Towards Resolving the American and West African Strombidae (Mollusca: Gastropoda: Neostromboidea) Using Integrated Taxonomy

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ABSTRACT The phylogeny of the American Strombidae the genus Lobatus is limited to the extant Lobatus raninus and several fossil precursors, the genera Macrostrombus, Aliger and Titanostrombus are re-installed as valid genera. The genus Persististrombus which was used as a sink for a plethora of species, is limited to the extant Persististrombus granulatus, fossil American species and a few Eocene to Miocene European species, which we enclose within Persististrombini nov. tribus along with Thetystrombus. Two new genera for the Miocene ancestral basal taxa of Aligerini nov. tribus, Edpetuchistrombus nov. gen. and Antestrombus nov. gen., both of which represent basal reference points enabling greater clarity in the resolution of early West African and American Strombidae radiations are proposed. This revised phylogeny informed by total evidence and historical revisions will assist in providing an evolutionary-based nomenclature that offers a structural basis for further explanation of the radiation and diversification of taxa within the Strombidae.

KEY WORDS Crown clade, East Africa, Strombidae, Edpetuchistrombus, Antestrombus, taxonomy, Western Atlantic

INTRODUCTION

Higher taxonomic classifications provide a framework for the ordering of species, and with the introduction of the PhyloCode, a revolution in the way that the nomenclature is formed is coming. This paper deals with the three forms of naming that can be applied to higher taxonomic groups and applies Bryant’s (1996) conventions for the defining of higher taxa. Bryant’s guidelines are practically applied to the resolution of the taxonomy of West African and American Strombidae. We first examined the literature and determined relational clades for this group based on molecular and internal and external morphological relationships, and then integrated these relationships in the standard type-based nomenclature. These relationships were contextualised with reference to ancestral relationships from the fossil record to formulate a theory of American Stromboid radiation. Associations between these clades were then defined using either stem or nodal definitions conforming to the principles of phylogenetic nomenclature. We also compared similarity-derived maximum-likelihood tree generated using combined histone 3 and cytochrome oxidise I data versus cytochrome oxidise I alone and found no difference in the level of taxonomic resolution achieved. We defined an anatomical character set which was much smaller through the removal of multiple
homeoplasies, this reduced character set had the same resolution as previous studies where those homeoplasies were included. Following construction of these trees, we mapped the published type-based taxonomy on the trees generated during the analyses to provide an insight into how alternative forms of evidence support current taxonomic understanding reflected in the nomenclature. All evidence from the relational clades and mapped taxa were considered, and a phylogeny explaining the internal relationships within the West African and American Strombidae was derived.

The West African and American Strombidae Rafinesque, 1815 have seen many taxa shuffled between genera as workers revise their understanding of morphological character relations. This rearranging of taxonomic relationships has led to cladistic instability and resulted in confusion in the nomenclature. This confusion is attributable to a major failing of modern taxonomic practice, in that it belies apomorphy-based definitions that define higher nomenclature, irrespective of the total evidence available (Latiolais et al. 2006; Dekkers 2008a, 2008b).

To resolve this issue and provide taxonomic clarity for the group, this review redefines the infra-familial relationships within the American and West African Strombidae Rafinesque, 1815, based on a new approach to higher taxonomic practice (Bryant 1996). In doing so, it provides a practical example of how clades are resolved and defined so as to provide a nomenclature that is stable. This stability comes with the grounding of the nomenclature in a well-resolved phylogeny and avoids the long-term problem of revisions generating paraphyletic higher taxa of older classifications (Abbott 1960, 1961; Latiolais et al. 2006).

We herein review the concept of clades and how they are formulated. We consider the rank of genus and subgenus as clades, as they form the first points where taxa are aggregated taxonomically. We argue that the currently accepted phylogeny of American and West African Strombidae is simplistic and is based on either a misunderstanding of the potential for reticulation among evolutionary units, or on the over-reach of generic inclusivity. These faults are grounded in a limited systematic approach that uses a purist biological concept of species but is morphologically defined in terms of criteria. This approach restricts the potential for a greater understanding in terms of a more taxonomically relevant nomenclature. We see no differentiation in the historical use of taxa at the levels of subgenera and genera for the purposes of clade recognition in this paper, as the names in use at these levels are often shuffled up and down cladistically. Therefore, we treat subgenera and genera as ranks, and application is governed by the zoological nomenclature codes on types and priority.

THE THEORY OF HIGHER CLASSIFICATION

Higher classification in biology has two fundamental roles: it provides a practical definition for the ordering of the reference list of species, and it provides a diagnosis that describes how that list can be derived (Benton 2000). Therefore, the role of higher classification is to elucidate the evolutionary relationships between organisms and serve to provide a tool for comparative evolutionary analyses (de Queiroz and Gauthier 1990; Benton 2000). Furthermore, the diagnosis is supplemented with a description that states the innate characteristics of the organisms that are to be included within a particular rank, enabling a high level of clarity on what is, or is not, to be
included within the erected clades (de Queiroz and Gauthier 1990).

Ranks have historically been based on a need to recognise the phenotypic variability of organisms that are included under each classification and have sought to encapsulate the innate breadth and uniqueness of the characters of the organisms included (Ereshefsky 2002). Furthermore, the problem with characters is that they create ambiguity, and this leads to problems of delineation in what is naturally a continuous process of evolutionary linkage within a phylogenetic system. Hennig (1965) argued for, but later abandoned, the idea that higher taxa need to be grounded by a taxon drawn from the particular time from which the lineage arose. Furthermore, the lack of explicit time grounding avoids arguments for the need to identify the monotypic origins of higher taxa and limits the subsequent inferred nature of nodal taxa to the organisms used in its definition (Platnick 1977). Cladistic analysis needs to find the point of equivalence at which there is maximum descriptive ability and maximum explanatory power, providing the optimal delineation of a taxon (Platnick 1986).

Rank hierarchy seeks to achieve a level of positioning of a taxon relative to another that allows the creation of a class of taxa that then forms the underlying argument for ranking and subsequent ordering of the natural system (Stevens 2002). Therefore, taxa and their ancestral relationships cannot be discerned from assigned higher Linnaean ranks, which are necessary under the restrictions of that system, as they are not grounded in the phylogeny of the organisms. Linnaean ranks serve no other purpose than to group ‘like’ organisms. The nineteenth century concepts of adaptation, in particular the ideas of Lamarck and Darwin, were yet to be formalised when Linné formulated the system of nomenclature. This lack of theoretical importance given to the asymmetry of ranks under the Linnaean system of nomenclature has led to the lack of evolutionary justification in tree topology and nomenclature, resulting in the assignment of higher taxa within the nomenclature that provide no insights as to the evolution of the organisms that are being classified. Therefore, there is a need for a complete restructure of the higher nomenclature (de Queiroz and Gauthier 1990, 1992, 1994; de Queiroz 1996). That is, under the Linnaean system of nomenclature, when a genus is compared to other genera, there is an implicit equality in rank, which in terms of an evolutionary grounded phylogeny, may not actually be equal.

In contrast to Linnaean nomenclature, phylogenetic nomenclature is designed to show relationships based upon a historically or evolutionary generated phylogeny. This hierarchical approach to the ordering of nature creates taxon-bearing reference points that then form the basis for relative comparisons, without any implications for the existence of ranks (Stevens 2002). Brochu and Samrall (2001) emphasize the benefit of explicitness and that universal meaning needs an explicit taxonomic name definition. That is, under phylogenetic nomenclature, name-bearing reference-points are used in formal definitions that are restricted by a diagnosis, thus enabling stable internal tree reconstruction (Schander 1998). This is in contrast to Linnaean nomenclature, where the assignment of taxa is singularly explicit in all definitions lacking relational explanations, thus giving rise to inherent paraphyletic problems. In contrast, phylogenetic nomenclature is fundamentally implicit. Instability in definition as a result of implicit description where relationships are given priority is only found if the definition fails to fulfil all the requirements needed to satisfy that formal definition (Benton 2000).
The use of structured or formulaic styled definitions for cladistic relationships brings clarity to the relationship between name and taxon in taxonomic definitions (Benton 2000). Much of the opposition to the acceptance of phylogenetic nomenclature is related to the misconception that it causes a loss of taxonomic freedom to deviate taxa outside the definitional framework (Lidén and Oxelman 1996; Lidén et al. 1997; Bryant and Cantino 2002). The disruption to the use of the nomenclature in the real world that may occur with the adoption of a phylogenetic rank-free system and the subsequent changes in nomenclature that result from different approaches to the construction of phylogenies, can be minimized if the existing type-based taxa has priority in determining the named regions of inclusivity. The use of types can avoid such instability by providing stable markers for defining the limits of inclusivity (Blackwell 2002).

Recent works that apply phylogenetic nomenclature to biological revisions have demonstrated that streamlined transitions from traditional Linnaean nomenclature to relationship-based phylogenetic nomenclature can be achieved (Cantino et al. 1997; Pleijel 1999; Härлин and Härリン 2001). In order to avoid ambiguity in the definition of a clade there needs to be accuracy in the wording of the definition, avoidance of reference inspecificity, and provision of phylogenetic definitions of included taxa (Bryant 1996).

**Practical Definitions in Higher Taxonomy**

With the soon to be introduced PhyloCode set to revolutionize the way in which definitions are used in taxonomy, a review of the principles that govern the defining of clades needs to be explored. There are three ways a clade can be defined in higher taxa: first, node-based, where the most common ancestor of two terminals or clades and all their descendants are included; second, stem-based, where all taxa more closely related to an organism than to another are included; and third, apomorphy-based, where all taxa that share particular unique characters are included (de Queiroz and Gauthier 1990, 1992, 1994; Bryant 1994; de Queiroz 1996; Sereno 1999; Benton 2000; Bryant and Cantino 2002).

