The Anisian (Middle Triassic) brachiopod fauna from Qingyan, Guizhou, southwestern China

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Abstract

Like most of the benthos, brachiopods suffered huge losses in biodiversity during the end-Permian extinction and did not fully recover until the Anisian (Middle Triassic). Anisian brachiopod faunas are thus a key clade characterizing the recovered marine ecosystems in the early Mesozoic. Of these, the brachiopod fauna from Qingyan Town in Guizhou Province, southwestern China has long been one of the best-known Anisian faunas in the world. The taxonomy of the Qingyan fauna, however, was last studied half century ago, and thus requires revision. Here we describe 34 species (and subspecies) (including seven undetermined species) assigned to 29 brachiopod genera from the Qingyan Formation from the Leidapo and Wachangpo localities in the Qingyan section. Of these, 11 species are described for the first time from this area. Two new genera: *Parabrekia* and *Caucasorhynchella* (= *Crurirhynchella* Xu & Liu, 1983, a *nomen nudum*) and seven new species (*Angustothyris dagysi*, *Angustothyris qingyanensis*, *Koeveskallina bifurcata*, *Neocyrtina xui*, *Nudirostralina minuta*, *Parabrekia yangi*, and *Rutorhynchia*? *trigonalis*) are also erected. The Qingyan brachiopod fauna is characterized by abundant endemic genera (33.3%) and exhibits a weak similarity with several coeval faunas reported from the western Tethys. In addition, faunal affinity analyses of 13 Anisian brachiopod faunas, overall, indicate that, at least, five biogeographical provinces: western Tethys, eastern Tethys, northern Siberia, Himalayas, and New Zealand were present during the Anisian, and the eastern Tethys province included three subprovinces: Yangtze, southern Qilian-western Qinling, and central Qinghai. However, most faunas mutually share rather low Jaccard similarity coefficients (< 0.4), except for those in the western Tethys, implying a continuity of the multi-provincial pattern established for Early Triassic brachiopod distributions.

Keywords: Brachiopoda; Middle Triassic; recovery; taxonomy; biogeography; South China

Introduction

Brachiopods suffered dramatic losses in biodiversity during the Permian–Triassic mass extinction (Sepkoski 1984; Carlson 1991; Sun & Shen 2004; Chen *et al.* 2005a, 2006; J. Chen *et al*. 2011; Ke & Zeng 2016). This clade experienced a rather slow but steady recovery in the Early Triassic and did not recover fully until the Anisian (early Middle Triassic) (Chen *et al.* 2005b, 2006; J. Chen *et al.* 2015; Ke & Zeng 2016). The Anisian brachiopods are thus the key to our understanding of the brachiopod recovery and subsequent radiation. Of these, the Qingyan section of Guizhou Province, southwestern China is one of the most classic and important Anisian (early Middle Triassic) fossil localities, worldwide. A total of more than 300 species belonging to 17 fossil groups: bivalves, brachiopods, gastropods, ammonoids, corals, crinoids, echinoids, nautiloids, ostracods, scaphopods, annelids, bryozoans, cnidarians, foraminifers, conodonts, sponges, and calcareous algae have been described from this locality since the 1900s (Koken 1900; Hsu & Chen 1943; Wang 1955a, b; Wang *et al.* 1964; Yang & Xu 1966; Feng & Jiang 1978; Gan & Yin 1978; Liao 1978; Kristan-Tollmann 1983a, b; Yin & Yochelson 1983a, b, c; Deng & Kong 1984, 2005; He 1984; Qi 1984; Qi & Stanley 1989; Stiller 1995, 1997, 1998, 1999, 2000, 2001a, b; Komatsu *et al.* 2004; Yao *et al.* 2004; Stiller & Chen 2004, 2006; Deng 2006; Stiller & Bucher 2008; Wu *et al.* 2008; J. Chen *et al.* 2010a; Ji *et al.* 2011; Song *et al.* 2015; Chen *et al*. 2018). The Qingyan fauna has become an important window on the recovery of marine ecosystems (Chen *et al.* 2010a, 2019; Chen & Benton 2012; Dineen *et al.* 2015).

Although important representatives of the Palaeozoic evolutionary fauna (Sepkoski 1984), brachiopods are still abundant and are one of major components of the Qingyan fauna. The Middle Triassic brachiopods from Qingyan were first described by Koken (1900), who reported two species, ‘*Retzia*’ *fuchsi* and ‘*Rhynchonella*’ *sinensis*. Later, several brachiopod species have been briefly described or listed in the literature (Hsu & Chen 1943; Wang 1955a, b; Wang *et al.* 1964). The Qingyan brachiopods were not systematically described until 1966 when Yang & Xu described 29 species (and subspecies) assigned to 23 genera from the Qingyan area (Chen *et al*. 2018). However, the taxonomy of the Qingyan brachiopod fauna has not been updated since then, although Stiller (1999) subsequently reported one new species, '*Neoretzia*' *wachangpoensis* from Qingyan and J. Chen *et al.* (2010a, b) also reported *Madoia* sp., *Costinorella* sp., and *Sinucosta* sp. from the Qingyan Formation in the same area. These taxa, however, also require proper description to ratify or revise taxonomic identifications. Accordingly, the Qingyan brachiopod fauna requires substantial taxonomic revision in order to present accurate and correct taxonomic information for the reconstruction and understanding of faunal recovery patterns and processes following the end-Permian mass extinction.

This paper systematically describes Anisian brachiopods based on more than 5300 specimens collected from two fossil localities in the Qingyan area, Guizhou Province, southwestern China (Fig. 1). Faunal composition is also analyzed and their affinities with coeval faunas from around the world are quantitatively evaluated based on the Jaccard coefficient, which also allows recognition of the palaeobiogeographical patterns amongst the recovering brachiopod faunas during the early Middle Triassic.

Geological setting

The brachiopods were collected from two major fossil localities: Leidapo (also named Fossil Hill and Bangtoupo in some literature; 26°20′22″ N, 106°41′37″ E) and Wachangpo (26°20′16″ N, 106°41′40″ E), in the vicinity of Qingyan Town (Fig. 1C), ~30 km south of Guiyang City, the capital of Guizhou Province (Fig. 1A, B). The Qingyan area was situated in the large ramp zone between the Upper Yangtze Platform in the north and deeper part of the Nanpanjiang Basin in the south (Enos *et al.* 1997, 2006; Huang *et al.* 2017). The Middle Triassic strata in Qingyan are usually assigned to the Qingyan Formation, which is subdivided into five members: Xiaoshan, Mafengpo, Yingshangpo, Leidapo, and Yuqing members in ascending order (Fig. 2). Both the Leidapo and Wachangpo localities are lithologically dominated by thinly-bedded, more or less marly and mostly slightly silty mudstones, interbedded with thin marls to argillaceous limestone (Stiller 1997; J. Chen *et al.* 2010a). These strata are assigned to the middle part of the Leidapo Member (Stiller & Chen 2006; Fig. 2). Stiller & Bucher (2008) placed the middle/upper Anisian boundary in the middle part of the Leidapo Member at Leidapo locality based on the first occurrence of ammonoid *Billingsites cordeyi* Subzone (or *Rieppelites cimeganus* Zone). Besides, the strata exposed at Wachangpo locality are slightly lower than that of Leidapo locality. Therefore, the brachiopods described here are from the Leidapo Member and of latest middle Anisian to earliest late Anisian in age (Stiller & Bucher 2008).

Material and analytical methods

More than 5300 brachiopod specimens were collected from the Leidapo and Wachangpo localities in Qingyan. Most specimens are preserved in the calcareous intercalations, and are naturally weathered out from the rock. All the brachiopod specimens found were collected, including those broken, deformed, disarticulated, and complete shells. The associated bivalves, gastropods, and crinoids were also collected. Rarefaction analysis is employed to evaluate sampling adequacy; the rarefaction trajectories exhibit banana-shaped patterns, indicating the sufficiency of the collections (see also Chen *et al.* 2010b; Fig. 3).

Brachiopod specimens were photographed in visible light following coating with a thin layer of magnesium oxide. Their morphologies were observed based on external and internal features recorded on external surfaces and excavated interiors as well as those revealed based on serial sections made through the specimens. All serial sections were photographed, and then traced using computing software.

Comparison of the faunal affinities and palaeobiogeography of the global Anisian brachiopods were accomplished using cluster and principal coordinates analysis (PCOa) with the Jaccard coefficient (Jaccard 1901). Except for the updated Qingyan fauna, other Anisian faunas were taxonomically assessed based on mainly original descriptions, illustrations, and some new taxonomic opinions before inclusion in the quantitative analyses. The raw data were transformed to binary data matrices with presence (1) or absence (0) of named genera. All calculations were executed using the Palaeontological Analysis Software Package (PAST; Hammer *et al.* 2001).

All the specimens described in this paper are housed in the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan), Wuhan, China, with the prefixes BGEG LDP for the specimens collected from the Leidapo locality and BGEG WCP for those from the Wachangpo locality.

Systematic palaeontology

The classification of the Brachiopoda adopted herein follows the revised Treatise on Invertebrate Paleontology, Part H (Williams *et al.* 2002, 2006), with the exception of the genera *Koeveskallina* and *Qingyenia* which follow Dagys (1996). Unless otherwise stated the occurrences are in the Anisian Stage. Measurements of registered specimens are provided in Supplementary Tables S1−S22.

Order **Rhynchonellida** Kuhn, 1949

Superfamily **Wellerelloidea** Licharew in Rzhonsnitskaia, 1956

Family **Allorhynchidae** Cooper & Grant, 1976

Genus *Caucasorhynchella* gen. nov.

1983 *Crurirhynchella* Xu & Liu: 83.

2002 *Crurirhynchella* Xu & Liu; Manceñido & Owen: 1376.

2017 *Crurirhynchella* Xu & Liu; Sun *et al.*: 900.

Type species. *Crurirhynchia subfissicostata* Yang & Xu, 1966.

Diagnosis. Medium-sized allorhynchid genus; foramen mesothyrid; deltidial plates disjunct. Costae radiating from umbo, occasionally bifurcating or intercalating. Dental plates short; hinge teeth denticulated; dorsal median septum short; septalium absent; crura short, horizontal and flat initially, becoming triangular and concave dorsally, distally bladelike, gently curved ventrally, nearly raduliform.

Etymology. *Caucasorhynchia*, a brachiopod genus, *ella* (Latin), small.

Remarks. The genus *Crurirhynchella* Xu & Liu, 1983 first occurred on a taxonomic list in Xu & Liu's (1983, p. 83) monograph. These authors questioned the generic assignment of *Crurirhynchia subfissicostata* Yang & Xu, 1966 from the Middle Triassic Qingyan Formation of Qingyan, Guizhou, and considered that the Qingyan species should be excluded from *Crurirhynchia* Dagys, 1961 due to the absence of a dorsal septalium (Xu & Liu, 1983). Moreover, Xu & Liu (1983) re-assigned the *subfissicostata* species to their new genus *Crurirhynchella*, but failed to provide a detailed diagnosis and description for the new genus. *Crurirhynchella* therefore is a *nomen nudum* (Manceñido & Owen 2002). Recently, Sun *et al.* (2017) documented descriptive characteristics of *Crurirhynchia subfissicostata* by Yang & Xu (1966), and gave a generic diagnosis for *Crurirhynchella* Xu & Liu, 1983, but these authors also agreed with Manceñido & Owen (2002) that *Crurirhynchella* Xu & Liu, 1983 should be abandoned and treated as an unavailable generic name (Sun *et al.* 2017, p. 888).

The newly obtained specimens of the *subfissicostata* species from its type locality in Qingyan indicate that the Qingyan species cannot be assigned to any known genera and represents a new genus. Consequently, we propose *Caucasorhynchella* gen. nov., instead of *Crurirhynchella*, to accommodate the *subfissicostata* species. This new genus is closely allied to *Caucasorhynchia* in shape and ornamentation, but differs from the latter externally in having simpler costae, an obviously mesothyrid foramen, and disjunct deltidial plates. They both have short and gently ventrally curved crura, however, the shape of crura are quite different. The crura of *Caucasorhynchella* are triangular and concave dorsally in section, with bladelike distal ends, in contrast to the typically hamiform crura of *Caucasorhynchia* (Fig. 4). *Crurirhynchia* Dagys, 1961 differs from this genus in its hypothyrid foramen, conjunct deltidial plates, simpler costae, and, most importantly, its septiform crura.

Caucasorhynchella subfissicostata (Yang & Xu, 1966)
(Figs 5A–I, 6)

1966 *Crurirhynchia subfissicostata* Yang & Xu: 27, pl. 3, figs 4–6.
1978 *Crurirhynchia subfissicostata* Yang & Xu; Feng & Jiang: 274, pl. 101, fig. 9.
1983 *Crurirhynchella subfissicostata* (Yang & Xu); Xu & Liu: 83.
?1992 *Crurirhynchia subfissicostata* Yang & Xu; Xu: 148, pl. 3, figs 5, 6.

Material. More than 350 articulated shells from Wachangpo. Registered specimens: BGEG WCP10032–10050.

Occurrence. Qingyan, Guizhou, southwestern China; ?Dangchang, western Qinling (Gansu), western China.

Description. Shell medium in size, 10–19 mm wide, 10–15 mm long (Table S1), transversely triangular in outline; anterior commissure uniplicate, lateral margins semicircular; both valves gently to moderately convex; thickest and widest at about midlength or slightly anterior to midlength.

Ventral valve slightly convex in lateral profile; beak short, gently to moderately curved; beak ridges rounded; foramen subcircular, small to large, mesothyrid; delthyrium small or not seen because of the curved beak; deltidial plates disjunct; sulcus shallow and broad, developing from midlength, equal to half to one-third of shell width at anterior margin; sulcus with slopes gently inclined, merging with lateral areas. Dorsal valve more convex than ventral valve; weak median depression developed near umbo; fold broad, more distinct at anterior part of shell. Shell ornamented by rounded costae; costae moderately coarse, radiating from beak, some bifurcating and intercalating near the beak; number of costae ranging from 12 to 20 on both valves.

Ventral interior lacking pedicle collar; hinge teeth strong and denticulated; dental plates strong but short, connected to floor posteriorly. Dorsal interior with short and low median septum, sometimes connected to dorsal walls and hinge plates near beak, but not forming a real septalium; hinge plates discrete, flat; crura short, flat and horizontal incipiently, becoming triangular in section and concave dorsally, distally bladelike, nearly raduliform (Fig. 6).

Remarks. Our specimens agree well with those described as *Crurirhynchia subfissicostata* by Yang & Xu (1966) in outline, ornamentation, and in the development of the fold and sulcus. The internal characteristics of this species were not studied in detail by Yang & Xu (1966) due to insufficient specimens. Yang & Xu (1966, p. 27) noted in the Chinese version of the monograph that this species possibly has a pedicle collar, but in the English summary (Yang & Xu 1996, p. 100), these authors stated that the pedicle collar is apparently present. The serial sections shown by Yang & Xu and our new materials, however, show that no pedicle collar occurs in the ventral valve (Fig. 6).

Many species of *Caucasorhynchia* described from the Upper Triassic of China embrace a closed delthyrium and allegedly hamiform crura (Jin *et al.* 1979; 1985). Perhaps, some can be assigned to *Caucasorhynchella* if their external and internal characteristics are better understood. '*Caucasorhynchia*' *zhidoensis* Jin, Sun & Ye in Jin *et al.* (1979, p. 137, pl. 38, figs 1–7) has initially horizontal and flat crura, which are close to that of this species, but it possesses a covered delthyrium.

Genus ***Septaliphorioidea*** Yang & Xu, 1966

Type species. *Septaliphorioidea paucicostata* Yang & Xu, 1966.

Septaliphorioidea paucicostata Yang & Xu, 1966
(Fig. 5J–S)

1966 *Septaliphorioidea paucicostata* Yang & Xu: 30, pl. 3, figs 7–9, pl. 4, figs 1–4.
1978 *Septaliphorioidea paucicostata* Yang & Xu; Feng & Jiang: 277, pl. 101, fig.

16.

Material. One hundred and sixty-two articulated shells and two ventral valves from Leidapo; 20 articulated shells from Wachangpo. Registered specimens: BGEG LDP10010–10019, BGEG WCP10051, WCP10052.

Occurrence. Qingyan, Guizhou, southwestern China.

Description. Shell small, 6–10 mm wide (Table S2), roundly triangular to pentagonal in outline, length slightly less than width; maximum width located at midlength or anteriorly; profile biconvex, depressed; posterolateral margins straight to gently curved, anterolateral margins semicircular; anterior commissure uniplicate. Ventral valve gently convex with anterior part flattened; beak small, straight to slightly curved; foramen small; deltidial plates narrow; sulcus well-defined, commencing from beak, widening and deepening anteriorly until at anterior margin it equals about one-third of shell width; tongue with truncated margin. Dorsal valve slightly convex; median fold beginning at beak with flat top, truncated at front. Shell covered by coarse plicae, subangular to rounded, radiating from beak, bifurcating on dorsal and intercalating on ventral; one to three within sulcus, two to four on fold and three to four on each lateral flank. Growth lines and lamellae developed near anterior commissure.

Remarks. Yang & Xu (1966) divided this species into three forms, based on the number of plicae within the ventral sulcus. The form I is the most abundant in our collection, which has only one plica in the sulcus. '*Septaliphorioidea*' *multicostata* Jin & Sun in Jin *et al.* (1976, p. 298, pl. 4, figs 7–11) from the Middle Triassic of Nyalam has a median septum and septalium, should be assigned elsewhere.

Superfamily **Rhynchonelloidea** d'Orbigny, 1847

Family **Rhynchonellidae** d'Orbigny, 1847

Subfamily **Piarorhynchiinae** Shi & Grant, 1993

Genus ***Rutorhynchia*** Sun, 1981

Type species. *Rutorhynchia jieshanensis* Sun, 1981.

Rutorhynchia*? *trigonalis sp. nov.

(Figs 5T–Y, 7)

Diagnosis. Shell very small, elongately subtrigonal in outline, equibiconvex; sulcus and fold low and ill defined. Ventral beak acute and suberect; beak ridges rounded; foramen small, hypothyrid. Few rounded plicae beginning at midlength of shell, sometimes bifurcating. Dental plates short and thin; lateral umbonal chambers small. Dorsal interior lacking septalium; median septum low, trigonal in section; hinge plates discrete; crura short, curved ventrally.

Etymology. Refers to the trigonal outline.

Material. Three articulated shells (BGEG LDP10020–10022) from Leidapo. One articulated shell (BGEG LDP10020) is designated herein as holotype, one deformed articulated shell (BGEG LDP10022) is selected herein as a paratype.

Occurrence. Leidapo locality, Qingyan, Guizhou, southwestern China.

Description. Shell very small, length less than 7 mm, width less than 6 mm (Table S3), subtrigonal in outline, maximum width anterior to midlength, greatest thickness at midlength, equibiconvex; anterior commissure weakly uniplicate.

Ventral valve moderately convex in lateral profile; beak pointed and suberect, ridges rounded; foramen small, hypothyrid; sulcus commencing from midlength of shell, shallow and ill defined, bounded by two plicae. Dorsal valve moderately convex; fold absent or very weak. Few rounded plicae near anterior margin, commencing from midlength, sometimes bifurcating once anteriorly, numbering five to six near anterior margin; comarginal growth lines fine, more distinct near margin.

Pedicle collar not observed; dental plates thin and short, ventrally divergent; lateral umbonal chambers small. Septalium absent; median septum low but strong, trigonal in section; hinge plates discrete and horizontal; crura short, curved ventrally (Fig. 7).

Remarks. A combination of the trigonal outline, biconvex shell, rounded plicae anteriorly, low dorsal median septum, and discrete hinge plates places the Qingyan materials close to *R. jieshanensis* Sun (1981, p. 202, pl. 4, figs 29–44) from the Upper Jurassic of Ngari, Xizang (Tibet), China, the type species of *Rutorhynchia* Sun, 1981. However, the Tibetan species possess a much larger size, a more strongly convex profile, and a better-developed sulcus, and thus cannot accommodate the Qingyan specimens. Accordingly, we propose herein a new species, *trigonalis* sp. nov. for these Qingyan specimens, and the new species is also tentatively assigned to the Jurassic genus *Rutorhynchia*.

Another new species *Nudirostralina minuta* sp. nov. described below is closely allied to the *trigonalis* species in outline and ornamentation, but the former has a larger size, a deeper sulcus, weaker plicae externally, and a distinct septalium internally. *Lissorhynchia pygmaea* Yang & Xu (1966, p. 14, pl. 1, figs 1, 2) also from Qingyan is distinguished from the new species in having a wider outline, a rudimentary dorsal median septum and undivided hinge plates. *Lissorhynchia*? *triloba* Yang & Xu (1966, p. 16, pl. 1, fig. 3) also has similar size and outline to the new species, from which the former differs clearly in having a strongly uniplicate anterior commissure and two grooves near the dorsal fold.

Superfamily **Norelloidea** Ager, 1959

Family **Norellidae** Ager, 1959

Subfamily **Holcorhynchellinae** Dagys, 1974

Genus ***Nudirostralina*** Yang & Xu, 1966

Type species. *Nudirostralina subtrinodosi* Yang & Xu, 1966.

Remarks. *Nudirostralina* is one of the most common genera in the Middle Triassic of China (Jin *et al.* 1979), but was never described in detail from outside China until 2018 when Gaetani *et al.* described a species from the Middle Triassic succession of the Socotra Island of Yemen. In contrast, *Piarorhynchella* Dagys, 1974 has been widely reported from the Lower and Middle Triassic all over the world except China. It should be noted that '*Piarorhynchia*' *gujiaoensis* Feng in Feng & Jiang (1978) from the Lower Triassic of Gujiao, Guizhou, southwestern China was tentatively assigned to *Piarorhynchella* by Chen *et al.* (2005) and Wang *et al.* (2017), but was assigned to *Abrekia* Dagys, 1974 by Sun & Shen (2004). In fact, in terms of its depressed shell and weak plicae, it is more similar to *Abrekia* than *Piarorhynchella*. *Nudirostralina* and *Piarorhynchella* are so close to each other in both external appearance and internal structures that *Piarorhynchella* was treated as a junior synonym of *Nudirostralina* by Jin *et al.* (1979).

After comparing the original descriptions of the two genera, we found that the only one distinct difference is that *Nudirostralina* has gently curved crura, while

Piarorhynchella possesses sharply curved and calcariform crura. Our new material of the type species of *Nudirostralina* shows that the crura of this genus are moderately to strongly curved ventrally, which agrees with those of *Piarorhynchella*. Besides, its crura are dorsally concave and close to canaliform crura (Fig. 9A). But sometimes the concavity of crura is weakened anteriorly so that the crura are calcariform (Fig. 9B). In summary, the crura of *Nudirostralina* are moderately to strongly curved ventrally, variably dorsally concave and calcariform or canaliform. *Piarorhynchella* and *Nudirostralina* are virtually identical, and thus the former should be regarded as a junior synonym.

Nudirostralina subtrinodosi Yang & Xu, 1966

(Figs 5Z–C', 8A–D, 9A, B)

?1965 *Rhynchonella trinodosi* Bittner; Ding: 271, pl. 4, figs 1, 2.

1966 *Nudirostralina subtrinodosi* Yang & Xu: 22, pl. 2, figs 1–4.

1978 *Nudirostralina subtrinodosi* Yang & Xu; Feng & Jiang: 276, pl. 101. fig. 13.

Material. About 90 articulated specimens from Leidapo, mostly deformed. Registered specimens: BGEG LDP10031–10045.

Occurrence. Qingyan and Yangpu, Guizhou, southwestern China; Tianjun, southern Qilian Mountains (Qinghai), western China. This species is also present in the Olenekian (Lower Triassic) of Tulong, Xizang (Chen 1983), but the Tibetan material is significantly different from the Qingyan species (see below).

Description. Shell medium to large in size, 9–15 mm in width (Table S4), subtrigonal to subpentagonal in outline, normally wider than long, dorsibiconvex; anterior margin uniplicate; widest at midlength or anterior to it. Ventral valve moderately convex at umbonal area; beak small, suberect to gently curved; beak ridges rounded; delthyrium small; deltidial plates disjunct; foramen small, submesothyrid to hypothyrid; sulcus originating from posterior half of shell to about midlength of shell, widening and deepening rapidly; lateral flanks gently convex; plicae commencing from posterior half to anterior half of shell, subangular, one to two in sulcus, two to three pairs on lateral flanks. Dorsal valve strongly convex, with a shallow depression near umbo; lateral slopes inclined rapidly; fold high, bearing two to three plicae. Fine growth lines and lamellae near anterior margin.

Ventral interior lacking pedicle collar; dental plates short, slightly divergent ventrally. Dorsal hinge plates disconnected and flat, merged with median septum; septalium V-shaped, shallow to deep, narrow to wide; median septum long, low to high, extending to anterior half of dorsal valve; crural bases subtriangular in section; crura moderately to strongly curved ventrally, variably concave dorsally, canaliform or calcariform (Fig. 9A, B).

Remarks. Chen (1983, pl. 1, fig. 2) described *N. subtrinodosi* from the Olenekian (Lower Triassic) of Tulong, Xizang (Tibet). The Tibetan specimen, however, possesses a thin shell, a slightly shallower ventral sulcus, and very short plicae, and thus cannot be assigned to the Qingyan species.

Both the length and strength of plicae are the two key features to distinguish various species within *Nudirostralina*. However, the plicae are usually variable even on the specimens collected from the same locality. Thus, other criteria such as outline and shell convexity are also important for distinguishing various species within this genus.

