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Small, flat, and gray: Cryptic diversity in chthamalid barnacles in the global context of marine coastal biogeography (Cirripedia: Balanomorpha: Chthamalidae)

John P. Wares^o

*Odum School of Ecology, Department of Genetics,
University of Georgia, Athens, GA 30602, USA*

Correspondence: J.P. Wares; e-mail: jpwares@uga.edu

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ABSTRACT

In the past 40 years, the ability to distinguish phenotypically similar species by using molecular methods has rapidly changed the study of taxonomy, biogeography, and community diversity. A cosmopolitan family of acorn barnacles, Chthamalidae Darwin, 1854, can be found on almost every non-boreal coast, with very similar habitat requirements, larval life histories, and external (test) morphologies among its species. Here I review how molecular methods have aided the description of new species as well as the characterization of phylogenetic diversity within species, and also broadened our understanding of the biogeography of this family. Multiple regional analyses have shown that the coastal habitat appears to drive diversity and diversification in generally similar ways regardless of location, while a global perspective allows us to identify regions and questions that merit further study. Variation in the spatial patterning of genomic diversity among species sometimes provides evidence as to how key life history parameters determine responses of species to ocean currents and forcing, thermal environments, and competition.

Key Words: barnacles, *Chthamalus*, divergence, intertidal zone, molecular diversity, phenotypic variation, population genetics, review, species

As Charles Darwin's reputation as a natural historian developed, his need to grapple with variation in form and function (something that would become the basis for his theory of natural selection) was among the more significant reasons for his decision to study the diversity and systematics of barnacles (Stott, 2003). Darwin's impact on the taxonomic study of barnacles has been immense, and to this day many of the species descriptions from his monographs (Darwin, 1851, 1854) are still used. Later revisions to the systematics of barnacles, based on additional careful observations and incorporating the extraordinary expertise of more recent and also present-day biologists, have demonstrated that certain characters display discrete forms among species (such as the number of plates, the type of basis, and traits of the mandibular or feeding appendages; Dando & Southward, 1980; Foster & Newman, 1987; Southward & Newman, 2003), whereas others, such as plate thickness, the form of the appendages, and the shape of the opercular opening, may vary according to the environment (Lively, 1986; Marchinko & Palmer, 2003; Ewers-Saucedo *et al.*, 2017). Inasmuch as the number of barnacles on this planet, including the diversity both among and within species, is immense

compared to the number of scientists studying them, these two categories of character may still be easily confused.

It has now been over 40 yrs since Alan Southward (Southward, 1976) pointed out that some of the initial species descriptions of chthamalid barnacles (Family Chthamalidae Darwin, 1854, from *χθαμαλός*, “flat” or “on the ground”) incorporated seemingly extraordinary levels of phenotypic and climatic variation, given that other recognized species of *Chthamalus* Ranzani, 1817, separated on the basis of a relatively small number of external (test) and more typical crustacean character states (inside the test), had far more limited geographic and environmental distributions. Southward (1976) recognized in particular how microhabitats contributed to variation in form and used this information to distinguish *Chthamalus montagui* Southward, 1976 from *C. stellatus* (Poli, 1791) along the British coasts, with *C. montagui* dominating in the highest regions of the intertidal. Major advances in understanding the evolutionary diversity of barnacles followed shortly after. Southward (1983: 62), referring to work initiated with Paul Dando (Dando *et al.*, 1979; Dando & Southward, 1980) and discussing the difficulty that Darwin had in separating species of barnacles, noted:

“Other examples of the despair and doubt induced in Darwin by cirripede classification can be found in the genus *Chthamalus*. As noted below it is now possible to obtain unequivocal biochemical evidence on which to separate species in this group, to compare with the varying morphological criteria that caused so much trouble to Darwin and still cause controversy.”

Molecular techniques have now become a common tool for exploring within-species diversity, frequently leading to the discovery of patterns that clearly identify species which are also proven to be separable on the basis of distinct traits and distributions (e.g., Hedgecock, 1979; Dando, 1987; Wares, 2001; Pitombo & Burton, 2007; Tsang, et al., 2012).

It is this last point that I address in this review, particularly insofar as molecular data relate to chthamalid barnacle diversity. These barnacles are small, nearly ubiquitous in the high intertidal throughout temperate and tropical ecosystems, and are often very difficult to distinguish without detailed dissection or molecular analysis (Miller et al., 1989; O’Riordan et al., 2010). As such, together they form a globally distributed band of “feeding rocks,” cleaning plankton from the passing seawater, with few obvious phenotypic shifts reflecting their ecology or response to the environment. Molecular analysis of this group of barnacles in particular has often been exploratory, leading to recognition of how the environment does, in fact, promote specific spatial patterns of distinct species (e.g., Chan et al., 2016) or to the recognition of evolutionarily distinct lineages within a taxon (e.g., Pannaciuoli et al., 2017). For the purposes of comparative biology and biogeography, this makes them a fascinating group because so much of their morphology and diet and habitat appear to be held relatively constant, whereas the actual separation of this diversity into distinct and often non-hybridizing evolutionary lineages (Southward, 1983; Dando, 1987) gives greater insight into how these same environmental transitions influence broader spatial and biogeographic patterns in the intertidal community (Wares et al., 2001; Ewers-Saucedo et al., 2016).

HOW HOMOGENEOUS ARE CHTHAMALIDS?

To avoid exaggerating the similarities among taxa, I will first briefly review what we know about the typical habitat, external morphology, larval biology, and feeding in chthamalid barnacles. Pérez-Losada et al. (2012) reviewed shell architecture and the broader phylogeny of the superfamily Chthamaloidea, including the families Catophragmidae Utinomi, 1968 and Chthamalidae. I will focus on the latter family here, but all chthamaloids are found predominantly intertidally (Foster & Newman, 1987; Poltarukha, 2006; O’Riordan et al., 2010). This zone of distribution, nearly as terrestrial as it is marine, is thought to be the product of both the barnacles’ high tolerance to desiccation and thermal stress (Foster, 1971), as well as strong competition from other space-utilizing intertidal organisms, often other barnacles (Stanley & Newman, 1980; Wethey, 1983).

The Family Chthamalidae currently comprises three subfamilies that are not themselves monophyletic with respect to one another (Pérez-Losada et al., 2012). This situation indicates that some of the phenotypic diversity documented to date is convergent and labile in form. Although there are variations in plate number in this group, some of this variability is age-dependent as plates fuse in larger individuals (Ross, 1971), and shell and opercular form in general remain poor criteria for classifying these barnacles (Wares et al., 2009; Pérez-Losada et al., 2012). Features of the feeding appendages (cirri) have been suggested as a primary basis for separating *Chthamalus* itself into four sub-generic groups (Dando & Southward, 1980), but these groupings do not seem to be supported by phylogenetic analysis (Pérez-Losada et al., 2012) and in some cases these features are variable within a single nominal species (Foster & Newman, 1987).

Furthermore, while various genera of chthamalids have been separated due to variation in the presence or absence of a calcareous basis, plate number, and cirral and mandibular traits, among others (Poltarukha, 2000), these genera themselves are not wholly monophyletic (Wares et al., 2009).

A few interesting phenotypic exceptions do stand out. As an example, *Chthamalus anisopoma* Pilsbry, 1916, has unusually asymmetrical opercular plates associated with a strong form of developmental plasticity; namely, a “defensive posture” (bent morph) is generated in the presence of gastropod predators (Lively, 1986). While some sympatric confamilials can be distinguished through careful evaluation of opercular shape or other features (Southward, 1976; Shinen & Navarrete, 2014), in other cases even evolutionarily distant species can only be consistently distinguished by using molecular techniques (Miller et al., 1989; O’Riordan et al., 2010), and very similar plate morphologies often arise in spatially and phylogenetically distinct species (Foster & Newman, 1987). For example, *C. dalli* Pilsbry, 1916 and *C. fissus* Darwin, 1854 have been placed in distinct subgeneric groups based on the morphology of feeding appendages (Dando & Southward, 1980) and phylogenetic analysis (Wares et al., 2009), but cannot be reliably distinguished in the field as either adults or larvae (Miller et al., 1989). These two species undergo a rapid transition in dominance near the southern edge of Monterey Bay, California, USA, as shown using restriction digest assays of PCR products (Wares & Castañeda, 2005); Southward (1975) had recognized the overlap in distribution but the molecular approaches used now provide finer detail in location and microhabitat transitions (Chan et al., 2016).

Larval development itself is poorly understood outside the laboratory. The period from release of planktotrophic nauplii to the cyprid stage in culture is generally about 2–3 weeks (Miller et al., 1989; Burrows et al., 1999; Venegas et al., 2000; Yan & Chan, 2001; Yan, 2003; Zabin et al., 2007; Cheang et al., 2012; Ewers-Saucedo & Pappalardo, 2019), depending on temperature and food availability. Evidence from field surveys suggests that the duration of the pelagic phase may be far longer than this in the wild (Southward, 1976). The most notable results to date concerning variation among species come from a study of *Jehlius cirratus* (Darwin, 1854) and *Notochthamalus scabrosus* (Darwin, 1854). These species, which are mostly codistributed along the Pacific coast of South America, exhibit much longer developmental times at colder temperatures than other chthamalids do (Venegas et al., 2000). At 15–18 °C, *J. cirratus* requires 31 d to develop to the cyprid stage whereas *N. scabrosus* requires 37 d.

