



## Frogs and tuns and tritons – A molecular phylogeny and revised family classification of the predatory gastropod superfamily Tonnoidea (Caenogastropoda)

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### ABSTRACT

The Tonnoidea is a moderately diverse group of large, predatory gastropods with ~360 valid species. Known for their ability to secrete sulfuric acid, they use it to prey on a diversity of invertebrates, primarily echinoderms. Tonnoideans currently are classified in seven accepted families: the comparatively well known, shallow water Bursidae, Cassidae, Personidae, Ranellidae, and Tonnidae, and the lesser-known, deep water Laubierinidae and Pisanianuridae. We assembled a mitochondrial and nuclear gene (COI, 16S, 12S, 28S) dataset for ~80 species and 38 genera currently recognized as valid. Bayesian analysis of the concatenated dataset recovered a monophyletic Tonnoidea, with *Ficus* as its sister group. Unexpectedly, *Thalassocyon*, currently classified in the Ficiidae, was nested within the ingroup as the sister group to *Distorsionella*. Among currently recognized families, Tonnidae, Cassidae, Bursidae and Personidae were supported as monophyletic but the Ranellidae and Ranellinae were not, with Cymatiinae, *Ranella* and *Charonia* supported as three unrelated clades. The Laubierinidae and Pisanianuridae together form a monophyletic group. Although not all currently accepted genera have been included in the analysis, the new phylogeny is sufficiently robust and stable to the inclusion/exclusion of nonconserved regions to establish a revised family-level classification with nine families: Bursidae, Cassidae, Charoniidae, Cymatiidae, Laubierinidae, Personidae, Ranellidae, Thalassocyoniidae and Tonnidae. The results reveal that many genera as presently circumscribed are para- or polyphyletic and, in some cases support the rescue of several genus-group names from synonymy (*Austrosassia*, *Austrotriton*, *Laminilabrum*, *Lampadopsis*, *Personella*, *Proxicharonia*, *Tritonoranella*) or conversely, support their synonymization (*Biplex* with *Gyrineum*). Several species complexes are also revealed that merit further investigation (e.g., Personidae: *Distorsio decipiens*, *D. reticularis*; Bursidae: *Bursa tuberosissima*; Cassidae: *Echinophoria wyvillei*, *Galeodea bituminata*, and *Semicassis bisulcata*). Consequently, despite their teleplanic larvae, the apparently circumglobal distribution of some tonnoidean species is the result of excessive synonymy. The superfamily is estimated to have diverged during the early Jurassic (~186 Ma), with most families originating during a narrow ~20 My window in Albian-Aptian times as part of the Mesozoic Marine Revolution.

### 1. Introduction

The Tonnoidea is a moderately diverse group of marine predatory gastropods, with 361 valid species in 51 genera (MolluscaBase, 2018) living mostly in subtropical to tropical waters of the continental shelf, and with a few species living in depths in excess of 2000 m (Beu, 1998). Commonly known as frog shells, tuns, helmets, and tritons among others, their large and charismatic shells have long been popular with collectors and shell enthusiasts. Among biologists, they are known for their long-lived, teleplanic larvae (Strathmann & Strathmann, 2007) and for their ability to secrete sulfuric acid. Produced by complex salivary glands as part of a cocktail that may also contain chelating agents, mucins, proteases, and low molecular weight peptide toxins, the highly acidic (pH ≤ 2) secretion may be used both for defense through forcible discharge, and for feeding in the immobilization of prey, dissolution of calcareous tests, and digestion both pre- and post-ingestion

(e.g., Houbrick & Fretter, 1969; Andrews et al., 1999; Barkalova et al., 2016; Bose et al., 2017). These moderately large to large snails (many species are in the 50–300 mm range) have been documented to feed on a diversity of invertebrates including other mollusks, echinoderms, polychaetes, sipunculans, barnacles, ascidians, even sponges and fish, but echinoderms appear to constitute their main diet and some species engulf their prey whole (Houbrick & Fretter, 1969; Riedel, 1995b; Andrews et al., 1999; Morton, 1991, 2012). They are such feared predators that their presence may elicit a dramatic flight response, the intensity of which has been hypothesized to increase with the risk of mortality (Legault & Himmelman, 1993). Triton's trumpet, *Charonia tritonis* (Linnaeus, 1758), famously preys on the crown-of-thorns starfish, among other taxa, and its salivary secretions have been found to contain 3800 toxin- and feeding-related proteins, including enzymes that play a role in neutralizing the toxins of its prey (Bose et al., 2017). Like other large predators, the larger tonnoidean species form sparse

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populations that can lead to over-harvesting, and *Cassia cornuta* (Linnaeus, 1758) or the species of *Charonia* Gistel, 1847 are locally protected in some areas. It has been debated whether outbreaks of crown-of-thorns starfish are caused by overfishing of its predator, *C. tritonis*, but this is very unlikely as *C. tritonis* is uncommon everywhere, and a 1994 proposal to list species of *Charonia* on CITES Appendix II was not passed.

