6 Historical Name-Bearing Types in Marine Molluscs

An Impediment to Biodiversity Studies?

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INTRODUCTION

Molluscs are the second largest animal phylum in terms of the global number of described species, and they have the largest known diversity of any marine group. We currently know about 82,000 valid described mollusc species (53,000 marine), with a yearly increment of about 580 new species descriptions (350 marine) (Bouchet 2006). Marine molluscs account for a quarter of all described marine biota. Gastropods make up roughly 85% of these and, specifically, the caenogastropods (comprising the vast majority of what people call "seashells") account for around two-thirds of total marine molluscan diversity. Seashells have attracted the interest of naturalists, amateurs, and collectors since well before Linnaeus, and the result has been both a blessing and a curse for biodiversity exploration. This chapter is mainly concerned with the impediments of historical and current taxonomic practices in documenting marine shelled gastropod diversity, and exploring ways to move forward in view of the daunting diversity that remains to be described. Other groups of molluscs (e.g., marine slugs) and certainly several other phyla of marine invertebrates suffer from similar types of problems, and would probably also benefit from the solutions explored here.

Linnaeus knew of roughly 870 species (H. Dekker, pers. com.) of "Vermes Testacea," a higher category that included the shells of molluscs and brachiopods, the tubes of serpulid polychaetes, and the plates of goose barnacles, while the shell-less molluscs (e.g., nudibranchs) were classified under "Vermes Mollusca," together with holothurians and annelid polychaetes. Leaving aside the phylogenetic rearrangements that have taken place since *Systema Naturae*, the significance of Linnaeus's classification is that species of "Testacea" were described and named exclusively based on their shells. This dichotomy between shell and animal was pursued to nomenclatural absurdity by several late 18th-century/early 19th-century zoologists. For example, Giuseppe Poli (1746–1825) used a parallel nomenclature for the shells and for the animals that occupied them. An example would be the animal *Callista* Poli, 1791 living in the shell *Callistoderma* Poli, 1795 (Bivalvia, Veneridae). Analogous systems have been developed in taxa with complex life cycles (e.g., hydroid and medusa stages of Hydrozoa), but Poli's approach differed in that different names were applied to different (and coexisting) parts of the same animal.

Although, very early on, authors such as Georges Cuvier (1769–1832), John Edward Gray (1800–1875), Franz Hermann Troschel (1810–1862), Otto Mörch (1828–1878), Paul Fischer (1835–1893), and Eugène Louis Bouvier (1856–1944) used anatomical characters as a basis for classification, and the radula and digestive tract anatomy, respiratory and excretory organs, nervous and circulatory systems are considered to be essential for the recognition of families, superfamilies, orders, and subclasses, by contrast the shell alone was considered adequate for species identification. The naming of shelled molluscs based exclusively on their shells has remained standard practice to this day, and over 80% of new descriptions of shelled marine gastropod species published in 2006 contained a description of the shell only. However, this time-honored system is compromised by the poor quality of much type material, and the resulting complexity poses a significant impediment to modern biodiversity studies.

MOLLUSCAN SHELLS IN BIODIVERSITY STUDIES

The shells of molluscs are a significant asset for biodiversity exploration because they make robust post mortem remains that potentially persist for a long time after the death of the animals that secreted them. This, of course, facilitates fossilization, and the fossil record of molluscs is exceptionally good. It also facilitates sampling and conservation of specimens; shells of molluscs do not require sophisticated preservation protocols, and sailors, missionaries, explorers, and travelers historically returned to their native countries with natural history collections, of which shells and corals, because of their hard parts, made up a significant proportion. In museum collections, the conservation of shells barely requires any maintenance at all and, except for Byne's disease (de Prins 2005) and—in the case of microshells—"glass disease" (Geiger et al. 2007), shells remain for centuries in museum drawers unaltered, whereas herbaria and insect collections require constant attention to prevent fungal and insect damage. Another advantage of the shells of molluscs is that they provide an important window on actual molluscan diversity, even if living animals are so rare, seasonal, or elusive that they are rarely or never sampled. After 25 years of intensive exploration in New Caledonia, as many as 73% of all 1,409 turrid gastropod species documented are represented only by empty shells, and 34% by a single empty shell (Bouchet et al. 2009).

But the shells of molluscs also have significant limitations. These external exoskeletons are susceptible to erosion after death, and even during the life of the animal. Shells are gradually eroded biologically (by the attack of boring and encrusting organisms), physically (by the mechanical movements of the waves), and chemically (by dissolution or diagenetic alteration of the minerals). But how these processes affect individual specimens is not uniform in space and time and there is no direct equivalence between the age of a shell and the quality of its preservation. Even ancient fossils hundreds of millions of years old may be exquisitely preserved, complete with the microsculpture of their protoconch (Bandel et al. 2002, Yoo 1994, Fryda 1999). By contrast, many shells collected on seashores may be (severely) worn—collectors use the expression "beach worn" to qualify seashells polished by sand and wave action so that details of sculpture and color are lost. However, such shells have been and occasionally still are described as new species (Turton [1932], for instance, did so on a massive scale).

