

<b>Zeitschrift:</b>	Eclogae Geologicae Helvetiae
<b>Herausgeber:</b>	Schweizerische Geologische Gesellschaft
<b>Band:</b>	77 (1984)
<b>Heft:</b>	3
<b>Artikel:</b>	The Benthopectinidae (asteroidea : echinodermata) of the Jurassic of Switzerland
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<b>DOI:</b>	<a href="https://doi.org/10.5169/seals-165525">https://doi.org/10.5169/seals-165525</a>

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# The Benthopectinidae (Asteroidea: Echinodermata) of the Jurassic of Switzerland

By DANIEL B. BLAKE<sup>1)</sup>

## ABSTRACT

The Jurassic Period is important in the history of sea stars because the first occurrences of many extant families are from rocks of this age. The range of the asteroid family Benthopectinidae is extended to the Hettangian, the lowest stage of the Jurassic System, with the transfer of *Plesiastropecten halloensis* to the family. The presence of *Plesiastropecten* in the Hettangian demonstrates that differentiation of modern sea stars had begun by very early in that period. In addition, *Xandarosaster hessi* n.gen., n.sp. is described from the Middle Jurassic (Bajocian). The new subfamily Paleobenthopectininae is recognized for the fossils and the Benthopectininae is redefined for the remainder of the family.

Modern benthopectinids are inferred to be partial suspension feeders. Morphologies of the fossils suggest a mosaic pattern in the evolution of the family with certain changes linked to improved adaptation to a suspension feeding life mode.

## 1. Introduction

The fossils discussed here are important because of their Jurassic occurrence, and because they suggest a sequence of events for the origins of certain unusual structural as well as behavioral characteristics of the family Benthopectinidae. Both fossils are from Switzerland, one representing a new genus and species, the other was previously assigned to the Astropectinidae.

Fossil benthopectinids are rare, perhaps because the family is largely known from deeper waters. DURHAM & ROBERTS (1948) described one under the name *Henricia* (?) *venturana* from the Late Eocene (considered Cretaceous at the time of publication) of California and BLAKE (1973) a second from the Oligocene of Oregon.

## 2. Systematic paleontology

Class *Asteroidea* DE BLAINVILLE 1830

Order *Notomyotida* LUDWIG 1910

Family *Benthopectinidae* VERRILL 1894

*Diagnosis.* – Arms five in number in all species, long, straight-sided, rectangular in cross section, arm tips pointed, terminal inconspicuous in larger individuals. Discs

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relatively small, with interbrachial arcs angular to weakly rounded, abactinal surface quite flat. Calycinals detectable, especially in smaller individuals. Madreporite quite large, offset toward marginals. Abactinals generally small, either simple, flattened to domed with few spinelets, or paxilliform, commonly with prominent basal facets, densely arranged spinelets and/or a central spine; a few abactinals, especially on disc, can be enlarged, bear larger spines and be more strongly differentiated; multiple abactinal types not developed in single species, abactinal arrangement aligned to rather irregular, especially in mid-arms; abactinals rather loosely interconnected, can be isolated in tissues in some taxa or individuals. Papulae in an oval or distally bifurcated patch at the base of each arm, or widespread on disc, proximal parts of arms. Marginals forming distinct lateral frame but generally rather inconspicuous from above, marginals numerous, tending to alternate in position; marginal form bulbous and elliptical, flattened and plate-like, or block-like but somewhat irregular with well-developed side faces, shallow intermarginal channels; marginals with single large central spine in most taxa, inferomarginals with smaller accessory spine below larger; unpaired, commonly enlarged interradial marginals present in some taxa. Actinal interbrachial areas small with few actinal ossicles extending beyond disc, only to proximal parts of arms, longest rows adradial; tube feet in two rows, with small suckered discs present, spicules lacking from discs. Pedicellariae common, usually pectinate, shared between two, or, in some examples on abactinal surface, three ossicles; can be fasciculate, with four or five spinelets clustered in group; bivalved in one genus. Thickened dermal layers not developed. Orals prominent, with marginal row of spinelets but typically few spinelets on remainder of surface. Interior of arms with pair of dorsal muscle bands extending from the arm tips to level with about the third to eighth superomarginal and attached to the ambulacrals, marginals or dorsal wall. Ampullae double; superambulacral ossicles lacking. Digestive system with three or four well developed rectal caeca, anus; cardiac, pyloric stomachs not clearly differentiated; digestive and reproductive organs largely restricted to disc, proximal portions of arms. Interbrachial septum organic throughout, ossicles lacking. Immature forms (from approx.  $R = 5$  mm) with stout skeletons but otherwise similar to adults.

#### Subfamily *Benthopectininae* VERRILL 1894

*Diagnosis.* — A subfamily of Benthopectinidae in which the abactinal ossicles are varied among taxa, including flat, typically scale-like ossicles; simple paxillae; stout tabulate paxillae; or simple columnar ossicles; basal digitations generally lacking and present in few ossicles on an individual where developed; abactinals of different sizes intermingled, not aligned in clearly defined rows. Ambulacrals high, ambulacral body moderately elongate, rectangular in outline, with moderately large podial pore, marginal brace developed on abradial end of abactinal ridge of arm ossicles in most species, distal ambulacral/adambulacral muscle surface very large, in life linked to similar surface on adambulacral. Adambulacral long, orientation subhorizontal, with angular furrow margin, prominent spine bases.

*Contents.* — Eight living genera (see A.M. CLARK 1981), *Mistia* BLAKE, 1973, *Henricia* (?) *venturana* DURHAM & ROBERTS (1948).

*Range.* — Eocene–Recent; worldwide.

Subfamily *Paleobenthopectininae* subfam. n.

*Diagnosis.* – A subfamily of the Benthopectinidae in which the abactinal skeleton consists of a large number of flat or low conical disc-like ossicles with a central spine base, digitate subcircular outline; ossicles relatively large, uniform in size, arranged in well-defined rows, overlap adjacent ossicles to form continuous pavement. Ambulacrals low, ambulacral body very elongate, attenuated triangular in outline, producing large podial pores; marginal brace not developed at abradial end of ambulacral abactinal ridge; enlarged distal ambulacral/adambulacral articular surface not developed. Adambulacrals either quite short, subvertical in orientation with transverse row of spine bases or elongate, subhorizontal in orientation, with single large spine base.

*Contents.* – *Plesiastropecten*, *Xandarosaster*. – *Range.* – Lower Jurassic (Hettangian) – Middle Jurassic (Bajocian); Switzerland.

Genus *Plesiastropecten* PEYER 1944

The genus is known from a single species.

