

Revision of clam shrimp (“conchostracan”) genus *Tylestheria*
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Revision of clam shrimp (“conchostracan”) genus *Tylestheria* from Late Cretaceous deposits of China

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Abstract

Restudy of the type species of *Tylestheria* from the First Member of the Upper Cretaceous Nenjiang Formation in Nenjiang County, north-east China under a scanning electron microscope (SEM) revealed morphological features on the carapace that had not been recognized previously: growth lines with serrated lower margins; growth bands near the umbo and in the middle part of the carapace with intercalated fine reticulation between relatively widely spaced radial lirae; growth bands in the ventral part of the carapace ornamented with radial lirae and punctae. According to the recent radiometric dating and magnetostratigraphic data of the Late Cretaceous deposits in the Songliao Basin, the *Tylestheria*-bearing horizons of the Nenjiang Formation (Songliao Basin) and the Majiacun Formation (dinosaur egg bearing Xixia Basin, Henan) were revised to be late Santonian in age.

Key words: fossil clam shrimps, taxonomy, biostratigraphy, Late Cretaceous, China.

Introduction

Tan and Wang (1929) established the Nenjiang Formation in the north-east of Nenjiang County, which is extensively developed in the Songliao Basin, north-east China. It is 500–1,235 m thick, and consists mainly of deep-water lacustrine dark grey mudstones with intercalations of very light grey fine-grained sandstones, but with red mudstones dominating the uppermost part (Chen, 2003). It has been subdivided into five members, labelled First to Fifth in ascending order. Fossil clam shrimps (“Conchostracans”) are

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abundant in the formation. The first paper on specimens of these crustaceans recovered from it was that of Chi (1931) who described *Estheria nengkiangensis* (now *Brachygrapta nengkiangensis* (Chi, 1931) Novojilov, 1954). This was followed by the publications of Kobayashi and Huzita (1942, 1943), Tani (1943), Chang (1957), Chang and Chen (1964), Zhang et al. (1976), Cui (1987), Li and Batten (2004b, 2005) and Li et al. (2004b, 2009b).

Age	Formation	Members	Clam shrimp zones
Campanian	Nenjiang Formation	5	<i>Mesolimnadiopsis anguagensis</i> Z.
		4	
		3	
		2	<i>Calestherites sertus</i> Z.
<i>Euestherites bifurcatus</i> Z.			
L. San.	1	<i>Halysesstheria yui</i> Z.	
		<i>Dictyestheria elongata</i> Z.	

Fig. 1. Clam shrimp zones of the Nenjiang Formation (revised after Li and Batten, 2005).

Zhang and Chen (in Zhang et al., 1976) recognized four clam shrimp zones in the Nenjiang Formation (Fig. 1): the *Halysesstheria yui* Zone in the First Member; the *Euestherites bifurcatus* and *Calestherites sertus* zones in the basal and upper parts respectively of the Second Member; and the *Mesolimnadiopsis anguagensis* Zone in the Fourth and Fifth members (Chen, 2003; Li et al., 2004a; Li, 2005; Li and Batten, 2005). Recently, Li et al. (2009b) recovered that the *Dictyestheria elongata* Zone, originally recognized in the underlying Yaojia Formation, extends into the basal part of the First Member of the Nenjiang Formation in the Yaojia area of Dehui, Jilin Province. All of the clam shrimp assemblages in the formation were considered by Zhang et al. (1976) to belong to the *Euestherites* fauna.

The clam shrimp genus *Tylestheria* Zhang and Chen in Zhang et al., 1976, an important associate occurring in the *Halysesstheria yui* Zone, was erected based on specimens from the First Member of the Nenjiang Formation of Jilin and Heilongjiang provinces (both northeastern China). A re-examination of the type species *Tylestheria shanhoensis* (Chang,

1957) under SEM revealed some morphological features not previously seen, as recorded below. Recent research progress on the Nenjiang Formation of the Songliao Basin, and the recovery of *Tylestheria* from the well-known, dinosaur egg bearing Xixia Basin in Henan Province, central China make further age determination and correlation of the fossil clam shrimp bearing beds possible.

