New Lopingian (Late Permian) rugosochonetid species from Sichuan, South China

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Two rugosochonetid species, *Neochonetes (Huangichonetes) geniculatus* sp. nov. and *Neochonetes (Zhongyingia) linshuiensis* sp. nov., are described from the Lopingian (Late Permian) of the Chuanmu section, Sichuan, South China. Ecological changes from the diverse upper Changhsingian brachiopod palaeocommunity to the depauperate post-extinction brachiopod community are briefly discussed.

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Key words: brachiopods, chonetids, ecology, Lopingian, Permian-Triassic boundary.

TWO NEW RUGOSOCHONETID species from the Changhsing and lowermost Feixianguan Formations at the Chuanmu section, Sichuan, South China are described in this paper. The Chuanmu section is located in the Huaying Mountains (Huayingshan) in eastern Sichuan, about 125 km northeast of Chongqing City (Fig. 1). Permian and Triassic sequences are well exposed along a road cutting at this section, which is fairly continuous from the Cisuralian Liangshan Formation to the Late Triassic. This work forms part of a larger study on the Permian Brachiopoda from the Chuanmu section by MJC.

**Lithology and biostratigraphy**

The Changxing Formation is the youngest Permian formation in South China, and is conformably overlain by Triassic marine sediments at the Chuanmu section. In this section and the surrounding area in Sichuan, the Changxing Formation is dominated by cherty limestone with subordinate argillaceous limestone and marl, representing a shallow carbonate platform environment (Fig. 2). The Feixianguan Formation at the Chuanmu section is a thick sequence (>1 000 m) of fairly monotonous thin-bedded marl and micrite. Brachiopods were only found at the very base of this formation at the Chuanmu section. Early Triassic sequences are fairly uniform across South China (Peng *et al.* 2001), and were deposited during a transgressional event and subsequent highstand following a regression that occurred towards the end of the Permian (Chert *et al.* 1998). They are characterised initially by thin bedded mudstone and shale, followed by fairly thinly bedded marly to argillaceous micritic facies, and are generally well laminated with little evidence of bioturbation.

The new species were collected from the upper half of the Changxing Formation and the lowermost 20 cm of the overlying Feixianguan Formation. The abundant and highly diverse brachiopod fauna of the upper half of the Changxing Formation yielded more than 70 identifiable species (304 individuals) associated with the two new species. The most common species was *Haydenella kiangsiensis* (Kayser, 1883), followed by *Spinomarginifera lopingensis*.
Fig. 1A-B. A, Location map of the Chuanmu section in Sichuan. 1: mountains; 2: rivers; 3: provincial boundaries. B, Distribution of formations at the Chuanmu section. 1: gravel road; 2: river.

(Kayser, 1883), Prelissorhynchia pseudoutah (Huang, 1933), Neochonetes (Zhongyingia) linshuiensis sp. nov., Spinomarginifera alpha (Huang, 1932), Acosarina minuta (Abich, 1878), Spinomarginifera chengyaoeyenensis (Huang, 1932), Crurithyris speciosa (Wang, 1955), Haydenella nasuta (Zeng, 1993), Linshuichonetes flatus (Shen & Archbold, 2002), Cathaysia orbicularis (Xu & Grant, 1994), Neochonetes (Huangichonetes) cursothornia (Xu & Grant, 1994), Neochonetes (Huangichonetes) sub-strophomenoides (Huang, 1932), Spirigerella? guizhouensis (Liao, 1980b), Huatangia sulcataferr (Liao & Meng, 1986) and Orthotetina frechi (Huang, 1933), which represented just over 60% of the collections; the other 60 species make up the remainder of the species diversity.

Neochonetes (Zhongyingia) linshuiensis sp. nov. is a relatively common species in the upper part of the Changxing Formation at this section, with twelve specimens collected from seven horizons in the upper 110 m of the Changxing Formation (Fig. 2). The second new species, Neochonetes (Huangichonetes) geniculatus sp. nov. appears to be much rarer, with only two specimens collected from two horizons, one within 20 cm (Bed 174) of the top of the Changxing Formation and the other in the basal 20 cm (Bed 178a) of the overlying Feixianguan Formation (Fig. 2).

