Zoological Studies

The Fossil Record of the Clam Shrimp (Crustacea; Branchiopoda)

Thomas A. Hegna[1,*] **and Timothy I. Astrop**[2]

[1]*Department of Geology and Environmental Sciences, SUNY Fredonia, 203 Jewett Hall, 280 Central Avenue, Fredonia, NY 14063, USA.*
 *Correspondence: E-mail: thomas.hegna@fredonia.edu (Hegna)
[2]*Fossil Forest Project, Blast Road, Brymbo, Wales, United Kingdom, LI11 5BT. E-mail: timastrop@gmail.com (Astrop)*

Special issue (articles 32-46) communicated by Thomas A. Hegna and D. Christopher Rogers

Clam shrimp (the paraphyletic assemblage of spinicaudatans, laevicaudatans, cyclestherids and the extinct leaiins) are small, bivalved branchiopod crustaceans that specialize in ephemeral freshwater habitats. They have a long fossil record (Devonian onward) that has often been overlooked. Here we briefly review the fossil record of the major groups of clam shrimp and clear up some misconceptions in the literature as to their origin. The dominant group of clam shrimp in the fossil record is the Spinicaudata, which have a diverse fossil record beginning in the Devonian. The clam shrimp suborder Laevicaudata are known from the Permian, with possible soft-part preservation from the Jurassic. However, owing the character-poor nature of these fossils, it is impossible to tell if they represent crown group or stem group laevicaudatans. In contrast, the total group Spinicaudata have a rich record of mostly carapace fossils— the earliest from the Early Devonian. The leaiins are an enigmatic extinct diplostracan lineage thought to be closely related to the spinicaudatans. They have a record that extends from the Middle Devonian to the Permian. The Cyclestherida have a somewhat problematic fossil record: there are no examples of cyclestherids preserved with soft-parts, so the only character used to assign fossils to this lineage is the carapace shape. According to that metric, cyclestherids have a record that begins in the Middle Devonian. Exceptionally preserved clam shrimp are found in the Paleozoic and Mesozoic. Assessing holistically what is known about the clam shrimp fossil record along with carapace morphology, carapace ornamentation and examples of exceptional preservation will ultimately contribute to a synthetic paleontological and neontological understanding of the group, its systematics and evolution.

Key words: Laevicaudata, Spinicaudata, Cyclestherida, Diplostraca, Onychocaudata.

What is a Clam Shrimp?

Clam shrimp are a paraphyletic group containing the clades Spinicaudata, Laevicaudata, Cyclestherida, and the extinct Leaiina. Morphologically diagnosing the extant clam shrimp is relatively easy—they have a bivalved carapace, biramous second antennae, more than 10 trunk limbs (Tasch 1969; Pennak 1989). Identifying clam shrimp in the fossil record by these characteristics is difficult. When presented as fossils, clam shrimp typically only display one valve, making 'bivalvedness' (and degree of lateral compression) an assumption drawn from the one valve. The second antennae and trunk limbs are almost never preserved. Of the four clades combined into the clam shrimp, three possess growth lines. This characteristic is easier to observe in the fossil record. However, as discussed below, its use yields some ambiguity—one cannot tell, based on growth lines alone if a fossil represents a crown group or stem group spinicaudatan/ cyclestherid.

Phylogenetic and apomorphic based clade defini-tions largely have no impact on clade membership for modern clam shrimp taxa; but how clade names are defined has significant implications for the membership

---

of fossil taxa as will be discussed below. We use a phylogenetic crown group definition for Spinicaudata, Laevicaudata, and Cyclestherida to align our definitions with those from molecular phylogenetics. Apomorphic clade definitions for Spinicaudata, Laevicaudata, and Cyclestherida cannot be applied to fossil taxa due to the fact that the relevant characteristics (*i.e.*, Fryer 1987) are almost always lost to decay.

Fossils and Phylogeny

Clam shrimp fossils are dominantly comprised of carapaces only. The reason is that the carapace is more heavily mineralized/sclerotized, and it is more resistant to decay than the 'soft parts' (the body and limbs). This leaves a relatively character-poor fossil, consisting of only the carapace and its growth lines, and under ideal circumstances, interval ornamentation patterns as well. As a result, the presence of growth lines has been a key character in clam shrimp systematics; 'growth lines' are exhibited by spinicaudatans, cyclestherids and a few species of cladocerans. The term 'growth lines', however, is a misnomer. The carapace is not formed by marginal accretion (as understood in brachiopods, corals, and molluscs, and implied by the term 'growth line'), but by incomplete molting. Each time the animal molts, it molts only the ventral cuticle of the carapace, as well as the cuticle of the body (Astrop and Hegna, unpublished). The carapace cuticle (as well as the head in cladocerans; see Kotov and Elias-Gutiérrez 2009; Kotov and Štifter 2006) is kept and a new layer grows underneath it. This extra thickening of the dorsal carapace no doubt serves to protect the animal.

The mere presence of carapace growth lines in fossil diplostracans has been previously interpreted as evidence of spinicaudatan affinities (Gallego 2010; Gueriau et al. 2016 2018; Li et al. 2009a b c d 2010a; Stigall and Hartman 2008; Stigall et al. 2014 2017). Carapace molt retention appears and disappears repeatedly. There is a population of spinicaudatans (formerly classed as the species *Eulimnadia alineata* Mattox, 1953, see Rogers 2020) that lacks *visible* growth lines. D.C. Rogers (pers. comm.) has encountered multiple populations of living spinicaudatas that appear to lack growth lines, and this seems to be the result of the food abundance and quality available to the animals (Rogers et al. 2012). There is also an anecdotal account of a laevicaudatan that possessed a growth line (Linder 1946; diligent searching (by TAH and others) of Linder's collections has failed to turn up this specimen, or specimens. It is assumed by Z. Sigvardt and J. Olesen (D.C. Rogers, pers. comm.) that Linder actually observed the inner verge showing through the carapace). Visible molt retention in several lineages of anomopod

cladocerans appears to have occurred multiple times independently (Kotov and Elias-Gutiérrez 2009; Kotov and Štifter 2006). Molt retention is even known in an extinct group of Paleozoic ostracods (Jones and Olempska 2013; Olempska 2012).

