



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

Ellen E. Strong<sup>a,\*</sup>, Nicolas Puillandre<sup>b</sup>, Alan G. Beu<sup>c</sup>, Magalie Castelin<sup>b</sup>, Philippe Bouchet<sup>b</sup>

<sup>a</sup> Department of Invertebrate Zoology, Smithsonian Institution, National Museum of Natural History, 10th and Constitution Ave NW, Washington DC 20560, USA

<sup>b</sup> Institut de Systématique, Évolution, Biodiversité, ISYEB, UMR7205 (CNRS, EPHE, MNHN, UPMC), Muséum National d'Histoire Naturelle, Sorbonne Universités, 43 Rue Cuvier, 75231 Paris Cedex 05, France

<sup>c</sup> GNS Science, PO Box 30-368, Lower Hutt 5040, New Zealand

### 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, *Thalassocycon*, 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, Thalassocyconidae 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

\* Corresponding author.

E-mail address: [StrongE@si.edu](mailto:StrongE@si.edu) (E.E. Strong).

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 Weeksidae 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

**Table 1**

Voucher and GenBank registration numbers, BOLD identification numbers, and locality information for sequenced specimens. All registration numbers refer to specimens deposited in the collection of the MNHN, Muséum National d'Histoire Naturelle, Paris (prefix "IM") or the collections of the Museum of New Zealand Te Papa Tongarewa (prefix "M"). The following refer to shallow-water, shore-based campaigns: ATIMO VATAE – South Madagascar; GUYANE 2014 – French Guiana; INHACA – Inhaca Island, Mozambique; KARUBENTHOS 2012 – Guadeloupe; PANGLAO 2004 – Panglao Island, Bohol, Philippines; SANTO 2006 – Espiritu Santo, Vanuatu; Tasmania – Tasmania, Australia; Western Australia 2011 – Esperance (WE), Albany (WA), Western Australia. The following refer to deep-water, ship-based campaigns: AURORA 2007 – Pacific Ocean, Luzon, Philippines; CONCALIS – New Caledonia; EBISCO – New Caledonia; KARUBENTHOS 2015 – Guadeloupe; MAINBAZA – Mozambique Channel, Madagascar; NORFOLK 2 – Norfolk Ridge; PAKAIHI I TE MOANA – French Polynesia, Marquesas; PANGLAO 2005 – Bohol Sea, Philippines; SALOMON 2 – Solomon Islands; TAIWAN 2004 – South China Sea; TERRASSES – New Caledonia; ZhongSha 2015 – South China Sea. RUNGIS 2009 refers to specimens purchased at the Rungis International Market, Paris. The listed individuals of *Charonia lampas*, *Tritonaranella latitudo*, *Bursina gnotina* and *Monoplex nicobaricus* were merged into composite terminals. Family and genus classification follows that proposed herein.

Taxon	Former taxonomic placement	BOLD IDs	Voucher	COI	16S	12S	28S	Campaign/Country, Station
<b>Outgroups</b>								
<b>Belontiidae</b>								
<i>Belomitra brachytoma</i>		NEOGA1132-11	IM-2009-11057	HQ401573	HQ401662	MH571234	JQ950186	SALOMON 2, CP2184
<b>Conidae</b>								
<i>Conus consors</i>		CONO513-08	IM-2007-17939	EU015751	HQ401672	HQ401605	EU015636	SANTO 2006, AT87
<b>Cypraeidae</b>								
<i>Purpuradusta gracilis</i>		TONO245-18	IM-2009-30992	MH581314	MH571331	MH571254		SANTO 2006, NR19
<b>Epitoniidae</b>								
<i>Surrepfungium</i> sp.		TONO247-18	IM-2009-30998	MH581374	MH571396	MH571306		SANTO 2006, NR16
<b>Ficidae</b>								
<i>Ficus filosa</i>		LIT0R137-10	IM-2007-33633	MH581334	MH571353	MH571267	MH571197	PANGLAO 2004, T31
<b>Harpidae</b>								
<i>Hapa kajiyamai</i>		TONO218-18	IM-2007-40569	EU685626	EU685783	EU685491		SANTO 2006, EP22
<b>Naticidae</b>								
<i>Polinices</i> sp.		TONO246-18	IM-2009-30995	MH581355	MH571374	MH571286		SANTO 2006
<b>Strombidae</b>								
<i>Laevistrombus canarium</i>		TONO281-18	IM-2009-11060	HQ401579	HQ401689	HQ401625		SANTO 2006, VM73
<b>Xenophoridae</b>								
<i>Xenophora solaroides</i>		TONO282-18	IM-2009-11061	HQ401587	HQ401719	HQ401656		SANTO 2006, AT55
<b>Tonnoidea</b>								
<b>Bursidae</b>								
<i>Bufofonia perelegans</i>		TONO034-12	IM-2007-43057	JX241364	JX241118	MH571236	JX241222	SANTO 2006, AT54
<i>Bursa affinis</i>		TONO098-12	IM-2007-43060	JX241367	JX241121	MH571238	MH571175	SANTO 2006, VM02
<i>Bursa awatii</i>		TONO044-12	IM-2007-43058	JX241365	JX241119	MH571243	MH571178	PANGLAO 2005, CP2372
<i>Bursa cubaniana</i>		TONO129-17	IM-2013-20121	MF124185	MH571316	MH571316		KARUBENTHOS 2012, GM02
<i>Bursa fijiensis</i>		TONO013-12	IM-2007-43430	JX241389	MH571315	MH571235	MH571173	TERRASSES, CP3049
<i>Bursa fosteri</i>		TONO096-12	IM-2007-43048	JX241356	JX241111	MH571245	JX241160	PANGLAO 2004, P1
<i>Bursa granularis</i>		TONO019-12	IM-2007-43071	JX241376	JX241130	MH571237	MH571174	SANTO 2006, VM62
<i>Bursa lamarekii</i>		TONO112-12	IM-2007-43046	JX241355	JX241109	MH571290	MH571176	PANGLAO 2004, R73
<i>Bursa quithorai</i>		TONO002-12	IM-2007-43587	JX241413	MH571318	MH571240	MH571162	TERRASSES, DW3102
<i>Bursa rosa</i>		TONO099-12	IM-2007-43045	JX241354	JX241108	MH571291	JX241162	SANTO 2006, DB20
<i>Bursa tuberosissima</i>		TONO106-12	IM-2007-43041	JX241350	JX241104	MH571289	JX241164	PANGLAO 2004, M8
<i>Bursa tuberosissima</i>		TONO113-12	IM-2007-43066	JX241371	JX241125	MH571289	JX241164	PANGLAO 2004, R24
<i>Bursina gnotina</i>		TONO021-18	IM-2009-7252	MH581305				MIRIKY, CP3241
<i>Bursina gnotina</i>		TONO047-12	IM-2009-7260		JX241135			MIRIKY, CP3208
<i>Bursina nobilis</i>		TONO190-18	IM-2007-42721	MH581306	MH571322	MH571247		CONCALIS, DW3000
<i>Lampadopsis rhodostoma</i>	<i>Bursa r. rhodostoma</i>	TONO009-12	IM-2007-43067	JX241372	JX241126	MH571241	JX241223	SANTO 2006, DB53
<i>Lampadopsis rhodostoma</i>	<i>Bursa r. rhodostoma</i>	TONO110-12	IM-2007-43068	JX241373	JX241127	MH571292	JX241224	PANGLAO 2004, R50
<i>Lampadopsis thomae</i>	<i>Bursa r. thomae</i>	TONO266-18	IM-2013-20452	MH581304	MH571321			KARUBENTHOS 2012, GB02
<i>Tritonaranella latitudo</i>	<i>Bursa</i>	TONO100-12	IM-2007-43589	JX241414	MH571317	MH571239		TERRASSES, DW3102
<i>Tritonaranella latitudo</i>	<i>Bursa</i>	MSM037-08	IM-2007-40291	JX241263			JX241184	NORFOLK 2, DW2040

(continued on next page)

Table 1 (continued)

Taxon	Former taxonomic placement	BOLD IDs	Voucher	COI	16S	12S	28S	Campaign/Country, Station
<i>Tritoronanella ranelloides</i>	Bursa	TONO082-12	IM-2009-5149	JX241428	JX241132			MAINBAZA, CP3144
<i>Tutufo bufu</i>		TONO094-12	IM-2007-43036	JX241346	MH571319	MH571242	MH571177	PANGLAO 2004, P3
<i>Tutufo tenuigranosa</i>		TONO031-12	IM-2007-43061	JX241368		MH571246		PANGLAO 2004, P4
<b>Cassidae</b>								
<b>Cassiniae</b>								
<i>Cassia fimbriata</i>		TONO241-18	IM-2009-23323	MH581307	MH571325		MH571180	WESTERN AUSTRALIA 2011, WE02
<i>Cassia flammica</i>		TONO254-18	IM-2013-19516	MH581308	MH571326			KARUBENTHOS 2012, GM02
<i>Cassia madagascariensis</i>		TONO253-18	IM-2013-19553	MH581309	MH571327		MH571181	KARUBENTHOS 2012, GM02
<i>Cypraeacassis rufo</i>		TONO248-18	IM-2013-40295	MH581316	MH571333		MH571184	PAKAHI I TE MOANA, MQ11/2/41 Madagascar
<i>Cypraeacassis testiculus</i>		TONO255-18	IM-2013-19567	MH581317	MH571334		MH571185	KARUBENTHOS 2012, GM14
<i>Dalium barbouri</i>	<i>Eucorys</i>	TONO274-18	IM-2013-61106	MH581331	MH571350		MH571194	KARUBENTHOS 2015, DW4602
<i>Dalium solidum</i>		TONO280-18	IM-2013-56835	MH581318	MH571335			GUYANE 2014, CP4407
<i>Galeodea bituminata</i>		TONO236-18	IM-2007-33627	MH581335	MH571354		MH571198	SANTO 2006, AT102
<i>Galeodea bituminata</i>		TONO192-18	IM-2007-34694	MH581336			MH571199	AURORA 2007, CP2708
<i>Galeodea echinophora</i>		TONO226-18	IM-2009-7834	MH581337	MH571355			RUNGIS 2009, 3
<i>Oocorys sulcata</i>		TONO260-18	IM-2007-33652	MH581349	MH571367		MH571280	SALOMON 2, CP2217
<i>Sconsia alexarhuri</i>		TONO273-18	IM-2013-61442	MH581368	MH571388		MH571220	KARUBENTHOS 2015, DW4638
<i>Sconsia grayi</i>		TONO272-18	IM-2013-60869		MH571389		MH571221	KARUBENTHOS 2015, DW4582
<b>Phaliinae</b>								
<i>Casmaria bohlemani</i>		TONO121-13	IM-2007-33625	KC970027	MH571323		MH571179	SANTO 2006, FR10
<i>Casmaria erinaceus</i>		TONO119-13	IM-2007-33621	KC970029	MH571324			PANGLAO 2004, R3
<i>Echinophoria kurodai</i>		TONO264-18	IM-2007-33650	MH581328	MH571347			EBISCO, CP2582
<i>Echinophoria wyvillei</i>		TONO237-18	IM-2007-33639	MH581329	MH571348		MH571192	SALOMON 2, CP2260
<i>Echinophoria wyvillei</i>		TONO224-18	IM-2007-33647	MH581330	MH571349		MH571193	PANGLAO 2005, CP2332
<i>Phidium areola</i>		TONO235-18	IM-2009-15913		MH571371			ATIMO VATAE, TP19
<i>Phidium glaucum</i>		TONO240-18	IM-2009-23317	MH581352	MH571370			INHACA 2011, MD3
<i>Semicassis bisulcata</i>		TONO228-18	IM-2007-34811	MH581369	MH571390		MH571222	PANGLAO 2005, CP2377
<i>Semicassis bisulcata</i>		TONO238-18	IM-2007-34812	MH581370	MH571391		MH571223	PANGLAO 2005, CP2377
<i>Semicassis</i> sp.		TONO198-18	IM-2007-33622	MH581371	MH571393		MH571225	PANGLAO 2004, P3
<i>Semicassis bulla</i>		TONO197-18	IM-2007-33618		MH571392		MH571224	PANGLAO 2004, P2
<b>Charoniidae</b>								
<i>Charonia lampas</i>	Raneliidae	TONO242-18	IM-2009-23327	MH581310	MH571328			WESTERN AUSTRALIA 2011, WE09
<i>Charonia lampas</i>	Raneliidae	TONO243-18	IM-2007-36559			MH571250		TERRASSES, DW3076
<i>Charonia trionis</i>	Raneliidae	TONO219-18	IM-2007-36517	MH581312	MH571329		MH571182	TERRASSES, CP3048
<i>Charonia variegata</i>	Raneliidae	TONO244-18	IM-2013-20073	MH581311		MH571251		KARUBENTHOS 2012, GM02
<i>Charonia variegata</i>	Raneliidae	TONO252-18	IM-2013-19537	MH581313	MH571330		MH571183	KARUBENTHOS 2012, GM02
<b>Cymatiidae</b>								
<i>Argobuccinum pustulosum</i>	Raneliidae	TONO256-18	M305635-1	MH485162	MH485172		MH485178	Stewart Island, New Zealand
<i>Austrosasia parkinsonia</i>	Raneliidae; Sasia	TONO258-18	IM-2013-42201	MH581364	MH571384		MH571217	TASMANIA, TA34
<i>Austrotriton bassi</i>	Raneliidae; Sasia	TONO257-18	IM-2013-42214	MH581363	MH571383		MH571216	TASMANIA, TA64
<i>Austrotriton subdistortus</i>	Raneliidae; Sasia	TONO257-18	IM-2013-42207	MH581367	MH571387			TASMANIA, TA43
<i>Cabestana tabulata</i>	Raneliidae	TONO267-18	M315865-1	MH485163	MH485173		MH485179	Chatham Islands, New Zealand
<i>Cymatella verrucosa</i>	Raneliidae	TONO223-18	IM-2013-42199	MH581366				TASMANIA, TA4
<i>Disorsomina pusilla</i>	Personidae	TONO223-18	IM-2007-33137	MH581327	MH571346		MH571191	PANGLAO 2004, B9
<i>Fusitriton laudandus</i>	Raneliidae	TONO251-18	M190343-2	MH485164	MH485174		MH485180	New Zealand
<i>Fusitriton magellanicus</i>	Raneliidae	TONO250-18	M305401-1	MH485165	MH485175		MH485181	Argentina
<i>Guttarium muricinum</i>	Raneliidae	TONO261-18	IM-2013-20180	MH581338	MH571356		MH571172	KARUBENTHOS 2012, GM15
<i>Gyrineum aculeatum</i>	Raneliidae; Biplex	TONO216-18	IM-2007-33078	MH581302				PANGLAO 2005, CP2350
<i>Gyrineum gyrinum</i>	Raneliidae	TONO216-18	IM-2007-33134	MH581339	MH571357		MH571200	PANGLAO 2004, B2
<i>Gyrineum hirasei</i>	Raneliidae	TONO204-18	IM-2007-33035	MH581340	MH571358		MH571272	EBISCO, DW2612
<i>Gyrineum lacunatum</i>	Raneliidae	TONO217-18	IM-2007-33149	MH581341	MH571359		MH571201	SANTO 2006, FR06

