THE EVOLUTION OF CANALICULATE RUDISTS IN THE LIGHT OF A NEW CANALICULATE POLYCONITID RUDIST FROM THE ALBIAN OF THE CENTRAL PACIFIC

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Abstract: A new polyconitid rudist, *Magallanesia canaliculata* gen. et sp. nov., of probably late Albian age, is described from the Pulangbato area, central Cebu Island, the Philippines in the western Central Pacific and Takuyo-Daini Seamount, now located in the Northwest Pacific. It is similar to *Praecaprotina* Yabe and Nagao, 1926, a Japanese–Central Pacific endemic genus of late Aptian – early Albian age, but differs in having canals that developed by partitioning of the large ectomyophoral cavity in the posterior part of the left valve. Its discovery strengthens the evidence for Pacific endemism in Albian times. Several other clades of canaliculate rudists flourished or evolved at the same time in different regions of the Tethyan Realm, suggesting the presence of common global biological and/or environmental factors stimulating the evolution of the canals despite such endemism. Furthermore, the finding of a canaliculate polyconitid provides evidence in favour of the evolutionary hypothesis of a polyconitid origin for the Late Cretaceous canaliculate rudist family Plagioptychidae Douvillé, 1888.

Key words: Polyconitidae, Plagioptychidae, *Magallanesia* gen. nov., pallial canals, Cebu Island, Takuyo-Daini Seamount.

SPATIO-TEMPORAL change in the distribution of rudists and other Tethyan biota provides clues for reconstruction of the palaeobiogeographical and palaeoclimatic history of the Cretaceous Pacific (Iba and Sano 2007, 2008; Iba *et al.* 2011*a*, *c*). Recently, Masse and Shiba (2010) proposed the presence of a Japanese – Western Pacific Province in the Aptian–Albian based on endemic rudists, such as the two species of the polyconitid genus *Praecaprotina* Yabe and Nagao, 1926: one, *P. kashimae* Masse and Shiba, 2010 known only from Daiichi-Kashima Guyot, probably located in the Central Pacific during the mid-Cretaceous, and the other, the type species *P. yaegashii* (Yehara 1920), from Japan. That conclusion was further reinforced by the recognition of three more, as yet unnamed Albian polyconitid taxa from the Japanese Seamounts and Cebu Island in the Philippines by Skelton *et al.* (2013). The endemism of the Tethyan biota and related palaeoceanographical conditions of the North to Central Pacific during the Albian are thus important considerations for future research on Cretaceous palaeobiogeography and palaeoclimatology.

The present article formally names and describes the first of the new taxa ('Polyconitid new taxon 1') recognized by Skelton *et al.* (2013) and discusses its particular implications for rudist phylogeny and palaeobiogeography. Formal descriptions of the other new taxa will follow in a later publication. The presence of a canaliculate rudist in Cebu Island in the Philippines was first reported by Wolcke and Scholz (1988). They considered this rudist to be an early Aptian ?*Amphitriscoelus* sp., and discussed its palaeobiogeographical significance. Later, Masse *et al.* (1996) revised its age to late Albian, based on the accompanying orbitolinid foraminifers and calcareous algae, and mentioned a questionable similarity of the Cebu rudist to the genus *Pachytraga* Paquier, 1900, to which another Japanese form, '*Pachytraga*' *japonica* Okubo in Okubo and

Matsushima, 1959, had previously also been referred. However, the latter species was subsequently re-assigned to the late Aptian – early Albian *Praecaprotina* (Skelton and Masse 1998). Meanwhile, further systematic and palaeobiogeographical studies of the Cebu rudist awaited completion.

GEOLOGICAL SETTING

The current Philippine Archipelago was located in the western equatorial Pacific during the Cretaceous Period (Honza and Fujioka 2004). Shallow marine carbonate sediments of the island arc system have been reported in the islands of Cebu and Catanduanes, and in the Caramoan Peninsula of Luzon Island by previous studies (Wolcke and Scholz, 1988; Militante-Matias 1995; Masse *et al.* 1996). Besides late Aptian orbitolinid assemblages from north-western Cebu and the Caramoan Peninsula (Militante-Matias 1995), a rudist '*Pachytraga*?' (= *Magallanesia canaliculata* gen. et sp. nov., herein), corals, stromatoporoids, calcareous red algae and orbitolinid foraminifers have also been reported from the Upper Albian of central Cebu Island (Masse *et al.* 1996).

In a collaborative palaeontological research project of the National Museum of Nature and Science, Tokyo, and the Mines and Geosciences Bureau, Philippines, the exact locality of the rudist-bearing limestone in Cebu Island was identified, allowing two of us (YI and SS) to collect additional rudist material from reddish tuffaceous limestones there. The rudist specimens described herein were recovered from carbonate sediments exposed along the Butuanon River in the Pulangbato area, central Cebu Island (N: 10°23.916′, E: 123°53.684′; Fig. 1), which is probably the same as, or very close to, the locality reported by Masse *et al.* (1996). The carbonate unit, 9.7 m thick, is intercalated in a volcaniclastic sequence at this locality and cannot be considered as an olistolith in the melange-type sequence. It contains abundant rudist individuals (mainly a few genera of polyconitids, but also a requieniid), corals, stromatoporoids and orbitolinid foraminifers with volcaniclastics in its matrix. They represent autochthonous occurrences and probably form a biostrome in the volcaniclastic sequence. Rudists are especially abundant in the lower part of the carbonate sequence. Late Albian orbitolinid foraminifers of the *Mesorbitolina texana* (Roemer, 1849) group and *Neorbitolinopsis conulus* (Douvillé, 1912) were reported from this carbonate unit by Masse *et al.* (1996).

