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LOPINGIAN (LATE PERMIAN) BRACHIOPOD FAUNAS FROM THE QUBUERGA FORMATION AT TULONG AND KUJIANLA IN THE MT. EVEREST AREA OF SOUTHERN TIBET, CHINA

HAI-PENG XU[1,2], CHANG-QUN CAO[1], DONG-XUN YUAN[1], YI-CHUN ZHANG[1] & SHU-ZHONG SHEN[1*]

[1*]Corresponding author. State Key Laboratory of Palaeobiology and Stratigraphy; Center for Excellence in Life and Paleoenvironment; Nanjing Institute of Geology and Palaeontology, CAS, 39 East Beijing Road, Nanjing 210008, China. E-mail: szshen@nigpas.ac.cn
[2]University of Science and Technology of China, 96 Jinzhai Road, Hefei 230026, China.

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Abstract. Permian strata containing abundant brachiopods are well developed in the Himalaya Tethys Zone. However, relatively few has been systematically described due to the difficult working condition for collecting. In this paper, we describe the brachiopods from the Qubuerga Formation at the Tulong and Kujianla sections in southern Tibet. The brachiopod faunas consist of 15 species belonging to 11 genera. Among the identified 15 species, *Retimarginfera xizangensis*, *Costiferina indica*, *Fusispirifer semiplicatus*, *Spiriferella sinica*, *Biplatyconcha grandis* and *Neospirifer* (*Quadrospina*) *tibetensis* are very common in the equivalents of the Himalaya Tethys Zone including the Selong Group at the Selong Xishan and Qubu sections in southern Tibet, the Senja Formation in northwest Nepal, the Zewan Formation in Kashmir, and the upper part of the Wargal Formation and the Chhidru Formation in the Salt Range, Pakistan. They are all comparable and can be assigned to the Wuchiapingian-early Changhsingian. Since the brachiopods from the Qubuerga Formation at Tulong and Kujianla are all composed of typical Gondwanan, bipolar or cosmopolitan elements, it is conclusive that the Himalaya Tethys Zone in the northern margin of the Indian Plate was still situated at southern high-latitudes under cold palaeoclimatic conditions during most of the Lopingian. The faunal succession at Tulong also recorded a rapid warming at the very end of the Changhsingian in view of the fact that the typical cold-water Lopingian brachiopod, gastropod and bivalve faunas were dramatically replaced by extremely abundant conodonts *Clarkina* in the basal part of the dolostone unit of the Tulong Formation. This end-Changhsingian warming is comparable with that recorded throughout the Permian-Triassic boundary interval at Selong, Qubu in southern Tibet, the Salt Range, Pakistan and the sections in Kashmir as well as South China.

Introduction

Permian faunal successions in the Himalaya Tethys Zone have long become the most crucial data to understand the palaeogeographical position and palaeoclimatic changes of the northern peri-Gondwanan region around the Permian-Triassic transition. As the southernmost terrane of the Qinghai-Tibet Plateau, this zone contains well-developed Permian strata and yields abundant brachiopods [Waterhouse 1966, 1975; Zhang (=Chang) & Jin (=Ching) 1976; Shen et al. 2000, 2001a]. However, relatively limited work has been undertaken in southern Tibet due to the difficult accessibility of this area and oxygen-deficit working condition.

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Only a few Permian brachiopods were reported from the Himalaya Tethys Zone before 1950s (e.g., Davidson 1862). Large collection of Permian brachiopod fossils was first reported by Muir-Wood & Oakley (1941) from North Sikkim (southern flank of Mt. Everest). Later, Ding (=Ting) (1962) described a small brachiopod fauna consisting of eight species belonging to five genera, which was collected by Li Pu in 1952 from the Permian deposits of the Qubu area, about 30 km north to Mt. Everest. Seven brachiopod genera from the Selong Group were mentioned by Mu et al. (1973) and eight brachiopod species collected from Surishan in Tingri were described by Yang & Zhang (1982). Permian brachiopod collections, mainly derived from a scientific expedition in the Mt. Everest region (1966-1968), were briefly described by Zhang & Jin (1976) in Chinese, and 13 species of those

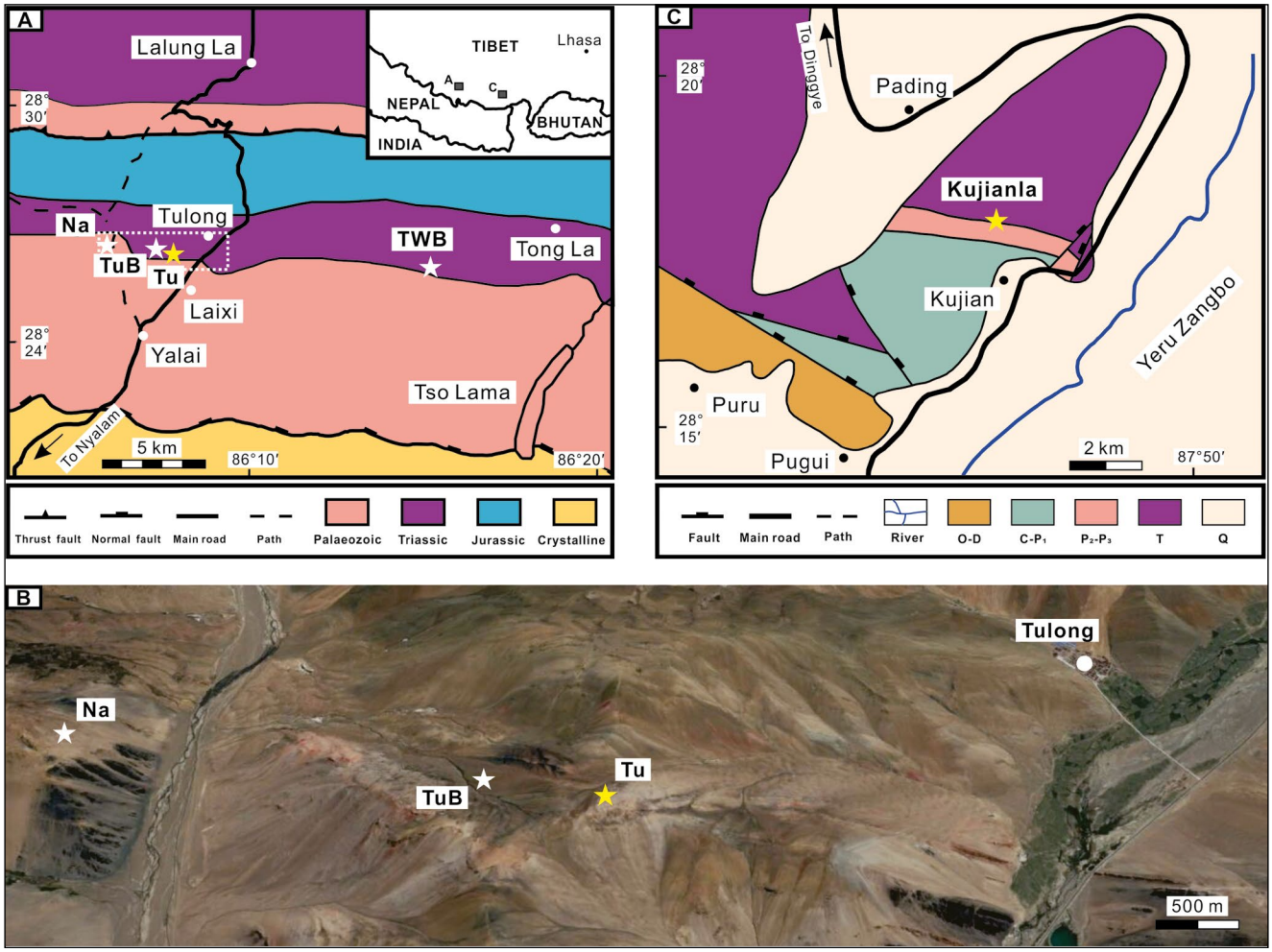


Fig. 1 - A) Geologic sketch map of the Tulong area with the location of the studied section (modified after Brühwiler et al. 2009, 2010), Tu: Tulong section in this paper. TuB: Tulong section; Na: Nazapuo section; TWA: Tong La West A section; TWB: Tong La West B section in Brühwiler et al. (2009, 2010). B) Google map of the area represented by the white dotted line in Fig. 1A showing the sampling sites in the Tulong area. C) Geologic sketch map of the Kujianla area with the location of the studied section (modified from Yin & Guo 1975, 1976).

collections are recorded from the Qubuerga Formation near the Tulong section but without description and detailed geographical and stratigraphic data. Monographic systematic works on the Permian brachiopods from the Selong Group at Selong Xishan and Qubu in southern Tibet were carried out in this century (Shen et al. 2000, 2001a, 2001b, 2002, 2003a, 2003c, 2006).

In this paper, we describe and illustrate two other brachiopod faunas from southern Tibet in the Himalaya Tethys Zone in the northern peri-Gondwanan region. The brachiopod specimens were collected from Tulong and Kujianla respectively. The Tulong section (86°09' E, 28°27' N) is about 2 km southwest of Tulong Village (Fig. 1A) which is approximately 40 km from Mt. Xixiabangma (+8012m). This section is relatively easy to access because the China-Nepal Highway (G318) from Lhasa to Nepal passes by the east side of Tulong Village. Brachiopods in this study were collected from the top of the Hill (Fig. 1B). Detailed conodont biozonation from the Triassic at Tulong was documented by Tian (1982) and Garzanti et al. (1998). Recently, more detailed paleontological researches in the Triassic have been undertaken at this section, including the middle and upper Smithian ammonoids (Brühwiler et al. 2010), and the Smithian to Anisian ostracods (Forel & Crasquin 2011; Forel et al. 2011). However, so far none of Permian brachiopods have been described although some of them (e.g., *Wyndhamia circularis*, *Cancrinella* sp., *Biplatyconcha grandis*) were listed by Rao & Zhang (1985) and Shen et al. (2006). In addition, a new section potentially containing extremely abundant brachiopods was briefly

investigated and some brachiopods were collected at Kujianla which is located at the mountainside of the southern slope of Kujianla (87°47' E, 28°17' N), about 1 km north to Kujian Village (Fig. 1C), Dinggye County and 90 km from Mt. Everest.

Stratigraphy

The Permian strata in the studied area were commonly divided into the Jilong, Qubu and Qubuerga formations in ascending order (Yin & Guo 1976). The Jilong Formation is mainly composed of diamictic sandstone and siltstone, which contains the typical Gondwanan-type brachiopod *Cimmeriella* (=previous "*Stepanoviella*") fauna and was generally assigned to a Sakmarian to Artinskian age (Jin 1979; Shen 2018). Some basalt interlayers were discovered by Garzanti et al. (1999) and subsequently confirmed by Zhu et al. (2002) in this formation. The Jilong Formation is in fault contact with the Qubu Formation. The missing strata between these two formations are unknown and probably equivalent to the Quga Formation which has only been reported from Zhongba County to Zanda County (Bureau of Geology and Mineral Resources of Xizang Autonomous Region 1997; Shi et al. 2003; Zhang et al. 2013).

The Qubu Formation at Tulong consists of white quartzose sandstone. At the Qubu and Kujianla sections, this formation contains an about 2 m-thick grey sandy shale yielding a *Glossopteris* flora which is about 10 m below the base of the overlying Qubuerga Formation (Hsü et al. 1990). This flora was once considered as early Late Permian (Wuchiapingian) in age, equivalent to the Raniganj Beds in India (Hsü 1976), subsequently changed to the Karharbari stage (Hsü et al. 1990) which is late Guadalupian, and later re-assigned to the Lopingian (Shen et al. 2003a, 2003c). However, the age of this formation has not been reliably determined because no marine fossils have been found yet. This flora has not been found at the Tulong section.

