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Comments on "The phylogeny of post-Palaeozoic Asteroidea (Neoasteroidea, Echinodermata)" by A.S. Gale and perspectives on the systematics of the Asteroidea

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Abstract

A new, morphologically based classification of extant asteroids with comments on select fossils was published by A.S. Gale. Research approaches used limited sampling, and much literature treatment is not accurate and therefore misleading. We review these concerns, seeking to clarify argumentation on differing interpretations.

Key words: Neoasteroidea, Echinodermata

Introduction and background

Gale (2011a, 2013) provided a revised classification and phylogeny of higher taxa of crown-group members of the class Asteroidea (Echinodermata). The author's cladistic analysis used an ingroup of 24 extant genera argued to represent 24 families, together with a late Paleozoic outgroup species, *Calliasterella mira* (Trautschold). Our views on the current status of crown-group asteroid classification and phylogeny were published in Mah and Blake (2012). The two interpretations differ primarily in that the former emphasizes newly delineated aspects of ossicular morphology whereas the latter integrates ongoing molecular results with more traditional morphologic interpretations. Conflicting interpretations and challenges to earlier interpretations of Blake were published in Gale (2011a, 2013). For clarification for future researchers, our perspectives on many of these issues are revisited here, including both concerns over research approaches of Gale and his interpretations of earlier papers. Original research is not our intent nor do we review in detail results of earlier research because such review of necessity would be incomplete and therefore misleading; the concerned reader is referred to earlier papers.

The development of taxonomic arrangement of extant asteroids was summarized by Spencer and Wright (1966) and more recently by Mah and Blake (2012). Taxonomy traditionally was morphologically based and developed largely during a period of intensive monographic study during the late 19th and early 20th centuries by a comparatively small number of researchers. Although uncertainties emerged, authors consistently separated the forcipulate groups (essentially, the zoroasterids, asteriids, and brisingids) from the remainder of the living asteroids (e.g. Fisher, 1911: 4).

The early monographers focused on arrangement and ranking of taxa. Phylogenetic interpretations were published (e.g., Döderlein 1920), but phylogenetic debate only began in earnest with the discussions among Bather (1921a, b; 1923), MacBride (1921, 1923a, b), Mortensen (1922, 1923), and Gemmill (1923). In brief, emphasizing select aspects of morphology, Mortensen found paxillosidans (e.g. *Astropecten* Gray, *Luidia* Forbes) to be primitive whereas MacBride argued that the pertinent morphologic expressions reflected later adaptations to environment; he did not designate a basal taxon. Reflecting the potential for fundamental differences of view in the interpretation of crown-group phylogeny, Blake (e.g. 1981a, 1987, 1989, 1990) developed the thinking of MacBride whereas Gale (1987, 2011a, 2013) followed the interpretations of Mortensen. Other phylogenetic perspectives have been published, some noted below, see also Mah and Blake (2012).

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Methods, Underlying Assumptions, and Outgroup Choice

Assumed monophyly. Sampling of Gale (2011a) was narrowly limited: this author (p. 49) chose "24 extant species that have traditionally been classified in as many families." It was further judged (p. 6) that "These species encompass a large portion of the morphological range of post-Palaeozoic asteroids." Gale (2011a) did not explain how he decided his select species were sufficient for each family, how the familial sampling was inferred to sufficiently explore the diverse extant fauna (Mah and Blake, 2012, recognized 37 extant families), nor how he decided that phylogenetic changes over hundreds of millions of years, including diversification of the crown group, were minor enough to suggest that a relatively few extant exemplars can sample a "large portion of the post-Palaeozoic" variation (p. 49), a conclusion at odds with his uncertainties about positioning of Triassic *Trichastopsis*, *Noriaster*, and *Migmaster*, see below. Selection of familial exemplars based on "traditional" assignments assumes familial monophyly. Survey of larger and even many smaller traditional families, however, demonstrates a broad range of variation that is not documented by a single representative. Basal taxa can be expected to be very different from the averaging of tradition.

In his review of Blake (1987), Gale (2011a: 49) opined "Blake effectively presumed the monophyly of major taxonomic groups and analyzed these without reference to any outgroup." Both portions of this statement are incorrect. Survey of all available specimens in many museums in the United States, Europe, and Australia led to a series of publications exploring affinities of taxa (Blake 1972; 1978; 1979; 1980; 1981b; 1982); museum survey syntheses, not assumptions of monophyly, formed the basis of Blake (1987). That the publication series of Blake remains incomplete, however, is implicit in treatment of *Goniaster* Agassiz in Blake and Portell (2011). Even if the misinterpretations of Gale (2011a) on an assumption of monophyly by Blake (1987) were correct, it would not validate following this approach in his own work. See discussion of outgroup selection below.

Support, Depth of Taxon Sampling, & Interpretation. Here, we address one of the primary shortcomings of Gale (2011a), which pertains to the use of exemplars that have insufficiently sampled asteroid diversity and represent choices that ignore taxa that have been historically relevant to phylogenetic discussions. Poor taxon sampling affects phylogenetic accuracy which undermines confidence in the classification (e.g. Zwicki & Hillis 2002). Gale's morphological dataset addresses only extant taxa (except outgroup *Calliasterella* Schuchert) and presents newly named clades based on his analysis of 24 exemplar species and 128 characters.

Gale's (2011a) character listing is extensive, but taxon sampling has a much more significant impact on the accuracy of the final tree. Small-scale exemplar-based studies are appropriate for making broader inference of larger taxonomic datasets (as discussed in Brusatte 2010, Prendini 2001, Yeates 1995), although large sample sizes become computationally difficult. Small taxon samples introduce significant difficulties (Predini 2001: 295): "As widely recognized, exemplar selection may seriously affect the outcome of phylogenetic analyses, because the derived character states of many extant species reduce the utility of these species as accurate estimators of the groundplans of their higher taxa (Donoghue *et al.*, 1989; Lecointre *et al.*, 1993; Adachi and Hasegawa, 1994; Doyle *et al.*, 1994)." Several important considerations for exemplar-based approaches were summarized in Brusatte (2010), Predini (2001) and Yeates (1995). Among the most significant considerations were the requirement that selected species occupy basal positions representing the greatest number of plesiomorphic character states with relatively short branch lengths thus allowing morphology to be most informative relative to the outgroup taxa. These authors also emphasized the need for an appropriate number of taxa in order to capture maximal diversity. Several taxa within Gale's (2011a) matrix are interpreted as derived based on independent phylogenetic surveys suggesting that taxonomic sampling is likely to have seriously affected the resultant tree topology. For example, within the Forcipulatacea, Mah (1998) presented a morphological phylogeny of the Brisingida, supporting *Odinella* Fisher, *Brisingaster* de Loriol, and *Novodinia* Dartnall, Pawson, Pope, and Smith as basal within the group whereas derived brisingid genera and species *Freyella elegans* (Verrill) and *Brisinga costata* Verrill were selected by Gale (2011a). Similarly, *Myxoderma* is basal within the Zoroasteridae whereas derived *Zoroaster* Thomson was selected (Mah 2007). Villier *et al.* (2004) provided preliminary phylogeny of the Pterasteridae supporting *Euretaster* Fisher and/or *Diplopteraster* Verrill as basal or sister taxa to more derived pterasterids, including *Pteraster* Müller and Troschel, the exemplar of Gale (2011a). Exemplar choice of Gale (2011a) appears to be of the commonly encountered rather than the potentially basal.

