

The genera that never were: The impact of *Janeia* and *Janacekia* on phyletic and taxonomic relations within the Solemyidae (Bivalvia: Protobranchia)

Jack Bowman Bailey

ABSTRACT

Proposed taxonomies of the Solemyoidea remain conflicted, particularly regarding the familiar genera, *Solemya* and *Acharax*, whose close phyletic kinship has been obscured by: 1) imperfect understanding of the chronological morphogenesis of diagnostically important ligament support structures, and 2) misconceptions triggered by two problematic Paleozoic genera, *Janeia* and *Janacekia*, including the prevalent mischaracterization that the primary ligament in *Janeia* was located in an internal chondrophore. Whereas *Janacekia* and certain *Janeia* are synonyms of *Acharax*, other alleged *Janeia* are shown to be clinopisthins such as *Dystactella* and *Clinopistha*. Morphological analysis supports DNA studies suggesting *Acharax* and *Solemya* are monophyletic, thereby challenging recent taxonomies placing them in separate families or superfamilies. The primary ligaments of *Acharax* and *Solemya* are basically similar (opisthodontic, parivincular, attached at nymphae), the main differences being placement: external in *Acharax* but slightly internal (submarginal) in *Solemya*. Character analyses suggest the external nymphae of *Acharax* are plesiomorphic, arising by the Early Devonian, whereas the submarginal placement of the nymphae in *Solemya* is shown to be a Mesozoic apomorphy involving depression and secondary enclosure of the ligament and nymphae by a shelly outer layer. Nymphal enclosure has had two concomitant effects: 1) dorsal occlusion of the posterior adductor muscle; 2) fusion of the nymphae to internal buttresses that plesiomorphically functioned as simple reinforcement for the anterior margin of the posterior adductor muscles whereas, by exaptation, they become apomorphically modified to serve as supporting braces for the submarginal nymphae by dorsally uniting with them.

Jack Bowman Bailey. Department of Earth, Atmospheric and Geographic Information Sciences Western Illinois University, 1 University Circle, Macomb, IL 61455 USA. jb-bailey@wiu.edu

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INTRODUCTION

Overview

Bivalve lineages are well known for evolutionary stasis, often showing only minor oscillations in shell morphology occurring over millions of years (Stanley and Yang, 1987). Throughout their roughly 475-million-year history, the Solemyidae have remained among the most conservative of bivalves in both morphology and chemosymbiotic autecology (Seilacher, 1990; Cope, 2000; Imhoff et al., 2003; Kiel, 2010; Bailey, 2011). Consequently, many fossil species have been reasonably placed within two ancient and enduring genera, *Solemya* Lamarck, 1818, and *Acharax* Dall, 1908. Commonly called “awning shells”, both genera uniquely share the same thickened frill of radially pleated periostracum extending well beyond the calcified shell margins (e.g., see various figures of Pojeta, 1988; Dell, 1995; Taylor et al., 2008; Oliver et al., 2011; Walton, 2015). The frill is an ancient character well documented in Pennsylvanian *Acharax* (see Bailey, 2011) with possible traces in an Ordovician antecedent, *Ovatoconcha* Cope, 1996 (see Cope, 2000, 2002).

In *Solemya*, minor differences in the ligament are used as a basis for division into subgenera. Although the resulting system has been confusing and its application often inconsistent, several studies (Pojeta, 1988; Carter, 1990; Taylor et al., 2008; Kamenev, 2009; Bailey, 2011) have provided much needed clarification. However, significant problems remain especially regarding the precise relation between *Solemya* and *Acharax*, whose intimate phyletic ties have been obscured by: 1) incomplete understanding of the chronological morphogenesis of the diagnostically important ligaments and their associated structures; and 2) confusion generated through the widespread and persistent use of the ambiguous names, *Janeia* King, 1850 and *Janacekia* Růžička and Řehoř, 1978 along with their attendant mischaracterizations of Paleozoic solemyids.

Terminology, Figure Scales, and Repositories

Due to inherent ambiguities, certain traditional terms used to describe the bivalve shell and its orientation are sometimes replaced herein by unbiased and directionally neutral terms proposed by Bailey (2009, 2011; see also Carter et al., 2012).

This system was designed to be useful in describing fossil bivalve specimens where recognition of the anterior and posterior ends of the shell is problematic due either to differences of opinion or data insufficiency. The system is especially useful in the present study inasmuch as edmondoids and several other posteriorly elongate fossil taxa have been historically confused with solemyids, all of which are anteriorly elongate.

Beginning with Children (1823, p. 300) the archaic spelling “*Solenomya*” [nomen vanum] and its variation, “*Solenimya*” were widely used by early authors in lieu of Lamarck’s (1818, p. 488) original spelling, *Solemya*. To avoid confusion in the text, uncorrected orthographies are here limited to the Appendix.

Illustrations of early authors reproduced herein are 600 dpi grayscale digital scans of the original physical publications, not screen captures borrowed from various online sources. Because authors rarely mention the size or dimensions of illustrated specimens, 1 centimeter bar scales shown in the figures herein were measured directly from the original printed sources.

Repository abbreviations are as follows: BGS - British Geological Survey, Keyworth, Nottinghamshire, UK; UM - University of Missouri, Columbia, MO; USNM - United States National Museum of Natural History, Washington, D.C. The specimen E1114 is in the collections of the Sedgwick Museum, Cambridge, UK.

SOLEMYA, ACHARAX, AND THE SOLEMYIDAE

Ligament and Support Structures in *Solemya* and *Acharax*

In the Solemyidae an understanding of the ligament and its supporting structures is fundamental in ascertaining the systematic relations among constituent genera. In the familiar solemyids *Acharax* and *Solemya*, the ligament is amphidetic, composed of two principal components: 1) a dorsally arched, parivincular portion posterior to the beaks (= primary ligament) consisting of an inner fibrous layer (Figure 1, lgf) attaching on each side at insertion grooves, bordered by narrow ridges (i.e., nymphae) (Figure 1, ne, ns) that function as attachment sites for an outer lamellar layer (Figure 1, lgl); and 2) an anterior extension (not shown) of the lamellar outer layer in front of the beaks that is often asym-

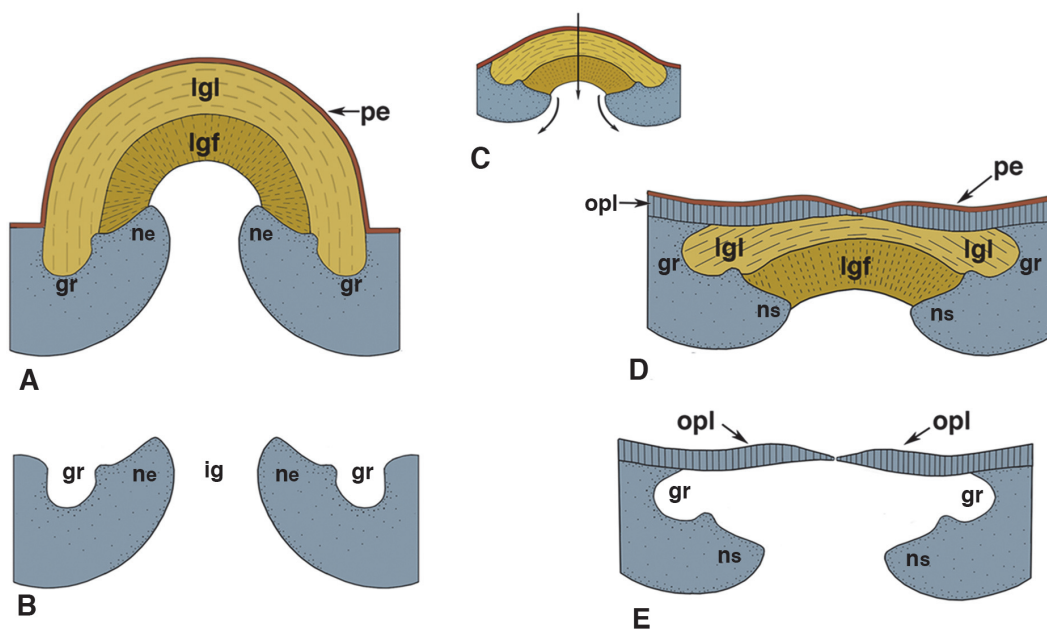


FIGURE 1. Diagrammatic transverse sections comparing the posterior portion of the ligament and nymphae of *Acharax* and *Solemya*. **A**, the upward-arching (parivincular) external ligament and nymphae, i.e., the plesiomorphic condition as seen in *Acharax*. (Drawing based on Carter, 1990, fig. 17D; Bailey, 2011, pl. 4, figs. 4-6; and Taviani et al., 2011, fig. 5). **B**, external nymphae of *Acharax* with the ligament removed. When the ligament is not preserved, the nymphae are visibly separated by an internymphal gap. **C**, hypothetical intermediate condition showing beginning stages of ligament depression and inward rotation of nymphae (arrows). **D**, submarginal ligament and nymphae - the apomorphic condition seen in *Solemya*. The depressed ligament is secondarily overgrown by a shelly outer prismatic layer. (After Carter, 1990, fig. 17A.) **E**, the submarginal nymphae of *Solemya* with the ligament removed. Notice the outer secondary layer that covers the former internymphal gap. Abbreviations: ne - external nymph, ns - submarginal nymph gr - ligament insertion groove, ig - internymphal gap, lgf - fibrous inner layer of ligament, lgl - lamellar outer layer of ligament, pe - periostracum, opl - outer (secondary) prismatic shell layer.

metrically attached between the left and right valves (see Carter, 1990, p. 174; Bailey, 2011, p. 19).

In *Acharax* the primary ligament is external, attaching at external nymphae (Figures 1, 2, ne) and insertion grooves (Figure 1, gr). However, in all subgenera of *Solemya* the primary ligament is sunken to a shallow internal (= submarginal) position immediately below the posterodorsal margins of the shell. There it is attached to a pair of submarginal nymphae and flanking grooves (Figure 1, ns, gr and Figure 2, ns), each supported at its anterior end by attachment to a ridge-like buttress (= rib, ridge, prop, or clavicle of various authors), i.e., a narrow thickening of the valve that extends along the anterior margin of the posterior adductor muscle (Figure 2, btc). Submarginal nymphae in *Solemya* are conventionally termed chondrophores (e.g., Dall, 1908) thus obscuring their homological relation to external nymphae. Unlike *Solemya*, the internal buttress (Figure 2, bts) of *Acharax* is not attached to nymphae and is variable in development, sometimes prominent but often weak or

obsolescent. Peripheral thickenings of adductor attachment sites in other bivalve taxa (Bailey, 1983; Taylor et al., 2008) suggest that the buttress in *Acharax* functions in part for added reinforcement of the thin valve along the posterior adductor margin (Bailey, 2016).

Because of its remarkable similarities to *Solemya* in gross morphology, *Acharax* was originally recognized as a subgenus of *Solemya* (see Dall, 1908, p. 2). Even the diagnostic primary ligament, aside from its external vs. submarginal location, is fundamentally similar in the two genera (Figure 1; see also Bailey, 2011, text-fig. 2). The homologies seem obvious. Together, *Acharax* and *Solemya* arguably form a monophyletic group (i.e., clade) in which the external ligament and nymphae of *Acharax*, the probable plesiomorphic condition (Figure 1A-B), later achieved submarginal (apomorphic) status in *Solemya* through depression of the nymphae and ligament below the posterodorsal margin (Figure 1C-E), along with attendant overgrowth of a thin outer prismatic layer (Carter, 1990, fig. 17; Bailey, 2011; Carter, et al., 2012, fig. 216). As

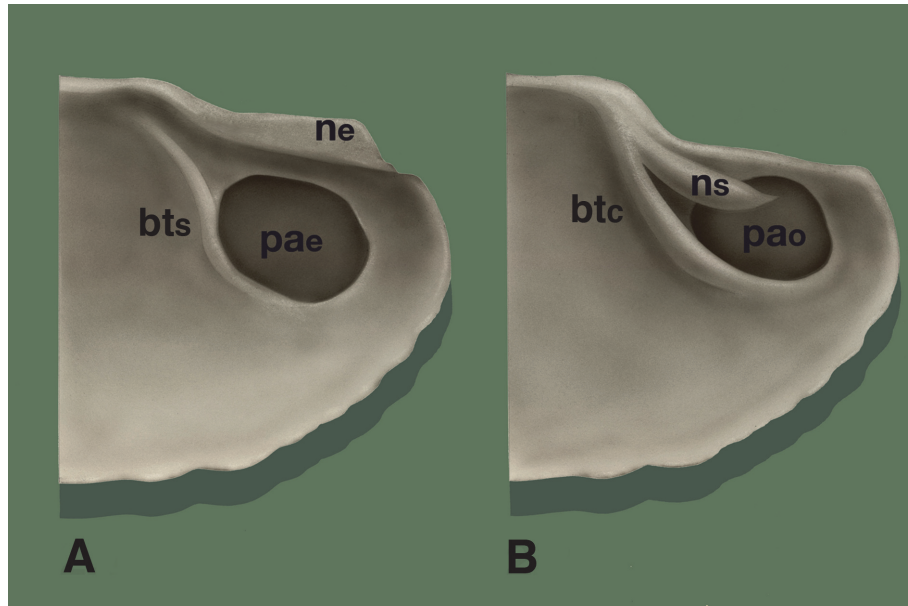


FIGURE 2. Comparative internal views of the posterior portion of the right valves of *Acharax* (A) and *Solemya* (B) showing character states of the nymphae, internal buttresses and posterior adductor scars. In *Acharax* the nymph (ne) is external, the condition of the internal buttress is simple (bts), and the condition of the posterior adductor muscle scar is entire (pae). In *Solemya*, depression of the nymph to a submarginal position (ns) results in a compound buttress (btc) and an occluded posterior adductor scar (pao).

noted by Waller (1998, p. 19), the outer prismatic layer (Figure 1, opl) covering the ligament “is a secondary [apomorphic] feature that is not present in the earliest ontogeny of the dissoconch...nor in the earliest members of the Solemyoidea and Solemyidae.” Depression of the nymphae may have been facilitated by the natural tendency of the thin shells and periostracum (Figure 1, pe) to crack and repair in the umbonal and ligamental regions during growth (Waller, 1990; Bailey, 2011).

In *Solemya*, depression of the nymphae below the hinge margin has resulted in: 1) fusion of the anterior end of each nymph directly to the internal buttress such that the function of the buttress becomes altered by exaptation from an original one of reinforcing the attachment site of the posterior adductor muscle along its anterior border (Figure 2A, bts) to one of serving as a supporting brace or prop for the submarginal nymph (Figure 2B, btc; see also Bailey, 2016); and 2) dorsal occlusion, either by embayment, truncation, or intersection, of the posterior adductor muscle by the nymph. In the case of intersection, the posterior adductor partially continues around the obstructing nymph, passing posteriorly above it (Figure 2B, pao). The resulting cross-cutting relationship firmly establishes the submarginal posterior ligament and nymphae in *Solemya* as apomorphic traits (see also pl. 4, fig. 2

of Pojeta, 1988, and figs. 3h, 3i of Hryniewicz et al., 2014).

Proxy Characters Linked to Nymphal Placement

In *Acharax* and *Solemya*, nymphal placement has a significant influence on the internal morphology of the shell. If neither nymphae nor ligament are preserved, the two genera may nevertheless be distinguished from each other in internal molds or incomplete specimens so long as traces of the buttresses and posterior adductor scars are present. Serving as proxies of nymphal placement, two functionally linked character states are here designated as follows: Where the nymphae are external (a plesiomorphy), the buttress will be simple and the posterior adductor will be entire. Where the nymphae are submarginal (an apomorphy), the buttress will be compound, and the posterior adductor will be occluded. In *Acharax*: 1) the buttress is simple (Figure 2A, bts), that is, from the anterior limit of the posterior adductor scar, it extends dorsally to the underside of the umbo without any evident attachment to a nymph; and 2) in the absence of a submarginal nymph the posterior adductor muscle is entire, that is, whole and unobstructed (Figure 2A, pae). The condition is reversed in *Solemya*: 1) the buttress is compound, that is, it adjoins the anterior terminus of the sub-

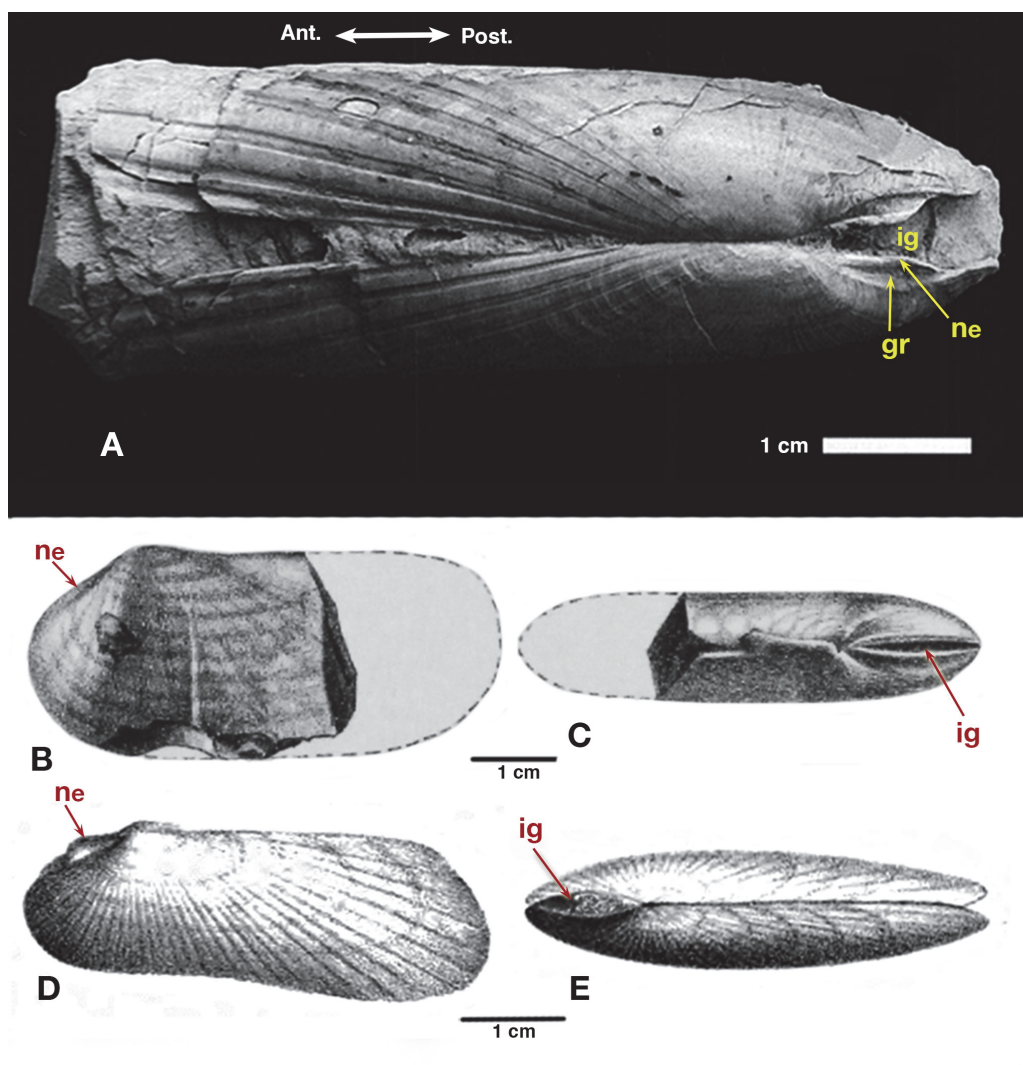


FIGURE 3. Internymphal gaps in fossil examples of *Acharax*. **A**, *Acharax doderleini* (Mayer, 1861), Pliocene of Italy; dorsal view showing external nymphae and ligament insertion grooves separated by internymphal gap that in life is covered by the ligament. In *Solemya*, the gap is secondarily closed off by the addition of a thin, outer prismatic shell layer. (Photo by permission, Taviani et al., 2011, fig. 5; yellow arrows with notations added here.) **B-E**, *Solemya puzosiana* de Koninck, 1842, Lower Carboniferous of Belgium. **B**, right lateral view of an incomplete articulated specimen (de Koninck, 1885, pl. 23, fig. 33). **C**, same specimen in dorsal view (de Koninck, 1880, pl. 23, fig. 34), reversed, anterior at left. **D**, right lateral view of an articulated specimen (de Koninck 1842, pl. 5, fig. 2b). **E**, same specimen in dorsal view (de Koninck 1842, pl. 5, fig. 2a). Hind (1900, p. 439) synonymized this specimen with *Solemya primaeva* Phillips, 1836, the type species of *Janeia* King, 1850. Internymphal gaps shown in de Koninck's figures are consistent with *Acharax* but not *Solemya*. Red arrows with notations added here. Abbreviations: ne - external nymph; ig - internymphal gap; gr - ligament insertion groove.

marginal nymph, the resulting configuration of the two forming a "7" shape (Figure 2B, btc); and 2) the posterior adductor is thereby occluded, becoming dorsally truncated, embayed, or intersected by the nymph (Figure 2B, pao).

