PERMIAN AND TRIASSIC STRATIGRAPHY AND FOSSILS OF THE HIMALAYA IN NORTHERN NEPAL

By

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PREFACE

This study focuses on Permian stratigraphy of the Manang district, north-central Nepal, and Carboniferous and Permian brachiopods significant from a regional Himalayan and world perspective.

Fossiliferous Late Paleozoic rocks in the Manang district of north-central Nepal are exposed north of the Annapurna Range along the north side of the Marsyangdi valley from east of Braga settlement (11500ft, 3505m) to beyond Manang settlement (11650ft, 3551m), south of the peaks of Chulu (21672ft, 6630m and 20321ft, 6200m). The rocks persist westwards for 15km across Puchenpra Peak (16883ft, 4950m) and an unnamed peak at 17315ft, 5146m, along the north and west side of a huge glacial amphitheatre called Plateau of Lakes, and continue to Mesokanto Pass (16730ft, 5099m), then descend 5km along the Thini River valley to the Kali Gandaki River and the settlement of Jomson (8900ft, 2713m). Further west lies the region of Dolpo in northwest Nepal, where similar Permian-Triassic rocks are exposed north of the Dhaulagiri massif (Fuchs 1967, 1975, 1977, Waterhouse 1977, 1978). Overall these geological observations on Late Paleozoic and Early Mesozoic rocks and fossils extend over 160km, in a band 5-20km broad.

General geological studies and maps of the Manang region by Bordet et al. (1975) and Fuchs et al. (1988) provide critical data on the regional setting, and Garzanti et al. (1994) measured four sections in the area. Five expeditions have been made to the area by the writer in 1977, 1981, 1987, 1988, 1989, each of 2-4 months duration, sufficient to allow for extensive mapping and collecting. General summaries have been published for Permian stratigraphy in Waterhouse (1979, 1987b, 1989, 1994) and Waterhouse & Shi (1991), underpinned by detailed Permian fossil studies (Waterhouse 1966, 1978, 1983a, 1988). Triassic ammonoids and stratigraphy have been examined in a series of monographs (Waterhouse 1994, 1996a, b, 1999a, b, 2002a, b) and members of the bivalve Subfamily Claraiinae and Family Posidoniidae have been described (Waterhouse 2000). In these articles a number of maps and illustrations of the region provide data on the regional topographic and geological setting, and general location for fossils. Brachiopoda and Mollusca from the Late Permian in Manang will be described separately in a study by Waterhouse & Chen (in prep.).

Summary

Part 1. Stratigraphy and Biostratigraphy

A - Stratigraphy

Formations and members of Permian age, together with the underlying Early Carboniferous, are summarized for north-central Nepal from the Kali Gandaki valley into the Manang district, and a number of sections documented to trace variation within units. The Thini Chu Group is restricted to beds of Early Carboniferous age, and is made up mostly of near-shore marine deposits, accumulated under conditions much warmer than glacial and subglacial deposits of Late Carboniferous age in east Australia and South America. The Permian involves the Chulu and Shokang Formations and Nar Volcanics of the newly proposed Ghyaru Group and the Senja and Marsyangdi Formations of the Namlang Group. The Chulu Formation is made up of Early Permian glacial diamictites and Shokang Formation is non-marine, and contains *Glossopteris* and other plant remains, possibly correlative with the Karharbari Formation of India. It is associated with the Nar Volcanics, representing part of the widespread Himalayan Panjal Volcanics. The Senja Formation is extended into the region from west Dolpo, and includes the Popa, Pija, Kyobra, Galte and Ngawal Members. Invertebrate marine fossils are abundant, and belong to the *Pyramus silicius*, *Lazarevonia arcuata* and *Biplatyconcha grandis* Zones, of Changhsingian and possibly late Wuchiapingian age. The topmost Permian Marsyangdi Formation is subdivided into thin and persistent Chho, Hongde, Munji, Braga, Tengi and Gungsang Members. Abundant marine invertebrate fossils belong to the *Retimarginifera xizangensis* Zone, shared with the Selong Group at the Selong Xishan section of south Tibet. The very latest Permian faunas, preserved in uppermost beds of the Selong Group, are not found in Nepal. Over the divide between the Kali Gandaki and Marsyangdi river systems, the Late Permian formations thin or disappear or pass into coarse marine sediments of the Puchenpra Member, to indicate shallow water and at times emergent upland, as an island or ridge termed the Kali Gandaki high.

B - Macro-invertebrate Biozones

Late Permian of the Himalayas is divided into 6 biozones, of which 4 and additional traces are represented in the Salt Range of Pakistan, 2 in Kashmir, 5 in Nepal and 4 in south Tibet.

Part 2. Systematics

A. Upper Paleozoic Brachiopoda

Chonetidina, Stenoscismatoidea

New genera are proposed, including *Nisalarinia*, type species *Rugaria nisalensis*

Waterhouse, 1978 (Family Rugosochonetidae), *Pitakpaivania*, type species *Kutorginella aprica* Grant, 1976 (Superfamily Productoidea), *Miniliconcha*, type species *Taeniothaerus miniliensis* Coleman, 1957 (Superfamily Aulostegoidea), *Sedecularia,* type species *Stenoscisma glabra* Waterhouse, 1987a, *Liufaia*, type species *Stenoscisma tetricum* Grant, 1976 and *Bicamella*, type species *Camarophoria timorensis* Hayasaka & Gan, 1940 (Superfamily Stenoscismatoidea). New species include *Chonetella semicostata, Retimarginifera sheni, Wyatkina tibetensis, Echinalosia zaga*, *Goleomixa? archboldi*, *Stenoscisma hamleti, Coledium? cheni*, *C. costacurtosus* and *Cyrolexis zhangi.* Rugariini is proposed as a new tribe within Plicochonetinae.

Spiriferidina

Permian members of spiriferoid, paeckelmannelloid and brachythyridoid brachiopods are described, classified and discussed from the Salt Range, Himalaya and elsewhere. Several species are delineated and offer moderately good potential for correlation. New genera include *Ovispirifer*, type species *Spirifer oldhamianus* Waagen, 1883, *Gobbettifera*, type species *G. angulata* n. sp., *Fasciculatia*, type species *S. greenlandicus* n. sp. (Subfamily Gypospiriferinae), *Maxwellispirifer*, type species *Neospirifer campbelli exora* McKellar, 1965 (Subfamily Neospiriferinae), *Wadispirifer*, type species *Neospirifer grandis* Archbold & Thomas, 1986 (Subfamily Kaninospiriferinae), *Cracowspira*, type species *Fusispirifer laminatus* Waterhouse, 1987a (Subfamily Fusispiriferinae), *Koenigoria,* type species *Trigonotreta neoaustralis* Archbold & Thomas, 1986 (Subfamily Trigonotretinae), and *Aequalicosta*, type species *Eliva inflata* Cooper & Grant, 1976 (Subfamily Purdonellinae). Angiospiriferin brachiopods are also discussed in part, with three new genera, *Varuna*, based on *Spirifer varuna* Diener, 1915, *Unicostatina*, type species *Sulciplica subglobosa* Clarke, 1990, and *Georginakingia*, type species *Spirifera avicula* Morris, 1845, and new genus *Costuloplica*, type species *Neospirifer senilis* Maxwell, 1964 (Subfamily Costuloplicinae). The pterospiriferin (paeckelmannelloid) new genus *Johncarteria*, type species *Spirifernaella scalpata* Cooper & Grant, 1976, is proposed. Additional new species are *Betaneospirifer shii, Costuloplica robertsi, Crassispirifer broilii*, *C. transversa*, *C. acuta*, *Cratispirifer macroplica, Fusispirifer jini, Kaninospirifer costellinus, Neospirifer poletaevi*, *N. kalashnikovi, Pterospirifer waageni*, *Sulciplica chatsworthensis* Balfe & Waterhouse, *Trigonotreta thomasi* and *Wadispirifer hongdeensis.* New subfamilies Gypospiriferinae, based on *Gypospirifer* Cooper & Grant, 1976, and Fusispiriferinae, name genus *Fusispirifer* Waterhouse, 1966, are proposed within Spiriferidae and Neospiriferidae , and new subfamily Costuloplicinae, name genus *Costuloplica* n. gen. is proposed within Trigonotretidae. Tribe Grantoniini, from *Grantonia*

Brown, 1953, is proposed within Trigonotretinae, and new tribe Georginakingiini from new genus *Georginakingia* within Angiospiriferinae.

Significant Afghanistan, Canadian, United States, Timor and other Spiriferellidae are examined for comparison with Himalayan genera and species. New genera are *Bamberina*, type species *Elivina? annectens* Cooper & Grant, 1976, *Canalisella*, type species *Spiriferella leviplica* Waterhouse & Waddington, 1982, *Quispira*, type species *Elvinia detecta* Cooper & Grant, 1976, and *Dissimiliplica*, type species *Spirifer mexicanus compactus* Girty, 1909 within Family Spiriferellidae. Newly named species are *Spiriferella grunti, S. legrandblaini, Arcullina angiolinii,* and *Elivina? termieri.* New Subfamily Elivininae is recognized within Spiriferellidae. Brachythyridoidea are rearranged, and new Family Brachthyrinididae, based on *Brachythyrina* Fredericks, 1929, and Subfamily Pustuloplicinae, based on *Pustuloplica* Waterhouse, 1968, are proposed, with new species *Brachythyrina boonlomi.*

Family Alphaneospiriferidae is proposed, based on *Alphaneospirifer* Gatinaud, and of uncertain affinities because of the apparent presence of tabellae, costate plicae and lack of adminicula.

B. Triassic Mollusca

Ammonoidea

Corrigenda and records of subsequently described taxa and illustrations are provided for the series of Palaeontographica monographs on Early and Middle Triassic ammonoids from the Himalaya.

Bivalvia

Figures are provided for species of Claraiinae and Posidoniidae from the Early Triassic of Dolpo and Manang, Nepal.

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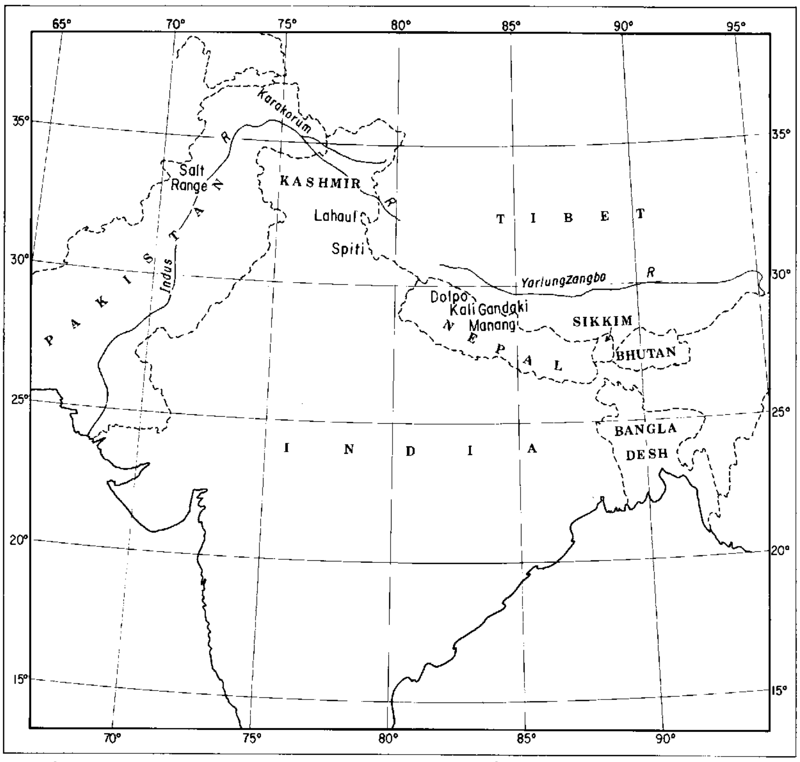
PART 1

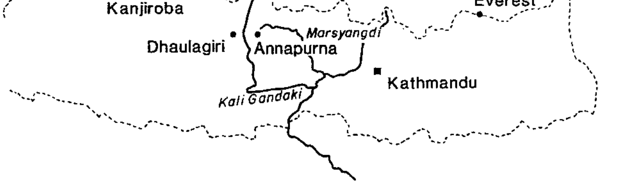
A. PERMIAN STRATIGRAPHY OF NORTH-CENTRAL NEPAL

Regional geology and structure

Paleozoic and younger rock formations lie north of the Himalayan "crystalline zone" of the Annapurna Range, in the area traversed from west to east by the Marsyangdi River (Text-fig. 1-4). Low in the valley, marine Devonian is overlain by marine Early Carboniferous Thini Chu Group, followed in turn by an incomplete marine and non-marine Permian succession (Table 2), and a much fuller marine Triassic sequence, Triassic being the period most fully represented by marine and fossiliferous rocks in the northern Himalaya. Most of the examined Permian and Triassic outcrops lie at altitudes between 14000 and 17000ft, 4000-5200m, but a few outcrops are found at little more than 12000ft (3600m). Overall, sequences are simple, and beds are upright and young northwards, but there are local folds and steep dips southwards.



Text-fig. 1. The Indian subcontinent, showing some of the principal areas with Permian sequences.



Text-fig. 2. The country of Nepal, showing the positions of the Dolpo region and the Kali Gandaki and Marsyangdi Rivers, and the capital Kathmandu. Peaks of Kanjiroba, Dhaulagiri and Annapurna overlook significant Permian rocks.

Some elaboration is required for the structure shown on the geological map of Bordet et al. (1975). The map depicts Triassic resting on Thini Chu rocks in faulted blocks north of Drakar (=Braga) and Bodzo, west of Chegaji Khola, but in the field fold axes are visible and the NNE-SSW cross faults seem less significant than shown on their map, and probably are not present. A large anticline is developed north of Braga, with Thini Chu core exposed over the south face of the Chulu massif and ridges southeast of Mt Chulu. The core of Thini Chu rocks is overlain by Permian and Triassic to the north and south (Bordet et al. 1975, text-fig. 56a). On the south flank of the anticline the Permian-Triassic is folded in a gentle syncline and anticline (Text-fig. 15C), and the south limb extends far downslope into the Marsyangdi valley. The folds die out west of Manang. These points are independently confirmed in the geological map and cross-sections presented by Fuchs et al. (1988).

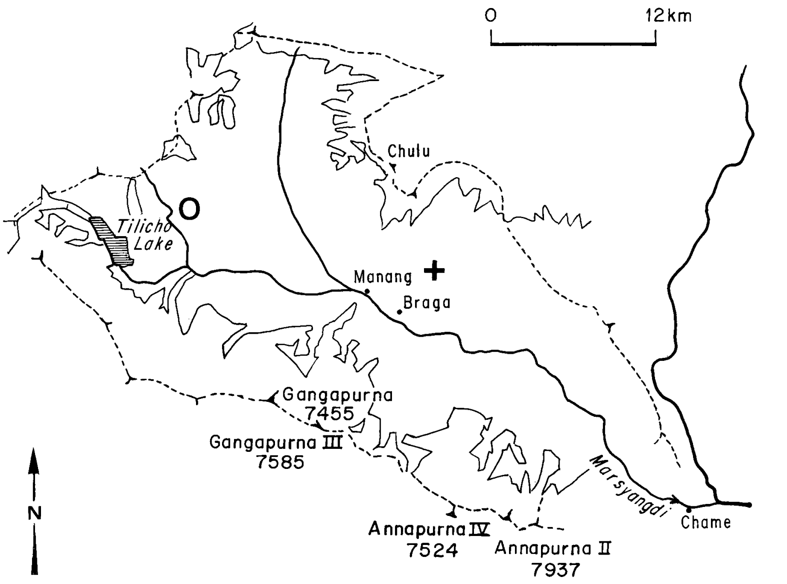
Pleistocene overburden

The lower slopes of the Marsyangdi Valley are cloaked with fanglomerate and debris-flow material with 0.4-0.5m angular breccia, principally of Mesozoic and some Paleozoic rock, at least 500m thick, with bedding in 10-50cm layers, dipping south or mostly north. Layers are cemented from calcareous or siliceous springs. The rock is very porous and now weathers into pillars and peculiar shapes, in part protected by a crust, in part soft and open to rapid erosion. The rocks were mapped and described by Fuchs et al. (1988, p. 604) as "older fluvio-glacial deposits" and it appears to me that the fluvial component was due to short-lived storm flushes. The formation was probably sourced from the Annapurna and Chulu ranges when aridity prevailed, preventing much vegetative cover, as in Zanskar today. The formation filled ancient valleys and then was perhaps river-planed, and probably re-excavated along the south (Annapurna) side, possibly by ice, then refilled by glacial detritus. Glaciation re-excavated a new valley floor in the formation to the north, depositing much till eastwards downvalley from Hongde, and passing into lake deposits mostly east of Chame. Although it has been suggested that the fanglomerate accumulated during glacial times, evidence indicates major aridification and might suggest deposition during the second to last interglacial.

Place names and source maps

Nepal is not provided with close coverage by detailed topographic maps. For years up to the 1980's, reliance for geological mapping had to be placed either on mapping by the research team (eg. Bordet et al. 1975), or on unofficial access to classified cartographic maps prepared by the Indian army, the Manang area being included in a 1963 sheet 62 P 14. Later, maps for trekking parties became commercially available.

Place and spellings have not been stabilized. The names used herein



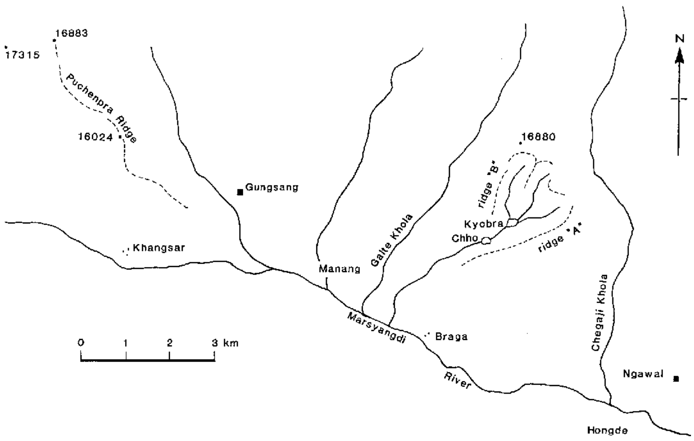
Text-fig. 3. The Manang district of north-central Nepal, north of the Annapurna Range, extending from the administrative centre at Chame west to the divide above the Kali Gandaki River. O indicates the area mapped geologically in Text-fig. 10. Cross marks the area mapped geologically in Text-fig. 11. Peak heights in metres.

come from a mixture of sources, including Fuchs (1967, 1977) and Bordet et al. (1971, 1975), and the trekking and Indian maps. A prime source is offered through the maps and accounts of journeys to Dolpo by the scholar of Tibetan ethnology and philology, David Snellgrove (1961, 1967, 1992), and even he, in his later work, changed a few of his early renditions. Names and spelling used herein have been selected with advise from sherpas, preferences for renditions close to common usage in English, and endeavours to maintain consistency throughout my publications.

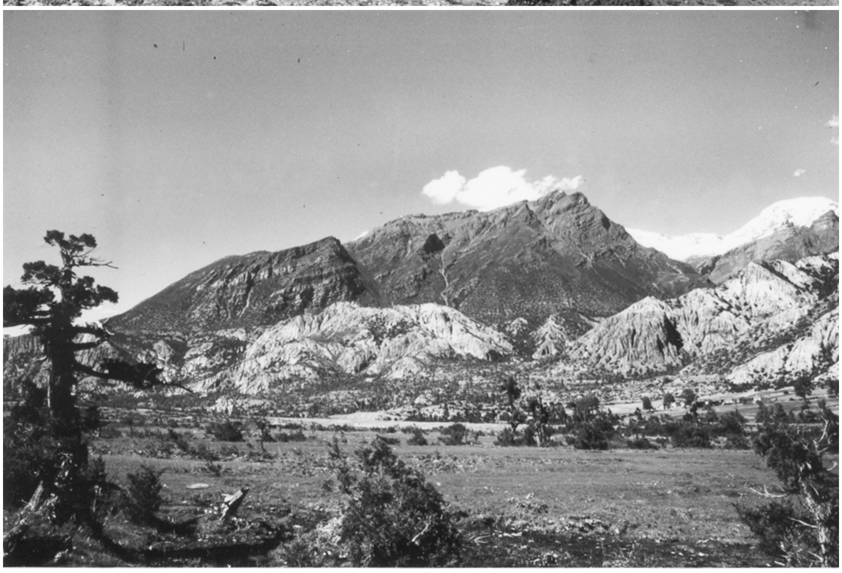
Stratigraphic sequence

DEVONIAN AND EARLY CARBONIFEROUS

Bodenhausen et al. (1964) recognized a Tilicho Pass Formation in the Kali Gandaki valley, and the formation was traced westwards by Fuchs (1967, pp. 17, 161-167, 1975, p. 27, 1988 et al. p. 598) across the valley into east Dolpo and eastwards into Manang. Fuchs assigned a Devonian age on the basis of fossils, and also reported 1000m of dolomite in east Dolpo. Later Waterhouse (1978) named the Langu Group for thick dolomite with few other rock types in west Dolpo (Text-fig. 5A). Talent et al. (1988, p. 16) misunderstood the relationships. They assigned all Dolpo Devonian to Langu Group, but the Langu Group applies to the dolomite, not the marine clastic and fossiliferous beds which interfinger to the east and south.



Text-fig. 4. Some geographic features of the Manang district, based on Manali Trekking Map 1: 250:000 (1985-6). Spot heights in feet. Ridges A and B have useful sections of Permian rocks, above the small lakes Chho and Kyobra, north of Braga settlement.



Text-fig. 5. A. Langu dolomite in the foreground across the Tar-Sebu River which flows north from Shey Gompa into the Langu River. Above lies Permian Senja Formation, followed by extensive Mesozoic, in western Dolpo, west Nepal.

B. The ruined village of Shokang, sited on Thini Chu rocks east of the Kali Gandaki River, north-central Nepal.

C. Ridge A south of Chulu massif, looking westnorthwest across the Marsyangdi river plain from east of Hongde airstrip, exposing Devonian to Triassic, as outlined in Waterhouse (1996b, text-fig. 1, 2). The pale coloured rock is Pleistocene. Manang district.

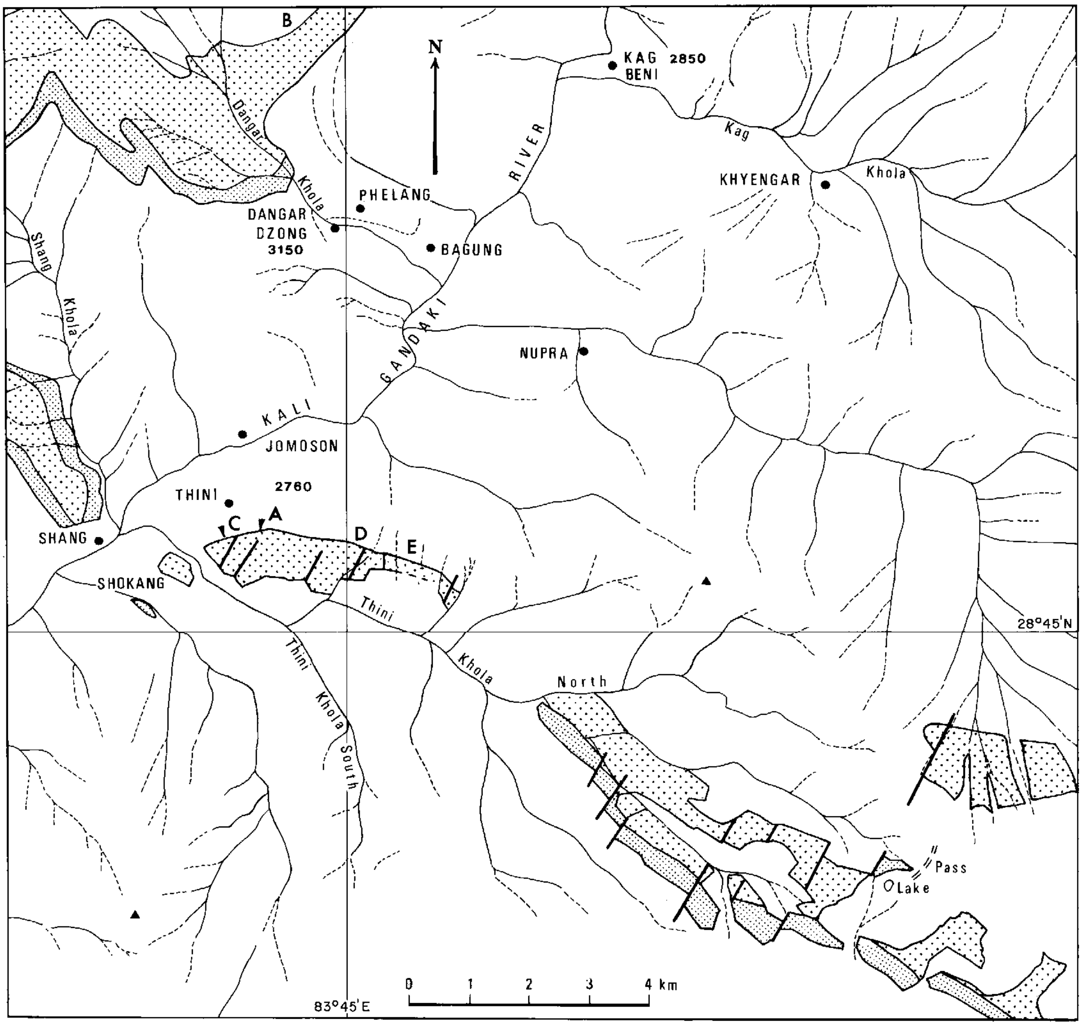
Further east in Manang, Bordet et al. (1975) recognized a “Série détritique de Bangba” - map caption - for Devonian, but the relationship to Tilicho Pass Formation was not clarified, a point also noted by Fuchs et al. (1988).

Above the Devonian in Kali Gandaki valley and east Dolpo is an Early Carboniferous Ice lake Formation (Text-fig. 6), named by Bodenhausen et al. (1964) and Bodenhausen & Egeler (1971), and recognized by Fuchs (1967, p. 167) and Waterhouse (1979) for grey-brown crystalline limestones with laminated calcilutites. It was rechristened Tilicho Lake Formation by Fuchs et al. (1988), and “formation du Lac de Tilicho” by Bordet et al. (1975, p. 95), and regarded as equivalent to the “formation du Gompa de Bangba” of Bordet et al. (1975, p. 94) in the Manang area. Fossils from Dolpo indicated a Tournaisian age according to Waterhouse (1966), qualified to upper Tournaisian - lower Visean by Bordet et al. (1975, p. 95). The proposed correlation with the Syringothyris limestones of Kashmir remains feasible. The unit was overlooked by Garzanti et al. (1994), who claimed that Thini Chu rested on Devonian even in Kali Gandaki valley.

THINI CHU GROUP

DEFINITION, NAME: The Thini Chu Formation (Text-fig. 5B, C, 6, 7) was proposed by Bodenhausen et al. (1964) for outcrops near Thini Khola in Kali Gandaki valley, across the river from the settlement of Jomson (Jomoson). It has been further described by Bordet et al. (1971), Fuchs (1967), Garzanti et al. (1994) and Waterhouse (1977, 1979, p. 199). Bordet et al. (1971) allowed ambiguity between Permian and Carboniferous age data, Fuchs et al. (1988) regarded the formation as Permian and upper Carboniferous, and Fuchs (1967, 1975, p. 77) considered the Thini Chu to be entirely Permian. Fuchs et al. (1988) and Garzanti et al. (1994) expanded the Thini Chu upwards from Carboniferous into Permian, to incorporate beds regarded as Triassic Thinigaon Formation by Bodenhausen et al. (1964) in the Kali Gandaki valley. Both articles by Garzanti et al. and Fuchs et al. failed to acknowledge previous studies and evidence for age, and incorporated Permian formations in the Manang area which are not represented in the type area of Thini Chu Group. Here it is preferred to restrict the Thini Chu to Carboniferous beds as a natural unit, very close to the original concept, and as exposed in the Kali Gandaki valley, where the unit was recognized, named and described. Arguably the Thini Chu could be grouped with the Ice (or Tilicho) Lake Formation.

A very brief account of an extended Thini Chu was provided for the Manang area by Fuchs et al. (1988, pp. 599, 600). Garzanti et al. (1994, October) examined parts of the Thini Chu rocks, which they accepted as a group, and



Text-fig. 6. Carboniferous outcrops of Ice (or Tilicho) Lake Formation (close stipple), and Thini Chu Group and including Permian Shokang Formation (open stipple), Kali Gandaki valley, from Waterhouse (1979, text-fig. 2).

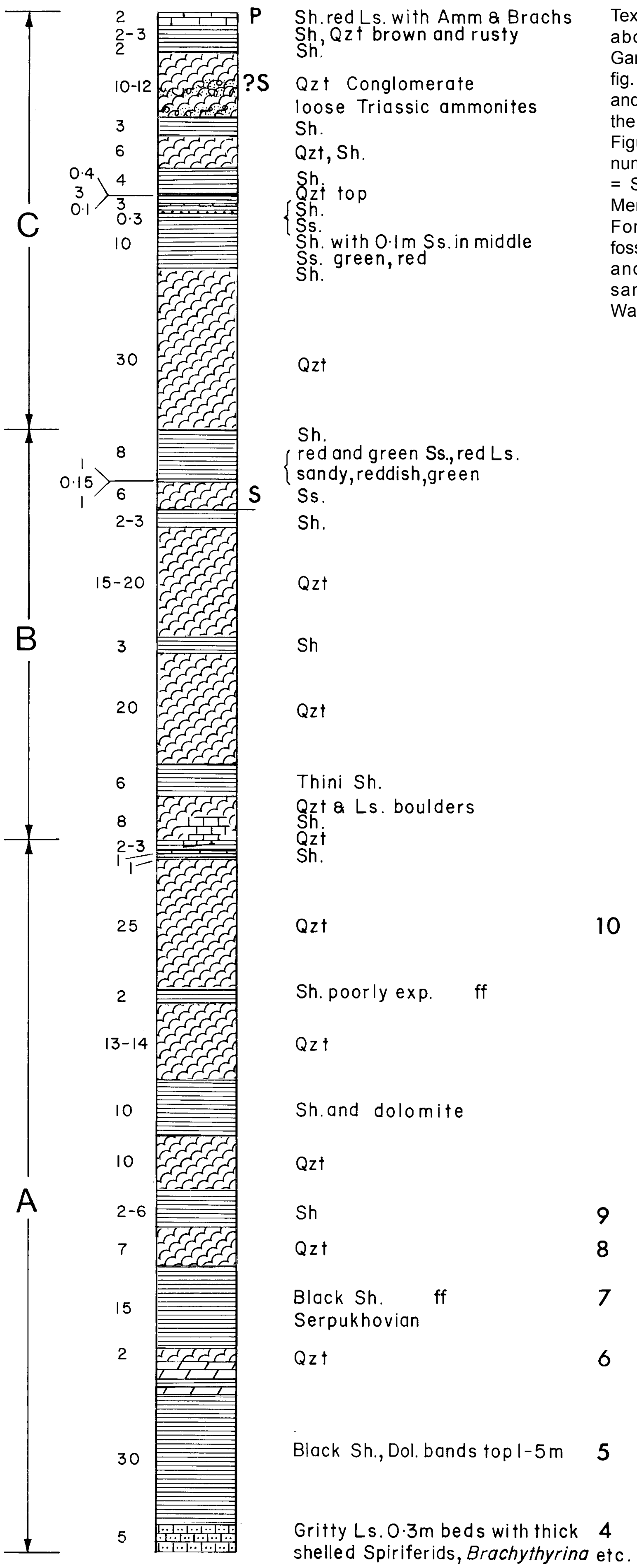
named a lower Marsyandi Formation for black shales and quartzites, with fossils. Contact with underlying beds was not explained, and the Tilicho Lake Formation ignored. The name Marsyandi (alt. Marsyangdi) was not available, having been used in a different application and earlier by Waterhouse & Shi (1991) and Waterhouse (1989, p. 97, 1994, September). Overlying black shales and thin quartzites were incorporated by Garzanti et al. (1994) in a newly proposed Col Noir Shale, 100 to 160m thick. This unit could prove to be a useful addition to stratigraphic nomenclature, but so far has not been mapped, or accurately located in different sections, or provided with a designated type section. The names must lapse, because the proposals failed to meet requirements of the Guide to Stratigraphic Nomenclature (Salvador 1994).

DESCRIPTION: The group is characterized by thick bands of quartzite alternating with thick bands of dark shale. The quartzites abruptly overlie the shale, are coarse to medium-grained, and include subarkoses, some with cross-laminations and ripples, angular mudstone clasts and rare fine conglomerate. Data on petrography and clay mineralogy were provided by Garzanti et al. (1994, pp. 172, 175). Shelly beds are most frequent in the Kali Gandaki valley, with brachiopods, fenestellids and crinoids prominent in quartz arenites and arkoses. The black shales include fine ripple-bedded subarkoses and quartzite layers and bands, and vary between shale and siltstone. Thin layers and concretions or lenses of dolomite or barite are found widely, 2-10cm by 12-25cm in size, and of orange or pink colour, with the shales approaching faint hues of red-orange or purple. Garzanti et al. (1994) suggested that the shales were deposited under mid-shelf conditions, but many aspects, involving micro-bedding, burrowing and biota, raise the possibility of shallow-water inshore deposition as extensive mud-flats. The abrupt change to marine quartzites may have reflected "forced regressions" as favoured by Garzanti et al. (1994) and supported by one or two bands with rare plant remains. But sudden transgressive influx of coarse sediment with marine fossils remains a likely alternative for most of the bands. From a regional mapping perspective, somewhat similar quartzite of the overlying Popa Member is definitely transgressive, overlying Devonian, Carboniferous and Permian rocks.

DISTRIBUTION: The group continues eastwards from the Kali Gandaki valley across Mesokanto Pass, Plateau of Lakes and Puchenpra Ridge into the Chulu massif north of Manang and Braga villages. The rocks are well exposed at various localities, notably on the east face of the ridge between Dent Carbonifère and Dent Permienne.

SECTION AT RIDGE A: Further east, and southeast of Mt Chulu, the rocks exposed over the ridges A-D north of Braga (Text-fig. 5C) reveal the following sequence:

[Chulu Formation]
(top) 65m shale and fine siltstone
20m quartz sandstone
25m 2-4cm layered siltstone with calcareous and subdolomitic or barite layers
18m shale, upper part covered by detritus
25m gap, probably shale
6m mostly quartz sandstone
8m quartzite (scarp)
?65m gap, probably shale
5m quartz sandstone
3m shale
3m quartzite
1m shale
0.6m pebbly siltstone, quartzite and shale
2.5m massive quartzite
2m of 4-5cm bedded undulating quartzite
3m chipwacke in 8-12cm beds of quartzite
12m gap (=shale)
3m 10-12cm beds of quartzite, some beds with mudstone flakes
7m cross-bedded massive quartzite, cross-beds up to 0.25m high
120m gap, presumably shale
24m siltstone, shale
10m gap
20m mudstone, some sandstone and concretions
18m gap (shale?)
12m mostly mudstone, some calcareous and dolomitic lenses
10m mostly siltstone, bioturbated
18m siltstone, mudstone
(cont'd p. 19)



Text-fig. 7. Rock column from ridge about 1km east of Thini in Kali Gandaki valley, sited below A on Text-fig. 6, showing faulted nature of rocks and repeated sequences. Figures at the left indicate thickness in metres. Figures at right repeat the bands as numbered by Bordet et al. (1971). S = Shokang Formation, P = Nisal Member, Pangjang and Marsyangdi Formations. Dol = dolomite, ff = fossils, Ls = limestone, Qzt = quartzite and arkose, Sh = shale, Ss = sandstone. Modified from Waterhouse (1979, text-fig. 3).

9m siltstone grades up to black mudstone, bioturbated. Green siltstone and minor burrowed sandstone
1.5m 2cm mudstone and 4-5cm sandstone and massive green siltstone
12m burrowed black siltstone, minor 1cm fine sandstone, weathering brown
(no basal contact exposed. High terrace in valley of Chegaji Khola. The contact with Devonian is exposed further north along the east face of Chulu ridge A, as indicated by Bordet et al. 1975, text-fig. 51).

There are crinoid stems and other macro-invertebrate fossils, including brachiopods such as *Dowhatania dowhatensis* (Diener) - see pl. 2, fig. 3 - at the east side of ridge B. The quartzites have rust flecks, and rarely contain what appear to be roots, 0.3-4mm in diameter.

CORRELATION: The age is Early Carboniferous, Visean-Serpukhovian, with numerous brachiopods and other macro-invertebrate fossils, shared with the "Fenestella Shales" of northwest India (Waterhouse & Gupta 1977, 1979a, Gupta et al. 1985). The zone is here termed the *Syringothyris lyddekeri* Zone. Species of the Fenestella Shales include *Streptorhynchus humilis* Waterhouse & Gupta, *Chonetes planatus* Waterhouse & Gupta, *Globosochonetes thibetensis* (Davidson), *Dowhatania dowhatensis* (Diener)*, *Flexaria spitiensis* (Diener), *Papiliolinus eishmakami* Waterhouse & Gupta*, *Rotaia dowhatensis* (Diener), *Adminiculoria middlemissi* (Diener)*, *Varuna varuna* (Diener)*, *Syringothyris lyddekeri* (Diener), *Hemiplethorhynchus kashmirensis* Waterhouse & Gupta and *Beecheria lidarensis* (Diener). Asterisked species are figured in this text. Stratigraphy is summarized by Fuchs & Gupta (1971) and it would be desirable to have detailed documentation of fossil distribution. In the Kali Gandaki valley, gigantoproductids or large chonetids are present, suggestive of a Serpukhovian age, and these are yet to be described.

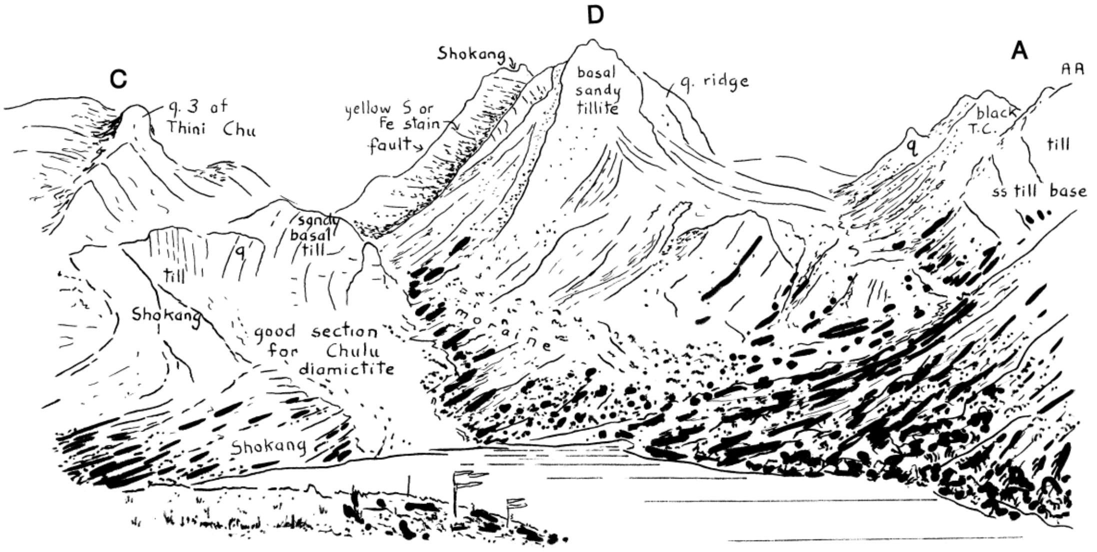
Garzanti et al. (1994) considered that the faunas were contemporaneous or almost contemporaneous with those of the *Levipustula levis* Zone of east Australia and Argentine (Gonzalez 1990, Roberts et al. 1995), judged to be of Serpukhovian and Bashkirian age. But the Indian-Nepal faunas share little in common with the *Levipustula levis* Zone, and unlike faunas of that biozone, are not indicative of cold-water conditions and glaciation. Gonzalez (2003) found evidence for four separate glacial phases in the Carboniferous of southern South America, and so far there is no firm evidence for a single one in the Carboniferous of the Himalaya. This may reflect the incompleteness of the stratigraphic record in the Himalaya or point to the need for further paleontological study, but at face value shows that glaciation did not affect the Himalayan region until Permian times. It is true that Garzanti et al. (1994) asserted that the Thini Chu Carboniferous fossils indicated cool or cold conditions, as productids were supposedly rare or absent. On the contrary, many productids are present (see lists in Bordet et al. 1971, Waterhouse & Gupta 1979a), and the fossils show little affinity with those of the cold-water glacial and subglacial faunas of east

Table 1. International standard for Permian stages (Waterhouse 2002c, table 27 p.168).

Series	Stage	Substage or level	Wardlaw 2000 age Ma
			251.4
	Changhsingian		
			253.4
Lopingian	Wuchiapingian		
		Lamar etc	
		McCombs	
	Capitanian	upper Pinery	
Guadalupian			265
		lower Pinery	
		Hegler etc.	
	Wordian	Vidrio	
		Appel Ranch	
		Willis Ranch	
		China Tank	
	Roadian	Road Canyon	
		Solikamian	
	Kungurian	Elkin	
		Nevolin	
		Filippovian	
Cisuralian		Saranin	
	Artinskian	upper Baigendzinian	
		lower Baigendzinian	
		Aktastinian	283
		Sterlitamakian	
	Sakmarian	upper Tastubian	
		lower Tastubian	
		Shikhanian - Kurmaian	
	Asselian	Uskalikian	290.6
		Surenan	

Table 2. Permian stratigraphy in the Manang district, Nepal.

Group	Formation	Member	Biozone
Namlang	Marsyangdi	Gungsang	*Retimarginifera*
		Tengi	*xizangensis*
		Braga	
		Mungji	
		Hongde	
		Chho	
	Senja	Ngawal	
		Galte	*Biplatyconcha*
		Kyobra	*grandis*
		Pija	*Lazarevonia arcuata*
		Popa	*Pyramus silicius*
Ghyaru	Shokang		
	Nar		
	Chulu		
(Thini Chu)			



Text-fig. 8. Field sketch of Chulu Ridge D, west face, with thick Chulu diamictite or tillite ("till") and recent moraine, from west side of Lake Kyobra. Ridge C has anticline with Thini Chu TC and Shokang Formation. q - quartzite, ss - sandstone. AA shows start of section along Chulu ridge A.

Australia and South America.

GHYARU GROUP (new)

The Ghyaru Group is proposed for Permian beds found between the marine Thini Chu Group (Carboniferous) and marine Namlang Group (Late Permian). The lower formation is the Chulu Formation, with diamictites, and this is followed by the Nar Volcanics and the Shokang Formation, which is akin to non-marine barren coal measures. The name is taken from the Manang village of Ghyaru on the north bank of the Marsyangdi River, east of Chegaji Khola (Table 2).

CHULU FORMATION

NAME, HISTORY: Glacial diamictites were recognized in the Nyi-Shang and Manang regions by Bordet et al. (1975, text-fig. 50b) and were formally named Chulu Formation, from Mt Chulu, by Waterhouse (1987b, p. 137, 1989, p. 97), following and modifying French usage (Bordet et al. 1975, p. 94), in which a "Formation du Chulu" was vaguely applied to diamictite and younger Permian, but not used in their map. Garzanti et al. (1994) sought to rename some of the beds Bangba Formation, but the beds had been clearly named much earlier, and moreover Bangba had already been used in a different sense by Bordet et al. (1975). Overlying diamictites in the same area east of Braga were termed Braga diamictites by Garzanti et al. (1994), but the same difficulties apply: the diamictite had already been named, and Braga as a name had already been preempted and applied in a different sense by Waterhouse & Shi (1991) and Waterhouse (1994, September). It was not available for use in the manner proposed by Garzanti et al. (1994, October). As well, it is preferred to refer all the diamictites to one unit. So far there is no evidence that the "Braga" and "Bangba" diamictites pass laterally into "Braga" and "Bangba" Formations further west: instead they constitute a different, younger formation, occupying a depression channelled into underlying Thini Chu Group.

TYPE SECTION: The type section EA, located as shown in Text-fig. 11 on "ridge A" southeast of Mt Chulu, commences with 4.7m of sandstone with grit and breccia, overlying Thini Chu beds. The basal beds are followed by 24m of siltstone and shale of purple and red hue, containing fine sandstone pebbles of mostly 0.5cm diameter, overlain by 58m of silty shale containing 2-5cm rounded polymict pebbles and some sandstone, with pebbles in occasional 0.5m heaps. At the top, 34m of fine siltstone, shaly to the top, contains rare 1cm pebbles. The formation is overlain by Shokang Formation.

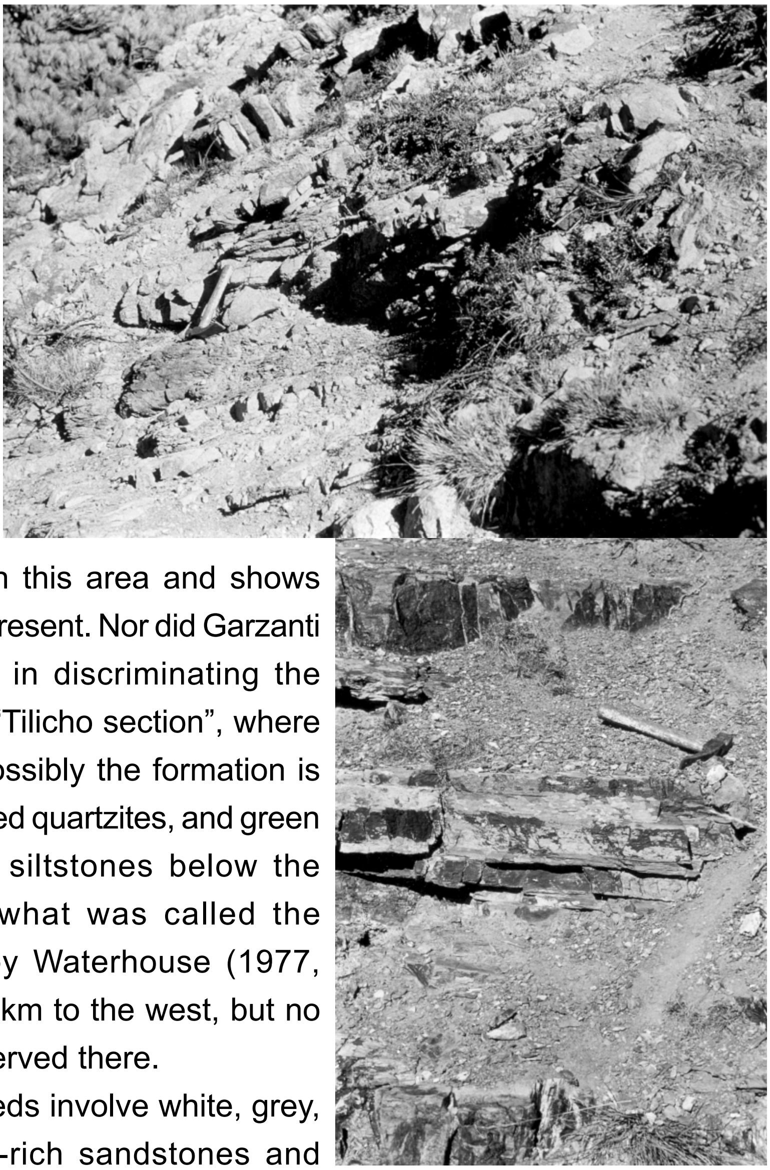
OTHER SECTIONS: At the south end of ridge A (section SA, Text-fig. 11), the Chulu beds are about 50m thick, mostly of purple-tinged shale, with some black sandstone. Occasional angular blocks are up to 20cm across, and pebbles are rare. Obscure shell-fossils are found some 15m from the top in sandy calcareous lenses. Boulders up to 40cm across are present over the ridge to the north, where pebbles are more common, and the fine beds more than 100m thick. At ridge D (Text-fig. 8), the Chulu Formation is well exposed below Shokang Formation, and diamictite commences with a 20m+ band overlain by 2-3m sandstone, followed by 10m of diamictite. This is followed by two 3m bands of quartzite separated by about 3m of shale, overlain by thick diamictite in excess of 100m. At section WB (see Text-fig. 11), 70m of diamictite lies over 10m quartzite in a restricted channel, above some 100m of further diamictite. This section is on the east side of Galte Khola.

DISTRIBUTION: The Chulu Formation varies in thickness, is very local in distribution, and is found mostly over Chulu ridges A and D, south of a well defined fault (Text-fig. 11). It extends west of Manang, where the contact with Thini Chu is exposed. Elsewhere, the Thini Chu Formation is overlain by Shokang Formation, with no intervening diamictite. There is no Chulu Formation to the west in the Plateau of Lakes, Kali Gandaki valley, or Dolpo, and Garzanti et al. (1994) confirmed that none was present at Dent Permienne on the southern side of the Plateau of Lakes. They interpreted the stratigraphy in a layer-cake model, with two formations extending throughout the area, and containing tilloid only near Bangba, on the east face of Chulu "ridge A". It is more likely that the tilloid does not pass laterally into the Thini Chu sediments of the Col Noir etc., but is channeled into Thini Chu. A significant discovery by Garzanti et al. (1994, p. 181) was the find of "euhedral yellow-brown Al-rich chromian spinel" and microlitic volcanic grains at the base of their "Braga" Formation and "the first appearance" of "dark reddish to coffee brown Cr-rich chromian spinel" in the middle of their "Puchenpra Formation." These minerals might with advantage be used to reinforce field-mapping and fossil studies as correlation tools, as well as provide source data. But the minerals were only found in one "Tilicho" column in beds here judged to be older than the diamictite (Garzanti et al., 1994, text-fig. 5) and the failure to find the minerals in supposedly correlative diamictite levels signals the need for thorough sampling, and revision of their stratigraphic model. Further afield, Garzanti et al. (1994, p. 182) reported that in central Dolpo, spinel occurs at the base of the "Upper Permian *Costiferina* arenites", and reported a Permian foraminifer *Nodosaria* aff. *grandis*, of supposed mid-Early Permian age. The data is not robust, and the misidentification of *Biplatyconcha* as *Costiferina* by Garzanti et al. (1994, pl. 1, fig. 1) underlines the need for careful stratigraphic control and paleontological evaluation.

CORRELATION: The age is not certain, but from regional considerations appears to be correlative with Early Permian diamictites found over Peninsular India, northwest India and Tibet. Scattered fossil evidence should enable the age to be determined more accurately. According to Sun (1993, p. 63), the Jilong Formation of south Tibet contains 30m of grey diamictite with calcareous siltstone at the top, which yields critical fossils such as *Globiella gracilis* (Jin) and *Attenuatella* to suggest an upper Tastubian age (Table 1). Part of the Agglomeratic Slate of Kashmir is likely to be correlative (Acharyya & Shah 1977), involving the 900m thick "diamictite division" of the lower Agglomeratic Slate, or "Bren bed" of Acharyya & Shah (1977), with *Eurydesma* and *Deltopecten* (Nakazawa & Kapoor 1977, p. 11). A range of latest Carboniferous well into Early Permian has been suggested by Garzanti et al. (1994).

SHOKANG FORMATION

NAME, HISTORY: The Shokang Formation was described and named for non-marine barren coal measure-type deposits by Waterhouse (1979, p. 203) for rocks in the east Kali Gandaki valley. The name Shokang was taken from the ruined village of Shokang (Text-fig. 5B), and the type section provided by a ridge about 1km south of Thini. Garzanti et al. (1994) wished to rename the beds as Member A of a Puchenpra Formation, but they did not take care to discuss previous work. Their proposal had long been preempted, and Puchenpra had already been used in a different sense by Waterhouse (1994). Furthermore Garzanti et al. (1994) wished to lump the restricted and non-marine Shokang beds with younger marine beds of quite different appearance and origin, already named Senja and Marsyangdi Formations (Waterhouse 1977, 1978, 1989, 1994 etc.). They failed to recognize the Shokang beds in the Kali Gandaki area



Text-fig. 9. Illustrations of Shokang Formation in Kali Gandaki valley, hammer approx. 0.3m long.

(Thinigaon section of Garzanti et al. 1994, text-fig. 5), asserting that a fault had removed various Permian formations. Detailed mapping shows that only thin Permian ever overlay the Thini Chu Group in this area and shows that Shokang is widely present. Nor did Garzanti et al. (1994) succeed in discriminating the Shokang beds in their “Tilicho section”, where it is well developed. Possibly the formation is correlative with pale or red quartzites, and green and dark shales and siltstones below the fossiliferous part of what was called the Nangung Formation by Waterhouse (1977, 1978, p. 8) in Dolpo 60km to the west, but no plant material was observed there.

DESCRIPTION: The beds involve white, grey, red and green quartz-rich sandstones and shales, accumulated in swamps with estuarine channels, and levee bank and splay channel deposits, revealing cross-bedding, pebbles, root remains, coal traces, leaf remains, mud-flakes and minor argillite partings, and varying from 10m to about 40m in thickness in the Kali Gandaki valley (Text-fig. 9A, B). Thin sections of the rock show a sedimentary matrix containing biotite, lithics, rare pyroxene fragments, and angular quartz fragments with strained extinction. Other detail is provided by Garzanti et al. (1994, p. 174). The rocks were derived from an igneous or metamorphic terrane, presumably of Proterozoic and Early Paleozoic age in the Lesser Himalaya to the south, supplemented by a component sourced from associated and underlying Nar Volcanics, as discussed shortly. Compared with Thini Chu shales, the shales are darker and contain more carbon and no fossil marine shells.

Overall, variation in the Shokang Formation is considerable, and its source varied between volcanics, quartzites and metamorphic terrain.

MESOKANTO, PLATEAU OF LAKES: Near the divide between the Marsyangdi and Kali Gandaki river systems, thin Permian is found north of Lake Tilicho close to Mesokanto Pass, poorly exposed and displaced by small 5-15m offsets vertical to bedding, with minor fold complexities, especially near the pass. The Shokang Formation is represented above Thini Chu beds by some 8.7m of red sandstone, and black shale and siltstone, followed by some 3m of white sandstone with root remains. Overlying beds belong to the Puchenpra Member of the Senja Formation.

At the Plateau of Lakes, Shokang Formation is some 12m thick at section 2 (Text-fig. 10), with sulphur efflorescence and red mudstone. Ferrous spots are found in the quartzite, and beds are 0.1-0.6m thick. At section 6 in this area, the Shokang Formation is made up of some 11-12m of fine beds, as follows:

[Puchenpra sandy conglomerate, 1m]
(top) 1m sandstone
1m shale
4m massive quartz-rich sandstone
0.3m shale
1.1m sandstone
0.3m conglomerate in 2-3 bands, pebbles 1cm in diameter
0.7m sandstone
0.5m fine beds, sandstone, mudstone
1m mudstone?
0.5m sandstone
?0.7m mudstone
[massive rust-stained Thini Chu Group].

At peak 17315ft (section 3, Text-fig. 10), Shokang Formation is some 11-12m thick, of sandstone in 1-2m beds, making up 3-4 bands of dirty quartzite with iron-oxide specks, rare green mafic bands, and plant stems about 1cm thick.

About 1km further east on the Puchenpra Ridge, the Shokang beds are well developed:

[Popa quartzite]
(top) 5m quartzite
3m quartzite and minor mudstone
42m quartzite
2.5m shale
1.2m sandstone, laminated mudstone
1.2m quartzite
4m shale and sandy shale
11m quartzite and 10cm conglomerate, quartz pebbles 1cm in diameter
[Thini Chu shale].

MANANG, BRAGA: To the east in the Manang district, outcrops of Shokang Formation are better exposed and thicker than in the Kali Gandaki valley or Puchenpra Ridge and Plateau of Lakes (Waterhouse 1989, p. 97). They overlie the Chulu diamictite (Waterhouse 1987b, p. 137, Waterhouse & Shi 1991, table 1, p. 383, Waterhouse 1994, p. 6, table 1, p. 7).

Along ridge B (Text-fig. 11, 15B, C) on the east side, north from the Senja

Formation, Shokang beds are well exposed:

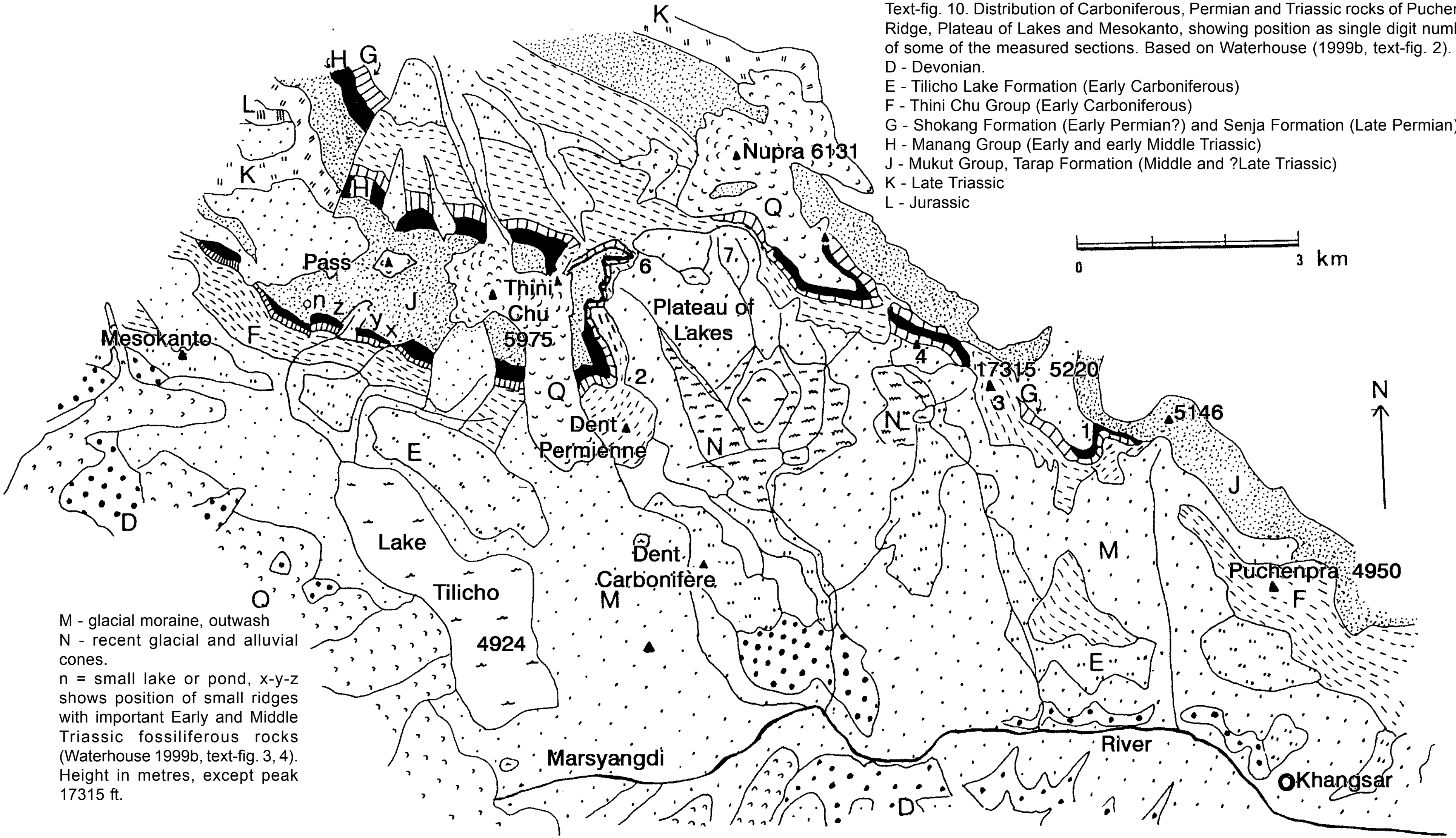
[Popa Member]
(top) 1m black shale with plant fragments
1.5m muddy quartzite
0.25m shale
0.6m 12-15cm quartzite beds
0.6m shale
ca 50m mostly quartzite with thin shale intervals, coarse 0.75-1m cross-bedding layers
0.6-1m greenschist
0.25m black shale
0.3 greenschist
2.2m iron-rich band
1m sandstone
3m quartzite
1.3m thin quartzite and shale beds, oily sheen
4m quartzite
3.9m black shale with subcalcareous beds near top. Some sandstone grading to mudstone and current-bedding
6m 6 quartzite units with 10cm shale in middle. Base swells 8-12cm high and 6-10cm long
[Thini Chu Group].

At ridge C Shokang sediments are about 100m thick and include dark green siltstone, shale and green sandstone, as well as quartzite and black shale.

In the syncline north of Braga and southeast of ridge B, the Shokang Formation is approximately 70m thick, with three major quartzite bands and black shale at the top, in 0.2m beds of shale, flinty shale and concretionary bands, and some volcanic-derived sediment. Plant remains, including *Glossopteris* leaves, are present in the upper 6m.

The Shokang beds are nearly 60m thick on the northwest side of ridge A. The crestal sequence of the ridge NA (Text-fig. 11) was measured as follows:

[Popa Member quartzite]
(top) ca 6m mixed shale, black to light brown and impure quartz-rich sandstone, 20-25cm beds
ca 6m quartz sandstone, current-bedded
1m black shale
ca 1m grey shale and dirty sandstone at top 20cm
18m quartzite, current-bedded
3m black shale
3m green sandstone and black shale
7m quartz sandstone
8m siltstone with tiny ferrous patches at top
3m fine greenish sandstone
1.2m siltstone with ferrous patches
0.3m fine green sandstone
1m shale
1.2m green sandstone
1.8m shale and some siltstone
1m shale
0.25m fine sandstone
0.5m black shale and 2-5cm grey sandstone beds
5m quartzose sandstone
7m black shale with a few small 2cm barren concretions
1m quartzose sandstone, faintly bioturbated
1-2m pure black shale and silty streaks. Minor quartzite and green sandstone to east in one bed
7m quartzite
0.1m dense mafic volcanic band
0.7 shale
3m quartzose sandstone
1m shale
0.4m fine green sandstone
0.6m shale, silty and sandy
11m two shale bands, some sandstone
1m black shale
[Chulu diamictite].



Text-fig. 10. Distribution of Carboniferous, Permian and Triassic rocks of Puchenpra Ridge, Plateau of Lakes and Mesokanto, showing position as single digit numbers of some of the measured sections. Based on Waterhouse (1999b, text-fig. 2).
D - Devonian.
E - Tilicho Lake Formation (Early Carboniferous)
F - Thini Chu Group (Early Carboniferous)
G - Shokang Formation (Early Permian?) and Senja Formation (Late Permian)
H - Manang Group (Early and early Middle Triassic)
J - Mukut Group, Tarap Formation (Middle and ?Late Triassic)
K - Late Triassic
L - Jurassic

M - glacial moraine, outwash
N - recent glacial and alluvial cones.
n = small lake or pond, x-y-z shows position of small ridges with important Early and Middle Triassic fossiliferous rocks (Waterhouse 1999b, text-fig. 3, 4).
Height in metres, except peak 17315 ft.

Green-coloured rock is not so well developed to the south end of exposures on Chulu ridge A (section SA):

[Popa Member]
(top) 5-8m black silty shale, slickensided and graphitic 4-12cm quartzose beds in 30-50cm bands, some dark
2m shale
3m quartzite
1m impure quartz sandstone
3.2m current-bedded quartzite
0.6m laminated quartzite
10m 10-40cm beds of dark sandstone and black shale, 10-15cm shale at base, above well laminated quartzose sandstone
35m mostly sandstone in 0.1-2m beds, quartz-rich especially to base. Lower 16m especially massive
10-15cm conglomerate, pebbles well rounded, up to 2cm diameter, varied
28m dense black streaky mudstone, showing basal contact well, appears to thin south
28-35m quartzite (joined across gulch by stone wall), basal relief of 10-15cm
[Chulu diamictite].

PLANT MATERIAL: In the original proposal of the Shokang unit, it was suspected that the beds would prove to be Permian (Waterhouse 1979, p. 205). This is now established by the presence of the Permian plant *Glossopteris* in beds north of Braga village (Text-fig. 16C, and Waterhouse 1989, p. 97, 1996a, text-fig. 2) and at Col Noir (Garzanti et al. 1994, p. 170). The best preserved plant material was collected during 1987 as leaf impressions from a band 6m thick in the upper Shokang Formation, in the syncline between ridges B and A, with the help of Sherpas Nore and Pisang. Some examples are figured herein as pl. 1. The material has been on loan to Dr John Rigby, Queensland University of Technology, Brisbane, and will be permanently housed at Canterbury Museum, Christchurch.

At first appraisal, the plant fossils appear to be like those of the younger Permian Gondwanas of India, and the plant beds of the Chubu Formation, south Tibet, described by Hsu (1976, in Li et al. 1985). The flora bears some resemblance to that of the Nishatbagh Formation in Kashmir (Singh et al. 1982). The age initially assigned to the Chubu flora was Wuchiapingian, but this was later revised to Maokouan (ie. Late Guadalupian), for example in Hsu et al. (1990), influenced by the misidentification of an Early Permian ammonoid from the overlying Qubuerga Formation. This ammonoid has been reidentified with a Guadalupian - early Lopingian genus (Dr Shen Shuzhong, pers. comm.). Given the possible affinities of the Shokang plants, stratigraphic position, and information on the sequences in south Tibet, it seems likely that the Chubu beds are of younger Guadalupian or Wuchiapingian age.

An initial assessment of the Shokang leaf remains by Dr John Rigby suggests that the *Glossopteris* comes closest to species from the Karharbari Formation of Bihar, India, and correlative floras. The Karaharbari beds lie above Talchir Formation with glacial boulder beds, and above the Umaria beds with marine fossils of likely upper Tastubian age (Sastry et al. 1977, Waterhouse, 1976). Garzanti et al. (1994) preferred a mid-early Permian correlation, which seems close to Dr Rigby's assessment.

NAR VOLCANICS

Bordet et al. (1975, p. 97, caption to map) described rare metamorphosed spilites from the Nyi-Shang region as "episode spilitique de Nar", and these occur at the base and within Shokang Formation (Le Fort 1975, Colchen et al. 1986, p. 85). They constitute a local representation of the Panjal Volcanics of Kashmir (Waterhouse (1987b, 1989, p. 97), and use of Nar is informal. In Kashmir, the volcanics start above the diamictite and below the pyroclastic division of the Agglomerate Slate, and the volcanics extend up into *Glossopteris* floras below the Zewan Formation (Nakazawa & Kapoor 1977, p. 11, table 3). The volcanics provided part of the source for the greenschists, shales and sandstone of the Shokang Formation in the Manang region.

NAMLANG GROUP

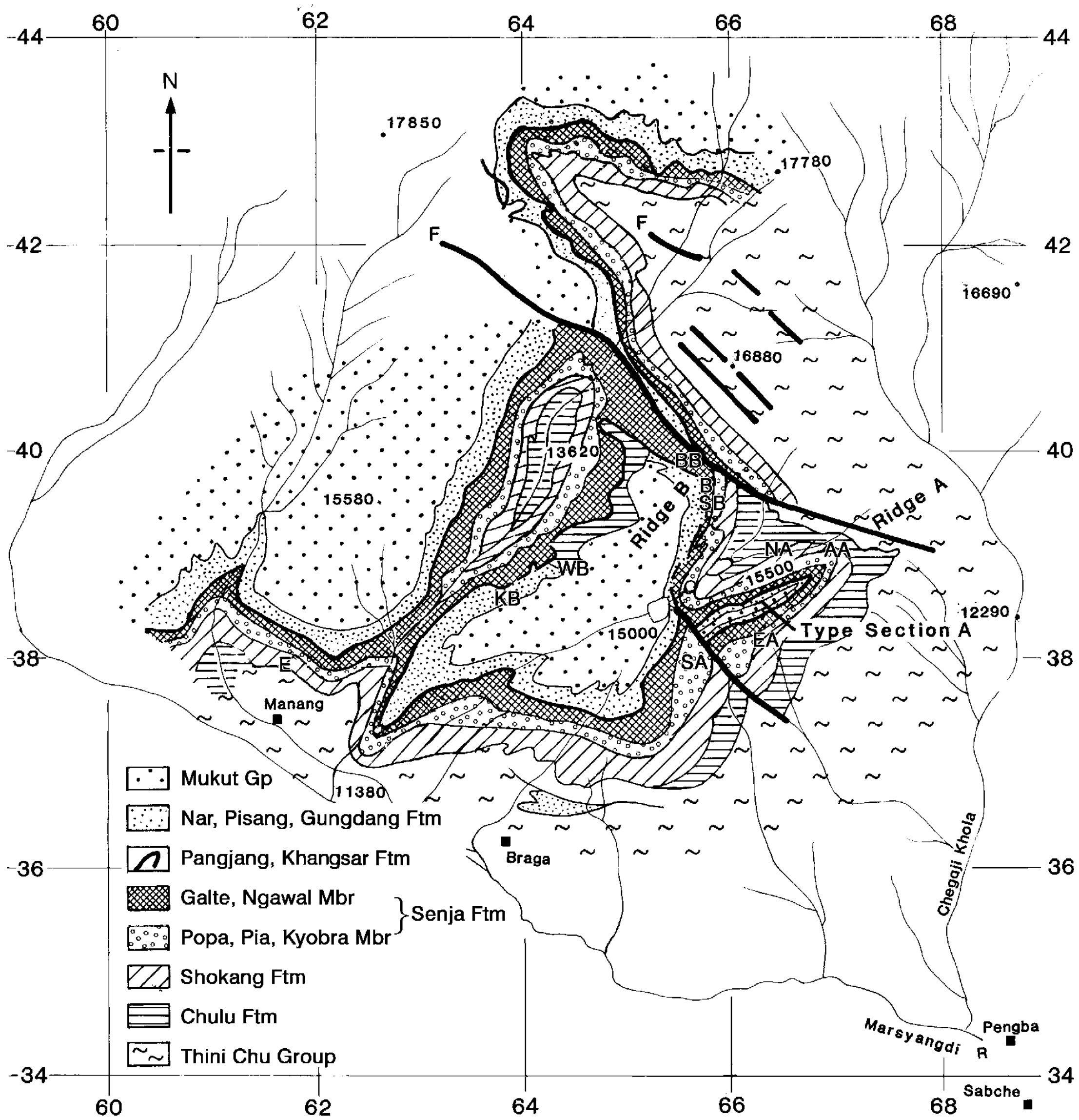
Namlang Group was proposed for marine Permian formations of Late Permian age, based on Namlang, an alternative name for Langu River (Waterhouse 1977, 1978). In Dolpo, the group commences with the Nangung Formation, followed by the Senja Formation. In Manang, the Nangung Formation is not developed, and the Senja Formation is followed by the Marsyangdi Formation, not found in Dolpo.

The Namlang Group, especially the younger formations, is closely examined from a stratigraphic and biostratigraphic standpoint. Eventually, it should be possible to fit the units into cyclothemic and sea-change patterns with correlates elsewhere, comparable to those established for the cyclothems of the North American Pennsylvanian (Heckel 2003).

SENJA FORMATION

NAME, HISTORY: The Senja Formation was proposed for Late Permian beds up to 150m thick in west Dolpo, west Nepal (Waterhouse 1977, 1978). It was named from Senja Khola near Popagaon in west Dolpo, and was divided into the Popa, Pija, Nisal, Nambdo, Luri and Kuwa Members (Text-fig. 12, 13), each distinguished by characteristic and widespread lithological attributes. Earlier, the members had been treated as part of the Thini Chu Formation (Fuchs 1967, 1977, Bordet et al. 1971), and the Early Carboniferous was muddled with Late Permian.

In the Manang region (Text-fig. 14, 15A), the Popa and Pija Members are



Text-fig. 11. Geological map of area north of Braga, north-central Nepal. Faults marked by heavy lines; A, B, AA etc. indicate positions of measured sections around Chulu ridges A and B; spot heights in feet, and 17850 and 17780 show small peaks south of main Chulu summit. Modified from Waterhouse (1994, text-fig. 5), with input from Mandala Trekking Map and 1963 Indian cartographic survey 62P/14.

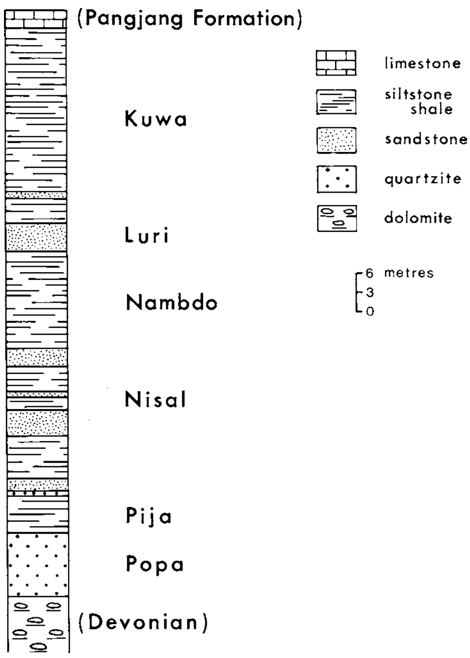
much the same as in Dolpo, but overlying rocks differ to some degree, and are named as different members. The Senja Formation was re-arranged as upper members of a Puchenpra Formation within the Thini Chu Group by Garzanti et al. (1994), but Senja and its constituent units enjoy long priority (eg. Waterhouse 1977, 1978, 1987b) and, as well, lumping marine Senja with non-marine Shokang is not acceptable. The term Puchenpra had already been applied to different rocks by Waterhouse (1994, as anticipated in 1987b), and was not available. Various members were touched on in the Garzanti et al. account, without regard to previous work or the Guide to Stratigraphic Nomenclature, and unfortunately their studies require substantial elaboration and much more extensive field work, and detailed paleontology, to substantiate various details and justify their suggested interpretations. As well, their sections show considerable misinterpretation in detail, with the “Bangba section” wrongly interpreted as less complete than their “Col Noir section”: the opposite is true.

Popa Member

NAME, HISTORY: The Popa Member was named from Popagaon, west Dolpo, for well-sorted white fine to medium-fine and coarse quartzite about 18m thick in the type section at the cave monastery some 2km west of Popagaon. The member overlies Langu Group, principally dolomite, of Devonian age (Text-fig. 13A). Locally, east of Pijagaon, dolomite rubble is developed up to tens of metres thick, below Popa quartzite, as a basal collapse breccia in abrupt contact with underlying Langu dolomite, like canyon or cavern fillings (Text-fig. 13B, Waterhouse 1989a, p. 94). In the Manang region, the Popa Member overlies Shokang Formation, which also includes quartzites, and the Popa quartzites differ in lacking plant remains and in having rare marine fossils. The member widely marks substantial transgression over beds as old as Devonian, Carboniferous and terrestrial Permian throughout western and central parts of Nepal. Beds look moderately like those of the Thini Chu quartzites, and map out as transgressive, not recessive as interpreted by Garzanti et al. (1994).
VARIATION: Over parts of Chulu ridge A the member is laminated in layers 2-3cm thick, and there is rare burrowed pelite, but on the whole the unit is massive and featureless. The thickness varies (Table 3). At the section on the west side of Chulu ridge C, across the glaciated valley from Chulu ridge B, the Popa Member commences with 2.5m of quartzite, followed by 1m of dark black shale, then 3m of quartzite, 0.8m of shale, and closes with 2.5m of quartzite, below Pija Member. In the syncline south of Chulu ridges B and C, the Popa quartzite is channelled 0.5m into the Shokang, in scours 1-2m across.

To the west along Puchenpra Ridge, the Popa quartzite involves some 25m of laminated quartzite, underlain by quartzites of the Shokang Formation. There appears to be no Popa Member exposed at the Plateau of Lakes, Mesokanto, or Kali Gandaki valley.
CORRELATION: Fossils are few, and include nuculanid- and *Schizodus*-like specimens south of Lake Chho at two localities, and other rare bivalves and brachiopods elsewhere. The fossils belong to the *Pyramus silicius* Zone (Waterhouse 1978, 2002c). The Popa Member is correlated through bivalves and some brachiopods with species in the Ganjaroh Member or Waagen’s bivalve fauna of the upper Chhidru Formation in the Salt Range of Pakistan (Waagen 1891, Waterhouse 1983b, 2002c, p. 182), and Zewan D of Kashmir (Nakazawa & Kapoor 1981). The age of the Ganjaroh Member is Lopingian according to conodonts (Wardlaw & Mei 1999, Nakazawa et al. 1975), possibly

early Changhsingian, or perhaps late Wuchiapingian (Waterhouse 2002c). By contrast, Garzanti et al. (1994, p. 170) claimed an early Permian age for the quartzite, in conflict with available stratigraphic, correlation and paleontological evidence (Grant 1970, Wardlaw & Mei 1999, Pakistan-Japanese Group 1985, Waterhouse 1978, 1994, 2002c, pp. 183, 184, Table 30).



Text-fig. 12. Stratigraphic column for Senja Formation (Late Permian) with constituent members in west Dolpo, measured just north of Popagaon (from Waterhouse 1978, text-fig. 3).

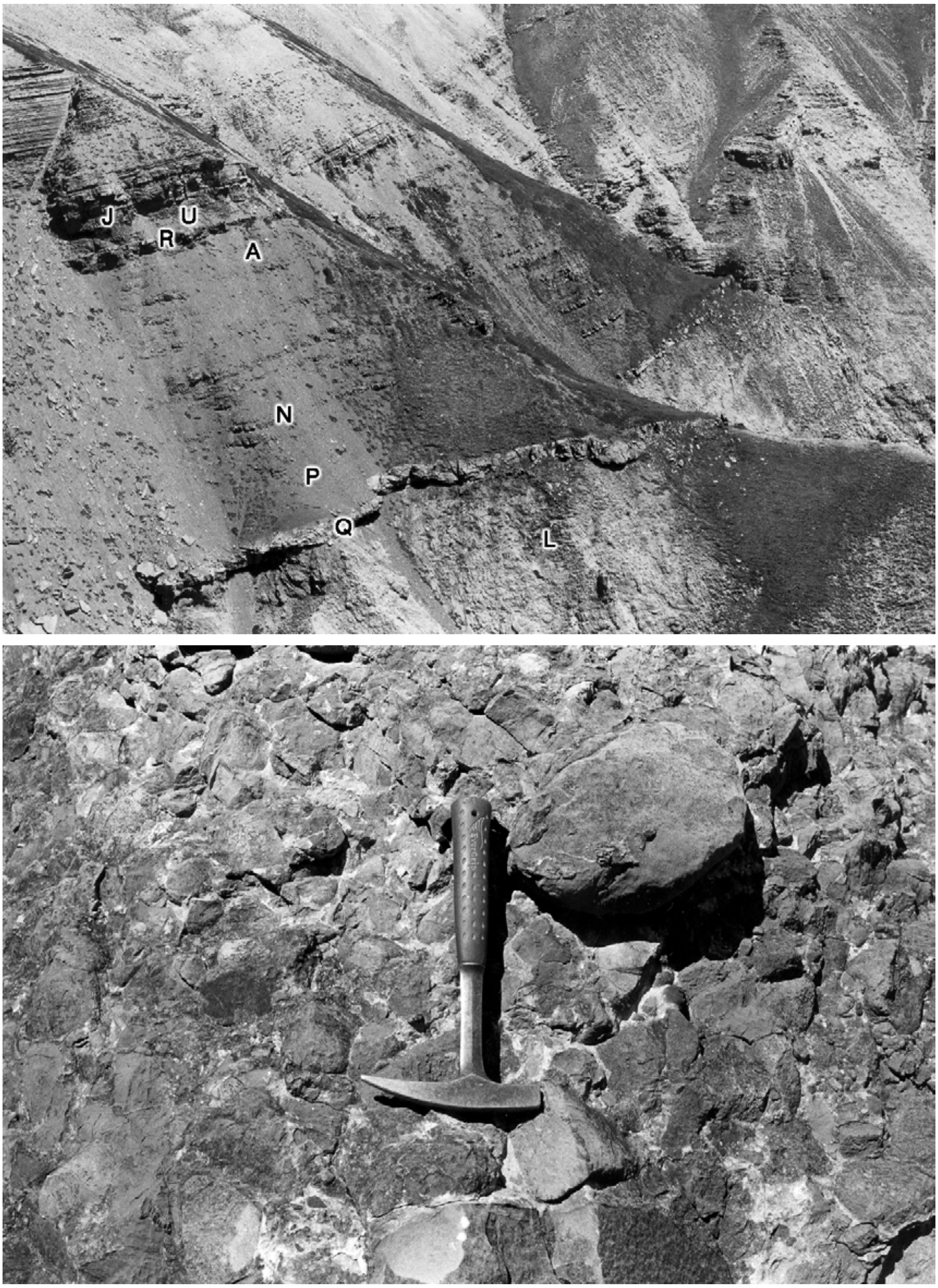
Pija Member

HISTORY, DESCRIPTION: The Pija Member was proposed for black shales about 25m thick in Dolpo, west Nepal, and includes minor sandstone and limestone. It was named from Pijagaon, with type section east of Pijagaon on the north bank of the Pangjang tributary that flows past the village (Waterhouse 1977, 1978, p. 13). A rich assemblage of brachiopods and some molluscs is found (Waterhouse 1978).

MANANG: The member is well developed in the Manang region, and a substantial fauna of brachiopods has been described (Waterhouse 1983a). Burrowed siltstone and thin pebbly sublitharenites are present, and fossils are moderately common, suggesting deposition about mid-shelf, at no great depth, but well seaward of the shore-line, in view of the scarcity of coarse clastics: superficially the member looks like the black shales of the Thini Chu Group, but in detail differs considerably.

Table 3 summarizes the variation in thickness at different sections. Overall the member is less varied than in Dolpo, and is comprised of shale and siltstone, with shell patches and scattered shells. On the east face of ridge A, north of Honde airstrip, the member involves these beds:

[Kyobra Member]
(top) 4m black shale
1m quartzite
3.5m shale
1m shale, sandstone
10m shale
1.2m calcareous sandstone
~30m black siltstone
8m quartz sandstone, sandstone, shale
4m quartzite
2m shale
1m quartzite
35m black siltstone and shale
[Popa Member].



Text-fig. 13. A. Senja Formation looking east across Tar-Sebu canyon, west Dolpo. Popa quartzite Member Q rests unconformably on Devonian Langu dolomite (L) at base, followed by Pija Member (P), Nisal Member (N), Nambdo Member (A), Luri Member (R), and Kuwa Member (U). Pangjang Formation (J) follows.

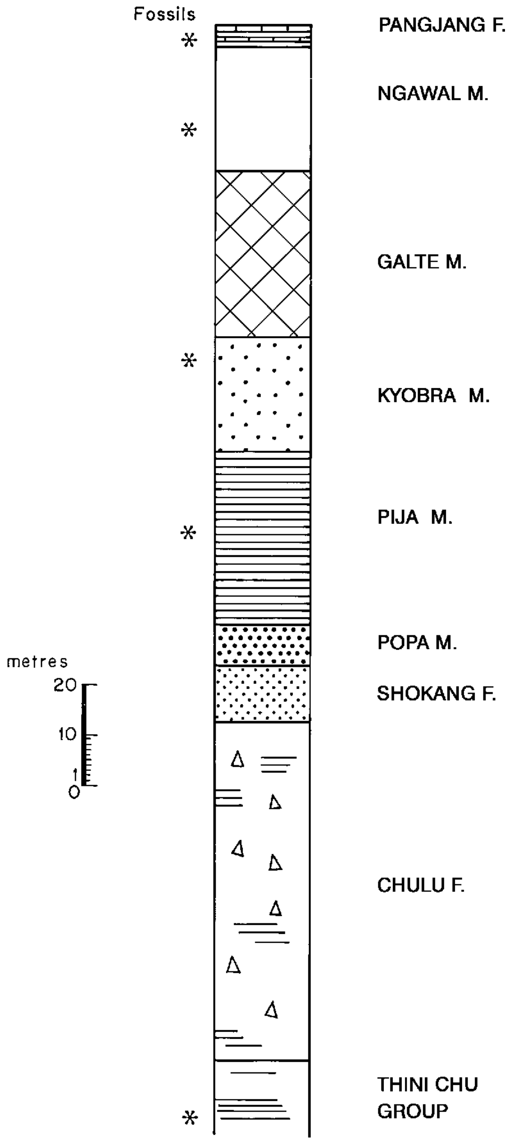
B. Dolomite breccia at base of Popa Member, east of Pijagaon, west Dolpo.

At ridge B, the south section along the east face is thick, and includes bryozoans in the lower shaly part and *Lazarevonia* brachiopods in the upper sandy limy beds. Beds are thin in the Galte Khola.

The facies change to the west (Waterhouse 1987b) into more calcareous beds. At Puchenpra Ridge, the Pija Member is represented as follows:

[Kyobra Member]
(top) 0.7m rust-stained sandstone, calcareous at top, with *Lazarevonia* brachiopods
13m brown to yellow sandstones up to 1.5m thick
10m shale, some subcalcareous, quartzite at 5m below top
8m black siltstone
0.2-1m rust-stained sandstone with weathered basal contact
[Popa Member].

The member is not found to the west in the Plateau of Lakes nor Mesokanto area, or Kali Gandaki valley, but resumes in Dolpo.
AGE: Fossils belong to the *Lazarevonia arcuata* Zone. The age is Changhsingian or perhaps late Wuchiapingian (Late Permian) from stratigraphic position and from study of faunas, as discussed by Waterhouse (2002c, p. 183).



Text-fig. 14. Generalized stratigraphic column for Late Paleozoic rocks at ridge A north of Braga, Manang district, modified from Waterhouse (1988, text-fig. 3). F. = Formation, M. = Member.

Kyobra Member

NAME: This member was tabulated and summarized by Waterhouse & Shi (1991) and Waterhouse (1994). It is named from Lake Kyobra, north of Lake Chho and Braga, with type section on the east face of Chulu ridge A.
CONTENT, DESCRIPTION: The member is mostly white fine to coarse quartzite, developed above the Pija black shales, and below the Galte Member, and formed from a sudden local influx of coarse clastics varying from very thin or up to 40m in thickness. On the northwest side of Chulu ridge A east of the Lakes Chho and Kyobra, the member is only 8m thick and includes 0.4cm shards of mudstone and pebbles up to 3cm in diameter in some layers, with minor interleaving of black shale. Beds at south ridge B are 4-12cm in thickness. The east side of Galte Khola exposes some 12m of quartzite with ferrous spots, as at section WB. To the west, along the Puchenpra Ridge, the member lies below Puchenpra Member:

[Puchenpra Member]
(top) 1.1m shale
0.2m quartz-rich sandstone, minor mudstone
(possible disconformity)

2m calcareous ferrous-specked sandstone and quartz sandstone
1m black mudstone and ferrous-specked minor sandstone
2.5m quartz-rich grey sandstone
sedimentary break
[Pija Member].

AGE, CORRELATION: Poorly preserved fossils found at Puchenpra and Galte Khola appear to belong to *Lazarevonia* and an indeterminate productidin. The member falls within the same biozone as the Galte and Puchenpra Members, judged from specific affinities of *Lazarevonia*, and is correlated with part of the Nisal Member to the west in Dolpo. The beds are of Changhsingian age.

Table 3. Thickness in metres of units at different sections, located as in Text-fig. 11.

Member	EA	WA	SB	B	KB	BB	WB	Puchenpra
Kyobra	35	8	10	12	11	12	13	0.7
Pija	100	45	50	35	25?	12	30?	31
Popa	10	5	35	11	5	30	-	25

Galte Member

NAME: This member was tabulated and diagnosed by Waterhouse & Shi (1991, p. 383) and Waterhouse (1994). It was named from Galte Khola west of Braga, Manang district, and southeast of Lake Chho.

DESCRIPTION: The beds are moderately close to those of Nisal Member in west Dolpo, but are more varied, with more mudstone and more conglomerate, deposited near-shore under fluctuating conditions of supply, storminess and water-depth. The beds, unlike those of the Nisal Member, were derived in part from Shokang Formation. The type section lies at ridge B southeast of Mt Chulu (Text-fig. 15B) north of Triassic and Kyobra Member outcrops.

TYPE SECTION: Rocks are exposed over the crest and east side of ridge B, and may be traced through a band 40-60m wide, so that patches of rock covered by rubble may be examined nearby.

[Ngawal Member]
(top) 0.3m quartz sandstone with 2-3 mudstone layers and current-bedding
0.3m calcareous sandy beds
5-10cm shales, 10cm conglomerate
1m calcareous red-green sandstone with golden patina, mudstone inclusions
0.4m sandstone and upper mudstone, red and green, brachiopod shells include *Biplatyconcha grandis, Pondospirifer, Cleiothyridellina accoliformis*, pebbles
1.7m quartz-rich sandstone, red at top, medium coarse, some 0.7cm grit of Shokang lithology
1.4m red and green sandstone and mudstone, lenticular, in 2-10cm beds
3m red and green sandstone and mudstone in 5-30cm beds, derived from Shokang Formation, moderately well bedded
0.4 quartz-rich sandstone
2.5m red sandstone and sandy siltstone
9.3m quartzose sandstone
1.2m impure quartzose sandstone, undulose base
0.6m fine 2-10cm beds of quartzose sandstone and minor dark siltstone, sandstone
2-8cm dark green sandy siltstone
0.3m calcareous red sandstone
1.2m beds 2-15cm thick of shelly calcareous sandstone
[Kyobra Member].

Text-fig. 15. Permian exposed along the east face of Ridge A, with Ridge D in background, looking north. M = Mukut Group (Anisian), J = Pangjang Formation with *Otoceras woodwardi* at base of Triassic, above Marsyangdi Formation, N = Ngawal Member and Galte Member.

Ridge B south of Chulu massif, looking northwest. C = Chini Thu Group, J = Pangjang Formation with *Otoceras woodwardi* at base of Triassic, above Ngawal and Galte Members.

Ridge B and Chulu massif looking northwest from Ridge A. Foreground includes Galte Member, Shokang Formation with *Glossopteris* leaves and Chulu diamictite. Ridge B with Carboniferous to Triassic. Chulu face with substantial overturned anticline, Pangjang Formation at J.

OTHER SECTIONS: In the syncline between Chulu ridges B and A the Galte Member is well exposed:

[Ngawal Member]
(top) 18m fractured fine bedded hard sandstone, some fossils and mudballs at base, 4mm pipes opening from below, some dark layers
1m massive Nisal-like red calcareous sandstone, sub-bedding, many fossils at top 0.2m
1m red-green sandstone, little fine, 5-20cm irregular beds
2-2.5m fine sandstone and siltstone-mudstone
1m quartzite
4m quartz-rich and fine beds, siltstone, mudstone, dark mudstone
2m basal sandstone, red calcareous and black mudstone, sandstone mostly in 0.1-0.3 beds, irregular undulose base, mica flakes
[Kyobra Member].