The brachiopod fauna in the Feixianguan Formation at the Chuanmu section is found only at the very base of this formation in one bed only (Bed 178a, CC-11). It consists entirely of Permian holdover taxa which did not immediately succumb to the end-Permian extinction. The brachiopod fauna from Bed 178a (CC-11) contains eight species along with an unidentifiable specimen belonging to the Rugosochonetidae. The species are Cathaysia orbicularis, Spinomarginifera lopingensis, Crurithyris sp., Linshuichonetes flatus, Neochonetes (Huangichonetes) sub-strophomenoides, Acosarina minuta, Neochonetes (Huangichonetes) geniculatus sp. nov. and Spirigerella? sp., in order of decreasing abundance.

As conodont work is yet to be fully completed on this section, the Permian-Triassic boundary was primarily located through the use of lithostratigraphy, biostratigraphy and eventostratigraphy (Peng & Tong 1999, Peng et al. 2001) mainly through correlation of the clay beds immediately above and below the boundary bed. From correlation with the PTBSS (Permian-Triassic Boundary Stratigraphic Set) of Peng et al. (2001) the Permian-Triassic boundary has
Fig. 2. Stratigraphic column of the Changhsing (top 110 m only) and Feixianguan Formations at the Chuanmu section. 1. limestone; 2. argillaceous limestone; 3. cherty limestone; 4. cherty bioclastic limestone; 5. mudstone; 6. calcareous mudstone; 7. claystone; 8. Neochonetes (Zhongyingia) linshuensis sp. nov.; 9. Neochonetes (Huangichonetes) geniculatus sp. nov.; 10. other brachiopods. The arrow marked ‘A’ at top right indicates the Permian-Triassic biostratigraphic boundary, which occurs between Beds 178a and b, about 20 cm above the top of the Changxing Formation. The arrow marked ‘B’ indicates the lithostratigraphic boundary between the Changxing and Feixianguan Formations.
been placed by us between Beds 178a and 178b, which appear to be the equivalents of Beds 27a/b and 27c/d of Meishan D section respectively (Peng et al. 2001, Yin et al. 1996). Placement of the boundary at this point locates the brachiopods of Bed 178a in the very last bed of the Permian, although they are above the event stratigraphic boundary marked by the clay beds (Beds 25 and 26 at the Meishan section), and the main extinction horizon, which is in Bed 176 at the Chuanmu section [this extinction event was discussed in detail in Campi (2003)]. This also means that the basal 20 cm of the Feixianguan Formation is Permian, as the lithostratigraphic boundary between the Feixianguan and Changxing Formations was placed by us at the top of Bed 174, in accordance with Yin et al. (2001). Peng et al. (2001) reported the conodont *Hindeodus parvus* from Bed 178 (their Bed 5) at the Chuanmu section; however, the exact identity of the specimen is somewhat questionable according to Peng Yuanqiao (pers. comm. 2003).

**Ecology**

These new species occur within the *Spinomarginifera* – *Haydenella* – *Neochonetes* (*S* – *H* – *N*) Palaeocommunity recognised in the upper part (top 40 m) of the Changxing Formation at the Chuanmu section (Campi 2003). *Neochonetes (Zhongyingia) linshuiensis* sp. nov. is a prominent member of this community, whereas *N. (Huangichonetes) geniculatus* sp. nov. played a very minor role, as it first appeared at the very top (top 20 cm) of the Changxing Formation. The *S* – *H* – *N* Palaeocommunity was very diverse (> 70 species) and was dominated by small, spiny productids and chonetids, in addition to genera such as *Prelissorhynchia* and *Acosarina*. It was generally found in micrite to cherty and bioclastic limestones and is interpreted as a relatively quiet environmental setting with a soft, muddy lime substrate. There is abundant pyrite in some beds at the Chuanmu section, which possibly indicates periodic presence of reducing conditions, and this is common in the limestone facies in the Changhsingian in South China (pers. obs.). The *S* – *H* – *N* Palaeocommunity was associated with an abundant invertebrate fauna dominated by crinoids, with bivalves, corals, ammonoids and trilobites present in smaller numbers (Fig. 3A).

