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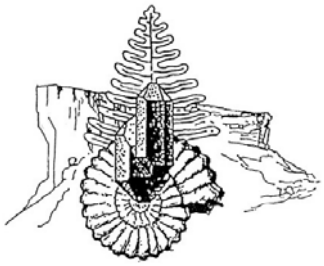

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TWO SPECIES OF *POROSOMA* (ECHINOIDEA) IN THE EOCENE AND OLIGOCENE OF NORTH-EASTERN ITALY

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Abstract: The taxonomy of *Porosoma* Cotteau, 1856 has long remained uncertain, owing to reliance on morphological traits subject to considerable variability. To address this issue, well-preserved specimens from the Eocene and Oligocene of the Veneto Region (Northeastern Italy) were examined. An extensive sample from the type horizon, the Calcareniti di Castelgomberto formation (Rupelian), confirms the diagnosis of the type species, *Porosoma cribrum* (Agassiz in Agassiz & Desor, 1846), including the distinctive composition of polygeminate ambulacral plates in echinid style. The study of topotypic specimens from the Priabonian of the Colli Berici further supports the reassignment of *Cyphosoma pulchrum* Laube, 1868 to *Porosoma*.
The diagnostic characters of *Porosoma* should include the composition of the ambulacral plates as in the type species. Based on this criterion, only three additional species are retained within *Porosoma*: *P. haimei* (Desor, 1856), *P. vidali* (Lambert, 1902) and *P. montserratense* Lambert, 1927.
Phylogenetic analysis recovers *Porosoma* in an unresolved polytomy with *Phymosoma* and *Gauthieria*, thereby corroborating its placement within the family Phymosomatidae Pomel, 1883.

Key words: *Porosoma*, cladistics, systematics.

Riassunto: ***DUE SPECIE DI* POROSOMA *NELL'EOCENE ED OLIGOCENE DEL NORD-EST ITALIANO.***
La tassonomia del genere Porosoma *Cotteau, 1856 è tuttora molto incerta e necessita di revisione dal momento che le differenze utilizzate per la separazione a livello specifico riguardavano sinora prevalentemente caratteri morfologici molto variabili, come altezza e contorno della teca, numero e distribuzione dei tubercoli secondari (vedi Carrasco, 2024 per una sintesi). Solo in rari casi è stato utilizzato il tipo di composizione delle piastre ambulacrali, come suggerito da Lambert (1927), anche perché le linee di sutura risultano raramente visibili nel materiale fossile. Per cercare di chiarire la questione, in questo lavoro ci si è basati su materiale proveniente dall'Eocene e Oligocene del Veneto, area in cui il genere* Porosoma *è relativamente frequente, e si è partiti dalla revisione della specie tipo,* Porosoma cribrum *(Agassiz in Agassiz & Desor, 1846). Di questa specie è stato esaminato un gruppo consistente di esemplari (130) provenienti dall'orizzonte tipico, la formazione delle Calcareniti di Castelgomberto (Rupeliano). Si conferma la diagnosi della specie fornita da Smith & Kroh (2011) e vengono aggiunti alcuni caratteri morfologici ancora non noti, come la presenza di piccole aree prive di tubercoli nella parte adapicale degli interradii, l'aspetto degli aculei primari e il campo di variabilità dei principali dati biometrici e dei rapporti di forma della teca.*
Alcuni esemplari provenienti dall'Eocene superiore della cava inattiva di Sossano (Cava di Via Piare) nei colli Berici (Vicenza) corrispondono a Cyphosoma pulchrum *Laube, 1868. Dal momento che la composizione delle piastre ambulacrali è identica a quella di* P. cribrum*, è possibile attribuire questa specie al genere* Porosoma e *ricombinarla come* Porosoma pulchrum *(Laube, 1868). Le buone condizioni di conservazione del materiale in studio, che proviene dall'orizzonte tipico per questa specie (formazione delle Marne di Priabona), consentono di completarne la descrizione morfologica*. P. pulchrum *si distingue da* P. cribrum *per le maggiori dimensioni della teca, il peristoma sensibilmente più piccolo in proporzione; inoltre l'apparato apicale è sub-pentagonale e si estende maggiormente nell'interradio posteriore.*
Smith & Kroh (2011) includono nei caratteri diagnostici di Porosoma *la composizione delle piastre ambulacrali di tipo echinide, come nella specie tipo; le specie attribuite in letteratura a questo genere che mostrano una diversa*

*composizione delle piastre (*e.g.*, in stile phymosomatide) devono quindi essere assegnate ad un genere diverso. Un confronto con le altre specie attribuite in letteratura a* Porosoma *basato su questo criterio porta ad includere con certezza solo 3 altre specie in questo genere:* P. haimei *(Desor, 1856),* P. vidali *(Lambert, 1902) e* P. montserratense *Lambert, 1927. Un'analisi filogenetica sviluppata includendo il materiale disponibile di* Porosoma pulchrum *e* Porosoma cribrum *ha consentito di chiarire la posizione sistematica di questo genere, che era sinora considerata incerta (Smith & Kroh, 2011; Carrasco, 2024; Kroh & Mooi, 2025): la nostra analisi di inferenza bayesiana colloca* Porosoma *in una politomia irrisolta insieme a* Phymosoma *e* Gauthieria*.* Porosoma *viene quindi assegnato alla famiglia Phymosomatidae Pomel, 1883*.

Parole chiave: Porosoma*, cladistica, sistematica*.

Figure 1 – Panoramic view of the abandoned limestone quarry of Sossano (Cava di Via Piave).

Figura 1 – Panoramica della cava inattiva di Sossano (Cava di Via Piave).

Introduction

The type species of the genus *Porosoma* Cotteau, 1856, *Porosoma cribrum* (Agassiz in Agassiz & Desor, 1846), is relatively frequent in the Calcareniti di Castelgomberto formation (Lower Oligocene) of the Veneto Region, which also represents the type-horizon (Desor, 1855, Laube, 1868; Dames, 1878). This species was originally attributed to *Cyphosoma* L. Agassiz, 1838, a genus that is no longer considered valid (Kroh & Mooi, 2025).

Three additional species formerly attributed to "*Cyphosoma*" have been reported from this region: *C. blanggianum* Desor, 1857, from the Upper Eocene of Priabona (Vicenza Province), *C. pulchrum* Laube, 1868, from the Priabonian of Val Scaranto (Colli Berici, Vicenza Province) and the Lutetian of San Giovanni Ilarione (Verona), and *C. superbum* Dames, 1878, from the Lutetian of San Giovanni Ilarione (Verona).

Species-level distinctions within *Porosoma* remain problematic (Carrasco, 2024), primarily due to reliance on morphological characters subject to high variability, such as test size and shape, and the size and arrangement of secondary tubercles. Even the systematic position of the genus *Porosoma* remains unresolved (Smith & Kroh, 2011; Carrasco, 2024; Kroh & Mooi, 2025).

The main aim of this study is to compare newly collected material from the Eocene and Oligocene of the Veneto Region with the "*Cyphosoma*" species previously recorded from the area and to clarify the systematic placement of *Porosoma*, through a Bayesian cladistic analysis statistical analysis. For this purpose, a large sample (130 specimens) of *P. cribrum* from the type-locality (Castelgomberto, Vicenza Province) and the type-horizon has been examined to reassess the type-species. Additionally, five large regular echinoids recently collected from the Priabonian (Upper Eocene) of Sossano in the Colli Berici (Vicenza Province, Fig. 1) have been analysed based on the composition of their ambulacral plates, a feature rarely preserved in fossil echinoids, and compared with the type species.

Material and methods

Porosoma cribrum (Agassiz, in Agassiz & Desor, 1846): a total of 130 specimens from the Lower Oligocene (Rupelian) Calcareniti di Castelgomberto formation in the Veneto Region were examined at the Museo Civico "Dal Lago" of Valdagno (MCV). Three specimens (MCV CDL864a-c) originate from Castelgomberto, while the remaining material (MCV 22.118, 136, 701, 740, 743-746, 756-759, 790-796, 817, 825-826, 869, MCV 25/25-28) was collected from San Gottardo (Colli Berici).
A specimen of *P. cribrum* illustrated by Smith & Kroh (2011), a complete test with D = 36 mm (University of Lyon, Ecole de Mines collection, uncatalogued) from Castelgomberto, was originally figured by Desor (1855; pl. 15, figs 8-10) as *Cyphosoma* (*Coptosoma) cribrum*. It corresponds to the cast ("moule M29") used by Agassiz (1840) in the first citation of this species (pers. comm. Philippe Nicolleau, November 2023).
The material attributed to *Porosoma pulchrum* (Laube, 1868), from Sossano, consists of 6 specimens housed at the Museo Civico "Dal Lago" of Valdagno (MCV 25/20-23, 29-30). All specimens originate from the Marne di Priabona formation (Upper Eocene) of the Colli Berici, near Vicenza.

Phylogenetic methods. A non-time-calibrated Bayesian inference phylogenetic analysis was undertaken in order to investigate the systematic position of *Porosoma*. Two new operational taxonomic units (OTUs) were scored into the Borghi *et al*. (2024b) dataset, a modified version of the Coppard *et al*. (2010) matrix, but excluding the *Gregoryaster* OTU which was added by Borghi *et al*. (2024b). The two new OTUs (*Porosoma cribrum*, based on the San Gottardo specimens and *Porosoma pulchrum*, based on the Sossano specimens only), were scored based on first-hand examination of the material described herein.
The Bayesian inference analysis was performed in MrBayes ver. 3.2.7 (Ronquist *et al*., 2012) using the Mkv model, with two runs of four chains each and the temperature set at 0.10. The analysis was run for 2.000.000 Markov chain Monte Carlo generations, sampling every 1000 generations and the first 25% of the sampled trees were discarded as burn-in. Convergence of independent runs was assessed in MrBayes using effective sample size (>400 for all parameters) and the average potential scale reduction factor (1.001 or less for all parameters). Characters 4, 6, 17, 38, 75, 80, 86, 202, 203 and 233 were treated as ordered, as in Kroh & Smith (2010).
Complete scorings for the new OTUs can be found in the appendix, along with the MrBayes script used to run the analysis.

