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Survival brachiopod faunas of the end-Permian mass extinction from the southern Alps (Italy) and South China

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Abstract – Eight brachiopod species in seven genera are described from the Permian–Triassic boundary beds of South China and northern Italy. The brachiopods from northern Italy are described for the first time and include two new species: *Orbicoelia dolomitensis* Chen and *Spirigerella*? *teseroi* Chen. The Permian affinity of these brachiopods and their stratigraphical position above the extinction horizon demonstrate that they are survivors from the end-Permian mass extinction. The surviving brachiopods from South China, which was located at the eastern margin of the Palaeo-Tethys Ocean, are considerably abundant and diverse and are dominated by geographically widespread generalist elements adapted to a wide variety of environments. They were mostly limited to the Upper Permian to lowest Griesbachian. In contrast, the survivors in northern Italy, which was situated at the western margin of the Palaeo-Tethys, comprise elements ranging from the Carboniferous to Permian or widespread Tethyan genera. These survivors did not occur in the pre-extinction western Tethyan oceans but migrated into this region after the end-Permian extinction event. Disaster taxon *Lingula* proliferated slightly earlier in western Tethyan oceans than in eastern Tethyan regions following the event. Survival brachiopods from both regions appear to have a generic affinity, although they do not share any species. Both South Chinese and Italian survival faunas support the view that the survival interval is the duration when survivors are dominated by geographically widespread generalist organisms adapted to a wide variety of ecological conditions.

Keywords: Permian–Triassic, mass extinction, surviving brachiopods, northern Italy, South China.

1. Introduction

The severest biotic crisis in the geological record, the end-Permian mass extinction, killed over 90 % of marine species (Erwin, 1993). Brachiopods were severely affected and are considered to be the second largest group of victims with more than 90 % families and up to 95 % of genera lost (Carlson, 1991; Erwin, 1993). As a result, the post-extinction brachiopods of the event experienced dramatic reduction in diversity and the Early Triassic was a bad time for brachiopod faunas (Ager, 1965). However, relict faunas of Permian affinity are locally preserved in the Permian–Triassic boundary beds and lowest Triassic (Chen, Kaiho & George, 2005*a*,*b*). These Permian brachiopods dominate the faunal assemblage, which typically includes Permian foraminifers and Triassic-type elements of ammonoids, bivalves and gastropods, all of which form the well-known ‘Mixed Faunas’ of the Permian–Triassic boundary (Sheng *et al.* 1984). However, the new Permian–Triassic boundary position (Yin *et al.* 2001) suggests most of these ‘Mixed Faunas’ are of latest Permian age (see Section 2), and the Permian brachiopods occurring in the true Triassic strata are very rare (Chen, Kaiho & George, 2005*b*). Thus, these post-extinction faunas are not ‘mixed faunas’. On the other hand, all of the brachiopod genera persist from the strata below the mass extinction horizon, which is well-defined and marks the abrupt disappearance of the majority of marine benthos at the Meishan section, South China (Jin *et al.* 2000), and thus are collectively treated here as the survivors of the end-Permian mass extinction (see Section 4).

The post-extinction Permian brachiopods survived only briefly after the end-Permian crisis with most species eventually extinct within less than one million years after the end-Permian extinction event. (Chen, Kaiho & George, 2005*a*). These unusual survivors have been reported numerous times worldwide in fossil lists (e.g. Liao, 1980*a*, 1984; Sheng *et al.* 1984; Neri & Pasini, 1985; Broglio Loriga, Neri & Posenato, 1988; Posenato, 1988, 2001) but have been rarely systematically studied, largely due to inadequate materials and/or poor preservation. These surviving brachiopods, therefore, remain poorly understood and many require thorough taxonomic revision. Here,

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we document new materials from strata directly overlying the end-Permian mass extinction horizon from South China and the southern Alps (Italy). The Italian brachiopods are described for the first time, although geological surveying in northern Italy has been conducted for many years (e.g. Stache, 1878; Merla, 1930; Broglio Loriga, Neri & Posenato, 1986, 1988; Posenato, 2001). Some taxa previously reported from both regions are also emended on the basis of topotype materials. In addition, South China and northern Italy were biogeographically and ecologically different regions at the end of the Permian due to their remote locations at the eastern and western margins of the Palaeo-Tethys (Ziegler, Gibbs & Hulver, 1998). The faunal correlation of both regions provides valuable insights into the environmental affects of surviving brachiopods at the eastern and western margins of the Palaeo-Tethys Ocean during the end-Permian mass extinction.

2. Permian–Triassic sections in South China

The specimens described here were collected from the Permian–Triassic boundary beds of the Meishan, Huangzhishan and Taping sections in South China and the Tesero section of the Dolomite region, northern Italy (Fig. 1). The Meishan Section is located at the town of Meishan in the northwestern Zhejiang Province, South China (Section 1 in Fig. 1; Fig. 2a) and is the Global Stratotype Section Point for the Permian–Triassic Boundary (Yin *et al.* 2001). The Permian–Triassic succession features dark grey, medium-bedded limestone (Bed 24) overlain by white claystone (Bed 25), black shale (Bed 26), marlstone (Bed 27) and white claystone (Bed 28). This upper white claystone is typically thicker than Bed 25 and is also widely recognized in Permian–Triassic sections in South China. These beds are overlain by alternations of greenish calcareous mudstones and marlstones

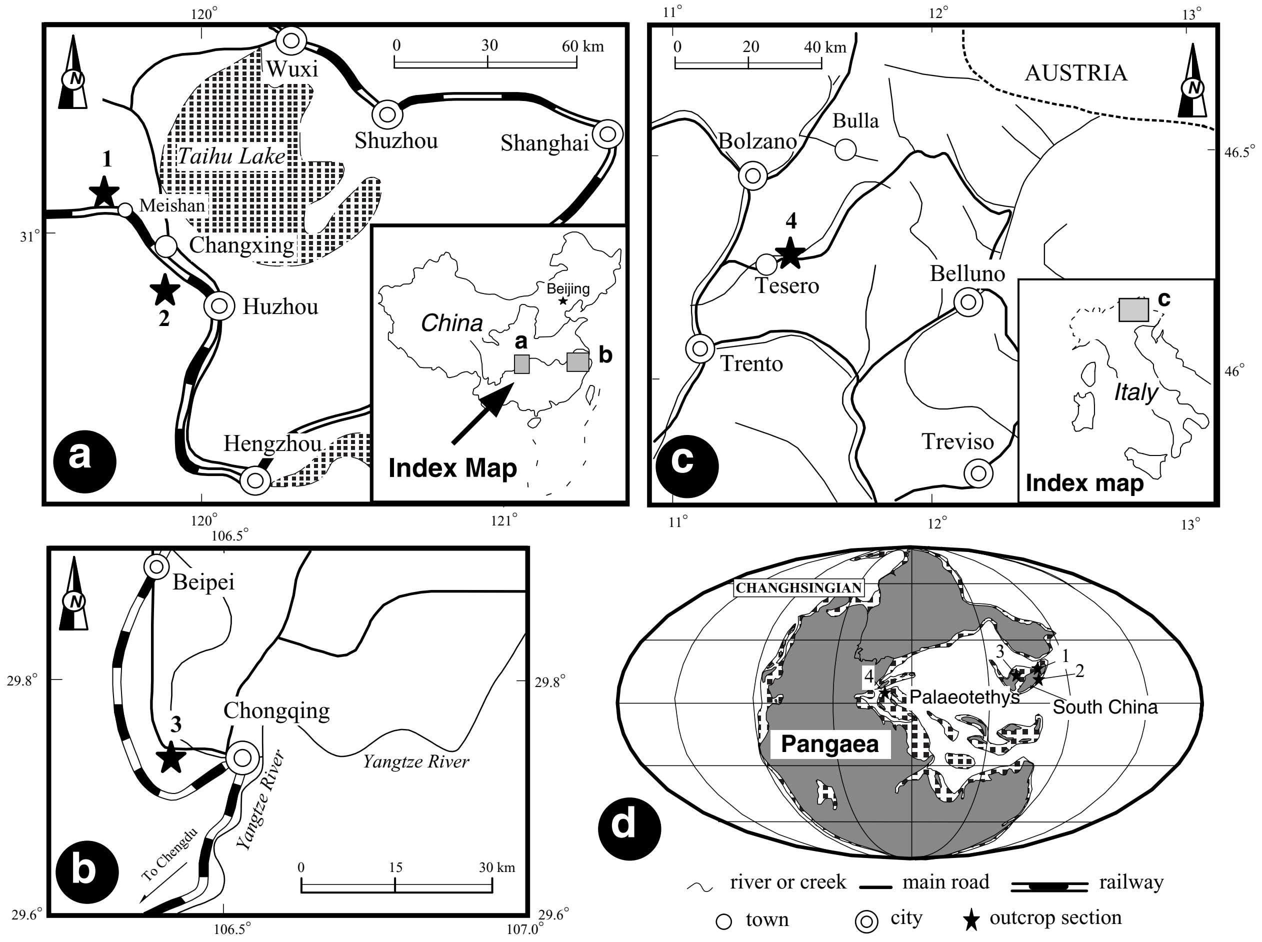


Figure 1. Geographical localities of the surviving brachiopod faunas from the end-Permian mass extinction in South China and northern Italy. (a) Locations of the Meishan and Huangzhishan sections. (b) Location of the Taiping section. (c) Location of the Tesero section. (d) Palaeogeographical positions of the studying sections (base map after Ziegler, Gibbs & Hulver, 1998). The studied outcrop sections include: 1 – Meishan section of Changxing, Zhejiang Province, South China; 2 – Huangzhishan section of Huzhou, Zhejiang Province, South China; 3 – Taiping section of Zhongliangshan, Chongqing City, South China; 4 – Tesero section of The Dolomites, northern Italy.

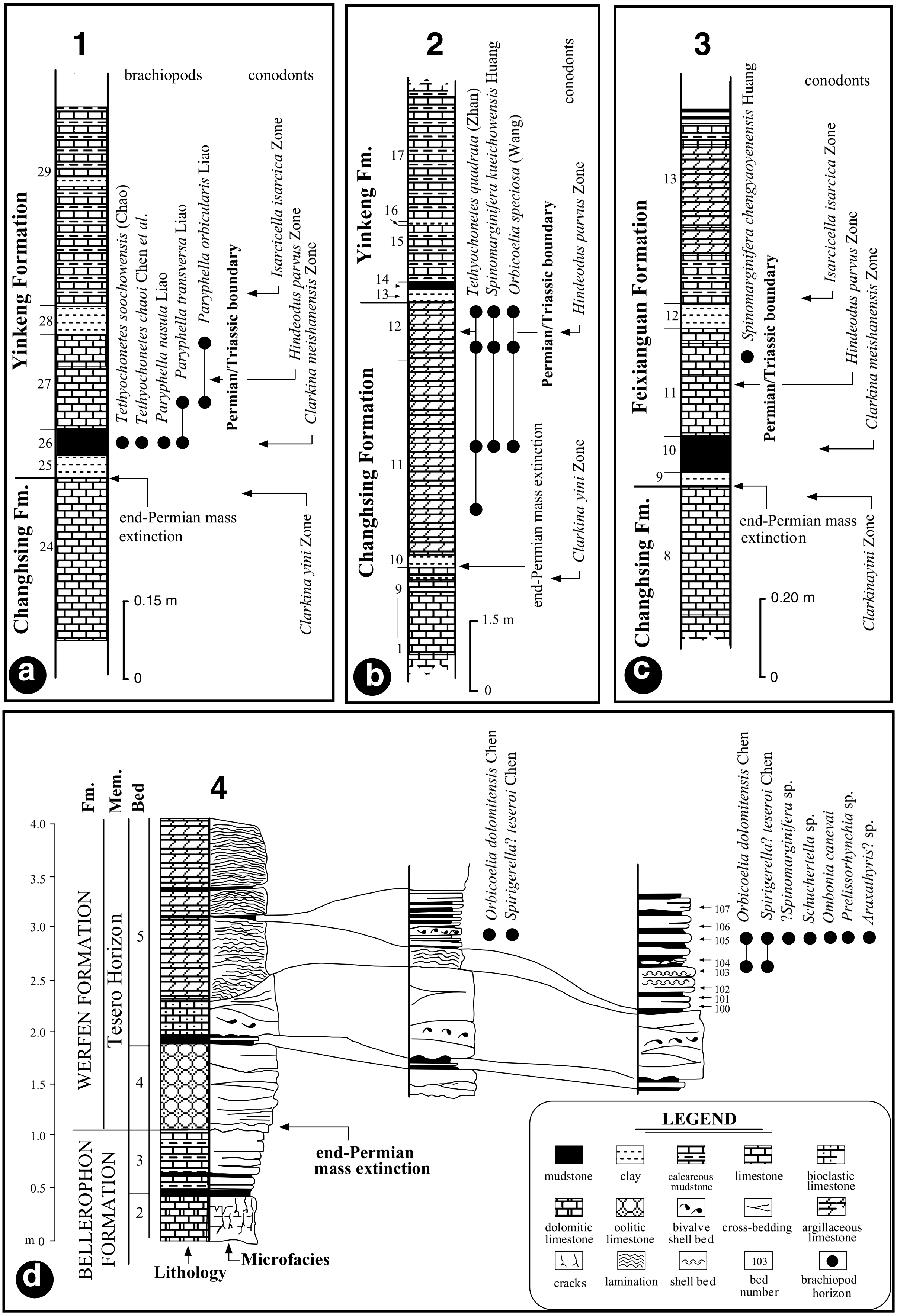


Figure 2. Stratigraphical distribution of the described brachiopods in the Permian–Triassic boundary beds of South China and northern Italy. (a) Meishan section. (b) Huangzhishan section. (c) Taiping section. (d) Tesero section (after Neri *et al.* 1999).

(Beds 29, 30). Five species of brachiopods, namely *Tethyochonetes chaoi*, *T. soochowensis*, *Paryphella orbicularis*, *P. nasuta* and *P. transversa*, are described from Beds 26 and 27 (Fig. 2a).

A dark grey limestone (Bed 24) forms the top of the Changhsing Formation and contains the latest Changhsingian conodont *Clarkina changxingensis yini* Zone and fusulinid *Palaeofusulina sinese* Zone (Yin *et al.* 2001). Bed 25 defines the base of the Yinkeng Formation (Fig. 2a) and forms a conspicuous, widely recognized marker bed of the Permian–Triassic boundary across South China. Beds 25 and 26 belong to the conodont *Clarkina meishanensis* Zone (Mei, Zhang & Wardlaw, 1998). Other important conodont elements include *Hindeodus latidentatus* and *H. typicalis*. In addition, Bed 26 also contains abundant bivalves (*Pteria ussurica variabilis*, *Palaeonucula* sp., *Eumorphotis*? sp., *Peribositra baoqingensis* and *Claraia* cf. *bioni*) and ammonoids (*Otoceras* sp., *Tompophiceras* sp. and *Hypophiceras* cf. *martini*) (Sheng *et al.* 1984). The middle part (Bed 27c) of Bed 27 is characterized by the first appearance of the earliest Triassic conodont *Hindeodus parvus*. Palaeontological and geochemical evidence has been used to place the end-Permian mass extinction boundary at the base of Bed 25 (Jin *et al.* 2000) or about 10 mm below the top of Bed 24 (Kaiho *et al.* 2001). Therefore, the brachiopods from the strata above Bed 24 are the post-extinction faunas.

The Huangzhishan section is located about 17 km west of Huzhou City of the Zhejiang Province (Section 2 in Fig. 1a,d; Fig. 2b) and is about 30 km from the Meishan section. The Permian–Triassic boundary beds of both sections are comparable to one another, and the Huangzhishan section is also subdivided into the Changhsing Formation and overlying Yinkeng Formation (Fig. 2b). Here, the limestone of the Changhsingian Formation represents a shallow-water platform facies (Wu, Wei & Zhang, 1986) and forms a much thicker section (about 121 m thick) than at Meishan (36 m thick; see also Sheng *et al.* 1984).

The Changhsing Formation contains abundant fossils including conodonts (*Hindeodus typicalis*, *Clarkina changxingensis*, *C. carinata* and *C. dicerocarinata*), foraminiferids (*Colaniella* sp.), fusulinids (*Palaeofusulina sinese*), brachiopods (*Araxathyris araxaensis*, *Terebratuloidea davidsoni* and *Pseudolabaia tumita*) and algae (*Mizzia* sp., *Permocalculus* sp. and *Gymnocodium* sp.) (Zhang, 1995; Chen & Shi, 1999; Chen, Shi & Kaiho, 2004). The upper portion of the Changhsing Formation is represented by massive bioclastic limestone (Bed 9), which contains conodont *Clarkina changxingensis*. This conodont species was later re-assigned to *Clarkina changxingensis yini* by Mei, Zhang & Wardlaw (1998), and nominated as the zonal element of the *Clarkina yini* Zone by these authors. The *C. yini* Zone occurs at the topmost Changhsing Formation, just below the end-Permian mass extinction horizon at the Meishan section (Yin *et al.* 2001). Accordingly, both conodont and fusulinid zones indicate that Bed 9 correlates well with Bed 24 of Meishan. Bed 10 is 6–8 cm thick white claystone, which is stratigraphically equivalent to Bed 25 of Meishan. Both clay beds immediately overlie the conodont *C. yini* Zone at both the Meishan and Huangzhishan sections. Bed 10 is overlain by calcareous mudstone and argillaceous limestone (Bed 11). Bed 11 contains abundant Permian brachiopods (Chen & Shi, 1999; Chen, Shi & Kaiho, 2004) and bivalves *Pteria ussurica variabilis*, *Towapteria* sp., *Claraia* cf. *bioni*, *C. huzhouica* and *Palaeolima* sp. (Chen, 2004). Of these, *Pteria ussurica variabilis*, *Towapteria* sp., *Claraia* cf. *bioni* and *Palaeolima* sp. are also present in Bed 26 at Meishan, suggesting that faunas from both beds are contemporaneous.

Bed 12 comprises brown-green argillaceous limestone to calcareous mudstone, from which abundant Permian brachiopods have been listed (Chen, Shi & Kaiho, 2004). Of these, *Tethyochonetes quadrata*, *Spinomarginifera kueichowensis* and *Orbicoelia speciosa* are described here. Associated bivalves include *Pteria ussurica variabilis*, *Pteria* sp., *Oxytoma scythicum*, *Ornithopecten* sp., *Entolium discites microtis*, *Bakevellia costata*, *Leptochondria virgalensis*, *L.* sp., *Promyalina* sp. and *Chlamys* (*Praechlamys*) *wuxingensis* (Chen, Shi & Kaiho, 2004). In addition, Chen (2004) reported *Eumorphotis venetiana*, *Towapteria scythica*, *Claraia griesbachi* and *Hollinella tingi* from the same horizon of the same section. The majority of these bivalves are characteristic of the earliest Triassic faunas across South China (Yin, 1985; Li, 1995). More recently, the conodont *H. parvus* has been found in the upper portion of Bed 12 (Y. P. Qi, pers. comm. 2005), suggesting that Bed 12 is equivalent to Bed 27 of Meishan (Fig. 2); both beds contain Permian brachiopods and earliest Triassic conodonts. This correlation also confirms that bivalve faunas from Bed 12 are latest Changhsingian to earliest Griesbachian in age.

