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Chronologie de la diversification des Bursidae Thiele, 1929 (Gastropoda, Tonnoidea)

Malcolm Sanders

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THESE

Pour obtenir le grade de

DOCTEUR DU MUSEUM NATIONAL D'HISTOIRE NATURELLE

Spécialité : Systématique, Paléontologie

Présentée et soutenue publiquement par

Malcolm T. SANDERS

Le 8 décembre 2017

**Chronologie de la diversification
des Bursidae Thiele, 1929
(Gastropoda, Tonnoidea)**

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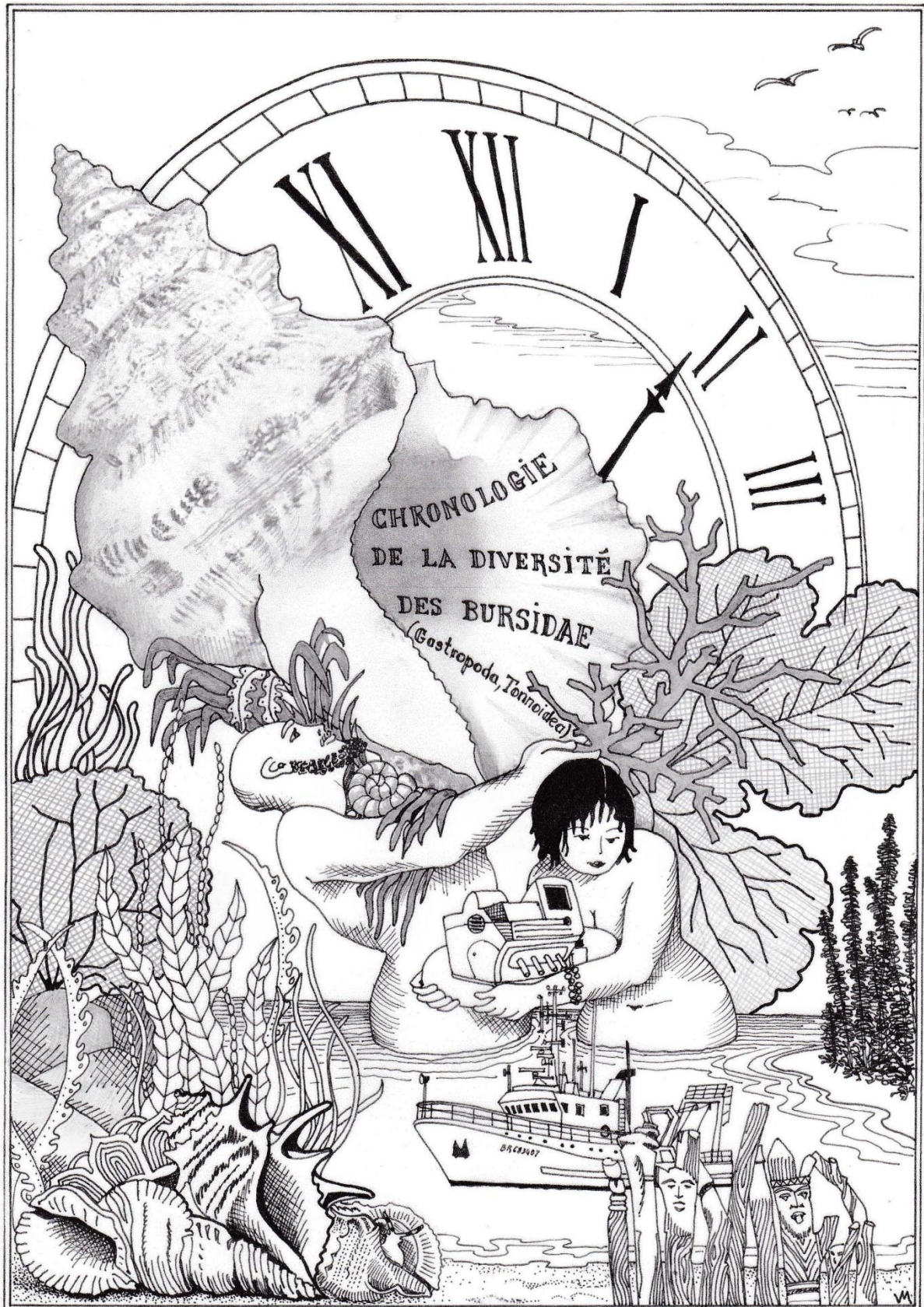
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La présente thèse ne constitue pas une publication au sens
du Code International de Nomenclature Zoologique.

[Code, Recommandation 8E]

FRONTISPICE



Véronique Petitjean

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CHAPITRE 1

INTRODUCTION



Les théories passent, la grenouille reste
J. Rostand, Carnets d'un biologiste

*People assume that time is a strict progression of cause to effect, but *actually* from a non-linear, non-subjective viewpoint - it's more like a big ball of wibbly wobbly, time-y wimey... stuff.*
Doctor who, Saison 3 épisode 10

A l'origine de la malacologie, la science de l'étude des mollusques, les fossiles étaient considérés de la même manière que les actuels. Et cela pour une très simple raison, l'objet d'étude était strictement le même : la coquille. En effet les premières classifications systématiques ont été réalisées par des naturalistes qui n'étaient pas nécessairement des hommes de terrain et à qui on confiait, en grande partie, du matériel séché (débarassé de toute partie molle).

Ce lien entre paléontologie et néontologie a perduré pendant tout le 19^{ème} siècle, et ce malgré les avancées technologiques telles que le microscope qui ont donné accès à de nouveaux caractères (radula, système nerveux etc...) non observables chez les fossiles.

Le divorce allait arriver au cours du 20^{ème} siècle.

A la suite des travaux de Darwin, la biologie allait devenir évolutive et pour refléter ce nouveau paradigme les classifications ne pouvaient plus être fondées sur des ressemblances globales mais sur des liens de parenté ; elles allaient devoir devenir phylogénétiques.

Une méthode qui connaîtra un grand succès pour reconstruire ces classifications est l'analyse cladistique. Popularisée par la traduction en langue anglaise des travaux de Willi Hennig (1966), il s'agit d'une méthode permettant, à partir de l'observation des différents caractères d'un ensemble de taxons, de reconstituer leur degré de parenté. En d'autres termes, l'analyse cladistique des caractères d'un ensemble de taxons (au minimum trois) va permettre de déterminer lequel, parmi ces taxons, est le plus proche d'un autre.

Pour que la méthode fonctionne il faut faire l'hypothèse que les caractères comparés, même s'ils sont très différents (on parle d'état de caractère) ont une origine unique. Le terme désignant cette hypothèse est homologie primaire. Cette hypothèse ne sera confirmée qu'à l'issue de l'analyse phylogénétique.

Les problèmes liés à la formalisation des hypothèses d'homologies primaires aboutissant à la faible résolution des analyses basées uniquement sur la coquille (Wagner, 2001) est possiblement à l'origine du désintérêt d'une grande partie des paléo-malacologues pour les questions de phylogénies. A part quelques exemples notables (Wagner, 1997, 2002, Merle, 2004, 2005, Neige et al. 2009, Bardin et al. 2017) les méthodes de classification des mollusques fossiles se sont très largement limitées et se limitent encore à l' α -taxonomie.

Le coup de grâce arriva à la fin des années 80 avec l'émergence de la phylogénie moléculaire. Ces approches basées sur des comparaisons de séquences nucléotidiques (ou protéiques) connurent un succès fulgurant. Elles permettent de poser des hypothèses d'homologie à grande échelle tout en limitant les effets liés à la subjectivité du chercheur. Leur

usage a abouti à une refonte importante des classifications de grands groupes de mollusques (Smith et al. 2011, Puillandre et al. 2011).

Avec la diminution des couts d'obtention des séquences ADN, les fossiles semblaient ne plus pouvoir apporter grand-chose au débat. Cependant les fossiles sont porteurs d'une information unique en leur genre. Ils sont inscrits dans le temps. En effet l'échelle des temps géologiques, qui est la référence temporelle de tous les évènements biotiques de l'Histoire de la Terre, a été entièrement défini à l'origine sur la base d'occurrence et de disparition d'organismes fossiles, principalement des mollusques (Gradstein et al. 2012). Cette notion de temps est reconnue comme étant le plus grand apport de la paléontologie à la théorie synthétique de l'évolution (Donoghue & Benton 2007). Et c'est avec ce rôle de « jalon » temporel qu'ils allaient faire leur retour dans le domaine de la biologie évolutive.

Cette thèse s'inscrit dans la dynamique de ce dialogue retrouvé entre données paléontologiques et néontologique avec comme objectif d'adapter les nouveaux outils, concepts et méthodes de la datation des arbres phylogénétiques à l'analyse d'un groupe de gastéropodes marins, les **Bursidae**. Ce groupe s'est révélé potentiellement prometteur pour de multiples raisons.

- Les collections ADN du MNHN constitué depuis 10 ans dans le cadre du renouveau des grandes expéditions naturalistes (MNHN/IRD) couvrent une majeure partie de la taxonomie et de la géographie de ce groupe. Alliées à l'utilisation des nouvelles technologies de séquençage développées au service de systématique moléculaire (UMS 2700) elles offrent l'opportunité d'établir une phylogénie moléculaire robuste de ce groupe.
- Leur registre fossile est bien documenté et bien représenté dans les collections de paléontologie du Muséum. Et le nombre potentiellement important de caractères permettraient de les placer avec une certaine confiance dans les phylogénies actuelles.

Autant de bonnes raisons d'utiliser les Bursidae comme un groupe modèle pour tester notre capacité, au sein d'un établissement comme le MNHN, à réconcilier ADN et morpho-anatomie pour répondre à une question évolutive.

LE GROUPE D'ETUDE : LES BURSIDAE

Les Bursidae Thiele, 1925 sont connus des collectionneurs de coquillage sous le nom d'escargots grenouilles (*Frog shells*) ou ranelles, un nom que l'on doit à Linné (1758) avec la

création dans le *Systema naturae* de *Murex rana* Linnaeus, 1758 (*rana* étant le latin pour grenouille) et *Murex rana* var. *rubeta* Linnaeus, 1758, les deux plus anciennes descriptions de Bursidae aux yeux du code.

A noter que le nom vernaculaire français est un regroupement non monophylétique des familles Ranellidae Gray, 1854, Cymatiidae Iredale, 1913 (1854) et Bursidae, ce que ne fait pas l'anglais.

Caractéristiques générales

Les Bursidae sont tout de suite identifiables à leur canal siphonal postérieur fortement marqué, qui peut parfois être tubulaire ou porter une épine).

Ils le sont aussi par leur coquille généralement épaisse et fortement ornementée avec des nodules, verrues et micro nodosités dans la plupart des espèces les faisant ressembler à certaines espèces de Cymatiidae actuelle ou Charoniidae fossile (Fig. 1.1). La téléoconque est de couleur brune ou blanche et sans periostracum. Les motifs de couleur sont rares et consistent toujours en des bandes spirales (qui peuvent être interrompues chez certaines espèces), situés au niveau des cordons primaires. Les varices sont proéminentes et espacés de 180°, 200° ou 240°. L'ouverture est généralement blanche ou crème sauf chez *Lampasopsis* et *Bursa* où elle peut être jaune, rose ou pourpre. Très variable en taille, la plus petite espèce *Lampasopsis lucaensis* (Parth, 1991) ne dépasse jamais les trois cm alors que certaines espèces du genre *Tutufa* peuvent arriver jusqu'au demi mètre, ce qui en fait un des plus gros gastéropode de la nature actuelle (la grande majorité des Bursidae ont une taille qui varie autour des 5 cm). La radula est taenioglosse et caractérisée par un processus à la base de la dent centrale qui s'emboîte dans la dent latérale. Il n'y a pas de plaque jugale sauf chez *Tutufa* chez qui elles sont très réduites. Une troisième glande salivaire s'ajoute aux deux communes chez les Tonnoidea (Beu, 1998).

Histoire de vie

Les Bursidae ont une distribution mondiale restreinte aux zones tropicales et subtropicales, mais c'est dans la zone tropicale de la région Indo-Pacifique qu'ils atteignent leur richesse maximale. En 2000, Delongueville & Scaillet font mention de la récolte par 100 m de profondeur d'un spécimen appartenant à *Bufonaria rana* (Linnaeus, 1758) dans le nord Finistère (Bretagne, France), bien au-delà de la distribution connue de l'espèce (ou de tout autre Bursidae). Les auteurs indiquant que *Bufonaria rana* est l'une des espèces de Bursidae les plus

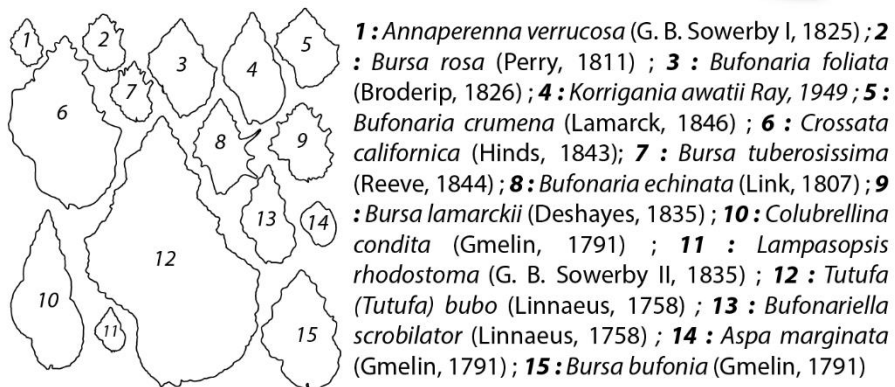


Fig 1.1. Variabilité morphologique des Bursidae

utilisées en décoration, ils concluent qu'il s'agit probablement d'un apport anthropique, ce qui ne retire rien au mystère de sa découverte à une telle profondeur.

Dans la nature on peut trouver des Bursidae depuis les domaines intertidaux jusqu'à la limite de la zone bathyale. Cependant la très vaste majorité des Bursidae vivent dans la zone photique du plateau continental, entre 0 et 100 m.

Reproduction et croissance

Les Bursidae sont des organismes dioïques à fécondation interne ; leur reproduction a été relativement peu étudiée et s'est généralement limitée à la description des pontes, *Crossata californica* (Hinds, 1843) (Fig. 1.1B) par Abbott (1954) et *Dulcerana* aff. *granularis* (Röding, 1798) par Cernohosky (1967). La seule étude à notre connaissance s'attardant plus avant sur le sujet a été réalisée par d'Asaro (1969) en utilisant *Talisman corrugata* (Perry, 1811) comme modèle. Ainsi, il indique que la ponte se produit en quelques heures à une semaine après la copulation. Les œufs sont préférentiellement déposés sur des substrats durs, que ce soit des rochers coralliens (Cernohosky, 1967), des coquilles de bivalves (Fig. 1.2 B, D) ou des débris végétaux terrigènes (Fig. 1.2A). Les femelles couvent les œufs jusqu'à l'éclosion. Les œufs fraîchement pondus sont blancs et brunissent avec le temps. Une ponte de Bursidae est généralement ovale (Fig. 1.2C1), légèrement concave et épouse la forme de l'ouverture de la femelle. Les capsules sont légèrement inclinées vers l'intérieur de la ponte et ont une forme vaguement triangulaire (Fig. 1.2C2-3) avec des capsules de plus grande taille dans la partie centrale de la ponte (Fig. 1.2C2) (d'Asaro, 1969, Thorson, 1940). Il n'y a pas de bouchon d'ouverture des capsules mais une faiblesse dans leur membrane. Le nombre de capsules par pontes est très variable (de 5 à plus d'une centaine) et est contrôlé par la surface que l'ouverture de la femelle peut couvrir lors de la couvée. L'éclosion a lieu après deux semaines. La durée précise de la phase larvaire est inconnue mais comme les protoconques de tous les Bursidae est téléplanique (du grec *teleplanos*, vagabond) on peut supposer qu'elle est relativement longue, entre quelques semaines à plusieurs mois (Scheltema, 1966, 1968, 1971, 1972, 1986a, b, 1988; Laursen, 1981; Pechenik et al. 1984).

Habitudes alimentaires

Peu de choses sont connues sur le régime alimentaire des Bursidae ; ils sont cependant supposés tous prédateurs. Seuls Houbriek & Fretter (1969), Taylor (1978) et Kohn (1983) ont discuté du sujet pour un nombre limité d'espèces (*Lampasopsis cruentata*, *Lampasopsis rhodostoma*, *Dulcerana granularis* et *Bursa bufonia*). Les proies sont d'une part des annélides, des holothuries ou des siponcles qui semblent être anesthésiés par une substance relâchée dans l'eau avant d'être avalé en entier (Houbriek & Fretter 1969) à la manière de certains cônes (Safavi-Hemami, 2015). Cette substance est très probablement une variante de Tetrodotoxine, une toxine déjà identifiée chez des représentants du genre *Tutufa* par Noguchi *et al.* (1983). Taylor (1978) et Kohn (1983) font état d'une prédation sur les echinoïdes, faisant appel à une stratégie différente. L'oursin est attrapé par le pied musculeux du Bursidae du genre *Bursa s.s*

et débarrassé d'une partie de ses épines (Fig.1.3). Par la suite le gastéropode utilise sa radula pour forer un orifice dans l'épiderme de sa proie. Il s'agit d'une stratégie semblable à celle employée par les Charoniidae (Beu, 1998).

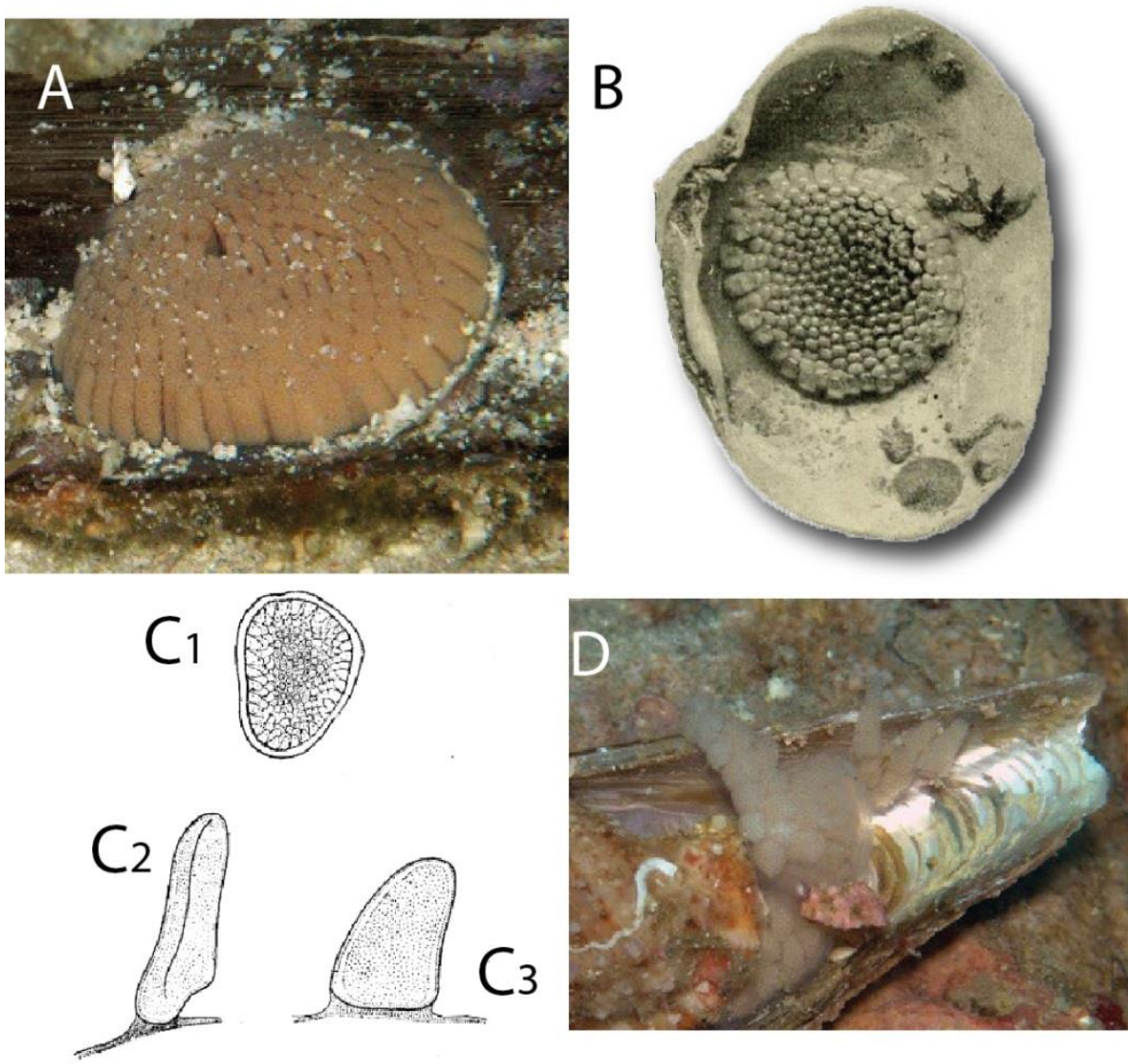


Fig. 1.2 Pontes de Bursidae : **A** Ponte de *Tutufa rubeta* déposée sur du bois coulé, Panglao, 2004, (Photo : Poppe-image.com) **B** Ponte de *Crossata californica* déposée sur une coquille de bivalve ; reproduit d'après Abbott (1953), **C** Capsule de Bursidae, **C1** vue apicale d'une ponte de *Talisman corrugata*, **C2** capsule centrale en vue latérale, **C3** capsule latérale. reproduit d'après d'Asaro,(1969), **D** Ponte de *Dulcerana* aff. *Granularis*, déposée sur une coquille de bivalve ; Panglao 2004, (Photo : Poppe-image.com)



Fig. 1.3 *Bursa bufonia* s'attaquant à un oursin. D'après Kohn, 1983

Bien que non documenté dans la littérature scientifique *Tutufa rubeta* est considéré comme un ravageur des cultures d'huitres perlières dans le Pacifique (Southgate & Lucas, 2011).

Prédation

Les Bursidae sont aussi des proies, notamment de crustacés décapodes et de poissons, et à ce titre ils ont développé un ensemble des stratégies de défense (Vermeij, 1994). Le premier étant la taille ; les représentants du genre *Tutufa* peuvent atteindre une taille de 45 cm de haut pour une largeur de 30 cm les mettant à l'abri de la plupart des prédateurs, d'autant qu'avec des varices espacées de 240° on peut supposer que leur croissance se fait relativement vite. D'autres ont fait le choix de la discrétion, les espèces des genres *Bursa*, *Lampasopsis* et certaines *Bursina* et *Bufonaria* ont leur coquille fortement colonisée par des algues encroûtantes et des bryozoaires, les dissimulant parfaitement aux yeux des prédateurs (Fig.1.4). Une autre stratégie, plus offensive ; est celle de certaines espèces du genre *Bufonaria* (*Bufonaria echinata* ou *Bufonaria perelegans*) qui possèdent des épines plus ou moins longues sur leurs varices. D'une manière générale les Bursidae ont des coquilles relativement épaisses et solides comparés à d'autres familles de gastéropodes avec des varices proéminentes dont la fonction pourrait être de renforcer la structure de la coquille (Webster & Vermeij, 2017). De plus on constate que toutes les espèces aux coquilles fragiles comme *Bursina awatii*, *Tritonoranella latitudo* ou

Korrigania quirihorai sont toutes inféodées à des milieux relativement profonds (au-delà de 200 m) où les pressions de prédation sont supposées moindres (Vermej, 1994).

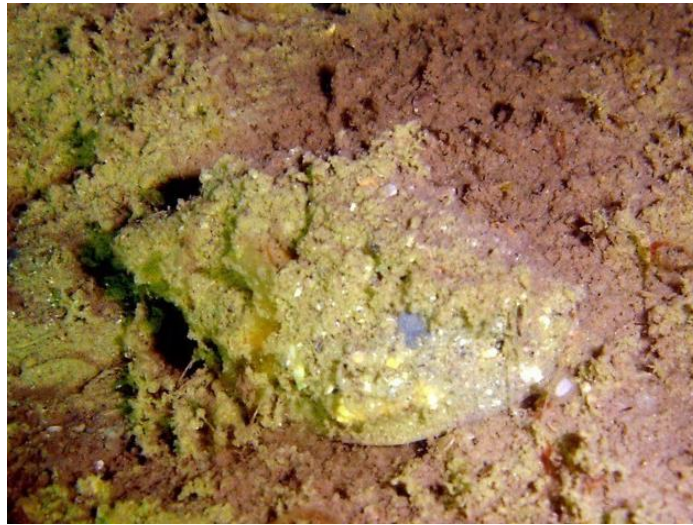


Fig. 1.4 *Bursina thersites* dissimulée par des algues se développant sur sa coquille (Photo : Poppe-image.com)

Des Bursidae et des hommes

Les Gastéropodes comme de nombreux autres mollusques jouent une grande variété de rôles pour les sociétés humaines, que ce soit comme source de nourriture ou de colorants, d'ornements décoratifs ou symboliques ou encore d'instruments de musique. Bien que d'une importance culturelle plus restreinte que celle des Murex (pourpre) ou des porcelaines (*shell money*), celle des Bursidae n'est pas pour autant négligeable.

Le plus ancien constat de l'usage de Bursidae par des populations humaines remonte à 46 000 ans au Nord de l'Italie (Peresani *et al.*, 2013). Elle consiste en un assemblage de coquille d'*Aspa marginata* (Gmelin, 1791) (Fig. 1.5C) teintées à l'ocre rouge et utilisées comme parure par les néandertaliens, les coquilles elles-mêmes ont été collectées à l'état fossile (Miocène Pliocène) à plus de 100 km du lieu de leur découverte. Au moment de sa découverte il s'agissait de la plus ancienne preuve de comportement symbolique chez les hommes de Neandertal.

D'autres données archéologiques, provenant du Néolithique d'Oman semblent indiquer l'usage de *Tutufa bardeyi* (Jousseume, 1881) comme mobilier funéraire (Charpentier *et al.*, 2003, Charpentier & Méry, 2010) ou trompette (Wilkins 2002).

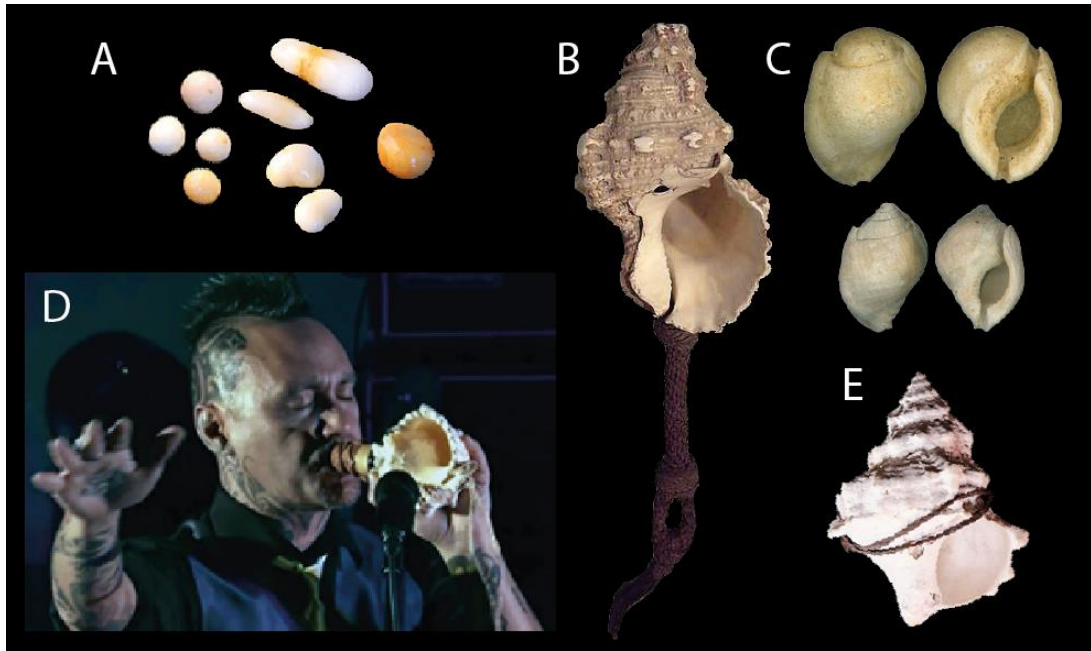


Fig. 1.5A : Perles de Bursidae [*Tutufa bubo* (Linnaeus, 1758)] ; **B** : Trompette de cérémonie (Davui), Fidji, 19^{ème} siècle (Metropolitan Museum of Art, 89.4.1823) ; **C** : coquilles d'*Aspa marginata* (Gmelin, 1791) fossiles (Miocène Pliocène) utilisés comme ornement par les néandertaliens du Piémont (45 000 ans, Italie, modifié d'après Peresani *et al.*, 2013) ; **D** : le chanteur Tiki Taane jouant du *Putatara* fabriqué à partir d'une coquille de *T. bubo* ; **E** : écarteur d'oreille « Sau mocemoce ni valu » du bete ni valu (prêtre de guerre) des gonedau de Wainawaqa, Fidji, 19^{ème} siècle en coquille de *Tutufa* sp. (Fiji Museum).

Dans la période historique c'est à Fidji que l'importance culturelle des Bursidae est la plus marquée. En effet les Bursidae du genre *Tutufa* (davisogasoga) sont sacrés et communément utilisés, dans la partie occidentale de l'île, pour la réalisation de *Davui*, (Fig. 1.5B) ou trompette de cérémonie remplaçant les coquilles de *Charonia* traditionnellement utilisées dans tout le Pacifique (Gatty, 2009).

Un autre usage, plus atypique, qui se pratiquait à Fidji était le port du *Sau mocemoce* (Fig. 1.5E). Il s'agit d'un écarteur d'oreille en coquille de *Tutufa* porté par le bete ni valu (prêtre de guerre) des gonedau de Wainawaqa (Sud-ouest de Fidji) durant les batailles et qui avait la propriété supposée d'endormir les guerriers ennemis (Fiji Museum, 2017). Le dernier usage attesté du *Sau mocemoce* remonte à 1844.

Il n'y a qu'une espèce de Bursidae dont la consommation est documentée (bien que non avérée, Bourquin, 2002) en Asie du sud-est et au Japon : *Bufonaria elegans* (Beck in Sowerby, G.B. II, 1836). La présence de tétrodotoxines en quantité dangereuse (sinon létale) chez les Bursidae de grande taille (ex. *Tutufa*, Noguchi *et al.*, 1984) expliquerait leur quasi non

consommation malgré leur abondance à faible profondeur. Une autre espèce de *Bufo*, *Bufo rana* (Linnaeus, 1758), est utilisée traditionnellement dans la pharmacopée chinoise pour guérir les ulcères (Ahmad *et al.*, 2018).

Ne bénéficiant pas de la renommée que possèdent d'autres groupes de gastéropodes comme les Murex (Muricidae Rafinesque, 1815) ou les Cônes (Conidae Fleming, 1822) ils sont néanmoins collectionnés, particulièrement les représentants du genre *Tutufa* qui sont parmi les plus gros gastéropodes du monde.

Ces mêmes *Tutufa* sont parmi les rares gastéropodes qui sont prélevés pour les perles qu'ils peuvent former. Ne produisant pas de nacre ces perles sont d'aspect crayeux (Fig. 1.5A).

Systématique des Bursidae

Les Bursidae forment une famille modestement diversifiées comprenant 59 espèces actuelles (Worms, 2017) et une dizaine d'espèces entièrement fossiles. Leur statut de famille ne fait plus réellement débat aujourd'hui. Ils furent élevés à ce rang et sortis de la famille Ranellidae en 1929 par le zoologiste allemand Johannes Thiele. Ce rang n'a été contesté à notre connaissance que par Riedel (1995, 2000), les considérant comme une sous-famille. Beu (1998, 2005 et 2010) cimentera ce statut d'indépendance vis-à-vis des Ranellidae en montrant qu'une partie des caractères distinctifs des Bursidae (présentés plus bas) les rapprochent plus des Cassidae et des Tonnidae.

La première étude scientifique des Bursidae est antérieure à l'émergence de la classification linnéenne, comme l'atteste les nombreuses figurations dans les premiers ouvrages d'Histoire naturelle ou de malacologie (Lister, 1691, d'Argenville, 1742, Seba, 1758 ; Fig. 1.6). La grande majorité des descriptions d'espèces ont été faites durant le 19ème et 20ème siècle (Fig. 1.7). Même si de nouvelles espèces ont été décrites au 21ème siècle le rythme s'est considérablement ralenti, laissant envisager que l'inventaire de la diversité des Bursidae approche de sa maturité. Ce n'est cependant pas le cas de leur classification. Comme tous les Tonnoidea, la classification des Bursidae a souffert d'un « grand écart » systématique voyant s'opposer d'une part, les intérêts des collectionneurs aboutissants à une multiplication des noms de rang spécifique (Cossignani, 1994 par exemple), et d'autre part les considérations portant sur les capacités dispersives que leur procure leur phase larvaire relativement longue qui ont abouti à des hypothèses d'espèces très englobantes (Beu, 1998, Chapitre 3 et 4).



Fig. 1.6 Figuration de Bursidae par des auteurs pré-linnéens : **A** Martin Lister et spécimens figuré dans *Historiae [...] Conchyliorum* (1691). **B** Antoine Joseph DeZallier d'Argenville et spécimens figurés dans *L'histoire naturelle éclaircie dans [...] la lithologie et la conchyliologie* (1742). **C** Albertus Seba et spécimens figurés dans *Locupletissimi rerum naturalium thesauri* vol. 3 (1758)

L'émergence des méthodes de phylogénie moléculaire dans les années 1980, puis leurs généralisations au cours des années 2000 ont généré de grands bouleversements des classifications du monde vivant et des gastéropodes en particulier, contredisant celles traditionnellement basées sur des caractères très généraux de la coquille ou de la radula (Fedosov *et al.* 2015, Galindo *et al.* 2017). C'est également ce qui s'est passé pour les Bursidae lors de la première étude moléculaire de la famille par Castelin *et al.* (2012). Sur les sept genres considérés valides à l'époque, quatre ont été inclus dans la phylogénie et deux se sont révélés être paraphylétiques. Le genre type de la famille *Bursa* Röding, 1798, s'est révélé être issu de au moins 3 évènements indépendants. La phylogénie générale du groupe reste à ce jour peu connue et fait l'objet du chapitre 3 de cette thèse.

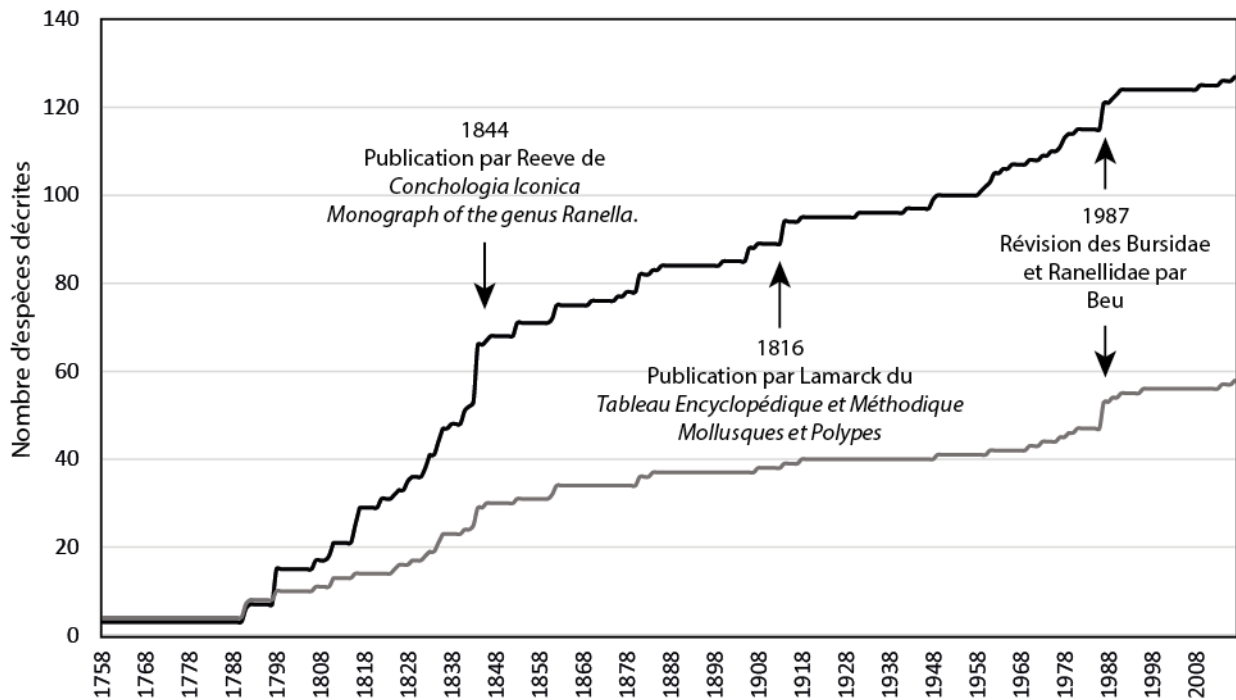


Fig. 1.7 Courbes cumulatives de la description des Bursidae, de Linné à nos jours, courbe grise : espèces considérées valide, Courbe noire : combinaisons originales (d'après WoRMS, 2017)

TEMPS ET DATATION EN SYSTEMATIQUE.

L'étude de la diversité d'un ensemble d'organismes est une entreprise en quatre dimensions. Les aspects phylogéniques et taxonomiques seront traités dans le manuscrit (Chapitres 3 et 4) La quatrième dimension, celle du temps, qui est probablement celle qui connaît le plus rapide développement en ce moment.

La partie suivante est une brève introduction historique de la notion de temps en systématique en gardant la paléontologie comme fil conducteur

Le temps des fossiles

L'étude de l'émergence dans le temps des organismes vivants, que ce soit dans un cadre évolutionniste ou non, a depuis l'origine été du ressort de la paléontologie.

En paléontologie le temps n'est pas directement accessible (mesurable) mais il est inféré à partir des fossiles. En eux-mêmes ils ne portent aucune information temporelle, cette information n'émerge que par leur relation les uns par rapport aux autres, les fossiles trouvés dans des séries plus basses sont successivement plus anciens que ceux trouvés au sommet de la série stratigraphique (sauf remaniement ultérieur) faisant du temps en paléontologie une notion fondamentalement relative.

Durant tout le 20^{ème} siècle la majorité des paléontologues ont « forcé » l'entrée de l'évolution dans cette vision successionniste et ainsi ont reconstruit l'histoire des lignées animales et végétales en lisant directement leur histoire dans les strates, Cette approche est connue sous le nom de stratophénétique (Gingerich, 1979) et est fortement liée à une vision gradiste de l'évolution où les groupes (ici des grades) émergent à partir d'autres groupes plus anciens. La révolution hennigienne allait totalement bouleverser cette lecture du temps en paléontologie.

Le temps des arbres phylogénétiques

Le livre fondateur de la pensée évolutionniste, *l'Origine des espèces*, ne contient qu'une seule et unique figure (Fig. 1.8, Darwin 1859), un graphe connexe sans cycle, que communément on appelle arbre. Ce type de diagramme allait devenir le modèle privilégié pour représenter aussi bien les patrons que les processus évolutifs.

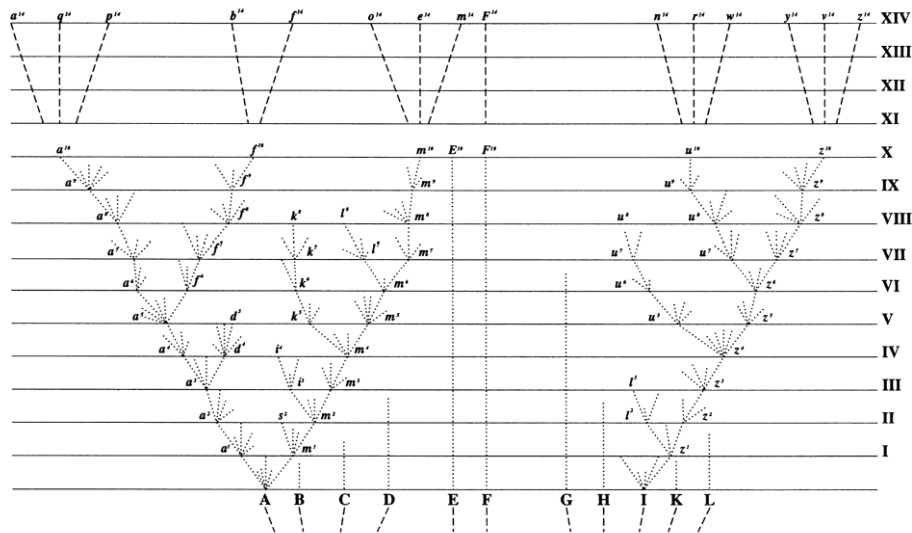


Fig. 1.8 La fameuse illustration de Darwin (1859): *diversification of species A–L through generations and geological time*

Dans cet arbre le temps est explicitement représenté (en chiffre romains à droite). Dès l'origine le temps est implicitement incorporé via la structure hiérarchique des arbres. Cette vision hiérarchique va à l'encontre de la pensée stratophénétique qui elle est fondée sur une succession de partitions

La stratigraphie est empirique car le temps peut être directement lu dans les couches géologiques alors que l'évolution est déductive, car ce sont les inférences réalisées à partir des données de ces mêmes couches qui nous donnent accès au temps (Tassy, 2017).

L'horloge moléculaire

La seconde moitié du vingtième siècle a vu apparaître de nombreuses méthodes pour estimer les âges de divergence des taxons à partir de phylogénies moléculaires et des données parcellaires du registre fossile. Elles ont connues un vif succès car elles permettent de répondre à de nombreuses questions évolutives (biogéographie, évolution des traits morphologiques, etc...) et aussi d'estimer l'âge d'apparition et de diversification (Fig. 1.9) des groupes pour lesquels aucun renseignement paléontologique n'était disponible.

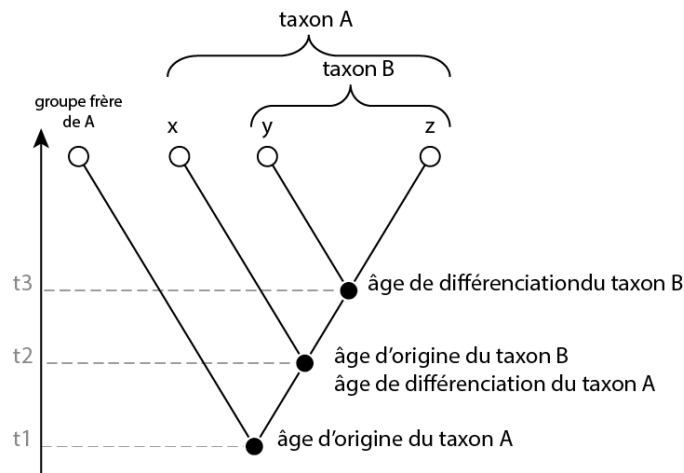


Fig. 1.9 différence entre origine et diversification (Modifié d'après Hennig, 1966)

Estimer un âge de diversification avec un modèle sans contrainte d'évolution de caractères est difficile car dans ce modèle chaque branche est un paramètre indépendant reflétant la quantité de divergences des caractères (généralement le nombre de substitution par site) plus que le temps. Cela est dû au fait que ce caractère est le produit du taux de substitution le long de la branche donnée par la « durée » de la branche (Thorne & Kishino, 2005).

Ainsi pour une même quantité de divergence observée une branche peut avoir un taux de substitution rapide sur une courte période et une autre branche un taux lent sur une longue période.

Pour contourner ce problème on fait une hypothèse forte : **l'horloge moléculaire**.

En 1962 Zuckerlandl et Pauling ont remarqué que la quantité de divergence entre les acides aminés de l'hémoglobine d'un grand nombre de vertébrés varie de manière linéaire en fonction du temps (estimé grossièrement à partir du registre fossile). Ils en extrapolèrent que le taux d'évolution de n'importe quelle protéine était relativement constant au cours du temps, indépendamment des lignées. Autrement dit la différence moléculaire entre une paire de taxons

est proportionnelle à l'âge de leur spéciation. L'horloge moléculaire était née (Zuckerlandl et Pauling 1965).

Tenant compte de cette hypothèse il suffit d'assigner un âge à un seul nœud pour obtenir tous les âges de divergences de l'arbre (Fig. 1.10)

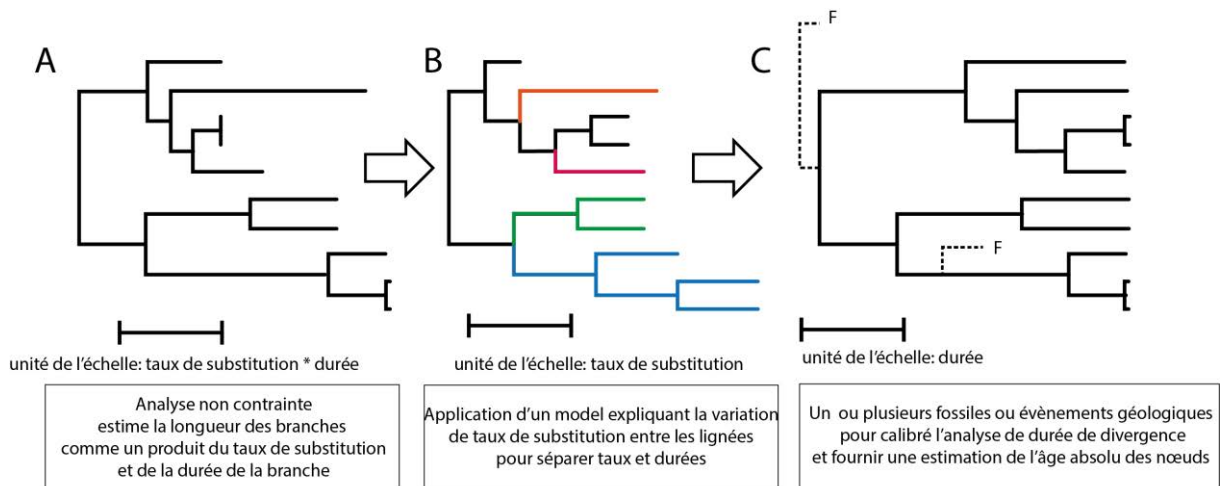


Fig. 1.10 Le principe de l'horloge moléculaire (Modifié d'après Douzery et al. 2005 et Heath 2014)

Hélas la réalité biologique s'accorde peu avec cette hypothèse. Les premières analyses empiriques ont produit des estimations de divergences extrêmement anciennes telles qu'une divergence Mésoproterozoïque (3 Milliard d'années !) pour les bilatériens (Wray et al. 1996) ou une origine Jurassique des Angiospermes (Heckman et al. 2001), ce qui défiait tout ce qu'on connaissait sur le registre fossile de ses groupes, mais aussi toutes les hypothèses macro évolutive (explosion Cambrienne ou émergences post crises par exemple) que 40 ans de paléontologie avait produites.

Cela a eu pour conséquence un rejet massif de cette approche rejetée par les paléontologues (Wray et al. 1996, Wikström et al. 2001, Donoghue & Smith 2003, Donoghue & Yang 2016), alors qu'il la voyait plutôt d'un bon œil à l'origine (Runnegar, 1982, Brown et al. 1972)

Le biais de l'horloge dite « strict » n'est pas surprenant, compte tenu des tous les facteurs susceptibles de faire changer la quantité moyenne de divergence d'une branche ; entre autre citons :

- Un taux d'évolution variable entre gènes, et même dans certaines parties des gènes (Kimura & Ohta 1973).
- La durée des générations : les mutations d'un éléphant mettront plus de temps à être transmises à la génération suivante que celles d'une souris.

- Le taux métabolique : les organismes aérobies à haut taux métaboliques ont une respiration produisant plus de radicaux libre de l'oxygène pouvant produire des mutations.
- La taille de population, très variable entre espèces.
- Les pressions de sélection, également très variables entre gènes et espèces.

Le désir de s'affranchir d'un modèle d'horloge strict pour se rapproche d'une horloge au comportement plus biologique a motivé le développement des horloges dites relâchées ou assouplies (*relaxed molecular clock models*).

Le développement méthodologique de ces horloges s'est d'abord fait dans le cadre du maximum de vraisemblance (Sanderson 1997, Yang & Yoder 2003). Mais c'est dans le cadre des inférences bayésiennes que des avancées majeures ont été faites et se font encore (Thorn et al. 1998, Kishino et al. 2001, Thorn & Kishino 2002, Drumond et al. 2006, Yang & Rannala 2006, Lartillot et al 2009, Ronquist et al 2012, Lartillot et al. 2016).

L'assouplissement de cette hypothèse est possible en autorisant des variations de taux d'évolution le long des branches de l'arbre phylogénétique. Sanderson (1997) a été le premier à mettre en œuvre un lissage des taux d'évolution dans lequel les écarts entre le taux de la branche descendante et celui de la branche parentale (immédiatement ascendante) sont limités (horloge autocorrélée). Depuis les années 2000, le nombre de modèles d'horloge a explosé, on en dénombre aujourd'hui pas moins d'une quinzaine et il serait trop long de les détailler ; Chen et al. (2015) ont fait une review complète de ces modèles et de leur justification.

Malgré toutes ces avancées en modélisation il a été montré (Yang & Rannala, 2006, Rannala & Yang 2007, Dos Reis & Yang 2013) que des distorsions de l'estimation de l'âge des nœuds demeurait significative. Il fallait donc ajouter un nouveau paramètre pour contraindre les analyses : la calibration des nœuds par les fossiles.

En effet le registre fossile nous informe sur l'âge minimum des clades à partir de l'âge de leur plus ancien représentant (Reisz & Muller 2004, Hedges & Kumar 2004), (l'âge maximum définit par une absence du clade est par nature très difficile à prouver).

Il s'agit d'un *prior* aussi fort que l'horloge stricte au titre qu'elle ne peut être modifiée par les autres priors de l'analyse. Le danger est donc qu'une mauvaise attribution à un nœud d'une calibration aboutit à des distorsions extrêmes des temps de divergence des taxons.

Conscient de cela Parham et al (2012) ont défini un ensemble de règle permettant de de minimiser les chances d'erreurs dans ces calibrations (ces paramètres sont discutés dans le chapitre 2).

OBJECTIFS ET PLAN DE LA THESE.

Dans le contexte actuel du changement climatique et de l'érosion accélérée de la biodiversité, les problématiques d'apparition, de diversification et d'extinction des groupes taxonomiques sont devenues une question centrale de la biologie évolutive.

En réponse à cela les projets de description de la biodiversité ont fleuri depuis une dizaine d'années, fort de la maturité des méthodes de reconstructions phylogénétiques et de la relative facilité d'acquisition des séquences moléculaires

Mais si on commence à bien appréhender la diversité de nombreux groupes d'invertébrés marins (via les approches de phylogénie et de taxonomie intégrative), leur dynamique dans le temps, quant à elle, reste fortement sous étudiée alors que le registre fossile de ces groupes, et des mollusques en particulier est particulièrement riche et potentiellement porteur d'un grand nombre d'informations.

L'objectif de cette thèse est de revisiter la systématique et d'établir la chronologie de la diversification Cénozoïque d'un groupe de gastéropode marin actuel au registre fossile relativement abondant : les Bursidae.

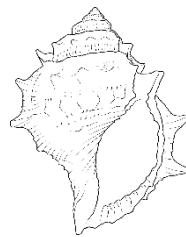
Le travail présenté ici commencera tout d'abord par la synthèse complète du registre fossile de cette famille (Chapitre 2, Article 1 formaté pour *Geodiversitas*). Elle a été réalisée dans le but de définir les limites temporelles du groupe et de chacune de ses espèces, de donner une idée de la qualité de son registre fossile et d'évaluer sa capacité à fournir des points de calibration dans une analyse phylogénétique.

Le chapitre suivant est consacré à la systématique des Bursidae par l'utilisation des outils de la biologie moléculaire. Cette étude s'est faite en deux temps. Une première étude visait à évaluer les capacités de dispersion transocéaniques des Bursidae en clarifiant la systématique de l'espèce possédant la plus grande répartition géographique de toute la famille (et de quasiment tous les gastéropodes), *Bursa granularis* (Röding, 1798). Cela a été fait par une approche de taxonomie intégrative mettant en relation les données moléculaires, la morphologie de la coquille et nos connaissances du registre fossile de ce groupe. Il s'est révélé que les taxons connus sous le nom de *B. granularis* correspondent en réalité à un ensemble d'au moins quatre espèces structurées géographiquement. Ces résultats ont fait l'objet d'une présentation au *Molluscan forum*, 2016 et d'une publication dans *Journal of Molluscan Studies* (article 2). Cela a permis d'éclaircir les hypothèses d'espèces de la famille avant d'en réaliser la phylogénie

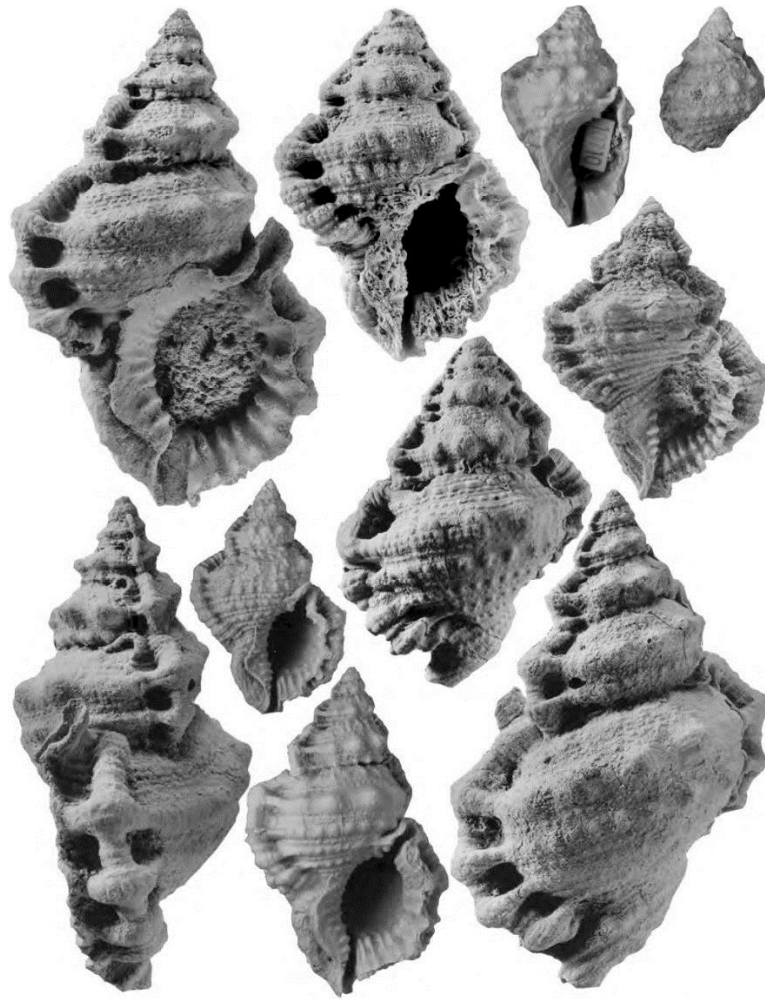
Par la suite j'expose les résultats obtenus concernant la phylogénie des Bursidae intégrant des mitogénomes complets et reconstruite par des méthodes probabilistes (Maximum de vraisemblance et inférence bayésiennes). Cette phylogénie datée (en *node* et *tip dating*, intégrant une vingtaine de points de calibration) nous a permis d'évaluer la diversification du groupe en relation avec les principaux évènements climatiques et géologiques du Cénozoïque. De plus elle a permis d'établir la base de la nouvelle classification générique des Bursidae qui fait l'objet d'une description complète pour les actuels et les fossiles dans le chapitre 4.

Le cinquième et dernier chapitre est une tentative de réconcilier morphologie et moléculaire en réalisant une étude phylogénétique des Bursidae réalisée en parcimonie standard à partir de caractères conchyliologiques uniquement, les seules caractères disponibles chez les fossiles. Les limites de la méthode seront discutées, mais l'importance du dialogue entre caractères moléculaires et morphologiques sera également soulignée.

Je dresse en conclusion le bilan des résultats obtenus et discute en perspective des possibilités futures que le développement récents de certaines méthodologies permettraient d'envisager, jusqu'à la réconciliation entre le morpho-anatomie et le moléculaire chez les mollusques.



CHAPITRE 2
REGISTRE FOSSILE
DES BURSIDAE



*L'homme ne peut lire dans l'avenir, et c'est là une des plus dures épreuves de sa destinée ;
mais il peut essayer de lire dans le passé*

Albert Gaudry, la revue des deux mondes, 1898

A REVIEW OF FOSSILS BURSIDAE AND COMMENTS ON THEIR USE FOR PHYLOGENY CALIBRATION.

by MALCOLM T. SANDERS^{1,2}, DIDIER MERLE¹ & NICOLAS PUILLANDRE²

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INTRODUCTION

The importance of phylogenetic reconstruction no longer needs to be proven and the advances of molecular phylogeny provided new possibilities for mollusc’s systematics, renowned for the difficulty to define primary homologies of 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 mean of calibration for dating of molecular phylogenies. A time-tree goes beyond patterns, it gives information regarding tempo of evolution, and allows the testing specific hypotheses. (e. g. biogeography, diversification rate...). For these reasons time trees has become common in systematics (Donoghue & Benton 2007). In the vast majority of cases researchers use 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 difficult to justify without proper homology hypotheses and phylogenetic assessment. A wrong node attribution could lead to a massive distortion of the divergence time (Douzery et al. 2006). Hence a review of the fossil record of the considered clade should be done prior to any analysis. In their 2012 article Parham *et al.* discussed a set of data paramount to be given in order to consider that a calibration is well justified; 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, (5) a reference to a published radioisotopic age and/or numeric timescale and details of numeric age selection should be given.

From all these points the most difficult to satisfy when dating a mollusc phylogeny is obviously the third one because of the homology issues cited above. Besides, few molluscan systematists took time to confront molecular and morpho-anatomical datasets and even recent examples (e. g. Strong *et al.* 2011) use around 10% of shell characters (9 in total), the rest being soft anatomy, making the impact of those characters uneasy to estimate.

In this paper we chose to review the fossil record of the Bursidae Thiele, 1925 (Tonnoidea). This tonnoidean family is currently under systematic revision by the authors who will produce a molecular phylogeny for which they'll need good calibrations.

Bursidae are a moderately diverse tonnoidean family with 59 extant species (Worms, 2017). Recent bursids have a sub-tropical distribution with a southernmost record in eastern South Africa, North New Zealand and Walters shoal. The northernmost record [*Bursa scrobilator* (Linnaeus, 1758)] is from Nice, southern France and Savona north western Italy. They are intertidal to subtidal species most often associated with hard substrate such as rocks, coral or sponges, where they can be abundant. They are active predator, 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 and by their thick, coarsely sculptured shells with knobs, warts, tubercles and nodules, hence their vernacular name: frog snails. Very variable in size, the smallest species, *Bursa lucaensis* (Parth, 1991) never exceeds 23 mm height while *Tutufa bardeyi* (Jousseume, 1881), with a height up to 450 mm and a width up to 300 mm, is one of the largest and most capacious of all gastropod shells (Beu, 1998). Most bursids size ranges between 40 and 50 mm.

As inferred from their protoconch, similar to all tonnoideans, they are supposed to have a long to extremely long larval stage granting for some of them trans-oceanic dispersal capabilities. However Sanders *et al.*, (2017) showed that such capabilities were greatly overestimated for one of the most widespread species of Bursidae: *Bursa granularis*.

The early evolution of the Bursidae remains shred in mystery. Pre-Eocene species describe as Bursidae (Kase, 1983, Adegoke, 1977) are regarded as very dubious in the literature and will be discussed here. The earliest seemingly undisputed species of Bursidae are known from the Americas Eocene (Beu, 1988). They are represented by the genus *Olequahia* Stewart, 1926 with it earliest from the Bartonian of Southern 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. Afterward no bursid has ever been found

until the late Chattian-early Aquitanian of the Aquitaine Basin (South western France). During the Middle Miocene up to the Pliocene the genus *Aspa* H. Adams & A. Adams, 1853 becomes one of the most commonly found gastropod in suitable shallow offshore facies of Aquitaine Basin, Western Tethys (Turin Hills) and Paratethys. So common that they were used by Neanderthal population as jewels and fineries (Peresani *et al.*, 2013)

This paper aim to review the fossil record of Bursidae, discussing the exclusion of several species from the Bursidae family. We will provide a morphological description i. e. apomorphy based diagnosis *sensus* Paraham *et al.* (2012) (2) for all known extinct genera. In addition we will listed and discussed all the necessary informations regarding their use in for time calibration. Two new genera are describe: *Olssonina* and *Aquitano bursa*.

SHELL DESCRIPTION

Shells were described 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 infrasutural 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: Muséum national d'Histoire naturelle, Paris, France.

NHMW: Naturhistorisches Museum Wien, Vienna, Austria

NMB: Naturhistorisches Museum, Basel, Switzerland.

PRI: Paleontological research institution, Ithaca, New York, USA

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, California, USA.

UIMG: University of Ife Museum of Geology, Nigeria

UMUT: University Museum, the University of Tokyo, Tokyo, Japan.

USNM: United States National Museum of Natural History, Washington D.C., USA.

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) 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 the oldest known bursid species. The relatively high spired shell with weak varices-like ridges every 90° of *H. aquilana* shows more similarities with batillariid gastropods and especially the genus *Pyrazopsis* Hacobjan, 1972, 1810 than with any other Tonnoidea. Furthermore the posterior siphonal canal doesn't seem to be homologous to the one of Bursidae, it looks like an adaxially extending fold within the outer lip. Riedel (1995) was the first to notice this resemblance with cerithoidean, we agree with him on that matter.

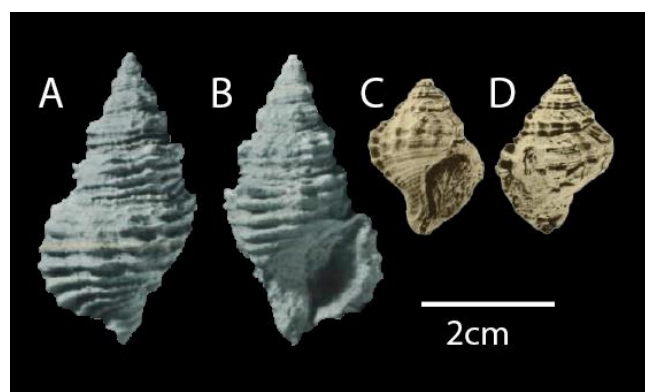


Fig. 1:Taxa excluded from Bursidae A-B *Hanaibursa aquilana* (Parona, 1909) UMUT MM15655, Hiraiga formations, (Aptian of Japan) A dorsal view, B Ventral view, C-D *Bursa saundersi* (Adegoke, 1977), UIMG 394 Ewekoro fm. (Selandian of Nigeria), C ventral view, D, dorsal view

Bursa saundersi Adegoke (1977: 209, pl. 31, figs. 27-28) was describe by Adegoke (1977) and recognized by Beu (1998, 2010) as a possible Paleocene bursid. It is true that the small specimen from the Selandian of Ewekoro formation (Nigeria) presents a true likeness with frog shells, showing aligned prominent varices and a coarse spiral ornamentation. However it lacks the key feature used to discriminate Bursidae from Ranellidae and Cymatiidae, the posterior siphonal canal.

According to Beu (1988, 2010) there is only one entirely fossil genus within the Bursidae family: *Olequahia* Stewart, 1926, with 5 accepted species (*Olequahia domenginica* (Vokes 1939), *Olequahia lincolnensis* (Weaver, 1916); *Olequahia lorenzana* (Wagner & Schilling, 1923), *Olequahia schencki* Durham, 1944, and *Olequahia washingtoniana* (Weaver, 1912)). Specimens presented here (Fig. 2) may challenge this classification. *Olequahia domenginica* (Fig. 2A-B) is the oldest known species of the genus. It has prominent varices every 200° or so over the entire teleoconch and is taller and narrower than the other species of the genus. Furthermore the shell has no anal notch casting doubts on its kinship with Bursidae. More recent species such as *O. washingtoniana* (Fig.2 C-H) share the same general ornamentation pattern constituted of spiral cords, more prominent on the primary cords than on the secondary ones but their general shape with a low spire and inflated last whorl is more reminiscent of Cassidae or Tonnidae shells than of Ranellidae, Bursidae or Cymatiidae. Varices are only present on the first whorl and as terminal varix. According to Beu (1988) pre-terminal varices are entirely lost in Oligocene species

Every single species of Bursidae (extant and extinct) possesses varices and considering that varices is most probably a plesiomorphic characters within tonnoidean families (with an apomorphic loss due to varix dissolution during ontogeny in the clade Tonnidae +Cassidae (Strong et al. unpub. data)) we find quite difficult to include *Olequahia* in the Bursidae family. However *Olequahia washingtoniana* shows a well-defined posterior siphonal canal resembling the one of Bursidae but this siphonal canal is structured by two rather large nodules on the parietal part of the collumela and on the inner part of the outer lip. Collumelar nodules may occur in bursid (e. g. *Bursa latitudo* Garrard, 1961) though never as large as in *O. washigtoniana* and, to our knowledge there is no Bursidae with a single large nodule or denticle in the outer lip, yet this feature occurs in several cassid species from the *Galeodea* genus (e. g. *Galeodea hoarai* Drivas & Jay, 1989). In the light of the reinterpretation of those characters we considers *Olequahia* to be a Cassidae, somewhat affiliated to the genus *Galeodea* Link, 1807, but not a Bursidae.

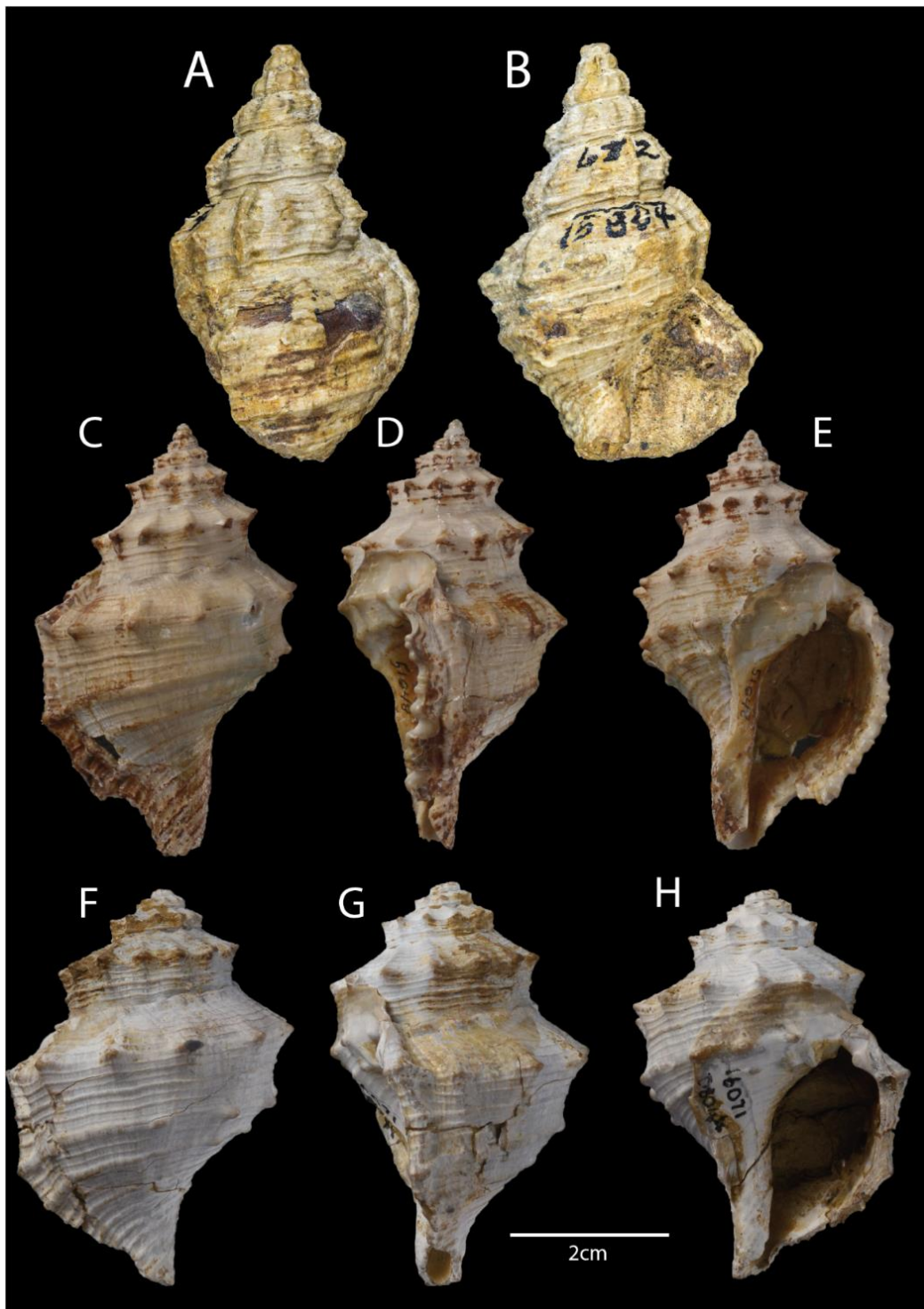


Fig. 2 A-B: *Olequahia domenginica* (Vokes, 1939): UCMP 15804 syntype of *Ranella domenginica*, **A** dorsal view, **B** ventral view. Tejon formation, California USA. **C-H** *Olequahia washingtoniana* (Weaver, 1912): UCMP D8044/16071 Dorsal view (**C,F**), Left lateral view (**D,G**), Ventral view (**E,H**) all from Cowlitz formation, Cowlitz river, Washington USA

TACKLEING *BURSA* IN THE FOSSIL RECORD

Under current acceptation *Bursa* Röding, 1798 is a very variable genus. So variable in fact that Beu (1998: 143) was forced to conclude 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*”. There is only one conclusion, *Bursa* is a “trash” genus, it exist only to classify species that do not fit anywhere else (such genera are rather common in gastropods e. g. *Vexillum* Röding, 1798 for Costellariidae MacDonald, 1860 or *Gemmula* Weinkauff, 1875 for Turridae Adams & Adams, 1853 (1838)). Being paraphyletic (or polyphyletic) by nature they are an impediment for every systematist aiming to describe biodiversity in its historic dimension (Faurby et al. 2016). Without providing a new classification Castelin et al (2012) cast some light on this matter by providing the first molecular phylogeny of the Bursidae (Fig. 3). Without surprise *Bursa* came out as polyphyletic.

