sponges	1	25		7		
Hydrozoa				3	15	6
Polychaeta - sea worms				2	6	
Sipunculida - sea worms	1	1			2	
Ascidiacea - tunicates	1	3		9		
Isopoda - sea lice		2		5		
Decapoda - crabs	4	2			4**	1
Echinodermata – feather/brittle stars			1	1		2
Mollusca	1		2*	6	2	2
TOTAL	8	33	3	33	29	11
Percentages	6.8%	28.2%	2.6%	28.2%	24.8%	9.4%

Table 1. Faunal Distribution. * One from fossil records. ** Three species recorded from False Bay to Natal, also from the Mediterranean, Northwest Atlantic and Angola. One species recorded from the east and south coasts of South Africa.

(Von der Heyden *et al.*, 2007). That shallow genetic separation is not reflected in the morphology of the Tristan and Vema rock lobster populations. This is significant as, initially, the fauna of Vema was thought to be closely aligned with Tristan. Except for fish species and *J. tristani*, the two locations have few species in common. *J. tristani* is relevant to this study and will be part of the discussion section below.

Seven species of isopods were collected at Vema with two newly described. As these are direct developers with affinity to South Africa, it has been posited that they may have reached Vema via drifting *Ecklonia biruncinata* (Bory de Saint-Vincent & Papenfuss, 1944) (kelp) which is abundant on the Vema plateau as well as the southern Cape Coast. The kelp provides ideal habitat for the species. The isopods are the only direct developers from Vema which have been studied (Kensley, 1980).

Studies of the affinities of 11 species of decapods (crabs) (Kensley, 1980), 13 species of ascidians (tunicates) (Millar, 1968) and 86 other invertebrate species (Berrisford, 1969) collected at Vema showed a wide variation in their affinities as shown in Table 1.

On Table 1: A) represents species to the north of Vema with no present day connectivity to the seamount. B) is confined to Vema endemics. The A & B populations, representing 35.0% of the invertebrate species at Vema, can be considered relictual. C) represents an overlap zone and at 2.6% is the smallest group at Vema with one of its species sharing affinity to fossil records. This suggests possible relictual status. D) illustrates the shared affinity of many species, 28.2% of the total, with the Atlantic side of South Africa. E) represents cosmopolitan species, 24.8% of the total, scattered over a variety of regions but not the Indian Ocean side of South Africa. The exception is the four crab species noted above. With the exception of D, this suggests that approximately 62% of the above species are relictual. F) represents Indo-Pacific species and, while only 9.4% of the total, best speaks to the possible connectivity of the Natal Region with Vema. Setting aside the Hydrozoa, there are only five other species with an Indo-Pacific affinity and only two are molluscs: the bivalves *Septifer bilocularis* (Linnaeus, 1758) and *Ventricolaria cf. toreuma* (Gould, 1850). This suggests that the connectivity of the Natal Region to Vema for larval distribution is not strong, or alternatively that it is a relictual population. Overall, if the sponges and hydrozoa are eliminated, Vema would be considered species poor, at least at the depths specimens were collected on the plateau (41-61 m).

Figure 3. *Erosaria cernica cernica* (Sowerby, 1870). Collected by diver at 150' (45 m), 1988. 23.9 mm. Chiapponi Lorenz Seashell Foundation (CLSF 9445).

However, it is possible, if not probable, that other species and greater numbers exist at greater depth off the plateau where they would not be subject to open ocean pressures, including the occasional cyclone, at shallower depths. Unfortunately, the only such collecting

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activity is conducted by sporadic rock lobster expeditions where traps are set at about 150 m. While craypot traps do not represent an efficient method of collecting small Cypreaidae specimens, a specimen of *O. c. violacea* was collected from a trap at that depth in 1991. Many other Cypreaidae species, including *O. c. violacea*, inhabit the Natal Bight at those deeper depths.

Figure 4. *Ovitipsa chinensis violace*a (Rous, 1905). Taken from a rock lobster, *Jasus tristani* (Holthuis, 1963), trap at 150 m at Vema Seamount, June, 1991 32.3 mm. Santa Barbara Museum of Natural History (SBMNH 159765).

Migration Routes

Of particular interest to this study are the present day currents which can shed light on the affinities of the invertebrate populations at Vema to other regions as outlined above. In addition, possible Pleistocene migration related to glacial events cannot be overlooked.