Morphological abbreviations:
D = diameter of the corona at the ambitus;
Da = diameter of the apical disc;
Dp = diameter of the peristome;
Dc = diameter of the periproct;
Hp, Wp = heigh and width, respectively, of an interambulacral plate at the ambitus;
na, nIA = number of plates in the ambulacral and interambulacral columns, respectively;
TH= height of the test;
WA, Wia = width of the ambulacral and interambulacral zones at the ambitus, respectively.
Measurements were taken with a precision of 0.5 mm.

Finding localities in the Colli Berici

Most of the fossil localities cited in this paper are situated in the Colli Berici (Vicenza Province; Fig. 2). These hills, covering an area of about 200 km², lie in the southern part of the Vicenza Plain, bounded to the northwest by the Monti Lessini (Verona Province), and to the southeast by the Colli Euganei. The eastern margin of the Colli Berici is marked by a steep escarpment descending towards the plain; while the western margin, where most of the limestone quarries cited in this paper (Alonte, Orgiano, Sossano) are located, slopes gently into the surrounding lowlands.
Geologically, these hills are interpreted as the south-western continuation of the Monti Lessini, sharing stratigraphic affinities with the Palaeogene formations of the Lessini Shelf (Mietto *et al.*, 1981).

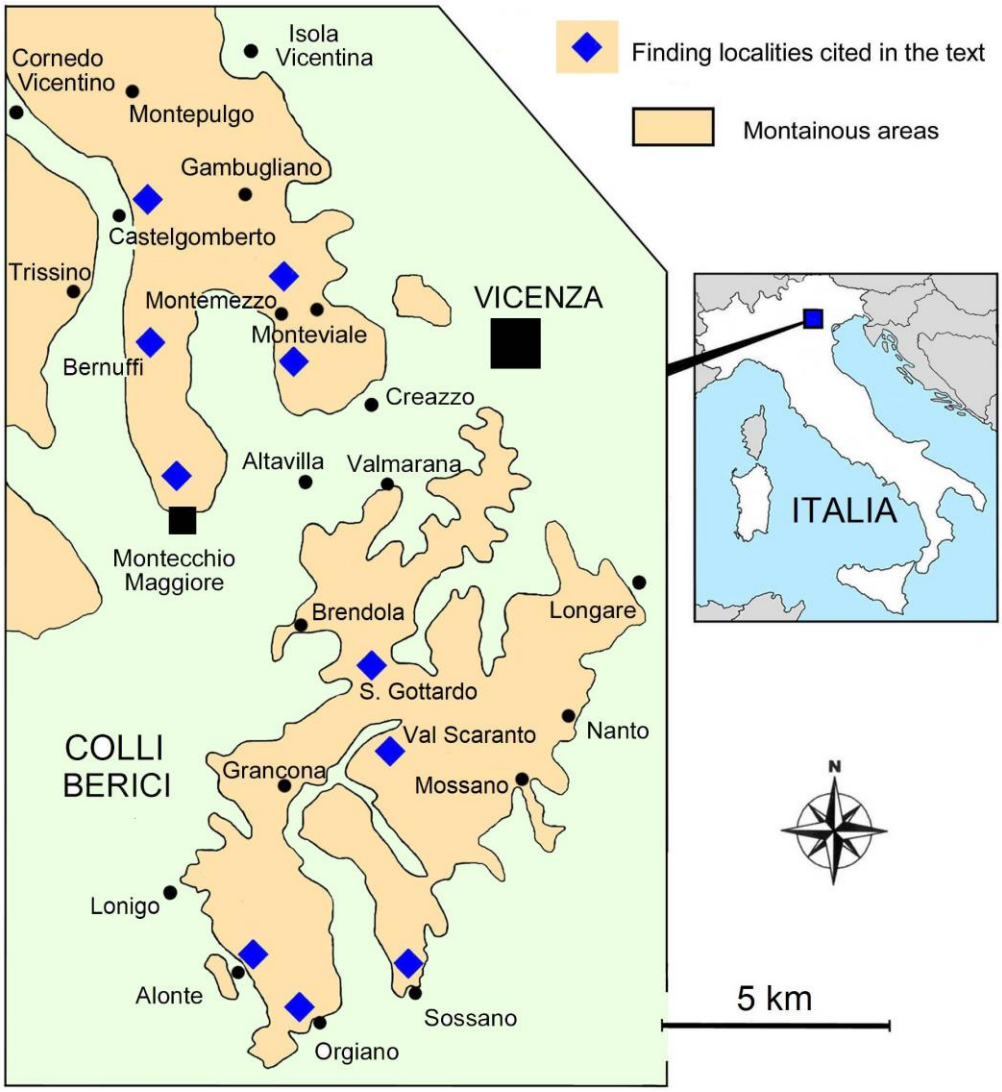


Figure 2 – Location map of the finding localities cited in the text (Vicenza Province).

Figura 2 – Ubicazione delle località di ritrovamento citate nel testo (Provincia di Vicenza).

The stratigraphical succession in this area is mainly composed of carbonates and igneous rocks, ranging from the Upper Cretaceous to the Lower Miocene (Antonelli *et al*., 1990). It was significantly influenced by the Alpone-Chiampo *graben* (Bassi *et al*., 2000): during the Early Eocene, a zone of pronounced subsidence developed in the eastern Lessini Shelf, encompassing the western Colli Berici. During the Paleocene to the Middle Eocene, basaltic flows were emplaced within this graben, effectively separating the Monti Lessini and the Colli Berici into two regions with different geological and stratigraphic histories. These two regions bean to evolve independently from the Late Eocene (Antonelli *et al*., 1990).

The stratigraphical succession of carbonate rocks in the Colli Berici begins with the Upper Cretaceous-Lower Eocene open marine deposits of the Scaglia Rossa, a unit a few tens of meters thick (Massari *et al*., 1976).

The Middle Eocene (Lutetian, Lucchi Garavello, 1980) Marne Euganee consist of alternating marly limestones, calcareous marls and calcarenites interbedded with tuffs (Massari *et al*., 1976), reaching a maximum thickness of about 35 m. The massive nummulitic limestones (Lower to Middle Eocene; Zorzin, 2021), overlie both the Marne Euganee and the volcanic deposits (Ungaro, 1979). These limestones are characterized by accumulations of large nummulites, especially in the lower part, and by coralline red algae occurring as rhodoliths or crusts.

In central and eastern Colli Berici the Upper Eocene Marne di Priabona formation forms a continuous succession with the Middle Eocene nummulitic limestones (Ungaro & Bosellini, 1965), while in the western sector it unconformably overlies the basaltic volcanics. This formation, renowned for its rich fossil content (Fabiani, 1911), reaches its maximum thickness in the Mossano area (Ungaro, 1969).
The Lower-Middle Oligocene Calcareniti di Castelgomberto formation occurs in the north-eastern and north-central Colli Berici, directly overlying the Marne di Priabona. It ranges in thickness from 80 to 200 m. It consists of shallow water, massive or irregularly bedded limestones and calcarenites with abundant coralline red algae. The rich fossil assemblage includes branching corals, molluscs and echinoids. On the eastern margin of the Colli Berici, massive coral colonies are predominant (Ungaro, 1979).

The specimens of *Porosoma cribrum* studied at the Museo Civico of Valdagno derive from the Calcareniti di Castelgomberto formation, which represents the type-horizon for this species. Extensive outcrops of this unit (Lower Oligocene, Rupelian), up to 200 m thick, are exposed in the eastern Monti Lessini and the Colli Berici (Bosellini & Trevisani, 1992). It corresponds to a reef-lagoonal complex: a barrier reef developed in the southeastern Colli Berici (Rossi & Semenza, 1958; Frost, 1981), while a shelf lagoon extended north-westward for approximately 30 km behind the reef (Bosellini & Trevisani, 1992). The Calcareniti di Castelgomberto overlie the Marne di Priabona (Upper Eocene) and are overlain by the Upper Oligocene Arenarie e Calcari di S. Urbano (Bassi *et al*., 2008). Deposition occurred in fully marine conditions within the euphotic zone in generally low-energy conditions, as reconstructed for the four facies identified by Nebelsick *et al*. (2012). The pervasive micritic matrix supports this interpretation. *P. cribrum* is especially abundant in facies 3, the "Coralline algal-larger foraminiferal facies". The occurrence of abundant Nummulites suggests a shallow, well-illuminated marine environment, either sparsely colonized or in proximity to seagrass meadows (Nebelsick *et al*., 2012).

The specimens attributed to *Porosoma pulchrum* were collected by one of the authors (F.C.) from an abandoned quarry (Cava di Via Piave) near Sossano in the Colli Berici. This site is well known for the large number of well-preserved Eocene fossils recovered during its operational phase, late 1960s-2005, although notable finds have also been made following environmental restoration.
The exposed Eocene section, approximately 50 m thick (Fig. 1), mainly consists of Middle Eocene (Lutetian) calcareous limestones, formerly quarried for concrete production, overlain by an 8 m thick Upper Eocene (Priabonian) unit of grey marly limestones (De Angeli & Caporiondo, 2009). These limestones are well stratified and turn yellowish upon weathering. They are rich in macrofossils, predominantly nummulites, bryozoans and less frequently, bivalves, crustaceans and fish teeth. The *Porosoma* specimens were collected from the uppermost marly limestones, in association with other echinoids such as *Gitolampas*, *Echinolampas, Scholechinus, Crucibrissus* and *Waurnia* (Borghi *et al*., 2022, 2024a).
A few specimens of *Porosoma pulchrum*, represented by incomplete coronas, have also been recovered from the Priabonian limestones and marly limestones of the Orgiano and Alonte quarries (Colli Berici). These occurrences are associated with other echinoids including: *Cidaris*, *Gitolampas*, *Echinolampas, Aguayoaster*, *Schizobrissus* and *Trachypatagus* (Bottazzi *et al.,* 2019; Borghi *et al.,* 2023).