The systematics of the Tonnoidea has been torn between collectors' interests – resulting in oversplitting and an inflation of names at all ranks – and consideration for their teleplanic larval development and presumed capacity to cross biogeographical barriers – resulting in broad species hypotheses. In combination with a complex nomenclatural history, the metrics of Recent tonnoidean systematics now amount to a formidable 23 family-group, 147 genus-group and 1052 species-group names. Currently, tonnoideans are classified in seven families – the comparatively well known and shallow-water Bursidae Thiele, 1925, Cassidae Latreille, 1825, Personidae Gray, 1854, Ranellidae Gray, 1854, and Tonnidae Suter, 1913 (1825), and the lesser-known, deep-water Laubierinidae Warén & Bouchet, 1990 and Pisanianuridae Warén & Bouchet, 1990. In recent years, the limits of the superfamily have been disputed, notably the inclusion or exclusion of the family Ficidae Meek, 1864 (1840) (Warén & Bouchet, 1990; Riedel, 1995a) and of the Laubierinidae and Pisanianuridae (Bandel & Riedel, 1994; Riedel, 1995b, 2000). The family and subfamily classification also has been debated, with Bursinae (in Ranellidae) and Cassinae (Tonnidae) recognized at the rank of subfamily in some schemes (Riedel, 1995b, 2000). The extension, rank and affinities of Oocorythinae Fischer, 1885 as either a separate family or as a subfamily in the Cassidae or Tonnidae also have been questioned (see e.g., Warén & Bouchet, 1990; Beu, 2008). Equally controversial is the higher phylogenetic placement of the superfamily. Traditionally perceived as “the most advanced superfamily of the mesogastropods” (Houbrick & Fretter, 1969: 415), morphological approaches to caenogastropod phylogeny inevitably place the Tonnoidea as sister to the Neogastropoda (e.g., Ponder et al., 2008; Simone, 2011), while molecular approaches typically resolve them among the neogastropods (e.g., Riedel, 2000; Colgan et al., 2007; Ponder et al., 2008; Osca et al., 2015). However, representation of Tonnoidea in gastropod phylogenies has been very sparse and has not allowed the circumscription of the superfamily and of its constituent families to be assessed robustly.

### 1.1. History of family classification

Until recently, the classification of the Tonnoidea followed that established by Thiele (1929), who recognized in “Stirps Doliacea” the six families Oocorythidae, Cassidae (as Cassidae), Cymatiidae Iredale, 1913 (1854), Bursidae, Tonnidae (as Doliidae Latreille, 1825) and Ficidae (as “Pirulidae”; = Pyrulidae Swainson, 1840). Thiele followed the traditional position of *Distorsio* Röding, 1798 and related taxa within Cymatiidae. Beu (1981) commenced a slightly more subdivided classification by establishing the subfamily Phaliinae Beu, 1981 for cassids with a strongly twisted anterior siphonal canal and a fan-shaped operculum with the nucleus near the centre of the columellar margin, essentially for the genus *Phalium* Link, 1807 as recognized by Abbott (1968). Beu & Cernohorsky (1986) pointed out that *Ranella* Lamarck, 1816 was considered at that time to be a genus of cymatiid, so Cymatiidae should be known by the much earlier name Ranellidae (which previously had been regarded as a synonym of Bursidae). In 1988, Beu recognized the family Personidae for *Distorsio* and related genera, given their distinctive radula and anatomy, including an extremely long and coiled proboscis, and a long fossil history extending to the Cretaceous.

