

Revision of *Praeacprina? pennyi* (Harris and Hodson) (Caribbean caprinoid rudist): its placement in *Pantojalaria* Alencáster; taxonomic, stratigraphic and evolutionary implications

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ABSTRACT. The revision of the type series of *Praeacprina? pennyi* from Trinidad, shows that this form should be assigned to the Caprinuloideidae (Amphitriscolitinae) and is a representative of the genus *Pantojalaria*. *Pantojalaria sphaerica* and *Pantojalaria estanciensis* from Mexico and *Pantojalaria pennyi* from Trinidad are distinctive species and differ by their biometric properties and the distribution of canals in the right valve. *Pantojalaria pennyi* has some affinities with *Conchemipora skeltoni*. The genus *Praeacprina* is absent in the New World. Among the three species of *Pantojalaria* two belong to the Barremian and one to the early Aptian, their evolution is marked by a size increase and a decrease in the variability of characters, mainly the canaliculation.

Key words: Caprinoidea, Caribbean, Barremian-early Aptian, taxonomic revision.

1. INTRODUCTION

Since its description by Harris and Hodson (1922), *Praeacprina? pennyi* has been regarded as a poorly defined taxon and most authors (Mac Gillavry, 1937; Skelton, 1982; Masse and Rossi, 1987; Chartrousse, 1998a) tend to reject both the specific and generic names. This rejection was mainly due to the poor state of preservation of the type material from Trinidad and/or its insufficient description. It is important to recall however that in the description of *Pantojalaria sphaerica* Alencáster (in Alencáster and Pantoja-Alor, 1996) the close similarity of *P. sphaerica* with *Praeacprina? pennyi* was pointed out. Moreover the two forms were also considered to have the same age, early Aptian, and a similar associated rudist fauna, therefore their possible synonymy was questioned. Similarly, Chartrousse and Masse (2004) suggested that *Praeacprina? pennyi* should be placed within the Caprinuloideinae, and probably in the genus *Pantojalaria*.

The present paper is based on an accurate revision of the type material from Trinidad and its comparison with *Pantojalaria estanciensis* (Pantoja-Alor et al., 2004) and *Pantojalaria sphaerica* from Mexico, including qualitative and quantitative aspects. The taxonomic, stratigraphic and evolutionary implications of this revision are discussed.

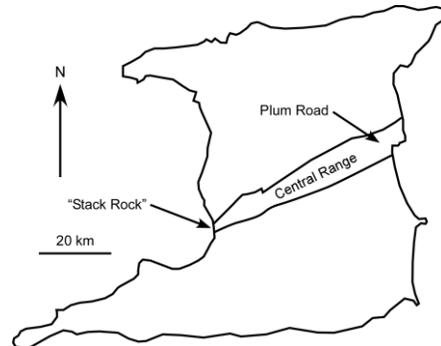


Figure 1. Location of rudist sections (Plum Road and "Stack Rock" in the Central Range of Trinidad.

2. PRAEACPRINA? PENNYI A REAPPRAISAL

In their original description Harris and Hodson (1922) described rudists from two locations in Trinidad. *Amphitriscoelus waringi* Harris & Hodson was collected from the locality at Plum Road (Figure 1) where it was assigned a most-likely Cenomanian age, but was stated to be possibly as old as Aptian. The *A. waringi* fauna is now well dated as early Aptian (Alencáster and Pantoja-Alor, 1996; Skelton and Masse, 1998). *Praeacprina? pennyi* was collected from the "Stack Rock" just offshore near Point-a-Pierre (Figure 1) which was mentioned by Wall and Sawkins (1860, p. 34) and to which Harris and Hodson (1922) assigned an age 'as equally as low' as that of the Plum Road

locality. A reinvestigation of the fauna of “Stack Rock” (which is now located in the Petrotrin car park at Pointe-a-Pierre) indicates that *P.?* pennyi is associated with *Amphitriscoelus primaevus* Pantoja-Alor, Skelton & Masse and not *A. waringi*, and that *P.?* pennyi should be assigned a Late Barremian age (Pantoja-Alor et al., 2004).

The type material of *P.?* pennyi is housed in the Paleontological Research Institution, Ithaca, New-York, and includes two isolated left valves (LV) (numbers 1551, 1553), an isolated right valve (RV) (number 1550), and a bivalve specimen with an eroded, partly broken LV (number 1552).

