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HIMALAYAN CAMBRIAN BRACHIOPODS

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Abstract: A synoptic analysis of previously published material and new finds reveals that Himalayan Cambrian brachiopods can be referred to 18 genera, of which 17 are considered herein. These contain 20 taxa assigned to species, of which five are new: Eohadrotreta haydeni, Aphalotreta khemangarensis, Hadrotreta timchristiorum, Prototreta? sumnaensis and Amictocracens? brocki. Well-preserved topotype material from the classic Parahio Valley section is described for three species that have not
previously been illustrated photographically. A biostratigraphic scheme based on
Cambrian brachiopod occurrence is integrated with that recently proposed for trilobites.
Regional correlations based on shared taxa within and across Himalayan lithotectonic
belts demonstrate that erosion of Cambrian rocks in the Kurgiakh ontogeny in the Parahio
Valley removed little of the Parahio Formation, and that all of the fossil-bearing
lithotectonic zones shared similar late early Cambrian brachiopods, suggesting regional
faunal continuity at the time. Palaeobiogeographical analysis of the Cambrian brachiopod
faunas from the Himalaya shows that they occupied a marginal position of the
Australasian segment of Gondwana.

Key words: Linguliform brachiopods, Gondwana, Kashmir, biogeography, taxonomy.

BRACHIOPODS were among the first Cambrian fossils reported from the Indian
subcontinent (Waagen 1882-1885) and are now known from six different areas of
Cambrian outcrop within the Himalaya (Figs 1, 2). Despite widespread occurrence and
local abundance, their taxonomy and stratigraphic distribution remains poorly resolved.
There have been only limited attempts to revise original descriptions or provide new
illustrations for type material, and this is unfortunate because the faunas include some of
the first Cambrian brachiopods to be described from Asia, and are thus potentially senior
synonyms of other taxa. This monograph, along with a recently published paper (Hughes
et al. 2010), provides a comprehensive description of Himalayan Cambrian brachiopods
in which previously described material is reillustrated (commonly for the first time
photographically) and redescribed, and in which new species are erected based on
collections located within measured stratigraphic sections from which other fauna, including trilobites, have been described. Some of these new collections have also provided topotype material that helps clarify and expand knowledge of previously described species. A summary of the stratigraphic occurrence of the brachiopods was constructed based on this synoptic review, and this enables erection of a biostratigraphic zonation based on brachiopod occurrence. This is then integrated with the existing trilobite zonation to provide a more comprehensive documentation of regional Cambrian biostratigraphy.

The distribution of particular brachiopod taxa also permits important regional correlation within the Himalaya based on shared occurrence. Firstly, it provides the first species-level, direct biostratigraphic correlation between horizons within the Parahio Formation in the Zanskar and Spiti valleys, substantiating previous indirect correlations based on trilobites. Secondly, it permits correlation of a specific horizon preserved in three Himalayan lithotectonic zones: the sub-Himalaya (Kußak Formation, Salt Range), the outer Lesser Himalaya (the lower part of the upper Tal Group) and the Tethyan Himalaya (the Parahio Formation of Zanskar and Spiti). These faunal links are important evidence for the biogeographic continuity of the Indian margin during Cambrian time. Furthermore, this new work also occasions a global scale biogeographical analysis of late lower Cambrian and middle Cambrian brachiopod distribution that is based on cluster analyses for two time slices (unnamed Stages 4 and 5). The analyses were hindered by low generic diversity and varying data quality, but indicate that the Himalayan faunas exhibit closest connection to fauna of the Australasian segment of Gondwana.
GEOLOGICAL SETTING AND BIOSTRATIGRAPHY

The Himalaya is comprised of four lithotectonic zones (Fig. 1), and Cambrian brachiopods are found in three of these, with occurrence in the Indian Tethyan Himalaya and Lesser Himalaya, in the Tethyan Himalaya of Bhutan, and also in the sub-Himalayan Salt Range of Pakistan. Brachiopod distribution along and across the ancient north Indian margin is thus extensive and of potential stratigraphic and palaeogeographical value both within the region and beyond.

Localities bearing Cambrian brachiopods span the interval between the western to eastern syntaxes of the Himalaya (Fig. 1) but all except the Bhutanese locality lie toward the western end of the orogeny. This is partly because the Southern Tibetan Fault System cuts up section further to the east with the result that the Tethyan Himalayan Cambrian is generally too metamorphosed to yield specimens in that area (Myrow et al. 2009). This paper describes Himalayan Cambrian brachiopods from all six outcrop regions bearing fossils that can be identified at least to generic level, except those recently described from the Black Mountain region of Bhutan, where the billingsellid *Billingsella cf. tonkiniana* Mansuy 1915 occurs in rocks of *Kaolishania granulosa* Zone age (Hughes, et al. 2010). That assemblage is the youngest Cambrian fauna yet described from the Himalaya.

Cambrian sedimentary rocks accumulated on a seaward facing shelf that deepened toward the present day north, with the result that that facies of the Tethyan Himalaya are generally more distal than those of the Lesser Himalaya and Salt Range. Brachiopods are found in a variety of lithologies, but mostly occur either in dark shales, or in comparatively thin carbonate layers from which phosphatic shells have been liberated via acid digestion. Within the Tethyan Himalaya these deposits form the deeper water parts
of sand-dominated shallowing upward cycles that are interpreted to represent the repeated progradation of delta lobes (Myrow et al. 2006a,b). All the specimens from this region figured herein are from the Parahio Formation, and come from two regions, the Purni section in the Zanskar Valley and Parahio Valley section that adjoins the larger Spiti Valley, and are about 150 km along strike from one another (Figs 1, 2). A similar environmental setting appears consistent with the mudstone that forms unit B of the upper Tal Group of the Lesser Himalaya, from which the great majority of Lesser Himalayan Cambrian brachiopods have been collected. In the Salt Range brachiopods are found in dark shales and in glauconitic sandstone at several horizons within the Khussak and Jutana formations, also in a shelf setting dominated by clastic deposits.

A result of deposition in deltaic conditions is that thick packages of sediment accumulated within a relatively short interval of time, with depositional rates for the Parahio Formation as much as 200 m per million years (as assessed over a 10 Ma time interval). Accordingly, although sections of Cambrian sedimentary rock within the Himalaya are reasonably thick, the time represented by these deposits is relatively short (Hughes et al. 2013).

PRIOR SYSTEMATIC AND BIOGEOGRAPHIC WORK
Brachiopods were important in the first recognition of Cambrian rocks within the Indian subcontinent, with a series of geological and palaeontological studies of the Salt Range carried out in the late 19th century commissioned by the Geological Survey of India. Relatively short sections in these sub-Himalayan hills (now part of Pakistan) yielded specimens from several horizons that were described in a series of palaeontological
studies (Waagen 1882-1885; Waagen 1891; Redlich 1891; Walcott 1905, 1912) along with detailed accounts of the geology (Middlemiss 1891; Noetling 1894). An important more recent palaeontological study of that succession was that of Schindewolf (1955) who illustrated a significant number of specimens photographically for the first time, and offered further revision of some of Waagen’s species. King (1941) mentioned the occurrence of known Salt Range brachiopod species at some newly recognized localities.

Hayden’s (1904) survey of the geology of Spiti revealed the first Cambrian rocks from the Tethyan Himalaya, defied a series of stratigraphic levels in the Parahio Formation in the Parahio Valley, and provided fossil material for the systematic analysis of Reed (1910). Several new brachiopod species were erected by Reed, based on material preserved in dark mudstone. The first report of Cambrian brachiopods from the Zanskar Valley (Dungrakoti et al. 1977, pl. 30, fid. 2a, b) provided no repository information for the specimen, and thus cannot be further evaluated. Late Cambrian rocks of Tethyan Himalayan affinity bearing brachiopods have been recently described from Bhutan (Hughes et al. 2010).

An account of middle Cambrian fossils from the Pohru Valley of Kashmir, also in the Tethyan Himalaya, included several brachiopods (Reed 1934), but featured material from a series of isolated localities rather than those located within a continuous section. Unfortunately, several brachiopod specimens attributed to genera such as Botsfordia, Lingulella, Dicellomus and Acrothele, including some figured, were deposited in the stratigraphic collection of the Geological Survey of India, rather than in the type and figured collection, and are presently unavailable. Kobayashi (1934) also figured a poorly preserved brachiopod from the Pohru Valley. Several subsequent papers have also
mentioned, but not illustrated, Cambrian brachiopods from that region (e.g. Suneja 1973, 1975, 1977). Three early Cambrian brachiopod specimens were figured from the top of the Lolab Formation of the Kupwara region of Kashmir (Shah et al. 1980), along with the trilobite *Redlichia takooensis* (see Jell and Hughes 1997).

A number of papers have been published on brachiopods from the Mussoorie and Korgai synclines of the Lesser Himalaya. Several have concerned material collected from a single horizon at a single locality (Tripathi et al. 1984; Tripathi et al. 1986; Mathur and Joshi 1989; Mathur and Srivastava 2005), although others have taken a wider perspective (Kumar et al. 1983). Most of this material was attributed at the generic level only. Cambrian brachiopods have also been reported from the Nigali Dhar Syncline near Ganog (Kumar et al. 1987) but have yet to be described. The claim of brachiopod or bivalve impressions along with trace fossils from the Mesoproterozoic Dharagad Group of the inner Lesser Himalaya (Rai et al. 1997) is here considered to have mistaken mud chips for body fossils.

A claimed occurrence of Cambrian *Orthis* from what is now known to be the Neoproterozoic Sonia Formation of the Jodhpur Group of Rajasthan (Khan 1973) which is part of the Indian craton, has been refuted (Kumar et al. 1997, p. 24), but the recognition of marine Cambrian deposits in the Nagaur Formation of Rajasthan means that Cambrian brachiopods might yet be found in this region (Kumar and Pandey 2008; McKenzie et al. 2011). Azmi’s (1998) claim of acrotretid brachiopods from the lower Vindhyan succession has been widely dismissed. Thus, in summary, to date brachiopods have played a minor role in biostratigraphic or biogeogeographic analysis of the Indian Cambrian. This has largely been due to their preservation in mudstones being generally
quite poor in quality, with relatively few diagnostic features of internal morphology sufficiently well preserved to permit accurate determination.

In 1990 N.C.H. began revising all previously described Himalayan Cambrian trilobites, including those housed in the collections of the Geological Survey of India in Kolkata. Where possible, casts were also made of figured Cambrian brachiopods. In 2000, N.C.H. and P.M.M. began fieldwork in the type section of the Parahio Formation in the Parahio Valley (Fig. 3), where Hayden (1904) established a continuous, well-exposed section, in order to collect fossils systematically in a measured sequence. This approach yielded a number of new “crack out” brachiopod specimens, but better material was obtained via the acid dissolution of carbonate horizons both in the Parahio Valley itself and in the Zanskar Valley to the northwest (Fig. 2). This substantial yield of new brachiopod material, some of it from the topotype localities of Reed’s (1910) original descriptions, occasions this review of all Himalayan Cambrian brachiopods available to us except that from Bhutan published recently elsewhere (Hughes, et al. 2010).

The conodont controversy. A further stimulus for this work was the report of fossils attributed to various euconodont and paraconodont genera from the upper part of the Parahio Formation in the Parahio Valley (Bhatt and Kumar, 1980), which has been referenced in recent compilations of the stratigraphic geology of India (Vaidyanadhan and Ramakrishnan 2008, p. 581). As some of the taxa reported by Bhatt and Kumar (1980) are not known from rocks older than Early Ordovician, their conclusions are of considerable potential biostratigraphic significance. We have re-evaluated the available specimens deposited in the Geological Survey of India in Kolkata. Three specimens
(GSI19604 to 19606) attributed to the Lower Ordovician euconodont genus *Oneotodus* are discussed elsewhere: none are conodonts and one or more of these may be a chancelloriid spicule (Gilbert et al., in press). The other specimens illustrated by Bhatt and Kumar (1980, figs 4-9; GSI19607 to 19612) are brachiopods. Unfortunately, as these specimens cannot be loaned, cast, or adequately photographed in Kolkata it is not possible to reillustrate them herein. However, between them, specimens illustrated on Bhatt and Kumar’s (1980) figs 4-7 are probably referable to *Prototreta? sumnaensis* sp. nov., whereas a specimen illustrated on their fig. 8 may represent an incomplete ventral valve of *Amictocracens? brocki* sp. nov.; all are from the same stratigraphic level and apparently the same locality as our PO9 collection. Attribution of a shell fragment, illustrated on their fig. 9 is uncertain. Accordingly, none of specimens figured by Bhatt and Kumar (1980) are either paraconodonts or euconodonts. Rather, they can be attributed to middle Cambrian species described by other workers from the same succession. Thus the paradox is resolved.

**PRESERVATION**

All studied lingulate and paterinate brachiopods described were originally composed of calcium phosphate. The best preserved faunas were isolated from carbonate horizons that are present only in the Tethyan part of the studied succession. A total of eleven sampled carbonate horizons were dissolved either in acetic or formic acid yielded identifiable brachiopods, mostly yielding acrotretides together with a few lingulides and paterinides. The majority of the specimens are preserved as incomplete, disarticulated valves. The shell structure and details of finer surface ornamentation are generally well preserved,
whilst some specimens have lost their surface micro-ornament, probably due to the

treatment in formic acid, which is necessary for the digestion of the dolomitic rock.

Cambrian brachiopods are also quite common in clastic rocks, but their

preservation varies significantly among the localities studied. The shells from the

*Neobolus* beds of the Salt Range are well preserved; while all shale specimens from the

Parahio valley section often are exfoliated and distorted, and consequently they lack

preserved micro-ornament, shell structure and larval shells, which are important for
detailed taxonomic discrimination. All specimens from the Tal Group of Garhwal

Himalaya are strongly affected by recrystallization and neomorphism of the original
organophosphatic fabric. They are also distorted and compressed, being often preserved
as composite moulds. As a result, even generic assignment is usually problematic. The
study of available specimens also confirmed that calcareous-shelled brachiopods are so

far entirely lacking in the early to mid-Cambrian succession of Himalaya; thus all

previous records of taxa such as *Nisusia, Magnicanalis* and *Obolella* remain doubtful.

