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Autor(en): **Hess, Hans / Blake, Daniel B.**

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Coulonia platyspina n.sp., a new astropectinid sea star from the Lower Cretaceous of Morocco

HANS HESS[1] & DANIEL B. BLAKE[2]

Key words: Asteroid, *Coulonia platyspina* n.sp., Barremian, Morocco, description, taphonomy, palaeoecology, phylogeny, morphology

ZUSAMMENFASSUNG

Der Seestern *Coulonia platyspina* n.sp. aus der Unterkreide (Barrémien) der Tamanar-Küste, N Agadir, Marokko gehört zu einer bislang nur aus dem Hauterivien des Neuenburger Juras bekannten Gattung. Die drei Funde, alles Ventralseiten, sowie Reste von irregulären Seeigeln liegen auf der Unterseite einer feinkörnigen Sandsteinbank. Schleifmarken auf dieser Schichtfläche zeigen, dass die Tiere als Folge einer Sturmlage eingebettet wurden.

Auffällig breite Inframarginalia mit tiefen Siebrinnen und säulenförmige Paxillen deuten auf eine mit rezenten Astropectiniden wie *Astropecten* und *Luidia* vergleichbare Fähigkeit zum Eingraben. Solche morphologischen Merkmale sind von den zahlreichen in der Literatur beschriebenen jurassischen Astropectiniden nicht bekannt. Aufgrund der stratigraphischen Gegebenheiten dürfte die Entwicklung von Siebrinnen zwischen den Randplatten eine phylogenetische Entwicklung darstellen, die den Astropectiniden im späten Mesozoikum neue ökologische Möglichkeiten erschloss. Dazu beigetragen hat möglicherweise ein durch das Aufkommen von Räubern erzeugter Selektionsdruck, wie er für andere Gruppen nachgewiesen wurde.

Der hier diskutierte Zeitablauf zeigt, dass phylogenetische Studien an Asteroiden auch scheinbar primitivere Formen der Paxillosida einschliessen müssen; solche Studien begnügten sich mit den Gattungen *Astropecten* und *Luidia*, die mit ihren Siebrinnen als typische Vertreter der Paxillosida gelten.