Nudirostralina trinodosi (Bittner, 1890, p. 13, pl. 32, figs 17–28) differs from the Qingyan species in having much weaker lateral plicae (Yang & Xu 1966). *N. mutabilis* (Stoliczka, 1866) from Spiti, India (Stoliczka 1866, p. 40, pl. 3, figs 6–9; refigured by Bittner 1899, p. 15, pl. 2, figs 11–13) and Socotra, Yemen (Gaetani *et al.* 2018, p. 252, figs 5A–F, 6) has long plicae starting at about shell midlength, which is quite similar to that of *N. subtrinodosi*. But, possibly *N. subtrinodosi* can be distinguished from the former in having angular plicae. The wide pentagonal species, *N. tenuicostata* Jin, Sun & Ye in Jin *et al.* (1979, p. 144, pl. 39, figs 43–46) can be differentiated from the *subtrinodosi* species in having relatively weaker plicae and a shallower sulcus. *Nudirostralina mangyshlakensis* (Dagys, 1974, p. 112, pl. 32, figs 8–10), the type species of *Piarorhynchella* (a junior synonym of *Nudirostralina*), can be discriminated from *N. subtrinodosi* in its much weaker and rounded plicae anteriorly.

Nudirostralina subtrinodosi multicostata Yang & Xu, 1966

(Fig. 8E–H)

1966 *Nudirostralina subtrinodosi multicostata* Yang & Xu: 24, pl. 2, figs 5, 6.

1978 *Nudirostralina subtrinodosi multicostata* Yang & Xu; Feng & Jiang: 276, pl. 101, fig. 14.

Material. One complete shell (BGEG LDP10046, 11.5 mm wide, 9.8 mm long) and one deformed articulated shell from Leidapo.

Occurrence. Qingyan, Guizhou, southwestern China.

Remarks. This subspecies differs from *Nudirostralina subtrinodosi subtrinodosi* in having more plicae anteriorly. *N. dieneri* (Bittner, 1899, p. 14, pl. 2, figs 8, 9) from Spiti, India has shorter plicae and thus is not confused with the present subspecies. The anterior margin of *N. tazawai* (Popov *in* Popov & Zakharov, 2017, p. 737, pl. 5, figs 1–7) from the Lower Triassic of South Primorye is also marked by dense plicae, but the Russian species commonly has an elongate outline.

Nudirostralina minuta sp. nov.

(Figs 8I–Q, 11)

Diagnosis. Small for genus, with subpentagonal outline, slightly longer than wide; umbonal angle of about 90°; sulcus beginning from anterior half of shell, deep; plicae numbering one in sulcus, strong but quite short, one to two on each lateral side, weaker than the median one; dorsal median septum high.

Etymology. *Minuta* (Latin), small, referring its small size.

Material. Four articulated shells (BGEG LDP10047–10050) from Leidapo. One articulated specimen (BGEG LDP10047) is designated as holotype and one articulated specimen (BGEG LDP10049) is selected as a paratype.

Occurrence. Leidapo locality, Qingyan, Guizhou, southwestern China.

Description. Small for genus, width less than 7 mm (Table S5), subpentagonal or subtrigonal in outline, umbonal angle about 90 degrees, slightly longer than wide, widest at midlength or slightly anterior to it; strongly biconvex; anterior commissure sulciplicate.

Ventral valve strongly convex near umbo; beak small and acute, slightly curved; deltidial plates small; foramen small, submesothyrid; sulcus deep, beginning from the central part of shell, equal to one-third of shell width at anterior margin; lateral slopes gently convex; shell smooth posteriorly, with few plicae anteriorly and laterally; plicae numbering one in sulcus, strong but short, one to two on each lateral side, much weaker than that within sulcus. Dorsal valve convex posteriorly with median region flat to slightly concave; lateral slopes strongly inclined; plicae short, numbering two on fold and two on each lateral slope. Fine growth lines developed near anterior margin.

Ventral interior with stout hinge teeth and dental plates; dental plates subparallel and short; median septum absent. Dorsal median septum high, about 2mm long, supporting a shallow and V-shaped septalium; crura short, ventrally curved (Fig. 11).

Remarks. Some specimens having very small size, longer than wide outline, and relatively weak plicae are pronounced in the Qingyan collections, and they are readily different from two known species/subspecies: *N. subtrinodosi* Yang & Xu, 1966 and *N. subtrinodosi multicostata* Yang & Xu, 1966 that are also described from the same section. A new species therefore is erected herein to accommodate these new data. The new species *N. minuta* sp. nov. also resembles *N. lissosinus* Xu & Liu (1983, p. 89, pl. 2, figs 3a–3e) from the Middle Triassic Junzihe Formation, Qinghai in relatively elongate outline and weak plicae, but the latter clearly differs from the new species in having a smooth sulcus and larger size.

Jin, Sun & Ye (in Jin *et al.* 1979) established two species *N. tenuicostata* and *N. longa* from the Middle Triassic of Qinghai. The former is wider than long and thus obviously different from the new species, while the latter shows similar outline and umbonal angle, but its plicae are denser and more prominent. *N. subsphaerica* Sun & Ye (1982, p. 156, pl. 1, figs 21–24) is also distinguished from *N. minuta* by its strongly swollen umbo and subspherical shell. *N. griesbachi* (Bittner, 1899, p. 12, pl. 2, figs 1–7) occasionally shares an elongate and subpentagonal outline with this species, from which the former differs clearly in having a larger size, a shallower sulcus and denser and more prominent plicae.

Some specimens of *N. trinodosi* described by Bittner (1890, p. 13, pl. 32, figs 18, 24) have elongate outlines and weak lateral plicae like *N. minuta*. However, the new species has much shorter plica in the sulcus, and on the opposite valve, the groove bounded by two plicae on the fold is also quite short, only developed near the anterior margin, which helps distinguish this species from *N. trinodosi*. The Early Triassic species *N. triassica* (Girty, 1927) from Idaho, USA is very similar to this species in size and outline, but differs in having longer and stronger plicae on both valves (Girty 1927, pl. 30, figs 1–4; Alexander 1977, pl. 1, figs 12–17; Perry & Chatterton 1979, pl.

1, figs 1–39).

Subfamily **Praemonticlarellinae** Manceñido & Owen in Manceñido *et al.*, 2002

Parabrekia gen. nov.

Type species. *Parabrekia yangi* sp. nov. from the Anisian Qingyan Formation of the Leidapo locality of the Qingyan section, Guizhou Province, southwestern China.

Diagnosis. Small norellid genus, depressed and equibiconvex; anterior commissure uniplicate. Deltidial plates disjunct; foramen hypothyrid. Dorsal depression weakly developed posteriorly. Fine capillae all over shell (on well-preserved specimens, otherwise smooth), few blunt plicae anteriorly and laterally. Dental plates subparallel; inner hinge plates connected to the dorsal floor near the beak, then merged with low median septum anteriorly to form a low septalium; low dorsal median septum appearing anterior to beak; crura initially elongate and subtriangular in section, distally bladelike, nearly raduliform.

Etymology. *Para* (Greek), near, *Abrekia*, an existing brachiopod genus name. Named for its similarity to *Abrekia* Dagys, 1974.

Remarks. This new genus bears a remarkable resemblance to *Abrekia* Dagys, 1974 in having a subpentagonal outline, depressed shell, weak dorsal sulcus, uniplicate anterior commissure, rounded plicae near anterior margin and other external characteristics, but differs clearly from the latter in that the latter has short and ventrally convergent dental plates and a developed dorsal median septum. Besides, the hinge plates of *Parabrekia* are connected to the dorsal floor posteriorly, and are apparently different from those of *Abrekia*, which are merged with a high median septum in the beak. Moreover, *Parabrekia* can be distinguished from the latter by its crura which are initially elongate and subtriangular in section.

Parabrekia gen. nov. may also be confused with *Pseudomonticlarella* Smirnova, 1987 in outline, plicae and low median septum, but the latter has a more convex shell and a *Monticlarella*-like anterior commissure. Internally, the new genus differs from the latter in having a unique median septum, which appears near beak and becomes higher and thinner at first and lower at last. *Meishanorhynchia* Chen & Shi in Chen *et al.* (2002) is distinguished on the basis of its gently sulcate anterior commissure, low median septum, laterally placed dental plates, and possibly spinuliform crura. *Lichuanorelloides* Wang, Chen & Song in Wang *et al.* (2017) is easily separated from the new genus in having flat inner hinge plates and a well-developed dorsal septalium.

Parabrekia yangi sp. nov.
(Figs 8R–Y, 12A–H, 13A, B)

Diagnosis. *Parabrekia* with maximum width at midlength; anterior commissure not strongly uniplicate. Dorsal depression very weak to absent. Rounded plicae originating at or after the shell midlength, numbering two to three in sulcus, weak or distinct, plicae on lateral flanks very weak. Internal structures as for the genus.

Etymology. Named after Professor Zunyi Yang, as a tribute to his important contributions to the study of Qingyan brachiopods.

Material. Fourteen articulated specimens from Leidapo. One articulated shell (BGEG LDP10051) is selected herein as holotype; three conjoined shells (BGEG LDP10052–10054) are selected as paratypes. Other registered specimens: BGEG LDP10055–10059, 10134–10136.

Occurrence. Leidapo locality of Qingyan, Guizhou, southwestern China.

Description. Shell small, 5–12 mm in width, 5–11 mm in length (Table S6), elongately oval to transversely subpentagonal in outline, anterior and lateral margins rounded, equibiconvex, moderately to strongly depressed in lateral profile; maximum width and thickness at midlength or slightly anterior to midlength; anterior commissure gently uniplicate to moderately uniplicate.

Ventral valve gently convex in anterior profile with the maximum convexity at midline, sometimes forming blunt ridge, lateral flanks slightly convex to flattened; beak acute and suberect, ridges subangular; deltidial plates disjunct; foramen hypothyrid; sulcus wide, beginning at valve midlength or only developed near anterior margin, shallow to moderately deep. Dorsal valve gently convex; dorsal sulcus restricted to posterior half of valve, very weak to completely absent. Fine capillation over entire shell, apparent if well preserved; blunt plicae beginning at midlength or anteriorly to midlength, numbering two to three in sulcus, weak or distinct, plicae on lateral flanks very weak or completely absent, numbering one to two if present;

growth lines variable.

Ventral interior lacking pedicle collar; dental plates thin and long, subparallel; lateral umbonal chambers small. Hinge plates horizontal to inclined dorsally; inner hinge plates connected to the floor of dorsal valve near the beak, then fused to median septum anteriorly, forming a wide and V-shaped septalium; median septum appearing anterior to beak, low and wide, trigonal in section, becoming higher and thinner anteriorly at first and then becoming lower, attaining about one-third of length of dorsal valve; crura initially elongate and subtriangular in section, distally bladelike, gently curved, nearly raduliform (Fig. 13A, B).

Remarks. The new species exhibits large morphological variability. First, the outline of the species is variable; it may have an elongately oval, triangular, equilateral subcircular or transversely subpentagonal outline. Second, the anterior commissure varies from gently uniplicate to moderately uniplicate, and the dorsal depression ranges from completely absent to clearly developed. Third, the length and the strength of plicae also vary greatly. The new species resembles *Abrekia sulcata* Dagys (1974, p. 99, pl. 31, figs 3, 4) in outline, profile, dorsal sulcus and anterior commissure, but their internal structures are quite different from one another, as discussed above.

Subfamily **Diholkorhynchiinae** Xu & Liu, 1983

Genus ***Diholkorhynchia*** Yang & Xu, 1966

Type species. *Rhynchonella sinensis* Koken, 1900.

Remarks. Several Triassic and Jurassic genera: *Holcorhynchia* Buckman, 1918, *Maxillirhynchia* Buckman, 1918, *Trigonirhynchella* Dagys, 1963, *Sinorhynchia* Yang & Xu, 1966, and *Holcorhynchella* Dagys, 1974 are closely allied to *Diholkorhynchia* in general outline and ornamentation. However, *Holcorhynchia* differs clearly from the present genus in having a depressed lateral profile, subcircular outline, denser costae, and a deep septalium. *Maxillirhynchia* is also easily distinguished from *Diholkorhynchia* by the presence of capillae and strong costae on both valves. *Trigonirhynchella* possesses comparable external morphology, such as the subtrigonal outline, sulci on both valves and rounded costae anteriorly, with *Diholkorhynchia*, from which the former differs clearly in having a weak dorsal median septum, connected hinge plates, and short dental plates that are virtually fused to the lateral walls.

Sinorhynchia has a ventral valve that is crest-like posteriorly, steep lateral flanks, a distinct triangular sulcus, and an anteriorly-elevated fold within the dorsal sulcus, and lacks dental plates and a dorsal septalium, thus cannot be confused with *Diholkorhynchia*. *Holcorhynchella* shares a similar subpentagonal outline and dorsal sulcus with *Diholkorhynchia*, from which the former differs in possessing the dorsal sulcus that is well developed on anterior half of shell. Dagys (1974) re-assigned many previously described species to his new genus. Nevertheless, some of these species (e.g. *Rhynchonella dinarica* Bittner, 1903) show marked dissimilarities with the type species, and, instead, are closer to *Diholkorhynchia*.

Diholkorhynchia sinensis (Koken, 1900)
(Figs 12I–O, 14)

1900 *Rhynchonella sinensis* Koken: 206, pl. 10, figs 1–8, 12.
1955b '*Maxillirhynchia*' *sinensis* (Koken); Wang: 136, pl. 74, figs 16–20.
1964 '*Maxillirhynchia*' *sinensis* (Koken); Wang *et al.*: 406, pl. 68, figs 28–31.
1966 *Diholkorhynchia sinensis* (Koken); Yang & Xu: 25, pl. 2, figs 7–12, pl. 3, figs 1–3.
1974 *Diholkorhynchia sinensis* (Koken); Liao & Sun, p. 353, pl. 184, figs 7–10.
1978 *Diholkorhynchia sinensis* (Koken); Feng & Jiang: 277, pl. 101, fig. 15.
1979 *Diholkorhynchia sinensis* (Koken); Jin *et al.*: 146, pl. 39, figs 47–50.
1982 *Diholkorhynchia sinensis* (Koken); Sun & Ye: 157, pl. 1, figs 25–28.

Material. More than 1000 articulated shells from Leidapo; more than 500 articulated shells from Wachangpo and some disarticulated valves. Registered specimens: BGEG WCP10053–10072, BGEG LDP10023–10030.

Occurrence. Qingyan, Yangpu and Machangping, Guizhou, southwestern China; Dangchang, western Qinling (Gansu); Burhan Budai Mountains, central Qinghai; Tulong, Nyalam, Xizang; Middle Triassic: Nierong, Xizang; Zeku, eastern Qinghai.

Description. Shell small to medium in size, 7–13 mm in width (Table S7), rounded triangular to subpentagonal in outline; hingeline short; biconvex; anterior commissure plicate; maximum width at midlength to two thirds of shell length; thickest at midvalve.

Ventral valve moderately convex in lateral profile; greatest convexity at middle of valve in anterior view; lateral flanks flattened; beak small, straight to moderately incurved; beak ridges rounded; foramen small and oval, submesothyrid to hypothyrid; interarea low and narrow with conjunct deltidial plates; sulcus distinct, limited to anterior part of shell. Dorsal valve evenly convex; median depression commencing from umbo, narrow, weak to deep, widening anteriorly. Shell lacking radial ornament posteriorly, rounded plicae near anterior and anterolateral margins; growth lines fine and closely-spaced, lamellae observed near anterior commissure.

Ventral interior with strong and denticulated teeth; dental plates almost parallel. Sockets crenulate; median septum high, slightly shorter than half of dorsal length, supporting a shallow septalium; hinge plates flat or gently convex ventrally; crura strongly curved ventrally (Fig. 14).

Remarks. This species displays large morphological variability, which have been discussed by Koken (1900) and Yang & Xu (1966). Another Middle Triassic species *D. multicostata* Xu (1978, p. 277, pl. 93, fig. 9) from Sichuan area, southwestern China has much denser costae in comparison with the type species. *D. minucosta* Xu (1992, p. 148, pl. 3, fig. 8) from the Middle Triassic Guojiashan Formation of Dangchang, western Qinling region can be differentiated from *D. sinensis* in having shorter and fewer plicae, a shorter ventral sulcus, and a shallower dorsal sulcus.

Dagys (1974) assigned *Rhynchonella dinarica* Bittner, 1903 to his new genus *Holcorhynchella*, with the type species of *Rhynchonella delicatula* Bittner, 1890. However, the *dinarica* species has a faint dorsal fold, and thus is readily different from *Holcorhynchella*. Instead, it is closely allied to *Diholkorhynchia* in almost all external characters, and thus is better re-assigned to that genus.

Superfamily **Hemithiridoidea** Rzhonsnitskaia, 1956

Family **Cyclothyrididae** Makridin, 1955

Subfamily **Cyclothyridinae** Makridin, 1955

Genus ***Costirhynchopsis*** Dagys, 1977

Type species. *Costirhynchia spatiosa* Dagys, 1974.

Costirhynchopsis sinensis (Yang & Xu, 1966)

(Fig. 12P–W)

1966 *Septaliphoria sinensis* Yang & Xu: 17, pl. 1, figs 4–7.
1978 *Septaliphoria sinensis* Yang & Xu; Feng & Jiang: 275, pl. 101, fig. 11.

Material. Two articulated shells (BGEG LDP10060, 10061) from Leidapo and one articulated specimen (BGEG WCP10073) from Wachangpo.

Occurrence. Qingyan and ?Yangpu of Guizhou, southwestern China; Dangchang, western Qinling (Gansu), western China.

Description. Shell about 12 mm in width (Table S8), rounded triangular in outline, slightly elongate to slightly transverse, maximum width anterior to midlength, greatest thickness at about midlength, anterior commissure uniplicate. Ventral valve strongly convex, slightly less convex than dorsal valve; beak moderately incurved, beak ridges subangular; pedicle foramen circular, permesothyrid; sulcus beginning at midlength, widening and deepening anteriorly. Dorsal valve strongly convex; beak strongly curved. Both valves ornamented by coarse angular to slightly rounded plicae; plicae commencing from beak, sometimes increasing by bifurcation and intercalation on both valves, numbering two to three in sulcus, three to four on the fold and on each lateral slope.

Remarks. The described species is characterized by the plicae that commonly increase by bifurcating and intercalating. But, in fact, some specimens of this species have plicae radiating from the beak, not bifurcating or intercalating anteriorly (Yang & Xu 1966, pl. 1, fig. 5; Fig. 12T–W). These specimens ornamented by simple plicae are somewhat close to *Costirhynchopsis rhomba* (Yang & Yin, 1962, p. 95, pl. 38, fig. 7) from the Middle Triassic Junzihe Formation of South Qilian Mountains in their ornamentation, but differ as the latter has a narrower ventral umbo and a protruding sulcus. The type species *C. spatiosa* (Dagys, 1974) has a widely triangular outline, a much-depressed shell, and a hypothyrid foramen, and thus is easily separated from the present species. Three species: *C. xingyiensis* (Yang & Xu, 1966, p. 19, pl. 1, figs 8–10) from Guizhou, *C. tienchungensis* (Yang & Yin in Yang *et al.*, 1962, p. 93, pl. 38, figs 1–3) and *C. pavoplicata* Xu & Liu (1983, p. 88, pl. 1, figs 13–16) from South Qilian Mountain are also distinguished from the present species in having relatively denser plicae.

Superfamily and family unknown

Rhynchonellida gen. and sp. indet. 1

(Fig. 12X–A')

Material. One articulated shell (BGEG LDP10062).

Occurrence. Leidapo locality, Qingyan, Guizhou, southwestern China.

Description. Shell of medium size, width 9.1 mm, length 9.2 mm, thickness 4.9 mm, subtrigonal in outline; greatest width anterior to midlength; moderately biconvex; anterior commissure slightly uniplicate. Ventral beak small, gently incurved; beak ridges subangular; foramen small, mesothyrid; sulcus beginning from midvalve, widening and deepening anteriorly. Dorsal valve slightly convex; sulcus commencing from beak, shallow and narrow. Both valves ornamented by subangular costae, starting from umbo, simple and coarse, not bifurcating or intercalating; fine growth lines near anterior margin.

Remarks. The assignment of the described material to a certain species and genus is difficult because only one specimen is available for study, and its internal structures remain unknown. In having a subtrigonal outline, moderately convex valves, an uniplicate anterior commissure, subangular costae, and a narrow dorsal sulcus, this specimen shows similarity to *Neofascicosta pulchra* Xu (1978, p. 278, pl. 94, figs 4, 5) from the Upper Triassic Kuahongdong Formation of Sichuan, southwestern China; but our material cannot be referred to the Xu's (1978) species due to the relatively narrower outline, and simpler but coarser costae. *N. simplexa* Sun & Li (1990, p. 112, pl. 1, figs 39–42) from the Upper Triassic Xiaoqiacuo Formation of Qinghai is comparable in having simple costae and a narrow outline, but differs from the Qingyan specimen in the absence of dorsal sulcus. *Pseudohalorella sibirica* Dagys, 1965 is also comparable, but its ventral valve is flattened medianly.

Rhynchonellida gen. and sp. indet. 2

(Fig. 15A–D)

Material. One articulated shell (BGEG WCP10074).

Occurrence. Wachangpo locality, Qingyan, Guizhou, southwestern China.

Description. Shell small, 8.8 mm wide, 9.8 mm long and 4.5 mm thick, subtriangular in outline, lateral margins straight; maximum width near to anterior margin; anterior margin uniplicate; gently ventribiconvex. Ventral valve weakly convex; beak narrow, acute and suberect; beak ridges angular; interarea gently concave, equilateral triangular in outline, slightly wider than long; deltidial plates not connected; foramen hypothyrid; median sulcus developed at anterior part of shell, broad and shallow. Dorsal valve almost flat; depression developed near dorsal umbo; fold very weak. Both valves ornamented by costellae; 13 costae (one median costa and six pairs laterally) originating at umbo on ventral valve, the median costa and the second pair bifurcating at about valve midlength; costellae numbering 16 near anterior margin of ventral valve, 15 on dorsal valve. Growth lines and lamellae, close-spaced, more distinct on the anterior half of shell.

Remarks. Another uncertain species and genus is proposed here for an articulated shell because it is distinct by having a subtriangular outline, longer than wide, gently convex shell, and sometimes bifurcating costellae, but its interior features remain unknown due to insufficient materials. This uncertain species is also comparable with Rhynchonellida gen. and sp. indet. 1 in having a dorsal depression and a trigonal outline, but their lateral profiles, beaks, foramens and costae are quite different from one another. By virtue of its median depression on dorsal valve, this uncertain species may belong to Norelloidea Ager, 1959. It may also be related to *Costinorella* Dagys, 1974 in its triangular outline, a dorsal depression and dense costae, but the latter has a unisulcate anterior margin and posteriorly, a smooth shell.

Rhynchonellida gen. and sp. indet. 3

(Fig. 15E–H)

Material. One articulated specimen (BGEG WCP10075).

Occurrence. Wachangpo locality, Qingyan, Guizhou, southwestern China.

Description. Shell small, 9.4 mm wide, 8.9 mm long and 3.8 mm thick, rounded triangular in outline, anterior commissure slightly uniplicate, gently biconvex. Ventral valve gently convex, more convex along midline; lateral flanks almost flat; beak acute and suberect; ridges rounded; deltidial plates disconnected; foramen small, mesothyrid; ventral sulcus beginning at midlength, shallow and not well defined.

Dorsal valve gently convex; a very weak depression posteriorly; fold inconspicuous. Ornamentation of dense costellae, increasing by bifurcating; growth lamellae near anterior and lateral margins.

Remarks. The third undetermined genus and species has a rounded triangular outline, a gently biconvex shell, and dense costae. It also differs from Rhynchonellida gen. and sp. indet. 2 in having a wider outline, a mesothyrid foramen and denser costellae. It is somewhat close to *Caucasorhynchella subfissicostata* (Yang & Xu, 1966), but that species has a larger, a more convex shell, a deeper ventral sulcus and simpler costae.

Rhynchonellida gen. and sp. indet. 4

(Fig. 15I–L)

Material. One articulated specimen (BGEG LDP10063).

Occurrence. Leidapo locality, Qingyan, Guizhou, southwestern China.

Description. Shell small, 7.5 mm wide, 8.4 mm long and 5.1 mm thick, elongately subtriangular in outline, posterolateral margins slightly curved; anterior commissure uniplicate; moderately biconvex. Ventral beak relatively long, moderately curved; beak ridges rounded; interarea concave; foramen possibly mesothyrid; ventral umbo slightly swollen; lateral flanks inclined rapidly; sulcus wide, restricted to anterior one-quarter of valve length. Dorsal valve with a shallow depression near the beak; fold low. Shell ornamented by coarse and rounded costae, rarely bifurcating.

Remarks. The present specimen apparently differs from the other three undetermined species described above in its longer outline, prominent and curved ventral umbo, and short sulcus. Its shape is comparable to that of the Middle Jurassic *Indorhynchia subtrigonalis* Ovcharenko, 1975, but further comparison is difficult because only one specimen is available for study and its internal structures are unknown.

Order **Athyridida** Boucot, Johnson & Staton, 1964

Suborder **Athyrididina** Boucot, Johnson & Staton, 1964

Superfamily **Athyridoidea** Davidson, 1881

Family **Diplospirellidae** Schuchert, 1894

Subfamily **Ochotathyridinae** Alvarez, Rong & Boucot, 1998

Genus ***Spirigerellina*** Dagys, 1974

Type species. *Spirigerellina pygmaea* Dagys, 1974.

Spirigerellina sulcata (Yang & Xu, 1966)

(Fig. 15M–P)

1966 '*Athyris*' *sulcata* Yang & Xu: 66, pl. 11, figs 2, 3.

1978 '*Athyris*' *sulcata* Yang & Xu; Feng & Jiang: 279, pl. 101, fig. 20.

Material. One articulated shell (BGEG WCP10016) from Wachangpo.

Occurrence. Qingyan, Guizhou, southwestern China.

Description. Shell small, 10.3 mm wide, 9.2 mm long, 6.1 mm thick, rounded pentagonal in outline, widest at midlength, anterior commissure strongly uniplicate, lateral margins evenly curved, biconvex. Ventral valve gently convex, posterior half moderately curved and anterior half gently convex; beak strongly curved; foramen subcircular, permesothyrid; sulcus starting from beak, narrow and deep, widening rapidly anteriorly, equaling to half of the shell width near anterior margin, forming a protruding tongue. Dorsal valve gently convex; umbo slightly swollen; fold broad, not well defined; lateral flanks gently concave. Comarginal growth lamellae well developed.

