

Original article

Systematics and palaeoecology of middle Toarcian Asteroidea
(Echinodermata) from the “Seuil du Poitou”, Western France

Systématique et paléoécologie des Asteroidea (Echinodermata)
du Seuil du Poitou (ouest de la France)

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Abstract

Complete, articulated starfish fossils are rare. However, more frequently encountered dissociated skeletal elements (ossicles) permit reliable taxonomic identification, making them a valuable data source for diversity estimates. Nearly 300 asteroid ossicles, collected from the middle Toarcian marls in western France can be assigned to five species. Four species and two genera are described: *Comptoniaster vrinensis* nov. sp. (Goniasteridae), *Poncetaster crateri* nov. gen. nov. sp. (Stauranderasteridae), *Galbaster recurrans* nov. gen. nov. sp. (Goniasteridae) and *Pentasteria? liasica* nov. sp. (Astropectinidae). The known diversity of Early Jurassic asteroids is increased from 12 to 16 species. These taxa illustrate the diversification of crown-group asteroids early in the Jurassic, following the Permo-Triassic crisis. They also reflect bias of the fossil record, and imply the existence of numerous ghost lineages in the evolutionary trees of extant groups. Variation in asteroid diversity across the “Seuil du Poitou” was driven by ecological constraints. The relative frequency (abundance of ossicles and diversity) of goniasterids and stauranderasterids increases in shallower environments. The Benthoplectinidae, represented by *Plesiastropecten hallovensis*, occurred primarily from deep-shelf sediments. Similar ecological patterns are observed for more recent fossil and extant relatives, which further supports the idea of conservative evolution in post-Palaeozoic starfishes since the Early Jurassic.

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Résumé

Les fossiles plus ou moins complets d'étoiles de mer sont extrêmement rares. Cependant, les éléments dissociés du squelette (ossicules) sont abondants et permettent une attribution taxinomique, ce qui fait des ossicules une source de donnée intéressante pour l'estimation de la paléobiodiversité. Cinq espèces ont été reconnues à partir d'environ 300 ossicules, collectés dans les marnes du Toarcien moyen de l'ouest de la France. Quatre espèces et deux genres sont nouveaux : *Comptoniaster vrinensis* nov. sp. (Goniasteridae), *Poncetaster crateri* nov. gen. nov. sp. (Stauranderasteridae), *Galbaster recurrans* nov. gen. nov. sp. (Goniasteridae) et *Pentasteria ? liasica* nov. sp. (Astropectinidae). La diversité des astérides connus au Jurassique inférieur est ainsi augmentée de 12 à 16 espèces. Ces taxons illustrent la diversification du « crown-group » des astérides très tôt dans le Jurassique, après la crise de la limite Permo-Trias. Ils reflètent également des biais du registre fossile et impliquent de nombreuses lignées fantômes dans les arbres évolutifs établis à partir des groupes actuels. Les variations de diversité des astérides le long du Seuil du Poitou étaient déterminées par des contraintes écologiques. L'abondance relative des ossicules et le nombre d'espèces de Goniasteridae et de Stauranderasteridae augmente dans les environnements les moins profonds. Les Benthoplectinidae, représentés par *Plesiastropecten hallovensis*, occupent préférentiellement les environnements échantillonnés les plus profonds (plate-forme

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distale). Les mêmes affinités écologiques s'observent chez les plus récentes, y compris les formes actuelles, ce qui suggère un conservatisme évolutif des étoiles de mer depuis le Jurassique inférieur.

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Mots clés : Asteroidea ; Toarcien ; Taxinomie ; Écologie ; Évolution

1. Introduction

Paleoenvironmental patterns in post-Palaeozoic benthic marine invertebrates provide a fundamental context for macroevolutionary, paleobiological, and contemporary biodiversity studies. Within the marine realm, bathymetric and spatial migration (i.e., “onshore–offshore”) patterns (Jablonski and Bottjer, 1990) have held particular interest. The Asteroidea (Echinodermata) represents a major group of exclusively marine invertebrates that has demonstrated bathymetric shifts between fossil and extant members (e.g. Blake and Aronson, 1998).

Blake (1987) and Gale (1987a) have independently reconstructed the phylogeny of the Asteroidea and demonstrated the monophyly of a post-Palaeozoic crown-group based on ambulacral characters. Gale (1987a) erected the subclass Neoasteroidea for all post-Palaeozoic asteroids. Blake (1987) reconstructed the Carboniferous *Calliasterella americana* as the sister taxon to the post-Palaeozoic crown group. Blake (1986) has interpreted subsequent evolution as very conservative with long-ranging taxa, frequent convergence, and few morphological innovations.

Crown group asteroids are first observed in the Triassic and although there are only a few forms known, they have been recently revised (Blake et al., 2000; Blake and Hagdorn, 2003). Most extant crown group taxa occur as fossils in the early Jurassic. Such an asymmetry in the fossil record and the evolutionary patterns implied by phylogeny suggest a radia-

tion of the crown-group Asteroidea in the early Mesozoic and a diversification event early in the Jurassic. However, only 12 starfish species have been described from the Lower Jurassic (Table 1). Most of these are known only from poorly preserved material and problematic localities. Thus, substantial gaps in the early fossil history of this group prevent a complete understanding of the diversification events and corresponding environmental shifts.

Starfish body fossils are rarely preserved intact. This implies that the low diversity attributed to fossil asteroid taxa is probably underestimated. Taxonomic studies of dissociated ossicles can, with some restrictions, permit reliable genus and species level identification. For example, marginal plates have had considerable taxonomic value in recognising astropectinids, goniasterids, pycinasterids, sphaerasterids and stauranderasterids from Cretaceous and Cainozoic sediments (e.g. Hess, 1974; Breton, 1992; Jagt, 2000). Thus, sampling ossicles may better reflect diversity, occurrence, and evolutionary events of the group in the fossil record, especially when placed within a phylogenetic context.

Detailed investigation of the Toarcian stage type section allows an estimate of diversity from the “Seuil du Poitou” (France) where no previous record of fossil starfish has been reported. Samples from coeval sites but from different palaeoenvironments or localities across the shelf were used to recognise ecological affinities between species and determine biases involved in sampling one site only.

Table 1

List of asteroid species known to date from the Lower Jurassic
Liste des espèces d'astérides décrites dans le Jurassique inférieur

Species	Family	Age	Geography
? <i>Pentasteria hastingiae</i> (Forbes, 1848)	?Astropectinidae	Pliensbachian	Yorkshire, England
<i>Plesiastropecten hallovensis</i> Peyer, 1944	Benthopectinidae	Hettangian	France, Germany and Switzerland
<i>Solaster' murchinsoni</i> (Williamson, 1836)	Solasteridae	Pliensbachian	Yorkshire, England
<i>Plumaster ophiuroides</i> Wright (1862)	Solasteridae	Pliensbachian	Yorkshire, England
<i>Tropidaster pectinatus</i> Forbes, 1850	Tropidasteridae	Pliensbachian	Gloucestershire, England
<i>Asterias' gaveyi</i> Forbes, 1850	Asteriidae	Pliensbachian	Calvados, France
<i>Asterias' radiatus</i> Wright, 1862	Asteriidae	Pliensbachian	Yorkshire, England
<i>Hystriasterias hettangiurnus</i> Blake, 1990	Asteriidae	Hettangian	Schwarzer Jura, Germany
<i>Germanasterias amplipapularia</i> Blake, 1990	Asteriidae	Hettangian	Schwarzer Jura, Germany
<i>Diclidaster gevreyi</i> de Loriol, 1887	?Valvatida	Hettangian	Ardèche, France
<i>Protenaster universalis</i> Smith and Tranter, 1985	Asterinidae	Sinemurian	Antarctic Peninsula
<i>Pycinaster' mortenseni</i> Mercier, 1935	?Pycinasteridae	Pliensbachian	Calvados, France
<i>Pentasteria? liasica</i> nov. sp.	?Astropectinidae	Toarcian	Deux-Sèvres, France
<i>Galbaster recurrans</i> nov. gen. nov. sp.	Goniasteridae	Toarcian	Deux-Sèvres, France
<i>Comptoniaster vrinensis</i> nov. sp.	Goniasteridae	Toarcian	Deux-Sèvres, France
<i>Poncetaster crateri</i> nov. sp. nov. sp.	Stauranderasteridae	Toarcian	Deux-Sèvres, France

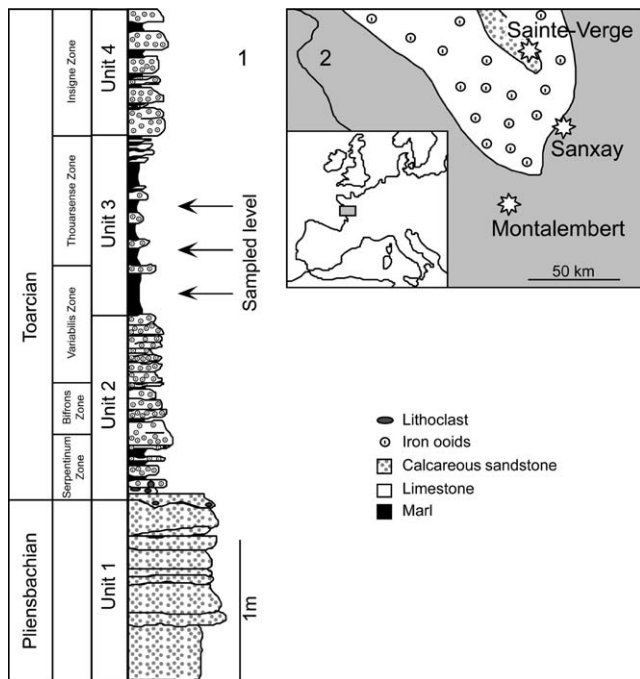


Fig. 1. Geographical and stratigraphical context. (1) Lithology and stratigraphy of the type section of the Toarcian at Sainte-Verge (Deux-Sèvres, France). (2) Localisation des sites et paléogéographie de la zone étudiée au Toarcien inférieur (d'après Gabilly, 1976).

Fig. 1. Cadre géographique et stratigraphique. (1) Lithologie et stratigraphie de la coupe stratotypique du Toarcien à Sainte-Verge (Deux-Sèvres, France). (2) Localisation des sites et paléogéographie de la zone étudiée au Toarcien inférieur (d'après Gabilly, 1976).

2. Material and methods

2.1. Stratigraphy

The type section of the Toarcian was chosen for reference in the present study. Two quarries close to d'Orbigny's original section are now in a Natural Reserve, which facilitates study of lithology, biostratigraphy, micropalaeontology and magnetostratigraphy (Magné et al., 1961; Gabilly, 1976; Galbrun et al., 1994). These quarries are located in the vicinity of Thouars, in the village of Sainte-Verge.

Four main lithological units compose the section (Fig. 1, (1)): (1) calcareous sandstone; (2) iron ooids rich, bioclastic limestone; (3) alternation of thick clayey marls with nodular marly beds; and (4) a more regular alternation of bioclastic limestone with marly layers.

The basal calcareous sandstone interval, dated to the Pliensbachian, is composed of coarse quartz grains cemented by a calcareous matrix. Beds are very different in thickness and shape. Most are discontinuous, with erosive casts and oblique litage. Fossils are rare, but bivalves (*Entolium*), belemnites and terebratulid brachiopods are encountered.