(continued on next page)

Table 1 (continued)

Taxon	Former taxonomic placement	BOLD IDs	Voucher	COI	16S	12S	28S	Campaign/Country, Station
<i>Gyrineum longicaudatum</i>	Ranellidae	TONO227-18	IM-2007-43376	MH581343	MH571361	MH571275	MH571203	TERRASSES, DW3129
<i>Gyrineum perca</i>	Ranellidae; <i>Biplex</i>	TONO212-18	IM-2007-33102	MH581303	MH571314			PANGLAO 2005, CP2348
<i>Gyrineum roseum</i>	Ranellidae	TONO207-18	IM-2007-33057	MH581342	MH571360	MH571274	MH571202	SANTO 2006, ZB09
<i>Monoplex aquatilis</i>	Ranellidae	TONO205-18	IM-2007-33039	MH581344	MH571362	MH571276		SANTO 2006, AT52
<i>Monoplex comptus</i>	Ranellidae	TONO210-18	IM-2007-33083	MH581345	MH571363	MH571277		PANGLAO 2004, M40
<i>Monoplex nicobaricus</i>	Ranellidae	TONO215-18	IM-2007-33124	MH581347	MH571365		MH571205	SANTO 2006, VM70
<i>Monoplex nicobaricus</i>	Ranellidae	TONO233-18	IM-2009-15903					ATIMO VATAE, TV21
<i>Monoplex krebsii</i>	Ranellidae	TONO268-18	IM-2013-55932	MH581346	MH571364	MH571278	MH571204	GUYANE 2014, CP4350
<i>Monoplex pilearis</i>	Ranellidae	TONO208-18	IM-2007-33064	MH581348	MH571366	MH571279	MH571206	PANGLAO 2004, R66
<i>Personella lewisi</i>	Ranellidae; <i>Sassia</i>	TONO271-18	IM-2013-61171					KARUBENTHOS 2015, DW4613
<i>Proxicharonia palmeri</i>	Ranellidae; <i>Sassia</i>		M314449-1	MH485166	MH485176		MH4851219	North Island, New Zealand
<i>Ranularia canadata</i>	Ranellidae	TONO206-18	IM-2007-33053	MH581360	MH571379	MH571293	MH571214	SANTO 2006, AT119
<i>Ranularia gutturnia</i>	Ranellidae	TONO234-18	IM-2009-15896		MH571380	MH571294		ATIMO VATAE, TM21
<i>Ranularia pyrum</i>	Ranellidae	TONO065-12	IM-2007-43051	JX241359	MH571320	MH571244	JX241159	PANGLAO 2004, R43
<i>Ranularia testudinaria</i>	Ranellidae	TONO213-18	IM-2007-33113	MH581361	MH571381	MH571295	MH571215	SANTO 2006, AT76
<i>Retacuriton pfeifferianus</i>	Ranellidae	TONO220-18	IM-2007-38126	MH581362	MH571382			MIRIKY, CP3204
<i>Sassia remensa</i>	Ranellidae	TONO203-18	IM-2007-33031	MH581365	MH571385	MH571298	MH571218	EBISCO, DW2528
<i>Sassia semitoria</i>	Ranellidae	TONO270-18	IM-2013-59481	MH581365	MH571378		MH571213	ZhongSha 2015, CP4160
<i>Septa rubecula</i>	Ranellidae	TONO265-18	IM-2007-33077	MH581372	MH571394	MH571304	MH571226	PANGLAO 2004, R8
<i>Septa rubecula</i>	Ranellidae	TONO214-18	IM-2007-33117	MH581373	MH571395	MH571305		SANTO 2006, ZB09
<i>Turritriton labiosus</i>	Ranellidae	TONO251-18	IM-2013-7817	MH581381	MH571403			KARUBENTHOS 2012, GS27
<i>Turritriton tenuiliratus</i>	Ranellidae	TONO229-18	IM-2007-38294	MH581382	MH571404	MH571311	MH571232	MAINBAZA, CP3144
<b>Laubierinidae</b>								
<i>Akiburnia orientalis</i>		TONO230-18	IM-2007-36364	MH581301	MH571313	MH571233	MH571171	Western Australia
<i>Laminilabrum brevixae</i>	Pisaniannuridae; <i>Pisaniannura</i>	TONO196-18	IM-2007-35025	MH581353	MH571372	MH571284	MH571208	NORFOLK 2, CH2115
<i>Pisaniannura grimaldii</i>	Pisaniannuridae	TONO191-18	IM-2007-34532	MH581354	MH571373	MH571285	MH571209	AURORA 2007, CP2753
<b>Personidae</b>								
<i>Disorsio clathrata</i>		TONO269-18	IM-2013-55936	MH581319	MH571336		MH571186	GUYANE 2014, CP4350
<i>Disorsio constricta</i>		TONO276-18	IM-2013-56468		MH571337		MH571187	GUYANE 2014, CP4378
<i>Disorsio constricta</i>		TONO277-18	IM-2013-56487		MH571338		MH571188	GUYANE 2014, CP4379
<i>Disorsio decipiens</i>		TONO194-18	IM-2007-34733	MH581323	MH571342	MH571259	MH571190	AURORA 2007, CP2665
<i>Disorsio decipiens</i>		TONO193-18	IM-2007-34718	MH581325	MH571344	MH571261		AURORA 2007, CP2666
<i>Disorsio euconstricta</i>		TONO225-18	IM-2007-33061	MH581320	MH571339	MH571256		PANGLAO 2005, DW2374
<i>Disorsio habei</i>		TONO263-18	IM-2007-33037	MH581321	MH571340	MH571257		EBISCO, CP2517
<i>Disorsio reticularis</i>		TONO262-18	IM-2007-33153	MH581326	MH571345	MH571262		SANTO 2006, AT43
<i>Disorsio reticularis</i>		TONO209-18	IM-2007-33079	MH581324	MH571343	MH571260		PANGLAO 2005, CP2377
<i>Personopsis grasi</i>		TONO275-18	IM-2013-60657	MH581350	MH571368		MH571207	KARUBENTHOS 2015, DW4565
<i>Personopsis purpurata</i>		TONO222-18	IM-2007-33107	MH581351	MH571369			EBISCO, DW2496
<b>Ranellidae</b>								
<i>Ranella australasia</i>		TONO239-18	IM-2009-23315	MH581357	MH571376		MH571211	WESTERN AUSTRALIA 2011, WA20
<i>Ranella australasia</i>		TONO259-18	IM-2013-42202	MH581356	MH571375	MH571287	MH571210	TASMANIA, TA34
<i>Ranella olearium</i>		TONO231-18	IM-2007-36318	MH581358	MH571377	MH571288	MH571212	MAINBAZA, CC3151
<b>Thalassocyoniidae</b>								
<i>Distorsionella lewisi</i>	Personidae	TONO211-18	IM-2007-33093	MH581322	MH571341	MH571258	MH571189	EBISCO, DW2578
<i>Thalassocyon tui</i>	Ficidae		M301820-1	MH485167	MH485177			New Zealand
<b>Tonnidae</b>								
<i>Eudolium bairdii</i>		TONO199-18	IM-2007-33624	MH581332	MH571351	MH571265	MH571195	SANTO 2006, AT59
<i>Eudolium crosseanum</i>		TONO202-18	IM-2007-33646	MH581333	MH571352	MH571266	MH571196	TAIWAN 2004, CH257
<i>Tonna allium</i>		TONO201-18	IM-2007-33632	MH581375	MH571397	MH571307	MH571227	PANGLAO 2004, M11
<i>Tonna dunkeri</i>		TONO232-18	IM-2009-15933	MH581376	MH571398	MH571228	MH571228	ATIMO VATAE, BM10
<i>Tonna galea</i>		TONO278-18	IM-2013-56652	MH581377	MH571399	MH571308	MH571229	GUYANE 2014, CP4391
<i>Tonna galea</i>		TONO279-18	IM-2013-56653	MH581378	MH571400		MH571230	GUYANE 2014, CP4391
<i>Tonna perlix</i>		TONO200-18	IM-2007-33629	MH581379	MH571401		MH571231	PANGLAO 2004, R34
<i>Tonna sulcosa</i>		TONO195-18	IM-2007-34839	MH581380	MH571402	MH571310		AURORA 2007, CP2764

assessed robustly with molecular data. To do so, we have assembled the most inclusive taxonomic and molecular data set compiled thus far, comprising four mitochondrial and nuclear genes (COI, 16S, 12S, 28S) for ~80 species and 38 genera currently recognized, or ~22% of accepted species diversity and ~75% of the 51 accepted Recent genera. This material has been assembled over the course of 21 shore- and ship-based expeditions in 12 countries (Australia, French Polynesia, Guadeloupe, Madagascar, Mozambique, New Caledonia, New Zealand,

Papua New Guinea, Philippines, Solomon Islands, Taiwan, Vanuatu) from intertidal to > 1500 m depth and includes many rare deep-water taxa ([expeditions.mnhn.fr](http://expeditions.mnhn.fr); Table 1). To test the possible affinities of ficoideans and tonnoideans we have included for the first time in any molecular analysis the singular, deep-water genus *Thalassocyon*. We also explore the timing of diversification of the group and the major lineages using fossil calibration.