In the original description, based on these four specimens, assumed to belong to the same taxon, no holotype was proposed by the authors. The principal characters summarized after Harris and Hodson (1922) are as follows:

The upper valve is closely coiled with the apex near the anterior shell margin; its outline is oval with an antero-posterior compression. An internal partition is present and few sub-quadrangular canals on the anterior and posterior margins too, no canals have been observed on the ventral side. The lower valve is elongated, slightly curved and somewhat twisted, without a partition, and thick

walled (**Figure 2**).

The overall morphology closely resembles that of the genus *Praeacprina* Paquier (Paquier, 1905), and the presence of canals, interrupted ventrally, and only clearly observed on the upper valve, tend to support this similarity, and therefore the assignment of the Caribbean form to the above European genus, as proposed by Harris and Hodson (1922).

We have studied transverse sections of the LV of the bivalve specimen (1552) and the isolated RV (1550), which show that (**Figure 3**):

- rounded canals are present on the relatively thick anterior side, their number ranges from 3 to 4 and their diameter decreases dorsally; canals are absent on the ventral side; they are suspected but hardly visible on the relatively thin posterior side, their absence being either effective or the result of diagenesis (i.e., sparitisation of the inner shell wall);

- there is a rather obtuse internal ridge on the ventral floor of the shell;

- the myocardinal apparatus conforms to the “coalcomanid type” as defined by Chartrousse (1998a) by reference to the former Coalcomaninae of Coogan (1973, 1977). The characteristic feature of the family Caprinuloideidae Damestoy (1971)

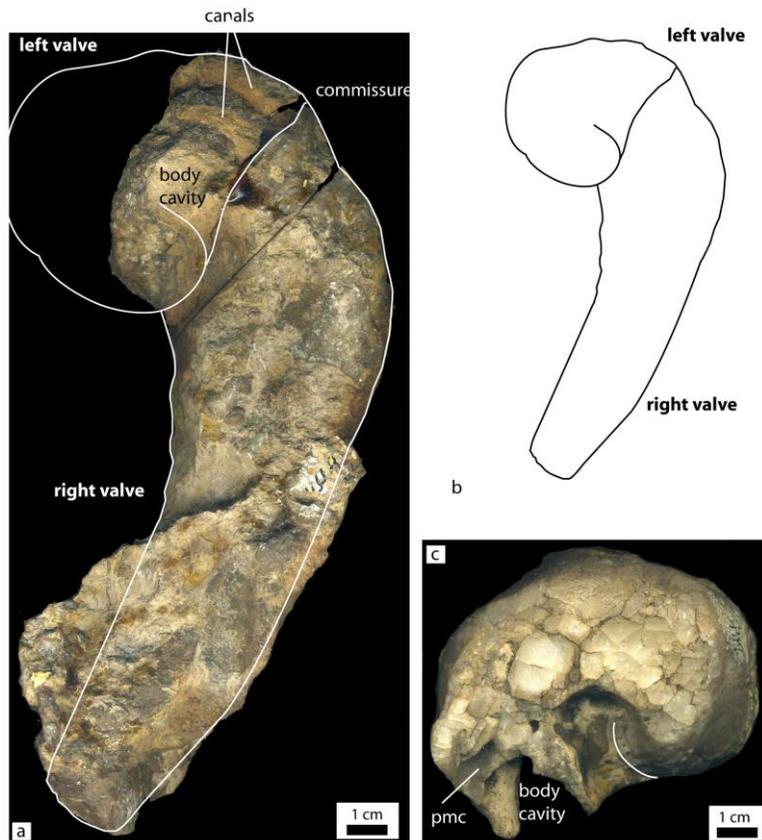


Figure 2. External characters of *Praeacprina?* pennyi: a, view of a bivalve specimen with upper valve partly broken (no. 1552); b, drawing of the same specimen, partly reconstructed, to show the overall morphology; c, external view of the left valve (posterior side) showing the coiling habit (specimen no. 1551).