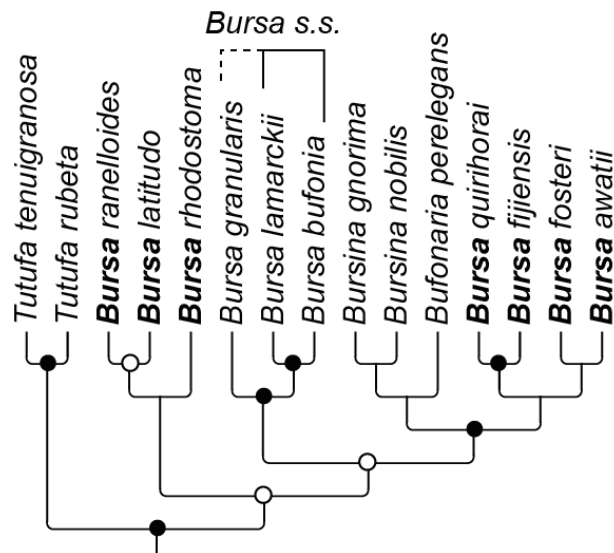


Fig. 3 Phylogeny of the Bursidae. Topology based on the multigene Bayesian analysis of Castelin et al. (2012), Black dots represent well supported nodes (posterior probabilities over 0.98), and white dots represent moderately supported nodes (PP over 0.90). *Bursa* written in bold are taxa that make the genus polyphyletic. Bracket on top indicates the phylogenetic extension of the genus *Bursa* if we consider the tubular posterior siphonal canal to be one of its synapomorphies, dotted bracket indicates the maximal extension of the genus considering the topology

To our knowledge there is 14 recognize extinct species of Bursidae with two third of them attributed to the *Bursa* genus, they are: *Bursa amphitrites* Maury 1917, *Bursa chipolana* Schmelz 1997, *Bursa grateloupi* (d'Orbigny, 1842), *Bursa inaequicrenata* (Cossmann & Peyrot, 1923), *Bursa sangirana* Beu 2005, *Bursa tuberosa* (Grateloup, 1833), *Bursa victrix* Dall 1916, *Apollon morrisi* (d'Archiac & Haimes, 1853), *Bursa landaui* Harzhauser, 2009,

Marsupina chira (Olsson, 1930), *Marsupina freya* (Olsson, 1932), *Marsupina yasila* (Olsson, 1930), *Marsupina judensis* Beu, 2010, *Marsupina strongi* (Jordan, 1936).

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

If we consider a phylogenetic definition of *Bursa* based on Castelin et al. phylogeny and the position of the type species of the genus (*B. bufonia*) we end up with a much smaller definition of *Bursa* containing only *B. bufonia* and *B. lamarckii* (to which we can add *Bursa 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* (Gmelin, 1791) and none of them are type species of a previously published name that could be resurrected. So we are left with only two options either create new genera (as few as possible) or propose primary homology hypotheses linking fossils with extant species (preferably type species).

Bursa sangirana Beu 2005 (Fig. 4 R-S): From Late Pliocene of Kalibeng layers, (Sangiran, central Java) is a low spire shell with a warty ornamentation. Its posterior siphonal canal is short it is very reminiscent of *Bursa rhodostoma* and is probably very closely related to it. They may all belong to a separate genus: *Lamapsopsis* Jousseume, 1881. The resurrection of this genus has been recently suggested by Strong et al. unpb data.

Bursa landaui Harzhauser, 2009 (Fig.4 P-Q): This slender shell is only known by two external molds from the Aquitanian of Ras Tipuli, Lindi Bay, Tanzania. It has a very fine granulate ornamentation and a weakly expressed shoulder slightly reminiscent of *Bursa granularis*, and very close to *Bursa condita*. This may be an indication of the close relationship of the three species for which there is two (maybe 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) with *B. granularis*.

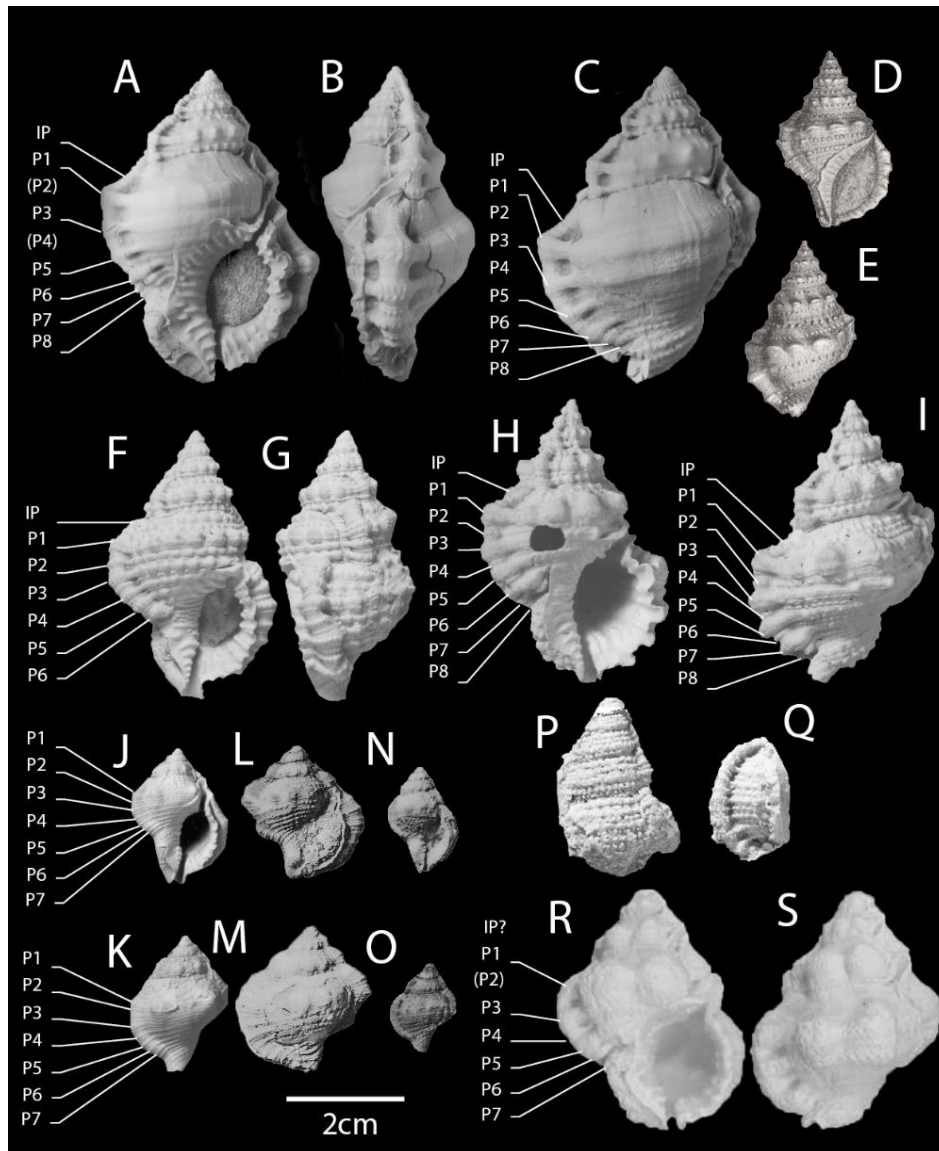


Fig. 4 A-C: *Marsupina judensis* Beu, 2010. NMB H 18308, holotype, Late Miocene, Punta Judas, Pacific Costa, reproduced from Beu, 2010 D-E *Aquitano bursa morrisi* (d'Archiac & Haimes, 1853), original representation of one of the syntypes by d'Archiac & Haimes (1853) F,G: *Aquitano bursa amphitrites* (Maury, 1917): 8. PRI 28763, holotype, Cercado Fm (Late Miocene), Maury's bluff 3, Cercado de Mao, Dominican Republic, reproduced from Beu, 2010, H,I *Tutufa chipolana* (Schmelz, 1997) USNM 647108, paratype, specimen illustrated by Vokes (1973: text-figs 2a-b). J,K *Olsson ia freya* (Olsson, 1932) PRI 2312, holotype, "Zorritos Miocene," divide between Quebrada Conchudo Bravo and Quebrada Seca, Mancora, Peru, Reproduced from Beu, (2010), L,M *Olsson ia chira* (Olsson, 1930) PRI 24257, holotype, Late Eocene/ Oligocene of Chira formation, Quercotilla, Peru. Reproduced from Olsson (1930). N,O *Olsson ia yasila* (Olsson, 1930), PRI 24254, Middle Eocene Talara Formation, Yasila, Peru. Reproduced from Olsson (1930). P,Q "*Bursa*" *landaui* Harzhauser, 2009 NHMW 2007z0181 /0029 (P) holotype and NHMW 2007z0181 /0030 (Q), both from Ras Tipuli, Lindi Bay, Tanzania, reproduced from Harzhauser, (2009). R,S ?*Lampasopsis sangirana* (Beu, 2005) RGM 456 230 holotype. Late Pliocene of Kalibeng layers, Sangiran, central Java

Bursa chipolana Schmelz 1997 (Fig. 4 H-I): This shell from the Chipola Formation (Burdigalian) Florida, USA possess eight distinct primary cords on the convex part of the whorl. In extant bursids there is only two genera displaying such character: *Tutufa Jousseume*, 1881 and *Marsupina* Dall, 1904. With its strong coarsely nodulose ornamentation, very well defined shoulder and the lack of dorsoventral compression we attribute *B. chipolana* to the genus *Tutufa*. However its varices are less displaced (around 200°) than in recent *Tutufa*. Finding a *Tutufa* in the western Atlantic is rather odd considering that in the recent it is restricted to the Indo-Pacific region. It may be a clue indicating a closer phylogenetic relationship between *Tutufa* and *Marsupina* with an American origin.

Bursa victrix Dall 1916 : This species only known by a poorly preserved external mold (USNM 166728) from the late Oligocene of Mascot Point, Flint River, Georgia, USA. 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 the species *Bursa corrugata* (Perry, 1811). We follow Beu's (2010) opinion keeping it as a separate species from *B. corrugata* pending the discovery of better preserved specimens.

Among the remaining extinct bursid species, three of them strikingly fit together: *Marsupina chira* (Olsson, 1930) *Marsupina freya* (Olsson, 1932) and *Marsupina yasila* (Olsson, 1930) for which we decide to give a new genus name: *Olssonia*.

In the same fashion *Bursa amphitrites* Maury 1917, *Bursa grateloupi* (d'Orbigny, 1842), *Bursa inaequicrenata* (Cossmann & Peyrot, 1923), *Bursa tuberosa* (Grateloup, 1833) and *Apollon morrisi* (d'Archiac & Haimes, 1853) are here attributed to a new genus: *Aquitano bursa*. These two new genera are describe in the following section.

SYSTEMATICS

MOLLUSCA Cuvier, 1795

GASTROPODA Cuvier, 1797

Superfamily **TONNOIDEA** Suter, 1913 (1825)

(Conserved under ICZN Article 40b)

Family **BURSIDAE** Thiele, 1925

Genus **OLSSONIA** Nov. Gen.

TYPE SPECIES. — *Bursa chira* Olsson, 1930

DERIVATIO NOMINIS — dedicated to the American palaeontologist A. A. Olsson.

SPECIES INCLUDED IN THE GENUS:

Olssonina chira (Olsson, 1930), *Olssonina freya* (Olsson, 1932) *Olssonina yasila* (Olsson, 1930).

DISTRIBUTION. — *Olssonina* is a genus restricted to the Eocene to Early Miocene of Peru

DIAGNOSIS — Shell biconic and dorsoventrally compressed, short spired, 7 primary cords in the convex part of the whorl, all but P1 evenly reduced in varical and intervarical intervals of the whorl (P1 is hardly more expressed), Posterior siphonal canal short varices strictly aligned, strong collumellar callus

COMPARISONS — *Olssonina* resemble *Marsupina* but possess a lesser number of primary chord in the convex part of the whorl (7 in *Olssonina*, 8 in *Marsupina*). Resemble *Aspa* but has a much stronger collumellar callus are much more granulose, has a more defined shoulder and a wider spire angle. Resemble *Bufo* with the same straighten anterior siphonal canal but lack a spine or a blade on the posterior siphonal canal

Remarks: The oldest representatives of this genus (*O. chira* and *O. yasila*) are the oldest confirmed Bursidae as such they can be used to calibrate the node Bursidae

Olssonina chira (Olsson, 1930)

Fig. 4 L,M

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

Marsupina chira (Olson, 1930) — Beu 1988: 71; 2010: 72.

TYPE LOCALITY. — Late Eocene/ Oligocene of Chira formation, Quercotilla, Peru

TYPE MATERIAL. — Holotype (PRI 24257), one paratype (PRI 24263).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Olssonina chira* seems to appear only on the Late Eocene/ Oligocene of Peru.

Olssonina freya (Olsson, 1932)

Fig.4 J,K

Bursa (Marsupina) freya Olsson, 1932: 187, pl. 21, figs 3, 4-6.

Bursa aff. B. (*Marsupina*) *freya* Olsson, 1932 — Marks 1951: 378.

Marsupina freya (Olsson, 1932) — Beu 2010: 75, Pl. 10, Figs 6, 8-9.

TYPE LOCALITY. — From “Zorritos Miocene,” divide between Quebrada Conchudo Bravo and Quebrada Seca, Mancora, Peru.

TYPE MATERIAL. — Holotype (PRI 2312) with two paratypes (PRI 2313 and PRI 2315).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Olssonia freya* has been recorded previously only from the early to middle Miocene of Ecuador and Peru, and the range is extended a long way northward to the Nicoya Peninsula, Costa Rica. All three localities apparently are Miocene, and all lie along the Pacific coast of tropical America.

Olssonia yasila (Olsson, 1930)

Fig. 4 N,O

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

Marsupina yasila (Olsson, 1930) — Beu 1988: 71.

TYPE LOCALITY. — Middle Eocene 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** Nov. Gen.

TYPE SPECIES. — *Ranella grateloupi* d'Orbigny, 1852.

DERIVATIO NOMINIS — Derived from Aquitaine the region of most of the species of the genus occur

SPECIES INCLUDED IN THE GENUS:

Aquitanobursa grateloupi (d'Orbigny, 1852), *Aquitanibursa amphitrites* (Maury, 1917), *Aquitanobursa inaequicrenata* (Cossmann & Peyrot, 1924), *Aquitanobursa morrisi* (d'Archiac & Haimes, 1853), *Aquitanobursa tuberosa* (Grateloup, 1833).

DIAGNOSIS — Thick shell, moderately short spired, varices slightly displaced, 6 primary cords on the convex part of the whorl, varical and intervarical P2 very reduced, axial ridges on the first whorl, strong parietal callus. Short well defined posterior siphonal canal. Weak projection of the outer lip.

COMPARISON — With their deeply marked and angular varices, strongly expressed shoulder *Aquitanobursa* resemble some deep sea species of the *Bursa* s.l. genus such as *Bursa quirihorai* Beu, 1987 however it is much strongly build with a thicker shell.

Remark: Phylogenetic relationship with other Bursidae remains unclear, this genus may be sister group to all recent which is unlikely considering that it occurs at the same time than *Aspa marginata* and *B. corrugata* (Fig. 6), a fair assumption would be that it is the sister group to every bursid except *Aspa* and *B. corrugata* but it would need a cladistics analysis to be confirmed.

Aquitanobursa grateloupi (d'Orbigny, 1852)

Fig. 5A

Ranella leucostoma (not Lamarck, 1822) — Grateloup 1833: 91, pl VI

Ranella semigranosa (not Lamarck, 1822) — Grateloup 1840 : pl XXIX, fig. 6.

Ranella gratteloupi (sic) d'Orbigny 1852: 76.

Apollon grateloupi (d'Orbigny, 1852) — Cossmann & Peyrot 1924: 305, Pl. XV, fig. 42-43

TYPE LOCALITY. — Lower Miocene of Aquitaine Basin, Bordeaux and Saint-Paul-lès-Dax.

TYPE MATERIAL. — Two syntypes (MNHN.F.B27595 and MNHN.F.A27211).

MNHN.F.A27211 (from Saint-Paul-lès-Dax) is here designated lectotype.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bursa grateloupi* is only known from the Lower Miocene of the Aquitaine Basin.

Remarks: *Aquitanobursa grateloupi* was originally written *gratteloupi* this name is obviously founded over Grateloup, in accord with ICZN 32.5.1. the correct name must be *Aquitanobursa grateloupi*.

Aquitanobursa amphitrites (Maury, 1917)

Fig. 5 FG

Bursa amphitrites Maury, 1917: 273, pl. 17, fig. 9;.

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

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

CHRESONYMY

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.

Aquitanobursa inaequicrenata (Cossmann & Peyrot, 1924)

Fig. 5 B

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

Bursa. (*Bufonariella*) *inaequicrenata* (Cossmann and Peyrot, 1924) — Beu 1981:258
Bursa inaequicrenata (Cossmann & Peyrot, 1924) — Landau *et al.* 2004 :68; Landau *et al.* 2009: 76.

TYPE LOCALITY. —Burdigalian of le Peloua, near Saucats, 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.)

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Only Known to the Atlantic Aquitaine Basin (Burdigalian) of France.

***Aquitnobursa morrissi* (d'Archiac & Haimès, 1853)**

Fig. 4 D,E

Ranella morrissi d'Archiac & Haimès, 1853: 309, pl. XXX, fig. 1, pl XXXI, fig. 3

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

Apollon morrissi (d'Archiac & Haimès, 1853) — Harzhauser *et al.* 2009: 360, tab. 1

TYPE LOCALITY. — “Calcaire grossier jaune de la chaîne d'Hala” Pakistan.

TYPE MATERIAL. — Two syntypes figured by d'Archiac & Haimès (1853) possibly in NHMUK

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — This species is only known by d'Archiac & Haimès (1853) specimens for the Lower Miocene of the Halla Mountain, Sindh, Pakistan.

Remark: this species is only putatively attributed to *Aquitnobursa*. We were not able to find the original material in NHMUK and the original figuration lack details.

***Aquitnobursa tuberosa* (Grateloup, 1833)**

Fig. 5 C

Ranella tuberosa Grateloup, 1833 : n°420, 92..

Ranella subtuberosa d'Orbigny, 1852 : n°1405, 76. 1872.

Ranella tuberosa Bonelli (m.s.) — Bellardi 1873 : 236, pl. 15 fig. 7.

Apollon pelouatensis Cossmann & Peyrot, 1924: n°842, pl. 15 figs 38-39, pl. 17 figs 1-2.

Bursa (*Bufonariella*) *pelouatensis* (Cossmann & Peyrot, 1924) — Beu 1981: 258, Schmelz, 1997: 106, pl. 1, fig.2.

Bursa tuberosa (Grateloup, 1833) — 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

TYPE MATERIAL. — *Ranella tuberosa* in Grateloup coll. University of Bordeaux, Talence, France, *Apollon pelouatensis* syntypes (MNHN.F.J06123-6).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Early Aquitanian to Middle Miocene of Aquitaine basin (France) and Po valley (Italy).

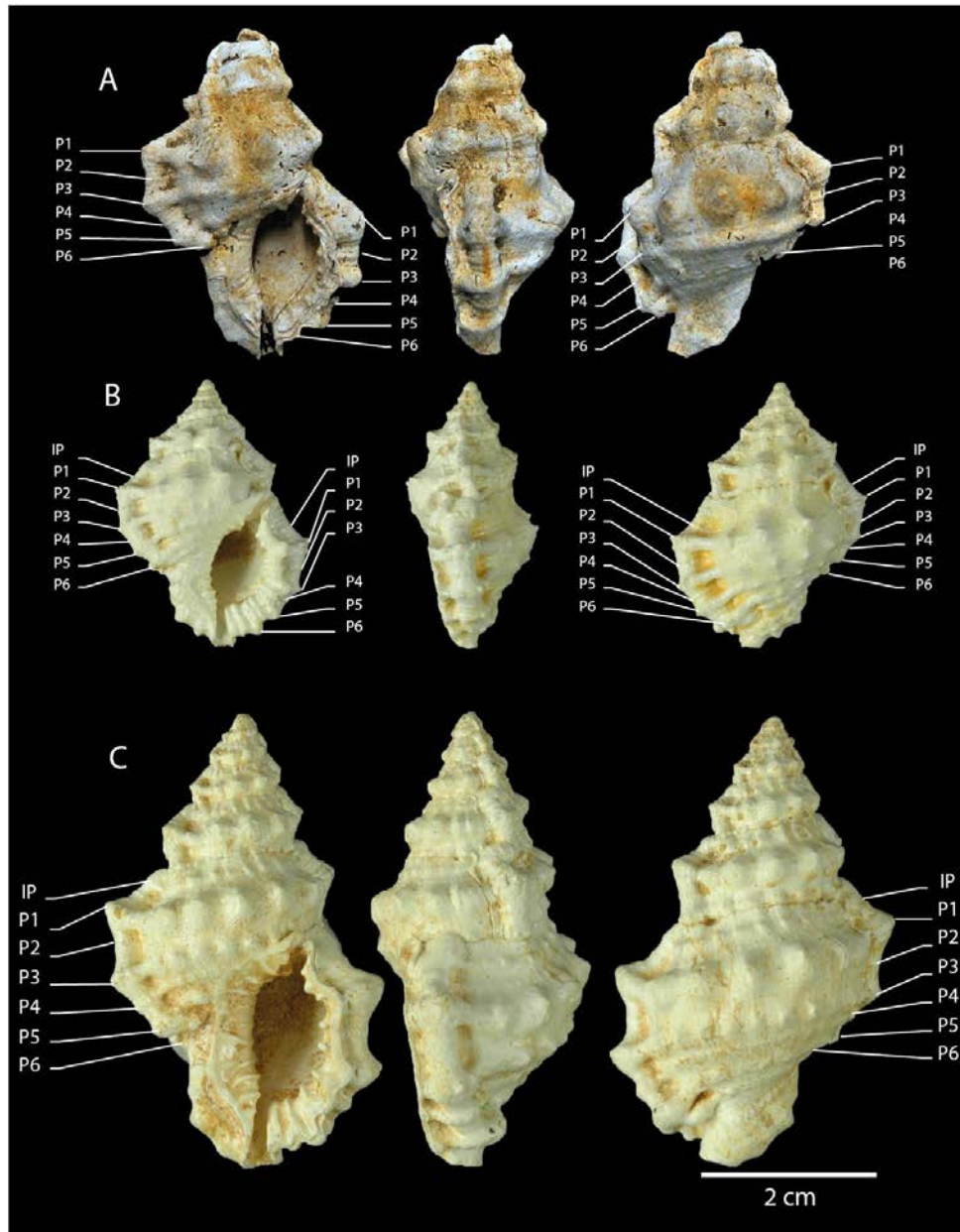


Fig. 5 *Aquitano-bursa* of Aquitaine Basin: **A** *Aquitano-bursa grateloupi* (d'Orbigny, 1852) MNHN.F.A27211 lectotype from Saint-Paul-les-Dax. **B** *Aquitano-bursa inaequicrenata* (Cossmann & Peyrot, 1924) MNHN.F Aquitanian of Gast, France. Faulumelle Coll. **C** *Aquitano-bursa tuberosa* (Grateloup, 1833) MNHN.F Burdigalien de le Peloua, Brongniart coll.

RECOMMENDATIONS

In regard to the first part we can provide some recommendations for calibration of the molecular tree of the Bursidae.

Numerical dating from this section are provided by the international geological time scale (Gradstein et al 2012), a complete stratigraphic distribution chart for the Bursidae can be found in annex 1, First occurrence and last occurrence data are provided in annex 2.

Node Calibration

Considering that they are the oldest undisputable Bursidae and apparently not closely related to another clade within the family, the Genus *Olssonina* seems to be the better candidate for the calibration of the whole Bursidae clade. The oldest representative of the genus is *O. yasila* from the early Bartonian (Beu, 1988, Olsson, 1932) for which we propose to use an age of 42.2 Ma. As for all following node calibrations we will propose 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 *Aspa* genus does not resemble any other Bursidae and considering its very long stratigraphic history (possibly anterior to the Neogene (Landau et al. 2004)) it may very well be a sister group the rest of Recent Bursidae. On the other hand the fossil genus *Aquitano bursa* look like some recent species such as *B. quirihorai*, or *B. granosa*. If *Aspa* where to branch at the basis of the Bursidae tree, the clade containing every other bursid but excluding *Aspa* could be calibrated by *Aquitano bursa*. The oldest representatives of the genus are *A. tuberosa* and *A. inaequicrenata* from the Chatian –Aquitanian of the Aquitaine Basin (Lozouet, 1998). we propose an age of 23 Ma for the node calibration.

The genus *Bursa*, under the acceptation 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 bear the long tubular posterior siphonal canal characteristic of the genus but it is far less warty and could very well be an undescribed species, the oldest of all *Bursa s.s.* We propose an age of 9 Ma.

All the species of the former *B. granularis* complex (resolved in 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 are not figured in Beu (2005). The relation of *B. landaui* to this clade remains too uncertain to be used as calibration.

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

Strong et al. unpub proposed to use the large specimen of *Tutufa* sp. Figured by Tomida et al. (2013) as a calibration point for the genus *Tutufa*, they calibrated it at 13.5 Ma. We accept their recommendation as *Tutufa chipolana* remains too dubious in its attribution to the genus.

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

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 as dating phylogenetic trees without proper fossil data. For this reason reviews such as the one done here are paramount in order to reliably apprehend the paleodiversity of a taxonomic group. 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 specimen institution numbers when possible. We hope the numerous calibrations provided here will help unveil the Paleogene diversification pattern of the Bursidae, a period for which few fossils are known.

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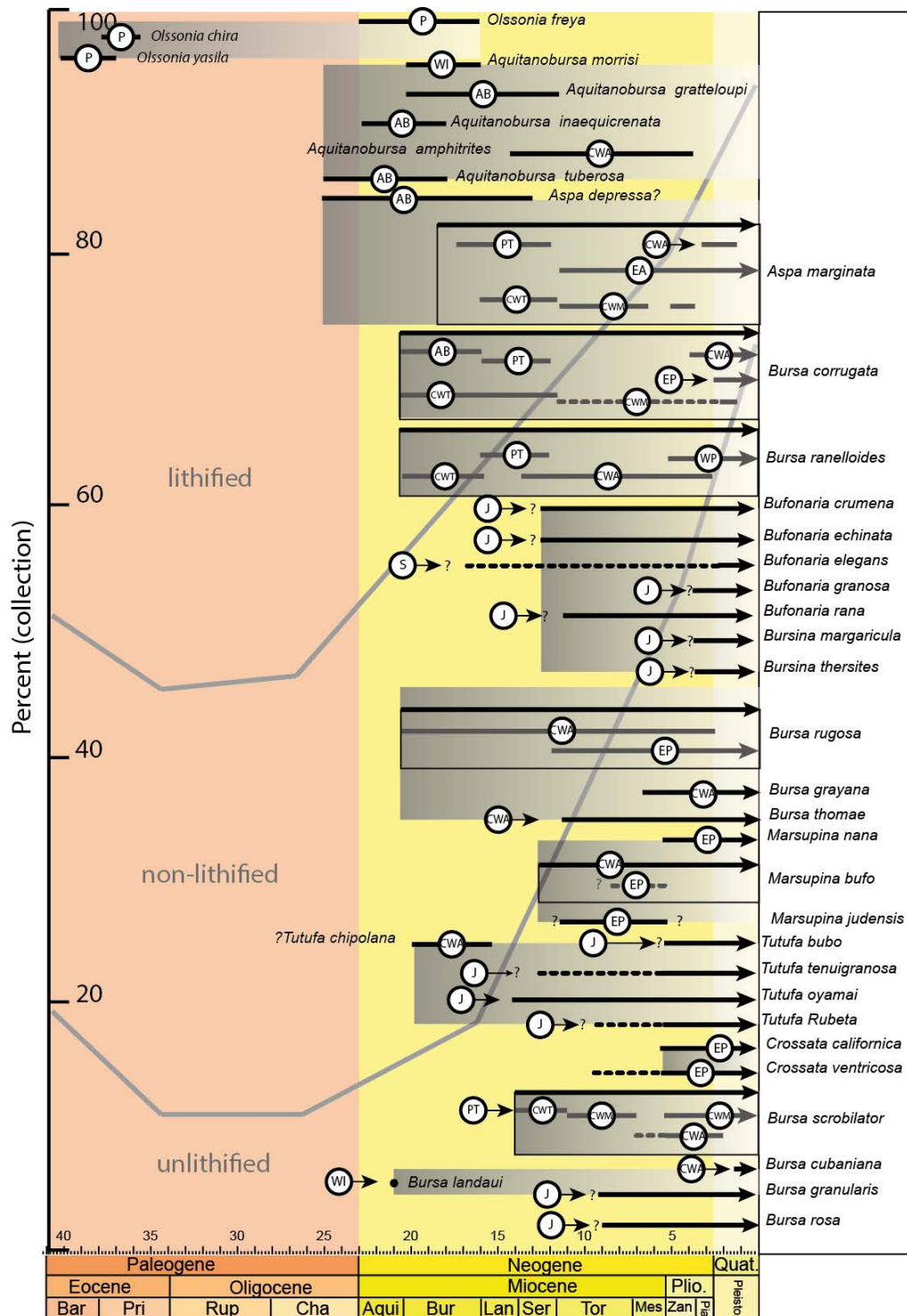
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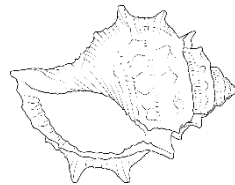


Annex 1 stratigraphic distribution of the extinct and extant Bursidae, black arrows indicates total stratigraphic extension, grey arrows indicates regional stratigraphic extension. Abbreviations: P: Peru, WI: Western Indian Ocean, AB: Aquitaine Basin, CWP: Caribbean, Western Atlantic Ocean, PT: Para-Tethys, 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. In the back ground curves are variation in proportion of collections derived from unlithified and non-lithified (combined unlithified and poorly lithified) sediments through the Cenozoic (after Hendy, 2011). Grey squares regroup accepted genera and putative genera within *Bursa*.

Annex 2 First occurrence and last occurrence data for every species of Bursidae

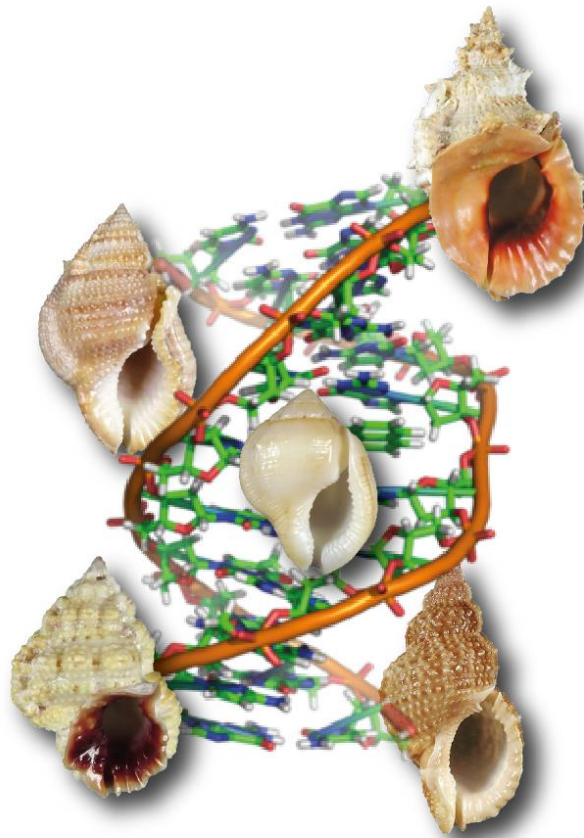
| Species | First occurrence | formation | reference of the occurrence | reference of the stratigraphy | Last occurrence | formation | reference for the occurrence | reference for the stratigraphy |
|--------------------------------------|------------------------------------|---|-------------------------------|---|-------------------|---------------------------------------|------------------------------|---|
| <i>?Tutufa chipolana</i> | Burdigalian | Chipola formation, Florida | Beu 2010 | Beu 2010 | Burdigalian | Chipola formation, Florida | Beu 2010 | Beu 2010 |
| <i>Aquitanoobursa amphitrites</i> | Tortonian | Buenevara Adentro beds, Venezuela | Beu 2010 | Beu 2010 | Zanclean | Gurabo Formation, Dominican republic | Beu 2010 | Beu 2010 |
| <i>Aquitanoobursa inaequicrenata</i> | Aquitanian | Le Peloua, Aquitaine Basin, France | Cossmann & Peyrot, 1924 | Lozouet 1998 | Lower Burdigalian | Le Peloua, Aquitaine Basin, France | Lozouet 1997 | Lozouet 1998 |
| <i>Aquitanoobursa morrisi</i> | Burdigalian | Calacaire 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 |
| <i>Aquitanoobursa tuberosa</i> | Rupelian | Aquitaine basin, France | Lozouet 1998 | Lozouet 1998 | Lower Burdigalian | Aquitaine basin | Lozouet 1998 | Lozouet 1998 |
| <i>Bufonaria crumena</i> | Middle Miocene (early Preangerian) | Robba's locality CIJ1, Cijarian, western Java | Beu, 2005 | Beu, 2005 | Extant | N.A | N.A | N.A |
| <i>Bufonaria echinata</i> | Middle Miocene (early Preangerian) | Robba's locality CIJ1, Cijarian, western Java | Beu, 2005 | Beu, 2005 | Extant | N.A | N.A | N.A |
| <i>Bufonaria elegans</i> | Pleistocene (Erly miocene) | Nias Island, Sumatra (Pakistan) | Beu, 2005 (Ligdoh et al 1999) | Beu, 2005 (Ligdoh et al 1999) | Extant | N.A | N.A | N.A |
| <i>Bufonaria granosa</i> | Late Pliocene (Piacenzian?) | Kalibeng layers , Sangiran, central Java | Beu, 2005 | Beu, 2005 | Extant | N.A | N.A | N.A |
| <i>Bufonaria rana</i> | Late Miocene | Kendeng beds, Jave | Beu, 2005 | Robba, 1996 & Sharaf et al., 2005 | Extant | N.A | N.A | N.A |
| <i>Bursa corrugata</i> | Burdigalian | Aquitaine basin, France | Cossmann & Peyrot, 1924 | Landau et al 2009 | Extant | N.A | N.A | N.A |
| <i>Bursa cubaniana</i> | Pleistocene | Various formations from Panama, Cuba, Dominican republic and Barbados | Beu, 2010 | Beu, 2010 | Extant | N.A | N.A | N.A |
| <i>Bursa granularis</i> | Late Miocene | Citalahab, West Java | Beu, 2005 | Beu, 2005 | Extant | N.A | N.A | N.A |
| <i>Bursa gratteloupi</i> | Burdigalian | Bordeau surroundings, aquitaine Basin, France | d'Orbigny, 1852 | d'Orbigny, 1852 | Serravalian | Tauziets Aquitaine basin, France | Lozouet 1997 | Lozouet 1998 |
| <i>Bursa grayana</i> | Messinian | Cercado formation, Dominican republic | Beu 2010 | Beu 2010 | Extant | N.A | N.A | N.A |
| <i>Bursa landaui</i> | Aquitanian | Ras Tipuli Tanzania | Harzhauser 2009 | Harzhauser 2009 | Aquitanian | Ras Tipuli Tanzania | Harzhauser 2009 | Harzhauser 2009 |
| <i>Bursa rosa</i> | Late Miocene | Citalahab, West Java | Beu, 2005 | Beu, 2005 | Extant | N.A | N.A | N.A |
| <i>Bursa rugosa</i> | Burdigalian | Cantaure, Venezuela | Beu 2010 | Beu 2010 | Extant | N.A | N.A | N.A |
| <i>Bursa scrobilator</i> | Langhian/Serravalian | Paratethys Austria and Poland | Landau et al., 2004 | Baluk 1995 | Extant | N.A | N.A | N.A |
| <i>Bursa thomae</i> | Burdigalian | Chipola formation, Florida | Beu, 2010 | Tulane fossile localities | Extant | N.A | N.A | N.A |
| <i>Bursina margaritula</i> | Pliocene | Tjikeusik [Cikeusik], Java | Beu, 2005 | Beu, 2005 | Extant | N.A | N.A | N.A |

| | | | | | | | | |
|----------------------------|---------------------|---|------------------------|-----------------------------------|----------------------|---|--------------|-------------|
| <i>Crossata ventricosa</i> | Tortonian | Tumbez Fm, Quebrada Tucillal, Zorritos, Peru | Olson, 1932; Beu, 2010 | Olson, 1932 | Extant | N.A | N.A | N.A |
| <i>Marsupina bufo</i> | Serravallian | Shoal River formation, Florida | Beu, 2010:74 | Gardner, 1947 | Extant | N.A | N.A | N.A |
| <i>Marsupina freya</i> | Chattian/Aquitanian | Malpais, SW coast of Nicoya Peninsula, Pacific Costa Rica | Beu, 2010:75 | Beu, 2010 | Burdigalian/Langhian | Subibaya Formation, Progreso Basin, SW Ecuador | Beu, 2010 | Beu, 2010 |
| <i>Marsupina judensis</i> | Late Miocene | Punta Judas, 40 km WNW of Quepos, Pacific coast of Costa Rica | Beu, 2010:76 | Beu, 2010 | Late Miocene | Punta Judas, 40 km WNW of Quepos, Pacific coast of Costa Rica | Beu, 2010:76 | Beu, 2010 |
| <i>Marsupina nana</i> | Zanclean | Charco Azul Group, Penita Fm, Quebrada La Penita, Burica Peninsula, Pacific coast of Costa Rica | Beu, 2010 | Olson 1942 | Extant | N.A | N.A | N.A |
| <i>Olssonina chira</i> | Priabonian | Chira formation, Quercotilla, Peru | Olson, 1930 | Stone 1949 | Bartonian | Chira formation, Quercotilla, Peru | Olson, 1930 | Stone 1949 |
| <i>Olssonina yasila</i> | Bartonian | talara formation, Peru | Olson, 1930 | Olson, 1930 | Bartonian | talara formation peru | Olson, 1930 | Olson, 1930 |
| <i>Tutufa bubo</i> | Late Miocene? | Pendopo Oilfield, 16 km east of Talang Akar, Sumatra | Beu, 2005:29 | Robba, 1996 | Extant | N.A | N.A | N.A |
| <i>Tutufa oyamai</i> | Langhian/Seravalian | Karas, Rembang, Ngrayong Formation, Java | Beu, 2005:31 | Robba, 1996 & Sharaf et al., 2005 | Extant | N.A | N.A | N.A |
| <i>Tutufa rubeta</i> | Late Miocene | Citalahab, West Java | Beu, 2005:32 | Beu, 2005 | Extant | N.A | N.A | N.A |
| <i>Tutufa tenuigranosa</i> | Miocene | Mount Butack, Rembang, central Java | Beu, 2005:30 | Beu, 2005 | Extant | N.A | N.A | N.A |



CHAPITRE 3

ETUDE MOLECULAIRE DE LA DIVERSIFICATION DES BURSIDAE.



Yet the discoveries and techniques of molecular biology have now provided an appropriate source for recovering homology... Molecular phylogenies work not because DNA is 'better,' more real, or more basic than morphology, but simply because the items of a DNA program are sufficiently numerous and independent to ensure that degrees of simple matching accurately measure homology.

Gould S.J. Evolution and the triumph of homology

Toute étude phylogénétique utilise des taxons comme entité terminales ou feuille (dans l'acceptation de la théorie des graphes). Par définition ces taxons sont des groupes d'organismes reconnus en tant qu'unité formelle à chacun des niveaux de la classification (Simpson, 1961). Le but de cette thèse étant de caractériser les relations de parenté des Bursidae, les taxons terminaux ne sauraient être que de niveaux générique ou spécifique. Par ailleurs les travaux récents de Castelin *et al.* (2012) ayant montré que la plupart des genres (au moins *Bursa* et *Bursina*) étaient polyphylétiques dans leurs définitions actuelles, nous sommes donc contraint à ce que les taxons incluent dans notre phylogénie soient de rang spécifique afin de pouvoir redéfinir les genres et établir leurs liens de parenté.

L'espèce est généralement considéré comme un taxon à part car c'est le seul qui aurait une « réalité » biologique objective (Darlu & Tassy, 1993). Les modalités de cette réalité dépassent largement le cadre de cette thèse et ici on considèrera qu'une espèce est un réseau d'organisme, définitivement divergent des autres (de Queiroz 1998, Samadi & Barberousse, 2006, Barberousse & Samadi 2010). Les propriétés dérivées de ce cadre conceptuel (ressemblance, biologique et phylogénétique) sont massivement utilisé dans le champ disciplinaire de la taxonomie intégrative (Pante *et al.* 2015).

La connaissance de la taxonomie d'un groupe est un prérequis à n'importe quelle phylogénie, et la taxonomie intégrative est d'une utilité précieuse lors de la phase exploratoire qu'est la constitution de l'échantillonnage.

Le premier article de ce chapitre est un exemple de la potentialité de qu'offre la Taxonomie intégrative dans le cas des Bursidae. Encore une fois les premiers indices qui allaient guidé notre recherche nous ont été fournis par Castelin *et al.* (2012). Dans leur étude j'avais remarqué que que les logiciels de délimitation automatique d'espèce que sont ABGD (Puillandre *et al.* 2012) et GMYC (Pons *et al.*, 2006; Monaghan *et al.* 2009) retrouvaient plusieurs espèces pour un seul même nom. Ces espèces était *Bursa lamarckii*, *Bursa rhodostoma* et *Bursa granularis*. Après réévaluation du matériel il s'est avéré que pour les deux premiers cas des juvéniles d'espèces proches avaient été mal identifiés ; mais le complexe *granularis*, lui, demeurait.

J'ai donc récolté tous le matériel de *B. granularis* séquençable du Muséum de Paris complété par un prêt du Muséum d'Histoire naturelle de Floride afin de couvrir la totalité de l'aire de répartition du complexe qui est quasi-mondiale.

Et pour c'est spécimens j'ai séquencé une partie du gène *cox-1*. Ce gène est bien connu des taxonomistes (Lipscomb et al. 2003, Weeler 2005, Godfrey 2006) pour ses propriétés de « Barcode » (Herbert et al. 2004). Il a un niveau de variabilité très faible au sein des espèces et très fort entre les espèces différentes ce qui permet en théorie une différenciation nette de celles-ci.

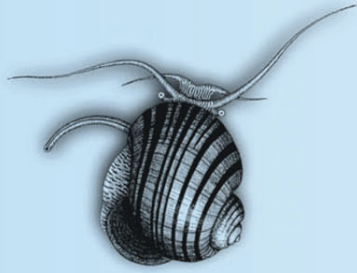
Cependant le *cox-1* peut présenter des limites, avec des biais relativement bien identifiés aujourd'hui : transmission maternel non homogène dans la population (Fu & Zeng 2008), ou encore variation des variables intra et interspécifiques au sein des groupes taxonomiques (Smith et al. 2008 ; Flot & Tillier 2007). C'est pour ces raisons qu'il est recommandé de tester nos hypothèses d'espèce avec au moins un autre gène indépendant.

Dans notre cas nous avons choisi le gène nucléaire 28s qui avait fait ses preuves chez d'autres gastéropodes (Puillandre et al. 2014, 2017) malheureusement nous n'avons pas réussi à amplifier ce gène malgré toutes les variations du protocole. Nous nous sommes reportés vers le H3 que nous avons amplifié avec succès mais ce dernier s'est révélé non variable.

C'est donc avec seulement un marqueur et l'anatomie de la coquille dont nous avons formalisé les caractères que nous avons déterminé que *B. granularis* était un complexe de au moins quatre espèces que nous avons redécrits. Ce résultat est important car les taxons de ce complexe vont former un genre dans la phylogénie moléculaire *Dulcerana* Oyama, 1964 (Article 3).

Cette étude c'est aussi fait dans l'optique d'une réévaluation des capacités dispersives des Tonnoidea à la lumière de ce taxon. Ces résultats préliminaires suggère que leur capacité dispersive qui avait été décrite comme transocéanique (Scheltema, 1966, 1968, 1986a, b, 1988; Laursen, 1981; Pechenik, Scheltema & Eyster, 1984) est probablement très surestimé et doit être réévalué chez d'autres taxons de la famille.

Ce travail a été le fruit d'une collaboration entre Le CR2P (UMR, 7207), l'équipe 3E de l'IsyEB (UMR 7205) et du *Geological survey of New Zealand*. Les résultats ont été publiés dans le *Journal of molluscan Studies*



One for each ocean: revision of the *Bursa granularis* (Röding, 1798) species complex
(Gastropoda: Tonnoidea: Bursidae)

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ABSTRACT

Bursa granularis (Röding, 1798) is a tonnoidean gastropod that is regarded as broadly distributed throughout the Indo-Pacific and tropical western Atlantic. Because of its variable shell it has received no less than thirteen names, now all synonymized under the name *B. granularis*. We sequenced a fragment of the *cox1* gene for 82 specimens covering a large part of its distribution and most type localities. Two delimitation methods were applied, one based on genetic distance (ABGD) and one based on phylogenetic trees (GMYC). All analyses suggest that specimens identified as *B. granularis* comprise four distinct species: one limited to the tropical western Atlantic, another to southwestern Western Australia and two in the Indo-Pacific (from the Red Sea to the open Pacific) that are partly sympatric—but not syntopic—in Japan, the Philippines, Vanuatu and New Caledonia. Based on comparison of shell characters, we applied the following available names to the four species, respectively: *B. cubaniana* (d'Orbigny, 1841), *B. elisabettae* Nappo, Pellegrini & Bonomolo, 2014, *B. granularis* s. s. and *B. affinis* Broderip, 1833. We provide new standardized conchological descriptions for each of them. Our results demonstrate that a long planktotrophic larval stage, common among Tonnoidea, does not necessarily ensure a circumtropical species distribution.

INTRODUCTION

Tonnoideans are a rather small superfamily of Caenogastropoda (about 357 species, WoRMS, 2017) related to the neogastropods, either as its sister group (Zou, Li & Kong, 2011) or belonging within Neogastropoda (Hayashi, 2005; Colgan *et al.*, 2007; Cunha, Grande & Zardoya, 2009; Williams, Foster & Littlewood, 2014; Osca, Templado & Zardoya, 2015). Notwithstanding the non-planktotrophic development of a few Australian species, one of the characteristic features of tonnoidean gastropods is their long to extremely long planktonic larval stages, termed teleplanic larvae (derived from the Greek *tele*, distant and *planos*, wandering; Scheltema, 1971). The record has been observed for a larva of *Fusitriton oregonensis* (Ranellidae), which lived in an aquarium for 4.5 years without metamorphosing (Strathmann & Strathmann, 2007). An indirect estimation of the duration of larval life was also proposed by Scheltema (1972) who, based on the extent of the distribution area and the speed of ocean currents, inferred the time it would take for the larvae to cross ocean basins—generally several months. Conversely, and in quite circular reasoning, the duration of this larval time led to the hypothesis that some species may have trans-oceanic dispersal capabilities (e.g. Scheltema, 1966, 1968, 1971, 1972, 1986a, b, 1988; Laursen, 1981; Pechenik,

Scheltema & Eyster, 1984), resulting in a cosmopolitan distribution. Scheltema (1971) also kept larvae that had been collected in the plankton alive in an aquarium, and found that some taxa lived as planktonic veliger larvae for several months or more (e.g. *Monoplex nicobaricus* lived for 390 d in captivity).

As in most other marine gastropods, tonnoidean species were first described based on features of the teleoconch, using a limited number of specimens and characters. The available material of many species of Bursidae described before 1960 rarely exceeded three specimens. Because of this limited evaluation of the intraspecific variability, numerous new species were described for every newly recognized morphological form. When additional material became available, malacologists realized that they might have greatly underestimated the intraspecific shell variability, since supposedly geographically restricted species were actually morphologically highly similar to other nominal species from other localities, to the extent that they shared identical protoconchs. This was the first step towards an important synonymization trend in tonnoidean systematics. Also, taking into account the expected great dispersal abilities, modern authors (e.g. Beu, 1998; Nappo, Pellegrini & Bonomolo, 2014) followed the lead of Scheltema to the point where some very well-defined morphs were ranked as no

more than subspecies. They thus recognized a smaller number of species, but with trans-oceanic distributions.

Among the Tonnoidea, the family Bursidae includes 54 Recent species (WoRMS, 2017), among which several are potentially species complexes, i.e. species for which alternative hypotheses of delimitation have been proposed in the literature. In particular, the *Bursa granularis* complex, already identified as such by Castelin *et al.* (2012), is typically recognized as a single species by modern authors (Beu, 1998, 2005, 2010), although sometimes with subspecies (Nappo *et al.*, 2014). According to both the literature and the GBIF (2016) database (Fig. 1), *B. granularis* has a subtropical and tropical distribution throughout the Indo-West Pacific, the eastern Pacific and the tropical western Atlantic. [In the eastern Atlantic, it has only been recorded from the Cape Verde Islands (García-Talavera, 1983, cited by Beu, 1998), but this record was not confirmed by Rolán (2005).] This distribution would make it one of the most widespread species among the Tonnoidea. However, this apparently cosmopolitan species has received no fewer than ten names (Beu, 1998). WoRMS (2017) lists 13 synonyms of *Tritonium granulare* Röding, 1798: *Tritonium jabick* Roding, 1798, *Biplex rubicola* Perry, 1811, *Ranella granifera* Lamarck, 1816, *Ranella affinis* Broderip, 1833, *Ranella cubaniana* d'Orbigny, 1841, *Ranella livida* Reeve, 1844, *Bursa cumingiana* Dunker, 1862, *Bursa alfredensis* Turton, 1932, *Bursa kowiensis* Turton, 1932, *Bursa cubaniana intermedia* Nowell-Usticke, 1959, *Bursa corrugata lineata* Nowell-Usticke, 1959 and *Bursa granularis elisabettae* Nappo *et al.* 2014. The numerous alternative species hypotheses led to various usages of these names in the literature; whereas 19th century authors (e.g. Reeve, 1844b) recognized up to four different species, the latest revision proposed to group them all under the name *B. granularis* (Röding, 1798) (Beu, 1998). Two of these names, however have been accepted by Nappo *et al.* (2014) at the rank of subspecies—*B. granularis cubaniana* and *B. granularis elisabettae*—in addition to the nominotypical subspecies *B. granularis granularis*.

Using several molecular markers, Castelin *et al.* (2012) identified two morphologically distinct clades within the *B. granularis* complex. Interestingly, these two clades were found in sympatry in Vanuatu, at similar depths, and the authors suggested that additional sampling would be needed to clarify species boundaries within the group. We increased the size of the dataset, including samples from the geographical region sampled by Castelin *et al.* (2012) as well as from other localities, with a particular focus on type localities, and covering a large part of the global distribution

of the *B. granularis* complex. Our goal was to clarify species delimitation within the *B. granularis* complex and to test the hypothesis that this supposed species has a world-wide geographical distribution.

The specimens were first separated tentatively into morphospecies based on shell characters. In a second step, all the specimens were sequenced (cytochrome *c* oxidase subunit I gene) to test whether the recognized morphogroups corresponded to distinct molecular clusters. Finally, we assigned available names to the different genetic and morphological groups identified within the complex and considered the implication in terms of their geographical distributions.

MATERIAL AND METHODS

Sampling

The material for this study was collected from various localities during a series of shallow-water and deep-sea expeditions to Saudi Arabia (University of Florida UF 2013), Vietnam (NT 2014), Vanuatu (UF 2005, Santo Marine biodiversity survey 2006), Mozambique (MAINBAZA 2009, INHACA 2011), Madagascar (UF 2008), the Philippines (PANGLAO 2004, UF 2015), Mariana Islands (UF 2008), Micronesia (UF 2008), Okinawa, Japan (UF 2010), Guam (UF 2010), Marquesas Islands (Pakaihi I Te Moana 2012), Papua New Guinea (PAPUA NIUGINI 2012), Marshall Islands (UF 2008), New Caledonia (TERRASSES 2008, UF 2013), Taiwan (UF 2005), Florida, USA (UF 2010), Guadeloupe (KARUBENTHOS 2012) and Western Australia (UF 2009, WESTERN AUSTRALIA 2011). MNHN specimens collected before 2012 were anaesthetized with an isotonic solution of MgCl₂ and fixed in 96% ethanol. Specimens collected after 2012 were processed with a microwave oven (Galindo *et al.*, 2014); the living molluscs in small volumes of sea water were exposed to microwaves for *c.* 30 s. Bodies were immediately removed from shells and dropped into 96% ethanol. UF specimens were directly put alive into 75% or 95% ethanol. The analysed material included 82 specimens, 42 deposited in the Muséum national d'Histoire naturelle, Paris (MNHN) and 40 in the Florida Natural History Museum (UF) collections (Supplementary Material Table S1). The specimens and corresponding sequences are also registered in the Barcode of Life Data System (project BURSA

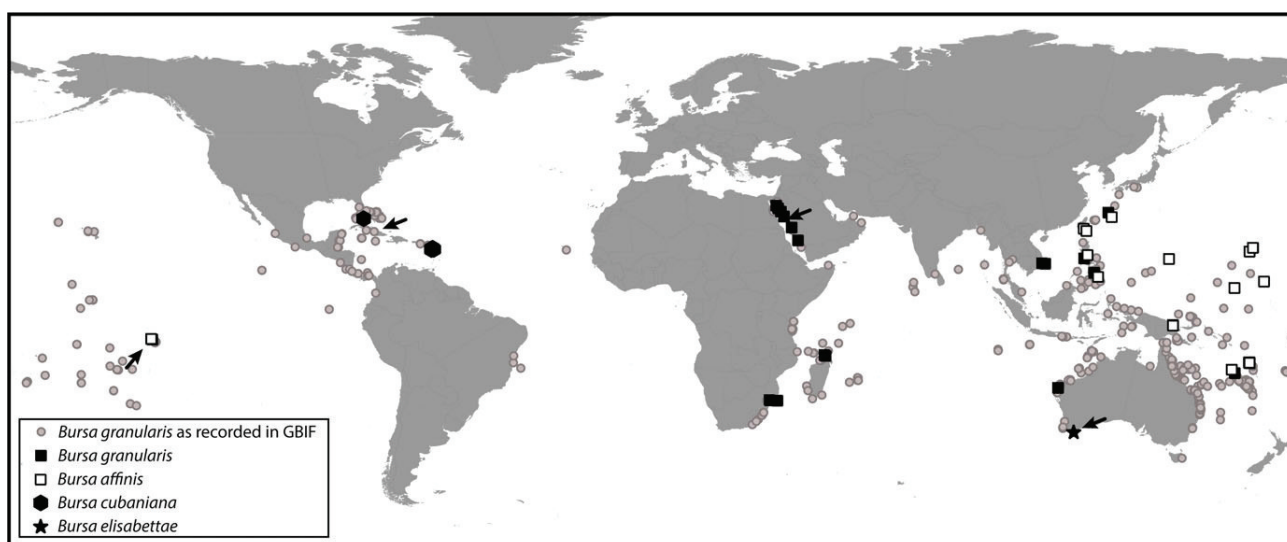


Figure 1. Distribution of the *Bursa granularis* complex recorded by the Global Biodiversity Information Facility (GBIF, 2016). Records from Senegal were removed after being reidentified as *Bursa scrobilator* (Linnaeus, 1758). Type localities of corresponding species are marked by arrows.

and GenBank. Maps showing the sampling localities of all the specimens were generated using Qgis v. 2.16.3 (Fig. 1).

DNA sequencing

DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the manufacturers' recommendations. A fragment of the cytochrome *c* oxidase subunit I (*cox1*) gene was amplified using the universal primers LCO1490/HCO2198 (Folmer *et al.*, 1994). PCR reactions were performed in volumes of 20 µl, containing 3 ng DNA, 1× reaction buffer, 2.5 mM MgCl₂, 0.26 mM dNTP, 0.3 mM of each primer, 5% DMSO and 1.5 units of Qbiogene Q-Bio Taq. The amplification consisted of an initial denaturation step at 94 °C for 5 min, followed by 40 cycles of denaturation at 94 °C for 30 s, annealing at 47 °C for 30 s, followed by extension at 72 °C for 1 min. The final extension was at 72 °C for 5 min. PCR products were purified and sequenced in both directions by the Eurofins sequencing facility.

Species delimitation

All specimens were first separated into morphogroups, using characters of the teleoconch and in particular of the outer lip. In a second step, the *cox1* sequences were analysed. Alignment was done by eye. Pairwise genetic distances were calculated using MEGA v. 6 (Tamura *et al.*, 2013). Phylogenetic trees were reconstructed using maximum likelihood (ML) and Bayesian inference (BI) approaches, with MEGA v. 7 (with Bootstraps 100 replications and default parameters for tree inference options) for ML analysis and, for the BI analyses, with MrBayes (Huelsenbeck, Ronquist & Hall, 2001) (six Markov chains and 10,000,000 generations, five chains, three swaps at each generation, a sampling frequency of one tree each 1,000 generations, chain temperature set at 0.02) and BEAST v. 1.8.3 (Drummond *et al.*, 2012) (with uncorrelated relaxed clock, and 10,000,000 generations). In all analyses the three codon positions of the *cox1* gene were treated

as independent partitions and the substitution model was set to GTR + G and GTR + I + G for the ML and BI analyses, respectively. Convergence for both BI analyses was evaluated using Tracer v. 1.4.1 (Rambaut *et al.*, 2014) to check that all effective sample size values exceeded 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. Nodal support was assessed as posterior probability (PP) in the BI analyses and as bootstraps (BS) for the ML analysis. Closely related bursid species were used as outgroups: *Bursa latitudo* Garrard, 1961, *Bursina ignobilis* (Beu, 1987) and *Tutufo bufo* (Röding, 1798), following Castelin *et al.* (2012).

Species delimitations were performed using the online versions of the Automatic Barcode Gap Discovery (ABGD; Puillandre *et al.*, 2012a) method using a simple distance (p-distance) model and default parameters. ABGD automatically detects the barcode gap in the pairwise distribution of genetic distances between low and high genetic distances, hypothesized to correspond to intra- and interspecific genetic distances, respectively. The General Mixed Yule Coalescent (GMYC) method (Pons *et al.*, 2006; Monaghan *et al.*, 2009) was also used, with default parameters (both single and multiple methods). GMYC defines the transition (unique in the single version, but variable between lineages in the multiple version) between speciation and coalescent events in the ultrametric tree obtained with BEAST, inferred from the rate of splits in the tree.

Shell description

Once the species were delimited based on molecular data, shells were described using the methods developed by 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 apical to abapical (P2 to P6, Fig. 2A). The primary cord of the infrasutural

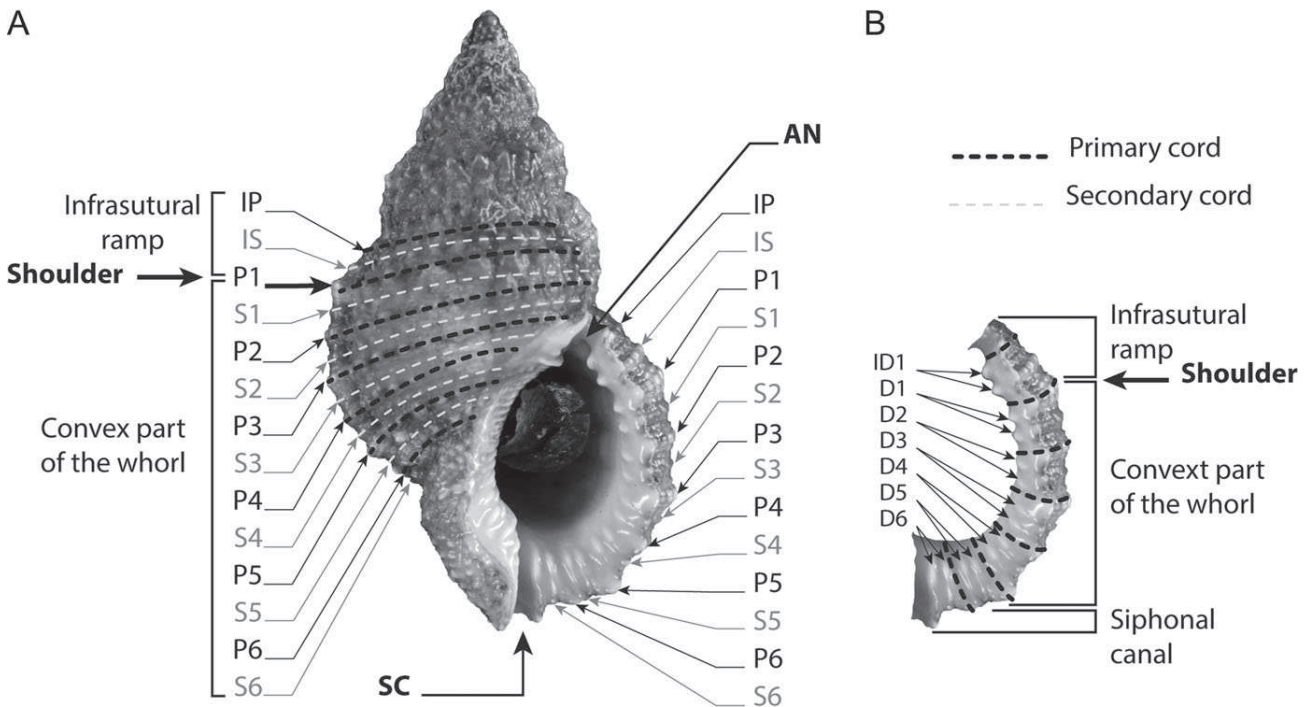
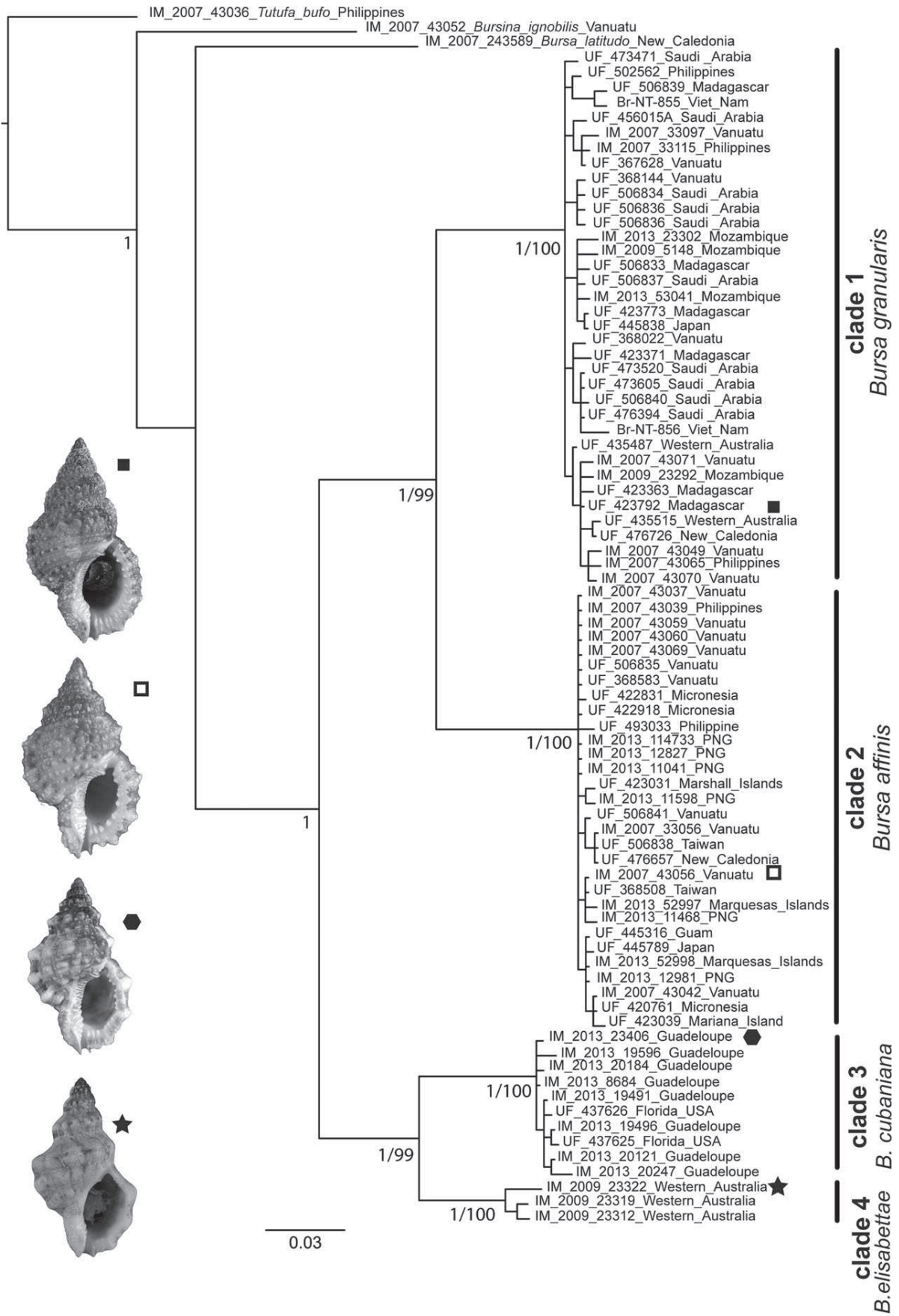


Figure 2. Shell characters of *Bursa granularis* complex. **A.** Apertural view. **B.** Outer lip. Specimen figured: UF-423792, UF cruise 2008 (Madagascar), Nosy Komba, NW side. Abbreviations: IP, infrasutural ramp primary cord; IS, infrasutural ramp secondary cord; P1-6, primary cords; S1-6, secondary cords; AN, anal notch; SC, siphonal canal; ID1, infrasutural denticle; D1-6, denticles of convex part of whorl.



ramp is designated IP and the secondary cord IS. Secondary cords on the convex part of the whorl are designated S1 to S6. Cords of the siphonal canal were not considered. Denticles inside the outer lip are named D1 to D6, starting under the shoulder cord and added from adapical to abapical; denticles above the shoulder are designed as ID1 and ID2 added from abapical to adapical (ID2 is not shown in Fig. 2). Denticles are bifid on most specimens, but can merge or further bifurcate. In order to describe the outer lip we introduce here the outer lip denticle formula (OLDF). This is a four-digit sequence representing the number of visible denticles (D) between a notch and the preponderant primary cord (P1, P3 and P5) or between two preponderant primary cords, starting from the anal notch in the direction of the siphonal notch. For example, in the specimen of *B. granularis* figured in Figure 2, the OLDF should be read as AN, 2, P1, 4, P3, 4, P5, 4, SC or 2,4,4,4 for short.

Abbreviations

Specimen repositories:

| | |
|--------|--|
| MAC.ML | Museo di Storia Naturale Aquilegia, Cagliari, Sardinia |
| MHNG | Muséum d'Histoire naturelle, Geneva |
| MNHN | Muséum national d'Histoire naturelle, Paris |
| NHMUK | Natural History Museum, London |
| RASM | Russian Academy of Science, Moscow |
| UF | Florida Natural History Museum, University of Florida, Gainesville, FL |

Shell characters:

| | |
|-------|---|
| AN | anal notch |
| D | denticles of the outer lip |
| D1-6 | denticles of the convex part of the whorl |
| H | height |
| ID1-2 | denticles of the infrasutural ramp |
| IP | infrasutural primary cord |
| IS | infrasutural secondary cord |
| OLDF | outer lip denticle formula |
| P | primary cord |
| P1 | shoulder cord |
| P2-6 | primary cords of the convex part of the whorl |
| S | secondary cord |
| S1-6 | secondary cords of the convex part of the whorl |
| SC | siphonal canal |
| W | width |

RESULTS

Among the 82 specimens, excluding outgroups, three morphogroups were initially recognized. The ABGD (both initial and recursive partitions) and GMYC (single threshold) methods consistently found four clusters. The only exception is the multiple-threshold approach of GMYC: five clusters were supported, one specimen (IM-2013–19496) from the Caribbean cluster (see below) being considered different. Given that this specimen is very close in molecular sequences to other Caribbean specimens, we conclude this to be an artefact of the multiple-threshold method of GMYC, which is known to oversplit (Fujisawa & Barraclough, 2013; Kekkonen & Hebert, 2014). Among the four clusters recognized with the *cox1* gene, two correspond to two morphogroups.

One morphogroup is thus divided into two genetic clusters, corresponding to the two clades revealed by Castelin *et al.* (2012). A *posteriori* re-examination of the shells revealed stable teleoconch characters distinguishing these two genetic clusters. The morphological characters used to recognize first the three morphogroups and, after the molecular analyses, the final four morphogroups, are described in the systematic section (below). The four genetic clusters also correspond to highly supported clades in both BI and ML analyses (PP > 0.99 and BS > 80) (Fig. 3). Pairwise genetic distances between clades were never less than 6.4%, while within cluster genetic distances never exceeded 1.8%, even between geographically distant localities such as Saudi Arabia and Western Australia. All clades correspond to geographically defined areas: Clade 1 ranges from Mozambique to the Red Sea, Vietnam, Japan, the Philippines, Western Australia, Vanuatu and New Caledonia, suggesting an occurrence throughout the Indian Ocean and western Pacific; Clade 2 is found in sympatry with Clade 1 in Okinawa, the Philippines, Vanuatu and New Caledonia, but is also present in Taiwan and Papua New Guinea and extends further east to Guam and French Polynesia; although Clades 1 and 2 can be found in sympatry they never occur in syntopy. Clade 3 is restricted to the Caribbean; and Clade 4 is limited to southernmost Western Australia.

Based on the original descriptions and type localities, we have attributed available names as follows: *B. granularis* to Clade 1, *B. affinis* to Clade 2, *B. cubaniana* to Clade 3 and *B. elisabettae* to Clade 4.

SYSTEMATIC DESCRIPTIONS

Superfamily TONNOIDEA Suter, 1913 (1825) Family BURSIDAE Thiele, 1925

Bursa Röding, 1798

Type species: *Bursa monilata* Röding, 1798, by subsequent designation (Jousseau, 1881: 174) (junior synonym of *Murex byfonius* Gmelin, 1791, by First Reviser's action of Winckworth, 1945: 137).

Bursa granularis (Röding, 1798) (Fig. 4A–D, J)

Tritonium granulare Röding, 1798: 127. (Red Sea, in accordance with ICZN Art. 76.3; original types lost; neotype MHNG 1098/85/1, designated by Beu, 1998: 150).