In addition, another specimen of the same taxon was discovered among samples dredged from Takuyo-Daini Seamount in the Japanese Seamounts, now located in the Northwest Pacific, but situated in the central equatorial Pacific at the time of formation (Skelton *et al.* 2013). The age of the rudist-bearing limestone of Takuyo-Daini Sea-
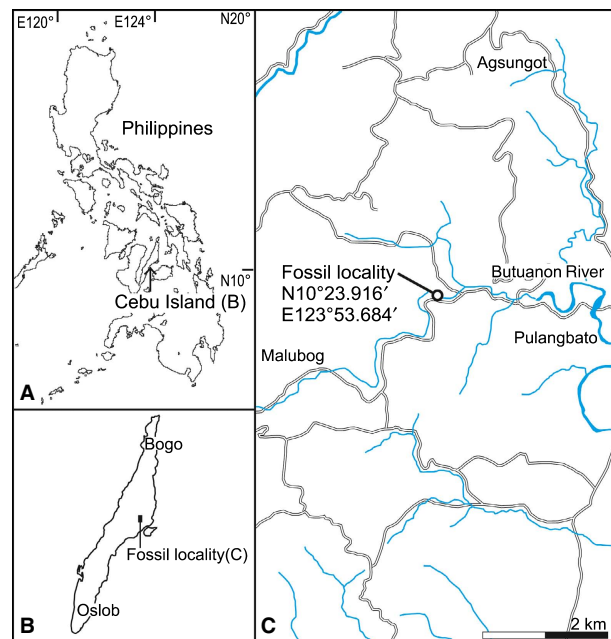

FIG. 1. Locality map for *Magallanesia canaliculata* gen. et sp. nov. in the Pulangbato area, central Cebu Island, the Philippines. Base map is 'Cebu City (Philippine Topographic Map Series Scale 1:50,000, 3721-I)' published by National Mapping and Resource Information Authority, Philippines.

mount is broadly assigned to the Aptian–Albian, according to the age of the shallow marine limestones from nearby Takuyo-Daisan Seamount (Arnaud-Vanneau and Premoli-Silva 1995).

RESULTS AND DISCUSSION

Investigation of collected samples and field photographs reveals that the Cebu rudist, *Magallanesia canaliculata* gen. et sp. nov., here described, is indeed a polyconitid rudist, similar to *Praecaprotina* (most particularly, *P. yaegashii*) but differing in having canals developed by partitioning of the posterior ectomyophoral cavity of the left valve (see Systematic Palaeontology section). In addition, a single specimen of the same taxon from Takuyo-Daini Seamount (Guyot) in the Japanese Seamounts, now located in the Northwest Pacific, was also discovered among dredged Pacific rudist samples in the Masse/Winterer collection of Scripps Institution of Oceanography (SIO), Université de Provence, Marseille, France (M/W coll.; see Systematic Palaeontology section).

Origin of the Cebu caniculate rudist

Magallanesia canaliculata gen. et sp. nov. lacks canals in the ventral shell wall, representing a primitive stage of

canal development by analogy with other canaliculate taxa. Thus, *M. canaliculata* itself probably originated from a noncanaliculate taxon. Besides its canals, the diagnostic characters of *M. canaliculata* are: (1) subequal teeth in left valve (LV) straddling a straight, erect central tooth in right valve (RV); (2) posterior myophoral plate in LV, flanked behind by an ectomyophoral cavity, projecting into a broad posterior cavity in the RV, where it faces inwards onto an erect (steeply backwardly tilted) posterior myophoral wall in the latter valve; and (3) the moderately thickened outer shell layer of the RV. The first of these last three features is characteristic of all Polyconitidae, while the other two are typical of advanced forms, including *Praecaprotina* (Fig. 2), described from late Aptian deposits in Tohoku and Hokkaido areas in Japan (*P. yaegashii*: Yabe and Nagao 1926; Skelton and Masse 1998; Skelton and Smith 2000; Skelton *et al.* 2013) and late Aptian – early Albian limestone of Daiichi-Kashima Seamount (*P. kashimae*). It is worth noting, in passing, that characters 1 and 2 above, relating to the dentition and the posterior myophore, respectively, are also recognized in polyconitid new taxa 2 and 3 of Skelton *et al.* (2013), who supposed that these co-provincial taxa were likewise derived from *Praecaprotina* (though, their possession of character 3 has yet to be verified, as the outer shell layer is not preserved in the investigated specimens). In *Magallanesia* gen. nov., the addition of a number of thin radial partitions in the broad ectomyophoral cavity of the LV gave rise to the single row of large, simple canals there. Thus, it can be interpreted as a derivative of *Praecaprotina*, most probably *P. yaegashii*, with which it shows the greater similarity in external shell form and size (compare Figs 2, 4), indicating that the latter gave rise to

a distinct lineage of canaliculate rudists, probably endemic in the Pacific in the late Albian.

It should be noted that an analogous mode of canal development, namely achieved by the subdivision of large ectomyophoral cavities, has already been proposed for *Neocaprina* of the Caprinulidae Yanin, 1990 by Steuber and Bachmann (2002, p. 745), who noted that 'in *Neocaprina* from Sinai, the shells are delicate, and canals are large and frequently of subrectangular shape. This suggests that the large posterior canals in the LV of *Neocaprina* are formed by the subdivision of large ectomyophoral cavities, and that the LV posterior myophore was not rooted directly on the posterior shell wall, as has been shown for the Caprininae'. A similar mode of canal formation in spaces external to the myophores can again be seen among certain Late Cretaceous radiolitids with a domed LV, such as *Colveraia* Klinghardt, 1921. Hence, partitioning of ectomyophoral cavities of various kinds can be considered as a frequently repeated (homeomorphic) developmental pathway towards the evolution of pallial canals in rudists.