Emphasizing the small overall sampling of Gale (2011a), there is significant disparity between the taxa coded and included in analysis and those quoted as having been available for study (tab. 1), including *Caymanostella*

Belyaev (Caymanostellidae), *Cheiraster* Studer (Benthopectinidae), *Diplopteraster* (Pterasteridae), *Korethraster* Thomson (Korethrasteridae), *Myxoderma* Fisher (Zoroasteridae), *Peribolaster* Sladen (Korethrasteridae), *Proserpinaster* Fell (Astropectinidae), and *Pseudarchaster* Sladen (Pseudarchasteridae). *Pseudarchaster* is particularly important because of its taxonomic instability (e.g., Sladen 1889, Fisher 1911, McKnight & H.E.S. Clark 1996) and emerging taxonomic position (Mah & Foltz 2011a). Blake (1987) separated *Pseudarchaster* from the Goniasteridae as the sister taxon to the other Valvatida and later Blake & Jagt (2005) followed Sladen (1889) in recognizing a subfamily Pseudarchasterinae, including extended discussion of the subfamilial concept. Gale (2011a) correctly pointed out that placement of *Pseudarchaster* Sladen by Blake (1987) constructed a paraphyletic Goniasteridae; however, in spite of the challenge and although a species of *Pseudarchaster* was included in his taxonomic listing, Gale (2011a, tab. 1), positioning of the genus and character significance were not tested (text-fig. 20: 49). It was left to Mah and Foltz (2011a) to transfer *Pseudarchaster* to the Paxillosida. Transfer is important in part because Gale (2011a) thought paxillosidans lack suckered tube feet; these are present in both *Pseudarchaster* and *Radiaster*, the latter coded by Gale (2011a) as having pointed tube feet. Gale (2013: 8r) retained the earlier evaluation.

Certain family-level taxa found to be phylogenetically important in other studies (e.g. Blake 1987, Mah and Foltz 2011a) were not included by Gale (1987, 2011a). For example, Gale (1987) indicated that the Asterinidae and Ganeriidae were treated as identical, and Gale (2011a) in a sense remained consistent with this perspective in including *Asterina gibbosa* (Pennant) (Asterinidae) but no ganeriids, or other potentially related taxa such as chaetasterids.

We realize that much of our criticism in this section is based on theoretical grounds addressing unsampled diversity but taxon sampling and its effect of different tree topologies, tree lengths, etc. has long been a factor relevant to phylogenetic accuracy (e.g., Zwicki & Hillis 2002). Although it was not within the scope of our review to completely reconstruct or comprehensively reanalyze Gale's (2011) tree, any opportunity or need to re-analyze these characters has essentially been rendered moot, as the full morphological data matrix was incomplete and has not been published or provided as an addendum to the published data. The combination of incomplete data matrix and subjective inclusion of taxa included in the study presents a possible bias which could affect the accuracy of the classification.

Outgroup Selection & Consideration of *Calliasterella*. Both explicitly and implicitly, many authors have agreed that the fossil record provides limited and uncertain evidence of the phylogenetic connection between Paleozoic and Mesozoic asteroids (Ubaghs 1953; Spencer and Wright 1966; Blake 1987; Blake and Hagdorn 2003; Gale 1987, 2011a). Although disagreeing on many issues, Gale and Blake agreed in selecting the nominal genus *Calliasterella* as the best-available candidate for interpretation of transitional events. (*Calliasterella* is nominal because the type species, *Calliasterella mira*, the focus of Gale, is distinctive in certain expressions from *Calliasterella americana* Kesling and Strimple, the focus of Blake. Revision is needed; however, the two species are similar enough in certain aspects to be treated in common here.)

Reasoning behind the selection of *Calliasterella* differed significantly between the two authors. In describing his choice of an outgroup taxon, Gale (2011a: 6) stated that "The Late Carboniferous *Calliasterella mira* was selected as an outgroup, because this is one of the few Palaeozoic asteroids for which almost all ossicle types can be examined in a dissociated state and thus can be compared individually with those of extant taxa." Gale (2011a) did not provide listing of other fossils among which *C. mira* is "one of the few," how their candidacy was rejected, or why "the few" were not used to test conclusions based on *C. mira*. Justification based on quality of preservation does not help to establish an exemplar as a member of an ancestral lineage nor as the appropriate sister taxon. Other candidates are available; Blake and Rozhnov (2007), for example, compared the articular faceting of Ordovician *Urasterella* McCoy adambulacral ossicles with that of extant *Echinaster* Müller and Troschel; the primary purpose of the study was analysis of life mode rather than phylogeny, but the similarities between the ancient and extant genera implicitly ask whether at least a part of the adambulacral morphology stressed by Gale ranges from the Ordovician. As a second example, Branstrator (1972) was so impressed with similarities between the Ordovician families Mesopalaeasteridae and Promopalaeasteridae and extant asteroids that he assigned the ancient families to the suborder of Asteriadina of the Forcipulatida. As implicit in Spencer and Wright (1966, fig. 38), perhaps crown-group diversification took place long before the time of *C. mira*.

Gale (2011a: 6) opined that "Blake (1987) based the polarity of his cladogram upon the supposition that the Carboniferous *Calliasterella* was a member of the extant superorder Forcipulatacea, following the interpretation of

Downey (1970) that *Calliasterella mira* fell close to the extant forcipulatid Zoroasteridae." Gale reiterated his view in arguing that Downey's placement of *C. mira* close to the Zoroasteridae "was the basis of the polarity determination in Blake's 1987 cladogram" (p. 76), and more recently, Gale (2013: fig. 1.1) suggested that the basal position of the Forcipulatida of Blake (1987) "is an assumption, and is not based on reference to an outgroup." Gale (2013: 6) suggested that Downey's noting similarities between *C. mira* and the zoroasterid *Doraster* "presumably prompted Blake's (1987) argument for the basal position of the Forcipulatida." The suggestions of Gale (2011a, 2013) are simply wrong. The character expressions behind selection of *C. americana* as the outgroup were identified (Blake, 1987: 500–501), revisited in Blake *et al.* (2000), Blake & Hagdorn (2003), and discussed in more detail in Blake (2000: 320). The outgroup taxon in Blake & Hagdorn (2003) was an Ordovican somasteroid; forcipulates and non-forcipulates emerged as the two branches of crown-group asteroids. Gale (2011a, 2013) reproduced cladograms of Blake but did not explain how he thought these were generated without use of an outgroup.

Similarities between calliasterellids and zoroasterids have long been recognized. Downey (1970: 2–4) listed many, and she cited observations in Thomson (1873), Schöndorf (1909), and Kesling and Strimple (1966). Since Downey (1970) and in addition to papers of Blake, Mah (2007) compared Paleozoic fossils with zoroasterids, and Gale (2011a: 83) also cited common expressions. In challenging the interpretation of Downey (1970), Gale (2011a: 83) acknowledged that *C. mira* shows various ambulacral and adambulacral characters found in the crown group but that "the mouth frame is primitive ... (T)he striking similarity between the zoroasterid *Doraster constellatus* and *Calliasterella mira* is therefore convergent." A similar viewpoint was repeated in Gale (2013: 6). "Primitive" is in essence a synonym of plesiomorphic, a status that does not affect the implications of similarities cited by Downey (1970) and others as potential apomorphies of a possible *Calliasterella*-zoroasterid lineage. Interpretation of ambulacral and mouth frame morphology as argued by Gale (2011a) implicitly indicates a need for rigorous and comprehensive morphometric treatment.

The many morphologic similarities between *Calliasterella* and *Zoroaster* yielded the cladogram of Blake (1987: fig. 10), in which *Calliasterella* and Triassic *Trichasteropsis* are basal to a dichotomy between surviving forcipulates and the remainder of the asteroids. The cladogram perhaps led to the interpretation of Gale (2011a: 70) that "Blake identified the Forcipulatida as the most plesiomorphic group"; a similar perspective was offered again in Gale (2013: 4). Instead, however, differentiation of the crown group was interpreted as representing a dichotomous branching of unknown ancestry between the forcipulates and the remainder of the surviving asteroids (Blake, 1987: 5151; 1989: 2082; Blake and Hagdorn, 2003: 50L5). The cladogram of Blake (1987) was supplemented by analyses of Blake *et al.* (2000) and Blake and Hagdorn (2003) in which separate branches emerged. *Calliasterella* was tentatively interpreted to be of forcipulatacean affinities in Blake (1987: 515), an interpretation dropped in Blake & Hagdorn (2003). Separation of forcipulates from the remainder of surviving asteroids was largely in accord with the taxonomic arrangements of monographers of the late19th and early 20th centuries.

