

A new species of the asteroid genus *Betelgeusia* (Echinodermata) from methane seep settings, Late Cretaceous of South Dakota

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Abstract.—*Betelgeusia brezinai* new species (Radiasteridae, Paxillosida, Asteroidea) is described from diversely fossiliferous Upper Cretaceous methane seep deposits of South Dakota. Asteroids are rare at modern chemosynthetic settings, although a hydrothermal vent occurrence is known, and two possible fossil methane seep occurrences have been reported. The Radiasteridae is important to the interpretation of crown-group asteroid phylogeny. Two extant genera are assigned to the family: *Radiaster* is known from relatively few but geographically widely dispersed largely deeper-water settings, and *Gephyreaster* is uncommon over a range of depths in the North Pacific Ocean. Jurassic and Cretaceous radiasterids have been described from geographically widely separated localities. In morphological-based phylogenetic analyses, the Radiasteridae has been assigned to the order Paxillosida, and *Gephyreaster* is similarly placed in a molecular evaluation; *Radiaster* has not yet been treated in a molecular study. In molecular treatment, an approximately traditional Paxillosida is a sister taxon to a significant part of the traditional Valvatida. Comparative morphology of Mesozoic and extant asteroids enables a hypothesis for a stemward, Mesozoic paxillosidan.

Introduction

Diverse invertebrate faunas have been described from the widely distributed methane seep deposits of the Upper Cretaceous Pierre Shale of the Western Interior (Landman et al., 2012). Echinoderms, including crinoids, echinoids, ophiuroids, and asteroids, have been collected; the known asteroid specimens are treated here. A guide and background to the Western Interior seep ecosystems was furnished by Shapiro and Fricke (2002), and an overview of ancient chemosynthetic settings was provided by Campbell (2006). Although echinoderms are important deep-water benthic invertebrates (Gage and Tyler, 1991), they are of limited and incompletely understood significance in chemosynthetic settings. In the Gulf of Mexico, an extant species of the upper-slope predatory forcipulate asteroid *Sclerasterias* Perrier, 1891, was reported to be a seep colonist (Carney, 1994), and a diversely fossiliferous Oligocene setting in Oregon provides another potential seep occurrence (Burns and Mooi, 2003, p. 95). Recently and for the first time, asteroids are reported from hydrothermal vents (Mah et al., 2015), these occurrences including a new family, a new genus, and two new species, the taxa emerging stemward in one major branch of forcipulatacean diversification.

All new Pierre Shale seep asteroid specimens, excepting a single fragment, are assigned to *Betelgeusia brezinai* new species, family Radiasteridae. The Radiasteridae today is known from relatively few but geographically widely separated largely deeper-water settings (448–2423 m, 245–1,325 fathoms; Clark, 1946), and because of its somewhat problematic morphology, the genus and family long have been taxonomically

difficult (Clark and Downey, 1992, p. 89). Positioning of the Radiasteridae within crown-group diversification (see the following) argues to its phylogenetic significance.

A single small Pierre Shale fragment is assigned to the Forcipulatida. Forcipulate subdivisions of Spencer and Wright (1966) are broadly typical of traditional morphology-based taxonomic arrangements whereas a recent molecular study (Mah and Foltz, 2011b) introduced significant changes placed in a historical biogeographic framework. Because of the limited data available for the single fossil, and because of taxonomic complexities, the fragment is assigned to the Pedicellasterinae in the traditional sense of Spencer and Wright (1966); placement in the updated framework (Mah and Foltz, 2011b) is not attempted.

Previous reports of Upper Cretaceous Western Interior asteroids

Two asteroids were reported from the Upper Cretaceous of the Western Interior, one from the Turonian–lower Campanian Cody Shale of Wyoming (Weller, 1905; Branson, 1947) and another from the Pierre Shale of Colorado (Griffitts, 1949, p. 2025). Gill and Cobban (1966, p. A23) reported arms of an asteroid associated with hundreds of small echinoids in a concretion collected from near the top of the upper Campanian *Baculites reesidei* Zone; although echinoids were illustrated, the asteroid was not. An asteroid arm was included among echinoderm remains in a middle Campanian cold seep setting (Kato et al., 2017).

Geologic setting

Locations of the collecting localities are illustrated in Figure 1 and their biostratigraphic positioning in Figure 2; locality AMNH 3529 is illustrated in Figure 3, and locality 3418 is documented in Landman et al. (2012). *Betelgeusia brezinai* is illustrated in Figures 4.1–4.7, 5.1–5.13 and pedicellasterid? sp. in Figure 5.14, 5.15.

Cretaceous seep deposits were first reported by Gilbert and Gulliver (1895), who provided detailed description of carbonate occurrences northeast of Pueblo, Colorado. The transition from the roughly cylindrical carbonate ‘core’ to the surrounding shale was found to be abrupt, with differential weathering and erosion yielding a distinctive conical pattern resembling Native American lodges, the structures therefore dubbed ‘tepee buttes.’ Several possible explanations for carbonate core origins were offered, but in the end it was concluded that “our present knowledge is not sufficient” (Gilbert and Gulliver, 1895, p. 340), and butte genesis remained enigmatic for 100 years. The diverse molluscan fauna of the carbonate cores includes the index ammonites *Didymoceras nebrascense* Meek and Hayden, 1856 and *Didymoceras cheyennense* Meek and Hayden, 1856, whereas the adjacent shales are devoid of fossils.

Chemosynthetic communities were first discovered in a modern cold seep setting in the Gulf of Mexico in 1983 using

the manned deep submergence vehicle (DSV) Alvin (Paull et al., 1984); since then, cold seeps and their faunas have been studied from locations around the globe (e.g., Levin, 2005). Extant seep sites were compared to the tepee butte structures and found to provide a compelling match (e.g., Kauffman et al., 1996). Further studies measuring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ levels in the carbonate core rocks support the methane (cold) seep hypothesis for tepee buttes and other carbonate mound structures, some retaining rich Late Cretaceous faunas (Landman et al., 2012; Cochran et al., 2015).