*Plesiastropecten hallovensis* PEYER 1944

Fig. 1A–G

1944 *P. hallovensis* PEYER, p. 231, Pl. 7, 8.

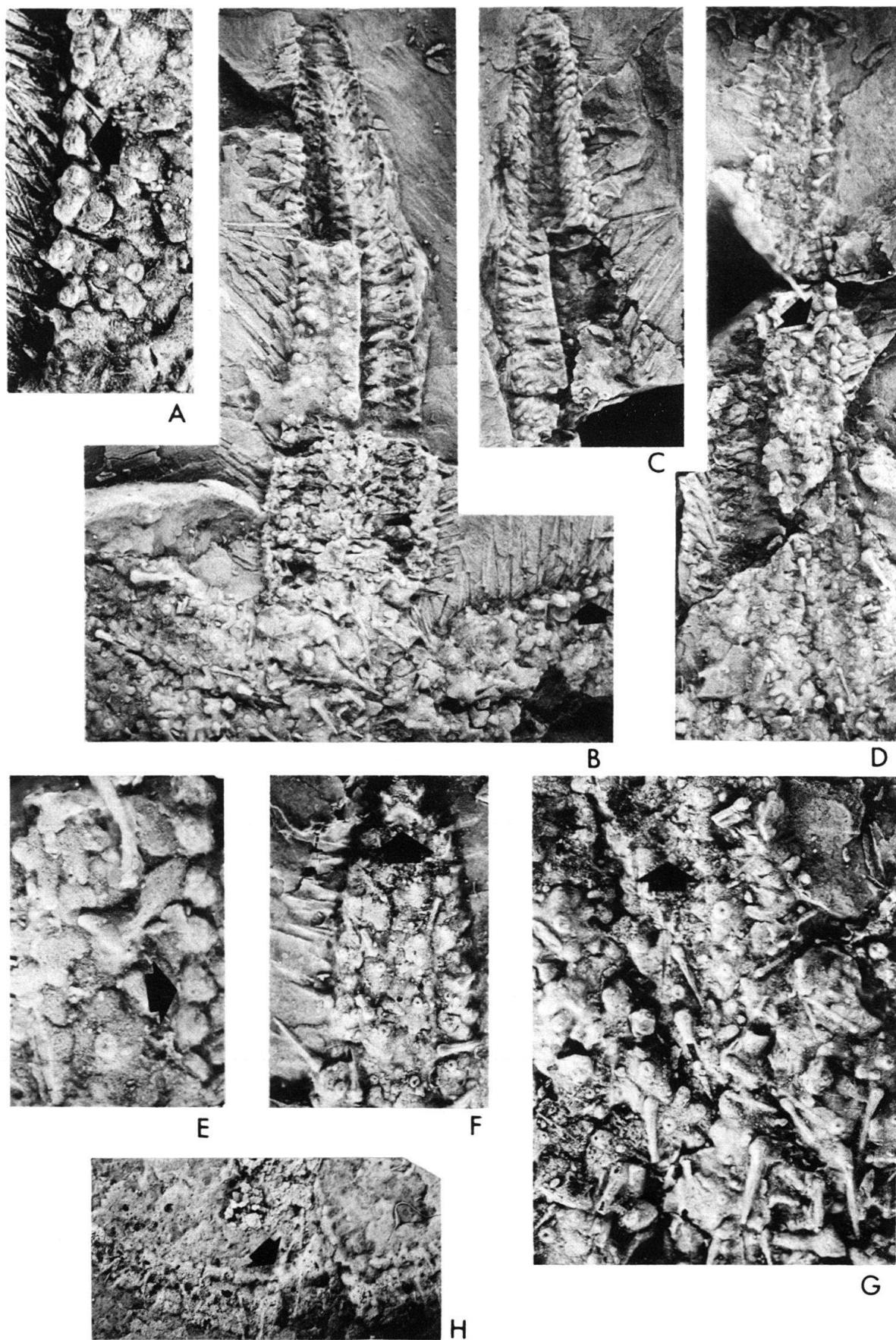
Three new specimens are available; because of very different sizes and preservational states, they are considered individually below. PEYER's description was extensive; descriptive material here stresses ossicle morphology and features important in the interpretation of affinities and evolution.

All specimens are from the lowest subzone of the Upper Hettangian (lowest Jurassic) at Hallau, Canton Schaffhausen. They were derived from the portlocki Subzone of the liasicus Zone sensu DONOVAN 1961, or the johnstoni or torus Subzone of the liasicus Zone, sensu LANGE 1942; and SCHLATTER 1983.

The specimens of *Plesiastropecten* described herein are preserved at the Museum zu Allerheiligen (Naturhist. Abteilung), Schaffhausen.

*MZA L 13b/32a–e.* – Specimen largely complete but fragmentary; buried with fragile arm spines in place, without indication of extensive pre-burial transport or decomposition. The counterparts show portions of both surfaces because fragments clung to each side, but the abactinal is the better exposed. The matrix is a green mudstone. Although buried intact, there has been leaching and ossicle loss. The specimen was crumbling, then coated with a varnish that serves to protect, but partially obscures detail.

*Description.* – Arms nearly parallel – sided proximally and medially, tapering distally to a pointed tip; R approx. 56 mm; r approx. 11 mm; arm width at base approx. 11 mm. Abactinals low, weakly conical, each with central spine base; outlines subcircular but with 6–8 articular facets. Larger ossicles in 4 (or 5) longitudinal rows proximally, 3 distally; apparently separated by overlapping smaller non-spine bearing



but otherwise similar ossicles. Abactinals form continuous skeletal surface of relatively large ossicles. Diameter of proximal ossicles 3–4 mm, distal ossicles less than 2 mm. Terminal forms arm tip; length, width approx.  $1\frac{1}{2}$  mm; with strong proximal reentrant; numerous small spine bases. Marginals small relative to body size; 15 present in 15 mm interval beginning 14 mm from disc center; mid arm ossicle length approx. 1.0 mm, width approx. 0.7 mm; superomarginals elliptical in outline, bulbous, elongate horizontally, tips overlapping, not extending significantly onto abactinal surface of arms. Outer face with one large medial spine base enclosed by scattered smaller bases. Inferomarginals not clearly exposed, appear to have been similar to superomarginals. Actinals cannot be distinguished; disc area available limited; arm form suggests actinals probably lacking or at most a single row of small ossicles present. Ambulacrals with low, rounded abactinal ridge; elongate, triangular ambulacral body; ambulacral/adambulacral muscle wings similar, broad; outline elliptical, podial pore large. Twelve ambulacral/adambulacral pairs present in  $9\frac{1}{2}$  mm interval beginning 24 mm from disc center. Neither superambulacrals nor superambulacral articular facets apparent. Adambulacrals short, broad, with transverse row of prominent spine bases. Ossicles appear to have been relatively upright and formed most of actinal surface of arms. Outer face wide, short, bearing transverse row of about 4 or 5 spine bases; not clearly differentiated into furrow and subambulacral spine series. First ambulacral abactinal edge stout, large. Marginal spines with bulbous base, slender, column tapering evenly to point; column consisting of several elongate elements, bearing distally directed barbs; up to approx. 7 mm in length; superomarginals with one large spine, inferomarginals not clearly exposed but spine number, disposition suggests one spine on each inferomarginal. Abactinal spines similar, primaries up to 4 mm in length; secondaries under 1 mm in length. Adambulacral spines similar, up to  $1\frac{1}{2}$  mm in length.