Bursa granularis—H. & A. Adams, 1853: 106; Barnard, 1963: 17; Hinton, 1972: 12, pl. 6, fig. 22; Hinton, 1978: 32, fig. 8; Kilburn & Rippey, 1982: 73, pl. 16, fig. 14, Drivas & Jay, 1988: 62, pl. 16, fig. 4; Wilson, 1993: 226, pl. 43, figs 11a–b, 12; Kubo *in* Kubo & Kurozumi, 1995: 74, 78, fig. 7; Beu, 1998: 150, figs 48a–e, 58d; Beu, 1999: 44, fig. 85; Beu, 2005: 19, figs 27, 28; Lee & Chao, 2003: 40, pl. 4, fig. 93; Castelin *et al.*, 2012: 4843, fig. 4; Dolorosa, Conales & Bundal, 2013: 8, fig. 3D.

Colubrellina granularis—Habe, 1961: 47, pl. 24, fig. 5; Okutani, 1986: 116–117, top left fig.

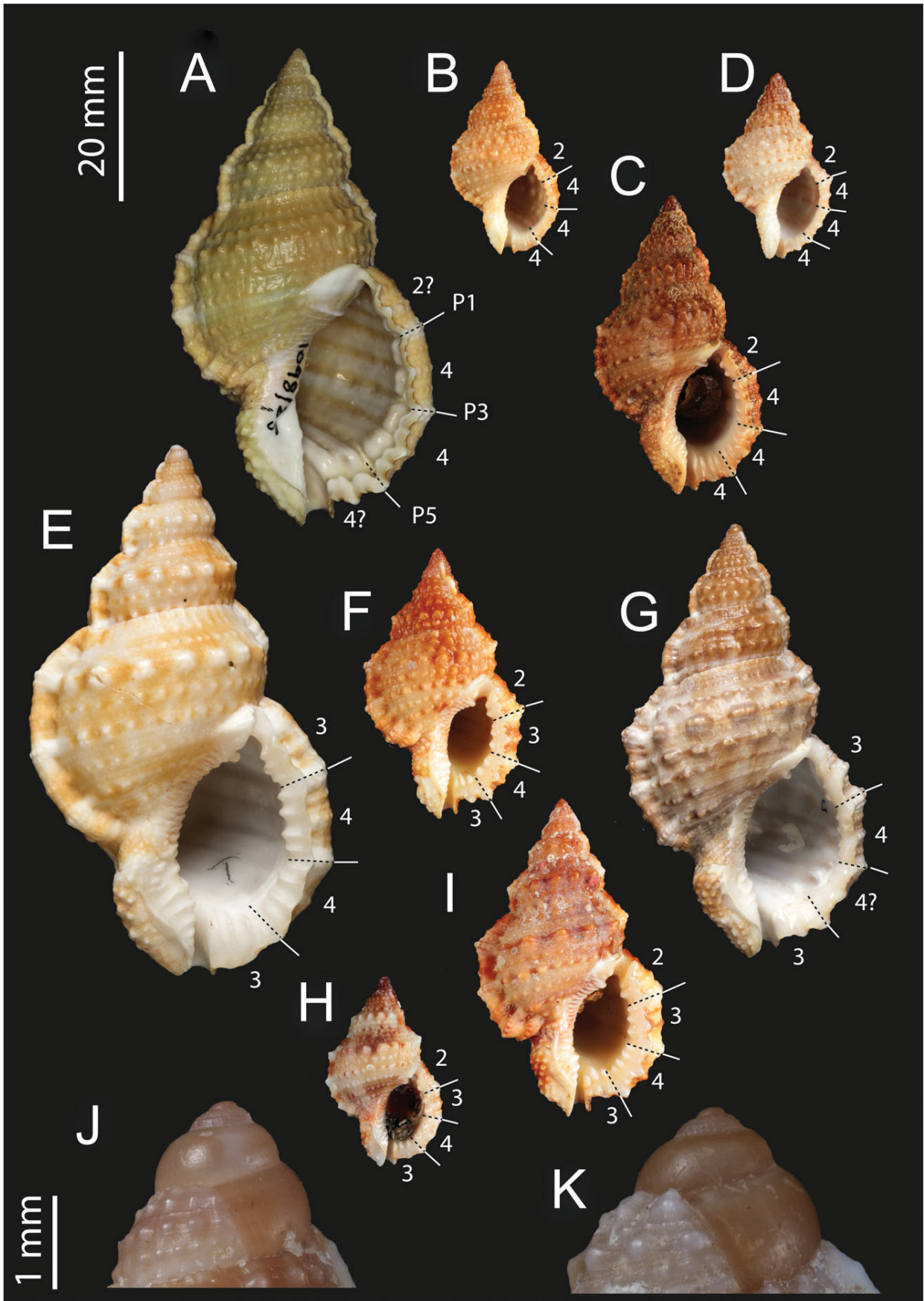
Colubrellina (Dulcerana) granularis—Habe, 1964: 76, pl. 24, fig. 5; Wilson & Gillett, 1971: 80, pl. 54, fig. 7, 7b.

Bursa (Colubrellina) granularis granularis—Beu, 1985: 64; Cossignani, 1994: 75–77; Nappo *et al.*, 2014: pl. 3, figs 1–3, pl. 4, figs 1–4, pl. 5, fig. 1, pl. 7, fig. 1.

Bursa (Byfonariella) granularis—Bosch *et al.*, 1995: 102, fig. 737.

Bursa (Colubrellina) granularis—Okutani, 2000: 269, pl. 133, fig. 1; Zhang & Ma, 2004: 182, text-figs 113a–c, pl. 5, figs 1–3.

Figure 3. Molecular tree for the *cox1* gene of the *Bursa granularis* complex. *Bursa granularis* is represented by shell of UF-423792 (indicated by black square); *B. affinis* by shell of IM-2007–43056 (white square); *B. cubaniana* by shell of IM-2009–23406 (black hexagon) and *B. elisabettae* by shell of IM-2009–23322 (black star). Support for nodes is given as PP/BS, where these exceed 0.95 and 95, respectively. Abbreviation: PNG, Papua New Guinea.



Tritonium jabick Röding, 1798: 127 (Red Sea, in accordance with ICZN Art. 76.3; original types lost; neotype MHNG 1098/85/1, designated by Beu, 1998: 150).

Dulcerana jabick—Iredale, 1931: 213.

Colibrellina jabick—Oyama & Takemura, 1960: *Colubrellina* pl., figs 3, 4.

Biplex rubicola Perry, 1811: pl. 5, fig. 4 (Red Sea, in accordance with ICZN Art. 76.3; original types lost; neotype MHNG 1098/85/1, designated by Beu, 1998: 150).

Ranella granifera Lamarck, 1816: pl. 414, fig. 4, 'Liste des objets': 4; 1822: 153 (Red Sea, designated by Beu 1998: 150; lectotype MHNG 1098/85/1, designated by Beu, 1998: 150); Kiener, 1841: 16, pl. 11, fig. 1; Deshayes, 1843: 548; Reeve, 1844a: pl. 6, fig. 30; Küster, 1871 [in Küster & Köbelt, 1870–1878]: 143, pl. 39, fig. 1.

Bursa cumingiana Dunker, 1862: 238; New Caledonia; lectotype NHMUK 1968530 designated by Beu 1998: 150; Dunker, 1863: 59, pl. 19, figs 7, 8.

Ranella (Lampas) granifera—Tryon, 1880 [in 1880–1881]: 41, pl. 22, figs 35–40.

Ranella semigranosa—Reeve, 1844b: pl. 6, fig. 25; Krauss, 1848: 113 (not Lamarck, 1822).

Material examined: Supplementary Material Table S1.

Diagnosis: Shell biconic, varices strictly aligned, numerous nodules on all primary, secondary and tertiary cords, OLDF: 2,4,4,4, or 2,4,4,3 in large specimens.

Description: Protoconch of 3.75 whorls (following counting method of Bouchet & Kantor, 2003), rather tall with weakly impressed sutures, with finely reticulate protoconch I of 0.5 whorls, reticulate sculpture on first whorl of protoconch II, becoming obsolete before end of last protoconch whorl. Teleoconch: tall, relatively narrow, 4–5 whorls (up to 6 in very large specimens). H about 40 mm, up to 60 mm. Spire angle 50°. Aperture 53% of W. Last whorl 54% of H. Varices strictly aligned for most of spire height, becoming slightly displaced only on last 1 or 2 whorls of large specimens. Abapertural face of each varix slightly excavated, buttressed by spiral cords. Spiral ornamentation of 7 primary cords, 1 on infrasutural ramp (IP) and 6 on convex part of whorl (P1–6). After whorl 2.5 (varix 5) IP becoming very reduced, noticeable only where it intersects varices. Secondary cords in interspaces between primary cords. Primary cord above IP remaining reduced throughout shell ontogeny whereas others growing in similar fashion to primary cords. On last whorl, spiral ornamentation composed of 9 nodules per primary cord between two varices (and secondary cords of infrasutural ramp) and double this number for secondary cords. Apertural lip well flared, bearing numerous prominent, narrow, transverse denticles. Outer lip bearing numerous denticles; ID1 bifid, ID2 absent, D1–4 bifid, D5 bifid but merged in large specimens, D6 bifid (Fig. 5).

Distribution and habitat: *Bursa granularis* has a tropical distribution throughout the Indo-West Pacific province (Fig. 1), from the Mozambique Channel throughout East Africa and the Red Sea to the northern Indian Ocean, in the western Pacific from Kii Peninsula and Yamaguchi Prefecture, Honshu, Japan (Beu, 1999), south to Rottnest Island in Western Australia (Wilson, 1993). Its eastward distribution in the Pacific extends from Japan to

Australia through the Philippines, Vanuatu and New Caledonia. *Bursa granularis* is commonly found in very shallow water but some specimens were found alive in about 100 m depth.

Remarks: The nomenclatural history of *B. granularis* is a particularly complex one. The types of *Tritonium granulare*, *T. jabick* and *Biplex rubicola* are lost. Beu (1998) designated the lectotype of *R. granifera* as neotype of the three other names. As a consequence these formerly subjective synonyms became objective synonyms and following ICZN Art. 76.3 they also all share the same type locality, the Red Sea. There is only one species belonging to the complex in this locality, to which the name *B. granularis* can thus unambiguously be attributed. Furthermore, the type specimen of *R. granifera* displays characters congruent with the description above (Fig. 4A).

Bursa cumingiana (type locality New Caledonia) is another available name in the *B. granularis* complex. There are two (and only two) molecular operational taxonomic units (MOTU) living sympatrically in this region and the lectotype of *Ranella cumingiana* (NHMUK 1968530) is a well-preserved adult specimen, which displays four distinctive denticles between P5 and the anterior canal, identifying it as *B. granularis*. The colour pattern of the teleoconch of *B. granularis* is highly variable, from off-white, pale brown or pale orange to deep reddish brown. Some specimens bear the same striped colour pattern as *B. cubaniana*. A few young specimens display the angular profile of *B. affinis*, especially in the Mozambique Channel, but it never occurs in fully grown specimens.

Bursa affinis (Broderip, 1833)

(Fig. 4E–I, K)

Ranella affinis Broderip, 1833: 179 ('Annaa,' Tuamotu Islands, lectotype NHMUK 1950.11.28.4, designated by Beu, 1998: 150); G.B. Sowerby II, 1835 [in 1832–1841]: pl. 89, fig. 12; Reeve, 1844b: pl. 4, fig. 19; Küster, 1871 [in Küster & Köbelt, 1870–1878]: 142, pl. 38a, fig. 5.

Bursa granularis affinis—Hertlein & Allison, 1960: 15.

Ranella livida Reeve, 1844a: pl. 6, fig. 28; ('Annaa,' Tuamotu Islands, lectotype NHMUK 1967657_1, designated by Beu, 1998: 150); Reeve, 1844b: 138; Krauss, 1848: 113.

Dulcerana granularis—Iredale, 1931: 213; Rippingale & McMichael, 1961: 69, pl. 7, fig. 19 (all not Röding, 1798).

Bursa granularis—Hertlein & Allison, 1960: 15; Salvat & Rives, 1975: 307, fig. 179; Kay, 1979: 227, fig. 80A; Severns, 2011: 150, pl. 59, fig. 6; Beu, Bouchet & Tröndle, 2012: 67, fig. E2 (all not Röding, 1798).

Bursa (Colubrellina) granularis—Kaiser, 2007: 39, pl. 26, fig. 7a–b (not Röding, 1798).

Material examined: Supplementary Material Table S1.

Diagnosis: Shell biconic, varices strictly aligned, numerous nodules on all primary, secondary and tertiary cords, shoulder angulation prominent, OLDF: 2,3,4,3 or 3,4,4,3 in particularly large specimens.

Description: Protoconch as in *B. granularis*. Teleoconch tall, relatively narrow, with 4–5 whorls (up to 6 on large specimens). H 40–50 mm, up to 80 mm. Spire angle 55°. Aperture comprising

Figure 4. Shells of *Bursa granularis* complex. **A–D.** *Bursa granularis* (Röding, 1798). **A.** MHNG 1098/85/1, lectotype of *Ranella granifera* Röding, 1798 and neotype of *Tritonium granulare* Röding, 1798, of *T. jabick* Röding, 1798 and of *Biplex rubicola* Perry, 1811, from Red Sea, H 64 mm. **B.** IM-2009–5148, MAINBAZA 2009 (Mozambique Channel), stn DW3168, H: 26 mm. **C.** UF-423792, UF 2008 (Madagascar), NW side Nosy Komba, H 40 mm. **D.** IM-2007–43071, Santo Marine Biodiversity Survey 2006 (Vanuatu), stn VM62, H 25 mm. **E–I.** *Bursa affinis* (Broderip, 1833). **E.** NHMUK 1950.11.28.4, lectotype of *Ranella affinis* Broderip, 1833, supposedly from 'Annaa,' Tuamotu Islands, H 62.5 mm. **F.** IM-2007–43056, Santo Marine Biodiversity Survey 2006 (Vanuatu), stn VM02, H 37 mm. **G.** NHMUK 1967657, lectotype of *Ranella livida* Reeve, 1844, supposedly from 'Annaa,' Tuamotu Islands, H 56.8 mm. **H.** UF-422918, UF 2008 (Federated States of Micronesia), Kosrae Letu, H 25 mm. **I.** IM-2007–43039, PANGLAO 2004 (Philippines), stn R24, H 41 mm. **J.** IM-2009–5148, *Bursa granularis* protoconch detail. **K.** IM-2007–43056, *Bursa affinis* protoconch detail. Abbreviations: P1, P3, P5, preponderant primary cords; numbers indicates the number of denticles.

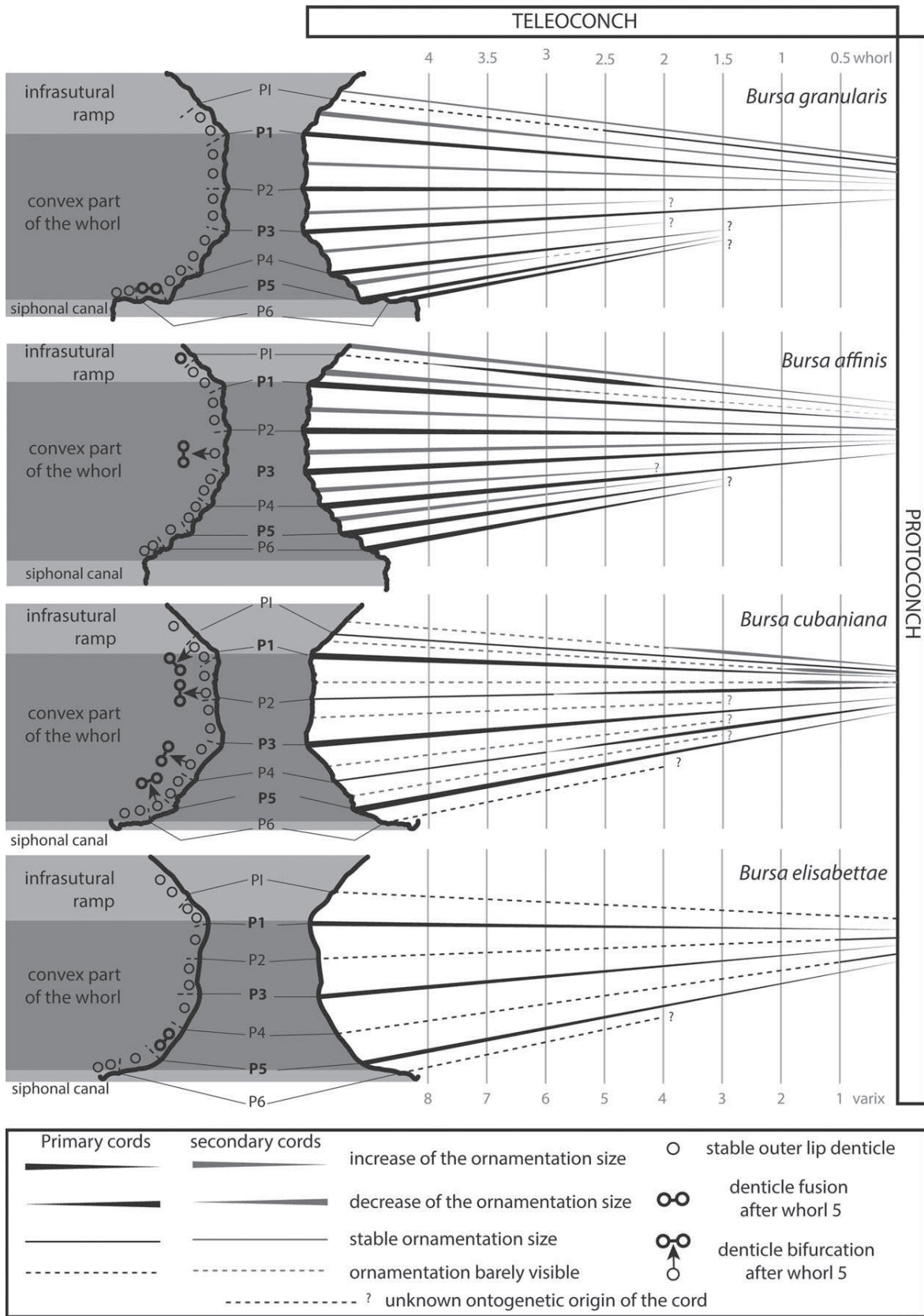


Figure 5. Diagrams showing the sequence of appearance of primary and secondary cords in the four species of the *Bursa granularis* complex. In all ontogenies, the primary cords (black lines) are numbered following their adapical to abapical order.

50% of W. Last whorl comprising 52% of H. Varices strictly aligned for most of spire height, becoming slightly displaced only on last 1 or 2 whorls of large specimens. Abapertural face of each varix deeply excavated, buttressed by spiral cords. Spiral ornamentation as in *B. granularis*. After whorl 2 (varix 4) IP increasing in importance to equal other cords, diminishing again after varix 6, allowing development of secondary cord above. Each primary cord bounded by two secondary cords, increasing in importance similarly to primary cords. On last whorl, spiral ornamentation composed of 9 nodules per primary cord between two varices except P1, which bears much bigger nodules, pointing slightly upwards, decreasing in number with ontogeny from 9 to 5. Secondary cords bearing same number of small nodules as *B. granularis*. Nodules on varices where they meet P1 angulating shoulder. Apertural lip well flared, bearing numerous prominent, narrow, internal transverse denticles. ID2 present in large specimens, ID1 bifid, D1 bifid, D2 single but bifid in large specimens, D3-4 bifid, D5 single, D6 bifid (Fig. 5).

Distribution and habitat: *Bursa affinis* has a tropical distribution throughout the Pacific Ocean (Fig. 1), from Okinawa, Japan to Sydney Harbour, New South Wales, Australia, and throughout Polynesia to Hawaii (Beu, 1998). In the eastern Pacific, particularly large specimens are common at Clipperton Island (Hertlein & Allison, 1960; Kaiser, 2007) and specimens were recorded by Emerson (1991) from the Revillagigedo Islands, Cocos Island and the mainland coast at Bahia Chamela, Jalisco, western Mexico (Beu, 2010). Its westward distribution in the Pacific extends from Japan to Australia through the Philippines, Papua New Guinea, Vanuatu and New Caledonia. *Bursa affinis* is commonly found in very shallow water, but specimens are occasionally found alive in about 40 m depth.

Remarks: *Bursa affinis* and *B. livida* have the same type locality, 'Anaa' [now Anaa], Tuamotu Islands. The type specimens (Fig. 4E, G) of both have the same OLDF and we consider the latter to be a junior synonym of the former. Considering that there is only one MOTU occurring in outer Oceania in general (Fig. 1) and French Polynesia in particular, we attribute to it the name *B. affinis*.

***Bursa cubaniana* (d'Orbigny, 1841)**

(Fig. 6A–D, L)

Ranella cubaniana d'Orbigny, 1841: 165, pl. 23, fig. 24 (Ste Lucie, West Indies, holotype NHMUK 1854.10.4.412); Mörch, 1877: 24.

Gyrineum affine var. *cubaninum*—Dall, 1889: 224.

Gyrineum affine (sic) *cubaninum*—Morretes, 1949: 92.

Bursa (*Colubrellina*) *cubaniana*—Abbott, 1958: 57, text-fig. 2, pl. 1, fig. k. Warmke & Abbott, 1962: 103, pl. 18, fig. i; Rios, 1970: 70; Coelho & Matthews, 1971: 52, figs 11, 12; Humfrey, 1975: 126, pl. 14, fig. 4, 4a; H. & E. Vokes, 1983: 23, pl. 11, fig. 14.

Bursa cubaniana—Nowell-Usticke, 1959: 61; Work, 1969: 663; Kaufmann & Gotting, 1970: 372, fig. 87; Matthews & Kempf, 1970: 28; de Jong & Coomans, 1988: 214, pl. 16, fig. 382.

Bursa cubaniana var. *intermedia* Nowell-Usticke 1959: 61-62, pl. 3, fig. 13 (North of Fredericksted, St Croix, Virgin Islands); Boyko & Cordeiro, 2001: 24.

Bursa corrugata var. *lineata* Nowell-Usticke 1959: 61-62, pl. 3, fig. 12 (North of Fredericksted, St. Croix, Virgin Islands); Boyko & Cordeiro, 2001: 24.

Bursa granularis cubaniana—Abbott, 1974: 167, pl. 7, fig. 1781 (as *B. granularis* in caption); Rios, 1975: 81, pl. 23, fig. 331; Finlay, 1978: 149; Bandel, 1984: 102, pl. 10, figs 3, 8; Diaz & Gotting, 1988: 156; Diaz, 1990: 19; Diaz & Puyana, 1994: 174, fig. 650; Redfern, 2001: 58, pl. 29, fig. 247 A, B. Nappo *et al.*, 2014: pl. 5, figs 2, 3, pl. 6, figs 1–3, pl. 7, fig. 2.

Bursa (*Colubrellina*) *granularis cubaniana*—Rios, 1975: 81, pl. 23, fig. 331; Beu, 1985: 64; Cossignani, 1994: 78.

Bursa (*Colubrellina*) *granularia* (sic) *cubaniana*—Rios, 1994: 92, pl. 31, fig. 365.

Bursa granularis—Leal, 1991: 111, pl. 16, figs C, D; Lipe & Abbott, 1991: 14-15, illus.; Beu 2010: 48, pl. 3, figs 1, 3; Redfern, 2013: 83, fig. 241 (not Röding, 1798).

Bursa (*Colubrellina*) *granularia* (sic)—Rios, 1985: 79, pl. 28, fig. 347 (not Röding, 1798).

Gyrineum affine—Dall, 1903: 132 (not Broderip, 1833).

Ranella (*Bursa*) *affinis*—Trechmann, 1933: 39 (not Broderip, 1833).

Material examined: Supplementary Material Table S1.

Diagnosis: Shell biconic, varices strictly aligned, varices abaperturally deeply excavated, relatively numerous nodules on all primary cords, particularly large one on P1, beige stripes following primary cords, OLDF: 3,5,4,3 or 3,5,5,4 in particularly large specimens.

Description: Protoconch similar to other species in the complex (see above). Teleoconch tall, relatively narrow with 4–5 whorls (up to 6 for larger specimens). H about 50 mm, up to 60 mm. Spire angle 55°. Aperture comprising 50% of W. Last whorl comprising 47% of H. Varices strictly aligned for most of spire height, becoming slightly displaced only on 1 or 2 last whorls in large specimens. Abapertural face of each varix deeply excavated, buttressed by spiral cords. Spiral ornamentation much reduced compared to *B. granularis* and *B. affinis*. P1, 3 and 5 much more pronounced than others. Primary cords (IP included) bearing 4 rather large nodules, with small nodules overlying large ones in large specimens. Secondary cords not visible on shell after whorl 1, except slightly visible at intersections with varices. Nodules on varices where they meet P1 angulating shoulder, not as sharp as on *B. affinis*. Apertural lip well flared, bearing numerous prominent, narrow transverse internal denticles; ID2 single, ID1 bifid, trifurcated in large specimens, D1 bifid, trifurcated in large specimens, D2 bifid, D3 bifid, trifurcated in large specimens, D4 bifid, D5 single, bifid in large specimens, D6 bifid (Fig. 5). Shells bearing distinctive beige-cream bands following spiral cords.

Distribution and habitat: *Bursa cubaniana* occurs in the western Atlantic (Fig. 1; Rosenberg, 2009), where it is recorded from southeastern Florida (Abbott, 1974; this study), Texas and Louisiana (Garcia, 1999) westwards to Mexico, Costa Rica, Panama and Colombia (Massemín *et al.*, 2009), the Bahamas (Redfern, 2013), Guadeloupe (this study), Jamaica, Cuba and St Lucia (d'Orbigny, 1841) south to French Guiana (Massemín *et al.*, 2009), Bahia and Pernambuco, Brazil (Matthews, 1968; Rios, 1985, 1994; Mello & Perrier 1986). In the eastern Atlantic, it has been recorded only from the Cape Verde Islands, but this record is unconfirmed (Rolán, 2005).

Remarks: The type locality of *B. cubaniana* is Cuba and there is only one MOTU in the Caribbean region (Fig. 1), so the name *B. cubaniana* is unambiguously attributed to this MOTU.

***Bursa elisabettae* Nappo *et al.* 2014**

(Fig. 6E–G, M)

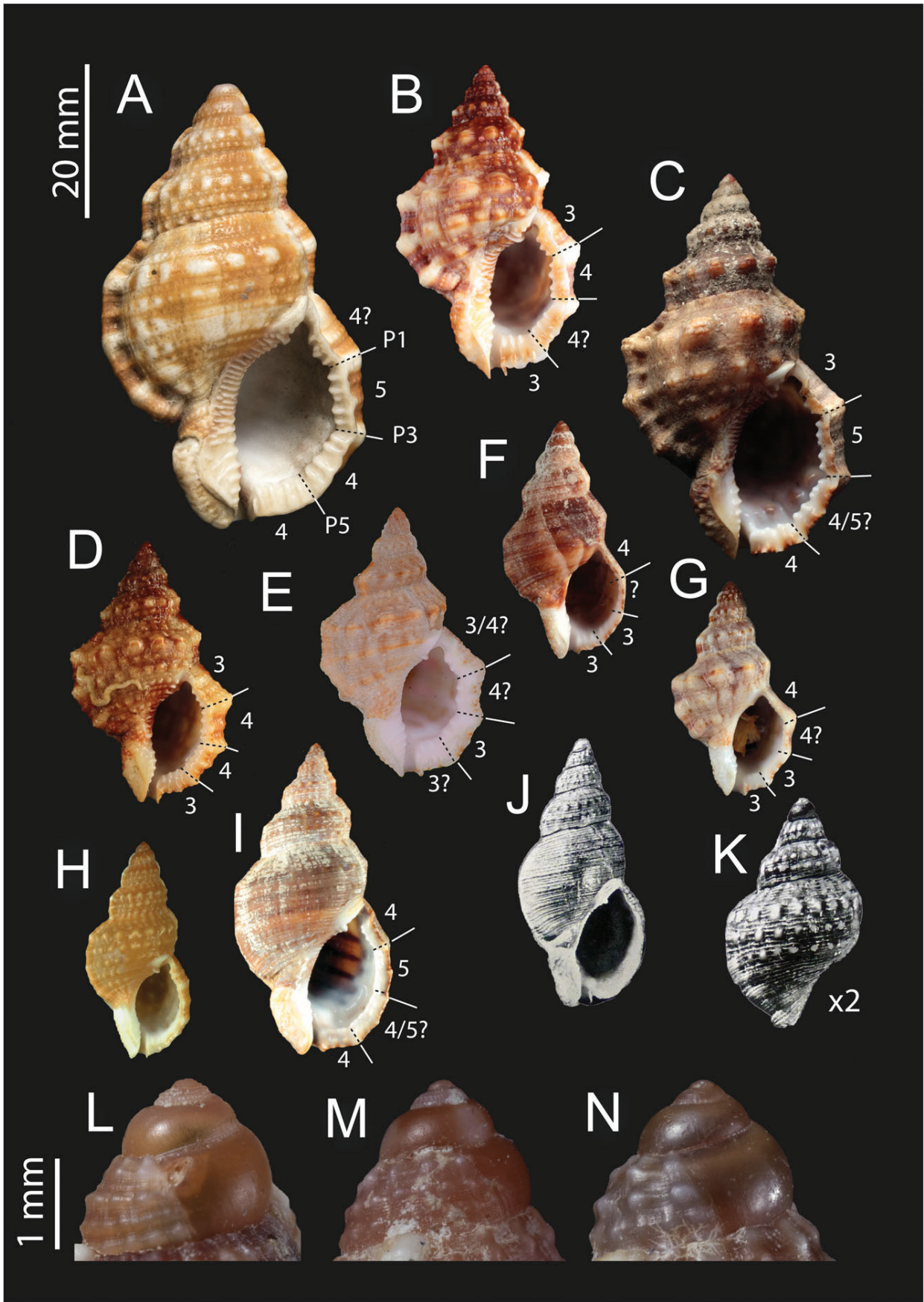
Bursa granularis elisabettae Nappo *et al.* 2014: 5, pl. 1, figs 1–3, pl. 2, figs 1–3, pl. 3, figs 1–3 (Flinders Bay, Cape Leeuwin, southern Western Australia, 12 m, MAC.ML 1536).

Bursa cf. *nodosa*—Bozzetti, 1991: 1, fig. 1 (not Borson, 1823).

Bursa granularis "affinis" form—Wilson, 1993: pl. 43, fig. 12 (not Röding, 1798).

Material examined: Supplementary Material Table S1.

Diagnosis: Shell biconic, varices strictly aligned, varices abaperturally rather excavated, nodules weak on first primary cords, brown



bands following primary cords, outer lip denticles small, OLF: 4,3,3,3 or 4,3,2,3 in large specimens.

Description: Protoconch similar to that of other species in the complex (see above). Teleoconch tall, relatively narrow, with 4–5 whorls, H about 50 mm. Spire angle 45°. Aperture comprising 52% of W. Last whorl comprising 52% of H. Varices strictly aligned, although low and indistinct in some specimens. Spiral ornamentation very reduced to absent in some specimens. Only primary cords P1, 3 and 5 visible; each bearing 4 nodules between 2 varices, especially visible on P1. Secondary cords lacking. Nodules on varices where they meet P1 angulating shoulder, although not as sharply as in *B. affinis*. Apertural lip well flared, bearing numerous prominent, narrow transverse internal denticles; ID2-1 bifid, D1 single, D2 bifid, D3 single, D4 bifid, merged in large specimens, D5 single, D6 bifid (Fig. 5).

Distribution and habitat: The known distribution of *B. elisabettae* is restricted to southwestern Western Australia, in shallow water.

Remarks: *Bursa elisabettae* is the last species to have been described in the complex. There is only one MOTU occurring around Cape Leeuwin, southwestern Australia (the type locality) to which we therefore attribute the name *B. elisabettae*. The possible occurrence of *B. elisabettae* in South Africa is discussed below.

DISCUSSION

Bursa granularis is considered to be easy to identify, although it is highly variable, hence the thirteen names it received through history and the innumerable subsequent references in the literature. Previous works failed to provide a comprehensive characterization of such variability, leading to the aggregation of the whole morphological spectrum under the single name *B. granularis* (Beu, 1998, 2005, 2010). An integrated taxonomic approach based on extensive sampling (geographical, bathymetrical and type locality of many nominal taxa), coupled with a detailed analysis of the shell variability and the sequencing of the *cox1* gene, analysed with two methods (ABGD and GMYC), revealed four groups within the *B. granularis* complex, here considered to be distinct species. However, our species hypotheses are supported by one gene and morphological data only; an independent genetic marker would help to determine whether the partition obtained with the *cox1* gene corresponds to the species limits.

Among the four delimited species, members of one pair, *B. granularis* and *B. affinis*, are difficult to distinguish morphologically and without molecular evidence there is little to suggest that they are separate species. Furthermore, intraspecific morphological variability sometimes exceeds interspecific disparity, particularly in shell coloration; the pinkish coloration of the first whorls, formerly used to discriminate *B. affinis* (see Reeve, 1844), can be found in specimens of both species and some specimens present the banded pattern usually attributed to *B. cubaniana* (for which this pattern is stable). Nevertheless, we were able to discriminate this pair of species according to their morphology through the detailed observation of the spiral ornamentation of the shells. The importance of

such ornamentation for systematics has previously been recognized in e.g. Muricidae (Merle, Garrigues & Pointier, 2001; Merle & Houart, 2003; Merle, 2005), Mathildidae (Bieler, 1995) and Calliostomatidae (Marshall, 1995). Although Muricidae and Bursidae are not closely related, they have a similar morphological organization of the sculptural elements and the methodology applies as well to Bursidae as to Muricidae. Other morphological characters, e.g. apertural colour, spire height and sculptural prominence (i.e. considering one cord at a time), are of very little value.

Other anatomical characters and radulae were not considered in the present study, but may perhaps provide useful information. Abbott (1958) pointed out differences between *B. cubaniana* and *B. granularis* in denticle size and number on the central teeth (Abbott, 1958: figs 1d, 2c), but radular studies are often based on too small a sample size and their results may not be significant. For good pictures of the radula of *B. granularis* see Barkalova, Fedosov & Kantor (2016) and for insight on the general anatomy of *B. cubaniana* see Simone (2011).

The integrated taxonomic approach followed here was thus effective to propose robust species hypotheses. It is yet another example of the value of molecular characters when species cannot readily be distinguished morphologically, a common pattern in gastropods (e.g. Duda *et al.*, 2008; Puillandre *et al.*, 2012b). However, if proposing putative species using DNA sequences is now a common practice, linking the species hypotheses to available names attached to nonsequenced name-bearing types remains daunting. Indeed, all the species in the *B. granularis* complex were described based on shell characters only, including *B. elisabettae*, which was described as recently as 2014. More generally, most known species of molluscs were described before the molecular era and the application of historical names remains based on non-sequenced, sometimes problematical, dry material (Bouchet & Strong, 2010).

Because we did not sample the entire distribution area of the complex, additional species may be recognized in the future. *Bursa alfredensis* and *B. koviensis* (Fig. 6I–K, N) were both described from Port Alfred, South Africa, and are the only two names that we have refrained from associating with one of the MOTUs of this study. The types of both display a loss of fine sculpture early in ontogeny. The adult South African specimen in Fig. 6I (for which we have no molecular data) certainly corresponds to the nominal species described as *B. koviensis* by Turton (1932). This loss of ornamentation resembles the one displayed by *B. cubaniana*, but even more by *B. elisabettae*. If *B. elisabettae*, *B. alfredensis* and *B. koviensis* were found to be a single species, then *B. koviensis* or *B. alfredensis*, both names established in 1932, would be the valid name. Such a scenario would be consistent with a Pleistocene colonization of the Caribbean from the Indian Ocean around South Africa and which corresponds to the stratigraphic distribution of *B. cubaniana* in the region (Beu, 2010). This scenario was discussed by Vermeij & Rosenberg (1993) for 17 Indo-West-Pacific species.

South African collectors (R. Aiken, personal communication) have also drawn our attention to a small form of *B. granularis* dredged from ‘deep water’ (Fig. 6H). We have not seen this variation anywhere else and the deep-water (100 m?) habitat is very unusual for *B. granularis* s. s., which has only exceptionally been

Figure 6. Shells of *Bursa granularis* complex. **A–D.** *Bursa cubaniana* (d’Orbigny, 1841). **A.** NHMUK 1854.10.4.412, holotype of *Ranella cubaniana* d’Orbigny, 1841, St Lucie, West Indies, H 51.7 mm. **B.** IM-2009–23406, Pointe Antisu, Port Louis, Guadeloupe, H 41 mm. **C.** IM-2013–20184, KARUBENTHOS 2012 (Guadeloupe), stn GM09, H 51 mm. **D.** UF 437626, UF 2010 (Florida, USA), Tennessee Reef, Monroe Co., FL, H: 35 mm. **E–G.** *Bursa elisabettae* Nappo *et al.* 2014. **E.** MAC.ML 1536, holotype of *Bursa granularis elisabettae* Nappo *et al.* 2014, Flinders Bay, Cape Leeuwin, south Western Australia, H 35 mm. **F.** IM-2009–23319, WESTERN AUSTRALIA 2011, stn WA17, H 31 mm. **G.** IM-2009–23313, WESTERN AUSTRALIA 2011, stn WB28, H: 28 mm. **H.** ‘Deep-sea’ form of South African *Bursa granularis* MNHN ex coll. Aiken, off Richard Bay, South Africa, H 24.8 mm. **I.** *Bursa* aff. *koviensis* MNHN ex coll. Aiken, Coffee Bay, South Africa, H 40 mm. **J.** Holotype of *Bursa koviensis* Turton, 1932, H 35 mm (reproduced from Turton, 1932). **K.** Holotype of *Bursa alfredensis* Turton, 1932, H 15 mm (reproduced from Turton, 1932). **L.** IM-2013–20247, *Bursa cubaniana* protoconch detail. **M.** IM-2009–23313, *Bursa elisabettae* protoconch detail. **N.** MNHN ex coll. Aiken, *Bursa* aff. *koviensis* protoconch detail. Abbreviations: P1, P3, P5, preponderant primary cords; numbers indicates the number of denticles.

dredged alive in 87–90 m (MNHN IM-2009–5148, sequenced). The status of this small, South African, deep-water form will have to be evaluated by sequencing.

Recent work (Nappo *et al.*, 2014) suggested that *B. granularis*, *B. cubaniana* and *B. elisabetae* were subspecies of *B. granularis*. We rank them here as full species. Firstly, as we showed above, the two species-pairs *B. granularis*–*affinis* and *B. cubaniana*–*elisabetae* have very distinct distributions and inferred biogeographical histories. Secondly, Castelin *et al.* (2012) demonstrated that the pair *B. granularis*–*affinis* diverged from each other over 11 Mya (the distance between *B. cubaniana* and *B. elisabetae* suggests a comparable time of divergence, although this was not tested). The divergence between the two pairs is necessarily older.

The estimated 11 Mya divergence between *B. granularis* and *B. affinis* corresponds to the Seravallian/Tortonian stages of the Miocene, a period of particularly low sea-level stand (around 100 m lower than today; Scotese, 2014). Australia, Papua New Guinea, Indonesia, Japan and the Philippines were all connected to Eurasia by a series of land bridges or very shallow seas, disrupting marine connectivity between the Pacific and Indian Oceans. Given the sympatric distribution of *B. granularis* and *B. affinis* in an area extending from Japan to eastern Australia through the Philippines, Papua New Guinea and New Caledonia, this speciation event could represent an example of allopatric speciation with secondary contact following recolonization. However, because our results are based only on mitochondrial data, we cannot rule out an alternative scenario in which both groups are still genetically connected. In this latter scenario, the pattern observed with the *cox1* gene would again be the result of an ancient allopatric divergence, but with the secondary contact being too recent to homogenize the two mitochondrial gene pools. Although the large number of sequenced specimens and the high genetic divergence between *B. affinis* and *B. granularis* do not support this hypothesis, nuclear data would help reject one of these scenarios.

One of the main general implications of the systematic revision proposed here is that larval duration alone does not explain geographical distributions. Other factors, such as availability of suitable habitats, may limit distribution areas regardless of dispersal capacity. A striking example is *Fusitriton oregonensis*; it is the only species for which the larval duration has been directly measured (although under laboratory conditions) and estimated at 5 years (Strathmann & Strathmann, 2007), but its distribution area is limited to the North Pacific from central Japan to California, extending south to off Panama in deep water (Smith, 1970).

While the distribution areas of at least two of the members of the *B. granularis* complex are indeed large, we have shown that the range of the classic taxonomic concept of ‘*B. granularis*’ was greatly overestimated. It is not unlikely that the same pattern—one very variable species with an extremely large distribution being in fact several species with smaller distributions—will be found in other tonnoideans. Considering only the Bursidae, *B. corrugata* (Perry, 1811) (with eight subjective synonyms and recorded from Eastern Pacific and Eastern Atlantic Oceans and Caribbean), *B. ranelloides* (Reeve, 1844) (with seven subjective synonyms, recorded from Indian and Atlantic Oceans, and Japan and Hawaii in Pacific) and *B. rhodostoma* (G.B. Sowerby II, 1835) (with six subjective synonyms, recorded from Indo-Pacific and Caribbean) are good candidates for integrative taxonomy-based revision.

However, achieving a representative sampling for molecular taxonomy is becoming increasingly difficult, considering the multiplicity of permits necessitated by sampling distribution areas that span numerous countries. The future will tell whether Article 8a of the Nagoya Protocol to the Convention of Biological Diversity (encouraging the Parties to the protocol to “create conditions to promote and encourage research [...] through simplified measures on access for noncommercial research purposes”) will reverse the trend (Bouchet *et al.*, 2016). For the time being, compliance with regulations on ‘Access and Benefit Sharing’ and ‘Prior Informed

Consent’ is a formidable obstacle to academic researchers investigating the limits and names of species.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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Supplementary material of: One for each ocean: revision of the *Bursa granularis* (Röding, 1798) species complex

| Species | Museum ID number | Expedition | Location | Depth (m) | Station | Latitude | Longitude | BOLD ID | Genbank COI |
|----------------------|--------------------|-------------------------|---|-----------|------------|----------|-----------|------------|-------------|
| <i>Bursa affinis</i> | MNHN IM-2007-33056 | SANTO 2006 | Vanuatu | 11 | NR08 | -15,60 | 167,12 | TONO140-17 | MF124239 |
| <i>Bursa affinis</i> | MNHN IM-2007-43037 | SANTO 2006 | Vanuatu | 6 | DR84 | -15,72 | 167,25 | TONO069-12 | JX241347 |
| <i>Bursa affinis</i> | MNHN IM-2007-43039 | PANGLAO 2004 | Philippines | 2 | R24 | 9,63 | 123,78 | TONO080-12 | JX241349 |
| <i>Bursa affinis</i> | MNHN IM-2007-43042 | SANTO 2006 | Vanuatu | 2-30 | DR03 | -15,52 | 167,26 | TONO058-12 | JX241351 |
| <i>Bursa affinis</i> | MNHN IM-2007-43056 | SANTO 2006 | Vanuatu | | VM02 | -15,58 | 167,04 | TONO059-12 | JX241363 |
| <i>Bursa affinis</i> | MNHN IM-2007-43059 | SANTO 2006 | Vanuatu | 1-42 | FR09 | -15,54 | 167,20 | TONO018-12 | JX241366 |
| <i>Bursa affinis</i> | MNHN IM-2007-43060 | SANTO 2006 | Vanuatu | | VM02 | -15,58 | 167,04 | TONO098-12 | JX241367 |
| <i>Bursa affinis</i> | MNHN IM-2007-43069 | SANTO 2006 | Vanuatu | | VM46 | -15,58 | 167,21 | TONO006-12 | JX241374 |
| <i>Bursa affinis</i> | MNHN IM-2013-11041 | PAPUA NIUGINI 2012 | Papua-New-Guinea | 22 | PR08 | -5,17 | 145,84 | TONO128-17 | MF124209 |
| <i>Bursa affinis</i> | MNHN IM-2013-11468 | PAPUA NIUGINI 2012 | Papua-New-Guinea | 2 | PFM01 | -5,18 | 145,80 | TONO139-17 | MF124191 |
| <i>Bursa affinis</i> | MNHN IM-2013-11598 | PAPUA NIUGINI 2012 | Papua-New-Guinea | 1 | PM12 | -5,00 | 145,79 | TONO133-17 | MF124217 |
| <i>Bursa affinis</i> | MNHN IM-2013-12827 | PAPUA NIUGINI 2012 | Papua-New-Guinea | 7 | PR27 | -5,08 | 145,81 | TONO134-17 | MF124248 |
| <i>Bursa affinis</i> | MNHN IM-2013-12981 | PAPUA NIUGINI 2012 | Papua-New-Guinea | | PR29 | -5,09 | 145,82 | TONO135-17 | MF124228 |
| <i>Bursa affinis</i> | MNHN IM-2013-14733 | PAPUA NIUGINI 2012 | Papua-New-Guinea | 0-1 | PM12 | -5,00 | 145,79 | TONO136-17 | MF124213 |
| <i>Bursa affinis</i> | MNHN IM-2013-52997 | Pakaihi I Te Moana 2012 | Marquesas Islands | | MQ11-II-01 | -32,97 | -140,23 | TONO145-17 | MF124220 |
| <i>Bursa affinis</i> | MNHN IM-2013-52998 | Pakaihi I Te Moana 2012 | Marquesas Islands | | MQ11-II-01 | -32,97 | -140,23 | TONO146-17 | MF124183 |
| <i>Bursa affinis</i> | UF_506835 | Vanuatu UF 2005 | Vanuatu, Sanma Province Aore island, Aore point | 30-40 | | 15,53 | 167,24 | TONO183-17 | MF124187 |
| <i>Bursa affinis</i> | UF_368508 | Taiwan UF 2005 | Taiwan, Kenting National park; Wanlitung fringing reef | 0-1 | | 21,93 | 120,82 | TONO153-17 | MF124219 |
| <i>Bursa affinis</i> | UF_506838 | Taiwan UF 2005 | Taiwan, Kenting National park; Wanlitung fringing reef | 0-1 | | 21,93 | 120,82 | TONO186-17 | MF124214 |
| <i>Bursa affinis</i> | UF_368583 | Vanuatu UF 2005 | Vanuatu, Shefa province, Epi island, Southern Lamén Bay | 1-3 | | 16,60 | 168,17 | TONO154-17 | MF124200 |
| <i>Bursa affinis</i> | UF_506841 | Vanuatu UF 2005 | Vanuatu, Shefa province, Epi Island, southern Lamén Bay | 1-3 | | 16,60 | 168,17 | TONO189-17 | MF124229 |

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|------------------------|--------------------|--------------------------|---|-------|------|----------|----------|------------|----------|
| <i>Bursa affinis</i> | UF_420761 | Micronesia UF 2008 | Federate states of Micronesia, Ksrae lelu, reef flat next to N side of Lelu Island | 0-1 | | 5,33 | 163,03 | TONO155-17 | MF124196 |
| <i>Bursa affinis</i> | UF_422831 | Micronesia UF 2008 | Federate states of Micronesia, Ksrae lelu, reef flat next to N side of Lelu Island | 0-1 | | 5,33 | 163,03 | TONO156-17 | MF124205 |
| <i>Bursa affinis</i> | UF_422918 | Micronesia UF 2008 | Federated states of Micronesia, Kosrae Letu, in front of Nautilus hotel | 0-0.5 | | 5,34 | 163,02 | TONO157-17 | MF124236 |
| <i>Bursa affinis</i> | UF_423031 | Marshall islands UF 2008 | Marshall Islands, Majuro Atoll, Eneko channel, W side of the island | 0 | | 7,1493 | 171,2829 | TONO158-17 | MF124232 |
| <i>Bursa affinis</i> | UF_423039 | Mariana island UF 2008 | Mariana Islands, Saipan Islands, Lau Lau | | | | | TONO159-17 | MF124231 |
| <i>Bursa affinis</i> | UF_445316 | Guam UF 2010 | Guam, Piti, Tepungan Channel, lagoon tunnel with constant high flow, under rock in tunnel, on cave wall | 1-4 | | 13,4649 | 144,6872 | TONO168-17 | MF124189 |
| <i>Bursa affinis</i> | UF_445789 | Japan UF 2010 | Japan, Okinawa Prefecture, Okinawa Island, White Beach | 0-4 | | 26,2928 | 127,9174 | TONO169-17 | MF124221 |
| <i>Bursa affinis</i> | UF_476657 | New Caledonia UF 2013 | France, New Caledonia, Huon atoll, N tip | 0-1 | | -17,9121 | 162,8987 | TONO177-17 | MF124218 |
| <i>Bursa affinis</i> | UF_493033 | Philippines UF 2015 | Philippines, Oriental Mindoro province, Minoro, Puerto Galera, The Boulders dive site | 5-20 | | 13,51 | 120,9824 | TONO179-17 | MF124230 |
| <i>Bursa cubaniana</i> | MNHN IM-2013-19491 | KARUBENTHOS 2012 | Guadeloupe | 16 | GR37 | 16,50 | -61,48 | TONO142-17 | MF124250 |
| <i>Bursa cubaniana</i> | MNHN IM-2013-19496 | KARUBENTHOS 2012 | Guadeloupe | 9 | GR33 | 16,38 | -61,52 | TONO138-17 | MF124199 |
| <i>Bursa cubaniana</i> | MNHN IM-2013-19596 | KARUBENTHOS 2012 | Guadeloupe | 1 | GM09 | 16,09 | -61,77 | TONO131-17 | MF124201 |
| <i>Bursa cubaniana</i> | MNHN IM-2013-20121 | KARUBENTHOS 2012 | Guadeloupe | 1 | GM07 | 16,17 | -61,78 | TONO129-17 | MF124185 |
| <i>Bursa cubaniana</i> | MNHN IM-2013-20184 | KARUBENTHOS 2012 | Guadeloupe | 1 | GM09 | 16,09 | -61,77 | TONO137-17 | MF124190 |
| <i>Bursa cubaniana</i> | MNHN IM-2013-20247 | KARUBENTHOS 2012 | Guadeloupe | 11 | GR13 | 16,13 | -61,78 | TONO130-17 | MF124204 |
| <i>Bursa cubaniana</i> | MNHN IM-2009-23406 | (Hors campagne INVMAR) | Guadeloupe, Port-Louis, Pointe Antisue | 12 | | | | TONO127-17 | MF124211 |
| <i>Bursa cubaniana</i> | MNHN IM-2013-8684 | KARUBENTHOS 2012 | Guadeloupe | 15 | GR49 | 16,16 | -61,13 | TONO132-17 | MF124224 |

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|--------------------------|--------------------|------------------------|---|-------|--------|----------|----------|------------|----------|
| <i>Bursa cubaniana</i> | UF_437625 | Florida UF 2010 | USA, Florida, Moneroc county, Florida Keys, Tennessee Reef | | | 24,7651 | -80,7542 | TONO166-17 | MF124241 |
| <i>Bursa cubaniana</i> | UF_437626 | Florida UF 2010 | USA, Florida, Moneroc county, Florida Keys, Tennessee Reef | 6 | | 24,7651 | -80,7542 | TONO167-17 | MF124210 |
| <i>Bursa elisabettae</i> | MNHN IM-2009-23312 | WESTERN AUSTRALIA 2011 | Australia | 4-12 | WA20 | -35,08 | 117,97 | TONO143-17 | MF124238 |
| <i>Bursa elisabettae</i> | MNHN IM-2009-23319 | WESTERN AUSTRALIA 2011 | Australia | 20 | WA17 | -35,11 | 118,02 | TONO144-17 | MF124184 |
| <i>Bursa elisabettae</i> | MNHN IM-2009-23322 | WESTERN AUSTRALIA 2011 | Australia | 4-12 | WA20 | -35,08 | 117,97 | TONO126-17 | MF124233 |
| <i>Bursa granularis</i> | MNHN IM-2007-33097 | SANTO 2006 | Vanuatu | 1 | VM61 | -15,48 | 167,26 | TONO123-17 | MF124192 |
| <i>Bursa granularis</i> | MNHN IM-2007-33115 | PANGLAO 2004 | Philippines | 3 | M7 | 9,60 | 123,75 | TONO141-17 | MF124186 |
| <i>Bursa granularis</i> | MNHN IM-2007-43049 | SANTO 2006 | Vanuatu | 1 | VM61 | -15,48 | 167,26 | TONO007-12 | JX241357 |
| <i>Bursa granularis</i> | MNHN IM-2007-43065 | PANGLAO 2004 | Philippines | 0-2 | M5 | 9,59 | 123,74 | TONO122-17 | MF124216 |
| <i>Bursa granularis</i> | MNHN IM-2007-43070 | SANTO 2006 | Vanuatu | 6 | DB83 | -15,72 | 167,25 | TONO017-12 | JX241375 |
| <i>Bursa granularis</i> | MNHN IM-2007-43071 | SANTO 2006 | Vanuatu | | VM62 | -15,48 | 167,26 | TONO019-12 | JX241376 |
| <i>Bursa granularis</i> | MNHN IM-2009-23292 | INHACA 2011 | Mozambique | 1 | MM2 | -26,04 | 32,89 | TONO124-17 | MF124212 |
| <i>Bursa granularis</i> | MNHN IM-2009-5148 | MAINBAZA 2009 | Mozambique | 87-90 | DW3168 | -26,20 | 35,05 | TONO057-12 | JX241427 |
| <i>Bursa granularis</i> | MNHN IM-2009-23302 | INHACA 2011 | Mozambique | 17-19 | MR4 | -26,11 | 32,97 | TONO125-17 | MF124240 |
| <i>Bursa granularis</i> | MNHN IM-2013-53041 | INHACA 2011 | Mozambique | 12 | MB6 | -25,98 | 32,91 | TONO147-17 | MF124226 |
| <i>Bursa granularis</i> | Br-NT-855 | NT-2014 | Viet-Nam, Nok id., Nha Trang bay | 10-20 | | | | TONO148-17 | MF124225 |
| <i>Bursa granularis</i> | Br-NT-856 | NT-2014 | Viet-Nam, Mun id., Nha Trang bay | 6-22 | | 12,16 | 109,31 | TONO149-17 | MF124223 |
| <i>Bursa granularis</i> | UF_367628 | Vanuatu UF 2005 | Vanuatu, Shefa Province Mapuna bay, NE of Epi Island | | | 16,59 | 168,21 | TONO150-17 | MF124197 |
| <i>Bursa granularis</i> | UF_368022 | Vanuatu UF 2005 | Vanuatu, Sanma Province Aore island, Million Dollar point | 30-40 | | 15,53 | 167,25 | TONO151-17 | MF124195 |
| <i>Bursa granularis</i> | UF_368144 | Vanuatu UF 2005 | Vanuatu, Sanma Province Aore island, Aore point | 30-40 | | 15,53 | 167,24 | TONO152-17 | MF124242 |
| <i>Bursa granularis</i> | UF_506834 | Saudi Arabia UF 2013 | Saudi Arabia, Thuwal | 2-20 | | 22,27 | 39,05 | TONO182-17 | MF124194 |
| <i>Bursa granularis</i> | UF_423363 | Madagascar UF 2008 | Madagascar, Nosy Be, W of Hellville | 0-10 | | -13,4156 | 48,2465 | TONO160-17 | MF124198 |
| <i>Bursa granularis</i> | UF_506833 | Madagascar UF 2008 | Madagascar, Nosy Be, W of Hellville | 0-10 | | -13,4156 | 48,2465 | TONO181-17 | MF124244 |
| <i>Bursa granularis</i> | UF_423371 | Madagascar UF 2008 | Madagascar, Nosy Tanikely, off S side | 0-20 | | -13,4789 | 48,2366 | TONO161-17 | MF124245 |
| <i>Bursa granularis</i> | UF_423773 | Madagascar UF 2008 | Madagascar, Nosy Tanikely, off S side | 0-20 | | -13,4789 | 48,2366 | TONO162-17 | MF124235 |

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|--------------------------|--------------------|---------------------------|--|---------|---------|----------|----------|------------|----------|
| <i>Bursa granularis</i> | UF_506839 | Madagascar UF 2008 | Madagascar, Nosy Tanikely, off S side | 0-20 | | -13,4789 | 48,2366 | TONO187-17 | MF124237 |
| <i>Bursa granularis</i> | UF_423792 | Madagascar UF 2008 | Madagascar, Nosy Komba, NW side | 0-12 | | -13,4462 | 48,3316 | TONO163-17 | MF124234 |
| <i>Bursa granularis</i> | UF_435487 | Western Australia UF 2009 | Australia, Western Australia, Ningaloo Reef, Norwegian Bommies | 5-6 | | -22,6232 | 113,6532 | TONO164-17 | MF124222 |
| <i>Bursa granularis</i> | UF_435515 | Western Australia UF 2009 | Australia, Western Australia, Ningaloo reef, Wreck Zirv reef front, in <i>Pocillopora</i> head | 15 | | -22,6083 | 113,6249 | TONO165-17 | MF124249 |
| <i>Bursa granularis</i> | UF_445838 | Japan UF 2010 | Japan, Okinawa prefecture, Okinawa Island, Okinawa, Cape Zanpa | 0-40 | | 26,4416 | 127,7127 | TONO170-17 | MF124247 |
| <i>Bursa granularis</i> | UF_456015 | Saudi Arabia UF 2013 | Saudi Arabia, Thuwal | 2-20 | | 22,2741 | 39,0512 | TONO171-17 | MF124193 |
| <i>Bursa granularis</i> | UF_463618 | Saudi Arabia UF 2013 | Saudi Arabia, Farasan Banks, Pelican (Ablo) Island | | | 18,6595 | 40,827 | TONO172-17 | MF124208 |
| <i>Bursa granularis</i> | UF_506836 | Saudi Arabia UF 2013 | Saudi Arabia, Farasan Banks, Pelican (Ablo) Island | | | 18,6595 | 40,827 | TONO184-17 | MF124246 |
| <i>Bursa granularis</i> | UF_506837 | Saudi Arabia UF 2013 | Saudi Arabia, Farasan Banks, Pelican (Ablo) Island | | | 18,6595 | 40,827 | TONO185-17 | MF124227 |
| <i>Bursa granularis</i> | UF_473471 | Saudi Arabia UF 2013 | Saudi Arabia Island near Jaz'air Sila | 10-30 | | 27,651 | 35,2832 | TONO173-17 | MF124206 |
| <i>Bursa granularis</i> | UF_473520 | Saudi Arabia UF 2013 | Saudi Arabia, Al Wajj, Shaybarah | 0-3 | | 25,3675 | 36,9097 | TONO174-17 | MF124215 |
| <i>Bursa granularis</i> | UF_473605 | Saudi Arabia UF 2013 | Saudi Arabia, Gulf of Aqaba, Magna Coast Guard | 0-2 | | 28,4039 | 34,7407 | TONO175-17 | MF124203 |
| <i>Bursa granularis</i> | UF_506840 | Saudi Arabia UF 2013 | Saudi Arabia, Gulf of Aqaba, Magna Coast Guard | 0-3 | | 28,4039 | 34,7407 | TONO188-17 | MF124243 |
| <i>Bursa granularis</i> | UF_476394 | Saudi Arabia UF 2013 | Saudi Arabia Island near Ras Al-Ubayd | 0-1 | | 26,7398 | 36,0426 | TONO176-17 | MF124202 |
| <i>Bursa granularis</i> | UF_476726 | New Caledonia UF 2013 | France, New Caledonia, Surprise Island | 0-2 | | -18,4879 | 163,0955 | TONO178-17 | MF124207 |
| <i>Bursa granularis</i> | UF_502562 | Philippines UF 2015 | Philippines, Batangas province Verde Island Channel, Mabini, Wside Bonito Island | 20-25 | | 13,6305 | 120,9472 | TONO180-17 | MF124188 |
| <i>Bursa latitudo</i> | MNHN IM-2007-43589 | TERRASSES | New Caledonia | 410-430 | DW 3102 | -22,98 | 168,38 | TONO100-12 | JX241414 |
| <i>Bursina ignobilis</i> | MNHN IM-2007-43052 | SANTO 2006 | Vanuatu | 78-91 | EP22 | -15,62 | 167,10 | TONO081-12 | JX241360 |

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|---|---------------------|------------------------|---|--------|------|--------|---------|------------|----------|
| <i>Tutufa bufo</i> | MNHN IM-2007-43036 | PANGLAO 2004 | Philippines | 100 | P3 | 9,52 | 123,68 | TONO094-12 | JX241346 |
| Supplementary material (not sequenced) | | | | | | | | | |
| <i>Bursa cubaniana</i> | MNHN IM-2013-8684 | KARUBENTHOS 2012 | Guadeloupe | 15 | GR49 | 16,16 | -61,13 | | |
| <i>Bursa elisabettae</i> | MNHN IM-2009-23321 | WESTERN AUSTRALIA 2011 | Australia | 4-12 | WA20 | -35,08 | 117,97 | | |
| <i>Bursa elisabettae</i> | MNHN IM-2009-23313 | WESTERN AUSTRALIA 2011 | Australia | 0-15 | WB28 | -33,67 | 114,94 | | |
| <i>Bursa granularis</i> | MNHN ex coll. Aiken | | Estern South Africa (Probably Natal) | | | | | | |
| <i>Bursa alfredensis</i> | MNHN ex coll. Aiken | - | Coffe Bay, South Africa | dived | | | | | |
| <i>Bursa granularis</i> | MNHN ex coll. Aiken | - | Richard Bay, South Africa | dredge | | | | | |
| <i>Bursa affinis</i> | UF_414132 | Hawaii UF 2006 | Hawaii, French frigate shoal | 10 | | 23,77 | -166,26 | | |

LE CHOIX DE L'APPROCHE MITOGENOMIQUE POUR AMELIORER LA PHYLOGENIE DES BURSIDAE.

Les choix des données est, comme toujours, dépendant de la question scientifique. Ici l'objectif est de retracer les relations de parenté entre les espèces et les groupes d'espèces auxquelles on attribue le rang de genres. La seule étude précédemment menée en partie dans ce but est celle de Castelin et al. 2012. Elle a montré qu'une approche multi gènes standard (deux gènes mitochondriaux, *cox-1* et *12S*, et un nucléaire : *28S*) était insuffisante pour établir avec certitude ces relations. Cependant l'irrésolution n'était pas complète, des liens forts entre *Bursa* et *Dulcerana* d'une part et *Korrigania* et *Bufo*+*Bursina* d'autre part avaient été mises en évidence avec un très fort support statistique aussi bien en approche Bayésienne qu'en maximum de vraisemblance. Il en était de même, avec des supports plus faibles, pour le clade contenant tous ces genres. Cela laissait supposer qu'obtenir une meilleure résolution ne nécessiterait pas nécessairement l'addition de beaucoup plus de caractères. C'est principalement pour cette raison que j'ai décidé en concertation avec Nicolas Puillandre de passer à une échelle mitogénomique pour retracer les relations de parenté des Bursidae. Cela a été également motivé par le fait que le ratio difficulté du traitement informatique (lié à l'assemblage des reads) / quantité de données était relativement faible par rapport à d'autres méthodes (assemblage de transcriptomes par exemple) et aussi parce qu'un mitogénome assemblé dans des conditions optimales à un coût inférieur à 10 €

Le choix des Long Range PCR

Le choix de cette méthode d'amplification pré-séquençage a été fait sur les conseils d'Agnès Dettai. Elle a l'avantage que le protocole est strictement identique à celui d'une PCR standard mais permet d'obtenir des amplicons de 7 ou 8 kb, nous permettant de reconstruire le mitogénome avec potentiellement seulement deux PCR (pour des raisons de mise au point des amorces, les notre ont été reconstruit à partir de quatre fragments). Cependant elle en a aussi les inconvénients, à savoir la nécessité d'avoir des extraits d'ADN de bonne qualité (les amplicons peuvent être jusqu'à 10 fois plus long que ceux d'une PCR standard). Un autres avantage était de pouvoir séquencer mes amplicons de manière multipléxé (inclus dans une même banque de séquençage) avec ceux d'autre utilisateurs travaillant sur des groupes suffisamment éloignés (rongeurs, téléostéens, crustacés décapodes...) et ainsi fortement diminuer les couts de production de séquence (Hinsinger *et al* 2015).

Echec de l'amplification de certains mitogenomes.

Sur la trentaine d'espèce de Bursidae (et la soixantaine de spécimens) pour lesquels l'amplification du mitogénome a été tentée, elle s'est révélée fructueuse pour seulement 10.

L'échec de l'amplification du mitogénomes des autres Bursidae peut être expliqué de plusieurs manières.

- Un ADN de mauvaise qualité : comme indiqué précisément un ADN trop fragmenté peut empêcher la bonne conduite de la réaction de PCR au moment de la phase d'élongation. Cependant la qualité et la taille de nos ADN ont été testées par *nanodrop* et par migration de l'ADN total sur gel, et la taille semblait satisfaisante.
- Problème d'amorces : les amorces utilisées ont été conçues de telle manière à ce qu'elles soient utilisables chez tous les Tonnoidea (sauf Personidae) (voir article 3). Elles devraient donc être efficaces pour tous les membres de la famille des Bursidae. Cependant, on observe qu'une grande partie des amorces se trouvent dans les ARNt, ce n'est pas surprenant, étant donné que ce sont des régions peu variables. Mais ces séquences sont aussi sujettes à des retournements complets, et si un tel retournement se produit, les amorces sens deviennent non-sens et inversement, et l'élongation se fera dans le même sens et l'hybridation ne se fera bloquant ainsi la PCR. Maintenant que nous avons une couverture raisonnable de la taxonomie des Bursidae en termes de mitogénomes, on peut envisager dans un futur proche la conception de nouvelles amorces Bursidae-centrées dans des régions géniques ou ribosomales.
- Les polysaccharides : les mollusques sont connus pour avoir un taux important de polysaccharides dans leur tissus (principalement du glycogène). Ce sont des inhibiteurs connus des réactions de PCR (Enriquez et al. 1992; Richards 1999, Schrader et al. 2012) dont l'effet est probablement d'autant plus important que la réaction est longue. Les kits d'extraction standard sont relativement inefficaces. De nouveaux tests réalisés avec un kit spécialisé dans les nettoyages des mucopolysaccharides (E.Z.N.A. Mollusc DNA Kit par exemple) seront réalisés dans le futur.

A time-calibrated phylogeny of frog shells (Bursidae, Tonnoidea, Gastropoda)

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Abstract

With around 60 Recent species, Bursidae known as « frog shells » are a small but widely distributed group of tropical and subtropical gastropods that are most diverse in the Indo-West Pacific. The present study aimed at the reconstruction of phylogenetic relationships of Bursidae gastropods based on representative taxon sampling. Four genetic markers [cytochrome c oxidase subunit I (cox-1), 16S and 12S rRNA mitochondrial genes, 28s and H3 (Histone 3) nuclear gene] were sequenced for over 30 species in every known genera but *Crossata*. Furthermore we sequenced the complete mt-genome of 10 species (*Aspa Marginata*, *Marsupina bufo*, *Korrigania quirihorai*, *Korrigania fijiensis*, *Tutufa rubeta*, *Bursa lamarckii*, *Lampasopsis rhodostoma*, *Bufonaria perelegans* and *Bursa* aff. *tuberosissima*). Our analysis recovered Bursidae as a monophyletic group. Whereas the genus *Bursa* was found to be polyphyletic. Genera *Bufonariella*, *Dulcerana*, *Lampasopsis*, *Tritonoranella* and *Talisman* are resurrected. Genus *Korrigania* is created. Dating analysis using 21 fossils as node and tip calibrations was performed. Good correlation with temperature curves indicates that climate may be a driving force for Bursidae diversification.

Key words: Bursidae, *Bursa*, Marine molluscs, time-tree, fossil calibration, Phylogeny

INTRODUCTION

Frog snails (Bursidae Thiele, 1925) are a moderately diverse tonnoidean family with 59 currently recognized extant species (Worms, 2017) and around 20 extinct one, downsized to 11 by Sanders *et al.* (in prep). Recent bursids have a sub-tropical distribution with a southernmost record in eastern South Africa, North New Zealand and Walters shoal. The northernmost record [*Bufonariella scrobilator* (Linnaeus, 1758)] is from Nice, southern France and Savona north western Italy [the specimen of *Bufonaria rana* (Linnaeus, 1758) recorded by Delongueville & Scaillet (2000) from northern Finistère, Brittany, France remains dubious]. They are intertidal to subtidal species most often associated with hard substrate such as rocks, coral or sponges, where they can be abundant. Very little is known about Bursidae diet; Houbrick & Fretter (1969) described it for three species (*Lampasopsis cruentata*, *Lampasopsis rhodostoma* & *Dulcerana granularis*), all of them where preying on polychaetes annelids and sipunculids by removing them from their tube or crevices and swallowing them. Kohn (1983) figured a specimen of *Bursa bufonia* predated an echinoid by gripping it with its muscular foot and using its radula to saw through the starfish's armoured skin, much in the same fashion as *Charonia*.

In South East Asia, Frog shells are consumed as food and as such constitute a human health issue since they produce tetrodotoxin (Nogushi *et al.* 1984). Shells of *Bufonaria rana* are used in traditional Chinese medicine to cure ulcers and furuncle carbuncle (Ahmad *et al.*, 2018). Bursid also have had cultural importance to Mankind since at least the Middle Palaeolithic; Peresani *et al.* (2013) showed that Neanderthals used fossil *Aspa* shells as fineries. The most culturally significant use of Bursidae is reported from western Fiji where *Tutufa* shells (called *davuisogasoga*) are considered sacred and are used as ceremony trumpets (Gatty, 2009) or worn as earlobe stretcher during battle (Sau mocemoce, Fiji Museum, 2017). In modern times, trumpets made of *Tutufa* shells have been sold throughout the Pacific instead of the much rarer (and pricy) Triton (*Charonia tritonis*), even in regions where it does not occur naturally (e. g. New Zealand).

Bursidae are readily recognizable by their well-defined posterior exhalant siphon (anal notch) at the top of the outer lip and by their thick, coarsely sculptured shells with knobs, warts, tubercles and nodules, hence their vernacular name: frog snails. Very variable in size, the smallest species, *Lampasopsis lucaensis* (Parth, 1991) never exceeds 23 mm height while *Tutufa bardeyi* (Jousseume, 1881), with a height up to 450 mm and a width up to 300 mm, is one of the largest and most capacious of all gastropod shells (Beu, 1998b). Most bursids size ranges between 40 and 50 mm. The radula is characterized by a basal interlocking processes on the

central tooth (Beu, 1998b), and by a flap on the outer posterior edge of each lateral tooth that overlaps the tooth in the preceding row (Barkalova *et al.*, 2016).

As inferred from their protoconch, similar to all tonnoideans, they are supposed to have a long to extremely long larval stage granting for some of them trans-oceanic dispersal capabilities. However Sanders *et al.*, (2017) showed that such capabilities were greatly overestimated for one of the most widespread species of Bursidae: *Dulcerana granularis*. This complex was once considered to be a single species with a worldwide distribution, but it is in fact constituted of at least four species, as confirmed by an integrative taxonomy approach combining molecular and morphological characters, restricted to one ocean each (plus one restricted to southernmost Western Australia). This result thus suggests that the species diversity of the family may be underestimated.