Previous work

Cotteau (1856) erected the genus *Porosoma* without designating a type-species, distinguishing it from *Cyphosoma* L. Agassiz, 1838, primarily by the uniserial (rather than biserial) arrangement of the adapical pore pairs. Mortensen (1935, p. 474) later designated *Cyphosoma cribrum* Agassiz in Agassiz & Desor, 1846 as the type-species of *Porosoma*. *Porosoma cribrum* was originally based on a cast ("moule M29") described by Agassiz (1840) and housed at the Museum of Neuchâtel. Sismonda (1843) regarded Agassiz (1840) to be the author of the species. Cast M29 corresponds to the specimen from Castelgomberto (Vicenza, Italy), currently held at the University of Lyon (uncatalogued), and figured in Smith & Kroh (2011). This specimen was illustrated by Desor (1855, pl. 15, figs. 8-10) and referred to as *Cyphosoma* (*Coptosoma*) *cribrum,* "*du Vicentin*". However, as noted by Smith & Kroh (2011), *Cyphosoma* (*Coptosoma*) Desor, 1855 is an unavailable name, being preoccupied by *Coptosoma* Laporte, 1833, a genus of hemipteran insects. The currently accepted combination is: *Porosoma cribrum* (Agassiz in Agassiz & Desor, 1846).

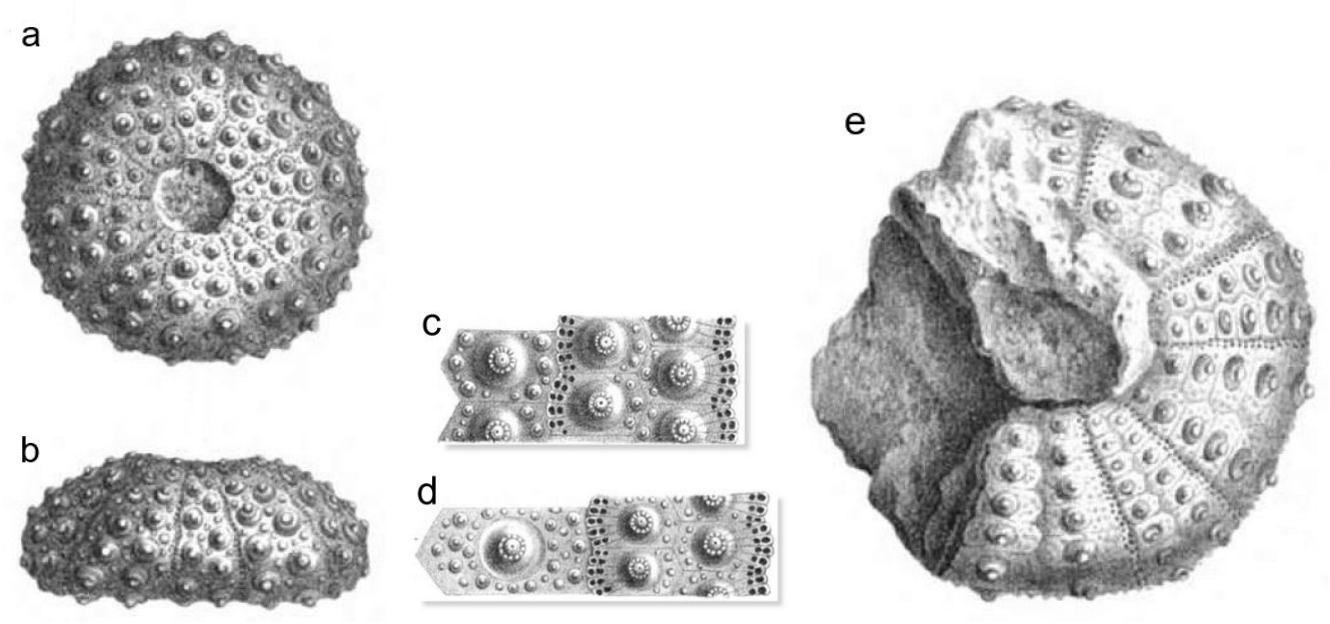
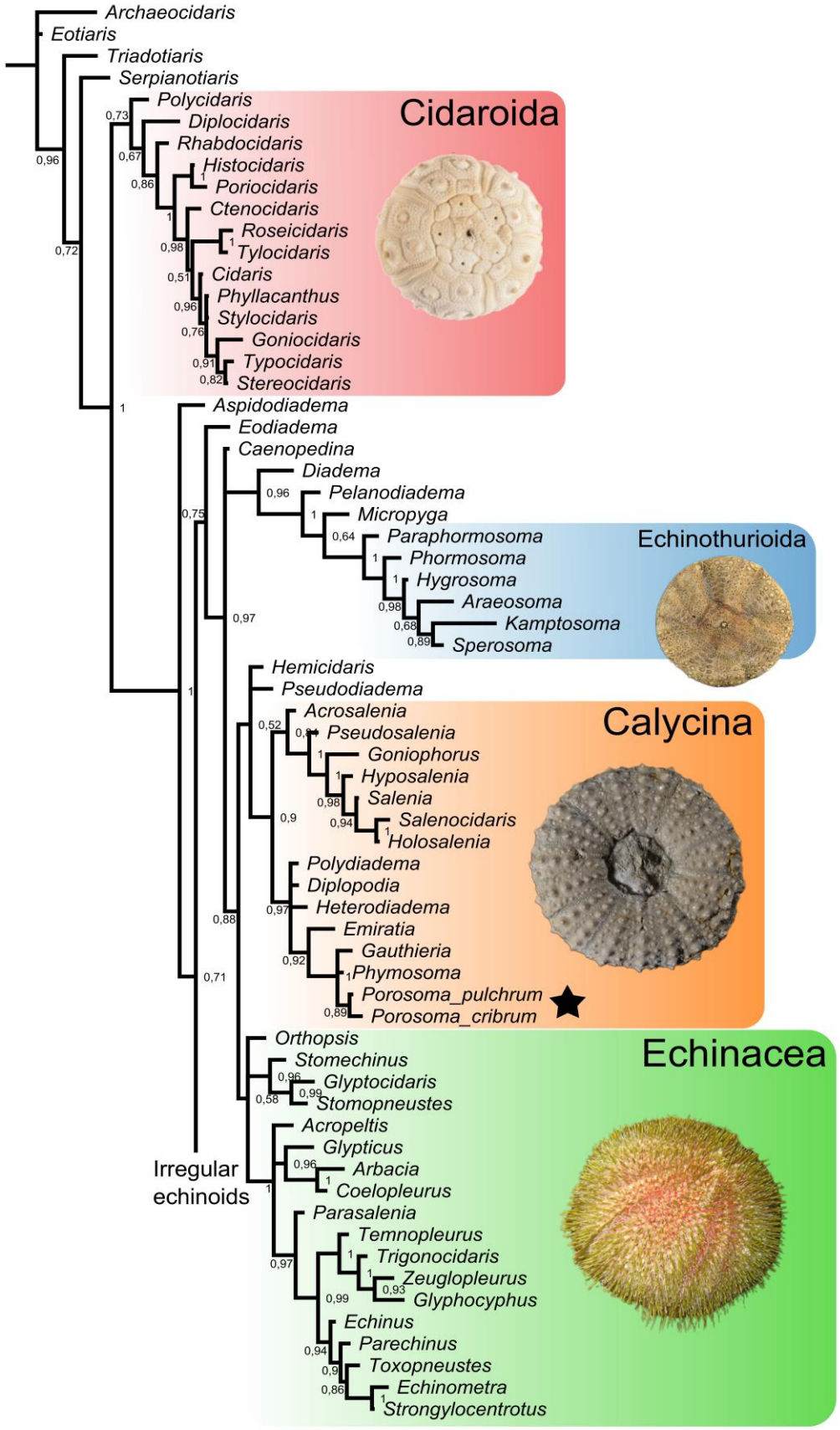


Figure 3 – Original illustration by Laube (1868); a-c) *Porosoma cribrum* (Agassiz, 1846), D = 29 mm, from the Oligocene of Vicenza: a) aboral and b) lateral views, c) detail of the primary tubercles arrangement; *d-e) Porosoma. pulchrum* Laube, 1868, D = 45 mm, from the Priabonian of Val Scaranto (Colli Berici): d) detail of primary tubercles, e) oral view.

Figura 3 – Illustrazioni originali di Laube (1868); a-c) Porosoma cribrum *(Agassiz, 1846), D = 29 mm, Oligocene del Vicentino: a) vista aborale e b) laterale, c) dettaglio dei tubercoli primari; d-e)* Porosoma pulchrum *Laube, 1868, D = 45 mm, dal Priaboniano di Val Scaranto (Colli Berici): d) dettaglio dei tubercoli primari, e) vista del lato orale.*

Four species of "*Cyphosoma*" have been reported from the Eocene and Oligocene of Veneto Region:
- *C. cribrum*: the type-species has been cited from numerous localities (Fig. 2), including Castelgomberto (the type-locality; Lower Oligocene), S. Trinità Bernuffi, Riva San Daniele, Monteviale, Montemezzo, Santo Stefano and Sant'Eusebio di Bassano (Desor, 1855, Laube, 1868; Dames, 1878).
- *C. blanggianum* Desor, 1857: a single specimen was recorded by Dames (1878) from the Upper Eocene of Priabona (Vicenza).
- *C. pulchrum* Laube, 1868: this species was established based on two incomplete specimens, the holotype, from the Priabonian of Val Scaranto in the Colli Berici (Dames, 1878), and a test fragment from the Lutetian of San Giovanni Ilarione (Verona). Oppenheim (1902) also reported a specimen from the Upper Eocene of Priabona.
- *C. superbum* Dames, 1878: known only from the type, an incomplete test from the Lutetian of S. Giovanni Ilarione.

Lambert (1927) proposed to use the structure of the ambulacral plates as the primary criterion for distinguishing species assigned to this genus, and provided schemes of some species.
After Mortensen (1935), more than 30 species, mainly from the Cretaceous and the Eocene, had been assigned to *Porosoma* at that time. However, Mortensen noted that the structure of the ambulacral plates was known for only a few of these, making it difficult or impossible to confirm their generic placement.
According to Carrasco (2024), the taxonomy of *Porosoma* needs comprehensive revision, primarily based on the ambulacral plate compounding, as previously suggested by Lambert (1927). Other features historically used to differentiate species within the genus, such as the number, size, and arrangement of secondary tubercles, are now recognized as highly variable within species and have contributed to considerable taxonomic confusion.
The systematic position of *Porosoma* also remains unresolved (Smith & Kroh, 2011; Carrasco, 2024). Smith & Kroh (2011) observed that *Porosoma* resembles toxopneustids in some respects, particularly in the echinid-style ambulacral plate compounding and the presence of deep buccal notches. However, it differs in possessing crenulate primary tubercles and polygeminate (rather than trigeminate) ambulacral plates.
Similarly, Kroh & Mooi (2025) actually refrain from assign *Porosoma* to any established echinoid family.