One additional proxy needs to be discussed. Among fossil solemyids, paired external nymphae are often visibly separated by a narrow space whenever the primary ligament is not preserved. In

error, Hind (1900, p. 442) referred to the space as a "slit for the ligament." Herein termed the internymphal gap (Figures 1B, 3A-E, ig), it is a character seen in living and fossil *Acharax* but not in *Solemya*. In his original diagnosis Dall (1908, p. 2) referred to it thusly: "Ligament opisthodic, wholly external, visible internally only where it crosses the gap between the margins of the valves." In *Acharax*, the internymphal gap is cov-

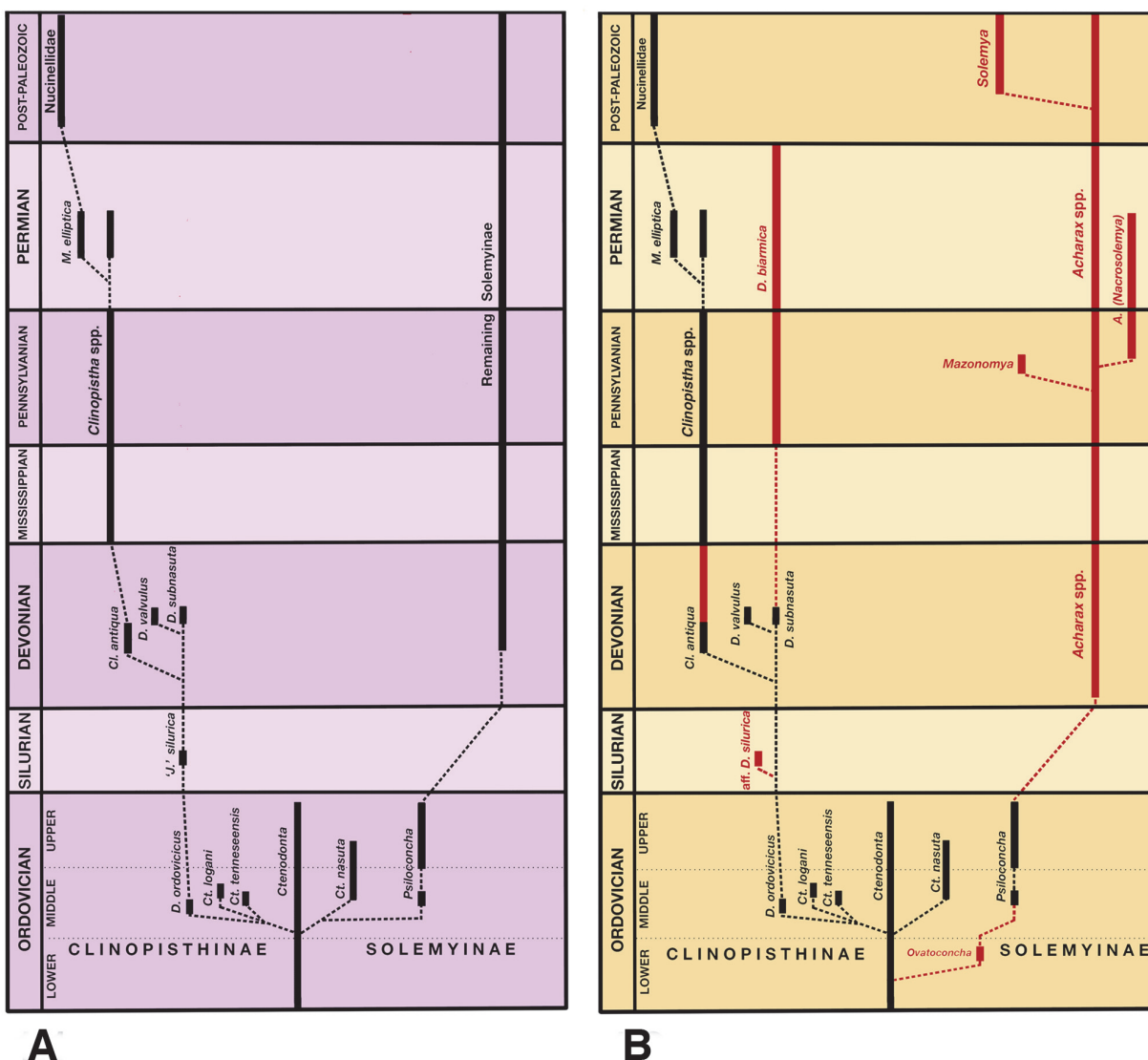


FIGURE 4. Phyletic schemes and biostratigraphic ranges (solid bars) of Paleozoic solemyoid genera. **A**, phyletic scheme of Pojeta (1988, fig. 3) postulating derivation of the Clinopisthinae and Solemyinae from nuculoid ancestors (i.e., *Ctenodonta*). **B**, proposed modifications (in red) of Pojeta's scheme based on studies herein. Abbreviations of generic names: A. = *Acharax*; Cl. = *Clinopistha*; Ct. = *Ctenodonta*; D. = *Dystactella*; 'J.' = *Janeia*; and M. = *Manzanella*.

ered in life by the arch of the external ligament and is thereby visible only when the ligament is not preserved. In contrast, the internymphal gap is missing in *Solemya* because the nymphae are submarginal and the former gap is secondarily covered over by the aforementioned outer prismatic shell layer (Figure 1D-E, opl). In addition to *Acharax*, the internymphal gap (a probable symplesiomorphy) is observed in other fossil solemyid genera with external nymphae including both *Clinopistha* Meek and Worthen, 1870, and *Dystactella* Hall and Whitfield, 1872.

Solemyid Origins and Phylogeny

Parivincular ligaments with supporting nymphae are key characters used in Pojeta's (1988) proposed phylogeny of fossil and extant Solemyidae (Figure 4A). Pojeta (1988) and Waller (1990, 1998) posited that these characters were acquired from nymph-bearing ctenodontid nuculoid ancestors such as *Ctenodonta nasuta* (Hall, 1847) and, especially, *Ctenodonta tennesseensis* Pojeta, 1988, which, aside from the taxodont hinge, is strikingly similar to the early solemyid *Dystactella*

Hall and Whitfield, 1872. Strong phylogenetic connections of the solemyids and nuculoids are supported by numerous other studies (e.g., Carter et al., 2000; Carter, 2001; Giribet and Distel, 2003; Giribet, 2008; Bailey, 2011; Carter et al., 2011; Bieler et al., 2014). However, based on stratigraphic occurrences Cope (2002) suggested that these characters might have arisen independently in the two groups. Whereas the solemyid *Ovatoconcha* is dated as late Early Ordovician, ligamental nymphae do not occur in ctenodontids until the Middle Ordovician. Alternatively, Cope also posited that nymphae could be persistent characters derived from earlier, as yet undocumented ctenodontid stock. Indeed, persistent solemyid traits are fairly common among much later nuculoids, for example, in *Spathelopsis oakvalensis* Peck, Bailey, Heck, and Scaiff, 2009 from the Mississippian of West Virginia (see Peck et al., 2009, p. 959; Bailey, 2011, p. 14).

Pojeta's (1988, fig. 3) phyletic scheme divided the Solemyidae into two sister subfamilies, the Clinopisthinae and the Solemyinae (Figure 4A). With the exception of *Solemya*, external placement of the nymphae and ligament is broadly shared in both subfamilies. Among the Solemyinae it occurs in *Psiloconcha* Ulrich, 1894 (Ordovician), *Acharax* (Devonian-Holocene), and *Mazonomya* Bailey, 2011 (Pennsylvanian). Among the Clinopisthinae, it occurs in *Clinopistha* Meek and Worthen, 1870 (Devonian-Permian) and *Dystactella* Hall and Whitfield, 1872 (Ordovician-Permian). Thus, it is likely to represent the primitive (symplesiomorphic) condition for the Solemyidae as a whole. In contrast, the submarginal ligament structure of *Solemya* is unique, representing a derived (autapomorphic) condition evidently not occurring prior to the Mesozoic (Figure 4B). Although ligament and nymphae are as yet unknown in *Ovatoconcha*, the genus is a near match for its possible congener, *Psiloconcha* with respect to: 1) shell profile, aspect ratio and shell gapes; 2) umbonal placement and elevation; 3) small size and high placement of the posterior adductors to accommodate the underlying hypertrophied gills and hypobranchial gland; and 4) pyriform outline and elevated placement of the anterior composite (adductor/visceral retractor) scars (Bailey, 2011, p. 12). Radial elements in the prosopon are not well developed in either genus, i.e., weak in *Ovatoconcha* and mostly lacking in *Psiloconcha*.

The Problem of Range

In order to establish a convincing phylogenetic derivation of *Solemya* from *Acharax* ancestry, the

geologic timing of the split must be consistent with the foregoing character analysis.

The Y-shaped burrows of the ichnogenus *Solemyatuba* Seilacher, 1990 occur as early as the Ordovician (Seilacher, 1990). Although they are usually attributed to *Solemya*, comparable burrows are also associated with *Acharax* (Stanley, 1970, Campbell et al., 2006; Ros-Franch et al., 2014). Thus, their occurrence cannot be attributed to a particular genus.

Early authors, including Beushausen (1895), Zittel (1913), Quenstedt (1930), Shimer and Shrock (1944), as well as more recent authors, notably Cox (1969), gave the stratigraphic range of *Solemya* as Devonian-Holocene under the apparent misapprehension that the submarginal ligament and compound buttress were primitive characters, whereas the external ligament and simple buttress of *Acharax* were tacitly regarded as later derivations. For example, Cox (1969) regarded *Acharax* as a later genus with a verified range limited to Miocene-Holocene. However, Pojeta (1988) subsequently emended the range of each genus thusly: For *Solemya*, Upper Pennsylvanian-Holocene; and for *Acharax*, Lower Permian-Holocene, (with a dubious Middle Devonian occurrence). Pojeta's basis for concluding that *Solemya* occurred as early as the Upper Pennsylvanian was a single specimen, "*Solemya* sp." (USNM 415967), from the Hertha Limestone, Erie, Kansas (Pojeta, 1988, pl. 23, figs. 5-8). However, this specimen is a probable *Acharax* because the alleged free ends of the "chondrophores" shown in his figure 8 are probably the compressed and broken termini of external nymphae, a conclusion supported by his figure 5 of the same specimen showing: 1) simple buttresses that dorsally reveal no indication of either added reinforcement or attachment to internal nymphae; and 2) posterior adductor scars that are entire, lacking the expected dorsal occlusion caused by submarginal nymphae.

Although the study of Dickins (1963), like that of Pojeta (1988), ostensibly provided support for the late Paleozoic occurrence of *Solemya*, Dickins himself was tentative regarding the final generic assignment of his material. His "*Solemya*" *holmwoodensis* Dickins (1963) from the Lower Permian of western Australia is herein assigned to *Acharax* inasmuch as the holotype and three paratypes show strong external nymphae as well as the anterior ligamental extension (Dickins, 1963, p. 60; pl. 7, figs. 1-9). Even a dorsally arched portion of the external parivincular ligament is preserved in the holotype (Dickins, 1963, pl. 7, fig. 2). In error, Hajkr

et al. (1978, p. 14) transferred this species to the Sanguinolitidae Miller, 1877.

Contemporary studies support the view that *Acharax* arose much earlier than Cox (1969) had supposed. For example, *Acharax* has been reported from the Early Devonian of Arctic Canada (Bailey, 2011, 2016; Bailey and Prosh, 2016). In addition, there are Pennsylvanian occurrences in both Kentucky (Carter, 1990) and the Mazon Creek Lagerstätte of Illinois (Bailey, 2011). Furthermore, all of the Devonian-Permian examples of alleged *Solemya* (and its doppelgänger, *Janeia* King, 1850) reviewed herein have external ligament and nymphae like *Acharax*, whereas the submarginal ligament and associated compounding of the buttress of *Solemya* appear to be Mesozoic modifications (see Appendix; also Bailey, 2011, 2016).

Unverified examples of *Solemya* have been reported from the Permian (Ciriacks, 1963; Sterren and Cisterna, 2010) and Triassic (Conrad, 1870). Ciriacks (1963, p. 42, pl. 5, figs. 12, 13) tentatively designated a nearly featureless internal mold of a possible solemyid as *Solemya* sp. (UM 5275 = “*S. radiata?*” sensu Branson, 1930) from the Park City Formation, near Cody, Wyoming. Although Ciriacks (p. 42) described the specimen as “insufficiently preserved for specific identification”, the form superficially resembles *Dystactella*. Sterren and Cisterna (2010, p. vi) reported an occurrence of *Solemya* from the Early Permian of Argentina, but they provided neither figure nor description. Conrad (1870, p. 102) described the shell exterior and radial prosopon of “an obscure cast” he designated *Solemya triasina* Conrad, 1870, from the Triassic of Perkiomen Creek, Pennsylvania. However, data on the hinge and ligament are lacking, and no figure of the specimen, now lost, was provided.

Other studies place the earliest occurrence of *Solemya* in either the Jurassic (Coan et al., 2000; Imhoff et al., 2003; Neulinger et al., 2006) or Cretaceous (Dechaseaux, 1952). Hryniewicz et al. (2014) reported convincing examples of *Solemya* from Late Jurassic-Early Cretaceous hydrocarbon seeps of Spitzbergen. The silicon rubber casts of their (fig. 3h-i) internal molds of *Solemya* (*Petrasma*) cf. *woodwardiana* Leckenby, 1859 clearly show the compound buttress and occluded posterior adductor scar. It should be noted, however, that alleged “*Solemya woodwardiana*” reported by Duff (1978) from the Lower Oxford Clay (Middle Jurassic of England) is a possible *Acharax*. Although data on the posterior adductor is lacking, a simple buttress is evident. In addition, the butterflyed specimen figured by Duff (1978, pl. 1, fig. 40)

shows what appear to be traces of a deltoid parivincular ligament stretching across an internymphal gap with a possible nymph and insertion groove preserved in the right valve.

The accumulation of 18S rRNA gene sequence disparities (Neulinger et al., 2006) separating extant species of *Acharax* and *Solemya* seem consistent with a Mesozoic (possibly Jurassic) split. The timing of the split is interesting. Among the Bivalvia in general, the Mesozoic is associated with episodes of rapid expansion and diversification (Ros et al., 2012).

Taxonomic Dissent

Despite extensive study, solemyoid classification remains in dispute, noticeably in regard to the systematic relations of *Solemya* and *Acharax* (Table 1). Owing to the external ligament, Cox (1969) in Part N of the *Treatise* first elevated *Solemya* (*Acharax*) Dall from subgeneric to full generic status while adding, in error, the vesicomid, *Adulomya* Kuroda, 1931 (i.e., see Amano and Kiel, 2011) to the Solemyidae and, unfortunately, giving full recognition to the problematic *Janeia* King, 1850 as a subgenus of *Solemya*.

Based on the ontogenetic expansion vector of the shell and underlying soft anatomy, Pojeta's (1988) landmark study argued for two main phylogenetic lines (Figure 4A) within the Solemyidae, thereby subdividing the Solemyidae into two subfamilies: 1) the Solemyinae for anteriorly elongated solemyids with “barely discernible” beaks and umbos (i.e., *Solemya*, *Acharax*, and *Psiloconcha*); and 2) the Clinopisthinae for anteroventrally elongated solemyids with more conspicuous umbos and beaks (i.e., *Clinopistha* and *Dystactella*). This system was followed by Bailey (2011) and used herein (see Figure 4B, Table 1 and Appendix).

Scarlato and Starobogatov (1979) split the order Solemyoida into two suborders, the Nucinelina and Solemyina. Emphasizing the relative significance of the submarginal vs. external ligament, they divided the Solemyina into two taxonomic divisions: 1) the Superfamily Solemyoidea/Family Solemyidae was proposed for genera with submarginal ligaments such as *Solemya*; and 2) the Superfamily Acharacoidea/Family Acharachidae was proposed for genera with an external ligament, including *Acharax* and, in error, the vesicomid *Adulomya* (see Amano and Kiel, 2011). A similarly divided system was endorsed by Zardus (2002), Nevesskaja (2009), and Nevesskaja et al. (2013).

Maxwell (1988) likewise placed *Acharax* and *Solemya* in separate superfamilies, the Acharac-

TABLE 1. Solemyoid classification schemes of various authors. *Acharax* and *Solemya* have been placed either in separate families (or superfamilies) or grouped together within the same family (or subfamily).**Cox, 1969**

Class BIVALVIA Linné, 1758

Subclass CRYPTODONTA Neumayr, 1884

Order SOLEMYOIDA Dall, 1889

Superfamily SOLEMYOIDEA Adams and Adams, 1857 (1840)

Family SOLEMYIDAE Adams and Adams, 1857 (1840)

(Includes *Solemya* and *Acharax*; *Clinopistha* [= *Dystactella*] placed in Ctenodontidae Wöhrmann)**Scarlato and Starobogatov, 1979**

Class BIVALVIA Linné, 1758

Superorder PROTOBRANCHIA Pelseneer, 1889 (= Nuculoida Dall, 1889)

Order SOLEMYIDA Newell, 1965

Suborder SOLEMYINA Newell, 1965 (= Solenomyina Dall, 1889)

Superfamily ACHARACOIDEA Scarlato et Starobogatov, 1979

Family ACHARACIDAE Scarlato et Starobogatov, 1979

(*Acharax* placed here)

Superfamily SOLEMYOIDEA H. Adams et A. Adams, 1857

Family SOLEMYIDAE H. Adams et A. Adams, 1857

(*Solemya* placed here)

Suborder NUCINELLINA Scarlato et Starobogatov, 1971

Superfamily AFGHANODESMATOIDEA Scarlato et Starobogatov, 1979

Family AFGHANODESMATIDAE Scarlato et Starobogatov, 1979

Superfamily MANZANELLOIDEA Chronic, 1952

Family MANZANELLIDAE Chronic, 1952

Family NUCINELLIDAE Vokes, 1956

Superfamily HUXLEYOIDEA Scarlato et Starobogatov, 1971

Family HUXLEYIIDAE Scarlato et Starobogatov, 1971

Allen and Hannah, 1986

Class BIVALVIA Linné, 1758

Subclass PROTOBRANCHIA Pelseneer, 1889

Order SOLEMYOIDA Dall, 1889

Family SOLEMYIDAE Gray, 1840

(Includes both *Solemya* and *Acharax*)

Family NUCINELLIDAE Vokes, 1956

Maxwell, 1988

(Class BIVALVIA)

(Subclass PROTOBRANCHIA)

Order SOLEMYOIDA Dall, 1889

Suborder SOLEMYINA Dall, 1889

Superfamily SOLEMYOIDEA Gray, 1840

Family SOLEMYIDAE Gray, 1840

(*Solemya* placed here)

Family ACHARACIDAE Scarlato and Starobogatov, 1979

(*Acharax* placed here)

TABLE 1 (continued).

Suborder NUCINELLINA Scarlato and Starobogatov, 1971
Superfamily MANZANELLOIDEA Chronic, 1952
Family MANZANELLIDAE Chronic, 1952
Cope, 1996
Class BIVALVIA Linnaeus, 1758
Subclass LIPODONTA Cope, 1995
Order SOLEMYOIDA Dall, 1889
Superfamily SOLEMYOIDEA Adams and Adams, 1857
Family SOLEMYIDAE Adams and Adams, 1857
Pojeta, 1988
Class PELECYPODA Goldfuss
Subclass PALAEOTAXODONTA Korobkov
(= Subclass PROTOBRANCHIA Pelseneer)
Superfamily SOLEMYOIDEA Adams and Adams
Family SOLEMYIDAE Adams and Adams
Subfamily SOLEMYINAE Adams and Adams
(Includes both <i>Solemya</i> and <i>Acharax</i>)
Subfamily CLINOPISTHINAE Pojeta, 1988
(includes both <i>Clinopistha</i> and <i>Dystactella</i>)
Superfamily NUCINELLOIDEA Vokes, 1956
Family NUCINELLIDAE Vokes, 1956
Family MANZANELLIDAE Chronic, 1952
Amler, 1999
(Class BIVALVIA)
Subclass LIPODONTA (Iredale, 1939) Cope, 1995
Order SOLEMYOIDA Dall, 1889
Superfamily SOLEMYOIDEA (Adams and Adams, 1857) Gray, 1840
Family SOLEMYIDAE (Adams and Adams, 1857) Gray, 1840
(<i>Solemya</i> placed here)
Family JANACEKIIDAE Růžička and Řehoř, 1978
(<i>Janacekia</i> placed here)
Family ACHARACIDAE Scarlato and Starobogatov, 1979
(<i>Acharax</i> placed here)
Nevesskaja, 2009; Nevesskaja et al., 2013
Class BIVALVIA
Superorder PROTOBRANCHIA Pelseneer, 1889
Order SOLEMYIDA Newell, 1965
Superfamily SOLEMYOIDEA H. et A. Adams, 1857
Family SOLEMYIDAE H. et A. Adams, 1857
(<i>Solemya</i> placed here)
Superfamily ACHARACOIDEA Scarlato et Starobogatov, 1979
Family ACHARACIDAE Scarlato et Starobogatov, 1979
(<i>Acharax</i> placed here)
Superfamily MANZANELLOIDEA Chronic, 1952

TABLE 1 (continued).

Family MANZANELLIDAE Chronic, 1952

Family NUCINELLIDAE Vokes, 1956

Beiler et al., 2010

Class BIVALVIA Linnaeus, 1758

Subclass PROTOBRANCHIA Pelseneer, 1889

(= Subclass PALAEOTAXODONTA Korobkov, 1954)

Order SOLEMYOIDA Dall, 1889

Superfamily MANZANELLOIDEA Chronic, 1952

Family MANZANELLIDAE Chronic, 1952

Superfamily SOLEMYOIDEA Gray, 1840

Family SOLEMYIDAE Gray, 1840

Subfamily SOLEMYINAE Gray, 1840

(= Family JANACEKIIDAE Růžička and Řehoř, 1978)

(Includes both *Solemya* and *Janacekia*)

Subfamily ACHARACINAE Scarlato and Starobogatov, 1979

(*Acharax* placed here)

Subfamily CLINOPISTHINAE Pojeta, 1988

Carter et al., 2011

Class BIVALVIA Linnaeus, 1758

Subclass PROTOBRANCHIA Pelseneer, 1889

(= Subclass PALAEOTAXODONTA Korobkov, 1954)

Superorder NUCULIFORMII Dall, 1889

(= Superorder FOLIOBRANCHIA Ménégaux, 1889)

Order SOLEMYIDA Dall, 1889

Superfamily SOLEMYOIDEA Gray, 1840

Family SOLEMYIDAE Gray, 1840

Subfamily SOLEMYINAE Gray, 1840

(Includes both *Solemya* and *Acharax*)

Subfamily JANACEKIINAE Růžička and Řehoř, 1978

(*Janacekia* placed here)

Family CLINOPISTHIDAE Pojeta, 1988

Family CTENODONTIDAE Wöhrmann, 1893

Family OVATOCONCHIDAE Carter, 2011

Bailey, 2011 (and herein)

Class BIVALVIA Linnaeus, 1758

Subclass PROTOBRANCHIA Pelseneer, 1889

(= Subclass PALAEOTAXODONTA Korobkov, 1954)

Superorder NUCULIFORMII Dall, 1889

Order SOLEMYOIDA Dall, 1889

Superfamily SOLEMYOIDEA Gray, 1840

Family SOLEMYIDAE Gray, 1840

Subfamily SOLEMYINAE Gray, 1840

(includes both *Solemya* and *Acharax*)

Subfamily CLINOPISTHINAE Pojeta, 1988

(includes both *Clinopistha* and *Dystactella*)

oidea and Solemyoidea, respectively, whereas Amler (1999) recognized only one superfamily, the Solemyoidea made up of three families, the Solemyidae, the Janacekiidae, and the Acharacidae.

Bieler et al. (2010) combined and modified the classifications of both Pojeta (1988) and Scarlato and Starobogatov (1979) by dividing the Solemyidae into three subfamilies, the Clinopisthinae, the Acharacinae, and the Solemyinae, the latter considered as a synonym of the Janacekiidae Růžička and Řehoř 1978. However, this system is problematic in that it results in the division of the *Acharax-Solemya* clade into two paraphyletic subgroups. Furthermore, treating the Janacekiidae as a synonym of the Solemyinae is antithetical because the namesake, *Janacekia* Růžička and Řehoř, 1978, has the external ligament and nymphae like *Acharax* but unlike *Solemya*, as discussed further below.

Carter et al. (2011) proposed dividing the order Solemyida into two superfamilies, the Solemyoidea and the Manzanelloidea. In this system, the Solemyoidea comprises four families: the Solemyidae, consisting of the subfamilies Solemyinae (containing both *Acharax* and *Solemya*), as well as the Janacekiinae, Clinopisthidae, Ctenodontidae, and Ovatoconchidae. However, because *Janacekia* is herein accepted as a junior synonym of *Acharax*, the Janacekiinae becomes superfluous. In addition, *Ovatoconcha*, because of its similarities to *Psiloconcha*, may arguably be placed in the Solemyinae.

