A NEW HOMOIOSTELEAN AND A NEW EOCRINOID FROM
THE MIDDLE CAMBRIAN OF UTAH

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Abstract—Castericystis vali, n. gen., n. sp., a solutan homoiostelean, and Marjumicystis
mettae, n. gen., n. sp., an eocrinoid, are described from the Marjum Formation of late
Middle Cambrian age in the House Range of west-central Utah. Castericystis vali is the
oldest described species of the class Homoiostelea and the first to be named from rocks
of Cambrian age. It is known from several hundred complete or partial specimens in
various stages of growth, with some juveniles apparently attached to adults. Mar-
jumicystis mettae, known from seven specimens, is characterized by a lack of sutural
pores or epispires and reduction or possible loss of the holdfast. The preserved biota
comprises echinoderms and arthropods in association with rare algae, hyoliths,
brachiopods, and sponges. Rare ichnofossils may indicate the activity of various
worms. This marine biota is inferred to have inhabited a mud substrate, below wave
base, on a gently sloping shelf ramp. Some assemblages may have been buried by
episodic storm deposits. Rare, fragmentary specimens of one or possibly two unnamed
solutans are described from the overlying Weeks Formation of the House Range.

Complete echinoderms are rarely found in rocks of Cambrian age. Of the eleven echi-
noziderm classes recorded from the Cambrian worldwide (Sprinkle, 1976), one of the rarest is
the Homoiostelea (order Soluta and class Car-

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reported from at least two other localities, one of early Late Cambrian age in Alabama (Bell and Sprinkle, 1980) and one of Early Cambrian age in Pennsylvania (Derstler, 1975, 1981; Paul and Smith, 1984). Thus, a recent discovery in Utah of hundreds of specimens of a new late Middle Cambrian homoiostelean is of special interest, not only because of the numerous complete specimens, but also because of the wealth of information they provide about an early representative of a little-known class of extinct echinoderms.

In 1982, R. A. Robison and Val Gunther discovered a fragmentary homoiostelean echinoderm in the Marjum Formation of the House Range, Utah. Further search of the locality resulted in a collection of almost 100 additional specimens, mostly from talus but a few from outcropping beds. Subsequent careful excavation, mainly by Lloyd, Metta, and Val Gunther, produced numerous well-preserved echinoderms and arthropods as well as rare specimens of other taxa. Also in 1982, K. D. Kehrberg discovered a few fragmentary homoiostelean in the upper Weeks Formation of the House Range, but further search of that locality failed to produce additional specimens. All these echinoderms are the subject of this paper and an accompanying one by James Sprinkle.

Like other Cambrian echinoderm faunas (Sprinkle, 1976, 1981), these are low in diversity. The Marjum material comprises several hundred specimens of a single homoiostelean species, a few specimens of an eocrinoid species, and one specimen of an edrioasteroid. The Weeks material represents one or possibly two undetermined species.

The larger echinoderm collection is from interbedded shale and limestone, 185 to 200 m above the base of the Marjum Formation. Descriptions of the locality, number 811 of R. A. Robison, are recorded in files of the U. S. National Museum of Natural History and the University of Kansas Museum of Invertebrate Paleontology. Other specimens were collected from the same interval for at least 3 km along strike. Index fossils from the stratigraphic section indicate a position in the middle Psychagnostus punctuosus Interval–zone (Robison, 1984) of the upper Middle Cambrian. The incidence of all taxa represented at locality 811 is recorded in the following list (vr, very rare, less than 10; r, rare, 10 to 100; c, common, 100 to 1,000; a, abundant, more than 1,000).

**Algae**
- *Margaretia dorus* Walcott
- *Yuknessia simplex*? Walcott

**Porifera**
- archaeocyathid, n. gen. & n. sp.
- *Brachiopoda*
- *Micromitra* sp.
- *Hyolitha*
- *Hyalithes* sp.

**Arthropoda**
- *Ballagnostus eurypyx* Robison
- *Bolaspidea* n. sp.?
- *Hemihodon amplifygy* Robison
- *Modocia laevinucha* Robison
- *Tuzoa guntheri* Robison & Richards

**Echinodermata**
- *Castericytis vali* Ubaghs & Robison
- *Marjumicytis mettae* Ubaghs & Robison
- *Totiglobus? lloyd* Sprinkle

**Ichnofossils**
- *Palaeophycus heberti* (Saporta)
- *Planolites beverleyensis* (Billings)
- *Tasmanadia?* sp.
- *Treptichnus?* sp.

The homoiostelean from the upper Weeks Formation were collected just above the small abandoned quarries along the north side of the road in North Canyon (Weeks Canyon of C. D. Walcott) in the central House Range. The locality is in the SE1/4 NW1/4 sec. 29, T. 18 S., R. 13 W. (Notch Peak 15-minute quadrangle map, U. S. Geological Survey, 1960). Trilobites at the locality represent the Cedaria Zone of traditional North American usage.

**Acknowledgments.**—Most of the specimens from the Marjum Formation were collected by the family team of Lloyd, Metta, and Val Gunther. Rare specimens from the upper Weeks Formation were donated by K. D. Kehrberg. An early draft of this paper was improved by reviews from M. N. Rees, A. J. Rowell, and James Sprinkle. Ichnofossils were identified by R. W. Frey. Some field work was supported by National Science Foundation grants EAR–8024066 to R. A. Robison and EAR–8201428 to J. K. Rigby. Expenses related to field excavation of specimens were paid by a special grant from the Smithsonian Institution, arranged with the help of P. M. Kier.

We were deeply saddened by the recent
death of Metta Gunther. Her friendliness, industry, patience, unselfishness, and quiet dignity remain as an inspiration to those who associated with her.

**GEOLOGIC SETTING**

The Marjum Formation of the House Range, with an average thickness of about 425 m, is predominately composed of interbedded fine-grained limestone and clayshale at its type locality near Marjum Pass. Marjum stratigraphy and faunas have been described most comprehensively by Robison (1964a, b). Within the Marjum Formation of the central House Range, Brady and Koepnick (1979) have documented a lateral transition from shallow platform to deeper shelf-basin lithofacies. Regionally, Rees (1984) has presented evidence for a northeast striking, high-angle fault that produced a large reentrant, the House Range embayment, into the Middle Cambrian shelf of western North America. According to Rees, the embayment was an asymmetrical trough that deepened and widened as it extended some 400 km westward across the shelf toward the edge of the continent.