Remarks. This species is characterized by its slim lateral profile, deep sulcus, and well-developed growth lamellae. It is assigned to *Spirigerellina* Dagys, 1974 in having a similar shape and internal structures to those of the type species *S. pygmaea* Dagys, 1974 (Yang & Xu 1966). But this species possibly has a short ventral median septum and rather narrow umbonal lateral chambers (Yang & Xu, 1966), and shows some differences from the type species. Thus, there is a possibility that the present species may represent a different genus if the distinct interior features are confirmed when more specimens are observed in future. This species can be distinguished from other *Spirigerellina* species in terms of its marked growth lamellae and slim lateral profile.

Suborder **Retziidina** Boucot, Johnson & Staton, 1964

Superfamily **Retzioidea** Waagen, 1883

Family **Neoretziidae** Dagys, 1972a

Subfamily **Neoretziinae** Dagys, 1972a

Genus ***Cassianospira*** Dagys, 1972a

Type species. *Retzia loczyi* Bittner, 1900.

Remarks. This genus has been reported from the Upper Triassic in the Southern Alps, Carpathians, and Hungary (Alvarez & Rong 2002). Recently, Halamski *et al.* (2015) described a species from the Ladinian of Croatia. The Qingyan species *Cassianospira wachangpoensis* (Stiller, 1999) is, to date, the known oldest species of the genus. *Neoretzia* Dagys, 1963 can be distinguished from this genus by its much larger size and shorter ventral umbo. *Schwagerispira* Dagys, 1972a is also closely allied to *Cassianospira* in ornamentation, but the former is larger, and has a shorter beak and a different type of jugum.

Cassianospira wachangpoensis (Stiller, 1999)

(Figs 15Q–Z, 16)

1999 *Neoretzia wachangpoensis* Stiller: 52, pls 1, 2.

Material. More than 90 articulated shells. Registered specimens: 10 articulated specimens (BGEG WCP10001–10010).

Occurrence. Wachangpo locality, Qingyan section, Guizhou, southwestern China.

Description. Shell small, width less than 6 mm, length less than 7 mm (Table S9), teardrop-shaped, longer than wide; greatest width at midlength of the dorsal valve or slightly posterior to midvalve; hingeline straight, equal to half the greatest shell width; anterior and lateral margins evenly rounded.

Ventral valve moderately convex; ventral beak ridges sharply angular; beak high, straight to slightly curved; foramen rounded, in submeso- to mesothyridid position; interarea apsacline; symphytium narrow, elongately triangular in outline, transversely and longitudinally gently concave, with a weak median line of junction. Dorsal valve moderately convex, subcircular in outline; dorsal umbo strongly curved; dorsal sulcus absent to weakly developed, extending from umbo to anterior margin, containing one relatively weak median costa. Ornamentation of rounded costae, separated by interspaces of similar width; eight to ten on ventral valve, seven to eleven on dorsal valve with the median costa slightly narrower; strength of costae gradually decreases laterally. Growth lines weak, and closely spaced near anterior margin.

Pedicle collar absent; cardinal flanges and hinge plates thick, supported by a long median septum, the length of the septum equaling about three quarters that of dorsal valve; spiralium not known (Fig. 16).

Remarks. Stiller (1999) emphasized that the variably twisted umbo is a diagnostic feature, when he established this species. However, the large number of specimens from the same locality shows that the specimens having twisted umbo are very rare. Instead, most specimens possess straight umbones. Besides, one of the specimens illustrated by Stiller (1999, pl. 2, fig. 7) shows an almost straight umbo. Thus, the 'twisted umbo' may be due to shell deformation during life and/or taphonomic process.

The umbo of the Qingyan species is moderately long when compared with other species within the same genus. *C. humboldtii* (von Klipstein, 1845 in 1843–1845; see also Bittner 1890, p. 88. pl. 2, fig. 33; Halamski *et al.* 2015, p. 557, fig. 3.1–3.16) differs from *C. wachangpoensis* in having a shorter umbo, a broader ventral symphytium, and wider dorsal valve. Three other allies: *C. klipsteinii* (Bittner, 1890, p. 89, pl. 2, figs 31, 32), *C. pseudolyrata* (Bittner, 1900, p. 28, pl. 2, fig. 24) and *C. lyrata* (Münster, 1841) figured by Bittner (1890, pl. 2, figs 29, 30) all have much longer beaks, and thus cannot be confused with the Qingyan species. When compared with *C. wachangpoensis*, the type species *C. loczyi* (Bittner, 1900; see also Dagys 1974, pl. 42, fig. 11) has a more depressed dorsal median costa and a moderately curved ventral umbo. *C. hungarica* (Bittner, 1900, p. 26, pl. 2, figs 21–23, pl. 5, figs 12, 13) is a species, which shows substantial morphological variability. It differs from *wachangpoensis* in its longer ventral umbo and wider dorsal valve.

Neoretzia jingguensis Jin & Fang (1977, p. 54, pl. 5, figs 9–12) described from the Upper Triassic Weiyuanjiang Formation of Yunnan Province, southwestern China is similar to *Cassianospira* species in having a very small size, subangular costae, and a weak dorsal median costa, but its ventral umbo is much shorter than that of *Cassianospira*. Instead, it is similar to that of *Schwagerispira*, which makes its current generic assignment doubtful. *Schwagerispira fuchsi* (Koken, 1900) and *S. subcircularis* (Yang & Xu, 1966) described below are closely allied to *C.*

wachangpoensis in ornamentation, but are distinguished from the latter by their larger size and short umbones, even though the jugum of *C. wachangpoensis* is unknown.

***Cassianospira* sp.**

(Fig. 18A–D)

Material. One articulated shell (BGEG WCP10011).

Occurrence. Wachangpo locality, Qingyan section, Guizhou, southwestern China.

Description. Shell very small (4.0 mm wide, 4.8 mm long, 2.8 mm thick), teardrop-shaped, greatest width at midlength; hingeline straight, about half of the maximum shell width. Ventral valve moderately convex; beak high, slightly incurved, ridges sharply angular; foramen rounded, mesothyrid; interarea high, apsacline; symphytium longitudinally trigonal in outline, slightly wider than long, gently concave, with a very weak median line of junction. Dorsal valve moderately convex, slightly wider than long; sulcus distinct, deep, commencing from dorsal beak, containing one median costa. Costae rounded, with interspaces of similar width, numbering eight on ventral valve and seven on dorsal valve; the median costa on dorsal valve very narrow and low.

Remarks. One complete specimen is characterized by a strongly depressed dorsal median costa and fewer costae, which distinguish it from all known species of the genus. The present specimen co-occurs with *C. wachangpoensis*, but is smaller than most individuals of the latter. Thus, the present material may be a juvenile of *C. wachangpoensis*. However, the juveniles of *C. wachangpoensis* possess longer ventral umbones, more costae, and a stronger dorsal median costa, and are almost identical to the mature form. Thus, the present material cannot be assigned to that species. Nevertheless, only one specimen was collected, insufficient to establish a new species. The potential new species is also comparable with the type species, *C. loczyi* (Bittner, 1900) in its depressed dorsal median costa, but the latter has a much higher ventral interarea and more costae. *C. laubei* (Bittner, 1890) is close to this species in having seven costae on the dorsal valve and a short ventral umbo, but its hingeline is quite short and the dorsal median costa is relatively strong.

Subfamily **Hustediinae** Grunt, 1986

Genus ***Schwagerispira*** Dagys, 1972a

Type species. *Retzia schwageri* Bittner, 1890.

Schwagerispira subcircularis (Yang & Xu, 1966)
(Fig. 18E–H)

1966 *Neoretzia subcircularis* Yang & Xu: 72, pl. 11, figs 7, 8.
1978 *Neoretzia subcircularis* Yang & Xu; Feng & Jiang: 279, pl. 101, fig. 19.
1982 *Schwagerispira subcircularis* (Yang & Xu); Sun & Ye: 165, pl. 3, figs 1–4.
1983 *Schwagerispira subcircularis* (Yang & Xu); Xu & Liu: 128, pl. 11, figs 8–10.
1999 *Schwagerispira subcircularis* (Yang & Xu); Stiller: 55, pl. 5.

Material. One articulated shell and one dorsal valve from Leidapo; 13 articulated shells, two ventral valves, and one dorsal valve from Wachangpo. Registered specimens: four articulated shells (BGEG WCP10012–10015).

Occurrence. Qingyan, Guizhou, southwestern China; southern Qilian Mountains (Qinghai); Burhan Budai Mountains, central Qinghai; Dangchang, western Qinling (Gansu), western China.

Description. Shell small, width less than 8 mm (Table S10), subcircular to elongately oval in outline; both valves moderately to strongly convex; thickest at or slightly posterior to midlength; anterior and lateral margins evenly rounded; hingeline short, equaling about 0.3 of the maximum width at about the midlength of shell. Ventral umbo slightly curved, prominent; beak ridges angular; foramen rounded, in permesothyridid position; interarea apsacline, wider than high. Dorsal valve lacking sulcus; beak strongly incurved. Shell ornamented by rounded costae; costae numbering ten to twelve on ventral valve, nine to eleven on dorsal valve, strength of costae gradually decreases laterally. Comarginal growth lines weakly developed near anterior margin.

Remarks. The present specimens agree well with those described by Yang & Xu (1966) in their shape and ornamentation. *Schwagerispira fuchsi* (Koken, 1900) differs from this species in having a more elongate outline, slightly higher interarea and the presence of a dorsal sulcus. Sometimes *S. subcircularis* displays a median costa on the dorsal valve, but the costa is coarse and strong, different from the feeble one in *S. fuchsi*. *S. sichuanensis* (Liao & Sun, 1974, p. 352, pl. 184, figs 4–6, 22) from the Middle Triassic of Sichuan, southwestern China shares many features with *S. subcircularis*, but differs from the latter in its elongate outline.

Schwagerispira pinguis Sun & Ye (1982, p. 165, pl. 2, figs 29–32) from the Middle Triassic of Qinghai, northwestern China is subtriangular in outline and has more costae on both valves, and thus is easily differentiated from the Qingyan species. *S. beneckei* (Bittner, 1890, p. 21, pl. 36, figs 5–7) resembles this species in its costae and outline, but differs in its larger size and strongly incurved ventral beak. *S. speciosa* (Bittner, 1890) described by Bittner (1892, p. 4, pl. 1, fig. 17) has a circular outline as well, but is distinguished by its denser costae.

Neoretzia tibetensis Jin & Sun in Jin *et al.* (1976, p. 313, pl. 7, figs 4–8, 41) from the Upper Triassic of Nyalam, Xizang (Tibet) is also almost identical with this species in shape and ornamentation, but it is larger in size and its jugum appears different.

Schwagerispira fuchsi (Koken, 1900)

(Fig. 18I–L)

1900 *Retzia fuchsi* Koken: 205, pl. 10, figs 9–11, 13–15.
1966 *Neoretzia fuchsi* (Koken); Yang & Xu: 67, pl. 11, figs 4–6, 9–10.
1978 *Neoretzia fuchsi* (Koken); Feng & Jiang: 278, pl. 101, fig. 18.
1982 *Schwagerispira fuchsi* (Koken); Sun & Ye: 166, pl. 3, figs 5–8.
?1983 *Schwagerispira fuchsi* (Koken); Chen: pl. 1, fig. 1.
1999 *Schwagerispira fuchsi* (Koken); Stiller: 54, pls 3, 4.

Material. Nine articulated shells, four ventral valves and three dorsal valves from Leidapo; three articulated shells and one dorsal valve from Wachangpo. Registered specimens: three articulated specimens (BGEG LDP10001–10003).

Occurrence. Qingyan, Guizhou, southwestern China; Burhan Budai Mountains, central Qinghai. This species is also reported from the Olenekian Kangshare Formation of Tulong, Nyalam, Xizang, but requires revision.

Description. Shell small, 5–7 mm in width (Table S11), elongately oval; greatest width at midlength; hingeline straight. Ventral valve moderately convex; beak short, gently curved; ridges of beak angular; foramen in permesothyridid position; interarea slightly curved, equilateral triangular in outline. Dorsal valve moderately convex; beak strongly incurved; sulcus narrow and shallow, originating at umbo, widening anteriorly, containing a median costa. Costae rounded, 12 on ventral valve, 11 on dorsal valve; the dorsal median costa slightly narrower and lower than the pair defining the sulcus, especially near the umbo.

Remarks. Our specimens are almost identical to *Schwagerispira fuchsi* described by Koken (1900) and Yang & Xu (1966). This species is closely similar to *S. schwageri* (Bittner, 1890, p. 21, pl. 36, figs 1–4) in outline and costae. The differences between these two species and other allied species have been noted by Koken (1900) and Yang & Xu (1966) and are not discussed here.

Order **Spiriferinida** Ivanova, 1972
Suborder **Cyrtinidina** Carter & Johnson in Carter *et al.*, 1994
Superfamily **Suessioidea** Waagen, 1883
Family **Laballidae** Dagys, 1962
Subfamily **Paralepismatininae** Carter in Carter *et al.*, 1994
Genus ***Paralepismatina*** Yang & Xu, 1966

Type species. *Paralepismatina semiconica* Yang & Xu, 1966.

Paralepismatina semiconica Yang & Xu, 1966
(Fig. 18M–O)

1966 *Paralepismatina semiconica* Yang & Xu: 38, pl. 5, figs 1–3.
1978 *Paralepismatina semiconica* Yang & Xu; Feng & Jiang: 284, pl. 102, figs 5, 6.
1983 *Paralepismatina semiconica* Yang & Xu; Xu & Liu: 119, pl. 9, figs 11–17.

Material. Twelve ventral valves and one dorsal valve from Leidapo; one articulated specimen and nine ventral valves from Wachangpo. Registered specimens: one articulated specimen (BGEG WCP10076) and three ventral valves (BGEG LDP10064–10066).

Occurrence. Qingyan, Guizhou, southwestern China; southern Qilian Mountains (Qinghai).

Description. Shell of small to medium size, 6–13 mm in width (Table S12), transversely semicircular in outline; ventribiconvex; maximum width at hingeline or slightly anterior to it; cardinal extremities subangular. Ventral valve subconical; beak acute, straight to curved; interarea low to very high, flattened, nearly catacline, ornamented by transverse lines; delthyrium narrow, not covered; sulcus absent or very weakly developed. Dorsal valve gently convex, fold absent. Costellae on both valves, numbering 12 to 22 on each valve, mostly simple on small specimens, some bifurcating or intercalating on large ones, especially those ribs within the sulcus or near the ventral interarea; regular growth lamellae developed near anterior margin.

Remarks. Our material agrees well with those specimens described by Yang & Xu (1966). Yang & Xu (1966) noted that the costellae of this species were simple. In fact, although small individuals (usually <10 mm wide) often have simple costellae, large ones (>10 mm wide) have more complex costellae. In large specimens, the costellae within sulcus are often finer than those on the flanks because of intercalation and bifurcation. The height of ventral interarea is also variable, with the ratio of height to width ranging from 0.5 to 0.65.

Family **Bittnerulidae** Schuchert, 1929

Subfamily **Bittnerulinae** Schuchert, 1929

Genus ***Leiolepismatina*** Yang & Xu, 1966

Type species. *Leiolepismatina semiconula* Yang & Xu, 1966.

Leiolepismatina semiconula Yang & Xu, 1966

(Fig. 18P, Q)

1966 *Leiolepismatina semiconula* Yang & Xu: 40, pl. 5, figs 4–6.

1978 *Leiolepismatina semiconula* Yang & Xu; Feng & Jiang: 285, pl. 102, fig. 7.

Material. One disarticulated ventral valve from Leidapo (BGEG LDP10082, 5.6 mm long, 7.3 mm wide).

Occurrence. Qingyan, Guizhou, southwestern China.

Remarks. This genus is monotypic. Though this specimen is incomplete, it can be safely assigned to *Leiolepismatina semiconula* Yang & Xu, 1966 in having fine growth lamellae, a catacline interarea and open delthyrium. *Thecocyrtelloidea tubulosa* is similar, but its delthyrium is covered, and it often has a weak sulcus so that the anterior margin is not evenly curved like that of *Leiolepismatina semiconula*.

Genus ***Thecocyrtelloidea*** Yang & Xu, 1966

Type species. *Thecocyrtelloidea tubulosa* Yang & Xu, 1966.

Thecocyrtelloidea tubulosa Yang & Xu, 1966
(Fig. 18R–U)

1943 *Cyrtina* (*Bittnerula*) *yini* Hsu & Chen, p. 132.
1966 *Thecocyrtelloidea tubulosa* Yang & Xu: 59, pl. 9, figs 1–14, pl. 10, figs 1, 2.
1978 *Thecocyrtelloidea tubulosa* Yang & Xu; Feng & Jiang: 285, pl. 102, fig. 3.

Material. Fifteen articulated shells, 47 ventral valves and 28 dorsal valves from Leidapo; six articulated shells, one ventral valve and two dorsal valves from Wachangpo. Registered specimens: five dorsal valves (BGEG WCP10077, BGEG LDP10067–10070), five ventral valves (BGEG LDP10071–10075) and five articulated specimens (BGEG LDP10076–10080).

Occurrence. Qingyan, Guizhou, southwestern China.

Description. Small, width less than 10 mm (Table S13), sub-semicircular in outline; anterior commissure rectimarginate to weakly uniplicate; ventribiconvex in profile; greatest width at hingeline; cardinal extremities subangular. Ventral valve subconical, strongly convex; beak acute, straight to strongly curved; interarea relatively low to high, flattened, catacline to procline, with fine transverse grooves; deltidium narrow and convex, with numerous fine pedicle tubules; sulcus flattened or slightly depressed at middle. Dorsal valve gently convex; fold bordered by a pair of grooves. Shell smooth; microornament absent except growth lines.

Remarks. The *tubulosa* species is easily identified because of its characteristic deltidium. It is comparable to the *Thecocyrtella* sp. described here, in having a subconical ventral valve, smooth shell and high ventral interarea. However, *Thecocyrtelloidea tubulosa* has a delthyrium, which is covered by a convex and complex plate. Therefore, the specimen of *Thecocyrtella* sp. cannot be confused with *Thecocyrtelloidea*, even though they are very close in external appearance.

Genus ***Thecocyrtella*** Bittner, 1892

Type species. *Cyrtotheca ampezzana* Bittner, 1890.

***Thecocyrtella* sp.**
(Fig. 18V–X)

Material. One disarticulated ventral valve (BGEG LDP10081).

Occurrence. Leidapo locality, Qingyan, Guizhou, southwestern China.

Description. Shell small, 5.5 mm long, 6.4 mm wide. Ventral valve strongly convex, pyramidal; beak incurved; interarea high, concave; delthyrium covered by deltidium, with a median line of junction; pedicle opening semicircular, situated near hingeline; sulcus shallow, initiated at beak; lateral slopes steeply inclined rapidly, smooth. Dorsal valve unknown.

Remarks. This specimen is assigned to *Thecocyrtella* Bittner, 1892 based on its shape, size, covered delthyrium and smooth shell. Two genera from the same localities, *Leiolepismatina* Yang & Xu, 1966 and *Thecocyrtelloidea* Yang & Xu, 1966 also possess a smooth shell without radial ornamentation, however, have different types of delthyrium covers. The material is comparable with *Thecocyrtella orientalis* Ivanova in Dagys (1965) in having a shallow sulcus on the ventral valve. It differs from *T. dagysii* Halamski *et al.* (2015, p. 559, figs 4.1, 4–34, 5) in having a shallower sulcus, and from *T. horogensis* Pálfy (2003, p. 148, pl. Br-I, figs 23, 34) and *T. ampezzana* (Bittner, 1890, p. 116, pl. 38, fig. 19) in having a deeper sulcus.

Subfamily **Hirsutellinae** Xu & Liu, 1983
Genus ***Neocyrtina*** Yang& Xu, 1966

Type species. *Neocyrtina mixodeltidiumosa* Yang & Xu, 1966.

Neocyrtina mixodeltidiumosa Yang & Xu, 1966

(Fig. 18Y–F')

1966 *Neocyrtina mixodeltidiumosa* Yang & Xu: 62, pl. 10, figs 3–8.
1978 *Neocyrtina mixodeltidiumosa* Yang & Xu; Feng & Jiang: 286, pl. 102, fig. 4.

Material. Seven complete specimens, seven ventral valves and one dorsal valve from Leidapo; three dorsal valves and three ventral valves from Wachangpo. Registered specimen: three complete specimens (BGEG LDP10083–10085) and three ventral valves (BGEG LDP10086–10088).

Occurrence. Qingyan, Guizhou, southwestern China.

Description. Shell small, width less than 10mm (Table S14); cardinal extremities angular; hingeline straight, equal to greatest width of shell. Ventral valve subconical; beak straight to curved; interarea high and flat, catacline to procline, transversely grooved; delthyrium narrow, with base about one-fifth of hinge length; deltidium with solid tubules or nodules apically and imbricating plates proximally; valve ornamented by rounded plica, numbering four to five on each slope, two median plica slightly higher than the lateral ones, forming an inconspicuous fold. Dorsal valve gently convex; median depression marked; seven to eight plicae on dorsal valve, with the median one slightly weaker.

Remarks. There are only two species currently assigned to this genus. The differences between this species and *Neocyrtina xui* sp. nov. will be given in the remarks for that species. Specimens of *Lepismatina hsui* illustrated by J. Chen *et al.* (2010a, fig. 6.17, 6.18) should be re-assigned to this species on the basis of a dorsal median depression.

Neocyrtina xui sp. nov.

(Fig. 19A–H)

Diagnosis. *Neocyrtina* with wide delthyrium, ill-defined plicae, and hingeline, which is narrower than the maximum width of shell, without dorsal depression.

Etymology. Named after Professor Guirong Xu, as a tribute to his contributions to the study of Permian and Triassic brachiopods of China.

Material. Two articulated shells. BGEG WCP10078 is designated herein as the holotype, BGEG WCP10079 is selected as a paratype.

Occurrence. Wachangpo locality, Qingyan, Guizhou, southwestern China.

Description. Shell of small size, width about 5–7 mm (Table S15), transversely oval in outline, anterior and lateral margins evenly rounded; cardinal extremities subangular; hingeline straight, slightly shorter than the maximum width at midlength.

Ventral valve subconical; beak acute and straight; interarea high, catacline, elongately triangular in outline, marked with transverse lines; delthyrium wide, about one-third of hinge length; deltidium with nodules apically and imbricating plates proximally; ventral valve ornamented by plicae; plicae rounded, ill defined, very weak near ventral beak, numbering eight to nine, the pair near the ventral interarea sometimes bifurcating once anteriorly, the median pair equally strong with lateral ones, not forming fold. Dorsal valve gently convex, without depression; seven to eight plicae on dorsal valve. Marked growth lines developed on anterior one-third of shell.

Remarks. The two specimens can be discriminated from other spiriferinids discovered from Qingyan in having a conical ventral valve, a truncated hingeline and ill-defined plicae, based on which a new species is proposed. This species is assignable to *Neocyrtina* Yang & Xu, 1966 in having a subconical ventral valve, coarse plicae and most importantly, *Neocyrtina*-like deltidial plates. Compared with the type species *N. mixodeltidiumosa*, the new species differs in having a wider delthyrium, shorter hingeline, more developed growth lines and ill-defined plicae, and in the absence of a ventral 'fold' formed by plicae and median depression on dorsal valve. This new species resembles *Thecocyrtelloidea tubulosa* in the shape of shell, but it has distinct plicae and a different type of deltidium.

Suborder **Spiriferinidina** Ivanova, 1972
Superfamily **Pennospiriferinoidea** Dagys, 1972b
Family **Spiriferellinidae** Ivanova, 1972
Genus ***Pseudospiriferina*** Yang & Xu, 1966

Type species. *Pseudospiriferina variabilis* Yang & Xu, 1966.

Pseudospiriferina sp.

(Fig. 19I, J)

Material. Two dorsal valves from Leidapo; one dorsal valve from Wachangpo. Registered specimens: BGEG LDP10089, 10090.

Occurrence. Qingyan, Guizhou, southwestern China.

Remarks. The two dorsal valves are moderately convex and bear coarse plicae. They differ from those of *Nudispiriferina minima* Yang & Xu, 1966 and *Lepismatina hsui* Wang, 1955a in having a larger convexity and stronger plicae. The external appearance suggests that the new material may be assigned to *Pseudospiriferina variabilis* Yang & Xu, 1966 or *P. pinguis* Yang & Xu, 1966, but the absence of ventral valves prevents further assignment to a certain species. *P. multicostata* Yang & Xu, 1966 is distinguished in having a median groove on the dorsal fold.

Family **Balatonospiridae** Dagys, 1974

Subfamily **Balatonospirinae** Dagys, 1974

Genus ***Nudispiriferina*** Yang & Xu, 1966

Type species. *Nudispiriferina minima* Yang & Xu, 1966.

Nudispiriferina minima Yang & Xu, 1966

(Fig. 19K–O)

1966 *Nudispiriferina minima* Yang & Xu: 47, pl. 6, figs 7–11.

1978 *Nudispiriferina minima* Yang & Xu; Feng & Jiang: 293, pl. 104, figs 9, 10.

Material. Thirty-five ventral vales and seven dorsal valves from Leidapo; two articulated shells, 49 ventral valves and one dorsal valve from Wachangpo. Registered specimens: eight ventral valves (BGEG WCP10081–10086, BGEG LDP10091, 10092) and one articulated specimen (BGEG WCP10080).

Occurrence. Qingyan and Yangpu, Guizhou, southwestern China.

Description. Small, width less than 12 mm (Table S16), semicircular in outline; anterior and lateral margins evenly rounded; cardinal extremities angular; plano-convex to slightly biconvex; hingeline straight, equaling to the greatest shell width. Ventral valve evenly convex; beak pointed and moderately incurved; interarea moderately high, concave longitudinally, ornamented by vertical striae; delthyrium open and narrow; sulcus narrow and smooth, defined laterally by first pair of plicae, initiating at beak; plicae rounded, six or eight in number. Dorsal valve plane to slightly convex; interarea very low; fold very low, slightly wider than lateral plicae; plicae numbering five or seven on dorsal valve. Shell densely punctate; microornament absent. Ventral teeth blunt, elongate transversely along hinge.