**Table 2**

Representatives of type species (or their synonyms) of available genus-group names included in the present analysis. Family and genus classification follows that proposed herein.

Family	Genus	Included species
<b>Bursidae Thiele, 1925</b>		
	<i>Dulcerana</i> Oyama, 1964	<i>Bursa granularis</i> (Röding, 1798)
	<i>Bursina</i> Oyama, 1964	<i>Bursina nobilis</i> (Reeve, 1844)
	<i>Lampadopsis</i> Jousseume, 1881	<i>Lampadopsis rhodostoma</i> (G.B. Sowerby II, 1835)
	<i>Tritonoranella</i> Oyama, 1964	<i>Tritonoranella ranelloides</i> (Reeve, 1844)
	<i>Tutufa</i> Jousseume, 1881	<i>Tutufa bubo</i> (Linnaeus, 1758)
<b>Cassidae Latreille, 1825</b>		
<b>Cassiniae Latreille, 1825</b>		
	<i>Hypocassis</i> Iredale, 1927	<i>Cassis fimbriata</i> Quoy & Gaimard, 1833
	<i>Cypraecassis</i> Stutchbury, 1837	<i>Cypraecassis rufa</i> (Linnaeus, 1758)
	<i>Dalium</i> Dall, 1889	<i>Dalium solidum</i> Dall, 1889
	<i>Galeodea</i> Link, 1807, <i>Morio</i> Montfort, 1810, <i>Cassidaria</i> Lamarck, 1816, <i>Echinora</i> Schumacher, 1817	<i>Galeodea echinophora</i> (Linnaeus, 1758)
	<i>Oocorys</i> P. Fischer, 1884	<i>Oocorys sulcata</i> P. Fischer, 1884
	<i>Sconsia</i> Gray, 1847	<i>Sconsia grayi</i> A. Adams, 1855
<b>Phaliinae Beu, 1981</b>		
	<i>Casmaria</i> H. Adams & A. Adams, 1853	<i>Casmaria erinaceus</i> (Linnaeus, 1758)
	<i>Phalium</i> Link, 1807, <i>Bezoardica</i> Schumacher, 1817,	<i>Phalium glaucum</i> (Linnaeus, 1758)
	<i>Semicassis</i> Mörch, 1852	<i>Semicassis bisulcata</i> (Schubert & J. A. Wagner, 1829)
<b>Charoniidae Powell, 1933</b>		
	<i>Charonia</i> Gistel, 1847	<i>Charonia tritonis</i> (Linnaeus, 1758)
	<i>Buccinatorium</i> Mörch, 1877	<i>Charonia variegata</i> (Lamarck, 1816)
<b>Cymatiidae Iredale, 1913 (1854)</b>		
	<i>Gondwanula</i> Finlay, 1926	<i>Argobuccinum pustulosum</i> (Lightfoot, 1786)
	<i>Austrosassia</i> Finlay, 1931	<i>Austrosassia parkinsonia</i> (Perry, 1811)
	<i>Negyryna</i> Iredale, 1929	<i>Austrotriton subdistortus</i> (Lamarck, 1822)
	<i>Cymatiella</i> Iredale, 1924	<i>Cymatiella verrucosa</i> (Reeve, 1844)
	<i>Distorsomina</i> Beu, 1998	<i>Distorsomina pusilla</i> (Pease, 1861)
	<i>Fusitriton</i> Cossmann, 1903, <i>Cryotritonium</i> Martens, 1904	<i>Fusitriton magellanicus</i> (Röding, 1798)
	<i>Gutturium</i> Mörch, 1852	<i>Gutturium muricinum</i> (Röding, 1798)
	<i>Gyrineum</i> Link, 1807	<i>Gyrineum gyrinum</i> (Linnaeus, 1758)
	<i>Biplex</i> Perry, 1810	<i>Gyrineum perca</i> (Perry, 1811)
	<i>Cymatriton</i> Clench & Turner, 1957	<i>Monoplex nicobaricus</i> (Röding, 1798)
	<i>Lampusia</i> Schumacher, 1817	<i>Monoplex pilearis</i> (Linnaeus, 1758)
	<i>Tritonocauda</i> Dall, 1904	<i>Ranularia caudata</i> (Gmelin, 1791)
	<i>Ranularia</i> Schumacher, 1817	<i>Ranularia gutturnia</i> (Röding, 1798)
	<i>Reticutriton</i> Habe & Kosuge, 1966	<i>Reticutriton pfeifferianus</i> (Reeve, 1844)
	<i>Phanozesta</i> Iredale, 1936	<i>Sassia remensa</i> (Iredale, 1936)
	<i>Septa</i> Perry, 1810, <i>Simpulum</i> Mörch, 1852	<i>Septa rubecula</i> (Linnaeus, 1758)
	<i>Tritoniscus</i> Dall, 1904, <i>Particymatium</i> Iredale, 1936	<i>Turritriton labiosus</i> (Wood, 1828)
<b>Laubierinidae Warén &amp; Bouchet, 1990</b>		
	<i>Laminilabrum</i> Kuroda & Habe in Habe, 1961	<i>Laminilabrum brevixae</i> Kuroda & Habe in Habe, 1961
<b>Personidae Gray, 1854</b>		
	<i>Rhysema</i> Clench & Turner, 1957	<i>Distorsio clathrata</i> (Lamarck, 1816)
	<i>Personopsis</i> Beu, 1988	<i>Personopsis grasi</i> (Bellardi in d'Ancona, 1872)
<b>Ranellidae Gray, 1854</b>		
	<i>Mayena</i> Iredale, 1917	<i>Ranella australasia</i> (Perry, 1811)
	<i>Ranella</i> Lamarck, 1816, <i>Gyrina</i> Schumacher, 1817, <i>Eugyrina</i> Dall, 1904	<i>Ranella olearium</i> (Linnaeus, 1758)
<b>Thalassocyonidae Riedel, 1994</b>		
	<i>Distorsionella</i> Beu, 1978	<i>Distorsionella lewisi</i> (Beu, 1978)
<b>Tonnidae Suter, 1913 (1825)</b>		
	<i>Eudolium</i> Dall, 1889	<i>Eudolium crosseanum</i> (Monterosato, 1869)
	<i>Tonna</i> Brünnich, 1771, <i>Dolium</i> Lamarck, 1801,	<i>Tonna galea</i> (Linnaeus, 1758)
	<i>Cadus</i> Röding, 1798, <i>Cadium</i> Link, 1807, <i>Foratidolium</i> Rovereto, 1899	<i>Tonna perdx</i> (Linnaeus, 1758)

## 2. Materials and methods

### 2.1. Taxon sampling

To test the monophyly of the superfamily, 10 outgroups were selected, representing several neogastropod families (Belomitridae, Conidae, Harpidae) and a variety of other caenogastropods (Cypraeidae, Epitoniidae, Ficidae, Naticidae, Strombidae, Xenophoridae). Among the ingroup, ~80 species as currently recognized were included, representative of the morphological diversity of the superfamily, including such rare and elusive genera, mostly from deep water, as *Akibumia*, *Dalium* Dall, 1889, *Distorsionella* [Beu, 1978](#), *Distorsomina* [Beu, 1998](#), *Personopsis*, *Pisanianura*, *Oocorys* P. Fischer, 1884 and *Thalassocyon* ([Table 1](#)). Among these species are 42 representatives of type species (or their synonyms) of available genus names ([Table 2](#)).

### 2.2. DNA sequencing and alignment

The majority of specimens included in this study were obtained during expeditions organized by the MNHN and Pro-Natura International as part of the *Our Planet Reviewed* program, and by the MNHN and the Institut de Recherche pour le Développement as part of the *Tropical Deep-Sea Benthos* program (see [Table 1](#) and Acknowledgements). These specimens were processed in the field specifically for molecular analysis and were anesthetized using magnesium chloride (MgCl<sub>2</sub>) or were microwaved to separate the animal from the shell ([Galindo et al., 2014](#)). Tissue clips of foot tissue were preserved in 95–98% ethanol. The shell vouchers of all sequenced specimens were kept intact for identification purposes and have been deposited in the collections of the Muséum national d'Histoire naturelle in Paris and of the Museum of New Zealand Te Papa Tongarewa in Wellington (see [Table 1](#)).

Two labs contributed sequences for this study, using slightly different protocols: the Muséum national d'Histoire naturelle in Paris (MNHN) and the National Museum of Natural History in Washington DC (USNM). The MNHN generated the mitochondrial cytochrome c oxidase I (COI) dataset, while both labs amplified fragments of the mitochondrial 16S rRNA and 12S rRNA genes as well as the nuclear 28S rRNA (MNHN – primers C1/D2; USNM – primers D23/D6). The primers used for amplification and sequencing are listed in [Table 3](#).

At the MNHN, total genomic DNA was extracted from foot tissue using NucleoSpinR 96 Tissues (Macherey-Nagel) and following the manufacturer's instructions. PCR reactions were performed in 25 µL final volume, containing approximately 3 ng template DNA, 1.5 mM MgCl<sub>2</sub>, 0.26 mM of each nucleotide, 0.3 µM of each primer, 5% DMSO and 0.75 U of Taq Polymerase (Qbiogene). Amplification products were generated by an initial denaturation step of 4 min at 94 °C followed by 35 cycles at 94 °C for 40 s, annealing at 50 °C for COI, 52 °C for 28S, 51 °C for 12S rRNA and 16S rRNA for 40 s and by an extension at 72 °C for 1 min. PCR products were purified and sequenced by sequencing

facilities (Genoscope and Eurofins).

At the USNM, total genomic DNA was extracted using a phenol-chloroform protocol on an AutoGen GenePrep965 (AutoGen, Holliston, MA) according to the manufacturer's mouse-tail protocol. Each locus was amplified using Bioline Biolase taq (BIO-21042) according to manufacturers instructions but modified to either 10 µL (16S, 12S) or 20 µL (28S) reaction volumes. Cycling parameters for each gene region were optimized as follows: 16S – initial denaturation for 5 min at 95 °C + 40 cycles (30 s at 95 °C + 30 s at 54 °C + 1 min at 72 °C) + 3 min at 72 °C; 12S – initial denaturation for 5 min at 95 °C + 35 cycles (30 s at 95 °C + 30 s at 52 °C + 45 s at 72 °C) + 7 min at 72 °C; 28S – initial denaturation for 3 min at 95 °C + 7 cycles (30 s at 95 °C + 30 s at 65 °C + 1 min at 72 °C) + 30 cycles (30 s at 95 °C + 30 s at 60 °C + 1 min at 72 °C) + 5 min at 72 °C. PCR products were visualized by agarose gel electrophoresis (1.5% agarose) and purified with ExoSAP-IT (Affymetrix) according to manufacturer's protocols prior to sequencing. Sequencing reactions were performed using 1 µL of purified PCR product in a 10 µL reaction containing 0.5 µL primer, 1.75 µL Big Dye buffer and 0.5 µL Big Dye (Life Technologies), and were carried out under standard cycling conditions (25 cycles of 5 s at 95 °C + 10 s at 50 °C + 4 min at 60 °C). Reactions were purified using Millipore Sephadex plates (MAHVN-4550) according to the manufacturer's instructions and sequenced on an ABI 3730XL automated DNA sequencer at the Laboratories of Analytical Biology at the USNM.

All genes were sequenced in both directions to ensure accuracy. Chromatograms were edited and assembled using CodonCode Aligner version 7.1.2 (CodonCode Corporation, Dedham, MA) (MNHN) or Sequencher v. 4.7 (GeneCodes, Ann Arbor, MI, USA) (USNM). All sequences have been deposited in BOLD and GenBank (see [Table 1](#)).

### 2.3. Alignment and phylogenetic analyses

Sequences were aligned separately for each gene partition with ClustalX ([Thompson et al., 1997](#)) using default parameter values as implemented in Geneious 10.1. Nonconserved regions were removed with Gblocks version 0.91b ([Castresana, 2000](#)) using all three options for a less-stringent selection (allowing “smaller final blocks”, “gap positions within the final blocks” and “less strict flanking positions”). The final aligned length for each partition, with and without nonconserved regions, is as follows: COI – 658 base pairs (bp); 16S – 514 (483) bp; 12S – 611 (489); 28S – 1245 (305). This resulted in an aligned concatenated dataset of 3028 bp including nonconserved regions, and of 1935 bp with nonconserved regions removed.