*MZA L 13b/27a-d.* – Specimen largely complete, counterparts present. Buried intact, but badly leached so that little detail is available, but portions of both surfaces are exposed. R approx. 35 mm, r approx. 6 mm. Abactinals approx. 2 mm in diameter, between 15 and 20 mm from arm tip. Marginals about 10 in number in 10 mm medially on arm.

Preserved in green mudstone. From 8 cm above upper Psilonotenbank.

*MZA L 13b/28a,b.* – Preservation similar to *MZA L 13b/27* except only abactinal surface exposed on one surface with impression of abactinal on counterpart, but nothing of actinal surface. R. approx. 9 mm, r approx. 2 mm.

Ossicles relatively large, especially first carinals, terminal; about ten marginals present along arm; small, odd interbrachial appears to occur at least in 2 interradii. Spines on carinals 1.4 mm in length.

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Fig. 1. *Plesiastropecten halloensis* PEYER. – A = Abactinal view; detail of 1B (lower right arm) showing abactinals, bulbous marginals (arrow), prominent spines;  $\times 4$ . – B = Abactinal view; overall form, abactinals, marginals (arrow corresponds to that of 1A), spines;  $\times 2$ ; MZA L 13b/32b. – C = Actinal view; adambulacrals, ambulacrals, spines;  $\times 2$ ; MZA L 13b/32a. D = Abactinal view; abactinals, terminal, ambulacral (arrow), marginals, spines;  $\times 2$ ; MZA L 13b/32b. – E = Abactinal view; detail of 1D showing ambulacral, bulbous marginals (arrow);  $\times 6$ . – F = Abactinal view; detail of 1D showing arm tip, detail of abactinal arrangement, marginals, terminal (arrow);  $\times 5$ . – G = Abactinal view of disc, base of arm; detail of abactinals, arrow lies to right of ambulacrals, points distally on arm;  $\times 4$ ; MZA L 13b/32b. – H = Abactinal of portion of disc, arms; arrow points to possible interbrachial ossicle; artificial cast;  $\times 4$ ; MZA L 13b/28b.

*Affinities and comparisons.* – Based on all available morphologic information, the new fossils are considered conspecific with the type of *Plesiastropecten halloensis*. Although ossicles are not exposed so that all their surfaces are visible, overall body form, marginals, ambulacrals and spines are all readily compared between PEYER's and the new specimens.

Most recently, SPENCER & WRIGHT (1966) included *Plesiastropecten* in the Astropectinidae. PEYER based the name on *Astropecten*, and many of his comparisons were with that genus, but Peyer also cited close affinities with the Archasteridae (p. 320). Most authors in this century have tended to restrict the Archasteridae to *Archaster* itself, but PEYER cites *Pararchaster* in his comparisons, and LUDWIG (1899) as one of his references. LUDWIG included *Pararchaster* in his concept of the Archasteridae, but other authors (e.g. A. M. CLARK 1981) synonymize it with *Benthopecten*, in the Benthopectinidae. Thus, PEYER's reference to the Archasteridae seems to have been what most authors consider to be the Benthopectinidae.

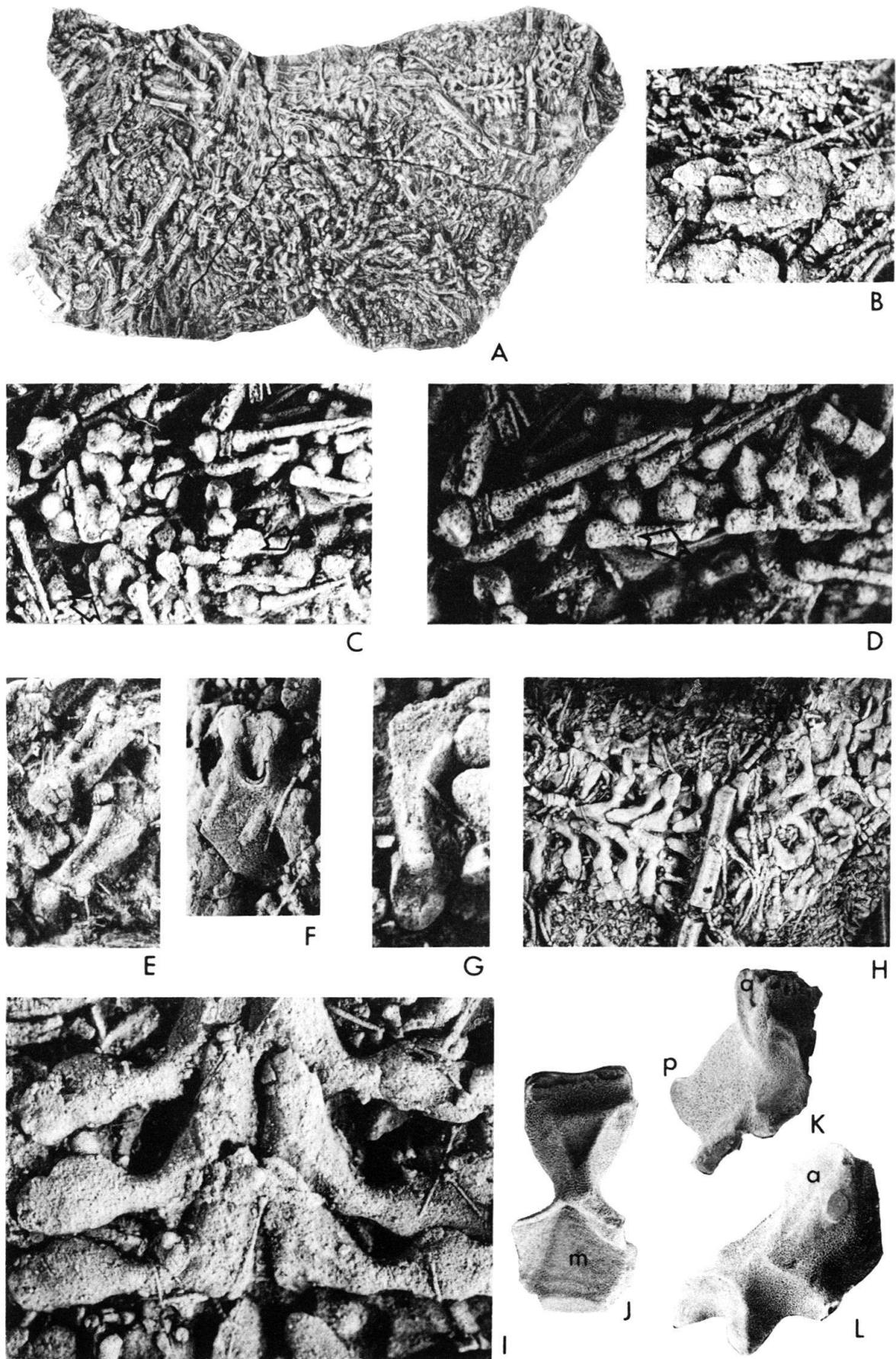
I consider the genus readily assigned to the Benthopectinidae (sensu SPENCER & WRIGHT 1966) based on the following criteria:

