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# A review of fossil Bursidae and their use for phylogeny calibration

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## ABSTRACT

Bursidae Thiele, 1925 is a moderately diverse group of extant tonnoidean gastropods with a significant fossil record. We review the fossil record of the family. We exclude some taxa from Bursidae, particularly the most ancient ones: *Hanaibursa aquilana* (Parona, 1909) (Aptian) and *Bursa saundersi* Adegoke, 1977 (Selandian). We exclude the genus *Olequahia* Stewart, 1926; its posterior siphonal canal is not analogous with that of Bursidae. We also discuss the possible revision of the type genus, *Bursa* Röding, 1798, on the basis of previously published phylogenies; the genus is not monophyletic. We create two new genera, *Olssonia* n. gen. (type species: *Bursa chira* Olsson, 1930) and *Aquitanobursa* n. gen. (type species: *Ranella grateloupi* d'Orbigny, 1852), containing only fossil species. Lectotypes are designated for *Ranella grateloupi* d'Orbigny, 1852, *Ranella morrisi* d'Archiac & Haime, 1853 and *Apollon pelouatensis* Cossmann & Peyrot, 1924. Based on this revision of the fossil record, we propose five fossil calibration points that can be used to date molecular phylogenetic trees of Bursidae.

KEY WORDS
Bursidae,
Tonnoidea,
node calibration,
lectotypifications,
new combinations,
new genera.

RÉSUMÉ
*Révision des Bursidae fossiles et leur utilisation dans la calibration des phylogénies.*
Les Bursidae Thiele, 1925 sont un groupe de Tonnoidea (Mollusca: Gastropoda) actuels modérément diversifiés possédant un registre fossile assez important. Dans ce travail nous faisons la revue de la totalité du registre fossile de la famille. Tout d'abord nous proposons d'exclure certaines espèces de Bursidae, en particulier les plus anciennes *Hanaibursa aquilana* (Parona, 1909) (Aptien) and *Bursa saundersi* Adegoke, 1977 (Sélandien). Nous excluons aussi la totalité des espèces du genre *Olequahia* Stewart, 1926 en discutant de l'analogie de leur canal siphonal postérieur avec celui des Bursidae. Ensuite nous révisons le genre *Bursa* Röding, 1798, genre type de la famille, sur la base d'une phylogénie précédemment publiée remettant en question la monophylie du genre. Nous créons deux nouveaux genres *Olssonia* n. gen. (espèce type : *Bursa chira* Olsson, 1930) et *Aquitanobursa* n. gen. (espèce type : *Ranella grateloupi* d'Orbigny, 1852) composés d'espèces fossiles. Nous désignons des lectotypes pour *Ranella grateloupi* d'Orbigny 1852, *Ranella morrisi* d'Archiac & Haime, 1853 et *Apollon pelouatensis* Cossmann & Peyrot, 1924. En se basant sur la révision du registre fossile, nous proposons également cinq points de calibration fossile pouvant être utilisés pour dater l'arbre phylogénétique moléculaire de la famille.

MOTS CLÉS
Bursidae,
Tonnoidea,
calibration des nœuds,
lectotypifications,
combinaisons nouvelles,
genres nouveaux.

## INTRODUCTION

The importance of phylogenetic reconstruction no longer needs to be proven and the advances in molecular phylogeny have provided new possibilities for molluscan systematics, renowned for the difficulty of defining primary homologies based on shell characters (Giribet 2015). However, the use of fossils, for which only the shells are available, is unavoidable in modern evolutionary biology because they are the favoured means of calibration for dating molecular phylogenies. A time-tree goes beyond patterns, it gives information regarding tempo of evolution, and allows testing specific hypotheses (e.g., biogeography, diversification rate, etc.). For these reasons time-trees have become used commonly in systematics (Donoghue & Benton 2007). In the vast majority of cases researchers have used fossils to calibrate molecular trees, providing information to constrain nodes (Donoghue & Benton 2007). To do so most of them assume that the taxonomy reflects the correct phylogenetic position of the fossils, something that is difficult to justify. Furthermore, it may lead to under-estimation of uncertainty in the resulting node ages if conducted without proper homology hypotheses or phylogenetic assessment (Sterli *et al.* 2013). Lastly, a wrong node attribution could lead to huge distortions of divergence time (Douzery *et al.* 2006). Therefore, a review of the fossil record of the considered clade should be done before any analysis.

Parham *et al.* (2012) discussed a set of data required to justify a fossil calibration. They are: 1) a museum numbers for the specimen(s) that demonstrate all the relevant characters and provenance data; 2) an apomorphy-based diagnosis of the specimen(s); 3) an explicit statement on the reconciliation of morphological and molecular data; 4) the locality and stratigraphic level(s) from which the calibrating fossil(s) was/were collected; and 5) a reference to a published radioisotopic age and/or numeric timescale and details of numeric age selection of the specimen(s). From all these criteria, the most difficult to satisfy when selecting fossils to calibrate a molluscan phylogeny is the third one, due to the homology issues cited above.

In this paper we review the fossil record of the Bursidae Thiele, 1925. This tonnoidean family is currently under systematic revision by the authors, who will produce a molecular phylogeny. In order to do it a re-evaluation of calibration points is required.

Bursidae are a moderately diverse group with 59 living species (Worms 2018). Recent bursids have a tropical and sub-tropical distribution with a southernmost record in eastern South Africa (Sanders *et al.* 2017), northern New Zealand (Spencer *et al.* 2016) and Walters shoal (Expeditions Muséum 2018). The northernmost record (*Bursa scrobilator* (Linnaeus, 1758)) is from Nice, southern France and Savona, north-western Italy (Landau *et al.* 2004). They are intertidal to subtidal species, most often associated with hard substrates such as rocks, coral or sponges, where they can be locally abundant. They are active predators, feeding on polychaetes, sipunculids and echinoderms (Houbrick & Fretter 1969; Taylor 1978).

Bursidae are readily recognizable by their well-defined posterior exhalant siphon (anal notch) at the top of the outer lip, attached to the suture and by their thick, coarsely sculptured shells with knobs, warts, tubercles and nodules, hence their vernacular name: frog shells. Their size range is great; the smallest species, *Bursa lucaensis* (Parth, 1991) never exceeds 23 mm in height whereas *Tutufa bardeyi* (Jousseaume, 1881), with a height up to 450 mm and a width up to 300 mm, has one of the largest and most capacious shell of all gastropods (Beu 1998). Most bursids range in size between 40 and 60 mm.

As inferred from their protoconch, they are assumed to have a long to extremely long larval stage granting, for some of them, trans-oceanic dispersal capabilities. However, Sand-

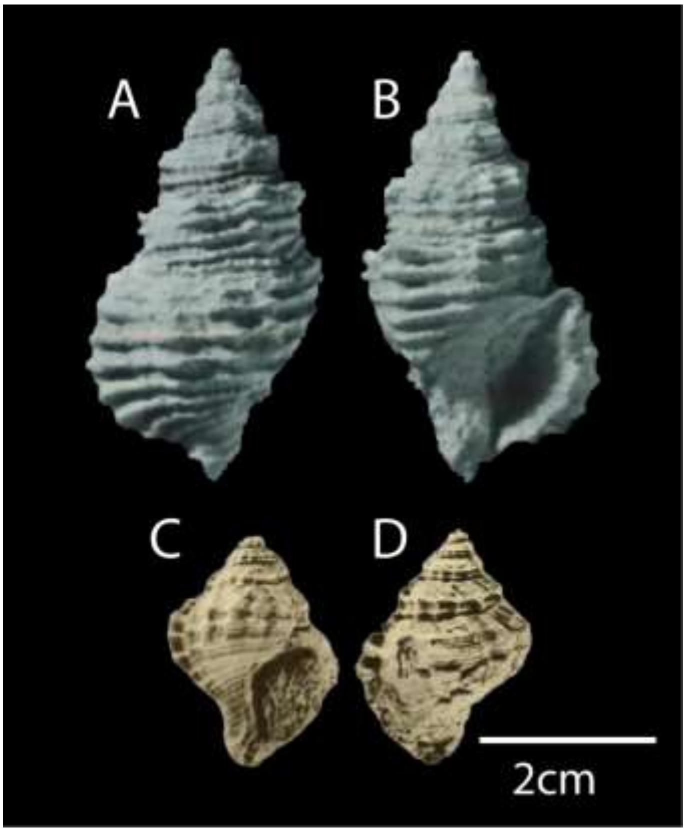


fig. 1. — Taxa excluded from Bursidae: **A**, **B**, *Hanaibursa aquilana* (Parona, 1909) UMUT MM15655, Hiraiga Formation (Aptian of Japan), reproduced from Kase (1984: pl. 28, fig. 16a); **A**, dorsal view; **B**, ventral view; **C**, **D**, *Bursa saundersi* Adegoke, 1977, UIMG 394, holotype, Ewekoro Formation (Selandian of Nigeria), reproduced from Adegoke (1977: pl. 31, figs 27, 28); **C**, ventral view; **D**, dorsal view. Scale bar: 2 cm.

ers *et al.* (2017) showed that such capabilities were greatly overestimated for one of the most widespread species of Bursidae, *Bursa granularis* (Röding, 1798).

The early evolution of the Bursidae remains shrouded in mystery. Pre-Eocene species described as Bursidae (Kase 1984; Adegoke 1977) have been ascribed to the family with reservation in the literature and will be discussed here. The earliest seemingly undisputed species of Bursidae are known from the American Eocene (Beu 1988). They are represented by the genus *Olequahia* Stewart, 1926 from the Upper Eocene (Bartonian) of Washington to California, USA and by two Peruvian species attributed by Beu (1988) to the genus *Marsupina* Dall, 1904, from the Bartonian of Talara Formation and Priabonian of Chira formation. Thereafter, no bursid is recorded until the Rupelian (Stampian) of the Aquitaine Basin (Southwestern France) (P. Lozouet pers. comm.). During the middle Miocene and throughout the Pliocene, the genus *Aspa* H. Adams & A. Adams, 1853 became one of the most abundant gastropods in suitable shallow offshore facies of the Aquitaine Basin, Guadalquivir Basin, Western Tethys (Turin Hills) and Paratethys (Landau *et al.* 2004, 2009, 2011).

This paper aims to review the fossil record of Bursidae, discussing the exclusion of several species from the family. We will provide a morphological description, i.e., an apomorphy-based diagnosis *sensu* Parham *et al.* (2012), for all known extinct genera. In addition, we will list and discuss all the necessary information regarding their use as calibration points in phylogenies. Two new genera are described.