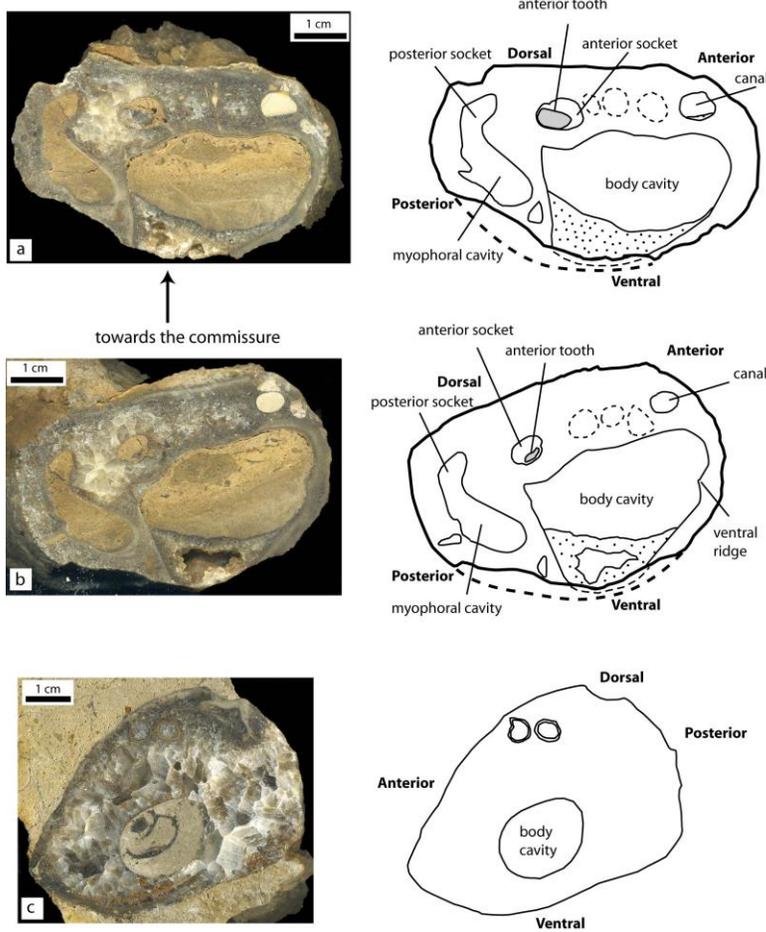


Figure 3. Internal characters of *Praeacprina? pennyi*: a-b, transverse sections of the RV (specimen no. 1552) showing the myocardial organisation, the arrangement of canals, and their interpretation; c, transverse section of RV (specimen no. 1553), showing the overall spartisation of the shell and preserved canals on the anterior side.

(*pro* Coalcomaninae *sensu* Coogan, but see Skelton, 2013 and Mitchell, 2013, for current classifications), being the downward development of the posterior myophoral plate (attached to the posterior tooth) of the LV, which projects into the broad posterior cavity (i.e., endomyophoral) of the RV with the posterior muscle scar external, that is located on the convex side of the myophoral plate or the concave side of the inner, shell wall. The myocardial cavity of the RV has a typical scoop or yellow squash shape (Chartrousse, 1998b); the socket and myophoral cavities are somewhat similar in size. The anterior tooth has a rounded elliptical transverse outline and is smaller than the posterior one, the anterior socket is larger than the corresponding tooth, and its distal portion bears a small gutter.

The above description of *Praeacprina? pennyi* testifies that this form has to be excluded from the genus *Praeacprina*, a representative of the Family Caprinidae d'Orbigny, and must be assigned to the subfamily Caprinuloideidae, namely the genus *Pantojaloria* Alencáster. The definition of the

genus based on *P. sphaerica* provided by Alencáster (in Alencáster and Pantoja-Alor, 1996) and complemented by Chartrousse (1998b) is as follows: “Shell large, inequivalve, LV tightly coiled in a whole whorl with beak prosogyrate and ventral side convex; RV subconical and straight with ventral slightly convex. Internal structure (**Figure 4**) similar in both valves; muscle insertions separated from shell wall by a posterior row and an antero-dorsal row of a few, large pallial canals; ventral margin without canals. Body cavity large, with a short longitudinal inner ridge near the anterior side of the ventral floor. Large ligamental cavity. Posterior myophoral cavity of “coalcomanid” shape in both valves”. In some specimens a thin (about 1 mm thick), silicified, outer shell layer has been observed, which documents the existence of the thin formerly calcitic layer usually found in the Caprinioidea.

