

Revision of Fossil Clam Shrimp Taxonomy and a Case Study on Palaobiogeography of Jurassic Clam Shrimps in China

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Abstract

Clam shrimp carapaces are normally preserved as the fossil records. This makes the morphological features of their carapaces important for the taxonomy of fossil clam shrimps, such as the size and shape of the carapaces, the position and size of the umbo, the number and frequency of growth lines, the ornamentation on growth bands, the presence and nature of radial carinae and costae. In this paper a short review has been made on the Chinese systematic framework for fossil clam shrimps. And a case study was carried out for the Jurassic clam shrimp biogeography, which may reflect the geographic barrier and/or palaeoclimate change.

Keywords: Fossil clam shrimp; Taxonomy; Palaeobiogeography

Introduction

Clam shrimps are large branchiopod crustaceans with laterally compressed bodies enclosed by a bivalved chitinous or complex chitin-mineral carapace [1,2]. They are widely distributed on all continents except Antarctica [3,4], and inhabit seasonally astatic wetlands such as playas, vernal (rain and snow-melt) pools, rice field or fishless lakes [3]. These habitats are normally dry for the most portion of the year, or several years [5]. This living environment is consistent with their relatively short life cycles, such as in the species *Eulimnadia texana* individuals disappeared two–three weeks after hatching from the egg [6]. Clam shrimps are important components of an ephemeral freshwater ecosystem [7-9] and successful colonizers under a wet and dry alternating climate setting in the earth history, as abundant fossils have been recorded worldwide in the Mesozoic fine lacustrine deposits [10-21].

Taxonomy of Fossil Clam Shrimps

The fossilized partial soft parts of clam shrimps are very rare in the geological records [22,23]. Clam shrimp fossils are commonly preserved as calcium phosphate carapaces [24], or the external or internal moulds of carapaces. This means that the classification theme of extant clam shrimps, basing mainly on soft body structures, cannot be directly applicable for fossil clam shrimp valves. Because the classification of the latter is mainly based on the carapace characters, such as the carapace outline, structure and the fine ornamentation patterns on growth bands (Figure 1). Nowadays fossil clam shrimps have been accommodated in four suborders: Laevicaudata Linder, 1945 [25], Spinicaudata Linder, 1945 [25], Estheriellina Shen, 2003 [26] and Leaiina Kobayashi, 1972 [27].

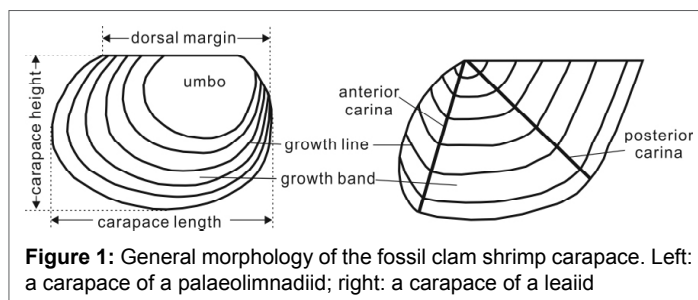


Figure 1: General morphology of the fossil clam shrimp carapace. Left: a carapace of a palaeolimnadiid; right: a carapace of a leaiid

Laevicaudata Linder, 1945

The fossil laevicaudatans, represented by the superfamily Paleolynceioidea Tasch, 1956 [28], are characterized by their carapaces that have one or no growth line. They have been recorded from the Upper Jurassic and the Lower Cretaceous.

Spinicaudata Linder, 1945

The suborder Spinicaudata includes three fossil superfamilies, i.e. the Lioestherioidea Raymond, 1946 [29], Eosestherioidea Zhang and Chen in Zhang et al., 1976 [30] and Estheriteoidea Zhang and Chen in Zhang et al., 1976 [30].