Archaeocidaris
Eotiaris
Triadotiaris
Serpianotiaris
Polycidaris
Diplocidaris
Rhabdocidaris
Histocidaris
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Ctenocidaris
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Goniocidaris
Typocidaris
Stereocidaris
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Aspidodiadema
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Caenopedina
Diadema
Pelanodiadema
Micropyga
Paraphormosoma
Phormosoma
Hygrosoma
Araeosoma
Kamptosoma
Sperosoma
Echinothurioida
Hemicidaris
Pseudodiadema
Acrosalenia
Pseudosalenia
Goniophorus
Hyposalenia
Salenia
Salenocidaris
Holosalenia
Polydiadema
Diplopodia
Heterodiadema
Emiratia
Gauthieria
Phymosoma
Porosoma_pulchrum
Porosoma_cribrum
Calycina
Orthopsis
Stomechinus
Glyptocidaris
Stomopneustes
Acropeltis
Glypticus
Arbacia
Coelopleurus
Parasalenia
Temnopleurus
Trigonocidaris
Zeuglopleurus
Glyphocyphus
Echinus
Parechinus
Toxopneustes
Echinometra
Strongylocentrotus
Echinacea
Irregular echinoids

Figure 3 (previous page) – Majority rule consensus tree resulting from the Bayesian inference phylogenetic analysis. Numbers at nodes and under branches are posterior probability values. All images, except *Porosoma pulchrum,* were taken from Wikimedia Commons (image credits can be found in the acknowledgements).

Figura 3 (pagina precedente) – Albero di consenso risultante dall'analisi filogenetica bayesiana. I numeri ai nodi e sotto i rami indicano i valori di probabilità a posteriori. Tutte le immagini, eccetto Porosoma pulchrum*, sono state prese da Wikimedia Commons (i relativi crediti sono riportati nella sezione dei ringraziamenti).*

Phylogenetic results

The Bayesian inference analysis (Fig. 3) recovered *Porosoma cribrum* and *Porosoma pulchrum* as sister taxa. The clade formed by the two *Porosoma* species, in turn, is found in an unresolved polytomy (*i.e*., a node where the current data does not allow complete resolution of phylogenetic relationships) with *Gauthieria* and *Phymosoma*. Support for this scenario is strong in the Bayesian analysis (posterior probability: 1), this indicates that *Porosoma* can be confidently assigned to Phymosomatidae based on the present data.
Characters supporting the new position for the genus include tubercle-free zone developed adapically down middle of interambulacral zones, apical disc large, with distinct pentagonal outline (both present only in *Porosoma pulchrum)*, pore-pairs forming a very small phyllode close to the peristome (in *Porosoma cribrum*), tubercles imperforate and crenulated and defined buccal notches without tag.
The general topology recovered by our analysis is congruent with topologies found by previous iterations of the Kroh & Smith (2010) dataset (Fig. 7).

Systematics

The systematic palaeontology follows Kroh & Mooi (2025).

Order Phymosomatoida Mortensen, 1904
Family Phymosomatidae Pomel, 1883
Genus ***Porosoma*** Cotteau, 1856

[= *Cyphosoma* (*Coptosoma*) Desor 1855, p. 91 (unavailable name); = *Microsoma* Cotteau, 1886 (subjective junior synonym of *Porosoma*, in Smith & Kroh, 2011)].

Type species: *Cyphosoma cribrum* Agassiz, in Agassiz & Desor, 1846, p. 352, by subsequent designation of Lambert (1927, p. 65) and Mortensen (1935, p. 474).

Description (partially emended from Smith & Kroh, 2011):
- Test medium to large, wheel-shaped, depressed above and below.
- Apical disc about one-third of the test diameter, with weak interradial and perradial indentations, sometimes more pronounced in the posterior interambulacrum. Plates not bound to the corona, always missing.
- Ambulacra straight; plating polygeminate (6-7 elements per compound plate at the ambitus), with echinid style compounding (Fig. 4a): the lowest element is the largest, the uppermost element also reaches the perradius and intermediate elements are demiplates. Pore-pairs are uniserial, arranged in arcs aborally and around the ambitus, and expanding into very short phyllodes adorally in the type species (Fig. 5g). A single primary tubercle dominates each compound plate, with small secondary tubercles and granules along the plate margins.
- Interambulacral plates wider than tall, dominated by a single centrally positioned primary tubercle. Secondary tubercles and granules are markedly smaller and predominantly restricted to the plate margins. Short interradial naked zones may occur adapically.
- Tubercles imperforate and crenulate.
- Peristome large to very large, circular, nearly flush with the test surface; buccal notches broad and deep with thickened lips and well-developed bar.
- Spines straight, cylindrical or flattened, tapering distally to a blunt point; shaft surface nearly smooth; ring conspicuous, base crenulate.

Remarks: The topotypic sample of *P. cribrum* examined in this study confirms the generic diagnosis of *Porosoma* proposed by Smith & Kroh (2011) and enables the addition of previously undescribed morphological features. Notably, these include the presence of small naked interradial zones in the adapical region and the distinctive morphology of the primary spines. These newly observed traits tracked in *Porosoma* are congruent with the diagnostic framework of the family Phymosomatidae Pomel, 1883. The sole exception lies in the echinid-style compounding of ambulacral plates, which deviates from the typical phymosomatid pattern. In the current phylogenetic context, this feature is best interpreted as a homoplasy, reflecting convergent evolution rather than shared ancestry, given the deeply nested position of *Porosoma* within the Phymosomatoida.

Comparison with other genera in the Phymosomatidae:

- *Porosoma* shows close affinities with *Phymosoma* Haime, in d'Archiac & Haime 1853. These two genera share several morphological characters; however, *Phymosoma* is distinguished by its phymosomatid-style compounding of ambulacral plates (Fig. 4b), adapically biserial pore columns and smaller buccal notches (Smith & Kroh, 2011). Stratigraphic range of *Phymosoma*: from the Middle Jurassic to the Paleocene.
- *Gauthieria* Lambert, 1888, Upper Cretaceous (Cenomanian-Maastrichtian), differs from *Porosoma* by a markedly larger apical disc (up to half test diameter), a deeply sunken peristome, smaller buccal notches and the absence of phyllodes. All known species are small-sized and the ambulacral plate compounding is different (Fig. 4c).
- *Rachiosoma* Pomel, 1883 (Upper Cretaceous), is distinguished by a relatively small apical disc (about one-quarter of the test diameter) with plates often preserved bound to the corona. Ambulacral plates are polygeminate, with 5 elements compounded as an echinid triad and an overlapping primary tubercle, alternating with one or two simple elements. Phyllodes are absent. Small pits and elongate sutural depressions occur at the ambitus and adapically giving the test a sculptured appearance.
- *Cosmocyphus* Pomel, 1883 (Upper Cretaceous to Paleocene), has polygeminate ambulacral plating with phymosomatid-style compounding (Fig. 4b) and adapically biserial pore pairs. Phyllodes are absent.
- *Kachchhia* Srivastava, Gupta and Jauhri, 2008 (late Middle Eocene, India) differs by phymosomatid-style ambulacral compounding, broad and depressed aboral interradial naked zones and a sunken peristome.
- *Miocyphosoma* Pomel, 1883 (Cretaceous) is distinguished by ambulacral plates compounded in phymosomatid style, small buccal notches and absence of phyllodes.

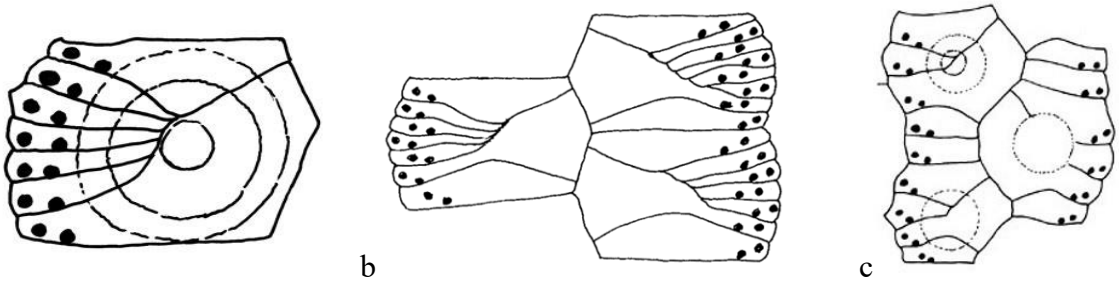

Figure 4 – Ambulacral plating schemes (from Smith & Wright, 1996; Smith & Kroh, 2011): a) *Porosoma*, b) *Phymosoma* and *Miocyphosoma*, c) *Gauthieria.*

Figura 4 – Schema della composizione delle piastre ambulacrali (da Smith & Wright, 1996; Smith & Kroh, 2011): a) Porosoma*, b)* Phymosoma *e* Miocyphosoma*, c)* Gauthieria.

Species included:

- *P. cribrum* (Agassiz, in Agassiz & Desor, 1846)	Eocene-Lower Oligocene, western Europe.
- *P. haimei* (Desor, 1856)	Middle Eocene, Europe.
- *P. pulchrum* (Laube, 1868)	Eocene (Lutetian-Pribonian), Italy.
- *P. vidali* (Lambert, 1902)	Eocene, Spain.
- *P. montserratense* Lambert, 1927	Eocene, Spain.

Taxonomic Concept and Revision: The concept of the genus *Porosoma* adopted herein follows the diagnosis provided by Smith & Kroh (2011), which accurately reflects the morphological characters observed in the type

species. In particular, the echinid-style compounding of the polygeminate ambulacral plates is regarded as a key diagnostic feature of the genus.
Among the species historically assigned to *"Cyphosoma*" from the Eocene-Oligocene of the Veneto Region, only *C. pulchrum* Laube**,** 1868 exhibits the defining traits of *Porosoma cribrum*. In contrast, *C. superbum* Dames, 1878 has trigeminate ambulacral plates which exclude it from *Porosoma*. The attribution of the incomplete specimen from the Eocene of Priabona attributed to *C. blanggianum* Desor, 1857 by Dames (1878) remains highly uncertain. According to Dames, the specimen closely resembles the illustration published by De Loriol (1875; pl. 1, figs. 14-15), which depicts trigeminate ambulacral plates.