1. Most important is the shape, orientation and spine arrangement of the marginals. Irregular, overlapping elliptical ossicles, their long axes inclined abactinally in the distal direction, and the very large medial spine base are all characters typical of certain benthopectinids, and members of no other families. Marginals in most astropectinids, in contrast, are tabular, with broad, vertical, abutted side faces and deep intermarginal channels.
2. An odd interradial marginal occurs in certain benthopectinids and *Plesiastropecten* but in members of few other families (e.g. Odontasteridae, Chaetasteridae).
3. Prominent slender spines on the abactinals and marginals are present in members of few other families, and those (e.g. Brisingidae) are unlike the benthopectinids in other characters.
4. General body shape is consistent with a benthopectinid assignment.
5. The entire skeletal framework was somewhat loosely interconnected by soft tissues, again a common feature of benthopectinids.

Most unusual for a benthopectinid is the shape of the ambulacrals and adambulacrals. In extant benthopectinids, ambulacrals have a high, rectangular ambulacral body, a high sharp ambulacral ridge typically with an abradial extension that serves to brace the marginal frame (Fig. 2K, p), and a broad flange like ambulacral/adambulacral muscle articular surface (Fig. 2J, m). Adambulacrals are very long, oriented sub-

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Fig. 2. *Xandarosaster hessi* gen.n., sp.n., M9683; unidentified benthopectinid, brisingid ossicles. – A = Overall view of slab bearing only known specimen of *X. hessi*; many of the visible ossicles are of crinoids  $\times 0.5$ . B = Marginals, with medial spine bases, see Figure 3A;  $\times 4$ . C = Abactinals, interior surface of adambulacral; arrows correspond with those on Figure 3B;  $\times 6$ . D = Adambulacral row with spines; arrow corresponds with that on Figure 3C;  $\times 4$ . E = Exterior of adambulacrals; see Figure 3E;  $\times 4$ . F = Oral; see Figure 3F;  $\times 4$ . G = Actinal view of ambulacral; see Figure 3D;  $\times 6$ . H = Ambulacral column, upper right of Figure 2A;  $\times 2$ . I = Abactinal view of ambulacrals; see Figure 3G;  $\times 6$ . J-L = Actinal (J) and lateral (K) views of ambulacral of a benthopectinid, and lateral (L) of brisingid; only the Benthopectininae has the large ambulacral/adambulacral muscle articular flange (m) and a process (p) to brace the marginals; compare with Figures 2G, I. Both the brisingid and benthopectinid have relatively large interambulacral articular surfaces (a), although they are larger in the brisingid. The contacts help construct a sturdy ambulacral column; approx.  $\times 5$ .



horizontally, and bear the large adambulacral/ambulacral articular surface. In *Plesiastropecten*, the long ambulacral body and the low abactinal ridge are distinctive. Modern species have large podial pores, but not as large as in the fossil. Because the basic ossicular form is suggestive of those found in other families (e.g. Astropectinidae) they are considered to be closer to the primitive state than are the shapes found in modern taxa.

In addition to the nature of the ambulacral/adambulacral system, *Plesiastropecten hallovensis* differs from other benthopectinids in the nature of the abactinals. Certain modern species also have subcircular abactinals with a central spine base, but the large size, relatively thin, disc like shape, and alignment in rows is distinctive in the fossil. Modern species typically have large numbers of smaller, simple ossicles of somewhat varying sizes, or ossicles scattered in the dermal tissue.

#### Genus *Xandarosaster* gen.n.

The genus is monospecific; *X. hessi* is the type species.

#### *Xandarosaster hessi* sp. n.

Fig. 2A–I; Fig. 3A–G

**Material.** – *Xandarosaster hessi* is known from a badly disrupted individual(s) on an irregular slab about 175 mm long, 95 mm broad (Fig. 2A). The fossil lies on the upper surface of a 1 cm thick slab consisting of *Chariocrinus andreae* (DESOR); on the lower surface completely articulated specimens of this crinoid are preserved (such a surface from the same bed has been figured by HESS 1972, Fig. 22) whereas the upper surface shows more or less disarticulated specimens. The lithology is a calcarenite, of crinoid and asteroid debris. The slab was enclosed in argillaceous shale; surfaces covered by the fine clastics are well preserved, but abutted ossicles have recrystallized and fused and therefore cannot be removed individually from the block. Except for intervals of the ambulacral column, the specimen is largely disarticulated, consisting of small fragments, disjunct ossicle clusters, and some scattered ossicles. Although a pair of orals occur, other disc ossicles cannot be identified. It is uncertain how many individuals might be represented; smaller ambulacral column ossicles are present that might represent either smaller individuals or distal parts of a single individual.

Unterer Hauptrogenstein (Bajocian), Middle Jurassic, Reigoldswil, Canton Basel-land; Naturhistorisches Museum Basel, Abteilung Geologie, Nr. M9683.

**Diagnosis.** – Benthopectinid with low, conical abactinals bearing medial spine base, prominent articular digitations; flattened, rectangular marginals with single medial spine base; low ambulacrals with very long triangular ambulacral body, lacking enlarged ambulacral/adambulacral articular surface; podial pore large; adambulacrals elongate, rectangular, with large spine.