Geological age of the Nenjiang Formation

The Third and Fourth members of the Nenjiang Formation belong to the important Heitimiao oil layer, which is the shallowest oil layer of the Songliao Basin. The sedimentary character and fossil contents of the formation have been studied in great detail since the early 20th century (Tan and Wang, 1929 ; Kabayashi, 1942a, b; Chen, 1983; Yu et al., 1983; Liu, 1990; Sha, 2007). However, its age determination has been disputed. Gu (1962, 1982) postulated possible seawater incursions into the Songliao Basin during the Cenomanian or Turonian high sea level period because of the discovery of marine or marginal marine bivalves *Musculus*, *Mytilus* and *Fulpioides* from the Nenjiang Formation. As a result, the base of the Upper Cretaceous in the Songliao Basin was defined at the base of the Nenjiang Formation. These early Late Cretaceous marine links with the Songliao Basin got supported by the discovery of marine water related fossil fish in the formation, including *Sungarichthys longicephalus* (Takai, 1942), *Hama macrostoma* Chow, 1976 and *Jilingichthys rapax* Chow, 1976 (Chang and Chow, 1978). Furthermore, the Cenomanian–Turonian age determination of the Nenjiang Formation got supported by the biostratigraphy of the palynomorph flora recovered from the Nenjiang Formation (Development and Research Institute of Daqing Oil Field, 1976). But the recovery of abundant Late Cretaceous megaspore *Balmeisporites* assemblages from the underlying Yaojia and Qingshankou formations made the lowering of the base of the Upper Cretaceous to the base of the Quantou Formation (Institute of Scientific Research and Designing, Daqing Oil Field, 1976). Thus, a late Turonian–Santonian age was proposed for the Nenjiang Formation (Chen, 2000, 2003). Later, according to more detailed palynomorph data, Gao et al. (1999) revised a much younger Santonian–Campanian (Late Cretaceous) age for the Nenjiang Formation. Recent years, the newest research achievement on the Cretaceous Continental Scientific Drilling borehole SK-1 in the Songliao Basin offers a unique opportunity to establish a more precise chronostratigraphic framework for the Upper Cretaceous sequence in the Songliao Basin (Wang et al., 2008, in press; Li et al., 2011; Scott et al., 2012; Feng et al., in press). The late Coniacian–Santonian foraminifers recovered from the First and Second members of the Nenjiang Formation are direct evidence of middle Late Cretaceous seawater incursions into the Songliao Basin (Xi et al., 2011). A bentonite bed yielding a weighted mean $^{238}\text{U} / ^{206}\text{Pb}$ age of 83.7 ± 0.8 Ma (He et al., 2012) is 2 m above the boundary between the First Member and the Second Member of the

Nenjiang Formation. The C33r/C33n geomagnetic reversal, which was determined to be 79.3 Ma (Mitchell et al., 2006), was recorded 1.2 m above the boundary between the Nenjiang and Sifangtai formations. Thereby, the Nenjiang Formation would be late Santonian–middle Campanian in age (Deng et al., in press).

During the Santonian the *Nemestheria* clam shrimp fauna evolved into four distinct faunas occupying three clam shrimp biogeographic provinces identified in Chinese Late Cretaceous non-marine deposits: (1) the North China Province, represented by the *Euestherites* Fauna in the Songhua Lake drainage system; (2) the South-East China Province containing the *Linhaiella* and *Tenuestheria* faunas in the Yunmeng Lake drainage system; and (3) the South-West China Province represented by the *Aglestheria* fauna in the south-western palaeolake drainage system (Chen, 1994). *Tylestheria shanhoensis* (Chang, 1957) and other two species mentioned below are known from the *Halysesstheria yui* Zone of the *Euestherites* Fauna in the late Santonian First Member of the Nenjiang Formation. *Tylestheria xixiaensis* Li et al., 2009a is the only spinicaudatan species to have been recovered from the Majiacun Formation in the well-known dinosaur egg bearing Xixia Basin, which was a part of the Yunmeng Lake drainage system during the Late Cretaceous. The occurrence of *Tylestheria* in both the Nenjiang and Majiacun formations suggests a late Santonian age for the fossil-bearing horizons of the North and South-East biogeographic provinces.