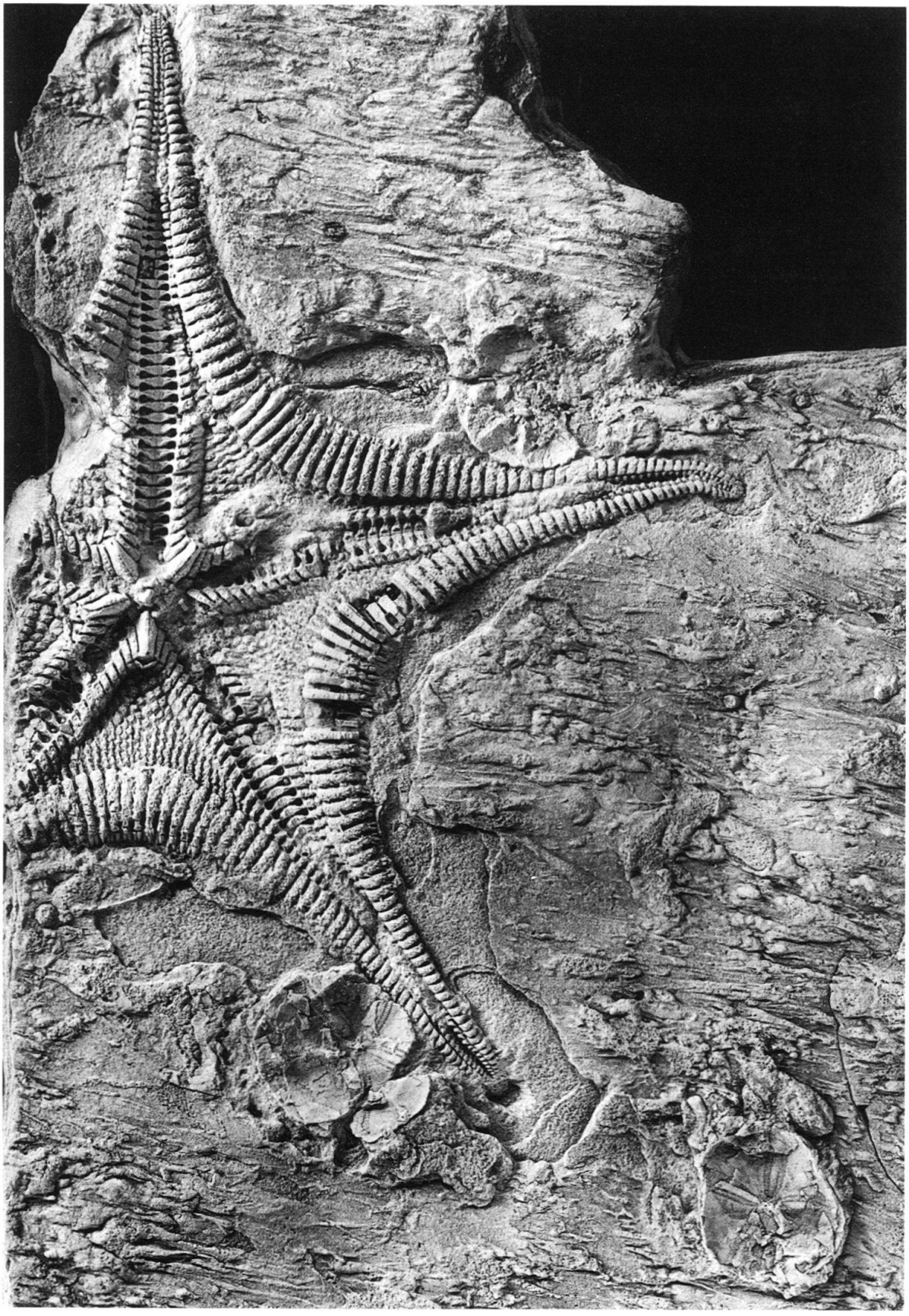
ABSTRACT

The asteroid *Coulonia platyspina* n.sp. from the Lower Cretaceous (Barremian) of the Tamanar coast, north of Agadir, Morocco, belongs to a genus hitherto known only from the Hauterivian of Switzerland. The ventral surface of the three specimens as well as remains of irregular echinoids are exposed on the lower surface of a fine-grained sandstone bed; presence of tool marks on this surface indicates that the animals were dragged along the bottom during a tempestite event before final burial.

Very broad inferomarginals with deep fasciolar channels and columnar true paxillae suggest the capability for self-burial comparable to that found in living *Astropecten* and *Luidia*. These morphological features are not known from Jurassic astropectinids, although numerous fossils from rocks of this system have been described. Based on stratigraphic position, fasciolar development appears to represent the phylogenetically derived state and suggests a broadening of astropectinid ecological capabilities during the later Mesozoic, possibly under the stimulus of the Mesozoic increase in predation pressure documented for other groups.

Timing discussed here indicates studies of asteroid phylogeny need to encompass apparently more primitive members of the Paxillosida than the fasciole-bearing genera *Astropecten* and *Luidia*, the typical paxillosidan examples of such studies.

[1] Naturhistorisches Museum, Augustinergasse 2, CH–4001 Basel
[2] University of Illinois at Urbana-Champaign, 1301 West Green Street, Urbana, IL 61801, USA



Introduction

The Lower Cretaceous along the Atlantic coast between Agadir and Essaouira (Mogador) is renowned for its rich invertebrate faunas, especially ammonites (Roch, 1950, p. 318). While collecting in this area, Serge Xerri, working for François Escuillié (Gannat, France) has found three specimens of an asteroid in loose rock material fallen from a cliff on the coast, west-south-west of the town of Tamanar; the locality is thus approximately 60 km north of Agadir. Despite considerable effort the asteroid-bearing bed could not be located in the outcrop. The fossils have been transferred to Beat and Thomas Imhof (Trimbach, Switzerland) for preparation by air-abrasive and potassium hydroxide. The better preserved of the two larger specimens (Fig. 1) was acquired through the senior author by the Basel Natural History Museum.