The overlying Qubuerga Formation was divided into two members (Shen et al. 2003a). The lower member is composed of grey brown siltstone interbedded with bioclastic limestone and containing abundant brachiopods, and the upper member is dominated by varicoloured shale with some argillaceous nodules containing a handful of gastropods such as species of *Bellerophon* (Pan & Shen 2008) and abundant bivalves (e.g., species of *Atomodesma*) (Rao & Zhang 1985), also numerous poorly preserved ammonoids (Rao & Zhang 1985; Shen et al. 2003a). The brachiopods described in this paper were collected from marly limestone, bioclastic limestone and mudstone at the Tulong section (Fig. 2A) and from sandstone in the lower member at the Kujianla section. The upper member was named Nimaluoshenza Member by Rao & Zhang (1985) at the Tulong section, and it is generally equivalent to the Kuling Shale in Spiti, India (Garzanti et al. 1996) and to units 23-24 at the Qubu section (Shen et al. 2003c). Brachiopods are very rare in this interval (Shen et al. 2006; Brühwiler et al. 2009) except for some small unidentified brachiopods around 60 cm below the top of this member, as mentioned by Rao & Zhang (1985). However, the bivalve *Atomodesma variabilis* is very abundant in the topmost 5-10 m which is consistent with the record from the Qubu section (Rao & Zhang 1985; Shen et al. 2003c, 2006; Pan & Shen 2008). In addition, microfossils like palynomorphs and acritarchs are very abundant in this member (Fig. 2A); the pollen-dominated palynological assemblage (Rao & Zhang 1985) shows a Permian-Triassic mixed character, as indicated by the presence of some elements reported in the Chhidru Formation (e.g., *Polypodiisporite*s cf. *mulabilis*, *Lueckisporites*, *Vitreisporites*) and the Kathwai Member (e.g., *Punctatisporites* sp., *Densoisporites* sp.) of the Salt Range, Pakistan (Balme 1970). In addition, the appearance of *Aratrisporites* sp. is considered to be the signal of the floral turnover near the Permian-Triassic boundary (Shen et al. 2006; Hermann et al. 2012). But palynological samples collected by Brühwiler et al. (2009) from this member are barren.

The multicoloured Nimaluoshenza Member (upper member in this paper) of the Qubuerga Formation is overlain by the very distinct reddish dolostone unit of the Tulong Formation. According to the conodont samples we collected and the data of Tian (1982), abundant latest Permian to basal Triassic conodonts including *Hindeodus* sp. (Fig. 3.1), *H. praeparvus* (Fig. 3.2), *Clarkina carinata* (Figs 3.3-3.4), *C. orchardi* (Figs 3.5-3.6), *C.* ?*orchardi* (transitional to *C. taylorae*) (Figs 3.7-3.8), *C.* ?*taylorae* (Figs 3.9-3.10) and *C. tulongensis* (Fig. 3.11) occur in the dolostone unit in the basal part of this formation at the Tulong section. This clearly indicates that the section

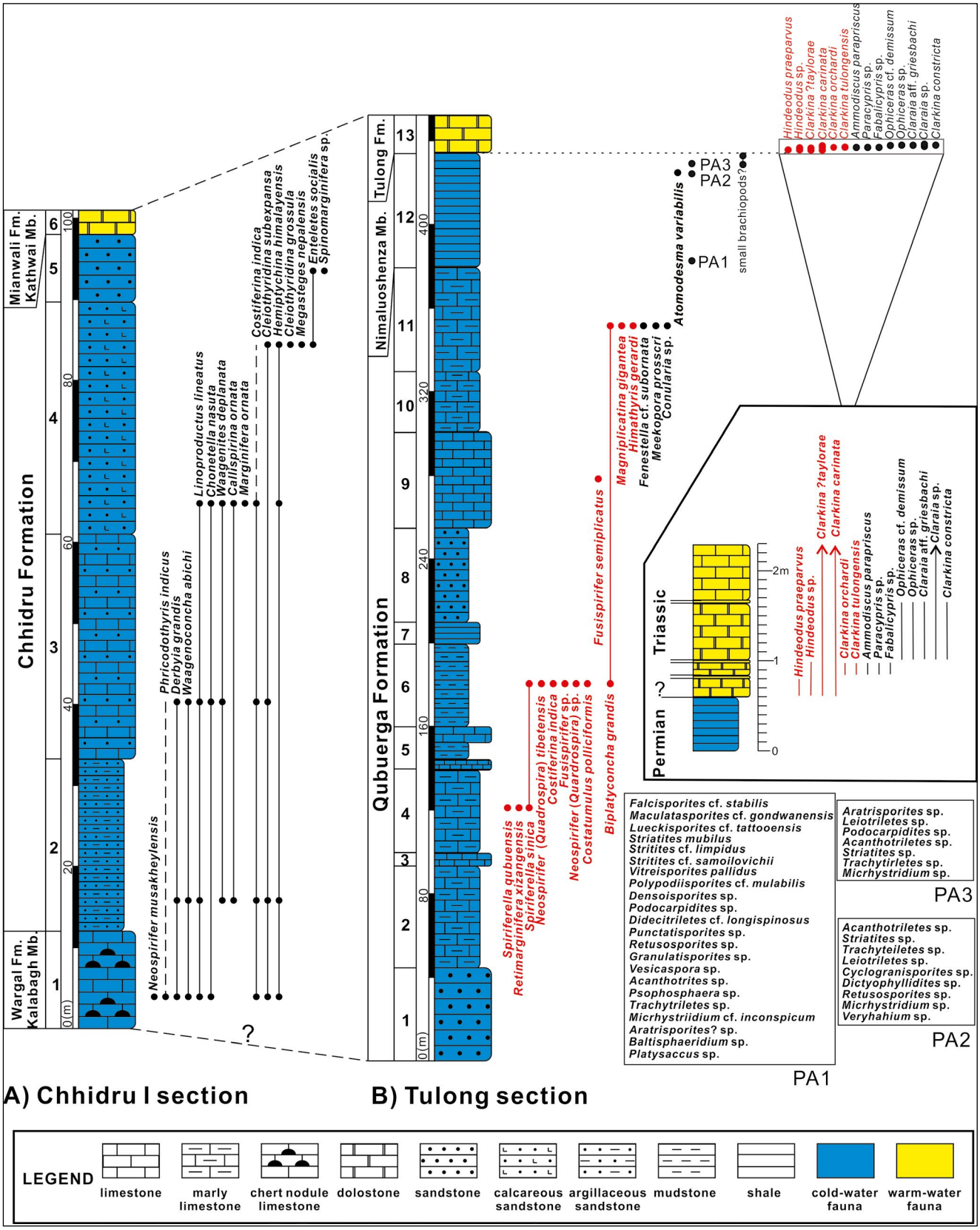


Fig. 2 - Correlation of stratigraphic successions of A) the Chhidru I section in the Salt Range, Pakistan with occurrences of brachiopods and B) the Tulong section with occurrences of various fossils. Some data are from Tian (1982), Rao & Zhang (1985), Pakistan-Japanese Working Group (1985) and Shen et al. (2006). Fossil names in red were collected by this study.

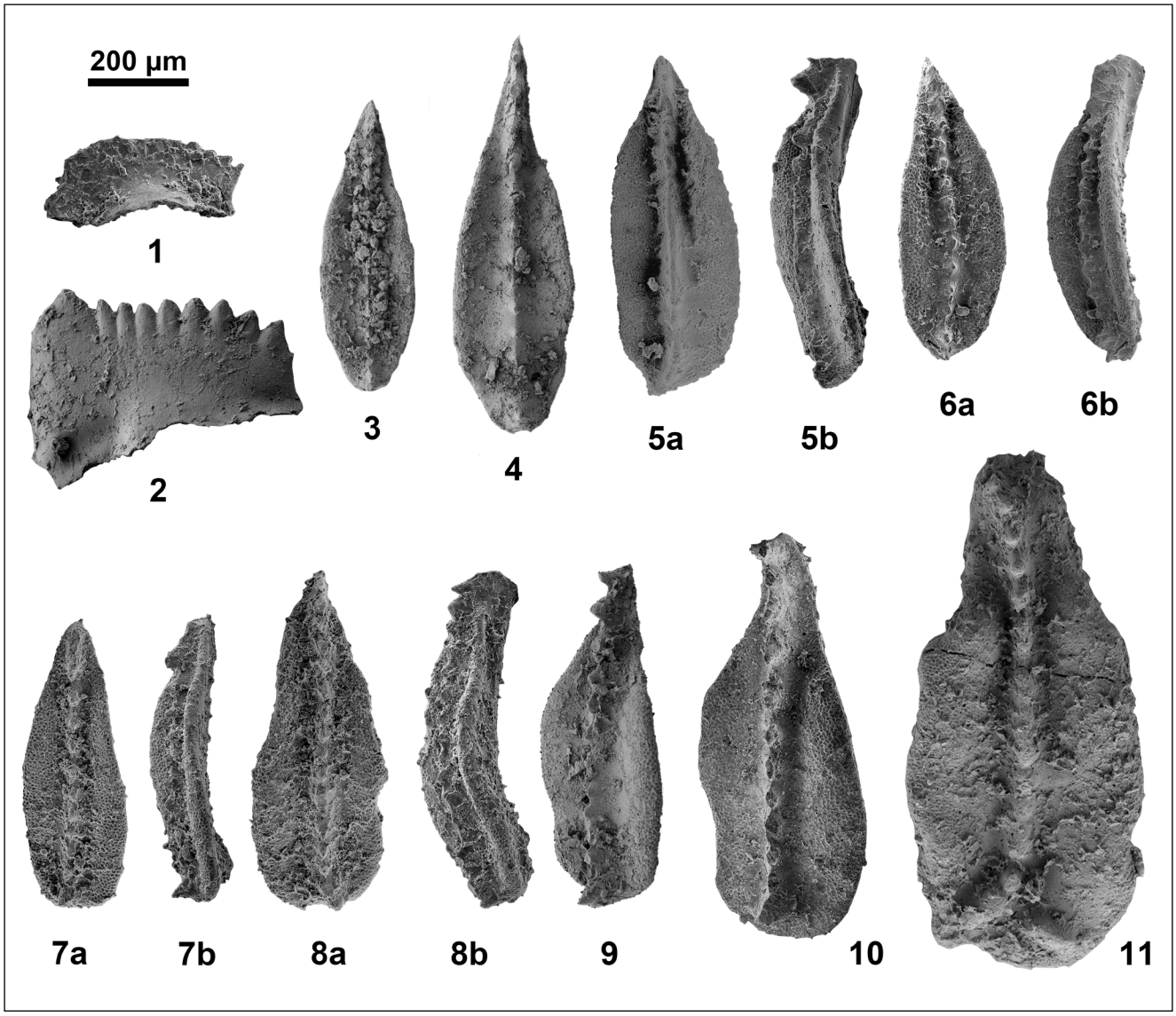


Fig. 3 - Conodonts from the basal part of the Tulong Formation. 1) *Hindeodus* sp., lateral view; 2) *Hindeodus praeparvus* (Kozur, 1996), lateral view; 3, 4) *Clarkina carinata* (Clark, 1959), upper view; 5a, 5b, 6a, 6b) *Clarkina orchardi* Mei, 1996, 5a, 6a, upper view, 5b, 6b, lateral view; 7a, 7b, 8a, 8b) *Clarkina* ?*orchardi* Mei, 1996 (transitional to *Clarkina taylorae*), 7a, 8a, upper view, 7b, 8b, lateral view; 9, 10) *Clarkina* ?*taylorae* (Orchard, 1994), upper view; 11) *Clarkina tulongensis* (Tian, 1982), upper view.

contains a generally continuous sequence across the Permian-Triassic boundary. Additionally, a foraminifer identified as *Ammodiscus parapriscus* and the ostracods *Paracypris* sp. and *Fabalicypris* sp. have been recorded from the lower part of the dolostone unit (Shen et al. 2006). About 34 cm above the base of this formation, ophiceratids and the bivalve *Claraia* start to occur (Fig. 2A). In addition, an age-mixed ammonoid assemblage probably due to coarse sampling was recorded in the limestone unit (Wang & He 1976; Rao & Zhang 1985); it is impossible that these ammonoids come from the same time interval (Brühwiler et al. 2009). Based on a recent detailed study of ammonoids and conodonts from its counterpart at the Qubu section, the Permian-Triassic boundary is about several tens of centimetres above the base of this dolostone unit (Shen et al. 2006; Zhang et al. 2017).