Materials and methods

The type specimens examined are deposited in the collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPCAS). They are all natural external moulds, and were originally collected from the Upper Cretaceous Nenjiang Formation at Shanhe, Nenjiang County of north-west Heilongjiang Province.

Most of the previous studies on the palaeontology of fossil clam shrimps have used a light microscope. This means that some potential characters of taxonomic value were difficult to see clearly. Here the authors have relied on examination of specimens using an SEM, a Leo 1530 VP, and a Leica light microscope. At the same time we also used the invert function of the software Adobe Photoshop to reverse images taken from external moulds of the specimens, as if they were taken directly of the carapace, so that the detailed ornamentation on the carapace could be clearly shown (Fig. 2).

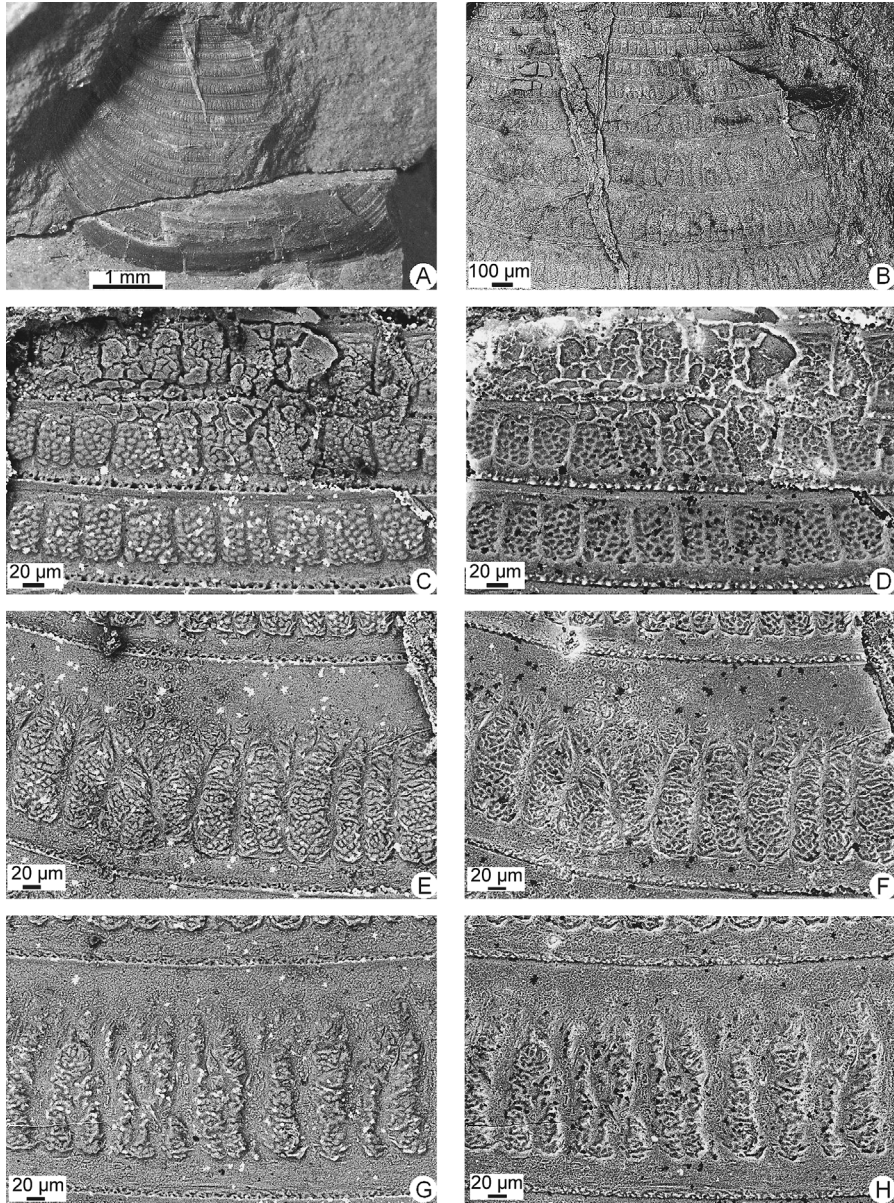


Fig. 2. A–H, *Tylestheria shanhoensis* (Chang, 1957) Zhang and Chen, in Zhang et al., 1976 emend., SEM images of damaged external mould of a right valve, from the First Member of the Nenjiang Formation, Nenjiang County, Heilongjiang Province. A, the counter part of the holotype, NIGPCAS 8549A. B, growth bands near umbo. C, external mould, showing growth bands near the umbo. D, reversed image of Fig. 2C, growth bands near the umbo showing fine reticulation between widely spaced radial lirae and serrated lower margins of growth lines. E, external mould, showing growth bands in the antero-middle part of carapace. F, reversed image of Fig. 2E, showing ornamentation located in the lower two-thirds of each growth band in the antero-middle part of carapace, leaving the upper one-third smooth, fine reticulation intercalated between widely spaced pronounced radial lirae, branching laterally. G, external mould, growth bands in the lower part of carapace. H, reversed image of Fig. 2G, prominent radial lirae intercalated with irregular reticulation, cross bar, punctae and short, fine ridial lines located in the lower one-third of the growth band.

Systematic palaeontology

The classification of recent spinicaudatans of Martin and Davis (2001) is followed here. Because *Cyclestheria* Sars, 1887 has been removed from the suborder Spinicaudata Linder, 1945 and placed in the suborder Cyclestherida Sars, 1899, which is on an equal footing with the remaining Spinicaudata and Cladocera Latreille, 1829, the Conchostraca Sars, 1867 as a taxonomic unit has been abandoned.

Class: Branchiopoda Latreille, 1817

Subclass: Phyllopoda Preuss, 1951

Order: Diplostraca Gerstaecker, 1866

Suborder: Spinicaudata Linder, 1945

