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Are the ICZN and PhyloCode that incompatible? A summary of the shifts in Stromboidean taxonomy and the definition of two new subfamilies in Stromboidae (Mollusca, Neostromboidae)

Stephen J. Maxwell [1] and Tasmin L. Rymer [1, 2]
[1] College of Science and Engineering, James Cook University, Cairns, Qld, 4870, Australia stephen.maxwell@my.jcu.edu.au
[2] Centre for Tropical Environmental and Sustainability Sciences, James Cook University, P.O. Box 6811, Cairns, Queensland, Australia

ABSTRACT The taxonomy of Stromboideans has, historically, been simplistic. However, recent revisions have seen new taxa introduced to distinguish relationships between species clusters. We discuss these numerous advancements in Stromboidean systematics, and describe two new subfamilies here. The key diagnostic characteristic, the basal peg on the first lateral tooth, splits the Strombidae into two clades similar to those observed with molecular data. In defining the new subfamilies, Neoaligerinae and Neostrombinae, we demonstrate that the practical application of the International Code of Phylogenetic Nomenclature (PhyloCode 2020), can also conform to the requirements of the International Code of Zoological Nomenclature (ICZN 1999). This revision further advances and strengthens the framework of Stromboidean nomenclature such that it is able to reflect the current understanding of the evolutionary relationships between members of the Stromboidea.

KEY WORDS ICZN, Neoaligerinae, Neostrombinae, PhyloCode, Sub-family, Stromboidea, Taxonomy, Crown Clade

INTRODUCTION

Historically the taxonomy of Stromboideans has been simplistic based on the utilisation of the taxonomic ranks of family, genera, and subgenera only (Figure 1). However, recent revisions of Stromboideans in Maxwell *et al.* (2020), Dekkers and Maxwell (2020) and Liverani *et al.* (2021) saw taxa introduced to distinguish the finer relationships between species clusters. These revisions were based on the principles of phylogenetic taxonomy, or the use of a relational definition in association with the normal diagnosis. Therefore, there revisions were compliant with both the guidelines of the International Code of Zoological Nomenclature (ICZN 1999) and the principles of the International Code of Phylogenetic Nomenclature (PhyloCode 2020). The purpose of erecting these taxa was to "demonstrate that nomenclature can reflect the current evolutionary understanding within that complex rather than the simple aggregation of taxa based on uncritical analysis of form alone" (Dekkers and Maxwell 2020, p. 40). The authors therein demonstrated the hypothetical evolutionary relationships used to underpin the proposed nomenclature can be formed under the framework of the ICZN. While there has been some resistance to the acceptance of the PhyloCode, the use of its diagnosis and description for the discernment of higher taxonomic meaning in the structure of the nomenclature does remain compliant with ICZN requirements (Maxwell *et al.* 2019, 2020; Dekker and Maxwell 2020; Liverani *et al.* 2021).

The application of the PhyloCode by Maxwell *et al.* (2019, 2020), Maxwell and Dekkers (2020) and Liverani *et al.* (2021), with the inclusion of a definition for taxonomic rank, shows a path to overcome the formulative rigidly of the ICZN's methodological approach to the construction of the nomenclature, without affecting its application in practice. The definition brings a statement of relatedness when formulating a new taxon and seeks to explain its relationship between closely related taxonomic outgroups. These two codes of nomenclature are not mutually exclusive, and the PhyloCode can be used for the formulation and defining process of identifying and defining clades that are then constructed to conform to the ICZN (Maxwell *et al.* 2019, 2020). It is this definition that allows clades to be reliably knitted into a hypothetical phylogeny. This placement allows us to draw a relational framework between those defined taxa. Similarly, when dealing with those taxa that have not been defined, they should not be included in the phylogeny or the taxonomy, other than given the rank applied per the pre-revision state, and they should be treated as undefined.

Crown clades are defined by using living taxa and their current hypothesised relationships. However, this does not mean that ancestral relatives are excluded. They are recognisable in the structure of the clade name, typically with the prefix 'Neo+" (Maxwell *et al.* 2019). The role of a crown clade is to form a tree-like structure based on extant evidence upon which the fossil branches can be attached. The use of extant taxa to define higher taxonomy provides the taxonomist with evidence, such as anatomy and genetics, for ancestral relationships, which gives a level of robustness to those relationships that are used to generate the phylogeny. The fossils can then be added where they appear to support the evolution of organisms that gave rise to what we see today, as with the case of *Aligerini* Maxwell, Dekkers, Rymer and Congdon, 2020. It is therefore wrong to assume that a crown clade does not include fossil taxa because they are omitted from the definition. Importantly, the definitions used to highlight relationships between taxa are not rigid, and are able to be modified as further information and understanding of those relationships becomes apparent. The rejection of crown clades based on the use of structural definitions and the belief that those definitions exclude fossil taxa, not only shows a lack of understanding of what crown clades are but seeks to collapse the taxonomy such that it reverts to some twentieth century simplified state and is, theoretically, retrogressive.