## SHELL DESCRIPTION

Shells are described here using the methods of Sanders *et al.* (2017) adapted from Merle (2001, 2005) for primary homology definition. Primary cords (P) are spiral ornamentations present from the first teleoconch whorl. Secondary cords (S) are spiral ornamentations appearing later during shell ontogeny. The shoulder cord is designated as P1. Cords of the convex part of the whorl are added from adapical to abapical (P2 to P8). The primary cord of the sutural ramp is designated IP and the secondary cord IS. Secondary cords on the convex part of the whorl are designated S1to S8. Cords of the anterior siphonal canal were not considered.

### Abbreviations

*Specimen repositories*

| | |
|---|---|
| MNHN-IM | Muséum national d'Histoire naturelle, collection de malacologie, Paris; |
| MNHN.F | Muséum national d'Histoire naturelle, collection de paléontologie, Paris; |
| NHMW | Naturhistorisches Museum Wien, Vienna; |
| NMB | Naturhistorisches Museum, Basel; |
| PRI | Paleontological Research Institution, Ithaca, New York; |
| RGM | Fossil collections of Netherlands Nationaal Museum van Natuurlijke Historie, Leiden (formerly Rijksmuseum van Geologie en Mineralogie); |
| UCMP | University of California (Museum of Paleontology), Berkeley; |
| UF | Florida Museum of Natural History, University of Florida, Gainesville; |
| UIMG | University of Ife Museum of Geology, Nigeria; |
| UMUT | University Museum, the University of Tokyo, Tokyo; |
| USNM | United States National Museum of Natural History, Washington D.C.; |
| TU | Tulane University, New Orleans. |

*Shell characters*

| | |
|---|---|
| AN | anal notch; |
| H | height; |
| P | primary cord; |
| P1 | shoulder cord; |
| P2-8 | primary cords of the convex part of the whorl; |
| S | secondary cord; |
| S1-8 | secondary cords of the convex part of the whorl; |
| SC | siphonal canal; |
| W | width. |

## EXCLUSION OF SPECIES FORMERLY INCLUDED IN BURSIDAE

The attribution of the Aptian (Hijochi and Hiraiga formations, Japan) species *Hanaibursa aquilana* (Parona, 1909) (Fig. 1A, B) to Bursidae by Kase (1984: fig. 16a, b) is most surprising considering that it bears few, if any, bursid characters. When published it was considered to be the oldest known bursid species. The relatively high-spired shell of *H. aquilana* with weak varix-like ridges every 90° shows greater similarity to batillariid gastropods such as *Pyrazopsis* Hacobjan, 1972, than with Tonnoidea. Furthermore, the posterior siphonal canal is not homologous to that of bursids, as it appears to be an adaxially extending fold within the outer lip. Riedel (1995) was the first to notice this resemblance with cerithoideans; we agree with him on this superfamily position.

*Bursa saundersi* Adegoke, 1977 (Fig. 1C, D) was described by Adegoke (1977: 209, pl. 31, figs 27-28) and recognized by Beu (1998, 2010) as a possible Paleocene bursid. With aligned prominent varices and coarse spiral sculpture, the small specimen from the Ewekoro Formation (Selandian of Nigeria) looks a lot like a frog shell. Nevertheless, it lacks the posterior siphonal canal, the key character used to discriminate Bursidae from Ranellidae and Cymatiidae. For this reason, we conclude that this species does not belong to crown-Bursidae; Strong *et al.*(2018) suggested that this species possibly belongs in a new family along with *Halgyrineum louisae* (Lewis, 1974) and "*Ranella*" *neuvillei* Cossmann & Peyrot, 1924 (both currently included tentatively in Cymatiidae, following the phylogeny of Strong *et al.* 2018).

According to Beu (1988, 2010), there is only one long-extinct genus within the family Bursidae: *Olequahia* Stewart, 1926, with five accepted species (*Olequahia domenginica* (Vokes, 1939), *O. lincolnensis* (Weaver, 1916), *O. lorenzana* (Wagner & Schilling, 1923), *O. schencki* Durham, 1944, and *O. washingtoniana* (Weaver, 1912)). Specimens presented here (Fig. 2) challenge this classification.

The type species of the genus, *Olequahia washingtoniana* (Fig. 2C-H), possesses an ornamentation pattern constituted mostly of spiral cords, the primary cords more prominent than the secondary ones. Nodules are consistently present on the shoulder. Two rows of nodules are present adapically; however, they fade into cords after half a whorl, an unusual feature among Bursidae, but found in *Galeodea* Link, 1807 (Cassidae). The low spire and inflated last whorl of *O. washingtoniana* are more reminiscent of shells of Cassidae or Tonnidae than of Ranellidae, Cymatiidae or Bursidae. In this species, varices are only present on the first whorl and as a terminal varix. According to Beu (1988), pre-terminal varices are entirely lost in Oligocene species.

Varices are an important character because every single species of Bursidae possesses them even though they may be reduced in some cases (e.g. in *Aspa marginata* (Gmelin, 1791)). According to Strong *et al.* (2018) tonnoidean varices are most probably a plesiomorphic character (with an apomorphic loss due to varix dissolution during ontogeny in the clade Tonnidae + Cassidae). This lack of a varix on every whorl suggests that *Olequahia* may not be correctly referred to Bursidae.

However, *Olequahia washingtoniana* has a well-defined posterior siphonal canal resembling that of Bursidae. This siphonal canal is unusually large, similar to that in species of *Crossata* Jousseaume, 1881; this led some authors (Beu 1988; Albi 2002) to consider *Olequahia* as possibly "ancestral" to *Crossata.* We consider the posterior siphonal canal of *Olequahia* to be structurally different from that of *Crossata* (or any other Bursidae). The siphonal canal of *Olequahia* is formed by two rather large tubercules, one on the parietal part of the columella and one on the inner part of the outer

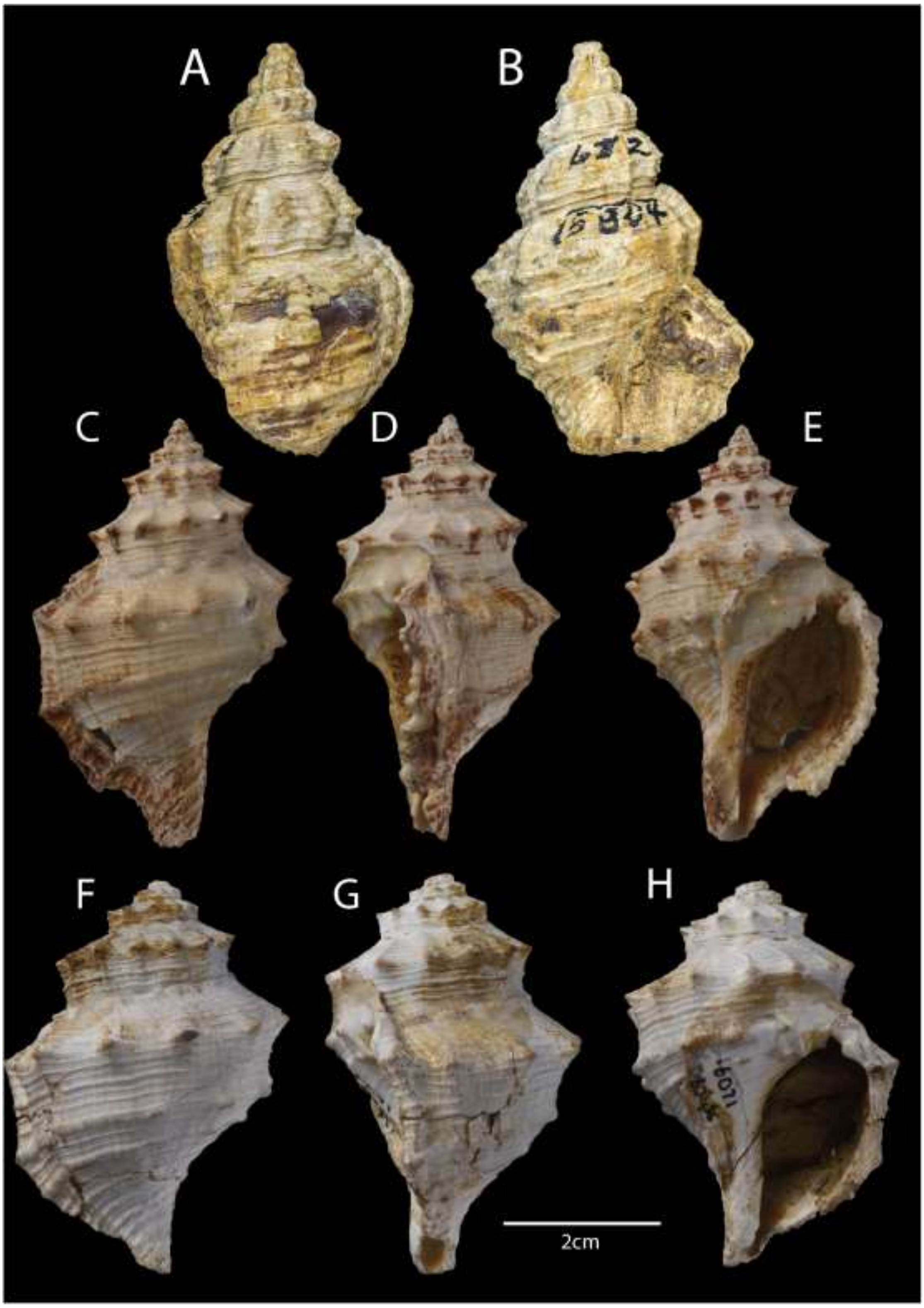


Fig. 2. — Taxa excluded from Bursidae. *Olequahia* Stewart, 1926 species: **A**, **B**, *Olequahia domenginica* (Vokes, 1939): UCMP 15804, syntype of *Ranella domenginica,* Tejon formation (Bartonian), California, United States; **A**, dorsal view; **B**, ventral view; **C**-**H**, *Olequahia washingtoniana* (Weaver, 1912): UCMP 16071 (loc. ID D8044) , in dorsal (**C**, **F**), left lateral (**D**, **G**) and ventral views (**E**, **H**), all from Cowlitz Formation (Priabonian), Cowlitz River, Washington, United States. Scale bar: 2 cm

lip. Columellar tubercules may occur in bursids (e.g. *Bursa latitudo* Garrard, 1961; see Fig. 3E[black arrow]), although never as large as in *O. washingtoniana* and, to our knowledge, there is no species of Bursidae with a single large tubercle or denticle inside the outer lip (in bursids there is either no denticle, or denticles are present throughout the outer lip). However, this feature occurs in several cassid species in the genus *Galeodea* (e.g., *Galeodea hoaraui* Drivas & Jay, 1989). In the light of our reinterpretation of these characters, we consider that *O. washingtoniana* is not a species of Bursidae.