With regard to the species from other regions currently attributed to *Porosoma*, we concur with Carrasco (2024) that the taxonomy of the genus requires thorough revision. Such a revision should follow the approach originally outlined by De Loriol (1875, p. 20) and Lambert (1927, p. 65), emphasizing the composition of ambulacral plates and the presence or absence of lower rows of secondary tubercles, as primary diagnostic characters. A comprehensive re-examination of well-preserved material from across the genus is essential to clarify the correlation between ambulacral plate architecture and other proposed diagnostic features (Carrasco, 2024).

Among the species revised by Carrasco (2024):
- *Porosoma blanggianum* (Desor, 1853), *P. pentagonale* (Cotteau, 1892), *P. dalloni* Lambert, 1927 and *P. distinctum* Lambert, 1927 exhibit a "*plaquita mediana*" (median small plate), indicative of phymosomatid-style ambulacral compounding. These species are therefore excluded from *Porosoma*.
- *Porosoma haimei* (Desor, 1855), *P. vidali* (Lambert, 1902) and *P. montserratense* Lambert, 1927, in contrast, have ambulacral plates compounded in the echinid style, consistent with the type-species of *Porosoma*.

Distribution: Eocene and Oligocene of Europe, Middle East, Northern and Sub-Saharan Africa, North America.

Porosoma cribrum (Agassiz, in Agassiz & Desor, 1846)
Fig. 5a-r, Tab. 1

1846 *Cyphosoma cribrum* – Agassiz in Agassiz & Desor: 48.
1857 *Cyphosoma* (*Coptosoma*) *cribrum* – Desor: 91, pl. 15, figs. 8-10.
1863 *Cyphosoma cribrum* Agassiz, 1840 – Cotteau: 40.
1868 *Cyphosoma cribrum* Agassiz, 1840 – Laube: 12, pl. 1, fig. 4.
1875 *Cyphosoma cribrum* Agassiz, 1840 – De Loriol: pl. 2, fig. 1.
1935 *Porosoma cribrum* (Agassiz, 1846) – Mortensen: 474, fig. 275.
2011 *Porosoma cribrum* (Agassiz in Agassiz & Desor, 1846) – Smith & Kroh.
2014 *Porosoma cribrum* (L. Agassiz, 1840) – Mikuz *et al*.: 13-14, pl. 2, figs. 4-7.
2016 *Porosoma cribrum* (Agassiz in Agassiz & Desor, 1846) – Boschele *et al*.: 118, pl. 6, fig. 23; pl. 7, fig. 1; pl. 17, fig. 4.

Type locality: Castelgomberto (Vicenza), Oligocene (Rupelian), Calcareniti di Castelgomberto formation.

Type material: the species was originally based by Agassiz (1840) on a cast (M29, Museum of Neuchâtel), corresponding to the specimen from Castelgomberto (Vicenza, Italy) housed at the University of Lyon (uncatalogued) illustrated in Smith & Kroh (2011).
Material studied: 130 specimens from the type horizon. Three of them (MCV CDL864a-c) from Castelgomberto, the type-locality; the remaining specimens (MCV 22.118, 136, 701, 740, 743-746, 756-759, 790-796, 817, 825-826, 869, MCV 25/25-28) from San Gottardo (Colli Berici).

Diagnosis: Small to medium-sized species of *Porosoma* characterized by the presence of large primary tubercles, with those in the interambulacra only slightly exceeding in size those in the ambulacra (Fig. 5o). In the interambulacral zones, secondary tubercles are less than half the size of the adjacent primary tubercles and do not form vertical series adorally. Apical disc with weak indentations, both interradially and perradially (Figs. 5a, o, q), slightly extending only into the posterior interambulacrum (Fig. 5h). Small interradial naked areas are present adapically especially in the posterior interambulacrum (Fig. 5h).

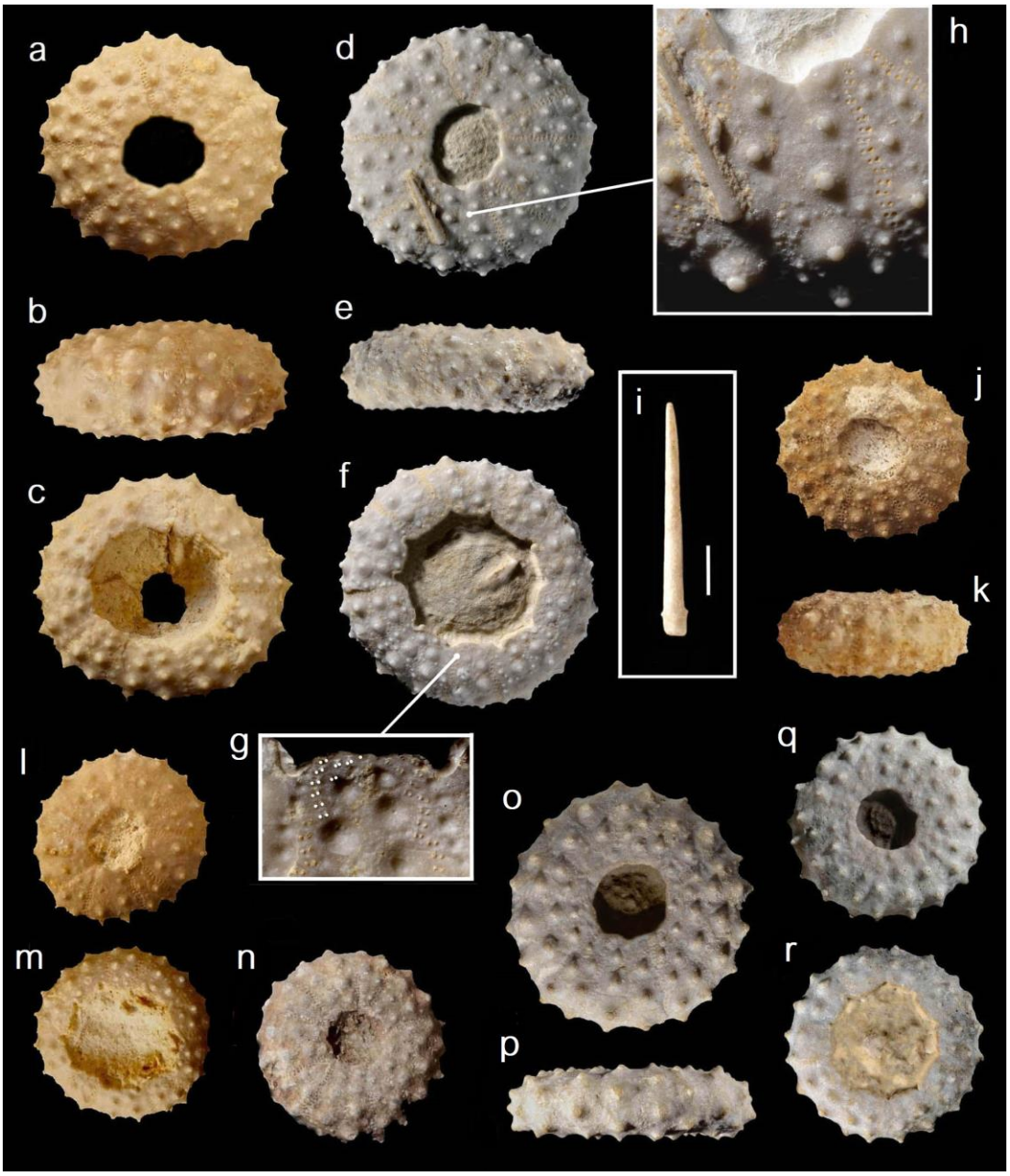

Figure 5 – *Porosoma cribrum* (Agassiz, in Agassiz & Desor, 1846), Lower Oligocene, Calcareniti di Castelgomberto formation. Specimens from San Gottardo (Vicenza): a-c) MCV 22.869a, D = 24.5 mm, aboral (a), lateral (b) and oral (c) views; d-i) MCV 25/25, D = 26 mm, aboral (d), lateral (e) and oral (f) views, g) detail of an adoral ambulacrum with short phyllodes (white dots), h) detail of the posterior interambulacrum displaying an adapical naked area, i) close up of a primary spine; j-k) MCV 22.869d, D = 22 mm, aboral (j) and lateral (k) views; l-m) MCV 22.869c, D =19.5 mm, aboral (l) and oral (m) views; o-p) MCV 25/27, D = 25 mm, aboral (o) and lateral (p) views; q-r) MCV 25/26, D = 20 mm, aboral (q) and oral (r) views. Specimen from Castelgomberto (Vicenza): n) CDL864c, D = 18.5 mm, aboral view. Scale bar equals 2 mm.

Figura 5 – Porosoma cribrum *(Agassiz, in Agassiz & Desor, 1846), Calcareniti di Castelgomberto, Oligocene inferiore. Esemplari da San Gottardo (Vicenza): a-c) MCV 22.869a, D = 24.5 mm, vista aborale (a), laterale (b), orale (c); d-i) MCV 25/25, D = 26 mm, vista aborale (d), laterale (e), orale (f), g) dettaglio di ambulacro adorale con piccole fillodi (punti bianchi), h) dettaglio dell'interambulacro posteriore con area nuda adapicale, i) ingrandimento di una spina primaria; j-k) MCV 22.869d, D = 22 mm, vista aborale (j) e laterale (k); l-m) MCV 22.869c, D =19.5 mm, vista aborale (l) e orale (m); o-p) MCV 25/27, D = 25 mm, vista aborale (o) e laterale (p); q-r) MCV 25/26, D = 20 mm, vista aborale (q) e orale (r). Esemplare da Castelgomberto (Vicenza): n) CDL864c, D = 18.5 mm, vista aborale. La barretta = 2 mm.*

Specimen	D	H		Da*		Dp		nA	nIA
		mm	%D	mm	%D	mm	%D		
CDL 864a	34	12	35	8.5	25	18.5	54	10-11	9-10
CDL 864b	29	10	34	8.5	29	17.5	60	-	-
CDL 864c	18.5	8.5	44	5.5	30	-	-	-	-
MCV 22.869A	25	10.5	42	6	24	12.5	50	10	9
MCV 22.869B	21.5	9.5	44	5	23	-	-	.-	--
MCV 22.869C	19.5	8.5	44	6.5	33	12	62	8-9	7-8
MCV 22.869D	22	8	36	-	-	-	-	9	7-8
MCV 22.869E	17.5	7.5	43	6	34	10	57	8	7-8
MCV 25/25	26	10	38	8.5	32.5	13.5	52	8-9	8
MCV 25/26	20	7	35	6	30	10	50	7-8	7
MCV 25/27	25	7	28	7	28	12.5	50	8	7
MCV 25/28	19	8	42	4.5	24	9.5	50	7-8	7
Mean	**23**		**39**		**28.5**		**54**		

Table 1 – *Porosoma cribrum* (Agassiz, in Agassiz & Desor, 1846), Lower Oligocene Calcareniti di Castelgomberto formation, Colli Berici (Vicenza): principal biometric parameters and mean shape-ratio values of the 12 best-preserved specimens.