Temperature does not affect development alone, but behavioral activity as well. Barnacles of the typical size of a chthamalid (ca. 1 cm in diameter) are difficult to evaluate in this regard, but Southward (1964) studied cirral activity (feeding rate) in a number of chthamalid species and other barnacles in numerous locations to evaluate how temperature influences their capacity for feeding. This trait can also be affected by local wave exposure and other flow effects (Marchinko, 2007), but certainly temperature is also an important determinant of where a species can feed and reproduce, and thus persist (Orton, 1920; Sunday et al., 2012). Key points for evaluating such data are whether the populations measured are representative of the taxon and how comprehensively this was checked. For example, different latitudinal populations of the copepod *Tigriopus californicus* Baker, 1912 that show very different thermal sensitivities also vary in the amount of additive genomic variation allowing adaptation to higher temperatures (Kelly et al., 2012). In some cases among chthamalids, we have good data demonstrating a stable, homogeneous taxon at multiple locations (e.g., *C. dalli* in Southward, 1964), but in other cases, measurements of cirral behavior may have included representatives of multiple taxa, thus confounding what were actually distinct temperature/activity profiles of cryptic diversity within that taxon. For example, such measurements of *C. fragilis* Darwin, 1854 in Miami, Florida, USA (Southward, 1964) were likely confounded with those of unrecognized but nonetheless codistributed congeners

and also may not represent the thermal optima of populations of *C. fragilis* from other parts of the species distribution (Wares *et al.*, 2018).

The depths at which larvae of different developmental stages are found are often poorly known (Govindarajan *et al.*, 2015a; Ewers-Saucedo *et al.*, 2016), but even across the range of Chthamalidae, it does not appear to vary significantly (Tapia *et al.*, 2010). Typically, chthamalid larvae are most dense at depths of 5–10 m (Tapia & Pineda, 2007; Tapia & Navarrete, 2010; Tapia *et al.*, 2010; Morgan, 2014), with later developmental stages occurring somewhat deeper than that range (Pfeiffer-Herbert *et al.*, 2007); these patterns appear to be driven by behavior related to bottom proximity, rather than to distance from the water surface (Hagerty *et al.*, 2018). Unclear features of larval biology and behavior better might be addressed more quickly by applying, at different locations and depths, and at different times of the year, molecular methods that are capable of quickly identifying taxa and distinguishing larval diversity by developmental stage (Chen *et al.*, 2012; Govindarajan *et al.*, 2015a; Hagerty *et al.*, 2019).

Because chthamalid barnacles are difficult to distinguish in terms of tidal height, external morphology, and larval form (e.g., Miller *et al.*, 1989; York, 2008; Tsang *et al.*, 2012), it is often difficult to ascertain whether the adults of different species play distinct ecological roles. Shinen & Navarrete (2014) suggested that *J. cirratus* and *N. scabrosus*, confamilials that likely diverged in the Miocene, are equally effective competitors across a broad stretch of central Chile, meaning that the dominance of either in a microhabitat is likely to be stochastic and temporary. In general, the difficulty in identifying chthamalid species in the field has limited direct studies of interactions between them, and they are often listed as “*Chthamalus* spp.” in such studies (O’Riordan *et al.*, 2010). Even the most notable study that came to define competition between species (Connell, 1961) did not recognize that not one, but two chthamalid species (*C. stellatus* and *C. montagui*) were in competition with the archaebalanid species *Semibalanus balanoides* (Linnaeus, 1767). While recruitment and abundance of barnacles are often associated with nearshore productivity (Kasten & Flores, 2013; Shanks *et al.*, 2017; Scrosati & Ellrich, 2019), the dietary profile of these tiny barnacles has not, to my knowledge, been evaluated other than the importance of availability; whether some thrive on distinct partitions of plankton (*sensu* Hutchinson, 1961) remains a matter of speculation.

HOW HETEROGENEOUS ARE CHTHAMALIDS?

One of the key aspects of external phenotypic stability in chthamalid barnacles is that their areas of provenance provide a rather important context for understanding patterns of cryptic diversity, biogeographic transitions, and gene flow, and perhaps even for narrowing the list of possible species for identification. Thus, this review will follow the temperate and tropical coasts illustrated in Figure 1, alphabetically, with the primary coastal biogeographic regions following those objectively defined, using data from many taxa, by Costello *et al.* (2017). Some regions share certain commonalities and could conceivably be grouped by prevailing limitations to dispersal, habitat differentiation, lack of exploration, or other key conceptual linkages. The story of exploration and understanding, however, is nevertheless so dependent on the particular coastlines and the history of cirripede study that a map-based summary may be more efficient in explaining what we currently know.

WESTERN EUROPE

Starting on the British coast (Fig. 1: A, region 3 of Costello *et al.*, 2017), the recognition of *C. montagui* as phenotypically and

genomically separable from *C. stellatus* (Southward, 1976; Dando *et al.*, 1979) represented the beginning of the rapid modern transformation of what we know of diversity in Chthamalidae. The realization that these species possess distinct electrophoretic alleles at several protein loci (allozymes) confirmed the initial morphological diagnosis (based in part on the junction of opercular plates), but also signaled the need for increased exploration of barnacle diversity using molecular markers (e.g., Hedgecock, 1979; Dando & Southward, 1980; Southward, 1983; Dando, 1987). The separation of these two species made it apparent that the huge amount of developmental and phenotypic variation originally perceived by Darwin was not necessarily so great for individual species after all. Researchers began to tease apart differences in their larval stages, including both morphology and phenology (Burrows *et al.*, 1999), and differences in the microhabitats preferred by or best suited to each species (Pannacciulli & Relini, 2000; Sousa *et al.*, 2000; Power *et al.*, 2001; O’Riordan *et al.*, 2004).

It became apparent upon closer examination that *C. stellatus* tends to dominate in the mid-intertidal and particularly in wave-exposed areas whereas *C. montagui* typically can be found higher in the intertidal (Southward, 1976; Sousa *et al.*, 2000, but see Pannacciulli & Relini, 2000) and is found further southward along the African coast (Shemesh *et al.*, 2009; O’Riordan *et al.*, 2010) and the Canary Islands (González *et al.*, 2012). Understanding these distinctions allowed biologists to make more accurate predictions about how species will respond to a changing environment (Southward, 1991). Hawkins *et al.* (2009) noted that distinct patterns of expansions toward poleward habitats have been observed in both species, although they retain some individual habitat preferences. Nevertheless, they are often still treated together, because the taxonomic distinctions between them require tedious and time-consuming examination to confirm (Poloczanska *et al.*, 2008; O’Riordan *et al.*, 2010).

MEDITERRANEAN AND NORTHWESTERN AFRICA

Recognition of the distinct distribution of *C. montagui* prompted a number of additional evaluations of how it has persisted across varied environments and marine provinces ranging from England to coastal Africa and into the Mediterranean. Almost immediately, allozyme data were used to identify the degree of evolutionary divergence of the Atlantic and Mediterranean populations of both *C. montagui* and *C. stellatus* (Dando & Southward, 1981; Pannacciulli *et al.*, 1997). A strong transition in intraspecific diversity is expected here (and observed in many other marine taxa) not only because of ancient changes in sea level during the Pleistocene that isolated the Mediterranean from the Atlantic, but also strong oceanographic and environmental transitions at what is known as the Almería-Oran front between southeastern Spain and the coast of Morocco (Gosling, 1992; Quesada *et al.*, 1995). These studies showed not only divergence between the basins, but also different levels of allelic variation, with higher heterozygosity and allelic diversity in both species in the Mediterranean (Pannacciulli *et al.*, 1997). Subsequently, Pannacciulli *et al.* (2017) used mitochondrial DNA sequence data (mtDNA) from individuals of *C. montagui* in the northeastern Atlantic, Mediterranean, and Black Sea (Fig. 1: B, region 5 of Costello *et al.*, 2017) to show robust evolutionary divergence (~1.7% in the mitochondrial cytochrome oxidase I (mtCOI) gene region) between individuals collected from the Atlantic (England to Morocco) and the western/central Mediterranean, and a reduced but still statistically supported divergence (0.6%) between these regions and the Aegean and Black seas. The latter disjunction is thought to be maintained by the unique hydrography of this region (Pannacciulli *et al.*, 2017). These patterns were echoed in a similar study by Shemesh *et al.* (2009), who noted very low regional genetic divergence

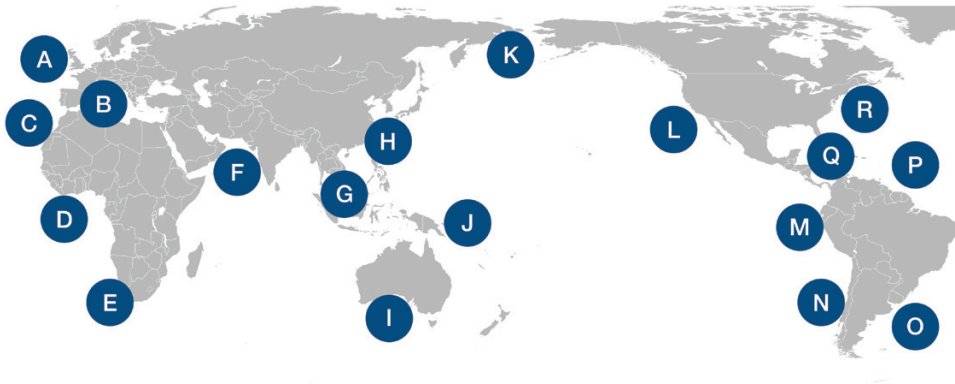


Figure 1. Regions for which the current status of molecular biogeographical study of chthamalid barnacles is discussed herein. Letters correspond to regions identified in the text and correspond with defined biogeographic regions and/or transitions identified in Costello *et al.* (2017).

among individuals of *C. stellatus*, with marginal isolation evident between the Mediterranean and Aegean populations as before for mtCOI. The spatial pattern shown in *C. stellatus*, however, is far weaker than shown in *C. montagui*, which has similar divergence patterns at two other loci. A nuclear gene region (elongation factor 1-alpha, EF1) was also investigated in these species, and strong spatial patterns were found in *C. stellatus* between the Atlantic and Mediterranean sites, just as with the earlier protein studies; this gene has often displayed intriguing spatial patterns in molecular studies of barnacles (Sotka *et al.*, 2004; Wares *et al.*, 2009) and other taxa. These results reinforce the importance of the paleoceanography of the Strait of Gibraltar and western Mediterranean in maintaining spatial structure in communities (Pannacciulli *et al.*, 2017), but also exemplify the importance of studying more genetic loci when possible. Shemesh *et al.* (2009) also evaluated the chthamalid *Euraphia depressa* (Poli, 1791), found only along the shores of the Mediterranean and Black seas, but identified no genetic structure in that species. As a historical note, prior to the use of allozyme data to separate chthamalid taxa (Dando *et al.*, 1979), Juan (1976) explored variation in *C. stellatus* and *E. depressa* (as *C. depressus*) among sites near Barcelona, Spain, recovering site-to-site variation that she considered evidence of local adaptation. As Dando (1987) pointed out, however, her results were confounded by not separating *C. stellatus* and *C. montagui*. The need to identify distinct evolutionary lineages is fundamental if one wishes to fully address questions of distribution, movement, and the potential for adaptation.