**BIOSTRATIGRAPHY**

A stratigraphic succession of brachiopod taxa can presently be observed within two
outcrop regions, the Salt Range in Pakistan, and the Parahio valley and Purni sections of
Spiti and Zanskar in India (Figs 3-5). In all other regions brachiopods are currently
known from a single stratigraphic level, although their stratigraphic context can often be
determined by correlation with other sequences based on the brachiopod fauna or co-
occurrence of trilobites. At present, Cambrian brachiopods and trilobites are known to co-
occur in the same beds in 14 Himalayan collections.
The succession of brachiopod species in the Salt Range sections represents our best understanding gleaned from earlier accounts, which discussed some nineteenth century conflicts regarding the age and order of faunal succession (see Noetling 1894, p. 71). Walcott (1905, p. 252) presented a stratigraphic table of occurrence that is consistent with subsequent discoveries made by Schindewolf (1955), and we adopt Walcott’s scheme herein. In this scheme *Wynnia warthi* occurs lowest in the section, and its three dimensional preservation suggests it was hosted in a sandy rather than shale matrix, so we accept Walcott’s placement in the “Upper Annelid Sandstone” part of Khussak Formation (Fig. 5).

*Schizopholis rugosa* is preserved in the overlying “Neobolus shales” but occurs below the level bearing *Botsfordia granulata*, which itself co-occurs with *Eoobolus fuchsi* and the trilobite *Redlichia noetlingi* in the very top of the Khussak Formation and, according to Schindewolf (1955, p. 61), also low in the subsequent Jutana Formation. In the Salt Range, these taxa also occur with *Eoobolus wanniecki* and the trilobite *Yuehsienszella szechuanensis* at the top of the “Neobolus shales” in the Khussak Formation. These occurrences allow the establishment of a level characterized by *Schizopholis rugosa* that is immediately succeeded by a zone bearing *Botsfordia granulata* (Fig. 5).

We have found *Eoobolus wanniecki* in float near the base of the Parahio Formation in the Parahio Valley (Fig. 3), which is consistent with earlier reports of *R. noetlingi* also from float at that location (Reed 1910). This suggests that the lower part of the Parahio Formation, immediately above the Khemangar Valley fault extends down
into the *R. noetlingi* Zone/*B. granulata* Zone and, given the thickness and lithofacies observed, likely no more or only a little beneath that level (Hughes et al. 2013).

Specimens here assigned to *Eoobolus?* sp. have also been recovered from several localities in the Krol-Tal belt of the Lesser Himalaya (Fig. 5). Here again, *R. noetlingi* is co-occurrent, suggesting that representation of the *R. noetlingi* Zone/*B. granulata* Zone extends between the Salt Range, the Lesser Himalaya and the Tethyan Himalaya. No occurrence of *Botsfordia* has yet been reported from the Lesser Himalaya. Nevertheless, the occurrences of *Eoobolus* suggest that an interval of late early Cambrian time, during part of Stage 4 of the Cambrian Period, is widely represented among Himalayan lithotectonic zones. The brachiopods thus confirm the conclusions of Jell and Hughes (1997) and Hughes et al. (2005) in this regard, based on the occurrence of *R. noetlingi*.

The succession in the Parahio Valley first described by Hayden (1904) has yielded the largest number of successive horizons bearing brachiopod and other body fossils specimens. Of the 14 brachiopod taxa found there *in situ*, three have observed ranges that likely extended for several million years and are longer than those of any trilobite known from these sections (Fig. 3). Nine species are presently known only from a single horizon. *Prototreta? sumnaensis* and *Amictocracens? brocki* occur in the Parahio Valley section above any trilobite yet found *in situ*. We use the occurrence of these brachiopods to define a series of levels and zones (Figs 3-5). Levels are where species are confined to one particular horizon, whereas zones are where they occur in two or more horizons, and this difference is important when considering the zonation shown in Figs 3-5.
Within the Parahio Valley, a sequence of brachiopod zones or levels has been established based on *in situ* occurrence, although the presence of *E. wanniecki* in float indicates rocks of the *B. granulata* Zone within the drainage basin (Fig. 3). The lowest of these is characterized by *Eohadreta haydeni*, which occurs both at 78.07 m in the section, and also at 439.44 m. The 78.07 m collection contains one of most diverse brachiopod faunas yet known from the Himalaya and includes the botosfordiid *Schizopholis napuru*, whilst the upper occurrence marks the incoming of the more derived acrotheloid *Acrothele vertex* (Fig. 3). This zone spans at least two trilobite zones, the latest Stage 4 *Haydenaspis parvatya* level and extends into the Stage 5 *Kaotaia prachina* Zone. Peng *et al.* (2009) proposed that the *Oryctocephalus indicus* Zone (which they did not locate *in situ*), a candidate horizon for the base of Stage 5, occurs within between these two trilobite zones, and thus within the range of the *Eohadreta haydeni* Zone.

The *Linnarssonia parahoensis* Zone begins at 580.2 m which is within but above the base of the *Kaotaia prachina* trilobite Zone, where it is the only brachiopod species found (Fig. 3). *Linnarssonia parahoensis* is also found at 765.14 m, within the subsequent *Paramecephalus defossus* trilobite Zone, along with *Aphelotreta khemangarensis*. The first appearance of *Hadrotreta timchristiorum* at 776 m, defines the next brachiopod biozone and is also found at 835.66 m, within the subsequent *Oryctocephalus salteri* trilobite Zone (Fig. 3). *Amictocracens teres* occurs at a single horizon at 836.66 m where it defines a level within the *Oryctocephalus salteri* trilobite Zone. Thus the bases of these three brachiopod zones are stratigraphically slightly higher than the bases of the accompanying trilobite zones (Figs 3, 5). The uppermost occurrence of brachiopods in the Cambrian of the Parahio Valley section is at 1242.4 m, and is represented by four
species of which *Prototreta? sumnaensis* is the most common. The name of that species is used to define a level of occurrence (Fig. 3).

The type locality of *Hadrotreta timchristiorum* lies within the Parahio Formation in the Purni section of the Zanskar Valley, where this brachiopod occurs in great numbers, along with a new chancelloriiid species (Gilbert *et al.* in press), some 500 meters below the base of the Karsha Formation (Figs 4, 5). As both these species are also found in the Parahio Valley section they permit the first direct correlation between the two sections based on shared species occurrence. This is important because previous correlations between the sections were indirect, and based on the order of succession of trilobite species seen in Chinese sections, with the youngest trilobites in the Parahio Valley section predating the oldest known from the Purni section (Peng *et al.* 2009). As the range of the new chancelloriiid species is extremely long (Gilbert *et al.* in press) the occurrence of *H. timchristiorum* is significantly more useful from a biostratigraphical perspective, because it correlates a specific parts of the Parahio Formation in both sections: in the Parahio Valley the range only extends for a few metres. The implications of this are discussed further below.

The Kashmiri species *Notiobolus? kashmiricus* co-occurs with the trilobites *Hundwarella memor, Tonkinella breviceps* and *Balliella lantenosei* (see Jell and Hughes 1997). As this species has not yet been not found elsewhere in Himalaya it does not help refine correlations further, but is occurrence is consistent with the previous inference that the age of the Kashmiri localities likely correlates with the higher parts of the Parahio Formation or with the Karsha Formation (Jell and Hughes 1997) (Fig. 5). In Antarctica, *Notiobolus tenuis* Popov *in* Popov and Solovyev, 1981, which is the type species of the
genus, co-occurs together with *Ptychagnostus gibbus* (Linnarsson, 1869) and *Ptychagnostus praecurrens* (Westergaard, 1936) suggesting a pre-Drumian age, while in Malyi Karatau in South Kazakhstan the genus is ranging up into the Furongian (Holmer *et al.* 2001).

The youngest Cambrian brachiopods from the Himalaya are the Jiangshanian (late Cambrian) *Billingsella cf. tonkiniana* from Bhutan (Hughes *et al.* 2010) (Fig. 5).

**GEOLOGICAL IMPLICATIONS**

The Himalayan Cambrian brachiopod fauna reinforces the conclusions of regional paleobiogeographical studies based on trilobites. In particular, the widespread shared occurrence of elements of the *Redlichia noetlingi Zone/Botsfordia granulata Zone* shows that this interval, deposited at ~512 Ma, offers the best opportunity for the regional reconstruction of the contemporaneous conditions across the Himalayan Cambrian margin (Fig. 5). At this time the trilobite and brachiopod faunas suggest biotic continuity between rocks from different Himalayan lithotectonic belts, and thus biotic data is consistent with other geological data arguing for a continuous, seaward facing, north Indian margin at the time (Myrow *et al.* 2003).

In Zanskar *H. timchristiorum* lies approximately 500 m below the base of the Karsha Formation, a carbonate unit that directly succeeds the Parahio Formation (Fig. 5). There, the Karsha Formation is directly overlain by the clastic Kurgiakh Formation, which is in turn truncated by the Cambrian–Ordovician unconformity caused by the Kurgiakh orogeny (Myrow *et al.* 2006a) (Fig. 5). Both the Kurgiakh and Karsha formations are absent in the Parahio Valley, which is located southeastwards along the strike of the Himalayan chain, and where Ordovician conglomerate sits directly on top of the Parahio Formation (Hayden 1904; Myrow *et al.* 2006b).
Up until now it has been unclear as to how much of the Parahio Formation has been eroded beneath the Kurgiakh orogeny unconformity in the Parahio Valley. The presence of conspicuous bands of dolomite that become progressively thicker towards the top of the Parahio Formation in both sections suggested that little of the Parahio Formation was eroded in the type section, and the brachiopod biostratigraphy now confirms this: in the Parahio Valley the *H. t\(\text{imchristiorum}\)* Zone lies almost exactly 500 m beneath the slight angular unconformity at the top of the Parahio Formation where the maximum thickness is preserved. As this is the same stratigraphic distance at which *H. t\(\text{imchristiorum}\)* occurs below the base of the Karsha Formation in Zanskar, erosion related to the Kurgiakh orogeny in the Parahio Valley apparently produced only minor erosion of the Parahio Formation, although more erosion likely took place to the south, given the orientation of the slightly tilted (a few degrees) strata.

Although on a regional scale this unconformity cuts down section to the east in the Spiti–Zanskar area (Myrow et al. 2006a), correlations with the Everest region indicate that a carbonate Karsha Formation equivalent is preserved further along strike (Myrow, et al. 2009). Furthermore, the presence of confirmed late Cambrian brachiopods in Tethyan rocks of Bhutan (Hughes et al., 2010), with facies that differ from those of India and Tibet, indicates important variation in Cambrian stratigraphy along the strike of the orogen (Fig. 5).

**FAUNAL AFFINITIES AND PROVINCIALITY**

The linguliform brachiopod faunas from the Himalaya described herein are from the as yet unnamed Cambrian Stages 4 and 5. Brachiopod faunas from these units are presently known from all main Early Palaeozoic continents; however, the quality of existing records varies significantly between localities both in terms of taxonomic attributions of
the reported taxa and in understanding of the correlation between faunas. The best known faunas are confined to the Australasian segment of Gondwana, whilst the faunas of the west Mediterranean segment of Gondwana are known from a few localities in Bohemia, Spain and Morocco where, most likely, the diversity of their lingulide component is strongly underestimated.

The Avalonian faunas have not been revised for almost a century, and the brachiopods described by Cobbold (1921) remain very poorly understood; the only available reliable data was published by Walcott (1912) for west Avalonia.

In Baltica, the transition from Cambrian Stage 4 to 5 coincides with a regional unconformity and widespread hiatus (the Hawke Bay unconformity of Nielsen and Schovsbo 2007). Thus, there are no published reports of Baltic linguliforms from Cambrian Stage 4, whereas the linguliform fauna from the Cambrian Stage 5 represents a composite list of genera from several localities, and in a part it is based on preliminary identifications (Streng et al. 2008). The Laurentian record of linguliforms is sparse and based on a few localities mainly from the eastern part of the continent, including Nevada (Rowell 1980, Skovsted and Holmer 2006) and the Mackenzie Mountains (Voronova et al. 1987), whereas faunas of the eastern Laurentian margin are represented by the small faunal assemblage described by Skovsted and Holmer (2005) from Greenland. The same is true for Siberia and peri-Siberian Altai-Sayany composite terrane. Consequently, the lingulate faunas of both these regions were compiled from composite lists based on publications of Pelman (1977), and Ushatinskaya and Malakhovskaya (2001). In South China linguliform brachiopods of the Unnamed Cambrian Stage 4 are known from a single publication by Li and Holmer (2004) and they are yet unknown from the Unnamed
Cambrian Stage 5. Cambrian linguliform brachiopods from North China (e.g. Huang et al. 1994) are too poorly understood to be included in the biogeographic analysis presented below.

The transition from the unnamed Cambrian Stages 4 to Stage 5 coincides with a two-fold increase in the taxonomic diversification of the lingulate brachiopod faunas, from 17 to 40 genera. This also coincides with a considerable increase in morphological diversity, particularly among acrotretides. The most important novelties in this group include: a pedicle foramen that is enclosed within the larval shell (*Amictocracens*), a larval shell that is ornamented with flat-based imprints (*Amictocracens, Kyrshabaktella*), a high, blade-like dorsal median septum with septal rod or platform (*Amictocracens, Prototreta*). In the lingulides there is comparatively rapid morphological change within the assumed evolutionary lineage *Botsfordia → Schizopholis → Eothele → Acrothele* associated with a transformation from a botsfordiid-like shell with a marginal ventral umbo, a rudimentary ventral interarea and a pedicle groove typical of Botsfordiidae (*Botsfordia, Schizopholis*) into a acrothelid-like shell with an enrolled ventral valve (characterised by hemiperipheral growth), where the posterolateral muscle fields migrate posterior to the umbo (*Acrothele*). These evolutionary changes occurred in a relatively short time during the transitional interval from the Unnamed Cambrian Stage 4 to Unnamed Cambrian Stage 5, probably in the Australasian segment of Gondwana and adjacent regions.