Superfamily: Estheriteoidea Zhang and Chen, in Zhang et al., 1976

Family: Halysesitheriidae Zhang and Chen, in Zhang et al., 1976

Genus *Tylestheria* Zhang and Chen, in Zhang et al., 1976 emend.

1976 *Tylestheria* Zhang and Chen gen. nov., Zhang et al., p. 217.

1980 *Tylestheria* Zhang and Chen, Wang, p. 107.

Type species. *Estherites shanhoensis* Chang, 1957, now *Tylestheria shanhoensis* (Chang, 1957) Zhang and Chen, in Zhang et al., 1976.

Occurrence. First Member of the Nenjiang Formation, Heilongjiang and Jilin provinces, north-east China; the Majiacun Formation, Henan Province; upper Santonian (Upper Cretaceous).

Diagnosis. Carapace small or of moderate size, elongate-elliptical, elliptical or oval in outline; growth lines prominent, with serrated lower margins; growth bands near the umbo ornamented with widely spaced long radial lirae with intercalated fine reticulation, sporadically occurring of one short fine radial line between two neighboring radial lirae in the lower part of each growth band; growth bands in the middle part of the carapace ornamented with more widely spaced, prominent long radial lirae with intercalated fine reticulation, and short fine radial lines occurring both in the lower and upper parts of each growth band, some pairs of fine radial lines even being radially connected to form long radial lines; on the external mould of the specimen every pair of rows of radially arranged, grouped tubercles on the middle part of the carapace are separated by deep grooves; growth bands in the lower part of the carapace ornamented with more pronounced radial lirae intercalated with cross bars and irregular reticulation or punctae.

Discussion. When the genus *Tylestheria* Zhang and Chen in Zhang et al., 1976 was erected, the microphotographs were taken under a light microscope, thus some morphological features could not be seen clearly in the low resolution images. Unfortunately, the holotype (NIGPCAS 8549, an external mould of a left valve) of the type species has been coated by varnish to protect it from damage, which means that it is impossible to re-examine it under SEM; as a result, all the images of the holotype are photographs taken under a light microscope (Fig. 3. A–F). It was, however, possible to re-examine the broken counter part of the holotype under SEM, i.e. an external mould of a damaged right valve. Our examination under SEM have revealed features not previously seen, namely: (1) serrated lower margins of growth lines; (2) reticulation intercalated between widely spaced, long radial lirae in the umbonal and middle parts of the carapace; (3) punctae between pronounce irregular radial lirae in the lower part of the carapace.