This series of studies in the Mediterranean highlights one of the most important reasons for using molecular approaches with barnacles, namely the application of population genetic data to specific models of molecular evolution that allow alleles to be ordered as a series of mutational steps (Avice, 2000). Because acorn barnacles are sessile, hermaphroditic, short-lived, and highly fecund, they have been used to explore how biological drifters (larvae) respond to upwelling, currents, and ways in which ocean dynamics direct dispersal (Wares *et al.*, 2001; Sotka *et al.*, 2004; Pringle & Wares, 2007; Galindo *et al.*, 2010; Barshis *et al.*, 2011; Chan *et al.*, 2012; Ewers-Saucedo *et al.*, 2016). The interaction of gene flow and local adaptations in broadly-dispersing species such as chthamalid barnacles may help to resolve a paradox noted by Palumbi (1992): we find a surprising level of genetic divergence among populations of marine species despite there being few apparent physical boundaries to dispersal and connectivity at many marine sites. The length of time spent by larvae in the plankton suggests a potential for larval dispersal as high as tens to hundreds of kilometers per generation, although successful dispersal and recruitment are far more likely to be restricted to shorter distances (Weersing & Toonen, 2009) because of larval behavior (e.g., Hagerty *et al.*, 2018). This balance of dispersal and successful recruitment underlies the

broad-scale patterns highlighted in chthamalids, and likely explains unusual finds such as the apparently isolated population of *C. montagui* identified on the coasts of Malta (Dando, 1987, Pannacciulli *et al.*, 2017). In any case, as ubiquitous representatives of the high intertidal community with planktotrophic larvae, chthamalid barnacles have played a key role in evaluation of ocean dynamics (Wares *et al.*, 2001, Tsang *et al.*, 2008, Ewers-Saucedo *et al.*, 2016, Pannacciulli *et al.*, 2017).

WESTERN AND SOUTHERN AFRICA

The major boundaries that isolate populations from one another, and which have been reinforced by oceanic circulation that limits larval transport among regions, are clearly important as abiotic, “neutral” drivers of speciation and divergence (Wares, 2016) among what might otherwise appear to be ecologically equivalent populations. Nevertheless, the huge environmental gradients covered by some species (Southward, 1976) prompt inquiry into what limits and trade-offs exist in the physiological needs of chthamalid barnacles, and how they vary in traits and genomic regions that have yet to be studied. O’Riordan *et al.* (2010) reviewed early work on physiological tolerances in chthamalids, but many of the species studied up until then have since been taxonomically split or re-identified, so the results may not apply to the current names.

In considering populations further to the south along the African coast from Morocco, where *C. montagui* is found and has been characterized using molecular data (Fig. 1: C, region 21 in Costello *et al.*, 2017), there is soon another transition into a distinct biogeographic region with distinct chthamalids. It is not well-characterized how *C. montagui* overlaps with the distribution of *C. dentatus* Krauss, 1848, which of the two species is found in a more sheltered habitat, which may be found higher on the shore, and so on. A thorough mapping of chthamalid diversity in this region was first attempted by Stubbings (1967), but the above-mentioned difficulties with older species lists apply to his work. More recently, *C. dentatus* has been reported from the Cape Verde Islands (O’Riordan *et al.*, 2010) and Cameroon (Wares *et al.*, 2009), whereas *C. montagui* has been collected as far south as Senegal (Wares *et al.*, 2009), which lies between those two locations. These reports, however, were not based on careful evaluations of the diversity at each site and so neither of these biotic transitions is informative about their relative intertidal distributions.

The phylogenetic analysis of Wares *et al.* (2009), a multilocus phylogeny of *Chthamalus* limited mostly to Western Hemisphere species, showed *C. montagui* and the Cameroon population of *C. dentatus* to be highly divergent (collected near D on Figure 1, biogeographic region 23 of Costello *et al.*, 2017).

Comparison of the latter with sequence data for South African *C. dentatus* published by Teske *et al.* (2013; GenBank accessions KC357047-KC357131; Fig. 1: E) show a divergence along the western coast of Africa of similar magnitude (roughly 11% sequence divergence for mtCOI; JW, unpublished data). The inclusion of three otherwise unpublished “DNA barcode” samples from Namibia near the Angola border (Ratnasingham & Hebert, 2007; BOLD identifiers HVDBC081-11, HVDBC082-11, HVDBM318-11; transition between region 23 and 27 of Costello *et al.*, 2017) indicate yet another clade within this group, approximately 5% divergent from the South African samples (Fig. 2). Here, again, the strong ocean currents and upwelling typical of mid-latitude temperate coasts seem to be important in maintaining the isolation of otherwise ecologically similar populations (Thiel *et al.*, 2007; Costello *et al.*, 2017). O’Riordan *et al.* (2010: 54) noted that:

“[Previous authors] described the distribution of *C. dentatus* on the East and South coasts of South Africa, where warm-water conditions dominate. There it occurs in the upper part of the midlittoral On the west coast of southern Africa, cold-water conditions dominate and *C. dentatus* disappears as one proceeds further north ... however when water conditions become warmer, it becomes more abundant and occurs as far north as Cape Verde ... as well as in Madagascar and Mauritius.”

Like the contrasts seen between *C. stellatus* and *C. montagu* in the Northern Hemisphere, Teske *et al.* (2013) also point out that there is statistically robust genetic differentiation (measured using permutational tests of standard differentiation statistics) between outer coast and sheltered populations of *C. dentatus* in South Africa. This is, however, a small divergence relative to the diversity seen among population samples on the Namibian coast and further north. No work to date has been done on the distribution or diversity of *C. dentatus* along the eastern coast of Africa, or in Madagascar. The species has been documented as far north as Kenya (Global Biodiversity Information Facility; GBIF, 2019).

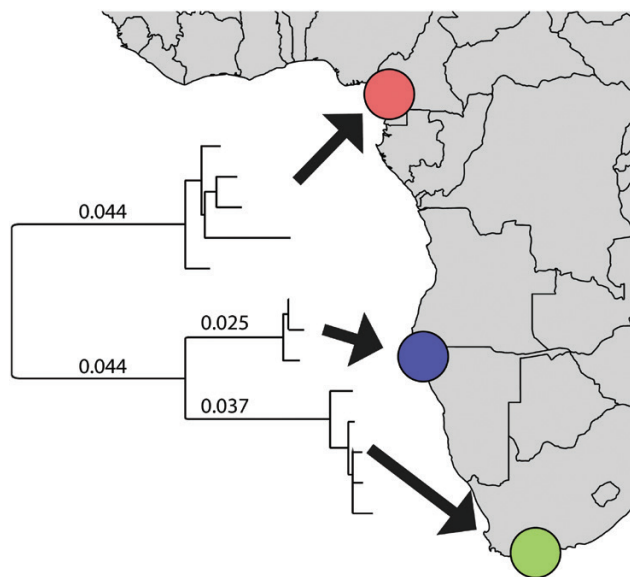


Figure 2. Alignments of mitochondrial COI sequence data from the barnacle *Chthamalus dentatus*, highlighting the issue of evolutionarily divergent populations within the same nominal species. Branch lengths on the neighbor-joining phylogram represent the proportion of divergent nucleotides among the studied populations in Cameroon (red; Wares *et al.*, 2009), Namibia (blue; data published online in Ratnasingham & Hebert, 2007), and South Africa (green; Teske *et al.*, 2013). Each site was subsampled to a maximum of five individuals for this visualization, but the result is the same when all specimens are included.

INDIAN OCEAN

It is difficult to make global generalizations about ecological and genomic diversification when there remain relatively understudied regions such as the eastern coast of Africa and the southwestern Asian coasts of the Indian Ocean (Fig. 1: F, region 19 of Costello *et al.*, 2017). GBIF (2019) catalogues only a few collections of chthamalids in this region, including *Microeuraphia permitini* (Zevina & Litinova, 1970) from the coast of Iran, and *C. barnesi* Aчитув & Safriel, 1980 in the Persian Gulf and Gulf of Oman (Shahdadi & Sari, 2011, Shahdadi *et al.*, 2014). Aчитув (1981) documents competitive interactions between *Tetrachthamalus obliteratus* Newman, 1967 and other barnacles in the Red Sea and western Indian Ocean, and Poltarukha (2000) described *C. southwardi* Poltarukha, 2000 from the relatively isolated Seychelles, adding to the potential diversity of the region. Without additional study and evaluation of molecular diversity in and among such isolated examples, it is hard to know how these taxa fall within the broader distribution of the dominant chthamalid in the Indian Ocean, *C. malayensis* Pilsbry, 1916 (cf Southward & Newman, 2003). The original diagnoses of these taxa did not involve any molecular markers, and I can find no reference to spatial genetic analysis (nor a comprehensive survey of distribution) of these chthamalids in this extensive portion of our world’s coastal oceans. The molecular diversity of *C. malayensis* has, however, been evaluated from eastern Indian Ocean localities in India as well as western Thailand and Malaysia (Tsang *et al.*, 2012), providing a contrast with the mitochondrial diversity of this species as it transitions into the Indo-West Pacific (IWP) and southeastern Asia, where very distinct lineages of this taxon occur (see below).