Phylogenetic reconstructions were conducted using Maximum Likelihood (ML) and Bayesian Inference (BI). The best fit partitions and models for phylogenetic analyses were determined with PartitionFinder 1.1.1 ([Lanfear et al., 2012](#)) which favored the following scheme: COI: SYM + I + G, GTR + I + G, HKY + G, for the first, second and third codon position, respectively; 16S, 12S, 28S: GTR + I + G. ML analyses of the concatenated datasets (including and excluding nonconserved regions) were performed using RAxML-HP2 (8.2.10) ([Stamatakis,](#)

**Table 3**  
Primers used for amplification and sequencing.

Gene	Primer	Sequence (5'-3')	Direction	Reference	Amplicon length
COI	LCOI1490	GGT CAA CAA ATC ATA AAG ATA TTG G	F	<a href="#">Folmer et al. (1994)</a>	660
COI	HCOI2198	TAA ACT TCA GGG TGA CCA AAA AAT CA	R	<a href="#">Folmer et al. (1994)</a>	
16S	16Sa-L	CGC CTG TTT ATC AAA AAC AT	F	<a href="#">Palumbi (1996)</a>	460
16S	16Sb-H2	CTC CGG TTT GAA CTC AGA TCA	R	<a href="#">Palumbi (1996)</a>	
12S	12SA	AAA CTG GGA TTA GAT ACC CCA CTA T	F	<a href="#">Palumbi (1996)</a>	370
12S	12SB	GAG GGT GAC GGG CGG TGT GT	R	<a href="#">Palumbi (1996)</a>	
28S	C1'	ACC CGC TGA ATT TAA GCA T	F	<a href="#">Jovelin and Justine (2001)</a>	830
28S	D2	TCC GTG TTT CAA GAC GGG	R	<a href="#">Jovelin and Justine (2001)</a>	
28S	D23	GAG AGT TCA AGA GTA CGT G	F	<a href="#">Park and O'Foighil (2000)</a>	670
28S	D6	CCA GCT ATC CTG AGG GAA ACT TCG	R	<a href="#">Park and O'Foighil (2000)</a>	

2006a; Stamatakis et al., 2008) on XSEDE V. 3.3 as implemented on the CIPRES Science Gateway (Miller et al., 2010). A mixed/partitioned model was selected, partitioned according to the partitions returned by PartitionFinder. GTRCAT (Stamatakis, 2006b) was used for the bootstrapping phase, and GTRGAMMA for final tree inference. Nodal support was assessed using 1000 nonparametric bootstrap replicates (Felsenstein, 1985). For BI of the concatenated datasets (including and excluding nonconserved regions) and of the individual gene partitions (including nonconserved regions, only), Bayesian phylogenies for each gene partition (COI, 16S, 12S, 28S) and for the two concatenated datasets (with and without nonconserved regions) were inferred with MrBayes 3.2.6 (Ronquist & Huelsenbeck, 2003) on the CIPRES Science Gateway, using the schemes and models indicated by PartitionFinder. Bayesian analyses, consisting of two independent replicates with four heated chains each (0.02), and three swaps per swapping cycle, were run for 50,000,000 Markov chain Monte Carlo (MCMC) generations with a sampling frequency of one tree every 1000 generations. The first 25% were discarded as burn-in. Tracer 1.6 (Rambaut et al., 2014) was used to assess MCMC convergence and to ensure that all ESS values exceeded 200. A majority rule consensus tree for each analysis was inferred with the `sumt` command in MrBayes. Nodal support was assessed with posterior probability of each node.

Nodes with posterior probabilities (PP) lower than 0.90 and bootstrap values (BS) lower than 70% were considered unsupported, those with between 0.90 and 0.95 and 71–90% as moderately supported, and those with greater than 0.95 and 90% as highly supported.

Fossil calibrations used in the MrBayes analysis are listed in Table 4. As has been noted before, one challenge of calibrating molecular phylogenies stems from the difficulty in allocating often fragmentary and/or morphologically divergent early fossils confidently to crown-group lineages. We faced the additional challenge that many early fossils have been assigned to genera that are para- or polyphyletic on our tree (e.g. *Sassia*, *Gyrineum* Link, 1807; see Results). Further, it seems likely that the genus-group assignment of some of these early fossils requires closer scrutiny. For example, species referred to *Gyrineum* before the Miocene fossils in southern Australia (*G. maccoyi* Pritchard, 1898) are not convincing members of this genus [e.g., *G. judithae* Zinsmeister, 1983 (Paleocene, California)]. Other putative early tonnoidean fossils appear upon closer examination to belong to other taxonomic groups. For example, in a work revising d'Orbigny's (1842–1843) Cretaceous gastropods, Kollmann (2005) established the new genus *Rouenia*, referred to Cassidae, for a rather globose species with spiral cords and a slightly flared lip that d'Orbigny (1843) had referred to *Pterocera* Lamarck, 1799 (Stromboidea). From the Cenomanian of the Paris Basin, it would be the earliest cassid, and among the earliest Tonnoidea, if the position were correct. We follow d'Orbigny (1843) and consider a placement in Stromboidea, possibly in the Aporrhaidae, to be more likely. Riedel (1995b: 123) accepted *Haydenia impressa* Gabb, 1865 as a likely Maastrichtian (Late Cretaceous) representative of Cassidae (Stewart, 1927: 381, pl. 20, Figs. 5, 5a). Again, this would represent one of the earliest fossil cassids if correct. However, with its straight, widely open, typically neogastropod siphonal canal and a low-spined bucciniform shape, it more closely resembles taxa of Pseudolividae (Neogastropoda). Kiel & Bandel (2003) referred a mid-Santonian–early Campanian (Late Cretaceous, ca. 85–80 Ma) species to *Galeodea* (*Taieria*)

Finlay & Marwick, 1931. However, their illustrated shell has a wide, concave sutural ramp demarcated by a peripheral keel, weak sculpture on the apical half of the whorls, prominent, rounded spiral cords on the abapical half, and a straight siphonal canal, and in our opinion is a muricoidean neogastropod. Kiel & Bandel (2003) and Bandel & Dockery (2016) also referred the Cretaceous genus *Anomalofusus* Wade, 1916 to the Ranellidae (=Cymatiidae of the present paper) on the basis of protoconch morphology, but again we interpret their illustrated shells as muricoidean neogastropods. Consequently, some early fossil occurrences as reported in the literature have not been used here.

MrBayes 3.2.6 was used to reconstruct a dated tree, using the same partitions and substitution models as defined before. Two parallel analyses were run, each consisting of four Markov chains of 100,000,000 generations with a sampling frequency of one tree every 10,000 generations, number of swaps set to three and the chain temperature to 0.02. A birthdeath clock model was applied for the branch length estimations, coupled with an Independent Gamma Rate (clockvarpr = igr) for the clock rate, with an IGR parameter (igrvarpr) set to exp(10). The base substitution rate of the tree (clockratepr) was set to follow a lognormal distribution (mean =  $-7.08069$ , s.d. =  $2.458582$ ). The age of the calibrated nodes followed a lognormal distribution (minimum ages are provided in the Table 4; mean ages = minimum ages + 5; s.d. = 1). Convergence of the analysis was evaluated using Tracer 1.6 (Rambaut et al., 2014), to ensure that all ESS values exceeded 200. A consensus tree was then calculated after omitting the first 25% trees as burn-in.

### 3. Results

*Ficus* is supported as the sister group to a monophyletic Tonnoidea, which also includes *Thalassocyon*, a genus currently placed in the Ficidae (Fig. 1; Supplementary Fig. 1). Monophyly of the ingroup was only returned in the 28S gene tree from among the four individual gene partitions (COI, 12S, 16S, 28S; Supplementary Figs. 2–5). The ingroup has moderate support in the concatenated analysis with nonconserved regions removed (Fig. 1; PP = 0.93), and forms two main clades, one without significant support (Clade A + B) and one with high support (Clade C-I; PP = 1). In the analysis including nonconserved regions, the ingroup does not have significant support (Supplementary Fig. 1; PP = 0.76), and forms a polytomy of three robustly supported clades (Clades A, B, C-I). Clade A unites *Thalassocyon* (Ficidae) with *Distorsionella* (Personidae) with high support (PP = 1; BS = 100) in both concatenated analyses. This clade was supported in the three gene trees for which both taxa were sequenced (COI, 16S, 12S). Clade B unites *Distorsio* and *Personopsis*, both currently placed in the Personidae, also with high support (PP = 1; BS = 100); both genera are supported as monophyletic with high support (PP = 1; BS = 100). These results were obtained in both concatenated analyses and in all individual gene trees, with the exception of the 12S and 28S gene trees, which could not evaluate monophyly of *Personopsis* as only a single specimen was sequenced for these two genes.

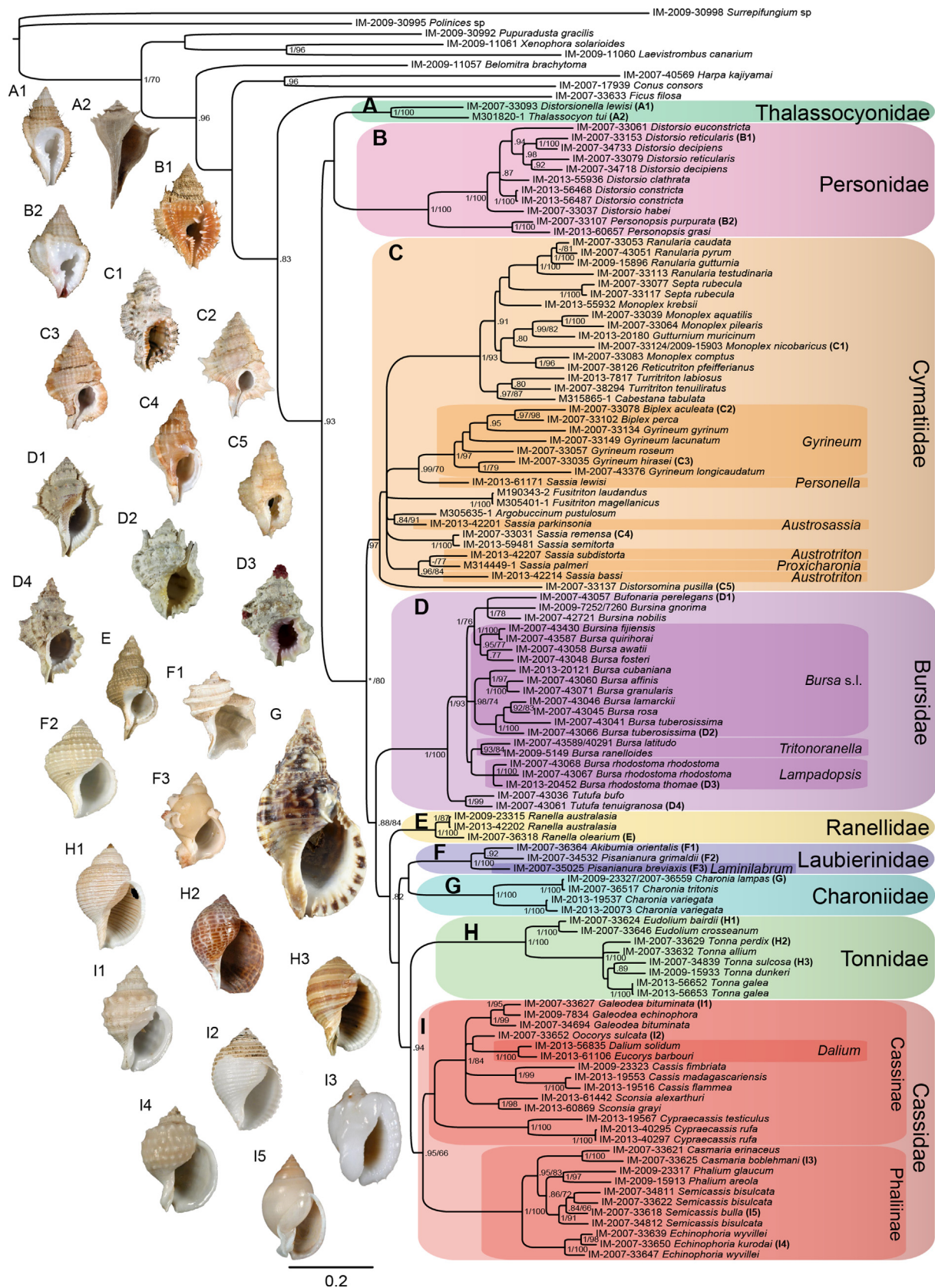
Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ymp.2018.09.016>.