There are three possible explanations for the migration of marine invertebrate veligers to Vema, including the two supported and one reported Cypreaidae species from the Indian Ocean: (1) Veliger transport from the affiliated regions to the north and east of Vema; (2) Veliger transport from the Natal Bight flowing southwest within the Agulhas Current, captured by Natal Pulses/Agulhas Rings and then transported to Vema within the Benguela Current flowing through the Cape Basin, and; (3) Population expansion during the Pleistocene as the result of oceanic flooding and extreme ENSO (El Niño-Southern Oscillation) events during inter-glacial periods. The first two explanations hinge on whether or not there is a viable means of transport of veligers from each region (*see* Figure 5).

North and East of Vema

Is Vema impacted by currents from the north? About once every ten years, the warm and salty waters of the Angola Current move south from southern Angola at 15° S into central Nambia as far south as 25° S. The waters in the current reach 150 km offshore and to a depth of 50 m. These events are known as the Benguela Niño and, while similar to Pacific ENSO events, their cause is not the same and, in fact, is not well understood. Vema at 31° S and 480 km off Namibia is well beyond the southernmost extension of the Benguela Niño. There are no

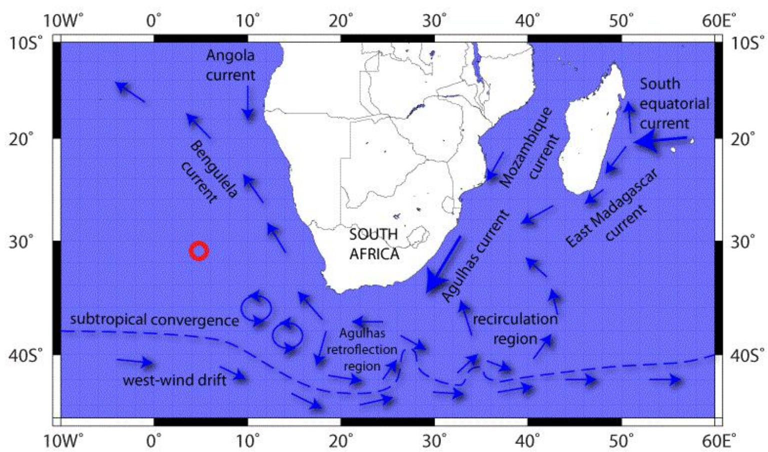

Figure 5. Map reflecting oceanic currents and reflection regions off the coast of South Africa (Walker, 1989; Stuvier *et al.* 2017). Red circle denotes relative location of Vema seamount.

other currents which have the potential to impact Vema from the north. In any event, there is no present day viable means of veliger transport to account for the invertebrate species at Vema with West African/Mediterranean affinities.

Is Vema impacted by currents from the east? As part of a study of water flow in the Benguela Current, six floats were launched within the Cape Basin in the easternmost part of the current at 30° S off South Africa, below the Namibian border. Surprisingly, five of the floats drifted to the south, one as far as 34° S, counter to the mean velocity of the Benguela Current, before drifting northwestward into the Benguela Current. Several floats passed close to Vema. The trajectories of the floats suggest that significant amounts of southward transport can occur in the Cape Basin. It is believed the floats were transported in or around the numerous rings there. (Richardson & Garzoli, 2003). As a result, there is a present day viable means of transport to account for the invertebrate species at Vema with South African affinities.

Natal to Vema

Is Vema impacted by currents originating from the Natal Region? The journey begins with the northern Agulhas Current which, fed by water flowing from the southern mouth of the Mozambique Channel, flows southwest along the South African coast out to the 200 m edge of the continental shelf. Along most of the coast, the shelf is narrow and the continental slope is steep. The only exception is the Natal Bight, between Richards Bay and Durban in the KwaZulu-Natal Province, where the shelf widens and slopes more gradually over a broader area.

The core of the current closely follows the shelf, meandering less than 15 km to either side. In the Natal Bight, surface speeds at the inshore edge of the current may reach 5.4 kilometers per hour. However, the behavior of the current is not very stable with surface current speed varying day to day, upwelling and downwelling events and current reversals at the edge of the current. Downstream of Durban to the Agulhas Bank, the shelf is narrow without any significant indentations in its shape. The current closely follows the shelf edge. Current speeds increase from 1.8 kilometers per hour just south of Durban, increasing steadily to 7.8 kilometers per hour off Port Elizabeth. Current speeds inshore are much slower and random, from 1.3 to 2.7 kilometers per hour.