SOUTHEASTERN ASIA

In coastal oceans of southeastern Asia and the rest of the IWP (Figs. 1 (G), 3, spanning regions 13, 20, 29 of Costello *et al.*, 2017), the intensity of study of taxonomic and genomic diversity in chthamalid barnacles has been high in recent decades (Chan *et al.*, 2009; Pochai *et al.*, 2017). As with Southward’s work on *C. stellatus*, initial work on chthamalid diversity in this region involved detailed morphological examination (Yan & Chan, 2004a) to identify a new species (originally as *C. neglectus* Yan & Chan, 2004 [in Yan & Yang, 2004a], but later recognized as synonymous with *C. sinensis* Ren, 1984; Chan & Cheang, 2015) from the region around Hong Kong amidst the more broadly distributed *C. malayensis*. Additional work (Yan & Chan, 2004b) confirmed apparent larval distinctions between these two species, which is itself remarkable as in many instances chthamalid larvae, even from evolutionarily distant congeners, are practically indistinguishable (Miller *et al.*, 1989).

The dominant warm-water chthamalid in the Indo-West Pacific region, *C. malayensis*, was next evaluated using molecular data over a much broader spatial region ranging from Sri Lanka and Malaysia in the Indian Ocean through coastal eastern and western Thailand and China, and north to Taiwan (Tsang *et al.*, 2008). This work was focused on size structure of these barnacle populations and the application of molecular data (mtCOI sequence data) to evaluate gene flow across the region; the results, however, indicated significant cryptic diversity within *C. malayensis*. Four phylogenetically robust clades emerged from these data (Fig. 3; one of those clades was only recovered from Christmas Island in the Indian Ocean, not shown). Because the specimens were sampled along low-shore, mid-shore, and high-shore transects, Tsang *et al.* (2008, 2012) were able not only to document deeply divergent lineages within *C. malayensis*, but to also show that they are ecologically (physiologically) divergent. For example, the “South China Sea” clade was limited to high-shore transects, whereas the “Indo-Malay” clade was found in mid- to low-shore transects). As with other regional chthamalid communities described earlier (e.g., Dando, 1987; Pannacciulli *et al.*, 2017), Tsang *et al.* (2008)

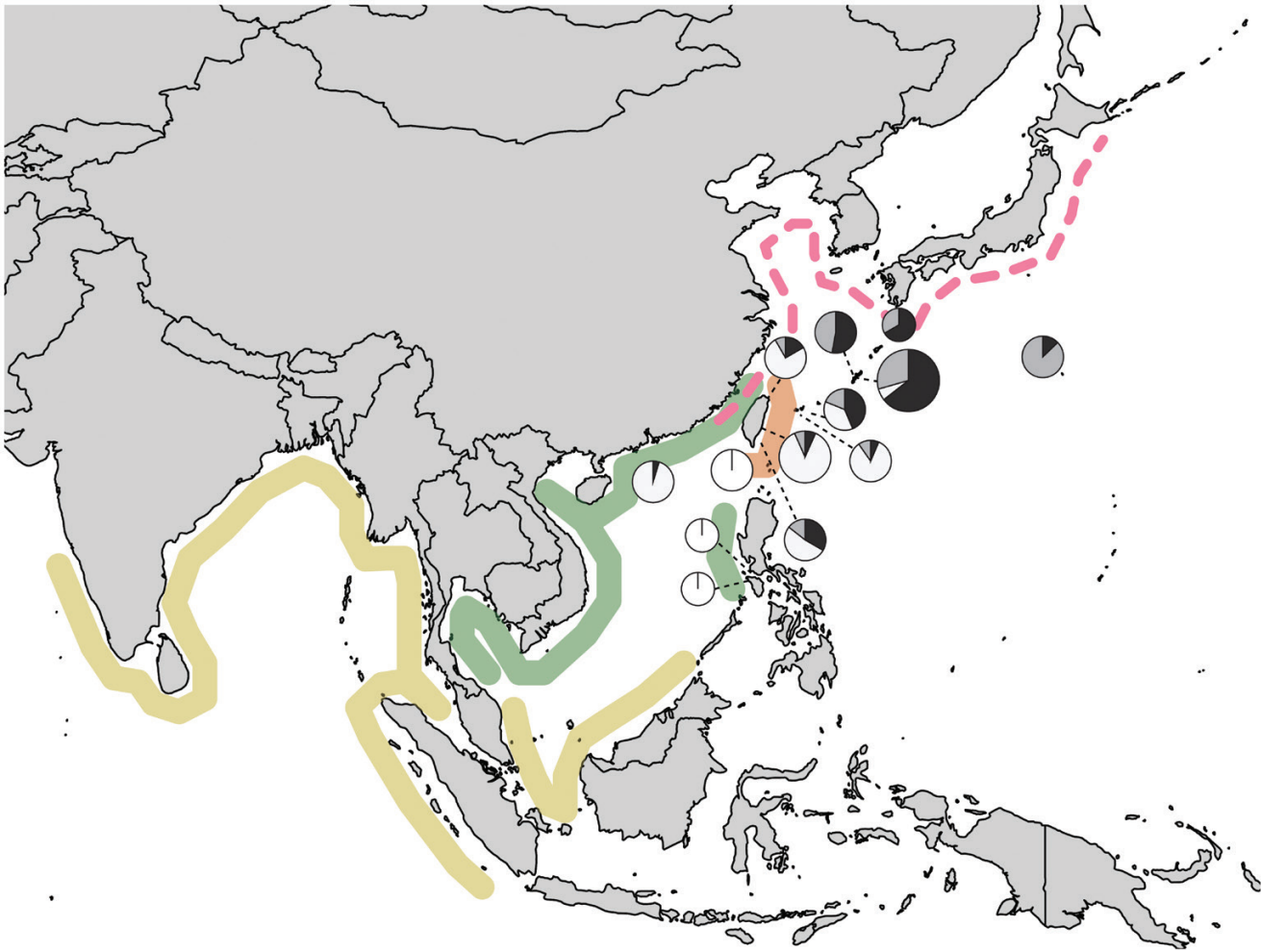


Figure 3. Overview of the approximate distribution of distinct mitochondrial clades in various Asian species of *Chthamalus*. Clades of *C. malayensis* (from Cheang *et al.*, 2012) are shown as colored bands, but the orange region east of Taiwan is now classified as *C. williamsi*. Three mitochondrial clades of *C. moro* at various sites are shown in pie graphs (after Wu *et al.*, 2015), with distinct colors indicating reciprocally monophyletic lineages within the species. The distribution of *C. challengeri*, representing a single mitochondrial clade, is shown as a dashed line. Together, and including some short-range endemics such as *C. sinensis* in southern China and Taiwan, these distributions demonstrate the important role that sea level change during Pleistocene glaciations had in the siting of significant contemporary biogeographic transitions.

suggested that Pleistocene sea-level changes may have initiated isolation among these lineages, but that they have been maintained by coastal currents including the South China Sea current, and the Kuroshio Current that sweeps across eastern Taiwan and gyres are likely involved in limiting the dispersal of some of these evolutionarily distinct lineages.

The above-cited work on diversity within *C. malayensis* provoked a molecular evaluation of *C. challengeri* Hoek, 1883, which is distributed along the more temperate coasts of eastern Asia. Sampling of this species took place in Taiwan and the East China Sea, as well as at numerous sites along the outer and inner coasts of Japan as far north as Hokkaido (Fig 3; Cheang *et al.*, 2012). Unlike *C. malayensis*, no cryptic diversity was found throughout this range despite the evaluation of multiple mitochondrial and nuclear sequence regions. The authors concluded that the lack of spatial diversity in *C. challengeri* may reflect a distinct history of post-glacial population recovery through this region. Building on this, Wu *et al.* (2015) re-examined the island-distributed *C. moro* Pilsbry, 1916, itself having a history of being split and re-lumped with *C. malayensis* (see Yan & Chan, 2004a), but clearly evolutionarily distinct when molecular markers are considered (Chan & Cheang, 2015). This species would be expected to have had much stronger responses to sea-level fluctuations during glacial maxima.

In fact, three deeply divergent lineages were found, as much as 8.3% different based on mitochondrial COI sequence data (Wu *et al.*, 2015), and they transitioned in dominance over very short geographic distances (Fig 3). The authors also noted tremendous variation in shell and cirral morphology in *C. moro*, features which, however, are known to show plastic responses to the environment in many barnacles (Southward, 1983; Marchinko & Palmer, 2003; Jarrett, 2008; Ewers-Saucedo *et al.*, 2017).

Remarkably, the strong transition in *C. moro* is spatially concordant with the transition between the warm-water *C. malayensis* (the northernmost lineage; Fig 3) and the cool-water *C. challengeri* lineages (corresponding to the transition between regions 20, 29 in Costello *et al.*, 2017). Additional analysis of co-distributed chthamalids across this zone have also exhibited a strong transition between Taiwan and southern Japan; Tsang *et al.* (2013) explored molecular (mtCOI) diversity in *Hexechamaesipho pilsbryi* (Hiro, 1936) to understand better the appearance of *H. pilsbryi* in Taiwan in recent decades. As it turns out, the absence of this species in surveys of coastal Taiwan may have been aberrant, as further surveys recovered this species throughout maritime southeast Asia (Tsang *et al.*, 2013). In addition, sequence data from across this extensive range, which spans a major biogeographic transition (Fig 3), cleanly separates the species into two lineages separated

by ~4.2% sequence divergence, with very little gene flow across this span (only three individuals from Taiwan are “northern”; only 1 individual from Okinawa represents the “southern” lineage).

This transitional zone, where *C. malayensis* and *C. challengeri* meet, among other major faunal transitions (Costello *et al.*, 2017), also appears to harbor short-range endemics (Newman, 1979; Engle & Summers, 1999) associated with the transition. One recently described chthamalid in the *challengeri* subgroup has only been reported in Taiwan (*C. williamsi* Chan & Cheang, 2015), though Southward & Newman (2003) reported what may be the same species in Hong Kong and Vietnam (Chan & Cheang, 2015). Given the strength of isolation generated by currents between Taiwan and Japan, as with *C. moro*, this population appears to have been isolated from other species in the *challengeri* subgroup for a very long time (Chan & Cheang, 2015).