The cladogram shown in Figure 3 (see Appendix and Sano *et al.* (2014) for character analysis) summarizes the phylogenetic position of *Magallanesia* gen. nov. within the polyconitid clade, as proposed here, based on the characters discussed above, together with selected representatives of other canaliculate groups for comparison. As already established in the analysis of Skelton and Smith (2000), the caprinoid clade is shown here to be clearly distinct from the main radiolitoid clade, which encompasses the remaining uncoiled rudists including the polyconitids and their derivatives (Skelton 2013). In the present analysis, two most parsimonious trees (of 29
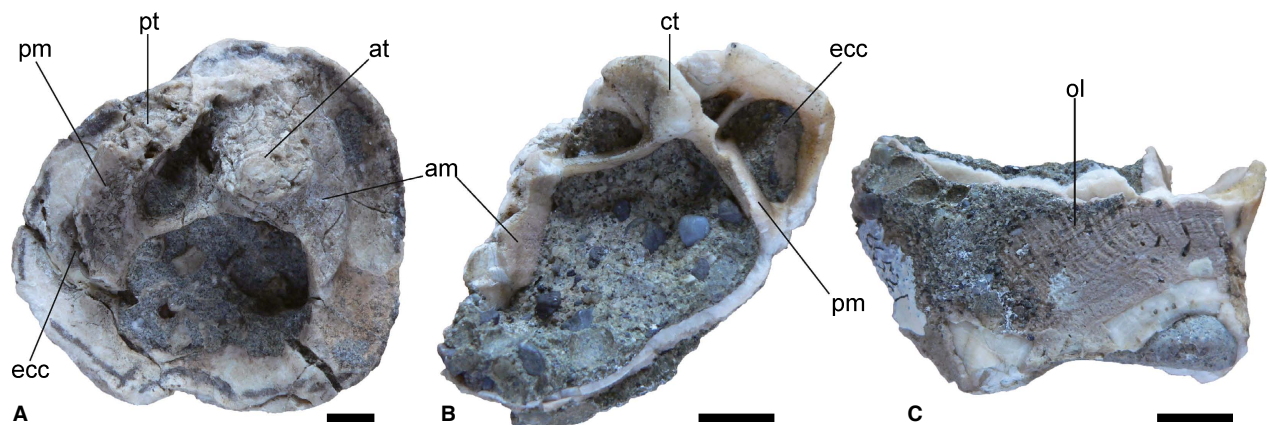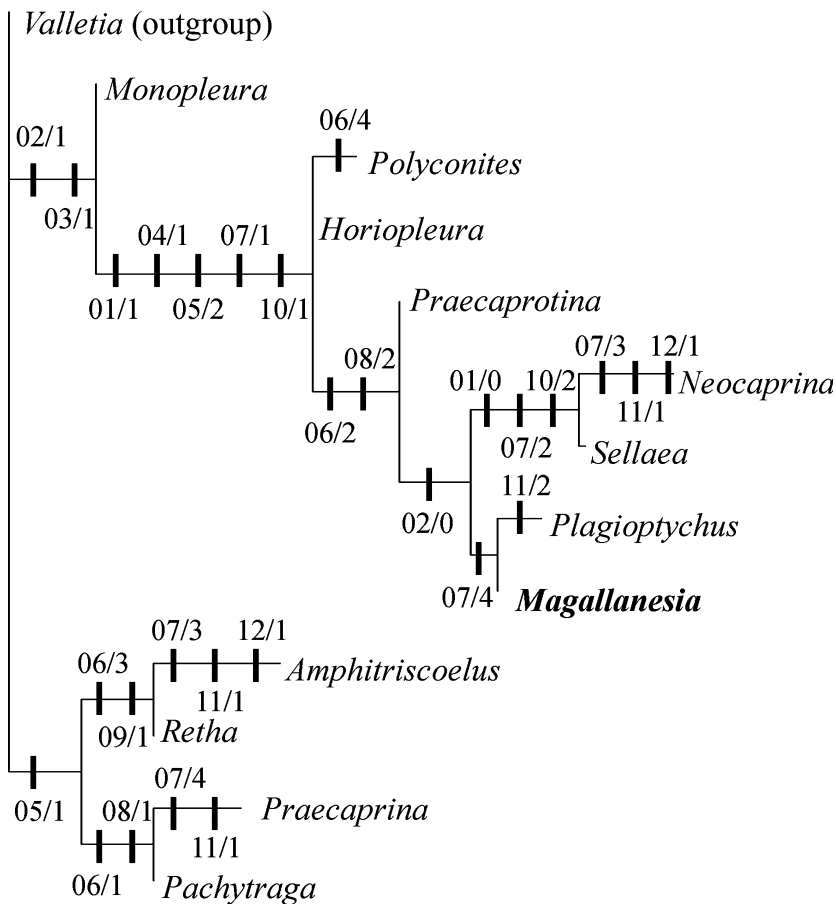

FIG. 2. *Praecaprotina yaegashii* (Yehara, 1920) from upper Aptian part of the Miyako Group in the Tanohata area, Iwate Prefecture, Northeast Honshu, Japan (collections of Institute of Geology and Palaeontology, Tohoku University, Sendai, Japan). A, left valve (IGPS 35442, 'near Hiraiga?'), internal view. B–C, right valve (IGPS 66521, northern beach cliff at Haipe); B, internal view; C, ventral view, showing partially preserved outer shell layer (ol). *Abbreviations*: am, anterior myophore; at, anterior tooth; bc, body cavity; ct, central tooth; cts, central tooth socket; ecc, ectomyophoral cavity; l, ligament; *LV*, left valve; pm, posterior myophore; pt, posterior tooth; ol, outer shell layer; RV, right valve. Scale bars represent 10 mm.

FIG. 3. Cladogram of selected rudist taxa showing inferred phylogenetic relationships of *Magallanesia canaliculata* gen. et sp. nov., and of other selected caniculate forms: preferred one of two most parsimonious trees of 29 steps produced by the PARS program of the PHYLIP package (Felsenstein 2005), version 3.65, with the following settings: number of trees saved, 1 000 000; input order randomized; outgroup, *Valletia tombecki* Munier-Chalmas, 1873; characters unweighted. Bars on branches represent implied character state transformations (see Appendix and Sano et al. (2014) for character data).

steps) were found, differing only slightly with respect to the position of the caprinulid pairing of *Sellaea* Di Stefano, 1889 and *Neocaprina*. The preferred option shown here designates the latter pairing as, itself, a sister group to another combining *Magallanesia* gen. nov. and *Plagioptychus* Matheron, 1842. The alternative tree, by contrast, identifies the former pairing as one branch of an unresolved trichotomy with the last two taxa, united by possession of posterior ectomyophoral canals but thereby involving the secondary loss of the radial partitions in *Sellaea*, which we regard as unlikely. Thus, the caprinulids, according to this analysis, may possibly constitute another stock of caniculate rudists derived from *Praecaprotina* or some allied form (with secondary thinning of the outer shell layer). Inclusion of *Himeraelites* Di Stefano, 1889 in the phylogenetic analysis, however, calls for a re-appraisal of the previously assumed kinship between *Himeraelites* and the *Sellaea–Neocaprina* lineage, both of which were included in the Caprinulidae (Skelton 2013). It yields a number of equally parsimonious trees some of which do group *Himeraelites* with *Sellaea* and *Neocaprina*, while others separate it from them – an ambiguity that must be addressed in a later publication. What is nevertheless reasonably clear from the present analysis is the independent evolution of pallial canals in the three canali-

culate clades (*Magallanesia* gen. nov., the caprinulids and the caprinoids) considered here.