If, indeed, as posited herein, *Solemya* was derived from *Acharax* ancestors by, perhaps, mid-Mesozoic times through depression of the primary ligament and nymphae to a submarginal position, the two genera are monophyletic, a conclusion independently corroborated by both Sharma et al. (2013) and Combosch et al. (2017) in each of their phylogenetic tests of molecular markers in the genomic DNA of *Solemya* and *Acharax*. The 18S rRNA analysis of these genera by Taylor et al. (2008) reached a similar conclusion. According to Mayr and Ashlock (1991) higher taxa should consist of monophyletic groups separated from groups of similar rank by a distinctive gap. Their understanding echoes Schenck's (1934, p. 55) classic criterion: "One basic principle is that a family should be monophyletic." When inherent misunderstandings associated with *Janeia* and *Janacekia* are eliminated, the morphologic and temporal gaps separating *Acharax* and *Solemya* are not only minimized, but also consistent with DNA studies. Thus, of the various systems described above, Pojeta's

(1988) taxonomic scheme combining both genera within a single subfamily (Solemyinae) remains a viable alternative to placement into separate (paraphyletic) superfamilies or families.

THE *JANEIA* PROBLEM

Key issues influencing the taxonomic debate are historical interpretations (sometimes incomplete or erroneous) of past authors regarding the placement of the primary ligament and its associated structures, specifically, the mistaken assumption that among Paleozoic Solemyidae, the primary ligament was placed internally, supported there by so-called "chondrophores" as in modern *Solemya*. This assumption has been largely based on a series of misapprehensions regarding a single illusory genus, *Janeia*.

In Search of a Concept

Janeia King (1850) may be justifiably regarded as a nomen dubium (Hryniewicz et al., 2017). Commenting on its ill-defined and confusing history, Pojeta (1988, p. 214) called it "a name looking for a concept." Nevertheless, *Janeia* continues to be widely applied in recent publications (e.g., Nevesskaja, et al., 2013) and many online databases, even though it is devoid of any essential meaning. Historically, the ongoing confusion began with King (1850) himself. In his celebrated monograph, *The Permian Fossils of England*, he first proposed the genus on page 177 of the text, but subsequently withdrew it in an appendix note (p. 246-247) of the same publication, concluding that *Janeia* and *Solemya* are synonymous. In addition, King's original diagnosis of *Janeia* is both ambiguous and inaccurate, reflecting not only a misunderstanding of the fossil material at hand but also a lack of familiarity with solemyid soft anatomy. In his diagnosis the anterior and posterior ends of the shell were reversed, and he mischaracterized the ligament (i.e., "cartilage") as "internal; attached to a considerable portion of, and a little within, the dorsal margin of the valves; dilated, and somewhat oval within the umbonal cavity; narrow and elongated behind [sic] it" (King, 1850, p. 177). The "considerable" dorsal attachment of the ligament possibly refers only to the secondary ligament, that is, the anterior extension of the ligament outer layer (seen in both *Acharax* and *Solemya*) that runs along much of the anterodorsal (longidorsal) length of the valves. The "somewhat oval" portion is more difficult to interpret; perhaps it refers to the variably developed subumbonal ligamental

demipads seen in *Solemya* and some *Acharax* (see Bailey, 2011).

King (1850, p. 247) reported that his withdrawal of *Janeia* was based on an evaluation of the anatomical and conchological figures of *Solemya mediterranea* Lamarck, 1818, as contained in Cuvier (1836, plate 115). Curiously, despite anatomical evidence to the contrary, King (1850, p. 247) persisted in his erroneous interpretation of shell orientation and criticized contemporary conchologists who disagreed. Despite King's withdrawal of *Janeia*, the name has had a lasting legacy inasmuch as it has been accepted by many subsequent authors who, in an attempt to salvage the concept, have ascribed to it additional characters far beyond those originally intended by King.

Historically, *Janeia* has been conceptually applied to Paleozoic solemyids having an internal (primary) ligament supported by internal "chondrophores" (= nymphae) as in extant *Solemya*. It must be emphasized that the nature of the primary ligament in *Janeia* is purely an unsupported assumption based on: 1) King's (1850, p. 177) mischaracterization of the ligament as internal; and 2) his subsequent conflation of *Janeia* with extant *Solemya*. Inasmuch as the name *Janeia* has been restricted to Paleozoic solemyids, the internal primary ligament has been accordingly presumed to be a primitive (plesiomorphic) character within the Solemyidae, whereas the external ligament in *Acharax*, is implicitly understood to be a post-Paleozoic derived (apomorphic) condition. However, evidence suggests the opposite to be true, given the many published examples of *Janeia* showing evidence of an external primary ligament similar to *Acharax* (see Logan, 1967; Carter, 1990; Dickins, 1999; Bailey, 2011, and Appendix herein), whereas other examples of putative *Janeia* with external ligaments are assignable to either *Dys-tactella* or *Clinopistha*.

Types and Archetypes

Each of the species of *Janeia* originally proposed by King is evaluated below:

***Janeia primaeva* (Phillips, 1836).** Logan's (1967) restudy of *Janeia primaeva* accepted the primary ligament as external, a conclusion later confirmed by Bailey (2011) who emended the name as *Acharax primaeva* (Phillips, 1836) (see Appendix).

As type species of *Janeia*, King (1850) selected *Solemya primaeva* Phillips, 1836 from the Lower Carboniferous (Tournaisian-Viséan) of Lowick, Northumberland, England (see Figure 5A), but he neither discussed it nor its relationship to his

two other exemplars, *Janeia biarmica* (de Verneuil, 1845) from the Upper Permian Magnesian Limestone at Tunstall Hill and Humbledon Hill, Durham, England, and *Janeia phillipsiana* (King, 1848), allegedly from Humbledon Hill.

Solemya primaeva was evidently based on a single specimen. Phillips' (1836, p. 209, pl. 5, fig. 6) original treatment consists of an imprecise diagnosis and simple drawing. The putative holotype consisted of a composite mold with attached shell showing no evidence of the ligamental condition aside from the apparent non-occlusion of the posterior adductor scar, suggestive of an external ligament as in *Acharax* (Figure 5A). The specimen, originally stored in Phillips' personal collection, is lost, allegedly stolen by thieves (see Hind, 1896 footnote, p. 19). Portlock's (1843, p. 441) subsequent re-description *S. primaeva* was based on a single unfigured hypotype collected from an alternate location, i.e., Carboniferous shales of Aghaloo Parish, County Tyrone, Northern Ireland. Portlock's hypotype, much larger and more elongated than Phillips' holotype, was later illustrated by Hind (1900) (see Figure 5B). In the same study, Hind illustrated five additional specimens of *S. primaeva* (e.g., Figure 5C-D). One of these, a topotype (Figure 5C), was reproduced by Cox (1969, fig. B1.1a) in Part N of the *Treatise* where it was used as a principal basis for accepting *Janeia* as a valid subgenus. Unfortunately, the *Treatise* figure is mistakenly credited to Phillips (1836) rather than Hind (1900). Apart from the significant size disparity, the morphologic similarities of Hind's topotypic example (Figure 5C) and Portlock's hypotype (Figure 5B) are compelling. Both lack direct ligament data but show simple buttresses and entire posterior adductors characteristic of *Acharax*.

M'Coy (1855) approved of King's decision to withdraw *Janeia* in favor of *Solemya* in apparent agreement with King's presumption that the primary ligament is internal. However, he disagreed with King on shell orientation, asserting correctly that the valves are anteriorly elongate. On page 519 of the same work M'Coy provided a detailed description of an additional topotype he identified as *Solemya primaeva* Phillips, although the shell shape significantly differs from the aforementioned specimens of Hind. As shown in Figure 5E-F, it appears to be either an internal or composite mold with well-marked adductor scars and radial striae. As in *Acharax*, the posterior adductor scar is entire, and the internal buttress is weak and simple, extending along the anterior border of the posterior adductor and diminishing in relief as it approaches

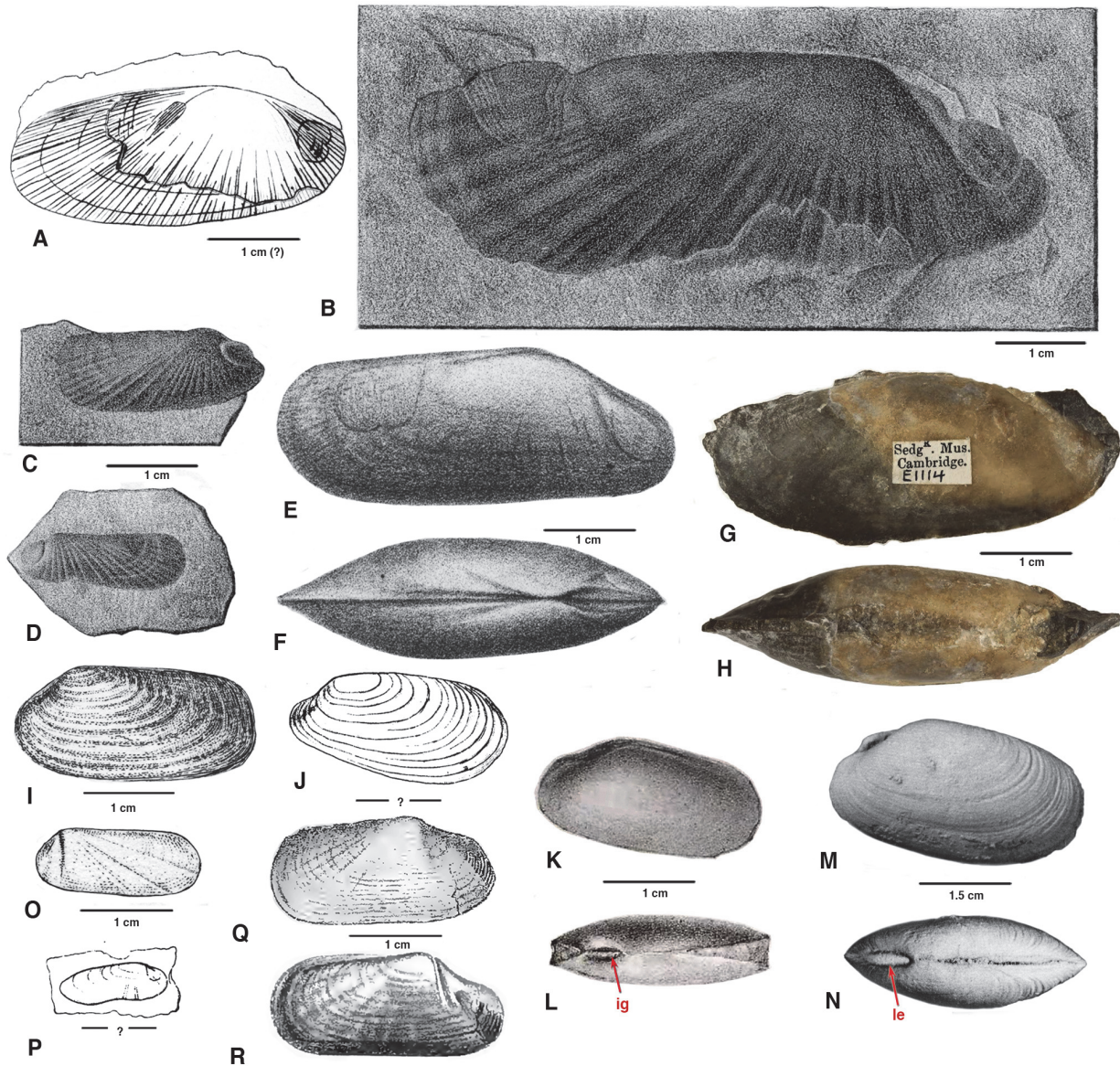


FIGURE 5 (caption on next page).

the interior of the umbo. The close-set nymphae shown on the brevidorsum appear to be external, recalling those of *Acharax* (*Nacrosolenya*) *trapezoides* (Meek, 1874) (see Beede and Rogers 1899, pl. 32, fig. 2b; Carter, 1990, fig. 17d), an interpretation that seems supported by M'Coy's own description (1855, p. 519): "...on its outer or posterior margin the slight thickening of the external cartilage support [= nymphae] is clearly seen, and the reflected gaping [= internymphal gap] edge of the lunette in some specimens..." Surprisingly, these features are not validated by M'Coy's actual topo-

type (Sedgwick Museum, no. E1114), a natural cast with attached matrix (Figure 5G-H) on which his illustrations (evidently interpretive reconstructions) were based. In particular, the hinge morphology of the topotype is inconsistent with M'Coy's figure, providing few clues concerning the exact mode of ligament attachment. Yet, the posterior adductor is simple, and the elevated brevidorsal feature that M'Coy called a "lunette" (p. 519) appears consistent with external nymphae. It is worth noting here that Hind (1900, p. 444)

regarded M'Coy's figures as "largely hypothetical, especially the view of the hinge-line and umbones."

Solemyids comparable to *S. primaeva* have been treated by several authors. De Verneuil's (1845, pl. 19, fig. 5) specimen of *S. primaeva* from the Lower Permian of Russia is fragmentary; only the anterior portion of the shell is preserved; the ligament-bearing posterior portion of shell is missing. Both M'Coy (1855 p. 520) and Hind (1900, p. 440) accepted *Solemya puzosiana* de Koninck, 1842, Carboniferous of Belgium (Figure 3B-E), as a synonym of *S. primaeva*. However, M'Coy (1855) separated the species into two varieties: *S. primaeva* of Phillips he informally called *S. primaeva* var. α whereas *Solemya puzosiana* de Koninck, 1842 (p. 60, pl. 5, fig. 2a, b; Carboniferous of Belgium) he formally named *S. primaeva* var. β . Similar shells, M'Coy noted, occur in the Lower Carboniferous dark limestone of Lowick and black beds of Derbyshire.

Zhang and Pojeta (1986, p. 670, fig. 5.4) reported *Solemya (Janeia) primaeva* (Phillips) from the Ceshui Formation (Lower Carboniferous of China). Their specimen resembles Hind's (1900) topotype and Portlock's hypotype (Figure 5B).

Janeia biarmica (de Verneuil, 1845). King's (1850, pl. 16, fig. 7) example of *J. biarmica* from the Upper Permian, Tunstall Hill, and Humbledon Quarry, is not a solemyid (Figure 5I). The umbos are too prominent, and the shell is marked by regular, broadly rounded comarginal ribs (radii lacking), and a subtruncate longiterminus. Rather, it is a probable pholadomyoid, i.e., *Wilkingia elegans* (King) (see Logan, 1967, p. 63). Richard Howse (1857a, p. 309), a colleague and collaborator of King's, called it a juvenile specimen of *Allorisma elegans* [= *Wilkingia elegans*], and Geinitz (1861, p. 57) agreed.

King (1850, p. 178) placed *Solemya abnormis* Howse, 1848 from the Upper Magnesian Limestone (Upper Permian), Tunstall and Silksworth, in synonymy with *J. biarmica*. Howse (1857a, p. 309) not only disagreed with King's conclusion but also professed reluctance in referring it to *Solemya*. His two figures of *S. abnormis* (Howse, 1857a, pl. 4, figs. 8, 9) are simple drawings. Although the ambiguous shell fragment in his figure 9 shows no distinguishing traits, the modioliform Silksworth shell shown in his figure 8 (Figure 5J herein) compares with *Stutchburia modioliformis* (King) sensu Logan (1967, p. 50, pl. 8, fig. 8a-e) from the reef

FIGURE 5 (figure on previous page). Classic exemplars of *Janeia* King of past authors. **A-H**, *Solemya primaeva* Phillips, 1836. **A**, putative holotype (lost) of Phillips, 1836, pl. 5, fig. 6 (= type species of *Janeia* by original designation of King, 1850, p. 177), Lower Carboniferous of Lowick, Northumberland, England. **B**, composite mold, left valve; a large hypotype identified by Portlock (1843, p. 441) as *S. primaeva* Phillips (figure of Hind 1900, pl. 50, fig. 1), Carboniferous shales of Aghaloo Parish, Co. Tyrone, N. Ireland. **C**, composite mold, left valve of a topotype (Hind, 1900, pl. 50, fig. 5); same figure used by Cox (1969, fig. B1.1a), Lower Carboniferous, Lowick, Northumberland. **D**, composite mold, right valve of a hypotype (Hind, 1900, pl. 50, fig. 6) (= type of *Sanguinolites radiatus* M'Coy, 1844, p. 50), Killymeal, Dungannon, Co. Tyrone. The simple buttresses and non-occluded posterior adductors in 5B-D are consistent with *Acharax*. **E-F**, *Solemya primaeva* Phillips as figured by M'Coy (1855), Lower Carboniferous, Lowick, Northumberland. **E**, left lateral view (M'Coy, 1855, pl. 3F, fig. 3). **F**, same specimen, dorsal view (M'Coy, 1855, pl. 3F, fig. 3a). **G-H**, actual specimen (Sedgwick Museum no. E1114) used by M'Coy as the basis for Figures 5E-F (photos by Matthew Riley). **G**, left lateral view. **H**, dorsal view. The details shown in M'Coy's figures appear to be largely hypothetical. **I**, *Janeia biarmica* (de Verneuil, 1845), figure of King, (1850, p. 178, pl. 16, fig. 7) [= *Wilkingia elegans* (King)], Upper Permian, Humbledon Quarry, Durham, England. **J**, *Solemya abnormis* Howse, 1848, p. 244; 1857a, p. 309, pl. 4, fig. 8; Upper Permian "Shell-Limestone", Silksworth, Durham; King (1850) accepted it as a synonym of *J. biarmica*; Logan (1967) called similar topotypic shells *Stutchburia modioliformis* (King). **K-L**, *Solemya biarmica* de Verneuil 1845, pl. 19, fig. 4a, 4b, Lower Permian, Nizhny, Novgorod Oblast, Russia; herein reassigned to *Dystactella* Hall and Whitfield. **K**, holotype, an internal mold, right lateral view. **L**, dorsal view of same showing anterior and posterior gapes; the infilling of the internymphal gap (ig) is evidence of an external parivincular ligament. **M-N**, *Dystactella subnasuta* (Hall and Whitfield, 1872), Lower Devonian (Upper Helderberg), Louisville, Kentucky. **M**, right lateral view of articulated specimen (= "Specimen A", USNM 145650) of McAlester (1968, pl. 5, fig. 7). **N**, dorsal view of "Specimen A" of McAlester (1968, pl. 5, fig. 9) showing cylindrical external ligament (le) on the posterodorsum; the similarities to *S. biarmica* de Verneuil are conspicuous. **O**, *Janeia phillipsiana* King, 1848 (from King, 1850, p. 179, pl. 16, fig. 8); Howse (1857b, p. 9) called it a "mere fiction." **P**, *Solemya normalis* Howse, 1848 as figured by Howse (1857a, pl. 4, fig. 7); placed in synonymy with *J. phillipsiana* by King (1850, p. 179), Upper Permian, Humbledon Hill, Durham. **Q**, *Solemya phillipsiana* King, figure of Schuchroth (1854, p. 553, pl. 21, fig. 5), lower Zechstein (Upper Permian), Bucha, Germany. **R**, same specimen reinterpreted by Geinitz (1861, p. 60, pl. 12, fig. 19) and placed by him in synonymy with *S. biarmica*. Note the marked differences in shell shape and detail; both the cleft formed by the buttress and adjacent adductor scar are missing in Schuchroth's figure.

facies, Middle Magnesian Limestone (Upper Permian), Tunstall Hill, Durham. Later, Howse (1858, p. 266, pl. 11, figs. 8, 9) published the same Silkworth shell under the name of "*Solemya biarmica*?" (see Appendix).

De Verneuil's (1845, pl. 19, fig. 4a, b) original specimen of *Solemya biarmica*, herein assigned to the clinopisthin, *Dystactella*, is a smooth internal mold from the Lower Permian of Nizhny Novgorod Oblast (Russia) (see Figure 5K-L). Unlike *Acharax* and *Solemya*, the umbos are broader, more elevated and more subcentrally placed than in either of these genera, and the shell is expanded antero-ventrally. Furthermore, the shell radii that often mark internal molds of both *Solemya* and *Acharax* are uncharacteristically absent. The thin cylindrical ridge along the brevidorsum is probably a sediment infilling of an internymphal gap associated with a strong external ligament. The characters and the shell profile of de Verneuil's figured type precisely match McAlester's (1968, pl. 5, figs. 3-11) and Pojeta's (1988, pl. 8, figs. 1-10) specimens of *Dystactella subnasuta* Hall and Whitfield, 1872 (type species of *Dystactella*) from the Silver Creek Limestone Member of the Sellersburg Limestone (Middle Devonian) of Clark County, Indiana. (compare Figure 5K-L with Figure 5M-N) Herein, de Verneuil's original figured type of *Solemya biarmica* is emended as *Dystactella biarmica* (de Verneuil, 1845) new combination (see Appendix).

A tiny specimen attributed to *S. biarmica* by Geinitz (1848, p. 8, pl. 3, fig. 34) from the Permian Kupferschiefer of Kamsdorf, Germany, is not instructive. However, a second example figured by Geinitz (1861, p. 60, pl. 12, fig. 18) superficially resembles de Verneuil's figured type (= *Dystactella*), but ligamental and other data are lacking. Logan's (1967, pl. 10, fig. 11, 12) figured specimens, hypotypes "A" and "B" respectively, from the Upper Permian Middle Magnesian Limestone, Durham, were described under the emended name, *Janeia biarmica* (de Verneuil, 1845). Hypotype "A", from Humbledon Hill, is an internal mold that generally agrees with de Verneuil's type. However, Logan's inferred profile of the incomplete hypotype "B" from Tunstall Hill is more like *Acharax* although the prosoponal radii characteristic of some (but not all) species of this genus are not evident. Unlike de Verneuil's figured type, hypotype "B" is far more inequiaxial with lower umbos. Significantly, it convincingly shows remains of paired external ligamental nymphae separated by a narrow oval cleft (internymphal gap), features associ-

ated with both *Acharax* and *Dystactella* but not *Solemya*.

***Janeia phillipsiana* (King, 1848).** King's figure (1850, pl. 16, fig. 8) shows an internal mold, extremely inequiaxial in form, with barely discernible umbo and beak. A few radial ribs are indistinctly shown along with a narrow furrow for a simple buttress extending vertically to the beak but lacking an adjoining groove for the diagnostic submarginal nymph of *Solemya* (see Figure 5O). Significantly, in a scathing denunciation of King's work, Howse (1857b, p. 9) accused King of specimen theft, plagiarism, and deceit, calling King's *Janeia phillipsiana* a "mere fiction", and asserting that his published description and figure were inventions based on non-existent fossil material. Accordingly, King's (1850, p. 179) placement of *Solemya normalis* Howse, 1848 in synonymy with *J. phillipsiana* was also denounced by Howse (1857a, p. 309; 1857b, p. 9; 1858, p. 266).

Howse's (1857a, pl. 4, fig. 7; 1858, pl. 11, fig. 7) own illustration of *S. normalis* is a simple drawing of an elongated shell with low umbos marked by comarginal lineations with few radii and, apparently, an entire posterior adductor scar (see Figure 5P). However, the shell is unusual in its slightly arcuate profile and broadly embayed ventral margin. In a footnote, Howse (1857a, p. 308; 1858, p. 265) admitted that anterior extremity of his drawing was not correctly represented. Thereby, placement within the Solemyidae cannot be fully confirmed. More recently, Logan (1967, p. 61) gave recognition to *Janeia normalis* (Howse) based on material from the Upper Permian Magnesian Limestone at Tunstall Hill. However, these are referable to *Acharax* inasmuch as Logan (p. 62) observed external ligamental nymphae in his hypotypes. Although prosoponal radii are either weak or lacking, the shell profiles (see Logan, 1967, pl. 10, figs. 13, 14) are intermediate between *Solemya parallela* Beede and Rogers, 1899, pl. 34, fig. 1 (= *Acharax parallela* (Beede and Rogers) emend. Bailey, 2011) and *Acharax primaeva* (i.e., *S. primaeva* sensu Hind, 1900, non Phillips, 1836).