Discussion on the age

As mentioned above, the presences of a *Glossopteris* flora of a late Guadalupian or Wuchiapingian age (Hsü et al. 1990) from the underlying Qubu Formation and the earliest Triassic conodonts such as *Hindeodus praeparvus*, *Clarkina carinata*, *C.* ?*taylorae* (Fig. 3), and ammonoids (e.g., ophiceratids) from

Species	Ventral valves	Dorsal valves	Conjoined shells
Tulong section			
Costiferina indica (Waagen)	2	1	
Retimarginifera xizangensis Shen et al.	17		
Biplatyconcha grandis (Waterhouse)	2		
Costatumulus polliciformis (Waterhouse)	2		
Magniplicatina gigantean Shen et al.	1		
Himathyris gerardi (Diener)			1
Neospirifer (*Quadrospira*) *tibetensis* Ding	1		
Neospirifer sp.	1		
Fusispirifer semiplicata Jin	2	1	
Fusispirifer sp.	1		
Spiriferella qubuensis Zhang	2		
Spiriferella sinica Zhang	15		
Kujianla section			
Biplatyconcha grandis (Waterhouse)		1	
Magniplicatina gigantean Shen et al.	2	1	
Echinalosia magnispina Waterhouse	3	7	
?*Derbyia* sp.		1	
Fusispirifer semiplicata Jin	2	1	
Fusispirifer marcouiformis Jin		1	

Tab. 1 - Brachiopod species from the Tulong and Kujianla sections.

the lowest part of the overlying Tulong Formation constrain the age of the Qubuerga Formation at Tulong to the Lopingian.

In total, 15 brachiopod species belonging to 11 genera (Tab. 1) were identified from the lower member of Qubuerga Formation at the Tulong and Kujianla sections. Among the identified 15 species, *Retimarginfera xizangensis, Costiferina indica, Fusispirifer semiplicatus, Spiriferella sinica*, *Biplatyconcha grandis* and *Neospirifer* (*Quadrospina*) *tibetensis*, are all very common elements in the Selong Group and its equivalents at the Selong Xishan, Qubu and Shengmi sections in southern Tibet (Shen et al. 2000, 2001a, 2001b, 2003c). Some of them have been widely known from the Senja Formation in northwest Nepal (Waterhouse 1966, 1978), the Zewan Formation in Kashmir (Shimizu 1981) and the upper part of the Wargal Formation and the Chhidru Formation in the Salt Range, Pakistan (Waterhouse & Gupta 1983). The upper part of the Wargal Formation is clearly of Wuchiapingian age as indicated by the presence of the ammonoid *Cyclolobus* (Furnish et al. 1973; Shen et al. 2001a), Wuchiapingian conodonts (Wardlaw & Pogue 1995; Wardlaw & Mei 1999), and some small foraminifers (Pakistan-Japanese Working Group 1985; Shen et al. 2003b).

Biplatyconcha grandis is very common in the Nisal Member of the Senja Formation in northwest Nepal (Waterhouse 1975, 1978, 1988). Within this member, a brachiopod fauna referred to the *Marginalosia kalikotei* Zone was assigned to the Dorashamian (=Changhsingian) Stage (Waterhouse 1988; Waterhouse & Gupta 1983). In addition, *Biplatyconcha grandis* is one of the dominant species in the *Biplatyconcha grandis-Quinquenella semiglobosa* Assemblage, which was given a late Wuchiapingian to early Changhsingian age at the Qubu section (Shen et al. 2003c). *Costiferina indica* is very common in the Wargal and Chhidru formations of the Salt Range, Pakistan (Davidson 1862; Muir-Wood & Cooper 1960; Waterhouse and Gupta 1983), the Basleo Bed of West Timor (Broili 1916), Upper Permian of northwest Nepal (Waterhouse 1966), and the Gyanyima Formation (Changhsingian) in southwestern Tibet (Shen et al. 2010), which have a Wuchiapingian-Changhsingian age. *C. indica* also occurs in the *Lamnimargus himalayensis* Zone in Divisions I, II and IV of the Zewan Formation in Kashmir which correspond to the Wargal and Chhidru formations (Nakazawa et al. 1975; Shen et al. 2003c). Similarly, *Retimarginifera xizangensis* is associated with or occur in the assemblages equivalent to the *L. himalayensis* Zone mainly from the Zewan Formation at Guryul Ravine and Spur in Kashmir, the lower member of the Gungri Formation of the Kuling Group in Spiti (Garzanti et al. 1996) and the middle part of the Selong Formation at the Selong Xishan section, southern Tibet (Shen et al. 2000; Shi & Shen 1997). *Spiriferella qubuensis* is close to *S. sinica* and these two species are associated to *S. rajah*. As remarked by Shen et al. (2003c), *S. rajah* is one of the most common elements that were never found below the "*L.*" *himalayensis* zone in the Himalayan region. Therefore, this taxon suggests an age ranging from the late Wuchiapingian to the early Changhsingian. *Neospirifer* (*Quadrospira*) *tibetensis* is closely related to *Neospirifer* (*Neospirifer*) *kubeiensis* which is the dominant species in the *Chonetella nasuta* Assemblage at the Selong Xishan section (Shen et al. 2000) and *Neospirifer* (*Neospirifer*) *kubeiensis-Chonetinella unisulcata* Assemblage at the Qubu section (Shen et al. 2003c). *Costatumulus polliciformis* and *Himathyris gerardi* were both recorded in the Kuling Formation in the Indian Himalayan region (Diener 1897), which were also referred to the "*L.*" *himalayensis* Zone (Waterhouse 1985; Garzanti et al. 1996). *Fusispirifer semiplicata* and *F. marcouiformis* are not only present in the Kuling Formation at Kiungling (Diener 1897)

and Spiti (Diener 1899), but they are also present in the Luri Member (Waterhouse 1966) and the Nisal Member (Waterhouse 1978) of the Senja Formation in northwest Nepal. Thus, it is clear that the brachiopod faunas from the Qubuerga Formation at Tulong and Kujianla are both comparable with those from the Selong Group at Selong and Qubu, the Senja Formation in northwest Nepal and the Wargal and Chhidru formations in the Salt Range, Pakistan. Their age can be safely assigned to the Wuchiapingian to early Changhsingian (Shen et al. 2003c). The overlying Nimaluoshenza Member, immediately below the dolostone unit, is of late Changhsingian age.

Palaeobiogeographical and Palaeoclimatic implications

Three Lopingian lithofacies with different brachiopod faunas were recognised in the Himalaya Tethys Zone. They are respectively: the Chitichun-type, the Selong-type and the Qubu-type lithofacies (Shen et al. 2003a). The Chitichun-type lithofacies is characterized by gray or purple pure bioclastic limestone containing compound rugose corals, fusulinids, ammonoids and mixed brachiopod faunas with palaeoequatorial to Gondwanan affinity, which probably represents disrupted and displaced carbonate or seamount deposits in the southern part of the Neotethys Ocean. The Selong-type Lopingian is represented by the Selong Group which is mainly composed of coarse bioclastic limestone, calcareous shale, crinoid grainstone. Brachiopods are extremely abundant in most part of the group with a typical Gondwanan affinity and solitary rugose corals are largely yielded from the topmost of the group. Notably, the Selong-type lithofacies does not have a multicoloured shale member in the uppermost part of the Selong Group, which was interpreted to suggest the occurrence of a long hiatus (e.g., Xia & Zhang 1992). The Qubu-type lithofacies refers to the Qubuerga Formation, which is characterized by a lower member containing abundant Gondwanan-type brachiopods and an upper member featured by muddy siltstone and varicoloured shale with abundant bivalves, gastropods and palynomorphs. Thus, it is clear that the brachiopod faunas and lithofacies at Tulong (Fig. 2A) and Kujianla indicate that they are comparable with those at Qubu and Shengmi in the Mt. Everest area, which clearly belong to the Qubu-type lithofacies. Moreover, the sedimentary environment of the Tulong section probably experienced a transgression-regression-transgression cycle as the Qubu section. Specifically, the sequence starts with a likely terrigenous environment (the Qubu Formation and the sandstone in the lowest part of the lower member) and then generally shifted to a shallow-water or coastal environment (bioclastic limestone of the lower member), and dropped to a sea-level lowstand (siltstone or shale of the main part of the upper member containing abundant palynomorphs), finally deepened again at the very end of the Permian as indicated by the shale in the topmost part of the upper member containing numerous poorly-preserved ammonoids and the distinct dolostone unit in the basal part of the Tulong Formation containing numerous conodonts *Clarkina* (Fig. 3).

Palaeobiogeographically, the brachiopods from the Qubuerga Formation at Tulong and Kujianla are all composed of typical Gondwanan, bipolar or cosmopolitan elements. Among the identified 11 genera, *Biplatyconcha*, *Retimarginifera*, *Magniplicatina*, *Echinalosia* are restricted to the Gondwanan Realm, while *Costiferina* and *Himathyris* are mainly distributed in the Gondwanan Realm and the Southern Transitional Zone during the Lopingian (Shi et al. 1995; Shen & Shi 2000; Shen et al. 2000). The other taxa, such as *Fusispirifer*, *Spiriferella*, *Neospirifer* and *Costatumulus* are typically bipolar or anti-tropical genera. Thus, it is clear that the Himalaya Tethys Zone, as a part of the Indian Plate, was still situated in the southern high-latitude region under cold palaeoclimatic conditions during the Lopingian (Shen et al. 2001b), which is different from the Cimmerian blocks such as southeast Pamir, Karakoram, South Qiangtang and Lhasa blocks in tectonic history (Fig. 4). All those blocks drifted northward significantly from late Cisuralian; therefore, they began to contain transitional and warm-water faunas after the Kungurian (Shi et al. 1995; Angiolini et al. 2013b, 2015; Shen & Shi 2000; Shen et al. 2016; Yuan et al. 2016).