Late Albian global diversification of caniculate rudists

In the late Albian, several caniculate taxa belonging to different lineages flourished or evolved in different regions, including: (1) several genera of the Caprinuloideidae Damestoy, 1971 in the Caribbean (Scott and Filkorn 2007; Mitchell 2013a) and possibly Central Pacific (Swinburne and Masse 1995); (2) *Caprina choffati* Douvillé, 1898 and *Caprina mulleri* Hamilton, 1956 of the Caprinidae d'Orbigny, 1847 in the western Mediterranean Tethys and Central Pacific, respectively (Douvillé 1898; Hamilton 1956; Chikhi-Aouimeur 2003; Skelton et al. 2011, 2013); (3) *Neocaprina raghawiensis* Steuber and Bachmann, 2002 and *N.?* sp. of the Caprinulidae, and probably *Ichthyosarcolites* Desmarest, 1817 of the Ichthyosarcolitidae Douvillé, 1887 in Egypt, in the Middle Eastern Tethyan Province (Steuber and Bachmann 2002), the latter family having already arisen in the Caribbean by the mid-Albian (Mitchell 2013b); and (4) *M. canaliculata* gen. et sp. nov. of the Polyconitidae in the Central Pacific. The presence of different caniculate rudists in each

region reflects the development of rudist endemism within the Tethyan Realm at that time. On the other hand, it should be noted that at least three lineages of canaliculate rudists existed in the Central Pacific in the late Albian, highlighting the importance of the region for rudist diversification in the mid-Cretaceous.

Neocaprina Pleničar, 1961 and *Magallanesia* gen. nov. first appeared in the late Albian, and *Ichthyosarcolites* in the middle Albian. The acme of the caprinuloideid diversification was in the late Albian. Although *Caprina* d'Orbigny, 1822 has a longer history compared with other lineages, starting from the Barremian, it revived in the late Albian following a long absence from the fossil record of the upper Aptian and most of the Albian (Skelton *et al.* 2013). The late Albian can thus be considered as a notable period of polyphyletic diversification and/or origination of canaliculate rudists. The nature of the implied influence of some common biological and/or global environmental factor(s) on the evolution of canals in different rudist lineages at the time remains an issue that should be addressed in future studies.

Implications for the hypothesis of polyconitid origin of the Plagioptychidae

Although the origin and phylogenetic development of canals have been discussed in detail for the Caprinidae and Caprinuloideidae (Skelton and Masse 1998) and the Caprinulidae (Steuber and Bachmann 2002), the origins of other canaliculate rudists, especially the Late Cretaceous families (the antillocaprinids, the trechmannellids, the plagioptychids and some of the radiolitids), remain less precisely resolved (Skelton 2003, 2013).

Cladistic analysis of rudists by Skelton and Smith (2000) has suggested a polyconitid origin for the plagioptychids. Now the derivation of the Plagioptychidae Douvillé, 1888, from *M. canaliculata* gen. et sp. nov., or a related form (Fig. 3) can be supposed to have been accomplished through ventralward extension of canals around the margin of the left valve, via a mode of canal development analogous to that within the Caprinulidae (Steuber and Bachmann 2002; Skelton 2013). With respect to canal development, the caprinulid *Sellaea*, which has a large ectomyophoral cavity without multiple radial partitions, corresponds homoplasiously to *Praecaprotina* of the Polyconitidae, primitive *Neocaprina* to *Magallanesia* gen. nov., advanced *Neocaprina* to *Plagioptychus*, and *Caprinula* d'Orbigny, 1847 to *Mitrocaprina* Boehm, 1895. On the other hand, as Skelton (2013) pointed out the similarity of myocardinal arrangements between the polyconitids and the plagioptychids, anagenetic evolution of the above-mentioned polyconitids and plagioptychids is more likely than the alternative hypothesis of conver-

gent acquisition of canals in these two families. Thus, *Magallanesia* gen. nov. may provide further evidence in favour of the evolutionary hypothesis of a polyconitid origin for the plagioptychids. However, a significant stratigraphical gap remains between *Magallanesia* gen. nov. (upper Albian) and the first plagioptychid, *Plagioptychus haueri* (Teller, 1877) from the Czech Republic and Austria (lower Turonian: Steuber 2004). Furthermore, it should be noted that there are almost no records so far of rudists or other Tethyan biota in the Pacific from the Cenomanian – early Campanian time interval (Iba and Sano 2007, 2008; Iba *et al.* 2011*a*, *b*; Skelton *et al.* 2013), although the Plagioptychidae show a cosmopolitan distribution including the Pacific in the late Campanian – Maastrichtian record (Premoli-Silva *et al.* 1995; Steuber 2004). Much of the early evolutionary history of the Plagioptychidae thus remains to be filled in – a quest in which regions around the Pacific can be expected from the present study to play a prominent role.

Institutional abbreviations. NMP, National Museum of the Philippines, Manila, Philippines; M/W, Masse/Winterer collection of Scripps Institution of Oceanography (SIO) dredged Pacific rudist samples, Université de Provence, Marseille, France; IGPS, Institute of Geology and Palaeontology, Tohoku University, Sendai, Japan.

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This published work and the nomenclatural act it contains have been registered in Zoobank: http://www.zoobank.org/References/urn:lsid:zoobank.org:pub:568F55BE-F54E-4068-B169-86F6CE0889B4.