AUSTRALIA AND PACIFIC ISLANDS

With so much phylogenetic diversity recovered from the evaluation of supposedly just three taxa across a relatively small but oceanographically complex portion of the Asian coastline, it is difficult at first to derive a single clear biogeographic story from comparing chthamalids alone. Together with data from other cryptic barnacle lineages (Tsang *et al.*, 2011; Chan *et al.*, 2012), it is clear, however, that the phenotypic and evolutionary diversity of barnacles of this region does include deterministic ecological and physiological variants that are suited to distinct microhabitats within the larger environmental gradients of the region. Among the coastal barnacle communities farther to the south in the IWP and Australia (Fig. 1: I, J, regions 10, 15, 16, 17, 26, 28 of Costello *et al.*, 2017), the *C. malayensis* complex (distributed in northern and western Australia; Southward & Newman, 2003) is gradually replaced with *C. antennatus* Darwin, 1854 (the chthamaloid *Catomerus polymerus* Darwin, 1854, also present in this region, belongs to a different family; see Jones (2012) for overall biogeography of Australian barnacles). While *C. polymerus* does show some genetic structure (east to west) along the breadth of the southern Australian coast (York *et al.*, 2008), *C. antennatus* does not (York, 2008). Additional species in the western and southern Pacific, certainly in more remote locations (e.g., Pope, 1965; Foster & Newman, 1987; Paulay & Ross, 2003), will merit further investigation for what they convey about ecological and evolutionary divergence. There has so far been little evaluation of spatial variation in morphology or genomic data for taxa like *Nesochthamalus intertextus* (Darwin, 1854), for example, although Foster & Newman (1987) noted important variations in some of the cirral characters of this species, including features often used to distinguish entire subgroups of *Chthamalus*. Nominally, *N. intertextus* has been reported from remote Pacific island chains covering over 80,000 km² of ocean (Foster & Newman, 1987), similarly distributed to the *devaneyi* Foster & Newman, 1987 group of *Euraphia*. Other species with more limited distributions, such as *Rehderella belyaevi* (Zevina & Kurshakova, 1973) (found only at Easter Island and Pitcairn Island, nearly 2,000 km apart) include populations so distant from one another that evolutionary divergences are to be expected among sites.

A key challenge in integrating our understanding of much of the chthamalid diversity in the Indian and Pacific oceans is the lack of a complete and well-supported phylogeny that integrates molecular and phenotypic information across time scales ranging from ancient to recent. Some studies have done a better job of sampling the genome and assessing deeper-scale questions (Pérez-Losada *et al.*, 2012), some have tackled regional biota well (e.g., Wares *et al.*, 2009, focusing primarily on North and Central America), and others have generated phylogenetic hypotheses that assume the four sub-generic groupings proposed by Dando & Southward (1980), based on microscopic details of the feeding appendages and mouthparts, properly circumscribe phylogenetic

clades (e.g., Chan & Cheang, 2015) though these groupings were not supported by Pérez-Losada *et al.* (2012). Several of the monotypic chthamalid genera are found in this region (Pope, 1965; Ross, 1971; Foster & Newman, 1987; Southward & Newman, 2003; Poltarukha, 2006), and while it is likely that there will be strong regional affiliations in a complete, deeply-sampled phylogeny of the chthamalid barnacles, the integration of understanding of within-taxon variation (molecular and morphological) with complete spatial sampling of representative specimens continues to be a challenge for researchers of this cosmopolitan family.

NORTHEASTERN ASIA AND WESTERN NORTH AMERICA

Continuing this survey into the north Pacific, only a single chthamalid is recognized in this region including northeastern Asia (Fig. 1: K, transition between regions 7 and 20 in Costello *et al.*, 2017) as far south as Hokkaido, Japan (Luckens, 1969; Poltarukha, 2000), along the coast of Alaska (even slightly into the Arctic, where they can still reproduce at temperatures as low as 6 °C; Southward, 1964; Southward & Southward, 1967) and common as far south as Point Conception, California (Fig. 1: L; Pitombo & Ross, 2002; Wares & Castañeda, 2005). *Chthamalus dalli* is, like most chthamalids, dominant in the high intertidal above the distribution of balanids and *Tetraclita* Schumacher, 1817. As with the initial observation of an extraordinary geographic and ecological range spanned by *C. stellatus* (Southward, 1976), the difficulty in distinguishing congeners may have masked additional ecological and physiological diversity.

In Wares *et al.* (2009), multilocus sequence data are presented from *C. dalli*, collected from a number of sites between northern Oregon and southern California (Wares & Castañeda, 2005). Specimens in that paper representing “*C. challengeri*” (mtCOI Genbank accessions FJ858068-076) had been collected in Hokkaido (but were presumed to be *C. dalli* based on the test morphology) and when the sequence divergence exhibited reciprocal monophyly and considerable divergence from *C. dalli*, the specimens were inferred, based on their area of provenance (where *C. dalli* and *C. challengeri* have been reported to overlap in distribution; Luckens, 1969; Poltarukha, 2000), to be *C. challengeri*. The more recent and detailed work in Cheang *et al.* (2012) fortunately provided additional reference data for *C. challengeri* throughout its range. New comparison of the sequence data from these publications show clearly that the diversity found in Hokkaido is highly divergent (6–7%) from both *C. challengeri* (Cheang *et al.*, 2012) and *C. dalli* (Wares & Castañeda, 2005; Wares *et al.*, 2009), and represents yet another cryptic lineage to explore in this taxon. At this point, no data are available for molecular diversity of *C. dalli* at locations between Hokkaido and British Columbia (see Chan *et al.*, 2016), all of which falls in biogeographic zone 7 of Costello *et al.* (2017).

Although *C. dalli* may be distinguished from the next species south along the temperate Pacific coast of North America (*C. fissus* Darwin, 1854) with careful observation of opercular traits (but see Miller *et al.*, 1989), many researchers (for example, the coastal long-term surveys by the Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO); piscoweb.org) still choose to lump distributional data for *C. dalli* and *C. fissus*, which is itself distributed to the south into Mexico, for ecological surveys. Wares & Castañeda (2005) developed a restriction digest assay of mtCOI for distinguishing the two species where they overlap; unfortunately, the quadrat sampling for that study was performed haphazardly. At many sites where both species were found it was clear that their distributions are clumped by microhabitat (Wares & Castañeda, 2005: table 1), with other surveys indicating that *C. dalli* are more often found in sheltered microhabitats (Chan *et al.*, 2016). The geographical overlap between these two species is narrow in comparison with other chthamalid taxa; *C. fissus* is very

rare in Santa Cruz, California (36.9°N) and *C. dalli* becomes rare only about 200 km to the south (Wares & Castañeda, 2005) with its limit near La Jolla, CA (Chan *et al.*, 2016; Table S1). By using this assay to avoid sequencing costs on a non-target species, a survey of sequence diversity in *C. dalli* from Cape Meares, Oregon (45.5° N) southward was done, but no spatial population structure was evident (Wares & Castañeda, 2005) even though other taxa with similar distributions along this coast do show significant intraspecific transitions (Sotka *et al.*, 2004; Kelly & Palumbi, 2010).

To the south of the distribution of *C. dalli* (Fig. 1: L, M), few studies have asked about such variation in *C. fissus*, samples from the northern part of its range and southward into Mexico (Guerrero Negro, 28.0° N) also showed no evidence of population structure (Wares *et al.*, 2001). In that study, phylogeographic methods were used to assess the probability of asymmetric gene flow and its relationship to coastal biogeography, but there was no evidence for cryptic diversity within *C. fissus* throughout this range. What variation in form exists has been shown, as with so much phenotypic diversity in this group, to be driven by local environment and plasticity (Jarrett, 2008). This is in part because the range of *C. fissus* had already been carved into cryptic taxa by one of the earliest molecular studies of barnacles. Hedgecock (1979) used allozyme diversity to support the evolutionary separation of *C. fissus* from *C. panamensis* (see Southward & Newman, 1977; Dando, 1987), and to recognize two cryptic species within this species complex. In later reports, these were called *C. "mexicanus"* and *C. "cortezianus"* (Laguna, 1990), unofficial names that ultimately promoted significant confusion in the taxonomic literature (Wares, 2001; Pitombo & Burton, 2007; Wares *et al.*, 2009; Chan *et al.*, 2016; Newman *et al.*, 2016; Pitombo & Burton, 2018; WoRMS, 2019). Nevertheless, the distinctness of these two taxa has been well supported by more recent molecular and morphological revisions (Wares *et al.*, 2009; Pitombo & Burton, 2007; Chan *et al.*, 2016). Notably, Chan *et al.* (2016) re-surveyed the North American coast from Alaska to Panama to confirm the distributions of *C. dalli*, *C. fissus*, *C. anisopoma*, and what have proved to be four distinct species in the *C. panamensis* complex (*C. panamensis*, *C. hedgecocki* Pitombo & Burton, 2007, *C. southwardorum* Pitombo & Burton, 2007 (see Pitombo & Burton, 2018), and *C. newmani* (Chan, Chen, Dando, Southward, & Southward, 2016; see Fig. 3).

The data from Chan *et al.* (2016) concord with previous studies on *C. anisopoma*, which is restricted to the Gulf of California (Sea of Cortez). *C. anisopoma* exhibits a remarkable plasticity in test development; in the presence of a gastropod predator they develop a 'bent' or defensive morph that limits predation (Lively, 1986), and Mokady *et al.* (2000) used mitochondrial sequencing to show no molecular distinction between the two morphs. Deng & Hazel (2010) subsequently evaluated the phylogeography of *C. anisopoma* more fully, using a restriction digest assay to ensure separation from the codistributed *C. southwardorum* and then sequencing mtCOI for the individuals of *C. anisopoma*. No consistent spatial structure was shown for *C. anisopoma* in that study, though further evaluation of populations that mark the transition to the other species along the Tropical Eastern Pacific region (TEP) coastline could be of interest. The complete history of taxonomic and phylogenetic exploration of this species complex will not be revisited here (Chan *et al.*, 2016; Pitombo & Burton, 2018), but Meyers *et al.* (2013) showed that the four species in the *C. panamensis* complex found in the TEP can be clearly distinguished using mitochondrial COI data and, as with overlapping distributions among barnacles such as *C. stellatus* and *C. montagu*, there is a clear signal of ecological separation into exposed *versus* sheltered habitats (Chan *et al.*, 2016), as well as biogeographic transition promoted by what appears to be unsuitable habitat (Meyers *et al.*, 2013).