As a result, the optimization of carapace molt retention in branchiopods is not simple (Fig. 1). Even if we ignore the two cases mentioned above (*i.e.*, Linder 1946 and Mattox 1953), molt retention may have originated independently in both spinicaudatans and cyclestherids (B and C in Fig. 1) or it could have originated at the base of the Spinicaudata + Cladoceromorpha clade and been lost at the base of the Cladocera (A and D in Fig. 1). The implications are that a fossil exhibiting growth lines could, in principle, be a (stem) spinicaudatan, a (stem) cyclestherid, a (stem) cladoceromorph, or a member of the Spinicaudata + Cladoceromorpha clade, Onychocaudata.

Early References

In the published literature, one finds reference to Cambrian (Howell 1963; Ulrich and Bassler 1931) and Ordovician (Soot-Ryen 1960) 'conchostracans' (the now-abandoned taxonomic term for clam shrimp). All of these fossils have, under subsequent study, been transferred into other groups. The small, bivalved bradoriids discussed by Howell (1963) and Ulrich and Bassler (1931) are now regarded as stem group crustaceans (Bradoriida + Eucrustacea sister to Marellomorpha (Hou et al. 2010)). *Eoasmussia*, described as a 'conchostracan' by Soot-Ryen (1960), has subsequently been referred to the pelecypod molluscs (Pojeta 1971).

Eridostracans are another group of crustaceans that has been allied with the Diplostraca throughout their history; their peculiar carapace which is mineralized and exhibits molt retention makes them difficult to place systematically. Today regarded as aberrant ostracods (Olempska 2012), a few workers once viewed them as clam shrimp (Schmidt 1941) or marine branchiopods (Jones 1968).

There are no credible references to any clam shrimp taxon prior to the Devonian.

Early Clam Shrimp

The Devonian sees the emergence and subsequent diversification of fossils attributed to the clam shrimp. Working out which clam shrimp is actually the oldest is difficult, owing to difficulties in stratigraphic correlation. There are several references to Early (or lower) Devonian clam shrimp (Cuvelier et al. 2015; Defretin 1950; Groß 1934; Maillieux 1939; Novozhilov

1961), but none are dated more precisely. These species include *Belgolimnadiopsis stockmansi* (Maillieux, 1939) (see also Cuvelier et al. 2015; Defretin 1950), *Concherisma eifelense* (Raymond, 1946), *Pseudestheria* (*Pseudestheria*) *diensti* (Groß, 1934), and *Pseudestheria* (*Tuvinopsis*) *arduennae* Novozhilov, 1961, (see Novozhilov 1961 for the most recent taxonomic treatment)—all are in need of re-evaluation and re-illustration, and their precise stratigraphic placement needs updating. As a result, it is difficult to place the fossils phylogenetically. It is unknown if they represent crown or stem group spinicaudatans, or even stem group onychocaudatans. Regardless, the fossils discussed above represent the earliest clam shrimp. A timeline of the appearance of different clades of diplostracans can be found in figure 2.

A reference to a supposed Late Silurian form, *Asmussia*? *buchoti* (Péneau, 1936) (Bate et al. 1967) was apparently made without consulting Novozhilov (1961), who had previously reclassified Péneau's (1936) taxonomy as *Glyptoasmussia buchoti*, and found its age to be Middle Devonian.

Leaiins

Leaiins are an enigmatic extinct diplostracan lineage thought to be closely related to the spinicaudatans. In form, they look like spinicaudatans with two or more ridges (carinae) running from the umbo to the edge of the carapace (a feature also noted in the extant spinicaudatans *Limnadopsis* (Astrop, pers. obs.) and *Metalimnadia* (Rogers, pers. comm.). They have a fossil record that extends from the Devonian to the Permian—casualties of the end-Permian mass extinction. Impressions of putative soft parts are known from several localities (Shen and Schram 2014), but they do not illuminate the detailed phylogenetic position of leaiins beyond being a part of the Diplostraca. The soft-part impressions are notable for the fact that they only seem to preserve the impression of one pair of male claspers—spinicaudatans possess two pairs of claspers while laevicaudatans and cyclestherids both possess a single pair. However, the nature of the impressions is such that two pairs of claspers could have easily been superimposed upon one another rendering one pair of claspers invisible in the fossils.

As leaiins are thought to have spinicaudatan affinities (based on gross carapace morphology including the presence of carinae, and the putative presence of claspers), they have been used to date the crown group appearance of diplostracans (Wolfe et al. 2016) as Middle Devonian.
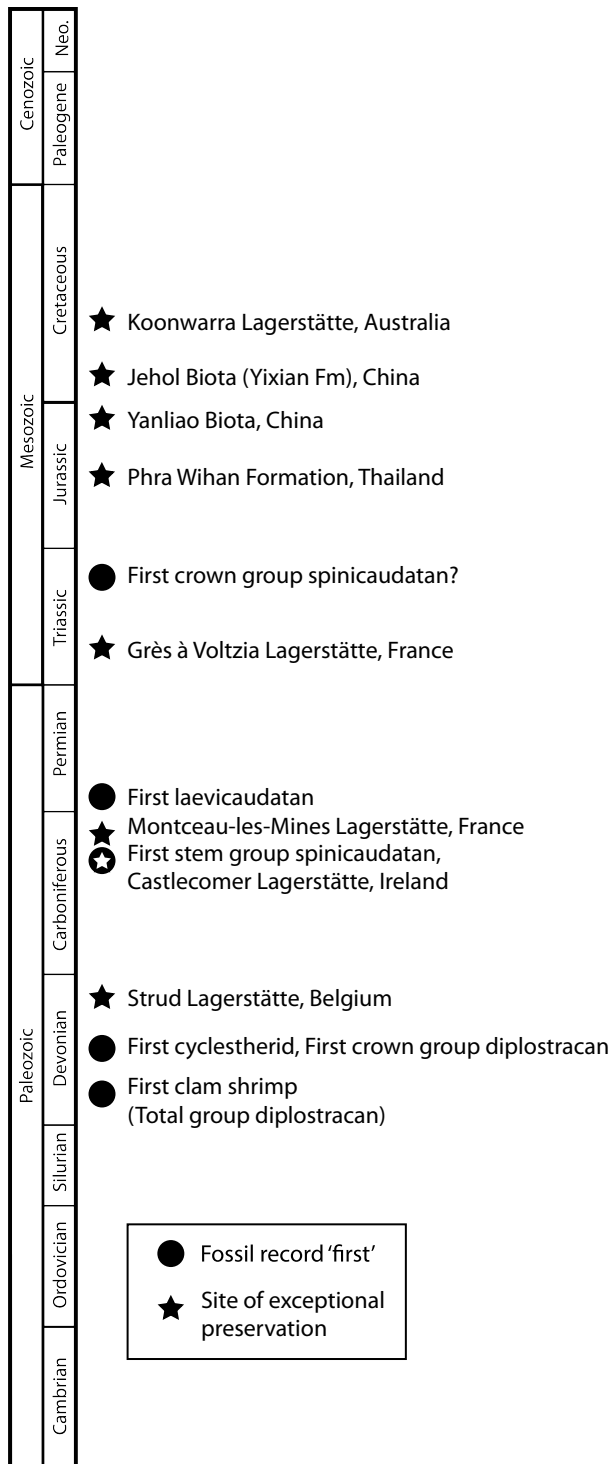
Spinicaudatans