The section NW for beds exposed on the northwest side of ridge A involves:

[Ngawal Member]
(top) 10m 1-2 fine mud-streaked barren sandstone beds, sandstone finer and more mudstone upwards, beds 1-2cm thick. Reddish limestone and occasional 2-10cm sandstone and fossils
1.7m 2-6cm scattered fossil bands, irregularly bedded sandstone and mudstone
1.2m 4-5 beds of sandstone, minor mudstone
1.2m shelly sandstone, *Biplatyconcha*
2.1m massive sandstone and 30cm inclusions of red sandstone
7m 4-20cm beds of fine green weathering rusty sandstone, streaky mudstone in 1cm beds. Slightly irregularly bedded, not knobbly, yet moderately lenticular
[Kyobra Member].

A major collecting area of 1981 lay at the crest of ridge A, towards the north end, and south of a prayer flag:

[Ngawal Member]
(top) 3-4m massive red beds
19m very shaly in poorly bedded 1-3cm layers, occasional 2cm harder layers of sandstone stand out, mudstone flakes
10m sandstone, pebbles 6.2m above base, fossils especially from 1m band about 2m above base, some higher. Locality PG1
1.1m sandstone and fine rare siltstone partings, many fossils
0.5m sandy siltstone
6m 0.1-0.2m impure quartz sandstone, silt and silty sandstone partings
[Kyobra Member].

In the Galte Khola west of ridge B, between Manang and Braga, section BB (Text-fig. 16) exposes almost 18m of mostly sandstone beds. But further up the valley, and about 1km west of the type section in section WB, beds above Kyobra Quartzite are more muddy than usual, with some 35m of multicoloured weathered sandy shale and siltstone in 0.1-0.6 beds, occupying the position of the Galte Member, but like Ngawal in appearance. Scattered 5cm rounded pebbles and black muddy siltstone in 1cm layers are present. A further 32m of beds above appears to be Ngawal Member.

CORRELATION: Fossils are common, and belong to the *Biplatyconcha grandis* Zone, of Changhsingian age, represented in the Nisal, Nambdo and Luri Members of west Dolpo, and upper Qubuerga Formation at Qubu, south Tibet.

Puchenpra Member

NAME: The Puchenpra Member was named and diagnosed by Waterhouse

(1994, p. 7) for conglomeratic sandstone, rich in fossils, constituting a shallow water deposit lapping on to the Kali Gandaki high (Waterhouse 1987b, 1989a, p. 96), and passing laterally into the Galte Member further east. The coarseness and variability of the sediment suggest a source of moderately steep topography drained by turbulent streams, and sifting of the sediment by wave action. The name is derived from Puchenpra Ridge, and the type section is found at peak 17315ft, on the northeast side of Plateau of Lakes. It was named before use of the name in a different sense by Garzanti et al. (1994) in applying the term redundantly to rocks already named Shokang (Waterhouse 1979), Senja (Waterhouse 1977) and Marsyangdi (Waterhouse 1989, Waterhouse & Shi 1991) Formations. Their name was not only a junior synonym, but not applicable in a group sense, for that had already been anticipated with the proposal of Namlang Group by Waterhouse (1977, 1978).

TYPE SECTION: The best developed beds are developed in a small area of the peak 17315ft at section 3 (Text-fig. 10):

[Ngawal Member]
(top) 18m subangular quartz conglomerate and coarse sandstone, 1-12cm layers, coarser red sandstone with fine pebbles. Pebbles of quartz 1-15cm in diameter, possibly derived from Shokang Formation, usually matrix-separated, subrounded, not flat, with grit and coarse sandstone matrix, a few pebbles weakly flattened, suggestive of inshore deposits. Lower 8m (PP2, PP3) contains brachiopods *Arctitreta* and *Betaneospirifer ravaniformis* in 4 fossil bands, and better preserved in upper bands (PP1), with brachiopods *Saeptathaerus, Biplatyconcha grandis, Fusispirifer jini, B. ravaniformis, and Cyrtella*. This constitutes a rich inshore fauna, winnowed and concentrated
[Shokang Formation].

OTHER SECTIONS: At Puchenpra Ridge about 1km to the east, and almost on strike, the member is represented by some 1-11m rust-coated conglomerate and sandstone. Fossils include crinoids, *Biplatyconcha grandis, Fusispirifer jini,* and *Betaneospirifer ravaniformis* 5m from base. Underlying 1.1m shale and 0.2-12m of quartz-rich sandstone are deemed to be Kyobra Member.

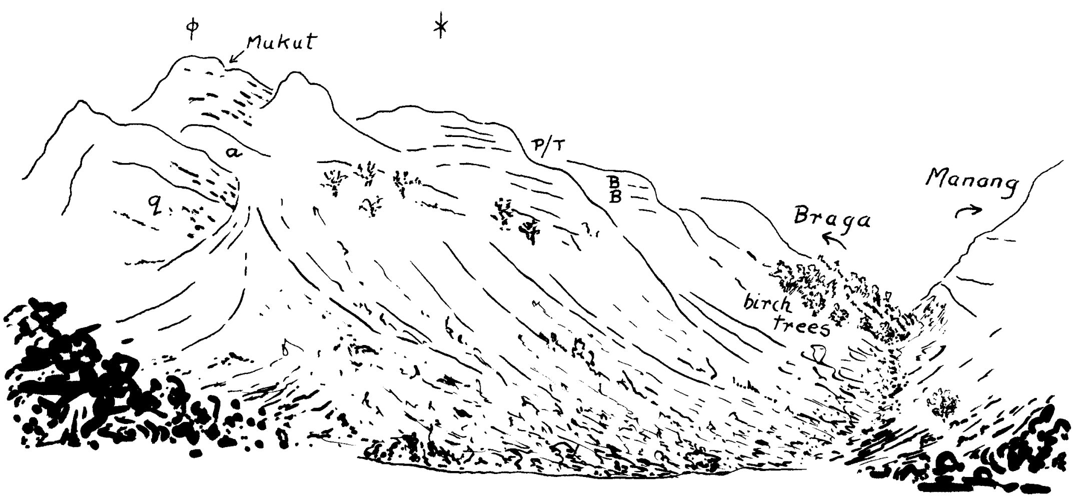
At section 6 in the Plateau of Lakes, there is about 1m red sandstone overlying 1m sandy red conglomerate, of rounded quartz pebbles. At section 4, which lay originally considerably north of other sections prior to deformation, the Puchenpra Member lies above Shokang Formation and below Ngawal beds. It is represented by some 6m conglomerate and quartz sandstone, chert pebbles, variously green, red and white, 1-15cm in diameter, mudstone flakes, some pebbles in contact, and mostly matrix-separated slabs of sandstone and mudstone. Fossil brachiopods *Biplatyconcha grandis* and *Spiriferella rajah* and nuculanid bivalve occur near the base. Section 2 exposes some 15cm of quartz conglomerate, with quartz pebbles that are rounded or subrounded, separated by grit matrix, above 10-12m of Shokang Formation, and below ca 2cm of shale of the Marsyangdi Formation.

Further west at Mesokanto Pass, limestone of the Marsyangdi Formation is underlain by some 5m of red pebbly sandstone, with 1-2m of mudstone

along strike. Gastropod *Retispira* and brachiopod *Echinalosia* are found in the topmost beds. On the one hand, these beds strongly approach thin Nisal Member of the Dolpo district, because the sandstones are less well sorted than those typical of the Puchenpra Member, but on the other hand, the beds are pebbly, approaching Puchenpra Member. The underlying 5-20cm is quartz-rich, above some 3m of white sandstone with roots, typical of Shokang Formation.
CORRELATION: The fossils belong to the *Biplatyconcha grandis* Zone, of Changhsingian age. They are much the same age as those of the Galte and Ngawal Members of Manang, and Nisal and Luri Members of Dolpo and Kali Gandaki valley.

Nisal Member

NAME: The member was named from Nisalgaon in west Dolpo, for mostly sandstones rich in fossils of the *Biplatyconcha grandis* Zone (Waterhouse 1977, 1978).
DISTRIBUTION: The member is well developed in west Dolpo and probably is widely present in east Dolpo. Thence it thins eastwards into the Kali Gandaki valley. North of the Thini Khola 100m above the main track to Mesokanto in a depression above a sheep enclosure, there is 1m or so of red green sandstone and red mudstone with 3cm black mudstone pebbles and large brachiopods including *Biplatyconcha grandis*. The sandstone is less well sorted than to the east at peak 17315ft, and so is like Nisal in appearance. The topmost 2-4cm of rock is bleached. In this general region, the Nisal beds consist of 1 to 3.5m of red green sandstone, minor conglomerate with limestone flakes, and layers of black argillite and grey siltstone, containing densely packed brachiopod shells of *Biplatyconcha grandis* and *Betaneospirifer ravaniformis*, lying on quartzite at



Text-fig. 16. Field sketch showing section BB, looking southwards down Galte Khola between Braga and Manang, as indicated by arrows. Also indicated are q - quartzite of Popa Member, a - argillite of Pija, Mukut Group, and positions of anticline and syncline. P/T = Permian - Triassic boundary.

the top of Shokang Formation (Waterhouse 1979, p. 206). These beds were classed as Early Triassic band 4 by Bordet et al. (1971, pp. 124, 125, text-fig. 47), and largely ignored in other studies on the region. Somewhat arbitrarily, it may be suggested that the Nisal Member replaces the Puchenpra Member near Mesokanto Pass and extends westwards at least as far as west Dolpo.

Ngawal Member

NAME: This member was named and diagnosed in Waterhouse & Shi (1991, table 1) and Waterhouse (1994). The name is derived from Ngawal village, Manang district, and the type section is at Ridge B southeast of Mt Chulu.

DESCRIPTION: The member is characterized by the predominance of shaly beds, generally multicoloured, with minor dolomite and shells, accumulated under what appear to have been fluctuating conditions of supply and water-depth. More shale is present than in the Galte or Puchenpra Members, or in the Luri Member of Dolpo, and there are more coarse clastics than in the Nambdo or Kuwa Members of west Dolpo. The Ngawal Member may contain equivalents of these members, as less distinctive units, and lacks some of the distinctive fossils of the Nambdo and Kuwa Members.

TYPE SECTION: The type section at ridge B is moderately well exposed along the crest and over the east face.

[Marsyangdi Formation]
(top) 7m shale, silty and sandy mudstone with thin dolomite layers, mostly 2-35cm beds, minor conglomerate
14-17m fine bedded, irregularly jointed and fractured black siltstone, mudstone, red sandstone, weathering to various hues of red, yellow and brown and orange, 10cm beds of sandstone, pebbles up to 0.3m from base, 7cm grit at 1.2m from top. Locality PN1 collected over an interval 3-6m from top
[Galte Member].

Pelite from near the base of the member (UQ 45890) is metamorphosed carbonaceous mudstone, with quartz, minor albite feldspar and detrital mica. Some secondary muscovite is aligned parallel to foliation, and there is also minor secondary biotite.

In the syncline between Chulu ridges A and B, fossils are difficult to extract, but beds are well exposed. There is no stratigraphic cap:

(top) 9m mostly siltstone and sandstone, fossiliferous beds up to 10cm thick, weathered yellow, orange and red
0.5m sandstone and mudstone
20cm conglomerate and 5cm igneous clasts, matrix supported
0.5m fine siltstone and sandstone, bedding fine
1-3cm dark siltstone
0.3m coarse sandstone bed, gently channeled (2cm) base, some mudstone, 1-3cm conglomerate, subangular, none flat, mudstone, derived most likely from Shokang Formation
[Galte Member].

Further to the east, on the northwest side of Chulu ridge A, similar beds are better exposed:

[Marsyangdi Formation]
(top) 1-2cm sublenticular fine red sandstone
12m poorly exposed silky silty mudstone, green hue

17m siltstone, mudstone, up to 0.6m sandstone
[Galte Member].

As discussed for the Galte Member, beds 1km west of the type section on ridge B at section WB involve 32m of multicoloured weathered mostly 2-3cm beds of sandstone and shale, quartzites in 0.2-1m beds and rust-stained dark sandstone and siltstone in 0.1-0.6m beds, largely typical of Ngawal Member. Underlying beds 35m thick are more shaly than the type Galte Member, or Galte Member further east.

Ngawal Member is exposed immediately north of Manang settlement, and is found further west on Puchenpra Ridge, with more dolomite than to the east. The bivalve *Atomodesma* is locally common:

[Marsyangdi Formation]
(top) 7m laminated shale and dolomite
5m dolomite and shale
4m mudstone with brachiopod *Biplatyconcha grandis* prominent 2m above base
0.3m matrix-supported green quartz sandstone
0.5m dolomite
1m shale
1m sandstone including dense metal-rich layer
0.2m mudstone with well preserved *Atomodesma* bivalve species, including *A. exaratum* and *A. multifurcata,* locality PN3
[Puchenpra Member].

At Section 3, peak 17315ft, 1km east of Puchenpra, Ngawal beds are 6-21m thick along strike, of micaceous black siltstone and black shale, dolomite and orange-weathered medium sandstone, poorly exposed, with brachiopod fossils of *Biplatyconcha grandis* and *Transversaria marcouiformis,* bivalve *Dolponella sulcata* and gastropod *Retispira* 8m below top (locality PN4). About 0.3m rusty red-weathered medium sandstone lies at the base, above Puchenpra Member.

At section 6 in the Plateau of Lakes, the Ngawal Member is represented by 10m shale, siltstone, dolomite, and fine sandstone in 8-25cm bands, with few shells, above 1m of red-weathered sandstone and conglomerate with rounded quartz pebbles like those of the Puchenpra Member. At section 4, Ngawal rocks are exposed as follows:

[Marsyangdi Formation]
(top) 6-7m quartzose shelly grit, dolomite up to 9cm thick, micaceous siltstone rich in bivalve *Atomodesma exaratum* and other species, including gastropods and brachiopods
2.5 sandstone and mudstone, brachiopod *Biplatyconcha grandis*
0.7m mudstone
0.2m sandstone
3.5m black silty mudstone
1.3m sandstone with bivalve *Clavicosta rugatula,* brachiopod *Biplatyconcha grandis*
1m black siltstone - mudstone
[Puchenpra Member].

Further westwards, there appears to be no Ngawal Member: the beds do not reach Mesokanto or Kali Gandaki valley.

CORRELATION: The fossils are those of the *Biplatyconcha grandis* Zone, and are of Changhsingian age. The member is correlative in part with the Kuwa Member of west Dolpo, with which it shares *Atomodesma* n. sp.

MARSYANGDI FORMATION

NAME, HISTORY: The Marsyangdi Formation was proposed in Waterhouse (1989, p. 97, 1994), and Waterhouse & Shi (1991) for the youngest of Permian formations in the region. It was named from Marsyangdi River, and the type section is based on the east face of Chulu ridge A, below the type section for the Early Triassic or Scythian formations and members of the Manang Group (Waterhouse 1994, p. 9). The formation is best developed as far as known over the ridges south of Mt Chulu, where it is subdivided into several thin members, named and briefly described in Waterhouse & Shi (1991) and Waterhouse (1994). It embraces part of the upper “Puchenpra Formation” of Garzanti et al. (1994), but unfortunately they provided no map or type section, and did not describe, measure or locate their rocks in detail, so that their observations find little applicability. Their names were informal, as they were proposed heedless of previous studies, and not in conformity with the Guide to Stratigraphic Nomenclature.

CONTENT: The members may be summarized as follows:

(base) Chho Member, named from small lake north of Braga, Manang district, for impersistent black or green-dark grey shale, with sulphur efflorescence, up to 2m thick near the type section on the west side of ridge A, but missing from many sections.

Hongde Member, named from Hongde airstrip in Manang district for dense and often dark sandy bioclastic limestone (rock sample UQ 45888).

Mungji Member, named from a village in the Manang district, for foetid shale. Rock sample UQ 45887 is of metamorphosed carbonaceous mudstone, with 25-30% graphite derived from carbonaceous material, minor muscovite, haematite staining, and considerable alteration.

Braga Member, named from the village of Braga for prominent red- or orange-patinaed limestone and intervening thin shale, especially rich in fossils, often with current bedding, or large fucoidal structures up to 20cm long inclined to the bedding. Rock sample UQ 45891 is bioclastic limestone stained by haematite, and comparatively pure. The name Braga was also applied by Garzanti et al. (1994) in a different sense to beds already named Chulu by Waterhouse (1987b): the present application has priority over the use by Garzanti et al. (1994).

Tengi Member, named from Tengi settlement, Manang district, for thin fossiliferous shale. Rock sample UQ 45885 of interbedded mudstone and fine sandstone shows concentration of graphite in the fine layers. The sandstone consists of quartz, sericitized feldspar, and minor lithics.

(top) Gungsang Member, named from Gungsang settlement, Manang district , for dark to red-, orange- or gold-patinaed limestone. Rock sample UQ 45884 involves recrystallized bioclastic limestone with dolomite, minor quartz and albite feldspar, and secondary calcite veining.

The Marsyangdi Formation is overlain paraconformably by the basal Triassic Pangjang Formation (Waterhouse 1978, 1989, 1994), and lies on a surface that is apparently conformable, or may show very slight relief of 1-2cm.

TYPE SECTION: The type section on the east face of Chulu ridge A shows the following sequence:

[Pangjang Formation]
Marsyangdi Formation
(top) Gungsang Member 0.3m limestone with martiniid brachiopod
Tengi Member 0.2-0.3m mudstone
Braga Member 10cm golden sandy limestone above 8-12cm black mudstone, above 40cm ripple-bedded golden limestone
Mungji Member 0.1-0.3m foetid mudstone in 1-3cm layers
Hongde Member 0.4-0.7m sandy calcareous band with fossils, laminated and current-bedded, black pebbles
Chho Member 0-2m black sandstone, and green-black shale with sulphur efflorescence
[Ngawal Member].

OTHER SECTIONS: A nearby section SA on south ridge A for Marsyangdi Formation above gulch leading to Hongde:

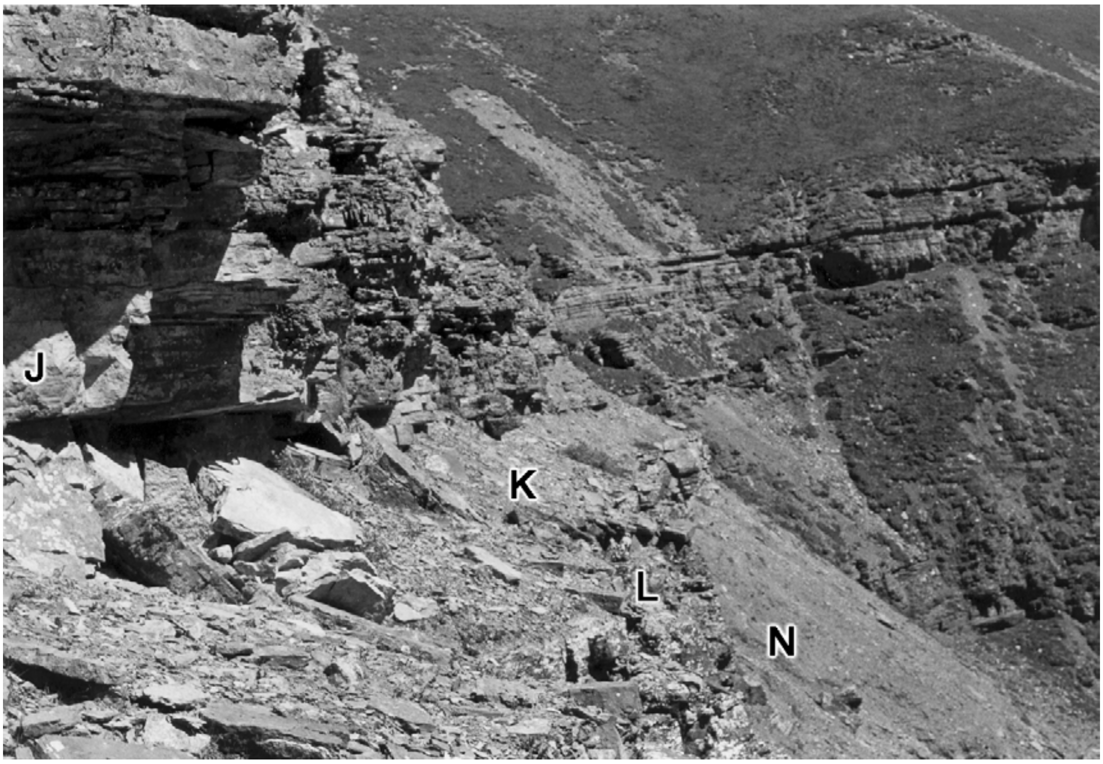
[Pangjang Formation]
(top) 30cm golden sandy limestone, Gungsang Member
0-20cm black shale, irregular top, and black mudstone balls, martiniid brachiopod, Tengi Member
15cm crinkle-sheared shale, Tengi Member
20-30cm massive golden sandy limestone, Braga Member
16 cm black shale, grading up from below, Braga Member
6cm limestone, Braga Member
8cm black shale, Mungji Member
3.2m golden sandy limestone, few fossils, Hongde Member
[Ngawal Member].

On the west face of ridge A above Lake Chho - section WA:

[Pangjang Formation]
(top) 0.8m massive red carbonate, split at 20cm from base, strong sulphurous odour, martiniid brachiopod, Gungsang Member
0.18-.24 m shale, Tengi Member
0.28m sandy red carbonate, productidins and spiriferidins, Braga Member
0.1-0.2m laminated dark grey dense shale, fossils at base, Braga Member
0.7m red sandy carbonate, corals at top, and other shells, Braga Member
ca 1m red-tinged dolomitic and grey mudstone, 1-5cm beds, Mungji Member
1.2m 4-5cm layers of red limestone, irregular shale bands, fossils 0.4m above base, Hongde Member
[thin sandstone and shale, Ngawal Member].

At Ridge B, north side, below Early Triassic, the sequence is:

[Pangjang Formation]
(top) 0.28-0.3m golden coloured sandy limestone, conglomerate, corals and martiniid brachiopod, some dense black pebbles, fossils may lie in channels, Gungsang Member
0.8-1m black shale, Tengi Member
0.28m limestone with corals and brachiopod *Spiriferella* or *Arcullina*, Braga Member
1.8m black shale, Mungji Member
0.7m sandy limestone, fossils at top, *Spiriferella*, Hongde Member
[Ngawal Member].



Text-fig. 17. A. Permian-Triassic contact in west Dolpo, Tar-Sebu canyon. J = Pangjang Formation (basal Triassic), K = Kuwa Member, L = Luri Member, N = Nambdo Member (Late Permian).
B. Pangjang Formation, east side of Kali Gandaki valley.

About 1km to the west in the Galte Khola at section WB:

[Pangjang Formation
massive dense beds with rare black pebbles up to 10cm above base, ammonoids in section, a few reworked brachiopods. Here the Gungsang beds are so thin that the basal Pangjang carbonate is well exposed as a ledge over readily back-weathered Tengi shale and may be easily collected.]
(top) 0-2-7cm limestone, jagged 1cm relief, suggesting surface cracking prior to consolidation, Gungsang Member
33cm shale, Tengi Member
12cm gold-coated current-bedded limestone, Braga Member
15-20cm shale, Braga Member
2-7cm gold-surface-coloured current-bedded limestone, Braga Member

5cm calcareous shale, Mungji Member
24cm current-bedded gold-surface-coloured limestone, Hongde Member
0-1cm shale, Chho Member
[Senja Formation].

Section BB, west side of Chulu ridge B above Galte Khola (Text-fig. 11, 16), 2 km south of WB:

[Pangjang Formation]
(top) 22cm golden fossiliferous limestone, Gungsang Member
14cm shale, Tengi Member
23cm current-bedded limestone, Braga Member
7cm shale, Mungji Member
1m limestone and shale, Mungji or Hongde Member
1.2m sandy *Spiriferella* limestone, calcareous concretions and black pebbles at base, Hongde Member
0-3cm shale, Chho Member
[Ngawal Member].

In the foothills north of Manang (section E), the Pangjang Formation is 1.25m thick, lower 0.5m massive, basal relief 2-3cm, scattered black pebbles up to 7cm diameter. The Marsyangdi Formation is subdivided as follows:

(top) 7-14cm black finely laminated shale, with 2-4cm relief at base, distinct unnamed unit above otherwise youngest known member of Marsyangdi Formation
6-8cm carbonate with martiniid at top, Gungsang Member
3cm shale, Tengi Member
18-32cm gold-coated carbonate, Braga Member
2cm shale, Braga Member
8cm gold-coated carbonate, Braga Member
1m fossiliferous shale, Mungji Member
0.6-0.7m gold-red-patinaed limestone, Hongde Member
[Ngawal Member].

To the west and north up a tributary of Jargeng Khola, west of the Chulu massif, a section was measured on the east side of the valley:

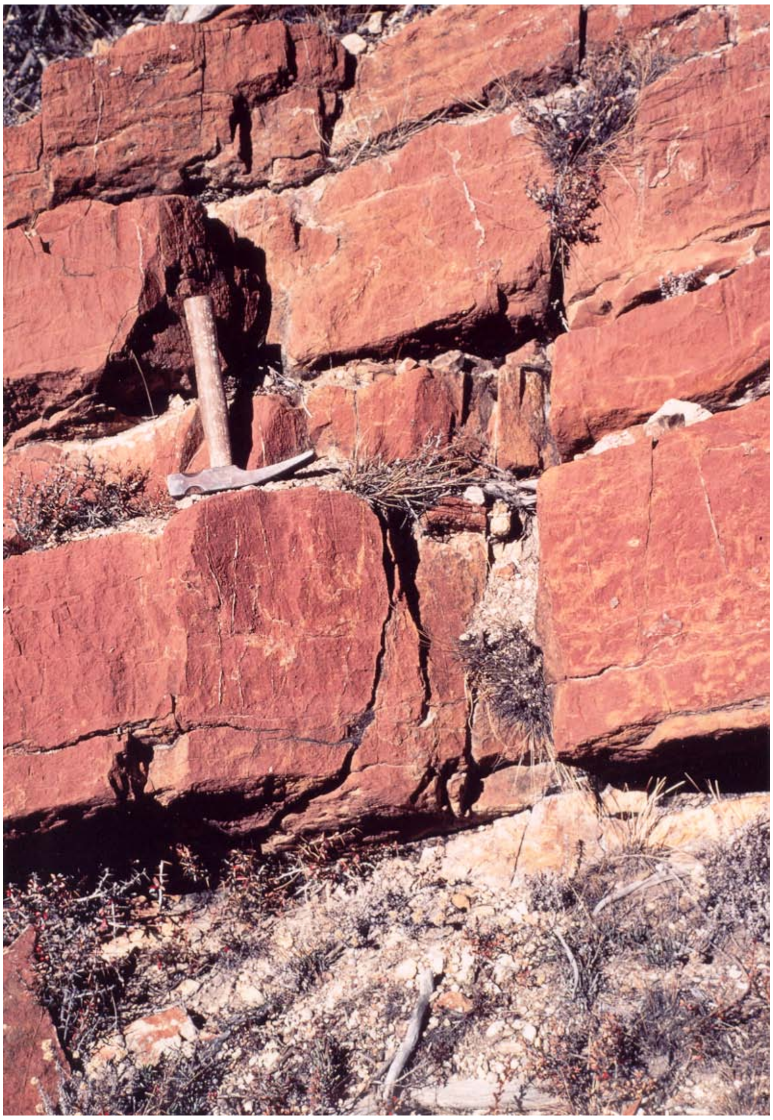
[Pangjang Formation]
(top) 10-18cm carbonate, Gungsang Member
44cm shale, carbonate rich, Tengi Member
56cm carbonate with ripples, 5cm black pebbles at base, channeled 10cm into underlying member, beds show swirl pattern, few shells other than some spiriferids, Braga Member
1m shale, pebbles, Mungji Member
15cm sandy carbonate, few shells, Hongde Member
60cm sandy carbonate, Hongde Member
[Senja Formation].

Another section to the north in this valley shows:

[Pangjang Formation, *Otoceras* in cross-section]
(top) 80cm shale, top channelled, Tengi Member
45cm limestone, upper 8-10cm very shelly, and top 20-25cm layered; lower part massive, with shells and 2cm black pebbles at base, Braga Member
1.60m shale, 40cm laminated, Mungji Member
[Ngawal dolomite and laminated sandstone and shale].

To the south a poor section on the east side shows 50cm of shale (Tengi Member), above 12cm gold-patinaed sandy limestone with shells (Braga Member) above 15cm of shale (Mungji Member), over Ngawal beds.

Further west, the beds become thinner, and are treated as Marsyangdi Formation, with discrimination of units not feasible. At Puchenpra Ridge the formation above the Ngawal Member is reduced to 1.3m of golden sandy



Text-fig. 18. Pangjang Formation (basal Triassic) east of Kali Gandaki River.

limestone with *Spiriferella* to top, in four thin bands. At section 3, peak 17315ft, the formation consists of 35-70cm golden sandy limestone with corals and brachiopods. Still further west and a little north beds are thicker at section 4:

[Pangjang Formation
7cm fine golden and slightly red limestone with *Otoceras*. Base undulose]
(top) 5cm gold-red limestone with brachiopod Anidanthin
88cm shelly gold-coated limestone with brachiopods *Spiriferella grunti, Retimarginifera xizangensis,* martiniid
7cm dense red siltstone, fenestellids
1m alternating dolomite and shale
[Ngawal Member].

At the west side of the Plateau of Lakes, section 7 (Text-fig. 10) is as follows:

[Pangjang Formation]
(top) 15cm muddy limy bands, gritty limestone to north with black pebbles, martiniid
15cm dense limestone
38cm dense orange-coated limestone with few fossils
37cm dense orange-red-coated limestone, light grey when fresh, with corals, productids, spiriferids
2cm shale
[Puchenpra Member].

At Mesokanto, the Marsyangdi Formation is represented by 0.8 to 1m of orange brown limestone, below Pangjang Formation and above Puchenpra Member. Shells are present, but difficult to collect.

Further west, about 100m above the track to Tilicho and east of a sheep camp, the Marsyangdi Formation is a band 38cm thick rich in bryozoans with few brachiopods. It is found above red and green sandstone and red mudstone like Nisal Member of west Dolpo. Elsewhere the lower 28cm of this band is sub-bedded, and the upper 7cm is free of fossils. Towards Thini village at site D of Waterhouse (1979), the bands A, B and C cited in the text belong to the

Marsyangdi Formation, commencing with A, 38cm of dense red-patinaed dolomitic carbonate with productid brachiopods, bryozoans and crinoids, overlain by B, 58cm of dense red-weathering carbonate with brachiopods *Betaneospirifer* and *Spiriferella*, and then 5-10cm pebbly layer C with crinoids and bryozoans (Waterhouse 1979, p. 208). Slightly different successions were also described nearby. Although the beds were initially assigned to Pangjang Formation, they should be re-allocated to Marsyangdi Formation. They were treated as unit 5 of the Triassic Thinigaon Formation by Bordet et al. (1971, p. 124). The cement or matrix is recrystallized with dolomitic and ferruginized components.

CORRELATION

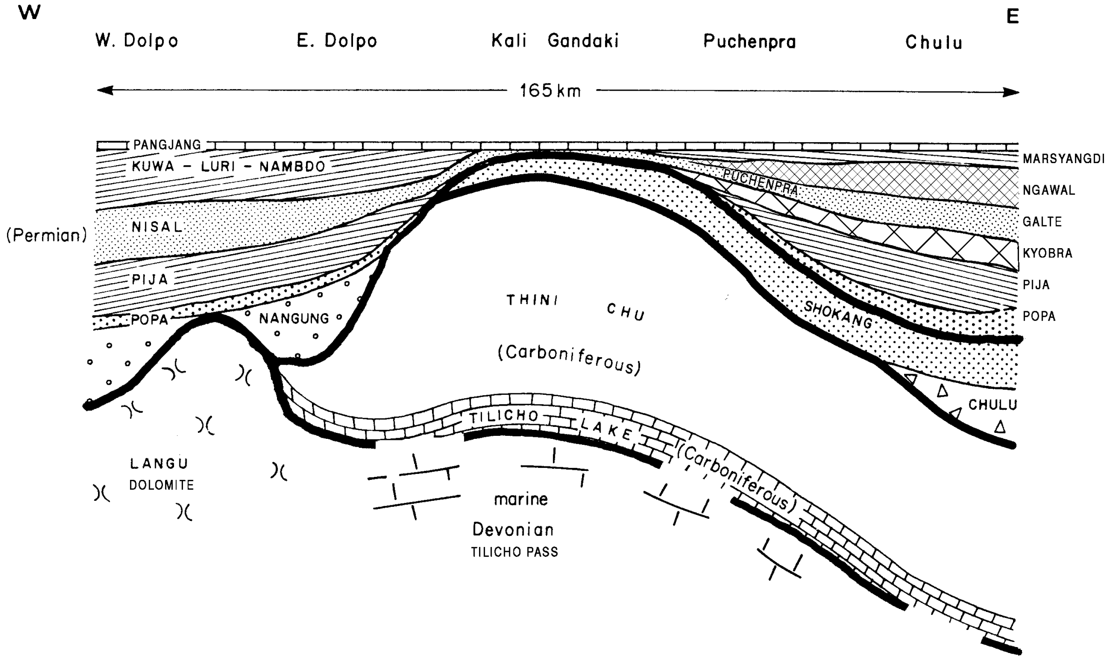
Brachiopods and molluscs are described by Waterhouse & Chen (in prep.) and are assigned to the *Retimarginifera xizangensis* Zone, which embraces the Marsyangdi Formation of Manang district, and is well represented in much of the Selong Group at the Selong Xishan section of south Tibet (Shen et al. 2000, 2001). Flügel in Garzanti et al. (1994, p. 171) identified the coral *Plerophyllum schindewolfi* Flügel, 1966, regarded by Garzanti et al. as "documenting the latest Permian", though the assertion was not supported by published evidence. The coral species was described by Flügel (1966) from east Dolpo, from rocks not as young as the *Retimarginifera xizangensis* Zone, and probably equivalent to the *Biplatyconcha grandis* Zone, equivalent to middle but not latest Changhsingian in age.

PANGJANG FORMATION

The Pangjang Formation (Text-fig. 17, 18) was named for dense dolomitic limestone 1-3m thick at Pangjang Khola, west Dolpo, by Waterhouse (1977, 1978), and extends across Dolpo and the Kali Gandaki valley to Manang (Waterhouse 1989a, p. 95). Similar rocks are found far to the west in Zanskar, Kashmir and western Himalaya, and also in south Tibet (Orchard et al. 1993). In the Manang district, the Pangjang Formation is divided into the Pengba and Chegaji Members, with *Otoceras woodwardi* and *Ophiceras tibeticum* Zones, and further fossil levels, as elaborated in Waterhouse (1994, table 5, p. 75, 2002b, pp. 96, 97).

THE KALI GANDAKI HIGH

Outcrops of the Kali Gandaki valley and eastwards across Mesokanto Pass, Plateau of Lakes and Puchenpra Ridge show Permian sediments that are much thinner than those of Dolpo or Manang district to the west and east. This area was called the Kali Gandaki high by Waterhouse (1987b, p. 137, text-fig. 3), and was a shallow-water area, at times emergent during Late Permian time.



Text-fig. 19. Impressionistic longitudinal section of Late Paleozoic rocks from west Dolpo to Manang district, showing the Kali Gandaki high, from Waterhouse (1987b, text-fig. 3), modified to include members of the Senja Formation in the Manang district. Heavy black lines follow unconformities.
Vertical not to scale.

Compared with outcrops at Chulu ridges A and B north of Braga, there is no tillite at Puchenpra Ridge. The Shokang Formation is mostly quartzite, the Popa also quartzite, without plant material, and the Pija more sandy and calcareous with little shale, suggesting an inshore position. Puchenpra Member is equivalent to Galte, but more pebbly and quartzose. The Ngawal Member was deposited in quiet inshore waters with reduced sediment supply and much mud, away from the main distribution source. The Pangjang Formation is similar to that elsewhere, and contains derived Permian fossils such as *Betaneospirifer* and *Biplatyconcha grandis,* as well as the basal Triassic ammonoid *Otoceras woodwardi*.

At section 3, Peak 17315ft, apparent Pija equivalents and any Popa plus Kyobra Member have wedged out. The Shokang Formation persists, diagnosed through the presence of roots and tubes, but is compact and approaches that of the Plateau of Lakes, with less red sandstone and less sulphur-encrusted mudstone than to the east. The Puchenpra Member was deposited very close to shore, with conglomerate containing fluviatile, not beach-flattened pebbles. Shells are found in a lower quartz sandstone conglomerate unit, and also in overlying less pebbly sandstone. The Ngawal Formation contains some sandstone bands and more shells than to the east, and fails to extend far west. The Marsyangdi Formation is present as compact carbonate, just as to the west, with no sign of the Hongde unit, nor shale. The Pangjang Formation is very similar overall to Pangjang further east, and the *Otoceras* layer is widely present.

In the Kali Gandaki valley there is thin Shokang Formation, no sign of Senja Formation units other than Nisal Member, and Marsyangdi Formation is reduced in thickness. This is the most accessible area for Permian in northern Nepal, so that it has been closely studied by several geological teams. But within a few kilometres the sediments change in nature (Text-fig. 19), so it is an error to regard the Kali Gandaki rocks as typical of Himalayan Permian.

B. LATE PERMIAN BIOZONES FOR THE HIMALAYAS

(Table 1, 2)

It is now possible to assign Late Permian macro-invertebrate faunas to biozones that apply along the Himalayan Range, thanks to clarification of the sequences in south Tibet by Shen et al. (2000, 2001, 2003a), coupled with study by Waterhouse & Chen in prep. and the systematic studies in the present work (Table 4). The broad general picture of Late Permian faunas may be summarized for the Salt Range of Pakistan, and throughout the Himalaya, involving northwest India, Sikkim, Bhutan, Nepal and south Tibet (Xizang), and extending into the southern Karakorum Range.

***Lamnimargus himalayensis* Zone**

Faunas of the *Lamnimargus himalayensis* Zone were extensively studied by Diener (1897b, 1899, 1903, 1915) particularly in Kashmir, and later extended through much of the northern Himalaya. Zewan Formation member C beds and faunas of Kashmir (Nakazawa & Kapoor 1981) provide the best example. The key fossils are *Lamnimargus himalayensis* (Diener), *Costiferina indicus* (Waagen) and *C. alatus* Waterhouse. *Lamnimargus* is particularly widespread, and remains highly useful, even though confused with *Retimarginifera* by some workers. It is diagnosed externally by its large and gently concavo-convex visceral disc with fine and numerous radial and concentric ribs. Unlike *Retimarginifera*, concentrics are predominant (see p. 66). Other wide-ranging and largely if not entirely restricted species include *Chonetinella unisulcata* Zhang, *Waagenoconcha gangeticus* (Diener), *Derbyia grandis* Waagen, *Wadispirifer ravana* (Diener) and *Fusispirifer nitiensis* (Diener). As well a number of other species have been described, including *Paramesolobus lissarensis* (Diener), *Sulcataria pentagonalis* Waterhouse, *Retimarginifera sheni* Waterhouse, *Wyatkina zaga* Waterhouse, *Echinalosia sheni* Waterhouse, *Etherilosia convexa* Shen et al., *“Linoproductus” tingriensis* Jin, *Orthotetes bisulcata* Waterhouse, *Spiriferella sinica* Zhang and *Arcullina qubuensis* (Zhang), the latter ranging possibly into the *Lazarevonia arcuata* Zone. Some spiriferid species are comparatively abundant in the zone, but have extended ranges. One such species is *Betaneospirifer neomarcoui* (Licharew), which includes *Neospirifer*

Table 4. Range of Himalayan Permian species described in this study.

Species	NEPAL					TIBET				
	1	2	3	4	5	6	7	8	9	10
Nisalarinia nisalensis	x									
Sulcirugaria transversa			x							
Chonetella semicostata									x	
Retimarginifera sheni				x		x				
Wyatkina tibetensis						x				
?Strophalosia gerardi			x							
Echinalosia magnispina			x							
E. zaga						x				
Stenoscisma cf. *vagata*	x									
Coledium selongensis										x
C? cheni							*x*			
Cyrolexis? zhangi								?		
Goleomixa? archboldi									x	
Betaneospirifer ambiensis	x			x						
B. neomarcoui				x		x				
B. ravaniformis				x						
B. shii					x				x	
Pondospirifer magnificus				x						
Quadrospira tibetensis			x			x			x	
Wadispirifer hongdeensis			x							
Fusispirifer semiplicata	x					x				
F. jini				x			?	x		
Transversaria marcouiformis				x		x	x	x		
Spiriferella rajah	x		x	x						
S. sinica						x				
S. nepalensis					x				x	
S. grunti					x				x	
Arcullina qubuensis			x			x				
A. oblata				x						
A. angiolinii					x					

Zones:
1 *Lamnimargus himalayensis* — 6 Equivalent *L. himalayensis*
2 *Pyramus silicius* — 7 "beds" 13-15
3 *Lazarevonia arcuata* — 8 *B. grandis*
4 *Biplatyconcha grandis* — 9 *R. xizangensis*
5 *Retimargifera xizangensis* — 10 *Coledium selongensis*
1-5, northern Nepal, west and central. 6-8 Qubu section, south Tibet. 9, 10 Selong Xishan section, south Tibet.

kubeiensis Ding, widely reported from south Tibet and Nepal. *Betaneospirifer ambiensis* and *Spiriferella rajah* are well known from this zone, but cannot be distinguished from younger occurrences.

Lamnimargus himalayensis faunas are found widely, including the Zewan members A, B and C in Kashmir, upper Nangung Formation in Dolpo, northwest Nepal, Tidong valley of Kinnaur district, Kuling Shales, Tingri Formation (Gupta & Waterhouse 1981) of northwest India, Sikkim and Bhutan (Gupta & Waterhouse 1979b). Equivalents are found in "beds" 1-12 of the lower Qubuerga Formation near Qubu, Zaga River, south Tibet (Shen et al. 2003a).

The faunas are judged to match those of the Kufri Member, lower Chhidru Formation (Table 5, 6) of the Salt Range, Pakistan (Waterhouse 2002c). Significant links are offered by *Chonetella nasuta* (Waagen), *Marginifera* aff. *typica* Waagen, *Costiferina indica* (Waagen), *Linoproductus abrupta* Reed, *Derbyia grandis* Waagen, *Betaneospirifer ambiensis* (Waagen) and *B.*

neomarcoui (Licharew). There are a number of other ties, involving chonetids, *Waagenoconcha*, *Lyttonia*, etc, and they are reinforced by the sharing of the ammonoid *Cyclolobus* between the Salt Range and Zewan C in Kashmir and Kuling Shale. Conodonts from the Kalabagh Member and Kufri Member (= lower Chhidru Formation), Salt Range, studied by Wardlaw & Pogue (1995), Wardlaw & Mei (1999) and Shen, Mei & Wang (2003) demonstrate a Wuchiapingian age, although this is not yet supported by full documentation or systematic validification.

***Pyramus silicius* Zone**

The *Pyramus silicius* Zone is based on faunas from the Popa Member of Nepal, overlying the *Lamnimargus himalayensis* Zone, and including, as well as the nominate species, *Waagenoconcha* s. l. *circularis* Reed and *Schizodus pinguis* Waagen, with other brachiopods and bivalves. Allied and identical bivalves are found in member D of the Zewan Formation in Kashmir, and both faunules have strong links with the distinctive and well known “bivalve fauna” of Waagen (1891) in the Salt Range. This is a restricted level with rich fossil assemblage dominated by gastropods and bivalves, and distinguished as the Ganjaroh Member (Waterhouse 1983b). The faunal level obviously represented a brief bioecological event, correlative across the Salt Range, Kashmir and northern Nepal. In efforts to oversimply Late Permian biostratigraphy, various accounts have left out consideration of Ganjaroh Member, and conodont studies have been made on the Salt Range with complete ignoral of Waagen’s “bivalve fauna”. Various articles, including Wardlaw & Mei (1999) and Shen, Mei & Yang (2003) in purporting to correlate the Chhidru Formation of the Salt Range, have failed to take account of the macro-invertebrate succession, even though clearly outlined in numerous studies (eg. Waagen 1891, Grant 1970, Waterhouse 1983b, 2002c), and failed to relate the conodonts to even the stratigraphic subdivisions. The “bivalve fauna” may, in the vague terms of reference offered by conodont studies, be Changhsingian, or possibly late Wuchiapingian (Waterhouse 2002c).

Two Late Permian sequences in south Tibet appear to lack the zone. Certainly, Kashmir, Nepal and the Salt Range have been studied from many more sequences, and the zone may be locally missing from Tibet, or not recognized because bivalves have not been closely studied.

***Lazarevonia arcuata* Zone**

The *Lazarevonia arcuata* Zone is best exemplified in the Pija Member of the Manang district of north-central Nepal, and extends into west Dolpo for a distance of more than 160km. It is characterized by a number of brachiopod species, including *Sulcirugaria transversa, S. subquadrata, Lazarevonia arcuata,* *Fostericoncha grandis, Platycancrinella grandauris, Wadispirifer hongdeensis, Pteroplecta sulcata, Reticulariina montana* and other species, as well as more long ranging species such as *Quadrospira tibetensis* (Ding) and *Arcullina qubuensis* (Ding). From superposition, the fauna seems likely to be Changhsingian, and there are some ties with Changhsingian faunas of south China (Waterhouse 1983a). But there are no clear cut links with faunas of Kashmir or the Salt Range. To some extent this might reflect both condensed sedimentation and patchy fossil record of those two areas. Neither this zone nor the underlying *Pyramus silicius* Zone have been recognized in south Tibet, and it should be noted that reports of *Krotovia arcuata* (now *Lazarevonia*) from the Selong Xishan section are discounted by Waterhouse & Chen (in prep.). Whilst there is still much to done in south Tibet, it is possible that the two zones are not represented by fossils there, or are represented by different fossils, perhaps of different lithofacies, or merged, or cryptic in some other way. Whatever the explanation, it should not mean that the reality, or limited reality, of the *Lazarevonia arcuata* Zone can be ignored.

***Biplatyconcha grandis* Zone**

This zone is very well represented in Dolpo, west Nepal, in the Nisal, Nambdo, Luri and Kuwa Members of the Senja Formation, and Manang in the Kyobra, Galte, Ngawal and Puchenpra Members of the same formation. The zonal name replaces the *Marginalosia kalikotei* Zone of Waterhouse (1978). The zone covers the same range, and *Biplatyconcha grandis* is preferred as zonal index because it is more common than *kalikotei* in central Nepal

Group	Formation		Earlier Names
	Mianwali Formation	Narmia Member	Topmost Limestone Dolomite
		Mittiwali Member	Ceratite Beds
		Kathwai Member	Upper Productus Limestone
ZALUCH	Chhidru Formation		
	Kalabagh M.		Middle Productus Limestone
50-300m	Wargal Limestone (plant beds)		
	Amb Formation		Lower Productus Limestone
NILAWAN	Sardi Formation		Lavender Clay
	Warchha Sandstone		Speckled Sandstone
			Conularia beds *Eurydesma* beds
200-300m	Tobra Formation		Talchir Boulder Beds

Table 5. Permian and Triassic stratigraphic units of Salt Range, Pakistan. From Teichert (1965) and Waterhouse (1976, table 28).

Table 6. Subdivisions of Chhidru Formation, Salt Range, Pakistan.

Formation	Member	Informal name
Chhidru	Khisor	white sand
	Ganjaroh	bivalve band
	Kufri	middle and lower beds, including Cephalopod or Jabi beds

and south Tibet. Just some of the critical fossils may be mentioned. In addition to the name fossil, brachiopod species include *Nisalarinia nisalensis*, *Qinquenella glabra, Glabrichonetina kuwaensis, Megasteges nepalensis, Anidanthus fusiformis, Betaneospirifer ravaniformis, Pondospirifer magnificus, Fusispirifer jini, Pteroplecta laminatus, Cleiothyridellina accoliformis*, and a number of Mollusca, including species of *Atomodesma* such as *exaratum* and *multifurcata*, *Dolponella sulcata*, and *Collabrina lunulata*.

The zone is meagrely represented in south Tibet by faunas of the upper Qubuerga Formation in "beds" 16-22 at Qubu, with *Biplatyconcha grandis* and *Fusispirifer jini*, as well as *Costatumulus policiformis* that appears to have a longer range in this section than in Nepal, and *Transversaria marcouiformis* which is restricted to the zone in Dolpo, Nepal, but ranges up from the equivalents of the *Lamnimargus himalayensis* Zone at Qubu in "beds" 1-12. Shen et al. (2003a) judged that the lower Qubuerga Formation matched part of the *Biplatyconcha grandis* Zone, and Senja Formation of Nepal. But to some extent this was based on misidentified species and genera. As shown in this study, *Echinalosia zaga* was mistaken for *E. ?magnispina, Retimarginifera sheni* for *R. xizangensis,* and *Wyatkina tibetensis* for *Megasteges nepalensis.* Waterhouse & Chen (in prep.) add to the list of generic and specific identifications that need to be adjusted. They show that no keys to the *grandis* Zone are present in Qubuerga "beds" 1-12. The result of present work is to sharpen faunal distinctions, and help resolve questions over correlation, so that the two closely studied sections in Tibet may be integrated with some 40 sections in Dolpo, about 20 in Manang, and more than 20 or so in the Salt Range and in northwest India.

Of particular interest in the Qubu section of south Tibet is the development of two collections more or less between the *himalayensis* and *grandis* Zones, from "beds" 13 and 15. These have a high diversity of brachiopods, including unique species, and include *Costiferina indica* and *Biplatyconcha* to suggest zonal overlap or reworking. Normal procedure is to treat the incoming as marking a significant biological event, and start of the zone. This is reinforced by *Streptorhynchus plata*, otherwise restricted to the *Biplatyconcha grandis* Zone of Dolpo, and *Fusispirifer jini*, found elsewhere only in the same zone in Dolpo and Manang. *Taeniothaerus qubuensis* Shen et al. (2003a), which was shown as persisting through both zones at Qubu, involves at least two different genera - one having buttress plates, the other belonging to *Taeniothaerus. Derbyia grandis* also appears to range through, but seems to be represented in the younger zone by a fragment that is arguably indeterminate. Various other species belong to long-ranging scattered forms, poorly known as to morphologic and temporal limits, including *"Tomiopsis"* (now *Ambikella*) *himalayanicus, Himathyris gerardi, Cleiothyridina*, *Hoskingia* spp. , and so-called *Megasteges geniculatus*, identified in south Tibet without the dorsal valve from younger localities, and therefore not necessarily identical. Possibly the faunas from "beds" 13-15 are equivalent to either the *Pyramus silicius* or *Lazarevonia arcuata* Zone in Nepal and involve a different biofacies. The present understanding, thanks to the careful collecting and fine illustrations of Qubu fossils by Shen et al. (2003a), marks a substantial advance for Himalayan correlation, and the problems raised here may be resolved by further detailed study, and also by search for further sections and fossil localities.

The age is deemed to be Changhsingian, presumably middle, but without precise ties to the world stratotype.

***Retimarginifera xizangensis* Zone**

The best exemplar for this zone is in the Selong Group of the Selong Xishan section of south Tibet, monographed for brachiopods by Shen et al. (2000, 2001). The zone is comparatively distinct. Typical and restricted species include *Retimarginifera xizangensis* Shen et al., *Megasteges densipustulata* (Shen et al.), *Lazarevonia inflata* (Shen et al.), *Chonetella semicostata* Waterhouse, *Auritusinia tazawai* (Shen et al.), *Goleomixa? archboldi* Waterhouse, *Betaneospirifer shii* Waterhouse, *Spiriferella grunti* Waterhouse, *S. nepalensis* Legrand-Blain, *Nakimusiella selongensis* Shen et al., and *Gruntea grunti* (Shi & Shen). These species are described by Shen et al. (2000, 2001), herein, and in Waterhouse (2002d). Species identified previously with *Marginalosia, Neospirifer kubeiensis, Spiriferella rajah, S. qubuensis* and others have had to be revised, as herein. Much the same faunas are found in the Marsyangdi Formation of Nepal, from many sections, and collected under tight control from 6 members. They will be mostly described by Waterhouse & Chen in prep., and include *Retimarginifera xizangensis, Betaneospirifer shii, Spiriferella grunti, S. nepalensis, Gruntea grunti* and a number of other species.

In the Salt Range, a white sand recognized by Waagen (1891) and named Khisor Member (Waterhouse 2002c, p. 182) includes possible *Chonetella semicostata* Waterhouse, *Linoproductus periovalis* Waterhouse and *Derbyia?*

postplicatella Waterhouse*.* There are few direct ties with the Himalayan faunas, and whereas *Megasteges* and *Linoproductus* suggest ties with the *Biplatyconcha grandis* Zone, a number of the genera are nowhere known in the Senja Formation or correlates, and probably indicate warmer waters and higher diversities of faunas, which is to be expected for correlates of the *xizangensis* Zone. Such a correlation is supported by the presence of *Chonetella semicostata* and *Callispirina.*

***Coledium selongensis* fauna**

At the top of the Selong Xishan section in south Tibet, Shen & Jin (1999) recognized three beds immediately below the basal Triassic. The middle one, the "Caliche Bed", yielded a strong negative excursion of $\delta^{13}C$, suggesting a position close to the Permian-Triassic boundary. The underlying "Coral Bed", characterized by an abundance of tabulate and solitary rugose corals, contains fossils *"Krotovia arcuata"*, Stenoscisma timorense, Cleiothyridina deroyssii*, Spiriferella rajah** and *S. nepalensis**, every species probably misidentified. Large *Stenoscisma gigantea* were also noted in the text (p. 552). Asterisked species were considered to extend into the overlying "Waagenites Bed", which was treated by Jin et al. (1996) as the basal unit of the Kangshare Formation, immediately below the basal Triassic ammonoid *Otoceras* and disconformably above the "Caliche Bed" at the top of the Selong Formation. Additional species at this level, immediately below the *Otoceras* band, include *Tethyochonetes liao* Chen et al., *Coledium selongensis* (Shen & Jin), *"Martinia" attenuatelloides* Shen & Jin, and *Bullarina* cf*. rostrata* Jin & Sun. The species *attenuatelloides* is particularly distinctive, and appears to be crurithyrid. Wang et al. (1989) reported a different assemblage from the same bed, involving elements of the *Waagenites barusiensis- Paracrurithyris pigmaea* Assemblage of the Changhsing Formation in south China, accompanied by Changhsingian conodonts such as *Neogondolella changxingensis*. There have been various articles on the conodonts from this level (Wang et al. 1993, 1996). As well, brachiopods *Araxathyris* and *Vediproductus tingriensis* were figured, but Shen & Jin (1999, p. 552) doubted the occurrences and questioned the identifications, without fully detailing the nature of the fossils or reasons for revision. They noted that the specimens were all small, but moderately close otherwise to some of the species from the underlying "Coral Bed".

There is no known equivalent in Nepal. Fossil fragments and specimens from the uppermost Permian of Kashmir may be correlative, but no fossil species are shared.

In the Salt Range of Pakistan, a small fauna from the Kathwai Member includes *Crurithyris? extima* Grant*, Martinia acutomarginiformis* Waterhouse*,* *Spinomarginifera kathwaiensis* Waterhouse and *Orthotetina* cf. *arakeljani* Sokolskaya (Grant 1970, Waterhouse 1983b). The fauna suggests a possible correlate of the Marsyangdi Formation of Nepal (which includes *Spinomarginifera*), or possibly a match with the Coral band at the top of the Selong Group in the Selong Xishan section, but there is no firm link. Revealingly, conodonts indicate mixing or severe condensation of faunas, with Wardlaw & Mei (1999) reporting *Clarkeina meishanensis* at the base, also found in the "boundary beds" below the Triassic at Meishan, China, followed by *Hindeodus parvus*, widespread key for basal Triassic, often with *Otoceras woodwardi* in the Himalaya, and *Isarcicella isarcica*, found with *Ophiceras* widely. *Ophiceras tibeticum* is also found in the Kathwai Member (Waterhouse 1994), as revised from the study of Schindewolf (1954). Thus the brachiopods possibly represent very latest Permian, conceivably slightly reworked, and most likely correlative with the "Coral" and "Waagenites" levels of Selong Xishan section.

Part 2 - Systematic Paleontology

FOSSIL LOCALITIES

Fossil localities are listed by code number, and are described in the text. Localities of various institutions have used the prefix L with a serial number.

REPOSITORIES

A few critical new species are described in subsequent chapters from Manang, and the bulk of Permian macro-invertebrate brachiopods and molluscs from the Galte, Kyobra, Ngawal, Puchenpra and Marsyangdi stratigraphic units in the Manang district will be published in Waterhouse & Chen (in prep.) The fossils are housed at the Canterbury Museum, Christchurch.

Repositories for other specimens mentioned in the text are indicated by prefix letters: AM - Australian Museum, Sydney, B - Museum of Natural History, London, BR - Institute of Geological and Nuclear Science, Lower Hutt, CASG - Centre of Advanced Studies in Geology, Chandigarh, CPC - Geoscience Australia, Canberra, FMo - Canterbury Museum, Christchurch, GSC - Geological Survey of Canada, Calgary, GSI- Geological Survey of India, Calcutta, GST - Geological Survey of Tasmania, Hobart, GSWA - Geological Survey of Western Australia, Perth, IGAS - Institute of Geology, Academy of Science, Beijing, IPI - Facultad de Ciencias Naturales e Instituto Miguel Lillo, San Miguel de Tucuman, MPUM - Museo di Paleontologia del Dipartimento di Scienze della Terra dell'Universita degli Studi di Milano, MUGD - Department of Geology, University of Melbourne, NMV - National Museum of Victoria, Melbourne, SME - Sedgwick Museum, Cambridge, TBR - Geological Survey Division, Department of Mineral Resources, Bangkok, TM - Tasmanian Museum, Hobart, UQ - University of Queensland collections, Queensland Museum, Brisbane, USNM - United States National Museum, Smithsonian Institution, Washington DC. Fossils are often allocated a number, with an additional prefix F. Other repositories are mentioned in the text.

ABBREVIATIONS

Abbreviations used are W = width, L = length, H = height, OD by original designation, SD by subsequent designation. Cited type species for genera were by original designation, unless otherwise stated.

TERMINOLOGY

In discussing distribution of taxa, reference may be made to bipolar and bitemperate. Some recent studies prefer the term “antitropical”, but this term is less precise, and fails to emphasize that the climatic belt is double, not singular. The term anti implies opposed, or opposite, whereas temperate and polar are different from, not opposite to, tropical. Bipolar also carries medical connotations, in a metaphorical sense, and should not be allowed to exile the original and geographic sense of the word.

Some special morphological terms are outlined in the introduction to Spiriferida. Vascular impressions and subdelthyrial plate or pseudodeltidium are illustrated in Pl. 1, fig. 7-10.

SOUTH TIBET SECTIONS

Frequent reference is made to invaluable studies on measured and carefully collected sequences through the Selong Group at Selong Xishan (Shen et al. 2000, 2001) and through the Qubuerga Formation at Qubu (Shen et al. 2003a) in south Tibet. The sequences were subdivided into serially numbered beds in their studies. Some of these subdivisions, called beds, are beds as generally understood according to the International Stratigraphic Guide. Others are bands, up to 40m thick. In my view the distinction between bed and band is significant, and in the following text, the beds of Shen and colleagues are enclosed in inverted commas, to signify that they might be a true bed, or a band.

A. CARBONIFEROUS AND PERMIAN BRACHIOPODA PRODUCTIDA

SYSTEMATIC DESCRIPTIONS

Order Productida Sarytcheva & Sokoskaya, 1959
Suborder Chonetidina Muir-Wood, 1955
Superfamily **CHONETOIDEA** Bronn, 1862
Family **RUGOSOCHONETIDAE** Muir-Wood, 1962
Subfamily **RUGOSOCHONETINAE** Muir-Wood, 1962
Genus ***Nisalarinia*** n. gen.

DERIVATION: Named from Nisalgaon, Nepal village in west Dolpo.

TYPE SPECIES: *Rugaria nisalensis* Waterhouse, 1978, p. 60, here designated.

DIAGNOSIS: Small transverse shells, shallow ventral sulcus, low fold, hinge alate and at maximum width, ears moderately large, without radial ornament. Ribs of moderate strength, branching and very fine anteriorly on both valves, forming fascicles anteriorly, concentric growth lines prominent on both valves, no spine bases over ventral disc, row of ventral hinge spines. Ventral interior with teeth, muscle scars, thickened median septum posteriorly, vascular trunks present but not clearly defined, low dorsal socket ridges, dorsal median septum extends to mid-length, well formed, anderidia long and distinct.

DISCUSSION: Unlike *Rugaria* Cooper & Grant or *Sulcirugaria* Waterhouse, this genus has long anderidia in the dorsal valve (Waterhouse 1978, pl. 7, fig. 11, 13), not visible in immature specimens (Waterhouse 1978, pl. 7, fig. 12). Although the ribs branch somewhat as in these genera, the branching gives rise to more and finer ribs over the anterior shell, with the branches remaining associated in fascicles. Ears remain smooth, apart from growth-lines, whereas ears of *Rugaria* and *Sulcirugaria* are costate. The ventral septum is thicker posteriorly in the new genus. The presence of comparatively smooth ears suggests an approach to *Waterhousiella* Archbold, 1983, type species *Waagenites speciosus* Waterhouse & Piyasin, 1970 from Thailand. Ribs are subject to much less splitting in this form, the cardinal extremities are more rounded, and the inflation greater. Internally the ventral median septum of *Waterhousiella* is thinner posteriorly, and the anderidia much less developed - indeed no septa are visible in some specimens described by Waterhouse & Piyasin (1970, pl. 19, fig. 5) and several figures and the text show that the septa may be no more than raised edges of the inner adductor scars, or what may be termed interadductorial ridges, whereas anderidia in the present form extend far forward from the adductors. Unlike *Rugaria*, as noted by Waterhouse & Piyasin (1970), body spines are lacking from *Waterhousiella*.

Neochonetes (Zhongyingia) zhongyinensis Liao - see Shen & Archbold (2002, p. 333) - from Changhsingian beds of Guizhou Province, south China, may show similar costation, but is more alate and lacks anderidia.

Tethyochonetes Chen et al. (2000), type species *Waagenites soochowensis quadrata* Zhan, 1979 and embracing several Late Permian species especially from China, has fewer bifurcating costae and somewhat shallower ventral sulcus, and 2-4 hinge spines and roughly comparable inflation. The dorsal exterior is scarcely mentioned in the descriptions of the genus. Internally the ventral septum is much thinner posteriorly, and what were termed lateral septa are thick but short, and brachial ridges thick and strongly defined.

Schistochonetes Roberts, 1971, type species *S. abruptus* Roberts from Visean of Australia, shows ventral ribbing somewhat similar to that of *Nisalarinia*, and has stronger vascular trunks and weaker anderidia, with other differences.

Sulcirugaria tibetensis Shen et al. (2003a, pl. 1, fig. 17-22) is possibly allied to *Nisalarinia*, being close in shape, with well developed sulcus and smooth ears, but shows only a hint of anterior costal splitting. No dorsal valve was described, nor the interior of the ventral valve, so that the species cannot be allocated precisely to any genus. The lack of costae from the ears distinguishes it from *Sulcirugaria*. *Waterhousiella* Archbold offers one alternative, possibly a preferable one, because its ribs are mostly simple, much as in *tibetensis*.

Nisalarinia nisalensis (Waterhouse, 1978)

1978 *Rugaria nisalensis* Waterhouse, p. 60, pl. 7, fig. 1-13.
HOLOTYPE: UQF 68841 figured by Waterhouse (1978, pl. 7, fig. 8) from Nisal Member, west Dolpo, OD.
DISCUSSION: Possibly allied material was recorded from the Nambdo Member of west Dolpo by Waterhouse (1978, p. 115, pl. 22, fig. 10), but the figured specimen cannot be securely matched with *nisalensis*, although it appears close. Shen, Archbold & Shi (2001, p. 279) retained the species *nisalensis* as *Rugaria*, but *Rugaria* lacks anderidia and has body spines, and shows various other distinctions. They recorded the species as coming from the Nanguang (sic = Nangung) Formation, but it definitely comes from the Senja Formation, Nisal Member, and belongs to the *Biplatyconcha grandis* Zone, not the *Lamnimargus himalayensis* Zone.

Subfamily **PLICOCHONETINAE** Sokolskaya, 1960

Tribe **PLICOCHONETINI** Sokolskaya, 1960

[nom. transl. hic ex Plicochonetinae Sokolskaya, 1960, p. 222]
NAME GENUS: *Plicochonetes* Paeckelmann, 1930.
DIAGNOSIS: Strongly concavo-convex shells with sturdy costae increasing by branching and some by intercalation, ventral sulcus and dorsal fold absent, ventral median septum, weakly defined vascular trunks, inner socket ridges, well formed median septum. There are no extended anderidia between the dorsal anterior and posterior adductor impressions, but interadductorial ridges lie between the adductor scars.
DISCUSSION: Racheboeuf (2000, p. 411) stressed the lack of sulcus for Plicochonetinae, and *Plicochonetes* lacks sulcus and branching costae and has short inner socket ridges. *Hemichonetes* is like *Plicochonetes* in lacking sulcus and branching costae, but has well developed inner socket ridges.

Tribe **RUGARIINI** n. tribe

NAME GENUS: *Rugaria* Cooper & Grant, 1969, p. 4.
DIAGNOSIS: Shells distinguished by presence of ventral sulcus and low dorsal fold, otherwise close to Plicochonetini. Short interadductorial ridges.
DISCUSSION: The genera *Rugaria, Sulcirugaria, Waterhousiella* and *Waagenites* are particularly close to each other in the strength of their costae and presence to varying degree of sulcus and fold. Plicochonetini are close but lack sulcus and fold and show more simple costae.

Fanichonetes Xu & Grant, 1994, from Late Permian of China is close in its branching ribs, and misrepresentations of its morphology in Xu & Grant have been corrected by Racheboeuf (2000, p. 405). The critical dorsal interior has not been described and no adequate comparison was made by Xu & Grant (1994) with *Rugaria* or *Sulcirugaria*. Unlike *Rugaria*, external body spines are not developed. The validity of the genus is precarious, but hinge spines appear to be more numerous than in *Rugaria* or *Sulcirugaria*, providing a possible means of distinction.

Fusichonetes Liao, 1981 is based on a poorly known species from the Late Permian of China, *Plicochonetes nayongensis* Liao, 1980, p. 256, and has simple ribs and shallow sulcus. Lack of information about the ventral and dorsal interior prevents certainty over subfamilial relationships.

The genus *Waterhousiella* Archbold, 1983, type species *Waagenites speciosus* Waterhouse & Piyasin, 1970 from Guadalupian Rat Buri Limestone of Peninsular Thailand, was classed in Rugosochonetinae by Racheboeuf (2000, p. 407), but the genus looks close in overall aspect to *Rugaria* in shape and costation, apart from having less branching costae, shallower sulcus, lower fold, and lack of body spines. Unlike members of Rugosochonetinae, there are no well developed long anderidia, and the dorsal septa stressed by Archbold (1983) are short low interadductorial ridges defining the posterior edge of the posterior adductor scars and not extending beyond the muscle field: they may be termed lateral septa, or truncated anderidia. The lack of long anderidia in *Rugaria, Sulcirugaria* and *Waterhousiella* means that the proposal by Shen et al. (2003a, p. 63) that they should be referred to Rugosochonetinae rather than Plicochonetinae must be rejected. The nature of septa which subdivide the muscle field is here deemed significant: they are long in members of Rugosochonetinae and short or subdued in Plicochonetinae. *Waagenites* Paeckelmann, 1930, type species *Chonetes grandicostus* Waagen, 1884 from Late Permian of the Salt Range, Pakistan, is distinguished by its strong and rarely branching ribs and deep sulcus. The interior as exemplified for *Waagenites yunnanensis* Fang, 1983, also figured by Chen et al. (2000, text-fig. 3) from mid-Permian of Xiaoxinzai, China, is essentially like that of *Waterhousiella.* There is a well developed ventral median septum, heavy lateral papillation, dorsal valve with well developed inner socket ridges, well developed median septum, and raised posterior edge to the posterior adductor scars, not extended beyond the muscle field. This suggests an alliance with *Rugaria* and allies, rather than with Rugosochonetinae.

Tethyochonetes Chen et al. (2000) is moderately close. What were termed lateral septa were described as short and strong, apparently like interadductorial ridges. The sulcus is shallow or absent, so that its position is ambiguous, close to both *Plicochonetes* and *Rugaria,* but radials are unusually fine.

Prorugaria Waterhouse, 1982b is a Carboniferous genus, so far known from Thailand, with few branching costae, shallow narrow sulcus and short median septa in each valve, and radially arranged endospines suggestive of accessory septa-like ridges or possible anderidia. It thus differs internally from *Rugaria*, yet externally looks close to this genus, apart from having few branching costae, and may be classed in Rugosochonetinae.

GENERA: *Rugaria* Cooper & Grant, ?*Fanichonetes* Xu & Grant, ?*Fusichonetes* Liao, *Sulcirugaria* Waterhouse, *Waagenites* Paeckelmann, *Waterhousiella* Archbold.

Genus ***Sulcirugaria*** Waterhouse, 1983a

TYPE SPECIES: *Sulcirugaria subquadrata* Waterhouse, 1983a, p. 112.

DIAGNOSIS: Shells with ventral sulcus and dorsal fold, branching well formed costae over corpus and ears, no trace of spines or hollow spine-bases over body of shell, ventral and dorsal median septa long, inner socket ridges.

DISCUSSION: This genus comes very close in many respects to *Rugaria* Cooper & Grant, 1969, 1975 as represented by two species in the late Early Permian of United States. Compared with *Sulcirugaria*, species of *Rugaria* show a shallower sulcus and lower fold commencing further from the hinge, and more branching complex costae, costae fine or absent over outer ears, and scattered rather than concentrated pustules in front of the dorsal median septum. Apart from these differences, which could be interpreted as signifying specific differences relating to an Early Permian suite of very small forms in United States, as compared with larger Late Permian species in Asia, *R. hessensis* has well formed low hollow spine-bases over the crests of costae, a significant difference, because none are developed in the well preserved material of *Sulcirugaria*. The commissure of the type species of *Rugaria, R. hessensis* (King), is unfolded to faintly uniplicate according to Cooper & Grant (1975, p. 1296), and is uniplicate in *Sulcirugaria.* [These commissure terms are used sensu Thomson 1927, not Williams et al. 1997. The definitions by Williams et al. (1997) are more logical, but consistent usage is highly desirable, and the Thomson terms are well established, as in Williams & Rowell 1965, and appear to have been followed in parts of the new brachiopod Treatise volumes].

Neochonetes (*Huangichonetes*) Shen & Archbold (2002, p. 337), type species *Chonetes substrophomenoides* Huang, 1932 from Changhsingian of south China, is alate with moderately defined sulcus, branching costae and ribbed ears. It is small in size, and has as few as 4 hinge spines, like *Sulcirugaria* (cf. Waterhouse 1983a, pl. 1, fig. 15). There is no clearly developed dorsal median septum, perhaps implying an early growth stage. Short “lateral” septa are recorded. Perhaps the chief difference from *Sulcirugaria* lies in its small size, but the validity remains open to question, because stunted size need not be critical for generic distinction.

Sulcirugaria transversa Waterhouse, 1983a
Pl. 2, fig. 1, Text-fig. 20

1983a *Sulcirugaria transversa* Waterhouse, p. 114, pl. 1, fig. 3-9.
1989a *S. transversa*. Waterhouse, text-fig. 2e.
HOLOTYPE: UQF 73587, figured by Waterhouse (1983a, pl. 1, fig. 3) and herein as Text-fig. 20, from Pija Member, Manang, OD.
DISCUSSION: The species is refigured. Racheboeuf (2000, p. 413) mistakenly cited it as type species of *Sulcirugaria*. He illustrated *Sulcirugaria subquadrata*, miscalling it *S. transversa* (Racheboeuf 2000, text-fig. 270.4a-c). Shen et al. (2003a, p. 64, pl. 1, fig. 17-22) added a species *S. tibetensis* Shen et al. from the Qubuerga Formation of south Tibet, without describing the dorsal valve, ventral interior, or hinge spine detail. The generic position remains uncertain, because the ears seem to be non-costate. A specimen figured by Zhang & Jin (1976, pl. 1, fig. 7) as *Waagenites* cf. *barusiensis* (Davidson) was included in synonymy of *tibetensis* by Shen et al. (2003a), but has costate ears.

Text-fig. 20. *Sulcirugaria transversa* Waterhouse x 4, specimen UQF 73587, holotype, with valves splayed open, from Pija Member, Manang district. Also figured by Waterhouse (1983a, pl. 1, fig. 3).

Sulcirugaria strophomenoides (Waagen, 1884)

1884 *Chonetes strophomenoides* Waagen, p. 628, pl. 58, fig. 10a-f.
HOLOTYPE: Sole specimen figured by Waagen (1884), from the Middle Productus Limestone (= Wargal Formation), Salt Range, Pakistan, by monotypy.
DISCUSSION: Shen, Archbold & Shi (2001, p. 277) and Shen & Archbold (2002, p. 334) referred the species *strophomenoides* to *Neochonetes (Sommeriella)* Archbold, but Waagen’s species has moderately coarse and branching costae and long and wide well formed costate ears, unlike either *Neochonetes* or especially *Sommeriella*. Shen, Archbold & Shi (2001) and Shen & Archbold (2002) synonymized *Neochonetes convexa* Liao, 1980 with Waagen’s species,

but the two forms are not conspecific or congeneric. Liao's species has a shallow sulcus, many costae, less rectangular smaller ears and smaller size. Possibly Waagen's species is allied to *Nisalarinia*, but overall the shape, sulcus, and strength, disposition and splitting of the costae suggest *Sulcirugaria. Waterhousiella* Archbold is perhaps an alternative genus for *strophomenoides*, but the type species *speciosus* Waterhouse & Piyasin has fewer branching costae and smooth dorsal ears. *Neochonetes* (*Nongtaia)* Archbold, 1999 from Khao Nong Ta On, Thailand, below the Rat Buri Limestone, has branching costae, and is closer internally to *Neochonetes* Muir-Wood, 1962.

From "Carboniferous Limestone of Tibet" *Chonetes hardrensis* var. *thibetensis* Davidson (1866, pl. 1, fig. 7 - B5952) is a transverse sulcate shell with some 14 costae, much as in the species *grandicostus* (Waagen), the type species of *Waagenites*. The costae do not branch, and although some aspects suggest *Tethyochonetes* Chen et al., its sulcus is better defined, and costae are fewer and coarser than in species figured by Chen et al. (2000). The interior and the dorsal valve are not known, preventing full assessment, but placement with *Waagenites* seems likely.

Suborder Productidina Waagen, 1883

Superfamily **PRODUCTELLOIDEA** Schuchert, 1929

[nom. transl. Waterhouse 1978, p. 20 ex Productellidae Schuchert in Schuchert & Le Vene, 1929, p. 17. See Waterhouse 2002d, p. 6].

Family **PRODUCTINIDAE** Muir-Wood & Cooper, 1960

Subfamily **CHONETELLINAE** Licharew, 1960

Genus ***Chonetella*** Waagen, 1884

Chonetella semicostata n. sp.

?1970 *Chonetella* sp. Grant, p. 136, pl. 1, fig. 20, a, b.

1976 *Chonetella nasuta* not Waagen Zhang & Jin, p. 172, pl. 4, fig. 4, 5.

1979 *C. nasuta.* Jin et al. pl. 24, fig. 6.

1985 *C. nasuta.* Jin, pl. 8, fig. 7.

1997 *C. nasuta.* Shi & Shen, p. 41, text-fig. 3C.

2000 *C. nasuta.* Shen et al., p. 739, text-fig. 9.23-28, table 6.

DERIVATION: semi - part, costa - rib, Lat.

HOLOTYPE: NMV 148888 figured by Shen et al. (2000, text-fig. 9.25, 26), from Selong Group, south Tibet, here designated.

DIAGNOSIS: Moderately large for genus, transverse with nasute anterior and ears of moderate size, ventral costae cover anterior shell, posterior shell smooth.

DESCRIPTION AND RESEMBLANCES: This species was recorded from "beds" 3, 4, 8, 9, 10, 11 of the Selong Group of the Selong Xishan section of south

Tibet. It is distinguished from *Chonetella nasuta* Waagen (1884, pl. 81, fig. 3-8) of the Jabbi beds in the Chhidru Formation (Kufri Member) by its smooth posterior ventral valve, in contrast to the ribbing on *nasuta*, which commences at the ventral umbo. Characteristic specimens of *Chonetella nasuta* include those shells figured by Waagen (1884), Muir-Wood & Cooper (1960, pl. 69, fig. 1-7) and Grant (1976, pl. 42, fig. 1-17) from the Salt Range, Pakistan, and from the *Lamnimargus himalayensis* Zone by Waterhouse & Gupta (1979b, pl. 1, fig. 7). Small non-nasute ventral valves from the Basleo faunas of Timor (Hamlet 1928, pl. 3, fig. 5-8, Rothpletz 1892, pl. 10 fig. 12) are covered by ribs and may belong to *nasuta*, because the lack of nasute anterior is possibly due to small size. Material from Tibet figured by Jin & Sun (1981, pl. 1, fig. 18, 19) seems to have posterior ribs and so might belong to *C. nasuta*. *Chonetella nasuta* is distinctly older than *C. semicostata*, and is of Wuchiapingian rather than Changhsingian age.

Grant (1970) figured very small *Chonetella* without costae from the Khisor Member, or white sand band, of the Salt Range. The material could be immature specimens of *C. semicostata*. A different species ascribed to *C. nasuta* by Renz (1940, pl. 2, fig. 7a, b) from Shaksgam valley of the Karakorum Range lacks ribs entirely, and has nasute anterior.

From the Maubisse Formation of west Timor, specimens figured as *Chonetella* by Archbold & Bird (1989, text-fig. 3A-B) are not congeneric, having low broad ribs that branch anteriorly, with small ears and no nasute anterior. Although figures suggest small spines arising from the crests of ribs, the text stated that no spines were present. *Parachonetella* Liao, 1980 has only anterior ribs, but these are irregular and so not like those of the present species.

Superfamily **MARGINIFEROIDEA** Stehli, 1954

[nom. transl. Waterhouse 2002d, p. 13 ex Marginiferidae Stehli, 1954, p. 321].

Family **PAUCISPINIFERIDAE** Muir-Wood & Cooper, 1960

[nom. transl. Waterhouse 2002d, p. 14 ex Paucispiriferinae Muir-Wood & Cooper, 1960, p. 319].

Subfamily **PAUCISPINIFERINAE** Muir-Wood & Cooper, 1960

Tribe **PAUCISPINIFERINI** Muir-Wood & Cooper, 1960

[nom. transl. Brunton et al. 1995, p. 927 ex Paucispiriferinae Muir-Wood & Cooper, 1960, p. 319].

Genus **Retimarginifera** Waterhouse, 1970a

Three Permian genera within Marginiferoidea share reticulate ornament of radial ribs crossing concentric ribs, and sometimes may be confused with each other.

Transennatia Waterhouse has very fine ribs which form a densely reticulate pattern, and lacks the strong ventral strut spines of the other two genera. *Lamnimargus* and *Retimarginifera* in particular have been confused, and it has been asserted that *Lamnimargus* does not always show the mutiple dorsal trails that were supposed to characterize the genus. That remains open for further study, based on specimens which first have to be verified as belonging to *himalayensis*, and not *Retimarginifera*. Externally, the radial and concentric ribbing of *Lamnimargus* are much finer and more numerous than in *Retimarginifera*, but are not as dense as in *Transennatia*.

Retimarginifera sheni n. sp.

cf. 1966 *Marginifera* sp. Waterhouse, p. 17, pl. 3, fig. 3, 4, not 5.
cf. 1978 *Transennatia* sp. Waterhouse, p. 118, pl. 22, fig. 13, 14.
2003a *Retimarginifera xizangensis* not Shen et al. Shen et al., p. 77, pl. 8, fig. 11-14, pl. 9, fig. 1-6, text-fig. 10, 11.

DERIVATION: Named for Shen Shuzhong.

HOLOTYPE: NMV P305961 figured by Shen et al. (2003a, pl. 9, fig. 2-4) from "bed" 9, lower Qubuerga Formation, south Tibet, here designated.

DIAGNOSIS: Moderately transverse shells with generally well defined sulcus and long subgeniculate trail.

DESCRIPTION: Shell of average size for genus, transversely subelliptical in outline with strongly convex ventral valve, concave dorsal valve with long trail, ears large and at maximum width of shell. Ventral umbo wide and low, sulcus commences at umbo, moderately deep and U or V-shaped in section on trail. Costae coarse, missing from ears, 4 in 5mm at mid-length, may bifurcate and weakly converge into trail anteriorly, crossed over visceral disc by some 4-7 prominent concentric rugae, missing or fine and imperceptible over umbonal region, and weakly developed on ears. Dorsal disc with similar ornament, and costae cover the trail. Ventral spines poorly preserved, with a strut pair visible on trail, no dorsal spines. Both valves carry marginal ridge, without mutiple trails. The species has been described and figured as shown in the preceeding synonymy. It will be further discussed by Waterhouse & Chen (in prep.).

RESEMBLANCES: This species is very close to *Retimarginifera xizangensis* Shen et al. (2001, text-fig. 10.1-18, 19, 20) from the Selong Group of the Selong-Xishan section in southern Tibet. The two are especially close in ribbed ornament, although concentric ribs tend to be more pronounced over the mid-disc in *xizangensis*. Further differences between the two involve the visceral disc, which is wider in the present species, with deeper sulcus, and shorter trail. Thus *xizangensis* tends to be more elongate, and includes specimens without sulcus or only very shallow sulcus, and specimens have a longer trail. As well the strut spines tend to be more prominent. However *xizangensis* suites do include transverse and also deeply sulcate specimens.

STRATIGRAPHY: Dolpo specimens from Nepal come from F108 in the upper beds of the Senja Formation (Waterhouse 1966), and from the Luri Member in the Senja Formation (Waterhouse 1978), in the *Biplatyconcha grandis* Zone. In south Tibet material comes from “beds” 6-9 in the lower Qubuerga Formation (Shen et al. 2003a), equivalent to the *Lamnimargus himalayensis* Zone.

Superfamily **PRODUCTOIDEA** Gray, 1840

Family **PRODUCTIDAE** Gray, 1840

Subfamily **PRODUCTINAE** Gray, 1840

Tribe **RETARIINI** Muir-Wood & Cooper, 1960

Genus ***Retaria*** Muir-Wood & Cooper, 1960

TYPE SPECIES: *Retaria umbonata* Muir-Wood & Cooper, 1960, p. 230.

DIAGNOSIS: Transverse shells with wide hinge and large ears, costae and spines on both valves, distinguished by scattered often paired strut spines, generally sited posterior laterally and anteriorly near middle of ventral valve. Umbonal slope row and row of spines near hinge. Dorsal spines fine, erect. Heavy marginal ridges and other features as in *Kutorginella* Ivanova.

DISCUSSION: The genera *Retaria* and *Kutorginella* were regarded as allied to Marginiferidae by Muir-Wood & Cooper (1960), Muir-Wood (1965) and Cooper & Grant (1975, p. 1023), until relationships to Productidae were clarified by Sarytcheva (1971), Sarytcheva & Waterhouse (1972), Shi & Waterhouse (1996, p. 82), Brunton et al. (1995, 2000) and Waterhouse (2002d). *Retaria* has been synonymized with *Kutorginella* Ivanova, 1951 (eg. Cooper & Grant 1975, p. 1023, Brunton et al. 2000, p. 472). The two are close in many respects, but Waterhouse (2002d) proposed to refer to *Retaria* the cluster of species so far known only in western United States, in the Cathedral Mountain and especially Road Canyon Formations, including *Retaria umbonata* Muir-Wood & Cooper, *R. robusta* (Cooper & Grant) and *R. sullivanensis* (King). They are characterized by the presence of prominent thick and long ventral strut spines, which are specialized unusually large halteroid spines near the posterior lateral margins and anteriorly on the trail near the mid-line. The spines are not clearly illustrated or described by Muir-Wood & Cooper (1960), but are well shown by Cooper & Grant (1975, pl. 343, fig. 18-33). Development of these spines is a little variable but they are few, slightly variable in position, and differ in each species of *Retaria*. *Kutorginella*, which has been extensively illustrated, and is represented in personal collections by topotype material from the Moscow Basin (Kasimovian), does not show such spines, and even though the spines are broken short, the width and size of their bases shows that anterior and lateral spines were not unduely prominent , even though Grant (1976) suggested otherwise.

Genus ***Calliomarginatia*** Jin, 1976

TYPE SPECIES: *Calliomarginatia himalayensis* Jin, 1976, p. 181.

DIAGNOSIS: Medium-sized shells with costae and posterior concentric wrinkles, no nasute trail, ears may be wide. Ventral spines in a row close to hinge and another row along posterior umbonal slopes, scattered body spines; no strut spines or dorsal spines. High marginal ridge developed in each valve around visceral disc, internal pustules dense.

DISCUSSION: This genus, figured by Zhang & Jin (1976, pl. 8, fig. 1-18, text-fig. 5), was synonymized with *Kutorginella* Ivanova, 1951, type species *K. mosquensis* Ivanova, 1951, by Brunton et al. (2000). In many details, the two are close, but *mosquensis* has dorsal spines, whereas such are missing from the dorsal valve of *Calliomarginatia*, at least as far as described and figured. Brunton et al. (2000, p. 472) regarded the development of dorsal spines as a variable affair, but the presence or absence constitutes an objective feature, and was not found to be variable in substantial populations of *Kutorginella* in Canada, for example (Sarytcheva & Waterhouse, 1972; Shi & Waterhouse 1996, p. 83), although admittedly dorsal spines are delicate, and require good conditions for preservation. Dorsal valves for the type species of *Kutorginella* have received less attention, largely due to the mode of preservation through which the dorsal valve is concealed by matrix that, although not particularly hard, is not easy to remove.

The type species of *Calliomarginatia, C. himalayensis*, also differs from *Kutorginella* in other respects. The visceral disc is comparatively less transverse than *Kutorginella*, and the diductor scars are deeply impressed. The spines over the anterior ventral valve are not clearly displayed, except in Zhang & Jin (1976, pl. 8, fig. 18), on which some spines of moderate strength are visible, close to those of *Kutorginella*. There appears to be a hinge row, and another row of spines over the umbonal slopes, as well as a few additional ear spines.

Kutorginella uddeni Cooper & Grant (1975, pl. 343, fig. 1-17) from the Gaptank and Neal Ranch Formations of Texas is more transverse, but otherwise moderately close externally. Lacking dorsal spines according to Cooper & Grant, and evidently lacking strut spines, it was made type species of a new genus *Aspinosella* Waterhouse, 1982b, which now appears to be a synonym of *Calliomarginatia*. Ventral spines are possibly close to those of *Calliomarginatia*. Internal details are not revealed.

An upper Carboniferous species from Huai Bun Nak, northeast Thailand, was assigned to *Aspinosella*, as *A. sinauris* Waterhouse, 1982b, p. 48, text-fig. 5. The Thai species not only lacks dorsal spines, but has only very fine and few spines over the anterior ventral valve, including hinge and umbonal slope rows. It lacks the dense internal pustules found in *Calliomarginatia*, has a very wide posterior hinge ridge, small dorsal adductor scars and short dorsal median septum.

OCCURRENCES IN NEPAL: Several specimens possibly related to *Calliomarginatia himalayensis* Jin were recorded from the *Lamnimargus himalayensis* Zone in the Nangung Formation of western Dolpo by Waterhouse (1978). Some poorly preserved specimens were assigned to Retariid gen. & sp. indet. (pl. 3, fig. 6), but cannot be adequately compared. An ear-baffle is illustrated as crossing the dorsal ears at higher angle than in figured *Calliomarginatia*. The dorsal valve of Dictyoclostid gen. & sp. indet. B of Waterhouse (1978, pl. 2, fig. 16) has a high posterior marginal ridge and ridge around the disc and broad posterior septum, and although more elongate in outline, is somewhat suggestive of the dorsal valve figured in Zhang & Jin (1976), with comparable ribs but better defined sulcus. Dictyoclostid gen. & sp. indet. A (Waterhouse 1978, pl. 2, fig. 18) perhaps is allied. However pustules are not dense as in the Tibetan taxon, but are large, elongate and scattered anteriorly. ?*Reticulatia* figured by Waterhouse (1978, pl. 2, fig. 19, 20) appears too transverse to be a likely ally, and also has broader ribs. None of these specimens has dorsal spines.

Genus ***Pitakpaivania*** n. gen.

DERIVATION: Named for K. Pitakpaivan.

TYPE SPECIES: *Kutorginella aprica* Grant, 1976, p. 143, here designated.

DIAGNOSIS: Distinguished from allied genera by obscure development of hinge and umbonal slope row of spines, and presence of large strut spines anteriorly, amongst very fine and medium-sized spines on ventral valve. Radial and concentric ornament fine, fine dorsal spines.

DISCUSSION: The type species is found in the lower Guadalupian Rat Buri Formation of south Thailand, and has been well described and illustrated by Grant (1976), with holotype USNM 212481, figured by Grant (1976, pl. 38, fig. 1-6) from the island of Ko Muk. It is close in most aspects to *Kutorginella, Retaria* and allied genera, and although Grant (1976) reported that no marginal ridge or ear baffle was present in the ventral interior, one is illustrated by Grant (1976, pl. 38, fig. 14). The distinguishing features involve the ornament. Concentric and radial ribbing is comparatively fine and close-set, compared with other Retariinae. Spine detail is distinctive. There appears to be no hinge row of spines, to judge from illustrations, but Grant (1976, p. 144) did report thin short suberect spines projecting posterolaterally along the hinge. An umbonal slope row is not clearly distinguished. Much of the ventral disc is covered by anteriorly inclined somewhat recumbent spines. Anterior spines are unlike those of other genera. They are comparatively numerous, and include 4-6 strut spines, including an anterior lateral pair, somewhat suberect moderately thick spines, and scattered very fine erect spines.

Superfamily **AULOSTEGOIDEA** Muir-Wood & Cooper, 1960

[nom. transl. Waterhouse 1978, p. 21 ex Aulostegidae Muir-Wood & Cooper, 1960. See Waterhouse 2002d, pp. 27, 49].

DIAGNOSIS: Shells generally attached by spines or direct cementation, ventral interarea present, dorsal interarea small or absent, no chilidium. Trails may be simple, geniculate or elaborate, conical in shells with deep corpus, brachial ridges enclose small shields, lateral to anterior adductors.

Family **AULOSTEGIDAE** Muir-Wood & Cooper, 1960

Subfamily **TAENIOTHAERINAE** Waterhouse, 2002d

DIAGNOSIS: Large shells with erect and/or prostrate spines on both valves, or only ventral valve, not rhizoid on dorsal valve, unlike those of Aulosteginae Muir-Wood & Cooper, spine bases variable. Cardinal process not supported by buttress plates.

Genus ***Wyatkina*** Fredericks, 1931

TYPE SPECIES: *Aulosteges gigas* Netschajew, 1894, p. 155.

DIAGNOSIS: Large shells with well developed ventral interarea and elytridium, ventral spines numerous, fine and close-set, mostly erect, some sessile. Fine erect dorsal spines?