The lithological characteristics and biozones of the overlying Yinkeng Formation compare very well with coeval strata at Meishan. The common occurrence of bivalves *Claraia griesbachi*, *C. wangi*, *C.* cf. *dieneri*, *Posidonia* sp. and ammonoids *Ophiceras* spp. is a feature of both successions. In addition, abundant *Lingula* are present in these strata in Huangzhishan (Chen, Shi & Kaiho, 2004).

The Permian–Triassic section at Taiping is situated about 15 km west of Chongqing City, South China (Section 3, Fig. 1b,d), and is assigned to the Changhsing and Feixianguan formations (Fig. 2c). The uppermost Changhsing Formation is composed of thick-bedded light grey limestone (Bed 8). It contains brachiopods (*Leptodus* sp., *Oldhammina* sp.), sponges and algae typical of the late Changhsingian faunas of South China (Yang *et al.* 1987). Bed 8 is overlain by white claystone (Bed 9) and brown mudstone (Bed 10) of the basal Feixianguan Formation, equivalent to the Beds 25 and 26 of the Yinkeng Formation at Meishan, respectively (Fig. 2c), indicating that the end-Permian extinction boundary potentially coincides with the base of Bed 9 at Taiping. The mudstone is overlain by a 21 cm thick marlstone (Bed 11), from which *Spinomarginifera chengyaoyenensis* is found in association with *H. parvus* of Griesbachian age (Yin *et al.* 2001). This indicates that *S. chengyaoyenensis* is earliest Griesbachian. Beds 12–15 are composed of alternations of greenish mudstone and marl, which are lithologically similar to the lower Yinkeng Formation at Meishan.

3. Permian–Triassic section in northern Italy

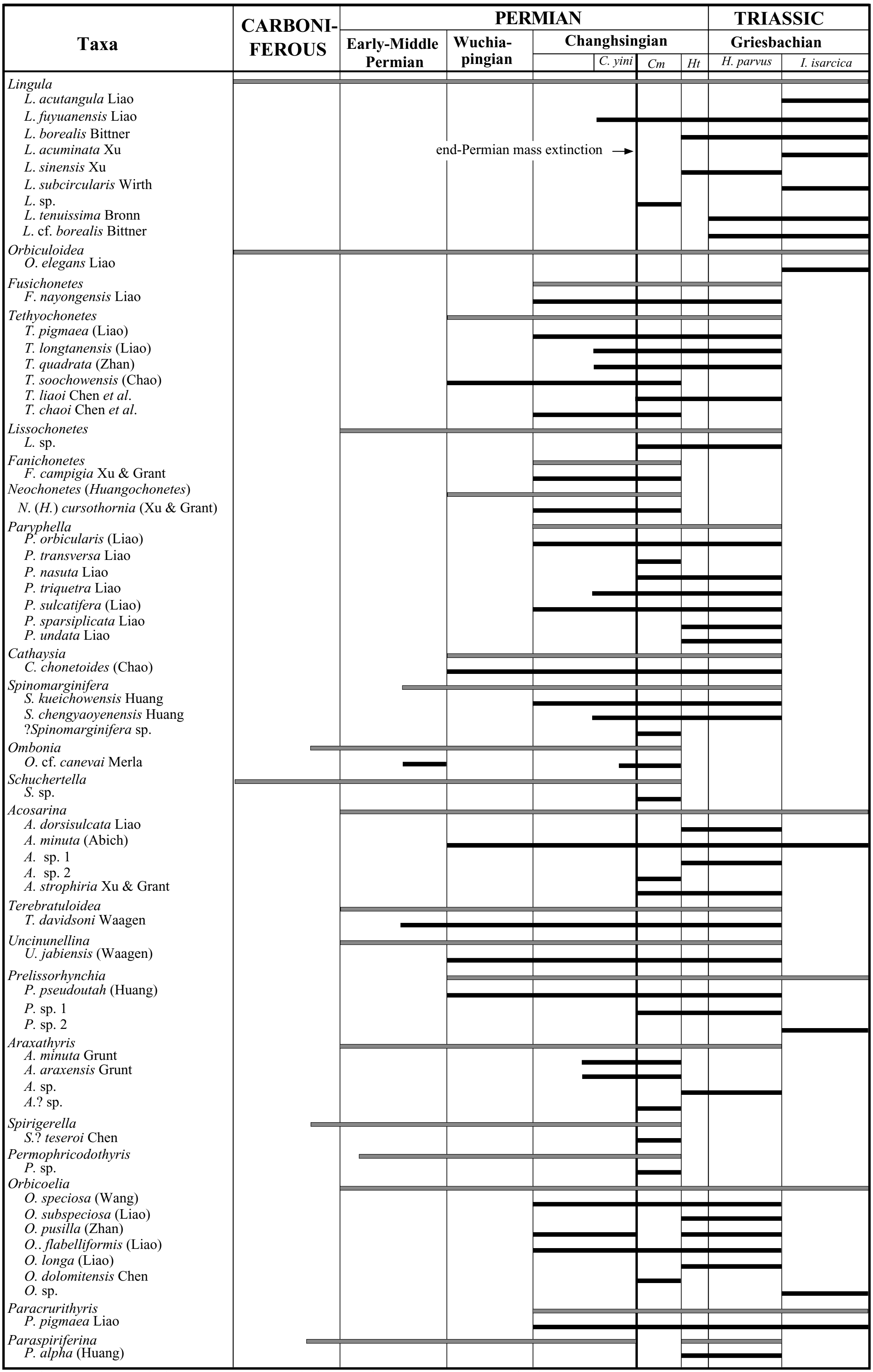
The Tesero section of the Dolomite area, northern Italy (Section 4 in Fig. 1c, d; Fig. 2d) has long been studied in terms of biostratigraphy, sedimentology and biotic events (e.g. Stache, 1878; Merla, 1930; Broglio Loriga, 1968; Assereto *et al.* 1973; Broglio Loriga, Neri & Posenato, 1980, 1986, 1988; Wignall & Hallam, 1992; Wignall, Kozur & Hallam, 1996; Hallam & Wignall, 1997; Twitchett, 1999). The Permian–Triassic boundary beds are assigned to the Bellerophon Formation and overlying Werfen Formation, which is further subdivided into the Tesero Horizon below and the Mazzin Member above (Fig. 2d). The Bellerophon Formation has been constrained as late Changhsingian in age by Broglio Loriga, Neri & Posenato (1988). This age determination is reinforced by recent discoveries of the ammonoid *Paratirolites* Zone (Posenato & Prinoth, 1999) and brachiopod *Comelicania* fauna (Posenato, 1998) from the lower and upper parts of the formation, respectively.

The overlying Tesero Horizon (lower Werfen Formation) is a 7 m thick succession composed of oolitic grainstone in the lower part and interbedded oolitic–bioclastic grainstone, wackestone and micrite in the upper part (Fig. 2d). The conodont *Hindeodus praeparvus* first appears about 35 cm above the base of the Tesero Horizon, whereas the first occurrence of *Hindeodus parvus*, the earliest Triassic marker (Yin *et al.* 2001), coincides with the lower part of the Mazzin Member, about 11 m above the base of the Werfen Formation (Nicora & Perri, 1999). It is noteworthy that *H. parvus* has its first occurrence at 1.3 m above the base of the Tesero Horizon at the Bulla section, about 20 km north of Tesero (Farabegoli & Perri, 1998). This horizon correlates with the upper part of Unit 5 in Tesero (Fig. 2d). As such, the precise position of the Permian–Triassic boundary has long remained obscure at the Tesero section.

The brachiopods described here were sampled from strata between the conodonts *Hindeodus praeparvus* and *Hindeodus parvus* zones. They include *Orbicoelia dolomitensis* n. sp., *Araxathyris*? sp. and *Spirigerella*? *teseroi* n. sp. In addition, Posenato (1999) listed *Shuchertella* sp., *Ombonia canevai*, ?*Spinomarginifera* sp., *Orbicoelia dolomitensis* (= *Crurithyris extima* Grant *in* Posenato, 1999), ?*Araxathyris* sp. and *Prelissorhynchia* sp. (= *Neowellerella* sp. *in* Posenato, 1999). These elements have been collectively named the ‘*Crurithyris*’ fauna (*sensu* Neri & Pasini, 1985; Broglio Loriga, Neri & Posenato, 1986, 1988; Posenato, 1988, 2001). Associated bivalves (*Towapteria scythica* and *Eumorphotis* sp.) and gastropods (*Bellerophon vaceki*) are also extremely abundant (Broglio Loriga, Neri & Posenato, 1988; Wignall, Kozur & Hallam, 1996). As well as these macrofaunas, the conodont *Hindeodus latidentatus* (Wignall, Kozur & Hallam, 1996; Farabegoli & Perri, 1998) has been reported from the Tesero Horizon. At Tesero, the end-Permian mass extinction horizon has been generally placed at the lower part of the Tesero Horizon (Fig. 2d; e.g. Magaritz *et al.* 1988; Wignall & Hallam, 1992; Hallam & Wignall, 1997; Twitchett, 1999). The placement of the end-Permian extinction horizon at the lower Tesero Horizon is also reinforced in the neighbouring Siusi section (Newton *et al.* 2004). In addition, *H. latidentatus* is characteristic of the strata above the end-Permian extinction horizon in many other Permian–Triassic boundary sections, such as the Meishan section (Yin & Tong, 1998). Thus, both extinction horizon and biostratigraphical correlations indicate that the brachiopods from the Tesero Horizon are post-extinction faunas although they may also be of latest Changhsingian age (e.g. Twitchett & Wignall, 1996; Kozur, 1998). Apart from the post-extinction brachiopods from the Tesero Horizon, *Lingula* is very abundant in the Mazzin Member of the earliest Triassic at almost all Permian–Triassic sections in the northern Italy (Broglio Loriga, Neri & Posenato, 1988). This inarticulate brachiopod has been regarded as the disaster taxon due to its global proliferation at the aftermath of the end-Permian mass extinction (e.g. Rodland & Bottjer, 2001).

4. Correlation of post-extinction brachiopods from South China and northern Italy

As stated in Sections 2 and 3, the so-called ‘Mixed Faunas’ of the Permian–Triassic boundary beds (Sheng *et al.* 1984; Chen, Shi & Kaiho, 2002) are actually post-extinction faunas, as indicated by their occurrence above the end-Permian mass extinction horizon. They are constrained by conodonts *Clarkina meishanensis*, *Hindeodus typicalis*, *H. parvus* and *Isarcicella isarcica* zones in ascending order (Yin *et al.* 2001). Stratigraphical distributions of the post-extinction brachiopods from both South China and northern Italy indicate that all genera persist from pre-extinction Permian strata (Fig. 3). This means that the post-extinction brachiopods can be collectively treated, at genus level, as the survivors of the end-Permian mass extinction,



Conodont zones: *Cy* = *Clarkina yini* Zone; *Cm* = *Clarkina meishanensis* Zone; *Ht* = *Hindeodus typicalis* Zone; *Hi* = *Hindeodus parvus* Zone; *Ii* = *Isarcicella isarcica* Zone

Figure 3. Global stratigraphical ranges of the post-extinction brachiopods from the Permian–Triassic boundary beds of South China and North Italy (for detailed spatio-temporal distributions of surviving brachiopods see Chen, Kaiho & George, 2005*a*, appendix).

although post-extinction faunas consist of survival species that extend from the pre-extinction Permian strata, newly originated species and uncertain species, respectively (Fig. 3).

Palaeogeographically, South China and northern Italy were situated at the eastern and western margins of the Palaeo-Tethys Ocean, respectively (Fig. 1d). In South China, Permian survival brachiopods are quite abundant and have been widely reported (Chen, Kaiho & George, 2005*a*, appendix). For the most part, they have been only listed and thus require taxonomic revision and updating of the stratigraphical data. The weakness of the taxonomic studies resulted in different statistical figures for the survival brachiopods conducted by various authors. In addition, the surviving faunas have been considered to comprise Permian relicts that persisted into the lowermost Triassic strata (Liao, 1979, 1980*a*; Xu & Grant, 1994). However, the end-Permian extinction horizon is positioned at least two conodont zones below the biostratigraphically defined Permian–Triassic boundary (Yin & Tong, 1998). Most of the survivors are, therefore, latest Permian in age. For these reasons, we have reassessed the surviving brachiopods and their stratigraphical distributions in South China (Fig. 3). In contrast to previously published statistics (e.g. Liao, 1979, 1980*a*; Xu & Grant, 1994; Rong & Shen, 2002), our data show that 50 species (including nine uncertain species) in 19 genera of 12 families have been reported from 32 localities. Of these, 33 species in 16 genera of 10 families are present in the *C. meishanensis* Zone, 34 species in 15 genera of 10 families in the *H. typlicalis* and *H. parvus* zones, and 10 species in six genera of six families in the *I. isarcica* Zone (Table 1). Although the recent additional data (e.g. Shen, He & Shi, 1995; Chen & Shi, 1999; Chen *et al.* 2000; Shen & Archbold, 2002; Chen, Shi & Kaiho, 2004; Chen, Kaiho & George, 2005*a*,*b*; this study) considerably modify the statistical figures for the survival brachiopods, the various datum sources and assignment to uncertain species listed in the literature by different authors may be largely responsible for the highly varied diversity figures for the survivors. We assessed brachiopod data from at least 32 Permian–Triassic boundary sections described above and published by previous authors (e.g. Zhao *et al.* 1981; Sheng *et al.* 1984; Yang *et al.* 1987; Zhan, 1989; He & Shen, 1991; Xu & Grant, 1994; Shen, He & Shi, 1995; Chen *et al.* 2000). The uncertain species are followed here, each indicating an independent species, although the inadequate materials or poor preservation prevent the precise taxonomic assignment.

The post-extinction brachiopods within the *C. meishanensis* Zone (Mei, Zhang & Wardlaw, 1998) are dominated by *Tethyochonetes*, *Paryphella*, *Orbicoelia* and *Prelissorhynchia* (Fig. 3). Twenty-four species (72.7 %) persist from the pre-extinction Permian strata and thus are the survivors of the event; nine species (27.3 %) originated newly after the extinction event or uncertain species (Fig. 3). Other associated faunas include conodont (*H. latidentatus*) and bivalves (*Pteria ussurica variabilis*, *Towapteria scythica* and *Claraia* cf. *bioni*). Brachiopods within the *Hindeodus typicalis* and *H. parvus* zones are dominated by *Paryphella* and *Spinomarginifera* (Fig. 3) and include 18 survival species (52.9 %); 16 species (47.1 %) originated after the event or are uncertain species. Brachiopods from the *I. isarcica* Zone are assigned to the *Lingula fuyuanensis–Paracrurithyris pigmaea* (*L–P*) Assemblage (Sheng *et al.* 1984) or the *Crurithyris–Lingula* (*C–L*) Assemblage of Xu & Grant (1994) (note we consider that *Crurithyris* of Xu & Grant is synonymous with *Paracrurithyris*; see taxonomic discussion in Section 5). Other than three species (*Lingula fuyuanensis*, *Ascoarina minuta* and *Paracrurithyris pigmaea*) that extend from the pre-extinction Permian strata, all brachiopods are newly originated after the event or are uncertain species (Fig. 3). Other important biozones associated with this conodont include the Early Triassic ammonoid *Ophiceras* Zone and bivalve *Claraia griesbachi* Zone.

In northern Italy, the post-extinction brachiopods which appeared immediately after the end-Permian extinction event (equivalent to the *C. meishanensis* Zone) have been only reported from the Tesero sections, although more than ten Permian–Triassic boundary sections in this region have been investigated (Neri & Pasini, 1985; Broglio Loriga, Neri & Posenato, 1986,

Table 1. Numbers of species, genera and families of the south Chinese survival brachiopods and comparison with the data previously published from South China

	This study				Liao, 1979, 1980*a*			Sheng *et al.* 1984		Xu & Grant, 1994		Rong & Shen, 2002	
Surviving brachiopods	Localities	No. of species	No. of genera	No. of families	No. of species	No. of genera	No. of families	No. of species	No. of genera	No. of species	No. of genera	No. of genera	No. of families
TSB	32	50	19	12	17	9	7	28	9	20	12	12	6
Cm Zone	15	33	16	10									
Ht and *Hp* Z.	23	34	15	10									
Ii Zone	19	10	6	6									

TSB – Total surviving brachiopods; *Cm* – *Clarkina meishanensis* Zone; *Ht* – *Hindeodus typicalis* Zone; *Hp* – *Hindeodus parvus* Zone; *Ii* – *Isarcicella isarcica* Zone.

1988; Posenato, 1988, 2001). As stated in Section 3, the Tesero brachiopod fauna co-occurs with the conodont *H. latidentatus*, which is also an important component of the *C. meishanensis* Zone in South China (Yin *et al*. 2001). This fact and the stratigraphical position above the end-Permian extinction horizon suggest that the *Orbicoelia* fauna of Tesero is comparable with survival faunas of the *C. meishanensis* Zone of South China. This correlation is reinforced by the common appearance of bivalves (*Towapteria scythica* and *Eumorphotis* sp.) and gastropods (*Bellerophon vaceki*) in both South China and northern Italy. Of the *Orbicoelia* fauna, other than *Ombonia* cf. *canevai* persisting from the pre-extinction Permian strata, all species are newly originated after the end-Permian event or are uncertain species. However, as stated above, all genera are survivors of the event and all species are morphologically similar to the pre-extinction allies (see taxonomic discussion in Section 5). Accordingly, they are also survivors of the end-Permian event.

In sharp contrast to the limited occurrence of the *Orbicoelia* fauna, the *Lingula* fauna, comprising *L. tenuissima* Bronn, *L.* cf. *borealis* and *L.* sp., is widely distributed in almost all Lower Triassic sections in northern Italy (Broglio Loriga, 1968; Broglio Loriga, Neri & Posenato, 1980, 1988). This fauna occurs in the Mazzin Member and is usually associated with conodont *H. parvus*, although it may extend to the *I. isarcica* Zone in some sections. Thus, the *Lingula* fauna of Italy is slightly older than the South Chinese *L–P* fauna and its counterparts, which are usually associated with *I. isarcica* Zone in South China (Xu & Grant, 1994). The *Lingula* fauna is very different from the survivors within the *H. parvus* Zone in South China in terms of faunal compositions, although both faunas are contemporaneous.

In brief, the Italian surviving faunas (eight monospecific genera) are generally less diverse than the South Chinese survivors (Fig. 4a), although sampling bias may affect the diversity figure of the Italian faunas to some extent. Taxonomically, the South Chinese faunas are dominated by such genera as *Lingula*, *Tethyochonetes*, *Paryphella*, *Spinomarginifera*, *Acosarina*, *Orbicoelia*, *Paracrurithyris* and *Prelissorhynchia*. Of these, the productids predominate (approximately 40 %; see also Fig. 4b), with subordinate inarticulate forms (16 %) and spiriferids (16 %). In comparison, there are no dominant groups (> 35 %) in the Italian faunas, with the athyridids representing the largest group (about 28.5 %). Moreover, the Italian faunas are characterized by abundant *Orbicoelia* and *Lingula*, both of which are abundant in South China.