Remarks. This species is characterized by its flat dorsal valve, inconspicuous sulcus and fold, and coarse plicae. *Pseudospiriferina variabilis* Yang & Xu, 1966 bears some resemblance to this species, but differs in its more convex valves, rounded outline and undeveloped ventral adminicula. *Balatonospira lipoldi* (Bittner, 1890, p. 139, pl. 28, figs 20, 21) is close to *Nudispiriferina minima* in internal features (Dagys 1974), but it has a strongly convex dorsal valve and a median plica within the ventral sulcus.

Subfamily **Dinarispirinae Dagys, 1996**

Genus ***Qingyenia*** Yang & Xu, 1966

Type species. *Qingyenia spinosa* Yang & Xu, 1966.

Qingyenia spinosa Yang & Xu, 1966

(Fig. 19P–U)

1966 *Qingyenia spinosa* Yang & Xu: 50, pl. 7, figs 2–4.

1978 *Qingyenia spinosa* Yang & Xu; Feng & Jiang: 293, pl. 104, fig. 12.

Material. Twenty-eight ventral valves and 10 dorsal valves from Leidapo. Registered specimens: six ventral valves (BGEG LDP10110–10115) and four dorsal valves (BGEG LDP10116–10119).

Occurrence. Qingyan, Guizhou, southwestern China.

Description. Shell small, 4–10 mm wide (Table S17), subquadrate in outline;

hingeline straight, equal to maximum width of shell; cardinal extremities subangular. Ventral valve strongly convex; beak pointed, gently incurved; beak ridges angular; interarea moderately high, concave; delthyrium narrow, open; sulcus shallow, initiated at umbo, bounded by two coarse plicae; plicae numbering two to three in sulcus, finer, starting anterior to ventral beak, numbering three to four pairs of plicae on each slope. Dorsal valve slightly concave; plicae often weaker in central part of shell, sometimes with a coarse median plica; interior with diverging crural plates. Both valves covered by dense spinules.

Remarks. This genus is monotypic and only the type species is included. *Pseudospiriferina multicostata* Yang & Xu figured by J. Chen *et al.* (2010a, fig 6.13, 6.14) from Qingyan is, in fact, *Qingyenia spinosa* in having a subquadrate outline, a weak ventral sulcus, which bears more than one plica.

Family **Lepismatinidae** Xu & Liu, 1983

Subfamily **Lepismatininae** Xu & Liu, 1983

Genus ***Lepismatina*** Wang, 1955a

Type species. *Lepismatina hsui* Wang, 1955a.

Lepismatina hsui Wang, 1955a

(Fig. 19V–D')

1955a *Lepismatina hsui* Wang: 108, pl. 6, figs 2.1–2.8.

1955b *Lepismatina hsui* Wang; Wang: 163, pl. 96, figs 1–9.

1964 *Lepismatina hsui* Wang; Wang *et al.*: 592, pl. 115, figs 6–10.

1966 *Lepismatina hsui* Wang; Yang & Xu: 35, pl. 4, figs 6–12.

1974 *Psioidea hsui* (Wang); Liao & Sun: 352, pl. 184, figs 16, 17.

1978 *Lepismatina hsui* Wang; Feng & Jiang: 284, pl. 102, figs 1, 2.

Material. Four complete specimens, 38 ventral valves and 19 dorsal valves from Leidapo; two conjoined shells, three ventral valves and four dorsal valves from Wachangpo. Registered specimens: four articulated shells (BGEG WCP10088, BGEG LDP10099–10101), five ventral valves (BGEG LDP10102–10106) and three dorsal valves (BGEG LDP10107–10109).

Occurrence. Qingyan, Guizhou, southwestern China.

Description. Shell small to medium in size, 4–17 mm width (Table S18); transversely subquadrate or trapezoidal in outline; maximum width at hingeline; cardinal extremities angular to strongly alate. Ventral valve subpyramidal; interarea high and flattened, low to relatively high, apsacline to procline, marked by vertical and transverse grooves; delthyrium narrow and open, with base about one sixth of hinge width; sulcus smooth, commencing from beak, widening and deepening anteriorly; lateral slopes with rounded plicae, numbering four to nine on each side. Dorsal valve weakly convex, with three to eight pairs of plicae on slopes. Both valves marked by regularly spaced and imbricate growth lamellae. For a description of internal features, see Yang & Xu (1966).

Remarks. This species shows marked variation in the number of plicae, its cardinal extremities, and interarea. In our collection, the number of plicae on ventral valves ranges from eight to sixteen, and the cardinal extremities may be subangular or strongly alate. However, because there is no stable character that can divide these specimens into several groups, they are treated as one species. Sun (1981, p. 209, pl. 8, figs 9, 10) described *L.* cf. *hsui* from the Middle Triassic Kangnan Formation of Xizang (Tibet) and stated that his specimens differ from *L. hsui* in having fewer plicae. In fact, considering the great variability in the number of plicae observed in our specimens, the Tibetan specimens described by Sun (1981) perhaps belong to this species.

Dagys (1965, 1974) misunderstood some aspects of this genus. He noted that *Lepismatina* has a spondylium. However, as shown by Yang & Xu (1966), true *Lepismatina* has discrete dental adminicula that are fused to the median septum by a callus. Both ‘*L.*’ *arctica* (Dagys, 1965, p. 95, pl. 14, figs 1, 2) and ‘*L.*’ *austriaca* (Suess, 1854; see also Dagys 1974, p. 144, pl. 40, figs 6, 7, text-fig. 98) have high spondylia, and are apparently different from those of the type species. Sun *et al.* (2017) mentioned that these species should be included in *Psioidea* Hector, 1879. Nevertheless, the lateral slopes of *Psioidea* are smooth, in contrast to the ribbed ones of *Lepismatina*. Possibly these species can be re-assigned to *Zugmayerella* Dagys, 1963 or *Spinolepismatina* Dagys, 1974.

Dagys (1974) included ‘*Spiriferina*’ *asiatica* Dagys (1965, p. 128, pl. 20, figs 1–6), ‘*S.*’ *terekhovi* Dagys (1965, p. 124, pl. 20, fig. 7), and ‘*S.*’ *viligensis* Dagys (1965, p. 129, pl. 19, figs 1–7) in his newly established genus *Costispiriferina* Dagys, which was proved to be a junior synonym of *Lepismatina* (Dagys 1996; Carter 2006a; Sun *et al.* 2017). These three species differ from *L. hsui* in having a concave interarea and a curved ventral umbo.

One species from the Middle Triassic Junzihe Formation, Qinghai, *L. qilianensis* Xu & Liu (1983, p. 121, pl. 10, figs 2, 3) is comparable with *L. hsui*, and only differs in having a wider delthyrium and a lower interarea. *L. shalshalensis* (Bittner, 1899, p. 42, pl. 4, fig. 1; see also Dagys 1974, p. 127, pl. 34, figs 7, 8, pl. 39, figs 4, 5, text-fig. 86) is also similar to this species, but differs in having a somewhat wider delthyrium and a lack of distinct growth lamellae.

Superfamily **Spiriferinoidea** Davidson, 1884

Family **Spiriferinidae** Davidson, 1884

Subfamily **Mentzeliinae** Dagys, 1974

Genus ***Dagyssia*** Gaetani & Mantovani, 2015

Type species. *Spiriferina paläo-typus* var. *lineolata* Loretz, 1875.

Dagyssia multicostata (Yang & Xu, 1966)

(Fig. 20A)

1966 *Mentzelia multicostata* Yang & Xu: 54, pl. 8, figs 3–7, 10, 11.

1978 *Mentzelia multicostata* Yang & Xu; Feng & Jiang: 300, pl. 106, fig. 4.

Material. One ventral valve (BGEG LDP10120) from Leidapo.

Occurrence. Qingyan, Machangping and Yangpu, Guizhou, southwestern China; Dangchang, western Qinling (Gansu), western China.

Remarks. The described specimen is incomplete and scratched, but the shape of the ventral valve, developed sulcus and obscure costae on the flanks suggests its assignment to this species.

This species was originally described as *Mentzelia multicostata* by Yang & Xu (1966) from Guizhou. Later, several authors (Sun & Ye 1982; Xu & Liu 1983) re-assigned the *multicostata* species to *Hirsutella* Cooper & Muir-Wood, 1951. Carter (2006b, p. 1889) also chose the illustrated specimens of '*Hirsutella multicostata*' by Xu & Liu (1983) in their description of the genus *Hirsutella* and attributed the authorship of this species to Yang & Yin. However, the authorship of the *multicostata* species is more correctly Yang & Xu, instead of Yang & Yin. Besides, the specimens described by Xu & Liu (1983) as *Mentzelia multicostata* Yang & Xu from the southern Qilian region, western China are better re-assigned to another species, rather than Yang & Xu's (1966) species. The detailed comparisons between the *multicostata* species and other allies show that the former is not *Hirsutella*, instead, is better attributed to *Dagyssia* Gaetani & Mantovani, 2015.

Xu & Liu (1983, p. 36) noted '*Hirsutella multicostata* = *Mentzelia multicostata*, *Aequspiriferina multiplicata* Yang and Yin' and in the description of *Hirsutella multicostata*, these authors incorrectly cited Yang & Yin as the authors of the species. Unfortunately, this erroneous authorship of the *multicostata* species was followed by Carter (2006b) who described and illustrated *Hirsutella multicostata*. Clearly, the authorship of *Mentzelia multicostata* should be attributed to Yang and Xu (1966) since these authors established the present species in 1966. Another allied species *Aequspiriferina multiplicata* Yang & Yin in Yang *et al.* (1962) was nominated as the type species of *Aequspiriferina* Yang & Yin in Yang *et al.* (1962), which has different internal features from the former (Xu & Liu 1983, pp. 120, 123).

The specimens described by Xu & Liu (1983, p. 120, pl. 9, figs 28, 29, pl. 10, fig. 1) from southern Qilian were reportedly identical with those of the Guizhou species. However, the Qilian specimens have a low interarea, curved ventral beak, and lack a distinct sulcus and fold, which distinguish it from the Guizhou form. *Hirsutella* is distinguished by a high interarea. Neither '*multicostata*' from southern Qilian nor true *multicostata* species from Guizhou can be assigned to that genus. The Guizhou species should be referred to *Dagyssia* in having a conspicuous sulcus, relatively coarse costae and a false spondylium. It differs from the type species *D. palaeotypus* (Loretz, 1875, p. 802, pl. 21, fig. 1) in having coarser costae and longer hingeline. The *multicostata* species also has similar ventral internal structures to those of *Koeveskallina bifurcata*, but is distinguishable in its coarse and simple costae and uniplicate anterior commissure.

Genus ***Koeveskallina*** Dagys, 1965

Type species. *Spiriferina koeveskalliensis* Böckh, 1872 = *Spiriferina koeveskalyensis* Stur, 1865.

Koeveskallina bifurcata sp. nov.

(Fig. 20B–H, 21)

Diagnosis. *Koeveskallina* with transversely oval outline, moderately convex ventral valve and gently convex dorsal valve; fold and sulcus absent; partial costellae increasing by bifurcation, sometimes by intercalation.

Etymology. *Bifurcata* (Latin), referring to the costellae increasing mainly by bifurcation.

Material. Six ventral valves and five dorsal valves from Leidapo; one ventral valve and one dorsal valve from Wachangpo, and some fragments. One ventral valve (BGEG WCP10087) is designated herein as holotype, two dorsal valves (BGEG LDP10096, 10097) and one ventral valve (BGEG LDP10093) are selected as paratypes. Other registered specimens: BGEG LDP10095, 10098, 10132, 10133.

Occurrence. Qingyan, Guizhou, southwestern China.

Description. Shell small to medium size, width less than 11 mm (Table S19), transversely oval in outline, moderately ventribiconvex; cardinal extremities rounded to subangular; hingeline straight, maximum width slightly anterior to hingeline, at midlength of shell; anterior commissure rectimarginate. Ventral valve moderately convex; beak acute, gently curved, beak ridges angular; interarea moderately high, concave, apsacline; delthyrium triangular and narrow, not covered, with base about one-fifth of hinge width; sulcus absent. Dorsal valve slightly convex; fold absent. Both valves ornamented by costellae, some bifurcating once anterior to beak or at anterior part of shell, some increasing by intercalation.

Ventral interior with high median septum, connected with long dental flanges to form a high and W-shaped false spondylium, protruding into the spondylial chamber (Fig. 21). Dorsal crural plates short, connected to dorsal floor apically.

Remarks. This new species is represented by a few disarticulated ventral valves, dorsal valves, and some fragments. When compared with the new species, the type species *K. koeveskalyensis* (Stur, 1865) shows a more elongate outline, a strongly convex ventral valve and simpler costae without bifurcation (Bittner 1890, p. 26, pl. 34, figs 29–32, 35; Pálfy 2003, p. 147, pl. Br-I, 17–21; Gaetani & Mantovani 2015, p. 173, pl. 2, figs 4–11). *K. pannonica* (Bittner, 1890, p. 25, pl. 34, fig. 36) has a ventral sulcus and strongly convex shell, and is apparently different. Two species from Qinghai, China: *K. epichara* Sun & Ye (1982, p. 163, pl. 2, figs 13–16) and *K. media* Sun & Ye (1982, p. 163, pl. 2, figs 17–20) can be distinguished from the new species by their coarser costellae.

The transversely oval outline and bifurcated costellae of the new species recall those of *Sinucosta bifucata* Sun & Shi in Jin *et al.* (1985, p. 220, pl. 17, figs 29–32), described from the Upper Triassic of Yunnan, southwestern China, but the Yunnan species has discrete dental adminicula internally and a weak sulcus externally. *Dagyssia* Gaetani & Mantovani, 2015, with *Spiriferina palaeotypus* Loretz, 1875 as the type species, differs from *Koeveskallina* in its less convex ventral valve, transverse outline and pronounced sulcus and fold. In having a less globose shell and transverse outline, the Qingyan species is consistent with an assignment to *Dagyssia*. However, this taxon lacks a sulcus and fold, and thus is referred to *Koeveskallina*, although it markedly differs from the type species *K. koeveskalyensis*.

Genus ***Mentzelia*** Quenstedt, 1871 in 1868–1871

Type species. *Spirifer medianus* Quenstedt, 1852 in 1849–1875 = *Spirifer mentzeli* Dunker, 1851.

Mentzelia mentzeli (Dunker, 1851)
(Fig. 20I–N)

1851 *Spirifer mentzeli* Dunker: 287, pl. 34, figs 17–19.
1890 *Spiriferina* (*Mentzelia*) *mentzeli* Dunker; Bittner: 22, pl. 34, figs 1–23, 27–28.
1912 *Spiriferina mentzeli* Dunker; De Toni: 328, pl. 1, fig. 5.
1955b *Mentzelia mentzeli* (Dunker); Wang: 165, pl. 98, figs 16–20.
1964 *Mentzelia mentzeli* (Dunker); Wang *et al.*: 586, pl. 113, figs 15–18.
1966 *Mentzelia mentzeli* (Dunker); Yang & Xu: 53, pl. 7, figs 5–9.
1967 *Mentzelia mentzeli* (Dunker); Casati & Gnaccolini: 124, pl. 9, figs 4, 9.
1969 *Mentzelia mentzeli mentzeli* (Dunker); Gaetani: 507, pl. 34, figs 8–10.
1972 *Mentzelia mentzeli mentzeli* (Dunker); Siblík: 183, pl. 42, fig. 1.
1974 *Mentzelia mentzeli* (Dunker); Dagys: pl. 40, fig. 1.
1978 *Mentzelia mentzeli* (Dunker); Feng & Jiang: 299, pl. 106, fig. 2.
1978 *Mentzelia mentzeli* (Dunker); Xu: 293, pl. 97, fig. 10.
1979 *Mentzelia mentzeli* (Dunker); Jin *et al.*: 175, pl. 53, figs 13–16.

1993 *Mentzelia mentzeli* (Dunker); Iordan: pl. 1, fig. 14.

1997 *Mentzelia mentzeli* (Dunker); Torti & Angiolini: 161, pl. 1, figs 20, 21, pl. 3, figs 7, 8.

2003 *Mentzelia mentzeli* (Dunker); Pálfy: 146, pl. Br-I, fig. 15.

2015 *Mentzelia mentzeli* (Dunker); Gaetani & Mantovani: 166, pl. 1, figs 1–8.

Material. One articulated specimen from Leidapo and numerous disarticulated valves from Leidapo and Wachangpo, mostly deformed or broken. Registered specimens: one articulated specimen (BGEG LDP10121), five ventral valves (BGEG LDP10122–10126) and five dorsal valves (BGEG LDP10127–10131).

Occurrence. Anisian, widely distributed across entire Tethys region; Ladinian, western Tethys.

Description. Small to medium size, 10–20 mm long, 11–21 mm wide (Table S20), transversely oval, subpentagonal or subrounded in outline, ventribiconvex; anterior margin broadly rounded, weakly uniplicate, almost rectimarginate in small specimens; widest at posterior third to midlength; hingeline straight, about half of shell width; cardinal extremities rounded. Ventral valve moderately to strongly convex; beak moderately incurved, beak ridges rounded; interarea concave, low to moderately high; delthyrium triangular, open; sulcus absent or weak in small specimens, conspicuous in large ones, starting at midlength or anterior to it. Dorsal valve moderately convex; fold low, more distinct near anterior margin. Shell without costae; growth lamellae prominent, covering entire shell or limited to anterior half of shell; micro-ornament of dense spinules.

Remarks. This taxon is a long-established and very variable species. The specimens from Guizhou possess a fold and sulcus developed near the anterior margin, and are different from the specimens figured by Dunker (1851, pl. 34, figs 17–19) and by Quenstedt (1871 in 1868–1871, pl. 54, figs 58–61), which show rectimarginate anterior commissures. Bittner (1890) established many subspecies within *M. mentzeli*, most of which have variably developed folds and sulci. Yang & Xu (1966) indicated that the Guizhou species is closer to *M. mentzeli illyrica*. But, according to Bittner's figure (Bittner 1890, pl. 34, fig. 28), this subspecies has a longer sulcus, which initiates at the umbo. Actually, in having a short sulcus and inconspicuous fold, our specimens show greatest similarity to *M. mentzeli mentzeli* figured by Bittner (1890, pl. 34, figs 1–19), and therefore can be included in the nominate subspecies.

Small specimens (<15 mm in width) of this species often have a very weak sulcus, and are easily confused with those of *M. subspherica* Yang & Xu, 1966 in the absence of sulcus (Fig. 20M). A great number of specimens from Qingyan Formation were referred to *M. subspherica* by Yang & Xu (1966) and only eight specimens were assigned to *M. mentzeli*. The former is said to be different from the latter in having a rounded or elongate outline and lacking a sulcus and fold (Yang & Xu 1966). These authors figured only three specimens of *M. subspherica* on their plates (Yang & Xu 1966, pl. 7, figs 10, 11, pl. 8, figs 1, 2). However, the three specimens are not very similar to each other. The two ventral valves shown on their plate 7 have an elongate outline and a high ventral interarea. Nevertheless, the holotype of the species, shown on plate 8 is transverse in outline and has a relatively low interarea. Although it differs from the sulcus-bearing *M. mentzeli* collected by Yang and Xu in the absence of a sulcus and fold, there is the possibility that it can still be referred to *M. mentzeli* due to its similarities with those figured by Dunker (1851) and Quenstedt (1871). If so, *M. subspherica* becomes a junior synonym of *Mentzelia mentzeli*. However, the specimens on plate 7 (Yang & Xu 1966) differ clearly from *M. mentzeli*. More material is needed to confirm or reject this synonymy.

One specimen illustrated by J. Chen *et al.* (2010a, fig. 4.5, 4.6) as *Madoia* sp. possesses a relatively high interarea and lacks subimbricate growth varices, and thus cannot be assigned to *Madoia* Sun & Ye, 1982, which is characterized by a low interarea and strong growth lamellae. Instead, the illustrated characteristics of J. Chen *et al.*'s (2010a) specimen agree with *Mentzelia mentzeli* described here, although its interiors remain unknown.

Order **Terebratulida** Waagen, 1883

Suborder **Terebratulidina** Waagen, 1883

Superfamily **Dielasmatoidea** Schuchert, 1913

Family **Dielasmatidae** Schuchert, 1913

Subfamily **Dielasmatinae** Schuchert, 1913

Genus ***Coenothyris*** Douvillé, 1879

Type species. *Terebratulites vulgaris* von Schlotheim, 1820.

Coenothyris elongata (Yang & Xu, 1966)

(Fig. 20O–R)

1966 *Adygella elongata* Yang & Xu: 73, pl. 12, figs 1, 2.
1974 *Adygella elongata* Yang & Xu; Liao & Sun: 351, pl. 184, figs 1–3.
1978 *Adygella elongata* Yang & Xu; Xu: 300, pl. 100, fig. 6.
1978 *Adygella elongata* Yang & Xu; Feng & Jiang: 302, pl. 108, fig. 1.
1992 *Adygella elongata* Yang & Xu; Xu: 150, pl. 4, fig. 3.

Material. Three articulated shells from Leidapo. Registered specimen: BGEG LDP10004 (19.9 mm long, 12.2 mm wide).

Occurrence. Qingyan, Guizhou, and Emei, Sichuan, southwestern China; Dangchang, western Qinling (Gansu), western China.

Remarks. Our material is assigned to this species on the basis of its elongately oval outline and the dorsal valves lacking a sulcus. This species was originally assigned to *Adygella* Dagys, 1959 by Yang & Xu (1966). They noted in the Chinese description that the species lacks a pedicle collar, however, as stated in the English description and shown by serial sections (Yang & Xu, 1966, text-fig. 73), the pedicle collar is quite distinct. In having a well-developed pedicle collar and a long loop, this species is now re-assigned to *Coenothyris*. It is distinguishable from other species of this genus in having a marked elongate outline. This species has different internal structures from *Angustothyris qingyanensis* sp. nov. described below. Externally, *Coenothyris elongata* is distinguished from the latter by the complete absence of a dorsal sulcus and a longer outline.

Family **Angustothyrididae** Dagys, 1972c

Genus ***Angustothyris*** Dagys, 1972c

Type species. *Angustothyris dagysi* sp. nov.

Type species now fixed (under Article 70.3 of the International Code of Zoological Nomenclature) as *Angustothyris dagysi* sp. nov., misidentified as *Waldheimia angustaeformis* Böckh, 1872 in the original designation by Dagys (1972c).

Remarks. When establishing *Angustothyris*, Dagys (1972c) designated *Waldheimia angustaeformis* as the type species. Dagys' new genus was defined based on specimens identified as *Waldheimia angustaeformis* from the Caucasus region. However, the *angustaeformis* species was established by Böckh (1872, pl. 11, fig. 20) based on specimens from Köveskál in Hungary, but its internal structures were not described at that time. Since then, many specimens from the Triassic of the Alps, Carpathians, Balkans, Crimea, Caucasus, and southwestern China have been collectively assigned to this species (Bittner 1890; Salomon 1895; Yang & Xu 1966; Siblík 1972; Dagys 1972c, 1974; Liao & Sun 1974).

In his description of *Angustothyris angustaeformis* (Böckh) based on specimens from Caucasus, Dagys (1972c) reported that '*A. angustaeformis* (Böckh)' is characterized by a pronounced septalium in the doral valve. However, Pálfy (2003) re-studied the specimens of *angustaeformis* from its type locality in Hungary and found that the Hungarian species indeed lacks a median septum and septalium in the dorsal valve. Accordingly, the Caucasus material identified as '*A. angustaeformis* (Böckh)' is not synonymous with the Hungarian species, and actually belongs to a different genus. A new species therefore is proposed here to include the Caucasus specimens and to unambiguously establish the type species of *Angustothyris* Dagys, 1972c. Moreover, the Hungarian material assigned to *angustaeformis* may represent a new genus since they are quite different from *Angustothyris* (Dagys 1972c, 1974; Pálfy 2003).

Angustothyris dagysi sp. nov.

1972c *Angustothyris angustaeformis* (Böckh); Dagys: figs 11–14, 25.
1974 *Angustothyris angustaeformis* (Böckh); Dagys: pl. 48, fig. 1.

Diagnosis. *Angustothyris* with sub-oval outline and slightly unisulcate anterior commissure; dorsal sulcus wide and shallow; inner socket ridges very high; outer hinge plates very narrow or absent; septalium prominent.

Etymology. Named after Algirdas Dagys, a Lithuanian paleontologist, in recognition of his contribution to the study of Triassic brachiopods.

Holotype. The specimen figured by Dagys (1974, pl. 48, fig. 1) which was collected from the Anisian of the northwestern Caucasus is selected as the holotype herein.

Remarks. The new species clearly differs from '*Waldheimia*' *angustaeformis* Böckh, 1872 from Hungary in the development of its internal structures. Externally, this species is distinguished from the Hungarian species by its ovate outline and relatively shallower dorsal sulcus. The differences between this species and *Angustothyris qingyanensis* sp. nov. will be given in the remarks for that species.

Angustothyris qingyanensis sp. nov.

(Figs 20S–V, 22A–I, 23)

1955b *Rhaetina angustaeformis* (Böckh); Wang: 170, pl. 102, figs 9, 10, 13, 14.

1964 *Rhaetina angustaeformis* (Böckh); Wang *et al.*: 680, pl. 136, figs 1, 2, 6, 7.

1966 *Rhaetina angustaeformis* (Böckh); Yang & Xu: 77, pl. 12, figs 3–8.

1978 *Rhaetina angustaeformis* (Böckh); Feng & Jiang: 303, pl. 108, fig. 2.