*Botsfordia* (basal member of lineage) and *Acrothele* (terminal member of the lineage) are cosmopolitan taxa, while during the Unnamed Cambrian Stage 4 *Schizopholis* is documented only from Antarctica, the Himalaya and Australia, all then
situated in subtropical and tropical Gondwana. *Eothele*, which is the earliest representative of the family Acrothelidae, has a wider geographical distribution. It occurs, in particular, in the Sekten Formation (*Orictocara* and *Kuanamkites* zones) of Siberia (Korovnikov, 1998), the Sidi-Saïd-Maâchou volcano-sedimentary complex of the Moroccan Coastal Meseta (Alvaro et al. 2008) and the Pioche Shale (uppermost *Bonnia—Olenellus* Zone) of Nevada in Laurentia (Rowell 1980). The Australasian segment of Gondwana was probably the centre of origin and dispersal of *Eothele*, as well as being the only region where *Schizopholis* is present. In the Himalayan succession the last occurrence of *Schizopholis* is in the *Haydenaspis parvarya* Level (sample PO3, uppermost Unnamed Cambrian Stage 4) whereas the earliest *Acrothele* is already present in sample PO15, in the lower part of the Cambrian Stage 5 (*Kaotaia prachina* Biozone).

Our biogeographical analysis of the early Cambrian linguliform brachiopods was significantly hampered by low generic diversity of the faunas and the varying quality of taxonomic data. Nevertheless, the diversification of lingulides and acrotretides recorded at the beginning of the Cambrian Stage 5 had a significant impact on linguliform biogeography patterns and it is possible to identify some biodiversity centres and directions of faunal exchange. Our interpretation of faunal affinities was facilitated by multivariate cluster analysis (based on Raup-Crick similarity), using the computer program PAST (Hammer et al. 2001). Analyses have been performed for two time slices. Ten faunas (A1-A10, Fig. 6; Attachment 2) representing Gondwana, Laurentia, Siberia, South China and Karatau-Naryn Microplate are available from the Unnamed Cambrian Stage 4. The diversity of these faunas was low (usually between 3 and 5 genera) and no distinct biofacies differentiation could be identified. They are defined by the occurrence
of the botsfordiids *Schizopholis* and *Botsfordia* and commonly include cosmopolitan lingulides such as *Eoobolus* and *Kyrshabaktella*. A further 12 faunas (C1-C12, Fig. 2; Attachment 2) are characterised by the occurrence of *Acrothele* and diverse acrotretide components, which are typical of the Unnamed Cambrian Stage 5. There are also a number of transitional faunas (B1-B7, Fig. 6; Attachment 2), which include *Eothele*, but lack *Acrothele* and *Schizopholis*. In Laurentia, these faunas occur in the upper part of *Bonnia—Olenellus* Zone and there they are considered to belong to the early Cambrian (Rowell 1980, Voronova et al. 1988), whereas in Gondwana they are assigned to the mid Cambrian (Roberts and Jell 1990). Due to the fact that the precise position of the Unnamed Cambrian Stage 5 boundary is not yet defined, *Eothele* faunas have been included in the data sets of both Cambrian stages.

The results from the cluster analysis of the linguliform faunas of the Unnamed Cambrian Stage 4 shows that the ‘*Eothele’* faunas of Laurentia are grouped together and form a separate cluster with low similarity to other faunas. This is defined by the occurrence of *Hadrotreta* and *Eothele*, which are unknown in other faunas of Unnamed Cambrian Stage 4. It is possible that ‘*Eothele’* faunas of Laurentia may be of somewhat younger age as compared with other Stage 4 faunas included in the analysis.

All other faunas can be grouped into two second-order clusters (Fig. 6A). One of them includes mainly faunas of low latitude eastern Gondwana (Antarctica, Australia and the Himalaya). It is defined mainly by the presence of *Schizopholis, Vandalotreta* and *Eoobolus*. *Schizopholis* and *Eoobolus* do not co-occur at any Himalayan horizon, but they do occur in the same section. The Laurentian assemblage from North-East Greenland also appears within this cluster and form a sub-cluster together with Australasian faunas. This
similarity is most probably superficial, caused by the low diversity of the fauna including mainly cosmopolitan genera (e.g. *Botsfordia*, *Eoobolus*, *Micromitra*) in association with *Vandalotreta*, which is the only occurrence of the genus outside Gondwana. *Botsfordia* is also known from the Gondwanan assemblage of the Salt Range, (Sub-Himalaya) and probably also from the Lesser Himalaya. Two Himalayan faunas (Fig. 6A; A8, Salt Range and A9, Spiti) are placed at the base of the cluster. Their links to the Australasian faunas are due to co-occurrence of *Eoobolus* and *Schizopholis*, while *Vandalotreta* is absent in both Himalayan faunas.

Another second-order cluster includes faunas of the Karatau-Naryn microplate (as defined by Holmer *et al*. 2001), South China and Siberia (Fig. 6A; A2, A5 and A6). Faunas of South China and Karatau-Naryn are linked by co-occurrence of *Lingulellotreta* and *Palaeobolus*, whereas the similarity of Karatau-Naryn and Siberia is mainly due to co-occurrence of *Botsfordia* and *Linnarssonia*.

The linguliform faunas of the Unnamed Cambrian Stage 4 have a very low generic diversity, and in their biogeographical differentiation, they closely follow the pattern of the inferred relative position of the Early Palaeozoic continents for that time. The main differences/links between these faunas are usually defined by a few endemic or common lineages. In particular, early Cambrian species of the acrotretide *Linnarssonia* seemingly initially had a restricted geographic distribution (being limited to Siberia and the Karatau-Naryn microplate), whilst species of this genus became cosmopolitan following the Drumian. *Lingulellotreta* is unknown outside of South China and Karatau-Naryn throughout the Cambrian. The most characteristic Gondwanan faunal element is *Schizopholis*. Known occurrences of paterinides (*Micromitra* and *Paterina*) are sparse
outside Laurentia. The only exceptions are the occurrence of *Paterina* in the Toyonian of Siberia and in the *Haydenaspis parvarya* Level of the Tethyan Himalaya (Fig. 6A), as well as the possible presence of *Micromitra* in the Australasian segment of Gondwana. The enigmatic paterinide *Wynnia* is endemic to the Himalayan fauna of the Salt Range (Fig. 6A; A8); however, it is rather distant from the genera of the Family Paterinidae and may be a last survivor of an older paterinide lineage.

During the transition from the Unnamed Cambrian Stage 4 to the Unnamed Cambrian Stage 5, background rates of extinction likely pertained. Only four genera, including *Lingulellotreta*, *Neobolus*, *Wynnia* and the problematic *Palaeoschmidtites* (possibly a junior synonym of *Eoobolus*) did not cross the stage boundary. Linguliform faunas from the Unnamed Cambrian Stage 5 are mainly characterised by a significant increase in biodiversity, especially of the acrotretide component of the assemblages. The faunas attain the maximum diversity in the *Pernopsis? ultimus* and *Ptychagnostus intermedius* biozones of the Karatau-Naryn microplate. Twenty-four of 40 genera documented from the stage are known only from a single locality. With the exception of *Eohadrotreta*, *Palaeobolus* and *Schizopholis*, which are transitional and became extinct by the beginning of the Drumian Stage, they all were newcomers, representing, probably, neo-endemics.

The results of the cluster analysis for the Unnamed Cambrian Stage 5 show significant separation of the lingulate faunas of the Kazakh terranes and microplates (Fig. 6B; C1, Karatau-Naryn; C2, North Tien Shan; C3, Tarbagatai) from other faunas of that age. With the exception of the assemblage from the Tarbagatai island arc, these faunas have a relatively high generic diversity and are dominated by micromorphic acrotretides.
Akmolina, Canthylotreta, Kostjubella, Neotreta, Stilpnotreta were endemic for one or other region. Several more genera have a restricted geographic distribution, in particular, Kotylotreta is otherwise known only from Baltica, whereas Kleithriatreta and Prototreta from Australasian Gondswana. These faunas also include the earliest representatives of the families Ceratretidae, Myotretidae and Scaphelasmatidae. Most of these taxa proliferated later in the Cambrian and acquired pan-tropical or cosmopolitan geographical distribution. Thus the isolated island shelves of the Kazakh microplates and island arcs may have represented ‘cradles’ for micromorphic linguliform brachiopod associations, which later spread worldwide. All other faunas of the Unnamed Cambrian Stage 5 are distributed between two major second-order clusters.

The first second-order cluster divided into two sub-clusters (‘a’ and ‘b’). All these faunas have peri-Iapetus locations.

Sub-cluster ‘a’ links faunas of the West Mediterranean segment of Gondwana (Fig. 6B; B5, Morocco and C12, Bohemia). These faunas include five endemic genera (Acanthatreta, Lindinella, Luhotreta, Treptotreta?, Almohadella, Tingitanella), plus Monophtalma, which are all known only from Morocco and Baltica. Unlike the acrotretides from the Kazakh terranes most of these genera are short lived taxa, except Treptotreta?; however, the precise generic affinities of the Bohemian taxa are difficult to evaluate.

It is possible that diversity of these faunas is underestimated, because lingulides are yet unknown from Morocco, and the generic affinities of four lingulide species from Bohemia, assigned to Lingulella, are questionable and they have not been considered in the analysis.
The Sub-cluster ‘b’ comprises faunas of Avalonia, Iberia, Laurentia and Novaya Zemlya (Fig. 6B; C4-C7). These are low diversity faunas, which include from three to six genera, where *Acrothele* is the only common taxon. Links between Avalonia, Laurentia, Novaya Zemlya are also accentuated by the co-occurrence of *Acrothyra*, whereas links with Iberian fauna are relatively weak and probably due to co-occurrence of the paterinide *Dictyonina* in Iberia and Laurentia. Iberia (Fig. 6B; C11) with six genera is distinct because of the occurrence of the endemic acrotretides *Genetreta* and *Iberotreta*, while *Luhotreta* is also present in Bohemia.

Another second-order cluster is more heterogeneous. It also comprises two sub-clusters (Fig. 6B; sub-clusters ‘c’ and ‘d’). Sub-cluster ‘c’ embraces closely related faunas of Siberia and pari-Siberian Altay-Sayany region (Fig. 6; B2, C10), and Baltic fauna. Affinity of the Siberian and Baltic faunas are supported by cosmopolitan genera *Acrothele*, *Eoobolus* and *Linnarssonia* and more restricted *Canalilatus* and *Oepikites*, which are also documented from Australasian Gondwana and Kazakh terranes.

Sub-cluster ‘d’ comprises ‘Eothele’ faunas of the Australasian segment of Gondwana and Laurentia (Fig. 6B; B1, B3, B4, B6, B7) plus faunas of the Himalaya (Fig. 6B; C11) and the peri-Gondwanan Alai Microplate (Fig. 6B; C9). The observed pattern can be explained by the major disruption in distribution of the tropical linguliform faunas at the beginning of the Unnamed Cambrian Stage 5 caused by dispersion of newly evolved taxa and the increased faunal exchange within the low latitudes. These faunas include the earliest acrothelid *Eothele* and acrotretide *Hadrotreta*, which probably evolved in Australasian Gondwana; whereas paterinides *Dictyonina*, *Micromitra* and *Paterina* most likely dispersed from Laurentia.
The close association of the fauna from peri-Gondwanan Alai terrane with Laurentian faunas (Fig. 6; B1) is defined by co-occurrence of the paterinid genera *Dictyonina*, *Micromitra* and *Paterina*; while *Kleithriotreta* is unknown outside of Australasian segment of Gondwana and Kazakh terranes.

The presence of the Himalayan fauna within the second major sub-cluster indicates that it was a part of the pantropical fauna, which was formed due to increased faunal exchange in low latitudes and especially between the eastern, Australasian segment of Gondwana and Laurentia at the beginning of the Unnamed Cambrian Stage 5.

Both analyses show that Himalayan faunas occupied a marginal position in relation to the Australasian segment of Gondwana. Within the Unnamed Cambrian Stage 4 the only distinct link with Australasian faunas is the presence of *Schizopholis*, whereas most of other genera, including *Botsfordia, Eoobolus, Neobolus* and *Wynnia* are probably survivors from older faunas. Two later genera are local endemics, whereas two former ones had cosmopolitan distribution. Acrotretide *Eohadrotreta* from the *Haydenaspis parvarya* Level of the Tethyan Himalaya gives a distinct link to the contemporaneous linguliform fauna of South China.

The linguliform brachiopods from the Unnamed Cambrian Stage 5 of the Tethyan Himalaya total 10 genera. The major component of the fauna are micromorphic acrotretides; however, unlike contemporaneous micromorphic brachiopod assemblages of Karatau-Naryn and North Tien Shan, they occur as recurrent oligotaxic associations, which usually include one or two acrotretide species and *Acrothele*, and they were restricted in their distribution to narrow stratigraphical intervals of carbonate sedimentation in a predominantly siliciclastic succession. It is possible that these taxa
were components of a more diverse microbrachiopod associations that inhabited the outer shelf nearby and represented a ‘reservoir’ for invaders during times when delta lobes switched.