DISCUSSION: This genus is based on well preserved specimens, and is distinguished from related genera in the nature of its ventral spines, which lack prolonged or swollen bases. Although figures appear to indicate fine dorsal spines, Brunton et al. (2000, p. 591) stated that the ornament of the dorsal valve remained uncertain.

Wyatkina tibetensis n. sp.

2003a *Megasteges nepalensis* not Waterhouse Shen et al., p. 71, pl. 4, fig. 11-14, pl. 5, fig. 1-4, pl. 6, fig. 1, 2-4.

DERIVATION: Tibet, place-name.

HOLOTYPE: NMV P305922 figured by Shen et al. (2003a, pl. 5, fig. 1) from "bed" 11, Qubuerga Formation, south Tibet, here designated.

DIAGNOSIS: Elongate asymmetric shell with high flat ventral interarea, shallow sulcus in front of umbo, ventral close-set spines, fine dorsal spines.

DESCRIPTION: The species has been described by Shen et al. (2003a). One specimen measured 67mm in length, 42.5mm wide and about 30mm high at geniculation. Shells are elongate, asymmetric, with high flat ventral interarea and convex elytridium, shallow sulcus commencing in front of umbo, and ornament of fine close-set spines, mostly erect, with a few sessile. The dorsal valve has numerous dimples and very fine erect spines. Ventral muscle scars are not impressed.

RESEMBLANCES: The suite figured by Shen et al. (2003a) tends to be slightly more elongate with slightly shallower sulcus than suites of *Megasteges nepalensis* Waterhouse, but differences in shape are neither substantial nor consistent. The most significant difference lies in the nature of the ventral spines, which are largely uniform in diameter, with a few sessile in the new species (Shen et al. 2003a, pl. 4, fig. 14, pl. 6, fig. 4). By contrast, ventral spines of *nepalensis* include a mix of coarse and fine spines, virtually all erect, as shown in Waterhouse (1978, pl. 9, fig. 5). There are further possible differences, but the failure to describe the dorsal interior for *tibetensis* prevents further analysis. The difference in ornament is regarded as highly significant in itself, and the possibility that different subfamilies are involved is high. If *tibetensis* does have buttress plates, it belongs to a new genus.

The Tibetan species is close to the type species *Wyatkina gigas* (Netschajew) and the rather similar species *W. tholus* (Keyserling) from Kazanian of Russia in size and ornament and interarea, but is more irregular in shape, and dorsal spines appear to be fine but somewhat sessile.

There is some approach to west Australian shells that have been referred to *Taeniothaerus*, involving those of more symmetrical outline, with low ventral interarea, and fine ventral spines, mostly erect, and some sessile. These are described below as a separate genus.

Genus ***Miniliconcha*** n. gen.

DERIVATION: Minilya River - Carnarvon Basin, concha - shell, Lat.

TYPE SPECIES: *Taeniothaerus miniliensis* Coleman, 1957, p. 96, here designated.

DIAGNOSIS: Large shells, wide hinge with comparatively low and curved ventral interarea, low dorsal interarea, fine closely spaced spines, mostly erect or with short bases, some sessile, on ventral valve, large spines at posterior lateral extremities, some radial rugae, dorsal spines fine and erect. Dorsal interior with high double-bladed cardinal process, no buttress plates, very long median septum, dendritic adductor scars.

DISCUSSION: This genus is close to *Wyatkina* Fredericks, and distinguished principally by its lower ventral interarea and coarser posterior lateral spines. *Taeniothaerus* Whitehouse, type species *Productus subquadratus* Morris, 1845, is close internally, and distinguished by the coarser more widely spaced and subprostrate spines with slightly elongated bases. *Lipanteris* Briggs has a very low ventral interarea and well spaced spines of two orders arising from short spine ridges that become elongate anteriorly. Posterior lateral spines project out laterally without forming a convergent brush. Other genera that superficially come close are distinguished chiefly by the nature of the ventral spines, and also by the presence of buttress plates in the dorsal valve.

The spines of this genus somewhat resemble those of *Waagenoconcha* Chao and allies, though as a rule not so prolonged at the base over the ventral valve. *Fostericoncha* Waterhouse, 2002d has broader spines laterally, but less clustered postero-laterally, and is characterized by having very large ears. These and allied genera lack a moderately well formed, although low ventral interarea.

The type species of *Miniliconcha* comes from the lower Wandagee Formation of the Carnavon Basin, and *Taeniothaerus irwinensis* Coleman, 1957 from the Fossil Cliff Formation of the Irwin Basin is congeneric. Both are found in Western Australia.

Superfamily **LINOPRODUCTOIDEA** Stehli, 1954
Family **KANSUELLIDAE** Muir-Wood & Cooper, 1960
Subfamily **AURICULISPININAE** Waterhouse, 1986
Tribe **AURICULISPININI** Waterhouse, 1986
Genus ***Papiliolinus*** Waterhouse & Gupta, 1977
Plate 2, fig. 14

TYPE SPECIES: *Papiliolinus eishmakami* Waterhouse & Gupta, 1977, p. 160.

DISCUSSION: This species and genus was misrepresented by me (Waterhouse 2002d, p. 51), as far as I can tell. I have found a photograph, here printed, of what appears to be the nominated type specimen, and it is clearly a dorsal valve, not ventral valve as I had stated. But this will have to be checked, because the photograph is not labelled, and I am relying on a match with the Diener figure. There are minute spines, and a little of the ventral valve.

Suborder Strophalosiidina Waterhouse, 1975
Superfamily **STROPHALOSIOIDEA** Schuchert, 1913
Family **STROPHALOSIIDAE** Schuchert, 1913
Subfamily **STROPHALOSIINAE** Schuchert, 1913

DIAGNOSIS: No spines on dorsal valve, two orders of spine on ventral valve.

Genus ***Strophalosia*** King, 1844

TYPE SPECIES: *Strophalosia gerardi* King, 1846, p. 92, SD Muir-Wood & Cooper 1960, p. 74.

DISCUSSION: The genus and synonymy are discussed by Waterhouse (2001, p. 54).

?***Strophalosia gerardi*** King, 1844

Plate 2, fig. 2, 4

?1846 *Strophalosia gerardi* King, p. 93.

?1850 *S. gerardi*. King, p. 96, pl. 19, fig. 6, 7.

?1960 *S. gerardi*. Muir-Wood & Cooper, p. 72, pl. 9, fig. 1, 2.

?1966 *S. gerardi*. Brunton, p. 186, pl. 1, fig. 7-9. (See for full references and typology etc.).

1983a *S. gerardi*. Waterhouse, p. 118, pl. 2, fig. 1, 2.

HOLOTYPE: Specimen figured by King (1850), Muir-Wood & Cooper (1960, p. 364), and Brunton (1966, p. 188), and in the brachiopod Treatises, kept at University College, Galway.

DIAGNOSIS: Moderately large for genus with narrow hinge and moderately concave dorsal valve, ventral spines fine and close-set over umbo and coarse anteriorly.

DISCUSSION: The original material for this genus and species is believed to have come from Ladakh, western Himalaya, and its stratigraphic source and age are not known. The species is reliably represented by a specimen with valves conjoined and a dorsal valve, kept at University College, Galway. There have been numerous references to the species, virtually all to be discounted, and for many years the nature of the genus was not correctly understood, even by Muir-Wood & Cooper (1960) and Muir-Wood (1965). Judicious preparation of the dorsal valve showed that tubercles were present, but dorsal spines were lacking (Waterhouse 1964, p. 28), as indeed inferred by King (1938). Brunton (1966) concluded that dorsal spines were definitely absent.

Although extensive geological field-work over much of Ladakh during the last decades of the 20th century has failed to discover further specimens of *Strophalosia gerardi,* this may not be significant, because teams have been little concerned with detailed stratigraphy or macro-invertebrate paleontology. *Strophalosia diadema* Waterhouse in Waterhouse & Gupta (1983, pl. 1, fig. 6-9, pl. 3, fig. 2-4, see pl. 2, fig. 5-8 herein), comes from the *Lamnimargus himalayensis* Zone in the upper Shyok valley in the southern Karakorum Range, not far from Ladakh. It does not appear to be conspecific with *gerardi*, having a ventral sulcus and wider hinge, and less concave and more geniculate dorsal valve. Spines are much the same as for *gerardi* on the ventral valve, but slightly finer posteriorly. From the Lower Productus Limestone, now Amb Formation, of the Salt Range, Pakistan, *Strophalosia (Heteralosia) sublamellata* Reed (1944, pl. 6, fig. 6, 6a, pl. 7, fig. 8, 8a, 9, 9a, 9b) is closer to *gerardi*, but has wider hinge and slightly finer spines.

About a dozen specimens from three localities in the Pija Member of the Manang district in Nepal show several attributes of the species *Strophalosia gerardi*, in having hinge of comparable width, and somewhat similar ventral spines, described in detail in Waterhouse (1983a, pp. 118, 119). On the other hand the dorsal valve is slightly less concave in the Manang material, and the dorsal valve is a little less disrupted by tubercles, unlike dorsal valves of *gerardi, diadema* and *sublamellata*.

Subfamily **ECHINALOSIINAE** Waterhouse, 2002d

DIAGNOSIS: Dorsal spines of one order.

Tribe **ECHINALOSIINI** Waterhouse, 2002d

DIAGNOSIS: Genera characterized by two orders of spines on ventral valve.
DISCUSSION: The genus *Marginalosia* Waterhouse which was included by Waterhouse (2001, p. 67, 2002d, p. 41) in Echinalosiini should be transferred to Arcticalosiini Waterhouse, because the ventral valve has spines of only one order. *Marginalosia* shares a thickened dorsal valve with other members of Articalosiini.

Genus ***Echinalosia*** Waterhouse, 1967

TYPE SPECIES: *Strophalosia maxwelli* Waterhouse, 1964, p. 32.

Echinalosia magnispina Waterhouse, 1983a

Plate 2, fig. 9-13

HOLOTYPE: UQF 73606 figured by Waterhouse (1983a, pl. 2. fig. 4, 5, 6, 7) and here as Pl. 2, fig. 9, 10, 12, 13, from locality UQL 4799, Pija Member, Manang, OD.
DIAGNOSIS: Moderately large shells with sturdy ventral spines and comparatively few dorsal spines. Ventral adductor platform subelongate and narrow.
DISCUSSION: Figures for this species were poorly reproduced in the original publication and so are re-illustrated - the CD version gives good figures. Closest of named species is *Echinalosia minuta* (Jin) from the Selong Formation of

south Tibet. It is smaller with large ventral spines, but otherwise poorly known.

Echinalosia zaga n. sp.

2003a *Echinalosia ?magnispina* not Waterhouse Shen et al., p. 67, pl. 2, fig. 14-23, pl. 3, fig. 1-3.

DERIVATION: Zaga, name of river near collecting point (see Shen et al. 2003a, text-fig. 2).

HOLOTYPE: NMV P305891 figured Shen et al. (2003a, pl. 2, fig. 23) from "bed" 6, Qubuerga Formation, south Tibet, here designated.

DIAGNOSIS: Moderately large shells, ventral valve highly convex, ventral spines mostly erect, somewhat erratic in distribution and opening into interior over anterior disc and posterior trail to leave internal ridges, rare spines thin and recumbent. Dorsal spines thin, erect, between dimples. Ventral adductor impressions short and posteriorly placed.

MATERIAL: Some 12 specimens recorded by Shen et al. (2003a), moderately well preserved.

DESCRIPTION: The species has been described and compared by Shen et al. (2003a). Shell large for Himalayan *Echinalosia*, transversely elliptical in outline, hinge slightly shorter than maximum width of shell, ears small, interarea low, no ventral sulcus or dorsal fold. Ventral valve strongly convex, dorsal valve concave with trail. Ventral spines about 0.7mm in diameter anteriorly, unevenly scattered, prostrate anteriorly. Dorsal valve with dense concentric lamellae and dimples and fine erect spines, well figured in detail by Shen et al. (2003a, pl. 3, fig. 3). Ventral muscle field posteriorly placed, adductor platform elongate, especially at early maturity, diductor scars large and striated longitudinally. Mature ventral shell interior marked by short strong ridges as posteriorly prolonged bases of spines. Fine pustules also prominent.

RESEMBLANCES: This species is new, and characterized by shape, ventral spines which are finer and less dense than in most other Himalayan species of *Echinalosia*, posteriorly placed ventral muscle field, and strong internal spine base ridges in the ventral valve. Shen et al. (2003a) tentatively compared the material with *Echinalosia magnispina* Waterhouse, but this species is smaller, more transverse, with strong ventral spines, and more anteriorly placed ventral muscle field, and no internal ventral spine ridges. Shen et al. (2003a) claimed that *magnispina* was poorly preserved. It is true that the illustrations were poorly reproduced, and although differences may be discerned, there is considerable difficulty in picturing the species. The types are, and have been since publication, available for inspection at Brisbane, but were not checked for the Tibetan studies.

Shells identified as *Multispinula* (now *Echinalosia*) *indica* (Waagen) from

F112 in the Senja Formation of Dolpo, west Nepal, by Waterhouse (1966, p. 12, pl. 1, fig. 2, 3, pl. 4, fig. 1, pl. 8, fig. 3) are close in shape and have similar ventral spines opening into the interior, but for the size of the shell, spines are larger. The dorsal exterior is poorly known, hindering identification, and the ventral adductors are small and narrow, and not so posteriorly placed. *Echinalosia* aff. *indica* (Waagen) recorded by Waterhouse (1978, pl. 7, fig. 15, 16) from the Nisal Member of Dolpo is close in shape and has posteriorly placed muscle field, but spines are coarse at 1mm in diameter. *E. indica* (Waagen) is close in general appearance but has radial ridges laterally and more numerous and differentiated ventral spines and prominent ventral cicatrix.

The specimens assigned to *Multispinula minuta* Jin from FdV-8 of the Qubuerga Formation near Mt Qomolungma, Tibet (Zhang & Jin 1976, pl. 1, fig. 25-27) are moderately close in shape and size, although more irregular, and have few well spaced large ventral spines, large attachment cicatrix and very irregular exterior surface, and appear to be less inflated.

STENOSCISMATOIDEA

Order Rhynchonellida Kuhn, 1949

Suborder Stenoscismatidina Waterhouse, 1981

The Stenoscismatoidea are a very distinctive superfamily, and it is believed that the morphological space between it and other superfamilies warrants full recognition as a suborder, as proposed by Waterhouse (1981, p. 91). Its shells are larger as a rule than the Rhynchonellida with which they mostly have been associated, and are characterized especially by the spondylium in the ventral valve, that is not replicated amongst rhynchonellidin shells. Further differences involve the lesser degree of foramenal development and function, the septum duplex, and dorsal structures involving camarophorium and intercamarophorial plate. Indeed relationships with Rhychonellida are not unambiguous, because Carter & Poletaev (1998) indicated a preference for placement within Pentamerida Schuchert & Cooper, 1931, members of which also have a spondylium. There are as yet no established rules for the establishment of higher categories of classification beyond superfamily level, and although it is believed that I was first to propose the recognition of the suborder, it may be noted that Sapelnikov & Mizens (1989) independently recognized Stenoscismatidina.

Superfamily **STENOSCISMATOIDEA** Oehlert, 1887

An excellent discussion of the Stenoscismatoidea is provided by Carlson in

Carlson & Grant (2003, pp. 1218-1219), building on the comprehensive monograph by Grant (1965). As explained in the following text, the classification is rearranged slightly, as follows:

Superfamily Stenoscismatoidea Oehlert
- Family Stenoscismatidae Oehlert
  - Subfamily Stenoscismatinae Oehlert
  - Subfamily Cyrolexinae Carlson
- Family Psilocamaridae Grant
  - Subfamily Psilocamarinae Grant
  - Subfamily Proatriboniinae Gratsianova
  - Subfamily Zhejiangellinae Liang.

Family **STENOSCISMATIDAE** Oehlert, 1887

Subfamily **STENOSCISMATINAE** Oehlert, 1887

Atriboniidae Grant, 1965 and Torenychinae Grant, 1965 have justifiably been merged with Stenoscismatinae by Carlson in Carlson & Grant (2003).

Genus ***Stenoscisma*** Conrad, 1839

TYPE SPECIES: *Terebratula schlottheimii* Buch, 1835, p. 59 (see Carlson in Carlson & Grant 2003, pp. 1220-1221).

Stenoscisma? hamleti n. sp.

Text-fig. 21C

1916 *Camarophoria purdoni* not Davidson Broili, p. 55, pl. 11, fig. 13a, b, 18-21, 23? (part, not pl. 11, fig. 7-12, 14, 16, 17 = *timorensis*, not fig. 15 = *crassa*, not fig. 20, 22 = indet.).

1965 *Stenoscisma purdoni*. Grant, p. 149, pl. 20, fig. 3 (part, not fig. 1, 2, 4 = *timorensis*).

1966 *S. "purdoni."* Shimizu, p. 408, pl. 15, fig. 24-28, pl. 16, fig. 1-10, text-fig. 2).

HOLOTYPE: Specimen figured by Shimizu (1966, pl. 15, fig. 22-28) from Basleo, Timor, here designated. Kept at Kyoto University,

DIAGNOSIS: Small generally transverse shells with well defined sulcus and fold commencing well in front of hinge, costae largely limited to anterior sulcus and fold, few or none on lateral flanks. Dorsal median septum thick, with hinge plate entire posteriorly, and apparently continuing well forward above intercamarophorial plate. Spondylium largely sessile, with low anterior septum.

DESCRIPTION: The species has been described especially by Shimizu (1966). The interior differs considerably from that of *timorensis*, a species which lacks an intercamarophorial ridge. Shimizu's thin sections are reproduced herein as Text-fig. 21C. Details do not fully conform with standard sections for *Stenoscisma*. The dorsal valve has a sturdy hinge plate, entire posteriorly, with probable but obscure cardinal process. The anterior hinge plate overlies the septum and intercamarophorium. Unlike typical *Stenoscisma*, the camarophorium which lies below the hinge plate and intercamarophorial ridge is not clearly distinguished. This probably reflects shell thickening and recrystallization, but might indicate a significantly different arrangement in which the camarophorium is not developed. No decision is possible in the absence of further material for sectioning, and the species is provisionally referred to *Stenoscisma*, with a query. The spondylium is large and sessile except anteriorly.

RESEMBLANCES: The species *hamleti* is based on mature specimens, as judged by ornament and development of the sulcus and fold. The shells are much smaller than the species *timorensis* to which they had been referred, and also differ in their more oval outline and less triangular shape. A few specimens figured by Broili (1916, eg. pl. 11, fig. 11) are somewhat uncertain in view of their small size, and might belong to *Coledium,* or to a different genus.

Stenoscisma schlottheimi Buch, 1835, with tight synonymy suggested by Grant (1965, p. 143), from the Zechstein of south Germany at Pössneck, and also from the Magnesian Limestone, England, is close in size, shape and ornament, but tends to have more lateral costae, and internally the camarophorium and intercamarophorial ridge are clearly developed (Grant 1965, text-fig. 34). *Stenoscisma ovalia* Liu & Waterhouse (1985, pl. 5, fig. 5-16) from the Houtoumiao Formation of Inner Mongolia shows considerable approach to *S? hamleti* in shape and size, but has slightly finer and more numerous costae over the anterior shell. An intercamarophorial plate in a small camarophorium was reported, as well as high septum and large cardinal process.

Stenoscisma vagata (Reed, 1944)

1944 *Camarophoria schlotheimi* (Buch) var. nov. *vagata* Reed, p. 136, pl. 23, fig. 7, 7a, pl. 24, fig. 6.

1944 *C.* cf. *thevenini* not Kozlowski Reed, p. 141, pl. 23, fig. 8.

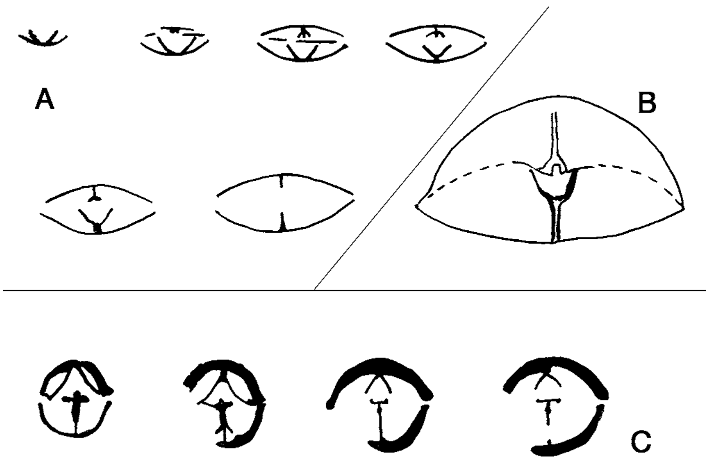
1944 *C. biplicata* not Stuckenberg Reed, p. 137, pl. 22, fig. 11, 11a, pl. 23, fig. 9, pl. 24, fig. 10, a, b (part, not pl. 23, fig. 10? = indet.).

?1978 *Stenoscisma* sp. Waterhouse, p. 36, pl. 3, fig. 8, 9.

LECTOTYPE: Specimen figured by Reed (1944, pl. 23, fig. 7, 7a) from Middle Productus Limestone (= Wargal Limestone, Kalabagh Member), Salt Range, here designated. Kept at Geological Survey of India, Calcutta.

DIAGNOSIS: Medium-sized triangular shells with long posterior walls and prominent ventral umbo, posterior third to half of shell smooth, costae arise over sulcus, fold and flanks, 2-4 or more in sulcus, and similar number on each flank.

DISCUSSION: The species was described as *Camarophoria schlotheimi (= schlottheimi) vagata* Reed. Here the species is elevated in rank from "var. nov." and is somewhat narrowly circumscribed, to include allied shells from the Wargal Formation that were ascribed to Early Permian taxa by Reed. These vary a little in number of costae. *C. humbletonensis* Howse var. nov. *divisa* Reed (1944, pl. 23, fig. 5, 5a) from the Kalabagh Member is close but distinguished by slightly finer and more numerous costae which cover more of the valve, and from the same stratigraphic level *C. cuneiformis* Reed (1944, pl. 24, fig. 5, a-c) also is more ribbed with angular crests and interspaces.



Text-fig. 21. Sections for Stenoscismatoidea.
A - Constructed serial sections for *Sedecularia glabra* (Waterhouse), at 1mm intervals from ventral umbo, ventral valve below, x 1.
B - *Bicamella timorensis* (Hayasaka & Gan), section from Broili (1916, pl. 125 (11), fig. 17), x 1. Ventral valve below.
C - Serial sections for *Stenoscisma? hamleti* n. sp. x 1, from Shimizu (1966, text-fig. 2). Dorsal valve below.

Stenoscisma sp. of Waterhouse (1978) from the *Lamnimargus himalayensis* Zone of the Nangung Formation of Dolpo, Nepal, is somewhat similar, and shows the spondylium and a little of the camarophorium and intercamarophorial plate, but is not well enough preserved to allow certainty.

Genus ***Coledium*** Grant, 1965

TYPE SPECIES: *Coledium erugatum* Grant, 1965, p. 98.

DIAGNOSIS: Small shells of oval rather than triangular shape with slight overlap of posterolateral margins, slight outpushing of anterior margins in some species and narrow stolidium in others, generally few costae limited to anterior shell, spondylium strongly curved longitudinally, on low septum duplex, intercamarophorial ridge.

DISCUSSION: Two species from the Himalaya closely conform in shape and ornament with the species of *Coledium* described by Grant (1965), apart from *C. undulatum* Grant (1965, pl. 14, fig. 1, 2, 2a, text-fig. 32), which is exceptional in having a number of fine anterior costae. Although neither these two Himalayan forms nor allied species from Timor and Salt Range, Pakistan, are well known internally, they will be provisionally referred to *Coledium,* following the lead set by Grant (1965) for *crassa* Hamlet.

Coledium crassa (Hamlet, 1928)

1916 *Camarophoria purdoni* not Davidson Broili, p. 55, pl. 11, fig. 15 (part, not fig. 13a, b, 18-21, 23? = *hamleti*, not pl. 11, fig. 7-12, 14, 16, 17 = *timorensis*, not fig. 20, 22 = indet.).

1928 *C. crassa* Hamlet, p. 60, pl. 9, fig. 10-14.

1965 *Coledium crassa*. Grant, p. 97, pl. 18, fig. 6.

1966 *Stenoscisma* sp. Shimizu, p. 410, pl. 16, fig. 11-15.

LECTOTYPE: Specimen figured by Hamlet (1928, pl. 9, fig. 13, 14), from Basleo, Timor, here designated.

DIAGNOSIS: Subrounded shells with very low ventral umbo and few strong very anteriorly placed costae ranging from one to 2-3 in sulcus, none on lateral flanks.

DISCUSSION: This species was transferred to *Coledium* by Grant (1965).

Coledium selongensis (Shen & Jin, 1999)

1999 *Stenoscisma timorense* (not Hayasaka & Gan) Shen & Jin, p. 555, text-fig. 3.1, 4.21-24.

1999 *S. selongensis* Shen & Jin, p. 555, text-fig. 3.2-8.

HOLOTYPE: Specimen 129360 figured by Shen & Jin (1999, text-fig. 3.6-8) from “Waagenites bed”, Selong Group, south Tibet, OD. Kept at Nanjing Institute of Geology & Palaeontology, China.

DIAGNOSIS: Shells convex and pentagonal in outline, bearing short thick anterior costae generally numbering 2 or 4, with median costa in ventral sulcus of some shells.

RESEMBLANCES: This is a very distinctive species, somewhat similar in appearance to *Coledium crassa* (Hamlet, 1928, pl. 9, fig. 12-14) from Basleo beds of Timor, but with shallower sulcus and more costae on some specimens. The Timor specimens show a tiny foramen, which is obscure in the Tibetan specimens. The interior is not known.

Coledium costacurtosus n. sp.

1884 *Camerophoria globulina* (not Phillips) Waagen, p. 443, pl. 33, fig. 14a-d (part, not fig. 13a-d = *Cyrolexis*?).

DERIVATION: costa - rib, curtosa - short, Lat.

HOLOTYPE: Specimen figured by Waagen (1884, pl. 33, fig. 14a-d), from Cephalopod bed of Chhidru Formation, Salt Range, here designated. Kept at Geological Survey of India, Calcutta.

DIAGNOSIS: Small subpentagonal equidimensional shells with few short anterior

costae, pair defining edges of sulcus and fold, a lateral pair and single costa along sulcus.
RESEMBLANCES: This species is very small, the holotype being about 7.5mm wide. It is indeed close to the species named *globulina* by Phillips (1834), extensively figured by Davidson (1858, 1863), and reassessed by Grant (1965, p. 119) as belonging to *Coledium*. The British species varies somewhat in appearance, and may show a median rib in the anterior sulcus as in the present form, but its sulcus and fold are not bordered by ribs. It is only 8-10mm across, and comes from the Magnesian Limestone of England, generally deemed to be of late Wuchiapingian age, and so close to the Salt Range species in age. Tiny specimens figured as *purdoni* not Davidson by Broili (1916, pl. 11, fig. 20, 22) show some approach. Another species of similar appearance is the Early Carboniferous species from England, *C. rhomboideum* (Phillips, 1836 - see Grant 1965), and this tends to have more ribs and is larger.

Coledium? cheni n. sp.

2000 *Stenoscisma timorense* (not Hayasaka & Gan) Shen et al. p. 746, text-fig. 13. 6-11, 13, 14, tab. 9.
DERIVATION: Named for Chen Zhong-Qiang.
HOLOTYPE: NMV P148934, figured by Shen et al. (2000, text-fig. 13.9, 11, 14) from Selong Group, south Tibet, here designated.
DIAGNOSIS: Moderately rather than well inflated shells characterized by low and weak costae limited to anterior shell, numbering up to 3 in sulcus and 4 on fold, may be fewer, absent from flanks, ventral posterior walls tend to be convex in outline, ventral umbo inconspicuous and strongly incurved over dorsal beak.
DESCRIPTION: This species comes from "beds" 13 and 15 of the Selong Group in the Selong Xishan section in south Tibet, and is described by Shen et al. (2000).
RESEMBLANCES: The species is readily distinguished from Timor shells described and named as *Camarophoria timorensis* by Hayasaka & Gan (1940), and now referred to *Bicamella*. In *timorensis* there are 4-6 ribs in the sulcus and 4-5 on the fold, and lateral costae as well, all commencing much closer to the umbo than in the Tibetan species. The Tibetan species is new and is provisionally referred to *Coledium*, although of unusually low inflation.

Coledium selongensis (Shen & Jin) from the topmost beds of the Selong Group, south Tibet, is smaller, less transverse, and more inflated with strong anterior costae, and lateral short costae on some specimens, and so is readily distinguished, although approaching the new species in outline and short costae. From Timor, *Coledium crassa* (Hamlet, 1928) is closer to the new species in outline, and is more inflated and has stronger costae, also limited to sulcus and fold, and comparatively deep and broad sulcus anteriorly. There is also some approach to material described as *Camarophoria (Laevicamera) sella* Kutorga var. nov. *praeacuta* Reed (1944, pl. 39, fig. 7, a, b) from the upper Middle Productus Limestone (= Wargal Formation, Kalabagh Member) of the Salt Range, Pakistan. The Salt Range species has a more prominent slender umbo, and narrow long ventral sulcus which becomes deep in front. The interior is not known, but its shape with narrow ventral umbo and extended posterior walls and very inconspicuous ribs suggest *Camerisma* Grant, or perhaps *Callaiapsida* Grant.

From Member E1 at the top of the Permian in Kashmir at the Guryul Ravine, Shimizu (1981, p. 77, pl. 7, fig. 12, 13) described as *Wellerella*? sp. a shell that possibly belongs to *Coledium*. It is only moderately close to the present species, and has three short ribs over the anterior median dorsal valve, and obscure ribs anteriorly on the ventral valve.

Coledium elivinia Waterhouse (1986b, pl. 14, fig. 30-34) from the Sakmarian Elvinia Formation of the southeast Bowen Basin, Queensland, is close from a ventral aspect, apart from more tapered ventral umbo, but has 4 costae along the anterior half of the dorsal fold.

Genus ***Sedecularia*** n. gen.

Text-fig. 21A, Text-fig. 22

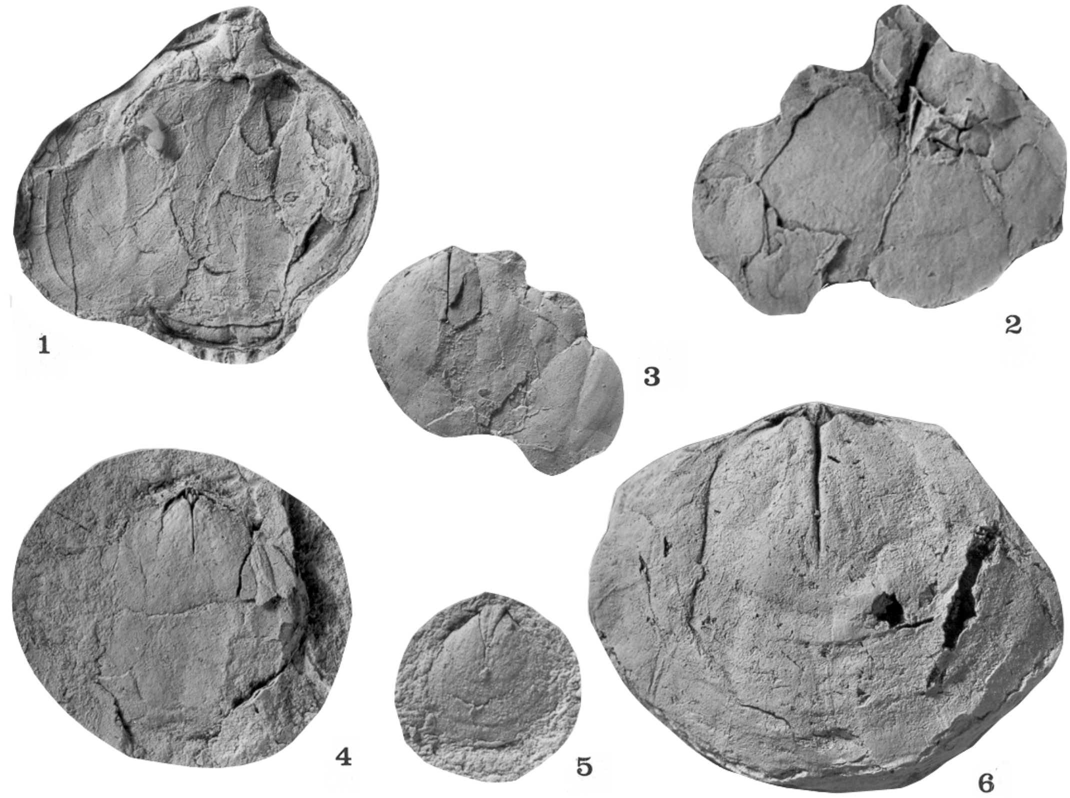
NAME: sedecula - low seat, Lat.

TYPE SPECIES: *Stenoscisma glabra* Waterhouse, 1987a, p. 67, here designated.

HOLOTYPE: UQF 70116 figured by Waterhouse (1986b, pl. 14, fig. 35, pl. 15, fig. 21) and Text-fig. 22.1,3 herein, from Brae Formation, Bowen Basin, Queensland, OD.

DIAGNOSIS: Medium-small oval to subrounded little inflated shells with comparatively wide and almost straight hinge, very shallow sulcus and low or no fold, no costae, no stolidium, ventral umbo not incurved but nature of delthyrium requires clarification. Spondylium sessile for most of length, very low septum anteriorly, persisting only a short distance; dorsal valve with horizontal hinge plate, short camarophorium in front supported by long septum duplex, short high intercamarophorium, laminated cardinal process, well formed dental sockets.

DISCUSSION: This genus is distinguished from *Stenoscisma* by its low inflation, subrounded shape and smooth ornament, some of these distinctions being similar to some of those between *Ussuricamara* Koczyrkevicz, 1969 and



Text-fig. 22. *Sedecularia glabra* (Waterhouse) from Brae Formation, Bowen basin, Queensland. 1, holotype dorsal external mould with part of ventral interior attached, UQF 70116 x 3. 2, partly crushed ventral interior with spondylium, unregistered specimen x 2. 3, dorsal aspect of internal mould, UQF 70116 x2. 4, internal mould of immature dorsal valve UQF 70117 x 3. 5, internal mould of small ventral valve UQF 70114 x 2. 6, internal mould UQF 70115 x 2.

Psilocamara Cooper, 1956. As well, the ventral spondylium is sessile posteriorly and only supported by a low septum anteriorly. *Ussuricamara* is distinguished internally from the present genus by its thick shell, high raised spondylium and lack of intercamarophorium etc. The present form is close in many respects to *Camerisma* Grant, 1965, p. 63, type species *C. prava* Grant. This is uniplicate according to Carlson & Grant (2003), not in the sense of Williams et al. (1997, p. 328) but as in Thompson (1927, p. 58), and is triangular in shape, with well developed anterior sulcus and fold, and no stolidium, though the valve edges overlap. The ventral umbo is strongly incurved, and the hinge of *Camerisma* diverges widely each side of the midline as in most stenoscismatids, and is not almost straight as in the present genus. The spondylium of *Camerisma* rests on a high septum duplex and intercamarophorial ridge is well developed. *Stenoscisma* is normally costate and has a stolidium, and is otherwise close to *Camerisma. Coledium* Grant, 1965 is a genus that also lacks or rarely shows a stolidium and has only short if any anterior costae, and the spondylium is often sessile posteriorly, and is well raised for most of its length on a high septum duplex. In shape *Coledium* species are well inflated and of oval outline, with well curved hinge and well developed anterior sulcus and fold.

Genus ***Liufaia*** n. gen.

DERIVATION: Named for Liu Fa.

TYPE SPECIES: *Stenoscisma tetricum* Grant, 1976, p. 185, here designated.

DIAGNOSIS: Stenoscismatid shells characterized by triangular outline with very long and almost straight posterior walls diverging narrowly to maximum width placed well forward, close to anterior margin. Ornament of relatively numerous and subequal costae, may be absent from umbo, sulcus shallow and fold very low, commissure uniplicate, stolidium present. Spondylium sessile posteriorly, raised on low median septum anteriorly, dorsal camarophorium and intercamerophorial plate, flat hinge plate bearing crura.

DISCUSSION: The type species comes from the early Guadalupian Rat Buri Limestone of Thailand, and has been well illustrated. It is characterized by its shape, ornament of ribs which increase by branching and intercalation, and may be missing laterally and from the umbonal region, and inconspicuous sulcus and fold. Allied species are widely scattered, and include *Stenoscisma margaritovae* (Tschernyschew, 1888, text-fig. 1-3, p. 355) from near Vladivostok, South Primoyre, also reported from the Chandalaz Suite with *Parafusulina stricta* in South Primoyre (Licharew & Kotlyar 1978, pl. 17, fig. 7), and from Ussuriland by Fredericks (1924b). It has also been reported from central and northeast Japan (Tazawa & Matsumoto 1998, p. 9, Tazawa et al. 2000, p. 10) with further synonymies and distribution data. Specimens assigned a nomen nudum by Liu & Waterhouse (1985, pl. 4, fig. 8-12) from the Zhesi Formation of Inner Mongolia are congeneric. From northeast China, *Stenoscisma giganteum elongatum* Lee & Su in Lee et al. (1980, pl. 173, fig. 1, 2) belongs to *Liufaia.*

Subfamily **CYROLEXINAE** Carlson, 2003

DIAGNOSIS: Genera suboval to subtriangular in shape, costae generally anterior or absent, stolidium rarely present, spondylium generally sessile posteriorly, intercamarophorial plate low.

DISCUSSION: The diagnosis here suggested, and not complete, appears to apply better to the genera included in Cyrolexinae than that proposed in the Treatise. The presence in some species of a very low intercamarophorial ridge raises the possibility that it is relict from stenoscismatid ancestry, and so is here provisionally moved to Stenoscismatidae. The genus *Callaiapsida* Grant is presumed to belong to Cyrolexinae, but the hinge plate is not known.

Genus ***Cyrolexis*** Grant, 1965

TYPE SPECIES: *Cyrolexis haquei* Grant, 1965, p. 91.

Cyrolexis zhangi n. sp.

1976 *Stenoscisma timorensis* (not Hayasaka & Gan) Zhang & Jin, p. 193, pl. 11, fig. 20-27, text-fig. 7.

?1981 *S*. cf. *timorensis.* Jin & Sun, pl. 7, fig. 29, 30.

DERIVATION: Named for Zhang Shouxin.

HOLOTYPE: Specimen 23404 figured by Zhang & Jin (1976, pl. 11, fig. 21-23) from JSB2, Selong Group, south Tibet, here designated. Kept at Nanjing Institute of Geology & Palaeontology.

DIAGNOSIS: Elongate shells of subtriangular outline with extended ventral umbo and long posterior walls, 2-3 lateral costae arising near umbo, 3-4 sulcal costae and 3 or more over fold. Low intercamarophorial ridge.

DESCRIPTION: Shells small, globose, elongate. Two sections of the interior and serial sections in Zhang & Jin (1976, text-fig. 7) indicate a very subdued intercamarophorial ridge along the camarophorium and no covering hinge plate, and the hinge plate does not appear to extend laterally along the sides of the camarophorium. The posterior spondylium is sessile, and the cardinal process is trilobed, judged from cross-sections. Possibly the obscure material compared to *timorensis* from Tibet by Jin & Sun (1981, pl. 7, fig. 29, 30) is congeneric.

RESEMBLANCES: The shells come from the Selong Group at Naxin, near the Selong Xishan section, but stratigraphic position is under poor control. They are moderately close to *Bicamella timorensis* (Hayasaka & Gan), but are smaller, more globose, and more elongate with fewer costae commencing in front of the umbo, except for one more costate specimen, figured in Zhang & Jin (1976, pl. 11, fig. 24).

The species is only moderately close to other species of *Cyrolexis*, which share an intercamarophorial plate that is weak or absent. The species so far referred to *Cyrolexis,* including the type species, and various species which have been described mostly by Tschernyschew (1902) and Diener (1915) and ascribed by external appearance to *Cyrolexis* by Grant (1965), are strongly biconvex, and have generally shorter costae and overall shape more rounded than the present form. *C*. *ussuricum* (Maslennikov 1950, pl. 3, fig. 4-10) with its variant *elongata* (Maslennikov, also Koczyrkevicz 1979, pl. 13, fig. 3-10), from the *Metadoliolina lepida* Zone of South Primoyre, is small with 3-9 ribs, greater inflation and more rounded outline*. C. antearcus* Xu & Grant (1994, text-fig. 25, 26) from the Changhsing Formation of Hunan, Sichuan and Zhejiang provinces of China has coarser anterior plicae, but *C. beccojectus* Xu & Grant (1994, text-fig. 27) is close in general appearance, including anterior costae, though less subtriangular in shape. It comes from the Changhsing Formation in the Zhejiang and Shansi provinces of China. Differences in shape are thus consistent, and the present species may have to be placed in a different, possibly new, genus.

Family **PSILOCAMARIDAE** Grant, 1965

[nom. transl. Koczyrkevicz 1969, p. 11 ex Psilocamarinae Grant 1965, pp. 29, 77].

DIAGNOSIS: Shells distinguished by absence of intercamarophorial plate.

DISCUSSION: Grant (1965) distinguished two families within Stenoscismatoidea, Atriboniidae and Stenoscismatidae, and assigned *Psilocamara* and allies to Psilocamarinae within Atriboniidae. He distinguished the two families on the basis of presence or absence of stolidium, deemed to be absent from Atriboniidae, and present in Stenoscismatidae. Yet one subfamily Torenychinae was recognized within Stenoscismatidae for genera which lacked stolidium, though it was later abandoned by Carlson & Grant (2003), and even amongst Stenoscismatinae, not all species and genera consistently show a stolidium. Koczyrkevicz (1969) was first to criticize the analysis and classification favoured by Grant (1965). Grant (1976) stoutly defended his own interpretation, appealing to the evidence offered by the succession of genera through the stratigraphic record, which he interpreted as indicating generic ties and evolution within the group, with no allowance for imperfection of the fossil record, or the complexifications normal for most groups, or the evidence for evolution and relationships offered by morphology. Nonetheless, Carlson & Grant, or perhaps Carlson in Carlson & Grant (2003), abandoned Grant's line of arguement and considerably modified the classification to suppress Atriboniidae and Torenychinae and recognize Psilocamaridae as a full family. It may be noted that in Carlson & Grant (2003), several text-figures are mislabelled Stenoscismatidae, and should be termed Psilocamaridae.

Subfamily **PSILOCAMARINAE** Grant, 1965

Genus ***Goleomixa*** Grant, 1976

TYPE SPECIES: *Goleomixa acymata* Grant, 1976, p. 180.

DIAGNOSIS: Shells with strong costae medianly, flanks and umbo may be smooth, open foramen, stolidium absent, no intercamarophorial plate.

DISCUSSION: *Goleomixa* Grant, 1976, initially described from the Rat Buri limestone of Thailand, was placed in Psilocamarinae by Carlson & Grant (2003), and lacks an intercamarophorial plate. *Goleomixa* is inflated with strong ribs medianly. Its hinge plate is long and not divided, and the camarophorium is overlain by the hinge plate posteriorly, and is open anteriorly.

Goleomixa? archboldi n. sp.

2000 *Stenoscisma gigantea* (not Diener) Shen et al., p. 745, text-fig. 13.1-5; 14.

DERIVATION: Named for N. W. Archbold.

HOLOTYPE: NMV P1449097 figured by Shen et al. (2000, text-fig. 13.3, 5) from Selong Group, south Tibet, here designated.

DIAGNOSIS: Large transverse ovally triangular shells, covered except at umbonal region by sturdy costae commencing 5-10mm in front of umbones, 2-4 costae in sulcus and 6-10 over flanks, 4 on fold at mid-length. Dorsal camarophorium long and high, no intercamarophorium, long dorsal median septum.

DESCRIPTION: The species is described by Shen et al. (2000). The cross-sections in Shen et al. (2000, text-fig. 14), although distorted and possibly of flawed material, indicate an approach to *Bicamella* as described below, but the hinge plate appears to cover the posterior camarophorium without extending laterally along the sides, and this strongly suggests, together with ornament and lack of stolidium and intercamarophium, an approach to *Goleomixa.*

RESEMBLANCES: This species is new, and comes from Late Permian faunas of the Selong Group at the Selong Xishan section at "bed" 11. It was identified with *Stenoscisma gigantea* (Diener, 1897a) from Chitichun no. 1, Himalaya, but is readily distinguished by its coarser and fewer costae. The sulcus of Diener's species has 7-10 costae in the sulcus and 7-8 costae laterally, compared with 2-4 sulcal costae and 6-10 lateral costae in the new form, and as well the new species is more inflated and the fold less raised and less distinguished from the lateral slopes. The generic position of *gigantea* Diener is not known, because the interior is so far uncertain, and the species might belong to *Stenoscisma*, *Goleomixa* or *Bicamella*. Tibetan specimens figured as *gigantea* by Zhang & Jin (1976, pl. 11, fig. 28) and by Jin & Sun (1981, pl. 7, fig. 31-34) are not conspecific with the present species, being much more costate.

Goleomixa acymata Grant (1976) is only moderately close, and has stronger ribs over the sulcus and fold, and fewer ribs laterally. There is some approach of the new form to shells described as *Stenoscisma ratmani* Archbold (1981, pl. 3, fig. 1-8, 11, 12) from the Aifat Formation of west Irian Jaya, but no internal detail was provided for *ratmani*, so that its generic position is yet to be ascertained: it may be referred to *Stenoscisma?*.

Subfamily **ZHEJIANGELLINAE** Liang, 1990

[nom. transl. hic ex Family Zhejiangellidae Liang, 1990, p. 247].

Liang (1990, p. 247) proposed a new Family Zhejiangellidae, which is here amended to subfamily status, as embracing variously ribbed shells with short complete dorsal hinge plate covering the camarophorium posteriorly, and extending laterally each side of the camarophorium. There is no intercamarophorial ridge. Such a group includes *Camarophorinella* Licharew, *Bicamella* n. gen., and *Ussuricamara* Koczyrkevicz. *Ussuricamara* is a little inflated smooth shell, with stolidium, no intercamarophorium and hinge plate figured as divided anteriorly. It was classed within Cyrolexinae by Carlson & Grant (2003), but lacks intercamarophorium. *Psilocamara, Camarophorina, Goleomixa* and *Careoseptum* are here retained in Psilocamarinae.

There is considerable approach to members of the Devonian Subfamily Proatriboniinae Gratsianova, 1967. The genus *Proatribonium* Gratsianova lacks an intercamarophorial plate, but unlike *Zhejiangella*, the camarophorium is not covered posteriorly by the hinge plate; instead this is subdivided anteriorly, and lies each side of the camarophorium. Carlson & Grant (2003) classed the subfamily in Stenoscismatidae, but no reason was provided.

Genus ***Bicamella*** n. gen.

DERIVATION: bi - two; camella, wide cup - Lat.

TYPE SPECIES: *Camarophoria timorensis* Hayasaka & Gan, 1940, p. 129, here designated.

DIAGNOSIS: Shell with subtriangular outline, extended posterior walls, moderately prominent ventral umbo incurved over delthyrium, shallow sulcus and low fold well formed anteriorly, numerous costae covering much to all of the valves, stolidium, ventral spondylium resting on high septum duplex, dorsal hinge plate very short and bearing small cardinal process, extending anteriorly each side of narrow camarophorium which rests on median septum duplex, no intercamarophorial ridge.

DISCUSSION: This genus is characterized by the lack of an intercamarophorial plate, hinge plate broad posteriorly and extending laterally each side of camarophorium, subtriangular outline, and presence of stolidium. A figure in Broili (1916, pl. 125 (11), fig. 17) of the species *timorensis* shows a divided hinge plate, joined at the edges to the small steep-sided and narrow camarophorium (Text-fig. 21B). In *Stenoscisma*, the hinge plate extends forward over the posterior camarophorium, and the camarophorium is otherwise open and unsupported anteriorly by a median septum, with no bordering hinge plate. Internally the new genus falls very close to *Camarophoria (Camarophorinella) caucasica* Licharew (1936, p. 63, text-fig. 4) from Late Permian of the Caucasus. Within *Camarophorinella* the edges of the camarophorium are attached to the sides of the divided hinge plate. In his wide-ranging monograph on Stenoscismatoidea, Grant (1965) recognized only one species of *Camarophorinella*, the type species, and *C. leveni* Grunt (Grunt & Dmitriev 1973, pl. 8, fig., 15, pl. 14, fig. 9, text-fig. 33) was later described from the Late Permian upper Taktabulakh beds of the Pamirs, and *C. gorodinskii* Zavodowsky (1970, p. 129, pl. 92, fig. 4) from the Late Permian Hivach Suite of Kolyma, with another occurrence in China mentioned by Carlson & Grant (2003). The species are of distinctive external appearance, subrounded in shape, and entirely covered by costae, and without stolidium. *Zhejiangella* Liang, 1990, type species *Z. sexplicata* Liang (1990, pl. 47, fig. 1-28, text-fig. 28, 29) carries close-set strong ribs, and the text-figures indicate that the hinge plate extends laterally as in *Camarophorinella* and *Bicamella*. *Zhejiangellina* Liang, type species *Z. wangi* Liang (1990, pl. 48, fig. 1-11 text-fig. 30), seems to be similar. These genera especially approach *Camarophorinella* Licharew in external appearance, and are moderately close internally.

Hybostenoscisma Liao & Meng, 1986, p. 83, type species *H. bambusoides* from China, is a small form with somewhat rounded triangular shape and high septa supporting the spondylium and camarophorium. The genus differs in having strong jointed ribs and a low intercamarophorial ridge, suggesting it should be placed in Cyrolexinae Carlson. The camarophorium is not bordered laterally by the hinge plate. *Careoseptum* Carter & Poletaev (1998, p. 139), type species *C. septentrionalis* Carter & Poletaev from the mid-Carboniferous Hare Fiord Formation of Arctic Canada, is distinguished by the lack of a dorsal septum. Its hinge plate is posteriorly placed and overlaps the camarophorium for a short distance, but is not extended laterally each side of the camarophorium.

Bicamella timorensis (Hayasaka & Gan, 1940)

Text-fig. 21B

1864 *Camarophoria crumena* (not Martin) Beyrich, p. 73, pl. 1, fig. 11a-c, 12.
1892 *Camarophoria pinguis* not Waagen Rothpletz, p. 48, pl. 10, fig. 2a, b.
1916 *Camarophoria purdoni* not Davidson Broili, p. 55, pl. 11, fig. 7-12, 14, 16, 17 (part, not fig. 13a, b, 18-21, 23? = *hamleti*, not fig. 15 = *crassa*, not fig. 20, 22 indet.)
1928 *C. purdoni.* Hamlet, p. 37, pl. 9, fig. 5-8.
1940 *C. timorensis* Hayasaka & Gan, p. 129, pl. 9, fig. 1-7.
1965 *Stenoscisma purdoni*. Grant, p. 149, pl. 20, fig. 1, 2, 4 (part, not fig. 3 = *hamleti*).
1989 *S. timorense*. Archbold & Bird, p. 110, text-fig. 5A-Z, AA-BB.

LECTOTYPE: Specimen figured by Broili (1916, pl. 11, fig. 10), refigured by Hayasaka & Gan (1940, pl. 9, fig. 2), designated subsequently by Waterhouse

(1964, p. 101). Hayasaka & Gan (1940) designated all the Broili specimens as syntypes. Kept at Geologisches-Paläontologisches Institut, Bonn University.
DIAGNOSIS: Weakly transverse shells with moderately prominent incurved ventral umbo, broad sulcus and fold commencing near posterior third of shell length, bearing 2-5 coarse costae, with 3-5 costae as a rule on flanks, though some specimens have non-costate flanks.
DESCRIPTION: The species is represented in my collections by plaster duplicates. It has been described by several authors. In the synonymy, small shells included with typical *timorensis* have been set aside, because they show a well developed and deep sulcus at a size of only 15mm, less than half the length of *timorensis* at comparable maturity and depth of sulcus. These include some of the specimens figured by Broili (1916) and one specimen of the suite figured by Grant (1965, pl. 20, fig. 3), that are now referred to *Stenoscisma? hamleti* n. sp. (p. 77).
RESEMBLANCES. *Camarophorinella caucasica* Licharew (1936, 1960, p. 250, text-fig. 292; Grant 1965, p. 87, pl. 4, fig. 5, text-fig. 17) is readily distinguished by the costae which cover the entire shell. As well, the fold and sulcus are more sharply defined, and the size smaller, giving an overall very different appearance. Internal detail seems much the same. The species *timorensis* is internally close to *Camarophorinella*, and externally is close to species of *Stenoscisma*, with their subtriangular outline and development, at least in some individuals, of a stolidium. A number of referrals of Asian species to *timorensis* have been made (see Archbold & Bird 1989, p. 112), but require substantiation. Several are externally similar to *Stenoscisma*, but differ internally, or are not known. For instance Licharew & Kotlyar (1978, pl. 17, fig. 8) recorded the species from the upper Barabash horizon of South Primoyre, but the interior is not known. Liu & Waterhouse (1985, pl. 4, fig. 13, 14, pl. 5, fig. 1-4) compared specimens from the Zhesi Formation of Inner Mongolia, but noted differences, and reported that the intercamarophorial ridge and hinge plate, if present, were obscured by poor preservation. A Tibetan form figured by Zhang & Jin (1976, pl. 11, fig. 28) from JSK1 shows only moderate approach. Koczyrkevicz (1979, p. 52, pl. 12, fig. 1-6) reported *Stenoscisma timorensis* from south Primoyre, in the Chandalaz Suite, but internal detail was not provided.

Stenoscisma papilio Waterhouse (1964) from the Wuchiapingian or early Changhsingian *Paucispinauria verecunda* Zone of New Zealand is externally somewhat like *Bicamella timorensis*, but has an intercamarophorial plate and belongs to *Stenoscisma*. Somewhat puzzlingly, Archbold (1981) asserted that the species was “poorly known”, but external and internal details are well established.

SPIRIFEROIDEA

Introduction

Spiriferidin brachiopods are moderately widespread in the Permian of the Himalaya and nearby Salt Range of Pakistan. They have been studied for more than a century, commencing with the pioneering study of Davidson (1862). Early descriptions based on material mainly from the Salt Range and northwest India have been reinforced by studies especially from Nepal and Tibet. The present overview brings together these studies, and although Himalayan material is subject to deformation and may be particularly difficult to collect because of logistic difficulties involving remoteness and altitude, species may be regarded now as sufficiently distinctive and well defined to act as keys for correlation and classification.

MORPHOLOGY: The term fastigium has been proposed for what used to be termed the fold in Spiriferida, as accepted by a number of authors, but the revised brachiopod Treatise (Williams et al. 1997) regarded the term as superfluous. Both terms are used interchangeably herein, but in essence, the assessment by Williams et al. is accepted.

In 1959, Campbell applied the term pleromal plate to thickening along the inside edge of the dental plate where it meets the adminiculum, and this is a useful term for the ridges that converge or meet under the delthyrium in a number of spirifers: they will be termed pleromal ridges, and characterize especially Late Carboniferous Spiriferida. Pleromal ridges that extend to meet across but below the delthyrium form what Carter (1974) termed a subdelthyrial plate, or pseudodeltidium according to some authors. Such is illustrated for *Brachythyrina boonlomi* in Pl. 1, fig. 9, 10. The nature of the delthyrial or subdelthyrial covering is likely to be significant, as summarized in Williams et al. (1997, pp. 357-358), and Poletaev (1997) reassessed the position of various genera as arranged by Carter et al. from the nature of the delthyrial cover. Unfortunately the delthyrium is often obscured, and indeed the covering plate may be lost, so that it is not known for a number of type species, and has not yet been studied in a large range of specimens from a variety of lithofacies.

Subplicae are here regarded as narrow plicae, and may support a narrow fascicle with generally 1-3 costae. Subplicae are developed laterally away from the sulcus in Trigonotretinae or Neospiriferinae, and occur to the exclusion of plicae and tend to be more numerous in members of Gypospiriferinae, but the term is not used in any tightly defined sense.

Table 7. Classification of Spiriferoidea.

Superfamily Spiriferoidea King
- Family Spiriferidae King
  - Subfamily Spiriferinae King
  - Subfamily Gypospiriferinae Waterhouse n. subfam.
- Family Neospiriferidae Waterhouse
  - Subfamily Imbrexiinae Carter
  - Subfamily Neospiriferinae Waterhouse
  - Subfamily Kaninospiriferinae Kalashnikov
  - Subfamily Fusispiriferinae Waterhouse n. subfam.
- Family Trigonotretidae Schuchert
  - Subfamily Sergospiriferinae Carter
  - Subfamily Angiospiriferinae Legrand-Blain
    - Tribe Angiospiriferini Legrand-Blain
    - Tribe Georginakingiini Waterhouse n. tribe
  - Subfamily Trigonotretinae Schuchert
    - Tribe Trigonotretini Schuchert
    - Tribe Grantoniini Waterhouse n. tribe
  - Subfamily Costuloplicinae Waterhouse n. subfam.
- Family Choristitidae Waterhouse
  - Subfamily Prospirinae Carter
  - Subfamily Choristitinae Waterhouse
  - Subfamily Purdonellinae Poletaev
- Family Spiriferellidae Waterhouse
  - Subfamily Spiriferellinae Waterhouse
  - Subfamily Hunzininae Angiolini
  - Subfamily Elivininae Waterhouse n. subfam.

Reticulate and ramiform lateral vascular impressions, or angioglyphs, (see Pl. 1, fig. 6-8, 10 herein) have been granted high significance by Legrand-Blain (1986b) and Carter et al. (1994), with detail provided by Legrand-Blain (1985a) and Legrand-Blain et al. (1984). Branching vascular impressions are developed close to the ventral muscle field in choristitinids (Barkhatova 1968, Legrand-Blain 1970), martiniids (Cooper & Grant 1976), and brachythyrids (Abramov & Grigorieva 1983, pl. 29, fig. 4), whereas they are laterally placed in *Angiospirifer* and *Anthracothyrina* (Angiospiriferinae) as shown by Legrand-Blain (1986b, text-fig. 24), and in *Aperispirifer* (Trigonotretinae), *Georginakingia* and *Sulciplica* (Angiospiriferinae), as shown herein. Ventral valves of the neospiriferin genus *Spiriferalaria* Waterhouse 2002d, eg. *Neospirifer bakeri columbarius* - Cooper & Grant (1976, pl. 598, fig. 26), and *N. bakeri bakeri* Cooper & Grant (1976, pl. 597, fig. 6) have spongiform thick ridges separated by small pits. As far as is known, no reticulate vascular impressions are developed in any Spiriferellidae, but for some spiriferoid subfamilies, the presence or absence is not established.

SYSTEMATIC DESCRIPTIONS

Order Spiriferida Waagen, 1883

Suborder Spiriferidina Waagen, 1883

Superfamily **SPIRIFEROIDEA** King, 1846

DIAGNOSIS: Usually large, transverse, ornamented by costae and/or plicae, well formed sulcus and fold, hinge line denticulate, ventral interior with dental plates and adminicula, dorsal interior without tabellae, variably developed crural plates (Table 7).

DISCUSSION: The classification presented by Carter et al. (1994, p. 342) is revised and elaborated, by building on previous work. Particular attention is paid to the nature of the sulcus and fold and how they are subdivided, and also to the number of plicae, and to the nature of the cardinal extremities. Some recent studies focus solely on the ventral valve, but this is believed to be an error, with even species difficult to circumscribe in the absence of the dorsal valve.

Family **SPIRIFERIDAE** King, 1846

DIAGNOSIS: Weakly to moderately transverse with well formed sulcus and fold, ornament predominantly costate with no or weak or impersistent fasciculation, delthyrium open or closed partly to entirely by stegidial plates.

DISCUSSION: Carter et al. (1994) assigned to Spiriferidae the subfamilies Spiriferinae, Prospirinae, Sergospiriferinae, and Purdonellinae. Here it is suggested that some of these subfamilies may be reassigned, and Spiriferidae used to incorporate the subfamilies limited to genera close to *Spirifer* itself, with large size, and prominent costae in narrow to substantial fascicles.

Subfamily **SPIRIFERINAE** King, 1846

DIAGNOSIS: Delthyrial cover weakly developed or absent, lateral slopes and fold-sulcus costate, increase by bifurcation, not raised as fascicles other than as very low and moderately numerous "subfascicles" often of only two costae, micro-ornament of concentric lamellae and radial capillae, vascular impressions simple.

GENERA: Genera include *Spirifer (Spirifer)* Sowerby, *S. (Grandispirifer)* Yang, *S. (Mesochorispira)* Carter, *Larispirifer* Enokjan & Poletaev, *?Warsawia* Carter.

Subfamily **GYPOSPIRIFERINAE** n. subfam.

NAME GENUS: *Gypospirifer* Cooper & Grant, 1976, p. 2210.

DIAGNOSIS: Costae branching, may form a number of narrow and comparatively low fascicles, usually distinct from the substantial fascicles developed in Neospiriferidae, plicae narrow, feeble or absent, shells weakly transverse, well defined fold and sulcus, sulcus bordered or entered by fascicle pair, micro-ornament of radial and concentric capillae or only concentrics, delthyrium bordered by flanges, may be open, or have low umbonal callosity or be partly or entirely closed by stegidial plates. Dental plates generally well formed, ventral median septum present or absent.

DISCUSSION: Genera of Gypospiriferinae are close to *Neospirifer* and allies, where classed by Cooper & Grant (1976) and Carter et al. (1994), but have more conspicuously bifurcate costae, which are not differentiated other than close to inception, and are associated in low, varyingly persistent narrow subplicae, or narrow bundles, more numerous than the much better developed and fewer plicae of Neospiriferidae. Costae are more differentiated than in Spiriferinae, which has costae either simple or rarely fasciculate. Poletaev (1997) preferred a strong linkage between *Gypospirifer* and Spiriferinae. The subfamily is believed to have arisen from Spiriferinae, with *Fasciculatia* n. gen. close to *Spirifer*.

Cooper & Grant (1976) stated that radial filae were absent from *Gypospirifer*, and the absence of radial capillae may constitute an important facet for some of the genera. But the lack possibly reflects preservation, as no radial filae were observed also in various species of neospiriferin affinity from the Glass Mountains, and Cooper & Grant (1976, p. 2195) observed that radial ornament could be destroyed in *Cartorhium latum* (King). An allied genus *Fasciculatia* n. gen. from Greenland shows radial filae (Dunbar 1955, pl. 28, fig. 6), and radial capillae were reported for *Lepidospirifer*, with the observation that tiny granules could be formed (Cooper & Grant 1976, p. 2203). *Ovispirifer* n. gen. also displays small granules, and radial as well as concentric filae.

For *Gypospirifer*, Cooper & Grant (1976) recorded stegidial plates that converge and partly or entirely close the delthyrium. In *Lepidospirifer* Cooper & Grant, the delthyrium is open with dental keels and very low umbonal callosity. *Cartorhium* Cooper & Grant has an open delthyrium, closed under the umbo by a small apical callosity, or what was called a pseudodeltidium. In *Gobbettifera* with allied ornament, the delthyrium is open with well developed median septum. Illustrations in various articles for the delthyrium in a number of species of various genera indicate an entire covering plate, its nature not described, and the figures not clear enough to show the structure. The significance of the delthyrial apparatus may need to be regarded with caution, until clarified for more type species of more genera, and indeed examined across a range of species within a genus.

Dental plates are known to be well formed in *Septospirifer*, *Gobbettifera* and *Fasciculatia*. Cooper & Grant (1976) did not distinguish dental plates from adminicula, and the dental plates were called dental ridges, which they described as deep for *Gypospirifer* and *Lepidospirifer*. Vascular impressions are poorly known, although in *Cartorhium*, Cooper & Grant (1976, pl. 618, fig. 29) indicate radial impressions around the ventral muscle field.

Three associations may be recognized amongst the genera, a transverse group generally with subalate hinge, including *Gypospirifer, Lepidospirifer,* and *Fasciculatia*, a group with obtuse cardinal extremities, involving *Ovispirifer* and *Cartorhium*, and genera with ventral median septum, *Septospirifer* and *Gobbettifera*.

GENERA: *Gypospirifer* Cooper & Grant, *Cartorhium* Cooper & Grant, *Fasciculatia* Waterhouse n. gen., *Gobbettifera* Waterhouse n. gen., *Lepidospirifer* Cooper & Grant, *Ovispirifer* Waterhouse n. gen., *Septospirifer* Waterhouse.

Genus ***Lepidospirifer*** Cooper & Grant, 1969

TYPE SPECIES: *Lepidospirifer angulatus* Cooper & Grant, 1969, p. 15.

DIAGNOSIS: Moderately large shells with obtuse but extended cardinal extremities, numerous round-crested costae with narrow interspaces, well developed “tiled” concentric laminae, narrow fascicles in some 3-4, rarely 5 pair, restricted to posterior shell, narrow pair passes into sulcus posteriorly at least in some species, hinge wide but cardinal interarea high and triangular in ventral valve. Little secondary thickening.

DISCUSSION: This genus has a small umbonal callosity and open delthyrium, and the dental plates do not fuse medianly (Waterhouse 2001, p. 94), but pleromal ridges are well formed. Strong radial capillae were observed for the American shells by Cooper & Grant (1976). *Lepidospirifer angulatus* Cooper & Grant, and *L. costellus* (King) are found in the Cathedral Mountain and Road Canyon Formations of the Glass Mountains. Shen et al. (2001, text-fig. 5.8) identified *Lepidospirifer* in the Late Permian of south Tibet, based on an exterior of a ventral valve, with no internal or delthyrial morphology.

A species *Lepidospirifer miyakei* Tazawa & Shen (1997, pl. 2, fig. 2-6) of Guadalupian age from Hiyomo, Japan, has well preserved micro-ornament of concentric lamellae without radial filae. But the genus was possibly misidentified. It might be purdonellid or a new spiriferoid genus, judged from shape and poor development of sulcus, and even the subfamily position remains obscure in the absence of data on the interareas, delthyrium, and internal plates.

Genus ***Fasciculatia*** n. gen.

DERIVATION: fascis - bundle, Lat.

TYPE SPECIES: *Fasciculatia greenlandicus* n. sp., here designated.

DIAGNOSIS: Large transverse shells with sulcus and fold and weakly alate cardinal extremities, ornament of well formed bifurcating costae associated in a number of low and narrow bundles, of which 1-2 pair enter sulcus, weak concentric lamellae and fine radial filae. Delthyrium open with small umbonal callosity, moderately developed dental plates and short adminicula, moderate secondary thickening, no ventral median septum or prominent myophragm.

DISCUSSION: This genus is very close to *Gobbettifera* n. gen. - see below - but lacks the prominent ventral median septum. Other genera within the subfamily differ in shape, or have less developed fascicles, except for *Septospirifer* Waterhouse, which has a median ventral septum.

The genus comes particularly close to *Spirifer* Sowerby, 1818 as exemplified by its type species *Spirifer striatus* (Martin, 1809) - see Dunbar (1955, p. 131) - which has been well figured in Archbold & Thomas (1984) and discussed by many authors, including Thomas (1971, p. 59). The costae develop low narrow fascicles, somewhat irregular in distribution. Those of *Fasciculatia* are slightly more regular and better developed, but overall the two are close, although *F. greenlandicus* is less transverse with fuller anterior lateral margins, and fuller sulcal tongue and less sharply defined fold, compared with *Spirifer striatus.* Unfortunately accounts of *S. striatus* have failed to confirm that radial capillae are absent, but I have not encountered statements that radial capillae are definitely present in *S. striatus*. Given these uncertainties, and the degree of similarity between the two, *Fasciculatia* may be regarded as either Spiriferinae or a reversionary member of Gypospiriferinae, and the latter option is favoured by the nature of fascicles, costae and micro-ornament.

There is also an approach to *Kaninospirifer* Licharew (see p. 130). *Fasciculatia* is close in general appearance, but has more fascicles laterally and has large dental plates, and concentric laminae are close-set and not prominent. Dunbar (1955) identified what is now *F. greenlandicus* with *striatoparadoxus* Toula, and Toula's species, especially well exemplied by various specimens described by Wiman (1914), has scarcely developed plicae or fascicles, and so in that regard could be a catagenic representation of either stock. But its dental plates are reduced, suggestive of *Kaninospirifer*.

Fasciculatia greenlandicus n. sp.

Text-fig. 23

1931 *Spirifer* cf. *marcoui* not Waagen Frebold, p. 16, pl. 4, fig. 2.

1931 *S. ravana* not Diener Frebold, p. 39, pl. 4, fig. 1, 1a, pl. 5, fig. 1.

1933 *S. cameratus* not Morton Frebold, p. 15, pl. 1, fig. 4.

1950 *S. ravana.* Frebold, p. 57, pl. 4, fig. 3, 3a, 6.

1950 *S. marcoui*. Frebold, p. 58, pl. 4, fig. 2.

1955 *S. striato-paradoxus* not Toula Dunbar, p. 131, pl. 23, fig. 1-7, pl. 24, fig.

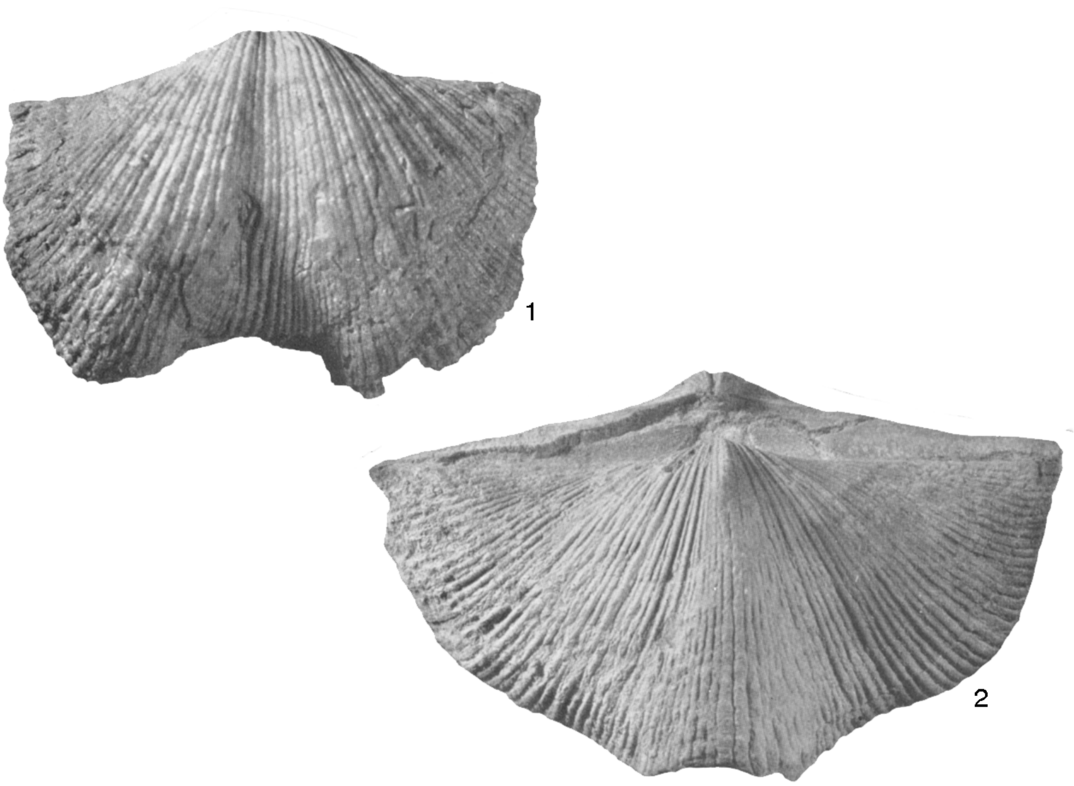
1-5, pl. 28, fig. 1-6.

DERIVATION: Named for Greenland, source of the species.

HOLOTYPE: Specimen figured by Dunbar (1955, pl. 24, fig. 4, 5) and Text-fig. 23.1 herein, from Clavering, Noe-Nygaard & Soderberg collection LK 20, "Productus Limestone", Foldvik Creek Group, here designated. Kept at Mineralogisk Museum, Copenhagen.

DIAGNOSIS: Large shells with small pointed cardinal extremities, deep sulcus and high fold, up to 7 pairs of subplicae on ventral valve, costae with rounded crests, concentric ornament subdued or absent, faint radial filae.

DESCRIPTION AND RESEMBLANCES: This species has been fully described and well illustrated by Dunbar (1955). The Dunbar material came from the Productus limestones of Greenland, which are regarded as Late Permian in age. They were identified with *Spirifer striatoparadoxus* Toula, 1873 and are certainly close to that species, but have finer ribs, and more numerous and more prominent fascicles. Interiors of ventral valves from the Spirifer Limestone of Spitsbergen that were figured by Wiman (1914, pl. 7, fig. 9-11) as *S. marcoui* not Waagen belong to *striatoparadoxus*, and clearly show a small umbonal callosity and absence of median septum, and reduced dental plates, suggestive of *Kaninospirifer*. The species *striatoparadoxus* was discussed by Gobbett (1964, p. 134), and lectotype designated as 1875 XLI 24, figured by Toula (1875, pl. 8, fig. 1) kept at the Naturhistorisches Museum, Vienna. The original figured



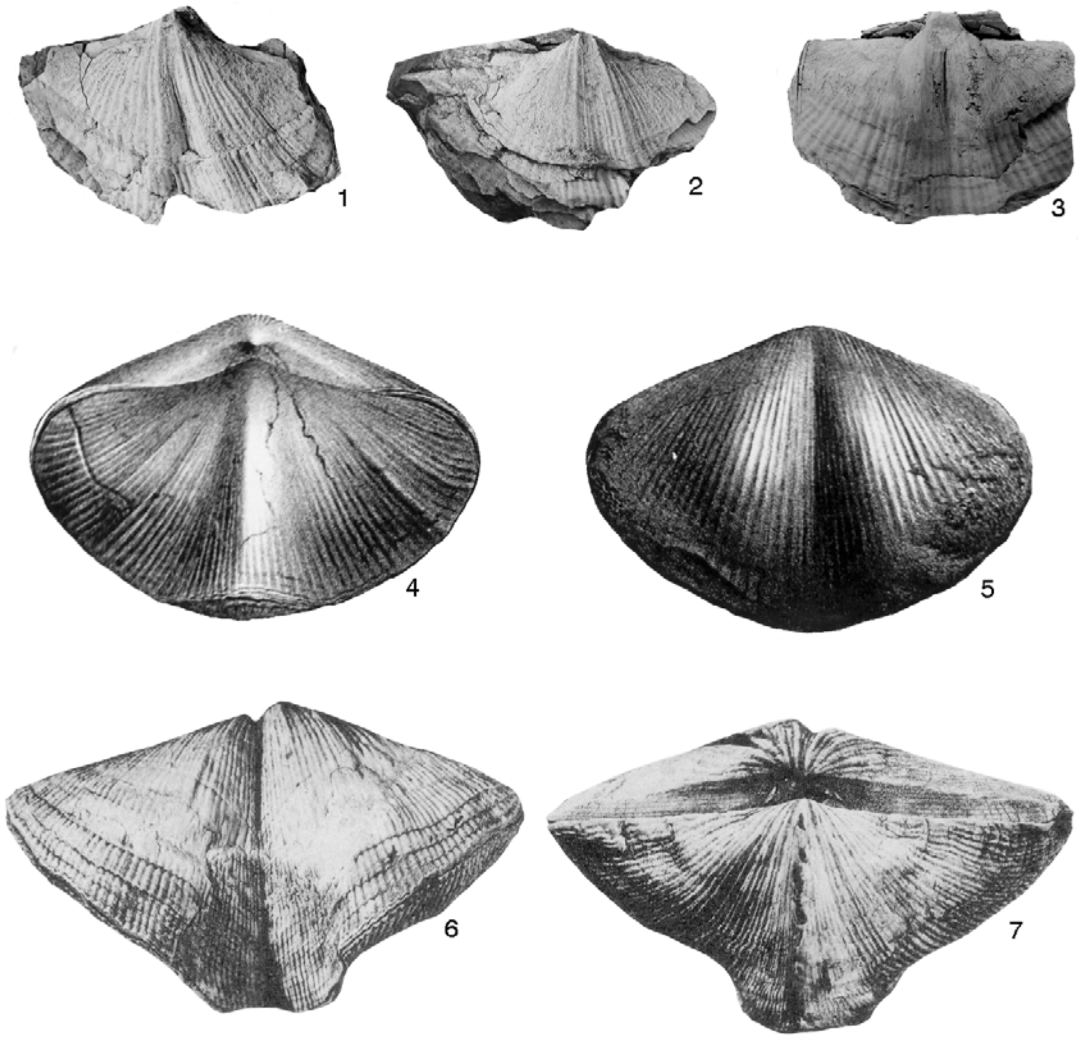
Text-fig. 23. *Fasciculatia greenlandicus* Waterhouse x 1. 1, ventral exterior, holotype. 2, dorsal view. Specimens altered from Dunbar (1955, pl. 25, fig. 3, 4) from "Productus limestone", Foldvik Creek Group, Greenland.

specimen has been lost. The species comes from the Spirifer Limestone of Spitsbergen, of Kungurian age. A number of occurrences have been identified with Toula's species, as in Gobbett (1964), but some must be weaned out.

Spirifer striatoplicatus Gobbett (1964, pl. 17, fig. 7-9, pl. 18, fig. 1) from the Kungurian Spirifer Limestone of Spitsbergen is regarded as a member of *Fasciculatia*, distinguished by its less emphasized sulcus and fold, and lacking medium septum or myophragm. The holotype SME 18588 carries irregular low plications and a number of subplicae and bifurcating costae, and has large dental plates. The ornament of a paratype figured by Gobbett (1964, pl. 17, fig. 7) involves 3 pairs of low plicae, suggestive of *Kaninospirifer*, and is not deemed to be conspecific.

AGE OF "PRODUCTUS LIMESTONES" OF GREENLAND

The Productus Limestone of the Foldvik Creek Group in Greenland is probably



Text-fig. 24. 1-3. *Septospirifer tatondukensis* Waterhouse x 1. 1, ventral exterior GSC 26434. 2, ventral exterior GSC 26435. 3, ventral internal mould, GSC 26437, holotype. Also figured by Bamber & Waterhouse (1971, pl. 27, fig. 1, 2, 4), from Jungle Creek Formation, Yukon Territory, Canada.
4, 5. *Ovispirifer oldhamianus* (Waagen), dorsal and ventral views of lectotype GSI 3519, also figured by Waagen (1883, pl. 46, fig. 1a, b) from Wargal Formation, Salt Range, Pakistan, x 1.
6, 7. *Gobbettifera angulata* Waterhouse, ventral and dorsal aspects of holotype, GSC 13748, x 1, also figured by Harker & Thorsteinsson (1960, pl. 19, fig. 1, 2), from Assistance Formation, Canada.

Late Permian in age. Kozur (1994) placed its conodonts as Djulfian (roughly Wuchiapingian), and regarded the Schuchert Dal Formation as close or slightly younger in age (Kozur 1998). It is true that Rasmussen et al. (1990) reported the conodont *Merrillina divergens* from the Foldvik Creek Group, and this conodont was said to occur in upper Wordian to early Capitanian beds in North America (Wardlaw & Collinson 1986). Revision of the stage boundaries now mean that the range is Wordian (Waterhouse 2002c, p. 204). But the North America conodont is regarded as *M. praedivergens* Kozur & Mostler by Dr Kozur, and he has found *M. divergens* in early Djulfian beds at Kuh-e-Ali Bashi (Jolfa) and Zal, northwest Iran, in the *Codonofusiella* beds (Dr Heinz Kozur, e-mail 24.9.03).

Genus ***Cartorhium*** Cooper & Grant, 1976

TYPE SPECIES: *Cartorhium retusum* Cooper & Grant, 1976, p. 2191.

DIAGNOSIS: Small to moderate in size, subcircular to transversely subelliptical in outline, widest in front of hinge, fold low and sulcus shallow, evenly concave or angular in section. Costae fasciculate, triplicate and frequently bifurcate, of uneven strength, strong posteriorly, becoming lower anteriorly, plicae low and posterior only or absent, fascicle pair may lie posteriorly within sulcus. Micro-ornament of concentric and radial filae. Delthyrium open except at apex, with reported deep-set pseudodeltidium or apical callosity.

DISCUSSION: A number of well-preserved species were described by Cooper & Grant (1976) from the Permian of the Glass Mountains. This genus is externally close to *Blasispirifer* Kulikov and is better known, particularly with regard to the interior and delthyrium, though various details of the species await closer examination. Plicae are less persistent in the American genus, and may include a pair distinctly within the sulcus.

Some uncertainty surrounds the subfamilial and tribal affinities. Judged from illustrations, the dental plates are comparatively low, as if there were possible relationships to Kaninospiriferinae, even though the nature of the fascicles show little similarity to the plicae developed on this subfamily.

Genus ***Ovispirifer*** n. gen.

Text-fig. 24.4, 5

DERIVATION: ovi - round, spirifer - brachiopod.

TYPE SPECIES: *Spirifer oldhamianus* Waagen (1883, p. 518, pl. 46, fig. 1a-d, 2a-c) from Middle Productus Limestone (Wargal Formation, Kalabagh Member), Salt Range, Pakistan, here designated.

LECTOTYPE: GSI 3512, figured by Waagen (1883, pl. 46, fig. 1a-d) and Text-fig. 24.4,5 herein, here designated.

DIAGNOSIS: Shells characterized by obtuse cardinal extremities, short subtriangular hinge, simple bifurcating costae, low ventral umbo, low and poorly discriminated but persistent few and narrow plicae.

DISCUSSION: The type species may be readily distinguished from the American species of *Gypospirifer* described by Cooper & Grant (1976), and various allies, through having rounded cardinal extremities and hinge much shorter than maximum width of the shell. Shells of *Gypospirifer* even at late maturity remain alate, and generally display at maturity small alate extensions of the hinge. The type species of *Ovispirifer* has inconspicuous ventral umbo, almost no trace of plicae on the ventral valve and faint irregular narrow plicae on the dorsal valve, sharply crested fold and grooved sulcus with ill-defined borders, whereas borders are more sharply delimited in *Gypospirifer*. The nature of the delthyrium requires clarification. For micro-ornament, Waterhouse (1966, p. 43) recorded pustules, possibly from intersection of radial and concentric capillae, as also reported for *Lepidospirifer* by Cooper & Grant (1976), and noted somewhat angular crests of costae.

Both *Blasispirifer* and *Cartorhium* come close in overall shape, but are smaller shells distinguished by their more numerous fascicles.

A number of other Salt Range species are allied, but tend to be more transverse than *oldhamianus,* with longer hinge. As the cardinal extremities are also rounded, they may be included provisionally within *Ovispirifer,* but require first-hand examination. Taxa described by Reed (1944) include:

Spirifer (Neospirifer) *cameratus* cf. *orientalis* Chao (Reed 1944, p. 207, pl. 27, fig. 9) from Lower Productus Limestone (now Amb Formation).

Spirifer (Neospirifer) *sodalis* Reed (1944, p. 203, pl. 26, fig. 4, 4a) from Middle Productus Limestone (Wargal Formation).

Genus ***Gobbettifera*** n. gen.

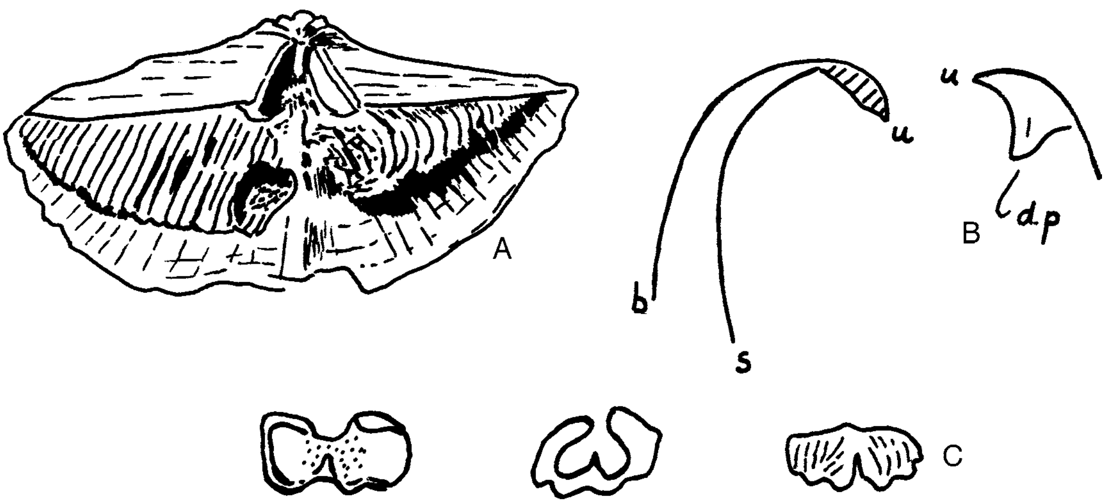
DERIVATION: Named for D. J. Gobbett.

TYPE SPECIES: *Gobbettifera angulata* n. sp., here designated.

DIAGNOSIS: Shells transverse with alate extremities at full maturity, deep and angular sulcus, high and narrow-crested fold, 5-7 moderately developed to persistent narrow subplicae pairs formed by branching costae in complex arrangement, one or two pair incorporated within sulcus anteriorly, concentric lamellae may be well developed. Delthyrium open as far as known, dental plates large, high stout ventral septum posteriorly. Shell thickening moderate along hinge of ventral valve.

DISCUSSION: This genus is based on well preserved and numerous specimens, mostly with valves conjoined, from the Assistance Formation of the Canadian Arctic Archipelago. *Septospirifer* Waterhouse, 1971 (see Text-fig. 24.1-3 herein) does have a posterior ventral septum, differing from that of the present genus in being longer and lower. The type species, *S. tatondukensis* Waterhouse from high in the Carboniferous of Yukon, Canada, is differently shaped, with more alate cardinal extremities and narrower sulcus lacking sulcal plicae. Plicae are narrow in three pair, and suggest subdivisions, with costae narrow and well defined, and bifurcate. There is thus considerable similarity between *Septospirifer* and *Gobbettifera*. Poletaev (1997) assessed the genus *Septospirifer* as belonging to Spiriferinae, but provided no specific discussion of the genus.

In a number of respects, *Gobbettifera* is close to *Gypospirifer* Cooper & Grant. It shares alate cardinal extremities and nature of costae with rounded crests, which bifurcate conspicuously, and form narrow and low couplets and triplets, not as high or as distinctive as those of *Gobbettifera*, but close. As well, tiled growth lamellae are developed. The sulcus is bordered throughout by narrowly diverging well defined crests in *Gypospirifer*, unlike the arrangement in *Gobbettifera*, in which the sulcus expands to incorporate the two inner fascicles. The dorsal fold of *Gypospirifer* is comparative low and broad with well defined edges, rather than high and narrow-crested as in *Gobbettifera,* and in the latter genus the innermost plicae pair disappears against the anterior fold, and the second plicae pair pass along the side of the fold, gradually disappearing. Internally, the delthyrium of *Gobbettifera* is preserved as open, whereas it is partly or entirely closed by arched stegidia in *Gypospirifer* (Cooper



Text-fig. 25. *Gobbettifera angulata* n. gen., n. sp. from GSC 26406, Assistance Formation, Canadian Arctic x1. 1, GSC 9822 showing ventral aspect of ventral valve with spiralia from dorsal valve, broken on the right side, median septum under umbo. 2A, longitudinal section of ventral valve GSC 9824 showing median septum in front of umbo u, base of sulcus s and crest of lateral plication b. 2B, longitudinal section showing relative height of dental plate dp and adminiculum. 3, sections across ventral umbo, showing median septum.

& Grant 1976; Legrand-Blain 1986a). No ventral median septum or myophragm is developed in *Gypospirifer*, and dental plates were described as deep, with no illustration, and secondary thickening was deemed to be considerable.

Ovispirifer n. gen. is less close to *Gobbettifera*, in having more obtuse cardinal extremities, and also has weak and narrow simple plicae, and gently rounded sulcus and fold. *Lepidospirifer* Cooper & Grant, 1976 has an open delthyrium with small apical callosity, and the bifurcating costae have round crests crossed by strong concentric lamellae and forming a number of narrow fascicles posteriorly. *Lepidospirifer* has a simple narrow sulcus with subdued subplicae posteriorly in at least some species, narrow subangular crested fold, high dental and adminicular plates, and no myophragm or ventral median septum.

The type species of *Gobbettifera* first was identified as *Spirifer striatoparadoxus* Toula, which has been referred subsequently to *Kaninospirifer* Stepanov & Kulikov, 1975. Compared with *Gobbettifera, Kaninospirifer* has a broader plication bordering the sulcus, with subdivision within the sulcus weakly indicated in some species such as *kaninensis* and *adpressum*, and more strongly in *borealis*. Overall, plicae are very subdued, simple and broad, unlike those of the present form. In the present genus, three major pairs of plicae may be discerned, but these are complex and varied, the first innermost pair often subdivided into two fascicles, and second pair narrow, the third pair broad with 2-3 narrow fascicles, and laterally 1-3 more narrow subplicae. Cardinal extremities near maturity in the type species of *Kaninospirifer* develop somewhat larger, longer ears, less narrow than in the present form. Internally, the dental plates of *Kaninospirifer* are very small, and there is no indication of any ventral median septum.

Differences from Neospiriferinae are more marked. Both *Neospirifer fasciger* (Keyserling) and *Betaneospirifer moosakhailensis* (Davidson) are much more strongly plicate, and the costae show less branching and no comparable subdivision into a number of subplicae. None have a strong ventral median septum, and the delthyrium in well preserved specimens has an arched cover. Dental plates are comparable.

Gobbettifera angulata n. sp.

Text-fig. 24.6, 7, Text-fig. 25

1960 *Spirifer striato-paradoxus* not Toula Harker, p. 67, pl. 19, fig. 1-7.

1968 *S. striatoparadoxicus*. Bamber et al., p. 630, pl. 14, fig. 9.

DERIVATION: angulatus - with corners or angles, Lat.

HOLOTYPE: GSC 13748, figured by Harker (1960, pl. 19, fig. 1-3) and Text-fig. 24.6,7 herein, from Assistance Formation, Ellesmere Island, here designated.

DIAGNOSIS: Shells with high angular-crested fold, deep and narrowly troughed sulcus, plicae moderately developed over posterior shell.
DESCRIPTION: This species was described by Harker (1960) from the Assistance Formation at GSC locality 26406, Grinnell Peninsula, Ellesmere Island, of Roadian age. Two ventral valves GSC 9822 and GSC 9823 have well developed dental plates, high sturdy posterior median septum, higher than the myophragm of many spiriferid genera, and open delthyrium. A small ventral valve GSC 9824 shows low dental plates.
RESEMBLANCES: The species is readily distinguished by its well developed sulcus and fold and ventral septum from another Arctic species described as *Spirifer striatoparadoxus* Toula, 1873. This species has been discussed in a number of studies, as summarized by Gobbett (1964). A further new species, *greenlandicus*, here proposed as type species of a new genus *Fasciculatia,* has a less angular less profound sulcus, and slightly less alate cardinal extremities, but subplicae are developed with bifurcating costae that are less concentrically laminated. Dental plates are well developed, and the delthyrium is either open with a small apical callosity, or partly closed. There is no median septum.