It is worth mentioning that the Lopingian brachiopod fauna in the Salt Range contains some tropical or subtropical genera such as *Enteletes* and *Spinomarginifera* (Fig. 2B) in the Kalabagh Member of the Wargal Formation and the Chhidru Formation, which are totally absent in the faunas from Tu-

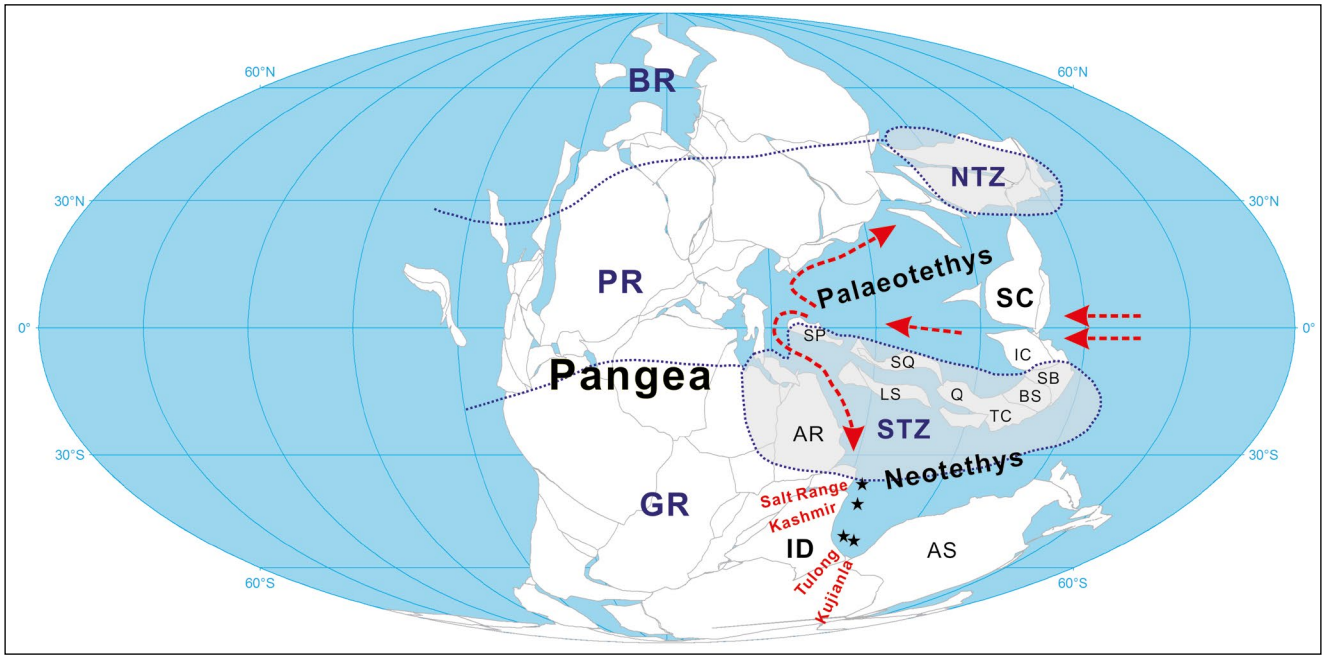


Fig. 4 - Palaeogeographic map of the Tethyan region showing the palaeopositions of Tulong, Kujianla, Kashmir and the Salt Range during the Lopingian. BR: Boreal Realm; PR: Palaeoequatorial Realm; GR: Gondwanan Realm; NTZ: Northern Transitional Zone; STZ: Southern Transitional Zone; SC: South China; IC: Indochina; AR: Arabian Plate; ID: Indian Plate; AS: Australia; LS: Lhasa Block; SQ: South Qiangtang Block; SP: South Pamir; Q: Qamdo Block; TC: Tengchong Block; BS: Baoshan Block; SB: Sibumasu Block; Red dotted line: warm-water currents; Blue dotted line: boundaries of the different palaeobiogeographic realms (base map modified after Ke et al. 2016).

long and Kujianla (Pakistan-Japanese Working Group 1985; Shen & Shi 2000) although all those localities were situated at the northern peri-Gondwanan margin and they generally share the similar palaeobiogeographical affinities, with more than 60-80% similarities (Shen et al. 2000; Ke et al. 2016). This difference may be explained by its more northerly palaeolatitude position along the northern margin of the Indian Plate (Fig. 4). Alternatively or both, the Salt Range of Pakistan was likely influenced by the southeasterly warm-water currents which were branched from the westward palaeoequatorial warm currents (Shen & Shi 2000; Angiolini et al. 2013a, 2013b). The Tulong and Kujianla areas were probably not affected by the warm currents due to their relatively far distance from the western coast of the Palaeotethys, being located at more southerly palaeolatitudes, close to Western Australia or northeastern India (Fig. 4).

Palaeoclimatically, the faunal succession at Tulong records a dramatic transition from cold to warm condition across the Permian-Triassic boundary. This is indicated by the typical cold-water brachiopods described herein from the lower member and the gastropods and bivalves in the upper member of the Qubuerga Formation, followed by the burst of extremely abundant conodonts *Clarkina* spp. (Fig. 3) in the dolostone unit of the basal part of the Tulong Formation. This is also supported by the replacement of ferns by the tropical gymnosperm and lycopod assemblages near the Permian-Triassic boundary (Hermann et al. 2012) and the presence of the typical lycopod spore *Aratrisporites* sp. in the uppermost part of the Permian (Rao & Zhang 1985).

This rapid changeover from cold to warm condition has been documented in the entire peri-Gondwanan region (Shen et al. 2006). For instance, in the Salt Range, Pakistan, the conodonts in the upper part of Chhidru Formation are characterized by typical cold-water elements in terms of the presence of the genera *Vjalovognathus* and *Merrillina* (Wardlaw & Mei 1999). The brachiopods in the Kalabagh Member and the Chhidru Formation are dominated by cold-water elements mixed with a few warm elements, which clearly indicate relatively cold conditions. This is followed by the presence of abundant conodonts including *Clarkina meishanensis* (Wardlaw & Mei 1999) and warm-water brachiopods (e.g., *Spinomarginifera, Ombonia, Orthothetina,* and *Enteletes*) in the Kathwai Member of the basal part of Mianwali Formation (Grant 1970). At the Selong Xishan sec-

tion, the Selong Group including the topmost part of Coral Bed, contains abundant cold-water brachiopods (Jin et al. 1996; Shi & Shen 1997; Shen & Jin 1999; Shen et al. 2000, 2001b) and it is overlain by the *Wagganites* Bed containing both cold-water and warm-water brachiopods (e.g., *Fusichonetes*) and extremely abundant conodonts *Clarkina* spp. At the Gyanyima section around the Yarlung-Zangbo Suture Zone, seawater temperature varied about 26°C from Unit 1 to the base of Unit 8 of the Gyanyima Formation and sharply exceeded 35°C at about 120 kyr before the Permian-Triassic boundary based on brachiopod $\delta^{18}O$ (Garbelli et al. 2016). Thus, it can be concluded that a significant climatic warming event occurred just beneath the Permian-Triassic boundary based on the sections in the peri-Gondwanan region (Shen et al. 2006, 2010). This warming is also clearly recorded based on the $\delta^{18}O_{apatite}$ excursion from conodonts in South China (Joachimski et al. 2012; Chen et al. 2016).

Systematic Palaeontology

Order **Productida** Sarytcheva & Sokolskaya, 1959
Suborder **Productidina** Waagen, 1883
Superfamily Productoidea Gray, 1840
Family Productellidae Schuchert, 1929
Subfamily Marginiferinae Stehli, 1954
Tribe Paucispiniferini Muri-Wood & Cooper, 1960
Genus *Costiferina* Muir-Wood & Cooper, 1960

Type species: *Productus indicus* Waagen, 1884 from the Wuchiapingian of Salt Range (Pakistan).

Costiferina indica (Waagen, 1884)

Pl. 1, figs 1-4

1862 *Productus costatus* - Davidson, p. 31, pl. 1, figs 20, 21.
1884 *Productus indicus* Waagen, p. 687, pl. 70, figs 1-6; pl. 71, fig. 1.
1915 *Productus indicus* - Diener, p. 66, pl. 6, figs 15a-d.
1916 *Productus spiralis* - Broili, p. 11, pl. 117, fig. 2 (non 1, 3-5).
1960 *Costiferina indica* - Muir-Wood & Cooper, p. 277, pl. 95, figs 6, 7; pl. 103, figs 1-12.
1966 *Costiferina alata* Waterhouse, p. 26, pl. 5, figs 1, 4, 5; pl. 6, figs 1-3; pl. 7, figs 3, 5; pl. 8, fig. 4.
1976 *Costiferina indica* - Zhang & Jin, p. 178, pl. 5, figs 11, 12; pl. 6, figs 11-13.
1976 *Costiferina spiralis* - Zhang & Jin, p. 179, pl. 5, figs 4, 7-10; pl. 7, fig. 2.
1981 *Costiferina indica* - Shimizu, p. 75, pl. 7, figs 17-19.
1992 *Costiferina indica* - Jiang & Yan, pl. 1, figs 7, 8.
2003c *Costiferina indica* - Shen et al., p.75, pl. 7, figs 13, 15, 16; pl. 8, figs 1-8.
2003 *Costiferina indica* - Shi & Shen, p. 1059, figs 3.9-3.14.

Material. Two ventral valves (NIGP 166727-166728); and an incomplete external cast of a dorsal valve (NIGP 166729).

Description. Medium sized shell, 35.1 mm long, 64.8 mm wide and about 33 mm thick (NIGP 166728); ventral outline subquadrate, greatest width at hinge; ears small, but distinct; cardinal extremities nearly at right angle. Ventral valve strongly convex; beak broad; umbonal slopes sharply inclined; sulcus broad, beginning from the umbo, widening and deepening anteriorly, becoming distinct on trail; costae very coarse on trail, slightly converging into sulcus anteriorly, numbering 3-4 in 1 cm anteriorly, interrupted by concentric wrinkles posteriorly to midvalve, forming delicate reticulate ornaments on the visceral region; erect spines found sporadically on costae, spine bases very obvious, about 1-2 mm in diametre; lateral slopes strongly inclined. Dorsal valve slightly concave and geniculated; radial costae fairly coarse, numbering 6-8 in 1 cm on trail, spines erect, evenly distributed on costae.

Discussion. Specimens referable to this species were first reported by Davidson (1862) as one of the most common species in the Carboniferous limestone which is actually from the Wargal and Chhidru formations of Lopingian (Late Permian) age at Moosakhail and Kafir Kote of the Salt Range, Pakistan. A specimen from the Basleo Bed of West Timor described as *Productus spiralis* by Broili (1916, pl. 117, fig. 2) is probably conspecific with *C. indica* in terms of similar size, outline and very coarse costae on the trail (Shen et al. 2003c; Shi & Shen 2003). *C. alata* Waterhouse (1966) from the Upper Permian of northwest Nepal was suggested by Shen et al. (2003c) to be assigned to this species in terms of same ornament details apart from some intraspecific variations like slightly larger size and broader plicae anteriorly. Specimens figured as *C. spiralis* by Zhang & Jin (1976) are also similar to this species. Although some characters such as trail, complete beak and ears are not observed in the present specimens, we feel confident that it belongs to *C. indica* in view of their subquadrate outline, coarse costae and clearly reticulate ornament. *Retimarginifera* can be readily distinguished from *Costiferina* in terms of its much smaller size, transverse outline with acute extremities and fine costae on the trail. Internally, *Costiferina* possesses very large and strong muscular scars in the ventral valve.

Occurrence. Bed 6 of the Qubuerga Formation at Tulong; Qubuerga Formation at Qubu in southern Tibet, China; Wargal and Chhidru formations in the Salt Range, Pakistan; Upper Permian Senja Formation in northwest Nepal; Member B of the Zewan Formation in Kashmir; Basleo Bed at Kampong in West Timor.

Genus *Retimarginifera* Waterhouse, 1970

Type species: *Retimarginifera perforata* Waterhouse, 1970 from the Kungurian of Western Australia.

