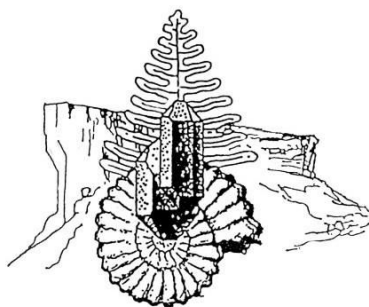




FIRST RECORD OF *GREGORYASTER* (ECHINOIDEA) IN THE EOCENE OF ITALY

Enrico Borghi, Lorenzo Emanuele Morra, Alberto Bottazzi, Fabio Caporiondo



Notiziario della Società Reggiana di Scienze Naturali, (2024): 114-136

Data di pubblicazione: 20 Dicembre 2024



FIRST RECORD OF *GREGORYASTER* (ECHINOIDEA) IN THE EOCENE OF ITALY

Enrico Borghi¹, Lorenzo Emanuele Morra¹, Alberto Bottazzi², Fabio Caporiondo³

¹ Società Reggiana di Scienze Naturali, Reggio Emilia; e-mail: enrico.borghi20@gmail.com, lorenzo.morra@gmail.com

² Museo Civico "Dal Lago", Valdarno (Vicenza); e-mail: alberto.bottazzi@virgilio.it

³ Museo Civico di Montecchio Maggiore (Vicenza); e-mail: fabiocaporiondo@gmail.com

Abstract: Two specimens recently collected from the Upper Eocene Priabona formation of Sossano, near Vicenza (Northeastern Italy), are assigned to *Gregoryaster* Lambert (1907). In Italy, this echinoid was so far known only in the Miocene (Aquitanian-Langhian) of Sardinia and the Northern Apennines. The morphological characters visible in the studied specimens are consistent with *Gregoryaster coranguinum* (Gregory, 1892), the type species of this genus. Morphological comparison highlights differences with *Trachyaster heberti* Cotteau, 1887, Eocene of Spain, here considered as a true *Gregoryaster*, *Hemiaster praeceps* Bittner, 1882 and *Hemiaster galantigensis* de Loriol, 1891, two species from the Eocene of Veneto possibly belonging to *Gregoryaster*.

A Bayesian phylogenetic analysis was performed in order to evaluate the uncertain systematic position of *Gregoryaster*. The results demonstrate that it is premature to assign *Gregoryaster* to a family other than the Schizasteridae and indicate that the possible attribution to the families Pericosmidae or Hemiasteridae should be discarded with the present data, thus supporting the results by the morphological analysis.

At Sossano *Gregoryaster* lived in the upper Circalittoral at a depth of about 50-100 m, in well oxygenated environments with a high-diversity fossil assemblage; it was an endobenthic deposit feeder, unable to burrow deeply into the fine-grained marly sediments of the Priabonian fossiliferous deposits at Sossano.

Key words: Echinoidea, *Gregoryaster*, Eocene.

Riassunto: PRIMA SEGNALAZIONE DEL GENERE *GREGORYASTER* (ECHINOIDEA) NELL'Eocene ITALIANO.

Due esemplari recentemente raccolti nel Priaboniano di Sossano, nei Colli Berici (Vicenza) consentono di accertare la presenza nell'Eocene del Veneto del genere *Gregoryaster* Lambert (1907), un'echinoide sinora noto in Italia solo nel Miocene: Aquitaniano-Langhiano della Sardegna (Stara *et al.*, 2022) e Langhiano inferiore dell'Emilia-Romagna (Rondelli & Battilani, 2023). I due esemplari in esame mostrano caratteri morfologici che corrispondono a quelli della specie tipo, *Gregoryaster coranguinum* (Gregory, 1892). Vengono indicate le differenze che separano i due esemplari di Sossano da *Gregoryaster cabiddui* Stara *et al.*, 2022, del Miocene inferiore della Sardegna. Il confronto viene esteso a *Trachyaster heberti* Cotteau, 1887, qui confermato come appartenente a *Gregoryaster*, e ad *Hemiaster praeceps* Bittner, 1882 ed *Hemiaster galantigensis* de Loriol, 1891, rispettivamente dell'Eocene di Negrar (Verona) e di Montecchio Maggiore (Vicenza), anch'essi probabilmente appartenenti a questo genere.

Un'analisi filogenetica bayesiana è stata effettuata allo scopo di chiarire l'incerta posizione sistematica di *Gregoryaster*. I risultati dimostrano che sarebbe prematuro assegnare *Gregoryaster* ad una famiglia diversa da Schizasteridae Lambert, 1905, e che la possibile attribuzione di questo genere alle famiglie Pericosmidae e Hemiasteridae è da scartare con i dati attuali, confermando quindi le conclusioni basate sull'analisi morfologica. Nel Priaboniano di Sossano *Gregoryaster* viveva a una profondità di ca. 50-100 m, nel piano Circalitorale superiore, in acque ben ossigenate e caratterizzate da una elevata diversità faunistica. In base alle caratteristiche morfologiche rilevate, si trattava di un echinoide endobenthico che non era però in grado di infossarsi profondamente nel sedimento marnoso a grana fine che costituiva i depositi fossiliferi del Priaboniano di Sossano.

Parole chiave: Echinoidea, *Gregoryaster*, Eocene, Veneto.

Introduction

Gregoryaster Lambert (1907) is an extinct echinoid known, for certain, from the Oligocene - Lower Miocene of Malta (Wright, 1855, 1864; Gatt, 2006), the Aquitanian-Burdigalian of Sardinia (Stara *et al.*, 2022) and the Lower Langhian of Emilia-Romagna (Rondelli & Battilani, 2023).

Gregoryaster has never been recorded from the Eocene of Italy. However, similar specimens from Veneto Region (Northeastern Italy) were attributed to *Hemiaster praeceps* Bittner, 1882, from Negrar (Verona Province), and to *Hemiaster galantigensis* (de Loriol, 1891, from Galantiga near Montecchio Maggiore (Vicenza Province). The attribution of these species to *Hemiaster* is doubtful, because in past times the interpretation of this genus was subjective due to the lack of clear distinctive morphological characters. Also, the specimens of *Gregoryaster* sp. from the Pantano Formation of Emilia Romagna (Rondelli & Battilani, 2023) were originally attributed to *Hemiaster* by Stefanini (1908).

Stara *et al.* (2022), when restudying the type material of *Gregoryaster* and *Opissaster* Pomel, 1883, two echinoids apparently closely related on the basis of their overall morphology, highlighted morphological differences clearly separating them and fixed the diagnostic characters for each genus.

The aim of this paper is to study two specimens recently collected in the Priabonian of Sossano in the Berici Hills (Vicenza Province, Fig. 1) and to compare them with the species of *Gregoryaster* considered as valid in Stara *et al.* (2022) and with the specimens earlier attributed to *Hemiaster* from the Eocene of Veneto.

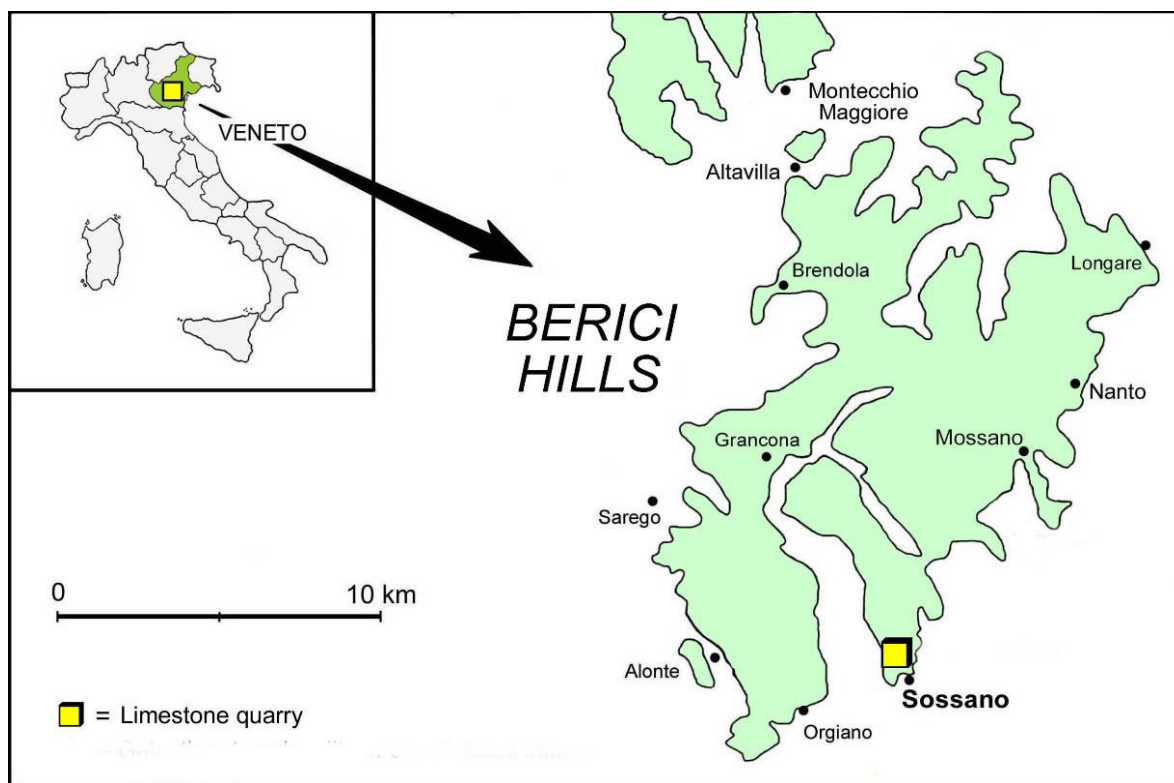


Figure 1 – Location map of the finding locality of *Gregoryaster*: Sossano, in the Berici Hills (Vicenza Province).

Figura 1 – Ubicazione della località di ritrovamento di *Gregoryaster*, presso Sossano, nei Colli Berici (Vicenza).

Material and methods

Phylogenetic analysis: A Bayesian phylogenetic analysis was carried out in order to evaluate the uncertain systematic position of *Gregoryaster*. A new operational taxonomic unit (OTU) was scored in the Coppard *et al.* (2010) dataset. The new OTU was scored based on first-hand examination of specimens described in this study and on the recent pertinent literature (Stara *et al.*, 2022 and Rondelli & Battilani, 2023). The character list for the

full matrix is after Kroh & Smith (2010) but excluding characters E23 and E24, which were removed by Coppard *et al.* (2010), and the 50 pedicellarial characters added by Coppard *et al.* (2010) which we removed; characters 4, 6, 17, 38, 75, 80, 86, 202, 203 and 233 were treated as ordered as in Kroh & Smith (2010).

The non-time-calibrated Bayesian analysis was carried out in MrBayes ver. 3.2.7 (Ronquist *et al.*, 2012) using the Mkv model with two runs of four chains each. The analysis was run for 2.000.000 generations, sampling every 1000 generations, with a burn-in of 25% and the temperature set at 0.10. Effective sample size was greater than 1000 for the tested parameters and average standard deviation of split frequencies was below 0.025 at the end of the run. For the full matrix and script used in the analysis see the Appendix.

Institutional abbreviations: MAC = Museo di Storia Naturale “Aquilegia” of Masullas; MCV = Museo Civico “Dal Lago” of Valdagno (Italy); MHNG = Musée d'Histoire Naturelle, Genève, Switzerland; NHM = Natural History Museum of London (UK); NMNH/TE = National Museum of Natural History of Mdina, Malta.

The two specimens under study from Sossano are housed at the Museo Civico “Dal Lago” of Valdagno (Italy) (inventory codes: MCV 24/120, MCV 24/121).

The illustration of the holotype (NHM E3429) of *Gregoryaster coranguinum* (Gregory, 1892), from Malta, is reported in Smith & Kroh (2011). Biometric data of 14 additional specimens from Malta (NHM E43308, E11683, E3405; NMNH/TE 314-324) have been provided by Stara *et al.* (2022; table 3).