Family **NEOSPIRIFERIDAE** Waterhouse, 1968

[nom. transl. hic ex Neospiriferinae Waterhouse, 1968, p. 9].
DIAGNOSIS: Generally transverse, weakly to strong plicate, overall costate, with delthyrial cover or stegidal plates, subdued or no umbonal callosity.

Subfamily **IMBREXIINAE** Carter, 1994

[nom. transl. hic ex Imbrexiidae Carter, 1994, p. 345].
DIAGNOSIS: Transversely rectangular shells with transverse and alate early growth stages after initial rounded growth stage, short delthyrial plate, moderately numerous simple and bifurcating costae over flanks, sulcus and fold, no well formed sulcal plicae, weak radial capillae and imbricate growth lamellae.
GENERA: Genera include *Imbrexia* Nalivkin, *Fernglenia* Carter, *Frechella* Legrand-Blain, *Tegulocrea* Carter.

Genus ***Frechella*** Legrand-Blain, 1985

The type species of *Frechella* is *Neospirifer fascicostatus gwinneriformis* Legrand-Blain, 1971, and it shows alate cardinal extremities, narrow sulcus, and tricostate fascicles in 3-5 pairs of somewhat ill-formed plicae with coarse primary and in some specimens fine secondary costae, and predominantly concentric micro-ornament. *Frechella* was included within Trigonotretinae by

Carter et al. (1994), but the delthyrium lacks the massive umbonal callosity typical of Trigonotretidae, Legrand-Blain (1986*a*, pl. 1, fig. 3) recording a thick delthyrial plate, and a delthyrial cover with concentric growth-lines was illustrated for *fascicostatus* by Legrand-Blain (1971, text-fig. 3).

There is considerable approach to Fusispiriferinae, especially *Cratispirifer* Archbold & Thomas, in its narrow sulcus with feeble or no subfascicles, its narrow and few plicae, and broad lateral shell ornamented by costae only, and although cardinal extremities are alate and the shell more elongate than in most forms of Fusispiriferinae, the genus *Frechella* may have been ancestral.

Subfamily **NEOSPIRIFERINAE** Waterhouse, 1968

DIAGNOSIS: Plicate costate shells with usually broad sulcus that expands to involve innermost pair of plicae in many genera, micro-ornament with concentric and generally radial filae, well formed sulcus and fold, delthyrium covered by delthyrial plate. Ventral interior has dental plates, teeth, short adminicula, often low myophragm, ventral adductors and diductor impressions, no umbonal callosity. Vascular impressions known to be branching in a few genera. Dorsal interior with inner and outer socket plates, crural plates, ctenophoridium, low median septum between adductor scars, spiralia.

DISCUSSION: Neospiriferinae are distinguished mostly by plication. They are not considered to fall within Trigonotretidae, unlike Carter et al. (1994), because of the difference in delthyrium. Carter et al. (1994) suggested that Neospiriferinae had evolved from *Imbrexia* and allies of Imbrexiinae, here regarded as a subfamily within Neospiriferidae.

Poletaev (1997) emphasized mutiple bifurcating costae and presence of delthyrial plate as characters of Neospiriferinae. On that basis he excluded *Gypospirifer* and *Septaspirifer*, as herein. *Lutuginia* Poletaev, 1997, type species *Spirifer lutugini* Rotai, 1931, was regarded as an ally of *Neospirifer*, and has a thin delthyrial cover, subparallel adminicula, very narrow subdued plicae and bifurcating costae, which also closely approach those of Spiriferinae and Gypospiriferinae. According to Poletaev (1997, p. 309), species of the *“Neospirifer” tegulatus* Trautschold group have a well developed stegidial plate, not as yet described or illustrated, and were to be referred to Trigonotretinae. Yet trigonotretids have no stegidial plates, and the original figures of *tegulatus* suggest a position close to Neospiriferinae (Trautschold 1876, pl. 35, fig. 6a-g). Cooper & Grant (1976) claimed that *tegulatus* belonged to *Gypospirifer*, but only, it would seem, on the presence of tegulate ornament, which is not restricted to *Gypospirifer* , as pointed out by Archbold & Thomas (1984). The well defined plicae, weakly defined sulcus and indications of sulcal plicae suggest that the species *tegulatus* is neospiriferin.

Gibbospirifer Waterhouse (Text-fig. 26) seems particularly hard to place, and was excluded from Neospiriferinae by Poletaev (1997), for reasons not clearly specified. It has subdued but distinct plicae separated by narrow interspaces and no sulcal plicae. Fine undifferentiated costae cover the plicae from umbo to anterior commissure, and the delthyrium as preserved is open and may have a small umbonal callosity. The hinge is wide and probably denticulate. It is here regarded as a member of Costuloplicinae, a small and unusual group descended from Angiospiriferinae (p. 188).

Tibetospirifer Liu & Wang, 1990 was included in the subfamily by Carter et al. (1994), but appears to fall within Fusispiriferinae.

GENERA: Genera include *Neospirifer* Fredericks, *Betaneospirifer* Gatinaud, *Lutuginia* Poletaev, *Maxwellispirifer* Waterhouse n. gen., *Pondospirifer* Waterhouse, *Simplicisulcus* Waterhouse, *Spiriferalaria* Waterhouse.

Genus ***Neospirifer*** Fredericks, 1923

TYPE SPECIES: *Spirifer fasciger* Keyserling, 1846, p. 231.

DIAGNOSIS: Shells small to medium-sized, generally of transverse suboval shape with rounded to weakly alate cardinal extremities, moderately narrow hinge, maximum width in front, wide deep sulcus and moderate to high fold, plicae well developed, including pair within sulcus from close to inception, shell overall costate, costae fasciculate, trifurcate posteriorly, bifurcating in front, growth lamellae well to moderately developed. Delthyrium partly to entirely covered.

DISCUSSION: Poletaev (1997) has clarified aspects of the type species *fasciger*, and there is now more information than previously available to reinterpret and refine the attributes and differences within the substantial array of species previously classed as *Neospirifer*. The type species has to be interpreted from two small individuals examined by Keyserling (1846): there seems to be no prospect of obtaining further material from a type locality. The lectotype 129/46 at the Museum of the Mining Institute, St Petersburg, is a dorsal valve showing costae, narrow dorsal fastigium with raised narrow crest, and plicae in 3 or 4 pair. The paratype 128/46 is a ventral valve of moderate size, possibly not fully mature, with sulcus V-shaped in section, not very deep or wide, and incorporating a distinct pair of plicae diverging at close to 20º, and bordered by a second stronger pair of plicae diverging at close to 50º, as estimated from the figures in Poletaev (1997), and also from figures provided by Archbold & Thomas (1984, text-fig. 1F, H, I, text-fig. 2C). Costae are fine, 4-5 in 5mm, and show mutiple bifurcations, but there is no published information on the presence or absence of radial filae. There are 2-3 well developed pair of plicae and further prominent costae or subplicae laterally.

Poletaev (1997, p. 306) identified with *Neospirifer fasciger* various specimens collected from the Middle and Upper Productus Limestones (mainly Kalabagh and Kufri Members) of the Salt Range, Pakistan, and kept at the Central Geological Prospecting (TsNIGR) Museum, St Petersburg, named after F. N. Tschernyschew. In the suite so identified, the ratio of the length of the cardinal margins to the shell width was stated to range from 1.3 to 1.2, and showed little change. This "first group" was distinguished from a "second group" of shells from the same localities, which has a changing ratio, the ratio of the hinge in juveniles being at 0.75 of the width, becoming 1:1 in adults, and later in more advanced specimens developed an even wider hinge. The shells of this group were identified by Licharew (1942) as "forma rectiareata". Poletaev (1997, p. 306) identified the first group as identical with *Spirifer fasciger* sensu Keyserling, and illustrated his interpretation by figuring several Salt Range individuals of the "first group" as *fasciger* (Poletaev 1997, pl. 4, fig. 4-7), and using the Salt Range specimens to provide external and internal detail for that species. Internal detail was supplied through referral to Salt Range thin sections ascribed to *moosakhailensis* by Waterhouse (1968), and reproduced by Poletaev (1997, text-fig. 2). Poletaev (1997, p. 307) equated *Spirifer fasciger* sensu Tschernyschew (1902) with the specimens of the second group, which he identified with *Neospirifer moosakhailensis* (Davidson).

The lack of reliability with regard to *fasciger* is obvious. For a start the Salt Range specimens are very much younger than the Russian types, and the Russian types are inadequate for firm identification with Salt Range species, because they allow only some of the important aspects of the exterior to be determined. Using Salt Range material is no substitute for retrieving good Russian material from at least close to the original locality. Licharew (1942) and Poletaev (1997) were right to recognize two different neospiriferin taxa amongst Salt Range collections, but they wrongly concluded that one was *fasciger*, an extremely doubtful suggestion even if the Salt Range specimens had in fact come from "the late Lower Permian" as asserted by Poletaev (1997, p. 307). As summarized in Waterhouse (2002c), conodont and other evidence suggests a Wuchiapingian, early Late Permian, age. The Salt Range species differs from *fasciger* in size and ornament. Nonetheless, the species *fasciger* from Russia appears to be congeneric with group 1 species from the Salt Range. Thus it remains necessary, given the lack of material for *fasciger*, to rely on the Salt Range specimens to provide information about the interior and micro-ornament. This is not satisfactory, but there appears to be no alternative.

The serial sections provided by Waterhouse (1968, text-fig. 8) for the *fasciger*-like Salt Range material came a moderately small and well preserved specimen from the Kalabagh Member of the Salt Range. I have a plaster mould that is labelled as having been sectioned and almost fitting the sections, but slightly smaller, although the caption states that the figures are x1. The mould has 5 well developed ventral plicae pairs, including strong sulcal pair. The hinge, though not so shown in the sections, is incomplete, being broken on both sides, so that the sections could mislead over the width of the hinge. But the interarea is high, with margins diverging at the same angle as in other short-hinge specimens. Waterhouse (1968, pl. 3, fig. 12) also figured a dorsal valve from the Kalabagh Member, now difficult to identify specifically, and likely to be conspecific with *poletaevi*, given the obtuse cardinal extremities and nature of the ornament.

A further caution to be kept in mind concerns uncertainty over the assertion by Poletaev (1997, p. 305) that B. K. Licharew had sent specimens of *Gypospirifer* rather than *Neospirifer* to J. B. Waterhouse. Some of the Licharew specimens were figured and sectioned by Waterhouse (1968, text-fig. 7a, pl. 16, fig. 3, 7), and came from the Schwagerina Horizon of Lipovaya Mt, near Asha village, Sim River, south Urals. Plaster duplicates were prepared prior to sectioning, and are still retained. One specimen (Waterhouse 1968, pl. 16, fig. 3, text-fig. 7A.1, 2, 4) shows persistent and well formed plicae, with no pair within the sulcus, and belonging to *Simplicisulcus*. The specimen is not *Gypospirifer* sensu Cooper & Grant, judged from the strength of plicae and the definition of the sulcus. The other specimen (Waterhouse 1968, pl. 16, fig. 7, text-fig. 7A.3) has moderately strong but narrow fascicles up to 40mm from the ventral umbo, and dorsal fascicles persist to the anterior margin, along with broad dorsal fastigium, and a pair of faint plicae within the posterior ventral sulcus. *Gypospirifer* lacks sulcal plicae, although bundles of three costae do form outside the sulcus and very close to the ventral umbo, within some 10mm. The costae in the sectioned Russian specimen are grouped posteriorly in threes as impersistent fascicles, and many costae anteriorly bifurcate, as in *Gypospirifer,* but also in *Neospirifer* and *Betaneospirifer*. The material is not *Gypospirifer*, as defined by Cooper & Grant (1976), and the plicae are narrower and more numerous than in *Kaninospirifer* Kulikov & Stepanov. Thus the specimen belongs to *Betaneospirifer* or *Fasciculatia*: the latter seems likely.

The new understanding of *Neospirifer*, following Poletaev, depicts *Neospirifer* as close to *Cartorhium* Cooper & Grant, 1976 in shape, with short hinge and extended posterior and high ventral interarea. Fascicles are not well defined in *Cartorhium* and often fade anteriorly, and the delthyrium is open except under the beak, where it is filled by a pseudodeltidium or apical callosity, according to Cooper & Grant (1976, p. 2191), not by a delthyrial plate which characterizes *Neospirifer*. Such an interpretation depends of course on the generic match of type *Neospirifer* with the Salt Range species.

Neospirifer is in summary to be distinguished from other allies within Neospiriferinae by its high triangular ventral interarea, comparatively short hinge, and suboval outline. The shape of the Salt Range specimens of *Neospirifer* changes into maturity, with the anterior lateral margins becoming more extended and lateral margins wider, so that specimens become more transverse, but do not achieve the more subrectangular outline of *Kaninospirifer* and *Betaneospirifer.*

Neospirifer poletaevi n. sp.

Plate 3, fig. 3

1862 *Spirifera moosakhailensis* not Davidson, p. 28, pl. 2, fig. 2c (part, not fig. 2a, b = *moosakhailensis*).

1942 *Spirifer moosakhailensis*. Licharew, p. 64, pl. 1, fig. 2-5 (part, not fig. 1 = *moosakhailensis*, not fig. 6, 7 = *ambiensis?*).

1944 *S. (Neospirifer) warchensis scabrosa* Reed, p. 199, pl. 27, fig. 8, 8a (part, not fig. 7 = *scabrosa*).

1968 *N. moosakhailensis*. Waterhouse, pl. 3, fig. 12, text-fig. 8.

1978 *N. moosakhailensis*. Waterhouse, p. 42, pl. 3, fig. 16-19 (part, not pl. 26, fig. 4-7 = *moosakhailensis*, not pl. 26, fig. 1-3 = *neomarcoui*).

1997 *N. fasciger* (not Keyserling) Poletaev, pl. 4, fig. 5-7, text-fig. 1, 2 (part, not pl. 4, fig. 2a-d, 3a-d = *fasciger*).

?2001 *N. moosakhailensis*. Shen et al. text-fig. 5.4-7 (part, not text-fig. 5.1-3 = *moosakhailensis*).

DERIVATION: Named for V. I. Poletaev.

HOLOTYPE: B 82373 figured by Davidson (1862, fig. 2c), Licharew (1942, pl. 1, fig. 2), Waterhouse (1978, pl. 3, fig. 16-19) and herein as Pl. 3, fig. 3, from Wargal Formation, Kalabagh Member, Salt Range, Pakistan, here designated.

DIAGNOSIS: Small suboval shells with comparatively narrow but well defined plicae in 4-5 pair, costae fine.

DESCRIPTION: Shell small, holotype measuring 30.5 in width, 18mm in length and 13.5mm in height, with hinge width 17mm. Outline transversely oval, maximum width just in front of mid-length, ventral interarea short and high, edges diverging at 100-110^{o} at interface with outer shell, delthyrium has angle close to 90^{o}, bordered by well defined teeth tracks. Dorsal interarea low. Sulcus well defined, commencing at umbo, bordered posteriorly by plicae diverging at 20^{o}, and anteriorly by second pair of plicae diverging at 40^{o}, floor concave; fold also well defined and broadening anteriorly. Shell bearing 4-5 pairs of ventral plicae and 4-5 pairs of dorsal plicae, curving outwards anteriorly, carrying sharply defined narrow fascicles of no more than 3 costae; costae with rounded crests and sharply defined interspaces. Costae moderately high, begin to bifurcate 7-8mm from umbonal tip, on either the outward or inward side along different fascicles. Lateral costae raised and prominent but not subdivided, further fine costae laterally. Shell crossed by well defined growth lamellae, but radial capillae not visible in available material and it requires further examination to determine if capillae are present. In small shells, the maximum width lies well in front of the hinge, and the posterior walls are long. Shape changes a little into maturity, with the anterior lateral margins becoming more extended and lateral margins wider, so that specimens become more transverse.

The interior is revealed by sectioning of a ventral valve by Poletaev (1997, text-fig. 1) and a complete specimen (Waterhouse 1968, text-fig. 8). Dental plates moderately well developed, supported by adminicula which are high and diverge strongly to the floor of the valve. Small delthyrial plate covers the upper delthyrium. Dorsal valve with socket and crural plates and extended spiralia.

There is a little variation in the fineness of costae and position at which bifurcations commence. The specimen figured by Poletaev (1997, pl. 4, fig. 5a) has broader inner plicae with more costae, and in other figured specimens the costae split anteriorly but remain close.

RESEMBLANCES: This species has been identified with *Neospirifer fasciger* (Keyserling), and is close in general appearance, involving shape, interareas and ornament. But the two are not conspecific. The Salt Range species has more sharply defined and narrower fascicles that are more numerous, and the fold is lower and and less narrowly crested, and the sulcal plication narrower and higher.

Reed (1944) figured specimens of two different genera as *Spirifer (Neospirifer) warchensis scabrosa*, and one, from the Kalabagh Member, is deemed to be conspecific with *poletaevi*. The other is made type of Reed's taxon *scabrosa*, and is provisionally referred to *Simplicisulcus* Waterhouse, as discussed below (p. 125). It comes from the Kufri Member in the Salt Range. *Spirifer (Neospirifer) warchensis* Reed (1931, p. 21, pl. 4, fig. 9; 1944, p. 198) apparently belongs to *Blasispirifer* Kulikov (p. 238).

A small specimen figured as *Spirifer musakheylensis* by Waagen (1883, pl. 45, fig. 5a-d) from the Wargal Formation is judged to be *moosakhailensis* rather than *poletaevi*, because it is shown as having fewer and broader plicae and slightly wider hinge and less oval shape. A specimen assigned to *Neospirifer moosakhailensis* by Shen et al. (2001, text-fig. 5.4-7) from the upper Wargal Formation of the Salt Range appears to have short hinge and high interarea as in *poletaevi*, but needs to be examined at first hand. It has 5 pair of well defined dorsal plicae.

Possibly *Neospirifer chivatschensis* Zavodowsky (see Zavodowsky 1970, pl. 76, fig. 1, 2, pl. 79, fig. 1) from the Omolon beds of Hivatch River, northwest Siberia, is allied. The posterior walls are long and the cardinal extremities obtuse. The outline suggests that the ventral interarea might well prove to be high and triangular, and the hinge short, but figures do not adequately show these aspects. A few other species from Asia might well be congeneric, but are not well portrayed.

Neospirifer kalashnikovi n. sp.

1944 *Spirifer (Neospirifer) subfasciger* not Licharew Reed, p. 207, pl. 27, fig. 5a, b.

DERIVATION: Named for N. V. Kalashnikov.

HOLOTYPE: Sole specimen figured by Reed (1944), from Lower Productus Limestone (Amb Formation), Salt Range, by monotypy. Kept at Geological Survey of India, Calcutta.

DIAGNOSIS: Plicae few, dominated by second broad pair, narrow sulcal pair, and low outermost pair.

DESCRIPTION: The holotype is well preserved, with moderately prominent umbo with angle of 110º, almost straight posterior umbonal walls, and width close to 25mm. The hinge is short with high triangular ventral interarea, and cardinal extremities close to mid-length. The sulcus is well formed, with pair of narrow sulcal plicae. Broad plicae border the sulcus, next to low outermost pair, with further costae laterally. Dorsal valve has moderate fold, narrow inner pair of plicae, wider second pair and moderately developed outermost pair. Costae are fine.

RESEMBLANCES: Reed (1944) compared his material to *Spirifer (Neospirifer) subfasciger* Licharew, 1934, but this species is shaped like typical *Betaneospirifer*. Reed's form, of Guadalupian age, is readily distinguished from the much younger species *Neospirifer poletaevi* by its different plicae and less sharply defined costae. *N. fasciger* (Keyserling) is closer in plication, but has better defined sulcal pair of plicae, and more sharply defined dorsal fold, and ventral posterior walls that are weakly convex in outline.

Genus ***Betaneospirifer*** Gatinaud, 1949

TYPE SPECIES: *Spirifer moosakhailensis* Davidson, 1862, p. 28.

DIAGNOSIS: Shells medium to large, generally of transverse subrectangular shape with rounded to weakly alate cardinal extremities, moderate to wide hinge, maximum width generally at hinge, wide deep sulcus and moderate to high fold, plicae well developed, including pair within sulcus from close to inception, shell overall costate, costae fasciculate, trifurcate posteriorly, bifurcating in front, growth lamellae well to moderately developed. Delthyrium partly to entirely covered.

DISCUSSION: Gatinaud (1949) erected what he called a “section” *Betaneospirifer* within genus *Neospirifer,* based on *Spirifer moosakhailensis* Davidson. Pitrat (1965, p. 699) considered that the name, together with others proposed by Gatinaud (1949), did not constitute a valid taxon, but it was listed as a genus within Neospiriferinae by Carter et al. (1994, p. 346). Poletaev (1997) also included the genus as a member of Neospiriferinae, yet included its type species *moosakhailensis* as a valid species of *Neospirifer*.

Two critical matters need to be resolved, concerning the validity of the proposal, and whether *moosakhailensis* is generically separate from *fasciger*. The first matter remains arguable, but in my opinion, Gatinaud came close enough to offering a valid proposal, with diagnosis and comparison. The nomination of a well known species as type makes his taxon readily open for interpretation. The second matter requires no conjecture. The shapes of the two type species differ considerably, and each is generically typical of a number of allied species. It is true that apart from Carter et al. (1994) all authors over the last decade seem to have used *Neospirifer* for *moosakhailensis* and closely allied species, but they have offered no discussion of the matter, and neglected to even refer to *Betaneospirifer*. Appeals to “customary use” retain little credibility when custom neglects to cover literature adequately: that would make a virtue of ignorance.

Betaneospirifer marcoui (Waagen, 1883)

1862 *Spirifera striatus* (not Martin) Davidson, p. 28, pl. 1, fig. 9, 10.
1883 *S. striatus*. Waagen, p. 509, pl. 44, fig. 3, 5? (part, not pl. 44, fig. 4).
1883 *Spirifer marcoui* Waagen, p. 510, pl. 47, fig. 1-3.
1902 *Spirifer marcoui.* Tschernyschew, p. 533, text-fig. 47 (part, not pl. 6, fig. 9, pl. 12, fig. 3).
1942 *Spirifer marcoui*. Licharew, pl. 2, fig. 2a, b.

LECTOTYPE: GSI 3519 figured by Waagen (1883, pl. 47, fig. 1a-c) from Amb Formation, Salt Range, here designated.

DIAGNOSIS: Moderately large shells with deeply troughed ventral sulcus, high fold, weakly defined plicae as a rule with subdued sulcal pair.

DESCRIPTION: These shells are of moderate size for the genus, with hinge close to maximum width. In the initial transverse growth phase of the shell up to a width of 30 or 40mm at most, cardinal extremities are alate and the antero-lateral margins then start to bulge out. Ventral sulcus deeply troughed with rounded floor, bearing moderate varying to very subdued pair of sulcal plicae which may be faint or disappear anteriorly, and the plicae bordering the sulcus are moderately to usually well defined, diverging forward at 40-50º. The dorsal fold is narrow and high anteriorly, and commences a little in front of the hinge. Plicae number 4-5 pairs, and laterally may be subdued, as in shells figured as *striatus*. Although the Waagen illustrations of type material indicate that plicae are very faint, the plicae are a little stronger on the actual specimens. There are 4 pair on specimen GSI 3521, including faint sulcal pair of plicae, and slightly stronger plicae in the lectotype GSI 3519, and very faint if any sulcal plicae. Costae are of moderate strength, stronger than in the younger species *ambiensis* Waagen and *neomarcoui* Licharew.

DISCUSSION: The subspecies *marcoui undata* Reed (1944, pl. 25, fig. 1, 2, 2a) has plicae that are comparatively strong on the ventral valve, very weak on the dorsal valve, sharp-crested high fold more prominent just in front of the hinge, and shallow narrow sulcus. There are 4 pair of plicae, including well defined pair in the sulcus, with suggestions of a fifth pair, and fine costae, and the shell is less elongate than *marcoui*, and close to *ambiensis* Waagen in several respects including shape and cardinal extremities. It is supposed to have come from the Lower Productus Limestone (Amb Formation), but morphology suggests that the source may be questioned.

Archbold & Thomas (1986, p. 143) noted various suggestions that the species *marcoui* approached specimens in Western Australia. These specimens were described as *Neospirifer amplus* Archbold & Thomas from the Wandagee Formation, of latest Cisuralian or possibly early Guadalupian age. The species *marcoui* does include specimens that show comparable profound sulcal tongue and high anterior dorsal fold, but *amplus* differs from *marcoui* in its transverse hinge, lower ventral umbo, larger size, and wider deeper sulcus, aspects all characteristic of the new genus *Wadispirifer* (see below).

Zhang in Zhang & Jin (1976, pl. 15, fig. 3, 4) described and named a solitary and incomplete ventral valve from Tibet as *Neospirifer striatiformis* which has coarse not fine costae and low plicae and moderately deep sulcus. It is too poorly known to be useful, with no data on ventral interior and dorsal valve. Short of finding more and better preserved material, the species seems indeterminate, although showing approaches to *Occidalia* and *Cratispirifer*. Zhang also referred better preserved specimens figured by Waagen (1883) from the Salt Range to his species *striatiformis*. These specimens are believed to be synonymous with *marcoui*.

Neospirifer marcoui tolingensis Xiong in Yang et al. (1990, pl. 23, fig. 23a, b) from south Tibet has fine ribs, wide sulcus, and high narrow-crested fastigium. It is poorly preserved, with poorly reproduced figures, and so is very difficult to interpret, and looks somewhat like *Wadispirifer* because the sulcus is wide and deep.

Betaneospirifer moosakhailensis (Davidson, 1862)

1862 *Spirifera moosakhailensis* Davidson, p. 28, pl. 2, fig. 2a-b (part, not fig. 2c = *poletaevi*).

1867 *S. moosakhailensis*. Verneuil, p. 210, pl. 3, fig. 1, 1a.

1883 *Spirifer musakheylensis*. Waagen, p. 512, pl. 45, fig. 1a-c (part, not 2, 3, 4, 5, ?6 = *neomarcoui*).

1942 *S. moosakhailensis*. Licharew, p. 64, pl. 1, fig. 1 (part, not fig. 2-5 = *poletaevi*, not fig. 6, 7 = *ambiensis*).

1978 *Neospirifer moosakhailensis*. Waterhouse, p. 42, pl. 26, fig. 4-7 (part, not pl. 3, fig. 16-19 = *poletaevi,* not pl. 26, fig. 1-3 = *neomarcoui*).

2001 *N. moosakhailensis*. Shen et al., p. 162, text-fig. 5.1-3 (part, not text-fig. 5.4-7 = *poletaevi*).

LECTOTYPE: For *moosakhailensis*, B 82371 figured by Davidson (1862, pl. 2, fig. 2a, b), SD Licharew (1942) from the lower Wargal Formation, Salt Range, Pakistan. Also figured by Licharew (1942, pl. 1, fig. 1), Waterhouse (1978, pl. 26, fig. 4-7) and Shen et al. (2001, text-fig. 5. 1-3).

DIAGNOSIS: Transverse moderately large shells, with fine costae posteriorly, coarse anteriorly, and close-set moderately well developed growth lamellae and fine radial capillae, comparatively well developed sulcus and fold, becoming emphasized anteriorly, plicae well defined, costae subangular to round in section posteriorly, subangular but worn anteriorly, plicae in sulcus not well defined, may not persist forward, lateral margins gently rounded, subparallel; sulcus wide and anteriorly deep, fold broadens in front to incorporate the inner pair of plicae towards midlength. Growth development distinctive, small specimens 13mm wide have short hinge less than 0.75 of shell width, and obtuse cardinal extremities. Immature and mature specimens, such as the lectotype, have hinge extending almost full width of shell.

DISCUSSION: This species was described from the Salt Range, probably from the base of the Wargal Formation. Waagen (1883) also named an immature transverse specimen as a new species *ambiensis*, which came from the younger Kufri Member in the Salt Range. The species *ambiensis* Waagen has more strongly emphasized sulcal plicae and five pair of plicae overall in the holotype, whereas *moosakhailensis* has 4 pair, and weak lateral fascicles suggested on the interior but not exterior shell. As a rule *ambiensis* has more prominent ventral umbo and slightly finer costae, especially anteriorly. It is more transverse at early growth stages and has a wider hinge early in ontogeny, and its cardinal area is rectilinear and slightly lower, and the sulcus is shallower. In the lectotype of *moosakhailensis*, the innermost pair of plicae has been damaged but is visible behind the lump of matrix on the shell, and fades anteriorly. The pair lies at the edge of the sulcus only for some 5mm from the umbo and is less conspicuous and less persistent than in *ambiensis*, and is stronger on one side than the other in the type. In the dorsal valve the innermost pair of plicae passes forwards into the fold, as also suggested for *ambiensis.*

The specimen from the Salt Range figured as *moosakhailensis* by Waagen (1883, pl. 45, fig. 1) appears to have the deep sulcus, high fold and subdued plicae indicative of *moosakhailensis,* although not exactly the same. It comes from the Katta beds, classed by Waagen (1883) at the base of the Middle Productus Limestone, but evaluated as top of the Lower Productus Limestone by some authors, as summarized in Waterhouse (1976).

Poletaev (1997, pp. 306-307) recognized two suites in the Salt Range collection of *moosakhailensis* at TsNIGRI Museum, St Petersburg, Russia. Poletaev stated group 1 was *fasciger*, and group 2 *moosakhailensis*. In reality, from consideration of suites of specimens, plaster moulds and illustrations of the two taxa, and disregarding claims of identity with Russian *fasciger*, group 1 is *Neospirifer poletaevi*, and group 2 is probably *ambiensis* or *neomarcoui*, judged from the width of hinge and number of plicae pairs, though there is uncertainty, because only dorsal aspects were figured, and the strength of plicae is the same in both species. I am inclined to favour *ambiensis* as the host, because the specimens were not identified as *neomarcoui* by Licharew. The lectotype of *moosakhailensis* has a subtriangular ventral interarea, and a hinge close to that of *ambiensis* and *neomarcoui*, but slightly shorter during early growth phases, and much longer than in *poletaevi.*

The species *moosakhailensis* differs from the older regional species *Betaneospirifer marcoui* (Waagen) in its better developed plicae, broader less profound sulcus and slightly lower broader fold, although overall shape and distribution of plicae are close. The ventral umbo is wider, cardinal extremities are less rounded, and the shell less elongate. The sulcal plicae are more conspicuous in the younger species, the costae slightly finer posteriorly with steeper flanks, and coarser anteriorly, and concentric laminae more prominent, and various other differences may be discerned. Further comparisons, especially with Himalayan species, will be enumerated below.

The species *moosakhailensis* has been widely reported (eg. Merla 1934, Astre 1934), but material is seldom preserved well enough to allow confidence. STRATIGRAPHIC SOURCE OF LECTOTYPE: According to Dr A. N. Fatmi, then at the Geological Survey of Pakistan, when he guided a small party made up of N. D. Newell, J. M. Dickins and me through the Salt Range in 1964, the limestones at Moosa Kheil (Musa Khel) consist mainly of Amb Formation, with some lower Wargal Formation (Waterhouse 1966, p. 40, Grant 1976, p. 213). This opens up possibilities of confusion over the original source for Davidson's material, or unrealized variation, and other possibilities, that will need to be resolved by matrix examination, and/or further study in the Salt Range. But present analysis supports Dr Fatmi's view of the stratigraphy, with *moosakhailensis* likely to have come from lower Wargal Formation, and a little older than the species *neomarcoui* and *ambiensis*. The lectotype of *moosakhailensis* differs from the types and other Amb specimens assigned to *marcoui*, most notably in the height of its plicae, and comes closer to Wargal - Chhidru *Betaneospirifer* apart from strength of sulcal plicae and depth of sulcus.

Betaneospirifer ambiensis (Waagen, 1883)

Plate 3, fig. 8

1866 *Spirifera moosakhailensis* not Davidson Davidson, p. 41, pl. 2, fig. 6.
1897a *S. musakheylensis.* Diener, p. 43, pl. 6, fig. 8.
1897b *S. musakheylensis*. Diener, p. 35, pl. 3, fig. 3, 4 (part, not pl. 4, fig. 1?, 2 = *ravana*, not pl. 5, fig. 1 = *macroplica*).
1899 *S. musakheylensis*. Diener, p. 63, pl. 5, fig. 6 (part, not fig. 3-5, 7 = *ravana* Diener).
1899 *Spirifer* sp. ind. aff. *musakheylensis.* Diener, p. 65, pl. 5, fig. 10.
?1942 *Spirifer moosakhailensis* Forma *rectiareata* Licharew, p. 69, pl. 1, fig. 6, 7 (part, not fig. 1 = *moosakhailensis,* not fig. 2-5 = *poletaevi*).
?1944 *S. (Neospirifer) marcoui* Waagen *undata* Reed, p. 200, pl. 25, fig. 1, 2, 2a.
cf 1944 *S*. (*Neospirifer*) *cameratus* not Morton Reed, p. 204, pl. 27, fig. 4.
1962 *Neospirifer moosakhailensis.* Ding, p. 452, pl. 1, fig. 1, 5, 6 (part, not 2, 4? = *tibetensis*?, not fig. 3 = aff. *Wadispirifer?*).
1966 *Neospirifer moosakhailensis*. Waterhouse, p. 34, pl. 8, fig. 1, 2, pl. 9, fig. 1, 4, pl. 10, fig. 2 (part, not pl. 10, fig. 1= *hongdeensis*).
1978 *Neospirifer* cf. *ambiensis*. Waterhouse, p. 41, pl. 4, fig. 8-14, 15?, 16.
1978 *N. ambiensis*. Waterhouse, pl. 26, fig. 8, 9.
1978 *Neospirifer* sp. A Waterhouse, p. 126, pl. 24, fig. 9 (not 10 = *hongdeensis*)
1978 *Neospirifer* sp. B Waterhouse, p. 126, pl. 24, fig. 12, 13.
1979b *N*. cf. *ambiensis*. Waterhouse & Gupta, p. 31, pl. 5, fig. 8, 9.

?1981 *N. moosakhailensis.* Shimizu, p. 80, pl. 8, fig. 24.
1982 *N. kubeiensis*. Zhan & Wu, pl. 5, fig. 14, 20?
?1982 *Neospirifer* sp. Zhan & Wu, pl. 5, fig. 15.
HOLOTYPE: By monotypy, GSI 3524 figured by Waagen (1883) and Waterhouse (1978, pl. 26, fig. 8, 9), from Kufri Member, Salt Range. Lectotype for *undata:* GSI 17026 figured by Reed (1944, pl. 25, fig. 1), here designated, supposedly from Lower Productus Limestone (Amb Formation), Salt Range, Pakistan.
DIAGNOSIS: Specimens characterized by wide hinge, alate cardinal extremities, transverse outline, five plicae pairs including well defined plicae pair within sulcus, sharply defined fold.
DESCRIPTION: Transverse moderately large shells, with fine costae and close-set moderately well developed growth lamellae, comparatively well developed sulcus and fold, becoming emphasized and wide anteriorly, 5 pair of plicae well developed especially on the ventral valve, subangular to round in section, plicae in sulcus generally well defined, lateral margins gently rounded, subparallel. In the dorsal valve of the holotype, the inner pair of plicae appear to merge with the fold flanks anteriorly, much as in *moosakhailensis*. Growth development distinctive, small specimens 30mm wide have wide hinge and acute cardinal extremities, and shells are highly transverse up to a width of 50 or 60mm from the Salt Range, and more in some Himalayan specimens, as from Marbal Pass (Waterhouse & Gupta 1979b) and Kashmir (Shimizu 1981). In these Himalayan shells, the sulcal plicae are less developed, with plicae in the Kashmir specimen figured by Shimizu unusually low for the species, and perhaps fewer in number. Mature specimens fill out antero-laterally and look like specimens of *moosakhailensis* and *neomarcoui,* but the dorsal fold may be slightly narrower and higher, the sulcal tongue a little narrower and deeper, and interarea lower and less triangular. The specimens figured by Diener (1899) are only moderately transverse but sulcal plicae are strong and ribs fine. The hinge is long and linear, and 5 pair of plicae are developed.
DISCUSSION: This species was described from the Salt Range, probably from the Kufri Member of the Chhidru Formation. The taxon *ambiensis* has more strongly emphasized sulcal plicae, and arguably more prominent ventral umbo and slight finer costae, compared with *moosakhailensis*, and the hinge is longer during early development, with slightly lower interarea. Such specimens are common in unfigured collections from Zewan C in Kashmir. The specimens figured by Diener (1897b, pl. 3, fig. 3, 4) as GSI 6197 and 6198 have inner plicae plunging into the sulcus within 5-7mm of the umbo, and wide hinge at immaturity. Specimens as figured by Diener (1899) have weakly obtuse cardinal

extremities, intermediate between *moosakhailensis* and *ambiensis*, and strong inner sulcal plicae as in *ambiensis*. The innermost pair of plicae lies at the edge of the sulcus only for some 5-10mm from the umbo before entering the sulcus, and is more conspicuous than in *moosakhailensis*. From east Dolpo specimens with wide sulcus, strong sulcal plicae, 5 plicae pairs overall, and fine costae come from the *Lamnimargus himalayensis* Zone, accompanied by *Costiferina alata* Waterhouse. Although obscured by deformation, they belong to *ambiensis*. *Neospirifer* sp. B of Waterhouse (1978) from the Luri Member, *Biplatyconcha grandis* Zone, of west Dolpo, is transverse with costae as numerous as 8-9 in 5mm, and is now deemed to belong to *Betaneospirifer ambiensis*. The material has 5 pair of plicae, as does *Neospirifer* A in part of Waterhouse (1978) from the same beds.

Spirifer (*Neospirifer*) *cameratus* not Morton Reed (1944, p. 204, pl. 27, fig. 4) from the Kufri Member is transverse with possibly 5 pair of somewhat subdued plicae. There is doubt over the stratigraphic source of *marcoui undata* Reed, but as discussed for *marcoui*, most available aspects of the morphology suggest a position with *ambiensis*, even though the specimen supposedly came from the Amb Formation in the Salt Range. The designated lectotype has the dorsal valve preserved, although not figured.

From younger Permian of northeast China, Lee et al. (1980, pl. 177, fig. 7, 10, 14) described specimens of which some show 5 pair of plicae, less transverse than *ambiensis*. The specimens were identified as *moosakhailensis* and *ambiensis*, together with others ascribed to various Himalayan species. They need further examination.

STRATIGRAPHIC RANGE: The type of species *ambiensis* comes from the Kufri Member of the lower Chhidru Formation and it is also found commonly in the underlying Kalabagh Member of the Wargal Formation, Salt Range, Pakistan. The species is widespread throughout the *Lamnimargus himalayensis* Zone of the Himalaya, including the correlative Zewan Formation of Kashmir, and extends upward in age into the Senja Formation of Nepal, including the Nisal, Luri, Galte and Ngawal Members of Dolpo and Manang, in the *Biplatyconcha grandis* Zone of the Senja Formation in Dolpo and Manang. It is also found in the Xiala Formation, Xianza district, south Tibet.

Betaneospirifer neomarcoui (Licharew, 1942)

Plate 3, fig. 7

1883 *Spirifer musakheylensis* not Davidson Waagen, p. 512, pl. 45, fig. 2, 3, 4, 5, ?6 (part, not fig. 1a-c = *moosakhailensis*).

?1941 *Neospirifer moosakhailensis.* Muir-Wood & Oakley, p. 30, pl. 2, fig. 12, 13.

1942 *Spirifer neomarcoui* Licharew, pp. 62, 65, pl. 2, fig. 1a, b, c.
1944 *Spirifer (Neospirifer) musakheylensis* Davidson var. nov. *humilis* Reed, p. 198, pl. 25, fig. 3.
1944 *S. (Neospirifer) ravana* Diener *plicatifera* Reed, p. 202, pl. 26, fig. 2, 2a, b, pl. 29, fig. 10.
1953 *Neospirifer fasciger* (not Keyserling) Brown, pl. 5, fig. 7.
1962 *N. kubeiensis* Ding, p. 453, pl. 2, fig. 1-3.
1978 *N. moosakhailensis.* Waterhouse, p. 42, pl. 26, fig. 1-3 (part, not pl. 3, fig. 16-19 = *poletaevi*, not pl. 26, fig. 4-7 = *moosakhailensis*).
1978 *N. kubeiensis.* Waterhouse, p. 125, pl. 24, fig. 5-7.
?1983 *N. ambiensis*. Waterhouse & Gupta, p. 239, pl. 2, fig. 7.
2003a *N. (Neospirifer) kubeiensis*. Shen et al., p. 84, pl. 11, fig. 23, pl. 12, fig. 1-4.

TYPES: Holotype for *neomarcoui*: specimen 6/5969, figured by Licharew (1942, pl. 2, fig. 1a, b, c) from Kalabagh Member, Wargal Formation, Salt Range, kept at Central Geological Prospecting Museum, St Petersburgh, OD. For *humilis* by monotypy, sole GSI specimen figured by Reed (1944), from upper Middle Productus Limestone (Kalabagh Member). Lectotype for *plicatifera*: GSI 17034 figured by Reed (1944, pl. 28, fig. 2, a, b) from lower Chhidru Formation, here designated. Lectotype for *kubeiensis*: IGAS 3602 figured by Ding (1962, pl. 2, fig. 1, 2) from lower Qubuerga Formation, Tibet, here designated. Ding (1962, caption, pl. 2) cited IGAS 3602 and 3592 as syntypes in Chinese and English, and here the first specimen is selected, and the second (Ding 1962, pl. 2, fig. 3 - IGAS 3592) established as paratype.

DIAGNOSIS: Shells large, transverse, wide hinge, plicae well defined within and each side of sulcus, numbering 4 pair in types, sulcus widens anteriorly, may widen anteriorly in large specimens to incorporate next lateral pair, costae fine. Dorsal fastigium possibly tent-shaped, low.

DISCUSSION: The species *neomarcoui* is judged to be close to *ambiensis* Waagen, because of long hinge and well developed inner sulcal pair of plicae. Both Licharew (1942) and Poletaev (1997) apparently overlooked and made no mention of *ambiensis*. Licharew's specimens came from the Kalabagh Member of the Wargal Formation, at Kalabagh. The holotype of *neomarcoui* is inflated and the ventral umbo incurved, and the sulcus wide, indicating full maturity, although it is not large. It has been overlooked in a number of recent studies, except by Lee et al. (1980) and by Archbold & Thomas (1986, p. 136), who suggested that *Neospirifer neomarcoui* showed some similarity to *N. plicatus*. This is now the type species of *Quadrospira*, but Licharew's type differs in alation and other detail.

Compared with *moosakhailensis, neomarcoui* has more strongly developed plicae, including sulcal plicae, but is close in shape, with slightly finer costae and shallower sulcus. The strong persistent inner dorsal plicae do not fade into the dorsal fold, unlike *moosakhailensis*. Specimens of *neomarcoui* at early maturity are highly transverse, approaching *ambiensis*, and include specimens mostly from the upper Wargal Formation figured by Waagen (1883). Uncertainty remains over aspects of the synonymy, because it appears that the species *neomarcoui* co-existed with *ambiensis*, so that stratigraphy cannot be used as a substitute for morphological discrimination. Not all specimens are well figured or preserved, and many are broken.

Betaneospirifer moosakhailensis humilis (Reed, 1944) was described from the upper Middle Productus Limestone (= Kalabagh Member of the Wargal Formation) of the Salt Range. It is not well circumscribed, and the inner sulcal pair diverge at 25-30°, more than in type *moosakhailensis*, and the main bordering plical pair diverge at 60-65°, much as in *moosakhailensis*. There are 4 pair of strong plicae in the ventral valve. Various other aspects were enumerated by Reed (1944), but the figure and description are difficult to interpret. *Spirifer (Neospirifer) ravana plicatifera* Reed (1944) from the upper Middle and Upper Productus Limestone is a mature *neomarcoui.* It has a high and curved ventral interarea, and 4 pair of strong plicae, the sulcal plicae rather high and close to the bordering pair, and fold and sulcus a little more emphasized and narrower than in *moosakhailensis* or typical *ambiensis*. The specimens are close in size and shape to type *neomarcoui*, though plicae differ a little.

To judge from poorly preserved material, the species is also possibly present in northwest India and Lachi series of Sikkim, within the *Lamnimargus himalayensis* Zone. The Bhutan material figured by Muir-Wood & Oakley (1941) is tentatively included, and indicates material with firm costae and narrow sulcus with a pair of plicae, but is poorly preserved, and not well figured. Shen et al. (2003a) suggested that the specimens belonged to *N. kubeiensis* Ding. The specimens are also very close to *neomarcoui* Licharew in the nature of the plicae and sulcal plicae, but the hinge length is not known.

The taxon *kubeiensis* Ding as circumscribed by the nature of type and allied material is identical with *neomarcoui* and close to *ambiensis*. The types of *kubeiensis* have a wide hinge, fine costae, well developed plicae, strong sulcal pair of plicae and strong lateral or bordering plicae, and wide shallow sulcus, with angle up to width of 60°. Shen et al. (2003a) reported counts of 7-9 costae in 10mm on the plicae and 10 laterally, but illustrations of the types, and the material in Shen et al. (2003a) show much finer costae, and 7 or so costae in 5mm would apply widely. It seems likely that *kubeiensis* is scarcely even a geographic variant of *neomarcoui* and very close in most repects to *ambiensis*, other than having one less pair of plicae. The angle of divergence for sulcal bordering plicae may be very roughly estimated from figures, and although not accurate, may be of value for comparing relative figures. The angle is 50^{o} for *plicatifera*, 40^{o} for type *ambiensis* and 60^{o} in *neomarcoui* of Waagen (1883, pl. 45, fig. 2), with sulcal plicae diverging at 28^{o}, 28^{o}, and 35^{o} respectively. The comparable angles for type *kubeiensis* are 60^{o} and 30^{o}; overall the sulcal border plicae diverge at 40^{o} to 60^{o} in both *ambiensis* and *kubeiensis*, and sulcal plicae diverge at between 35^{o} and 28^{o} in each. The angles for *neomarcoui* appear almost identical at 50^{o} and 30^{o}. Unfortunately a number of studies have tried to circumscribe *kubeiensis* without paying attention to *ambiensis* and *neomarcoui*. The dorsal valve of *kubeiensis* is poorly known, but has a low broad fold and moderately defined plicae. Internal detail is also poorly known from Ding's study. Separation of *neomarcoui* and *kubeiensis* is thus precarious, and objectively, the two have to be merged. There may be more justifiable dispute about the value of separating *neomarcoui-kubeiensis* from *ambiensis,* because they occur together in the Salt Range and possibly Qubuerga Formation, and share strong plicae and wide hinge and other detail. Provisonally, the two are separated through plicae counts. In summary:

moderately wide early hinge - *moosakhailensis,* weak sulcal plicae, 4 pair of plicae overall

wide early hinge - *neomarcoui, kubeiensis* and *ambiensis*

4 pair plicae - *neomarcoui* and *kubeiensis,* strong sulcal plicae

5 pair plicae - *ambiensis,* strong sulcal plicae.

Shen et al. (2003a) figured further specimens of *kubeiensis* from "beds" 6-11 of the Qubuerga Formation and greatly clarified the succession and occurrence of brachiopod species throughout the formation. Their specimens mostly have 4 pair of plicae. Some, not figured, were reported to have 5 pair, as in *ambiensis*. The figured specimens are very like *Neospirifer neomarcoui.*

Neospirifer kubeiensis was identified by Zhan & Wu (1982, pl. 5, fig. 14, 20, part, not fig. 13) from the Xiala Formation, Xianza district, Tibet. The specimen of fig. 14 has 5 pair of plicae as in *ambiensis*, and fig. 20 is an elongate shell and no clear sulcal pair. So-called *N. kubeiensis* of Jin & Sun (1981, pl. 10, fig. 9, 10) from Tibet shows little similarity to the species, and is not *Betaneospirifer* in any strict sense.

Various specimens from several localities were ascribed to *moosakhailensis* by Ding. The specimen figured by Ding (1962, pl. 1, fig. 1) is clearly *ambiensis* and has 5 pair of plicae, and specimens in pl. 1, fig. 4, 6 are close. The specimen of fig. 2 has unusually narrow sulcus, perhaps indicating affinity with *Quadrospira tibetensis*, and fig. 3 differs from others, approaching *Wadispirifer*. However Shen et al. (2003a) referred all specimens to *kubeiensis*. Material described from the Luri Member of the upper Senja Formation of west Dolpo by Waterhouse (1978) as *kubeiensis* conforms moderately well with the ventral valves described by Ding (1962). This material provides data on stratigraphic position, ventral interior, and the dorsal valve. The well preserved dorsal valve of Waterhouse (1978, pl. 24, fig. 6) has plicae weaker than on the ventral valve.

Shen et al. (2001) reinterpreted Ding's species, but most of their specimens have narrower deeper sulcus, less well developed sulcal plicae, 4 pair of plicae overall, and notably coarser costae, which number about 3-4 in 5mm. Such coarse costae contrast with counts of 7-8 costae in 5mm measured from figures of type *kubeiensis,* and as few as 4 costae in 5mm anteriorly on type *moosakhailensis*. Their material is deemed to belong to a different species, *Betaneospirifer shii*, discussed below. *Neospirifer (Neospirifer*) sp. A (Shen et al. text-fig. 4.4) has strong plicae, and wide sulcus with short faint sulcal plicae visible in the figure, and the plicae bordering the sulcus are narrow and the shell is transverse, unlike individuals of *Wadispirifer*. The weakness of the sulcal plicae suggests *shii.* Figures of some of the specimens that Shen et al. (2001) referred to *Neospirifer (Quadrospira) tibetensis* do not appear to show subalate cardinal extremities and are transverse with some 4 pair of plicae, and approach *kubeiensis,* but also come close to *B. shii,* described below - identity will depend on the coarseness of the costae.

The specimen figured as *Neospirifer kubeiensis* by Yang et al. (1990, pl. 25, fig. 9a, b) has massive dorsal fold and massive ventral muscle field, indicating *Wadispirifer*, possibly *hongdeensis* n. sp. (see p. 140).

RANGE: According to Ding (1962), type *kubeiensis* occurred with *Costiferina indica* (Waagen), which is a key for upper Wargal and lower Chhidru fossils and indicates likely correlation with the *Lamnimargus himalayensis* Zone of the Himalaya. This was confirmed by Shen et al. (2003a), who showed the taxon as ranging through "beds" 5-12 in the lower Qubuerga Formation. This is equivalent to the *Lamnimargus himalayensis* Zone elsewhere in the Himalaya. Younger specimens come from the Luri Member of the *Biplatyconcha grandis* Zone in west Nepal. Specimens identified as *kubeiensis* by Shen et al. (2001) from the *Retimarginifera xizangensis* Zone of the Selong Group in the Selong-Xishan section of south Tibet are here reassigned to *Betaneospirifer shii* n. sp.

Betaneospirifer ravaniformis Waterhouse, 1978

1978 *Neospirifer ravaniformis* Waterhouse, pp. 90, 124, pl. 15, fig. 1-4, 6-10, pl. 24, fig. 8, pl. 26, fig. 11.

HOLOTYPE: UQF 68965 figured by Waterhouse (1978, pl. 15, fig. 2-4, 7, pl. 26, fig. 11) from Nisal Member, Dolpo, OD.

DIAGNOSIS: Large with inconspicuous ventral umbo, low narrow plicae and subdued to distinct sulcal subplication, fine undifferentiated costae, sulcus deep and wide anteriorly, fold high. Muscle field large in ventral valve.

DESCRIPTION: This is a distinctive species, first described from the Nisal Member of Dolpo, and characterized by very subdued plicae, especially on the ventral valve. Shells are transverse, with ventral sulcus very deep and broad anteriorly, and massive prominent fold with broad crest. The delthyrial plate is well developed under the umbo. A myophragm is present posteriorly in some shells, dividing the posterior muscle field, and the dorsal median septum is well developed. Specimens to be described from the Galte Member, Manang, show reticulate vascular impressions laterally (Waterhouse & Chen, in prep.).

RESEMBLANCES: *Betaneospirifer neomarcoui* (Licharew) and *Neospirifer kubeiensis* Ding, 1962, regarded as a junior synonym, show considerable approach in size, shape, and sulcus and have costae that are as fine, or almost as fine. Ding's specimens have a slightly higher fold and plicae that persist much more strongly to the anterior margin, and the sulcal pair of plicae are more strongly defined. In *ravaniformis*, dorsal plicae are slightly stronger than ventral plicae, whereas the reverse may be possibly true of Luri Member specimens and possibly type *kubeiensis* (Ding 1962, pl. 2, fig. 1). The species *ravaniformis* seems unlikely to be even a geographic variant of *kubeiensis*, comments by Shen et al. (2001, p. 162) notwithstanding, because although the two are comparable in shape and costation, *kubeiensis* has well defined sulcus and plicae, close in such respects to *ambiensis*, and identical with *neomarcoui*, whereas *ravaniformis* has weakly defined sulcus and plicae. In Nepal, *ravaniformis* follows and accompanies *ambiensis* stratigraphically, but simple linear evolution seems unlikely.

The species *Betaneospirifer moosakhailensis* (Davidson) is smaller, with fine passing to coarse costae, well defined plicae, and narrower sulcus, and comparably high dorsal fold. The species *ravaniformis* is distinctly younger, and is closer to *ambiensis* and *neomarcoui* in being transverse at an immature stage.

Betaneospirifer shii n. sp.

Plate 3, fig. 1, 2, 4, 5, 6

1997 *Neospirifer kubeiensis* not Ding Shi & Shen, p. 51, text-fig. 7B-D.

2001 *N. (Neospirifer) kubeiensis.* Shen et al., p. 160, text-fig. 3.1-3,?4, 7-13 (part, not text-fig. 3.5, 6 = *tibetensis*).

2001 *Trigonotreta* sp. Shen et al., p. 165, text-fig. 5.17, 18.

?2001 *N. (Quadrospirifer) tibetensis* not Ding Shen et al., p. 162, text-fig. 4.2, 5 (part, not text-fig. 4.3, 6?, 7, 8 = *tibetensis*).

2001 *Neospirifer* sp. A Shen et al., p. 142, text-fig. 4.4.

DERIVATION: Named for G. R. Shi.

HOLOTYPE: Specimen figured in Pl. 3, fig. 1, 4, 5 from PMb5, Braga Member, Marsyangdi Formation, crest and east side of Chulu ridge B (see Text-fig. 11), kept at Canterbury Museum.

DIAGNOSIS: Large transverse shells with wide sulcus, moderately high fold, 4 pair of well developed plicae, including pair within sulcus, variable mostly medium to coarse costae and wide ventral muscle field.

MATERIAL: A number of ventral valves and several dorsal valves from the Marsyangdi Formation. They will be further described in Waterhouse & Chen in prep.

DESCRIPTION: Large transverse shells up to 120mm across with alate cardinal extremities, becoming obtuse in mature shells, ventral umbo broad with angle close to 110^{o}, but only 80^{o} in one specimen, incurved but not prolonged or prominent, maximum shell width lies just in front of hinge. Interarea high, gently concave, delthyrial angle 50-70^{o}, delthyrium bordered by dental rims, no specimen preserved with delthyrial cover intact. Dorsal interarea low, at high angle to commissure, with wide notothyrium. Sulcus commences at ventral umbo, of moderate width and depth, angle 60^{o} in large specimens, 45^{o} in smaller shells, profile slightly angular; fold narrow and of moderate height with narrow crest. Sulcal pair of plicae well developed, especially in material within shale matrix, and three well developed pair lie to each side, the sulcal bordering pair wide in some specimens. Additional lateral 1-3 weak and subdued subplicae pairs developed. Dorsal plicae number 4 pairs. Costae may be fine at 5 in 5mm but typically coarse at 2-3 in 5mm over midlength and anteriorly in largest specimens, tend to be broad then split into two, with broad well rounded crests and comparable interspaces, costae a little finer in sulcus and number some 23 in holotype between crests of bordering plicae. Fine radial and concentric capillae: holotype has concentric laminae more prominent at 2-5mm intervals, but laminae not preserved in all specimens.

Dental plates supported by short adminicula. Ventral muscle field moderately wide, with narrow longitudinally ridged adductors that may be sharply defined by lateral ridges, wide diductor scars with a set of longitudinal ridges and a set of ridges parallel to oblique anterior lateral margins. No umbonal callus but delthyrial or stegidial plates not exposed. Posterior shell considerably thickened and floor marked by elongate short irregular ridges.

Dorsal valve with low ctenophoridium, small sockets supported by socket plates, low crural plates, presence of dorsal septum not well established, other detail not clear.

RESEMBLANCES: This species is more plicate than *Betaneospirifer ravaniformis* (Waterhouse, 1978) and is shaped differently from *B. moosakhailensis* (Davidson), with wider muscle field and sulcus, coarser costae and plicae better defined anteriorly. The new species shares with *B. ambiensis* and *neomarcoui* a wide hinge, but has weaker sulcal plicae, coarser costae and wider muscle field. Although costae were stated to be coarse in Ding's species *kubeiensis* by Shen et al. (2001), some 7-8 costae are visible in 5mm in Ding's types, compared with 2-4 in 5mm in *shii* as figured by Shen et al. (2001, text-fig. 3.3) and 3-4 in 5mm in Shen et al. (2001, text-fig. 3.1) and 2-3 in 5mm on Nepal specimens. It is not easy to measure costal counts accurately from figures, but the difference involves an order of magnitude.

Specimens figured as *kubeiensis* by Shi & Shen (1997) and Shen et al. (2001, text-fig. 3) from the Selong Group in the Selong Xishan section of south Tibet appear to be conspecific with *shii*, in so far as they display comparable shape, sulcus, well defined plicae including faint to moderately developed sulcal pair, and, over parts of the shell, coarse costae (see Shen et al. 2001, text-fig. 3.1, 2, 3, 11, 13). Other figures in Shen et al. (2001, text-fig. 3.7-10) show small specimens difficult to evaluate, and text-fig. 3.12 presents the muscle field, shaped as in present material. Specimens shown as *kubeiensis* in Shen et al. (2001, text-fig. 3. 5, 6) have fine costae (5 in 5mm) and may be conspecific as a variant, or not related, being also close to *kubeiensis,* but having less persistent and lower plicae in the sulcus than normal for *kubeiensis, neomarcoui* or *ambiensis*, and 3 lateral pairs of plicae, which suggests *Quadrospira tibetensis*. The general range of the Selong Xishan specimens were stated to be "beds" 1, 6, 8-11, 15. *Neospirifer* sp. B of Shen et al. (2001, p. 162, text-fig. 4.1) is elongate with fine costae and no strong plicae. *Neospirifer* sp. A (Shen et al. (2001, text-fig. 4.4) has a wide deep sulcus, low short sulcal plicae and high plicae, as possibly an unusual form of *kubeiensis* (ie. *neomarcoui*), but given the coarse costae and inconspicuous sulcal plicae, seems most likely to belong to *shii.*

Genus ***Pondospirifer*** Waterhouse, 1978

Pondospirifer magnificus Waterhouse, 1978

1978 *Pondospirifer magnificus* Waterhouse, p. 93, pl. 16, fig. 1, 3, 4, 6, 7.

HOLOTYPE: UQF 68971 figured by Waterhouse (1978, pl. 16, fig. 1, 3, 4, 6, 7) from Nisal Member, Dolpo, OD.

DISCUSSION: This is a very distinctive genus and species, massive with inconspicuous ventral umbo and plicae and swollen lateral flanks. The species is restricted to the Nisal Member in west Dolpo, and specimens have been reported from the lower Qubuerga Formation of south Tibet by Shen, Archbold & Shi (2001, text-fig. 5.1, 2, 3), though their figures (fig. 5.2, 3) indicate a more prominent ventral umbo and deeper ventral sulcus than is typical of the species, suggesting a different species. Rare specimens of the genus have been found in the Galte Member of Manang, central Nepal, and these possibly belong also to a separate species.

Genus ***Simplicisulcus*** Waterhouse, 2002c

TYPE SPECIES: *Neospirifer arthurtonensis* Waterhouse, 1968, p. 28.

DIAGNOSIS: Small shells with generally strong costae (though fine through splitting in some specimens) increasing by bifurcation, fasciculate, well formed plicae, deep sulcus without subplicae and not entered by lateral plicae, fold low to high, not joined anteriorly by innermost pair of plicae, prominent concentric lamellae and fine radial filae. Delthyrium covered in part or entirely by plate.

DISCUSSION: The type species is the only member of this genus to be so far named in New Zealand, in the Arthurton Group, in the *Martiniopsis woodi* and *Paucispinauria verecunda* Zones, of Changhsingian age. *Neospirifer concentrica* Waterhouse (1987a, pl. 4, fig. 7-13) from the early Guadalupian *Echinalosia discinia* Zone of the Brae Formation of southeast Bowen Basin is congeneric. The genus is widespread in Asia, and includes so-called *Neospirifer fasciger* (not Keyserling) of Licharew & Einor (1939, pl. 16, fig. 3) from Novaya Zemlya, and *N. permicus* Ivanova, 1972. Although *Gypospirifer* and allies also have a simple sulcus with bordering pair of plicae, the sulcus is less sharply edged, and the costae are bundled much more and differentiated more in *Simplicisulcus*, and are much more rarely bifurcate. As well, radial filae are well developed in *Simplicisulcus*, and *Gypospirifer* has stegidial plates rather than a delthyrial plate. Therefore the similarity is believed to be due to convergence.

The way in which the innermost plicae border, but do not enter the sulcus is also to be observed in some species from Texas that were described by Cooper & Grant (1976), including species characterized by wide alate cardinal extremities, and referred to *Spiriferalaria* Waterhouse, 2002c, p. 231. As in *Simplicisulcus*, costae may be differentiated, and often are trifurcate. Cooper & Grant (1976) reported a flatly convex plate in the delthyrium, fused to a thick apical callosity. No radial filae were preserved. The type species of *Spiriferalaria* is *Neospirifer thescelus* Cooper & Grant (1976, p. 2189) from the Road Canyon Formation of the Glass Mountains, Texas, and the genus also appears to be represented in the Pennsylvanian of United States.

Possibly the species *striatiformis* Zhang in Zhang & Jin (1976) from south Tibet belongs to *Simplicisulcus* Waterhouse, 2002c, but the type species and allied species of this genus have higher narrower plicae and higher narrower ventral umbo and lower ventral interarea. The large sulcal bordering plicae of *striatiformis* suggest *Wadispirifer* as a possibility, but the sulcus is much narrower than in this genus. Although the species *striatiformis* was referred to *Kaninospirifer* by Kalashnikov (1998), the type specimen has a sulcus that is narrower than in typical *Kaninospirifer,* and the size of its dental plates is not known.

Simplicisulcus? scabrosa (Reed, 1944)

1944 *Spirifer (Neospirifer) warchensis scabrosa* Reed, p. 199, pl. 27, fig. 7, 7a (part, not 8, 8a = *poletaevi*).

LECTOTYPE: Specimen figured by Reed (1944, pl. 27, fig. 7, 7a) from Kalabagh Member, Salt Range, here designated. Kept at Geological Survey of India, Calcutta.

DISCUSSION: *Spirifer (Neospirifer) scabrosa* of Reed (1944) from the Kalabagh Member of the Salt Range is small, and shows some 5 pairs of fascicles, with well defined inner pair apparently bordering the sulcus, and well defined concentric laminae. The material is more elongate with hinge not as wide and cardinal extremities more obtuse than in *Betaneospirifer ambiensis* (Waagen), and growth-lines show transverse early outline. Its outline and ornament differ from that of the other specimen figured as *scabrosa* by Reed (1944, fig. 8, 8a), deemed to belong to *Neospirifer poletaevi* n. sp.

Simplicisulcus? semicircularis (Shen, Shi & Zhu, 2000)

2000 *Trigonotreta semicircularis* Shen, Shi & Zhu, p. 273, pl. 3, fig. 5-8.

Internal detail has not been provided for *Trigonotreta semicircularis* Shen, Shi & Zhu (2000, pl. 3, fig. 5-8) from Early Permian of Yunnan. If it belongs to Trigonotretinae, it doubtfully could be classed as *Aperispirifer*, given the wide hinge, fine costae well developed close to the umbo, and few plicae pair. But there does not appear to be a pair of plicae within the sulcus, which would distinguish the species from both *Aperispirifer* and *Trigonotreta*. Its generic position remains obscure, unless the species belongs to *Simplicisulcus* Waterhouse. Delthyrial data must be ascertained for *semicircularis* before generic placement can be secured.

Simplicisulcus sp.

2003 *Neospirifer (Neospirifer) moosakhailensis* (not Davidson) Shen, Dongli & Shi, text-fig. 6.1-5.

Transverse shells with blunt cardinal extremities, well defined moderately deep sulcus and low broadly rounded fold, 3-4 well defined plicae pairs and 2-3 narrow lateral subplicae, no sulcal plicae, costae of moderate strength, coarse anteriorly, 3 in 5mm. The specimens were figured but not described by Shen, Dongli & Shi (2003). They come from an exotic limestone block at Xiukang, Lhaze county, Tibet, and are distinctive. The transverse outline suggests an approach to *Occidalia* Archbold, 1997, a genus which appears to differ through having sulcal plicae.

Genus ***Maxwellispirifer*** n. gen.

DERIVATION: Named for W. G. H. Maxwell.

TYPE SPECIES: *Neospirifer campbelli exora* McKellar, 1965, p. 10, here designated.

DIAGNOSIS: Small transverse shells with well rounded cardinal extremities, delthyrium open as preserved, low pleromal ridges, three pair of plicae commencing over umbonal region, and innermost pair entering broad well formed sulcus, costae over sulcus, fold, plicae and lateral flanks coarse, with rounded crests, fine concentric laminae. Dental plates short, adminicula very short, secondary thickening low, muscle field elongate, lightly impressed, extends well in front of adminicula, divided by well defined myophragm, dorsal valve with ctenophoridium, very low median septum, slender socket plates and low thick crural plates, elongate muscle field.

DISCUSSION: This genus is provisionally treated as a member of Neospiriferinae, although no delthyrial plate is so far known. It might have been lost, or might have never been present, and in aspects of plication and costation, the genus stands apart from other members of the subfamily, yet does not appear close to any particular genus within other subfamilies. Further study is required, for some aspects suggest the possibility of placement within Gypospiriferinae, and the delthyrium, shape, and well developed myophragm may point to alliance with *Cartorhium* or *Septospirifer*.

Maxwellispirifer differs from a number of genera in its rounded cardinal extremities, few plicae of which inner pair enters sulcus, and tiny ventral plates. *Neospirifer* and *Betaneospirifer* are distinguished by having more bundled and relatively finer costae, and longer adminicula and dental plates. Amongst other genera, *Septospirifer* is characterized by its ventral low septum and more angular costae and *Gibbospirifer* Waterhouse by its more numerous and finely costate plicae with no sulcal plicae. *Frechella* Legrand-Blain is larger with better defined plicae not entering the sulcus, and well defined ribs, and larger internal plates with more compact ventral muscle field. Permian forms such as *Crassispirifer*

Archbold & Thomas, *Pondospirifer* Waterhouse and *Wadispirifer* n. gen. are all much larger with distinctive plication, and *Simplicisulcus* Waterhouse has strong costae in more plicae, and no plicae within the sulcus. *Spiriferalaria* Waterhouse has fine costae, more plicae, no sulcal plicae and alate cardinal extremities. *Cartorhium* Cooper & Grant and *Blasispirifer* Kulikov are readily distinguished by plication. *Cartorhium* is somewhat similar in general appearance, but has a shorter hinge, differently bundled costae, less persistent plicae, and longer dental plates and adminicula. *Kaninospirifer* Stepanov & Kulikov has wider pair of plicae bordering the sulcus and dental rims rather than plates, fine costae, and distinct ears.

Trigonotretinae are distinguished by their large umbonal callosity. Closest amongst the genera are *Grantonia* Brown and *Aperispirifer* Waterhouse, as described below, because these genera also have few plicae with inner pair entering the sulcus. *Grantonia* is moderately close, with slightly more differentiated costae branching nearer the umbonal tip. The ventral muscle field is much better defined, and adminicula and dental plates are much larger, and a myophragm is not developed, at least in known species. *Aperispirifer* is further removed, with more angular costae as a rule, commencing nearer the umbo, and more alate cardinal extremities, as well as large adminicula and dental plates, and well developed ventral muscle field.

Maxwellispirifer exora (McKellar, 1965)

1965 *Neospirifer campbelli exora* McKellar, p. 10, pl. 4, fig. 1-6.

HOLOTYPE: GSQF8926a, b figured by McKellar (1965, pl. 4, fig. 2a, b) from Branch Creek Formation, Queensland, OD.

DIAGNOSIS: Small slightly transverse oval shells with wide sulcus, costae over narrow plicae in 3 pair.

DESCRIPTION: Costae in *exora* are sturdy with round crests, and well developed concentric lamellae, and increase by branching some distance in front of the umbo. There are faint signs of radial filae, but they are not clear, perhaps because of poor preservation. The adminicula measure only 2.5mm in length in UQF 46509, which is about 25mm long, and this length does not allow for the incurved and partly deformed ventral umbonal part of the specimen. This specimen was well figured by McKellar (1965, pl. 4, fig. 4a, b) to illustrate the shortness of the adminicula. The muscle field extends well beyond the adminicula and is rather diffuse, subdivided by a low myophragm, and surrounded by an area of valve floor marked by radiating low grooves and ridges. The development of pleromal plates under the delthyrium is also found to some extent in *Neospirifer*, but there is no sign of a delthyrial plate in *Maxwellispirifer*.

RESEMBLANCES: *Neospirifer gruenewaldtianus* (Yanischevsky, 1900) as figured in Einor (1973, pl. 28, fig. 2-5) appears to be close in external detail, with comparable plicae and costae. The text in Einor (1973, p. 105, pl. 32, fig. 4, 5) described different and less well preserved material, and cited a neotype. The species is recorded from Bashkirian faunas of north Urals, Russia (Einor 1973, table 4).

Subfamily **KANINOSPIFERINAE** Kalashnikov, 1996

[Kaninospiriferinae Kalashnikov, 1996, p. 133].

NAME GENUS: *Kaninospirifer* Stepanov & Kulikov, 1975, p. 63.

DIAGNOSIS: Weakly transverse shells with wide hinge and well formed interareas, delthyrium of only moderate width, sulcus and fold well defined, may be narrow, plicae in few pair, may be broad bordering sulcus, pair may be incorporated within sulcus, costae well developed, weakly fasciculate, crossed by concentric laminae that impart tiled effect especially anteriorly. Delthyrium bordered by keels, or very low dental plates, adminicula. Delthyrium variably open or closed partly by small delthyrial plate, small umbonal callus in adult specimens from Australia and Arctic.

DISCUSSION: *Kaninospirifer* Stepanov & Kulikov (1975) is based on the species *Spirifer kaninensis* Licharew, 1943, which has been illustrated in various studies, including Grunt et al. (1998) and Kalashnikov (1983, 1986, 1990, 1998). Although figures convey somewhat variable limitations, it appears that the species is transverse with subalate to alate extremities, and comparatively well defined sulcus not widening very substantially. There are subdued plicae, of which the sulcal bordering pair is very broad, and in some specimens the sulcus has a low inner subplication. The costae have rounded crests anteriorly, and narrow interspaces, with “tiled” appearance at least anteriorly. Internally, the dental plates are very low.

There is considerable approach to *Imperiospira* Archbold & Thomas, 1993 from Western Australia, as pointed out by Kalashnikov (1998). The type species of this genus has subdued narrow plicae, and deeper sulcus and upturned ventral lateral margins, but is overall close in general appearance, and has radial filae and reduced dental plates. Other species of *Imperiospirifer* have better defined plicae, usually amounting to no more than 4 pair.

Herein, two further genera are referred to Kaninospiriferinae, *Quadrospira* Archbold, and *Wadispirifer* n. gen. These share reduced dental plates, and overall look close to *Kaninospirifer* in shape, being less transverse than a number of neospiriferin genera, and having only 3-4 plicae pairs, one or two pair fewer than in *Betaneospirifer*.

In *Spirifer hardmani* Foord, regarded as a likely member of Kaninospiriferinae, Archbold & Thomas (1986, p. 130) reported a small overhanging delthyrial plate in some submature specimens, and thickened overhanging callosities in gerontic individuals. For the type species of *Quadrospira* Archbold, Archbold & Thomas (1986, p. 134) stated that delthyrial structures were variable, either absent or flattened, with apical callus at the apex of the delthyrium. *Wadispirifer amplus* (Archbold & Thomas) has what appear to be two plates, one each side, with small pad of callus under the umbo. *W. grandis* (Archbold & Thomas, 1986, p. 147) displays a small delthyrial plate in juvenile stages, and a posterior pad of callus in adult specimens. For *Imperiospira*, Archbold & Thomas (1993) reported that a "true delthyrial plate was apparently absent" (p. 319) and that the delthyrium showed remnants of a delthyrial cover (p. 323). In summary, Australian species often possess a delthyrial plate early in ontogeny, suggestive of neospiriferins, replaced later by delthyrial thickening. The differences from Neospiriferinae involve the presence of small umbonal callosity in at least some members of the subfamily, and the severely reduced dental plates, shown in section by Kalashnikov (1998) for *Kaninospirifer kaninensis*, and by Archbold & Thomas (1993) for *Imperiospira franzjosefi.* Even so, species of similar appearance are known that have dental plates much as *Betaneospirifer*. *Imperiospira* finds an external match in *Neospirifer sulcoprofundus* Liu & Waterhouse, 1985, at least in the upturning of the lateral margins, and Archbold & Thomas (1986) referred the species in *Imperiospira*. Yet *sulcoprofundus* has well developed developed dental plates. If this means that dental plate size is simply a specific variant, then value as a tribal or subfamilial distinction for Kaninospiriferinae may prove to be negligible. It seems more likely that the Archbold & Thomas identification must be set aside.

There is less approach to members of Gypospiriferinae in delthyrial apparatus, and considerable difference in external features.

Genus ***Kaninospirifer*** Stepanov & Kulikov, 1975

TYPE SPECIES: *Spirifer kaninensis* Licharew, 1943, p. 279.

DIAGNOSIS: Weakly to moderately transverse shells which may develop small narrow long wings with lateral margin embayed, maximum width in front of hinge, large pair of plicae bordering fold, and generally two further plicae pairs laterally, weak to strong plication or none within sulcus, costae fine to moderate in strength, may be tegulate. Dental plates low, adminicula short, moderately high.

DISCUSSION: Species which appear to be referable to *Kaninospirifer* are widespread. Kalashnikov (1998) listed a number from especially Arctic regions, as well as Inner Mongolia, and a species is named herein from Oman, of the southern paleohemisphere during Permian time. *Aperispirifer crassicostatus* Waterhouse, 1983d from the *Terrakea dickinsi* Zone of the Takitimu Group of New Zealand and upper Tiverton Formation of Bowen Basin, Queensland (Archbold & Thomas 1984, Waterhouse 1987a), appears to belong to *Kaninospirifer* . There is a broad sulcus, wide plicae bordering the sulcus, subdued other plicae, and low dental plates. Costae are broad, and do not bifurcate much. The cardinal extremities, as in the holotype (Waterhouse 1964, pl. 22, fig. 4-8), are alate and project beyond the well rounded and prominent lateral margins, so that overall shape is close to that of *Quadrospira*, but the ears are smaller and plication less developed. In its small but pointed ears and coarse costae the species is moderately close to *Neospirifer (Quadrospira) woolagensis* Archbold, 1997 from the Artinskian High Cliff Sandstone of the Perth Basin. *Spirifer hardmani* Foord, 1890 from Western Australia is also likely to belong to *Kaninospirifer*.

Shi et al. (2002, p. 294) presented a different view of *Kaninospirifer*, claiming that adminicula (ventral adminicula) were not developed. This is not confirmed in original descriptions and is denied by serial sections of the type species presented by Kalashnikov (1998, text-fig. 6). Their diagnosis and distribution for the genus are therefore set aside.

Kaninospirifer costellinus n. sp.

?1959 *Neospirifer hardmani* (not Foord) Hudson & Sudbury, p. 50, pl. 6, fig. 1, text-fig. 12.

1959 *N.* aff. *moosakhailensis* (not Davidson) Hudson & Sudbury, p. 49, pl. 6, fig. 3a, b (part, not fig. 2, 4 = *Neospirifer?*, 5 = indet.).

1997 *Neospirifer* aff. *hardmani.* Angiolini in Angiolini et al., p. 390, text-fig. 15.4-10, table 4.

DERIVATION: costa - rib, linea - line, Lat.

HOLOTYPE: MPUM 7947 figured by Angiolini in Angiolini et al. (1997, text-fig. 15.4) from the Sakmarian Saiwan Formation, Oman, here designated.

DIAGNOSIS: Characterized by comparatively narrow sulcus, obtuse cardinal extremities and fine costae.

DESCRIPTION: The material has been described and illustrated from several localities in the Saiwan Formation, and the type locality OL18 has yielded a number of specimens. The species is comparatively small, with low broad ventral umbo and obtuse cardinal extremities, but lateral margins are poorly preserved and whether the lateral margins extended more at greater maturity is not revealed, but is possible. The sulcus is narrow with U-shaped floor, increasing in width and angle anteriorly, and the fold narrow and well defined, with narrowly rounded crest. Plicae are not prominent, and the pair that borders the sulcus for most of its length from just in front of the ventral umbo is comparatively broad, and carries a faintly defined subplication along its inner side. There are two further pairs laterally, and weak suggestions of another lateral pair. The dorsal valve has only two pair of plicae that are moderately defined. Costae are fine, and Angiolini has described the bundling and provided counts and other documentation. There are 5-6 costae in 5mm close to the anterior margin on several specimens, and tegulate growth lamellae. The ventral interior has been well figured, and shows very low dental plates, supported by high adminicula, and well delimited muscle platform, with considerable secondary thickening. A small delthyrial plate was recorded by Angiolini, with various other significant observations.

RESEMBLANCES: Kalashnikov (1998, p. 50) indicated a number of possible members of *Kaninospirifer* that come close in the nature of ornament, including subdued plicae as a rule and tegulate ornament, and reduced dental plates. The Middle Permian species from Russia and Arctic, and *adpressum* Liu & Waterhouse from Inner Mongolia, are more rectangular in shape, and generally have slightly better defined sulcal plicae, compared with the new species. A number of the species have small posterior wings, and maximum width lying in front, but present material is a little obscure in this regard.

A ventral valve figured as *Neospirifer* sp. by Angiolini et al. (1997, p. 390, text-fig. 15, 11) from the Saiwan Formation of Oman comes from a different locality, and is distinguished from *Kaninospirifer costellinus* by its stronger plicae, but shows otherwise identical sulcus and somewhat comparable costae. It might be a variant or subspecies of *costellinus.*

Angiolini (in Angiolini et al. 1997) justifiably compared the Oman material to S*pirifer hardmani* Foord, 1890 from the Callytharra Limestone, Jimba Jimba Calcarenite and Fossil Cliff Member of Western Australia. This species, as revised by Archbold & Thomas (1986, text-fig. 1A-N, 2A-I, 3A-I; Hogeboom & Archbold 1999, text-fig. 8H-L), is moderately close, and is less transverse than northern hemisphere Middle Permian *Kaninospirifer*, and shows a tendency for small posterior ears to be differentiated at maturity (Archbold & Thomas 1986, text-fig. 2C, 3H) . There are up to 4 pair of plicae, the main pair bordering the sulcus being broad with a weakly defined inner sulcal pair, and two moderately defined lateral pair; some shells have only 3 plicae pair: the sulcal pair is not always clearly developed, and in others a lateral pair is not well differentiated.

The inner pair of dorsal plicae is incorporated anteriorly in the dorsal fold. Dental plates are comparatively small. In many details the Oman species comes close, but has a narrower sulcus, and its dorsal fold does not show quite the same incorporation of plicae anteriorly into the fold. This could be because of small size and less maturity, but the difference seems actual, given the suggestion of maturity by the amount of secondary thickening in the Oman shells. Costal counts were not provided for *hardmani*, and appear from figures to vary, generally 3-4 per 5mm, but may carry splits to reach 5 in 5mm. The ribs of the Oman species are distinctly finer, and their number has not been increased by costal splitting. As well, tegulate ornament is less prominent for *hardmani* than in *K. costellinus*, although the extent to which this reflects wear of specimens is not known.

The Oman specimen figured as *Neospirifer hardmani* by Hudson & Sudbury (1959) was regarded as conspecific by Angiolini in Angiolini et al. (1997). It is a large specimen, distorted and shaped much as the other specimens, but with coarser costae at least anteriorly, and obscure plicae and sulcus. The specimen figured as *N*. aff. *moosakhailensis* by Hudson & Sudbury seems close, with more grooved sulcus and 5-6 costae in 5mm. Other specimens ascribed to aff. *moosakhailensis* (pl. 2, fig. 2, 4) have more plicae with wide hinge and might belong to *Neospirifer* or *Aperispirifer*, and the specimen of pl. 6, fig. 5 is shown only in hinge view. These comments rely only on assessment of figures, and not only did Angiolini refer the specimens to aff. *hardmani*, but Hudson & Sudbury remarked on the approach shown by the plicae - including the specimen of pl. 6, fig. 3 - to those of *Spirifer kaninensis.*

As pointed out by Angiolini in Angiolini et al. (1997), material identified with Salt Range species described by Reed (1944) by Termier et al. (1974) from upper Sakmarian near Wardak, Afghanistan, also looks similar, although it was not included in her synonymy. The specimens were identified as *Neospirifer trimurensis* (Termier et al. 1974, p. 101, pl. 11, fig. 10) and *Aperispirifer undatus* (Termier et al. 1974, p. 102, pl. 12, fig. 4-8, pl. 13, fig. 1-4, text-fig. 18, 19). Four plicae pairs are shown on the dorsal valve (Termier et al. 1974, pl. 12, fig. 8, text-fig. 18), more than visible in the Oman shells. The Wardak specimens are larger and possibly more mature than those from Oman, and show anterior costae as coarse as 3 or slightly fewer per 5mm, and 4-5 in 5mm posteriorly, and costae rarely bifurcate. The plicae are scarcely visible, especially on the ventral valve, whereas dorsal plicae are clearly defined. Like the Oman shells, the sulcus appears to be narrower than in *hardmani*. Internal detail is not known, and subject to the nature of the dental plates, placement with *Neospirifer* or *Aperispirifer* seems likely.

NOTE ON DESIGNATED LECTOTYPE OF HARDMANI

The lectotype of *Spirifera hardmani* Foord, 1890 is the ventral valve figured by Foord (1890, pl. 7, fig. 1), designated by Waterhouse (1964, p. 122). Archbold & Thomas (1986, p. 128) reported that this specimen could not be found at the British Museum (Natural History) - now Museum of Natural History, and indicated the second specimen figured by Foord (1890, pl. 7, fig. 1a) as lectotype (sic), a poorly preserved specimen figured as a ventral interior, and catalogued as GSWAF10078. This specimen should surely be termed a neotype rather than "lectotype", as replacing a type that has been lost. Notes show that I had inspected the first specimen at the Museum of Natural History in 1956, and whether it has since been lost, or I erred, remains open. Collections when inspected in those days were segregated according to publication, and since, they have been rearranged systematically and according to country, with figured material scattered amongst an array of collections, often not clearly identified or readily located. The original specimen designated as lectotype is apparently not to be found at the Geological Survey of Western Australia. It remains possible that the lectotype will be refound, somewhere, sometime. Fortunately Archbold & Thomas (1986) have been able to describe and figure a fine suite of specimens in its place.

Genus ***Quadrospira*** Archbold, 1997

TYPE SPECIES: *Neospirifer plicata* Archbold & Thomas, 1986, p. 133.

DIAGNOSIS: Shells subquadrate, hinge generally auriculate at maturity, and anterior lateral margins as wide or wider than hinge, sulcus may be deep and fold high. Sulcal plicae high and may lie close to sulcal bordering pair of plicae, only 2-3 lateral pair. Ventral muscle field broad, dental plates form flanges.

DISCUSSION: Archbold (1997) and Shen et al. (2001) treated *Quadrospira* as a subgenus of *Neospirifer*, but it is here preferred to grant full generic standing. Rather than having its closest ally as *Neospirifer*, the genus in several respects falls very close to *Kaninospirifer* Stepanov & Kulikov, 1975. Species of *Kaninospirifer* may show comparable outline with prominent posterior cardinal extremities. For instance *Neospirifer adpressum* Liu & Waterhouse (1985, pl. 12, fig. 5-10) from the Zhesi Formation of Inner Mongolia is close to *Quadrospira* in shape, although it has the sulcus and plicae typical of *Kaninospirifer* Stepanov & Kulikov, 1975, as pointed out by Kalashnikov (1998). Specimens referred to the type species of *Kaninospirifer, Spirifer kaninensis* Licharew, 1943 also come close in shape to *Quadrospira*, as in Grunt et al. (1998, pl. 13, fig. 1a, b), with somewhat similar plicae and lateral ears in some specimens. *K. kaninensis* has a plication each side of the sulcus broader than that of the type species of

Quadrospira, but very like that of the species *hardmani* Foord, assigned to *Quadrospira* by Hogeboom & Archbold (1999). *K. kaninensis* carries an inner subplication within the sulcus that is less well developed than in *Quadrospira*. In what has been stated to be an allied species, *Kaninospirifer borealis* Stepanov & Kulikov (1975, pl. 3, fig. 6, 7), the sulcal plicae are well defined, and lateral plicae narrow and well defined, approaching plication in *Quadrospira.* Perhaps it should be reallocated to *Quadrospira*. The dental plates of the type species of *Quadrospira* appear to be less well developed than in *Neospirifer,* and reference to dental flanges was made by Archbold & Thomas (1986) in describing the type species, and its ally *postplicatus*. The species described as *Neospirifer (Quadrospira) preplicatus* Hogeboom in Hogeboom & Archbold (1999, text-fig. 8A, D, E) clearly has reduced dental flanges, as documented and well figured. The two might be one genus with somewhat variable species. But here *Quadrospira* is provisionally retained, and distinguished from *Kaninospirifer* by its more consistently developed cardinal extremities, plicae and radial micro-ornament.

Quadrospira tibetensis (Ding, 1962)

Plate 4, fig. 2, 3

1962 *Neospirifer tibetensis* Ding, p. 454, pl. 2, fig. 4, 5.

1962 *N. moosakhailensis* (not Davidson) Ding, p. 452, pl. 1, fig. 2, 4? (part, not fig. 1, 5, 6 = *ambiensis*, fig. 3 = *Wadispirifer*?).

1976 *N. kubeiensis* not Ding, Zhang & Jin, p. 203, pl. 14, fig. 1-4, 8, 9, pl. 15, fig. 1, 2, pl. 16, fig. 8?, pl. 19, fig. 2, text-fig. 10, 11.

1982 *N. tibetensis*. Yang & Zhang, p. 312, pl. 3, fig. 2-4, text-fig. 1.

1983a *N. kubeiensis* not Ding Waterhouse, p. 136, pl. 6, fig. 11, 12 (part, not pl. 7, fig. 3, 4, 8 = *hongdeensis)*.

1994 *N. kubeiensis*. Fang & Fan, p. 86, pl. 31, fig. 10-12, pl. 32, fig. 1, 2.

2001 *N. (Neospirifer) kubeiensis*. Shen et al., p. 160, text-fig. 3.5, 6 (part, not text-fig. 1-3, 4?, 7-13 = *shii*).

2001 *N. (Quadrospira) tibetensis*. Shen et al., p. 162, text-fig. 4.3, 6?, 7, 8 (part, not text-fig. 4.2, 5 = *shii)*.

2003a *N. (Quadrospira) tibetensis*. Shen et al., p. 84, pl. 12, fig. 5-8, pl. 13, fig.1.

LECTOTYPE: Specimen IGAS 3609 figured by Ding (1962, pl. 2, fig. 4) from lower Qubuerga Formation, Tibet, here designated. Ding (1962) cited both of his figured specimens as holotypes.

DIAGNOSIS: Shells with deep ventral sulcus and high narrow dorsal fold, costae fine, plicae within sulcus moderately developed, two major pair laterally, weak sulcal and outermost pair, ventral muscle field wide.

DISCUSSION: This species was clarified by Shen et al. (2001), in demonstrating a close relationship to earlier Permian species described from Western Australia by Archbold & Thomas (1986). The material circumscribed by Shen et al. (2001) comes from various levels in the Selong Group at the Selong Xishan section of south Tibet, and some specimens, as figured in Shen et al. (2001, text-fig. 4.2, 5), are more transverse than the types and have mostly shallower sulcus than the original specimens, and possibly finer ribs. Conceivably these specimens belong to a new species, but the lack of figured dorsal valves makes species delineation hazardous. Some of the specimens assigned to *kubeiensis* by Zhang in Zhang & Jin (1976) obviously belong to *Quadrospira*, even though Shen et al. (2001, 2003a) retained all except pl. 15, fig. 1, 2 as *kubeiensis*. Some of the Zhang & Jin specimens have lower plicae and shallow sulcus, and the outer pair of plicae and inner sulcal plicae are generally better defined. Yang & Zhang (1982) showed well the interior and the dorsal plicae on the flanks of the fold, with only two main pairs of plicae laterally. There seem to be very low dental plates (pl. 31, fig. 12a, b), although first hand confirmation is necessary. Typical specimens from the upper part of the lower Qubuerga Formation were figured by Shen et al. (2003a). Fang & Fan (1994) recorded the species from the Xiaoxingzhai and Guanyinshan Formations of west Yunnan, of late Guadalupian age. In their specimens, plicae lie close together, within extended lateral costate shell.

The Pija Member specimens figured as *Neospirifer kubeiensis* by Waterhouse (1983a, pl. 6, fig. 11, 12) do not have alate cardinal extremities. But they are small and, as shown from growth lines on the Ding's original specimens, agree with *tibetensis* at a comparable size in shape, fineness of costae with up to 6-10 costae in 5mm, and narrowly diverging sharply defined plicae with only two lateral pair. Up to 8 costae occur in 5mm on Ding's specimens. Shen et al. (2003a, p. 85) also noted the change in shape with advance in ontogeny of *tibetensis*.

STRATIGRAPHIC RANGE: The species is best known from the equivalent of the *Lamnimargus himalayensis* Zone and ranges into the *Retimarginifera xizangensis* Zone of south Tibet.

Genus ***Imperiospira*** Archbold & Thomas, 1993

TYPE SPECIES: *Imperiospira franzjosefi* Archbold & Thomas, 1993, p. 317.

DIAGNOSIS: Large ventrally curved lateral margins, extended anterior lateral margins, sulcal tongue deep, fold high, spiralia directed posterolaterally. No true delthyrial plate, slight umbonal callus under the beak.

DISCUSSION: This genus is represented by several species in the Early Permian of Western Australia. An allied species is recognized in the *Lamnimargus himalayensis* Zone of northwest India, of Late Permian age.