The echinoderm-bearing shale and limestone in the middle of the Marjum Formation seemingly represents deposition by alternating and episodic fluxes of fine-grained carbonate and clastic sediment into the axial, deep-ramp part of the House Range embayment (Rees, 1984). Regular alignment of fossils, especially the homoiostelean described here, is indicative of current action at the time of burial. The fossils show many features of the Silurian "smothered-bottom assemblages" described by Brett (1983), which were interpreted as being buried by storm-generated sediment on a gently sloping seafloor below wave base.

The Weeks Formation, with an estimated thickness of about 370 m, is predominantly composed of thin-bedded, shaly limestone and interbedded shale (Hintze and Robison, 1975). Topographically, it forms slopes and valleys between more resistant units, and is one of the most poorly exposed formations in the House Range. The lower part of the formation contains a fauna representative of the Lejopyge laevigata Zone of late Middle Cambrian age (Robison, 1984). Fauna from the middle of the formation is virtually unknown, whereas tri-lobites of the Cedaria Zone are common but not well documented in the uppermost Weeks. It is presently unclear whether the fauna of the upper Weeks correlates with that of the uppermost Middle Cambrian or lowermost Upper Cambrian as traditionally defined in northwestern Europe. Rare, poorly preserved homoiosteles of undetermined genus and species are described here from the upper part of the Weeks and are the first echinoderms to be reported from the formation. Depositional environments of the Weeks Formation remain to be documented in detail, but the upper, echinoderm-bearing strata probably represent deposition in an open-shelf environment shallower than that of the echinoderm-bearing strata in the middle Marjum Formation.

**MATERIAL AND PRESERVATION**

From several hundred complete or partial homoiostelean specimens from the Marjum Formation, about 125 were chosen for detailed study and description, together with seven eocrinoids. A single associated edrioasteroid is described in an accompanying paper (Sprinkle, 1985). Many homoiosteles retain the arm and stele, which suggests rapid burial at or near the place where they lived.

The manner of preservation varies with lithology. In soft, yellowish or light-gray shale, dark-gray or black homoiosteles commonly have the thecal plates fused, and the outer surface of the theca is altered to a pustulated calcitic crust (see Fig. 2,1,2). Plate sutures on arms and steles (mainly mesi- and dististeles) are generally evident, although unweathered surfaces are commonly covered by a thin calcareous layer of diageneric origin. Thecae are considerably flattened but arms and steles, especially dististeles, are little deformed. Stereocomic meshwork is perceptible on some weathered specimens. Homoiosteles are most abundant in this light-colored shale, several being preserved per square meter on some parting surfaces. Many specimens are large (thecal length up to 28 mm) and complete. Juveniles are common, free or apparently attached to an adult. Most specimens have the arm, theca, and stele approximately aligned, or the stele may be gently curved. Few steles are sharply bent and rarely is one dislocated. On most bedding surfaces, strong orientation pre-
vails, the specimens lying with their main axes parallel.

In harder, thinner beds of medium- to dark-gray shale, homoiosteleans are preserved either as yellowish sheets of calcite or as impressions coated by extremely thin films of organic matter that is slightly darker than the matrix (see Fig. 11.3-5), or the original skeletal calcite has been replaced by limonite. In the first case, the plates are rarely distinct. In the second case, little more than the outline of the body is ordinarily perceptible; however, when immersed in alcohol, boundaries between plates, particularly in the arm and stele, may appear as dark lines. In the third case, the plates are more or less distinct, though considerably flattened. In all cases, most specimens are complete and ordinarily much smaller than those in the light-gray shale (thecal length usually less than 15 mm). Commonly, the stele is bent back to the point of lying along or across the theca, or it has a sharp bend or two as if broken into two or three parts that remain connected. The arm may show similar disruptions and the theca may have an irregular outline, suggesting some plate disordering. Particularly noteworthy is the presence of juveniles, preserved as dark films, which appear to be attached to the arm, stele, or theca of an adult.

In interbedded limestone, homoiosteleans are preserved on silty parting surfaces of thin beds. The dark-gray or black calcite endoskeleton stands out clearly against the lighter color of the rock (see Fig. 2.3-5). Specimens are more or less flattened, and weathering may expose stereomic meshwork. The fragmentary condition of most of these specimens appears to be the result of weathering or partial decomposition before burial, or both. In fact, virtually no complete individual has been observed in this type of rock. The stele, especially the dististele, is the body part usually found because its plates are thick and closely fitted. In comparison, thecae and arms are rare; however, many fragments of thecal wall are preserved, some with plates still tessellate and others with plates more or less disordered. Commonly, the stele is sharply bent at its juncture with the theca and it may even lie under or over the theca, probably as a result of postmortem shifting of specimens on the seafloor.

Eocrinoids are present in limestone and shale, but not in dark shale. In limestone, they are preserved in the same manner as the associated homoiosteleans; in shale, the original calcite has been partly or wholly replaced by limonite. In both lithologies, they still retain brachioles.

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![Fig. 1. Reconstruction of Castericyttis valli as viewed from the left lateral side, with cross sections of the stele; ×2.3.](image-url)
SYSTEMATIC DESCRIPTIONS

Class HOMOIOSTELEA Gill and Caster, 1960
Order SOLUTA Jaekel, 1901
Family uncertain

CASTERICYSTIS, new genus

Etymology.—The generic name is intended to honor K. E. Caster for his outstanding contributions to paleontology, and particularly to knowledge of the Homoioastelea.

Type species.—Castericystis call, new genus and new species (Fig. 1).

Diagnosis.—Medium-sized solutan with ovoid, probably inflated theca, without lobes except a weak proximal one; thecal faces virtually undifferentiated; thecal plates thin, large, nonimbricate; marginal frame not developed. Anus on adoral thecal face, covered by elongate plates forming conical projection at summit of proximal lobe. Pore (probably hydropore) on conical tubercle of adbranchial plate on adoral side of arm. Arm long, robust, with blunt distal end; almost axial in position; brachial plates and cover plates slightly imbricating; cover plates thick and large with outwardly, slightly protuberant tips. Stele long and stout; proxistele long, inflated, subcircular in cross section, with scalelike, somewhat irregular skeletal platting; mesistele long (relative to other genera), making gradual transition to dististele; dististele long, depressed, asymmetrical, with differentiated faces, provided with prominent keel separated from rounded opposite edge by discontinuous string of intercalated platelets on both faces; as many as 6 or 7 long spines obliquely inserting on edge opposite keel; stele ending in short, round, tail-like process.