*Eothele* is not documented in the Himalayan linguliform faunas, while *Schizopholis* is still present in the Parahio Formation, *Haydenaspis parvarya* Level (sample PO3), just below the *Oryctocephalus indicus* Level, whereas the earliest *Acrothele* is already present at the *Paramecephalus defossus* Biozone. In Laurentia (Nevada) according to Rowell (1980) *Eothele* is confined to the upper *Bonnia—Olenellus* Biozone and replaced by *Acrothele* in the Susan Dustor Limestone, which contains trilobites of pre-*Albertella* Biozone. In Siberia *Eothele* is confined to the *Oryctocara* Biozone and is replaced by *Acrothele* in the upper *Kounamkites* Biozone (Korovnikov 1998). Therefore the narrow stratigraphical range of *Eothele* is mainly confined to the *Oryctocephalus indicus* Biozone and its correlatives, and dispersion of the genus from the Australasian segment of Gondwana to west Mediterranean Gondwana, Laurentia and Siberia occurred almost isochronously, close to the proposed position of the lower boundary of the Unnamed Cambrian Stage 5 at the base of the *Oryctocephalus indicus* Biozone (Babcock et al. 2005). *Acrothele* evolved and started its dispersion probably at the mid part of the Unnamed Cambrian Stage 5.

**SYSTEMATIC PALAEONTOLOGY**

Measurements (in millimetres if not stated otherwise) are as follows: W, L, T=width,
length, height of valve; $I_w, I_l=$ width, length of pseudointerarea; $P_w=$ width of median groove; $C_w, C_l=$ width, length of cardinal muscle field; $V=$ length of visceral area; $S_I=$ length of dorsal median ridge/septum. $S=$ standard deviation, $N=$ number of measurements, $M A X=$ maximum value, $M I N=$ minimum value.

The illustrated and/or discussed material is deposited in the United States National Museum, Washington D.C. (USNM), Geological Survey of India, Kolkata (Calcutta) (GSI), Cincinnati Museum Center (CMCIP), the Wadia Institute of Himalayan Geology, Dehradun, Uttarkhand, India (WIF/A [for material numbered on individual slabs] and WIMF/A/ [for isolated microfossil specimens mounted on SEM stubs]), Tübingen University (TU), South Australian Museum, Adelaide (SAM) and Museum of the Geological Committee of Uzbekistan, Tashkent (MGCU).

Class LINGULATA Gorjansky and Popov, 1985

Order LINGULIDA Waagen, 1885

Superfamily LINGULOIDEA Menke, 1828

Family OBOLIDAE King, 1846

Subfamily OBOLINAE King, 1846

Genus AKSARINAIA Koneva, 1992

Type species. By original designation Aksarinaia triquetra Koneva, 1992, middle Cambrian, Pernopsis ultimus to Ptychagnostus intermedius biozones, Kyrshabakty, Malyi Karatau Range.
**Aksarinaia? sp.**

*Figure 7A-L*

**Material.** Total four ventral and four dorsal valves, including: WIMF/A/3751 (Lv=1.9, W=1.3, Il=0.8, Iw=1.1, Pl=0.35; Fig. 7A, B, E), WIMF/A/3752 (W=1.1, Il=0.3, Iw=0.65; Fig. 7C-D), WIMF/A/3753 Fig. 7F-H), WIMF/A/3754 (Ld=1.6, W=1.15), WIMF/A/3755 (Fig. 7I), WIMF/A/3756 (Fig. 7J), WIMF/A/3757 (Fig. 7K), WIMF/A/3758 (Fig. 7L); sample PO3 (78.07 m above the base of the Parahio Valley section), west side of the Parahio River, Spiti region, Himachal Pradesh.

**Remarks.** These smooth, slightly biconvex strongly elongate, subtriangular shells with an acutely acuminate ventral valve shows closest similarity to *Aksarinaia* Koneva, 1992. In particular, they are comparable to *Aksarinaia triquetra* Koneva, 1992 in having a characteristic ‘V-shaped’ ventral interarea with elevated, oblique pseudointerareas bearing flexure lines and a broad and narrow median groove; however, the Himalayan shells differ considerably in having an undivided dorsal pseudointerarea lacking flexure lines. In addition, the larval shell in *Aksarinaia triquetra* has a distinct median mound (protegulum) and a pair of lobes representing imprints of larval setal sacks (Holmer *et al.*, 2001, pl. 3, fig. 13), whereas the dorsal larval shell in studied specimens is completely smooth. The interior of both valves in the Himalayan shells lack distinctive features, which in addition to their small sizes (less than 2 mm), may suggest that they belong to juvenile individuals, and they may represent a new species.
Genus NOTIOBOLUS Popov (in Popov and Solovyev), 1981

*Type species*—By original designation *Notiobolus tenuis* Popov in Popov and Solovyev, 1981, Cambrian, Drumian Stage, erratic boulder from Shackleton Range, west Antarctica.

*Notiobolus? kashmiricus* (Reed, 1934)

Figure 8A, B

1934 *Obolus kashmiricus* Reed; p. 29, pl. 2, figs 19-21.

*Types.* Lectotype (here selected), GSI 15627 (=CMCIP 71494), partly exfoliated ventral valve; paratype GSI 15626 (=CMCIP 71495), exfoliated ventral valve; middle Cambrian Nutunus Formation, 2.8 km WNW of Wadapur, Kashmir.

*Remarks.* This taxon is known only from two partly exfoliated specimens. They are characterised by having a slightly transverse, subtriangular ventral valve, a smooth postlarval shell ornamented with fine growth lines, a low ventral pseudointerarea with a deep pedicle groove and flattened, elevated propareas with flexure lines. The ventral valve has a gently impressed, subtriangular visceral area, bordered anteriorly by a rim and bisected by a v-shaped pedicle nerve impression, and arcuate *vascula lateralia*. All listed features suggest affinity to *Notiobolus*, but in the absence of data on the dorsal interior, generic affiliation of the specimens is provisional and a detailed comparison with
two other species of the genus (the type species and *Notiobolus indefinites* Holmer, Popov, Koneva and Bassett, 2001) is difficult.

Genus *OEPIKITES* Khazanovich and Popov (*in* Khazanovich *et al*.), 1984

_Type species.* *Oepikites macilentus* Khazanovich and Popov in Khazanovich *et al*., 1984; middle Cambrian, Sablinka Formation, Gertovo Member, St. Petersburg Region, Russia.

*Oepikites? haimantensis* (Reed, 1910)

Figures 7M-T; 8C-L

1910 *Lingulella haimantensis* Reed; p. 50, pl. 6, figs 6-9.

1910 *Lingulella spitiensis* Reed; p. 51, pl. 6, figs 10-13.

?1910 *Lingulepis?* sp.: Reed, p. 51, pl. 6, figs 16, 16a.

non 1984 *Lingulella* cf. *haimantensis* Reed; Tripathi *et al*., pl. 1, fig. 12.

_Lectotype*–GSI 9899 (=CMCIP 71496), dorsal valve (illustrated as ventral valve by Reed, 1910, pl. 6, fig. 6), Parahio Formation, _Paramecephalus defossus_ Biozone, Hayden’s (1904) level 6, north side of the Parahio River, Spiti region, Himachal Pradesh.

_Material*–GSI 9900 (=CMCIP 71497), dorsal valve (illustrated by Reed, 1910, pl. 6, fig. 7); GSI 9901 (=CMCIP 71498) (illustrated by Reed, 1910, pl. 6, figs 8, 8a); GSI 9902 (=CMCIP 71499), illustrated by Reed, 1910, pl. 6, fig. 9), three dorsal valves; GSI 9903
(=CMCIP 71500), here selected as lectotype of *Lingulella spitiensis* (illustrated by Reed, 1910, pl. 6, fig. 10), GSI 9904 (=CMCIP 71501)), two ventral valves; GSI 9905 (=CMCIP 71502)), poorly preserved shell fragment; Parahio Formation, *Paramecephalus defossus* Biozone, Hayden’s (1904) level 6, Parahio Valley section. Three ventral and two dorsal valves, including WIMF/A/3761 (Fig. 8Q), 3762 (Fig. 8S), 3763, 3764 (Fig. 5R), 3765, from the Parahio Formation, *Kaotaia parchina* Biozone sample PO15 at 439.44 m above the base of the Parahio Valley section. WIMF/A/3766 (Fig 7T), a pair of conjoined valves and WIMF/A/3767, ventral valve fragment, from the Parahio Formation, sample at 917.47 m above the base of the Parahio Formation, sample at 917.47 m above the base of Parahio Valley section. Two ventral valves and four dorsal valves, including WIF/A331, 591, 598 (Fig. 8E, C, D), 950, 1052, 1053 from the Parahio Formation, *Paramecephalus defossus* Biozone, sample PO21 at 765.14 m above the base of the Parahio Valley section, Hayden’s (1904) level 6. WIMF/A/3759 (Fig. 7M, T), dorsal valve and WIMF/A/3760 (Fig. 7O, P), ventral valve from the Parahio Formation sample PO9 at 1242.4 m above the base of the Parahio Valley section; GSI 9908a, b, (=CMCIP 71503) ventral and dorsal valves (illustrated by Reed, 1910, pl. 6, fig. 16, 16a as *Lingulepis?* sp.), from Changnu encamping ground.

*Remarks.* The shells recovered from the residuals show dorsal and ventral interarea with raised propareas and well defined flexure lines, and a broad median groove excavated medially suggesting that they may be conditionally attributed to *Oepikites*. All the specimens that originally were assigned by Reed (1910) to *Lingulella haimantensis* represent dorsal valves; however, he also confusingly described *Lingulella spitiensis*
from the same horizon (Reed 1910, pl. 6, figs 10, 11). The dorsal valve GSI 9899, is selected here as the lectotype of *Lingulella spitiensis* and synonymised with *Oepikites*? *haimantensis*. In addition there are also a few specimens collected from Hayden’s (1904) level 6 (*Paramecephalus defossus* Biozone, sample PO21, Fig. 8C-E), which are the only topotypes available for study. Two incomplete dorsal valves between all these specimens (Fig. 8D, F) show a weakly impressed visceral area extending far beyond mid-length, with a narrow median tongue bisected by a faint median ridge, while information on the larval shell pseudointerareas of both valves and ventral interior cannot be observed on the types. Poorly preserved shells of lingulides occur occasionally also in the limestone beds in the lower part of the *Kaotaia parchina* Biozone, below Hayden’s (1904) level 4, and in the uppermost part of the Parahio Formation in the Parahio Valley. These specimens have a smooth larval and postlarval shell, and similar dorsal interior to the specimens from Hayden’s (1904) level 6; we consider these to be conspecific with *Oepikites*? *haimantensis*.

Specimens dissolved from sample PO21, which are here assigned to *Oepikites*? *haimantensis* are closely comparable to *Lingulella bynguanoensis* Roberts and Jell (1990) from the Coonigan Formation of western New South Wales. In particular, they have an identical morphology of the dorsal pseudointerarea, which has a characteristic medially excavated dorsal median groove and raised narrow dorsal propareas with flexure lines, accentuated by growth lines, as well as a strongly elongate, thickened medially visceral area bisected anteriorly by the short median edge. All these features are characteristic for *Oepikites*, though the Australian shells should be re-assigned to this genus.
Two specimens from the Changnu camping ground, assigned by Reed (1910) to *Lingulepis*? sp. can also be provisionally assigned to *Oepikites? haimantensis*.

Tripathi *et al.* (1984) illustrated a dorsal valve assigned to ‘*Lingulella cf. haimantensis*’ from the Pulchatti Quartzite Member of the basal Upper Tal Group exposed at 1.6 km south-east of Loarkha; however, the identification made in that publication is doubtful. This specimen may belong to *Eoobolus*. Bhargava *et al.* (1998) suggested *L. haimantensis* to be a provincial form but did not give reasons for this view.

**Family EOOBOLIDAE** Holmer, Popov, and Wrona, 1996

**Genus EOOBOLUS** Matthew, 1902

*Type species.* Subsequent designation by Rowell (1965) *Obolus triparilis* Matthew, 1902, middle Cambrian, Bourinot Group, Cape Breton, Canada.

*Eoobolus fuchsi* (Redlich, 1899)

Figure 9A-D

1899 *Lingulella fuchsi* Redlich; p. 7, pl. 1, fig. 10a-e.

1905 *Obolus (Lingulella) fuchsi* (Redlich); Walcott, p. 332.

1912 *Lingulella fuchsi* Redlich; Walcott, p. 502, pl. 39, figs 2, 2a-c, 3.

1955 *Lingulella fuchsi* Redlich; Schindewolf, p. 307, pl. 39, figs 2, 2a-c, 3.
Lectotype. GSI 7241 (=CMCIP 71505) (L=5.3, W=3.1, Il=2.2, Iw=2.0, Pl=1.4), partly exfoliated ventral valve, lower Cambrian, shale within the Jutana Formation (Magnesian Sandstone), lower Cambrian, Salt Range, Pakistan. Lectotype, here selected, is a single specimen from the original Redlich’s collection preserved in the Geological Survey of India. It is difficult to decide which of two ventral valves illustrated it represents, because original drawings are imprecise and lack individual details. The specimen illustrated by Redlich (1899) as pl. 10, fig. 10a is considerably smaller. Another alternative is the specimen illustrated on pl. 10, fig. 10b, c. The image shows a dorsal view of conjoined valves, but it well may erroneously represent a ventral valve with exfoliated umbonal area, as this can be seen on the specimen GSI 7240 (Fig. 9D).

Material. USNM 51546a (L=3.2, W=1.85, Vl=1.4; Fig. 9A), partly exfoliated ventral valve (Walcott, 1912, pl. 39, fig. 2); USNM 51546d (L=3.0, W=2.4; Fig. 9B), exfoliated dorsal valve exterior (Walcott, 1912, pl. 39, fig. 2c); USNM 51546b (L=1.7, W=1.35; Fig. 9C), dorsal internal mould, all specimens are from Redlichia noetlingi Biozone at Khussak; TU Br 1080/52, conjoined valves; TU Br 1080/51 (Schindewolf, 1955, pl. 8, fig. 23), TU Br 1080/53, 54; Br1080/57, dorsal valve; all from the uppermost Khussak Formation (upper Neobolus shales) and the basal Jutana Formation (Magnesian Sandstone) of Khussak, Salt Range, Pakistan.