Although serrations along the lower margins of growth lines were originally considered as a diagnostic feature for the family Afrograptidae Novojilov, 1957 (Chen and Shen, 1977, 1982, 1985; Shen and Chen, 1979, 1982; Cui, 1987; Chen and Hudson, 1991), recent studies on living clam shrimps (Shen, 2003) have shown that they are remains of broken setae or points at or through which setae articulated along the lower margins of growth lines. It has also been demonstrated that this feature is of taxonomic significance at generic or subgeneric level but not at higher (family) groupings of fossils (Li, 2004, 2005; Li and Batten, 2004a, b, 2005; Li et al., 2004b, 2006). Hence, *Tylestheria* is, as originally determined, maintained here in the family Halyssestheriidae Zhang and Chen, in Zhang et al., 1976.

Tylestheria shanhoensis (Chang, 1957) emend.

Figs. 2–3.

1957 *Estherites shanhoensis* Chang sp. nov., p. 485, pl. 6, figs. 1–2.

1976 *Tylestheria shanhoensis* (Chang), Zhang et al., p. 217, pl. 100, figs. 1–6.

Material. Holotype NIGPCAS 8549, and a damaged counter part of the holotype, NIGPCAS 8549A, Shanhe Farm, Nenjiang County, north-west Heilongjiang Province, north-east China.

Emended diagnosis. In addition to the diagnosis of the genus, the type species has an elongate-elliptical outline, and the ornament of the growth bands located in the lower two-thirds of each growth band in the middle and lower parts of the carapace.

Dimension of the holotype. In order: specimen no.; number of growth lines; length of carapace (mm); heigh of carapace (mm); NIGPCAS 8549; 24; 5.6; 3.2.