Discussion.—Assignment of the specimens in hand to the class Homoioastelea is indicated by the typical structure of the stele, appended to a multiplated theca, itself provided with a single biserial arm. Because there is no established genus of the class to which they can be assigned, the new genus Castericystis is defined to accommodate them.

Comparison of Castericystis with Minervaecystis from the Lower Ordovician of France and questionably the uppermost Cambrian of Nevada is warranted because, until now, Minervaecystis was the oldest described homoioastelean genus (Ubaghs and Caster in Caster, 1968; Ubaghs, 1969). Both genera possess: 1) a more or less inflated, ovoid theca without marked lobation or differentiated margins; 2) thecal faces without notable differences; 3) thecal plates that are large, thin, and nonimbricate; 4) an arm and an anus on opposite sides of the main body axis; 5) a long inflated proxistele, comprising a large number of imbricate plates in vertical succession; and 6) a long asymmetrical dististele. Castericystis differs from Minervaecystis by: 1) the position of the arm almost opposite the stele rather than a considerable distance from the distal pole of the theca; 2) characters of the arm, which is larger, more robust, and possesses solid, peculiarly shaped cover plates; 3) more irregular arrangement of the proxistele plates, which in adults do not form regular, tetrigenous, telescopically imbricating rings; 4) greater length of the mesistele, being truly transitional from the proxistele to the dististele (in Minervaecystis the mesistele is short to the point of being almost lacking in some individuals); 5) many peculiarities of the dististele, such as a well-developed keel, long submarginal spines, a presence on two faces of an almost continuous string of intercalated platelets between dimere series (i.e., keel-forming plates and rounded plates on the opposite edge), and its termination in an unusual tail-like process.

Differences are even greater between Castericystis and other known homoioastelean genera, except possibly one unnamed from the Upper Cambrian of Alabama. According to Bell and Sprinkle (1980), some specimens from Alabama have an ovoid theca with numerous polygonal plates, an adoral arm, and a large multiplated stele bearing several long spines. These are all features diagnostic of Castericystis.

The similarities between Castericystis and Minervaecystis are not unequivocal evidence of close relationship, for most of the shared characters are probably primitive; that is, features inherited from some common, possibly remote, ancestor. Moreover, some of the differences between Castericystis and Minervaecystis may have disappeared during their phylogenies. For example, the rather irregular platting of the proxistele may have become progressively more regular, or the number of intercalated platelets between the dimere series in the dististele may
Fig. 2. *Castericytis* sp. from different lithologies. —1, 2. Complete specimens flattened in light-gray shale; note anal lobe, pustulated calcitic crust covering theca and proxistele, and juveniles apparently attached (arrows); 1, holotype, USNM 393391; 2, USNM 393390; both × 1.5. —3-5. Specimens preserved on silty surfaces of limestone, showing thecal plating; 3, almost complete specimen with prominent anal cone on lower left of theca (compare side with Fig. 9, 7), USNM 393369; 4, two thecae, the one below with stele flexed upward along right side, USNM 393357; 5, theca with arm (compare Fig. 3, 7), USNM 393365; all × 3.

have been gradually reduced. Yet, the features of *Castericytis* are too distinctive to be ascribed with any confidence to an ancestor of *Minervacystis*, or of any other known homoiostelean genus. Its systematic position is uncertain and will probably remain so until more information is gathered on Cambrian genera and criteria for definition of families are better defined. At present, it seems best to leave its family assignment open.

*Castericytis* shows that diagnostic features of the class Homoiostelea were fully acquired by Middle Cambrian time. Undescribed specimens may document an even earlier acquisition (Derstler, 1975, 1981; Paul and Smith, 1984). The stele of *Castericytis* is particularly instructive in this respect, for it has the same distinctive organization as the stele of all other members of the class. It displays characters judged primitive because of their significant
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Fig. 3. Thecal plating of Castericystis vali, as preserved in limestone (1) and shale (2-4), all x6. — 1. USNM 393365 (compare Fig. 2,5). — 2. USNM 393378. — 3. USNM 393371. — 4. USNM 393386.

reduction or absence in post-Cambrian homoiostelean. Such characters are the great length of the proxistele, the gradational passage from the proxistele to the dististele, and especially the presence on both faces of the dististele of an almost uninterrupted series of intercalated platelets that, like the dimeres, are in perfect transitional continuity with plates of the proxistele. This suggests an originally tetrarmorous organization for the whole organ, the intercalates being probably remnants of the two tetramerous series that, according to Caster (1968), disappeared in the passage from proxistele to dististele in most homoiostelean genera. Nevertheless, despite its primitiveness, Castericystis betrays no tendency to approximate other carpoid groups in its stele or other parts of the body; no phylogenetic connection is suggested. In our opinion, the concept of carpoids as a natural taxon remains purely conjectural; the classes included have not been demonstrated to form a phylogenetically connected group nor to possess demonstrably homologous structures (see Derstler, 1981).

CASTERICYSTIS VALI, new species
Figures 1-12

Etymology.—Named for Val Gunther, one of the discoverers of specimens assigned to the species.

Holotype.—Specimen USNM 393391 (Fig. 2,1).

Diagnosis.—Characters of the genus.

Description.—As in all other homoiosteleans, the body of Castericystis vali, which reaches at least 80 mm in total length, is composed of a single arm, theca, and stele (Fig. 1). Relations of symmetry between these parts are difficult to ascertain. Although there is no evidence of a
well-developed extensiplane in the theca, a plane of flattening is evident in both the arm and the stele, especially in the mesistele and dististele. These latter parts lie generally parallel to the bedding—a position that does not necessarily reflect their position in life.

Although the theca is always compressed, the condition is probably a consequence of the thinness of plates, decay of soft tissues, and compaction in sediment rather than its shape in life. The lack of angled edges or differentiated margins, the absence of significant plating differences on opposite faces, the common preservation of distinct plate convexity, and rare compression of specimens in the same plane, all suggest that the theca was inflated and an extensiplane was feebly, if at all, developed. The outline is an elongated, somewhat asymmetrical oval, the ratio of length to width varying from 1.1 to 1.8. Proximal lobation is weak, though an anal lobe is distinct and anal plates form a conical projection at its summit. As generally preserved, the arm and the stele are located at or near opposite ends of the theca, but probably the arm is not strictly axial and possibly the stele insertion is slightly lateral.