The role of name-bearing types is to provide an anchor for the virtual world of names in the real world of animals. In common with many—perhaps most—other animal taxa, the historical descriptions of new recent shelled molluscs lack many characters that are today considered essential for proper (super) family assignment and species discrimination. But as progress is made in the understanding of characters and character-states, entomologists can still return to name-bearing types to, for example, mount sclerotised pieces from the internal genital anatomy, acarologists can examine the position of setae with the scanning electron microscope (SEM), ichthyologists can do meristic counts from x-rays of preserved specimens, etc. All this is feasible because name-bearing types of insects, mites, or fish were (with a few rare, exceptions) alive when they were collected. By contrast, the name-bearing types of shelled molluscs were mostly empty shells at the time they were collected. In such cases it is not only impossible to examine standard anatomical characters, including the radula, but very often the shell itself lacks important diagnostic features such as the protoconch, color, and microsculpture.

THE PROTOCONCH REVOLUTION

With their accretionary growth, gastropod shells typically exhibit at their apex a protoconch secreted by the embryo or veliger larva before hatching or metamorphosis, whereas the rest of the shell (the teleoconch) is secreted by the post-metamorphic snail. The morphology of the protoconch reflects the larval ecology of the animal that secreted it (Jablonski and Lutz 1980, 1983). A protoconch with a large initial nucleus, consisting of 1–2 whorls (i.e., "paucispiral"), and a single protoconch/teleoconch discontinuity, is characteristic of species with non-planktotrophic larval development (also called lecithotrophic or (improperly) direct development). A protoconch with a small initial nucleus and two distinct accretionary stages, including protoconch I (typically comprising less than one-half whorl secreted by the embryo in the egg-case) and protoconch II (secreted by the swimming veliger typically consisting of 3–5 whorls, i.e., "multispiral"), is characteristic of species with planktotrophic larval development. Protoconch II is also frequently adorned with complex sculpture patterns that provide additional morphological characters. The size of protoconchs is usually in the range of 0.5–2 mm, and they are thinner—thus less solid—than subadult and adult teleoconch whorls. These characteristics mean that the protoconch is the most vulnerable part of the shell and is often the first to become damaged or corroded, even during the lifetime of the animal.

The value of the protoconch as a taxonomic character was first highlighted by Dall (1924), and Powell (1942) even attributed genus-level importance to the paucispiral vs. multispiral protoconchs of Turridae (but see Bouchet 1990). With the advent of SEM, malacologists were prompt to understand its potential for examining and illustrating protoconchs (e.g., Robertson 1971, Thiriot-Quiévreux 1972). Indeed, protoconchs are so essential in the systematics of certain shelled gastropod families that Marshall (1983) wrote:

> I cannot emphasize too strongly that under absolutely no circumstances should further new species [of Triphoridae] be proposed unless a complete, unworn protoconch can be illustrated. Protoconchs should always be illustrated by scanning electron micrographs.

It has been demonstrated that the mode of larval development (i.e., planktotrophic vs. non-planktotrophic), is a species-specific character of shelled molluscs (Hoagland and Robertson 1988, Bouchet 1989). The two modes of larval development often coexist in the same genus, and there are numerous examples of species pairs/complexes, with very similar or even indistinguishable teleoconchs, but distinct—multispiral vs. paucispiral—protoconchs (e.g. Boisselier-Dubayle and Gofas 1999, Véliz et al. 2004) (Figure 6.1). Historically, such species pairs/complexes were considered to be one species. When two species are recognized, the question that arises is to which of the two species the name in current use should be applied. In principle, the answer should be straightforward: examine the name-bearing type, and confirm its protoconch type. Many times, however, the name-bearing types of shelled molluscs, especially those described before the 1970s, lack protoconchs, are fragmentary, or lack both the tip of the shell and its base, obliterating characters now considered important or essential.

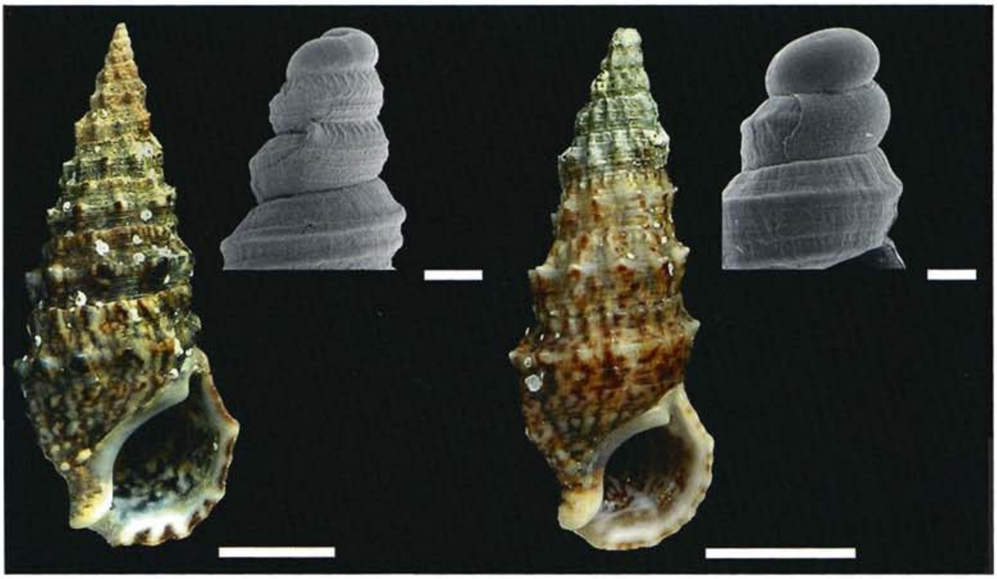

FIGURE 6.1 Two species of *Cerithium* from the Mediterranean formerly included in the highly variable species *Cerithium vulgatum* Bruguière, 1792. Based on protoconchs, spawn and allozyme data, two species are recognized, one with multispiral protoconch (left), one with paucispiral protoconch (right) (see Boisselier-Dubayle and Gofas 1999). *Cerithium vulgatum* is the oldest name and there are 38 available names currently included in its synonymy. When type material is extant, it lacks the discriminating protoconch that is always eroded in the subadults and adults, and it is conjectural which name applies to each species. The minor differences apparent between the two specimens are less than the range of variation within each species. Scale bars: 10 mm (adults) and 100 µm (protoconchs). (Photos courtesy of S. Gofas.)