The original illustration of the type of *Trachyaster heberti* Cotteau, 1877 (Musée d'Histoire Naturelle, Genève, Switzerland, de Loriol Collection, inventory code: MHNG.27808), and the figure of another specimen from the Eocene of Callosa (Spain) reported by Smith & Kroh (2011), have been utilized for comparison.

The interpretation of *Hemiaster praeceps* Bittner, 1882, and *Hemiaster galantigensis* (de Loriol, 1891) have been based on the respective original description and illustration.

Exhaustive illustration and biometric data of *Gregoryaster cabiddui*, Aquitanian-Burdigalian of Ales (Sardinia), were provided by Stara *et al.*, 2022. The type-material consists of 8 specimens (inventory MAC PL2115-2121, PL2332, 2502).

Morphological abbreviations: (Fig. 2): α = angle between the anterior paired petals; L1 = distance between the apical disc to the anterior test margin; L2, L3 = length of the anterior and posterior paired petals, respectively; L4, L5, L6 = maximum width of anterior and posterior paired petals and of the frontal ambulacrum, respectively; L7 = height of the periproct; L8 = distance between the tip of the labrum and the anterior test margin; L9 = length of the labral plate, TL, TH and TW = length, height and width of the test, respectively.

The systematic palaeontology follows Kroh & Mooi (2024), although no valid species are assigned to this genus.

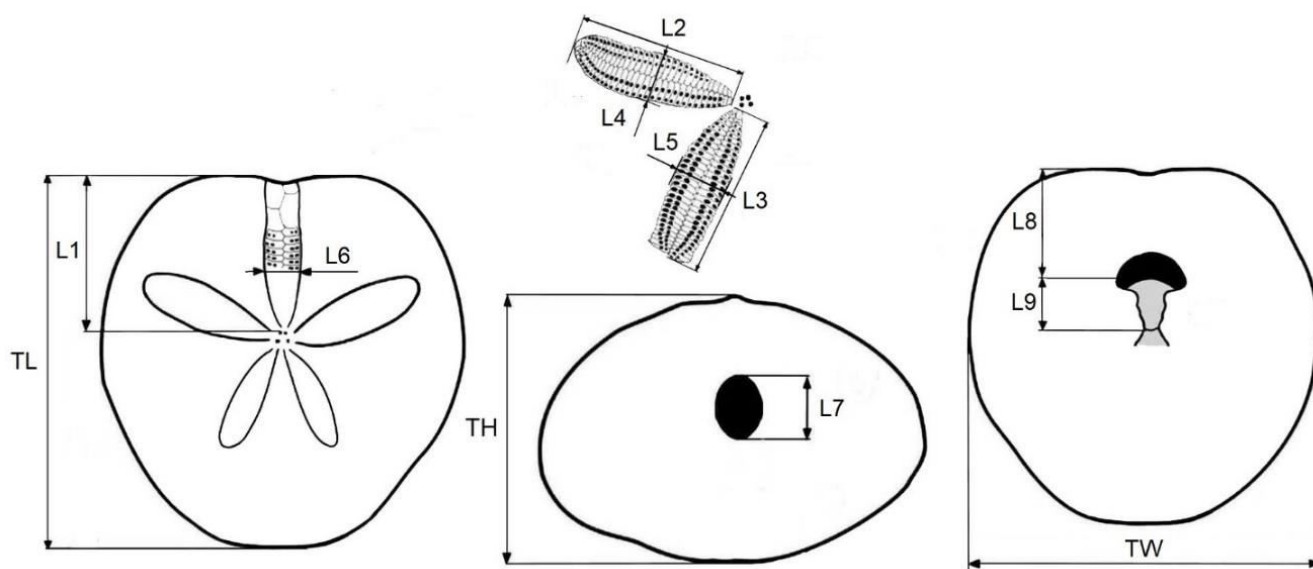


Figure 2 – Scheme of the morphometric measures taken in the examined specimens.

Figura 2 – Schema delle misure rilevate sugli esemplari studiati



Finding localities

The two specimens under study were collected by one of the authors (F.C.) in a limestone quarry of Sossano, located in the south-western slope of the Berici Hills (Fig. 1).

Geo-stratigraphy and paleoenvironments of the Eocene deposits in this area have been studied by Fabiani (1908, 1915), Ungaro (1978), Mietto (1988, 2003) and Bassi (1995). A paleosinecological analysis of the community present at Sossano in an Upper Eocene level rich in the annelid polychaete *Rotularia spirulea* Lamarck, 1818, has been provided by Accorsi Benini *et al.* (1988).

This quarry (Cava di Via Piare) was active since the end of the 1960s to the 2005; after that time the quarry was abandoned and underwent an environmental reinstatement. Notwithstanding the restoration works, the Eocene section, about 50 m thick, is still well visible. It consists mainly of middle Eocene (Lutetian) calcareous limestones, utilised in concrete production, overlaid by about 8 m of Upper Eocene grey marly limestones (De Angeli & Caporiondo, 2009) belonging to the Priabona Formation. The marly limestones are well stratified and become yellowish when weathered. They are rich in macrofossils, consisting above all of nummulites, bryozoans and, less frequently, bivalves, crustaceans, fish teeth and echinoids.

The two specimens under study were collected in the Upper Eocene marly limestones, associated with other echinoids, such as *Scholechinus*, *Clypeaster*, *Gitolampas*, *Echinolampas*, *Trachypatagus*, *Waurnia* and *Crucibrissus* (Borghi *et al.*, 2022, 2024).

Previous work

The genus *Gregoryaster* was established by Lambert (1907) on the basis of a specimen originally assigned by Wright (1855) to the genus *Hemiaster* Desor, in Agassiz and Desor, 1847, as *Hemiaster grateloupi*, and was subsequently transferred by the same author (Wright, 1864) to *Brissopsis* L. Agassiz, 1840, as *Brissopsis grateloupi*. Later on, the type specimen was reassigned to a new species, *Pericosmus coranguinum*, by Gregory (1892). The generic position of the type species has been changed several times since then, due to the lack of adequate diagnostic features distinguishing *Gregoryaster* from other similar spatangoids.

Several species have been attributed to the genus (or subgenus) *Gregoryaster*, from the Cretaceous to the Lower Miocene (e.g., Forbes, 1856; Lambert & Thiery, 1921). However, Smith & Kroh (2011) affirmed that, although Lambert & Thiery (1921) included many species in *Gregoryaster*, most of them cannot be included for certain and need confirmation. They also considered *Trachyaster heberti* Cotteau, 1887 from the Eocene of France and Spain (Cotteau, 1890), as possibly belonging to *Gregoryaster*.

Gregoryaster is accepted as a valid genus in Kroh & Mooi (2024) but no valid species are indicated in that web site (WoRMS), thus underlying the uncertainty affecting the taxonomy of this genus.

A recent revision (Stara *et al.*, 2022) of *Gregoryaster* and *Opissaster* Pomel 1883, two echinoids apparently closely related on the basis of their overall morphology, cleared the morphological differences between them and fixed the diagnostic characters of *Gregoryaster* on the basis of the study of topo-typic material.

After Stara *et al.* (2022), *Gregoryaster* is present for certain only in the Oligocene (Chattian) and Lower Miocene of Malta (Wright, 1855, 1864; Gatt, 2006; Challis, 1980; Cappelletti, 2008) and in the Aquitanian-Burdigalian of Sardinia, where a new species *G. cabiddui* Stara *et al.*, 2022, has been described.

Gregoryaster has been recently recognised also in the Middle Miocene of the Northern Apennines (Rondelli & Battilani, 2023), on the basis of specimens from the Lower Langhian of the Pantano Formation previously attributed by Stefanini (1908) to the genus *Hemiaster*.

Results

Phylogenetic results: Our analysis (Fig. 3) places *Gregoryaster* immediately stemwards of a clade containing *Periaster*, *Brisaster* and *Schizaster* (posterior probability= 0.81). This clade is here interpreted as Schizasteridae (we follow Stockley *et al.*, 2005 and Smith & Kroh, 2011 in considering *Periaster* a schizasterid). These results clearly demonstrate it is premature to assign *Gregoryaster* to a family other than Schizasteridae Lambert, 1905 until more precise phylogenetic analyses, containing other similar taxa (eg. *Linthia*), are carried out. Our analysis



- Ambulacrum III narrow, with very shallow sulcus aborally which shallows close to the ambitus. Pore-pairs closely spaced, with enlarged periporal bulge.
- Paired ambulacra petaloid; petals long, straight and sunken. Anterior petals widely diverging; posterior pair almost as long as anterior pair.
- Peristome small, kidney-shaped, rather close to the anterior test margin.
- Labrum elongated, extending to the second adjacent ambulacral plates and partially covering the peristome; sternal plates large and symmetrical; forming most of oral surface. Episternal plates biserially offset.
- Periproct small, commonly oval and vertically elongated, located on the upper part of the posterior truncate face.
- Peripetalous fasciole present, indented behind the anterior paired petals in the interambulacral columns 1b and 4a. Traces of a thin marginal fasciole may be present in the posterior aboral part of the test.
- Aboral tuberculation uniform and dense.

Remarks: in past times, the type species of *Gregoryaster* has been assigned to other genera, such as *Hemiaster* Desor, in Agassiz & Desor, 1847, and *Pericosmus* Agassiz, in Agassiz & Desor, 1847, on the basis of the overall test morphology. Also, *Opissaster* Pomel 1883, is apparently closely related.

The main characters separating among these four genera are reassumed in Stara *et al.* (2022, tab. 6).

Hemiaster is nowadays restricted to forms having an ethmophract apical system, a labrum in contact with three ambulacral plates per side and asymmetric sternal plates separated by an oblique suture (Smith & Kroh, 2011). Additionally, the peripetalous fasciole is not deeply indented in the interambulacra 2 and 3 and behind the paired anterior ambulacra.

Pericosmus includes exclusively forms with an ethmolytic apical system bearing three gonopores; additionally, it has a peripetalous fasciole doubling in the interambulacra 2 and 3 (Smith & Kroh, 2011) and the frontal ambulacrum is continuous (not petaloid).

Opissaster differs from *Gregoryaster* by the course of the peripetalous fasciole, which is deeply indented in the interambulacra 2 and 3 and behind the paired anterior ambulacra; additionally, in *Gregoryaster* the labrum is in contact with two ambulacral plates instead of one, and the periproct is vertically-elongated (Stara *et al.*, 2022).

Gregoryaster has been assigned to different families, such as the Hemiasteridae Clark, 1917, and the Pericosmidae Lambert, 1905. However, the pathway of the peripetalous fasciole, which crosses the first ambulacral plate under the petaloid tract and plates 4a and 4b in the interambulacra 2 and 3, the presence of an ethmolytic apical disc and of differentiated pore pairs in the ambulacrum III, confirm the affinities of *Gregoryaster* to the family Schizasteridae Lambert, 1905. After Stara *et al.* (2022), this placement requires further investigations on possibly related spatangoids, because *Gregoryaster* differs from most schizasterids by the absence of the anterior sulcus, anterior and posterior paired-petals almost similar in length, the absence of the latero-anal fasciole and the labrum reaching the second ambulacral plate. This placement is actually accepted in Kroh & Mooi (2024) and our cladistic analysis supports it (Fig. 3).

Trachyaster heberti Cotteau, 1887 is here considered as a true *Gregoryaster*: only the peripetalous fasciole is present and it is not deeply indented in the interambulacra 2 and 3 (Cotteau, 1887: pl. 113, fig 2; 1890, pl. 5, fig. 6), the periproct is vertically elongated. Additionally, a specimen (HMNG.27808) from the Eocene of Callosa (Spain) shows the labrum extending back to the second ambulacral plate (see Smiht & Kroh, 2011): this feature was not known in the type material.