Orientation is difficult, if not impossible, to determine in most specimens because of the absence or weak development of an extensiplane. Where visible, an adbrachial pore, generally interpreted as the hydroapore, is invariably located near the aboral side of the arm. The thecal surface on which it lies may therefore be designated as aboral and the opposite surface as adoral, as in the Iowacystidae (Kolata, Strimple, and Levoirson, 1977). It is on the adoral face that the anus opens. This can easily be deduced from specimens compressed in a plane passing approximately through this orifice and the adbrachial pore. If the latter is on the right side of the body axis, the anus is on the left side, and conversely (Fig. 1). Other features have not been detected for consistently distinguishing the two opposite thecal surfaces.

The thecal plates are tessellated. Imbrication, where present, probably is the result of deformation (Figs. 2, 3). The plates are polygonal, varying in number as well as size and shape in each specimen. Excluding adbrachial, adanal, and adsteleal plates, maximum plate diameter in medium-sized individuals does not exceed 5 mm and minimum diameter is rarely less than 1 mm. The largest specimens, which are preserved in soft yellowish shale, rarely show sutures between thecal plates.

The thecal plates are thin (0.07 to 0.15 mm). When eroded, they are smooth; however, close examination of the external surface of some specimens reveals traces suggesting a finely granular ornamentation. A few larger plates appear to have a weak central umbo. Otherwise, the plates are flat or slightly swollen, the latter probably a remnant of original convexity. Where exposed, the stereom consists of a fairly homogeneous network with meshes 0.03 to 0.05 mm wide.

Size of the thecal plates tends to decrease toward both the stele and the arm. Thecal plates around the stele insertion seem to be relatively small; but, as preservation generally is poor, neither shape, nor number (questionably 6 or 7), nor arrangement have been established with certainty (Fig. 3,4). There is no indication that they form a gradational passage into the steleal skeleton. Neither grooves nor ridges for attachment of proxistele muscles or ligaments have been observed, but they may be present.

The thecal region around the arm base is barely better known than that around the stele. It is composed of medium-sized plates, possibly encasing the arm base. One of the adbrachial plates, always located on the aboral side of the arm and sutured to the proximal pair of brachial plates, bears a relatively high, slightly conical, perforated protuberance, the axis of which is at an oblique angle to the surface of the
Fig. 5. Plating of anal cone of Castericycits vahii.—1. USNM 393361 (compare Fig. 4,1), x 8.—2. USNM 393387 (compare Fig. 4,2), x 8.

The anus is located near the steele on the adoral face of the theca and at the summit of a broadly conical lobe (Figs. 1; 2,2,3; 3,2,4). It is closed by a pyramid (1.9 mm high, 3.3 mm wide at base in USNM 393387) of thin, long, pointed platelets. These are supported by larger elongated skeletal elements, themselves carried by polygonal plates of moderate size that pass into the general thecal pavement (Figs. 4, 5).

The arm is inserted at the distal end of the theca, slightly aboral to the main axis of the body. It is flattened and more or less distorted in most specimens. The fact that it is generally preserved in lateral position suggests that it had a certain amount of lateral compression in life. In the holotype, one of the largest specimens observed, the arm is 15 mm long. It is about one-fourth shorter than the theca. Its width and thickness decrease progressively in distal direction, but its free end is blunt rather than pointed, and weakly curved. Though stoutly built, it was quite flexible, for several arms display strong curvature without any trace of breakage (Fig. 6,1,2).

The skeleton of the arm consists of two series of brachial plates and two series of cover plates (Figs. 6, 7). The brachial plates alternate and meet on the aboral side along a zigzag suture (Fig. 7,2,5). They number 19 to 21 on a side in 5 mm. They imbricate, each plate covering a part of the outer face of the next distal one in the same series (Figs. 6,4; 7,2). The ratio of width (external dimension normal to length of arm) to height (dimension parallel to length of arm) of individual brachial plates ranges from 2.60 proximally to 1.75 distally. The proximal pair, which connects the arm to the adbrachial thecal plates, differs in shape from those following and is larger; probably erect, it may have formed a more or less rigid half-ring bracing the arm base (Fig. 7,3,5).

Like the brachial plates, the cover plates are arranged in two alternating series with each plate resting on a brachial plate (Figs. 6,3,4; 7,1,2). Two or three extra pairs of cover plates, possibly incorporated into the theca, seem to occur proximally. They probably protected a passageway leading to a subthecal mouth. The cover plates are remarkably large and stout. Near the arm base, they occupy a little less than half of the arm flanks, but in the middle and distal parts they form more than half of the arm flanks.

Each cover plate may be divided into two portions of about equal width (same definition as for brachial plates) but different shape. The lower portion, which articulates with a brachial plate, has a slightly convex profile (Figs. 6,3,4; 7,6). Its distilateral face overlaps the exposed surface of the next plate, causing a slight imbrication of the plates in distal direction. The proxilateral face is convex and it fits the distilateral face of the preceding cover plate. The face articulating with a brachial plate is bevled, weakly hollowed, and externally limited by a straight or feebly curved ridge. At the distal end of the ridge is a small depression that fits the proximal outer corner of the next following cover plate—a feature probably facilitating lateral movement of the arm (Fig. 7,7).

The summit portion of the cover plate is
conical, with a slightly concave outer profile. Its tip tends to flex outward and to form a small, yet distinct, protuberance (Fig. 6,1,3,4), which is commonly altered or removed by etching. The tip of a cover plate does not meet those of adjacent cover plates of the same series, but it interlocks with the summit portion of the cover plates of the opposite series when the ambulacrum is closed (Figs. 6,2; 7,1).

As no specimen has been observed in which the ambulacral groove is well preserved, its shape, size, and depth remain conjectural (Fig. 7,8).

The stele is the most conspicuous part of the body, being about twice as long as the theca. It is circular or subcircular in proximal cross section (Fig. 8,3) and progressively flattens in a distal direction. The two faces of the flattened portion are separated on one side by a sharp keel and on the other side by a rounded margin carrying several fixed lateral spines. The stele ends in a short, narrow, tail-like process (Fig. 1).