From the lower Zechstein (Upper Permian) of Germany, Schauroth (1854, p. 553, pl. 21, fig. 5) described a specimen he hesitatingly referred to *Solemya phillipsiana* (King). His figure shows a relatively featureless internal mold with an anomalously thick shell remnant attached just above the "posterior" (breviventral) margin (Figure 5Q). The shape of the bivalve superficially agrees with other solemyins and is subtly marked by a few radial elements. Subsequently, Geinitz (1861, p. 60, pl. 12,

fig. 19) refigured Schauroth's original specimen but assigned it to *Solemya biarmica* de Verneuil, although the similarities to that species are few. Interestingly, Geinitz's figure of the same specimen is startlingly different from Schauroth's. Although Geinitz's figure, like that of Schauroth, shows the same telltale shell remnant, the overall profile of the bivalve is noticeably altered (see Figure 5R). More significantly, the internal mold in Geinitz's figure is marked by a deep groove for an internal buttress flanked by an adductor scar. Surprisingly, these features are altogether missing in Schauroth's figure. If Geinitz's illustration is accurate, the septum-like buttress is simple but appears unusually deep and well defined but does not appear to directly border the adductor scar as expected. The adductor scar, though entire, is unusual in its more breviventral placement. Although the shell profile superficially recalls *Acharax parallela* (Beede and Rogers), the umbos are more prominent and less extreme in posterior placement, and strong comarginal lirae adventitiously mark the outer surface of the shell remnant. Because of the many disparities, taxonomic placement of this specimen is undetermined, and its location is unknown.

A PERPLEXING LEGACY

Janeia Reinvented

Despite King's own abandonment of *Janeia* and Howse's recriminations, subsequent authors found various problematic reasons for reinstating the name. Fielding Bradford Meek (in Meek and Worthen, 1870, p. 44) suggested reviving *Janeia* as a subgenus of *Solemya* for Carboniferous-Permian shells similar to those of King (1850) but showing left-over-right overlap of the beaks. Meek speculated that King's failure to mention overlap in his original diagnosis of *Janeia* may have been due to an insufficiency in available material. In 1871, Meek (p. 66) described *Solemya (Janeia) vetusta* from the Corniferous Limestone (Devonian), Franklin Co., Ohio, and published a figure of it two years later (Meek, 1873, pl. 18, fig. 4). The distinctive shell (Figure 6A) shows the marked anteroventral expansion vector and prominent external ligament seen in the Clinopisthinae (i.e., *Clinopistha* and *Dystactella*). The similarities to *Dystactella valvulus* (Hall and Whitfield, 1872) from the Middle Devonian (Silver Creek Limestone Member, Sellersburg Limestone) of Indiana are fairly strong although Pojeta (1988, p. 217) rejected conspecificity (but compare with Pojeta, 1988, pl. 10, fig. 1). The low, subcentrally placed umbos, long, low-angled pos-

terodorsal slope, weakly developed radii, and narrow posterior adductor bordered by a thin, weak buttress led Meek to compare it to *Solemya biarmica* de Verneuil, suggesting that King's abandoned genus, *Janeia*, should perhaps be reinstated and applied to solemyids with similar characters. James Hall (1885) followed Meek's precedent; his specimens of *Solemya (Janeia) vetusta* from the Middle Devonian Hamilton Group, near Louisville, Kentucky and Charlestown, Indiana, superficially agree with Meek's material (Figure 6B-D). Pojeta (1988, p. 217) placed all of Hall's figured specimens of *Solemya (Janeia) vetusta* in *Dystactella valvulus*. All of Hall's (1885) figured specimens show evidence of an external ligament in the form of narrow ridges (= external nymphae) along the brevidorsum. In particular, the uniquely scalloped radial elements in the prosopon (Figure 6E) shown in one of Hall's *S. (J.) vetusta* exactly match those of *D. valvulus* illustrated by Pojeta (1988, pl. 10, fig. 1). Kindle's (1901) figures show similarities (Figure 6F-G). In addition, the paired external nymphae (Figure 6G, ne) are visibly separated by a narrow internymphal gap (Figure 6G, ig). All aforementioned *biarmica-vetusta* specimens of de Verneuil (1845), Meek (1873), Hall (1885), and Kindle (1901) are herein reassigned to *Dystactella* (see Appendix). Compare with figured specimens of McAlester (1968, pl. 5, figs. 1-11) and Pojeta (1988, pls. 6-10).

Valve Inequality and Overlap

In Dechaseaux's (1952, p. 264) treatment of solemyid genera, *Janeia* is given a range of Devonian-Permian and distinguished from *Solemya* only by being "légèrement inéquivalve." The roots of this problematic trait are traceable not only to Meek (p. 44 in Meek and Worthen, 1870; Meek, 1876, p. 127) but also to Beushausen (1895, p. 292). Both authors stressed the need for full reinstatement of *Janeia* in application to Paleozoic specimens similar to *Solemya* but showing a slight umbonal overlap (often left-over-right) of the opposing valves. However, Beushausen's (1895) emphasis on valve asymmetry in diagnosing *Janeia* must be seen within the larger context of his erroneous belief that, in general, valve inequality and overlap were natural characteristics of most Paleozoic bivalves.

Bailey (1983, figs. 34, 35, and p. 280) documented minor left-right inequalities in non-solemyoid protobranchs, for example, left-right valve height and depth inequalities in the Nuculidae (i.e., *Nuculoidea deceptiformis* Bailey, 1983) and left-right ligamental inequalities in the Malletiidae, i.e.,

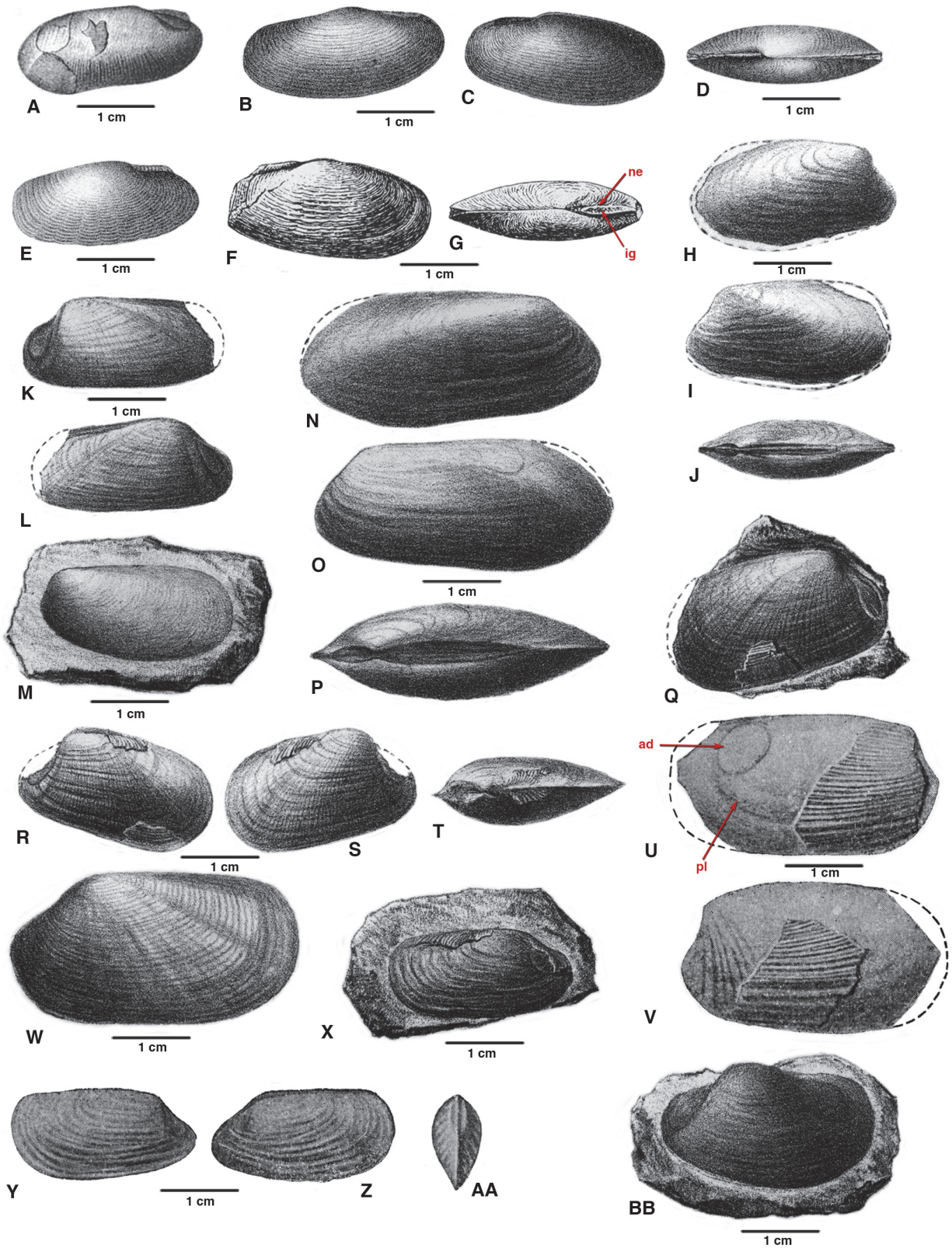


FIGURE 6 (caption on next page).

Palaeoneilo filosa (Conrad, 1842). Among the Solemyidae, Bailey (2011) showed that valve overlap and inequality (including ligament lateralization) are common among the Solemyidae and by no means restricted to species referred to *Janeia*. Růžicka and Řehoř (1978) likewise reported umbonal overlap in their Carboniferous genus, *Janacekia*, although it is a persistent character among the Solemyidae described as early as the Silurian (i.e., *Janeia silurica* Liljeldahl, 1984). Meek (1873) reported it in Devonian *Clinopistha*. It has also been observed in an undescribed species of Early Devonian *Acharax* (Bailey, 2011; Bailey and Prosh, 2016), as well as two common Pennsylvanian species, *Acharax* (*Nacrosolemya*) *trapezoides* (Meek, 1874) and *Acharax radiata* (Meek and Worthen, 1860) (see Carter, 1990; Bailey, 2011, text-fig. 4.2). In addition, it also occurs in extant *Solemya*, notably, *Solemya* (*Zesolemya*) *parkinsoni* Smith, 1874, and *Solemya* (*Austrossolemya*) *australis* Lamarck, 1818 (Carter, 1990; Carter et al., 1990; Bailey 2011).

Possible causes of the overlap summarized by Bailey (2011) include: 1) cracking and repair of the fragile umbonal region during growth (Waller, 1990); 2) reclining on one valve within the burrow as in extant *Solemya* (*Petrasma*) *velum* Say, 1822;

and 3) the effects of post-mortem sedimentary compaction on the thin, pliable valves.

Based upon his incorrect assumptions regarding valve inequality and overlap, Beushausen (1895, p. 290) placed Paleozoic so-called “*Solemya*” of previous authors in *Janeia*. In addition, he expanded and shaped his understanding of *Janeia* to include both *Dystactella* and *Clinopistha*. As Beushausen admitted on page 294: “Eine generische Verschiedenheit von *Clinopistha* und *Janeia* kann ich jedenfalls nicht anerkennen.” As exemplars of his broad vision of *Janeia*, he chose four species from the Devonian of the Rhineland previously placed by Goldfuss (1840) in *Sanguinolaria* Lamarck, 1799. Each of these is evaluated below: ***Janeia? compressa* (Goldfuss, 1840)**. Beushausen’s placement of this species in *Janeia* was tentative. Neither his designated type (*Sanguinolaria compressa* Goldfuss, 1840, p. 280, pl. 159, fig. 16a-b) nor his figured specimen (Figure 6H-J) is a solemyid. Both are somewhat modioloid in form with a laterally compressed shell (height/total width = 1.73). Alternatively, both favorably compare with published examples of *Pleurophorella* Girty, 1904, e.g., *Pleurophorella transversa* (de Koninck, 1842) (see Morris et al., 1991, fig. 41) from the Lower Carboniferous of Tournai, Belgium (see Appendix).

FIGURE 6 (figure on previous page). Classic exemplars of *Janeia* King of past authors. **A-G**, *Solemya* (*Janeia*) *vetusta* Meek, 1871 [= *Dystactella* Hall and Whitfield]. **A**, left lateral view, internal mold with partial shell (Meek, 1873, pl. 18, fig. 4), Devonian, Ohio. **B-D**, articulated specimen, Middle Devonian, Louisville, Kentucky. **B**, left lateral view (Hall, 1885, pl. 47, fig. 53). **C**, right lateral view (Hall, 1885, pl. 47, fig. 54). **D**, dorsal view, anterior to right (Hall, 1885, pl. 47, fig. 55). **E**, a left valve showing scalloped radii and cylindrical external ligament, Middle Devonian, Charlestown, Indiana (Hall, 1885, pl. 94, fig. 10). **F-G**, articulated specimen, Middle Devonian, Charlestown, Indiana. **F**, right lateral view (Kindle, 1901, pl. 16, fig. 1). **G**, dorsal view, posterior at right (Kindle, 1901, pl. 16, fig. 1a) showing external nymphae (ne) and internymphal gap (ig). **H-J**, *Janeia? compressa* (Goldfuss, 1840) of Beushausen (1895), an internal mold [= *Pleurophorella? aff. transversa* (de Koninck)], ?Middle Devonian, Daleiden, Germany. **H**, right lateral view (Beushausen, 1895, pl. 26, fig. 1a). **I**, left lateral view (Beushausen, 1895, pl. 26, fig. 1b). **J**, dorsal view showing lunule and escutcheon (Beushausen, 1895, pl. 26, fig. 1c). **K-P**, *Janeia laevigata* (Goldfuss, 1840). **K-L**, an internal mold [= ?*Pleurophorella cf. tricostrata* (Portlock)], Middle Devonian, Gerolstein, Germany; note prosoponal radii and short buttress bordering deeply impressed anterior adductor scar. **K**, left lateral view (Beushausen, 1895, pl. 26, fig. 3a). **L**, right lateral view (Beushausen, 1895, pl. 26, fig. 3b). **M**, lateral view of type (Goldfuss, 1840, pl. 159, fig. 14), gen. indet., Devonian, Eifel; also figured in Beushausen (1895, pl. 26, fig. 8). **N-P**, an articulated specimen [= *Pleurophorella? sp.*], Devonian, Daleiden. **N**, right lateral view (Beushausen, 1895, pl. 26, fig. 2a). **O**, left lateral view (Beushausen, 1895, pl. 26, fig. 2b). **P**, dorsal view (Beushausen, 1895, pl. 26, fig. 2c); note strong similarities to Figure 6J. **Q-V**, *Janeia truncata* (Goldfuss, 1840). **Q**, internal mold with attached shell fragments, left lateral view [= *Clinopistha* Meek and Worthen], Middle Devonian, *Stringocephalus* Limestone, Gerolstein (Beushausen, 1895, pl. 26, fig. 5). **R-T**, internal mold with attached shell fragments [= *Clinopistha*], Devonian, Eifel. **R**, right lateral view (Beushausen, 1895, pl. 26, fig. 4b). **S**, left lateral view (Beushausen, 1895, pl. 26, fig. 4a). **T**, dorsal view, anterior at right (Beushausen, 1895, pl. 26, fig. 4c). **U-V**, internal mold with partial shell [not a solemyid]; lateral views showing circular adductor scar (ad) and distinct pallial line (pl) (Beushausen, 1895, text-fig. 32, p. 297), Middle Devonian, Gerolstein. **W-BB**, *Janeia phaseolina* (Goldfuss, 1840). **W**, lateral view of type (Goldfuss, 1840, p. 279, pl. 159, fig. 15), gen. et sp. indet., Devonian, Eifel; also figured by Beushausen (1895, pl. 26, fig. 9). **X**, lateral view of an internal mold (Beushausen, 1895, pl. 26, fig. 6), Devonian, Eifel [= ?*Edmondia* de Koninck]. **Y-AA**, articulated specimen [= ?*Edmondia*], Gerolstein (Beushausen, 1895, text fig. 31, p. 296). **Y**, right lateral view. **Z**, left lateral view. **AA**, end view. **BB**, lateral view of an internal or composite mold, lower Middle Devonian, Gerolstein (Beushausen, 1895, pl. 26, fig. 7) [possible sanguinolitid; = ?*Myofossa* Waterhouse].

Although the hinge, ligament and internal morphology of *Janeia? compressa* are unknown, the dorsal views of both Goldfuss' shell and Figure 6J are similar. Each is posteriorly elongate with a well-defined lunule and escutcheon.

***Janeia laevigata* (Goldfuss, 1840).** Beushausen described neither the hinge nor internal characters. His first example (Figure 6K-L) favorably compares with *Sanguinolites striatograunulatus* Hind, 1900 (p. 393, pl. 42, figs. 6-22). Though superficially resembling a solemyid in profile and prosopon radii, it is posteriorly elongate. Like *Acharax*, it has an internal buttress, but here it is shorter and posteriorly borders a well-marked anterior adductor. Based on their restudy of Hind's syntypes from the Lower Carboniferous of the Isle of Man and Yorkshire, Morris, et al. (1991, p. 87, fig. 38c-h) judged *S. striatograunulatus* to be a likely synonym of *Pleurophorella tricostata* (Portlock, 1843). Beushausen's second example (Figure 6M), his designated type of *Janeia laevigata*, is a copy of *Sanguinolaria laevigata* Goldfuss, 1840, p. 279, pl. 159, fig. 14. However, because much of it is embedded in sedimentary matrix, the generic identity of the type is indeterminate. His third example (Figure 6N-P) compares in profile to the following: 1) *?Pleurophorella cuneata* (Phillips, 1836) (Morris et al., 1991, p. 88, fig. 42) from the Lower Carboniferous, Bolland, Yorkshire; 2) *Pleurophorella* sp. from the Upper Pennsylvanian of Texas (Morris et al., 1991, fig. 40), and 3) *Pleurophorella?* sp. from the Pennsylvanian of Brazil (Anelli et al., 2009, fig. 2H). The laterally compressed shell (dorsal view, Figure 6P), and well-marked lunule and escutcheon, are notably similar to Beushausen's *Janeia? compressa* (dorsal view, Figure 6J).

***Janeia truncata* (Goldfuss, 1840).** Two of the figured specimens of *J. truncata* on Beushausen's (1895) plate 26 are solemyids (i.e., clinopisthins), probably *Clinopistha* Meek and Worthen (see Figure 6Q-T) although the ligament is not preserved. Beushausen (1895, p. 297) compared *J. truncata* to *Janeia* (*Solemya*) *vetusta* (= *Dystactella valvulus* sensu Pojeta, 1988, non Meek, 1871), whereas Hind (1900) compared it to *Clinopistha*. However, one of Beushausen's examples of alleged *J. truncata* is problematic (Figure 6U-V). The pallial line (pl) is far too distinct for a solemyid (see Cox, 1969, p. N241). In addition, the well-delimited circular profile of the "anterior" adductor scar (ad) suggests a discrete muscular unit, whereas among the Solemyidae it is typically a pyriform composite scar formed by the contiguous placement of the anterior adductor muscle and the visceral/pedal retractor

and protractor muscle complex (Bailey, 2011, p. 12). Cox (1969, p. N242) considered the composite anterior scar to be a distinctive feature of the Solemyidae.

***Janeia phaseolina* (Goldfuss, 1840).** The figured specimens of *J. phaseolina* on Beushausen's (1895) plate 26 appear to be a heterogeneous mix of bivalves none of which are solemyids (see Appendix). Goldfuss's type, *Sanguinolaria phaseolina* Goldfuss, 1840 (see Figure 6W) is generically indeterminate (possible edmondiid?), whereas two of Beushausen's shells (Figure 6X, Y-AA) appear to be edmondiids, possibly *Edmondia* de Koninck, 1841 (see remarks of Hind, 1900, p. 297). A third specimen (Figure 6BB), is substantially different from the others. Although the hinge and ligamental attachment are not shown, the short, sulcate shell with tumid umbo recalls certain sanguinolitids, possibly *Myofossa* Waterhouse, 1969 (see Morris et al. 1991, p. 61, fig. 8).

In his celebrated monograph on Carboniferous bivalves of Great Britain and Ireland, Hind (1900) was critical of Beushausen's (1895) reinstatement and emendation of *Janeia*, suggesting that the dorsal overlap emphasized by Beushausen was largely accidental due to simple displacement of the valves owing to the lack of dentition, noting similar displacement in unrelated bivalve taxa. Moreover, he observed, the left-over-right displacement, though common, was inconsistent. In many cases the displacement was the reverse, and in still other cases displacement was lacking altogether. As a result, Hind reassigned King's type species, *Janeia primaeva* once again to *Solemya*. Although Hind did not discuss the ligament, the internal molds figured specimens in his plate 50 (*Solemya primaeva* Phillips, *Solemya excisa* de Koninck, 1885, and *Solemya costellata* M'Coy, 1844), the simple buttresses and entire posterior adductors favor reassignment to *Acharax*.

The Ligament Puzzle

As noted above, King (1850, p. 247) in his final analysis judged *Janeia* to be identical with *Solemya*. As a result, the placement of the ligament of *Janeia* was presumed to be internal, attached at chondrophores. However, in order to explain the external ligament preserved on some fossil specimens, de Ryckholt (1854, p. 49) surmised that, although the ligament of *Solemya* was attached internally, it nonetheless protruded to the outside. Of particular interest here is Beushausen's (1895, p. 290) observation of a small opening ("schmale Oeffnung") bordered on each side by

“verdickten, schrägen Ligamentstützen” (= external nymphae) in published figures of, for example, *Solemya puzosiana* de Koninck (1842, pl. 5, fig. 2a, 2b; 1885, pl. 23, fig. 34) (i.e., Figure 3B-E herein). Like de Ryckholt before him, Beushausen incorrectly hypothesized the opening (= internymphal gap) to be a dorsal orifice through which King’s alleged internal ligament was permitted to protrude to the exterior. Hind (1900, p. 442) held a similar view. However, Beushausen accorded no particular taxonomic significance to this feature, noting that the opening was seen in some specimens of *Janeia* but not others. Among the Solemyinae, it must be again emphasized here that the presence of the internymphal gap argues for an external ligament as in *Acharax*. Generic placement in *Solemya* is thereby excluded because, as previously noted, the ligament is secondarily enclosed by an outer prismatic layer.