Examination in the Muséum National d'Histoire Naturelle (MNHN) and the National Museum of Natural History (USNM) (Figure 6.2) of the name-bearing types of 64 and 61 nominal species of Triphoridae, respectively, shows that only roughly one-third have a protoconch in good condition, and another third have only remains that allow some "guesswork," while the remaining third are in an atrocious condition, i.e., beach worn (see, for example, Figure 6.2A); rarely do such historical types rise to the level of modern, live-collected shells in excellent condition. Buried in the taxonomic literature on molluscs, not infrequently one finds observations such as: "The holotype of *Murex mundus* Reeve, 1849 [...] is beachworn, probably subadult, and lacks the protoconch and the first teleoconch whorl. [Its] identity remains thus uncertain" (Houart 2003). Common sense would perhaps recommend that such name-bearing types be discarded and replaced by a neotype. However, a replacement must be approved by the International Commission on Zoological Nomenclature (ICZN) following an application, on a case-by-case, name-by-name, basis. Furthermore, the judgment of one author who regards a specimen as unrecognizable can be challenged by another author, even purely on principle. Also, the eyes of two taxonomists with different training and experience may not "see" exactly the same thing on the same shell. As a result, such an application would be considered ineffectual by many zoologists, except in the case of emblematic or biologically or ecologically important species. But what about an insignificant species such as *Murex mundus*? It is symptomatic that so few molluscan petitions in the *Bulletin of Zoological Nomenclature* are for replacement of existing type material by a neotype, whereas such petitions are not rare for arthropods or vertebrates. The implicit significance is that malacologists are perhaps either more pragmatic or more cynical about the taxonomical value of types.

Taxonomists are thus often left to guess from subtle differences in teleoconch sculpture to which of two or more biological species a name-bearing type belongs. After reasonable guesswork and

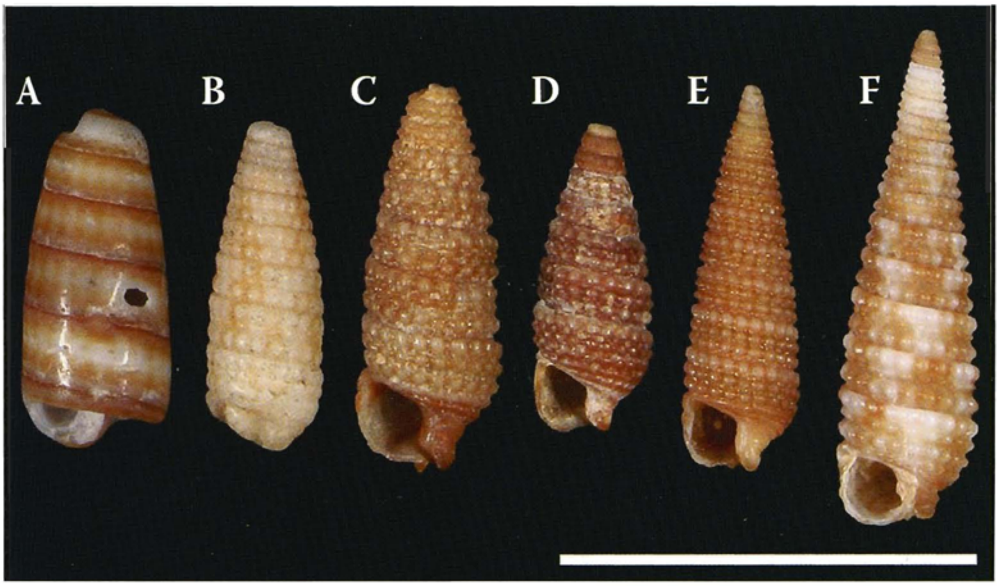

FIGURE 6.2 Types of triphorid species described by Paul Bartsch and deposited in the USNM; A to F, worst to best. A. *Triphoris montereyensis* Bartsch, 1907, figured holotype, USNM 32216. B. *Triphoris stearnsi* Bartsch, 1907, figured holotype, USNM 32259. C. *Triphoris pedroanus* Bartsch, 1907, figured syntype, USNM 152206. D. *Triphoris peninsularis* Bartsch, 1907, figured holotype, USNM 106424. E. *Triphoris africana* Bartsch, 1915, figured holotype, USNM 186804A. F. *Triphoris dalli* Bartsch, 1907, figured holotype, USNM 195375. Scale 1 mm.

inference from type localities (when the two species in a pair have partly non-overlapping distributions), the type can often be pinned down to a certain species. But for how long? Only until one discovers there is not one, but a species complex, that matches the fragmentary type? The following quote was written by Marshall (1983) with Triphoridae in mind, but could apply just as well to Cerithiopsidae and many other caenogastropods and shelled heterobranchs:

> Many species based on imperfect type specimens will be impossible to identify, at least until the faunas of particular type localities are sufficiently well known for topotypes to be identified with confidence. In cases where the type locality is unknown, or when a type specimen comes from a locality where two or more species with indistinguishable teleoconchs occur, species based on specimens lacking the protoconch or lacking even the first whorl may be permanently unrecognizable.