Geological setting

Above the beach north of Tillelt, WSW of Tamanar, approximately 20 m of fine-grained sandstone beds alternate with marly layers. The asteroids are all on the same bedding plane, presumably from about the middle of the section. Other beds of this cyclic rock sequence are very rich in irregular echinoids (*Toxaster* sp.). This sequence is overlain by bioherm-like structures with oysters and irregular echinoids. Approximately 2 km to the south, the strata pass laterally into limestone beds and marls with heteromorphous ammonites (ancyloceratids), nautiloids and *Toxaster* of Barremian age. A few hundred metres to the north they pass into marls with sandy layers and numerous specimens of *Toxaster* sp. as well as worn ammonites, indicating current activity. The inferred age of the asteroid bed is therefore Barremian.

Material

All three asteroids found by Mr. Xerri present the ventral side with widely opened ambulacral furrows. The presence of tool marks indicates this to be the lower bedding plane. A limonitic crust covered part of the 25 mm thick slab, a fine-grained sandstone with clay-laminae. Remains of irregular echinoids (*Toxaster* sp.) also occur on the bedding plane. It is the interior of the dorsal surface of their test that is exposed; thus, at some point, the ventral surface was truncated. The following description is based on the type specimen (Fig. 1). The second specimen is somewhat smaller (R = 74 mm, r = 35 mm). The third, possibly juvenile, specimen (Escuillié collection) is complete; its disc has a radius of 26 mm and its arms a length of 55 mm, with 32 inferomarginals on each ray.

Description of *Coulonia platyspina* n.sp.

The asteroid presents the ventral surface and has the ambulacral furrows widely opened, presumably partially spread by taphonomic processes. Three of the arms of the holotype

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Fig. 1. *Coulonia platyspina* n.sp. ventral view of holotype. Note tool marks with current from the right and three ventrally truncated tests of irregular echinoids (*Toxaster* sp.). 0.8 X. Barremian, WSW of Tamanar (Morocco). Natural History Museum, Basel, M 9925. Details are enlarged (approximately 3 X) in Figs. 2–6.


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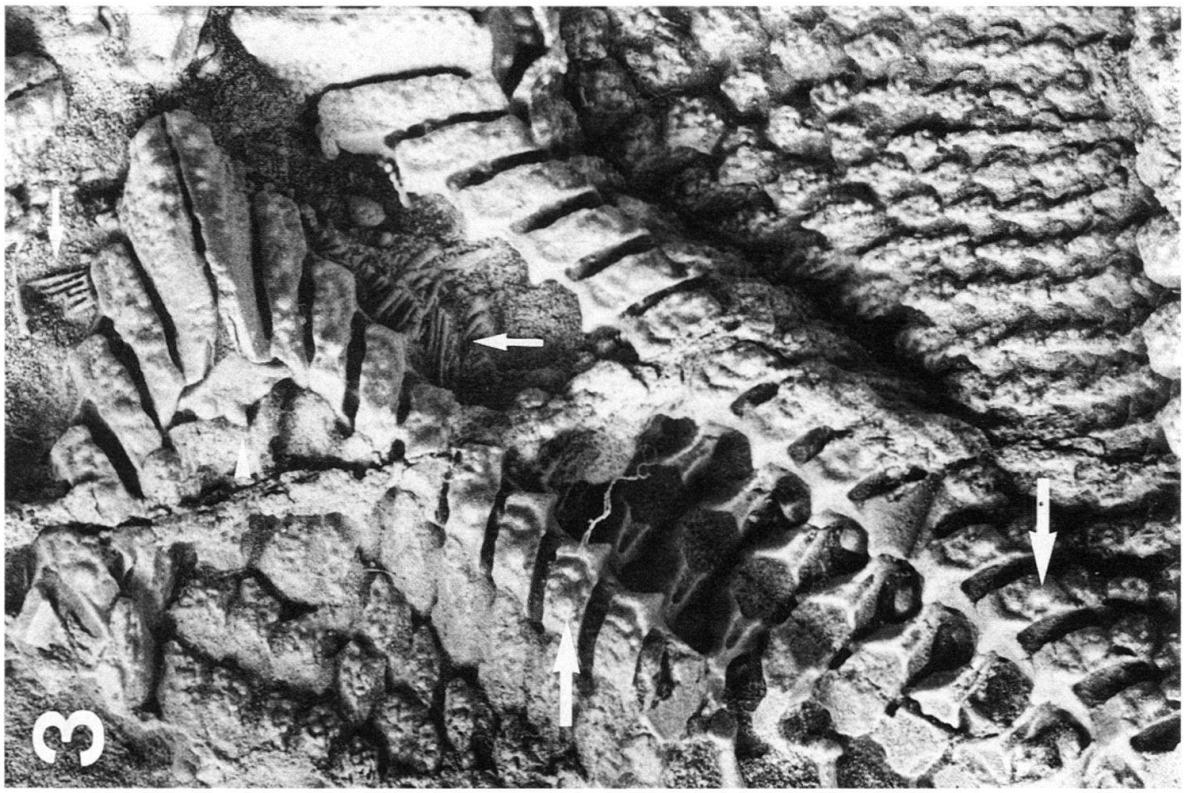
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are preserved in their entire length of 103 mm. The radius of the disc is 40 mm (R/r = 2.5), or 2–3 mm more with the fringe of protruding marginal inferomarginal spines included. Most of the disc is preserved. The approximately 45 inferomarginals on each ray are very wide and short on the disc but narrow significantly distally, producing attenuated arms. Near the tip of the arm they are nearly quadratic (Fig. 5). The terminal plate is quite inconspicuous. The margin formed by the wide inferomarginals with their large ventral face must have been even more apparent in the living animal, with partly or completely closed ambulacral furrows. The outer surface of the inferomarginals is covered with numerous smaller and three larger spines articulating with tubercles of different size. On the abradial margin each protruding inferomarginal carries two larger, flattened, blunt spines; a third such spine of similar size is situated just adradially so that the margin is armed with three flat spines (Fig. 6).