Lioestherioidea Raymond, 1946: The superfamily Lioestherioidea was first proposed by Kobayashi (1972) [27], and its authorship has been credited to Kobayashi, 1954 (Kobayashi, 1973) [31,32], because he has nominated the subfamily Lioestheriinae Kobayashi, 1954 [31]. While Zhang et al. (1976) [30] credited the authorship of the Lioestherioidea to Raymond (1946) [29], because his nomination of the family Lioestheriidae in 1946 antedated that of Kobayashi. Later, Kozur et al. (1981) [33] revised the genus *Lioestheria* as forms with a semi-globular tubercle and a postero-ventrally directed radial rib on a relatively large umbo. Thus, Chen and Shen (1985) [6] subsequently revised the Lioestherioidea (although they used an -acea suffix) to include forms with a large umbo, on which spines, nodules, a muscle scar or a carapace gland can occur; carapaces normally with a few growth lines, which recurved at the dorsal margin, sometimes they extend above the dorsal margin to form a jagged edge. The geological range of the Lioestherioidea is from the Middle Devonian through the Cenozoic. The Lioestherioidea includes seven families as following:

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Palaeolimnadiidae Tasch, 1956 [28]: The carapace has a large umbo and fewer growth lines (Figure 1); ranging from the Late Devonian through the Late Cretaceous.

Palaeolimnadiopseidae Defretin-Lefranc, 1965 [34]: The umbo is not so large, the growth lines recurved at the postero-dorsal margin; ranging from the Middle Devonian through the Late Cretaceous.

Sinoestheriidae Chen and Shen, 1982 [35]: Carapace thin and large; dorsal margin not thickened or ridge-like and serrated; growth lines stout and convex, with a row of nodes, slightly recurved near the postero-dorsal margin; growth bands broad, ornamented with veins, large polygonal reticulation, fine and sparse radial lirae or bifurcated fibrous sculptures; ranging from the Late Jurassic to the Cretaceous [36,37].

Ipsiloniidae Novojilov, 1958c [38]: The carapace has a spine or wing-like process on the dorsal margin behind (sometimes in front) of the umbo; ranging from the Middle Devonian to the Early Cretaceous.

Lioestheriidae Raymond, 1946 [29]: The carapace has a large umbo, on which spines, nodules and radial ribs occur; ranging from Late Carboniferous to Triassic.

Molinestheriidae Kozur, 1980 [39]: The carapace has a large umbo; a long spine extending from the dorsal ridge; occurring in the Lower Triassic.

Perilimnadiidae Chang and Chen in Chen, 1975 [40]: The carapace has a large umbo, on which carapace gland or muscle scar occurs, ranging from the Late Permian through the Early Cenozoic.

Eosestherioidea Zhang and Chen in Zhang et al., 1976 [30]: The superfamily Eosestherioidea includes forms with small umbo and a large number of growth lines. The umbo and dorsal margin have no special structure. The Eosestherioidea ranges from the Middle Devonian through the Cenozoic, and includes nine families as following:

Ulugkemiidae Novojilov, 1958a [41]: The family is characterized by the development of growth line indentation in the later stage; its geological range is from the Middle Devonian to the Permian.

Euestheriidae Defretin-Lefranc, 1965 [13]: The family is characterized by the small-sized reticulation (mesh diameter normally smaller than 0.02 mm) on growth bands. It ranges from the Middle Devonian to the Cretaceous [42,43].

Loxomegaglyptidae Novojilov, 1958a [41]: Growth bands are ornamented with large-sized reticulations. It ranges from the Late Permian to the Cenozoic.

Orthothemosiidae Defretin-Lefranc, 1965 [13]: Growth bands are punctate or smooth. It ranges from Late Permian to Triassic.

Aquilonoglyptidae Novojilov, 1958b [44]: Growth bands are ornamented with scale-like ornamentation. It occurs in the Lower Triassic.

Eosestheriidae Zhang and Chen in Zhang et al., 1976 [30]: The ornamentation transitions from reticulation in upper and antero-ventral part of the carapace to radial lirae in the ventral and postero-ventral part of the carapace. It occurs in the Lower Cretaceous [45,46,47].

Diestheriidae Zhang and Chen in Zhang et al., 1976 [30]: Ornamentation on growth bands as that in Eosestheriidae, with large transversely elongated reticulation superimposed over the radial lirae on the ventral or postero-ventral part of the carapace. It occurs in the Lower Cretaceous [48].