There are two areas of Stromboidean taxonomic practice that have generated considerable public debate: 1) the revisions to the nomenclature that have been undertaken, and are necessary to enable Stromboidean taxonomy to move forward; and 2) the use of the International Code of Phylogenetic Nomenclature (PhyloCode 2020), and how its practical application can also conform to the requirements of the International Code of Zoological Nomenclature (ICZN 1999). In conjunction with the demonstrated reconciliation of the PhyloCode and ICZN practice, we present the current hypothetical state of Stromboidean taxonomy showing practically how these two systems are compatible. Furthermore, we outline the benefits of crown clades for the definition of higher taxa, and particularly that extant taxa are not excluded from inclusion in clades defined with the use of the PhyloCode by the sole use of extant taxa to formulate those definitions. This will be achieved through the recognition of two crown clades within Strombidae.

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METHODS

The two clades represent two divergent evolutionary lines in radula development. One line has developed a basal peg on the first lateral tooth, and a second evolutionary line has no basal peg. The taxa without a basal peg tend to be larger than those with basal pegs. The clade of taxa with the basal peg can be distinguished from those without a peg genetically in most cases (Latiolais *et al.* 2006; Irwin *et al.* 2021); only *Conomurex* Fischer, 1884, a taxon with a basal peg, did not conform, and its placement is discussed below.

Clade recognition and name construction followed principles of Bryant (1996) outlined in Maxwell *et al.* (2020). The names circumscribed herein follow the practice of Maxwell *et al.* (2019) with the use of the prefix "Neo+" designating that a crown clade is being described. The ICZN (1999) makes no comment on the use of prefixes.

The taxonomy presented is an amalgamation of the definitions and their relationships for each clade (Maxwell *et al.* 2019, 2020; Dekkers and Maxwell 2020; Liverani *et al.* 2021; Irwin *et al.* 2021). Where taxa have not been defined they have been aggregated at the same status as their sister taxa; not all undefined taxa have been listed in the figures.

SYSTEMATICS

Phylum: Mollusca Linné, 1758
Order: Sorbeoconcha Ponder & Lindberg, 1997
Superfamily: Stromboidea Rafinesque, 1815

Neostromboidae Maxwell, Dekkers, Rymer & Congdon, 2019

Type Genus. *Strombus* Linné, 1758.

Original Definition. "The clade is nested within Stromboidea, with the characteristics outlined in the diagnosis, and contains taxa more closely related to *Strombus pugilis* Linné, 1758 (Strombidae), *Terebellum terebellum* (Linné, 1758) (Seraphsidae) and *Tibia fusus* (Linné, 1758) (Rostellariidae) than Struthiolariidae Gabb, 1868 and Aporrhaidae Gray, 1850" (Maxwell *et al.* 2019) (Figure 2).

Diagnosis. Eyes positioned distally on peduncles that also have the cephalic tentacle attached.

Original Description. "The animal possesses eyes on the end of the peduncles. The cephalic tentacle is also located on the peduncle towards the distal end. The radula has a central rachidian tooth with three lateral teeth either side. The foot is laterally compressed, with a defined propodium and a metapodium. The shell form changes upon maturation with the development of an outer lip structure" (Maxwell *et al.* 2019).

Remarks. The epifamily Neostromboidae incorporates an evolutionary line where the eyes of the animal have evolved to be on the end of peduncles. There are three extant clades incorporated within the Neostromboidae.

Strombidae Rafinesque, 1815

Type Genus. *Strombus* Linné, 1758.

Definition. The clade is nested within Neostromboidae, with the characteristics outlined in the diagnosis, and contains taxa more closely related to *Aliger gigas* (Linné, 1758) (Neoaligerinae n. subfam.) and *Strombus urceus* (Linné, 1758) (Neostrombinae n. subfam.) than to *Terebellum terebellum* (Linné, 1758) (Seraphsidae) and *Tibia fusus* (Linné, 1758) (Rostellariidae).