Further morphological characteristics are a spiral ornamentation of the convex part of the whorl composed of 6 to 8 primary cords (*sensus* Merle 2004 and Sanders *et al.*, 2017) that can be lost during the ontogeny. Secondary and ternary ones can appear later on and sometimes grow in such importance that they can be confused with primary cords [e.g. *Dulcerana granularis* (Röding, 1798)]. Such characters, sometimes difficult to observe for shallow water species, whose shells are often colonized and strongly encrusted by coralline algae (especially in the genera *Bursa*, *Lampasopsis* and *Tutufa*), can be also difficult to interpret, and consequently, the systematics of the Bursidae, largely based on the morpho-anatomical work carried out by Alan Beu (1981, 1986, 1998b) and Tiziano Cossignani (1994), remains confused. The current classification recognizes seven bursid genera: *Aspa*, *Bufoaria*, *Bursa*, *Bursina*, *Crossata*, *Marsupina* and *Tutufa*. As happened for many other gastropod taxa in the last decade, molecular phylogenies challenge this shell-based classification. Although based on a limited number of species, Castelin *et al.* (2012.) demonstrated that the genera *Bursa*, supposed to include nearly half of the bursid species, and *Bursina* are polyphyletic, which suggests that an extended dataset may reveal other discrepancies and calling for a new classification for the group.

The main goal of this study is to propose a phylogeny of the Bursidae using several genetic markers, including full mitogenomic coding regions and nuclear genes. We added several species compare to the work of Castelin *et al.* (2012) (from 17 to 33), focusing on the type species of the available genus names, in order to convert the molecular phylogeny into a new genus-level nomenclature of the frog shells. Furthermore the fossil record of the bursid family is rather good: a recent review (Sanders *et al.* in prep) showed that, in addition to the 11 extinct species mentioned in the literature, 26 extent ones have an exceptionally long fossil

distribution (reaching the Miocene for some), making the Bursidae a good empirical model for testing multiple calibration strategies (tip and node dating).

MATERIAL AND METHODS

Sampling

The material for this study was collected from various localities during a series of shallow-water and deep-sea expeditions in Vanuatu (Santo 2006), the Philippines (PANGLAO 2004, PANGLAO 2005), French Guiana (GUYANE 2014), Guadeloupe (KARUBENTHOS 2012, KARUBENTHOS 2015), Marquesas Islands (PAKAIHI I TE MOANA), Western Australia (WESTERN AUSTRALIA 2011), New Caledonia (CONCALIS, EBISCO, EXBODI, NORFOLK 1, NORFOLK 2, TERRASSES), French Polynesia (Tuhaa Pae 2013), Mozambique (INHACA 2011, MAINBAZA), Madagascar (ATIMO VATAE, MIRIKY), Salomon Islands (SALOMON 2), Papua New Guinea (PAPUA NUIGINI) Taiwan (Zhong Sha 2015) Viet Nam (NT-2014), Mauritania (MIWA), Azores, Panama and California. MNHN (Muséum national d'Histoire naturelle) specimens collected before 2012 were anaesthetized with an isotonic solution of MgCl₂ and fixed in 96% ethanol. Specimens collected after 2012 were processed with a microwave oven (Galindo *et al.*, 2014); the living molluscs in small volumes of sea water were exposed to microwaves for c. 30 s. Bodies were immediately removed from shells and dropped into 96% ethanol. The analysed material included 398 specimens, 388 deposited in the Muséum national d'Histoire naturelle, Paris (MNHN), one in the Natural History Museum of Santa Barbara (SBMNH), 4 in the Zoology department of the University of Bergen ZMB), Furthermore, sequences from five species [*Bufonaria nana* (Broderip, & Sowerby, 1829), *Galeodea echinophora* (Linnaeus, 1758), *Cymatium parthenopeum* (Salis Marschlins, 1793) *Cymatium cingulatum* (Lamarck, 1822) and *Tonna galea* (Linnaeus, 1758)] were mined from GenBank. Sequences from four of these taxa (*G. echinophora*, *C. parthenopeum* *C. cingulatum* and *T. galea*) and used as outgroups. The specimens and corresponding sequences are also registered in the Barcode of Life Data System and GenBank (Supp. Material Table 1).

Sampling was selected to be as taxonomically extensive as possible, covering all the currently recognized genera. Particular effort was put into adding type species in order to be able to provide a sound systematic revision of the group.

DNA extraction, PCR amplification and Sanger sequencing

DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the manufacturers' recommendations. Fragments of five genes were analysed: (i) the cytochrome c oxidase subunit I (cox1) using primers LCO1490/HCO2198 (Folmer *et al.*, 1994), (ii) mitochondrially encoded 12S ribosomal RNA (12s) using primers 12SA/12SB (Palumbi, 1996), (iii) mitochondrially encoded 16S RNA (16s) using primers 16SH/16LC (Palumbi, 1996), (iv) the nuclear 28S rDNA gene using primers C1 and D2 (Jovelin & Justine 2001) and the nuclear Histone H3 gene using primers H3F/H3R (Colgan *et al.*, 2000). PCR reactions were performed in volumes of 20 µl, containing 3 ng DNA, 1× reaction buffer, 2.5mM MgCl₂, 0.26mM dNTP, 0.3mM of each primer, 5% DMSO and 1.5 units of Qbiogene Q-Bio Taq. The amplification consisted of an initial denaturation step at 94°C for 5 min (3 min for H3), followed by 40 cycles of denaturation at 94°C for 35 s (20 s for H3), annealing at 47°C for cox-1, 62°C for 12s, 54°C for 16s, 52°C for 28s and 58° for H3 during 35s (20 s for H3) followed by extension at 72°C for 1 min (30 s for H3). The final extension was at 72°C for 5 min. PCR products were purified and sequenced in both directions by the Eurofins sequencing facility.

Primer design for long range PCR

The Myseq shotgun sequencing of a specimen of *Lampasopsis rhodostoma* (G.B. Sowerby II, 1835) (MNHN-IM-2013-11042) was subcontracted to Genome Quebec, using the Illumina Genomic DNA Sample Preparation protocol for libraries preparation. The mitogenome of this specimen was reconstructed over the closest tonnoidean mitogenome available in the literature: *Galeodea echinophora* (Linnaeus, 1758) (GenBank accession number: NC_028003.1, Osca *et al.* 2015) using the Map-to-reference tool of Geneious 9.1.7 (<http://www.geneious.com>, Kearse *et al.*, 2012) set on medium sensitivity (allowing 15% of gaps per read and 30% of mismatches). These two mitogenomes where then aligned using MAFFT (Kato *et al.*, 2002) with the only other Tonnoidean mitogenome available in the literature *Cymatium parthenopeum* (Salis Marschlin, 1793) (GenBank accession number: NC_013247, Cunha *et al.*, 2009). Conserved regions (identified by eye) were analysed using the primer design option of Geneious for temperature of melting calculation (Breslauer *et al.*, 1986). Following the recommendations of Hinsinger *et al.*, (2015), we select primers with little or no self- or heterodimer, and closely matching annealing temperatures with primer melting temperatures selected between 50 and 65°C. We also used universal cox-1 primers. Primers are provided in Table 1. Only 10 over the 13 primers where used for amplify the complete mitogenomes; they were chosen in order to minimize the number of fragments needed for

reconstructing a mitogenome. When two primers were neighboring, they were pooled in the mix to minimize the number of PCR and maximize the probability of amplification in case of mutation within the primers (they are noted “bis” in the first column of Table 1).

Table 1: Primers for the long range PCRs, including primers designed for the Bursidae. F: forward, R: Reverse. TM: temperature of melting

| Fragment in fig. 1 | Primer name | 5'-3' sequence | F/R | TM (°C) | Publication |
|--------------------|-------------|-------------------------------|-----|---------|---------------------|
| Frag. 1 F | Folmer_F/L | GGTCAACAAATCATAAAGATATTGG | F | 51,1 | Folmer et al.(1994) |
| Frag. 4 R | Folmer_R/H | TAAACTTCAGGGTGACCAAAAAATCA | R | 51 | |
| Frag. 2 F | MS_12SF4669 | GTGCCAGCATCCGCGGTTA | F | 61 | This study |
| | MS_16SF6214 | CGGTACTCTGACCGTGCAAAGG | F | 64 | |
| | MS_16SR6691 | AGATAGAAACTGACCTGGCTCACG | R | 62,7 | |
| Frag. 1 R | MS_R7937 | TATTTACCTAATYTTTAGCTTCCAATGCT | R | 58,9 | |
| Frag. 3 F | MS_F9734 | ACCTTTGGCTTACAAGACCAATGCT | F | 61,3 | |
| Frag. 3 F bis | MS_F9649 | TTCCTGGGGACAATTTGTCTTGAAAAC | F | 61,9 | |
| Frag. 2 R | MS_R11502 | ATTTTATCTTCAACTCCACAGATTGATGT | R | 59,6 | |
| | MS_R13295 | CCTTAGCATCTTCAGTGCTATGCTC | R | 63 | |
| Frag. 4 F | MS_F14405 | AGCGAGAAATTTGCATTTCGGTTTC | F | 59,3 | |
| Frag. 4 F bis | MS_F14480 | AATAGAGGCGCCTAGCTGTTAATTAG | F | 61,6 | |
| Frag. 3 R | MS_R15004 | AGTTAGCAGCCCTGTTTACTCCAAG | R | 63,2 | |

Long range PCRs for complete mitogenome amplification and sequencing.

In order to complete the mitogenome amplification, we amplified four overlapping fragments (Figure 1). We used a modified protocol of Hinsinger *et al* (2015): PCR reactions were performed in 18 µl volume including 5X LongAmp Taq Reaction Buffer, 0.4 ng/µl Bovine Serum Albumin (BSA), 3.5% DMSO, 300 nM of each primer, 300 µM of dNTPs, and 1 unit of LongAmp Taq polymerase. After an initial denaturation of 30 s at 94°C, the DNA was amplified through 60 cycles of 20 s at 94°C, 30 s at 55°C, and 15 min at 65°C, with a terminal elongation for 15 min at 65°C.

The PCRs were visualized on ethidium bromide stained agarose gel, and we estimated the amounts for pooling from the intensity of the bands (Timmermans *et al.*, 2010), taking into account PCR size and using one of our own PCRs as intensity standard across gels. Libraries for genome sequencing approach were generated using NEBNext© Fast DNA Fragmentation & Library Prep Set for Ion Torrent™ (E6285L, New England Biolabs), loaded onto Ion

316V2chips. The sequencing was performed at the *Service de Systématique Moléculaire* (UMS 2700, OMSI)

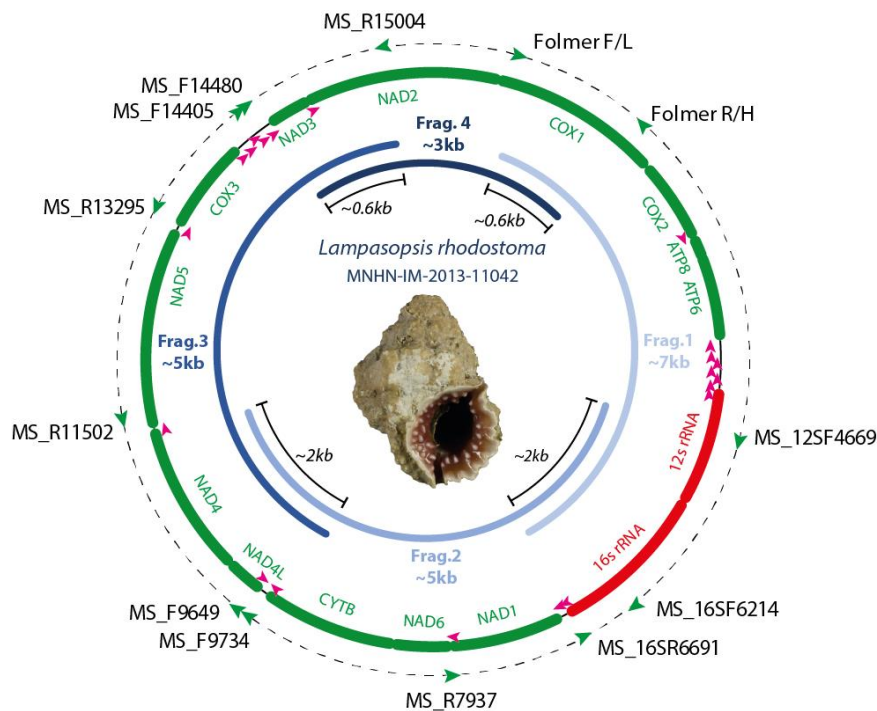


Fig.1: Position of the primers on the mitogenome of *Lampasopsis rhodostoma*. Blue lines represent the fragments of mtDNA amplified by the long range PCRs. Black lines represent the overlapping sections of the amplified fragments, green lines represent coding genes, red lines represent rRNA genes, clockwise green arrows represent forward primers, contraclockwise green arrows represent revers primers, pink arrows represents tRNA .

Genome assembly

Short-read DNA sequences from Ion Torrent were assembled into a single sequence corresponding to a complete mt genome using the Map to reference tool of Geneious (using the *Lampasopsis rhodostoma* MNHN-IM-2013-11042 reconstructed mt genome as reference) set on custom sensitivity (Min map quality: 30, Allowing 10% gap per read and 20% mismatch per read). The 13 mt protein-coding genes were annotated by identifying their open reading frames and by comparing them with other reported tonnoidean mt genomes. The transfer RNA (tRNA) and the ribosomal RNA (rRNA) were annotated by comparing them with other reported tonnoidean mt genomes and assumed to extend to the boundaries of adjacent genes (Boore *et al.*, 2005).

Sequence alignment

Sequences were aligned for each gene independently using MAFFT (Katoh *et al.*, 2002). The accuracy of automatic alignments was confirmed by eye using BioEdit v. 7.0.9.0 (Hall, 1999). No indels were detected in the protein-coding genes.

Data sets

The first dataset corresponds to all available cox-1 DNA sequences. The second dataset represents the cox-1, 12s, 16S, H3 and 28S concatenated sequences of one specimen of each of the 33 independent lineages (accepted as species) previously recognized morphologically (and confirmed as independent lineages with the cox-1 dataset). In order to minimize the number of missing data, in several cases conspecific specimens were concatenated (Table 2). It was done only if their Cox-I sequences had less than 2% pairwise genetic distances. For the same reason, outgroup sequences downloaded from GenBank were concatenated when they belonged to the same family (Strong *et al.* unpub.) (the correspondence is shown in supplementary material, Table 1). The third and fourth dataset represents the concatenated analysis of the 13 protein-coding genes, using DNA and amino-acids sequences, respectively. The fifth dataset is a concatenation of the second and third dataset.

Phylogenetic analyses

Best-scoring maximum likelihood (ML) trees were estimated using RaxML (Stamatakis, 2006) from 100 independent searches, each starting from distinct random trees. Robustness of the nodes was assessed using the thorough bootstrapping algorithm (Felsenstein, 1985) with 1000 iterations. RaxML analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>), using RAXML-HPC2 on XSEDE. Bayesian analyses (BA) were performed by running two parallel analyses in MrBayes (Huelsenbeck, Ronquist, & Hall, 2001). For cox-1 analyses, each run consisted of 8 Markov chains and 10,000,000 generations, three swaps at each generation, a sampling frequency of one tree each 1,000 generations, and the chain temperature set at 0.02; for the datasets 2 to 5 the number of generation was increased (30,000,000 for dataset 2 to 4 and 70,000,000 for the last one). Convergence of each analysis was evaluated using TRACER 1.4.1 (Rambaut *et al.*, 2014) to check that all effective sample size values exceeded 200. Consensus trees were calculated after omitting the first 25% of the trees as burn-in. Analyses were performed on the Cipres Science Gateway, using MrBayes 3.2.2 on XSEDE. In all analyses (ML and BA), genes were separated into unlinked partitions;

additionally, all protein-coding genes were separated in three partitions, one for each codon position. The substitution model was set to GTR + I + G for both ML and BI analyses

Calibration strategy and molecular dating

Dating was performed by running two parallel analyses in Mr Bayes 3.2.6 (Ronquist *et al.* 2012), with prior probability distribution on branch lengths set on a birth-death model, with an independent gamma rate (igr) relaxed clock model (variance distribution of the prior set on exponential 10). Each run consisted of 8 Markov chains and 100,000,000 generations, three swaps at each generation, a sampling frequency of one tree each 1,000 generations and the chain temperature set at 0.02. The analysis was done combining tip and node dating.

All node calibrations were done using 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. The clades *Bursidae*, *Bursa*, *Bufo*, *Lampasopsis*, *Tritonoranella*, *Marsupina*, *Dulcerana*, *Korrigania*, *Bursina* and the clade excluding *Aspa* and *Talisman* were constrained.

All tip calibrations were set to follow a uniform distribution of the prior as it is the only distribution that allows the implementation of a wide stratigraphic range. Information regarding the fossils used in calibration, the parameters of the calibration prior distribution and references for fossils identifications and stratigraphic attributions are reported in the Table 3.

Table. 3 Prior information for fossil calibration

| calibrated taxon | calibration prior distribution | Mr Bayes parameters | fossil used | Period | Origine / Formation | Ref for systematic attribution | Ref for stratigraphy |
|---|--------------------------------|---------------------|---|--|--|--------------------------------|--------------------------------|
| Bursidae | | (41.2,46.2,1); | <i>Olssonina yasila</i> | Bartonian | Yasila formation Peru | Beu, 1988 | Olsson, 1930 |
| Bursidae without <i>Aspa</i> & <i>Talisman</i> | | (23,26,1); | <i>Aquitano bursa tuberosa</i> & <i>inaequicrenata</i> | Chatian / Aquitanian | Aquitaine Basin France | This study | Lozouet 1998 |
| <i>Bursa</i> | | (9, 12, 1); | <i>Bursa</i> cf. <i>rosa</i> | Late Miocene | Citalahab, West Java | Sanders et al in prep | Beu 2005 |
| <i>Dulcerana</i> | | (9, 12, 1); | " <i>Bursa</i> " cf. <i>granularis</i> | late Miocene | Citalahab, West Java | Sanders et al in prep | Beu 2005 |
| <i>Lampasopsis</i> | | (20, 22, 1); | <i>B. (Marsupina) albofasciata</i> <i>boussingaulti</i> (= <i>Lampasopsis</i> cf. <i>rugosa</i>) | Aquitanian/ Burdigalian | Punta Gavilán formation, northern Venezuela | Sanders et al in prep | Beu 2010 |
| <i>Marsupina</i> | offsetlognormal | (14, 16, 1); | <i>Marsupina</i> cf. <i>bufo</i> | middle Miocene | Shoal River formation Florida, USA | Sanders et al in prep | Beu 2010 |
| <i>Tritonoranella</i> | | (14, 16, 1); | <i>Tritonoranella</i> cf. <i>ranelloides</i> | middle Miocene | Trinity Hill Sandstone member of Moruga Formation, Trinidad | This study | Beu 2010 |
| <i>Tutufa</i> | | (13.5,18.5,1); | <i>Tutufa</i> sp. | Middle Miocene | Ena Limestone Japan | Tomida <i>et al.</i> (2013) | Tomida <i>et al.</i> (2013) |
| <i>Aspa Marginata</i> | | (0,18); | <i>Aspa Marginata</i> | Middle Miocene | Po valley Italy & Paratethys | Landau et al., 2004 | Landeau et al., 2004 |
| <i>Bufonaria perelegans</i> | uniform | (0,11); | <i>Bufonaria perelegans</i> | Middle Miocene (early Preangerian) | Cijarian, western Java | Beu 2005 | Beu 2005 |

| | | | | | | |
|-----------------------------------|----------|-----------------------------------|-------------------------|---|-----------------------|------------------------|
| <i>Bufo nariella scrobilator</i> | (0,14); | <i>Bufo nariella scrobilator</i> | Langhian/ Seravalian | Paratethys Austria and Poland | Landau et al., 2004 | Baluk 1995 |
| <i>Bursina margaritula</i> | (0,3.5); | <i>Bursina margaritula</i> | Pliocene | Tjikeusik, Java | Beu 2005 | Beu, 2005 |
| <i>Dulcerana cubaniana</i> | (0,2); | <i>Dulcerana cubaniana</i> | Pleistocene | Various formation from Panama, Cuba, Dominican republic and Barbados | Sanders et al. 2017 | Beu 2010 |
| <i>Lampasopsis thomae</i> | (0,12); | <i>Lampasopsis thomae</i> | Burdigalian | Chipola formation, Florida, USA | this study | Beu 2010 |
| <i>Marsupina bufo</i> | (0,7); | <i>Marsupina bufo</i> | Tortonian Messinian | Gurabo formation in Dominican republic Charco Azul Group, Penita Formation , | Sanders et al in prep | Beu 2010 |
| <i>Marsupina nana</i> | (0,5); | <i>Marsupina nana</i> | Early Zanclean | Quebrada La Penita, Pacific coast of Costa Rica | Beu 2010 | Beu 2010 |
| <i>Talisman corrugata</i> | (0,20); | <i>Talisman corrugata</i> | Burdigalian | Aquitaine basin | Landau et al., 2009 | Landau et al., 2009 |
| <i>Tritonoranella latitudo</i> | (0,2.5); | <i>Tritonoranella latitudo</i> | late Pliocene | Kendeng beds, Java | Beu 2005 | Beu 2005 |
| <i>Tritonoranella ranelloides</i> | (0,2.5); | <i>Tritonoranella ranelloides</i> | Pliocene | Cayo Agua Formation Panama | Beu 2010 | Beu 2010 |
| <i>Tutufa bubo</i> | (0,5); | <i>Tutufa bubo</i> | Late Miocene | Pendopo Oilfield, east of Talang Akar, Sumatra | Beu 2005 | Robba, 1996 |
| <i>Tutufa rubeta</i> | (0,7); | <i>Tutufa rubeta</i> | Late Miocene | Citalahab, West Java | Beu 2005 | Beu 2005 |

Transforming a phylogeny into a genus level classification.

Following the guidelines of Puillandre *et al.*, 2014, genus names were given only to well-supported clades. Then, genus names were applied based on the position of their type species in the tree. If the type species of a nominal genus had not been sequenced, application of the name was determined by reference to the morphologically most similar species used in the molecular analysis. If more than one name was applicable for a clade, the valid name was determined by the rule of priority.

Providing an extended classification of the Bursidae including the attribution of all currently accepted species to the new genera goes far beyond the scopes of this paper and will be treated in an upcoming article.

RESULTS

Mitochondrial genome organization

The complete mt genomes of *Tutufa rubeta*, *Marsupina bufo*, *Lampasopsis rhodostoma* (two specimens), and the partial mt genome of *Bufo nana perelegans*, *Aspa marginata*, *Bursa* cf. *tuberosissima*, *Korrigania quirihorai* and *Korrigania fijiensis* were sequenced and assembled (see Table 4 for genome length and sequencing coverage). Like most animal mt genomes (Boore & Brown, 1994), they encode for 13 protein-coding genes, 22 tRNAs, and 2 rRNAs (Fig 1) The gene order of the newly sequenced mt genomes is identical to the gene arrangement of other reported tonnoidean mt genomes (Osca *et al.*, 2015)

Table 4 Complete and partial mt genomes sequenced and reconstructed in this study

| Species | repository accession number | proportion assembled | mitogenome size | number of read assembled | Coverage | | | |
|---------------------------------------|-----------------------------|----------------------|-----------------|--------------------------|----------|-----|------|---------------|
| | | | | | Min | Max | Mean | Standard dev. |
| <i>Tutufa rubeta</i> | IM -2013-10139 | 100 | 15397 | 7421 | 12 | 438 | 122 | 101 |
| <i>Bufo nana perelegans</i> | IM-2007_43034 | 52 | | 2574 | 0 | 273 | 46 | 63 |
| <i>Aspa marginata</i> | ZMB-92447 | 56 | | 3568 | 0 | 522 | 66 | 100 |
| <i>Marsupina bufo</i> | IM-2013-56144 | 100 | 15403 | 3736 | 9 | 200 | 51 | 32 |
| <i>Bursa</i> aff <i>tuberosissima</i> | IM-2007_43041 | 69 | | 507 | 0 | 22 | 7 | 6 |
| <i>Lampasopsis rhodostoma</i> | IM-2013-11043 | 100 | 15392 | 6604 | 14 | 284 | 86 | 46 |
| <i>Korrigania quirihorai</i> | IM-2013_52981 | 93 | | 955 | 0 | 75 | 12 | 9 |
| <i>Bursa lamarkii</i> | IM-2013_13449 | 100 | 15407 | 4760 | 10 | 218 | 62 | 38 |
| <i>Korrigania fijiensis</i> | IM-2009_5459 | 86 | | 765 | 0 | 42 | 10 | 9 |
| <i>Lampasopsis rhodostoma</i> | IM-2013-11042 | 100 | 15392 | 22176 | 138 | 536 | 217 | 42 |

Phylogenetic analyses

Single gene (dataset 1) and protein (dataset 2) datasets yield poorly resolved phylogenies and do not present any evidence of conflict in their topology. These trees will not be discussed further. As shown by Castelin *et al.* (2012), the monophyly of the Bursidae is well supported in the tree obtained with the fifth dataset (posterior probabilities PP = 1, bootstrap BS = 100) (Fig. 2). The first dichotomy divides two poorly supported clades, an Atlantic clade containing *Aspa marginata* and *Talisman corrugata*, and a second clade that contains the rest of the Bursidae. The early branching of *Aspa* and *Talisman* is consistent with the fact that they are the only extant genera with a potential Paleogene record. Nine supported major clades can be recognized within the main bursid grouping (highlighted in fig. 2). These clades, in addition with three other clades composed of a single species each, are each attributed to a distinct genus (see discussion for name attribution). Relationships between genera have various levels of support, ranging from fully supported (PP = 1, BS = 96) for Clade A minus *Korrigania* and clade B, to weakly supported for clade C (Fig. 2).

Compared with earlier work (Castelin *et al.*, 2012), the main difference lie in the phylogenetic position of the genus *Tutufa*; in Castelin *et al.* (2012), it originates early, as a sister group of all the other bursids, but with the increased sampling, in particular in the *Lampasopsis* clade, and the addition of *Marsupina*, it is well imbedded within the Bursidae. The deep sea (200 to 1000m deep) genus *Tritonoranella* was closely related to *Lampasopsis* (with low support); it is now sister group to the clade containing *Korrigania*, *Bufonaria* and *Bursina* (still with low support). All the species belonging to these clades are commonly found in deep water (to the exception of some species of *Bufonaria*), unlike *Lampasopsis* that never occurs below 100 m deep. The species *Lampasopsis thomae* and *L. rhodostoma* were still recently accepted as a single species, though our work refutes this; furthermore, they are not even sister species.

Dating analysis

Among all the nodes, only those that have been calibrated have a divergence standard deviation lower than two Myr. Frog shell genera appearance is not synchronic, with *Aspa* and *Talisman* being the oldest (around 40 Myr) and *Bursa* and *Dulcerana* the youngest (around 13 Myr). The Bursidae found their origin during the early Lutetian period. Afterwards, bursids seem to have diversified in two relatively synchronic phases during the Paleogene. The first phase was in the mid-Bartonian, with the dichotomy *Aspa-Talisman* in one hand and clades A-

B+C on the other hand. Then, we observe a synchronic diversification of the genera *Tritonoranella* – *Korrigania*+*Bufonaria*+*Bursina* and *Lampasopsis*-*Marsupina*+*Tutufa*. Those diversifications occurs around the Eocene-Oligocene transition. No broad general pattern of diversification is readily observable during the Neogene.

NOMENCLATURE

Name attribution

Clades containing type species are readily nameable: *Aspa* (type species *Ranella laevigata* Lamarck, 1822 = *Buccinum marginatum* Gmelin, 1791), *Tritonoranella* (type species *Triton ranelloides* Reeve, 1844), *Lampasopsis* (type species *Ranella rhodostoma* G. B. Sowerby II, 1835), *Marsupina* (type species *Buffo spadiceus* Montfort, 1810 = *Murex bufo* Bruguière, 1792), *Tutufa* (type species *Murex rana bubo* Linnaeus, 1758), *Dulcerana* (type species *Tritonium granulare* Röding, 1798), *Bufonariella* (type species *Murex scrobilator* Linnaeus, 1758) and *Bursa* (type species *Bursa monitata* Röding, 1798 = *Murex bufonius* Gmelin, 1791). However, the type species of *Bufonaria* and *Bursina*, respectively *Bufonaria spinosa* Schumacher, 1817 (a junior synonym of *Bufonaria echinata* (Link, 1807)) and *Ranella nobilis* Reeve, 1844, were not included in this study. *Bufonaria perelegans* Beu, 1987 is morphologically extremely similar to *Bufonaria echinata*; the only noticeable difference is that *Bufonaria echinata* has much longer spines on its sutural, first and third primary chords. *Bursina nobilis* and *ignobilis* (Beu, 1987) can only be differentiated by their size when they are adult, *Bursina nobilis* being slightly larger and taller. Consequently, well supported clades containing *Bufonaria perelegans* and *Bursina nobilis* are attributed to the genera *Bufonaria* and *Bursina*, respectively. *Talisman* is a genus name based on *Talisman parfaiti* Folin, 1884; Warén & Bouchet (1990) considered this genus to be a *nomen dubium* based on a juvenile of either *Bufonariella scrobilator*, *Aspa marginata* or *Talisman corrugata*. de Folin (1884) described a reduction of the ornamentation on the last whorl for *Talisman parfaiti*, absent in *Bufonariella*, and a reddish aperture, unlike *Aspa*, which is white to pale beige.

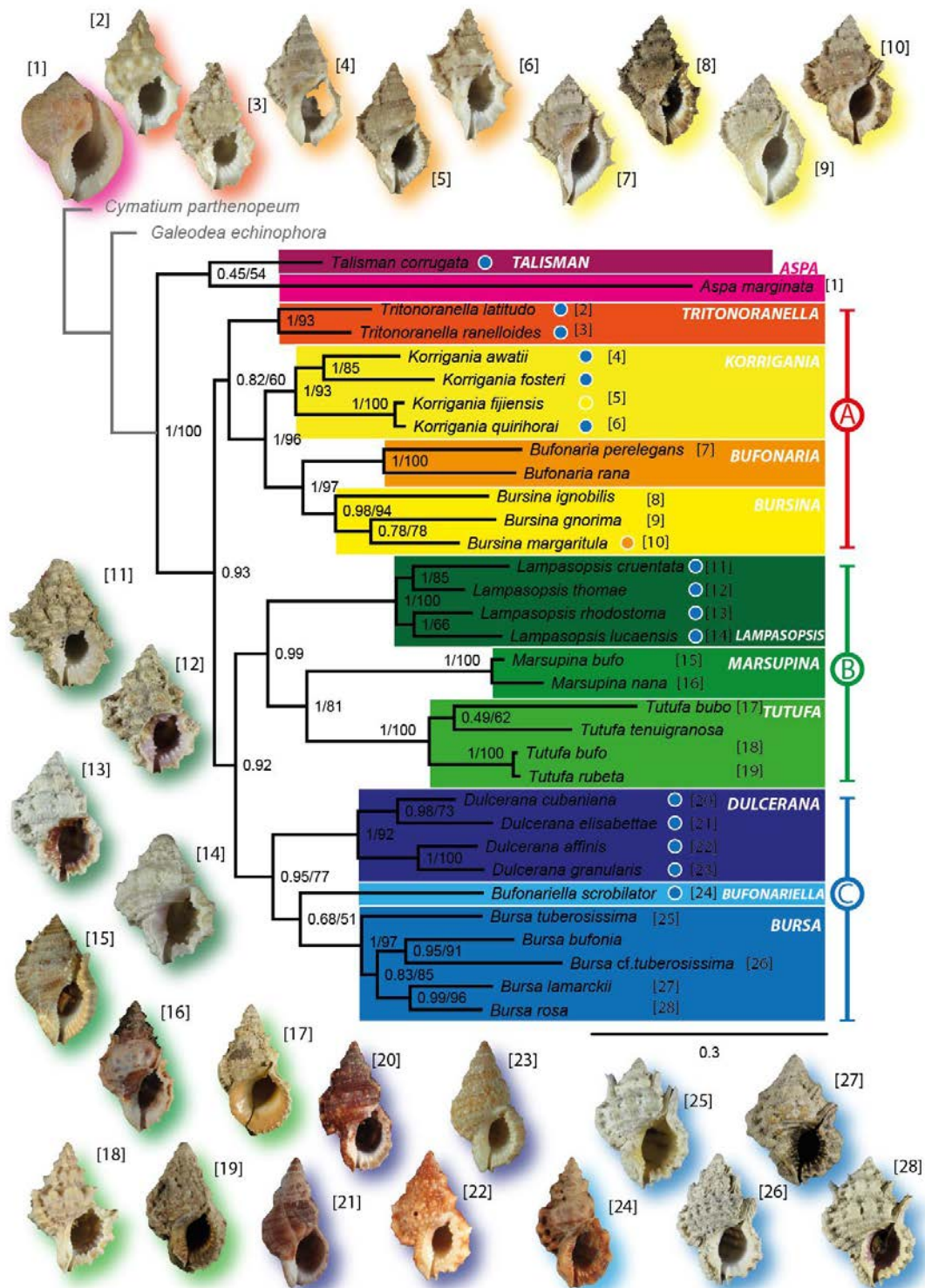


Fig.2 Bayesian phylogram based on a concatenated mitochondrial and nuclear gene dataset. Support for nodes is given as PP/BS. Figured specimens are sequenced vouchers. Scale bar indicates number of nucleotide substitutions per site. Blue dots indicate species previously attributed to *Bursa*, yellow dots indicates species previously attributed to *Bursina* and orange dot indicates species previously attributed to *Bufonaria*. Outgroup branches, in grey, are not to scale.

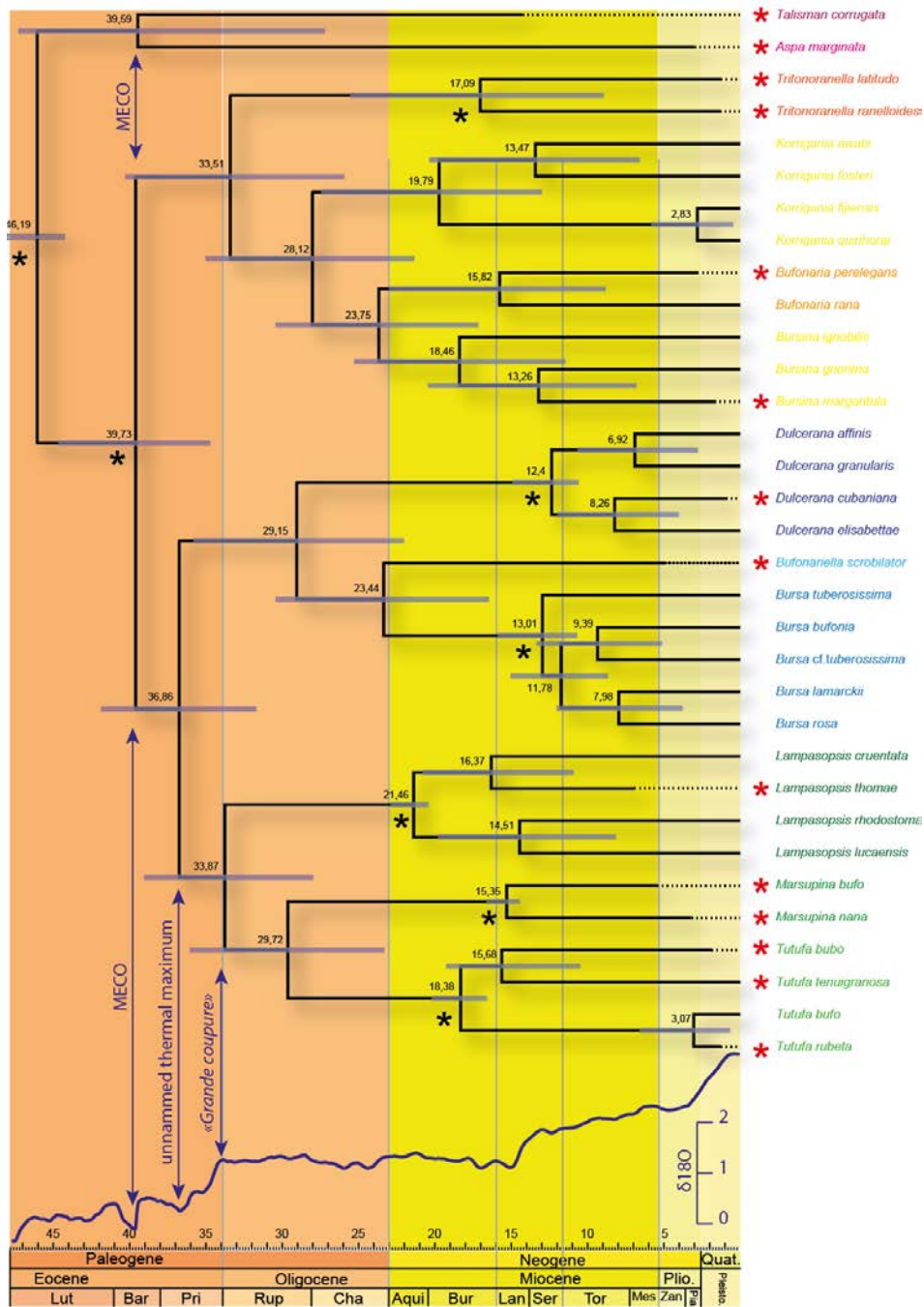


Fig.3 Maximum clade credibility chronogram obtained from the Bayesian analyses performed on dataset 5 with *Galeodea echinophora* and *Cymatium parthenopeum* as outgroup (not shown). Node values are posterior mean ages (Myr), with node bars representing their 95% HPD intervals. Black * indicates calibrated nodes and red * indicates calibrated tips. The blue curve represents the benthic foraminiferal oxygen isotopic ($\delta^{18}O$) trends through time (reproduced from Cramer *et al.* 2009) which is anti-correlated to temperature. Geological time scale in Myr with abbreviations: Lut, lutetian, Bar, Bartonian, Pri, Priabonian, Rup, Rupelian, Cha, Chattian, Aqu, Aquitanian, Lan, Langhian, Ser, Serravalian, Tor, Tortonian, Mes, Messinian, Zan, Zanclean, Pia, Pliocene, Pleisto, Pleistocene.

We consider *Talisman parfaiti* to be a junior synonym of *Biplex corrugata* Perry, 1811 and we attribute the name *Talisman* to the *corrugata* clade. We still consider *Crossata* (not included in the sampling) to be a valid genus under the current delimitation (Powell & Berschauer, 2017). “*Bursa*” *verrucosa* (G. B. Sowerby I, 1825) and “*Bursa*” *condita* (Gmelin, 1791) are two morphologically distinct species that we were unable to obtain for this phylogenetic study, and they are not readily attributable solely based on their morphology to any newly delimited genus; fortunately, they are both type species of *Annaperenna* and *Colubrellina* respectively. These two monospecific genera are considered valid, pending their inclusion in a molecular phylogeny. The only clade that we consider to be of generic level without previously published name is the well supported one containing “*Bursa*” *awatii*, “*Bursina*” *fijiensis*, “*Bursa*” *fosteri*, and “*Bursa*” *quirihorai*; we decided here to create a new name for it: *Korrigania*

Systematics

Phylum **MOLLUSCA** Cuvier, 1795

Class **GASTROPODA** Cuvier, 1795

Order **NEOGASTROPODA** Milne Edwards, 1848

(Following Osca *et al.*, 2015)

Superfamily **TONNOIDEA** Suter, 1913 (1825)

Genus *Korrigania*, gen. nov

Type species: Ranella fijiensis Watson, 1881 here designated

Included species:

Korrigania awatii (Ray, 1949) n. comb., ***Korrigania fijiensis*** (Watson, 1881) n. comb., ***Korrigania fosteri*** (Beu, 1987) n. comb., ***Korrigania quirihorai*** (Beu, 1987) n. comb.

Derivatio nominis: founded over the Britany dwarf-like spirit Korrigan.

Diagnosis: (Following the cord nomenclature of Sanders *et al.*, 2017) Fusiform, very light built shell (extremely light in *K. awatii*), 7 primary cords (P) on the convex part of the whorl, P2 and P4 atrophied, P6 and P7 reduced varices displaced but less than in *Tutufa* or *Tritonoranella*,

ovate operculum, subanterior nucleus. Resemble *Tritonoranella* but lack black stripes on the columella.

DISCUSSION

Lutetian diversification

The very early diversification of the Bursidae remains obscure due to the fact that no undisputable bursid fossil has ever been found in strata older than those belonging to the Eocene Peruvian genus *Olssonina* (Beu, 1988, Sanders et al in prep). Molecular dating indicates that the radiation of the crown Bursidae originates during the Lutetian; this is consistent with the fact that the Thanetian fossil species “*Bursa*” *saundersi* Adegoke, 1977 from West Africa (Nigeria) bears numerous characters resembling those of bursids (the varices closely spaced and nearly aligned up the whorls, the sculpture of coarse nodes and the short spire place it in the Bursidae rather than in the Ranellidae or the Cymatiidae). However, it lacks the distinctive anal notch of the family. It may very well be an early, stem-bursid anterior to the acquisition of the posterior siphonal canal. Yet the biogeographic pattern between West Africa and Peru remain difficult to explain considering the absence of known record in the early Eocene of the Americas. This would need further paleontological research and perhaps a re-evaluation of some “ranellid” forms of the rich deposit of the Gulf coast of the United States.

Bartonian diversification

The Bartonian diversification pattern described above is concomitant to the last supra-regionally recognized Eocene thermal event, the MECO (Mid Eocene Climatic Optimum) (Vandenbergh *et al.*, 2012). Such thermal events are recognized to be biodiversity drivers (Erwin, 2009). As stated earlier, the speciation event giving birth to the clades A and B+C is most certainly caused by bathymetric isolation. Clade A is composed of species commonly found more than 300 m deep, and up to 1000 m for some species of *Korrigania* and *Tritonoranella*. On the other hand, species within B+C are rarely collected alive below 100 m deep (*Tutufa tenuisgranosa* is the sole species to be found under 100 m but never over 220 m). *Aspa* and *Talisman* being shallow water species as well, deep sea colonization by the clade A is then considered as an apomorphy of the clade. Speciation induced by bathymetry has already been hypothesized in the Bursidae by Castelin *et al.*, (2012). Bathymetric speciation may have been induced by the appearance of new deep-sea niches created by the global sea transgression peak in the mid-Bartonian (P13 Planktonic foraminifera zonation). Considering that the fossil

genus *Aquitnobursa*, closely related to the clade ABC, has a Tethysian distribution, it is reasonable to suppose that this Bartonian diversification occurred in the Tethys as well.

Two hypotheses can be proposed to explain why *Talisman* and *Aspa* fossil are not found in Eocene and Oligocene deposits. (1) Early Eocene *Aspa* and *Talisman* occur in the Aquitaine Basin where deposits of that period are poorly preserved. This may prevent the discovery of early forms of those genera. (2) The evolutionary rates of this part of the tree is apparently different from the rest the Bursidae tree (*Aspa* shows quite a longer branch compared to its sister group - Fig. 2). It is then possible that the clock model used in the analysis artificially gave an older diversification time. Such artefacts have been consistently shown in other groups (Alaya, 1997, Schwartz & Maresca 2006). Pending for new fossil discoveries, this problem could be addressed by increasing the number of molecular characters for *Talisman corrugata*, the only extant species of its genus.

Priabonian diversification.

The Priabonian diversification of the clades B and C could be explained in the same manner, due to its synchronicity with an unnamed local thermal maximum (Fig. 3).

The “Grande Coupure”

All the extant genera of Bursidae (except *Aspa* and *Talisman*), as delimited here and if conceptualized as total taxa (including their stem), found their origin in the Oligocene or the Eocene. This major radiation seems to be a post-crisis recovery following the biodiversity crisis known as “Grande coupure” (Stehlen, 1910), which is characterized by a global cooling (Ivany et al., 2000). There is no bursid fossil record from late Priabonian to late Chattian. Hence, molecular dating is the only mean to recover information regarding Oligocene diversification of the group.

Panama isthmus closure

Among the sampled species, two are geographically restricted to western Atlantic and the Caribbean: *Lampasopsis thomae* and *Marsupina bufo*. Separation with their sister group, respectively *Marsupina nana* from eastern Pacific and *Lampasopsis cruentata* from the East Indo-Pacific, are both estimated to have occurred around 15 Myr, which corresponds to the initial closure of the Panama isthmus (Montes et al., 2015). Global climatic impact of the closure remain unclear to this day (a small peak in $\delta^{18}\text{O}$ can be observed at the 15 Myr), though

it is difficult to say if any other speciation event occurring in this period but not in the region can be attributed to this event.

Conclusion

With 56% of the extent species represented in the dataset, this work constitutes the first large-scale revision of the Bursidae. A new classification of the frog snails is proposed, including a tentative solution to the decade-long debate regarding the delimitation of the family type genus, *Bursa*. The integrative approach using mitogenomic data and the extensive fossil record allowed us to reconstruct the chain of events leading to the extent biodiversity of the Bursidae. However, further work needs to be done in order to provide a complete phylogeny of the Bursidae. First, shifting to the genomic scale has been proven to significantly improve the resolution of the trees, but to this day, we have no full mitogenomic data for *Dulcerana*, *Talisman* and *Tritonoranella*. Second, taxonomic sampling should be increased, including in particular the species *Annaperenna verrucosa*, *Colubrellina condita* and *Bufo naria foliata*, respectively type species of *Annaperenna* Iredale, 1936, *Colubrellina* Fischer, 1884 and *Chasmotheca* Dall, 1904. To this day, we are not aware of any material preserved for molecular analysis for these species. Furthermore, *Bufo naria* is among the most diverse bursid genus (nine recognized species), but it is greatly under-sampled in this study. To thoroughly test the monophyly of this group, several species need to be added to the tree. If generating genomic-scale molecular data is becoming easier, achieving a representative sampling for molecular systematics is becoming increasingly difficult, considering the multiplicity of permits required to sample the whole distribution area of the targeted taxa, spanning numerous countries. The future will tell whether the Article 8a of the Nagoya Protocol for the Convention of Biological Diversity (encouraging the Parties to the protocol to “create conditions to promote and encourage research [...] through simplified measures on access for non-commercial research purposes”) will reverse the trend (Bouchet *et al.*, 2016). For the time being, compliance with regulations on ‘Access and Benefit Sharing’ and ‘Prior Informed Consent’ is more an obstacle than a facilitating tool for academic researchers studying the biodiversity.

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Supplementary material: List of specimens analyzed.

| institution number | Genus | Species | Campagne | Station | LAT | LONG | | BOLD | cox-1 | 12s | 16s | 28s | H3 | Mitogenome |
|--------------------|-------------|-------------------------|-----------------------|------------|------------|-----------------|---------|------|-------|-----|-----|-----|----|------------|
| ZMB-92447 | <i>Aspa</i> | <i>Marginata</i> | Mauritania | | | | | | x | x | | | x | x |
| MNHN-IM-2007-43034 | <i>Bufo</i> | <i>perelegans</i> | SANTO 2006 | EP04 | 15°33'S | 167°12,7'12,8'E | 89-109 | x | | | | | | x |
| MNHN-IM-2007-43043 | <i>Bufo</i> | <i>perelegans</i> | SANTO 2006 | EP04 | 15°33'S | 167°12,7'12,8'E | 89-109 | x | | | | | | |
| MNHN-IM-2007-43057 | <i>Bufo</i> | <i>perelegans</i> | SANTO 2006 | AT54 | 15°32,1'S | 167°14,1'E | 68-79 | x | x | x | x | x | x | |
| LSGB-22701 | <i>Bufo</i> | <i>rana</i> | mined from gene bank | | | | | x | x | x | | | x | |
| ZMB-86382-A | <i>Bufo</i> | <i>scrobilator</i> | Porto da horta Azores | | | | | | | | | | x | |
| ZMB-86382-B | <i>Bufo</i> | <i>scrobilator</i> | Porto da horta Azores | | | | | x | x | | | | | |
| MNHN-IM-2013-52974 | <i>Bufo</i> | <i>bufonia</i> | PAKAIHI I TE MOANA | MQ16 M | 10°27,84'S | 138°39,97'W | 0-1 | x | | | | | | |
| MNHN-IM-2013-52977 | <i>Bufo</i> | <i>bufonia</i> | PAKAIHI I TE MOANA | MQ16 M | 10°27,84'S | 138°39,97'W | 0-1 | x | | | | | x | |
| MNHN-IM-2013-52978 | <i>Bufo</i> | <i>bufonia</i> | PAKAIHI I TE MOANA | MQ16 M | 10°27,84'S | 138°39,97'W | 0-1 | x | | | | | | |
| MNHN-IM-2013-52979 | <i>Bufo</i> | <i>bufonia</i> | PAKAIHI I TE MOANA | MQ16 M | 10°27,84'S | 138°39,97'W | 0-1 | x | x | x | | | | |
| MNHN-IM-2013-52980 | <i>Bufo</i> | <i>bufonia</i> | PAKAIHI I TE MOANA | MQ16 M | 10°27,84'S | 138°39,97'W | 0-1 | x | | | | | | |
| MNHN-IM-2007-43041 | <i>Bufo</i> | <i>cf.tuberosissima</i> | PANGLAO 2004 | M5 | 09°35,5'N | 123°43,3'44,3'E | 0-2 | x | x | x | | | x | x |
| MNHN-IM-2013-18934 | <i>Bufo</i> | <i>gnorima</i> | PAPUA NIUGINI | CP4053 | 03°03'S | 142°19'E | 300-308 | x | | | | | | |
| MNHN-IM-2013-18935 | <i>Bufo</i> | <i>gnorima</i> | PAPUA NIUGINI | CP4053 | 03°03'S | 142°19'E | 300-308 | x | | | | | | |
| MNHN-IM-2013-18936 | <i>Bufo</i> | <i>gnorima</i> | PAPUA NIUGINI | CP4053 | 03°03'S | 142°19'E | 300-308 | x | | | | | | |
| MNHN-IM-2013-18937 | <i>Bufo</i> | <i>gnorima</i> | PAPUA NIUGINI | CP4053 | 03°03'S | 142°19'E | 300-308 | x | | | | | | |
| MNHN-IM-2013-18938 | <i>Bufo</i> | <i>gnorima</i> | PAPUA NIUGINI | CP4053 | 03°03'S | 142°19'E | 300-308 | x | x | | | | x | |
| MNHN-IM-2013-19029 | <i>Bufo</i> | <i>gnorima</i> | PAPUA NIUGINI | CP4054 | 03°03'S | 142°20'E | 380-384 | x | | | | | | |
| MNHN-IM-2013-19062 | <i>Bufo</i> | <i>gnorima</i> | PAPUA NIUGINI | CP4053 | 03°03'S | 142°19'E | 300-308 | x | | | | | | |
| MNHN-IM-2007-43046 | <i>Bufo</i> | <i>lamarckii</i> | PANGLAO 2004 | R73 | 09°30,9'N | 123°40,8'E | 2-30 | x | | | | | | |
| MNHN-IM-2007-43054 | <i>Bufo</i> | <i>lamarckii</i> | SANTO 2006 | DR87 | 15°38,5'S | 167°15,1'E | 13 | x | | | x | x | | |
| MNHN-IM-2007-43062 | <i>Bufo</i> | <i>lamarckii</i> | PANGLAO 2004 | R43 | 09°41,3'N | 123°49,5'E | 3-41 | x | | | | | | |
| MNHN-IM-2013-13449 | <i>Bufo</i> | <i>lamarckii</i> | PAPUA NIUGINI | PM25 | 05°01,1'S | 145°47,9'E | | | | | | | | x |
| MNHN-IM-2013-13452 | <i>Bufo</i> | <i>lamarckii</i> | PAPUA NIUGINI | PM25 | 05°01,1'S | 145°47,9'E | - | x | | | | | | |
| MNHN-IM-2013-15805 | <i>Bufo</i> | <i>lamarckii</i> | PAPUA NIUGINI | PR115 | 05°18'S | 145°46,1'E | 17 | x | | | | | | |
| MNHN-IM-2013-16520 | <i>Bufo</i> | <i>lamarckii</i> | PAPUA NIUGINI | PR128 | 05°18'S | 145°46,7'E | 0-30 | x | | | | | | |
| MNHN-IM-2007-43045 | <i>Bufo</i> | <i>rosa</i> | SANTO 2006 | DB20 | 15°36,5'S | 167°01,4'E | 22-25 | x | | | x | x | | |
| MNHN-IM-2009-15927 | <i>Bufo</i> | <i>rosa</i> | ATIMO VATAE | TV13 | 25°04,4'S | 46°57,1'E | 4-5 | x | | | | | | |
| MNHN-IM-2009-22265 | <i>Bufo</i> | <i>rosa</i> | INHACA 2011 | MM18 | 26°03,5'S | 32°52,9'E | 0-1 | x | | | | | | |
| MNHN-IM-2009-22268 | <i>Bufo</i> | <i>rosa</i> | INHACA 2011 | MR27 | 26°06,3'S | 32°58,0'E | 17 | x | x | | | | | |
| MNHN-IM-2013-52996 | <i>Bufo</i> | <i>rosa</i> | PAKAIHI I TE MOANA | MQ11 II 01 | 08°55,8'S | 140°13,6'W | 38 | x | | | | | | |
| MNHN-IM-2007-43066 | <i>Bufo</i> | <i>tuberosissima</i> | PANGLAO 2004 | R24 | 09°37,5'N | 123°46,8'E | 0-2 | x | x | x | x | | | |

| | | | | | | | | | | |
|--------------------|------------------|----------------------|----------------------|--------|----------------|----------------|---------|---|---|-----|
| MNHN-IM-2013-10059 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR214 | | | 1-8 | x | | |
| MNHN-IM-2013-10236 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR04 | 05°10,1'S | 145°50,5'E | 30 | x | | x |
| MNHN-IM-2013-11544 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR13 | 05°12,3'S | 145°48,8'E | 8-10 | x | | |
| MNHN-IM-2013-11859 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR15 | 05°17,9'S | 145°46,7'E | 21 | x | | |
| MNHN-IM-2013-12023 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR16 | 05°12,5'S | 145°49,1'E | 13 | x | | |
| MNHN-IM-2013-12072 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR18 | 05°10,9'S | 145°48'E | 0-2 | x | | |
| MNHN-IM-2013-12098 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PB12 | 05°11,8'S | 145°48,8'E | 7-15 | x | | |
| MNHN-IM-2013-12297 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PM12 | 05°00,2'S | 145°47,6'E | 0-1 | x | | |
| MNHN-IM-2013-13150 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR35 | 05°06,3'S | 145°49,3'E | - | x | | |
| MNHN-IM-2013-13756 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PM25 | 05°01,1'S | 145°47,9'E | - | x | | |
| MNHN-IM-2013-14088 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR62 | 05°02,2'S | 145°48,4'E | - | x | | |
| MNHN-IM-2013-14727 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PM12 | 05°00,2'S | 145°47,6'E | 0-1 | x | | |
| MNHN-IM-2013-14749 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PM12 | 05°00,2'S | 145°47,6'E | 0-1 | x | | |
| MNHN-IM-2013-14970 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PB27 | 05°03,9'S | 145°48,8'E | 12 | x | | |
| MNHN-IM-2013-17422 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PD66 | 05°15,5'S | 145°47,3'E | 26 | x | | |
| MNHN-IM-2013-18014 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR203 | 05°10,3'S | 145°48,5'E | 1-19 | x | | |
| MNHN-IM-2013-18064 | <i>Bursa</i> | <i>tuberosissima</i> | PAPUA NIUGINI | PR211 | 05°15,5'S | 145°47,3'E | - | x | | |
| MNHN-IM-2009-7251 | <i>Bursina</i> | <i>gnorima</i> | MIRIKY | CP3260 | 15°35'S | 45°45'E | 179-193 | x | | |
| MNHN-IM-2009-7252 | <i>Bursina</i> | <i>gnorima</i> | MIRIKY | CP3241 | 14°30'S | 47°27'E | 274-325 | x | | |
| MNHN-IM-2009-7260 | <i>Bursina</i> | <i>gnorima</i> | MIRIKY | CP3208 | 12°41'S | 48°17'E | 231-237 | | x | |
| MNHN-IM-2007-42721 | <i>Bursina</i> | <i>ignobilis</i> | CONCALIS | DW3000 | 18°31'S | 163°07'E | 210-212 | x | | |
| MNHN-IM-2007-42722 | <i>Bursina</i> | <i>ignobilis</i> | CONCALIS | DW3000 | 18°31'S | 163°07'E | 210-212 | x | | |
| MNHN-IM-2007-42723 | <i>Bursina</i> | <i>ignobilis</i> | CONCALIS | DW3000 | 18°31'S | 163°07'E | 210-212 | x | | |
| MNHN-IM-2007-43052 | <i>Bursina</i> | <i>ignobilis</i> | SANTO 2006 | EP22 | 15°37,3'37,4'S | 167°05,8'6,0'E | 78-91 | x | x | x |
| MNHN-IM-2009-15944 | <i>Bursina</i> | <i>ignobilis</i> | ATIMO VATAE | CP3623 | 25°41,4'S | 45°59,2'E | 74-80 | x | | |
| MNHN-IM-2009-22029 | <i>Bursina</i> | <i>ignobilis</i> | TERRASSES | DW3106 | 23°02'S | 168°21'E | 180-220 | x | | |
| MNHN-IM-2009-7246 | <i>Bursina</i> | <i>ignobilis</i> | MIRIKY | DW3244 | 14° 54,67' S | 46° 55,54' E | 58-87 | x | | |
| MNHN-IM-2009-7250 | <i>Bursina</i> | <i>ignobilis</i> | MIRIKY | DW3244 | 14° 54,67' S | 46° 55,54' E | 58-87 | x | x | |
| MNHN-IM-2009-7249 | <i>Bursina</i> | <i>margaritula</i> | MIRIKY | CP3288 | 14° 31,9' S | 47° 26,54' E | 46-54 | | x | x |
| AF033686.1 | <i>Cabestana</i> | <i>spengleri</i> | mined from gene bank | | | | | | | x x |
| LSGB22602 | <i>Cymatium</i> | <i>cingulatum</i> | mined from gene bank | | | | | | | x |
| NC-013247 | <i>Cymatium</i> | <i>parthenopeum</i> | mined from gene bank | | | | | x | x | |
| MNHN-IM-2007-33056 | <i>Dulcerana</i> | <i>affinis</i> | SANTO 2006 | NR08 | 15°35,7'S | 167°07,4'E | 11 | x | | |
| MNHN-IM-2007-43037 | <i>Dulcerana</i> | <i>affinis</i> | SANTO 2006 | DR84 | 15°43,4'S | 167°15'E | 6 | x | | |
| MNHN-IM-2007-43039 | <i>Dulcerana</i> | <i>affinis</i> | PANGLAO 2004 | R24 | 09°37,5'N | 123°46,8'E | 0-2 | x | | |
| MNHN-IM-2007-43042 | <i>Dulcerana</i> | <i>affinis</i> | SANTO 2006 | DR03 | 15°31,1'S | 167°15,8'E | 2-30 | x | | |

| | | | | | | | | |
|--------------------|------------------|---------------------|------------------------|------------|------------|-----------------|-------|-------|
| MNHN-IM-2007-43056 | <i>Dulcerana</i> | <i>affinis</i> | SANTO 2006 | VM02 | 15°34,9'S | 167°02,4'E | 0-1 | x |
| MNHN-IM-2007-43059 | <i>Dulcerana</i> | <i>affinis</i> | SANTO 2006 | FR09 | 15°32,4'S | 167°11,8'E | 1-42 | x |
| MNHN-IM-2007-43060 | <i>Dulcerana</i> | <i>affinis</i> | SANTO 2006 | VM02 | 15°34,9'S | 167°02,4'E | 0-1 | x |
| MNHN-IM-2007-43069 | <i>Dulcerana</i> | <i>affinis</i> | SANTO 2006 | VM46 | 15°34,5'S | 167°12,3'E | - | x |
| MNHN-IM-2013-11041 | <i>Dulcerana</i> | <i>affinis</i> | PAPUA NIUGINI | PR08 | 05°09,9'S | 145°50,4'E | 22 | x |
| MNHN-IM-2013-11468 | <i>Dulcerana</i> | <i>affinis</i> | PAPUA NIUGINI | PFM01 | 05°11'S | 145°48,1'E | 2 | x |
| MNHN-IM-2013-11598 | <i>Dulcerana</i> | <i>affinis</i> | PAPUA NIUGINI | PM12 | 05°00,2'S | 145°47,6'E | 0-1 | x |
| MNHN-IM-2013-12827 | <i>Dulcerana</i> | <i>affinis</i> | PAPUA NIUGINI | PR27 | 05°04,7'S | 145°48,8'E | 7 | x |
| MNHN-IM-2013-12981 | <i>Dulcerana</i> | <i>affinis</i> | PAPUA NIUGINI | PR29 | 05°05,6'S | 145°49,4'E | - | x |
| MNHN-IM-2013-14733 | <i>Dulcerana</i> | <i>affinis</i> | PAPUA NIUGINI | PM12 | 05°00,2'S | 145°47,6'E | 0-1 | x |
| MNHN-IM-2013-52997 | <i>Dulcerana</i> | <i>affinis</i> | PAKAIHI I TE MOANA | MQ11 II 01 | 08°55,8'S | 140°13,6'W | 38 | x |
| MNHN-IM-2013-52998 | <i>Dulcerana</i> | <i>affinis</i> | PAKAIHI I TE MOANA | MQ11 II 01 | 08°55,8'S | 140°13,6'W | 38 | x |
| MNHN-IM-2013-19491 | <i>Dulcerana</i> | <i>cubaniana</i> | KARUBENTHOS 2012 | GR37 | 16°30,04'N | 61°28,79'W | 16 | x |
| MNHN-IM-2013-19496 | <i>Dulcerana</i> | <i>cubaniana</i> | KARUBENTHOS 2012 | GR33 | 16°22,88'N | 61°31,43'W | 9 | x |
| MNHN-IM-2013-19596 | <i>Dulcerana</i> | <i>cubaniana</i> | KARUBENTHOS 2012 | GM09 | 16°05,44'N | 61°46,02'W | 1 | x |
| MNHN-IM-2013-20121 | <i>Dulcerana</i> | <i>cubaniana</i> | KARUBENTHOS 2012 | GM07 | 16°10,45'N | 61°46,78'W | 1 | x |
| MNHN-IM-2013-20184 | <i>Dulcerana</i> | <i>cubaniana</i> | KARUBENTHOS 2012 | GM09 | 16°05,44'N | 61°46,02'W | 1 | x |
| MNHN-IM-2013-20247 | <i>Dulcerana</i> | <i>cubaniana</i> | KARUBENTHOS 2012 | GR13 | 16°07,61'N | 61°46,53'W | 11 | x |
| MNHN-IM-2013-8684 | <i>Dulcerana</i> | <i>cubaniana</i> | KARUBENTHOS 2012 | GR49 | 16°09,71'N | 61°07,73'W | 15 | x |
| MNHN-IM-2009-23312 | <i>Dulcerana</i> | <i>elisabettiae</i> | WESTERN AUSTRALIA 2011 | WA20 | 35°04,54'S | 117°58,35'E | 4-12 | x |
| MNHN-IM-2009-23319 | <i>Dulcerana</i> | <i>elisabettiae</i> | WESTERN AUSTRALIA 2011 | WA17 | 35°06,46'S | 118°01,28'E | 20 | x |
| MNHN-IM-2009-23322 | <i>Dulcerana</i> | <i>elisabettiae</i> | WESTERN AUSTRALIA 2011 | WA20 | 35°04,54'S | 117°58,35'E | 4-12 | x |
| MNHN-IM-2007-33097 | <i>Dulcerana</i> | <i>granularis</i> | SANTO 2006 | VM61 | 15°28,5'S | 167°15,5'E | 0-1 | x |
| MNHN-IM-2007-33115 | <i>Dulcerana</i> | <i>granularis</i> | PANGLAO 2004 | M7 | 09°36,1'N | 123°45,2'E | 0-3 | x |
| MNHN-IM-2007-43049 | <i>Dulcerana</i> | <i>granularis</i> | SANTO 2006 | VM61 | 15°28,5'S | 167°15,5'E | 1 | x |
| MNHN-IM-2007-43064 | <i>Dulcerana</i> | <i>granularis</i> | PANGLAO 2004 | M5 | 09°35,5'N | 123°43,3'44,3'E | 0-2 | x |
| MNHN-IM-2007-43070 | <i>Dulcerana</i> | <i>granularis</i> | SANTO 2006 | DB83 | 15°43,4'S | 167°15'E | 6 | x |
| MNHN-IM-2007-43071 | <i>Dulcerana</i> | <i>granularis</i> | SANTO 2006 | VM62 | 15°28,8'S | 167°15,3'E | 0-1 | x |
| MNHN-IM-2009-15888 | <i>Dulcerana</i> | <i>granularis</i> | ATIMO VATAE | TR13 | 25°08.1'S | 46°47.7'E | 16-20 | x |
| MNHN-IM-2009-15950 | <i>Dulcerana</i> | <i>granularis</i> | ATIMO VATAE | TM16 | 25°06.7'S | 46°49.9'E | 0-1 | x |
| MNHN-IM-2009-23292 | <i>Dulcerana</i> | <i>granularis</i> | INHACA 2011 | MM2 | 26°02.5'S | 32°53.5'E | 0-1 | x |
| MNHN-IM-2009-23302 | <i>Dulcerana</i> | <i>granularis</i> | INHACA 2011 | MR4 | 26°06.3'S | 32°58.0'E | 17-19 | x |
| MNHN-IM-2009-24728 | <i>Dulcerana</i> | <i>granularis</i> | | | | | - | x |
| MNHN-IM-2009-5148 | <i>Dulcerana</i> | <i>granularis</i> | MAINBAZA | DW3168 | 26°12'S | 35°03'E | 87-90 | x |
| MNHN-IM-2013-53041 | <i>Dulcerana</i> | <i>granularis</i> | INHACA 2011 | MB6 | 25°59.5'S | 32°54.3'E | 2-10 | x |
| NC-028003.1 | <i>Galeodea</i> | <i>echinophora</i> | mined from gene bank | | | | | x x x |

| MNHN-IM-2013-53010 | <i>Gen.</i> | <i>sp.</i> | PAKAIHI I TE MOANA | MQ11 II 01 | 08°55,8'S | 140°13,6'W | 38 | x |
|--------------------|-------------------|------------------|--------------------|------------|-----------|------------|---------|---|
| MNHN-IM-2007-43030 | <i>Korrigania</i> | <i>awatii</i> | SALOMON 2 | DW2302 | 09°07'S | 158°22'E | 254-341 | x |
| MNHN-IM-2007-43031 | <i>Korrigania</i> | <i>awatii</i> | PANGLAO 2005 | CA2337 | 09°32'N | 123°42'E | 362 | x |
| MNHN-IM-2007-43032 | <i>Korrigania</i> | <i>awatii</i> | PANGLAO 2005 | CA2337 | 09°32'N | 123°42'E | 362 | x |
| MNHN-IM-2007-43033 | <i>Korrigania</i> | <i>awatii</i> | PANGLAO 2005 | CA2337 | 09°32'N | 123°42'E | 362 | x |
| MNHN-IM-2007-43058 | <i>Korrigania</i> | <i>awatii</i> | PANGLAO 2005 | CP2372 | 08°39'N | 123°16'E | 255-301 | x |
| MNHN-IM-2007-33147 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |
| MNHN-IM-2007-40279 | <i>Korrigania</i> | <i>fijiensis</i> | NORFOLK 2 | CP2139 | 23°01'S | 168°23'E | 372-393 | x |
| MNHN-IM-2007-40280 | <i>Korrigania</i> | <i>fijiensis</i> | NORFOLK 2 | CP2139 | 23°01'S | 168°23'E | 372-393 | x |
| MNHN-IM-2007-40281 | <i>Korrigania</i> | <i>fijiensis</i> | NORFOLK 2 | CP2139 | 23°01'S | 168°23'E | 372-393 | x |
| MNHN-IM-2007-40282 | <i>Korrigania</i> | <i>fijiensis</i> | NORFOLK 2 | CP2139 | 23°01'S | 168°23'E | 372-393 | x |
| MNHN-IM-2007-40283 | <i>Korrigania</i> | <i>fijiensis</i> | NORFOLK 2 | CP2139 | 23°01'S | 168°23'E | 372-393 | x |
| MNHN-IM-2007-40284 | <i>Korrigania</i> | <i>fijiensis</i> | NORFOLK 2 | CP2139 | 23°01'S | 168°23'E | 372-393 | x |
| MNHN-IM-2007-40285 | <i>Korrigania</i> | <i>fijiensis</i> | NORFOLK 2 | CP2139 | 23°01'S | 168°23'E | 372-393 | x |
| MNHN-IM-2007-40286 | <i>Korrigania</i> | <i>fijiensis</i> | NORFOLK 2 | CP2139 | 23°01'S | 168°23'E | 372-393 | x |
| MNHN-IM-2007-40318 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |
| MNHN-IM-2007-40319 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |
| MNHN-IM-2007-40320 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |
| MNHN-IM-2007-40321 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2612 | 19°35'S | 158°41'E | 392 | x |
| MNHN-IM-2007-40322 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2612 | 19°35'S | 158°41'E | 392 | x |
| MNHN-IM-2007-40323 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2612 | 19°35'S | 158°41'E | 392 | x |
| MNHN-IM-2007-40324 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2607 | 19°33'S | 158°40'E | 400-413 | x |
| MNHN-IM-2007-40325 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2607 | 19°33'S | 158°40'E | 400-413 | x |
| MNHN-IM-2007-40326 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2607 | 19°33'S | 158°40'E | 400-413 | x |
| MNHN-IM-2007-40327 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2607 | 19°33'S | 158°40'E | 400-413 | x |
| MNHN-IM-2007-40328 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2607 | 19°33'S | 158°40'E | 400-413 | x |
| MNHN-IM-2007-40329 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2607 | 19°33'S | 158°40'E | 400-413 | x |
| MNHN-IM-2007-40330 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2608 | 19°33'S | 158°40'E | 393-396 | x |
| MNHN-IM-2007-40336 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |
| MNHN-IM-2007-40341 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2526 | 22°46'S | 159°23'E | 330-340 | x |
| MNHN-IM-2007-40343 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2525 | 22°48'S | 159°23'E | 408-410 | x |
| MNHN-IM-2007-40347 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2577 | 20°20'S | 158°39'E | 399-602 | x |
| MNHN-IM-2007-40348 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2577 | 20°20'S | 158°39'E | 399-602 | x |
| MNHN-IM-2007-40349 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2577 | 20°20'S | 158°39'E | 399-602 | x |
| MNHN-IM-2007-40351 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |
| MNHN-IM-2007-40352 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |

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|--------------------|-------------------|------------------|--------------|--------|---------|----------|---------|---|
| MNHN-IM-2007-40358 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2577 | 20°20'S | 158°39'E | 399-602 | x |
| MNHN-IM-2007-40359 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2606 | 19°37'S | 158°42'E | 442-443 | x |
| MNHN-IM-2007-40360 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2606 | 19°37'S | 158°42'E | 442-443 | x |
| MNHN-IM-2007-40361 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW2606 | 19°37'S | 158°42'E | 442-443 | x |
| MNHN-IM-2007-42671 | <i>Korrigania</i> | <i>fijiensis</i> | CONCALIS | DW2996 | 18°01'S | 163°01'E | 487-500 | x |
| MNHN-IM-2007-42724 | <i>Korrigania</i> | <i>fijiensis</i> | CONCALIS | CP2959 | 19°00'S | 163°14'E | 394-407 | x |
| MNHN-IM-2007-42725 | <i>Korrigania</i> | <i>fijiensis</i> | CONCALIS | CP2959 | 19°00'S | 163°14'E | 394-407 | x |
| MNHN-IM-2007-43416 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | CP3089 | 22°17'S | 167°12'E | 390-410 | x |
| MNHN-IM-2007-43420 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3114 | 22°44'S | 167°14'E | 350-380 | x |
| MNHN-IM-2007-43421 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3077 | 23°15'S | 168°14'E | 420-540 | x |
| MNHN-IM-2007-43423 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43430 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | CP3049 | 23°42'S | 168°16'E | 380-410 | x |
| MNHN-IM-2007-43431 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3105 | 22°59'S | 168°22'E | 420 | x |
| MNHN-IM-2007-43435 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3105 | 22°59'S | 168°22'E | 420 | x |
| MNHN-IM-2007-43436 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3105 | 22°59'S | 168°22'E | 420 | x |
| MNHN-IM-2007-43437 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3077 | 23°15'S | 168°14'E | 420-540 | x |
| MNHN-IM-2007-43548 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43550 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3127 | 23°00'S | 167°16'E | 400-420 | x |
| MNHN-IM-2007-43552 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3121 | 22°45'S | 167°13'E | 380-400 | x |
| MNHN-IM-2007-43553 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3127 | 23°00'S | 167°16'E | 400-420 | x |
| MNHN-IM-2007-43562 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3127 | 23°00'S | 167°16'E | 400-420 | x |
| MNHN-IM-2007-43571 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3127 | 23°00'S | 167°16'E | 400-420 | x |
| MNHN-IM-2007-43572 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43596 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3127 | 23°00'S | 167°16'E | 400-420 | x |
| MNHN-IM-2007-43597 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43598 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43599 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3127 | 23°00'S | 167°16'E | 400-420 | x |
| MNHN-IM-2007-43602 | <i>Korrigania</i> | <i>fijiensis</i> | TERRASSES | DW3121 | 22°45'S | 167°13'E | 380-400 | x |
| MNHN-IM-2009-28468 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW3785 | 22°15'S | 167°10'E | 386-387 | x |
| MNHN-IM-2009-28471 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW3785 | 22°15'S | 167°10'E | 386-387 | x |
| MNHN-IM-2009-28472 | <i>Korrigania</i> | <i>fijiensis</i> | EXBODI | DW3930 | 18°37'S | 164°26'E | 448-464 | x |
| MNHN-IM-2009-5458 | <i>Korrigania</i> | <i>fijiensis</i> | CONCALIS | DW2995 | 18°00'S | 163°04'E | 450-495 | x |
| MNHN-IM-2009-5459 | <i>Korrigania</i> | <i>fijiensis</i> | CONCALIS | DW2995 | 18°00'S | 163°04'E | 450-495 | x |
| MNHN-IM-2009-5460 | <i>Korrigania</i> | <i>fijiensis</i> | CONCALIS | DW2995 | 18°00'S | 163°04'E | 450-495 | x |
| MNHN-IM-2007-43048 | <i>Korrigania</i> | <i>fosteri</i> | PANGLAO 2004 | P1 | 09°36'N | 123°45'E | 90-200 | x |
| MNHN-IM-2009-22032 | <i>Korrigania</i> | <i>fosteri</i> | CONCALIS | DW2932 | 19°05'S | 163°30'E | 215-225 | x |

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|--------------------|-------------------|-------------------|-----------|---------|---------|----------|---------|---|
| MNHN-IM-2009-5461 | <i>Korrigania</i> | <i>fosteri</i> | CONCALIS | DW2932 | 19°05'S | 163°30'E | 215-225 | x |
| MNHN-IM-2007-40259 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2528 | 22°49'S | 159°23'E | 320-345 | x |
| MNHN-IM-2007-40260 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2528 | 22°49'S | 159°23'E | 320-345 | x |
| MNHN-IM-2007-40261 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2526 | 22°46'S | 159°23'E | 330-340 | x |
| MNHN-IM-2007-40262 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 2 | DW2040 | 23°41'S | 168°01'E | 285 | x |
| MNHN-IM-2007-40263 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 2 | DW2093 | 24°44'S | 168°09'E | 230 | x |
| MNHN-IM-2007-40264 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 2 | CP2140 | 23°00'S | 168°22'E | 270-350 | x |
| MNHN-IM-2007-40275 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | no data | | | | x |
| MNHN-IM-2007-40276 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40277 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | no data | | | | x |
| MNHN-IM-2007-40278 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40298 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40299 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1675 | 24°44'S | 168°09'E | 231-233 | x |
| MNHN-IM-2007-40300 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40301 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40302 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40303 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40304 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40305 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40306 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40307 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40308 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40309 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x |
| MNHN-IM-2007-40331 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2564 | 20°25'S | 158°41'E | 333-386 | x |
| MNHN-IM-2007-40332 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2564 | 20°25'S | 158°41'E | 333-386 | x |
| MNHN-IM-2007-40334 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |
| MNHN-IM-2007-40335 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |
| MNHN-IM-2007-40337 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x |
| MNHN-IM-2007-40350 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2577 | 20°20'S | 158°39'E | 399-602 | x |
| MNHN-IM-2007-40353 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | DW1727 | 23°19'S | 168°15'E | 190-212 | x |
| MNHN-IM-2007-40354 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 2 | DW2040 | 23°41'S | 168°01'E | 285 | x |
| MNHN-IM-2007-40355 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 2 | DW2040 | 23°41'S | 168°01'E | 285 | x |
| MNHN-IM-2007-40356 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 2 | DW2040 | 23°41'S | 168°01'E | 285 | x |
| MNHN-IM-2007-40357 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 2 | DW2040 | 23°41'S | 168°01'E | 285 | x |
| MNHN-IM-2007-40567 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW2564 | 20°25'S | 158°41'E | 333-386 | x |
| MNHN-IM-2007-42267 | <i>Korrigania</i> | <i>quirihorai</i> | NORFOLK 1 | no data | | | - | x |

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|--------------------|-------------------|-------------------|-----------|--------|---------|----------|---------|---|
| MNHN-IM-2007-42738 | <i>Korrigania</i> | <i>quirihorai</i> | CONCALIS | DW2951 | 18°58'S | 163°25'E | 300 | x |
| MNHN-IM-2007-42739 | <i>Korrigania</i> | <i>quirihorai</i> | CONCALIS | DW2951 | 18°58'S | 163°25'E | 300 | x |
| MNHN-IM-2007-43408 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3101 | 22°59'S | 168°21'E | 320-390 | x |
| MNHN-IM-2007-43409 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3101 | 22°59'S | 168°21'E | 320-390 | x |
| MNHN-IM-2007-43410 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3056 | 23°42'S | 168°01'E | 250-330 | x |
| MNHN-IM-2007-43411 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3056 | 23°42'S | 168°01'E | 250-330 | x |
| MNHN-IM-2007-43413 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3090 | 22°16'S | 167°08'E | 260 | x |
| MNHN-IM-2007-43414 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43422 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | CP3055 | 23°42'S | 168°01'E | 250-320 | x |
| MNHN-IM-2007-43432 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3110 | 23°02'S | 168°16'E | 270-310 | x |
| MNHN-IM-2007-43433 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3056 | 23°42'S | 168°01'E | 250-330 | x |
| MNHN-IM-2007-43439 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3056 | 23°42'S | 168°01'E | 250-330 | x |
| MNHN-IM-2007-43554 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3069 | 23°18'S | 168°05'E | 300-320 | x |
| MNHN-IM-2007-43555 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43563 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3090 | 22°16'S | 167°08'E | 260 | x |
| MNHN-IM-2007-43564 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43566 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | CP3054 | 23°42'S | 168°01'E | 240-260 | x |
| MNHN-IM-2007-43567 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3069 | 23°18'S | 168°05'E | 300-320 | x |
| MNHN-IM-2007-43569 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43570 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43587 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43590 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2007-43593 | <i>Korrigania</i> | <i>quirihorai</i> | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x |
| MNHN-IM-2009-28423 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x |
| MNHN-IM-2009-28425 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3896 | 22°19'S | 168°41'E | 340-343 | x |
| MNHN-IM-2009-28426 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x |
| MNHN-IM-2009-28428 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3896 | 22°19'S | 168°41'E | 340-343 | x |
| MNHN-IM-2009-28431 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | CP3788 | 22°13'S | 167°07'E | 264-273 | x |
| MNHN-IM-2009-28432 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | CP3898 | 22°18'S | 168°42'E | 340-346 | x |
| MNHN-IM-2009-28434 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3896 | 22°19'S | 168°41'E | 340-343 | x |
| MNHN-IM-2009-28435 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3896 | 22°19'S | 168°41'E | 340-343 | x |
| MNHN-IM-2009-28439 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3896 | 22°19'S | 168°41'E | 340-343 | x |
| MNHN-IM-2009-28440 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | CP3898 | 22°18'S | 168°42'E | 340-346 | x |
| MNHN-IM-2009-28441 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3896 | 22°19'S | 168°41'E | 340-343 | x |
| MNHN-IM-2009-28442 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | CP3788 | 22°13'S | 167°07'E | 264-273 | x |
| MNHN-IM-2009-28443 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3784 | 22°13'S | 167°09'E | 353-365 | x |

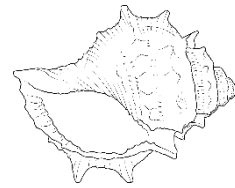
| | | | | | | | | | | | | | |
|--------------------|--------------------|-------------------|--------------------|------------|------------|-------------|---------|---|---|---|---|--|---|
| MNHN-IM-2009-28444 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | | | | | |
| MNHN-IM-2009-28447 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | CP3898 | 22°18'S | 168°42'E | 340-346 | x | | | | | |
| MNHN-IM-2009-28448 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | | | | | |
| MNHN-IM-2009-28449 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3784 | 22°13'S | 167°09'E | 353-365 | x | | | | | |
| MNHN-IM-2009-28450 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3900 | 22°17'S | 168°41'E | 355-357 | x | | | | | |
| MNHN-IM-2009-28451 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3900 | 22°17'S | 168°41'E | 355-357 | x | | | | | |
| MNHN-IM-2009-28455 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | CP3789 | 22°11'S | 167°07'E | 335-350 | x | | | | | |
| MNHN-IM-2009-28456 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3928 | 18°38'S | 164°20'E | 362-402 | x | | | | | |
| MNHN-IM-2009-28457 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3900 | 22°17'S | 168°41'E | 355-357 | x | | | | | |
| MNHN-IM-2009-28459 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3896 | 22°19'S | 168°41'E | 340-343 | x | | | | | |
| MNHN-IM-2009-28475 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | | | | | |
| MNHN-IM-2009-28476 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | | | | | |
| MNHN-IM-2009-5454 | <i>Korrigania</i> | <i>quirihorai</i> | CONCALIS | DW2973 | 18°14'S | 163°06'E | 275-288 | x | | | | | |
| MNHN-IM-2009-5455 | <i>Korrigania</i> | <i>quirihorai</i> | CONCALIS | DW2973 | 18°14'S | 163°06'E | 275-288 | x | | | | | |
| MNHN-IM-2009-5466 | <i>Korrigania</i> | <i>quirihorai</i> | CONCALIS | CC2929 | 19°56.5'S | 163°50.1'E | 28-30 | x | | | | | |
| MNHN-IM-2013-52981 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | CP3898 | 22°18'S | 168°42'E | 340-346 | x | | | | | x |
| MNHN-IM-2013-52984 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | CP3856 | 22°19'S | 168°41'E | 338 | x | | | | | |
| MNHN-IM-2013-52985 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | CP3898 | 22°18'S | 168°42'E | 340-346 | x | | | | | |
| MNHN-IM-2013-52990 | <i>Korrigania</i> | <i>quirihorai</i> | EXBODI | DW3896 | 22°19'S | 168°41'E | 340-343 | x | | | | | |
| MNHN-IM-2013-11043 | <i>Lampasopsis</i> | <i>rhodostoma</i> | PAPUA NIUGINI | PR08 | 05°09,9'S | 145°50,4'E | 22 | | | | | | x |
| MNHN-IM-2009-15907 | <i>Lampasopsis</i> | <i>cruentata</i> | ATIMO VATAE | TA52 | 25°02,4'S | 46°59,6'E | 8-14 | x | | | | | |
| MNHN-IM-2013-12462 | <i>Lampasopsis</i> | <i>cruentata</i> | PAPUA NIUGINI | PR20 | 05°17,8'S | 145°46,9'E | 22 | x | x | | | | |
| MNHN-IM-2013-12992 | <i>Lampasopsis</i> | <i>cruentata</i> | PAPUA NIUGINI | PR29 | 05°05,6'S | 145°49,4'E | - | x | | | | | |
| MNHN-IM-2013-18273 | <i>Lampasopsis</i> | <i>cruentata</i> | PAPUA NIUGINI | PB47 | 05°11,3'S | 145°49,6'E | 5 | x | | | | | |
| MNHN-IM-2013-52966 | <i>Lampasopsis</i> | <i>cruentata</i> | TUHAA PAE 2013 | ARU02 | 22°26,5'S | 151°20,5'W | 19 | x | | | | | |
| MNHN-IM-2013-52999 | <i>Lampasopsis</i> | <i>cruentata</i> | PAKAIHI I TE MOANA | MQ1 GR | 08°56,21'S | 140°05,45'W | 8-10 | x | | | | | |
| MNHN-IM-2013-53005 | <i>Lampasopsis</i> | <i>cruentata</i> | PAKAIHI I TE MOANA | MQ2 GR | 08°56,23'S | 140°07,24'W | 20-23 | x | | | | | |
| MNHN-IM-2013-53006 | <i>Lampasopsis</i> | <i>cruentata</i> | PAKAIHI I TE MOANA | MQ11 II 09 | 07°54,3'S | 140°34,1'W | 28 | x | | | | | |
| MNHN-IM-2013-53008 | <i>Lampasopsis</i> | <i>cruentata</i> | PAKAIHI I TE MOANA | MQ24 R | 09°23,71'S | 140°07,76'W | 6-12 | x | | | | | |
| MNHN-IM-2013-53009 | <i>Lampasopsis</i> | <i>cruentata</i> | PAKAIHI I TE MOANA | MQ11 II 04 | 08°48,2'S | 140°03,1'W | 28 | x | | | | | |
| MNHN-IM-2013-53012 | <i>Lampasopsis</i> | <i>cruentata</i> | PAKAIHI I TE MOANA | MQ11 II 13 | 08°55,4'S | 140°01,2'W | 36 | x | | | | | |
| MNHN-IM-2013-53013 | <i>Lampasopsis</i> | <i>cruentata</i> | PAKAIHI I TE MOANA | MQ11 II 13 | 08°55,4'S | 140°01,2'W | 36 | x | | x | | | x |
| MNHN-IM-2007-43068 | <i>Lampasopsis</i> | <i>rhodostoma</i> | PANGLAO 2004 | R50 | 09°35,7'N | 123°44,4'E | 3-7 | x | x | x | x | | x |
| MNHN-IM-2009-15916 | <i>Lampasopsis</i> | <i>rhodostoma</i> | ATIMO VATAE | TA52 | 25°02,4'S | 46°59,6'E | 8-14 | x | | | | | |
| MNHN-IM-2009-15917 | <i>Lampasopsis</i> | <i>rhodostoma</i> | ATIMO VATAE | TS04 | 25°02,3'S | 47°00,3'E | 22-24 | x | | | | | |
| MNHN-IM-2009-5146 | <i>Lampasopsis</i> | <i>rhodostoma</i> | MAINBAZA | DW3168 | 26°12'S | 35°03'E | 87-90 | x | | | | | |

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|--------------------|-----------------------|-------------------|------------------|---------|------------|------------|---------|---|---|---|---|
| MNHN-IM-2009-5147 | <i>Lampasopsis</i> | <i>rhodostoma</i> | MAINBAZA | DW3168 | 26°12'S | 35°03'E | 87-90 | x | x | | x |
| MNHN-IM-2013-15499 | <i>Lampasopsis</i> | <i>rhodostoma</i> | PAPUA NIUGINI | PR107 | 05°10,2'S | 145°50,4'E | 17 | x | | | |
| MNHN-IM-2007-43067 | <i>Lampasopsis</i> | <i>rhodostoma</i> | SANTO 2006 | DB53 | 15°28,8'S | 167°15,2'E | 5 | x | | | |
| MNHN-IM-2013-20452 | <i>Lampasopsis</i> | <i>thomae</i> | KARUBENTHOS 2012 | GB02 | 16°21,97'N | 61°37,98'W | 11 | x | | | |
| MNHN-IM-2013-8179 | <i>Lampasopsis</i> | <i>thomae</i> | KARUBENTHOS 2012 | GM08 | 16°07,57'N | 61°46,45'W | 1 | x | | | |
| MNHN-IM-2013-8181 | <i>Lampasopsis</i> | <i>thomae</i> | KARUBENTHOS 2012 | GR13 | 16°07,61'N | 61°46,53'W | 11 | x | | | |
| MNHN-IM-2013-8184 | <i>Lampasopsis</i> | <i>thomae</i> | KARUBENTHOS 2012 | GR13 | 16°07,61'N | 61°46,53'W | 11 | x | | | |
| MNHN-IM-2013-8185 | <i>Lampasopsis</i> | <i>thomae</i> | KARUBENTHOS 2012 | GR13 | 16°07,61'N | 61°46,53'W | 11 | x | | | |
| MNHN-IM-2013-8776 | <i>Lampasopsis</i> | <i>thomae</i> | KARUBENTHOS 2012 | GB08 | 16°02,38'N | 61°45,71'W | 17 | x | x | x | x |
| MNHN-IM-2013-56124 | <i>Marsupina</i> | <i>bufo</i> | GUYANE 2014 | CP4344 | 05°08,7'N | 51°58,7'W | 47 | x | | | |
| MNHN-IM-2013-56144 | <i>Marsupina</i> | <i>bufo</i> | GUYANE 2014 | CP4344 | 05°08,7'N | 51°58,7'W | 47 | x | x | x | x |
| SBMNH-460303 | <i>Marsupina</i> | <i>nana</i> | | | | | | x | x | | |
| MNHN-IM-2009-28473 | <i>Talisman</i> | <i>corrugata</i> | - | | 01°39,0' N | 07°17,7' E | 4-8 | x | x | x | |
| MNHN-IM-2013-56022 | <i>Talisman</i> | <i>corrugata</i> | GUYANE 2014 | CP4357 | 06°33,8'N | 53°07,8'W | 60-61 | x | | | |
| MNHN-IM-2013-56022 | <i>Talisman</i> | <i>corrugata</i> | GUYANE 2014 | CP4357 | 06°33,8'N | 53°07,8'W | 60-61 | x | | | |
| MNHN-IM-2007-40255 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40256 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40257 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40258 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40265 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40266 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40267 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40268 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40269 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40270 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40271 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40272 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40273 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | no data | | | | x | | | |
| MNHN-IM-2007-40274 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | | | |
| MNHN-IM-2007-40287 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 2 | DW2135 | 23°02'S | 168°21'E | 295-330 | x | | | |
| MNHN-IM-2007-40288 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 2 | DW2093 | 24°44'S | 168°09'E | 230 | x | | | |
| MNHN-IM-2007-40289 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 2 | DW2093 | 24°44'S | 168°09'E | 230 | x | | | |
| MNHN-IM-2007-40290 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 2 | DW2126 | 23°16'S | 168°14'E | 398-550 | x | | | |
| MNHN-IM-2007-40291 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 2 | DW2040 | 23°41'S | 168°01'E | 285 | x | | | |
| MNHN-IM-2007-40292 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 2 | DW2040 | 23°41'S | 168°01'E | 285 | x | | | |
| MNHN-IM-2007-40293 | <i>Tritonoranella</i> | <i>latitudo</i> | NORFOLK 2 | DW2040 | 23°41'S | 168°01'E | 285 | x | | | |

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| MNHN-IM-2007-40294 | <i>Tritonoranella</i> | latitudo | NORFOLK 2 | DW2040 | 23°41'S | 168°01'E | 285 | x | |
| MNHN-IM-2007-40295 | <i>Tritonoranella</i> | latitudo | NORFOLK 2 | CP2095 | 24°46'S | 168°10'E | 283-310 | x | |
| MNHN-IM-2007-40296 | <i>Tritonoranella</i> | latitudo | NORFOLK 2 | CP2095 | 24°46'S | 168°10'E | 283-310 | x | |
| MNHN-IM-2007-40297 | <i>Tritonoranella</i> | latitudo | NORFOLK 2 | DW2151 | 22°43'S | 167°14'E | 353-368 | x | |
| MNHN-IM-2007-40310 | <i>Tritonoranella</i> | latitudo | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | |
| MNHN-IM-2007-40311 | <i>Tritonoranella</i> | latitudo | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | |
| MNHN-IM-2007-40312 | <i>Tritonoranella</i> | latitudo | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | |
| MNHN-IM-2007-40313 | <i>Tritonoranella</i> | latitudo | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | |
| MNHN-IM-2007-40314 | <i>Tritonoranella</i> | latitudo | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | |
| MNHN-IM-2007-40315 | <i>Tritonoranella</i> | latitudo | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | |
| MNHN-IM-2007-40316 | <i>Tritonoranella</i> | latitudo | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | |
| MNHN-IM-2007-40317 | <i>Tritonoranella</i> | latitudo | NORFOLK 1 | DW1659 | 23°38'S | 167°42'E | 449-467 | x | |
| MNHN-IM-2007-40333 | <i>Tritonoranella</i> | latitudo | EXBODI | DW2576 | 20°20'S | 158°43'E | 390-394 | x | |
| MNHN-IM-2007-40338 | <i>Tritonoranella</i> | latitudo | EXBODI | DW2526 | 22°46'S | 159°23'E | 330-340 | x | |
| MNHN-IM-2007-40339 | <i>Tritonoranella</i> | latitudo | EXBODI | DW2526 | 22°46'S | 159°23'E | 330-340 | x | |
| MNHN-IM-2007-40340 | <i>Tritonoranella</i> | latitudo | EXBODI | DW2526 | 22°46'S | 159°23'E | 330-340 | x | |
| MNHN-IM-2007-40342 | <i>Tritonoranella</i> | latitudo | EXBODI | DW2530 | 22°48'S | 159°23'E | 338-343 | x | |
| MNHN-IM-2007-40344 | <i>Tritonoranella</i> | latitudo | EXBODI | DW2525 | 22°48'S | 159°23'E | 408-410 | x | |
| MNHN-IM-2007-40345 | <i>Tritonoranella</i> | latitudo | EXBODI | DW2634 | 21°05'S | 160°46'E | 342-347 | x | |
| MNHN-IM-2007-40346 | <i>Tritonoranella</i> | latitudo | EXBODI | DW2504 | 24°48'S | 159°46'E | 390-600 | x | |
| MNHN-IM-2007-43419 | <i>Tritonoranella</i> | latitudo | TERRASSES | DW3069 | 23°18'S | 168°05'E | 300-320 | x | |
| MNHN-IM-2007-43589 | <i>Tritonoranella</i> | latitudo | TERRASSES | DW3102 | 22°59'S | 168°23'E | 410-430 | x | x |
| MNHN-IM-2007-43604 | <i>Tritonoranella</i> | latitudo | TERRASSES | DW3056 | 23°42'S | 168°01'E | 250-330 | x | |
| MNHN-IM-2009-22055 | <i>Tritonoranella</i> | latitudo | CONCALIS | DW2963 | 18°22'S | 162°59'E | 220-240 | x | |
| MNHN-IM-2009-22175 | <i>Tritonoranella</i> | latitudo | CONCALIS | DW2932 | 19°05'S | 163°30'E | 215-225 | x | |
| MNHN-IM-2009-28427 | <i>Tritonoranella</i> | latitudo | EXBODI | DW3857 | 22°18'S | 168°42'E | 342 | x | |
| MNHN-IM-2009-28463 | <i>Tritonoranella</i> | latitudo | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | |
| MNHN-IM-2009-28464 | <i>Tritonoranella</i> | latitudo | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | |
| MNHN-IM-2009-28465 | <i>Tritonoranella</i> | latitudo | EXBODI | DW3896 | 22°19'S | 168°41'E | 340-343 | x | |
| MNHN-IM-2009-28466 | <i>Tritonoranella</i> | latitudo | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | |
| MNHN-IM-2009-28467 | <i>Tritonoranella</i> | latitudo | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | |
| MNHN-IM-2009-5457 | <i>Tritonoranella</i> | latitudo | CONCALIS | DW2932 | 19°05'S | 163°30'E | 215-225 | x | |
| MNHN-IM-2009-5463 | <i>Tritonoranella</i> | latitudo | CONCALIS | DW2949 | 19°00'S | 163°28'E | 261-272 | x | |
| MNHN-IM-2013-52982 | <i>Tritonoranella</i> | latitudo | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | x |
| MNHN-IM-2013-52986 | <i>Tritonoranella</i> | latitudo | EXBODI | DW3867 | 22°52'S | 169°26'E | 146-610 | x | |
| MNHN-IM-2013-52987 | <i>Tritonoranella</i> | latitudo | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | x |

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| MNHN-IM-2013-52988 | <i>Tritonoranella</i> | <i>latitudo</i> | EXBODI | DW3855 | 22°19'S | 168°41'E | 340-345 | x | | | | |
| MNHN-IM-2013-61403 | <i>Tritonoranella</i> | <i>latitudo</i> | KARUBENTHOS 2015 | CP4636 | 15°51'N | 61°26'W | 262 | x | | | | |
| MNHN-IM-2009-5149 | <i>Tritonoranella</i> | <i>ranelloides</i> | MAINBAZA | CP3144 | 23°33'S | 35°41'E | 171-180 | x | | x | | |
| MNHN-IM-2009-5149 | <i>Tritonoranella</i> | <i>ranelloides</i> | MAINBAZA | CP3144 | 23°33'S | 35°41'E | 171-180 | x | | | | |
| MNHN-IM-2013-60314 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4538 | 16°38'N | 61°31'W | 320-338 | x | | | | |
| MNHN-IM-2013-60315 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4538 | 16°38'N | 61°31'W | 320-338 | x | | | | |
| MNHN-IM-2013-60316 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4538 | 16°38'N | 61°31'W | 320-338 | x | | | | |
| MNHN-IM-2013-60317 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4538 | 16°38'N | 61°31'W | 320-338 | x | | | | |
| MNHN-IM-2013-60503 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4554 | 16°21'N | 60°56'W | 300-370 | x | | | | |
| MNHN-IM-2013-60523 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4555 | 16°24'N | 60°51'W | 100-258 | x | | | | |
| MNHN-IM-2013-60560 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4556 | 16°24'N | 60°49'W | 367-428 | x | | | | |
| MNHN-IM-2013-60561 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4556 | 16°24'N | 60°49'W | 367-428 | x | | | | |
| MNHN-IM-2013-60671 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4566 | 16°21'N | 60°51'W | 165-260 | x | | x | | |
| MNHN-IM-2013-60752 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4573 | 16°20'N | 60°55'W | 389-413 | x | | | | |
| MNHN-IM-2013-60753 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4573 | 16°20'N | 60°55'W | 389-413 | x | | | | |
| MNHN-IM-2013-61153 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4612 | 16°20'N | 60°51'W | 250-290 | x | | | | |
| MNHN-IM-2013-61187 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4615 | 16°23'N | 60°50'W | 226-270 | x | | | | |
| MNHN-IM-2013-61199 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4615 | 16°23'N | 60°50'W | 226-270 | x | | | | |
| MNHN-IM-2013-61200 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4615 | 16°23'N | 60°50'W | 226-270 | x | | | | |
| MNHN-IM-2013-61365 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4634 | 15°48'N | 61°26'W | 304-310 | x | | | | |
| MNHN-IM-2013-61366 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4634 | 15°48'N | 61°26'W | 304-310 | x | | | | |
| MNHN-IM-2013-61367 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4634 | 15°48'N | 61°26'W | 304-310 | x | | | | |
| MNHN-IM-2013-61368 | <i>Tritonoranella</i> | <i>ranelloides</i> | KARUBENTHOS 2015 | DW4634 | 15°48'N | 61°26'W | 304-310 | x | | | | |
| MNHN-IM-2013-14386 | <i>Tutufa</i> | <i>bubo</i> | PAPUA NIUGINI | PR67 | 05°01,6'S | 145°48,1'E | - | x | x | x | | x |
| MNHN-IM-2007-43036 | <i>Tutufa</i> | <i>bufo</i> | PANGLAO 2004 | P3 | 09°31,1'N | 123°41,5'E | 100 | x | x | x | | x |
| MNHN-IM-2007-43050 | <i>Tutufa</i> | <i>rubeta</i> | PANGLAO 2004 | B40 | 09°34,6'N | 123°49,9'E | 22 | x | | | | |
| MNHN-IM-2007-43063 | <i>Tutufa</i> | <i>rubeta</i> | SANTO 2006 | FR65 | 15°35,4'S | 166°59,2'E | - | x | | | | |
| MNHN-IM-2013-10178 | <i>Tutufa</i> | <i>rubeta</i> | PAPUA NIUGINI | PR04 | 05°10,1'S | 145°50,5'E | 30 | x | x | | | |
| MNHN-IM-2013-10179 | <i>Tutufa</i> | <i>rubeta</i> | PAPUA NIUGINI | PR04 | 05°10,1'S | 145°50,5'E | 30 | x | | | | x |
| MNHN-IM-2013-10488 | <i>Tutufa</i> | <i>rubeta</i> | PAPUA NIUGINI | PR01 | 05°11,3'S | 145°49,4'E | 22 | x | | | | |
| MNHN-IM-2013-10813 | <i>Tutufa</i> | <i>rubeta</i> | PAPUA NIUGINI | PR04 | 05°10,1'S | 145°50,5'E | 30 | x | | | | |
| MNHN-IM-2013-10855 | <i>Tutufa</i> | <i>rubeta</i> | PAPUA NIUGINI | PR05 | 05°11,3'S | 145°49,6'E | - | x | | | | |
| MNHN-IM-2013-11738 | <i>Tutufa</i> | <i>rubeta</i> | PAPUA NIUGINI | PB11 | 05°12,5'S | 145°49,1'E | 13 | x | | | | |
| MNHN-IM-2013-12519 | <i>Tutufa</i> | <i>rubeta</i> | PAPUA NIUGINI | PB14 | 05°13,8'S | 145°48'E | 15 | x | | | | |
| MNHN-IM-2013-14779 | <i>Tutufa</i> | <i>rubeta</i> | PAPUA NIUGINI | PB26 | 04°59,1'S | 145°47,7'E | 22 | x | | | | |
| MNHN-IM-2013-16045 | <i>Tutufa</i> | <i>rubeta</i> | PAPUA NIUGINI | PB34 | 05°07,1'S | 145°49,4'E | 15 | x | | | | |

| | | | | | | | | | | | |
|--------------------|---------------|---------------------|----------------|--------|-----------|------------|---------|---|---|---|---|
| MNHN-IM-2007-43044 | <i>Tutufa</i> | <i>tenuigranosa</i> | SALOMON 2 | DW2236 | 06°51'S | 156°23'E | 208-230 | x | x | x | x |
| MNHN-IM-2007-43061 | <i>Tutufa</i> | <i>tenuigranosa</i> | PANGLAO 2004 | P3 | 09°31,1'N | 123°41,5'E | 100 | x | | | |
| MNHN-IM-2009-15969 | <i>Tutufa</i> | <i>tenuigranosa</i> | ATIMO VATAE | CP3589 | 25°03'S | 44°00'E | 132-153 | x | | | |
| MNHN-IM-2013-61690 | <i>Tutufa</i> | <i>tenuigranosa</i> | ZHONG SHA 2015 | CP4135 | 19°59'N | 114°38'E | 211-218 | x | | | |



CHAPITRE 4

NOUVELLE CLASSIFICATION DES BURSIDAE



Espèces types de tous les genres de Bursidae (legende page suivante)

*Books are not made for furniture, but there is nothing else that so beautifully furnishes a house
[Or a lab...].*

Henry Ward Beecher

*Splitters make very small units - their opponents say that if they can tell two animals apart,
they place them in different genera, and if they cannot tell them apart, they place them in
different species. Lumpers make large units - their opponents say that if a carnivore is neither
a dog nor a bear they call it a cat.*

George Gaylord Simpson

1 : *Aquitanobursa grateloupi* (d'Orbigny, 1852), 2/ *Bufo echinatus* (Link, 1807), 3 : *Bursa bufonia* (Gmelin, 1791), 4 : *Olssonina chira* (Olsson, 1930), 5: *Crossata ventricosa* (Broderip, 1833), 6: *Bursina nobilis* (Reeve, 1844), 7: *Bufo variabilis* (Linnaeus, 1758), 8: *Korrigania fijiensis* (Watson, 1881), 9: *Aspa marginata* (Gmelin, 1791), 10: *Colubrellina condita* (Gmelin, 1791), 11: *Dulcerana granularis* (Röding, 1798), 12: *Lampasopsis rhodostoma* (G. B. Sowerby II, 1835), 13: *Marsupina bufo* (Bruguière, 1792), 14: *Bufo foliatus* (Broderip, 1826) espèce type de *Chasmotheca* Dall, 1904, 15: *Tutufa bubo* (Linnaeus, 1758), 16: *Anaperenna verrucosa* (G. B. Sowerby I, 1825), 17: *Tritonoranella ranelloides* (Reeve, 1844), 18: *Talisman corrugata* (Perry, 1811),

VERS UNE NOUVELLE CLASSIFICATION

Même si toutes les relations intrafamiliales ne sont pas encore résolues au sein des Bursidae (notamment les nœuds reliant les clades A, B et C de la fig.2 de l'article 3) les nouvelles hypothèses apportées par les analyses du chapitre précédent (article 3 principalement) nous permettent de proposer une nouvelle classification. En effet les profondeurs de nœud que nous avons utilisé pour définir les genres sont bien soutenues et ont peu de chance de changer dans l'avenir même avec l'ajout de nouvelles espèces. Cependant leurs relations intra et inter générique sont à même de varier avec l'apport de données futures.

Pour cette raison nous nous sommes retenus de créer des sous-familles (Par exemple Bursinae et Aspanae) ou d'utiliser les sous genres considérés comme valide (*Tutufa* (*Tutufella*) Beu, 1981 par exemple) même si ils ne sont compatibles avec la topologie actuelle de l'arbre.

A l'issue du travail effectué dans le chapitre précédent il ne nous restait plus qu'à attribuer à chaque espèce valide un genre nouvellement définie, cette attribution se faisant uniquement sur des critères morphologique il a été nécessaire de produire une diagnose pour chacun des genres

Le nombre d'espèces décrites dépassant largement le nombre d'espèce valide (Fig. 1.7) il nous a été nécessaire de réévaluer l'ensemble des nomina

L'article qui suit a comme but de faire une synthèse générale des noms disponibles dans la littérature et de leur attribution à des espèces que nous considérons comme valide. Pour cela nous avons clarifié le statu nomenclatural de 12 spécimens types (principalement déposés au Muséum de Londres et de Paris) et avons réalisé la synonymie exhaustive de toutes les espèces. A cela s'ajoute une chrésonymie étendue suivi de toutes les informations disponibles concernant le matériel type, les localités type et les répartitions connues de toutes les espèces, aussi bien dans l'espace que dans le temps

Le but in fine était de produire une nomenclature stable et de fournir toutes les clés pour faciliter sa modification si cela s'avérait nécessaire.

SYSTEMATIC REVISION OF THE EXTENT AND EXTINCT FROG SNAILS
(BURSIDAE THIELE, 1925)

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INTRODUCTION

Frog snails (Bursidae Thiele, 1925) are a moderately diverse tonnoidean family with 59 extent species (Worms, 2017) and 11 extinct one (Sanders *et al.* in prep).

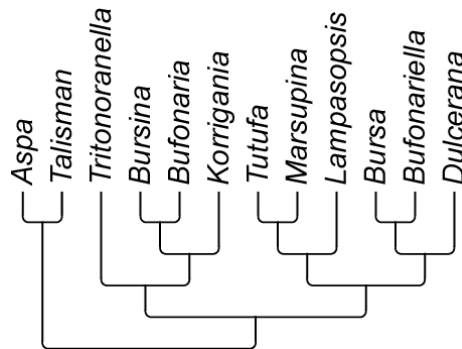


Fig.1 Phylogenetic relationships among the Bursidae, Modified after Sanders *et al.* in prep#2

Bursids are readily recognizable by their thick, coarsely sculptured shells with knobs, warts, tubercles and nodules, hence their vernacular name: Frog snails. Spiral ornamentation of the convex part of the whorl is composed of 6 to 8 primary cords (sensus Merle 2004 and Sanders *et al.*, 2017) that can be lost during the ontogeny. Secondary and ternary ones can appear later on and sometimes grow in such importance that they can be confused with primary cords [e.g. *Dulcerana granularis* (Röding, 1798)]. The most paramount feature, the key for frog snails recognition, is the well-defined posterior exhalant siphon (anal notch) at the top of the

outer lip. The basal interlocking processes of the central radular tooth (Beu 1998b), a flap on the outer posterior edge of each lateral tooth that overlaps the tooth in the preceding row (Barkalova *et al.* 2016) and an accessory salivary gland (Beu 1981) are also distinctive of the Bursidae family.

In the recent bursids have a sub-tropical distribution with a southernmost record in eastern South Africa, North New Zealand and Walters shoal. The northernmost record is from Nice, southern France and Savona north western Italy.

If the family Bursidae is well characterized by several synapomorphies, it is not the case for most of the bursid genera. Until recently the systematic of the Bursidae was largely based on the work carried out by Alan Beu (1981, 1986, 1998b) and the book “Bursidae of the world” written by Tiziano Cossignani (1994). However, relationships within this family remained poorly understood. Castelin *et al.* (2012) provided the first phylogeny of the group showing its monophyly and pointing out the paraphyly of some accepted genera. Using an extensive sampling, Sanders *et al.* (in prep) clarified the generic limits of the family (Fig. 1) splitting the genus *Bursa* in no less than seven genera, all of them but one preexisting in the literature.

In our previous work (Sanders *et al.* inprep article 3) every accepted bursid genera were redefined on the basis of the clades of the phylogeny to which we attributed a previously published name (plus a new one). As a consequence all the species in the phylogeny are now attributed to a genus. Yet most of the recent and all of the extinct species have not been included in this new classification, furthermore there is more than a few synonyms in the literature and it's necessary to revised them.

The main goal of this paper is to propose a complete revision of the Bursidae taxonomy by attributing every single considered valid names to genera defined in Sanders *et al.* in prep (article 3). We will provide a complete overview for the whole family with a diagnosis for each genus; and a complete synonymy, extensive cresonymy, indication regarding all the known type specimens, type locality and range (Geographic and stratigraphic) for each species.

Shells will be described using the methods developed by Merle (2001, 2005) for primary homology definition, adapted for Bursidae by Sanders *et al.* 2017. Primary cords (P) are spiral ornamentations present from the first teleoconch whorl, in opposition to secondary cords (S) that appear 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 (Fig. 1). The primary cord of the

infrasutural ramp is designated IP and the secondary cord IS. Cords of the siphonal canal were not considered.

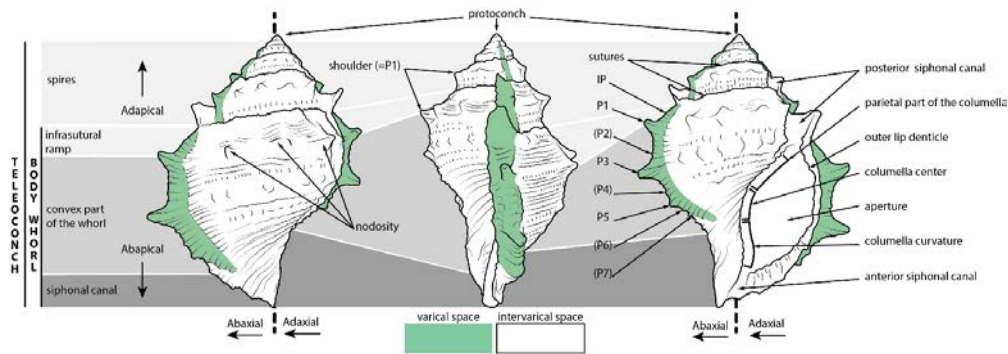


Fig. 2 General characters of a bursid shell; IP: infrasutural ramp primary cord, P1-7: primary cords if P is between parentheses it means that the cord is weakly expressed.

ABBREVIATIONS USED IN THE TEXT

AMNH: American Museum of Natural History, New York, USA.

AMS: The Australian Museum, Sydney, Australia

NHMUK: The Natural History Museum, London, UK

BPBM: Bernice P. Bishop Museum, Honolulu, Hawaii, USA.

FAU: Florida Atlantic University, Boca Raton, Florida, USA.

IMT: Institute of malacology, Tokyo, Japan.

LACM: Los Angeles County Museum of Natural History, California, USA.

MHNG: Muséum d'Histoire naturelle de Genève, Geneva, Switzerland.

MMM: Museo Malacologico Piceno di Cupra Marittima, Italy.

MNHN.F: Muséum national d'Histoire naturelle, Paleontology collection, Paris, France.

MNHN-IM: Muséum national d'Histoire naturelle, Malacology collection, Paris, France.

MNRJ: Museu Nacional de Rio de Janeiro, Brazil

MORG: Museu Oceanográfico de Rio Grande, Rio Grande do Sul, Brazil.

MV: Museum of Victoria, Melbourne, Australia.

MZUSP: Museu de Zoologia, Universidade de São Paulo, São Paulo, Brasil.

NMB: Naturhistorisches Museum, Basel, Switzerland.

NMP: Natal Museum, Pietermaritzburg, South Africa.

NSMT: National Science Museum, Tokyo.

NZGS: New Zealand geological survey, Lower Hutt, New Zealand (non-New Zealand mollusks prefixed "WM,").

Table 1 Comparative morphology of Bursidae genera

| | general shape | Number of cord in the CPW | varix allignement | operculum | outter lip lamellar projection | anterior siphonal canal | posterior siphonal canal | dorso ventral compression | Thickness of the shell |
|---------------------|---------------|---------------------------|-------------------|------------------------------------|--------------------------------|-----------------------------|---|---------------------------|-------------------------|
| <i>Bursa</i> | biconic | 6 | aligned | ovate, anterior nucleus | reduced | strongly curved | long tubular, extending abaxially | yes | Heavy to very heavy |
| <i>Annaperenna</i> | biconic | 6? | offset | ovate operculum, subapical nucleus | reduced? | strongly curved | simple notch with parietal lamella | no | ? |
| <i>Aquitnobursa</i> | biconic | 6 | aligned | ? | reduced | slightly curved | simple notch with parietal lamella | yes | Heavy |
| <i>Aspa</i> | ovoid | 7 | aligned | ovate, subanterior nucleus | absent | straight | notch structured by the infrasutural ramp | yes | very heavy |
| <i>Bufonaria</i> | biconic | 7 | aligned | ovate, anterior nucleus | reduced to extensive | straight | simple notch with parietal lamella and structur a spine derived from SP | yes | Moderatly heavy |
| <i>Bufonariella</i> | biconic | 6 | displaced | ovate, subanterior nucleus | reduced | slightly to strongly curved | simple notch with parietal lamella | no | Moderatly heavy |
| <i>Bursina</i> | biconic | 7 | aligned | ovate, apical nucleus | reduced to extensive | straight | simple notch with parietal lamella | yes | Moderatly heavy |
| <i>Colubrellina</i> | fusiform | 6 | offset | ovate , anterior nucleus | absent | slightly curved | simple notch with parietal lamella | no | Moderatly heavy |
| <i>Crossata</i> | biconic | 7 | offset | ovate, subanterior nucleus | reduced to extensive | strongly curved, very open | simple notch with parietal lamella | no | Moderatly heavy |
| <i>Dulcerana</i> | biconic | 6 | aligned | ovate, subanterior nucleus | reduced | strongly curved | simple notch with parietal lamella | no | Moderatly heavy to thin |
| <i>Korrigania</i> | biconic | 7 | offset | ovate, subanterior nucleus | extensive | straight | simple notch with parietal lamella | no | Thin |
| <i>Lampasopsis</i> | biconic | 7? | aligned | ovate , anterior nucleus | extensive | strongly curved | simple notch with parietal lamella | no | Heavy |
| <i>Marsupina</i> | biconic | 8 | aligned | ovate , anterior nucleus | absent to reduced | straight | notch partly structured by the infrasutural ramp | yes | Moderatly heavy |

| | | | | | | | | | |
|-----------------------|----------------|---|---------|--|-----------|--------------------------------------|------------------------------------|-----|---------------------------|
| <i>Olssonina</i> | <i>biconic</i> | 6 | aligned | ? | reduced? | straight | simple notch with parietal lamella | yes | Heavy |
| <i>Talisman</i> | <i>biconic</i> | 6 | offset | ovate, subanterior nucleus | extensive | slightly curved to straight | simple notch with parietal lamella | no | Thin |
| <i>Tritonoranella</i> | <i>biconic</i> | 7 | offset | ovate, subanterior nucleus | yes | slightly curved | simple notch with parietal lamella | no | Thin |
| <i>Tutufa</i> | <i>biconic</i> | 8 | offset | fan shape , lateral nucleus in central right | extensive | slightly to strongly curved, pinched | simple notch with parietal lamella | no | Moderately heavy to heavy |

PRI: Paleontological research institution, Ithaca, New York, USA

SBNHM: Santa Barbara Museum of Natural History, Santa Barbara, Florida, USA.

TU: Tulane University, New Orleans, USA

UCMP: University of California (Museum of Paleontology), Berkeley, California, USA.

UF: Florida Museum of Natural History, Florida, USA

UFC LCM: Universidade Federal do Ceara, Laboratorio de Ciencias do Mar, Ceara, Brazil.

UNAM IG: Universidad Nacional Autonoma de Mexico, Instituto de Geologia, Mexico city, Mexico.

USBF: United States Bureau of Fisheries, USA.

USNM: United States National Museum of Natural History, Washington D.C., USA.

WAM: Western Australian Museum, Perth, Australia.

ZSI: Zoological Survey of India, Madras, India.

SYSTEMATICS

Phylum **MOLLUSCA** Cuvier, 1795

Class **GASTROPODA** Cuvier, 1795

Order **NEOGASTROPODA** Milne Edwards, 1848

(Following Osca *et al.*, 2015)

Superfamily **TONNOIDEA** Suter, 1913 (1825)

(Following Bouchet *et al.*, 2005: 11,253)

Suter (1913) placed *Dolium* Lamarck, 1801, in synonymy of *Tonna* Brünnich, 1772, and replaced DOLIIDAE Latreille, 1825, with the new name TONNIDAE. TONNIDAE is in prevailing usage and is to be maintained, with the precedence of DOLIIDAE

Family **BURSIDAE** Thiele, 1925

Genus **BURSA** Röding, 1798

Bursa Röding, 1798: 128.

TYPE SPECIES. — *Bursa monitata* Röding, 1798 by subsequent designation (Jousseume, 1881: 174) (subj. jr. syn. of *Murex bufonius* Gmelin, 1791), by first reviser's action of Winckworth, 1945: 137), Recent, Indo-West Pacific.

Pseudobursa Rovereto, 1899: 6.

TYPE SPECIES. — *Gyrineum bufonium* (Gmelin, 1791) (= *Bursa bufonia* (Gmelin, 1791))
Unnecessary replacement name for *Bursa* Röding, 1798.

SPECIES INCLUDED IN THE GENUS:

Bursa bufonia (Gmelin, 1791), *Bursa lamarckii* (Deshayes, 1853), *Bursa luteostoma* (Pease, 1861), *Bursa rosa* (Perry, 1811), *Bursa tuberosissima* (Reeve, 1844)

DIAGNOSIS:

Moderately short spired (except *Bursa luteostoma*) thick shell, varices aligned, 6 primary cords on the convex part of the whorl, Varical P2 reduced; Intervarical P1 and P3 merged with warty ornamentation, P2 not visible, anterior siphonal canal pinched, Posterior siphonal canal long and tubular, extending abaxially; ovate operculum, anterior nucleus. Aperture often coloured

Bursa bufonia (Gmelin, 1791)

Murex bufonius Gmelin, 1791: 3534.

Bursa bufonia (Gmelin, 1791) — Cernohorsky 1967a: 312, pl. 42, fig. 4, Rehder 1969: 31; Cossignani 1994: 44, 5 unnamed figs.; Tröndlé & Cosel 2005: 288; Tröndlé & Boutet 2009: 22; Severns 2011: 154, pl. 61, figs 2a, b.; Beu *et al.* 2012: 64, Fig. 2D; Kil *et al.* 2012:

Bursa mammata Röding, 1798: 128.

Bursa monitata Röding, 1798: 129.

Bursa dunkeri Kuroda ms Kira, 1954: 43, pl. 21, fig. 18. (*nomen nudum*) — Kira 1959: 54, pl. 21, fig. 18; Kira 1962: 54, pl. 22, fig. 18.

TYPE LOCALITY. — Unknown

TYPE MATERIAL. — Gmelin (1791: 3534) cited as illustrations of *Murex bufonius*: Dezallier D'Argenville (1742: pl. 9, [error for pl. 12] fig. R), Seba (1758: vol. 3, pl. 60, figs 14, 20), Schröter (1782: pl. 39 [error for pl. 36], fig. 234b), and Martini (1780: pl. 129, figs 1240–1241).

The specimen illustrated by DeZallier D'Argenville (1742: pl. 12, fig. R) have been designated the lectotype of *Murex bufonius* Gmelin, 1791 by Beu *et al.* (2012). They also designated it lectotype of both *Bursa mammata* Röding, 1798 and *B. monitata* Röding, 1798. The location of any type material of *Bursa dunkeri* is unknown. It presumably consists of the specimen illustrated by Kira (1959).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE: — No fossil records. *Bursa bufonia*, the type species of *Bursa*, occurs widely in the central Indo-West Pacific, from East Africa and Mauritius to an eastern limit at the Marquesas and Tuamotu Islands. Richard (1985) and Tröndlé & Boutet (2009) recorded *B. bufonia* from all island groups of French Polynesia. It is largely replaced in Hawaii by the similar but taller, narrower, more elaborately sculptured, restricted Hawaiian species *Bursa luteostoma* (Pease, 1861) (Kay 1979: fig. 80G, identified as *B. bufonia*; Severns 2011: 150, pl. 59, fig. 5), a single occurrence in Hawaii (Severns 2011: 154, pl. 61, figs 2a, b). Southern Japan (Ryukyu Islands). One occurrence in South Korea (Jeju Island) (Kil *et al.* 2012). *B. bufonia* does not occur in New Caledonia or northern Australia, and seems to extend only as far south as northern Papua New Guinea. Marquesan Islands (Ua Huka), where it occurs moderately commonly and reaches a large size (Beu *et al.* 2012). Occurs at Tahuata and Ua Pou Islands. Specimens are fairly common in Tahiti (Society Islands) and the Tuamotu Islands and two specimens are reported from the Austral Islands (Beu *et al.* 2012).

***Bursa lamarckii* (Deshayes, 1853)**

Ranella lamarckii (*sic*) Deshayes, 1853, "Explications des planches": 67, pl. 112, figs 1-2 .

Bursa muehlhaeusseri Parth, 1990:217, figs 1 a, 2 a, 3.

Bursa (Bursa) muehlhaeusseri Parth, 1990 — Cossignani 1994: 42, illus.

Bursa angioyorum Parth, 1990: 220, figs 1 b, 2 b, 4.

Bursa (Bursa) angioyorum Parth, 1990 — Cossignani 1994: 54, 55, illus.

Bursa lamarckii (Deshayes, 1853) — Beu 1985: 63, fig. 40 ; Springsteen & Leobrera 1986: 120, pl. 33, fig. 2 ; Lai 1987: 20, fig. 5 ; Wilson 1993: 227, pl. 43, figs 7 a-b, Cossignani 1994: 49, illus, Beu 1997: 150 ; Beu *et al.* 2012: 68, fig 2F ; Dolorosa *et al.* 2013 : 8, fig. 3C

Bursa lamarckii (*sic*) (Deshayes, 1853) — Castelin *et al.* 2012: 4843, fig. 4

Bursa bufonia (not Gmelin, 1791) — Oyama & Takemura 1963: *Bursa* pl., fig. 9; Shikama 1964: 64, pl. 49, fig. 1.

Ranella bufonia var. b Reeve, 1844a: pl. 5, fig. 23 a.

Bursa venustula Habe & Kosuge 1966: 45, pl. 16, fig. 4.

Bursa sp. Cernohorsky, 1967: 316, pl. 42, fig. 2; 1967b: 46, pl. 1, fig. 2 — Hinton 1972: 12, pl. 6, fig. 24; 1978: pl. 32, fig. 2.

TYPE LOCALITY. — *Ranella lamarckii* from recent Island of Capul, Philippines (Designated by Beu 1998: 115). *Bursa muehlhaeusseri* and *B. angioyorum* from recent Cebu, Philippines

TYPE MATERIAL. — There is one specimen (MNHN-IM-2000-4108) in MNHN marked as a Deshayes's syntype of *Ranella lamarckii*, but it does not closely resemble Deshayes's figure and Virginie Heros (MNHN) says that according to the label it is very unlikely that it belongs to Deshayes's collection; No other specimens in MNHN are identified as Deshayes's type(s) of *R. lamarckii*. Neither has it been recognized by Dr A. Prieur, curator of paleontology at Centre des Sciences de la Terre, Université Claude Bernard, Lyon, where the former collection of Ecole des Mines has been transferred. Jérôme Thomas (UB) manager of the e-recolnat project reached the same conclusion. The whereabouts of any original material is therefore unknown. Reeve (1844b: caption to pl. 5, fig. 23 a) illustrated this species very clearly, as "*Ranella bufonia* variety b", and stated that, although Deshayes (1843: 546) had proposed to separate this form from *R. bufonia*, he thought earlier authors were correct to treat it as part of the variation of *R. bufonia*. The specimen illustrated by Reeve from "Island of Capul, Philippines" (NHMUK 1995224/1 ex Cuming coll.) has been designated neotype of *Ranella lamarckii* by Beu 1998: 155) Reeve's figured specimen is accompanied by two smaller specimens (NHMUK 1995224/2-3).

Bursa muehlhaeusseri and *B. angioyorum*: holotypes both from Cebu, Philippines, in Zoologischen Staatssammlung, München; (parth 1990, Beu *et al.* 2012).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. Occurs throughout the recent tropical Indo-West Pacific, from Madagascar (NZGS WM12478, Tuléar) and presumably East Africa to the Red Sea (2 lots NZGS), and from the southern Great Barrier Reef, eastern Australia (NZGS WM11634, One Tree I., Capricorn Group) (Beu 1998) to at least as far north as Okinawa (Oyama & Takemura, 1963: *Bursa* pl., fig. 9), the Solomon Islands (NZGS, 2 lots), and east to French Polynesia (Beu, 1998). One specimen from New Caledonia and another is present in recent MNHN collections from Lifou. Richard (1985) also reported it from the Society Islands.

Remarks: *Bursa lamarckii* was originally written *lamarkii* by Deshayes, 1853 this name was obviously dedicated to Lamarck, in accord with ICZN 32.5.1. the correct name must be *Bursa lamarckii*.

***Bursa luteostoma* (Pease, 1861)**

Ranella luteostoma Pease, 1861: 397

Bursa luteostoma (Pease, 1861) — Kay 1979: 226, figs 80; Beu 1985: 55.

Bursa (Bursa) luteostoma (Pease, 1861) — Cossignani 1994: 53

TYPE LOCALITY. — Sandwich Islands (Hawaii)

TYPE MATERIAL. — No specimen of *Bursa luteostoma* were to be found in the Cuming coll. (NHMUK) by Kay (1965). The type material is presumed lost.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. This species seems to be strictly restricted to Hawaii.

***Bursa rosa* (Perry, 1811)**

Biplex rosa Perry, 1811: pl. 4, fig. 1.

Bursa rosa (Perry, 1811) — Wilson & Gillett 1971: 80, pl. 54, figs 4-4 a; Hinton 1972: 12, pl. 6, fig. 26; 1978: 32, fig. 4. Kay 1979: 229, figs 80 E-F; Beu 1985: 63. Springsteen & Leobrera 1986: 123, pl. 34, fig. 5; Short & Potter 1987: 44, pl. 21, fig. 7; Drivas & Jay 1988: 60, pl. 15, fig. 6; Lai 1987: 19, figs 3-4; Wilson 1993: 227, pl. 43, figs 6 a-b; Cossignani 1994: 58-59, Beu 1998: 166, figs 52i, j; Tröndlé & Boutet 2009: 22; Severns 2011: 154, pl. 61, figs 1a, b.

Bursa rosea (sic) (Perry, 1811) — Okutani 1986: 116; 117, top tight fig.

Ranella siphonata Reeve, 1844b: pl. 7, fig. 38 (excluding variety b) — Reeve 1844b: 138; Kobelt 1876: 328.

Bursa siphonata (Reeve, 1844) — Edmondson 1946: 143, fig. 61 j.

Bursa siphonata (not Reeve, 1844) — Oliver 1915:528.

Argobuccinum siphonatum (not Reeve, 1844) — Iredale 1910: 73.

Ranella (Lampas) bufonia var. *venustula* Tryon, 1880: 39, pl. 19, fig. 11.

Bursa mammata Röding, 1798 — Habe 1961: 47, pl. 24, fig. 2; Oyama & Takemura 1963:

Bursa fig. 1-3; Habe 1964: 76, pl. 24, fig. 2; Salvat *et al.* 1988: 103, pl. 13, fig. 13.

Bursa bufonia dunkeri (Kira, 1959) — Ladd 1982: 41, pl. 8, figs 6-7 (only; not pl. 33, figs 15-16 = *Bursina nobilis*).

TYPE LOCALITY. — Recent Philippine Islands.

TYPE MATERIAL. — *Biplex rosa*, neotype, and lectotype of *Ranella siphonata* (NHMUK1967658/1 ex Cuming coll.) both by designation of Beu (1998: 166) and two paralectotypes (NHMUK 1967658/2-3).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bursa rosa* occurs from South Africa, East Africa and the Red Sea eastwards to Hawaii and French Polynesia, and from Kii Peninsula, Honshu, Japan, south to the southern Great Barrier Reef, Australia. The six Marquesan specimens reported by Beu *et al.* (2012) (plus one) are the only Polynesian ones in MNHN collections, but a few specimens are also reported above from the Society and Tuamotu Islands, where Robert Gourguet (Beu *et al.* 2012) reported that it is rare. There are no known records from the Austral Islands or the Atlantic. They are fairly common in Papua New Guinea. Two late Pliocene early Pleistocene specimens from Java (Beu, 2005) are the only fossils specimens known.

***Bursa tuberosissima* (Reeve, 1844)**

Ranella tuberosissima Reeve, 1844: sp 39, pl VII.

Bursa (Ranella) tuberosissima (Reeve, 1844) — Schepman 1909: 118

Bursa (Bursa) tuberosissima (Reeve, 1844) — Cossignani 1994: 61, 2 figs.

Bursa tuberosissima (Reeve, 1844) — Dharma 2005: 194, pl. 72 fig. 194-195.

Ranella siphonata var. B Reeve, 1844: sp 38, pl VII

Bursa leo Shikama, 1964 in Shikama & Horikoshi 1964: 115, pl 62, fig. 10, text fig. 194.

Bursa (Bursa) leo (Shikama, 1964 in Shikama & Horikoshi, 1964) — Cossignani 1994: 50, 6 figs.

TYPE LOCALITY. — *Ranella tuberosissima* and *Ranella siphonata* var B from recent Philippines Islands.

TYPE MATERIAL. — *Ranella tuberosissima* holotype (NHMUK 1967660 H.ex Cuming coll.) by monotypy. *Ranella siphonata* var B, one lectotype designated, here (NHMUK 1967659).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. Common in the Philippines, Papua New Guinea, Taiwan and Indonesia.

Genus *ANNAPERENNA*, Iredale, 1936

Annaperenna Iredale, 1936: 310.

TYPE SPECIES. — *Ranella verrucosa* G. B. Sowerby I, 1825, by original designation, Iredale, 1936: 337 Recent, southwestern Pacific.

SPECIES INCLUDED IN THE GENUS:

Annaperenna verrucosa (G. B. Sowerby I, 1825)

DIAGNOSIS:

Short shell, varices slightly displaced, 6 (maby 7) primary cords on the convex part of the whorl, Varical and interverical P2, P4 and P6 extremely reduced to the point that they are no longer visible, P1, P3, P5 bear large black nodules contrasting over the white background of the shell, ovate operculum, subapical nucleus. Relatively strong projection of the outer lip.columella striped like *Tritonoranella*.

Annaperenna verrucosa (G. B. Sowerby I, 1825)

SYNONYMY:

Ranella verrucosa G. B. Sowerby I 1825: sp 24, pl V— Kiener 1841: 24, pl. 14, fig. 1; Tryon 1880:279, pl. 21, fig. 27

Annaperenna verrucosa (G. B. Sowerby I, 1825) — Iredale 1936: 310; Powell 1967: 190

Bursa verrucosa (G. B. Sowerby I, 1825) — Beu 1985: fig. 46.

Bursa (Columbrellina) verrucosa (G. B. Sowerby I, 1825) — Cossignani 1994: 90, 3 figs.

Murex papilla Wood, 1828: 14

Argobuccinum papilla (Wood, 1828) — Iredale 1910:73

TYPE LOCALITY. — *Ranella verrucosa* from Recent Norfolk Island, New Zealand. Type locality of *Murex papilla* is here designated as Recent Norfolk Island, New Zealand.

TYPE MATERIAL. — *Ranella verrucosa* & *Murex papilla* holotype (NHMUK 20100624) both founded on the same unique shell.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records From Australia and northern New Zealand (Kermadec Island) where it is quite rare.

Genus *AQUITANOBURSA* Sanders *et al.*, in prep (article 1)

Aquitanoobursa Sanders *et al.*, in prep:

TYPE SPECIES. — *Ranella grateloupi* d'Orbigny, 1852, original designation

SPECIES INCLUDED IN THE GENUS:

Aquitanoobursa grateloupi (d'Orbigny, 1852), *Aquitanoobursa amphitrites* (Maury, 1917), *Aquitanoobursa inaequicrenata* (Cossmann & Peyrot, 1924), *Aquitanoobursa morrissi* (d'Archiac & Haimes, 1853), *Aquitanoobursa tuberosa* (Grateloup, 1833).

DIAGNOSIS:

Moderately short spired, varices slightly displaced, 6 primary cords on the convex part of the whorl, Varical and intervarical P2 very reduced, axial ridges on the first whorl, strong parietal callus. Short well defined posterior siphonal canal. Weak projection of the outer lip.

Aquitanoobursa grateloupi (d'Orbigny, 1852)

Ranella leucostoma (not Lamarck, 1822) — Grateloup 1833: 91, pl VI

Ranella semigranosa (not Lamarck, 1822) — Grateloup 1840 : pl XXIX, fig. 6.

Ranella grateloupi (sic) d'Orbigny 1852: 76.

Apollon grateloupi (d'Orbigny, 1852) — Cossmann & Peyrot 1924: 305, Pl. XV, fig. 42-43

TYPE LOCALITY. — Lower Miocene of Aquitaine Basin, Bordeaux and Saint-Paul-lès-Dax.

TYPE MATERIAL. — Two syntypes (MNHN.F.B27595 and MNHN.F.A27211). MNHN.F.A27211 (from Saint-Paul-lès-Dax) is here designated lectotype.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bursa grateloupi* is only known from the Lower Miocene of the Aquitaine Basin.

Remarks: *Aquitanobursa grateloupi* was originally written *gratteloupi* this name is obviously founded over Grateloup in accord with ICZN 32.5.1. the correct name must be *Aquitanobursa grateloupi*.

***Aquitanobursa amphitrites* (Maury, 1917)**

Bursa amphitrites Maury, 1917: 273, pl. 17, fig. 9; Pilsbry 1922: 360; Beu 2010 : 42, pl. 1, figs 1-4, 8.

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

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

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, Denniston *et al.* 2008) in the Dominican Republic and from the early Middle Miocene Buenevara Adentro beds of the Paraguaná Peninsula, Venezuela.

***Aquitanobursa inaequicrenata* (Cossmann and Peyrot, 1924)**

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

Bursa. (Bufonariella) inaequicrenata (Cossmann & Peyrot 1924) — Beu 1980: 258

Bursa inaequicrenata (Cossmann & Peyrot, 1924) — Landau *et al.* 2004 :68; Landau *et al.* 2009: 76.

TYPE LOCALITY. — Burgidalian of le Peloua, near Saucats, Aquitaine Basin.

TYPE MATERIAL. — *Apollon inaequicrenatus*, holotype (MNHN-F-J06127 Cossmann Coll.) from the Burdigalian of le Peloua and one paratype (MNHN-F-J06128 Cossmann Coll.)

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Only known to the Atlantic Aquitaine Basin (Burdigalian) of France.

***Aquitanobursa morrиси* (d'Archiac & Haimes, 1853)**

Ranella morrиси d'Archiac & Haimes, 1853: 309, pl. XXX, fig. 1, pl XXXI, fig. 3 — Fischer-Piette 1887: 656

Ranella elegans (not Beck in G.B. Sowerby 2nd, 1836 in G.B. Sowerby 1st & G.B. Sowerby 2nd, 1832-1841) — Kostak 1884:137

Apollon morrиси (d'Archiac & Haimes, 1853) — Harzhauser *et al.* 2009: 360, tab. 1

TYPE LOCALITY. — “Calcaire grossier jaune de la chaîne d'Hala” Pakistan.

TYPE MATERIAL. — Two syntypes figured by d'Archiac & Haimes (1853) possibly in NHMUK (not checked)

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — This species is only known by d'Archiac & Haimes (1853) specimens for the Lower Miocene of the Halla Mountain, Sindh, Pakistan.

***Aquitanobursa tuberosa* (Grateloup, 1833)**

Ranella tuberosa Grateloup, 1833 : n°420, 92. Grateloup 1847 : pl. 29 fig. 7.

Ranella subtuberosa d'Orbigny, 1852 : n°1405, 76. 1872.

Ranella tuberosa Bonelli (m.s.) — Bellardi 1872 : 236, pl. 15 fig. 7.

Apollon pelouatensis Cossmann & Peyrot, 1924: n°842, pl. 15 figs 38-39, pl. 17 figs 1-2.

Bursa (Bufonariella) pelouatensis (Cossmann & Peyrot, 1924) — Beu 1981: 258, Schmelz, 1997: 106, pl. 1, fig.2.

Bursa tuberosa (Grateloup, 1833) — Lozouet *et al.* 2001 : 45, pl. 19, figs. 3a-3b ; Landau *et al.* 2004 : 68.

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

TYPE MATERIAL. — *Ranella tuberosa syntypes* probably in Grateloup coll. University of Bordeaux, Talence, France, *Apollon pelouatensis* syntypes (MNHN.F.J06123-6).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Early Aquitanian (Lozouet 1998) to Middle Miocene of Aquitaine basin (France) and Po valley (Italy).

Genus **ASPA** H. Adams & A. Adams, 1853

Aspa H. & A. Adams, 1852: 106

TYPE SPECIES. — *Ranella laevigata* Lamarck, 1822 by original designation (= *Buccinum marginatum* Gmelin, 1791), Late Paleogene to Recent, Mediterranean and West Africa; Late Pliocene-Early Pleistocene, Costa Rica.

Biconic (fossil only) to ovoid, very low spires, wide aligned varices, smooth surface, very flattened spiral cords in some specimens, primary cords nearly indistinguishable (probably 7 on the convex part of the whorl), poorly expressed to no nodules at all on P1, first whorl lost in nearly every specimens; posterior siphonal canal integrated to the infrasutural ramp; fan-shaped operculum, nucleus halfway along the columellar margin.

SPECIES INCLUDED IN THE GENUS

Aspa marginata (Gmelin, 1791)

DIAGNOSIS:

Biconic (fossil only) to ovoid, very low spires, wide aligned varices, smooth surface, very flattened spiral cords in some specimens, primary cords nearly indistinguishable (probably 7 on the convex part of the whorl), poorly expressed to no nodules at all on P1, first whorl lost in nearly every specimens; posterior siphonal canal integrated to the infrasutural ramp; fan-shaped operculum, nucleus halfway along the columellar margin.

Aspa marginata (Gmelin, 1791)

Buccinum marginatum Gmelin, 1791: 3486 — Brocchi 1814: 332, pl. 4, fig. 17

Cassis marginata (Gmelin, 1791) — Borson 1821: 228, pl. 1, fig. 19.

Ranella marginata (Gmelin, 1791) — J. Sowerby & G. B. Sowerby I 1824: pl. 233, fig. 2; de Serres 1829: 114; Locard 1897: 298.

Ranella (Aspa) marginata (Gmelin, 1791) — Bellardi 1873: 243; Tryon 1880: 42, pl. 23, fig. 52; Dautzenberg 1891: 23; Sacco 1904: 40, pl. 11, figs 13-14; Cossmann & Peyrot 1924: 315.

Ranella (Lampas) cruentata (not G. B. Sowerby II, 1835) — Gabb 1881: 353

Apollon marginatus (Gmelin, 1791) — Cossmann 1903: 118.

Bursa (Aspa) marginata (Gmelin, 1791) — Thiele 1929: 284; Settepassi 1970: Cymatiidae xviii, pl. 10, figs 29a-b, 30a-b, with var. *tuberculata*, appendix p. xi, illus..

Bursa marginata (Gmelin, 1791) — Nickles 1950: 88, fig. 136 ; Bernard 1984: 64, pl. 52, fig. 103; Gofas *et al.* 1984: 132.