Ancient methane seep deposits ranging in age from late Cenomanian to early Maastrichtian are widely distributed throughout the Upper Cretaceous of the Western Interior (Metz, 2008; Landman et al., 2012; Larson et al., 2014; Hunter et al., 2016) and have been further documented from east-central Montana, south-central Colorado, western Kansas, north-western Nebraska, western South Dakota, eastern Wyoming (Metz, 2010; Landman et al., 2012; Larson et al., 2014), and southern Utah (Kiel et al., 2012).

The seep deposits from the Black Hills of South Dakota to southern Colorado were formed between 76 Ma and 70 Ma

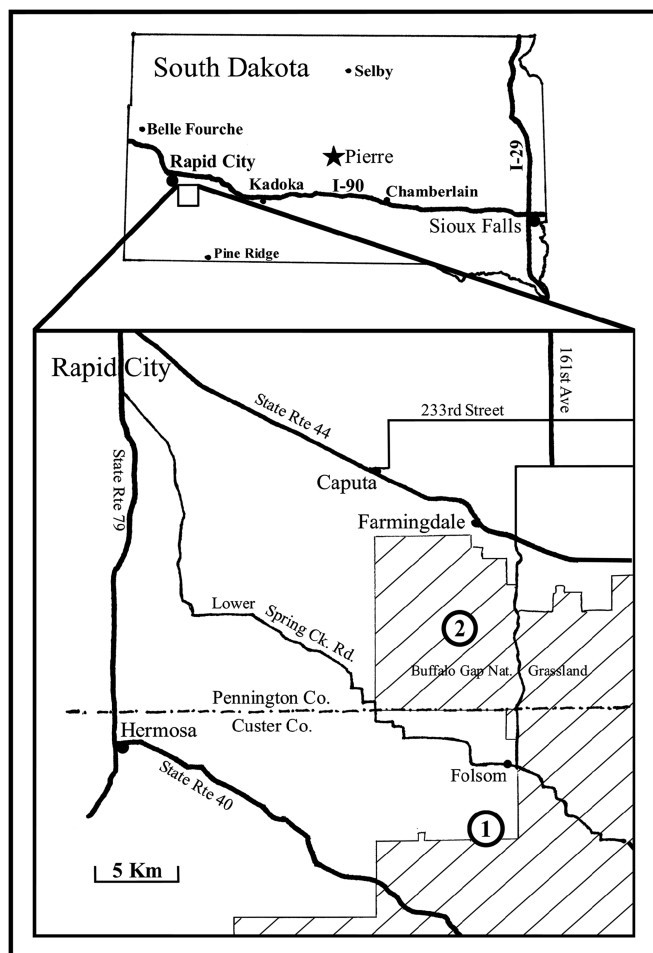


Figure 1. Map of South Dakota, USA, showing approximate asteroid collecting localities.

| Stage | US Western Interior Ammonite Zone | Age Ma* |
|-----------------|---------------------------------------|---------------------|
| Upper Campanian | <i>Baculites eliasi</i> | 71.98 ± 0.31 |
| | <i>Baculites jenseni</i> | |
| | <i>Baculites reesidei</i> | 72.94 ± 0.45 |
| | <i>Baculites cuneatus</i> | |
| | <i>Baculites compressus</i> | 73.52 ± 0.39 |
| | <i>Didymoceras cheyennense</i> | 74.67 ± 0.15 |
| | <i>Exiteloceras jenneyi</i> | 75.08 ± 0.11 |
| | <i>Didymoceras stevensoni</i> | |
| | <i>Didymoceras nebrascense</i> | 75.19 ± 0.28 |

Figure 2. Upper Campanian ammonite zonal table of the Western Interior. *Age dates from Cobban et al. (2006). Zone of occurrence of the asteroid *Betelgeusia brezinai* n. sp. in bold.



Figure 3. AMNH loc. 3529. All asteroid specimens at this locality were found within the black outline, 2–3 m north of the micritic mass of the carbonate core (arrow).

(Larson et al., 2014) in response to methane seepage through seafloor faults (Metz, 2010). Larson et al. (2014) hypothesized that they developed along fault lines due to tectonic activity, allowing for dewatering of the thick Cretaceous shales prior to and coincident with the Black Hills uplift. At any one locality, the seeps typically occur in groups of three or more, representing either closely connected conduits or movement of a single seep through time. Howe (1987) reported that most fossil seep core dimensions near Pueblo, Colorado, range from 1 to 8 m in width and up to 30 m in height, whereas many seep deposits around the Black Hills are larger (Larson et al., 2014).

The lithology of ancient seeps has been described by a number of authors (Kauffmann et al., 1996; Metz, 2008; Hendricks et al., 2011). Using the seep structure model of Handle (2014), Meehan and Landman (2016) related faunal expressions to seep architecture, with variation among seep occurrences resulting from variation among causal factors of original depth, lateral extent of seepage, methane flux, oxygen levels, water temperature (Levin, 2005), seep longevity (Larson et al., 2014), and perhaps as yet unrecognized factors; additional work is needed.

Regardless of the lithology and architecture, most of the carbonate core intervals are micritic and were formed by bacterial-mediated anaerobic oxidation of methane (AOM) coupled with sulfate reduction, the overall chemical reaction being: $\text{CH}_4 + \text{SO}_4^{-2} \rightarrow \text{HCO}_3^{-} + \text{HS}^{-} + \text{H}_2\text{O}$ (Levin, 2005). Carbonate precipitation commonly occurred from the seafloor surface to several meters within the substrate (Hendricks et al., 2011; Cochran et al., 2015). Inoceramid bivalve accumulations together with fine clastics provided a varied substrate that supported a diverse primary autotrophic fauna of tube worms and bivalves nourished by methane and/or sulfide chemosymbionts. The autotrophs were prey for predatory gastropods, crabs (MacAvoy et al., 2002), and cephalopods (Landman et al., 2012). Cemented ‘shell hash’ and seep-associated concretions can be present at the periphery of the main micritic mass (‘core’; Hunter et al., 2016, fig. 3).