Superfamily RADIOLITOIDEA d'Orbigny, 1847
Family POLYCONITIDAE Mac Gillavry, 1937

Genus MAGALLANESIA gen. nov.

LSID. urn:lsid:zoobank.org:act:315D8BEC-60D2-413E-8673-B36D0EE393DE

Type species. *Magallanesia canaliculata* sp. nov., by monotypy.

Derivation of name. Dedicated to Ferdinand Magellan (in Spanish: Fernando de Magallanes), a Portuguese explorer, who led the Spanish expedition in the early sixteenth Century in search of a westward route from Europe to Asia, known as the first circumnavigator of the Earth. He discovered the route to the huge ocean behind the American continents and named that ocean as 'the Pacific', crossed it and finally arrived at Cebu Island in the Philippines where he died. As Magellan's expedition, the lineage for the Cebu rudist, the Polyconitidae, is also supposed to have originated in the western Mediterranean Tethys, and to have

entered the equatorial Pacific, evolving new taxa there. Although the famous explorer is better known across the world by the anglicized form of his name, 'Magellan', the genus name derived from it is preoccupied (by the extant terebratulide brachiopod *Magellania* Bayle, 1880), so we have chosen the Spanish form of his name, 'Magallanes', as the root for the new genus erected herein, to avoid confusion.

Diagnosis. Large-sized polyconitid (antero-posterior commissural diameter reaches about 15 cm) with a single row of large, simple pallial canals of radially elongate oval to rounded-subrectangular cross-sectional shape in the posterior part (behind posterior myophore) only of LV. Attached RV of wide conical to cylindrical form; LV capuloid in shape; commissural outline subrounded to subquadrate, usually somewhat compressed dorso-ventrally, with gently indented ventral margin; subequal teeth in LV straddling straight and erect central tooth in RV; anterior myophores forming broad comarginal thickenings, tilted so as to leave a broad but shallow accessory cavity separating the myophore from the anterior shell wall in LV; posterior myophore of LV projecting into broad posterior ectomyophoral cavity in RV, and facing in towards posterior myophoral wall in RV.

Comparisons. Development of a single row of large, simple canals only in the posterior shell part of the LV is the most notable character of *Magallanesia* gen. nov. Absence of canals in the ventral shell wall is uncommon in most taxa of canaliculate rudists and can be considered primitive by analogy with the progressive evolution of canals in the early caprinids of the Hauterivian – early Aptian (Skelton and Masse 1998), caprinuloideids of the Barremian–Albian (Mitchell 2013*a*) and the late Albian caprinulid, *N. raghawiensis* and *Neocaprina*? sp. from Sinai, Egypt (Steuber and Bachmann 2002; Skelton, 2013).

Among early taxa of the Caprinidae *Praecaprina* Paquier, 1905 and *Offneria simplex* Chartrousse and Masse, 1998*a* show the primitive condition of absence of canals in the ventral shell wall. However, the former genus develops the canals also in the anterior shell part of the LV, and the latter also in the anterior and dorsal shell wall of the LV, as well as in the RV. Species of the Caprinidae coeval with *Magallanesia* gen. nov., namely *C. choffati* from the western Mediterranean Tethys and *C. mulleri* from the Mid-Pacific Mountains, have canals in the posterior, postero-dorsal, and ventral shell walls of the LV (Skelton *et al.* 2013).

In the Caprinuloideidae the Barremian – early Aptian *Amphitriscoelus* Harris and Hodson, 1922, Barremian – early Aptian *Pantojaloria* Alencáster (in Alencáster and Pantoja-Alor, 1996), early Aptian *Conchemipora* Chartrousse and Masse, 1998*b*, Aptian Osaka new caprinuloideid (Sano 2012; Mitchell 2013*a*; Skelton *et al.* 2013) and late Albian 'Coalcomanid indet. 1' (Swinburne and Masse 1995) likewise share the distinctive absence of canals in the ventral shell wall of the LV with *Magallanesia* gen. nov. However, these caprinuloideids, with the exception of Barremian species of *Pantojaloria*, again consistently have canals not only in the posterior shell wall, but also in the anterior shell wall of the LV. Primitive *Pantojaloria*, namely *P. pennyi* (Harris and Hodson, 1922) and *P. estanciensis* Pantoja-Alor *et al.*, 2004, may have up to a few subrounded pallial canals, only, in the anterior shell wall of the LV (Pantoja-Alor *et al.* 2004; Masse *et al.* 2013). In contrast, the Osaka new caprinuloideid and 'Coalcomanid indet. 1' even develop additional polygonal canals in the shell.

Furthermore, the subequal teeth in the LV and a moderately thickened outer shell layer in the RV in *Magallanesia* gen. nov. are relatively derived character states that contrast with the primitively unequal teeth (posterior markedly smaller than the anterior) and thin outer shell