Nestoriidae Shen and Chen, 1984 [49]: Carapace large; growth lines stout and convex; broad growth bands ornamented with large and shallow polygonal reticulations. Radial lirae may occur on growth bands near the venter. It ranges from the Late Jurassic to the Early Cretaceous [50].

Triglyptidae Wang, 2014 [51]: Carapace ornamented with three kinds of ornamentation: the dorsal part of the carapace is ornamented with puncta; the middle part of the carapace with punctate small reticulations; the lower part of the carapace with radial lirae intercalated with radially aligned puncta. It occurs in the Middle and Upper Jurassic [49].

Estheriteoidea Zhang and Chen in Zhang et al., 1976 [30]: The superfamily Estheriteoidea is characterized by linear, dendritic, lattice-shaped, chain-like ornamentation on growth bands. It ranges from the Devonian to the Cenozoic, and includes six families as following:

Asmusiidae Kobayashi, 1954 [31]: Growth bands are ornamented with fine fiber-like ornamentation. It ranges from the Middle Devonian to the Early Carboniferous.

Fushunograptidae Wang in Hong et al., 1974 [53]: Growth bands are ornamented with simple radial lirae, which are straight, curving or with intercalated cross bars. Fushunograptids range from the Late Permian to the Cenozoic [54,55,56]

Jilinstheriidae Zhang and Chen in Zhang et al., 1976 [30]: Growth bands in the upper part of the carapace are ornamented with widely spaced radial lirae with intercalated fine reticulations and short radial lirae; growth bands in the lower part of the carapace are ornamented with irregular reticulations, which are formed by adding short cross bars between radial lirae. Members of this family occur in the Cretaceous.

Halysesstheriidae Zhang and Chen in Zhang et al., 1976 [30]: Growth bands near the umbo are ornamented with widely spaced radial lirae with intercalated fine reticulations and short radial lirae; growth bands in the lower part of the carapace ornamented with chain-like reticulations. Halysesstheriids occur in the Cretaceous [58,59,60,61].

Estheriteidae Zhang and Chen in Zhang et al., 1976 [30]: Growth bands near the umbo are ornamented with widely spaced radial lirae, intercalated with fine reticulations; growth bands in the lower part of the carapace are ornamented with cavernous ornamentation, which appear as isolated stout tubercles on the external mould. The members of the family occur in the Upper Cretaceous [61].

Dimorphostracidae Chang and Chen, 1964 [63]: Growth bands on the upper part of the carapace are ornamented with branching, dendritic radial lirae; growth bands on the lower part of the carapace with dense, fine and curving radial lirae. It occurs in the Upper Cretaceous.

Estheriellina Shen, 2003 [26]

The family Estheriellidae Kobayashi, 1954 was first elevated to the superfamily Estherielloidea [27], including forms with dense radiating costae (more than five) and were assigned to the suborder Leaiina Kobayashi, 1972 [30,6]. Then, in considering that the multiple radiating costae become obsolete near the umbonal area, it was further elevated to the suborder Estheriellina Shen, 2003, including two superfamilies: Estherielloidea and Afrograptioidea Novojilov, 1957 [64].

Estherielloidea Kobayashi, 1954 [31]: Carapace has multiple radiating costae that become obsolete near the umbonal area. It includes the family Estheriellidae Kobayashi, 1954 [31], and occurs in the Lower Triassic.

Afrograptioidea Novojilov, 1957 [64]: Chen and Shen (1985) [6] elevated the family Afrograptidae Novojilov, 1957 [64] to a superfamily, and assigned it to the suborder Estheritina Kobayashi, 1972 [27]. Shen (2003) [26] revised the Afrograptidae to include forms with multiple radiating costae or stout tubercles perpendicular to growth lines present from the umbo through later growth bands, and suggested its close relationship with Estherielloidea. The superfamily ranges from the Late Jurassic to the Early Cretaceous.

Leaiina Kobayashi, 1972 [27]

The leaiids have a carapace with up to five radial carinae present from the umbo through the later growth bands. They range from the Devonian to the Late Permian, and are accommodated in the superfamily Leaiioidea Raymond, 1946 [29].