The second interval of iron ooid rich, bioclastic limestone lies in unconformity on the Pliensbachian sandstones. Between one and seven biostratigraphic horizons (sensu Gabilly, 1976) comprise the hiatus associated with this unconformity. In the Toarcian type section two horizons are

lacking. The lowest levels of the second interval are dated to the Serpentinum Zone. The series starts with two discontinuous beds containing lithoclasts and quartz grains. Overlapping these beds are marly, bioclastic and phosphate-rich limestone with many small iron ooids. Bedding varies considerably. The series may be compacted in a 1-m bed of limestone with iron ooids and ammonites as it occurs in the north quarries of the Natural Reserve. Two hundred meters south, in the other quarry, calcareous beds, of 5–30 cm in thickness, alternate with thin marly layers. Beds consist of bioturbated limestone with iron ooids. The base of these beds is probably erosive. Ooid size and frequency decrease from the base to the top of the thicker beds. Two small beds with oblique litage appear in the upper part of the unit (Variabilis Zone). Such features may indicate the presence of tempestites.

The third interval represents the upper part of the Variabilis Zone and the Thouarsense Zone, comprising an alternation of clayey marls with small nodular, in some cases discontinuous, marly limestone with a variable amount of iron ooids. The clayey beds are generally thicker than the limestone ones (between 20 and 30 cm vs. 5 and 10 cm). These levels contain a variety of bioclasts, among which complete or fragmentary shells of *Camptonectes pumilus* (Bivalvia), Foraminifera (*Lenticulina*, *Falsopalmula*, *Nodosariidae*), and Ostracoda (*Kinkelinella*, *Cytherelloidea*). Echinoderm remains are frequently encountered (columnals, brachials and cirri of crinoids, vertebrae and lateral shields of ophiuroids, marginals of asteroids and sclerites of holothurians).

The fourth interval represents a time range from the base of the Insigne Zone to the Early Aalenian and consists of irregular 10–20 cm bioclastic marly layers alternating with marly limestone beds each of which are only a few centimetres in thickness. In this fourth unit, the density of iron ooids progressively decreases whereas bioclasts increase in number.

2.2. Palaeogeography

The three first lithologic units (calcareous sandstone, ooid-rich, bioclastic limestone and the alternation of thick clayey marls with nodular marly beds) represent different depositional environments. Gabilly (1976) showed that early in the Toarcian, these three facies were spatially distributed across the "Seuil du Poitou" allowing a specific palaeoenvironmental gradient to be recognised (Fig. 1, (2)). The "Seuil du Poitou" was a shallow zone during the Early Jurassic, joining the Armorican to the Central Massif and separating the Aquitaine and Paris basins. Near Sainte-Verge, calcareous sandstones are common and characterise a shoreface environment. Sand deposited between the granitic islands are remains of the southeastern part of the Armorican massif. Where detrital material was not available, this sandstone formation is replaced by crinoid-rich calcarenites (Galbrun et al., 1994). Among the "Seuil du Poitou" from the north (Paris Basin) to the south (Aquitaine Basin), there is a facies change

as the iron ooids-rich limestones occur first, followed by clayey marls. These two facies are characteristic of the upper offshore and of the lower offshore, respectively, which suggests an environmental gradient from shallow to deep waters.

As a result of global transgression, sediments are more homogeneous during the middle Toarcian, and offshore marls are found all over the “Seuil du Poitou”. However, the thickness of the series varies. For example, the Bingmann horizon, 0.3 m thick in the stratotypical section, reaches nearly 1 m at Sanxay, and 2.5 m in Montalembert (Gabilly, 1976). Depositional rate is controlled by topography of the shelf assuming homogenous sedimentation. Changes in fossil associations and abundance suggest conspicuous variation in environmental conditions.

2.3. Sampling methods

We sampled sediments at three sites (Sainte-Verge, Sanxay and Montalembert see Fig. 1(2)) to test possible variations in diversity related to depth and environmental changes. Fifty kilograms of marls were collected from the middle Toarcian Variabilis and Thouarsense zones. Bioclastic marls were collected at the type section and more than 10 kg of marls from coeval levels at the Sanxay and Montalembert quarries. Additional material is from approximately coeval sites in western France, namely the upper Toarcian of Champdeniers (Deux-Sèvres), and the middle Toarcian of the Moulin de la Ronce (Sarthe), of Moiran and of Mondrainville (Calvados).

Sampled marls were broken down with water and detergent (washing powder) for 48 h before being washed through

2–0.2 mm sieves. Several hundred dissociated echinoderm ossicles were removed and sorted under a binocular microscope, yielding 298 dissociated asteroid ossicles (Table 2). Asteroid ossicles were the least abundant of those sampled and were only obtained after sorting of the complete sediment sample. In contrast, significant numbers of ophiuroid and holothurian ossicles were readily obtained from smaller quantities of the sediment sampled. To accelerate the sampling process, emphasis was placed on the coarser size fraction and on marginal plates. Marginals have been considered the most relevant elements for taxonomic assignment. Other plate types were more problematic at the species level. As a consequence, our sampling is homogeneous across sites but is not representative of the fossil record of these asteroids. In particular, ambulacral plates and adambulacral plates are poorly represented.

All analysed material is housed at the Muséum d’Histoire Naturelle of Le Havre. Only figured and type specimens received collection numbers.

2.4. Preservation and taphonomy

Toarcian ossicle samples show good preservation of the fine skeletal structure. The original stereom mesh is frequently preserved, despite local reworking into micrite. In the best-preserved ossicles, small crystals (<2 µm) of low magnesium calcite (LMC) replace the original High Magnesium Calcite (HMC) of the stereom. Pyrite crystals occur between stereom trabeculae or on the surface of some ossicle. Pyritization might be favoured by early diagenesis of

Table 2

List of species recognised in material and frequency of each plate type. Four localities are added to the middle Toarcian samples from the Thouars area: Champdeniers, Deux-Sèvres (Upper Toarcian), Moulin de la Ronce, Sarthe (Middle Toarcian), Moiran, Calvados (Middle Toarcian), and Mondrainville, Calvados (Middle Toarcian)

Liste des espèces reconnues dans les échantillons analysés et fréquence de chaque type de plaques. Quatre localités complètent l'échantillonnage du Toarcien moyen de la région de Thouars : Champdeniers, Deux-Sèvres (Toarcien supérieur), Moulin de la Ronce, Sarthe (Toarcien moyen), Moiran, Calvados (Toarcien moyen), et Mondrainville, Calvados (Toarcien moyen)

	Sainte-Verge	Montalembert	Sanxay	Moiran	Moulin	Champdeniers	Mondrainville
<i>P. hallovensis</i>	9	5	2	0	0	0	0
Ambulacrals	3	1	0	0	0	0	0
Abactinals	4	2	1	0	0	0	0
Terminals	2	2	1	0	0	0	0
<i>P.?</i> <i>liasica</i> nov. sp.	41	4	4	1	0	63	6
Inferomarginals	22	3	2	0	0	32	4
Superomarginals	16	1	2	1	0	31	2
Terminals	3	0	0	0	0	0	0
<i>C. vrinensis</i> nov. sp.	13	0	0	0	5	6	0
Superomarginals	5	0	0	0	1	3	0
Inferomarginals	7	0	0	0	4	3	0
Actinolaterals	1	0	0	0	0	0	0
<i>G. recurans</i> nov. gen. nov. sp.	26	2	4	2	0	5	2
Superomarginals	12	1	3	1	0	2	1
Inferomarginals	14	1	1	1	0	3	1
<i>P. crateri</i> nov. gen. nov. sp.	3	0	0	0	0	0	0
Carinals	2	0	0	0	0	0	0
Marginals	1	0	0	0	0	0	0
Indetermined ossicles	27	1	1	0	6	58	2
Sum	119	12	11	3	11	132	10

organic matter within a skeletal structure (Hudson, 1982) and suggests rapid burial of the ossicles. Nevertheless, some Toarcian ossicles show post-mortem decay and bioerosion, which indicate maceration of ossicles on the sediment surface. The surface of the ossicles may be covered by irregular, deep rounded holes (diameter of 10–100 μm , see Fig. 2(2,5,6) and Fig. 3(4–6)). The ossicle edges may be eroded or decayed resulting in an irregular surface (see Fig. 2(2)). Breton (1992) has observed similar surface textures and has suggested that sponges and/or algae may be responsible.

When asteroid ossicles are subjected to mechanical erosion, ossicle edges are blunt, ornament is abraded, and undulating lines on the surface of the ossicles reveal the stereom network. These features are particularly common in fossil ossicles sampled from the shallow-shelf environments (shoreface) and imply reworking. There is no evidence of this in our samples.

2.5. Taxonomic value of dissociated ossicles

Asteroids are fragile organisms that rapidly break up after death into easily scattered skeletal elements (Spencer and Wright, 1966). While near complete body fossils are extremely rare, dissociated skeletal plates are preferentially preserved and locally, are extremely common in shelf sediments.

Dissociated starfish ossicles have been recognised since the 19th century (e.g. Goldfuss, 1831; Desmoulins, 1832). At this time, taxonomy was typological and many types of ossicles received independent specific names. Spencer (1907, 1913) was one of the earliest to utilise comparative taxonomy to identify and classify dissociated ossicles. He compared complete specimens and dissociated plates of valvatan starfishes (Goniasteridae, Pycinasteridae and Stauranderasteridae) from the English Chalk (Upper Cretaceous). Following Spencer's approach, species described from complete specimens can be accurately identified from dissociated plates, and vice versa. Taxonomy of ossicles based on comparisons with complete specimens or extant taxa has been developed for fossil groups and for extant groups with fossil members (e.g. Pycinasteridae and Stauranderasteridae, Goniasteridae) (Spencer, 1907, 1913; Müller, 1953; Rasmussen, 1950; Gale, 1987b, 1987c; Breton, 1992; Jagt, 2000). The comparative approach is a reliable, well-established, and useful basis for assigning taxonomic identifications to dissociated ossicles.

In contrast, species based on dissociated ossicles without formal comparison with extant or well-defined fossil forms would be more poorly supported and more inclined to be problematic. In this respect, studies of Jurassic material lag behind the more extensively studied Cretaceous asteroid faunas. Many Cretaceous species have been developed in conjunction with comparisons of complete or partially complete forms (e.g. Spencer, 1907, 1913; Breton, 1992) whereas relatively few Jurassic forms have been comparably described (e.g. Hess, 1955; Breton, 1992).

The asteroid skeleton provides the main source of characters used in the systematics of extant and fossil taxa. Because morphology and orientation of articulation faces reflect architecture the overall morphology can be reconstructed from isolated ossicles (Gale, 1987b; Breton, 1992, 1995; Villier, 1999). External faces can provide detailed information on type and distribution of ornaments (e.g. granule-pits, pedicellariae-pits, tubercles for articulation of spines). Depending on the kind of plates, features of isolated ossicles can be diagnostic for different taxonomic ranks (Viguier, 1879; Müller, 1953; Blake, 1973, 1987; Gale, 1987b; Breton, 1992). Ambulacral, adambulacral, abactinal, marginal and mouth angle plates may be informative in recognising taxa from orders to species (see discussion in Hess, 1974; Breton and Ferré, 1995).

However, there are limitations in accurately applying taxonomy to dissociated ossicles. Because ossicles are dissociated, exact diagnostic features may not always be available for precise identification at lower levels. Hess (1955) classified marginal plates of the Mesozoic astropectinid genus *Pentasteria* within "species groups", rejecting the possibility of species recognition. Rasmussen (1972) acknowledged this when he noted taxonomic inconsistencies in his systematic account of Cainozoic Astropectinidae. Furthermore, there is a lack of comprehensive data on plate morphology of extant taxa for full comparisons with fossil forms (Blake, 1976). In spite of these difficulties, however, diagnostic ossicle features in astropectinids permit genus level identification (Hess, 1955; Rasmussen, 1972; Breton and Vizcaíno, 1997; Jagt, 2000).