Both *C. hedgecocki* and *C. southwardorum* occur in the Gulf of California and northern Mexico. Chan *et al.*, 2016 reported that *C. hedgecocki* can also be found on the outer Pacific coast of the Baja Peninsula, typically with *C. southwardorum* in more sheltered

microhabitats (Fig. 4; Chan *et al.*, 2016; Pitombo & Burton, 2018). Corresponding to the "Central American Gap" and the Gulf of Tehuantepec, southern Mexico, there is a significant biogeographic transition on the Mexican coast for many taxa (Hastings, 2000; Meyers *et al.*, 2013; Chan *et al.*, 2016), and south of this region both *C. panamensis* and *C. newmani* are found, with *C. panamensis* in exposed habitats and *C. newmani* in more sheltered ones (Chan *et al.*, 2016). Additional study is needed to fully evaluate the ranges of these tropical eastern Pacific taxa. Importantly, this tremendous diversity of often-sympatric chthamalid species in the Tropical Eastern Pacific was recognized early (A.J. Southward, personal communication) and then validated through the use of molecular markers. Subsequent to the molecular separation, however, biologists were able to carefully evaluate and identify distinguishing morphological details (Pitombo & Burton, 2007; Chan *et al.*, 2016), though these features are largely microscopic and cannot readily be used for field identification.

PANAMA AND WESTERN SOUTH AMERICA

The vicariant mechanism that isolated historic populations into distinct species is rather obvious in some instances. Taxa separated by the Isthmus of Panama have long been regarded as "geminant taxon pairs," likely conspecific until the rise of the Isthmus approximately 3.5 million years ago (Knowlton & Weigt, 1998). Laguna (1987) used this logic and molecular analysis of *Euraphia* Conrad, 1837 to recognize the specific distinction between *Microeuraphia rhizophorae* (de Oliveira, 1940) in the Caribbean and *M. eastropacensis* (Laguna, 1987) on the Pacific coast. As a clear geminant species pair, these taxa have been used to help calibrate divergence times among other chthamalid barnacles (Wares, 2001; Wares *et al.*, 2009), although the phylogenetic relationships of *Chthamalus* and *Microeuraphia* appear to need reconsideration (Shemesh *et al.*, 2009; Wares *et al.*, 2009; Pérez-Losada *et al.*, 2012). *Microeuraphia eastropacensis* is thought to be distributed similarly to the Tropical Eastern Pacific species of *Chthamalus* (Laguna, 1990), but its molecular diversity has only been evaluated on the two coasts of Panama (Fig. 4). *Microeuraphia rhizophorae* is distributed along the northern coast of South America as far as northeastern Brazil (Farrapeira, 2010).

There has been very little work on the morphological or genetic diversity of chthamalids on the northwestern coast of South America (Fig. 1: M). Laguna (1990) listed no chthamalids in the Galapagos Islands. The only taxon recorded at GBIF (2019) for the Colombian coast is *C. panamensis*. Laguna (1987) showed *C. panamensis* as far south as the Gulf of Guayaquil, Ecuador, which bridges the Ecuador/Peru border, and it could be that another novel species of *Chthamalus* can be found south of this location (based on unpublished work by A.J. Southward; Chan *et al.*, 2016). The only chthamalids recorded for the Peruvian coast are *Notochthamalus scabrosus* and *Jehlius cirratus* (Laguna, 1990; GBIF, 2019). Both of these species are found along the entire Chilean coast (Ewers-Saucedo *et al.*, 2016), and *N. scabrosus* has been further recorded from the Patagonian region of southern Argentina and the Falkland Islands. *N. scabrosus* and *J. cirratus* present an outstanding opportunity to evaluate variation in ecology and gene flow between very similar co-distributed taxa along a topologically "simple" coastline (Navarrete *et al.*, 2008; Zakas *et al.*, 2009).

Both *N. scabrosus* and *J. cirratus* can be found in the mid-to-high intertidal along the entire coast of Chile, with populations in Peru and southernmost Argentina as well (Curelovich *et al.*, 2009). Typically, they overlap greatly in vertical range, with *J. cirratus* tending to be more abundant in the high intertidal and *N. scabrosus* more abundant in the mid-intertidal (Shinen & Navarrete, 2014); yet there is no evidence that they competitively exclude each other from these zones (Shinen & Navarrete, 2014) nor that they have distinct thermal tolerances (Lamb *et al.*, 2014). The one somewhat clear exception to their similarities in life history is their speed of

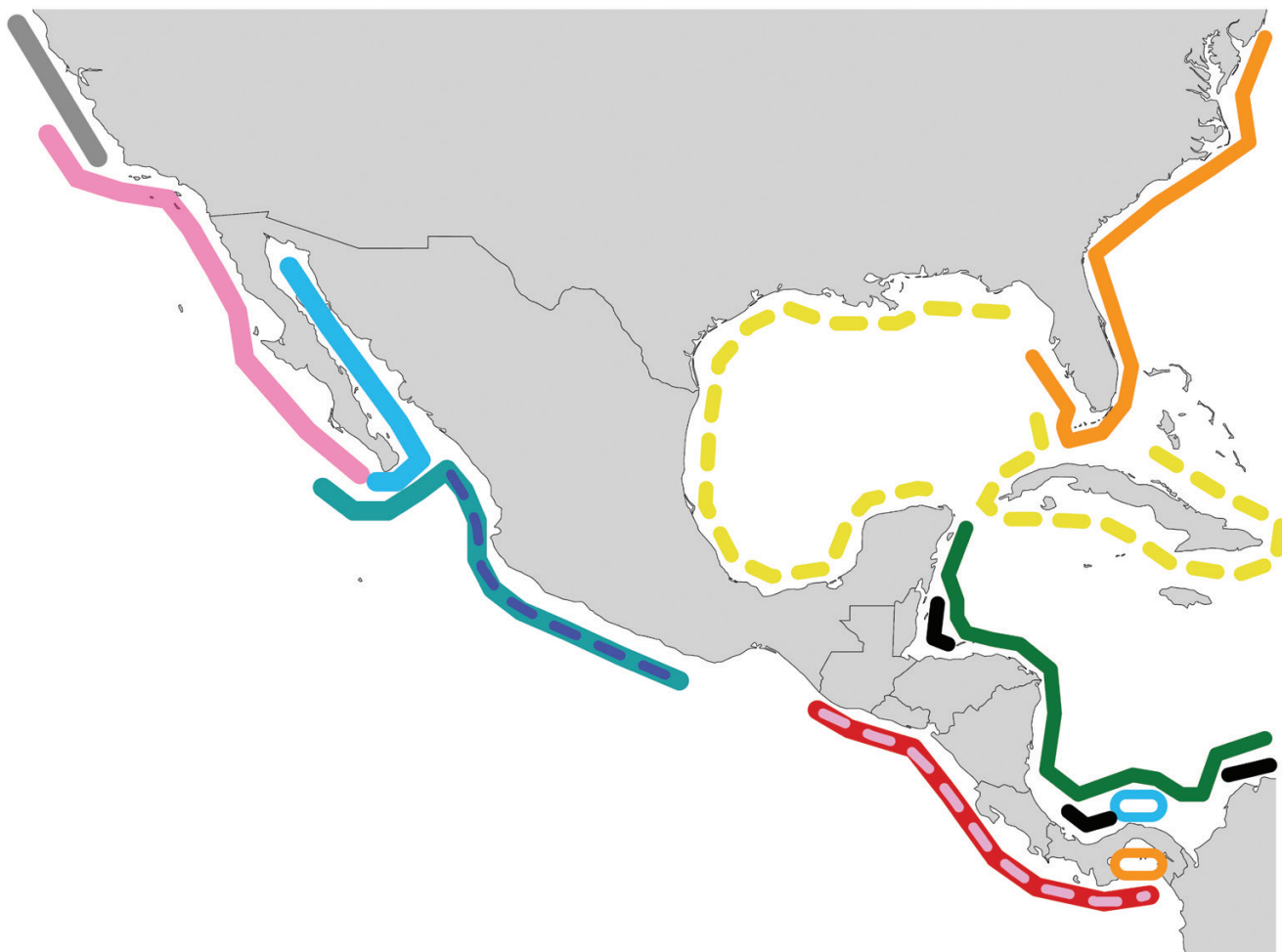


Figure 4. Overview of chthamalid diversity in North and Central America. In the Pacific, the northernmost species is *C. dalli* (grey), overlapping briefly with *C. fissus* (pink) between Monterey Bay and Point Conception in California; neither exhibits mitochondrial structure. *Chthamalus anisopoma* (light blue) is largely confined to the Gulf of California (Sea of Cortez). Two species with largely overlapping ranges that are separable by microhabitat are *C. hedgecocki* (green) and *C. southwardorum* (dashed blue) to the north of the “Central American Gap;” south of this region are *C. panamensis* (red) and *C. newmani* (dashed pink), both presumably also being found down onto the Colombian coast. In the Caribbean, much of the distributional data follow Southward (1975) and have not been explicitly re-evaluated with molecular data or phenotypic surveys; dashed yellow lines indicate uncertain chthamalid diversity. *Chthamalus proteus* (dark green) is suggested to have a more continuous distribution along the continental and island coasts; *C. angustitergum* (black) is believed to have an interrupted distribution (Dando & Southward, 1980), and this is reflected in the divergence between populations from Belize and Panama (Wares *et al.*, 2009). *Chthamalus fragilis* is indicated in Florida and along the eastern US coast. Ovals on the coast of Panama represent the isolation of Atlantic *Microeuraphia rhizophorae* and Pacific *M. eastropacensis*.

larval development. Venegas *et al.* (2000) assessed the time from release to development of the cyprid stage (which is competent to settle) at two locations with distinct temperature profiles. Although laboratory studies of larval development may not reflect the natural time series, *J. cirratus* consistently developed to the cyprid stage about a week faster than *N. scabrosus*.