FIG. 4. *Magallanesia canaliculata* gen. et sp. nov. from the Pulangbato area, central Cebu Island, the Philippines and Takuyo-Daini Seamount, Japanese Seamounts in the Northwest Pacific. A–D, specimens from the Pulangbato area, central Cebu Island, the Philippines. A, photograph of natural transverse section of LV taken at the outcrop; adapical view. Note the polyconitid-type myocardinal arrangements (compare with Fig. 2), gently indented ventral margin, and the presence of a single row of large, simple, rounded-subrectangular canals around the posterior shell margin. B, paratype (NMP-1375); LV, adapical view. Note that the section in the posterior part is oblique to that in the anterior-central part of the valve on this photograph. C, holotype (NMP-1376); natural transverse section of RV near the commissure, with elements of the LV, including the anterior tooth (at) and posterior tooth (pt) in their respective sockets and the posterior myophore (pm) with ectomyophoral canals in the posterior myophoral cavity. Adapical view. Note shallowly invaginated ligament (l) and moderately thickened outer shell layer (ol) in RV. D, photograph of natural antero-posterior section (oblique to the commissure) of both valves taken at the outcrop. Note capuloid LV and broad cylindrical RV in section. Posterior myophore of LV projects into the broad posterior cavity of RV and faces inwards on to erect (steeply backward tilted) posterior myophoral wall in RV. Note the presence of large canals in the ectomyophoral cavity situated in the posterior part of LV. E–F, LV (M/W coll., A5 D39-F2) of *Magallanesia canaliculata* gen. et sp. nov. from the Takuyo-Daini Seamount, Japanese Seamounts in the Northwest Pacific. Outer shell layer missing. E, posterior view of valve, showing exposed canals in the large ectomyophoral cavity (ecc). F, internal view. Adapical view. Note the polyconitid-type myocardinal arrangements and gently indented ventral valve margin, lacking canals. See Figure 2 caption for abbreviations. Scale bars represent 10 mm.
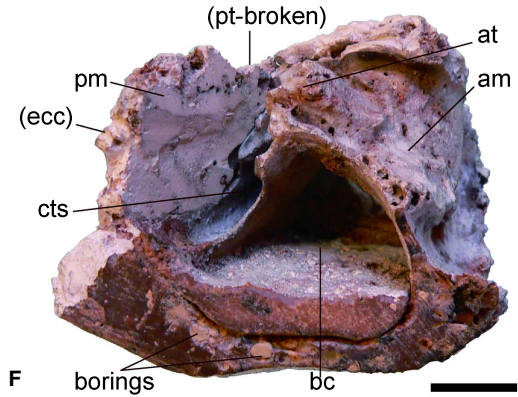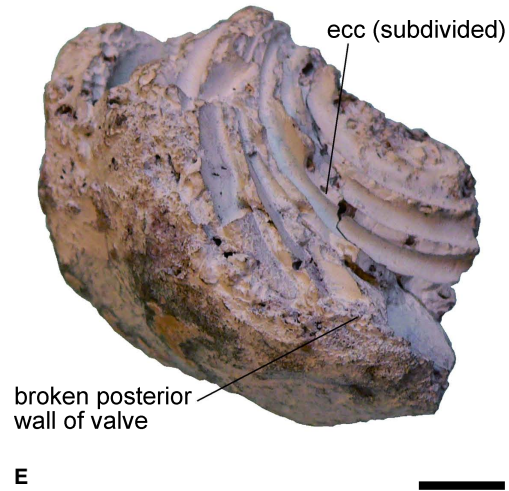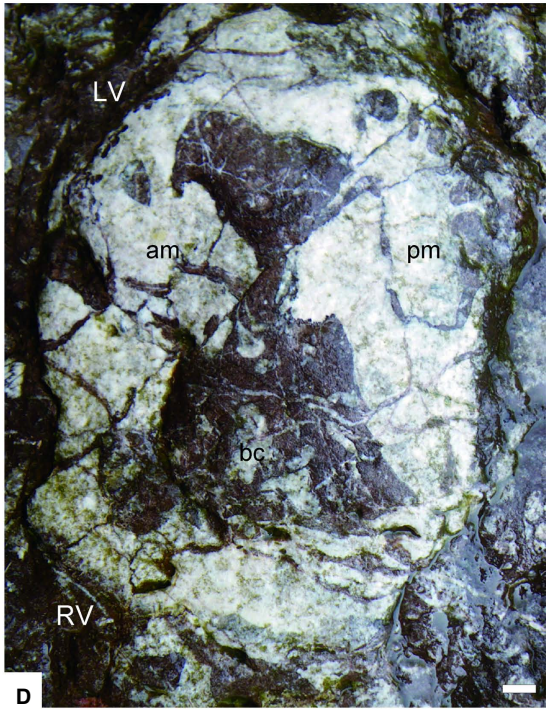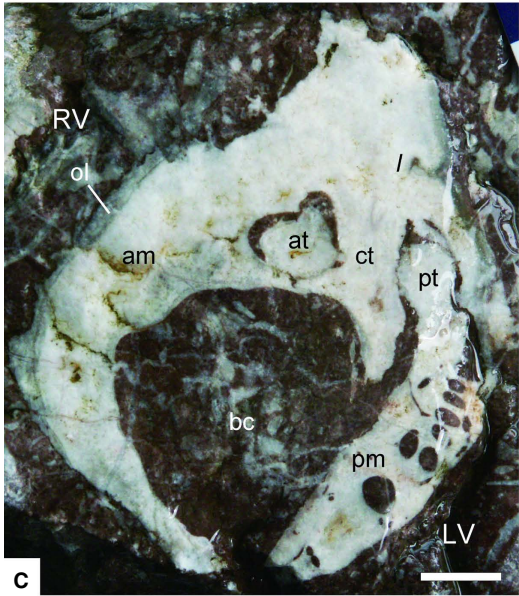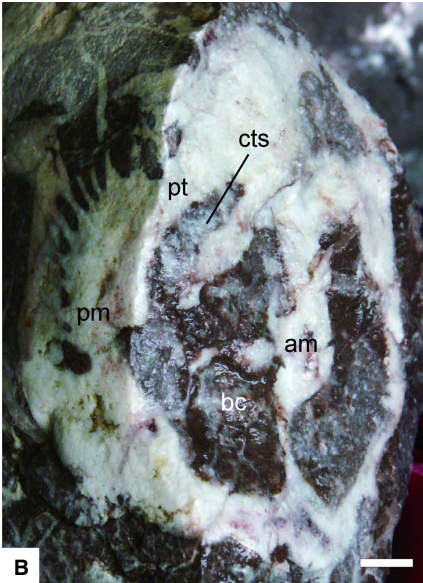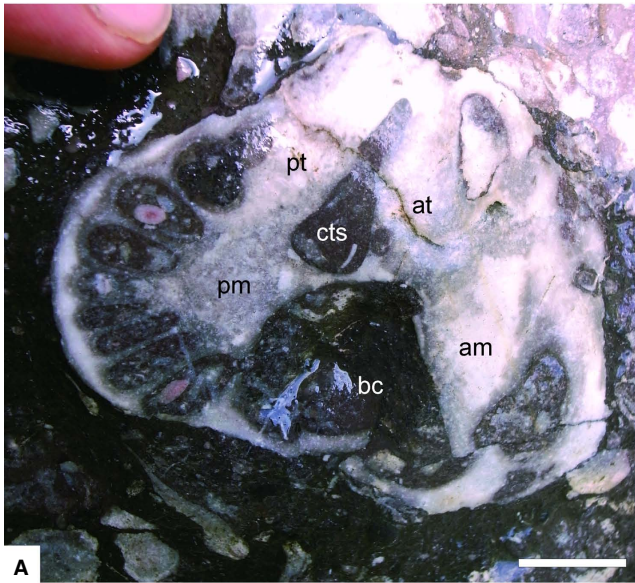
layer of the Caprinoidea d'Orbigny, 1847 in general (Skelton 2013).