Below, we present morphological descriptions and taxonomic assignments of dissociated ossicles of uncommon or new taxa from poorly studied stratigraphic levels and localities. In many ways, marginal plates provide the most useful features for identifying fossil species. Marginal plates can be differentiated based on shape, ornamentation, and articulation faces and provides a criteria for recognising species. Although most can be identified and clearly differentiated from previously known forms, others were more problematic and depending on the absence of clearly diagnostic characters, or the difficulty of interpreting morphological features some species were unidentifiable even to genus or family level.

3. Systematic palaeontology

Order VALVATIDA Perrier, 1884

Family GONIASTERIDAE Forbes, 1841

Genus *Comptoniaster* Breton, 1984

Comptoniaster vrinensis nov. sp.

Fig. 2(1,2) and Fig. 4(1–3)

Derivation of name: From Vrines, village close to the type locality.

Stratum typicum: Middle Toarcian, Variabilis to Thouarsense Zones.

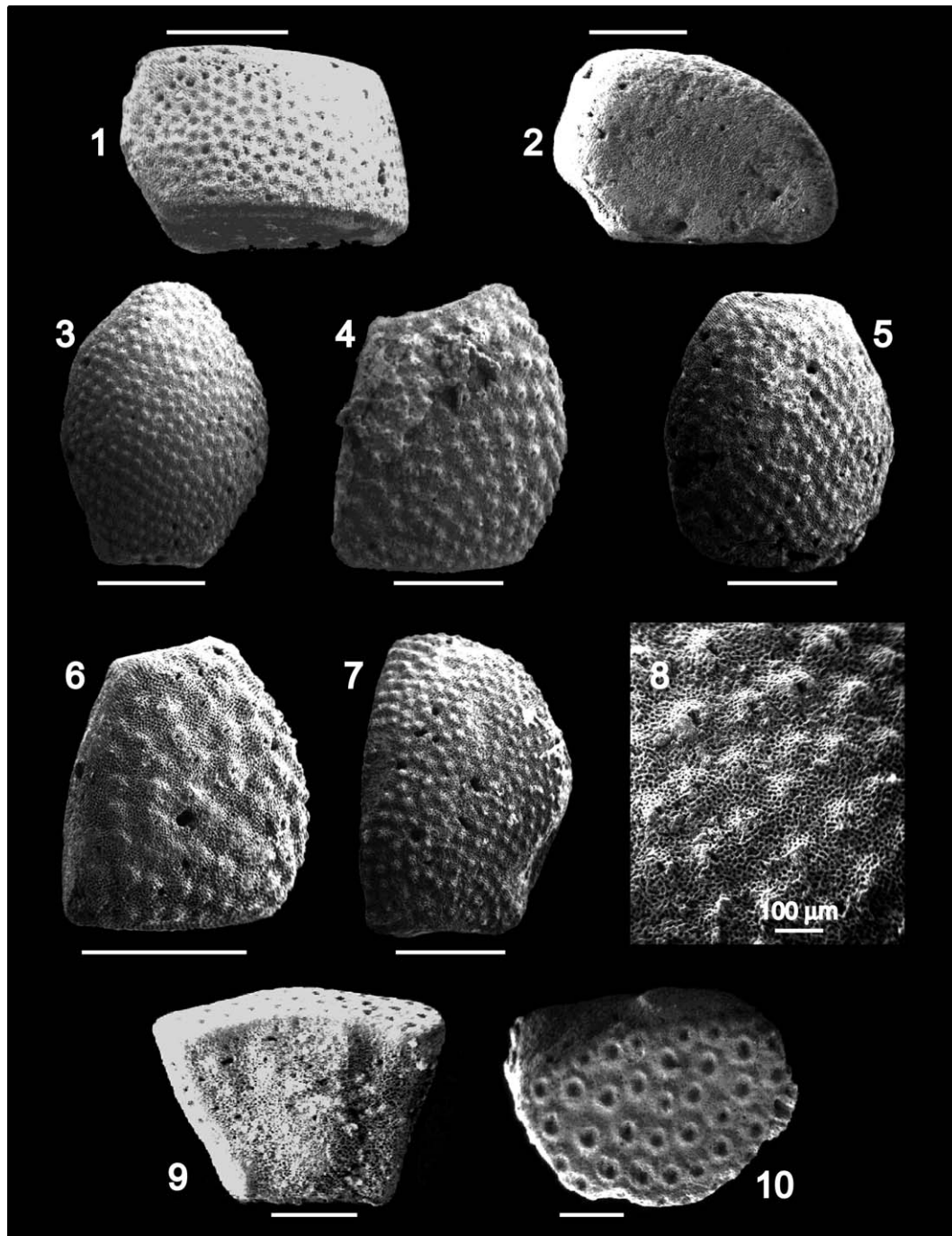


Fig. 2. Scanning electronic microscope pictures of the Middle Toarcian asteroids from Sainte-Verge (Deux-Sèvres, France). (1) *Comptoniaster vrinensis* nov. sp., inferomarginal plate, Holotype MHNH 8995. (2) *C. vrinensis* nov. sp., inferomarginal plate, MHNH 9115. (3) *Galbaster recurrans* nov. gen. nov. sp., superomarginal plate, Holotype MHNH 8997 \times 18. (4) *Galbaster recurrans* nov. gen. nov. sp., inferomarginal plate, Paratype MHNH 9000. (5) *Galbaster recurrans* nov. gen. nov. sp., superomarginal plate, MHNH 9117. (6) *Galbaster recurrans* nov. gen. nov. sp., inferomarginal plate, MHNH 9118. (7) *Galbaster recurrans* nov. gen. nov. sp., superomarginal plate, MHNH 9119. (8) *Galbaster recurrans* nov. gen. nov. sp., detail of ornamentation of inferomarginal plate, MHNH 9120. (9) *Poncetaster crateri* nov. gen. nov. sp., radial plate, Holotype MHNH 9001. (10) *Poncetaster crateri* nov. gen. nov. sp., marginal plate, Paratype MHNH 9002. Scale bar: one millimetre.

Fig. 2. Clichés réalisés au microscope électronique à balayage des ossicules d'astérides du Toarcien moyen de Sainte-Verge (Deux-Sèvres, France). (1) *Comptoniaster vrinensis* nov. sp., inféromarginale, Holotype MHNH 8995. (2) *C. vrinensis* nov. sp., inféromarginale, MHNH 9115. (3) *Galbaster recurrans* nov. gen. nov. sp., supéromarginale, Holotype MHNH 8997. (4) *Galbaster recurrans* nov. gen. nov. sp., inféromarginale, Paratype MHNH 9000. (5) *Galbaster recurrans* nov. gen. nov. sp., supéromarginale, MHNH 9117. (6) *Galbaster recurrans* nov. gen. nov. sp., inféromarginale, MHNH 9118. (7) *Galbaster recurrans* nov. gen. nov. sp., supéromarginale, MHNH 9119. (8) *Galbaster recurrans* nov. gen. nov. sp., détail de l'ornementation des inféromarginales, MHNH 9120. (9) *Poncetaster crateri* nov. gen. nov. sp., plaque radiale, Holotype MHNH 9001. (10) *Poncetaster crateri* nov. gen. nov. sp., marginale, Paratype MHNH 9002. Barre d'échelle : un millimètre.

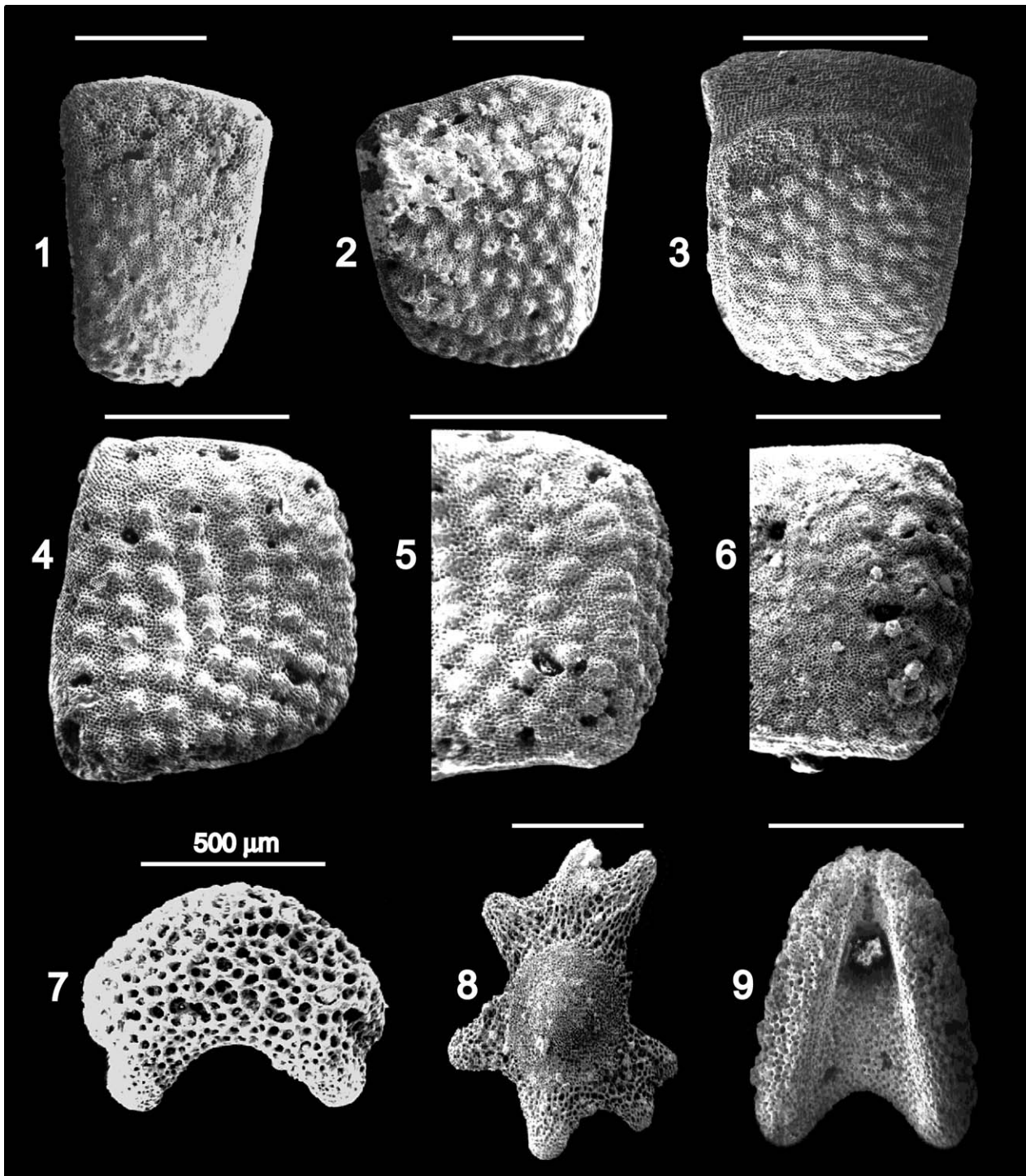


Fig. 3. Scanning electronic microscope pictures of the Middle Toarcian asteroids from Sainte-Verge (Deux-Sèvres, France). (1) *Pentasteria? liasica* nov. sp., inferomarginal plate, MHNH 9122. (2) *P.? liasica* nov. sp., inferomarginal plate, Paratype MHNH 9005. (3) *P.? liasica* nov. sp., inferomarginal plate, Paratype MHNH 9006. (4) *P.? liasica* nov. sp., inferomarginal plate, Holotype MHNH 9003. (5) Details of the ornament of the abradial side, Holotype MHNH 9003. (6) *P.? liasica* nov. sp., inferomarginal plate, arrangement of the horse-shoe shaped tubercles of the abradial flange, MHNH 9123. (7) *Pentasteria? liasica* nov. sp., terminal plate, MHNH 9124. (8) *Plesiastropecten hallovensis* Peyer, 1944, centrodorsal plate, MHNH 9011. (9) *P. hallovensis*, terminal plate, MHNH 9012. Scale bar: one millimetre.