Diagnosis. Shell with a body whorl that is longer than the combined teleoconch, stromboidal notch well formed, and body whorl sculpture may vary significantly from that of the teleoconch.

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Original Description. "2. S. F. *Strombia*. Les Strombiens. Bord de la base ou bouche, dilaté en aile latérale. G. 15. *Strombus* L. 14. *Pterocera* Lam. 17. *Rostellaria* Lam." (Rafinesque, 1815, p. 145).
Remarks. This family historically contained a number of genera that have now been elevated to family level: *Terebellum* (Seraphsidae) and *Tibia* (Rostellariidae). Similarly, the subgenera have all been elevated to genera.

Neostrombinae Maxwell & Rymer, new subfamily

Type Genus. *Canarium* Schumacher, 1817.
Definition. Contains all recent and ancestors of Dolominini Dekkers and Maxwell, 2020 and Neostrombini Liverani, Dekkers and Maxwell, 2021 and does not include those ancestors more closely related to members of Neoaligerinae n. subfam. (Figure 3)
Diagnosis. There is a basal peg on the radula first lateral tooth.
Description. The shells are small to medium in size. The posterior canal is straight and extended. There is basal peg on the first lateral tooth. Dorsum of the body whorl often smooth or with limited shoulder ornamentation.
Etymology. The name if formed from the combination of the genus *Neostrombus*, as "Neo +strombus+" where the prefix "Neo+" is also used to denote a crown clade, and the subfamily suffix "+inae" is used to reflect the taxon's position within the nomenclature.
Remarks. This clade is able to be recognised in the published gene trees (Latiolais *et al.* 2006). One taxon however, did not conform to this character based hypothesis. *Conomurex* fell genetically within the taxonomic cluster of Neoaligerinae n. subfamily. However, the presence of the basal peg on the first lateral tooth requires it to be contained with Neostrombinae n. subfam. where it forms the basal taxon within this hypothesised taxonomy, although this placement is contested with mitochondrial analyses (Latiolais *et al.* 2006; Irwin *et al.* 2021). While there is no anatomical evidence available on the radula formula, the general similarity for *Barneystrombus* Blackwood, 2009 in the formation of the outer lip conforms to the morphology of other members of the Neostrombinae. However, exact relationships are unclear, and *Barneystrombus* is treated as currently undefined (Figure 3). The positions of *Conomurex* and *Laevistrombus* Abbott, 1960 are undefined, but these taxa possess a basal peg on the radula's first lateral tooth.

Neoaligerinae Maxwell & Rymer, new subfamily

Type Genus. *Aliger* Thiele, 1929.
Definition. Contains all recent taxa of the most common ancestors of Aligerini Maxwell, Dekkers, Rymer and Congdon, 2020 and Persististrombini Maxwell, Dekkers, Rymer and Congdon, 2020 and does not include those ancestors more closely related to members of Neostrombinae n. subfam. (Figure 4).
Diagnosis. There are no basal pegs on the radula first lateral teeth. Body whorl dorsum often well ornamented with axial chords, knobs or plaits, flaring or ornamented outerlips.
Description. The shells are medium to large in size. The posterior canal may be extended.
Etymology: The name is formed from *Aliger* Thiele, 1929, as "+aliger+", and the prefix "Neo+" here used to denote a crown clade, and the subfamily suffix "+inae" to reflect the taxon's position in the nomenclature.
Remarks. This clade has no basal peg on the first lateral tooth, and are generally of a larger size than members of Neostrombinae. As this clade undergoes revisions, further natural clusters will be found and it is expected that the definitions will need to be amended (Figure 4).

DISCUSSION

The two new clades erected in this paper, combined with those taxa that have previously been defined, provide a sound structural framework upon which the undefined stromboidean taxa can be integrated as reviews are completed. However, while there are murmurings in the Mordorian Halls for a return to a more simplified state of higher taxonomy, to do so would lose the evolutionary meaning that has been achieved with recent revisions, with the loss of definitions contained therein. Therefore, the benefits for understanding the relationships between the different branches of stromboideans cannot be so flippantly disregarded based on a "clutter" argument, unless this heralds a call to return to the dark ages of mass synonymisation of much of stromboidean taxonomy. The integrated use of the PhyloCode and ICZN has been demonstrated to illustrate significant advancements in the understanding of stromboidean systematics.