The faunas from the two regions do not share any species, although *Lingula*, *Spinomarginifera*, *Orbicoelia*, *Prelissorhynchia* and *Araxathyris* are common in both regions, suggesting a generic affinity between the two faunas. In addition, all of the post-extinction brachiopod genera from South China persisted from the Changhsingian and are dominated by palaeogeographically widespread generalist elements such as *Tethyochonetes*, *Paryphella*, *Spinomarginifera*, *Orbicoelia*, *Paracrurithyris*, *Prelissorhnychia* and *Araxathyris*, which dispersed over the South China block (Liao, 1979, 1984; Sheng *et al*. 1984; Yang *et al*. 1987; Xu & Grant, 1994), and some of which spread to the Salt Range (Grant, 1970) and northern Italy (e.g. Posenato, 1988, 1998, 2001). Alternatively, the Italian faunas are dominated by the elements (e.g. *Lingula*, *Shuchertella* and *Ombonia*) that range from the Carboniferous to Permian and/or widespread Tethyan genera (e.g. *Spinomarginifera*, *Orbicoelia* and *Araxathyris*). Their absence in the underlying Permian sequences, which are characterized by the *Comelicania* and *Janiceps* faunas (Posenato, 1998, 2001), supports the interpretation that these elements migrated into this region after the end-Permian extinction event. The

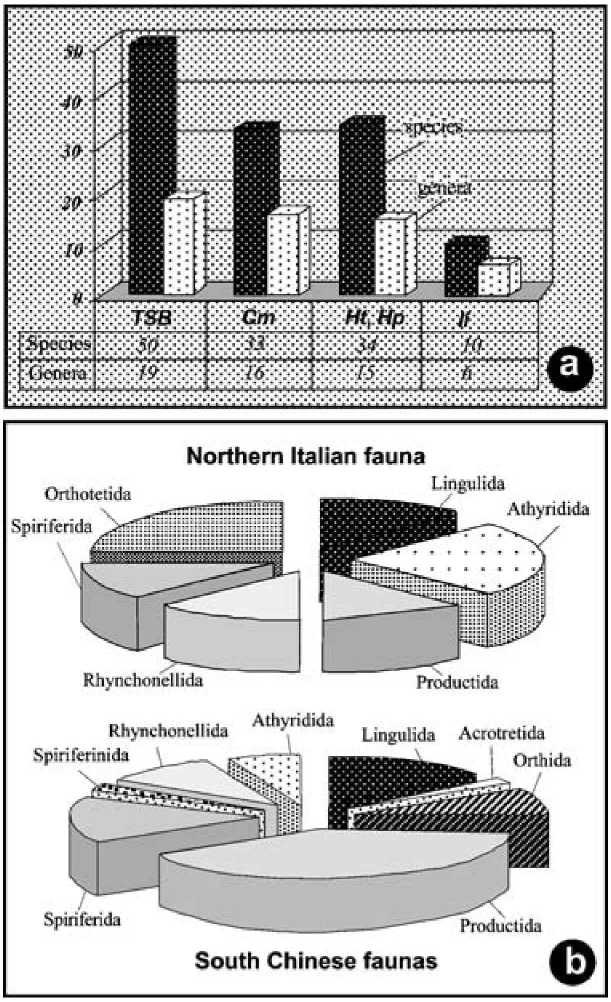


Figure 4. (a) Numbers of species and genera of the post-extinction brachiopods in the Permian–Triassic boundary beds of South China. TSB – Total survival brachiopods; *CM* – *Clarkina meishanensis* Zone; *Ht* – *Hindeodus typicalis* Zone; *Hp* – *Hindeodus parvus* Zone; *Ii* – *Isarcicella isarcica* Zone. (b) Comparison of taxonomic compositions of post-extinction brachiopod faunas from South China and northern Italy.

post-extinction brachiopods survived in diverse benthonic niches along the eastern margins of the Palaeo-Tethys (South China, for example). Along the western margins of the Palaeo-Tethys, only widespread, widely adapted elements survived the event. Both survival faunas from South China and northern Italy support the view that the survival interval is the duration when survivors are dominated by geographically widespread generalist organisms adapted to a wide variety of ecological conditions (Erwin, 2001).

5. Systematic palaeontology (Z. Q. Chen)

Repositories. All illustrated specimens are housed in the museum of School of Earth and Geographical Sciences, The University of Western Australia (UWA).

Class STROPHOMENATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order PRODUCTIDA Sarycheva & Sokolskaya, 1959
Suborder CHONETIDINA Muir-Wood, 1955
Superfamily CHONETOIDEA Bronn, 1862
Family RUGOSOCHONETIDAE Muir-Wood, 1962
Subfamily CHONETINELLINAE Muir-Wood, 1962
Genus *Tethyochonetes* Chen, Shi, Shen & Archbold, 2000

Type species. *Waagenites soochowensis quadrata* Zhan, 1979.

Tethyochonetes soochowensis (Chao, 1928)
Figure 5a–c, i

1928 *Chonetes soochowensis* Chao, p. 31, pl. 1, figs 14–16.
1932 *Chonetes soochowensis* Chao; Huang, p. 5, pl. 1, figs 8, 9.
1962 *Chonetes soochowensis* Chao; Chi-Thuan, p. 489, pl. 2, fig. 8a, b.
1964 *Chonetes soochowensis* Chao; Wang, Jin & Fang, pp. 241–2, pl. 37, figs 20, 21.
1977 *Waagenites soochowensis* (Chao); Yang *et al.*, p. 332, pl. 135, fig. 22.
1978 *Waagenites soochowensis* (Chao); Feng & Jiang, p. 243, pl. 88, fig. 4.
1979 *Waagenites soochowensis* (Chao); Zhan, p. 72, pl. 11, fig. 7.
1980*a* *Waagenites soochowensis* (Chao); Liao, pl. 1, fig. 2; pl. 2, fig. 7.
1980*b* *Waagenites soochowensis* (Chao); Liao, pl. 5, fig. 4.
1982 *Waagenites soochowensis* (Chao); Wang *et al.*, p. 198, pl. 91, figs 3, 4; pl. 95, figs 7, 8.
1984 *Waagenites soochowensis* (Chao); Liao, pl. 1, fig. 10.
1987 *Waagenites soochowensis* (Chao); Xu, pl. 8, figs 15, 16.
1990 *Waagenites soochowensis* (Chao); Zhu, pp. 64–5, pl. 18, figs 1, 2.
1995 *Waagenites soochowensis* (Chao); Zeng, He & Zhu, pl. 3, figs 13, 14.
1998 *Waagenites soochowensis* (Chao); Shi & Shen, p. 509, fig. 4: 6.
2000 *Tethyochonetes soochowensis* (Chao); Chen *et al.*, table 1.
2002 *Tethyochonetes soochowensis* (Chao); Shen & Archbold, p. 338, fig. 5O–R.
2002 *Tethyochonetes* cf. *soochowensis* (Chao); Liao & Xu, pl. 1, fig. 45.

Material. One ventral valve (UWA133439), about 6.5 mm long, 12.8 mm wide and 3 mm thick; one ventral internal mould (UWA133440) and one dorsal external mould (UWA133441).

Description. Medium-sized to large *Tethyochonetes*; outline very transverse, usually twice as wide as long; widest at hingeline; cardinal extremities forming angles of about 80–90°; ears rather broad, triangular, flat, demarcated from remainders of shell by a pronounced concavity. Ventral valve strongly convex; beak incurved, slightly extending beyond hingeline; umbo high, narrow, triangular, flanked by steep slopes, medially separated by a distinct median sulcus; median sulcus well developed, commencing anterior to beak, rapidly broadening and deepening anteriorly, separating body disk into two lobes. Dorsal valve moderately concave, median fold narrow, low. External ribs dense, with narrower interspaces, commencing at beaks, about 2–3 in 5 mm at anterior margins, rarely bifurcating; posterior margins marked by 3–4 spines on each side, projecting laterally. Internal features of both valves not observed.

Remarks. Small chonetids are very common in the Changhsingian and the Permian–Triassic boundary beds in South China. By comparing true *Waagenites grandicosta* (Waagen), type species of the genus, Chen *et al.* (2000) transferred these small chonetid species, previously ascribed to *Waagenites*, to their new genus *Tethyochonetes*. Of the five *Tethyochonetes* species re-described or proposed by Chen *et al.* (2000), *T. wongiania* (Chao, 1928) is closely allied to the present species, with both species sharing a transverse outline, but *T. wongiana* differs strikingly from *T. soochowensis* in having much more robust, unbranching costae with relatively broader costal interspaces. The type species *T. quadrata*, described below, is also indistinguishable in general ornamentation from *T. soochowensis*, but it is less transverse and has a relatively shallower ventral median sulcus, unlike *T. soochowensis*.

Occurrence. Yinkeng Formation Bed 26 (latest Changhsingian), Meishan section (Quarry Z) of Zhejiang, South China. Other occurrences include the Luntan Formation (Wuchiapingian), Sichuan,

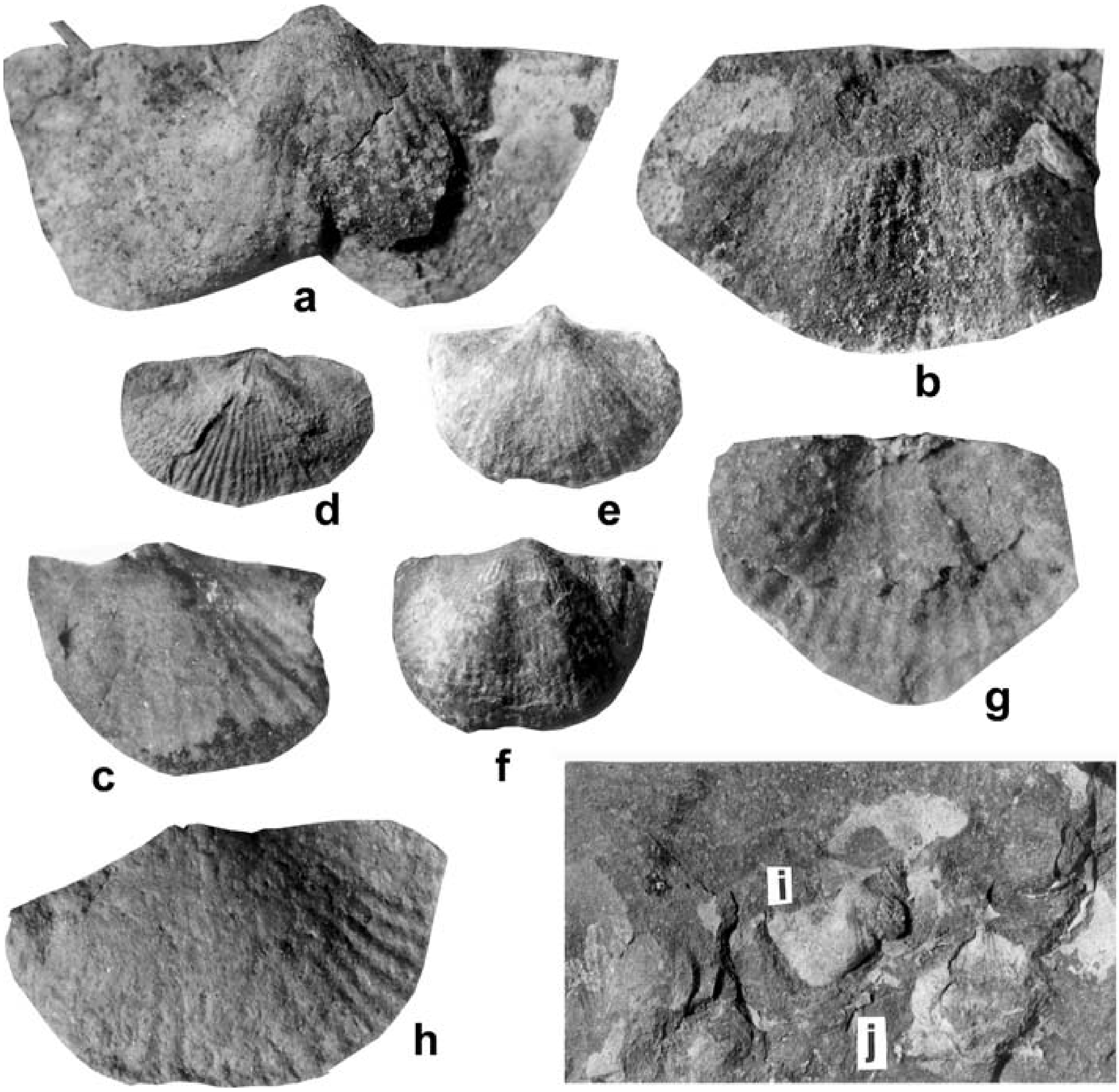


Figure 5. (a–c, i) *Tethyochonetes soochowensis* (Chao, 1928) from Bed 26 of the lower Yinkeng Formation (latest Changhsingian) of the Meishan section (Quarry Z), Zhejiang, South China. (a) UWA133439, ventral view of a ventral valve, × 6. (b) UWA133441, ventral view of a ventral internal mould, × 6. (c) UWA133440, dorsal view of an incomplete dorsal external mould, × 3.8. (i, j) shell bed showing preservation of *Tethyochonetes soochowensis* (i) and *Paryphella nasuta* (j), × 1.5. (d–f) *Tethyochonetes quadrata* (Zhan, 1979) from topmost Changhsing Formation (earliest Griesbachian), Huangzhishan section of Zhejiang, South China. (d) UWA133442, internal view of a dorsal valve showing thick socket ridges, a pair of short anderidia, and the broken median septum, × 3.8. (e, f) UWA133443–444, ventral views of two ventral valves, both × 3.8. (g, h) *Tethyochonetes chaoi* Chen, Shi, Shen & Archbold, 2000 from Bed 26 of the lower Yinkeng Formation (latest Changhsingian) of the Meishan section (Quarry D), Zhejiang, South China, UWA133445-446, ventral views of two broken ventral valves, both × 5.

Guizhou and Hunan, South China; Changhsing Formation (Changhsingian), Guizhou and Hunan, South China; Shuizutang Formation (Changhsingian), Guangdong, South China; Talung and Yanshi formations (Changhsingian), Fujian and Hunan, South China.

Tethyochonetes quadrata (Zhan, 1979)
Figure 5d–f

1979 *Waagenites soochowensis quadrata* Zhan, p. 70, pl. 4, figs 16–19.
2000 *Tethyochonetes quadrata* (Zhan); Chen *et al.*, p. 9, fig. 4A–D, G.
2002 *Tethyochonetes quadrata* (Zhan); Shen & Archbold, p. 339, fig. 6A–E.

Material. One dorsal valve (UWA133442) 5.8 mm long, 8.7 mm wide and 1.5 mm thick; two ventral valves (UWA133443) 6.0 mm long, 8.8 mm wide and 2.5 mm thick and (UWA133444) 6.9 mm long, 9.0 mm wide and 2.8 mm thick).

Remarks. When describing the species, Chen *et al.* (2000, pp. 9–10) summarized the internal features based on the figured specimens by Zhan (1979, pl. 4, fig. 16). Here, an additional dorsal valve is figured to illustrate the dorsal internal features, which confirm the previous observation by Chen *et al.* (2000). Internally, the dorsal valve has a round, blunt cardinal process with a shallow alveolus; the socket ridges are nearly parallel to the hinge margins; the median septum is short, moderately high and flanked by a pair of broad, short anderidia.

Tethyochonetes guizhouensis (Liao, 1980*b*, p. 258, pl. 5, figs 5–7), assigned by Waterhouse (1983*a*, p. 117) to his new genus *Sulcirugaria*, also approaches the type species in the high convexity and distinct costae. However, *T. guizhouensis* is differentiated from *T. quadrata* in being more transverse, twice as wide as long, and having broader ears and simple costae.

Occurrence. Beds 11 and 12 of the Changhsing Formation (latest Changhsingian to earliest Griesbachian), Huangzhishan section of Zhejiang, South China.

Tethyochonetes chaoi Chen, Shi, Shen & Archbold, 2000
Figure 5g, h

1922 *Chonetes barusiensis* (Davidson); Hayaskaya, p. 100, pl. 5, figs 7–10.
1928 *Chonetes* cf. *barusiensis* (Davidson); Chao, p. 30, pl. 1, fig. 18.
1964 *Chonetes barusiensis* (Davidson); Wang, Jin & Fang, pp. 240–1, pl. 27, figs 27, 33.
1976 *Waagenites* cf. *barusiensis* (Davidson); Zhang & Jin, p. 165, pl. 1, fig. 7.
1977 *Waagenites barusiensis* (Davidson); Yang *et al*., p. 332, pl. 135, fig. 4.
1979 *Waagenites barusiensis* (Davidson); Jin *et al*., p. 80, pl. 23, figs 16, 17.
1979 *Waagenites barusiensis* (Davidson); Zhan, p. 71, pl. 4, fig. 15, 20.
1978 *Waagenites barusiensis* (Davidson); Feng & Jiang, p. 244, pl. 88, fig. 6.
1987 *Waagenites barusiensis* (Davidson); Xu, 1987, pl. 8, figs 17, 18; pl. 9, figs 7, 8, 21.
1989 *Waagenites barusiensis* (Davidson); Zhan, pl. 25, fig. 9.
1989 *Waagenites barusiensis* (Davidson); Wang *et al*., pl. 1, fig. 6.
2000 *Tethyochonetes chaoi* Chen *et al*., p. 11, fig. 4J, K.

Material. UWA133445–446.

Description. Small size for genus with trapezoidal outline; ears broad, smooth and slightly inflated, bounded by furrows or shallow concavities from disk of shell; external costae with rounded crest, rarely bifurcate, about 5–6 costae in 10 mm near anterior margins. Other features are not observed.

Remarks. To distinguish the South Chinese materials from true *Waagenites barusiensis* (Davidson, 1866), Chen *et al*. (2000) proposed *Tethyochonetes chaoi* to include these small chonetids bearing a moderately convex ventral valve, a relatively broader, shallower ventral median sulcus and relatively finer ribs. These characteristics distinguish *T. chaoi* from other *Tethyochonetes* species.

Occurrence. Yinkeng Formation Bed 26 (latest Changhsingian), Meishan section (Quarry D) of Zhejiang, South China. Other occurrences include: Lungtan Formation (Wuchiapingian), Guizhou, Jiangxi, Jiangsu and Fujian, South China; Changhsing Formation (Changhsingian), Hubei and Sichuan, South China; Talung Formation (Changhsingian), Sichuan, South China; Upper Permian, Qinghai and Tibet, West China.

Suborder PRODUCTIDINA Waagen, 1883
Superfamily PRODUCTOIDEA Gray, 1840
Family PRODUCTELLIDAE Schuchert (*in* Schuchert & LeVene, 1929)
Subfamily PRODUCTININAE Muir-Wood & Cooper, 1960
Tribe PARAMARGINIFERINI Lazarev, 1986
Genus *Paryphella* Liao (*in* Zhao *et al*. 1981)

Type species. Cathaysia sulcatifera Liao, 1980*b*.