In one interradius a few inferomarginals are missing so that the superomarginals are exposed ventrally (Fig. 6). The two series of marginals are subequal, with the wide inferomarginals strongly protruding and forming the edge with their spines. Between both series are deep intermarginal channels (fasciolar grooves); the articulation face between neighbouring ossicles is limited to about half of the ossicles. The protruding inferomarginals with their fringe of spines compare well with the arrangement in the holotype of *Coulonia neocomiensis*. The same is true for the articulation surfaces of the marginals (see Hess, 1955, Fig. 16–22).

From the oral frame only the orals (mouth angle plates) are visible, the first ambulacrals are hidden in the sediment. The orals are stout and wide; their surface is covered with tubercles; these are somewhat larger near the mouth and along the sutures between these plates (Fig. 2). None of the corresponding spines is preserved, however.

The ambulacrals show the prominent head and elongated abradial extension typical of astropectinids (Fig. 2–4). The adambulacrals are very wide near the center of the disc but become rapidly narrower, without losing much of their length. The first three or four of these ossicles are somewhat gradational in morphology, approaching that of the mouth angle plate (Fig. 2, 3). The adambulacrals are distally strongly overlapping, their distal articulation surface forming a wing-like extension on which the next ossicle is imbricated (Fig. 2–4). The ventral surface of the adambulcarals is covered with tubercles; one of these is larger and carries a long spine (Fig. 4). A ridge at the adradial end (furrow ridge) supported a row of approximately 5 closely spaced, slender furrow spines; these are preserved in the ambulacral furrow of the mouth region (Fig. 2, 3).

The rhomboid actinals, developed to about half the arm length, are strongly imbricated on the adambulacrals and on each other (Fig. 3). They are arranged in well-defined transverse rows and decrease in size from orals and adambulacrals to the marginals. The