Though many clues may indicate that *Olequahia washingtoniana* belongs in *Galeodea*, some characters do not point in that direction. The high-spired protoconch of this species (Beu 1988: fig. 1F) is quite different from the short, wide protoconch of one whorl in *Galeodea*; the columella is curved in *Galeodea* and straight in *Olequahia*; and finally, the wavy, frilly outer lip extension of *O. washingtoniana* is quite unique among tonnoideans. The position of *O. washingtoniana* in *Galeodea*, as a genus of Cassidae or even as a new family of Tonnoidea requires further attention but is beyond the scope of this paper.

*Olequahia domenginica* (Fig. 2A, B) is the oldest known species referred to the genus. The figured syntype has prominent varices every 200° or so over the entire teleoconch and is taller and narrower than its congeners. However, the general ornamentation resembles that of *O. washingtoniana*. Furthermore, the shell has no anal notch, casting doubts on its kinship with Bursidae. This shell is more reminiscent of a cymatiid such as *Monoplex* Perry, 1810. It is quite possible that it is more closely related to *Monoplex* than to *O. washingtoniana*. Either way, it is not a species of Bursidae. The other syntype of *O. domenginica* (UCNP 15803, not figured) is slightly larger than the illustrated specimen, but otherwise quite similar. However, the ventral side is not preserved in this specimen.

## TACKLING *BURSA* IN THE FOSSIL RECORD

As currently understood, *Bursa* Röding, 1798 is very morphologically variable, so variable in fact that Beu (1998: 143) gave the broad generic description that "*Bursa* is a large genus containing species with short to tall spires, weak to coarse sculpture, heavy and thick to light, thin shells, with varices variable in position […] and with or without a red colour area on the parietal lip". One conclusion may be that *Bursa* is a "trash" genus, and exists only to classify species that do not fit anywhere else (this status was confirmed by Castelin *et al.* 2012 [Fig. 4] and Strong *et al.* 2018). Being paraphyletic (or polyphyletic), such genera are an impediment for every systematist aiming to describe biodiversity in its historical dimension (Faurby *et al.* 2016).

To our knowledge there are 14 recognized extinct species of Bursidae, two-thirds of them referred to *Bursa* (*Bursa amphitrites* Maury, 1917, *B. chipolana* Schmelz, 1997, *Ranella grateloupi* d'Orbigny, 1852, *Apollon inaequicrenatus* Cossmann & Peyrot, 1924, *B. sangirana* Beu, 2005, *R. tuberosa* Grateloup, 1833, *B. victrix* Dall, 1916, *R. morrisi* d'Archiac & Haime, 1853 and *B. landaui* Harzhauser, 2009) and the rest to *Marsupina* Dall, 1904 (*Bursa chira* Olsson, 1930, *Bursa* (*Marsupina*) *freya* Olsson, 1932, *Bursa chira* var. *yasila* Olsson, 1930, *Marsupina judensis* Beu, 2010, and *Gyrineum strongi* Jordan, 1936).

Following Beu's (1988, 2010) opinion we consider *Marsupina freya*, *M. judensis* and *M. strongi* to be correctly attributed to the extant genus *Marsupina*.

As we want *Bursa* to be monophyletic, based on the phylogeny of Castelin *et al.* (2012) and considering the position of the type species of the genus (*B. bufonia* (Gmelin, 1791)), we end up with a narrower definition of *Bursa*; it contains only *B. bufonia* and *B. lamarckii* (Deshayes, 1853), to which we can add *B. luteostoma* (Pease, 1861), *B. rosa* (Perry, 1811) and *B. tuberosissima* (Reeve, 1844), on the basis of their tubular and elongated posterior siphonal canal.

None of the fossil species mentioned above are closely similar to *Bursa bufonia* and none of them are type species of a previously published name that could be resurrected. So we are left with two options: either erect new genera (as few as possible) or propose phylogenetic hypotheses linking fossils with extant species (preferably type species).

*Bursa sangirana* Beu, 2005 (Fig. 5E), from the late Pliocene Kalibeng layers (Sangiran, central Java), has a low spire with a warty ornamentation. Its posterior siphonal canal is short; it is very reminiscent of *Bursa rhodostoma* (G. B. Sowerby II, 1835) (Fig. 3F) and is probably closely related to it. Both species may be included in the separate genus *Lampadopsis* Jousseaume, 1881 for which *B. rhodostoma* is the type species. The resurrection of this genus was suggested recently by Strong *et al.* (2018).

*Bursa landaui* Harzhauser, 2009 (Fig. 4C, D): this slender shell is only known by two external molds from the Aquitanian of Ras Tipuli, Lindi Bay, Tanzania. It has a very fine granulose ornamentation and a weakly expressed shoulder, slightly reminiscent of *Bursa granularis* (Röding, 1798) (Fig. 3G) and similar to *Bursa condita* (Fig. 3A). This may be an indication of the close relationship of the three species, for which there are two or possibly three available generic names: *Colubrellina* Fischer, 1884 and *Dulcerana* Oyama, 1964. *Bufonariella* Thiele, 1929 is possibly another available name considering the close resemblance of its type species, *Bursa scrobilator* (Linnaeus, 1758), to *B. granularis*.

*Bursa victrix* Dall, 1916: this species is only known from a poorly preserved external mold (USNM 166728) from the late Oligocene of Mascot Point, Flint River, Georgia, United States. The almost evenly inflated whorl profile, with a slightly protruding shoulder angle formed by a row of rounded nodules at approximately the upper third of the whorl height on the spire, the numerous lower rows of nodules extending down over the anterior canal, and the deeply buttressed abapertural face of the varix on the ultimate whorl are all characters in common with *Bursa corrugata* (Perry, 1811) (Fig. 3D). We follow Beu's (2010) opinion, keeping it as a species separate from *B. corrugata* pending the discovery of better-preserved specimens.

Among the remaining extinct bursid species, two are strikingly similar: *Marsupina chira* (Olsson, 1930) and *M. yasila*

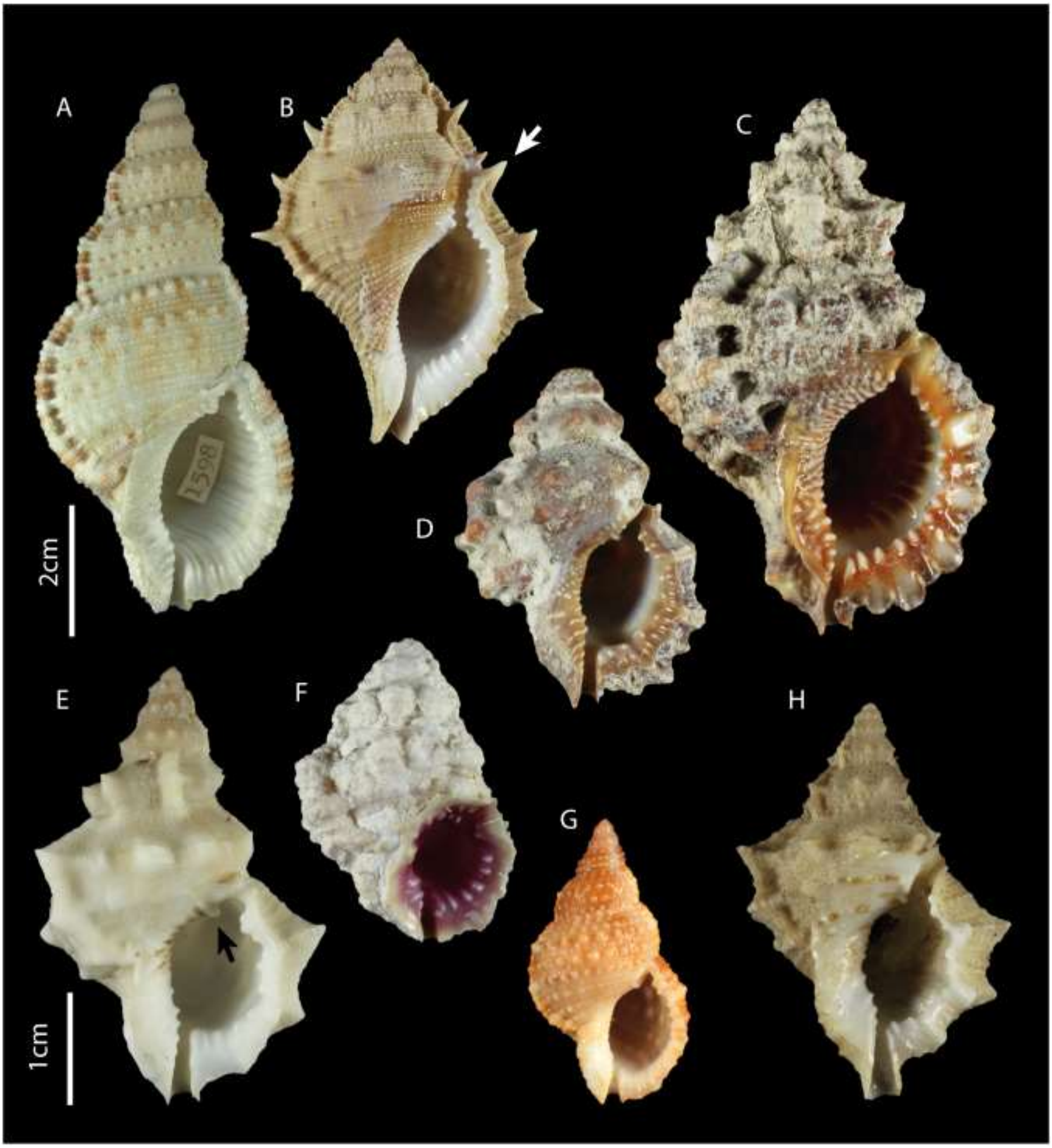


fig. 3. — Recent Bursidae: **A**, IM-2008-5350, *Bursa condita* (Gmelin,1791), « Nouvelle Calédonie », Jousseaume coll.; **B**, IM-2007-43072, *Bufonaria perelegans* Beu, 1987, Santo Marine Biodiversity Survey 2006, Vanuatu; **C**, IM-2009-11906, *Bursa corrugata* (Perry, 1811), Dakar'09, Senegal; **D**, IM-2007-43063, *Tutufa rubeta* (Linnaeus, 1758), Santo Marine Biodiversity Survey 2006, Vanuatu; **E**, IM-2007-40338, *Bursa latitudo* Garrard, 1961, Exploration de la Biodiversité et Isolement en mer du Corail, Nouvelle Calédonie; **F**, IM-2009-5150, *Lampadopsis rhodostoma* (G.B. Sowerby II, 1835), MAINBAZA, Mozambique channel; **G**, IM-2009-5148, *Bursa granularis* (Röding, 1798), juvenile, MAINBAZA, Mozambique channel; **H**, IM-2009-11653, *Bursa quirihorai* Beu, 1987, Exploration de la Biodiversité et Isolement en mer du Corail, New Caledonia. All are ventral views. Scale bars: A-D, 2 cm; E-H, 1 cm.