Imperiospira bambadhuriensis (Diener, 1903)

1903 *Spirifer bambadhuriensis* Diener, p. 108, pl. 4, fig. 8-10.

LECTOTYPE: GSI 7386, figured by Diener (1903, pl. 4, fig. 9a, b), from Productus Shales, northwest India, designated by Waterhouse (1978, p. 94).

DIAGNOSIS: Transverse, ventral umbo protrudes a little beyond the hinge, lateral margins upturned, plicae low and posterior, costae fine.

DESCRIPTION: This species comes from the Productus Shales of Lissar Valley, northwest India. The ventral umbo protrudes beyond the hinge, and low plicae are visible posteriorly on the ventral valve and persist faintly to the anterior margin on the dorsal valve. Costae are fine. The characteristic upturn of the ventral posterior extremities is shown by Diener (1903, pl. 4, fig. 8) and less in fig. 10. The lateral anterior margins are not preserved.

DISCUSSION: The west Australian species of *Imperiospira* are all larger, with stronger plicae and costae, and are considerably older than the Himalayan species. Archbold & Thomas (1993) noted the close approach of Diener's species to *Imperiospira*, and this appears to be correct, although the nature of the dental plates still needs to be determined. A number of other species were referred to *Imperiospira* by Archbold & Thomas (1993), but not all are necessarily congeneric. *Spirifer striatus* mut. *neostriatus* Fredericks (1924b, p. 37, 1925, pl. 4, fig. 111, 112) from Cape Kalouzin, Ussuriland, also reported by Fredericks (1934, pl. 3, fig. 26) from the Ashi-ho River, North Manchuria, is based on large ventral valves which show abundant rib splitting, but nothing of the interior or dorsal valve, or the lateral upturn of shell. *Neospirifer sulcoprofundus* Liu & Waterhouse (1985) from the Zhesi 4 Formation of outer Mongolia is an unusual species and shows aspects of *Imperiospira*, with costal splitting and tendency for upturned lateral margins (Liu & Waterhouse 1985, pl. 12, fig. 1, 3). But shells are more transverse and alate, the costae very coarse, and the dental plates well developed. The nature of the sulcus, although somewhat obscured by decortication and deformation, appears to rule out an approach to *Spiriferalaria* Waterhouse, because this genus lacks the sulcal subplicae exhibited in *Imperiospira* and in the species *sulcoprofundus*. The South Primoyre ventral valve figured by Licharew & Kotlyar (1978, pl. 18, fig. 1) as *Neospirifer striatoparadoxus* and referred to *Imperiospira* by Archbold & Thomas (1993) is elongate and moderately like *Imperiospira*, but does not show any characteristic lateral upturn, and in some respects looks closer to *Kaninospirifer*. Dental plates are not revealed.

Genus ***Wadispirifer*** n. gen.

DERIVATION: wadi - dry gulch, Sansk., spirifer, brachiopod genus.

TYPE SPECIES: *Neospirifer grandis* Archbold & Thomas, 1986, p. 143, here designated.

DIAGNOSIS: Large elongate shells of subpentagonal outline with hinge generally close to maximum width, cardinal extremities obtuse, ventral umbo broad and low, sulcus very broad and deep, weakly defined sulcal plicae, not persisting far from umbo in some species, plicae weakly to well defined and in few pair, sulcal bordering pair wide and high, dorsal fold high, narrow or broad, costae fine or coarse, micro-ornament of radial filae, low concentric laminae. Dental plates low and ventral muscle field very large. Small delthyrial plate in juvenile, posterior callus in adult; stegidial plates known rarely.

DISCUSSION: *Neospirifer grandis* Archbold & Thomas from the Hardman Formation of the Canning Basin, Western Australia, is a large species well described by Archbold & Thomas (1986). The low dental plates are indicated by Archbold & Thomas (1986, text-fig. 11E, F) and shape and muscle field shown by Archbold & Thomas (1986, text-fig. 13C, D). *N. amplus* Archbold & Thomas (1986) from the Wandagee Formation of the Carnarvon Basin, Western Australia, also belongs to the genus. For *grandis*, Archbold & Thomas (1986) recorded a minor delthyrial plate in juveniles, and posterior pad of callus in adult specimens. For *amplus*, Archbold & Thomas (1986) recorded a small callus pad, and loose plates (stegidal plates or a fractured delthyrial plate) over the delthyrium (Archbold & Thomas 1986, text-fig. 10B, C). From the Himalaya, *ravana* Diener and *hongdeensis* n. sp. are congeneric.

Species of *Wadispirifer* are much larger than the types of *Neospirifer fasciger*, and show broad generally deep sulcus and massive swelling along the sulcal sides, and generally a subdued pair of inner sulcal plicae or subplicae. The dorsal plicae are generally a little better defined than those of the ventral valve, and the dorsal fold is variably narrow and high, or broad. The new genus is less transverse with inconspicuous sulcal plicae, and broader more conspicuous sulcus and fold than exhibited by *Betaneospirifer*. Plicae are often as few as 2 up to 4 pair. *Wadispirifer* shows considerable approach to *Betaneospirifer marcoui* (Waagen) in sulcus and plicae with low sulcal pair of plicae, but Waagen's species is less pentagonal in outline, and is much smaller and has a high narrow fold and smaller ventral muscle field. The shell is more massive and is shaped differently from the distinctive and strongly plicate *Quadrospira*, and lacks alate cardinal extremities. There is some approach to *Kaninospirifer*, but shells are large with deeper wider sulcus, larger plicae bordering sulcus, weak concentric lamellae and wider ventral muscle field.

Wadispirifer ravana (Diener, 1897b)

1897b *Spirifer ravana* Diener, p. 34, pl. 3, fig. 1a-c, 2.

1897b *S. moosakhailensis* not Davidson Diener, p. 35, pl. 4, fig. 1?, 2 (part, not pl. 3, fig. 3, 4 = *ambiensis*, not pl. 5, fig. 1 = *macroplica*).

1899 *S. musakheylensis.* Diener, p. 63, pl. 5, fig. 3-5, 7 (part, not fig. 6 = *ambiensis*).

1903 *S. marcoui* not Waagen Diener, p. 187, pl. 9, fig. 1a-d.

1979b *Neospirifer ravana*. Waterhouse & Gupta p. 32, pl. 5, fig. 10.

LECTOTYPE: GSI 6195 figured by Diener (1897b, pl. 3, fig. 1a-c) from Zewan Formation, Kashmir, SD Waterhouse (1966, p. 40).

DIAGNOSIS: Large subquadrate to subtriangular highly inflated shells with well spaced costae, 3-4 in 5mm anteriorly, low and broad plicae, very wide sulcus anteriorly.

DISCUSSION: This is a moderately well known species from the *Lamnimargus himalayensis* Zone of the Himalaya. It is distinguished by its deep and broad sulcus, subdued plicae, broad-crested ribs which tend to bifurcate and stay paired, narrow intercostal spaces, and inconspicuous ventral umbo. Specimens have been figured and described from the *Lamnimargus himalayensis* Zone by Diener, including one (GSI 7465) from sandstone below the Kuling Shales with less stratigraphic control (Diener 1903), but possibly equivalent to the Testha Sandstone Member, recognized by Waterhouse (1985) in south Zanskar. This specimen shows broadly convex ventral plicae, and narrowly crested higher dorsal plicae. The figures in Diener (1897b) are a little restored, and the specimen is slightly damaged in the umbonal region. The specimens figured as *moosakhailensis* by Diener (1897b, pl. 4, fig. 1, 2 - GSI 6200-6201) show the posterior shell well. GSI 6200 has a well developed sulcal pair of subplicae. Of the material figured as *musakheylensis*, that of Diener (1899, pl. 5, fig. 4 - GSI 6275) is well preserved, and shows the broad ventral sulcus without sulcal subplicae, as well as the dorsal valve, not figured. The specimen is probably at late immaturity, and is transverse. The specimen GSI 6278 (pl. 5, fig. 7) is a ventral interior, showing the characteristic wide muscle field. Specimens of Diener (1899, pl. 5, fig. 3, 5) seem likely to be conspecific. They all come from the Spiti valley and from Zewan beds of Kashmir valley. An internal mould of a ventral valve was figured from Marbal Pass, Kashmir, by Waterhouse & Gupta (1979b).

There have been various other reports of the species from further afield, and they can probably be discounted: Archbold & Thomas (1986) outlined some of them. A number of Arctic specimens have been identified with *ravana* and do come close to the species (eg. Stepanov 1937, pl. 7, fig. 5, 6), but require further examination. A large ventral interior figured by Jin & Sun (1981, pl. 11, fig. 1) needs to have more known about the external ornament before the species can be determined. Zhang in Zhang & Jin (1976, p. 208, pl. 16, fig. 9, 10, 13) identified specimens as *Neospirifer ravana* from south Tibet at JSJ17 and JSQ9, but the specimens have coarse costae, 2 in 5mm anteriorly, and relatively elongate ventral muscle field.

The species is moderately close to *Neospirifer grandis* Archbold & Thomas (1986, text-fig. 11-13) from the Hardman Formation of Wuchiapingian age in the Canning Basin, Western Australia, apart from stronger costae, wider sulcus and less transverse trigonal shape, though shape probably changed with increased maturity in the Australian species. Archbold & Thomas (1986, p. 148) suggested that the delthyrium was wider, the sulcal tongue less angular, the sulcus narrower and plicae weaker in their species, as compared with *ravana*. The west Australian species has some 4-5 costae in 5mm anteriorly.

Wadispirifer hongdeensis n. sp.

Plate 4, fig. 1, 5, 6, Plate 5, fig. 1

1966 *Neospirifer ravana* (not Diener) Waterhouse, p. 40, pl. 9, fig. 2, pl. 10, fig. 4.

1966 *Neospirifer moosakhailensis* (not Davidson) Waterhouse, p. 34, pl. 10, fig. 1 (part, not pl. 8, fig. 1, 2, pl. 9, fig. 1, 4, pl. 10, fig. 2 = *ambiensis*).

1978 *Neospirifer* sp. A Waterhouse, p. 126, pl. 24, fig. 10 (part, not fig. 9 = *ambiensis*).

1983a *N. kubeiensis* not Ding Waterhouse, p. 136, pl. 7, fig. 3, 4, 8 (part, not pl. 6, fig. 11, 12 = *tibetensis*).

DERIVATION: Named from Hongde, Manang place-name and airstrip.

HOLOTYPE: Specimen figured by Waterhouse (1966, pl. 10, fig. 4) from F 112, upper Namlang Group, east Dolpo, here designated. Kept at Geologische Bundesanstalt, Vienna.

DIAGNOSIS: Large shells with obtuse cardinal extremities close to maximum width, wide sulcus and broad strong fold, fine costae posteriorly, 5-6 in 5mm midvalve, 2-3 in 5mm anteriorly, wide ventral muscle field.

ADDITIONAL MATERIAL: A large specimen with valves conjoined from PJ1, Pija Member, southeast of Lake Chho and south side of ridge A over gentle hill-slopes high above Braga village, about 0.5km from cattle pound.

DIMENSIONS IN MM: internal mould

Width	Length	Height
110	82	55

DESCRIPTION: The PJ1 specimen is large, with hinge slightly less than maximum width, very wide deep sulcus, moderately high but damaged dorsal fold, and two pairs of strong plicae on each valve, and 1-2 additional narrow pairs laterally; ventral plicae broad and rounded in section, dorsal plicae fitting into ventral interspaces and narrow but well defined, not involved in dorsal fold in PJ1 specimen, but lie along base of fold flanks in holotype. Costae broad, 2-3 in 5mm, but only visible anteriorly on the newly illustrated mould. In the holotype, costae number 5-6 in 5mm medianly near midlength, some 40mm from the umbo, and in the specimen UQF 73653 (Waterhouse 1983a, pl. 7, fig. 3) costae number 6-8 at comparable position, and 6 in 5mm on UQF 73656 (Waterhouse 1983a, pl. 7, fig. 8): posteriorly costae are a little coarser, before splitting. Cardinal extremities at or near maximum width, may be obtuse or weakly alate in the large internal mould, with margin retracted a little in front, not as much as in *Quadrospira*. In the two moderately large fragments figured in Waterhouse (1983a), the cardinal extremities are more alate, and indicate that shape changed from transverse to subrectangular or pentagonal with increase in size.

The ventral muscle field is large, broad and somewhat elongate, dorsal muscle scars not strongly impressed. The partly visible spire is posteriorly directed, but may have been disarranged.

Dolpo material also large with similar attributes. The large specimen of Waterhouse (1966, pl. 10, fig. 4), now holotype, also shows the ventral valve, not figured, with strong ventral plicae and sulcus and part of the ventral muscle field. A weak swelling suggests the presence of posterior and impersistent sulcal plicae, and weak sulcal plicae are present in the ventral valves figured in Waterhouse (1983a). Dorsal costae number 4 in 5mm at some 30mm from the beak and 2-3 in 5mm anteriorly in holotype.

RESEMBLANCES: The species is close to *Wadispirifer ravana* (Diener) from the older *Lamnimargus himalayensis* Zone of Nepal and northwest India, but is larger, with slightly better defined plicae, and fine costae posteriorly and coarser costae anteriorly, and comparable or more elongate ventral muscle field. Archbold & Thomas (1986, p. 148) pointed out that the Waterhouse (1983a) specimens were close to *ravana.* Less appositely, Waterhouse (1978) and Shen et al. (2003a) referred 1966 specimens *to kubeiensis* Ding, but there is little similarity in inflation, fold, sulcus and costae, other than at subfamily level. The species *Neospirifer grandis* Archbold & Thomas (1986, text-fig. 11-13) from the Hardman Member of the Canning Basin, Western Australia, has fine costae and lower plicae and falls closer to *ravana* than to the present species.

Small specimens figured by Waterhouse (1983a, pl. 6, fig. 11, 12) as *Neospirifer kubeiensis* have 8 costae in 5mm at about 40mm from the ventral umbo, compared with 6 or so in the present species, and the sulcus is much narrower and shallower, and growth stages are more elongate. They are deemed to belong to *Quadrospira tibetensis* (Ding). Specimens figured as *ravana* by Zhang & Jin (1976, pl. 16, fig. 9, 10, 13) from JSJ 17 and JSQ 9, south Tibet, appear to have 3-4 costae in 5mm posteriorly, perhaps 30mm from the beak, coarser it appears than on *Wadispirifer hongdeensis*, and 2-3 costae in 5mm anteriorly, and large but elongate ventral muscle field.

STRATIGRAPHIC SIGNIFICANCE OF PRINCIPAL NEOSPIRIFERIN AND KANINOSPIRIFERIN SPECIES

It appears that most if not all of the neospiriferine species found in the Indian subcontinent are of limited distribution world-wide. This is partly because many of the species come from very Late Permian, with correlative marine faunas few and mostly coming from different paleolatitudes. *Betaneospirifer marcoui* (Waagen) is reasonably well circumscribed, of Guadalupian age in the Amb Formation of the Salt Range, Pakistan, and although the species has been reported elsewhere, no reports are convincing, and Archbold & Thomas (1986) have shown that the species differs from a supposedly comparable form in the Canning Basin of Western Australia. *B. moosakhailensis* (Davidson) comes from lower Wargal or upper Amb Formation, and is very widely reported. *B. neomarcoui* (Licharew, syn. *kubeiensis* Ding) is distinguished by well defined plicae and is found especially in the Kalabagh and Kufri Members of the Salt Range and lower Qubuerga Formation of south Tibet, ranging as high as the *Biplatyconcha grandis* Zone in western Nepal. *Betaneospirifer ambiensis* (Waagen) is a close ally, with wide hinge and one more pair of plicae, and the two appear to co-exist in the Kalabagh and Kufri Members of the Salt Range, of Wuchiapingian age. The latter species is found in the *Lamnimargus himalayensis* Zone of Kashmir and elsewhere in the Himalaya, and persisted into the *Biplatyconcha grandis* Zone of western Nepal. *Wadispirifer ravana* (Diener) is restricted to the *Lamnimargus himalayensis* Zone in western Himalaya of India and west Nepal.

Another distinctive form *Quadrospira tibetensis* (Ding) is mostly found in Tibet, and rarely in Nepal, in equivalents of the *Lamnimargus himalayensis* Zone, and, with modifications, in the younger *Lazarevonia arcuata* Zone of Nepal and *Retimarginifera xizangensis* Zone of Tibet. A number of species are found as minor occurrences, such as *Neospirifer poletaevi* n. sp. , *Neospirifer kalashnikovi* n. sp. and *Blasispirifer warchensis* (Reed), only in the Salt Range, and *Imperiospira bambadhuriensis* (Diener), in the Productus Shales of northwest India. *Wadispirifer hongdeensis* occurs in the *Lazarevonia arcuata*

Zone of the Pija Member, and the overlying Nisal Member yields *Betaneospirifer ravaniformis* and *Pondospirifer magnificus,* in the *Biplatyconcha grandis* Zone. The species *B. shii*, a large and coarse-ribbed species of the Marsyangdi Formation and Selong beds in south Tibet, is of Late Permian age, in the *Retimarginifera xizangensis* Zone.

Subfamily **FUSISPIRIFERINAE** n. subfam.

NAME GENUS: *Fusispirifer* Waterhouse, 1966, p. 43.

DIAGNOSIS: Very transverse shells with obtuse cardinal extremities, well formed cardinal areas, delthyrium generally closed by plate under umbo, sulcus and fold well formed, sulcus in many forms without plicae, plicae as a rule few, 2-6 pair, low and narrow with few costae, lateral shell as a rule ornamented by simple or rarely bifurcating costae, low growth lamellae, fine radial capillae. Interior as in *Spirifer* and *Neospirifer*, with no exceptional features, secondary thickening may be modest to considerable.

DISCUSSION: Genus *Fusispirifer*, with its type species *F. nitiensis* (Diener) of the Himalaya (Text-fig. 26. 1, 2) and widespread other species, is characterized by its highly transverse outline and ornament of some 2-5 narrow inner pairs of persistent plicae, with costae in fascicles of bifid or trifurcate nature, and extended lateral ornament of simple costae. The sulcus is bordered throughout its length by a pair of narrow plicae, and as a rule plicae have no more than 2-3 rarely up to 5 costae. Plicae are strong and few in *Occidalia* Archbold, but are faint in *F. kennediensis* Archbold & Thomas, 1987, and fascicles are narrow and only developed posteriorly in *Transversaria* Waterhouse & Gupta and *Latispirifer* Archbold & Thomas. *Costatispirifer* Archbold & Thomas rarely has fascicles or plicae in which costae are fine and bifurcate, but not repeatedly, and stay close to each other. Concentric lamellae are seldom prominent in *Fusispirifer* itself. Although they are well developed in *F. carnarvonensis* and *F. wandageensis* as described by Archbold & Thomas (1987), these species are deemed to belong to other genera within the subfamily, namely *Cratispirifer* and *Crassispirifer* respectively. A delthyrial cover is often preserved, and in the species *carnavonensis* is composed of arcuate plates in pairs, suggestive of stegidia found in various Spiriferidae, including *Gypospirifer*. One species *Fusispirifer avicula* (Morris) has been recorded by Clarke (1987, text-fig. 5D) as showing an umbonal callosity. This is not known for other species, but the species *avicula* is regarded as a member of Angiospiriferinae not Fusispiriferinae (p. 185). *Cratispirifer* Archbold & Thomas is particularly close to *Fusispirifer*, with more plicae and high ventral interarea, and *Crassispirifer* Archbold & Thomas has a number of comparatively well formed plicae, approaching those of neospiriferine species, and including 1-2 narrow pairs within the sulcus. Western Australia has provided the finest array of genera and species amongst Fusispiriferinae, and occurrences extend into east Australia and New Zealand, and throughout the Himalaya, and also in high paleolatitudes of Siberia. No paleotropical examples are known.

Tibetospirifer Liu & Wang, 1990, p. 388, type species *T. xizangensis* Lui & Wang, is transverse with oval cardinal extremities, showing some approach to *Cratispirifer*, apart from being less transverse and having perhaps 6 pair of plicae. The height of the ventral interarea is poorly known, as is the nature of the delthyrium, which needs to be clarified for subfamily and family placement. Internal moulds figured by Lui & Wang (1990) appear to suggest short adminicula and no tabellae, but a transverse form figured as *Zhejiangospirifer giganteus* Shen, Shi & Archbold (2003b) from south Tibet that looks somewhat similar was reported to lack dental plates and presumably adminicula: the approach is therefore presumably from convergence.

Warsawia Carter, 1974, type species *Spirifer lateralis* Hall, is transverse with numerous fine simple costae, rarely bifurcating, and not fasciculate. Of Lower Carboniferous (Meramecian, Visean) age, it could be regarded as the oldest member of Fusispiriferinae, or ancestral to the subfamily. But it lacks adminicula from at least the mature ventral valve according to Carter (1974, p. 685), leading to some doubt, and is provisionally retained as a member of Spiriferinae, following Carter et al. (1994). However this may require reassessment, as the adminicula might be short and buried in secondary shell.

RELATIONSHIP TO SPIRIFERINAE AND NEOSPIRIFERINAE

There is some ambivalence in the relationship of Fusispiriferinae to other spiriferid and trigonotretin groups. The preponderance of solitary or bifurcate usually undifferentiated costae points to spiriferin affinities, whereas the development of some tricostate fascicles, concentric laminae and radial filae tends to be better known amongst Neospiriferinae. The degree of plication is generally greater than that exhibited in most if not all gypospiriferin genera, but less than in Neospiriferinae and Trigonotretinae. As a rule, the nature of the sulcus more closely approaches that of Spiriferidae. The delthyrium is generally covered by a plate formed by fusion of plates from the delthyrial edges, but its nature has not been closely studied. *Occidalia* Archbold is particularly close to Neospiriferinae, having few strong plicae, and its position may require reassessment.

Fusispiriferinae are treated as a member of Neospiriferidae, because of overall shape and ornament, and presence of delthyrial plate. The species *Neospirifer licharewi* Abramov (in Kotlyar & Popeko (1967) from the early Late

Carboniferous Shazagaituisk Suite of Zabaikal shows strong attributes of *Crassispirifer*. Thus it appears that the group arose in the Late Carboniferous and flourished in higher to moderate temperate latitudes during the Permian Period. The genera are all large, and include forms with subdued and narrow plicae and extensive lateral shell with simple costae.

What may prove to have been ancestral is the genus *Frechella* Legrand-Blain. This has weak plicae in which primary ribs predominate, lateral costae, and narrow sulcus, with the bordering pair of plicae rarely subdivided on the inner side. The genus has extended alate cardinal extremities, especially into early maturity, weak fascicles and a thick delthyrial cover. *Frechella* is of Carboniferous age, Serpukhovian especially, first described from North Africa, and is putatively classed as a member of Imbrexinae Carter.

GENERA: *Fusispirifer* Waterhouse, *Costatispirifer* Archbold & Thomas, *Cracowspira* Waterhouse n. gen., *Crassispirifer* Archbold & Thomas, *Cratispirifer* Archbold & Thomas, ?*Latispirifer* Archbold & Thomas, ?*Occidalia* Archbold, ?*Tibetospirifer* Liu & Wang, *Transversaria* Waterhouse & Gupta.

Genus ***Fusispirifer*** Waterhouse, 1966

Text-fig. 26. 1, 2

TYPE SPECIES: *Spirifer nitiensis* Diener, 1897b, p. 41.

DIAGNOSIS: Transverse shells with alate cardinal extremities, narrow sulcus without subplicae or plicae, low fold, 2-5 pairs of narrow plicae, shell covered by bifurcating and more rarely trifurcating generally fine costae, costae may be missing from lateral shell.

DISCUSSION: Archbold & Thomas (1987) and Shen et al. (2003a) confused *Transversaria* with *Fusispirifer*, but the two genera are quite different. *Transversaria* lacks the narrow plicae of *Fusispirifer*, and has a fold that commences in front of the umbones, and becomes much broader than in *Fusispirifer*.

Fusispirifer semiplicata Jin, 1976

1966 *Fusispirifer nitiensis* (not Diener) Waterhouse, p. 44, pl. 9, fig. 5, pl. 11, fig. 1, pl. 12, fig. 1 (part, not pl. 11, fig. 3, 4 = *marcouiformis*).

1973 *F. nitiensis*. Mu et al. pl. 3, fig. 7, 8.

1976 *F. nitiensis semiplicata* Jin in Zhang & Jin, p. 209, pl. 12, fig. 1-6.

1985 *F. nitiensis semiplicata*. Jin, pl. 3, fig. 10.

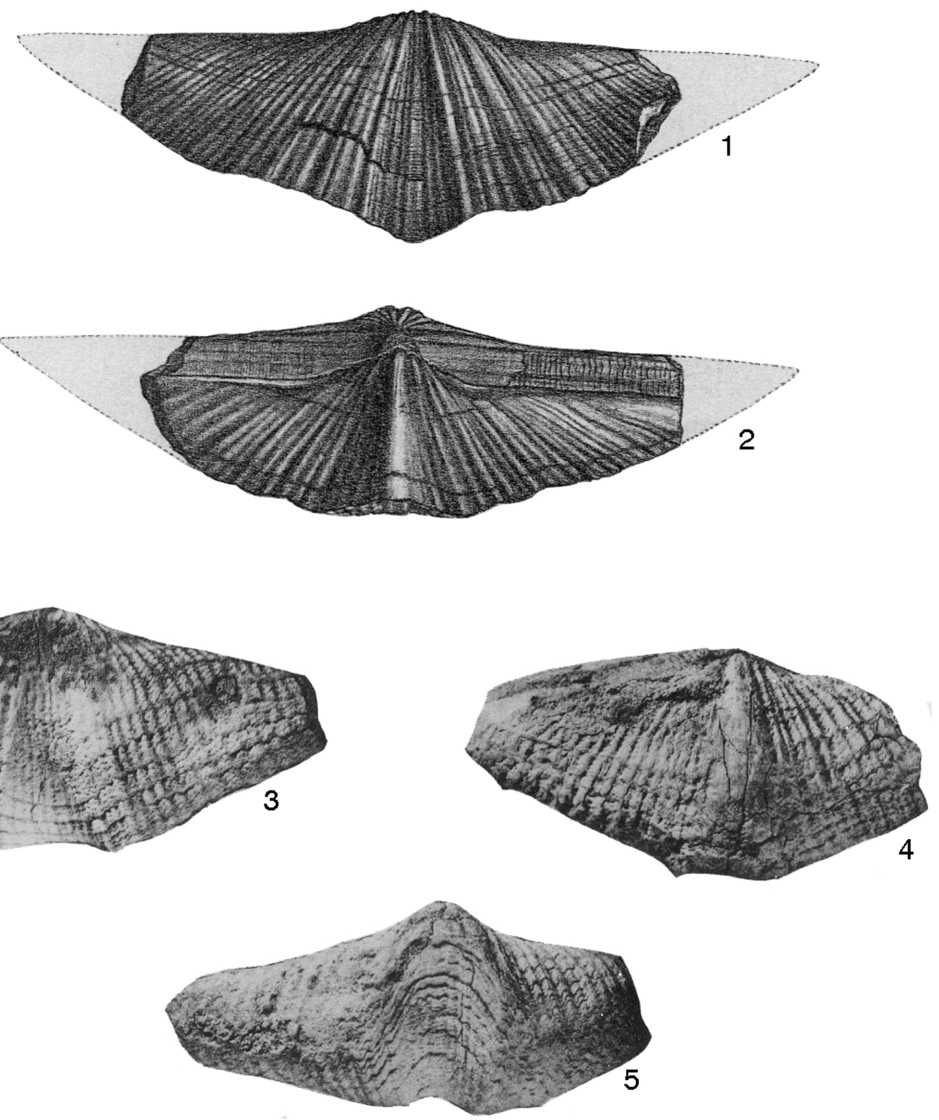
HOLOTYPE: Specimen 23407 figured by Jin (1976, pl. 12, fig. 1-3, 6) from FdV-8, lower Qubuerga Formation, south Tibet, OD. Kept at Nanjing Institute of Geology & Paleontology.

DIAGNOSIS: Transverse shells with narrow posterior plicae, fading anteriorly, but with large broad swelling along sides of sulcus in ventral valve, dorsal plicae fade anteriorly, poorly known posteriorly.

DISCUSSION: *Fusispirifer nitiensis semiplicata* Jin in Zhang & Jin (1976, pl. 12, fig. 1-6) from FdV8 and JSPf17 in the Qubuerga Formation, Tingri County, south Tibet, has a narrow sulcus and subdued plicae, and swollen flanks along the sulcal edges. The taxon may be treated as a full species, as also agreed by Shen et al. (2003a). It is found in what was termed the *Calliomarginatia* assemblage in south Tibet by Jin (1985), in the lower Qubuerga Formation at Qubu, south Tibet. Jin in Zhang & Jin (1976) pointed out that the Dolpo specimens figured by Waterhouse (1966) from locality 58 in east Dolpo were identical. They come from low in the Late Permian, probably Nangung Formation, in the *Lamnimargus himalayensis* Zone. Jin (1976) also included the specimen compared to *nitiensis* by Diener (1899, pl. 5, fig. 9) but its inner plicae are narrow without the broad bordering plication of *semiplicata*. Shen et al. (2003a) synonymized *Fusispirifer nitiensis* of Yang & Zhang (1982, pl. 3, fig. 1a, b) with *semiplicata*, but the specimen has robust plicae and may be *Occidalia* Archbold, although it is difficult to be sure, because only an internal mould was figured. They also treated a Dolpo specimen of Waterhouse (1966, pl. 11, fig. 3, 4) as *semiplicata*, but the specimen belongs to *Transversaria marcouiformis*.

Fusispirifer jini n. sp.

1978 *Fusispirifer nitiensis* (not Diener) Waterhouse, pp. 94, 127, pl. 17, fig. 1, 6, pl. 24, fig. 11, 14.
2001 *Fusispirifer* sp. Shen, Archbold & Shi, p. 281, text-fig. 5.8-11.
2003a *F. semiplicata* not Jin Shen et al., p. 86, pl. 13, fig. 10-17.
DERIVATION: Named for Jin Yugan.
HOLOTYPE: NMV P306025 figured by Shen et al. (2003a, pl. 13, fig. 13) from “bed” 15, upper Qubuerga Formation, Tibet, here designated.
DIAGNOSIS: Transverse *Fusispirifer* characterized by narrow sulcus with angle of 15-20° and fine costae on subdued not raised flanks, 4-5 pair of plicae very narrow and either fading anteriorly or persistent. Inner plicae have 2-3 broad costae near umbo, in contrast to slender costae over lateral shell.
RESEMBLANCES: This species was described by Waterhouse (1978), Shen, Archbold & Shi (2001) and Shen, Shi & Archbold (2003a). It is close to *Fusispirifer nitiensis* (Diener, 1897b, 1899) from the Productus Shales of Niti Pass and Lissar Valley in the *Lamnimargus himalayensis* Zone, but has narrower plicae and finer costae with 4-5 ribs in 5mm at midlength, compared with 3 - rarely 4 - in 5mm on Diener’s types, and a slightly narrower sulcus, close to 15-20°, compared with 28-30° in Diener’s types. Amongst specimens described from



Text-fig. 26. Genera of Subfamily Fusispiriferinae.
1, 2. *Fusispirifer nitiensis* (Diener), lectotype, ventral and dorsal aspects, as figured by Diener (1897b, pl. 4, fig. 5). Productus Shales, northwest India x 1.
3-5. *Cracowspira laminatus* (Waterhouse), holotype, ventral, dorsal and anterior views, UQF 74179, figured by Waterhouse (1987a, pl. 5, fig. 11-13) x 1. Rose's Pride Formation, Queensland.

the *Biplatyconcha grandis* Zone in west Dolpo by Waterhouse (1978), a ventral valve (pl. 17, fig. 1) shows 4-5 pairs of very narrow and low but distinct fascicles, some with 2 ribs, others with 3 ribs, scarcely plicating the shell. Another ventral valve (pl. 17, fig. 6) is more worn, with prominent swelling bordering the sulcus, suggestive of *semiplicata,* but the apparent swelling is probably due to wear and lighting, and is only on one side of the shell. *Fusispirifer* sp. of Shen, Archbold & Shi (2001) from the Qubuerga Formation near Mt Qomolungma, south Tibet, is allied.

Fusispirifer nitiensis semiplicata Jin in Zhang & Jin (1976, pl. 12, fig. 1-6), now regarded as a full species, has swollen flanks along the sulcal borders, and sulcus with angle close to 25^{o}. Specimens from the upper Qubuerga Formation ("beds" 15-22) that were referred to *semiplicata* by Shen et al. (2003a) do not belong to Jin's species, because they lack the parasulcal swelling of the ventral valve. Instead they show a very narrow sulcus with angle close to 15^{o}, low scarcely raised fold, and some 4 pairs of plicae and many lateral costae, typical of *F. jini*.

Neospirifer? subovalis Abramov & Gigorieva (1988, p. 165, pl. 26, fig.3) from the upper Echisk Suite of Verchoyan, belongs to *Fusispirifer* and is only moderately close, being smaller in size with low inner fascicles of 2 or 3 narrow costae.

Genus ***Transversaria*** Waterhouse & Gupta, 1983, p. 240.

TYPE SPECIES: *Fusispirifer marcouiformis* Jin, 1976, p. 209.

DIAGNOSIS: Large transverse shells with weak bundling of 2 or rarely 3 ribs limited to umbones, well developed fold and sulcus, that commence in front of the umbones, widen anteriorly to become broad and low. Shell very thick posteriorly in ventral valve.

DISCUSSION: Writers have gone to some length to discredit the validity of *Transversaria*, in order to synonymise it with *Fusispirifer*, asserting for instance that the genus was based entirely on internal moulds, and that the genus had been justified on the basis that plicae were lacking from the internal mould. These assertions are not true. Shen et al. (2003a) retained the type species *marcouiformis* as *Fusispirifer*, but figured external shells, to make it clear that the species is not *Fusispirifer*. The specimens lack fasciculae, just like one specimen of the original suite (Zhang & Jin 1976, pl. 12, fig. 10, 11) which shows the exterior, and have massive anterior fold, unlike any species of *Fusispirifer*. One figure (Shen et al. 2003a, pl. 14, fig. 5) shows the delthyrial cover.

The genus *Latispirifer* Archbold & Thomas, 1985b shows similar weak bundling over the umbonal region, and so is threatened with being a junior synonym of *Transversaria*. But whereas the fold becomes very wide in *marcouiformis*, it remains high and narrow in species of *Latispirifer*, as in most genera within Fusispiriferinae.

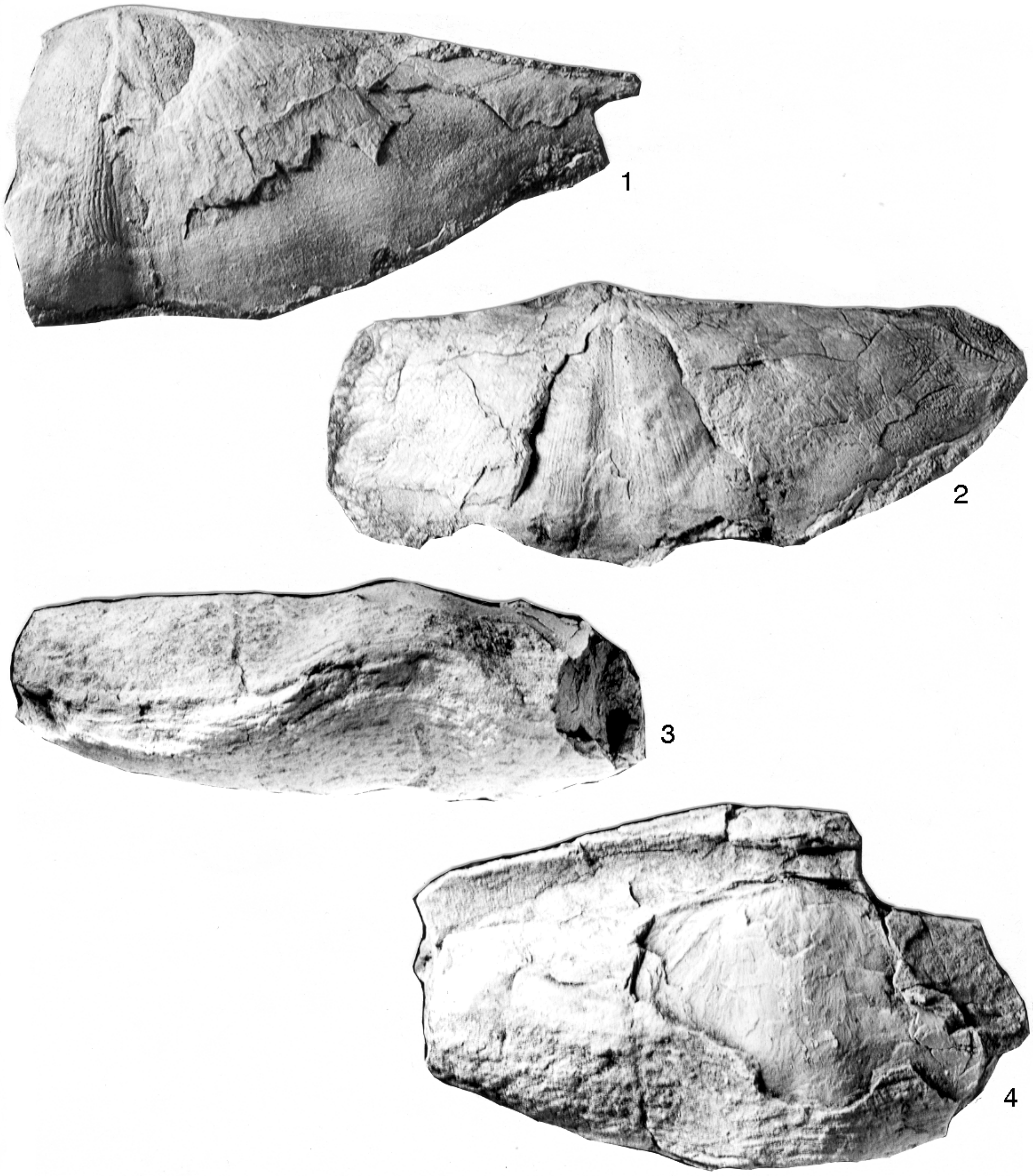
Transversaria marcouiformis (Jin, 1976)

Text-fig. 27

1966 *Fusispirifer nitiensis* (not Diener) Waterhouse, pl. 11, fig. 3, 4 (part, not pl. 9, fig. 5, pl. 11, fig. 1, pl. 12, fig. 1 = *semiplicata*).

1976 *Fusispirifer marcouiformis* Jin in Zhang & Jin, p. 209, pl. 12, fig. 7, 9-11, pl. 13, fig. 1, 2, 21-23.

1982 *Neospirifer* sp. Yang & Zhang, p. 313, pl. 2, fig. 3, 4.



Text-fig. 27. *Transversaria marcouiformis* (Jin) from lower Qubuerga Formation, south Tibet, x 1. 1, unregistered NMV ventral valve. 2, NMV P306029. 3, 4, anterior and dorsal aspects of NMV P306031. Specimens figured in Shen et al. (2003a, pl. 14, fig. 2-4), photographs supplied by Dr Shen.

1983 *Transversaria marcouiformis*. Waterhouse & Gupta, p. 240.

1985 *F. marcouiformis*. Jin, pl. 2, fig. 14.

2003a *F. marcouiformis*. Shen et al. p. 86, pl. 13, fig. 10-17.

HOLOTYPE: Specimen IGAS 00925 figured by Jin (1976, pl. 13, fig. 1, 2, 22, 23) from Qubuerga Formation, south Tibet, OD.

DISCUSSION: The original figures and the additional figures in Shen et al. (2003) show that the ribs of *marcouiformis* are not strongly fasciculate, and that there are no plicae.

Shen et al. (2003a) referred specimens from west Dolpo figured by Waterhouse (1978) to *marcouiformis*, but the specimens have narrow plicae extending to the anterior margin, and completely different sulcus. The material belongs to *Fusispirifer*, not *marcouiformis* or allied species.

Transversaria pauciplicus (Waterhouse, 1987a)

Text-fig. 28

1987a *Fusispirifer pauciplicus* Waterhouse, p. 23, pl. 5, fig. 15, pl. 6, fig. 1-4 text-fig. 4 (part, not fig. 5-7 = *acuta*).

HOLOTYPE: UQF 42221 figured by Waterhouse (1987a, pl. 6, fig. 1, 2, 4) and herein as Text-fig. 28, from Barfield Formation, Bowen Basin, OD.

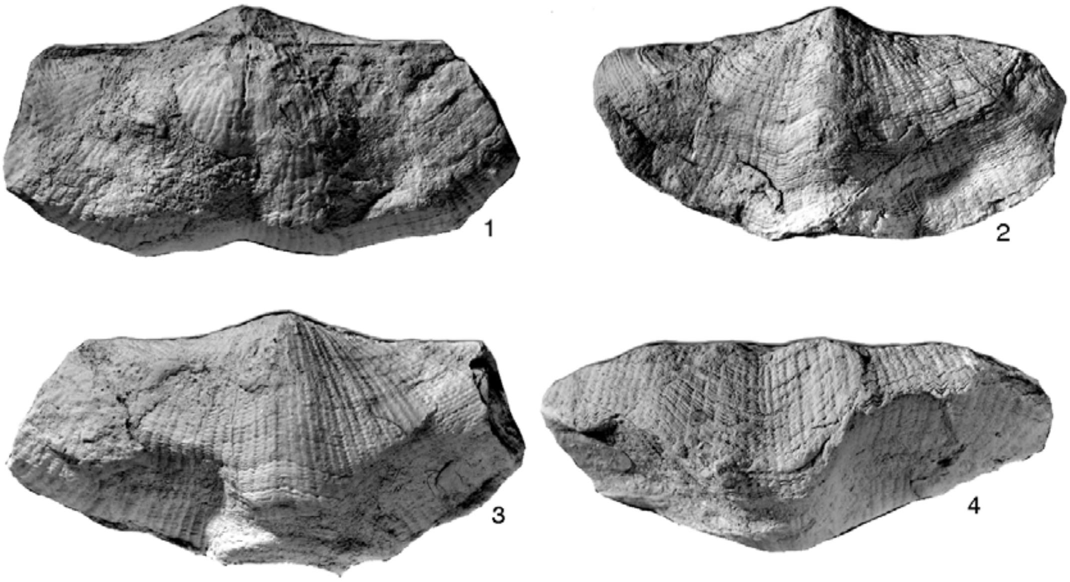
DISCUSSION: This species is smaller than the Tibetan form *marcouiformis*, and has low broad fold and shallow anterior sulcus. Full comparison of ornament is difficult, because the umbonal ornament is essentially poorly known for the ventral valve of this species, and for both valves of the Tibetan species, but the shape and nature of the characteristic fold and sulcus are similar for both species, and much of what is known of the ornament is comparable. The fold is almost half the width of the shell, compared with a third to a quarter in *Transversaria marcouiformis*, and is a third of the height, compared with a third to half the height in *Transversaria*. In other fusispiriferin genera, the fold is narrower, and higher. There are no plicae, but costae may form low posterior fascicles through splitting into pairs and persisting as doubles, and costae also bifurcate anteriorly and laterally. Ventral costae are mostly broad and solitary, with a few fine lateral costae, not raised as fascicles. The ornament agrees especially with the specimens described by Shen et al. (2003a), and costae are less even than in the large exterior figured by Jin & Zhang (1976, pl. 14, fig. 11). Concentric laminae are moderately well developed. The species is found in the Barfield Formation, of Roadian age (Waterhouse 2002c). Specimens assigned to the species from the overlying Flat Top Formation (Waterhouse 1987a, pl. 6, fig. 5-7) have more attenuate cardinal extremities and appear to have narrow fold and are assessed as belonging to *Crassispirifer* Archbold & Thomas (p. 158).

Genus **Latispirifer** Archbold & Thomas, 1985b

TYPE SPECIES: *Latispirifer amplissimus* Archbold & Thomas, 1985b, p. 273.

DIAGNOSIS: Transverse shells with weakly developed fasciculate bundling of costae in pairs or triplicate over umbones; dorsal fold high, narrow, ventral sulcus commences at umbo.

DISCUSSION: This genus is provisionally recognized and tentatively placed as a member of Fusispiriferinae. It is represented by species in Western Australia, and judged to be fusispiriferin because of its transverse outline and the nature of the sulcus and fold, which are very close to those of *Fusispirifer* and allies. The fold is over half up to 0.75 of the shell in height, and narrow at a quarter to a tenth of the shell width, with high tented crest. Feeble bundling is



Text-fig. 28. *Transversaria pauciplicus* (Waterhouse) from Barfield Formation, Bowen Basin, x 1. 1, 2, 4, ventral, dorsal and anterior view (ventral valve on top) of holotype, UQF 42221. 3, dorsal valve UQF 42220. Also figured by Waterhouse (1987a, pl. 6, fig. 1-4).

developed posteriorly, but in detail there is variation. Fascicles are well developed on some small specimens, such as those figured by Archbold & Thomas (1985b, text-fig. 3C, 4D, F, 6B), with costae in triplets and doublets, indicating that the umbonal region is fasciculate and gently plicate, in 3-4 pair. In larger specimens the costae may be even, or rather irregular and associated in pairs, but plicae are virtually absent; the variation seems greater than in suites of *Transversaria*. However specimens of *Transversaria* are not well preserved over the umbonal region for the ventral valve, so that this also may have displayed umbonal bundling.

From almost inception, the very similar genus *Transversaria* has been misrepresented and alleged to be *Fusispirifer*. But despite claims to the contrary, and mis-statements over the type material, *Transversaria* lacks plicae, and has a wider lower fold and broader shallow sulcus. It is considered that *Latispirifer* may be distinguished by the nature of its sulcus and fold, which suggest that the genus may be a relapsed and catagenic derivative from *Fusispirifer,* or more likely, *Crassispirifer,* given the way that the innermost bundles enter the posterior sulcus, especially in *L. amplissimus* Archbold & Thomas. By contrast, the fold of *Transversaria* commences in front of the umbones, and is much broader and lower.

Genus ***Cracowspira*** n. gen.

Text-fig. 26.3-5

DERIVATION: Cracow - Queensland mining town, spira - coil, Lat.

TYPE SPECIES: *Fusispirifer laminatus* Waterhouse, 1987a, p. 23, here designated.

HOLOTYPE: UQF 74179 figured by Waterhouse (1987a, pl. 5, fig. 11-14) and herein as Text-fig. 26.3-5, from Rose's Pride Formation, Bowen Basin, OD.
DIAGNOSIS: Small transverse shells with alate cardinal extremities, very low ventral interarea, narrow fold and sulcus, 3 weak plicae or fascicle pairs posteriorly and narrow single bold costa each side of sulcus. Characterized by stout rarely bifurcating subangular costae, concentric laminae well developed.
DISCUSSION: This genus is based on a species from the Sakmarian Rose's Pride Formation of the southeast Bowen Basin of central Queensland. In most respects *Cracowspira* falls very close to the genus *Fusispirifer*, being largely identical in shape, with narrow well formed sulcus and fold and wide cardinal areas, alate at the extremities, and three pair of extremely low and narrow fascicles. Costae bifurcate and bear strong concentric lamellae. The main difference from *Fusispirifer* lies in the coarse nature of the lateral costae. In species of *Fusispirifer*, the lateral costae are finer than those of the median shell, and in some species lateral costae can scarcely be discerned. In the type species of *Cracowspira*, the lateral costae are sturdy, with rounded tending to subangular crests, and interspaces of similar width. The ornament somewhat approaches the relatively strong lateral costae found in species of *Cratispirifer* Archbold & Thomas, 1985b, and *Crassispirifer* Archbold & Thomas, 1985b, but the new genus is distinguished from those genera by the paucity of plicae, narrow deep sulcus and low interareas. A stout costa traverses each side of the sulcus in the type species, along the inner side of the sulcal bordering pair of plicae, unlike *Fusispirifer*. This somewhat approaches the arrangement seen in some species of *Cratispirifer,* to suggest a possible origin from that genus. *Transversaria* Waterhouse & Gupta is also close, with broader fold, less developed fascicles and narrower costae.

Latispirifer Archbold & Thomas has finer costae, weaker and less organised fascicles, better defined sulcus and lower broader ventral umbo.

Genus ***Cratispirifer*** Archbold & Thomas, 1985b

TYPE SPECIES: *Cratispirifer nuraensis* Archbold & Thomas, 1985b, p. 280.
DIAGNOSIS: Transverse with high ventral interarea and thick posterior shell, coarse costae and weak to strong plicae, fastigium high and narrow, delthyrium narrow with delthyrial plate, sulcus narrow, without extended tongue, well defined sulcal borders and either devoid of plicae or bearing a low pair of subplicae along sulcal side of border pair.
DISCUSSION: *Cratispirifer* was based on a species from the Nura Nura Member of the Canning Basin, Western Australia. It was considered to differ from *Fusispirifer* through its high ventral interarea and coarse costae. A species from

the southern Karakorum and Himalaya has moderately high interarea and coarse costae, and is referred to the genus.

Cratispirifer macroplica n. sp.

Plate 5, fig. 4

1897b *Spirifer musakheylensis* not Davidson Diener, p. 35, pl. 5, fig. 1 (part, not pl. 3, fig. 3, 4 = *ambiensis,* not pl. 4, fig. 1?, 2 = *ravana*).

?1897b *Spirifer* sp. aff. *fasciger* not Keyserling Diener p. 40, pl. 5, fig. 2, 3.

1903 *S. nitiensis* not Diener Diener, p. 106, pl. 4, fig. 6a, b, 7a, b.

DERIVATION: macro = large, plica = fold, Lat.

HOLOTYPE: GSI 7385 figured by Diener (1903, pl. 4, fig. 6) from *Lamnimargus himalayensis* Zone, Lissar valley, northwest India, here designated.

DIAGNOSIS: Transverse not very inflated shells with alate cardinal extremities and high ventral interarea, shallow well defined ventral sulcus, narrow high fold, 4 pair of well defined plicae and coarse costae with rounded crests.

MATERIAL: A specimen with valves conjoined from *Lamnimargus himalayensis* Zone of Shyok valley, southern Karakorum Range.

DIMENSIONS IN MM: ventral valve

Width	Length	Height
118	33	20est.

DESCRIPTION: Transverse with very low broad ventral umbo not projecting far beyond hinge, high gently concave ventral cardinal area with wide delthyrium, acute cardinal extremities becoming obtuse with increase in size. Dorsal valve with very low concave interarea at high angle to ventral interarea, and moderately high and narrow fold with narrow crest, carrying subdivision low on each flank. Plicae in 4 pair, well defined, slightly stronger on dorsal valve, with narrow somewhat tented crests, persisting to anterior margin, pair bordering sulcus narrow, with subsidiary pair on flanks, within sulcus for most of length. Costae broad with rounded crests, numbering up to 13 in sulcus, including central costa, 3-5 over inner plicae.

Ventral muscle field large and long, broad adductors marked by longitudinal grooves and other grooves parallel to anterior margin, secondary shell thick below cardinal area and each side of muscle field. Dorsal adductor scars lightly impressed, irregularly marked, and divided by median ridge, secondary thickening moderate.

RESEMBLANCES: This species is distinguished from *Fusispirifer nitiensis* (Diener) by its less transverse outline, higher ventral interarea, more plicae, coarser costae and greater secondary thickening in the ventral valve. It is best represented by material from Lissar valley, northwest India. The specimen figured by Diener (1897b, pl. 5, fig. 1) as *musakheylensis* is a transverse shell with narrow ventral sulcus, weak sulcal subplicae and coarse costae, but the nature of the interarea is not figured. The accompanying dorsal valves, also from Kiunglung, were figured by Diener as *fasciger* and are here tentatively assigned to the same species. They are comparable in shape (ie. pl. 5, fig. 2, the other being a fragment), but the costae appear finer. Archbold & Thomas (1985b, p. 822, 1987, p. 177) suggested that the specimens of Diener (1903) belonged to *Crassispirifer* Archbold & Thomas, 1985b, but the ventral interarea is much higher, and the sulcus narrower than in species of *Crassispirifer* from Western Australia and Siberia.

Cratispirifer nuraensis Archbold & Thomas (1985b, p. 280, text-fig. 8A-F) has slightly higher ventral interarea, less persistent less well defined plicae, and coarse costae that flatten anteriorly on the dorsal valve. The species was described from the Nura Nura Member of the Poole Sandstone, Canning Basin, of Sakmarian age. From the upper Echisk Suite of west Verchoyan, of late Cisuralian age, *C. barchatovae* Abramov & Grigorieva (1988, pl. 28, fig. 2-4, pl. 29, fig. 4) is smaller, with slightly lower ventral interarea and relatively coarse costae and narrow sulcus.

Genus ***Crassispirifer*** Archbold & Thomas, 1985

TYPE SPECIES: *Spirifer rostalinus* Hosking, 1931, p. 24.

DIAGNOSIS: Moderate to large and transverse shells with largely transverse and even alate early ontogeny, later developing more extended antero-lateral margins, but some species remain alate at a large size. Plicae in a number of narrow not well emphasized pairs, one or two pair within anterior sulcus; costae cover both valves, moderate to coarse in strength.

DISCUSSION: Three species were recognized in the Permian of Western Australia by Archbold & Thomas (1985b, p. 282), and it appears that *Fusispirifer wandageensis* Archbold & Thomas, 1987 from the Wandagee Formation of the Carnarvon Basin, Western Australia, is congeneric. Unlike species of *Fusispirifer*, this species has a broad sulcus entered for much of its length by at least one pair of plicae or subplicae, and at least 5 plicae pairs overall. Archbold & Thomas (1985b) acceptably regarded *Fusispirifer* as a close ally of *Crassispirifer*, and distinguished the genus on the basis of its thick shell, change in shape during development from transverse to subrectangular, and reported "subequidimensional costae", presumably in section, of flattish appearance. The broad sulcus and number of plications which are comparatively low and narrow, with few costae, constitute significant differences from *Neospirifer* and *Betaneospirifer*, reinforced by the way in which the anterior sulcus may expand, gradually, to incorporate two rather than just one pair of plicae. *Fusispirifer* has only 2-4, rarely 5, pair of subdued narrow plicae, and none are present within the sulcus. *Cratispirifer* Archbold & Thomas is close in transverse outline and a number of strong plicae, but its sulcus is narrower, with no or only very subdued sulcal plicae, thereby approaching *Fusispirifer*, and shell thickening is substantial and ventral interarea high.

Various Russian forms were recognized as related by Archbold & Thomas (1985b), and several species were described as *Crassispirifer* from northeast Russia by Abramov & Grigorieva (1988). The Russian shells are transverse on the whole, with a number of plicae, of which two pair may enter the anterior sulcus. They differ from west Australian species in their smaller size, finer costae, and tendency for individuals, especially *C. monumentalis* Abramov & Grigorieva (1988, pl. 27, fig. 1-6), to be less alate and slightly more elongate during early growth stages.

The species *Neospirifer licharewi* Abramov in Kotlyar & Popeko (1967, p. 162, pl. 45, fig. 13-18, pl. 46, fig. 1-5) comes from the Upper Carboniferous Shazagaituisk Suite of Zabaikal. There are some 6 pairs of narrow plicae, including one or two pair within the sulcus, which persist to the anterior margin, and the plicae carry 2 or rarely 3 costae. It seems likely that the costae arise further from the umbones than in typical *Crassispirifer*, but this is difficult to ascertain, because mostly internal moulds were described. There is some approach also to *Costuloplica* n. gen. (p. 188), but the species appears to have sulcal plicae, unlike members of that genus.

Archbold & Thomas (1985b, p. 822) asserted that *Neospirifer striatiformis* Zhang, 1976 clearly belonged to their genus *Crassispirifer*, but this species, although close, is characterized by narrow sulcus that lacks sulcal plicae.

Material figured by Angiolini (1995, pl. 2, fig. 10-13, 15-18, pl. 8, fig. 4-6) as *Trigonotreta lyonsensis* has a much broader sulcus and fold than the species so-named by Archbold & Thomas (1986), and being transverse, with two plicae pairs entering the sulcus, might prove to belong to *Crassispirifer*. The specimens come from the Early Permian Gircha Formation of Chapursan valley in the Karakorum Range.

HOMONYMY: Abramov & Grigorieva (1986) also proposed a genus named *Crassispirifer*, and their genus was renamed *Doescherella* by Abramov & Grigorieva (1987).

Crassispirifer broilii n. sp.

?1915 *Spirifer fasciger* not Keyserling Broili, pl. 21, fig. 9.

1916 *Spirifer fasciger.* Broili, p. 34, pl. 120 (6), fig. ?10, 11, pl. 121 (7), fig. 1a, b?, 2-3 (part, not pl. 120, fig. 12, 13, 14 = Bitauni specimens, species not known; not fig. 15 = indet., pathological according to Broili 1916).

DERIVATION: Named for F. Broili.

HOLOTYPE: Specimen figured by Broili (1916, pl. 120, fig. 11) from Basleo, Timor, here designated, kept at Geologisches-Paläontologisches Institut of Bonn University.

DIAGNOSIS: Very large and transverse shells with comparatively narrow sulcus widening anteriorly, low fold, fine costae and well defined narrow plicae, numbering 6-7 pairs, counting those within sulcus, innermost pair incorporated early within sulcus and a second pair within the sulcus for most of the length.

DESCRIPTION: This species is based on specimens described by Broili (1916) from the Basleo collections of Timor. There are some 5-6 costae in 5mm, and growth lines are dense and low, the fastigium broad, and the sulcus widens at about 55°. The species is very distinctive. I have a plaster duplicate of the holotype, an internal mould of both valves, as figured by Broili (1916, pl. 120, fig. 11), and this shows that a deltidial plate was present, now lost, with no umbonal callosity. Adminicula are visible, and the ctenophoridum is well developed, with a slender median septum in front, small crural plates, and lightly impressed subrectangular adductor scars. Specimens are very large, one (Broili 1916, pl. 121 (7), fig. 2) being over 130mm across and the largest specimen (pl. 121 (7), fig. 3) over 150mm wide.

RESEMBLANCES: This species is referred to *Crassispirifer* because it has a number of plicae pairs, with two pair incorporated in the sulcus, and large size. The species is distinguished from west Australian species of *Crassispirifer* Archbold & Thomas by its plication, high ventral umbo and fine costae. It also has a slightly different growth pattern, in which the early shell is transverse, but less alate than in the west Australian species, and slightly more elongate. Reaching a large size of more than 100mm, the cardinal extremities become more alate, whereas those of type *Crassispirifer* tend to become slightly obtuse. The species is much larger and has more plicae than *Neospirifer fasciger* or *Betaneospirifer moosakhailensis* and allies. Quite possibly the Timor specimens had not yet reached full maturity, and later would have displayed the same growth phases as in the types of *Crassispirifer*. On the other hand the Russian species do not conform exactly with the growth development for West Australian species either, and include individuals and species with moderately prominent umbones, fine costae, and obtuse cardinal extremities. Such variations are here regarded as reflecting slight differences by well dispersed species. It is particularly noticeable amongst brachiopods from Western Australia that species and genera remain rather similar to each other through time, and do not display the degree of variability through time found in successions elsewhere. This implies that evolution developed mostly in situ from within local species, rather than through migration and replacement by species from elsewhere.

The present form is the youngest species yet known, at Wuchiapingian, as compared with middle Cisuralian to possibly as young as early Guadalupian in Western Australia, and starting in the early Cisuralian in Russia, or, if *licharewi* Abramov is *Crassispirifer*, in the Late Carboniferous.

Crassispirifer transversa n. sp.

1990 *Fusispirifer plicatus* not Waterhouse Xiong in Yang et al., pl. 25, fig. 1a, b, 4a, b.

DERIVATION: transversa - across, sideways, Lat.

HOLOTYPE: Specimen 74102 figured in Yang et al. (1990, pl. 25, fig. 4a, b) from upper Manzongrong Formation at Zanda, Tibet, here designated. Kept at Beijing Campus of China University of Geosciences.

DIAGNOSIS: Transverse shells with low broad ventral umbo, broad shallow sulcus, moderately high ventral interarea, some 6 pairs of plicae, inner pair entering sulcus just front of ventral umbo, coarse costae.

DESCRIPTION: Shell very transverse with extended but obtuse cardinal extremities, low broad ventral umbo, high ventral interarea and moderately wide delthyrium. Sulcus wide and shallow, angle close to 50º, and fold broad and low with narrow crest and outward sloping flanks. Plicae numerous and persisting to anterior margin, numbering 6 pair in holotype, narrow with interspaces just as wide, innermost pair enters sulcus early; 5 pair each side of fold on holotype, and fold flanks subdivided. Costae coarse, tending to extend along inner flank of plicae, generally solitary, becoming 2 then 3 anteriorly, a single costa traverses sulcus, and several costae lie over fold; outer flanks towards cardinal extremities may be smooth, especially on dorsal valve, with costae arising anteriorly.

RESEMBLANCES: This species is distinguished by its transverse outline and coarse costae. Species from Western Australia protrude more medianly in front, but young individuals of *Crassispirifer rostalinus* (Hosking) from the Madeline Formation, Carnarvon Basin, come close in shape (Archbold & Thomas 1985b, text-fig. 10F, G). *C. pinguis* Archbold & Thomas (1985b) from the Wandagee Formation of the same basin is close in plication and costae, but differs in shape and detail of ornament.

Russian specimens described by Abramov & Grigorieva (1988) have finer costae and generally are more elongate. *Neospirifer* sp. of Liu & Wang (1990, pl. 3, fig. 8, 9) from the Early Permian Mamixueshan Formation of Tibet is likely to belong to *Crassispirifer*, but has more pairs of narrow plicae, and is more elongate. *C. koargychanensis* (Zavodowsky 1970, pl. 31, fig. 3, pl. 32, fig. 1, 2; Abramov & Grigorieva 1988, pl. 24, fig. 1, pl. 23, fig. 2, 3) from the Lower Permian Echisk Suite of west Verchoyan is moderately close, with coarse costae and fewer plicae and lower interarea.

Shen et al. (2003a, p. 86) claimed that the present species as figured in Yang et al. (1990) was close to *Fusispirifer nitiensis* and *F. semiplicata*, but these species, typical of *Fusispirifer*, have fewer plicae, narrower sulcus, no sulcal plicae, lower interarea and finer costae, with other differences.

Crassispirifer acuta n. sp.

1987a *Fusispirifer pauciplicus* not Waterhouse Waterhouse, p. 23, pl. 6, fig. 5-7 (part, not pl. 5, fig. 15, pl. 6, fig. 1-4, text-fig.4 = *pauciplicus*).

DERIVATION: acutus - sharp, pointed, Lat.

HOLOTYPE: UQF 74182 figured by Waterhouse (1987a, pl. 6, fig. 5) from Flat Top Formation, Bowen Basin, here designated.

DIAGNOSIS: Transverse with acute cardinal extremities, wide but shallow sulcus and low fold, 4 pair of low plicae, with sulcal pair, costae moderately fine.

DESCRIPTION: A number of specimens are available from the Flat Top Formation of late Guadalupian age in the southeast Bowen Basin. They are characterized by subdued and few plicae and only moderately defined costae. The ventral interarea is of moderate height, with broad delthyrium largely closed by a plate on each side (unless it is fractured - see Waterhouse 1987a, pl. 6, fig. 6); the dorsal interarea is very low. Cardinal extremities are acute, close to 45^{o}. The sulcus is shallow and widens at approximately 50^{o}, to incorporate a broad inner plicae pair, and possibly a second pair anteriorly. The fold is low and moderately broad. Plicae are best displayed on small specimens (eg. Waterhouse 1987a, pl. 6, fig. 7), broad, low, bearing 3 costae, and fading somewhat towards the anterior margin. There are only 4 pair overall, and the outermost pair is not developed in all specimens. Costae have rounded crests and number about 3 in 5mm at the anterior margin. Concentric growth lines are feebly developed. The ventral muscle field is of moderate breadth, and not long, and secondary thickening is not great. Dental and adminicular plates are short.

RESEMBLANCES: This species is exceptional in its very alate extremities and low plicae and subdued costae. The specimens are less transverse, with more prominent ventral umbo and lower fewer plicae than species described from Western Australia by Archbold & Thomas (1985b), and readily distinguished from the south Asian and Timor forms described herein. The species is a little closer in shape and ornament to Siberian species described by Abramov & Grigorieva (1988), but differ in many details.

Genus ***Occidalia*** Archbold, 1997

TYPE SPECIES: *Occidalia shahi* Archbold, 1997, p. 218.

DIAGNOSIS: Transverse moderately to strongly plicate and costate shells with high fold and pronounced sulcal tongue.

DISCUSSION: This genus is known in Peninsular India and Western Australia, and Shen et al. (2003a, pl. 13, fig. 3-9) have recognized the genus in the Qubuerga Formation of south Tibet, as a very distinctive, as yet unnamed form. With high fold, several plicae pairs, and strong concentric lamellae, the genus approaches *Pteroplecta* Waterhouse, 1978 but plicae are fewer, in no more than 5 pairs, whereas *Pteroplecta* may have 7 or more pairs of plicae, and the plicae tend to be lower and narrower. Costae are finer and more numerous in *Occidalia* than in *Pteroplecta*. Sulcal plicae are indicated for *Occidalia mingenewensis* (Archbold, 1996, text-fig. 10.I, J) and vaguely for the mostly internal moulds described as *O. shahi* Archbold (1997, text-fig. 12.D, 13D, I).

Neospirifer striatiformis Zhang, 1976 from south Tibet shows some approach to *Occidalia* Archbold, in its transverse shape, deep narrow sulcus, number of plicae and strong costae (cf. Archbold 1997, text-fig. 13I). But the species of *Occidalia* so far described carry a subplication, or a strong rib, on the sulcal side of the bordering plicae, whereas this is not apparent in the figure of *striatiformis*.

Occidalia plicatus (Waterhouse, 1966)

Plate 5, fig. 7

1928 *Spirifer nitiensis* not Diener Bion, p. 24, pl. 1, fig. 1, 2a, b, pl. 4, fig. 8-13.

1928 *S. nitiensis*. var B Bion, p. 26, pl. 5, fig. 9.

?1928 *Spirifer fasciger* not Keyserling Bion, p. 29, pl. 4, fig. 14 (part, not pl. 1, fig. 5 = *Grantonia*).

1966 *Fusispirifer plicatus* Waterhouse, p. 47.

2003a *Occidalia plicatus*. Shen et al., p. 86.

HOLOTYPE: GSI 13186 figured by Bion (1928, pl. 4, fig. 11a, b) from Agglomeratic Slate, Kashmir, OD.

DIAGNOSIS: Very transverse shells with high ventral interarea, narrow and comparatively well defined inner plicae, high narrow fold and fine costae.

DESCRIPTION: This species has some 4 pair of plicae, and fine costae over sulcus, fold, plicae and laterally with fine concentric laminae. Most specimens are internal casts, leading to some obscurity, but there appears to be a sulcal pair of plicae. The specimen of Bion (1928, pl. 4, fig. 14) is costate and plicate like dorsal valves of *Betaneospirifer*.

RESEMBLANCES: The present species is less elongate and less robust with finer costae than *Occidalia shahi* (Archbold, 1997) from the High Cliff Sandstone of the Perth Basin or *O. mingenewensis* (Archbold, 1996) from the Mingenew Formation, both of younger Cisuralian age in Western Australia. *Occidalia* sp. from the Qubuerga Formation of south Tibet as figured by Shen et al. (2003a, p. 85, pl. 13, fig. 3-8) is also more elongate with median ridge along the anterior sulcus and strong lateral pair of costae within the sulcus, and costae coarser than in *plicatus*.

Zhang & Jin (1976, p. 210, pl. 12, fig. 8) identified a specimen from south Tibet as *"Fusispirifer" plicatus*, correctly drawing attention to the misassignment to *Fusispirifer*. Their specimen has a fastigium higher than in *plicatus*, and comes from JSJ24, its stratigraphic position far from clear. The species was further elaborated and "emended" by Xiong in Yang et al. (1990), based on material from Nagri, south Tibet, but the Nagri material belongs to *Crassispirifer,* and is described herein as a new species *C. transversa.*

DISCUSSION: Shen et al. (2003a) drew attention to the probable identity of the species *plicatus* with *Occidalia*. Archbold & Thomas (1985b, pp. 287-288, 1987, p. 177) stated that the species *plicatus* represented small specimens of *Crassispirifer*, but the sulcus, plication and ribbing are quite different. *Cratispirifer* Archbold & Thomas is similar in having a high and wide ventral interarea, but is less transverse and more elongate, with inconspicuous concentric lamellae.

Occidalia n. sp.

Plate 5, fig. 5, 8

1983 *Fusispirifer nitiensis* (not Diener) Waterhouse & Gupta, p. 240, pl. 2, fig. 9, 12.

DESCRIPTION: A small collection of several ventral and dorsal valves and specimens with valves conjoined comes from the *Lamnimargus himalayensis* Zone in the upper Shyok valley. They are highly transverse shells with wide sulcus and broad fold, alate cardinal extremities, and strong plicae, including pair within sulcus, and coarse costae. Vestiges of a median costa lies along the sulcus. Specimens are kept at the Centre of Advanced Studies in Geology, Chandigarh.

A transverse internal mould from Dingri, south Tibet, described as *Fusispirifer nitiensis* (not Diener) by Yang & Zhang (1982, pl. 3, fig. 1a, b) might prove to be *Occidalia*. It shows strong and costate plicae and possible sulcal plicae and median sulcal rib, and is somewhat suggestive of *Occidalia* described by Shen et al. (2003a) from the Qubuerga Formation of south Tibet. These specimens have a narrower higher fold than in the Shyok valley specimens.

TRIGONOTRETIDAE

The family Trigonotretidae has suffered vicissitudes of neglect and differing interpretations, and understanding of what genera it encompasses remains incomplete. Carter et al. (1994) recognized two subfamilies, Trigonotretinae and Neospiriferinae within Trigonotretidae. Here a different interpretation is proposed, that Trigonotretidae and Neospiriferinae arose from different stock, so that the two should be separated to family level, and tentatively retained as Spiriferoidea. Angiospiriferinae Legrand-Blain and Sergospiriferinae Carter are included within Trigonotretidae. They have numerous narrow plicae and are seldom costate, and so approach Paeckelmannelloidea (p. 227), a matter requiring further study.

Family **TRIGONOTRETIDAE** Schuchert, 1893

DIAGNOSIS: Small to large, hinge denticulate, moderate to numerous plicae, costae rare to covering shell, umbonal callosity developed in most forms. Vascular impressions laterally reticulate or ramiform.

Subfamily **TRIGONOTRETINAE** Schuchert, 1893

NAME GENUS: *Trigonotreta* Koenig, 1825, p. 3.

DIAGNOSIS: Characterized primarily by open delthyrium with umbonal callosity, sulcus and fold, ornament of moderate number of 3-9 pairs of plicae, bearing few to many costae, micro-ornament of radial and concentric filae. Cardinal extremities obtuse to alate, ventral valve with dental plates and short adminicula, as a rule largely buried in heavy secondary thickening, dorsal valve with ctenophoridium, low median septum, dental sockets formed by outer and inner hinge plates, crural plates, no tabellae. Lateral vascular impressions may be reticulate or ramiform (Text-fig. 33).

DISCUSSION: Trigonotretinae are centred in the Permian of Australia, and based on the long established genus *Trigonotreta* Koenig, 1825. The subfamily was widely dispersed within Gondwana, with no occurrences so far established from high latitudes of the northern paleohemisphere. The genus *Trigonotreta* was largely neglected in most studies based on northern hemisphere faunas, but after World War 11, a number of researchers in Australia (eg. Maxwell 1954, Armstrong 1968, Roberts et al. 1976) became concerned that *Trigonotreta* possibly had priority over *Neospirifer* Fredericks, 1923, even though *Neospirifer* had been used widely. On the contrary, it was shown by Waterhouse (1968) that a trigonotretin form *Aperispirifer* lacked the delthyrial plate found in

Neospirifer and developed large umbonal callosity, and Archbold & Thomas (1984) established that Trigonotretinae and Neospiriferinae could be distinguished with help from that difference. Clarke (1979) was not convinced and pointed to North American species assigned to *Neospirifer* and characterized in part by lack of delthyrial plate and presence of umbonal callosity. Why that was deemed significant was not made clear. North American species are not type material for *Neospirifer*: the types of *Neospirifer* come from Russia, and no effort was made to verify the nature of type *Neospirifer*, or verify whether North American species were neospiriferin or trigonotretin. At least one Permian species described as *Neospirifer* by Cooper & Grant (1976) is clearly trigonotretin, and belongs to a distinct genus (Waterhouse 2001, 2002c). This is *Neospirifer amphigyus* Cooper & Grant (1976, pl. 593, fig. 2), now type species for *Trigorhium* Waterhouse (p. 173). The Carboniferous genera in the United States, as figured by Dunbar & Condra (1932), to which Clarke (1979) referred, may include, subject to the nature of the largely undescribed delthyrial apparatus, *Betaneospirifer* (*N. latus* Dunbar & Condra), *Spiriferalaria* (*N. triplicatus alatus* Dunbar & Condra), and *Simplicisulcus* (*triplicatus* Hall), to judge from illustrations. The only form to show an umbonal callosity appears to be *Neospirifer texanus* (Meek) as shown by Dunbar & Condra (1932, pl. 38, fig. 13). This belongs to Spiriferellidae, not *Neospirifer*.

Even Archbold & Thomas (1986) played down the possible significance of the delthyrial apparatus, and various articles since have ignored it. Nonetheless, the morphological difference is objective, and remains the prime discriminant. The development of an umbonal callosity appears to be variable amongst a number of spiriferoids, but not apparently for trigonotretids. Archbold & Thomas (1986) and Archbold (1991) have pointed to prominent concentric lamellae, and to the branching of costae further from the umbo as characteristics of *Trigonotreta*. But a number of non-trigonotretin genera and species show similar concentric laminae, and the spacing between lamellae varies considerably, and may be just as emphatic for *Neospirifer* and *Betaneospirifer* as in type *Trigonotreta.* Multiplication of costae occurs close to the umbo in the trigonotretin species *cracovensis* Wass and *hobartensis* Brown and in species of *Aperispirifer*. These aspects are elaborated below.

Poletaev (1997, p. 308) sought to distinguish Neospiriferinae from Trigonotretinae by the numerous costae, weakly developed callosity, and barely developed stegidial structures. *Aperispirifer* and to less extent *Grantonia* etc. have just as fine costae as many Neospiriferinae, and reference to stegidial structures for *Trigonotreta* requires explanation: no stegidial plates in any trigonotretin are known to me. Poletaev (1997) evidently considered that the dental tracks or ridges which border the edges of the delthyrium, and separated from the interarea by a groove, point to a resting place for stegidial development. This is not entirely convincing, and the structure may simply be as it seems, teeth tracks separated from the interarea by a groove. Such are well developed in numerous individuals of trigonotretins that never show any delthyrial or stegidial plates, and are also developed in neospiriferin shells with well developed delthyrial plate.

During the 1980's and 1990's a considerable array of species came to be referred to *Trigonotreta*. They show as much variation as species which used to be assigned to *Neospirifer*, and were aggregated on the basis that ribbing was sometimes coarse, growth lamellae sometimes moderately developed, and secondary thickening sometimes substantial. None of these attributes are restricted to Trigonotretinae, and may be shared, to varying degree, with Spiriferinae, Neospiriferinae and Paeckelmannelloidea. Closer scrutiny of various attributes involving costation, sulcus and fold, plication and alation enables species identified as *Trigonotreta* to be re-allocated to various genera, just as species have been recognized as generically discrete from *Neospirifer*, notably by Archbold & Thomas (1985b). Therefore the group of trigonotretins is reviewed, and species are associated in different groupings, largely in genera that authors have sought to synonymize, by disregarding or minimizing the differences shown from the type species of *Trigonotreta*. It is shown that the subfamily is a moderately large and wide-ranging group, with representatives in the paleotropics as well as southern hemisphere. At the same time, caution is expressed over the identification of some species in Asia, Australia and South America, which have been identified as *Trigonotreta* solely on the basis of prominent ribbing or concentric lamellae, with little or no clarification of the delthyrium, and no assessment of plicae, sulcus and fold, shape or nature of costation.

Most of the Trigonotretinae, Neospiriferinae and Fusispiriferinae that I have examined have pitted impressions over the floor of the valve medianly, close to the muscle field, and are comparatively smooth laterally. But individuals of *Trigorhium amphigyus* (Cooper & Grant), and also *Aperispirifer archboldi* Waterhouse, 2001, as shown in Text-fig. 33, have reticulate vascular impressions, or angioglyphs.

RELATION OF TRIGONOTRETINAE TO OTHER BRACHIOPOD FAMILIES

A few other spiriferidin genera come moderately close to *Trigonotreta* and allies in the presence of umbonal callosity, or feebly or non-costate plicae, costate sulcus and fold, and largely identical micro-ornament, or even better defined concentric ornament, and identical internal plates and musculature. The genus

Pteroplecta Waterhouse, 1978, a modest component of Late Permian faunas in the Himalaya, tends to be a transverse shell with wide hinge, and has weakly costate sulcus, fold, and plicae, with well defined concentric laminae, and fine radial capillae. The genus differs from *Trigonotreta* in having a delthyrial cover, and lacking an umbonal callosity. Otherwise it is distinguished largely by shape and number of plicae. *Pteroplecta* is classed, as in Carter et al. (1994, p. 348), in Pterospiriferinae Waterhouse, 1975, based on *Pterospirifer* Dunbar, 1955, a genus which also has a delthyrial covering. This genus is transverse and alate, with radial filae, non-branching plicae, and median sulcal rib. Allied genera, as listed by Carter et al. (1994), include *Spiriferinaella* Fredericks and *Xizispirifer* Liang.

As what may have been a forebear of trigonotretin shells, *Varuna* n. gen. is subequilateral with a number of narrow fastigate plicae that develop variable coarse costation, thick secondary thickening, and umbonal callosity. These are features shared to some extent with members of Angiospiriferinae Legrand-Blain, which is a Carboniferous-Permian group that displays a number of narrow plications, and costae over the sulcus and fold and in some genera over the plicae. An umbonal callosity may be well developed, and micro-ornament consists of radial and concentric capillae. *Angiospirifer* (Angiospiriferinae), *Aperispirifer* and *Trigorhium* (Trigonotretinae) share reticulate vascular impressions.

If the suggestion can be sustained that Sergospiriferinae are related to and preceeded Angiospiriferinae as suggested by Carter et al. (1994) and supported herein, then trigonotretids extend into the Early Carboniferous. Such a proposal implies that Neospiriferinae should be divorced from Trigonotretidae, and related more closely to Spiriferidae. Genera within Neospiriferinae nearly always show the fine costation present from almost inception, and tend to have fewer plications than several Trigonotretinae. According to this proposal, in Neospiriferinae, plication arose to diversify from costate Spiriferinae: whereas in Trigonotretinae, costation arose over plicae, as a divergence from plicate Angiospiriferinae.

Carter et al. (1994) referred *Frechella* Legrand-Blain and *Sulciplica* Waterhouse to Trigonotretinae, but these are reassessed as belonging to Imbrexinae and to Angiospiriferinae respectively (pp. 103, 179).

GENERA: *Trigonotreta* Koenig, *Aperispirifer* Waterhouse, *Brachythyrinella* Waterhouse & Gupta, *Grantonia* Brown, *Koenigoria* Waterhouse n. gen., *Trigorhium* Waterhouse.

Tribe **TRIGONOTRETINI** Schuchert, 1893

[nom. transl. hic ex Trigonotretinae Schuchert, 1893, p. 156]

DIAGNOSIS: Genera with comparatively numerous plicae in 5-9 pairs, costae few and coarse, cardinal extremities obtuse.

GENERA: *Trigonotreta* Koenig, *Brachythyrinella* Waterhouse & Gupta.

Genus ***Trigonotreta*** Koenig, 1825

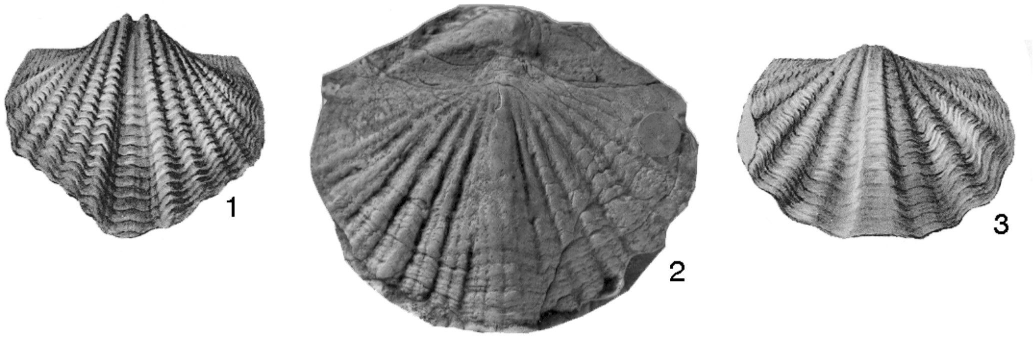
Text-fig. 29.2, Text-fig. 30.A

TYPE SPECIES: *Trigonotreta stokesii* Koenig, 1825, p. 3.

DIAGNOSIS: Medium-sized spiriferidin shells with moderately wide hinge, rounded cardinal extremities, interarea high and wide, open delthyrium and no closing apparatus, large umbonal callosity. Well defined and costate sulcus and broad costate fastigium, plicae well developed, numbering 5-7 or more pairs in ventral valve with further strong costae laterally, and inner pair of plicae entering sulcus early, dorsal plicae number 5-7 or more pairs. Costae broad and with rounded or tented crests, arise 10mm or more in front of umbo as a rule, 2-3 up to 5 costae on plicae, tend to be more numerous on ventral valve, but not always so. Crossed by close-set subevenly spaced and subevenly developed concentric laminae, fine radial filae sometimes visible. Interior much as in spiriferid genera, dental plates well developed, adminicula short and may be largely buried in heavy secondary thickening, myophragm often developed in somewhat elongate muscle field. Dorsal valve includes inner and outer socket plates, very low crural plates, median septum low, not always visible, spiralia.

DISCUSSION: The type species *Trigonotreta stokesii* Koenig (1825, pl. 6, fig. 70) has been well illustrated by Clarke (1979, 1990) and synonymy provided. Other species include *Trigonotreta victoriae* Archbold, 1991 from Victoria, *T. occidentalis* Thomas, 1971 from the upper Lyons Group of Western Australia, and *T. thomasi* n. sp. from the Garhwal Himalaya. Angiolini (1995) has described allied material from the Early Permian Gircha Formation of the Karakorum, and Fantini Sestini (1966) illustrated material from Geirud Formation member D of Iran.

Previous discussions of the genus have been very generalized, but the new analysis highlights several diagnostic features previously overlooked. Cardinal extremities are seldom or never even weakly alate, the interareas are high and wide, plicae are narrow and comparatively numerous for the subfamily, and include a narrow pair within the sulcus, and concentric laminae are fine, low and close-spaced. The costae, on which emphasis has been placed, are sturdy, moderately numerous, arise well in front of the umbo, and have broad and somewhat rounded crests. The fastigium is closely costate. Clarke (1979) drew attention to the elongate ventral muscle field.



Text-fig. 29. 1, 3. *Brachythyrinella narsahensis* (Reed) x 1.5. 1, ventral valve. 3, dorsal valve, assigned to *narsahensis pauciplicata* by Reed (1928). Figured by Reed (1928, pl. 36, fig. 2, 6). From Umaria coal field, India.
2. *Trigonotreta stokesii* Koenig x 1, holotype BM (NH) B 4798, from Swifts Jetty Sandstone, Tasmania, cast provided by British Museum, London.

Trigonotreta thomasi n.sp.

Plate 7, fig. 6-9

1978 *Brachythyrinella* cf. *narsahensis* (not Reed) Waterhouse & Gupta, p. 426, pl. 4, fig. 2-6.

DERIVATION: Named for G. A. Thomas.

HOLOTYPE: CASGF 596, figured by Waterhouse & Gupta (1978, pl. 4, fig. 4) and herein, Pl. 7, fig. 8, from Bijni tectonic unit, Garhwal Himalaya, here designated.

DIAGNOSIS: Moderately small shells with obtuse cardinal extremities, 5-7 pair of plicae, sulcus narrow, fastigium broad with rounded subplication along lateral flanks anteriorly and closely costate, costae few on lateral ventral valve and only a little more prominent on dorsal valve, concentric laminae well developed. Short dental plates and adminicula, and heavy secondary thickening posteriorly in ventral valve.

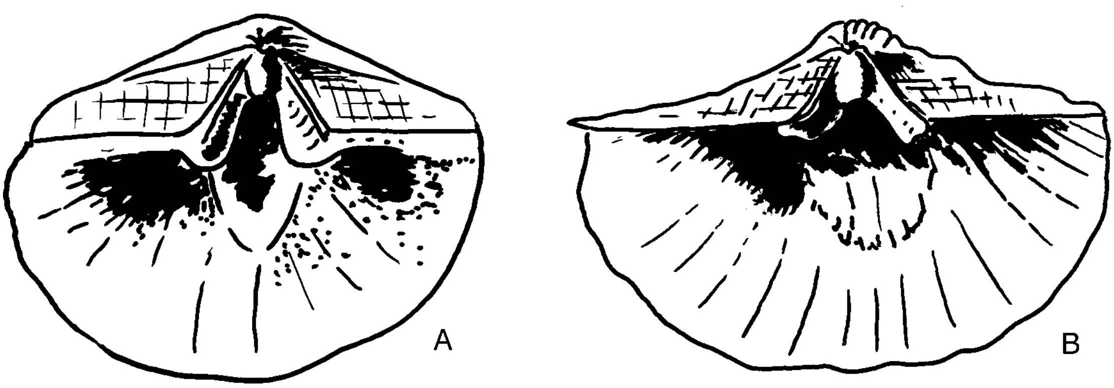
DESCRIPTION: This species has been described and illustrated.

RESEMBLANCES: The species is not deemed to belong to *Brachythyrinella*, in contradistinction to the view of Waterhouse & Gupta (1978), because although close in size and many aspects of ornament, including rarely costate and moderately numerous plicae and well developed concentric laminae, the fastigium is broader with rounded crest and a number of costae. By contrast, the fastigium of *Brachythyrinella* has few costae limited to the lateral flanks, and the crest carries a median flattening or groove.

Clarke (1990, p. 62) stated that the ventral valve compared to *Brachythyrinella narsarhensis* by Waterhouse & Gupta (1978, pl. 4, fig. 2-6) belonged to *Trigonotreta stokesii*, and certainly secondary thickening is considerable. But the specimen is an internal mould, and it is likely that the specimen is simply a gerontic individual. Archbold & Singh (1993, p. 187) misquoted Clarke (1979) to claim that Clarke had referred all the Waterhouse-

Gupta specimens to *Trigonotreta stokesii*. This is not correct. Archbold & Singh (1993, pl. 1, fig. 8, 9) referred the specimens to *Trigonotreta* sp. Their own figured "*Trigonotreta* sp." has wide sulcus and is not congeneric with either *Brachythyrinella* or *Trigonotreta*.

Thomas (1971, p. 108, pl. 19, fig. 1-6, 9-13) ascribed a rather similar form to *Trigonotreta narsahensis occidentalis* from the upper Lyons Group of Western Australia. It also differs from *narsahensis* in the costate nature of the rounded fastigium and belongs to *Trigonotreta* s. s., but like the new species, differs from east Australian species in its more prominent and broader fastigium, narrow ventral umbo and smaller size, and fewer costae over the more rounded, less angular plicae. A slender subplication extends along the inner base of the sulcal bordering pair of plicae. *T. occidentalis* is more inflated with more obtuse cardinal



Text-fig. 30. Interior of ventral valves x1. A, *Trigonotreta stokesii* Keonig, drawn from cast of TMF 368405 in Clarke (1979, pl. 1, fig. 9) from Swifts Jetty Sandstone, Tasmania.
B, *Trigorhium amphigyus* (Cooper & Grant) USNM 152894 from China Tank Member, Word Formation, Glass Mountains, Texas, figured by Cooper & Grant (1976, pl. 593, fig. 2).

extremities, broader fastigium, and less well spaced concentric laminae, compared with *T. thomasi*. The new species is closer to *Trigonotreta victoriae* Archbold (1991, text-fig. 2A-X) from Early Permian of Victoria, Australia, than to the type species, but has more secondary thickening and less conspicuous ventral myophragm, fewer costae, more separated dorsal plicae and better spaced more conspicuous concentric laminae. A more prominent inner pair of plicae enters the sulcus or forms a subplication on the border pair of plicae in *victoriae*.

Trigonotreta stokesi of Angiolini (1995, p. 179, pl. 2, fig. 2-9, 14, pl. 8, fig. 1-3, text-fig. 10) is close to type *stokesii*, with slightly lower posterior plicae and 6-7 pairs of narrow plicae, including a sulcal pair, and a pair close to the fold on the dorsal valve. The dorsal plicae are more costate. An Iran specimen from Geirud Formation member D described as *Neospirifer fasciger paucicostulatus* Reed by Fantini Sestini (1966, pl. 5, fig. 3a, b, not fig. 2) has 6-7 pairs of costate narrow plicae, and rounded outline, showing a strong approach to *Trigonotreta*.

Angiolini (1995) excluded *Trigonotreta stokesii* of Bion (1928, pl. 1, fig. 7, pl. 5, fig. 6-8) from her view of the species. The Bion specimens possibly are the same as the material figured by Bion (1928, pl. 5, fig. 2-5) as *keilhavii*. They have rounded cardinal extremities, narrow sulcus with narrowly diverging sulcal plicae, involving apparently only 4 lateral pairs. The dorsal valve has high rounded costate fold with basal plicae pair and 3-4 pair of lateral costate plicae in all. Shell is very thick posteriorly in the ventral valve, and adminicula are short. The dorsal valve shows a large ctenophoridium. The low number of plicae is significant, and indicates that the genus is not likely to be *Trigonotreta.*

NOTE ON SYNONYMY: The synonymy for this species is possibly incomplete, as an article that figured specimens as cf. *narsahensis* by Gupta (1982) is not available to me, and another by Bhatt & Singh (1981, pl. 1, fig. 1) that seems perfunctory at best in its identifications, to judge from reassessments by Archbold & Singh (1993, p. 184), is also not available. *Trigonotreta* sp. as reported by Archbold & Singh (1993) from the Bijni tectonic unit, and regarded by them as identical, needs to be examined and described more fully with regard to delthyrium and sulcus. The authors seemed unaware that a possible neospiriferine or transverse trigonotretin species is present in the Garhwal fauna, as noted by Waterhouse & Gupta (1978), and their figured specimen appears to have a very wide sulcus, suggestive of a neospiriferin or perhaps *Aperispirifer*.

NOTE ON AGE: The age is regarded as Sakmarian, and probably Tastubian, as established by Waterhouse & Gupta (1978, 1979c), although Archbold & Singh (1993) ignored that determination, and pronounced that it was they who had established a Tastubian age. They relied at least in part on reassessment of some genera, but their assignment of dorsal valves which lack spines to *Cancrinella* is certainly incorrect, with Brunton et al. (2000) confirming that *Cancrinella* has dorsal spines.