The difference in the application of the codes with the formulation of names is the use of the first part of the binominal. The ICZN requires the use of the genus for this position, while the PhyloCode (Article 21) "is independent of categorical ranks (Art. 3.1), the first part of a species binomen is not interpreted as a genus name but simply as the name of a taxon that includes that species". In practice, under the ICZN the need to state the specific rank of genus to form a binominal means that a sample taxon *Canarium* (*Stereostrombus*) *hellii* Kiener, 1843 would have to have its ranks below genus listed in brackets. In contrast, the applied PhyloCode may have the same taxon as *Stereostrombus hellii* Kiener, 1843, which ties the first part of the binominal name to the lowest cladistic rank. Another notable difference between the codes when applied is the convention for all equivalent intermediary ranks to be recognised implicitly under the ICZN and the understanding that these are irrelevant, being a repetition of the higher rank, and practically omitted when working within the PhyloCode.

CONCLUSION

We argue that the PhyloCode and ICZN are not mutually exclusive, and that the use of ICZN conforming taxonomy, with the inclusion of a definition, does not exclude either taxonomic systems, but rather improves the ability to bring evolutionary meaning to the nomenclature. We have demonstrated that the use of crown clades forms a strong framework upon which the taxonomy of complex systems can be constructed, and that they do not exclude fossil taxa by their definitional structure. As more revisions of this superfamily are undertaken, there will be a need to utilise other ranks, such as supertribe. The lack of use of these ranks in molluscan studies should not preclude their introduction, as to do so would limit the taxonomist's ability to bring evolutionary and relational meaning to the nomenclature.

LITERATURE CITED

Blackwood, T.J. 2009. *Barneystrombus*, a new genus of Strombidae (Gastropoda) from the Indo-West Pacific, with discussions of included taxa and the general morphology of their shells. Visaya 2(5):11-17.

Dekkers, A.M. & S.J. Maxwell. 2020. An Examination of the Relationships Between Extant *Dolomena* Wenz, 1940, *Doxander* Wenz, 1940, *Mirabilistrombus* Kronenberg, 1998, *Neodilatilabrum* Dekkers, 2008 and *Labiostrombus* Oostingh, 1925 (Stromboidea: Neostromboidae: Strombidae). The Festivus 52(1):39-59.

Fischer, P. 1884. Manuel de Conchyliologie et de Paleontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivants et Fossiles. Paris, Librairie F. Savy.

Gabb, W.M. 1868. An attempt at a revision of the two families Strombidae and Aporrhaidae. American Journal of Conchology 4:137-149.

Gray, J.E. 1850. Figures of molluscous animals, selected from various authors. Longman, Brown, Green and Longmans, London.

International Code of Zoological Nomenclature (ICZN). 1999. 4 Ed.. International Commission on Zoological Nomenclature, London.

International Code of Phylogenetic Nomenclature (PhyloCode). 2020. Phylocode. Cantino P. D. and K. De Queiroz K. Eds.. International Society for Phylogenetic Nomenclature. http://phylonames.org/code/

Irwin, A.R., E.E. Strong, Y. Kano, E.M. Harper, & S.T. Williams. 2021. Eight new mitogenomes clarify the phylogenetic relationships of Stromboidea within the caenogastropod phylogenetic framework. Molecular Phylogenetics and Evolution, in press.

Kiener, L.C. 1843. Famille des Ailées, volume III. Spécies général et iconographie des coquilles vivantes, comprenant la collection du Muséum d'Histoire naturelle de Paris, La collection Lamarck, celle de Prince Massena, (appartenant maintenant à M. le baron Benjamin Delessert) et les découvertes récentes des voyageurs. Chez Rousseau and J.B. Bailliè, Paris.

Latiolais, J.M., M.S. Taylor, K. Roy, & M.E. Helleberg. 2006. A molecular phylogenetic analysis of stromboid gastropod morphological diversity. Molecular Phylogenetics and Evolution 41:436-444.

Linné, C. 1758. Systema naturae, per Regna tria Naturae secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Tomus, Holmiae.

Liverani, V., A.M. Dekkers, & S.J. Maxwell. 2021. Resolving phylogenetic and classical nomenclature: A Revision of *Canarium* Schumacher, 1817 (Mollusca, Neostromboidae, Strombidae). The Festivus 53(1):26-43.

Maxwell, S.J., A.M. Dekkers, T.L. Rymer, & B.C. Congdon. 2019. Recognising and defining a new crown clade within STROMBOIDEA Rafinesque, 1815 (MOLLUSCA, GASTROPODA). ZooKeys 867:1-7.