The node-based structural definition is defined in terms of the point of delineation of two or more taxa from a common ancestor (de Queiroz and Gauthier, 1992; Sereno 1999). Any node-based definition must use taxa that are least inclusive and well nested within the clade to avoid relocation and internal inconsistency resulting in the creation of impossible clades (de Queiroz and Gauthier 1990; Schander and Thollesson 1995; Sereno 1999; Bryant and Cantino 2002). The use of names of multiple subordinate taxa in the node-based definition is only an issue in terms of stability if the taxa used in the definition are poorly supported (Sereno 1999; Bryant and Cantino 2002). All taxa that are basal need not be included. However, the definition needs to comprise enough basal taxa to avoid a more reduced inclusive clade than was originally intended. This use of designated phylogenetic context (Bryant and Cantino 2002), is a means of maximizing stability within a node-based definition. Cantino et al. (1997) outlined recommendations in the definition in order to maximize stability. First, there must be a level of ‘substantial evidence’. Without this, there would be confusion through proliferation of phylogenetic synonyms. Second, a taxon whose membership is questionable should be avoided. Third, Sereno (1999) argued that the numbers of inclusive taxa used in the definition is dependent upon whether the clade content is well supported and nested. The use of well-supported and nested taxa will increase the
clade stability even as taxa are internally redistributed.

The stem-based structure for naming clades is based on the closer relationship between an ancestral taxon and its descendants than to more distant taxa (de Queiroz and Gauthier 1992; Sereno 1999). The stem-based definition in phylogenetic nomenclature is suited to revisions that have a lack of prior tree resolution (de Queiroz and Gauthier 1990; Sereno 1999; Bryant and Cantino 2002). The use of stem-based nomenclature also allows future division of all levels of taxa, and free movement within, or out of, a particular clade, which in turn eliminates the restrictions that the assignment of apomorphy and node-based definitions create. Dyke (2002) suggested that the movement of taxon would cause greater inclusion than the definition intended if the taxon that is used in the definition is involved in the movement. However, in his example of theropod dinosaurs, the principle concerns were of synonymic duplication as resolution increases. This is an issue for stem-based definitions only if ‘proper’ formulation of the principle definition from the start is lacking. Therefore, Dyke (2002) failed to recognise stability and unambiguous interpretation as having priority. It is only when priority is given to stability and clarity that the problem of proliferation of unnecessary definitions can be overcome, a concern of those who would oppose phylogenetic stem-based definitions (Dyke 2002). The stem-based definition grants higher significance to terminals, avoids ranking into unnecessary Linnaean categories, gives priority to clades, irrespective of characters and the need for inclusiveness, and is determined principally by historical phylogeny (Härlin 1999).

The apomorphy-based definition of a clade is based on the synapomorphy of the first ancestor in which it arose and includes all its descendants (Sereno 1999; de Queiroz and Gauthier 1992). The use of apomorphy-based definitions in phylogenetic nomenclature is a major area of contention (Bryant 1994; Schander and Thollesson 1995; Pleijel 1999; Sereno 1999; Bryant and Cantino 2002). The apomorphy-based structure seeks to directly tie the actual empirical evidence to the recognition of taxa (Pleijel 1999). However, it is a fundamental concept to the study of taxonomic biology, with the focus on historicity rather than morphology that makes apomorphy-based definitions principally non-evolutionary (de Queiroz and Gauthier 1992). Bryant (1994) argued for the avoidance of apomorphy-based definitions. The restriction that this definition imposes upon the tree structure, and patterns that are absent in node and stem-based definitions, is the major fallibility in this descriptive approach. Apomorphy-based definitions are fundamentally flawed because they rely on homoplasy to allow cladistic discernment, with the actions of evolutionary processes that cause the loss of primary apomorphs, and levels of continued congruence with other apomorphs of near taxon. While Bryant and Cantino (2002) rightly point out that apomorphs do have a role in phylogenetic nomenclature, their use should be incorporated into either node or stem-based definitions as a means to give added stability.

**BRYANT AND CROWN CLADE DEFINITIONS**

A crown taxon differs from other taxa formulations by its definition being restricted to living taxa that have an immediate extinct outgroup (Sereno 1999). While it is possible to describe a crown taxon or clade with a stem-based definition, the inadvertent use of a node-based definition is the form most widely encountered within the nomenclature (de Queiroz and Gauthier 1992; Rowe and Gauthier 1992; Wyss and Meng 1996). The use of crown
clades is common in much of the taxonomy, but this does not necessarily improve taxonomic clarity or stability unless it is accompanied by a structured definition (Lee 1996). The aim must be for the taxonomist to obtain maximum stability, and the definition of a crown clade must be determined by the state of resolution of the basal dichotomy (Sereno 1999). The use of a crown clade as a mode of definition does not preclude the recognition of ancestral taxa within it, only that these taxa are not used in the formulation of the definition. Bryant (1996) argued for eight conventions that facilitate effective phylogenetic taxonomic definitions of clades:

1. **Phylogenetic definitions should name clades identified through phylogenetic analysis.**

There needs to be an explicit phylogenetic context and pattern to the naming of a clade (de Queiroz 1994). Clades need to have a basis in evolutionary fact that supports their erection. It is unnecessary to generate ranks within a hierarchy that are “space fillers” and do not contribute to the evolutionary contextualisation of the nomenclature.

2. **Phylogenetic definitions should have standardised formats.**

There needs to be a standardised format in the naming of taxa. The use of a stem or node-based definition is the individual concern for the taxonomist and is dependent on the level of resolution of the clade under consideration (Sereno 1999). A clade that has a high level of internal resolution is more suited to the node-based definition, and is independent of outgroup relations, compared to a clade that has a low level of internal resolution, which is more suited to a stem-based definition.

3. **Typification of taxa is an optional heuristic device for standardising hierarchical relationships among clades with particular taxon names.**

It is not necessary to include a terminal taxon in the definition at every level of the hierarchy, with higher order taxonomic ranks being sufficient if inclusivity is codified (Cantino et al. 1997). While the use of types is redundant in phylogenetic taxonomy, as the diagnosis fulfils the role of grounding the rank in the real world, types may assist with the standardising of hierarchical relationships and in defining the most inclusive taxa (de Queiroz and Gauthier 1992; Sundberg and Pleijel 1994; Bryant 1996). Bryant (1994) argued that, for a definition to achieve accuracy, there needs to be an explicit reference to a single common ancestor in the wording. Bryant (1994) also argued that providing an ancestral basis upon which a clade is grounded needs to be with the inclusion of “most recent”, which has significant implications for the clad structure that is chosen. A clade with a poorly resolved basal relationship is best defined by a stem-based definition because the reference upon which it is founded is based on outgroups, which by definition implicitly creates the ancient ancestor. Another ambiguity in wording is created when the definition of a crown clade is dependent on the current non-extinction of members, where future extinctions would change the clade definition (Lucas 1992). This problem can be avoided if the terms ‘extant’ and ‘living’ are not used in the definition (Bryant 1994, 1996). This allows evolution of the definition and retains stability in meaning while losing extant taxa to extinction. Tautology also causes a level of ambiguity in the wording of cladistic definitions (Bryant 1996).
4. Emendation of phylogenetic definitions is necessary in particular instances but should preserve the association between taxon names and clades.

The need for emendation of cladistic names is often required when there is confusion in the wording of the definition and where there is a lack of clarity in meaning, or appropriateness of the taxa that are included (Bryant 1996). This is particularly relevant as the suffixes used under the codes for nomenclature that are attached to a name may not truly reflect the organizational position when contextualized with evolutionary evidence. There are no ICZN rules governing the use of prefixes, but the inclusion of “Neo+ type taxon” is advantageous to the recognition that a crown clade has been defined. This was the basis for the erection of Neostrombioidae: Prefix + type genus + suffix: Neo + Stromb + oidae for the epifamily rank.

5. Crown clades should have “widely known taxon names”.

Where possible, existing taxonomic crown clade names should be retained in order to maintain stability. The current state of taxonomy often reflects the underlying phylogenetic understanding, albeit tied to ranks that obscure this. Therefore, a revision may involve a review and possible rejection of rules of priority in the ordering of ranks in nomenclature to save this taxonomy (Rowe 1998; de Queiroz and Gauthier 1992; Anderson 2002). This can be achieved if names are crown clades (Bryant 1996). The issue of implied ranking based on the Linnaean suffix means that the suffix should be amended to reflect the nature of the definition (convention 8 vide infra). Cantino et al. (1997) argued that current suffixes utilised by existing taxonomy could be maintained to avoid unnecessary changes and make the shift to a phylogenetic system more acceptable. In addition, taxonomists familiar with a particular taxon would still be able to recognize the cladistic group that is implied, irrespective of the suffix.

6. Given several “widely known taxon names” that could be used for a crown clade, the one at the lowest rank in the Linnaean hierarchy should often be chosen.

If more than one name is available within the Linnaean hierarchical system, then the lowest rank should be applied. This would leave the higher ranks available for use for more inclusive clades (Bryant 1996).

7. Stem-based taxon names could be formed from the name of the appropriate less inclusive node-based taxon and an appropriate suffix.

The use of a suffix should be used to indicate whether the definition is based on the node, apomorph, or stem structure. De Queiroz and Gauthier (1992) suggested -gens or -genea, and Bryant (1996) suggested -morpha or -formia. However, recent revisions make the use of these suffixes somewhat problematic due to an inconsistent application to one level of rank as internal clade structures change (Bryant 1996). Furthermore, the conflagration of stem and node names, with shifts in stem structure, may obscure the evolutionary meaning that each different approach to formulating a definition brings. In the present paper, stems are formulated in order of nomenclatural position under the ICZN (1999).