Fig. 3. Clichés réalisés au microscope électronique à balayage des ossicules d'astérides du Toarcien moyen de Sainte-Verge (Deux-Sèvres, France). (1) *Pentasteria ? liasica* nov. sp., inféromarginale, MHNH 9122. (2) *P. ? liasica* nov. sp., inféromarginale, Paratype MHNH 9005. (3) *P. ? liasica* nov. sp., inféromarginale, Paratype MHNH 9006. (4) *P. ? liasica* nov. sp., inféromarginale, Holotype MHNH 9003. (5) Détails de l'ornementation de la face abradiale, Holotype MHNH 9003. (6) *P.? liasica* nov. sp., inféromarginale montrant l'arrangement des tubercules en fer à cheval le long du bord abradial, MHNH 9123. (7) *Pentasteria ? liasica* nov. sp., plaque terminale, MHNH 9124. (8) *Plesiastropecten hallovensis* Peyer, 1944, centrodorsale, MHNH 9011. (9) *P. hallovensis*, plaque terminale, MHNH 9012. Barre d'échelle : un millimètre.

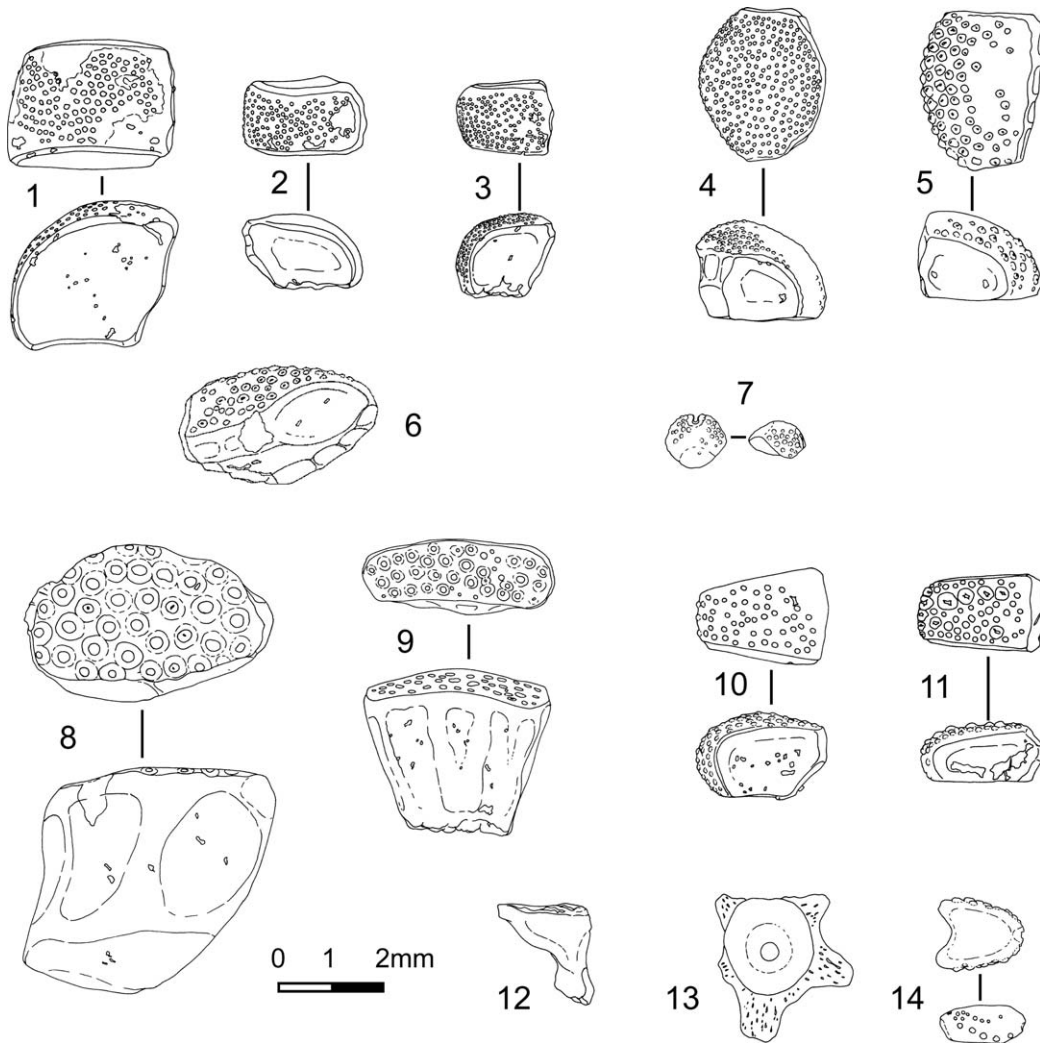


Fig. 4. Camera Lucida drawings of the Middle Toarcian asteroids from Sainte-Verge (Deux-Sèvres, France). (1) *Comptoniaster vrinensis* nov. sp. Inferomarginal plate, Paratype MHNH 8996. (2) *C. vrinensis* nov. sp. superomarginal plate, MHNH 9116. (3) *C. vrinensis* nov. sp. superomarginal plate, MHNH 9125. (4) *Galbaster recurrans* nov. gen. nov. sp. superomarginal plate, Holotype MHNH 8997. (5) *Galbaster recurrans* nov. gen. nov. sp. Inferomarginal plate, Paratype MHNH 8999. (6) *Galbaster recurrans* nov. gen. nov. sp. enlarged ultimate superomarginal, Paratype MHNH 8998. (7) *Galbaster recurrans* nov. gen. nov. sp. terminal plate, MHNH 9121. (8) *Poncetaster crateri* nov. gen. nov. sp., marginal plate, Paratype MHNH 9002. (9) *Poncetaster crateri* nov. gen. nov. sp., radial plate, Holotype MHNH 9001. (10) *Pentasteria? liasica* nov. sp., superomarginal plate, Paratype MHNH 9007. (11) *P.? liasica* nov. sp., inferomarginal plate, Paratype MHNH 9004. (12) *Plesiastropecten hallovensis* Peyer, 1944, ambulacral plate, MHNH 9008. (13) *P. hallovensis*, centrodorsal plate, MHNH 9009. (14) *P. hallovensis*, terminal plate, MHNH 9010.

Fig. 4. Dessins à la chambre claire des ossicules d'astérides du Toarcien de Sainte-Verge (Deux-Sèvres, France). (1) *Comptoniaster vrinensis* nov. sp. Inféromarginale, Paratype MHNH 8996. (2) *C. vrinensis* nov. sp. supéromarginale, MHNH 9116. (3) *C. vrinensis* nov. sp. supéromarginale, MHNH 9125. (4) *Galbaster recurrans* nov. gen. nov. sp. supéromarginale, Holotype MHNH 8997. (5) *Galbaster recurrans* nov. gen. nov. sp. Inféromarginale, Paratype MHNH 8999. (6) *Galbaster recurrans* nov. gen. nov. sp. supéromarginale distale, Paratype MHNH 8998. (7) (?) *Galbaster recurrans* nov. gen. nov. sp. plaque terminale, MHNH 9122. (8) *Poncetaster crateri* nov. gen. nov. sp., marginale, Paratype MHNH 9002. (9) *Poncetaster crateri* nov. gen. nov. sp., plaque radiale, Holotype MHNH 9001. (10) *Pentasteria? liasica* nov. sp., supéromarginale, Paratype MHNH 9007. (11) *P.? liasica* nov. sp., inféromarginale, Paratype MHNH 9004. (12) *Plesiastropecten hallovensis* Peyer, 1944, plaque ambulacraire, MHNH 9008. (13) *P. hallovensis*, centrodorsale, MHNH 9009. (14) *P. hallovensis*, plaque terminale, MHNH 9010.

Locus typicus: Hauts-Coteaux quarry, Sainte-Verge (Deux-Sèvres, France).

Type material: Holotype number MHNH 8995 is the inferomarginal plate preserved at the Muséum d'Histoire Naturelle of Le Havre, France (Fig. 2(1)). Another inferomarginal plate is the paratype (number MHNH 8996, Fig. 4(1)).

Diagnosis: Marginal plates convex in profile. External face of the inferomarginal plates covered by fine, dense and

contiguous granule pits (30–40 per square mm). External face of superomarginal plates covered by dense small tubercles. Intermarginal face flat. External face bordered with an oblique, depressed rim on distal side. Interradial marginal plates broad, with concave lateral faces oriented under a convergent angle towards the outside of the body. Marginal plates of arms are less broad with lateral faces parallel. Faces of articulation with ventral plates represent two-thirds of the plate height.

Description: Available material is limited (24 marginal plates) but is sufficient to distinguish inferomarginal from superomarginal plates. Marginal plates are small by comparison with other species of *Comptoniaster*. Dimensions are approximately 4 mm in width and 2 mm in length. The profile of each marginal plate is convex with a more or less domed surface that reaches the vertical abradial side (Fig. 4(1–3)). A narrow depressed rim borders the external face, distally (Fig. 2(1)). By comparison with extant and fossil goniasterids of stellate shape (e.g. *Calliderma*, *Comptoniaster*, *Nymphaster*), marginal plates that are distinctly wider than long with convergent lateral faces are assumed to be interrarial marginal plates. Near the tip of the arm, the shape of the marginal plates is squarer, higher, weakly convex with a nearly upright adradial face and with parallel lateral faces. Inferomarginal and superomarginal plates differ mainly in ornament. The external face of the inferomarginal plates has granule pits varying in density from 30 to 40 per square mm (Fig. 2(1) and Fig. 4(1)). The ornament of the superomarginal plates consists of especially fine, dense tubercles (Fig. 4(2,3)). Inferomarginal plates can also be differentiated by their oblique to near-vertical faces for the articulation of the ventral plates (Fig. 2(1) and Fig. 4(1)). Superomarginal plates are moderately asymmetrical with one lateral face flat and the other weakly concave. They articulate with three abactinal plates. The more distal the superomarginal plates were along the arm, the shorter, more convex and hooked they become. Despite substantial differences, the two types of plates described here are assigned to a single taxon for two reasons: first they can be recognised as inferomarginals and superomarginals, respectively, and secondly, they are found in approximately the same proportion.

Only a single actinal plate may be assigned to *C. vrinensis* nov. sp. due to its compatible size and its typical valvatidan shape. It shows a prismatic, sloping shape with lozenge cross-section. The external face is covered with about 20 large, discontinuous granule pits.

Taxonomic affinities: A combination of characters, including large marginal plates covered only by granule pits, the absence of lateral fascioles, and well-differentiated faces of articulation with abactinal or ventral plates are present in several valvatidan starfishes (sensu Blake, 1987), including the Goniasteridae, Oreasteridae, Asterodiscididae and Ophidiasteridae. Asterodiscidids have never been described as fossils. Ophidiasterids and oreasterids appear first during the Middle Cretaceous and Eocene, respectively (Blake, 1979, 1986; Blake and Aronson, 1998; Blake and Reid, 1998). However, goniasterids have occurred since the Bajocian and many genera are described from the Middle and Upper Jurassic of Europe (viz. *Comptonia*, *Comptoniaster*, *Cottreauaster*, *Miopentagonaster*, *Noviaster*, *Pulcinellaster*, *Tylasteria*). No goniasterids have been found from the Early Jurassic, and only a single species, *Tylasteria aalensis* (Mercier, 1935) in the Aalenian.