All the seeps from Colorado to the Black Hills occur in the Pierre Shale, a thick, homogenous deposit of black shale more than 1,000 m thick deposited from the early Campanian through early Maastrichtian in a seaway generally 300 m deep or less (Gill and Cobban, 1966). Pierre Shale ammonite paleontology and biostratigraphy were summarized by Larson et al. (1997), the pertinent Campanian zonation summarized in Figure 2. The fossil methane seeps encircling the Black Hills are from the *Didymoceras nebrascense* Zone (base of upper Campanian) through the *Baculites grandis* Zone (lower Maastrichtian) (Larson et al., 2014), the asteroids from two sites in the *Didymoceras cheyennense* Zone (upper Campanian), AMNH loc. 3418 and AMNH loc. 3529; a partial arm from AMNH loc. 3495 is lost. Additional asteroid specimens were found at an undocumented seep site in the 1990s, their present location unknown. All asteroid specimens were found on the flanks of the main core micritic masses (Fig. 3).

Echinoderm paleoecology of Pierre Shale cold seep environments has been studied on the basis of skeletal elemental chemical analyses and stable carbon isotopes (Kato et al., 2017). A crinoid species recovered from seep settings was found to be both morphologically and geochemically differentiated as to

argue that this species is endemic and specialized to the seep environments, whereas Western Interior Seaway echinoids also based on morphologic and geochemical data were judged to have been a part of the background fauna and not restricted to seep settings. Geochemical data are not available for *B. brezinai* but its morphology does not differ in any obvious manner from morphologies of species of *Betelgeusia* that are not associated with seep settings, and therefore the new asteroid, like the echinoids, likely is a part of the background fauna.

Terminology.—Terminological usage for the asteroids follows Spencer and Wright (1966) and Blake (2013). The primary skeleton forms the body wall. The accessory skeleton includes the generally abundant spines, granules, and pedicellariae seated on all primary ossicles except ambulacrals. Ambulacrals form a double series along the axis of the arm and serve as the foundation for the water vascular system. Ambulacrals are vaulted to form the ambulacral furrow, and the mouth angle ossicles (MAO) are the proximal-most ossicles of the ambulacral series. Ambulacrals articulate with and are immediately dorsal to the adambulacrals. Marginal ossicles form either a single inferomarginal series or a double inferomarginal plus superomarginal series, one or both positioned near the margin of the asteroid. A primary circlet of abactinials can be differentiated on the dorsal disk, and dorsal midarm ossicles can be enlarged and/or otherwise differentiated to form a carinal series. The madreporite is the outlet of the water vascular system, on the dorsal disk surface of radiasterids. No, few, or many actinials occur between the inferomarginals and adambulacrals.

Repository and institutional abbreviation.—All specimens are housed in the collections at American Museum of Natural History (AMNH), Division of Paleontology.

Systematic paleontology

Order Paxillosida Perrier, 1884

Family Radiasteridae Fisher, 1916

Known genera.—*Betelgeusia* Blake and Reid, 1998 (middle Cretaceous); *Gephyreaster* Fisher, 1910 (extant); *Indiaster* Rao, 1957 (Middle Jurassic); *Radiaster* Perrier, 1881 (extant).

Remarks.—Although only two extant genera are assigned to the Radiasteridae, taxonomic interpretations of the family have differed (Fisher 1911, 1919; Clark, 1946; Blake, 1987; Clark and Downey, 1992). Two extant genera, *Radiaster* Perrier, 1881 (= *Mimaster*), represented by four species, and monospecific *Gephyreaster* Fisher, 1910 (not *Gephyriaster* Spencer and Wright, 1966) have been assigned to the family. Because of ambiguities in the literature as well as the relatively robust construction of *Gephyreaster* as compared to *Radiaster*, Blake (1987) and Blake and Reid (1998) limited treatment of extant Radiasteridae to *Radiaster* itself.

Molecular methodologies are of increasing importance in the study of evolution and biogeography, these approaches potentially particularly useful for complex settings and

evolutionary histories (Hardy et al., 2010) such as those represented here by both seep occurrences and problematic taxa such as the Radiasteridae. As true of other invertebrates, phylogenetic relationships among major subdivisions of the crown-group Asteroidea are undergoing significant revision with evolving molecular results. At writing, *Radiaster* has not yet been treated in a molecular phylogenetic analysis whereas *Gephyreaster* clustered with *Pseudarchaster* Sladen, 1889, the two assigned to the Pseudarchasteridae within an otherwise traditional paxillosidan and notomyotidan (Benthopectinidae) complex (Mah and Foltz, 2011a). Middle Cretaceous *Betelgeusia* Blake and Reid (1998) was the first fossil radiasterid to be recognized. *Indiaster* Rao, 1957 was originally assigned to the Goniasteridae but later transferred to the Radiasteridae (Blake and Reboul, 2011), the genus originally described as “probably of Upper Bathonian age” (Middle Jurassic) (Rao, 1957, p. 213). Given molecular analysis together with the closing of the morphologic gap between *Radiaster* and *Gephyreaster* as based on species of *Betelgeusia*, five fossil and extant genera, *Betelgeusia*, *Gephyreaster*, *Indiaster*, *Pseudarchaster*, and *Radiaster*, form a monophyletic complex. Molecular positioning of *Radiaster* and subsequent status evaluation of the terms ‘Radiasteridae’ and ‘Pseudarchasteridae’ are left for the future.

Genus *Betelgeusia* Blake and Reid, 1998

Type species.—*Betelgeusia reidi* Blake and Reid, 1998, by monotypy.

Other species.—*B. exposita* Blake and Jagt, 2005; *B. orientalis* Blake and Reboul, 2011.