Clades C-I are united in a large monophyletic group with moderate to high support in both concatenated analyses, both with (PP = 1;

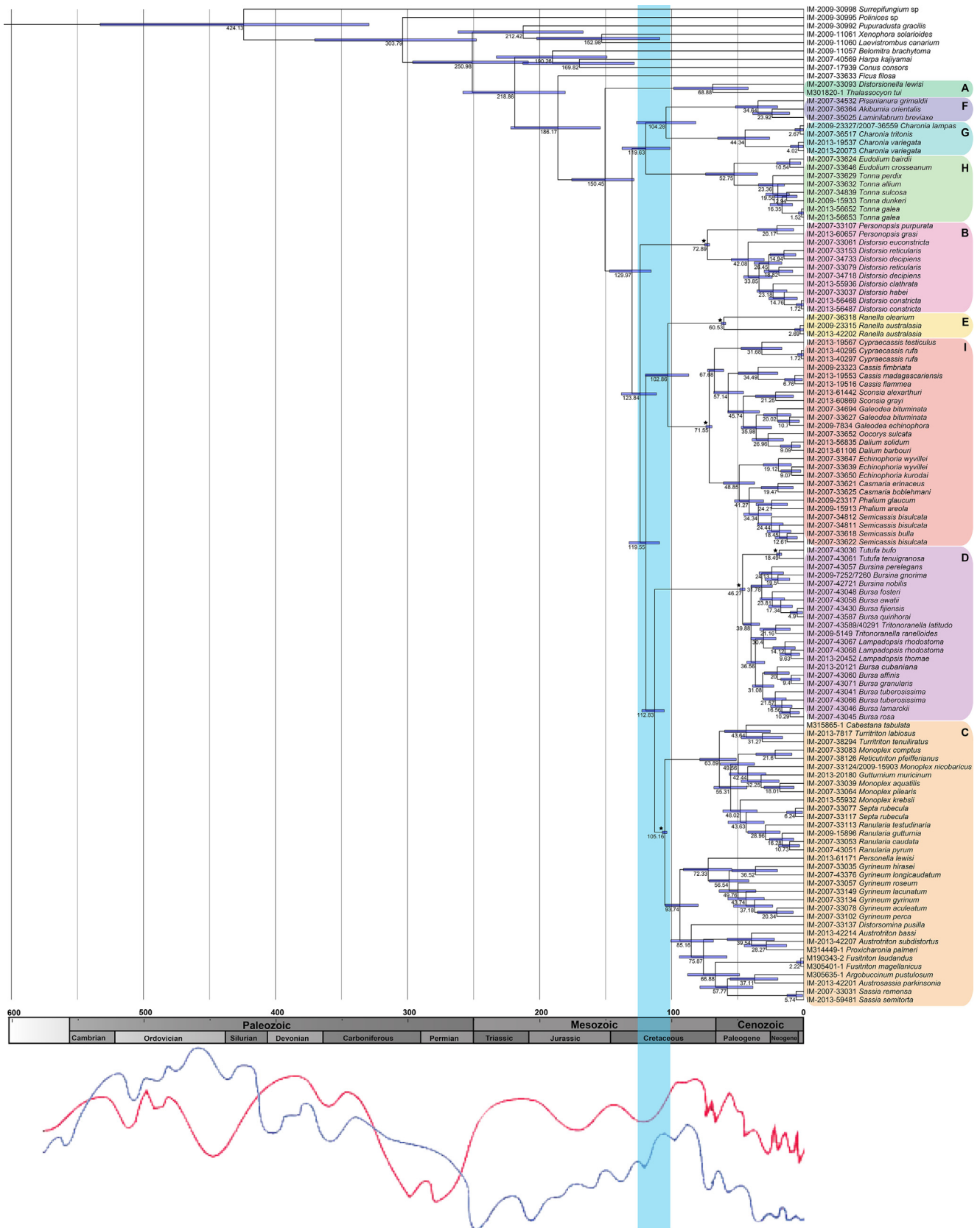
**Table 4**  
Fossil calibrations used in MrBayes analysis. Dates are from Gradstein et al. (2012).

Taxon	Node	Epoch/Stage	Age (Ma)	References
Gen. sp. indet.	Cymatiidae	Albian	113–100.5	Schröder (1995), Mutterlose et al. (2003)
<i>Galeodea</i> spp.	Cassidae	Maastrichtian	72.1–66.0	Riedel (1995b)
<i>Distorsio praegransosa</i> (Cottreau, 1922)	Personidae	basal Upper Maastrichtian	70–68	Cottreau (1922), Kennedy (1986)
<i>Ranella louellae</i> Beu, 1988	Ranellidae	Late Paleocene	59.2–56	Beu (1988)
<i>Marsupina yasila</i> (Olsson, 1930)	Bursidae	Middle Eocene	47.8–41.2	Olsson (1930), Fildani et al. (2008)
<i>Tutufa</i> sp.	<i>Tutufa</i>	Middle Miocene	15.5–13.5	Tomida et al. (2013), Okada (1987)





**Fig. 1.** Bayesian phylogram based on a concatenated mitochondrial (COI, 12S, 16S) and nuclear gene (28S) dataset, with nonconserved regions removed. Bayesian posterior probabilities (PP  $\geq 0.75$ ) and bootstrap values (BS  $\geq 65\%$ ) are indicated at the nodes. Figured specimens are sequenced vouchers; voucher registration numbers are indicated for each terminal. Terminal tips are labeled according to the current taxonomy; revised genus- and family-level classification follows that proposed herein. See Table 1 for sources. Scale bar indicates number of nucleotide substitutions per site.



**Fig. 2.** Maximum clade credibility chronogram obtained from Bayesian analysis of the concatenated dataset, with nonconserved regions removed, calibrated with six fossils. Genus-level classification follows that proposed herein. Time indicated in millions of years; posterior mean ages at the nodes. Blue bars, 95% credibility intervals. Stars indicate calibrated nodes. ~20 My interval during early Cretaceous marking origin of most family crown group lineages in light blue. Global sea level curve (blue) and mean global temperature (red) modified from <http://www.open.edu/openlearn/science-maths-technology/science/geology/geological-processes-the-british-isles/content-section-3#fig003-002>. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

BS = 80) and without (PP = 0.96; BS = 81) nonconserved regions removed, and was united in the 28S gene tree with high support (PP = 1), but was not obtained in any other gene tree. This assemblage contains seven major clades, recognized at the family level, almost all resolved with high support (PP  $\geq$  0.95; BS  $\geq$  95), excluding only Clades C and I, which did not receive significant bootstrap support in either of the concatenated analyses. Relationships among the seven clades that comprise this assemblage are supported weakly and sensitive to the exclusion of nonconserved regions.

Within Clade C are the majority of taxa included in the analysis presently classified in the Ranellidae and spanning both currently recognized subfamilies, Cymatiinae and Ranellinae: *Argobuccinum* Herrmannsen, 1846, *Biplex* Perry, 1810, *Cabestana* Röding, 1798, *Fusitriton*, *Gutturium* Mörch, 1852, *Gyrineum*, *Monoplex* Perry, 1810, *Ranularia* Schumacher, 1817, *Reticutriton* Habe & Kosuge, 1966, *Sassia*, *Septa* Perry, 1810, and *Turritriton* Dall, 1904. Among the genera represented by more than a single species, *Fusitriton* and *Ranularia* are supported robustly (PP = 1; BS = 100) as monophyletic, while *Turritriton* is monophyletic but without significant support. *Biplex* is monophyletic in both concatenated analyses (PP  $\geq$  0.97; BS  $\geq$  98), but is placed robustly (PP = 1; BS  $\geq$  97) within a paraphyletic *Gyrineum*. The clade *Gyrineum* + *Biplex* was recovered also on the COI and 28S gene trees, but not on the 16S tree. *Monoplex* as presently conceived is polyphyletic; the monotypic genus *Gutturium* is nested within a clade containing a subset of *Monoplex* species, while *M. comptus* (A. Adams, 1855) is resolved robustly (PP = 1; BS  $\geq$  96) as the sister group of *Reticutriton pfeifferianus* (Reeve, 1844). The relationship of *M. krebsii* (Mörch, 1877) is not resolved. *Sassia* is highly polyphyletic, comprising four separate lineages, with affinities of many of the species unsupported. *Distorsomina*, previously classified in the Personidae, is the sister group to all other members of Clade C in the analysis excluding nonconserved regions, or as sister to (*Gyrineum* + *Biplex*) in the analysis including nonconserved regions; but both results are not supported significantly. *Cymatiella verrucosa* (Reeve, 1844) (Ranellidae), for which only the COI gene was successfully sequenced, is supported as the sister group of *Distorsomina* in the COI gene tree (Supplementary Fig. 2). Clade D comprises the Bursidae as presently conceived and contains representatives of *Bufonaria* Schumacher, 1817, *Bursa*, *Bursina* Oyama, 1964 and *Tutufa* Jousseume, 1881; this group was supported as monophyletic in all analyses with uniformly high support (PP = 1; BS + 100) except on the 12S gene tree (PP = 0.91). Among the genera represented by more than a single species, only *Tutufa* is monophyletic with high support (PP = 1; BS  $\geq$  99). The single sequenced specimen of *Bufonaria* is supported in both concatenated analyses in a clade with two species of *Bursina*, although only with significant support under BI (PP  $\geq$  0.97; BS  $\geq$  66); this result was returned also in the COI (PP = 0.98) and 12S (PP = 0.94) gene trees, but not in that for 16S. *Bursina fijiensis* (Watson, 1881) is nested robustly (PP  $\geq$  0.95; BS = 100) in a clade with *Bursa quirihorai* Beu, 1987, *B. awatii* Ray, 1949, and *B. fosteri* Beu, 1987, but this relationship received only modest bootstrap support (BS = 79) in the concatenated analysis including nonconserved regions (Supplementary Fig. 1). *Bursa* is highly polyphyletic with members dispersed among several clades with high support (PP = 1; BS  $\geq$  97), including: (1) the *Bursa granularis* (Röding, 1798) complex; (2) *B. rhodostoma rhodostoma* (G.B. Sowerby II, 1835), *B. rhodostoma thomae* (d'Orbigny, 1847), *B. rosa* (Perry, 1811); (3) *B. lamarckii* (Deshayes, 1853), *B. rosa* (Perry, 1811), *B. tuberosissima* (Reeve, 1844). Clade E comprises the only two living species of *Ranella*, *R. australasia* (Perry, 1811) and *R. olearium* (Linnaeus, 1758); this group was supported robustly as monophyletic in both concatenated analyses (PP = 1; BS = 100) and was monophyletic on all individual gene trees, but its placement is sensitive to the exclusion of nonconserved regions. Clade F unites two genera presently allocated to two different families: *Akibumia* (Laubierinidae) and *Pisanianura* (Pisanianuridae). This group is supported robustly in both concatenated analyses (PP = 1; BS = 100) and is monophyletic in all individual gene trees. Like Clade E, the

placement of Clade F is sensitive to the exclusion or inclusion of non-conserved regions, and is supported as sister to Clade G in the former, but as sister to Clade E in the latter. Clade G includes representatives of the genus *Charonia*, presently classified in the Ranellidae, and was supported in all analyses. Clade H includes representatives of the genera *Eudolium* Dall, 1889 and *Tonna*, presently classified in the Tonnidae, and each supported as monophyletic with high support (PP = 1; BS = 100) in both concatenated analyses, but was supported as sister to Clade G in the analysis including nonconserved regions, and as sister to Clade I in the analysis excluding nonconserved regions. Monophyly of this group and of both genera was also obtained on all individual gene trees although, in contrast to *Tonna*, *Eudolium* did not receive consistently high support. Clade I unites members of the Cassidae as presently defined (*Casmaria* H. & A. Adams, 1853, *Cassis* Scopoli, 1777, *Cypraecassis*, *Dalium*, *Echinophoria* Sacco, 1890, *Eucorys* Beu, 2008, *Galeodea* Link, 1807, *Oocorys*, *Phalium*, *Sconsia* Gray, 1847, *Semicassis* Mörch, 1852) and was recovered in both concatenated analyses with PP  $\geq$  0.95, albeit with low to no bootstrap support (< 71%), and in the 12S gene tree but without support. All genera represented by more than a single representative (excluding *Eucorys*, *Oocorys* and the monotypic *Dalium*) were recovered as monophyletic with high support in both concatenated analyses (PP = 1): *Casmaria*, *Cassis*, *Cypraecassis*, *Echinophoria*, *Galeodea*, *Phalium*, *Sconsia* and *Semicassis*. The monophyly of *Echinophoria* and *Phalium* on the 16S gene tree, and of *Semicassis* on the COI, 12S and 16S gene trees, was not obtained.