Diagnosis. Small productellid; widest at hinge; ginglymus short; ears broad, varyingly enrolled. Ventral median sulcus variously developed. Dorsal valve slightly concave; corpus cavity moderately deep. Costae robust, simple, confined to anterior regions of shell; rugae on ears; numerous spines along hinge margins. Ventral muscle fields striped; cardinal process small; dorsal median septum low, short; rows of coarse endospines arranged near anterior margin.

Remarks. Prior to formal description of the genus, Liao (1979, pl. 1, figs 19, 20; 1980a, pl. 1, fig. 19; pl. 2, fig. 10) figured his new species *Paryphella sulcatifera*. Later, Liao (1980b, p. 261, pl. 6, figs 8–10) assigned *sulcatifera* to *Cathaysia* Jin (*in* Wang, Jin & Fang, 1966). In 1981, Liao (*in* Zhao *et al*. 1981) designated *C. sulcatifera* as the type species and described the genus *Paryphella*. Apparently, these artificial confusions hindered later authors from fully understanding this genus. For example, Xu & Grant (1994) considered that *Cathaysia sulcatifera* (Liao) is synonymous with *Cathaysia sinuata Zhan* (1979, p. 78, pl. 8, figs 7–9). They also referred *Paryphella* as a junior synonym of *Cathaysia*. Although they treated *Paryphella* as a valid genus, Brunton *et al*. (2000, fig. 282: 1c) selected a replica of the dorsal valve interior of '*C. chonetoides* (Chao)' from the upper Changhsingian of Fujian, South China (Xu & Grant, 1994, fig. 18: 27) to demonstrate the dorsal features of *Cathaysia*. In fact, these Fujian specimens possess much more robust costae, and are not conspecific with the types of *C. chonetoides* from the Wuchiapingian and lower Changhsingian of South China (see Chao, 1927, pp. 62–3, pl. 16, figs 1–5). Accordingly, *Paryphella* remains poorly understood and requires restudy of the type materials.

After re-examining all *Paryphella* type specimens published by Liao (1979, 1980*a*,*b*, 1984), housed in the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences (by ZQC), we found that lack of a nasute structure at the anterior margin and possession of the strongly laterally enrolled ears justify distinction of *P. sulcatifera* from *C. sinuata*. The latter has a distinctive nasute structure and more flattened ears.

In brief, the important differences between *Paryphella* and *Cathaysia* (*sensu* Jin *in* Wang, Jin & Fang, 1966) are summarized as follows: the ears of *Paryphella* are broader and strongly enrolled laterally, whereas *Cathaysia* has two more flattened ears; *Paryphella* has fewer, much coarser ribs that are simple and weaken posteriorly; in comparison, *Cathaysia* embraces a greater number of costae that are relatively finer but throughout the valves and often bifurcate; the dorsal valve of *Paryphella* is much less concave than that of *Cathaysia* so that *Paryphella* has a much deeper corpus cavity than *Cathaysia*. In addition, Jin (*in* Wang, Jin & Fang, 1966) pointed out that the thin lamellae forming a concentric zone on the gutter of the ventral valve are also diagnostic of *Cathaysia*; this structure has not been observed in *Paryphella*.

Paryphella orbicularis Liao, 1980*a*
Figure 6a–g

1980*a* *Paryphella orbicularis* Liao, pl. 1, figs 17, 18; pl. 2, fig. 3.
1980*b* *Cathaysia orbicularis* (Liao): Liao, p. 261, pl. 6, figs 1–4.
1982 *Paryphella orbicularis* Liao; Wang *et al.*, p. 205, pl. 96, fig. 16.
1984 *Paryphella orbicularis* Liao; Liao, pl. 2, fig. 19.
1994 *Cathaysia orbicularis* (Liao); Xu & Grant, p. 34, fig. 19: 13–16, 21, not 19: 3–6.

Material. UWA133447–454.

Description. Small to medium-sized *Paryphella*, with subrectangular outline; widest at hinge; ears broad, triangular, enrolled laterally in various degrees, separated from ventral disk by a concavity; geniculation not preserved. Ventral beak blunt, incurved; umbo broad, rounded, evenly convex; median sulcus absent. Dorsal valve moderately concave; corpus cavity moderately deep.

External costae coarse, rounded in cross-section, with slightly narrower costal interspaces, simple, commencing anterior to umbo; about 5–7 costae in juveniles and about 10–12 costae in adults; rugae on ears; 2–3 spines on each side of hinge margins, projecting laterally; one spine present on the left side of ventral disc. Internal features of both valves are not observed.

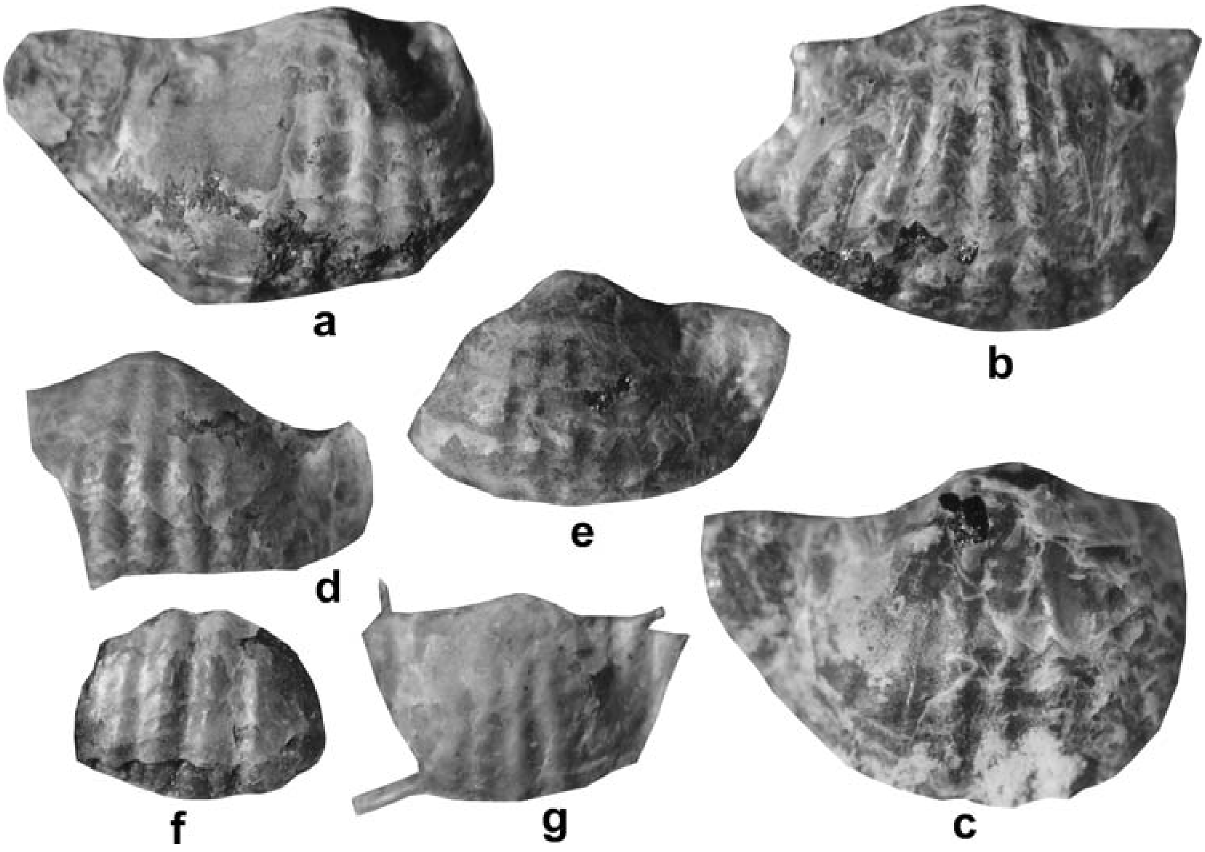


Figure 6. *Paryphella orbicularis* Liao, 1980*a* from Bed 27 of the lower Yinkeng Formation (earliest Griesbachian), Meishan section (Quarry D) of Zhejiang, South China. (a–g) UWA133447–453, ventral views of eight incomplete ventral valves: (a, b) showing pyrite grains on the shell; (c) illustrating costae commencing anterior to umbo; (e) showing large, slightly horizontally enrolled ear; (f) showing robust costae; (g) showing cardinal spines. (a–c) × 5. Others × 3.8.

Remarks. The morphologically closest species to *Paryphella orbicularis* is *P. triquetra* Liao (1979, pl. 1, fig. 18; see also Liao, 1980*a*, pl. 1, fig. 22; Zhao *et al*. 1981, p. 53, pl. 8, figs 18–22; Wang *et al*. 1982, p. 205, pl. 96, figs 14, 15; Liao, 1984, pl. 2, fig. 25); both species share similar shell outline, ornamentation, convex ventral umbo and lack of a ventral median sulcus. However, *P. triquetra* differs clearly from *P. orbicularis* in possessing a much smaller size, a more strongly convex ventral umbo, a pair of proportionally broader and more extended ears that are usually more strongly enrolled laterally. If these criteria are followed, some of the specimens (Xu & Grant, 1994, fig. 19: 3–6) under the name *P. orbicularis* by Xu & Grant are assignable to *P. triquetra*, although these authors insisted on *P. triquetra* being synonymous to *P. orbicularis*.

The type species *Paryphella sulcatifera* from the Changhsingian and Permian–Triassic boundary beds of South China (Liao, 1980*b*, p. 261, pl. 6, figs 8–10; Liao, 1984, pl. 2, fig. 18) is distinguished from the present species by its much larger size and deeper ventral median sulcus.

Occurrence. Yinkeng Formation Bed 27 (earliest Griesbachian), Meishan section (Quarry D) of Zhejiang, South China. Other occurrences include: Changhsing Formation (Changhsingian), Guizhou, Zhejiang and Hunan, South China; Talung Formation (Changhsingian), Jiangsu, Anhui and Fujian, South China; Lower Qinglong Formation (earliest Griesbachian), Jiangsu and Anhui, South China; Yinkeng Formation (earliest Griesbachian), Anhui and Zhejiang, South China.

Paryphella transversa Liao, 1984
Figure 7a

1980*a* *Paryphella* cf. *sulcatifera* Liao, pl. 2, fig. 4.

1984 *Paryphella transversa* Liao, p. 280, pl. 2, figs 10–12.

Material. UWA133456.

Description. Medium-sized for genus; transversely rectangular in outline; longer than wide; widest at hinge; ears broad, triangular, moderately enrolled laterally. Ventral umbo broad, moderately convex; median sulcus broad, shallow, beginning anterior to beak. External costae coarse, rounded, simple, commencing anterior to umbo; about 14–16 costae on disc; rugae on ears. Other features not observed.

Remarks. The presence of a transverse outline, a shallow ventral median sulcus and 14–16 costae justifies assignment of the examined specimen to Liao's species even if the studied material is inadequate and fragmentary. *P. transversa* is most allied to *P. sulcatifera*, from which the present species is distinguishable in having a relatively more transverse outline, a shallower ventral valve and greater number of costae.

Occurrence. Yinkeng Formation Bed 26 (latest Changhsingian), Meishan section (Quarry A) of Zhejiang, South China.

Paryphella nasuta Liao, 1984
Figures 5j, 7b

1984 *Paryphella nasuta* Liao, p. 281, pl. 2, figs 13, 14.

Material. UWA133455.

Description. Small species for genus, with chonetid-shaped shells; widest at hinge; ears moderately broad, triangular, enrolled laterally, demarcated from ventral disc by a concavity. Ventral valve evenly strongly convex with greatest convexity at umbo; beak broad, rounded, slightly incurved; umbonal region rounded,

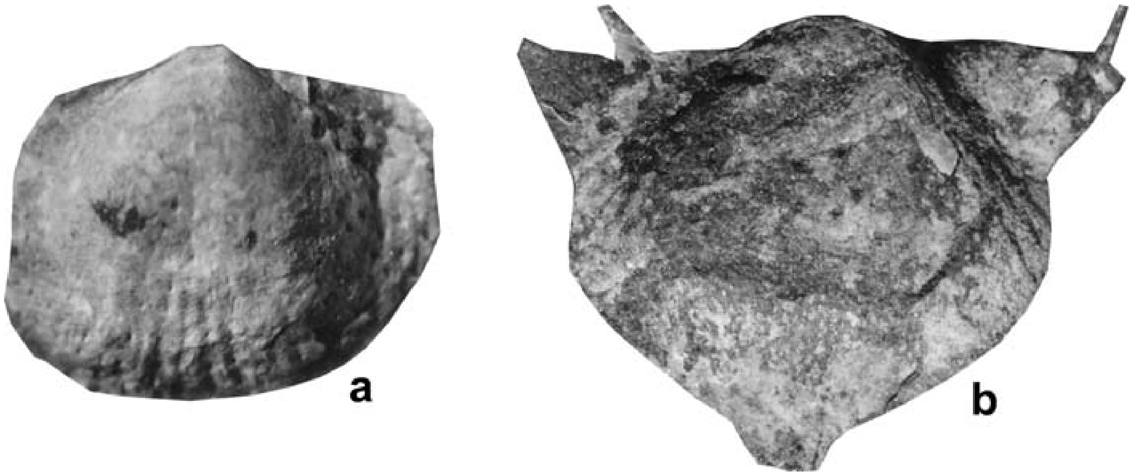


Figure 7. (a) *Paryphella transversa* Liao, 1984 from Bed 26 of the lower Yinkeng Formation (latest Changhsingian), Meishan section (Quarry A) of Zhejiang, South China, UWA133456, ventral view of an incomplete ventral valve with ears broken. (b) *Paryphella nasuta* Liao, 1984 from Bed 26 of the lower Yinkeng Formation (latest Changhsingian), Meishan section (Quarry Z) of Zhejiang, South China, UWA133455, ventral view of a ventral valve. Both × 5.

evenly convex; median sulcus absent; a small nasute extension present anterior margin.

External costae coarse, rounded in cross-section, with narrower interspaces, simple, commencing anterior to umbo; umbo smooth; about 12 costae on disk; rugae on ears; 2–3 spines on each side of hinge margins, projecting laterally. Other features not observed.

Remarks. The unique *Paryphella*-like outline and a nasute extension justify the assignment of the examined specimen to Liao's species even if its internal features are unknown. The latter characteristic also distinguishes *Paryphella nasuta* from other species of the genus. On the other hand, the nasute extension of *P. nasuta* recalls that of *Cathaysia sinuata* Zhan (1979, p. 78, pl. 8, figs 7–9) from the Changhsingian of Guangdong, South China and *Chonetella nasuta* Waagen (1884, p. 658, pl. 18, figs 3–8) from the Upper Permian of the Salt Range, Pakistan. However, Zhan's species is distinguished from the present species in having more flattened ears, finer ribs originating from anterior to beaks, and a distinctive ventral median sulcus; the Salt Range species is much larger than *P. nasuta* and has a longer, broader nasute extension. In addition, *Chonetella nasuta* possesses much weaker costae and is very different in the dorsal interior.

Occurrence. Yinkeng Formation Bed 26 (latest Changhsingian), Meishan section (Quarry Z) of Zhejiang, South China.

Subfamily OVERTONIINAE Muir-Wood & Cooper, 1960
Tribe MARGINIFERINI Stehli, 1954
Genus *Spinomarginifera* Huang, 1932

Type species. *Spinomarginifera kueichowensis* Huang, 1932.

Spinomarginifera kueichowensis Huang, 1932
Figure 8a–e; Table 2

1932 *Spinomarginifera kueichowensis* Huang, pp. 56–60, pl. 5, figs 1–11.

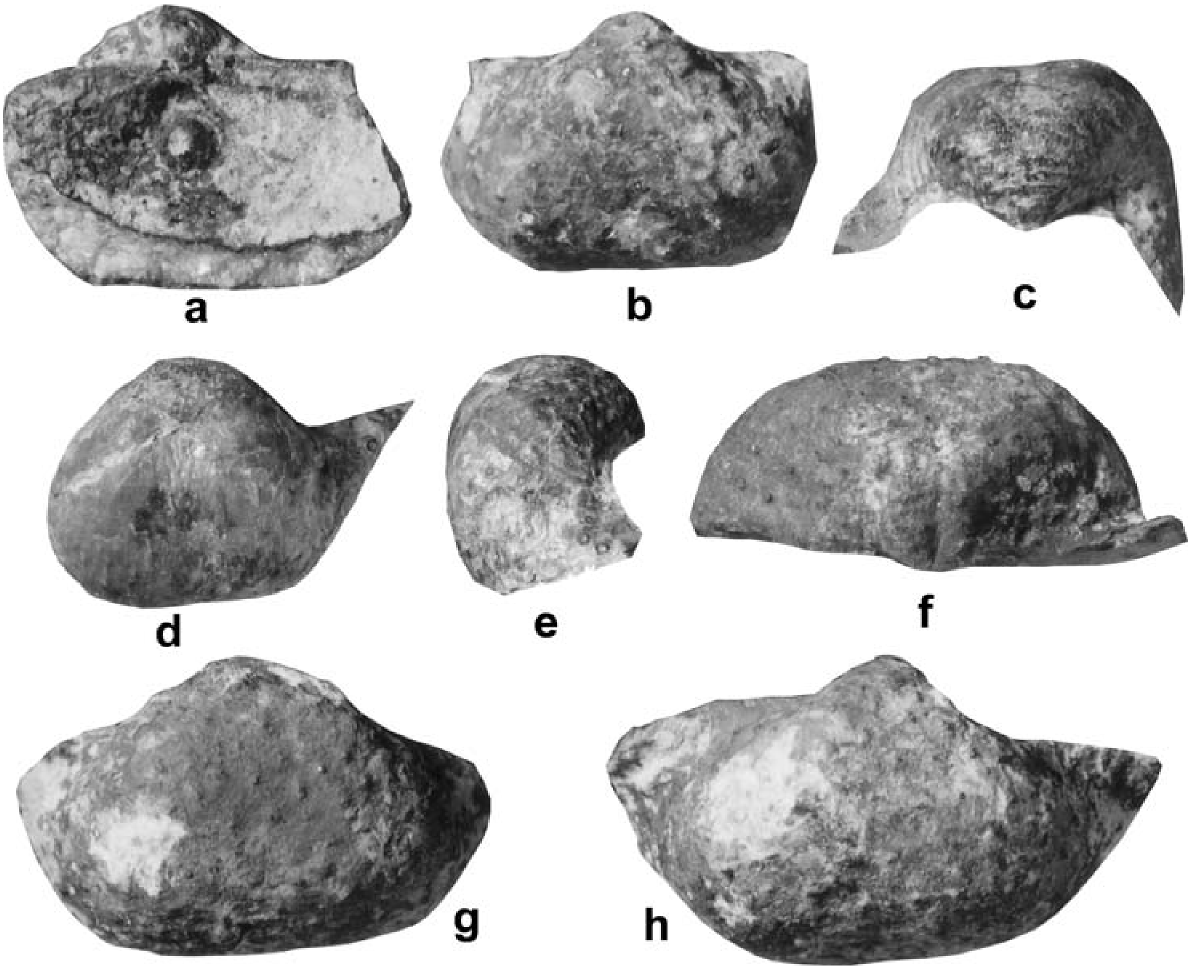


Figure 8. (a–e) *Spinomarginifera kueichowensis* Huang, 1932 from the topmost Changhsing Formation (earliest Griesbachian), Huangzhishan section of Zhejiang, South China. (a, b) UWA133479, dorsal and ventral views of a specimen. (c–e) UWA133457–458, UWA133478, three specimens in posterior, antero-ventral and postero-ventral views, respectively. (f–h) *Spinomarginifera chengyaoyenensis* Huang, 1932 from the lowest Feixianguan Formation (earliest Griesbachian), Taiping section of Chongqing, South China, UWA133459, posterior, ventral, and lateral views of a ventral valve. All × 3.8.