8. Taxon names should have recommended usages.

Bryant (1996) argues that there may be a limitation of the use of names to particular contexts, and this may reflect the level of
meaning intended at the time by the taxonomist formulating the definition. That is, there may be a need to restrict the inclusivity of a definition as the understanding of the phylogeny expands and more taxa are brought into a particular cladogram.

**TARGET TAXA AND THEIR HISTORICAL GENERIC AFFILIATIONS**

We examined the taxonomy attributed to extant Strombidae Rafinesque, 1815 on the West African coast and in the Americas, and explored how the nomenclature of the subfamilies, genera, subgenera of those taxa reflects and explains the current evolutionary understanding of the relationships between those taxa. We used fossil taxa to define basal clades and to provide markers for understanding Atlantic radiations.

A list of all extant American and West African Strombidae Rafinesque, 1815 currently in general use was formulated. Each taxon was revised in order of date of description using first principles. From this list of species, their current cladistic checklist of taxa and their cladistic position was confirmed by literature review to enable a basic framework upon which to commence the revision (Table 1). Where necessary the taxonomic list was updated as the revision and higher taxonomic relationships identified were resolved and defined. All amended taxonomic positions were applied retrospectively throughout. This enabled the discussions throughout to reflect the current taxonomy and to avoid nomenclatural confusion within the text, particularly with taxa that have been moved repeatedly between genera. The checklist, therefore, represents the currently accepted living species and their generic placement (Table 1). We focused on supra-specific ranks, hence forms and subspecies were omitted. An overview of the taxonomic ranks from subfamily to genera is presented as the systematic part of this paper.

There is a significant level of taxonomic inflation in the supra-species nomenclature. In particular, this has involved the elevation of subgenera to genera, and the displacing of the unifying genus *Strombus* Linné, 1758. We do not deal with the arguments for or against the position of infra-subtribal ranks. Rather, we treated them all based on definitional form, and they were discussed and applied appropriately and equally without rank bias. The genus and subgenus are the basal ranks, defined as the first aggregative rank in systematics.

**CURRENT TAXONOMIC RELATIONSHIPS**

There have been four major systematic revisions on the nature of stromboids after Abbott (1960, 1961). Latiolais *et al.* (2006) based their work on a mix of morphology and genetics. However, the sample used was small and not representative of the diversity across the strombid complex. Simone (2005) utilized anatomical information. However, only American and Caribbean taxa were studied. Bandel (2007) and Dekkers (2008a, 2008b) used morphology, fossil and geographical relationships, and Dekkers (2008a, 2008b) based much of his revision on the phylogeny generated by Latiolais *et al.* (2006). When these four approaches are compared, some well-defined clades are clear overall, which enable the contextualization of more focused monographs and papers within the broader clade structure (Figure 4). There have been a number of other smaller targeted monographs and papers that have contributed to understanding aspects of the cladistic relationships between West African and American taxa, and these fall into two groups: those grounded in a phenetic approach (Clench and Abbott 1941; Abbott
1960); and those that use morphology and some form of spatiotemporal evidence (Petuch 1994).

Latiolais et al. (2006) and Simone (2005) determined *Strombus* Linné, 1758 to contain *Strombus pugilis* Linné, 1758, *Strombus alatus* Gmelin, 1791 and *Strombus gracilior* Sowerby, 1825. Bandel (2007) combined *Strombus pugilis* Linné, 1758 with another species, *Macrostrombus costatus* (Gmelin, 1791) into the clade *Strombella* Schlüter, 1838. However, the inclusion of *Macrostrombus costatus* (Gmelin, 1791) within *Strombella* Schlüter, 1838 is problematic as it is contrary to the phylogenies presented by Simone (2005) or Latiolais et al. (2006) that hold for independent linages. Clench and Abbott (1941) lumped all the Caribbean taxa within the clade *Strombus* Linné, 1758, a classification that fails to offer an explanatory reflection of the taxonomy in the nomenclature, which is a reflection on the taxonomic thinking of that time.

Latiolais et al. (2006) singled out *Strombus* (s.l.) *granulatus* (Swainson, 1822) and placed it in *Lentigo* Jousseaume, 1886. In contrast, Bandel (2007) and Dekkers (2008a) placed this taxon within *Persististrombus* Kronenberg and Lee, 2007. Similarly, *Thetystrombus latus* (Gmelin, 1791) has been shuffled with the family phylogeny during revisions, having been included in both *Lentigo* Jousseaume, 1886 (Abbott 1960) and *Persististrombus* Kronenberg and Lee, 2007 (Harzhauser and Kronenberg 2013). With the description of *Thetystrombus* Dekkers, 2008, the evolutionary understanding of the Strombidae Rafinesque, 1815 was enhanced through the provision of a West African focal point on which to base radiation theory.

The use of this name is systematically problematic and reflects the broad lumping of species under the revisions of Abbott (1960). The genus *Tricornis* Jousseaume, 1886 (type – *Strombus tricornis* Lightfoot, 1786) currently contains two species (Bandel 2007; Dekkers 2008a), namely: *Tricornis tricornis* (Lightfoot, 1786) and *Tricornis oldi* (Emerson, 1965), considered restricted to the Indo-Pacific region (Bandel 2007).

Bandel (2007) was not so conservative in dividing up the West African-American complex, erecting three subgenera of *Strombus*: *Strombella* Schlüter, 1838 (type – *Strombus pugilis* Linné, 1758) *Mondactylus* Klein, 1753 (Type – *Strombus gallus* Linné, 1758) and *Eustrombus* Wenz, 1939 (sic = 1940) (Type – *Strombus gigas* Linné, 1758). The American stromboid taxonomy of Bandel (2007) is problematic because it does not reflect upon the cytochrome oxidase I (COI), or anatomically derived phylogenies (Latiolais et al. 2006; Simone 2005), which were already available, nor was it supported by Dekkers (2008a, 2008b). The use of *Aliger* Thiele, 1929 (Type – *Strombus gallus* Linné, 1758) over its junior synonym *Eustrombus* Wenz, 1940 (Type – *Strombus gigas* Linné, 1758) is correctly reflected in other revisions (Bandel 2007, Simone 2005). The use of *Lobatus* Iredale, 1921 for some members of the *Aliger* Thiele, 1929 shows a lack of understanding of the original definition of *Lobatus* Iredale, 1921 and its sister genera (Dekkers 2008b).

It is clear that the ongoing shifting of internal cladistic relationships in this complex is largely justified by the use of only a single form of evidence. The names that are applied to these clades vary, and this reflects the opinion of each taxonomist, and their understanding of what is the internal relationship, which can compound and cement taxonomic errors. These revisions
are also greatly influenced by the current state of taxonomy in the general literature, which is often grounded on smaller revisions that can overreach with the purported understanding of wider internal infra-familial relationships.

**METHODOLOGY FOR DISCERNING PHYLOGENY**

Pure cladistics searches are the most parsimonious hierarchical arrangements based on character scoring of terminal taxa that do not include evolutionary considerations, nor the geographical distribution of the characters used (Davis and Nixon 1992). Thus, cladistical hierarchy is purely an epistemological axiom that is without an explanatory causal hypothesis (Brower 2000). In contrast, phylogenetics is a form of cladistics that seeks to reconstruct relationships that are dependent on the distribution of characters (Davis and Nixon 1992). In order to achieve this, species must be treated as separate terminals (Yeates 1995). In creating terminals, the taxonomist is then able to either intuitively deduce ground plan character states of the higher clades, or choose exemplars that represent real species, both of which have the same goal of providing the basis for coding (Yeates 1995). The discovery of islands of individuals within multiple most parsimonious trees enables the determination of these exemplars (Maddison 1991). Definitions should only be applied to clades after considered analysis and a sound basis for need has been established, particularly with reference to the delineation of islands out of greater diverse organism character set (Brochu and Samrall 2001). This need is systematically subjective and may be argued on a basis of phylogenetic support, phenotypic distinctiveness, ecological significance, economic importance or some other argument made by the taxonomist (Forey 2002). However, it is a phylogenetic principle that the formation of the definition of higher taxa has stability and that there is unambiguous interpretation of what taxa are to be included and excluded. That is, uses of the name in association with a particular key stone taxon, represented by a type, must have priority (de Queiroz and Gauthier 1990).

Two forms of evidence were used to generate phylogenies for West African and American Strombiidae. The cytochrome oxidise I (COI) mitochondrial subunit evidence comprised the first data set derived from Latiolais et al. (2006). Anatomical character states form Simone (2005) formed a second set of data. The results of this analysis were examined within the context of Bandel’s (2007) and Dekkers’ (2008a, 2008b) hypothetical relationships.