The stele is divided into three parts, which merge into one another. These are the proxistele, a relatively long, wide, subcircular, proximal region; the mesistele, a shorter intermediate region; and the dististele, a long flat-
Fig. 7. Plating of the arm of *Castericyctis oaki*. — 1. Arm in side view proximally, then progressively turning adoral face toward observer and showing interlocking of partially etched cover plates (compare Fig. 6,2), USNM 393360, ×15. — 2. Arm in side view showing imbrication of brachial plates (compare Fig. 6,3,4), USNM 393363, ×10. — 3. Proximal part of arm and adbrachial pore plate, USNM 393380, ×10. — 4. Adbrachial pore plate in lateral view, USNM 393362, ×20. — 5. Proximal part of arm in side view with adbrachial pore plate (compare Figs. 2,3,3,1), USNM 393365, ×30. — 6. Middle part of arm showing imbrication of cover plates, USNM 393359, ×30. — 7. Two cover plates, oblique side view showing articulation with brachial plates, USNM 393366. — 8. Diagrammatic section of arm.

tened region that passes distally into the tapering tail-like process (see Fig. 10).

The proxistele constitutes about one-third to nearly one-half of the entire stele. Its strong skeletal covering consists of numerous thin plates imbricating in both distal and lateral directions (Figs. 8,1; 9,1,2,4). The scalelike plates enclose a wide hollow space, continuous with the thecal cavity. Based on the manner of preservation, it is obvious that the plates could easily slide over one another, enabling great flexibility in this part of the stele during life but commonly resulting in irregular plate arrangements after death. The plates form neither definite rings nor columns, but there is some tendency to align vertically as well as transversely. Their number is approximately 20 to 25 along a vertical line. Although the fundamental structure is probably tetramerous, generally more than four plates are present in any
cross section. The plates are smooth and convex with a curving distal edge.

The mesistele begins proximally with appearance in the skeleton of the first components of a long series of plates that are triangular in cross section, which form the prominent keel along one edge of the mesistele and the dististele except its caudal terminus (Figs. 8,1; 9,3,4). These plates, initially small and thick, in a short distance become larger and thinner. In some specimens, the free edge, which is rather sharp, begins with a slight deviation to the right and then maintains the same direction, suggesting a feeble twisting of the stele. Opposite the keel, the scalelike plating of the proxistele changes progressively to a pavement of closely fitting plates covering a wide, rounded surface. The shape of these plates gradually changes from transversely elongate to polygonal, and coincidentally differentiates into larger elements (dimeres) and smaller accessory ones (located on the flanks). It is in the mesistele that the flattening of the stele originates or at least begins to be distinct, though it is only in the dististele that it becomes strongly developed, allowing recognition of two distinct faces.
These faces generally lie parallel to the bedding. Depending whether the keel is on the observer's right or left, with the theca being away from the observer, the upper face may conventionally be called right or left.

The transition from the mesistele to the dististele is gradational. The boundary between these two parts is approximately at the level of the first spine-bearing plate (Fig. 1).

The dististele is the longest part of the stèle, being as long as or slightly longer than the remainder of the organ (Figs. 1; 8,1,2; 9,4,5).
Its width and thickness decrease regularly in distal direction until it abruptly narrows into a rounded, tapering, caudal process. The two flattened faces differ in shape and ornamentation. Still more distinct are the two edges limiting the faces, so that the dististele appears asymmetrical with regard to both its axial plane and its flattening plane.

The dististele is invariably composed of four series of plates: the keel-like dimere series, the dimere series forming the opposite edge, and two series (one on each lateral face) of intercalated platelets. All these skeletal elements were so firmly united that in most specimens they are still closely associated.

In side view, the keel of the dististele is proximally narrow, but widens rapidly and covers more than half of both faces. Generally, the keel plates have a sharp free edge, proximally concave sides that tend to flatten distally, and gently hollowed inner faces. On each end of the keel, the plates are shorter; in between they are the same length, though here and there some may be shorter or longer than others. The sutures are thin and straight or slightly curved (Fig. 9,4,5). Ornamentation has not been observed on these plates, but a few scattered, tiny protuberances are present. On weathered specimens, shallow depressions develop on the plate flanks (Fig. 8,1,2).

Opposite the keel, the dististele margin is composed of a more complex dimere series. The margin is broadly rounded proximally and progressively contracts distally. The right side remains convex but the left side tends to flatten (Fig. 9,8). Although rather large, the plates are shorter than those of the keel and are associated, mainly in the proximal part, with smaller polygonal plates (Fig. 9,3,4). Among these skeletal elements, on the left side and more or less spaced, are inserted as many as 6 or 7 large and conspicuous ossicles, each provided with a long spine (longest observed, 1.6 mm) directed obliquely upward and outward when viewed from the left side (Figs. 8,2,4; 9,5–7). The spine series does not extend onto the distal third of the stele.

Between the dimere series, on each face, a strip of smaller polygonal plates intercalates. Like the dimere series, it originates in the mesistele, rapidly narrows, and extends discontinuously almost to the end of the stele (Fig. 9,3–5). It forms a rounded, in places swollen, ridge along the right face and a rather angular ridge along the left face.

Within the tail-like terminus of the stele, the keel disappears either progressively or abruptly (Fig. 10). The stele is then reduced to a narrow, rounded, tapering process composed of two series of more or less alternating, elongated ossicles, with or without intercalated platelets. The process is straight or curved, is about one-tenth of the total length of the stele, and apparently was rigid.

An inner cavity extends throughout the stele. It communicates with the thecal cavity through a large circular opening, has a large and rounded cross section in the proxistele (Fig. 8,3), and progressively narrows in the mesistele and the dististele (Figs. 8,4; 9,6,8), becoming reduced to a tiny axial canal in the caudal process. Its walls are relatively thin in the proxistele, being less than one-tenth of the lumen diameter, and thicken in the mesistele and the dististele. Walls along the keel and the opposite edge also are thicker than along the middle of the lateral faces (Fig. 9,8).

How the stele was oriented relative to the theca is far from obvious, as no plane of symmetry has been detected in the proxistele. Although the dististele generally lies with its flanks parallel to the bedding as a result of its flatness, it too gives no clue to its position in life. The quadriserial structure of the dististele suggests, however, a basic tetrumerous organization for the whole stele, which is fundamentally similar to
that of other known homoiosteleans (Caster, 1968). This may indicate a morphological orientation, but does not indicate which side of the stele was aborally or adorally directed in life.