Gyrineum (Aspa) marginatum (Gmelin, 1791) — Malatesta 1974: 273, pl. 23, figs 6a-d; Nordsieck & Garcia-Talavera 1979: 127, pl. 28, fig. 6.

Bufonaria (Aspa) marginata (Gmelin, 1791) — Beu 1985: 65, fig. 51 ; Robinson 1991: 340, pl. 14, figs 11-12; Cossignani 1994: 12; Giannuzzi-Savelli *et al.* 1997: 242, figs 905a-b, 906; Guerreiro & Reiner 2000: 122; Landau *et al.* 2004: 69, pl. 5, figs 6-7, pl. 10, fig. 2.

Bufonaria marginata (Gmelin, 1791) — Waren & Bouchet 1990: 80, figs 113-114 ; Gofas & Beu 2002: 102; Ardovini & Cossignani 2004: 132, upper left 2 figs; Chirli 2007: 105, pl. 38, figs 5-16 (with long synonymy).

Ranella laevigata Lamarck, 1822: 154.

Ranella (Aspa) laevigata (Lamarck, 1822) — H. & A. Adams 1852: 106 ; Chenu 1859: 156, fig. 721; Coulon 1933: 139.

Aspa laevigata (Lamarck, 1822) — Rochebrune 1881: 303 ; Gray 1839: 110, pl. 36, fig. 18; Kiener 1841: 34, pl. 13, fig. 2; Deshayes 1843: 550; Philippi 1844: 183; Reeve 1844b: pl. 8, fig. 50; Michelotti 1847: 254; D'Ancona 1872: 176, pl. 8, figs 3-4; Martens 1877: 236.

Eione inflata Risso, 1826: 172. — Arnaud 1977: 120, pl. 4, fig. 52.

Ranella brocchii Bronn, 1828: 533.

Murex depressus Grateloup, 1840 (1833): 97

Apollon (Aspa) depressus (Grateloup, 1840) — Cossmann & Peyrot 1924: 606, pl. 16, figs 1-2, pl. 17, figs 8-9.

Bursa (Aspa) marginata depressa (Grateloup, 1840) — Strausz 1966: 251, pl. 29, figs 5-6: pl. 63, figs 14-18.

Buccinum pleurotoma Calcara, 1841: 61, pl. 2, fig. 6.

Ranella subgranulata d'Orbigny, 1852: 76

Apollon (Aspa) subgranulatus (Orbigny, 1852), — Cossmann & Peyrot 1924: 313–316, pl. 15, Fig. 54; pl. 17, Fig. 7

Bursa (Aspa) subgranulata (Orbigny, 1852) — Beu 1981:262

Aspa subgranulata (Orbigny, 1852) — Beu 2010: 66

Ranella submarginata d'Orbigny 1852: 174

TYPE LOCALITY. — *Buccinum marginatum*, Italian Piedemontio. *Ranella laevigata*, Italian Piémont. *Eione inflata*, La Trinité, France. *Murex depressus*, Dax, France. *Ranella subgranulata* Dax, France. Type locality unknown for *Ranella submarginata* and *Buccinum pleurotoma*.

TYPE MATERIAL. — *Buccinum marginatum*, *Ranella laevigata* and *Eione inflata* Neotype (NHMUK GG9183a Palaeontology Department) designated by Beu (2010: 67). *Ranella submarginata* two syntypes [MNHN.F.B33829 (6 specimens) and MNHN.F.B36400 (7 specimens)] from the Piazancian of Languedoc-Roussillon. The type specimens of *Ranella subgranulata* is presumably in Grateloup coll. at the university of Bordeaux. *Buccinum pleurotoma* type whereabouts are unknown.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE.

Aspa marginata lives today in the Ibero-Moroccan Gulf and down the coast of West Africa from southern Spain to Angola (Gofas *et al.* 1984: 132), and at the Canary and Cape Verde Islands and at Madeira. A single juvenile specimen was recorded from Seine Bank, Lusitanian seamounts, eastern Atlantic, (Gofas & Beu 1993: 102). The first Recent specimen seems to have been recorded by von Martens (1877: 236), who gave a description of a specimen taken off of the Cape Verde Islands, pointed out that Gmelin's name *Buccinum marginatum* was the

earliest for the species, and commented at length on Brocchi's (1814) "sub-appenine" fossils found living off of West Africa, but not in the Mediterranean. Records of Recent specimens from the western Mediterranean is unlikely. Fossils occur widely in central and southern Europe in Miocene and Pliocene rocks of suitable shallow offshore facies. The southernmost known specimen is a Pleistocene fossil from 55 km north of Swakopmund, Namibia (NMP 7868, 1 abraded specimen). In the Americas, the one fossil record is in the latest Pliocene-earliest Pleistocene Moín Formation at Limón, Costa Rica, where a total of 5 specimens is recorded at present (Beu, 2010).

Genus **BUFONARIA** Schumacher, 1817

Bufonaria Schumacher, 1817:251.

TYPE SPECIES. — *Bufonaria spinosa* Schumacher, 1817 [junior synonym of *Gyrineum echinatum* Link, 1807] subsequent designation of Herrmannsen (1846: 135), Miocene to Recent, central-northern Indo-West Pacific and Red Sea.

Chasmotheca Dall, 1904: 118

TYPE SPECIES. — *Ranella foliata* Broderip, 1826, recent, Indian Ocean.

SPECIES INCLUDED IN THE GENUS

Bufonaria cavitensis (Beck in Reeve, 1844), *Bufonaria cristinae* Parth, 1989, *Bufonaria crumena* (Lamarck, 1816), *Bufonaria echinata* (Link, 1807), *Bufonaria elegans* (G.B. Sowerby II, 1836 in G.B. Sowerby I & G.B. Sowerby II, 1832-1841), *Bufonaria foliata* (Broderip, 1826), *Bufonaria granosa* (Martin 1884), *Bufonaria perelegans* Beu, 1987, *Bufonaria rana* (Linnaeus, 1758).

DIAGNOSIS:

Biconic shell, dorsoventrally compressed shape, evenly granulose sculpture over the entire teleoconch, varices alligned 7 primary cords on the convex part of the whorl, P2 and P4 atrophied, P6 and P7 reduced; pointy ornamentation on intervarical P1, P3 and P5 abapically reducing in importance, pointy to spiny ornamentation on varical P1,P3 and P5 reaching

maximum in P1 (e. g. *Bufonaria foliata*) or P3 (e. g. *Bufonaria echinata*); spine on the posterior siphonal canal; fan-shaped operculum, nucleus halfway along the columellar margin

Bufonaria echinata (Link, 1807)

Gyrineum echinatum Link, 1807: 123.

Bufonaria (Bufonaria) echinata (Link, 1807) — Beu 1985: 65; Cossignani 1994: 20.

Bufonaria echinata (Link, 1807) — Okutani 2000: 271, pl. 134, fig. 14; Beu 2005: 10, Figs. 6-9.

Ranella spinosa Lamarck, 1816: pl. 412, fig. 5a, b, “Liste des objets” p. 4 — Lamarck 1822: 152; Kiener, 1842: 7, pl. 5, figs. 1, 2; Reeve 1844b, pl. 11, fig. 7; van der Vlerk 1931: 24.

Bufonaria spinosa Schumacher, 1817: 252. (homonym, not Lamarck, 1816)

Ranella (Bufonaria) spinosa var. (Schumacher, 1817) — Martin 1899: 147, pl. 23, figs. 343-345.

Bursa (Bufonaria) spinosa (Schumacher, 1817) — Cox 1948: 41, pl. 3, fig. 8a, b; Skwarko & Sufiati 1994, p. n1.

Bursa suensonii Mörch, 1853: 106 (according to Beu, 1987: 333).

TYPE LOCALITY. — *Gyrineum echinatum*, *Ranella spinosa*, *Bufonaria spinosa* and *Bursa suensonii* type locality unknown.

TYPE MATERIAL. — No material is known today from the collections of Link (1807) or Schumacher (1817). For *Ranella spinosa*, the specimen hold in Geneva (MHNG 1098/81) has abusively been designated as “holotype” by Beu (2005: 10) (ICZN 74.6). This specimen is here designated lectotype of *Ranella spinosa*. Furthermore, following Beu’s (2005:10) opinion this specimen is also designated the neotype of both *Gyrineum echinatum*, and *Bufonaria spinosa* Schumacher, 1817. For *Bursa suensonii* there are two possible syntypes (labelled by Mörch) in ZMC [more information in Beu (2005)].

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bufonaria echinata* occurs throughout the northern and northwestern Indian Ocean, the Gulf of Arabia and the Red Sea. More rarely, specimens occur in the northwestern Pacific Ocean, as far north as southern Japan

(Okutani 2000). Fossils seem to have been reported only from middle to late Miocene of Java and Sumatra (Beu 2005).

***Bufonaria cavitensis* (Beck in Reeve, 1844)**

Ranella cavitensis Beck in Reeve, 1844: pl 4, fig 17a

Bursa crumena (not Lamarck, 1816) — Hinton 1972: 12, pl. 6, fig. 19; Hinton 1978, pl. 32, fig. 9.

Bufonaria (Bufonaria) crumena cavitensis (Beck in Reeve, 1844) — Beu 1987: 9; Cossignani 1994: 19.

Bufonaria (Bufonaria) cavitensis (Beck in Reeve, 1844) — Beu 2005: 337

Bufonaria cavitensis (Beck in Reeve, 1844) — Beu 2010: 22

TYPE LOCALITY. — Recent Bay of Manila (Philippines) by designation of Beck (*in* Reeve, 1844: pl 4 caption)

TYPE MATERIAL. —The specimen from the Cuming collection (NHMUK 2015056) figured by Reeve (1844) is here designated lectotype of *Ranella cavitensis*.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. *Bufonaria cavitensis* range from north-eastern Australia to the Philippine Islands and Taiwan.

***Bufonaria cristinae* Parth, 1989**

Bufonaria (Bufonaria) cristinae Parth, 1989: 51, second figure; Cossignani, 1994: 16.

TYPE LOCALITY. — Recent Davao, Philippines.

TYPE MATERIAL. — Holotype (NHMUK 1990019) (designated in Parth 1989: 53, deposited in NHMUK in Parth 1991: 21), one paratype (AMNH 246026), the location of the four other paratypes mentioned in Parth (1989) is unknown.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. *Bufo* *crumena* is known only to the Philippines.

Bufo crumena (Lamarck, 1816)

Ranella crumena Lamarck, 1816: 4, pl. 412, fig. 3, “Liste des objets” ; Lamarck 1822: 151; Broderip 1826, pl. 11, fig. 2; G.B. Sowerby II 1835 in G.B. Sowerby I & G. B. Sowerby II 1832-1841, pl. 88, fig. 9; Reeve 1844b, pl. 4, fig. 17b (typical form only, not form B= *Bufo crumena* *cavitensis*); Boettger 1883: 149, pl. 5, fig. 14; pl. 6, fig. 1; Martin 1899: 145; Martin 1919: 89, 122, 123, 126; Martin 1928: 8; van der Vlerk 1931: 240.

Bursa (Chasmotheca) crumena (Lamarck, 1816). — Oostingh 1935: 61.

Bufo (Bufo) crumena crumena (Lamarck, 1816). — Beu 1987: 336, fig. 231-233; Cossignani 1994: 17-18.

Ranella crumenoides Blainville in Valenciennes, 1832: 297.

Bufo crumenoides (Blainville in Valenciennes, 1832) — Kilburn & Rippey 1982: 72, pl. 16, fig. 13.

Ranella elegans (not *Ranella elegans* G.B. Sowerby II, 1836 in G.B. Sowerby I & G. B. Sowerby II, 1832-1841) – Kiener 1841: 4, pl. 3, fig. 1.

Ranella crumena var *paucinodosa* Boettger, 1883: 36, pl. 1, fig. 9a, b.

?*Ranella* (*s. str.*) sp. indet. — Icke & Martin 1907: 238, pl. 15, figs. 19, 19a.

Ranella (Bursa) affinis (not Broderip, 1833) — Tesch 1920: 42, pl. 129, fig. 154.

TYPE LOCALITY. — Type locality unknown for both *Ranella crumena* and *Ranella crumenoides*. *Ranella crumena* var *paucinodosa* from the late Miocene of Eburnamergel, Pfahl 65, Seluma, Sumatra.

TYPE MATERIAL. — *Ranella crumena* Lamarck, lectotype (MHNG 979/331) by designation of Beu (1987: 336). It is the specimen illustrated by Lamarck (1816, pl. 412, fig. 3). *Ranella crumena* var. *paucinodosa* Boettger, 1883, holotype (SMF XII/2880a). No type material seems still to exist for *Ranella crumenoides* Blainville in Valenciennes, 1832; none is present in MNHN.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bufonaria crumena* occurs throughout the Indian Ocean and Gulf of Arabia, as far south as South Africa, but not in the Red Sea. Specimens occur off western and central Indonesia. In northern Indonesia and the Philippine Islands the species is replaced by *B. cavitensis* (Reeve, 1844). Fossils of *B. crumena* are moderately common at some Miocene (Seravallian?) and Pliocene localities in Java (see Beu 2005).

Bufonaria elegans (G.B. Sowerby II, 1836 in G.B. Sowerby I & G.B. Sowerby II, 1832-1841)

Ranella elegans G.B. Sowerby II, 1836:pl. 92, fig. 17 —Martin 1884:137.

Gyrineum (Gyrineum) subgranosum (not G.B. Sowerby II, 1836) —Wissema 1947: 160

Bufonaria (Bufonaria) elegans (G.B. Sowerby II, 1836) — Beu 1987: figs. 207-210; Cossignani 1994: 21-22; Beu 2005: 11, figs. 10-15.

TYPE LOCALITY. — Recent, Nicobar Islands (India)

TYPE MATERIAL. — *Ranella elegans* three syntypes (NHMUK 20030451), the biggest one is here designated lectotype.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — At present, *Bufonaria elegans* has quite a limited distribution, as it occurs only in the eastern Bay of Bengal and northeastern Indian Ocean, between the Andaman Islands, western Thailand and the southwest coast of Sumatra. There is also records from the central western Indian Ocean that require confirmation. The only fossils reported by Beu (2005) are from Nias Island and a single specimen from Java

in addition of those reported by Tiwari & Kachhara (2004) from the Burdigalian of Upper Bhuban Formation, zone 4, Mizoram, India.

Bufonaria foliata (Broderip, 1826)

Ranella foliata Broderip, 1826: 199 — Lamarck 1835:535; Martini 1837: 134, Pl. 39, Fig. 1; Reeve 1844a, plate 2 sp 8.

Bursa crumena form *foliata* (Broderip, 1826) — Abbott & Dance 1986: 128.

Tutufa (*Tutufa*) *foliata* (Broderip, 1826) — Oliver 1989: 154.

Bufonaria (*Bufonaria*) *foliata* (Broderip, 1826) — Cossignani 1994: 24-25.

TYPE LOCALITY. — Mauritius.

TYPE MATERIAL. — Two syntypes in NHMUK (1837.12.1.1062), the biggest one is here designated lectotype of *Ranella foliata*.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. *Bufonaria foliata* lives now throughout the Indian Ocean and Gulf of Arabia, as far south as South Africa, and the Red Sea. Specimens occur rarely off western and central Indonesia. Further East it's replaced by *Bufonaria crumena* and *B. cavitensis*

Bufonaria granosa (Martin, 1884)

Ranella leucostoma (not Lamarck, 1822) – Martin 1879: 55, pl. 10, figs. 4, 4a, b.

Ranella spinosa var. *granosa* Martin, 1884: 201, pl. 9, fig. 5.

Bufonaria (*Bufonaria*) *granosa* (Martin, 1884) – Beu 2005 p.12 Figs. 16, 17: 170

?*Ranella* (*Argobuccinum*) *leuconostoma* (sic) – Zwierzycki 1915: 105.

Ranella (Bursa) subgranosa (not G.B. Sowerby II, 1836) – Tesch 1915: 70, pl. 82, fig. 152a, b.

?*Argobuccinum leucostoma* (not Lamarck, 1822) – van der Vlerk 1931: 238; Skwarko & Sufiati 1994: m4.

?*Ranella leuconostoma* (not Lamarck, 1822) – van der Vlerk 1931: 241.

Bursa (Bufonaria) spinosa (not Schumacher, 1817 in part) – Skwarko & Sufiati, 1994: n1.

TYPE LOCALITY. — Miocene of Mount Sela, Java

TYPE MATERIAL. — *Ranella spinosa* var. *granosa* one syntype (RGM 9907) here designated lectotype.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bufonaria granosa* occurs in New Caledonia and Vanuatu (Beu, 1998, 2005) northern Borneo (Beu 2005, Han Raven coll. the Philippine Islands (?), Taiwan (?) and southern Japan (?), Queensland, Australia. A few fossil specimens are recorded from the Pliocene of Indonesia and Viti Levu, Fiji (Beu 2005).

***Bufonaria perelegans* Beu, 1987**

Gyrineum elegans (not Sowerby II, 1836) — Oyama & Takemura 1960: *Gyrineum* figs 11-12.-
Habe & Kosuge 1966: 46, pl. 16, fig. 6,

Bursa (Gyrineum) elegans (not Sowerby II, 1836) — Shikama 1964: pl. 62, fig. 9.

Bufonaria sp. — Springsteen & Leobrera 1986: 123, pl. 34, figs 1 a-b,

Bufonaria albivaricosa (not Reeve, 1844) — Lai 1987: 24, figs 1-3,

Bufonaria (Bufonaria) perelegans Beu, 1987: 328, figs 211-217.

Bufonaria perelegans Beu, 1987 — Cossignani 1994: 31-32; Beu 1998: 170, figs 53 f, h, 54

Bursa rana (not Linnaeus, 1758) — Salvat *et al.* 1988: 103, pl. 13, fig. 15.

Bufonaria albivaricosa (not Reeve, 1844) — Lai 1987: 24, figs 1-3,

TYPE LOCALITY. — Recent southwestern Taiwan

TYPE MATERIAL. — Holotype (USNM 849005) (Beu, 1987: 332) , trawled, “deep water” off southwestern Taiwan; one paratype, (NZGS, WM13597); trawled off Kaioshung, Taiwan, 2 paratypes, (WM13263, NZGS); off southwest Taiwan, one (paratype, NZGS WM 1 3262); trawled on a muddy substrate, with *B. rana*, in 200 m deep, southwest of Taiwan, 2 paratypes, (NZGS, WM13175); trawled off Thailand one paratype, (NZGS WMI3925); native fishermen's tangle nets in relatively shallow water, Samar, Philippine Islands, one paratype, (NZGS WM13676); native fishermen's tangle nets, Visayan Sea, Philippines Islands 5 paratypes, (NZGS WM13071); common in drag nets in moderately deep water, Palawan, Philippine Islands, 6 paratypes, (NZGS WM13196); deep water off Palawan, Philippine Islands one paratype, (NZGS WM 13064); Tayabas Bay, Marinduque, Philippines, one paratype, (NZGS WM12428)

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bufonaria perelegans* only occurs from the northwestern Pacific (Taiwan, Philippines, and Thailand) New Caledonia and Vanuatu. The specimens from Vanuatu are from significantly deeper water than the New Caledonian ones, so it is possible that *B. perelegans* occurs uncommonly throughout the western Pacific archipelagoes in depths greater than 150 m. The specimens from the Pliocene of Fiji suggest that this species formerly was more widespread than it is now, so that the apparently disjunct range is possibly a remnant of a wider range (Beu 1998).

***Bufonaria rana* (Linnaeus, 1758)**

Murex rana Linnaeus, 1758: 748 (typical form only) —Linnaeus 1767: 1216.

Bursa (Bufonaria) rana (Linnaeus, 1758) — MacNeil 1961: 60, pl. 13, fig. 5; Schmid & Walther 1962: 258, pl. 26, fig. 13; Noda 2002: 106, fig. 18-11a, b (as *Bufonaria* in fig. caption).

Bufonaria (Bufonaria) rana (Linnaeus, 1758) — Beu 1987: 333, figs. 222-228; Wilson 1993: 226, pl. 43, fig. 1a, b; Cossignani 1994: 33-35; Parth 1996: 132; Beu 1999: 47, figs. 89-97.

Bufonaria rana (Linnaeus, 1758) — Okutani 2000: 271, pl. 134, fig. 11.

Ranella subgranosa Beck in Sowerby II, 1836 in G.B. Sowerby I & G.B. Sowerby II, 1832-1841: pl. 92, figs. 18 — Martin 1899: 146; Martin 1919: 88, 125, 132, 141, 145; Martin 1926:

10; van der Vlerk 1931: 240; van der Vlerk 1932: 111; Martin 1932: 114; Kutassy 1934: 307, 315, pl. 6, figs. 14, 15; Oostingh 1935: 226.

Ranella (Bursa) subgranosa (Sowerby 1836) — Fischer 1927: 65.

Ranella (Apollon) subgranosa (Sowerby 1836) — Koperberg 1931: 121.

Bursa (Bursa) subgranosa (Sowerby 1836) — van Regteren Altena 1942: 112; Skwarko & Sufiati 1994: n2; van den Hoek Ostende *et al.* 2002: 36.

Bufonaria (Bufonaria) subgranosa. (Sowerby 1836) — Cossignani 1994: 36, 37.

Ranella beckii Kiener, 1841: 5, pl. 4, fig. 1.

Ranella albivaricosa Reeve, 1844b: pl. 1, fig. 2 — Reeve 1844b: 136; A. Adams & Reeve 1850: 37, pl. 13, fig. 4; van der Vlerk 1931: 240.

Ranella interrupta Martin, 1884: 138, pl. 7, figs. 138, 138a, b.

Gyrineum scelestum Yokoyama, 1928: 44, pl. 3, figs. 5, 6.

Bufonaria perelegans (not Beu, 1987) — Okutani 2000, p. 271, pl. 134, fig. 13.

TYPE LOCALITY. — *Murex rana* and *Ranella subgranosa* type locality is unknown. *Ranella albivaricosa* from “Ceylon”. *Gyrineum scelestum* from the upper Miocene and Pliocene of the Byoritz Beds, Taiwan.

TYPE MATERIAL. — *Murex rana* lectotype (LSL 448) designated by Beu (1987: 335) as the specimen marked “527” inside the aperture (species number for *Murex rana* in Linnaeus, 1767). *Ranella subgranosa*, three syntypes (NHMUK 20030451), the middle size one is here designated lectotype. *Ranella albivaricosa*, one lectotype, (NHMUK 1967651/1) designated by Beu (1999 47) and five paralectotypes (NHMUK 1967651/2-3 and NHMUK 1967652/1-3). Every specimen of *Gyrineum scelestum* from Yokoyama (1928: 45) are syntypes; presumably in the Geological Survey of Japan.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bufonaria rana* occurs commonly throughout the western Pacific from central Japan to Queensland, Australia, and throughout Indonesia. Late Miocene and Pliocene fossils are common in both Japan and Indonesia (Beu, 2005).

Genus **BUFONARIELLA** Thiele, 1929

Bufonariella Thiele, 1929: 284.

TYPE SPECIES. — *Murex scrobilator* Linnaeus, 1758, by monotypy. Pliocene to Recent, Mediterranean and eastern Atlantic; Pliocene and Pleistocene, Atlantic tropical America.

SPECIES INCLUDED IN THE GENUS:

Bufonariella scrobilator (Linnaeus, 1758)

DIAGNOSIS:

Fusiform shell of relatively light build, with moderately tall spire, short anterior siphonal canal, posterior canal short and shallow, varices situated at every 2/3 whorl, 6 primary cords on the convex part of the whorl P2 and P4 totally atrophied (P6 less reduced than in *Dulcerana*). P1 and P3 can merge in big specimens (not as strong as in *Bursa* and *Lampasopsis*) weak variceal ornamentation,. Relatively strong projection of the outer lip. ovate operculum, subanterior nucleus.

Bufonariella scrobilator (Linnaeus, 1758)

Murex scrobilator Linnaeus, 1758: 749; 1767: 1218.

Tritonium scrobilator (Linnaeus, 1758) — Philippi 1844: 184.

Bursa (Bufonariella) scrobilator (Linnaeus, 1758) — Nordsieck & Garcia-Talavera 1979: 126, pl. 28, fig. 1.

Bursa scrobilator (Linnaeus, 1758) — Russo 1981: 20, illus. (living animal); Robinson 1993: 253; Cachia *et al.* 1996: 116, pl. 12, fig. 2; Gofas & Beu 2002: 102; Ardovini & Cossignani 2004: 133, three central figs; Landau *et al.* 2004: 66, pl. 5, figs 3-5, pl. 10, fig. 1; Chirli 2007: 103, pl. 37, figs 11-16, pl. 38, figs 1-4 (with long synonymy), Landau *et al.* 2009: 75, Pl. 7, Figs. 10–11; Segers *et al.* 2009: 173, pl. 35, fig. 7-7a-7b; Beu 2010: pl. 7, figs 3-4, 6-7.

Bursa (Colubrellina) scrobilator scrobilator (Linnaeus, 1758) — Beu 1985: 64; Cossignani 1994: 88-89; Giannuzzi-Savelli *et al.* 1997: 242, figs 903-904.

Murex scrobiculator Gmelin, 1791: 3535.

Tritonium scrobiculator (Gmelin, 1791) — Röding 1798: 127.

Triton scrobiculator (Gmelin, 1791) — Lamarck 1816: pl. 414, fig. 1, “Liste des objets”: 4; 1822: 180; Deshayes 1843: 626; Bellardi & Michellotti 1840: 33, pl. 2, fig. 7; Philippi 1843: 213; Reeve 1844a: pl. 8, fig. 28; Petit de la Saussaye 1852: 194.

Ranella scrobiculata (Gmelin, 1791) — G. B. Sowerby II 1836: pl. 93, fig. 21.

Tritonium scrobiculator (Gmelin, 1791) — Röding 1798: 127; Drouet 1858: 34.

Ranella scrobiculator (Gmelin, 1791) — Weinkauff 1868: 73.

Bursa (Bufonariella) scrobiculator (Gmelin, 1791) — Thiele 1929: 284, illus.

Bursa (Bufonariella) scrobiculata (Gmelin, 1791) — and var. *nodulosa* Segre 1954: 64, pl. 3, figs 4-6d.

Bursa (Bufonariella) scrobiculata (Gmelin, 1791) — with vars. *major*, *peculiaris*, *fasciata*, *undulata*, *nodulata*, *nodulosa elongata*, *seminodulosa*, and *seminodulosa fasciata* Settepassi 1970: Cymatiidae vii, pl. 5, figs 14ab, 15a-b, pl. 6, figs 16a-b, 17-18 (with further synonymy).

Bursa (Bufonariella) scrobiculator nodosa (Borson, 1825) — Caprotti 1970: 172, pl. 6, fig. 3.

Bursa scrobiculator (Gmelin, 1791) — Micali 1975: 202, illus. (living animal); Melone 1975: 203, illus. (radula); Avila *et al.* 1998: 500; Verdejo Guirao 2001: 14-18, figs 2-17.

Murex rana var. (not Linnaeus, 1758) — Brocchi, 1814: 401.

Bufonaria pesleonis Schumacher, 1817: 252.

Murex nodosus Borson, 1825: 310.

Ranella nodosa (Borson, 1825) — Sismonda, 1847: 40 ; D’Ancona 1872: 61, pl. 8, figs 5a-b; Bellardi 1873: 233, pl. 15, fig. 5.

Bursa (Bufonariella) nodosa (Borson, 1825) — Pavia, 1976: 153, pl. 2, figs 2, 5; Baluk 1995: 210, pl. 18, figs 4-5.

Ranella tuberculata Risso, 1826: 203, pl. 9, fig. 123 — Arnaud 1977: 139, pl. 10, fig. 167.

Ranella coriacea Reeve, 1844b: pl. 4, fig. 26.

Bufonaria scrobiculatoria (sic) Locard, 1886: 153.

Bursa (Colubrellina) scrobilator coriacea (Reeve, 1844) — Beu, 1985: 64, fig. 43; Cossignani 1994: 89.

Bursa scrobilator f. *coriacea* (Reeve, 1844) — Ardovini & Cossignani 2004: 133, two upper right figs.

Apollon quercina Mörch, 1853: 106.

Bufonaria scrobiculator var. *minor* Pallary, 1900: 296.

Ranella (Apollon) nodosa vars. *subanodosa* and *mioinquieseriata* Sacco, 1904: 39, pl. 11, figs 1-2.

Bursa scrobilator (*sic*) Guerreiro & Reiner, 2000: 120-121.

TYPE LOCALITY — *Murex scrobilator* and *Bufonaria pesleonis* from Recent Palermo, Sicily, by designation of Beu (2010: 64); *Ranella coriacea* from Recent Ile Goree, Senegal by designation of Beu (2010: 64).

TYPE MATERIAL. — *Murex scrobilator*, lectotype [LSL.455 The larger specimen (H 61.9 mm) bearing the number “537”] designated by Beu (2010: 64). In the absence of any known type material of Schumacher (1817), the lectotype of *M. scrobilator* has also been designated the neotype of *Bufonaria pesleonis* and *Apollon quercina* (Beu 2010: 64). *Ranella coriacea*, 3 syntypes (NHMUK 1967656). Beu (1987: 333) discussed the identity of *Apollon quercina* Mörch (1853: 106), and designated the lectotype as the unlocated specimen figured by Lister (1691: 943, fig. 39).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bufonariella scrobilator* lives today only in the Mediterranean Sea, along the coast of West Africa at least as far south as Ghana (southern limit not well established; recorded from Gabon by Bernard, 1984: 126, fig. 266), and at the Atlantic islands; it is recorded from the Azores (Ávila *et al.* 1998), Canary and Cape Verde Islands and at Madeira (Segers *et al.* 2009). Fossil specimens of *B. scrobilator* are recorded from a Pleistocene shellbed behind the beach at Praia, Santa Maria Island, Azores (Garcia-Talavera 1990), and were recollected by Alan Beu and Bernard Landau in 1998, from a Pleistocene shellbed ca. 2 m above sea level at Tenerife, Canary Islands (Garcia-Talavera *et al.* 1978), and from a Pleistocene shellbed on Selvagem Pequenha Island, Selvagem Islands, off of West Africa (Garcia-Talavera 2001). Meco *et al.* (2002: table 2) also recorded fossils from uplifted Pleistocene terraces at Arucas and Las Palmas, Canary Islands. Fossils also are widespread in the Miocene and Pliocene rocks of Europe and the Mediterranean region. Early Miocene (Burdigalian) of Italy: Turin Hills (Sacco 1904). Middle Miocene Paratethys (Langhian): Austria: Soß (Hoernes & Auinger 1884); Romania: Costeiu de Sus (= Kosteji) (Boettger 1902). Middle Miocene western Atlantic: Trinity Hill Sandstone member of Moruga Formation, Trinidad (Beu 2010). Pliocene western Atlantic: Panama: Cayo Agua Formation, Bocas del Toro Basin (Beu 2010); Pleistocene, Italy: Details to add from Beu (2010); material in collection of Paolo Crovato, Naples. Fossils of *Bufonariella. scrobilator* in the Americas are limited to Pliocene and Early Pleistocene rocks along the Atlantic coasts of Costa Rica, Panama,

and Colombia (the sole Colombian record possibly is as old as Late Miocene, but its age is poorly constrained). Fossil occurrence from Japan (Osagawara 2002) are dubious.

Genus **BURSINA**, Oyama 1964

Bursina, Oyama 1964: 333

TYPE SPECIES. — *Ranella nobilis* Reeves, 1844 by original designation.

SPECIES INCLUDED IN THE GENUS

Bursina borisbeckeri (Parth, 1996), *Bursina fernandesi* (Beu, 1977), *Bursina gnorima* (Melvill, 1918), *Bursina ignobilis* (Beu, 1987), *Bursina nobilis* (Reeve, 1844), *Bursina thersites* (Redfield, 1846)

DIAGNOSIS:

Very similar to *Bufonaria* in size, shape, varices alignment, intervarical expression of the primary cords and ornamentation, intervarical spines sometime pinch (e.g. *Bursina thersites*); varical P1 and P3 are relatively of the same size, no spine on the posterior siphonal canal; ovate operculum with apical nucleus.

Bursina nobilis (Reeve, 1844)

Ranella nobilis Reeve 1844a: pl. 4, fig. 16 — Reeve 1844b: 137; Martin 1899: 146, pl. 23, figs. 340-343 (in part); van der Vlerk 1931: 241.

Bursa (Bursa) nobilis (Reeve 1844) – van Regteren Altena 1942: 111 (in part).

Bursina nobilis (Reeve, 1844) — Oyama 1964: 330, 332; Beu *in* Poppe 2008: 612, pl. 251, figs 6, 7, Beu *et al.* 2012: 71, Figs 2J, K ; Lozouet *et al.* 2011: 31, Fig. 17, 1-2.

Gyrineum nobilis (Reeve 1844) – Habe & Kosuge 1966:46, pl. 16, fig. 8.

Bufonaria (Bufonaria) nobilis (Reeve 1844) – Beu 1985: 65; Cossignani 1994: 29-30.

Gyrineum (Chasmotheca) nobilis (Reeve 1844) – Skwarko & Sufiati 1994: m14.

Bursa bufonia dunkeri (not Kira, 1961) – Ladd 1982: 41, pl. 33, figs. 15, 16 (not pl. 8, figs. 6, 7 = *Bursa rosa* Perry, 1811).

Bursina ignobilis (not Beu, 1987) — Tröndlé & Boutet 2009: 22.

TYPE LOCALITY. — Recent Taiwan by designation of Beu (1998: 169)

TYPE MATERIAL. — Holotype (NHMUK 1967655ex Cuming Coll.) by monotypy.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Recent *Bursina nobilis* occurs uncommonly throughout the Indo-West Pacific, from Natal, Mozambique, and either Mauritius or Réunion (Drivas and Jay 1988) and the western Pacific to the Marquesas Islands, but not in the Red Sea or in southeastern Polynesia (Tuamotu, Society, and Austral Islands). Three large, typical specimens of *B. nobilis* in MNHN were collected as empty shells off Fiji during Musorstom 10 (Beu 1998: 169). *B. nobilis* is unexpectedly common around the Marquesas Islands. Ladd (1982, pl. 33, figs. 15, 16) and Lozouet *et al.* (2011: fig. 17, 1-2) illustrated typical specimens from the upper Pleistocene deposit at the Kere River, southern Espiritu Santo Island, Vanuatu.

***Bursina borisbeckeri* (Parth, 1996)**

Bufonaria (Bufonaria) borisbeckeri Parth, 1996: 129 figs 1-5

Bursina borisbeckeri (Parth, 1996) — Beu 2005: 24.

TYPE LOCALITY. — from deep water of Cebu, Philippines Islands (Parth 1996: 129).

TYPE MATERIAL. — Holotype (ZSM 1996 0001) and three paratypes in Parth coll.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. Only known from the Philippines Islands.

***Bursina fernandesi* (Beu, 1977)**

Bufonaria fernandesi Beu 1977: 89, figs 1-5.

Bufonaria (Bufonaria) fernandesi Beu, 1977 — Cossignani 1994: 23.

Bursina fernandesi (Beu, 1977) — Beu 2005: 24

TYPE LOCALITY. — From coast of Mozambique between Cabo das Correntes and Punta da Barra Falsa.

TYPE MATERIAL. — Holotype (NMP G8236/T2050) (Beu 1997: 90) paratype in C. P. Fernandes coll.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. Only known from the coast of Mozambique and Somalia.

Bursina gnorima (Melvill, 1918)

Bursa subgranosa (not G.B. Sowerby II, 1836 in G.B. Sowerby I & G.B. Sowerby II, 1832-1841) – Schepman 1909: 117

Bursa gnorima Melvill, 1918: 138, pl. 4, fig. 1.

Bufonaria (Bufonaria) gnorima. (Melvill, 1918) – Cossignani 1994: 26.

Bursa (Bursa) koperbergae van Regteren Altena, 1942: 109, figs. 4a, b, 5 – Skwarko & Sufiati 1994: n1.

Bursa koperbergae. van Regteren Altena, 1942 – Robba et al. 1989: 78, pl. 1, fig. 4.

Ranella (Bursa) nobilis (not *Ranella nobilis* Reeve, 1844) – Tesch 1920: 41, pl. 129, fig. 153a, b.

Ranella (Apollon) nobilis subsp. *timorensis* Koperberg, 1931: 120 (junior primary homonym of *Ranella pulchra timorensis* Koperberg, 1931: 119).

?*Gyrineum (Chasmotheca) nobile* (not Reeve, 1844) – Shuto 1969: 93, pl. 7, figs. 2, 7, 11; text-fig. 22.

TYPE LOCALITY. — *Bursa gnorima* Recent Jask, Gulf of Oman. *Bursa koperbergae* from the Pliocene of Toi Osapi Soka or Nono Fatoe Fekoe, province of Amanoeban” (Indonesia).

TYPE MATERIAL. — *Bursa gnorima*, lectotype (NHMUK1921.1.28.1) by designation of Beu (1987: 340). *Bursa koperbergae* lectotype (formerly in Instituut voor Mijnbouwkunde, Delft, no. 13846, now in RGM)

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — The distribution of *Bursina gnorima* is poorly known because of its deep-water habitat. It is known from Madagascar the

northern Indian Ocean and Gulf of Arabia, and throughout the central western Pacific in the Philippine Islands, Papua New Guinea and Indonesia.

Bursina ignobilis (Beu, 1987)

Ranella elegans (in part not G.B. Sowerby II, 1836 in G.B. Sowerby II & G.B. Sowerby II, 1832-1841); – Martin 1879: 55, pl. 10, fig. 3, 3a ;Martin 1884: 137 (in part).

Ranella nobilis (in part not Reeve, 1844) – Martin 1899: 146, pl. 23, figs. 340-342; Zwierzycki 1915: 109; Martin 1919: 88, 126, 128, 130, 141; van der Vlerk 1931: 241; van der Vlerk 1932: 111; Martin 1932: 114.

Bursa (Bursa) nobilis (not Reeve, 1844) – van Regteren Altena 1942: 111.

Bursa (Colubrellina) nobilis (not Reeve, 1844) – Ladd 1977: 35, pl. 12, figs. 1-3.

Bufonaria (Bufonaria) ignobilis Beu, 1987: 344, figs. 221, 257-263. — Cossignani 1994: 27; Beu 1998: 167, fig. 53g.

Bursina ignobilis (Beu, 1987) — Beu 2005: 26, figs. 42-53.

TYPE LOCALITY. — From Punta Engaño, Mactan Island, Cebu, Philippine Islands.

TYPE MATERIAL. —Holotype (USNM 849010).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Bursina ignobilis* occurs throughout the tropical Indian Ocean and the western Pacific. Recent collections from the Marquesas Islands, in eastern Polynesia, demonstrate that only *B. ignobilis* occurs there and *B. nobilis* seems not to occur so far to the east. Fossils are common in the richly diverse Pleistocene locality on Espiritu Santo Island, Vanuatu [recorded by Ladd (1977: 35) as *Bursa nobilis*] and are moderately common in the late Miocene of Indonesia (Beu 2005).

Bursina thersites (Redfield, 1846)

Ranella thersites Redfield, 1846: 166, pl. 10, fig. 6a, b.

Ranella californica (in part not Hinds, 1843) — Tryon 1880: 40.

Gyrineum (Chasmotheca) cavitense (not Reeve, 1844) — Oyama & Takemura 1960, *Gyrineum* figs. 3, 4.

Bursa nobilis (not Reeve, 1844) — Cernohorsky 1967a: 314, pl. 42, fig. 5; Cernohorsky 1967b: 46, pl. 2, fig. 6; Hinton 1978: 32, fig. 1.

Bufonaria (Bufonaria) thersites (Redfield, 1846) — Beu 1987: 342, figs. 254-256; Cossignani 1994: 38, Beu 2005: 18.

Bursa thersites (Redfield, 1846) — Short & Potter 1987: 44, pl. 21, fig. 1.

Bufonaria thersites (Redfield, 1846) – Wilson 1993: 226

Bursa crumena (not Lamarck, 1816) — Salvat *et al.* 1988: 103, pl. 13, fig. 17.

Bufonaria thersites (Redfield, 1846) – Beu 1998: 171, figs. 53b, d, e, 58a.

TYPE LOCALITY. — Recent New Caledonia by subsequent designation of Beu (1998:171).

TYPE MATERIAL. — location of type material not confirmed, presumably in the State Museum of New York, Albany; Redfield's (1846, pl. 10, fig. 6a, b).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Beu (1998: 172) recorded specimens of *Bursina thersites* from the Philippine Islands south to northeastern Australia, New Caledonia, and Fiji. He also recorded Pliocene fossils from Fiji (2, AMS C302629), the only other fossils he is aware of recent specimens occur uncommonly in populations of the much more abundant *Bufonaria margaritula* and the single record from Java suggests that they also did so during Pliocene time (Beu 2005).

Genus *COLUBRELLINA* Fischer, 1884

Colubrellina Fischer, 1884b: 656.

TYPE SPECIES. — *Ranella candisata* Lamarck, 1822 (= *Murex conditus* Gmelin, 1791) by monotypy Recent, western Pacific.

Extremely tall, narrowest shape of all Bursidae species. Varices unaligned. 6 primary cords on the convex part of the whorl, visible only on varical. Strong sutural cord. Uniform sculpture of many rows (a least 4 between each primary cord) of fine beads (micronodosity) lack protruding posterior siphonal spines up the spire; weak lamellar projection of the outer lip; operculum D shape, sub apical nucleus in lower right.

SPECIES INCLUDED IN THE GENUS

Colubrellina condita (Gmelin, 1791)

DIAGNOSIS:

Extremely tall, narrowest shape of all Bursidae species. Varices unaligned. 6 primary cords on the convex part of the whorl, visible only on varical. Strong sutural cord. Uniform sculpture of many rows (a least 4 between each primary cord) of fine beads (micronodosity) lack protruding posterior siphonal spines up the spire; weak lamellar projection of the outer lip; operculum D shape, sub apical nucleus in lower right.

Colubrellina condita (Gmelin, 1791)

Murex conditus Gmelin, 1791: 3565.

Colubrellina (Dulcerana) condita (Gmelin, 1791) — Oyama & Takemura 1960; *Colubrellina* fig. 12; Habe 1961: 46, pl. 23, fig. 12.

Colubrellina condita (Gmelin, 1791) — Habe 1964: 75, pl. 23, fig. 12.

Bursa (Colubrellina) condita (Gmelin, 1791) — Cernohorsky 1972b: 200, figs 12-13; Beu 1985: 64, Springsteen & Leobrera 1986: 120 pl. 33 fig. 5; Cossignani 1994: 68.

Bursa condita (Gmelin, 1791) — Wilson 1993: 226; Beu 1998: 143, Figs. 45 a-d. Beu *et al.* 2012: 66, fig. 6A.

Tritonium candidatum Röding, 1798: 126.

Murex candidatus (Röding, 1798) — Dillwyn 1817: 699,

Ranella candidata Lamarck 1822; 150 — J. Sowerby & G.B. Sowerby I 1823: part 19, pl. 233, fig. 1; Kiener 1841: 35, pl. 13, fig. 1 [as *candidata* in text]; Deshayes 1843:542; Reeve 1844b: pl. 1, fig. 5.

Apollon candidatus (Röding, 1798) — Kobelt 1876: 327.

Ranella (Lampas) candidata (Lamarck 1822) — Tryon 1880:41, pl. 22, fig. 43.

Colubraria granulate Schumacher, 1817: 251 (in part).

TYPE LOCALITY. — Ambon Island (Amboina), Indonesia, designated by Beu (1998: 145)

TYPE MATERIAL. — *Ranella candidata*, lectotype, (MHNG 993.102) and neotype of *Murex conditus* and *Tritonium candidatum* Röding, 1798, all designated by Beu (1998:145).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. Three specimens recorded from Tahiti and from the Tuamotu Islands (Beu *et al.*, 2012). *Colubrellina condita* is rare throughout its range, and is not recorded from Hawaii (Severns 2011). The first record from the Indian Ocean is the specimen illustrated from Kandholhudhoo Islet, North Maalhosmadulu Atoll, Maldive Islands, by Delsaerdt (2011: 17, 31, pl. 2, figs 10–11). *Colubrellina condita* therefore seems to occur rarely throughout the Indo-West Pacific province from the Maldives to as Far East as the Tuamotu Islands in eastern French Polynesia.

Genus **CROSSATA** Jousseume, 1881

Crossata Jousseume, 1881

TYPE SPECIES. — *Ranella ventricosa* Broderip, 1833 by original designation Pliocene to Recent, southern California to Peru

SPECIES INCLUDED IN THE GENUS

Crossata ventricosa (Broderip, 1833), *Crossata californica* (Hinds, 1844), *Crossata barbarajeanae* Powell & Berschauer, 2017, *Crossata calcipicta* (Dall, 1908) (*taxon inquirendum*)

Crossata ventricosa (Broderip, 1833)

Ranella ventricosa Broderip, 1833: 178. G. B. — Sowerby II 1836: pl. 92, fig. 16; d'Orbigny 1841b: 451, pl. 62, figs 11-12; Kiener 1842: pl. 14, fig. 2; Deshayes 1843: 555; Reeve 1844b: pl. 2, fig. 6; Hupé 1854: 184; Tapparone-Canefri 1876: 118; Küster & Kobelt 1871: 140, pl. 38a, figs 3-4.

Ranella (Lampas) ventricosa Broderip, 1833 — Tryon 1880: 40, pl. 20, figs 16-18.

Crossata ventricosa (Broderip, 1833) — Jousseume 1881: 175 (reprint: 4); Beu 1985: 66; Parth 1996: 135; Cossignani 1994: 95; Beu 2001: 711, fig. 1.8.

Bursa ventricosa (Broderip, 1833) — Dall 1909: 226; Basly Santa Maria 1983: 19, pl. 5, fig. 43.

Bursa (Crossata) ventricosa (Broderip, 1833) — Olsson 1932: 186, pl. 21, fig. 1; Pilsbry & Olsson 1941: 39; Ramirez 1987: 150, fig. 186; Guzman *et al.* 1998: 46, illus.

Ranella (Lampas) ventricosa (Broderip, 1833) — Coulon 1933: 138.

Ranella tenuis Potiez & Michaud, 1838: 426, pl. 34, figs 1-2.

TYPE LOCALITY. — *Ranella ventricosa* from Recent “Bay of Callao, Peru.” *Ranella tenuis* from Recent Chili.

TYPE MATERIAL. — *Ranella ventricosa*, lectotype (NHMUK 1950.11.28.1, marked holotype) by designation of Beu (2010: 70), with two paralectotypes (NHMUK 1950.11.28.2-3). *Ranella tenuis*, neotype (NHMUK 1950.11.28.1) by designation of Beu (2010: 70) type material originally in the Museum de Douai, northern France, but it has been destroyed during World War II.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Peruvian Province. Warm temperate zone south of the Gulf of Guayaquil (Powell & Berschauer 2017), Ecuador in the north through Peru, and rarely into northern Chile. Specimens are known to have been collected from 15 to 170 m water depth. Pliocene fossils are known from: Canoa Formation, Ecuador (Pilsbry & Olsson, 1941), Esmeraldas Formation, Ecuador (Jung 1989), Onzole Formation, Ecuador (Landau & Marques da Silva 2010), Shark Hole Formation, Panama (Collins & Coates 1999; Beu 2010), and Taie Formation, Peru (DeVries 1988). Pleistocene: San Juan Terrace, Peru (Ortlieb *et al.* 1990), Caleta Patillos, Chile (Rivadeneira & Carmona 2008).

Crossata californica (Hinds, 1844)

Ranella californica Hinds, 1844: 255. — Reeve 1844b: pl. 2, figs 9a-b; Hinds 1844b: 12, pl. 2, fig. 4; Küster & Kobelt 1871: 141, pl. 39, fig. 5; Arnold 1903: 287.

Ranella (Lampas) californica Hinds, 1843 — Tryon 1880: 40, pl. 22, fig. 42.

Crossata californica (Hinds, 1843) — Jousseume 1881: 175 (reprint: 4); Beu 1988: 74; Albi 2002: 33, figs 2-5, 7 (lower row), 8 (lower), 9 (lower row).

Bursa (Bufonaria) californica (Hinds, 1843) — Dall 1921: 141; Oldroyd 1927: 241, pl. 33, figs 7-8.

Bursa californica (Hinds, 1843) — Jordan 1924: 149; Jordan 1926: 246; Jordan 1936: 113; Oldroyd 1927: 241, pl. 33, figs 7-8; Grant & Gale 1931: 731; Durham 1950: 115, pl. 35, fig. 10; Keen 1958: 348; McLean 1978: 40, fig. 21.1.

Bursa (Crossata) californica (Hinds, 1843) — Abbott 1954: 199, pl. 20r; Abbott 1974: 167, pl. 7, fig. 1783.

Crossata californica californica (Hinds, 1843) — Beu 1985: 66; Cossignani 1994: 91-92.

Bursa californica sonorana Berry, 1960: 118 — Hertz 1984: 24, fig. 50.

Bursa sonorana Berry, 1960— Keen 1971: 509, fig. 967.

Crossata californica sonorana (Berry, 1960) — Beu 1985: 66, fig. 52; Cossignani 1994: 93-94; Schneider 1999: table 1.

TYPE LOCALITY. —*Ranella californica* from recent Bay of San Diego, California. *Bursa sonorana* near Guaymas, Sonora, Mexico by original designation of Berry (1960: 118)

TYPE MATERIAL. — *Ranella californica*, neotype (NHMUK, no. 1842.1.2(2).634) by subsequent designation of Beu (2010: 70). *Bursa sonorana*, holotype (CASIZ 43931 *ex* Stanford University coll., SU 9510), with one paratype, (SDNHM 42802).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Generally found from Point Conception, California, USA south through Baja California, Mexico. Occasional specimens are found as far north as the Monterey Peninsula, California, USA. Guaymas, Mexico. Miocene specimens reported from the Tumbes sandstone, Que. Tucillal at Zorritos, Peru (Olsson, 1932); Pliocene: “Fernando” Formation – Brea Canyon, Orange County, California (Carson 1925); Los Angeles, Los Angeles County, California (Davis, 1998); Niguel Formation, Mission Viejo, Orange County, California (Stadum 1984); San Diego Formation (Hertlein & Grant 1960; Albi 2002; Powell *et al.* 2009; Vendrasco *et al.* 2012); “Santa Barbara” Formation, Rincon Point, Santa Barbara/Ventura counties, California (Powell *et al.* 2009). Provisionally (cf.) identified specimens - location, “Pico” Formation (Powell *et al.* 2009). Pleistocene: Lomita Marl - San Pedro, Los Angeles County, California (Wooding *et al.* 1946); Palos Verdes Sand, San Pedro, Los Angeles County, California (Mount 1970); “San Pedro” Formation - Coyote Hills, Los Angeles/Orange counties, California (Powell & Stevens 2000); Unnamed formations/terraces,

Potrero Canyon, Los Angeles County, California (Woodring *in* Hoots 1931; Valentine 1956; Albi 2002); Isla Coronado, Baja California, Mexico (Durham 1950); Bahia Tortuga, Baja California, Mexico (Chase 1956), Rosarito Beach, Baja California, Mexico (Valentine 1957), Punta Baja, Baja California, Mexico (Emerson & Addicott 1958); Punta Cabras, Baja California, Mexico (Addicott & Emerson 1959); San Nicolas Island, Southern California Bight (Vedder & Norris 1963), Isla Coronados, Baja California, Mexico (Emerson & Hertlein 1964), Bahia Santa Rosalia quadrangle, Baja California, Mexico (Fife 1968), San Clemente Island, southern California Bight (Susuki & Stadum 1978), Isla de Guadalupe, Mexico (Lindberg *et al.* 1980), Newport Bay, Orange County, CA (Powell *et al.* 2004), All those localities has been listed by Powell & Berschauer (2017).

Crossata barbarajeanae Powell & Berschauer, 2017

Crossata barbarajeanae Powell & Berschauer, 2017: 184, Fig. 4, Gig. 10, I.

TYPE LOCALITY. — *Crossata barbarajeanae* from Bahia de la Independencia, central Peru.

TYPE MATERIAL. — Holotype (LACM holotype 3472, from lot number LACM 35-25.1). Five paratypes (LACM paratype 3473 from the same lot as holotype).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. *Crossata barbarajeanae* is only known from the Peruvian province.

Crossata calcipicta (Dall, 1908) (*taxon inquirendum*)

Bursa (Lampadopsis) calcipicta Dall, 1908: 320.

Bursa calcipicta Dall, 1908 — Keen 1958: 348, fig. 328; Keen 1971: 508, fig. 965 (in part, = *Ranella rugosa* G. B. Sowerby II, 1835).

TYPE LOCALITY. — *Bursa (Lampadopsis) calcipicta* from recent Cocos Island, Gulf of Panama

TYPE MATERIAL. — *Bursa (Lampadopsis) calcipicta*, holotype (USNM 123027)

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. *Crossata calcipicta* occurs from Bahia de Panamá, Panama to Ecuador and Galapagos Islands.

Genus **DULCERANA** Oyama, 1964

***Dulcerana* Iredale, 1931**: 213

Invalid nomina Iredale doesn't differentiate the genus from related taxa (no type species).

***Dulcerana* Oyama, 1964**: 332.

TYPE SPECIES. — *Tritonium granulare* Röding, 1798, Pleistocene and Recent, Indo-West Pacific, eastern and western Atlantic, and eastern Pacific (Clipperton Island).

SPECIES INCLUDED IN THE GENUS:

Dulcerana granularis (Röding, 1798), *Dulcerana affinis* (Broderip, 1833), *Dulcerana cubaniana* (d'Orbigny, 1841), *Dulcerana elisabettae* (Nappo *et al.* 2014), *Dulcerana alfredensis* (Turton, 1932) (*taxon inquirendum*), *Dulcerana kowiensis* (Turton, 1932) (*taxon inquirendum*)

DIAGNOSIS:

Very similar in broad shape and colour to *Bufo nariella*, varices aligned (can be slightly displaced in the last whorl), granulose ornamentation, secondary cords can grow as important as primary ones. P2, P4, P6 reduce in varical and intervarical, (very slightly in *D. granularis* to fully atrophied in *D. elisabettae*) Weak projection of the outer lip, ovate operculum, subanterior nucleus

***Dulcerana granularis* (Röding, 1798)**

Tritonium granulare Röding, 1798: 127.

Bursa granularis (Röding, 1798) — H. & A. Adams 1853: 106; Barnard 1963: 17; Hinton 1972: 12, pl. 6, fig. 22; Hinton 1978: 32, fig. 8; Kilburn & Rippey 1982: 73, pl. 16, fig. 14, Drivas & Jay 1988: 62, pl. 16, fig. 4; Wilson 1993: 226, pl. 43, figs 11a-b, 12; Kubo *in* Kubo & Kurozumi 1995: 74, 78, fig. 7; Beu 1998: 150, figs 48a-e, 58d; Beu 1999: 44, fig. 85; Beu 2005: 19, figs

27, 28; Lee & Chao 2003: 40, pl. 4, fig. 93; Castelin *et al.* 2012: 4843, fig. 4; Dolorosa *et al.* 2013: 8, fig. 3D; Sanders *et al.* 2017 fig. 4A–D, J.

Colubrellina granularis (Röding, 1798) — Habe 1961: 47, pl. 24, fig. 5; Okutani 1986: 116–117, top left fig.

Colubrellina (Dulcerana) granularis (Röding, 1798) — Habe 1964: 76, pl. 24, fig. 5; Wilson & Gillett 1971: 80, pl. 54, fig. 7, 7b.

Bursa (Colubrellina) granularis granularis (Röding, 1798) — Beu 1985: 64; Cossignani 1994: 75–77; Nappo *et al.* 2014: pl. 3, figs 1–3, pl. 4, figs 1–4, pl. 5, fig. 1, pl. 7, fig. 1.

Bursa (Bufonariella) granularis (Röding, 1798) — Bosch *et al.* 1995: 102, fig. 737.

Bursa (Colubrellina) granularis (Röding, 1798) — Okutani 2000: 269, pl. 133, fig. 1; Zhang & Ma 2004: 182, text-figs 113a–c, pl. 5, figs 1–3.

Tritonium jabick Röding, 1798: 127

Dulcerana jabick (Röding, 1798) — Iredale 1931: 213.

Colubrellina jabick (Röding, 1798) — Oyama & Takemura 1960: *Colubrellina* pl., figs 3, 4.

Biplex rubicola Perry, 1811: pl. 5, fig. 4.

Ranella granifera Lamarck, 1816: pl. 414, fig. 4, ‘Liste des objets’: 4; 1822: 153; Kiener 1841: 16, pl. 11, fig. 1; Deshayes 1843: 548; Reeve 1844a: pl. 6, fig. 30; Küster & Köbel 1871: 143, pl. 39, fig. 1.

Bursa cumingiana Dunker, 1862: 238 — Dunker 1863: 59, pl. 19, figs 7, 8.

Ranella (Lampas) granifera Lamarck, 1816 — Tryon 1880: 41, pl. 22, figs 35–40.

Ranella semigranosa (not Lamarck, 1822) — Reeve 1844b: pl. 6, fig. 25; Krauss 1848: 113

TYPE LOCALITY. — . *Tritonium granulare*, *Tritonium jabick*, *Biplex rubicola*, *Ranella granifera*, Red Sea, in accordance with ICZN Art. 76.3 (see below). *Bursa cumingiana*, New Caledonia.

TYPE MATERIAL. — *Tritonium granulare*, *Tritonium jabick*, *Biplex rubicola*, original types lost; neotype MHNG 1098/85/1, designated by Beu, 1998: 150. *Ranella granifera*, lectotype MHNG 1098/85/1, designated by Beu, 1998: 150. *Bursa cumingiana*, lectotype NHMUK 1968530 designated by Beu 1998: 150.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Dulcerana granularis* has a tropical distribution throughout the Indo-West Pacific province, from the Mozambique Channel throughout East Africa and the Red Sea to the northern Indian Ocean, in the western Pacific from Kii Peninsula and Yamaguchi Prefecture, Honshu, Japan (Beu, 1999), south to Rottneest Island in Western Australia (Wilson 1993). Its eastward distribution in the Pacific extends from

Japan to Australia through the Philippines, Vanuatu and New Caledonia. *Dulcerana granularis* is commonly found in very shallow water but some specimens were found alive in about 100 m depth. *D. granularis* has a Miocene-Recent time range in the Indian Ocean (Beu 2005).

***Dulcerana affinis* (Broderip, 1833)**

Ranella affinis Broderip, 1833: 179 G.B. — Sowerby II 1835 [*in* 1832–1841]: pl. 89, fig. 12; Reeve 1844b: pl. 4, fig. 19; Küster & Köbelt 1871: 142, pl. 38a, fig. 5.

Bursa granularis affinis (Broderip, 1833) — Hertlein & Allison 1960: 15.

Bursa affinis (Broderip, 1833) — Sanders *et al.* 2017: Fig. 4E–I, K.

Ranella livida Reeve, 1844a: pl. 6, fig. 28—Reeve 1844b: 138; Krauss 1848: 113.

Dulcerana granularis (not Röding, 1798)—Iredale 1931: 213; Rippingale & McMichael 1961: 69, pl. 7, fig. 19.

Bursa granularis—Hertlein & Allison 1960: 15; Salvat & Rives 1975:

307, fig. 179; Kay 1979: 227, fig. 80 A; Severns 2011: 150, pl. 59, fig. 6; Beu *et al.* 2012: 67, fig. E2 (all not Röding, 1798).

Bursa (Colubrellina) granularis (not Röding, 1798) — Kaiser 2007: 39, pl. 26, fig. 7a-b.

TYPE LOCALITY. — *Ranella affinis*, *Ranella livida* ‘Annaa,’ Tuamotu Islands

TYPE MATERIAL. — *Ranella affinis*, lectotype, NHMUK 1950.11.28.4, designated by Beu 1998: 150. *Ranella livida*, lectotype, NHMUK 1967657_1, designated by Beu 1998: 150.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. *Dulcerana affinis* has a tropical distribution throughout the Pacific Ocean, from Okinawa, Japan to Sydney Harbour, New South Wales, Australia, and throughout Polynesia to Hawaii (Beu 1998). In the eastern Pacific, particularly large specimens are common at Clipperton Island (Hertlein & Allison 1960; Kaiser 2007) and specimens were recorded by Emerson (1991) from the Revillagigedo Islands, Cocos Island and the mainland coast at Bahia Chamela, Jalisco, western Mexico (Beu 2010). Its westward distribution in the Pacific extends from Japan to Australia through the Philippines, Papua New Guinea, Vanuatu and New Caledonia. *Dulcerana affinis* is commonly found in very shallow water, but specimens are occasionally found alive in about 40m depth.

***Dulcerana alfredensis* (Turton, 1932) (*taxon inquirendum*)**

Bursa alfredensis Turton, 1932: 107, pl. 24, fig. 781. — Sanders *et al.* 2017: fig. 6 K.

TYPE LOCALITY. — *Dulcerana alfredensis* from Port Alfred, South Africa (supposed type locality).

TYPE MATERIAL. — Presumably in the collection from Port Alfred, South Africa, presented to the Oxford University Museum by Turton (1932).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — If *Dulcerana alfredensis* were to be genus species its known range would be the eastern coast of South Africa

***Dulcerana cubaniana* (d'Orbigny, 1841)**

Ranella cubaniana d'Orbigny, 1841: 165, pl. 23, fig. 24.) — Mörch 1877: 24.

Gyrineum affine var. *cubanianum* (d'Orbigny, 1841) — Dall 1889: 224.

Gyrineum affine (sic) *cubanianum* (d'Orbigny, 1841) — Morretes 1949: 92.

Bursa (Colubrellina) cubaniana (d'Orbigny, 1841) — Abbott 1958: 57, text-fig. 2, pl. 1, fig. k. Warmke & Abbott 1962: 103, pl. 18, fig. i; Rios 1970: 70; Coelho & Matthews 1971: 52, figs 11, 12; Humfrey 1975: 126, pl. 14, fig. 4, 4a; H. & E. Vokes 1983: 23, pl. 11, fig. 14.

Bursa cubaniana (d'Orbigny, 1841) — Nowell-Usticke 1959: 61; Work 1969: 663; Kaufmann & Gotting 1970: 372, fig. 87; Matthews & Kempf 1970: 28; de Jong & Coomans 1988: 214, pl. 16, fig. 382., Sanders *et al.* 2017: fig. 6 A–D, L.

Bursa cubaniana var. *intermedia* Nowell-Usticke 1959: 61–62, pl. 3, fig. 13 — Boyko & Cordeiro 2001: 24.

Bursa corrugata var. *lineata* Nowell-Usticke 1959: 61–62, pl. 3, fig. — Boyko & Cordeiro 2001: 24.

Bursa granularis cubaniana (d'Orbigny, 1841) — Abbott 1974: 167, pl. 7, fig. 1781 (as *B. granularis* in caption); Rios 1975: 81, pl. 23, fig. 331; Finlay 1978: 149; Bandel 1984: 102, pl. 10, figs 3, 8; Diaz & Gotting 1988: 156; Diaz 1990: 19; Diaz & Puyana 1994: 174, fig. 650; Redfern 2001: 58, pl. 29, fig. 247 A, B. Nappo *et al.* 2014: pl. 5, figs 2, 3, pl. 6, figs 1–3, pl. 7, fig. 2.

Bursa (Colubrellina) granularis cubaniana (d'Orbigny, 1841) — Rios 1975: 81, pl. 23, fig. 331; Beu, 1985: 64; Cossignani, 1994: 78.

Bursa (Colubrellina) granularia (sic) *cubaniana* (d'Orbigny, 1841) — Rios 1994: 92, pl. 31, fig. 365.

Bursa granularis (not Röding, 1798) — Leal 1991: 111, pl. 16, figs C, D; Lipe & Abbott 1991: 14–15, illus.; Beu 2010: 48, pl. 3, figs 1, 3; Redfern 2013: 83, fig. 241.

Bursa (Colubrellina) granularia (sic) (not Röding, 1798) — Rios 1985: 79, pl. 28, fig. 347.

Gyrineum affine (not Broderip, 1833) — Dall 1903: 132.

Ranella (Bursa) affinis (not Broderip, 1833) — Trechmann 1933: 39.

TYPE LOCALITY. — *Ranella cubaniana*, Ste Lucie, West Indies, *Bursa cubaniana* var. *intermedia*, and *Bursa corrugata* var. *lineata*, north of Fredericksted, St Croix, Virgin Islands

TYPE MATERIAL. — *Ranella cubaniana* holotype NHMUK 1854.10.4.412. *Bursa corrugata* var. *lineata*, holotype (AMNH 195427). *Bursa cubaniana intermedia* type material not recognizable in Nowell-Usticke's collection (now in AMNH), as was also stated by Faber (1988: 81).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Dulcerana cubaniana* occurs in the western Atlantic (fig. 1; Rosenberg 2009), where it is recorded from southeastern Florida (Abbott 1974; this study), Texas and Louisiana (Garcia 1999) westwards to Mexico, Costa Rica, Panama and Colombia (Massemin *et al.* 2009), the Bahamas (Redfern 2013), Guadeloupe (this study), Jamaica, Cuba and St Lucia (d'Orbigny 1841) south to French Guiana (Massemin *et al.* 2009), Bahia and Pernambuco, Brazil (Matthews 1968; Rios 1985, 1994; Mello & Perrier 1986). In the eastern Atlantic, it has been recorded only from the Cape Verde Islands, but this record is unconfirmed (Rolán 2005). It is recorded only from Pleistocene rocks and in the living fauna in the western Atlantic, and so apparently is a geologically recent arrival there. The record by Gregory (1895: 288, table) from Pleistocene rocks of Barbados as "*Ranella (Lampas) aff. affinis*" presumably refers to this species (Robinson 1991).

***Dulcerana elisabettae* (Nappo *et al.*, 2014)**

Bursa granularis elisabettae Nappo *et al.*, 2014: 5, pl. 1, figs 1–3, pl. 2, figs 1–3, pl. 3, figs 1–3

Bursa cf. nodosa (not Borson, 1823) — Bozzetti 1991:1, fig.1.

Bursa granularis "affinis" form (not Röding, 1798) — Wilson 1993: pl. 43, fig. 12.

Bursa elisabettae Nappo *et al.*, 2014 — Sanders *et al.* 2017: fig. 6E–G, M.

TYPE LOCALITY. — Flinders Bay, Cape Leeuwin, southern Western Australia, 12 m deep.

TYPE MATERIAL. — Holotype (MAC.ML 1536).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. The known distribution of *Dulcerana elisabettae* is restricted to southwestern Western Australia, in shallow water.

Dulcerana kowiensis (Turton, 1932) (*taxon inquirendum*)

Bursa kowiensis Turton, 1932: 108, pl. 24, fig. 782. — Sanders *et al.* 2017: fig. 6, j

TYPE LOCALITY. — *Dulcerana kowiensis* from Port Alfred, South Africa (supposed type locality).

TYPE MATERIAL. — Presumably in the collection from Port Alfred, South Africa, presented to the Oxford University Museum by Turton (1932).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — If *Dulcerana kowiensis* were to be genus species its known range would be the eastern coast of South Africa

Genus **KORRIGANIA**, Sanders *et al.* in prep. (article 3)

Korrigania, Sanders *et al.* in prep: (article 3)

TYPE SPECIES. — *Ranella fijiensis* Watson, 1881

SPECIES INCLUDED IN THE GENUS

Korrigania awatii (Ray, 1949), *Korrigania fijiensis* (Watson, 1881), *Korrigania fosteri* (Beu, 1987), *Korrigania quirihorai* (Beu, 1987).

DIAGNOSIS:

Fusiforme very light built shell (extremely light in *K. awatii*), 7 primary cords on the convex part of the whorl, P2 and P4 atrophied, P6 and P7 reduced varices displaced but less than *Tutufa* or *Tritonoranella*, ovate operculum, subanterior nucleus. Resemble *Tritonoranella* but lack black stripes on the columella.

Korrigania fijiensis (Watson, 1881)

Ranella fijiensis Watson, 1881: 270 — Watson 1886: 397, pl. 34, figs 7 a-b.

Bursa (Bufonariella) fijiensis (Watson, 1881) — Beu 1978: 26, fig. 10; Cossignani 1994: 73-74.

Bursa (Colubrellina) fijiensis (Watson, 1881) — Beu 1985: 64.

Bursina fijiensis (Watson, 1881) — Beu, 2005: 24; Beu *et al.* 2012: 71, fig. 2I.

TYPE LOCALITY. — From "*Challenger*" sta. 173, 19°9'35" S, 170°41'50" E, off Fiji, in 576 m deep.

TYPE MATERIAL. — Holotype (NHMUK 1887.2.9.1217) Paratype, (NHMUK 1887.2.9.1218), from "*Challenger*" sta. 204A, 12°43' N, 112°9' E, 183-210 m, Philippine Islands (a fragmentary specimen of *Korrigania awatii*).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — The range of *Korrigania fijiensis* is poorly known, as it lives in c.300–600 m throughout its range. Beu (1998) recorded specimens from the Philippine Islands, the New Caledonian region (51 samples) and Vanuatu, and other samples are present in MNHN from recent expeditions to the Norfolk Ridge and the Solomon Islands. Along with the type locality of Fiji and the present record of a single specimen from off Rurutu in the Austral Islands, these records indicate that *K.fijiensis* is very widespread throughout the western Pacific from the western archipelagos to eastern Polynesia. However, it is not present in samples collected so far from the Marquesas, Society, or Tuamotu Islands.

Korrigania awatii (Ray, 1949)

Bursa awatii Ray, 1949: 100, pl.1 fig. 3-5; Abbott & Dance, 1981: 127, Castelin *et al.*, 2012 : 4843, Fig. 4.

Bursa (Colubrellina) awatii. Ray, 1949; Cossignani, 1994:63-67, 11 unnamed figs.

fBursa (Bufonariella) rehderi Beu, 1978: 25, figs. 1-8.

TYPE LOCALITY. — *Bursa awatii*: Coromandel coast of India, Madras, India. *Bursa (Bufonariella) rehderi*: Abgao, Leyte, Philippine Islands (USBF Station 5403, 333 m deep).

TYPE MATERIAL. — *Bursa awatii*, holotype (ZSI Reg. No. M 15942/2) and one paratype (ZSI Reg. No. M 15945/2) from the same locality. *Bursa (Bufonariella) rehderi*, Holotype (USNM 240450) USNM 240450 and NZGS WM 12070 from the same locality. Three paratypes, USNM 238820 from off Pt. Tagolo, Mindanao, Philippines (USBF Station 5518, 365 m deep). One Paratype USNM 230654 from Tanon Strait, Philippines (USBF Station 5191, 490 m deep). One paratype, USNM 205474 from Tanon Strait due west of Alegraia, Cebu I, and midway between coasts of Cebu and Negros Islands, Philippines (USBF Station 5188, 9° 44'N, 123° 14' 20"E, 547 m deep).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE: — No fossil record. Throughout the Indian ocean, Western India (Ray, 1949), quite abundant in the Philippines islands, Bohol sea. Less common in Indonesia (Tanimbar and Kai Islands). Rather common in Somalia (Cossignani 1994).