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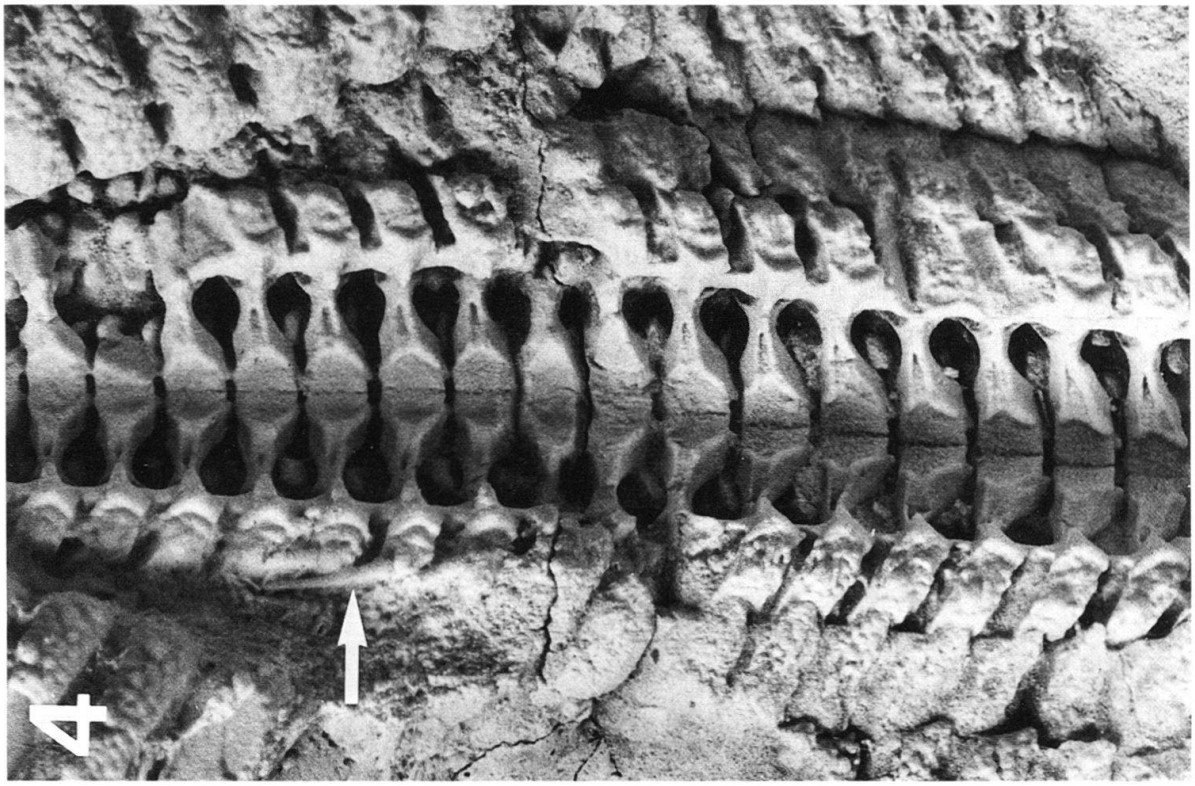
Fig. 2. Mouth region with orals and rows of adambulacrals, note slender furrow spines in left furrow (small arrow) and paxillae (large arrows).

Fig. 3. Disc near mouth. Note adambulacral furrow spines (small arrows), large tubercle on free surface of adambulacrals (large arrows), and rhomboid, imbricated actinals (lower right and upper left). The unpaired odontophore is at the abradial tip (to the left, short arrow) of the mouth angle plates.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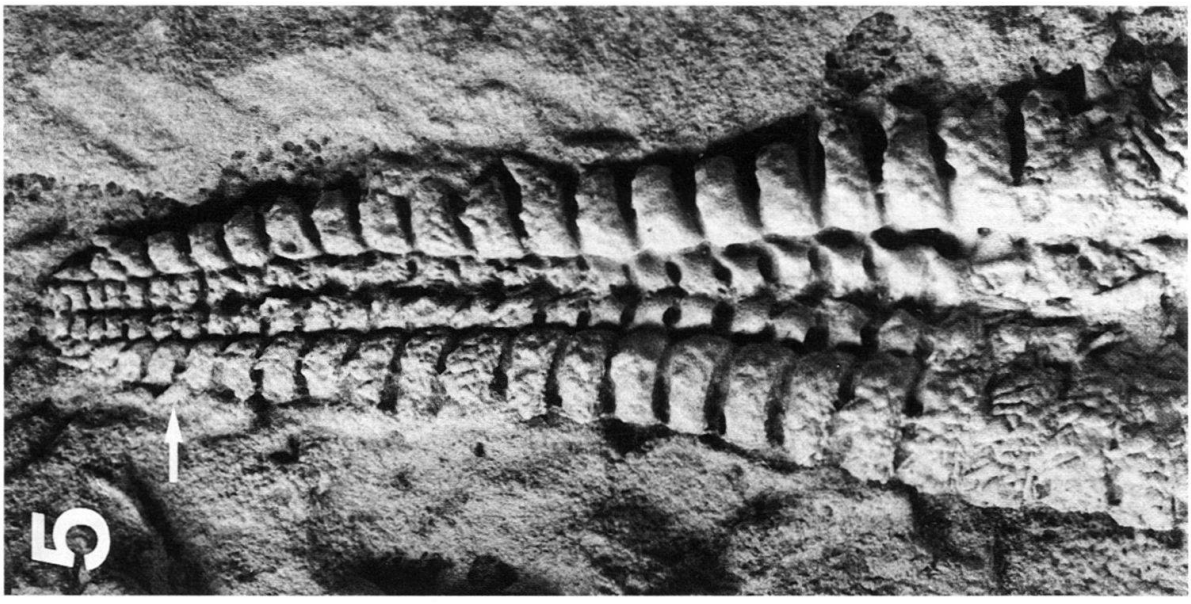
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Fig. 6. Margin of disc with inferomarginals and their armature (with fringe of flattened spines); four of the inferomarginals are missing so that the superomarginals (s) are seen ventrally. Note articular ridges limited to about half the articulation face (large arrows) and the deep fasciolar channels (small arrows).

