

BIOGEOGRAPHY OF THE DEEP-SEA GASTROPOD *OOCORYS SULCATA* FISCHER 1884

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Abstract The deep-sea gastropod *Oocorys sulcata* attains unusually large size, has a broad geographic range including the Atlantic and Indo-Pacific, maintains a global bathymetric range from the shelf-slope transition to the abyss, and is locally very rare. The extreme scale of its body size-distribution-abundance relationships presents a theoretical challenge to deep-sea ecology.

Key words Deep sea, *Oocorys sulcata*, Gastropod, Biogeography, Body size

INTRODUCTION

On a recent deep-sea sampling expedition along the Gay Head-Bermuda Transect south of New England, we recovered a living specimen of the exceptionally large and locally rare snail *Oocorys sulcata* Fischer 1884 (Fig. 1). *Oocorys* is a genus of caenogastropods residing in the family Cassidae (Warén & Bouchet, 1990; Bouchet & Warén, 1993; Beu, 2008). It has undergone a relatively modest adaptive radiation in the deep sea estimated to include 6–10 species globally (Bouchet & Warén, 1993). Bouchet & Warén (1993) synonymized *O. sulcata* Fischer 1884 with *Benthodolium abyssorum* Verrill & Smith 1884, *O. watsoni* Locard 1897, *O. fischeri* Locard 1897, and *O. umbilicata* Quinn 1980, based on finding continuous variation in shell form among nearly 300 museum specimens representing these named taxa. More recently, Beu (2008) added *O. rotunda* Dall 1908, *O. elongata* Schepman 1909, *O. weberi* Schepman 1909, *O. schepmani* Turner 1948, and *Eudolium aulacodes* Tomlin 1927, to the synonymy based on examining a larger collection. The strong jaws and radula of *O. sulcata* suggest that it is a predator, probably on Annelida (Quinn, 1980). Its protoconch morphology clearly indicates planktotrophic larval development (Bouchet & Warén, 1993).

Oocorys sulcata has large body size, low population density, and an extensive geographic range. These macroecological features are often found in combination (Brown, 1995), for example, in many solitary mobile predators inhabiting more familiar environments. However, in *O. sulcata*, the scaling of the relationships is



Figure 1 *Oocorys sulcata* Fischer 1884, collected at station 14A, 3300 m, 38°17.71'N, 70°29.64' W, 16 June 2008, R.V. Endeavor, Cruise 447. Shell height 45.2 mm, shell width 31.0 mm. Catalogue number MCZ 361869, Department of Mollusks, Museum of Comparative Zoology, Harvard University. Photograph by Leo Kenney.

extreme, revealing several aspects of deep-sea ecology that are potentially important and unique.

RESULTS AND DISCUSSION

In Fig. 2 we compare the size of *O. sulcata* to the size spectrum of caenogastropods and vetigastropods collected in earlier extensive surveys between 1964 and 1973 along the same Gay Head-Bermuda Transect (c.f. Sanders *et al.*, 1965; Sanders, 1977; McClain *et al.*, 2005). The earlier data represent measurements on 3,426 individuals of 83 species retrieved from 41 epibenthic sled samples and one anchor dredge sample taken between 196 m and 5042 m (from McClain *et al.*, 2005 with additions). *O. sulcata* is by far the largest snail reported from this region. It is approximately an order of magnitude larger than the average body size (shell height + width = 8.2 mm) and nearly three orders of magnitude larger in biovolume. No *O. sulcata* were found in the earlier sampling program, although there are records in the western North Atlantic from nineteenth century dredging expeditions (Fig. 3). There are three other species that do reach unusually large size represented in earlier collections: *Gymnobela bairdii* Verrill & Smith 1884; *Belomitra quadruplex* (Watson 1882); and *Mohnia abyssorum* (Fischer 1883) (Fig. 2). The conspicuous displacement of size between these large species and the rest of the snail fauna may represent the well-known dichotomy of miniaturisation and gigantism found in some other deep-sea taxa (Gage & Tyler, 1991; McClain *et al.*, 2006). This size divergence has not been recognized previously in deep-sea molluscs. The fact that it emerges only at lower bathyal to abyssal depths (> 2800 m), where average size in the rest of snail fauna declines significantly (Fig. 2), suggests that severely limited food supply may somehow drive the evolution of highly disparate body sizes, but the precise selective mechanisms remain unclear.