Diagnosis. *Angustothyris* with rounded subpentagonal outline and mostly truncated anterior margin; anterior commissure rectimarginate to slightly unisulcate; dorsal sulcus deep, originating at umbo; dorsal median septum and inner socket ridges relatively low; outer hinge plates broad; septalium short; fine capillae all over shell (on well-preserved specimens).

Etymology. After Qingyan Town, where the specimens were collected.

Material. Numerous specimens. One complete specimen (BGEG WCP10017) is designated herein as holotype, three articulated specimens (BGEG WCP10018, BGEG LDP10005, 10006) are selected as paratypes. Other registered specimens: BGEG WCP10019–10030, BGEG LDP10007, 10008.

Occurrence. Qingyan and Yangpu, Guizhou, southwestern China.

Description. Small to medium in size, width less than 14 mm, length less than 20 mm (Table S21), rounded subpentagonal in outline, longer than wide; anterior margin rectimarginate to slightly unisulcate, straight and truncated, rarely broadly rounded; lateral margin gently curved; biconvex with ventral valve more convex; greatest width at midlength or slightly anterior to midvalve; thickest at midlength or posterior to midlength.

Ventral valve moderately convex in lateral profile, maximum curvature at the posterior part of shell; moderately convex in anterior profile, with greatest convexity near midline, forming blunt ridge; beak short and strong, slightly to moderately curved; beak ridges subangular; umbonal slopes steeply inclined, but flanks gently inclined; foramen large, elongate oval, mesothyrid. Dorsal valve gently convex, with maximum convexity near umbo; dorsal umbo moderately curved; sulcus distinct, initiated in umbonal region, narrow and deep, widening gradually to anterior margin where it is almost as wide as anterior margin or slightly narrower. Shell ornamented by fine capillae when preserved, distinct comarginal growth lines near anterior commissure.

Ventral interior with strong teeth, lacking dental plates; pedicle collar complete and distinct. Dorsal interior with relatively low inner socket ridges; outer hinge plates flat and broad, slightly inclined, merging with inner socket ridges; crural bases attaching to inner ends of outer hinge plates; inner hinge plates joining with median septum to form a short, V-shaped septalium; median septum relatively long and low, loosing contact with hinge plates rapidly, slightly shorter than half of shell length; loop long, with arched transverse band and long flanges, extending to about two thirds of dorsal length (Fig. 23).

Remarks. Similar specimens from Qingyan have previously been assigned to *Rhaetina angustaeformis* (Böckh) by Chinese authors (e.g. Wang 1955b; Wang *et al.* 1964; Yang & Xu 1966) because they are closely allied, externally, to '*Waldheimia*' *angustaeformis* Böckh figured by Bittner (1890). However, the presence of a strong doral medium septalium distinguishes the Qingyan material from '*Waldheimia*' *angustaeformis* Böckh (assigned to *Rhaetina* by Chinese paleontologists) that lacks a median septum and septalium in the dorsal valve (Pálfy 2003). Thus, a new species is proposed to accommodate the Qingyan specimens, and the new species agrees well with the diagnosis of *Angustothyris* Dagys, 1972c, proposed by the author.

Externally, *Angustothyris qingyanensis* differs from the Caucasian species *A. dagysi* in having a more pentagonal outline, a truncated anterior margin, and a deeper dorsal sulcus. Internally, the Qingyan species has broader outer hinge plates and much lower inner socket ridges. In addition, the median septum of *A. qingyanensis* is lower and loosely in contact with the hinge plates (Fig. 24).Popiel-Barczyk & Senkowiczowa (1983) reconstructed the loop stages of specimens identified as *A.* '*angustaeformis*' from the Middle Triassic of Poland. Compared with the mature specimens of *A. qingyanensis*, the Polish specimens of *A.* '*angustaeformis*' have a higher median septum, a longer septalium, and a shorter loop. Externally, they have a drop-shaped outline and rounded anterior and lateral margins, differing from those of

A. qingyanensis. *A.* '*angustaeformis*' described by Torti & Angiolini (1997, p. 168, pl. 1, figs 35, 36) from Val Parina, Bergamasque Alps, Italy has a broadly rounded anterior margin and a shallow and broad dorsal sulcus, and is closely allied to the species illustrated by Dagys (1974, pl. 48, fig. 1). The species described by Liao & Sun (1974, p. 351, pl. 184, figs 18–21) from the Middle Triassic of Sichuan has a rounded anterior commissure and lacks a dorsal sulcus, thus is obviously different from the Qingyan species.

The type specimen of '*Waldheimia*' *angustaeformis* figured by Böckh (1872, pl. 11, fig. 20) is 16 mm long, 14 mm wide, 7 mm thick, and subpentagonal in outline. It has a strongly unisulcate anterior margin and a wide and deep sulcus beginning at the umbo. Greatest width and thickness are at the midlength of shell. Compared with *Angustothyris qingyanensis*, it differs in having a more pentagonal outline, strongly unisulcate anterior commissure, and steep flanks of ventral valve (Fig. 24). Although the specimens collected by Pálfy (2003, p. 152, pl. Br-I, 32–33) from the type locality are not completely identical with the one figured by Böckh, they are also strongly unisulcate. Besides, they have shallower and wider sulci than those of *Angustothyris qingyanensis* (Fig. 24).

Suborder **Terebratellidina** Muir-Wood, 1955

Superfamily **Zeillerioidea** Allan, 1940

Family **Zeilleriidae** Allan, 1940

Subfamily **Zeilleriinae** Allan, 1940

Genus ***Sacothyris*** Jin, Sun & Ye in Jin *et al.*, 1979

Type species. *Aulacothyropsis sinosa* Jin & Fang, 1977.

Sacothyris angustaeformis (Yang & Xu, 1966)

(Fig. 22P–S)

1966 *Aulacothyris angustaeformis* Yang & Xu: 87, pl. 14, figs 9, 10.

1978 *Aulacothyris angustaeformis* Yang & Xu; Feng & Jiang: 304, pl. 108, fig. 8.

Material. One articulated specimen from Leidapo; two articulated shells from Wachangpo. Registered specimens: BGEG LDP10009, BGEG WCP10031.

Occurrence. Qingyan, Guizhou, southwestern China; Dangchang, western Qinling

(Gansu), western China.

Description. Shell very small, length less than 9 mm, width less than 8 mm (Table S22), subcircular to oval in outline, slightly longer than wide, widest and thickest at midlength; anterior commissure sulcate, lateral margin broadly curved. Ventral strongly convex along midline, forming blunt ridge; lateral flanks gently convex, steeply inclined; beak strongly curved, beak ridges rounded; pedicle foramen oval, permesothyrid. Dorsal valve moderately to strongly convex in lateral profile; sulcus commencing from beak, widening and deepening anteriorly, lateral slopes gently inclined. Shell smooth with comarginal growth lines.

Remarks. Our material is identical to those specimens described by Yang & Xu (1966) in having a very small size, a deep and broad ventral sulcus, and the strongly convex shell. This species was assigned to *Aulacothyris* Douvillé, 1879 by Yang & Xu (1966). But, *Aulacothyris* has a short dorsal median septum, thin ascending branches, and lacks a pedicle collar, thus cannot accommodate the present species. In having an *Aulacothyris*-like shape, a conspicuous pedicle collar, a pronounced dorsal septalium, a long median septum and a teloform loop with plate-like ascending lamellae (Yang & Xu 1966), the *angustaeformis* species should be re-assigned to *Sacothyris* Jin, Sun & Ye in Jin *et al.*, 1979. The type species, *S. sinosa* (Jin & Fang, 1977, p. 64, pl. 6, figs 5–8) from the Upper Triassic of Yunnan, southwestern China is different from the Qingyan species in being larger and having a short ventral sulcus near anterior margin. *S. deqinica* (Jin & Fang, 1977, p. 65, pl. 6, figs 1–4) from the same localities with the type species lacks a ventral sulcus, but has a much longer outline in comparison with *S. angustaeformis*.

Aulacothyropsis reflexa (Bittner, 1890) is close to this species in shape, but the former lacks a developed septalium and possesses a loop with connecting bands and undivided descending and ascending branches (diploform). *A. megaeminens* Xu (1978, p. 311, pl. 103, figs 13, 14) from the Upper Triassic Kuahongdong Formation of Sichuan, southwestern China has a dorsal septalium, but its loop was not studied in detail, and thus its assignment at genus level is difficult. Xu's (1978) species also differs clearly from *Sacothyris angustaeformis* in having a larger size and thinner shell.

Discussion

Brachiopod faunal composition

A total of 2789 specimens assigned to 28 species (and subspecies) within 25 genera and 2586 specimens assigned to 22 species within 19 genera were collected from the Leidapo and Wachangpo localities, respectively. These two fossil localities are similar in lithology and very close in age, but yield different brachiopod assemblages. The Wachangpo assemblage is dominated by *Angustothyris qingyanensis* (41.1%), with abundant *Diholkorhynchia sinensis* (20.8%), *Mentzelia mentzeli* (14.5%), and *Caucasorhynchella subfissicostata* (13.7%), together with a minor constituent of *Cassianospira wachangpoensis* (4.3%) (Fig. 25). The predominant elements of the Leidapo assemblage are *D. sinensis* (36.1%) and *A. qingyanensis* (23.1%). Both *M. mentzeli* (19.4%) and *Septaliphorioidea paucicostata* (5.9%) are also common in this assemblage (Fig. 25).

When compared with the Wachangpo assemblage with a Shannon index of 1.65, and Dominance index of 0.26, the Leidapo community possesses a relatively higher diversity and lower dominance index (Shannon index = 1.83, Dominance index = 0.23), and has more specimens of *D. sinensis* and fewer *A. qingyanensis*. Both diagnostic elements, *C. subfissicostata* and *C. wachangpoensis* in the Wachangpo assemblage are very rare or absent in the Leidapo community. Instead, the Middle Triassic diagnostic genus, *Nudirostralina* Yang & Xu (Jin *et al.* 1979) is rather common, with about 100 specimens assignable to *N. subtrinodosi subtrinodosi*, *N. subtrinodosi multicostata*, and *N. minuta* at Leidapo, but is absent at Wachangpo. The fossil horizon of the Wachangpo locality equates to the '*Rhaetina angustaeformis* shell bed' of J. Chen (2010a), and is slightly lower than those of the Leidapo locality. The Wachangpo assemblage therefore is slightly older than the Leidapo fauna. Both the Leidapo and Wachangpo localities share a similar lithology and are very close to each other, so the difference between the two assemblages is possibly because they are derived from different stratigraphical horizons.

Faunal affinity of the Qingyan brachiopods

To date, 40 species (and subspecies) belonging to 31 genera have been described from Qingyan. The Qingyan fauna therefore is one of the most diverse Anisian brachiopod faunas. The Qingyan brachiopods, as a whole, are characterized by a large proportion of endemic genera especially spiriferinids. Nine of the 27 (33.3%) genera (*Qingyenia*, *Thecocyrtelloidea*, *Leiolepismatina*, *Neocyrtina*, *Parabrekia*, *Septaliphorioidea*, *Sinorhynchia*, *Caucasorhynchella*, and '*Rutorhynchia*') have not been reported elsewhere. Moreover, a large number of widespread genera also characterize the Qingyan fauna. Of these, 11 genera: *Angustothyris*, *Schwagerispira*, *Spirigerellina*, *Coenothyris*, *Nudirostralina*, *Costirhynchopsis*, *Koeveskallina*, *Lepismatina*, *Dagyssia*, *Thecocyrtella*, and *Mentzelia* have been widely reported from the eastern and western Tethyan regions, with some elements even occurring in the Himalayan region, suggesting the development of near-global distributions. Moreover, *Cassianospira* is confined to Qingyan during the Anisian, but this taxon spread rapidly to Croatia, Alps, Hungary, and Carpathians in the western Tethys region during the Ladinian and late Triassic (Alvarez & Rong 2002; Halamski *et al.* 2015). *Lissorhynchia* was present only in Guizhou and southern Qilian during the Anisian, however, this genus had already appeared in the western Tethys during the Early Triassic (Dagys 1974). The Qingyan brachiopod fauna therefore is a combination of endemic and widespread genera. Except for Qingyan, Anisian brachiopods have also been reported from Yangpu in Anshun, Machangping in Fuquan, Xinmin in Panxian, and Shaiwa in Ziyun within Guizhou Province, Southwestern China (Yang & Xu 1966; Sun *et al.* 2009; He *et al.* 2015; Table 1). The latter faunas, however, are much less diverse and abundant than the Qingyan assemblage. Outside Guizhou, Anisian brachiopods have also been described from Yunnan (one species belonging to one genus) and Sichuan (10 species belonging to 10 genera) (Liao & Sun 1974; Xu 1978), southwestern China. Like the Qingyan fauna, the Yunnan and Sichuan brachiopods are dominated by either cosmopolitan (e.g. *Adygella*, *Mentzelia*, *Costirhynchopsis*, and *Lepismatina*) or endemic elements (*Emeithyris* and *Triseptothyris*).

In the Tethys region, the only brachiopod fauna which shows a strong affinity with the Qingyan fauna is that from the upper Guojiashan Formation in Dangchang, western Qinling. It consists of 24 species, and shares 11 species with the Qingyan fauna and 11 species with the brachiopod assemblage from southern Qilian Mountains, which builds a bridge between these two localities (Xu 1992). Nevertheless, the common genera in the Dangchang and Qingyan faunas are mostly cosmopolitan. By contrast, it shares many endemic taxa with the southern Qilian fauna. Thus, the Dangchang fauna bears a closer relationship with the latter. The brachiopod assemblage from the Junzihe Formation in southern Qilian Mountains consists of 59 species belonging to 25 genera and is characterized by a high diversity of terebratulids (Yang *et al.* 1962; Jin *et al.* 1979; Xu & Liu 1983). Seven genera belong to Terebratulida and most are endemic (e.g. *Parantiptychia*, *Eoantiptychia*, *Parasulcatinella*, *Athyrorhynchia*, and *Thyratryaria*). Jin *et al.* (1979) and Sun & Ye (1982) described 19 genera of brachiopods from the Naocangjiangou Formation in central Qinghai. The assemblage shows a similarity with that in southern Qilian but shares only six widespread genera with the Qingyan fauna. In contrast to the diverse spiriferinids in Qingyan, this assemblage contains abundant, endemic rhynchonellids.

In the western Tethys, Anisian brachiopods have been reported from the Alps, Carpathians, Dinarids, Hungary, northern Caucasus and other places, but they are quite similar and have many genera and species in common (Bittner 1890; Dagys 1965, 1974; Pálfy 2003). *Dinarispira*, *Decurtella*, *Volirhynchia*, *Tetractinella* and *Pexidella* are very common in European Tethys, but are very rare in eastern Tethys at least during the Anisian. Of these, only one species *Mentzelia mentzeli* is shared with the Qingyan fauna.

Jin *et al.* (1976), Chen (1983) and Xu & Liu (1983) described seven species belonging to six genera from Nyalam and Dingri, Xizang, which are situated on the northern margin of the pre-Gondwana region during the Anisian. *Yalongia* is endemic and *Tulungospirifer* is distributed in the Himalayas and Siberia (Dagys 1993). The other four genera *Nudirostralina*, *Koeveskallina*, *Diholkorhynchia* and *Adygella* are widely distributed. A similar fauna which contains only six species have been discovered from Socotra, Yemen by Gaetani *et al.* (2018). Though most of the determinable species are known only from Himalayan region, these genera, *Nudirostralina*, *Spirigerellina*, *Adygella*, *Koeveskallina* and *Lepismatina* are cosmopolitan. Excepting these diverse faunas, some smaller brachiopod assemblages have been described from Israel, Iran, northern Siberia, Turkey, north America, Far East (Russia), Xizang (Lhasa, Shuanghu, Nierong), New Zealand, Spiti (India) and Nepal (Bittner 1899; Diener 1907, 1908, 1913; Smith 1914; Dagys 1972c, 1974; Siblík 1975, 1991; Jin *et al.* 1979; Sun 1981; Sun *et al.* 1981; Dagys & Kurushin 1985; MacFarlan 1992; Feldman 2005, 2017; Ruban 2006, 2010; Gaetani 2016).

Compared with coeval brachiopod faunas elsewhere in the world, the Qingyan fauna has a very high endemicity (except for the New Zealand fauna that lacks widespread genera). With respect to the Early Triassic and Ladinian brachiopods, the Yangtze block (South China) evolved as a center for brachiopod recovery and origination after the end-Permian mass extinction. During the Griesbachian (early Induan), the first two Mesozoic-type brachiopods *Meishanorhynchia* and *Laevorhynchia* occurred sporadically in South China (Shen & He 1994; Chen *et al.* 2002). Later, another endemic genus *Lichuanorelloides* and other common elements appeared during the Early Triassic in South China (Chen *et al.* 2005b; Wang *et al.* 2017). As discussed above, many characteristic genera that did not originate in other regions, appeared first in South China during the Anisian. Most of them, though, became extinct at the end of the Anisian (e.g. *Qingyenia*, *Thecocyrtelloidea*, *Leiolepismatina*, *Neocyrtina*, *Parabrekia*, *Septaliphorioidea*, *Sinorhynchia*, *Caucasorhynchella*, *Liaous*, *Emeithyris*, and *Triseptothyris*), while several of them spread to the western Tethys during the Ladinian (e.g. *Cassianospira*). Koninckinids, a peculiar group of brachiopods that are common members of the Late Triassic and Early Jurassic faunas in the Tethys region, also originated in South China (Baeza-Carratalá *et al.* 2015; Guo *et al.* 2017). The first reliable koninckinid fauna was reported from the Ladinian of southwestern Guizhou (Guo *et al.* 2017). In the Late Triassic, due to the regional regression across the entire South China, brachiopods became rare, but some unique koninckinids occurred occasionally. Therefore, from the earliest Triassic (Griesbachian) to Middle Triassic, South China became an important center for the origination and radiation of brachiopods following the end-Permian extinction.

Global palaeobiogeography of Anisian brachiopods

Recently, Ke *et al.* (2016) studied brachiopod palaeobiogeography from the Changhsingian to Rhaetian including Anisian, but some of the data are in need of revision and some new data are now available from this study. Here we apply cluster analysis and PCOa based to 13 relatively diverse Anisian brachiopod faunas [faunas in Qingyan, western Qinling (Gansu, western China), southern Qilian (Qinghai, western China), central Qinghai (western China), Alps, Hungary, northern Caucasus, northern Siberia, Xizang (Himalayas), Socotra (Yemen), Iran, northwestern Turkey, and New Zealand] and our result show some contrasts with that reported by Ke *et al.* (2016) (Figs 26, 27). The occurrence data of the Anisian brachiopod faunas used in this study are provided in Supplementary Table S23.

Cluster analysis of global Anisian brachiopods shows five major groups: western Tethys, eastern Tethys, northern Siberia, Himalayas and New Zealand, each of which suggests an independent biogeographical province. Besides, the Jaccard similarity coefficients of these groups are very low (<0.2), implying a multi-provincial distribution pattern (Figs 26, 28). Although the percentages of the first three axis are not very high (less than 20%), in the plots of PCOa (Fig. 27), these provinces are easily to be identified. The eastern Tethys province includes Qingyan (or Yangtze), western Qinling, southern Qilian and central Qinghai. Though these four localities are grouped together, they share rather low Jaccard similarity coefficients (< 0.4) with one another, which is consistent with their marked mutual dissimilarities discussed above. According to the dendrogram, this province consists of three subprovinces, which agrees well with the deduction of Sun *et al.* (2017) (Figs 26, 28). The Yangtze subprovince is characterized by the abundant spiriferinids such as *Pseudospiriferina*, *Neocyrtina*, *Thecocyrtelloidea*, *Qingyenia*, and *Nudispiriferina*. The western Qinling-southern Qilian subprovince is dominated by the diverse terebratulids such as *Parantiptychia*, *Parasulcatinella* and *Thyratryaria*, as well as the norellid *Qilianoconcha*. In addition, the central Qinghai subprovince (Burhan Budai) is distinguished by its rhynchonellids: *Uniplicatorhynchia*, *Nucleusorhynchia* and *Paranudirostralina*.

In the dendrogram, the Alps, Hungary and northern Caucasus are grouped and they have relatively low similarity coefficient with each other, which differs from the results of Ke *et al.* (2016) (Fig. 26). In fact, the Anisian brachiopod faunas in the western Tethys have been discovered from many localities of different countries, however, they are quite similar in taxon composition and local faunas differs mainly in the number of genera identified (Dagys 1993), so the dissimilarities between these localities shown by Ke *et al.* (2016) are possibly due to the sample sizes but not taxon differences. Therefore, these localities are included within a province. This province is characterized by *Dinarispira*, *Decurtella*, *Volirhynchia*, *Tetractinella*, and *Pexidella*.

Socotra (Yemen) and Xizang in the Himalayan region are grouped, belonging to one province, which confirms their connection during the Middle Triassic (see Gaetani 2018) (Figs 26, 27). In addition, the north Siberia assemblage in the northern hemisphere is grouped with the first two because of the presence of *Lepismatina*, *Spirigerellina* and *Tulungospirifer*, which reflects a temperature control, like the pre-extinction faunas in Changhsingian (Chen *et al.* 2005a; Fig. 28). Additionally, Iran, Turkey and New Zealand are also isolated and developed as individual provinces, but these faunas consist of only four or five identified genera so the result lacks rigour (Fig. 28). Nevertheless, the fauna in New Zealand is fairly unique and shares no genera with other faunas; it is thus identified as a separate province.

Overall, the Anisian brachiopods were distinctly provincialized, implying a continuity of the multi-provincial pattern established for the global distributions of Olenekian (late Early Triassic) brachiopods (Chen *et al.* 2005b). In the aftermath of the end-Permian mass extinction, the surviving brachiopods are dominated by geographically widespread elements that adapted to a wide variety of environments, although some endemic Mesozoic-type brachiopods (such as *Meishanorhynchia*, *Laevorhynchia* and *Lichuanorelloides*) occurred sporadically. During this interval, brachiopods endured the survival stage and began to recover, but the biogeographic pattern of post-extinction brachiopods still appeared unchanged, due to limited data.

Thus, the global Induan brachiopods shared the same biogeographic provincial patterns (Chen *et al*. 2005b). The Olenekian (late Early Triassic) brachiopod faunas are characterized by widespread brachiopod dispersal, multiprovincialism, with an increasing number of endemic elements (i.e., *Periallus*, *Portneufia*, *Protogusarella*, and *Vex* in North America, and *Compositella*, *Antezeilleria*, and *Proanadyrella* in southern Qilian; Table S23) and four provinces are recognized within the global Olenekian brachiopod faunas (Ke *et al.* 2016). Later, global provincialism became more and more prominent during the recovery stage in the Middle Triassic, and reached a peak during the Carnian (Late Triassic) (Ke *et al.* 2016).

Conclusions

Qingyan brachiopod fauna is one of the most important and diverse Anisian (Middle Triassic) brachiopod assemblages in the world. In this paper 34 species (and subspecies) assigned to 29 genera are described from the Qingyan Formation from the Leidapo and Wachangpo localities, Qingyan, Guizhou, southwestern China. Eleven species within 11 genera are described for the first time from this area, including one new genus (*Parabrekia*), six new species (*Angustothyris qingyanensis*, *Koeveskallina bifurcata*, *Neocyrtina xui*, *Nudirostralina minuta*, *Parabrekia yangi*, and *Rutorhynchia*? *trigonalis*) and seven undetermined species. *Angustothyris dagysi* sp. nov. is proposed to include the Caucasus specimens previously ascribed to *Angustothyris angustaeformis* (Böckh) by Dagys (1972c, 1974), and fixed as the type species of *Angustothyris* Dagys, 1972c. The Qingyan specimens previously described as '*Rhaetina angustaeformis*' are now re-assigned to a new species *Angustothyris qingyanensis*. In addition, *Crurirhynchella* Xu & Liu, 1983 is treated as a *nomen nudum* and abondened. Instead, a new generic name, *Caucasorhynchella*, is proposed to accommodate the Qingyan specimens. Compared with other Anisian brachiopod assemblages, the Qingyan fauna is characterized by abundant endemic genera (33.3%) and fewer cosmopolitan taxa. The cluster analysis of 13 Anisian brachiopod faunas, distributed globally, identifies at least five provinces: western Tethys, eastern Tethys, northern Siberia, Himalayas and New Zealand are present during the Anisian, and the eastern Tethys province includes three subprovinces: Yangtze, southern Qilian-western Qinling and central Qinghai (Burhan Budai). Additionally, most faunas share rather low Jaccard similarities (< 0.4) with one another, implying the continuity of multi-provincial distribution patterns established in Early Triassic brachiopod assemblages.

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Figure and table captions

Figure 1. Geological setting of the fossil localities. **A,** general map of China with locations of Guizhou and Qingyan marked; **B,** map of central Guizhou Province showing the location of Qingyan; **C,** geological map of the vicinity of Qingyan town showing the fossil localities (after Stiller & Bucher 2008). T_1a = Lower Triassic Anshun Formation; T_2q = Middle Triassic Qingyan Formation, T_2q^1 = Xiaoshan Member, T_2q^2 = Mafengpo Member, T_2q^3 = Yingshangpo Member, T_2q^4 = Leidapo Member, T_2q^5 = Yuqing Member; T_2h = Middle Triassic Huaxi Formation.