**Ontogeny.**—About 30 immature specimens at various stages of growth have been observed. Their thecal length ranges from about 0.6 to 6.5 mm. The plates are partially distinct in some larger individuals, but not in the smallest ones, which are preserved as carbonaceous films on dark shale and are only recognizable from their outlines. The largest specimens are isolated on the rock, but as a rule the smallest ones are associated with various parts (arm, theca, or stele) of adult specimens, as if attached to them by the stele in life (Figs. 2,1,2; 11,3-5; 12,6,7). Conditions of preservation do not permit positive determination as to whether this association was fortuitous or the result of a larval fixation. Nevertheless, the high frequency and the near uniform orientation of juveniles with their distal stele directed toward an adult very likely indicate that the early growth stages were effectively attached.

Very early, the theca seems to have acquired a shape and proportions similar to those of adults. The number of plates in a theca 5.5 mm long probably does not exceed 60, the greatest diameter for a single plate being 1.5 mm. The thecal plates are very thin, some appearing as retiform stereomic lamellae with meshes averaging 0.04 mm in width. They are tesselated, but probably not firmly articulated. No ornamentation has been observed. Great differences in plate size in a single individual indicate that new plates were introduced between older and larger ones. An anal pyramid has been observed on a theca as short as 6.5 mm; however, proximal (anal?) lobation seems already distinct in the outline of much smaller individuals. The arm appears as an extremely short distal protuberance on very small thecae (Fig. 12,6). This protuberance grew relatively rapidly; it is 0.1 mm high in a theca 1.0 mm long, 0.4 mm in a theca 2.2 mm long, and 5.0 mm in a theca 10.0 mm long. In the latter specimen, the number of brachial plates per biseries is about 28, and the cover plates show the same shape as those of fully grown individuals. In an arm 1.4 mm long, the proximal brachial plates, which connect the arm with the theca, tend to differentiate and to be much larger than the following plates (Fig. 12,5). Most likely, new plates were added at the distal end of the arm.

The transition from theca to stele is well marked, at least in outlines, even in the earliest observed growth stages (Fig. 12,6,7). In a specimen possessing a theca 2.2 mm long, the stele has a length of 5.3 mm. In another one with a theca 7.0 mm long, the stele is 14.0 mm long, the ratio being about the same as that in adults: Division of the stele into three sections is not recognizable in the smallest specimens, the stele of which seems to taper regularly; however, division is clearly shown in individuals with a theca 3 to 4 mm long (Fig. 12,2,3). In one of the few immature steles showing plating, the proxistele comprises about one-third of the organ; it shows the same irregular scalalike skeletal covering as in adults, and passes progressively into the mesistele and dististele. The keel, opposite dimere, intercalated platelets, and spines are differentiated in the immature dististele, but there is no clear indication of a tail-like terminus, the stele appearing to taper distally. If and where new plates were introduced during growth has not been detected from available material.

**Mode of life.**—The lack of any structure serving for permanent fixation suggests eleutherozoic tendencies in *Castericystis vali*, except probably in larvae and juvenile growth stages, as discussed under Ontogeny. This does not imply, however, that this homoiostelean was not mainly sedentary. Most certainly the proxistele was extremely flexible and capable of movement in any direction, as shown by its imbricate plating and the contorted positions preserved in many specimens. In comparison, the dististele with its thick, closely joined plates has the appearance of a stiff and heavy structure, little fit for active swimming or wriggling motions. It is invariably straight or widely curved, but never sinuous. That the dististele mostly rested on the seafloor is suggested by its flatness, the dissimilarity of its two faces, and the presence of long spines on the left side of the edge opposite the keel and their absence on the right side. The latter feature would have resulted in a tilting to the left if the keel was downwardly directed in life.

The spines could hardly have functioned for defense. Their position in the stele immediately adjacent to the main zone of flexibility seems to indicate that they acted as an anchor and a fulcrum on which the muscles of the proxistele
Fig. 11. Ontogeny of *Castericyclus sali.*—1, 2. Imature specimens flattened in light-gray shale; USNM 393373 and 393372, respectively (compare Fig. 12, 2 and 12, 1, respectively); both ×5.—3–5. Early growth stages apparently attached to various parts of adult specimens, preserved as carbonaceous films on dark shale, immersed in alcohol; USNM 393375–393377 (compare 3 with Fig. 12, 6; 5 with 12, 7); all ×3.
Fig. 12. Ontogeny of Castericystis vali. — 1,2. Immature specimens flattened in light-gray shale; USNM 393372, 393373 (compare Figs. 11,2 and 11,1, respectively); both ×6. — 3,4. Incomplete steles preserved on limestone, showing progressive differentiation of dististele; USNM 393368 and 393364, respectively; both ×10. — 5. Young arm preserved on limestone, USNM 393364, ×18. — 6,7. Outlines of early growth stages preserved as films on dark shale, apparently fixed on theca and arm (6) and on distal end of stele (7) (compare Fig. 11,3,5); USNM 393375, 393377; both ×5.

could raise the theca. They were possibly assisted in this function by the insertion of the rigid distal process into mud. The keel probably gave stiffness to the dististele and helped the organism to balance in currents or when it moved. Because the dististele is more symmetrical distally than proximally, it conceivably may have served, when necessary, as a sculling organ operated by the proxistele.

If morphology points to a prostrate habit for the dististele, no feature indicates that in life the theca also lay on the seafloor. Its probably inflated shape, lack of marked differentiation of faces, and absence of lateral extensions lead one rather to suppose that it floated slightly above the sediment so that it could swivel to meet food-bearing currents. If such was its usual way of life, Castericystis vali should be viewed as a low-level suspension feeder rather than as an organism feeding on organic detritus on the substrate.

This species was apparently gregarious, judging from the occurrence of numerous, well-preserved, complete specimens at several stratigraphic horizons. This abundance contrasts with the scarcity of associated remains of eocrinoids and edrioasteroids.

GENUS AND SPECIES UNDETERMINED
Figures 13, 14

Material.—Fragments of a theca, two arms, and a stele are preserved on two small slabs of grayish-orange limestone from the upper Weeks
Formation. All of these parts are considerably flattened and eroded.