What is known about the global distribution of *O. sulcata* is shown in Fig. 3. Compared to coastal gastropod species, its geographic range is remarkably broad. It includes eastern and western corridors of the Atlantic and reaches well into the Indian Ocean to the western Pacific. There is also one locality record in the eastern Pacific off Panama. Since most of the deep sea is unexplored, particularly in the Indo-Pacific, the geographic range of *O. sulcata* may be even wider. Its bathymetric range is similarly impressive, extending from the outer continental shelf to the abyss (150–5073 m), although its distribution is

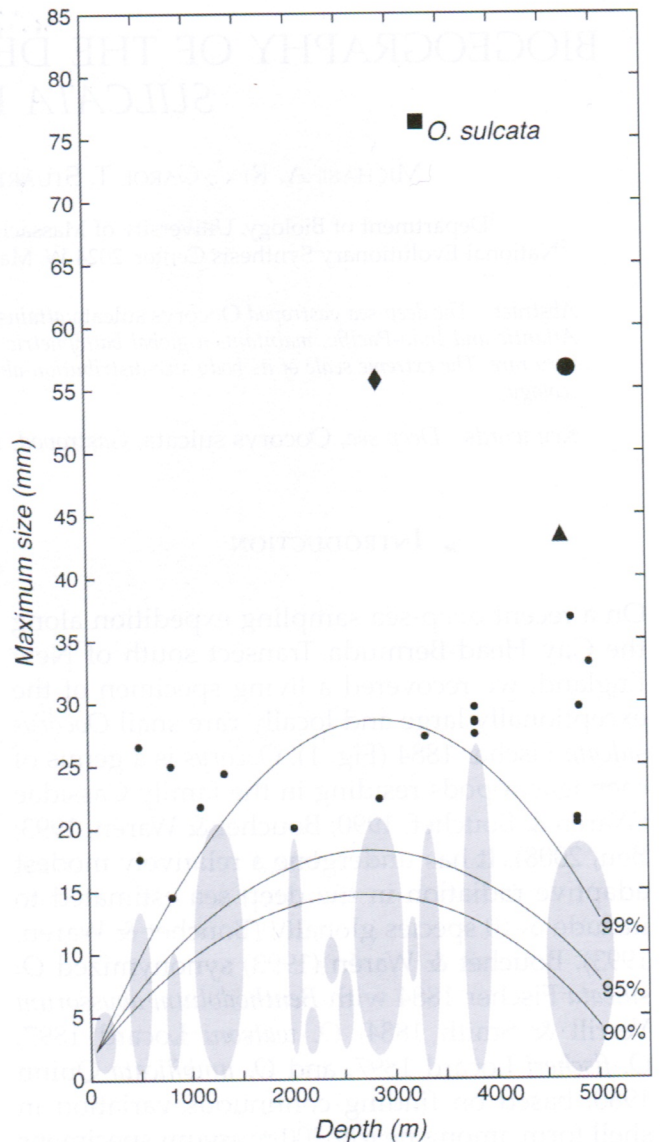


Figure 2 The shell size (height + width) of the specimen of *Oocorys sulcata* shown in Fig. 1 (solid square) compared to shell sizes of all caenogastropod and vetigastropod species collected previously along the Gay Head-Bermuda Transect south of New England. Other unusually large snails include *Gymnobela bairdii* (solid diamond), *Belomitra quadruplex* (solid circle), and *Mohnia abyssorum* (solid triangle). Shaded ovals contain dense clusters of data from an earlier analysis of snail size in this region (see McClain *et al.*, 2005, Fig. 2 for a plot of all individuals), and small dots are larger individuals at these depths. The three curves are the 99, 95 and 90% percent quantile regressions that show the relationship of maximum size to depth. All three regressions are significant at $P=0.0002$. See McClain *et al.* (2005) for regression equations.

primarily mid-bathyal and abyssal. Although the relative distribution of range sizes in deep-sea mollusks is still poorly documented at oceanic