Tabella 1 – Porosoma cribrum *(Agassiz, in Agassiz & Desor, 1846), Oligocene inferiore, formazione delle Calcareniti di Castelgomberto, Colli Berici (Vicenza): dati biometrici principali e valori medi dei rapporti di forma nei 12 esemplari meglio conservati.*

Description: As for the generic diagnosis. Newly observed features include the presence of small adapical naked interradial areas, which are not visible in the type specimen, likely due to surface abrasion (Smith & Kroh, 2011). Primary spines are short (length ~1 cm in a specimen with D = 26 mm), straight and tapering distally to a blunt point (Fig. 5i); the shaft is nearly smooth, bearing only faint longitudinal ridges.

Remarks: Specimens of *P. cribrum* preserved as complete coronas are relatively frequent within the Calcareniti di Castelgomberto formation, although the test surface is often abraded, as observed in the type specimen (Smith & Kroh, 2011). The large sample examined confirms the diagnostic features previously established for the species and allows for a detailed assessment of biometric variability. The corona is of small to medium size (mean D = 27.5 mm, range = 8-45 mm, in the whole studied sample), relatively low in profile (mean H = 37% D, range 34-44% D; Figs. 5b, e, k, p), with a large peristome (mean Dp = 50% D, range 47-62% D; Figs. 5c, f, m, r), and a comparatively small apical disc (mean Da = 30.5% D, range 23-35% D; Fig. 5a, d, j, l, n, o, q). Ambulacral plates typically consist of 6 elements at the ambitus (range: 5-7; Fig. 4a).
Detailed biometric data, including previse counts of ambulacral and interambulacral plates, taken from a group of 12 well-preserved specimens, are presented in Table 1.

Distribution: Eocene-Lower Oligocene of Western Europe (Smith & Kroh, 2011). Cotteau (1863) recorded it as very rare in the Eocene of France, at Biarritz (Rocher du Goulet) and Sabarat (Ariège). Most records from the Veneto Region (North-eastern Italy) are Oligocene in age: S.S. Trinità Bernuffi, Riva di S. Daniele, Monteviale, Montemezzo and S. Stefano near Castelgomberto (Laube, 1868); Fabiani (1915) also recorded this species in the Priabonian. Boschele *et al.* (2016) described 3 specimens from the Oligocene (Rupelian) of Colle S. Pietro and Torrente Ceggio, in the Val Sugana (Trentino Region).

Porosoma pulchrum (Laube, 1868)
Figs. 6a-e, 7a-i, Tab. 2

1868 *Cyphosoma pulchrum* – Laube: 12, pl. 1, fig. 5
1902 *Cyphosoma pulchrum* Laube – Oppenheim: 175, figs 5-8.
? 2014 *Phymosoma istrana* (nov. sp.?) – Mikuz *et al.*: 12-13, pl. 1, figs. 15-19.

Type locality: Val Scaranto (Colli Berici, Vicenza Province), Priabonian (Oppenheim, 1902).

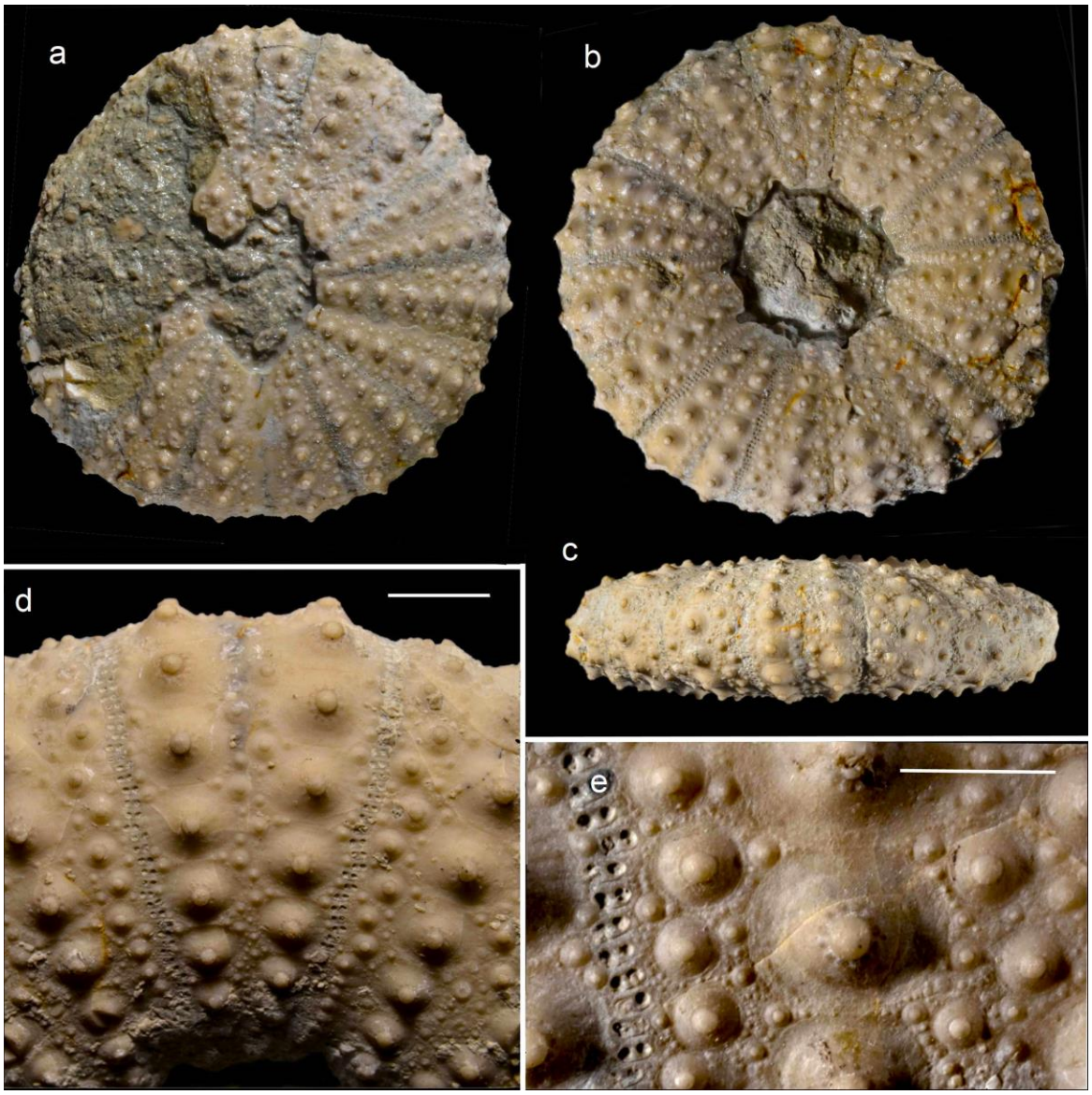

Figure 6 – *Porosoma pulchrum* (Laube, 1868), (MCV 25/29), D = 73 mm, Upper Eocene Marne di Priabona formation, Sossano (Vicenza): a) aboral view; b) oral view; c) lateral view; d) detail of an oral ambulacral area; e) close up of an interambulacral area at the ambitus. Scale bar equals 5 mm.

Figura 6 – Porosoma pulchrum *(Laube, 1868), (MCV 25/29), D = 73 mm, Eocene superiore, formazione delle Marne di Priabona, Sossano (Vicenza): a) vista aborale; b) orale; c) laterale; d) ingrandimento di un'area ambulacrale del lato orale; e) ingrandimento di un'area interambulacrale all'ambitus. La barretta = 5 mm.*

Type material: Laube (1868) described two incomplete specimens, one of them from the Priabonian of Val Scaranto (Colli Berici), the other from the Lutetian volcanic tuffites of San Giovanni Ilarione (Verona), but he did not designate a holotype. After Oppenheim (1902), the type is the specimen figured by Laube (1868, fig. 5), from Val Scaranto.

Material studied: 6 specimens (MCV 25/20-23, MCV 25/29-30) from Sossano and one (T560) from Alonte, all from the Upper Eocene Marne di Priabona formation of the Colli Berici (Vicenza Province).
Diagnosis: Large-sized species of *Porosoma* (D up to 75 mm), characterized by the apical disc that indents the posterior interambulacrum and by the presence of adapical naked interradial zones.

Description (biometric data in Tab. 2): Test medium to large in size (D up to 73 mm in the studied sample, mean D = 57.5 mm), very low (mean H = 28.5% D), dorsoventrally depressed (Figs. 6c, 7h).