Description. Shell dorsibiconvex strongly elongate, subtriangular, about 170-185% as long as wide with the maximum width at about one third valve length from the ventral umbo. Ventral valve acutely acuminate with apical angle 60-70° and with high triangular
pseudointerarea bisected by a very narrow and shallow pedicle groove. Propareas slightly elevated above the valve floor, bisected by very fine flexure lines running close to the proparea outer margins. Dorsal valve elongate, suboval, about 125% as long as wide with maximum width slightly anterior to mid length. Dorsal interarea high, mainly occupied by a shallow concave median grove. External surface of post-larval shell finely and densely pustulose.

Ventral interior with a weakly impressed visceral area extended anteriorly at about 45% valve length from the umbo and bisected medially by a pair of narrowly divergent grooves representing a pedicle nerve impression. Individual muscle scars indiscernible. Ventral *vascula lateralia* almost straight, narrowly divergent. Dorsal interior unknown.

*Remarks.* The species exhibits all characteristic features of *Eoobolus* including a high ventral pseudointerarea with a very narrow pedicle groove, a weakly impressed ventral visceral area not extending to the mid length, straight, slightly divergent ventral *vascula lateralia* and most importantly a finely pustulose postlarval shell. It differs from the type species *Eoobolus triparilis* (Matthew) mainly in having a more elongate, acutely acuminate ventral valve with a higher ventral pseudointerarea; however, in the absence of data on the dorsal valve interior further comparison is difficult.

*Eoobolus wanniecki* (Redlich, 1899)

Figures 8M-O; 9E, 10A-M
1899 *Lingulella Wanniecki* Redlich; p. 7, pl. 1, fig. 9a-d.

1905 *Obolus* (*Lingulella*) *wanniecki* (Redlich); Walcott, p. 332.

1912 *Lingulella Wanniecki* Redlich; Walcott, p. 528, pl. 39, figs 1, 1a-n.

1955 *Lingulella Wanniecki* Redlich; Schindewolf, p. 304, pl. 39, figs 1-20, text-figs 6-7.

2001 *Eoobolus* aff. *E. viridis* (Cobbold); Ushatinskaya and Holmer, p. 123, pl. 16, figs 10-13, pl. 17, figs 1-5.

**Lectotype.** GSI 7240a (=CMCIP 71504) ventral valve (L=4.2, W=4.0; Fig. 7 A, L) illustrated by Redlich (1899, pl. 1, fig. 9a), lower Cambrian, uppermost Khussak Formation (upper *Neobolus* Beds), *Redlichia noetlingi* Biozone, Salt Range, Pakistan.

**Material.** USNM 55744a (Lv=2.2, W=1.9; Fig. 10B), USNM 55744b (Lv=5.1, W=4.7; Fig. 10C), USNM 51744e (Lv=4.9, W=4.3, Il=1.3, Iw=2.55, Pl=1.0, Vl=2.3, Vw=2.2; Fig. 10E), 55744o (L=5.35, W=4.35; Fig. 10H), all from locality 15r, TU Br 1060/4, TU Br 1080/31, TU Br 1080/32, ventral valve (L=2.6, W=2.3, Il=0.9, Pl=0.5, Vl=1.25, Vw=1.05; Fig. 10N), TU Br 1080/33, (L=3.1, W=2.85; Fig. 10M); TU Br 1080/41-44, 45, 47, 48, ventral valves; USNM 51744d (Lv=5.1, W=4.35, Il=1.9, Iw=3.1, Pl=1.1, Vl=2.55, Vw=2.2; Fig. 10D), ventral internal mould; USNM 51744g (L=5.5, W=5.4; Fig. 10F), USNM 51744h (L=4.9, W=5.1), USNM 51744i, 51744j (Fig. 10G), 51744k, 51744n (Fig. 10J), all from locality 15r; TU Br 1080/39, 40, dorsal valves; USNM 51744l-m, sample 15r. All these specimens are from the *Neobolus* Beds, *Redlichia noetlingi* Biozone at Khussak. WIF/A100A.1-275; total 275 ventral and dorsal valves from locality PO1 (loose sample), Parahio Formation, Parahio Valley section,
WIF/A101.1 (Fig. 8M) 101.2 (Fig. 8N), 101.3 (Fig. 8O), 101.4-101.195; total 195 ventral and dorsal valves also from locality PO1 (loose sample), Parahio Formation, Parahio Valley section, Himachal Pradesh.

_Description._ Shell slightly dorsibiconvex, elongate, subtriangular to almost suboval, about 115% as long as wide, with maximum width anterior to mid-length. Ventral valve gently and evenly convex, obtusely acuminate. Ventral pseudointerarea high, triangular, almost orthocline, about one-quarter as long as wide and two-thirds as wide as the valve. Pedicle groove deep, narrow with subparallel lateral margins; propareas slightly elevated about the valve floor, bisected by deep flexure lines. Dorsal valve gently convex; dorsal pseudointerarea moderately high, orthocline, about two thirds as wide as the valve, mainly occupied by a broad, shallow median groove weakly separated from the narrow propareas bearing faint flexure lines. Postlarval shell densely pustulose.

Ventral valve interior with a slightly thickened visceral area not extending to the mid valve. Ventral umbonal muscle scars paired, bisected by a V-shaped pedicle nerve impression. Combined scars of outside lateral, middle lateral and central muscles form a pair of gently impressed subtriangular anterior muscle fields divided by a pair of grooves forming a distal part of the pedicle nerve impression. Ventral transmedian and anterior lateral muscle scars situated on a callus of secondary shell along the posterolateral margins of the visceral area. Ventral _vascula lateralia_ straight, divergent. Dorsal interior with a visceral area situated on a callus of secondary shell. Narrow anterior median tongue extending at same distance anterior to mid valve, with a pair of elongate tracks of the anterior lateral muscles bounded laterally by a pair of slightly divergent ridges and
divided by a faint median ridge (Fig. 10J). Large, gently impressed dorsal central muscle scars situated posterior to the centre of the valve. Combined transmedian, middle lateral and outside lateral muscle scars situated on a callus of secondary shell along the posterolateral margins of the visceral area. Dorsal *vascula lateralia* marginal, arcuate; dorsal *vascula media* short, straight, divergent.

**Remarks.** The specimens of *Eoobolus wanniecki* show considerable variation, mostly related to ontogeny. Smaller specimens tend to be slightly elongate, suboval with maximum width displaced anterior to mid length, whereas larger shells become more subtriangular. Shells described and illustrated by Ushatinskaya and Holmer (2001) from the Parara Formation of Yorke Peninsula, South Australia as *Eoobolus* aff. *E. viridis* (Cobbold, 1921) have no any substantial differences from *Eoobolus wanniecki* except being considerably smaller, therefore they are considered here as conspecific. *Eoobolus wanniecki* also shows close similarity to the shells described and illustrated by Holmer et al. (1996) and Ushatinskaya and Holmer (2001) as *Eoobolus* aff. *elatus* (Pelman in Pelman and Pereladov, 1986). *Eoobolus wanniecki* differs from the latter mainly in its less transverse, subtriangular shell outline and coarsely pustulose micro-ornament.

The shells described by Roberts and Jell (1990) from the Coonigan Formation of western New South Wales as *Palaeoschmidtites horizontalis* show distinct similarity to *Eoobolus wanniecki* in general shell outline, morphology of interareas in both valve and ventral visceral area; however, there is no report on the presence of finely pustulose micro-ornament in the original publication. The Australian shells differ from *Eoobolus*
wanniecki in having a more strongly impressed dorsal interior and in having a stronger dorsal median ridge. It is likely that *Palaeoschmidites horizontalis* should be re-assigned to *Eoobolus*.

The occurrence of *Eoobolus wanniecki* in float collected near the base of the Parahio Formation is biostratigraphical consistent with the recovery of a specimen of *Redlichia noetlingi* also found in loose material from the same location (Reed, 1910; Jell and Hughes, 1997). Based on the trilobite succession in south China, *Redlichia noetlingi* can be anticipated to occur stratigraphically shortly below the *Haydenaspis parvatya* level. If the loose material originated from the poorly exposed basal part of the Parahio Formation, its stratigraphic occurrence is consistent with the presence of *Haydenaspis parvatya* at the base of the continuous section exposed immediately above (Peng *et al.* 2009). This suggests that the base of the Parahio Formation at the section above the Khemangar river is likely equivalent in age to the Tsanglangpuan, as suggested by Hughes *et al.* (2013) and not significantly older (*contra* Parcha *et al.* 2005; Parcha and Pandey 2011).

*Eoobolus?* sp.

Figures 9 F-H; 10 O, P; 11

1984 *Lingulella* cf. *haimantensis* Reed; Tripathi *et al.* 1984, pl. 1, fig. 12.

1984 *Obolella* cf. *crassa* Reed (sic!); Tripathi *et al.* 1984, pl. 1, fig. 11.

1984 *Magnicanalis* sp.; Tripathi *et al.* 1984, pl.1, figs 2, 14, 17.

1984 *Obolus* sp.; Tripathi *et al.* 1984, pl.1, figs 3, 4, 8, 15.
1984 *Obolella* sp.; Tripathi et al. 1984, pl.1, figs 1, 3, 7.

1986 *Lingulella* sp.; Tripathi et al. 1986, fig. 3.5.

1986 *Lingulella* sp. A; Tripathi et al. 1986, fig. 3.6.

1986 *Lingulella* sp. B; Tripathi et al. 1986, fig. 3.7.

1984 *Obolus* sp.; Tripathi et al. 1986, fig. 3.1.

**Material.** GSI 20126 (=CMCIP 71506), dorsal valve, sample SM/34, Morora section (Tripathi et al. 1986, fig. 3.4, as *Lingulella* sp.); GSI 20016 (=CMCIP 71507), ventral external mould (Tripathi et al. 1984, pl. 1, fig. 9, as *Lingulella* sp.), sample KT/262, Dhanulti; GSI 20129 (=CMCIP 71508), ventral external mould, sample SM/37, Morora section (Tripathi et al. 1986, fig. 3.7, as *Lingulella* sp. B); GSI 20128 (=CMCIP 71509), dorsal internal mould (SM/37, Tripathi et al. 1986, fig. 3.6, as *Lingulella* sp. A); GSI 20127 (=CMCIP 71510), ventral internal mould (SM/38, Tripathi et al. 1986, fig.3.5, as *Lingulella* sp.); GSI 20022 (=CMCIP 71511), ventral valve from sample KT/26, Dhanulti (Tripathi et al. 1984, pl. 1, fig. 15, as *Obolus* sp.); GSI 20019 (=CMCIP 71512), dorsal valve from KT/266 Dhanulti (Tripathi et al. 1984, pl. 1, fig. 12, as *Obolus* sp.); GSI 20009 (=CMCIP 71513), dorsal valve, sample KT/266, Dhanulti (Tripathi et al. 1984, fig. 3.2 as *Magnicanalis* sp.); GSI 20010 (=CMCIP 71514), dorsal valve, sample KT/264, Dhanulti (Tripathi et al. 1984, pl. 1, fig. 3 as *Obolella* sp.); GSI 20018 (=CMCIP 71515), one dorsal and one ventral valve, sample KT/263, Dhanulti (Tripathi et al. 1984, Pl. 1, fig. 11 as *Obolella* cf. *crassa* Reed); GSI 20013 (=CMCIP 71516), dorsal valve, sample KT/266, Dhanulti (Tripathi et al. 1984, pl. 1, fig. 6 as *Lingulella* sp.); GSI 20123 (=CMCIP 71517), dorsal internal mould, sample, SM/38A, Morora section (Tripathi et
al. 1986, fig.3.1, as *Obolus* sp.), GSI 20131 (=CMCIP 71518), dorsal valve, sample SM/38, Morora section (Tripathi *et al.* 1986, fig.3.9), GSI 20012 (=CMCIP 71519), ventral valve, sample KT/264, Dhanulti (Tripathi *et al.* 1984, pl. 1, fig. 5, as *Obolus* sp.); GSI 20014 (=CMCIP 71520), dorsal and ventral internal moulds from KT/266 Dhanulti (Tripathi *et al.* 1984, pl. 1, fig. 7 as *Obolella* sp.); GSI 20017 (=CMCIP 71521), ventral internal mould from KT/266 Dhanulti; CMCIP 71522, ventral valve; CMCIP 71523, dorsal valve along with one unnumbered ventral valve and 5 unnumbered dorsal valves; CMCIP 751767-751769, ventral values on same slab as CMCIP 71523: CMCIP 71524, contains four ventral and five dorsal valves; CMCIP 71525, contains two ventral and three dorsal valves; CMCIP 71526, two ventral and three dorsal valves; all from the Member B of the upper Tal Group; about 1.5 km from Dhaulagiri towards Maldeota, Mussoorie Syncline, Garhwal Himalaya. Additional material CMCIP 70361-70453 from GKM-11 (N 30˚ 20.634’, E 078˚ 09.659’, 1650 m altitude) on roadside from Maldeota to Gopi Chandka Mahal, Mussoorie Syncline, Garhwal Himalaya.

*Remarks*. These small lingulides are rather common in the shales of Member B of the upper Tal Group. They are characterised by having a slightly dorsiibiconvex shaped shell, varying in outline from subtriangular to slightly elongate, suboval (Figs 9G, H: 10O). The ventral valve is usually subacuminate, with narrow subtriangular pseudointerarea, and visceral area not extending to the mid-valve and straight, almost parallel *vascula lateralia* (Figs 9G, O). The dorsal valve has a visceral area bisected by a median ridge, which is terminated anterior to mid-length with a narrow tongue bearing a pair of anterior lateral muscles tracks, bounded laterally by a pair of slightly divergent ridges (Fig. 6F, 8C).
Listed features suggest strong affinity to *Eoobolus wanniecki* (Redlich, 1899); however, pustulose micro-ornament, which is the most distinctive feature of the Family Eoobolidae, has not been observed on the shells from the Tal Group, probably, because of inadequate preservation due to re-crystallisation and neomorphism of the original organophosphatic fabric. Most of the shells illustrated by Tripathi *et al.* (1984, 1986) under the generic names *Lingulella, Magnicanalis, Obolus* and *Obolella* (Fig. 11A-C, E-H) represent a single lingulide species and they can be provisionally assigned to *Eoobolus*.