Korrigania fosteri (Beu, 1987)

Bursa (Colubrellina) latitudo fosteri Beu, 1987:325, figs 195-199,202-206 — Cossignani 1994: 81, four unnamed figs.

Bursa fosteri Beu, 1987: 22 — Castelin *et al.* 2012: 4843, Fig 4.

TYPE LOCALITY. — Tangled nets in 100-200 m deep, north side of Panglao Peninsula, Bohol, Philippine Islands

TYPE MATERIAL. — Holotype (USNM 849013) 1 paratype from type locality in Abbey Specimen Shells, Santa Barbara, 4 paratypes from Punta Engano, Mactan I., Cebu (2 NZGS WM13166 and 2 in F.J. Springsteen coll.), 2 paratypes from Mactan I., Cebu (NZGS WM14441), 1 paratype, off Cebu, (NSMT 55501).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. *B. fosteri* is recorded only from the Philippine Islands (Beu 1987, 1998; Castelin *et al.* 2012), New Caledonia (Beu 1998; Castelin *et al.* 2012) and Vanuatu (Beu, 1998).

Korrigania quirihorai Beu, 1987

Bursa (Colubrellina) quirihorai Beu, 1987: 321, figs 182-192 — Cossignani 1994: 85,

Bursa quirihorai Beu, 1987— Beu 1998: 162, Figs 47 e, 52 a-g, 58 b ; Castelin *et al.* 2012: 4843, fig .4

TYPE LOCALITY. — Recent Panglao Peninsula, Bohol, Philippines.

TYPE MATERIAL. — Holotype (USNM 849004) and 12 paratypes (6 NZGS WM14093 (Beu, 1998: figs 52 e-f), 3 Abbey Specimen Shells, 1 SBNHM 33909), tangle nets in 275-460 m, off Balicasag Island, a few km south of Panglao Peninsula, Bohol, Philippines, 1 paratype (NZGS WM14442), off Punta Engafto, Mactan I., Cebu, 1 paratype (MNHN-IM-2000-4126), off New Caledonia, 300-315 m (Beu 1998: fig. 52 d).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. *B. quirihorai* is recorded from the Philippine Islands Tonga Islands, Fiji Islands and New Caledonia, from off the Kai Islands in eastern Indonesia and a single specimen from Vanuatu.

Genus *LAMPASOPSIS* Jousseau, 1881

Lampadopsis Jousseau, 1881: 175.

TYPE SPECIES. — *Ranella rhodostoma* G. B. Sowerby II, 1835. Miocene (Serravallian?) to Recent, Indo-West Pacific and eastern and western Atlantic [*Lampadopsis* Jousseau, 1881, justifiably emended to the genitive form *Lampasopsis* by Fischer (1884: 656)].

SPECIES INCLUDED IN THE GENUS:

Lampasopsis asperrima (Dunker, 1862), *Lampasopsis cruentata* (G.B. Sowerby II, 1835), *Lampasopsis davidboschi* (Beu, 1987), *Lampasopsis grayana* (Dunker, 1862), *Lampasopsis lucaensis* (Path, 1991), *Lampasopsis rhodostoma* (G. B. Sowerby II, 1835), *Lampasopsis rugosa* (G. B. Sowerby II, 1835) *Lampasopsis sangirana* (Beu 2005), *Lampasopsis thomae* (d'Orbigny, 1842),

DIAGNOSIS:

Very similar to *Bursa*, though shorter, with a smaller and less tubular posterior siphonal canal short spired thick shell, varices aligned, 7 primary cords on the convex part of the whorl, Varical P2 reduced; Intervarical P1 and P2 merged with warty ornamentation, P2 and P7 not visible, D7 not visible, anterior siphonal canal strongly adaxially turned. Strong projection of the outer lip. Aperture often coloured, Columella can display dots (*L. cruentata*)

Lampasopsis rhodostoma (G. B. Sowerby II, 1835)

Ranella rhodostoma G. B. Sowerby II, 1835: pl. 88, fig. 10; 1841b: 52 — Deshayes 1843: 552; Reeve 1844b: pl. 7, fig. 32; Chenu 1859: 155, fig. 712; Küster & Kobelt 1871: 155, pl. 34a, fig. 11.

Ranella (Lampas) cruentata var. *rhodostoma* (G. B. Sowerby II, 1835) — Tryon 1880: 40, pl. 21, fig. 25.

Lampadopsis rhodostoma (G. B. Sowerby II, 1835) — Habe 1961: 47, pl. 24, fig. 1; Oyama & Takemura 1963: *Lampadopsis* plate, figs 1-2; Habe 1964: 75, pl. 24, fig. 1; Okutani 1986: 116-117, top center fig.

Bursa rhodostoma (G. B. Sowerby II, 1835) — Cernohorsky 1967a: 314, Pl. 43, Fig. 9; Text fig. 5.); Salvat & Rives 1975: 307, fig. 181; Hinton 1978: 32, figs 5, 5a; Kay 1979: 229, figs 80C-D; Garcia-Talavera 1983: 33, 135; Drivas & Jay 1988: 60, pl. 15, fig. 9; Lai 1989: 21, fig. 4; Wilson 1993: 227, pl. 43, fig. 5; Kubo *in* Kubo & Kurozumi 1995: 78, fig. 5; Beu 1998: 163, fig. 47g, 52h, k, 58e; Zhang & Ma 2004: 176, text-fig. 109; Tröndlé & Cosel 2005: 288; Tröndlé & Boutet 2009: 22; Beu 2010: 57, Pl. 5, Figs 5, 7, 10-12, 15; Severns 2011: 150, pl. 59, fig. 2; Beu *et al.* 2012: 69, Fig. 2H; Castelin *et al.* 2012: 4843, fig. 4.

Bursa (Lampasopsis) rhodostoma (G. B. Sowerby II, 1835) — Nordsieck & Garcia-Talavera 1979: 126, pl. 28, fig. 2.

Bursa (Bursa) rhodostoma rhodostoma (G. B. Sowerby II, 1835) — Beu 1985: 63; Cossignani 1994: 56.

Bursa (Bursa) rhodostoma (G. B. Sowerby II, 1835) — Springsteen & Leobrera 1986: 124, pl. 34, fig. 9.

Bursa (Ranella) rhodostoma (G. B. Sowerby II, 1835) — Okutani 2000: 269, pl. 133, fig. 4.

Ranella venustula Reeve, 1844b: pl. 7, fig. 37; Reeve 1844d: 138.

Bursa venustula (Reeve, 1844) — Drivas & Jay 1988: 60, pl. 15, fig. 10.

Bursa (Bursa) venustula (Reeve, 1844) — Cossignani 1994: 62, illus.

Ranella paulucciana Tapparone-Canefri, 1876: 244 — Tapparone-Canefri 1881: 51, pl. 2, figs 16-17.

Ranella rhodostoma var. *xantostoma* Tapparone-Canefri, 1878: 249.

Ranella bergeri (Sowerby, *in schedis*) Tapparone-Canefri, 1881: 50, pl. 2, fig. 1, 2.

Bursa bergeri (Tapparone-Canefri, 1881) — Drivas & Jay 1988: 60, pl. 15, fig. 8.

Gyrineum cruentatum cruentata (not G. B. Sowerby II, 1835) — Dall & Simpson 1901: 416.

Bursa mammata (not Röding, 1798) — Hedley, 1914: 28; Iredale 1931: 212; Iredale & McMichael 1962: 55.

TYPE LOCALITY. — *Ranella rhodostoma* from Island of Masbate, of the Philippines. *Ranella venustula* from Lord Hood's Island' (South Marutea Island, Gambier Islands).

TYPE MATERIAL. — *Ranella rhodostoma*, lectotype (NHMUK 1966542/1) by designation of Beu (1998: 165) and two paralectotypes (NHMUK 1966542/2-3). *Ranella venustula*, three

syntypes NHMUK 1966541. The type material of *Ranella paulucciana*, *Ranella rhodostoma* var. *xanthostoma* and *Ranella bergeri* is presumably in Museo Civico di Storia Naturale ‘Giacomo Doria’, in Genoa (Cossignani 1994: 57).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. Occurs throughout the Indo-West Pacific Province, from Madagascar (and possibly eastern South Africa) to the northern Indian Ocean and the Red Sea, from southern Honshu, Japan, south to Sydney Harbour, New South Wales (where a specimen was collected alive at Bottle and Glass Rocks during the 19th century (Beu 2010), and eastward throughout Melanesia and Polynesia to Hawaii (Beu 1998).

Lampasopsis asperrima (Dunker, 1862)

Bursa asperrima Dunker, 1862: 238; 1863: 57, pl. 19, figs 5-6 — Yen 1942: 217, pl. 19, fig. 114; Emerson 1991: 68; 1994: 69; Finet 1994: 41; Beu 1998: 146, fig. 43f; Kaiser 2007: 39, pl. 26, figs 5a-b; Beu 2010: 43, pl. 1, Fig. 9; Beu *et al.* 2012: 63.

Bursa (Bursa) asperrima. Dunker, 1862 — Beu 1985: 63; Cossignani 1994: 43; Kaiser 1997: 32.

Ranella cruentata. (not G. B. Sowerby II, 1835) — Stearns 1893: 347

Bursa cruentata. (not G. B. Sowerby II, 1835) — Hertlein & Allison 1960: 15 Cernohorsky 1970: 180 (in part); Salvat & Rives 1975: 307, fig. 180; Okutani 1986: 116-117, middle fig. second column; Okutani 2000: 269, pl. 133, fig. 5.

Lampadopsis cruentata (not G. B. Sowerby II, 1835) — Oyama & Takemura 1963: *Lampadopsis-Tutufa* pl. 1, fig. 5.

TYPE LOCALITY. — Hawaii designated by Beu (2010).

TYPE MATERIAL. — Lectotype of *Bursa asperrima*, Dunker’s (1863: pl. 19, figs 5-6) figured syntype, NHMUK 1968566/1, from Cuming coll., designated by Yen (1942: 217); two paralectotypes, NHMUK 1968566/2-3.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE: — No fossil record. Appears throughout the eastern and western Pacific Ocean. NOT in the Indian or the Atlantic Oceans, Common by itself (i.e., without *B. cruentata*) at Clipperton Island, eastern Pacific (Hertlein & Allison, 1960; Kaiser, 2007: 39, pl. 26, figs 5a-b). In eastern French Polynesia (Beu *et al.*, 2012), is replaced by *Bursa cruentata* (G.B. Sowerby II, 1835) in the Marquesas Islands. As common as *B. cruentata* in Hawaii, but is exceedingly rare further west in the western Pacific.

Recorded as *Ranella cruentata* Sowerby (i.e., *B. asperrima*) from the American coast in the eastern Pacific: near Cape San Lucas, Baja California Sur, in 56 m deep, 22°52'N, 109°55'E (USNM 125665), and at Utila Island, Honduras (Stearns 1893: 347). Recorded from the Galápagos Islands (two specimens in CAS, from Jervis and James islands) (Emerson 1991: table 1). A single specimen from Pitcairn Island (NMP, K2826). Hachijo Island, southern southern Japan (Oyama & Takemura 1963: *Lampadopsis-Tutufa* pl. 1, fig. 3) Southern Japan (Okutani 1986: 117; 2000: pl. 133, fig. 5). An occurrence at Niue Island (Cernohorsky's 1970: 180 (Salvat & Rives 1975: 307, fig. 180) Moderately common in Makemo Island, Tuamotu Islands 180 (Salvat & Rives 1975: 307, fig. 180). *Bursa asperrima* seems to be basically a far-eastern western Pacific species, in the case of *B. asperrima* extending rarely to the eastern Pacific mainland. It occasionally extends its range to the west as planktotrophic larvae, but apparently is essentially outcompeted by the closely similar *B. cruentata* to the west of its normal range.

***Lampasopsis cruentata* (G.B. Sowerby II, 1835)**

Ranella cruentata G.B. Sowerby II, 1835: pl. 85, figs 5 — G.B. Sowerby II 1841: 51; Kiener 1841: 13. pl. 7, fig. 2. Reeve 1842: 196, pl. 241, figs 5; Reeve 1844b: pl. 5, fig. 20, Kobelt 1876: 330. Schmeltz 1877: 81. Tapparone-Canefri 1881:49.

Lampas cruentata (G.B. Sowerby II, 1835) — Mörch 1852: 105.

Ranella (Lampas) cruentata (G.B. Sowerby II, 1835) — Tryon 1880: 39, pl. 21, fig. 24 (only).

Lampasopsis (sic) cruentatum (G.B. Sowerby II, 1835) — Jousseaume 1881: 176 (reprint p. 5).

Bursa cruentata (G.B. Sowerby II, 1835) — Ostergaard 1939: 72; Cernohorsky 1967a: 312, pl. 43, fig. 7. Houbrick & Fretter 1969: 416, figs 1-2 A. Wilson & Gillett 1971: 80, pl. 54, fig. 5; Hinton 1972: 12, pl. 6, fig. 27; 1978: 32, fig. 10. Kay 1979: 227 (but not fig. 80 B); Beu 1985: 63; Springsteen & Leobrera 1986: 123, pl. 34, fig. 7. Drivas & Jay 1988: 60, pl. 15, fig. 7. Salvat *et al.* 1988: 103, pl. 13, fig. 18; Lai 1987: 21, figs 5-6. Wilson 1993: 226, pl. 43, fig. 8. Cossignani 1994:46, 4 unnamed figs. Beu 1998: 145, Figs. 45 e, g; Beu *et al.* 2012: 67, figs. 2B, C.

Lampadopsis cruentata (G.B. Sowerby II, 1835) — Habe & Kosuge 1966: 4b, pl. 16, fig. 9.

TYPE LOCALITY. — Recent 'Ticao, Philippines'

TYPE MATERIAL. — Lectotype (NHMUK 1950.11.28.10) designated by Beu (1998: 146) with two paralectotypes, (NHMUK 1950.11.28.11–12), all from 'Ticao, of the Philippines'.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. *Bursa cruentata* is moderately common throughout the Indian Ocean, in the western Pacific from southern Japan south to northern Australia, the Coral Sea and New Caledonia, and eastwards to the Hawaiian Islands. *B. cruentata* occurs in smaller numbers in the Marquesas, Society and Tuamotu Islands. It occurs syntopically with, but less commonly than, *B. asperrima* at the Society and Tuamotu Islands.

***Lampasopsis davidboschi* (Beu, 1987)**

Bursa bufonia (not Gmelin, 1791) — Bosch *et al.* 1983: 83, lower fig.

Bursa (Bursa) davidboschi Beu, 1987: 318 Fig. 165-175.

TYPE LOCALITY. — East coast of Masirah I., Oman, Gulf of Arabia

TYPE MATERIAL. — Holotype (USNM 849006), one paratype (NZGS WM14096), 17 paratypes (2 paratypes, USNM849007; 15 paratypes, NZGS WM13260) from Rassier Beach, Masirah I., Oman. 1 paratype in Mrs K. Smythe's collection, Bognor Regis, England; "shallow water", Medina, Misamis Province, Mindanao, Philippine Islands (3 paratypes, NZGS WM13972; 6 paratypes in collection of The Abbey Specimen Shells, Santa Barbara).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. The species is probably widespread, but rare, throughout the northern tropical Indian and Pacific oceans, and is probably the basis of previous records of *Lampasopsis grayana* in the Indo-West Pacific. Recorded in the Gulf of Aden, Oman, Somalia (Beu 1987, Cossignani 1994) and in the Philippines islands (Beu 1987).

***Lampasopsis grayana* Dunker, 1862**

Bursa grayana Dunker, 1862: 238 — Dunker 1863: pl. 19, figs 5-6, Beu 2010: 50, pl. 3, Figs 2, 4-9.

Bursa (Bursa) grayana Dunker, 1862 — Beu 1985: 63; Beu 1987: 317, figs 157-164, Rios 1985: 78, pl. 28, fig. 343; Rios 1994: 92, pl. 30, fig. 361; Cossignani 1994: 48.

Bursa bufoniopsis Maury, 1917: 108, pl. 17, fig. 8 — Pilsbry 1922: 360.

Bursa aff. thomae Matthews & Kempf, 1970: 28.

Bursa (Bursa) pacomoni Matthews & Coelho, 1971: 2, figs 1-5 — Coelho & Matthews 1971: 48, figs 4-8; Leal 1991: 113, pl. 16, fig. E.

TYPE LOCALITY. — *Bursa grayana* from recent Mucuripe, Fortaleza, Brazil (Designated by Beu 2010: 51); *Bursa bufoniopsis* from recent Rio Gurabo at Los Quemados, Dominican Republic; *Bursa pacomoni* from stomach of “pacomon” recent Mucuripe, Fortaleza, Ceara, Brazil.

TYPE MATERIAL. — *Bursa grayana* lectotype (NHMUK 1988064/1, designated by Beu, 1987:318) and four paralectotypes (NHMUK 1988064/2 and NHMUK 1968529/1- 3). *Bursa bufoniopsis*, holotype (PRI 28762). *Bursa pacomoni*, holotype (MNRJ 3528), 3 paratypes in MNRJ, 4 paratypes in Laboratorio de Ciencias do Mar, Universidade de Rio Grande, Rio Grande do Sul, Brazil; and 4 paratypes in Museu Oceanografico de Rio Grande, Rio Grande do Sul, Brazil (see Matthews & Coelho 1971: 6, table).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Lampasopsis grayana* occurs in the living fauna from southern Florida, USA, throughout the western Atlantic to Bahia, Brazil, and to Fernando de Noronha Island and Atol das Rocas (Rios 1994), although it is much less common in collections than the shallow-water species *Talisman corrugata*, *Dulcerana cubaniana*, and *Lampasopsis thomae*. Most specimens are from divers or from fish stomachs, although a few have been found cast ashore on beaches. There are no records from either the eastern Atlantic or the eastern Pacific. Miocene and Pliocene fossils are moderately common in the northern Dominican Republic, probably reflecting the offshore habitat of the species at present, and the correspondingly offshore deposition sites of most Dominican Republic units. However, the only other fossils are two specimens from the Pliocene Cayo Agua Formation in the Bocas del Toro Basin, eastern Panama, and one poorly localized specimen from Mexico, of Pliocene age (Beu 2010).

***Lampasopsis rugosa* (G. B. Sowerby II, 1835)**

Ranella rugosa G. B. Sowerby II, 1835: pl. 85, fig. 71835 — G. B. Sowerby II, 1841: 53; Reeve 1844b: pl. 5, figs 21a-b.

Bursa (Bursa) rugosa. (G. B. Sowerby II, 1835) — Beu 1985: 63, fig. 39; Cossignani 1994: 50; Kaiser 1997: 33.

Bursa rugosa (G. B. Sowerby II, 1835) — Beu 2001: 711, figs 1.3, 1.5 ; — Beu 2010: 59, pl. 5, figs 9, 13-14; Pl. 6, figs 1-10.

Bursa (Marsupina) albofasciata boussingaulti Rutsch, 1934: 58-59, fig. 7; pl. 3, figs 3-4.
Bursa (Ranella) sp. Trechman, 1935: 542, pl. 21, fig. 20 (as *Bursa (Ranella)* cf. *amphitrites* in caption to pl. 21).
Bursa (Colubrellina) caelata amphitrites (not Maury, 1917). — Woodring 1959: 207, pl. 28, figs 1-2, 7-8; Jung 1965: 513, pl. 68, figs 12-13, pl. 69, fig. 2; Perrilliat 1972: 76, pl. 37, figs 12-15.
Bursa calcipicta (not in part Dall, 1908) — Keen 1958: 348, fig. 328; Keen 1971: 508, fig. 965; Finet 1991: 270.
Bursa (Bursa) calcipicta (not in part Dall, 1908) — Kaiser 1997: 32.
Bursa (Colubrellina) sp. — Olsson 1964: 172, pl. 30, fig. 4; Perrilliat 1987: 15, pl. 4, figs 3-4.
Bursa (Colubrellina) sp. A — Jung 1971: 189, pl. 11, figs 5-7.
? *Bursa* sp. — Cosel 1984: 221.
Bursa amphitrites (not Maury, 1917) — Petuch 1992: 108, fig. 3G.
Bursa (Lampasopsis) (sic) amphitrites (not Maury, 1917) — Petuch 1994: 120, pl. 39, figs. L-M; Petuch 1997: 224, fig. 83J

TYPE LOCALITY. — *Ranella rugosa* from recent, Perlas Islands, Panama Bay, by subsequent designation of Beu (2010: 61). *Bursa (Marsupina) albofasciata boussingaulti*, from early Pliocene Punta Gavilan, Venezuela

TYPE MATERIAL. — *Ranella rugosa*, three syntypes (NHMUK 1989133); the largest syntype figured by Sowerby (1835: pl. 85, fig. 7) is here designated lectotype. *Bursa (Marsupina) albofasciata boussingaulti*, holotype (NMB H 1870) (Beu 2010: pl. 5, fig. 14); with 2 paratypes (NMB H 1871/1-2); one paratype (NMB H 1872), Punta Gavilan beds, coast near Sabanas Altas, northern Venezuela (localities shown by Rutsch 1934: fig. 2).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Lampasopsis. rugosa* lives from southern Mexico to at least Paita, Peru. Records of “*Bursa calcipicta*” from Cocos Island, Costa Rica (Montoya 1983, 1984; Skoglund 1992) and the Galápagos Islands (Finet 1985) almost certainly are also based on *L. rugosa*. Certainly, *L. rugosa* is limited to tropical western America at present. It is therefore particularly interesting for Panamic biogeography that *L. rugosa* occurs in Florida [if rarely; specimens identified by Petuch (1992, 1994, 1997) as *B. amphitrites*], USA, and is abundant in Caribbean, Venezuelan, and Colombian shallow-water fossil localities of Early Miocene to Pliocene age; this is one of the clearest examples of a paciphile tonnoidean species (Beu 2010). Other than in the Panama Isthmus itself, where it is common in Pliocene rocks on both coasts, there seem to be no records of *B. rugosa* in the

western Atlantic after the end of Pliocene time. In 1985, Beu identified a specimen in USGS 8343 (Moín Formation, latest Pliocene-Early Pleistocene, Limón, Atlantic Costa Rica) as possibly *L. rugosa*. There are also no records at all from the Dominican Republic, apparently reflecting the mostly coral reef or offshore, soft-bottom nature of the Dominican Republic units, and the shallow rocky habitat of *L. rugosa* (Beu, 2010). The specimens identified as *B. (Colubrellina)* sp. by Perrilliat (1987: pl. 4, fig. 3, 4) also are clearly *L. rugosa*, from the Middle Miocene Ferrotepec Formation in Michoacan, Mexico.

***Lampasopsis sangirana* (Beu, 2005)**

Bursa sangirana Beu 2005: 22, figs. 36-38.

TYPE LOCALITY. — Late Pliocene of Kalibeng layers, Sangiran, central Java. Precise localities are unknown for most of B. Dharma's material (Beu 2005).

TYPE MATERIAL. — Holotype (RGM 456 230), one paratype (NZGS WM17456), and two paratypes in B. Dharma coll.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Lampasopsis sangirana* is only known from the Late Pliocene of Sangiran, central Java.

***Lampasopsis thomae* (d'Orbigny, 1842)**

Ranella thomae d'Orbigny, 1842: 250, pl. 23, figs 23-24. —Mörch 1877: 24; Smith 1890: 269.

Ranella (Lampas) thomae (d'Orbigny, 1842) — Watson 1886: 400; Gregory 1895: 288.

Ranella (Lampadopsis) cf. thomae. (d'Orbigny, 1842) — Trechmann 1930: 208, pl. 12, fig. 18.

Ranella (Bursa) thomae. (d'Orbigny, 1842) — Trechmann 1933: 39.

Bursa (Bursa) thomae. (d'Orbigny, 1842) — Morrison 1949: 11.

Bursa thomae. (d'Orbigny, 1842) — McGinty 1962: 40; Warmke & Abbott 1962: 103, pl. 18j; Humfrey 1975: 126, pl. 14, figs 5, 5a; Finlay 1978: 149; Bandel 1984: 101, fig. 162, , pl. 10, fig. 4; de Jong & Coomans 1988: 70; Diaz & Gotting 1988: 156; Leal 1991: 112; Lipe & Abbott 1991: 14-15, illus.; Diaz & Puyana 1994: 174, fig. 652; Segers *et al.* 2009: 174, Pl. 35, fig. 2-3.

Bursa (Bursa) aff. thomae (d'Orbigny, 1842) — Jung 1969: 486, pl. 49, figs 1-2; Rios 1970: 74.

Bursa (Bursa) thomae (d'Orbigny, 1842) — Matthews & Coelho 1971: 4, figs 6-7; Abbott 1954: 197; Rios 1975: 81, pl. 22, fig. 329.

Bursa (Lampasopsis) thomae. (d'Orbigny, 1842) — Abbott 1974: 166, pl. 7, fig. 1777.

Bursa (Bursa) rhodostoma thomae. (d'Orbigny, 1842) — Beu 1985: 63; Rios 1985: 79 (not pl. 28, fig. 344, = *Lampasopsis grayana*); Cossignani 1994: 57; Rios 1994: 92 (not pl. 30, fig. 362, = *Lampasopsis grayana*); Guerreiro & Reiner 2000: 119-120; Redfern 2001: 57, pl. 29, figs 245A-B, pl. 109, fig. 245C.

Bursa rhodostoma thomae (d'Orbigny, 1842) — Ardovini & Cossignani 2004: 132, 2 lower right figs, 133, upper left fig.

TYPE LOCALITY. —Recent St Thomas, Lesser Antilles, Caribbean.

TYPE MATERIAL. — Holotype (NHMUK 1854.10.4.414).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Lampasopsis thomae* occurs in the western Atlantic, it ranges from South Carolina (Merrill & Petit 1965: 63), USA, to Bahia, Brazil (Abbott 1974; Coelho & Matthews 1971), including Louisiana (USA), and from Fernando de Noronha and Martin Vas Islands and many seamounts off of Brazil (Rios 1994: 92; Leal 1991: 112). Matthews (1968) recorded specimens found commonly in the gut of the toadfish or “pacomon,” *Amphichthys cryptocentrus*, caught off of Fortaleza, Ceará, Brazil. E. A. Smith (1890) recorded it also from St. Helena, and specimens are listed above from St. Helena and Ascension Island. In the eastern Atlantic, it is recorded from Madeira, the Canary Islands, and the Cape Verde Islands (Nordsieck & Garcia-Talavera 1979; and above). Fossils range in age from late Early Miocene (Burdigalian) to late Pleistocene, although this is a very uncommon fossil (Beu 2010). Gregory (1895: 288) recorded Pleistocene fossils from Barbados.

Genus **MARSUPINA** Dall, 1904

Marsupina Dall, 1904 (*nomen protectum*).

TYPE SPECIES. — Replacement name for *Buffo* Montfort, 1810, supposedly a junior homonym of *Buffo* Lacepède, 1788 (Amphibia; rejected by ICZN Opinion 2104, 2005)

Buffo Montfort, 1810 (*nomen oblitum*)

TYPE SPECIES. — *Buffo spadiceus* Montfort, 1810 (= *Murex bufo* Bruguière, 1792) by monotypy, Pliocene to Recent, western Atlantic.

Bechtelia Emerson & Hertlein, 1964

TYPE SPECIES. — *Gyrineum strongi* Jordan, 1936, by original designation of Emerson & Hertlein (1964: 360), Pleistocene, Gulf of California.

Evenly biconic shell, dorsoventrally compressed (more than in *Bufo*), varices strictly aligned, 8 primary cords in the convex part of the whorl, all but P1 evenly reduced in varical and intervarical parts of the whorl. Posterior siphonal canal forming a semicylindrical gutters without columellar blade extending up the opposing sides of the spire; outerlip denticles extending inside the posterior siphonal canal; no lamellar projection of the outerlip; ovate operculum, anterior nucleus.

SPECIES INCLUDED IN THE GENUS

Marsupina bufo (Bruguière, 1792), *Marsupina judensis* Beu, 2010, *Marsupina nana* (Broderip & G. B. Sowerby I, 1829), *Marsupina strongi* (Jordan, 1936)

DIAGNOSIS:

Evenly biconic shell, dorsoventrally compressed (more than in *Bufo*), varices strictly aligned, 8 primary cords in the convex part of the whorl, all but P1 evenly reduced in varical and intervarical parts of the whorl. Posterior siphonal canal forming a semicylindrical gutters without columellar blade extending up the opposing sides of the spire; outerlip denticles extending inside the posterior siphonal canal; no lamellar projection of the outerlip; ovate operculum, anterior nucleus.

Marsupina bufo (Bruguière, 1792)

Murex bufo Bruguière, 1792: 126.

Bursa (Marsupina) bufo (Bruguière, 1792) — Jung 1969: 487, pl. 49, figs 3-6; Abbott 1974: 167, pl. 7, fig. 1782; Rios 1975: 82, pl. 23, fig. 333; Rios 1994: 93, pl. 31, fig. 367; Macsotay *et al.* 2001: 70.

Marsupina bufo (Bruguière, 1792) — Vokes 1973: 100; Beu 2001: 711, Beu 2010: 72, Pl. 9, Figs 1, 3-15, Pl. 10, Figs 1-3, 5.

Bursa (Colubrellina) bufo (Bruguière, 1792) — Okutani 1983: 263, illus.

Bufo (Marsupina) bufo (Bruguière, 1792) — Beu 1985: 65, fig. 48 ; Rios 1985: 80, pl. 28, fig. 350; Cossignani 1994: 39-40.

Bufo bufo (Bruguière, 1792) — Calvo 1987: fig. 84 (radula).

Bursa bufo (Bruguière, 1792) — Finlay 1978: 150 ; Princz & Pacheco 1981: table; Cosel 1986: 241, fig. 155; Lipe & Abbott 1991: 14, illus.

Bursa gibbosa Röding, 1798: 128.

Buffo spadiceus Montfort, 1810: 575.

Ranella spadicea (Montfort, 1810) — Morch 1877: 23 ; van Regteren Altena 1975: 38, pl. 6, figs 8-9; Diaz & Gotting 1988: 156; Diaz & Puyana 1994: 174, fig. 651.

Bursa spadicea (Montfort, 1810) — McGinty 1940: 71; 1962: 41.

Bursa (Bufo) spadicea (Montfort, 1810) — Morrison 1949: 11 ; Abbott 1954: 198, pl. 25, fig. p; Warmke & Abbott 1962: 103, pl. 18, fig. 1; Humfrey 1975: 127, pl. 14, figs 7-7a; Rios 1970: 75, pl. 18, lower left fig.

Bursa (Marsupina) spadicea (Montfort, 1810) — Coelho & Matthews 1971: 55, figs 16- 17.

Ranella granulata Lamarck, 1816: pl. 412, fig. 4, “Liste des objets”: 4 — Lamarck 1822: 152; Kiener 1841: 18, pl. 12, fig. 1; Deshayes 1843: 547

Murex crassus Dillwyn, 1817: 692.

Ranella crassa (Dillwyn, 1817) — d’Orbigny 1841a: 134 ; Reeve 1844b: pl. 4, figs 18ab; Krebs 1864: 25; Guppy 1866: 288, pl. 18, fig. 9; Guppy 1874: 438; 1876: 522; Tryon 1880: 38, pl. 19, fig. 10.

Bursa crassa (Dillwyn, 1817) — Gabb 1873: 212.

Gyrineum crassum (Dillwyn, 1817) — Dall 1903: 1584.

?*Bursa nana* (not Broderip & Sowerby, 1829) — Gabb 1881: 353.

Bursa crassa proavus Pilsbry, 1922: 360, pl. 29, figs 4-5 — Maury 1917: 108, pl. 17, figs 6-7; Olsson 1922: 306, pl. 15, fig. 19; Maury 1925: 217; Smith 1948: 24, pl. 9, fig. 8

Bursa proavus (Pilsbry, 1922) — Petuch 1992: 108, fig. 3H.

Bursa (Marsupina) proavus (Pilsbry, 1922) — Petuch 1994: pl. 39, figs D-E; Petuch 1997: 223.

Bursa crassa bowdenensis Pilsbry, 1922: 360, pl. 29, fig. 8.

Bursa (Marsupina) proavus bowdenensis (Pilsbry, 1922) — Woodring 1928: 303, pl. 19, fig. 4.

Bursa crassa colombiana Weisbord, 1929: 41, pl. 8, figs 1-2.

Bursa crassa caribbaea Smith, 1948: 25, pl. 9, fig. 10.

Bursa amphitrites (in part not Maury, 1917) — E. H. Vokes 1973: 100.

TYPE LOCALITY. — Type locality unknown for *Murex bufo*, *Buffo spadiceus*, *Bursa gibbosa*, *Murex crassus* and *Bursa crassa caribbaea*. *Ranella granulata* from off of Cayenne, Guiana by designation of Beu (2010: 73). *Bursa crassa proavus* from the Late Miocene-Early Pliocene of Dominican. *Bursa crassa bowdenensis* from Bowden shellbed, Jamaica, Late Pliocene. *Bursa crassa colombiana* from near Tuhera Cedral, Morro Hermoso, Departamento de Atlantico, Colombia, “Middle Miocene”.

TYPE MATERIAL. — *Murex bufo* neotype (MHNG 1098/84) by designation of Beu (2010: 73). *Bursa gibbosa* neotype (MHNG 1098/84) by designation of Beu (2010: 73). *Buffo spadiceus* lectotype (the specimen illustrated by Montfort, 1810: 573) by designation of Beu (2010: 71) and neotype (MHNG 1098/84) by designation of Beu (2010: 73). *Ranella granulata* lectotype (MHNG 1098/84) by designation of Beu (2010: 73). *Murex crassus* neotype (MHNG 1098/84) by designation of Beu (2010: 73). *Bursa crassa proavus* holotype (ANSP.IP 3227). *Bursa crassa bowdenensis* holotype (ANSP.IP 3747 labeled syntype) (1922: 360). *Bursa crassa colombiana* holotype (PRI 22964). *Bursa crassa caribbaea* type location unknown.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Marsupina bufo* is dredged commonly on the shelf in ca. 30-200 m deep at the present day, from southeastern Florida (McGinty, 1940; Abbott, 1974: 167), USA, south to Bahia, Brazil (Rios, 1994). Specimens are abundant in relatively shallow water along the northern coast of Venezuela, Suriname, and Guiana. Fossils are common at a few middle Miocene to Pleistocene localities, notably in the Early Pliocene of Cubagua Island, Venezuela, but are uncommon to rare at other localities, or somewhat surprisingly absent at still others. Specimens are rare in Dominican Republic localities. The specimens recorded by Gabb (1881: 353) from Limón, Costa Rica, as *Bursa nana* seem likely to refer to *Marsupina bufo*, because there are several other records of *M. bufo* from Limón (Beu, 2010). Rutten (1931: 664) recorded fossils [as *Bursa (M.) crassa*] from

Pleistocene localities in Suriname. All fossil localities where *M. bufo* has been collected are either on the Caribbean islands or on the Atlantic coasts of Florida (rare), Costa Rica, Panama, Colombia, Venezuela, and Suriname; there are virtually no records from the Pacific coast of western America. The one exception is a specimen from the Río Vaca (Plio-Pleistocene?), Puntarenas Province, Costa Rica.

***Marsupina judensis* Beu, 2010**

Marsupina judensis Beu, 2010: 75, Pl. 10, Figs 4, 7, 10.

TYPE LOCALITY. — from Punta Judas, 40 km WNW of Quepos, Pacific coast of Costa Rica, Late Miocene.

TYPE MATERIAL. — Holotype (NMB H 18308); 2 incomplete paratypes (NMB 17753); 3 incomplete paratypes (NMB 17754); 1 incomplete paratype (NMB 17755).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Marsupina judensis* is known only from Punta Judas, Pacific coast of Costa Rica.

***Marsupina nana* (Broderip & G. B. Sowerby I, 1829)**

Ranella nana Broderip & G. B. Sowerby I, 1829: 376 — Sowerby II 1835 “small sheet”: caption to pl. 85, fig. 6; Sowerby II 1841: 51; Kiener 1841: 21, pl. 9, fig. 2; Reeve 1844b: pl. 6, fig. 29; Menke 1850: 189; C. B. Adams 1852: 119; Stearns 1894: 188.

Bursa nana (Broderip & G. B. Sowerby I, 1829) — Pilsbry & Olsson 1941: 39, pl. 5, fig. 6; Keen 1971: 509, fig. 966.

Bufonaria (Marsupina) nana (Broderip & G. B. Sowerby I, 1829) — Beu 1985: 65, fig. 50; Cossignani 1994: 41.

Marsupina nana (Broderip & G. B. Sowerby I, 1829) — Lopez de la Fuente & Ramos 2004: 86; Beu 2010: 76, pl. 10, figs 11-12, Pl. 11, figs 1-2, 5, 7-8.

Ranella pulchra G. B. Sowerby II, 1835, “small sheet”: caption to pl. 89, fig. 14 (senior primary homonym of *R. pulchra* G. B. Sowerby II, 1836, “small sheet”: caption to pl. 93, fig. 19).

Ranella albofasciata G. B. Sowerby II, 1841: unpaginated catalog of *Ranella species* — G. B. Sowerby II 1841: 52.

Ranella albifasciata (sic) G. B. Sowerby II, 1841— Reeve 1844b: pl. 6, fig. 27; Tryon 1880: 38, pl. 19, fig. 9.

Bursa (Colubrellina) nana albofasciata (G. B. Sowerby II, 1841) — Hertlein & Strong 1955: 264.

?*Bursa nana jamanensis* Pilsbry & Olsson, 1941: 8 — Olsson 1942: 170 (*nomen nudum*).

Bursa (Colubrellina) caelata amphitrites (not Maury, 1917) — Aguilar & Fischer 1986: 223, pl. 2, fig. 7.

TYPE LOCALITY. — *Ranella rana* from recent “Panama, coarse sand, 10 fathoms”. *Ranella albofasciata*, Recent Panama Bay by subsequent designation of Hertlein & Strong (1955b: 264).

TYPE MATERIAL. — *Ranella nana*, lectotype (NHMUK 1950.11.28.14) by designation of Beu (2010: 78) with two paralectotypes (NHMUK 1950.11.28.15-16). There is no separate type material labeled *R. pulchra* that applies to the present species. *Ranella albofasciata*, lectotype (NHMUK 1950.11.28.20) by designation of Beu (2010:78) with two paralectotypes (NHMUK 1950.11.28.21- 22), with identical locality label to that of the syntypes of *R. nana*.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Marsupina nana* lives today in the eastern Pacific from the outer coast of Baja California Peninsula (32°24'N) throughout the Gulf of California and along the western coast of tropical America, southward to northern Peru (to at least 3°28'S). Specimens have been collected alive from the shallow subtidal to a depth of 100 m deep. Fossil specimens are recorded from Pliocene and Pleistocene rocks along the western coasts of Costa Rica and Panama, well within the living range.

***Marsupina strongi* (Jordan, 1936)**

Gyrineum strongi Jordan, 1936: 160, pl. 18, fig — Durham 1950: 28, 115, pl. 29, figs 19, 22; Schneider 1999: fig. 10.

Gyrineum (Bechtelia) strongi Jordan 1936 — Emerson & Hertlein 1964: 360, fig. 5g.

Marsupina strongi (Jordan 1936) — Beu 2010: 78, pl. 11, figs 4, 6

TYPE LOCALITY. — Late Pleistocene, Bahia Magdalena, Baja California Sur, Mexico.

TYPE MATERIAL. — Holotype (CAS 5480) with one paratype (CAS 5481).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Marsupina strongi* is recorded only from late Middle Pleistocene (Last Interglacial period, oxygen isotope stage 5e, ca. 125,000-130,000 years old) terrace faunas of Isla Coronado, northern Mexico, and Isla Monserrate and Isla San Diego in the southwestern Gulf of California (Emerson & Hertlein 1964), from the mainland coast of western Mexico at Bahia Magdalena (Jordan 1936), on the inner coast of Baja California Peninsula at Bahia Concepción and in the Santa Rosalia area (Durham 1950) and at three localities in Mulegé Terrace cover beds near Punta Chivato, south of Santa Rosalia (Schneider: 1999: table 1; at Punta Gallito, sea cliffs north-west of Punta Prieta, and northern end of Punta Santa Inés).

Genus **OLSSONIA** Sanders *et al.* in prep.(article 1)

Olssonina Sanders *et al.* in prep

TYPE SPECIES. — *Bursa chira* Olsson, 1930 by original designation

SPECIES INCLUDED IN THE GENUS

Olssonina chira (Olsson, 1930), *Olssonina freya* (Olsson, 1932), *Olssonina yasila* (Olsson, 1930).

DIAGNOSIS:

Very similar to *marsupina*, as it is biconic though less dorsoventrally compressed, varices strictly aligned, short spired; 6 primary cords in the convex part of the whorl, all but P1 evenly reduced in varical and intervarical parts of the whorl (P1 is hardly more expressed), Posterior siphonal canal short

Olssonina chira (Olson, 1930)

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

Marsupina chira (Olson, 1930) — Beu 1988: 71; 2010: 72.

TYPE LOCALITY. — Late Eocene/ Oligocene of Chira formation, Quercotilla, Peru.

TYPE MATERIAL. — Holotype (PRI 24257), one paratype (PRI 24263).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Olssononia chira* seems to appear only on the Late Eocene/ Oligocene of Peru.

***Olssononia freya* (Olsson, 1932)**

Bursa (Marsupina) freya Olsson, 1932: 187, pl. 21, figs 3, 4-6.

Bursa aff. B. (*Marsupina*) *freya* Olsson, 1932 — Marks 1951: 378.

Marsupina freya (Olsson, 1932) — Beu 2010: 75, Pl. 10, Figs 6, 8-9.

TYPE LOCALITY. — From “Zorritos Miocene,” divide between Quebrada Conchudo Bravo and Quebrada Seca, Mancora, Peru.

TYPE MATERIAL. — Holotype (PRI 2312) with two paratypes (PRI 2313 and PRI 2315).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Olssononia freya* has been recorded previously only from the early to middle Miocene of Ecuador and Peru, and the range is extended a long way northward to the Nicoya Peninsula, Costa Rica. All three localities apparently are Miocene, and all lie along the Pacific coast of tropical America.

***Olssononia yasila* (Olsson, 1930)**

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

Marsupina yasila (Olsson, 1930) — Beu 1988: 71.

TYPE LOCALITY. — Middle Eocene 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 *TALISMAN* de Folin, 1884

Talisman de Folin, 1884: 212.

TYPE SPECIES. — *Talisman parfaiti* de Folin, 1884 by monotypy.

SPECIES INCLUDED IN THE GENUS:

Talisman corrugata (Perry, 1811), *Talisman victrix* (Dall, 1916)

DIAGNOSIS:

Fusiform though less high spired than *Korrigania* or *Tritonoranella*, Shell of relatively light build varices aligned (can be slightly displaced in the last whorl), 6 primary cords on the convex part of the whorl P2 and P4 totally atrophied in varical and intervarical, P6 reduced in intervarical and atrophied in varical only, large nodules on variceal P1 and P3, disappearing entirely on the last whorl (like *Aspa*), Varical P1 is split first whorl lost in nearly every specimens (like *Aspa*), strong projection of the outer lip, second row of denticle on the outerlip. ovate operculum, subanterior nucleus

Talisman corrugata (Perry, 1811)

Biplex corrugata Perry, 1811: pl. 5, fig. 1.

Ranella (Lampas) corrugata (Perry, 1811) — Mörch 1877: 24.

Bursa (Colubrellina) corrugata (Perry, 1811) — Abbott 1954: 198, pl. 9, fig. k; 1958: 60, text-fig. 2, pl. 1, fig. i; Warmke & Abbott 1962: 103, pl. 18, fig. m; Coelho & Matthews 1971: 51, figs 9-10; Rosewater 1975: 18, fig. 8; H. & E. Vokes 1983: 23, pl. 11, fig. 13; Rios 1985: 79, pl. 28, fig. 345.

Bursa corrugata (Perry, 1811) — Kaufmann & Gotting 1970: 372, fig. 88; Abbott 1974: 167, pl. 7, fig. 1780 (as *B. caelata* in plate caption); Rios 1975: 81, pl. 22, fig. 330; Cosel 1984: 221; Calvo 1987: fig. 82 (radula); Leal 1991: 110 (not pl. 16, figs C-D); Lipe & Abbott 1991: 14, illus.; Paulmier 1994: 9, fig. 22; Diaz & Puyana 1994: 174, fig. 649.

Bursa (Colubrellina) corrugata corrugata (Perry, 1811) — Beu, 1985: 64; Cossignani 1994: 69; Kaiser. 1997: 33; Lopez de la Fuente & Ramos 2004: 86; Kaiser 2007: 39, pl. 26, figs 6a-b.

Bursa corrugata corrugata (Perry, 1811) — Hickman & Finet, 1999: 73, fig. 66.

?*Bursa (Colubrellina) cf. corrugata* (Perry, 1811) — Macsotay & Campos Villarroel 2001: 70.

Ranella semigranosa Lamarck, 1822: 153 — Kiener 1841: 19, pl. 11, fig. 2 ; Deshayes 1843: 548; ? Coulon 1933: 137.

Ranella caelata Broderip, 1833: 179 — G. B. Sowerby II 1835: pl. 85, fig. 8.

Ranella (Apollon) caelata (Broderip, 1833) — Mörch 1860: 81.

Ranella calata (sic). (Broderip, 1833) — Coulon 1933: 137.

Bursa caelata louisa (Broderip, 1833) — Smith 1948: 28, pl. 9, fig. 4.

Bursa (Colubrellina) caelata (Broderip, 1833) — Hertlein & Strong 1955: 263.

Bursa caelata (Broderip, 1833) — Keen 1971: 508, fig. 964; Deshayes 1843: 554; Reeve 1844: pl. 3, fig. 10; C. B. Adams 1852: 118.

Ranella ponderosa Reeve, 1844: pl. 3, fig. 14— Reeve 1844d: 137.

Bursa (Colubrellina) corrugata ponderosa (Reeve, 1844) — Beu 1985: 64; Cossignani 1994: 70; Rios 1994: 92, pl. 31, fig. 363; Rios 2001: 57, pl. 29, figs 246 A-B.

Ranella pustulosa Reeve, 1844: pl. 3, fig. 11; 1844d: 137.

Bursa pustulosa var. *jabik* Fischer-Piette, 1942: 216.

Bursa pustulosa (Reeve, 1844) — Burnay & Monteiro 1977: 34, fig. 27.

Bursa (Colubrellina) corrugata pustulosa (Reeve, 1844) — Beu 1985: 64; Cossignani 1994: 71-72.

Bursa (Bursa) corrugata pustulosa (Reeve, 1844) — Guerreiro & Reiner 2000: 118- 119.

Bursa corrugata pustulosa (Reeve, 1844) — Ardovini & Cossignani 2004: 132, upper right fig. and central left 2 figs.

Bursa mexicana Perrilliat, 1963: 19, pl. 4, figs 18-19.

Bursa (Colubrellina) granularis cubaniana (not Röding, 1798) — Macsotay & Campos Villarroel 2001: 70, pl. 13, fig. 5.

TYPE LOCALITY. — Type locality unknown for, *Ranella semigranosa* and *Ranella ponderosa*, *Biplex corrugata*. *Ranella caelata*, recent Panama Bay, eastern Pacific in accordance with ICZN Art. 76.3(see below). *Bursa pustulosa* var. *jabik*, Senegal, West Africa. For *Ranella pustulosa*, recent Ascension Island. *Bursa caelata louisiana*, recent Perlas Archipelago, Gulf of Panama. *Bursa mexicana* from Agueguexquite Formation (Pliocene), Isthmus of Tehuantepec, Mexico.

TYPE MATERIAL. — *Biplex corrugata* Perry, 1811, neotype (NHMUK 1950.11.28.7-9, the one labelled Holotype) designated by Beu (2010: 45). *Ranella semigranosa* Lamarck, 1822 lectotype (MHNG 1098/86/2), with one paratype (MHNG 1098/86/1) designated by Beu (1998: 154). *Ranella caelata* lectotype (NHMUK 1950.11.28.7-9, the one labelled holotype) and two paralectotypes designated by Beu (2010: 45). *Ranella ponderosa*, two syntypes (NHMUK 1967654 and 20150505) the one figured by Reeve (1844) (NHMUK 20150505) is here designated lectotype. *Ranella pustulosa*, 3 syntypes (NHMUK 1967653), the specimen (NHMUK 1967653/1) called lectotype in Beu (2010, pl. 2, fig. 6-7) is not valid (ICZN 74.7.3. [amendment]), the same specimen is here designated lectotype. *Bursa pustulosa* var. *jabik*, three syntypes in Adanson coll. (MNHN-IM-2000-31761-31763), the specimen figured by Fisher Piette (MNHN-IM-2000-31761) is here designated lectotype. *Bursa caelata louisiana* type material unknown. *Bursa mexicana*, holotype [UNAM IG no. 1109-G according to Perrilliat (1963: 43)].

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Talisman corrugata* lives at present in Panamic western America, from Sonora to northern Peru (Keen 1971 and Beu 2010), in the western Atlantic, from Florida, USA, and the Bahamas to northern Brazil (Abbott 1974 and Beu 2010; “Ceará to São Paulo; Trindade I.”, Rios 1994), at St. Helena and Ascension Island in the mid-Atlantic (Rosewater 1975: 18, fig. 8; and Beu 2010), and in tropical West Africa, from Madeira (Beu 2010), the Canary Islands (Nordsieck & Garcia-Talavera 1979: 127, pl. 28, fig. 5), and Mauretania to at least as far south as Gabon (Bernard 1984: 64, fig. 102) and Angola (Gofas et al. 1984: 132, as *B. pustulosa*). It was recorded also from the Galápagos

Islands by Hickman & Finet (1999), Cocos Island, Costa Rica, eastern Pacific, by Montoya (1983, 1984) and Skoglund (1992), from Clipperton Island by Kaiser (2007: 39) and from Gorgona Island, Pacific Colombia, by Cantera et al. (1979) and Cosel (1984). Specimens from 125 m, off of Martinique, Caribbean, were illustrated by Paulmier (1994: 9, fig. 22). Matthews (1968) recorded specimens found rarely in the gut of the toadfish or “pacomon,” *Amphichthys cryptocentrus* (Valenciennes, 1837), caught off of Fortaleza, Ceará, Brazil. Fossils are widespread in Europe in Miocene, Pliocene, and late Pleistocene rocks (Cossmann & Peyrot, 1924). In the Americas are recorded only from the Agueguexquite Formation, Isthmus of Tehuantepec, Mexico (Pliocene), and the Galápagos Islands (Pleistocene), *Talisman corrugata* does not live in the Mediterranean at present, but young Pleistocene (Tyrrhenian) fossils occur at at least one locality in southern Italy, demonstrating that it entered briefly during interglacial warm periods. *Talisman corrugata* is among the widest-ranging of the Tonnoideans that have not entered the tropical Indo-West Pacific, and its full range – both geographical and stratigraphical – is still poorly known.

***Talisman victrix* (Dall, 1916)**

Bursa victrix Dall, 1916: 507, pl. 88, fig. 10— Beu 2010: 65, Pl. 2, Fig. 5.

TYPE LOCALITY. — Eastern bank of Flint River, Georgia, to be equivalent to the *Orthaulax pugnax* zone of Florida, of Late Oligocene age (Beu 2010).

TYPE MATERIAL. — *Bursa victrix* holotype (USNM 166728) by monotypy.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Only known from the late Oligocene of Mascot Point, Flint River, Georgia, United States.

Genus TRITONORANELLA Oyama, 1964

***Tritonoranella* Oyama, 1964: 332.**

TYPE SPECIES. — *Triton ranelloides* Reeve, 1844, Pliocene to Recent, eastern and western Atlantic, South Africa, Indian Ocean, Hawaii, and Japan-Taiwan.

SPECIES INCLUDED IN THE GENUS

Tritonoranella ranelloides (Reeve, 1844), *Tritonoranella latitudo* (Garrard, 1961),
Tritonoranella humilis (Beu, 1981), *Tritonoranella natalensis* (Coelho & Matthews, 1970)

DIAGNOSIS:

Very similar in shape and colour to *Korrigania* anterior siphonal canal more bent, varices situated at each 240° around the spiral, collumella striped (like *K. fosteri*), ovate operculum, subanterior nucleus

Tritonoranella ranelloides (Reeve, 1844)

Triton ranelloides Reeve, 1844a: pl. 3, fig. 10. — Reeve 1844c: 111

Lotorium ranelloides (Reeve, 1844) — G. B. Sowerby III 1902: 95.

Bursa (Lampas) ranelloides var. *tenuisculpta* (Reeve, 1844) — Dautzenberg & Fischer 1906: 36, pl. 2, figs 15-18.

Bufonariella ranelloides (Reeve, 1844) — Oyama & Takemura 1960: pl. *Colubrellina-Bufonariella*, figs 8-11; Habe 1961: 47, pl. 24, fig. 3; 1964: 76, pl. 24, fig. 3; Beu 1971: 110, pl. 8, fig. 8; Kuroda *et al.* 1971: 203, pl. 33, figs 5-6.

Tritonoranella ranelloides (Reeve, 1844) — Oyama 1964: 332.

Bursa ranelloides (Reeve, 1844) — Finlay 1978: 148; Gofas & Beu 2002: 102, figs 8A-J; Beu 1998: figs 49f-g; Zhang & Ma 2004: 180, text-fig. 112, pl. 4, fig. 8, Segers *et al.* 2009: 173, pl. 35, fig. 4; Castelin *et al.* 2012: 4843, fig. 4

Bursa (Bufonariella) ranelloides ranelloides (Reeve, 1844) — Beu 1981: 290, figs 18d, f-i.

Bursa (Colubrellina) ranelloides ranelloides (Reeve, 1844) — Beu 1985: 64.

Bursa (Colubrellina) ranelloides (Reeve, 1844) and formae *tenuisculpta* and *benvegnuae*.— Cossignani 1994: 86-87.

Bursa (Tritonoranella) ranelloides (Reeve, 1844) — Okutani 2000: 269, pl. 133, fig. 3; Higo *et al.* 2001: pl. 49, fig. G1622.

Simpulum papillosum A. Adams, 1870: 49 — Beu 1971: 110, pl. 8, fig. 8.

Bursa finlayi McGinty, 1962: 39, pl. 3, fig. 2 (in part; holotype only).

Bursa (Colubrinella) (sic) canarica Nordsieck, 1975: 4, fig. 16.

Bursa (Colubrellina) benvegnuae Penna-Neme & Leme, 1973: 285, figs 25-26.

Bursa (Colubrellina) ranelloides benvegnuae (Penna-Neme & Leme, 1973) — Rios 1985: 79, pl. 28, fig. 348.

Bursa ranelloides benvegnuae (Penna-Neme & Leme, 1973) — Coltro 1995: 52, fig. 4.

Bursa (Colubrellina) tenuisculpta Abbott, 1974: 166, fig. 1778 — Penna-Neme & Leme 1973: 284, figs 1, 10, 24, 27.

Bursa (Bufonariella) ranelloides tenuisculpta (Abbott, 1974) — Beu 1981: 292, figs 19a-k.

Bursa (Colubrellina) ranelloides tenuisculpta (Abbott, 1974) — Beu 1985: 64; Rios 1985: 79, pl. 28, fig. 349; Rios 1994: 92, pl. 31, fig. 366.

Bursa ranelloides tenuisculpta (Abbott, 1974) — Paulmier 1994: 9, fig. 24 ; Ardovini & Cossignani 2004: 132, central right and lower left figs.

Bursa pygmaea Kosuge, 1979: 31, pl. 5, fig. 5, pl. 6, fig. 23.

TYPE LOCALITY. — *Triton ranelloides* Sagami Bay, Honshu, Japan (designated by Beu 2010: 56). *Simpulum papillosum* “Takano-Sima,” Japan. *Bursa (Lampas) ranelloides* var. *tenuisculpta* Princess Alice Bank, Azores Islands, North Atlantic. *Bursa finlayi* from Triton sta. 615, dredged on Pourtales Plateau off of Sombrero Key Light, Florida Keys, in 210 m deep. *Bursa (Colubrinella) (sic) canarica* from Gran Canaria. *Bursa (Colubrellina) benvegnuae* from Mostardas, Rio Grande do Sul, Brazil. *Bursa pygmaea* from Midway, Hawaiian Islands.

TYPE MATERIAL. — *Triton ranelloides*, holotype (NHMUK 1967594) by monotypy (see Beu 2010:56). *Simpulum papillosum*, holotype (NHMUK 1967680). *Bursa (Lampas) ranelloides* var. *tenuisculpta*, most syntypes are in the Musée Océanographique, Monaco (see Beu: 2010); two syntypes in MNHN (MNHN-IM-2008-5172 *ex* collection H. Fischer). *Bursa finlayi*, holotype (USNM 634570); 3 paratypes in T. L. McGinty collection, dredged off of Sand Key Light, Florida, in 130-137 m deep; further paratypes from fish traps off of Gibara, Oriente Province, Cuba, collected by C. J. Finlay, and from Matanzas Bay, Cuba, collected by C. J. Finlay, in USNM, collections of T. L. McGinty and of C. J. Finlay (now at FAU) (but all except the holotype are specimens of *B. natalensis*). *Bursa (Colubrinella) (sic) canarica*, holotype originally in Nordsieck collection, no. 67.02, present location not known. *Bursa (Colubrellina) benvegnuae*, holotype (MZUSP no. 18477); 2 paratypes (MZUSP 18478) from the same station. *Bursa pygmaea*, holotype in IMT (Kosuge 1979).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Tritonoranella ranelloides* is moderately common in offshore (particularly rocky) habitats in the eastern and western

Atlantic. In the western Atlantic, it is recorded from Bermuda and southern Florida, USA, south to “northeast Brazil” (Rios 1994: 92). Paulmier (1994: 9, fig. 24) illustrated a specimen from 320 m deep, off of Martinique, West Indies. Its range is poorly documented in the central and eastern Atlantic, but it is recorded from at least the Azores (Gofas & Beu 2002), Madeira, and the Cape Verde Islands and on many of the offshore banks, and presumably occurs much more widely than this in depths of 100 m to more than 1,200 m deep. However, no specimens have been collected from close to the African mainland. An interesting record is from Vema Seamount, east of Walvis Ridge, SE Atlantic (NMP D.4374, 1). In South Africa, it is recorded from 168 m, 13 km WNW of Scottsburgh Lighthouse, Natal (G. B. Sowerby III 1902: 95).. In Japan, *Tritonoranella ranelloides* is a well known shell in relatively shallow water, from Boso Peninsula southward (Kuroda *et al.* 1971: 134); Okutani (2000: 269) recorded that in Japan, specimens occur from the “intertidal zone down to 200 m deep,” whereas it is definitely an outer shelf and upper bathyal species throughout the rest of its range (Beu, 2005). Kuroda *et al.* (1971: 134, as *Bufonariella ranelloides*) recorded specimens dredged in Sagami Bay, Honshu (its northern limit, Boso Peninsula, forms the northern margin of Sagami Bay), at five localities in 65-87 m deep. Specimens were recorded also from Taiwan by Lai (1987: 20, fig. 3, as *Tutufa ranelloides*), and material in MNHN was dredged off of eastern and northeastern Taiwan . Fossils are recorded from a few Miocene and Pliocene localities in the western Atlantic. There is no authentic records from the Philippine Islands (despite the original locality data for the holotype of *Triton ranelloides*) or from the northwestern Pacific area between Taiwan and the northern Indian Ocean. Fossil specimens have been reported previously from the Pliocene Shinzato Fm of Okinawa, Japan, (Ogasawara 2002: 328) and the late Middle Pleistocene (oxygen isotope stage 5e) Ryukyu Limestone of Kikaijima, Ryukyu Islands, southern Japan (Ogasawara 2002: 329), but the only others known to us are those listed By Beu (2010) from the middle Miocene of Trinidad and Pliocene of Panama.

***Tritonoranella humilis* Beu, 1981**

Gyrineum ranelloides (not Reeve, 1844) — Verco 1912: 219, pl.16, figs 6, 7; Hedley 1916: 196.

Bursa (Bufonariella) ranelloides humilis Beu, 1981: 290, Figs 10, r; 2b; 4j; 5a; 18a-c, e.

Bursa humilis Beu, 1981 — Wilson 1993:

Bursa (Colubrellina) humilis Beu, 1981 — Cossignani 1994: 79,

TYPE LOCALITY. — Recent Western Australia

TYPE MATERIAL. — Holotype (WAM 305-72) and nine paratypes (WAM 305-72, WAM 309-72, WAM 310-72, WAM 312-72).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. To our knowledge every specimens of *Tritonoranella humilis* have only been found in Western Australia

Tritonoranella latitudo Garrard, 1961

Bursa latitudo, Garrard, 1961: 15, pl. 2, fig. 2. — Kay 1979: 227, fig. 80 H; Parth 1991: 209. Wilson 1993: 227, pl. 43, fig. 13; Beu 2005: 20, Figs. 29, 30; Beu *et al.* 2012: 69, Fig. 2G; Castelin *et al.* 2012:4843

Bursa (Bufonariella) latitudo latitudo Garrard, 1961 — Beu 1981: 287, figs 16 g-i.

Bursa (Colubrellina) latitudo latitudo Garrard, 1961 — Beu 1985: 64; Cossignani 1994: 80.

Bursa (Bufonariella) latitudo wolfei Beu 1981: 289, figs 17 a-f.

Bursa (Colubrellina) latitudo wolfei Beu, 1981 — Beu 1985: 64 ; Cossignani 1994: 83-84.

Bursa lampas (not Linnaeus, 1758) — Tinker 1952: 98-99, centre fig.

Bursa finlayi (not McGinty, 1962) — Wolfe 1975: 12, figs 1-2.

Bursa nigrita (not Mulhauser & Blocher, 1979) — Wells *et al.* 1990: 40, pl. 19, fig. 123.

TYPE LOCALITY. — *Bursa latitudo* off Moreton Island, southern Queensland, in 230 m deep; *Bursa latitudo wolfei* from crab trap in 58 m deep, off Makahu, Hawaii.

TYPE MATERIAL. — Holotype (MV F21111); paratype AMS C63353 [a badly damaged specimen of *Ranella australasia* (Perry, 1811)], from the same locality as the holotype. *Bursa latitudo wolfei*: holotype (BPBM 8936); 2 paratypes, (1 in C.S. Wolfe Collection, 1 in S. Handrahan Coll.); paratype, off Haleiwa, 120 m deep, Oahu, Hawaii, in C.S. Wolfe Coll.; paratype, off Nanakuli, Oahu, Hawaii, in Honolulu Aquarium Collection.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Tritonoranella latitudo* is abundant in moderately deep water (250–700 m deep, a few empty shells to 1145 m deep) in the Southwest Pacific, particularly around New Caledonia, and occurs uncommonly in similar depths throughout the western Pacific, from the Philippine Islands and eastern Australia (where it is rare) to Hawaii and French Polynesia. Although no material has been seen from the Indian Ocean, the specimen from Christmas Island identified as *Bursa nigrita* by Wells *et al.* (1990: 40, pl. 19, fig. 123) is actually *Tritonoranella latitudo*, and all MNHN expeditions throughout the Western Pacific region have taken it in moderate to large numbers in deep water. Beu (1998: 157) recorded this species previously from the Marquesas Islands. Only two fossils are listed by Beu (2005). From Cosijn Coll., upper Kendeng beds, Pleistocene: RGM 46 582; Sangiran, central Java, Late Pliocene in B. Dharma coll.).

Tritonoranella natalensis (Coelho & Matthews, 1970)

Bursa finlayi McGinty, 1962: 39, pl. 3, figs 1-1a, 2 (in part; holotype is *Tritonoranella ranelloides* (Reeve, 1844) — Laursen 1981: 30, pl. 3, figs 2ab.

Bursa (Colubrellina) natalensis Coelho & Matthews 1970: 1, figs 1-3.

Bursa (Colubrellina) tenuisculpta natalensis Coelho & Matthews, 1970 — Abbott 1974:167.

Bursa (Bufonariella) latitudo natalensis Coelho & Matthews, 1970 — Beu 1981: 288, figs 16a-f.

Bursa (Colubrellina) latitudo natalensis Coelho & Matthews, 1970 — Beu 1985: 64; Cossignani 1994: 82.

Bursa latitudo natalensis Coelho & Matthews, 1970 — Calvo 1987: fig. 83 (radula); Paulmier 1994: 9, fig. 23.

Bursa natalensis Coelho & Matthews, 1970— Leal 1991: 113.

Bursa (Colubrellina) finlayi Coelho & Matthews, 1971: 53, figs 13-15.

TYPE LOCALITIES. — *Bursa (Colubrellina) natalensis* from off of Natal, Rio Grande do Norte, Brazil. *Bursa finlayi* from off of Sombrero Key Light, Florida Keys (*Triton* sta. 615 dredge in 210 m deep).

TYPE MATERIAL. — *Bursa (Colubrellina) natalensis*, holotype (MNRJ 3527); one paratype (UFC LCM no. 462); one paratype (MORG no. 14731). *Bursa finlayi*, holotype (USNM 634570), a specimen of *B. ranelloides* (Reeve, 1844); all paratypes are *Tritonoranella natalensis*: 3 paratypes in McGinty coll.; paratype in McGinty coll. from fish traps in 180-200 m deep, off of Gibara, Oriente Province, Cuba; paratypes from the same station in FAU (ex Finley coll.), and one in USNM.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Tritonoranella natalensis* lives now in the western Atlantic, from southern Florida, USA, to Bahia, Brazil, in relatively deep water (ca. 100-500 m deep). From the Lesser Antilles, particularly near Guadeloupe. Paulmier (1994: 9, fig. 23) illustrated a specimen, and reported *B. natalensis* from depths of 125-380 m off of the French Antilles, Caribbean. the only one fossil specimen (and a possible second specimen) is recorded from Limón, Costa Rica (Latest Pliocene-EarlyPleistocene) (Beu 2010).

Genus **TUTUFA** Jousseume, 1881

Tutufa Jousseume, 1881 : 175

TYPE SPECIES. — *Murex rana bubo* Linnaeus, 1758; ICZN Opinion (1977:1074), Middle Miocene to Recent, Indo-West Pacific.

Lampas Schumacher, 1817

TYPE SPECIES. — (by monotypy) *Lampas hians* Schumacher, 1817 (= *Murex rana rubeta* Linnaeus, 1758), Recent, Indo-West Pacific. Junior homonym of *Lampas* Montfort, 1810 (Foraminifera).

Tutufella Beu, 1981 Replacement name for *Lampas* Schumacher, 1817, preoccupied.

SPECIES INCLUDED IN THE GENUS

Tutufa bardeyi (Jousseume, 1881), *Tutufa boholica* Beu, 1987, *Tutufa bubo* (Linnaeus, 1758), *Tutufa bufo* (Röding, 1798), *Tutufa chipolana* Schmelz, 1997 *Tutufa nigrita* Mühlhäusser & Blöcher, 1979, *Tutufa oyamai* Habe, 1973, *Tutufa rubeta* (Linnaeus, 1758), *Tutufa tenuigranosa* (Smith, 1914).

DIAGNOSIS:

Large size, relatively tall, narrow shape for a Bursidae, varices situated at each 240° around the spiral, 8 primary cords on the convex part of the whorl, P1, P3, P5 and P7 nodulous, P1 and P3 sometimes splited (e.g. *Tutufa bubo*) P2 and P4 atrophied, P6, P7 and P8 reduced (P6 and P8 atrophied in intervarical), subcircular to fan shape operculum, lateral nucleus in central right.

Tutufa bubo (Linnaeus, 1758)

Murex rana bubo Linnaeus, 1758: 748 — Gmelin 1791: 3532.

Murex lampas bubo (Linnaeus, 1758) — Linnaeus 1767: 1216.

Bursa bubo (Linnaeus, 1758) — Vanatta 1914: 80 (in part); Hedley 1916: 42; Cernohorsky 1967b: 311, pl. 42, fig. 1; 1972a: 118, pl. 32, fig. 7 (only); Hinton 1972: 14, pl. 7, fig. 3; Salvat & Rives 1975: 307, fig. 178.

Bursa bubo (not Linnaeus, 1758) — Vanatta 1914: 80 (in part); Salvat *et al.* 1988: 103, pl. 13, fig. 14.

Tutufa bubo (Linnaeus, 1758) — Oyama & Takemura 1963: *Tutufa* pl. 2, fig. 5; Habe & Kosuge 1966: 46, pl. 16, fig. 10; Hinton 1978: 31, fig. 1.; Short & Potter 1987: 44, pl. 21, fig. 4; Lai 1987: 18, fig. 4.

Tutufa (Tutufa) bubo (Linnaeus, 1758) — Beu 1981: 277, figs 2 d, 4 a, 11 b, 12 f, 13-14 a, c-d; Beu 1985: 66; Springsteen & Leobrera 1986 122 pl 33 figs 8 ab; Wilson 1993: 228, pl. 43, fig. 16; Cossignani 1994: 98, 99; Beu 1998: 172, fig. 55c; Tröndlé and Cosel 2005: 288; Tröndlé and Boutet 2009: 22; Beu *et al.* 2012: 72, fig. 3A.

Tutufa bubo (in part not Linnaeus, 1758) — Wilson & Gillett 1971: 80, pl. 54, figs 2-2 a (in part) (= *T. oyamai*).

Triton lampas (Linnaeus, 1758) — Lamarck 1822: 180 (in part); Reeve 1844a: pl. 9, fig. 30 a (only); Lischke 1870: 47 (in part); Lischke 1871: 34; 1874: 29.

Bursa (Bufonaria) lampas (Linnaeus, 1758) — Schepman 1909: 118.

Bursa (Tutufa) rubeta var. *gigantea* E.A. Smith, 1914: 230, pl. 4, fig. 4 (only).

Bursa rubeta gigantea (E.A. Smith, 1914) Rippingale & Mc Michael, 1961: 69, pl. 7, fig. 20,

TYPE LOCALITY. — Recent Philippines islands.