Although Quenstedt (1930), a follower of Beushausen, attempted to describe and illustrate the ligament support structures of *Janeia*, his conclusions are unsupported. At the outset, it must be emphasized that Quenstedt, like his antecedents, began with the erroneous assumption that the ligament of *Janeia*, like that of *Solemya*, was internal. His ink drawings (Quenstedt, 1930, pl. 1, figs. 3-4) compared transverse sections through the beaks,

one in extant *Solemya* (*Zesolemya*) *parkinsoni* Smith, 1874, and the other in a specimen Quenstedt identified as *Janeia truncata* (Goldfuss, 1840), from the Middle Devonian, Gerolstein, Germany. The transverse section of the internal nymph in the former appears, as expected, as a simple, recumbent, distally thickened, sublamellar plate, whereas the transverse section of the latter unexpectedly shows a robust, L-shaped ossicle (Figure 7A) alleged by Quenstedt to be a chondrophore for attachment of an internal ligament, a conclusion derided by Hajkr, et al. (1978, p. 11) as unnatural (i.e., “unnatürlich”). Although the strong angle and upright prolongation of the ossicle are generally consistent with an external nymph, the structure is so unnaturally thick and large that neither it nor the associated ligament could believably be accommodated internally if a similarly structured opposing valve (Figure 7B) were fitted into place (Figure 7C). However, if an internymphal gap is introduced between the ossicles (Figure 7D), a reasonable configuration results. Thus, the problematic ossicles take on the form and placement of paired nymphae. By implication, the restored ligament was probably external.

A second problem in Quenstedt’s (1930) study is his inappropriate choice of *Janeia truncata* as a basis for comparison with *Solemya*. As noted

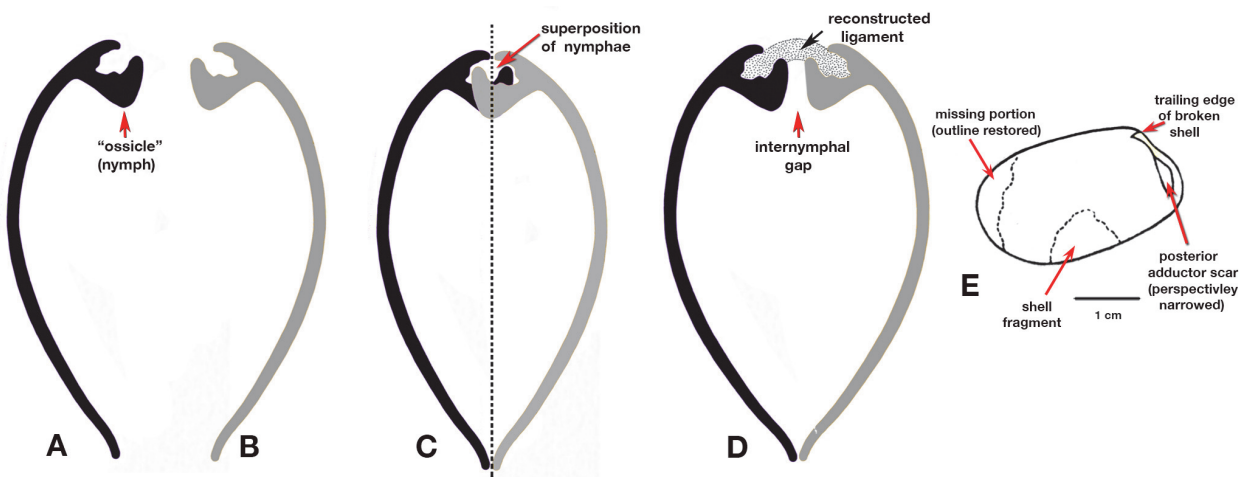


FIGURE 7. Interpretations of a transverse section through the beak of *Janeia truncata*, Middle Devonian of Gerolstein as figured by Quenstedt (1930, pl. 1, fig. 4) and reproduced in the *Treatise* by Cox (1969, N242, fig. B1,1b). **A**, Quenstedt’s original ink sketch, a left valve, showing nymph-like ossicle (arrow) alleged to be a chondrophore for attachment of an internal ligament. **B**, inferred transverse section of right valve. **C**, incompatibility of right and left valves when fitted together with closed dorsal margins. As shown, the ossicle and its inferred counterpart irreconcilably overlap (arrow). **D**, a workable solution achieved by addition of an internymphal gap (arrow) separating the valves posterodorsally. By inference, the ossicles functioned as nymphae supporting an external ligament (stippled pattern, here reconstructed). **E**, Quenstedt’s (1930, pl. 1, fig. 5) diagrammatic reconstruction of *Janeia truncata* based on the internal mold of a left valve figured by Beushausen (1895, pl. 26, fig. 5). For clarification, arrows and explanatory labels are added here.

above, *J. truncata* is a clinopisthin, probably *Clinopistha*, a genus known to have strong external ligaments and nymphae (McAlester, 1968; Pojeta, 1988). Quenstedt's drawing of *J. truncata* (Figure 7E) is a reconstructed outline of the left valve of an anteriorly incomplete internal mold earlier figured by Beushausen (1895, pl. 26, fig. 5). The missing portion of the specimen was restored differently by the two authors. Judging the anterior margin to be relatively short, Beushausen's reconstruction closely resembles *Clinopistha*, whereas Quenstedt's reconstruction shows anterior elongation comparable to *Dystactella*. In either case, the anteroventral growth vector (sensu Pojeta, 1988) is consistent with both *Dystactella* and *Clinopistha* but dissimilar to either *Acharax* or *Solemya*.

The diagrammatic markings along the posterior margin of Quenstedt's reconstruction were explained by Quenstedt in the explanation of his plate 1: 1) the narrow form and triangular outline of the posterior adductor is the result of perspective; 2) the vertical line running dorsally along the anterior margin of the posterior adductor represents the internal curvature of the umbo; 3) the sharp angle and short connecting line directly behind the beak corresponds to the trailing edge of the broken shell remnant and is indicative of the umbonal thickness of the shell (see Figure 7E).

The *Treatise* and Beyond

In Part N of the *Treatise*, Cox (1969, p. N242-N243) accepted *Janeia* as a legitimate Paleozoic subgenus of *Solemya*. His diagnosis (p. N243) of *S. (Janeia)* reads as follows: "Resembling *S. (Solemya)* in external features and in presence of internal chondrophore; with internal ridge [= buttress] originating at anterior end of chondrophore and diverging from it at acute angle, passing below posterior adductor scar. Dev.-Perm., cosmopolitan." Unlike previous authors, Cox mentioned neither valve inequality nor umbonal overlap in his diagnosis. As exemplars, Cox chose a topotype of *Solemya primaeva* Phillips of Hind (1900) (see Figure 5C) and the transverse section of *Janeia truncata* (Goldfuss) of Quenstedt (1930) (see Figure 7A). Cox's conclusions are rejected here for three reasons:

1. As noted by Logan (1967), Pojeta (1988), Bailey (2011) and herein, there is no evidence as alleged that the ligament was internally placed either in the type species or, indeed, any of the other species of *Janeia* proposed by King (1850) or subsequent authors. Cox's conclusion was apparently based on the L-

shaped "chondrophore" in *Janeia truncata* figured by Quenstedt (Figure 7A). As shown above, *J. truncata* is a clinopisthin (probably *Clinopistha*). The L-shaped structures are nymphae supporting an external ligament.

2. Although the figured topotype *S. primaeva* used by Cox is a solemyin, the simple buttress and entire posterior adductor are consistent with *Acharax* but not *Solemya*. Previously, Bailey (2011, p. 30) argued that *S. primaeva* (and its possible variant, *S. parallela* Beede and Rogers, 1899) should be placed in *Acharax* (see Appendix).

3. Cox's conclusion that the internal "ridge" (= buttress) originates at the anterior end of the "chondrophore" and diverges from it at an acute angle was questioned by Dickins (1999) and is unsupported by the many published internal molds attributed to *Janeia*. Whereas it is true that the anterior end of the "chondrophore" (i.e., submarginal nymph) joins the buttress in modern *Solemya*, the two structures show no such connection in published specimens attributed to *Janeia*. Instead, the buttress in the topotypes is simple, continuing, as in *Acharax*, without connection or interruption along its entire length.

In a notable departure from the *Treatise* diagnosis, Liljedahl's (1984b, p. 27) reinterpretation of *Janeia* represents a revival of the criteria of valve inequality and overlap formerly advocated by Meek (1876), Beushausen (1895), and Dechaseaux (1952). His species, *Janeia silurica* Liljedahl, 1984a (Silurian of Mölbos, Gotland), is herein placed in the Clinopisthinae. As shown in his photographs (Liljedahl, 1984a, fig. 14A-J; 1984b, text-fig. 1.1-1.6), the primary ligament (parivincular, opisthodontic) was attached at strong external nymphae. The parivincular primary ligament, internal features, and anteroventrally extended shell profile all support Pojeta's (1988, p. 217) contention that *J. silurica* should be reassigned to *Dystactella*. However, the left-over-right umbonal overlap in *J. silurica* is associated with a minor subumbonal ossicle (Liljedahl, 1984b, fig. 14H, 14I) present only in the right valve. The significance of this unique feature, which has elsewhere not been reported in *Dystactella*, was discussed by Bailey (2011).

Other studies accepting *Janeia* as a valid genus include Zhang (1977), Kłapciński and Karwowski (1978), Bernard (1980), Muromtseva (1981), Muromtseva and Guskov (1984), and Zhang and Pojeta (1986) (see Appendix). Like Cox (1969) before them, these studies either incorrectly

accepted the ligament of *Janeia* as internal or do not mention the ligament at all. Bernard (1980, p. 21) regarded *Janeia* as a Permian subgenus of *Solemya* marked by prominent umbos at the posterior $\frac{1}{4}$ of the shell. Treating *Janeia* as a separate genus with a range of Silurian-Triassic, Nevesskaja, et al. (2013, p. 90) placed diagnostic emphasis on valve overlap.

JANEIA VERSUS JANACEKIA

There is a significant complication to the *Janeia* story. Růžicka and Řehoř (1978) were critical of King's (1850) withdrawal of the name *Janeia* in favor of *Solemya*, arguing that King had failed to provide objective evidence that *Janeia* was related to *Solemya*. Determination of the anterior and posterior ends of the shell, placement of the ligament, and organization of the internal anatomy, they asserted, were King's personal opinions. Yet, because King's original diagnosis of *Janeia* is both ambiguous and subjective, they were also critical of subsequent authors who adopted the name. Curiously, however, Růžicka and Řehoř (1978) agreed with King's erroneous opinion that the long end of the shell is posterior. In their study of an assemblage of *Janeia*-like shells from the Carboniferous of the Czech Republic, Růžicka and Řehoř (1978) concluded that the ligament was external, rather than internal, as King (1850) and subsequent authors had alleged. By comparing their shells to those of extant *Solemya togata*, Poli 1795, they also affirmed that King (1850) was wrong in asserting that the ligament of *Janeia*, like that of *Solemya*, was internal. Unfortunately, the authors did not compare their material with extant examples of *Acharax*, comparing them instead to the solecurtid genus *Tagelus* Gray, 1847, which they selected as an archetype. Because their interpretations agreed neither with *Solemya* nor *Janeia* sensu King, they proposed a new genus, *Janacekia* Růžicka and Řehoř, 1978, herein accepted as a junior synonym of *Acharax*. Thus, there is neither justification for recognition of Růžicka and Řehoř's family Janacekiidae nor any basis for regarding it as synonym of the Solemyinae as opposed to the Acharachinae (contra Bieler, et al., 2010, p. 115).

Both *Acharax* and *Janacekia* share the same shell profile, the same thick periostracum marked by radial ribs and lirae, and the same primary ligament (external, parivincular, opisthodontic). Significantly, the ligament of *Janacekia* as originally described by the authors is ironically in agreement with *Acharax* but not *Solemya*: "Ligament ist ein äußeres, kurz und opisthodont." (Růžicka and

Řehoř, 1978, p. 37). However, because their understanding of anterior and posterior is reversed, the term "opisthodont" was incorrectly applied. Thus, this portion of their description becomes essentially correct but for the wrong reason.

Of critical importance in diagnosing *Janacekia* is a unique feature Růžicka and Řehoř termed the "pseudolunula", consisting of paired external lamellae located on the brevidorsum. Having observed an equivalent feature in "*Solemya radiata*" Meek and Worthen, 1866 (Pennsylvanian of Illinois), they suggested that "*S. radiata*" would more reasonably be placed in *Janacekia* rather than *Solemya*. However, based on examples with well-preserved ligaments from the Mazon Creek Lagerstätte (Pennsylvanian of Illinois), Bailey (2011) transferred "*S. radiata*" to *Acharax*. Visual comparison of the brevidorsum of *Janacekia* (e.g., fig. 64 of Růžicka and Řehoř, 1978) with that of *Acharax* (e.g., pl. 2, fig. 2 of Pojeta, 1988) demonstrates that the "pseudolunula" and external nymphae are synonymous.

Janacekia and *Acharax* show additional similarities that further secure their identity. As shown in figure 61 of Růžicka and Řehoř (1978), the buttress in *Janacekia*, as in *Acharax*, is simple, extending dorsally from the anterior limit of the posterior adductor scar to the underside of the umbo without any suggestion of attachment to nymphae, and the posterior adductor muscle shows no indication of dorsal occlusion.

Although the analysis of *Janacekia* by Růžicka and Řehoř (1978) is comprehensive, it contains numerous errors and internal contradictions. For example, in their extensive biometric section (p. 18-27) the anteriorly elongate shell orientation is understood correctly, whereas, in the systematic section, the incorrect orientation (posteriorly elongate) is applied beginning on their page 37: "Der Vorderteil der Schalen ist kurz, enger als die Hinterseite. Die hintere Teil ist stets länger als die Vordere." In addition, the authors provided a detailed reconstruction (their fig. 65) of the foot and pedal accessory musculature (pedal protractor, retractors, and elevators) placed at the short end of the shell, which they regarded incorrectly as the anterior.

Interpretative errors notwithstanding, the deltoid outline of the distinctive external, convex-upward ligament of *Acharax* is documented in those authors' photos of *Janacekia herberti* (pl. 1, fig. 2, showing collapsed ligament with nymph termini), and *Janacekia leosi* (pl. 7, fig. 9). Moreover, deltoid traces (or possible traces) of the external

ligament of *Janacekia herberti* and *Janacekia leosi* seem evident in several of their other photos (pl. 3, fig. 12; pl. 8, fig. 9; pl. 11, fig. 4; and especially both pl. 7, fig. 9 and pl. 14, fig. 6). Traces of the anterior ligamental extension like *Acharax radiata* (Meek and Worthen, 1860) as figured by Bailey (2011, pl. 3, 4) are evident in their pl. 6, fig. 8. The type species, *Janacekia herberti* from the Carboniferous (Namurian) Ostrava Schichtengruppe, Upper Silesian Coal Basin, Czech Republic, is so remarkably similar to *Acharax radiata* (Meek and Worthen) from the Mazon Creek Lagerstätte that, aside from differences in the relative relief of the radial ribs, the two are nearly indistinguishable. For example, compare Růžicka and Řehoř (1978, pl. 7, fig. 9) with Bailey (2011, pl. 3, figs. 1-9; pl. 4, figs. 1-7). Interestingly, Růžicka and Řehoř listed numerous specimens referred by various authors to *Solemya primaeva* Phillips (= type species of *Janeia* King, 1850) as synonyms of both *Janacekia herberti* and *Janacekia leosi*. However, as noted above and by both Bailey (2011, 2016) and Logan (1967), *S. primaeva* is a probable *Acharax*.

In addition to *J. herberti*, three additional species of *Janacekia* (i.e., *J. leosi*, *J. mariae*, and *J. talboti*) were described by Růžicka and Řehoř (1978) (see Appendix). However, the apparent differences in shell profile and prosopon, which both seem fairly minor, are possibly due to variable taphonomic effects on the thin shells and compliant periostracum.

CONCLUSIONS

Character state analysis of the primary ligament and its support structures argues that *Acharax* and *Solemya* are monophyletic, a conclusion now in harmony with 18S rRNA and DNA studies (Taylor et al., 2008; Sharma et al., 2013). Thus, classification systems placing the two genera in separate families or superfamilies are not supported; Pojeta's (1966) placement of the two genera together in a single family and subfamily (Solemyidae: Solemyinae) is preferred.

Within the Solemyidae the external ligament and nymphae of *Acharax*, *Clinopistha*, *Dystactella*, and *Psilooncha* are shared primitive (symplesiomorphic) characters, whereas the unique submarginal ligament and nymphae of *Solemya* are shown to be derived (autapomorphic) characters.

The submarginal nymphae of *Solemya* arose through depression of the external nymphae of *Acharax* ancestors followed by secondary overgrowth of a thin outer shelly layer, thus covering the ligament as well as its supporting nymphae and

the internymphal gap separating them. Previously, submarginal nymphae in *Solemya* have been unsuitably termed "chondrophores", thus obscuring their homological relation to external nymphae of *Acharax*.

The adjusted ranges of *Acharax* and *Solemya* are: Lower Devonian-Holocene for *Acharax*; and Mesozoic (possibly Jurassic)-Holocene for *Solemya*.

Where ligaments are not preserved, fossil *Acharax* and *Solemya* are distinguishable from internal molds. New terms representing these characters are introduced: An internymphal gap, evident in *Acharax*, is absent in *Solemya*; a simple buttress, evident in *Acharax*, is compound in *Solemya*; an entire posterior adductor scar, evident in *Acharax*, is occluded in *Solemya*.

Misconceptions relating to King's (1850) Paleozoic genus *Janeia* have been instrumental in obscuring the monophyletic connections between *Acharax* and *Solemya*. Especially significant is the erroneous belief that *Janeia*, like *Solemya*, possessed an internal ligament - incorrectly presumed to represent a primitive (plesiomorphic) condition.

King's (1850) material basis for *Janeia* is critically reviewed. Although the figured type of *J. primaeva* (Phillips, 1836) (= King's selection as type species) is lost, topotypes have an external primary ligament and should be placed in *Acharax*. The remaining designated species of King (1850) are *J. biarmica* (de Verneuil, 1845) and *J. phillipsiana* (King, 1848). King's example of *J. biarmica* is a misidentified *Wilkingia elegans* (King, 1850), whereas de Verneuil's (1845) figured type designated *Solemya biarmica* is a clinopisthin, probably *Dystactella*. *Janeia phillipsiana* of King is an alleged fiction based on non-existent fossils.

In this study, Paleozoic solemyids previously placed in *Janeia* have been found to be mainly assignable either to *Acharax*, *Dystactella*, or *Clinopistha*. Other alleged *Janeia* (misidentifications) are not solemyids (see Appendix).

Based on King's (1850) erroneous assertions, subsequent authors were persuaded that Paleozoic solemyids possessed an internal ligament. De Ryckholt (1854), Beushausen (1895), and Hind (1900) misinterpreted the internymphal gap as an orifice (or slit) through which a presumed internal ligament was permitted to emerge to the outside. The small ossicle shown in Quenstedt's (1930) transverse section of *J. truncata*, is reinterpreted herein as an external nymph rather than an internal chondrophore as he had originally supposed. Unfortunately, Quenstedt's misinterpretation cou-

pled with King's erroneous conclusions formed the principal basis for acceptance of *Janeia* as a valid subgenus by Cox (1969) in the *Treatise*, Part N.

Janacekia is a problematic genus originally proposed by Růžička and Řehoř (1978) as a rejection of *Janeia* based on its inherent ambiguity and confusing history. Present analysis shows their interpretation of the shell orientation and ligamental structure to be incorrect. *Janacekia* is herein accepted as a junior synonym of *Acharax*.

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APPENDIX

PALEOZOIC SOLEMYIDAE - REVIEW AND REVISION OF SELECTED TAXA

The following treatise is a preliminary assessment and taxonomic review of Paleozoic bivalves misclassified either as *Janeia*, *Janacekia*, or *Solemya* (including nomina vana variants, *Solenomya* or *Solenimya*) based in part on the unsubstantiated assumption that among Paleozoic examples the primary ligament was set in internal chondrophores. Emphasis here is mostly on generic level evaluation and revision. Within synonymies, descriptive annotations and provenance are provided for most listings. The format in part follows recommendations of Matthews (1973) and Bengtson (1988). Publication dates given by de Ryckholt for various portions of his *Mélanges Paléontologiques* are revised based on Rosenberg and Petit (1987).

Abbreviations. Diagnostic character states observed: Bts = simple buttress; Dp = ligamental demipad; IG = internymphal gap; Le = ligament visibly external; Ne = nymphae external; PAe = posterior adductor entire; PP = traces of periostracal 'awning'. Prosopon: Pc = comarginal lirae/rugae; Pc0 = comarginal elements lacking; Pr0 = radii absent or not observed; Pr1f = fine, closely spaced radii; Pr1 = radii weak or obsolescent; Pr2 = radii marked; Pr3 = radii strongly marked; Prs = radii with scalloped pattern.

SYSTEMATIC PALEONTOLOGY

- Class BIVALVIA Linnaeus, 1758
- Subclass PROTOBRANCHIA Pelseneer, 1889
- Superorder NUCULIFORMII Dall, 1889
- Order SOLEMYOIDEA Dall, 1889
- Superfamily SOLEMYOIDEA Gray, 1840
- Family SOLEMYIDAE Gray, 1840
- Subfamily SOLEMYINAE Gray, 1840
- Genus ACHARAX DALL, 1908
- [= *Janacekia* Růžička and Řehoř, 1978]

Type species. By original designation, *Acharax johnsoni* (Dall, 1891), Holocene, NE Pacific.

Acharax primaeva (Phillips, 1836)

Remarks. Lost holotype of Phillips (1836) was imperfectly illustrated and diagnosed. Useful if Hind's (1900, in part, pl. 50, figs. 4, 5) topotypes are given priority (e.g., Cox, 1969). If so, *Solemya puzosiana* de Koninck, 1842 is a probable synonym. Hind (1900, p. 441) compared it with *S.*

costellata and *S. excisa* but with stronger radial ribs.