Family NEOBOLIDAE Walcott and Schuchert, 1908

*Diagnosis.* Pseudointerareas of both valves narrow, lacking flexure lines; ventral pseudointerarea with a deep pedicle groove and high propareas; dorsal pseudointerarea as a narrow, crescent shape rim. Ventral interior with a visceral area on the tri-lobate platform. Dorsal interior with variably developed platforms under central muscle scars and posterolateral muscle fields on a thick callus of secondary shell. Larval and postlarval shell smooth; dorsal larval shell bilobate.

*Remarks.* The Family Neobolidae is re-introduced here to include several early Cambrian lingulide genera formerly assigned to the Family Botsfordiidae (Holmer and Popov 2000, 2006). The original concept of the taxon (Walcott and Schuchert *in* Walcott, 1908) has been emended to include genera which are characterised by a smooth larval and postlarval shell, a strong, tri-lobate platform in the ventral valve, a prominent dorsal
median ridge and variably developed muscle platforms in the dorsal valve. All these features are neither characteristic of the Family Botsfordiidae, nor of the Superfamily Acrotheloidea, which typically have a pitted larval shell, a finely pustulose postlarval shell and lack muscle platforms and a prominent dorsal median ridge. Hence as the genera included within the Neobolidae show distinct affinities to the Linguloidea they are considered within that superfamily. The Neobolidae are also somewhat similar to the Cambrian – Ordovician family Elkaniidae, in having strongly developed muscle platforms, but latter is characterised by having a finely pitted larval, and postlarval shell and well developed flexure lines on ventral propareas.


Genus NEOBOLUS Waagen, 1885

**Type species.** By original designation *Neobolus warthi* Waagen, 1885, lower Cambrian, Khussak Formation (*Neobolus* beds), Salt Range, Pakistan.

*Neobolus warthi* Waagen, 1885

Figure 12; 13A, B
1885 *Neobolus warthi* Waagen; p. 758, pl. 84, figs 3-8.

1955 *Neobolus warthi* Waagen; Schindewolf, p. 325, pl. 14, figs 1f-h, 2-9, pl. 15, figs 1, 3 (non fig. 2), text-figs 13-20 (full synonymy).

*Lectotype.* GSI 3776 (=CMCIP 71529) (Fig. 9B), illustrated by Waagen (1885, pl. 84, fig. 4), ventral valve; lower Cambrian, Khussak Formation (lower *Neobolus* beds), Kiura, Salt Range, Pakistan.

*Material.* GSI 3775 (=CMCIP 71528), (Waagen 1885, pl. 84, fig. 3b), GSI 3776 (=CMCIP 71529), (Fig. 12B); Waagen 1882-85, pl. 84, fig. 4), GSI 3778 (=CMCIP 71530), (Waagen 1885, pl. 84, fig. 6), GSI 3781 (=CMCIP 71531), (Waagen 1885 pl. 85, fig. 3a-b), GSI 3782 (=CMCIP 71532) (Waagen 1885, pl. 85, fig. 2; Waagen 1891, pl. 2, fig. 11), GSI 3783 (=CMCIP 71533) (Fig. 12E; Waagen 1885, pl. 82, fig. 2), GSI 3786 (=CMCIP 71534) (Fig. 12D; Waagen 1885, pl. 85, fig. 5, as 1891, pl. 2, fig. 3c), GSI 3787 (=CMCIP 71535) (Fig. 12A; Waagen 1885, pl. 86, fig. 1), GSI 3795 (=CMCIP 71536), Waagen 1885, pl. 86, fig. 9), TUBr 1080-102 (Fig. 12L), ventral valves; GSI 3777 (=CMCIP 71537), (Fig. 12C, F; Waagen 1882-85, pl. 84, fig. 5a, b), GSI 3779 (=CMCIP 71538) (Fig. 12I; Waagen 1885, pl. 84, fig. 7), GSI 3781 (=CMCIP 71539), GSI 3784 (=CMCIP 71540), (Fig. 12H; Waagen 1885, pl. 85, fig. 4 as *Davidsoniella linguloides*), GSI 3785 (=CMCIP 71527) (Fig. 12G; Waagen 1885, pl. 85, fig. 5; 1891, pl. 2, fig. 4c as *Davidsoniella linguloides*), Tu M Br 1080-6, (Fig. 12J; Schindewolf 1955, pl. 14, fig. 3), TUBr 1080-100, (Fig. 9K; Schindewolf 1955, pl. 14, fig. 7), dorsal
valves; lower Cambrian, lower *Neobolus* beds of Chel Hill, Jutana and Kiura, Salt Range, Pakistan.

*Remarks*. Walcott (1912) and subsequently Schindewolf (1955) gave a detailed description and discussion of the species, and considered *Neobolus wynnei* Waagen, 1885, *Davidsoniella linguloides* Waagen, 1885, *Davidsoniella squamma* Waagen, 1885 and *Lingulella? kiurensis* Waagen, 1885 as junior synonyms of *Neobolus warthi* Waagen, 1885.

Unlike species of *Schizopholis* and *Botsfordia*, the shell of *Neobolus warthi* is smooth, ornamented only by dense, regular concentric fila. The dorsal larval shell in *N. warthi* is also smooth and distinctly bilobed. The preservation and condition of the specimens available for study is not favourable for more detailed study of the larval shell morphology in *Neobolus*; however, it shows distinct similarity with that of *Minlatonia* (Ushatinskaya and Holmer 2001, pl. 23, fig. 5b). The dorsal larval shell in *Minlatonia* is about 230 μm wide, it is smooth and has a pair of inflated lobes divided by the median cleft. These lobes show position of the larval setal sacks.

Figured specimen GSI 7256 (Redlich, 1899, pl. 1, figs. 25a, b) was reported missing from the Kolkata collection in January 1901 and has yet to be returned.

A ventral internal mould of a lingulid from the *Redlichia noetlingi* Zone of the upper part of the Lolab Formation in Kupwara, Kashmir, questionably assigned by Shah *et al*. (1980) to *Neobolus* is very poorly preserved, and its generic assignment is highly doubtful.
Remarks. Revision of the specimens deposited in the Geological Survey of India, Kolkata has revealed that in many cases taxonomic identifications given by Reed (1910), Kumar et al. (1983), Tripathi et al. (1984, 1986), Mathur and Joshi (1989), Mathur and Srivastava (2005) cannot be confirmed and must be disregarded. An important point is that none of the specimens illustrated in these publications show calcareous shell fabric or any other feature diagnostic for rhynchonelliform brachiopods in general or Obolellida in particular; therefore, previous identification of Himalayan material as Magnicanalis and Obolella (e.g. Fig. 11C, E, K) are likely shells representing Eoobolus? sp. or unidentified lingulides.

*Nisusia depsaensis* Reed, 1910 from Depsa Khad in the Parahio Valley is based on a single lingulide shell fragment (specimen GSI 9898). The shell is definitely organophosphatic and cannot be assigned either to *Nisusia* or to Rhynchonelliformea. Because of poor and incomplete preservation of the type, this taxon cannot be positively identified and the binomen itself can be declared as *nomen dubium*.

*Lingulella* cf. *caelata* (Hall), briefly described and illustrated by Reed (1910, pl. 6, fig. 14) from Hayden’s (1904) level 2 of the Parahio Valley section represents a single lingulide shell fragment (Fig. 11L, GSI 9907) lacking taxonomically informative characters, thus its genus and species affiliation given by Reed cannot be adequately supported by existing material.
Obolus (Westonia)? sp. from Hayden’s (1904) level 9, briefly described and illustrated by Reed (1910, pl. 6, fig. 17) is a strongly exfoliated ventral valve, which does not preserve surface ornament of irregular transverse lines indicative of Westonia (Fig. 11D). In the absence of data on the characters of the interior and pseudointerarea, its generic affiliation within Linguloidea is uncertain.

Specimens identified by Mathur and Joshi (1989) as Paterina sp. and Obolopsis sp. (Fig. 11J) and by Kumar et al. (1983) as Diandongia cf. D. pista Rong (Fig. 11I) do not exhibit features that indicate generic affiliation within Lingulida or Paterinida; they more likely belong to Linguloidea. The specimens of Mathur and Joshi (1989) were reported to occur at a stratigraphically lower level within the Tal Group than the Eoobolus? sp. described above, but others have questioned whether the stratigraphic position attributed by the authors was correct, and suggested that the specimens more likely belong to Member B of the upper part of the Tal Group (Hughes et al. 2005, p. 63).

A shell fragment from beds bearing Tonkinella breviceps from the Pohru Valley illustrated by Kobayashi (1934) probably belongs to the Linguloidea, but because of poor preservation further taxonomic determination is impossible.

Superfamily ACROTHELOIDEA Walcott and Schuchert, 1908
Family ACROTHELIDAE Walcott and Schuchert, 1908
Subfamily ACROTHELINAE? Walcott and Schuchert, 1908
Genus ACROTHELE Linnarsson, 1876
Type species. Subsequent designation by Oehlert (1887) Acrothele coriacea Linnarsson, 1876, middle Cambrian, Sweden,

Acrothele? praetans Reed, 1910

Figure 14C

1910 Acrothele praetans Reed; p. 55, pl. 6, figs 26, 26a, 27, 27a.

?1910 Obolella cf. atlantica Walcott; Reed, p. 55, pl. 6, fig. 25.

Holotype. GSI 9915 (=CMCIP 71541), ventral valve (Reed 1010, pl. 6, fig. 26), Parahio Formation, Paramecephalus defossus Biozone, Hayden’s (1904) level 6, Parahio Valley section.

Material. GSI 9914 (=CMCIP 71542), incomplete dorsal valve from Parahio Formation, Paramecephalus defossus Biozone, Hayden’s (1904) level 6 (Reed 1010, pl. 6, fig. 25 as Obolella cf. atlantica), Parahio Valley section, Himachal Pradesh.

Remarks. The holotype and only specimen is characterised by having a submarginal apex with an umbonal foramen and finely pustulose ornament of the postlarval shell, suggesting affiliation to the Family Acrothelidae. It can be only tentatively assigned to Acrothele because the characters of the larval shell and interiors of both valves are unknown. An elongate, suboval shell outline is not common in Acrothele, but it may be result of post-mortem distortion of the specimen. A shell briefly described and illustrated
by Reed (1910) as *Obolella cf. atlantica* Walcott, 1890, from Hayden’s (1904) level 6 exhibits remnants of finely pustulose micro-ornament on the organophosphatic shell and probably represents a dorsal valve of *Acrothele praetans*.

*Acrothele vertex* Reed, 1910

Figures 13C-L; 14A, B, D; 15A-D, I-P

1910 *Acrothele vertex* Reed; p. 56, pl. 6, figs 28, 29.

1910 *Acrothele cf. spurri* Walcott; Reed, p. 56, pl. 6, fig. 30.

1910 *Obolella cf. crassa* (Hall); Reed, p. 56, pl. 6, figs 23, 24.

*Lectotype*. GSI 9917 (=CMCIP 71543), ventral valve (Fig. 14B), Parahio Formation, *Oryctocephalus salteri* Biozone, Hayden’s (1904) level 9, Parahio Valley section.

*Material*. GSI 9912 (=CMCIP 71544), ventral valve (Fig. 14A) illustrated by Reed, 1910 as *Obolella cf. crassa* (Hall) (Reed, 1910 pl. 6, figs 23, 24); GSI 9919 (=CMCIP 71545), ventral valve (illustrated by Reed, 1910 as *Acrothele cf. spurri* Walcott, pl. 6, fig. 30); 10 ventral and one dorsal valves, including WIMF/A/3786, 3787 (Fig. 13D), 3788 (Fig. 13C), from the Parahio Formation, *Kaotaia prachina* Biozone, sample PO15 at 439.44 m above the base of the Parahio Valley section; WIMF/A/1520, ventral valve from sample PO13 at 836 m above the base of the Parahio Valley section; WIMF/A/3768 (Fig. 13H) and 3769, two ventral valves Parahio Formation from sample at 917.47 m above the base of Parahio Valley section. Four ventral and one dorsal valves, including WIMF/A/3770
(Fig. 13E, I), 3771-3774, from sample PO32 at 836.66 m above the base of Parahio Valley section. WIF/A595 (Fig. 14K), ventral valve, from Parahio Formation, *Paramecephalus defossus* Biozone, sample PO21 at 765.14 m above the base of Parahio Valley section. One ventral and five dorsal valves, including WIMF/A/4044, from Parahio Formation, sample PO31 at 836.36 m above the base of Parahio Valley section. Twelve ventral and ten dorsal valves, including WIMF/A/3776-3785, WIMF/A/3786 (Fig. 15A-C), WIMF/A/3787 (Fig. 15D-F), WIMF/A/3788 (Fig. 15G), WIMF/A/3789 (Fig. 15H), WIMF/A/3790, 3791 (Fig. 15M-P), 3792 (Fig. 15J, K), 3793 (Fig. 15I, L), WIMF/A/3794-3796 (Fig. 13F), from sample PO9 at 1242.4 m above the base of Parahio Valley section.