Both the Eocene species *Hemiaster praeceps* Bittner, 1882, from Negrar (Verona Province), and *Hemiaster galantigensis* de Loriol, 1891, from Galantiga near Montecchio Maggiore (Vicenza Province), possibly belong to *Gregoryaster*, based on the original description and illustration. In the types, the sole specimens so far known of these species, the pathway of the peripetalous fasciole and the other visible features are consistent with those in *Gregoryaster*, the periproct is vertically elongate, no other fascioles are visible. Unluckily, the oral plating is unknown and re-examination of the respective type specimens is needed to confirm their systematic position.

After Smith & Kroh (2011), *Brissus expansus* Forbes, 1856, Campanian-Maastrichtian of southern India, possibly belongs to *Gregoryaster*, however, its sharp frontal groove extending from apex to mouth is very different from the shallow anterior sulcus in *G. coranguinum*.

Distribution: Eocene, Oligocene and Lower to Middle Miocene, Malta, Spain, France and Italy.

Species included:

- *Gregoryaster heberti* (Cotteau, 1887): Eocene of Spain and southern France.
- *Gregoryaster coranguinum* (Gregory, 1892): Priabonian of Italy, Chattian to Aquitanian of Malta.
- *Gregoryaster cabiddui* Stara *et al.*, 2022: Aquitanian-Burdigalian of Sardinia (Italy).

***Gregoryaster coranguinum* (Gregory, 1892)**

Figg. 3-4, Tab. 1

Simplified synonymy:

1855 - *Hemiaster grateloupi* non Sismonda – pars; Wright: 189-190

1892 - *Pericosmus coranguinum* Gregory: 615-616

1907 - *Gregoryaster coranguinum* (Gregory, 1892); Lambert: 61

1975 - *Hemiaster* (*Gregoryaster*) *coranguinum*; Rose: 79

1979 - *Hemiaster coranguinus* (Gregory, 1892); Menesini: 60

1980 - *Hemiaster* (*Gregoryaster*) *coranguinum* (Gregory, 1892); Challis: 187-190

2006 - *Hemiaster* (*Gregoryaster*) *coranguinum* (Gregory, 1892); Gatt: 243-244

2008 - *Hemiaster* (*Gregoryaster*) *coranguinum* (Gregory, 1892); Cappelletti: 113.

Type species: *Pericosmus coranguinum* Gregory, 1892, by original designation.

Type material: Holotype (NHM E3429).

Material examined: MCV 24/120 and MCV 24/121, Priabonian of Sossano (North Italy).

Diagnosis (from Stara *et al.*, 2022): a medium to large-sized species of *Gregoryaster*, with a test almost as long as wide, globose and with height from medium-high to high; posterior face tilted upwards with periproct visible from above; very shallow anterior sulcus; labrum long and narrow, widening over the stoma and in contact with two ambulacral plates on each side.

Remarks: the specimens from Sossano match with the description and the biometric data provided by Stara *et al.* (2022) for *Gregoryaster coranguinum*. Slight differences can be found only in the petals, that are shorter in proportion to the test length, and the peristome, which is farther from the anterior test margin. No traces of fascioles other than the peripetalous are visible.

		TL	TW	TH	L1	L2	L3	L2/L3	L4	L5	L6	L7	L8	L9	α
MCV 24/120	mm	67	63	46	29	24	16	1.5	6	4	4.5	7	20	8	122°
	%TL	-	94	69	42	36	24	-	9	6	7	10	30	12	-
MCV 24/121	mm	69	66	-	27	22	14	1.2	6	4	4.5	-	19	-	130°
	%TL	-	96	-	39	32	20	-	9	6	6.5	-	28	-	-

Table 1 – *Gregoryaster coranguinum* (Gregory, 1892), Upper Eocene of Sossano: main biometric data.

Tabella 1 – *Gregoryaster coranguinum* (Gregory, 1892), Eocene superiore di Sossano: dati biometrici principali

The attribution to *Gregoryaster* of *Hemiaster praeceps* Bittner, 1882, and *H. galantigensis* de Loriol, 1891, from the Eocene of Veneto, is doubtful and needs confirmation. Anyway, *H. praeceps* differs from the specimens from Sossano by smaller and much higher test (TH = 91% TL) and the peripetalous fasciole is more indented behind the anterior paired petals. In *H. galantigensis* the anterior ambulacrum is much larger and the peripetalous fasciole is not indented at all behind the anterior paired petals,

Gregoryaster heberti (Cotteau, 1887), from the Eocene (Lutetian) of Spain, has the peripetalous fasciole deeply indented behind the ambulacra II and IV and the anterior sulcus is deeper.

Gregoryaster cabiddui Stara *et al.*, 2022, differs from the two specimens under study by its much lower test (mean TH = 42.7% TL against 63% TL) and less numerous tubercles. In *G. cabiddui* the peristome opens much closer to

the anterior margin ($L8 = 13.3\% \text{ TL}$, against $28\% \text{ TL}$) and the posterior face is inclined towards the posterior, while it is almost vertical in the specimens from Sossano.

Distribution: Upper Eocene Priabona formation of North-eastern Italy, Chattian to Aquitanian of Malta.

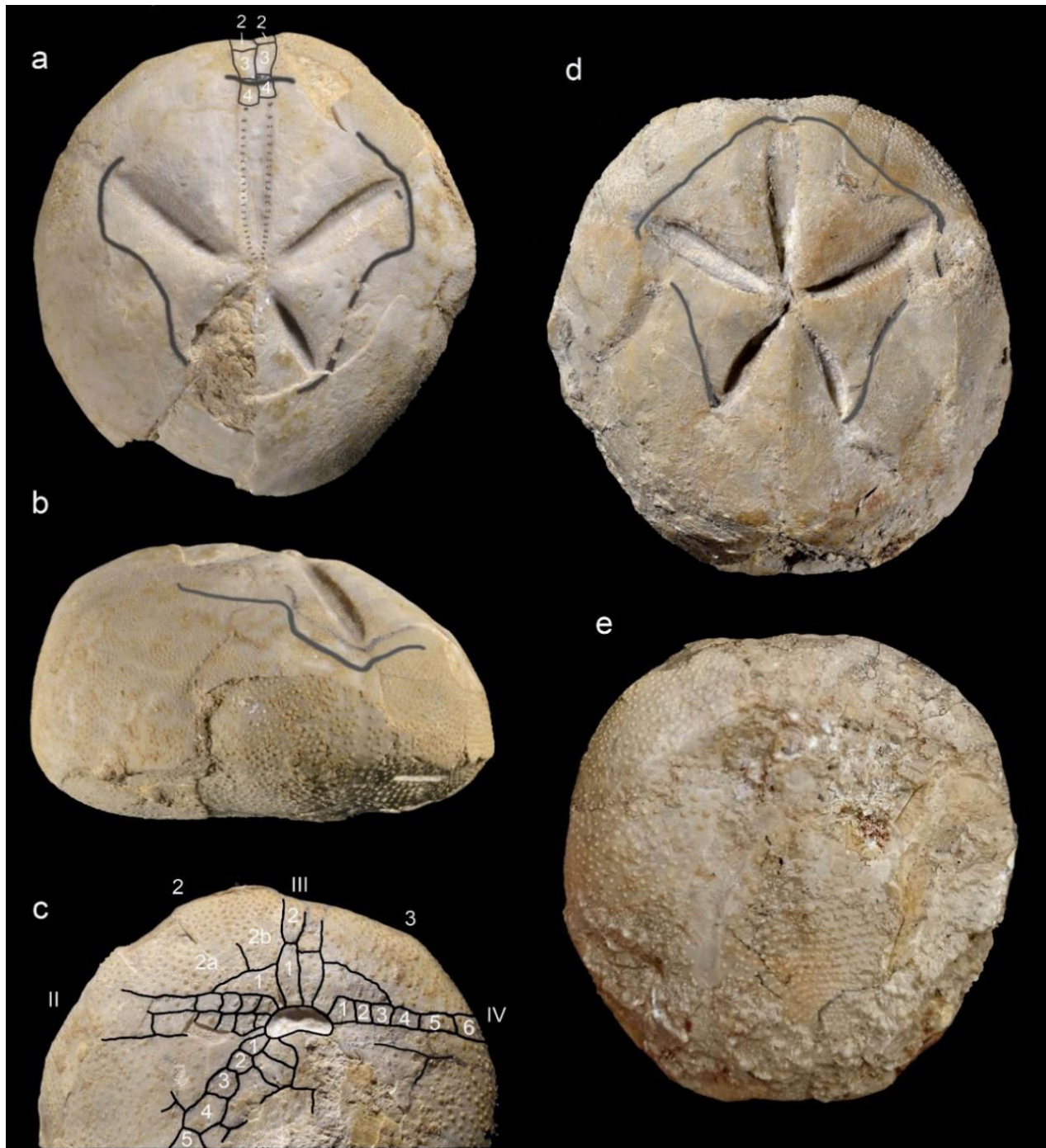


Figure 4 – *Gregoryaster coranguinum* (Gregory, 1892) Upper Eocene of Sossano; a-c) MCV 24/120, TL = 67 mm: a) aboral, b) lateral and c) oral views (with plating scheme); d-e) MCV 24/121, TL = 69 mm: aboral (d) and oral (e) views. The scale bar equals 1 cm.

Figura 4 – *Gregoryaster coranguinum* (Gregory, 1892), Eocene superiore di Sossano; a-c) MCV 24/120, TL = 67 mm: a) vista aborale, b) laterale e c) orale (con schema delle piastre); d-e) MCV 24/121, TL = 69 mm: vista aborale (d) e orale (e). La barretta indica 1 cm.



Palaeoecological remarks

Gregoryaster is an extinct echinoid and no closely related genera are present in Recent seas. The reconstruction of its paleoecology is therefore based on the functional morphological interpretation of test features (Smith, 1980a, b; Smith, 1984). In particular, some traits indicate infaunal, deposit feeding, lifestyle:

- the partitioned isopores present in the frontal ambulacrum supported funnel building tube feet
- the peripetalous fasciole was used to create ciliary currents within the burrow in endobenthic echinoids (Smith & Stockley, 2005)
- the fine, almost uniform and dense aboral tuberculation supported a dense canopy of spines enabling burrowing within fine-grained substrates, using the dorsal spines to support the top of the burrow and to maintain a space for water circulation (Gale & Smith, 1982)
- the plastron is densely covered by crenulated tubercles with a posterior areole enlargement, while tubercles on both sides of the oral face do not reach such high density and have a reduced, slightly asymmetric areole; plastron tubercles are associated to spines with a locomotory function, whereas lateral tubercles are associated with digging spines (Smith, 1984)
- phyllodes are well developed: they consist of enlarged pores with an extensive peri-poral area which supported specialized (penicillate) tube feet for picking up sediment particles (Smith, 1980b).

The tubercles arrangement, the presence of peripetalous fasciole and phyllodes indicate that *Gregoryaster* was a deposit feeder unable to burrow deeply into fine-grained sediments.

In the Priabonian of Sossano this echinoid lived in the upper Circalittoral at a depth of about 50-100 m, in well oxygenated environments, within a highly diverse faunal assemblage (Bassi, 1995). This is corroborated by the frequent occurrence in the same marly deposit of typical shallow to moderate depth echinoids, such as *Clypeaster*, *Gitolampas*, *Echinolampas* and *Trachypatagus* (Borghi *et al.*, 2024).

Acknowledgements

The authors warmly thank Bernardetta Pallozzi (Museo Civico “Dal Lago”, Valdarno), for allowing access to the specimens studied, and Riccardo Rondelli (Società Reggiana di Scienze Naturali), for helpful suggestions to the first manuscript. Many thanks also to Zilio Zordan (Valdarno), for translation of ancient German texts.