**Description.** – An evaluation of general body form is desirable because of the highly fragmentary nature of the specimen. The longest arm fragment suggests the presence of a large individual. The fragment is approximately 50 mm in length; in a 35 mm interval, width of the ambulacrals declines from 6 mm to 5 mm. If taper were constant

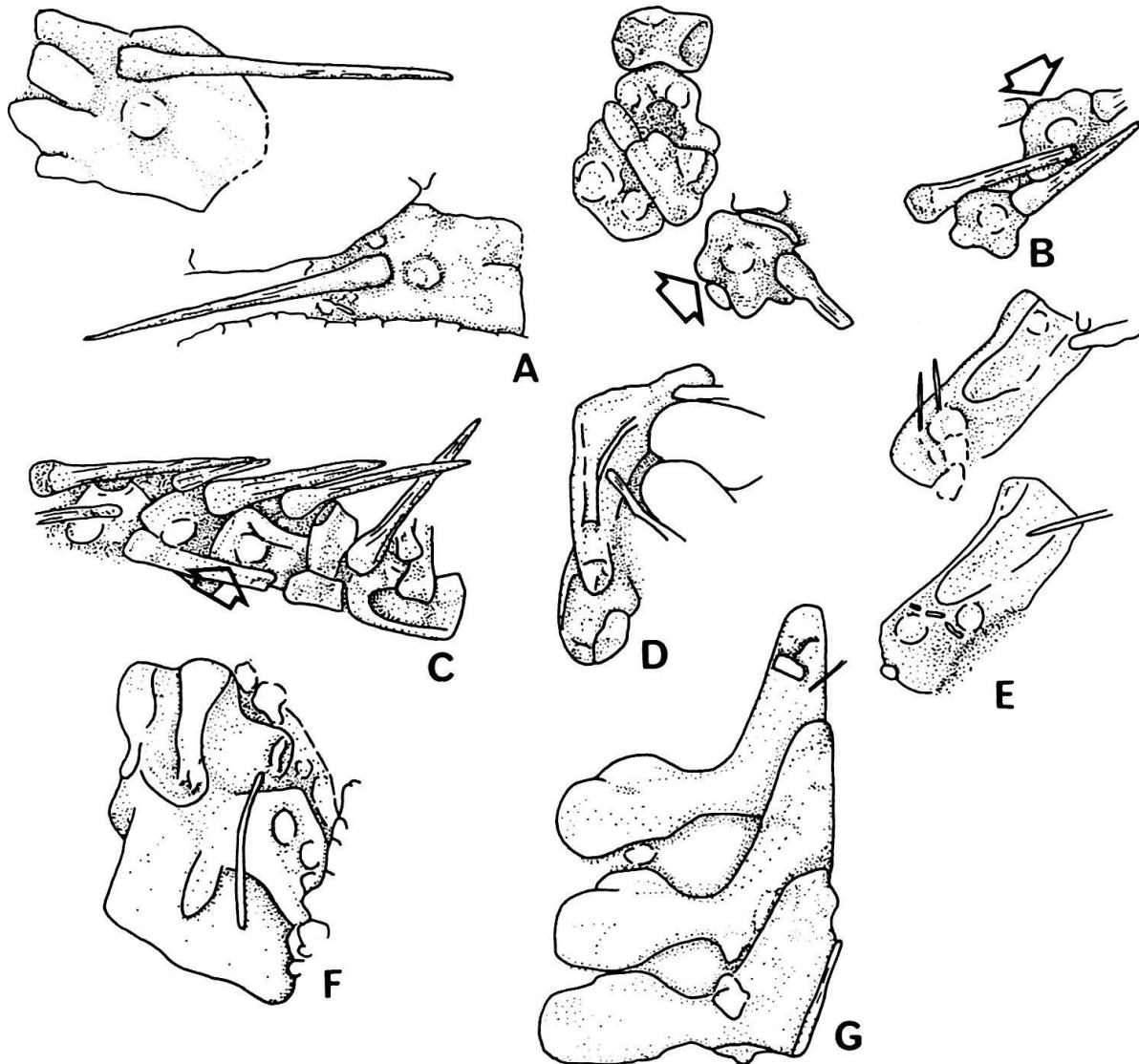


Fig. 3. *Xandarosaster hessi* gen.n., sp.n. – Camera lucida drawings of representative ossicles, see Figure 2 for photographic equivalents.

(which is reasonable) then the principal radius was at least 210 mm. There are no readily identifiable disc ossicles other than a single pair of orals. The disc apparently was relatively small, the arms long and probably strap-like, based on general appearance in comparison with other species. Abactinal ossicles are disc like and they were in contact laterally, forming a more or less continuous surface over at least part of the arm. Spine bases are numerous, suggesting a spiny appearance. Ambulacrals and adambulacrals are elongate, and the podial pores and presumably the tube feet were large. The structure of the ambulacral column is relatively open, with small articular facets on the ossicles, suggesting a relatively weak structure.

Abactinals very low, conical, with one, or in some ossicles, perhaps two prominent medial spine bases; outline subcircular but with prominent lateral articular facets. Facets suggest development of closely spaced, continuous covering on arm. Ossicle diameter approx. 1.5 mm, position on arm unknown. Marginals cannot be identified with certainty, however several ossicles near to the articulated ambulacrals are reasonable in

size, form and position and are therefore interpreted as marginals. Marginals flat, shield like, elliptical or polygonal, long axis approximately horizontal, with large central spine base; length approx. 4.5 mm; height 2.5 mm; with spine approx. 6.5 mm long. Ambulacral abactinal ridge low, broadly rounded; ambulacral body very long, triangular, moderately overlapping; articular surfaces subhorizontal, of low relief; actinal cross furrow muscle depression very large; ambulacral arm straight; ambulacral/adambulacral articular surfaces large, subequal but proximal muscle surface notched abradially; adradial ambulacral/adambulacral articular facet prominent. Neither superambulacrals nor facets for these ossicles apparent. Adambulacrals very elongate, long axis subhorizontal in life; with single prominent spine base; large adambulacral/adambulacral muscle depression present on outer face; inner surface poorly exposed, adambulacral/ambulacral muscle scars occupying proximal edges of ossicle, not central area. The distal half of two orals are exposed; ossicles high with small articular surface for first adambulacral. Actinally, ossicle blade-like, smooth, attaining narrow edge; with prominent spine base row; first ambulacral articular shaft near distal edge. Large spines are associated with some ossicles, and therefore clearly belong to the sea star. Spines simple, with enlarged base and long, conical, evenly tapered shaft, pointed tip; longitudinally striate. Spine 2.7 mm long with base length, width 0.5 mm associated with adambulacral 1.2 mm long. Neither pedicellariae valves nor their articular bases were recognized.