The three papers (Blake 1987; Blake *et al.* 2000; Blake and Hagdorn 2003) provide phylogenetic reconstructions from somewhat differing perspectives. The character suite of these studies provided the basis for recognition of the subclass Ambuloasteroidea, which included both Paleozoic fossils and the crown group. The hypothesis of the Ambuloasteroidea exploited readily observable morphologic expressions and encompasses what can be determined of comparative life modes. The concept of the Ambuloasteroidea was not treated by Gale (2011a, 2013) nor did this author provide perspective of his own interpretations through inclusion of *Trichasteropsis* or other fossil asteroids in the ingroup of his own phylogenetic analysis; without such inclusion, direct comparisons of results are not possible. A useful concept proposed by Gale (1987), the Neoasteroidea, was retained for extant asteroids in Blake and Hagdorn (2003).

Comparative life modes. Gale (2011a) stressed putative morphologic similarities between *Calliasterella* and *Luidia ciliaris* in his phylogenetic reconstruction. Interpretation of the ecology of extinct organims, especially those of generalists such as asteroids, is problematic; nevertheless, comparative morphology of *Calliasterella* and *L. ciliaris* documents significant differences. *Luidia* and many other extant paxillosidans are at least semi-infaunal; water-current passageways occur between the larger ossicles, the currents protected by spinelet tufts. Life habits of extinct *C. mira* naturally are uncertain, but *Zoroaster* and *Calliasterella* share small disks, columnar arms, and relatively smooth body surfaces; no similar extant species known to us is infaunal. If the phylogeny of Gale (2011a) is accepted, paxillosidan infaunal adaptations must have emerged after the evolutionary grade of *C. mira*, that species retaining an ancestral configuration and epifaunal behavior. This implication is counter to the conclusion of Gale (2011a: 77), that the common ancestor of the crown group probably was infaunal.

Select concerns

Marginal ossicles. Differentiated body frame ossicles, typically termed "marginals," occur in some or most members of different echinoderm groups, including cyclocystoids, edrioasteroids, somasteroids, ophiuroids, and asteroids. Commonality of derivation (i.e. homology) of "marginals" among groups has received some discussion (e.g. Shackleton, 2005; Blake, 2013). Ossicles labeled "marginals" are not homologous among all groups where the term has been used.

Based on molecular work, Janies *et al.* (2011) posited the Pterasteridae as basal within surviving asteroids. Gale (2011a) coded two rows of marginals for this family, although we have not been able to identify these series in any available representative. Body wall ossicles in the family typically are uniform and proportionately small, and verification of status is difficult.

Within living asteroids, ossicles of most series (e.g. marginals, ambulacrals) are readily recognized, and identification seldom has been a serious issue. Nevertheless, differentiation of marginal ossicles was recognized to be varied enough (e.g. *Astropecten* vs. *Asterias*) to be addressed by Verrill (1914: 29), who in focusing on the Asteriidae, noted that the inferomarginal row reaches the terminal whereas adjacent ventral series rarely do. Blake (1978: 241) broadened the perspective of Verrill (1914) in arguing that "…almost invariably in the sea-stars a double series of ossicles arises near the actinal lateral margin of each side of the terminal, and that this series can be traced along the arm, recognizable through position and alignment, size or morphology, or some combination of these criteria." Identification of the marginal series was important to the phylogeny of Blake (1987), in which only a single marginal series was recognized in the Zoroasteridae. Expression is most readily observed in those zoroasterids with proportionally large marginal ossicles, including *Zoroaster* itself. Concerns of Verrill appear to have been limited to lower taxonomic levels because his discussions of *Zoroaster* (1914: 27–30) did not address marginal row number, although text seems to imply an interpretation of presence of two rows. Discussions of Verrill as well as some of other earlier systematists, including W.K. Fisher, suggest presence of two rows among living asteroids was simply assumed; it is differences among Paleozoic asteroids that raised the question of expression in basal crown-group asteroid(s). Reasoning of Blake (1978) was followed by Mooi and David (2000) and by Mah (2006, 2007), the latter for the aberrant asterozoan *Xyloplax* as well as for the Zoroasteridae.

Sumida *et al.* (2001) provided a post-settlement *Zoroaster fulgens* displaying one clear marginal series in several different individuals of different sizes. Marginal plate terminology applied to these images was not developed with an explicit homology, i.e., the authors assumed *Z. fulgens* had two series of marginal plates (Sumida pers. comm. to Mah) as assumed by Gale (2011a: 100). Although we find Gale's so-called inferomarginal ossicle difficult to interpret from Sumida's figure, we have further examined small specimens of *Z. fulgens* (including USNM E18539, arm radius=8 mm) that show features similar to those in Sumida's (2001: fig. 11). The short series of ossicles extends from the interradius, ossicles sequentially smaller and the series "pinching off" midway along the arm, indicating that these plates are actinals rather than inferomarginals, which originate next to the terminals. Another figured example of *Zoroaster* configuration as well as interpretation of marginal series expression is provided in Blake and Elliott (2003).

Presence of a single marginal row was important to the formulation of the phylogeny of Gale (2011a) in that only a single row occurs in his outgroup genus *Calliasterella*, and presence of only a single row was posited for the paxillosidan species *Luidia ciliaris* (p. 11), which this author stressed in his comparisons with *Calliasterella.* Gale (2011a) did not discuss interpretation of Döderlein (1920: 200, 218, pls. 18, 19), who recognized two rows in *L. ciliaris*, nor did he accomodate interpretation of this species with another species of the genus that he accepted as having two rows of marginals (p. 70). Although not explicit, all species of *Luidia* were interpreted as having two marginal rows in Blake (1987), and we retain Döderlein's (1920) reasoning and interpretation.

Gale (2011a: 96, 98, 100) suggested a "Forcipulatid Plating Rule" (FPR) that was offered as a tool for the identification of marginal-series ossicles in the forcipulates. The FPR was based on "arrangement and imbrication pattern," but rows termed "marginal" were not required to reach the terminal in this formulation. Diverse diagrammed forcipulate examples suggested to exhibit two rows of marginals included *Zoroaster* (fig. 36), although earlier in the same paper, Gale (2011a: 11; table 6, p. 50) identified only a single marginal series in this genus. Both terminologically ("Forcipulatid Plating Rule") and in discussions, Gale (2011a) applied the FPR only to forcipulates. There is no suggestion as to phylogenetic positioning of the putative FPR apomorphy, but the rule is not suggested to apply to other crown group asteroids, which indicates it is a character independent of series origin behind the terminal (Verrill 1914; Blake 1978).

The Absence of the Brachiolaria Larvae. Gale (2011a) embraced a major argument of Mortensen (1921), that absence of brachiolarian larvae from the Paxillosida is basal or "primitive"; McEdward and Janies (1993) was cited as a later source for this reasoning. Publications unavailable at the time of Mortensen (1921) argued instead that absence is likely derived. Gale (2011a: 75) incorrectly cited McEdward and Janies (1993) as an advocate of the brachiolaria as the "primitive condition."; McEdward and Janies (1993: 265) argued that absence represented derived loss in the Paxillosida relative to the ancestral asteroid life cycle. Following publication of two early molecular studies on asteroid phylogeny favoring a basal positioning for paxillosidans (LaFay *et al.* 1995; Wada *et al.* 1996), McEdward and Miner (2001) took a more cautious approach, suggesting other hypotheses including the possibility that the ancestral life cycle could have consisted of both bipinnaria and brachiolaria stages with subsequent loss.