The Spinicaudata are the most diverse group of
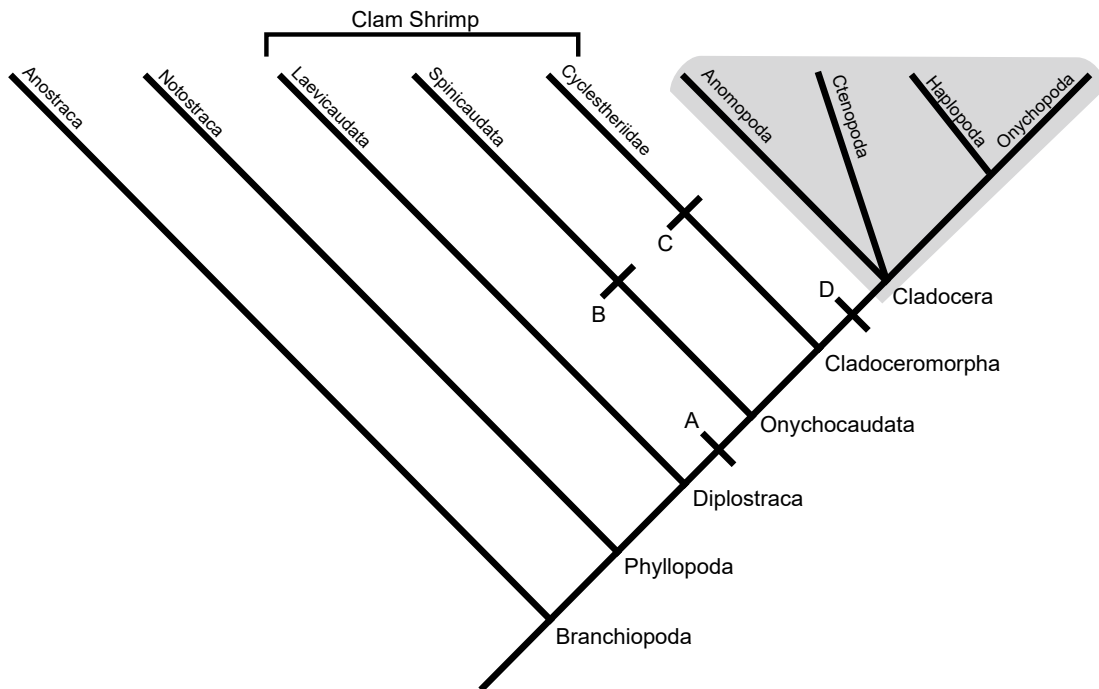
Fig. 1. A phylogeny of extant Diplostraca, with several scenarios for growth line (incomplete molting) evolution mapped onto it. A and D represent the scenario of a gain (A) and subsequent loss (D) of incomplete molting. B and C represent the scenario of two independent gains of incomplete molting.

extant clam shrimp with approximately 194 species in around 16 genera (new species are identified relatively frequently) (Rogers 2020). The four living families,

Fig. 2. A timeline for the first appearance of several groups of fossil diplostracans (circles), as well as for fossil lagerstätten that contain exceptionally preserved fossil clam shrimp (stars).

Leptestheriidae, Eocyzicidae, Cyzidae and Limnadiidae (Schwentner et al. 2020), are distributed globally and are the subject of many studies as model organisms relating to their systematics (*i.e.*, Rogers and Cruz-Rivera 2020; Sanomuang et al. 2020; Timms and Rogers 2020), ecology (*i.e.*, Hethke and Weeks 2020; Meyer-Milne et al. 2020), functional morphology (*i.e.*, Liu et al. 2020), and mating systems (*i.e.*, Weeks et al. 2014). Fossils of this group are diagnosed by the gross morphological features and ornamentation of the carapace and the number of fossil clam shrimp attributed to this suborder is large in comparison to the Laevicaudata and Cyclestherida and many Devonian and Carboniferous clam shrimp are attributed to the Spinicaudata based on the presence of growth lines. However, as discussed above, this alone is insufficient to place them within the stem or crown of Spinicaudata, other characters such as gross carapace morphology, carapace ornament and where possible, soft part morphology must be assessed. Fossils preserving more than just carapaces shed more light on the matter. The Westphalian age (Late Carboniferous) *Limnestheria arda* Wright, 1920 has males with two pairs of claspers (Orr and Briggs 1999), putting this species in, at least, the stem group to the spinicaudatans, as all living spinicaudatan males have two pairs of claspers (despite being relatively heavily chitinised, claspers still do not approach the requisite mineralization to experience the same preservation potential as the carapace and are here considered 'soft parts'). Thus, stem group spinicaudatans originated by the Late Carboniferous.

