TOWARD A HISTORY OF THE PALEOZOIC ASTEROIDEA (ECHINODERMATA)

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ABSTRACT

Existing taxonomic and evolutionary interpretations of stem-group (Paleozoic) Asteroidea differ significantly. Molecular methodologies are unavailable, and because of a fossil record consisting largely of incomplete specimens, comprehensive morphology-based phylogenetic treatments yield equivocal results. Because of axial ossicular vaulting to form the ambulacral furrow, exposure of axial and the adjacent adaxial ossicles is limited in both ancient and modern asteroids and, as a result, taxonomic focus traditionally has been extraxial. Interpretation largely separating the less varied axial-adaxial elements from the more varied extraxial offers a fresh approach; here, primacy is axial-adaxial.

Evolution of the Asteroidea from the Somasteroidea accentuated two adaptive sequences: The axial or ambulacral skeleton was vaulted to form the furrow, and the adaxial virgal series was reduced to a single adambulacral ossicle. Taxonomic interpretation begins with *Ophioxenikos*, judged closest to asteroids among known somasteroids. Three extinct new orders, the Euaxosida, Hadrosida, and Kermasida, are based on axial and adaxial character expressions. Extraxial evolution accompanying and following virgal-series reduction led to varied and homoplastic body configurations; extraxial development traditionally was and remains basic to taxon recognition below the ordinal level. Two familial clusters of uncertain phylogenetic linkages are recognized for each order, one centered on presence of an extraxial skeleton of small ossicles logically derived from an *Ophioxenikos*-grade ancestry, and a second in which extraxials became enlarged and plate-like. Aspects of Paleozoic stem group diversification were later mirrored by the Ambuloasteroidea, balancing adaptations for protection against demands of active life modes. The families Lacertasteridae, Permasteridae, and Illusioluididae are new.

INTRODUCTION

Delineation of the history of the Paleozoic Asteroidea begins at the subphylum level. Researchers have almost entirely agreed on content and limits of the subphylum Asterozoa as summarized by Spencer (1914–1940) and Spencer and Wright (1966), and it has been treated as monophyletic, although paraphyly or even polyphyly cannot be wholly dismissed; some authors have aligned the small lower and middle Paleozoic Ophiocistioidea Sollas, 1899 with ophiuroids, a notion rejected for example by Ubaghs (1967, p. 58). Viewpoints on subphylum ancestry within the Echinodermata have varied. An edrioasteroid ancestry traditionally has been supported, with early thinking summarized and endorsed by Spencer (1914, p. 6); more recent advocates of an edrioasteroid ancestry include Smith and Jell (1990), Shackleton (2005), and Jell (2014). Support was further posited based on a comparative appraisal of ambulacra of asteroids with those of a new edrioasteroid (Sumrall and Sprinkle, 2008), it later recognized as *Kailidiscus*, Zhao *et al.*, 2010. Spencer (1951) assigned the then-new class Somasteroidea to a basal position within the Asterozoa, finding that the absence of an ambulacral furrow from somasteroids challenged posited linkages between asterozoans and edrioasteroids (p. 88). Argumentation countering currently-available edrioasteroid derivation hypotheses were developed around *Kailidiscus* (Blake and Guensburg, 2015), the exemplar of Sumrall and Sprinkle (2008). Parallel thinking applies to other genera, including the superficially asterozoan-like *Stromatocystites* (*e.g.*, Zamora *et al.*, 2014), its Cambrian age positioning it stratigraphically prior to the earliest-known skeletal asterozoan, and therefore allowing it to serve as a potential outgroup candidate.

Argumentation advocating a crinoid ancestry was developed in a series of papers by Fell (*e.g.*, 1963), a perspective accepted by Spencer and Wright (1966), but challenged by others (Madsen, 1966; Blake, 1982; Shackleton, 2005). The crinoid *Apektocrinus* Guensburg and Sprinkle, 2009, is superficially asteroid-like, a crinoid ancestry thereby retaining some cogency at least for this class.

Using "starfish" as an informal term for the Asterozoa, Spencer (1951, p. 88) noted "that starfish arose at a very early stage in the development of echinoderm stocks," but a specific ancestry was not designated. Blake (2013, 2014) and Blake and Guensburg (2015) argued that identity of asterozoan ancestry within the Echinodermata is unknown, a view retained here.

The timing of skeletal origin is germane. Trace fossils suggestive of asterozoans have been reported from the Early Cambrian (Alpert, 1976; Mikulás, 1992), well before the earliest skeletal remains from the Early Ordovician (Spencer, 1951; Blake, 2013; Blake and Guensburg, 2015), and if the traces are of the asterozoan clade then homologies between asterozoans and other skeletonized echinoderms might be