*Molecular Information*

We revisited molecular data and generated new phylogenies to confirm hypothetical relationships postulated in Latiolais et al. (2006). Eleven COI sequences were obtained from GenBank: DQ52522 Strombus gigas Linné, 1758 (= Eustrombus gigas (Linné, 1758)) (Latiolais et al. 2006); DQ52523 Strombus granulatus Swainson, 1822 (= Persististrombus granulatus (Swainson, 1822)) (Latiolais et al. 2006); DQ52524 Strombus latus Gmelin, 1791 (=Thetystrombus latus (Gmelin, 1791)) (Latiolais et al. 2006); DQ52527 Strombus peruvianus Swainson, 1823 (= Lobatus peruvianus (Swainson, 1823)) (Latiolais et al. 2006); DQ52526 Strombus raninus Gmelin, 1791 (= Lobatus raninus (Gmelin, 1791)) (Latiolais et al. 2006); DQ52525 Strombus costatus Gmelin, 1791 (= Macrostrombus costatus (Gmelin, 1791)) (Latiolais et al. 2006); DQ52521 Strombus gallus Linné, 1758 (= Aliger gallus (Linné, 1758)) (Latiolais et al. 2006); DQ52520 Strombus galeatus Swainson, 1823 (= Titanostrombus galeatus (Swainson, 1823)) (Latiolais et al. 2006); DQ52520

The species database was generated through this analysis, which included the following key species:

- **Strombus gigas**: Common name: Giant Strombus. Known distribution: West African and American Strombiidae. COI GenBank accession: DQ52522
- **Strombus latus**: Common name: African Giant Strombus. COI GenBank accession: DQ52524
- **Strombus peruvianus**: Common name: Peruvian Strombus. COI GenBank accession: DQ52527
- **Strombus gallus**: Common name: Aliger Strombus. COI GenBank accession: DQ52521

These species were selected for their ecological relevance and distribution, providing a comprehensive understanding of the phylogenetic relationships within the Strombiidae family.
Molecular data were entered into MEGA X (Kumaer et al. 2018; Saitou and Nei 1987; Rzhetsky and Nei 1992). All trees generated were tested using 50 bootstrap replicates, the level of bootstrapping reflects the data matrix size and lack of gaps in alignment. Where multiple trees were generated, only the consensus tree is presented unless any divergence indicated a significant cladistic anomaly from another tree. Two forms of analysis were undertaken: Maximum Likelihood evolutionary history was inferred based on the Jukes-Cantor model (Jukes and Cantor 1969) and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA; Sneath and Sokal, 1973), with the base assumption of a uniform rate of evolution under the Jukes-Cantor model (Nei and Kumar 2000). The ability to choose the evolutionary model overcomes many of the black box issues associated with earlier models of the MEGA software.

**Anatomical Information**

Simone (2005) provided a seminal overview of the anatomy of American Strombidae Rafinesque, 1815, and the anatomical characters for eight taxa were derived from that work and used in this review: *Aliger costatus* (Gmelin, 1791) (= *Macrostrombus costatus* (Gmelin, 1791)); *Aliger galius* (Linné, 1758); *Aliger gigas* (Linné, 1758); *Eustrombus goliath* (Schröter, 1805) (= *Titanostrombus goliath* (Schröter, 1805)); *Strombus alatus* Gmelin, 1791; *Strombus gracilior* Sowerby, 1825; *Strombus pugilis* Linné, 1758; and *Tricornis raninus* (Gmelin, 1791) (= *Lobatus raninus* (Gmelin, 1791)). Fourteen characters were utilized and coded for, and these represented differences in the anatomy of the reproductive system, buccal structure, kidneys, mantle and the organs within the cavity formed by it, and body dorsal surface textures (Table 2). Analyses of anatomical characters coded for were conducted in MEGA X (Kumaer et al. 2018). Trees were generated using Maximum Likelihood with a neutral evolutionary model. Character states were transcribed and coded (1 = A, 2 = G, 3 = C, 4 = T) to represent states. Maximum Likelihood evolutionary history was inferred based on the Jukes-Cantor model (Jukes and Cantor 1969). All trees generated were tested using 50 bootstrap replications, which is reflective of the data matrix size. This novel approach of using software developed for molecular analysis for character states was tested using anatomical characters against known trees that were generated with traditional software and using the same character sets and indicates no difference in internal relationships (Simone 2005).

**RESULTS**

**Molecular Analyses**

The maximum likelihood analysis of the COI data produced one tree with log likelihood of -3152.21 (Figure 2B). The tree generated during this retesting conformed completely to Latiolais et al.’s (2006) COI and H3 combined maximum likelihood gene tree (Figure 1A). The UMPGA analysis resulted in a COI gene consensus tree similar in overall branch structure and internal resolution presented by Latiolais et al.’s (2006) COI and Histone 3 (H3) combined maximum likelihood gene tree (Figure 2A). However, there were some differences between the two
trees. First the positioning of Lentigo Jousseaume, 1886 (= Persististrombus Kronenberg and Lee, 2007; = Thetystrombus Dekkers, 2008) was paraphyletic in Latiolais et al. (2006) but is presented as the sister taxon to Persististrombus Kronenberg and Lee, 2007 and Thetystrombus Dekkers, 2008 in this analysis. Another difference is the treatment of the internal content of the Latiolais et al. (2006) clade Tricornis Jousseaume, 1886 which is currently restricted to the extant Indo-Pacific. The position of Titanostrombus Petuch, 1994 in relation to its sister taxon remains unclear, and its position within the phylogeny is dependent on the phylogenetic methodology used (Figure 2A, B). However, results indicate a sister taxa relationship between Macrostrombus Petuch, 1994, Aliger Thiele, 1929 and Titanostrombus Petuch, 1994.

Anatomical Analysis

There was no difference between the tree generated using anatomical data analysed with Mega X and that illustrated by Simone (2005) generated using more conventional cladistic programmes (cf. Figure 1B and 2C). The anatomical maximum likelihood analysis produced one tree with log likelihood of -84.77. Cladistic analysis of the anatomical evidence indicated two distinct clades. The first contained Strombus Linné, 1758 and this formed Simone’s (2005) unidentified clade 15. The second clade, clade 16 in Simone (2005), is more complex and is represented by the Aligerina nov. subtribus, and is divided between: 1) Macrostrombus Petuch, 1994, Lobatus Iredale, 1921, and Aliger Thiele, 1929 which Simone (2005) identified as clade 18; and 2) the Simone (2005) clade 17 containing both Titanostrombus Petuch, 1994 and Aliger Thiele, 1929.

OVERVIEW OF SYSTEMATICS

Historically, the Western Atlantic and Eastern Pacific (Panamic) stromboid species, including Thetystrombus latus Gmelin, 1791 from West Africa were considered monophyletic and derived from a single radiation event (Clench and Abbott 1941; Kronenberg and Vermeij 2002). Kronenberg and Lee (2007) proposed several theories to explain radiation of American stromboids. The first accepted theory is premised on the Persististrombus Kronenberg and Lee, 2007 arriving in one or two waves: one resulting in Strombus Linné, 1758 and the other accounting for all the remaining stromboids species (Kronenberg and Lee 2007). The second theory, while rejected by Kronenberg and Lee (2007), is premised on a common ancestry derived out of Dilatilabrum Cossmann, 1904 from the Lutetian (Middle Eocene) of Italy based on the widely extended outer lip. Purportedly, the line terminated with the Oligocene Dilatilabrum roegli Harzhauser, 2001. However, the placement of this taxon within Dilatilabrum Cossmann, 1904 needs review. The third theory also rejected by Kronenberg and Lee (2007) is grounded in Beneventi and Piccoli (1969) and Sacco (1893), where a relationship exists between American and European stromboids through the Strombus (s.l) coronatus (Defrance, 1827) complex, which is the possible ancestor of Thetystrombus Dekkers, 2008. We reject all these hypotheses and argue that the radiation occurred twice at different times and from different lineages.

Furthermore, this paper addressed both the irregularities in American stromboid taxonomy. This was achieved through the use of total evidence, which brings previous revisions that used different methodological approaches together, to generate a phylogeny that illustrates the relationships between extant members of the Strombidae (Figure 3). Two clades that were
resolved here have not been identified previously, and we suggest that these represent the possible independent ancestral incursions into the Americas: Aligerini nov. tribus and Persististrombini nov. tribus. The Persististrombini nov. tribus includes two clades at the generic level, Thetystrombus Dekkers, 2008 and Persististrombus Kronenberg and Lee, 2007. Thetystrombus Dekkers, 2008 is postulated to have arisen out of a common ancestor shared with Persististrombus Kronenberg and Lee, 2007 (Dekkers 2008a; Harzhauser and Kronenberg 2013). This occurred during the upper Paleogene. Furthermore, the varying placement of these two clades in relation to other taxa indicates they have different evolutionary trajectories. The limitation on inclusivity within this paper makes drawing conclusions on the basal relationships between these clades problematic. This is because there is no ancestral context relative to the wider familial group outside of the defined taxa. However, the fossil records indicate a divergence between the Persististrombini nov. tribus and the Aligerini nov. tribus occurring within the upper Paleogene (Dall 1890; Petuch 2004).

Based on the distribution of the fossil records, the remaining American Strombidae Rafinesque, 1815 are not all related to Persististrombus granulatus Swainson, 1822, but fall into the natural clade Aligerini nov. tribus. Given that there is no definitively resolved outgroup to provide ancestral grounding within this study, the most appropriate definition is nodal in form. Aligerina nov. subtribus forms a monophyletic, enclosed and definable clade that is robustly divided into two sub-clades namely the stem clade Strombus Linné, 1758; and the nodal clade containing Aligerina nov. subtribus. These two clades represent robust clades that have evolved defining anatomical and morphological characters that enable clear delineation. However, both share a pre-Miocene common ancestry, and we hypothesize that both are derived from a single and independent colonising event giving rise first to Edpetuchistrombus nov. gen. and then Antestrombus nov. gen. in the early Miocene of Florida.

The erection of Aligerina nov. subtribus represents the point of a common ancestry between Edpetuchistrombus nov. gen. and Antestrombus nov. gen.. The fossil record indicates however, that there has been a long period of divergence between these two taxa (Petuch 1994). Lobatus Iredale, 1921 and its Aligerina nov. subtribus sister crown clade share some unifying morphological characteristics, such as the tendency for distinctive uniform ribbing dorsally, the somewhat flaring lip, and the lack of sculpture within the aperture. The extant remaining members of these groups are represented by a limited number of taxa. However, each represents a greater number of fossil taxa, such that the extant taxa represent only the tip of an historical extinction iceberg. Nomenclatural significance of these taxa should not be governed only on criteria that seeks to avoid monotypicity in extant taxa. The reduction of higher taxonomic relationships based, in part, on hybridization fails to understand that successful mating can occur between genetically dissimilar organisms (Soltis and Soltis 2009). This taxonomic collapse limits the ability to construct a phylogeny that assists in explaining evolutionary theory.