Emended diagnosis.—Radiasterid with relatively robust, fasciolate marginals; fascicular expression, particularly superomarginal expression, varied among species. Abactinals subgranular to robust paxillae, not tabulate. Actinal ossicles many, small, aligned in strongly imbricate series that extend from inferomarginals to adambulacrals; well-defined grooves separate exposed crowns of adjacent series. Accessories varied: granules, robust short spinelets, or elongate delicate spinelets; pedicellariae not recognized.

Remarks.—A range of marginal, accessory, and abactinal variation is developed among the four species of *Betelgeusia*, although generic subdivision is not deemed justified. *Indiaster* is incompletely known, but unlike *Betelgeusia*, the actinal ossicles appear to be relatively robust, rectangular, and at most, only weakly imbricate. The two marginal series of *Indiaster* appear to be similar, robust, and closely fitted, the two series not distinctive as in *Betelgeusia*. Enough remains of the *Indiaster* specimens to suggest that accessory development was subdued. All primary ossicles of extant *Radiaster* are small and delicate, the marginals blade-like or subpaxilliform, and paxillae are delicate. Spinelets are small. Diagnostic separation of *Gephyreaster* and *Radiaster* (= *Mimaster*) was based on presence of stout tabulate paxillae and a peculiar MAO accessory arrangement in the former (Fisher, 1911, p. 175), criteria that also serve to separate *Gephyreaster* from *Betelgeusia*. In *Gephyreaster* as in *Betelgeusia*, marginals and,

in particular, inferomarginals are comparatively robust and closely fitted, although smaller accessories are similar between *Gephyreaster* and some *Betelgeusia*.

The strongly imbricate, paddle-like actinals of *Betelgeusia* aligned in well-defined series form a distinctive generic character complex. The almost upright actinal occurrences of some fragments of *B. brezinai* (Fig. 5.10, 5.11) might have been accentuated taphonomically, but not significantly so from natural positioning assumed during normal life activities.

Betelgeusia brezinai new species

Figures 4.1–4.7; 5.1–5.13

2017 asteroid; Kato et al., p. 223, fig. 2I.

Holotype.—Locality AMNH 3529, holotype AMNH-FI 111823: a small individual in overall good condition and exposing both surfaces, although distorted through sediment compaction and breakage, and partially obscured by foreign shell fragments. Remaining arm radii R = 18, 12, 12, 4, and 11 mm; r of three remaining interbrachia 8–10 mm.

Paratypes.—Locality AMNH-FI 3529, paratypes: an illustrated, nearly complete specimen exposed in ventral aspect, AMNH-FI 111824, an arm tip with both surfaces exposed, paratype AMNH-FI 111825; five illustrated small fragments, AMNH-FI 111825–AMNH-FI 111830; seven partial paratypes, relatively complete to fragmentary, AMNH-FI 111831–AMNH-FI 111837; and 14 small to tiny paratype fragments of larger specimens, AMNH-FI 111838–AMNH-FI 111851.

Locality AMNH 3418, a single paratype, AMNH-FI 111852, exposed in ventral aspect, on a small block of fossiliferous carbonate matrix. Two arms are nearly complete, R = 19 mm; truncated R between about 9 and 12 mm, interbrachial radius 10 mm. Inferomarginals of interbrachia are complete; a single superomarginal series is visible, but no abactinals; no accessory ossicles remain. Approximately 14 inferomarginals between the interbrachial plane and arm tip of nearly complete arm R = 19 mm, r ~ 9 mm. About 13 to 15 marginal pairs between interbrachial midline and terminal.

Occurrences.—Locality AMNH-FI 3529: *Didymoceras cheyennense* Zone, Pierre Shale, upper Campanian, Late Cretaceous; Pennington County, South Dakota. Exact locality information is available to qualified researchers from the American Museum of Natural History. All available specimens but one were collected at locality 3529.

The locality is a low-profile mound consisting of tan-weathered shales at the top with less-weathered black and dark-gray shales at its base. A 1–2 m main carbonate micritic mass (‘core’) is exposed with associated concretions and cemented shell hash carbonates on the core flanks; weathered carbonates are scattered downslope. The original Pierre Shale surrounding the seep was eroded during the Paleocene through early Eocene, exposing the carbonates to weathering. The seep was later reburied by Chadron Formation deposition during the middle to late Eocene, composite sediments including volcanic ash from the west and alluvial gravels and clay from the Black Hills. The seep was reexposed as a result of weathering during the

Pleistocene and Holocene. The seep supported a highly diverse fauna including ammonites, crinoids (*Lakotacrinus brezinai* Hunter et al., 2016 and an unknown feather star), two types of tubeworms, two types of bryozoans, various gastropods and bivalves (including teredinids and inoceramids), unidentified crabs, a ghost shrimp, and echinoids (Larson et al., 2014). Preservation of the asteroids is varied, including both articulated and fragmentary specimens, exposing both surfaces, the suite recovered both from an approximately 3 × 5 m area in the carbonate shell hash and loose in the weathered tan shale (Fig. 3).

Locality AMNH-FI 3418: *Didymoceras cheyennense* Zone, Pierre Shale, upper Campanian, Late Cretaceous; Custer County, South Dakota. Exact locality information is available to qualified researchers from the American Museum of Natural History.

A vertically exposed carbonate seep cross section measuring 13 m high and 20 m wide, surrounded by black and gray shales with orange and yellow partings near the carbonates (Landman et al., 2012). The base is buried beneath slumped black and dark-gray shale, but the roughly cylindrical carbonate ‘core’ and its conduit-like structures are readily visible. A detailed map of the seep face (Landman et al., 2012, fig. 2) and site photographs (Larson et al., 2014, fig. 9a, b) have been published. The seep contains a diverse fauna of well-preserved fossils including many ammonites, a nautiloid, bivalves, gastropods, the articulate crinoid *Lakotacrinus brezinai* Hunter et al., 2016, tube worms, sponges, fish, and crabs (Landman et al., 2012; Larson et al., 2014).