**Remarks.** Specimens of *Acrothele* are common within the interval from sample PO15 to sample PO9 of the Parahio Valley section, corresponding to the interval from Hayden’s (1904) level 4 to 9 and higher (all within the informal global Cambrian stage 5). All these shells show little variation in morphology and they are considered as conspecific with the lectotype of *Acrothele vertex*. It is also probable that the only specimen assigned to *Acrothele? praetans* Reed, 1910 may represent an aberrant or distorted individual conspecific with *Acrothele vertex*; however, due to inadequate preservation of the holotype of the former binomen, it is practical to keep the species name for its type, considering it as *nomen dubium.*

*Acrothele vertex* is among the oldest yet known species of the genus. Its ventral brephic shells retain a rudimentary pedicle groove and propareas (Fig. 10L) and strongly
elongate pedicle opening mainly outside of the larval shell unlike the type species
*Acrothele coriacea* (see Holmer and Popov, 2000, fig. 45a-n).

Specimens assigned by Reed (1910) to *Acrothele cf. spurri* Walcott and *Obolella cf. crassa* (Hall) have a characteristic pustulose ornament and phosphatic composition of the shell. They came from the same horizon as the types of *Acrothele vertex* and are here reassigned to this species. Among them the partly exfoliated ventral valve GSI 9812 shows the internal pedicle foramen perforating a thickened umbal part of the valve and a pair widely divergent *vascula lateralia* that are typical for *Acrothele*.

*Acrothele vertex* differs from *Acrothele exquisita* Aksarina 1975, which occurs in the Cambrian *Pseudanomocarina* Beds of Alai Range, Kyrgyzstan, in having a strongly elongate foramen and more posteriorly placed ventral apex.

There are a number of *Acrothele* species described from various parts of Baltica, Laurentia, Siberia, Gondwana and its associates. Differences between species are mainly based on characters of the pedicle foramen and its position relative to the boundary of the ventral larval shell, the development of spines on the dorsal and ventral larval shell, and the position of the ventral umbo. Other reported differences in shell outline and profile of both valves are too imprecise to make accurate discrimination between species possible. Most of the listed diagnostic features can be recognised with confidence only after SEM studies, thus affinities of many formally defined *Acrothele* species remain unresolved pending taxonomic revision.

*Acrothele?* sp.
Fig. 16J-L

Material. WIF/A1058, dorsal valve (Fig. 16J), sample PI18; WIF/A1059, dorsal internal mould (Fig. 16K), sample PI4; WIF/A1060, composite mould of dorsal valve (Fig. 16L), sample PI9; all from the Parahio Formation, PU-3 section in Purni, Zanskar valley.

Remarks. A few acrotheloid shells occur in argillites belonging to the uppermost part of the Parahio Formation in Purni, Zanskar valley. They are usually preserved as compressed and distorted specimens or as composite moulds, though pustulose micro-ornament (Fig. 16J) and some details of the interior (Fig. 16K) can be observed. These shells probably belong to *Acrothele*, but in the absence of data on the ventral valve morphology this taxonomic affiliation is highly provisional.

Family BOTSFORDIIDAE Schindewolf, 1955

Genus BOTSFORDIA Matthew, 1891

Type species. *Obolus pulcher* Matthew, 1889, lower Cambrian, Hanford Brook Formation, Catons Island, New Brunswick, Canada.

*Botsfordia granulata* (Redlich, 1899)

Figures 14O, P; 16A-I

1899 *Mobergia granulata* Redlich; p. 5, pl. 1 figs 11-16.
1955 *Botsfordia granulata* (Redlich); Schindewolf, p. 314, pl. 9, figs 1-10, pl. 10, figs 1-10, pl. 11, figs 1-7, pl. 12, figs 1-8, pl. 13, figs 1-4, text-figs 8-12 (full synonymy).

**Lectotype**, Here selected, GSI 7242 (=CMCIP 71546) (Fig. 16G-I), ventral valve, Cambrian, Khussak Formation, *Redlichia noetlingi* Biozone, eastern Salt Range, Pakistan. (Redlich in 1899 did not specify the locality, but it seems probable from the description of the collector, Dr. Fritz Neotling [1894], that it was the southern slope of Khussak Fort Hill. Other possibilities are Khewra Gorge, or on the northern side of Khussak Fort Hill.)

**Paratypes.** GSI 7244 (=CMCIP 71547), dorsal valve (Fig. 14O; Redlich, 1899, pl. 1, fig. 13, as *Mobergia granulata*), locality and horizon the same as lectotype.

**Other material.** TU Br 1060-2 (Fig. 16C), TU Br 1060-3b (Fig. 16F), 1060-7, 1080-3g (Fig. 16B), 1080-58, 1080-70, 1080-71, 1080-80, 1080-86, 1080-87, 1080-92, 1080-94, ventral valves; TU 1060-3 (Fig. 16D-E), TU 1060-5, 1060-6, 1080-50 (Fig. 16A), 1080-95, 1080-97, all from Khussak; GSI 7234 (=CMCIP 71548) (Fig. 14P), dorsal valve, locality in the eastern Salt Range (no locality data given by Redlich 1899). This species co-occurs with *Redlichia noetlingi* both in the uppermost Khussak Formation (upper *Neobolus* beds) and in the lower part of the Jutana Formation (Magnesian Sandstone).

**Remarks.** This species was described, discussed and illustrated in great detail by Schindewolf (1955). Some types from the original Redlich (1899) collection, along with
some specimens deposited in Tübingen University are re-illustrated here. Figured specimens GSI 7243, and GSI7247-49 (Redlich, 1899, pl. 1, figs. 12, 16-18 respectively) were reported missing from the Kolkata collection in January 1901 and have yet to be returned.

_Botsfordia? sp._

Figure 16M

1980 _Botsfordia granulata_ (Redlich); Shah et al. 1980, p. 516, pl. 1, figs 11, 15.

_Material._ GSI 20124 (=CMCIP 71549), dorsal internal mould, sample, SM/38A, Morora section (Tripathi _et al._ 1986, fig. 3.2, as _Magnicanalis_ sp.), Mussourie syncline; upper Tal Group, Member B.

_Remarks._ Shells questionably assigned to _Botsfordia_ may occur in the Tal Group. In particular, we consider that specimen illustrated by Tripathi _et al._ (1986, fig. 3.2) as _Magnicanalis_ sp. from Member B of the upper Tal Group represents an exfoliated dorsal valve of _Botsfordia_. Lingulide shells from the upper part of the Lolab Formation in Kupwara, Kashmir, assigned by Shah _et al._ (1980) to _Botsfordia granulata_ probably indeed belong to _Botsfordia_, but specimens illustrated in that publication are too poorly preserved for detailed taxonomic determination.

Genus _SCHIZOPHOLIS_ Waagen, 1885
Type species. By original designation *Schizopholis rugosa* Waagen, 1885, lower Cambrian, Khussak Formation (lower *Neobolus* beds), Salt Range, Pakistan.

*Diagnosis.* Shell almost equally biconvex, ventral valve with a submarginal umbo and a narrow triangular procline to catacline pseudointerarea bearing a deep pedicle groove with steep lateral slopes and vestigial pseudointerareas. Margins of the delthyrium may converge distally, but always separated by a narrow cleft. Dorsal valve gently convex, with a marginal umbo and a shallow median sulcus. Dorsal pseudointerarea vestigial with a shallow median groove. Ventral larval shell with three tubercles; dorsal larval shell with one or two pairs of tubercles. Larval shell finely pitted; postlarval shell densely pustulose. Dorsal visceral field small, on callus of secondary shell; median tongue narrow, extending to mid-valve, bisected by median ridge. Mantle canal system baculate in both valves with straight, submedian, divergent *vascula lateralia*; dorsal *vascula media* long, divergent.

Remarks. For a long time the relationship of *Schizopholis* to other acrotheloid genera was uncertain because of inadequate knowledge of the ventral interior and characters of the pedicle opening. In the original description, Waagen (1885) reported the presence of narrow slit posterior to the apex; however, Walcott (1912) after study of the types of *Schizopholis rugosa* suggested that this species has a pedicle opening as a narrow slit
immediately posterior to the apex, which does not reach the posterior valve margin. At the same time he suggested that in *Discinolepis granulata* Waagen, 1885, the pedicle opening represents a narrow, subtriangular cleft open posteriorly and Walcott further confirmed it by illustration based on Waagen’s types (Walcott, 1912, pl. 81, fig. 3). Schindewolf (1955) re-described *Schizopholis rugosa* based on newly available material. He provided, for the first time, description and illustration of the dorsal interior and gave a very schematic illustration of the ventral interior based on the specimen TU Br 1080/12 (Schindewolf, 1955, text-fig. 22). He considered shells described by Waagen (1885) as *Discinolepis granulata* and *Schizopholis rugosa* to be conspecific, which makes *Discinolepis* the junior synonym of *Schizopholis*. Our restudy of the type specimens of both taxa has led us to the same conclusion. However, our observations including the study of type specimens (as subsequently defined by Walcott 1912) of *Schizopholis rugosa* (GSI 3790, Fig. 14J), *Discinolepis granulata* (GSI 3792, Fig. 14G, L) and specimens TU 1080/107 and TU 1080/12 illustrated by Schindewolf (1955, pl. 15, figs 4-5) do not support a presence of the posteriorly confined pedicle foramen in *Schizopholis rugosa*. Instead, the pedicle opening in *Schizopholis rugosa* resembles closely that of *Eothele napuru* Kruse, 1990. In both taxa the pedicle opening is formed by posteriorly converging delthyrial margins, but they are not merged completely and a narrow cleft is invariably preserved. Both taxa are congeneric and externally they are very similar to *Eothele* Rowell, 1980, but differ in having a delthyrial opening and a rudimentary ventral interarea, which are diagnostic features of the Family Botsfordiidae. It becomes also certain that *Karathele* Koneva, 1986, as re-defined by Holmer et al. (1996) represents the junior objective synonym of *Schizopholis*. 
Species assigned. In addition to the type species the genus includes: (1) Eothele napuru Kruse, 1990, from Cambrian (Ordian) Jinduckin Formation of Daly Basin, Northern Territory, Australia and erratic boulders of King George Island, Antarctica; (2) Karathele coronata Koneva, 1986, from Peronopsis? ultimus and Ptychagnostus atavus biozones of Malyi Karatau Range, Kazakhstan; (3) Karathele yorkensis Holmer and Ushatinskaya in Ushatinskaya and Holmer, 2001 from the Parara Formation of Yorke Peninsula, South Australia.

Schizopholis rugosa Waagen, 1885

Figure 14, E-J, L

1885 Schizopholis rugosa Waagen; p. 753, pl. 14, fig. 1a-e, pl. 15, figs 4-7.
1885 Discinolepis granulata Waagen; p. 750, pl. 86, figs 2-4.
1891 Schizopholis rugosa Waagen; Waagen, pl. 2, figs 12-14.
1891 Discinolepis granulata Waagen; Waagen, pl. 2, figs 15-16.
1892 Schizopholis rugosa Waagen; Hall and Clarke, p. 95, figs 50-51.
1892 Discinolepis granulata Waagen; Hall and Clarke, p. 90, figs 45-46.
1912 Schizopholis rugosa Waagen; Walcott, p. 609, pl. 81, figs 1, 1a-e (non pl. 1, fig. 4c).
1912 Discinolepis granulata Waagen; Walcott, p. 664, pl. 81, figs 3, 3a-b.
1955 Schizopholis rugosa Waagen; Schindewolf, p. 331, pl. 14, figs 1a-e, 10, pl. 15, figs 4-7, text-figs 21-23.
1955 Neobolus warthi Waagen; Schindewolf, pl. 15, fig. 15.

2000 Schizopholis rugosa Waagen; Holmer and Popov, fig. 45.2a-d.

non 1979 Schizopholis rugosa Waagen; Koneva, p. 44, pl. 13, figs 1-7.

**Lectotype.** Selected by Walcott (1912), GSI 3790 (=CMCIP 71575), ventral valve exterior (Fig. 11J; Waagen 1885, pl. 86, fig. 4a-d; 1891, pl. 2, fig. 3a-b), Kiura, Khussak Formation (lower Neobolus beds), eastern Salt Range, Pakistan.

**Material.** GSI 3788 (=CMCIP 71576) (Waagen 1885, pl. 86, figs 2a, 2b), GSI 3789 (Fig. 11I, Waagen 1885, pl. 86, figs 3a, 3b), GSI 3791 (=CMCIP 71577) (Waagen 1885, pl. 86, figs 4; 1891, pl. 2, fig. 15, as Discinolepis granulata), Jutana, GSI 3792 (=CMCIP 71578) (Fig. 11G, L; Waagen 1885, pl. 86, fig. 6, 1891, pl. 2, fig. 16, as Discinolepis granulata, selected by Walcott, 1912 as lectotype) from Jutana, TU Br 1060/12a, TU Br 1060/13b, TU Br 1080/103 (Fig. 11F, Schindewolf 1955, pl. 15, fig. 2, as Neobolus warthi), TU Br 1080/107 (Fig. 11H), TU Br 1060/14d, ventral valves; TU1060/14 (Fig. 11E), dorsal valve. All from Khussak Formation (lower Neobolus bed), eastern Salt Range, Pakistan.

**Remarks.** Schizopholis rugosa is closely similar to Schizopholis napuru in characters of the pedicle opening, which is formed from posteriorly converging delthyrial margins, but they are not merged completely and a narrow cleft is invariably preserved. In characters of the dorsal interior both species are almost undistinguishable and the main difference is in the more marginal position of the ventral umbo in Schizopholis rugosa, which also has
an almost catacline ventral pseudointerarea. In that respect illustrations of the ventral valves given by Waagen (1885, pl. 86, figs 5b, 6b) are inaccurate, if compared with actual specimens (Fig. 14G, J, L).

The ventral valve TU Br 1080/103 (Fig. 14F), illustrated by Schindewolf (1955, pl. 15, fig. 2) as *Neobolus warthi*, shows remnants of pustulose ornament and a characteristic median tubercule on the larval shell in front of the delthyrium. Thus it is reassigned here to *Schizopholis rugosa*.

Specimens from the Cambrian Edrei Formation of the Edrei Mountains in Kazakhstan described by Koneva (1979) as *Schizopholis rugosa* are characterised by the umbo situated at a considerable distance from the posterior margin and they have a pedicle foramen. Therefore they represent different genus and species, probably an early species of *Acrothele*.