Bibliography

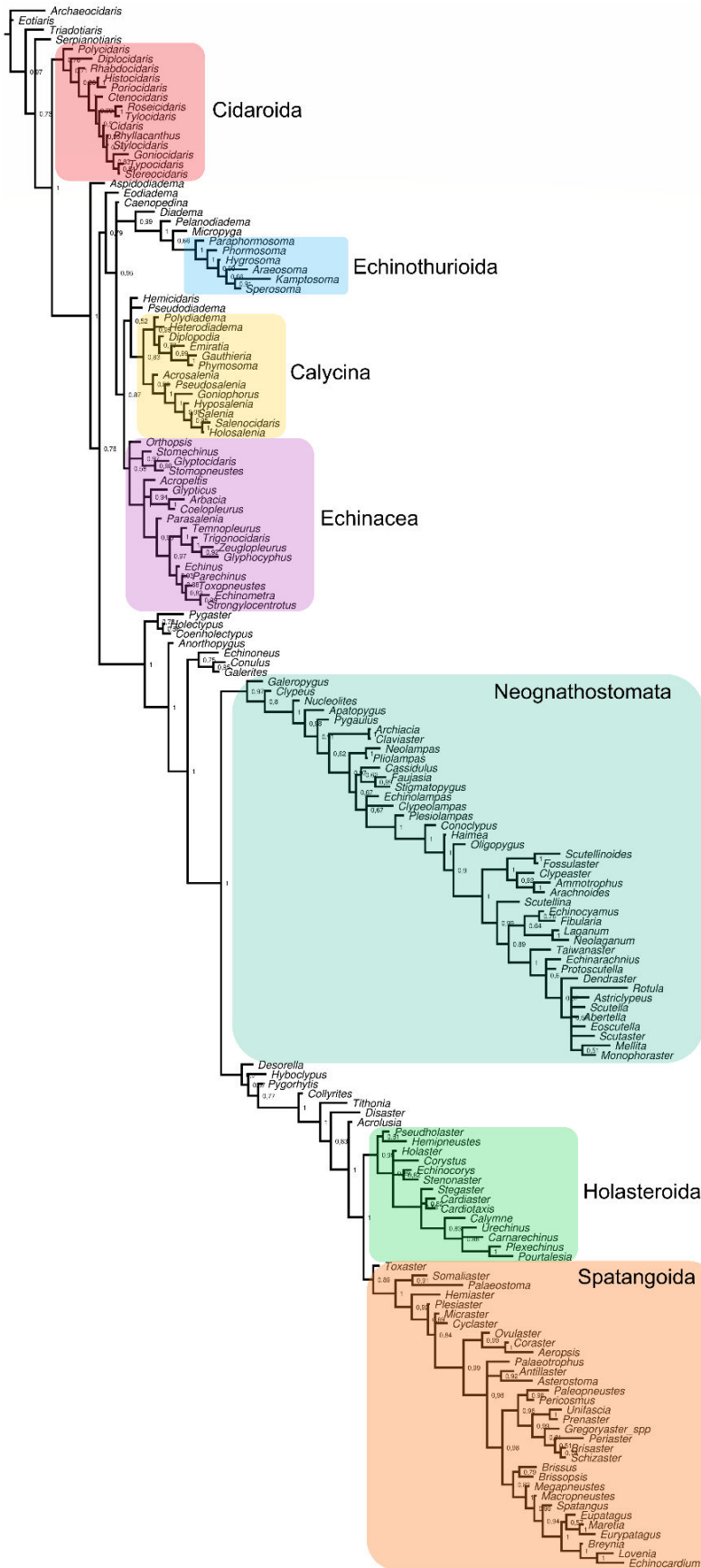
- AGASSIZ L. (1840). Catalogus systematicus Ectyporum Echinodermatum fossilium Musei Neocomiensis, secundum ordinem zoologicum dispositus; adjectis synonymis recentioribus, nec non stratis et locis in quibus reperiuntur. Sequuntur characteres diagnostici generum novorum vel minus cognitorum. 1-20 pp. Neuchâtel (O. Petitpierre).
- AGASSIZ L. & DESOR P.J.E. (1847). Catalogue raisonné des familles, des genres, et des espèces de la classe des échinodermes. *Annales des Sciences Naturelles, Troisième Série, Zoologie* 8: 5-35, 355-380.
- BASSI D. (1995). Crustose coralline algal pavements from late Eocene Colli Berici of Northern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 101(1): 81-92.
- BITTNER A. (1882). Beiträge zur Kenntnis alttertiärer Echinidenfaunen der Südalpen. Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, 1/2: 73-110.
- BORCHI E., BOTTAZZI A. & CAPORIONDO F. (2022). A new species of *Scoelechinus* (Echinoidea) from the Eocene of Italy. *Studi e Ricerche*, Museo Civico “G. Zannato”, Montecchio Maggiore (Vicenza), 28 (2021): 13-19.
- BORCHI E., BOTTAZZI A. & CAPORIONDO F. (2024). *Crucibrissus* and *Waurnia*, two rare echinoids in the Eocene of north-eastern Italy. *Notiziario della Società Reggiana di Scienze Naturali*, (2023): 18-30.
- CAPPELLETTI E. (2008). Gli echinoidi miocenici dell’Arcipelago Maltese: studio sistematico ed affinità biogeografica. Unpublished thesis, University of Pisa, pp. 225.



- CHALLIS G.R. (1980). Palaeoecology and Taxonomy of Mid-Tertiary Maltese Echinoids. Unpublished Ph.D. thesis, Bedford College, University of London, pp. 401.
- COPPARD S.E., KROH A. & SMITH A.B. (2010). The evolution of pedicellariae in echinoids: an arms race against pests and parasites. *Acta Zoologica*, 93: 125-148. <https://doi.org/10.1111/j.1463-6395.2010.00487.x>
- FORBES E. (1846). Report on the Fossil Invertebrata from Southern India, collected by Mr. Kaye and Mr. Cunliffe. *Transactions of the Geological Society*, London, 7(2): 1-160.
- GALE A.S. & SMITH A.B. (1982). The palaeobiology of the Cretaceous irregular echinoids *Infulaster* and *Hagenowia*. *Palaeontology*, 25: 11-12.
- GATT M. (2006). Il-Geologija u l-Paleontologija tal-Gzejjer Maltin. Pubblikazzjonijiet Indipendenza, Malta, Vol. 2, i-viii, 265-470.
- GREGORY J.W. (1892). The Maltese fossil Echinoidea and their evidence on the correlation of the Maltese rocks. *Transactions of the Royal Society of Edinburgh*, 36: 585-639.
- KROH A. & MOOI R. (2024). World Echinoidea Database. *Gregoryaster* Lambert, 1907. Accessed through: World Register of Marine Species at: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=512838> on 2024-06-24.
- KROH A. & SMITH A.B. (2010). The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology*, 8(2): 147-212.
- LAMBERT J.M. (1907). Description des Echinides Fossiles des Terrain Miocéniques de la Sardaigne. *Mémoires de la Société Paléontologique Suisse*, 34: 1-72.
- LAMBERT J.M. & THIERY P. (1921). Essai de Nomenclature Raisonnée des Échinides. fasc. 5: 321-384 (Septembre 1921). Chaumont (L. Ferrière).
- LOVEN S. (1874). Etudes sur les Echinoidees. *Kongelige Svenska Vetenskaps-Akademiens Handlingar*, 11: 1-91.
- MENESINI E. (1979). Echinidi Fossili dell'Arcipelago Maltese. *Atti della Società Toscana di Scienze Naturali, Memorie, Serie A*, 86: 51-64.
- RONDELLI R. & BATTILANI D. (2023). Il genere *Gregoryaster* nel Langhiano dell'Appennino emiliano. *Atti della Società dei Naturalisti e Matematici di Modena*, 154: 141-156.
- RONQUIST F., TESLENKO M., VAN DER MARK P., AYRES D.L., DARLING A., HOHNA S., LARGET B., LIU L., SUCHARD M.A. & HUELSENBECK J.P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61: 539-542.
- ROSE E.P.F. (1975). Oligo-Miocene Echinoids of the Maltese Islands. Proceedings of the VIth Congress Regional Committee on Mediterranean Neogene Stratigraphy, Bratislava, 1: 75-79.
- SMITH A.B. (1980a). The structure and arrangement of echinoid tubercles. *Philosophical Transaction of the Royal Society of London B*, 289: 1-54.
- SMITH A.B. (1980b). The structure, function, and evolution of tube feet and ambulacral pores in irregular echinoids. *Palaeontology*, 23: 39- 83.
- SMITH A.B. (1984). Echinoid Palaeobiology. George Allen and Unwin Ltd, London, 199 pp.
- SMITH A.B. & KROH. A. (Eds.) (2011). The Echinoid Directory. World Wide Web electronic publication. <http://www.nhm.ac.uk/scienceprojects/echinoids> (accessed June, 2024).
- STOCKLEY B., SMITH A.B., LITTLEWOOD T., LESSIOS H.A., MACKENZIE-DODDS J.A. (2005). Phylogenetic relationships of spatangoid sea urchins (Echinoidea): taxon sampling density and congruence between morphological and molecular estimates. *Zoological Scripta*, 34(5): 447-468.
- WRIGHT T. (1855). On Fossil Echinoderms from the Island of Malta; with notes on the stratigraphical distribution of the fossil organisms in the Maltese Beds. *Annals and Magazine of Natural History*, 15: 101-276.
- WRIGHT T. (1864). On the fossil Echinidea of Malta – with additional notes on the Miocene Beds of the Island, and the Stratigraphical Distribution of the Species therein. *Quarterly Journal of the Geological Society of London*, 20: 470-191.

Figure 5 (next page) – Complete cladogram.

Figure 5 (pagina seguente) – Cladogramma completo.





APPENDIX: FULL MATRIX AND SCRIPT USED FOR THE BAYESIAN PHYLOGENETIC ANALYSIS

```
#NEXUS
BEGIN DATA;
DIMENSIONS NTAX=163 NCHAR=304;
FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = " 0 1 2 3 4 5 6 7 8 9 ";
MATRIX
Archaeocidaris 01010000000-0-0000100000-000000000110000?????????10-1005060?11?00000???000010-0-000-1-
-0--0000000000000000001100000-000000000-?000000-0-00-000-----
0010000----0000--000020?0----0-00--00-110011000203001000--000030000000000000-0110?0-
000000110001000102001000?0-1000000000000000-----00-00000?00-00000----
Triadotiaris 00010000000-0-0000100000-000000000?00020----012010-1105150??10000000100000?010-?-020-0-
532?00000000000000001201100000-000000000-?000000-0-00-000-----
0110000----0000--000020?0----0-00--00-110011100223000000--000030000000000000-
01?0?2200000011000100010200111100-0000?00000000?????00-00000?00-00000----
Roseicidaris 00010000000-0-002100000?-000000000?0000?0??0??10-?????????????????????????0-0-000-1--0--
0000000000000000001100000-000000000-?000001-0-00-000-----
0110000----0000--000010?0----0-00--00-110011011103110000--000030000000000000-
0???2?00000011???????????1?????????????????0?0?0???00-00000?00-00000----
Typocidaris 00010000000-0-002100001?2000000000000000?0??0?0??10-?????????????????????????0-?-000-1--0--
0000000000001000001100000-000000000-?000001-0-00-000-----
0110000----0000--000010?0----0-00--00-110011011203000000--000030000000000000-
0???2?00000011???????????1?????????????????0?0?0???00-00000?00-00000----
Phyllacanthus 00010000000-0-0021000000-000000000?00003-----012010-11051500000000000000000000-0-000-1--
0--0000000000001000001100000-000000000-5000001-0-00-000-----
0110000----0000--000020?0----0-00--00-110011001203000000--000030000000000000-
0110021000000110001000?0??111101020010000000000-----00-00000?00-00000----
Serpianotiaris 00010000000-0-0020100000-000000000?00003-----012010-1105150?00000000000000000000-0-010-
01532?0000000000000000001110000-0000000002?000001-0-00-000-----
0110000----0000--000020?0----0-00--00-110001000223001000--000030000000000000-
01?0?2000000?1100?1000?0?00111100-0000?00000000?????00-00000?00-00000----
Polycidaris 00010000000-0-0011000000-000000000?00000-----012010-1105150?0000000001010000000-0-020-
00030?0000000000000000001100000-000000000-?000001-0-00-000-----
0110000----0000--000020?0----0-00--00-110010-00223000000--000030000000000000-
0???2?0000001100?0?0?000001?101010??00000000?????00-00000?00-00000----
Diplocidaris 00010000000-0-0021000000-000000000?00002-----012000-100515001000000000000001??0-0-020-
00020?00000000000002001101100000-000000000-?000001-0-00-000-----
0110000----0000--000020?0----0-00--00-110011000223000000--000030000000000000-
0???2100000011000?0????001?1?01010??00000000?????00-00000?00-00000----
Rhabdocidaris 00010000000-0-0021000000-000000000100003-----012010-1105150?0000000001000000000-0-040-
00020?0000000000001000001100000-000000000-?000001-0-00-000-----
0110000----0000--000020?0----0-00--00-110011000223000000--000030000000000000-
0???2100000011???????????1?110102000?000000000-----00-00000?00-00000----
Histocidaris 00010000000-0-0021000000-000000000100003-----012010-110515010000000000000000000-0-000-1--
0--0000000000000000001100000-000000000-5000001-0-00-000-----
0110000----0000--000020?0----0-00--00-110011100223000000--000030000000000000-
0110121000000110001000?0?00111101020100000000000-----00-00000?00-00000----
Poriocidaris 00010000000-0-0021000000-000000000?00003-----012010-110515110000000000000000000-0-000-1--
0--0000000000000000001100000-000000000-5000001-0-00-000-----
0110000----0000--000020?0----0-00--00-110011100223000000--000030000000000000-
011012?000000110001000?0?00111101100100000000000-----00-00000?00-00000----
Stylocidaris 00010000000-0-0021000000-0000000000000003-----012010-11051500000000000000000000-0-000-1--
0--0000000000001000001100000-000000000-5000001-0-00-000-----
0110000----0000--000020?0----0-00--00-110011001203000000--000030000000000000-
011002100000011000100000000111101020010000000000-----00-00000?00-00000----
```