One of the most significant changes to the extension and classification of the Tonnoidea was that by Warén & Bouchet (1990), who described the new family Laubierinidae for *Akibumia* Kuroda & Habe, 1959 (previously included in Trichotropidae Gray, 1850; = Capulidae Fleming, 1822) and *Laubierina* Warén & Bouchet, 1990, and by

including *Pisanianura* Rovereto, 1899 (previously included in Buccinidae Rafinesque, 1815) in a new subfamily Pisanianurinae Warén & Bouchet, 1990 of the Ranellidae. They also treated *Laminilabrum* Kuroda & Habe, 1961 (also previously included in the “Trichotropidae”) as a synonym of *Pisanianura*. Warén & Bouchet (1990) also pointed out the unique anatomical characters and distinctive protoconch of Ficidae, suggesting it might not be correctly included in Tonnoidea. Riedel (1995a) followed these suggestions, recognizing a separate superfamily Ficoidea. He also proposed the family Thalassocyonidae Riedel, 1995 (as “Thalassocyonidae”) for *Thalassocyon* Barnard, 1960, previously included in the Ficidae. Bandel & Riedel (1994) suggested that Laubierinidae was more closely related to Calyptraeioidea Lamarck, 1809 than to Tonnoidea, and proposed recognition of the superfamily Laubierinoidea. Bandel & Riedel (1994) and Riedel (1995b, 2000) proposed an even more condensed classification of Tonnoidea (as “Cassoidea”) with only three families, such that Cassidae included the subfamilies Cassinae, Oocorythinae, Phaliinae and Tonninae, and Ranellidae included Ranellinae, Bursinae and Cymatiinae. Ranellinae and Oocorythinae were considered paraphyletic stem groups from which the other subfamilies evolved. The Personidae was considered to have diverged early during the Late Cretaceous from a common ancestor with the Ranellidae. Beu (in Beesley et al., 1997) separated the Pisanianurinae from the Ranellidae and elevated it to family rank; Riedel (2000) later transferred the family to the Laubierinoidea.

Beu (1998, 2008, 2010) returned to a modified version of Thiele's (1929) classification, recognizing Bursidae, Cassidae, Laubierinidae (= Pisanianurinae), Personidae, Ranellidae and Tonnidae within Tonnoidea, but separating Ficoidea. Cassidae was subdivided into Cassinae, Oocorythinae and Phaliinae, and Ranellidae was subdivided into Ranellinae, for taxa with varices aligned along opposing sides of the spire, and Cymatiinae, for taxa with varices at each two-thirds of a whorl. Bouchet & Rocroi (2005) adopted a slightly modified view based on Warén & Bouchet (1990) and Beu (1998), retaining Ficoidea as distinct and recognizing six families in the Tonnoidea: Bursidae, Laubierinidae, Personidae, Pisanianuridae, Ranellidae and Tonnidae. Cassinae was included at the rank of subfamily in the Tonnidae along with Tonninae, Oocorythinae and Phaliinae. Cassidae has since been re-elevated to the rank of family (Beu, 2008). Most recently, Bandel & Dockery (2016) transferred Thalassocyonidae to among the Cretaceous stem-group neogastropods Sarganidae Stephenson, 1923 and Weeksiidae Sohl, 1961.

### 1.2. Previous phylogenetic hypotheses

Higher order phylogenetic analyses of caenogastropods typically have included only one or two representative tonnoideans (e.g., Colgan et al., 2007; Ponder et al., 2008; Osca et al., 2015); no molecular investigation has included members of both Ficoidea and Tonnoidea except that of Riedel (2000). The only analysis with sufficient sampling to assess monophyly and relationships among tonnoidean families is that of Simone (2011) based on morphological data. His analysis was based on 32 species from 14 genera of Tonnoidea, which included Ficidae (*Ficus* Röding, 1798, *Thalassocyon*). His results supported a monophyletic Tonnoidea as circumscribed therein as the sister group to the Neogastropoda. *Ficus* was resolved as the sister group to all other tonnoideans, including *Charonia* (Ranellidae) on an isolated branch, Bursidae (*Bursa* Röding, 1798), Tonnidae (*Tonna* Brünnich, 1771), Cassidae (*Cypraeacassis* Stutchbury, 1837, *Phalium*), the remaining ranellids as a paraphyletic assemblage (*Sassia* Bellardi, 1873 + *Fusitriton* Cossmann, 1903, and “*Cymatium*” Röding, 1798), and *Thalassocyon* as the sister group to the Personidae (*Personopsis* Beu, 1988, *Distorsio*). Although his proposed classification recognized both Cymatiidae and Ranellidae at the rank of family, it was not explained how the three pertinent resulting lineages should be distributed among them.

Thus, the monophyly and extension of the Tonnoidea as a whole, its constituent families, and the relationships among them have never been

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