The superfamily is estimated to have diverged ~186 Ma, with the median age of the crown group estimated as ~150 Ma. Most major clades (Fig. 2; B-I) are estimated as having arisen between ~103 and ~124 Ma.

## 4. Discussion

### 4.1. Comparison with previous phylogenetic analyses

Simone's (2011) phylogeny of the Caenogastropoda based on morphological data shows several similarities to the present results. Simone (2011) considered Ficoidea synonymous with Tonnoidea and in his phylogeny, *Ficus* was resolved as the sister group to all other tonnoideans. Both Simone's (2011) analysis and the morphological phylogeny of Ponder et al. (2008) resolved tonnoideans as sister to the neogastropods, but there was no support in Ponder et al. (2008) for the idea that ficids are tonnoideans and they were not closely related. Prior to the present study, the only molecular analysis that included representatives of both tonnoideans and ficids was that of Riedel (2000). Based on 16S and 18S rDNA sequences, Riedel's (2000) results invariably placed the single tonnoidean sequenced for each marker among the neogastropods, and a sister group relationship between *Ficus* and *Bufonaria* (Bursidae) was obtained only on the 18S parsimony tree. Despite the present results speaking to a close affinity between the two, the taxon sampling among neogastropods and their close relatives among the former "mesogastropods" is insufficient to resolve robustly the question of whether Ficoidea should be included in the Tonnoidea. We prefer a conservative approach to the classification and retain Ficoidea as distinct pending further study.

Support for the uniqueness of *Charonia*, separate from the other ranellids among which it is currently classified, also echoes the results of Simone (2011) which resolved *Charonia "laevigata"* [error for *Charonia variegata* (Lamarck, 1816)] on an isolated branch based on its distinct anatomy. However, the Cymatiidae as circumscribed herein was paraphyletic in his analysis, with *Sassia kampyla* (Watson, 1883) (type species of *Cymatona* Iredale, 1936) and *Fusitriton* in one subclade, separated from five species of "Cymatium" [= *Cymatium femorale* (Linnaeus, 1758), *Ranularia cynocephala* (Lamarck, 1816), *Monoplex nicobaricus* (Röding, 1798), *M. parthenopeus* (Salis Marschlin, 1793), and *M. pilearis* (Linnaeus, 1758)] in another.

One of the more surprising results is the placement of *Thalassocyon*

(Ficidae) as sister to *Distorsionella* (Personidae), despite the marked dissimilarity in their shells. From an anatomical point of view, this placement has some precedent. Similar to *Distorsio*, the proboscis of both *Distorsionella* and *Thalassocyon* is very long and coiled when retracted, and the small, irregular, black operculum of *Thalassocyon* is also identical to that of *Distorsio*, whereas *Ficus* does not have an operculum (Beu, 1969, 1978, 1981). Simone (2011) also found that Ficidae as presently conceived (*Ficus*, *Thalassocyon*) is not monophyletic, and that *Thalassocyon* is more closely related to personids.

Possible similarities in foregut organization between personids and ficids have been interpreted differently by past workers. Personidae are unique amongst tonnoideans in possessing undivided salivary glands that consist of histologically differentiated branching tubules, whereas other tonnoideans possess salivary glands that are externally differentiated and, in most species, subdivided into anterior and posterior lobes (see Barkalova et al., 2016; and references therein). In contrast, the salivary glands of ficids form “spacious tubular pockets” (Barkalova et al., 2016). Both ficids and personids possess an unusually long proboscis that forms multiple coils within the rhynchodaeum when contracted, but the proboscis of personids is introvertible, while that of *Ficus* is not (Golding, 2009). When recognizing the Personidae as a distinct family, Beu (1988) found the foregut anatomy of Personidae more similar to that of Ficidae than of Ranellidae. In contrast, Golding (2009) concluded that there are few synapomorphies uniting Ficoidea with either Tonnoidea or Neogastropoda. Barkalova et al. (2016) similarly concluded the similarity between ficids and personids in foregut organization to be superficial, while somewhat paradoxically concluding that the personid foregut morphology was “...less derived than in other tonnoideans” (2016: 17), and going so far as to question their placement in the superfamily. Simone’s phylogeny placed *Thalassocyon* as the sister group to Personidae with the two only distantly related to Ficidae, which would support the view that the similarity is superficial. Our results confirm the close affinity of *Thalassocyon* and Personidae, possibly as sister taxa and themselves sister to the remaining tonnoideans. The fact that there is a possible sister group relationship between Ficoidea and Tonnoidea supports the idea that the similarity in foregut organization between personids and ficids is not a result of homoplasy but may be symplesiomorphic in the two superfamilies.

#### 4.2. Revised family-level classification of the Tonnoidea

Prior to the present study, the classification of Tonnoidea recognized seven taxa at the rank of family: Tonnidae, Bursidae, Cassidae, Laubierinidae, Personidae, Pisanianuridae and Ranellidae (with Ranellinae and Cymatiinae). All except the Laubierinidae (*Akibumia*) were represented in the present analysis by more than a single species. Of these, only three, Bursidae, Cassidae and Tonnidae, were supported as monophyletic. Members of the Personidae were found to be distributed among three distinct clades (clades A, B, C; Fig. 1), as were members of the Ranellidae (clades C, E, G; Fig. 1), rendering both polyphyletic. The Pisanianuridae was supported as paraphyletic, with *Akibumia* (Laubierinidae) nested within it (Fig. 1; Clade F).

Bayesian analysis of the concatenated datasets, both including and excluding nonconserved regions, resulted in nine robustly supported clades, which we here recognize at the rank of family. The placement of *Thalassocyon* as sister to *Distorsionella* on an isolated branch (Clade A) is here recognized as the Thalassocyonidae, a family until now (Bouchet & Rocroi, 2005) placed in the synonymy of Ficidae. Although the ingroup node has modest support only in the analysis with nonconserved regions removed (Fig. 1; PP = 0.93), and relationships at the base of the Tonnoidea are essentially unresolved, there is no support for a relationship between *Ficus* and *Thalassocyon*, either in the concatenated analyses, or in the individual gene trees. *Thalassocyon* + *Distorsionella* are supported as sister taxa with high support (PP ≥ 0.99) in both concatenated analyses, and in all individual gene trees for which both were sequenced (COL, 12S, 16S). Consequently, we here retain

Thalassocyonidae in the Tonnoidea.

The Personidae included four Recent genera (*Distorsio*, *Distorsionella*, *Distorsomina*, and *Personopsis*) and representatives of all four were included in the analysis (the type genus, *Persona* Montfort, 1810, is a synonym of *Distorsio*). The results support retaining only two genera in the family (Clade B; *Distorsio*, *Personopsis*). As mentioned, *Distorsionella* is placed in the Thalassocyonidae, while *Distorsomina* is transferred to the Cymatiidae.

The Cymatiinae was conceived as a subfamily of Ranellidae and included 14 genera (*Cabestana*, *Charonia*, *Cymatium*, *Cymatiella* Iredale, 1924, *Gelagna* Schaufuss, 1869, *Gutturium*, *Linatella* Gray, 1857, *Lotoria* Emerson & Old 1963, *Monoplex*, *Ranularia*, *Reticutriton*, *Sassia*, *Septa*, *Turritriton*; MolluscaBase, 2018), ten of which were represented in the analyses, six by more than a single terminal. The Cymatiinae is here elevated once again to the rank of family (Clade C) to include the majority of genera formerly placed in this subfamily. Of the ten included in the analyses, nine are retained in the family as redefined here, excluding only *Charonia*, and only three of the six represented by more than a single terminal are supported as monophyletic: *Ranularia*, *Septa*, *Turritriton*. As mentioned, *Distorsomina* is transferred here from the Personidae. *Eosassia* Bandel & Dockery, 2012 was named to include Cretaceous species referred to *Sassia*. Although this is a useful concept for Cretaceous species previously referred to this highly polyphyletic genus, this renders Eosassiidae Bandel & Dockery, 2012 a synonym of Cymatiidae as redefined here.

The Ranellinae as circumscribed prior to this study contained eight genera, representatives of five of which were included in the analyses (*Argobuccinum*, *Biplex*, *Fusitriton*, *Gyrineum* and *Ranella*), four by more than a single species. *Halgyrineum* Beu, 1998, *Obscuranella* Kantor & Harasewych, 2000 and *Priene* H. & A. Adams, 1858 were not included. All genera previously assigned to the subfamily that were analyzed here, excluding *Ranella*, are now included in an expanded concept of the Cymatiidae. Of the three retained in Cymatiidae and represented by more than a single species, *Fusitriton* was returned as monophyletic, as was *Biplex*, but *Biplex* was nested within a paraphyletic *Gyrineum*.

Although the large polytomy within the Cymatiidae prevents us from recognizing taxa formally at the rank of subfamily, one well supported clade includes *Cabestana*, *Gutturium*, *Monoplex*, *Septa*, *Ranularia*, *Reticutriton* and *Turritriton*, and could arguably represent the subfamily Cymatiinae. However, the type species of *Cymatium*, *C. femorale* (Linnaeus, 1758), was not included in the analysis. Depending on the resolution of the polytomy, the family-group name Argobuccininae Kilius, 1973, formerly in the synonymy of Ranellinae, is available for a clade including *Argobuccinum*.

*Ranella* is supported as an isolated lineage distinct from all other Tonnoidea at the family level, and for which we retain the name Ranellidae (Clade E). *Charonia*, previously classified in the Cymatiinae, is similarly supported as an isolated lineage and unrelated to the taxa among which it was formerly placed. For this clade, the name Charoniinae Powell, 1933 is available and we use here at the rank of family (Clade G). Given the molecular distinctiveness of *Charonia variegata*, it is arguable that a second genus, *Buccinatorium* Mörch, 1877 (type species *C. variegata*), could be recognized in the family. However, the shells of charoniids appear to have been morphologically conserved since the Oligocene (Lozouet, 1998), and the shells of *C. tritonis* are much more similar to those of *C. variegata* than to those of its sister taxon *C. lampas*. Furthermore, there are no known anatomical characters to support such a wide distinction. Additional study is needed to resolve this issue.

The close relationship between *Pisanianura* and *Akibumia* (Clade F) justifies the synonymization of the Pisanianuridae (containing *Pisanianura*) with the Laubierinidae (containing *Akibumia* and *Laubierina*). *Laminilabrum* is currently accepted as a synonym of *Pisanianura*. However, the type species of *Laminilabrum*, *L. breviace* Kuroda & Habe, 1961, is sister to *Pisanianura grimaldii* (Dautzenberg, 1899) only on the 16S gene tree, so we here resurrect from synonymy

the genus *Laminilabrum* for its type species. The question of whether *Akibumia* and *Laubierina* should be synonymized requires analysis of the type species of *Laubierina*, *L. peregrinator* Warén & Bouchet, 1990, which was not available to us.