Cidaris 0001000000-0-002100000-0000000000000003-----012010-110515000000000000000000-0-000-1--0--
0000000000000000001100000-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110011001203000000--000030000000000000-
01100210000001100010000000011101020010000000000-----00-00000?00-00000----
Ctenocidaris 0001000000-0-002100000-000000000?00003-----012010-110515010000000000000000000-0-000-1--
0--0000000000000000001100000-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110010-01203000000--000030000000000000-
0110021000000110001000?0?001110103000000000000000-----00-00000?00-00000----
Goniocidaris 0001000000-0-0021000010200000000000000000-----012010-110515010000000001010000000-0-000-1-
-0--0000000000000000001100000-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110011001203000000--000030000000000000-
0110021000000110001000?0?0011101010010100000000-----00-00000?00-00000----
Tylocidaris 0001000000-0-002100000-000000000?00002-----012010-11051500000000000000000000-0-000-1--
0--0000000000000000001100000-000000000-?000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110011011003110000--000030000000000000-
0100021000000110001000?0?00111?01020000000100000-----00-00000?00-00000----
Eotiaris 0001000000-0-002010000?000000000?0000??????0??10-
1?????????????????????0-?0???0??-0-??-??0-----
0110000----0000--000020??0----0-00--00-11001100022?000000--0000?000?00000000-
0????200??0011000?000?0?00110000-1000?00000000?0000?00-00000?00-00000----
Stereocidaris 0001000000-0-0021000010200000000000000003-----012010-11051500000000000000000000-0-000-1--
0--0000000000001000001100000-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110011011203000000--000030000000000000-
01100210000001100010000000011101020010100000000-----00-00000?00-00000----
Pelanodiadema 0?010000000-0-0010000000-000000000?00000-----012010-1005150??1000000010000?0?0-0-
0221011321000-000000000002201110000-00000000033000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110100-00202000000--
000020000000000001101000?0??000110111000?0000111?00-0000?00?00000?0??0-00000?00-00000----
Araeosoma 0101000000-0-0000001100-0000000001100000-----012010-1005153?1100000001000000010-0-020-
012321011-000000000002213300000-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-10--00-100000-00202000000--000020000000000000-
010001202100011011100010000110000-000021100000010300000-00000?00-00000----
Hygrosoma 0101000000-0-0000000000-000000000?00020-----012010-1005153?1102000001000000010-0-020-
012321011-000000000002211100100-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-00--00-101000-00201000000--000020000000000000-
01000?0?0001101?1000?0000110000-000021100000010300100-00000?00-00000----
Kamptosoma 0101000000-0-0000000000-000000000?00020-----012010-10051?0?1000000001100000010-0-020-
012321011-010000003000010000100-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-?0--00-110000-00223000000--000010000000000000-020000-
02?0001101?1000?0000110000-000020000000010300000-00000?00-00000----
Paraphormosoma 0101000000-0-0000000000-000000000?00020-----012010-1005150?1000000001000000010-0-020-
014321001-010000000002201100000-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-00--00-101000-00201000000--000020000000000000-
01000120210001101?1000?0000110000-000020010000010300000-00000?00-00000----
Phormosoma 0101000000-0-0000000000-0000000001100020-----012010-10001530-10200000-000000010-0-020-
011321011-000000000002011100000-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-?0--00-101000-00201000000--000020000000000000-
010002202100011011100010000110000-000020010000010300100-00000?00-00000----
Sperosoma 0101000000-0-0000000000-000000000?00020-----012010-1005153?1102000001100000010-0-020-
014321001-000000000002210000100-000000000-5000001-0-00-000-----
0110000----0000--000020??0----0-00--00-100000-00201000000--000020000000000000-
01000?0?0001101?1000?0000110000-000021100000010300000-00000?00-00000----
Aspidodiadema 0001000000-0-002100000-0000000001100000-----012010-100515000000000001000000030-0-020-
00030?0000000000000000000100000-000000000-3000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110000-00221000000--000020000000000010020000-
020000110111000?0000112000-010000000000011300000-00000?00-00000----

Diadema 00010000000-0-0011000000-000000000110000101100012010-10051500110000000000000010020-0-02210003010002000000000000001110000-00000000033000001-0-00-000-----
0110000---0000-000020??0---0-00--00-101000-0022000000--
000020000000000011020002202100011011100010000110010-0100?0010000010300000-00000?00-00000----
Micropyga 01010000000-0-0010000000-0000000001100000----012010-100515001100000001000000010-0-0221011321000-000000000001101100000-000000000-3000001-0-00-000-----
0110000---0000-000020??0---0-10--00-101000-00201000000--00002000000000001020000-
020000110111000?0000110000-000001000000010300000-00000?00-00000----
Caenopodina 00010000000-0-0021000000-0000000001100002----012000-10051500000000000000000010010-0-02210003010002000000000000001110000-0000000003?000001-0-00-000-----
0110000---0000-000020??0---0-00--00-110000-00203000000--000020000000000010020000-
020000110111000?0000111000-000000000000010300000-00000?00-00000----
Eodiadema 00010000000-0-0021000000-000000000?0000101110012000-1005150?0100000000000{01}1???0-?-012000030?0000000000000000001100000-000000000-?000001-0-00-000-----
0110000---0000-000020??0---0-00--00-110010-01223000000--
0000200000000000100?0??0??0??001101?1000?000011?000-0000?0??000?0?0??00-00000?00-00000----
Orthopsis 00010000000-0-0021000000-000000000?00002----012000-100515000000000000000000{01}1???0-?-022000030?0000000000000000001110000-0000000001?000001-0-00-000-----
0110000---0000-000020??0---0-00--00-110100-10201000000--0000200000000000100?0??0-
021000110111100?000011?00-0000?00000000?0??00-00000?00-00000----
Acrosalenia 00010000000-0-0021000000-000000000110000101110012000-11051500000000000000000221??0-?-02200003010002000000000000001110000-0000000001?000001-0-00-000-----
0110000---0000-000020??0---0-10--00-110010-00223000000--000020000000000011020000-
02100011010?10010000111?010000000000000010200000-00000?00-00000----
Hyposalenia 00010000000-0-0021000001-000000000?00002----012000-111515000000010000000221??0-?-022000020?0002000000000000001110000-0000000001?000001-0-00-000-----
0110000---0000-000010??0---0-00--00-110010-00023000000--0000300000000000100?0??0-
02000011?0??0??0??0??0?1?0110000?00000000?0??00-00000?00-00000----
Salenia 00010000000-0-0021000001-0000000001100002----012000-111515000000010000000222010-0-022000020?0002000000000000001110000-00000000013000001-0-00-000-----
0110000---0000-000020??0---0-00--00-110010-00023000000--000030000000000010020000-
020000110101100100001110010000000000000010-1-200-00000?00-00000----
Salenocidaris 00010000000-0-0021000000-000000000110000101111012000-111515000000000000000222010-0-012000020?0002000000000000001100000-000000000-3000001-0-00-000-----
0110000---0000-000020??0---0-00--00-110011100023000000--0000300000000000010020000-
020000110101100100001110010000000000000010111200-00000?00-00000----
Gauthieria 00010000000-0-0021000000-000000000?00000----012010-1105150?01000000010000210?0-?-02220014320002000000000000001110000-000000000-?000001-0-00-000-----
0110000---0000-000020??0---0-10--00-110000-00011001000--
0000200000000000100?0??1202000011?0??0??0??0??0?100100000?00000000?0??00-00000?00-00000----
Arbacia 00010000000-0-0021000000-0001000000(01)00002----012000-100515000000001000001010110-0-0221001321000-000000001000001111000-00000000033000001-0-00-000-----0100000000000002000020000----
02(01)0-100-101000-0000110000--0000200000000000010120000-02000011011110010000111000-000000000000011001-00-00000?00-00000----
Glypticus 00010000000-0-0021000001-0001000000100002----012000-100515000000001010000{01}1???0-?-022100131?0002000000002000001110000-0000000001?000001-0-00-000-----
0110000---0000-000010??0---0-00--00-110000-00002100000--
0000200000000000100?0??0??0??0??0?1?01020??00000000?0??00-00000?00-00000----
Acropeltis 00010000000-0-0021000000-000000000?00002----012000-100515100100000200000{01}1???0-?-022100131?0002000000000000001110000-0000000001?000001-0-00-000-----
0110000---0000-000010??0---0-00--00-110000-00001100000--
0000200000000000100?0??0??0??0??0?1?01?0000?00000000?0??00-00000?00-00000----
Coelopleurus 00010000000-0-0021000000-000100000?00002----012000-100515000000001100001010110-0-0221001321000-0000000000000011(01)1000-000000000(01)3000001-0-00-000-----0100000000000002000020000----
0210-100-110000-00001000000--000020000000000010120000-
021000110111100100001110011000000000000011201000-00000?00-00000----