Retimarginifera xizangensis Shen et al., 2000

Pl. 1, figs 5-9

1976 *Marginifera himalayensis* - Zhang & Jin, p. 174, pl.10, figs 17-21; pl. 15, fig. 10.
1981 *Marginifera himalayensis* - Shimizu, p.72, pl. 8, figs 5-8 (non 1-4).
1989 *Marginifera himalayensis* - Wang et al., pl. 1, figs 10, 11.
1996 *Lamnimargus himalayensis* - Garzanti et al., p. 194, pl. 1, figs 1, 2.
1997 *Lamnimargus himalayensis* - Shi & Shen, p. 43, figs 3E, G, H.
2000 *Retimarginifera xizangensis* Shen, Archbold, Shi & Chen, p. 741, figs 10.1-10.7, 10.19, 10.20, 11.
2003c *Retimarginifera xizangensis* - Shen et al., p. 77, pl. 8, figs 11-14; pl. 9, figs 1-6; text-figs 10, 11.

Material. Seventeen ventral valves. Registered specimens: three complete ventral valves (NIGP 166730-166732).

Description. Small sized shell, 17.3-20.7 mm long, 23.7-27.6 mm wide and about 12.3 mm thick, transversely elliptical in outline, apparently concavo-convex in lateral profile; widest at hinge; ears large, alate, triangular in shape, demarcated from visceral disc by grooves clearly; lateral margin rounded; ventral valve strongly geniculated; beak very low and slightly incurved; umbonal slopes slowly inclined; sulcus commencing from beak, slightly widening and deepening anteriorly; costae beginning from beak, nearly straight and relatively coarse, crossed by 5-7 distinct concentric rugae from umbo to about midvalve, numbering 5-6 in 5 mm anteriorly.

Discussion. *Lamnimargus himalayensis* was first named by Waterhouse (1975) with type-species *Marginifera himalayensis*, which is distinguished from *Marginifera* by its reticulate ornament and from *Retimarginifera* by a cluster of spines over the ears and occasionally two or three trails arising from the marginal ridge in both valves. Although the specimens reported by Zhang & Jin (1976) from southern Tibet were assigned to *M. himalayaensis*, they did not feature a more flattened and longer visceral disc, finer costae and more reticulation. Therefore, they were re-assigned to the present species by Shen et al. (2000). Shen et al. (2000) defined *Retimarginifera xizangensis* as characterized by marginal ridges in both valves, but no more trails based on the specimens from the Selong Xishan Section, southern Tibet. Notably, several specimens reported by Shimizu (1981) from Kashmir were divided into two species by Shen et al. (2000, 2003c), specimens from the Unit E1 of the Khunamuh Formation at Guryul Ravine are probably identical with *R. xizangensis* while the others from Member b of the Zewan Formation at Barus are clearly different from those of the Unit E1 by their more extensively reticulated disc and relatively weaker concentric rugae, which characterize *Lamnimargus*. Also, the specimens described as *L. himalayensis* by Garzanti et al. (1996) from the Gungri Formation at Muth and the Selong Group of the Selong Xishan Section by Shi & Shen (1997) are considered to be *R. xizangensis*. This species is similar to *R. gaetanii* Angiolini, 1995 in Angiolini (1995, 2001) reported from Karakorum, from which it can be distinguished by its coarser costae and less reticulate visceral disc.

PLATE 1

Figs 1-4 - *Costiferina indica* (Waagen, 1884). 1, 2, ventral and postero-ventral views of a ventral valve, NIGP 166727; 3, ventral valve, NIGP 166728; 4, ventral view of interior of a dorsal valve, NIGP 166729.

Figs 5-9 - *Retimarginifera xizangensis* Shen et al., 2000. 5, 6, ventral and anterior views of a ventral valve, NIGP 166730, ×1.5; 7, 8, ventral and anterior views of a ventral valve, NIGP 166731, ×1.5; 9, antero-ventral view of a ventral valve, NIGP 166732, ×1.5.

Figs 10-12 - *Biplatyconcha grandis* (Waterhouse, 1975). 10, internal mould of a ventral valve, NIGP 166733; 11, a fragment of a ventral valve, NIGP 166734; 12, external cast of a dorsal valve, NIGP 166751.

Figs 13-16 - *Costatumulus polliciformis* (Waterhouse, 1978); 13, antero-ventral view of internal mould of a ventral valve, NIGP 166735; 14, 15, 16, antero-ventral, ventral and lateral views of a ventral valve, NIGP 166736.

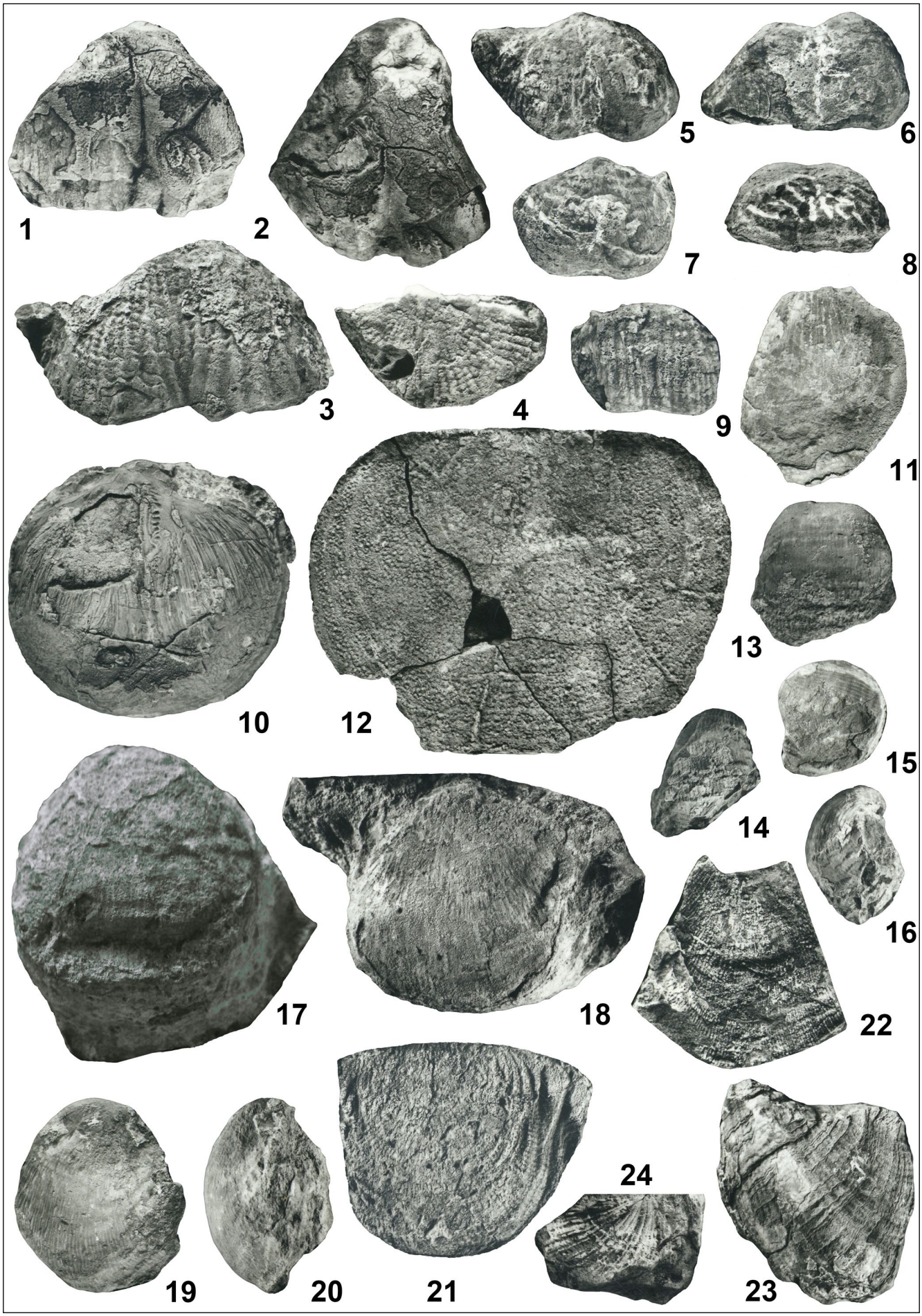
Figs 17-21 - *Magniplicatina gigantea* Shen, et al. 2003c. 17, internal mould of a ventral valve, NIGP 166752; 18, internal mould of a ventral valve, NIGP 166753; 19, 20, latero-ventral and lateral views of a ventral valve, NIGP 166737. 21, incomplete internal mould of a dorsal valve showing a median ridge, NIGP 166754.

Fig. 22 - ?*Derbyia* sp. dorsal view, NIGP 166756.

Fig. 23 - *Neospirifer* (*Quadrospira*) *tibetensis* Ding, 1962. incomplete ventral valve, NIGP 166739.

Fig. 24 - *Neospirifer* sp. external cast of an incomplete ventral valve, NIGP 166740.

All figures are in natural size unless otherwise illustrated.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Occurrence. Bed 4 of the Qubuerga Formation at Tulong, southern Tibet, China; Gungri Formation at Spiti of Indian Himalaya; Zewan Formation in Kashmir.

Superfamily Echinoconchoidea Stehli, 1954
Family Echinoconchidae Stehli, 1954
Subfamily Juresaniinae Muri-Wood & Cooper, 1960
Tribe Waagenoconchini Muri-Wood & Cooper, 1960
Genus *Biplatyconcha* Waterhouse, 1983a

Type species: *Platyconcha grandis* Waterhouse, 1975 from the Late Permian of Nepal.

Biplatyconcha grandis (Waterhouse, 1975)

Pl. 1, figs 10-12

1975 *Platyconcha grandis* Waterhouse, p. 8, pl. 2, figs 1-4.
1976 *Wyndhamia circularis* Zhang in Zhang & Jin, p. 166, pl. 2, figs 1-15; text-fig. 3.
1978 *Platyconcha grandis* - Waterhouse, p.73, pl. 10, figs 11-14; pl. 11, figs 1-5.
1998 *Platyconcha grandis* - Briggs, fig. 59.
1988 *Megalosia chuluensis* Waterhouse, p. 42, figs 4, 5.
2001a *Biplatyconcha grandis* - Shen et al., p. 279, figs 4.1-4.4.
2003c *Biplatyconcha grandis* - Shen et al., p. 69, pl. 3, figs 16-18; pl. 4, figs 1-7; text-fig. 7.

Material. A complete internal mould of ventral valve (NIGP 166733); a fragment of ventral valve (NIGP 166734); and an external cast of dorsal valve (NIGP 166751).

Description. Shell relatively large for genus; 51.4 mm long, 54 mm wide and about 26 mm thick (NIGP 166733), elliptical to suborbicular in outline; hinge slightly shorter than greatest width at about shell midlength; cardinal extremities rounded. Ventral valve moderately convex, mostly convex at midvalve; beak low and blunt; interarea low; sulcus unconspicuous or absent; costae fine, numbering 4 in 5 mm; spines over ventral valve closely set and slightly coarse, somewhat in rows. Dorsal valve gently concave or nearly flat; anterior side broadly rounded while lateral margins nearly flat; surface evenly covered by closely set and quincunxially arranged dimples; relatively dense concentric stripes distributed near the anterior margin. Ventral adductor scar elongate in shape; diductor scars well developed, shallowly impressed, separated by a median trough.