The Toarcian marginal plates, described herein, are morphologically close to those of the Mesozoic genera *Compto-*

niaster and *Tylasteria*, suggesting they are indeed goniasterids. The Jurassic species of *Comptoniaster* and *Tylasteria* are difficult to distinguish (Breton, 1992) even when complete specimens are compared. Marginal plates differ mainly by ornament and shape of the intermarginal face. Very wide interrarial marginal plates and large, deep unequal granular pits on the outer face distinguish *Tylasteria* from *Comptoniaster*. None of the marginal plates of *C. vrinensis* nov. sp. bears the ornament typically found on *Tylasteria*. However, these characters are progressively expressed during ontogeny making it difficult to identify the genera from juvenile specimens (Breton, 1992). This feature is not present in *Tylasteria*. Marginal plates generally alternate in *Tylasteria* whereas they are vis-à-vis in *Comptoniaster*. Alternation of superomarginal and inferomarginal plates of *Tylasteria* can be recognised in angular shape of the intermarginal faces (Breton, 1992). Intermarginal faces are flat and never angular in the Toarcian material. As described in *C. sharpii* (Wright, 1880), *C. godeti* Breton, 1992 many species of the genus have a narrow depressed rim, which borders the external face, distally. This is also present in the Toarcian species and justifies its assignment to *Comptoniaster*.

Compared to other Jurassic and Cretaceous goniasterids, *Comptoniaster* seems to be defined based on an association of primitive character states. A non-cladistic phylogeny for Jurassic and Cretaceous goniasterid genera (Breton, 1992: 442) suggests *Comptoniaster* may be paraphyletic, forming sister taxa for multiple stellate Mesozoic goniasterid lineages.

The genus *Comptoniaster* includes 13 species of Bajocian to Maastrichtian age species. Cretaceous species are easily distinguished from Jurassic species by the presence of large oval pedicellariae pits on the marginal plates. There are six Jurassic species of *Comptoniaster*. The marginal plates of *C. spongiarum* Breton, 1992, differ from those of *C. vrinensis* nov. sp. by their larger size, an abrupt abradial area and an adradial ledge near the convex summit of superomarginal plates. The marginal plates of *C. basseti* (de Loriol, 1887) are characterised by an ornament of dense granule pits (between 30 and 60 per square mm). The interrarial marginal plates are larger but shorter and less convergent. The terminal plate is heart-shaped with a size nearly equal to the marginal plate of the arm. Such a large size of terminal plates is apparently absent in *C. vrinensis* nov. sp. *C. jangouxii* Breton, 1992 shows wide marginal plates of a large size with parallel lateral sides, with a vertical abradial side and an domed outer face with 10–20 granule pits per square mm. The marginal plates of *C. sharpii* (Wright, 1880) are smaller in size and have a domed outer face with 10–20 granule pits per square mm. The inferomarginal plates are 2–3 mm long and 2–5 mm wide, depending on their position. *Comptoniaster meyeri* Breton et al., 1994, is distinguished by tall marginal plates, strongly convergent marginal plates in the interradius, low inferomarginal plates twice as long as wide in the interradius, and an external face weakly domed and covered by tiny dense granule pits. *Comptoniaster berthandi* (Wright, 1880)

has a more flattened external face with fine, dense granule pits, and large marginal plates in the interradius, which are triangular in outline.

Comptoniaster vrinensis nov. sp. can be easily distinguished from these other species by the high density of the granule pits (30–40 per square mm), the relatively small size, and the weakly convex shape of the interradiial marginal plates. The fine tubercles covering the superomarginal plates are especially diagnostic.

Genus *Galbaster* nov. gen.

Derivation of name: The name refers to the curved shape of the marginal plates (Latin *galba* = curved).

Type species: *Galbaster recurrans* nov. gen. nov. sp. by monotypy.

Diagnosis: The arms terminate in differentiated ultimate plates or large penultimate and reduced ultimate superomarginal plates. If present, ultimate superomarginal plates are large, triangular in shape, and show a low and oval adradial face representing a third of plate length. Marginal plates (superomarginals as well as inferomarginals) are long (length greater than width), barrel shaped, outer face very convex. Lateral faces irregular, oriented under an angle pointing adradially. The ornament varies from a network of small and dense to large and perforate tubercles. The lateral faces are relatively small, unequal and triangular. The largest lateral face is separated from the external face by a small rim. The abradial side of the marginal vertical or in slightly reflex angle.

Galbaster recurrans nov. gen. nov. sp.

Fig. 2(2–8) and Fig. 4(4–7).

Derivation of name: The name of the species alludes to the recurrent and convergent state of ornament and the ability to produce enlarged ultimate superomarginal plates, both characters known from independent genera of Goniasteridae in the Late Cretaceous.

Stratum typicum: Middle Toarcian, Variabilis to Thoursense zones.

Locus typicus: Hauts-Coteaux quarry, village of Sainte-Verge (Deux-Sèvres, France).

Diagnosis: Same as the genus by monotypy.

Type material: Holotype is a superomarginal plate, MHNH 8997 (Fig. 2(3)). The type series also includes an ultimate superomarginal, MHNH 8998 (Fig. 4(6)) and two inferomarginal plates, MHNH 8999 (Fig. 4(5)) and MHNH 9000 (Fig. 2(4)).

Description of material: One enlarged ultimate superomarginal plate was collected (Fig. 4(6)). It is triangular in shape in abactinal view. The ventral side shows a row of five small faces for articulation with the inferomarginal plates. The adradial face is very low, oval and short (nearly a third of plate length). There is a low occurrence of enlarged ultimate superomarginal plates *Galbaster recurrans* nov. gen. nov. sp. samples, implying that the structure was only present in some individuals. Large penultimate superomarginals are more common. They represent approximately 50% of the sample

of superomarginals (4 out of 9 sufficiently well-preserved, large superomarginal plates), which suggests that the marginal frame was typically made up of one large interradiial pair, one large penultimate pair and one reduced ultimate pair of marginals on each side of arms. Marginal plates of *Galbaster recurrans* nov. gen. nov. sp. are elongate with a domed external face (Fig. 2(3–8) and Fig. 4(4,5)). The outline is barrel shaped in dorsal view. One side corresponds to the dome of the external face and the other to the curve of the articulation faces between the marginal and abactinal or ventral plates. The lateral faces are small, unequal and triangular (Fig. 4(4,5)). The largest lateral face is slightly sunken. Ornament varies from a framework of dense fine tubercles, mainly on superomarginal plates (Fig. 2(3,5,7) and 4(4)) to a coarser framework of perforate tubercles, mainly on inferomarginal plates (Fig. 2(4,6,8) and Fig. 4(5)). The intermarginal face is large, plane to possibly convex abradially. The abradial margin of the external face is vertical or in a slight angle (Fig. 4(4,5)). Some smaller and shorter marginal plates are characteristic of a more distal position. These are interpreted as distal superomarginals or inferomarginals in contact with an enlarged ultimate or penultimate superomarginal. Most marginal plates bear irregular lateral faces, oriented under an angle pointing adradially. This implies a pentagonal to subcircular body shape (see Breton, 1992: 47; Fig. 8.10) as found in *Metopaster downendensis* Gale, 1987b or *Metopaster hunteri* (Forbes, 1848).

A single terminal plate is tentatively attributed to *Galbaster recurrans* nov. gen. nov. sp. (Fig. 4(7)). This is a conical plate with tiny tubercular ornaments and angular proximal sides. Angular proximal sides are found when abactinal plates do not reach the arm tip and when superomarginal plates of two sides are in contact in the mid-axis of the arm. Such architecture is consistent with the reconstruction of *Galbaster recurrans* nov. gen. nov. sp. and similar terminal plates are typical of some pentagonal goniasterid (e.g. *Crateraster*, *Fomalhautia*, *Metopaster*, *Peltaster*, *Tosia*) that can be compared with *Galbaster recurrans* nov. gen. nov. sp.

Taxonomic affinities: *Galbaster* nov. gen. *recurrans* nov. sp. possesses a suite of characters, which was previously unknown in the fossil record prior to the Callovian but has been observed more frequently since the Late Cretaceous in the family Goniasteridae: enlarged ultimate or penultimate superomarginal plates, marginal plates clearly differentiated according to their position in the marginal frame, subcircular or pentagonal body outline. For example, large distal superomarginal plates similar to those of *Galbaster recurrans* nov. gen. nov. sp. are known in other fossil genera including *Metopaster*, *Miopentagonaster* and *Parametopaster* as well as in several recent valvatidan starfishes (e.g. species of the genera *Asterodiscides*, *Goniaster*, *Pentagonaster*, *Plinthaster*, *Tosia*, etc.). All of these genera belong to the family Goniasteridae, except *Asterodiscides* of the family Astero-discididae, but this is closely related to Goniasteridae according to Blake (1987). This supports attribution of *Galbaster recurrans* nov. gen. nov. sp. to the Goniasteridae.

Jurassic *M. calloviensis* and *Galbaster recurrans* nov. gen. nov. sp. share a pentagonal outline and a reduced number of large marginal plates. Both are morphologically distinct from other Jurassic goniasterids, which possess numerous, short marginal plates, with progressively decreasing in size to the arm tip, such as *Comptonia*, *Comptoniaster*, *Cotreauaster* and *Tylasteria*. *Galbaster recurrans* nov. gen. nov. sp. differs from *M. calloviensis* on the basis of its low, smaller sized, distal superomarginals (highly swollen in *M. calloviensis*), its equally sized inferomarginals and superomarginals, and its fine tubercles. The relative length of the marginal plates, the fine perforated tubercles, and lack of a raised central area clearly differentiates *Galbaster recurrans* nov. gen. nov. sp. from Cretaceous and Extant goniasterids.

Within goniasterids, fine or perforated tubercles, such as those found in *Galbaster recurrans* nov. gen. nov. sp. appear in the “*Crateraster-Spenceraster*” group (sensu Breton, 1992), which also includes *Fomalhautia hortensae* Blake and Reid, 1998, and are known only from the Albian to the Lutetian. However, other characters between taxa within the “*Crateraster-Spenceraster*” group do not correspond, suggesting that these taxa are probably not related.

For either of the characters described above, a developed phylogenetic reconstruction of these groups would be necessary to determine whether these characters comprise apomorphies for monophyletic clades or convergent associations of characters across disparate lineages.

Family STAUANDERASTERIDAE Spencer, 1913

Genus *Poncetaster* nov. gen.

Derivation of name: The genus is named after Didier Poncet, geologist at the “Réserve Naturelle géologique du Toarcien”.

Type species: *Poncetaster crateri* nov. gen. nov. sp. by monotypy.

Diagnosis: External face covered with large, widely spaced crater-like spine bases. Carinal plates rectangular, highly wider than long. Carinals and marginals morphologically distinct. The proximal and distal faces of the marginal and abactinal plates show large triangular faces for plate articulation. No granule-pits.

Poncetaster crateri nov. gen. nov. sp.

Fig. 2(9,10) and Fig. 4(8,9).

Derivation of name: The name of the species alludes to the crater-like shape of the surface concavities.

Stratum typicum: Middle Toarcian, Variabilis and Thouarsense zones.

Locus typicus: Hauts-Coteaux quarry, Sainte-Verge (Deux-Sèvres, France).

Type material: Holotype is a radial plate MHNH 9001 (Fig. 2(9) and Fig. 4(8)). Paratype is a marginal MHNH 9002 (Fig. 2(10) and Fig. 4(9)).

Diagnosis: Same as the genus by monotypy.

Description of the material: Only three isolated plates can be referred to *Poncetaster crateri* nov. gen. nov. sp. Two of these plates are carinals and the third is a marginal plate.