The depositional environment for this community is interpreted as a back reef or lagoonal environment, below wave base, rather than in a reef or bioherm deposit. Reefs and bioherm build-ups were quite common in the Changhsingian in South China, and were usually characterised by abundant corals and calcareous algae, along with reef-building brachiopod genera.

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*Fig. 3. Palaeocommunity reconstructions. A, typical members of the *Spinomarginifera* – *Haydenella* – *Neochonetes* Palaeocommunity from the upper part of the Changxing Formation; a, crinoids; b, ammonoid; c, *Prelissorhynchia*; d, *Acosarina*; e, *Schuchertella*; f, chonetids; g, *Spirigerella*; h, trilobite; i, *Crurithyris*; j, productids (e.g. *Spinomarginifera* and *Haydenella*); k, bioturbation. B, holdover taxa found in Bed 178a, Feixianguan Formation; a, *Crurithyris*; b, *Cathaysia*; c, *Acosarina*; d, chonetids; e, *Spinomarginifera*. 
such as Richthofenia, Perigeyereella, Leptodus and Laterispira (Liao & Meng 1986, Shen & He 1994a). Corals are rare at the Chuanmu section and, although both Leptodus and Perigeyereella are present, they are not abundant.

Neochonetes (Huangichonetes) geniculatus sp. nov. was only found at the very top of the Changhsingian (Fig. 2) at the Chuanmu section, and it appears to be one of the few species that survived for a short period after the end-Permian mass extinction. The effect of this extinction event on the Permian brachiopod fauna at the Chuanmu section is discussed in greater detail in Campi (2003). Other species that also were present in the 'holdover' fauna in the aftermath of the end-Permian mass extinction at this section were Cathaysia orbicularis, Spinomarginifera lopingensis, Linshuichonetes flatus, Neochonetes (Huangichonetes) substrophomenoides, Acosarina minuta, Crurithyris sp. and Spirigerella? sp. (Fig. 3B).

These species were all small and the 'holdover' fauna at this section appears to be quite similar in general composition to that found in other areas of South China immediately above the mass extinction horizon. For example, Xu & Grant (1994) recognised a suite of Permian-type survivors in the lower Griesbachian at several sites in South China that included Acosarina, Araxathyris, Crurithyris and Prelissorhynchia in addition to several species of chonetids. The composition of the 'holdover' fauna in bed 178a at the Chuanmu section is quite similar in composition to the Transitional Bed Lingula fuyuanensis – Crurithyris flabelliformis Assemblage Zone of Shen & He (1994b).

There appears to have been an environmental change associated with the mass extinction, as the Changxing Formation is dominated by cherty and bioclastic limestone indicative of a relatively clear and normal marine environment, whereas the basal Feixianguan Formation is dominated by marl and thin-bedded micrite. This facies change has been recognised from elsewhere in Sichuan (Wignall & Hallam 1996, Ezaki et al. 2003), and has been interpreted as resulting from a transgressive event and associated development of dysaerobic benthic conditions. However, in the Chuanmu section pyrite crystals are commonly disseminated through the limestones in the upper part of the Changxing Formation, with little other evidence of dysaerobic conditions, as the abundant and diverse brachiopod fauna otherwise indicates a relatively tolerant environment.