The original argument by Mortensen (1921) can be applied to other taxa. For example, McEdward and Janies (1993) introduced the concept of a mesogen, a novel larval type occurring in multiple species of *Pteraster* [Pterasteridae; Velatida sensu Mah & Blake (2012)]. Recent phylogenetic arguments supporting velatidans in stemward positions (e.g. Janies et al 2011; Mah and Foltz 2011b) suggest the mesogen might be basal, and presence of a brachiolaria becomes a separate issue.

Strenger and Erber (1983) and Erber (1985) argued that reduced brachiolarian larval stages can be recognized in both astropectinid and luidiid paxillosidans. Work of these authors calls for further research on early development, which has been studied in only few of the known paxillosidan genera (*Astropecten* and the very similar *Ctenopleura*; *Luidia*). All three are shallower water genera found in sandy and muddy habitats potentially less suitable for the brachiolaria (MacBride, 1921). Such settings likely would be conducive to the brachiolarian reduction identified in these papers; a test for such a possibility would be the study of development in paxillosidans that live in deeper, quiet settings on stable substrates.

Phylogenetic interpretations. Arguments by Gale (1987, 2011a) have consistently favored a basal or stemward position for the Paxillosida among post-Paleozoic, crown-group asteroids. This interpretation is not supported by a number of other molecular and morphological phylogenetic studies. Congruence or agreement among independent data sets is essential for the reconciliation of phylogenetic hypotheses and tree topologies (e.g. Eernisse and Kluge, 1993, Patterson *et al.*, 1993) including those based on morphology and those based on molecular analyses.

Among available evidence for phylogenetic hypotheses within the Asteroidea, molecular treatments by Knott & Wray (2000), Janies *et al.* (2011) and Mah and Foltz (2011a, 2011b) have shown greater overall agreement with fossil and morphological trees as presented by Blake (1987) and Blake and Hagdorn (2003) than those of Gale (1987, 2011a), including dichotomous separation of forcipulataceans from the remainder of the crown group as favored in the former, which contrasts with the recognition of a forcipulatacean clade embedded within a larger clade containing valvatidan taxa, all emerging from a basal Paxillosida, as favored by Gale. A critical shortcoming of Gale (2011a) was his very limited exemplar sampling. The extant asteroid fauna, including approximately 1900 species assigned to 36 families (Mah & Blake 2012); from this fauna, Gale (2011a) sampled 24 species, each assigned to a separate traditional family. Several families with phylogenetic importance, such as the Pedicellasteridae within the Forcipulatacea and at least eight families within the Valvatacea from Foltz and Mah (2011a,b) are not represented.

LaFay *et al.* (1995) and Wada *et al.*(1996) were cited as providing support for proposed phylogenetic interpretations by Gale (2011a), but these are among the earliest of molecular studies, and they are significantly undersampled for taxa and number of genes relative to more recent efforts; they have been superseded by the later work. Studies following this early period began to show patterns contrary to the Paxillosida-as-primitive notion. Matsubara *et al.* (2005) showed paxillosidans as derived relative to *Asterias, Pisaster*, and an echinoid+holothuroid outgroup**.** Other studies, with increasing more sampling, such as those of Knott and Wray (2000) and Matsubara *et al.* (2004) showed more ambiguous results casting doubt on the earlier conclusions.

Current studies in asteroid phylogeny have further broadened taxonomic sampling as well as the amount of sequence data used in estimation. Mah and Foltz (2011a, 2011b) reconstructed the phylogeny of the Valvatacea and the Forcipulatacea, the two most diverse groups of asteroids. Their results also included significant taxonomic representation from the Velatida. The Valvatacea, Forcipulatacea, and the Velatida represent three of the four major lineages within the modern Asteroidea. Only the Spinulosida was not included in their trees. The Mah and Foltz (2011a,b) trees are consistent with one another in that Velatida occurs stemward in both trees as the Valvatacea and Forcipulatacea were used as outgroups to one another. Further corroboration comes from Janies *et al.* (2011) in his effort to place *Xyloplax* among the Echinodermata. Their work used seven genes and places *Xyloplax* among the Asteroidea relative to Echinoidea, Holothuroidea, Ophiuroidea, and Crinoidea as variously placed sister taxa. Topology of the Asteroidea within Janies *et al.* (2011) is largely consistent with topologies observed by Mah and Foltz (2011a, 2011b); two echinasterids were included in this study, thereby representing the Spinulosida. Janies *et al.* (2011) presented a derived Paxillosida among the Valvatacea on a separate branch from the Forcipulatacea, all of which are subtended by the Velatida in a basal position on the tree relative to the outgroups.

Poorly sampled exemplar-based approaches are problematic for several reasons. Brusatte (2010) and Yeates (1995) have argued that inclusion of stemward or plesiomorphic taxa are more desirible for recovering phylogeny and providing phylogenetic signal than highly derived, apomorphic taxa. This is a criterion which has been applied to both molecular and morphological approaches. This can be observed when contrasting the use of *Astropecten irregularis* as an exemplar in Lafay *et al.* (1995) with the *Astropecten* global population phylogeographic study of Zulliger & Lessios (2010), the latter authors demonstrating that the species occupies a highly placed, recently derived branch tip, a positioning consistent with fossils of *Astropecten*. Similarly, the asteriid forcipulate *Asterias* was used by both Gale (2010) and LaFay *et al.* (1995), rather than a more stemward taxon, such as a pedicellasterid or a zoroasterid, which may have obscured the phylogenetic positioning as interpreted by prior workers.

It is important to note that these and other older molecular studies attempting to assess questions of divergence (i.e., "is the Paxillosida basal/primitive?) might have become obsolete as a result of recent phylogenetic data from Janies *et al.* (2011) and Mah and Foltz (2011a,b) indicating that the Velatida, including *Xyloplax*, pterasterids, korethrasterids, and myxasterids, represent a distinct branch apart from the other surviving crown-group lineages. If velatidans are a previously unrecognized primary lineage representing an early divergence from other extant asteroid lineages, then all exemplar-based studies that do not include velatidans (as listed above) fail to address the question of basal positioning within the crown-group Asteroidea.

Pedicellariae: Homology vs. Convergence. Gale (2011a) presented a novel grouping, the Tripedicellariae, which is a cluster that places a monophyletic Forcipulatida+*Echinaster* clade alongside several nominal taxa that have been historically placed in the Valvatida [e.g. *Acanthaster planci* (Linnaeus), *Protoreaster nodosus* (Linnaeus), *Nardoa variolata* (Retzius)]. The historical basis of classification of the Valvatida is both named for and defined by perceived homologies of pedicellariae morphology, which were argued as shared among these taxa. Gale's (2011a) topology represents a radical repositioning of these groups that finds no agreement with other phylogenetic data. Molecular studies by Mah and Foltz (2011a, b), Janies *et al.* (2011) and others (Yasuda *et al.* 2006; Matsubara *et al.* 2004; Knott & Wray 2000) as well as morphological studies by Blake (1987) have not recovered forcipulates as derived within a broader phylogeny of the Valvatacea. None of the pre-cladistic historical classicifications, such as those of Fisher (1911), Sladen (1889) or Perrier (1884, 1894), placed forcipulates within valvatidans.

Thus, it seems that the most likely explanation for Gale's (2011a) Tripedicellariae is to be found in his morphological interpretations and overdependence on a series of related but convergent characters. Jangoux and Lambert (1988) reviewed asteroid pedicellariae anatomy and classification and argued that pedicellariae types were more likely the result of convergence than homology. Within a phylogenetic context, Coppard *et al.* (2010) concluded that pedicellariae types in echinoids displayed high levels of homoplasy relative to other skeletal structures; based on the bulk of phylogenetic evidence; conclusions of Coppard *et al.* are judged appropriate for asteroids as well.