*Affinities and comparisons.* – Characters of *Xandarosaster hessi* are compared with those of living sea star orders in the table. The concept of the Valvatida here follows BLAKE (1981) whereas the Velatida includes all families assigned to the Spinulosida except the Echinasteridae, which alone forms the Spinulosida. In summary, *Xandarosaster hessi* can be separated from the Paxillosida on the lack of paxillae, and from the Brisingida on the structure of the ambulacral column ossicles, the oral frame, and the shape of the arms. The presence of spines and the general structure of the ambulacral column ossicles separate it from the Spinulosida. Valvatidans mostly have stout marginals, few have spines, and those spines typically are quite stout. The morphology of both ambulacral column ossicle types is stout and block-like in valvatidans; the abactinals are varied, but not like those of fossil. The Velatida lack elongate spines, and abactinals are almost always paxilliform. Ambulacrals are varied among velatidans but they are broadly similar to those of *Xandarosaster*, but less stout, in the pterasterids and the myxasterids. *Xandarosaster* is compatible with living Notomyotida (monofamilial, Benthopectinidae) in all characters except those of the ambulacral column. Important similarities are the development of spines, abactinals, and marginals. Orals in living benthopectinids are varied, but they typically have a broad, actinally directed outer surface. The keel-like edge of *Xandarosaster* is distinct, but the differentiation of a broad actinal margin bordered by a row of stout spine bases, as in *Xandarosaster*, is also typical of extant benthopectinids. The ambulacrals are similar to those of *Plesiastropecten*, and therefore *Xandarosaster* is assigned to the Benthopectinidae.

Distinguished from all benthopectinids except *Plesiastropecten* on the nature of the ambulacral column and the abactinals; see further comparisons below. Distinguished from *Plesiastropecten* on the form of the adambulacrals which are elongate and subhorizontal rather than short and subvertical, and marginals, which are shield like rather than bulbous and elliptical.

Table: Compatibility of *Xandarosaster hessi* and *Plesiastropecten hallovensis* with orders of living sea stars for selected important characters. – Key: X = *Xandarosaster hessi*; P = *Plesiastropecten hallovensis*; plus means essentially compatible, minus means essentially incompatible.

Character	Taxon		Paxillosida	Notomyotida	Valvatida	Spinulosida	Velatida	Brisingida	Forcipulitida
	X	P							
General body form	X	+	+	-	-		+	-	-
	P	+	+	-	-		+	-	-
Body construction light	X	-	+	-	-		+	+	+
	P	-	+	-	-		+	+	+
Ambulacral morphology	X	-	-	-	-		-	-	-
	P	-	-	-	-		-	-	-
Adambulacral morphology	X	+	-	-	+		+	-	-
	P	+	-	-	+		+	-	-
Oral morphology	X	+	+	-	-		+	-	-
	P	unavailable							
Marginal morphology	X	-	+	-	-		-	-	-
	P	-	+	-	-		-	-	-
Abactinal morphology	X	-	+	-	-		-	-	-
	P	-	+	-	-		-	-	-
Spines	X	-	+	-	-		-	+	+
	P	-	+	-	-		-	+	+
Large, open podial pores	X	+	+	-	-		+	+	-
	P	+	+	-	-		+	+	-

*Etymology.* – *Xandaros*, Gr., is a fabulous sea monster; the fossil was large, spinose, and like all good monsters, of peculiar construction (for benthopectinids, because of the nature and apparent operation of the ambulacrinal column). The species name is in honor of the contributions of Dr. Hans Hess to knowledge of Mesozoic echinoderms; he has also discovered the present specimen.

### 3. Discussion

*Comparisons of the fossils with living benthopectinid genera.* – A. M. CLARK (1981) reviewed the living benthopectinid genera, providing a comparative tabular key (p. 96) of their characters. Unfortunately, some of her characters cannot readily be determined for fossils, but to aid comparisons, those that can be are listed below.

1. Interradial suture, and presence of differentiated, unpaired interradial marginal.

*P. hallovensis*: Odd interradial appears to be present in one specimen.

*X. hessi*: Unknown.

2. Papular areas.

*P. hallovensis*: Abactinals appear digitate wherever exposed; assuming digitations outline papular pores, the papulae probably were widespread.

*X. hessi*: The few ossicles available are similar to those of *P. hallovensis* but there is no certainty that all were similar, nor that papular distribution was the same.

3. Superomarginal ossicle alignment.

*P. hallovensis*: Superomarginals probably mainly on lateral surfaces and inconspicuous in abactinal view.

*X. hessi*: The thin marginals would have been inconspicuous in abactinal view.

4. Abactinal ossicles.

Both taxa: Subcircular with prominent lateral digitations; low, with medial central spine.

5. Abactinal armament.

*P. hallovensis*: Central primary spine; possible ring of smaller bases around primary.

*X. hessi*: Large central spine base; no smaller bases evident.

6. Central armament of primary and some other proximal ossicles.

*P. hallovensis*: Large spines more than 2 mm long present.

*X. hessi*: Unknown.

7. Subambulacrinal spine number.

*P. hallovensis*: Not clearly differentiated from furrow spines; transverse row of 4 (or 5) spines.

*X. hessi*: Single large spine base.

8. Dorsal arm muscles.

Both taxa: Unknown.

## 9. Pedicellariae.

Both taxa:

Unknown; specimens of *P. hallovensis* are complete enough that pedicellariae bases should be recognizable if common; among the spines preserved in the *X. hessi* specimen, none are suggestive of pedicellariae, although these small ossicles might not be preserved.

*Phylogenetic and paleoecologic significance of the Paleobenthopectininae.* – Benthopectinids share a number of unusual characters that suggest a mosaic pattern in the evolution of a suspension feeding life mode. Comparisons with the Brisingidae provide support for the interpretation.

The brisingids are deep water sea stars with small, round discs and very long, slender cylindrical arms. The arms have only weak abactinal and lateral skeletal development, they lack papulae, and internal organs are restricted to proximal intervals near the disc. The sides of ambulacral ossicles (Fig. 2L) are flat, and adjacent ambulacrals are firmly linked by strong soft tissues. PAWSON (1978) published a photograph of living brisingids with many arms extended into the water column in an apparent suspension feeding orientation. The arrangement of ossicles appears to provide sturdy support for the arms while they are extended.

In contrast, the arm of living benthopectinids is strap-like, and of moderate length. Although not as sturdy as the arrangement in the brisingids, the sides of the benthopectinid ambulacrals are also somewhat flattened (Fig. 2K) and provide attachment areas for extensive soft tissues. The arm marginal ossicles are braced from the inside by a process on the abradial end of the ambulacral (Fig. 2K, p). An unusual feature of the benthopectinid ambulacral/adambulacral articulation structure is the presence of a broad, flat articular surface (Fig. 2J).