Laevicaudata

Laevicaudata are distinguished from other clam shrimp by a smooth carapace that is devoid of growth lines, a unique anatomy including a proportionally large head and diagnostic reproductive features (Rogers and Olesen 2016). Extant Laevicaudata are a low diversity suborder containing 42 species in three genera and one family worldwide (Rogers and Olesen 2016; Sigvardt et al. 2019 2020, Shu et al. 2019) and have a poor fossil record. Fossil laveicaudatan identification is based on the presence of a roundish carapace devoid of growth lines and possessing the impression of a maxillary gland. The Laevicaudata sister group, Onychocaudata, has likely stem- or crown group fossils in the Devonian as discussed above. This implies a significant ghost range for the Laevicaudata. Fossil laevicaudatans are mostly only known from the Jurassic and Cretaceous (see Krasinetz 1964 1966; Oleynikov 1975; Shen and Chen 1984; Tchernyshev 1940). The most reliable of these are the specimens of Shen and Chen (1984), which seem to have the distinctive laevicaudatan-style telsons

preserved. Older specimens are known from the Middle Permian (Schneider et al. 2006) and Early Permian (earliest Asselian, J. Schneider, pers. comm.; Schneider et al. 2016). Fossil laevicaudatans are very character poor, so it is impossible at this time to tell if these fossils represent crown or stem group laevicaudatans.

Cyclestherida

The Cyclestherida are recognized by a rounded carapace and are unique among clam shrimp in that they harbor developing embryos within the carapace brood chamber (it should be noted that cladocerans do this as well). Extant cyclestherids are currently only known from one described species, *Cyclestheria hislopi*, however numerous cryptic species are known (Schwentner et al. 2013). Representatives of the Cyclestherida have been identified in the fossil record more frequently than the Laevicaudata and as far back as the Middle Devonian (Novozhilov 1953 1961) and molecular clocks suggest they originated in the Cretaceous (Schwentner et al. 2013). This discrepancy is likely explained by the fact that their identification in the fossil record is based on a single characteristic—round shape (in addition to the growth lines). However, it should be noted that a subrounded shape is exhibited in females of a few species of the living spinicaudatan genera *Eulimnadia* and *Limnadia* (Daday de Deés 1925 1926; Mattox 1937 1939 1953) and that there is an undescribed triangular *Cyclestheria* from Paraguay (D.C. Rogers, pers. comm.), further muddying the identification of fossil Cyclestherida. Thus, the early supposed fossil cyclestherids may belong to the spinicaduatan lineage.

Cyclestherida's sister group, the Cladocera, may have a fossil record extending to the Devonian. The Devonian record is supported by relatively ambiguous fossils that may be related to the Cladoceromorpha lineage (specifically, Cladocera—Anderson et al. 2003). Less ambiguous cladocerans fossils are known from the Jurassic (Kotov 2007).

Exceptionally Preserved Clam Shrimp

Exceptionally preserved clam shrimp fossils do occur at several lagerstätten throughout the world. These sites are scattered in age from Late Devonian to Early Cretaceous (Fig. 2). The fossil clam shrimp there are disappointing from the perspective of a modern clam shrimp taxonomist, because despite the fact that claspers, limbs, and telsons are preserved, they are preserved without the fine detail that modern taxonomists use to tell apart living species.

The oldest site that preserves clam shrimp soft-parts is the Strud Lagerstätte in Belgium (Gueriau et al. 2016 2018), which is Famennian (Devonian) in age. In addition, this site also has notostracans (Lagebro et al. 2015) and anostracans (Gueriau et al. 2016 2018). Next in age is the Castlecomer Lagerstätte in Ireland (Wright 1920; Orr et al. 1996), which is approximately dated to lower Westphalian (= Bashkirian; Early Pennsylvanian; Carboniferous) (Orr and Briggs 1999). Slightly younger is the Late Carboniferous (Late Pennsylvanian) Montceau-les-Mines Lagerstätte in France (Vannier et al. 2003). It should be noted that the notable American Mazon Creek Lagerstätte, which is slightly older than Montceau-les-Mines, does contain clam shrimp, but they do not preserve soft parts (though specimens illustrated in Shabica and Hay (1997) may preserve casts of the thorax). The Middle Triassic (Anisian) Grès à Voltzia is next in age (Gall 1971; Gall et al. 2006). A possible exuvium from a clam shrimp is known from the Middle Jurassic Phra Wihan Formation of northern Thailand (Heggemann et al. 1990). The Phra Wihan specimens were originally interpreted as fossil amphipods (Heggemann et al. 1990), but have been more plausibly reinterpreted as clam shrimp remains (Hegna et al. 2020). The fossils described by Zhang et al. (1987 1990) are likely a part of the Yanliao Biota in the Middle-Late Jurassic (Xu et al. 2017). The Yanliao Biota is notable because it also contains fossil anostracans (Huang et al. 2006; Luo et al. 2020; Shen and Huang 2008). The Jehol Biota is Early Cretaceous in age (Zhou et al. 2017) and contains exceptionally preserved clam shrimp (Shen 2011; Pan et al. 2015) and notostracans (Hegna and Ren 2010; Wagner et al. 2019). The youngest lagerstätten containing clam shrimp with soft parts (Hegna, pers. obs.) is the Koonwarra Lagerstätte in Australia which is Aptian in age (Poropat et al. 2018). A timeline showing the appearance of these clam shrimp containing fossil lagerstätten can be found in figure 2.

DISCUSSION

Despite over a century of research into clam shrimp paleontology, very little consensus exists regarding what is, and what is definitively not, a clam shrimp fossil and furthermore, what characters provide discrete delineation of phylogenetic groupings in higher taxa. The systematics of extant clam shrimp is predominantly based on characters that do not preserve in the fossil record including soft parts and, of course, molecular data. How then, are we to resolve relationships between the abundant fossils of obvious 'clam shrimp' affinity, accessioned in their thousands in global collections, with the phylogenetic history

elucidated using modern taxa?

An initial step is to identify, utilize and expand a standardized set of morphological characters seen in both modern and fossil taxa that allow identification of both definitive clam shrimp carapaces in the fossil record and the major clam shrimp groups to which they may belong; but there are some serious obstacles. We will never get the same level of detail out of a fossil clam shrimp as that we can get from a modern clam shrimp. Thus, fossil and modern species will never be directly equivalent. Fossil clam shrimp are comparatively character-poor, and unfortunately, may never truly be able to generate a resolved phylogeny without input from modern clam shrimp characters. Phylogenies created with molecular data, like that of Schwentner et al. (2020) may become vital tools to use in concert with fossil data to understand clade origins and historical biogeography.