Among the Caprinuloideinae: *Amphitruscoelus* Harris & Hodson, *Pantojaloria* Alencáster and *Conchemipora* Chartrousse & Masse are the only forms having pallial canals absent on the

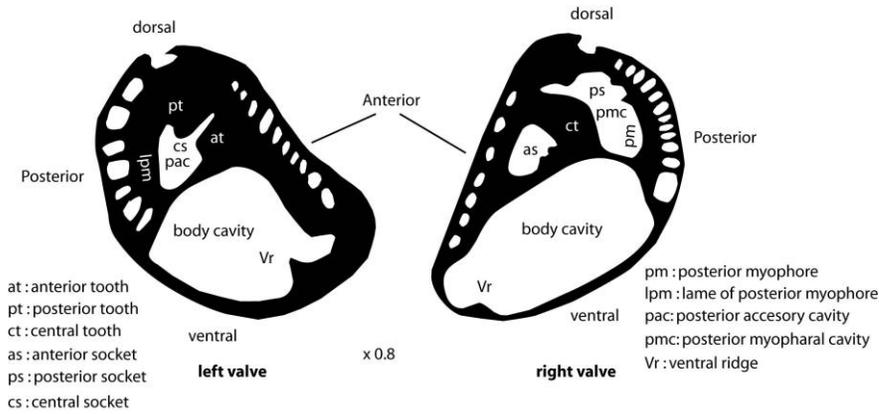


Figure 4. Internal characters of *Pantojaloria sphaerica* (Huetamo region, Mexico), based on transverse sections of right and left valves (after Chartrousse, 1998b) to illustrate the characters of the genus.

ventral side of both valves (Alencáster in Alencáster and Pantoja-Alor, 1996, Chartrousse, 1998a, Chartrousse and Masse, 1998). The LV of *Amphitriscoelus* is short and capuloid, the canals tend to be numerous and subquadrangular, there is an internal cavity in the anterior tooth and no inner ventral ridge. By contrast in *Pantojaloria* the LV is usually tightly coiled, pallial canals are few and tend to be subrounded, and there is an inner ventral ridge in the body cavity. In the more primitive forms such as *P. estanciensis* and *P. pennyi* canals are variable and virtually absent on either the anterior or posterior shell side. In *Conchemipora* the distribution of canals is asymmetric, they are absent on the posterior side.

The virtual absence of canals on the posterior side in *P. pennyi* indicates some affinities between this species and *Conchemipora skeltoni* Chartrousse & Masse, with a canalication limited to the antero-dorsal side (Chartrousse and Masse, 1998). The critical differences between the two forms are with the geometry and number of canals: numerous, rectangular with thin radial walls (as in *A. waringi*) and with bifurcations, and the absence of an inner ventral ridge. Moreover we did not observe in the specimens from Trinidad the presence of minute longitudinal tubes within the calcitic outer shell layer, as found in *C. skeltoni* (Chartrousse and Masse, 1998).

3. MORPHOLOGICAL INTERNAL AND EXTERNAL RELATIONSHIPS BETWEEN *PANTOJALORIA PENNYI*, *PANTOJALORIA ESTANCIENSIS* AND *PANTOJALORIA SPHAERICA*

Canals are present (8 to 10) in both valves of *P. sphaerica* on both the anterior and the posterior side, they are also found in smaller numbers (3 to 4) on the anterior side of *P. pennyi* but appear to be very limited or virtually absent on the posterior side. Canals are also poorly developed in *P.*

estanciensis and as noticed by Pantoja-Alor et al. (2004) there is a strong variability in their number and arrangement, and the anterior ones are very shallow and assumed to be absent in the RV. Assuming that the absence of canals on the anterior side of the RV of *P. estanciensis* and on the posterior side of the same valve of *P. pennyi* are not due to diagenetic alteration (i.e., sparitisation) of the inner shell wall, the two species therefore appear to be different, and also different from *P. sphaerica* which possesses canals on both sides of both valves. The inner ridge is rather obtuse and located on the anterior side of the ventral margin in *P. sphaerica* and *P. pennyi* whereas it tends to be more acute with a “mid-ventral” position in *P. estanciensis*. The LV of *P. estanciensis* is capuloid with a prosogyrally twisted umbo whereas it tends to be spirogyrate in *P. pennyi* and *P. sphaerica*.

Internal and external dissimilarities observed or inferred in the three species tend to support their taxonomic individuality.