Table 2. Measurements (in mm) of *Spinomarginifera kueichowensis* Huang, 1932

Specimens	Width	Length	C-length	Thickness
UWA133457	15.9	9.9	19.1	7.2
UWA133458	18.4	11.1	20*	9.2
UWA133478	16.6	10.7	22.6	6.7
UWA133479	13.5*	10*	19*	6.8
UWA133480	14.7	11.6	22.5	9.2
UWA133481	14.3	11.4	18.9	8.5
UWA133482	14.1	11.9	19.4	6.5
UWA133483	13.7	10*	19*	6.5*
UWA133484	15.5	10*	20*	7.5*
UWA133485	14.3	11*	19*	7.0*

C-length: curvature length; *value is estimated.

1960 *Spinomarginifera kueichowensis* Huang; Muir-Wood & Cooper, p. 216, pl. 65, figs 15–22, 24.
1962 *Spinomarginifera kueichowensis* Huang; Chi-Thuan, p. 493, pl. 2, fig. 1.
1965 *Spinomarginifera kueichowensis* Huang; Fantini Sestini, p. 994, pl. 94, fig. 1a, b.
1974 *Spinomarginifera kueichowensis* Huang; Jin, Liao & Hou, p. 312, pl. 164, fig. 13.
1976 *Spinomarginifera kueichowensis* Huang; Tazawa, p. 184, pl. 2, fig. 1a, b.
1977 *Spinomarginifera kueichowensis* Huang; Yang *et al*., p. 349, pl. 139, fig. 11.
1978 *Spinomarginifera kueichowensis* Huang; Feng & Jiang, p. 252, pl. 89, figs 5, 6;
1978 *Spinomarginifera kueichowensis* Huang; Tong, p. 222, pl. 79, fig. 5.
1979 *Spinomarginifera kueichowensis* Huang; Zhan, p. 80, pl. 11, figs 14–17, 20.
1980 *Spinomarginifera kueichowensis* Huang; Tien, p. 80, pl. 26, figs 4–10.
1980*a* *Spinomarginifera kueichowensis* Huang; Liao, pl. 4, fig. 29.
1982 *Spinomarginifera kueichowensis* Huang; Wang *et al*., p. 219, pl. 92, fig. 3.
1995 *Spinomarginifera kueichowensis* Huang; Zeng, He & Zhu, pl. 5, fig. 10.
2002 *Spinomarginifera kueichowensis* Huang; Tazawa, fig. 10: 11a, b.

Material. Ten specimens are measured (Table 2). Of these, UWA133457–459 and UWA133478–479 are illustrated here.

Description. Various sizes for genus (see measurements); subpentagonal outline; concave–convex in profile; widest at hingeline; both valves strongly geniculate; cardinal extremities acute; ears broad, slightly inflated. Ventral beak stout, strongly incurved, slightly overhanging hingeline; umbo strongly convex with steep slopes to flanks; median sulcus indistinct. Dorsal valve moderately concave; corpus cavity deep; fold absent; trail broken.

Ventral external surface ornamented with elongate concentric rugae and spine bases; rugae confined to ears; spine bases arranged on disk, ears and posterior margins; those on umbo arranged by the form of rounded tubercles on umbo, elongate anteriorly, forming insistent ‘costae’. Dorsal valve with similar ornamentation to ventral valve, but with numerous coarse dimples and rare, rather fine spine bases. Internal features not observed.

Remarks. The specimens examined agree well with Huang’s description of the species except for the small size. The type specimens are usually twice the size of the described materials (see above for measurements). Therefore, the present specimens are tentatively assigned to Huang’s species. *S. lopingensis* (Kayser, 1883; see also Liao, 1980b; Chen *et al.* 2005) is distinguished from the present species by the possession of an elongate–oval outline, coarser pustules on the ventral umbo, and more pronounced costae on the trails. *S. pseudosintanensis* Huang from the Upper Permian of the western Hubei Province, South China (Huang, 1932) is comparable with the examined materials in many aspects, but the Hubei species embraces a more rounded outline and hingeline that is slightly shorter than the shell width.

Occurrence. Beds 11 and 12 of the Changhsing Formation (latest Changhsingian to earliest Griesbachian), Huangzhishan section of Zhejiang, South China. Other occurrences include: Changhsing Formation (Changhsingian), Sichuan, Guizhou, Hunan, Guangdong, Fujian, Zhejiang and Jiangsu, South China; Middle to Upper Permian, Cambodia and northern Iran; Upper Permian, Russian Far East and northeastern Japan.

Spinomarginifera chengyaoyenensis Huang, 1932
Figure 8f–h

1932 *Spinomarginifera chengyaoyenensis* Huang, pp. 60–1, pl. 5, figs 12, 13.
1964 *Spinomarginifera chengyaoyenensis* Huang; Wang, Jin & Fang, p. 314, pl. 50, figs 12, 13.
1979 *Spinomarginifera chengyaoyenensis* Huang; Zhan, p. 81, pl. 13, fig. 12.
1980*a* *Spinomarginifera chengyaoyenensis* Huang; Liao, pl. 5, figs 27–32.
1980*b* *Spinomarginifera chengyaoyenensis* Huang; Liao, p. 292, pl. 2, figs 12, 13.
1987 *Spinomarginifera chengyaoyenensis* Huang; Liao, 1987, pl. 5, figs 3, 4.
1987 *Rugosomarginifera chengyaoyenensis* Huang; Xu, p. 224, pl. 11, figs 9, 17, 18; pl. 13, figs 1–4.
1998 *Spinomarginifera chengyaoyenensis* Huang; Shi & Shen, p. 509, fig. 4: 8–10.
2002 *Spinomarginifera* cf. *chengyaoyenensis* Huang; Liao & Xu, pl. 1, fig. 25.

Material. UWA133459.

Description. Small to medium-sized *Spinomarginifera*, about 13 mm long, 11 mm wide and 6 mm thick; oval outline; concave–convex shells; hingeline straight and equal to greatest width of shell; cardinal extremities acute; ears broad and flattened. Ventral valve strongly convex, geniculate anteriorly; beak strongly enrolled, slightly overhanging hingeline; umbonal region strongly convex, prominent; median sulcus absent. Dorsal valve not observed.

Remarks. Externally, the examined material agrees well with Huang's (1932) description for the species. *S. chengyaoyenensis* is distinguished from *S. kueichowensis* in having a smaller size, a more strongly convex ventral valve and stronger rugae covering the posterior regions of the shells. In particular, the latter feature has been treated as the main criteria to distinguish his new genus *Rugosomarginifera*, with type species *S. jisuensis* (Chao), from *Spinomarginifera* by Xu (1987). *Rugosomarginifera* is said to have distinct concentric wrinkles, spines on both valves, spines arranged in a curved row near ears and the gently concave–convex profile. However, these characteristics are specific variations within *Spinomarginifera* (Liao, 1980*b*).

The re-examination of the type specimens of *S. kueichowensis* housed in the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences (by Z.Q.C. in 2000) reveals that the true *Spinomarginifera* is also dorsally spinose, confirming the clarification of Waterhouse (1983*b*) and Liao (1987). In addition, both *Rugosomarginifera* and *Spinomarginifera* are exactly the same internally. Subsequently, *Rugosomarginifera* cannot be generically differentiated from *Spinomarginifera*.

Like *Spinomarginifera jisuensis*, *S. chengyaoyenensis* possesses distinct rugae, but they are confined to the umbonal regions, whereas *S. jisuensis* embraces the rugae covering the entire shells. Moreover, the elongate shell outline of *S. jisuensis* is also noteworthy.

Occurrence. Lowest Feixianguan Formation (earliest Griesbachian), Taiping section of Chongqing, South China. Other occurrences include: Changhsing Formation (Changhsingian), Sichuan, Guizhou and Hunan, South China.

Class RHYNCHONELLATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order SPIRIFERIDA Waagen, 1883
Suborder SPIRIFERIDINA Waagen, 1883
Superfamily AMBOCOELIOIDEA George, 1931
Family AMBOCOELIIDAE George, 1931
Subfamily AMBOCOELIINAE George, 1931
Genus *Orbicoelia* Waterhouse & Piyasin, 1970

Type species. *Orbicoelia fraterculus* Waterhouse & Piyasin, 1970.

Diagnosis. Small biconvex or planoconvex, without fold or sulcus; interareas narrow, proportionately high for Ambocoeliinae; surface bearing tiny, indistinct concentric spines; teeth supported by low dental plates, without adminicula or median septum; cardinal process low, flat, not tuberculate; crural plates sturdy, supported by floor plates.

Remarks. The most important difference between *Orbicoelia* and *Crurithyris* George, 1931 is that the former lacks a median sulcus on both valves. In addition, *Orbicoelia* is distinct from *Crurithyris* in the possession of a relatively more strongly inflated dorsal valve, a narrower, higher ventral interarea and more rounded cardinal extremities. Unlike *Orbicoelia* that bears tiny, indistinct spines, *Crurithyris* includes forms with distinct, concentrically arranged spines (George, 1931; Veevers, 1959; Waterhouse & Piyasin, 1970).

Another ally is *Crurícella* Grant, 1976, which is similar to *Orbicoelia* in having a rectimarginate commissure and an inflated dorsal valve. However, Grant's genus is smaller and proportionately more elongate and has a higher, flattened ventral interarea. The Devonian genus, *Ambocoelia* Hall, 1860, also resembles *Orbicoelia* externally. However, the re-examination by Goldman & Mitchell (1990) reveals that *Ambocoelia* possesses a planoconvex to concavo-convex profile, a distinct ventral median sulcus and a bifid cardinal process. Moreover, lack of parallel crural plates also distinguishes *Ambocoelia* from *Orbicoelia*.

Paracrurithyris Liao (*in* Zhao *et al*. 1981) is also externally comparable with *Orbicoelia* in many aspects. Although Xu & Grant (1994) treated *Paracrurithyris* as a synonym of *Crurithyris*, this poorly known genus includes specimens lacking a median sulcus on both valves, and thus differs clearly from *Crurithyris*. Liao's genus is said to be very small and stratigraphically restricted to the Permian–Triassic boundary beds in South China. However, the poor knowledge of the internal features prevents a full comparison between *Paracrurithyris* and *Orbicoelia*.

Jin & Sun (1981, p. 157) proposed *Speciothyris* to include '*Crurithyris*' *speciosa* Wang (1956), which is defined by lack of a median sulcus on both valves. However, Wang's species, described below, fully agrees with *Orbicoelia*. As a result, *Speciothyris* is considered to be a synonym of *Orbicoelia*.

In brief, although Waterhouse & Piyasin (1970) proposed *Orbicoelia* to include the *Crurithyris*-like specimens but lacking a median sulcus, these small ambocoelids have long been collectively ascribed to *Crurithyris* (Table 3). As such, to clarify the relationship between these two genera, we describe several *Orbicoelia* species based on new materials from both South China and northern Italy as below, and re-assign several other species previously ascribed to

Table 3. Species previously ascribed to *Crurithyris* from the Upper Permian and Permian–Triassic boundary beds and their revisions

Species	Authors	Age	Locality	Revision
Crurithyris pusilla n. sp.	Zhan (1979, p. 96, pl. 13, figs 24, 25)	Changhs.	Guangdong, S. China	*Orbicoelia pusilla* (Chan)
C. pusilla Chan	Zhu (1990, p. 82, pl. 18, fig. 17)	Changhs.	Fujian, S. China	*O. pusilla* (Chan)
C. pusilla Chan	Yang (1984, p. 234, pl. 37, fig. 22)	Changhs.	Hubei, S. China	*O. pusilla* (Chan)
C. pusilla Chan	Xu (1987, p. 230, pl. 15, figs 4–18)	Changhs.	Sichuan, S. China	*O. pusilla* (Chan)
C. pusilla Chan	Xu & Grant (1994, p. 43, fig. 34: 1–47, 52)	Changhs., Griesba.	Sichuan, Chongqing, Fujian, S. China	*O. pusilla* (Chan)
C. speciosa obovata n. subsp.	Zeng, He & Zhu (1995, p. 122, pl. 12, figs 17, 18)	Changhs.	Sichuan, S. China	*O. obovata* (Zeng, He & Zhu)
Crurithyris sp.	Zhu (1990, p. 83, pl. 16, figs 9–12)	Changhs.	Fujian, S. China	*O. sp.*
C. shizhongensis n. sp.	Zhu (1990, p. 82, pl. 16, figs 6–8)	Changhs.	Fujian, S. China	*O. shizhongensis* (Zhu)
C. speciosa Wang	Wang (1956, p. 389, pl. 6.1, figs 1–6)	Changhs.	Guizhou, S. China	*O. speciosa* (Wang)
C. speciosa Wang	Wang, Jin & Fang (1964, p. 546, pl. 104, figs 13–16)	Changhs.	Guizhou, S. China	*O. speciosa* (Wang)
C. speciosa Wang	Tong (1978, p. 254, pl. 89, fig. 6)	Changhs.	Guizhou, S. China	*O. speciosa* (Wang)
C. speciosa Wang	Feng & Jiang (1978, p. 283, pl. 102, fig. 10)	Changhs.	Guizhou, S. China	*O. speciosa* (Wang)
C. speciosa Wang	Liao (1979, pl. 1, fig. 21)	Changhs.	Guizhou, S. China	*O. speciosa* (Wang)
C. speciosa Wang	Liao (1980*b*, p. 276, pl. 8, figs 16, 17)	Changhs.	Guizhou, S. China	*O. speciosa* (Wang)
C. speciosa Wang	Liao (1980*b*, p. 290, pl. 1, figs 14–16)	Griesba.	Guizhou, S. China	*O. speciosa* (Wang)
C. cf. *speciosa* Wang	Liao (1980*b*, p. 265, pl. 8, fig. 15)	Changhs.	Guizhou, S. China	*O.* cf. *speciosa* (Wang)
C. longa n. sp.	Liao (1980*b*, p. 265, pl. 8, figs 11–14)	Changhs	Guizhou, S. China	*O. longa* (Liao)
C. flabiliformis n. sp.	Liao (1979, pl. 1, fig. 2)	Changhs.	Guizhou, S. China	*O. flabiliformis* (Liao)
C. flabiliformis Liao	Liao (1979, pl. 1, fig. 3)	Griesba.	Fujian, S. China	*O. flabiliformis* (Liao)
C. flabiliformis Liao	Liao (1980*b*, p. 290, pl. 1, figs 12, 13, 30)	Changhs.	Guizhou, S. China	*O. flabiliformis* (Liao)
C. flabiliformis Liao	Liao (1987, p. 109, pl. 6, figs 6–14)	Changhs.	Guangxi, S. China	*O. flabiliformis* (Liao)
C. cordata n. sp.	Shen, He & Zhu (1992, p. 186, pl. 4, figs 25–28)	Changhs.	Chongqing, S. China	*O. cordata* (Shen, He & Zhu)
C.? extima n. sp.	Grant (1970, p. 142, pl. 3, figs 1–3d)	Griesba.	Salt Range, Pakistan	*O. extima* (Grant)
?C. extima Grant	Posenato (1988, pl. 2, fig. 6)	Changhs.	Tesero, S. Alps	*O. dolomiteensis* Chen
C.? extima Grant	Broglio Loriga, Neri & Posenato (1988, pl. 2, figs 7–9)	Changhs.	Tesero, S. Alps	*O. dolomiteensis* Chen
C. extima Grant	Posenato (1999, pl. 5, figs 17–19)	Changhs.	Tesero, S. Alps	*O. dolomiteensis* Chen

Changhs. – Changhsingian; Griesba. – Griesbachian.

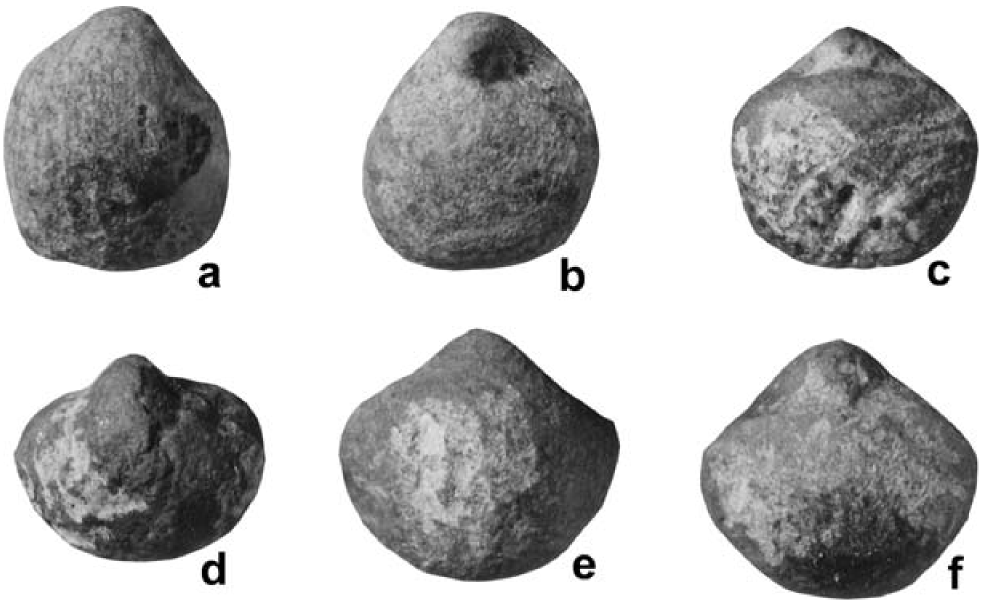


Figure 9. *Orbicoelia speciosa* (Wang, 1955) from topmost Changhsing Formation (earliest Griesbachian), Huangzhishan section of Zhejiang, South China. (a, b) UWA133460, a complete specimen in ventral and dorsal views. (c, d) UWA133462, a complete specimen in dorsal and ventral views. (e, f) UWA133461, a complete specimen in ventral and dorsal views. All × 3.8.

Crurithyris from the Permian–Triassic boundary beds to *Orbicoelia* (Table 3).

Orbicoelia speciosa (Wang, 1955)

Figures 9a–f, 10; Table 4

1955 *Crurithyris speciosa* Wang, p. 146, pl. 83, figs 1–4.

1956 *Crurithyris speciosa* Wang, pp. 389–90, pl. 6.1, figs 1–6.