External marginal plate ornaments are restricted to several large, disjoint, wide crater-shaped concavities covering the entire external face (Fig. 2(10)).

The two radial plates show a trapezoidal profile with a narrow internal face that is nearly horizontal (Fig. 2(9) and Fig. 4(9)). The external face expresses a weak convexity. This face is rectangular with rounded extremities, extremely wide (width/length ratio higher than two). Thin furrows indicate the position of the papular area at the corner of the plates.

The marginal plate is asymmetrical with a short, straight adradial margin (Fig. 4(8)). It has large concave articular faces on the proximal and distal faces. The side of articulation with the other marginal row is long, oblique and weakly concave. The lower and upper sides show thin furrows for the papulae. In external view, this plate is nearly polygonal with each ridge corresponding to an articular face.

Taxonomic affinities: Large block-like ossicles with marginal and abactinal plates of similar size, with furrows for papulae are present only in the extinct Stauranderasteridae. Initially, genera in this family were established on the basis of overall arm morphology and to a lesser extent on broad skeletal plate architecture. As a consequence, it was difficult to identify dissociated plates at a generic level. Some species were described from individual ossicles leading to erroneous species concepts. Villier et al. (in press) has recently completed a phylogenetic and systematic review and provided revised apomorphy-based diagnoses for genera within the Stauranderasteridae. Results supported five genera that are distinguishable based on overall shape, plate architecture, ornament and plate morphology. Genera and species can be identified from dissociated ossicles as well as from complete or fragmentary specimens. However, further work is required for fully, comprehensive knowledge of plate types (marginal, carinal and disc plates). Five genera (*Aspidaster*, *Hadrandaster*, *Manfredaster*, *Stauranderaster*, and *Stauraster*) can be defined as follows (Villier et al., in press).

Aspidaster de Loriol, 1884: Arms long and slender. Differentiated superomarginal and radial plates. Single row of radial plates on the dorsal face of the arm (no other abactinal plates). Primary plates of the disc well developed. Indentation of plate angles for passage of the papulae. External face with weakly differentiated central area and depressed margin. Ornament consists of large deep granular pits, articulation faces reniform. No pedicellariae known.

Hadrandaster Spencer, 1907: Arms short with semicircular cross section. Marginal and radial plates of similar size and shape: hexagonal to rounded, very thick with a rectangular outline. Several rows of abactinal plates. Passage for papulae at truncated angles of the plates. Ornament of fine, joint and dense granular pits. No central area. Few spine bases may be present on marginal and abactinal plates. Plates of disc articulated by small, irregular, draught-like faces that become wider and flatter in the arms. Wing-shaped pits of bivalve pedicellariae: in two lateral casts around a central rounded hole. Reduced external face, narrower than basement of the plate. Plates of the disc large with irregular outline. Articulation faces without pits.

Manfredaster Villier et al., in press: Disc high, domed. Arms short widened. Primary plates of the disc hypertrophied, domed. Marginal plates and only one row of abactinal plates (carinal) in the arm. Carinal and marginal plates high, triangular articulating through a reniform process at the base of the arm or more flattened faces distally. Ornament consisting often of a central area with a depressed margin, covered with dense, small granular pits. Fluting on plate corners for passage of the papulae. No spine. Pits of pedicellariae wing-shaped.

Stauranderaster Spencer, 1907: Arms long, slender, of triangular cross section. Primary plates of the disc hypertrophied, domed. Carinal plates absent or reduced to diamond-shape prism. Ornament generally composed of a rabbit edge surrounding a central area, smooth to cover by granular pits. Carinal and marginal plates articulated through a reniform process. Small pits generally present on the articulation faces. Fluting for passage of the papulae. No spine. Pedicellariae pits wing-shaped or oval.

Stauraster Valette, 1929: articulation processes as vertical blades at angles of the plates. No spines. Radial plates wider than tall, rectangular to trapezoidal in shape. External face of plates without central area. Ornament of disjoint, large and deep granular pits. Large area between articulation blades for papulae. Primary plates of the disc irregular as large as plates of the arm. No pedicellariae known. Marginal and radial plates weakly differentiated.

Poncetaster crateri nov. gen. nov. sp. is distinguished from other stauranderasterids based on the possession of large, numerous, crater-shaped, spine bases, the absence of granule-pits, and the shape of carinal plates which are short and wide with flattened lateral faces. *Hadrandaster* is the morphologically closest form: crater-shaped spine bases are rare but occur occasionally (see Spencer, 1907: Fig. 6). Plate shape is relatively simple and resembles marginals of *Poncetaster crateri* nov. gen. nov. sp. These features are putative

plesiomorphies for the Stauranderasteridae and do not suggest direct relationship between *Poncetaster* nov. gen. and *Hadrandaster*. It is therefore difficult to analyse the phylogenetic position of *Poncetaster crateri* nov. gen. nov. sp. pending more precise understanding of character evolution in primitive stauranderasterids. *Hadrandaster* is clearly defined by similar morphology of marginal and abactinal plates, by occurrence of several rows of abactinals in the arm and by reduced external face in disc plates.

Hadrandaster is inferred as basal within the Stauranderasteridae, but occurs only from the Late Cretaceous (Fig. 5). This implies a ghost lineage of nearly 80 million years. Villier et al. (in press) discusses several explanations. The lack of fossil data during the Jurassic and Early Cretaceous seems to be most plausible. Unpublished Toarcian stauranderasterid remains (housed in the Muséum d’Histoire Naturelle de Grenoble, France) are close to *Hadrandaster*, and suggest an Early Jurassic appearance.

Order PAXILLOSIDA Perrier, 1884
 Family ASTROPECTINIDAE Gray, 1840
 Genus *Pentasteria* Valette, 1929
Pentasteria? liasica nov. sp.
 Fig. 3(1–7) and Fig. 4(10, 11)

Derivation of name: The name refers to the Early Jurassic (Liassic) age of the species.

Stratum typicum: Middle Toarcian, Variabilis and Thouarsense zones.

Locus typicus: Hauts-Coteaux quarry, village of Sainte-Verge (Deux-Sèvres, France).

Type material: Holotype is an inferomarginal plate (MHNH 9003, Fig. 3(4)). Four paratypes, two inferomarginal (MHNH 9004 and MHNH 9005, Fig. 3(2) and Fig. 4(11)) and two superomarginal plates (MHNH 9006, Fig. 3(3) and 9007, Fig. 4 (10)).

Diagnosis: Marginal plates are bordered by shallow lateral fascioles. Inferomarginal plates show a rectangular and

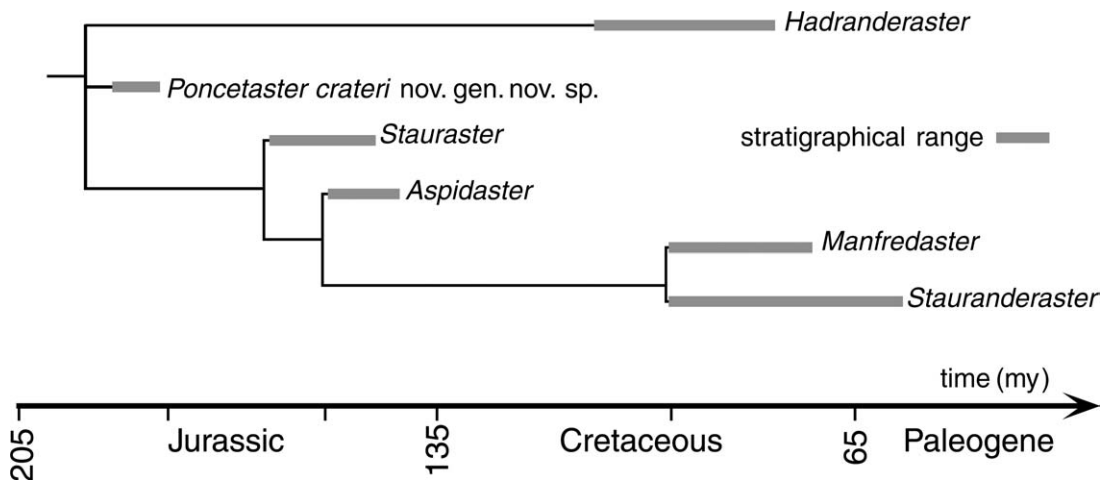


Fig. 5. Phylogenetic tree for the family Stauranderasteridae (modified from Villier et al., in press). Tree is based on a cladistic analysis calibrated against stratigraphical range of the taxa.

Fig. 5. Arbre phylogénétique de la famille des Stauranderasteridae (d’après Villier et al., in press, modifié). L’arbre est fondé sur une analyse cladistique calibrée dans le temps grâce aux extensions stratigraphiques des taxons.

hooked profile. The ornament consists of a network of rounded tubercles. Two rows of tubercles occur on the abradial side one of those made up of enlarged horseshoe-shaped tubercles. Abradial tubercle rows may be prolonged on the abactinal side by an alignment of enlarged tubercles. Superomarginal plates are square, nearly as long as wide in the arms. The external face is slightly convex and covered by tubercles smaller those of inferomarginals. The faces articulated with the abactinal plates are vertical to oblique.

Description of the material: Inferomarginal plates show a low rectangular, hooked profile (Fig. 4(10,11)). They are characterised by a row of horseshoe-shaped tubercles on the abradial side adjoined by a second row of rounded or dissected tubercles (Fig. 3(5,6)). On some plates, abradial rows are prolonged on the abactinal face by an alignment of enlarged tubercles (Fig. 3(4–6)). The remaining ornament consists of a dense network of small and fine tubercles on the abradial face becoming coarser and more organised in parallel rows on the actinal side (Fig. 3(4)). The lateral sides of the interradial inferomarginal plates are convergent towards the abradial side (Fig. 3(1)). Shallow fascioles border the external face of the marginal plates (Fig. 3(2,3)). Along the arm, the faces that articulate with the ventral plates vary from vertical and straight to slightly convex. The inferomarginal plates of the arm articulate with two to three adambulacral plates.

Superomarginal plates have planar to slightly convex lateral faces. Ornament of the external face includes rounded tubercles, which express a large variation in size and density. Such ornament is coarser than on the inferomarginal plates. Very shallow fascioles border the external sides of the plates. Occasionally, the adoral side of the lateral faces has a row of small pits. Interradial superomarginal plates are nearly twice as wide than long. The external face is weakly rounded. The zone of articulation with the abactinal plates overhangs the internal face. Faces of articulation are vertical or oblique. The superomarginal plates of the arm are relatively square, length and width being nearly equal.

Five shield-like terminal plates of median size (maximum length near to 0.6 mm) are referred as *Pentasteria? liasica* sp. nov. They are characterised by a coarse labyrinthic stereom on the upper face that becomes denser on the lower side and especially on the articulation face (Fig. 3(7)). A proximal concavity indicates that the abactinal plates reached the arm tip. The distal margin of the plate makes a round angle with two sides affected by a weak concavity. The lower opening is more rounded. The thickened lateral sides show six tubercles that are probably spine bases.

The terminal plates described here as *Pentasteria? liasica* nov. sp. were previously referred to *Terminaster* sp. (Kutscher and Hary, 1991; Villier and Kutscher, 1999). After a more detailed comparison with material of the type species, *Terminaster cancriformis* (Quenstedt, 1876), we are now certain that there is a significant difference in terminal plate size and shape between *Terminaster* and *Pentasteria*. In the Toarcian sample from the type section, the terminals do not

resemble *T. cancriformis* plates as described by Hess (1974), and are not *Terminaster*. The shield-like shape and well-defined contacts with abactinal and marginal plates suggest that they belong to *Pentasteria? liasica* nov. sp.