One obvious environmental consequence of the facies change from the Changhsing to the Feixianguan Formations, aside from any background phenomena operating on a larger scale to cause the global signature of this mass extinction, is the sudden influx of argillaceous material, indicated by the argillaceous micrite of Bed 178 compared to the cleaner limestones of the Changxing Formation. This influx may have affected the feeding efficiency and respiration of many of the brachiopod species adapted to the less turbid conditions prevalent in the Changxing Formation. There is some support for this argument as the 'holdover' species that were present in the basal Feixianguan Formation were all small and relatively thin-shelled. These morphological adaptations have been suggested to be a consequence of lowered oxygen levels (Allison et al. 1995). Small size alone may be a result of benthic environmental conditions only being adequate for life for short periods of time, so not allowing organisms to attain their full growth potential (Ferguson 1985).

Several chonetid species were also present in the 'holdover' group at the Chuanmu section, and are very common at this level across South China (Xu & Grant 1994). This eurytopic group is often a dominant element of brachiopod communities which experienced less than ideal environmental conditions (Simanauskas & Cisterna 2000, Shen & Archbold 2002, Campi & Shi 2002).

It is interesting that characteristic disaster taxa such as Lingula have not been found in the Permian-Triassic boundary sequence at the Chuanmu section. This genus is extremely abundant above the boundary in other areas of Sichuan and across South China (Xu & Grant 1994, He & Shi 1996), where it often forms high
abundance, low-diversity shell beds with bivalve genera such as *Claraia*. At the Chuanmu section Triassic bivalves, such as *Towaptera*, first appear in Bed 180e, about 32 cm above the holdover Permian fauna in Bed 178a, or 50 cm above the lithological boundary between the Changhsing and Feixianguan Formations. *Claraia* appears about 70 cm above the boundary (Peng et al. 2001) and *Lingula* may appear above this level, as it has been found in the Lower Triassic of nearby sections (Xu & Grant 1994), but not yet at the Chuanmu section. From our unpublished observations in areas around Chongqing (about 125 km from the Chuanmu section), *Lingula* can appear some metres above the boundary between the Changhsing and Feixianguan Formations.

**Systematic palaeontology**

The material studied for this paper is deposited in the Museum of Victoria (NMV P). The specimens were whitened with an aerosol of ammonium chloride for photography. Latex casts were also made from some of the specimens.

Suborder CHONETIDINA Muir-Wood, 1962

Superfamily CHONETOIDEA Bronn, 1862

Family RUGOSOCHONETIDAE Muir-Wood, 1962

Subfamily RUGOS~ONETINAE Muir-Wood, 1962

**Neochonetes** Muir-Wood, 1962

*Type species*. *Chonetes dominus* King, 1938, p. 259, pl. 36, figs 1-7. Late Carboniferous, West Texas (USA).

**Comments.** Shen & Archbold (2002) discussed in detail the various subgenera of *Neochonetes* that occur in South China, and their diagnoses are followed herein.

**Neochonetes (Huangichonetes)** Shen & Archbold, 2002

*Type species*. *Chonetes substrophomenoides* Huang, (1932, p. 3, pl. 1, figs 3-7). Lopingian, South China.

**Neochonetes (Huangichonetes) geniculatus** sp. nov. (Figs 4A, G, I – O, Fig. 5)

**Etymology.** From the geniculate longitudinal profile of the ventral valve of this species.

**Material.** The holotype is a ventral valve external mould and corresponding ventral internal mould, NMV P309550a-b. The paratype is a fragmentary ventral valve, NMV P309551.

**Diagnosis.** Small subquadrate *Neochonetes (Huangichonetes)* with highly convex ventral valve, very small ears, shallow median sulcus.

**Description.** Small for genus, subquadrate to trapezoidal in outline, moderately transverse; strongly inflated; ears very small, flat and triangular, well demarcated from body; hingeline straight, forming maximum width, bearing hinge spines; shallow sulcus.