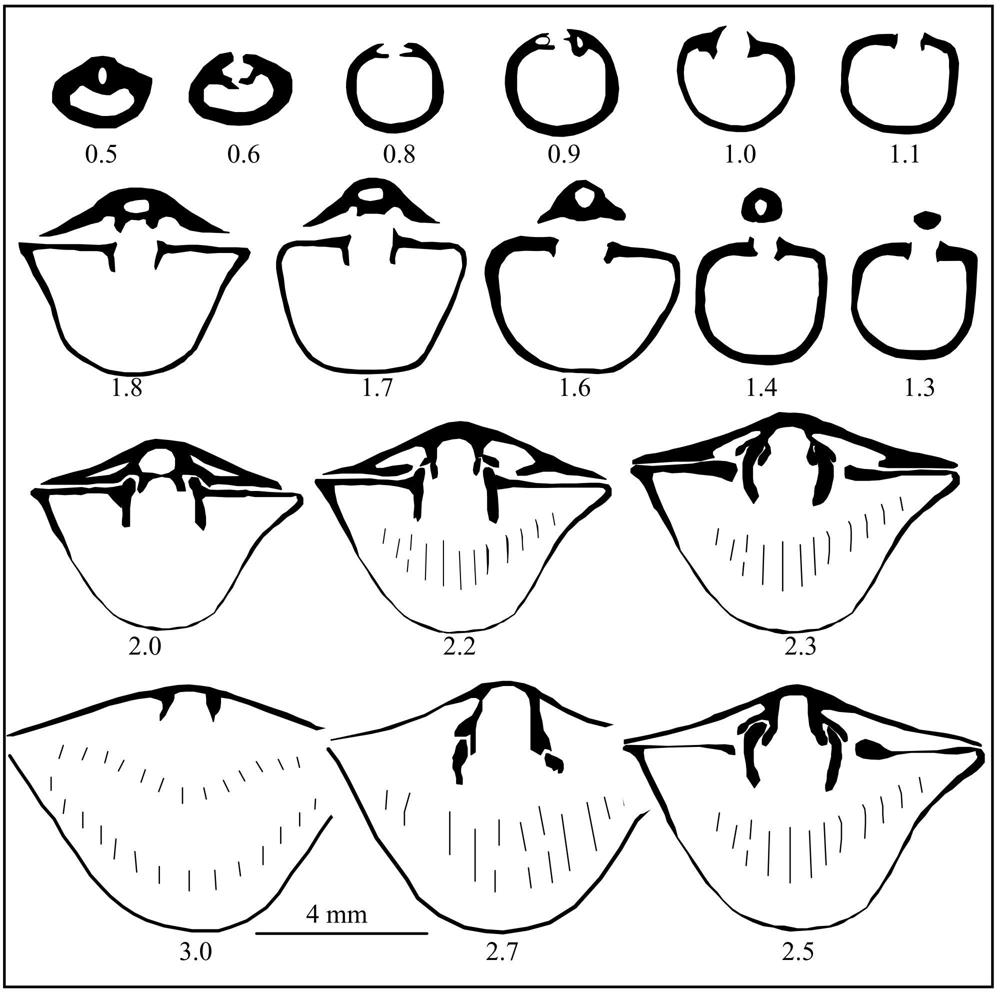


Figure 10. Selected serial sections of *Orbicoelia speciosa* (Wang, 1955) (based on specimen UWA133476). The numbers represent the distance from the ventral beak; the orientation of the sections is with the ventral valve downwards except where noted; horizontal line represents the scale (hereafter the same).

Table 4. Measurements (in mm) of *Orbicoelia speciosa* (Wang, 1956)

Specimens	Width	Length	Thickness
UWA133460	8.4	9.2	5.6
UWA133461	9.48	9.0	6.2
UWA133462	8.5	6.1	5.4
UWA133476	7.9	6.0	5.5

1964 *Crurithyris speciosa* Wang; Wang, Jin & Fang, p. 546, pl. 104, figs 13–16.
1978 *Crurithyris speciosa* Wang; Tong, p. 254, pl. 89, fig. 6.
1978 *Crurithyris speciosa* Wang; Feng & Jiang, p. 283, pl. 102, fig. 10.
1979 *Crurithyris speciosa* Wang; Liao, pl. 1, fig. 21.
1980*b* *Crurithyris speciosa* Wang; Liao, p. 276, pl. 8, figs 16, 17.
1980*b* *Crurithyris* cf. *speciosa* Wang; Liao, p. 265, pl. 8, fig. 15.
1981 *Speciothyris speciosa* Wang; Jin & Sun, pp. 156–7, text-fig. 17.
1994 *Crurithyris speciosa* Wang; Xu & Grant, p. 45, figs 33, 34: 48–51.

Material. Five specimens are available for study. Of these, UWA133460–133462 are figured here, and UWA133476 is sectioned.

Description. Medium to large *Orbicoelia* (measurements see Table 4); subcircular in outline; widest posterior to mid-length of shell; ventrobiconvex in profile; cardinal extremities rounded; anterior commissure rectimarginate; sulcus and fold absent. Ventral valve strongly convex; beak pointed, slightly incurved over delthyrium; umbo broad, evenly convex with gentle lateral slopes; delthyrium triangular, moderately high, open. Dorsal valve moderately convex. Externally, concentric growth lines and tiny spine bases occasionally visible when shell well preserved.

Ventral interior with pedicle collar and delthyrial plates near apex of delthyrial cavity; teeth stout; dental plates absent. Dorsal interior crural plates thin, nearly parallel, reaching valve floor; median ridge absent; numerous spiralia on each side of body cavity with axes of coiling directed slightly obliquely posteriorly (Fig. 10).

Remarks. The present species is very common in the Upper Permian and Permian–Triassic boundary beds in South China. It differs clearly from *Crurithyris urei*, type species of the genus, in lack of a median sulcus on both valves. Based on this distinction, Jin & Sun (1981) created *Speciothyris* to include *speciosa*. However, the external features observed by Wang (1956), internal structures revealed by Jin & Sun (1981) and our new topotype materials suggest that Wang's species fit well within the concept of *Orbicoelia*. As such, we here assign Wang's species to *Orbicoelia*.

Externally, *O. speciosa* is closely allied to *Orbicoelia extima* (Grant, 1970, pp. 142–4, pl. 3, figs 1–3d, text-fig. 1) from the dolomite unit of the Kathwai Member (Mianwali Formation) of the Salt Range, Pakistan. However, *O. extima* can be distinguished from Wang's species by its more posteriorly situated shell width, less incurved ventral beak, much thicker delthyrial plates and a smaller number of spiral turns. *Orbicoelia pusilla* (Zhan, 1979; see also Table 4) is also confined to the latest Changhsingian of South China and thus contemporaneous to *O. speciosa*. However, unlike *O. speciosa*, the *pusilla* species is significantly smaller and has a relatively more flattened dorsal valve.

Occurrence. Topmost Changhsing Formation (earliest Griesbachian), Huangzhishan section of Zhejiang, South China. Other occurrences include: Changhsing Formation (Changhsingian), Sichuan, Guizhou, Hunan and Guangdong, South China; Yinkeng Formation (earliest Griesbachian), Zhejiang and Anhui, South China.

Orbicoelia dolomitensis n. sp.
Figures 11a–l, 12, 13

Etymology. Named for the Dolomite region, northern Italy, where the studied sections are exposed.

Material. 20 specimens are available for study. Of these, UWA133463–133471 are figured; UWA133477 is sectioned.

Holotype. UWA133468, 4.6 mm long, 4.7 mm wide and 2.9 mm thick.

Diagnosis. Small *Orbicoelia* (measurements see Fig. 12) both valves moderately convex; convex regions confined to umbonal regions, with broad, slightly flattened lateral and anterior margins.

Description. Subcircular in outline; slightly ventrobiconvex in profile; fold and sulcus absent; cardinal

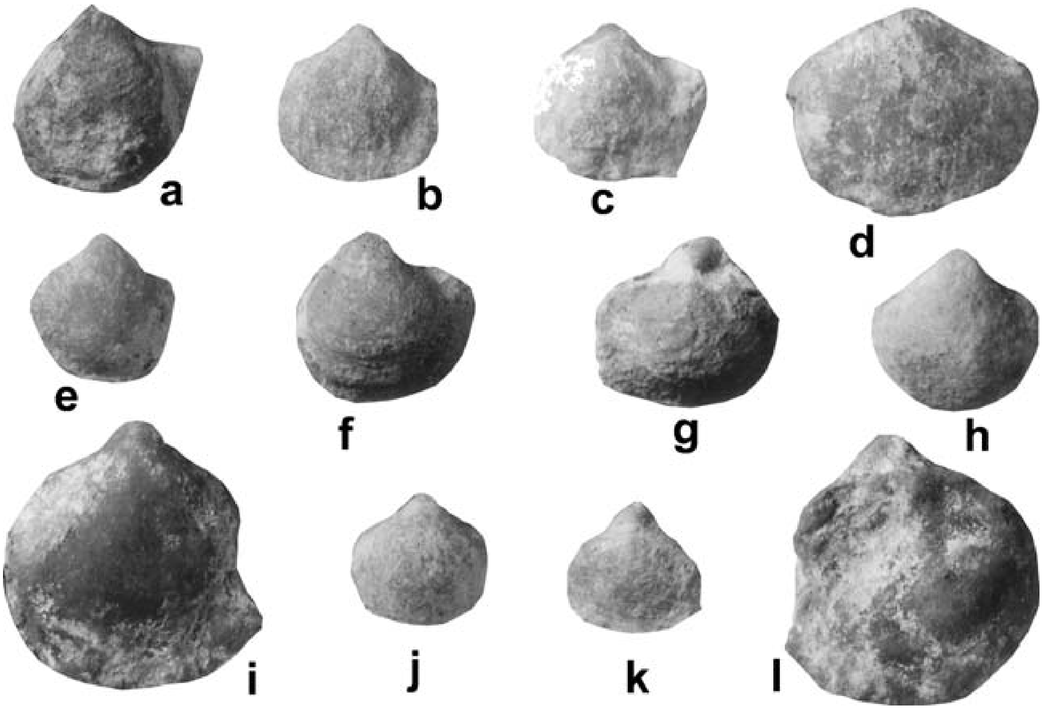


Figure 11. *Orbicoelia dolomitensis* n. sp. from the middle Tesero Member (Werfen Formation) of the Tesero section, Dolomites, northern Italy. (a) UWA133464, a complete specimen in ventral view. (b) UWA133467, a specimen in ventral view. (c) UWA133465, a specimen in ventral view. (d) UWA133470, a specimen in dorsal view. (e) UWA13469, a specimen in ventral view. (f, g) UWA133463, a complete specimen in ventral and dorsal views. (h) UWA133466, a specimen in ventral view. (i, l) UWA133471, a specimen in ventral and dorsal views. (j, k) UWA133468, holotype, a specimen in ventral and dorsal views. (d, i, l) × 5. Others × 3.8.

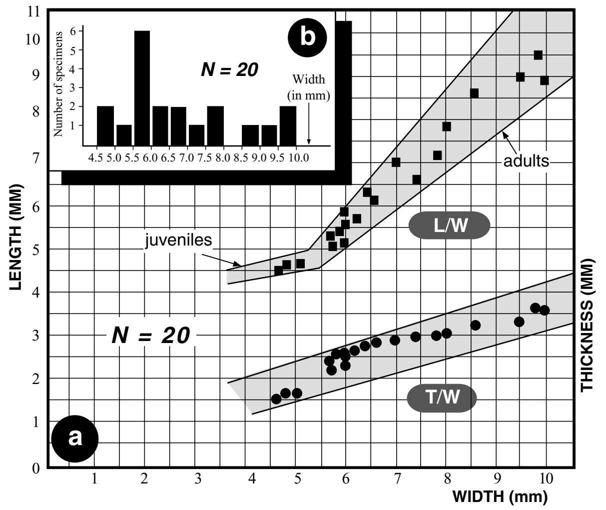


Figure 12. Measurements of *Orbicoelia dolomitensis* n. sp. (a) Variation of shell length, maximum width and thickness of twenty specimens. L/W, ratio of shell length and maximum width; T/W, ratio of shell thickness and maximum width. The ratios of juveniles are usually greater than 1.1; the ratios of adults are smaller than 1.1. (b) Frequency distributions of the maximum width in twenty specimens. Maximum widths vary between 5.5 mm and 6.0 mm are frequently counted, with an occurring frequency of 30 %.

extremities rounded; anterior commissure rectimarginate. Ventral valve with greatest convexity at umbo; beak small, pointed, incurved, slightly overhanging above delthyrium; interarea narrow, slightly concave; umbo convex with gentle lateral slopes; anterior and lateral margins broad, slightly flattening; Dorsal valve moderately convex; beak small, strongly incurved; umbo moderately convex; lateral and anterior margins broad, slightly flattening.

External surfaces generally smooth, with micro-ornaments of fine concentric growth lines. Internally, ventral valve with blunt teeth, short, thin delthyrial plates; dental plates absent; dorsal interior crural plates subparallel, reaching valve floor posteriorly, suspending anteriorly; median ridge low, indistinct (Fig. 13).

Remarks. The small, *Crurithyris*-like specimens from the Tesero section, northern Italy have long been ascribed to *Crurithyris*? *extima* Grant (e.g. Broglio Loriga, Neri & Posenato, 1988). Of particular note is that Grant (1970, p. 142) considered that *extima* maybe generically distinct from the true *Crurithyris*. However, when they applied this Pakistan species to the Italian materials, some authors treated *extima* as a distinct *Crurithyris* species (e.g. Posento, 1999, 2001). In fact, all characteristics described by Grant (1970) suggest *extima* is a typical *Orbicoelia* species. When compared with *O. extima*, these Tesero specimens possess a relatively smaller size, a lower convexity on both valves, much broader, flattened anterior and lateral margins and much thinner, shorter delthyrial plates. They thus are excluded from *O. extima*. These Tesero materials also approach moderately the South Chinese species *O. speciosa* Wang and *O. pusilla* (Zhan). However, Wang's species is much larger and has more strongly convex valves and thus cannot include the Tesero material. Zhan's species is of comparable size with the Tesero

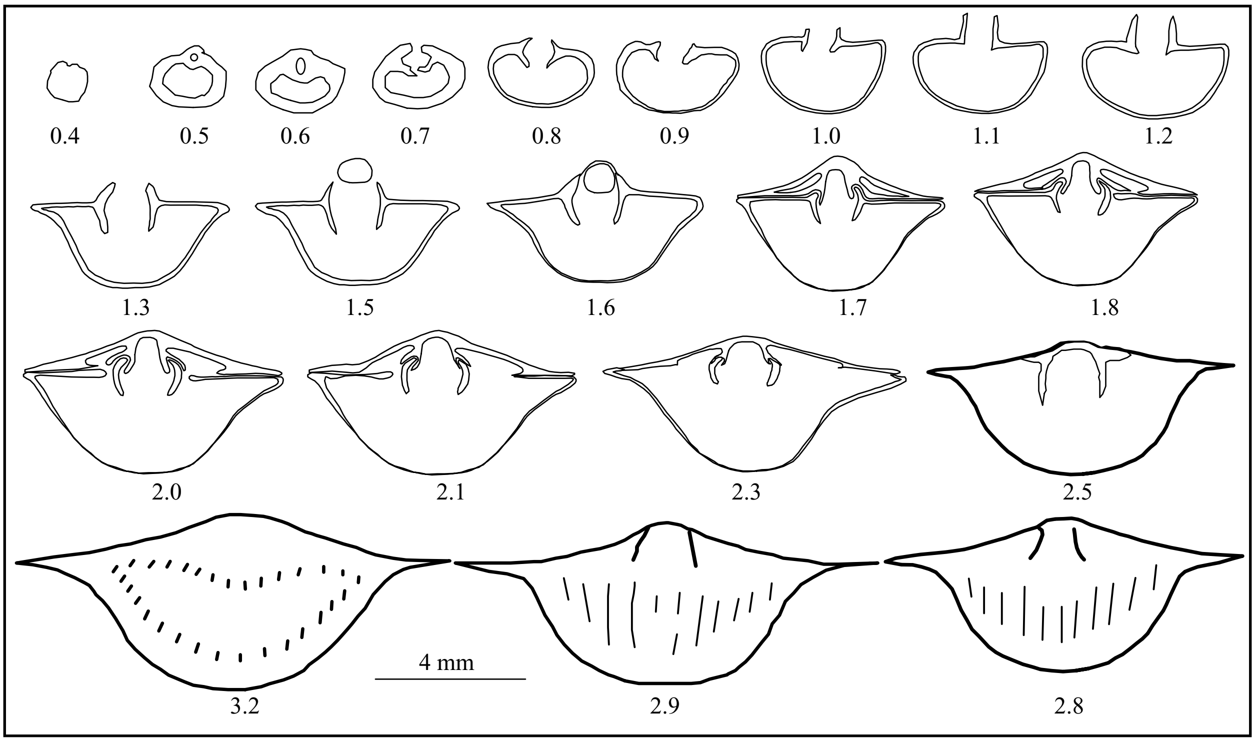


Figure 13. Selected serial sections of *Orbicoelia dolomitensis* n. sp. (based on specimen UWA133477).

specimens, and its dorsal valve is also moderately convex to slightly flattened, like the Italian specimens. However, the examined material is also not suitable for Zhan's species, as they possess much broader and slightly flattened anterior and lateral margins. As a result, these unique features of the described material justify establishment of a new species.

Occurrence. Tesero Horizon of the Werfen Formation (latest Changhsingian), Tesero section of Dolomite, northern Italy.

Order ATHYRIDIDA Boucot, Johnson & Staton, 1964
Suborder ATHYRIDINA Boucot, Johnson & Staton, 1964
Superfamily ATHYRIDOIDEA McCoy, 1844
Family ATHYRIDIDAE McCoy, 1844
Subfamily SPIRIGERELLINAE Grunt, 1965
Genus *Spirigerella* Waagen, 1883

Type species. *Spirigerella derbyi* Oehlert, 1887.

Spirigerella? *teseroi* n. sp.
Figures 14a–e, 15

Etymology. Named for the Tesero section, from which the described specimens were collected.

Material. Three specimens are available for study. Of these, UWA133472–133474 are figured here; UWA133486 is sectioned.

Holotype. UWA133474, 8.4 mm long, 8.2 mm wide and 3.9 mm thick.

Diagnosis. Subcircular athyridid; anterior commissure emarginated to slightly uniplicate; median sulcus broad, distinct; median fold absent.

Description. Medium-sized athyridid; outline subcircular, nearly wide as long; slightly dorsibiconvex in profile; widest at mid-length of shell; foramen round, large; cardinal extremities rounded; anterior commissure emarginated to slightly uniplicate. Ventral valve moderately convex; beak stout, nearly occupied by a large, circular, open foramen; umbo evenly convex with gentle slopes to lateral margins; median sulcus broad, variously developed, originating anterior to umbo, broadening near anterior margin. Dorsal valve evenly convex, with greatest convexity present at umbo; beak strongly incurved, under ventral foramen; median fold absent, lateral slopes gentle. External surfaces smooth except for poorly preserved laminae near anterior margins. Ventral interior teeth small; dental plates thin, slightly close to valve walls but not confused with wall; dorsal interior with undivided cardinal plate; inner socket ridges moderately high (Fig. 15).