The clade Strombus Linné, 1758 is well resolved out of the more inclusive Strombidae Rafinesque, 1815, with a diverse and rich fossil history arising out of the Miocene Lower Gatun Edpetuchistrombus aldrichi (Dall, 1890) complex. Practically, there is no explanatory advantage in erecting the subtribe to include
only *Strombus* Linné, 1758 as the definition of the clades is evolutionarily explicit and can be compared with taxa at any level.

*Edpetuchistrombus nov. gen.* is erected to encapsulate the lower Miocene Chipola River taxa that are directly related to *Edpetuchistrombus aldrichi* (Dall, 1890) that arrived between the Oligocene to very Early Miocene from Europe. *Strombus (s.l) lioclyclus* Dall, 1915, a very rare species from the Tampa Silex beds, Florida, most likely of Late Oligocene beds, is also one of the early intruders, and its placement is uncertain.

The extant *Strombus* Linné, 1758 have generally smooth body whorls except for the sometimes-strong knobs (or even spine-like knobs) and some axial growth lines. There is a general difference in form between *Edpetuchistrombus nov. gen.*, which tends towards being ovate, and the bicone form of *Antestrombus nov. gen.*. *Antestrombus nov. gen.* is herein erected to encapsulate the lower Miocene (Burdigalien) Chipola River species related to *Antestrombus chipolanus* (Dall, 1890) and *Antestrombus mardieae* (Petuch, 2004). With the erection of *Edpetuchistrombus nov. gen.* and *Antestrombus nov. gen.*, we hypothesise that the Miocene *Edpetuchistrombus aldrichi* (Dall, 1890) and *Antestrombus chipolanus* (Dall, 1890) complexes represent the split and transition towards *Aligerina nov. subtribus* and *Strombus* Linné, 1758. Notwithstanding, this paper argues that there were two waves, the first bringing the *Persististrombini nov. tribus* and the second wave bringing the *Tersusini nov. tribus*.

The clade *Pyramis* Röding, 1798 (Type *Strombus lucifer* Linné, 1758 = *Strombus gigas* Linné, 1758) is herein not considered taxonomically sound. The internal content of the clade indicates that Röding (1798) may have intended this to contain juveniles of many families, that prior to reaching terminal growth, have remarkable growth similarity in shape and lip structure, and not to describe the Strombidae Rafinesque, 1815 members that are clearly placed in *Lambis* Röding, 1798.

The use of types to define basal taxa avoids paraphyletic genera as they are independent terminals of the tree. As a result of the internal resolution of the phylogeny of the American Strombidae, the genus *Lobatus* Swainson, 1837 is limited to the extant *Lobatus raninus* (Gmelin, 1791) and several fossil precursors. The genera *Macrostrombus* Wenz, 1940, *Aliger Thiele*, 1929 and *Titanostrombus* Petuch, 1994 are reinstated as valid genera. The genus *Persististrombus* Kronenberg and Lee, 2007, which was used as a pit for a plethora of species, is now limited to the extant *Persististrombus granulatus* (Swainson, 1822), fossil American species and a few Oligocene to Miocene Indo-European species. Two new genera for the Miocene ancestral basal taxa of *Aligerini nov. tribus*, *Edpetuchistrombus nov. gen.* and *Antestrombus nov. gen.*, are proposed, both of which represent basal reference points, enabling greater clarity in the resolution of early West African and American Strombidae Rafinesque, 1815.

**SYSTEMATICS**

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Mollusca Linné, 1758</th>
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<tbody>
<tr>
<td>Superorder</td>
<td>Caenogastropoda Cuvier, 1797</td>
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<tr>
<td>Order</td>
<td>Sorbeconcha Ponder &amp; Lindberg, 1987</td>
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<tr>
<td>Superfamily</td>
<td>Stromboidea Rafinesque, 1815</td>
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<tr>
<td>Epifamily</td>
<td>Neostromboidea Maxwell, Dekkers, Rymer &amp; Congdon, 2019</td>
</tr>
<tr>
<td>Family</td>
<td>Strombidae Rafinesque, 1815</td>
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</table>
Persististrombini nov. tribus

Type. Persististrombus Kronenberg and Lee, 2007 (Type: Strombus granulatus Swainson, 1822).

Definition. Contains all recent taxa of the most common ancestors shared between Persististrombus Kronenberg and Lee, 2007 and Thetystrombus Dekkers, 2008, and does not include those ancestors more closely related to Aligerini nov. tribus.

Diagnosis. A small to medium sized shell with a thin edged outer lip that may be lightly calloused in part. The outer lip is not expanded, and attaches at the shoulder of the body whorl. The sculpture of the aperture wall is variable, ranging from smooth to granulate. The columella is smooth and calloused anteriorly. The basal sinus is well developed. Shell sculpture with shoulder knobs.


Persististrombus Kronenberg & Lee, 2007

Type species. Strombus granulatus Swainson, 1822.

Definition. All members more closely related to Persististrombus granulatus (Swainson, 1822) and the clade bound by it.


Original Diagnosis. “Shell of moderate size for family, fusiform, shoulder knobs distinct on body whorl, slightly expanded outer lip with sharp, unglazed rim and no extensions, regularly divided callus on columella, anterior canal short, posterior canal or groove absent or obsolete. Protoconch elongate and conical with four to five smooth whorls. Adaxial side of outer lip smooth, plicate, or granulate” (Kronenberg and Lee 2007, p. 257).

Description. The shell with a sharp outer lip, anteriorly strongly quadrate and not axially reflected. The inner lip is granulated or lirate. The mid-body whorl with rows of nodules. The shell is solid and heavy, with an anterior canal that is reflected.

Assigned Taxa: Strombus baltrae Garcia-Talavera, 1993 [Pliocene, Galapagos, Ecuador], Strombus (Lentigo) barrigonensis Jung & Heitz, 2001 [Early Pliocene, Venuzuela], Strombus granulatus Swainson, 1821 [Pliocene to Recent, tropical eastern Pacific] (Figure 4A), Strombus (Lentigo) insulanus Jung & Heitz, 2001 [Middle Pliocene, Caribbean Panama], Mitra nodosa Borson, 1820 [Lower Miocene, Italy], Strombus bonelli Brongniart, 1823 [Lower Miocene, Italy], Strombus obliratus Hanna, 1926 [Pliocene, California, USA], Strombus praecedens Schaffer, 1912 [Lower Miocene, Austria], Pteroceras radix Brongniart, 1823 [Lower Oligocene, Italy], Strombus (lentigo) torenoensis Jung & Heitz, 2001 [Early Pliocene, Panama].

Thetystrombus Dekkers, 2008

Type species. Strombus latus Gmelin, 1791.

Definition. All taxa more closely related to Thetystrombus latus (Gmelin, 1791) and the clade bound by it, than to Persististrombus Kronenberg and Lee, 2007.


Original Diagnosis. “Shell large to very large, solid but mostly thin walled, light to medium weight shells. The form of the shell is ovoid. Outer lip has a striking thin end which characterizes the genus. Body whorl decorated with knobs on the shoulder, sometimes nearly smooth and sometimes large to very large knobs reflecting to spines. Stromboidal notch is present, mostly large. The base left of the canal is rounded and smooth, no finger like small projections. The sculpture of the body whorl is
besides the aforementioned knobs rather smooth and consists merely of small growth line. The inside of the lip is smooth, just as the columella” (Dekkers 2008, p. 55).

**Description.** The shell with an outer lip that is centrally calloused and not axially reflected; teleoconch with regular nodulations; inner lip smooth; body whorl without striae; shell thin and light; and the anterior canal is straight.

**Assigned Taxa:** *Strombus coronatus* (Defrance, 1827) [Pliocene, Italy etc.], *Strombus exbonellii* Sacco, 1893 [Middle Miocene, Austria], *Strombus inflexus* Eichwald, 1830 [Middle Miocene, Ukraine], *Strombus lapugyensis* Sacco, 1893 [Middle Miocene, Hungary], *Strombus latus* Gmelin, 1791 [Pleistocene – Recent, Mediterranean – West Africa] (Figure 4B), *Persististrombus panonicus* Harzhauser & Kronenberg, 2013 [Middle Miocene, Austria].

**Aligerini nov. tribus**

**Type.** *Aliger* Thiele, 1929 (Type: *Strombus gallus* Linné, 1758).

**Definition.** Contains all recent taxa of the most common ancestor between *Strombus* Linné, 1758 and *Aligerina nov. subtribus* and does not include those ancestors more closely related to *Persististrombini nov. tribus.*

**Diagnosis.** The shell is solid, heavy, with a smooth and calloused outer lip. The body whorl is smooth or with uniform axial sculpture. The basal sinus is variable in depth.

**Etymology.** Derived from the subordinate genus *Aliger* Thiele, 1929.

**Aligerina nov. subtribus**

**Type.** *Aliger* Thiele, 1929 (Type species: *Strombus gallus* Linné, 1758).

**Definition.** Contains all members of the *Aligerini nov. tribus* that are not encapsulated within *Strombus* Linné, 1758.

**Diagnosis.** The shell is heavy and moderately large with a broad outer lip that is calloused and thickened. The basal sinus is present.

**Etymology.** Derived from the subordinate genus *Aliger* Thiele, 1929.

*Aliger Thiele, 1929*

**Type species.** *Strombus gallus* Linné, 1758.

**Definition.** Contains all recent members of the *Aligerina nov. subtribus* that are not encapsulated within *Macrostrombus* Petuch, 1994, *Titanostombus* Petuch, 1994 or *Lobatus* Iredale, 1921.