The most striking feature of the benthopectinid arm, however, is the presence of dorsal arm muscles (see familial diagnosis). A number of authors have suggested these muscles are used for swimming. LUDWIG (1910) perhaps developed the idea most completely. He pointed out that the benthopectinid arm is flexible because the abactinals do not form a solid pavement, and because of the offset nature of the marginals. Further, he noted papulae, digestive and reproductive organs are restricted to the disc and the base of the arms, and thus the arms are not encumbered with organs that would hinder swimming. As demonstrated by LUDWIG, the benthopectinid arm is a relatively light and flexible structure, and the dorsal muscles seemingly could only function to lift the arms, but these relationships do not establish how arm flexibility is used. Two major factors mitigate against swimming. First, there appears to be no effective musculature for the power stroke. Seemingly, the only available muscles are the interadambulacral muscles, which are as many in number as there are adambulacrals. There are no long muscles comparable to the dorsal bands to produce a smooth, continuous and powerful stroke. Secondly, there is no indication of bilateral symmetry, nor gliding surfaces to help maintain the animal in the water column. Swimming structures in stelleroids are possible; DIETL & MUNDLOS (1972) suggested certain paddle-shaped spines in a Jurassic ophiuroid aided swimming. Rapid contraction of the muscles might be used as an escape mechanism, but it seems difficult to picture how abrupt lifting of the arms and exposure of the tube feet would help the sea star to evade predation.

The similarities in arm structure between brisingids and benthopectinids suggests a function for the construction of the benthopectinids. The dorsal muscles lift the arms into the water currents for suspension feeding and along with the stout, abutted ambulacrals, provide support while the arms are extended. Longitudinal muscles extend between each successive pair of adambulacrals. Contraction of each of these muscles toward the proximal ossicle of the pair, along with gravity, would pull the arm downward and therefore provide a counter to the lifting action of the dorsal arm muscle. The dorsal muscles and the interadambulacral muscles together would also help balance the upright arm. The function of the broad ambulacral/adambulacral surface (Fig. 2J) isn't clear, but attached muscles might help stabilize the arm while extended.

Although brisingids are apparent suspension feeders, SLOAN (1980) and JANGOUX (1982), from literature surveys, cited the presence of annelids, crustaceans and detritus in the gut of these animals. Living benthopectinids also are deeper water organisms for which only limited feeding data are available; JANGOUX (1982) cited stomach contents including ophiuroids, arthropods, fecal pellets, microorganisms and detritus. Many sea stars are varied in both food materials and feeding modes; the benthopectinids, like the brisingids, appear to be suspension feeders as well as scavenger/carnivores and detritus feeders. Although now only conjectural, habits of benthopectinids presumably will eventually be documented with deep-sea photography.

The ambulacral column of the fossils is unlike that of extant species. Instead of a compact, sturdy arrangement, both fossils have a somewhat loosely linked system with relatively weak articular facets, small muscle surfaces, and large openings for the tube feet. On initial inspection, these arms would appear unable to maintain the arms in an upright feeding position, rather the arrangement is similar to that of the Astropectinidae and Luidiidae, whose members are predators on solitary, mobile invertebrates (SLOAN 1980; JANGOUX 1982). In *Xandarosaster*, large, sturdy subambulacral spines are present (Fig. 2D, 3C); these would seem to confer little benefit if the actinal surfaces of the arms were always directed toward the substrate. The spines might have agitated the substrate in search of food, but the tube feet, which have been shown to be highly extensible in the asteriid *Pisaster* (VAN VELDHUIZEN & PHILLIPS 1978) would seem much more effective for such use. Spines appear to be poor feeding aids in other ways. Flattened spines, broadest at their tips, are known in sea stars and would appear to be the best shape for sediment agitation, yet those of the fossils are columnar and pointed. Further, spines are powered by muscles at the base, hence seemingly they would be moved effectively only through soft sediment. In addition, they would have to be retracted for efficient locomotion, and they lack sensory receptors. Prominent spines would, however, provide a protective device if the arms were held upright in the water for suspension feeding. The occurrence of *Xandarosaster hessi* in a dense colony of crinoids adds to the plausibility of this mode of life.

The similarity between ambulacral column structure in the two fossils and the Astropectinidae suggests the fossil arrangement is nearer to the primitive state for the benthopectinids than is the modern pattern. Astropectinids are predators, suggesting predatory behavior in the fossils as well, but the prominent spines also suggest the arms of *Xandarosaster* were held upright, even if they were not as sturdy as the arms of their modern equivalents. Did the Jurassic fossils have dorsal arm muscles? Because

muscles in modern species can attach to the dorsal wall, marginals, or ambulacrals (A. M. CLARK 1981), presence or absence of muscles in fossils will be difficult to establish. LUDWIG's (1910) arguments provide the best guides. He suggested that light construction and the small, offset marginals in living benthopectinids provide flexibility, and these characters are correlated with dorsal muscles; the fossils are similarly constructed. Unlike the modern forms, the abactinal skeleton is quite stout in at least *Plesiastropecten*, and papulae might have extended well out onto the arms. The abactinal skeleton of *Plesiastropecten* is nevertheless likely to have been flexible because the plane of the articular facets lies close to the plane of the dorsal surface of the arm, and facet surfaces could have readily moved past one another. Free dorsal arm muscles are therefore inferred to have been present to support the arm during suspension feeding,