(Olsson, 1930), for which we propose a new genus, *Olssonia* n. gen.

In the same fashion, *Bursa amphitrites* Maury, 1917, *B. grateloupi* (d'Orbigny, 1842), *B. inaequicrenata* (Cossmann & Peyrot, 1923), *B. tuberosa* (Grateloup, 1833), *Bursa chipolana* Schmelz, 1997, and *Ranella morrisi* d'Archiac & Haime, 1853 are here attributed to a new genus: *Aquitanobursa* n. gen. These new genera are described below.

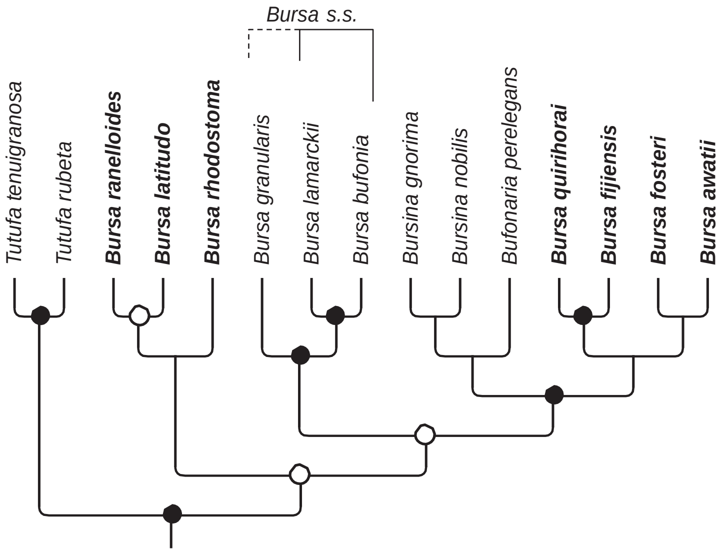


Fig. 4. — Phylogeny of the Bursidae. Topology based on the multigene Bayesian analysis of Castelin *et al.* (2012); black dots (●) represent well supported nodes (posterior probabilities over 0.98) and white dots (○) represent moderately supported nodes (PP over 0.90). *Bursa* species **in bold** type are taxa that make the genus polyphyletic. Bracket on top indicates the phylogenetic extent of the genus *Bursa* if we consider the tubular posterior siphonal canal to be one of its synapomorphies, dotted bracket indicates the maximum extent of the genus considering the topology.

## ON THE GENUS *ASPA*

*Aspa* is the most abundant fossil bursid. This is possibly due to its extremely thick shell. Some authors (Malatesta 1974; Baluk 1995; Solsona 1998) suggested that *Aspa* was monospecific with the extant species *Aspa marginata* ranging from the earliest Miocene (Aquitanian of Landes or Rupelian, France [Beu 2010]) to the Recent. However, early specimens possess a higher spire, coarser sculpture, a row of nodules at P1 persisting onto the last whorl and an obsolescent lower row of nodules, and larger nodules inside the outer lip than in Recent specimens of *A. marginata*. This led Landau *et al.* (2004, 2009) and Beu (2010) to the conclusion that the earliest specimens of *Aspa* belong to another species, for which they considered the valid name to be *Aspa subgranulata* (d'Orbigny, 1852) (Fig. 6). The exact upper range of *A. subgranulata* and the exact lower range of *A. marginata* are not well defined due to the use of the name *A. depressa* (Grateloup, 1833) for either of the two species. This species was originally considered as a "transition" species by Cossmann & Peyrot (1924), ranging from the Langhian to the Messinian. This species is currently considered a junior synonym of *A. marginata* (Landau *et al.* 2004, 2009; Beu 2010). Further quantitative studies should be conducted to determine the exact ranges of the two (or three) species.

## SYSTEMATICS

Phylum MOLLUSCA Cuvier, 1795
Class GASTROPODA Cuvier, 1797
Superfamily Tonnoidea Suter, 1913 (1825)
(Conserved under ICZN Article 40b)

Family Bursidae Thiele, 1925

Genus *Olssonia* n. gen.

Type species. — *Bursa chira* Olsson, 1930.

Derivatio nominis. — Dedicated to the American palaeontologist A. A. Olsson.

Species included. — *Olssonia chira* (Olsson, 1930) n. comb., *O. yasila* (Olsson, 1930) n. comb.

Distribution. — *Olssonia* n. gen. is a genus restricted to the Eocene to early Miocene of Peru.

Diagnosis. — Shell biconic, dorsoventrally compressed, short-spired, with 7 primary cords on the convex part of the whorl, all but P1 evenly reduced in variceal and intervariceal intervals of each whorl (P1 hardly more expressed than other cords); posterior siphonal canal short; varices strictly aligned; prominent columellar callus.

Comparisons. — *Olssonia* n. gen. resembles *Marsupina* but possesses a lesser number of primary cords on the convex part of the whorl (7 in *Olssonia* n. gen., 8 in *Marsupina*). It resembles *Aspa* but has a much more prominent columellar callus, it is much more granulose, and it has a more sharply defined shoulder and a wider spire angle. *Olssonia* n. gen. resemble *Bufonaria* (Fig. 3B), with the same straight anterior siphonal canal, but lacks a spine or blade on the posterior siphonal canal (Fig. 3B; white arrow).

### Remarks

The representatives of this genus are the oldest confirmed Bursidae; as such they can be used to calibrate the node Bursidae.