**Synonymy.** *Strombus* (Aliger) Thiele, 1929, p. 254; *Eustrombus* Wenz, 1940, p. 945 (Type: *Strombus gigas* Wenz, 1940) [Note: A uninominal name proposed for a genus-group division of a genus, even if proposed for a secondary (or further) subdivision, is deemed to be a subgeneric name even if the division is denoted by a term such as “section” or “division”; but a name used for an aggregate of species, which is denoted by a term such as “superspecies”, is not deemed to be a genus-group name (ICZN 1999, art. 6.2)]

**Original Diagnosis.** “Schale mit starken Knoten und Spiralreifen, Mundrand bedeutend erweitert und oben einen splitten Flügel bildend” (Thiele 1929, p. 254). Shell with strong knobs and spiral ribbing, apertural rim rather broad and on the upper part winged and pointed. (Translation AMD)

**Description.** The shell outer lip is inflated, with widely, expanded, uniformly thickened lips as adults, but is not axially reflected; posterior end of lip narrowing to projection or point, giving the aperture a triangulate shape; shoulders often ornamented with large knobs; shell moderately heavy and solid; and an anterior canal that is reflected.

**Assigned Taxa:** *Strombus dominator* Pilsbry & Johnson, 1917 [upper Miocene-lower Pliocene, Dominican Republic], *Strombus galliformis*
Pilsbry & Johnson, 1917 [Pliocene, Dominican Republic], Strombus gallus Linne, 1758 [Pleistocene – Recent, Caribbean] (Figure 5A), Strombus gigas Linne, 1758 [Pleistocene-Recent, Caribbean] (Figure 5B).

Lobatus Iredale, 1921

Type species. Strombus bituberculatus Lamarck, 1822 (= Lobatus raninus (Gmelin, 1791)).

Definition. Contains all recent members of the Aligerina nov. subtribus that are not encapsulated within Macrostrombus Petuch, 1994, Titanostrombus Petuch, 1994 and Aliger Thiele, 1929.

Synonymy. Lobatus Swainson ex Iredale, 1921, p. 208.

Original Diagnosis. Iredale provides a scant reference to a purported Swainson (1837) manuscript where the remark Lobatus is inserted next to Strombus bituberculatus Lamarck, 1822. “Only three names appear to be of importance: thus on p. 67, under the genus Turbinella, against a series beginning with T. capitellum, there is noted in brackets Plicatella, Swainson, and on p. 75, in the same manner, Lobatus, Swainson, is recorded for Strombus bituberculatus; and on p. 81. Buccinulum, Swainson is referred to in connection with Buccinum lineatum, lineolatum, maculosum and coromandelianum” (Iredale 1921: p.208).

Description. The shell is trianguar, heavy and solid; outer lip axially reflected and posteriorly tricornate with uniform callosity; mid-dorsal body whorl with striae and rows of nodules; and the anterior canal is reflected.

Assigned Taxa: Strombus peruvianus Swainson, 1823 [Pleistocene-Recent, tropical eastern Pacific] (Figure 5C), Strombus raninus Gmelin, 1791 [Pleistocene-Recent, Caribbean] (Figure 5D).

Macrostrombus Petuch, 1994

Type species. Strombus costatus Gmelin, 1791.

Definition. Contains all recent members of the Aligerina nov. subtribus that are not encapsulated within Aliger Thiele, 1929, Titanostrombus Petuch, 1994 or Lobatus Iredale, 1921.


Original Diagnosis. “Strombus shells that are much larger than Strombus s.s., massive, inflated, with widely, expanded, thickened lips as adults; posterior end of lip rounded, not narrowing to projection or point; body whorls sculptured with large flattened cords, giving shells ribbed appearance; shoulders often ornamented with large spike-like knobs” (Petuch 1994: p. 258). [Comment – Petuch (1994, p. 258): “This endemic western Atlantic strombid radiation, which appears to have been centred on the Floridian Peninsula, has traditionally been placed in the subgenus Eustrombus Wenz, 1940 (type: S. gigas Linnaeus, 1758) (note: Abbott (1960) incorrectly placed S. gigas in Tricornis Jousseaume, 1886 - an unrelated, endemic Indo-Pacific, Red Sea subgenus). Since members of Macrostrombus, although large like Eustrombus, lack the large shoulder spikes of the S. gigas complex, have heavily-ribbed body whorl sculptures, and have more rounded, non-projecting lips, I felt it necessary to erect a separate subgenus for this compact western Atlantic group.”]

Description. The shell dorsum with uniform striae; teleoconch whorls knobbed; body whorl with shoulder nodulations; outer lip centrally calloused, posteriorly quadrate and thinned; outer lip edge axially reflected with glazing; aperture smooth; shell heavy and solid and an anterior canal that is reflected.

Assigned Taxa: Macrostrombus bartoni Petuch & Drolshagen, 2011 [Plio-Pleistocene,

Diagnosis. Shells of moderate size; ovate; spire with spiral lines and knobs; body whorls with evenly spaced spiral ribbing that run also on the relatively large shoulder knobs; lip flaring, aperture straight, not glazed within; aperture extends posteriorly before the pre-ultimate whorl. The spiral ribbing runs over the extended lip, bending backwards. Apertural rim not glazed. The anterior canal not broad and a little reflected to the left. The Stromboid notch is present but shallow.

Etymology. The name Edpetuchistrombus nov. gen. is chosen in honour of Edward J. Petuch, Florida, USA, for the inspiring work he has done on extant and fossil molluscs in Florida and the Caribbean and especially the research on Strombidae species and genera, with his ground-breaking ideas on the seas and sub-seas and the formations from the Miocene to present.

Assigned Taxa: Strombus aldrichi Dall, 1890 [Lower Miocene, Florida, USA] (Figure 6A).

Titanostrombus Petuch, 1994

Type species. Strombus goliath Schröter, 1805.
Definition. Contains all recent members of the Aligerina nov. subtribus that are not encapsulated within Aliger Thiele, 1929, Macrostrombus Petuch, 1994 or Lobatus Iredale, 1921.


Original Diagnosis. “Strombus shells that reach the largest sizes for the family, massive, inflated, with uniformly thin, expanded lips as adults; posterior end of lip rounded; body whorls sculptured with wide, closely-packed, flattened ribs; spire whorls low and generally flattened; spire whorls often with large spike-like knobs; knobs become obsolete on body whorl; body whorl rounded, without spikes or knobs; shoulder rounded, often with faint axial undulations” (Petuch, 1994: p. 261). [Comment – Petuch (1994, p. 261): "This group

Edpetuchistrombus nov. gen.

Type species. Strombus aldrichi Dall, 1890.
Definition. Contains all ancestral members of Aligerini nov. tribus more closely related to Aligerina nov. subtribus than to Strombus Linné, 1758.
of giant strombids is unique to the tropical Americas, with a living species in both the Eastern Pacific and western Atlantic (Brazil). The only known fossil species, *S. williamsi* (Plate 20, Figure A) is found only in the Holey Land Fauna of the Everglades region, and is known from fewer than a dozen specimens. While *S. (Titanostrombus) goliath* is the largest living species, *S. (Titanostrombus) williamsi* is the largest-known fossil strombid (with specimens in excess of 300 mm). *Titanostrombus* is similar to *Macrostrombus*, but differs in being consistently larger, in having more rounded shoulders, and in having large, spikelike knobs on the early whorls. In this last character, *Titanostrombus* is similar to *Eustrombus* (type *S. gigas*). The co-occurrence of three giant strombid genera, *Macrostrombus*, *Eustrombus*, and *Titanostrombus*, together in southern Florida during Holey Land time, is truly remarkable.*]

**Description.** The shell outer lip is uniformly thin on the border, thickened centrally, expanded and rounded posteriorly; body whorl sculptured with broad narrow interspaced ribs; teleoconch often with large knobs; knobs become obsolete on body whorl; shell moderately heavy and solid; and an anterior canal that is reflected.

**Assigned Taxa:** *Titanostrombus immokaleensis* Petuch & Droshagen, 2011 [Pliocene, Florida, USA], *Strombus galeatus* Swainson, 1823 [Pleistocene – Recent, tropical East Pacific] (Figure 5F), *Strombus goliath* Schröter, 1805 [Recent, Brazil] (Figure 5G).

**Strombina nov. subtribus**

**Type.** *Strombus* Linné, 1758 (*Strombus pugilis* Linné, 1758 by subsequent designation Lamarck (1799)).

**Definition.** Contains all recent members of the *Aligerini nov. tribus* that are not encapsulated within *Aligerina nov. subtribus*.

**Diagnosis.** Shells biconic with the apertural rim not glazed. The edge of lip somewhat thickened posteriorly and calloused, becoming thinner and sharper anteriorly.

**Etymology.** Derived from subordinate genus *Strombus* Linné, 1758.

**Antestrombus nov. gen.**

**Type species.** *Strombus chipolanus* Dall, 1890.

**Definition.** Contains all ancestral members of the clade *Strombini nov. tribus* more closely related to *Strombus* Linné, 1758 than to *Aligerina nov. subtribus*.

**Diagnosis.** Shells of moderate size. Spire acute, with spiral lines and axially aligned knobs. Body whorl reversed conoidal form. The body whorl has evenly spaced spiral ribbing that is almost smooth, with relatively large and sharp shoulder knobs. The non-flaring lip with a straight side. The aperture large but narrow and not extending posteriorly before the body whorl. The spiral ribbing runs over the extended lip and bends slightly backwards at the posterior end. The apertural rim not glazed but a little thickened by shell material added from theinside of the aperture. Inside outer lip smooth. The anterior canal not broad, but deep, and slightly reflected to the left. Stromboid notch present but shallow.

**Etymology.** The name *Antestrombus nov. gen.* is chosen to indicate the close resemblance with fossil and extant species of the genus *Strombus* Linné, 1758. The prefix *ante* is indicative that species belonging to the new genus are precursors of a plethora of species that evolved and thrived in the Plio-Pleistocene of Florida and the Caribbean Seas.