Diagnosis.—Betelgeusid in which ossicles of marginal series are similar, relatively robust, rectangular in outline. Marginal fascioles narrow, deep; intermarginal articular ridges subdued, closely fitted, overlapping flanges not strongly differentiated. First actinal row overlapping onto adambulacrals. First adambulacrals strongly overlapping MAO. Accessories include granules and short, robust spinelets; elongate, delicate spines lacking.

Description.—Disk large, interbrachia broadly rounded, arms triangular, tapering abruptly to rounded tips; overall body form low arched in life. Abactinals small but proportionately robust, granular to weakly paxilliform. Abactinal size diminishing distally and radially but otherwise uniform, abactinals aligned in longitudinal and transverse rows; no apparent differentiation of carinal series or primary circlet. Abactinals covered by closely fitted, uniform, small, robust spinelets or granules; abactinals and granules forming closely fitted surface lacking distinct gaps suggestive of respiratory papulae. Madreporite not recognized, although potentially occurring in lost portions of available disks.

Marginal ossicles in two series; series paired, ossicles of both series robust, block-like, rectangular in vertical outline. Inferomarginals protrude slightly laterally beyond margins of superomarginals, more strongly so at interbrachia, protrusion

less distinct more distally. Marginal fascioles narrow, well defined, angular. Superomarginal dorsal surface weakly arched longitudinally; transverse profile broadly rounded adradially, more sharply curved toward arm margin. Superomarginal ossicular surfaces closely covered by uniform, closely spaced small granules; small, thickened spinelets can occur at abradial edge, preservational textures suggesting spinelets might not have been developed on all ossicles or all specimens. Both longitudinal and transverse inferomarginal ventral profiles nearly flat, transverse profile curving sharply near abradial margin, abradial inferomarginal edge upright, tightly rounded. Ventral inferomarginal surfaces bearing about five rows of small pustules; accessories entirely granulate, or with scattered spinelets; abradial margin granulate or bearing short, robust spinelets. Elongate spines lacking from both marginal series.

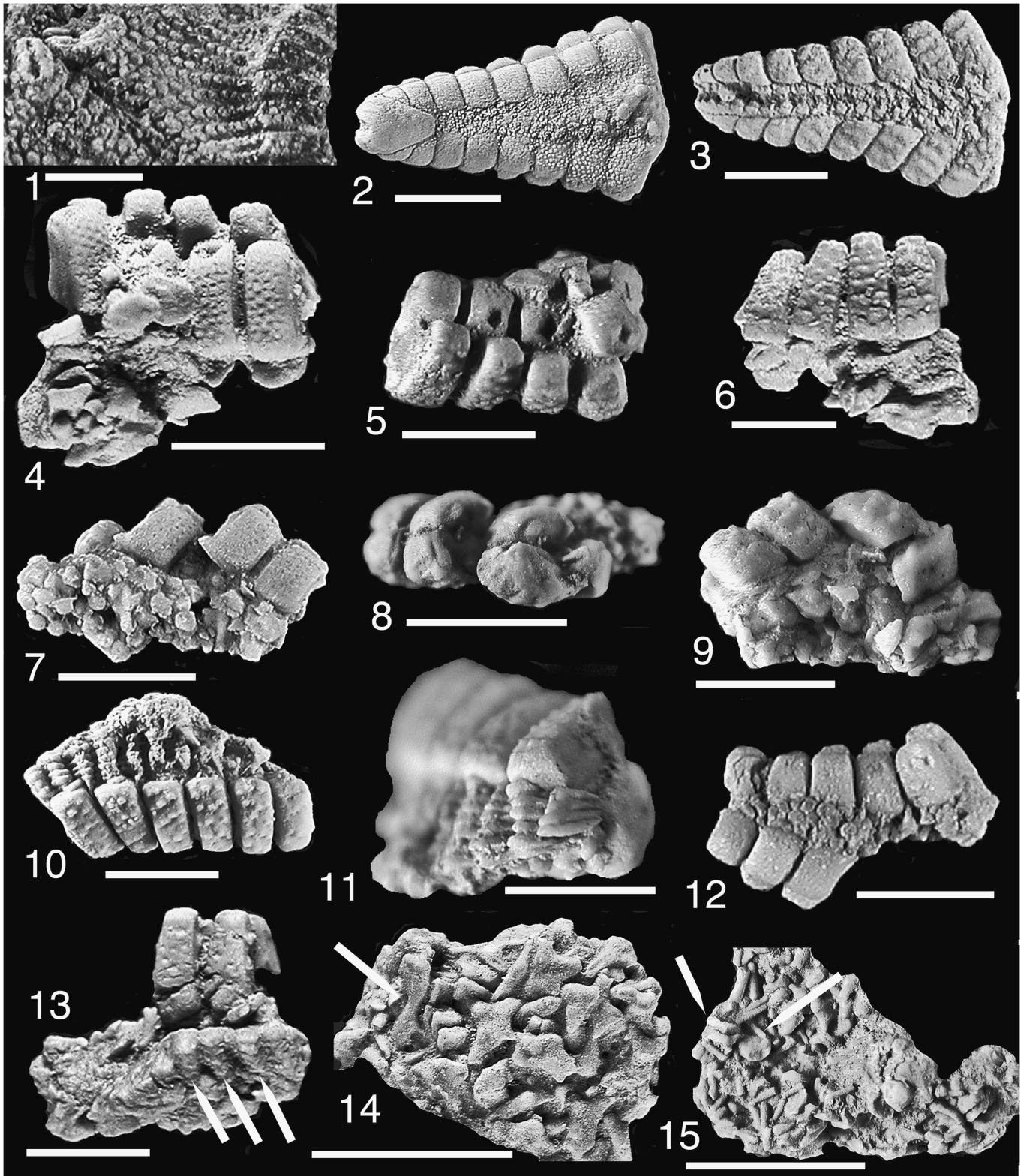
Actinal fields large, two ossicular series aligned with each inferomarginal, although arrangement locally somewhat irregular. Ten to 12 actinals in those inferomarginal series arising at interbrachial midline in specimens R ~ 18–20 mm. Actinal series diminishing uniformly in ossicular number, terminating at about seventh or eighth marginal, at which point inferomarginal series abut adambulacrals. Supplemental actinal series intercalated on disk away from inferomarginals. Actinals of each series aligned, successive series separated by a distinct but shallow groove; actinal grooves approximately, not sharply, aligned with inferomarginal fascioles and tissue gaps between successive adambulacrals. Actinals small, exposed surfaces subcircular, bearing one or more pustules; ossicles strongly overlapping, imbricated toward furrow. Actinal series aligned with interbrachial inferomarginals diverge toward adambulacrals leaving triangular area immediately distal to mouth-angle pair occupied by somewhat irregularly arranged actinals. Actinal ossicular surfaces bearing small spinelets or granules. Actinals adjacent to adambulacrals raised, bearing spinelets differentiated to form part of subadambulacrals spinelet series.