By leaving so much open to personal interpretation and appreciation, name-bearing types clearly do not fulfill their function to anchor nomenclature in verifiable statements.

NO RADULA OR GENETIC MATERIAL FROM EMPTY SHELLS

The situation becomes even worse when anatomical characters are essential to discriminate between species or to allocate species to the correct genus and family. The genital anatomy of seaslugs is routinely used for species-level discrimination, but the anatomy of shelled molluscs is considered to be informative primarily at higher taxonomical levels—genus, family, or superfamily (e.g. Strong 2003; but see Reid 1996). Most anatomical characters are time-consuming to observe, interpret, and illustrate, especially on large suites of specimens, but the radula is an exception. Radulae are relatively easy to extract (also from dried soft parts) and, starting with Solem (1972), their examination and illustration has become greatly facilitated by SEM. The radula is a ribbon situated in the buccal bulb of a gastropod; it consists of a chitinous membrane carrying rows of minute mineralized or sclerotised teeth, each measuring a few microns to several tens or even hundred microns, coming in all sorts of shapes and numbers depending on the taxon considered. Radulae provide superb taxonomical characters at family, genus, or even species level.

Not infrequently, species or genera with featureless shells that are indecisively attributable to one of several possible families can be unambiguously classified in the correct family based on their radula (e.g. *Onoba bassiana* Hedley, 1921, the type species of *Botelloides* Strand, 1928, originally described as a rissoid, and transferred to Trochidae by Ponder [1985]; *Daphnellopsis lamellosus* Schepman, 1913, originally described as a turrid, and transfered to Muricidae by Houart [1986]). Species of Triphoridae with indistinguishable shells can have strikingly different radulae, indicative not only of species-level, but also of genus-level differences. For instance, *Marshallora adversa* (Montagu, 1803) and *Similiphora similior* (Bouchet and Guillemot, 1978) have virtually indistinguishable protoconchs and teleoconchs, but very different radulae (Bouchet 1985) (Figure 6.3). When name-bearing types are empty shells, even with well-preserved protoconchs, none of these characters are available for scrutiny. This is another situation where name-bearing types fail to fulfill their taxonomical and nomenclatural function.

Finally, there is the issue of molecular characters. Historical sea-fan, insect, or crustacean types may have faded colors, broken legs or branches, yet they were alive (or at least freshly dead) at the time they were collected or preserved, and in principle their preserved or dried remains contain genetic material. Similarly, types of vertebrates often contain useable DNA in the bones and teeth, although not necessarily alive when originally collected. The DNA may be degraded and technically difficult to extract and sequence with current routine techniques (e.g., Hajibabaei et al., 2006), but the fact is that name-bearing types of octocorals, insects, or crabs do contain tissues with potentially sequenceable DNA (e.g., Berntson and France, 2001; Hylis et al., 2005; Fisher and Smith, 2008; Zhang et al., 2008). By contrast, classical molluscan types do not contain any DNA, and no technological advance will improve the situation. As molecular sequencing, especially COI, is just becoming a routine taxonomic character in marine molluscs (e.g., Kelly et al., 2007; Mikkelsen et

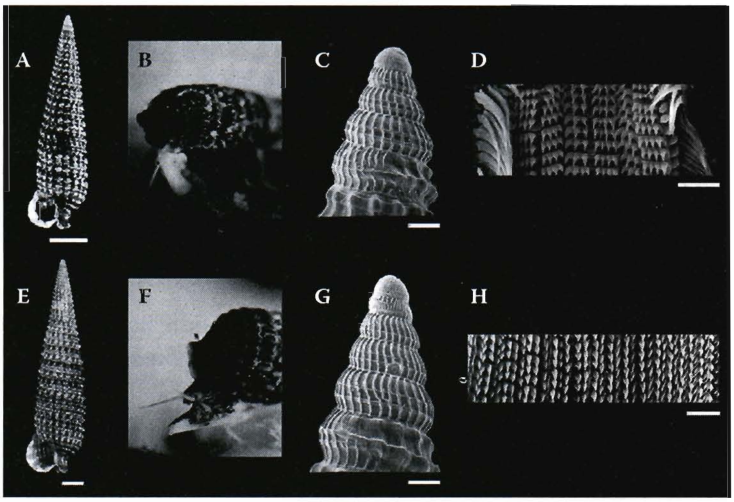

FIGURE 6.3 *Marshallora adversa* (Montagu, 1803) (A–D) and *Similiphora similior* (Bouchet and Guillemot, 1978) (E–H). Note the indistinguishable teleoconchs (A, E, scale 1 mm) and protoconchs (C, G, scale 100 µm) (the very minor differences between the two specimens are of the same magnitude and nature as differences between two conspecific specimens), but very different head–foot pigmentation and radulae (D, H, scale 10 µm). The name *Murex adversus* Montagu, 1803, was resurrected from the synonymy of *Trochus perversus* Linnaeus, 1758, and, in the absence of extant type material, a live-taken neotype was designated. *Triphora similior* was described as a new species, and a live-taken holotype was designated. After Bouchet (1985).

al., 2007; Johnson et al., 2008), we are already facing cases of barely distinguishable shells that can be recognized as distinct species only by molecular and radular characters (Kantor et al., 2008) (Figure 6.3).