Genus ***Brachythyrinella*** Waterhouse & Gupta, 1978

Text-fig. 29.1, 3

TYPE SPECIES: *Spirifer narsarhensis* Reed, 1928, p. 379.

DIAGNOSIS: Small shells with comparatively narrow to moderately wide hinge and triangular ventral interarea, well rounded cardinal extremities, moderate number of narrow plicae in 5-7 pairs, no sulcal pair other than sulcus widening at maturity to incorporate inner border pair, fastigium of moderate width and typified by flat or gently to moderately concave crest, costae few, low, broad, concentric laminae may be well developed and well spaced. Delthyrium open, umbonal callosity small to well formed. Adminicula short to moderate in length.

DISCUSSION: The lectotype for *narsahensis* Reed is the specimen figured by

Reed (1928, pl. 33, fig. 7, a, b), here designated. The lectotype for *narsahensis pauciplicatus* Reed is the specimen figured by Reed (1928, pl. 36, fig. 6), here designated. Specimens are kept at the Geological Survey of India, Calcutta, and come from the Umaria beds of India.

The genus was originally erected on the misunderstanding that adminicula were lacking, and this was clarified by Archbold & Thomas (1984), and by Waterhouse (1983c, p. 158) in acknowledging a correct assessment by Thomas (1971, pl, 19, fig. 8). Although some authors have proceeded to lump *Brachythyrinella* with *Trigonotreta*, the lack of posterior sulcal plicae, presence of grooved or flat-crested fold, and sparsity of costae provide firm differences. The type species is also distinguished by its short hinge and rounded cardinal extremities, well developed regularly spaced concentric laminae, and comparatively little shell thickening.

The poorly reproduced figures in Jin & Sun (1981, pl. 1, fig. 7-12) of *Trigonotreta* cf. *narsahensis* from the upper Jilong Formation of south Tibet show a dorsal fold with narrow median groove, indicative of the genus *Brachythyrinella*. *Spirifer duttai* Sahni & Srivastava, 1956 from the eastern Himalaya is a close ally*. S. hesdoensis* Sahni & Dutt, 1959 (p. 664, pl. 26, fig. 3, 5) from Peninsular India (?Asselian) is also close, but, with no data on the dorsal valve, needs further investigation. Taboada (1999) reported this species from the Argentine, but confirmation is required.

Trigonotreta narsarhensis occidentalis Thomas, 1971 from the Asselian upper Lyons Group of Western Australia is close at a casual assessment, but has a very broad and costate fold without flattened or grooved crest, and should be treated as a full species of *Trigonotreta,* not related to *narsahensis*. Jin (1985, pl. 1, fig. 13, 14) reported *Trigonotreta* cf. *narsahensis* from the Jilong Formation of Tingri County, Tibet. The specimens are possibly not trigonotretin, and indicate a non-costate sulcus and fold, if the specimen of fig. 13 is a dorsal valve and not a ventral ("pedicle") valve as claimed in the caption.

From the Early Permian of Argentine, several species tend to be a little more transverse, with wider hinge, but share with type *Brachythyrinella* the 5-7 pairs of narrow plicae, no posterior sulcal plicae, and grooved fastigium. In the Tupe Formation, San Juan Province, *Spirifer (Spirifer) pericoensis* Leanza, 1945, assigned to *Trigonotreta* by Cisterna et al. (2002), is close in most respects. Some specimens indicate a wide hinge, and secondary thickening is considerable. The sulcal border pair of plicae develop an inner branch anteriorly, but there is no pair within the sulcus comparable to that of *Trigonotreta, Grantonia* or *Aperispirifer*. The crest of the fastigium is traversed by a moderately well defined groove, deeper than in Indian species, but comparable overall. Allied species include *T. riojanensis* (Lech & Aceñolaza, 1987) from the Río del Peñon Formation, with fewer costae and less fasciculation, and *T. sanjaunensis* Lech & Aceñolaza, 1990 from the Del Salto Formation, Calingasta area of Argentine. In addition *Spirifer saltensis* Reed (1927a, pl. 14, fig. 8a, b) from the Esquina Gris Formation, Barreal, appears to belong to the same subset.

Tribe **GRANTONINI** n. tribe

NAME GENUS: *Grantonia* Brown, 1953, p. 61.
DIAGNOSIS: Transverse genera with 3-6 pairs of plicae, including sulcal pair, moderately numerous coarse, fine or varied costae.
DISCUSSION: Constituent genera are readily distinguished from Trigonotretini by the lesser number of more costate plicae, and generally alate cardinal extremities.
GENERA: *Grantonia* Brown, *Aperispirifer* Waterhouse, *Koenigoria* Waterhouse n. gen., *Trigorhium* Waterhouse.

Genus ***Grantonia*** Brown, 1953

Plate 4, fig. 4, 7, 8, Plate 5, fig. 2, 3, 6, 9

TYPE SPECIES: *Grantonia hobartensis* Brown, 1953, p. 61. This species, from the Berriedale Limestone, Tasmania, is a subjective synonym of *Spirifer stokesii* var. *australis* Bion, 1928, p. 30 (Waterhouse 1987a, pp. 17, 18). Foord (1890, p. 147, pl. 7, fig. 2) had already used the name *australis* as *Spirifera musakheylensis* Davidson var. *australis* var. nov., also mentioned by Hosking (1931, p. 23), and Reed (1932, p. 30). This never came to be of species rank, and Archbold & Thomas (1986, p. 128) referred *australis* Foord to synonymy of *Neospirifer hardmani* (Foord, 1890).
DIAGNOSIS: Moderately large shells with wide hinge, rounded to weakly alate cardinal extremities, 4-5 pairs of plicae, including narrow but well developed pair within sulcus, strongly costate with high primary costa upstanding, close-set growth laminae, faint to moderately developed radial filae. Dental plates and short adminicula, muscle field broad and generally lacks myophragm or median ridge through muscle field.
DISCUSSION: *Grantonia* is close to *Trigonotreta*, and has been synonymized with that genus, especially since a study by Armstrong (1968). But compared with *Trigonotreta*, the type species has wider hinge, fewer plicae, and higher primary costae over the plicae, and overall is more costate posteriorly, with costae arising very close to the umbones, especially on the ventral valve. It seems possibly to have been root-stock for *Koenigoria* n. gen. and ultimately *Trigorhium* Waterhouse. Clarke (1979) noted the difference in ventral muscle

field in the type species of *Trigonotreta* and *Grantonia*. The type species was described originally from the Berriedale Limestone of Tasmania, of Sakmarian age. Waterhouse (1987a) pointed out that material from the Sakmarian Homevale beds of Queensland was similar, as is apparent from inspection of collections kept at the University of Queensland or Queensland Museum, Brisbane, and in figures by Hill & Woods (1964b, pl. 8, fig. 8) and Hill et al. (1972, pl. 8, fig. 8). The Queensland specimens were initially described by Etheridge (1892, pl. 10, fig. 2, 3, pl. 39, fig. 2-4) and named as variety *australis* by Bion (1928) not Foord (1890). An older species *Grantonia cracovensis* Wass, 1966 from the Fairyland and possibly Dresden beds of the Bowen Basin, Queensland, shows somewhat comparable attributes (Waterhouse 1987a). Its possibly Late Carboniferous age is discussed by Waterhouse (1987c, d, 1988b).

A number of individual specimens from the Agglomeratic Slate of Kashmir and nearby areas are shaped and ornamented like *Grantonia*. These include specimens identified as *Spirifer fasciger musakheylensis* not Davidson of Reed (1925, pl. 6, fig. 2), *Spirifer fasciger* not Keyserling of Bion (1928, pl. 1, fig. 5), *Spirifer (Neospirifer) fasciger paucicostulata* not Reed of Reed (1932, p. 30, pl. 5, fig. 3, 4) and *S. (Neospirifer) fasciger australis* not Foord of Reed (1932, p. 30, pl. 5, fig. 6).

Over recent years *Grantonia* has always been placed in synonymy with *Trigonotreta*, but the wider hinge, reduced number of plicae and considerable height of the primary costae along plicae, high number of costae, and broader ventral muscle field allow discrimination.

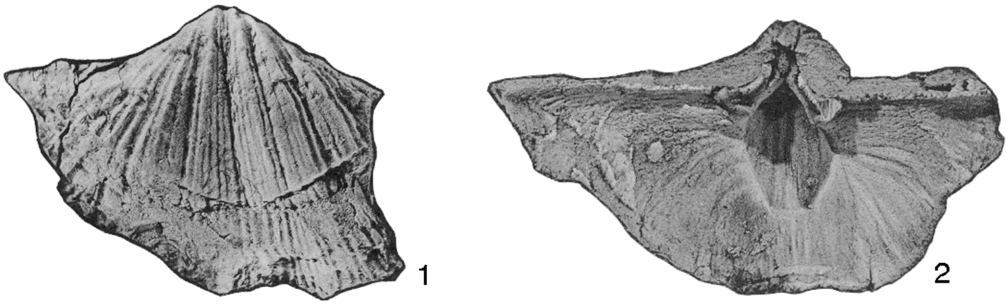
Genus ***Aperispirifer*** Waterhouse, 1968

Text-fig. 31-33

TYPE SPECIES: *Neospirifer wairakiensis* Waterhouse, 1964, p. 127.

DIAGNOSIS: Medium to large with wide hinge, high interareas, alate to subalate cardinal extremities, extended anterior-lateral margins, sulcus with well developed sulcal pair of plicae and 2-3 lateral pair only in Middle and Late Permian, 3-5 pair in possible Early Permian species, may fade anteriorly, costae numerous and fine, differentiated only close to umbo, generally angular crested, concentric laminae generally close-set, may be well developed. Ventral muscle field generally elongate. Ventral floor with angioglyphs laterally (Text-fig. 33).

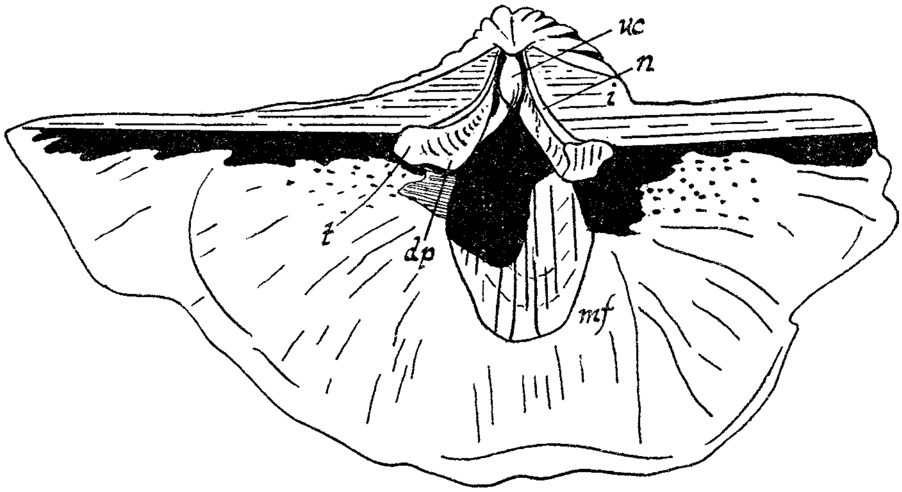
DISCUSSION: This genus is distinguished by its fine, fastigate and poorly differentiated costae, with primary costa not persistently prominent. Costae are more numerous than those of *Trigonotreta* and *Grantonia*. As well the hinge is more alate, and plicae in species from New Zealand and Queensland are few and generally limited to the posterior shell. Species range from late Cisuralian



Text-fig. 31. 1. *Aperispirifer wairakiensis* (Waterhouse) holotype BR 482 x 1 figured by Waterhouse (1964, pl. 23, fig. 4) from Letham Burn Member, Mangarewa Formation, New Zealand.
2. *A. archboldi* Waterhouse, ventral interior BR 467 from basal Letham Formation, New Zealand, x 1. Also figured by Waterhouse (1964, pl. 25, fig. 3).

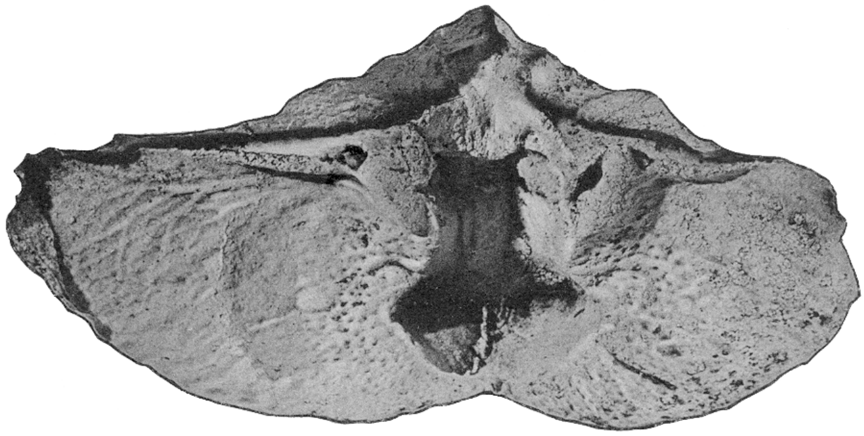
to Lopingian in age, and include *Aperispirifer archboldi* Waterhouse, *A. lethamensis* Waterhouse, *A. wairakiensis* (Waterhouse), *A. parfreyi* Waterhouse, *A. nelsonensis* (Waterhouse), and *A. ovalis* Waterhouse. Some of these species appear also in New South Wales (Waterhouse 2002c).

Further afield, species possibly have been confused with *Trigonotreta*.



Text-fig. 32. *Aperispirifer archboldi* Waterhouse, ventral interior BR 467 from Letham Formation, x 2.5 approx. dp - dental plate, i = interarea, mf = muscle field, n = dental ridge, t = tooth, uc = umbonal callosity. See Waterhouse (1964, text-fig. 61A).

Trigonotreta sp. of Shi & Shen (1997, text-fig. 7A, E-G) from the Selong Group of south Tibet is possibly *Aperispirifer*, as it fails to show the numerous plicae of *Trigonotreta*, but on the other hand delthyrial detail was not provided, and the identification remains uncertain. Internal detail has not been provided for *Trigonotreta semicircularis* Shen, Shi & Zhu (2000, pl. 3, fig. 5-8) from Early Permian of Yunnan. There does not appear to be a pair of plicae within the sulcus, and the species apparently belongs to *Simplicisulcus* Waterhouse, a neospiriferin genus with tricostate fascicles and delthyrial plate. Supposed *Trigonotreta* sp. of Angiolini et al. (1997, text-fig. 15.12) from Early Permian of southeast Oman is difficult to identify with full confidence, but has only 4 pair of



Text-fig. 33. *Aperispirifer archboldi* Waterhouse x2, PVC cast of interior, dorsal valve on top, showing vascular impressions, BR 476, Letham Formation, Southland, New Zealand. From Waterhouse (1964, pl. 25, fig. 7).

prominent plicae, and very tented or sharply angled primary costae, as in *Aperispirifer*.

Genus ***Trigorhium*** Waterhouse, 2001

Text-fig. 30B

TYPE SPECIES: *Neospirifer amphigyus* Cooper & Grant, 1976, p. 2175.

DIAGNOSIS: Large transverse shells with alate cardinal extremities, 5-6 pairs of plicae, primary costa higher than other costae which are few and coarse, sulcus with median and two lateral prominent costae or fascicles.

DISCUSSION: This distinctive genus is based on a Glass Mountains species from the China Tank and Appel Ranch Members of the Word Formation (Guadalupian), West Texas. It shows strong links with *Grantonia* Brown and especially *Koenigoria* (see below) from Western Australia, and is distinguished by its three sulcal fascicles, attenuated cardinal extremities, more lateral plicae, and shallow sulcus. A dense reticulate pattern of vascular impressions is shown for the ventral valve by Cooper & Grant (1976, pl. 594, fig. 9).

Genus ***Koenigoria*** n. gen.

DERIVATION: Named for C. Koenig.

TYPE SPECIES: *Trigonotreta neoaustralis* Archbold & Thomas, 1986, p. 152, here designated.

DIAGNOSIS: Transverse shells of somewhat triangular shape with wide hinge and lateral margins converging to anterior mid-line, alate or subalate cardinal extremities, tendency for sulcus to be angular and deep anteriorly, bearing sulcal plicae which fade anteriorly to become narrow and not conspicuous, lateral plicae in generally 4 pair, costae moderately numerous, primary costa retaining dominance. Growth laminae moderately to well spaced.

DISCUSSION: The genus embraces Western Australian species *Trigonotreta* *neoaustralis* from Callytharra Formation and correlates, and *T. dickinsi* from the Nooncanbah Formation of the Canning Basin, both species named by Archbold & Thomas (1986). The primary ribs remain prominent and suggest an alliance with *Grantonia*, which also has reduced number of plicae, and differs mostly by being much less alate and less deeply and more widely sulcate, with more rounded and protruding anterior-lateral margins. *Aperispirifer* is closer to *Grantonia* in shape, and may be more transverse with protruding anterior margins. It is densely costate, and the primary costae of fascicles near the umbones may be slightly raised and often fastigate, but are matched in strength by secondary costae within a few mm.

Singh & Archbold (1993, p. 70, text-fig. 10A-J) considered that their species *Trigonotreta orientensis* from the Garu Formation of the eastern Himalaya was close to *neoaustralis.* Depending on the nature of the delthyrium, which was not determined by Singh & Archbold (1993), *orientensis* also belongs to *Koenigoria,* and this is supported by the broadly triangular shape of specimens, including those figured in a study by Singh (1979), as summarized in the synonymy provided by Singh & Archbold (1993).

Trigonotreta lightjacki Archbold & Thomas, 1986 from the Lightjack Formation of the Canning Basin, Western Australia, is similar in some respects, although there seems to be no sulcal pair of plicae and the delthyrium was recorded only as “open” with no further detail. The generic position therefore requires clarification, but appears to have a number of attributes of *Koenigoria*, although there are also strong approaches to *Pteroplecta* Waterhouse. Shen et al. (2001, text-fig. 5.9-16) reported *lightjacki* from Late Permian of the Selong Group in south Tibet, but no delthyrial detail was provided, nor analysis of plicae and costation. One or two specimens (see Shen et al. 2001, text-fig. 5.14-16) suggest possible *Pteroplecta*, with fastigate plicae and subdued costae, whereas others have fine costae in the style of either a neospiriferine or *Aperispirifer*.

Archbold (1999) claimed that *Trigonotreta* was present in the Ko Yao Noi faunas described by Waterhouse (1981, pl. 25, fig. 3-5, pl. 26, fig. 1-7) as *Neospirifer*. Some specimens (eg. pl. 26, fig. 7), as was allowed, are indeed *Neospirifer*. Others, although superficially approaching *Trigonotreta*, might be juvenile *Neospirifer* as interpreted, or might be *Pteroplecta*. Any relationship with *Trigonotreta* must be dismissed, because the ventral valves have a delthyrial covering plate.

Trigonotreta lyonsensis Archbold & Thomas (1986) from the upper Lyons Group of the Carnarvon Basin, Western Australia, is a very distinctive transverse form with extended alate cardinal extremities, fine costae, and fewer plicae than in *Trigonotreta*, numbering 4-5 pair in the dorsal valve. The ventral exterior is obscure, and it is far from clear whether there was a pair of sulcal plicae. Similarly, the delthyrial apparatus was not described. The species therefore cannot be determined to generic level, and in the meantime could be left as *"Trigonotreta" lyonsensis*. Somewhat comparable material was recorded as this species from the Gircha Formation of Chapursan valley, Karakorum Range, by Angiolini (1995), but the Karakorum specimens have two pair of plicae entering the sulcus, and four pair of lateral plicae, and a fastigium that is very broad anteriorly. Crowded and subequal costae arise close to the umbo, and growth laminae are close-set. The delthyrium was described as open, but this does not of itself show its original nature, which may have been open, or may have been covered by a plate now lost. The shape and ornament invite consideration of possibilities of a new genus and species, but the nature of the delthyrium should be determined first. On available evidence of shape, plication, sulcus-fastigium and costation, the material appears to be allied to *Crassispirifer* Archbold & Thomas, 1985b.

Possibly *Koenigoria* is represented in the Early Permian Agglomeratic Slate of Kashmir as *Spirifer kimsari* Bion (1928). Reed (1932) later declared Bion's species to be punctate, but this is not supported by casts of figured types in my possession. A range of specimens have been illustrated by Reed (1932), involving specimens like *Koenigoria* and *Aperispirifer*, and further study is required to clarify if one or more species is involved, and the nature of generic affinities.

Transverse ventral valves with few coarse costae were figured from Khao Bat Kwang, Thailand, just below the Rat Buri Limestone, by Archbold (1999, text-fig. 51-N), but claims that they belonged to *Trigonotreta* have not been substantiated by determination of the nature of the delthyrium, and the specimens are much more transverse than *Trigonotreta*, with alate cardinal extremities, and fewer plicae. They might prove to belong to *Koenigoria*. A transverse ventral valve figured as *Trigonotreta* by Shi, Fang & Archbold (1996, text-fig. 5C) from Early Permian of the Baoshan block, western Yunnan, has a number of simple plicae, and was compared most closely with the species *Trigonotreta neoaustralis*, now the type species of *Koenigoria*. It shows little similarity, having more and simpler non-costate plicae, and even its family ties remain to be determined.

Koenigoria? kimsari (Bion, 1928)

1928 *Spirifer kimsari* Bion, p. 22, pl. 1, fig. 3, 4, pl. 4, fig. 1-7.

1928 *S. stokesii* Koenig *australis* var. nov. not Bion Bion, p. 30, pl. 1, fig. 7a-c.

1932 *Spiriferina (Spiriferella) personata* Reed, p. 32, pl. 5, fig. 1.

1932 *S. (Spiriferella) kimsari*. Reed, p. 31, pl. 5, fig. 2, a.

TYPES: Lectotype for *kimsari,* GSI 13148 figured by Bion (1928, pl. 1, fig. 3) from Agglomeratic Slate, Kashmir, here designated. Holotype for *personata*, GSI 15525, sole specimen figured by Reed (1932), from Agglomeratic Slate, Kashmir, by monotypy.

DIAGNOSIS: Large transverse moderately inflated shells with coarse costae, broad primary costae. Sulcal plication not certain.

DESCRIPTION: The Bion material, represented in my collections by plaster duplicates and rubber latex moulds, includes moderately transverse and alate shells of characteristic subtriangular outline, with strong costae of which the central one along the crest of plicae is broader than others. There are 3-4 pair of plicae, the inner one close to the base of the dorsal fold. The dorsal median septum is long. No ventral valves were included amongst the specimens figured by Bion (1928), but the specimen assigned to *stokesii australis* by Bion (1928, p. 31, pl. 1, fig. 7a-c) is an internal mould with both valves conjoined (GSI 13152) and shows 3 strong and one faint pair of plicae. There is no sign of sulcal plicae, but this could have been obscured by the specimen being an internal mould. However this is a matter critical for generic determination, and is still not resolved. As well, the nature of the delthyrium is not preserved. Two dorsal valves figured as *personata* and *kimsari* by Reed (1932) from the Agglomeratic Slate agree in subtriangular shape and coarse costae, and show long dorsal median septum. Reed (1932) stated that the shell was punctate, but this is judged to be most unlikely, and I noticed no punctae in inspecting the specimens.

RESEMBLANCES: Various other specimens ascribed to different taxa by Bion (1928) may be allied, but this is not certain, and they show differences. Full comparison is hindered by the lack of exteriors. *Spirifer stokesii* var. A of Bion (1928, pl. 5, fig. 6, 7) has a high narrow fold, and comparatively strong costae, but is elongate. *S. stokesii* var. B looks somewhat similar. The dorsal internal mould assigned to *S. fasciger* by Bion (1928, pl. 1, fig. 5 - GSI 13150) has strong plicae and costae, and the median costae is broader than the others. But plicae are lower and more close-set than in *kimsari*, and anterior lateral margins are more extended, and the costae are more numerous. From shape, plicae and costae, the specimen is most like *Grantonia.* A second specimen allocated to that species by Bion (1928, pl. 4, fig. 14) differs, with fine costae.

Koenigoria neoaustralis Archbold & Thomas, 1986 from the Callytharra Formation of the Carnarvon Basin and correlative levels in Western Australia is close in shape, but is smaller and has finer costae overall, with other differences.

Koenigoria? paucicostulata (Reed, 1925)

1925 *Spirifer fasciger* var. nov. *paucicostulata* Reed, p. 43, pl. 6, fig. 1a, b.
1925 *S. fasciger musakhaylensis* not Davidson Reed, p. 43, pl. 6, fig. 2a, b.
1993 *Trigonotreta* sp. Angiolini, p. 291, pl. 4, fig. 5-8.
1995 *Trigonotreta paucicostulata*. Angiolini p. 183, pl. 3, fig. 1-10, pl. 9, fig. 1-4, table 12.

HOLOTYPE: Specimen figured by Reed (1925) from Cisuralian of Baroghil Ailak, Chitral, north Pakistan, by monotypy. Kept at Geological Survey of India, Calcutta.

DESCRIPTION: The holotype is a large dorsal valve with sharp-crested fastigium, at least 4 pair of plicae and moderately coarse costae and outline shown as subtriangular. A ventral valve identified with *musakhaylensis* by Reed (1925) from the same locality is also large, with what appear to be comparable costae over perhaps 5 pair of plicae, including pair within sulcus. The partly restored margins show a less triangular shape, with anterior lateral margins subrounded in outline. To determine whether they are conspecific will require first-hand inspection. Specimens figured from the Karakorum by Angiolini (1995) are smaller than the holotype, and appear to have slightly finer costae, 5-6 pairs of plicae including a sulcal pair, and a somewhat subtriangular shape, and close-set growth lamellae.

RESEMBLANCES: This species is referred provisionally to *Koenigoria*, but the nature of the costae in the holotype requires examination, and the nature of the delthyrium is not known. Indications of a likely affinity with *Koenigoria* are provided by the strong costae, triangular shape and 5 pairs of plicae. Angiolini (1995) stated that primary costae remained prominent for their length in her material. *Trigonotreta* has more pairs of plicae, fewer costae and less fasciculate ornament, and rounded not alate cardinal angles (see Angiolini 1995, pl. 3, fig. 1). The precise age of the material in the synonymy is not known, and whether the age is the same as that of *Koenigoria? kimsari* remains open for further study.

Costae are finer and more numerous than those of *Koenigoria? kimsari* (Bion), described above. A dorsal valve figured by Bion (1928, pl. 1, fig. 5) as *Spirifer fasciger* Keyserling from the Agglomeratic Slate has moderately strong costae, and more roundly produced anterior lateral margins. The specimen is close to *Grantonia*.

GSI 14769 described by Reed (1930, p. 32, pl. 2, fig. 1, 1a) as *Neospirifer fasciger paucicostulatus* from Early Permian of Tibet is externally like *Grantonia*, as judged from a plaster duplicate. Its primary ribs are coarser than others on the dorsal valve, and shape is like that of *Grantonia* and *Aperispirifer*. Costae branch close to the umbo, and there are 4 pair of plicae and a fifth outermost fascicle, with inner pair incorporated in the sulcus anteriorly.

Finely costate shells from Cisuralian of Tezak, Afghanistan, were described by Legrand-Blain (1968, pl. 3, fig. 1a, b, 2, 3, 4a, b) as *Neospirifer fasciger*, and included in synonymy with *paucicostulata* by Angiolini (1995). These have some 3 pairs of plicae, fine costae, wide sulcus and subpentagonal outline. They belong to *Kaninospirifer, Neospirifer*, or *Aperispirifer*, depending on internal features and on the nature of the delthyrial cover. Further Afghanistan material described as *Neospirifer paucicostulatus* by Termier et al. (1974, pl. 6, fig. 6, text-fig. 9) might be allied: it has large sulcus and few plicae, so it is unlikely to belong to *paucicostulata*, and certainly differs from Angiolini's material. The delthyrium has a cover, and the material may well belong to *Kaninospirifer.* From the Agglomeratic Slate of Kashmir, a ventral valve figured by Reed (1932, pl. 5, fig. 7) as *hardmani* might also be close, and has narrow moderately prominent fascicles.

A Karakorum specimen from Geirud Formation member D of northern Iran that was ascribed to *paucicostulata* by Fantini Sestini (1966, pl. 5, fig. 2a, b) has the shape of *Koenigoria*, with 5 pair of plicae, simple sulcus and very coarse costae. It approaches *Koenigoria? kimsari,* but lack of sulcal plicae and presence of 5 plicae pair indicate possible *Cratispirifer* Archbold & Thomas. The other specimen (pl. 5, fig. 3a, b) has a more rounded outline and 6-7 pairs of costate narrow plicae, much as in *Trigonotreta*.

Angiolini (1995) noted some similarity between *paucicostulata* and material figured as *Neospirifer joharensis* (not Diener) by Grunt & Dmitriev (1973, p. 132, pl. 9, fig. 10-13, pl. 16, fig. 1) from the Sakmarian Tashkazyk Formation of the Pamirs. Possibly the material is allied or conspecific, but the Pamirs material appears to be more transverse with different sulcal angle.

DISTRIBUTION AND AGE

It is clear that a number of reported Trigonotretinae, especially from Asia, cannot be verified even to subfamily level, but on the other hand, the group is widespread throughout Gondwana, and extended into the Glass Mountains of Texas. Most species are Permian, especially Early Permian, but possibly *Grantonia cracovensis* is Late Carboniferous. *Grantonia* is thus amongst the oldest of genera, and mostly limited to east Australia, apart from possible occurrences in northwest India. *Trigonotreta* is found in Asselian faunas of east and Western Australia, northwest India, Iran and Karakorum. *Grantonia* persisted into Sakmarian faunas of east Australia, with an allied and descendent genus

Koenigoria in Sakmarian faunas of Western Australia, and this ranged as far as the Himalaya. A largely contemporary genus *Brachythyrinella,* derived from *Trigonotreta,* is represented by species in India and especially Argentine. *Aperispirifer* is best known in Guadalupian and Lopingian faunas of New Zealand and Queensland, with some presence in New South Wales. What might prove to be related species, subject to delthyrial clarification, appeared earlier in Sakmarian deposits of south Asia, and these forms have 1-2 more pairs of plicae, that are more persistent than in younger species. A close ally of *Koenigoria* appeared in Middle Permian of Glass Mountains, Texas, as *Trigorhium.*

Several species attributed to *Trigonotreta* require corroboration of delthyrial structure, which, when determined, may clarify the evolution of the group. The impression so far is of a diverse and well dispersed group, mostly from southern paleolatitudes, but penetrating paleotropics in the late Early Permian and Middle Permian, and a very incomplete fossil record.

Subfamily **SERGOSPIRIFERINAE** Carter, 1994

DIAGNOSIS: Cardinal extremities round in juveniles, outline variable in adults; lateral slopes with few, simple or bifurcating subplicae, lateral sulcal costae usually simple, derived from bounding subplicae, fold usually well delimited by bounding interspaces, adminicula well developed.

DISCUSSION: This diagnosis follows that offered by Carter in Carter et al. (1994, pp. 343, 344). The subfamily commenced in ?Upper Devonian. It differs from Angiospiriferinae in lacking large umbonal callosity.

Subfamily **ANGIOSPIRIFERINAE** Legrand-Blain, 1985

DIAGNOSIS: Shells transverse, plicae numerous, either simple or subcostate, sulcus and fold may be plain or generally costate. Micro-ornament of radial and well developed concentric laminae, delthyrium open with large umbonal callosity, no delthyrial plate, dental plates supported by short adminicula, crural plates and sockets moderately developed, no tabellae. Vascular impressions ramiform, or weakly to moderately reticulate, but may be obscure.

DISCUSSION: This group includes a Carboniferous and Permian association of shells distinguished by the open delthyrium, large umbonal callosity, and ribbing, generally in the sulcus and fold, and in some genera over the plicae. Several Permian genera from Gondwana are allocated to this subfamily on the basis of shape, delthyrium, ornament and internal plates. *Brachythyrina* Fredericks and *Anthracospirifer* Legrand-Blain, which fail to develop adminicula, are placed in a separate subfamily (p. 236), rather than with Angiospiriferinae as preferred by Legrand-Blain (1986b) and Carter et al. (1994).

Genera typical of Angiospiriferinae are *Angiospirifer* Legrand-Blain, *Adminiculoria* Waterhouse & Gupta and *Varuna* n. gen., of middle Carboniferous age. *Alispirifer* Campbell, 1961 is of comparable age, and lacks costae but has large umbonal callosity, and is similar in many respects. Genera *Cancellospirifer* Campbell, *Sulciplica* Waterhouse, *Unicostatina* n. gen. and *Georginakingia* n. gen. are Permian members. An alliance is indicated by members of Trigonotretinae, with *Trigonotreta* and *Brachythyrinella* showing considerable approach in internal plates, umbonal callosity, plicae, costae and concentric laminae to *Varuna,* and reticulate or ramiform vascular impressions shared by *Aperispirifer, Trigorhium, Georginakingia* and *Sulciplica.*

Tribe **ANGIOSPIRIFERINI** Legrand-Blain, 1985a

[nom. transl. hic ex Angiospiriferinae Legrand-Blain, 1985a, p. 574]
DIAGNOSIS: Transverse shells with round-crested plicae bearing no costae, sulcus and fold smooth or with few costae of even strength.
GENERA: Genera include *Angiospirifer* Legrand-Blain, *Adminiculoria* Waterhouse & Gupta, *Alispirifer* Campbell, ?*Cancellospirifer* Campbell, *Sulciplica* Waterhouse, *Unicostatina* Waterhouse n. gen.

Genus ***Cancellospirifer*** Campbell, 1953

TYPE SPECIES: *Cancellospirifer maxwelli* Campbell, 1953, p. 11.
DIAGNOSIS: Very small shells with comparatively narrow hinge, obtuse cardinal extremities, a number of simple plicae in about 7 pair, sulcus may carry 2-3 costae, cancellate micro-ornament. Open delthyrium, no umbonal callosity.
DISCUSSION: This genus is poorly known, and Waterhouse (1968, p. 25) suggested that it might be allied to *Sulciplica* Waterhouse, with Hill et al. (1972, pl. P7, fig. 13) illustrating well a small ventral valve with costate sulcus. This also suggests the presence of a plication bifurcating anteriorly. Carter et al. (1994, p. 344) referred the genus to Sergospiriferinae Carter, 1994, so the classification is far from resolved. The type and only known species is very small, up to 25mm wide, and might be based on immature specimens.

Genus ***Adminiculoria*** Waterhouse & Gupta, 1979a

This genus is very close in many respects to the Early Carboniferous genus *Angiospirifer* Legrand-Blain, 1985a, based on *Spirifer trigonalis* (Martin). So far no specimens have been found to show angioglyphs, but shape, ornament and plates are very similar between the two.

Adminiculoria middlemissi (Diener, 1915)

Plate 6, fig. 1-11

1899 *Spirifer* cf. *triangularis* (not Martin) Diener, p. 59, pl. 5, fig. 8.
1903 *Spirifer* sp. indet. ex aff. *curzoni* not Diener Diener, p. 150, pl. 7, fig. 7.
1903 *S*. cf. *strangwaysi* not Verneuil Diener, p. 146, pl. 7, fig. 8.
1910 *Spirifer grandicostatus* not M'Coy Middlemiss, p. 229.
1915 *S. middlemissi* Diener, p. 41, pl. 4, fig. 9-12.
1915 *S. trigonalis* (not Martin) Diener, p. 40, pl. 4, fig. 8 (part, not fig. 7a, b = *varuna*).
1977 *Brachythyrina middlemissi*. Waterhouse & Gupta, p. 176, pl. 5, fig. 9-16.
1979a *Adminiculoria middlemissi* Waterhouse & Gupta, p. 134, pl. 12, fig. 1-6, 8, pl. 13, fig. 1.
1985: *A. middlemissi*. Gupta et al., pl. 3, fig. 3, 5, 8, 9, 11.

LECTOTYPE: GSI 11099 figured by Diener (1915, pl. 4, fig. 9) and Waterhouse & Gupta (1979a, pl. 12, fig. 1) from Fenestella Shales, Kashmir, SD Waterhouse & Gupta (1977, p. 176).

DISCUSSION: Some specimens are refigured herein. Fine radial lirae have been observed in the specimen figured by Diener (1915, pl. 4, fig. 9). There is considerable approach to specimens figured as *Spirifer* sp. indet. ex aff. *curzoni* from flaggy limestone west of Muth, northwest Himalaya, by Diener (1903, pl. 7, fig. 7) and *S*. cf. *strangwaysi* Verneuil by Diener (1903, pl. 7, fig. 8) from the same beds, also near Muth. The species *curzoni* is syringothyrinid and lacks costae from sulcus and fold.

Genus ***Sulciplica*** Waterhouse, 1968

TYPE SPECIES: *Sulciplica transversa* Waterhouse, 1968, p. 27.

DIAGNOSIS: Large transverse shells with wide hinge, obtuse to weakly alate cardinal margins, a number of strong plicae pairs in each valve, and costate sulcus and fold, micro-ornament of radial and concentric threads, sometimes apparently pustulose. Interior with spiriferoid plates and large umbonal callosity, subdelthyrial plate may be present in early growth stages.

DISCUSSION: *Sulciplica* was referred with a query to Trigonotretinae by Carter et al. (1994). The type species is *Sulciplica transversa* Waterhouse from Guadalupian faunas of Tasmania. It is like trigonotretin genera internally, and has large ventral umbonal callosity and no delthyrial plate. Micro-ornament involves fine concentric laminae and somewhat finer radial capillae (Clarke 1987, p. 269). The prime ornament consists of simple narrow plicae, and narrow subplicae or costae are usually limited to the sulcus and fold, so that the overall appearance is very different from Trigonotretinae. Instead, aspects of the shell, especially the high number of plicae, suggest *Angiospirifer* Legrand-Blain and other genera classed in the Angiospiriferinae Legrand-Blain, 1985.

The vascular imprints on ventral valves of the type species of *Sulciplica*, as figured by Clarke (1987, text-fig. 6C, 8E), suggest a ramiform pattern more complex than in *Angiospirifer*.

The relationship between *Cancellospirifer* and *Sulciplica* remains problematical. The differences between the two, such as absence of umbonal callosity from *Cancellospirifer*, might be due to the possibility that *Cancellospirifer* is based solely on juvenile shells.

Sulciplica is moderately widespread as a genus, and includes *S. transversa* Waterhouse, *S. vellai* Waterhouse and *S. occidentalis* Archbold in west and east Australia and New Zealand of Guadalupian age, older species such as *S. tasmaniensis* (Morris) from Tasmania as revised by Clarke (1973), and *S. chatsworthensis* Balfe & Waterhouse and *S. stutchburii* Etheridge of the Bowen and Gympie Basins of Queensland. The Early Permian pebbly mudstones of Thailand contain S. *thailandica* (Hamada) - see Waterhouse 1982c, p. 347 - and Shi et al. (1997) recorded a new species from Malaysia, with another new species to be described from Thailand (Dr G. R. Shi pers. comm.).

Sulciplica chatsworthensis Balfe & Waterhouse n. sp.

1969 "*Spirifer*" cf. *stutchburii* not Etheridge Jr Runnegar & Ferguson, pl. 3, fig.1-4.

1987 *Sulciplica* n. sp. Waterhouse & Balfe, pl. 2, fig. 7-11.

DERIVATION: Named from Chatsworth, place near Gympie, southeast Queensland.

HOLOTYPE: UQF 454266 figured by Runnegar & Ferguson (1969, pl. 3, fig. 2) from lower South Curra Limestone, Gympie, here designated.

DIAGNOSIS: Species with 3-5 lateral plicae and further costae each side of sulcus, sulcus bearing 3 costae which may branch, subsidiary pair of subplicae on outer flanks of sulcus and fold, sulcus wide and deep.

DESCRIPTION: Shells up to 55mm wide and 25mm long (internal mould), with broad sulcus having sulcal angle up to 45°, weak median costa and 5-6 lateral ribs, 5-7 fastigate lateral plicae, micro-ornament of fine radial and concentric lirae. Hinge denticulate, secondary shell thick, adminicula short, muscle platform long, extending to mid-length. Dorsal valve with ctenophoridium, large dental sockets, no tabellae, spiralia with about 14 turns. The species will be further described.

RESEMBLANCES: *Sulciplica transversa* Waterhouse, 1968 of mid-Guadalupian age in Tasmania has many more pairs of plicae and is more transverse, and *S. vellai* Waterhouse, 1999c from slightly younger beds in the Flowers Formation of west Nelson, New Zealand, is even more transverse with more plicae. *S. occidentalis* Archbold, 1995 from the mid-Guadalupian of the Perth Basin in Western Australia has numerous fastigate plicae and is highly transverse. *S. tasmaniensis* (Morris,1845) of Sakmarian age in Tasmania is more elongate with well rounded anterior lateral margins and a number of fine subplicae and a few sulcal costae. *Spirifer stutchburii* Etheridge, 1892, pl. 38, fig. 4-6 has a stronger sulcal rib and weak lateral sulcal ribs.

AGE: The age is not certain, with suggestions ranging from Sakmarian to Wuchiapingian (Waterhouse 2002c, p. 158).

AUTHORSHIP: Paul Balfe, Geological Survey of Queensland, Brisbane, studied the brachiopod faunas from Gympie with me, and first analysed the present species.

Sulciplica stutchburii (Etheridge, 1892)

1892 *Spirifera stutchburii* Etheridge Jr, p. 232, pl. 38, fig. 4-6.

1968 *Sulciplica stutchburii*. Waterhouse, p. 24.

LECTOTYPE: Sole specimen figured by Etheridge (1892) from Tiverton Group, Bowen Basin, SD Waterhouse (1968, p. 24). Kept at Geological Survey of Queensland, Brisbane.

DIAGNOSIS: Small transverse shells with high angular plicae in 6 pairs, deep sulcus with central rib and faint lateral costae, dorsal fold with narrow concave crest.

RESEMBLANCES: The species is distinguished by the low number of strong plicae, more regular than in *Sulciplica chatsworthensis*, as described above, and by the faint costae within the sulcus, and narrow fold. No other species comes close.

DISCUSSION: This species was described from what is now the Tiverton Formation of Bowen Basin, Queensland, of Sakmarian age. Etheridge (1892) grouped the specimen with individuals described by Koninck (1877), and as these were later destroyed by fire, Waterhouse (1968) nominated the Etheridge specimen as lectotype. It must be allowed that Etheridge proposed the taxon with diffidence "If the latter, and the figures cited in De Koninck's work are in want of a name, I would propose to call them *Spirifera stutchburii*..." The name is deemed acceptable, because it is a conditional name published before 1960 (ICZN 2000, article 15). No diagnosis was offered, nor type cited, but the species was described and contrasted with other forms.

Genus ***Unicostatina*** n. gen.

DERIVATION: uni - one, costa - rib, Lat.
TYPE SPECIES: *Sulciplica subglobosa* Clarke, 1990, p. 64, here designated.
DIAGNOSIS: Medium-sized moderately inflated ovally subquadrate or subrectangular shells with bluntly obtuse to well rounded cardinal extremities, open delthyrium with umbonal callosity, ornament of generally 5-8 pair of round-crested to subfastigate plicae, without costae, single costa traverses sulcus for full length, no other costae, fold narrow with rounded crest, micro-ornament of radial and concentric capillae. Dental plates, short adminicula largely buried in secondary shell.
DISCUSSION: This genus is based on *Sulciplica subglobosa* Clarke from the "Spirifer Zone" of Maria Island, of basal Permian age in Tasmania. Clarke (1990) also described an allied species *S. crassa* from beds of much the same age. *Spirifera stutchburii* Etheridge (1892, pl. 38, fig. 4-6) from the Tiverton Group of the Bowen Basin, Queensland, of slightly younger Sakmarian age, looks close, but is more transverse with more angular cardinal extremities, and is described as having several sulcal costae, as in *Sulciplica*.

Tribe **GEORGINAKINGIINI** new tribe

NAME GENUS: *Georginakingia* n. gen., here designated.
DIAGNOSIS: Transverse shells with a number of somewhat fastigate plicae, bearing few to a number of costae generally arising well front of umbones. Concentric laminae well developed, umbonal callosity prominent.
DISCUSSION: This tribe involves genera close to *Angiospirifer* and allies, with plicae that tend to be more fastigate, and tend to give rise to branching costae. The costation differs from that found in *Costuloplica*, in which costae are of even size and arise uniformly over the plicae. It appears likely that the georginakingiin type of plication and costation exemplified by *Varuna* gave rise to Trigonotretinae.
GENERA: *Georginakingia* Waterhouse n. gen., *Varuna* Waterhouse n. gen.

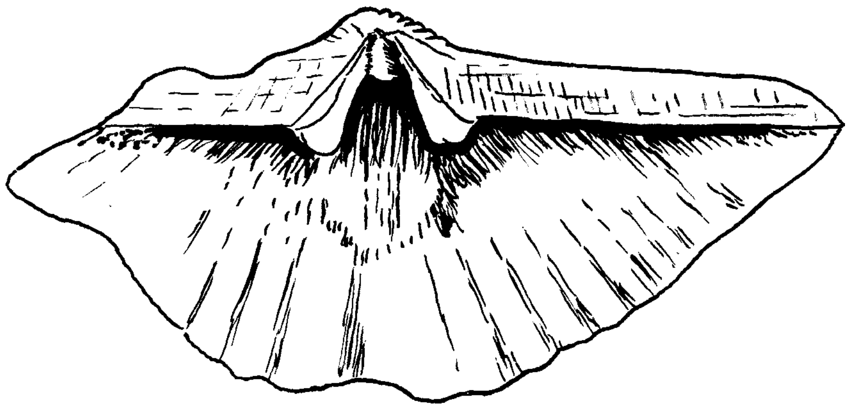
Genus ***Georginakingia*** n. gen.

Text-fig. 34

DERIVATION: Named for Georgina King, who collected fossils and minerals with great care and skill, little acknowledged, during the 19th century in Australia.
TYPE SPECIES: *Spirifera avicula* not Sowerby Morris, 1845, p. 282, here designated.
DIAGNOSIS: Large transverse shells with subalate cardinal extremities, well developed simple sulcus and fold, 8 or more pairs of narrow costate plicae,

concentric and radial micro-ornament, interior as in spiriferids, with no median ventral septum. Obliquely ramiform vascular impressions laterally.

DISCUSSION: The species *avicula* Morris, 1845 was first referred to *Fusispirifer* Waterhouse by Clarke (1973, pp. 50, 59), and has been well illustrated as *Fusispirifer avicula* (Morris) by Archbold & Thomas (1987, text-fig. 12A-D, 13A-G, 14A-C) and Clarke (1987, text-fig. 5A-E). Many more plicae are found in *avicula* than in *Fusispirifer*. The gross external ornament of *Fusispirifer*, both for type and a number of other species, mostly from Asia and Western Australia, consists of 2-5 pairs of costate plicae, with many fine costae covering an extended lateral shell. By contrast, Archbold & Thomas (1987, p. 199) recorded up to 8 pairs of plicae, in describing material from the Westley Park Sandstone Member of the "Budgong Sandstone", or better, Broughton Formation, south Sydney Basin. Judging from figures, this count is conservative. For material from Eaglehawk Neck, Clarke (1987, p. 267) recorded 12-20 "well developed fasciculate lateral plications". This number is very much higher than in



Text-fig. 34. *Georginakingia transversa* (Waterhouse), ventral interior, drawn from latex cast of ventral valve GST 8319 figured by Clarke (1987, text-fig. 5d) from Malbina Formation, Eaglehawk Neck, Tasmania, x1.

Fusispirifer, as cautioned by Waterhouse (1987a, p. 24) in rejecting any generic relationship to genuine fusispiriferins from Queensland. Moreover the number is greater than in other members of Spiriferidae and Trigonotretinae, and together with shape, suggests a closer approach to members of Angiospiriferinae and Strophopleuridae. The genus is characterized further by its costae, which are well developed, and, on the type species, increase close to the umbo, and arise through both bifurcation and more rarely, by intercalation. The holotype of the species is an internal mould. A squeeze of the lateral interior shows that complexly branched vascular impressions are developed, of unusual pattern. Branching vascular impressions are illustrated in the ventral interior of a specimen by Archbold & Thomas (1987, text-fig. 14C) and possibly in Clarke (1987, text-fig. 5D). Clarke (1987, text-fig. 5D) figured a large umbonal callosity in a ventral valve from Minnie Point Formation, Tasmania, whereas Archbold & Thomas (1987, p. 196) recorded a small delthyrial plate. Whether the nature of the delthyrium varied or not requires further study. This uncertainty complicates the subfamily position, because the genus shows similarities to Strophopleurinae, Angiospiriferinae, and Pterospiriferinae. The angiospiriferin genus *Sulciplica* shows considerable approach to *Georginakingia*, but has stronger sulcal subplicae, often fastigate, with rare if any costae over the plicae, and large well developed umbonal callosity. Both genera are much larger than related genera from older deposits further afield, suggesting ecological factors. The presence of costation suggests an approach to *Pteroplecta*, and the high number of plicae indicates an approach to Angiospiriferinae, or to Strophopleurinae.

The specific affinities of the Westley Park material may repay further study, although close in age to the upper Malbina Formation (Waterhouse 2002c). A number of specimens show a fold with shallow median depression and apparently less costation than in specimens from the Malbina Formation of Tasmania.

TAXONOMY: The original material of *Spirifera avicula* Sowerby, 1844, of uncertain provenance, is lost, so that the species has been based on *S. avicula* as described and figured by Morris (1845, pl. 17, fig. 6), with holotype by monotypy BB6248, from Malbina Formation member E, Eaglehawk Neck, southeast Tasmania.

Genus ***Varuna*** n. gen.

DERIVATION: varuna, species name from Indian word used by Diener (1915).

TYPE SPECIES: *Spirifer varuna* Diener, 1915, p. 43 from Fenestella Shales, Kashmir, here designated.

DIAGNOSIS: Small transverse shells with wide hinge and costate fold, plicae numerous and angular, bearing angular costae anteriorly, especially on dorsal valve, radial capillae and concentric laminae well developed. Dental plates, very short adminicula, socket and crural plates, denticulate hinge.

DISCUSSION: This genus is close to *Adminiculoria*, but more costate, and with fewer and more angular and branching plicae. In the nature of its few costae it approaches *Pteroplecta* Waterhouse, but has more fastigate and stronger plicae, and the ventral umbonal callosity is large, with no sign of a delthyrial cover. There is also some approach to members of Trigonotretinae, but costae are fewer and stronger than in members of this subfamily.

Varuna varuna (Diener, 1915)

Plate 7, fig. 1-5

1915 *Spirifer varuna* Diener, p. 43, pl. 4, fig. 13-15.

1915 *S. trigonalis* (not Martin) Diener, p. 40, pl. 4, fig. 7a, b (not fig. 8 = *middlemissi*).

1928 *Spirifer* sp. indet. aff. *niger* not Waagen Bion, p. 41, pl. 3, fig. 5, 6?

1977 Neospiriferine gen. & sp. indet. Waterhouse & Gupta, p. 171, pl. 5, fig. 3, 4 (part, not fig. 1, 2?, pl. 4, fig. 10 = neospiriferid).

1977 ?Gen. indet. *varuna*. Waterhouse & Gupta, p. 171, pl. 5, fig. 5.

1979a *Spirifer varuna*. Waterhouse & Gupta, p. 136, pl. 12, fig. 7.

LECTOTYPE: GSI 11104 figured by Diener (1915, pl. 4, fig. 14) and Waterhouse & Gupta (1979a, pl. 12, fig. 7), and Pl. 7, fig. 4 herein, from Fenestella Shale, Kashmir, SD Waterhouse & Gupta (1977, p. 172).

DISCUSSION: The species is refigured. Dorsal valves that belong to *Trigonotreta thomasi* from the Bijni tectonic unit of the Garhwal Himalaya come very close to some specimens of *varuna*, other than in their somewhat rounded plicae and more costate fold (Pl. 7, fig. 6, 8, 9).

Some accompanying specimens from the Fenestella Shales are more transverse, with more bundled inner plicae. These might be neospiriferid (Pl. 7, fig. 10, 11), as they not display any prominent umbonal callosity.

Subfamily **COSTULOPLICINAE** n. subfam.

NAME GENUS: *Costuloplica* n. gen.

DIAGNOSIS: Moderate number of narrow plicae, with low fine costae. Delthyrium open, dental plates may fuse medianly or be joined by pleromal ridges, passing posteriorly into elongate umbonal callosity.

DISCUSSION: *Costuloplica* is like Angiospiriferinae in having a number of narrow simple plicae, but these anteriorly develop fine costae. The costae are fine and subequal, unlike the coarse costae found in *Georginakingia* or *Varuna*, or within the sulcus and over the fold of *Angiospirifer* and allies. *Gibbospirifer* Waterhouse has somewhat comparable ornament, with a number of subdued and narrow plicae that are finely costate throughout their length. This genus is otherwise unlike any other within Spiriferoidea. It is more elongate with narrower hinge than in *Costuloplica*, and apparently is somewhat younger. In both genera the dental plates converge under the delthyrium, and carry pleromal ridges, which may form an elongate and slender umbonal callosity under the ventral umbo.

GENERA: *Costuloplica* Waterhouse n. gen., *Gibbospirifer* Waterhouse,

Genus ***Costuloplica*** n. gen.

DERIVATION: costa - rib, plica - fold, Lat.

TYPE SPECIES: *Neospirifer campbelli senilis* Maxwell, 1964, p. 31, here designated.

DIAGNOSIS: Small generally transverse moderately to well inflated shells characterized by ornament of 6-9 pair of ribs or subplicae posteriorly, separated by generally narrow interspaces, posterior plicae without costae, passing forward into finely costate plicae, radial filae very fine, sometimes absent possibly due to preservation, concentric growth increments stronger than radial filae but fine. Ventral interior with low dental and short adminicular plates, dental plates converge under top of delthyrium, with no visible well formed cover, umbonal callosity present as broad thickening not highly raised or swollen. Dorsal valve with dental sockets, low crural plates and spiralia, median septum low or not developed.

DISCUSSION: *Costuloplica* is based principally on Carboniferous species found in New South Wales and Queensland, within the range of the *Levipustula levis* brachiopod zone, deemed typical of southerly cold-water faunas of east Australia and South America. The type species *Neospirifer campbelli senilis* comes from the “Namurian” Branch Creek Formation of the Yarrol Basin, Queensland, and Roberts et al. (1976) reported the species from the Yagon Siltstone of Myall, New South Wales. *Neospirifer campbelli* Maxwell, 1964 was initially described from the Branch Creek Formation, Yarrol Basin, and later recorded from the Monto district of Queensland by McKellar (1965) and Yagon Siltstone by Roberts et al. (1976), and figured by Hill & Woods (1964a, pl. C11, fig. 13-15; 1973). Roberts et al. (1976) suggested that *N. tomskiensis* Benedictova, as figured by Kotlyar & Popeko (1967, pl. 43, fig. 1-6) and *N. profasciger* Maslennikov (Kotlyar & Popeko 1967, pl. 44, fig. 6-11) from the Lake Baikal region, were related to *N. campbelli.* The species *profasciger* has broad posterior ribs that split into fine costae, finer than in east Australian species. *Neospirifer virgatus* (Litvinovitch, 1962, pl. 33, fig. 3, 4 and Kotlyar & Popeko 1967, pl. 45, fig. 1-3) is also possibly congeneric. Roberts et al. (1976) also noted that *N. leoncitensis* (Harrington) from Argentina was related to *pristinus* or to *campbelli*. Thus the genus, like *Levipustula levis*, appears to typify early Late Carboniferous faunas, when glacial conditions prevailed in Argentine and east Australia.

Internally, the delthyrium is partly closed posteriorly by pleromal extensions from the dental plates, with heavy thickening along the hinge and under the ventral umbo, and none show a delthyrial plate. As well the dorsal septum appears to be feebly developed. The Argentinian species *leoncitensis* (Harrington) shows an umbonal callosity (Amos et al. 1964, pl. 1, fig. 6, 7).

Secondary thickening is considerable for *senilis* (Maxwell 1964, pl. 6, fig. 31-33) with callus thick below the delthyrium.

Overall, affinities are judged to lie with Trigonotretidae, because of the number of posterior subplicae at 6 or more pairs, variable costation, and substantial secondary thickening with thick callus under the ventral umbo. At an immature growth phase, *Costuloplica* shells look like Angiospiriferinae and allies, and also Strophopleurinae, with a number of simple ribs, and fine costae in the sulcus and over the fold. With advanced ontogeny, the ribs divide in a short space into 2-5 fine costae, not robustly with strong divergence of ribs as in *Neospirifer* or *Trigonotreta*, but through the introduction of fine interspaces. Thus the genus is readily distinguished from genera so far classed Trigonotretinae or Angiospiriferinae.

Although the type and other species have generally been referred to *Neospirifer* Fredericks and *Spirifer* Sowerby, with some caution expressed, they may readily be distinguished from members of these genera by the different ornament, in which posterior ribs are broad before passing into fine costae. As well, radial filae are feebly if at all developed, and the sulcus is bordered throughout by a feebly developed plication, and the posterior ribs and anterior bundles are more numerous, at least 6 pair, compared with the 2-5 plicae each side of the sulcus in *Neospirifer*. Similar observations hold for *Betaneospirifer*. Amongst neospiriferin genera of Late Carboniferous age, the well known species generally assigned to *Neospirifer* in the United States are costate and bundled much as *Neospirifer.*

Gibbospirifer Waterhouse is a subelongate form with fine costae in 8-10 bundles, narrow interspaces, somewhat approaching the present genus, and with dental plates extended to meet under the umbo (Text-fig. 35) and low umbonal callosity in some specimens. Differences are that costae arise and branch closer to the umbo, and the sulcus is very narrow. The type species comes from Late Carboniferous Ettrain Formation of Yukon Territory, Canada. It is an exceptional genus, and it shows no closer relationship to any other genus. *Septospirifer* Waterhouse of slightly younger age in the same region has high well formed bundles of somewhat raised and differentiated costae starting very close to the umbo, like those of Gypospiriferinae, and internally has a low median septum in the ventral valve.

Purdonellin species assigned to the genus *Podtsheremia* Kalashnikov, 1965 and *Kazakhstania* Besnosova, 1968 may have lengthy primary ribs or plicae, that subdivide near mid-length into 2-3 costae (see Kalashnikov 1974, pl. 49). The species are all elongate and inflated, with high adminicula, subdelthyrial plate, and moderately short hinge.

Costuloplica senilis (Maxwell, 1964)

1964 *Neospirifer campbelli senilis* Maxwell, p. 31, pl. 6, fig. 26-33.

1976 *N. senilis*. Roberts et al., p. 222, text-fig. 16.

HOLOTYPE: UQF 43206, figured by Maxwell (1964, pl. 6, fig. 31-33) from the Branch Creek Formation, Yarrol Basin, Queensland, OD.

DISCUSSION: The type material is kept in University of Queensland collections at the Queensland Museum, Brisbane. It was originally treated as a new variety, but was elevated to species rank by Roberts et al. (1976). It has more costae and longer undivided plicae than seen for *campbelli.*

Neospirifer pristinus Maxwell, 1951 from much the same levels as *Costuloplica* species is readily distinguished by its more elongate outline and bifurcating costae (Campbell 1962, Roberts et al. 1976, Hill & Woods 1964a, 1973, pl. C11, fig. 16-18). Campbell's (1962) suggestion that the species differed generically from *campbelli* and belonged to *Spirifer* Sowerby was not accepted by McKellar (1965), but was followed by Roberts et al. (1976). The exterior does show some attributes of the present genus in ornament, but there are clear differences in shape, because *pristinus* is an inflated elongate shell, and internally a ventral myophragm and dorsal median septum may be well developed, and secondary thickening is considerable in the ventral valve, and covered by deep pits. Campbell (1962, pl. 11, fig. 5) figured as *pristinus* a well preserved dorsal exterior that shows the ornament typical of *Costuloplica*, but McKellar (1965) challenged the identification, suggesting the specimen belonged to *campbelli.* That was not accepted by Roberts et al. (1976), but I believe McKellar was correct. McKellar (1965, pl. 4, fig. 10, 11) refigured from Maxwell exteriors that show very narrow primary ribs posteriorly on the dorsal valve with inner ribs in feeble bundles of duplicate or triplicate costae, coarser than in *Costuloplica campbelli* and *C. senilis*. McKellar (1965, p. 11) traced a distinct ontogeny for the species, noting well rounded cardinal extremities in juveniles, that become obtusely angular, right angled, and finally, at maturity, auriculate. The specimens referred to *pristinus* by Roberts et al. (1976, text-fig. 13) appear to be more transverse than Maxwell's types, but are internal moulds, and they appear to have narrow primary ribs posteriorly, which bifurcate in front. Overall, the external ornament is obscure, and the generic position requires further study.

Costuloplica robertsi n. sp.

1976 *Spirifer?* sp. Roberts, Hunt & Thompson, p. 219, text-fig. 14A-F.

DERIVATION: Named for J. Roberts.

HOLOTYPE: AM57771 figured by Roberts et al. (1976, text-fig. 14F), from Yagon

Siltstone, Myall, New South Wales, here designated.
DIAGNOSIS: Transverse small shells with rounded cardinal extremities and a large number of simple narrow plicae over lateral slopes, occasional but rare bifurcations, costae fine in sulcus and over fold.
DESCRIPTION: The material has been described from two localities L126-5, by Roberts et al. (1976).
RESEMBLANCES: The species is distinguished by having comparatively few anterior costae, with the ribs or subplicae branching rarely, and generally remaining simple. The costae within the sulcus and over the fold are much like those of *Costuloplica senilis* and *C. campbelli*, and the species is similar in overall shape and nature of the sulcus, fold, and internal detail. Therefore, despite the greater simplicity of ornament, the species is referred to the same genus. *Spirifer (Cyrtospirifer) leoncitensis* Harrington in Keidel & Harrington (1938, text-fig. 3d, 4, pl. 5, fig. 2, 3), as revised with references by Amos in Amos et al. (1963, pl. 1, fig. 5-9) is close, with more massive ventral umbo, broader though shallow sulcus with more costae, and slightly more costal splits over the anterior plicae.

There is some similarity in outline to *Neospirifer campbelli exora* McKellar, 1965 from the Monto district of Queensland, but this species has a broader sulcus and more costate lateral slopes with fewer plicae. Moreover the costae of *exora* are much stronger than in *Costuloplica*. McKellar's form is now referred to the genus *Maxwellispirifer* (p. 127).

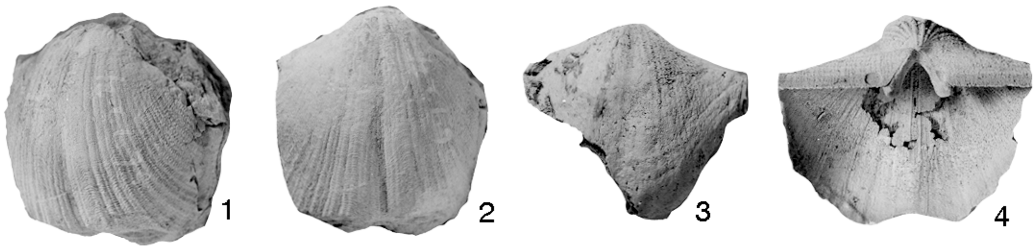
Some approach was noted by Roberts et al. (1976) of the Yagon Siltstone species to species of *Podtsheremia*? described by Roberts (1971) from the Burville beds of the Bonaparte Gulf, Western Australia. These are variably costate, and come close overall, but have more prominent adminicula, that appear to cut across the innermost pair of plicae. The apical callosity may form a hood-like structure.

Genus ***Gibbospirifer*** Waterhouse, 1971

Text-fig. 35

HOLOTYPE: GSC 26439, figured by Bamber & Waterhouse, pl. 27, fig. 7, 8, 13) from Ettrain Formation, Yukon, OD.
DIAGNOSIS: Medium small elongate shells with narrow sulcus, 8-10 plicae pairs, may fade anteriorly, bearing fine costae throughout length, fine close-set concentric laminae and fine radial filae. Weakly alate cardinal extremities, open delthyrium with dental plates convergent and extended by pleromal ridges, may form small umbonal callosity. Immature shells transverse.
DISCUSSION: This genus is unusual, and fails to fit amongst Neospiriferidae,

but possibly shows some approach to Spiriferinae and Gypospiriferinae in its delthyrium, and to Gypospiriferinae in the high number of subdued plicae. But these are more organized and simple than in the closest of genera, such as *Fasciculatia*, and the costae are finer. The genus is therefore provisionally regarded as an ally of *Costuloplica*, from which it is distinguished principally by its more elongate shape, weakly alate cardinal extremities, and more costate posterior shell.



Text-fig. 35. *Gibbospirifer ettrainensis* Waterhouse, 1971 from upper Ettrain Formation, Yukon Territory, x 1. 1, 2, ventral valve GSC 26439, holotype. 3, ventral valve GSC 26440. 4, ventral interior GSC 26441. From Bamber & Waterhouse (1971, pl. 27, fig. 7, 8, 10, 12).

Family **CHORISTITIDAE** Waterhouse, 1968

[nom. transl. Ivanova 1972, p. 40 ex Choristitinae Waterhouse, 1968, p. 9].

DIAGNOSIS: Shape distinctive, elongate and subglobose, simple or bifurcate costae over both valves, micro-ornament with radial filae, high and often long adminicula.

Subfamily **CHORISTITINAE** Waterhouse, 1968

DIAGNOSIS: Subelongate shells with both valves inflated, hinge wide and interarea moderately high, prominent fold, costae well developed, may bifurcate, adminicula of moderate length, high, no delthyrial plate. Vascular impressions may be reticulate, sited close to muscle field.

DISCUSSION: The vascular impressions of *Choristites fritschi* (Schellwien) as figured in Sarytcheva (1968, pl. 28, fig. 1) show a very coarse and open network. Similar impressions have been figured by Legrand-Blain (1970, pl. 3, fig. 10, 11, p. 1069) for what is now *Parachoristites* (Dr Legrand-Blain, pers. comm.)

GENERA: Genera include *Choristites* Fischer de Waldheim, *Choristitella* Ivanov & Ivanova, *Ectochoristites* Campbell, *Parachoristites* Barkhatova, *Trautscholdia* Ustritsky.

Subfamily **PROSPIRINAE** Carter, 1974

DIAGNOSIS: Cardinal extremities extended in juveniles, growth form varied in

adults, lateral costae mostly simple, fold clearly delimited, adminicula well developed as a rule, umbonal callosity generally developed.
GENERA: Genera include *Prospira* Maxwell and *Parallelora* Carter. The placement within Spiriferoidea, and the inclusion of genera requires further study, but the adult shape suggests Choristitidae rather than Spiriferidae as favoured in Carter et al. (1994).

Subfamily **PURDONELLINAE** Poletaev, 1986

DIAGNOSIS: Outline brachythyrid, with moderately prominent umbones and concave posterior walls, narrow hinge, elongate shape, fold, multicostate, simple or subfasciculate laterally, subdelthyrial plate, moderately long and high adminicula, indistinct vascular impressions.
DISCUSSION: According to Carter et al. (1994, p. 344), Purdonellinae were to be grouped with Spiriferidae, and not with Choristitidae, because they lack reticulate vascular impressions, and have a subdelthyrial plate, unlike Choristitinae. On the other hand, the overall shape and the ornament and moderately developed adminicula involve choristitin aspects, but the shortness of hinge for a number though not all genera and species distinguish the group from other spiriferin and choristitin genera. Poletaev (1984) illustrated the nature of the high adminicula, passing at low angle into the dental plates in the type species *Purdonella nikitini* (Tschernyschew), and also revealed the presence of a subdelthyrial or pleromal plate crossing the delthyrium from the junction of the dental plates and adminicula (Poletaev 1984, text-fig. 1). Genera within the subfamily may display some degree of plication and fasciculation, as illustrated for *Podtsheremia* Kalashnikov, for which the range of morphologies is well shown in Kalashnikov (1974, pl. 49). This latter genus also has high adminicula and may have a subdelthyrial plate, or prominent pleromal ridges (Kalashnikov 1974, text-fig. 16-18). Radial capillae are well developed (Besnosova 1968, pl. 27, fig. 12).
GENERA: Genera include *Purdonella* Reed, *Aequalicosta* Waterhouse, n. gen., *Ala* Nalivkin, *Darbandia* Angiolini, *Domokhotia* Abramov & Grigorieva, *Kasakhstania* Besnosova, *Podtsheremia* Kalashnikov.

Genus ***Aequalicosta*** n. gen.

DERIVATION: aequali - equal, similar, costa - rib, Lat.
TYPE SPECIES: *Eliva inflata* Cooper & Grant, 1976, p. 2239, here designated.
DIAGNOSIS: Shells small, hinge only half of maximum shell width, triangular interarea with apparently open delthyrium, sulcus well defined, fastigium very low and narrow, lateral costae low, numerous, bifurcating asymmetrically to

form a few weak fascicles of 3 costae, fine costae in sulcus and over fold and lateral slopes. Micro-ornament of concentric and radial filae, no pustules. Fastigium formed by single fascicle of costae, starting with one costa, that branches to form two, and the two bifurcate again. Dental plates supported by moderately high adminicula which extend in individuals almost as far as the anterior ventral muscle field; long and well developed myophragm; dorsal sockets well formed, bases of crura extend along socket plates, moderately well formed crural plates.

DISCUSSION: The type species was described from the Bell Canyon and Capitan Formations of western United States. It is selected as type because the text and figures provided by Cooper & Grant (1976) clearly document and illustrate the critical nature of the posterior fastigium. The holotype is USNM152887k (Cooper & Grant, 1976, pl. 633, fig. 49-53). A second species *Eliva shumardi* Cooper & Grant (1976, p. 2240, pl. 632, fig. 1-54, holotype USNM154567b, pl. 632, fig. 25-29) from the Hegler, Rader and Lamar Members of the Bell Canyon Formation, and Capitan Formation, western United States, shows more of the interior and micro-ornament. The median posterior rib of the fastigium is indicated in Cooper & Grant (1976, pl. 632, fig. 28).

In general aspect this genus looks like *Quispira*, described on p. 225 as a member of Spiriferellidae, but has a different posterior fold. It is triangular in shape, with scarcely raised fastigium or plicae, both valves being ornamented by fine subequal ribs. The interareas in both valves are triangular, adminicula are long, and ventral myophragm and crural plates prominent. The family placement of *Aequalicosta* may appear contentious, because in many respects, the new genus looks like a member of Spiriferellidae in shape, ornament and internal detail. But differences from Spiriferellidae are revealed by the origin and development of the fastigium, which was regarded as a significant feature for *Spiriferella* and allies by Cooper & Grant (1976) and Waterhouse & Waddington (1982). In *Elivina, Quispira* and other allies of the Spiriferellidae, the dorsal ornament on the fold commences with two costae, separated by groove, and the costae branch only or chiefly on one side. In *Aequalicosta*, the fold commences as one costa, which divides into two, and laterally splits to give 4 or 6 costae overall (Cooper & Grant 1976, p. 2238).

The type species of *Aequalicosta* was initially referred by Cooper & Grant (1976) to *Eliva* Fredericks, 1924a, based on *Spirifer lyra* Kutorga, 1844, but *Eliva lyra*, well figured by Tschernyschew (1902, pl. 6, fig. 6, 7, pl. 7, fig. 7, pl. 8, fig. 4, 5, text-fig. 150, Kulikov 1974, pl. 7, fig. 1, Kalashnikov 1998, pl. 12, fig. 4-6), differs in having fine costae in the sulcus and a number of narrow plicae laterally, with or without costae, and the dorsal median groove extends forward over the fastigium from the umbo. Pitrat (1965) implied that adminicula were lacking, but the genus is classed within Purdonellinae Poletaev in recent studies, along with *Elivina* and *Elinoria*, for instance by Kalashnikov (1998), and Carter et al. (1994). *Eliva* is here deemed to stand with *Elivina*, separate from Purdonellinae (p. 223).

There is some approach by *shumardi* and *inflata*, as noted by Archbold & Bird (1989, p. 119), to *Eliva lyra* not Kutorga from Noil Simaan, Timor, described by Hamlet (1928, pl. 6, fig. 5, 6). But the Timor shell is more elongate with coarser costae, well defined fold and broader sulcus. A slit is shown along the full length of the fold, suggesting that Hamlet's specimens do not belong to *Aequalicosta*. Compared with *Elivina*, the present form is fasciculicostate and its fascicles rarely make weak plicae, whereas in *Elivina* the costae bifurcate symmetrically and seldom form bundles with 3 costae at the anterior margin. *Gypospirifer* Cooper & Grant and *Purdonella* Reed both have stronger better defined fold and differ considerably in shape and costation.

Spirifer tibetanus Diener *occidentalis* Schellwien (1900, pl. 11, fig. 10-13) from the Trogkopfel beds of Austria is possibly congeneric with or allied to *Aequalicosta*, because a rib in the figure seems to form the start of the fastigium. It then appears to split into two ribs a little in front of the dorsal umbo. Figured specimens include some with massive ventral shoulders and incurved ventral umbo, and some shells have narrow plicae that branch little. Specimens somewhat akin to the Austrian form were recorded from the Cisuralian of Laos as *Spirifer tibetana* not Diener by Mansuy (1913, pl. 5, fig. 11, pl. 6, fig. 1).

A specimen from the "lower Murgabian" of Afghanistan, described as *Spiriferella mexicana* (not Shumard) by Termier et al. (1974, p. 137, pl. 31, fig. 3-5) is similar in the nature of its ribs, but the pattern of ribbing on the first formed part of the fastigium may not conform, and Termier et al. (1974) described granules as part of the micro-ornament.

Genus ***Darbandia*** Angiolini, 2001

TYPE SPECIES: *Darbandia vagabunda* Angiolini, 2001, p. 336.

DISCUSSION: This genus was classed as a member of Hunzininae, Spiriferellidae, by Angiolini (2001). It is based on a few specimens described by Angiolini (2001) and characterized by a very high ventral interarea. Costae are broad and rarely bifurcate. Micro-ornament was recorded as comprising only concentric growth increments, without radial filae or pustules. The nature of the fastigium was not described, but it was figured, and appears to be upstanding and to bear 4 costae, with a median at least anterior interspace. Interior not known. The type species comes from the Panjshah Formation of the Karakorum, judged to be of Late Wordian age.

In many respects, from what is so far known about the genus and species, including the upright and prominent ventral umbo and nature of ornament, sulcus and fold, and micro-ornament, *Darbandia* appears to be a member of Purdonellinae Poletaev, rather than Spiriferellidae. More detail on morphology is required, including the nature of internal plates and secondary thickening.

SPIRIFERELLIDAE

Introduction

Spiriferella and allied brachiopods are moderately common in the Late Permian rocks of northwest and central northern Nepal, and in comparable faunas of northwest India and south Tibet. They have been studied for well over a century, and the present overview reassesses their familial and generic attributes and stratigraphic range. Significant Afghanistan, Canadian, United States, Timor and other taxa are also examined for comparison with Himalayan genera and species.

The Himalaya belonged to the southern hemisphere during Permian time, and one of its faunal attributes was the comparative abundance of Spiriferellidae, shared to some extent with Western Australia and New Zealand. In the northern hemisphere, Spiriferellidae are common in Permian rocks of the present Arctic region, including the successions of northern Russia and Canada in the Canadian Arctic Archipelago and Yukon Territory, so that the two dissociated regions were paired and latitudinally equivalent. They are “bitemperate”, a term preferable to “antitropical”, because this word lacks the implication of double as opposed to singular, and carries inappropriate implications in its prefix “anti”. The temperate climatic belt is not opposed to tropical, but is different from tropical. Species are common in the late Guadalupian of western United States, indicating an influx from temperate latitudes, permitted by opening of seaways, evolutionary expansion, or climatic change. Reassessment of some of these spiriferellids is also provided.

MORPHOLOGY: The nomenclature used herein classes the larger radial folds or rugations near sulcus and fold as plicae. The outer lateral finer non-costate rugations are called subplicae or costae, and the ribs carried over or between the plicae are costae. Some authors apply the term costae to what are here termed plicae, but then proceed to describe costae on the costae: this is confusing, and to be avoided. As for other spiriferidins, fold and fastigium are used interchangeably.

RELATIONSHIPS: Family Spiriferellidae was classed within Spiriferoidea King by Carter et al. (1994). Waterhouse (1982a, p. 53) suggested that *Spiriferella* should be allied with *Licharewia* Slussareva. For Licharewiidae and Spiriferellidae to be separated in Spiriferinida and Spiriferida seemed incorrect. Licharewiidae and Spiriferellidae share heavy secondary thickening in the ventral valve, plicate ornament and finely cancellate and often pustulose ornament, impunctate shell, and internal features in both valves. Various authors have outlined the morphology of Spiriferellidae, including Cooper & Grant (1976) and Waterhouse & Waddington (1982), and members of Licharewiinae have been closely examined by Slussareva (1960) and Grigorieva & Kotlyar (1966). Some authorities have opposed the association, but no author seems to have provided an analysis of the placement or differences between the two families. Both are exceptional associations in their respective superfamilies of Spiriferoidea and Syringothyridoidea, where placed by Carter et al. (1994). Spiriferellidae has pustular micro-ornament and Licharewiidae has impunctate shell and lacks syrinx and other attributes of Syringothyridoidea.

Nonetheless, there are differences between the two groups. Most Licharewiinae are more transverse with wider hinge than seen in Spiriferellidae, other than the spiriferellid *Timaniella* Barkhatova, and have more plicae, apart from *Licharewia rugulata* (Kutorga) which is close to *Spiriferella* in shape, and *L. grewingi* (Netschajew) which has sulcal costae. These exceptional species may point to the possibility of linkage, but not necessarily so. Micro-ornament is not the same, with radial capillae better developed amongst Spiriferellinae, and the pustules arise from the junction of radial and concentric filae, whereas pustules are coarser amongst Licharewiinae. Perhaps the first step in resolving relationships is to determine whether Licharewiinae should be grouped with Syringothyrinidae. If this is to be ruled out, then the family may have to be treated as spiriferoid s. l., and possibly close to Spiriferellidae.

No other family or subfamily seems to be very close. The plicae and ribbing of Spiriferellinae finds some match amongst members of Purdonellinae. There are a number of differences between members of the two subfamilies, involving ornament, micro-ornament, shell thickening, delthyrial structures and vascular impressions, but the two do share somewhat similar-looking and prominent adminicula as in *Purdonella nikitini* and *Spiriferella saranae* (see Tschernyschew 1902, text-fig. 41-46). Genera within Elivininae seem intermediate between the two subfamilies in some respects. That further raises the question of possible links with Choristitinae, which share similar overall shape and prominence of adminicula.

Family **SPIRIFERELLIDAE** Waterhouse, 1968

[Used as full family in independent proposal by Termier et al. 1974, and separately upgraded by Carter in Carter et al. 1994, p. 346, Shi & Waterhouse 1996, p. 30 and Grigorieva in Kalashnikov 1998, p. 44 ex Spiriferellinae Waterhouse, 1968, p.10].

DIAGNOSIS: Generally broad plicae and costae and micro-ornament often with tiny pustules, hinge short to very wide, and delthyrium open or partly to completely closed by single or double plate. Dental plates, adminicula may be extended and high, crural plates but no tabellae, teeth, and varied amount of secondary thickening over posterior ventral valve. No reticulate vascular impressions known.

DISCUSSION: Two spiriferellid species long recognized in the late Middle or Late Permian of the Himalayas, including Kashmir, Tibet and Nepal, have been *Spiriferella rajah* (Salter) and *Elivina tibetanus* (Diener). Several additional species were named by Zhang in Zhang & Jin (1976) from Tibet, and single species from Nepal named by Legrand-Blain (1977) and Waterhouse (1978). There has in recent years been a tendency to focus only on the ventral valve, and ignore micro-ornament and the dorsal valve, but genera of Spiriferellidae show great variation in attributes involving these aspects. Taxa named without knowledge of the dorsal valve offer considerable difficulties for interpretation and application, to the extent that some taxa cannot be applied other than speculatively. If the dorsal valve is not preserved, the species should not be named, unless the ventral valve is outstandingly distinctive, as is the case for *Nakimusiella* Shen et al. (2001).

Subfamily **SPIRIFERELLINAE** Waterhouse, 1968

DIAGNOSIS: Genera characterized by moderately to well developed dorsal fold, which may be entire, costate or subplicate, with or without narrow or broad median furrow. Micro-ornament of concentric and radial filae, bearing tiny pustules. Considerable secondary thickening as a rule in ventral valve.

GENERA: Genera include *Spiriferella* Tschernyschew, *Alispiriferella* Waterhouse & Waddington, *Arcullina* Waterhouse, *Bamberina* n. gen., *Canalisella* n. gen., *Eridmatus* Branson, *Nakimusiella* Shen et al., *Plicatospiriferella* Waterhouse & Waddington, *Rhombospirifer* Duan & Li, *Spiriferellaoides* Lee, Gu & Li?, *Timaniella* Barchatova.

Genus ***Spiriferella*** Tschernyschew, 1902

TYPE SPECIES: *Spirifer saranae* Verneuil, 1845, p. 169.

DIAGNOSIS: Ventral valve, rounded posterior walls, ornament of rounded plicae, variably costate; dorsal valve less inflated and less thickened, with fold traversed by slender median groove, plicae and variable costation; micro-ornament on both valves of transennate radial and growth filae forming pustules at some intersections. Hinge of varying width, with well developed ventral interarea. Delthyrium closed by small or large delthyrial plate, or open with umbonal callosity, short to long adminicula and dental plates, spiriferidin muscle field, heavy secondary thickening. Dorsal valve with inner and outer socket plates, crural plates, spiralia, low median septum, no tabellae, low rectangular adductor scars, shell thin.

DISCUSSION: Shen et al. (2001, p. 166) discounted the genus *Tintoriella* Angiolini (1996), and treated it as a junior synonym of *Spiriferella*. *Tintoriella* was based on type species *Spiriferella rajah* (Salter), said to be distinguished from type *Spiriferella* by its longer adminicula and dental plates less buried in apical callus, and by the absence of the delthyrium plate. Shen et al. (2001) judged such features to be variable or unreliable. Waterhouse (2001) has also drawn attention to uncertainty stemming from the apparently variable development of the delthyrial plate. For instance individuals of *Spiriferella gravis* described by Cooper & Grant (1976, pl. 630, fig. 17, 22, 27, 29, 31, 39) vary in the presence or absence of delthyrial plate and umbonal callosity. The adminicula of *Spiriferella saranae* are quite as long as those of *S. rajah* (see Tschernyschew 1902, text-fig. 41-46).

In describing the type species *saranae,* Verneuil (1845) had recorded 5-6 costae in the sulcus, simple costae, high enrolled umbo, and possible dorsal valve with narrow fold bearing a narrow median slit and about 3 costae (Verneuil 1845, pl. 6, fig. 15a, b). From inspection of specimens from the upper Artinskian at Ufa River, it appears that *Spiriferella saranae* is typified by a rounded fold with shallow median groove (Waterhouse & Waddington 1982, p. 19). The ventral umbo is well incurved and posterior walls diverge and extend well forward, imparting a lozenge shape. The specimens described as *saranae* by Tschernyschew (1889, pl. 7, fig. 25 a, b, c) are close to typical *saranae*, although they also approach *S. pseudotibetana* Stepanov. They show more costae than Verneuil's figures, a grooved dorsal fold, widening anteriorly, and prominent ventral sulcus.

Angiolini (1995) interpreted *Spiriferella saranae* from the specimens described by Tschernyschew (1902) from the Schwagerinakalk at Sula River. The ventral valve figured by Tschernyschew (1902, pl. 12, fig. 4) has well defined sulcus and simple firmly defined plicae, and the dorsal valve figured by Tschernyschew (1902, pl. 40, fig. 7) shows narrow fold with well rounded crest and no median groove, as shown in the figure and confirmed from observation.

It is clear from several aspects of the morphology that Tschernyschew's specimens are not type *saranae,* and they are not like type *saranae*. After examining the type suites at the Tschernyschew Museum, Waterhouse & Waddington (1982, p. 19) placed the material of Tschernyschew (1902, pl. 12, fig. 4, pl. 40, fig. 7) in a new species, *Spiriferella barchatovae*, evaluated now as a species of *Arcullina*. The holotype is the specimen figured by Tschernyschew (1902, pl. 12, fig. 4). By contrast, different specimens figured by Tschernyschew (1902, text-fig. 41-46, pp. 524, 525) are closer to *saranae*, and come from Artinskian beds. They show well the delthyrial covering and the ventral plates, including long adminicula, muscle field, apical filling, and micro-ornament.

Various other Russian species, and those described from the Glass Mountains of Texas by Cooper & Grant (1976) and from the Canadian Arctic by Waterhouse & Waddington (1982) also have a sulcus that, whilst not always as well defined as in *Spiriferella saranae*, is wider than the narrow sulcus of most Himalayan species attributed to *Spiriferella*, including *S. rajah*. This may yet be deemed to justify *Tintoriella*, with its narrow sulcus, but at present the width of the sulcus is considered to be of specific rather than generic importance.

Spiriferella rajah (Salter, 1865)

Plate 8, fig. 1, 2

1831 *Producta* sp. Herbert, p. 271, pl. 17, fig. 2a, b.

1833 *Producta* sp. Everest, p. 114, pl. 2, fig. 22, 23.

1865 *Spirifer rajah* Salter in Salter & Blanford, pp. 59, 111.

1866 *Spirifer rajah*. Davidson, p. 40, pl. 2, fig. 3.

1899 *Spirifer rajah*. Diener, p. 68, pl. 4, fig. 1-7, pl. 5, fig. 1.

1903 *Spirifer rajah*. Diener, pp. 105, 131, 186, pl. 4, fig. 3-5.

1915 *Spirifer rajah*. Diener, p. 86, pl. 9, fig. 5, 6.

1941 *Spiriferella rajah*. Muir-Wood & Oakley, p. 36, pl. 2, fig. 2, 3, 9-11.

1966 *S. rajah*. Waterhouse, p. 48, pl. 1, fig. 5, pl. 3, fig. 2?, pl. 7, fig. 1, 2, 4, pl. 11, fig. 2, pl. 12, fig. 2.

1966 *S. tibetana* (not Diener) Waterhouse, p. 52, pl. 2, fig. 2, pl. 9, fig. 3, pl. 13, fig. 5 (part, not pl. 12, fig. 3, 4, pl. 13, fig. 1, 2, 4 = *oblata*).

1978 *S. rajah*. Waterhouse, pp. 38, 88, 123, pl. 4, fig. 1-5, pl. 14, fig. 1-8, 11-13 (part, not pl. 3, fig. 14, 15 = *legrandblaini*, not pl. 4, fig. 6?, 7?, pl. 14, fig. 9, 10, pl. 24, fig. 2 = *oblata,* not pl. 4. fig. 6, 7 = *Arcullina* sp.).

1979a *S. rajah*. Waterhouse in Gupta & Waterhouse, pp. 11, 16, pl. 1, fig. 10-14, pl. 2, fig. 1-10, pl. 3, fig. 1, 9, 10.

1982 *S. salteri* not Tschernyschew Zhan & Wu, pl. 5, fig. 17.

1983a *S. rajah.* Waterhouse, p. 135, pl. 6, fig. 5, 6.

1983 *S. rajah*. Waterhouse & Gupta, p. 238, pl. 2, fig. 1, 2.

1996 *Tintoriella rajah*. Angiolini in Garzanti et al., p. 195, pl. 1, fig. 6-13.
2001 *T. rajah*. Angiolini, pl. 4, fig. 8-11.
HOLOTYPE: B 82086 figured by Davidson (1866, pl. 2, fig. 3) from *Lamnimargus himalayensis* Zone, Zewan Formation, Kashmir, by monotypy.
DIAGNOSIS: Moderately large shells with wide hinge, ventral umbo incurved and posterior walls concave in outline, sulcus narrow and well formed, dorsal fastigium high, narrow with median groove. Plicae well formed, convex in section, with very narrow interspaces, number about 7 pair on each valve, grading laterally from plicae into subplicae, and into further costae, plicae bear narrow costae anteriorly, especially on ventral valve, dorsal plicae may lack costae.
DISCUSSION: The preceeding diagnosis is based on a plaster duplicate of the holotype (which is not well figured in Davidson) and on various specimens from the *Lamnimargus himalayensis* Zone and elsewhere, best illustrated by Diener (1899) and Gupta & Waterhouse (1979a). Other Himalayan material, as figured by Diener (1903, 1915), Angiolini (1996) and Waterhouse & Gupta (1983a), fall within this narrow circumscription. Material figured as *Spiriferella rajah* by Zhang & Jin (1976, pl. 17, fig. 3-12), if representing a genuine suite of one species, does not appear conspecific. A number of specimens suggest a wider sulcus than is normal for *rajah*, with the edge of the sulcus lying anteriorly at the second major pair of plicae from the midline, not the first pair as in *rajah,* and they are placed in a separate species *S. grunti,* described below. Similarly the specimens identified as *rajah* by Shen et al. (2001, text-fig. 6.3, 5, 8) show wider sulcus, narrower ventral interspaces, flatter ventral rib crests, and overall lower, less massive and less incurved ventral umbo, compared with *S. rajah*. Specimens from the *Tethyochonetes* bed figured by Shen & Jin (1999, text-fig. 3.17-20) are poorly preserved, but differ from *rajah* in the high plicae and wide interspaces on both valves. The figures offered for aff. *rajah* by Legrand-Blain (1977, text-fig. 4-6) are too incomplete to be recognized, but plaster moulds indicate that they belong to the slightly younger species, *S. nepalensis* Legrand-Blain and *Arcullina angiolinii* n. sp., as recorded below. *S. rajah* recorded from Shyok melange of Baltistan by Brookfield & Gupta (1984, text-fig. 5, 6, 8) might well be conspecific, but the figures are too poor to allow certainty. It can be confirmed that specimens present with *Costiferina* and *Lamnimargus himalayensis* in the Khimokul section of Tidong Valley, Kinnaur Himalaya, belong to *S. rajah* (Gupta & Waterhouse 1979b, 1981, p. 346). *S. salteri* (not Tschernyschew) of Zhan & Wu (1982, pl. 5, fig. 17) is very poorly preserved but shows the typical narrow sulcus of *rajah*. It comes from the Lia Formation of the Xainza district of south Tibet. A publication figuring *S. rajah* by Chopra et al. (1980, pl. 1, fig. 1-3. 6, 7, 8, pl. 2, fig. 1, 2, 7, 9, 13, 16) is not available to me for assessment.

Spiriferella rajah of Shimizu (1981, pl. 8, fig. 8, fig. 21, 22) from Kashmir is small, and the exterior suggests an affinity with *Nakimusiella* Shen et al. (2001) because the sulcus appears to be either missing or very shallow, or the shell has been deeply worn. *S. rajah* of Jin & Sun (1981, pl. 11, fig. 2, 10) from Tibet shows little similarity at a specific level.

Various specimens from the Late Permian of east Dolpo, western Nepal, described by Waterhouse (1966) include some with few costae, that might be distorted *Arcullina oblata*.