Although Gale (2011a) stressed he complexity of three-element pedicellariae in recognizing his Tripedicellariae, he did not comment on the morphologic expressions cited by Blake (1979) arguing that *Acanthaster* is of oreasterid ancestry. In the formulation of Blake (1979), the basal piece of the *Acanthaster* three-piece pedicellaria is readily derived through reduction of the larger and more robust primary ossicle of the oreasterid; pedicellariae of forcipulates and *Acanthaster* are judged not to be homologous and therefore the Tripedicellariae Gale (2011) is grounded in part on homoplasy. The interpretation of Blake (1979) was supported by the molecular analysis of Mah and Foltz (2011a).

Gale's phylogenetic interpretations are considered to reflect evolutionary convergences that do not justify rejecting multiple earlier phylogenetic studies with historical and morphological corroboration.

Interpretation of a meager but important fossil ecord

Overview of the fossil record of the Asteroidea. Interpretation of the fossil record of asteroids is important yet difficult. Fossil asteroids are rare, and Carboniferous through Triassic representatives are particularly uncommon. This is unfortunate because the interval spans from the late Paleozoic stem groups to the crown group(s), the latter first clearly identified from Triassic rocks. Given current knowledge of global geology, significant enlargement of this transitional record appears unlikely. A few relatively rich and diverse fossil faunas (e.g. Lehmann 1957; Hess 1972) argue an enduring success of the class and therefore apart from potentially geologically rapid major extinction and rediversification events such as might have accompanied the Paleozoic-Mesozoic transition, rarity likely relates more to preservational vulnerability than to small living faunas. This in turn indicates that by chance alone the few fossils that are found need not lie on or near major diversification pathways. It is not known whether the early diversification of the asteroid crown-group is better envisioned as a complex bush of many branches, these potentially arising well before the end of the Paleozoic, or as separation and survival of one (or few) lineage(s), perhaps as constrained by comparatively harsh conditions of the Paleozoic-Mesozoic transition. Given the limited but diverse record and barring an unforeseen increment in knowledge, debate over taxonomic assignments and phylogenetic implications of fossils are likely to be enduring.

Although the fossil record is scanty, it should not be lightly dismissed. Because the record is poor, timing of emergence of the crown group is uncertain. Earlier authors, such as Spencer and Wright (1966), suggested that major modern asteroid clades or taxa appeared early in asteroid history but that a major shift took place around the end-of-Paleozoic extinctions whereas both Gale (1987) and Blake (1987) argued that crown-group taxa are not known from the Paleozoic; interpretations were reviewed by Mah and Blake (2012). In spite of their rarity, Triassic asteroids are taxonomically diverse. Earlier monographers of asteroids consistently separated forcipulates from the remainder of the extant asteroids, and arguments of Blake (1987) and Blake *et al.* (2000) date both forcipulates and non-forcipulates from the Triassic. Although not recognizing Triassic forcipulates, the many uncertainties of assignment of Triassic asteroids opined by Gale (2011a) are here considered to indicate that this author favored significant early Mesozoic diversity.

Late Paleozoic *Calliasterella* bears much in common with extant zoroasterids, and Triassic trichasteropsiids share many expressions with both calliasterellids and surviving forcipulates; in Blake (1987) these similarities were inferred to reflect ongoing apomorphic steps emerging during the early evolution of the forcipulate clade. In contrast, even superficially paxillosidan-like coeval or earlier asteroids were not identified by Gale (2011a). Paxillosidans, basal in the crown group in the view of Gale (2011a, 2013), are quite robust and widely distributed today on soft-sediment continental shelves. Although rocks from such environments are common in the marine stratigraphic record, paxillosidans were not recognized by Gale (2011a: 57) from strata older than Jurassic whereas they are comparatively common (for asteroids) from younger intervals, as is consistent with their environmental preferences. Changing environmental settings [e.g. the concept of the Mesozoic Marine Revolution introduced by Vermeij (1977) and partially anticipated by MacBride (1921, 1923a, 1923b, in suggesting that the larval development of certain paxillosidans is associated with unstable substrates)] provide explanation for geologically late paxillosidan appearance. Shallow-water semi-infaunal luidiids, important to the Gale (2011a) phylogeny, do not appear in the geologic record until the comparatively recent Miocene, long after the documented Triassic diversification.

Approaching a bad fossil record. Disagreement among paleontologists on the taxonomic assessment of fossils is not new, and it can be particularly difficult for those groups such as asteroids with a "bad" (sensu Jefferies 1986:10) fossil record. In the past, phylogenetic interpretations of all organisms were limited by the necessary reliance on morphologic data, a difficulty now reduced for extant taxa by emerging molecular approaches (Losos and Mahler 2010). Lacking molecular data, paleontologists must turn to other guidelines. Systematists traditionally have relied on detailed comparision of many characters, as was articulated long ago by Simpson (1961: 88), who noted: "As far as characters in common are concerned, two criteria are fairly obvious: minuteness of resemblance and multiplicity of similarities. ... it is a sound principle of all taxonomy that conclusions on affinities ... are stronger the more characters are involved. The probabilities are cumulative ... "; ultimately important to the interpretation of *Trichasteropsis* by Blake and Hagdorn (2003) was presence of many strong character similarities. The major contribution of Henning (1966) to phylogenetic interpretation that was not exploited by Simpson (1961) is the concept of polarity; Blake (1987), Blake *et al.* (2000), and Blake and Hagdorn (2003) worked the complex of characters of *Trichasteropsis* into phylogenetic analyses, the several hypotheses beginning with differing perspectives and evolving data. The approach of Gale (2011a) was enumeration of putative similarities between *Trichasterpsis* and other taxa, but he did not include *Trichasteropsis* or any other crown-group fossil in his phylogenetic analysis. As exemplified below, the similarities posited by Gale (2011a) lack minuteness of detail (as sought by Simpson), and because they are scattered among taxa; the similarities are not cumulative. Without phylogenetic analysis, the Gale approach was not placed in an evolutionary context.

Another guideline for taxonomic assessment of fossils is provided by ranges of variation among widely accepted extant taxa, although environmental and evolutionary uncertainties complicate interpretation. Stratigraphic sequence can help, although the very sketchy early record of crown-group asteroids is a serious impediment, and finally, as indicated by MacBride (1922, 1923a, b), evaluation of life mode is useful for interpretation of taxonomy and phylogeny in spite of the difficulties of homoplasy.

Many changes to the taxonomic assignments of Blake (1986), Blake and Reid (1998), Blake *et al.* (2000), Blake and Hagdorn (2003), and Blake *et al.* (2006) were proposed by Gale (2005, 2011a). All suggestions are rejected here and in Blake & Reboul (2011). Interpretations of Gale (2011a) were not tested through inclusion of fossils in his phylogenetic analysis; perhaps such inclusion would have enabled a single integrated systematic section in his study, rather than division of an inferred single phylogenetic sequence into separate extant and fossil sections.

Minuteness of resemblance and multiplicity of similarities: *Trichasteropsis*. The Triassic family Trichasteropsiidae was treated in Blake and Hagdorn (2003) and Blake *et al.* (2006). The family was assigned to the order Trichasteropsida Blake, superorder Forcipulatacea, in effect arguing that the forcipulates are the earliest crown-group taxon with significant representation in the fossil record. Similarities among *Trichasteropsis*, *Calliasterella americana*, and the extant Zoroasteridae provided the foundation for the subclass Ambuloasteroidea. Blake (1987: 516) provided diagnoses of the Forcipulatacea and Trichasteropsida, summarized similarities and differences between trichasteropsiids and surviving asteroids, and provided some interpretations of earlier authors, these further discussed by Gale (2011a). Other comments on trichasterposiid affinities are in Blake *et al.* (2000) and Blake and Hagdorn (2003).