**Assigned Taxa:** *Strombus chipolanus* Dall, 1890 [lower Miocene, Florida, USA] (Figure 6 B), *Strombus dodoneus* Gardner, 1947 [Late Miocene, Florida, USA], *Strombus mardieae* Petuch, 2004 [lower Miocene, Florida, USA] (Figure 6 C). Note: *Strombus dodoneus* Gardner,
1947 is bridging between Antestrombus nov. gen. and Strombus Linné, 1758.

**Strombus Linné, 1758**

**Type species.** Strombus pugilis Linné, 1758 by subsequent designation Lamarck (1799).

**Definition.** Contains all recent members of the Aligerini nov. tribus that are not encapsulated within subtribe Aligerina nov. subtribus.

**Synonymy.**

Strombus Linné, 1758, p. 742;
Strombella Schlüter, 1838, p. 22 (Type: Strombus pugilis Linné, 1758);
Pyramis Röding, 1798 (Type: Pyramis striata Röding, 1798 = Strombus pugilis Linné, 1758).

**Description.** The shell triangulate to fusiform, medium in size, the columella smooth, and the outer-lip strongly axially quadrate posteriorly. The edge of the lip somewhat thickened posteriorly and calloused, becoming thinner and sharper anteriorly. The shoulder with nodules, and the body whorl is smooth or with fine axial uniform striations. The outer aperture smooth, or with fine short lirations.

**Assigned Taxa:** Strombus acanthspera Landau, Kronenberg, Herbert & Silva, 2011 [Calabrian: Pleistocene, Panama], Strombus alatus Gmelin, 1791 [Pleistocene - Recent, Florida & Caribbean] (Figure C), Strombus arayaensis Landau and Silva, 2010 [Pleistocene, Venezuela], Strombus ayersensis Petuch & Drolshagen, 2011 [Pleistocene, Florida, USA], Strombus bifrons Sowerby, 1850 [Late Miocene, Dominican Republic], Strombus capelletii Petuch, 1994 [Middle Pleistocene, Florida, USA], Strombus canoni Petuch & Drolshagen, 2011 [Pliocene, USA], Strombus elegantissimus Landau, Kronenberg, Herbert & Silva, 2011 [Late Pliocene, Panama], Strombus erici Petuch, 1994 [Calabrian Pleistocene, USA], Strombus evergladesensis Petuch, 1991 [Pleistocene, USA], Strombus floridanus Mansfield, 1930 [Upper Miocene, USA], Strombus gatunensis Toula, 1909 [Miocene, Panama], Strombus gracilior Sowerby, 1825 [Recent, Eastern Pacific] (Figure 4D), Strombus jenniferae Petuch & Drolshagen, 2011 [Pleistocene, USA], Strombus keatonorum Petuch, 1994 [Lower Pleistocene, Florida, USA], Strombus leurus Woodring, 1928 [Pliocene, Jamaica], Strombus lindae Petuch, 1991 [Pleistocene, USA], Strombus propegracilior Dall & Ochsner, 1928 [Pliocene, Galapagos], Strombus proximus Sowerby, 1850 [Miocene, Dominican Republic], Strombus pugilis Linné, 1758 [Recent, Caribbean] (Figure 4E). Strombus pugiloides Guppy, 1873 [Pliocene, Jamaica], Strombus sarasotaensis Petuch, 1994 [Pliocene, USA], Strombus subgracilior Durham, 1950 [Middle and Upper Pliocene], Strombus vermeiji Landau, Kronenberg, Herbert & Silva, 2011 [Neogene, Panama], Strombus worki Petuch, 1983 [Recent, Brazil] (Figure 4F).

**DISCUSSION**

One of the most significant problems in bringing an evolutionary understanding to the nomenclature is the blurring of ancestral relationships through overreach within the census literature in attribution to Persististrombus Kronenberg and Lee, 2007. The blurring of ancestral relationships through the oversimplification of the higher taxonomy has decreased the contribution that these genera can make to the evolutionary understanding of taxonomic radiations on a global scale (Dekkers 2008b). Lozouet and Meaestraiti (1986) demonstrated the link between the European Early Oligocene Persististrombus radix (Brongniart, 1823) (France, Aquitaine Basin) and the extant Persististrombus granulatus (Swainson, 1822). The overreach of the consensus in definable inclusivity within Persististrombus Kronenberg and Lee, 2007 has had the negative side effect of creating a level of
taxonomic inflation, where the increase in attributed taxa with more diverse morphology indirectly expands the accepted character set, and where the importance of the inclusivity within the genus appears to override the original description. The genus Persististrombus Kronenberg and Lee, 2007 is herein restricted to the American species: *P. granulatus* (Swainson 1822), *P. barrigonensis* (Jung and Heitz, 2001), *P. toroensis* (Jung and Heitz, 2001), *P. insulanus* (Jung and Heitz, 2001), *P. obliteratus* (Hanna, 1926) and *P. baltrae* (Garcia-Talavera, 1993). Kronenberg and Lee (2007) included ancestral species that fall outside the defining characteristics of that clade Persististrombus Kronenberg and Lee, 2007, such as *Edpetuchistrombus aldrichi* (Dall, 1890), *Antestrombus mardiae* (Petuch, 2004) and *Antestrombus chipolanus* (Dall, 1890).

*Thetystrombus* Dekkers, 2008 is found only in the tropical part of West Africa, with records indicating that *Thetystrombus latus* (Gmelin, 1791) entered the Mediterranean basin during a relatively short period of warming in the Pleistocene (Taviani 2014). The evidence in the form of *Thetystrombus coronatus* (Defrance, 1827) places this genus from as early as the Pliocene of Spain and Italy. There is a high degree of phenotypic plasticity in the recent shells of *Thetystrombus latus* (Gmelin, 1791) ranging from slender smooth shells without shoulder knobs to large and broad shells with strong shoulder knobs. Fossil Mediterranean examples clustered within *Thetystrombus bubonius* (Lamarck, 1822), a probable synonym of *Thetystrombus latus* (Gmelin, 1791). *Thetystrombus coronatus* (Defrance, 1827) from the Pliocene of Spain and Italy represents the ancestral Mediterranean species, however, lacks the variability in morphology commonly observed in modern *Thetystrombus* Dekkers, 2008 taxa.

*Strombus* Linné, 1758 have generally rather smooth shells with more or less strong spines on the shoulder of the body whorl and the spire whorls, and a smooth inside of the outer lip. They are confined to the tropics of the Caribbean and the East Pacific coastline from northern Peru to Mexico. *Strombus* Linné, 1758 arose in the late Miocene/Early Pliocene most likely sharing a common ancestry with a Miocene member of *Antestrombus* nov. gen. Species of *Strombus* Linné, 1758 show remarkable differences in shell form and shoulder knobs (or spines) in time and space. The genus shows remarkable adaptability demonstrated by rapid radiation and shift in morphological form (Petuch 2004).

*Lobatus* Iredale, 1921 is limited to two extant species: *Lobatus raninus* (Gmelin, 1791) and *Lobatus peruvianus* (Swainson, 1823) (Kronenberg and Lee 2007; Landau et al. 2008). The modern re-introduction of *Lobatus* Iredale, 1921 (Petuch 1994) was contested (Jung and Heitz 2001), but later restabilised (Kronenberg and Lee 2007), and there has been a level of taxonomic overreach with the problematic collapse of *Macrostrombus* Petuch, 1994, *Titanostrombus* Petuch, 1994 and *Aliger* Thiele, 1929 into *Lobatus* Iredale, 1921 (Freiheit and Geary 2009), which we reject. *Strombus* (Lentigo) *fetus* Jung and Heitz, 2001 and *Strombus* (s.l.) *dominator* Pilsbry and Johnson, 1917 are designated here as *Lobatus* Iredale, 1921 species. “*Lobatus*” first appeared in 1837 in an anonymous catalogue of the Manchester museum where Swainson was working on the collection.

Based also on classical Swainson spelling errors, Iredale (1921) attributed the work to him; however, this cannot be verified. Therefore, according to ICZN (1999) article 14, anonymous authorship before 1951 does not prevent availability of a new name or
nomenclatural act. The anonymous work attributed to Swainson was a simple catalogue listing shells in the collection of the Manchester Natural Museum and elucidated upon first by Iredale (1921). Iredale (1921) accepted Lobatus as an available name drawn for the anonymous booklet, and confirmed the type as Strombus bituberculatus Lamarck, 1822 (= Lobatus raninus Gmelin, 1791). Consequently, Iredale (1921) offered the formal name and defined the taxa and takes authorship.

The genus Macrostrombus Petuch, 1994 was introduced as a new subgenus (the modus operandi at that time) with the type species being the extant Macrostrombus costatus (Gmelin, 1791). This large species with a rounded flaring lip, coarse spiral ribbing, and lacking large shoulder spike is an endemic West Atlantic radiation with numerous species, especially in the Plio-Pleistocene of the Florida fossil beds. Approximately 20 were described by Petuch (1991, 1994; Cf. Petuch and Drolshagen 2011) with the main focus around Florida, which was part of the Caloosahatchian Province, where Petuch (1982) proposed a centre of radiation. Macrostrombus haitensis Sowerby, 1850 from the Lower Gatun is the earliest known member of the clade in the Americas. Diversification within Macrostrombus Petuch, 1994 was primarily during the Middle Gatun. Edpetuchistrombus nov. gen. from the Miocene of Florida is seen as the immediate ancestral clade to the crown clade Macrostrombus Petuch, 1994. Macrostrombus haitensis (Sowerby, 1850) is bridging between Edpetuchistrombus nov. gen. and Macrostrombus Petuch, 1994, but the general characters of the shells (larger size, more reflected outer lip, glazed rim) shows it belongs to Macrostrombus.