outer surface of the actinals is covered with tubercles that supported small spines, some preserved on the specimen. A somewhat larger, shield-like, tubercled ossicle, the odontophore, is exposed (Fig. 3) as it is in *Patagiaster* FISHER.

The dorsal surface of the specimen is not exposed. However, a few paxillae are visible, e.g. in the mouth region (Fig. 2). These have an expanded base and an elongated

Fig. 4. Ambulacral furrow at approximately half the arm length; near the top of the photograph the inferomarginals meet the adambulacrals. Note first (adradial) row of actinals imbricated on adambulacrals and large single adambulacral spine (arrow).

Fig. 5. Distal part of same arm as Fig. 4. Note flattened large spine of inferomarginals close to the very tip (arrow)

stem. In other places, where the ossicles of the ventral side are not preserved, the base of the paxillae is visible ventrally. There can be hardly any doubt that the entire dorsal surface between the superomarginals was filled up with such paxillae, similar to the holotype of *Coulonia neocomiensis* (De Loriol, 1873, Pl. 2, fig. 1b). None of the spinelets, presumably inserted on the head of the stem during life, is preserved.

Affinities

The genus *Coulonia* (with the single species *C. neocomiensis*) was established by de Loriol (1873) on the basis of a unique specimen presenting its dorsal view. It was found in the "Pierre Jaune" (Upper Hauterivian) of Neuchâtel. De Loriol recognized its astropectinid features but discussed also a relationship with "Pentacerotidae" (comprising goniasterids) on the basis of the large disc. A more exact systematic positioning had to be left open in view of the unknown ventral side. Subsequently, isolated marginals were found by Hess (1955) near Ste-Croix and Neuchâtel in Hauterivian marls. The true taxonomic position of these ossicles was not recognized at the time and Hess (1955, p. 58) proposed for them a new genus and species, *Cuneaster hauteriviensis*. However, in a subsequent paper Hess (1970) synonymized *Cuneaster hauteriviensis* with *Coulonia neocomiensis*, following the discovery of some juvenile specimens in the "Pierre Jaune" of St-Blaise near Neuchâtel. The juvenile specimens have all the characters of the holotype: a rather large disc, deep intermarginal channels, very wide and protruding inferomarginals with a fringe of spines forming the edge; the superomarginals are granulated and the dorsal side is covered with true paxillae. *Coulonia* was not mentioned by Spencer & Wright (1966). *Coulonia platyspina* n.sp. can be distinguished from *Coulonia neocomiensis* by the comparatively longer arms and the flattened and shorter spines on the abradial margins of the very wide inferomarginals, forming the edge (see Fig. 1 in comparison with de Loriol, 1873, Pl. 2, fig. 1c).

Astropectinid genera are varied but familial affinities of *Coulonia* are clear, based largely on aspects of plate form that are very similar to those of many other members of the family. Important is the presence of numerous broad inferomarginals with deep, sharp-edged fascioles and a well-developed marginal spine fringe and the comparatively wide interbrachial inferomarginals that give way distally to more nearly rectangular representatives. Plates of the ambulacral column are typical of astropectinids, including prominent, keel-like mouth angle plates. As in other astropectinids, the proximal-most three or four adambulacrals are gradational in morphology (in the superficially similar Goniasteridae, the first adambulacral is very similar to subsequent plates). The rather sturdy ambulacrals, with their rectangular heads, and the broad, rectangular adambulacrals with deep fascioles and prominent spine bases are also typical of many astropectinids.