Taxonomic affinities: A shallow fasciole along the lateral faces of the marginal plates, inferomarginal plates ornamented with large spines fixed on horseshoe-shape tubercles and forming an abradial flange are typical of some astropectinid starfishes (Hess, 1955) and the goniasterid genus *Pseudarchaster* (see Blake, 1986). All known fossil and extant species of *Pseudarchaster* have narrow marginal plates (similar to astropectinids) with a convex outer face. Therefore, the rectangular, hooked-shape marginals of the Toarcian form differ from marginals of *Pseudarchaster*. The most common Mesozoic astropectinid, *Pentasteria* spp., and the recent *Astropecten* spp. are characterised by a low number of adambulacral spines and distribution of horseshoe-shape tubercles in one curved row on the inferomarginal plates (Hess, 1955). Diagnostic astropectinid adambulacral or ambulacral plates have not been recognised from our samples. However, numerous Toarcian inferomarginals express an association of horseshoe-shaped tubercles in a similar pattern to the “*Pentasteria-Astropecten*” group (sensu Hess, 1955: 102), which is diagnostic of this group. Assignment of the Toarcian material to the Astropectinidae and to the genus *Pentasteria* is based on this single diagnostic character and remains tentative pending additional morphological information.

Hess (1955) and Rasmussen (1972) emphasised the difficulty of classifying marginal plates of astropectinids at the species level. *Pentasteria? liasica* nov. sp. is differentiated from previously known *Pentasteria* based on the presence of shallower fascioles and lower, rectangular marginal plates, justifying erection of a new species name. The ornament of the external face of marginals consisting of a network of fine tubercles in *Pentasteria? liasica* nov. sp. closely resembles *Pentasteria* gr. *huxleyi* (sensu Hess, 1955), whereas it comprises mostly granular pits in other Middle Jurassic and Cretaceous species of *Pentasteria*.

Kutscher (1988) illustrated isolated ossicles from the upper Pliensbachian of Grimmen (Germany) and attributed them tentatively to *Pentasteria* (*Archastropecten*)? *hastingsiae* (Forbes, 1848). Shape and ornament of the marginal plates look similar to those of *P.? liasica*, and both specimens from the middle Toarcian of Sainte-Verge and from the upper Pliensbachian of Grimmen are probably conspecific. According to Hess (1955), *P.? hastingsiae*, from the Hettangian of England, is diagnosed as a distinct astropectinid-like genus (but was unnamed due to poor preservation of the specimen) characterised by its small size, short and triangular arms, wide as long marginal plates, abactinal, ventral and adambulacral plates as large as the marginal plates, ventral plates extending into the proximal half of the arms and most plates bearing spines. *P.? hastingsiae* differs from *Pentasteria? liasica* nov. sp. in having laterally triangular marginals and fewer spines (one or two) on the inferomarginals, while *Pentasteria? liasica* nov. sp. has four to six.

The oldest unambiguous astropectinid dates back to the Aalenian (Hess, 1955). Several taxa suggest a first appearance in the Early Jurassic, including *P.?* *hastingsiae* from the Hettangian of England (see Hess, 1955), *P.?* *liasica* nov. sp. from the Late Pliensbachian to middle Toarcian of France and Germany (this paper and M. Kutscher unpublished data), an undescribed astropectinid from the Sinemurian of England (L. Villier unpublished data), and another from the Pliensbachian of England (Blake, 1996: 179).

Order: NOTOMYOTIDA Ludwig, 1910

Family: BENTHOPECTINIDAE Verrill, 1894

Genus: *Plesiastropecten* Peyer, 1944

?*Plesiastropecten hallovensis* Peyer, 1944

Fig. 3(8,9) and Fig. 4(12–14).

Figured material: An ambulacral plate (Fig. 4(12)), two centrodorsal plates (Fig. 3(8) and Fig. 4(13)) and two terminal plates (Fig. 3(9) and Fig. 4(14)) bear registration numbers MHNH 9008 to 9012.

Description of the material: The ambulacral plates show a large triangular, proximal expansion of the ambulacral body (Fig. 4(12)). The zone of articulation with the symmetrical ambulacral plate is reduced between half or a third of the length of the ambulacral body. The tabula and the oral groove are slightly marked. The ambulacral notch is weakly curved. The ambulacral wings are reduced to subvertical and oval faces of articulation with the adambulacral plates.

The centrodorsal plates of ?*P. hallovensis* are large ossicles (4 mm in length) with a lobate outline (Fig. 3(8) and Fig. 4(13)). The centre of the plate shows a large, single tubercle within a raised circular area of dense stereom. The peripheral zone and the abactinal side of the lobes are made of labyrinthic stereom. The lobes are of unequal size and number (between six and eight). The internal face of the lobes has a shallow groove.

The plates of the disk are of the same type, looking quite similar to the centrodorsal plates. They are more asymmetrical with reduced lobes and without a raised circular area around the central tubercle. In the arm, abactinal plates are small, polygonal with a small central tubercle and occasionally several peripheral ones.

Terminal plates are relatively large (>1 mm), long and flattened (Fig. 3(9) and Fig. 4(14)). The oral face shows a deep triangular groove ending on the distal side with a tiny furrow where the terminal podion was located. The stereom of the external face is dense with nodes forming tenuous granules. The proximal side is rounded and wide. A coarse alignment of rounded to horseshoe-shape tubercles borders the lateral face.

Taxonomic affinities: All plates correspond to the diagnostic characters of the Paleobenthopectininae Blake, 1984, including an abactinal skeleton that consists of low conical disc-like ossicles with a central spine base, low ambulacrals with a very elongate ambulacral body that are triangular in outline, and the absence of a developed distal ambulacral/adambulacral articular surface (Blake, 1984; Blake and Reid, 1998). The Paleobenthopectininae includes

Table 3

Pairwise comparison of the mean size of marginal plates from Montalembert, Sanxay and Sainte-Verge: results of non-parametric Kolmogorov–Smirnov test. Values of *p* are not significant, which suggests no statistical differences between two given samples. Lower left-half of the table: results for *Pentasteria?* *liasica* nov. sp. Upper right half of the table: results for *Galbaster recurrans* nov. gen. nov. sp. ID is labelled for insufficient data and—for inappropriate comparisons

Comparaison de la taille moyenne des plaques dans les gisements de Montalembert, Sanxay et Sainte-Verge. Le tableau fournit les résultats de comparaisons des gisements deux à deux par un test non-paramétrique de Kolmogorov–Smirnov. Les valeurs non-significatives de *p* suggèrent l'absence de différence entre les deux échantillons considérés. La partie en bas à gauche du tableau donne les valeurs de *p* pour les comparaisons des plaques de *Pentasteria?* *liasica* nov. sp. et la partie en haut à droite les valeurs pour *Galbaster recurrans* nov. gen. nov. sp. ID mentionne les cas où les données sont insuffisantes et—les comparaisons inappropriées

	Sanxay	Sainte-Verge	Montalembert
Sanxay	–	ID	ID
Sainte-Verge	0.74	–	0.67
Montalembert	0.99	0.99	–

only three monospecific genera *Alkaidia* Blake and Reid, 1998, *Plesiastropecten* Peyer, 1944, and *Xandarosaster* Blake, 1984. Following the description of the abactinal and ambulacral plates by Peyer (1944) and Blake (1984) all the Toarcian benthopectinid ossicles described can be assigned to *P. halloviensis*. Abactinal plates of *Alkaidia sumralli* Blake and Reid, 1998 are very different in outline and ornament from the material of the “Seuil du Poitou”. *X. hessi* has large rectangular and subhorizontal adambulacral plates and shield-like marginal plates rather than the short vertical adambulacral and bulbous marginal plates seen in *P. hallovensis*.

4. Palaeobiological results

4.1. Distribution patterns

The predominance of marginal plates in our samples suggests there is a bias against smaller plates. Additionally, bioerosion destroys primarily small and fragile ossicles, such as ambulacral plates. However, sorting and taphonomic influences appear homogeneous, which permits comparisons across sampled sites. After ossicles were identified to species, size distribution of marginal plates of *Galbaster recurrans* nov. gen. nov. sp. and *Pentasteria?* *liasica* sp. nov. was compared across the three sites. No significant difference between the sites was observed (Table 3), suggesting that no hydrodynamic sorting had taken place. Further taphonomic evidence suggests limited post-mortem transport or reworking of sediment. Fossil assemblages sampled from the study sites are considered representative of local diversity. Analysis of sediment samples suggests that abundance and diversity of the Toarcian asteroid species described herein are principally dictated by ecological factors.

The three sampled localities, Sainte-Verge, Sanxay and Montalembert, compose an environmental sequence begin-

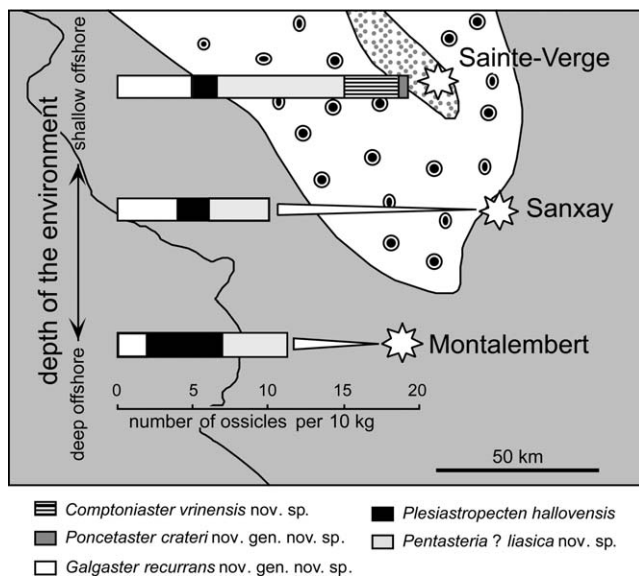


Fig. 6. Variation of ossicle abundance and taxon diversity across the "Seuil du Poitou". Size of the bars indicates the number of ossicles estimated for a sample of 10 kg of sediment. Palaeogeographical map for the Early Toarcian (from Gabilly, 1976) is drawn in the background for information on environmental shifts.

Fig. 6. Variations de l'abondance des ossicules et du nombre de taxons le long du Seuil du Poitou. La taille des barres indique le nombre d'ossicules estimés pour un échantillon de dix kilogrammes de sédiment. Un fond paléogéographique pour le Toarcien inférieur (d'après Gabilly, 1976) est proposé en arrière plan de manière à souligner les variations environnementales.

ning with shallower sediments at Sainte-Verge, shifting to deeper offshore sediments at Montalembert. Species diversity of fossil asteroids is higher in the shallower environments (Fig. 6). Five species were recognised at Sainte-Verge but only three each at Sanxay and Montalembert. *Comptoniaster vrinensis* nov. sp. and *Poncetaster crateri* nov. gen. nov. sp. were known only from the shallower environments at Sainte-Verge. Ossicle abundance follows the same trend, reaching almost 20 ossicles per 10 kg at Sainte-Verge but 50% less at the other sites. Relative abundance of *P. hallovensis* increases with depth whereas that of *Galgaster recurrans* nov. gen. nov. sp. decreases. Thus, the pattern of species and ossicle abundance are consistent with the interpretation of ecologically constrained distribution, in spite of potential sampling biases, such as small samples and selective sorting of marginal plates.

Comparable large-scale environmental distribution patterns in starfish based on relative abundance and diversity of fossil taxa (Villier et al., 1997; Villier and Odin, 2001) have been recognised in the European fossil record. For example, in the Upper Cretaceous of Western Europe, the highest species diversity recorded is reached in upper offshore sediments (Villier et al., 1997). Remains of astropectinids (*Aldebarania*, *Dipsacaster*, *Pentasteria*, *Lophidiaster*) are found predominantly on shallow shelf environments, while goniasterids remains are more frequently encountered on the mid-shelf environments (upper offshore) (Villier et al., 1997).