Glyptocidaris 00010000000-0-0021000000-000000000??00001011110120?0-100515001000000000000112010-?-
02220014210002000000000002201110000-00000000023000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110100-00021000000--
00002000000000001002000??02100011011110010000111?01000000000000010200000-00000?00-00000----
Stomechinus 00010000000-0-0021000000-0000000001100002-----012000-100515001000000000000{01}1??0-?-
02210003010002000000000002201110000-00000000023000001-0-00-000-----
0110000----0000--000020??0----0-10--00-110100-00001100000--
0000200000000000110????12021??110111100100001110?0-0000?00000000?00000?00-00000----
Stomopneustes 00010000000-0-0021000000-0000000001100001011100120?0-100515001000000000000{01}10010-0-
02220014311002000000000002201310000-00000000033000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110100-00001000000--000020000000000011020000-
02100011011110010000111000-000000000000010200000-00000?00-00000----
Hemicidaris 00010000000-0-0021000000-0000000001100002-----012000-100515000000000000000{01}1??0-?-
022(12)0003010002000000000000001110000-0000000003?000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110011100223000000--0000200000000000110?0??0-
020000110111100?0000111?0100000?0000000010200000-00000?00-00000----
Pseudodiadema 00010000000-0-0021000000-000000000??00002-----012000-100515001000000000000{01}1??0-?-
02220003010002000000000000001110000-0000000003?000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110000-00221010000--
0000200000000000110????1202100011011110010000111?0110000?00000000?00000?00-00000----
Echinus 00010000000-0-0021000000-0000000000000002-----012010-100515000000000000000112010-0-
02210113100002000000000002201100000-000000000-3000001-0-00-000-----
0110000----0000--000020??0----0-00--00-1(01)0(01)00-10001100000--
000020000000000010020001202100011010111010000111000-000000000000010201000-00000?00-00000----
Echinometra 20010000000-0-0021000000-0000000001100002-----012010-100515001000000000000(01)10010-0-
02220014300002000000000002201100000-000000000-3000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110100-00002100000--
000020000000000010020001202100011010111110000111000-000000000000010201000-00000?00-00000----
Parasalenia 20010000000-0-0021000000-0000000000000002-----012010-100515000000000000000010110-0-
02210013100002000000000000001110000-00000000013000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110000-00001100000--
000020000000000010020001202100011010111010000111000-000000000000010201?00-00000?00-00000----
Parechinus 00010000000-0-0021000000-000000000000000101110012010-100515001000000100000112010-0-
02210013100002000000000002201100000-000000000-3000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110100-10001100000--
000020000000000010020002202100011010111010000111000-000000000000010201000-00000?00-00000----
Strongylocentrotus 00010000000-0-0021000000-000000000110000101110012010-100515001000000000000112010-0-
02220014300002000000000002201100000-000000000-3000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110100-10002100000--
000020000000000010020001202100011010111110000111000-000000000000010201000-00000?00-00000----
Zeuglopleurus 00010000000-0-00210000122100000000??0000101110012000-1105150000000000000002220?0-0-
02210003000002000000000000001100000-000000000-?000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110000-10011001000--
0000200000000000100????2202000011?1????????????????????????00000?00000?00-00000----
Glyphocyphus 00010000000-0-00210000102100000000?0000000000012000-100515000000000001000{01}1??0-
0-0221000300000200000000000001100000-000000000-?000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110000-10211001000--
0000200000000000100????2202000011????????????????????????00000?00000?00-00000----
Toxopneustes 00010000000-0-0021000000-000000000000000101110012010-100515001000000000000012010-0-
02210113100002000000000002201100000-000000000-3000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110100-10001100000--
000020000000000012020001202100011010111110000111000-000000000000010201000-00000?00-00000----
Trigonocidaris 00010000000-0-0021000002-1000000000000002-----012000-100515000000000200000112010-?-
02210013100002000000000000001100000-000000000-?000001-0-00-000-----
0110000----0000--000020??0----0-00--00-110000-10011001000--
00002000000000001002000??02000011010111010000111000-00000000000001?201?00-00000?00-00000----

Tennopleurus 0001000000-0-00210000010200000000000000000000-----012000-1005150000000000000000112010-0-

02210013100002000000000000001100000-000000000-3000001-0-00-000-----

0110000---0000--000020?0----0-00--00-110100-1001100000--

000020000000000010020002202100011010111010000111000-000000000000011201000-00000?00-00000----

Conulus 10110000000-0-0021000000-001000000??0210-----0(02)4100-10041400100000000000001???3703020-0-

131?00000000000000000001110000-0000000003?000001-0-00-000-----0100000000000000000020??0000?0200-

1010000000-10221-00000--10002000001000000-000000-00001?0?------?------???0-0000?00000001?????00000000?00-

00000----

Galerites 00110000000-0-0021000000-011000000110210-----023100-10041400(01)00000000000001???3703000-0-

---00000000000000000001100000-0000000000?000001-0-00-000-----0100000000000000000020??000020200-

1011000000-10221-00000--10002000001000000-000?00-00001?0?------?------???????????0?0?1?????00000000?00-

00000----

Echinoneus 10010000000-0-0021000000-011000000110210-----023100-

00041400(01)00000000000001(03)014207020-0-131?00000000000000000001100000-00000000003000001-0-00-000-----

-0100000000000000000100000020000000(23)0200-1011000000-10001-00000--00002000002200000-000000-

00000001010120010000?1?0?0-000000000000111200200000000?00-00000----

Anorthopygus 00010000000-0-0021000000-000000000??0210-----000100-000414001000000000000011011707000-

0--3--00000000000000000001100000-0000000000?000001-0-00-000-----

011?000---0000--000020?0----0-00--011000000-10221-00000--1000200000200000100????0-

0{12}000?11?????????????????????????????0?0?1?????00000000?00-00000----

Holactypus 00010000000-0-0021000000-000000000110210-----002100-000514001000000000000001???4206010-0-

030-00000000000000000001100000-00000000003000001-0-00-000-----

0110000---0000--000020?00---0-00--010101000-00221-00100--100020000020000011000000-

02000?110101200100001110?0-0000?0000000011200010000000?00-00000----

Coenholactypus 00010000000-0-0021000000-000000000??0210-----002100-000515001000000000000001???3206010-

0-030-00000000000000000001100000-0000000000?000001-0-00-000-----

011?000---0000--000020010---0-00--010101000-00221-00100--1000200000200000110????0-

02000?11?????????????????????????0?0?0?????10000000?00-00000----

Pygaster 00010000000-0-0021000000-000000000??0000-01110011(01)10-01041400100000000000002???1909010-

0-030-00000000000000000001100000-0000000000?000001-0-00-000-----

0110000---0000--000020?00---0-00--010101000-00201-00100--1000200000200000110????0-

02000?11?1?2?2?10?00??1????0000?000000001?????10-00000?00-00000----

Pygorhytis 10010000000-0-0021000000-000000000??0121-01110021001101041400000000000100001???29?6140-

0-331?00000000000000000001210000-0001000002?000001-0-00-000-----0100000000000000-00002000000030200-

1010000000-10221-00000--10002000010000100-000?00-?????0?------?------???????????0?0?111200000000000000-

00000----

Nucleolites 10010000000-0-0021000000-000000000110210-----

0(02)41010000414001000000000000{01}1???090(34)140-0-331?0000100000001000000210000-

0000?00003?000101000000000-----01000000000000010000020?000?0?0001010000000-10221-00010--

00002000014101100-000?00-0000000?------?------?????????????000?1?????00000000000-00000----

Apatopygus 10010000000-0-0021000000-000000000??0210-----0231010000414001000000000000011010906140-0-

331?00000000000001010000211000-0001100003?000100200001000-----

01000000000000010000020010????020001011000000-10221-00010--00002000014500100-000100-

00000001110020021100011000-000000000000111201200000000000-00000----

Pygausus 10010000000-0-0021000000-000000000??0210-----0041011000414001000000000000{01}1???3?03140-

0-031?00000000000001000000311000-0001?00002?000101000000000-----

01??000000000??1?000020??0000?020001010000000-10221-000?0--00002000000200100-000?00-?????0?------?------

-?????????????000?1?????00000000000-00000----

Archiacia 10021100000-0-0021000000-000000000??1210-----000100-000414001000000000000{01}1???3???140-

0-331?0000?00??0001000000321000-00???00003?111111000001000-----

01??000????0????00?????0????0?0101?10000000-10??1-????0--00002000000001100-000?00-?????0?------?------

-?????????????000? ??????00000000000-00000----

Claviaster 10021100000-0-0021000000-000000000??1210-----000100-000414001000000000000{01}1???3??4140-0-

331?0000?00??0001000000321000-00???00003?111111000001000-----

01??000????00????00??20??0????0?0?0????10000000-10??1-00??0--?0002000000001100-000?00-?????0?------?------

-?????????????000? ??????00000000000-00000----



Cassidulus 100100000000-0021000000-000000000110210-----0-0-011200114101000000000000011011903140-0-0-0?0000100000001010000121000-0001100101?000101200001000-----
01000000000000010000020010010602011121100000-10221-00010--00002010013101100-000100-0000000?-----?-----
0010-000010000000111201200000000000-00000----

Faujasia 100100000000-0021000000-000000000?0210-----0-0-00-100114201000000000000{01}1???3402140-0-331?0000100000001010000321000-0001?00102?000111000001000-----
01000000000000030000020011010902010121100000-10221-00010--00002000013301100-000?00-0000000?-----?-----
-????????????000?111201200000000000-00000----

Stigmatopygus 100100000000-0021000000-000000000?0210-----
0001011000414101000000000000{01}1???2804140-0-3?1?0000100000001010000321000-
0001?00102?000111040101000-----01000000000000030000020011010902010121100000-10221-00010--
00002000013101100-000?00-?????0?-----?-----????????????000?111201200000000000-00000----

Echinolampas 10(01)1000000000-0021000000-000000000110210-----0-0-00-2001141010000000000000011014703140-0-331?0000100000001010000321000-000110010310001(01)1000101000-----
01000000000000010000020010?8020(01)01011000000-10221-00010--00002000013100100-000000-
0101000111002002110001(01)0(01)0-000010000000111201200000000000-00000----

Clypeolampas 1011000000000-0021000000-000000000?0210-----0-0-00-
2001140010000000000000{01}1???3903140-0-343?1000100000001010000321000-000?00103?000101000001010-----
01000000000000010000020?2222102010101100000-10221-00010--10002000013101100-000?00-?????0?-----?-----
-????????????000?111201200000000000-00000----

Neolampas 100100000000-0021000000-000000000?0210-----0-0-011100117011000000000000013013712140-0-331?0000100000003010000321000-0001000001000000--0-00--00-----
01000000000000010000020010010602000101100000-10221-00010--00002000013400100-000100-0000000?-----?-----
0010-000010000000111201200000000000-00000----

Pliolampas 100100000000-0021000000-000000000?0210-----0-0-01110011701100000000000001?013?03140-0-331?0000100000001010000321000-000?00101?000100000001000-----
010000000000000?000020?0?0?0?000101100000-10221-00010--00002000013400100-000?00-?????0?-----?-----
0?10-0000?0000000111201200000000000-00000----

Plesiolampas 100100000000-0021000000-000000000110210-----0-0-00-000114101000000000000{01}1???35?4140-0-131?0000000000001010001100000-000?00102?000101000001000-----
01000000000000010000020?0?0?902000101100000-10221-00010--10002000013501000-000?00-?????0?-----?-----
-????????????000?111201200000000000-00000----

Oligopygus 100100000000-0021000000-01?0000001(01)0210-----0-0-00-10012411-
000000000000{01}1???4511110-0-143?000-100100011010101100010-000010010-?000101000001000-----
010000000000000000000200?0111302000101100000-10221-00000--00002000012500000-000?00-
0101001110002002112101????????????000?111201100000000000-00000----

Haimea 100100000000-0021000000-0?000000110210-----0-0-00-10012411-000000000000{01}1???45?2110-0-121?000-100100011010001100010-000010010-?000101000001000-----
01000000000000000000020012111302000101100000-10221-00000--00002000013001000-000?00-
0101001110002002112101????????????000?111201100000000000-00000----

Clypeaster 100100000000-0021000000-000001210110210-----0-0-00-100125(12)01000000000000010013512130-
00121?0000020100001010----000111000000000-20001110010010010--0-0-0100222----00003-
000020010111412000101100000-10221-00000--1000200001200000-000000-010000111000200211210100(01)0-
000000000000112100-00000000000-00000----

Ammotrophus 120100000000-1021000000-011001210?0210-----0-0-00-10012410100000000000000100142?1130-
00121?0000020110001010----000110000000010-00001010000010010--0-1-0100111----00003-
000020010111412000101100000-10221-00000--0100200001100000-000000-01000011?000200211?0100?0-
00000000000112100-00000000000-00000----

Arachnoides 020100000000-1021000000-000001200110210-----0-0-00-100124101000000000000001--113?2130-
00121?0000020110001010----000110000000010-00001010000010010--0-1-0100222----00103-
000000?0111412000101100000-10221-00000--0100200001100000-000000-01000011100020021121010010-
00000000000112100-00000000000-00000----