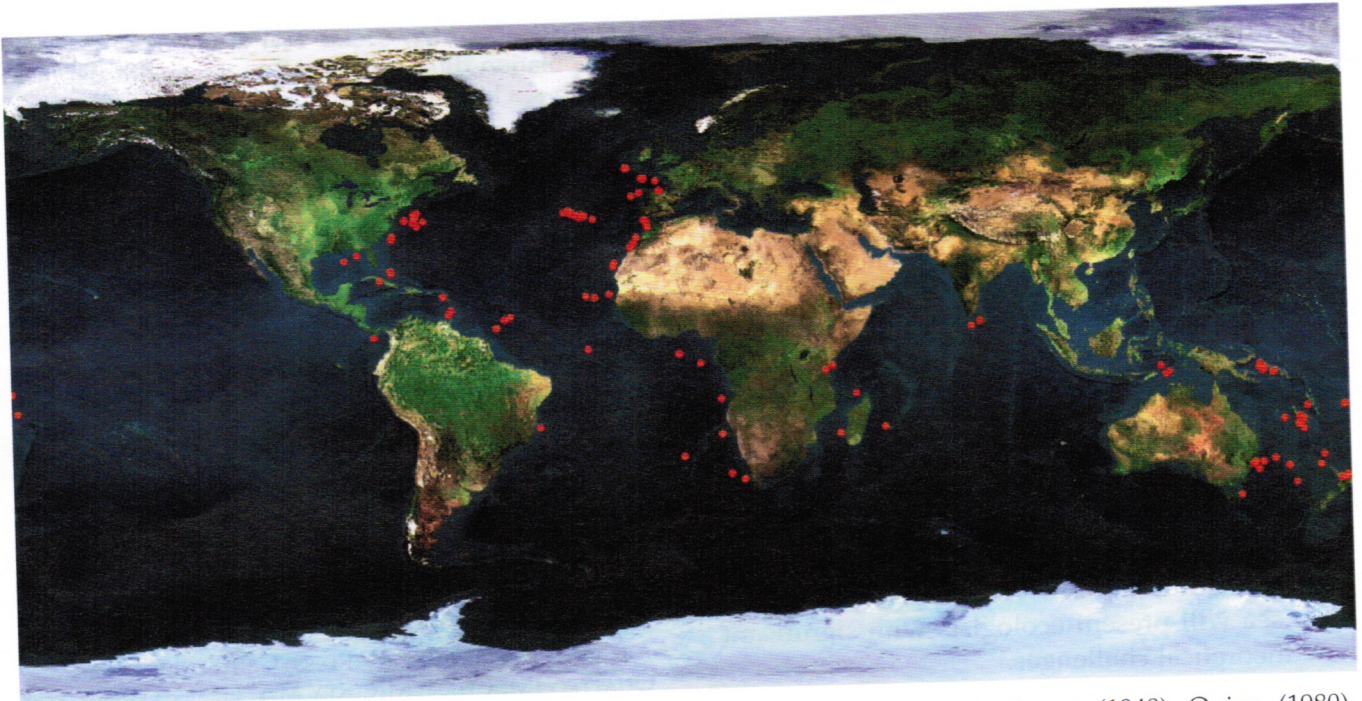


Figure 3 The global distribution of *Oocorys sulcata*. Data from Smith (1906), Turner (1948), Quinn (1980), Bouchet & Warén (1993), Beu (2008) and this paper. Some points represent multiple samples. Map from iMap 3.1 (www.bioevolution.com).

and global scales, very large ranges like those found in *O. sulcata* appear to be fairly common (Allen, 2008; Rex & Etter, 2010).

These enormous horizontal and bathymetric distributions have implications for the current debate surrounding the relative amount of biodiversity in the deep sea. In a pivotal paper, Grassle & Maciolek (1992) predicted total macrofaunal diversity to be 10^7 – 10^8 species based on extrapolating regional rates of species accumulation in the western North Atlantic to global scales. However, there is growing evidence that many deep-sea species are more broadly distributed than coastal species, suggesting that overall deep-sea diversity may be considerably lower (Carney, 1997; Rex *et al.*, 2005; McClain *et al.*, 2009). Any discussion of deep-sea biodiversity must include the caveat that existing estimates are based entirely on morphologically-defined species. Recent studies of population genetic structure show that some phenotypically coherent deep-sea mollusks contain deep cladal divisions comparable to those between well-established congeners in coastal systems (Etter *et al.*, 1999; Quattro *et al.*, 2001; Etter *et al.*, 2005; Zardus *et al.*, 2006). This suggests that some morphospecies may actually be complexes of cryptic species. We do not know whether this

is the case in *O. sulcata*, and its rarity and the paucity of specimens collected alive make it an unpromising candidate for genetic analysis.

South of New England, *O. sulcata* appears to be very rare in terms of its local and regional abundance. It was not found in any of the 41 epibenthic sled samples taken earlier along the Gay Head-Bermuda Transect, nor in the other 24 sled samples taken during the recent *R.V. Endeavor* Cruise 447 that yielded the single specimen from 3300 m shown in Fig 1. For the transect as a whole, its relative abundance among all gastropods collected is on the order of 10^{-4} , and below 1000 m on the order of 10^{-3} . Since epibenthic sleds sample roughly 1000 m² of sea floor, a crude estimate of *O. sulcata*'s density in this region is 1.5×10^{-5} individuals m⁻², or 15 individuals km⁻². Among all 87 records of *O. sulcata* reported by Bouchet & Warén (1993), 70% were single dead shells or living specimens, and only a third of the samples contained living individuals. This raises the perennial question of how such sparsely distributed, slow moving, gonochoristic species can possibly maintain reproductively viable populations in the deep sea. Part of the answer may be that *O. sulcata* has diffusive rarity (*sensu* Schoener, 1987); it may be common at some sites and rare elsewhere. For example, Quinn (1980)

noted that 25–30 living specimens were present among 55 lots of *O. umbilicata* (= *O. sulcata*) collected in the Tongue of the Ocean (1234–2780 m), a deep trough that cuts into the Bahama Bank. It was the most common snail collected there. It is conceivable that *O. sulcata* maintains its broad range, often represented by isolated individuals, as a metapopulation through dispersal by its planktotrophic larvae from more dense populations. Such a tenuous existence may be offset by the well-known adaptive advantages associated with large body size including greater longevity and fecundity, higher individual growth rate and metabolic efficiency, more mobility, broader diet, and protection from predators (Peters, 1983). This is entirely speculative, but it is becoming clear that large-scale patterns of biogeography in the deep sea will present ecologists with significant new theoretical challenges.

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