Leaiioidea Raymond, 1946 [29]: The superfamily is represented by four families: i.e. Monoleiophidae Novojilov, 1954 [65], Leaiidae Raymond, 1946 [29], Praeleiidae Novojilov, 1956 [66] and Rostroleiidae Novojilov, 1956 [66].

Monoleiophidae Novojilov, 1954 [65]: The carapace has one radial carinae. The family occurs in the Upper Carboniferous.

Leaiidae Raymond, 1946 [29]: The carapace has two radial carinae (Figure 1). The family ranges from the Middle Devonian to the Late Permian.

Praeleiidae Novojilov, 1956 [66]: The carapace has 3–5 radial carinae. The family ranges from the Middle Devonian to the Late Permian.

Rostroleiidae Novojilov, 1956 [66]: The carapace has up to five radial carinae; growth lines recurve at antero-dorsal and/or postero-dorsal margins. The family ranges from the Middle Devonian to the Permian.

Ontogeny

Spinicaudatans have carapaces with growth lines that reflect successive moultings. During ecdysis spinicaudatans only cast off an inner skeletal duplicature, but they do not shed their carapace, a growth line is added peripherally to each valve [1]. Thus, there would be the possibility to draw ontogenetic information within an individual carapace. In the case of the Middle Jurassic species *Shizhuetheria truncata* the first 10–14 growth bands are wide and relatively thin, while the later growth bands are narrow. This indicates a rapid growth rate during the junior stage, and a lower growth rate during the adult stage. The transition of growth bands from wide to narrow is clearly exhibited. This shift in carapace accretion rate could be attributed to the onset of the sexual maturity, and to the transition in biological priorities from rapid juvenile growth to reproductive activities [67].

Jurassic Clam Shrimp Biogeographic Provinces in China

Jurassic is a warm greenhouse period in the deep time of the earth history. In China the Jurassic is mainly of non-marine origin. Abundant fossil clam shrimps have been recorded in the Jurassic lacustrine deposits [30,70,71]. This made it possible to discuss the palaeobiogeographic province subdivision.

During the Early Jurassic, in southern China, the palaeo-Yangtze river, starting from the east, ran westwards along the Yunmeng, Ba-Shu and Yunnan lakes into Tethys in southwestern Yunnan (Figure 2). In northern China the biggest lake Qingyang occupied the Ordos basin, and the water replenishment was supplied by three big rivers, e.g. the Yan and Central Plains rivers in the east, and the Corridor river in the west. East Tethys occupied Tibet and southwestern Yunnan Province. The Guangdong-Jiangxi bay separated the southeastern coastal region from mainland China, and the Ussuri bay reached the eastern Heilongjiang region [68]. The Early and Middle Jurassic warm and humid climate made clam shrimp faunas evenly distributed in China. The Early Jurassic *Palaolimnadia baitianbaensis* fauna and the Middle Jurassic *Euestheria ziliujingensis* fauna flourished in the palaeo-Yangtze and the Qingyang lake drainage systems, in the Junggar, Turpan and Qaidam basins, and also occurred in the southeastern coastal region. The late Early Jurassic *Eosolimnadiopsis* fauna distributed mainly in the southeastern coastal region and the Qingyang lake [61].

Since the Late Jurassic with the gradual break-up of the Eurasian continent, the warm, humid climate of the Early–Middle Jurassic period [72] gave way to a warm, extremely arid climate in East Asia. Clam shrimps differentiated into three faunas, e.g. the Tithonian *Pseudograptia* fauna in northern China and the Kimmeridgian *Qinghaiaestheria-Mangyalimnadia* fauna in the Qaidam Basin, and the Kimmeridgian–Tithonian *Eosetheriopsis* fauna in southwestern China [61] (Figure 3). *Qinghaiaestheria* is a common component of the latter two faunas, which indicates that they belong to the same southern palaeobiogeographic province. Thus, researchers should pay more attention on the detailed distribution of fossil clam shrimps to reconstruct palaeo-drainage system and palaeogeography.