Crown group spinicaudatans are difficult to identify in the fossil record as their identity must rely on carapace ornamentation characters, which have been incompletely documented for all (fossil and modern) clam shrimp. The oldest crown group spinicaudatan has been identified as *Dundgobiestheria mandalgobiensis* Li et al., 2014 (Wolfe et al. 2016) which is upper Middle Jurassic in age. However, a suite of Late Triassic species belonging to the genus *Menucoestheria* Gallego in Gallego & Covacevich 1998 possess a reticulate ornamentation that transitions to lirae (Gallego 2010). This ornamentation pattern places them in the Eosestheriidae, which according to the phylogenetic hypothesis of Astrop and Hegna (2015) is the sister group to the Cyzicidae. This makes *Menucoestheria* a putative crown group spinicaudatan in the Late Triassic. It should be noted that sampling of clam shrimp ornamentation patterns is very poor prior to the Jurassic, and that, as noted by Wolfe et al. (2016, p. 79), this revision of the crown group age of Spinicaudata may still severely underestimate the antiquity of the group. The phylogenetic hypothesis of Astrop and Hegna (2015), was heavily based on the work of Schwentner et al. (2009) on modern taxa, and needs to be re-evaluated in light of the new hypothesis of Schwentner et al. (2020).

The reliance, in both Laevicaudata and Cyclestherida fossils, on a single problematic character is a cause for concern. Both laevicaudatans and cyclestherids should have the same preservation potential as spinicaudatans (with the caveat that the laevicaudatan carapace may be less durable due to the absence of molt retention). Furthermore, spinicaudatans are identified as spinicaudatans in the fossil record largely on the basis of a single character—the presence of molt retention. And, as discussed above, that character is problematic (Fig. 1). Thus, even when talking about spinicaudatans, we are likely including an array of stem lineages and extinct side branches unrelated to crown group spinicaudatans.

Expanding and standardizing the use of characters based on carapace ornamentation, gross carapace morphology (Scholze and Schneider 2015) and where possible, soft parts may shed light on the evolution and origin of the crown group clades.

Authors' contributions: The authors designed the study and wrote the manuscript.

Availability of data and materials: Not applicable.

Competing interests: The authors declare that they have no conflict of interests.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Anderson LI, Crighton WRB, Hass H. 2003. A new univalve crustacean from the Early Devonian Rhynie chert hot-spring complex. Trans Roy Soc of Edin: Earth Sci **94:**355–369. doi:10.1017/S0263593300000742.

Astrop TI, Hegna TA. 2015. Phylogenetic relationships between living and fossil spinicaudatan taxa (Branchiopoda Spinicaudata): reconsidering the evidence. J Crustacean Biol **35:**339–354. doi:10.1163/1937240X-00002317.

Bate RH, Collins JSH, Robinson JE, Rolfe WDI. 1967. Arthropoda: Crustacea. *In*: Harland WB, Holland CH, House MR, Hughes NF, Reybolds AB, Rudwick MJS, Satterthwaite GE, Tarlo LBH, Willey EC (eds.) The Fossil Record. Geological Society of London Burlington House, London, pp. 535–563.

Cuvelier J, Hennion M, Gallego O, Vachard D. 2015. Palaeontological collections of Lille University - Sciences and Technologies. II - Diplostraca (types and figured specimens). Ann Soc Géol Nord **22:**119–134.

Daday de Deés E. 1925. Monographie systématique des Phyllopodes Conchostracés. III. Limnadiidae. Ann Sci Nat Zool, 10e sér **8:**143–184.

Daday de Deés E. 1926. Monographie systématique des Phyllopodes Conchostracés. III. Limnadiidae (suite). Ann Sci Nat Zool, 10e sér **9:**1–81.

Defretin S. 1950. Crustacés fossiles du Dévonien de l'Artois et du Boulonnais. Ann Soc Géol Nord **70:**55–66.

Fryer G. 1987. A new classification of the branchiopod Crustacea.

Zool Jour Linn Soc **91**:357–383.

Gall J-C. 1971. Faunes et paysages du Grès à Voltzia du nord des vosges. Essai paléoécologique sur le Buntsandstein supérieur. Mém Ser Carte Géol d'Alsace Lorraine **34**:1–318.

Gall J-C, Grauvogel-Stamm L, Papier F. 2006. Archive de Grès: L'Alsace il y a 240 Millions d'Années. PIERRON, Sarreguemines, France.

Gallego OF. 2010. A new crustacean clam shrimp (Spinicaudata: Eosestheriidae) from the Upper Triassic of Argentina and its importance for 'conchostracan' taxonomy. Alcheringa **34**:179–195. doi:10.1080/03115510903546152.

Gallego OF, Covacevich CV. 1998. Conchostracos triásicos de las regiones de Antofagasta, Atacama y Coquimbo, Chile. Rev Geol Chile **25**:115–273.

Groß W. 1934. Eine *Estheria* aus dem rheinischen Unterdevon. Senckenbergiana **16**:309–313.

Gueriau P, Rabet N, Clément G, Lagebro L, Vannier J, Briggs DEG, Charbonnier S, Olive S, Béthoux O. 2016. A 365-million-year-old freshwater community reveals morphological and ecological stasis in branchiopod crustaceans. Cur Biol **26**:383–390. doi:10.1016/j.cub.2015.12.039.

Gueriau P, Rabet N, Du Tien Hat E. 2018. The Strud crustacean fauna (Late Devonian, Belgium): updated review and palaeoecology of an early continental ecosystem. Earth Env Sci Trans Roy Soc Edin **107**:79–90. doi:10.1017/S1755691017000275.

Heggmann H, Kohring R, Schlüter T. 1990. Fossil plants and arthropods from the Phra Wihan Formation, presumably Middle Jurassic of northern Thailand. Alcheringa **14**:311–316.

Hegna TA, Lazo-Wasem EA, Serrano-Sánchez ML, Barragán R, Vega FJ. 2020. A new fossil talitrid amphipod from the lower early Miocene Chiapas amber documented with microCT scanning. J South Am Ear Sci **90**:102462. doi:10.1016/j.jsames.2019.102462.

Hegna TA, Ren D. 2010. Two new "notostracans", *Chenops* gen. nov. and *Jeholops* gen. nov. (Crustacea: Branchiopoda: ?Notostraca) from the Yixian Formation, northeastern China. Acta Geol Sinica (Eng ed) **84**:886–894. doi:10.1111/j.1755-6724.2010.00232.x.

Hethke M, Weeks SC. 2020. Population density effects on carapace growth in clam shrimp: implications for palaeontological studies. Zool Stud **59**:33. doi:10.6620/ZS.2020.59-33.