- ? 1836 *Solemya primaeva* Phillips, p. 209, p. 247, pl. 5, fig. 6 [Pr3?, PAe?; nom. dub.; figure and diagnosis insufficient; holotype lost]; Lower Carboniferous, Lowick, Northumberland, England.
- 1842 *Solemya puzosiana* de Koninck, p. 60, pl. 5, fig. 2a, b [Pr3, Ne?, IG; = *A. cf. primaeva*, i.e., similar to Hind's (1900) topotypes and Portlock's (1836) hypotype of *S. primaeva*]; Lower Carboniferous, (Tournaisian), Belgium.
- 1843 *Solemya primaeva* Phillips; Portlock, p. 441 [no figure; later figured by Hind (1900)]; Carboniferous, Aghaloo, Co. Tyrone, N. Ireland.
- 1844 *Sanguinolites radiatus* M'Coy, 1844, p. 50, pl. 13, fig. 4 [Pr3; synonym of Hind (1900, p. 438)]; Carboniferous, Killymeal, Dungannon, Co. Tyrone, N. Ireland.
- ? 1845 *Solemya primaeva* Phillips; de Verneuil, p. 295, pl. 19, fig. 5 [Pr2; gen. et sp. indet.; partial valve; hinge unknown]; Lower Carboniferous, Tarusa, Oka River, Russia.
- ? 1849 *Solemya primaeva* Phillips; Brown, p. 230, pl. 93, fig. 10 [Pr3?; stylized drawing after Phillips, 1836, pl. 5, fig. 6]; Lower Carboniferous limestone, Heiton and Lowick, Northumberland, England, and Co. Fermanagh, N. Ireland.
- 1850 *Janeia primaeva* (Phillips); King, p. 177 [no figure].
- 1850 *Solemya primaeva* Phillips; King, p. 246-247 [no figure].
- ? 1855 *Solenimya? primaeva* Phillips; M'Coy (?M'Coy), p. 519, pl. 3F, fig. 3, 3a [hypothetical reconstruction]; Lower Carboniferous limestone, Lowick, Northumberland, England.
- 1855 *Solenimya primaeva* Phillips var. *β puzosiana* M'Coy, p. 520 [no figure]; Carboniferous, Derbyshire, and Northumberland, England [Accepted by M'Coy (1855) as a variety of *S. primaeva*].
- non 1859 *Solenomya primaeva* Phillips; Eichwald, [plates pub. 1859, text pub. 1860]; p. 5, pl. 39, fig. 10a-b (1859) [Pr2; highly elongated shell with aberrant (upwardly curving) longiterminus; gen. et. sp. indet.; possibly not a solemyid]; p. 1040-1041 (1860); Carboniferous limestone, Tarusa and Peredki, Novgorod Oblast, Russia.
- p 1885 *Solemya puzosiana* de Koninck; de Koninck, p. 120, pl. 23, fig. 41 [Pr3, Ne?]; fig. 29? [Pc, Pr0]; figs. 33?, 34? [Pr2, Ne, IG]; [possibly

- composed of more than one species; see Bailey, 2011, p. 30]; fig. 41 [= *A. cf. primaeva*]; Lower Carboniferous (Tournaisian), Belgium.
- 1896 *Solemya primaeva* Phillips; Hind, p. 6, 27, 53.
- 1900 *Solenomya primaeva* Phillips; Hind, pl. 50, fig. 1 (not fig. 2 as stated by Hind in error on p. 440) [Pr3, Bts, PAe; Portlock's (1836) unfigured hypotype; compares with topotypes but much larger and anteriorly more expanded]; Carboniferous, Aghaloo, Co. Tyrone, N. Ireland.
- ? 1900 *Solenomya primaeva* Phillips; Hind, pl. 50, fig. 2? [Pr3; provenance?], pl. 50, fig. 3? [Pr3; valves shorter and dissimilar in profile to Hind's topotypes; = *A. cf. costellata*?]; Carboniferous limestone series, Ardross, Fife, Scotland.
- p 1900 *Solenomya primaeva* Phillips; Hind, p. 438, pl. 50, figs. 4, 5 [topotypes, herein given priority; Pr3, Bts, PAe, IG]; Lower Carboniferous limestone, Lowick, Northumberland, England; non pl. 50, fig. 2 [Pr3; provenance?]; non pl. 50, fig. 3 [a hypotype, Pr3; shorter, more ovoid in profile], Carboniferous limestone series, Ardross, Fife, Scotland.
- 1900 *Solenomya primaeva* Phillips; Hind, pl. 50, fig. 6 [Pr3, Bts, PAe?; copy of M'Coy's 1844 hypotype of *Sanguinolites radiatus*; like Portlock's hypotype but much smaller]; Carboniferous, Killymeal, Dungannon, Co. Tyrone, N. Ireland.
- 1969 *Solemya (Janeia) primaeva* (Phillips); Cox, p. N243, fig. B1, 1a [topotype, Pr3, Bts, PAe; copy of Hind, 1900, pl. 50, fig. 5]; Lower Carboniferous limestone, Lowick, Northumberland, England.
- 1986 *Solemya (Janeia) primaeva* (Phillips); Zhang and Pojeta, p. 670, fig. 5.4 [Pr3, PAe, Bts(weak)]; Lower Carboniferous (Viséan), China.
- 2011 *Acharax primaeva* (Phillips); Bailey, 2011, p. 30
- 2013 *Janeia primaeva* (Phillips); Nevesskaja, et al., p. 90, pl. 12, fig. 12.5 [copy of Hind, 1900, pl. 50, fig. 5].
- Acharax costellata* (M'Coy, 1844) sp. inq.
- Remarks.** Needs further study. Reviewed by Bailey (2011, p. 30). Hind (1900, p. 441) compared the form as similar to *S. primaeva* but with radial ribs weak to obsolescent. M'Coy's (1844, p. 48) original description is limited; the holotype, figured both by M'Coy (1844) and by Hind (1900), is an ambiguous shell fragment. Possibly useful if Hind's (1900, in part, pl. 50, figs. 8-10, non fig. 7) hypotypes are given priority. If so, one of de Koninck's (1885, pl. 23, fig. 31) examples of *Solemya saginata* is a possible synonym. Compares with *Acharax radiata* (Meek and Worthen) but not with *A. primaeva* (Phillips).
- ? 1844 *Sanguinolites costellatus* M'Coy, p. 48, pl. 8, fig. 5 [nom. dub.; gen. et. sp. indet. Pr2; fragmentary; longiterminal half missing; hinge unknown; short radial ribs faint but limited to breviventral margin]; Carboniferous, Ireland.
- non 1854 *Solemya saginata* de Ryckholt, ("1847"), p. 53, pl. 11, figs. 9, 10 [= *Dystactella cf. subnasuta*]; l'argile carbonifère, Antoing, Belgium.
- ? 1885 *Solemya saginata* de Ryckholt; de Koninck, p. 121, pl. 23, figs. 31 [Pr2, Pc Ne?], 32? [Pr2, Pc]; Lower Carboniferous (Tournaisian), calcaire carbonifère, Tournai, Belgium.
- ? 1900 *Solemya costellata* M'Coy; Hind, p. 442, pl. 50, fig. 13 [Pr2, fragmentary; gen. et sp. indet.; Hind's own figure of M'Coy's (1844) holotype]; Carboniferous, Killyclogby, Lisbellaw, Co. Tyrone, N. Ireland.
- p 1900 *Solenomya costellata*; Hind, p. 442, pl. 50, fig. 8 [Pr2, PAe], fig. 9 [Pr3, Bts?], fig. 10 [Pr2]; non fig. 7; Lower Carboniferous, Lowick and Redesdale, Northumberland, England.
- ? p 1900 *Solemya excisa* de Koninck; Hind, p. 441, pl. 50 figs. 12, 16 [Pc, Pr2, Bts, PAe, = *Acharax cf. costellata*]; Carboniferous, Ardross, Scotland; non pl. 50, figs. 11, 14, 15 [ventrally embayed; Pc, Pr1; = *Acharax cf. normalis* sensu Howse]; Lower Carboniferous, Lowick, Northumberland. [See also *Dystactella excisa* (de Koninck)].
- Acharax cf. normalis* (Howse, 1848) n. comb.
- Remarks.** No figure accompanied Howse's (1848) description; his subsequent (1857a) figure is rudimentary and is, as he personally remarked, inaccurate; holotype lost. Useful if Logan's (1967, pl. 10, figs. 13, 14) material is given priority. If so, *Solemya excisa* de Koninck of Hind (1900, in part, pl. 50, figs. 11, 14, 15) is a possible synonym.
- ? 1848 *Solenimya normalis* Howse, p. 244 [nom. dub.; description only; no figure; radii described as lacking]; Upper Permian, Magnesian Limestone, Humbleton Hill Quarry, Durham, England.
- non 1848 *Solemya phillipsiana* King, p. 11 [allegedly fictitious (nom. nud.) but accepted by King as senior synonym of *S. normalis* Howse].
- non 1850 *Janeia phillipsiana* King; King, p. 179, pl. 16, fig. 8 [description and figure, allegedly fictitious (nom. nud.) but accepted by King as senior synonym of *S. normalis* Howse].

- ? 1857a *Solemya normalis* Howse; Howse, p. 25, pl. 4, fig. 7 [Pr1; nom. dub.; rudimentary drawing; anterior margin described by Howse as inaccurate; holotype lost]; Upper Permian, Magnesian Limestone, Humbledon Hill, Durham, England.
- ? 1861 *Solemya normalis* Howse; Geinitz, p. 61, pl. 12, figs. 20, 21? [gen. et sp. indet.; prosopon with fine comarginal growth lines and a few obsolescent radii]; Upper Permian (lower Zechstein), Thieschitz bei Gera, Germany.
- non 1894 *Solemya normalis* Howse; Netschajew, p. 303, pl. 10, fig. 7 [gen. et sp. indet.; possible edmondii?]; Permian, Volga River, mouth of Kama, Russia.
- ? p 1900 *Solenomya excisa* de Koninck; Hind, pl. 50, figs. 11, 14, 15, [ventrally embayed; Pc, Pr1; = *Acharax* cf. *normalis*]; Lowick, Northumberland; non pl. 50, figs. 12, 16 [= *Acharax* cf. *costellata*]; Carboniferous, Ardross, Scotland. [See also *Dystactella excisa* (de Koninck)].
- 1967 *Janeia normalis* (Howse); Logan, p. 61, pl. 10, figs. 13, 14 [best published examples; Pr1, Le]; Upper Permian, Middle Magnesian Limestone, Tunstall Hill, Durham, England.
- ? 1978 *Janeia normalis* (Howse); Kłapciński and Karwowski, p. 73, pl. 3, figs. 1, 2 [Bts?; = aff. *Acharax*]; Upper Permian (middle Zechstein), Main Dolomite, Stassfurt Cyclothem, Poland.
- non 1981 *Solemya (Janeia) normalis* (Howse); Muromtseva, p. 29, pl. 10, fig. 18 [Pc, Pr0; very small, gen. et sp. indet.; possible edmondii? or nuculoid?]; Upper Permian, Novaya Zemlya.
- non 1984 *Solemya (Janeia) normalis* (Howse); Muromtseva and Guskov, p. 35, pl. 24, fig. 15, Seregov, Komi Republic, Russia; pl. 41, fig. 18 [Pc, Pr0; very small, gen. et sp. indet.; edmondii?]; Upper Permian (Kazanian) Novaya Zemlya.
- Acharax radiata* (Meek and Worthen, 1860)
- Remarks.** Figures, missing in Meek and Worthen's (1860) original publication, were later added by the same authors (1866, pl. 26, figs. 10a-b). Compares with *A. costellata* (M'Coy), *A. herberti* (Růžička and Řehoř), and *A. cylindrica* (Hind), but not with *A. primaeva* s. s. Widely accepted; reviewed by Pojeta (1988) and Bailey (2011).
- 1860 *Solemya radiata* Meek and Worthen, p. 457 [no figure]; Pennsylvanian Coal Measures, Grayville, Illinois; [figure published by the authors in 1866].
- 1866 *Solenomya radiata* Meek and Worthen; Meek and Worthen, p. 349, pl. 26, fig. 10a-b [Pr2, Ne]; Pennsylvanian Coal Measures, Schuyler Co., Illinois.
- ? 1872 *Solenomya* sp. Meek, pl. 2, fig. 12a-b [figures only; no description; partial internal mold with attached shell fragment; Pr0, Bts?, Ne?]; Pennsylvanian, Upper Coal Measures, Rock Bluff, Nebraska.
- 1877 *Solenomya radiata* Meek and Worthen; Miller, p. 204 [no figure].
- 1889 *Solenomya radiata* Meek and Worthen; Miller, p. 512 [no figure].
- 1896 *Solemya radiata* Meek and Worthen; Hind, p. 32 [no figure].
- 1900 *Solenomya radiata* Meek and Worthen; Beede, p. 160, pl. 22, fig. 5-5a [Pr2-3, Ne?; copy of Meek and Worthen's description]; Pennsylvanian, Topeka, Kansas.
- 1922 *Solenomya radiata* Meek and Worthen; Morningstar, p. 193-194 [description but no figure]; Pennsylvanian, lower Mercer Limestone, Muskingum Co., Ohio.
- non 1930 *Solenomya radiata?* Meek and Worthen; Branson (?Branson), p. 41, pl. 9, figs. 21, 22 [Pr0, Pc0; featureless cast of an internal mold, gaping (?) at both ends; ligament and hinge unknown; same specimen (UM 5275) tentatively called *Solemya* sp. by Ciriacks (1963); profile resembles *Dystactella*]; Upper Permian, Park City Formation, Ervay Member, near Cody, Wyoming.
- 1961 *Solemya radiata* Meek and Worthen; Hoare, p. 94, pl. 12, fig. 12 [Pr2]; Middle Pennsylvanian (Desmoinesian), Tiawah Limestone, St. Clair Co., Missouri.
- ? 1961 *Solemya* sp. Hoare, p. 96, pl. 12, fig. 13 [Bts, PAe; partial internal mold; possibly *Acharax radiata?*]; Middle Pennsylvanian (Desmoinesian), Seville Limestone, Henry Co., Missouri.
- 1979 *Solemya (Janeia) radiata* (Meek and Worthen); Hoare, Sturgeon and Kindt, p. 29, pl. 2, fig. 12 [Pr2], fig. 13? [Pr2]; Middle Pennsylvanian, Putnam Hill Shale, Ohio.
- 1983 *Solemya (Janeia) radiata* (Meek and Worthen); Kues, p. 80 [no figure]; Middle Pennsylvanian, Upper Los Moyos Limestone, Cedro, New Mexico.
- 1988 *Solemya radiata* Meek and Worthen; Pojeta, p. 215, pl. 22, figs. 1, 2, 5 [Pr3], fig. 4 [Pr3, Bts], Pennsylvanian Coal Measures, New Lisbon, Ohio; pl. 22, fig. 3 [Pr2], Pennsylvanian, Schuyler Co., Illinois; figs. 6, 7 [Pr2], fig. 10 [Pr3], pl. 23, figs. 1, 2 [Pr2], figs. 3, 4 [Pr2, Bts, PAe]; Pennsylvanian, Henry Co., Missouri.
- non 1988 *Solemya radiata* Meek and Worthen; Pojeta, pl. 24, figs. 2, 3 [Pr1, Bts, PAe]; Pennsylvanian, Illinois?; figs. 4, 6 [Pr2, Bts, PAe; =

- Acharax (Nacrosolenomya) trapezoides*; Pennsylvanian, Kansas City, Missouri.
- 1992 *Solenomya radiata* Meek and Worthen; Kues, p. 91, figs. 2.7, 2.8 [Pr3, Bts, PAe]; Upper Pennsylvanian, basal limestone, Kinney Quarry, Manzanita Mts., New Mexico.
- 1997 *Solenomya radiata* Meek and Worthen; Cope, pl. 1, fig. 10 [Pr3, Le(?)]; Upper Carboniferous, Ohio.
- 1997 "*Solenomya radiata*" Meek and Worthen; Bailey and Sroka, p. 101, fig. 8A.2, C-E [Pr2, Le]; Middle Pennsylvanian (Westphalian D), Francis Creek Shale, Carbondale Formation, Will-Kankakee counties, Illinois.
- 2011 *Acharax radiata* (Meek and Worthen); Bailey, 2011, p. 27, pl. 3, figs. 1-6, 9; pl. 4, figs. 1-7 [based on topotypes; Pr2-3, Bts, PAe, Ne, Le, IG, PE]; Middle Pennsylvanian (Westphalian D), Francis Creek Shale, Carbondale Formation, Will-Kankakee and Fulton counties, Illinois.
- Acharax (Nacrosolenomya) trapezoides* (Meek, 1874)
- Remarks.** First published as a figure (*Solenomya* sp. undet. Meek and Worthen, 1873, pl. 27, fig. 1a-b); later named by Meek (1874, p. 583) but only briefly characterized. Beede and Rogers (1899, p. 132) gave the first detailed description. Reviewed by Pojeta (1988) and Carter (1990); lectotype nominated by Bailey (2011).
- 1873 *Solenomya* sp. undet. Meek and Worthen, pl. 27, fig. 1a-b [Pc, Pr0, Ne, Dp]; same specimen (USNM 36315; labeled, "Coal Meas. Illinois?") later figured by Bailey (2011, p. 31, pl. 5, figs. 1-5) and nominated as lectotype of *Acharax trapezoides* (Meek and Worthen)].
- 1874 *Solenomya* sp. undet. Meek, p. 582 [ref. Meek and Worthen, 1873, pl. 27, fig. 1a-b].
- 1874 *Solenomya (Janeia) trapezoides* Meek, p. 583 [ref. Meek and Worthen, 1873, pl. 27, fig. 1a-b].
- 1899 *Solenomya trapezoides* Meek; Beede and Rogers, p. 132, pl. 34, fig. 2a-b [Pc, Pr0/Pr1, Bts, PAe, Ne, IG]; Pennsylvanian, Coal Measures, Westport, Missouri, and Porterville, Kansas.
- 1900 *Solenomya trapezoides* Meek; Beede, p. 159, pl. 21, fig. 2a-b [Pc, Pr0, Bts, PAe, Ne]; near junction of Upper and Lower Coal Measures, Porterville, Kansas, and Westport, Missouri.
- ? 1961 *Solenomya trapezoides* Meek; Hoare, 1961, p. 96, pl. 12, fig. 14 [Pr0; few details; more smoothly rounded than other *A. (N.) trapezoides*]; Weir-Pittsburg Coal, Henry Co., Missouri.
- ? 1979 *Solenomya (Janeia) trapezoides* Meek; Hoare, Sturgeon and Kindt, p. 30, pl. 2, figs. 14? (fragment), 15? (fragment), 16, 17 [Pc]; Pennsylvanian, Putnam Hill Shale, Ohio.
- 1988 *Solenomya trapezoides* Meek; Pojeta, p. 215, pl. 22, figs. 8, 9 [Pr1, Bts, PAe.]; Pennsylvanian, Henry Co., Missouri; pl. 24, fig. 1? [Pr2, Bts, PAe]; Pennsylvanian, Beatrice, Nebraska; pl. 24, fig. 5? [Pr2, Bts, PAe]; Pennsylvanian, Clover Land, Clay Co., Indiana; pl. 24, figs. 7, 8 [Pr1, Bts, PAe]; Pennsylvanian, Kansas City, Missouri.
- 1988 *Solenomya* sp. Pojeta, pl. 23, figs. 5-8 [Pr1, Bts, PAe, Ne, IG]; Pennsylvanian, Hertha Limestone, Kansas.
- ? 1988 *Acharax?* sp. Pojeta (?Pojeta), pl. 20, fig. 9 [left internal mold; Pc, Pr1, PAe, Bts(weak); compares with *A. (N.) trapezoides*]; Permian, near Wymore, Nebraska.
- 1990 *Acharax (Nacrosolenomya) trapezoides* (Meek); Carter, 1990, p. 174, figs. 17, 18 [Pr0/Pr1, Le, Ne]; Upper Carboniferous, Breathitt Formation, Eastern Kentucky.
- 1992 *Solenomya trapezoides* Meek; Kues, p. 93, fig. 2.9 [Pc, Bts?, Ne], fig. 2.10 [Pc, Pr1]; Upper Pennsylvanian, basal limestone, Kinney Quarry, Manzanita Mts., New Mexico.
- 1997 *Acharax (Nacrosolenomya) trapezoides* (Meek); Bailey and Sroka, p. 102 [no figure].
- 2002 *Solenomya trapezoides* Meek; Kues et al., 2002, p. 129, fig. 4Q [Pc]; Upper Pennsylvanian, Derry Hills, New Mexico.
- ? 2003 *Solenomya trapezoides* Meek; Krainer, et al., 2003, fig. 7L [Pc, Pr0 Le; Bts; poorly preserved composite mold; shell profile short and rounded, nearly ovoid; intermediate (?) between *A. trapezoides* and *A. radiata*]; Upper Pennsylvanian, Zuni Mts., New Mexico.
- 2011 *Acharax (Nacrosolenomya) trapezoides* (Meek); Bailey, p. 31, text-fig. 3, Middle Pennsylvanian, Carbondale Formation, Canton, Illinois; pl. 5, figs. 1-5; = lectotype, USNM 36315, "Coal Meas., Illinois?" [Pc, Pr1, Bts, PAe, Ne, IG]; pl. 5, fig. 6 [Pr1]; Middle Pennsylvanian, Carbondale Formation, Will Co., Illinois.
- Acharax parallela* (Beede and Rogers, 1899)
- Remarks.** Junior homonym of *Solenomya parallela* de Ryckholt. Known mostly from original designation by Beede and Rogers (1899). Subsequent reports are questionable. Compares with *A. primaeva* (Phillips) (see Bailey, 2011, p. 30, 37). Logan's (1967, in part) example of *Janeia biarmica* is a possible synonym.

- non 1853 *Solemya parallela* de Ryckholt, ("1854"), p. 51, pl. 11, figs. 11, 12 [senior homonym; not a solemyid; = *Wilkingia*?, i.e., *W.*? aff. *abramovi* Muromtseva in Biakov, 2019, pl. 3, fig. 20]; Lower Carboniferous, (Tournaisian) l'argile carbonifère, Tournai, Belgium.
- 1899 *Solenomya parallela* Beede and Rogers, p. 131, pl. 34, fig. 1 [Pr3, Bts, PAe]; Pennsylvanian Coal Measures, Kansas City and Lawrence, Kansas.
- ? 1952 *Solemya (Janeia) parallela* (Beede and Rogers); Chronic, p. 153 [fragmentary, no figure]; Middle Permian, Kaibab Formation, Arizona.
- ? p 1967 *Janeia biarmica* (de Verneuil, 1845); Logan, p. 60, pl. 10, fig. 12 [Le, IG], non fig. 11; Upper Permian, Tunstall Hill, Durham, England.
- ? 1986 *Solemya (Janeia) parallela* (Beede and Rogers); Zhang and Pojeta, p. 669, fig. 5.14 [PAe; shorter than expected for *A. parallela*; compares with *A. radiata* and *A. costellata*]; Lower Carboniferous, Ceshui Formation, China.
- 2011 *Acharax parallela* (Beede and Rogers); Bailey, 2011, p. 30, 37 [possible variant (?) of *Acharax primaeva* (Phillips)].

Acharax cylindrica (Hind, 1907) n. comb.

Remarks. Poorly known. The syntype (BGS GSE6465) clearly shows a simple buttress and entire posterior adductor scar. Radii weak; compares with *A. costellata* (M'Coy) and *A. radiata* (Meek and Worthen).

- 1907 *Solemya cylindrica* Hind, p. 351, pl. 2, figs. 60, 61 [Pr1; Bts?]; Carboniferous (Namurian), Millstone Grit, Coatbridge, Dumbartonshire, Scotland [ref.: BGS GSE6465 (syntype), Pr1, Bts, PAe; labeled "*Solemya costellata*?" (McCoy), Carboniferous (Namurian), Millstone Grit, Gain Quarry, Glenboig, Lanarkshire, Scotland.

Acharax holmwoodensis (Dickins, 1963) n. comb.

Remarks. Useful but not widely studied.

- 1963 '*Solemya*' *holmwoodensis* Dickins, p. 59, pl. 7, figs. 1-9 [Pc, Pr1f(internal), Bts, Le, Ne]; pl. 8, figs. 17, 18; Lower Permian (Sakmarian) Holmwood Shale, W. Australia.

Acharax herberti (Růžicka and Řehor, 1978) n. comb.

Remarks. Shell compares in profile to both *A. radiata* and *A. costellata*, but radial ribs are more conspicuous; *J. herberti* has priority; *J. leosi*, *J. mariae*, and *J. talboti* are probable synonyms; differences are judged to be taphonomic in origin.