As the current continues southwest of Port Elizabeth, it enters the Agulhas Bank. The latter represents the triangular continental shelf off the south of Africa. Lying between Port Elizabeth in the east and Cape Town in the west, it extends about 250 km to its widest point south southeast of Cape Town where the shallow Alphard Rise delineates the border between the eastern and western Agulhas Bank. The warm waters of the intense southern Agulhas Current follow the shelf edge but not as closely as further upstream. The current begins to meander with much of the warm water spreading across the Agulhas Bank. Past the Alphard Rise, the Agulhas Current proper moves offshore. (Lutjeharms, 2006). About 85% of the current's volume turns back on itself in the Agulhas Retroflection due to shear interactions with the strong Antarctic Circumpolar Current and returns to the Indian Ocean Gyre. Only about 15% of the current leaks into the Atlantic. Filaments and plumes make up small portion of the leakage which then mix with cold water upwellings and travel north along the western edge of the Agulhas Bank. The balance is subsumed into the Benguela Current. If this were all there is, the transport of veligers from Natal to Vema would be problematic at best.

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Natal Pulses, Agulhas Rings and the Benguela Current

However, that is not all there is. Returning to the Natal Bight, near the beginning of the journey, there is actually another journey within the journey. Anticyclonic eddies originating in the southern Mozambique Channel first meet the northern Agulhas Current at the Natal Bight where the interaction between the anticyclonic eddies with the western boundary current (Agulhas Current) trigger solitary cyclonic meanders which follow the current along its southwestern course. These cyclonic meanders have been named Natal Pulses. The pulses are generated exclusively off the Natal Bight. About 4-5 pulses are generated per year. The diameters of the pulses are about 30 km near the bight but increase in size as they travel downstream. Diameters sometimes exceed 200 km as they near Port Elizabeth. The meanders of the pulses also cover the entire depth of the Agulhas Current. As the pulses reach the Agulhas Retroflection, some are shed or pinched off and enter the Atlantic Ocean as large, anticyclonic Agulhas rings where they enter the Benguela Current (Tsugawa & Hasumi, 2010). Natal Pulses would constitute a hypothetical vehicle for the transport of Cypraeidae veligers from Natal to the Atlantic Ocean.

The Benguela Current consists primarily of the cold, offshore waters of the Antarctic Circumpolar Current (ACC) which combine with cold, deep water upwellings from inshore waters. These upwellings give form to the current and direct it to the north and northwest to cross the Cape Basin. The current extends 100-300 km west from the offshore waters in the Agulhas Basin, adjacent to the western boundary of the Agulhas Bank, to an ill defined western boundary. It then widens as it proceeds north. Agulhas Rings, representing the only sustained warmer water in the current, are initially scattered chaotically across the southern section of the current as they are expelled from the Agulhas Current. From there, they begin their trajectories across the Cape Basin. Surviving rings eventually reach the Walvis Ridge where they either disintegrate or pass over in weakened form.

For 13 years (from October 1992 to December 2006), a study of the 102 rings formed at the Agulhas Current Retroflection focused on their actions during their life cycle. The average of almost eight rings formed per year versus the 4-5 Natal Pulses generated per year is explained by eddies formed south of Madagascar joining the Agulhas Current south of the Natal Bight. Agulhas Rings can be formed from the pulses or the eddies. At any one time, about 6.6 rings were simultaneously present in the basin.

The 102 rings produced 199 trajectories as the rings subdivided or combined. All but 18 trajectories were found to follow one of three main routes: Southern, Central and Northern. Eighteen trajectories were not allocated a route as they were either east or west of the main routes and, in any event, were not on courses which would impact Vema. The Southern Route, representing 37 or 20% of the trajectories, are captured by the ACC and pass to the south and west into subantarctic waters before turning to the northwest or rejoining the Agulhas Retroflection to the east. The Central Route, representing, 90 or 48% of the trajectories, is the preferred route for the rings. The route originates west of the Agulhas Basin in an area bordered by the Erica seamount to the north, the Schmidt-Ott seamount to the west and the Agulhas Ridge to the south. Approximately 76% of the rings passing through this area subdivide as they pass bathymetric subdivision locations in the area. This route passes west of Vema with a rare meander into the Vema vicinity. The Northern Route, representing 59 or 32% of the trajectories, originates in the Agulhas Basin. Less than half of the rings (45%) on the Northern Route subdivided versus 76% on the Central Route. This is likely the result of the absence of obstacles in the basin where the rings begin their north northwest journey. The subdivisions which do occur mostly take place north in the shallowest part of the Cape Basin along the African coast. This route had the most trajectories which passed over or within the vicinity of Vema (Dencausse *et al.*, 2010).