**Description.**—The theca has only distal (including arm base) and medial regions preserved (Figs. 13,1; 14,1). Its lateral margins seem to curve and converge on the arm, which was probably distal. The pavement of the exposed face is composed of tessellated, mostly hexagonal plates, the largest being 2.5 mm long and 1.8 mm wide. A few smaller plates are intercalated. Although represented only by remnants, the most distinctive feature is the presence of rounded, relatively thick, marginal plates that seem to frame the theca. Differentiated margins suggest some flattening of thecal faces.

The adbrachial area of the theca is partially concealed by a trilobite cranidium. Immediately distal to it is a node (possibly a pore node) succeeded by a median triangular plate. This is followed by two geniculate plates that apparently formed a sheath about the base of the arm. Similar adbrachial plates are present in *Dendrocystoides* (see Caster, 1968, p. S613, fig. 386) and *Minervaecystis* (see Ubaghs, 1969, pl. 17, fig. 7).

Two fragments of arms (8 and 12 mm long) are preserved on the same piece of rock as the theca. The brachial plates alternate, numbering 16 or 17 on a side in 5 mm. The ratio of width (normal to arm length) to height (parallel to arm length) of individual brachial plates is approximately 2.6. Cover plates, occupying slightly less than half of the arm flank, are bent in a distal direction. At first sight, there seems to be two cover plates for each brachial plate, but this is a false appearance resulting from erosion of one series of cover plates and exposure between them of the other alternating series.

A remnant (11.8 mm long, 2.9 mm at the widest) of a distitele (Figs. 13,2; 14,2) is present on the other piece of rock. Two series of plates are preserved. One, composed of large subquadrate plates, certainly formed a keel. The other, composed of indistinct plates, probably smaller and polygonal, formed a thicker and more irregular margin than the opposite one. Between these two series of plates, an empty space suggests that intercalated platelets could have been present. Distally, a separated...
tiny (1.0-mm-long), narrow (0.2-mm-wide), calcitic, rodlike structure indicates that the stele possibly ended in a tail-like process similar to that of *Castericystis vali*.

**Discussion.**—As these various remains are not connected, it is not certain that they belong to the same species. The stele, with its well-developed keel and possible distal tail-like process, could represent *Castericystis vali* or a closely allied species. The isolated arms do not show enough morphology to allow detailed comparison; however, like the arm of *Castericystis*, they have large cover plates. The theca, on the other hand, seems to differ markedly from that of *Castericystis* by apparent possession of differentiated margins (entirely lacking in *Castericystis*), more regular size and shape of pavement plates, and differently shaped adbrachial plates sheathing the arm base. These differences suggest a genus other than *Castericystis*, possibly a new one. If the thecal margins are differentiated, it is the earliest known occurrence of a feature that finds its full development in such advanced Ordovician solutans as the Syringocrinidae and Iowacystidae. Yet all of this needs to be taken cautiously on account of the poor preservation of such incomplete remains.

**Fig. 14.** Plating of genus and species undetermined; 1, USNM 393393 (compare Fig. 13,1); 2, USNM 393394 (compare Fig. 13,2).

**Class EOCRINOIDEA Jackel, 1918**

**Family uncertain**

**MARJUMICYSTIS, new genus**

**Etymology.**—The name refers to the Marjum Formation in which the type species was found.

**Type species.**—*Marjumicystis mettae*, new genus and new species.

**Diagnosis.**—Eocrinoids with irregular multi-plated theca, lacking sutural pores or epispires. Holdfast extremely reduced or possibly without attachment appendage. Ambulacrual system confined to oral surface, consisting of an elongate mouth and ambulacra leading to probably five groups of generally two slender, unbranched, biserial brachioles. Anus, hydropore, and gonopore unknown.

**Discussion.**—*Marjumicystis* conforms with the diagnosis proposed by Sprinkle (1973) for the class Eocrinoida, which includes species with or without epispires. A reappraisal of the Eocrinoida—apparently a paraphyletic group (Smith, 1984)—has led Broadhead (1982) to reject from it all species without epispires. That proposal is not accepted here because *Marjumicystis*, which lacks epispires, appears so
Fig. 15. *Marjumicystis mettae* preserved in various lithologies. — 1. Holotype preserved as limonite cast on shale (compare Fig. 16, 1); remnant of basal disk (arrow) seemingly attached to foreign body; USNM 393383, ×5.5. — 2. Counterpart of basal disk, same specimen as 1, ×12. — 3. Specimen flattened on limestone, lying on undetermined object, and apparently provided with large basal disk (arrow); USNM 393392, ×5. — 4. Specimen flattened on limestone, USNM 393370, ×5. — 5. Oblique view of the oral area of a partly disarticulated specimen on limestone (compare Fig. 16, 2); USNM 393351, ×10. — 6, 7. Imprints of basal disks apparently fixed on a disarticulated homoiostelean specimen (compare Fig. 16, 4), preserved as carbonaceous film on dark shale, immersed in alcohol; USNM 393385; ×8.7 and 17.0, respectively.
closely similar in organization to Gogia, which has epispines, that it seems inadvisable, based on present knowledge, to place them in two different classes.

Marjumicystis shares the lack of epispines and irregular arrangement of thecal plates with three North American genera of Cambrian age: Eustipocystis, Nolichuckia, and Trachelocrinus, all usually classified with the eocrinoids. It differs from Eustipocystis in its lack of a stem, its relatively larger thecal plates, and the probably different structure of its oral region (poorly known in Eustipocystis, but apparently with fewer brachioles attached to a more restricted area than in Marjumicystis). It differs more from Nolichuckia, which is much larger, has a few (4, possibly 5 or 6) powerful armlike processes very different from the slender brachioles of Marjumicystis, and possesses a well-developed multiplated holdfast. It is no less different from Trachelocrinus, which is characterized by a columnal-bearing stem and erect food-gathering appendages with biserial "pinnules."

A theca composed of numerous irregularly arranged plates without epispines occurs also in several post-Cambrian genera commonly considered to be eocrinoids. These include Balantiozys and Bockia, but all are easily distinguished from Marjumicystis. Balantiozys is characterized by its spindle-shaped theca, tripartite conical base, and a stem composed of typical columnals; Bockia by its biserial "pinnule-bearing" appendages, somewhat similar to those of Trachelocrinus (Bockelie, 1981).

If Marjumicystis has no holdfast or only an extremely reduced one, it is not alone among Cambrian eocrinoids in being without an an-
chorage structure. *Lichenoides* from the Middle Cambrian of Bohemia is another example, but a quite different one. That genus has a theca composed of three circles of plates, a high degree of pentameral symmetry, a complex system of epispires, and erect brachioles inserted along food grooves extending down over the theca.