- 1978 *Janacekia herberti* Růžicka and Řehor, p. 63, pl. 1, figs. 1-8; pl. 2, figs. 1-8; pl. 3, figs. 1-13; pl. 4, figs. 2-9; pl. 5, figs. 1-9; pl. 11, fig. 1; pl. 14, fig. 6; [Pc, Pr3, Bts, PAe, Le]; Carboniferous, Ostrava Schichtengruppe, Upper Silesian Coal Basin, Czech Republic.
- 1978 *Janacekia leosi* Růžicka and Řehor, p. 66, pl. 4, fig. 1; pl. 6, figs. 1-12; pl. 7, figs. 1-10; pl. 8, figs. 1-9; pl. 9, figs. 1-9; pl. 10, figs. 1-10; pl. 11, figs. 2-6; pl. 12, figs. 1-10; pl. 13, figs. 1-10; pl. 14, figs. 2, 8; pl. 15, figs. 2-4; [PP?, Pc, Pr3, Bts, PAe, Le, Ale]; Carboniferous, Ostrava Schichtengruppe, Upper Silesian Coal Basin, Czech Republic.
- 1978 *Janacekia mariae* Růžicka and Řehor, p. 69, pl. 14, figs. 1, 3, 5; pl. 16, figs. 1, 2 [PP?, Pc, Pr3, Bts]; Carboniferous, Ostrava Schichtengruppe, Upper Silesian Coal Basin, Czech Republic.
- 1978 *Janacekia talboti* Růžicka and Řehor, p. 69, pl. 14, figs. 4, 7 [Pc, Pr3]; Carboniferous, Ostrava Schichtengruppe, Upper Silesian Coal Basin, Czech Republic.

Acharax solikamica (Muromtseva, 1981) n. comb.

Remarks. Compares with *A. radiata*, *A. costellata*, and *A. herberti*. Ligament described by Muromtseva (1981, p. 30) as posteriorly placed, external.

- 1981 *Solemya (Janeia) solikamica* Muromtseva, p. 30, pl. 7, figs. 12, 16, 17 [Le, Pr2/3]; Upper Permian, North European part of Russia.
- 1984 *Solemya (Janeia) solikamica* Muromtseva; Muromtseva and Guskov, p. 35, pl. 24, figs. 11, 13, 14 [Pr2, Bts]; Upper Permian, West Verkhoysk, Russia; pl. 37, figs. 9?, 11, 12 [Pr2; Bts?, PAe?]; Permian, Novaya Zemlya.

Acharax? petschorica (Guskov, 1984) n. comb.

- ? 1984 *Solemya (Janeia) petschorica* Guskov (in Muromtseva and Guskov, 1984), p. 35, pl. 24, fig. 10 [Pr2, Bts? PAe?; possible *Acharax*]; Lower Permian (Kungurian), Pechora Basin, Russia.

Acharax sp. Pojeta, 1988

Remarks. Three shell fragments; two indeterminate, showing only prosopon; a third showing external nymph, small buttress (simple) and posterior adductor (entire).

- p 1988 *Acharax* sp. Pojeta, pl. 20, fig. 6? [indet. fragment, Pc, Prs, Pr2-3], fig. 7? [indet. fragment, Pc; Pr2-3], pl. 20, fig. 8, pl. 23, fig. 9 [fragment, Le(with insertion groove), Bts, Pae]; Lower Permian, Bone Springs Limestone, Sierra Diablo, Texas.

aff. *Acharax incertis* (Dickins, 1999) n. comb.

Remarks. Unnamed new solemyid genus; well-preserved impressions of adductor musculature; anterior adductor clearly showing visceral retractor band. Like *Acharax* but distinguished by thickened, finely dentate hinge plate.

1999 *Janeia? incertis* Dickins (?Dickins), 1999, pl. 1, figs. 13-18 [Bts, PAe, IG, Ne (traces)]; Middle Permian, Khuff Formation, Oman.

Acharax sp. Bailey, 2011

Remark. Unnamed new species.

1988 *Solemya (Janeia)* sp. Prosh, 1988, p. 162, pl. 23, fig. 4; Lower Devonian, Disappointment Bay Formation, Young Island, Nunavut, Canada.

2011 *Acharax* [sp.] Bailey, 2011, p. 26, pl. 3, fig. 7 [Pr2, Bts, PAe, IG]; Lower Devonian, Disappointment Bay Formation, Young Island, Nunavut, Canada.

2016 *Acharax* sp. Bailey and Prosh, abst. 12-12.

2016 *Acharax* sp. Bailey, abst. 118-2.

Subfamily CLINOPISTHINAE Pojeta, 1988

Genus CLINOPISTHA Meek and Worthen, 1870

Type species. By monotypy, *Clinopistha radiata* var. *levis* Meek and Worthen, 1870, p. 44 (= *Clinopistha levis* Meek and Worthen, 1870, p. 45); Coal Measures (Pennsylvanian), west-central, Illinois. Reviewed by McAlester (1968, p. 20) and Pojeta (1988, p. 216).

Clinopistha truncata (Goldfuss, 1840) n. comb.

Remarks. Beushausen's type (*Sanguinolaria truncata* Goldfuss, 1840) is a generically indeterminate shell fragment. Useful if Beushausen's (1895, pl. 26, figs. 4, 5) topotypes are given priority. Compares with certain examples of *Clinopistha levis* showing fine prosoponal radii, especially on the inner surface of the shell (e.g., Pojeta, 1988, pl. 9, fig. 8; pl. 11, figs. 1-9).

? 1840 *Sanguinolaria truncata* Goldfuss, p. 279, pl. 159, fig. 13a, b; [gen. et sp. indet.; breviterminus encased in matrix; poorly exposed; possibly not a solemyid]; Devonian, Eifel.

? 1858b *Edmondia? radiata* Hall (?Hall); p. 716, pl. 29, fig. 3 [Pr1; = *Clinopistha*; like *C. levis* Meek and Worthen (1870, p. 45) but fine prosoponal radii more pronounced; holotype lost]; Coal Measures (Pennsylvanian), Iowa.

p 1895 *Janeia truncata* (Goldfuss); Beushausen, p. 296, pl. 26, figs. 4, 5, [Pr1f; like *C. levis* but prosoponal radii more pronounced; non text-fig. 32, p. 297]; Devonian, Eifel and Gerolstein, Germany.

1930 *Janeia truncata* (Goldfuss); Quenstedt, pl. 1, figs. 4, 5, Middle Devonian, Gerolstein, Germany.

1969 *Solemya (Janeia) truncata* (Goldfuss); Cox, 1969, p. N243, fig. B1, 1b (copy of Quenstedt, 1930, pl. 1, fig. 4).

Clinopistha abbreviata (de Ryckholt, 1854)

Remarks. Ligament posterodorsal, parivincular, external. Compares with *Clinopistha levis* Meek and Worthen, 1870; Hind (1900, p. 447) agreed.

1854 *Solemya abbreviata* de Ryckholt, p. 53, pl. 16, figs. 18, 19 [short, anteroventrally extended shell, Pr0, Le]; Lower Carboniferous, (Tournaisian) Tournai, Belgium.

1885 *Clinopistha abbreviata* (de Ryckholt); de Koninck, pl. 14, figs. 48-50; pl. 23, figs. 15-19 [short, anteroventrally extended shell; Pr0, Le]; Lower Carboniferous, (Tournaisian), calcschiste de Tournai, Belgium.

1900 *Clinopistha abbreviata* (de Ryckholt); Hind, p. 446, pl. 50, fig. 17; Lower Carboniferous, Fourlaws Limestone, Coombs Quarry, Redesdale, Northumberland.

Clinopistha curta (Walcott, 1884) n. comb.

Remarks. Name originally applied to two different taxa: Walcott (1884, pl. 22, fig. 6) is *Clinopistha*, i.e., *C. cf. levis* Meek and Worthen, but pl. 22, fig. 11 is probably *Dystactella*, i.e., *D. cf. subnasuta* (Hall and Whitfield). By priority, the trivial name, *curta*, is herein assigned to *Clinopistha* as it appears first on Walcott's plate 22.

p 1884 *Solenomya curta* Walcott, p. 242, pl. 22, fig. 6 [Pc, Pr1; = *Clinopistha cf. levis* Meek and Worthen], non fig. 11 [Pc, Pr1; = *Dystactella cf. subnasuta* (Hall and Whitfield, 1872)]; Lower Carboniferous, Eureka District, Nevada.

? 1889 *Solenomya curta* Walcott; Miller, p. 512 [no figure]; Subcarboniferous, Nevada.

Clinopistha? kasanensis (Netschajew, 1894) n. comb.

Remarks. Generic identity of the Netschajew's (1894) type material (internal molds) is questionable; shell profiles resemble *Clinopistha* but diagnostic characters are lacking. Kłapciński and Karwowski's (1978) specimen is indeterminate, whereas examples of Muromtseva (1981) and Muromtseva and Guskov (1984) appear to be edmondidiids.

? 1894 *Solemya (Janeia) kasanensis* Netschajew, p. 304, pl. 10, fig. 16 [possible *Clinopistha?*]; Volga River, mouth of the Kama; pl. 10, fig. 20? [gen. indet.], Permian, Krasnowidowo, Volga River, Russia; pl. 10, fig. 21 [possible

- Clinopistha*?]; Permian, Bogorodskoye, Volga River, Russia.
- ? 1978 *Janeia kasanensis* (Netschajew); Kłapciński and Karwowski, p. 73, pl. 2, fig. 14 [internal mold; Bts?; gen. indet.]; Upper Permian (middle Zechstein), Main Dolomite, Stassfurt Cyclothem, Poland.
- non 1981 *Solemya (Janeia) kasanensis* Netschajew; Muromtseva, p. 30, pl. 10, fig. 17 [gen. indet.; possible edmondiiid]; Upper Permian, Novaya Zemlya.
- non 1984 *Solemya (Janeia) kasanensis* Netschajew; Muromtseva and Guskov, p. 35, pl. 41, fig. 17 [gen. indet.; possible edmondiiid]; Permian, Novaya Zemlya.

Genus *DYSTACTELLA* Hall and Whitfield, 1872
[= *Palaeosolemya* Pojeta and Runnegar, 1985]

Type species. By monotypy, *Tellinomya subnasuta* Hall and Whitfield, 1872, lower Givetian (upper Middle Devonian) near Louisville, Kentucky.

Dystactella biarmica (de Verneuil, 1845) n. comb.

Remarks. Holotype of de Verneuil (1845) is an internal mold with profile and ligament (external, parivincular) similar to *Dystactella subnasuta* (Hall and Whitfield). Shell exterior and prosopon not preserved in the holotype. Judged by Meek (1871, p. 67) to be possible synonym of *Solemya (Janeia) vetusta* Meek (= *Dystactella*; see below). *Solemya saginata* of de Ryckholt 1854 is a possible synonym.

- 1845 *Solemya biarmica* de Verneuil, p. 294, pl. 19, fig. 4a-b [IG, Le]; Lower Permian, Nizhny Novgorod Oblast, Russia.
- ? 1848 *Solemya biarmica* de Verneuil; Geinitz, p. 8, pl. 3, fig. 34. [Tiny oval shell with low umbos; gen. et sp. indet.] Upper Permian, Kupferschiefer, Kamsdorf, Germany.
- non 1850 *Janeia biarmica* (de Verneuil); King, p. 178, pl. 16, fig. 7 [= probable pholadomyid, i.e., *Wilkingia elegans* (King); see Logan, 1967, p. 63]; Upper Permian, Humbledon Hill, Durham, England.
- ? 1854 *Solemya saginata* de Ryckholt, p. 53, pl. 11, figs. 9, 10 [Pc, Pr0; = *Dystactella* cf. *subnasuta*; compares with Pojeta (1988, pl. 8 figs. 1, 2)]; Lower Carboniferous, (Tournaisian), l'argile carbonifère, Tournai, Belgium.
- non 1858 *Solemya biarmica*? de Verneuil; Howse (?Howse), p. 266, pl. 11, figs. 8, 9 [formerly, *Solenimya abnormis* Howse, 1848, and *Solemya abnormis* Howse, 1857a] [= *Stutchburia*? cf. *modioliformis* (King) sensu Logan (1967, p. 51)]; Upper Permian, Silksworth, Durham, England.

- ? 1860 *Solenomya biarmica*? de Verneuil; Swallow and Hawn (?Swallow and Hawn), p. 190. [Material described as "imperfect"; no description, no figure; Swallow was doubtful about generic placement]; Upper Permian, Council Grove, Kansas.
- p ? 1861 *Solemya biarmica* de Verneuil; Geinitz, p. 60, pl. 12, fig. 18 [Pc; shell form fairly consistent with *D. biarmica*; ligament unknown]; Upper Permian, Zaufensgraben bei Gera, Germany; non pl. 12, fig. 19 [= type of *Solemya phillipsiana* sensu Schauth; Upper Permian (lower Zechstein), Bucha, Germany.
- non 1866 *Solemya biarmica* de Verneuil; Geinitz, p. 15, pl. 1 fig. 22; [gives size but no description; hinge, ligamental and interior unknown; the smoothly ovoid profile, pointed subcentral umbo, and fasciculate comarginal growth laminae are unlike known solemyids; gen. et sp. indet.] Pennsylvanian, Plattsmouth Limestone Member, Oread Limestone, Nebraska City, Nebraska.
- 1877 *Solenomya biarmica* de Verneuil; Miller, p. 204 [no figure].
- 1889 *Solenomya biarmica* de Verneuil; Miller, p. 512 [no figure].
- non 1894 *Solemya biarmica* de Verneuil; Netschajew, p. 302, pl. 10, fig. 13 [gen. et sp. indet.; probably not a solemyid]; Permian, Volga River at the mouth of the Kama.
- 1896 *Solemya biarmica* de Verneuil; Hind, p. 24, 36 [no figure].
- non 1897 *Solemya (Janeia) biarmica* (de Verneuil); Diener, p. 173, pl. 8, figs. 7, 8 [= *Sanguinolites*? M'Coy, 1844]; Upper Permian, Kuling Shales, south of Pomerang, India.
- ? 1967 *Janeia biarmica* (de Verneuil); Logan, p. 60, pl. 10, fig. 11?, fig. 12? [possible *Dystactella*, sp. indet.; Pc, Ne, IG]; Upper Permian, Middle Magnesian Limestone, Tunstall Hill, Durham, England.
- ? 1978 *Janeia biarmica* (de Verneuil); Kłapciński and Karwowski, p. 72, pl. 2, figs. 12, 13; [poor preservation; gen. et sp. indet.]; Upper Permian (middle Zechstein), Main Dolomite, Stassfurt Cyclothem, Poland.
- non 1984 *Solemya (Janeia) biarmica* (de Verneuil); Muromtseva and Guskov, p. 34, pl. 24, fig. 4a-b [= cf. *Acharax* sp.; Pr0, Ne, Bts?, IG]; non fig. 5 [gen. et sp. indet.]; fig. 6a-b [= clinopisthin, cf. *Clinopistha* sp.; Pc, Ne, IG]; fig. 7 [= *Dystactella*?]; Lower Permian (Kungurian), Pechora Basin, Russia.

Dystactella vetusta (Meek, 1871) n. comb.

Remarks. Judged by Meek (1871, p. 67) to be possible synonym of *Solemya biarmica* de Ver-

neuil. Pojeta (1988, p. 217) placed Hall's (1885) examples of *Dystactella vetusta* (Meek) in *Dystactella valvulus* (Hall and Whitfield). See *D. valvulus* (below).

- 1871 *Solemya (Janeia) vetusta* Meek, p. 66 [description only; no figure]; Devonian, Corniferous Group, Dublin, Franklin Co., Ohio.
- 1873 *Solemya (Janeia) vetusta* Meek; Meek, p. 206, pl. 18, fig. 4 [Pr1, Ne]; Devonian, Corniferous Group, Dublin, Franklin Co., Ohio.
- 1877 *Solenomya vetusta* Meek; Miller, p. 204 [no figure].
- 1878 *Solenomya vetusta* Meek; Bigsby, p. 76 [no figure]; Corniferous Limestone, Dublin, Franklin Co., Ohio.
- non 1885 *Solemya (Janeia) vetusta* Meek; Hall, p. 463, pl. 45, figs. 53-55; pl. 94, fig. 10 [= *Dystactella valvulus* (Hall and Whitfield); see Pojeta, 1988, p. 217].
- 1889 *Solenomya vetusta* Meek; Miller, p. 512, fig. 922 [figure copied from Meek, 1873, pl. 18, fig. 4].
- 1890 *Solemya (Janeia) vetusta* Meek; Lesley, p. 972 [figure copied from Meek, 1873, pl. 18, fig. 4].
- 1901 *Solemya (Janeia) vetusta* Meek; Kindle, p. 690, pl. 16, figs. 1, 1a-b, 2 [Pc, Pr1, Ne, IG]; Middle Devonian, Sellersburg beds; Watson, Indiana, and Falls of the Ohio.
- non 1944 *Solemya? vetusta* Meek; Shimer and Shrock (?Shimer and Shrock), p. 369, pl. 44, figs. 1, 2 [with figure copies of Hall, 1885, pl. 47, figs. 53, 55; Pojeta (1988, p. 217) referred these to *Dystactella valvulus*.]; Middle Devonian (Onondaga-Hamilton), New York, Pennsylvania, Ohio, Indiana, Kentucky.

Dystactella cf. *subnasuta* Hall and Whitfield, 1872

Remarks. *Dystactella subnasuta* Hall and Whitfield was reviewed by Pojeta (1988, p. 217); items in his brief synonymy are omitted here as none were referred either to *Solemya* or *Janeia*.

- p 1884 *Solenomya curta* Walcott, p. 242, pl. 22, fig. 11 [Pc, Pr1; = *Dystactella* cf. *subnasuta* (Hall and Whitfield, 1872); hinge, ligament and interior unknown]; non pl. 22, fig. 6 [Pc, Pr1; = *Clinopistha* cf. *levis* Meek and Worthen]; Lower Carboniferous, Eureka District, Nevada.
- ? 1889 *Solenomya curta* Walcott; Miller, p. 512 [no figure]; Subcarboniferous, Nevada.

Dystactella valvulus (Hall and Whitfield, 1872)

Remarks. Reviewed by Pojeta (1988, p. 217). Hall (1885) placed *Yoldia? vetusta* Hall and Whitfield in

synonymy with *Solemya (Janeia) vetusta* Meek. Pojeta (1988, p. 217) placed Hall's (1885) examples of *Dystactella vetusta* (Meek) in *Dystactella valvulus* (Hall and Whitfield). See *D. vetusta* (above).

- non 1871 *Solemya (Janeia) vetusta* Meek, p. 66 [description only; no figure]; Devonian, Corniferous Group, Dublin, Franklin Co., Ohio.
- 1872 *Yoldia? valvulus* Hall and Whitfield (?Hall and Whitfield), p. 190 [description only; figures published in Hall and Whitfield, 1875, pl. 11, figs. 18-20]; Middle Devonian, Hydraulic Beds near Louisville, Kentucky.
- non 1873 *Solemya (Janeia) vetusta* Meek; Meek, p. 206, pl. 18, fig. 4 [Pr1, Ne]; Devonian, Corniferous Group, Dublin, Franklin Co., Ohio.
- 1875 *Yoldia? valvulus* Hall and Whitfield (?Hall and Whitfield), pl. 11, figs. 18-20 [Pc, Ne; figures to accompany description in Hall and Whitfield, 1872, p. 190].
- 1883 *Yoldia? valvulus* Hall and Whitfield (?Hall and Whitfield); Hall, pl. 47, figs. 53-55 [Pc, Ne; figures copied from Hall and Whitfield, 1875, pl. 11, figs. 18-20].
- 1885 *Solemya (Janeia) vetusta* Meek; Hall, p. 463, pl. 47, figs. 53-55 [Pc, Ne; figures copied from Hall and Whitfield, 1875, pl. 11, figs. 18-20]; Middle Devonian Hamilton Group, near Louisville, Kentucky; pl. 94, fig. 10 [Prs, Ne]; Hamilton Group, Charlestown, Indiana.
- 1889 *Yoldia? valvulus* Hall and Whitfield (?Hall and Whitfield); Nettleroth, p. 223, pl. 4, figs. 4, 5 [Pc, Pr0, Ne]; Devonian, from the cherty layers above the Hydraulic Limestone, Jefferson Co., Kentucky, and Clark Co., Indiana.
- 1944 *Solemya? vetusta* Meek; Shimer and Shrock (?Shimer and Shrock), p. 369, pl. 44, figs. 1, 2 [figures copied from Hall, 1885, pl. 47, figs. 53, 55], Middle Devonian (Onondaga-Hamilton), New York, Pennsylvania, Ohio, Indiana, Kentucky.
- 1988 *Dystactella valvulus* (Hall and Whitfield); Pojeta, p. 217, pl. 10, figs. 1-4 [Prs, Pr1, Ne; these specimens used by Nettleroth (1889) for his description and figures]; Middle Devonian (Lower Givetian), Silver Creek Limestone Member, Falls of the Ohio, Clark Co., Indiana.

Dystactella excisa (de Koninck, 1885)

Remarks. A species of *Dystactella* with large, well-defined external ligament on the brevadorsum. The lost undescribed (nom. nud.) specimen of *Solemya symesii* figured by Baily (1880) is nearly identical to de Koninck's (1885, pl. 9, figs. 13, 14) type of *Solemya excisa*; other specimens of de Koninck

attributed to *S. excisa* are indeterminate. Because the trivial name, *excisa*, is applied first to pl. 9, figs. 13, 14, it is here given priority.

- 1880 *Solemya symesii* Baile, p. 22. [no description (nom. nud.); based on two unnumbered figures of a single specimen, now lost; strong external ligament; similar to de Koninck's (1885, pl. 9 figs. 13, 14) examples of *Solemya excisa*]; lower limestone series, Easky, Bunowna, Co. Sligo, Ireland.
- p 1885 *Solemya excisa* de Koninck, p. 122, pl. 9, figs. 13, 14, pl. 23, figs. 30, 39, 40, non pl. 23, fig. 42, 43 [gen. et sp. indet.]; Lower Carboniferous, (Tournaisian) calcaire carbonifère, Tournai, Belgium.
- non 1900 *Solemya excisa* de Koninck; Hind, p. 441, non pl. 50, figs. 11, 14?, 15 [ventrally embayed; Pc, Pr1; = *Acharax* cf. *normalis* sensu Howse]; Lower Carboniferous, Lowick, Northumberland; non pl. 50 figs. 12, 16 [Pc, Pr2, Bts, PAe; = *Acharax* cf. *costellata*]; Carboniferous, Ardross, Scotland.

Dystactella? silurica (Liljedahl, 1984) n. comb.

Remarks. Possibly a new subgenus of *Dystactella*. Pojeta (1988) reassigned *Janeia silurica* to *Dystactella*, but because of its uniquely asymmetric ligament support structures, Bailey (2011, p. 20) suggested placement in a new genus very close to *Dystactella* s. s.].

- 1984a *Janeia silurica* Liljedahl, p. 28, figs. 4, 13-15, 34:5. Silurian (Upper Wenlockian), Halla beds, Mölbos, Gotland.
- 1984b *Janeia silurica* Liljedahl; Liljedahl, p. 693-698, text-figs. 1-3. Silurian (Upper Wenlockian), Halla beds, Mölbos, Gotland.
- 1988 *Dystactella silurica* (Liljedahl); Pojeta, 1988, p. 215.
- 1991 *Janeia silurica* Liljedahl; Liljedahl, p. 222, text-figs. 2E-G, 3.
- 1994 *Janeia silurica* Liljedahl; Liljedahl, p. 12, etc.
- 2011 *Dystactella? silurica* (Liljedahl); Bailey (?Bailey), 2011, p. 20; text-fig. 4.