Lastly, satellite observations have shown that rings do reach Vema where they loop and sometimes subdivide as they approach the seamount. (Richardson & Garzoli, 2003). Agulhas Rings would, therefore, constitute a hypothetical vehicle for the transport of Natal Cypraeidae veligers from the Agulhas Retroflection to Vema.

Stepping Stones

The potential transport of veligers from Natal to Vema follows a long and sometimes complex route. If there were stepping stones, *i.e.* intermediate habitats where veligers could settle, develop and produce new veligers for onward transport, the viability of such transport would be considerably enhanced.

Turning to the Indian Ocean off Natal and southeast and southern South Africa, the Agulhas Current follows the coastline southwest to Port Elizabeth. Here the continental slope is very steep and absent the terrain features prevalent in the Natal Bight. Past Port Elizabeth, portions of the current flow into the Agulhas Bank to the regions occupied by the endemic *Cypraeovula* Gray, 1824. Extensive collecting activity by divers and trawlers in these regions does not support the existence of any stepping stones in the Indian Ocean.

In the Atlantic, there are a two seamounts which must be considered. In the area where Central Route rings originate, there are the Schmidt-Ott and Erica seamounts. The Schmidt-Ott seamount is the shallower of the two, with the top of the seamount rising to 1,095 m. As the rings passing this area are transitory, any veligers deposited here would be subject to the deep, cold waters of the Benguela Current. That, and the great depth of the seamounts, would not support the status of stepping stone for Natal Cypraeidae veligers.

The author is not aware of any other potential stepping stones.

Time Travel

With the potential for the transport of Natal veligers to Vema, the timeline for such transport must be considered. It has been generally accepted that the Agulhas Current flows from Durban southeast at 20 km per day. As the distance between Durban and the Alphard Rise is approximately 1,200 km, a transport time of 60 days can be calculated. However, it is not that simple. Natal Pulses are considered meanders for a reason. Periodically, the pulses bulge landward followed by a bulge seaward. During the landward bulge, the current can actually reverse for a time before resuming its journey southwest. A more accurate estimate of travel time can be derived from satellite imagery. These show that Natal Pulses form about a half year before they are shed as Agulhas Rings. (Tsugawa & Hasumi, 2010).

Timing the journey of the Agulhas Rings is even more complex. The routes along which they travel are not well defined and narrow. Rather, they are broad corridors through which they meander, loop back on themselves, deform, subdivide, combine and interact with cyclones. The average life of a ring is 3-4 years. This makes the calculation of the timing of rings reaching Vema to be problematic at best. However, the distance between the Alphard Rise and Vema is approximately 1,230 km, about the same distance between Durban and the Alphard Rise. As the Durban route is more defined and less complex, assigning a faster travel time to the ring route does not seem supportable. Actually, a half year seems optimistic, but will be used for this study.

Therefore, travel from Durban to Vema would likely take at least a year and this is probably on the optimistic side.

Pleistocene Glacial Events

The Pleistocene epoch was a period of repeated glacial events with intervals of glacial retreat resulting in the fall and rise of ocean levels by as much as 130 m. Sea levels were <40 m below present day for the majority of the Pleistocene epoch. Prior to the mid-Pleistocene transition 900 thousand years ago, intervals between sea level fluctuations occurred approximately every 41 thousand years ago while, subsequently, every 100 thousand years ago until the end of the Pleistocene. During the last 250 thousand years ago, sea-level lows lasted only 6% of the time (Ludt & Rocha, 2015).