The interpretations of Blake & Hagdorn (2003) and Blake *et al.* (2006) were challenged by Gale (2011a), who focused on criteria opined to indicate taxonomic ambiguity, this author specifically citing (p. 64) the number of rows of tube feet, the nature of the mouth frame, the nature of the abactinal skeleton, and presence of a single row of marginal ossicles. None of the suggested ambiguities would disqualify trichasteropsiids as forcipulataceans, but argue simply that inferred comparable expressions occur elsewhere. The cited examples of Gale (2011a) were taken from taxonomically diverse living asteroids, an approach likely to identify homoplasy. This is a matter of particular concern in a group such as the Asteroidea that exhibits many recurring morphologic expressions through its long geologic range. The totality of argumentation on the forcipulate affinities of trichasteropsiids (Blake & Hagdorn 2003) cannot be repeated but here we continue to adhere to the forcipulatacean interpretation as developed in Blake (1987) and Blake and Hagdorn (2003). Further, we note a striking contrast within the approaches of Gale; although challenging assignment of comparatively well understood *Trichasteropsis*, Gale (2011b: 86), this author proposed a new genus and species of posited asteriid forcipulates, *Savignasterias villieri,* based on 18 isolated ossicles whose very combination into a single taxon is a first highly speculative interpretation. In addition to the holotype, a putative carinal (or "radial"), abactinals and marginals were included by Gale, as well as "possible adambulacrals"; thus neither ambulacral column nor jaw frame ossicles are considered definitely available in spite of their treatment as key to the phylogenetic interpretations of Gale (2011a). Basing taxon names on isolates was judged to be of very questionable reliability (Blake and Portell 2009; Blake 2010).

Challenge to the positioning of *Trichasteropsis* raises the broader issue of evaluation of affinities in general. Many cladistic results document widespread homoplasy in nature, which perhaps influenced Gale (2011a: 76 left) to point out that "... detailed morphological similarities between taxa seem so convincing that experienced workers have been reluctant to ... admit the possibility ..." of evolutionary convergence. The concerns of Gale all but demand reliance on the guidelines such as those of Simpson (1961: 88) for separating homology from homoplasy.

It is argued here that proposed similarities proposed by Gale are generalized, taxonomically scattered, and taken from modern exemplars far removed from the Triassic time of diversification of trichasteropsiids and the crown group, whereas and in contrast, character detail and their concentration in *T. weissmanni* carry the weight of minuteness of resemblance and multiplicity of similarities sought by Simpson (1961), thereby supporting an interpretation of forcipulatacean affinities for trichasteropsiids.

Among concerns, Gale (2011a: 64) first cited rows of tube feet. In his comprehensive and detailed study, Viguier (1879) separated forcipulates from all other extant asteroids based on three character groups, the widespread occurrence of four rows of tube feet in forcipulataceans, the presence of a so-called ambulacral-type mouth frame, and the nature of the pedicellariae. It was the view of Gale that use of presence of four rows in certain non-forcipulataceans compromised use of row number in *T. weissmanni* by Blake and Hagdorn (2003). Viguier (1879, trans. J. Lawrence, 1983: 32) found that rows of tube feet are useful "in the vast majority of cases," noting that G.O.Sars discovered four rows in the non-forcipulatacean *Pteraster multipes* Sars (now assigned to *Diplopteraster* Verrill), but Viguier went on to observe that "*Pteraster* has an appearance so special that it is absolutely unthinkable that he (i.e., in reference to Sars) made an error in classification"; Viguier (1879) thus relied on minuteness of resemblance. As noted by Gale, four tube-foot rows have been recognized elsewhere among extant taxa (e.g., the Asterinidae), but to our knowledge, only that of Ordovician *Promopalaeaster* Schuchert (see Spencer and Wright, 1966, fig. 50.2b) has suggested affinities with forcipulates to any author (Branstrator 1972). Adding to the multiplicity of similarities bearing on rows of tube feet and based on illustrations of Schöndorf (1909), Downey (1970: 3) thought alternately carinate and non-carinate adambulacral ossicles occur in *Calliasterella mira*. Gale (2011a: 83) did not comment on the Downey observation. Alternate adambulacrals are also found in the Zoroasteridae and *Trichasteropsis weissmanni* but they have not been reported from the Paxillosida.

Construction of the mouth frame further exemplifies minuteness of resemblance. Viguier (1879) separated the "ambulacral mouth frame" of the forcipulates from the "adambulacral mouth frame" of all other asteroids, introducing a concept that has endured, explicitly in the characterization of Spencer and Wright (1966) and implicitly, for example, in the diagnosis of the forcipulates of Fisher (1928: 2, 3). In challenging mouth frame construction of *Trichasteropsis*, Gale (2011a: 64, pl. 11:4) cited traits of Jurassic *Plumaster* Wright and modern echinasterids, suggesting presence of adoral carina in these genera, as well as a posited actinostome in *Echinaster*. We are in accord with Viguier and others, and do not recognize an actinostome in echinasterids, nor do we recognize the single abutted adambulacral pair behind the MAO in extant *Echinaster* as an adoral carina. A single abutted adambulacral pair occurs in other taxa as well, including specimens of Ordovician *Urasterella*; Blake and Rozhnov (2007) argued that mobility in this genus might even have yielded a "facultative adoral carina" (p. 526). The *Trichasteropsis* mouth frame shares enough minuteness of resemblance with extant forcipulataceans as to verify recognition as of an ambulacral type.

Regardless of his application of mouth frame characters sensu Viguier (1879) in the comparative interpretation of *Echinaster* and *Trichasteropsis*, Gale (2011a: 100) decided for Jurassic *Terminaster* Hess that "... presence of an adoral carina and an actinostome are ... forcipulatid features."

In pointing out that a reticulate dorsal skeleton occurs in poraniids as well as *Trichasteropsis*, Gale (2011a) challenged the importance of such a skeleton in *Trichasteropsis*; we argue that minuteness of resemblance justifies the interpretation of Blake & Hagdorn (2003: fig. 1). In challenging marginal row expression, Gale (2011a: 64) said “A single marginal row is present in various neoasteroids” although his data matrix (p, 50) identified only two candidates, *Luidia ciliaris* and *Zoroaster*. We agree with Döderlein (1920) that, like other species of *Luidia*, two marginal rows are found in *L. ciliaris*. Presence of one series remains a similarity shared among certain Paleozoic fossils, trichasteropsiids, and only zoroasterids within the crown group (regardless of the potential phylogenetic significance of possible marginal absence from the Pterasteridae).

An important difference between trichasteropsiids and modern forcipulates recognized by both Blake & Hagdorn (2003) and Gale (2011a) is the absence of pedicellariae from the former. (Given the nature of trichasteropsiid preservation, as summarized in Blake & Hagdorn, 2003, small and delicate pedicellariae as yet plausibly remain unrecognized.) Absence of pedicellariae does not preclude forcipulatacean affinities because they need not represent a basal apomorphy, a possibility shared with echinasterids in the Gale (2011a) interpretive assignment of this family to his Tripedicellaria. Further, crossed pedicellariae are not found in zoroasterids and they have not been recognized in certain Jurassic asteriids or near-asteriids (Gale 2011a: 60). Absence from these taxa raises the possibility that crossed pedicellariae are a later apomorphy, originating well after the origin of both the Forcipulatacea and of uncrossed three-element pedicellariae.

Gale (2013: 8) noted that *Trichasteropsis* has "a number of distinctive characters, such as the very broad adambulacrals that are never seen in later taxa" from there concluding that association of *Trichasteropsis* with living groups did not seem justified. Proportionately enlarged adambulacrals have been noted in both species of *Calliasterella* (for *C. mira*, Schöndorf, 1909: pl. 23.3 reproduced by Downey 1970: fig. 2b; for *C. americana*, Blake and Guensburg 1988: figs. 2, 5, 6), which imposes the same limitation on the *Calliasterella-Luidia* linkage of Gale as that he proposed for interpretation of *Trichasteropsis*. Enlarged adambulacrals occur in many Paleozoic asteroids, including the Australian Permian *Permaster* (Kesling & Strimple: fig. 2, 4), which was emphasized by Gale. Enlarged adambulacrals appear to represent a plesiomorphy retained as late as *Trichasteropsis*, with smaller sizes apomorphic within ambuloasteroid lineages.