Spiriferella subsalteri Shen et al. (2003a) may well be synonymous with *S. rajah*, but the species has so incompletely circumscribed, with no dorsal valve described or figured, that the generic position remains speculative. The specimens show a sulcus like that of type and other *rajah* specimens, and 3-5 costae over plicae. There appear to be only 5 conspicuous pair of plicae, fewer than in type *rajah*, so that this offers a possible means of distinction. The dorsal valve needs to be found and described, so that the species can be adequately distinguished from *rajah*.

RANGE: The species *Spiriferella rajah* appears to range in western and central Nepal from the *Lamnimargus himalayensis* Zone of Nangung Formation, of Wuchiapingian age, into the *Lazarevonia arcuata* and *Biplatyconcha grandis* Zones of Changhsingian age. The younger specimens cannot be distinguished by any particular feature from the older material.

Spiriferella sinica Zhang, 1976

1976 *Spiriferella sinica* Zhang in Zhang & Jin, p. 213, pl. 15, fig. 11-17.

1990 *S. rajah* not Salter Yang et al. pl. 25, fig. 2.

HOLOTYPE: IGAS 00929 figured by Zhang & Jin (1976, pl. 15, fig. 13-15) from Qubuerga Formation, JSPf22, Tibet, OD.

DIAGNOSIS: Subrounded shells with enrolled massive ventral umbo, widely diverging ventral posterior walls, gently convex in outline, sulcus typically shallow, may be moderately well formed, ventral plicae bearing only anterior if any costae, only 4 plicae pair conspicuous, dorsal fold may broaden anteriorly, and carries a median groove, 3-4 pair of dorsal plicae, costate anteriorly.

DISCUSSION: This species, very inadequately known and therefore subject to speculation over its definition, range and limitations, is presumed to be characterized by its shape, sulcation and ornament. The outstanding feature lies in its small size and hunched ventral umbo with posterior walls convex in outline. The figure of Zhang & Jin (1976, pl. 15, fig. 15) indicates a groove on the fold that is either lateral or median, or lateral with a median groove damaged. Dr Shen has kindly resolved this critical question and informed me that the fold definitely has a median groove, to indicate that the species belongs to *Spiriferella*, not *Arcullina*. The age and stratigraphy for the types remain under poor control, coming from the Qubuerga Formation in the Qubu area. Shen et al. (2001) placed *S. rajah* of Yang et al. (1990) in *S. qubuensis*, but the figure in question does not show the long posterior walls and prominent ventral umbo of *qubuensis*. Instead the posterior walls are convex as in *S. sinica* Zhang, although the plicae are more costate. *S. subsalteri* Shen et al. (2003a) comes from the lower Qubuerga Formation but has posterior walls that are concave in outline.

Compared with *Spiriferella rajah*, the species *sinica* has more incurved ventral umbo, posterior walls convex not concave in outline, similar convex plicae with interspaces as narrow or slightly wider, tendency for fewer pairs of plicae to be conspicuous on each valve, and plicae that may be broader and more costate anteriorly on the dorsal valve.

Shen et al. (2001) recorded the species *sinica* from levels 3, 6c, 8 and 9 of the Selong Xishan section and stressed the shallow nature of the sulcus, suggesting that the species may have been a forebear to the distinctive genus *Nakimusiella* Shen et al. (2001) from “bed” 12 of the Selong Xishan section. Reassessment fails to find convincing evidence that the material figured as *sinica* by Shen et al. (2001) belongs to Zhang’s species. None of their specimens is close in the nature of the ventral umbo or shows convex posterior walls or for the most part, a shallow sulcus. Rather, the specimen of Shen et al. (2001, text-fig. 10.1, 2) shows a very shallow ventral sulcus, and the size and shape and other detail indicative of *Nakimusiella*. The remaining specimens differ in sulcus, shape, size and ontogenetic development from *sinica* (text-fig. 10. 3, 4, 5, 6, 7, 8) and agree with the new species *Spiriferella grunti.*

Shen et al. (2001, p. 173) suggested that material recorded from the *Lamnimargus himalayensis* Zone of west Dolpo by Waterhouse (1978, pl. 4, fig. 1-5) was similar. One ventral valve (fig. 2) is close in simplicity of ornament, but lacks convex posterior walls and incurved ventral umbo, and so is closer to *Spiriferella rajah* (Salter). Some (fig. 3-5) show interiors, and cannot be compared with *S. sinica*, because no interiors are reliably known for *sinica*, and the interiors do agree with those of *rajah*.

Spiriferella unicostata Zhang (1976 , pl. 16, fig. 1, 2) might be conspecific with *S. sinica*. The sole figured ventral valve comes from Tibet, with no detail provided on critical morphological attributes, including the dorsal valve. The plicae are simple, the shape broad with incurved ventral umbo, the posterior walls convex in outline. The sulcus appears a little deeper and wider than in *sinica*, and the interspaces are wider as well. Shen et al. (2003a, p. 83) preferred a match with *nepalensis*-*qubuensis*, but the outline and length of the posterior walls do not appear to support this. Unless further topotypes can be discovered, the species may have to be abandoned, or at least pass into limbo. Basing a taxon on a single valve is certainly acceptable for some fossils in some circumstances, but not for spiriferellins of the Himalayan Permian.

Spiriferella sp. of Grunt & Dmitriev (1973, pl. 9, fig. 9) from the Kigiltass Suite of the Pamirs has posterior walls that are convex in outline, but the species is poorly known, and is of Sakmarian age.

Spiriferella nepalensis Legrand-Blain, 1977

Plate 8, fig. 6-8

1977 *Spiriferella nepalensis* Legrand-Blain, p. 242, text-fig. 7-11.
1977 *S*. aff. *rajah* not Tschernyschew Legrand-Blain, p. 245, text-fig. 4a,b, ?5 (part, not fig. 6a, b = *angiolinii*).
2001 *S. qubuensis* not Zhang Shen et al. p. 169, text-fig. 7.17-29, text-fig. 9.

HOLOTYPE: NP 136 bl, figured by Legrand-Blain (1977, text-fig. 7a, b) OD, from Permian of Nyi-Shang, probably from Late Permian Marsyangdi Formation, kept at Laboratoire de Géologie Historique, Paris.

DIAGNOSIS: Narrow elongate or transverse large shells, moderately inflated and weakly incurved ventral umbo, moderate to usually long posterior ventral walls generally concave in outline, hinge close to maximum width of shell, ventral interarea high. Narrow shallow sulcus with subgrooved floor, sulcus may widen anteriorly to 20°, dorsal fold low, narrow, with slender median groove, few costae. Plicae in 6-7 pairs, inner sulcal border pair rarely subdivided, apparently with anterior costae not branching, interspaces and plicae well spaced near umbo, but anteriorly the plicae become lower and broader, and interspaces narrower.

MATERIAL: A number of chiefly ventral valves are found in the Marsyangdi Formation of the Manang district in Nepal and will be described by Waterhouse & Chen (in prep.). Plaster replicates of the types and additional specimens have been provided by Dr Legrand-Blain.

DESCRIPTION: A dorsal groove is developed along the dorsal fold, as reported by Legrand-Blain (1977). It should be noted that some of the specimens of *nepalensis* were figured at less than natural size, and measurements were provided for the species in Legrand-Blain (1977, table 1).

RESEMBLANCES: This species is distinguished by its shallow narrow sulcus with somewhat angular cross-profile, and plicae which become lower and broader anteriorly, developing costae, whereas interspaces become narrow and grooved. This change in interspaces is the prime characteristic of the species. Plicae are fewer and lower than in *Spiriferella rajah*, and the fold is lower, and overall shape different. Manang specimens include a number that are more transverse with shorter posterior walls than in the types, but they show the same change in plication-interspaces as in the types and so are assumed to be infra-subspecific variants, and indeed shape is likely to have been affected by tectonic deformation. A moderately transverse specimen figured by Legrand-Blain (1977) as aff. *rajah*, from PL 136, is deemed to belong to *nepalensis*, because of its ornament.

Shen et al. (2001) ascribed a suite of specimens to *Spiriferella qubuensis* from Selong Group, in the Selong Xishan section at "beds" 6-10, 16, 17, and referred *nepalensis* to synonymy of the species *qubuensis*. Several of the Selong specimens carry simple especially anterior costae (text-fig. 7.25, 28, 29), suggestive of the longer costae figured for *nepalensis* (Legrand-Blain 1977, text-fig. 7a, 10b), and some of the shells figured by Shen et al. (2001) are elongate with long ventral posterior walls, indicating overall approach to *nepalensis*.

The species *Spiriferella nepalensis* is only superficially close to the species *qubuensis* Zhang, 1976, here described separately as a possible member of genus *Arcullina*. It is larger and less inflated with less incurved ventral umbo, and 1-2 more pair of plicae, and plicae and interspaces that change in nature anteriorly. Posterior walls are less convex in outline, plicae are more costate, the sulcus is rarely bordered by subplicae or prominent costae, and is more angular than concave in cross-section. *S. nepalensis* is younger than *qubuensis*, coming from the *Retimarginifera xizangensis* Zone, as compared with faunas equivalent to *Lamnimargus himalayensis* Zone for *qubuensis*.

Compared with *Arcullina oblata* Waterhouse, *Spiriferella nepalensis* has more costate plicae which with interspaces change anteriorly, more attenuated ventral umbo, longer posterior walls concave in outline, deeper and more concave sulcus, and grooved dorsal fold.

PUBLICATION DATE: The species *qubuensis* was published in December 1976, with no day indicated, and therefore 31 December. Shen et al. (2003a, p. 82) referred *qubuensis* to synonymy of *nepalensis*, on the basis that the two were conspecific, and on the basis that *nepalensis* was published before *qubuensis*. They stated that *nepalensis* had been published 7-10 December, 1976. This date refers to the conference dates on Himalayan Geology, and I assume a publication date in 1977, as confirmed by Dr. M. Legrand-Blain (pers. comm.). No date within the year was provided, so that the publication date was 31 December, 1977.

STRATIGRAPHIC SOURCE OF NEPALENSIS: The type specimens of *Spiriferella nepalensis* come from an uncertain stratigraphic level. Legrand-Blain (1977, p. 242) indicated the upper part of the Formation de Chulu, on what is here called “ridge A” above Chegaji Khola, and also the upper Thini Chu Formation at Thakkola. A reference to level F in Bordet et al. (1975, p. 89) is not explained in that work, and perhaps a critical digit was left out, or lost. On p. 88 in Bordet et al. (1975), *Spiriferella* and *Neospirifer* were recorded from F6, at the base of “unit 5” (see Bordet et al. 1975, text-fig. 51). Dr M. Colchen, through Dr M. Legrand-Blain, has clarified the stratigraphy. The fossils listed from F5 come in fact from level 4, and the fossils of 6 come instead from F5, above the diamictites. For the material illustrated by Legrand-Blain, fig. 7 (holotype) and 8 come from either level F5 or 6, and the remainder from level F5.

Dr Legrand-Blain kindly sent two specimens with matrix attached, and the matrix indicates Hongde Member in the middle of the Marsyangdi Formation. One specimen belongs to *nepalensis* (NP 136) and the other to *Spiriferella grunti* n. sp. (PL 157).

Spiriferella legrandblaini n. sp.

1916 *Spirifer rajah* not Salter Broili, p. 34, pl. 118 (4), fig. 19, pl. 119 (5), fig. 1-11, pl. 120 (6), fig. 1-6.

1978 *Spiriferella rajah.* Waterhouse, p. 39, pl. 3, fig. 14, 15 (part, not pl. 4, fig. 1-5, 6?, 7?, pl. 14, fig. 1-8, 11-13 = *rajah*, not pl. 14, fig. 9, 10, pl. 24, fig. 2 = *oblata*).

DERIVATION: Named for Marie Legrand-Blain.

HOLOTYPE: Specimen figured by Broili (1916, pl. 119 (5), fig. 4a, b, c) and Waterhouse (1978, pl. 3, fig. 14, 15), kept at Free University, Amsterdam, here designated.

DIAGNOSIS: Large shells characterized by broad interspaces between plicae which are moderately high and rather narrow, plicae in 5-6 pair on each valve, with lateral costae, plicae become moderately costate 15-20mm in front of umbo. Sulcus well formed, fold narrow and bearing median groove, fold broadens anteriorly. Hinge less than maximum width, may be very weakly projecting at cardinal extremities. Ventral interarea concave and not very high. Dental and adminicular plates moderately free of secondary thickening, although this is substantial.

DISCUSSION: Specimens of this species are described and well illustrated by Broili (1916), and plaster casts are available. *Spiriferella rajah* is somewhat similar in shape, with usually narrower sulcus and wider hinge. The plicae in the new species are narrower and more tented in section than the swollen convex plicae of *rajah*, and are separated by much wider interspaces in the Timor specimens. The plicae grade more laterally in size and height, whereas those of *rajah* tend to be narrow, high and simple. Some of the small specimens figured from Timor by Broili (1916) were excluded from synonymy by Shen et al. (2001), but available evidence suggests they are conspecific. They lack costae, but so do the large specimens over their early growth stages. Micro-ornament is preserved and described by Broili, the critical nature of the dorsal fold is well displayed, and the holotype, but no paratype, appears to have a delthyrial plate.

A possibly contemporaneous species was described as *Spiriferella orientensis* Archbold & Bird (1989, text-fig. 7A-N, 8A-H) from near Kasliu village, west Timor. This has even sharper fold and very sharply crested plicae and costae and more elongate outline.

Shells figured as *Spiriferella rajah* by Shimizu (1966, pl. 17, fig. 1-13) from Basleo equivalents in Timor have simple rather broad plicae or ribs. Archbold & Barkham (1989, p. 136) suggested the specimens belonged to *Elivina*, but they appear to have relied largely if not entirely on the subtriangular shape, and the fold is raised with apparent fine median slit, not suggestive of *Elivina*.

From nearby Late Permian beds at Ajer Mati, Timor, *Spirifer interplicata* Rothpletz (1892, pl. 9, fig. 6, a-c) is not regarded as conspecific. It is small, with fine costae commencing earlier on the broad and rounded plicae than in the new species, and displaying a grooved fold that widens more at the anterior margin, whereas the fold in the new species remains narrow for a much greater distance from the umbo. The sulcus has a median rib, and some 4 costae lie on the inner plicae at 18mm from the umbo. The delthyrial angle measures 90-100^{o}, and the cardinal extremities are weakly alate. The type material is kept at Utrecht. Rothpletz (1892, pl. 9, fig. 6c) showed micro-ornament for what might be the second specimen in the collection, so that the specimen of Rothpletz (1892, pl. 9, fig. 6, a, b) is cited as lectotype.

Spiriferella hoskingae (Archbold & Thomas, 1985a)

1985a *Elivina hoskingae* Archbold & Thomas, p. 44, text-fig. 3. (See for further references).

1993 *E. hoskingae* Archbold et al. pl. 42, fig. 15, 16, 21, 22.

HOLOTYPE: GSWAF 9187 figured by Archbold & Thomas (1985a, text-fig. 3F, G), Archbold et al. (1993, pl. 42, fig. 21, 22) and Waterhouse et al. (1978, pl. 3, fig. 8-11) from Callytharra Formation, Western Australia, OD.

DISCUSSION: This species has been well described by Archbold & Thomas (1985a). The generic position needs to be reassessed. Although the triangular shape strongly approaches that of *Elivina,* the greatly thickened ventral valve and the presence of fine pustules show that the species belongs to *Spiriferella*. The dorsal fold is obscure in the figure provided, but seems to be that of *Spiriferella*. To judge from the shell thickening in the ventral valve, *Spiriferella*? sp. of Legrand-Blain (1968, pl. 4, fig. 10, 11) is *Spiriferella*, not *Elivina* as supposed by Archbold & Thomas (1985a, p. 46). *Elivina yunnanensis* Shi, Fang & Archbold (1996, text-fig. 5D-M), based solely on ventral valves, belongs to Spiriferellinae, having pustules, but the genus could be either *Spiriferella* or *Arcullina*, with no dorsal valve known. It may be best called *Spiriferella? yunnanensis*, until the genus can be determined through discovery of dorsal valves.

Spiriferella grunti n. sp.

Plate 8, fig. 3-5

1976 *Spiriferella rajah* (not Salter) Zhang & Jin, p. 215, pl. 17, fig. 3-12.

2001 *S. rajah.* Shen et al. p. 167, text-fig. 6.1-11, 7.1-16, 8.

2001 *S. sinica* not Zhang Shen et al., p. 171, text-fig. 10.3-8 (part, not text-fig. 10.1, 2 = *Nakimusiella selongensis*).

DERIVATION: Named for T. G. Grunt.

HOLOTYPE: Specimen figured herein as Pl. 8, fig. 4, 5 from PMh5, Hongde Member, Marsyangdi Formation, crest of Chulu ridge B (see Text-fig. 11) and towards east side, here designated. Kept at Canterbury Museum.

DIAGNOSIS: Large transverse to subelongate species with incurved ventral umbo, posterior walls concave in outline, hinge comparatively narrow and may be alate, shape elongate, becoming very broad anteriorly, moderately well formed sulcus widening at 20^{o}, broad fold with costae and median groove, subplicae or innermost pair of plicae may be attached or separated only by narrow groove from flanks of the fold posteriorly and separate within 10mm, ventral inner plicae broad and prominent, 3-4 pair on ventral valve grading in size and well formed, lateral narrow subplicae and costae, 4 or so plicae pair on dorsal valve, ribs laterally.

MATERIAL: A number of ventral and dorsal valves, including specimens with valves conjoined, from Marsyangdi Formation, Manang. Further occurrences in Manang are enumerated in Waterhouse & Chen, in prep.

DIMENSIONS IN MM: holotype, slightly distorted

Width	Length	Length dorsal	Height ventral	Height dorsal	Hinge width
49	49	42	19	7	27

DESCRIPTION: Specimens of the Nepal suite moderately large, subelongate or equidimensional, umbonal angle of 90º, posterior walls steeply convex in section, sulcus commences at umbonal tip and widens at angle of 20º. Dorsal valve little inflated, with broad rounded fold standing a little above rest of shell and bearing narrow median groove. Maximum width placed well forward, hinge weakly alate, ventral interarea gently concave, with open delthyrium having angle of 45-50º, no delthyrial covering preserved, but no umbonal callosity. Plicae number generally 3-4 well developed pair and 4-7 lateral subplicae on ventral valve, also 3-4 pair and further 4-6 lateral costae or subplicae on dorsal valve, innermost pair commences on flank of fastigium some 10mm from beak. One specimen has the innermost plicae separate from the fold, and the fold is very broad anteriorly, possibly signalling a different taxon or damage. Costae prominent, generally a median costa along sulcus, additional costa each side from about mid-length, especially prominent along inner side, may bifurcate anteriorly. Innermost plicae with 2-3 costae, often central costa with broad and gently convex crest, some plicae bear 5 costae of subequal strength; lateral shell with a number of costae. Dorsal fold carries medium slit for full length, and 3 costae each side anteriorly. Plicae bundled with 3-5 costae, and a few costae cover shell laterally. Shell crossed by low concentric growth increments, 6 per mm, crossed by fine radial threads forming low pustules, very tiny and probably involving only single growth increments.

Ventral teeth supported by sturdy short dental plates which converge on short adminicula, largely to completely buried in secondary shell which is almost 10mm thick posteriorly. Adductor scars form low ridge between diductors in smallest of internal moulds, marked by finer longitudinal striae compared with coarser grooves over diductors. A larger specimen has two well formed adductor ridges separated by groove, and broad longitudinally striated diductors to each side. Posterior shell to each side bears low pustules.

RESEMBLANCES: This species is close in overall shape, inflation, ornament and dorsal fold to *Spiriferella rajah* (Salter). It is distinguished by its wider sulcus, with an angle of 20º, as compared to 12º average for *rajah*, and fewer, mostly 3-4, pair of prominent plicae, followed laterally by fine subplicae or coarse costae, as compared with up to 5-7 pair in *rajah,* followed by coarse costae. The fold is different in *grunti*, being much broader and more costate over the central portion. *S. rajah* (Salter) has a narrower and deeper sulcus, narrower higher fold, and more numerous narrower dorsal plicae with fewer costae, and narrower interspaces, judged from comparison with type and other Kashmir material. Specimens from the Nisal, Luri and Pija Members of the Senja Formation referred herein to *Spiriferella rajah* are slightly more elongate and less broad anteriorly, with slightly shallower and narrower ventral sulcus and lower dorsal fold, but the fold does show some approach. The ventral valves named *subsalteri* Shen et al. (2003a, pl. 11, fig. 18-22) from the lower Qubuerga Formation are moderately close to *grunti*, with narrower sulcus like that of *rajah*, and less elongate shell, and 5 pair of plicae. Attributes of the dorsal valve are not known. The species *S. grunti* seems likely to have evolved from *Spiriferella rajah* and is not very close in shape, sulcus-fold and ornament to *S. sinica* Zhang.

A species that is moderately close was described as *Spiriferella nepalensis* Legrand-Blain from the Marsyangdi Formation of Nepal. The two species evidently co-existed. Legrand-Blain's species has a narrower, lower, and less costate fold, often longer posterior walls and more extended ventral umbo, shallower narrower sulcus, and higher ventral interarea. The plicae and interspaces in *nepalensis* change anteriorly, the interspaces becoming shallower and the plicae becoming broader, but this change is not so well developed in *grunti*.

The new species is deemed to include the material or most of the material described as *Spiriferella rajah* and *S. sinica* from the Selong Group in the Selong Xishan section by Shen et al. (2001). These specimens are close in sulcus and shape, may have a wider or comparable hinge, and show similar costae and fold. The specimens are large like a number of Nepal specimens. The dorsal fold appears to have a median slit (Shen et al. 2001, text-fig. 7.6) and innermost plicae are attached posteriorly or placed very close to the fold. The shells have similar large ventral muscle field and some show a number of lateral plicae, as in shells from Nepal locality PMh5, Hongde Member. Shells ascribed to *S. rajah* from south Tibet by Zhang & Jin (1976, pl. 17, fig. 3-12), mostly at localities JSQ 3, 4, 5, 9, 10, 11, 12, appear to be conspecific.

The species *Spiriferella qubuensis* Zhang (1976, p. 212, pl. 18, fig. 1-5; Shen et al. 2003a, pl. 11, fig. 7-17) from the lower Qubuerga Formation of south Tibet differs from *S. grunti* in being elongate with prominent ventral umbo, long posterior walls and usually well defined rib along each side of the sulcus. Plicae have few costae. It might belong to *Arcullina*.

A specimen with valves conjoined from the "Waagenites Bed" at the top of the Selong Group in the Selong Xishan section was figured as *Spiriferella rajah* by Shen & Jin (1999, text-fig. 3.17-20) and Jin et al. (1996, pl. V2, fig. 17-20). It has comparatively well defined costae and plicae, and apparently high broad fold. A ventral valve figured as *S. nepalensis* not Legrand-Blain by Shen & Jin (1999, text-fig. 4.4) has at least 7 pair of plicae, and differs from *nepalensis* both in this feature and in its greater width. Its identity is difficult to decipher without first-hand examination, or further elaboration of its attributes.

Genus ***Arcullina*** Waterhouse, 1986a

TYPE SPECIES: *Spiriferina polaris* Wiman, 1914, p. 39.

DIAGNOSIS: Small to medium-sized Spiriferellinae distinguished by having entire dorsal fold without median groove. Plicae well developed, costae few, micro-ornament pustulose.

DISCUSSION: This is a bitemperate genus, with species recognized in paleotemperate latitudes of both hemispheres. Kalashnikov (1998) ascribed three Russian species to the genus; one species is known in New Zealand, and others in Western Australia and Thailand (Waterhouse 2001). At least three species are developed in the Late Permian of the Himalaya, and their recognition substantially clarifies the affinities and species limits within Spiriferellidae of the Himalaya.

Arcullina kupangensis (Beyrich, 1864)

1864 *Spirifer kupangensis* Beyrich, p. 78, pl. 1, fig. 6a, b, c.

cf. 2003b *Elivina tibetana* (not Diener) Shen et al., p. 244, pl. 4, fig. 7-10.

HOLOTYPE: Sole specimen figured by Beyrich (1864), by monotypy. Its whereabouts are not known to me.

DIAGNOSIS: Subelongate shells with comparatively narrow hinge, long posterior walls somewhat concave in outline, and plicae with few or no costae, fold with entire crest, sulcus with median and flank ribs.

DISCUSSION: This species was described from Kupang, Timor. The geological setting was not provided in modern terms, but various of the illustrated species, such as *Bicamella timorensis* (Hayasaka & Gan) figured by Beyrich (1864, pl. 1, fig. 11, 12), suggest a Basleo or correlative source. The specimen of *kupangensis*, figured as being complete, is closely similar to material referred to *Spiriferella qubuensis* Zhang, 1976, apart from smaller size. The illustration suggests a subplication along the inner side of the plicae bordering the sulcus.

Shen et al. (2003b) recorded somewhat similar material from an exotic block of Wuchiapingian age in the Indus-Tsangpo suture zone of south Tibet. The shell is elongate and highly inflated with long posterior walls gently concave in outline, at least 4 pair of simple plicae on each valve, sulcus narrow with median rib and boundary ribs on flanks, and fold simple with rounded crest. Although ascribed to *Elivina tibetana*, the fold is not made up of two strong costae separated by a median groove that is characteristic of *Elivina*. The specimen is close to *Arcullina kupangensis* (Beyrich), and only slightly more inflated, with thinner median rib, and ventral valve extending further beyond the dorsal valve. *A. oblata* (Waterhouse) has more attenuate ventral umbo and wider hinge and lower inflation, with more pairs of plicae, and *A? qubuensis* (Zhang) is particularly close, and possibly conspecific.

Broili (1915, pl. 21, fig. 17a, b, 18) figured material from Letti that has extended posterior walls, anterior placed well forward, narrow well defined sulcus, a number of slender plicae, fine costae, and entire dorsal fold. It constitutes an unusual species of *Arcullina*, but the whereabouts of the specimens is not known to me.

Arcullina? qubuensis (Zhang, 1976)

Plate 8, fig. 9-11

?1962 *Spiriferella salteri* not Tschernyschew Ding, pp. 455, 462, pl. 3, fig. 2a-c.
1976 *Spiriferella qubuensis* Zhang in Zhang & Jin, p. 212, pl. 18, fig. 1-5.
?1983a *S. oblata* not Waterhouse, Waterhouse p. 135, pl. 6, fig. 7-10.
2003a *S. nepalensis* not Legrand-Blain Shen et al., p. 81, pl. 11, fig. 7-17, text-fig. 12.

HOLOTYPE: IGAS 00933 figured by Zhang & Jin, 1976, pl. 18, fig. 4, 5, from lower Qubuerga Formation, south Tibet, OD.

DIAGNOSIS: Highly inflated shells with strongly incurved ventral umbo, posterior ventral walls generally moderately long, concave or convex in outline, hinge close to maximum width of shell. Narrow and moderately shallow sulcus. Plicae in 4-5 prominent pairs and possibly costae laterally, inner sulcal border pair generally subdivided along sulcus, median sulcal costa often present, costae rare, anterior and not branching. Dorsal valve not so far figured or described amongst type material, but possibly with moderately wide hinge, non-costate plicae and simple fold without median groove, bordered by costa on each side at base.

DISCUSSION: This species is tentatively deemed to belong to *Arcullina*, but the dorsal valve has not been described amongst the types by Zhang (1976) or Shen et al. (2003a), so that the generic position is insecure. However Zhang (1976) included a specimen with valves conjoined in his synonymy for *qubuensis*, though this was left out by Shen et al. (2001, 2003a). This specimen was figured as *Spiriferella salteri* Tschernyschew by Ding (1962, pl. 3, fig. 2a-c). It has an inflated ventral valve with incurved ventral umbo, narrow sulcus with median rib, and 5 pair of simple plicae with bordering rib each side within the sulcus. The dorsal valve has a simple fold, as in *Arcullina*. At the base of the fold on each side is a bordering rib. The hinge width is moderate. Should this specimen be deemed conspecific with *qubuensis*, as seems likely, then *qubuensis* may be referred to *Arcullina*. The Ding specimen was described from the lower Qubuerga Formation of south Tibet, equivalent to the *Lamnimargus himalayensis*

Zone, and is readily distinguished from *Spiriferella salteri* Tschernyschew (1902, p. 528, pl. 12, fig. 5, 6) described from Cisuralian beds of the Urals, and also Timan (Barkhatova 1970, pl. 19, fig. 6, 7, 9-14). The Russian species has a massive incurved ventral umbo, wide alate hinge, and grooved dorsal fold as in *Spiriferella*. The Tibet specimen belongs to *Arcullina*. The species comes very close to *Arcullina kupangensis* (Beyrich), of the same age, although displaying a more incurved umbo and wider plicae, and subdued median sulcal rib in only some specimens: conspecificity cannot be ruled out, without further clarification of *qubuensis*.

Of other species found in the Late Permian faunas of the Himalaya, *Arcullina oblata* (Waterhouse, 1978) comes closest in size, appearance and ornament. This has a described dorsal valve, the nature of which which indicates placement with *Arcullina.* The species *qubuensis* appears to have a narrower hinge, though this is not fully certain because of the limited nature of description and illustrations for the species. It has a more prominent sulcal border pair of ribs, often missing in *oblata*, a more inflated ventral valve with more incurved umbo, and often posterior walls that are more convex in outline. A low rib lies along the flanks of the fold in some specimens. The species *qubuensis* comes from equivalents of the *Lamnimargus himalayensis* Zone, whereas *oblata* comes from the *Biplatyconcha grandis* Zone. Specimens from the intervening *Lazarevonia arcuata* Zone in the Pija Member of Manang have the prominent sulcal ribs (Waterhouse 1983a), and so are provisionally referred to *qubuensis,* but do lack the median sulcal rib. Pija material shows the micro-ornament well.

Spiriferella subsalteri Shen et al. (2003a) comes from much the same stratigraphic level as *qubuensis*, but is wider with broader costate plicae and so does not look very close.

Shen et al. (2003a) also figured a suite of ventral valves - no dorsal valves - from the lower Qubuerga Formation of south Tibet, and these differ from the type and other Tibetan shells in having long posterior walls that as a rule are convex in outline. The specimens were referred to *Spiriferella nepalensis*, regarded by Shen et al. (2003a) as senior synonym for *qubuensis*. The specimens are smaller than *nepalensis*, and more inflated, with more incurved ventral umbones, coming close in these respects to type *qubuensis.* The sulcus is slightly less narrowly subangular in cross-section than in *nepalensis*, and has a fine sulcal median rib in some specimens, the bordering pair of ribs is better developed, the interspaces wider, and the plicae less costate. In these respects, and notwithstanding the more convex ventral posterior walls, the Qubuerga shells are identical with type *qubuensis*, and differ from type *nepalensis*. The specimens described as *qubuensis* by Shen et al. (2001) on the other hand are close to typical *nepalensis*, rather than *qubuensis*.

Two small and obscure specimens from the *Lamnimargus himalayensis* Zone of west Dolpo, figured as *Spiriferella rajah* from the Nangung Formation by Waterhouse (1978, pl. 4, fig. 6, 7), might be related, but have a simple sulcus and fold without median groove, and apparently no sulcal bordering costae.

Shen & Jin (1999, text-fig. 4.4) reported *Spiriferella nepalensis* from the “Waagenites Bed” at Selong Xishan, and synonymized *S. qubuensis* Zhang with *nepalensis*, but *qubuensis* has priority. They also reported somewhat similar specimens as *S. rajah* (Shen & Jin 1999, text-fig. 3.17-20), and reported a narrow groove along the dorsal fold. The Tibet specimens are less elongate with shorter ventral posterior walls than in some of the type *nepalensis*, and have few costae with wide interspaces and dorsal fold widely sulcate and bearing a median costa. They show little similarity to *S. rajah*, differing in shape, hinge, sulcus and fold as well as other morphological aspects, and are of uncertain identity.

Elivina bisnaini Archbold & Barkham (1989, p. 132, text-fig. 6A-Z, AA-LL) from the Early Permian Cisuralian Series of west Timor is shaped like *Elivina*, but shows the attributes of *Spiriferella,* including thick shell and pustules. The nature of the dorsal fold, figured only in text-fig. 6.P, Y, is obscure. The species somewhat approaches *S. qubuensis* Zhang in shape and ornament, but is distinguished by size and in having more costae on the sulcal plicae. Archbold & Barkham (1989, p. 136) judged *Spirifer rajah* of Broili (1915, pl. 21, fig. 11a, b - not fig. 17a, b, 18 = *Arcullina*) to be *Elivina*, but it has a fastigium typical of *Spiriferella*. The plicae of Broili’s specimen are narrower than in *S. legrandblaini* n. sp. from Timor. The species *bisnaini* has fewer and coarser plicae than in the *Arcullina* figured by Broili (1915).

Arcullina oblata (Waterhouse, 1978)

1966 *Spiriferella tibetana* (not Diener) Waterhouse, p. 52, pl. 12, fig. 3, 4, pl. 13, fig. 1, 2, 4 (part, not pl. 2, fig. 2, pl. 9, fig. 3, pl. 13, fig. 5 = *rajah*).

1978 *S. oblata* Waterhouse, pp. 89, 123, pl. 14, fig. 15-18, pl. 24, fig. 3.

1978 *S. rajah* (not Salter) Waterhouse, pp. 88, 123, pl. 14, fig. 9-10, pl. 24, fig. 2 (part, not pl. 3, fig. 14, 15 = *legrandblaini*, not pl. 4, fig. 1-5, 6?, 7?, pl. 14, fig. 1-8, 11-13 = *rajah,* not pl. 4. fig. 6, 7 = *Arcullina* sp.).

HOLOTYPE: UQF 68960 figured by Waterhouse (1978, pl. 14, fig. 14, 15) from Nisal Member, Dolpo, OD.

DIAGNOSIS: Shells with moderate to long posterior ventral walls, wide hinge, simple plicae numbering 5-7 pair, may be costate anteriorly. Sulcus narrow with angle close to 12-15^{o}, fold entire or laterally costate, inner plicae simple or subdivided.

DISCUSSION: The holotype has been crushed laterally, but shows both valves. Accompanying dorsal valves show the wide hinge.

This species has been forced through vicissitudes of misinterpretation. It has a rounded dorsal fold with no median groove, and is a member of *Arcullina*, not *Spiriferella*. Together with *nepalensis* Legrand-Blain, the species *oblata* was lumped with *qubuensis* Zhang by Shen et al. (2001, 2003a). The original type material of both *nepalensis* and *oblata* is much better known than the original types of *qubuensis*. The species *oblata* belongs to *Arcullina*. If the present interpretation is correct, based on a Ding specimen, *qubuensis* also belongs to *Arcullina.* In *oblata*, the hinge is wider than in *qubuensis*, the dorsal valve is more transverse, possibly an extra pair of plicae present, the two plicae bordering the sulcus are often not subdivided, and the ventral umbo is less enrolled and less massive than in *qubuensis*. The dorsal fold has a costa each basal flank of the fold in the Ding specimen, here assigned to *qubuensis*, but these costae are sometimes present, sometimes absent from *oblata*. Differences are not great, and both *qubuensis* and *oblata* could arguably be gathered within *kupangensis*.

The species *Arcullina oblata* is typical of the Nisal and Luri Members of Dolpo, and in the Galte Member in Manang, in the *Biplatyconcha grandis* Zone.

Arcullina angiolinii n. sp.

Plate 9, fig. 1-4, Text-fig. 36

1977 *Spiriferella* aff. *rajah* (not Salter) Legrand-Blain, p. 245, text-fig. 6a, b (part, not fig. 4a, b, 5? = *nepalensis*).

DERIVATION: Named for Lucia Angiolini.

HOLOTYPE: Specimen figured herein as Pl. 9, fig. 1-3, Text-fig. 36 from PMb2, Braga Member, Marsyangdi Formation, northwest side of Chulu ridge A, here designated. Kept at Canterbury Museum.

DIAGNOSIS: Moderately large shells with generally elongate outline, prominent ventral umbo, wide hinge and entire dorsal fold; plicae in 5-7 pairs, simple or closely costate over inner pairs, sulcus variable, narrow or moderately wide and well defined to deep.

MATERIAL: Many specimens including dorsal as well as ventral valves from Marsyangdi Formation, Manang, including material figured herein from PMb5 - Braga Member, crest and some 20m east of Chulu ridge B, PMh5 - Hongde Member, crest of Chulu ridge B and towards east side, and PMg3 - Gungsang Member, south end of Chulu ridge A.

DIMENSIONS IN MM:

Width	Length	Height
52	50	20
60	48	15
27	42	12
70	35	14

DESCRIPTION: Ventral umbo broad to attenuate and slender, hinge moderately wide with bluntly obtuse extremities and high concave ventral interarea, disrupted by a large open delthyrium. Dorsal valve moderately inflated with low interarea and wide notothyrium. Sulcus commences at the umbo, generally narrow at 12-15^{o}, angle up to 22^{o}, fastigium moderately high, with rounded crest. Plicae number 5 to generally 6 or 7 round-crested ventral pairs with narrow interspaces, gradually diminishing laterally in size and strength, and the sulcal border pair of plicae are generally subdivided, with firm rib along sulcal side. Dorsal valve has 3-5 pair of plicae with narrow crests and wide interspaces, inner plicae complexly costate as a rule, costae may lie over only the innermost pair, or on the inner 2-3 pairs, or involve 4th and 5th pairs as well. In a few transverse specimens the costae have broad flattened crests. A rib extends along the sulcus. Dorsal fastigium is bordered laterally over anterior half by subplication and raised anteriorly: second strong costa or subplication arising near umbo and second inner pair arising anteriorly. Next three plicae carry inner costa arising anteriorly, and outer costa arising before mid-length of plication. Outer cardinal extremities on both valves either smooth, or more usually faintly or closely costate. Micro-ornament consists of fine radial and stronger transverse capillae, 4-6 in 1mm, with small pustules.

Ventral valve with short adminicula and dental plates largely buried in secondary thickening, posterior wall carries low and short median ridge but no large umbonal callosity; no delthyrial plate preserved in mature specimens. Muscle field moderately large, with weakly defined adductors and diductors, both traversed by longitudinal grooves and ridges, short myophragm may be present posteriorly, oblique ridges parallel to anterior lateral margins over diductor impressions. Floor with short pits.

A small specimen 15mm wide has well defined adductors and separate diductor scars; delthyrial plate over upper delthyrium. Adminicula subvertical and diverging narrowly; dental plates high and not diverging widely from adminicula. Little of dorsal interior preserved.

RESEMBLANCES: A specimen drawn as aff. *rajah* from the Manang region by Legrand-Blain (1977, text-fig. 6) appears to have a broad deep sulcus and well formed plicae as in *angiolinii*, with well developed concentric lirae, judged from a plaster duplicate. Other figured specimens aff. *rajah* are close in sulcus and ornament to *nepalensis*. The critical dorsal valve was not figured. The text recorded a groove on the dorsal fold, presumably for *nepalensis.*

The species *Arcullina angiolinii* is associated with *Spiriferella grunti,* which is a more costate form with broad ventral umbo, higher more angular ventral subplicae and deeper interspaces, wider dorsal plicae with narrower interspaces, and grooved dorsal fold. The species is also accompanied by *S. nepalensis*, which is distinguished by its shallower and narrower sulcus, shallower interspaces and plicae which change in relative depth and width from umbo to anterior, and grooved dorsal fold.

Text-fig. 36. *Arcullina angiolinii* n. sp. , dorsal valve of holotype, x 1 approx., from PMB2, Braga Member, Marsyangdi Formation. 1 = anterior end of fold, u = umbo.

In many respects the specimens are close to *Arcullina qubuensis* (Ding) and *A. oblata* (Waterhouse, 1978) in the restricted narrow sulcus, number of plicae with inner sulcal plicae subdivided in some specimens, and round-crested fastigium. What distinguishes the present form is the larger size, more costate nature of the plicae, and narrower dorsal plicae with wider interspaces and different fold with more complex ribbing. As well, the species is more variable in shape and width of sulcus. A number of the specimens from the Selong Group of the Selong Xishan section, south Tibet, ascribed by Shen et al. (2001, text-fig. 7.1-16) to *Spiriferella rajah* (not Salter) fall moderately close to transverse specimens of the present form. But the nature of the dorsal valve was not described, and plicae tend to be less conspicuous, and the dorsal fastigium illustrated in Shen et al. 2001, text-fig. 7.6 suggests a low median slit, indicative of *Spiriferella*, and the species *grunti*.

Genus ***Canalisella*** n. gen.

DERIVATION: canalis, groove - Lat.

TYPE SPECIES: *Spiriferella leviplica* Waterhouse & Waddington, 1982, p. 26, here designated.

DIAGNOSIS: Close to *Spiriferella*, with hinge shorter than maximum width and obtuse cardinal extremities, fold bearing well formed groove for full length, plicae moderate in number, costae generally few, may be missing from fold.

DISCUSSION: Whereas *Spiriferella* is characterized by moderately well developed fastigium bearing a narrow groove for its full length, the fastigium on the present genus has a broader more strongly defined groove. It is the depth and width of the groove that constitutes the prime discriminant. As well, plicae in *Canalisella* are often smooth, without costae, but individuals in collections may be costate. In other respects, involving shape, micro-ornament and internal detail, the genus is close to *Spiriferella*. The groove along the fold is even more strongly developed in genera such as *Alispiriferella* Waterhouse & Waddington, 1982, and to less extent in *Timaniella* Barkhatova, 1968, but these genera have hinge at the maximum width of the shell and alate cardinal extremities, imparting a different appearance.

The type species *leviplica* is found in the late Guadalupian Degerbols and Van Hauen Formations of Ellesmere Island, Canadian Arctic Archipelago, with somewhat allied material known from the early Guadalupian faunas of the Tatonduk Formation of Yukon Territory. *Spirifer parryana* Toula, 1875 (not Hall 1858), renamed *S. loveni* by Diener (1903, p. 17), is related. *Spiriferina hoeferiana* Toula (1874, p. 35, pl. 1, fig. 1a-d) from Spitsbergen is possibly a senior synonym for *loveni*, as discussed by Waterhouse & Waddington (1982, p. 28). Further allied material is discussed by Waterhouse & Waddington (1982, pp. 22-26, 28, left upper column.) From the Zhesi Formation of Inner Mongolia, *Elivina* - now *Canalisella - sinensis* Liu & Waterhouse (1985) is a member of the genus, with well developed groove along the dorsal fold, and unusually elongate outline with prominent ventral umbo and high cardinal interarea. Costae are few.

PUBLISHING COMMENT: The publication of the study of Spiriferellinae by Waterhouse & Waddington (1982), despite our careful proof-reading, came out muddled, and far from easy to interpret. One critical text-figure was replaced by an older version. The text on *Spiriferella leviplica* starts in the lower right hand column of p. 26, and then jumps to the left hand column of p. 29. The discussion of *keilhavii* von Buch starts on the right column of p. 28, and reverts to the whole of p. 27, and then left hand column of p. 26. The description of *S. ?loveni* starts on p. 22, through p. 23, 24, 25, and ends in the left column of p. 28. Evidently the printers got confused, and the text was too technical for the editors to unravel. They distributed a statement purporting to correct the text, but the statement was not correct.

Genus ***Bamberina*** n. gen.

DERIVATION: Named for E. W. Bamber.

TYPE SPECIES: *Elivina*? *annectens* Cooper & Grant, 1976, p. 2242, here designated.

DIAGNOSIS: Small shells with very narrow hinge and triangular cardinal interarea, open delthyrium, moderately inflated ventral valve, little inflated dorsal valve, sulcus shallow with median groove, may be deep anteriorly, fastigium low posteriorly, broad and scarcely to well distinguished anteriorly, principally represented by two parallel costae with intervening groove, and with additional costae anteriorly, contributing as a rule to only a slight to moderate change in transverse convexity of the valve. Low and distinctive moderately broad plicae developed on both valves as two pair with bundles of 3 costae each side of sulcus and fold; lateral shell covered by some 6 or more costae, rarely bifurcate, dorsal valve with costae, some bifurcate. Micro-ornament of concentric growth lines, with fine radials in interspaces, and scattered pustules. Ventral valve with dental plates and adminicula that extend as low ridges for most of length of ventral muscle field, dental plates joined below delthyrium, may carry low callosity; little or no secondary thickening. Dorsal valve has well formed sockets with inner sides of plates bearing small thick crural plates, low median septum between adductors.

DISCUSSION: The type species of this genus is found in the Hegler?, Pinery, Rader and Lamar Members of the Bell Canyon Formation. It is well preserved, with two pairs of prominent costate plicae on the ventral valve, costae in twos or threes, and two pairs of very subdued dorsal plicae with bifurcate costae. Small pustules are developed rarely. There is virtually no secondary thickening, and Cooper & Grant (1976, p. 2242) stated that a pseudodeltidium, nature unexplained, covered the delthyrium.

Cooper & Grant (1976) considered that the species was exceptional, and morphologically intermediate between *Spiriferella* and *Elivina*. The genus is deemed to be spiriferellin rather than an ally of *Elivina*, contrary to Cooper & Grant (1976). The genus does approach *Elivina* in terms of its overall shape, short interarea, and predominant ornament of subplicae or costae, but unlike that genus, plicae with bundled costae are developed each side of the sulcus and fold, and pustules are present in the micro-ornament. Chief differences from *Spiriferella* and other close allies involve the very short hinge and triangular interarea, restricted number of plicae confined to two pair on each valve, very low fold as a rule, and lack of secondary thickening. The genus somewhat approaches members of Purdonellinae, but has pustules.

Hunzina Angiolini is close in plication and costae, but lacks pustules, and possibly lacks a median groove from the fastigium, which is much more prominent. Internal plates, including adminicula, are short.

Bamberina cordiformis (Waterhouse & Waddington, 1982)

1982 *Elivina cordiformis* Waterhouse & Waddington, p. 34, pl. 8, fig. 1-7, text-fig. 16j.

1988 *E. cordiformis*. Abramov & Grigorieva, p. 161, pl. 29, fig. 6-8.

HOLOTYPE: GSC 27034 figured by Waterhouse & Waddington (1982, pl. 8,

fig. 1-3) from north Richardson Mountains, Yukon, Canada, OD.
DISCUSSION: *Elivina cordiformis* Waterhouse & Waddington (1982) is regarded as a member of *Bamberina*. It displays two pair of low plicae, especially well illustrated for the smaller figured paratype (Waterhouse & Waddington 1982, pl. 8, fig. 6, 7, text-fig. 16j). The plicae fade anteriorly on the holotype, and they may split into two or sometimes three costae. There is virtually no secondary thickening, and micro-ornament includes concentric growth-increments, but is poorly preserved. The species is exceptional in having an incurved ventral posterior, and unusually deep and wide sulcus anteriorly. A rib lies along the sulcus. The fastigium in the smaller specimen is formed by two upstanding costae in parallel, and the large specimen has an array of additional costae diverging over the median part of the dorsal valve, and opposed to the ventral sulcus. This species is striking in aspects of its hunched ventral umbo and profound angular sulcus, and Angiolini (2001) noted an approach to *Spiriferella* rather than *Elivina*. It comes from beds of probable Guadalupian age in the North Richardson Mountains, Yukon Territory. Abramov & Grigorieva (1988) recorded the species from the Echisk Suite of west Verchoyan.

Elivina tschernyschewi Waterhouse & Waddington (1982, p. 33) from the Early Permian of the Urals is based on material figured as *tibetana* by Tschernyschew (1902, pl. 7, fig. 2-6). The plate number for the holotype was incorrectly cited - it is pl. 7, not pl. 17 as quoted by Waterhouse & Waddington (1982), as also noted by Archbold & Barkham (1989, p. 136). The species looks somewhat like *Bamberina* in shape, but has more plicae especially on the dorsal valve, and slightly less incised sulcus, and so probably belongs to *Spiriferella*: Angiolini (2001) has pointed out that the shells are plicate as in *Spiriferella* (see Tschernyschew 1902, pl. 7, fig. 2c, 3c). No pustules are present, but preservation of surface ornament is poor.

Eliva timorensis Archbold & Bird (1989, text-fig. 9A-N) has a similar grooved sulcus and short hinge, with little internal thickening. An inner pair of plicae are suggested in figures of the ventral valve, with perhaps a weak second bundling. The fastigium is weakly defined and low, with narrow median slit. The micro-ornament of radials and apparent pustules and other aspects of shape and ornament suggest that the species belongs to *Bamberina*. It comes from the Maubisse Formation, near Kasliu, West Timor, and equivalent to the Basleo fauna.

Subfamily **HUNZININAE** Angiolini, 2001

[Hunzininae Angiolini, 2001, p. 332].

DIAGNOSIS: Hinge narrow, delthyrium open or partly to completely closed by plate or plates, stated to be stegidial, lateral slopes with only one or two plicae pair, dorsal fastigium moderately well formed, not fully known, considerable secondary thickening in ventral valve. Micro-ornament predominantly concentric.
DISCUSSION: *Hunzina* is close to *Spiriferella* and allies, but is said to lack pustular micro-ornament and rarely shows radial filae. Angiolini stated that lateral slopes were non-plicate, and ornamented by bifurcating costae which rarely form fascicles, but *Hunzina* has ventral valves that are plicate in the sense used herein for *Spiriferella* and *Arcullina,* and the innermost plicae are well formed in the ventral valve, perhaps less so in the dorsal valve. Angiolini also included the genus *Darbandia* Angiolini, 2001, but this genus seems to be purdonellin (see p. 195).
GENUS: *Hunzina* Angiolini.

Genus ***Hunzina*** Angiolini, 1995

TYPE SPECIES: *Hunzina electa* Angiolini, 1995, p. 186.
DIAGNOSIS: Medium-small, sulcus well formed, bordered by one or usually two pair of costate or subcostate plicae and a number of narrow subplicae or strong single costae laterally. Dorsal valve with raised and round-crested fold, possibly no median groove, though this remains uncertain, lateral subplicae narrow, rarely costate. Micro-ornament predominantly of transverse filae, no pustules.
DISCUSSION: *Hunzina* Angiolini, 1995 is based on *H. electa* Angiolini, 1995 of Cisuralian age in the Karakorum Range. Angiolini (1995) regarded the genus as distinguished by its lack of a convex deltidial plate across the delthyrium, unlike specimens of *Spiriferella saranae*. Also it was noted that the ventral plates were short and covered by apical callus, and that ornament involved fine to coarse costae, rarely fasciculate. Sections provided by Angiolini (1995), confirm that adminicula are short and embedded in secondary shell. Species from Western Australia, including *Spiriferella cundlegoensis* Archbold & Thomas, *S. australasica* (Etheridge) and *S. etheridgei* Archbold & Thomas were referred to *Hunzina* by Angiolini (1995). These are well preserved, and show 4-5 pair of plicae, pustules in the micro-ornament, heavy secondary thickening, and an umbonal callosity: they seem to belong to *Spiriferella* and *Arcullina* as interpreted herein (Waterhouse 2001, p. 96).

Shen et al. (2001, pp. 165, 167) rejected the significance of the presence or absence of a delthyrial cover (“pseudodeltidium”), because there are such uncertainties over the likelihood of its preservation. They stressed the shortness of the curved hinge-line, the strongly incurved beak, low and inconspicuous plications with fine costellae, narrow and shallow sulcus, fairly elongate outline and strongly extended triangular anterior portion as prime descriptors for *Hunzina*. Their analysis was based on two specimens of *Hunzina electa* sent to them. These specimens (Shen et al. 2001, text-fig. 5.19-24) show a hunched elongate shell with swollen posterior valve and incurved ventral umbo. But the type and figured specimens in Angiolini (1995, pl. 3, fig. 11-23, pl. 4, fig. 1-14) suggest that such an analysis was in need of expansion. Many shells are wide, with no hunched posterior, and with ventral umbones not strongly incurved; some shells have a well formed sulcus, in some costae are moderately well developed on plicae, in others, missing; in none is the hinge unduely narrow, although it must be allowed that few figures show the hinge, and few of the ventral valves are unduely elongate. Nor is it likely that such criteria are powerful indices of generic as opposed to specific distinction.

The designated holotype for *Hunzina electa*, MPUM 7439 (Angiolini 1995, pl. 3, fig. 13, 14), is a ventral valve as wide as long, with slightly incurved ventral umbo, costate plicae in two pair and strong costae (or narrow simple subplicae) laterally, moderately narrow and moderately deep ventral sulcus, and interspaces narrower than plicae. In other specimens figured by Angiolini, the ventral valve has a broad costate inner pair of plicae, and narrow numerous lateral simple radial ribs. The sulcus is narrow. The dorsal valve in Angiolini (1995, pl. 4, fig. 19) lacks a median groove, whereas it has a median groove in pl. 14, fig. 18. This must raise the question about conspecificity. All known *Elivina, Eridmatus, Spiriferella, Bamberina*, *Quispira* and *Dissimiliplica* carry a median groove along the fastigium. The numerous specimens figured as *electa* by Angiolini (1995) come from an array of localities, not shown in maps or sections, and suggest, *if* conspecific, a diversity of features, or more likely, that two species and two genera are involved.

Material figured by Shen et al. (2001, text-fig. 5. 20, 23) is difficult to interpret, and the fold seems to carry a median groove, though this is far from certain. The specimens have a number of simple plicae, with a few anterior costae.

Later another critical aspect was uncovered: the fact that micro-ornament lacked pustules (Angiolini 2001), counter to the claim in Angiolini (1995, p. 186) that pustules were present. This marks a significant difference from *Spiriferella* or its allies. It also signifies a significant difference from *Arcullina*, which has a fastigium that lacks a median groove. So far no illustration has been provided to show the micro-ornament.

Bamberina n. gen. is close in the development of two pair of lateral plicae.

The fold is lower and grooved, micro-ornament includes radial filae and pustules, and adminicula are longer.

Spirifer tibetanus var. *tenuisulcata* Merla (1934, pl. 26, fig. 14-21) from the northeast Karakorum, which had been referred to *Elivina* by Branson (1948, p. 356) and Fantini Sestini (1965, p. 198), was reallocated to *Hunzina* by Angiolini (1995, pl. 4, fig. 15-20, pl. 5, fig. 1-3, pl. 6, fig. 31-40, pl. 9, fig. 5, 6, text-fig. 13, 15. In Merla (1934, pl. 26, fig. 20), the dorsal fastigium appears to have a long median groove. His figures indicate shells very close to *Elivina*, with apparently comparable dorsal radial ribs and fold.

Subfamily **ELIVININAE** n. subfam.

NAME GENUS: *Elivina* Fredericks, 1924a.

DIAGNOSIS: Small triangular shells with short hinge, plicae virtually absent, fastigium formed as narrow median pair of elevated ribs separated by distinct groove, flanks may be weakly raised and costate, ribs increase by bifurcation, micro-ornament without pustules, little or no secondary thickening.

DISCUSSION: This group is separated from Spiriferellinae and Hunzininae most readily by the lack of a conspicuous broadly elevated fastigium, and also by lack of substantial thickening in the ventral valve. Arguably it differs more from *Spiriferella* than does *Hunzina*, but it does approach Hunzininae in the reported lack of pustules in the micro-ornament.

Eliva Fredericks is regarded as a member of the subfamily, rather than Purdonellinae as in Carter et al. (1994) and Kalashnikov (1998). It has the typical fold, and simple lateral ornament, and stands apart from members typical of Purdonellinae.

The lack of pustules and the moderately well developed adminicula, and generally short hinge, open the question of relationship to Purdonellinae. The two may often appear close, other than the more irregular branching and broad radials in Purdonellinae, and the distinctive fastigium in Elivininae, which lack a subdelthyrial plate as far as known, and may have a small umbonal callosity, unlike *Purdonella*. The relationship between the two requires further consideration, and although most authors have favoured a relationship between *Elivina* and *Spiriferella*, this is not unanimous. A conservative position is adopted, but data points to the possibility of placing Elivininae and Purdonellinae together in a separate family, or regarding the two groups as providing evidence of linkage between Spiriferellinae and Choristitinae.

GENERA: *Elivina* Fredericks, *Dissimiliplica* Waterhouse n. gen., *Eliva* Fredericks, *Quispira* Waterhouse n. gen.

Genus ***Elivina*** Fredericks, 1924a

TYPE SPECIES: *Spirifer tibetana* Diener, 1897a, p. 45.

DIAGNOSIS: Medium to small elongately oval shells with narrow hinge and delthyrium open as far as known; sulcus well formed and fastigium very low and broad, scarcely raised, lateral shell on both valves with low gently rounded or flat-crested subplicae, some may bear fine ribs which increase rarely by bifurcation. No pustules as far as known, micro-ornament of radial and concentric threads. Interior with dental plates and slender adminicula, not buried in secondary thickening. Dorsal valve has socket plates, crural plates and low median septum and muscle impressions, no secondary thickening.

DISCUSSION: Shells from the Late Permian of Wesleo, Timor, that were reported by Hamlet (1928, pl. 7, fig. 1, 2) are moderately close to *Elivina tibetana*, and have a slender fastigium posteriorly, formed by two costae separated by median groove. Unlike *tibetana*, costae are not developed on the subplicae. Specimens allocated to subspecies of *Elivina* by Reed (1944) need to be examined further, and do not appear to belong to Fredericks' genus.

Hunzina Angiolini lacks pustules according to Angiolini (2001), and has stronger, wider and higher and more costate fastigium, and the ventral valve has one or usually two pair of well developed plicae and narrow plicae or subplicae laterally. Secondary thickening is considerable, and the delthyrium is open, but the nature of any umbonal callosity is not certain, and the presence or absence of dorsal median groove requires clarification.

Elivina? termieri n. sp.

1974 *Spiriferella tibetana* (not Diener) Termier et al., p. 131, pl. 29, fig. 5, pl. 30, fig. 2-5, pl. 31, fig. 1, 2.

DERIVATION: Named for Genevieve Termier.

HOLOTYPE: Specimen figured in Termier et al. (1974, pl. 30, fig. 2-4) from "lower Murghabian" of Wardak, central Afghanistan, here designated. Kept at Institut Geologique A. de Lapparent Centre Polytechnique St Louis, Cergy Pontoise.

DIAGNOSIS: Moderately inflated shells with broad ventral umbo and massive posterior walls extending for comparatively short distance, hinge comparatively wide. Ventral sulcus shallow and narrow posteriorly, better defined at anterior margin, fastigium low but unusually well defined for genus. Subplicae and costae on both valves fine, not subdivided.

RESEMBLANCES: This species has been described in Termier et al. (1974). It is distinguished from *Elivina tibetana* (Diener) through its shorter posterior walls, more incurved ventral umbo, wider hinge, narrower sulcus posteriorly, slightly raised fastigium and narrow subplicae that seldom divide. The fastigium, especially for the specimen figured by Termier et al. (1974, pl. 30, fig. 5), suggests an approach to *Hunzina*, but lacks the sulcal bordering plicae, and there are no costae.

Genus *Quispira* n. gen.

DERIVATION: qui - which, spira - spire, coil, Lat.

TYPE SPECIES: *Elivina detecta* Cooper & Grant, 1976, p. 2244, here designated.

DIAGNOSIS: Small shells distinguished by absence of plicae, both valves covered by uniform costae, splitting dichotomously, rarely in threes, normally not fasciculate, no fastigium differentiated except in early growth stage, median groove commences at dorsal umbo. Micro-ornament without pustules. Hinge short, delthyrium open, umbonal callosity under umbo, sulcus moderately well formed, dental plates small, adminicula long, secondary thickening slight, dental sockets well formed but crural plates poorly developed or absent.

DISCUSSION: The type species has been well described and illustrated as *Elivina detecta* Cooper & Grant (1976, pl. 634, fig. 1-49) from the Lamar Member of the Bell Canyon Formation (Capitanian Stage), United States, with holotype USNM 152568f.

Hunzina has only subplicae over most of the lateral shell, but they are few and coarse, and its sulcus is bordered by one or two plicae pair, and the fastigium is better defined. *Bamberina* n. gen., has two plicae each side of the sulcus and well formed crural plates and low but distinct and complexly costate fold. *Elivina* Fredericks is morphologically close, but the sides of the sulcus are raised, the fold more elevated medianly, and in many species some subplicae bifurcate conspicuously and rarely, and costae are differentiated. Species of *Elivina* without bifurcations have stronger and fewer radials. By contrast, the costae on *Quispira* are numerous and subequal, and bifurcations are of subequal to comparable strength. The genus looks to be close to *Aequalicosta* as described earlier in its numerous costae and subdued fastigium, but the branching of costae and nature of the first formed part of the fastigium differs.

Spirifer (*Spiriferella*) *scopulosus* Reed (1944, p. 209, pl. 27, fig. 1, 2) from the Middle Productus Limestone (Kalabagh Member) of the Salt Range is possibly allied to *Quispira*, but the fold needs first hand examination. The specimen described as *Spiriferella mexicana* (Shumard) from the lower Murghabian of Afghanistan by Termier et al. (1974, p. 131, pl. 31, fig. 3-5) is possibly allied. Both valves are covered by slender costae with little sign of

fasciculation, plicae or fastigium and no reported pustules. The dorsal umbo seems to indicate a median groove, but this requires confirmation. If there is a single costa, the species belongs to *Aequalicosta* n. gen. (see p. 193).
FAMILY POSITION: The ornament and long high adminicula suggest a possible relationship with Purdonellinae. But there are also similarities with Elivininae, here treated as related to Spiriferellidae.

Genus ***Dissimiliplica*** n. gen.

DERIVATION: dissimilis - different, plica - fold, Lat.
TYPE SPECIES: *Spirifer mexicanus* var. *compactus* Girty, 1909, p. 361, here designated.
DIAGNOSIS: Small well inflated shells with relatively broad ventral plicae and narrow dorsal ribs fitting between each other along the commissure, fastigium narrow and high with median groove between two costae.
DISCUSSION: This genus is distinguished by the highly differentiated radial ornament which differs substantially on the two valves, the radials on the ventral valve being broad, the dorsal radials being narrow. Bifurcations are rare and micro-ornament consists of fine concentrics and radial filae in interspaces, but no pustules have been observed. The fastigium is well defined for the group, consisting of two upstanding costae separated by a groove and no further ribs. Ventral plates are short, and the delthyrium is not known to have a covering plate.

The type species was described by Girty (1909, p. 361, pl. 13, fig. 7-9) and later elevated to a full species of *Elivina* by Cooper & Grant (1976, p. 2243, pl. 633, fig. 1-20) from the Capitan Formation (holotype USNM 118589) and also the Lamar Member of the Bell Canyon Formation, of Capitanian age. Internal detail is not well preserved, thanks to calcification. Overall the genus comes closest to *Elivina*, especially those species that have few bifurcations of the radial ornament. Ventral radial ornament is not as fine as that of *Aequalicosta* or *Quispira*, but the fastigium is very simple.

STRATIGRAPHIC SUMMARY

In the Late Permian of Nepal, *Spiriferella rajah* (Salter) is found to range through the *Lamnimargus himalayensis, Lazarevonia arcuata* and *Biplatyconcha grandis* Zones, judged to be of Wuchiapingian and Changhsingian age. *Spiriferella sinica* Zhang is a poorly known species from south Tibet, associated possibly with the *Lamnimargus himalayensis* Zone, and *Arcullina qubuensis* (Zhang) is found mostly in the lower Qubuerga Formation of south Tibet, equivalent to the

Lamnimargus himalayensis Zone, but ranges up into the *Lazarevonia arcuata* Zone, in the Pija Member of Manang. *A. oblata* (Waterhouse) is found in the *Biplatyconcha grandis* Zone of Nepal. *Spiriferella grunti* n. sp., *S. nepalensis* Legrand-Blain and *Arcullina angiolinii* n. sp. come from high in the Permian in the *Retimarginifera xizangensis* Zone of Manang, and *S. grunti* and *S. nepalensis* are present in the zone in the Selong Group in the Selong Xishan section of south Tibet.

PAECKELMANNELLOIDEA

These brachiopods make up a minor part of the Spiriferidina in the Himalaya.

Superfamily **PAECKELMANNELLOIDEA** Ivanova, 1972

[nom. corr. ex Carter, 1994, p. 347, as Paeckelmanelloidea pro Paeckelmanellacea Ivanova, 1981, p. 22 ex Paeckelmanellidae Ivanova 1972, p. 40. *Paeckelmanella* Licharew was named after W. Paeckelmann. Most authors have retained the original spelling, whereas others (eg. Reed, 1944, Gobbett 1964) corrected the spelling. Reed (1944, p. 211, footnote) wrote “as it was named after Paeckelmann, the second n is inserted as a reasonable emendation and in conformity with his other generic name *Paeckelmannia”*. Given the absence of unaminity, and given the fact that Reed despite exigencies of war was not slow to emend the name, it would seem justifiable to follow the intention of B. K. Licharew, and have the genus named after and in honour of the German paleontologist. No one has contradicted Reed’s analysis, just ignored or overlooked it. The overlooking by a majority of Reed’s correction does not justify or validate the continued misspelling].

Family **STROPHOPLEURIDAE** Carter, 1974

[nom. transl. Carter, 1994, p. 347 ex Strophopleurinae Carter, 1974, p. 677].

Subfamily **PTEROSPIRIFERINAE** Waterhouse, 1975

DIAGNOSIS: Medium sized, generally transverse, with numerous simple ribs, rarely also involving fine costae, sulcus smooth or costate, delthyrium closed or partly closed from each side, adminicula short.

Genus ***Pterospirifer*** Dunbar, 1955

TYPE SPECIES: *Terebratulites alatus* Schlottheim, 1813, p. 58.

DIAGNOSIS: Transverse shells with alate or extended cardinal extremities, up to 10 or more simple plicae on both valves, with rare increase by implantation, wide sulcus and broad round-crested fold, low concentric lamellae and very fine radial capillae, delthyrial cover, short adminicula and dental plates.

DISCUSSION: Pterospiriferinae was placed by Carter et al. (1994) within Strophopleuridae Carter 1974 with Strophopleurinae, which includes such genera as *Strophopleura* Stainbrook, *Acuminothyris* Roberts, *Avisyrinx* Martinez-Chacon, *Cantabriella* Martinez-Chacon & Rio Garcia and *Voiseyella* Roberts. Data on delthyrium is of varied quality, but where clear, as for *Cantabriella* for example, indicates a covering like that of Pterospiriferinae, and the two groups appear closely allied. Bashkiriinae Nalivkin, regarded as a member of Strophopleuridae by Carter et al. (1994), differs in having high interarea and long or prominent adminicula and short tabellae, indicative of differences likely to be highly significant, should the presence of tabellae ("dorsal adminicula") be confirmed. *Adminiculoria* Waterhouse & Gupta was included by Carter et al. (1994) in Bashkiriinae, but it differs and is regarded as a member of Angiospiriferinae (p. 181). Strophopleuridae is treated as a member of Paeckelmannelloidea Ivanova, 1972 by Carter et al. (1994). There is a degree of similarity to Angiospiriferinae, and the main difference appears to lie in the nature of the delthyrium.

Whilst there remain uncertainties over the classification, the outlines are far improved from the scheme adduced by Brunton & Rissoné (1976), in which *Fusella*, now a member of Bashkiriinae, was regarded as an ally of spiriferids *rhomboidea* Phillips, *convoluta* Phillips, and doubtfully *trigonalis* Martin, with *Brachythyrina* as a descendent. There are substantial external as well as internal differences, and the claim by Brunton & Rissoné (1976) that Waterhouse (1970) had separated various taxa from *Fusella* on the basis of endopunctae was not true - endopunctae had only been noted as a possibility in *Fusella*: there are other more definite differences, made apparent in this overview. Thus now *Fusella*, *Angiospirifer trigonalis* and *Brachythyrina* are placed in three different families.

Pterospirifer waageni n. sp.

1883 *Spirifer alatus* (not Schlottheim) Waagen, p. 519, pl. 48, fig. 7 (part, not fig. 2 = *devia*).

DERIVATION: Named for W. Waagen.

HOLOTYPE: GSI 3530 figured by Waagen (1883, pl. 48, fig. 7a-d) from Lower Productus Limestone (Amb Formation), Salt Range, here designated.

DIAGNOSIS: Elongate shells with alate but not extended cardinal extremities, moderately but not very high cardinal interarea, sulcus narrow with median rib, a number of simple lateral plicae.

DESCRIPTION: The species has been described by Waagen (1883). It is represented by a figured specimen which is slightly worn, but well preserved. It shows a single sulcal rib.

RESEMBLANCES: The species is close to *Terebratulites alatus* Schlottheim from the Zechstein of Europe and Foldvik Creek Group of Greenland (see Dunbar 1955), but has less extended cardinal extremities, narrower sulcus and less broad fold. *P. cordieri* (Robert, 1845), as summarized by Gobbett (1964, p. 158), from early Guadalupian of Spitsbergen has slightly wider sulcus and fold, with pronounced concentric lamellae, more pronounced sulcal tongue, and slightly higher ventral interarea.

Waagen (1883, pl. 48, fig. 2a-d) also recorded another specimen which comes from the same locality and has more sulcal costae. It is here reassigned to *Johncarteria.*

Genus ***Pteroplecta*** Waterhouse, 1978

TYPE SPECIES: *Pteroplecta laminatus* Waterhouse, 1978, p. 86.

DIAGNOSIS: Transverse alate shells with high ventral interarea, delthyrial cover, well formed ventral sulcus and dorsal fold, both costate (Pl. 9, fig. 5), and a number of plicae with rather narrow and rounded to fastigate crests, bearing differentiated generally broad costae, concentric laminae well spaced and prominent, radial capillae fine. Ventral interior with short adminicula and dental plates, probably denticulate hinge, dorsal inner and outer socket plates and crural plates, no tabellae.

DISCUSSION: *Pteroplecta* is close in overall shape to Strophopleuridae Carter, 1974, but apart from shape shows many of the attributes of Neospiriferinae. The number of plicae is somewhat variable in the type and other species, and is greater than so far known in any neospiriferin genus.

Pteroplecta sulcata Waterhouse, 1983a

Plate 9, fig. 6-14

1983a *Pteroplecta sulcata* Waterhouse, p. 132, pl. 5, fig. 8-18, pl. 6, fig. 21.

HOLOTYPE: UQF 73638 figured by Waterhouse (1983a, pl. 5, fig. 10, 13) and herein in Pl. 9, fig. 11, 12, from Pija Member north of Braga, Nepal, OD.

DIAGNOSIS: Moderately transverse shells with few costae and shallow sulcus and low fastigium.

DISCUSSION: Several species of *Pteroplecta* are found in the Salt Range. *Spirifer (Paeckelmannella) varuniformis* Reed (1944, pl. 27, fig. 3, 3a) from the Amb Formation has a prominent median rib and faint lateral costae in the ventral sulcus, and apparently smooth dorsal fold, but Reed (1944, p. 211) reported a few costae along the base of the fold. Plicae carry a rib on each side. The species is a member of *Pteroplecta*. Another Amb species, *Spirifer (Paeckelmannella) middlemissi biplicata* Reed (1944, pl. 29, fig. 3 - GSI 17054) has a ventral valve like that of *Pteroplecta*, with somewhat fastigate plicae and few costae other than in the sulcus. Its dorsal valve is not known. *Spirifer joharensis* Diener (1897b, pl. 4, fig. 3) from the *Lamnimargus himalayensis* Zone of the Lissar Valley of northwest India is also congeneric.

Pteroplecta niger (Waagen, 1883)

1883 *Spirifer niger* Waagen, p. 522, pl. 48, fig. 4, 6 (part, not fig. 5 = neospiriferin).
LECTOTYPE: GSI 3529, figured by Waagen (1883, pl. 48, fig. 6a-d), from "Chonetes" bed, Lower Productus Limestone (Amb Formation), Salt Range, here designated.
DIAGNOSIS: Transverse, numerous plicae bearing fine costae, sulcus narrow and costate, fold high with no costae other than along base.
DESCRIPTION: The lectotype has costate sulcus, 2-3 costae over anterior dorsal plicae, and only faint traces on the dorsal fold. Growth lines show that the specimen was suboval in early growth stages, and then became transverse. The species is distinguished principally by the lack of well defined costae over much of the fold, as reported by Waagen (1883, p. 522) and confirmed by Diener (1897b, p. 42) and Reed (1944, p. 213). The specimen figured as *Spirifer niger* by Waagen (1883, pl. 48, fig. 4 - GSI 3527) is fragmentary, and sulcal costation not clear, but lateral plicae seem to have low costae. Lee et al. (1980, pl. 178, fig. 1, 2, 14) reported moderately close specimens from northeast China. More costae are present in the specimen figured in Waagen (1883, pl. 48, fig. 5), and it may be a juvenile *Neospirifer* or more likely *Betaneospirifer,* illustrated as having some 5 or 6 pairs of plicae.

Archbold & Thomas (1985b, p. 290) suggested that *Spirifer niger* Waagen was like *Spirifera kimberleyensis* Foord (1890, p. 105, pl. 5, fig. 11) from the Gascoyne River, Western Australia. Archbold & Thomas referred Foord's species tentatively to *Crassispirifer* (see p. 154). Waagen's species shows little similarity to *Crassispirifer*, in which the plicae have fine costae, unlike those of Waagen's species.

Genus ***Johncarteria*** n. gen.

DERIVATION: Named for J. L. Carter.
TYPE SPECIES: *Spirifernaella scalpata* Cooper & Grant, 1976, p. 2217, here designated.
DIAGNOSIS: Small transverse alate spiriferids with moderately high ventral interarea, alate cardinal extremities, well formed sulcus and fold, 8-12 plicae

pairs on both valves, 1-6 and usually 3-4 costae in sulcus, also along flanks and in some species over crest of fold, little or no costation over plicae, concentric laminae well developed. Hinge denticulate, dental plates low, adminicula short, delthyrium partly covered by cover plate.

DISCUSSION: This genus is moderately close to *Pterospirifer* Dunbar, 1955, and to *Spirifernaella* Fredericks, 1926, and is distinguished by having costae within the sulcus, and costae along the basal flanks of the fold, and in some forms over the crest. *Spirifernaella,* type species *Spirifer artiensis* Stuckenberg, 1898 from the Cisuralian of the Urals, Russia, has simple sulcus and fold and rather few plicae. *Pteroplecta* Waterhouse, 1978 has broader, fewer and more costate plicae adjoining the sulcus and fold, and generally has more conspicuous costae over the fold.

Johncarteria is represented by species in the Word Formation and Getaway Member of the Cherry Canyon Formation in the Glass Mountains of Texas. The species are very transverse with interarea much lower than in Russian species assigned to *Spirifernaella*, and have two sulcal costae, and fold that varies in costation, generally with a pair along the base, and median rib that may subdivide. In the species *S. limata* Cooper & Grant, 1976, the median rib also may carry a central split, and there are more flank ribs laterally near the anterior margin. Species from the Salt Range differ in having an undivided median rib along the centre of the sulcus. There are generally two further sulcal costae, and the fold has a rib along each flank near the base, and may have ribs over the crest.

Johncarteria devia (Reed, 1944)

1883 *Spirifer alatus* not Schlottheim Waagen, p. 519, pl. 29, fig. 2 (part, not fig. 7 = *waageni*).

1944 *Spirifer (Paeckelmannella) niger* var. nov. *devia* Reed, p. 213, pl. 29, fig. 1, 2, 2a.

LECTOTYPE: GSI 17052 figured by Reed (1944, pl. 29, fig. 1) from Lower Productus Limestone (= Amb Formation), Salt Range, here designated.

DIAGNOSIS: Transverse shells with 10-12 pairs of non-costate plicae, 3-5 costae within sulcus, fold smooth apart from costae along base.

DESCRIPTION: The species is transverse, with low ventral umbo, and 10-12 narrow round-crested plicae separated by narrow interspaces. The suggestion of ribs on the plicae in the figure of Reed (1944, pl. 29, fig. 1) is misleading - none are present, to judge from a plaster duplicate in my possession. The sulcus carries a median rib and another well developed rib each side a little below the crest of the adjoining plication. The fold on the unfigured dorsal side carries a suggestion of a rib each side well below the fold crest. Reed (1944) reported one or two ribs near the base of the fold for the second figured specimen (pl. 29, fig. 2) and a possible rib is developed anteriorly each side within the sulcus. Several faint ribs may be discerned over the fold.

A specimen figured as *alatus* not Schlottheim by Waagen (1883) from the Lower Productus Limestone, now Amb Formation, of the Salt Range may be conspecific. The figure indicates a largely smooth fold, costae within the sulcus, and similar simple plicae.

RESEMBLANCES: *Spirifer niger protracta* (Reed, 1944, pl. 29, fig. 8 - GSI 17059) is a very transverse form with few costae over the plicae. Reed (1944, p. 214) stated that on each side of the sulcus, the ventral valve bears 3-4 plicae "which usually become triplicate towards their distal ends" and the lateral shell has a further 8-10 simple ribs. The same pattern was reported for the dorsal valve. Such observations suggest a possible approach to *Pteroplecta*, but the figure shows narrow and close-set plicae like those of *Johncarteria devia* (Reed). The figure does not show the "distal" costae described by Reed (1944), leaving the genus difficult to determine.

Species described as *Spirifernaella* by Cooper & Grant (1976) from the Guadalupian faunas of the Glass Mountains of Texas, and now referred to *Johncarteria*, are more transverse and have two costae in the sulcus: none are very close.

Pterospirifer terechovi Zavodowsky in Marcovskii (1968, pl. 43, fig. 1) is moderately close to *Johndearia devia*, but the sulcal rib fades anteriorly, and the cardinal extremities are alate. There are traces of faint ribbing posteriorly over the fold. The species comes from the Cisuralian Irbichan Suite of northwest Russia.

Spirifernaella tastubiensis Tschernyschew (1902, pl. 9, fig. 1-3) from the Schwagerinakalk of the Urals is closer to the present genus in size and shape, with traces of costae in the sulcus (see Kalashnikov 1998, pl. 29, fig. 1). *S. seziemensis* Kalashnikov (1983, pl. 54, fig. 4, 5) from the Sezim Suite of Petchoraland, north Russia, is an elongate shell with plicae and costae and wide groove along the dorsal fold: it seems unlikely to be congeneric.

BRACHYTHYRIDOIDEA

Introduction

Carter et al. (1994, p. 348-9) classed Brachythyridoidea as containing two families, characterized by rounded cardinal extremities at all growth stages, with micro-ornament absent or weakly developed, delthyrium partly covered by thin deltidial or stegidial plates, and no adminicula, subdelthyrial plate or tabellae. Here stress is laid on the absence of adminicula. Micro-ornament and delthyrial apparatus are considered to be more variable, and the cardinal extremities allowed to be obtusely subalate. Subfamily Tangshanellinae Carter, 1994 is transferred from Choristitidae. Unlike Choristitidae, *Tangshanella* and allies lack adminicula, and their suboval shape is close to that of Brachythyrididae. In its fine radial ribs, *Tangshanella* is similar to choristitinids, but its interarea is narrow and high, like that of brachythyridids. Radial striae are developed in *Tangshanella*, unlike Brachythyrididae according to Carter et al. (1994). This may well point to a significant difference, but further study is required, centred on the dorsal interior. Fine and continuous radial filae, 3 per mm, were recorded in specimens of the type species *Brachythyris* M'Coy, *Spirifer ovalis* Phillips, by Waterhouse (1968, p. 46), and radial lirae were recorded by Waterhouse (1968, p. 46) on Australian species *Brachythyris pseudovalis* Campbell (1957, pl. 14, fig. 13) and *B. elliptica* Roberts (1963, pl. 4, fig. 1-4), although perhaps these are surface effects caused by weathering.

A new subfamily is erected for another group, which like Brachythyridinae, lacks adminicula, has short hinge and radial ribs, and has concentric growth lamellae and small elongate pustules. Another group may be recognized for genera that agree internally with *Brachythyris*, and are distinguished by the extended hinge. Reticulate vascular impressions are developed in *Anthracothyrina* Legrand-Blain and *Brachythryina* Fredericks. From shape and vascular impressions, *Anthracothyrina* and *Brachythyrina* have in the past been deemed to be closely allied to Angiospiriferinae. But here the internal plates are regarded as a prime feature, outweighing, so far, the significance of angioglyphs for which presence or absence, and overall significance, is still poorly established. The width of hinge is not regarded as a prime discriminant amongst Brachythyridoidea.

The revised classification is therefore as follows:

Family Brachythyrididae Fredericks, 1924
- Subfamily Brachythyridinae Fredericks, 1924
- Subfamily Pustuloplicinae n. subfam.

Family Brachythyrinidae n. fam.

Family Skelidorygmidae Carter, 1994
- Subfamily Skelidorygminae Carter, 1994
- Subfamily Tangshanellinae Carter, 1994

Superfamily **BRACHTHYRIDOIDEA** Fredericks, 1924a

DIAGNOSIS: Suboval to transverse shells with generally poorly developed

interareas, ornament of plicae which may branch or be diversified through branching or costation, sulcus and fold developed and variably costate or smooth, micro-ornament subdued and usually simple with growth increments, may be diversified by radial lirae or pustules. Delthyrium open, or closed by delthyrial plate, or subdelthyrial plate. Teeth low, dental ridges not supported by adminicula. Muscle field diffuse with elongate ventral adductor platform. Inner and outer hinge plates, spiralia, no tabellae.
DISCUSSION: The diagnosis for this superfamily is expanded to include taxa with delthyrial or subdelthyrial plate, and genera with broad radial plicae, and/or narrow costae, and micro-ornament of concentric growth-lines, and in some forms, small pustules. As a consequence, the superfamily is interpreted as showing more diversity than understood previously. In the classification, the outline follows that proposed by Carter et al. (1994) as closely as possible. But perhaps more weight should be granted to the nature of the delthyrium and the delthyrial plate or subdelthyrial plate. *Blasispirifer*, Pustuloplicae and *Brachthyrina bonloomi* all have a subdelthyrial plate, whereas *Brachythyris, Skelidorygma* and other forms have a delthyrial plate.

Family **BRACHYTHYRIDIDAE** Fredericks, 1924a

DIAGNOSIS: Hinge short, cardinal extremities obtuse, interarea high, delthyrium partly closed by plate, ornament of plicae, simple or branching, sulcus and fold, may be costate. Micro-ornament variable, subdued, concentric or radial filae, may be pustular.
DISCUSSION: A delthyrial plate is developed in *Brachythyris*, as elaborated in Waterhouse (1968), and illustrated for example in Waterhouse (1968, pl. 6, fig. 4).

Subfamily **PUSTULOPLICINAE** n. subfam.

NAME GENUS: *Pustuloplica* Waterhouse, 1968, p. 45.
DIAGNOSIS: Small subrounded to subtriangular shells with prominent ventral umbo and obtuse cardinal extremities, short hinge, delthyrium partly closed by small plate or thickening which merges with pleromal ridges. Ornament of low ribs which may branch anteriorly, costae within sulcus, micro-ornament of short radially elongate pustules and grooves and concentric lamellae. Small dental plates, no adminicula or tabellae, ventral muscle field elongate.
DISCUSSION: This subfamily is most readily distinguished by its micro-ornament, because pustules are not known in other members of the Brachythyridoidea. Carter et al. (1994, p. 349) therefore regarded the genus as exceptional, and suggested that the micro-ornament was reminiscent of several

martiniid genera. These have been carefully scanned, and it has not been possible to point to any exactly comparable example. It is therefore concluded that *Pustuloplica* falls within the Brachythyridoidea. Members of Perissothyrididae Carter lack adminicula and have a “pseudodelthyrial plate” but differ in shape and macro- and micro-ornament. Genera within Martiniidae and allies seldom display coarse radial ribs, and often have pitted micro-ornament and a much more compact ventral muscle field. *Pustuloplica cooperi* Waterhouse, 1981, p. 110, named for shells described from the Rat Buri Limestone of south Thailand by Grant (1976, p. 230, pl. 55, fig. 28-52), has pustular ornament, but the overall shape of the shell is more martiniid, and the plicae very subdued, indicating that the generic position must be revised.

The ornament of several members of Ingelarellidae Campbell (see Waterhouse 1998) does have pits and raised lunular ridges, and one form has spines, and genera amongst Notospiriferidae Archbold & Thomas show some approach, but in none is the micro-ornament identical, and all the genera have well developed dental plates and adminicula, and generally tabellae as well. Gerkispiridae Carter differs substantially in micro-ornament, shape, macro-ornament and ventral plates.

There are additional lines of support. The Chinese genus *Zhejiangospirifer* Liang, 1982, 1990 lacks adminicula and tabellae, and so is identical internally with *Pustuloplica*, as far as known, apart from the muscle field which is poorly known. Externally the genus looks very close to *Pustuloplica* in shape, hinge, and the mode of its ribbing with branching. Micro-ornament was described as “a few weak concentric lines and grooves besides the strong costae, which are incised by the former and usually slightly raise a low node in the point of intersections” (Liang 1990, p. 476). The meaning is not entirely clear to me. Colleagues Drs Chen and Shen have kindly sent translations from the original Chinese text, but they differ little from the published English version. The micro-ornament could be identical with that of *Pustuloplica*, but perhaps not, and the position and nature of the “nodes” remain obscure. The genus was classed by Carter et al. (1994) with *Tangshanella* Chao, 1929, a genus which is identical internally as far as known, but has finer more numerous costae over the entire shell, with concentric micro-ornament, and no recorded nodes.

A further line of enquiry should centre on species ascribed to *Brachythyris* itself. Under certain light, shells of *Brachythyris elliptica* Roberts have the concentric growth-lines divided into small pits or pustules (F5192, 5194, specimens originally kept at University of New England, now transferred to Australian Museum, Sydney).

GENERA: *Pustuloplica* Waterhouse, ?*Zhejiangospirifer* Liang.

Family **BRACHYTHYRIDINIDAE** n. fam.

NAME GENUS: *Brachythyrina* Fredericks, 1929, p. 385.
DIAGNOSIS: Transverse shells with wide hinge and narrow cardinal extremities, delthyrium generally open or with subdelthyrial plate, ornament of a number of plicae pairs, and costae over sulcus and fold, micro-ornament of concentric growth increments, dental ridges, no large dental plates or adminicula, no tabellae. Reticulate vascular impressions laterally in at least some forms. Ventral adductor scars elongate.
DISCUSSION: Unlike other members of Brachythyridoidea, the hinge is wide. Plicae are numerous and simple, and costae occur over sulcus and fold. Reticulate vascular impressions are reported in *Anthracothyrina* Legrand-Blain (1986b) and *Brachythyrina*.
GENERA: Genera include *Brachythyrina* Fredericks (=*Anelasmina* Semikhatova), *Anthracothyrina* Legrand-Blain, *Elinoria* Cooper & Muir-Wood, *Eobrachythyrina* Lazarev & Poletaev.

Genus ***Brachythyrina*** Fredericks, 1929

TYPE SPECIES: *Spirifer strangwaysi* Verneuil, 1845, p. 164.
DIAGNOSIS: Transverse shells with extended and often alate hinge, costate sulcus and fold, numerous simple plicae, concentric micro-ornament. Delthyrium with subdelthyrial plate and forming swelling or callus under umbo, dental plates low, no adminicula or tabellae, vascular impressions form open network.

Brachythyrina boonlomi n. sp.

Pl. 1, fig. 6-10

1981 *Brachythyrina rectangulus* (not Kutorga) Waterhouse, p. 96, pl. 21, fig. 1-14, pl. 22, fig. 1-8, pl. 23, fig. 1.
DERIVATION: Named for Boonlom Tabtimtong.
HOLOTYPE: TBR 159 figured by Waterhouse (1981, pl. 21, fig. 1-3) and Pl. 1, fig. 6 herein, from Ko Yao Noi Formation, south Thailand, here designated.
DIAGNOSIS: Relatively elongate for genus, with alate cardinal extremities, 7-9 pair of plicae with usually 2 pair in sulcus, fold low posteriorly.
DESCRIPTION: This species is based on substantial collections of material from the Ko Yao Noi Formation, and has been described and extensively illustrated. Of particular interest to the overall theme on spiriferid morphology and classification is the way that specimens show a subdelthyrial plate, and vascular impressions. The subdelthyrial plate is illustrated in Pl. 1, fig. 9, 10, to show probable pleromal ridges curving up and fusing from the ventral edges of the dental plates, to form a swelling below the ventral umbo. The vascular

impressions, as illustrated, form an open and complex network close to the muscle field.

RESEMBLANCES: This species is very close to *Brachythyrina rectangulus* (Kutorga, 1844) from chiefly Sakmarian faunas in the Urals, and the species was surveyed with other references in Waterhouse (1981, p. 97). The hinge and sulcal costation are very close. Thai specimens are more elongate, and have 7-9-11 pairs of plicae, whereas *rectangulus* may have up to 20 pair of plicae and lateral costae. As well, the posterior fold is higher in *rectangulus*. Various other species are compared in Waterhouse (1981).

Family **SKELIDORYGMIDAE** Carter, 1994

DIAGNOSIS: Sulcus with primary median costa, often with additional sulcal costae that bifurcate from sulcal bounding ribs, ribs comparatively numerous.

Subfamily **SKELIDORYGMINAE** Carter, 1994

[nom. transl. hic ex Skelidorygmidae Carter, 1994, p. 349].

DIAGNOSIS: Ribs moderately coarse to fine.

DISCUSSION: This small group was recognized by Carter for genera of Upper Devonian (Famennian) to Upper Carboniferous (Bashkirian) age. Micro-ornament is of light concentric growth lines, and *Litothyris* has a subdelthyrial plate. For *Skelidorygma*, Carter (1974, pl. 4, fig. 5-7) figured what appears to be a small delthyrial plate rather than subdelthyrial plate, more like that of *Brachythyris.*

Subfamily **TANGSHANELLINAE** Carter, 1994

DIAGNOSIS: Subovate shells with rounded cardinal extremities, low dental ridges without high plates or adminicula, vascular impressions poorly known. Shell covered by fine subeven costae.

DISCUSSION: Various aspects of *Tangshanella* remain to be clarified - such as the nature of delthyrial cover, vascular markings, and dorsal interior. *Tangshanella* shares with *Litothyris* Roberts the ventral interior, general shape and fine costae, so it is provisionally placed close to that genus, but this remains in contention. Whereas Skelidorygminae are definitely brachythyriform, some doubt remains over the position of *Tangshanella*, because of uncertainty about the dorsal interior.

Carter in Carter et al. (1994) followed Roberts (1971) in claiming that *Tangshanella* was related to *Choristites*, but the ventral interior is so different that the external similarity would appear to be due to evolutionary convergence from different stock.

GENERA: *Tangshanella* Chao, ?*Blasispirifer* Kulikov.

Genus ***Blasispirifer*** Kulikov, 1950

TYPE SPECIES: *Spirifer blasii* Verneuil, 1845, p. 168.

DIAGNOSIS: Small with narrow well formed fascicles, hinge wide, ventral interarea high, triangular, sulcus and fold of moderate depth and height, costae comparatively coarse, bifurcating, fascicles few, trifurcate. Delthyrium apparently open, but with subdelthyrial plate or thickening. Dental plates not supported by adminicula.