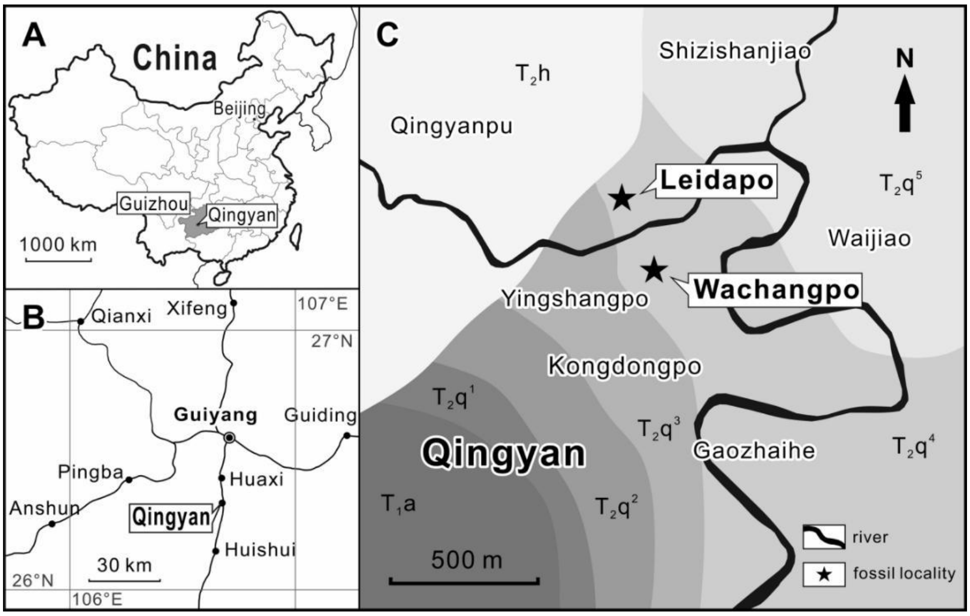


Figure 2. Middle Triassic (Anisian) stratigraphy in the Qingyan region. Thickness of the members after Guizhou Bureau of Geology and Mineral Resources (1987). Position of the two fossil localities marked by the grey band, after Stiller & Bucher (2008).

Figure 3. Rarefaction curves with 95% confidence limits for the brachiopod samples from the two localities in Qingyan.

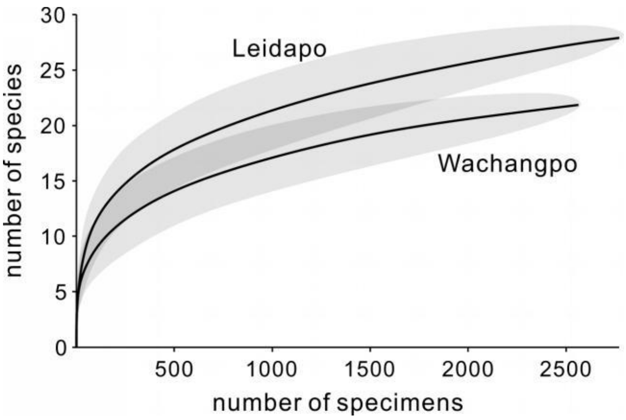


Figure 4. Comparisons of the crura of *Caucasorhynchella* gen. nov. and *Caucasorhynchia* Dagys, 1963. **A,** reconstruction of the crura of *Caucasorhynchella*, based on Fig. 6; **B,** reconstruction of the crura of *Caucasorhynchia*, based on its type species, *Caucasorhynchia kunensis* Dagys (Dagys 1963).

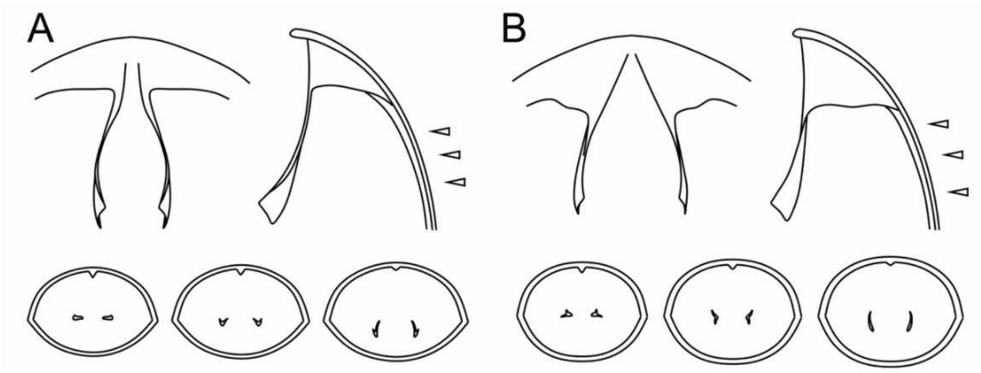


Figure 5. A–I, *Caucasorhynchella subfissicostata* (Yang & Xu, 1966); **A–D,** BGEG WCP10032, dorsal, ventral, lateral, and anterior views of an articulated shell; **E,** detail of the ventral umbo of BGEG WCP10032, showing the mesothyrid foramen and disjunct deltidial plates; **F–I,** BGEG WCP10034, dorsal, ventral, lateral, and anterior views of an articulated shell. **J–S,** *Septaliphorioidea paucicostata* Yang & Xu, 1966; **J–M,** BGEG LDP10010, dorsal, ventral, lateral, and anterior views of an articulated shell; **N–Q,** BGEG LDP10011, dorsal, ventral, lateral, and anterior views of an articulated shell; **R, S,** BGEG LDP10012, dorsal and ventral views of an articulated shell. **T–Y,** *Rutorhynchia*? *trigonalis* sp. nov.; **T–W,** holotype, BGEG LDP10020, dorsal, ventral, anterior and lateral views of an articulated shell; **X, Y,** paratype, BGEG LDP10022, dorsal and ventral views of a deformed and articulated shell. **Z–C',** *Nudirostralina subtrinodosi* Yang & Xu, 1966, BGEG LDP10031, dorsal, ventral, lateral and anterior views of an articulated shell.

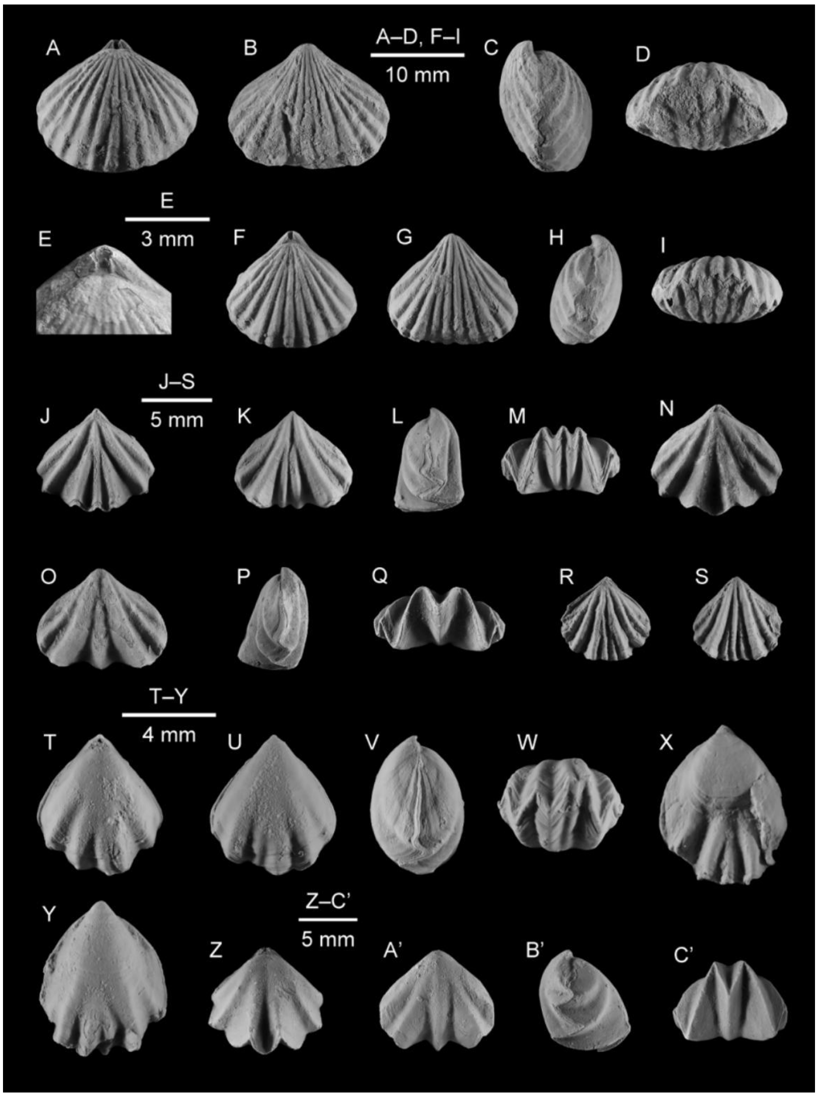


Figure 6. Serial sections of *Caucasorhynchella subfissicostata* (Yang & Xu, 1966) (based on specimen BGEG WCP10035). The numbers indicate distances (in mm) from the ventral beak. The specimen is 13.7 mm long.

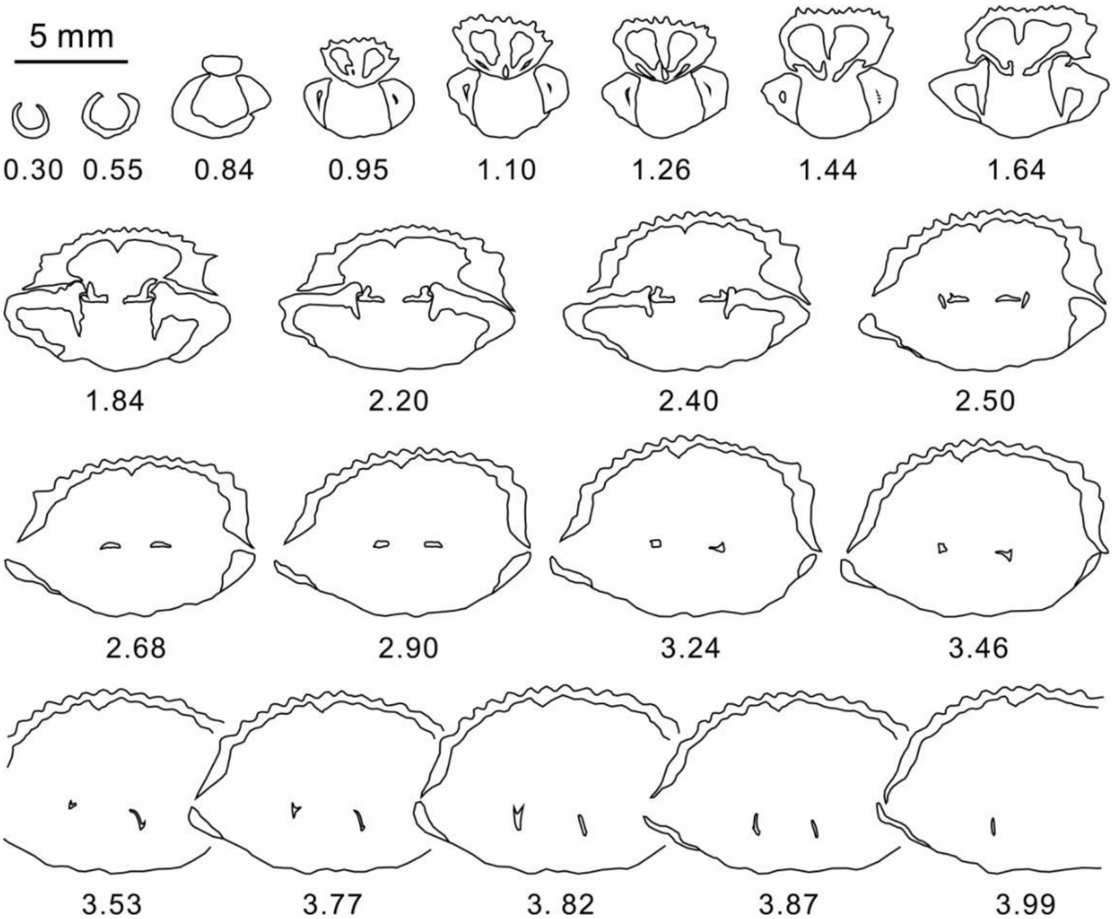


Figure 7. Serial sections of *Rutorhynchia*? *trigonalis* sp. nov. (based on specimen BGEG LDP10021). The numbers indicate distances (in mm) from the ventral beak. The specimen is 5.3 wide, and its anterior part is deformed.

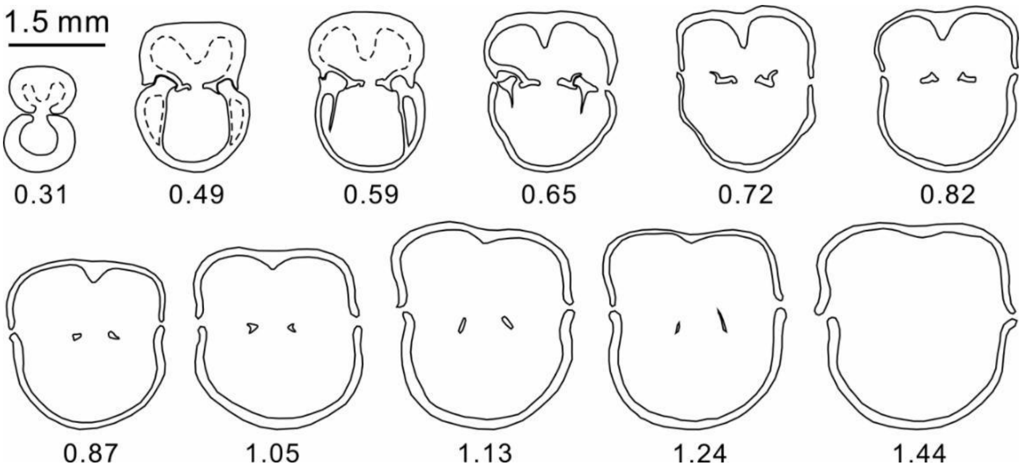


Figure 8. A–D, *Nudirostralina subtrinodosi* Yang & Xu, 1966, BGEG LDP10033, dorsal, ventral, lateral, and anterior views of an articulated shell. **E–H,** *Nudirostralina subtrinodosi multicostata* Yang & Xu, 1966, BGEG LDP10046, dorsal, ventral, lateral, and anterior views of an articulated shell. **I–Q,**

Nudirostralina minuta sp. nov.; **I–L,** paratype, BGEG LDP10049, dorsal, ventral, lateral, and anterior views of an articulated shell; **M,** BGEG LDP10050, ventral view of a deformed articulated specimen; **N–Q,** holotype, BGEG LDP10047, dorsal, ventral, anterior, and lateral views of an articulated shell. **R–Y,** *Parabrekia yangi* sp. nov.; **R–U,** paratype, BGEG LDP10052, dorsal, ventral, lateral, and anterior views of an articulated shell; **V–Y,** paratype, BGEG LDP10053, dorsal, ventral, anterior and lateral views of an articulated shell.

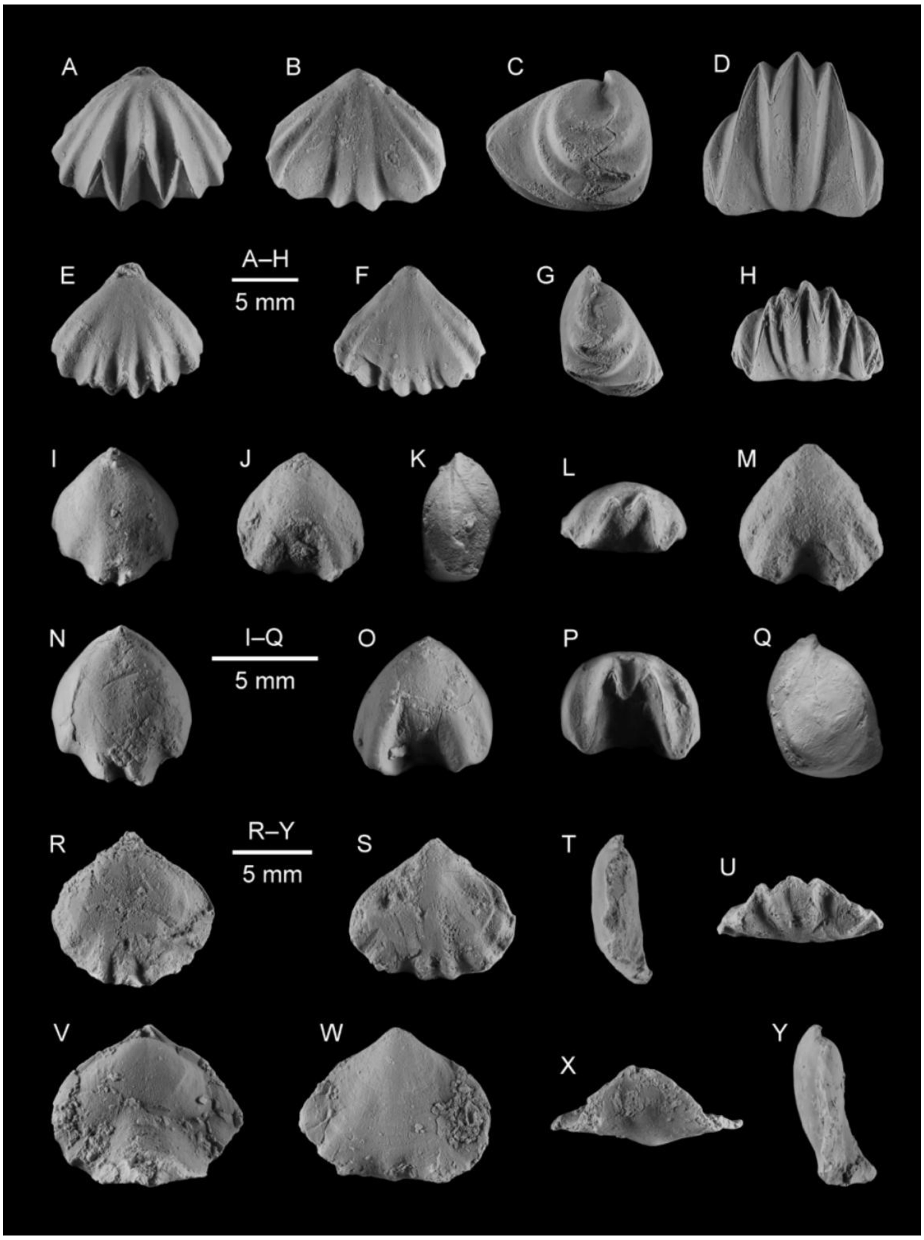


Figure 9. Serial sections of *Nudirostralina subtrinodosi* Yang & Xu, 1966. **A,** serial sections of specimen BGEG LDP10034 (9.5 mm long), showing the canaliform and strongly curved crura; **B,** serial sections of specimen BGEG LDP10035 (nearly 10 mm long, but the ventral umbo is deformed), showing the calcariform

crura. The numbers indicate distances (in mm) from the ventral beak.

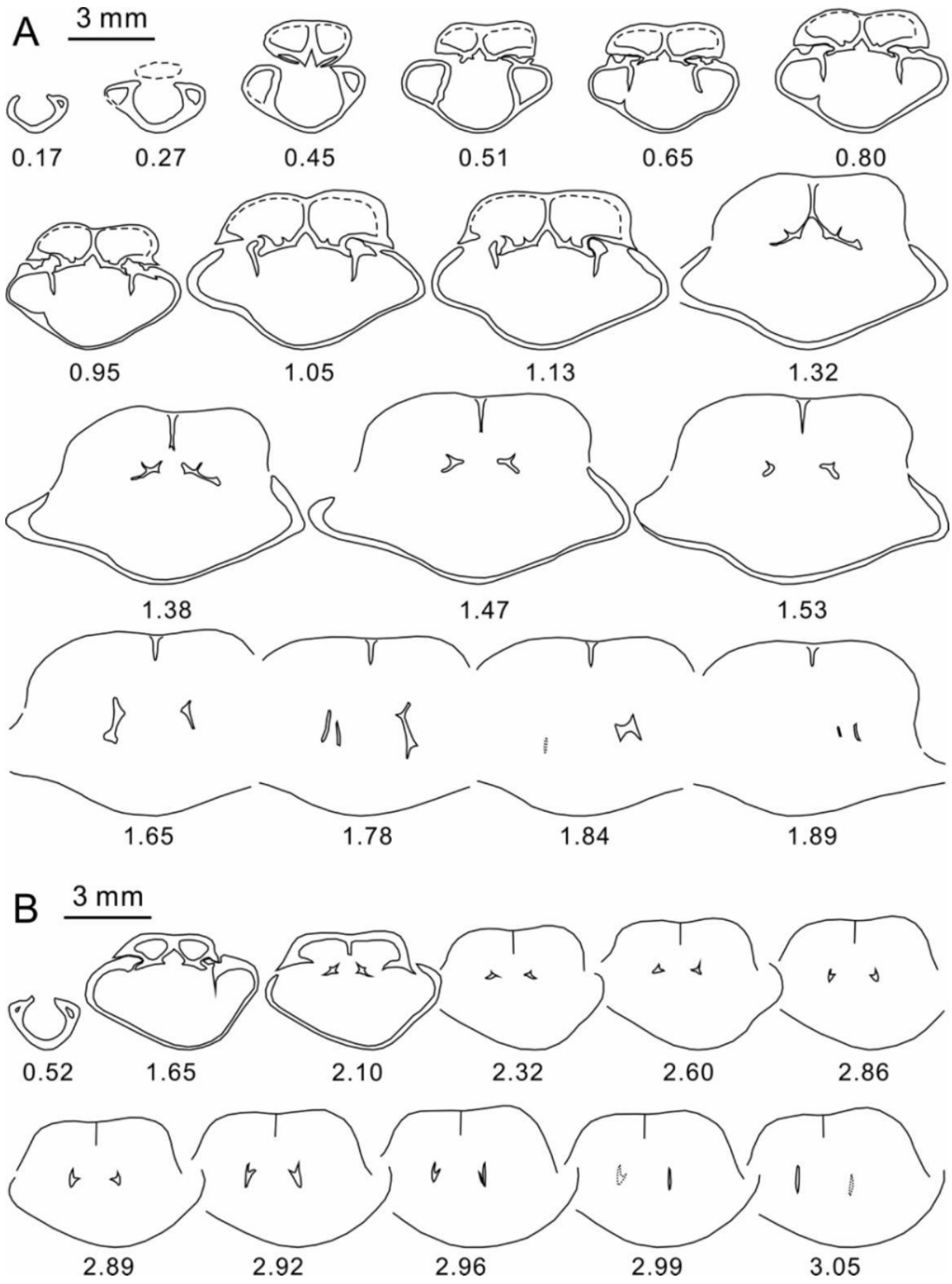


Figure 10. Comparison of the species of *Nudirostralina*. The sketches of *N. subtrinodosi* and *N. subtrinodosi multicostata* are based on our specimens; others are based on their respective holotype or syntype. Abbreviations: W, shell width; L, shell length; NF, number of plicae on dorsal fold; NL, number of plicae on

lateral flanks.

Species	Size (mm)	Outline (W/L)	Umbonal angle	Ventral sulcus	Number of plicae (NF/NL)	Strength and length of plicae	Sketch
N. dieneri (Bittner, 1899)	moderate (12–16)	equilateral to transverse (1.0–1.2)	95°–110°	deep	4/3	strong, short (<1/5L)	
N. griesbachi (Bittner, 1899)	moderate (10–12)	usually slightly transverse, rarely elongate (0.9–1.1)	95°–105°	shallow	2–4/3–4	strong, short (<1/5L)	
N. lissosinus Xu & Liu, 1983	moderate (12)	equilateral (~1.0)	92°	moderate	0/1	very weak, possibly short	
N. longa Jin, Sun & Ye in Jin *et al.*, 1979	moderate (12)	slightly transverse (~1.1)	90°	moderate	2–5/1–2	strong, moderate (~1/3L)	
N. mangyshlakensis (Dagys, 1974)	moderate (10–12)	transverse (~1.3)	110°–120°	deep	2–4/2	strong, long (~1/2L)	
N. minuta sp. nov. this paper	small (6–7)	elongate to equilateral (0.9–1.0)	90°–95°	deep	2/1–2	distinct on fold, weak on flanks, short (<1/5L)	
N. mutabilis (Stoliczka, 1866)	moderate (12–20)	equilateral to slightly transverse (1.0–1.1)	85°–105°	deep	2–4/2–4	strong, moderate to long (1/3–2/3L)	
N. subsphaerica Sun & Ye, 1982	moderate (12)	slightly transverse (~1.1)	~100°	shallow	2/1	weak, short (<1/5 L)	
N. subtrinodosi Yang & Xu, 1966	moderate (10–14)	equilateral to transverse (1.0–1.4)	80°–105°	deep	2–3/2–3	strong, moderate to long (1/3–2/3 L)	
N. subtrinodosi multicostata Yang & Xu, 1966	moderate (10–13)	transverse (1.2–1.3)	95°–115°	deep	4–5/2	strong, moderate to long (1/3–1/2L)	
N. tazawai (Popov in Popov & Zakharov, 2017)	moderate (8–15)	usually elongate, rarely transverse (0.8–1.1)	85°–100°	shallow	2–7/2–3	strong, short (<1/3L)	
N. tenuicostata Jin, Sun & Ye in Jin *et al.*, 1979	moderate (9–15)	equilateral to transverse (1.0–1.2)	95°–110°	moderate	4–6/2–3	strong, short (<1/5L)	
N. triassica (Girty, 1927)	small (usually<6, rarely >10)	usually elongate, rarely transverse (0.9–1.1)	85°–100°	deep	2–3/1–2	usually strong, short to long (1/5–1/2L)	
N. trinodosi (Bittner, 1890)	moderate (7–12)	usually transverse, rarely elongate (0.9–1.3)	75°–110°	deep	2–3/1–2	strong, long (~1/2L)	

Figure 11. Serial sections of *Nudirostralina minuta* sp. nov. (based on specimen BGEG LDP10048). The numbers indicate distances (in mm) from the ventral beak. The specimen is 7.4 mm long.