- Apical disc about one-third of test diameter (mean Da = 30.5% D), sub-pentagonal, showing slight to moderate indentation into the posterior interradius (Figs. 6a, 7a-b, 7g).
- Ambulacral plates polygeminate (7 elements per plate, at the ambitus), compounded in the echinid-style: the lowest element is the largest, the uppermost element also reaches the perradius and all intermediate elements are demiplates (Figs. 7c-d). Pore-pairs undifferentiated, arranged in arcs (Figs. 6d,e). A single primary tubercle occurs in each compound plate, with much smaller secondaries and granules at the plate edges (Fig. 6d).
- Interambulacral plates distinctly wider than tall (ratio = 0,40; Fig. 6e), dominated by a central primary tubercle. Much smaller secondary tubercles are present, mainly along the plate margins, some larger secondaries forming irregular vertical series parallel to the pore zones at the ambitus and adorally (Figs. 6d.e). Small, nearly naked interradial zones present adapically, especially in the posterior interambulacrum (Figs. 6a, 7a,b).
- Tubercles imperforate and crenulate, their base occupies nearly the entire plate heigh (Fig. 6e).
- Peristome about one-third of test diameter (mean Dp = 30.5% D), sub-circular, nearly flush or slightly sunken (Figs. 6b, 7i). Buccal notches "U" shaped, rather large and deep, with thickened lips (Fig. 7e).
- Oppenheim (1902, fig. 6) described short spines in the holotype (length 12 mm in a specimen with D = 45 mm). However, spines may reach up to 27 mm in length. They taper to a blunt point and have a prominent ring; the shaft is smooth, cylindrical or flattened distally (Fig. 7f).

Remarks: The specimens examined in this study closely match the original description and illustration of *Cyphosoma pulchrum* provided by Laube (1868), as well as to the subsequent interpretation provided by Oppenheim (1902). Both authors considered *P. pulchrum* to be closely related to *Cyphosoma pellati* Cotteau, 1863, from the Eocene of Biarritz (France). However, *C. pellati* differs markedly in having a significantly smaller apical disc (Cotteau, 1863, fig. 2); additionally, the generic placement of this species remains unresolved, as its ambulacral plate compounding has not been documented.

Specimen	**D**	**H**		**Da**		**Dp**		**nA**	**nIA**
		mm	**%D**	**mm**	**%D**	**mm**	**%D**		
MCV 25/20	60	-	-	18	30	-	-	-	-
MCV 25/29	73	21	29	21	29	22	30	19-20	18
MCV 25/21	31	8	26	10	32	10.5	34	11-12	10-11
MCV 25/30	66	20	30	-	-	22	33	18-19	16-17
Mean	**57.5**		**28.5**		**30.5**		**32.5**		

Table 2 – *Porosoma pulchrum* (Laube, 1868), Upper Eocene Marne di Priabona formation, Colli Berici (Vicenza): main biometric data and mean values of the shape ratios derived from 4 well-preserved specimens.

Tabella 2 – Porosoma pulchrum *(Laube, 1868), Eocene superiore, formazione delle Marne di Priabona, Colli Berici (Vicenza): dati biometrici principali e valori medi dei rapporti di forma in 4 degli esemplari meglio conservati.*

- *Porosoma cribrum* differs from *P. pulchrum* by smaller test, markedly wider peristome (mean Dp = 50% D, vs. 31.5% D) and taller interambulacral plates at the ambitus (height ~ 60% of width in *P. cribrum*, vs. 40% in *P. pulchrum*). The apical disc is less indented and the adapical interradial naked zones are more reduced.
- *P. haimei* (Desor, 1855) shares with *P. pulchrum* the presence of indentations in the apical disc outline and the occurrence of naked areas in the interradial zones (see Smith & Kroh, 2011, specimen A20112, Muséum National d'Histoire Naturelle, Paris, Eocene of Montserrat, Spain). However, in differs by having ambulacral plates composed of six elements at the ambitus and a much smaller apical disc (Da ~ 20% D; Carrasco, 2024).
- *P. vidali* (Lambert, 1902) has ambulacral plates composed by 8 elements at the ambitus.
- *P. montserratense* Lambert, 1927, is morphologically similar to *P. pulchrum* and has ambulacral plates made of 7-8 elements: it may represent a junior synonym of *P. pulchrum*. However, the specimens studied by Carrasco (2024) are much smaller (maximum test diameter = 50 mm) than those from the Colli Berici.

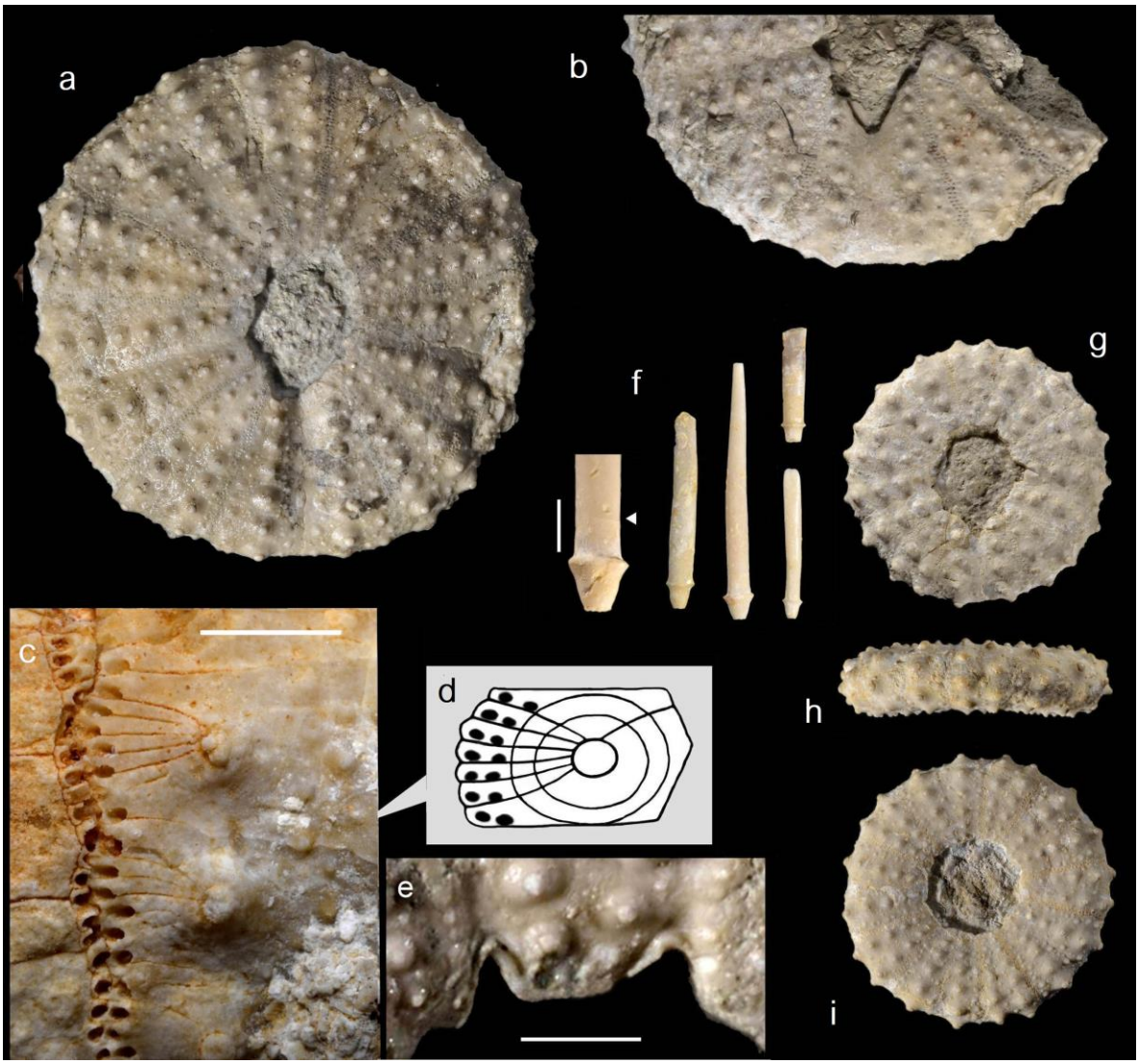

Figure 7 – *Porosoma pulchrum* (Laube, 1868), Upper Eocene Marne di Priabona formation, Sossano (Vicenza): a) MCV 25/20, D = 60 mm, aboral view; b) MCV 25 MCV 25/30, D = 62 mm, aboral view with deep interradial indentation and naked area in the adapical posterior interambulacrum; c) detail of ambulacral plates at ambitus (T560). Scale bar equals 5 mm; d) scheme of the ambulacral plate composition; e) close up view of buccal notches (MCV 25/29), D = 73 mm; f) primary spines (MCV 25/24), scale bar = 3 mm; g-i) small specimen (MCV 25/21), D = 31 mm, aboral (g), lateral (h) and oral (i) views. The scale bars equal 5 mm.

Figure 7 – Porosoma pulchrum *(Laube, 1868), Eocene superiore, formazione delle Marne di Priabona, Sossano (Vicenza): a) MCV 25/20, D = 60 mm, vista aborale; b) MCV 25/30, D = 62 mm, vista aborale con profonda indentazione interradiale e aree nude nell'interambulacro posteriore; c) ingrandimento di piastre ambulacrali all'ambitus (T560). La barretta = 5 mm; d) schema della composizione di una piastra ambulacrale; e) ingrandimento degli intagli boccali (MCV 25/29), D = 73 mm; f-g) piccolo esemplare (MCV 25/21), D = 31 mm, viste aborale (f) e orale (g). Barretta = 5 mm.*

- *Porosoma pentagonale* (Cotteau, 1892), *P. blanggianum* (Desor, 1853), *P. dalloni* Lambert, 1927 and *P. distinctum* Lambert, 1927 exhibit phymosomatid style compounding (Carrasco, 2024) and are therefore excluded from *Porosoma*.

Distribution: Upper Eocene Marne di Priabona formation of the Colli Berici (Vicenza) and Lutetian of San Giovanni Ilarione in the Lessini Mountains (Verona). Oppenheim (1902) also reported the species from the Upper Eocene of Priabona (Vicenza).

Conclusions

The taxonomy of *Porosoma* Cotteau, 1856 remains largely unresolved, as species differentiation has traditionally relied on morphological traits subject to considerable variability, such as test height, overall size, and the arrangement of secondary tubercles. By contrast, the composition of ambulacral plates has seldom been employed, partly due to the difficulty of observing suture lines in fossil material.

To address this issue, well-preserved specimens from the Eocene and Oligocene of the Veneto Region (Northeastern Italy) were examined.