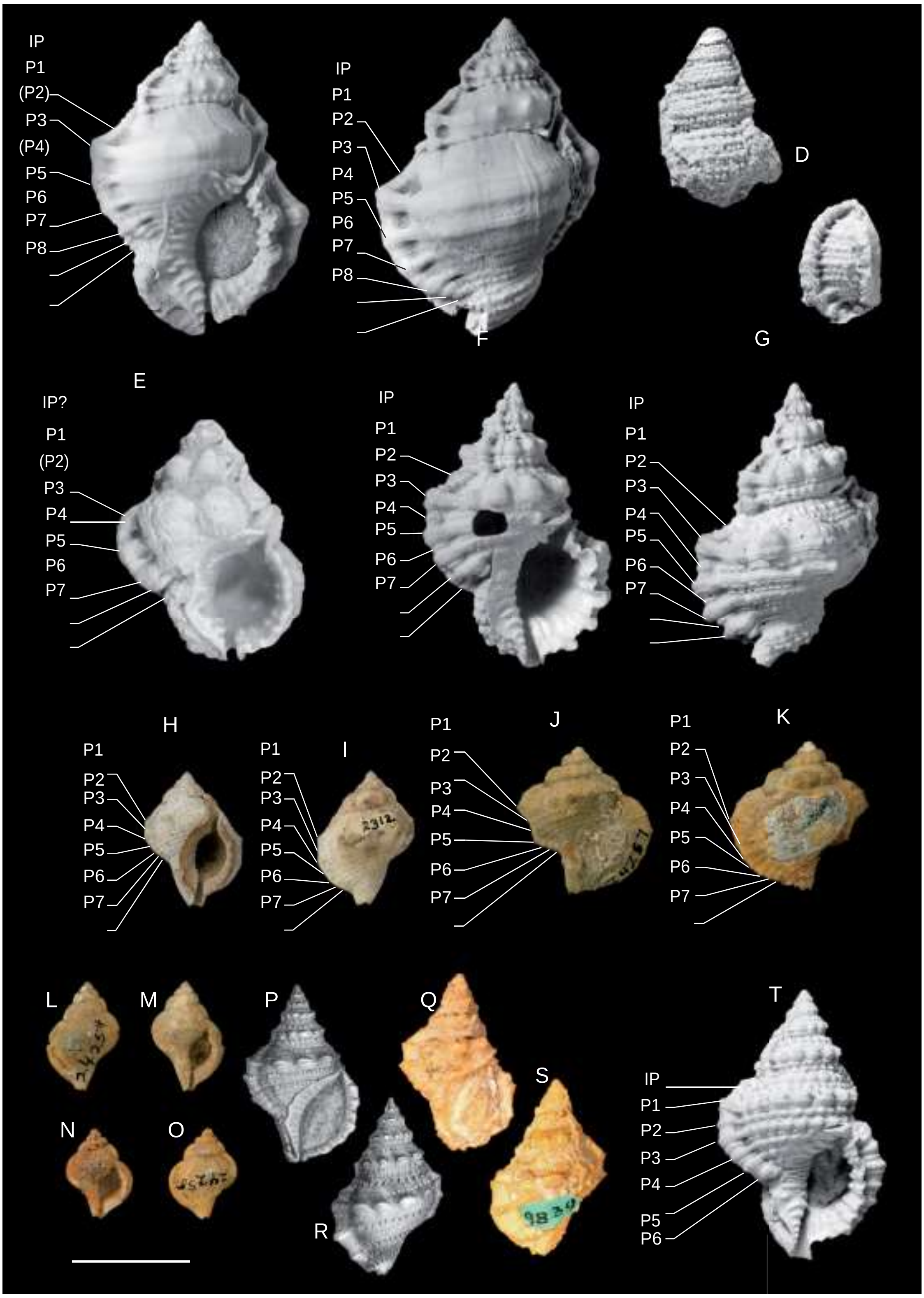


Fig. 5. — Extinct Bursidae species: A, B, *Marsupina judensis* Beu, 2010; NMB H 18308, holotype, late Miocene, Punta Judas, Pacific Costa Rica, reproduced from Beu (2010); **C**, **D**, "*Bursa*" *landaui* Harzhauser, 2009, NHMW 2007z0181/0029 (**C**) holotype and NHMW 2007z0181/0030 (**D**), both from the Aquitanian of Ras Tipuli, Lindi Bay, Tanzania, reproduced from Harzhauser (2009); **E**, *Lampadopsis sangirana* (Beu, 2005), RGM 456 230, holotype, late Pliocene of Kalibeng layers, Sangiran, central Java, reproduced from Beu (2005); **F**, **G**, *Aquitanobursa chipolana* (Schmelz, 1997) n. comb., USNM 647108, paratype, specimen illustrated by Vokes (1973: text-figs 2a, b), coral reef facies of Chipola Formation (late Early Miocene), loc. TU547, reproduced from Beu (2010); **H**, **I**, *Marsupina freya* (Olsson, 1932), PRI 2312, holotype, "Zorritos Miocene," divide between Quebrada Conchudo Bravo and Quebrada Seca, Mancora, Peru; **J**, **K**, *Olssonia chira* (Olsson, 1930) n. comb., PRI 24257, holotype, Late Eocene/Oligocene of Chira Formation, Quercotilla, Peru; **L**-**O**, *Olssonia yasila* (Olsson, 1930) n. comb., PRI 24254 (**L**, **M**) and PRI 24255 (**N**, **O**), Middle Eocene Talara Formation, Yasila, Peru; **P**-**S**, *Aquitanobursa morrisi* (d'Archiac & Haime, 1853) n. comb., original representation of one of the syntypes by d'Archiac & Haime (1853) (**P**, **R**) and (NHMUK PI TG 27045) lectotype, from "Calcaire grossier jaune de la chaîne d'Hala" (Aquitanian?) Pakistan; **T**, *Aquitanobursa amphitrites* (Maury, 1917) n. comb., PRI 28763, holotype, Cercado Fm (Late Miocene), Maury's bluff 3, Cercado de Mao, Dominican Republic, reproduced from Beu (2010). Scale bar: 2 cm.

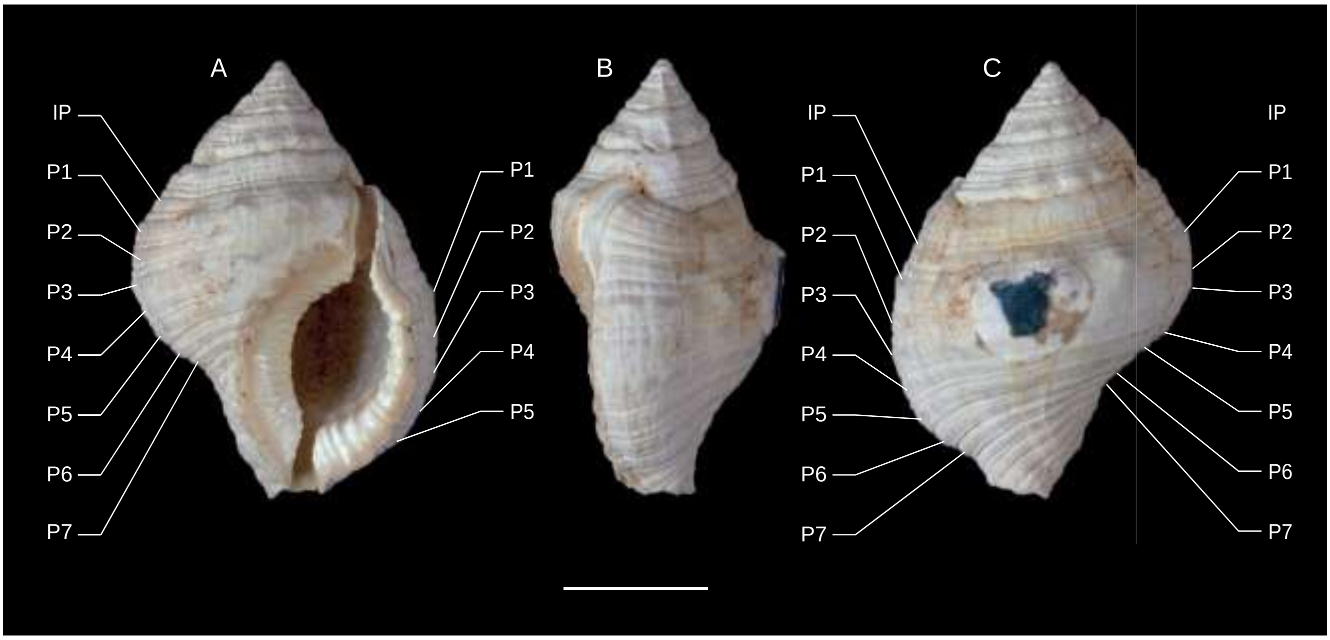


Fig. 6. — *Aspa subgranulata* (d'Orbigny, 1852). MNHN.F.A70283 (Brongniart coll.), ventral (**A**), lateral left (**B**) and dorsal (**C**) views, Miocene of Le Peloua, Landes, France. Scale bar: 2 cm.

### *Olssonia chira* (Olsson, 1930) n. comb.
### (Fig. 5L, M)

*Bursa chira* Olsson, 1930: 62, pl. 10, figs 5-7,13.

*Marsupina chira* – Beu 1988: 71; 2010: 72.

Type material. — Holotype (PRI 24257), one paratype (PRI 24263).

Type locality. — Late Eocene/Early Oligocene of Chira Formation, Quercotilla, Peru.

Geographic and stratigraphic occurrence. — *Olssonia chira* n. comb. seems to occur only on the Late Eocene/Early Oligocene of Peru.

### *Olssonia yasila* (Olsson, 1930) n. comb.
### (Fig. 5N, O)

*Bursa chira* var. *yasila* Olsson, 1930: 63, pl. 10, figs 3, 4.

*Marsupina yasila* – Beu 1988: 71.

Type locality. — Middle Eocene (Bartonian) Talara Formation, Yasila, Peru

Type material. — Holotype (PRI 24254), with two paratypes (PRI 24255 and PRI 24262).

Geographic and stratigraphic occurrence. — Known only from the Bartonian of Peru.

## Genus *Aquitanobursa* n. gen.

Type species. — *Ranella grateloupi* d'Orbigny, 1852.

Derivatio nominis. — Derived from Aquitaine (Aquitania in Latin), the region where most of the species of the genus occur.

Species included. — *Aquitanobursa grateloupi* (d'Orbigny, 1852) n. comb., *Aq. amphitrites* (Maury, 1917), n. comb., *Aq. inaequicrenata* (Cossmann & Peyrot, 1924) n. comb., *Aq. morrisi* (d'Archiac & Haimes, 1853) n. comb., *Aq. tuberosa* (Grateloup, 1833) n. comb.

Diagnosis. — Shell thick, moderately short-spired, varices slightly displaced, 6 primary cords on the convex part of the whorl, variceal and intervariceal P2 very reduced, axial ridges on the first whorl, parietal callus prominent. Posterior siphonal canal short, well-defined; outer lip with weak projection.

Comparison. — With their deeply marked and angular varices and strongly expressed shoulder, *Aquitanobursa* n. gen. species resemble some deep-sea species of the *Bursa s.l.* genus such as *Bursa quirihorai* Beu, 1987 (Fig. 3H); however, *Aquitanobursa* n. gen. species are much strongly built, with a thicker shell.
Atavistic features displayed by deep-sea gastropods are a well-known phenomenon, described recently for Muricidae by Merle (2012). The phylogenetic relationships of *Aquitanobursa* n. gen. with other Bursidae remain unclear; this genus is possibly a sister group to all Recent Bursidae, but that in unlikely considering that it occurs at the same time as *Aspa marginata* and *Bursa corrugata*. A fair assumption would be that it is the sister group to all bursids except *Aspa* and *B. corrugata,* but that would need a phylogenetic analysis for confirmation.

### *Aquitanobursa grateloupi* (d'Orbigny, 1852) n. comb.
### (Fig. 7A)

*Ranella gratteloupi* [sic] d'Orbigny, 1852: 76.

*Ranella leucostoma* – Grateloup 1833: 91, pl VI (not Lamarck, 1822).

*Ranella semigranosa* – Grateloup 1845: pl. XXIX, fig. 6 (not Lamarck, 1822).