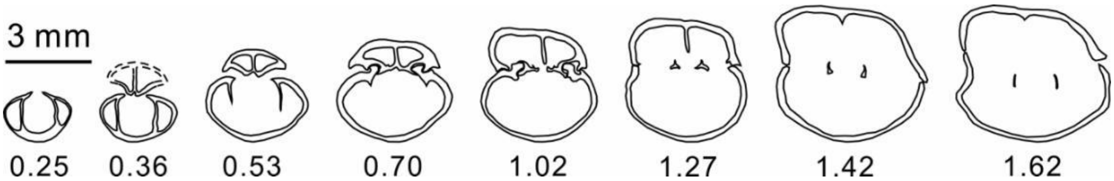


Figure 12. A–H, *Parabrekia yangi* sp. nov.; **A–D,** holotype, BGEG LDP10051, dorsal, ventral, lateral, and anterior views of an articulated shell; **E–H,** paratype, BGEG LDP10054, dorsal, ventral, lateral, and anterior views of an articulated shell. **I–O,** *Diholkorhynchia sinensis* (Koken, 1900); **I–L,** BGEG WCP10053,

dorsal, ventral, anterior, and lateral views of an articulated specimen; **M–O,** BGEG WCP10056, dorsal, ventral, and anterior views of an articulated shell. **P–W,** *Costirhynchopsis sinensis* (Yang & Xu, 1966); **P–S,** BGEG LDP10060, dorsal, ventral, lateral, and anterior views of an articulated shell; **T–W,** BGEG WCP10073, dorsal, ventral, lateral, and anterior views of an articulated shell. **X–A’,** Rhynchonellida gen. and sp. indet. 1, BGEG LDP10062, dorsal, ventral, anterior, and lateral views of an articulated shell.

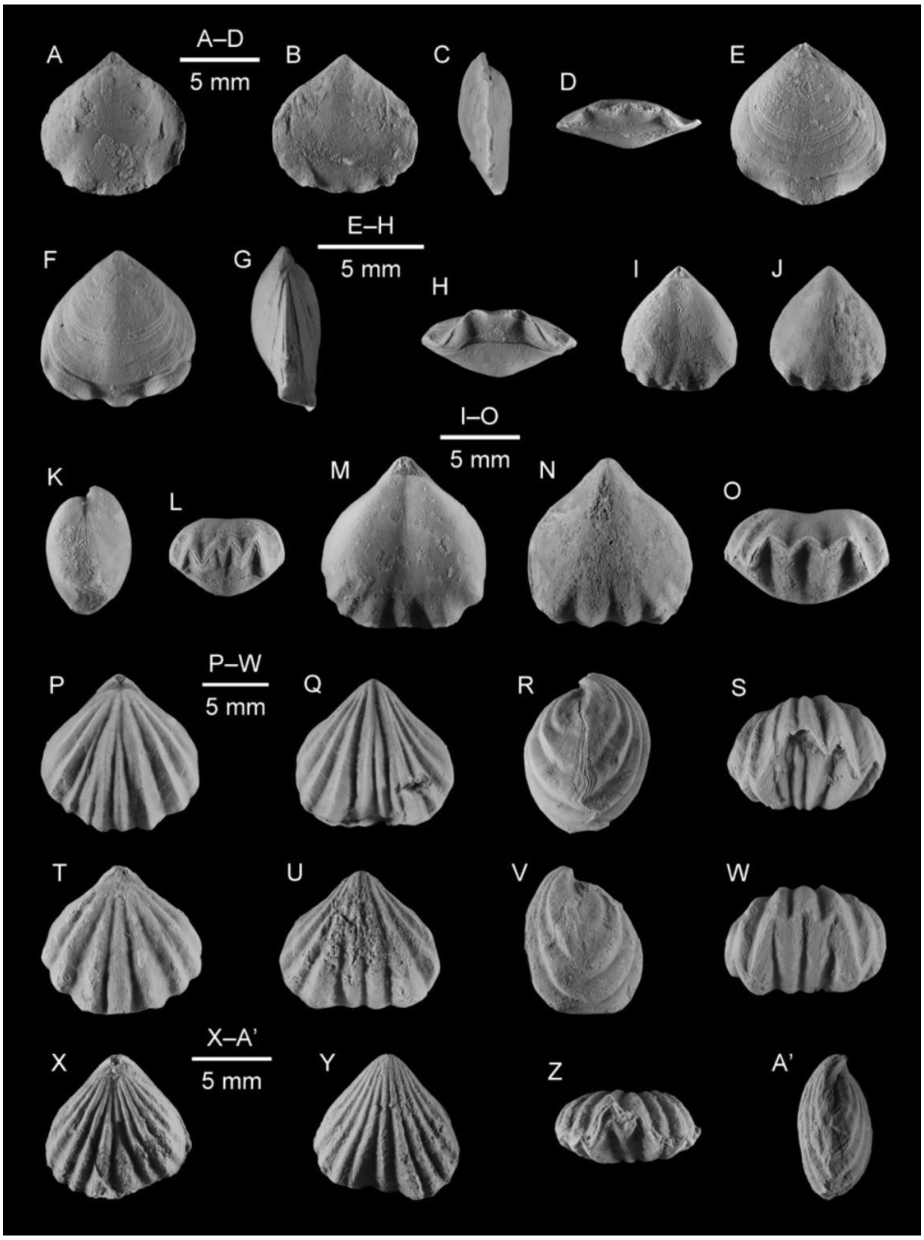


Figure 13. Serial sections of *Parabrekia yangi* sp. nov. **A,** serial sections of a large specimen (BGEG LDP10059, 9.8 mm long); **B,** serial sections of a small specimen (BGEG LDP10055, 5.9 mm long). The numbers indicate distances (in mm) from the ventral beak.

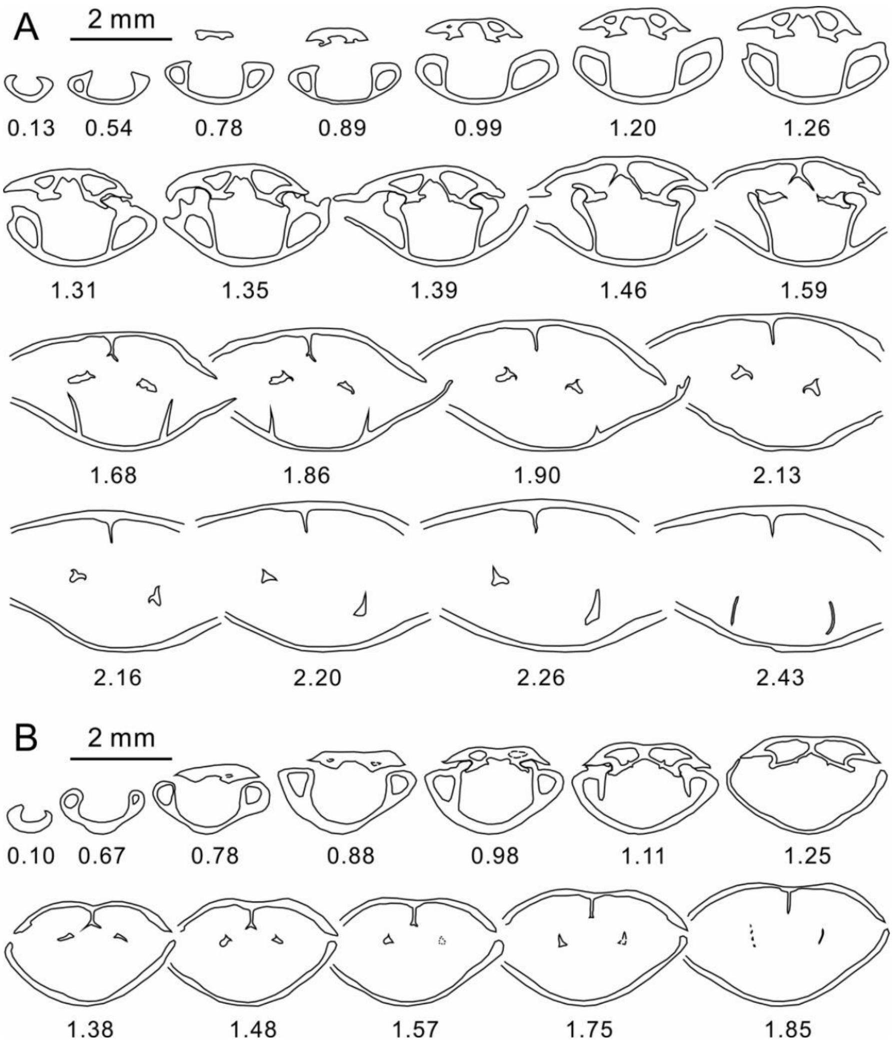


Figure 14. Serial sections of *Diholkorhynchia sinensis* (Koken, 1900) (based on specimen BGEG WCP10057). The numbers indicate distances (in mm) from the ventral beak. The specimen is 12 mm long.

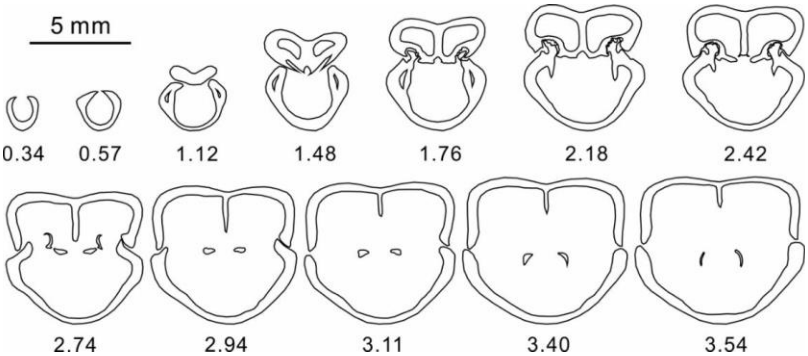


Figure 15. A–D, Rhynchonellida gen. and sp. indet. 2, BGEG WCP10074, dorsal, ventral, lateral and anterior views of an articulated shell. **E–H,** Rhynchonellida gen. and sp. indet. 3, BGEG WCP10075, dorsal, ventral, anterior and lateral views of an articulated shell. **I–L,** Rhynchonellida gen. and sp. indet. 4, BGEG

LDP10063, dorsal, ventral, lateral, and anterior views of an articulated specimen. **M–P,** *Spirigerellina sulcata* (Yang & Xu, 1966), BGEG WCP10016, dorsal, ventral, lateral and anterior views of an articulated shell. **Q–Z,** *Cassianospira wachangpoensis* (Stiller, 1999); **Q–T,** BGEG WCP10001, dorsal, ventral, lateral, and anterior views of an articulated shell; **U–W,** BGEG WCP10002, dorsal, ventral, and lateral views of an articulated shell; **X–Z,** BGEG WCP10003, dorsal, ventral, and lateral views of an articulated shell.

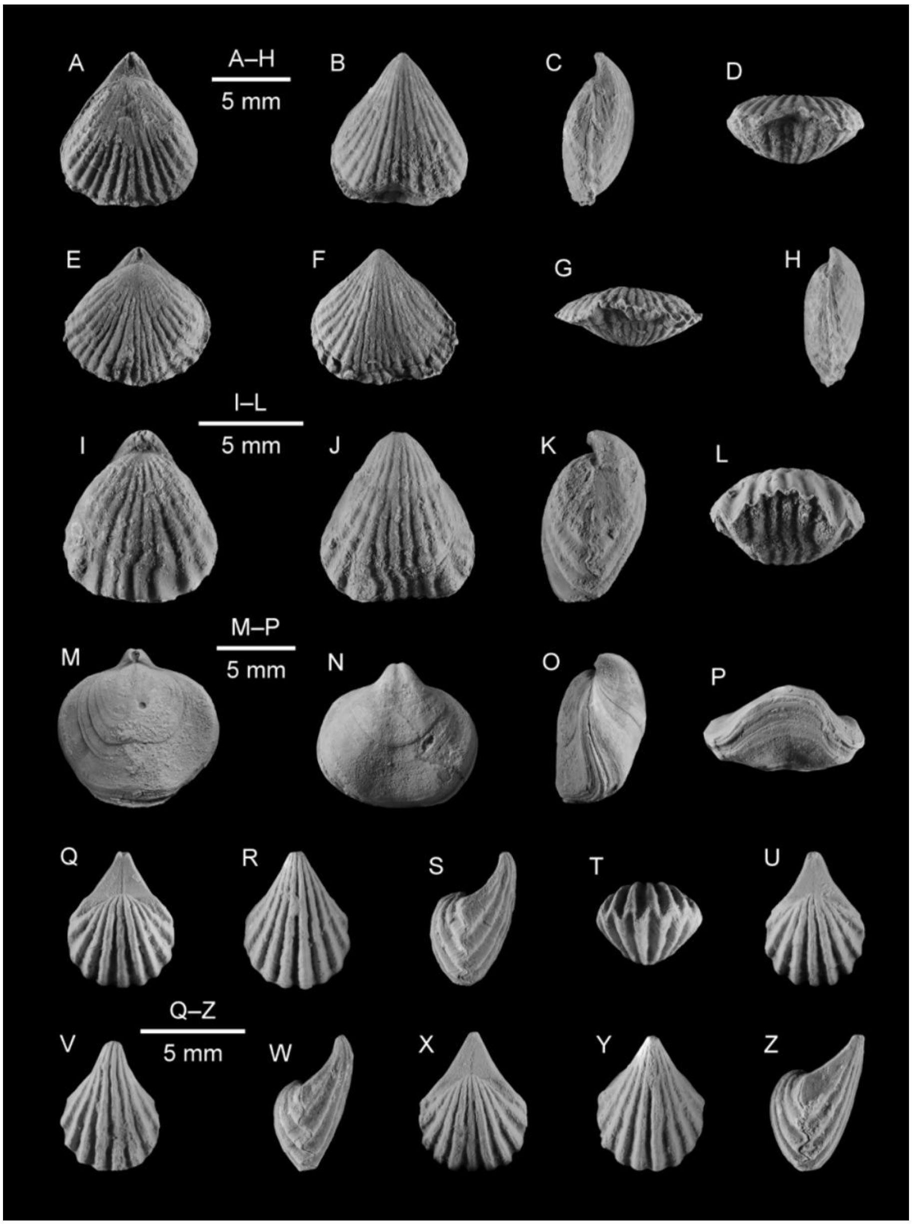


Figure 16. Serial sections of *Cassianospira wachangpoensis* (Stiller, 1999) (based on specimen BGEG WCP10004). The numbers indicate distances (in mm) from the ventral beak. The specimen is 7.1 mm long.

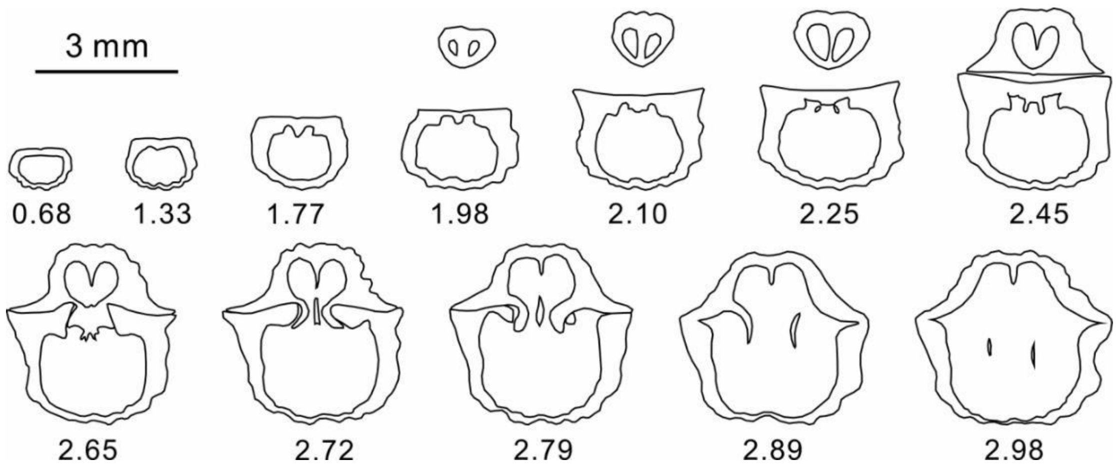


Figure 17. Comparison of the species of *Cassianospira.* The characters of *C. humboldtii* are based on Bittner (1890); others are based on their original descriptions. Abbreviations: HL, hingeline width; SW (= DW), shell width (= dorsal valve width); HI, interarea height; DL, dorsal valve length.

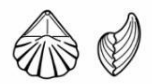
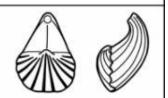
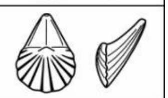
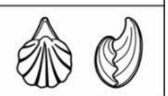
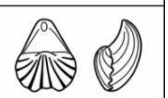
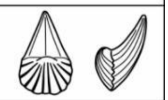
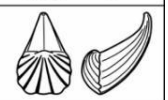
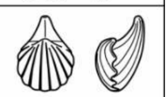
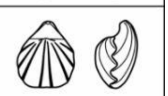
Species	Hingeline (HL/SW)	Ventral interarea (HI/DL)	Ventral umbo	Dorsal valve (DW/DL)	Dorsal median costa	Number of dorsal lateral costae (pairs)	Sketch
C. humboldtii (von Klipstein, 1845)	wide (~0.7)	low (~0.6)	gently curved	very wide (~1.5)	slightly depressed	3 or 4	
C. hungarica (Bittner, 1912)	moderate to wide (0.6–0.8)	moderate to high (0.7–1.0)	straight to moderately curved	very wide (1.2–1.3)	slightly depressed	4 or 5	
C. klipsteinii (Bittner, 1890)	moderate (~0.6)	high (~1.0)	straight	very wide (~1.3)	slightly depressed	5	
C. laubei (Bittner, 1890)	narrow (~0.4)	low (~0.5)	gently curved	equilateral (~1.0)	slightly depressed	3	
C. loczyi (Bittner, 1912)	moderate to wide (0.6–0.7)	moderate to high (0.8–1.0)	gently curved	slightly wide to almost equilateral (1.0–1.2)	strongly depressed	4 or 5	
C. lyrata (Münster, 1841)	moderate (~0.6)	high (~1.1)	straight	very wide (1.2–1.3)	slightly depressed	4	
C. pseudolyrata (Bittner, 1912)	wide (~0.7)	high (~1.4)	gently curved	very wide (~1.3)	slightly depressed	4	
C. wachangpoensis (Stiller, 1999)	moderate (0.5–0.6)	moderate (0.6–0.7)	gently curved	slightly wide (~1.1)	not depressed	4 or 5	
C. sp. in this paper	moderate (~0.6)	very low (~0.3)	gently curved	slightly wide (~1.1)	strongly depressed	3	

Figure 18. A–D, *Cassianospira* sp., BGEG WCP10011, dorsal, ventral, lateral and anterior views of an articulated specimen. **E–H,** *Schwagerispira subcircularis* (Yang & Xu, 1966), BGEG WCP10012, dorsal, ventral, anterior and lateral

views of an articulated shell. **I–L,** *Schwagerispira fuchsi* (Koken, 1900), BGEG LDP10001, dorsal, ventral, lateral and anterior views of an articulated shell. **M–O,** *Paralepismatina semiconica* Yang & Xu, 1966, BGEG LDP10064, anterior, ventral and posterior views of a ventral valve. **P, Q,** *Leiolepismatina semiconula* Yang & Xu, 1966, BGEG LDP10082, anterior and posterior views of a ventral valve. **R–U,** *Thecocyrtelloidea tubulosa* Yang & Xu, 1996; **R, S,** BGEG LDP10071, anterior and posterior views of a ventral view; **T, U,** BGEG WCP10077, dorsal and ventral views of a dorsal valve. **U–W,** *Thecocyrtella* sp., BGEG LDP10081, ventral, lateral, and posterior views of a ventral valve. **Y–F',** *Neocyrtina mixodeltidiumosa* Yang & Xu, 1966; **Y–B',** BGEG LDP10083, dorsal, ventral, posterior, and anterior views of an articulated shell; **C'–F',** BGEG LDP10084, anterior, dorsal, ventral, and lateral views of an articulated shell.

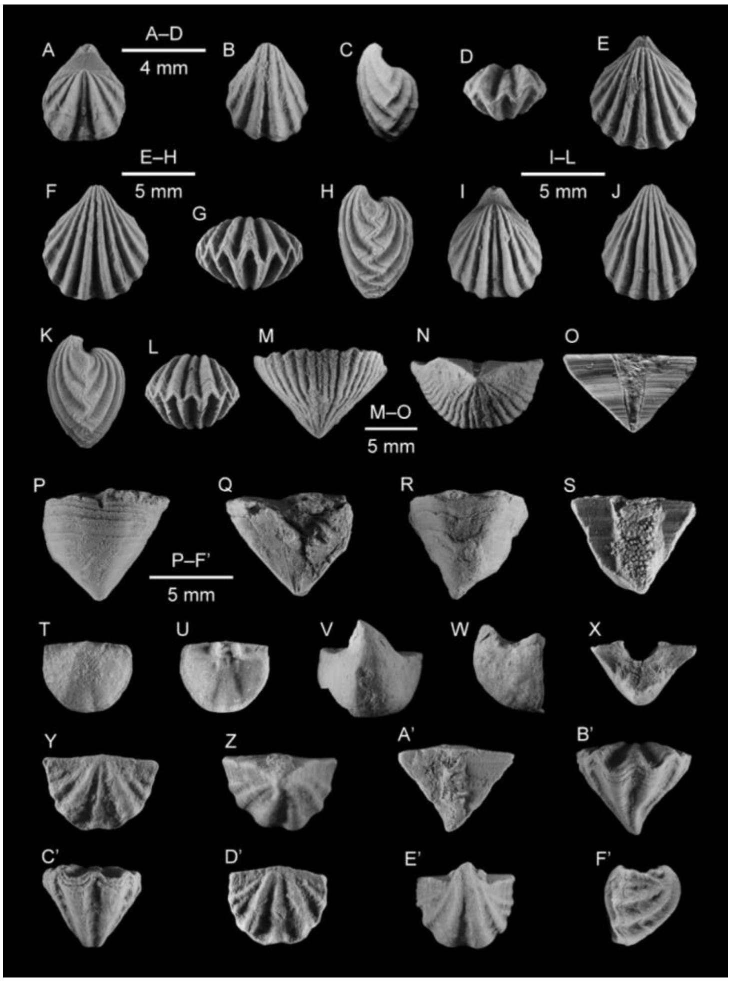


Figure 19. A–H, *Neocyrtina xui* sp. nov.; **A–D,** holotype, BGEG WCP10078, anterior, posterior, lateral, and dorsal views of an articulated shell; **E–H,** paratype, BGEG WCP10079, lateral, dorsal, anterior, and posterior views of an

articulated shell. **I, J,** *Pseudospiriferina* sp., BGEG LDP10089, BGEG LDP10090, dorsal views of two dorsal valves. **K–O,** *Nudispiriferina minima* Yang & Xu, 1966; **K–N,** BGEG WCP10080, dorsal, ventral, lateral, and posterior views of an articulated shell; **O,** BGEGECP 083, posterior view of a ventral valve. **P–U,** *Qingyenia spinosa* Yang & Xu, 1966; **P, Q,** BGEG LDP10116, dorsal and ventral views of a dorsal valve; **R, S,** BGEG LDP10112, BGEG LDP10113, ventral views of two ventral valves; **T, U,** BGEG LDP10117, dorsal and ventral views of a dorsal valve. **V–D',** *Lepismatina hsui* Wang, 1955a; **V–Z,** BGEG WCP10088, dorsal, ventral, lateral, anterior, and posterior views of an articulated specimen; **A'–D',** BGEG LDP10100, dorsal, ventral, anterior, and posterior views of an articulated shell.

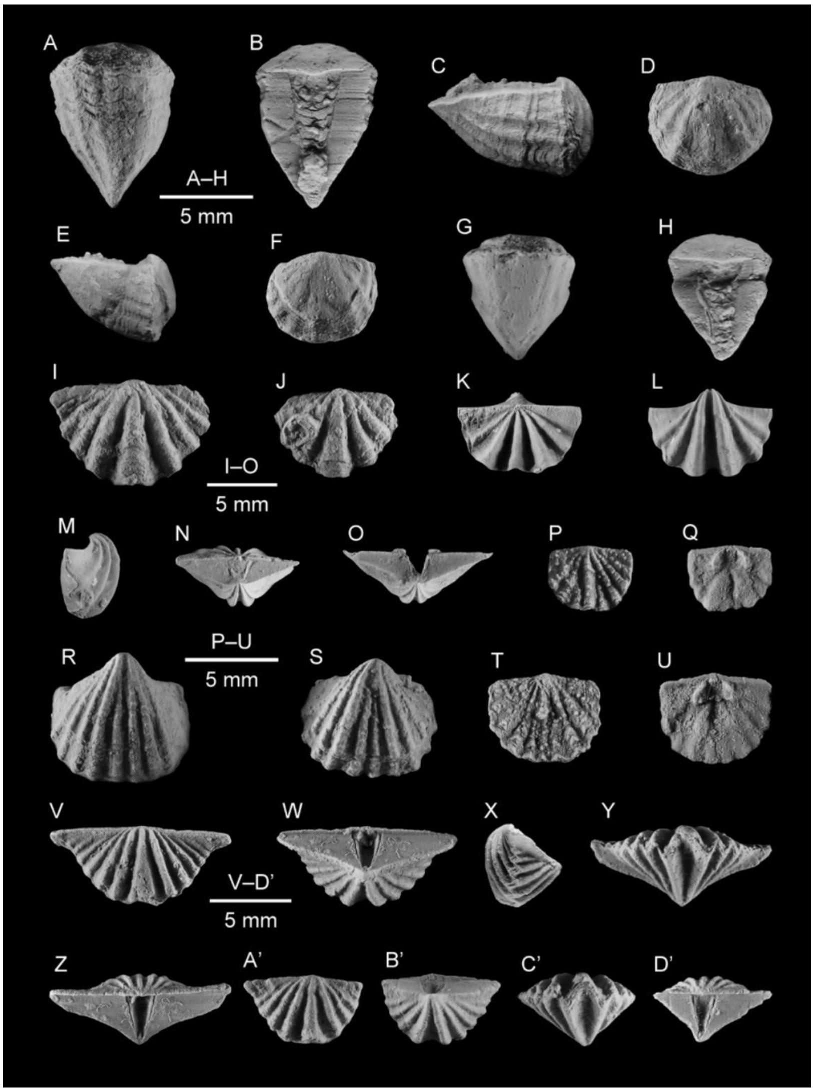


Figure 20. A, *Dagyssia multicostata* (Yang & Xu, 1966), BGEG LDP10120, ventral view of a ventral valve. **B–H,** *Koeveskallina bifurcata* sp. nov.; **B,** paratype,

BGEG LDP10093, ventral view of a broken ventral valve; **C,** paratype, BGEG LDP10097, dorsal view of a dorsal valve; **D,** holotype, BGEG WCP10087, ventral view of a ventral valve; **E, F,** paratype, BGEG LDP10096, dorsal and ventral views of a dorsal valve; **G, H,** BGEG LDP10095, ventral and posterior views of a broken ventral valve. **I–N,** *Mentzelia mentzeli* (Dunker, 1851); **I–L,** BGEG LDP10121, dorsal, ventral, lateral, and anterior views of an articulated shell; **M,** BGEG LDP10122, ventral view of a ventral valve; **N,** BGEG LDP10127, dorsal view of a dorsal valve. **O–R,** *Coenothyris elongata* (Yang & Xu, 1966), BGEG LDP10004, dorsal, ventral, lateral, and anterior views of an articulated specimen. **S–V,** *Angustothyris qingyanensis* sp. nov., paratype, BGEG LDP10005, dorsal, ventral, anterior, and lateral views of an articulated shell.