In spite of the many typical familial characters and a wealth of genera assigned to the Astropectinidae (Clark & Downey [1992] recognized 26), *Coulonia* is suggestive of members of the Goniasteridae in that the interbrachia are broadly rounded and arm outline is curved rather than straight.

Surviving astropectinids perhaps most similar in form to *Coulonia* are *Dipsacaster, Leptychaster* and *Trophodiscus. Dipsacaster* is quite similar superficially in fasciolar depth and presence of a comparatively large disc but it differs significantly in shape (the interbrachial angles are more angular and the arms less acute), proportionate inferomarginal width (narrower in *Dipsacaster*) and armament (the lateral fringe is lacking). In

Dipsacaster and *Leptychaster*, the ambulacral heads are long and triangular in outline, and therefore the articulated ambulacrals have a less sturdy appearance. Further, *Coulonia* has more robust, transversely aligned adambulacral spines and more expanded bases of the paxillae. *Leptychaster* has a comparatively large disc but interbrachia are less broad, and the arms are of typical astropectinid shape. Marginals lack prominent spines, as do the adambulacrals, which also lack a strong furrow prominence. Ambulacrals are low and triangular in *Leptychaster*. *Trophodiscus* has a large disc but triangular arms and it lacks well-developed spines.

Less similar are *Blakiaster* and *Bunodaster*, which have more angular interbrachial angles, less prominent spines, and enlarged paxillae. Plates of *Patagiaster, Koremaster, Tethyaster*, and *Plutonaster* and especially *Craspidaster* are comparatively stout and tightly arranged, more typical of certain goniasterids; further spines are less prominent. *Macroptychaster* and *Mimastrella* are poorly understood, but appear to have distinctive plate morphology. The remaining extant genera (e.g. *Bathybiaster, Dytaster*) have comparatively small discs and long, slender arms.

Appearance of the aligned actinals of *C. platyspina* n.sp. is suggestive of that of *Radiaster* (Paxillosida; Radiasteridae). Although actinals are generally well aligned both transversely and longitudinally in asteroids, it is only in those species with a large disc and protected, semi-enclosed channels that the radial arrangement is obvious. As a taxonomic character, alignment must be used with great care; characters of body form and ossicle morphology suggest no close affinities between *Radiaster* and *Coulonia*.

As noted above, Jurassic and earlier Cretaceous astropectinids lack the well-developed fasciolar grooves found in *Coulonia* and many extant genera. The Maastrichtian *Aldebariana arenitea* Blake & Sturgeon (1995) has well-developed fascioles and large disc similar to those of *Coulonia*, but arms are distinctively triangular.

Class Asteroidea DE BLAINVILLE, 1830
Order Paxillosida PERRIER, 1884
Family Astropectinidae GRAY 1840

Genus *Coulonia* DE LORIOL 1873

Amended diagnosis: Body form stellate; disc large with broadly rounded interbrachial angle and curved tapering (not straight, triangular) arm outlines; actinal area large. Paxillae elongated, columnar, with distinctly expanded base. Inferomarginals very wide on disc, with deep intermarginal channels (fasciolar grooves); abradial margin of inferomarginals with prominent fringe of spines; superomarginals narrower than inferomarginals. Ambulacral head rectangular in outline so that ambulacrals are stout and closely articulated. Terminals small. Mouth angle plates prominent, keel-like, with tip of odontophore exposed on the ventral surface.

Coulonia platyspina n.sp.

Holotype: Fig. 1–6, Natural History Museum Basel, M 9925.
Derivatio nominis: Refers to the fringe of flattened spines on the abradial margin of inferomarginals.
Stratum typicum: Lower Cretaceous, Barremian.

Locus typicus: Coast WSW of Tamanar, Morocco.
Diagnosis: Arms comparatively long (R/r = 2.5). Spines on abradial margin of inferomarginals short and flattend. Adambulacrals strongly overlapping distally, with row of slender furrow spines and single long spine on the free surface. Actinals rhomboid, strongly imbricated.