*Marjumicystis* may be most closely related to *Gogia* from the Lower and Middle Cambrian of western North America (Robison, 1965; Sprinkle, 1973; Durham, 1978). Both have the same organization, except that *Marjumicystis* lacks epispires and a holdfast, or the holdfast is much reduced. These characters, however, are variously developed in *Gogia* according to species. For example, *Gogia longidactylus*, *G. kitnerensis*, and an unnamed species from the Spence Shale (Sprinkle, 1976, pl. 1, fig. 5) have or may have epispires strongly restricted to the adoral portion of the theca. Yet epispires always appear to be present, at least in specimens similar in size to those described here. Similarly, the holdfast may be very short, as in *G. hobbsi*, but it is never altogether absent as it apparently is in *Marjumicystis*. For these reasons, *Marjumicystis* is thought to be distinct from, though possibly related to, *Gogia*.

It is not clear to which family *Marjumicystis* belongs, because the criteria for definition of eocrinoid families are still uncertain. Depending on whether primary importance is given to the arrangement of the thecal plates and ambulacral system, or to the presence or absence of epispires, it may or may not be classified with *Gogia* in the Eocrinidae. *Marjumicystis* is less similar to genera of other named families. Until more is learned about its morphology, variability, and phylogeny, it seems best to leave open its family status, as Sprinkle (1973) did for *EusttytPocystis* and *Nolichuckia*.

**MARJUMICYSTIS METTAE, new species**

*Figures 15, 16*

**Etymology.**—Named for Metta Gunther, whose collection of material was an important contribution to this study.

**Holotype.**—Specimen USNM 393383 (Figs. 15,1,2; 16,1).

**Diagnosis.**—Characters of the genus.

**Material.**—Seven specimens, five in lime-}

stone and two in shale; none are complete. Several rosette-shaped impressions probably represent bases of thecae.

**Description.**—All specimens are small, the largest being 11 mm long and 9 mm wide. The theca is rounded, conical to elongate bowl-shaped, with a length to width ratio of about 1.7. It is widest near the summit, which is flattened (Fig. 15, 1, 4). The thecal plates, though appearing to have been generally flattened during fossilization, are distinctly tumid in two specimens preserved in shale, but with original calcite replaced by limonite. In the most complete specimen—a small one 3.3 mm long—35 plates are exposed, 28 on one face and 7 on the other. An estimated total of 50 to 60 thecal plates comprised this individual, and the number may have increased had ontogeny continued (Fig 16,3). Thecal plates are relatively large (though none exceeds 2.2 mm in greatest diameter), rather thick (0.07 mm), and mostly hexagonal. The largest plates are in the middle of the theca. They are irregularly arranged, except around the proximal pole. There is no indication of epispires or sutral pores. The plates are nonimbricate and smooth.

The base of the theca can be observed clearly in only one small specimen having a thecal length of 3.3 mm. It consists of a low protuberance (0.55 mm in greatest diameter) made of about 30 tiny convex plates, and is surrounded by 8 thecal plates (Fig. 16,3). A similar, but somewhat larger (1.2 mm in greatest diameter) cluster of tiny plates is present in another, poorly preserved specimen. Such a structure probably represents either an extremely reduced or an incipient holdfast. Another specimen seems to be provided with a basal disk (best seen on counterpart) comprising a small, central, polygonal space (questionably occupied by a plate) that is surrounded by 6 or 7 pentagonal or hexagonal plates. The small rosette-shaped structure, 1.6 mm wide, rests on or is possibly attached to an undetermined object (Figs. 15,1; 16,1b). Several similar, but isolated, rosette-shaped impressions have been observed on the thecal wall of two homioosteleans (Figs. 15,6,7; 16,4). They somewhat resemble the attachment disk of *Totiglobus*, and could have been made by an edrioasteroid (James Sprinkle, personal communication, 1985). If, however, they belong to
Marjumicystis mettae, then the species may have been attached in life either by means of a very small holdfast or directly by the base of the theca adhering to some foreign object on the seafloor. Although there is no clear indication that the thecal base was cemented to a substrate, it may have been fastened by the epidermis, as has been suggested for Sphaeronites (Paul and Bockelie, 1983).

The adorai portion of the theca is shown by one specimen, but it is rather poorly preserved (Figs. 15, 5; 16, 2). It consists of an area about 2 mm wide, surrounded by relatively small thecal plates of undetermined number and arrangement. On one edge, 6 brachioles were partially preserved, but 2 were accidentally destroyed during preparation. A rather high ridge, composed of alternating narrow plates, extends across the area, likely protecting an elongate mouth. At both ends of the ridge, a few larger protruding polygonal plates seemingly covered the entrance of food grooves into the mouth. Remnants of 2 or possibly 3 such grooves are evident at one end. A pentameral arrangement of ambulacra appears likely: 3 ambulacra leading to the 6 brachioles mentioned above, and 2 leading to unpreserved brachioles on the opposite edge. Such arrangement of food grooves around the mouth is present in many early echinoderms (Sprinkle, 1973).

The brachioles are inserted on low projections at the periphery of the oral region. The observed number of these biserial appendages ranges from 2 to 7, and probably did not exceed 10 or 11. The longest observed brachiole is 5 mm, which is about half the length of the theca on which it is inserted. They are slender, simple, and probably were flexible, as suggested by the aspect of the best preserved ones (Fig. 15, 3). They are usually attached to the theca in groups of 2 or 3. The brachial plates alternate, numbering about five per millimeter (Fig. 16, 5). They are elongate, with a length to breadth ratio of 1.6 to 1.7. As preserved, their outer aboral face is smoothly rounded.

Cover plates are more numerous than brachial plates, in a ratio of 7 to 8 to 5. In side view, each cover plate shows a straight edge that meets the externally exposed part of a brachial plate, a proxilateral edge curving or bent in distal direction, and a concave opposite edge (Fig. 16, 6). The outer surface curves inward (i.e., in direction of the brachiole midline) and distally, showing a characteristic warped appearance. Coincidentally, the cover plate becomes thinner and forms a scalelike projection (beaklike in lateral view), which partially covers the next following plate. This scalelike portion is commonly separated from the remainder of the plate by what appears to be a fracture rather than a suture, resulting in a false appearance of two sets of cover plates (Fig. 16, 7).

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