Mode of life of *Trichasteropsis*. The predatory life mode typical of living asteriids is widely documented in the literature, these asteroids wrapping arms about prey, the actinostome and reduced mouth frame ossicles providing a pocket during predation. Strong morphologic similarities among asteriids, *Trichasteropsis*, and Ordovician *Promopalaeaster* favor parallel behavior. Similarities are almost certainly homoplastic between *Promopalaeaster* and the later asteroids, whereas *Trichasteropsis* indicates emergence of habits further developed later in forcipulate history. Donovan & Gale (1990) focused on asteriids in developing an argument attributing the post-Paleozoic decline of brachiopods in part to the radiation of crown-group asteroid predators. *Trichasteropsis* was described as a "possible forcipulatidid" (p. 81) by these authors, thereby attesting to Gale's earlier recognition of striking similarities of form and potential behavior between trichasteropsiids and asteriids, as well as to potential phylogenetic significance.

Although Donovan and Gale (1990) found Paleozoic asteroids to be distinctive, Branstrator (1972) emphasized similarities between *Promopalaeaster* and asteriids, and Blake (1981a) argued that if *Promopalaeaster* were asteriid-like in behavior, then a fossil might be found in which the specimen was preserved in the apparent act of predation. Blake and Guensburg (1994) described such an example.

Strong morphologic similarities between *Trichasteropsis* and certain extant forcipulates likely reflects commonality of behavior (Donovan & Gale 1990), and shared minuteness of resemblance and multiplicity of similarities reflect propinquity of descent (Blake & Hagdorn 2003). The *Promopalaeaster* specimen, buried while attacking a bivalve, emphasizes the significance of constructional morphology (Seilacher 1970; Reif *et al.* 1985) and provides added if indirect support for the assignment of *Trichasteropsis* to the Forcipulatacea. In contrast, *Echinaster*, in our view erroneously interpreted by Gale as showing such asteriid expressions as an adoral carina and an actinostome, specialize on small and relatively passive food items (Jangoux 1982; Mah & Blake 2012).

***Phylogenetic position of* Trichasteropsis weissmanni.** Gale (2011a: 63) pointed out that the cladogram of Blake (1987: fig. 10) positioned the Trichasteropsiidae as a monophyletic sister group of all other neoasteroids, and based on Blake (1987) and Blake and Hagdorn (2003), he further opined that the fossils form "part of the implicit evidence for the basal position of forcipulatids in the neoasteroid tree." Gale did not point out that the cladogram of Blake (1987) was further developed in Blake and Hagdorn (2003: fig. 6), which separated the forcipulate branch including *Trichasteropsis* from the remainder of the crown group. The cladogram reported the results of cladistic analysis of available data whereas Blake favored a scenario in which a phylogenetic dichotomy separated forcipulataceans from the remainder of the crown group. Although Gale (2011a, 2013) challenged the phylogenetic interpretations of *Trichasteropsis*, he did not include this genus in his own phylogenetic analysis and therefore results of the different studies cannot be directly compared.

***Selected taxa*: Palaeoctenodiscus campaniurnus and Betelgeusia**. The proposed transfer of *Paleoctenodiscus campaniurnus* Blake, 1988, to the Porcellanasteridae (Gale 2005) is rejected. *Paleoctenodiscus* shares marginal morphology throughout the length of the arm, including morphology of cribriform organs, with all members of the Goniopectinidae. Marginal ossicles of specimens of *Ctenodiscus* are varied, but nevertheless sharing ossicular breadth, height, and expression of the vertical ossicular ridges with *Paleoctenodiscus.* It also shares overall form and very probably presence of channels on the ventral surface with this family. Expression of the cribriform organs differs between *Paleoctenodiscus* and porcellanasterids. Gale (2005) compared specific expressions *Paleoctenodiscus* with those of a number of extant porcellanasterids, an approach intrinsically likely to identify homoplasies. Gale (2005) correctly noted presence of cribriform organs throughout the length of the arm of the porcellanasterid *Benthogenia cribellosa*, an expression otherwise unknown among porcellanasterids.

Benthogenia cribellosa is peculiar in a number of other aspects, perhaps most obvious, the comparatively extended arms, an oddity of uncertain significance found in other Phillippine asteroids (Fisher 1919).

Gale (2011a: 57) proposed transfer of *Betelgeusia* Blake & Reid to the Astropectinidae; radiasterid affinities were reaffirmed in Blake & Reboul (2011).

Selected taxa: Pseudarchaster portlandicus. *Archastropecten portlandicus* Hess was transferred by (Blake 1986: 1112) to *Pseudarchaster* based on arm shape, expression of the abactinal field, marginal shape including presence of shallow fascioles, ambulacral and adambulacral form, and expression of accessories (termed "encrusting ossicles"). Two species of *Pseudarchaster* (*P. gracilis, P. dissonus*) judged to have inferomarginal spinulation comparable to that of *P. portlandicus* were cited.

In questioning the proposed transfer, Gale (2011a: 57) did not treat the criteria of the primary ossicles cited by Blake (1986), an approach contrasting with his reliance elsewhere on morphology of isolated primary ossicles [e.g. in phylogenetic reconstruction, in the interpretation of the St. Cassian isolates (2011a: 65), and in the coining of *Savignasterias villieri* (Gale 2011b: 86)]; emphasis by Gale on *P. portlandicus* instead was placed on accessory (e.g. spinelets, granules) ossicular expression. The comparative species cited by Blake (1986) were not considered; instead *P. parelli* was chosen, a species contrasted with *P. portlandicus* in the comparisions of Blake (1986). Gale (2011a: fig. 23) described spines of *P. parelli* as "typical" but he did not explain how “typical” was determined nor why the comparative species cited in Blake (1986) were not considered. Twenty-two species of *Pseudarchaster* were recognized by A.M. Clark (1993), these widely distributed both geographically and in water depth, and although not well-documented in the literature, their ossicular morphology, including that of the accessories, is varied. The transfer of *Archasteropecten portlandicus* to *Pseudarchaster* by Blake (1986) is not challenged by Gale (2011a) because criteria pertinent to transfer were not considered.

Selected taxa: the concept of *Migmaster*. Description of *Migmaster angularis* Blake, *et al.* (1986) was based on a larger holotype and three small paratypes. Two of the smaller expose the dorsal surfaces whereas the third and the holotype show the ventral.

Gale (2011a: 64, 65) opined that there are "a number of problems with the published interpretation, the major one being the major constructional differences between the larger holotype and much smaller paratypes." Gale (2011a: 65) thought that "the smaller paratype (sensu Blake *et al.*, 2006) ... clearly has two marginal rows ... which precludes its inclusion in the Trichasteropsidae." Inclusion of the smaller and larger specimens of *Migmaster angularis* in a single taxon was thought to be "highly speculative," this author preferring to separate the larger from the smaller specimens and to "retain the name *Migmaster angularis* for the larger holotype." A family Migmasteridae was based on the holotype (Gale, 2011a: 102).

The taxonomy of suites consisting of few specimens, whether all of similar sizes or of disparate sizes, can be difficult (e.g. Clark and Downey 1992: 197, on *Leilaster*; see also Blake and Ettensohn 2009).