Hou X, Williams M, Siveter DJ, Siveter DJ, Aldridge RJ, Sansom RS. 2010. Soft-part anatomy of the Early Cambrian bivalved arthropods *Kunyangella* and *Kunmingella*: significance for the phylogenetic relationships of Bradoriida. Proc Roy Soc B **277**:1835–1841. doi:10.1098/rspb.2009.2194.

Howell BF. 1963. New Cambrian conchostracans from Wyoming and Newfoundland, brachiopods from Vermont, and worm, hydrozoan and problematicum from Newfoundland. J Paleo **37**:264–267.

Huang D, Nel A, Shen Y, Selden PA, Lin Q. 2006. Discussions on the age of the Daohugou fauna—evidence from invertebrates. Prog Nat Sci **16(Sp Issue)**:308–312.

Jones PJ. 1968. Devonian Ostracoda and Eridostraca from the Bonaparte Gulf Basin, Northwestern Australia. Bureau Min Res, Geol Geoph Bul **99**:1–109.

Jones PJ, Olempska E. 2013. The ostracode suborder Eridostracina Adamczak, 1961. Neues Jahr Geol Pal Abh **267**:341–352. doi:10.1127/0077-7749/2013/0315.

Kotov AA. 2007. Jurassic Cladocera (Crustacea, Branchiopoda) with a description of an extinct Mesozoic order. J Nat Hist **41**:13–37. doi:10.1080/00222930601164445.

Kotov AA, Elias-Gutiérrez M. 2009. A phylogenetic analysis of *Ilyocryptus* Sars, 1862 (Cladocera: Ilyocryptidae). Int Rev Hydrobiol **94**:208–225. doi:10.1002/iroh.200811102.

Kotov AA, Štifter P. 2006. Cladocera: Family Ilyocryptidae (Branchiopoda: Cladocera: Anomopoda) (22). Kenobi Productions, Ghent Backhuys Publishers, Leiden.

Krasinetz SS. 1964. Novye Lynceidae (Conchostraca, Crustacea) iz nižnego mela vostočnogo zabajkal'â [New Lynceidae (Conchostraca, Crustacea) from Lower Cretaceous, eastern Probaikal]. Geol Geof **9**:115–120.

Krasinetz SS. 1966. Rannemelonye dvystvorčatye listonogie (Conchostraca) vostočnogo zabajkal'â [Early Cretaceous bivalved crustaceans from eastern Transbaikalia]. Mat Po Geol Pol Isk Čit Obl **2**:126–196.

Lagebro L, Gueriau P, Hegna TA, Rabet N, Butler AD, Budd GE. 2015. The oldest notostracan (Upper Devonian Strud locality, Belgium). Palaeontology **58**:497–509. doi:10.1111/pala.12155.

Li G, Ando H, Hasegawa H, Yamamoto M, Hasegawa T, Ohta T, Hasebe N, Ichinnorov N. 2014. Confirmation of a Middle Jurassic age for the Eedemt Formation in Dundgobi Province, southeast Mongolia: constraints from the discovery of new spinicaudatans (clam shrimps). Alcheringa **38**:305–316. doi:10.1080/03115518.2014.870834.

Li G, Chen P-J, Wang D, Batten DJ. 2009d. The spinicaudatan *Tylestheria* and biostratigraphic significance for the age of the dinosaur eggs in the Upper Cretaceous Majiacun Formation, Xixia Basin, Henan Province, China. Cretaceous Res **30**:477–482. doi:10.1016/j.cretres.2008.09.002.

Li G, Hirano H, Batten DJ, Wan X-Q, Willems H, Zhang X-Q. 2010. Biostratigraphic significance of spinicaudatans from the Upper Cretaceous Nanxiong Group in Guangdong, South China. Cretaceous Res **31**:387–395. doi:10.1016/j.cretres.2010.05.003.

Li G, Hirano H, Kozai T, Sakai T, Pan Y-H. 2009a. Middle Jurassic spinicaudatan *Shizhuestheria* from the Sichuan Basin and its ontogenetic implications. Sci in China (Ser D): Earth Sci **52**:1962–1968. doi:10.1007/s11430-009-0161-5.

Li G, Shen Y, Liu Y, Bengtson P, Willems H, Hirano H. 2009b. Revision of the clam shrimp genus *Magumbonia* from the Upper Jurassic of the Luanping Basin, Hebei, Northern China. Acta Geol Sinica **83**:46–51. doi:10.1111/j.1755-6724.2009.00006.x.

Li G, Wan X-Q, Batten DJ, Bengtson P, Xi D, Wang P. 2009c. Spinicaudatans from the Upper Cretaceous Nenjiang Formation of the Songliao Basin, northeast China: taxonomy and biostratigraphy. Cretaceous Res **30**:687–696. doi:10.1016/j.cretres.2008.12.008.

Linder F. 1946. Affinities within the Branchiopoda, with notes on some dubious fossils. Arkiv Zool **37**:1–28.

Liu J-Y, Wang C-C, Rogers DC. 2020. Developmental and functional morphology of *Eulimnadia braueriana* Ishikawa, 1895 (Branchiopoda: Spinicaudata) feeding structures: combination of filtering and scraping feeding mechanisms. Zool Stud **59**:35. doi:10.6620/ZS.2020.59-35.

Luo C, Jarzembowski EA, Fang Y, Wang B, Xiao C. 2020. First Anostraca (Crustacea: Branchiopoda) from the Middle Jurassic of Daohugou, China. Proc Geol Assoc **131**:67–72. doi:10.1016/j.pgeola.2019.11.004.

Maillieux E. 1939. Un conchostracé nouveau de l'assise des grès et schistes de Wépion (Emsien inférieur). Bull Mus Royal d'Hist Nat Belg **15**:1–7.

Mattox NT. 1937. Studies on the life history of a new species of fairy shrimp, *Eulimnadia diversa*. Trans Amer Micro Soc **56**:249–255.

Mattox NT. 1939. Description of two new species of the genus *Eulimnadia* and notes on the other Phyllopoda of Illinois. Amer Mid Nat **22**:642–653.

Mattox NT. 1953. A new conchostracan phyllopod, *Eulimnadia alineata*, from Arkansas. Amer Mid Nat **49**:210–213.