The Bursidae, Tonnidae and Cassidae are the only families unchanged in their circumscription as a result of the present analysis, at least with the present sampling. The Bursidae (Clade D) currently includes seven genera: *Aspa* H. & A. Adams, 1853, *Bufonaria*, *Bursa*, *Bursina*, *Crossata* Jousseume, 1881, *Marsupina* Dall, 1904 and *Tutufa* (MolluscaBase, 2018). Of the seven, we included representatives of only four (*Bufonaria*, *Bursa*, *Bursina*, *Tutufa*), making it one of the more incompletely represented families in the analysis. However, the results reveal it to be one of the most complex in terms of genus-level relationships (see below) and only *Tutufa* was returned as monophyletic. Similar to the results of Castelin et al. (2012), there is a basal split between *Tutufa* and all other bursids, but this result is not supported in a more detailed analysis of bursid relationships (M. Sanders et al., unpubl. data). The Tonnidae (Clade H) comprises the clearly distinct *Eudolium* and *Tonna*, both monophyletic with high support (PP = 1). Of the three currently recognized genera, only *Malea* Valenciennes, 1832 was not included. The Cassidae (Clade I) currently includes 12 genera (*Casmaria*, *Cassis*, *Cypraecassis*, *Dalium*, *Echinophoria*, *Eucorys*, *Galeodea*, *Microsconsia* Beu, 2008, *Oocorys*, *Phalium*, *Sconsia*, *Semicassis*; MolluscaBase, 2018), 11 of which were represented in the analysis, eight by more than a single terminal. The analyses returned two well supported clades, equivalent to the rank of subfamily: 1) Cassinae, including *Cassis*, *Dalium*, *Eucorys*, *Galeodea*, *Oocorys* and *Sconsia*; *Cypraecassis* clearly belongs here based on its *Cassis*-like shell morphology and its oval rather than fan-shaped operculum, although its placement has no statistical support. 2) Phaliinae, with four genera: *Casmaria*, *Echinophoria*, *Phalium*, and *Semicassis*. Debate surrounding the extension, affinities and rank of Oocorythinae (see Beu, 2008) is resolved, as it is confirmed to be a synonym of Cassinae. All eight genera represented by more than a single terminal were supported as monophyletic.

While the present analyses cannot inform the family-level classification of exclusively fossil lineages, and a comprehensive reanalysis of fossil families beyond the scope of our analysis, we here exclude one family included recently in the Tonnoidea by Bandel & Dockery (2012). The Mataxidae Bandel & Dockery, 2012 is here excluded from the Tonnoidea based on the presence of columellar plaits visible in the illustration of the type species of the type genus, *Mataxa elegans* (Bandel & Dockery, 2012; pl. 3, Fig. 16), which are unknown in the superfamily. We suggest that Mataxidae may be a synonym of Cancellariidae.

Important taxa to include in future analyses include the type species of the type genus of Cymatiidae, *Cymatium femorale*. The affinities of *Obscuranella* Kantor & Harasewych, 2000 are also unclear and sequencable material was not available, but teleoconch similarities suggest that it likely belongs in a clade close to *Fusitriton*. The family position of *Halgyrineum louisae* (Lewis, 1974) is similarly ambiguous. Its anatomy is unknown and the shell with its combination of variceal position (each 180°), *Gyrineum*-like form, distinctive sculpture, and trochiform, reticulate-sculptured protoconch, does not readily suggest an affinity to any known family. However, a reticulate protoconch is otherwise seen in *Sassia* s.s., Laubierinidae and *Oocorys* (Bouchet & Warén, 1990), with affinities possibly among the poorly resolved cymatiids. Two distinctive, small fossil species, “*Bursa*” *saundersi* Adegoke, 1977 (Paleocene, Nigeria) (Adegoke, 1977) and “*Ranella*” *nevillei* Cossmann & Peyrot, 1924 (Miocene, Aquitaine, France) (Cossmann & Peyrot, 1924) resemble *Halgyrium louisae* in size, shape and sculpture, suggesting they comprise a further, poorly known tonnoidean family, although the fossils lack reticulate sculpture on the protoconch.

#### 4.3. Problematic genera

Resolving the systematics of included genera was not feasible with the present sampling, and was not an intended goal. However, the results have implications for the systematics of several genera that are clearly para- or polyphyletic even with this level of resolution. Within the Cymatiidae, *Biplex* was nested within *Gyrineum*, with a representative of the type species of both genera included in the analyses. Despite the distinctive shell morphology of *Biplex*, this result supports synonymy of the two genera, with *Gyrineum* having priority. The monotypic genus *Gutturnium* was nested within *Monoplex* in part. However, the type species of *Monoplex* was not included, consequently it is unclear to which clade the name *Monoplex* should be applied, and we refrain from taking any formal taxonomic action.

*Sassia*, as recognized by Beu (1998, 2010) and Beu & Maxwell (1990), is found to be highly polyphyletic, and it is clear that this heterogeneous group requires subdivision. The only species now retained in *Sassia* are elongate and relatively small, with a reticulate protoconch and teleoconch sculpture of several rows of small nodules, as in the type species *S. apenninica* (Sassi, 1827) from the Miocene and Pliocene of Europe. For Recent species formerly assigned to *Sassia*, the present analysis indicates, as discussed below, the recognition of *Austrosassia*, *Austrotriton*, *Cymatiella* and *Proxicharonia*; for *Sassia lewisi*, the genus *Personella* Conrad, 1865 (type species *Distorsio septemdentata* Gabb, 1860, from the Eocene of Texas) may tentatively be used. Additional genera are required for the many fossil forms, including more than 130 Cenozoic fossil species alone. The placement of *Sassia palmeri* (New Zealand) with respect to *S. bassi* and *S. subdistorta* (both from southern Australia) is sensitive to the inclusion or exclusion of non-conserved regions, with trees including nonconserved regions placing *S. palmeri* sister to a *bassi*-*subdistorta* clade, and trees excluding non-conserved regions placing *palmeri* within the *bassi*-*subdistorta* clade. The fossil record has been interpreted by Beu & Darragh (unpubl. data) as indicating that a southern Australian clade (for which the name *Austrotriton*, type species, *Tritonium radiale* Tate, 1888, Oligocene, is available) evolved through the loss of planktotrophy during the early Miocene, whereas a New Zealand clade, typified by *Charonia arthritica* Powell & Bartrum, 1929 (Miocene) and differing by protoconch and teleoconch characters, is referable to *Proxicharonia* Powell, 1938; *Sassia palmeri* was originally described in *Proxicharonia* (Powell, 1967), and is here interpreted as a living representative of this restricted New Zealand genus. We therefore use the fossil record to give preference to the molecular phylogenetic tree including nonconserved regions and treat *Austrotriton* Tate, 1888 (synonyms *Negyryna* Iredale, 1929 [4 September] and *Charoniella* Thiele, 1929 [before 21 October], both with *Triton subdistortus* as the type species) and *Proxicharonia* Powell, 1938, as distinct genera. *Austrosassia* Finlay, 1931 is also here rescued from synonymy with *Sassia* for its type species, *Austrosassia parkinsonia* (Perry, 1811).

Within the Bursidae, the genus *Bursa* is similarly highly polyphyletic with a number of well supported clades resolved among this heterogeneous assemblage. The clade including *Bursa rhodostoma*, the type species of *Lampadopsis*, is here assigned to that genus. A representative of the type species of *Bursina*, *B. nobilis* (Reeve, 1844), was also included and is united in a highly supported clade with *Bufonaria perelegans* Beu, 1987. *Bursina* and *Bufonaria*, as currently recognized, possess different operculae, and as the type species of *Bufonaria*, *B. echinata* (Link, 1807), was not included in our analysis, the two genera are kept separate at present. *Bursina fijiensis* should be classified in *Bursa* s.l., with *B. quirihorai*, *B. awatii*, and *B. fosteri*, pending a more complete re-evaluation of bursid relationships (M. Sanders et al., unpubl. data); a sister group relationship between *B. fijiensis* and *B. quirihorai* also was recovered by Castelin et al. (2012). We tentatively assign *Bursa latitudo* Garrard, 1961 and *B. ranelloides* (Reeve, 1844) to *Tritonoranella* Oyama, 1964, the latter the type species, despite that they do not form a clade in the Bayesian analysis of the concatenated dataset including nonconserved

regions (Suppl. Fig. 1). The clade received moderate bootstrap and posterior probability support in the other concatenated analyses and the two species are sisters on the COI tree, but are paraphyletic on the 16S tree, and only one species was successfully sequenced for the 12S and 28S datasets. Consequently, the lack of resolution undoubtedly reflects the large amount of missing data. The complex of *Bursa granularis* (sensu Sanders et al., 2017) could be assigned to a re-instated genus *Dulcerana* Oyama, 1964, of which it is the type species, but there are older available genus-group names that may apply (e.g., *Colubrellina* Fischer, 1884, *Bufonariella* Thiele, 1929) for which the types were not included. The type species of *Bursa*, *B. bufonia* (Gmelin, 1791), was not included in the analysis, leaving the circumscription of this genus uncertain. Clearly, the systematics of the Bursidae at genus level requires more work, with the status of several species and genera in our analysis remaining unresolved at present; a comprehensive revision of the genera of Bursidae is currently being undertaken by M. Sanders et al. (unpubl. data).

In the Cassidae, the close affinity between *Dalium* and *Eucorys*, shown by even the rapidly evolving COI gene, indicates that *E. barboursi* should be transferred to *Dalium*, and possibly that the two genera should be synonymized, with *Dalium* Dall, 1889 taking priority over *Eucorys* Beu, 2008. But confirmation of the synonymy of the two requires inclusion of the type species of *Eucorys*, *E. bartschi* (Rehder, 1943), in the analysis.

#### 4.4. Species relationships

As stated, tonnoideans are known for their long-lived teleplanic larvae with competent larvae reared in culture in excess of 4.5 years (Strathmann & Strathmann, 2007). These large larvae have been frequently described as holoplanktonic species by 19th century naturalists and occasionally still are, and a handful of genus-group names based on tonnoidean larvae have been established (Warén & Bouchet, 1990). Concomitant with such long larval durations, a large number of tonnoidean species as currently recognized have amphi-Atlantic, amphipacific or even circum-global distributions. Among the gastropods they are rivaled in the breadth of their ranges only by some Architectoniciidae (Heterobranchia) (Landau et al., 2009).

Resolving relationships at the species level was not our primary goal and would require denser taxonomic and geographic sampling. Nonetheless, even with the present sampling effort, our results have revealed or confirmed several species complexes that require further study and revision. Within the Personidae, *Distorsio decipiens* (Reeve, 1844) and *D. reticularis* (Linnaeus, 1758) are both revealed to be species complexes. Within the Bursidae, despite the resolution of the *Bursa granularis* species complex (Sanders et al., 2017), the results of our analysis indicate that many other species in the family merit further attention and revision. Contrary to Beu's (1998, 2010) synonymy, *Lampadopsis thomae* from the western Atlantic, currently recognized at the rank of subspecies (MolluscaBase, 2018), is separated from the Indo-West Pacific *L. rhodostoma* by 5.9–8.5% uncorrected pairwise divergence in COI, exceeding levels typically attributed to geographic structuring. The lack of resolution in the concatenated analyses can be attributed to the quantity of missing data for *L. thomae* and the two are here considered to be distinct at the species level. The results also reveal that *Bursa tuberosissima* comprises a species complex. Surprisingly, *Bursa fosteri* Beu, 1987 is shown to be quite molecularly distinct from *Tritonoranella*, despite being almost indistinguishable from *T. latitudo*, differing primarily in its taller, narrower protoconch. Within the Cassidae, *Semicassis bisulcata* (Schubert & Wagner, 1829) and *Galeodea bituminata* (K. Martin, 1933) were not supported as monophyletic, neither in the concatenated analyses nor on the individual gene trees, and hence both are revealed to be species complexes, although this was already suspected for *S. bisulcata* (AGB, unpubl. data). The two sequenced individuals of *Echinophoria wyvillei* (Watson, 1886) are paraphyletic with respect to *E. kurodai* (Abbott, 1968), which was formerly

synonymized with *E. wyvillei* by Beu (2008). Hence, *E. wyvillei* as presently understood constitutes a species complex as well. Consequently, despite their teleplanic larvae, the apparently circumglobal distribution of at least some tonnoidean species is the result of excessive synonymy.