Discussion. The type species *Platyconcha grandis* Waterhouse, 1975 was first reported from the Nisal Member of the Senja Formation at Dolpo, northwest Nepal by Waterhouse (1975). *Megalosia chuluensis* Waterhouse (1988) is considered to be a junior subjective synonym of *Biplatyconcha grandis*, following Briggs (1998). *Wyndhamia circularis* Zhang in Zhang & Jin (1976) from the Selong Group in southern Tibet was renamed as *Megalosia chuluensis* by Waterhouse (1988) because they have almost identical external features except for the slightly wider hinge. Later, they were all re-assigned to *Biplatyconcha grandis* by Shen et al. (2001a, 2003c) in terms of similar outline, size, profile, short hinge, close-set dimples over the dorsal valve, and comparable internal details.

Occurrence. Beds 6, 11 of the Qubuerga Formation at Tulong; Qubuerga Formation at Kujianla and Qubu; Selong Group at Quzong and Surishan in southern Tibet, China. This species was also recorded from the Nisal Member of the Senja Formation in northwest of Nepal.

Superfamily Linoproductoidea Stehli, 1954
Family Monticuliferidae Muri-Wood & Cooper, 1960
Subfamily Auriculispininae Waterhouse, 1986
Genus *Costatumulus* Waterhouse, 1986

Type species: *Auriculispina tumida* Waterhouse in Waterhouse et al., 1983 from the Artinskian of eastern Australia.

Costatumulus polliciformis (Waterhouse, 1978)

Pl. 1, figs 13-16

1897 *Productus cancriniformis* - Diener, p. 31, pl. 1, figs 7-10.
1978 *Cancrinella polliciformis* Waterhouse, p. 76, pl. 11, figs 9-12.
2003c *Costatumulus polliciformis* - Shen et al., p. 80, pl. 10, figs 15-22.

Material. An incomplete ventral valve and an incomplete internal mould of ventral valve (NIGP 166735, NIGP 166736).

Description. Small to medium sized shell, more than 27 mm long and 29 mm wide; elongate or slightly elliptical in outline. Ventral valve moderately convex in lateral profile; beak strongly incurved and relatively broad; umbonal slopes inclined sharply. Costae fine and nearly vertical, numbering 6-7 in 5 mm; rugae evenly distributed, becoming coarser and more distinct anteriorly; spines closely set, especially anteriorly, more or less in rows, bases slightly swollen. Dorsal valve unknown.

Discussion. *Productus* (=*Cancrinella*) *cancrini-*

formis described by Tschernyschew (1889) from the central Urals looks close to this species in similar size and ornamentation on the ventral valve, but its slightly transverse outline and weaker longitudinal curvature are apparently different from the present species. Later, the specimens from the *Productus* shales of the Indian Himalaya figured as *Productus cancriniformis* by Diener (1897) were suggested by Shen et al. (2003c) to be re-assigned to *Costatumulus polliciformis* in the light of elongate outline, strong longitudinal curvature and the absence of spines on the dorsal valve. In addition, *Linoproductus tingriensis* designated by Zhang & Jin (1976) from the Selong Group is pretty like this species in view of size, outline, longitudinal curvature, but differs by its finer costae anteriorly, and sparser and more scattered spines. This species is easily confused with the species of *Cancrinella* or *Magniplicatina* based on its costation, concentric rugation and numerous spines on the ventral valve. However, it differs from *Magniplicatina* species by its stronger convexity, sharper lateral flanks and strongly incurved ventral beak. It can be distinguished from all *Cancrinella* species by the absence of spines on the dorsal valve. Our specimens are basically identical with those described by Shen et al. (2003c) from the equivalent horizons at the Qubu section.

Occurrence. Bed 6 of the Qubuerga Formation at the Tulong section; Qubuerga Formation at Qubu in southern Tibet, China; *Productus* shales of Indian Himalaya; Nisal Member of the Senja Formation in northwest Nepal.

Genus *Magniplicatina* Waterhouse, 1983a

Type species: *Cancrinella magniplica* Campbell, 1953 from the Kungurian of Eastern Australia.

Magniplicatina gigantea Shen et al., 2003c

Pl. 1, figs 17-21

2003c *Magniplicatina gigantea* Shen et al., p. 78, pl. 9, figs 7-16.

Material. Two incomplete internal moulds of ventral valve; an incomplete ventral valve; and an incomplete internal mould of a dorsal valve (NIGP 166737, NIGP 166752-166754).

Description. Large sized shell; 48 mm long, 68 mm wide and about 36 mm wide (NIGP 166753); subquadrate in outline; widest at hinge or slightly anterior to hinge; ears flat and alate, well demarcated from visceral disc; cardinal extremities acute. Ventral disc roundly triangular; strongly convex in lateral profile, maximum convexity slightly anterior to midvalve; umbonal slopes sharply inclined. Costae fine and dense, numbering 10-12 in 1 cm at about midvalve, crossed by concentric wrinkles over lateral slope; wrinkles clear and delicate, distributed evenly on lateral slopes; spines closely set over valve, especially numerous near anterior margin; spine bases swollen, some up to 1 mm in diameter, slightly elongated anteriorly.

Discussion. This species was first reported by Shen et al. (2003c) from the Qubuerga Formation at the Qubu section. It can be distinguished from all other species of *Magniplicatina* reported from the Bowen Basin in eastern Australia by Waterhouse (1986) in view of its coarser costae and spines over the lateral slope. The present specimens can be assigned to *M. gigantea* based on their size and outline, fine costae, concentric wrinkles on lateral slopes and closely set spines over valve, apart from the ears not preserved.

Occurrence. Bed 11 of the Qubuerga Formation at Tulong; Qubuerga Formation at Kujianla and Qubu in southern Tibet, China.

Suborder **Strophalosiidina** Schuchert, 1913

Superfamily Strophalosioidea Schuchert, 1913

Family Strophalosiidae Schuchert, 1913

Subfamily Dasyalosiinae Brunton, 1966

Genus *Echinalosia* Waterhouse, 1967

Type species: *Strophalosia maxweli* Waterhouse, 1964 from the Kungurian of New Zealand.

Echinalosia magnispina Waterhouse, 1983a

Pl. 2, figs 1-2

1983a *Echinalosia magnispina* Waterhouse, p. 120, pl. 2, figs 3-8.
2003c *Echinalosia magnispina* - Shen et al., p.67, pl. 2, figs 14-23; pl. 3, figs 1-3.

Material. Ten specimens on a block of sandstone (NIGP 166755).

Description. Medium sized shell, transversely elliptical in outline; hinge slightly shorter than greatest width at about shell midlength. Ventral valve moderately convex in lateral profile; maximum convexity slightly posterior to midvalve; beak short, acute and a little incurved; interarea low; umbo-

nal slopes sharply inclined; ears not preserved or absent; cardinal extremities rounded; sulcus absent. Spines distinct, distributed from about midvalve to anterior margin, somewhat in rows but mostly scattered irregularly, about 1 mm in diameter. Dorsal valve poorly preserved; slightly concave in profile; only scattered erect spines observed.

Discussion. The type specimen of this species from northwest Nepal reported by Waterhouse (1983a) was so poorly preserved that it is difficult to judge whether the present specimens are really identical with the Nepalese specimens or not. Shen et al. (2003c) described some specimens from the Qubuerga Formation at the Qubu section, southern Tibet as *Echinalosia magnispina* in view of similar outline, spinosity on both valves when compared with those described by Waterhouse (1983a). Similarly, our specimens are supposed to be assigned to *E. magnispina* in light of their size, outline, spines on both valves, except for the dimples not preserved on the dorsal valve.

Occurrence. Qubuerga Formation at Kujianla and Qubu in southern Tibet, China; Pija Member of the Senja Formation in northwest Nepal.

Order **Orthotetida** Waagen, 1884
Suborder **Orthotetidina** Waagen, 1884
Superfamily Orthotetoidea Waagen, 1884
Family Derbyiidae Stehli, 1954
Genus *Derbyia* Waagen, 1884
Type species: *Derbyia regularis* Waagen, 1884 from the Wuchiapingian of Salt Range (Pakistan).

?*Derbyia* sp.

Pl. 1, fig. 22

Material. An incomplete external cast of dorsal valve (NIGP 166756).

Description. Large sized shell, more than 37 mm long and 45 mm wide; subquadrate in outline. Dorsal valve moderately convex in lateral profile, maximum convexity at midvalve; costae fine, delicate and dense, numbering 6-8 in 5 mm near anterior margin, crossed by several concentric wrinkles unevenly.

Discussion. This dorsal valve has the features of delicate and dense costae and several concentric wrinkles that suggest a possible species of *Derbyia*, but the ventral valve is not available for further examination. Although the present specimen resembles *Derbyia grandis* according to the similar size and almost the same features of the dorsal valve, it is hard to refer it to *Derbyia grandis* owing to the lack of essential features of ventral valve.

Occurrence. Qubuerga Formation at Kujianla in southern Tibet, China.

Order **Athyridida** Boucot, Johnson & Staton, 1964
Suborder **Athyrididina** Boucot, Johnson & Staton, 1964
Superfamily Athyridoidea Davidson, 1881
Family Athyrididae Davidson, 1881
Subfamily Cleiothyridininae Alvarez, Rong & Boucot, 1998
Genus *Himathyris* Waterhouse, 1985
Type species: *Athyris gerardi* Diener, 1899 from the Late Permian of Indian Himalaya.

Himathyris gerardi (Diener, 1899)

Pl. 2, figs 3-6

1897 *Athyris roysii* Diener (not Léveillé), p. 47, pl. 5, fig. 5 (not fig. 7).
1899 *Athyris gerardi* Diener, p. 56, pl. 6, figs 12-14.
1903 *Spirigera gerardi* - Diener, p. 184, pl. 5, figs 10, 11; pl. 9, figs 6, 7.
1966 *Cleiothyridina gerardi* - Waterhouse, p. 64.
1985 *Himathyris gerardi* - Waterhouse, p. 215, pl. 2, figs 1-8.
1996 *Cleiothyridina gerardi* - Garzanti et al., p. 194, pl. 1, figs 3, 4.
2003c *Himathyris gerardi* - Shen et al., p. 90, pl. 14, figs 14-17.

Material. A complete conjoined shell (NIGP 166738).

Description. Shell 30 mm long, 37 mm wide and 12.5 mm thick; transversely elliptical in outline; slightly convex-concave in lateral profile; widest at about shell midlength; posterior side broadly rounded; anterior side nearly flat with a very shallow middle grove; lateral sides perfectly rounded. Ventral valve nearly flat, slightly concave at the central portion of valve; beak broad; beak ridges almost overlapping with hinge line; sulcus beginning from umbo, narrow and shallow posteriorly, tending prominent and distinct around midvalve, becoming distinct again at anterior margin; concentric lamellae fine and dense, numbering 5-7 in 5 mm, with very fine and dense spines, almost

invisible. Dorsal valve evenly and moderately convex in lateral profile with maximum convexity at about midvalve; fold absent; concentric lamellae as dense as on ventral valve and possessing some fine spines.

Discussion. Specimens referred to this species from the Kuling Formation were first described as *Athyris royssii* by Diener (1897) and then reassigned as *Athyris gerardi* (Diener, 1899) although the specimens are poorly preserved. Specimens from the *Productus* shales of the Lissar Valley were later recorded as *Spirigera gerardi* by Diener (1903). Waterhouse (1985) synonymized this species to *Himathyris gerardi* from the Testha Sandstone Member of the Gungri Formation. (=Kuling Formation.) in South Zanskar; whereas Garzanti et al. (1996) included this species in the genus *Cleiothyridina* following Waterhouse (1966) in terms of large size and the flat ventral valve with a poorly defined sulcus. It is noticeable that *H. gerardi* is the only known species of *Himathyris*.