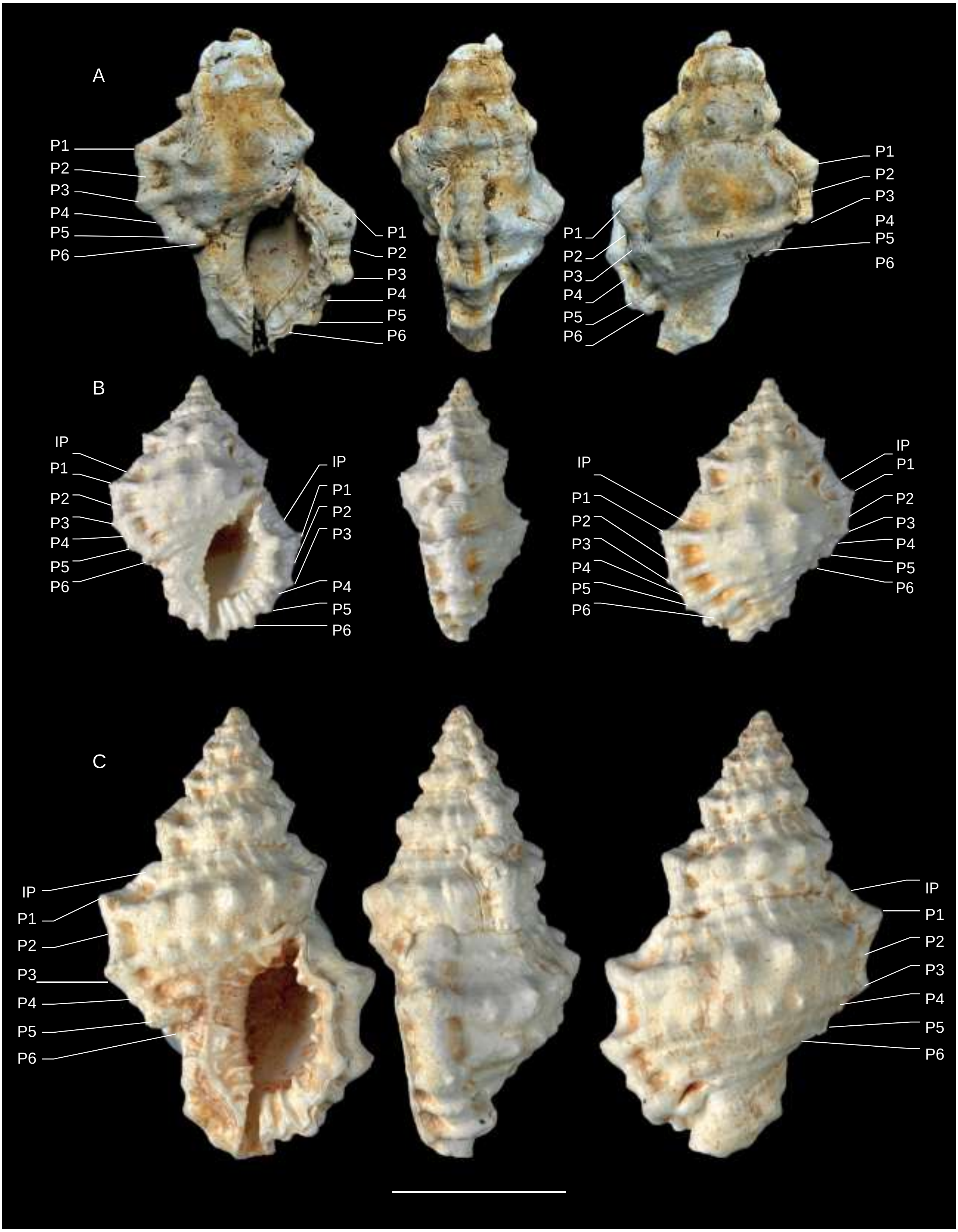


Fig. 7. — *Aquitanobursa* n. gen. of Aquitaine Basin: **A**, *Aquitanobursa grateloupi* (d'Orbigny, 1852) n. comb., MNHN.F.A27211, lectotype from the Aquitanian of Saint-Paul-les-Dax, France; **B**, *Aquitanobursa inaequicrenata* (Cossmann & Peyrot, 1924) n. comb., MNHN.F.A70284, Burdigalian of le Peloua, France; Faullummel coll.; **C**, *Aquitanobursa tuberosa* (Grateloup, 1833) n. comb., MNHN.F.A70285, Burdigalian of le Peloua, Staadt coll.

*Apollon grateloupi* – Cossmann & Peyrot 1924: 305, pl. XV, figs 42, 43.

Type locality. — Lower Miocene of Aquitaine Basin, Bordeaux and Saint-Paul-lès-Dax, France.

Type material. — MNHN.F.A27211 (from Saint-Paul-lès-Dax) is here designated as lectotype. One paralectotype (MNHN.F.B27595).

Other material examined. — 13 specimens from Brongniart coll. from le Peloua, Burdigalian.

Geographic and stratigraphic occurrence. — *Bursa grateloupi* is only known from the lower Miocene of the Aquitaine Basin.

Remarks

*Aquitanobursa grateloupi* n. comb. was originally written *gratteloupi*. This name is obviously based on that of J.P.S. de Grateloup, and in accord with ICZN 32.5.1 the correct spelling is *Aquitanobursa grateloupi* n. comb.

### *Aquitanobursa amphitrites* (Maury, 1917) n. comb.
(Fig. 5T)

*Bursa amphitrites* Maury, 1917: 273, pl. 17, fig. 9. — Beu 2010: 42, pl. 1, figs 1-4, 8.

*Bursa amphitrites* – E. Vokes 1973: 100 (in part = *Marsupina bufo*) (not Maury, 1917).

*Bursa* (*Colubrellina*) *caelata amphitrites* – Aguilar *in* Seyfried *et al.* 1985: 64, appendix (not Maury, 1917).

Type locality. — Bluff 3, Cercado de Mao, Dominican Republic; Cercado Formation, late Miocene.

Type material. — Holotype (PRI 28763).

Geographic and stratigraphic occurrence. — Occurs from the Late Miocene to Early Pliocene Gurabo Formation (Tortonian to Piacenzian, according to Denniston *et al.* 2008) in the Dominican Republic and from the early Middle Miocene Buenevara Adentro beds of the Paraguaná Peninsula, Venezuela (Beu 2010).

### *Aquitanobursa chipolana* (Schmelz, 1997) n. comb.
(Fig. 5F, G)

*Bursa* (*Bufonariella*) *chipolana* Schmelz, 1997: 105, pl. 1, figs 1a-c; pl. 2, figs 1a-b, 2a-b. — Vokes 1997: 212.

*Bursa* (*Bufonariella*) *pelouatensis* – Vokes 1973: 97, text-fig. 2 (not Cossmann & Peyrot, 1924).

*Bursa chipolana* – Beu 2010: 44, pl. 1, figs 5-7, 10.

Type locality. — Tulane University locality TU546, Chipola Formation (Burdigalian), Tenmile Creek, Florida, United States.

Type material. — *Bursa* (*Bufonariella*) *chipolana*, holotype (UF 73199), figured paratype (USNM 647108), from TU547, west bank Chipola River 600 m upstream from Fourmile Creek, Calhoun Co. (specimen figured by Vokes 1973: text-figs 2a-b, refigured in good quality by Beu 2010: pl. 1, figs 6, 7); figured paratype (UF 73200), from TU951, Tenmile Creek, Calhoun Co.; nine further paratypes from localities on or near the Chipola River listed by Schmelz (1997).

Geographic and stratigraphic occurrence. — *Aquitanobursa chipolana* n. comb. is recorded only from the Chipola Formation (Burdigalian) on and near the Chipola River, Calhoun Co., Florida, United States.

Remarks

*Aquitanobursa chipolana* n. comb. seems to have a slightly greater number of primary cords than other species referred to *Aquitanobursa* n. gen. This species possibly belongs in another genus, for which a new name needs to be created.

### *Aquitanobursa inaequicrenata* (Cossmann & Peyrot, 1924) n. comb.
(Fig. 7B)

*Apollon inaequicrenatus* Cossmann & Peyrot, 1924: 311 pl. 15, figs 44-45.

*Bursa* (*Bufonariella*) *inaequicrenata* – Beu 1981: 258.

*Bursa inaequicrenata* – Landau *et al.* 2004: 68; 2009: 76.

Type locality. — Burdigalian of Le Peloua, near Saucats (Gironde), Aquitaine Basin, France.

Type material. — *Apollon inaequicrenatus*, holotype (MNHN.F.J06127 Cossmann coll.) from the Burdigalian of Le Peloua and one paratype (MNHN.F.J06128 Cossmann coll.).

Other material examined. — Five specimens from Brongniart coll., three from le Peloua, Burdigalian, one from Saint-Paul-les-Dax (Cabannes), Burdigalian, one from Saubrigues, Burdigalian; one specimen from Jussieu coll., from Mérignac, Burdigalian; one specimen from Lhomme coll., from Saucats, Aquitanian; all housed in the collection de Paléontologie, MNHN.

Geographic and stratigraphic occurrence. — Only known from the Atlantic Aquitaine Basin of France (Aquitanian and Burdigalian).

### *Aquitanobursa morrisi* (d'Archiac & Haime, 1853) n. comb.
(Fig. 5P-S)

*Ranella morrisi* d'Archiac & Haime, 1853: 309, pl. XXX, fig. 1, pl XXXI, fig. 3.

*Ranella elegans* – Martin 1884: 137 (not G.B. Sowerby 2nd , 1836 *in* G.B. Sowerby 1st & G.B. Sowerby 2nd, 1832-1841).

*Apollon morrisi* – Harzhauser *et al.* 2009: 360, pl. 1.

Type locality. — "Calcaire grossier jaune de la chaîne d'Hala", Pakistan.

Type material. — Types figured by d'Archiac & Haime (1853) previously in UK Geological Survey, now in NHMUK. The complete specimen (NHMUK PI TG 27045) is here designated as the lectotype. One paralectotype (NHMUK PI TG 27046).

Geographic and stratigraphic occurrence. — This species is only known by d'Archiac & Haime's (1853) specimens for the lower Miocene of Halla Mountain, Sindh, Pakistan.

### *Aquitanobursa tuberosa* (Grateloup, 1833) n. comb.
(Fig. 7C)

*Ranella tuberosa* Grateloup, 1833: 92, no. 420. — Bellardi 1873: 236, pl. 15, fig. 7.

*Ranella subtuberosa* d'Orbigny, 1852: 76, no. 1405.

*Apollon pelouatensis* Cossmann & Peyrot, 1924: no. 842, pl. 15, figs 38-39, pl. 17, figs 1-2.

*Bursa* (*Bufonariella*) *pelouatensis* – Beu 1981: 258. — Schmelz 1997: 106, pl. 1, fig. 2.

*Bursa tuberosa* – Lozouet *et al.* 2001: 45, pl. 19, figs 3a-3b. — Landau *et al.* 2004 : 68.

TYPE LOCALITY. — *Ranella tuberosa* and *Apollon pelouatensis* both from the Aquitanian of Saint-Paul-Lès-Dax, France.

TYPE MATERIAL. — *Ranella tuberosa* syntypes in Grateloup coll., University of Bordeaux, Talence, France (not seen); *Apollon pelouatensis*: the specimen MNHN.F.J06123 is here designated as lectotype. Three paralectotypes (MNHN.F.J06124, J06125, J06126). .

OTHER MATERIAL EXAMINED. — Two specimens from Hofstetter coll., from le Peloua, Burdigalian, and one from Saubrigues, Burdigalian; 13 specimens from Brongniart coll., from le Peloua, Burdigalian; 15 specimens from Staadt coll., from le Peloua, Burdigalian; one specimen from Lhomme coll., from le Peloua, Burdigalian; two specimens (MNHN.F.A70577, A70578) from Gaas "Lagouarde", Rupelian; all in the collections de paléontologie, MNHN.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Rupelian to middle Miocene of the Aquitaine basin (France) and Po Valley (Italy).

## RECOMMENDATIONS FOR CALIBRATION

In regard to the systematic considerations, we can provide some recommendations for calibration of the molecular tree of the Bursidae. Numerical dating for this section is provided by the international geological time scale (Gradstein *et al.* 2012); a complete stratigraphic distribution chart for the Bursidae is shown in Figure 8. First occurrence and last occurrence data are provided in Appendix 1.

Considering that it is the oldest undisputable taxon included in Bursidae and apparently is not closely related to other clades within the family, the genus *Olssonia* n. gen. seems to be the best candidate for the calibration of the whole Bursidae. The oldest representative of the genus is *O. yasila* n. comb. from the early Bartonian (Olsson 1932, Beu 1988) for which we propose to use an age of 41.2 Ma. As for all the following node calibrations, we propose to apply a truncated log normal distribution, as it places the highest probability on ages somewhat older than the fossil, diversification being necessarily older than the observed fossil record (Ho & Phillips 2009).