It is intriguing to note what appear to be contrasting responses in *N. scabrosus* and *J. cirratus* to the broad environmental gradient present along the Chilean coast. Particular oceanic features such as diverging currents near 42°S (Acha *et al.*, 2004) and a persistent shift in the upwelling regime near 30°S (Navarrete *et al.*, 2008) together appear to drive the overall coastal biogeography of Chile (Thiel *et al.*, 2007). Analyses of gene flow in *J. cirratus* show minimal spatial structure in mitochondrial COI sequences from samples spanning greater than 3000 km (Guo & Wares, 2017). In contrast, *N. scabrosus* presents two clearly distinct evolutionary lineages that are wholly fixed in the northernmost and southernmost sampled regions of the Chilean coast (Laughlin *et al.*, 2012; Ewers-Saucedo *et al.*, 2016), with a broad range of distributional

overlap that mirrors the coastal biogeographic patterns and suggests that a combination of current-promoted dispersal and environmental gradients may underlie the patterns of most taxa on this coast (Thiel *et al.*, 2007; Fig. 1: N).

The findings for *N. scabrosus* (Ewers-Saucedo *et al.*, 2016) reflect not only mitochondrial sequence data, but also nuclear sequence data and single nucleotide polymorphism arrays (Zakas *et al.*, 2014). As such, these data are among the few for chthamalid barnacles that give deeper genomic insight into the possibility of hybridization and introgression between the two detected lineages. Early work with multilocus allozyme data (Southward, 1983; Dando, 1987) suggested that *Chthamalus* species do not hybridize when in sympatry, despite their need as sessile arthropods to copulate with nearby neighbors. Chan *et al.* (2016) revisited this question when they quantified the mitochondrial sequence disparity between two of the Tropical Eastern Pacific taxa. Even though large numbers of molecular markers are available (130 polymorphic markers plus mitochondrial DNA in *N. scabrosus*; Ewers-Saucedo *et al.*, 2016) it is nevertheless difficult to know which

markers reflect strong selection rather than introgression, or ancestral polymorphism in an evolutionarily recent separation (Bulgin *et al.*, 2003). Perhaps further genomic evaluation of *J. cirratus* will highlight stronger spatial patterning than the mitochondrial data exhibit (Guo & Wares, 2017), but the *N. scabrosus* and *J. cirratus* species pair presents an intriguing question: why do two very similar species, nearly indistinguishable in ecology and physiology (but not so similar in larval life history) respond distinctly in terms of spatial genetic structure to the same oceanic and environmental conditions? Can similar larval contrasts be demonstrated for co-distributed taxa such as *C. montagui*, *C. stellatus*, and *E. depressa* in the Mediterranean, or the chthamaloids *Catomerus polymerus* and *C. antennatus* along the southern Australian coast (York, 2008)? Our knowledge of potentially distinctive aspects of larval behavior, development, and temperature tolerance is imperfect for many of these overlapping chthamalid species.

EASTERN SOUTH AMERICA AND THE CARIBBEAN

A noteworthy and unusual temperate-zone gap in the distribution of Chthamalidae is found along the Argentinean coast (Fig. 1: O, transition from zone 24 to 21 in Costello *et al.*, 2017). Although the very southern coast and the Falkland Islands harbor *N. scabrosus*, the rest of the Argentinean coast has had no native barnacles in the intertidal (Eliás & Vallarino, 2001; Savoya & Schwindt, 2010). Eliás & Vallarino (2001) noted similar gaps along the Mexican coast (the “Central American Gap;” Hastings, 2000), as discussed above, and the Venezuelan coast. Further north along the South American coast, *C. bisinuatus* Pilsbry, 1916 (recorded from Uruguay) and *C. proteus* Dando & Southward, 1980 are found, with *C. proteus* extending all the way into the Caribbean (with a significant gap around the mouth of the Amazon; Zardus & Hadfield, 2005). Unfortunately, we do not know which of these latter two species tends to be found higher in the intertidal where they are co-distributed (but see Farrapeira, 2010, which indicates that *C. bisinuatus* tends to be in more exposed habitats than *C. proteus*), nor anything about other microhabitat preferences, because they have been considered indistinguishable in the field (Masi *et al.*, 2009) despite being highly divergent by molecular criteria (Wares *et al.*, 2009).

No molecular work has been done to evaluate spatial or cryptic diversity in *C. bisinuatus*, but *C. proteus* is one of the more intriguing chthamalids with respect to the patterns revealed by cryptic molecular diversity within its geographic range. Concerning the introduction of *C. proteus* to the Hawaiian Islands (Southward *et al.*, 1998), Southward (1983: 68) suggested that chthamalids, “with the exception of *proteus* [sic] and an Indian Ocean species, are rarely found as fouling growth.” To understand this introduction of *C. proteus* better, Zardus & Hadfield (2005) began to sequence samples of *C. proteus* across the Caribbean and Western Atlantic. The species itself was originally defined by molecular means, as Dando & Southward (1980) had initially identified *C. proteus* as being highly distinct from *C. fragilis* by using allozyme markers, and later on the basis of morphological features, and some discussion of the likely spatial/microhabitat distribution of *C. proteus* was included in their article. The mitochondrial sequence data for *C. proteus* collected from nine sites in its native range revealed four reciprocally monophyletic clades of mitochondrial diversity, ranging from 2.2% to 3.8% in sequence divergence among themselves. One of these clades is from southern Brazil; inasmuch as the northern coast of Brazil may not harbor these barnacles (Fig. 1: P, transition from zone 21 to 11 in Costello *et al.*, 2017; Dando & Southward, 1980; Zardus & Hadfield, 2005), this spatial and phylogenetic isolation makes sense and the southern Brazilian populations may represent yet another species-level taxon (Dando, 1987). The other clades included one endemic to the coast of Panama and

two that are broadly distributed in the Caribbean. As for the introduced *C. proteus* in the Pacific (and possibly in the Canary Islands; Gonzalez *et al.*, 2012), the authors concluded that there had been multiple introductions from different regions of the Atlantic and the Caribbean and suggested that *C. proteus* has a good capacity to be transported via human activity (Zardus & Hadfield, 2005; Zabin *et al.*, 2007).

Because congeners within *Chthamalus* are often difficult to distinguish in the field, we may have a poor sense of whether other global introductions have occurred (Gonzalez *et al.*, 2012). Ashton *et al.* (2016) sampled barnacles from ships’ hulls and used molecular barcoding to identify the members of the fouling community. Among the diversity recognized were six species of *Chthamalus*, all with broad “native” distributions (Ashton *et al.*, 2016). *Chthamalus* and other barnacles have also been identified rafting on plastic in the North Pacific (Goldstein *et al.*, 2014). Because many species may be first identified based on their provenance (i.e., one would not be looking for *C. dalli* in Europe), future molecular monitoring of coastal barnacle communities may reveal a much broader problem of anthropogenic introductions (Chen *et al.*, 2012). Most known introductions of barnacles have been to areas where there previously were no barnacles or none similar in phenotype (Allen *et al.*, 2006; Savoya & Schwindt, 2010). These observations pose a puzzle for biologists studying spatial patterns of cryptic diversity in such organisms as chthamalids. If these organisms are readily transported by anthropogenic activity, how have we so often seen strong and exclusive patterns of genealogical structure (Chan *et al.*, 2016; Ewers-Saucedo *et al.*, 2016; Pannacciulli *et al.*, 2017), and are these patterns transient in the long-term?

The other wholly Caribbean species (Fig. 1: Q, zone 11 in Costello *et al.*, 2017), *C. angustitergum* Pilsbry, 1916, has not been intentionally explored for spatial population structure with molecular markers. Wares *et al.* (2009), however, recovered *C. angustitergum* from the coasts of Panama and Belize (ca 1,500 km apart), and found that individuals from these two sites are reciprocally monophyletic. Dando & Southward (1980) suggested that there is little appropriate habitat for chthamalids in the intervening coastline, and so this disjunction may simply reflect the lack of gene flow over this distance, as in Meyers *et al.* (2013) and other studies reported above. *Chthamalus angustitergum* is thought to have a much broader distribution in the rest of the Caribbean besides Panama and Belize, and may be dominant on more exposed coastlines (Dando & Southward, 1980). According to the distribution maps of Southward (1975), both *C. bisinuatus* and *C. angustitergum* ought to be broadly distributed throughout the Caribbean and into the Gulf of Mexico, and Dando (1987) indicated that *C. angustitergum* may also be recovered in southern Florida. These distribution patterns, however, were established before the identification of *C. proteus* in these locations, and what few DNA sequence data are currently available from southern Florida all represent *C. fragilis* (Govindarajan *et al.*, 2015b). The tropical western Atlantic and Caribbean are due for a new survey of phenotypic and corresponding molecular diversity in these barnacles.

EASTERN NORTH AMERICA

Only one chthamalid remains to discuss on the Gulf and Atlantic coasts of the United States. Despite its proximity to many ecologists studying marine habitats with molecular markers, *C. fragilis* has until recently been neglected with regards to genomic diversity apart from its separation from *C. proteus* (Dando & Southward, 1980). Govindarajan *et al.* (2015b) sampled these barnacles from the Gulf coast of Florida, the Florida Keys, and along the east coast of the USA throughout its range (Fig. 1: R, entirely within what is still zone 11 of Costello *et al.*, 2017), including southern New England, where it is believed to have arrived in the late 19th century from the southeastern coast of the USA (Carlton *et al.*,

2011). Govindarajan *et al.* (2015b) identified three distinct clades, with one of them only found at Cape Hatteras, North Carolina and northwards (Wares *et al.*, 2018). This discovery of evolutionary diversity within what appeared to be a homogeneous but variable and plastic species (*C. fragilis* is unusual among its congeners in tending to recruit to the cordgrass *Spartina*; O’Riordan *et al.*, 2010) shines light on the processes of historical isolation and ecological divergence that are universally important in evolutionary diversification. It may also give us insights into general rules or foci for diversification in this part of the North American coast (Wares, 2002), even when there is no apparent functional distinction between the lineages involved. The phylogenetic diversity may also be of interest in the context of the competitive interactions that appear to be preventing further expansion into New England; Wethey (1983, 2002) showed that the balanid *Semibalanus balanoides* competitively excludes *C. fragilis* where they overlap, and this is precisely where the northern-restricted clade of *C. fragilis* is dominant. This interaction is unusual and is not found among chthamalids in Europe, where they again overlap the range of *S. balanoides*. The range in Europe has advanced northward with anthropogenic climate change (O’Riordan *et al.*, 2010), whereas the northern boundary of the range of *C. fragilis* appears to have moved only in concert with the southern range boundary of *S. balanoides* on the American coast (Wares *et al.*, 2018).