Distribution patterns of extant goniasterids and shallow-water astropectinids parallel those seen in asteroid species from Cretaceous and Toarcian sediments. Extant, shallow-water astropectinids, such as *Astropecten*, occur primarily on the upper shelf, whereas most extant goniasterids occur predominantly on deep shelf habitats and on the continental slope (Maluf, 1988; Clark, 1989, 1993; Clark and Downey, 1992). Although many of these taxa may be broadly distributed with depth, relative abundance may be limited to a narrow bathymetric range (Howell et al., 2002). If ecology constrains the distribution of asteroid plates, this pattern may help explain the abundance of plates found in sedimentary environments sampled for this study.

4.2. Palaeoecology

Data restricted to Late Cretaceous goniasterids suggest a relationship between the general shape of the body and depth of the environment (Villier et al., 1997). Pentagonal forms with enlarged marginal plates, such as *Parametopaster*, *Metopaster* and *Recurvaster*, occurred broadly on the shelf, but were best represented in offshore environments. Stellate forms with a robust marginal frame and superomarginals in contact along the arm, such as *Nymphaster*, *Comptonia*, and *Ophryaster*, preferentially lived in the upper offshore and lower shoreface (Villier et al., 1997; Villier and Odin, 2001). These examples suggest ecological constraints on species distribution. Unfortunately, the relationships between species distribution and environment are poorly understood. Substrate does not appear to constrain distribution. Late Cretaceous species, for example, are known from limestones, and sands, as well as marls (e.g. *Metopaster loirensis* Gale, 1987; see Breton, 1997). Comparisons of depth occurrence between Cretaceous and extant species are unclear.

Comptoniaster vrinensis nov. sp. is relatively common in upper offshore and shoreface sediments from the Toarcian of north-western France (e.g. Moulin de la Ronce, Sarthe). Most of the Jurassic species of the genus *Comptoniaster* are found in shallow-water sediments including reefal, lagoonal, and sandy formations representing shoreface or upper offshore environments. Several recent taxa occupy parallel habitats but are morphologically dissimilar. For example, three tropical Pacific genera, *Iconaster*, *Pentagonaster*, and *Tosia* all include species whose members occupy littoral to shallow habitats but possess smooth marginal plate surfaces compared to the granulated marginal plate surfaces found in *Comptoniaster*. Likewise, *Ogmaster* and *Stellaster*, occupy littoral to shallow habitats in the Indo-Pacific and although fine granulation may occur on the skin of some species, these species possess skin-covered rather than granulated surfaces. Granulated marginal plate surfaces similar to those found in *Comptoniaster*, tend to be found only in cold-water inhabiting species from shallow-water, less than 100 m (e.g. *Mediaster aequalis*) and deeper-water greater than 100 m (e.g. *Peltaster*, *Nymphaster*) environments (C. Mah, unpublished data).

Galbaster recurrans nov. gen. nov. sp. is more frequent in upper offshore sediments (Sainte-Verge, Deux-Sèvres), becoming less abundant to the south (Sanxay, Montalembert). As discussed above, *Galbaster*'s robust marginal plates resemble those of Cretaceous *Metopaster* in addition to extant forms, such as *Tosia* or *Pentagonaster*, which have a very distinct marginal frame, enlarged ultimate or penultimate superomarginal plates and a raised marginal plate area. All of which are taxa that inhabit relatively shallow habitats (0–200 m). *Galbaster* possess a similar morphology and is recovered from sediments of similar depth (nearly 150 m for the type Toarcian, [Gabilly, 1976](#)), suggesting a parallel ecology and distribution.

Plesiastropecten hallovensis occurs predominantly from deep-shelf sediments. Occurrence of fossil benthopectinids in relatively shallow, shelf settings is documented during the Jurassic and the Cretaceous ([Blake, 1984](#); [Blake and Reid, 1998](#); [Jagt, 2000](#)). Less than half of the total number of recent benthopectinid species occupy depths below 1000 m with deeper water species occurring as deep as 3250 m ([Clark, 1981](#)). [Blake and Reid, \(1998: 514\)](#) suggested that the “depth range of the family might have been generally broader in the past”. All recognised fossil benthopectinids belong to a single extinct clade (the subfamily Paleobenthopectininae), which suggests that paleobenthopectinids were found preferentially on shelves and that their selective extinction might have restricted some benthopectinids to deep waters.

Poncetaster crateri is relatively rare, occurring only in shallow water sediments. A shallow paleoenvironment is consistent with interpretations of the Stauranderasteridae possessing morphology similar to members of the extant Oreasteridae, including robust, arched to triangular-shaped arms, highly developed skeleton, and large papular areas at the corners of the plates. Extant oreasterids are restricted to tropical waters from the Indo-Pacific and Atlantic Oceans, occurring predominantly in shallow environments (<50 m) on reefs, sand flats and seagrassbeds ([Clark and Rowe, 1971](#)).

Toarcian *Pentasteria? liasica* is encountered from shallow to deep-water shelf-sediments. *Pentasteria* spp. are typically recorded from sandy to muddy Jurassic shelf sediments ([Courville and Villier, 1993](#)). Extant *Astropecten* occupy a similar depth range ([Clark, 1989](#)) and occupy parallel habitats with sandy to muddy substrates ([Clark and Downey, 1992](#)). Characters such as fascioles between marginal plates, paxillae, and superambulacral ossicles are associated with burrowing behaviour in astropectinids ([Blake and Sturgeon, 1995](#); [Hess and Blake, 1995](#); [Blake, 1996](#)). The marginals of *Pentasteria? liasica* nov. sp. have rudimentary fascioles suggesting a mode of life similar to those of extant astropectinids.

4.3. Evaluation of Early Jurassic diversity

All post-Palaeozoic starfishes constitute the crown-group Asteroidea. This group of modern starfishes roots with late

Palaeozoic forms close to the Pennsylvanian genus *Calliasterella* ([Blake, 1987](#)). Rapid diversification of the crown group Asteroidea during the Late Triassic and the Early Jurassic has been inferred by independent workers ([Blake, 1987](#); [Gale, 1987a](#); [Villier and Kutscher, 1999](#)). Some Triassic and Jurassic species are basal, extinct relatives of extant groups (e.g. Paleobenthopectininae, Tropidasteridae, *Paleoctenodiscus*, *Pseudarchaster*), while others are closely related to recent groups, and still others represent original groups restricted to the Mesozoic for which phylogenetic relationships are particularly unclear (e.g. Stauranderasteridae, Pycnasteridae, Sphaerasteridae, *Arthraster*, *Diclidaster*).

A list of Lower Jurassic species occurrences is shown in Table 1. These were analysed for patterns at higher levels. Taxonomic classification is that of [Blake \(1987\)](#), which is the most commonly used (e.g. [Clark and Downey, 1992](#)), modified to accommodate fossil taxa. When starfish phylogenies ([Blake, 1987](#); [Gale, 1987a](#); [Lafay et al., 1995](#)) are compared with fossil occurrence, the data implies an origination for almost all high-ranking post-Palaeozoic taxa during the Late Triassic or the Early Jurassic ([Villier and Kutscher, 1999](#)). All but one order and nearly two thirds of the 24 families that occur as fossils are expected to appear first during the Late Triassic and Early Jurassic. Within these families, 7% (2) appear during the Triassic, 54% (13) during the Jurassic, 32% (7) during the Cretaceous and 7% (2) during the Cainozoic. The number of first occurrence of families and orders has decreased since the Jurassic while the number of species increased significantly. This pattern cannot be explained by simple bias of the fossil record. It suggests a high rate of diversification of orders and families during the Late Triassic and Early Jurassic, although there are few known fossils during these intervals. Such a diversity pattern with an increase of higher-level taxa followed by an increase in the number of genera and species is typical of adaptive radiation (e.g. [Gould, 1989](#); [Sprinkle, 1983](#)). Disparity is likely to have reached a high level at the beginning of the radiation, as taxa underwent exploration of a wide range of morphological and ecological-space (adaptive zones, see [Blake, 1990](#)). Next, a progressive deceleration in morphological diversification occurred, as a function of clade extinction (Paleobenthopectininae, Pycnasteridae, Stauranderasteridae, Sphaerasteridae, Trichasteropsida, Tropidasteridae, and several incertae family taxa like *Arthraster*, *Asteriaceros*, *Diclidaster*, *Valetaster*), with a corresponding decrease in the rate of morphological innovation. Following this interpretation, adaptive zones occupied by starfishes today had been reached early in the Mesozoic. Subsequent evolution is interpreted as conservative, with prevalent convergence, and no significant innovation in morphologies or change in diversity structure ([Blake, 1986](#)).

Unfortunately, Lower Jurassic strata have not been closely studied for asteroid fossils, and our understanding of early starfish diversity are strongly influenced by work on preferentially complete specimens and geographic bias. For ex-

ample, the British faunas represent nearly two-thirds of the known complete or fragmentary specimens from the Lower Jurassic. All known English specimens come from only four horizons where well-preserved starfishes are relatively frequent, each with a specific depositional setting (Bucklandi Zone in the Sinemurian, Jamesoni, Capricornus and Spinatus Zones of the Pliensbachian, see Wright, 1869). Such narrow windows sample only taxa of the local or regional diversity. Ideally, taxon sampling should comprehensively include a diversity of regions, environments, and time periods in order to recover a relevant diversity signal. Additional consideration of disarticulated fossil material makes our estimates of asteroid species more comprehensive and serves to improve our understanding of the diversity for this group. Standardised, comprehensive surveys for sediments containing disarticulated asteroid ossicles also permits direct comparison with other localities sampled with identical sampling regimes. More consistent sampling can compensate for regional variance and might better represent trends in the fossil record.

For example, previous data listed only 12 species in the Lower Jurassic (Table 1). Based on material described herein, species diversity from the Lower Jurassic is increased from 12 to 16 species. Discoveries in the Toarcian of western France extend our knowledge of early Jurassic taxonomic diversity, increasing the number of known post-Palaeozoic fossil asteroid species.

5. Conclusion

A comprehensive sampling from Sainte-Verge sediments significantly improves the previously known diversity of Mesozoic asteroid fossil species from Lower Jurassic deposits. Terminal plates previously recognised as *Terminaster* sp. are assigned to *P.?* *liasica* nov. sp. Two new genera and four new species (*P. liasica* nov. sp., *Galbaster recurrans* nov. gen. nov. sp., *Poncetaster crateri* nov. gen. nov. sp. and *C. vrinensis* nov. sp.) are described. *Galbaster recurrans* nov. gen. nov. sp. plus *C. vrinensis* nov. sp. and *Poncetaster crateri* nov. gen. nov. sp. document the earliest occurrence for the Goniasteridae and the Stauranderasteridae, respectively, extending the first occurrence of these two families from the Aalenian and late Bathonian to the middle Toarcian. These newly discovered taxa are consistent with the notion that the diversity of fossil starfishes was substantially higher than currently known.

Taxa from the Toarcian show strong morphological and ecological similarities with geologically recent forms. Even when there are differences, starfishes from the Toarcian show close affinities with Jurassic, Cretaceous, and Cainozoic taxa. Ecologically, some Toarcian species may be compared with offshore shelf habitats from recent oceans.

Results highlight the inclusion of lower Jurassic starfishes as members of the post-Palaeozoic asteroid lineage and support the hypothesis of a rapid radiation in the early Mesozoic.

Fossil data support Jurassic taxonomic associations and ecology as close to those in contemporary oceans and that habits expressed in extant groups were explored early in the historical record of asteroids. This suggests conservative evolution in starfish since the Jurassic.

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