Neocaprina raghawiensis and *N.*? sp. of Steuber and Bachmann (2002) have a single row of large canals of more or less rectangular cross-sectional form, divided by narrow radial laminae and of somewhat broader aspect than those of *Magallanesia* gen. nov. Moreover, these canals develop not only in the posterior shell wall but, as with the caprinoids, also along the antero-dorsal shell wall. In addition, *Neocaprina* also lacks the thickening of the outer shell layer of the RV seen in *Magallanesia* gen. nov.

On the other hand, several derived character states in *Magallanesia* gen. nov., namely, subequal teeth in the LV straddling an erect, straight central tooth in the RV, a posterior myophoral plate in the LV flanked posteriorly by an ectomyophoral cavity and projecting into a broad posterior ectomyophoral cavity in the RV, and a moderately thickened outer shell layer in the RV, strongly suggest polyconitid affinity (Skelton 2013). Thus, *Magallanesia* can be considered as a new taxon of canaliculate rudist in the Polyconitidae. Its relationships within the latter family and in particular with the noncanaliculate but closely similar *Praecaprotina* is discussed in a previous section ('Origin of the Cebu canaliculate rudist').

Age and distribution. Late Albian for the rudist locality in Cebu Island, the Philippines, and Aptian–Albian for the rudist-bearing limestone of Takuyo-Daini Seamount in the Japanese Seamounts. Both localities were located in the Central Pacific in Aptian–Albian times. As the age of the Takuyo specimen is only roughly estimated, but *Magallanesia* gen. nov. has relatively derived characters compared with other Aptian–Albian polyconitids, we judge that a late Albian age is more likely for this new rudist genus, based on currently available evidence.

Magallanesia canaliculata sp. nov.
Figure 4

LSID. urn:lsid:zoobank.org:act:BF3B23A6-9B37-4E85-A6F0-625A3DF7EC0D

1988 ?*Amphitriscoelus* sp.; Wolcke and Scholz, p. 124, plates I–II.
1996 Rudist; Masse *et al.*, pp. 973–974, 978.
1998 Coalcomaninae? indéter. 3; Chartrousse, p. 196–197, plate 36, figs 5, 6.
2012 Polyconitid gen. et sp. nov.; Sano, pp. 74–77, figure III-2-8.
2013 Polyconitid new taxon 1; Skelton *et al.*, p. 519, fig. 6d, e, table 1.

Derivation of name. According to the notable shell character of this taxon, having canals in the posterior shell wall of the LV.

Holotype. RV with parts of posterior tooth and myophore of LV inserted into the corresponding cavities in the RV, shown in a natural transverse section (NMP-1376, Fig. 4C; =Skelton *et al.* 2013, fig. 6e).

Paratype. LV showing natural transverse section (NMP-1375, Fig. 4B).

Additional materials. Natural transverse sections of several individuals, photographed at the type locality (e.g. Fig. 4A, D). Also, LV (M/W coll., A5 D39-F2) recovered from the Takuyo-Daini Seamount (Fig. 4E–F).

Type locality. Pulangbato area, central Cebu Island, the Philippines (N: 10°23.916′, E: 123°53.684′; Fig. 1).

Another locality. Takuyo-Daini Seamount in Japanese Seamounts, now located in the Northwest Pacific.

Diagnosis. As for genus.

Description. The attached RV (Fig. 4C–D) is apparently of wide conical to cylindrical form; the LV is prominently capuloid in shape (Fig. 4D). Commissural outline is subrounded to subquadrate, usually somewhat compressed dorso-ventrally (antero-posterior commissural diameter is larger than dorso-ventral one), with very shallowly indented ventral sulcus (Fig. 4A–C, F). Outer shell layer of RV is moderately thick (up to 5 mm), and its inner shell is compact, without canals (Fig. 4C–D). In the LV, a single row of several (up to 12), large canals, which are separated by thin partitions, is developed along the posterior shell wall, behind the posterior myophore; the moderately close spacing of the partitions gives the canals a radially elongate oval to rounded-subrectangular aspect in transverse section (Fig. 4A–E). Ligament of RV is shallowly invaginated (Fig. 4C).

Subequal teeth (anterior tooth larger than posterior tooth) in LV straddle a straight and erect central tooth in RV (Fig. 4A–C, F). Salient ridge connects anterior tooth to inner margin of posterior myophore, separating central tooth socket from body cavity (Fig. 4A, F). Anterior myophores in LV and RV are broad comarginal thickenings (Fig. 4A–D, F); that in LV adjoins anterior tooth dorsally and passes to ventral shell wall, with a shallow accessory cavity or gutter separating it from the anterior shell wall (Fig. 4A–B, F); the corresponding myophore in the RV is shown to be nearly flat in antero-posterior section (Fig. 4D). Posterior myophore of LV connects to posterior tooth and to ventral margin of shell; it has a broad appearance (much wider than posterior tooth) in transverse section and is separated from posterior shell margin by a broad ectomyophoral cavity subdivided by radial laminae into the simple canals described above (Fig. 4A–B, F). In antero–posterior section, posterior myophore of LV projects into the broad posterior cavity of RV and faces inwards onto erect, steeply backwardly tilted posterior myophoral wall in RV (Fig. 4D). Posterior ectomyophoral cavity in RV is large, adjoining posterior tooth socket dorsally and extending ventrally subparallel to valve margin (Fig. 4C).