Freshly collected specimens can, with some difficulty, be attributed to one of the species, based on subtle characters of the teleoconch, but older, beach-worn specimens—including name-bearing types—remain in limbo. In the example discussed by Kantor et al. (2008) (Figure 6.4), the authors stated:

> The syntypes of *Pleurotoma cingulifera* Lamarck, 1822 are badly-worn specimens that render their identification difficult. [...] Although some ambiguity persists, we apply the name *cingulifera* to the form with "semi-enrolled" marginal radular teeth. We are of the opinion that this is nomenclaturally more stable than leaving *cingulifera* as a *nomen dubium* and describing the form with "semi-enrolled" marginal radular teeth as a new species. Ideally, the current name-bearing types of *Pleurotoma cingulifera* Lamarck, 1822 and *Xenuroturris legitima* Iredale, 1929 should be replaced by live-taken neotypes with known radular and molecular characteristics. This can be done only by a decision of the International Commission on Zoological Nomenclature, but we are of the opinion that this is unnecessary as long as the systematic and nomenclatural conclusions of this paper are accepted by zoologists.

As molecular barcoding becomes routine in marine molluscan taxonomy, such cases are bound to become more and more common, and this will be yet another situation where name-bearing types fail to fulfill their nomenclature stabilizing function.

In this chapter we have focused on those situations where species are distinguishable by trivial differences in teleoconchs, but significant differences in protoconchs, radulae, living animal features, or molecular characters, a situation particularly profound among the multitudes of similar species of gastropods in the five most diverse molluscan families—Cerithiopsidae, Triphoridae, Pyramidellidae, Turridae, and Eulimidae. Some may argue that all marine molluscs do not fall into this situation, and that there are many instances of clear-cut species with highly distinct teleoconch characters. In these cases, the name-bearing types are unambiguous and hence the taxonomy is also unambiguous and uncontroversial. In such cases, the existence of types may

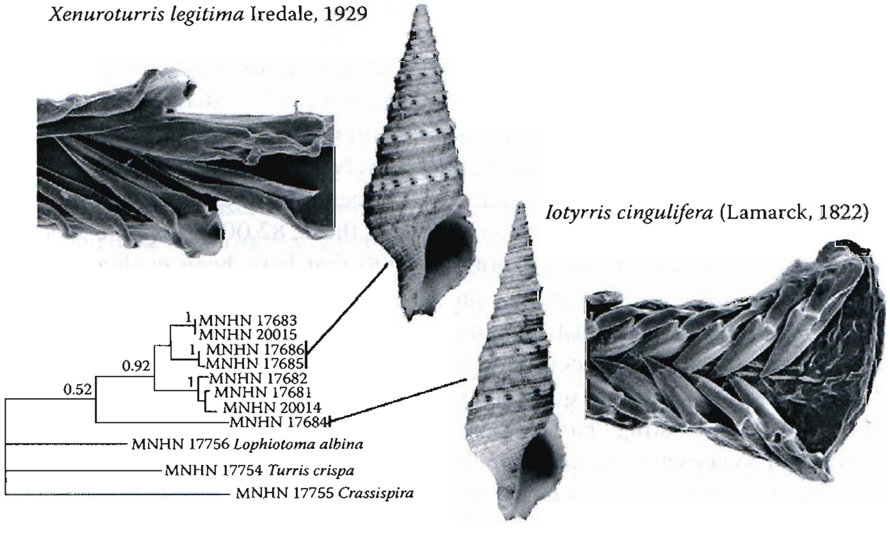

FIGURE 6.4 *Xenuroturris legitima* Iredale, 1929 (above) and *Pleurotoma cingulifera* Lamarck, 1822 [now *Iotyrris cingulifera*] (below). Closely resembling turrid species distinguished by molecular and radular characters, but with almost identical teleoconchs (the minor differences apparent between the two specimens are mainly due to size). The badly worn syntypes of *P. cingulifera* are not attributable with absolute certainty to one of the two biological species, and remain in limbo. After Kantor et al. (2008).

not be absolutely essential for the stability of nomenclature. For example, we may not need to have a name-bearing type for the dogwhelk *Nucella lapillus* (Linnaeus, 1758) as long as nobody suspects it hides a species complex. But even the iconic common cowrie *Cypraea tigris* Linnaeus, 1758 has been shown to harbor cryptic diversity based on molecular characters (Meyer, 2003), and taxonomic ambiguity of nomenclatural types may be more widespread than we currently are prepared to accept.