Titanostrombus Petuch, 1994 arose in the Middle Gatun and holds the largest stromloid species in the American radiations. The two attributable species to Titanostrombus Petuch, 1994, one each side of the Panama Isthmus, indicate a shared common ancestor from at the latest 3 million years ago. The shifting taxonomic placement of Titanostrombus galeatus (Swainson, 1823) under differing modalities may be reflective of the potential for rapid divergence, given the significant impacts of historical sea level oscillations on the narrow habit range potential for West American coastal marine species. The analysis of the provinces, and the splitting in two separate Miocene to Pleistocene Pacific-Caribbean provinces before the closure of the Isthmus, is important to understand the connection between the two gigantic stromboid species that are descendants of the southern Gatunian Province of Petuch (2004). The extant Brazilian Titanostrombus goliath (Schröter, 1905) and Titanostrombus galeatus (Swainson, 1823) from the Panamic Province, Eastern Pacific tropical coasts, are both survivors that were parted by the closure of the Central American Seaway. This Titanostrombus Petuch, 1994 lineage was confined to the southern part of the Pacific-Caribbean Miocene-Early Pleistocene Sea centred on Florida (Woodring 1959, 1966, 1974).

Further Research

This review did not consider the relationships between the early Indo-Pacific and the American taxa, primarily due to the lack of detailed distributional and stratigraphic knowledge and resolution in the Indo-pacific fossil taxa. Notwithstanding, the level of convergence in shell morphology in the fossil record between American and Indo-Pacific taxa presents an avenue for global perspectives of Strombidae radiation theory to be developed. Examples of this convergence include: Tricornis maximus (Martin, 1883) and Aliger
gigas (Linné, 1758), and Tricornis tuberosus (Martin, 1883; Indonesian Miocene) and Macrostrombus costatus (Gmelin, 1971). These similarities were also noted by Abbott (1960, p. 62), particularly with relation to Tricornis tuberosus (Martin, 1883): “I know of no recent Indo-Pacific species resembling it, although Strombus costatus Gmelin, 1971 of the West Indies is somewhat similar.”

CONCLUSION

We proposed that the American Tersusini nov. tribus and Strombus Linné, 1758 are derived from a common ancestor that arrived into the Americas well before the Miocene, probably from the European Tethys. Furthermore, we argue that the ancestor of Persististrombus Kronenberg and Lee, 2007 arrived in the Americas prior to the closure of the Panama Isthmus, and also prior to the arrival of the ancestral lines of the Tersusini nov. tribus. The clades erected here are primarily monotypic in terms of extant taxa, and the fossil taxa are mostly well attributable. Similar to an iceberg, the extant taxa represent only a small portion of the taxa encompassed with the definition, while the bulk of taxa are fossils that are unseen or ignored by many extant-focused researchers. The importance of these monotypically extant clades as markers in the understating of the entire evolution and radiation of the West African and American Strombidae is through the establishment of nomenclatural reference points that enable phylogenetic explanations, without falling into the pitfalls of inclusivity debates regarding the content of the clade. Furthermore, failing to recognize iceberging with genera with limited extant taxa, and understanding the role that genera play in enabling the recognition of discrete and evolutionary progression is one of the major failings of the historical revisions into Strombidae, where the focus has been bogged at the interspecies level without resolution. The use of phylogenetic nomenclature, and stem and nodal definitions give a level of stability in definition to the hypothesized phylogeny that has been lacking in previous attempts to resolve the West African and American Strombidae Rafinesque, 1815. Clench and Abbott (1941) applied a fundamentalist biological concept of species to their revision of American stromboids, and this is reflected in their approach to taxonomic practice. That is, the propensity for the crown clades to throw up inter-clade hybrids led to the conceptualization of closeness in relation, and therefore species were classified and aggregated in that light. This rigid adherence to a specific species concept reflects the breaking of the phenetic dominance of the past two centuries. However, one of the natural consequences was the over simplification through synonymization of many taxonomic groups. We demonstrate that a greater resolution can be achieved with a level of conceptional flexibility and a pluralist approach to the definition of taxonomic entities. The new definition explicitly defines the level of inclusivity, and places that taxonomic entity within a nomenclature that is founded on an evolutionary framework. We suggest that over simplification of higher clades based on a singular conceptualization is poor systematic practice.

ACKNOWLEDGEMENTS

We thank Edward Petuch, Florida, USA, for the inspiration for us to study the American stromboid radiations. Also, we thank A.J.F. Janssen, Bovenkarspel, of the Netherlands for the help in getting literature written by Edward Petuch. The second author wishes to thank Henk Dekker, Winkel, of the Netherlands, for sharing ideas and opinions on the evolution and radiations of stromboid genera and species. A special mention goes to Trevor and Marguerite
Young of Cannonvale, Queensland whose invaluable assistance was gratefully accepted in the editing of this manuscript.

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<tr>
<th>Extant Taxa</th>
<th>Accepted Generic Affiliation (Base Clade)</th>
<th>Alternative Generic Affiliations</th>
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*Table 1.* The extant American and West African Strombidae taxa with the accepted and alternative generic affiliations that have been applied to those taxa.
### Table 2: The table of comparative anatomy for members of the American Strombidae.

<table>
<thead>
<tr>
<th>Anatomical Character</th>
<th>Mouth-anterior margin</th>
<th>Foot-dorsal surface texture</th>
<th>Dihyphragmal septal muscle</th>
<th>Operculum spines</th>
<th>Mantle margin</th>
<th>Osphradium posterior extremity</th>
<th>Osphradium central region</th>
<th>Kraken lobes</th>
<th>Buccal mass muscle 3 pair</th>
<th>Verge dorsal appendage</th>
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Simone (2005) coding states: 8 – 0 = Smooth, 1 = Papillate; 20 – 0 = Smooth, 1 = Reticulate; 21 – 0 = Present, 1 = Double layered; 26 – 0 = No spines, 1 = With spines; 28 – 0 = Smooth, 1 = Anterior tentacle; 33 – 0 = Anterior of gill, 1 = At gill level; 34 – 0 = Simple weakly curved, 1 = Sigmoid region; 51 – 0 = Similar size, 1 = Single ventral lobe; 63 – 0 = United with each other anterior to the radula nucleus, 1 = Inserted into the radula nucleus; 90 – 0 = Flat with longitudinal appendage, 1 = Semi-circular with central undulating folds; 91 – 0 = Absent, 1 = With apical projection; 93 – 0 = Entirely open, 1 = Partially opened; 94 – 0 = Separate from oviduct, 1 = Secondary expansion of the oviduct; 96 – 0 = Without folded dorsal wall, 1 = With folded dorsal wall.
Figure 1. The hypothesised phylogenies of extant West African and American Strombidae and the hypothesised cladistic arrangements presented by each taxonomist: A) after Latiolais et al. (2006) maximum likelihood gene tree generated using combined COI and H3 molecular data; B) after Simone (2005) cladistic tree showing the anatomical relationships and significant taxonomic stem points identified by that author; C) inferred tree after Bandel (2007) based on the morphological and fossil relationships defined within the work; and D) the inferred tree after Dekkers (2008a, 2008) literary evidence, morphological, fossil and geographical relationships outlined within that work.
Figure 2. The morphological and anatomical cladistic trees: A) The tree generated to show similarity using COI molecular data analysis using maximum likelihood, set to zero branch collapse; B) The consensus tree generated to show hypnotized evolutionary relationships based on COI molecular data UMPGA; and C) The tree generated to show similarity using anatomical data analysis using maximum likelihood.
Figure 3. Hypothesized internal resolution of the American and West African genera of Strombidae based on anatomical, morphological and molecular evidence contextualized with the fossil record.
Figure 4. Extant members of Persististrombus, Thetystrombus and Strombus: A = Persististrombus granulatus (Swainson, 1821) – Manabi, Equador, 72 mm (collection Stephen Maxwell); B = Thetystrombus latus (Gmelin, 1791) – St Vincente Channel, Cape Verde Islands, 98 mm (collection Trevor and Marguerite Young); C = Strombus alatus Gmelin, 1791 – Marco Island, Florida, 84 mm (collection Stephen Maxwell); D = Strombus gracilior Sowerby, 1825 – Mexico, 71 mm (collection Stephen Maxwell); E = Strombus pugilis Linné, 1758 – Aruba, Dutch Antilles, 90 mm (collection Trevor and Marguerite Young); F = Strombus worki Petuch, 1983 – Brazil, 83 mm (collection Stephen Maxwell). Images not to scale.
Figure 5. Extant members of Aliger, Lobatus, Macrostrombus and Titanostrombus: A = Aliger gallus (Linné, 1758) – Porto Segura, Brazil 90 mm (collection Stephen Maxwell); B = Aliger gigas (Linné, 1758) – Dominican Republic, 306 mm (collection Jeroen Braakman); C = Lobatus peruvianus (Swainson, 1823) – Islas Cocinas, Mexico, 93 mm (collection Stephen Maxwell); D = Lobatus raninus (Gmelin, 1791) – Honduras, 51 mm (collection Stephen Maxwell); E = Macrostrombus costatus (Gmelin, 1791) – Bahamas, 110 mm (collection Stephen Maxwell); F = Titanostrombus galeteus (Swainson, 1823) – West Panama 198 mm (collection Jeroen Braakman); G = Titanostrombus goliath (Schröter, 1805) – Ceará, Brazil, 316 mm (collection Jeroen Braakman). Images not to scale.
Figure 6. Fossil Edpetuchistrombus and Antestrombus species. A = Edpetuchistrombus aldrichi (Dall 1890) – Ten Mile Creek, Florida, 53 mm (Aart Dekkers Collection no. STR9470); B = Antestrombus chipolamus (Dall 1890) – Ten Mile Creek, Florida, 62 mm (Aart Dekkers Collection no. STR9469); C = Antestrombus mardiaeae (Petuch 2004) – Ten Mile Creek, Florida, 42 mm (Aart Dekkers Collection no. STR9468). Images not to scale.