Maxwell, S.J., A.M. Dekkers, T.L. Rymer, & B.C. Congdon. 2020. Towards Resolving the American and West African Strombidae (Mollusca: Gastropoda: Neostromboidae) Using Integrated Taxonomy. The Festivus 52(1):3-38.

Ponder, W.F. & D.R. Lindberg. 1997. Towards a phylogeny of gastropod mollusks: An analysis using morphological characters. Zoological Journal of the Linnean Society 119:83-265.

Rafinesque, C.S. 1815. Analyse de la Nature, ou tableau de l'Univers et des Corps Organise´es. L'Imprimerie de Jean Barravecchia, Palermo.

Schumacher, C.F. 1817. Essai d'un Nouveau Système des Habitations des vers Testacés. Schultz, Copenhagen.

Thiele, J. 1929. Handbuch der systematischen weichtierkunde, Volume 1. Gustav Fischer Verlag, Jena.

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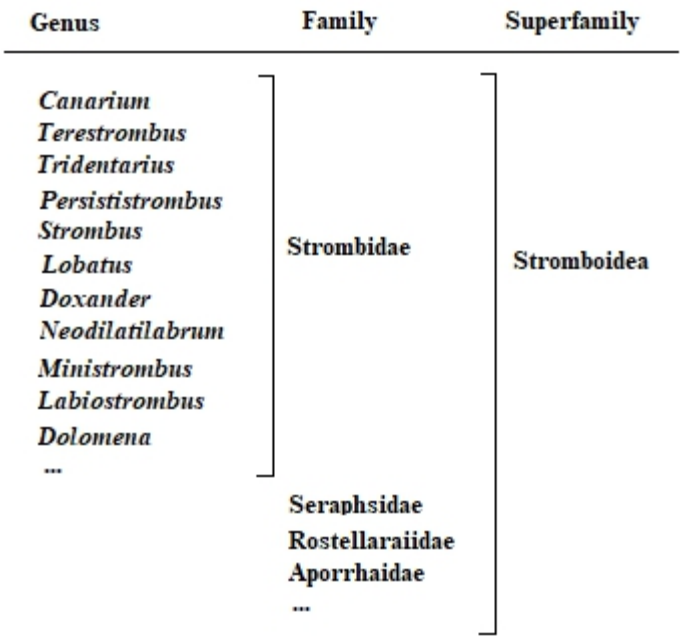

Figure 1. The historical arrangements of Stromboidae (Abbott 1960; Liverani 2013).

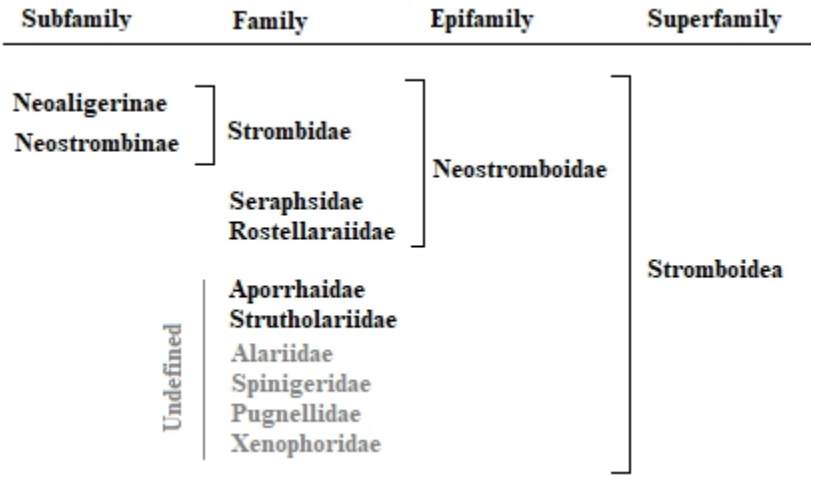

Figure 2. The hypothesised phylogeny of Neostromboidae (Maxwell *et al.* 2019; Irwin *et al.* 2021).