DOCUMENTING AND DESCRIBING THE MOLLUSCAN FAUNA OF THE WORLD

The description of marine molluscs currently continues unabatedly at the pace of roughly 350 new species per year. Not only is there no sign of leveling off, but there was, in fact, a steady increase of 68% in the naming of new marine molluscs between the 1960s and the 1990s (Bouchet 1997), and this trend is sustained. Even in European seas, where the shallow-water mollusc fauna was reputed to be completely inventoried since the beginning of the 20th century, in the late 1960s new species started again to be named and described, as a result of attention given to micromolluscs and nudibranchs. However, the main reservoirs of undescribed marine molluscs are in the tropics and the deep sea. Inspired by the work of entomologists in the canopies of tropical rainforests, recent large-scale marine expeditions are returning from the field with fantastic collections of molluscan specimens—with postlarvae, juvenile, subadult, and adult—live-taken, with digital images of living animals and clips of tissue for sequencing. Whereas "seashell" families (cowries, cones, volutes, miters, etc.) are fairly well known, with few new shallow-water species remaining to be discovered, the percentage of new species in hyper-diverse families of micromolluscs can be as high as 80–90% (Anders Warén, pers. com. cited by Bouchet et al. 2002). In deeper water, the Turridae (*s.l.*) is represented in New Caledonia alone by 1,409 morphospecies, with estimates that over 80% of these are undescribed (Alexander Sysoev, pers. com.). Preliminary examination of collections from other South Pacific island groups suggests that an estimate of 5,000, mostly undescribed, deep-water species of turrids is not beyond the realm of possibility (Bouchet et al. 2009).

A bottleneck shared by entomology and malacology is the assignment of names to the morphospecies or operational taxonomic units (OTUs) generated by such massive sampling exercises. There is justifiable concern for the broadening gap between discovering and documenting the diversity of the world and backing this exercise with sound nomenclature (Thompson 1997). Admittedly, molluscan systematics is not the only branch of zoology that suffers from the instability of names in taxonomic limbo, but with taxonomic inflation fueled by shell collecting, the magnitude of the problem is certainly unique to malacology. No one has ever evaluated the magnitude of the bank of nomenclaturally available names for Recent molluscs, but we believe that it is on the order of 300,000–500,000 species-group names; of these, 82,000 designate species currently considered valid, with an estimated 150,000–250,000 that have been evaluated as synonyms, and possibly another 100,000 in taxonomic purgatory (not evaluated, not in use, *nomina dubia*, etc.). How many are based on an existing name-bearing type in a publicly accessible institution? How many of these are based on specimens that defy modern standards as acceptable biological vouchers? Nobody knows. Without question, there is a critical need to evaluate the quality and quantity of names in the existing "name bank." Gittenberger (1993) used the expression "digging in the graveyard of synonymy" to describe the unrewarding task of confronting modern taxonomic hypotheses to nominal species currently considered invalid. We can extend the notion of a "graveyard" to encompass not only the names that are currently considered synonyms but also the taxonomic purgatory of names that have yet to be assessed. There are probably 100,000–150,000 molluscan species still to be named, and although we respect the history of our discipline and the work of our predecessors, too much is at stake in the face of a sixth extinction to waste our efforts digging in the graveyard of synonymy and matching modern live-taken specimens with ineffective name-bearing types.

DO WE NEED A MALACOLOGICAL "REVOLUTION"?

Biodiversity studies gain nothing by trying to resurrect or preserve ambiguous nominal species. Given this burden, the artisanal pace of the documentation and description of molluscan diversity can never hope to keep up with the industrial scale at which new species are discovered based on gene sequences alone. Not surprisingly, some researchers are advocating the development of name-free taxonomy for molecular OTUs (Klee et al., 2007), and molluscan systematics is effectively rooted in quicksand if (tens of) thousands of names in current use are backed by name-bearing types that do not fulfil their nomenclature stabilizing function.

In 250 years of morphology-based nomenclature, taxonomists have had time to accept that taxonomy is fallible and open to disputes and mistakes. But through reference to name-bearing types deposited in publicly accessible collections, the rules of nomenclature that have been in place since the latter half of the 19th century have permitted the correction of such mistakes and have brought remarkable stability. By contrast, much of molecular sequencing is effected by individuals who have no background in species identification, and who tend to view the historical heritage of taxonomy, including nomenclature, as a burden and a thing of the past. However, there is a growing body of literature (e.g., Vilgalys 2003) that documents the unreliability of many identifications associated with sequences deposited in public DNA databases. Before we declare traditional specimen-based nomenclature obsolete, modern sequence-based taxonomy must accept binding nomenclatural rules that guarantee stability and permit the correction of errors. The molecular systematists of today must develop a culture of vouchering specimens in long-term publicly accessible collections. Only then will there be a verifiable link between a specimen, a sequence, and a name. We praise the Data Submission Protocol for the Barcode of Life Database (BOLD), which requires vouchers and voucher information for all submissions of new molecular sequences (http://www.barcodinglife.org/docs/BOLD%20Data%20Submission.pdf), and we advocate that this should be mandatory practice in other molecular databases and for publication of research papers in molecular systematics journals.

A malacological revolution could take valuable lessons from other fields of biodiversity, namely bacteriology and botany, that have faced these challenges and already implemented solutions. In the 19th century and first half of the 20th century, bacteriologists tried to follow the provisions of the Botanical Code of Nomenclature, because bacteria had traditionally been considered fungi, the Schizomycetes. Methods of study were, however, very different. Also, much emphasis was placed on cultural characteristics, so that type cultures were of critical importance. In the 1960s and 1970s, bacteriological systematics was making fantastic progress thanks to new molecular approaches that facilitated discrimination between species and less ambiguous species definitions, while at the same time bacteriological nomenclature was being hampered by a very large percentage of published names that could not be used, due to lack of good descriptions and type cultures. A decision was then made to make a completely new start for nomenclature of bacteria on January 1, 1980. Lists were made of names that could be satisfactorily associated with known bacteria, and these formed the foundation document, the *Approved Lists of Bacterial Names* (1980). Names not on these lists lost standing in nomenclature (although provisions were made to revive old names subject to certain safeguards).