One of the keys to understanding this genomic variation with respect to environment, is that some deep phylogenetic separation may be expected in even a “neutral” relationship of genomic diversity to environment (Maggs *et al.*, 2008; Wakeley, 2008). The mitochondrial clades identified in many chthamalid lineages likely represent distinct evolutionary lineages, but this will not always be true as they are hypotheses to be tested with additional data. In the case of *C. fragilis*, the exploration of this diversity has been in part because of early allozyme data suggesting allele frequency variation in *C. fragilis* from the northern populations towards the south (Dando & Southward, 1980), which does not align with the observed mitochondrial clades (Wares *et al.*, 2018). Additional genomic data, obtained using restriction site associated DNA markers (RAD-seq), are preliminary but also do not support deep divergences among the mitochondrial lineages of *C. fragilis* (JPW, unpublished data) and so it may be key to understand how mitonuclear interactions drive very specific patterns of selection in crustacean genomes (e.g., Barreto *et al.*, 2018) to better understand this pattern in *C. fragilis*.

GENERALITIES IN CHTHAMALID DIVERSITY

Several taxonomic and phylogenetic puzzles remain to be sorted out in Chthamalidae, as noted above. Some species have scarcely been studied since their initial description (e.g., *Jehlius gilmeri* Ross, 1971 and *C. southwardi* Poltarukha, 2000) and thus remain phylogenetically unlinked to the other dominant regional chthamalid taxa. Study has been obviously more intense where research groups with sufficient resources have been active nearby. Questions remain as to where we may expect to find additional evolutionary diversity in this group, and how often descriptions of new species (e.g., *C. barnesi*) have been based on distinct phenotypes within the range of plasticity encompassed by such broadly-distributed species such as *C. malayensis*. We expect vicariance and restricted gene flow to be important contributors to diversification (Dando, 1987; Avise, 2000; Wares, 2016). To be sure, ancient geologic and hydrologic processes, as well as contemporary habitat disruptions, are of key importance in the cryptic diversity identified in almost every species named in this review. It is likely, after all, that spatially or oceanographically isolated populations of chthamalids will diverge both in DNA sequence and phenotype.

Many clues suggest that these distinct species or lineages respond to habitat differences on much smaller scales as well, even when gene flow appears to be more than capable of homogenizing or admixing populations. Where there is an intermixing of wave-exposed and wave-sheltered habitats, likely resulting in differences in temperature, food availability, larval retention, and other factors, evolutionarily divergent lineages tend to be sorted by these habitats (noted for *C. stellatus/montagui*; *C. hedgecocki/southwardorum*; *C. panamensis/newmani*; *C. dalli/fissus*; *C. proteus/angustitergum*, among others). This is also true for interspecific comparisons (*C. stellatus* and *C. montagui*; the two pairs of *Chthamalus* species in the Tropical Eastern Pacific) and is likely involved in maintaining the divergent lineages so far documented within species, whether or not specific status is warranted is a distinct question in most cases. A recurrent pattern in molecular analyses of these cryptic lineages is that the sheltered-shore species appear to have higher genetic diversity within populations than otherwise co-distributed, exposed-shore species do (Pannacciulli *et al.*, 1997; Chan *et al.*, 2016). This could be a genomic response to the greater environmental variation in the sheltered habitats.

Other environmental characteristics appear to be important in determining the distributions of lineages (for example, the latitudinal patterns in *N. scabrosus* and *C. fragilis*), but they do not always generate comparable patterns in co-distributed species. *Jehlius cirratus* appears homogeneous along thousands of kilometers of Chilean coast, whereas *N. scabrosus* displays strong population structure; *C. dalli* appears homogeneous along the temperate eastern Pacific coast of Oregon and California even though other sympatric acorn barnacles (*Balanus glandula* Darwin, 1854) exhibit significant, environmentally-associated population structure (Sotka & Wares, 2004; Wares & Skoczen, 2019). Chthamalids tend to exhibit population structure in areas of high evolutionary diversity or divergence for other species or communities (Chan *et al.*, 2012; Ewers-Saucedo *et al.*, 2016; Pannacciulli *et al.*, 2017; Wares *et al.*, 2018). At the broadest scale, there is general concordance with the biogeographic provinces identified in the recent synthesis study by Costello *et al.* (2017). There tend to be transitions among chthamalid taxa (for example, western Africa, eastern Asia, and major transitions along the eastern Pacific) where there are major faunal boundaries. Significant cryptic diversity in areas such as the Caribbean, however, are more likely maintained by regional-scale oceanography, as discussed in Baums *et al.* (2006) and Diaz-Ferguson *et al.* (2011), or habitat-driven differentiation as in the Tropical Eastern Pacific.

It will be instructive to evaluate for cryptic diversity in broadly distributed taxa that appear to consist of phenotypically homogeneous members (Rocha-Olivares *et al.*, 2001; Sotka *et al.*, 2003; Pfenninger & Schwenk, 2007; Chen & Hare, 2011). Such studies may lead us to grand-scale general understanding about how habitat and abiotic forcing drive global biogeography and diversity (Wares *et al.*, 2001; Pringle *et al.*, 2005; Cook *et al.*, 2017). Acorn barnacles have the additional advantage of still providing a relatively complete view of their biogeography and interactions inasmuch as they have not yet been reduced in number for their economic value (as with many fishes, for example (Roberts, 2008)) or by disease, as is seen in a growing number of marine taxa (Harvell *et al.*, 2002).

CONCLUSIONS

Molecular data have accelerated the discovery of biodiversity in many taxa (Pfenninger & Schwenk, 2007; Pringle *et al.*, 2011), but particularly in species that share a relatively static, but also high plastic, body plan with their congeners and confamilials (Dando & Southward, 1980; Foltz *et al.*, 1996; Rocha-Olivares *et al.*, 2001). In most cases, the molecular data have not replaced careful field observations and morphological examination for distinguishing

these species (Southward, 1976; Yan & Chan 2004a; Pitombo & Burton, 2007), but have prompted careful re-evaluation based on the latter criteria. In this sense, the use of molecular markers to study chthamalid diversity and distributions is an example of both “reverse ecology” (Li *et al.*, 2008; Marmeisse *et al.*, 2013) and revolutionary improvement of the process of taxonomic revision (Dando & Southward, 1980, Pitombo & Burton, 2007). It should be clarified that this review does not cover the distribution of all chthamalids, only those for which there is information about whether there is cryptic diversity within their recognized boundaries; there are many more to be explored for cryptic variation. As noted above, the exploration of cryptic diversity may also help identify cryptic introductions (Ashton *et al.*, 2016), the source of known introductions (Zardus & Hadfield, 2005), or the genomic composition of climate-related range expansions (Dawson *et al.*, 2010; Wares *et al.*, 2018).

As chthamalid barnacles are not often used in experimental studies, we often know little about their genomic diversity other than from allozyme studies or the sequencing of their mitochondrial DNA; this is changing quickly, however (Pannacciulli *et al.*, 2005; Shemesh *et al.*, 2009; Zakas *et al.*, 2014; Ewers-Saucedo *et al.*, 2016). New survey work to identify evolutionarily distinct lineages and reconstruct their phylogenetic relationships must be followed by the work needed to understand how traits vary with the environmental and evolutionary background, thus separating species by ecological role, and what this means in the context of the biogeography of co-distributed taxa (Wheeler, 2018). The survey data amassed to date will also likely prove to be valuable as we continue to monitor how barnacle species respond to warming oceans and a changing climate (Southward, 1991; Sunday *et al.*, 2012; Dawson *et al.*, 2010; Tsang *et al.*, 2013; Wares *et al.*, 2018; Wares & Skoczen, 2019; Sanford *et al.*, 2019).

Some focal areas that could benefit from further examination are clear. Such work could show, for example, how coastal upwelling and habitat availability influence diversity patterns in western Africa (Stubbings, 1967; O’Riordan *et al.*, 2010); how major river systems influence distributions in Brazil, China, and elsewhere (Zardus & Hadfield, 2005); and how coastal topography promotes or maintains diversification (Hellberg, 1998; Costello *et al.*, 2017) in other regions where cryptic diversity are highlighted in this review. Basic questions of biogeography and thermal tolerance require a better understanding of the dominance of a species or lineage at a given tidal height or degree of exposure (Southward, 1975: 33), but few of the distributional overlaps in Chthamalidae are sufficiently well characterized to reach general conclusions about how intertidal zonation and overall physiological niche are related in this group. Finally, it is of persistent interest that these barnacles possess numerous measurable traits that vary among environments (e.g., Lively, 1986; Jarrett, 2008), evolutionary lineages (Southward, 1983), and species (Chan *et al.*, 2016), yet the immense diversity found within species poses a distinct problem for delimiting them (Southward, 1983; de Queiroz, 2007; Galtier, 2019). We have a poor understanding of how barnacle species seem to become reproductively isolated so quickly (Dando, 1987) – by behavior, environmental cues, sensory hairs, and cues we have yet to recognize – because without a more thorough biogeographic synthesis, one that allows repeated observation of similar processes (Navarrete *et al.*, 2008), it is difficult to know what changes trigger the splitting off of yet another lineage. What features are so strong as to send them on their own evolutionary paths, focused on a particular microhabitat, diet, or phenology? Whatever the mechanism, it seems to have served them well as animals

“...so common, yet so implausible. In millions along every shoreline in the world...these hermaphrodites were fishing away with their feet, glued by their heads to rocks.” (Stott, 2003: 72).

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