As sea water levels lowered, the habitat for shallow water specimens was severely reduced and, particularly in the Western and Central Pacific, populations became isolated and extinctions occurred in lagoon and other shallow water habitats. Current flows were also reduced during these glacial events, thereby exacerbating conditions. Subsequent flooding as each Glacial Maximum receded restored connectivity between many populations and resulted in the repopulation of these habitats. Despite these extremes, few marine species became extinct [Author's Note: Florida is an exception due to unique circumstances]. Genetically, "most marine clades exhibit patterns indicative of population expansion following bottlenecks associated with low sea-level stands". Pelagic larval duration (PLD) was not a strong indicator of population dispersal and range in the Pleistocene. (Ludt & Rocha 2015). Rather, flooding and exceptionally strong ENSO (El Niño-Southern Oscillation) events during inter-glacial periods made PLD irrelevant to a great extent. Speciation/ subspeciation resulted when populations invaded and adapted to different ecological environments, resulting in Divergent Evolution.

While most studies of the impact of Pleistocene glacial events are based on Indo-Pacific studies and to a lesser extent Caribbean studies, some inferences can be drawn with regard to the Natal Region marine habitat. As a result of continual continental uplifting, especially during the last 20 million years, South Africa's east and west coastlines as well as the Namibian coastline are remarkably linear. With the exception of the Cape Agulhas to Cape of Good Hope coastline, there are only a few large bays which form natural harbors and the continental shelf (shelf) lies close offshore. There are no lagoons or other substantial shallow water habitats other than wave benches lying close to shore.

In the KwaZulu-Natal Region, the continental slope (slope) has a steep gradient and the shelf is narrow. However, within the Natal Region between Durban and Richards Bay to the northeast, the slope has a much more gradual slope and the shelf is much broader out to a depth of 200 m. This region is known as the Natal Bight. (Lutjeharms, 2006). The region also provides the habitat for a number Cypraeidae species which are found at diveable depths (to 50 m) but are also trawled or taken ex-pisces to depths of 100-150 m. In addition to *O. c. violacea* and *E. c. cernica*, many other

Cypraeidae species have been collected at both depths. To illustrate, other species include, but are not limited to, *Talostolida pellucens natalensis* (Heiman & Meinis, 2002), *Erosaria citrina citrina* (Gray, 1825), *Erosaris gangranosa gangranosa* (Dillwyn, 1817), *Erosaris helvola meridionalis* Schilder & Schilder, 1938, *Palmadusta contaminata distans* Schilder & Schilder, 1938, *Purpuradusta fimbriata durbanensis* (Schilder & Schilder, 1938).

To say that this is unusual would not be an overstatement as there is no other region with as so many Cypraeidae species inhabiting such varied depths. How could this have occurred? Within the Natal Bight there are no barriers to seaward migration. As sea levels dropped during Pleistocene glacial events, populations probably retreated to deeper depths along the gradual slope existing there, establishing populations at what are now at 100-150 m depths. As sea levels rose during inter-glacial periods, populations followed the rising waters, repopulating the areas they had originally inhabited. This is the most likely explanation for this unusual phenomenon.

DISCUSSION

A hypothetical route proposed for the present day transport of the rock lobster, *J. tristani*, larvae from Tristan da Cunha to Vema turned out to be just that, *i.e.* hypothetical. Instead, genetic studies showed shallow but significant genetic separation between the Vema population and all other populations from Tristan to New Zealand. The studies also showed that these populations share a common ancestry which dates back at least one million years ago during the Pleistocene epoch.

A hypothetical route also exists for the present day transport of *O. c. violacea* and *E. c. cernica* veligers from Natal to Vema. However, it is likely to remain hypothetical. Neither present day Vema faunal affinities, the distance and time required to traverse the Natal to Vema route nor the complex/chaotic nature of ring progression within the Benguela Current support the viability of the route. The two species also fall within the *Erroneinae* Troschel, 1863 genus whose veligers have the shortest lives of all the genus. (Pauley & Meyer, 2006). Veliger duration is an issue. In other words, present day migration of Indo-Pacific Cypraeidae species in general and Natal species specifically is improbable.

Rather, any Cypraeidae populations at Vema are likely to predominately, but not exclusively, inhabit the more hospitable areas off the plateau at the deeper depths where the Natal populations are also found. In any event, a Pleistocene invasion, similar to the *J. tristani* invasion, would be a more likely explanation for any such presence as pelagic larval duration (PLD) was not a strong indicator of population dispersal and range in the Pleistocene. (Ludt & Rocha, 2015). Rather, flooding and exceptionally strong ENSO (El Niño-Southern Oscillation) events during inter-glacial periods made pelagic larval duration irrelevant to a great extent.

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