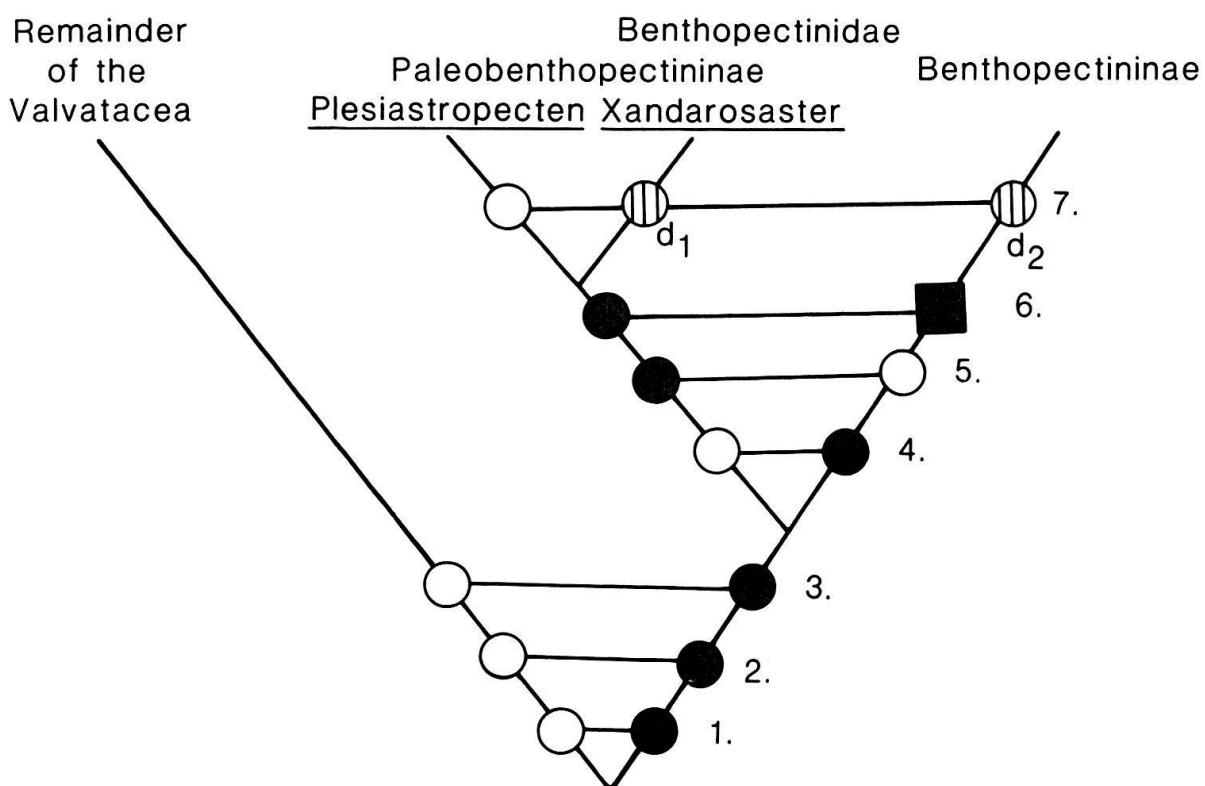


Fig. 4. Cladogram of certain events in the evolution of the Benthopectinidae. See remarks in text.

Primitive

1. No dorsal arm muscle bands.
2. Marginals not flat, elliptical, bulbous.
3. No prominent spines.
4. Typical asteroid ambulacral/adambulacral articulation.
5. Abactinals not a pavement of flat stellate discs.
6. Unknown.
7. Adambulacrals short, subvertical in orientation.

Derived

1. Dorsal arm muscle bands present.
2. Marginals flat or elliptical or bulbous.
3. Prominent spines.
4. Benthopectinid ambulacral/adambulacral articulation (see text).
5. Abactinals form pavement of flat stellate discs.
- 6d<sub>1</sub>. Ambulacrals very low, ambulacral body highly elongate, attenuated, triangular; podial pore very large.
- 6d<sub>2</sub>. Ambulacrals low, ambulacral body moderately elongate, rectangular; podial pore large.
7. Adambulacrals elongate, subhorizontal in orientation.

although because of the relatively weak articular structure perhaps periods of suspension feeding activity were relatively brief. Thus, a shift in primary feeding mechanism and efficiency taking place as the family evolved is suggested. The Benthopectinidae demonstrates a clear mosaic pattern in evolution, emerging as a morphologically recognizable entity before the origin of its now-characteristic ambulacral column articular structures.

A cladogram (Fig. 4) summarizes the sequence of certain hypothesized early events in the history of the family. The remainder of the Valvatacea sensu McKNIGHT (1975) was selected as the sister group of the Benthopectinidae whereas the Platyasteracea (essentially the Astropectinidae and allies) sensu McKNIGHT provides the outgroup for comparisons. Derived states are restricted to the Benthopectinidae, or certain members of that family only. Evolution of dorsal arm muscles is inferred to have marked the origin of the family (character 1), along with the development of typical benthopectinid marginal forms (no. 2) and prominent spines (no. 3), both known in the fossils. The peculiar ambulacral/adambulacral articulation clearly separates the modern genera from the fossils (no. 4), whereas the nature of the abactinals (no. 5) unites the fossils. In different ways, ambulacral form of both subfamilies is unlike that of other sea stars, and therefore both are considered to represent derived states (no. 6). The two represent different trends, toward foreshortening of the ambulacral body in the Benthopectininae and toward elongation and attenuation in the Paleobenthopectininae; primitive states and evolutionary sequences are unknown and the character is plotted only to provide a derived, unifying character for each taxon. Basic form and orientation of the adambulacrals of *Plesiastropecten* adambulacrals are typical of many sea stars, and by outgroup comparison, considered primitive (no. 7). In both *Xandarosaster* and the Benthopectininae, the adambulacrals are subhorizontal in the body, and of elongate, rectangular outline; these somewhat vague similarities are considered less significant than the articular structures (no. 4) and the nature of the ambulacrals (no. 6) and therefore character 7 is treated as convergent.

Although the specimen of *Xandarosaster* is fragmentary, I consider it complete enough to justify ready assignment to the Benthopectinidae and recognition of a new genus and species. It is important, however, that few changes of the above interpretations would be necessitated by rejection of this taxonomic assessment. Removal of *Xandarosaster* from the Benthopectinidae leaves functional interpretations of both *Plesiastropecten* and the modern benthopectinids unaltered (in *Plesiastropecten*, based on the presence of a typical benthopectinid flexible arm). Because of the prominent adambulacral spines, *Xandarosaster* seems to be a suspension feeder regardless of taxonomic position. Transfer of *Xandarosaster* would not alter the basic structure of the cladogram, but it would eliminate convergence in adambulacral form.

Finally, the age of *Plesiastropecten* is important for the determination of the timing of the diversification of the modern sea star fauna. No member of a living sea star family has been recognized from pre-Jurassic strata although representatives of many families are known from the Jurassic. The presence of an unequivocal benthopectinid in Hettangian rocks demonstrates that the differentiation of the modern sea stars had begun by very early in the Jurassic.

### Acknowledgments

I would like to thank Hans Hess and the authorities of the Naturhistorisches Museum Basel and the Museum zu Allerheiligen (Naturhistorische Abteilung), Schaffhausen, for generously making the specimens available to me for study. A. M. Clark and M. E. Downey reviewed the manuscript, and Rudolf Schlatter kindly provided information on the stratigraphic setting about the new material of *Plesiastropecten* (excavation by Schlatter at Hallau, 1981). Research funded in part through a grant from the National Science Foundation of the United States.

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