Remarks. The overall appearance of the new species recalls several allied genera such as *Araxathyris*, *Composita* and *Spirigerella*. However, *Araxathyris protea* (Abich), type species of *Araxathyris*, possesses a small foramen, a pronounced ventral median sulcus and

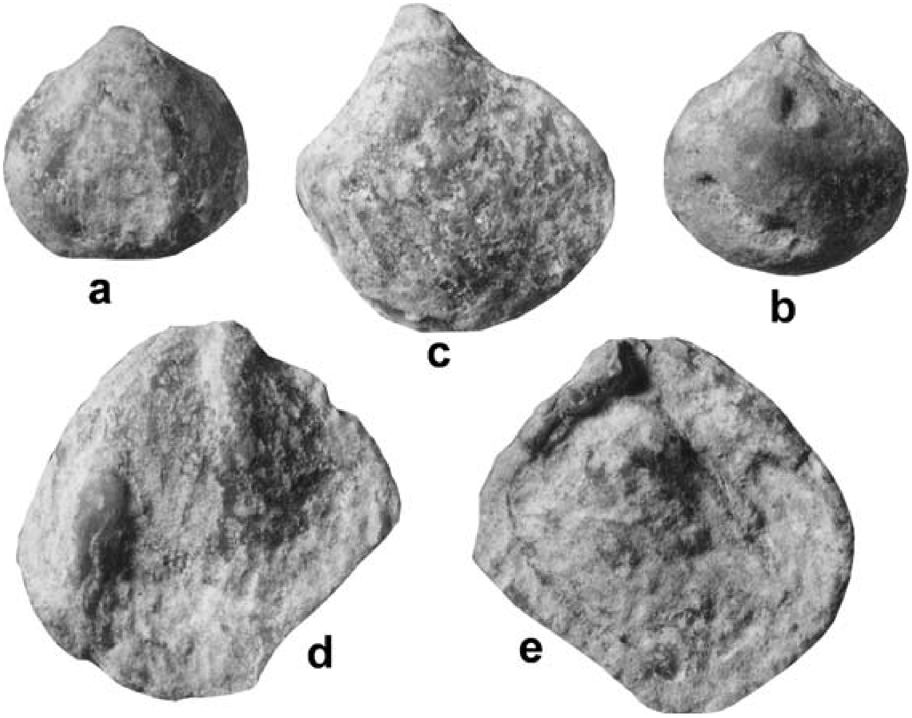


Figure 14. *Spirigerella*? *teseroi* n. sp. from the middle Tesero Member (Werfen Formation) of the Tesero section, Dolomite, northern Italy. (a, b) UWA133474, holotype, a complete specimen in ventral and dorsal views. (c) UWA133472, a crushed specimen in dorsal view. (d, e) UWA133473, a crushed specimen in ventral and dorsal views. (a, b) × 5. Others, × 3.8.

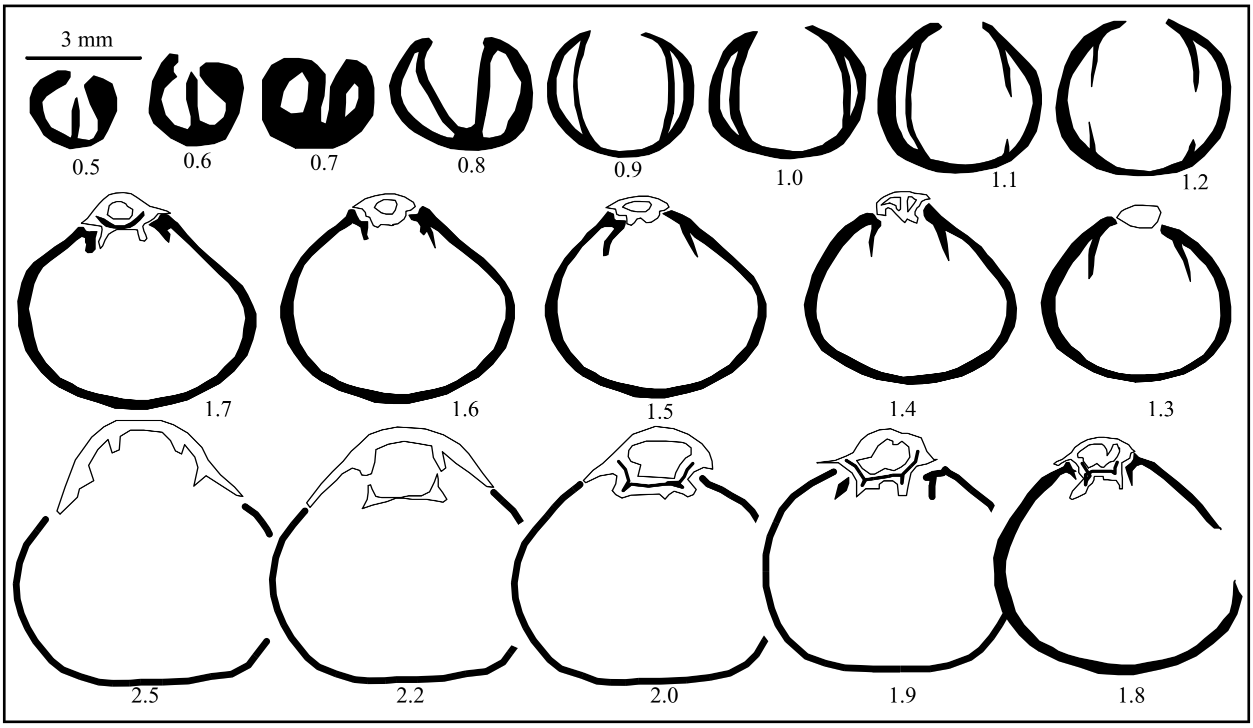


Figure 15. Selected serial sections of *Spirigerella*? *teseroi* n. sp. (based on specimen UWA133486).

a dorsal median fold that tend to flatten and broaden anteriorly, and a parasulcate anterior commissure. In addition, a distinctive median groove is present at the crest of the dorsal median fold of *A. protea*. Internally, *Araxathyris* possesses the dental plates widely separated from the valve walls and a short median ridge in the dorsal valve. Accordingly, *Araxathyris* cannot include the new species.

Compared with *Composita ambiguus* (*sensu* Brunton, 1980; Alvarez & Rong, 2002), type species of the genus *Composita*, the new species is indistinguishable from the latter in having a large, rounded foramen and similar overall appearance. However, *C. ambiguus* is distinguished from the new species by a distinctive ventral median sulcus and a median groove on the dorsal median fold. In addition, the more medially situated dental plates in *Composita* are also noteworthy. As a result, these differences suggest that the new species is excluded from *Composita*.

The true *Spirigerella* species embrace a small foramen and very thin dental plates buried by the secondary materials of the valve walls. Of these, the presence of a foramen in *Spirigerella* remains varied. Grant (1976, p. 204) argued that the beak of some *Spirigerella* specimens is broken so as to resemble a large foramen. The specimens examined appear to have a large foramen. Their poor preservation, however, renders this characteristic unconvincing. On the other hand, the dental plates close to the valve walls of the Tesero materials (Fig. 15) suggest a *Spirigerella* species. As a consequence, the new species is provisionally assigned to *Spirigerella*.

Of the athyridids described by Posenato (2001) from the transitional bed between the Bellerophon and Werfen formations of the Tesero section, a specimen named Spirigerellinae gen. and sp. indet. by Posenato (2001, p. 219, pl. 1, fig. 14) bears close resemblance to our new species in the emarginated anterior commissure and the internal features, and thus may be congeneric with our materials. However, Posenato's specimen differs clearly from the new species in having a much more convex dorsal valve, an indistinct foramen, more pronounced laminae and much thicker cardinal plate. None of the other athyridids from Tesero approaches the new species as these materials have a conspicuous deep median sulcus in both valves.

Occurrence. Tesero Horizon of the Werfen Formation (latest Changhsingian), Tesero section of Dolomite, northern Italy.

Genus *Araxathyris* Grunt, 1965

Type species. *Spirigera protea* Abich, 1878.

Araxathyris? sp.
Figure 16a–c

Material. UWA133475.

Description. Medium size, 9.2 mm long, 9.8 mm wide and 5.4 mm thick; moderately biconvex; outline subpentagonal, slightly wider than long; widest slightly anterior to mid-length of shell; anterior commissure strongly parasulcate; cardinal extremities subangular to rounded. Ventral valve with greatest convexity at umbo; beak strongly incurved; umbo broad, evenly

Figure 16. *Araxathyris*? sp. (a–c) UWA133475, a complete specimen in dorsal, ventral and lateral views. All × 3.8.

convex with gentle slopes to lateral margins; median sulcus originating anterior to umbo, deep, broad and forming conspicuous tongue-shaped extension at anterior margin. Dorsal valve moderately convex; umbo broad; median fold raised anterior to umbo, broad, high near anterior margin, flanked by deep, broad sulci from lateral flanks, bearing trace of a median groove at its crest. External surfaces generally smooth except for few concentric laminae, most pronounced near anterior margins. Internal features of both valves not observed.

Remarks. The external characteristics of the described specimen, in particular the development of a median sulcus and fold, suggest an *Araxathyris* species. When compared with the type species *A. protea* (*sensu* Grunt, 1965, 1980; Alvarez & Rong, 2002), the Tesero material is distinct in the possession of a much smaller size, a shallower, more anteriorly originated ventral median sulcus, and a much shallower median groove on the dorsal median fold. However, the inadequate materials prevent examination of the internal features and thus do not allow a full comparison with other known *Araxathyris* species. As a consequence, a provisional species is applied to the Tesero specimen, and its generic assignment also remains tentative.

Occurrence. Tesero Horizon of the Werfen Formation (latest Changhsingian), Tesero section of Dolomite, northern Italy.

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References

Abich, H. 1878. Geologische forschungen in den Kaukasischen Ländern. Th. 1. *Eine Bergkalkfauna aus der Araxesenge bei Djoulfa in Armenien* **7**, 1–126.

Ager, D. V. 1965. The adaptation of Mesozoic brachiopods to different environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* **1**, 143–72.

Alvarez, F. & Rong, J.Y. 2002. Athyridida. In *Treatise on Invertebrate Paleontology, Part H, revised, Brachiopoda, volume 4: Rhynchoneliforea (part)* (eds A. Williams, C. H. C. Brunton, S. J. Carlson, F. Alvarez, R. B. Blodgett, A. J. Boucot, P. Copper, A. S. Dagys, R. E. Grant, Yu-gan Jin, D. I. Mackinnon, M. O. Mancenido, E. F. Owen, Jia-yu Rong, N. M. Savage and Dong-li Sun), pp. 1475–1604. Lawrence: Geological Society of America and University of Kansas Press.

Assereto, R., Bosellini, A., Fantini Sestini, N. & Sweet, W. C. 1973. The Permian–Triassic boundary in the southern Alps (Italy). In *The Permian and Triassic Systems and their mutual boundary* (eds A. Logan and L. V. Hills), pp. 176–99. *Canadian Society of Petreoleum Geologists, Memoir* **2**.

Boucot, A. J., Johnson, J. G. & Staton, R. D. 1964. On some atrypoid, retzioid, and athyridoid Brachiopoda. *Journal of Paleontology* **38**, 805–22, 4 pls.

Broglio Loriga, B. 1968. Alcune considerazioni su *Lingula tenuissima* Bronn del Werfeniano delle Dolomiti. *Annali dell'Universita di Ferrara, Sezione 9* **4**(12), 189–202.

Broglio Loriga, B., Neri, C. & Posenato, R. 1980. La "*Lingula*" Zone delle Scitico (Triassic Inferiore). *Annali dell'Universita di Ferrara, Sezione 9* **6**(6), 91–130.

Broglio Loriga, B., Neri, C. & Posenato, R. 1986. The early macrofaunas of the Werfen Formation and the Permian–Triassic boundary in the Dolomites (southern Alps, Italy). *Studi Trentini di Scienze Naturali* **62**, 3–18.

Broglio Loriga, B., Neri, C. & Posenato, R. 1988. Marine fossil assemblages from Upper Permian to lowermost Triassic in the western Dolomites (Italy). *Memorie della Società Geologica Italiana* **34**, 5–44.

Bronn, H. G. 1862. *Die Klassen und Ordnungen der Weichthiere (Malacozoa)*, Volume 3(1), 518 pp., 44 pls. Berlin: Leipzig & Heidelberg.

Brunton, C. H. C. 1980. Type specimens of some Upper Palaeozoic Athyridide brachiopods. *Bulletin of the British Museum (Natural History) Geology* **34**(4), 219–34.

Brunton, C. H. C., Lazarev, S. S., Grant, R. E. & Jin Yu-gan. 2000. Productidina. In *Treatise on invertebrate palaeontology, Part H, Brachiopoda, Volume 2–3* (eds A. Williams, C. H. C. Brunton, S. J. Carlson and 44 others), pp. 424–644. Lawrence: Geological Society of America and University of Kansas Press.

Carlson, S. J. 1991. A phylogenetic perspective on articulate brachiopod diversity and the Permo-Triassic extinction. In *The Unity of Evolutionary Biology.*

Proceedings of the 4th International Congress of Systematic and Evolutionary Biology (ed. E. Dudley), pp. 119–42. Portland, Oregon: Dioscorides Press.

Chao, Y. T. 1927. Productidae of China. Part I: Productinae. *Palaeontologica Sinica, Series B* **5**(2), 1–192, 16 pls.

Chao, Y. T. 1928. Productidae of China. Part II: Chonetinae, Productinae and Richthofeninae. *Palaeontologica Sinica, Series B* **5**(3), 1–81, 6 pls.

Chen, J. H. 2004. Macroevolution of Bivalvia after the end-Permian mass extinction in South China. In *Biotic mass extinction and recovery – Evidences from the Palaeozoic and Triassic of South China* (eds J. Y. Rong and Z. J. Fong), pp. 647–700. Heifei: China University of Science and Technology Press.

Chen, Z. Q., Campi, M. J., Shi, G. R. & Kaiho, K. 2005. Post-extinction brachiopod faunas from the Late Permian Wuchiapingian coal series of South China. *Acta Palaeontologica Polonica* **50**(2), 343–63.

Chen, Z. Q., Kaiho, K. & George, A. D. 2005*a*. Survival strategies of brachiopod faunas from the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **224**(1–3), 232–69.

Chen, Z. Q., Kaiho, K. & George, A. D. 2005*b*. Early Triassic recovery of the brachiopod faunas from the end-Permian mass extinction: A global review. *Palaeogeography, Palaeoclimatology, Palaeoecology* **224**(1–3), 270–90.

Chen, Z. Q. & Shi, G. R. 1999. Revision of *Prelissorhynchia* Xu & Grant, 1994 (Brachiopoda) from the Upper Permian of South China. *Proceedings of the Royal Society of Victoria* **111**, 15–26.

Chen, Z. Q., Shi, G. R. & Kaiho, K. 2002. A new genus of rhynchonellid brachiopod from the Lower Triassic of South China and implications for timing the recovery of Brachiopoda after the end-Permian mass extinction. *Palaeontology* **45**, 149–64.

Chen, Z. Q., Shi, G. R. & Kaiho, K. 2004. New ophiuroids from the Permian–Triassic boundary beds of South China. *Palaeontology* **47**, 1301–12.

Chen, Z. Q., Shi, G. R., Shen, S. Z. & Archbold, N. W. 2000. *Tethyochonetes* gen. nov. (Chonetida, Brachiopoda) from the Late Permian of China. *Proceedings of the Royal Society of Victoria* **112**, 1–15.

Chi-Thuan, T. T. 1962. Les brachiopodes permiens de Cam-lô (Province de Quang-Tri). *Annales de la Faculté des Sciences, Université de Saigon* **1962**, 485–98, 2 pls.

Davidson, T. 1866. Notes on the Carboniferous Brachiopoda. *Quarterly Journal of the Geological Society of London* **22**(1), 39–45, 1 pl.

Erwin, D. H. 1993. *The great Paleozoic crisis*. New York: Columbia University Press, 327 pp.

Erwin, D. H. 2001. Lessons from the past: Biotic recoveries from mass extinctions. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 5399–403.

Fantini Sestini, N. 1965. Permian fossils of the Upper Hunza Valley. In *Italian expeditions to the Karakorum (K2) and Hindu Kush. IV* (ed. A. Desio), *Palaeontology, Zoology, Botany* **1**(1), 135–48.

Farabegoli, E. & Perri, M. C. 1998. Stop 4.3 – Permian/Triassic boundary and Early Triassic of the Bulla section (southern Alps, Italy): lithostratigraphy, facies and conodont biostratigraphy. *Giornale di Geologia, ser. 3* **60**, 292–311.

Feng, Ru-lin & Jiang, Zong-long. 1978. Brachiopods. In *Palaeontological Atlas of southwestern China*, pp. 231–305, pls 85–108. Beijing: Geological Publishing House.

George, T. N. 1931. *Ambocoelia* Hall and certain similar British Spiriferidae. *Quarterly Journal of the Geological Society of London* **87**(1), 30–61, pls 3–5.

Goldman, D. & Mitchell, C. E. 1990. Morphology, systematics, and evolution of Middle Devonian Ambocoeliidae (Brachiopoda), western New York. *Journal of Paleontology* **64**, 79–99.

Grant, R. E. 1970. Brachiopods from Permian–Triassic boundary beds and age of Chhidru Formation, West Pakistan. In *Stratigraphic boundary problems: Permian and Triassic of West Pakistan* (eds B. Kummel and C. Teichert), pp. 117–51. University of Kansas, Department of Geology, Special Publication no. 4.

Grant, R. E. 1976. Permian brachiopods from southern Thailand. *Journal of Paleontology* **50**(3), *Paleontological Society, Memoir* **9**, 1–269.

Gray, J. E. 1840. *Synopsis of the Contents of the British Museum, 42nd edition*. London: The British Museum, 370 pp.

Grunt, T. A. 1965. Nadsemeistvo Athyridacea. In *Razvitie i Smena Morskikh Organizmov na Rubezhe Paleozoia i Mezozoia* (eds V. E. Ruzhentsev and T. G. Sarytcheva), pp. 237–54, pls 41–4. *Trudy Academiia Nauk SSSR, Paleontogicheskii Institut* **108**.

Grunt, T. A. 1980. Atiridida Russkoi platformy. *Trudy Academiia Nauk SSSR, Paleontogicheskii Institut* **182**, 1–163, 17 pls.

Hall, J. 1860. Observations on Brachiopoda. *New York State Cabinet of Natural History, Annual Report* **13**, 65–75.

Hallam, A. & Wignall, P. B. 1997. *Mass extinctions and their aftermath*. Oxford: Oxford University Press, 320 pp.

Hayaskaya, I. 1922. Paleozoic brachiopods from Japan, Korea and China. Part 1. Middle and Southern China. *Tohoku Imperial University Science Reports, Series 2 (Geology)* **6**, 1–137.

He, Xi-lin & Shen, Shu-zhong. 1991. Permo-Triassic mixed biota in South China and Permo-Triassic boundary. *Journal of Changchun University of Earth Sciences* **21**(2), 121–9.

Huang, T. K. 1932. Late Permian Brachiopods of Southwestern China. Part 1. *Geological Survey of China, Palaeontologica Sinica, Series B* **9**(1), 138 pp., 9 pls.