Visceral disk strongly inflated, maximum inflation anterior of midvalve, almost geniculate in longitudinal outline (Figs 4G, 5A); lateral flanks steep; umboonal flanks slightly swollen; cardinal extremities acute, lateral margins tapering sharply anterior to ears; shallow median sulcus originating on umbo; about 25 fine capillae, reaching 4 per mm at anterior margin, capillae distinct with steep sides in cross section, wider than interspaces, ornament very faint to imperceptible on ears.

Ventral interior (Fig. 4M, Fig. 5B) with short median septum, about one-third of valve length; strong, short vascular trunks, originating close to anterior end of median septum; hinge spines not preserved but spine canals present, pointing towards umbo; interarea shallow, triangular; pseudodeltidium rounded; teeth rounded internally, tapering laterally and angled anteriorly; surface coarsely radially papillose, ears with much finer, fainter papillae. Dorsal valve unknown.

**Table 1.** Measurements of *Neochonetes (Huangichonetes) geniculatus* in mm: ml = maximum valve length; mw = maximum valve width; hw = hinge width; t = valve thickness; v = ventral valve; + = incomplete specimen.
Discussion. This new species is placed in Neochonetes (Huangichonetes) on the basis of the highly convex ventral valve, small ears, fine capillation, well defined ventral median sulcus, and ventral internal structure, especially the presence of vascular trunks and a short median septum. The highly convex ventral valve is also characteristic of Tethyochonetes Chen et al., 2000, and specimens described as Tethyochonetes sp. by Shen & Archbold (2002, figs 60-P) appear quite similar to the new species in terms of convexity and outline of the ventral valve, although Shen & Archbold’s specimens do not seem to have vascular trunks and are more finely papillose internally than the new species.

Two other subgenera of Neochonetes are present in the Permian of South China, and the new species can be separated from these. The highly convex dorsal valve and small ears clearly differentiate the new species from Neochonetes (Zhongyingia) Shen & Archbold, 2002, which has a gently to moderately convex ventral valve and extended, acute cardinal extremities. Neochonetes (Sommeriella) Archbold, 1982 can be separated from the new species as the former is widest at the midvalve rather than the hinge line and has larger ears. The new species can be differentiated from Neochonetes convexa (Zhongyingia) Shen & Archbold, 2002 placed in Neochonetes (Sommeriella) strophomenoides (Waagen, 1884) as Liao’s material is more transverse than the new species and has rounder rather than acute cardinal extremities.

Neochonetes (Huangichonetes) geniculatus sp. nov. can be easily differentiated from N. (H.) substrophomenoides (Huang, 1932) and N. (H.) cursothornia (Xu & Grant, 1994) as the latter two species have more moderately convex ventral valves and much larger ears. Neochonetes (H.) cursothornia also has square cardinal extremities rather than the more acute cardinal extremities of the new species and some specimens of N. (H.) substrophomenoides. However, two specimens of N. (H.) cursothornia figured by Xu & Grant (1994, figs 15.4, 15.8) appear similar in general shape and convexity to the new species, as they are less transverse and more inflated than the other figured specimens of this species. This may simply be a reflection of the close generic relationship, or these two specimens may actually belong to the new species, but the figures are not clear enough to be certain at this stage.

Shen et al. (2002) illustrated a very similar new species of this genus from the Yongde Formation of Yunnan. This species, N. (H.) inflatus Shen et al. (2002, p. 671, fig. 3: 1-9) appears very similar to the Sichuan species as both are finely capillate, have a conspicuous median sulcus, small ears and are strongly convex. They can be differentiated by the detail of the inflation of the ventral valve, as N. (H.) inflatus is most strongly inflated at the umbo, while N. (H.) geniculatus is most inflated at the midvalve. The latter species also has acute, well-defined ears whereas the former has obtuse, ill-defined ears.

Occurrence. Specimens were collected from Bed 174 in the Changxing Formation and Bed 178 of the Feixianguan Formation at the Chuanmu section.

Neochonetes (Zhongyingia) Shen & Archbold, 2002

Type species. Neochonetes zhongyingensis Liao, 1980a, p. 257, pl. 5, figs 10-13. Changhsingian (Lopingian), South China.