Meyer-Milne E, Mlambo MC, Rogers DC. 2020. Distribution of clam

shrimps (Crustacea: Laevicaudata and Spinicaudata) in South Africa, with new records from the Northern Cape Province. Zool Stud **59**:39. doi:10.6620/ZS.2020.59-39.

Novozhilov NI. 1953. Novyj kompleks dvustvorčatyh listonogih rakoobraznyh iz Devona karatau (čimkentskaâ obl., kazahskaâ SSR) [A new complex of bivalved crustaceans from the Devonian of Karatau (Chimkent region, Kazakh SSR)]. Dokl Akad Nauk SSSR **91(5)**:1207–1209.

Novozhilov NI. 1961. Dvustvorcatye Listonogie Devona [Devonian Conchostracans]. Akad Nauk SSSR Trudy Paleo Inst **81**:1–132.

Olempska E. 2012. Morphology and affinities of Eridostracina: Palaeozoic ostracods with moult retention. Hydrobiol **688**:139–165. doi:10.1007/s10750-011-0659-7.

Oleynikov AN. 1975. Stratigrafiya i fillopody yury i mela vostochnogo Zabaikalya [Stratigraphy and phyllopods of the Jurassic and Cretaceous of the Eastern Transbaikal region]. Trudy Vsesoyuznogo Nauchnogo-Issledovatel'skogo Geol Inst (VSEGEI), N.S., **138**:1–172.

Orr PJ, Briggs DEG. 1999. Exceptionally preserved conchostracans and other crustaceans from the Upper Carboniferous of Ireland. Sp Pap Pal **62**:1–68.

Orr PJ, Briggs DEG, Parkes MA. 1996. The "Castlecomer fauna"; a new Konservat-Lagerstätte from the Upper Carboniferous of Ireland. Irish J Ear Sci **15**:93–106.

Pan Y, Wang Y, Sha J, Liao H. 2015. Exceptional preservation of clam shrimp (Branchiopoda Eucrustacea) eggs from the Early Cretaceous Jehol Biota and implications for paleoecology and taphonomy. J Paleo **89**:369–376. doi:10.1017/jpa.2015.24.

Péneau J. 1936. Présence d'*Estheria* dans les schites attribués au Gothlandien du Synclinal de Laval. Bul Soc Sci nat Ouest France, 5, VI, pp. 219–226.

Pennak RW. 1989. Fresh-Water Invertebrates of the United States, 3rd Edition. John Wiley Sons, Inc., New York, USA.

Pojeta J. 1971. Review of Ordovician pelecypods. USGS Prof Paper **695**:1–43

Poropat SF, Martin SK, Tosolini A-MP, Wagstaff BE, Bean LB, Kear BP, Vickers-Rich P, Rich TH. 2018. Early Cretaceous polar biotas of Victoria, southeastern Australia—an overview of research to date. Alcheringa **42**:158–230. doi:10.1080/03115518.2018.1453085.

Raymond PE. 1946. The genera of fossil Conchostraca—an order of bivalved Crustacea. Bul Mus Comp Zool **96(3)**:217–307.

Rogers DC. 2020. Spinicaudata Catalogus (Crustacea: Branchiopoda). Zool Stud **59**:45. doi:10.6620/ZS.2020.59-45.

Rogers DC, Cruz-Rivera E. 2020. A New *Eulimnadia* (Branchiopoda: Spinicaudata: Limnadiidae) from the US Virgin Islands. Zool Stud **59**:42. doi:10.6620/ZS.2020.59-42.

Rogers DC, Olesen J. 2016. Laevicaudata Catalogus (Crustacea: Branchiopoda): an overview of diversity and terminology. Arthropod Syst Phylo **74(3)**:221–240.

Rogers DC, Rabet N, Weeks SC. 2012. Revision of the extant genera of Limnadiidae (Branchiopoda: Spinicaudata). J Crustacean Bio **32**:827–842. doi:10.1163/193724012X637212.

Sanomuang L, Padhye SM, Rogers DC. 2020. Review of the *Eulimnadia* (Branchiopoda: Spinicaudata: Limnadiidae) of Tropical Asia, with the description of a new species. Zool Stud **59**:41. doi:10.6620/ZS.2020.59-41.

Schmidt EA. 1941. Studien im böhmischen Caradoc (Zahoran-Stufe). I: Ostracod en aus den Bohdalec-Schichten und über die Taxonomie der Beyrichiacea. Abh Senckenb Naturf Ges **454**:1–96.

Schneider J, Werneburg R, Gand G, Vianey-Liaud M, Steyer S. 2006. First Permian playa fossil lagerstätte. *In*: Yang Q, Wang Y, Weldon EA, (eds) Ancient Life and Modern Approaches: Abstracts of the Second International Palaeontological Congress. University of Science and Technology of China Press, Beijing, pp. 74.

Schneider JW, Lucas SG, Trümper S, Stanulla C, Krainer K. 2016. Carrizo Arroyo, central New Mexico - A new late Paleozoic taphotype of arthropod Fossillagerstätte. New Mex Geol Soc Guidebook **67**:107–116. doi:10.19080/OFOAJ.2018.07.555710.

Scholze F, Schneider JW. 2015. Improved methodology of 'conchostracan' (Crustacea: Branchiopoda) classification for biostratigraphy. Newsl on Strat **48**:287–298. doi:10.1127/nos/2015/0065.

Schwentner M, Clavier S, Fritsch M, Olesen J, Padhye S, Timms BV, Richter S. 2013. *Cyclestheria hislopi* (Crustacea: Branchiopoda): A group of morphologically cryptic species with origins in the Cretaceous. Mol Phylogenet Evol **66**:800–810. doi:10.1016/j.ympev.2012.11.005.

Schwentner M, Rabet N, Richter S, Giribet G, Padhye S, Cart J-F, Bonillo C, Rogers DC. 2020. Phylogeny and Biogeography of Spinicaudata (Crustacea: Branchiopoda). Zool Stud **59**:44. doi:10.6620/ZS.2020.59-44.

Schwentner M, Timms BV, Bastrop R, Richter S. 2009. Phylogeny of Spinicaudata (Branchiopoda, Crustacea) based on three molecular markers - an Australian origin for *Limnadopsis*. Mol Phylo Evol **53**:716–725. doi:10.1016/j.ympev.2009.07.021.