The revision focused on the type species, *Porosoma cribrum* (Agassiz in Agassiz & Desor, 1846), based on an extensive sample from the type horizon, the Calcareniti di Castelgomberto formation (Rupelian). The results confirm the diagnosis of this species as provided by Smith & Kroh (2011), including the composition of the ambulacral plates: polygeminate plates, with the lowest element being the largest, the uppermost element reaching the perradius, and all intermediate elements represented by demi-plates (echinid style). In addition, new data are introduced, such as variability in test shape ratios, the presence of small naked interradial areas aborally, and the morphology of primary spines.

Some large specimens from the Upper Eocene Marne di Priabona formation in the Colli Berici (Vicenza Province) correspond to the original description of *Cyphosoma pulchrum* Laube, 1868. The composition of the ambulacral plates in this material is identical to that of *Porosoma cribrum*, thereby supporting its attribution to *Porosoma*. Accordingly, the new combination proposed here is *Porosoma pulchrum* (Laube, 1868). The newly available, well-preserved material from the type horizon allows a more complete morphological characterization and clarifies its relationship to the type species: *P. pulchrum* differs from *P. cribrum* by its larger test size, smaller peristome, and a sub-pentagonal apical disc that indents the posterior interradius.

According to Smith & Kroh (2011) and Carrasco (2024), the diagnostic characters of *Porosoma* should include the composition of the ambulacral plates as in the type species. Consequently, species previously assigned to *Porosoma* that exhibit different plate compositions likely belong to other genera. Based on this criterion, only three additional species are retained within *Porosoma*: *P. haimei* (Desor, 1856), *P. vidali* (Lambert, 1902) and *P. montserratense* Lambert, 1927.

A phylogenetic analysis including *Porosoma pulchrum* and *Porosoma cribrum* clarifies the systematic position of the genus, which had remained uncertain. Bayesian inference recovers *Porosoma* in an unresolved polytomy with *Phymosoma* and *Gauthieria*, leading to its placement within the family Phymosomatidae Pomel, 1883.

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Appendix

Complete scorings for the new OTUs used in the phylogenetic analysis:

Porosoma_pulchrum 00010000000-0-0021000000-0000???????00????????????10-1????????1????????0???????0-?-022200143000020000000000000011?0000-000000000??000001-0-00-000-------
0110000----0000--000020??0----0-10--00-110100-0001100000???0?002000000000000110??????????????????????????????100??0000000000000?????00--0000?00-00000----

Porosoma_cribrum 00010000000-0-0021000000-0000???????00????????????10-1????????0????????0???????0-?-022200143000020000000000000001110000-000000000??000001-0-00-000-------
0110000----0000--000020??0----0-00--00-110100-0001100000???0?002000000000000110??????????????????????????????100??0000000000000?????00--0000?00-00000----

MrBayes script used to run the analysis:

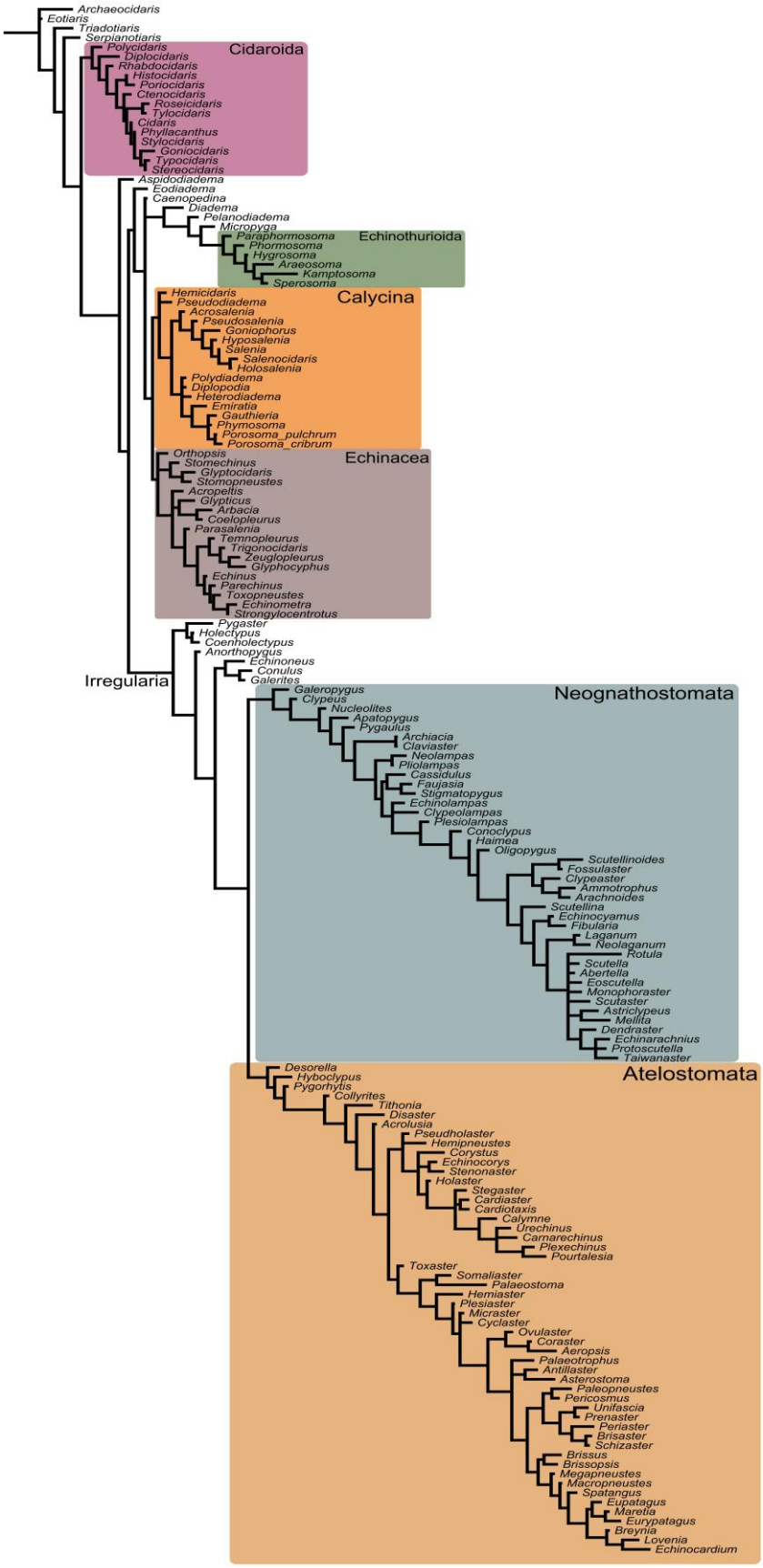
```
begin mrbayes;
set autoclose=yes nowarn=yes;
lset rates=gamma;
      lset coding=variable;
      ctype ordered: 4 6 17 38 75 80 86 202 203 233;
mcmcp ngen= 2000000 relburnin=yes burninfrac=0.25  printfreq=1000  samplefreq=1000 nchains=4 nruns=2 temp=0.10 savebrlens=yes;
mcmc;
sump;

sumt contype=allcompat Outputname=Echino164PoroOK_MCC.t;
sumt contype=halfcompat Outputname=Echino164PoroOK_MRC.t;

end;
```

Figure 7 (next page) - Full results of the Bayesian phylogenetic analysis.

Figura 7 (pagina seguente) - Risultati completi dell'analisi filogenetica Bayesiana. ⇨


Archaeocidaris
Eotiaris
Triadotiaris
Serpianotiaris
Cidaroida
Polycidaris
Diplocidaris
Rhabdocidaris
Histocidaris
Poriocidaris
Ctenocidaris
Roseicidaris
Tylocidaris
Cidaris
Phyllacanthus
Stylocidaris
Goniocidaris
Typocidaris
Stereocidaris
Aspidodiadema
Eodiadema
Caenopedina
Diadema
Pelanodiadema
Micropyga
Echinothurioida
Paraphormosoma
Phormosoma
Hygrosoma
Araeosoma
Kamptosoma
Sperosoma
Calycina
Hemicidaris
Pseudodiadema
Acrosalenia
Pseudosalenia
Goniophorus
Hyposalenia
Salenia
Salenocidaris
Holosalenia
Polydiadema
Diplopodia
Heterodiadema
Emiratia
Gauthieria
Phymosoma
Porosoma_pulchrum
Porosoma_cribrum
Echinacea
Orthopsis
Stomechinus
Glyptocidaris
Stomopneustes
Acropeltis
Glypticus
Arbacia
Coelopleurus
Parasalenia
Temnopleurus
Trigonocidaris
Zeuglopleurus
Glyphocyphus
Echinus
Parechinus
Toxopneustes
Echinometra
Strongylocentrotus
Pygaster
Holectypus
Coenholectypus
Anorthopygus
Echinoneus
Conulus
Galerites
Irregularia
Neognathostomata
Galeropygus
Clypeus
Nucleolites
Apatopygus
Pygaulus
Archiacia
Claviaster
Neolampas
Pliolampas
Cassidulus
Faujasia
Stigmatopygus
Echinolampas
Clypeolampas
Plesiolampas
Conoclypus
Haimea
Oligopygus
Scutellinoides
Fossulaster
Clypeaster
Ammotrophus
Arachnoides
Scutellina
Echinocyamus
Fibularia
Laganum
Neolaganum
Rotula
Scutella
Abertella
Eoscutella
Monophoraster
Scutaster
Astriclypeus
Mellita
Dendraster
Echinarachnius
Protoscutella
Taiwanaster
Atelostomata
Desorella
Hyboclypus
Pygorhytis
Collyrites
Tithonia
Disaster
Acrolusia
Pseudholaster
Hemipneustes
Corystus
Echinocorys
Stenonaster
Holaster
Stegaster
Cardiaster
Cardiotaxis
Calymne
Urechinus
Carnarechinus
Plexechinus
Pourtalesia
Toxaster
Somaliaster
Palaeostoma
Hemiaster
Plesiaster
Micraster
Cyclaster
Ovulaster
Coraster
Aeropsis
Palaeotrophus
Antillaster
Asterostoma
Paleopneustes
Pericosmus
Unifascia
Prenaster
Periaster
Brisaster
Schizaster
Brissus
Brissopsis
Megapneustes
Macropneustes
Spatangus
Eupatagus
Maretia
Eurypatagus
Breynia
Lovenia
Echinocardium