Neochonetes (Zhongyingia) linshuiensis sp. nov. (Figs 4B – F, H, P – R)

Etymology. From Linshui county, in which the Chuanmu section is located.

Material. Twelve specimens from the Changxing Formation. The holotype is a dorsal valve, NMV P309559; the paratypes are a ventral valve, NMV P309561, and a dorsal valve, NMV P309562; and the remaining material consists of one conjoined specimen, NMV P309553a and counterpart, NMV P309553b; two ventral valves, NMV P309557, NMV P309554a and counterpart, NMV P309554b; four dorsal valves, NMV P309552, NMV P309555, NMV P309556 and NMV P309558 and two fragmentary specimens, NMV P309560 and NMV P309563.
Diagnosis. Small Neochonetes (Zhongyingia), subquadrate to trapezoidal in outline, with flattened ears, cardinal extremities acute. Ventral valve moderately inflated for genus with a shallow, broad median sulcus and coarse capillation. Dorsal interior with indistinct median septum.

Description. Small for subgenus, subquadrate to trapezoid outline, hingeline close to straight, forming maximum width; 4 pairs of hinge spines; corpus cavity moderately inflated, ears flattened; longitudinal profile steeper at umbo and close to anterior margin, flatter medianly.

Ventral umbo pointed, extending short distance posterior to hinge, slightly elevated; shallow median sulcus extending from umbo; coarsely capillate (2 per mm at anterior margin), capillae low and rounded, equal to interspaces and bearing elongate spinule apertures, sometimes bifurcating. Dorsal valve flat or slightly convex; coarsely capillate (2 per mm); low median fold sometimes developed, containing 3 capillae.

Ventral interior with median septum and vascular trunks; vascular trunks originating anterior to umbo, shorter than median septum; surface radially papillose, including ears, papillae fine, except for coarse papillae ornamenting median septum and vascular trunks.

Dorsal interior with indistinct median septum; cardinal process small, rounded, internally bifid; alveolus small and rounded (Figs 5D, H); hinge sockets shallow, socket ridges short, extending laterally, diverging at about 20° from hingeline. Internal surface ornamented with radial rows of fine rounded papillae, with short rows of finer papillae intercalating close to anterior margin (Figs 5E, H), 5-6 rows on each interspace at anterior margin, internal surface of ears smooth.

Discussion. This new species is closest to Neochonetes (Zhongyingia) zhongyingensis Liao, 1980b, especially in internal features, although the dorsal median septum and ventral vascular trunks are more prominent in Liao’s species. Both species have quite fine papillae.

Table 2. Measurements of Neochonetes (Zhongyingia) linshuiensis in mm: c = conjoined valves; d = dorsal valve; other abbreviations as above.

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![Fig. 5. Neochonetes (Huangichonetes) geniculatus sp. nov.](image-url)
internally, which become much finer anteriorly. Neochonetes (Z.) zhongyingensis also has coarser costellation, and is slightly more semicircular in outline.

The new species appears similar to Neochonetes (Huangichonetes) substrophomenoides (Huang, 1932) in general size, shape and external ornament. However, there are several significant differences, as N. (H.) substrophomenoides has a more strongly inflated ventral valve compared to the moderate inflation of N. (Z.) linshuiensis, and the median sulcus of the former is deep and broad, while the new species has a shallower sulcus. Internal features are similar, reflecting the generic level relationship, although N. (H.) substrophomenoides has coarser papillae on the internal surface.

Tethyochonetes Chen et al., 2000 is another genus common to the Lopingian of South China, and the new species can be easily distinguished from members of this genus. Tethyochonetes has different internal features, as it possess much stronger median and lateral septa in the dorsal valve, while vascular trunks are absent from the ventral interior.

Occurrence. Specimens were collected from Beds 126, 134, 150, 152, 161, 172, and 174 from the Changxing Formation, Chuanmu section, Sichuan.

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