Jin, Yu-gan, Liao, Zhu-ting & Hou, Hong-fei. 1974. Permian Brachiopoda. In *Stratigraphical and Palaeontological Handbook of Southwest China* (ed. Nanjing Institute of Geology and Paleontology, Academia Sinica), pp. 308–13. Beijing: Science Press.

Jin, Yu-gan & Sun, Dong-li. 1981. Paleozoic brachiopods from Xizang. *Series of the Scientific Expedition to Qinghai-Xizang Plateau, Palaeontology of Xizang* **3**, 127–76, 12 pls.

Jin, Yu-gan, Wang, Yue, Wang, Wei, Shang, Qing-hua, Cao, Chong-qun & Erwin, D. H. 2000. Pattern of marine mass extinction near the Permian–Triassic boundary in south China. *Science* **289**, 432–6.

Jin, Yu-gan, Xu, Han-kui, Sun, Dong-li & Ye, Song-lin. 1979. Brachiopoda. In *Palaeontological Atlas of northwestern China, Qinghai Volume*, pp. 60–225, pls 18–57. Beijing: Geological Publishing House.

Kaiho, K., Kajiwara, Y., Nakano, T., Miura, Y., Chen, Z. Q. & Shi, G. R. 2001. End-Permian catastrophe by a bolide impact: evidence of a gigantic release of sulfur from the mantle. *Geology* **29**, 815–18.

Kayser, E. 1883. Obercarbonische Fauna von Lo-Ping. In *China 4(8)* (ed. F. von Richthofen), pp. 160–208, pls 19–29. Berlin: D. Reimer.

Kozur, H. 1998. Some aspects of the Permian–Triassic boundary (PTB) and of the possible causes for the biotic crisis around this boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143**, 227–72.

Lazarev, S. S. 1986. Otriad Productida. In *Atlas fauny verkhnego karbona i nizhnei permi Samarskoi Luki* (eds I. S. Muravyev and A. D. Grigor'eva), pp. 91–107. Kazan: Izdatel'stvo Kazanskogo Universiteta.

Li, Ning. 1995. Evolutionary change of bivalves from Changxingian to Griesbachian in South China. *Acta Palaeontologica Sinica* **34**, 350–69, 6 pls.

Liao, Zhuo-Ting. 1979. Brachiopod zones of Changhsingian stage and brachiopod of the mixed fauna in South China. *Journal of Stratigraphy* **3**(3), 200–13.

Liao, Zhuo-Ting. 1980*a*. Brachiopod assemblages from the Upper Permian and Permian–Triassic boundary beds, South China. *Canadian Journal of Earth Sciences* **17**(2), 289–95.

Liao, Zhuo-Ting. 1980*b*. Upper Permian brachiopods from western Guizhou. In *Stratigraphy and palaeontology of Upper Permian coal-bearing formations in western Guizhou and eastern Yunnan, China* (ed. Nanjing Institute of Geology and Palaeontology, Academia Sinica), pp. 241–77, 9 pls. Beijing: Science Press.

Liao, Zhuo-Ting. 1984. New genera and species of Late Permian and earliest Triassic brachiopods from Jiangsu, Zhejiang and Anhui provinces. *Acta Palaeontologica Sinica* **23**, 276–85, 2 pls.

Liao, Zhuo-Ting. 1987. Paleoecological characters and stratigraphic significance of silicified brachiopods of the Upper Permian from Heshan, Laibin, Guangxi. In *Stratigraphy and paleontology of systemic boundaries in China, Permian and Triassic boundary 1* (ed. Nanjing Institute of Geology and Palaeontology, Academia Sinica), pp. 81–125, 8 pls. Nanjing: Nanjing University Press.

Liao, Zhuo-Ting & Xu, Jun-Tao. 2002. Late Permian brachiopods from the lower part of the Wuli Group, southwestern Qinghai and the Geographic distribution of *Waagenites*. *Acta Palaeontologica Sinica* **41**(1), 130–6.

Magaritz, M., Baer, R., Baud, A. & Holser, W. T. 1988. The carbon isotope shift at the Permian–Triassic boundary in the southern Alps is gradual. *Nature* **331**, 337–9.

McCoy, F. 1844. *A synopsis of the characters of the Carboniferous limestone fossils of Ireland*. Dublin: University Press, 207 pp., 29 pls.

Mei, S. L., Zhang, K. X. & Wardlaw, B. R. 1998. A refined succession of Changhsingian and Griesbachian Neogondolellid conodonts from the Meishan section, candidate of the Global Stratotype Section and Point of the Permian–Triassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143**(4), 213–26.

Merla, G. 1930. La fauna del calcare a Bellerophon della regione dolomitica. *Istituto Geologico e Mineralogico della Universita di Padova, Memorie* **9**(2), 1–221, 11 pls.

Muir-Wood, H. M. 1955. *A history of the classification of the Phylum Brachiopoda*. London: British Museum, 124 pp.

Muir-Wood, H. M. 1962. *On the morphology and classification of the brachiopod suborder Chonetoidea*. London: British Museum (Natural History), pp. 1–132, 16 pls.

Muir-Wood, H. M. & Cooper, G. A. 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). *The Geological Society of America Memoir* **81**, 447 pp., 135 pls.

Neri, C., Beretta, C., Cimmino, F. & Radrizzani, S. 1999. Lithology and Sedimentology. In *Stratigraphy and facies of the Permian deposits between eastern Lombardy and the western Dolomites, Field Trip Guidebook* (eds G. Cassinis, L. Cortesogno, L. Gaggero, F. Massari, C. Neri, U. Nicosia and P. Pittau), pp. 90–7. Pavia.

Neri, C. & Pasini, M. 1985. A mixed fauna at the Permian–Triassic boundary, Tesero section, western Dolomites (Italy). *Bollettino della Società Paleontologica Italiana* **23**, 113–17.

Newton, R. J., Pevitt, E. L., Wignall, P. B. & Bottrell, S. H. 2004. Large shifts in the isotopic composition of seawater sulphate across the Permo-Triassic boundary in northern Italy. *Earth and Planetary Science Letters* **218**, 331–45.

Nicora, A. & Perri, M. C. 1999. Conodonts. In *Stratigraphy and facies of the Permian deposits between eastern Lombardy and the western Dolomites, Field Trip Guidebook* (eds G. Cassinis, L. Cortesogno, L. Gaggero, F. Massari, C. Neri, U. Nicosia and P. Pittau), pp. 97–100. Pavia.

Oehlert, D. P. 1887. Brachiopodes. In *Manuel de conchyliologie et de paleontologie conchyliologue, ou historie naturelle des mollusques vivants et fossiles* (ed. P. Fischer), pp. 1189–1334, 15 pls. Paris: F. Savy.

Posenato, R. 1988. The Permian/Triassic boundary in the western Dolomites, Italy: review and proposal. *Annali dell' Universita di Ferrara* **1**(3), 31–45.

Posenato, R. 1998. The gen. *Comelicania* Frech, 1901 (Brachiopoda) from the southern Alps: morphology and classification. *Rivista Italiana di Paleontologia e Stratigraphia* **104**, 43–68.

Posenato, R. 1999. Brachiopods and molluscs. In *Stratigraphy and facies of the Permian deposits between eastern Lombardy and the western Dolomites, Field Trip Guidebook* (eds G. Cassinis, L. Cortesogno, L. Gaggero, F. Massari, C. Neri, U. Nicosia and P. Pittau), pp. 104–9. Pavia.

Posenato, R. 2001. The athyridids of the transitional beds between Bellerophon and Werfen Formations (uppermost Permian, southern Alps, Italy). *Rivista Italiana di Paleontologia e Stratigraphia* **107**, 197–226.

Posenato, R. & Prinoth, H. 1999. Discovery of *Paratirolites* from the Bellerophon Formation (Upper Permian, Dolomites, Italy). *Rivista Italiana di Paleontologia e Stratigraphia* **105**, 129–34.

Rodland, D. L. & Bottjer, D. J. 2001. Biotic recovery from the end-Permian mass extinction: Behavior of the inarticulate brachiopod *Lingula* as a disaster taxon. *Palaios* **16**, 95–101.

Rong, Jia-Yu & Shen, Shu-Zhong. 2002. Comparative analysis of the end-Permian and end-Ordovician brachiopod mass extinctions and survivals in South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* **188**, 25–38.

Sarycheva, T. G. & Sokolskaya, A. V. N. 1959. O klassifikatsin lozhnoporistykh brakhiopod. *Akademiia Nauk SSSR, Doklady* **125**, 181–4.

SCHUCHERT, C. & LEVENE, C. M. 1929. Brachiopoda (Generum et genotyporum index et bibliographia). In *Fossilium Catalogus I: Animalia, Part 42* (ed. J. F. Pomeckj), pp. 1–140. Berlin: W. Junk.

SHEN, SHU-ZHONG & ARCHBOLD, N. W. 2002. Chonetoidea (Brachiopoda) from the Lopingian (Late Permian) of South China. *Alcheringa* **25**, 327–49.

SHEN, SHU-ZHONG, HE, XI-LIN & ZHU, MEI-LI. 1992. Changxingian brachiopods from Zhongliang Hill of Chongqing, Sichuan Province. In *Stratigraphy and palaeontology of oil and gas bearing areas in China 3* (ed. Dao-yuan Gu), pp. 171–96. Beijing: Petroleum Industry Press.

SHEN, SHU-ZHONG, HE, XI-LIN & SHI, G. R. 1995. Biostratigraphy and correlation of several Permian–Triassic boundary sections in southwestern China. *Journal of SE Asian Earth Sciences* **12**, 19–30.

SHENG, JIN-ZHONG, CHEN, CHU-ZHENG, WANG, YI-GONG, RUI, LIN, LIAO, ZHUO-TING, BANDO, Y., ISHII, K., NAKAZAWA, K. & NAKAMURA, K. 1984. Permian–Triassic boundary in middle and Eastern Tethys. *Journal of Faculty Science, Hokkaido University, Series 4* **21**(1), 133–81.

SHI, G. R. & SHEN, SHU-ZHONG. 1998. A Changhsingian (Late Permian) brachiopod fauna from Son La, northwest Vietnam. *Journal of Asian Earth Sciences* **16**, 501–11.

STACHE, G. 1878. Beitraege zur fauna der Bellerophonkalke Suedtirols. *Kaiserlich-Koenigliche Geologische Reichsanstalt, Jahrbuch* **28**(1), 93–168, pls 1–5.

STEHLI, F. G. 1954. Lower Leonardian Brachiopoda of the Sierra Diablo. *American Museum of Natural History, Bulletin* **105**, 257–358, pls 17–27.

TAZAWA, J. 1976. The Permian of Kesennuma, Kitakami Mountains: A preliminary report. *Earth Science, Journal of the Association for Geological Collaboration in Japan* **30**(3), 175–85, 3 pls.

TAZAWA, J. 2002. Late Paleozoic brachiopod faunas of the South Kitakami Belt, northeast Japan, and their paleobiogeographic and tectonic implications. *The Island Arc* **11**, 287–301.

TIEN, BAO-LIN. 1980. *Fossil Atlas of Wangchiazai coal field, Shuicheng County, Guizhou Province*. Beijing: Geological Publishing House, 110 pp.

TONG, ZHENG-XIANG. 1978. Permian and Carboniferous brachiopods. In *Palaeontological Atlas of Southwest China, Sichuan Volume*, pp. 210–67, pls 77–92. Beijing: Geological Publishing House.

TWITCHETT, R. J. 1999. Palaeoenvironments and faunal recovery after the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **154**, 27–37.

TWITCHETT, R. J. & WIGNALL, P. B. 1996. Trace fossils and the aftermath of the Permo-Triassic mass extinction: evidence from northern Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **124**, 137–51.

VEEVERS, J. J. 1959. The type species of *Productella*, *Emanuella*, *Crurithyris*, and *Ambocoelia* (Brachiopoda). *Journal of Paleontology* **33**, 902–8.

WAAGEN, W. H. 1882–1885. Salt Range Fossils: Productus Limestone fossils, Part 4(2–4): Brachiopoda. *Palaeontologica Indica, Series 13* **1**, 329–770, pls 25–86.

WANG, GUO-PING, LIU, QING-ZHAO, JIN, YU-GAN, HU, SHI-ZHONG, LIANG, WEN-PING & LIAO, ZHUO-TING. 1982. Brachiopoda. In *Palaeontological Atlas of Eastern China*, pp. 186–256, pls 74–102. Beijing: Geological Publishing House.

WANG, YI-GONG, CHEN, CHU-ZHENG, RUI, LIN, LIAO, ZHUO-TING & WANG, ZHI-HAO. 1989. A potential global stratotype of Permian–Triassic boundary. In *Developments in Geosciences* (ed. Chinese Academy of Sciences), pp. 221–8. Beijing: Science Press.

WANG, YU. 1955. Phylum Brachiopoda. In *Index Fossils of China, 2*, pp. 109–71. Beijing: Science Press.

WANG, YU. 1956. New species of brachiopods (II). *Scientia Sinica* **4**(3), 387–407, pls 6–10.

WANG, YU, JIN, YU-GAN & FANG, DA-WEI. 1964. *Brachiopod fossils of China*. Beijing: Science Press, 777 pp.

WANG, YU, JIN, YU-GAN & FANG, DA-WEI. 1966. *Brachiopod fossils*. Beijing: Science Press, 702 pp.

WATERHOUSE, J. B. 1983*a*. Permian brachiopods from Pija Member, Senja Formation, in Manang district of Nepal, with new brachiopod genera and species from other regions. *Bulletin of the Indian Geologists' Association* **16**, 111–51.

WATERHOUSE, J. B. 1983*b*. A Late Permian Lyttonid fauna from Northwest Thailand. *University of Queensland, Department of Geology, Papers* **10**(3), 111–53.

WATERHOUSE, J. B. & PIYASIN, S. 1970. Mid-Permian brachiopods from Khao Phrik, Thailand. *Palaeontographica, Abteilung A* **135**, 83–197, 19 pls.

WIGNALL, P. B. & HALLAM, A. 1992. Anoxia as a cause of the Permian/Triassic mass extinction: facies evidence from northern Italy and the western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* **93**, 21–46.

WIGNALL, P. B., KOZUR, H. & HALLAM, A. 1996. On the timing of palaeoenironmental changes at the Permo-Triassic (P/T) boundary using conodont biostratigraphy. *Historical Biology* **12**, 39–62.

WILLIAMS, A., CARLSON, S. J., BRUNTON, C. H. C., HOLMER, L. E. & POPOV, L. 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London, Series B* **351**, 1171–93.

WU, SHUAN-BAO, WEI MING & ZHANG, KE-XING. 1986. Facies changes and controlling factors of the Late Permian Changxing Limestone in the Changxing area. *Geological Review* **32**, 419–25.

XU, GUI-RONG. 1987. Brachiopoda. In *Permian–Triassic boundary stratigraphy and fauna of South China* (eds Zuan-yi Yang, Hong-fu Yin, Shuan-bao Wu, Feng-qing Yang, Mei-hua, Ding and Gui-rong, Xu), pp. 45–53, 154–7, 215–35, 317–26, pls 7–16. Beijing: Geological Publishing House.

XU, GUI-RONG & GRANT, R. E. 1994. Brachiopods near the Permian–Triassic boundary in South China. *Smithsonian Contributions to Paleobiology* **76**, 1–68.

YANG, DE-LI. 1984. Brachiopoda. In *Biostratigraphy of the Yangtze Gorge area, 3, Late Paleozoic Era* (ed. Geological and Mineral Resources Institute of Hubei Province), pp. 203–39. Beijing: Geological Publishing House.

YANG, DE-LI, NI, SHI-ZHAO, CHANG, MEI-LI & ZHAO, RU-XUAN. 1977. Brachiopods. In *Palaeontological Atlas of Central-South China*, pp. 306–470, pls 129–88. Beijing: Geological Publishing House.

YANG, ZUAN-YI, YIN, HONG-FU, WU, SHUAN-BAO, YANG, FENG-QING, DING, MEI-HUA & XU, GUI-RONG. 1987. Permian–Triassic boundary stratigraphy and fauna of South China. *China Ministry of Geological and Mineral Resources, Geology, Memoir, Series 2* **6**, 1–379.

YIN, HONG-FU. 1985. Bivalves near the Permian–Triassic boundary in South China. *Journal of Paleontology* **59**, 572–600.

YIN, HONG-FU & TONG, JIN-NAN. 1998. Multidisciplinary high-resolution correlation of the Permian–Triassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143**(4), 199–212.

YIN, HONG-FU, ZHANG, KE-XIN, TONG, JIN-NAN, YANG, ZUAN-YI & WU, SHUAN-BAO. 2001. The Global Stratotype Section and Point (GSSP) of the Permian–Triassic Boundary. *Episodes* **24**(2), 102–14.

ZENG, YONG, HE, XI-LIN & ZHU, MEI-LI. 1995. *Permian brachiopods and community succession in the Huayin mountains, Sichuan*. Xuzhou: China University of Mineralogy Press, 187 pp.

ZHAN (CHAN), LI-PEI. 1979. Brachiopods. In *The coal-bearing strata and fossils of Late Permian from Guangtung* (eds H. F. Hou, L. P. Zhan and B. W. Chen), pp. 20–30. Beijing: Geological Publishing House.

ZHAN (CHAN), LI-PEI. 1989. Brachiopods. In *Study on the Permo-Triassic biostratigraphy and eventostratigraphy of northern Sichuan and southern Shaanxi* (ed. Z. S. Li), pp. 205–11. *China Ministry of Geological and Mineral Resources, Geology, Memoir, Series 2,* **9**.

ZHANG, KE-XIN. 1995. Late Permian Changhsingian ecostratigraphy of Lower Yangtze region. In *Dongwuan-Indosinian (Late Permian–Middle Triassic) ecostratigraphy of the Yangtze region and its margins* (eds H. F. Yin, M. H. Ding, K. X. Zhang, J. N. Tong, F. Q. Yang and X. L. Lai), pp. 80–95. Beijing: Sciences Press.

ZHANG, SHOU-XING & JIN, YU-GAN. 1976. Late Paleozoic brachiopods from the Mountain Jolmo Lungma Region. In *A report of the scientific expedition in the Mountain Jolmo Lungma Region (1966–58) (Palaeontology) 2* (ed. Nanjing Institute of Geology and Palaeontology, Academia Sinica), pp. 159–270. Beijing: Science Press.

ZHAO, JIN-KE, SHENG, JIN-ZHANG, YAO, ZHAO-QI, LIANG, XI-LU, CHEN, CHU-ZHENG, RUI, LIN & LIAO, ZHUO-TING. 1981. The Changhsingian and Permian–Triassic Boundary of South China. *Bulletin, Nanjing Institute of Geology and Palaeontology, Academia Sinica* **2**, 1–95.

ZHU, TONG. 1990. *Permian coal bearing strata and Palaeobiocoenosis of Fujian*. Beijing: Geological Publishing House, 127 pp., 47 pls.

ZIEGLER, A. M., GIBBS, M. T. & HULVER, M. L. 1998. A mini-atlas of oceanic water masses in the Permian period. *Proceedings of the Royal Society of Victoria* **110**, 323–44.