Shabica CW, Hay AA. 1997. Richardson's Guide to the Fossil Fauna of Mazon Creek. Northeastern Illinois University Press, Chicago.

Shen Y-B. 2011. Soft body preservation in the conchostracan *Eosestheria lingyuanensis* Chen from the Jehol Biota and its taxonomic significance. Acta Pal Sinica **50**:275–283.

Shen Y-B, Chen P-J. 1984. Late Middle Jurassic conchostracans from Tuchengzi Formation of W. Liaoning, NE China. Bul Nanjing Inst of Geol Pal, Acad Sinica **9**:309–326.

Shen Y-B, Huang D-Y. 2008. Extant clam shrimp egg morphology: taxonomy and comparison with other fossil branchiopod eggs. J Crustacean Biol **28**:352–360. doi:10.1163/20021975-99990380.

Shen Y-B, Schram FR. 2014. Soft-body preservation in the leaiid clam shrimp (Branchiopoda, Diplostraca) and its palaeoecological implications. Crustaceana **87**:1338–1350. doi:10.1163/15685403-00003349.

Shu S, Sigvardt ZMS, Chen X, Olesen J, Rogers DC, Sanoamuang L. 2019. *Lynceus amplopedia* sp. nov., a new laevicaudatan clam shrimp with asymmetrically modified thoracopods from Yunnan, China (Crustacea: Branchiopoda). Zool Stud **58**:28. doi:10.6620/ZS.2019.58-28.

Sigvardt ZMS, Rogers DC, De los Rios P, Palero F, Olesen J. 2019. First molecular phylogeny of Laevicaudata (Crustacea: Branchiopoda) with description of a new species of *Lynceus* from Chile and an updated key to species in the Americas. Invertebr Syst **33**:597–617. doi:10.1071/IS18073.

Sigvardt ZMS, Shu S, Alonso M, Ventura M, Sanoamuang L, Rogers DC, Palero F, Olesen J. 2020. A new northeast Asian *Lynceus* (Crustacea: Branchiopoda: Laevicaudata) with uniquely modified thoracopods and an evaluation of DNA barcoding for clam shrimp species identification. Nauplius **28**:e2020013. doi:10.1590/2358-2936e2020013.

Soot-Ryen H. 1960. The middle Ordovician of the Oslo region, Norway; 12, Notostraca and Conchostraca. Norsk Geol Tidsskrift **40**:123–131.

Stigall AL, Hartman JH. 2008. A new spinicaudatan genus (Crustacea: 'Conchostraca') from the late Cretaceous of Madagascar. Palaeontology **51**:1053–1067. doi:10.1111/j.1475-4983.2008.00799.x.

Stigall AL, Hembree DI, Gierlowski-Kordesch EH, Weismiller HC. 2014. Evidence for a dioecious mating system in Early

Jurassic *Hardapestheria maxwelli* gen. et sp. nov. (Crustacea, Branchiopoda, Spinicaudata) from the Kalkrand Formation of Namibia. Palaeontology **57:**127–140. doi:10.1111/pala.12055.

Stigall AL, Plotnick RE, Park Boush LE. 2017. The first Cenozoic spinicaudatans from North America. J Paleo **91:**467–476. doi:10.1017/jpa.2017.15.

Tasch P. 1969. Branchiopoda. *In*: Moore RC (ed) Treatise on Invertebrate Paleontology (Part R, Arthropoda 4(1)). The Geological Society of America and The University of Kansas, Boulder CO and Lawrence, KS, pp. R141–R163.

Tchernyshev BI. 1940. Mesozoic Branchiopoda from Turkestan and the Transbaikal. J Geol, Acad Sci Ukr SSR, Inst Geol Sci **7:**5–46.

Timms BV, Rogers DC. 2020. Diagnosing *Eulimnadia* and *Paralimnadia* (Branchiopoda: Spinicaudata: Limnadiidae). Zool Stud **59:**38. doi:10.6620/ZS.2020.59-38.

Ulrich EO, Bassler RS. 1931. Cambrian bivalved Crustacea of the order Conchostraca. Proc USNM **78:**1–130.

Vannier J, Thiéry A, Racheboeuf PR. 2003. Spinicaudatans and ostracods (Crustacea) from the Montceau Lagerstätte (Late Carboniferous, France): morphology and palaeonenvironmental significance. Palaeontology **46:**999–1030. doi:10.1111/1475-4983.00330.

Wagner P, Haug JT, Haug C. 2019. A new calmanostracan crustacean species from the Cretaceous Yixian Formation and a simple approach for differentiating fossil tadpole shrimps and their relatives. Zool Let **5:**1–14. doi:10.1186/s40851-019-0136-0.

Weeks SC, Brantner JS, Astrop TI, Ott DW, Rabet N. 2014. The evolution of hermaphroditism from dioecy in crustaceans: selfing hermaphroditism described in a fourth spinicaudatan genus. Evo Bio **41:**251–261. doi:10.1007/s11692-013-9265-0.

Wolfe JM, Daley AC, Legg DA, Edgecombe GD. 2016. Fossil calibrations for the arthropod Tree of Life. Earth-Sci Rev **160:**43–110. doi:10.1016/j.earscirev.2016.06.008.

Wright MC. 1920. *Limnestheria*: a new conchostracan genus from the Kilkenny Coal-Measures. Proc Royal Irish Acad B **35:**187–204.

Xu X, Zhou Z, Sullivan C, Wang Y. 2017. The Yanliao Biota: a trove of exceptionally preserved Middle-Late Jurassic terrestrial life forms. *In*: Fraser NC, Sues H-D (eds) Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land. Dunedin Academic Press, Edinburgh, pp. 131–167.

Zhang W-T, Shen Y-B, Niu S-W. 1987. Discovery of Jurassic conchostracans with well-preserved soft parts and notes on its biological significance. Acta Pal Sinica **26:**111–129.

Zhang W-T, Shen Y-B, Niu S-W. 1990. Discovery of Jurassic conchostracans with well-preserved soft-parts and notes on its biological significance. Pal Cathayana **5:**311–352.

Zhou Z, Wang Y, Xu X, Ren D. 2017. The Jehol Biota: an exceptional window into Early Cretaceous terrestrial ecosystems. *In*: Fraser NC, Sues H-D (eds) Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land. Dunedin Academic Press, Edinburgh, pp. 169–214.