The genus *Aspa* does not resemble any other Bursidae closely and, considering its very long stratigraphic history, possibly commencing before the Neogene (Landau *et al.* 2004), it may very well be a sister group to the rest of the Recent Bursidae. On the other hand, the fossil genus *Aquitanobursa* n. gen. looks like some Recent species such as *B. quirihorai* and *B. granosa.* If *Aspa* were to branch at the base of the Bursidae tree, the clade containing every other bursid but excluding *Aspa* could be calibrated by *Aquitanobursa* n. gen. The oldest representative of the genus (two specimens MNHN.F.A70577, A70578) is *A. tuberosa* n. comb. from the Rupelian (Stampian) of the Aquitaine Basin. We propose an age of 27.82 Ma (Rupelian/Chattian transition) for the node calibration.

*Bursa,* under the definition suggested in this paper, could be calibrated by the specimen resembling *B. rosa* from middle-late Miocene of Citalahab, West Java mentioned by Beu (2005: fig. 33). He attributed this specimen to *B. rosa.* Indeed, this specimen bears the long tubular posterior siphonal canal characteristic of the genus, but it is far less warty and could warrant erecting a new species, becoming thus the oldest species of all *Bursa* s.s. We propose an age of 9 Ma.

All the species of the former *Bursa granularis* complex (Sanders *et al.* 2017) could have their clade calibrated by the three specimens from Citalahab, West Java attributed by Beu (2005) to *B. granularis*, with an age of 9 Ma as for *Bursa* s.s. This calibration should not be blindly trusted, because we have not seen the specimens and they were not figured by Beu (2005). The relationship of *B. landaui* to this clade remains too uncertain to be used as a calibration.

The genus *Marsupina* could be calibrated by the Shoal river formation specimen (USNM 647109), middle Miocene, figured by Beu (2010: pl. 9, fig. 6). This juvenile specimen strikingly resembling *M. bufo,* but has a more coarsely sculptured shell than later specimens of *Marsupina*, too much so to be conspecific. We propose an age of 14 Ma for the calibration of crown *Marsupina*.

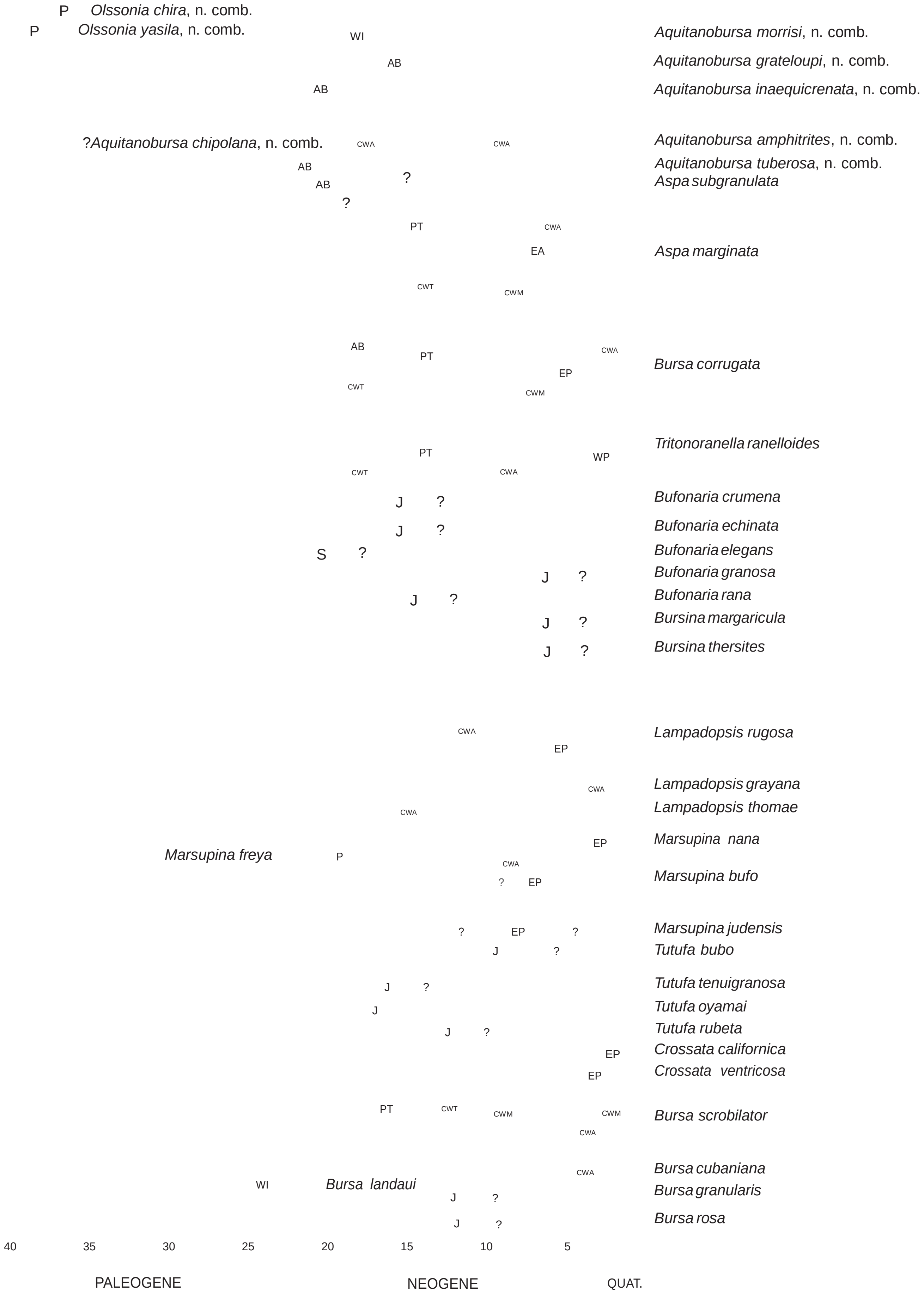
Strong *et al.*(2019) proposed to use the large specimen of *Tutufa* sp. Looking a lot like *T. bubo* figured by Tomida *et al.* (2013) as a calibration point for the genus *Tutufa*, calibrated at 13.5 Ma. We follow their recommendation.

No other node could be calibrated easily based on what we know currently of the systematics of Bursidae.

## TIMING OF DIVERSIFICATION OF BURSIDAE BASED ON THE FOSSIL RECORD

Providing a scenario explaining the diversification of a highly dispersive family like the Bursidae is not an easy task, especially without a proper phylogenetic context. What we can say, however, is that the diversification of the Bursidae happened in three phases (Fig. 8).

Strong *et al.* (2018) estimated (with very low support regarding its relationship with its sister family) the origin of the family at around 113 Ma but, as stated above, we have no trace of morphologically recognizable bursids prior to the middle Eocene (40 Ma) Peruvian fauna. Following this record there is no other trace of Bursidae in the Paleogene. A possible explanation of this lack of fossils is a general diminution of fossil-rich (unlithified) marine outcrops in the late Paleogene (Hendy 2011). This tendency dramatically shifts in the Neogene, as we found an already well diversified fauna throughout the lower Miocene Tethyan realm.


P Olssonia chira, n. comb.
P Olssonia yasila, n. comb.
WI
Aquitanobursa morrisi, n. comb.
AB
Aquitanobursa grateloupi, n. comb.
AB
Aquitanobursa inaequicrenata, n. comb.
?Aquitanobursa chipolana, n. comb.
CWA
CWA
Aquitanobursa amphitrites, n. comb.
AB
Aquitanobursa tuberosa, n. comb.
AB
?
Aspa subgranulata
?
PT
CWA
EA
Aspa marginata
CWT
CWM
AB
PT
CWA
EP
Bursa corrugata
CWT
CWM
Tritonoranella ranelloides
PT
WP
CWT
CWA
J ?
Bufonaria crumena
J ?
Bufonaria echinata
S ?
Bufonaria elegans
J ?
Bufonaria granosa
J ?
Bufonaria rana
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Bursina margaricula
J ?
Bursina thersites
CWA
Lampadopsis rugosa
EP
CWA
Lampadopsis grayana
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Lampadopsis thomae
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Marsupina nana
Marsupina freya
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Marsupina bufo
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Marsupina judensis
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Tutufa bubo
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Tutufa tenuigranosa
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Tutufa oyamai
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Tutufa rubeta
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Crossata californica
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Crossata ventricosa
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Bursa scrobilator
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Bursa cubaniana
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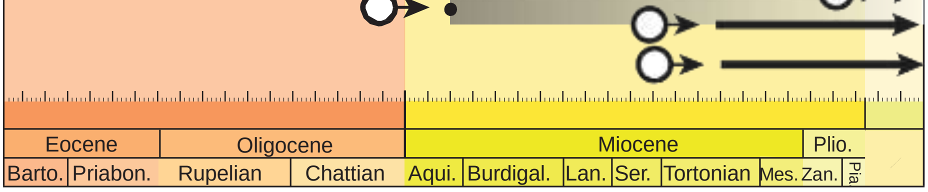

Fig. 8. — Stratigraphic range of the extinct and extant Bursidae. **Black arrows** indicate total stratigraphic range; **grey arrows** indicate regional stratigraphic range. Abbreviations: **P**, Peru; **WI**, Western Indian Ocean; **AB**, Aquitaine Basin; **CWA**, Caribbean, Western Atlantic Ocean; **PT**, Paratethys, CWT: Central Western Tethys; **EA**, Eastern Atlantic; **CWM**, Central Western Mediterranean; **WP**, Western Pacific Ocean; **J**, Java, Indo-Pacific; **S**, Sumatra, Indo-Pacific; **EP**, Eastern Pacific Ocean. **Grey squares** regroup accepted genera and putative genera within *Bursa.*

In the west (Aquitaine Basin) most species of the genus *Aquitanobursa* n. gen., *Aspa subgranulata* and *Bursa corrugata* occur. In the "Mediterranean region" (*sensu* Harzhauser *et al.* 2002) *Bursa corrugata* and *Bursa ranelloides* occur. The presence of *B. corrugata* in both regions is a clear indication of a connection between the westernmost Tethys and the Atlantic. In the Eastern Proto-Indo-West-Pacific region, Bursidae are represented by *Aquitanobursa morrisi* n. comb. in the north (Pakistan) and by *Bursa landaui* in the southwest (Tanzania). The arrival of *A. morrisi* n. comb. in the Proto-Indo-West-Pacific region was most certainly through the Tethys, as most of the species of the genus are found in the Aquitaine Basin. On the other hand, the arrival *B. landaui* in the region is more difficult to explain.