4. QUANTITATIVE RELATIONSHIPS BETWEEN *PANTOJALORIA PENNYI*, *PANTOJALORIA ESTANCIENSIS* AND *PANTOJALORIA SPHAERICA*

Dimensional data (Figure 5) are illustrated by measurements of the dorso-ventral and antero-posterior diameter of transverse sections of the RV and LV, all derived from Alencáster and Pantoja-Alor (1996), Chartrousse (1998a, b) and Pantoja-Alor et al. (2004), and the specimens belonging to the Harris and Hodson collection. Figure 5 also illustrates the mean diameter obtained by the addition of the antero-posterior and dorso-ventral ones divided by two ($d_{Average} = (d_{DV} + d_{AP})/2$).

The antero-posterior diameter of *P. pennyi* varies from 35 to 50 mm, its mean value being 41 mm, the dorso-ventral diameter ranges from 40 to 60 mm, mean 48 mm, its minimum mean diameter is 40 mm, maximum 52 mm, with mean

	<i>Pantojalaria pennyi</i>	<i>Pantojalaria estanciensis</i>	<i>Pantojalaria sphaerica</i>
Number of specimens	4	8	9
Antero-posterior diameter			
Mean (mm)	41	49	79
Standard deviation (mm)	6	3	7
Min (mm)	35	43	70
Max (mm)	50	52	93
Dorsa-ventral diameter			
Mean (mm)	48	64	79
Standard deviation (mm)	11	13	11
Min (mm)	40	37	69
Max (mm)	60	82	105
Average diameter			
Mean (mm)	45	56	79
Standard deviation (mm)	6	8	7
Min (mm)	40	42	72
Max (mm)	52	67	92

Figure 5. Values of biometric attributes of *Pantojalaria* specimens from Mexico and Trinidad.

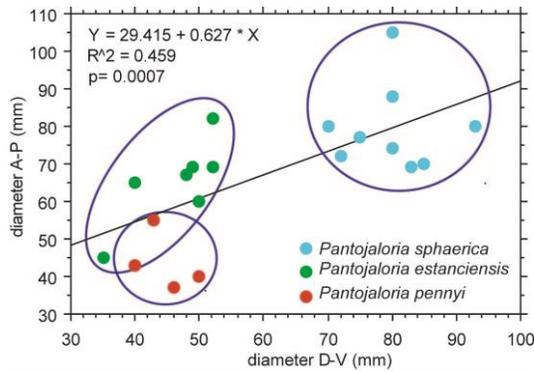


Figure 6. Cross plots and regression graph corresponding with the three species of *Pantojalaria*.

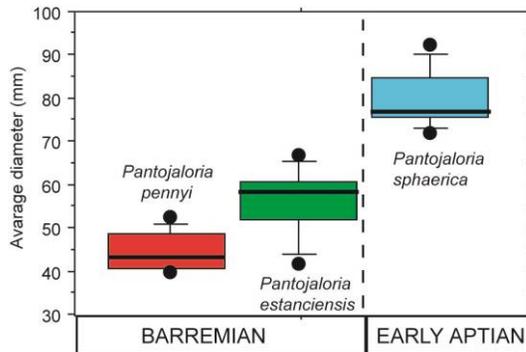


Figure 7. Box plot graph based on average shell diameter showing the size increase through time of *Pantojalaria* species.

	Mean Difference	Critical Difference
A- <i>Pantojalaria sphaerica</i> , B- <i>Pantojalaria pennyi</i>	34.861	10.158
A- <i>Pantojalaria sphaerica</i> , C- <i>Pantojalaria estanciensis</i>	23.299	8.357
B- <i>Pantojalaria pennyi</i> , C- <i>Pantojalaria estanciensis</i>	-11.563	8.357

Figure 8. Results of ANOVA method (based on average diameter) applied to *Pantojalaria* species to document statistically their distinctiveness.

45 mm. The dimensions of *P. estanciensis* are slightly greater than that of the above species, the antero-posterior diameter is in the range of 43-52 mm its mean value being 49 mm, the dorso-ventral diameter fluctuates from 37 to 82 mm, the mean being 64 mm.

Pantojalaria sphaerica is the largest species, the antero-posterior, dorso-ventral and mean diameter varies from 70-93 mm, 69-105 mm and 72-92 mm respectively, the mean being the same: 79 mm.