Remarks. A single LV (M/W coll., STYX D17 F-1, illustrated by Skelton *et al.* (2013, fig. 6f therein), from Darwin Seamount (Guyot) in the Mid-Pacific Mountains, is possibly attributable to *Magallanesia* gen. nov., as it likewise shows subdivision of the posterior ectomyophoral cavity by radial laminae to form simple pallial canals within it. However, it differs slightly from the Cebu and Takuyo-Daini specimens in being somewhat smaller and dorso-ventrally elongate instead of having a rounded to subquadrate commissural plan. Its stratigraphical level is unrecorded, and additional materials are necessary to confirm its systematic placement.

Age and distribution. As for genus.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.hm021.

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APPENDIX: CHARACTER DATA

Character data for phylogenetic analysis of *Magallanesia caniculata* gen. et sp. nov. and of other selected caniculate forms. For detailed descriptions of character states, see Skelton and Masse (1998), Skelton and Smith (2000), Skelton (2013), Skelton *et al.* (2013) and herein.

Abbreviations. at, anterior tooth; bc, body cavity; ct, central tooth; ecc, ectomyophoral cavity; enc, endomyophoral cavity; LV, left valve; pt, posterior tooth; RV, right valve.

Right valve (RV) outer shell layer

01. Outer shell layer thickness: 0, thin (up to c. 1 mm, cf., *Diceras);* 1, thickened (to 2 mm or more).

Left valve (LV) shape

02. 0, umbo extended capuloid/enrolled; 1, depressed (low-domed to operculiform).

Dentition

03. LV teeth: 0, pt considerably smaller than at; 1, pt enlarged (subequal or equal to at).

04. RV teeth: 0, ct curved conspicuously around dorsal side of at; 1, ventral part of ct prominent, forming erect wedge-like ridge oriented subperpendicular to dorsal margin, with reduced dorsal end sharply tapered around at.

Posterior myophores and associated accessory cavities

05. Position of LV myophore: 0, lying flush on myocardinal platform; 1, rooted on posterior valve wall (with or without bounding narrow ectomyophoral gutter or pallial canals) and separated from bc by large enc; 2, myophore distinctly separated from posterior valve wall by wide ecc (which may or may not be subdivided), and partially from bc by small enc forming ventral appendix to socket for ct.

06. Orientation of muscle insertion surfaces: 0, more or less parallel to commissural plane; 1, on posterior surface of erect RV myophoral plate projecting across commissural plane into LV and facing back onto inner surface of LV myophore (= caprinid configuration); 2, on steep posterior surface of myophoral wall within RV, facing back onto inner surface of strongly projecting LV myophore (= derived polyconitid and caprinulid configuration); 3, on posterior surface of strongly projecting LV myophore, facing back onto depressed inner surface of RV myophore (= caprinuloideid configuration); 4, on anterior surface of projecting LV myophore, reflexed so as to face down out onto depressed inner surface of RV myophore.

07. LV ecc: 0, absent or narrow gutter only; 1, cavity undivided; 2, cavity may be subdivided by a radial lamina; 3, cavity subdivided by several widely spaced radial laminae to yield large pallial canals of more or less rectangular cross-sectional form; 4, cavity subdivided by numerous moderately closely spaced radial laminae to yield pallial canals of radially elongate oval to rounded subrectangular cross-sectional form.
08. RV ecc: 0, absent; 1, narrow and comarginally elongated; 2, broad.
09. RV enc: 0, absent; 1, present, separated from bc by narrow lamina.

Anterior myophores

10. 0, flat or gently tilted on myocardinal platform; 1, LV myophore tilted up against at and separated from anterior valve margin by broad but shallow depression; 2, LV myophore tilted up against at and separated from anterior valve margin by deep accessory cavity (which may be subdivided).

Distribution of pallial canals

11. LV: 0, none (or sparsely present in some specimens only); 1, around both anterior and posterior valve margins but not continuing around entire ventral margin; 2, continuous around anterior, ventral and posterior valve margins.
12. RV: 0, none (or sparsely present in some specimens only); 1, around both anterior and posterior valve margins, but not continuing around entire ventral margin.

TABLE A1. Character matrix for selected rudist taxa.

Taxon/Character	01	02	03	04	05	06	07	08	09	10	11	12
Outgroup												
Valletia	0	0	0	0	0	0	0	0	0	0	0	0
Caprinoidea												
Pachytraga	0	0	0	0	1	1	0	1	0	0	0	0
Praecaprina	0	0	0	0	1	1	4	1	0	0	1	0
Retha	0	0	0	0	1	3	0	0	1	0	0	0
Amphitriscoelus	0	0	0	0	1	3	3	0	1	0	1	1
Radiolitoidea												
Monopleura	0	1	1	0	0	0	0	0	0	0	0	0
Horiopleura	1	1	1	1	2	0	1	0	0	1	0	0
Polyconites	1	1	1	1	2	4	1	0	0	1	0	0
Praecaprotina	1	1	1	1	2	2	1	2	0	1	0	0
Magallanesia	1	0	1	1	2	2	4	2	0	1	0	0
Plagioptychus	1	0	1	1	2	2	4	2	0	1	2	0
Sellaea	0	0	1	1	2	2	2	2	0	2	0	0
Neocaprina	0	0	1	1	2	2	3	2	0	2	1	1

Based on: *Valletia tombecki* Munier-Chalmas, 1873; *Pachytraga tubiconcha* Astre, 1961; *Praecaprina varians* Paquier, 1905; *Retha tulae* (Felix, 1891); *Amphitriscoelus primaevus* Pantoja-Alor, Skelton and Masse, 2004; *Monopleura varians* Matheron, 1842; *Horiopleura lamberti* (Hébert, 1867); *Polyconites verneuili* (Coquand, 1865); *Praecaprotina yaegashii* (Yehara, 1920); *Magallanesia canaliculata* gen. et sp. nov.; *Plagioptychus toucasi* Matheron, 1842; *Sellaea*/'*Caprotina*' species-group of Di Stefano (1889); *Neocaprina raghawiensis* Steuber and Bachmann, 2002.