The next phase of diversification happened during the middle Miocene with the closure of the Tethys Ocean in the east. Following this closure, we observed a relocation of the main coral biodiversity hotspot from the Mediterranean to the present-day coral triangle (Leprieur *et al.* 2016). This hot spot shift could explain the radiation of the coral-dependent bursids (*Tutufa*, *Bufonaria*, *Bursa* s.s.). An eastward colonization of most of those species is probable, although some genera (e.g. *Lampadopsis*) possibly arrived from the Pacific.

In the west, also during the middle Miocene, *Aspa marginata* entered the Eastern Atlantic and *Lampadopsis rugosa* entered the Pacific Ocean from the Caribbean. The genus *Aquitanobursa* n. gen. entered the Western Atlantic (*A. amphitrites* n. comb.) and the genus *Marsupina* appeared. In the Proto-Mediterranean Atlantic region the species *Bursa scrobilator* appeared.

The high species-level diversity of tonnoideans in general during the middle Miocene was already pointed out by Landau *et al.*(2009).

At the Miocene-Pliocene transition we see the appearance of the last currently admitted genera: *Bursina* in the Indo-Pacific and *Crossata* in western America (there is an unconfirmed occurrence of *Crossata* in the middle Miocene (Beu 2010; Powell & Berschauer 2017).

Following the Messinian salinity crisis in the Mediterranean Sea, we observe the return of *Bursa scrobilator* to this domain. In the Recent fauna it is the only bursid species in the Mediterranean. *Bursa corrugata* returned briefly as well, but disappeared from the Mediterranean during the Pleistocene (Landau *et al.* 2009). It was also during the Pliocene that *B. corrugata* entered the western Atlantic, from which it reached the Eastern Pacific during the Pleistocene (Beu 2010). *Aspa marginata* reappeared briefly in the Mediterranean at the beginning of the Pliocene and reached its maximum geographic extension during the late Pliocene/early Pleistocene by entering the Western Atlantic. At present it occurs only in the Eastern Atlantic and at some mid-Atlantic islands.

## CONCLUDING REMARKS

Dating biological events such as diversification or speciation in the fossil record remain a daunting task without a proper phylogenetic background, at least as much so as dating phylogenetic trees without proper fossil data. For this reason, reviews such as this one are paramount in order to understand the paleobiodiversity of a taxonomic group reliably. We followed as much as possible the recommendations of Parham *et al.* (2012) by systematically referring to the literature and by providing characters linking the fossils to extant clades and providing institution specimen numbers when possible. We hope the calibrations provided here will help unveil the Paleogene diversification pattern of the Bursidae, a period from which few fossils are known.

## Acknowledgements

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Appendix 1. — First occurrence and last occurrence data for all species of Bursidae. **N.A.**, not applicable.

| **Species** | **First occurrence** | **Formation** | **Reference to the occurrence** | **Reference to the stratigraphy** | **Last occurrence** | **Formation** | **Reference for the occurrence** | **Reference for the stratigraphy** |
|---|---|---|---|---|---|---|---|---|
| *Aquitanobursa chipolana* n. comb. | Burdigalian | Chipola formation, Florida | Beu 2010 | Beu 2010 | Burdigalian | Chipola formation, Florida | Beu 2010 | Beu 2010 |
| *Aquitanobursa amphitrites* n. comb. | Tortonian | Buenevara Adentro beds, Venezuela | Beu 2010 | Beu 2010 | Zanclean | Gurabo Formation, Dominican republic | Beu 2010 | Beu 2010 |
| *Aquitanobursa inaequicrenata* n. comb. | Lower Burdigalian | Le Peloua, Aquitaine Basin, France | Cossmann & Peyrot 1924 | Lozouet 1998 | Lower Burdigalian | Le Peloua, Aquitaine Basin, France | Lozouet 1997 | Lozouet 1998 |
| *Aquitanobursa morrisi* n. comb. | Burdigalian | Calcaire grossier de la chaine d'Hala, Pakistan | D'Archiac & Haime 1853 | Vredenburg 1925 Harzhauser *et al.* 2009 | Burdigalian | Calacaire grossier dela chaine d'Hala | D'Archiac & Haime 1853 | Vredenburg 1925 Harzhauser *et al.* 2009 |
| *Aquitanobursa tuberosa* n. comb. | Rupelian | Aquitaine basin, France | Lozouet 1998 | Lozouet 1998 | Lower Burdigalian | Aquitaine basin | Lozouet 1998 | Lozouet 1998 |
| *Bufonaria crumena* | Middle Miocene (early Preangerian) | Robba's locality CIJ1, Cijarian, western Java | Beu 2005 | Beu 2005 | Extant | N.A. | N.A. | N.A. |
| *Bufonaria echinata* | Middle Miocene (early Preangerian) | Robba's locality CIJ1, Cijarian, western Java | Beu 2005 | Beu 2005 | Extant | N.A. | N.A. | N.A. |
| *Bufonaria elegans* | Pleistocene (Early Miocene) | Nias Island, Sumatra (Pakistan) | Beu 2005 | Beu 2005 | Extant | N.A. | N.A. | N.A. |
| *Bufonaria granosa* | Late Pliocene (Piacenzian?) | Kalibeng layers, Sangiran, central Java | Beu 2005 | Beu 2005 | Extant | N.A. | N.A. | N.A. |
| *Bufonaria rana* | Late Miocene | Kendeng beds, Jave | Beu 2005 | Robba 1996 Sharaf *et al.* 2005 | Extant | N.A. | N.A. | N.A. |
| *Bursa corrugata* | Burdigalian | Aquitaine basin, France | Cossmann & Peyrot 1924 | Landau *et al.* 2009 | Extant | N.A. | N.A. | N.A. |
| *Bursa cubaniana* | Pleistocene | Various formations from Panama, Cuba, Dominican republic and Barbados | Beu 2010 | Beu 2010 | Extant | N.A. | N.A. | N.A. |
| *Bursa granularis* | Late Miocene | Citalahab, West Java | Beu 2005 | Beu 2005 | Extant | N.A. | N.A. | N.A. |
| *Aquitanobursa grateloupi* | Burdigalian | Bordeau surroundings, Aquitaine Basin, France | d'Orbigny 1852 | d'Orbigny 1852 | Serravallian | Tauziets Aquitaine basin, France | Lozouet 1997 | Lozouet 1998 |
| *Bursa grayana* | Messinian | Cercado formation, Dominican republic | Beu 2010 | Beu 2010 | Extant | N.A. | N.A. | N.A. |
| *Bursa landaui* | Aquitanian | Ras Tipuli Tanzania | Harzhauser 2009 | Harzhauser 2009 | Aquitanian | Ras Tipuli Tanzania | Harzhauser 2009 | Harzhauser 2009 |
| *Bursa rosa* | Late Miocene | Citalahab, West Java | Beu 2005 | Beu 2005 | Extant | N.A. | N.A. | N.A. |
| *Bursa rugosa* | Burdigalian | Cantaure, Venezuela | Beu 2010 | Beu 2010 | Extant | N.A. | N.A. | N.A. |
| *Bursa scrobilator* | Langhian/Serravallian | Paratethys Austria and Poland | Landeau *et al.* 2004 | Baluk 1995 | Extant | N.A. | N.A. | N.A. |
| *Lampadopsis thomae* | Burdigalian | Chipola formation, Florida | Beu 2010 | Tulane fossil localities | Extant | N.A. | N.A. | N.A. |

Appendix 1. — Continuation.

| Species | First occurrence | Formation | Reference to the occurrence | Reference to the stratigraphy | Last occurrence | Formation | Reference for the occurrence | Reference for the stratigraphy |
|---|---|---|---|---|---|---|---|---|
| *Bursina margaricula* | Pliocene | Tjikeusik [Cikeusik], Java | Beu 2005 | Beu 2005 | Extant | N.A. | N.A. | N.A. |
| *Crossata ventricosa* | Tortonian | Tumbez Fm, Quebrada Tucillal, Zorritos, Peru | Olsson 1932; Beu 2010 | Olsson 1932 | Extant | N.A. | N.A. | N.A. |
| *Marsupina bufo* | Serravallian | Shoal River formation, Florida | Beu 2010 | Gardner 1947 | Extant | N.A. | N.A. | N.A. |
| *Marsupina freya* | Chattian/ Aquitanian | Malpais, SW coast of Nicoya Peninsula, Pacific Costa Rica | Beu 2010 | Beu 2010 | Burdigalian/ Langhian | Subibaya Formation, Progreso Basin, SW Ecuador | Beu 2010 | Beu 2010 |
| *Marsupina judensis* | Late Miocene | Punta Judas, 40 km WNW of Quepos, Pacific coast of Costa Rica | Beu 2010 | Beu 2010 | Late Miocene | Punta Judas, 40 km WNW of Quepos, Pacific coast of Costa Rica | Beu 2010 | Beu 2010 |
| *Marsupina nana* | Zanclean | Charco Azul Group, Penita Fm, Quebrada La Penita, Burica Peninsula, Pacific coast of Costa Rica | Beu 2010 | Olsson 1942 | Extant | N.A. | N.A. | N.A. |
| *Olssonia chira* n. comb. | Priabonian | Chira formation, Quercotilla, Peru | Olsson 1930 | Stone 1949 | Bartonian | Chira Formation, Quercotilla, Peru | Olsson 1930 | Stone 1949 |
| *Olssonia yasila* n. comb. | Bartonian | talara formation, Peru | Olsson 1930 | Olsson 1930 | Bartonian | Talara Formation Peru | Olsson 1930 | Olsson 1930 |
| *Tutufa bubo* | Late Miocene? | Pendopo Oilfield, 16 km east of Talang Akar, Sumatra | Beu 2005 | Robba 1996 | Extant | N.A. | N.A. | N.A. |
| *Tutufa oyamai* | Langhian/ Serravallian | Karas, Rembang, Ngrayong Formation, Java | Beu 2005 | Robba 1996; Sharaf *et al.* 2005 | Extant | N.A. | N.A. | N.A. |
| *Tutufa rubeta* | Late Miocene | Citalahab, West Java | Beu 2005 | Beu 2005 | Extant | N.A. | N.A. | N.A. |
| *Tutufa tenuigranosa* | Miocene | Mount Butack, Rembang, central Java | Beu 2005 | Beu 2005 | Extant | N.A. | N.A. | N.A. |
| *Aspa subgranulata* | Rupelian | Gaas, Landes | Beu 2010 | Beu 2010 | Middle Miocene | ? | Landau *et al.* 2004 | Landau *et al.* 2004 |
| *Aspa marginata* | Burdigalian | Po valley and Paratethys | Landau *et al.* 2004, 2009 | Landau *et al.* 2004, 2009 | Extant | N.A. | N.A. | N.A. |