DISCUSSION: *Blasispirifer* Kulikov, type species *Spirifer blasii* Verneuil (1845, pl. 6, fig. 9a-d; Kulikov 1974, pl. 4, fig. 4), represented in my collections by a specimen provided by Dr Kulikov from the Pinega River, is like a juvenile *Neospirifer*, with 4 pairs of costate plicae, and moderately well to weakly defined sulcus, but differs internally, with no adminicula. This was clearly demonstrated by Licharew (1931, p. 37, pl. 3, fig. 16) and confirmed by Kulikov (1950, p. 6). The internal detail therefore appears to be brachythyriform. But externally, the genus approaches *Neospirifer* or *Betaneospirifer*, and so was included, with a query, in Neospiriferinae by Carter et al. (1994), Poletaev (1998) and Tazawa (2001), amongst others. Here the internal plates are regarded as critical, and the exterior is considered to characterise genus and subfamily. Plications are not as strong as in the neospiriferin genera, and fascicles have often two rather than three costae, which are broad with convex crests and narrow interspaces. There is no clearly separated pair of plicae within the sulcus, but borders of the sulcus are not clear defined, so that the sulcal border may lie between the two innermost pair of plicae. The combination of numerous costae and lack of adminicula suggests an approach to *Tangshanella* Chao, which is distinguished by the broader and flat-crested costae and lack of plicae. The assumption in virtually all studies of *Tangshanella* is that tabellae are lacking. This is also true of a specimen figured as *Blasispirifer* by Shi & Tazawa (2001, text-fig. 2.6), but the particular specimen has costae, but no plicae or fasciculation. The dorsal umbonal region of *Blasispirifer blasii* provided by Dr Kulikov has been ground down, but is obscure, because matrix is not very different from shell, and there is the possibility of extraneous shell material or calcite. With considerable reservation, there could be possibly short convergent tabellae, but uncertainty is too great to allow the possibility to have weight. The ventral umbonal region of the same specimen, ground down for 3mm, suggests a subdelthyrial plate. Serial sections of *Blasispirifer multiplicicostatus* (Netschajew) in Gubareva & Boltaeva (1998, text-fig. 1) show no adminicula or tabellae, and separate dental plates and crural plates anteriorly. Secondary thickening is substantial in both valves, so that sections of specimens at immaturity could be very useful.

In its fine ribs, *Blasispirifer* approaches the genus *Litothyris* Roberts, 1971, p. 237 from Famennian of Bonaparte Gulf Basin in Western Australia, and this genus in turn approaches some forms of *Skelidorygma* Carter. *Blasispirifer* is also like *Litothyris* is having a subdelthyrial plate. This may well constitute a significant aspect that requires some shuffling in disposition of genera. Both *Skelidorygma* and *Litothyris* are undoubted members of Brachythyridoidea.

Blasispirifer? warchensis (Reed, 1944)

1931 *Spirifer (Neospirifer) warchensis* Reed, p. 21, pl. 4, fig. 9.

1944 *Spirifer (Neospirifer) warchensis* Reed, p. 198.

HOLOTYPE: Sole specimen figured by Reed (1931), from Kufri Member, Salt Range, by monotypy. Kept at Geological Survey of India, Calcutta.

DISCUSSION: The species is characteristic, small in size, with strong persistent plicae, sturdy costae and prominent ventral umbo. Waterhouse (1966, p. 37) stated that the innermost plicae plunged early into the sulcus of *warchensis*, but perhaps this is a matter of how the sulcus is defined, with Reed (1931, pl. 4, fig. 9b) showing the second pair of plicae just ventral to the innermost pair, much as in type *Blasispirifer*. The dorsal innermost pair of plicae curve away from the fold anteriorly in the holotype. Many details of the species remain unknown. The umbo is prominent, and extends further from the hinge, and is narrower than in accompanying species of *Betaneospirifer*. The species apparently belongs to *Blasispirifer*, with Reed (1944) pointing to similarities to species now assigned to that genus. Both *B. blasii* (Verneuil 1845, pl. 6, fig. 9; Licharew 1913, pl. 3, fig. 9, 11) and also *B. vagaensis* (Licharew, 1931, pl. 3, fig. 9, 10, 11a, b, 16) from Guadalupian of north Russia are close in size, shape and ornament, with slightly narrower fascicles and less protruding ventral umbo.

Stratigraphic detail was not provided by Reed (1931), but Reed (1944) in reporting additional material stated it came from the base of the Upper Productus Limestone, now Kufri Member.

Spirifer (Neospirifer) warchensis var. nov. *scabrosa* Reed, p. 199, pl. 27, fig. 7, 7a, (part, not 8, 8a = *poletaevi*) is distinguished by its smaller umbo and straighter posterior outline, and more prominent concentric lamellae. It is tentatively regarded as a possible member of *Simplicisulcus* Waterhouse, a neospiriferin (p. 126). The other figured specimen belongs to *Neospirifer poletaevi* n. sp.

incerte sedis

Family **ALPHANEOSPIRIFERIDAE** n. fam.

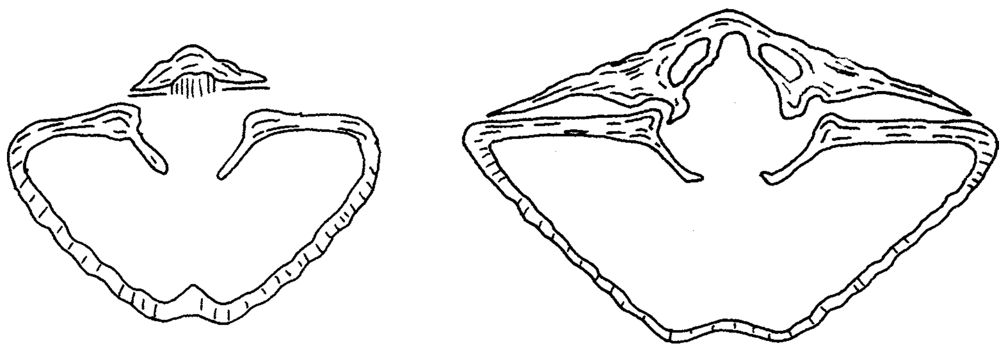
NAME GENUS: *Alphaneospirifer* Gatinaud, 1949, p. 491.

DIAGNOSIS: Closely costate shells with plicae, approaching neospiriferin shells in appearance. Ventral interior with low dental tracks, no dental plates or adminicula, subdelthyrial plate. Dorsal valve with crural plates supported by tabellae (= "dorsal adminicula").

DISCUSSION: *Alphaneospirifer,* type species *Spirifer mahaensis* Huang, 1933 (syn. *Semibrachythyrina* Yang & Chang 1962, type species *S. fasciculata* Yang & Chang, 1962, p. 104, pl. 42, fig. 8-10) was deemed to be a valid genus by Carter et al. (1994), although dismissed by Pitrat (1965, pp. 699-700). Its history is like of *Betaneospirifer*, discussed previously under Neospiriferinae (p. 110). *Alphaneospirifer* is a most unusual genus, of moderate to large size, transverse and neospiriferin in appearance, apart from a high interarea. Internally, the ventral valve is brachythyrid, with low dental plates and no supporting adminicula. There is a posterior median ridge, too low to be called a septum, and possibly no more than myophragm or raised adductor ridges. The dorsal interior, as figured from cross-sections by Liang (1990, text-fig. 42, p. 331) shows ctenophoridium, dental sockets, large crural plates resting on low tabellae, as shown herein in Text-fig. 37. Such plates are found elsewhere in members of Bashkiriinae Nalivkin, as discussed on p. 228.

Blasispirifer Kulikov is similar in some respects, and looks so neospiriferin that it has been classed within Neospiriferinae over recent years. It is smaller and less transverse than *Alphaneospirifer*, and lacks adminicula and tabellae, as far as known, although there is need to study specimens at immaturity, before the umbonal region became infilled with secondary shell.

GENUS: *Alphaneospirifer* Gatinaud (syn. *Semibrachythyrina* Yang & Chang).



Text-fig. 37. *Alphaneospirifer pyridamidiformis* (Liang), from sections presented by Liang (1990, text-fig. 42) at 8 and 9.5mm from umbonal tip, x 2.

B. TRIASSIC MOLLUSCA

1. COMMENTS AND CORRECTIONS FOR THE STUDIES ON EARLY AND MIDDLE TRIASSIC AMMONOIDS FROM THE HIMALAYA

INTRODUCTION

Studies on Triassic ammonoids by the writer were published as a seven part series entitled “The Early and Middle Triassic ammonoid succession of the Himalayas in western and central Nepal” in Palaeontographica Abteilung A. The studies were completed in 1994 and issued piecemeal between 1994 and 2002. The first monographs were integrated as far as possible with later volumes, and occasionally involved the publication of nomen nuda before validification; this was deemed justifiable because within a few years all volumes would be available and the series could be treated as a whole. Otherwise the early volumes would become superseded or require various corrections and elaborations, and clarity would be reduced. Of course the taxa date from time of validification.

It may also be noted that as elsewhere in my studies, the rules of Zoological Nomenclature are transgressed in granting naming rights to the first proposer, even though they failed to conform with procedures by not providing a diagnosis, for example. There is no wish to dispute the code, but at times courtesy should prevail over the acquisition of naming rights which conform with the Code but set aside the fact that the original concept and insight belong to someone else. Exploitation of legalisms to gain naming rights seems to be against what should be the ethos of scientific endeavour and discovery, and in its drive to ensure clear rules of procedure for taxonomic nomenclature, the ICZN (2000) has yet to address this problem adequately, and guard against intellectual theft and self-aggrandisement through exploitation of rules and procedures. So far, no weight has been granted to intellectual property rights, and law is considered to prevail over originality. The responsibility of granting taxon authorship to someone who has conceived the taxon without publishing it, or granting the name to someone who has published but failed to meet all the rules, should lie with the first revisor, who has met the necessary demands of the Code. Examples include *Pseudoproptychites* Bando, and Noetlingitinae Parnes, for which no diagnoses were provided. These omissions have been repaired in my studies, and the names should stand, with their authors, as originally conceived (see Part 1, p. 46 and Part 5, p. 14). Of course, principal first revisors who clarify and justify a taxon remain free to claim authorship, but it should then become mandatory to also refer to the original author. Such references would read - Koken in Spath (1934), or, to make up an example, author Y (1980), following or after author X (1975). "After" may be accurate in instances where concepts were not subsequently copied and self-attributed, but arose afresh, due to failure to adequately peruse the literature. Conduct within the scope of zoological nomenclature needs a procedure to mandate clarification of who originated the name and concept, and who "fixed" and adjusted the concept to conform with the rules.

Identifications of some Bivalvia and Brachiopoda are here added, following further study, and reference offered to illustrations of geology and fossil localities. For the most part, punctuation lapses are set aside. The text to be corrected is enclosed in brackets. Punctuation and capitalization for this chapter follows that of the articles in Palaeontographica, but names of authors are left in lower case.

THE EARLY AND MIDDLE TRIASSIC AMMONOID SUCCESSION OF THE HIMALAYAS IN WESTERN AND CENTRAL NEPAL

Part 1.

STRATIGRAPHY, CLASSIFICATION AND EARLY SCYTHIAN AMMONOID SYSTEMATICS.

***Palaeontographica Abt. A, Bd 232,* Lfg. 1-3, pp. 1-83, 6 pls. September 1994.**

p. 6. Line 12, *Favreticeras* (not *Ceratites*).

p. 8. For Ridge A, see Part 3, Text-fig. 1-3.

p. 9. For Ridge B, see Part 2, Text-fig. 2; Part 5, Text-fig. 1.
For Pangjang Formation, see Part 7, Text-fig. 33.
Line 25. Gungsang (not Gunsang).

p. 11. Text-fig. 5. The heavy black lines, some with F, mark faults.

p. 12. Table 3, Upper Marsyangdi. *Gruntea* (a spirigerellid) found rather than *Spirigerella*, also a martiniid.
For Plateau of Lakes, see Part 4, Text-fig. 1; Part 5, Text-fig. 2; Part 6, Text-fig. 3.
For Mesokanto, see Part 5, Text-fig. 2-4.

p. 16. Pangjang Formation of Dolpo. See Part 4, Text-fig. 1, 2; Part 7, Text-fig. 35.

p. 20. Lines 16, 19, and throughout this text. I used an awkward counting system and it should be changed to 8 [principal] lobes for Xenodiscida and 10 [principal] lobes for Meekoceratida.

p. 21. Line 39, basic eight-lobed (not ten) ... distinct from the ten-lobed (not twelve) suture.

p. 22. Line 8, Paraceltitida (not Paraceltida).
Line 52, approaches (not appraoches).

p. 23. Line 7, ten-lobed (not twelve) to eight-lobed (not ten).
Line 40, ten (not twelve) lobes.

p. 24. Line 26, ten not eight saddles (rather than twelve not ten).

p. 25. Line 6, Eoptychitidae (not Eoptychidae). See Part 3.
Line 13, ten-lobed (not twelve).
Line 26, Ussuriidae (not Ossuriidae).

p. 27. Line 18, multisellate (not multicellate).
Right column near base, insert Inyoitinae Spath 1934 and.
Subcolumbitinae Waterhouse 1999 [Part 4, p. 132].

p. 29. Right column, line 46, Shevyrev (not Shervyrev).

p. 30. Repository of collections. As announced in Part 2, the type collections are housed at the Canterbury Museum, Christchurch, New Zealand.

p. 31. Line 3, eight lobes (not ten).

p. 34. Text-fig. 6C. The sutures are visible on the flanks, with the largest of saddles likely to be the first lateral saddle.

p. 35. Last line, Sarytcheva (not Sarytceva).

p. 39. For further discussion of *woodwardi*, see Part 7, pp. 94ff.

p. 40. For further discussion of *latilobatum*, see Part 7, p. 93, Text-fig. 34.

p. 41. Lines 41, 42, eight-lobed (not ten).
Line 43, ten-lobed (not twelve).

p. 46. Line 6, Ussuriidae (not Ossuriidae).

p. 49. Line 10. The 8-10 saddles are exposed on single flank.

p. 50. Text-fig. 9A, suture on shell flank, position of ventral saddle uncertain.

p. 52. Line 29, 8 lobes (not 10).

p. 54. Line 7, 12 lobes (not 14).
Line 8, 14 lobes in Otoceratidae (not 16).
Line 13, 12 well formed lobes (not 14).
Line 15, twelve (not fourteen) well formed lobes.

p. 55. Text-fig. 10.2, 3. The base of the ventral saddle is represented to the left of the suture line.

p. 65. Text-fig. 12D, E. First lateral saddle to left.
Line 15 below Text-fig. 12 and caption, *Khangsaria* described in Part 2, p. 61.

p. 68. Line 16. For *Radioceras*, see Part 2, p. 40.

p. 70. Line 5, Arctic (for *Arctic*).

p. 82. Lines 3, 10, Pengba Member, *Otoceras woodwardi* Zone (not *concavum*).

Part 2.
SYSTEMATIC STUDIES OF THE EARLY MIDDLE SCYTHIAN.

***Palaeontographica Abt. A, Bd 241,* Lfg. 1-3, pp. 27-100, 12 pls. September 1996.**

p. 27. Lines 17, 32. *Kummelea* was proposed as a replacement name for *Kummelia*, preoccupied, by Waterhouse. See Part 7, p. 49.

p. 28. Line 26, *Kummelea* (not *Kummelia*).

p. 29. Line 14, ten-lobed (not twelve). See Part 1, explanation for p. 20.

p. 32. Text-fig. 3. The image has been reversed, and the left side should be to the right.

p. 39. Line 28, *candidus* (ital. not reg.).

p. 44. Lines 4, 19, *Kummelea* (not *Kummelia*).

p. 46. Line 1, *Kummelea*.

p. 56. Text-fig. 7E, line 10, first lateral saddle to left (not right).

p. 72. Lines 23, 25, *Kummelea.* See Part 7, p. 49.

p. 75. Line 46, Clypeoceratidae (not Aspenitidae).

p. 77. Line 30, ie. *Radioceras radiosum*.

pp. 82, 83. These pages are correctly numbered, but the order transposed.

p. 84. Line 31, ten-lobed (not twelve).

p. 85. Line 14, delete “by”.

p. 93. Line 3. *Lilangia* n. gen. (not sp.).

Part 3.
LATE MIDDLE SCYTHIAN AMMONOIDS.

***Palaeontographica Abt. A, Bd 241*, Lfg. 4-6, pp. 101-167, 11 pls. November 1996.**

p. 101. Line 19, *Beoflemingites* not *Boeflemingites* (see p. 153).

p. 104. Line 5. Pija Member may be Changhsingian in age. See Waterhouse 2002c, p. 183.

p. 105. Table 1, Upper Marsyangdi. The *Spirigerella* may be *Gruntea* or ally. A martiniid is also common.

p. 108. Text-fig. 4C. The suture (upper right) shows umbilical edge, but position of ventral saddle not certain.

p. 116. Line 5, *cheneyi* (not *chenezi*).

p. 128. Line 8, saddle (not sadle).

p. 132. Line 35, *Kummelea* (not *Kummelia*). See Part 7, p. 49.

p. 139. Line 13, multisellate (not multicellate).

p. 146. Text-fig. 11A, only umbilical shoulder clear, position of venter and ventral saddle not certain.

Line 4, below Text-fig. 11 caption, *pisangensis* (not *pisangi*).

p. 150. Line 8, Text-fig. 11F4 (not 12F4).

p. 153. Line 41, spiral ribs (not spirals ribs).

p. 160. Lines 16, 18, Pangjang (not Panjang).

p. 167. Line 5, *Xenoceltites*? (add query).

Part 4.

LATE SCYTHIAN.

***Palaeontographica Abt. A, Bd 254*, Lfg. 4-6, pp. 101-190, 11 pls. November 1999.**

p. 103. Line 2, right column, *Palaeophyllites* n. sp. p. 176 (not p. 178).

Line 48, the radially ribbed bivalve is now called *Chuluaria bragaensis* Waterhouse 2000.

p. 104. Line 38. Bivalve is *Chuluaria*, as above.

p. 107. Line 4, most of [inserted] the ammonoids.

p. 109. Line 7, Hedenstroemioidea.

p. 116. Line 30, Dinaritoidea (reg. not ital.).

p. 117. Line 18, Columbitinae (not Columbinae).

p. 119. Line 31, *Olenikites* (ital. not reg.).

p. 126. Line 24, it is [inserted] doubtful.

p. 137. Line 3, 1886 (not 1986).

p. 138. Line 25, Khangsariidae (not Khangsaridae).

p. 141. Line 7, multisellate (not multicellate).

p. 142. Line 8, delete &z.

p. 148. Text-fig. 14A3, first lateral saddle lies at right side.

Text-fig. 14D2, first lateral saddle at right side.

Text-fig. 14D3, first lateral saddle at left side.

p. 152. Line 2, Text-fig. 15A, whorl (not worl).

p. 154. Line 30, replace comma with period.

p. 157. Line 16, multisellular (not multicellular).

p. 159. Line 20, olistostrome not olistrostrome.

p. 160. Line 30, *Claraia* now *Chuluaria* Waterhouse 2000.

p. 163. Line 41, *Pseudoceltites* (ital. not reg.).

p. 166. Text-fig. 18.5, first lateral saddle at left.

p. 167. Line 40, n. fam. (not fa.).

p. 168. Line 17, Leiophyllitidae (not Leiophyllitiidae).

p. 170. Line 12 below the text-figure and caption, delete “the most”.

p. 172. Line 15 below the text-figure and caption, *Glyptophiceras* (not

Glyptohiceras).

p. 174. Text-fig. 22B, whorl height 12 mm.

p. 177. Line 40, *thalmanni* (ital. not reg.).

p. 179. Line 30, *Keyserlingites* (ital. not reg.).

p. 181. Line 39, Pangjang (not Panjang).

p. 183. Line 30, band (not beds).

Part 5.

SYSTEMATIC STUDIES OF THE EARLY ANISIAN.

***Palaeontographica Abt. A, Bd 255*, Lfg. 1-3, pp. 1-84, 10 pls. December 1999.**

p. 1. Line 35, (Superfamily Danubitoidea) - [add front bracket].

p. 2. Left column, base, Sunjar Formation. Add *Stenopopanoceras kukrii* n. sp.

p. 3. *costatus* (ital. not reg.).

p. 5. Line 20. Bivalve aff. *Claraia* is now *Chuluaria bragaensis* Waterhouse 2000, p. 176.

p. 9. Line 30, *kaisangensis* (ital. not reg.).

Line 31, *simplex* (ital. not reg.).

p. 12. Text-fig. 5E, black oval represents spine base.

p. 15. Line 44, p. (not pi.).

p. 26. Line 21 and 26, *thorongensis* (ital. not reg.).

p. 28. Line 8, *welteri* (ital. not reg.).

p. 29. Line 6, insert “up to” before 20.

p. 31. Line 33, *attenuatus* (ital. not reg.).

p. 35. Line 21, *Xenoceltites* and (insert space).

p. 36. Line 39. In Part 4 *Eophyllites* was classed in Leiophyllitidae but the position remains uncertain.

p. 39. Line 21, *involucrum* (not *Involucrum*).

p. 45. Line 44, faintly (not faintyly).

p. 47. Line 1, Family Albanitidae Waterhouse 1999b. See Part 4, p. 110.

p. 51. Text-fig. 17A4, arrow misplaced to left for ventral saddle.

p. 54. Lines 39-44, *Prosphingites coombsi* is now the type species of genus *Kakaria* Waterhouse (2001, p. 159).

p. 55. Line 1, falling (not failing).

p. 57. Line 5, multisellate (not multicellate).

p. 63. Text-fig. 20. Solid black shows nodes or bullae.

p. 65. Line 28, *Kummelea* replaces *Kummelia*. See Part 7, p. 49.

p. 71. Line 19, its (not it).

p. 77. Second last line, the bivalve is now called *Chuluaria bragaensis*

Waterhouse 2000.

Part 6.
SYSTEMATIC STUDIES OF THE MUKUT (MOSTLY ANISIAN) AMMONOIDS FROM MANANG.

***Palaeontographica Abt. A, Bd 266*, Lfg. 4-6, pp. 121-198, 8 pls. November 2002.**

p. 149. Line 20, Trachyceratid (not Trachyceraid).
p. 157. Line 18, it looks more like [add it].
p. 159. Line 14, tapered venter (not rounded).
p. 160. Line 39, figured (not figued).
p. 165. Line 29, Tozer took a broad view (insert a).
p. 167. Line 28, delete comma after Danubitidae.
p. 170. Line 26, *Ussurites* (not *Ussurires*).
p. 171. Line 26, marked (instead of scored).
p. 173. Line 7, Hollanditid (not Holanditid).
p. 186. Table 6. The x for *Paradanubites* should be transferred to the Kummel - Wang column.
p. 197. Pl. 6, fig. 7, *Japonites* aff. (not cf.) *hei.*

Part 7.
LATE ANISIAN AMMONOIDS FROM WEST NEPAL, AND WORLD WIDE CORRELATIONS FOR EARLY AND EARLY MIDDLE TRIASSIC AMMONOID FAUNULES.

***Palaeontographica Abt. A, Bd 267*, Lfg. 1-6, pp. 1-118, 8 pls. December 2002.**

p. 11. Line 21, Beyrichitidae (not Beyrichtitidae).
p. 12. Line 12, 1863 (not 1963).
Line 22, indicate (not indicates).
p. 17. Line 23, *hatschekii* (not *hatscheki*).
p. 18. Lines 25, 29, 32, 34, 36, *hatschekii* (not *hatscheki*).
p. 19. Line 2, *hatschekii* (not *hatscheki*).
p. 31. Line 5, without (not with).
p. 42. Text-fig. 24C, *Amphipopanoceras* (not *Parapopanoceras*).
p. 44. Line 6, his (not this).
p. 45. Line 44, succession (not succesion).
p. 48. Line 4 below Table, Gungdang (not Gundang).
p. 58. Line 26, delete bracket before 1981.
Line 31, *Prionolobus* (not *Prinolobus*).

Line 40, add bracket to read (Text-fig. 31).
p. 60. Line 44, base (not Base).
p. 66. Line 29, have (not has).
p. 88. Line 13, delete bracket.
p. 106. Line 6, interpreted (not interreted).
p. 107. Line 44, *bhaktabahadhuri*.
p. 109. Line 11, Xenodiscida (not Xenodisida).
p. 116. Line 25, brachiopod (not brachipod).
p. 117. Line 18, *hatschekii* (not *hatscheki*).

2. EARLY TRIASSIC AVICULOPECTINIDINA (MOLLUSCA: BIVALVIA) FROM DOLPO AND MANANG, NEPAL HIMALAYA

Plates 10 - 13

Pectinoid bivalves (Phylum Mollusca) were described from the Scythian (Early Triassic) beds of the Himalaya in the Manang and Dolpo districts of Nepal by Waterhouse (2000). The species belong to *Posidonia,* Family Posidoniidae, and to *Claraia* and its close allies classed in Subfamily Claraiinae Gavrilova, Family Pterinopectinidae. Two new genera were recognized, *Rugiclaraia* Waterhouse, type species *Claraia aurita* (Hauer) in Tribe Pseudoclaraiini Gavrilova, and *Chuluaria* Waterhouse, type species *C. bragaensis* Waterhouse in Tribe Claraiini Gavrilova. New species *Claraia nakazawai, C. kashmirensis, Crittendenia alta, C. langpoensis,* and *Posidonia elegantula* were named. The figures as published in Waterhouse (2000) were poorly reproduced, and here the figures are re-issued, with slight rearrangement and re-numbering. Use of a CD will provide clear detail. The figured material is kept at the Canterbury Museum, Christchurch.

In 2001 the classification of the Pectinida Newell & Boyd, 1995, was expanded in a major overview, with proposal of new suborders Aviculopectinidina and Monotidina. Within Aviculopectinidina, Claraiinae Gavrilova, 1996 were retained as a subfamily of Pterinopectinidae Newell, 1938, and shown to strongly approach Halobiidae Kittl, 1912. Posidoniidae Frech, 1909 were regarded as too poorly known to be classed with confidence (Waterhouse 2001, p. 134).

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Plate 1

Fig. 1-5. Plant impressions from Shokang Formation, north of Lake Kyobra, collected by the writer in 1987.

Fig. 6-10. *Brachythyrina boonlomi* n. sp. from Ko Yao Noi Formation, south Thailand. 6, rubber latex cast of ventral valve TBR 159 exterior, holotype, x 1. 7, ventral internal mould TBR 167 x 1. 8, ventral internal mould TBR 348 x1. 9, rubber latex cast of ventral interior TBR 160 x 2. 10, rubber latex cast of ventral interior TBR 159, x 2. Fig. 9 and 10 tilted to low angle from commissure. Also figured in Waterhouse (1981, pl. 21, fig. 1, 10, 13, pl. 22, fig. 6, 1) respectively.

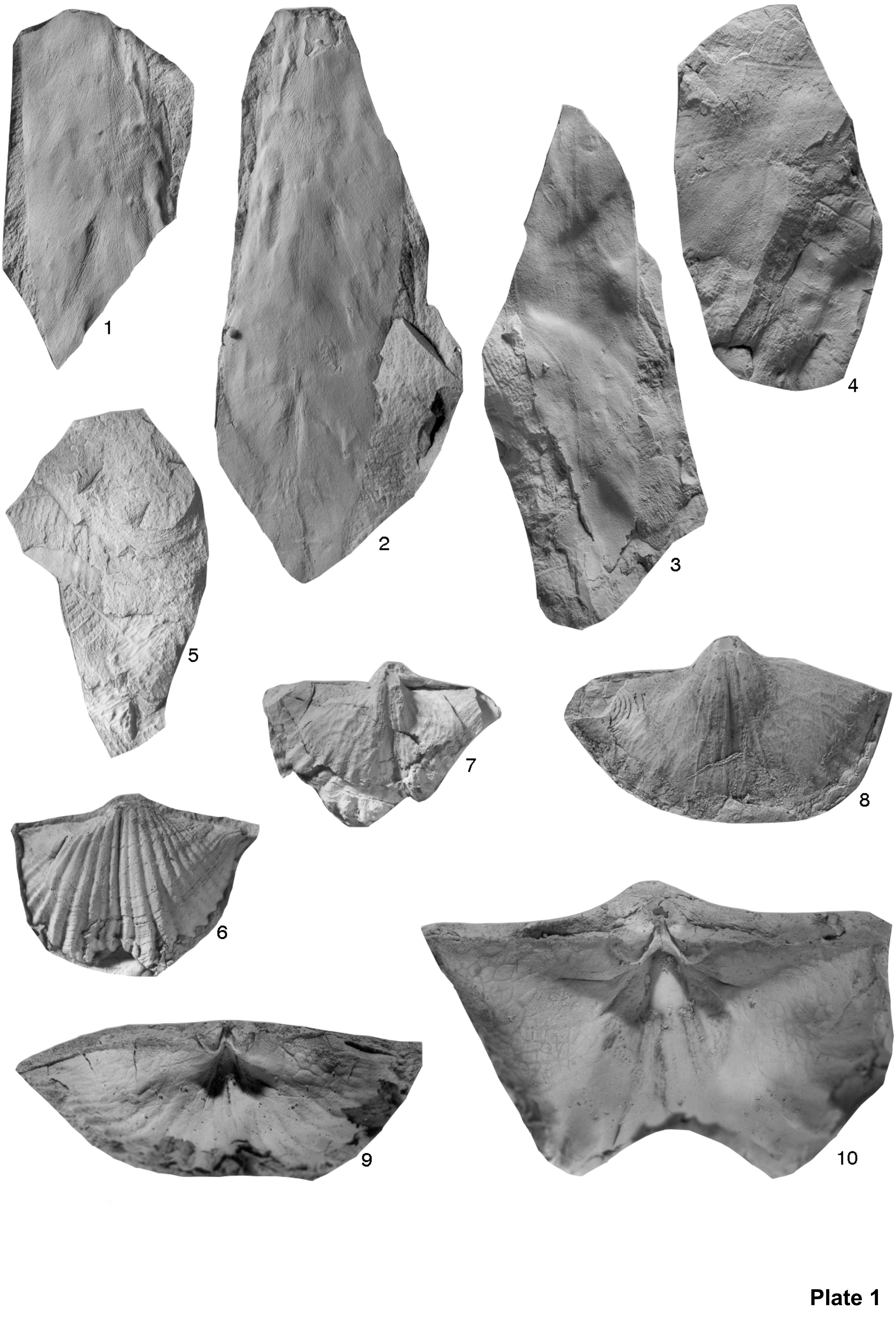

Plate 1

Plate 2

Fig. 1. *Sulcirugaria transversa* Waterhouse, UQL 73588 from UQL 4903, Pija Member, north of Braga, x 2. Also figured by Waterhouse (1983a, pl. 1, fig. 5).

Fig. 2, 4. ?*Strophalosia gerardi* King from UQL 4801, Pija Formation north of Braga, x 2. 2, dorsal view of exterior, rubber latex cast, UQF 73603. 4, ventral external mould of immature specimen UQF 73604. Figured by Waterhouse (1983a, pl. 2, fig. 1, 2).

Fig. 3. *Dowhatania dowhatensis* (Diener) from Fenestella Shales, Kashmir, rubber latex cast x 2, dorsal valve interior and surrounding ventral external spines, GSI 11071, figured by Diener (1915, pl. 2, fig. 10). This species is also found in the Thini Chu rocks of Manang district.

Fig. 5-8. *Strophalosia diadema* Waterhouse from *Lamnimargus himalayensis* Zone of upper Shyok Valley, south Karakorum, India. 5, 8, ventral valve internal mould x 2, x 1, after and before leaching. 6, 7, external mould and rubber latex cast, dorsal valve holotype x 1. CASG specimens also figured by Waterhouse & Gupta (1983, pl. 1, fig. 7, 9, pl. 1, fig. 6, and pl. 3, fig. 3 respectively).

Fig. 9-13. *Echinalosia magnispina* Waterhouse from UQL 4799, Pija Member, north of Braga. 9, 10, dorsal and ventral aspects of rubber latex cast, UQF 73606, holotype, x 2. 11, ventral view rubber latex cast UQF 73605 x 2. 12, 13, ventral and dorsal views of internal mould UQF 73606, holotype, x 2. Figured by Waterhouse (1983a, pl. 2, fig. 3-7).

Fig. 14. *Papiliolinus eishmakami* Waterhouse & Gupta, latex cast of dorsal exterior, presumed to be holotype, GSI 6226, x 2, from Fenestella Shale, Kashmir.

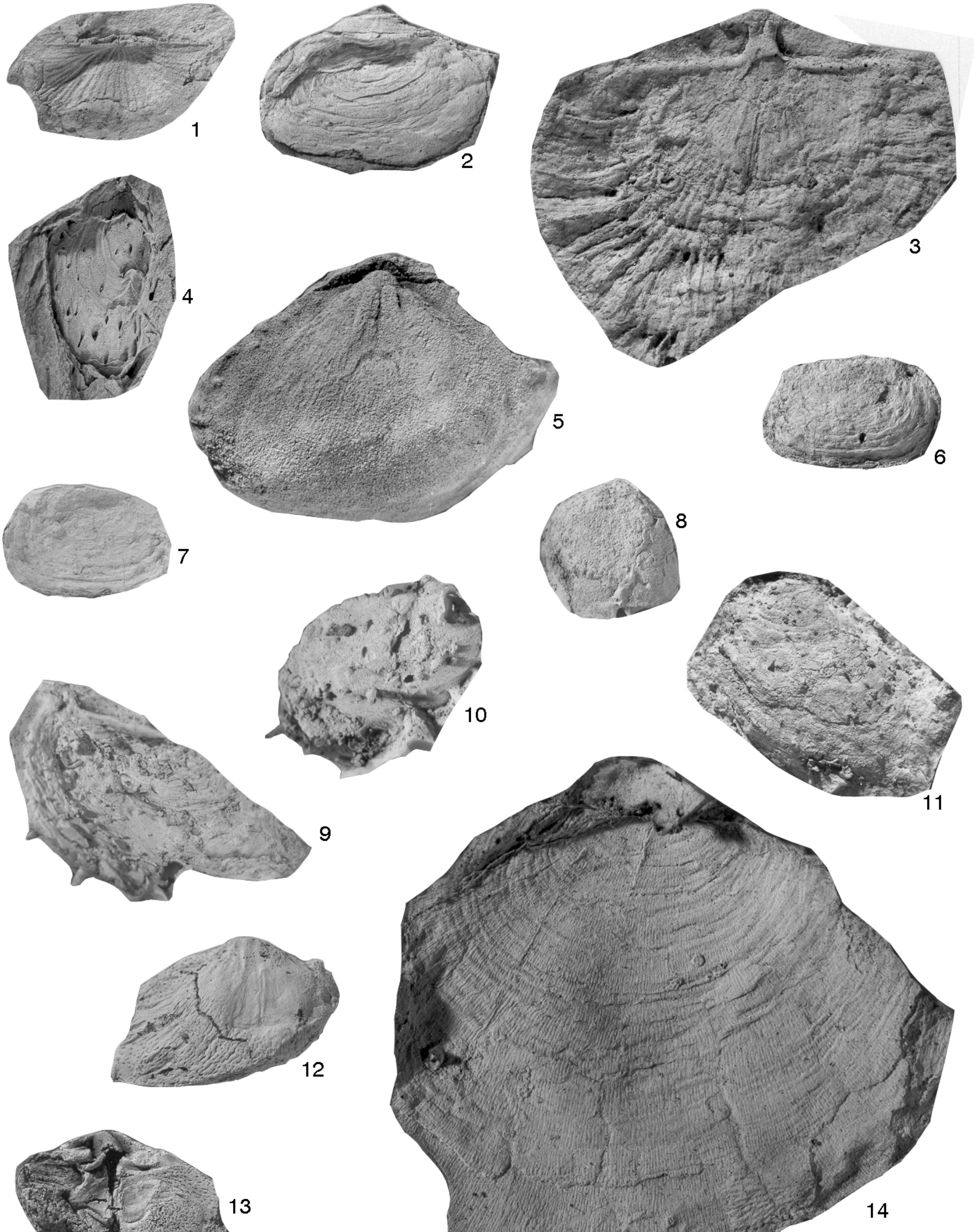

Plate 2

Plate 3

Fig. 1, 2, 4, 5, 6. *Betaneospirifer shii* n. sp. from Marsyangdi Formation, north of Braga, x 1. 1, 4, 5, holotype, ventral valve, exterior, valve with posterior shell lifted to show muscle field, and external mould from PMb5, Braga Member. 2, small dorsal valve from PMb5. 6, ventral valve from PMh5, Hongde Member. Kept at Canterbury Museum.

Fig. 3. *Neospirifer poletaevi* n. sp. holotype, B 82373, also figured by Davidson (1862, pl. 2, fig. 2c) and Waterhouse (1978, pl. 3, fig. 19) x 2. Kept at Museum of Natural History, London.

Fig. 7. *Betaneospirifer neomarcoui* (Licharew) with valves conjoined, dorsal valve on top, from upper Shyok valley, southern Karakorum Range, also figured by Waterhouse & Gupta (1983, pl. 2, fig. 7), x 1, CASG specimen.

Fig. 8. *Betaneospirifer ambiensis* (Waagen), flawed rubber latex cast of specimen figured by Diener (1899, pl. 5, fig. 6), from Zewan Formation, Kashmir, GSI 6277, x 2.

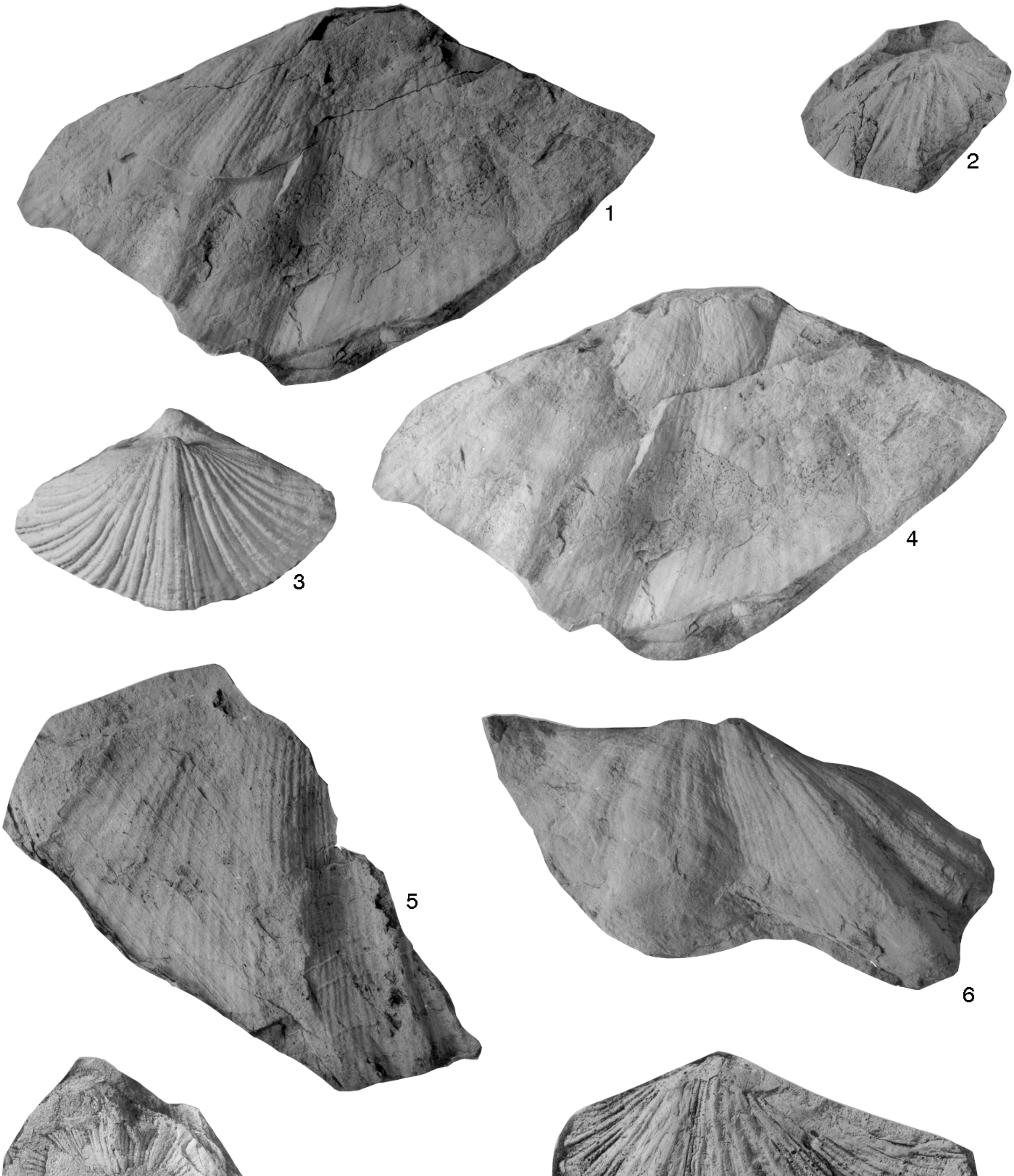

Plate 3

Plate 4

Fig. 1, 5, 6. *Wadispirifer hongdeensis* n. sp. 1, ventral valve UQF 73656 from UQL 4795, Pija Member north of Braga, x 1. The valve was originally figured as *kubeiensis* Ding by Waterhouse (1983a, pl. 7, fig. 8). 5, 6, ventral and dorsal aspects of internal mould from PJ1, Pija Member, north of Braga, x 1. Kept at Canterbury Museum.

Fig. 2, 3. *Quadrospira tibetensis* (Ding) from UQL 4795, Pija Member north of Braga, x 1. 2, rubber latex cast of immature ventral valve UQL 73654. 3, juvenile ventral valve, rubber latex cast UQF 73649. These specimens were originally figured as *Neospirifer kubeiensis* Ting (= Ding) by Waterhouse (1983a, pl. 6, fig. 11, 12).

Fig. 4, 7, 8. *Grantonia cracovensis* Wass from Fairyland Formation, Cracow, southeast Bowen Basin, Queensland, x 1. 4, 8, dorsal and ventral aspects of internal mould UQF 74156, also figured by Waterhouse (1987, pl. 3, fig. 9, 12). 7, dorsal aspect, unregistered specimen.

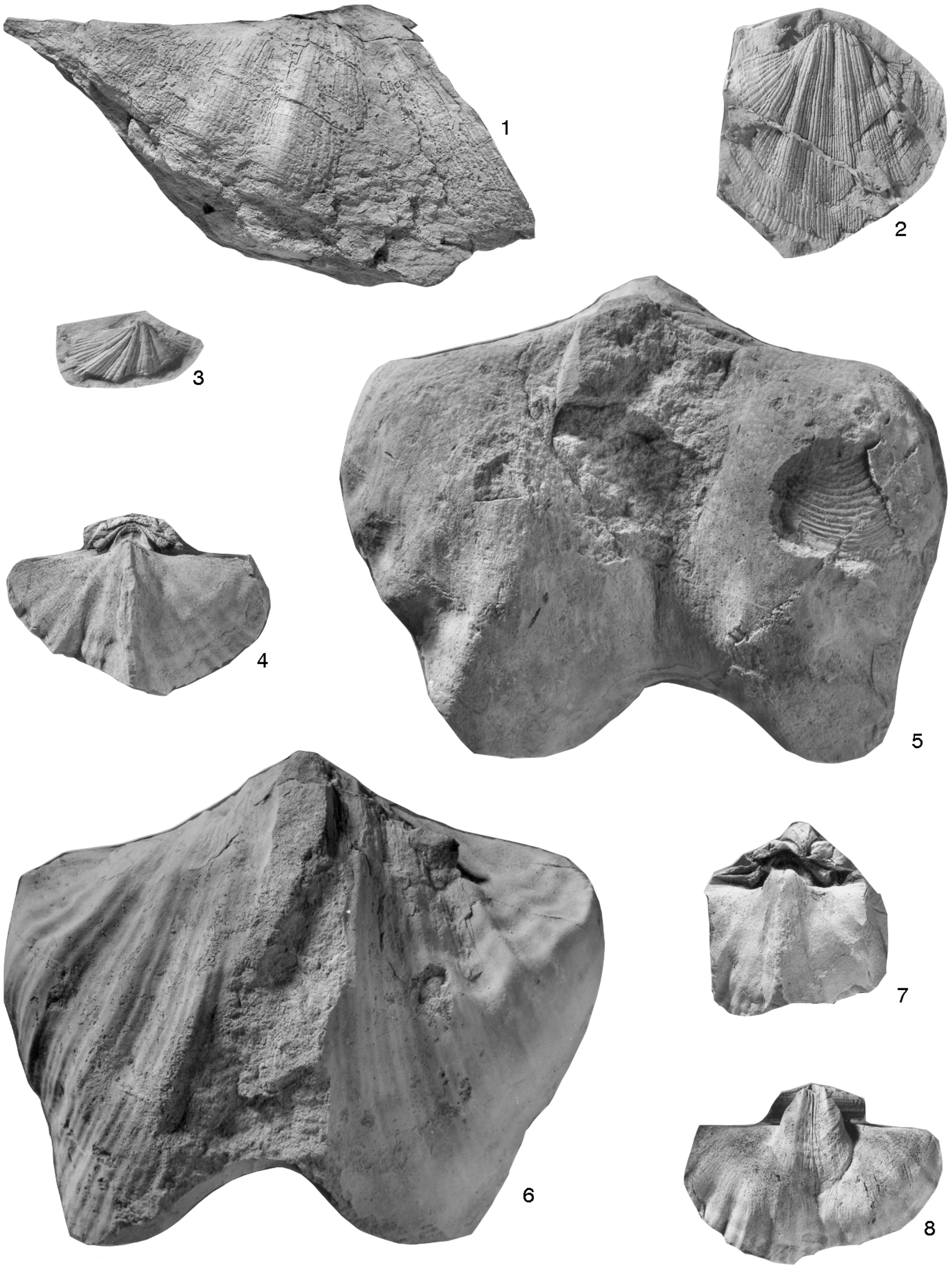

Plate 4

Plate 5

1, *Wadispirifer hongdeensis* Waterhouse n. sp. damaged ventral valve UQF 73653, x 1. This specimen was originally figured as *Neospirifer kubeiensis* Ting (Ding) by Waterhouse (1983a, pl. 7, fig.3).

Fig. 2, 3, 6, 9. *Grantonia cracovensis* Wass from Fairyland Formation, Cracow, southeast Bowen Basin, Queensland, x 1. 2, 3, ventral and dorsal aspects of internal mould UQF 43597 also figured by Waterhouse (1987a, pl. 3, fig. 6, 11). 6, ventral aspect of UQF 275431. 9, dorsal aspect UQF 74155. Also figured in Waterhouse (1987a, pl. 3, fig. 8, 10).

Fig. 4. *Cratispirifer macroplica* n. sp. from *Lamnimargus himalayensis* Zone, upper Shyok valley, southern Karakorum Range, x 1, ventral aspect, kept at Canterbury Museum.

Fig. 5, 8. *Occidalia* sp. from *Lamnimargus himalayensis* Zone, upper Shyok valley, southern Karakorum Range, ventral and dorsal aspects x 1, also figured by Waterhouse & Gupta (1983, pl. 2, fig. 9, 12). Kept at Centre of Advanced Study in Geology, Chandigarh.

Fig. 7. *Occidalia plicatus* (Waterhouse), rubber latex cast x 1, dorsal aspect, from Agglomeratic Slate, Kashmir, also figured as GSI external mould by Bion (1928, pl. 5, fig. 9).

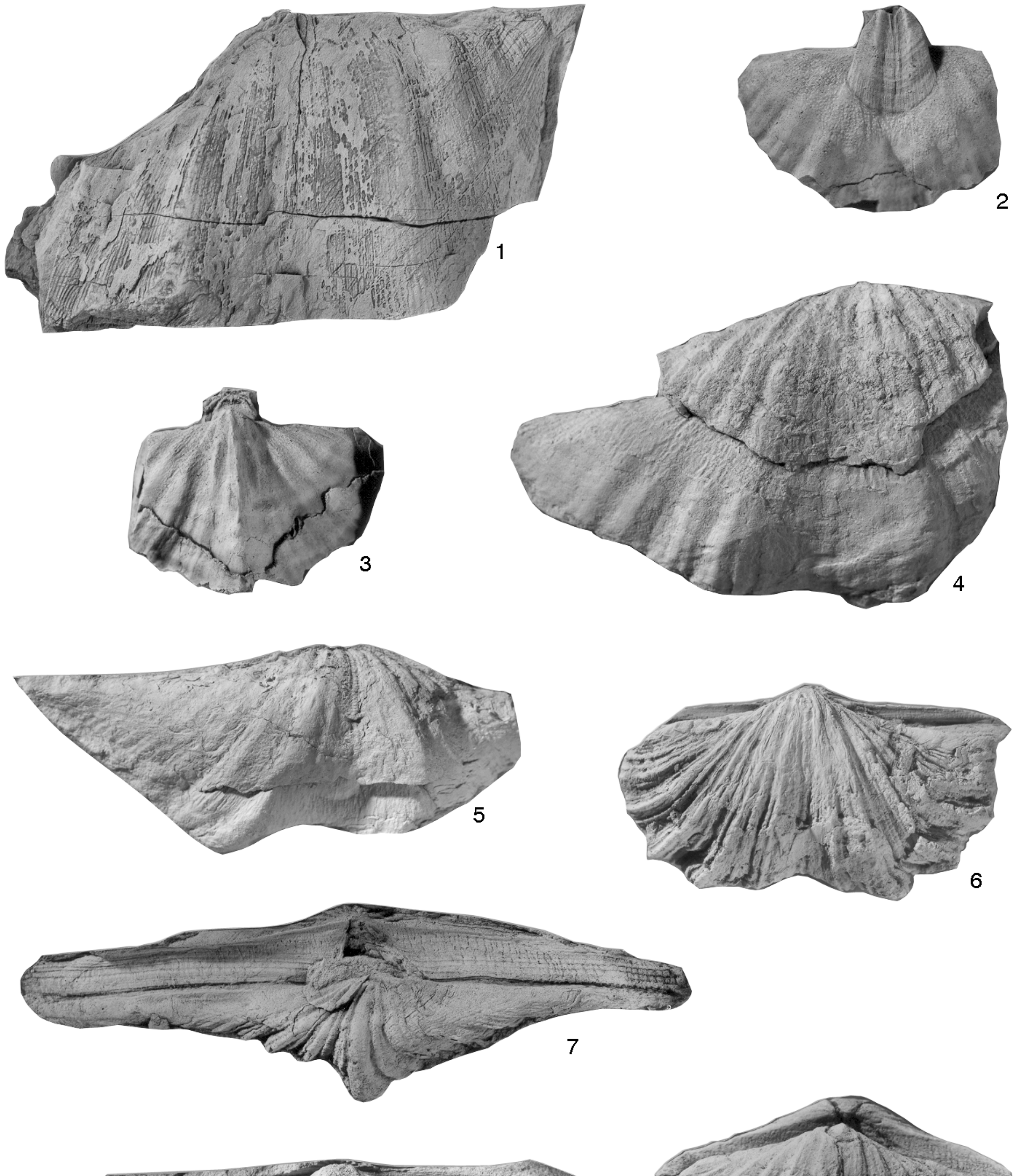

Plate 5

Plate 6

Fig. 1-11. *Adminiculoria middlemissi* (Diener) from Fenestella Shales, Kashmir, x 1 except fig. 1 x 2. 1, latex rubber cast of dorsal valve and ventral valve GSI 11100 figured by Diener (1915, pl. 4, fig. 10) and Waterhouse & Gupta (1979a, pl. 12, fig. 5). 2, rubber latex moulds of CASG 516, 517, figured in Waterhouse & Gupta (1977, pl. 5, fig. 13). See fig. 3. 3, ventral internal mould, CASG 516, figured by Waterhouse & Gupta (1977, pl. 5, fig. 10). 4, ventral internal mould CASG 517, figured by Waterhouse & Gupta (1977, pl. 5, fig. 11). See fig. 2. 5, ventral internal mould CASG 518, figured by Waterhouse & Gupta (1977, pl. 5, fig. 12). See fig. 11. 6, dorsal internal mould CASG 521 figured by Waterhouse & Gupta (1977, pl. 5, fig. 16). 7, ventral internal mould, unregistered. 8, ventral exterior CASG 519, figured in Waterhouse & Gupta (1977, pl. 5, fig. 9). 9, dorsal internal mould, CASG 520, figured by Waterhouse & Gupta (1977, pl. 5, fig. 15). 10, rubber latex of ventral interior, CASG 688, figured by Waterhouse & Gupta (1979a, pl. 12, fig. 8). 11, rubber latex of ventral interior CASG 518, figured also by Waterhouse & Gupta (1977, pl. 5, fig. 14). See fig. 4.

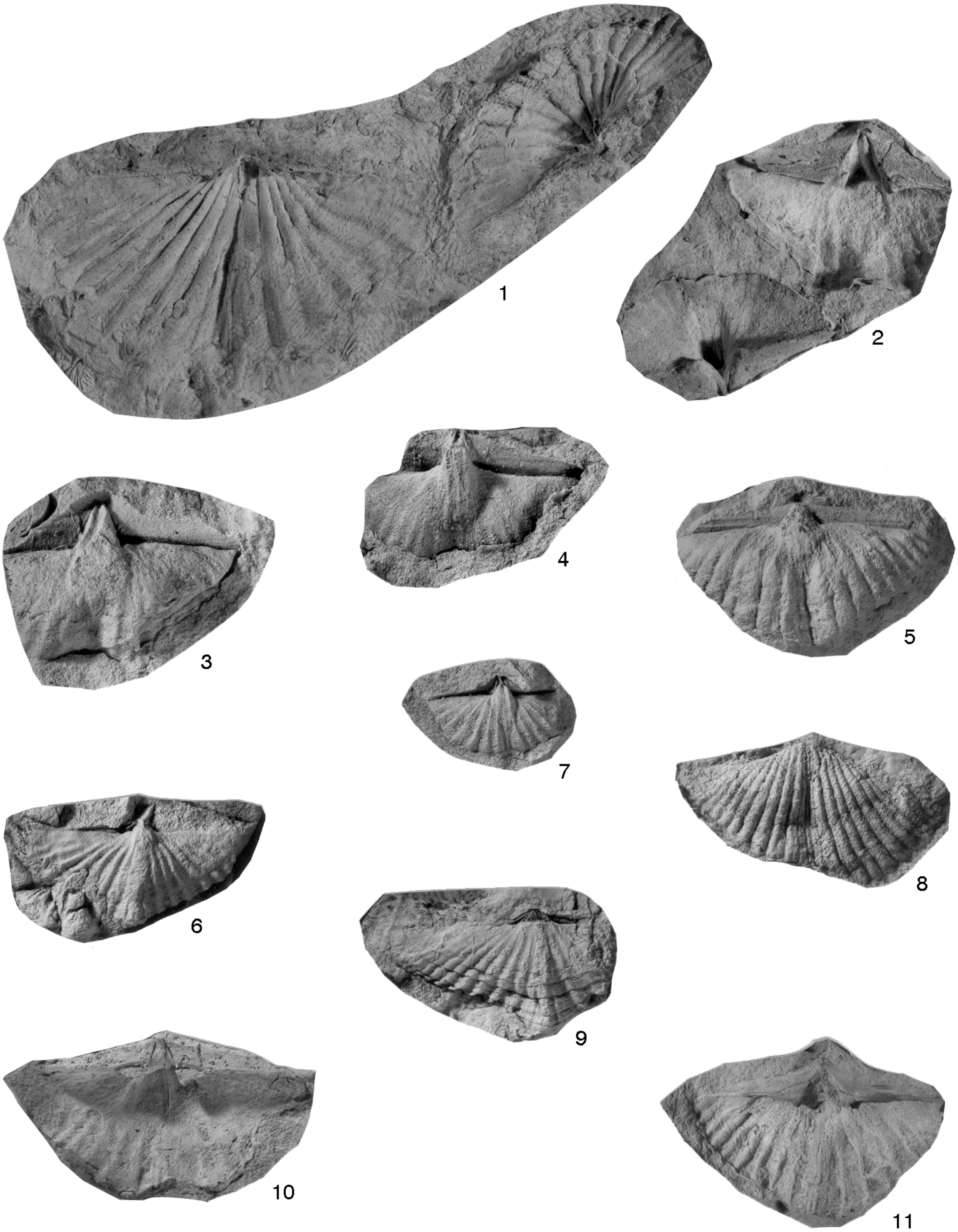

Plate 6

Plate 7

Fig. 1-5. *Varuna varuna* (Diener) from Fenestella Shales, Kashmir, x 2. 1, rubber latex cast of valve, GSI 11103, figured by Diener (1915, pl. 4, fig. 13). 2, dorsal internal mould CASG 506 figured by Waterhouse & Gupta (1977, pl. 5, fig. 2). 3, rubber latex cast of ventral interior, unregistered specimen. 4, lectotype GSI 11104 figured by Diener (1915, pl. 4, fig. 14) and Waterhouse & Gupta (1979a, pl. 12, fig. 7). 5, rubber latex exterior of dorsal valve CASG 507, figured by Waterhouse & Gupta (1977, pl. 5, fig. 4) as neospiriferine.

Fig. 6-9. *Trigonotreta thomasi* Waterhouse n. sp. from Bijni tectonic unit, Garhwal Himalaya. 6, 8, 9, dorsal rubber latex casts x 2, for comparison with *Varuna varuna*. 6, CASGF 596. 8, holotype CASGF 532. 9, CASGF 547. Refigured from Waterhouse & Gupta (1978, pl. 4, fig. 3, 4, 6). 7, internal ventral mould CASG 595 x 2 figured by Waterhouse & Gupta (1978, pl. 4, fig. 5). This was wrongly judged to belong to *Trigonotreta stokesii* Koenig by Clarke (1990).

Fig. 10, 11. Neospiriferid gen. & sp. indet. from Fenestella Shales, Kashmir, x 1. 10, rubber latex cast of ventral interior CASG 505 figured by Waterhouse & Gupta (1977, pl. 5, fig. 1). 11, ventral internal mould CASG 504 figured by Waterhouse & Gupta (1977, pl. 4, fig. 10).

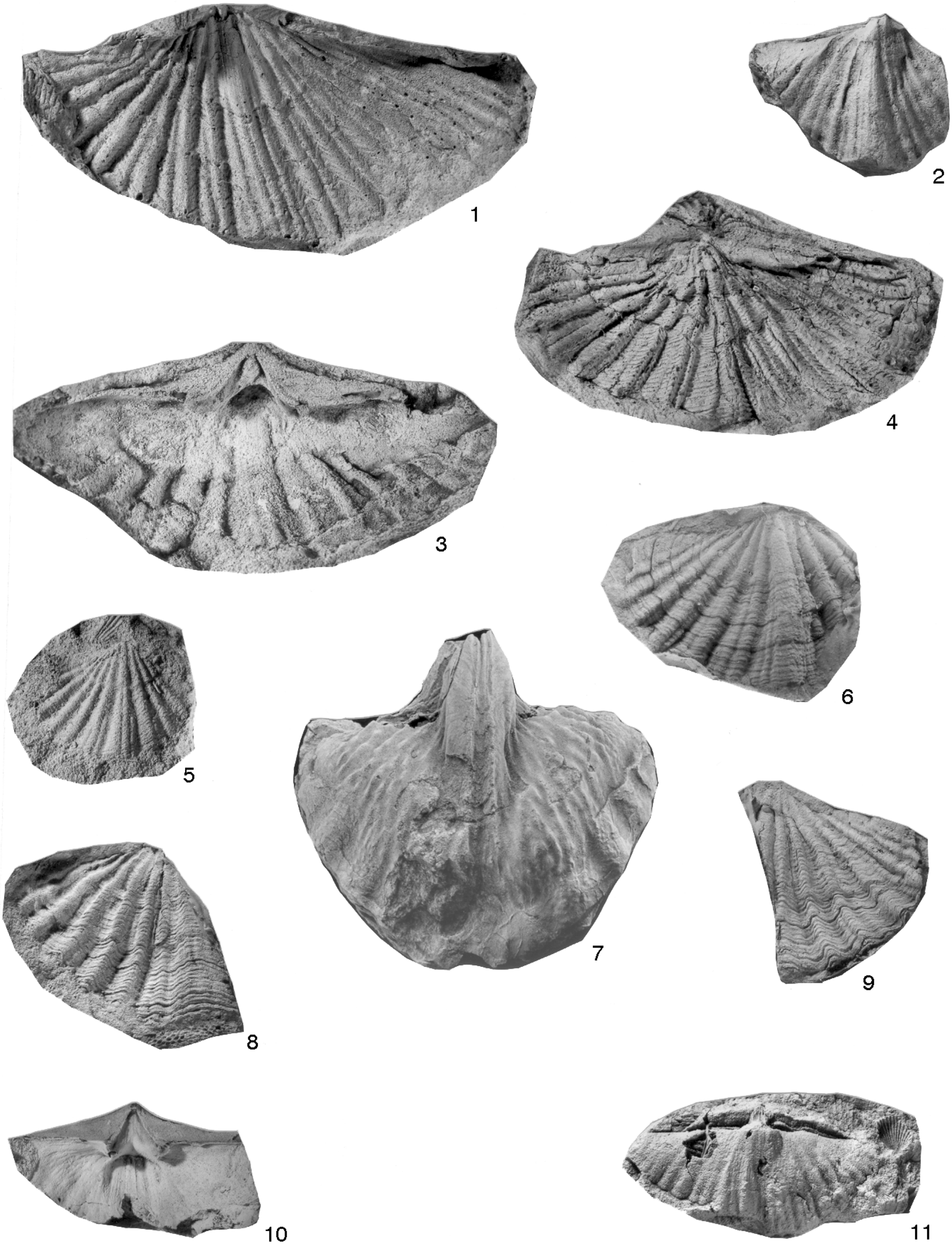

Plate 7

Plate 8

Fig. 1, 2. *Spiriferella rajah* (Salter) from Pija Member north of Braga.
1, ventral valve UQF 73646 from UQL 4805 x 1. 2, dorsal exterior, rubber latex cast UQF 73647 from UQL 4807, x 2. Figured also by Waterhouse (1983a, pl. 6, fig. 5, 6).

Fig. 3-5. *Spiriferella grunti* Waterhouse n. sp. from Marsyangdi Formation, Manang district, x 1. 3, ventral valve from PMh5, Hongde Member. 4, 5, ventral and dorsal aspects of holotype from same locality. Kept at Canterbury Museum.

Fig. 6-8. *Spiriferella nepalensis* Legrand-Blain from Marsyangdi Formation x 1. 6, ventral valve from PMh5, Hongde Member. 7, ventral valve from PMb5, Braga Member. 8, ventral valve from PMg3, Gungsang Member. Kept at Canterbury Museum.

Fig. 9-11. *Arcullina? qubuensis* (Ding) ventral valves from Pija Member north of Braga. 9, detail of micro-ornament on external mould UQF 73650 x 6. 10, UQF 73649 from UQL 4807 x 1. 11, UQF 73648 from UQL 4804 x 2. Also figured by Waterhouse (1983a, pl. 6, fig. 7, 9, 10).

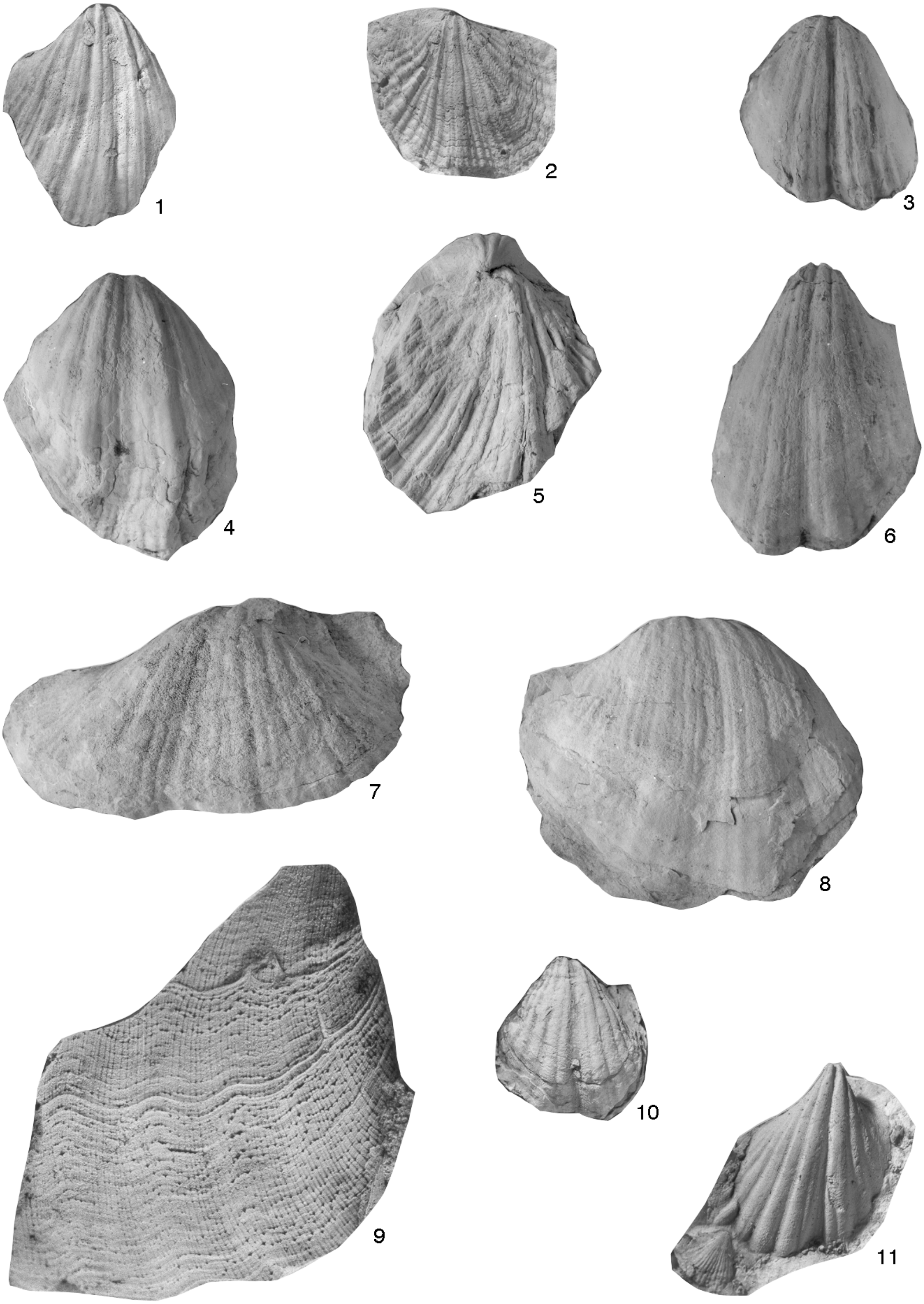

Plate 8

Plate 9

Fig. 1-4. *Arcullina angiolinii* Waterhouse n. sp. 1-3, ventral, dorsal and lateral aspects of holotype from PMb2, Braga Member, Marsyangdi Formation, x1. See Text-fig. 36. 4, ventral internal mould from PMb5, Braga Member, x 1. Kept at Canterbury Museum.

Fig. 5. *Pteroplecta* sp. from Braga Member, Marsyangdi Formation, showing costate fastigium. Rubber latex cast of dorsal valve, x 1.

Fig. 6-14. *Pteroplecta sulcata* Waterhouse from Pija Member north of Braga. 6, ventral valve rubber latex cast UQF 73645 from UQL 4807 x 1. 7, unregistered dorsal valve, rubber latex cast, with *Cleiothyridina*. 8, dorsal interior UQF 73643 from UQL 4792. 9, dorsal rubber latex cast, UQF 73637 from UQF 4803 x 1. 10, ventral valve UQF 76340 from UQL 4792 x 1. 11, 12, holotype UQF 73638 ventral valve rubber latex cast and internal mould, from UQL 4792 x 1. 13, dorsal valve UQF 73642 from UQL 4805 x 2. 14, dorsal internal mould UQF 73644 from UQL 4803 x 2. Also figured by Waterhouse (1983a).

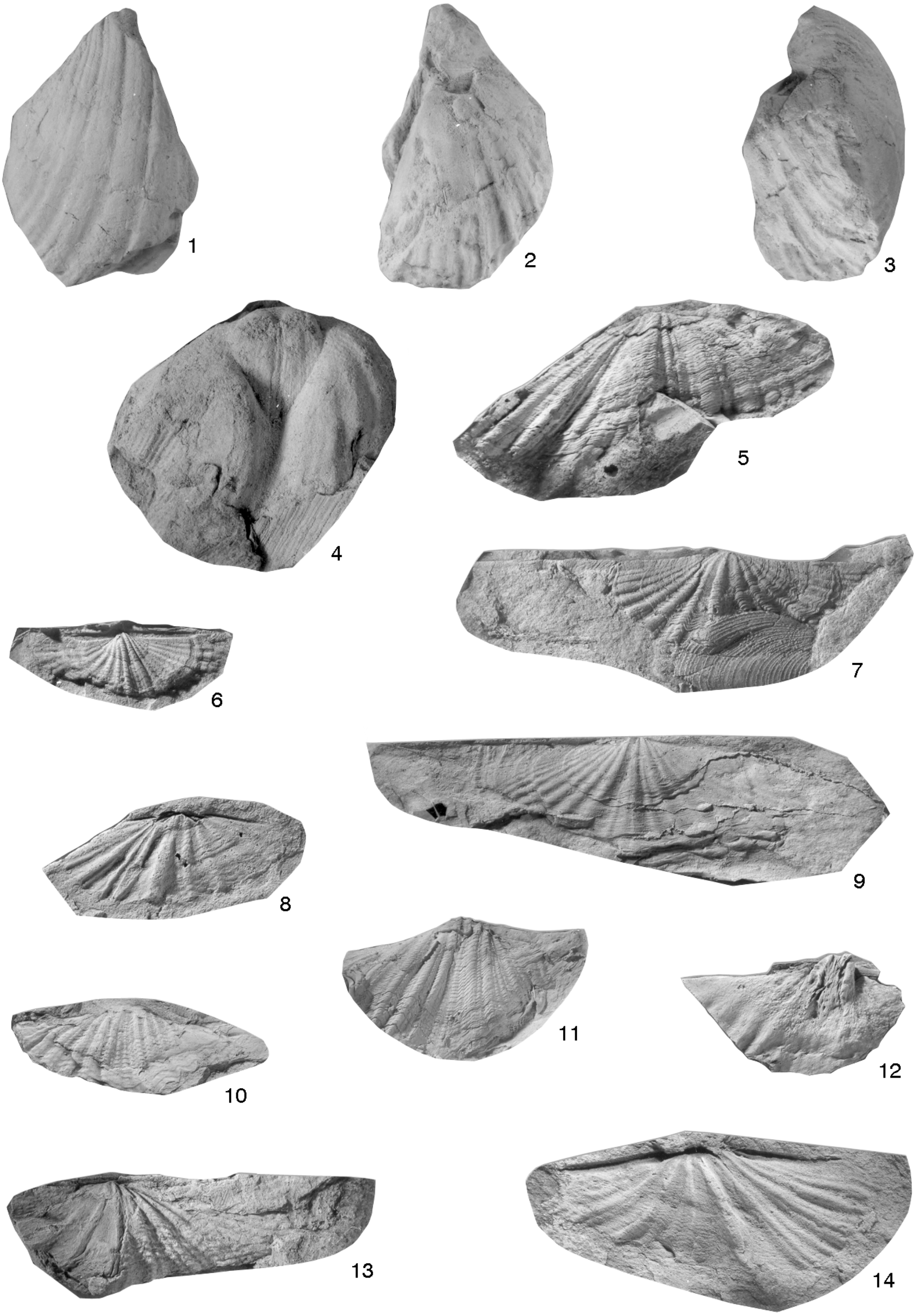

Plate 9

Plate 10

Fig 1-4. *Claraia dieneri* Nakazawa from Pengba Member, Manang x 1.
1, right valve FMo 3364. 2, external mould of right valve FMo 3361. 3, broken left valve FMo 3362. 4, right valve FMo 3363.
Fig. 5-11 *Claraia griesbachi* (Bittner) from Chegaji Member, Manang.
5, left valve FMo 3371. 6, 9, external moulds of mostly left valves under different lighting, FMo 3372 (lower right), small right valve FMo 3368 to right above, FMo 3373 to left in fig. 9. 7, left valves including FMo 3366 to right and FMo 3367 to left. 8, right valve FMo 3396 x 2. 10, right valve with anterior auricle outlined FMo 3548 x 2. 11, left valve FMo 3369. Specimens x 1 except Fig. 8 x 2.
Fig. 1-4 originally figured as Waterhouse (2000, text-fig. 1A-D) and fig. 5-11 as Waterhouse (2000, text-fig. 3A-G).

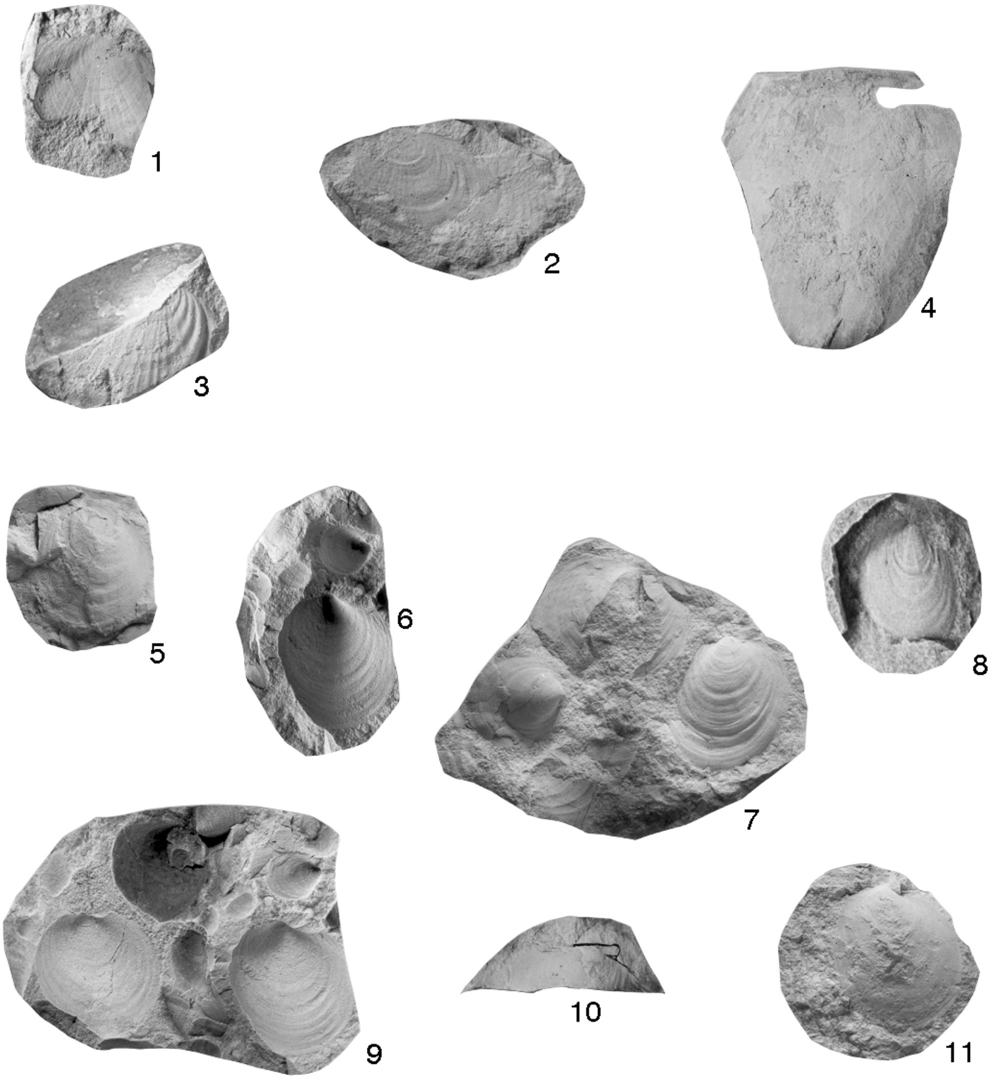

Plate 10

Plate 11

Fig. 1-3, 6. *Claraia nakazawai* Waterhouse x 1 from Sabche Member, Manang. 1, 2, left and right aspects of holotype FMo 3389. 3, left valve FMo 3387. 6, left valve FMo 3383.

Fig. 4. *Crittendenia painkhandana* (Bittner) left valve FMo 3395 x 2, Sabche Member, Manang.

Fig. 5. *Claraia kashmirensis* Waterhouse right valve FMo 3390 x 2, Kangla Member, Manang.

Fig. 7. *Crittendenia nammalensis* (Nakazawa) - left valve FMo 3406 x 1, from Sungjar Formation, Dolpo.

Fig. 8-10. *Crittendenia punjabiensis* (Wittenburg). 8, left valve FMo 3407 x 1 from Sungjar Formation, Dolpo. 9, right valve FMo 3405 x 2, Sungjar Formation, Dolpo. 10, left valve FMo 3403 x 2, Kone Member, Manang.

Fig. 11-15. *Crittendenia langpoensis* Waterhouse x 1 from Langpo Member, Manang. 11, left valve FMo 3551. 12, right valve with umbonal cicatrix FMo 3404. 13, holotype right valve FMo 3397. 14, left valve FMo 3398. 15 right valve with umbonal cicatrix, FMo 3398.

Fig. 1-6 originally figured as Waterhouse (2000, text-fig. 4A-F) and fig. 7-15 as Waterhouse (2000, text-fig. 6A-I).

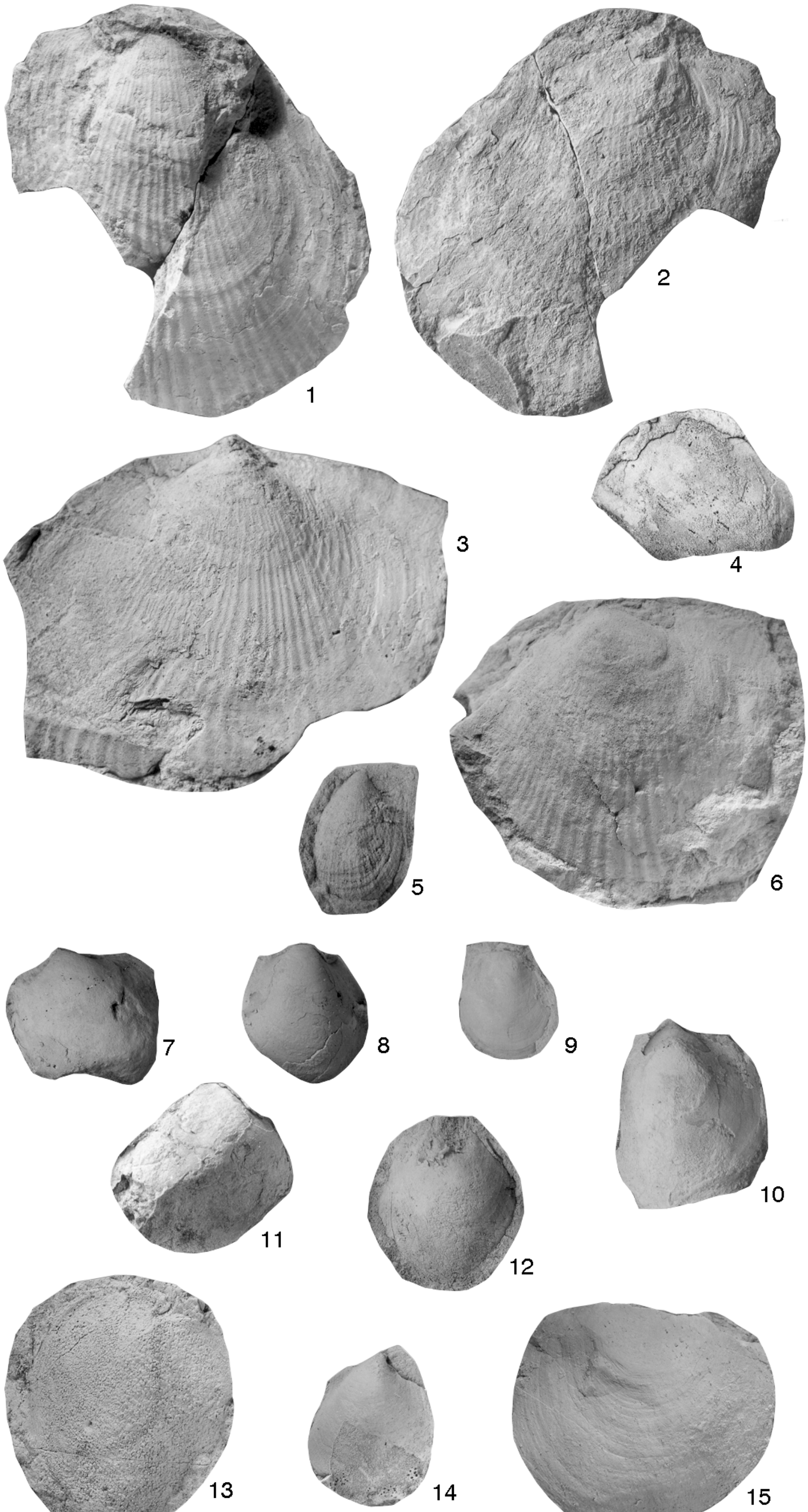

Plate 11

Plate 12

Fig. 1-4. *Claraia nakazawai* Waterhouse x 1 from Sabche Member, Manang. 1, left valve FMo 3549. 2, right valve FMo 3381 and part of left valve, possibly *Rugiclaraia?* sp. A. 3, right valves FMo 3380 (exterior) and FMo 3379 (interior) and part of left valve. 4, right valve FMo 3384 and small left valve FMo 3385.

Fig. 5. *Pteroclaraia* sp. right valve FMo 3427 x 1 from Sabche Member, Manang. u = umbo.

Fig. 6-10. *Chuluaria bragaensis* Waterhouse from Langpo Member, Manang. 6, holotype right valve FMo 3414 and also right valve FMo 3415, x 2. 7, left valve FMo 3409 x 1. 8, left valve FMo 3419 x 1. 9, right valve with anterior auricle FMo 3417 x 2. 10, small block with mostly left valves, including FMo 3410 and FMo 3411, x 1.

Fig. 1-5 originally figured as Waterhouse (2000, text-fig. 5A-E) and fig. 6-10 as Waterhouse (2000, text-fig. 9A-E).

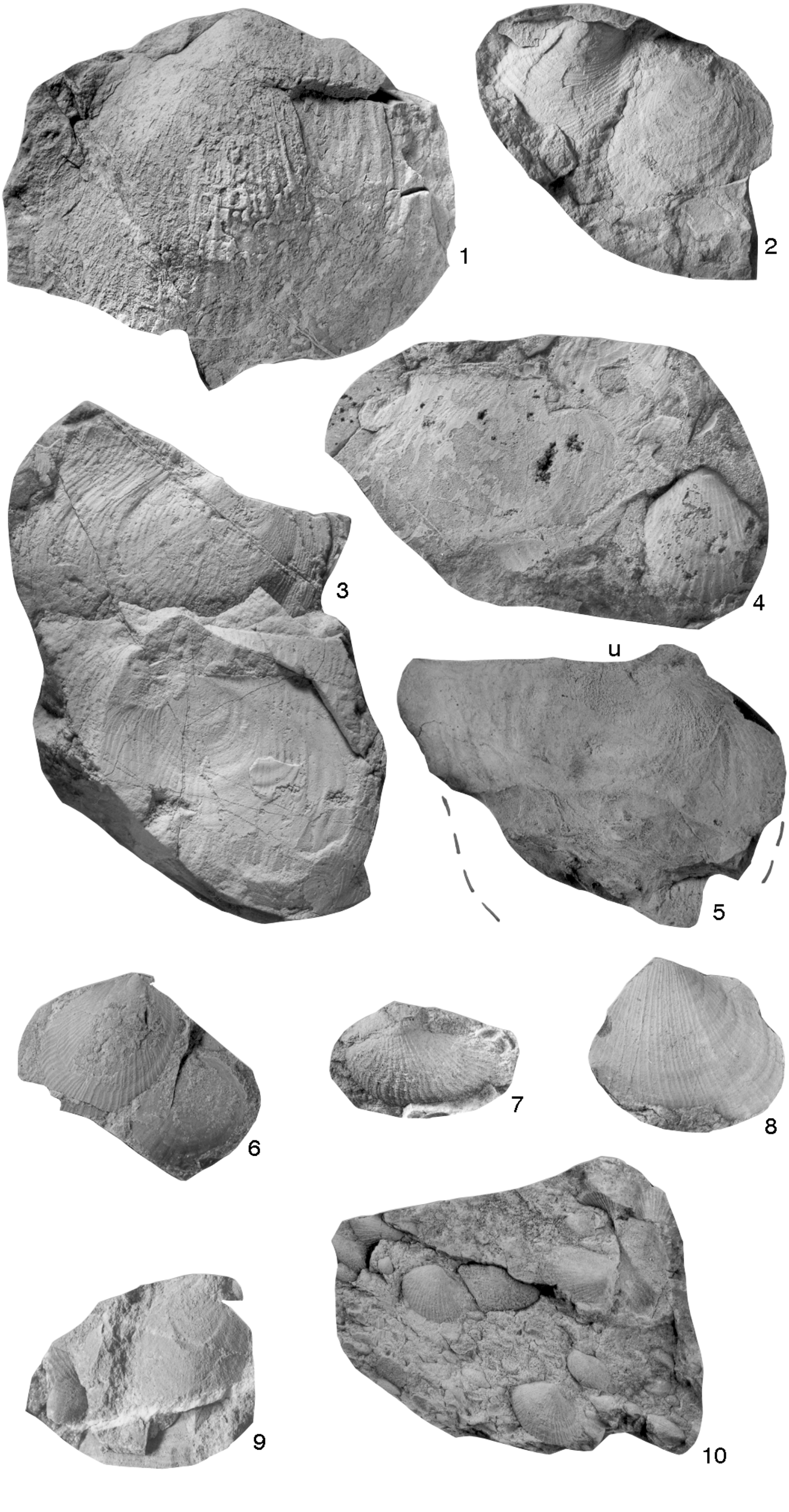

Plate 12

Plate 13

Fig. 1, 2. *Rugiclaraia?* sp. A from Sabche Member, Manang, x 1. 1, left? valve external mould FMo 3546. 2, left? valve external mould FMo 3547.

Fig. 3, 4. *Rugiclaraia* sp. B from Nar Formation, Manang, x 1. 3, obscure right valve external mould FMo 3424. 4, left valve external mould FMo 3423.

Fig. 5. *Posidonia* sp. A left valve FMo 3386, Sabche Member, Manang, x 1.

Fig. 6-12. *Posidonia elegantula* n. sp. from Jargeng Member, Manang, x 1. 6, holotype left valve FMo 3429. 7, right valve FMo 3542 above FMo 3543. 8, left valve FMo 3541. 9, left valve FMo 3542. 10, left valve FMo 3539. 11, right valve FMo 3428. 12, valves including FMo 3538.

Fig. 13. *Posidonia* sp. B left valve FMo 3544 from Naurchuli Member, Manang, x 1, resting against ammonoid *Euflemingites maharajah* Waterhouse.

Fig. 1-5 originally figured as Waterhouse (2000, text-fig. 10A-E) and fig. 6-13 as Waterhouse (2000, text-fig. 11A-H).

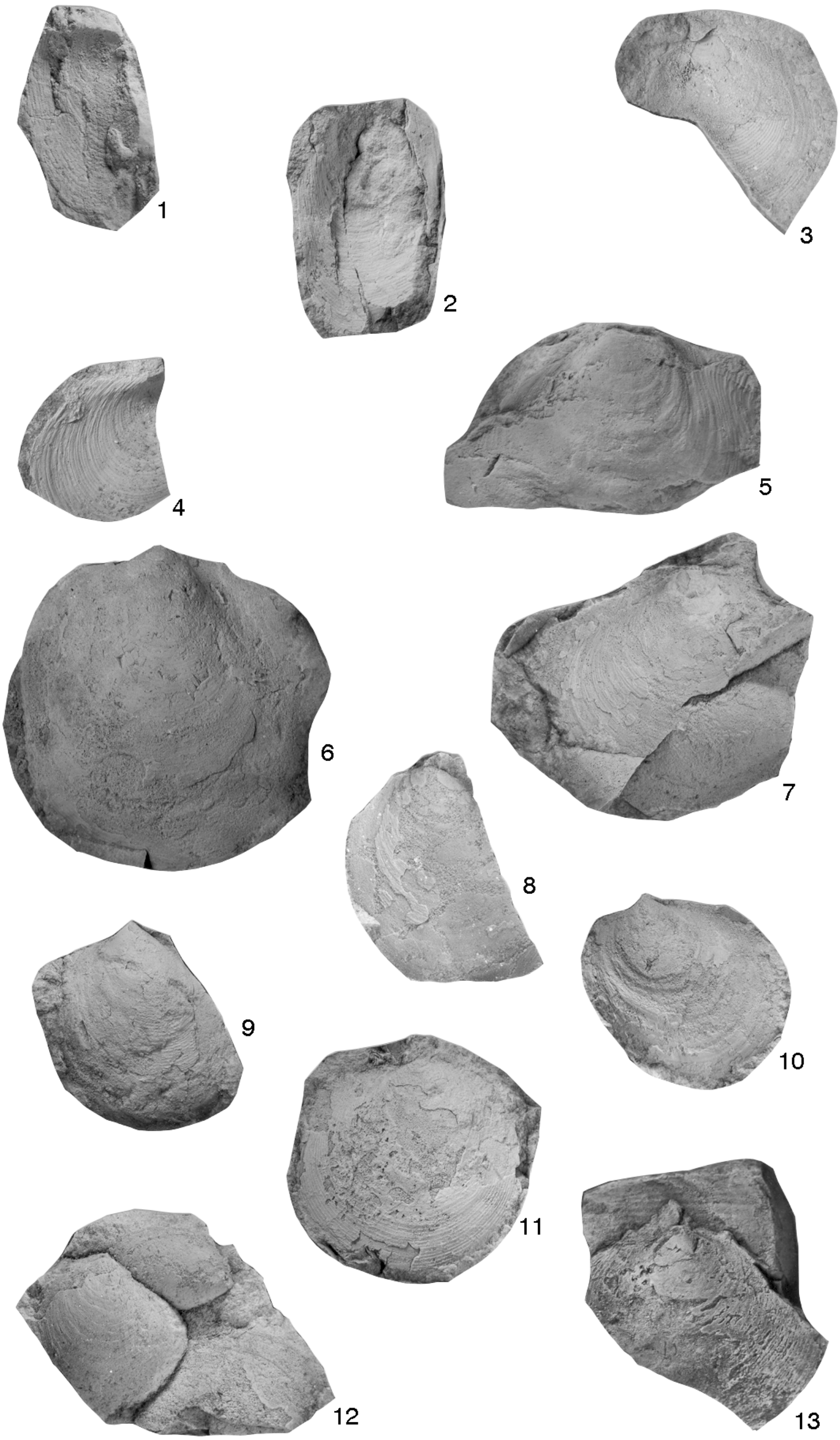

Plate 13