Gale (11a) thought two marginal rows to be present in one of the small *Migmaster* specimens, concluding that two rows would preclude assignment to the Trichasteropsiidae. Gale did not explain why presence of two rows (even if correct) would preclude such assignment. Discussion of *Migmaster* was immediately followed by consideration of *Berckhemeraster* Blake and Hagdorn, 2003, which he thought "appears to have two marginal rows" (p. 65) although this genus later was assigned to the Trichasteropsiidae (p. 102). Further, Gale (2011a) would have only a single marginal row in *Luidia ciliaris* although *Luidia* (*Platasterias*) *latiradiata*, with two clearly differentiated marginal rows, was accepted as a "true *Luidia*" (Gale 2011a: 70).

Blake *et al.* (2006: 288, 290) provided extended discussion of specimen sizes and morphologic interpretation of *Migmaster*; the new genus was found to share important similarities with *Trichasteropsis*, and configurations support interpretation of a growth series among specimens. Two enlarged series of ossicles are present at specimen edges, and evaluation of all specimens indicates that the lower series terminates without reaching the terminal ossicle (Blake *et al.*, 2006: 290 left), comparable to expression in *Trichasteropsis* and zoroasterid forcipulates; actinal ossicular series arrangement is as is found in all forcipulataceans. Only a single marginal series is present; Gale misinterpreted the outermost actinal row as a marginal series.

After rejection of assignment of all four *Migmaster* specimens to a single species, Gale (2011a: 102) proposed a new family Migmasteridae based on the holotype of Blake *et al.* (2006). Presence of two marginal rows was included in the diagnosis of the putative Migmasteridae although evaluation of this specimen by Gale (2011a: 64) appears to acknowledge presence of only a single series. The diagnosis of the Migmasteridae overlooks that the earlier interpretation of marginal row number was based on a smaller specimen to be excluded from *Migmaster* (p. 64) rather than on the holotype. Original morphologic and taxonomic interpretations of *Migmaster* are retained.

***Migmaster* and interpretation of the odontophore.** Among extant species, the odontophore is an unpaired ossicle distal and dorsal to each mouth-angle pair; Gale (2011a: 30R; 2013) considered this ossicle to be homologous with the axillary of Paleozoic asteroids. Blake *et al.* (2006: 292-293) discussed problems of odontophore interpretation and they argued that an enlarged, offset ossicle near the disk edge in the interbrachial angle of *Migmaster* as a possible axillary-odontophore equivalent. Gale (2011a: 64) opined that the " enlarged ... actinal/marginal plate is not homologous with the axillary of Palaeozoic asteroids because it does not articulate with the orals."

There are many publications in the complex history of interpretation of the axillary and odontophore; only a few are cited. Schuchert (1915) considered the axillary to be a part of the marginal ossicular series, a view that remains viable, and if the axillary is a part of the marginal series, there is no reason why it must abut the mouth frame. Small ossicles are intercalated between the enlarged marginal axillary and the mouth frame in a specimen of *Hudsonaster* Stürtz (Blake 2008, fig. 4.4).

Gale (2011a, 2013) considered the odontophore (characteristic of asteroids of the post-Paleozoic) to be a derivative of the axillary (a term traditional in the terminology of Paleozoic asteroids), but relationships are complex. An Ordovician *Hudsonaster* with a single external small ossicle together with a typical axillary was illustrated by Spencer and Wright (1966, fig. 47.3c), and a specimen with a fully internal ossicle together with a typical external axillary was illustrated by Schuchert (1915, pl. 1) and again by Blake (2008, fig. 4.6). These small ossicles are positioned as is the odontophore as identified by Gale (2011a, fig. 30F). Blake (2008) identified two apparent marginal-axillaries in an early species assigned to the Asteroidea, and Branstrator (1972: 186) was of the view that an internal, V-shaped ossicle was the "true" odontophore in *Promopalaeaster* rather than the "single, upaired inferomarginal axillary" identified by earlier authors. The proposal that the offset interbrachial ossicle described in *Migmaster* is a possible axillary remains fully viable, and the fate of a second axillary in the remainder of the crown group remains unknown. A typical internal odontophore might occur in *Migmaster*, although presence could not be verified among available specimens.

Selected taxa: *Berckhemeraster charistikos.* *Berckhemeraster charistikos* Blake and Hagdorn is a difficult taxon based on four incompletely preserved and exposed specimens; the genus was tentatively assigned to the Trichasteropsiidae in the original description. Gale (2011a: 65 opined "this genus should not be referred to the Trichasteropsidae" although later it was so assigned (p. 102). *Berckhemeraster* helps to document the diversity of Triassic asteroids and difficulties encountered in seeking to interpret crown-group history based on only a small sampling of extant species.

Selected taxa: *Noriaster barberoi.* Gale (2011a: 65) contested assignment of *Noriaster barberoi* to the Poraniidae by Blake *et al.* (2000), finding "the presence of large supermarginals and abactinal ossicles is quite unlike that seen in any living member of the family." Gale (2011a: 49) critiqued treatment of both his own earlier work and that of Blake for using "gradational and proportional characters that are impossible to code accurately"; "quite unlike" is such a gradational descriptor. We instead find the marginals and abactinals of *Porania antartica* Smith to be remarkably similar (using another such term) to those of *N. barberoi* based on direct specimen comparisons (Blake *et al.* 2000, figs. 1–4; Blake & Hotchkiss 2004, fig. 1.2). However, given phrasing difficulties, another criterion is important. Although Gale (2011a: 65) acknowledged that the original interpretation of *Noriaster barberoi* was "largely on the basis of similarities of ossicle arrangement of the actinal surface with that family," he did not note the crucial alignment of the actinal ossicles with the marginal frame, an expression emphasized in poraniids by Hotchkiss and Clark (1976) and reviewed for asteroids of all ages by Blake and Hotchkiss (2004). Such alignment is suggested in certain members of the Porcellanasteridae (Madsen 1961) but it is otherwise unknown beyond the poraniids and forcipulataceans, and it thereby provides an objective rather than a subjective criterion. [Any hypothesis of porcellanasterid affinities for *Noriaster* is rejected based on the totality of expressions, see Madsen (1961) and Blake *et al.* (1986)]. Assignment of *Noriaster* to the Poraniidae is consistent with the phylogenies of Blake and Hagdorn (2003) and Foltz and Mah (2011a). Similarities between *Noriaster* and e.g. *Porania antartica* demand little of the approximately 200 ma of evolution available since the time of *N. barberoi*.

Future directions

Our views on many aspects of asteroid biology and crown-group phylogeny were summarized in Mah and Blake (2012). For the future, we expect evolving molecular and statistical applications to significantly affect diverse interpretations of asteroid phylogeny at multiple levels, from species to higher-order classification. Future application of morphometrics adds a quantitative element to assessing morphologic boundaries, which previously have been the domain of qualitative assessment. As argued in Blake and Reboul (2011: 1022) "Quantitative approaches can help delineate ranges of variation and ultimately provide guides for the recognition of apomorphies. Blake and Portell (2009) and Blake (2010) argued that taxonomy of isolated ossicles (or select ossicles of more complete specimens) can be tested and verified or rejected based on computer imaging and statistical analysis; such approaches have been employed elsewhere (e.g., Hageman, 1991, 1995). Landmark analysis could prove as productive with asteroids as it has with trilobites (Webster, 2011) because asteroid ossicles and trilobite segments both are complex, three- dimensional objects. Cluster analysis could be used to develop blind tests for the assignment of isolated ossicles to single taxa; Lane and Rowe (2009) based phylogenetic interpretation of an asteroid genus on such techniques." The scanty fossil record favors a relatively ancient arguably relatively rapid divergence of crown-group lineages, and such histories elsewhere in biology have been shown to complicate phylogenetic interpretations. Morphologic research on both ancient and modern asteroids therefore can be expected to continue to be critical, but broad taxon sampling and comprehensive treatment of individual taxa using modern analytical techniques as appropriate are essential. We expect all approaches to play important roles in long-term, iterative re-evaluations of the history and biology of the class Asteroidea.

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