Scutellinoides 110100000000-0021000000-0?000121???0210-----0-0-00-100124101000000000000{01}1???14?3100-
0--00-0000020101000010----0001110-000000-?0000--0-00--00-----
0111222----00?00-000010?00004?0000101100000-10221-00000--0000-000000000000-000?00-
01000011????????????0?0?0?0?000?1?????00000000000-00000----

131



Galeropygus 00010000000-0-0021000000-00000000011010010010001101100104140000000000000001?0?090?110-0-131?00000000000000000001210000-0000?00003?000101000000000-----
01??0000000000000000020?0?0?0?000101100000-10221-00010--1000200000100000-000?00-0000000?-----?-----
-????????????000?1?????00-00000000-00000----
Disaster 10010000000-0-0021000000-000000000111111-01110021100-10041400100000000000001??29?6100-0--0-000000000000000000001000-00?1010001?100001-1-00-000-----1100000(01)00(01)000010000020000??(12)30200-101000000-10221-00000--10122000000000100-000?00-?????0?-----?-----????????????0?0?011200200000000000-00000----
Desorella 10010000000-0-0021000000-000000000?0220-----01100110104140?000000000000001??29?7140-0-030-0000000000000000001100000-00?000002?000001-0-00-000-----?100000000000000-000020?000030200-??10000000-10221-00000--10002000010300000-0???0-0{12}00000?-----?----
-?-????????????0?0?1?????000000000000-00000----
Hyboclypus 10010000000-0-0021000000-000000000?0220-----01102110010010514000000000001000{01}1??19?7140-0-331?0000000000000000001210000-0000000002?000001-0-00-000-----01?000??00000?000020?0?0?0?00-1010000000-10221-00000--00002000010000100-000?00-?????0?--
---?-----?-----????????????0?0?11120000000000000000-00000----
Toxaster 10010200000-0-0021000000-000000000110210-----024100-000414000000000000000?1??26?3100-0--00-0000000000001000010021000-00?1000001?010100100000010-----
110000000000000410000200002126010001010000000-10221-00000--10102000000000100-000?00-?????0?-----?-----
00?0-0000?00000?00?0?0?0?000000000000-00000----
Pseudholaster 10010200000-0-0021000000-000000000?0220-----224000-100414000000000001000?1??27?4100-0--00-0000000000001000010021000-00?1000001?110101100000010-----
1100000000000004100002000021130200-1010000000-10221-00000--10102000000100100-0?0?0?-0000000?-----?-----
-????????????0?0?0?0?0?0?00000000000000000000----
Holaster 10010200000-0-0021000000-000000000110220-----224000-100414000000000001000{01}1??2713100-0--00-0000000000001000010021000-00?1000001?110101000000100-----11000001101002010000020--021250200-1010000000-10221-00000--10102000000100100-000?00-0000000?-----?-----??0-0000?0000?0?0?0?000000000000-00000----
Hemipneustes 10110200000-0-0021000000-000000000110220-----224000-100414000001000001000{01}10012615100-0--00-0000000000001000010021000-00?1000001?110101000000310-----
11000000000010021010020--021130100-1010000000-102?1-00000--10102000000110110-0?0?0?-0000?0?-----?-----
-??0-0000?0000?0?0?0?0?00000000000000000000----
Echinocorys 10110000000-0-0021000000-000000000110220-----0224(01)00-100414000000000001000{01}1??3613100-0--00-0000000000001000010021000-00?1000001?000101000000000-----
1100000111100201000002000011240200-1010000000-10221-00000--10102000000100100-000000-0000000?-----?-----
-??0-0000?00000000102002000000000000-00000----
Cardiaster 10010200000-0-0021000000-000000000?0220-----224000-000414000000000001000{01}1??2613100-0--00-0000000000001000010001000-00?1000000?111101100000100-----11000001111010010000020--011130100-1010000000-10221-00000--101020000001(01)0110-000000-0000?0?-----?-----??0-0000?0000?0?0?0?01000000101100010----
Cardiotaxis 10010200000-0-0021000000-000000000?0220-----224000-000414000000000001000{01}1??2713100-0--00-0000000000001000010001000-00?1000000?111101100000100-----1100000111122010010020--011130200-1010000000-10221-00000--10102000000100120-000?00-0000?0?-----?-----??0-0000?0000?0?0?0?01000000101100010----
Stegaster 10110200000-0-0021000000-000000000?0220-----224000-100414000000000001000{01}1??27?3100-0-00-0000000000001000010001000-00?000000?11110-10000000-----
11000001111002010000020?01013020?-?010000000-102?1-00000--?0122000000000110-000?00-?????0?-----?-----
-????????????0?0?0?0?0?01000000101110010----
Stenonaster 10110000000-0-0021000000-000000000?0210-----024000-100414000000000000000{01}1??35?3100-0--00-0000000000001000010021000-00?1000001?00010-000000000-----
11000000001000010000020?02125020?-?010000000-10221-00000--?0102000000100100-000?00-?????0?-----?-----
-????????????0?0?0?0?0?000000000000-00000----
Somaliaster 10010100000-0-0021000000-000000000?0210-----004100-100414001000000000000{01}1??25?3100-0--00-0000000000001000010001000-00?1000001?{23}10100000001100-----110000010010000300000100-02127010?01010000000-10221-00000--10100000000000100-000?00-?????0?-----?-----
-????????????0?0?0?0?0?01200100000100000----



Periaster 10010000000-0-0021000000-000000000?0210-----023100-00041400000000000000{01}1???2???100-0-00-0000000000001000010021000-00?10?0000?020100100011100-----
1100000???00011100000?0?0?1?0{01}0001010000000-10221-00000--0010100?000110110-000?00-00000?0?-----?-----
--????????????0?0?0?0?0?01210100011010010----

Plesiaster 10010200000-0-0021000000-000000000?0210-----004100-1004140000000000000000{01}1???27?(23)100-0--00-0000000000001000010021000-00?1010001?{23}2010000?011100-----
11000000000000310000200002115010001010000000-10221-00000--10110000000110110-000?00-?????0?-----?-----
-????????????0?0?0?0?0?01000000000-000010000

Micraster 10010200000-0-0021000000-000000000110210-----004100-1004140010000000000000{01}1???271(23)100-0--00-0000000000001000010021000-00?1010001?{23}20100000011100--
-----110000000000011300000200002115010001010000000-10221-00000--10110000000110120-000000-0000000?-----?-----
-----0010-0000?00?0000011200201000000000-000010000

Cyclaster 10000200000-0-0021000000-000000000?0210-----024100-1004130100000000000000010012612100-0--00-0000000000001000010021000-0011010001-220100000011100-----
110000000000011300000200002215010001010000000-10221-00000--10110000000110110-000000-0000000?-----?-----
-?0?0-000000000000011200201(02)(01)(01)00000000(01)0010000

Coraster 10010(01)00000-0-0021000000-000000000?1210-----004100-1004140000000000000000{01}1???16?2100-0--00-0000000000003000010001000-00?1010000?110001-0-00-000-----
110000000000011300000100001114020001010000000-10221-00000--00102000000110120-000?00-?????0?-----?-----
-????????????0?0?0?0?0?01210100000?10000----

Antillaster 10010200000-0-0021000000-000000000?0210-----000100-10041(34)0010000000000000{01}1???25?4100-0--00-0000000000001010010021000-00?1011001?100101211001000-----
-11000000000001110100010?0?0?26010?01010100000-10221-00000--00102000000110110-000?00-?????0?-----?-----
-????????????0?0?0?0?0?00000000000-00000----

Unifascia 10010100000-0-0021000000-000000000?1210-----000100-0004140010000000000000{01}1???25?4100-0--00-00000000000001010010021000-00?1010001?110100010011000-----
110000000000011100000?0?02106000100010000000-10221-00000--00100000000110110-000?00-?????0?-----?-----
-????????????0?0?0?0?0?01210010000110000----

Corystus 10010000000-0-0021000000-000000000?0220-----224000-2004140000000000001000010012613100-0--00-0000000000001000010021000-0011001000-100101000000000-----1100000000110201001102000021140100-
1010000000-10221-00000--10102000000100100-000000-00000000-----?-----?0?0-000000000000011200301000000000-
000011120

Calymne 10010000000-0-0021000000-000000000?0220-----224000-0004110?0000000001000010012713100-0--00-0000000000003010010000000-0011000000-00100--0-00--0-----
1100(01)001101102010001020--010130100-1010000000-10221-00000--00112000000000110-000000-00000000-----?-----
--0010-0000?0000100010200201000000101?10010----

Palaeostoma 10000100000-0-0021000000-000000000?0210-----000100-1004120010000000000000010012613100-0--00-0000000000001010010001000-0011010000-200100100011100-----1100100111000003-
0100000?01013010001010000000-10221-00000--00100000000000100-030000-00000100-----?-----0010-
0000?0000010010200201210100000000000----

Hemiaster 10000100000-0-0021000000-000000000110210-----024100-1004140000000000000000{01}100126?2100-0--00-0000000000001000010021000-0011010001-220100100011100-----
1100000000000041000010000226010001010000000-10221-00000--00101000000110110-000000-0000000?-----?-----
00?0-0000?0000?100?0?0?01211000000001000----

Ovulaster 10010(01)00000-0-0021000000-000000000?1210-----024100-1004140000000000000000{01}1???25?(23)100-0--00-0000000000003000010001000-00110?0001?11000100-00-000-----
010000000000011100000200001114010001010000000-102?1-00000--00102000000110120-000?00-?????0?-----?-----
-????????????0?0?0?0?0?01000000000-000011020

Maretia 10010100000-0-0021000000-000000000?0210-----000100-10041400100000000000000100124?5100-0--00-0000000000001010010021000-0011011002-100111201001100-----
11000000000001130100000000225020100110101000-10221-000010000112000000110110-000000-00000100-----?-----
-0010-0000?0000010011200201000000000-000011120

Spatangus 10010200000-0-0021000000-000000000110210-----000100-0004140010000000000000010012514100-0--00-0000000000001010010021000-0011011001-110111001011100-----
110000000000011101000000002205000001010101000-10221-000010000122000000110110-000000-00000100-----?-----
-0010-0000?0000010011200201000000000-000011110



Euryptagus 1001000000-0-002100000-00000000??0210-----000100-000414001000000000000010012415100-
0--00-0000000000001010010021000-0011011002-100100210001100-----
1100001000-001130100000000225020100210101000-10221-000010000112000000110110-000000-00000100-----?-
-0010-0000?000001001020020100000000-000011120
Eupatagus 1001000000-0-002100000-000000000110210-----000100-000414001000000000000010012415100-
0--00-0000000000001010010021000-0011011001-100111001001100-----
110000000000011301000000001125020100010101000-10221-000010000112000000110100-000000-00000100-----?-
-0010-0000?0000010011200201201000000-010011110
Brissus 1001000000-0-002100000-000000000111210-----000100-000414001000000000000010012414100-
0--00-0000000000001010010021000-0011011001-100100011011000-----
11000001100001120100000000220500000101000000-10221-00000-00121001000110110-000000-00000100-----?-
0010-0000?00000100112002012110000000010011110
Macropneustes 10010200000-0-002100000-000000000??0210-----000100-
00041400100000000000{01}1???25?4100-0--00-0000000000001010010021000-00?1011001?110110000011000-----
110000000000011301000000002215000001010101000-10221-000010000122000000110110-000?00-?????0?-----?-
-?????????????0? ??????????012010000000010011110
Plexechinus 10010110000-0-002100000-000000000??1221-----224000-
20031(134)000000000001000010011613100-0--00-000000000000301001000000-0011000000-00000--1-00---0-----
0100001111110201-001020--011130101-0010000000-10221-00000--10112000000000100-000000-00000000-----?
1000-00000000000?010100201000000000-000010120
Pourtalesia 10010110000-0-002100000-000000000??1221-----223000-20041400001?000001000010011713100-0--
00-0000000000003010010000000-0001000000-01100--1-00---0-----
0100002????1?2????0?10--0????0001-0010000000-10221-00000--10112000000000120-000?00-0000000?-----?-
0010-000000000000010100201000000000-000011120
Urechis 10010000000-0-002100000-000000000??0220-----224000-1004130000000000001000010013514100-0--
00-00000000000000010010000000-0011000000-00000--0-00---0-----01000001111102010001020--011130100-
1010000000-10221-00000--10102000000000100-000000-0000000?-----?------0010-00000000000000?????00000000000-
00000----
Carnarechinus 1?0?0000000-0-0021000000-000000000??210-----02410???004140?00010000000000???????1?100-0--
00-0000000000003010010000000-00?10?000?00000--0-00---0-----
?10000011111020000?10?0?0?0????10????10000000-????1-?0?00--?????0?000?000?00-000?00-?????0?-----?-
0000?0000????????????????????????????????
Lovenia 10010200000-0-002100000-000000000110210-----0001021100414001000000000000013012415100-0--
00-0000000000001010010021000-0011011011-110121000011200-----
110000000000011301000000000115010100110101010-10221-00001110001110110-000000-00000100-----?-
-0010-0000?00000100112200201000000000-001011110
Breynia 10010200000-0-002100000-000000000110210-----000100-100414001000000000000010012415100-0--
00-0000000000001010010021000-0011011001-110121001001200-----
110?00000000011301000000002225010100010101010-10221-000011100112100000110110-000000-00000100-----?-
-0010-0000?00000100112002012010000000011011120
Paleopneustes 10010000000-0-002100000-000000000110210-----000100-100413001000000000000010012514100-0--
00-0000000000001010010021000-0011000001-100100001001000-----
110000010000011101000100?02226000001010000000-10221-00000-00101000000110110-000000-00000100-----?-
1010-000000000000010000201201001001011010----