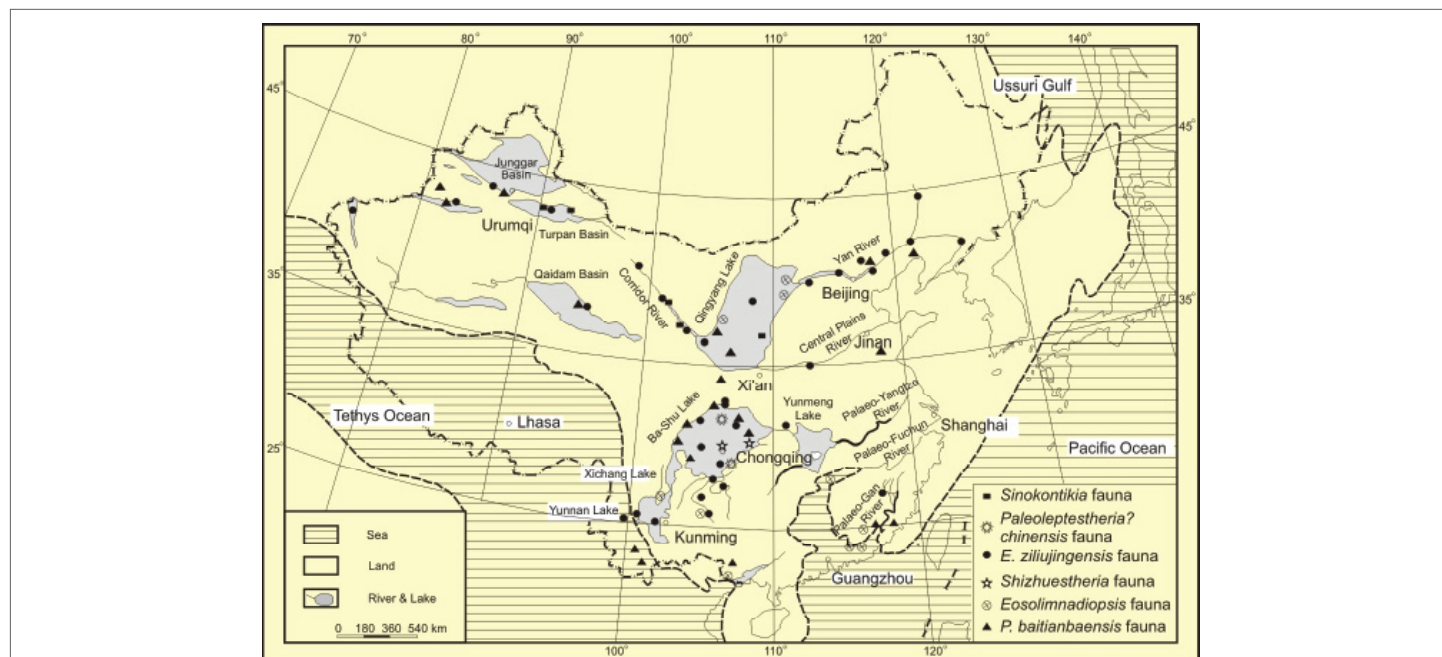


Figure 2: Distribution of Early and Middle Jurassic clam shrimp faunas in China (after Chen, 1979 [68]; Chen and Shen, 1983 [69]; Li and Matsuoka, 2012 [61])



Figure 3: Distribution of Late Jurassic clam shrimp faunas in China (after Chen, 1979 [68]; Chen and Shen, 1983 [69]; Li and Matsuoka, 2012 [61])

Conclusion

In China the non-marine deposits yield abundant clam shrimp fossils, which would be a great help to propose a systematic framework. In combining the recent clam shrimp classification theme, fossil clam shrimps have been accommodated in four suborders: Laevicaudata Linder, 1945 [22], Spinicaudata Linder, 1945 [22], Estheriellina Shen, 2003 [26] and Leaiina Kobayashi, 1972 [27]. The Chinese Jurassic clam shrimp data are used to delineate the palaeobiogeographic provinces, and to reconstruct the old drainage systems. The Early and Middle Jurassic warm and humid climate made clam shrimp faunas evenly distributed in China. While during the Late Jurassic clam shrimps have differentiated into the northern and southern palaeobiogeographic provinces, i.e. the *Pseudograptia* fauna in the north, and the *Qinghaiestheria-Mangyalimnadia* fauna and the *Eosestheriopsis* fauna in the south.

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