Adambulacrals approximately aligned with actinal rows. Adambulacrals broadly rectangular in outline, wider than long; proximal-adradial extremity angled toward mouth area. Tissue gaps between sequential adambulacrals well defined. Furrow accessory ridge V-shaped, directed toward furrow; furrow spine ridge clearly set off from subambulacrals spine bases and rows, these two or three in number. Abradial margin of adambulacrals overlapped by first actinal. Adambulacrals spinelets short, robust. Ambulacrals not exposed in available specimens.

Mouth-angle pair narrow, outline elliptical to weakly ovate, broader end of oval directed toward mouth area. Mouth-angle pair surface broadly arched, bearing spinelets similar to those of adambulacrals. First adambulacrals enlarged, abutting adradial lateral faces of mouth-angle pair, together forming robust, bud-like configuration. Actinal series nearly reaching distal edge of mouth-angle pair.

Figure 4. *Betelgeusia brezinai* n. gen. n. sp. (1–4) American Museum of Natural History, holotype AMNH-FI 111823; (1, 2) dorsal and ventral views, the primary ossicles partially obscured by accessories and foreign shelly material; (3) interbrachium toward top of (2); mouth frame to right, many accessories remaining, fasciolar channeling between actinal series is not closely aligned with marginal series (to left); (4) marginal form, fascioles, and accessories. (5, 6) Paratype AMNH-FI 111824; (5) ventral lateral view of arm, superomarginals granulate, inferomarginal with robust edging spinelets, accessories more nearly granular on ventral surface; edges of actinal rows, these aligned, separated by fasciolar grooving; (6) ventral view showing adambulacrals form, alignment of actinals, marginal form; comparatively few accessories remain. (7) Paratype AMNH-FI 111852, the only specimen derived from locality AMNH-FI 3418; MAO, form and positioning of actinals and marginals; see Fig. 5.1. (1, 2, 6, 7) Scale bars = 10.0 mm; (3–5) scale bars = 5.0 mm.





Etymology.—The species is named for Jamie Brezina, who discovered all but one of the available specimens, made them available for research, and donated them to the collections of the American Museum of Natural History.

Remarks.—Known species of *Betelgeusia* are generally similar in overall form, expressions of the abactinal, actinal, and, insofar as is known, ambulacral skeletons, including the mouth frame; they differ largely in marginal ossicular form and accessory development. *Betelgeusia brezinai* n. sp. is most similar to *B. exposita*, the latter known from a single incomplete specimen exposed in ventral view. The holotype of *B. exposita* is not significantly distorted or disrupted, and internal morphology is not available. Marginal ossicles of *B. brezinai* are more robust and fascioles less sharply defined than in *B. exposita*; although data are limited, actinals appear to be fewer in *B. exposita* and the first actinal does not overlap onto the adambulacral; the first adambulacral is proportionately smaller in *B. exposita*. Superomarginal accessories of *B. brezinai* are granules rather than spinelets as in *B. exposita*, and although exposure is limited, superomarginals do not appear to be inset in *B. exposita*. Marginals and proximal actinals of *B. orientalis* are similar to those of *B. exposita* rather than like those of *B. brezinai*, and MAO pair of *B. orientalis* are comparatively narrow and keel-like. Overall ossicular form of *B. reidi* is more delicate than that of *B. brezinai*, and spines of the former are much elongate and slender whereas those of *B. orientalis* are intermediate between those of *B. reidi* and *B. exposita*.

Superorder Forcipulatacea

Subfamily Pedicellasterinae? Perrier, 1884

Genus indeterminate species indeterminate

Fig. 5.14–5.15

Material.—Locality AMNH 3529, one small arm fragment, hypotype AMNH-FI 111853.

Remarks.—In a traditional arrangement of the Forcipulatacea (Spencer and Wright, 1966), the Pedicellasterinae is separated from the Asteroidea by absence of an adoral carina (the proximal-most adambulacrals abutting across the interbrachium immediately distal to the mouth-angle pair to form the ‘adoral carina’), and podial arrangement is biserial at least distally, rather than quadriserial throughout. The molecular phylogeny of Mah and Foltz (2011b) introduced significant changes to

forcipulate classification, the pedicellasterids separating into a more basal cluster, and a six-armed cluster that was imbedded among more derived forcipulates.

In the Pierre Shale fragment, the cross-shaped body wall ossicles with overlapping articular flanges are typical of Forcipulatacea. The shape of the single available ambulacral (Fig. 5.14), exposed in dorsal aspect, documents an arm that had only two rows of tube feet, a generalized configuration nevertheless typical of pedicellasterids in the traditional sense. Adambulacral form is typical of pedicellasterids, although not diagnostic. Familial assignment is traditional; available data are not sufficient for familial assignment following Mah and Foltz (2011b) or for generic and species assignments.