#### 4.5. The fossil record

The fossil record of Tonnoidea has been discussed by Beu (1988, 2010, among others), Riedel (1995b) and Bandel & Dockery (2012, 2016) and dates back to the Cretaceous. Bandel & Dockery (2016: 56–66) attempted to separate tonnoideans from neogastropods by their protoconch characters, and classified in Tonnoidea 16 genera with, in our opinion, typical neogastropod teleoconchs that we regard as mainly Muricoidea or Buccinoidea, with some Cancellarioidea. Taxa referred by Bandel & Dockery (2016) to *Sassia* s.l., *Gyrineum* s.l. and *Tintorium* Sohl, 1960 are the only ones we refer to Tonnoidea.

The earliest undisputed tonnoidean occurrence is a cymatiid represented by a damaged juvenile with a densely cancellate larval shell and a half postlarval whorl with ribs from the Lower Albian *tardefurcata* Zone (late Early Cretaceous, 113–100.5 Ma; dates from Gradstein et al., 2012) of the Gault Formation of northern Germany (Schröder, 1995). Although Schröder (1995) compared it to a *Sassia* s.l. species from the Coffee Sand (Maastrichtian, latest Cretaceous, USA), he admitted the placement was problematic and we hesitate to place it in a genus given the fragmentary nature of the specimen. Late Cretaceous records for the family include the slightly younger *Sassia* s.l. *kanabensis* (Stanton, 1893) (Cymatiidae) from the Turonian (Late Cretaceous, 93.9–89.8 Ma) of Utah, USA (Stanton, 1893) and a few species of *Sassia* s.l. and species at least superficially resembling *Gyrineum* from Maastrichtian (latest Cretaceous) rocks of the eastern USA (Sohl, 1960; Dockery, 1993). Other possible Maastrichtian species of *Sassia* s.l. have been described from Libya (Wanner, 1902), Tennessee (Wade, 1926) and Madagascar (Basse, 1932). As mentioned, the only species we retain in *Sassia* s.s. are those resembling the type species, *S. apenninica*; *Eosassia* and *Tintorium*, the type species of which (*T. pagodiforme* Sohl, 1960; Late Cretaceous, Coon Creek Formation, Tennessee) resembles a *Sassia* species with only a terminal varix, are available for Cretaceous species assigned previously to *Sassia*.

The next earliest group with a clear fossil record is the Personidae, of which there is a convincing record of a reasonably large species, *Distorsio praegransosa* (Cottreau, 1922) from late Cretaceous rocks of Madagascar. This internal mould has strongly distorted coiling and coarsely cancellate sculpture. Although the taxonomic position is somewhat unclear, it seems to be a species of *Distorsio*, although this requires confirmation from external teleoconch characters. A definite age is not determinable from the original work, but Cottreau (1922: pl. 9, Fig. 10) recorded a specimen of the zonally restricted ammonite *Pachydiscus gollevillensis* (d'Orbigny, 1850) from one of the *Distorsio* localities. Kennedy (1986: 28) confirmed this identification in his synonymy of *P. gollevillensis* when establishing its age at the type locality on the Cotentin Peninsula, France. *Pachydiscus gollevillensis* is limited to rocks of basal Upper Maastrichtian age (70–68 Ma). We are not aware of other Cretaceous records of Personidae. *Personopsis* species are first recorded from Paleocene rocks of Poland [*P. rutoti* (Krach, 1963); Beu, 1988].

Cassidae is the only other family of Tonnoidea with a Cretaceous fossil record. The earliest genus to appear, *Galeodea*, has been recorded from Maastrichtian time (late Cretaceous, 72.1–66.0 Ma). Riedel (1995b: 123) accepted *Galeodea* sp. of Wanner (1902), *Galeodea* sp. of Poyarkova & Dzhaliilov (1985) and *Galeodea truncata* (Abdel-Gawad, 1986) all as likely Maastrichtian taxa of Cassidae.

Most other families are known as fossils from Paleocene and Eocene time. Recognition of Ranellidae as a separate family for *Ranella* alone is not surprising in view of its relatively early fossil record, as it is known since the late Paleocene of California (Beu, 1988). A similar history is implied for *Charonia* by the recognition of the separate family

Charoniidae Powell, 1933, although its early fossil record is much more meagre than that of *Ranella*. One of the earliest undisputed records comprises two small species described from the Late Eocene of Italy, *Triton* (*Semiranella*) *gemmalearoi* Gregorio, 1880 and *T. (Semiranella) valrovinensis* Gregorio, 1894 (Gregorio, 1880, 1894). They are indistinguishable from immature specimens of *Charonia lampas* (Linnaeus, 1758) and although [Beu \(2010: 121\)](#) regarded them as synonyms of *C. lampas*, their small size suggests they represent a distinct, small, Eocene species.

The early fossil history of Bursidae is obscure, and the few relatively early records are widely separated and do not represent the main living Indo-West Pacific genera. The earliest definite bursid is *Marsupina yasila* (Olsson, 1930) from the Lutetian (Middle Eocene) of Peru. A similar species, *M. chira* (Olsson, 1930) occurs in Late Eocene rocks nearby. An unusual genus from Eocene and Oligocene rocks of western North America, *Olequahia* Stewart, 1927, has a wide, inflated teleoconch and a straight columella and siphonal canal and had been tentatively placed in the Bursidae ([Beu, 1988, 2010](#)). Reinterpretation of features of the wide posterior siphonal notch has resulted in transfer of the genus to the Cassidae ([Sanders et al., in press](#)). No other bursids are recorded from pre-Miocene rocks. The Late Eocene–Early Oligocene Nanggulan fauna of Java ([Martin, 1914](#)) includes only *Cassis*, *Sassia* and possibly a *Eudolium* species, and an incomplete species possibly of Cymatiidae, and provides little information on the origins of extant Indo-West Pacific Tonnoidea. There also are no fossil Bursidae in the Paris Basin Eocene or any of the other classical Paleocene–Eocene faunas. *Tutufa* has a fossil record only from Miocene time onwards. [Tomida et al. \(2013\)](#) recorded a large, typical *Tutufa* specimen resembling *T. bubo* (Linnaeus, 1758) from the Middle Miocene Ena Limestone in Japan.

The shallow-water family with the poorest fossil record is Tonnidae [[Beu \(in Vos, 2007: 11, 12; Beu, 2010: 264\)](#)]. Several records of *Eudolium* from Eocene and Oligocene rocks are convincingly referred there, including *E. mutica* (Michelotti, 1861) (Oligocene, Italy; type species of the synonym *Galeodolium* Sacco, 1891) and *E. antiquum* (Sacco, 1891) (Oligocene, Italy; type species of the synonym *Tuberculodolium* Sacco, 1891). The several Oligocene species referred to *Galeodaria* Conrad, 1865 by [MacNeil & Dockery \(1984\)](#) also belong in *Eudolium*, although the Eocene type species of *Galeodaria* is a species of *Galeodea*. We are not aware of any records of *Tonna* or *Malea* from Paleogene rocks.

Thalassocyoniidae and Laubierinidae are notable for their poor fossil record. Few taxa have been referred to Laubierinidae, and the only fossils convincingly referred there are the few species of *Pisanianura* from Early Miocene–Pliocene rocks of Europe, New Zealand and Fiji ([Warén & Bouchet, 1990; Landau et al., 2004; Landau & Harzhauser, 2012](#)). We can also record an unnamed species of *Akibumia* from Early Miocene rocks of New Zealand (Beu, unpubl. data). It seems likely that restriction to a specialized offshore habitat has limited their fossil record. However, we suggest that Middle Eocene (Lutetian) species of the very small (height to 10 mm), extremely thin-shelled genus *Monocirsus* Cossmann, 1889 from the Paris Basin are also members of Laubierinidae. Numerous unnamed species of *Monocirsus* have been shown to us by J. Le Renard (MNHN). The composition of this family is poorly understood as yet. We know of no fossils convincingly referable to the Thalassocyoniidae, again presumably because of their primarily deep-water habitat.

#### 4.6. Timing of diversification of Tonnoidea

Based on Bayesian analysis of the concatenated dataset excluding nonconserved regions, and calibrated with six fossil occurrences ([Table 4](#)), the superfamily is estimated to have its origins during the early Jurassic (~186 Ma), with the median age of the crown group estimated as late Jurassic (~150 Ma). Diversification of crown group families occurred during three main phases in the late Cretaceous (Cassidae, Cymatiidae, Personidae, Thalassocyoniidae), Paleocene

(Ranellidae, Tonnidae) and Eocene (Bursidae, Charoniidae, Laubierinidae). Most major tonnoidean crown group lineages, excluding only the Thalassocyoniidae, are estimated as having their roots in a roughly 20 My period between ~103–124 Ma in the Early Cretaceous, during Aptian–Albian times. For all families but the Cymatiidae, if true this estimate requires a sometimes substantial evolutionary history unrecorded by fossils. In some cases, this is a consequence of life in a habitat not favourable to preservation (e.g., deep-water Thalassocyoniidae, Laubierinidae). In other instances it may also be ascribed to the poor preservation potential of their comparatively lightly constructed shells (e.g., Tonnidae). For other families, it is more difficult to explain, but we attribute it at least in part to the fact that the early fossil history of some groups and their constituent taxa remain obscure. The often long branches separating the crown groups from their origins also may be explained by incomplete sampling and/or the extinction of major lineages.

That said, the estimated origination of most major tonnoidean lineages during Aptian–Albian times coincides with the radiation of other predatory gastropods near the end of the Mesozoic Marine Revolution, which marked a profound restructuring of marine ecosystems during the Jurassic and Early Cretaceous (e.g., [Vermeij, 1977, 1987; Taylor et al., 1983; Bambach, 2002; Finnegan et al., 2011](#)). This reorganization was driven by increases in energy budgets of marine ecosystems that allowed, among other things, the proliferation of active, large bodied predators such as tonnoideans. Against this backdrop of global change and restructuring of marine communities, the Early Cretaceous in particular was a time of pronounced climatic and oceanographic upheaval. During this interval, sea levels experienced a prolonged period of sustained increase leading to the formation of vast epicontinental seas. This time was also marked by increasing global temperatures and atmospheric CO<sub>2</sub> levels leading to super-greenhouse conditions and high ocean surface water productivity. This increase in productivity and the accompanying changes in ocean energetics are thought to have been key players in driving turnover at the top of the food chain (e.g., [Bambach, 1999; Pereira et al., 2016](#)).

## 5. Conclusions

The present study has resulted in significant changes to the family classification of the Tonnoidea, requiring the resurrection of three family-group names (Thalassocyoniidae, Cymatiidae, Charoniidae) and synonymy of one (Pisanianuridae with Laubierinidae), increasing the number of recognized families from seven to nine. The extension and composition of the Ranellidae is the most changed, with three families now recognized for the taxa formerly assigned there. At the genus level, the present sampling does not allow us to tackle the classification in a comprehensive way, and would require the addition of the type species of many further nominal genera. Nevertheless, the results have implications for the synonymy (*Biplex*) or resurrection (*Austrosassia*, *Austrotriton*, *Laminilabrum*, *Lampadopsis*, *Personella*, *Proxicharonia*, *Tritonoranella*) of several genera, and indicate that more merit revision (e.g., *Monoplex*, *Sassia*, *Bursa*, *Bursina*). The status of several subfamily-level clades for which names are available remains unresolved (e.g., Argobuccininae, Cymatiinae, Tutufinae). The results also have implications for species relationships with the disclosure of a number of species complexes (*Distorsio*, *Bursa*, *Echinophoria*, *Semicassis*, *Galeodea*), although in most cases it is not possible to make formal taxonomic recommendations at this time. The fossil-calibrated analysis suggests that most families of these large-bodied predators originated during a period of sustained warming and sea-level rise during the late stages of the Mesozoic Marine Revolution as part of the global reorganization of food webs and increases in benthic marine energy budgets that promoted the diversification of top predators. The rapid origin of major clades during such a narrow window explains the difficulty in resolving the relationships between them and with robust support. Robust resolution of the relationships among families, extension of the

superfamily (i.e. inclusion or exclusion of Ficoidea) and relationship of the Tonnoidea to other higher Caenogastropoda will require more extensive sampling among “advanced mesogastropods” and neogastropods, and the inclusion of genes capable of robustly resolving branching events that occurred during the Jurassic and Cretaceous.

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