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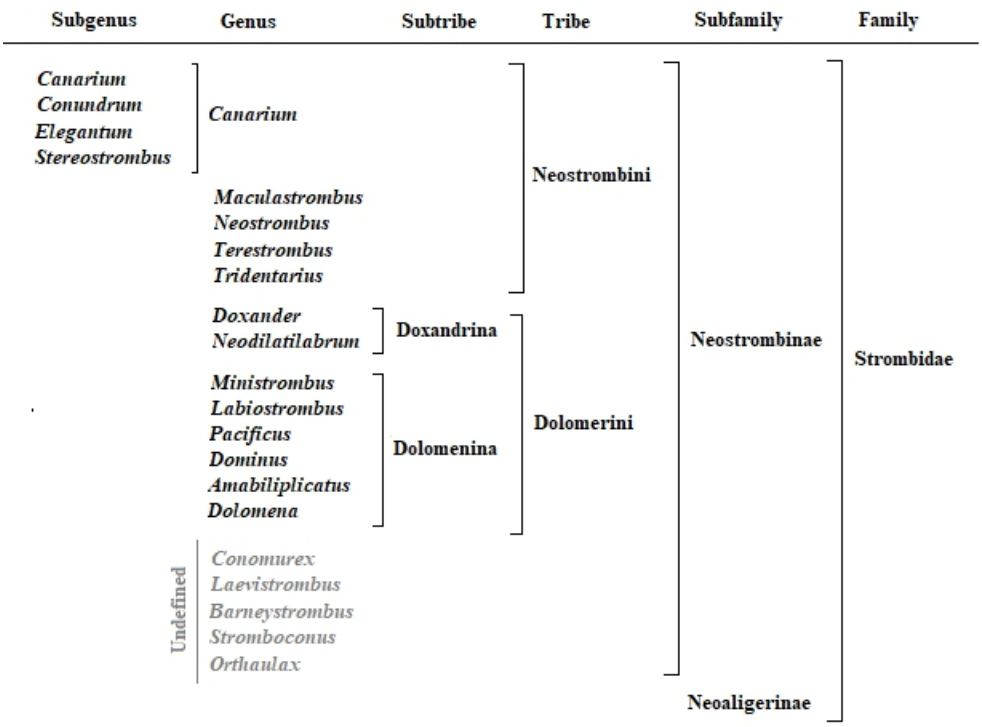

Figure 3. The hypothesised phylogeny of Neostrombinae n. subfam. (Dekkers and Maxwell 2020; Liverani *et al.* 2021).

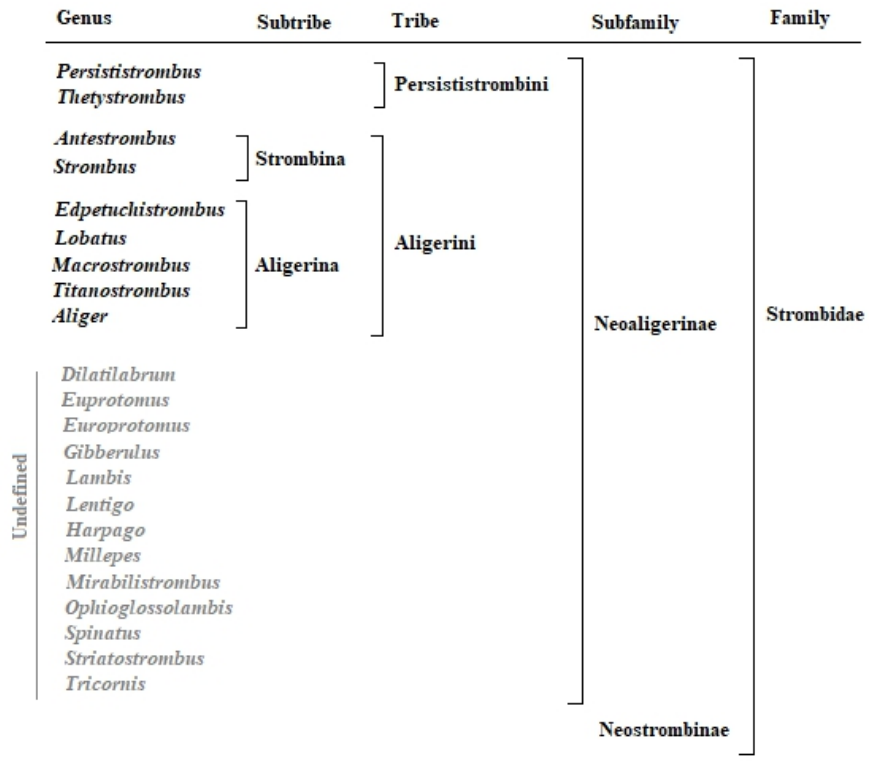

Figure 4. The hypothesised phylogeny of Neoaligerinae n. subfam. (Maxwell *et al.* 2020).