Diversification of the Paxillosida

The extant Radiasteridae based on morphologic data and represented by *Radiaster* is assigned to the order Paxillosida (Blake, 1987; Gale, 2011); in the literature, the Paxillosida traditionally has been envisioned as a major subdivision of the extant Asteroidea (Spencer and Wright, 1966), the order including the comparatively familiar fossil and extant *Luidia* Forbes, 1839 and *Astropecten* Gray, 1840. The molecular analysis of Mah and Foltz (2011a) recognized paxillosidan affinities for both the second known extant radiasterid genus, *Gephyreaster*, and *Pseudarchaster* Sladen, 1889, the latter traditionally considered to be a goniasterid valvatidan rather than a paxillosidan (Spencer and Wright, 1966). Drawing on these results, *Radiaster* here is aligned with *Gephyreaster*, and together with *Pseudarchaster*, the three are accepted as a monophyletic paxillosidan cluster. Mah and Foltz (2011a) argued for a broadly sister-group status between the Paxillosida plus the Notomyotida (monofamilial, Benthopectinidae), and the bulk of the traditional Valvatida including the Goniasteridae plus many extant members of the Spinulosida sensu Spencer and Wright (1966). Goniasterids and *Pseudarchaster* are widely distributed in modern oceans, and in part because of a comparatively robust construction, goniasterids predominate in the Cretaceous chalk asteroid faunas of Europe.

Although a number of Triassic crown-group asteroids are known, the Paxillosida has not been recorded from pre-Jurassic rocks (Gale, 2011, familial summary, p. 57) whereas Hess (1987, p. 907) found that the paxillosidan astropectinids radiated in the Middle Jurassic. Two Jurassic astropectinids have

Figure 5. (1–13) *Betelgeusia brezinai* n. gen. n. sp. (1) Paratype AMNH-FI 111852, disk in ventral aspect, aligned series of imbricate actinals separating two mouth angle ossicle (MAO) pairs (upper left) from inferomarginal series (far right); compare (10, 11). (2, 3) Paratype AMNH-FI 111825, arm tip in dorsal and ventral aspect; (2) the terminal is large, as is common among paxillosidans (including the Radiasteridae) with attenuated arm tips; (3) arm tip upturned as is common in life, an orientation enabling extension of sensory distal tube feet into the environment; marginals with aligned, transverse accessory pustules; marginals about spinose adambulacrals. (4–6) Paratype AMNH-FI 111826, marginal series and associated ossicles in dorsal, lateral, and ventral views; (4) ossicular debris including few abactinals and actinals that were displaced dorsally; (5) angular openings at abradial edge of superomarginals suggest pedicellariae openings, these otherwise unknown among radiasterids; (6) inferomarginal pustule configuration and a few remaining accessories; actinals largely disrupted. (7–9) Paratype AMNH-FI 111827; (7) superomarginals and displaced small paxilliform abactinals; (8) both marginal series, lateral surfaces showing fasciolar ridges; (9) inferomarginals above with spinelet pustules; displaced actinals below. (10, 11) Paratype AMNH-FI 111828, actinal and marginal series in ventral and inclined ventral views; the strongly imbricating and aligned actinals are characteristic of radiasterids, here potentially partially displaced taphonomically, but of overall orientation likely similar to those assumed during normal body flexure. (12) Paratype AMNH 111829, dorsal aspect near juncture of arm and disk, compare (1); superomarginal form, inferomarginals extending laterally beyond superomarginals; abactinal form. (13) Paratype AMNH-FI 111830, fragment in ventral aspect, shingled actinal rows (arrows) extend adradially from two inferomarginals. (14, 15) Pedicellasterinae? gen. indet. sp. indet., figured specimen AMNH-FI 111853, two views of the single available fragment; (14) dorsal ossicular views, cross-shaped body-wall ossicles are characteristic of forcipulates; a single ambulacral (arrow) is comparatively large, the figure ‘8’ or wasp-shape indicates a single row of podia rather than offset podial series of the Asteriidae; (15) dominantly ventral ossicular views, adambulacral (arrows) form is consistent with a pedicellasterid assignment. (1–13) Scale bars = 1.0 mm; (14, 15) scale bars = 2.0 mm.

been recognized, the relatively species-rich *Pentasteria* Valette, 1929 and monospecific *Advenaster* Hess, 1955. *Pentasteria* has been discussed by a number of authors, most notably by H. Hess, whose many papers provide perspective on both this genus and *Advenaster* (Hess, 1955, 1960a, 1960b, 1968, 1970, 1972, 1987; Enay and Hess, 1970). Another Jurassic genus, *Archastropecten* Hess, 1955, was later relegated to a subgeneric status within *Pentasteria* (Hess, 1960a).

Indiaster, sourced from Pachham Island (Kutch, Gujarat, India), was based on two specimens and a fragment thought derived from one of the larger specimens. The specimens unfortunately “are not traceable” and “probably misplaced” (personal communication, D. Srivastava, 2009), and available morphologic data are limited. Published photographs of Rao show both surfaces but only a single surface of each specimen, that in ventral aspect later reproduced by Spencer and Wright (1966, fig. 56.2). Five ossicular outline drawings accompanied the original photographs. The specimens appear abraded, limiting potential information. Specimen sizes appear to approximate those of *Betelgeusia brezinai*. When described, *Indiaster* was assigned to the Goniasteridae whereas here, following Blake and Reboul (2011), it is transferred to the Radiasteridae.

Betelgeusia currently is known only from Cretaceous occurrences. The type species, *B. reidi*, is represented by many specimens from several formations of the complex middle Cretaceous (Albian, Cenomanian) of Texas; *B. exposita* is known from a single incomplete Late Cretaceous (Maastrichtian) specimen from Europe; and *B. orientalis* is known from numerous Early Cretaceous (Barremian) specimens from Morocco.