In botany, the concept of epitype (initially termed "protypus"), was proposed by Barrie et al. (1991) with words that could be applied almost without change to the situation we have described above:

> Inadequate type material is frequently encountered when working with older names. All too often the surviving original material consists of poorly preserved or poorly collected specimens, vague drawings or sketches lacking the characters crucial to precise identification. The [Botanical] Code requires that a name be typified by original material if it exists, but if the obligate element is ambiguous the resulting typification does little to promote nomenclatural stability.

This new category of type, adopted in the Tokyo Code (1994) of Botanical Nomenclature, is intended to provide the necessary diagnostic characters to unambiguously fix the identity of the primary type. The epitype does not displace the primary type it is to interpret, but rather supplements it.

Just as the *Approved Lists of Bacterial Names* laid new foundations for the modern era of prokaryote taxonomy, an ideal hypothetical "*Approved List of Molluscan Names*" would contain all 82,000 molluscan names in current use, backed by name-bearing types that can be confronted to modern morphological and molecular screening; this would necessitate the establishment of thousands of neotypes/epitypes. Such an ideal approved list would have no sympathy for wobbly nominal species backed by beach-worn empty shells.

If molluscs were birds, mammals, or frogs, such a revolution might perhaps not be completely unrealistic, but the level of scientific effort devoted to the systematics of molluscs and other invertebrates is two orders of magnitude less than that devoted to tetrapod vertebrates and one order of magnitude less than that devoted to plants (Gaston and May 1992). The vast purgatory of nominal species is undoubtedly the main reason preventing a world register of mollusc species. Most of the hyper-diverse and most taxonomically challenging molluscan families are essentially without a single expert, and there simply is not the workforce to build an approved list of molluscan names that would stand the test of time, let alone to evaluate the contents of the "name bank." Rather than being elevated by the fantastic opportunities made possible by SEM, digital photography, and the molecular revolution, it is unacceptable that species-level systematics in the most diversified marine phylum is progressing at a snail's pace because of the burden of this historical legacy.

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REFERENCES

Bandel, K., A. Nützel, and T.E. Yancey. 2002. Larval shells and shell microstructures of exceptionally well-preserved Late Carboniferous gastropods from the Buckhorn Asphalt deposit (Oklahoma). *Senckenbergiana Lethaea*, 82(2): 639–689.

Barrie, F.R., J.L. Reveal, and C.E. Jarvis. 1991. Proposals to permit the designation of a discriminating element to allow the precise interpretation of an ambiguous type. *Taxon*, 40(4): 667–668.

Berntson, E.A. and S.C. France. 2001. Generating DNA sequence information from museum collections of octocoral specimens. *Bulletin of the Biological Society of Washington,* 10: 119–129.

Boisselier-Dubayle, M.C. and S. Gofas. 1999. Genetic relationships between marine and marginal-marine populations of *Cerithium* species from the Mediterranean Sea. *Marine Biology*, 135(4): 671–682.

Bouchet, P. 1985. Les Triphoridae de Méditerranée et du proche Atlantique. *Lavori della Societa Italiana di Malacologia*, 21: 5–58.

Bouchet, P. 1989. A review of poecilogony in gastropods. *Journal of Molluscan Studies*, 55: 67–78.

Bouchet, P. 1990. Turrid genera and mode of development: The use and abuse of protoconch morphology. *Malacologia*, 32: 69–77.

Bouchet, P. 1997. Inventorying the molluscan diversity of the world: What is our rate of progress? *The Veliger*, 41(1): 1–11.

Bouchet, P. 2006. The magnitude of marine biodiversity. In: C.M. Duarte (Ed.). *The exploration of marine biodiversity. Scientific and technological challenges*. Bilbao: Fundación BBVA, 31–62.

Bouchet, P., P. Lozouet, and A. Sysoev. 2009. http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6VGC-4WF4J21-2&_user=10&_rdoc=1&_fmt=&_orig=search&_sort=d&_docanchor=&view=c&_searchStrId=1068383053&_rerunOrigin=google&_acct=C000050221&_version=1&_urlVersion=0&_userid=10&md5=4af72f07a091b62c51a3499b13da5d42. *Deep Sea Research Part II: Topical Studies in Oceanography,* 56: 1724–1731.

Dall, W.H. 1924. The value of the nuclear characters in the classification of marine gastropods. *Journal of the Washington Academy of Sciences*, 14: 177–180.

De Prins, R. 2005. Deterioration of shell collections: causes, consequence and treatment. *Gloria Maris*, 43: 1–75.

Fisher, B.L. and M.A. Smith. 2008. A revision of Malagasy species of *Anochetus* Mayr and *Odontomachus* Latreille (Hymenoptera: Formicidae). *PLoS ONE*, 3: e1787.

Frýda, J. 1999a. Higher classification of the Paleozoic gastropods inferred from their early shell ontogeny. *Journal of the Czech Geological Society*, 44: 137–153.

Gaston, K.J. and R.M. May. 1992. Taxonomy of taxonomists. *Nature*, 356: 281–282.

Geiger, D.L., B.A. Marshall, W.F. Ponder, T. Sasaki, and A. Warén. 2007. Techniques for collecting, handling, preparing, storing and examining small molluscan specimens. *Molluscan Research*, 27: 1–50.