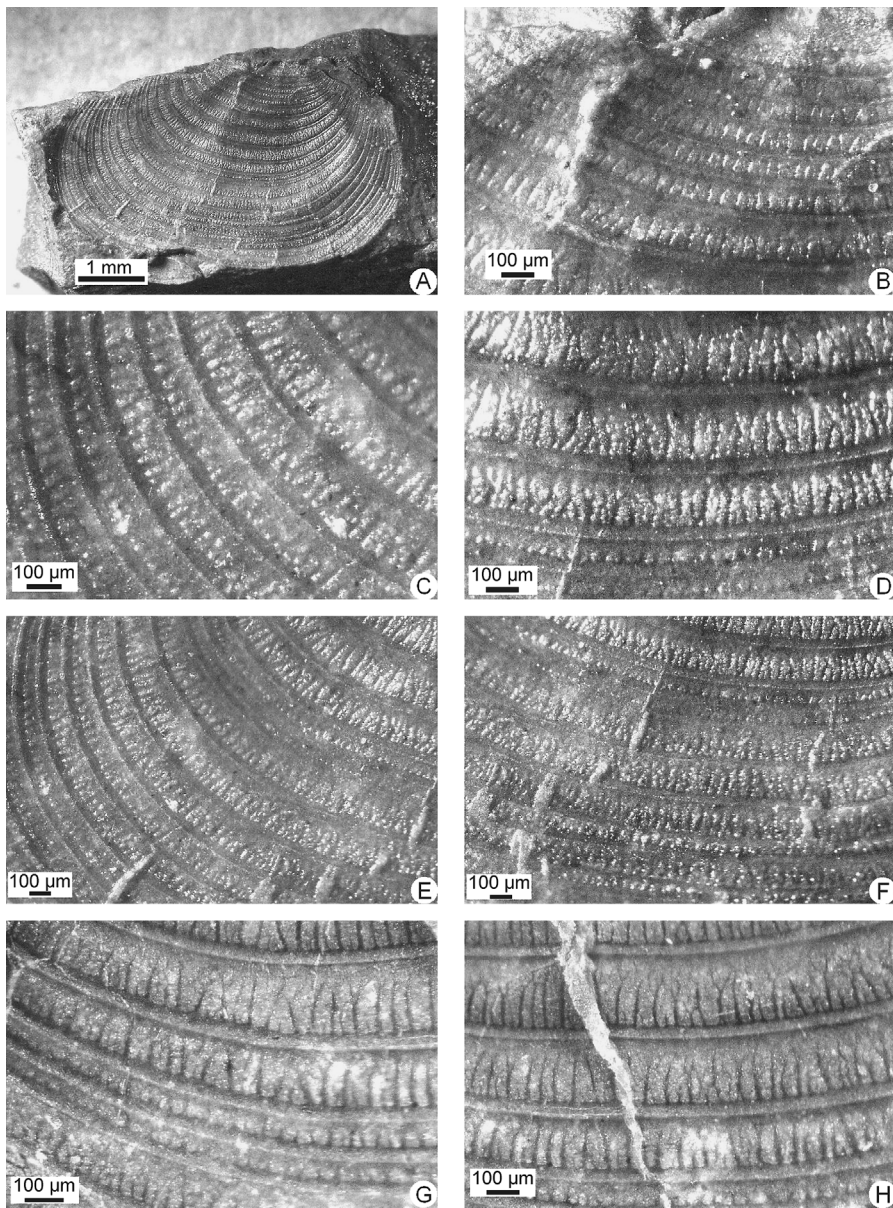


Fig. 3. A–H, *Tylestheria shanhoensis* (Chang, 1957) Zhang and Chen, in Zhang et al., 1976 emend., light microscope images of specimens, from the First Member of the Nenjiang Formation, Nenjiang County, Heilongjiang Province. A–F, holotype, NIGPCAS 8549. A, external mould of a left valve. B, narrow growth bands near umbo, showing widely spaced grooves. C, E, ornament on growth bands in antero-ventral part of carapace. D, F, ornament on growth bands in ventral part of carapace. G–H, ornamentation of counterpart specimen of the holotype, NIGPCAS 8549A. G, ornament on growth bands in antero-ventral part of carapace. H, ornament on growth bands in middle part of carapace.

Description. Carapace of small to moderate size, gently convex, elongate-elliptical in outline; umbo small, slightly projecting beyond the anterior one-third of the long and straight dorsal margin; 24 or more prominent growth lines have serrated lower margins. Growth bands in the umbonal area narrow, wider below, and become narrower again in the lower part of the carapace. Growth bands in the umbonal area ornamented by relatively widely spaced long radial lirae with intercalated reticulation, normally one short fine radial line occurs within the reticulation between two neighboring widely spaced long radial lirae. Growth bands in the middle part of the carapace are wider with smooth upper part of each growth band, while the lower two-thirds of each growth band decorated with ornaments including more widely spaced, more prominent, upwardly branching long radial lirae with intercalated reticulation, short fine radial lines occurring either in the lower part or middle part of each growth band, some pairs of fine radial lines extends to meet in the middle part of each growth band, as a result, on the external mould of the holotype every pair of rows of radially arranged grouped tubercles in the middle part of the carapace are separated by deep grooves; growth bands in the ventral part of the carapace are relatively narrow, ornamented with more pronounce irregular radial lirae with intercalated fine radial lines, cross bars and punctae, so that in the external mould the growth bands are decorated by radially arranged tubercles, i.e. a kind of chain-like ornament.

Discussion. *Tylestheria shanhoensis* is similar to *T. xixiaensis* Li et al., 2009a from the Upper Cretaceous Majiacun Formation of the dinosaur egg bearing Xixia Basin in Henan. Both have carapaces that are elongate-elliptical in outline. However, the carapace of *T. shanhoensis* is larger, the ornaments are restricted to the lower two-thirds and making the upper one-third smooth of each growth band in the middle and lower parts of the carapace. *Tylestheria shanhoensis* is easily differentiated in carapace outline from *T. kanqinshikouensis* Zhang and Chen, in Zhang et al., 1976 from Nenjiang and *T. compta* Zhang and Chen, in Zhang et al., 1976 from Da'an in Jilin, both of which are either elliptical or oval (not elongate) in outline respectively. No other species have been described.

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