Taphonomy, palaeoecology and evolutionary ecology

The asteroids and the echinoids were living in a shallow sea, presumably some cm beneath the sediment surface. A storm event, that would have exhumed the animals, dragged them for some distance along the sea floor, leaving tool marks (Fig. 1).

Coulonia is the oldest astropectinid genus now known that combines wide inferomarginals and pronounced marginal fascioles with true paxillae differentiated into expanded base and stem. These are characteristics of genera capable of self-burial, and they are further differentiated in the Goniopectinidae and the Porcellanasteridae. The Jurassic astropectinids, by contrast, have rounded ossicles or "low, stout paxillae" on the dorsal side (see Hess, 1955, Fig. 10–12; Blake, 1986, Fig. 1–3 and 1–5)[3]. The articulation faces between marginals are large and the articular ridges comprise most of the face, permitting only shallow marginal fascioles (see Hess, 1955, Fig. 23–60: 1975, Pl. 8, fig. 6, 8, 13–14; Blake 1986, Fig. 1)[4]. The Jurassic astropectinids share these characteristics with goniasterids, asteroids known to feed on small particles from the surface of the substrate (Blake, 1990; Hess, 1994). Based on the appearance of widened inferomarginals, deepened marginal fascioles, and true paxillae it appears probable that self-burial in paxillosidans was developing during the Early Cretaceous. A Cretaceous framework for these events is further suggested by the Campanian occurrence of a primitive ctenodiscid (Blake, 1988a), which represents a level of organization directed toward self-burial beyond that of the astropectinids but primitive to that of extant *Ctenodiscus* and porcellanasterids. *Astropecten matilijaensis* DURHAM & ROBERTS (1948), from the Late Eocene of California (see Blake 1981), shares the subequal marginal series, the fasciolar channels and the presence of true paxillae with *Coulonia.*

The presence of water currents over the surface of asteroids was described by Gislén (1924), and the function and value of well-developed, protected passageways (such as are found in *Coulonia* and *Astropecten*) in infaunal species were documented by Shick et al. (1981) for *Ctenodiscus* (Paxillosida; Goniopectinidae).

Evolution of fasciolar channels, here suggested to be related to the appearance of infaunal habits, might have been predation-driven. In an extensive literature survey of species abundances through time, Aberhan (1994) documented an increase in shallow to

[3] Hess figured (1975, Pl. 3, fig. 3) a paxilla, with broad base and slender stem, from the Lower Oxfordian of the Swiss Jura and provisionally assigned it to the astropectinid *Pentasteria (Pentasterias) longispina* HESS. This species, has, however, rounded dorsal ossicles, similar to the ones figured in Hess (1955, Fig. 10–12). The assignment of the Oxfordian paxilla remains open.

[4] The Jurassic genus *Eokainaster*, established by Blake (1981) for *Astropecten pewei* MILLER & UNKLESBAY, has block-like marginals that appear to be articulated over most of their lateral faces.

moderately deep infaunal suspension-feeding life habits (typical of certain bivalves) that he attributed to a rise in Mesozoic predation pressure. Within echinoderms, Aronson (1991) documented a lower incidence of non-lethal predation damage in an Early Jurassic population of ophiuroids than he found in extant populations from Jamaica and Belize. In an evaluation of high density so-called "ophiuroid beds" through geological time, Aronson (1992) recognized significant increase in predation on ophiuroids during the Jurassic, probably by durophagous teleosts, neoselachian sharks, and decapod crustaceans then evolving. Blake (1988b) correlated a complex of inferred derived characters in the Paxillosida to changing conditions during the Mesozoic, of which predation pressure was considered to be one aspect. The fossil record, including the presence of *Coulonia platyspina* n.sp., helps document the timing of the origin of the infaunal habit, in the Paxillosida. Increase in predation pressures, and their correlated evolutionary responses, are complex processes that took place over a prolonged geological interval; it is not surprising that the apparent Lower Cretaceous origin of fascioles and infaunal habits is later than Jurassic decline of ophiuroid mats inferred by Aronson (1992).

Because of their accessibility in north-temperate shallow waters, *Astropecten* and *Luidia* (a non-astropectinid paxillosidan similar to *Astropecten*) have traditionally represented the order Paxillosida in functional and phylogenetic surveys; the present historical documentation clearly indicates the need to treat other, perhaps more primitive extant paxillosidans in these evaluations.

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