Gittenberger, E. 1993. Digging in the graveyard of synonymy, in search of Portuguese species of *Candidula* Kobelt, 1871 (Mollusca: Gastropoda Pulmonata: Hygromiidae). *Zoologische Mededelingen*, 67: 283–293.

Hajibabaei, M., M.A. Smith, D.H. Janzen, J.J. Rodriguez, J.B. Whitfield, and P.D.N. Hebert. 2006. A minimalist barcode can identify a specimen whose DNA is degraded *Molecular Ecology Notes*, 6: 959–964.

Hoagland, K.E. and R. Robertson. 1988. An assessment of poecilogony in marine invertebrates: phenomenon or fantasy? *Biological Bulletin*, 174: 109–125.

Houart, R. 1986. Mollusca Gastropoda: Noteworthy Muricidae from the Pacific Ocean, with description of seven new species. *Mémoires du Muséum National d'Histoire Naturelle, Paris*, ser. A, 133: 427–455.

Houart, R. 2003. Description of a new muricopsine species (Gastropoda: Muricidae) from the Southwestern Indian Ocean. *Iberus*, 21(2): 91–98.

Hylis, M., J. Weiser, M. Obornik, and J. Vavra. 2005. DNA isolation from museum and type collection slides of microsporidia. *Journal of Invertebrate Pathology*, 88: 257–260.

Jablonski, D. and R. Lutz. 1980. Molluscan larval shell morphology. Ecological and paleontological applications. pp., I: Skeletal growth of aquatic organisms (D. Rhoads, R. Lutz, Eds). New York: Plenum. 323–377.

Jablonski, D. and R. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews*, 58: 21–89.

Johnson, S.B., A. Warén, and R.C. Vrijenhoek. 2008. DNA barcoding of *Lepetodrilus* limpets reveals cryptic species. *Journal of Shellfish Research*, 27: 43–51.

Kantor, Yu., N. Puillandre, and P. Bouchet. 2008. Morphological proxies for taxonomic decision in turrids (Mollusca, Neogastropoda): A test of the value of shell and radula characters using molecular data. *Zoological Science*, 25: 1156–1170.

Kelly, R.P., I.N. Sarkar, D.J. Eernisse, and R. Desalle. 2007. DNA barcoding using chitons (genus *Mopalia*). *Molecular Ecology Notes*, 7: 177–183.

Klee, B., I. Hyman, A. Wiktor, and G. Haszprunar. 2007. Cutting the Gordian knot of a taxonomic impediment. A plea for MOTU–numbers (Molecular Operational Taxonomic Units). Abstracts, World Congress Malacologia July 20–25, Antwerp, Belgium. 115.

Marshall, B.A. 1983. A revision of the Recent Triphoridae of southern Australia. *Records of the Australian Museum*, suppl. 2: 1–119.

Meyer, C.P. 2003. Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society*, 79: 401–459.

Mikkelsen, N.T., C. Schander, and E. Willassen. 2007. Local scale DNA barcoding of bivalves (Mollusca): A case study. *Zoologica Scripta*, 36: 455–463.

Ponder, W.F. 1985. A revision of the genus *Botelloides* (Mollusca: Gastropoda: Trochacea). *South Australia Department of Mines and Energy, Special Publication*, 5: 301–327.

Powell A.W.B. 1942. The New Zealand Recent and fossil Mollusca of the family Turridae. *Bulletin of the Auckland Institute and Museum*, 2: 1–188.

Reid, D. 1996. *Systematics and evolution of* Littorina. London, The Ray Society. 463 pp.

Robertson, R. 1971. Scanning electron microscopy of larval marine gastropod shells. *The Veliger* 14:1–12.

Solem, A. 1972. Malacological applications of scanning electron microscopy II. Radular structure and functioning. *The Veliger* 14, 327–336.

Strong, E.E. 2003. Refining molluscan characters: Morphology, character coding and a phylogeny of the Caenogastropoda. *Zoological Journal of the Linnean Society*, 137(4): 447–554.

Thiriot-Quiévreux, C. 1972. Microstructures de coquilles larvaires de Prosobranches au microscope électronique à balayage. *Archives de Zoologie Expérimentale et Générale*, 113: 553–564.

Thompson, F.C. 1997. Names: The keys to biodiversity. In: Reaka-Kudla, M.L., D.E. Wilson and E.O. Wilson (Eds.), *Biodiversity II*. Washington D.C.: Joseph Henry Press, 199–211.

Turton, W. H. 1932. *The marine shells of Port Alfred, S. Africa*. London: Oxford University Press. 331 pp.

Veliz, D., F.M. Winkler, and C. Guisado. 2004. Developmental and genetic evidence for the existence of three morphologically cryptic species of *Crepidula* in northern Chile. *Marine Biology*, 143(1): 131–142.

Vilgalys, R. 2003. Taxonomic misidentification in public DNA databases. *New Phytologist*, 160: 4–5.

Yoo, E.K. 1994. Early Carboniferous Gastropoda from the Tamworth Belt, New South Wales, Australia. *Records of the Australian Museum*, 46(1): 63–120, pls. 1–23.

Zhang, D.-Z., B.-P. Tang, and S.-L. Yang. 2008. Improved methods of genome DNA extraction and PCR for old crab samples including lectotype of museum. *Sichuan Journal of Zoology*, 27: 31–34.