TYPE MATERIAL. — *Murex rana* var. *bubo* neotype (NHMUK 1974147) by designation of Beu (1981: 278). *Bursa rubeta* var. *gigantea*, lectotype (NHMUK 1914.6.29.1) by designation of Beu (1981: 278).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Tutufa bubo* occurs throughout the tropical Indo-West Pacific region from Mozambique and the Seychelles Islands to eastern Polynesia, and from Tosa Bay, Shikoku, southern Japan (Oyama and Takemura 1963) to off Minnie Waters, northern New South Wales, eastern Australia (Beu 1981, 1998). One specimen seen by Beu (1986) is from off the Three Kings Islands, northernmost New Zealand. It is the one large *Tutufa* species occurring uncommonly subtidally around coral reefs throughout this region, including the Red Sea, although there are no records from Hawaii (Severns 2011). NHMUK has a specimen from Flint Island (southernmost of the Line Islands, between the Cook and Marquesas Islands) collected by Siméon Krauser. As noted by Tröndlé & Cosel (2005: 288), it was recorded previously from the Marquesas Islands by Rehder (1969: 31), Lavondes *et al.* (1973: 133), Salvat and Rives (1975: 307, fig. 178) and Richard (1985: 423), but elsewhere in French Polynesia there are only a few records from the Society and Tuamotu Islands. The only fossils comes from the Pleistocene of Sumatra and Java.

***Tutufa bardeyi* (Jousseume, 1881)**

Lampas bardeyi Jousseume, 1894:98.

Bursa (Tutufa) rubeta var. *gigantea*. E. A. Smith, 1914:230, pl. 4, fig. 5 (only).

Bursa (Bufonaria) rubeta var. *bardeyi* (Jousseume, 1894) — Bayer 1933: 231.

Tutufa (Tutufa) bardeyi (Jousseume, 1894) — Beu 1981: 312, Figs 9a, b, d; 10a, d

TYPE LOCALITY. — Gulf of Aden.

TYPE MATERIAL. — Holotype (MNHN-IM-2000-4095) and one paratype probably also in MNHN.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil record. *Tutufa bardeyi* occurs in the north-western Indian Ocean, and probably the Red Sea, from Kenya to at least the Gulf of Oman. Throughout its range it is sympatric with *T. bubo*.

***Tutufa boholica* Beu, 1987**

Tutufa (Tutufella) boholica Beu, 1987:347, fig. 269-274 — Cossignani 1994: 104.

TYPE LOCALITY. — Panglao Peninsula, Bohol I., Philippine.

TYPE MATERIAL. — Holotype (USNM 849014), 1 paratype in NZGS (WM I 4099), one paratype in The Abbey Specimen Shells coll.; Punta Engaio, Mactan I., Cebu, Philippines, and a small paratype in NZGS (WMI4029).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records is only known from recent Philippines Islands.

***Tutufa bufo* (Röding, 1798)**

Tritonium bufo Röding, 1798: 128.

Bursa bufo (Röding, 1798) — Hedley 1916a: 42; Hedley 1918b: M67.

Bursa bufo (Röding, 1798) — Kira 1954:43, pl. 21, fig. 20.

Bursa (Tutufa) bufo (Röding, 1798) — Kira 1961: 55, pl. 21, fig. 20; Kira 1962: 57, pl. 22, fig. 20.

Tutufa bufo (Röding, 1798) — Iredale & Mc Michael 1962: 55; Oyama & Takemura 1963: Tutufa pl. 2, figs 2-4; Powell 1967: 189, pl. 36, fig. 8; Wilson & Gillett 1971. 80, pl. 50, fig. 1; Kay 1979: 229, flg. 801; Okutani 1986: 116; 117, 3rd fig. from top left; Short & Potter 1987:44, pl. 21, fig. 3; Lai 1987: 18, fig. 1.

Tutufa (Tutufa) bufo (Röding, 1798) — Beu 1981: 272, figs 1 d, g, p; 2 c; 5 b-e, f; 6; 11 a, c-f; 12 a, g; Beu 1985: 66; Springsteen & Leobrera 1986: 120 l 33fig. 1; Wilson 1993; 228, pl. 43, fig. 17; Cossignani 1994: 100-102; Bosch *et al.* 1995: 104 fig. 376. p.

Bursa (Tutufa) rubeta var. *lissostoma* E.A. Smith, 1914: 230, pl. 4, fig. 3.

Tutufa lissostoma (E.A. Smith, 1914) — Iredale 1931: 214, pl. 23, fig. 5; Okutani 1970; 124, pl. 8, fig. 1; Kuroda *et al.* 1971: 134, pl. 34,

Bursa bubo forma lissostoma (E.A. Smith, 1914) — Cernohorsky 1972a: 118, pl. 32, fig. 7 a; Cernohorsky 1967b: 152; Cernohorsky 1979: 168, pl. 33, fig. 12.

Bursa bubo lissostoma (E.A. Smith, 1914) — Powell 1974: 205.

Bursa rubeta (not Linnaeus, 1758) — Bosch *et al.* 1982: 84.

Triton lampas (not Linnaeus, 1758) — Lamarck 1822; 180; Kiener 1842: pl. 5, fig. 1.- Reeve 1844a: pl. 10, fig. 30 b (only); Lischke 1869: 47; Lischke 1871: 34; Küster & Kobelt 1871: 175, pl. 37, figs 3-4; Lischke 1874: 29; Kobelt 1876 : pl. 9 fig. 2.

Ranella lampas (not Linnaeus, 1758) — Tryon 1880: pl. 19, fig. 12.

Bursa (Lampas) hians (not Schumacher, 1817) — Angas 1877: 179.

Tutufa (Crossata) californica (not Hinds, 1843) — Suter 1906: 328.

Argobuccinum siphonatum (not Reeve, 1844) — Iredale 1910: 73.

Bursa bubo (not Linnaeus, 1758) — Vanatta 1914: 80; Salvat *et al.* 1988: 103, pl. 13, fig. 14.

Bursa siphonata (not Reeve, 1844) — Oliver 1915: 528.

Tutufa robusta Cossignani, 2009: 27.

TYPE LOCALITY. —Madagascar by busequent designation of Kuroda *et al.* (1971: 134).

TYPE MATERIAL. —*Tritorium bufo*, neotype (NHMUK 197384) by designation of Beu (1998: 175). *Bursa rubeta* var. *lissostoma* lectotype by designation of Beu (1981: 273). *Tutufa robusta* holotype in MMM

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Tutufa bufo* is very wideranging throughout the Indo-West Pacific province. A record from Natal, South Africa, has been confirmed since 1981 (Beu 1981) and it occurs throughout the Indian Ocean, Gulf of

Arabia (Bosch *et al.* 1982: 84; Bosch *et al.* 1995: 104, fig. 376) and Red Sea. In the western Pacific it ranges as far north as central Honshu, Japan (Kira 1962: 57) and as far south as northeastern New Zealand, where the southernmost recorded locality is White Island, Bay of Plenty (5 specimens NZGS RM5069). Records extend throughout the central Pacific as Far East as Hawaii where, however, only one specimen has been reported (Kay 1979: 229).

Tutufa chipolana (Schmelz, 1997)

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

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

Bursa chipolana Schmelz, 1997—Beu 2010: 44, Pl. 1, Figs 5-7, 10

TYPE LOCALITY. — TU 546, Chipola Formation (Burdigalian), Tenmile Creek, Florida, United States

TYPE MATERIAL. — *Bursa (Bufonariella) chipolana*, holotype (UF 73199), figured paratype (USNM 647108), from TU 547, west bank Chipola River 600 m upstream from Fourmile Creek, Calhoun Co (Pl. 1, Figs 6-7; specimen figured by Vokes 1973: text-figs 2a-b); figured paratype UF 73200, from TU 951, Tenmile Creek, Calhoun Co; 9 further paratypes from localities on or near the Chipola River listed by Schmelz (1997).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE: — *Tutufa chipolana* is recorded only from the Chipola Formation (Burdigalian) on and near the Chipola River, Calhoun Co, Florida, USA.

Tutufa nigrita Mühlhäusser & Blöcher, 1979

Tutufa (Tutufella) nigrita Mühlhäusser & Blöcher, 1979: 210, fig. 1 — Drivas & Jay 1988:62; Cossignani 1994:105.

TYPE LOCALITY. — Recent Tulear, South west of Madagascar.

TYPE MATERIAL. — Holotype (ZSM 1688 Mollusca) 2 figured paratypes 1 in ZSM and 1 in Mühlhäusser coll., Freiburg. 10 other paratypes, 2 in ZSM, 1 in Mühlhäusser coll., Freiburg, 7) in Blöcher coll., Duisburg (Partially transferred in other museum).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — No fossil records. *Tutufa nigrita* occurs in the recent only in Madagascar, Mozambique and Réunion where it's very rare.

Tutufa oyamai Habe, 1973

Tutufa oyamai Habe, 1973: 140, fig. 2 — Wilson 1993: 228, pl. 43, fig. 14a, b; Higo *et al.* 2001: 49, fig. 1632.

Tutufa (Tutufella) oyamai. Habe, 1973 — Beu 1981: 283, figs. 1f, i, l, q, 2e, 4b-f, 15d-i.; Beu 1985: 66, fig. 54; Cossignani 1994: 106-108; Beu 1998: 177, fig. 55c; Okutani 2000: 271, pl. 134, fig. 17 (not fig. 16).

Ranella (Lampas) lampas (not Linnaeus, 1758) — Martin 1899: 148, pl. 23, figs. 346, 346a.

Ranella lampas (not Linnaeus, 1758) — Schepman 1907: 181; Martin 1919: 88, 132; van der Vlerk 1931: 241.

Bursa (Ranella) rubeta, (not Röding, 1798) — van Regteren Altena 1942: 108.

Tutufa tenuigranosa (not E.A. Smith, 1914) — Habe 1961: 47, pl. 24, fig. 4; Habe 1964: 76, pl. 24, fig. 4.

TYPE LOCALITY. — Recent Taiwan, South China Sea.

TYPE MATERIAL. — Holotype (NSMT 42372) and two paratype (NSMT 42373 NZGS WM11274)

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Tutufa oyamai* occurs throughout the Indian Ocean and the western Pacific archipelagos, as far south as southern Mozambique and as far north as Oman in the Indian Ocean, and from Taiwan to northern Australia and New Caledonia (Beu 1998). Although there are no records from Polynesia, some extension east of New Caledonia seems likely. Fossils are moderately common from the late Pliocene to Pleistocene of Java, but seem not to be recorded from elsewhere.

Tutufa rubeta (Linnaeus, 1758)

Murex rana rubeta Linnaeus, 1758: 748 — Linnaeus 1767: 1216; Gmelin 1791: 3532.

Tritonium rubeta (Linnaeus, 1758) – Röding 1798: 128.

Bursa (Tutufa) rubeta, typical var. (Linnaeus, 1758) – E.A. Smith 1914: 228, pl. 4, figs. 1, 2.

Bursa rubeta (Linnaeus, 1758) – Vanatta 1914: 80; Hedley 1916: 41; Hinton 1972: 14, pl. 6, fig. 23; pl. 7, fig. 2; Cernohorsky 1972b: 118, pl. 1, fig. 5; Drivas & Jay 1988: 62, pl. 16, fig. 2; Salvat *et al.* 1988: 103, pl. 13, fig. 16.

Tutufa rubeta (Linnaeus, 1758) – Oyama & Takemura 1963: *Tutufa* pl. 2, fig. 1; Habe & Kosuge 1966: 46, pl. 16, fig. 8; Hinton 1978: 31, fig. 2; Okutani 1986: 116, 117, fig top row, 5th from left; Short & Potter 1987: 44, pl. 21, fig. 5; Lai 1987: 18, fig. 2.

Tutufa (Tutufella) rubeta (Linnaeus, 1758) – Beu 1981: 280, figs. 1b-c, e, j, k, 3, 4g-i, 5d, e, 7, 9c, 12b, c, 14d; Springsteen & Leobrera 1986: 120, pl. 33, fig. 6a, b; Wilson 1993: 228, pl. 43, fig. 18; Cossignani 1994: 109-110; Beu 1998: 178, figs. 55b, 56a, 57b, d, e; Beu 2005: 32.

Tritonium tuberosum Röding, 1798: 127.

Biplex tuberculus Perry, 1811: pl. 4, fig. 3.

Lampas hians Schumacher, 1817: 252.

Lampas caledonensis Jousseaume, 1881: 177.

Triton lampas Lamarck, 1816: 420, fig. 3a, b, “Liste des objets”:5— Lamarck 1822: 180.

Murex lampas (not Lamarck, 1816) — Wood 1828: pl. 25, *Murex* fig. 28d.

Tritonium lampas (not Lamarck, 1816) — Anton 1838: 83.

Triton lampas var. (not Lamarck, 1816) — Küster & Kobelt 1871: 175, pl. 40, figs. 7, 8.

TYPE LOCALITY. — *Lampas caledonensis*, *Murex rana rubeta*, *Tritonium tuberosum*, *Biplex tuberculus* and *Lampas hians*, all form Recent New Caledonia in accordance with ICZN Art. 76.3.

TYPE MATERIAL. — *Lampas caledonensis*, lectotype (MNHN-IM-2000-4130) designated by Beu, 1998: 179 with 3 paralectotypes (MNHN-IM-2000-4132); the lectotype was also designated by Beu (1998) as the neotype of *Murex rana rubeta*, *Tritonium tuberosum*, *Biplex tuberculus* and *Lampas hians*. Five specimens in Lamarck's collection, in MHNG, are labelled as syntypes of *Triton lampas* Lamarck, but the syntype illustrated by Lamarck (1816: pl. 420, fig. 3a, b) is not among them.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — Beu (1998) recorded the range of *Tutufa rubeta* as East Africa (perhaps as far south as Durban, South Africa) and throughout the Red Sea, through out the indo-Pacific, Philippines and Papua New Guinea, as far east as French Polynesia (although there are no records from Hawaii), and from the Ryukyu Islands, southern Japan, to Coff's Harbour, northern New South Wales, Australia. The only known fossils of *Tutufa rubeta* are those from the late Miocene, Pliocene of Sangiran, central Java (Beu 2005).

Tutufa tenuigranosa (Smith, 1914)

Bursa (Tutufa) rubeta var. *tenuigranosa* E.A. Smith, 1914: 231, pl. 4, fig. 6.

Bursa tenuigranosa Smith, 1914 – Vanatta 1914: 80; Hedley 1916: 42.

Tutufa tenuigranosa (Smith, 1914) – Habe 1973: 139, text-fig. 1.

Tutufa (Tutufella) tenuigranosa (Smith, 1914) – Beu 1981: 285, fig. 15a-c.

Tutufa (Tutufa) tenuigranosa (Smith, 1914) – Beu 1985: 66, fig. 53; Beu 1987:346; Wilson 1993: 228, pl. 43, fig. 15; Cossignani 1994: 103; Beu 1998: 175, fig. 56b, c.

Tutufa (Tutufa) bubo form *tenuigranosa* (Smith, 1914) – Springsteen & Leobrera 1986: 122, pl. 33, fig. 13.

TYPE LOCALITY. — Taiwan by subsequent designation of Beu (1998: 175).

TYPE MATERIAL. — Lectotype (NHMUK 1914.6.29.4) by designation of Beu (1981: 286) with several paralectotypes in NHMUK.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE. — *Tutufa tenuigranosa* is recorded in the recent fauna from Taiwan, the Philippine Islands and Indonesia; it seems to be

limited to the most central western Pacific archipelagoes. The single fossil specimen recorded is from the Miocene of central Java.

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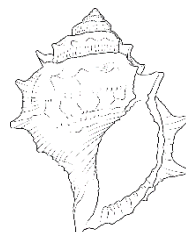
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CHAPITRE 5
PHYLOGENIE
FONDEE SUR LES CARACTERES DE LA
COQUILLE
DES BURSIDAE

La systématique moléculaire possède un désavantage certain qui est celui de la fragilité de son objet d'étude l'ADN. Se procurer du matériel de qualité suffisance pour pouvoir être utilisé dans des analyses de délimitation d'espèce ou de phylogénie peut parfois se révéler être un défi. Si l'échantillon n'est pas fixé tout de suite dans l'alcool (à 90° ou 100°) après la collecte l'ADN se dégrade très rapidement au point de devenir inutilisable.

Même si il est vrais que les avancées en séquençages font que nous somme à même d'obtenir de plus en plus de séquence issues de spécimens dégradés (Cole & Wood, 2017) et que d'autre part nos protocoles de collecte sont de plus en plus optimisé pour conserver l'ADN de nos spécimens (Galindo et al. 2014) il sera toujours difficile de se procurer du matériel rare (mais indispensable pour certains échantillonnages) ou des données issues d'holotypes qui le plus souvent sont conservé à l'état de coquilles séchées chez les mollusques. A cela s'ajoute la difficulté croissante de se procurer du matériel moléculaire provenant de l'étranger à cause des restrictions imposées par le protocole de Nagoya.

Face à ces problèmes la morphologie reste la seule alternative et elle est, de plus l'unique moyen d'intégrer des fossiles à une étude.

Cependant les problèmes de formulation d'homologie rendent son utilisation difficile dans un cadre phylogénétique (Scotland et al. 2003).

Dans ce chapitre nous proposons de tester notre capacité à retrouver une phylogénie des Bursidae basé sur leurs caractères anatomiques en se concentrant uniquement sur ceux de la coquille et de comparer ces résultats avec ceux de de l'analyse moléculaire.

Les Bursidae ont une coquille très fortement ornementé, avec un pattern spirale sériel, Il a été montré chez les gastéropodes ornementés tels que les murex (Merle 2001, 2004) que la coquille était potentiellement porteuse d'homologie et que ses caractères pouvaient être discrétisé afin d'être implémenté dans une matrice taxon caractère. Bien qu'ils ne soient pas phylogénétiquement proche Bursidae et Muricidae ont des coquilles qui peuvent être traité de la même manière en analyse phylogénétique.

MATERIEL ET METHODES

Matériel

Le matériel de l'étude morphologique est entièrement listé dans l'annexe 1, il est composé de matériel provenant des collections du MNHN (collections actuels noté IM et collections paléontologiques noté P), du muséum de Santa Barbara, et de l'université de de

Californie, Berkeley. Certains spécimens (listé dans l'annexe) ont été codés uniquement à partir de photo. Dans le matériel à notre disposition, quand nous avons plusieurs spécimens nous avons choisi le spécimen le plus grand afin de coder l'expression maximale des caractères. Ces spécimens n'ont pour la plupart pas de numéro de collection récent (IM ou F) nous leur avons attribué une étiquette pour signaler qu'ils ont été utilisés dans cette étude, en attendant qu'ils reçoivent un numéro de collection.

Visant un échantillonnage quasi exhaustif il est composé de 48 taxons actuels et 6 taxons fossiles.

Méthode d'identification des caractères :

La sculpture de la coquille des Bursidae est organisée en 4 complexes majeurs de caractères: (1) les côtes, (2) l'ornementation columellaire, (3) les cordons spiraux et (4) les denticules internes du labre. Pour les côtes, l'identification des caractères homologues est associée au type de construction. Au niveau de la téléoconque, elles sont de deux types: les côtes correspondant à des arrêts de croissance majeurs que l'on nomme varices (Webster & Wermeij 2017) et les côtes intermédiaires. Pour l'ornementation columellaire, les cordons spiraux de la téléoconque et pour les denticules internes du labre, il est possible de parler d'homologie sérielle. L'homologie sérielle est l'ensemble des caractères ayant un plan de construction commun et une morphologie plus ou moins semblable. Chaque caractère constitue alors un élément de la série. Bouligand (1989) fit une synthèse du travail de Grandjean (1948) qui définit 3 types de caractères distribués en série (Tableau 5.1).

Tableau 5.1 : Différents types de caractères sériels, modifié d'après Grandjean (1948) et Bouligand (1989)

| | | Pléthotaxiques | Cosmiothaxique | | Orthotaxique |
|------------------------------|----------|-----------------------------|---------------------|-------------------|--------------|
| Caractéristique | | | | | |
| alignement | | Pas de position définie | alignés | alignés | alignés |
| nombre | | illimité | variable, illimité | variable, limité | invariables |
| Possibilité d'identification | | non | non | oui | oui |
| Exemples | Homme | Cheveux | inexistante | dents | bras |
| | Bursidae | ornementation collumellaire | cordons secondaires | Cordons primaires | inexistante |
| Catégories | | 1 | 2 | 3 | 4 |

Le critère ontogénétique

Ce critère (Cox 1960), a été utilisé au départ pour l'étude des cordons des coquilles holostomes (Bieler 1988, 1995, pour les Mathildidae ; Allmon 1994 pour les Turritellidae ; Marshall 1995 pour les Calliostomatidae). Il a été adapté par Merle (2001, 2002, 2005), Merle *et al.* (2001), Merle & Pacaud (2002) et Merle & Houart (2003) aux Muricidae, Merle & Pacaud (2004) pour les Harpidae puis plus récemment pas nous (Article 2) pour les Bursidae. Ce critère permet la distinction de différentes séquences d'apparition des cordons. En effet, chez les Bursidae comme chez beaucoup de gastéropodes, les descriptions classiques étaient largement fondées sur l'étude des adultes et ne reposaient pas sur l'ontogenèse des organismes. Ainsi, les séquences d'apparition n'étaient pas considérées. Par conséquent, des cordons n'appartenant pas à la même séquence pouvaient être considérés comme homologues alors qu'en fait ils ne l'étaient pas. Grâce à ce critère, il est possible de mettre en évidence deux séquences majeures d'apparition des cordons. D'une part elles sont les premières à apparaître lors de l'ontogenèse et d'autre part, elles donnent l'aspect général de la sculpture de la coquille. Les cordons de la première séquence seront qualifiés de primaire (P) et ceux de la deuxième de secondaire (S). Les cordons tertiaires (Tableau 2, catégorie 2) de la troisième séquence, ne seront pas pris en compte car non aisément homologable.

Le critère de position topologique

La deuxième étape de l'analyse consiste à détecter les positions topologiques à l'intérieur de chaque séquence. Ceci est possible car chaque caractère de chaque séquence a une position particulière que l'on peut déduire de son environnement immédiat. Durant leur croissance, les cordons ne changent pas de position car ils ne se croisent pas. De plus, le cordon P1 qui correspond à l'épaulement est un bon point de repère. L'alignement des caractères au sein de la séquence a pour conséquence que le cordon primaire P2, par exemple, est défini ainsi car il se situe entre les cordons primaires P1 et P3 (Merle 2001), (Fig. 5.1).

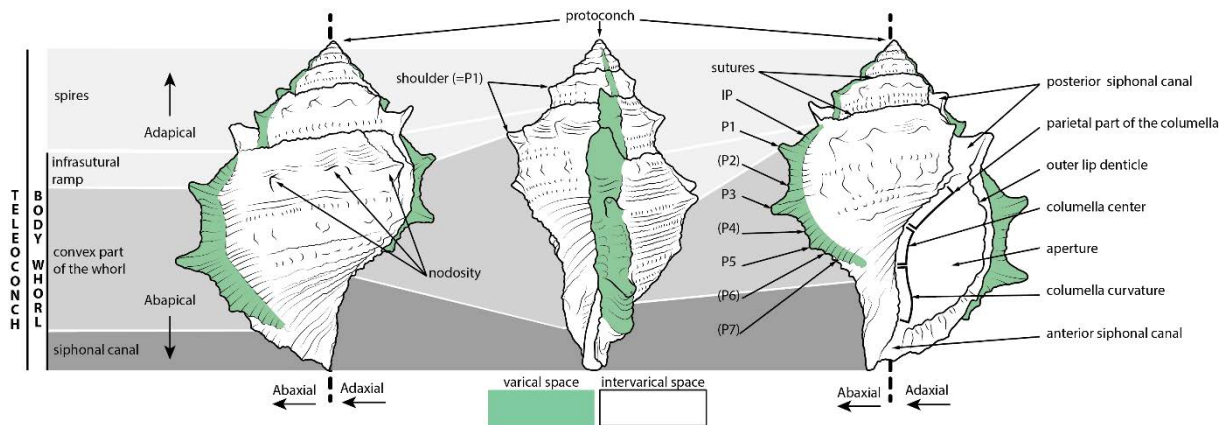


Fig. 5.1 : Caractères généraux de la coquille des Bursidae ; les cordons marqués entre () indique que le cordon est atrophié à cette position

Le critère de conjonction (mise en évidence des structures maximales)

La dernière étape de l'analyse permet de déterminer le nombre maximum de positions topologiques (Test de conjonction, Patterson (1982)) rencontrés dans la famille. Ceci va permettre d'une part de proposer une terminologie générale pour tous les taxons (ce qui a été fait dans l'article 2) et d'autre part d'éviter de revenir à la terminologie au cours de l'étude. Chez les Bursidae la structure maximale est composé d'un cordon suturale, un cordon infra sutural et au maximum de huit cordons dans la partie convexe du tour (c'est le cas chez tous les *Tutufa* et *Marsupina*), Tous les cordons primaires sont exprimés dès le premier tour

Traitement des données

L'analyse des données a été effectuée en maximum de parcimonie sous Paup 4.0 a157 (Swofford, 2002). Pour l'étude, la parcimonie de Wagner a été privilégiée car elle admet à la fois convergences et réversions. Les caractères sont traités de manière non ordonnées, non additifs et sans pondération. Le nombre de taxons étant important (55), une recherche heuristique a été réalisée avec les options Strepwise addition et Random (30 réplicats). En optimisation ACCTRAN (Accelerated Transformation) qui favorise les transformations au niveau des morphotypes ancestraux. La robustesse des nœuds sera évaluée sur le consensus.

Choix du groupe externe.

Comme groupe externe nous avons choisi deux Cassidae (un Cassidae sp, et *Galeodea kurodai*, (Abbott, 1968) imposé comme *out group* dans l'analyse) et le genre fossile *Olequahia* représenté par *Olequahia washingtoniana*

LISTE DES CARACTERES MORPHOLOGIQUES DES BURSIDAE ACTUELS ET FOSSILES

Les termes d'orientation de la coquille sont représentés sur la Fig. 5.5

CARACTERES GENERAUX DE LA TELEOCONQUE

Caractère 1 : varices

Etat : **0** : varice absente ou terminale, **1** : alignement des varices **2** : décalage des varices.

Note : les varices dites terminales observés notamment chez les Cassidae ne sont pas homologues à celles observées chez les Charoniidae ou les Bursidae. Elles ne suivent pas le même processus de formation : Les varices terminales de Cassidae sont issues d'un retournement complet du labre (Fig. 2) (flèche orange Fig. 2 state 0)) alors que les varices de discontinuité de croissance (qui peuvent être en position terminale) sont un bombement adaxiale de ce dernier (flèche bleue). De plus les Cassidae dissolvent leurs varices à chaque phase de croissance

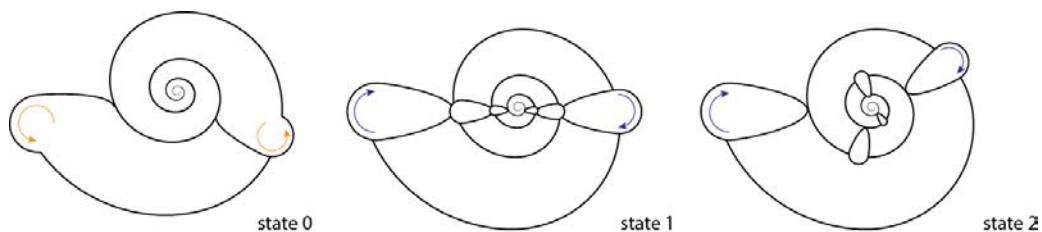


Fig. 5.2 processus de formation des varices (les states correspondent aux états de la matrice)

Caractère 2: Canal siphonal postérieur ou encoche anale (Fig. 3)

Etat : **0** : absente, **1** : encoche simple sans lamelle pariétale, **2** : la rampe infrasuturale fait partie intégrante de l'encoche (pas de séparation pariétale), **3** : encoche tubulaire avec déplacement adaxial, **4** : encoche simple avec extension d'une lamelle pariétale.

Notes : La dent labral (flèche figure C) d'Olequahia en relation avec sa dent collumelaire forme un « pseudo canal » non homologue à celui des Bursidae. L'expression varicale en épine du cordon sutural chez Bufonaria echinata (flèche figure E), influence la forme de l'encoche anal cependant elle reste à l'état 1.

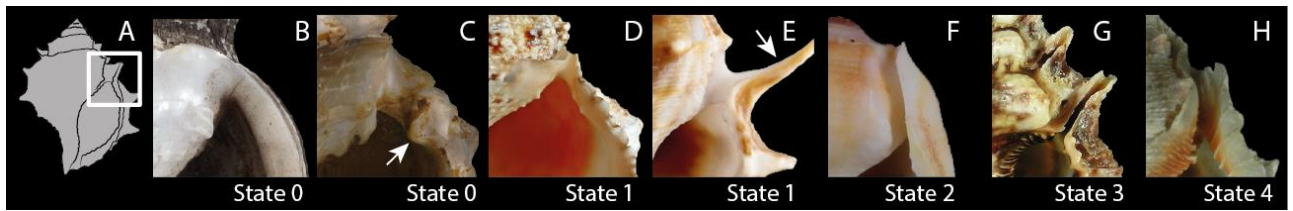


Fig. 5.3 variabilités des encoches anales

Caractère 3 : obturation du canal siphonal antérieur

0 : ouvert, **1** : légèrement fermé (structuré par une lamelle du labre) avec ouverture abaxiale, **2** : pincé, **3** : légèrement fermé (structuré par une lamelle du labre) avec ouverture adaxiale

Caractère 4. Résorption de la protoconque et des premiers tours chez l'adulte (Fig. 4)

0 : conservé, **1** : résorbé

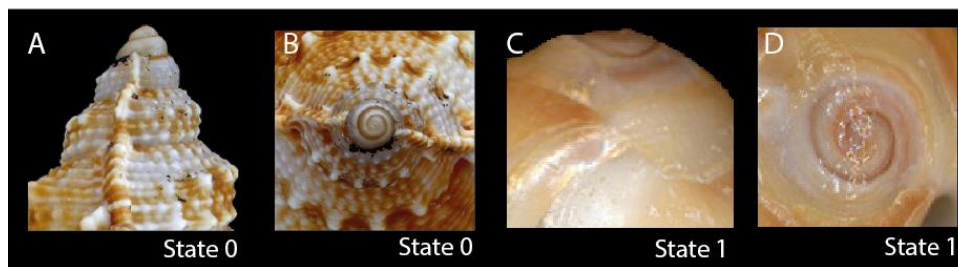


Fig. 5.4 perte des premiers tours.

Caractère 5. Nombre de cordons primaires impliqués dans la partie convexe du tour

0: 5 cordons, **1** : 7 cordons, **2** : 6 cordons, **3** : 8 cordons,

CARACTERES INTRAVARICAUX

P1 ADULTE

Caractère 6. Morphologie des nodosités intervaricales du cordon P1 chez l'adulte (Fig. 5.5)

0 : rond, **1** : pointu, **2** : pincé par des cordons secondaires, **4** : cordon **5**: pincé (pas par des cordons primaires ex *Bursina thersites*)

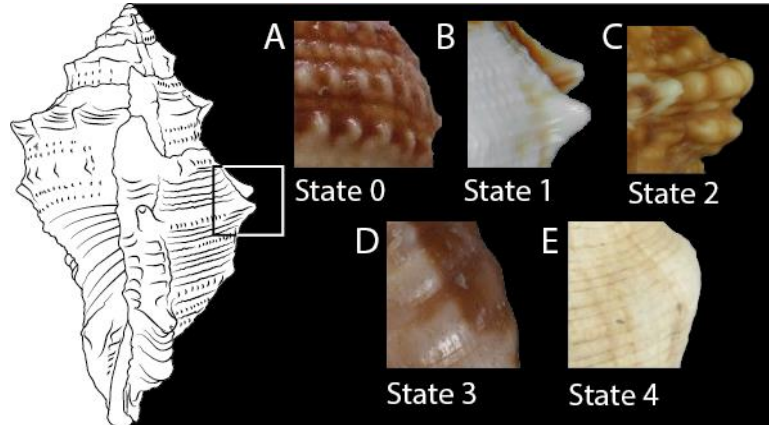


Fig. 5.5 nodosités intervaricales

P2 ADULTE

Caractère 7. Morphologie des nodosités intervaricales du cordon P2 chez l'adulte

0 : rond, **1** : cordon **2** : pas exprimé

P3 ADULTE

Caractère 8. Morphologie des nodosités intervaricales du cordon P3 chez l'adulte

0 : rond, **1** : pointu, **2** : pincé par des cordons secondaires, **3** : cordon **4** : pas exprimé

P4 ADULTE

Caractère 9. Morphologie des nodosités intervaricales du cordon P4 chez l'adulte

0: cordon, **1**: rond, **2** : pas exprimé

P5 ADULTE

Caractère 10. Morphologie des nodosités intervaricales du cordon P5 chez l'adulte

0 : rond, **1** : pointu, **2** : cordon **3** : pas exprimé

P6 ADULTE

Caractère 11. Morphologie des nodosités intervaricales du cordon P6 chez l'adulte

1 : rond, **0**: cordon **2** : pas exprimé

P1 JUVENILE

Caractère 12. Morphologie des nodosités intervaricales du cordon P1 chez le juvénile (tour deux)

0: rond, **2** : pointu, **1**: caréné,

CARACTERES VARICAUX

Caractère 13. Expression de P1 dans l'espace varicale chez l'adulte

0 : Pas exprimé, **1** : pointu, **2** : en cordon, **3** : nodosité, **4** : épine saillante, **5** : pincé

Caractère 14. Expression de P2 dans l'espace varicale chez l'adulte

1 : Pas exprimé, **0** : en cordon,

Caractère 15. Expression de P3 dans l'espace varicale chez l'adulte

0 : Pas exprimé, **1** : pointu, **2** : en cordon, **3** : nodosité, **4** : pincé

Caractère 16. Expression de P4 dans l'espace varicale chez l'adulte

1 : Pas exprimé, **0** : en cordon,

Caractère 17. Expression de P5 dans l'espace varicale chez l'adulte

0 : Pas exprimé, **1** : pointu, **2** : en cordon, **4** : pincé

Caractère 18. Expression de P6 dans l'espace varicale chez l'adulte

0 : Pas exprimé, **1** : pointu, **2** : en cordon.

Caractère 19. Expression relative des ornements varicales entre P1 et P3

0 : semblable, **2** : P1 grand – P2 atrophié – P3 plus grand que P1, **3** : P1 grand – P2 atrophié – P3 plus petit que P1, **1** : P1 grand – P2 atrophié – P3 aussi grand que P1

Caractère 20. Expression relative des ornements varicales entre P3 et P5

0 : semblable, **1** : diminution constante en direction abapicale, **3** : P3 grand – P4 atrophié – P5 plus petit que P3, **4** : P3 grand – P4 atrophié – P5 aussi grand que P3.

Caractère 21. Position de P6 par rapport au canal siphonal.

0 : P8 ou plus borde le canal siphonal, **1** : P6 borde le canal siphonal, **2** : P7 borde le canal siphonal

Caractère 22. Presence d'un cordon sub sutural (SP) dans l'espace intervarical

0 : pas exprimé ; **1** : exprimé

Caractère 23 Expression varicale de SP chez l'adulte

0 : ne s'exprime pas, **1** : provection abaxiale en lamelle, **2** : projection abaxial en épine

DENTICULES INTERNE DU LABRE

Caractère 24. SD

0 : simple, **1** : bifide, **2** : trifide avec bifurcation du denticule adapicale, **3** : trifide avec bifurcation du denticule abapicale.

Caractère 25. ID1

0 : simple, **1** : bifide

Caractère 26. ID2 (ID pour les Bursidae)

0 : simple, **1** : bifide, **2** : trifide avec bifurcation du denticule adapicale, **3** : trifide avec bifurcation du denticule abapicale.

Note : *Marsupina bufo* a 3 denticules formé par des cordons secondaires entre SP et IP

Caractère 27. D1

0 : simple, **1** : bifide, **2** : trifide avec bifurcation du denticule adapicale, **3** : trifide avec bifurcation du denticule abapicale.

Caractère 28. D2

0 : simple, **1** : bifide, **2** : trifide avec bifurcation du denticule adapicale, **3** : trifide avec bifurcation du denticule abapicale.

Caractère 29. D3

0 : simple, **1** : bifide, **2** : trifide avec bifurcation du denticule adapicale, **3** : trifide avec bifurcation du denticule abapicale.

Caractère 30. D4

0 : simple, **1** : bifide, **2** : trifide avec bifurcation du denticule adapicale, **3** : trifide avec bifurcation du denticule abapicale.

Caractère 31. D5

0 : simple, **1** : bifide, **2** : trifide avec bifurcation du denticule adapicale, **3** : trifide avec bifurcation du denticule abapicale.

Caractère 32. D6

0 : simple, **1** : bifide, **2** : trifide avec bifurcation du denticule adapicale, **3** : trifide avec bifurcation du denticule abapicale.

Caractère 33. D7

0 : simple, **1** : bifide, **2** : trifide avec bifurcation du denticule adapicale, **3** : trifide avec bifurcation du denticule abapicale.

AUTRES CARACTERES

Caractère 34. Morphologie de l'ornementation de P1

Voir figure 5.6

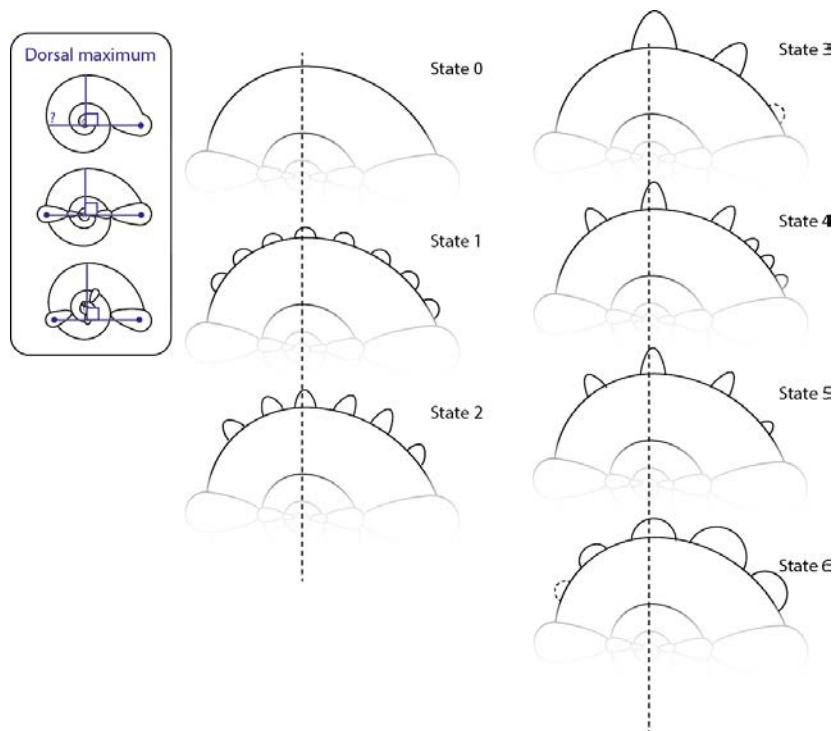


Fig. 5.6 conformation de l'ornementation de P1 chez les Bursidae (en vue apicale)

Caractère 35. Fusion P1, P2 et P3 dans l'intervaricale

0 : non fusioné, **1** : fusioné

Caractère 36. Perte complète de l'ornementation sur le dernier tour

0 : conservé **1** : perdu

Caractère 37. Split de P1

0 : non **1** : oui

Caractère 38. Ornementation secondaire

0 : Pas d'ornementation secondaire **1** : micronodosité, **2** : micronodosité jointive **3** : cordonnet

4 : cordonnet aplatis

Caractère 39. Présence de zébrure sur la columelle

0 : présent, **1** : absent

Matrice de caractère

La matrice de caractère est fournie en annexe 2

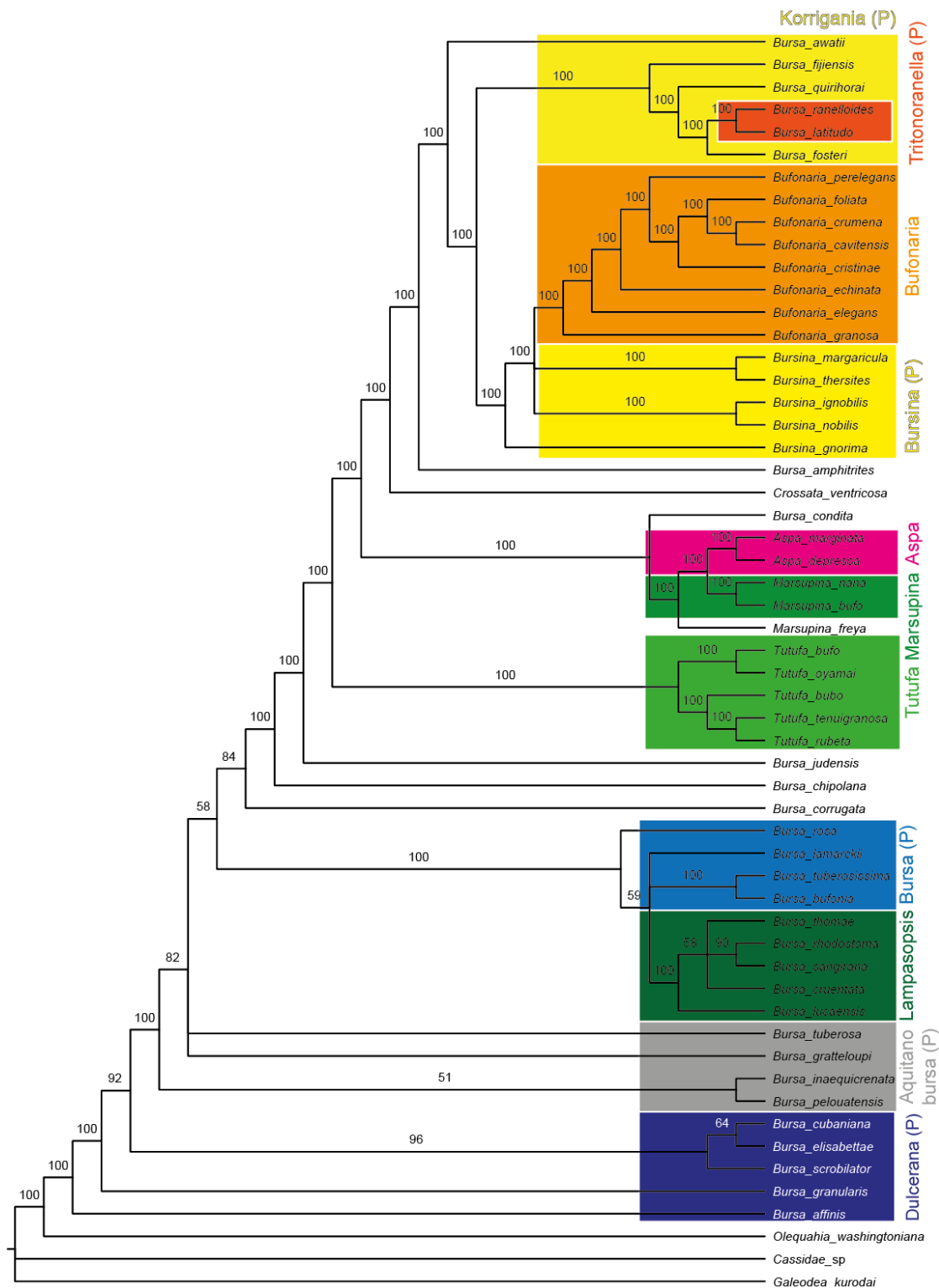


Fig. 5.7 Consensus Majoritaire 50% des 480 arbres de 301 pas de l'analyse heuristique, la valeur des branches indiquent la proportion d'arbre ayant retrouvé cette branche avant le consensus, seules les branches à 100 sont retenu dans le consensus strict ; CI : 0.35 ; RI : 0.71 ; (P) indique les groupes paraphylétiques par rapport à la classification du chapitre 3.

COMPARAISON AVEC L'ARBRE MOLECULAIRE (CHAPITRE 3, ARTICLE 3)

Les groupe (pas nécessairement les clades) sont représentés avec les mêmes couleurs que celles employées dans l'arbre de l'article 3.

L'indice de rétention relativement haut (0.7) semble indiquer que les caractères choisis pour l'analyse sont en adéquation avec l'arbre final mais l'indice de cohérence faible (0.35) semble indiquer quant à lui que l'homoplasie est importante dans l'arbre même si cet indice est difficile à réellement interpréter (Darlu & Tassy, 1993).

Cependant les relations sont très peu résolues. Et peu de relations communes sont retrouvées entre les deux phylogénies.

Parmi tous les genres redéfinis dans les deux derniers chapitres, seuls cinq sont retrouvés monophylétique dans l'analyse.

Il s'agit des genres *Aspa*, *Tutufa*, *Bufonaria Tritonoranella* et *Lampasopsis* et ils ne sont soutenus par aucune synapomorphie exclusive.

Le clade des Bursidae profonds retrouvé dans l'analyse moléculaire est retrouvé ici aussi quoi qu'avec une conformation différente dans ses relations internes

Bursina est retrouvé paraphylétique mais forme un clade avec *Bufonaria*, cela correspond à la définition du genre *Bufonaria* selon Cossignani (1994).

Tutufa chipolana n'est pas retrouvé dans les *Tutufa* actuels

Les *Marsupina* actuels forment un clade mais les taxons fossiles attribués à ce genre (ici *M. judensis*) ne sont pas retrouvé particulièrement proche.

LES LIMITES ET PERSPECTIVES DE L'USAGE DE LA COQUILLE DANS LA PHYLOGENIE DES BURSIDAE

Comme nous l'avons vu il n'y a pas de réconciliation stricte entre les phylogénies moléculaires et morphologiques. Il n'est probablement pas possible en l'état de justifier la calibration de l'âge d'un nœud par un fossile dans une phylogénie moléculaire en se basant sur son emplacement dans la phylogénie en morphologie. Cependant l'utilisation des homologies primaires sérielles nous permet de retrouver certains genres et c'est probablement la force de cette méthode car elle nous force à formaliser les caractères de la coquille et à s'assurer que

l'on parle de la même chose quand on compare des structures chez des Bursidae d'espèces différentes. Cette formalisation a été un outil précieux dans tous les articles de cette thèse.

Annexe 1 : matériel d'étude de la phylogénie morphologique. MNHN : Museum nationale d'Histoire naturelle, IM : collections mollusques, F :collections fossiles, SBMNH : Santa Barbara Museum of natural History

| Taxon | fossil/extant | collection | Taxon | fossil/extant | collection |
|-----------------------------|----------------------|-------------------|----------------------------|----------------------|-------------------|
| <i>Aspa depressa</i> | Fossile | MNHN-F | <i>Bursa latitudo</i> | actuel | MNHN-IM |
| <i>Aspa marginata</i> | actuel | MNHN-F | <i>Bursa lucaensis</i> | actuel | MNHN-IM |
| <i>Bufonaria cavitensis</i> | actuel | MNHN-IM | <i>Bursa pelouatensis</i> | actuel | MNHN-IM |
| <i>Bufonaria cristinae</i> | actuel | MNHN-IM | <i>Bursa quirihorai</i> | actuel | MNHN-IM |
| <i>Bufonaria crumena</i> | actuel | MNHN-IM | <i>Bursa ranelloides</i> | actuel | MNHN-IM |
| <i>Bufonaria echinata</i> | actuel | MNHN-IM | <i>Bursa rhodostoma</i> | actuel | MNHN-IM |
| <i>Bufonaria elegans</i> | actuel | Sanders coll. | <i>Bursa rosa</i> | actuel | MNHN-IM |
| <i>Bufonaria foliata</i> | actuel | MNHN-IM | <i>Bursa sangirana</i> | actuel | sur photo |
| <i>Bufonaria granosa</i> | actuel | MNHN-IM | <i>Bursa scrobilator</i> | actuel | MNHN-IM |
| <i>Bufonaria perelegans</i> | actuel | MNHN-IM | <i>Bursa thomae</i> | actuel | MNHN-IM |
| <i>Bursa affinis</i> | actuel | MNHN-IM | <i>Bursa tuberosa</i> | actuel | MNHN-IM |
| <i>Bursa amphitrites</i> | actuel | MNHN-IM | <i>Bursa tuberosissima</i> | actuel | MNHN-IM |
| <i>Bursa awatii</i> | actuel | MNHN-IM | <i>Bursina gnorima</i> | actuel | MNHN-IM |
| <i>Bursa bufonia</i> | actuel | MNHN-IM | <i>Bursina ignobilis</i> | actuel | MNHN-IM |
| <i>Bursa chipolana</i> | actuel | sur photo | <i>Bursina margaricula</i> | actuel | MNHN-IM |
| <i>Bursa condita</i> | actuel | MNHN-IM | <i>Bursina nobilis</i> | actuel | MNHN-IM |
| <i>Bursa corrugata</i> | actuel | MNHN-IM | <i>Bursina thersites</i> | actuel | MNHN-IM |
| <i>Bursa cruentata</i> | actuel | MNHN-IM | <i>Cassidae sp</i> | actuel | MNHN-IM |
| <i>Bursa cubaniana</i> | actuel | MNHN-IM | <i>Crossata ventricosa</i> | actuel | MNHN-IM |

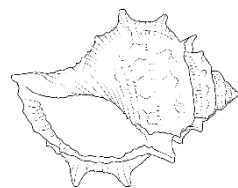
| | | | | | |
|-----------------------------|---------|-----------|---------------------------------|---------|-----------|
| <i>Bursa elisabettae</i> | actuel | MNHN-IM | <i>Galeodea kurodai</i> | actuel | MNHN-IM |
| <i>Bursa fijiensis</i> | actuel | MNHN-IM | <i>Marsupina bufo</i> | actuel | MNHN-IM |
| <i>Bursa fosteri</i> | actuel | MNHN-IM | <i>Marsupina freya</i> | fossile | sur photo |
| <i>Bursa granularis</i> | actuel | MNHN-IM | <i>Marsupina nana</i> | actuel | SBNHM |
| <i>Bursa gratteloupi</i> | Fossile | MNHN-F | <i>Olequahia washingtoniana</i> | fossile | UCMP |
| <i>Bursa inaequicrenata</i> | Fossile | MNHN-F | <i>Tutufa bubo</i> | actuel | MNHN-IM |
| <i>Bursa judensis</i> | fossile | sur photo | <i>Tutufa bufo</i> | actuel | MNHN-IM |
| <i>Bursa lamarckii</i> | actuel | MNHN-IM | <i>Tutufa oyamai</i> | actuel | MNHN-IM |
| <i>Bursa latitudo</i> | actuel | MNHN-IM | <i>Tutufa rubeta</i> | actuel | MNHN-IM |
| <i>Bursa lucaensis</i> | actuel | MNHN-IM | <i>Tutufa tenuigranosa</i> | actuel | MNHN-IM |

Annexe 2 : Matrice taxons caractères

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | |
|---------------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|
| <i>Galeodea kurodai</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>Cassidae sp</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Olequahia washingtoniana</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 3 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | |
| <i>Bursa fijiensis</i> | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 3 | 3 | 2 | 1 | 0 | 0 | 2 | 3 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | |
| <i>Bursa chipolana</i> | 1 | 1 | 3 | ? | 3 | 0 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | ? | 5 | 0 | 0 | 1 | 2 | 0 | 0 | |
| <i>Tutufa bufo</i> | 2 | 3 | 3 | 2 | 3 | 0 | 2 | 2 | 2 | 2 | 0 | 2 | 0 | 5 | 0 | 4 | 0 | 4 | 2 | 3 | 3 | 2 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | 5 | 0 | 0 | 1 | 1 | 0 | 0 | |
| <i>Tutufa bubo</i> | 2 | 3 | 3 | 2 | 3 | 0 | 2 | 2 | 2 | 2 | 0 | 2 | 2 | 5 | 0 | 4 | 0 | 2 | 2 | 3 | 3 | 2 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 6 | 0 | 0 | 1 | 1 | 0 | 0 | |
| <i>Tutufa oyamai</i> | 2 | 3 | 3 | 2 | 3 | 0 | 2 | 2 | 2 | 2 | 0 | 2 | 0 | 5 | 0 | 4 | 0 | 4 | 2 | 3 | 3 | 2 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 5 | 0 | 0 | 1 | 1 | 0 | 0 | |
| <i>Tutufa tenuigranosa</i> | 2 | 3 | 3 | 2 | 3 | 0 | 2 | 2 | 2 | 2 | 0 | 2 | 0 | 5 | 0 | 4 | 0 | 4 | 2 | 3 | 1 | 2 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 6 | 0 | 0 | 0 | 1 | 0 | 0 | |
| <i>Tutufa rubeta</i> | 2 | 3 | 3 | 2 | 3 | 0 | 2 | 2 | 0 | 2 | 0 | 2 | 0 | 5 | 0 | 4 | 0 | 2 | 2 | 3 | 1 | 2 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 6 | 0 | 0 | 1 | 1 | 0 | 0 | |
| <i>Crossata ventricosa</i> | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 3 | 2 | 0 | 1 | 0 | 1 | 0 | 2 | 2 | 3 | 3 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 |
| <i>Bursina gnorima</i> | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 2 | 4 | 2 | 3 | 2 | 2 | 1 | 0 | 2 | 0 | 2 | 2 | 1 | 3 | 2 | 1 | 0 | 1 | 3 | 2 | 1 | 3 | 2 | 1 | 1 | 2 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | |

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|------------------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| <i>Bufo naria perelegans</i> | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 2 | 3 | 4 | 2 | 4 | 2 | 1 | 2 | 2 | 5 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bufo naria echinata</i> | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 0 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 0 | 3 | 2 | 2 | 4 | 2 | 1 | 1 | 2 | 5 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bufo naria foliata</i> | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 3 | 3 | 2 | 1 | 1 | 2 | 4 | 4 | 2 | 2 | 2 | 2 | 2 | 4 | 5 | 0 | 0 | 0 | 3 | 0 | 0 |
| <i>Bufo naria crumena</i> | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 3 | 3 | 2 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 4 | 4 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bufo naria elegans</i> | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 2 | 1 | 1 | 2 | 5 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bufo naria granosa</i> | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 1 | 2 | 2 | 4 | 2 | 1 | 1 | 1 | 2 | 5 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bufo naria cavitensis</i> | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 3 | 3 | 2 | 1 | 1 | 2 | 2 | 4 | 2 | 4 | 4 | 2 | 2 | 2 | 4 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bursina margaricula</i> | 1 | 3 | 1 | 1 | 1 | 0 | 5 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 1 | 3 | 2 | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 5 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Bursina thersites</i> | 1 | 3 | 1 | 1 | 1 | 0 | 5 | 2 | 1 | 2 | 3 | 2 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 1 | 3 | 2 | 1 | 0 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 5 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bufo naria cristinae</i> | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 2 | 3 | 2 | 1 | 2 | 3 | 4 | 4 | 2 | 4 | 2 | 1 | 2 | 2 | 5 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bursa cubaniana</i> | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 2 | 0 | 2 | 3 | 2 | 0 | 2 | 1 | 2 | 1 | 2 | 2 | 2 | 3 | 1 | 0 | 0 | 0 | 2 | 4 | 2 | 4 | 2 | 2 | 4 | ? | 7 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Bursa elisabettae</i> | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 1 | 2 | 1 | 2 | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 2 | 1 | 2 | 2 | 2 | 1 | 2 | ? | 7 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Bursa granularis</i> | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 2 | 3 | 1 | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | ? | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Bursa affinis</i> | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 2 | 2 | 3 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Bursa scrobilator</i> | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 1 | 0 | 3 | 1 | 3 | 1 | 2 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 2 | 2 | 2 | 2 | 1 | 3 | 4 | ? | 7 | 1 | 0 | 0 | 2 | 0 | 0 |
| <i>Bursa quirihorai</i> | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 3 | 3 | 2 | 1 | 0 | 0 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 5 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Bursa condita</i> | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 4 | 2 | 3 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 1 | 4 | 4 | 2 | 1 | 2 | 4 | 2 | 4 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bursa ranelloides</i> | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 3 | 3 | 2 | 1 | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 1 |
| <i>Bursa latitudo</i> | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 3 | 3 | 2 | 1 | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 1 |
| <i>Bursa lamarckii</i> | 1 | 4 | 2 | 4 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | ? | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 3 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | ? | 3 | 1 | 0 | 1 | 1 | 0 | 0 |
| <i>Bursa tuberosissima</i> | 1 | 4 | 2 | 4 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 2 | 0 | 2 | 1 | 2 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | ? | 3 | 1 | 0 | 1 | 1 | 0 | 0 |
| <i>Bursa bufonia</i> | 1 | 4 | 2 | 4 | 2 | 0 | 1 | 2 | 0 | 2 | 0 | 2 | ? | 2 | 1 | 2 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | ? | 5 | 1 | 0 | 1 | 1 | 0 | 0 |
| <i>Bursa rosa</i> | 1 | 4 | 2 | 4 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | ? | 2 | 0 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | ? | 5 | 1 | 0 | 1 | 1 | 0 | 0 |
| <i>Bursina ignobilis</i> | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 3 | 2 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 3 | 5 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bursina nobilis</i> | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 3 | 2 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 3 | 5 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bursa fosteri</i> | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 3 | 3 | 2 | 1 | 0 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 7 | 0 | 0 | 0 | 1 | 1 | 1 |
| <i>Bursa awatii</i> | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 3 | 2 | 0 | 1 | 0 | 1 | 0 | 2 | 2 | 3 | 3 | 2 | 1 | 0 | 0 | 2 | 1 | 1 | 2 | 4 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Bursa thomae</i> | 1 | 3 | 1 | 2 | 1 | 0 | 0 | 2 | 0 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 1 | 2 | ? | 1 | 3 | 2 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 3 | 1 | 0 | 1 | 1 | 0 | 0 |
| <i>Bursa rhodostoma</i> | 1 | 3 | 1 | 2 | 1 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 3 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 8 | 1 | 0 | 1 | 1 | 0 | 0 |

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|-----------------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| <i>Bursa cruentata</i> | 1 | 3 | 1 | 2 | 1 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 3 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 8 | 1 | 0 | 1 | 1 | 0 | 0 |
| <i>Bursa lucaensis</i> | 1 | 3 | 1 | 2 | 1 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 2 | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 2 | 1 | 1 | 2 | 2 | 1 | 2 | 0 | 8 | 1 | 0 | 1 | 1 | 0 | 0 | |
| <i>Bursa corrugata</i> | 2 | 1 | 2 | 1 | 2 | 1 | 0 | 2 | 4 | 2 | 3 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 5 | 0 | 1 | 1 | 0 | 0 | 0 | |
| <i>Aspa marginata</i> | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 4 | 2 | 3 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | |
| <i>Aspa depressa</i> | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 4 | 2 | 3 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | |
| <i>Bursa inaequicrenata</i> | 1 | 1 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | ? | 8 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>Bursa pelouatensis</i> | 2 | 1 | 2 | 1 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 3 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | ? | 1 | 0 | 0 | 0 | 1 | 0 | 0 | |
| <i>Bursa tuberosa</i> | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 2 | 3 | 2 | 2 | 2 | 1 | 2 | 0 | 2 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | ? | 5 | 0 | 0 | 0 | 1 | 0 | 0 | |
| <i>Bursa gratteloupi</i> | 1 | 1 | 2 | 1 | 2 | ? | 1 | 2 | 3 | 2 | 2 | 0 | 1 | ? | 1 | ? | 1 | ? | 2 | 1 | 3 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | ? | 5 | 0 | 0 | 0 | 3 | 0 | 0 | |
| <i>Bursa amphitrites</i> | 2 | 1 | 2 | ? | 2 | 0 | 1 | 2 | 0 | 2 | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | ? | 2 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | |
| <i>Bursa sangirana</i> | 1 | 1 | 1 | ? | 1 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | 2 | 1 | 2 | 1 | 2 | ? | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | ? | 8 | 1 | 0 | 1 | 1 | 0 | 0 | |
| <i>Marsupina freya</i> | 1 | 1 | 1 | 1 | 1 | ? | 0 | 2 | 4 | 2 | 3 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 3 | 0 | 0 |
| <i>Bursa judensis</i> | 1 | 1 | 3 | 1 | 3 | 0 | 0 | 2 | 4 | 2 | 3 | 2 | 1 | 0 | 0 | 2 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 4 | ? | 5 | 0 | 0 | 1 | 1 | 0 | 0 | |
| <i>Marsupina nana</i> | 1 | 1 | 3 | 1 | 3 | 0 | 1 | 2 | 4 | 2 | 3 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 1 | 0 | 2 | ? | 0 | 0 | 2 | 2 | 1 | 2 | 1 | 2 | 2 | 2 | ? | 0 | 1 | 0 | 0 | 0 | 0 | |
| <i>Marsupina bufo</i> | 1 | 1 | 3 | 1 | 3 | 0 | 1 | 2 | 4 | 2 | 3 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | |



CONCLUSION

VERS UN RETOUR DU DIALOGUE.

Apports

L'analyse taxonomique de la famille des Bursidae aura non seulement permis de proposer une nouvelle classification via l'apport de nouvelles hypothèses phylogénétiques et de délimitation d'espèces, mais elle aura surtout été l'occasion de tester notre capacité à utiliser les données actuelles (moléculaires principalement) et fossiles de manière cohérente et intégrative pour retracer le patron de diversification de ce groupe au cours de Cénozoïque. Cette approche pluridisciplinaire nous a permis d'avoir un regard critique sur nos résultats, et je propose ci-dessous plusieurs exemples, tirés des résultats de ma thèse présentés en détail dans les chapitres précédents, illustrant ce dialogue entre approches morphologiques et moléculaires et entre études des taxons fossiles et récents.

L'exemple de *Bursa chipolana* Schmelz, 1997 (maintenant placé dans *Tutufa*) est un bel exemple où la taxonomie des fossiles a été éclairée par la phylogénie moléculaire. Sans elle il aurait probablement été classé dans le genre *Lampasopsis* « faute de mieux », car il s'agit du seul genre qui lui ressemblait vaguement dans la région de sa découverte, faisant de *Lampasopsis* le nouveau groupe « poubelle » des Bursidae. C'est avec le rapprochement, dans la phylogénie moléculaire, des genres morphologiquement très différents *Tutufa* et *Marsupina* (Article 3) qu'on a pu faire le lien entre ce fossile américain et le genre *Tutufa* : ces deux genres sont les seules à posséder huit cordons primaires dans la partie convexe de leur tour ce qui est le cas de *B. chipolana*. Cette similarité morphologique serait passée inaperçue sans la phylogénie moléculaire, d'autant plus que le genre *Tutufa* est absent de la région Caribéenne.

Un exemple de cas où le registre fossile nous a permis de soutenir une relation de parenté révélée par l'approche moléculaire est la position externe des genres *Aspa* et *Talisman*, en groupe frère de tous les autres Bursidae. Dans l'arbre phylogénétique moléculaire (article 3), les soutiens statistiques appuyant la position de ces deux genres est très faible ; cependant ils sont les seules genres actuelles dont le registre fossile remonte indiscutablement jusqu'au début du Miocène, une observation en accord avec une divergence ancienne de ce groupe par rapport aux autres Bursidae.

De façon plus générale, la réinterprétation des caractères morphologiques grâce aux approches moléculaires, et le renforcement des hypothèses moléculaires par l'analyse formalisée des caractères morphologiques, et en particulier chez les fossiles, comme illustrés par les quelques exemples ci-dessus, ont permis de proposer une révision complète de toutes

les espèces fossiles et récentes de Bursidae (Articles 1 et 4 surtout), résultat qui n'aurait pas été possible sans l'intégration de ces deux disciplines que sont la paléontologie et la systématique moléculaire.

Limites et perspective d'amélioration

Des études récentes (Ronquist et al. 2012, Heath et al. 2014, Davesne et al. 2015) indiquent clairement que l'ajout de fossiles dans les phylogénies a une influence positive sur leur résolution. Malheureusement l'obtention de phylogénies résolues basées uniquement sur des caractères de la coquille reste encore un défi pour les malacologues, même avec de très haut standard d'hypothèse d'homologie primaire. Malgré l'effort réalisé pendant cette thèse pour intégrer approches morphologiques et moléculaires, certains caractères morphologiques restent difficiles à interpréter, et l'allocation de certaines espèces fossiles et récentes (non intégrées dans la phylogénie moléculaire) à un genre reste discutable. Nous sommes donc dépendants de l'émergence de nouvelles méthodes ou de l'amélioration de celles existantes aujourd'hui pour retracer les relations de parenté sur les caractères de la coquille (le traitement en vraisemblance de Bardin et al. 2017 pour reconstruire la phylogénie d'une famille d'ammonites Jurassique est prometteuse bien que pas directement transposable aux gastéropodes). Les coquilles en tant qu'objet ont toujours suscité l'intérêt des scientifiques et des méthodes mathématiques puissantes ont été adaptées pour les décrire, que ce soit par des approches de morphométrie inspirées du model de Raup (Chirat et al.2010, Chirat et al. 2013, Gerber, 2016) ou via des modèles de morphogenèse de Turing (déclencheurs inhibiteurs, Meinhardt, 2009). Cependant ces études s'intéressent peu ou pas aux questions d'homologie.

Malgré la taille de notre jeu de données, recouvrant une grande partie de la diversité de la famille, un relativement grand nombre de marqueur, et un grand nombre de point de calibration par des fossiles (un des plus grand employé chez les mollusques), une forte incertitude demeure quant aux soutient des relations de parenté et de l'âges de diversification des clades, et ce même malgré la grande attention qu'il a été apporté au choix des points de calibration (articles 1, 2). Cela nous amène à nous demander quelle est la valeur des phylogénies datées uniquement par un seul nœud et dont l'attribution au clade relève en partie de l'argument d'autorité. La plupart des phylogénies datées de mollusques disponibles (et elles ne sont pas légion) se basent sur un nombre faible (entre 1 et 3) de fossiles, dont le statut taxonomique et l'âge n'ont pas été vérifié et éventuellement corrigé, comme nous l'avons fait pour les Bursidae,

mais seulement repris de la littérature (parfois assez ancienne) (Conidae, ...). C'est pour limiter ce genre de biais qu'en 2014 fut créée la *Fossil calibration database*, mais à ce jour il n'y a aucune calibration pour les mollusques dans cette base.

Les méthodes de datation des arbres avec les fossiles sont probablement un des domaines les plus actifs de la biologie évolutive moderne et certaines limites auquel j'ai été confronté au cours de ma thèse sont en train de tomber. Notamment le traitement des répartitions stratigraphiques non plus traitées comme un manque de précision (traiter avec une fonction de distribution uniforme dans l'article 3) mais comme une donnée sur la structure de l'horloge moléculaire et de la topologie de l'arbre (Stadler et al. 2017) on peut par ce même moyen traiter des arbres non entièrement dichotomique (gestion des anagenèses). On arrive maintenant à utiliser conjointement plusieurs types d'horloge dans plusieurs régions de l'arbre pour s'affranchir des biais des horloges relaxées (Lartillot et al. 2016). Nul doute que l'implémentation prochaine de ses méthodes dans des logiciels tel que BEAST2 (Bouckaert et al. 2014) et leur emploi sur des jeux de donnée toujours plus grand risque de remettre en question certaines hypothèses évolutives formulées lors de la dernière décennie.

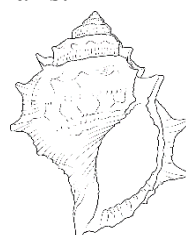
Pour ce qui est de l'amélioration des jeux de données moléculaires en général, il est souvent recommandé, quasiment comme une litanie, d'augmenter le nombre de taxons et d'augmenter le nombre de caractères. Pour ce qui est de notre jeu de données il n'est pas certain que ce soit nécessaire, comme argumenté dans l'article 3. Ajouter quelques espèces dans certaines régions sous-échantillonnées de l'arbre, comme les *Bufo naria*, ou pas du tout, comme les *Crossata*, serait effectivement intéressant car cela augmenterait la représentativité des données et la résolution des arbre (Nabhan & Sarka 2012), mais rajouter des spécimens de genres bien représentés (comme *Bursa* ou *Tutufa* par exemple) n'apporteraient que peu de chose (si ce n'est de confirmer l'allocation générique de ces espèces, qui comme nous l'avons vu plutôt reste incertaine sur la base des caractères morphologiques seuls). Cependant, pour ce qui est de la quantité de caractères, je doute qu'il faille changer d'échelle. Les mitogénomes semblent en effet fournir une quantité et qualité d'information suffisante, mais trop peu de mitogénomes ont été obtenus dans le cadre de cette thèse pour espérer résoudre l'ensemble des relations phylogénétiques au sein des Bursidae. Plutôt que d'ajouter de nouveaux caractères, je propose que diminuer la quantité de données manquantes, par l'obtention du mitogénome d'au moins un représentant de chaque genre nouvellement défini, Cela devrait permettre de résoudre la phylogénie de ce groupe.

L'arbre qui cache la forêt

Le systématicien classe le vivant, et obtenir un arbre totalement résolu et la classification qui en découle pourrait en théorie le satisfaire pleinement. Mais aujourd'hui à la suite d'avancées dans les techniques analytiques, les arbres phylogénétiques ne constituent plus une finalité, mais également un outil privilégié pour répondre à un nombre important de questions scientifiques lié à l'évolution du taxon considéré. Cela s'observe dans les politiques éditoriales de certaines revues comme *Molecular Phylogenetics and Evolution*, dont la plupart des phylogénies moléculaires publiées s'accompagnent maintenant d'une reconstruction d'un arbre daté, associé par exemple à un scénario biogéographique ou à la reconstruction d'états de caractères ancestraux.

D'un point de vue méthodologique, un grand nombre de méthodes nécessitent en amont l'obtention d'un arbre phylogénétique ultramétrique (calibré ou non). En dresser la liste complète n'est pas l'objectif ici, mais citons par exemple l'analyse des taux d'évolution des caractères (Rabosky et al 2012, Rabosky et al 2014), la reconstruction d'aire (biogéographiques) ancestrales (Yu et al. 2012), L'estimation les taux de spéciation, extinction, et fossilisation (Didier et al. 2015), ou encore les relations entre spéciation et évolution moléculaire (Ezard et al. 2013).

Toutes ses approches impliquent la collaboration entre diverses communautés scientifiques dont le premier maillon est le systématicien ; c'est lui qui fournit l'information taxinomique nécessaire à toutes ces analyses qui utilisent en particulier des arbres phylogénétiques. Cette première étape du processus étant maintenant, si ce n'est totalement abouti, en tout cas bien entamée, nous pouvons maintenant envisager d'utiliser les conclusions taxonomiques issues de ma thèse pour répondre à des questions liées à l'évolution des Bursidae. L'analyse des âges des nœuds de l'arbre présentée dans l'article 3 en est un premier exemple, mais il reste encore beaucoup d'inconnues, et si je devais ne citer qu'un exemple, je m'attaquerai à la comparaison des taux de spéciation et d'extinction estimés à partir des arbres phylogénétiques et, indépendamment, à partir du registre fossile, projet que je compte mener à bien au cours de mon année d'attaché temporaire d'enseignement et de recherche (A.T.E.R.) au Muséum national d'histoire naturelle à Paris.



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