Subclass AUTOBRANCHIA Grobбен, 1894

Order HIATELLIDA Carter, 2011

Superfamily EDMONDIOIDEA King, 1850

Family EDMONDIIDAE King, 1850

Genus EDMONDIA De Koninck, 1842

Type species. By original designation, *Isocardia unioniformis* Phillips, 1836, Carboniferous, Bolland, Yorkshire.

Edmondia? soleniformis (Cox, 1857) new comb.

Remarks. Cox's (1857) type incomplete; umbo subcentral, broad and elevated; prosopon with reg-

ular comarginal lirae, closely spaced and distinct; radii lacking; hinge, ligament and interior unknown. Placed in *Solemya* by Cox (1857), Keyes (1888) and Hind (1896). Not a solemyid; probable edmondidiid: *Edmondia?*

- ? 1857 *Solenimya soleniformis* Cox, p. 573, pl. 9, fig. 5; [Pc(strong), Pr0; = *Edmondia?*]; Pennsylvanian, Coal Measures, Union Co., Kentucky.
- 1877 *Solenomya soleniformis* Cox; Miller, p. 204 [no figure].
- 1888 *Solenomya soleniformis* Cox; Keyes, 1888, p. 234 [no figure or description; Keyes compared it to *Solenimya soleniformis* sensu Cox but larger]; Lower Coal Measures (Pennsylvanian), Des Moines, Iowa.
- 1889 *Solenomya soleniformis* Cox; Miller, p. 512 [no figure].
- 1896 *Solemya soleniformis* Cox; Hind, 1896, p. 29 [no figure].

Edmondia anodontoides (Meek, 1875)

Remarks. Studies prior to Morningstar (1922) placed the species in *Solemya*. Restudy of Hoare, Sturgeon, and Kindt (1979) accepted it as *Edmondia*.

- 1875 *Solenomya? anodontoides* Meek (?Meek), p. 339, pl. 19, fig. 11 [hinge, ligament and interior unknown; Meek called it a possible *Edmondia*]; Pennsylvanian, Newark, Ohio.
- 1877 *Solenomya anodontoides*, Meek; Miller, p. 204 [no figure].
- 1886 *Solenomya anodontoides* Meek; Claypole, p. 241-242 [no description, or figure]; Pennsylvanian, Wilkes-Barre, Pennsylvania.
- 1887 *Solenomya? anodontoides* Meek (?Meek); Herrick, p. 29, pl. 4, fig. 10 [Pc(strong); possible *Edmondia*, but hinge, ligament and interior unknown. Herrick was doubtful about generic placement]; Pennsylvanian, Flint Ridge, Ohio.
- 1889 *Solenomya anodontoides* Meek; Miller, p. 512 [no figure].
- 1922 *Edmondia anodontoides?* (Meek); Morningstar (?Morningstar), p. 196 [description/discussion but no figure; judged Meek's and Herrick's specimens to be disparate species]; Pennsylvanian, Perry Co., Ohio.
- 1979 *Edmondia anodontoides* (Meek); Hoare, Sturgeon and Kindt, p. 57, pl. 15, figs. 12-14; Pennsylvanian, Brush Creek, Ohio.

Edmondia meekiana (Herrick, 1887)

Remark. *Solemya? meekiana* Herrick subsequently accepted as *Edmondia*.

- 1887 *Solenomya? meekiana* Herrick (?Herrick), p. 30, pl. 4, fig. 9 [hinge, ligament, interior

- unknown; probable *Edmondia*. Herrick noted similarities to *Edmondia reflexa* Meek (1872, p. 233, pl. 4, fig. 7) but did not accept it as a synonym]; Pennsylvanian Coal Measures, Flint Ridge, Ohio.
- 1922 *Edmondia meekiana?* (Herrick); Morningstar (?Morningstar), p. 198, pl. 10, fig. 6; Pennsylvanian, Lower Mercer Limestone, Flint Ridge, Ohio.
- ? 1958 *Edmondia meekiana* (Herrick); Wanless, p. 44 [no figure]; Pennsylvanian, Liverpool Cyclothems, western Illinois.
- 1979 *Edmondia meekiana* (Herrick); Hoare, Sturgeon and Kindt, p. 58, pl. 16, figs. 6, 7; Pennsylvanian, Lower Mercer unit, Flint Ridge, Ohio.
- ? 1983 *Edmondia* aff. *E. meekiana* (Herrick); Kues (aff. Kues), p. 80 [no figure]; Middle Pennsylvanian, Upper Los Moyos Limestone, Cedro, New Mexico.

ORDER CARDIIDA Férussac, 1822
 SUPERFAMILY KALENTEROIDEA Marwick, 1953
 FAMILY KALENTERIDAE, Marwick, 1953
 Genus PLEUROPHORELLA Girty, 1904

Type species. *Pleurophorella papillosa* Girty, 1904 by original designation, Graham Limestone, Pennsylvanian (Cisco), Young County, Texas.

Remarks. *Janeia? compressa* (Goldfuss) Beushausen (1895) and *Janeia laevigata* (Goldfuss) Beushausen (1895) are not solemyids; both are here provisionally placed in *Pleurophorella*. Shell posteriorly elongated, somewhat modioliform, laterally compressed with well-defined lunule and long escutcheon; hinges and internal morphologies unknown.

Pleurophorella? aff. *transversa* (de Koninck, 1842)

Remarks. *Janeia? compressa* (Goldfuss) Beushausen compares with *Sanguinolaria compressa* Goldfuss and with *Pleurophorella transversa* (de Koninck). Beushausen himself was uncertain about generic placement.

- ? 1840 *Sanguinolaria compressa* Goldfuss, 1840, p. 280, pl. 159, fig. 16a-b [= Beushausen's type of *J.? compressa*; hinge and interior unknown; well-defined lunule and long escutcheon]; Devonian, Uebergangskalk, Eifel.
- ? 1842 *Cypricardia transversa* de Koninck, p. 94, pl. 1, fig. 3, pl. 3, fig. 8? [compares with but not identical to *S. compressa* Goldfuss]; Lower Carboniferous, (Tournaisian), Tournai, Belgium.
- 1895 *Janeia? compressa* (Goldfuss); Beushausen (?Beushausen) 1895, p. 297, pl. 26, fig. 1a-c [compares with *S. compressa* Goldfuss;

hinge and ligament unknown; Pr0]; Devonian, Daleiden, Germany.

- ? 1991 *Pleurophorella transversa* (de Koninck); Morris et al. (1991, p. 87, fig. 41) [compares with *J.? compressa* sensu Beushausen]; Lower Carboniferous, (Tournaisian) Tournai, Belgium.

Pleurophorella? sp.

Remarks. Beushausen's poorly exposed type of *Janeia laevigata* (i.e., *Sanguinolaria laevigata* Goldfuss) is indeterminate. Beushausen's (1895, pl. 26, fig. 2a-c) example of *Janeia laevigata* compares with *Pleurophorella* sp. Morris et al., 1991, fig. 40, Upper Pennsylvanian, Graham Formation, Texas, and also with *?Pleurophorella cuneata* (Phillips) (Morris et al., 1991, p. 88, fig. 42), Lower Carboniferous (Viséan), Yorkshire.

non 1840 *Sanguinolaria laevigata* Goldfuss, p. 279, pl. 149, fig. 14; [gen. indet., nom. dub.; a partially exposed, unidentifiable shell; probably not a solemyid]; Devonian, Eifel.

p 1895 *Janeia laevigata* (Goldfuss); Beushausen, p. 294, pl. 26, fig. 2a-c [possible *Pleurophorella*; hinge and interior unknown]; Devonian, Daleiden, Germany; non pl. 26, fig. 8 [copy of Goldfuss' type, gen. indet.].

Pleurophorella? cf. *tricostata* (Portlock, 1843)

Remark. Different from Beushausen's other *Janeia laevigata*; compares with *Sanguinolites striatogranulatus* Hind, considered by Morris et al. (1991) as possibly synonymous with *Pleurophorella tricostata* (Portlock).

p 1895 *Janeia laevigata* (Goldfuss); Beushausen, p. 294, pl. 26, fig. 3a-b [Pc, Pr2; with buttress-like feature]; Middle Devonian, Gerolstein, Germany; non pl. 26, fig. 2a-c; Devonian Daleiden, Germany.

? 1900 *Sanguinolites striatogranulatus* Hind, p. 393-394, pl. 42, figs. 16-22; Lower Carboniferous, Isle of Man, Yorkshire, and Ireland.

? 1991 *Pleurophorella tricostata* (Portlock); Morris et al., p. 87, fig. 38a-h; Lower Carboniferous, Isle of Man, Yorkshire, and Ireland.

Genus STUTCHBURIA Etheridge, 1900

Type species. By original designation, *Orthonota? costata* Morris, 1845; Permian, southeastern Australia.

Remarks. Needs further study. Logan's (1967) placement of *Cardiomorpha modioliformis* King in *Stutchburia* is uncertain. Although the subquadrate shell profile and coarse radial ribs of the type species are lacking, Logan (1967, p. 50) argued that Etheridge's original definition of *Stutchburia* was

broadly defined to include forms with a modioloid outline and variable prosopon.

Stutchburia? cf. *modioliformis* (King, 1850) sp. inq.

Remark. Howse's (1857a, pl. 4, figs. 8, 9) simple drawing of *Solemya abnormis* Howse superficially compares with *Stutchburia modioliformis* (King, 1850), but hinge, ligament, and interior unknown.

1848 *Solenimya abnormis* Howse, p. 244 [description only; Pc, Pr0; prosopon with comarginal "waves"; anisomyarian; adductor muscles deeply impressed; hinge and ligament unknown; not a solemyid]; Upper Permian, Magnesian Limestone, Silksworth and Tunstall.

non 1850 *Janeia biarmica* (de Verneuil); King, p. 178 (non de Verneuil, 1845); [no figure; in error, King considered *Solenomya abnormis* of Howse to be a junior synonym of *J. biarmica* (de Verneuil)].

? p 1850 *Cardiomorpha modioliformis* King, p. 180, pl. 14, 20-22; non figs. 18, 19, 23; Upper Permian, "Shell-Limestone", Tunstall Hill, Ryehope Field-House-Farm and Humbleton Quarry, Durham, England.

1857a *Solemya abnormis* Howse; Howse, p. 309; pl. 4, figs. 8, 9 [figures to accompany 1848 description; Pc, Pr0; modioloid profile, anisomyarian, not a solemyid]; Upper Permian, "Shell-Limestone", Silksworth, Durham, England.

1858 *Solemya biarmica*? de Verneuil; Howse (?Howse), p. 266, pl. 11, figs. 8, 9 [same specimen was shown by Howse (1857a) under the name of *Solemya abnormis*]; Upper Permian, "Shell Limestone", Silksworth, Durham, England.

? 1967 *Stutchburia modioliformis* (King); Logan, p. 51, pl. 8, fig. 8a-e (= lectotype); [compares with both *Solemya abnormis* Howse and *Cardiomorpha modioliformis* King]; Upper Permian, Middle Magnesian Limestone, Tunstall Hill, Durham, England.

? p 1981 *Stutchburia modioliformis* (King); Muromtseva, p. 41, pl. 10, fig. 11?, non 12a [gen. et sp. indet.]; Permian, Novaya Zemlya.

? 1984 *Stutchburia modioliformis* (King); Muromtseva and Guskov, p. 85, pl. 5, pl. 5, figs. 2, 10, 11; pl. 24, fig. 9a-b [compares with *Solemya abnormis* Howse]; Upper Permian, Russian Platform, Urals and Pechora Basin.

PROBLEMATICA (incertae sedis)

Remarks. The following listings marked ?? are either generically indeterminate or misidentified, etc. See comments in brackets.

?? *Solenomya phillipsiana* King, 1850, p. 179, pl. 16, fig. 8. [nom. dub.; Howse (1849, p. 9) called it a "mere fiction" based allegedly on nonexistent material from the "Shell-Limestone"]; Humbleton Quarry, Durham, England.

non 1854 *Solenomya phillipsiana* King; Schaubroth, p. 553, pl. 21, fig. 5 [Pc, Pr1; gen. indet.]; Upper Permian (lower Zechstein), Bucha, Germany.

non 1861 *Solemya biarmica* de Verneuil; Geinitz, p. 60, pl. 12, fig. 19a-c [gen. indet.; Schaubroth's original specimen of *S. phillipsiana* was refigured but significantly altered and reassigned in error by Geinitz to *S. biarmica*]; Upper Permian (lower Zechstein), Bucha, Germany.

?? *Solemya arcuata* (Phillips); de Ryckholt, (1847) 1854, p. 52 [no figure; not a solemyid; based solely on earlier studies of Phillips and King]; Lower Carboniferous, (Tournaisian) l'argile carbonifère, Tournai, Belgium.

? 1836 *Sanguinolaria*? *arcuata* Phillips (?Phillips) 1836, p. 209, pl. 5, fig. 4 [possible mytilid, aff. *Lithophaga* Röding, 1798]; Harelaw, Northumberland, England.

non 1849 *Sanguinolites arcuatus* (Phillips); Brown, p. 219, pl. 90, fig. 16 [drawing after Phillips; possible mytilid, aff. *Lithophaga*].

non 1850 *Edmondia arcuata* (Phillips); King, p. 164 [no figure].

non 1899 *Edmondia arcuata* (Phillips); Hind, p. 310, pl. 35, fig. 2 [= *Acharax*?; solemyiform shell, expanded brevidorsal auricle; Bts?, PAe?, Pc, Pr0]; fig. 3 [like fig. 2 but with fine radial ornament; Pc, Pr1]; Carboniferous, Redesdale Ironstone series, Northumberland; non pl. 35, figs. 1, 4, 6-10; Hurler Limestone, St. Monans, Fife, and Redesdale Ironstone, Northumberland.

non 1903 *Edmondia*? *arcuata* Cleland (?Cleland), 1903, p. 44, pl. 4, figs. 5-7 [= possible *Edmondia* but junior homonym of *Edmondia arcuata* (Phillips)]; Ordovician (Beekmantown), New York.

?? *Solemya devonica* de Ryckholt (1847) 1854, p. 51, pl. 16, figs. 16, 17; [gen. indet.; possible solemyid based on description, but fig. 16 is badly flawed, described by de Ryckholt himself, p. 51, as "plus inexacte"]; Devonian, Eifel.

1878 *Solenomya devonica* de Ryckholt; Bigsby, p. 76 [no figure]; Devonian, Eifel, Paffrath, Germany.

?? *Solemya parallela* de Ryckholt, (1847) 1854, p. 51, pl. 11, figs. 11, 12. [non *Solenomya parallela* Beede and Rogers (1899); Pr0; parallel dorsal and ventral margins; beaks placed at extreme breviterminus; treated by Hind (1899, p. 318) as possible synonym of *Edmondia sulcata* Phillips, 1836; not a solemyid; possible pholadomyid, cf. *Wilkingia* Wilson, 1959]; Lower Carboniferous, (Tournaisian) Tournai, Belgium.

non 1885 *Solemya parallela* de Ryckholt; de Koninck, p. 121, pl. 23, figs. 35, 36 [possible solemyid?, Pr0, Ne?]; non figs. 37, 38 [= *Edmondia*, cf. *arcuata* (Phillips)]; Lower Carboniferous, (Tournaisian), calschiste de Tournai, Belgium.

?? *Solemya* (?) *recurvata* Swallow (?Swallow) 1858, p. 208-209 [gen. indet.; description only; no figure; described as showing the remains of an external ligament; recurving gibbous shell, large beaks; comarginal growth laminae described; radii not indicated]; Upper Coal Measures, Clifton Park, Kansas.

1877 *Solenomya recurvata* Swallow; Miller, p. 204 [no figure].

1889 *Solenomya recurvata* Swallow; Miller, p. 512 [no figure].

1896 *Solemya recurvata* Swallow; Hind, p. 29 [no figure].

?? *Solenomya monroensis* Worthen, 1884, p. 13. [gen. indet.; description only; no figure; size small with comarginal growth lines; ligament, hinge and interior unknown]; Mississippian, St. Louis Limestone, Monroe Co., Illinois.

1889 *Solenomya monroensis* Worthen; Miller, p. 512 [no figure].

1896 *Solenomya monroensis* Worthen; Hind, p. 52 [no figure].

1890 *Solenomya monroensis* Worthen; Worthen, p. 131, pl. 18, fig. 5, 5a [copy of 1884 description; figure 5 shows umbo too narrow and prominent for a solemyid; radii lacking; evenly spaced comarginal growth varices; oblique longiterminus with longidorsum slightly elevated; dorsum (Worthen's fig. 5a) shows no evidence of ligament; form suggestive of *Edmondia*].

?? *Solenomya varsoviensis* Worthen, 1884, p. 12 [no figure; description of the shell form and size; ligament, hinge, and interior unknown]; Mississippian, Keokuk Limestone, Warsaw, Illinois.

1889 *Solenomya varsoviensis* Worthen; Miller, p. 512 [no figure].

? 1890 *Solenomya varsoviensis* Worthen; Worthen, p. 131 [copy of 1884 description], pl. 19, fig. 7 [not a solemyid; featureless; outline com-

pares with *Edmondia ovata* Meek and Worthen, 1873]; non pl. 19, fig. 8, 8a [not a solemyid; smooth outer surface; posteriorly elongate and expanded; dorsal view shows no ligament; concave posterodorsal margin; possibly with large posterior gape; probable pholadomyid, cf. *Chaenomya* Meek, 1864; compares with Anelli et al., fig. 7A]; Mississippian, Keokuk Limestone, Warsaw, Illinois.

1896 *Solenomya varsoviensis* Worthen; Hind, 1896, p. 52 [no figure].

?? *Solenomya iowensis* Worthen (?Worthen), 1884, p. 13 [no figure; size (small) and shell shape described; ornament, ligament and internal features unknown]; Mississippian, St. Louis Limestone, Pella, Iowa.

1889 *Solenomya iowensis* Worthen; Miller, p. 512 [no figure].

1890 *Solenomya iowensis* Worthen (?Worthen); Worthen, p. 132 [copy of 1884 description]; pl. 19, fig. 5, 5a [not a solemyid; possible kalenterid, cf. *Pleurophorella*? Girty, 1904; compares with Anelli et al., 2009, fig. 2H]; Mississippian, St. Louis Limestone, Pella, Iowa.

1896 *Solenomya iowensis* Worthen (?Worthen); Hind, p. 52 [no figure].

?? *Solenomya subradiata* Herrick, 1887, p. 30, pl. 3, fig. 8. [gen. indet.; possible solemyid? Shell thin, somewhat solemyiform with prosoponal radii, but umbos too prominent; protruding heel on breviterminus; hinge, ligament, and interior unknown]; Coal Measures, (Pennsylvanian), Flint Ridge, Ohio.

?? *Solenomya cuyahogensis* Herrick (?Herrick), 1888, p. 115, pl.10, fig. 1 [gen. indet.; short valves, very small and conjoined; probably not a bivalve; possible conchostracan. Herrick thought it might be *Edmondia*]; Lower Mississippian, Waverly Group, Cuyahoga Falls, Ohio.

? 1895 *Solenomya cuyahogensis* Herrick (?Herrick); Herrick, pl. 22, fig. 25 [gen. indet.; short valves, very small and conjoined – possible conchostracan]; Carboniferous, Cuyahoga Shale, Cuyahoga Falls, Ohio.

?? *Janeia phaseolina* (Goldfuss); Beushausen, 1895, p. 295 pl. 26, figs. 6, 7, 9 [a heterogeneous mix].

? 1840 *Sanginolaria phaseolina* Goldfuss, p. 279, pl. 159, fig. 15 [gen. et sp. indet; Pc, Pr1; elevated umbos, hinge, ligament and interior unknown]; Devonian, Eifel.

non 1855 *Edmondia phaseolina* (Goldfuss); M'Coy, 1855, p. 502. Lower Carboniferous limestone, Lowick, Northumberland; [= *Edmondia lowickensis* Hind, 1899, p. 296, pl. 33, figs. 1-

- 4]; Carboniferous, Fourlaws Limestone, Coombs, Northumberland, etc.
- ? 1895 *Janeia phaseolina* (Goldfuss); Beushausen, pl. 26, fig. 9 [copy of Goldfuss's type; differs slightly, hinge, ligament and interior unknown; Pc; gen. et sp. indet.; possible edmondii?].
- ? 1895 *Janeia phaseolina* (Goldfuss); Beushausen, p. 296, text-fig. 31 [differs from Goldfuss' type; hinge, ligament, and interior unknown = *Edmondia*?]; Middle Devonian, Gerolstein, Germany.
- ? 1895 *Janeia phaseolina* (Goldfuss); Beushausen, pl. 26, fig. 6 [differs in form Goldfuss' type and from text-fig. 31; shell thick; Pc (strong), buttress lacking; hinge and ligament unknown; = *Edmondia*?]; Devonian, Eifel.
- ? 1895 *Janeia phaseolina* (Goldfuss); Beushausen, pl. 26, fig. 7, [significantly differs from Beushausen's other examples of *J. phaseolina*; short, sulcate shell with tumid umbos; possible sanguinolite, = *Myofossa*? Waterhouse]; Middle Devonian, Gerolstein, Germany.
- ?? *Solenomya brevis* Hind, 1907, p. 351, pl. 2, figs. 45, 47 [Pr0; gen.indet.; non-solemyid shell profile; hinge, ligament and interior unknown]; Carboniferous, Millstone Grit, Coatbridge, Dumbartonshire, Scotland.
- ?? *Solenomya? sharonensis* Morningstar (?Morningstar), 1922, p. 194, pl. 10, figs. 1, 2, [not a solemyid; characters include small but prominent umbos, nasute longiterminus; straight/slightly declining hinge line; possible modiomorphoid, aff. *Sphenotomomorpha* Williams and Breger, 1916]; Pennsylvanian, Scioto Co., Ohio.
- ?? *Solenomya* sp. McKee, 1938, pl. 15, fig. 4. [gen. indet; not a solemyid; Pr0; ventrally embayed; alate; elevated subcentral umbos]; pl. 15, fig. 10 [gen. indet.; Kues and Lucas (1989, p. 171) called it *Sanguinolites*?]; Permian, 'β' member, Kaibab Formation, Grand Canyon, Arizona.
- ?? *Solemya (Janeia) elliptica* Zhang, 1977, p. 526, pl. 200, figs. 16, 17 [Pr2; possible solemyin, cf. *Acharax*?, but ligament and internal morphology not observed]; Permian, south-central (Hubei, Hunan), China.
- ?? *Solemya (Janeia) minuta* Zhang, 1977, p. 526, pl. 200, fig. 18 [Pr2; hinge, ligament not observed, possible solemyin?]; Permian, south-central (Lichuan, Hubei) China.
- ?? *Solemya (Janeia)* sp. Kues and Lucas, 1989, p. 171, fig. 3A-C [gen. indet.; poorly preserved]; Permian, San Andres Formation, Ojo Caliente, New Mexico.
- ?? *Solemya (Janina)* [sic] sp. Hoare, 2007, p. 65, fig. 3.20; [gen. indet.; broken shell with radiating ridges intersected by coarse comarginal discontinuities; probably not a solemyid]; Mississippian, Maxville Limestone, Ohio.

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