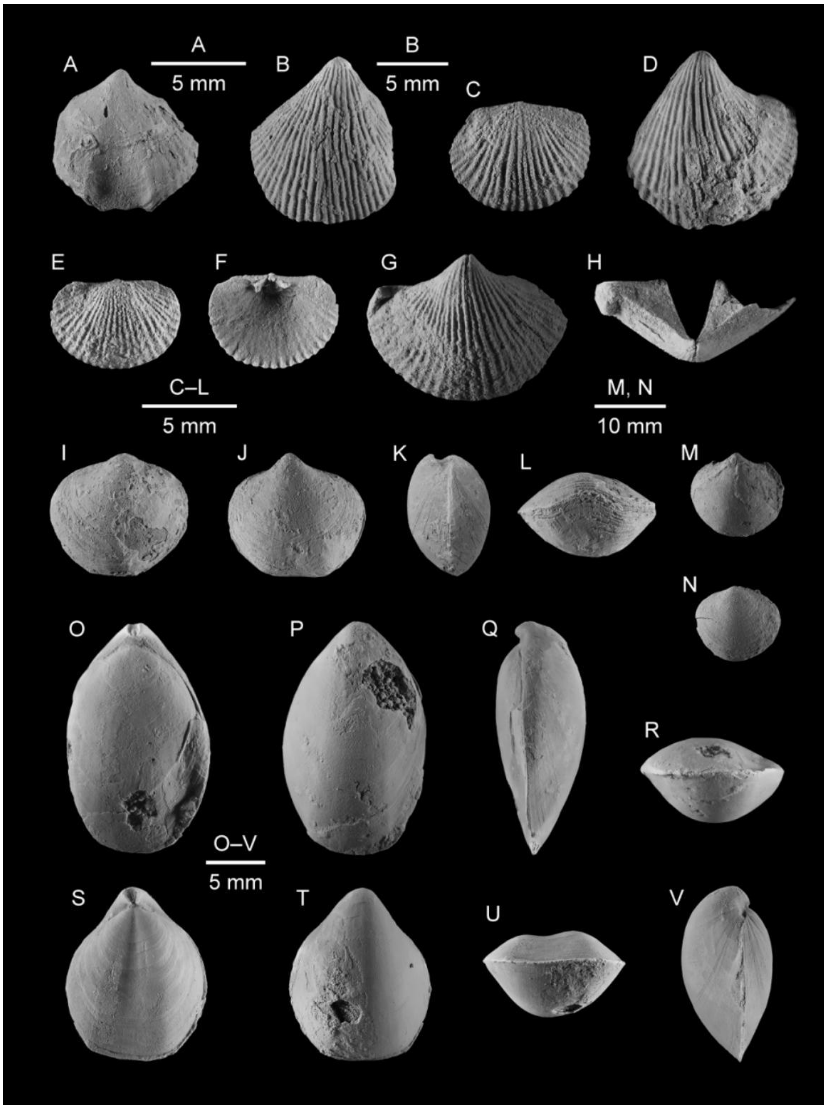


Figure 21. Serial sections of a ventral valve of *Koeveskallina bifurcata* sp. nov. (based on specimen BGEG LDP10094). The numbers indicate distances (in mm)

from the ventral beak.

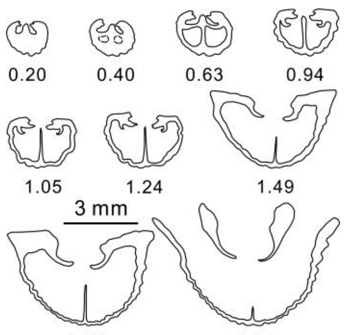


Figure 22. A–I, *Angustothyris qingyanensis* sp. nov.; **A–D,** paratype, BGEG LDP10006, dorsal, ventral, anterior, and lateral views of an articulated shell; **E,** enlarged view of the dorsal valve of BGEG LDP10006, showing the capillae and growth lines; **F–I,** holotype, BGEG WCP10017, dorsal, ventral, lateral, and anterior views of an articulated shell; **J–L,** paratype, BGEG WCP10018, dorsal, lateral, and anterior views of an articulated shell; **M–O,** BGEG WCP10020, dorsal, lateral, and anterior views of an articulated shell. **P–S,** *Sacothyris angustaeformis* (Yang & Xu, 1966), BGEG LDP10009, dorsal, ventral, lateral, and anterior views of an articulated specimen.

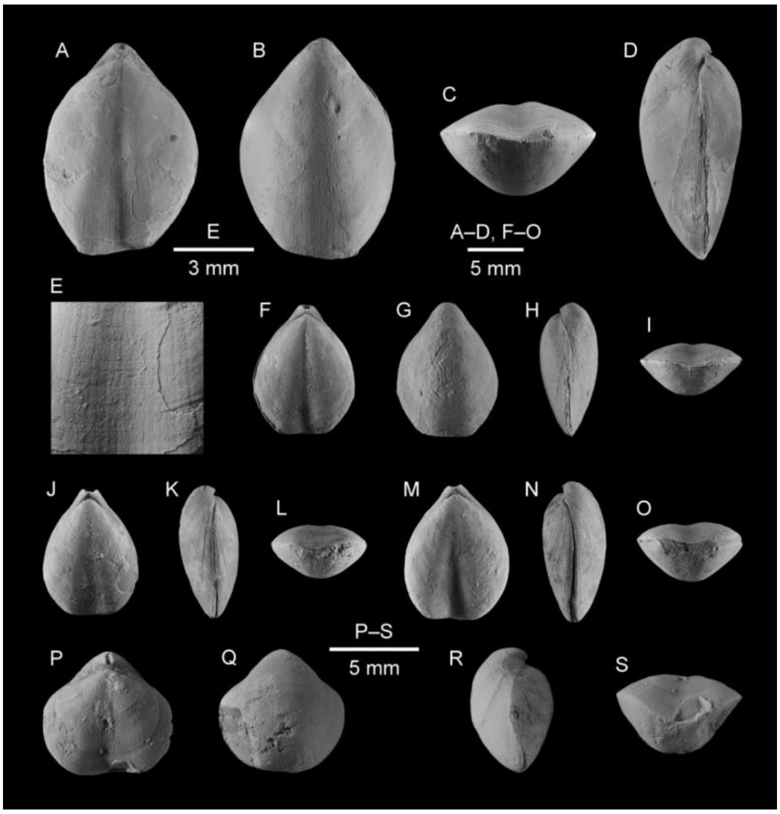


Figure 23. Serial sections of *Angustothyris qingyanensis* sp. nov. (based on specimen BGEG WCP10021). The numbers indicate distances (in mm) from the ventral

beak. The specimen is 14.5 mm long.

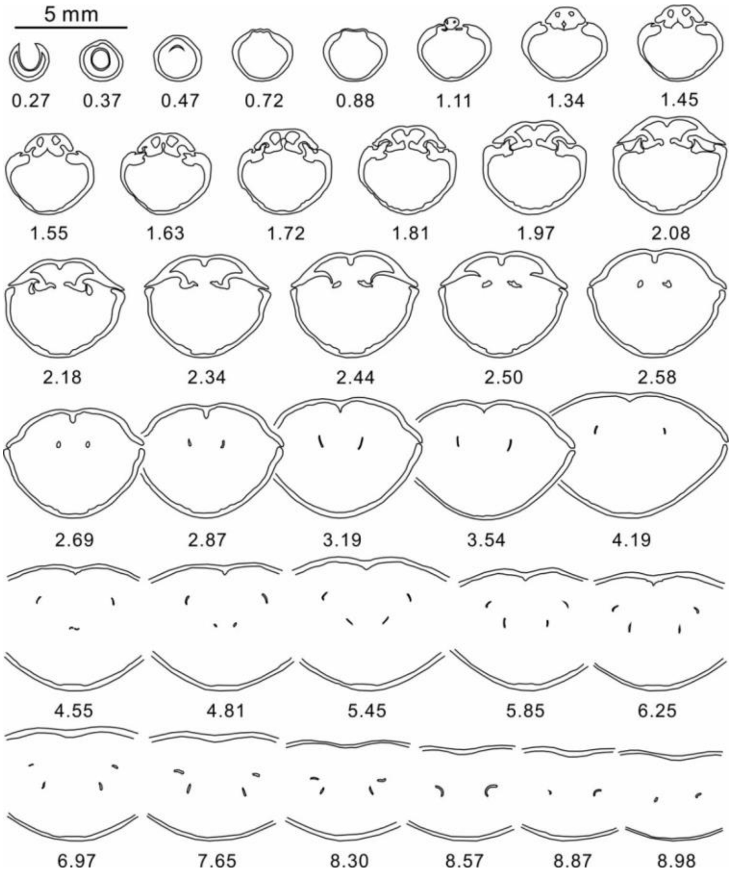


Figure 24. Comparisons of *Angustothyris qingyanensis* sp. nov., *Angustothyris dagysi* sp. nov., and '*Waldheimia*' *angustaeformis* Böckh (1872). The internal structures of '*Waldheimia*' *angustaeformis* in Böckh (1872) are not clear, and the characteristics marked by '*' are based on the specimens collected from its type locality (Pálfy 2003). The characters of *Angustothyris dagysi* sp. nov. are observed based on Dagys (1972c, 1974).

Species	External characteristics					Internal characteristics				
	Dorsal view	Outline	Anterior commissure	Ventral beak	Sulcus	Septalium	Outer hinge plates	Median septum	Inner socket ridges	Transverse sections
'*Waldheimia*' *angustae-formis* Böckh, 1872		pentagonal	strongly unisulcate	strongly curved	deep	absent*	?*	absent*	high*	
Angustothyris dagysi sp. nov.		suboval	weakly unisulcate	strongly curved	shallow	present, long	very narrow or absent	high	very high	
Angustothyris qingyanensis sp. nov.		rounded pentagonal	weakly unisulcate	gently curved	deep	present, short	relatively wide	low	low	

Figure 25. Species compositions of the brachiopod assemblages from Leidapo and

Wachangpo.

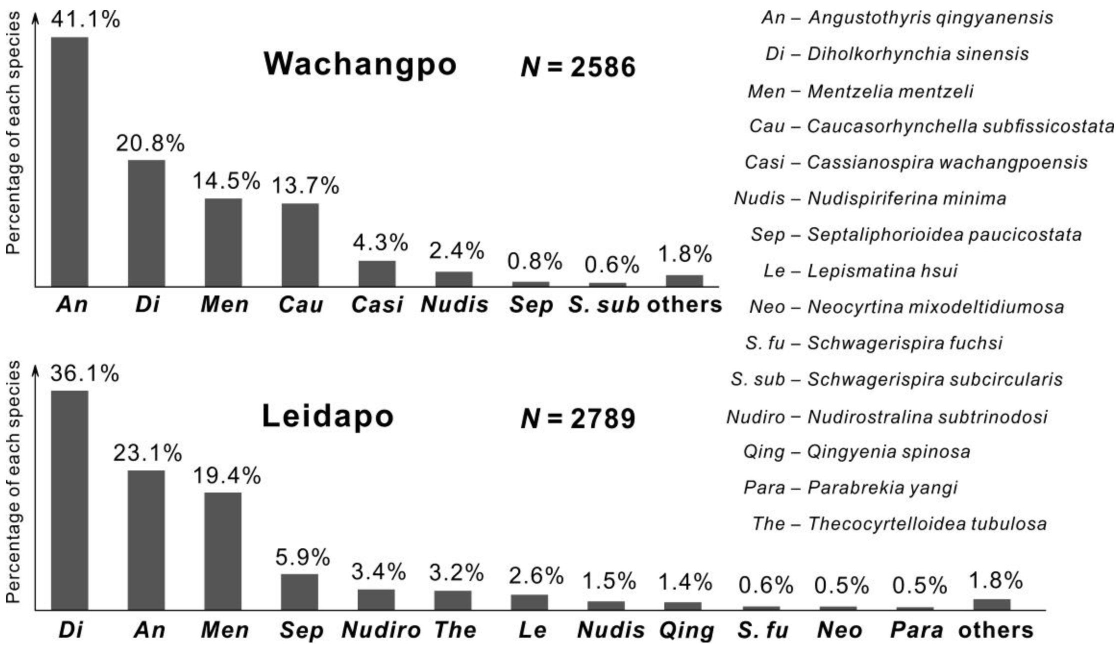


Figure 26. Dendrogram of 13 selected brachiopod faunas in the Anisian derived from cluster analysis based on the Jaccard similarity coefficient. Abbreviations: N Siberia, Northern Siberia; N Caucasus, Northern Caucasus; C Qinghai, Central Qinghai; S Qilian, Southern Qilian (Qinghai); W Qinling, Western Qinling (Gansu); NW Turkey, Northwestern Turkey.

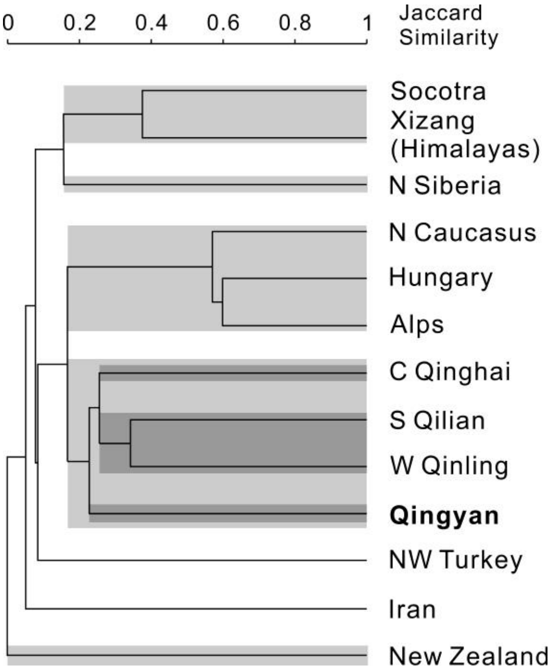


Figure 27. Results of principal coordinates analysis (PCOa) of 13 selected Anisian

brachiopod faunas based on the Jaccard similarity coefficient. The left part of the diagram showing the plots of PCOa axes 1 and 2, and the right part showing the plot of PCOa axes 2 and 3. Abbreviations: SC, Socotra (Yemen); XZ, Xizang (Himalayas); NS, Northern Siberia; NZ, New Zealand; NWT, Northwestern Turkey; IR, Iran; HUN, Hungary; NC, Northern Caucasus; QY, Qingyan; CQ, Central Qinghai; SQ, Southern Qilian (Qinghai); WQ, Western Qinling (Gansu).

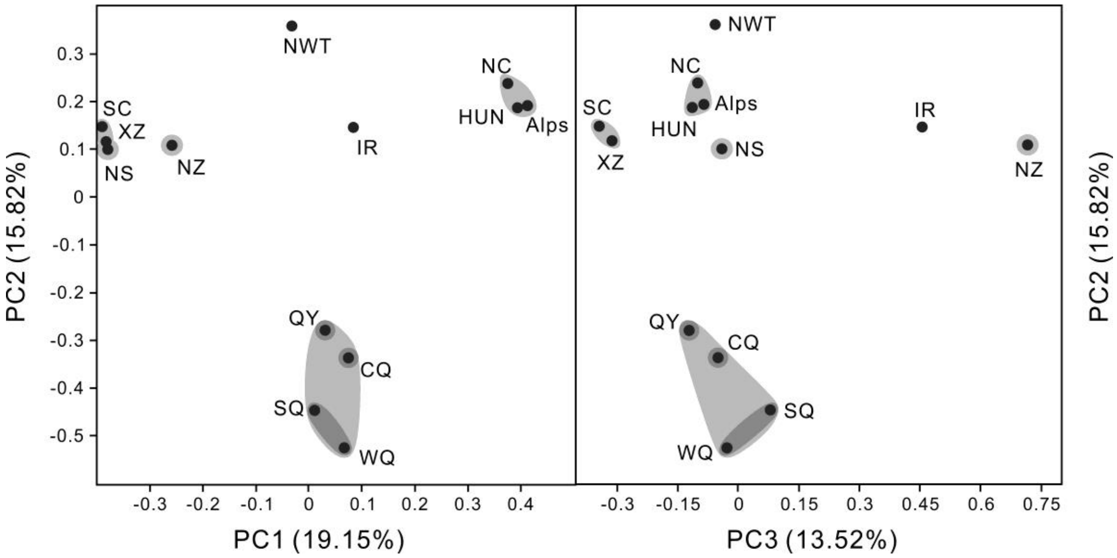


Figure 28. Brachiopod palaeobiogeography during the Anisian showing the provinces and subprovinces (base map after Ke *et al.* 2016).

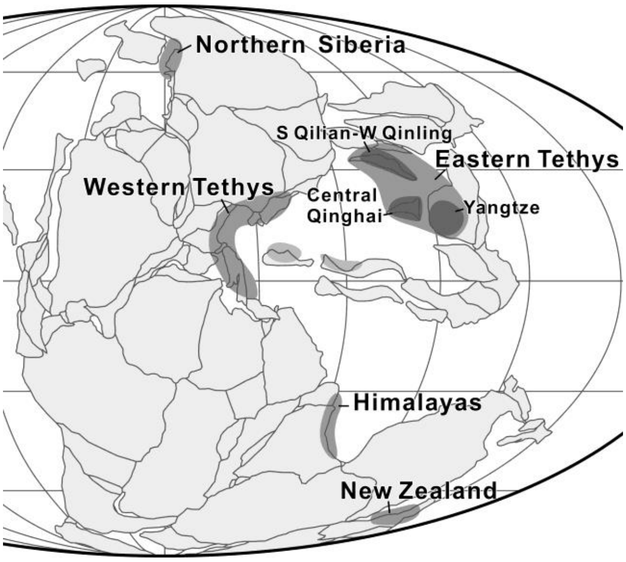


Table 1. List of the Anisian brachiopod species in Guizhou. Only the species

described in detail are listed. ‘Original species name’ refers to the species name used when it is firstly described from Guizhou. ‘Distribution’ refers to the distribution in Guizhou. All species described by Yang & Xu (1966) were re-described by Feng & Jiang (1978), thus the latter are not listed in the references. Abbreviations: QY, Qingyan; LDP, Leidapo, Qingyan; WCP, Wachangpo, Qingyan; YP, Yangpu, Anshun; MCP, Machangping, Fuquan; XM, Xinmin, Panxian; SW, Shaiwa, Ziyun; XY, Xingyi.

Species	Original species name	Distribution	References
Caucasorhynchella subfissicostata (Yang & Xu, 1966)	*Crurirhynchia subfissicostata*	QY	Yang & Xu 1966; this paper
Septaliphorioidea paucicostata Yang & Xu, 1966	*Septaliphorioidea paucicostata*	QY	Yang & Xu 1966; this paper
Rutorhynchia? *trigonalis* sp. nov.	*Rutorhynchia*? *trigonalis*	QY	this paper
Nudirostralina subtrinodosi Yang & Xu, 1966	*Nudirostralina subtrinodosi*	QY; ?YP	Yang & Xu 1966; this paper
Nudirostralina subtrinodosi multicostata Yang & Xu, 1966	*Nudirostralina subtrinodosi multicostata*	QY	Yang & Xu 1966; this paper
Nudirostralina minuta sp. nov.	*Nudirostralina minuta*	QY (LDP)	this paper
Parabrekia yangi sp. nov.	*Parabrekia yangi*	QY (LDP)	this paper
Diholkorhynchia sinensis (Koken, 1900)	*Rhynchonella sinensis*	QY; MCP; YP	Koken 1900; Wang 1995b; Wang *et al.* 1964; Yang & Xu 1964; this paper
Lissorhynchia pygmaea Yang & Xu, 1966	*Lissorhynchia pygmaea*	QY	Yang & Xu 1966
Lissorhynchia? *triloba* Yang & Xu, 1966	*Lissorhynchia*? *triloba*	QY	Yang & Xu 1966
Sinorhynchia bifaceta Yang & Xu, 1966	*Sinorhynchia bifaceta*	QY	Yang & Xu 1966
Costirhynchopsis sinensis (Yang & Xu, 1966)	*Septaliphoria sinensis*	QY; ?YP	Yang & Xu 1966; this paper
Costirhynchopsis xingyiensis (Yang & Xu, 1966)	*Septaliphoria xingyiensis*	QY; XY	Yang & Xu 1966
Rhynchonellida gen. and sp. indet. 1	Rhynchonellida gen. and sp. indet. 1	QY (LDP)	this paper
Rhynchonellida gen. and sp. indet. 2	Rhynchonellida gen. and sp. indet. 2	QY (WCP)	this paper
Rhynchonellida gen. and sp. indet. 3	Rhynchonellida gen. and sp. indet. 3	QY (WCP)	this paper
Rhynchonellida gen. and sp. indet. 4	Rhynchonellida gen. and sp. indet. 4	QY (LDP)	this paper
Spirigerellina sulcata (Yang & Xu, 1966)	‘*Athyris*’ *sulcata*	QY	Yang & Xu 1966; this paper
Spirigerellina subquadrata (Yang & Xu, 1966)	‘*Athyris*’ *subquadrata*	QY; ?YP	Yang & Xu 1966
Cassianospira wachangpoensis (Stiller, 1999)	*Neoretzia wachangpoensis*	QY (WCP)	Stiller 1999; this paper
Cassianospira sp.	*Cassianospira* sp.	QY (WCP)	this paper
Schwagerispira subcircularis (Yang & Xu, 1966)	*Neoretzia subcircularis*	QY	Yang & Xu 1966; Stiller 1999; this paper
Schwagerispira fuchsi (Koken, 1900)	*Retzia fuchsi*	QY	Koken 1900; Yang & Xu 1966; Stiller 1999; this paper
Paralepismatina semiconica Yang & Xu, 1966	*Paralepismatina semiconica*	QY	Yang & Xu 1966; this paper

Leiolepismatina semiconula Yang & Xu, 1966	*Leiolepismatina semiconula*	QY	Yang & Xu 1966; this paper
Thecocyrtelloidea tubulosa Yang & Xu, 1966	*Thecocyrtelloidea tubulosa*	QY	Yang & Xu 1966; this paper
Thecocyrtella sp.	*Thecocyrtella* sp.	QY (LDP)	this paper
Neocyrtina mixodeltidiumosa Yang & Xu, 1966	*Neocyrtina mixodeltidiumosa*	QY	Yang & Xu 1966; this paper
Neocyrtina xui sp. nov.	*Neocyrtina xui*	QY (WCP)	this paper
Pseudospiriferina variabilis Yang & Xu, 1966	*Pseudospiriferina variabilis*	MCP	Yang & Xu 1966
Pseudospiriferina pinguis Yang & Xu, 1966	*Pseudospiriferina pinguis*	MCP; XM	Yang & Xu 1966; Sun *et al.* 2009
Pseudospiriferina multicostata Yang & Xu, 1966	*Pseudospiriferina multicostata*	QY; XM	Yang & Xu 1966; Sun *et al.* 2009
Punctospirella fragilis (von Schlotheim, 1814)	*Punctospirella fragilis*	XM	Sun *et al.* 2009
Nudispiriferina minima Yang & Xu, 1966	*Nudispiriferina minima*	QY, YP	Yang & Xu 1966; this paper
Qingyenia spinosa Yang & Xu, 1966	*Qingyenia spinosa*	QY	Yang & Xu 1966; this paper
Lepismatina hsui Wang, 1955a	*Lepismatina hsui*	QY	Wang 1955a, b; Wang *et al.* 1964; Yang & Xu 1966; this paper
Dagyssia multicostata (Yang & Xu, 1966)	*Mentzelia multicostata*	QY; MCP; YP	Yang & Xu 1966; this paper
Koeveskallina bifurcata sp. nov.	*Koeveskallina bifurcata*	QY	this paper
Mentzelia mentzeli (Dunker, 1851)	*Mentzelia mentzeli*	QY	Wang 1955b; Yang & Xu 1966; this paper
Mentzelia subspherica Yang & Xu, 1966	*Mentzelia subspherica*	QY	Yang & Xu 1966; this paper
Mentzelia? *paucicostata* Yang & Xu, 1966	*Mentzelia paucicostata*	MCP	Yang & Xu 1966
Liaous shaiwensis He & Chen in He *et al.*, 2015	*Liaous shaiwensis*	SW	He *et al.* 2015
Coenothyris elongata (Yang & Xu, 1966)	*Adygella elongata*	QY	Yang & Xu 1966; this paper
Angustothyris qingyanensis sp. nov.	*Rhaetina angustaeformis*	QY; YP	Wang 1955b; Yang & Xu 1966; this paper
Sacothyris angustaeformis (Yang & Xu, 1966)	*Aulacothyris angustaeformis*	QY	Yang & Xu 1966; this paper

Online Supplementary **Tables S**1–**S22**. Measurements of registered specimens.

Online Supplementary **Table S**23. List of Anisian brachiopods of the other 12 faunas from around the world analyzed in this paper.