Occurrence. Bed 11 of the Qubuerga Formation at Tulong; Qubuerga Formation at Qubu in the southern Tibet, China; Kuling Shale in Spiti; *Productus* shales at Kiunglung in the Niti Pass area of Indian Himalaya.

Order **Spiriferida** Waagen, 1883
Suborder **Spiriferidina** Waagen, 1883
Superfamily Spiriferoidea King, 1846
Family Trigonotretidae Schuchert, 1893
Subfamily Neospiriferinae Waterhouse, 1968
Genus *Neospirifer* Fredericks, 1924

Type species: *Spirifer fasciger* Keyserling, 1846 from the Lower Permian of Russia.

Subgenus *Neospirifer* (*Quadrospira*) Archbold, 1997

Type species: *Neospirifer plicatus* Archbold & Thomas, 1986 from the Artinskian of Western Australia.

Neospirifer (*Quadrospira*) *tibetensis* Ding, 1962

Pl. 1, fig. 23

1962 *Neospirifer tibetensis* Ding, p. 454, pl. 2, figs 4-5.
1976 *Neospirifer kubeiensis* - Zhang & Jin, p. 203, pl. 15, figs 1, 2.
1982 *Neospirifer tibetensis* - Yang & Zhang, p. 312, pl. 3, figs 2-4.
1994 *Neospirifer kubeiensis* - Fang & Fan, p. 86, pl. 31, figs 10-12; pl. 32, figs 1, 2.
2001b *Neospirifer tibetensis* - Shen et al., p. 162, figs 4.2, 4.3, 4.5-4.8; tab. 2.
2003c *Neospirifer tibetensis* - Shen et al., p. 84, pl. 12, figs 5-8; pl. 13, fig. 1.

Material. An incomplete ventral valve (NIGP 166739).

Description. Large sized shell, more than 51.1 mm long and 79.5 mm wide; somewhat subquadrate in outline; greatest width slightly anterior to hinge, cardinal extremities subquadrate, with an angle more than 90 degrees. Ventral valve moderately convex in lateral profile; sulcus originating from beak, but its shape is not observable owing to the poor preservation; two plicae observed on the right part of ventral valve, inner plica greatly prominent and raised, likely the boundary plicae; costae coarse, numbering 9-10 in 1 cm near anterior margin, bifurcating several times from the middle to anterior part of the shell; growth lamellae (concentric lines) well developed and imbricate anteriorly, convergent toward cardinal extremities.

Discussion. Ding (1962) clearly defined *Neospirifer tibetensis* from the Permian deposits in Kubei and Tsunbu district, southern Tibet, and he distinguished it from *N. kubeiensis* based on its semicircular outline, and its hingeline shorter than the greatest width. Zhang & Jin (1976) strongly suggested *N. tibetensis* should be assigned to *N. kubeiensis* owing to the fact that the hinge of specimen 3510 of Ding (1962) is almost equal to the shell width. However, through a detailed comparison between *N. kubeiensis* and *N. tibetensis*, Shen et al. (2001b) showed that *N. tibetensis* has a relatively shorter hinge line, more convex lateral sides, larger cardinal angles, more strongly emarginate anterior commissure and usually more attenuated ears than *N. kubeiensis*. By contrast, *N. kubeiensis* normally has the greatest width at the hinge, a more triangular outline, and acute cardinal extremities without attenuated ears. Our specimen is closer to *Neospirifer* (*Quadrospira*) *tibetensis* because the specimen has subquadrate cardinal extremities that indicate the greatest width is slightly anterior to the hinge. In addition, the specimens figured as *N. kubeiensis* from the Xiaoxinzhai and Guanyinshan formations in western Yunnan by Fang & Fan (1994) were re-identified by Shen et al. (2001b, 2003c) as *N. tibetensis* according to their short hingeline and attenuated ears.

Occurrence. Bed 6 of the Qubuerga Formation at Tulong; Selong Group at Qubu, Selong and Tsunbu; Upper Permian at Surishan in southern Tibet; Xiaoxinzhai and Guanyinshan formations (Late Guadalupian) of the Tengchong Block in western Yunnan, China.

***Neospirifer* (*Quadrospira*)** sp.

Pl. 1, fig. 24

Material. An incomplete external cast of ventral valve (NIGP 166740).

Discussion. The ventral valve is medium sized and possesses a moderate convex profile, two apparent plicae on the same side and posterior half of sulcus, which clearly indicates a species of *Neospirifer* (*Quadrospira*). The costae starting from umbo are very fine and dense, about 4 in 5 mm near anterior margin.

Occurrence. Bed 6 of the Qubuerga Formation at Tulong.

Genus *Fusispirifer* Waterhouse, 1966

Type species: *Spirifer nitiensis* Diener, 1897 from the Late Permian of Spiti, Indian Himalaya.

Fusispirifer semiplicata Jin in Zhang & Jin, 1976

Pl. 2, figs 7-12

1966 *Fusispirifer nitiensis* - Waterhouse, p. 44, pl. 9, figs 5; pl. 11, figs 1, 3, 4; pl.12, fig. 1.
1973 *Fusispirifer nitiensis* - Mu et al., pl. 3, figs 7, 8.
1976 *Fusispirifer nitiensis semiplicata* Jin in Zhang & Jin, p. 209, pl. 12, figs 1-6.
1978 *Fusispirifer nitiensis* - Waterhouse, p. 127, pl. 24, figs 11, 14 (non p. 94, pl. 17, figs 1, 6).
1982 *Neospirifer nitiensis* - Yang & Zhang, p. 313, pl.3, fig.1.
1985 *Fusispirifer nitiensis* - Jin, pl. 3, figs 10.
2003c *Fusispirifer semiplicata* - Shen et al., p. 86, pl. 13, figs 10-17.

Material. An incomplete ventral valve and two incomplete internal moulds of ventral valve (NIGP 166741, NIGP 166757-166758); a complete dorsal valve and a complete internal mould of dorsal valve (NIGP 166743, NIGP 166759); and a fragment of external cast of ventral valve (NIGP 166742).

Description. Large sized shell, more than 43 mm long and more than 100 mm wide; extremely transverse in outline, gently biconvex in lateral profile; widest at hinge; cardinal extremities acute; cardinal angles about 30 degrees. Ventral beak low and broad; beak ridge nearly flat; interarea low, concave and broadly triangular; delthyrium in an equicrural triangular shape; flanks slightly convex in adult specimens; sulcus commencing from umbo, evenly widening and deepening anteriorly; plicae not preserved in all specimens, costae becoming evenly spaced anteriorly, numbering 6-8 in 1 cm, somewhat fasciculate on the anterior part. Dorsal beak low and very wide; interarea low, slightly concave and almost linear in shape; fold relatively broad, swelling moderately. Costae fine and dense in immature specimens, numbering 10-12 in 1 cm, weakly fasciculate.

Discussion. The specimens from the Qubu section in southern Tibet were first proposed by Zhang & Jin (1976) as *Fusispirifer nitiensis semiplicata* through detailed comparison with *Fusispirifer nitiensis* defined by Diener (1897) from the *Productus* shales at Kiunglung, Indian Himalaya, in view of the larger size of the shell, and finer and denser costae. Zhang & Jin (1976) and Shen et al. (2003c) also reported the specimens assigned to *F. nitiensis* from the Luri Member of the Senja Formation in northwest Nepal by Waterhouse (1966, 1978) to be comparable with those from the Qubu section in terms of their similar outline, size and fine costae. Shen et al. (2003c) considered that ontogenetic variations make specimens of this species to be easily confused and treated as belonging to different species. For instance, small shells of this species are usually less transverse and have a narrower sulcus and more prominent fasciculate plications,

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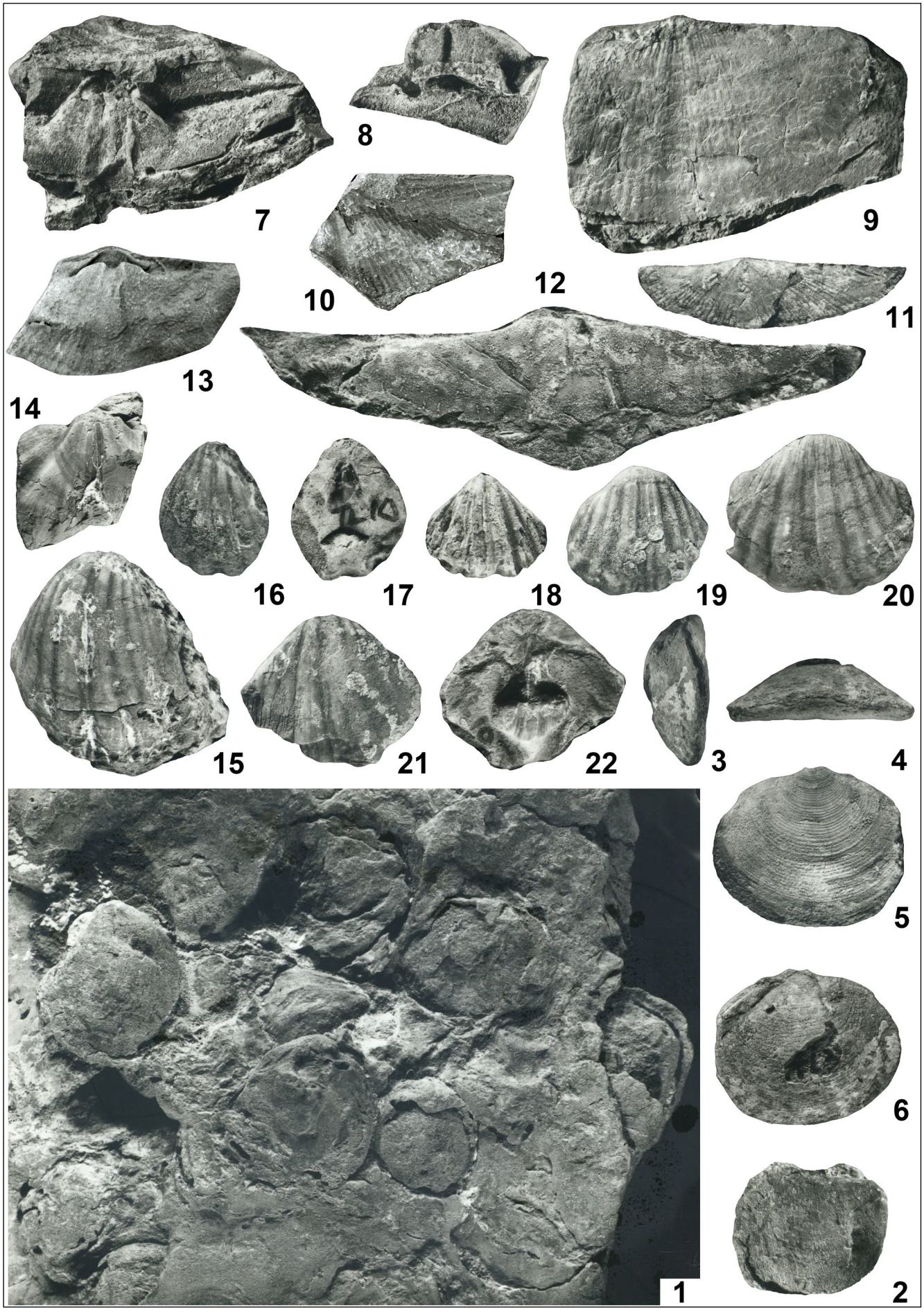
PLATE 2

Figs 1-2 - *Echinalosia magnispina* Waterhouse, 1983a. 1, one block of sandstone with ten internal moulds; 2, one representative specimen, NIGP 166755.
Figs 3-6 - *Himathyris gerardi* (Diener, 1899). lateral, anterior, ventral and dorsal views of a conjoined shell, NIGP 166738.
Figs 7-12 - *Fusispirifer semiplicata* Jin in Zhang & Jin, 1976. 7, internal mould of an incomplete ventral valve, NIGP 166757; 8, dorsal view of internal mould of an incomplete ventral valve, NIGP 166758; 9, ventral valve, NIGP 166741; 10, a fragment of external cast of a ventral valve, NIGP 166742; 11, dorsal valve, NIGP 166743; 12, internal mould of a dorsal valve, NIGP 166759.
Fig. 13 - *Fusispirifer marcouiformis* Jin in Zhang & Jin, 1976. internal mould of a dorsal valve, NIGP 166760.
Fig. 14 - *Fusispirifer* sp. internal mould of an incomplete ventral valve, NIGP 166744.
Figs 15-17 - *Spiriferella qubuensis* Zhang in Zhang & Jin, 1976. 15, ventral valve, NIGP 166745; 16, 17, ventral and dorsal views of a ventral valve, NIGP 166746.
Figs 18-22 - *Spiriferella sinica* Zhang in Zhang & Jin, 1976. 18, ventral valve, NIGP 166747; 19, ventral valve, NIGP 166748; 20, ventral valve, NIGP 166749; 21, 22, ventral and dorsal views of a ventral valve, NIGP 166750.
All figures are in natural size unless otherwise illustrated.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whereas adults often have more evenly spaced costae and a broad and shallow sulcus. Immature specimens are ornamented with a denser and more delicate costation.