The cross plot and regression graph (Figure 6) illustrate graphically the foregoing results (i.e., specimens of *P. sphaerica* have the largest diameter, and those of *P. pennyi* the smallest, *P. estanciensis* being somewhat in between but close to the latter. Statistic parameters support significantly ($p = 0.0007$) the distinctiveness of the three species of *Pantojalaria*.

In the box plot graph (Figure 7) each box illustrates the mean values of the mean diameter of specimens belonging to the three species of *Pantojalaria*. The box plot analysis includes the following statistical measurements: median, upper and lower quartiles (the box bounds these quartiles), dots figure the minimum and maximum values. Each box accounts for 50% of the data and the line in the middle indicates the median values. The box plot graph shows that 50% of the mean diameter fluctuates as follows: for the Barremian species (*P. pennyi* and *P. estanciensis* respectively) it ranges from 40 to 48 mm and 52 to 58 mm, and for the early Aptian species (*P. sphaerica*) from 75 to 85 mm.

To test the validity of the statistical analysis of the above three species we focused on the mean diameter. The measurements were compared by applying the analysis of variance: the one-way ANOVA (Figure 8) method, then followed by the post-hoc-Student-Newman-Keuls test (usually applied for biometric data) using the software STATVIEW with a 0.05 significance level. Results of the test show that three species of *Pantojalaria* are significantly different from each other.

The combination of results from the regression graph, box plot and ANOVA methods applied to the three species documents a size increase from the Barremian to the early Aptian. This pattern conforms to Cope's rule in the strict sense (Jablonski, 1997).

5. STATUS, DIAGNOSIS, EVOLUTIONARY STATE AND BIOGEOGRAPHY OF *PANTOJALORIA PENNYI*

Pantojalaria pennyi is regarded as a valid species for which we propose specimen 1552 of the Harris and Hodson collection as lectotype; its diagnosis is as follows: *Pantojalaria* with moderate-sized shell (antero-posterior commissural diameter 41 mm), LV with limited coiling, 3 to 4 rounded canals on the anterior side of both valves, canals poorly developed or virtually absent on the posterior side; obtuse inner ridge located on the anterior side of ventral margin.

The smaller size, more limited coiling habit of the LV and a smaller number of canals, show that *P. pennyi* and *P. estanciensis* are more primitive than *P. sphaerica*. The evolutionary state of the two Barremian species *P. pennyi* and *P. estanciensis* is comparable, but the difference in the two species is the average size which suggests that *P. pennyi* is more primitive than *P. estanciensis* and might be the oldest one, an hypothesis still to be checked by using other chronologic markers.

The placement of *Praeacprina?* pennyi in the genus *Pantojalaria*, bears out the absence of *Praeacprina* in the new World, as stated by most of the antecedent workers (e.g., Chartrousse and Masse, 2004) and documents the geographical extent of *Pantojalaria* to the southern Caribbean

domain. Affinities between *Pantojalaria pennyi* and *Conchemipora skeltoni* corroborate the paeobiogeographic link between the Caribbean and the Mid Pacific domains during the Barremian-early Aptian (Skelton et al., 2011).

6. CONCLUSIONS

The revision of the type material of *Praeacprina?* pennyi from Trinidad, usually rejected in the former literature as a *nomen nudum*, shows that this form is a Caprinuloideidae and must be ascribed to the genus *Pantojalaria*. *Pantojalaria sphaerica* and *P. estanciensis* from Mexico and *P. pennyi* represent distinctive species and differ by their biometric properties; values of the dorso-ventral, antero-posterior transverse diameters, are smaller in the Trinidad than in the Mexican forms. In addition the distribution of canals in the RV appears somewhat distinct, with more developed in the Mexican species than in the Trinidad species. We note some similarities between *P. pennyi* and the primitive *Conchemipora skeltoni* from the early Aptian of the Mid-Pacific Mountains. The placement of *Praeacprina?* pennyi in the genus *Pantojalaria* corroborates that this genus is a marker of the Barremian-early Aptian and bears out the absence of *Praeacprina* in the New World. The affinities between *Pantojalaria pennyi* and *Conchemipora skeltoni* support the paeobiogeographic link between the Caribbean and the Mid Pacific domains during the Barremian-early Aptian.

Acknowledgements. For his pertinent and helpful review of an earlier draft of the manuscript we thank Gavin C. Gunter.

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Accepted 14th June 2013