Pericosmus 10010200000-0-002100000-000000000110210-----000100-200413001000000000000010012514100-0--
00-0000000000001010010021000-0011010001-(12)20110001011000-----
1100000(01)0000011101000100002115000001010000000-10221-00000-00101000000110110-000000-00000100-----?---
---0010-0000?0000010010000201211001001011010----

Brisaster 10000200000-0-002100000-000000000??0210-----000100-000413001000000000000010012514100-0--
00-0000000000001010010021000-0011010001-220110100011100-----
110000000000011100000100002105000100010000000-10221-00000-00120001000110110-000000-00000100-----?-
0010-0000?0000110010000201210100011010010---

Gregoryaster_spp 10000200000-0-002100000-0000??????0210-----000100-00041400100000000000001?0?15?4100-0--
0--00-0000000000001010010021000-00110?0001-220100000011000-----
110000000000011300000100002015000100010000000-10221-00000-001?0001000110110-0000?????????0?-----?-
-?????????????????????????0121110000?010000----

Schizaster 1000200000-0-0021000000-000000000112210-----000100-0004140010000000000000010012514100-0--
00-00000000000001010010021000-0011010001-220100100011100-----
110000000000011100000100002106000100010000000-10221-00000--00120001000110110-000000-00000100-----?-----
0010-0000?0000110010000201210100011010010----
Prenaster 10010000000-0-0021000000-000000000??1210-----000100-000414001000000000000{01}1???25?4100-
0--00-00000000000001010010021000-00?1010001-100100010011000-----
110?00000000011100000?0??0210?000000011000000-102?1-00000--00100000000110110-000?00-??????0?------?-----
-?????????????0? ??????????01210010011110010----

Palaeotrophus 10010000000-0-0021000000-000000000??0210-----0?3?00-10011200?000000000000000100124?4100-0-
-00-0000001000003010010001000-0011011001-10000-?0-00--00-----
110000000000011101000100002115000000010000000-10221-00000--00102000000110110-000000-00000100-----?-----
0010-0000?0000010010200201000000000-000011120

Asterostoma 10010000000-0-0021000000-000000000??1210-----000100-
100414001000000000000{01}1???25?4100-0--00-00000000000001010010001000-00?1000003?102101210001000-----
11000000000001110000020??02219000?01010000000-10221-00000--00102000000101110-000?00-??????0?------?-----
-?????????????0? ??????????000000000000-00000----

Aeropsis 10010000000-0-0021000000-000000000??1210-----004100-100(24)120000000000000000000100116?2100-
0--00-00000000000003010010001000-0011000000-210001-0-00-000-----
110000000000011300000100100014020101010000000-10211-00000--00102000000400100-000000-00000?00-----?-----
0010-0000?00000000? ??????01200100000?10000----

Megapneustes 10010200000-0-0021000000-000000000??0210-----000100-
100414001000000000000{01}1???25?4100-0--00-00000000000001010010021000-00?101100??100100000001000-----
110000????00011301000?0??022??0?0?01010101000-10221-0000100001210000001?0110-000?00-??????0?------?-----
-?????????????0? ??????????0120??000000010011?10

Brissopsis 10010200000-0-0021000000-000000000110210-----000100-1004140010000000000000010012514100-0--
00-00000000000001010010021000-0011011001-220100001011100-----
110000000000011101000000?02105000100010000000-10221-00000--00121001000110110-000000-00000100-----?-----
0010-0000?00001100112002012110000000010011110

Echinocardium 10000200000-0-0021000000-000000000110210-----000100-
(01)0041400100000000000000010012415100-0--00-00000000000001010010021000-0011011011-310121000011200-----
11000000000001110100000001115000000010000000-10221-00000--00112101000110110-000000-00000100-----?-----
0010-0000?000011001120020100000000-001011121

Goniophorus 00010000000-0-0021000003-000000000??00002-----012000-110515000000010010000221??0-?
012000020?00020000000000000001100000-000000000-?000001-0-00-000-----0110000---0000--000020??0---0-00--00-
110001000023000000--00003000000000000100?????????????11?????????????????1000-000?0000000011200000-00000?00-
00000----

Pseudosalenia 00010000000-0-0021000001-000000000??00002-----012000-1105150000000000000000221??0-?
012100030100020000000000000001110000-0000000001?000001-0-00-000-----0110000---0000--000010??0---0-00--
00-110010-00223000000--00003000000000000100?????????????11?????????????????1?01?000?00000000?????00-
00000?00-00000----

Holosalenia 00010000000-0-0021000001-000000000??0000101111012000-1115150000000000000000222??0-?
022000020?00020000000000000001100000-000000000-?000001-0-00-000-----0110000---0000--000020??0---0-00--00-
110011000023000000--00003000000000000100?????????????11?????????????????????????????????00000? ??????00-00000?00-
00000----

Emiratia 00010000000-0-0021000000-000000000??00000-----012010-1105150?1000000000000{01}210?0-?
0222000402000200000000000001001100000-000000000-?000001-0-00-000-----0110000---0000--000020??0---0-10--00-
101000-00221000000--00002000000000000110?????????????11?????????????????????????????????00000? ??????00-00000?00-
00000----

Polydiadema 00010000000-0-002100000? -000000000??0000? ??????0{01}??10-1?0? ??????1 ??????????0 ??????????0-?
022100030100020000000000000001110000-0000000001?000001-0-00-000-----0110000---0000--000020??0---0-10--
00-110000-00221000000--00002000000000000120?????1?02100011?????????????????????????????????0?0? ??????00-00000?00-
00000----

Diplopodia 00010000000-0-002100000? -000000000110000? ??????0{01}??10-1?0? ??????1 ??????????0 ??????????0-?
022100030100020000000000000001001110000-0000000001?000001-0-00-000-----0110000---0000--000020??0---0-10--
00-110100-00221000000--00002000000000000110?????????????11?1?1?1?10?00111?0100000?000000000? ??????00-
00000?00-00000----

```
Phymosoma          00010000000-0-0021000000-000000000?0000?????012010-1?0?????1???????0??????0?-
02220014320002000000000001001110000-0000000001?000001-0-00-000-----0110000----0000--000020??0---0-10--
00-110100-00011000000--0000200000000000100200012020000110101100?00001110010000000000000000?????00-
00000?00-00000----
Taiwanaster                    1102000000000-0021000000-0??010000??0210-----0-0-00-1001241?-
000000000000{01}1???1{34}?2100-0--00-0000010010101010----0001?1?00000010-4000100000001000-----0100111---
-00103-0000100101114?20001011000000-10221-00000--00002000011000000-000?00?100000110?????????????0?0-
0000200000?1112001-00000000000-00000----
Heterodiadema      00010000000-0-002100000?-000000000?0000?????0??10-0?0?????????????????????????0-?
02210003010002000000000000001100000-000000000-?000001-0-00-000-----0110000----0000--000020??0---0-10--00-
110000-01221000000--0000200000000000110?????????????110?????????0011?????????????00000???????0-00000?00-
00000----
Conoclypus           0011000000000-0021000000-000000000110210-----0-0-01100012410-00000000000001???3???140-0-
121?0000100100011010001100000-000010010-?000101000001000-----
01000000000000002000020??2??13020001011000000-10221-00000--00002000013101000-000?00-
010?0011??????????0?0?????????????000?1?????00000000000-00000----
Fossulaster                  1001000000000-0021000000-00000121???0210-----0-0-00-
100124(01)1100000000000{01}1???15?2100-0--00-0000020101001010----0001?1000000010-?000101000001000-----
0111222----00000-000000?00004?00001011000000-10221-00000--00002000011000000-000?00-
01000011?????????????0?????????????000?1?????00000000000-00000----
Neolaganum       1101000000000-0021010000-0110????0110210-----0-0-00-1001240010001000000000(01)1???42?2130-
001(23)(12)?0000020110001010---000111100000010-?0001110010010110---0--
010000000000011300001211000003120001011000000-10221-00000--00002000011000000-000?00-
10000011?????????????0?????????????000?112001-00000000000-00000----
Scutellina            0101000000000-0021000000-011110000??0210-----0-0-00-100124101000000000000(01)1???2512100-
0--00-0000020000001010----000102000000010-?000101000000000-----
010000000000000320000200101103120001011000000-10221-00000--00002000011000000-000?00-
10000011?????????????0?????????????000?1?????00000000000-00000----
Abertella             1201000000000-1021000000-000002301110210-----0-0-00-10012410-100000000000{01}1???43?1100-
0--00-0000020110101?10---0001?1?000000?0-?000110001001011112200000100111---00113-
0000200101114100001011000000-10221-00000--000020000?0000000-000?00-
10000011?000?00211?01?????????????000?1?????00000000000-00000----
Eoscutella            1201000000000-1021000000-00?0?0?????0210-----0-0-00-10012410-000000000000{01}1???44?2100-0-
00-0000020100?01?10----
0001?1?000000?0-?00011000100101111???00?010000000000010320001200101114?10001011000000-10??1-00000--
0?0020000?0000000-000?0?0?????????????????????????????????????00?0???????00000000000-00000----
Monophoraster         1201000000000110021000000-001002200??0210-----0-0-00-10012410-
1000000000000{01}1???42?1100-0--00-0000020100101010----
000101?00000010-?0001100010010111122000001000000000001130000120010111(34)120001011000000-10221-00000--
01002000111000000-000?00-10000011?000200211?01?????????????00?1?????00000000000-00000----
Scutaster              1201000011020-0021000000-00?0?0?????0210-----0-0-00-100124?0-?00000000000{01}1???43?1100-0-
-00-0000020000?01?10---0001?1?000000?0-?0001110010010?1110-000-0100001110-00103-
0001200101114?00001011000000-10??1-00000--0?0020000?0000200-
000?0?0?????????????????????????????????????00?0?????????00000000000-00000----
;
begin mrbayes;
set autoclose=yes nowarn=yes;
lset rates=gamma;
    lset coding=variable;
        ctype ordered: 4 6 17 38 75 80 86 202 203 233;
mcmc ngen= 200000 relburnin=yes burnfrac=0.25   printfreq=1000   samplefreq=1000 nchains=4 nruns=2 temp=0.10
savebrlen=yes;
mcmc;
sump;
sumt contype=allcompat Outputname=Echino163Greg_MCC.t;
sumt contype=halfcompat Outputname=Echino163Greg_MRC.t;
end;
```