Occurrence. Bed 9 of the Qubuerga Formation at Tulong; Qubuerga Formation at Kujianla and Qubu; Selong Group at Surishan in southern Tibet, China; Luri Member of the Senja Formation in northwest Nepal.

Fusispirifer marcouiformis Jin in Zhang & Jin, 1976

Pl. 2, fig. 13

1976 *Fusispirifer marcouiformis* Jin in Zhang & Jin, p. 209, pl. 12, figs 7, 9-11; pl. 13, figs 1, 2, 21-23.
1978 *Fusispirifer nitiensis* - Waterhouse, p. 94, pl. 17, figs 1, 6 (not p. 127, pl. 24, figs 11, 14).
1982 *Neospirifer* sp. - Yang & Zhang, p. 313, pl. 2, figs 3, 4.
1983 *Transversia marcouiformis* - Waterhouse & Gupta, p. 240.
1985 *Fusispirifer marcouiformis* - Jin, pl. 2, fig. 14.
2001a *Fusispirifer marcouiformis* - Shen et al., p. 281, fig. 5.11.
2003c *Fusispirifer marcouiformis* - Shen et al., p. 86, pl. 14, figs 4, 5.

Material. An incomplete internal mould of dorsal valve (NIGP 166760).

Description. Large sized shell; extremely transverse in outline; widest at hinge; cardinal extremities acute, cardinal angles about 45 degrees. Dorsal valve gently convex in lateral profile; beak low and broad; interarea broadly triangular; notothyrium nearly equilaterally triangular; fold commencing from beak, relatively wide, gently elevated; costae fine and spaced evenly, numbering 6-8 in 1 cm anteriorly.

Discussion. Zhang & Jin (1976) defined this species as *Fusispirifer marcouiformis* which differs from *F. nitiensis* and *F. semiplicata* by its larger shell, absence of plication and more evenly distributed fine costae. Specimens described as *F. nitiensis* from the Nisal Member of the Senja Formation in northwest Nepal by Waterhouse (1978) were reassigned to this species by Shen et al. (2003c) in view of their huge size and inconspicuous plicae. Also, *Neospirifer* sp. (Yang & Zhang 1982) collected from Suri Hill, Tingri was included in this species by Shen et al. (2003c).

Occurrence. Qubuerga Formation at Kujianla and Qubu; Selong Group at Surishan in southern Tibet, China; Nisal Member of the Senja Formation in northwest Nepal.

Fusispirifer sp.

Pl. 2, fig. 14

Material. An incomplete internal mould of ventral valve (NIGP 166744).

Description. Large sized shell; transverse in outline. Ventral valve moderately convex in lateral profile; beak low and wide; interarea low, broadly triangular; flanks distinct and slightly convex, well demarcated from visceral disc by grooves; sulcus beginning from beak, steadily widening anteriorly, well defined by two relatively wide radial plicae; two or three pairs of plicae spaced symmetrically; costae greatly fine and delicate but becoming relatively coarse on ears.

Discussion. The above specimen can be safely assigned to a species of *Fusispirifer* according to its transverse outline, flat shell and narrow sulcus. This specimen differs from *F. semiplicata* and *F. marcouiformis* by its small size and two or three apparent pairs of plicae, it is mostlysimilar to *F. nitiensis* (Diener 1897) from the *Productus* shales at Kiunglung, Indian Himalaya, in outline, size and plicae, except for its delicate and dense costae.

Occurrence. Bed 6 of the Qubuerga Formation at Tulong.

Family Spiriferellidae Waterhouse, 1968

Genus *Spiriferella* Tschernyschew, 1902

Type species: *Spirifer saranae* de Verneuil, 1845 from the Lower Permian of Russia.

Spiriferella qubuensis Zhang in Zhang & Jin, 1976

Pl. 2, figs 15-17

1962 *Spiriferella salteri* - Ding, p. 455, pl. 3, figs 2a-c.
1966 *Spiriferella rajah* - Waterhouse, p. 48, pl. 1, fig. 5; pl. 7, figs 1, 2, 4; pl. 11, fig. 2
1966 *Spiriferella tibetana* - Waterhouse, p. 52, pl. 12, fig. 4; pl. 13, fig. 1 (non pl. 2, fig. 2; pl. 9, fig. 3; pl. 13, figs 2, 4, 5).
1976 *Spiriferella qubuensis* Zhang in Zhang & Jin, p. 212, pl. 18, figs 1-5.
1976 *Spiriferella nepalensis* Legrand-Blain, p. 242, pl. 1, figs 7, 11.
1978 *Spiriferella rajah* – Waterhouse, pl. 14, fig. 5.
1978 *Spiriferella oblata* Waterhouse, p. 89, pl. 14, figs 14-18.
1983a *Spiriferella oblata* Waterhouse, p. 135, pl. 6, figs 7-10.
1990 *Spiriferella rajah* - Yang et al., pl. 25, fig. 2.
2001b *Spiriferella qubuensis* - Shen et al., p. 169, figs 7.17-7.29; 9; tab. 4.
2003c *Spiriferella nepalensis* - Shen et al., p. 81, pl. 11, figs 7-17; text-fig. 12.
2003 *Spiriferella qubuensis* - Shi & Shen, p. 1062, figs 5.10, 5.11, 5.15-5.17.

Material. Two ventral valves (NIGP 166745-166746).

Description. Medium sized shell, the largest one more than 48 mm long and 34 mm wide; elongate in outline; hinge slightly shorter than greatest width at about shell midlength; ears small or nearly absent. Ventral valve moderately to strongly convex in lateral profile; beak narrow and acute, strongly incurved; interarea high, about 7 mm, triangular in shape, strongly concave; delthyrium large, trangular in shape; umbonal slopes sharply inclined; sulcus originating from beak, well defined by two coarse boundary costae, with a slender central costa along midline, always narrow and becoming deeper anteriorly; sulcal bounding costae bifurcating at about midvalve, stronger and higher anteriorly, costae on lateral slopes fairly simple, slightly coarse, usually not bifurcating; grooves evenly spaced between two adjacent costae; fine concentric ornament preserved on the left posterolateral flank.

Discussion. The specimens referred to this species from the Himalayan region were respectively described as *Spiriferella qubuensis* by Zhang & Jin (1976), *S. nepalensis* by Legrand-Blain (1976), and *S. oblata* by Waterhouse (1978). Based on a close comparison of these species, Shen et al. (2001b) and Shi & Shen (2003) proposed that the latter two species were conspecific with *S. qubuensis* except for some minor intraspecific morphological differences. However, *S. nepalensis* was suggested to have priority by Shen et al. (2003c), although the exact publication date of *S. qubuensis* is unknown. We prefer to assign our specimens to *S. qubuensis* owning to their close provenance to the locality of Zhang & Jin (1976). Specimens figured as *S. rajah* by Waterhouse (1966, 1978) were assigned to *S. qubuensis* by Shen et al. (2001b) and Shi & Shen (2003) ibecause of their smaller size, elongate outline, shorter hinge line and simple costae. Our specimens are also somewhat similar to those of *Elivina* from Karakorum (Angiolini 2001), but can be distinguished from the latter by their wider hinge, narrower sulcus and very coarse costae or plicae.

Occurrence. Bed 4 of the Qubuerga Formation at Tulong; Qubuerga Formation at Qubu; Selong Group at Selong in southern Tibet, China; upper Manzongrong Formation of Zanda in southwestern Tibet; Upper Permian in the Nyi and Dolpo districts, west and northwest of Nepal.

Spiriferella sinica Zhang in Zhang & Jin, 1976

Pl. 2, figs 18-22

1976 *Spiriferella sinica* Zhang in Zhang & Jin, p. 213, pl. 15, figs 11-17.
1978 *Spiriferella rajah* - Waterhouse, p. 38, pl. 4, figs 1, 2.
2001b *Spiriferella sinica* - Shen et al., p. 171, figs 10.1-10.8; tab. 5.

Material. Fifteen ventral valves. Registered specimens: four complete ventral valves (NIGP 166747-166750).

Description. Medium sized shell, 19.7-34.6 mm long and 23.9-40.3 mm wide; transversally oval in outline; hinge apparently shorter than greatest width at shell midlength; cardinal extremities slightly rounded. Ventral valve moderately to strongly convex in lateral profile; greatest convexity at midvalve; beak short and pointed, strongly incurved; interarea high, about 9-10 mm, broadly triangular in shape, strongly concave; delthyrium distinct; umbo well rounded, umbonal slopes inclined sharply; sulcus originating from beak, well defined by two coarse boundary costae, widening and deepening anteriorly, with a slender central costae along midline; sulcal slopes with costae bifurcating unconspicuously from the boundary costae; costae on flanks 4-5 pairs, simple, coarse, occasionally bifurcating near anterior margin; grooves formed between two adjacent costae; concentric lines on the posterolateral flank.

Discussion. This species can be safely assigned to *Spiriferella sinica* which was first defined by Zhang & Jin (1976) from the Selong Group at the Qubu section, southern Tibet. Zhang & Jin (1976) also remarked that this species is most like *S. qubuensis*, but the outlines of these two species are really different, one is much more transverse and the other is elongate. The specimens of *S. rajah* reported from Locality 1370 in Nepal (Waterhouse 1978) are identical with the present species. Shen et al. (2001b) suggested that *S. sinica* represents an intermediate species between species of *Spiriferella* and *Nakimusiella* in view of its costation and shallow sulcus and probably it is closer to species of *Nakimusiella*. However, this opinion is questionable based on the fact that *S. sinica* has a distinct shallow sulcus and fairly coarse costae, whereas the sulcus is basically absent and costae are simple and less coarse in the species of *Nakimusiella*.

Occurrence. Beds 4, 6 of the Qubuerga Formation at Tulong; Selong Group at Selong and Qubu in southern Tibet, China; Nisal Member of the Senja Formation in northwest Nepal.

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