Overall form and ossicular morphologies of Mesozoic fossils together with those of extant astropectinids and pseudarchasterids (Fisher, 1911, 1919; Hess, 1955, 1968, 1972, 1987; Blake and Jagt, 2005; Blake and Reboul, 2011) suggest a hypothetical configuration for a primordial paxillosidan species, although no species is considered adequately documented as to serve as an outgroup exemplar for phylogenetic analyses. The posited basal paxillosidan species would have been low-arched with a relatively large disk, broadly curved interbrachia, and triangular, comparatively abruptly tapering arms. A differentiated dorsal midarm series of abactinals together with a differentiated ring or primary cirlet of dorsal disk ossicles are typical of most crown-group asteroid clades, but lacking from radiasterids and astropectinids, and generally only weakly differentiated in *Pseudarchaster*. Interpretation of carinal or primary cirlet presence in fossils and even some modern specimens can be difficult because specimen symmetry and sediment compaction can elevate the midarm series as to suggest carinals, and the eye can interpret disk ossicles as concentric in arrangement, suggesting a cirlet. Accepting the Paxillosida as a sister group of a part of the terminologically traditional Valvatida (Mah and Foltz, 2011a), abactinal differentiation was likely plesiomorphic within early paxillosidans, and retained in *Pseudarchaster*.

In the hypothetical basal paxillosidan, two robust, similar, abutted marginal series would have defined the ambitus and separated an abactinal field of uniform, relatively robust paxilliform abactinals from the more or less enlarged field of actinals, these abutted and aligned in series. Except for

B. reidi, available data for ambulacral and adambulacral internal morphology of Mesozoic radiasterids are limited, but adambulacral likely were rectangular in the basal paxillosidan and bore well-developed spines; granules or small spinelets were common on other ossicles. If pedicellariae were differentiated, blades were simple and spinelet-like.

The strong but generically distinctive marginal differentiation seen in *Astropecten* and *Luidia* did not occur in Jurassic *Indiaster* or *Pentasteria* whereas complex marginals, ambulacrals, and delicate paxillae suggestive of *Astropecten* occur in middle Cretaceous *B. reidi* but not in younger Cretaceous *B. brezinai* (Blake and Reid, 1998, fig. 8.17; Fig. 5.7 herein), the latter then an inferred more stemward configuration surviving in similar form today not only in *Pseudarchaster* but also in some astropectinids (*Plutonaster* Sladen, 1889; *Tethyaster* Sladen, 1889), goniasterids (*Mediaster* Stimpson, 1857; *Ceramaster* Verrill, 1899), and other valvatidan families (Ganeriidae, Odontasteridae). Expressions of *B. reidi* might be either basal among those paxillosidans that led to *Astropecten* and *Luidia*, or homoplastic. Strongly imbricate actinals of *Betelgeusia* (Fig. 5.10, 5.11) and *Radiaster* are not known among the Jurassic paxillosidans.

Expression of the termini of the tube feet might have been emergent within early paxillosidans, but fossilized tube feet are unavailable. Traditionally, termini of the tube feet of all taxa assigned to the Paxillosida are pointed whereas in the remainder of the crown-group Asteroidea, termini are expanded and suckered or disk-like; expressions, however, likely were more complex than the simple two-fold terminology would suggest (Vickery and McClintock, 2000; Santos et al., 2005). Unlike other paxillosidans, *Gephyreaster*, *Radiaster*, and *Pseudarchaster* have disk-like tube feet. In separating *Radiaster* (= *Mimaster* Sladen, 1882) from the astropectinids *Plutonaster* and *Leptychaster* Smith, 1876, the essential difference in the structure of the tube feet was thought to be “a more important barrier [to combining taxa] than is commonly supposed,” the large sucking disks of *Pseudarchaster* found to ally this genus with *Radiaster* and *Gephyreaster* (Fisher, 1911, p. 175). It was, however, also pointed out, “In passing,” that presence of “conical tube feet with a little button (as in the Astropectinidae) at the tip” occur in *Radiaster cognatus* (Fisher, 1911, p. 175). However, as discussed in some detail by Clark (1962, p. 11), even familial assignment of this species and genus (under *Mimastrella* Fisher, 1916) is unclear, Clark including *Mimastrella* in the Astropectinidae but also finding aspects that “strongly suggest an affinity with the family Solasteridae.” Regardless of ultimate species disposition, complimenting Fisher’s observation on tube feet of ‘*R. cognatus*,’ occurrence of expanded termini were reported in the early ontogeny of a species of *Astropecten* (Oguro et al., 1976). Modern expressions together with the phylogeny of Mah and Foltz (2011a) and the complexities noted by Vickery and McClintock (2000) and Santos et al. (2005) suggest an emergent status for tube foot differentiation in early paxillosidans, rather than a single simple ordinal-level apomorphy.

Actinal ossicular alignment immediately adjacent to the mouth frame of *B. brezinai* appears to have been somewhat irregular, reminiscent of corresponding expressions in both Triassic *Trichasteropsis* Eck, 1879 (Blake and Hagdorn, 2003)

and a species of *Pycinaster* Spencer, 1907 (Blake et al., 2015). Abundant actinals, uncommon among Paleozoic asteroids, might have arisen as a space-filling device for disk enlargement, the ossicles only later and homoplastically becoming more strongly aligned, perhaps to form efficient water channels or to enhance body flexibility (Blake and Hotchkiss, 2004).

Taxonomic changes

A new asteroid species, *Betelgeusia brezinai* (Radiasteridae), is described; four species of *Betelgeusia*, all Cretaceous in age, now are known. A second radiasterid genus, *Indiaster*, is Jurassic in age. Fossil radiasterids have been recorded from Africa, western Europe, India, and North America. A single fragment is assigned to the forcipulate Pedicellasterinae. Data are insufficient for formal phylogenetic analysis but enough is known to reconstruct many likely aspects of morphology of the ancestral species of Paxillosoida.

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