*Schizopholis napuru* (Kruse, 1990)

Figures 14D, 17

1990 *Eothele napuru* Kruse; p. 31; pl. 12A-K, text-fig. 16.

1991 *Eothele napuru* Kruse; Kruse, p. 178 fig. 7A-E.

1993 *Eothele napuru* Kruse; Brock and Cooper, p. 782, fig. 15.1-14.

1996 *Karathele napuru* Kruse; Holmer, Popov and Wrona, p. 45; pl. 11, figs 1-8; pl. 12, figs 1-5; text-fig. 3C-D).
**Holotype.** SAM P85206, ventral valve; Cambrian (Ordian) Jinduckin Formation of Daly Basin, Northern Territory, Australia.

**Material.** Total 220 incomplete ventral valves and 82 incomplete dorsal valves, including WIF/A1057 (Fig. 14D), WIMF/A/3800 (Fig. 17A, B, E, K), WIMF/A/3801 (Fig. 17C), WIMF/A/3802 (Fig. 17D, G), WIMF/A/3803 (Fig. 17F, I), WIMF/A/3804 (Fig. 17H), WIMF/A/3805 (Fig. 17J); all from the Parahio Formation, *Haydenaspis parvatia* Biozone, sample PO3 at 78.07 m above the base of the Parahio Valley section, Kashmir.

**Remarks.** The studied shells are assigned to *Schizopholis napuru* because they are characterised by the pitted larval shell with a high median tubercle above the pedicle notch and a pair posterolaterally situated tubercles in the ventral valve, and a single pair of strong tubercles in the dorsal valve, finely pustulose postlarval shell, a deep pedicle groove in the ventral valve and vestigial ventral propareas and a procline pseudointerarea. All studied specimens are incomplete, but the largest shell fragment is about 6 mm wide, which closely approach the largest size (7.6 mm) of the specimens in the type series described by Kruse (1990). The only observed difference is the shape of the pedicle notch in large individuals, which has a form of a narrow slit with subparallel lateral margins not convergent distally as in some specimens of *Schizopholis napuru* illustrated by Kruse (1990).

Order ACROTRETIDA Kuhn, 1949

Superfamily ACROTRETOIDEA Schuchert, 1893
Family ACROTRETIDAE Schuchert, 1893

Genus AMICTOCRACENS Henderson and MacKinnon, 1981


_Remarks._ Restudy of Amictocracens teres from the Georgina Basin confirmed that this species has a larval shell about 180-185 µm wide, with a micro-ornament of flat-based circular imprints varying in diameter from 2 to 4 µm with vertical walls, separated by flat-topped interspaces bearing very fine, hemispherical pits less than 1 µm across (Fig. 15B, K).

The pedicle foramen is confined to the larval shell, whereas the dorsal larval shell has a shallow median cleft. Flat-based imprints are characteristic of Scaphelasmatidae, Eoconulidae and early Biernatidae, but also occur in some Acrotretidae (Williams 2003). Amictocracens together with scaphelasmatid Kotylotreta are probably the earliest yet known acrotretide genera with this kind of larval shell micro-ornament.

Amictocracens teres Henderson and MacKinnon, 1981

_Figure 18_

_Material._ Total of seven ventral and five dorsal valves, including WIMF/A/3806 (Figs 18A), WIMF/A/3807 (Figs 18B-D), WIMF/A/3808 (Fig. 18E), WIMF/A/3809 (Fig. 18F, G),
WIMF/A/3810 (Fig. 18H), WIMF/A/3811, (Fig. 18I), from the Parahio Formation, *Oryctocephalus salteri* Biozone, sample PO31 at 836.36 m above the base of the Parahio Valley section.

**Remarks.** The specimens described here are closely similar to those described by from Australia and New Zealand (Henderson and MacKinnon 1981; Engelbretsen 1996) in the main morphological characters and we consider them to be conspecific. However, the ventral interior with a characteristic boss-like apical process is not well preserved (Fig. 18I). The exact position of the pedicle foramen and morphology of the ventral larval shell cannot be seen in the earlier published descriptions of *Amictocracens teres*, but in our material the pedicle foramen is close to circular and inside the larval shell, which is about 170 µm wide (Fig. 18A). The umbonal region in most of the specimens is exfoliated, while flat-based circular imprints varying in diameter from 2 to 4 µm with vertical walls, separated by flat-topped interspaces preserved in a few ventral valves (Fig. 18B). Specimens of *Amictocracens teres* from the Georgina Basin, kindly presented by Glen Brock (Macquarie University, N.S.W.) show closely similar larval shell morphology, including micro-ornament and position of the pedicle foramen (Fig. 18K). One specimen appears to have a circular borehole drilled into the shell (Fig. 18C).

*Amictocracens? brocki* sp. nov.

Figures 19, 20A-J

1980 *Furnishina* sp.; Bhatt and Kumar; p. 357, fig. 8.
Derivation of name. After Dr. Glenn Brock (Macquarie University, N.S.W.) in appreciation of his valuable contributions to Cambrian brachiopod studies.

Holotype. WIMF/A/3812, holotype, dorsal valve (Fig. 19B, C), from the Parahio Formation, sample PO9 at 1242.4 m above the base of the Parahio Valley section.

Material. A pair of conjoined valves and several thousand dorsal and ventral valves, including paratypes WIMF/A/4045 (Fig. 19A), WIMF/A/3813 (Fig. 19D, G), WIMF/A/3814 (Fig. 19E), WIMF/A/3815 (Fig. 19F), WIMF/A/3816, WIMF/A/3817 (Fig. 19H, I), WIMF/A/3818 (Fig. 19J), WIMF/A/3819 (Fig. 19K), WIMF/A/3820 (Fig. 20A, C, G), WIMF/A/3821 (Fig. 20B), WIMF/A/3822 (Fig. 20E), WIMF/A/3823 (Fig. 20F, I), WIMF/A/3824 (Fig. 20H), WIMF/A/3825 (Fig. 20J); locality and horizon as for holotype.

Diagnosis. Ventral valve conical, less than half as high as long; dorsal median septum variable, from simple low triangular blade with upper rod to high, slightly folded blade that may be strongly folded and spinose in gerontic individuals; median buttress poorly developed.

Description. Shell transversely oval, about 80-90% as long as wide. Ventral valve conical less than half as high as long in adult specimens, up to 1.04 mm wide, 0.92 mm long, and 0.25 mm high. Anterior slope of ventral valve gently convex. Ventral pseudointerarea
flattened, most commonly catacline to slightly procline, with a variably developed
triangular intertrough. Pedicle foramen almost circular, around 40-50 µm wide,
posteriorly directed and located entirely within larval shell. Dorsal valve lowly convex in
lateral profile, up to 1.36 mm wide and 1.07 mm long. Dorsal pseudointerarea orthocline,
wide and short, occupying up to almost half valve width and around 10% of length.
Dorsal median groove shallow and wide. Dorsal propareas small and anacline. Dorsal
larval shell variably expressed, sometimes with a shallow median sulcus, and in some
valves with two indistinct nodes. Larval shell of both valves around 150-200 µm wide,
with characteristic pitting with large flat-based circular imprints around 3-4 µm across,
surrounded by clusters of small pits up to 1 µm across situated on flat-topped interspaces.

Ventral interior with a small apical process, forming a broadening triangular ridge
along the anterior slope and perforated by the well-defined preserved tube. Ventral
*vascula lateralia* short and straight poorly impressed directly lateral to the apical process.
Ventral cardinal muscle scars well-defined small on posterior slope. Ventral apical pits
poorly defined.

Dorsal cardinal muscle fields strongly impressed, very wide and long, occupying
up to 75% of valve width and almost half as long as the valve. Dorsal median septum
very variable in morphology, ranging from a simple, low, triangular blade in brephic
shells, to a high, rod-like, slightly folded blade in larger individuals, or becoming very
high, strongly folded and spinose. Median septum starting at distance from poorly
developed median buttress and extending up to 75% of valve length.
Discussion. Only the middle Cambrian type species from Australia, New Zealand, and the new record above has so far been assigned to *Amictocracens* with certainty (Henderson and MacKinnon 1981; Engelbreten 1996). *Amictocracens? brocki* differs from the type species in several important characters, particularly the much more variable dorsal median septum that is most commonly high and distinctly folded with spines. Other dorsal valves among our new material have a simple low triangular blade with an upper rod (Fig. 19F, J), or higher, slightly folded blades (Fig. 19B, C, E, K). The material of *Amictocracens teres* described by Engelbreten (1996) also include valves with a folded dorsal median septum, showing that this character is variable within other species in the genus. The strongly spinose dorsal valves are most similar to those in the Ordovician Ephippelesmatidae *Lurgiticoma* (see Popov and Holmer 2000, fig. 69), but *Amictocracens? brocki* differs from all Ephippelesmatidae in having a well-developed apical process, in the lack of an external pedicle tube and in details of the larval pitting.

*Amictocracens? brocki* also differs from *Amictocracens teres* in lacking the boss-like apical process. Species of *Prototreta* Bell and *Angulotreta* Palmer are also characterized by sometimes having a spinose septum, but species of *Prototreta* differ from *Amictocracens? brocki* in having a larger dorsal pseudointerarea and a foramen that is not enclosed within the larval shell, whilst species of *Angulotreta* have a ridge-like, high apical process and apical pits (Holmer and Popov, 2000). The larval pitting of *Amictocracens? brocki* is identical to that of species of the middle Cambrian – Silurian Scaphelasmatidae (e.g. Popov and Holmer 1994).

Genus APHELOTRETA Rowell, 1980
Type species. *Aphelotreta minuta* Rowell, 1980 from Cambrian Stage 5, upper part of Pioche Shale Formation, *Albertella* Zone, Nevada, USA.

*Aphelotreta khemangarensis* sp. nov.

Fig. 21

*Derivation of name.* After the Khemangar River, that flows near the type locality.

*Holotype.* WIMF/A/3826, a pair of conjoined valves (Fig. 21 A-C, F, I; Lv, 0.43; Ld, 0.38; W, 0.375; T, 0.21), from the Parahio Formation, *Paramecephalus defossus* Biozone, sample PO21 at 765.14 m above the base of the Parahio Valley section.

*Paratypes.* Total two pairs of conjoined valves, four ventral valves and five dorsal valves, including, WIMF/A/3827 (Lv, 0.445; W, 0.47D, E; Fig. 18), WIMF/A/3828 (Lv, 0.43; W, 0.39; Fig. 21G, K), WIMF/A/3829 (Fig. 21H), WIMF/A/3830 (Fig. 21J), WIMF/A/3831 (Fig. 21L), WIMF/A/3832 - WIMF/A/3836 (unfigured); locality and horizon the same as for the holotype.

*Diagnosis.* Small for genus, with strongly aspalcine to almost orthocline ventral interarea and differentiated pitted micro-ornament of larval shell, with hemispherical imprints of two varying sizes.
Description. Shell subequally biconvex, slightly elongate, suboval, about 95-110% as long as wide and slightly less than 50% as high as long. Anterior commissure rectimarginate. Ventral valve lateral profile moderately convex with maximum height at one-third valve length from the apex. Ventral pseudointerarea undivided, low, triangular, strongly apsacline to almost orthocline. Pedicle foramen elongate suboval, up to 340 µm long and 200 µm wide, crossing the boundary of the larval shell. Dorsal valve evenly convex with rudimentary pseudointerarea mainly occupied by a broad, concave median groove. Larval shell about 120 µm wide with micro-ornament of fine circular to suboval, hemispherical pits of two variable sizes. Larger pits about 1-2 µm in diameter separated by clusters of smaller pits less than 80 µm wide. Postlarval shell with very fine, evenly spaced fila.

Ventral interior with thickened umbonal area, but lacking discernible apical process. Muscle scars and mantle canals not impressed. Dorsal interior with a broad, triangular median buttress, and a short median ridge not extending to mid-valve. Cardinal muscle fields small, weakly impressed.

Remarks. Aphelotreta khemangarensis sp. nov. differs from the type species A. minuta in being almost half the size, strongly apsacline ventral interarea and in its strongly differentiated pitted micro-ornament of the larval shell with hemispherical pits of two varying sizes.

Genus EOHADROTRETA Li and Holmer, 2004

Type species. Eohadrotreta zhenbaensis Li and Holmer, 2004 from the Early Cambrian (Qiongzhusian Stage), Shuijingtuo Formation, South Shaanxi, China.
**Eohadrotreta haydeni** sp. nov.

**Figure 22**

*Derivation of name.* In honour of the late Sir Henry H. Hayden in appreciation of his pioneering work on the early Palaeozoic geology of Spiti.

*Holotype.* WIMF/A/3837, ventral valve (Fig. 22D) from the Parahio Formation, *Kaotaia prachina* Biozone, sample PO-15 at 439.44 m above the base of the Parahio Valley section.

*Paratypes.* 42 ventral and 60 dorsal valves, including WIMF/A/3838 (Fig. 22A), WIMF/A/3839 (Fig. 22B, C), WIMF/A/3840 (Fig. 22E), WIMF/A/3841 (Fig. 22G), WIMF/A/3842 (Fig. 22H), WIMF/A/3843-3850, from the Parahio Formation, *Kaotaia prachina* Biozone, sample PO-15 at 439.44 m above the base of the Parahio Valley section.

*Other material.* 219 ventral and 82 dorsal valves, including WIMF/A3851 (Fig. 22F, I, J), WIMF/A/3852 (Fig. 22K), WIMF/A/3853 (Fig. 22L), WIMF/A/3854 (Fig. 22M), WIMF/A/3855-WIMF/A/3861, from the Parahio Formation, *Haydenaspis parvatia* Biozone, sample PO-3 at 78.07 m above the base of the Parahio Valley section.

*Diagnosis.* Ventral valve very widely conical. Ventral pseudointerarea procline with shallow intertrough. Dorsal valve with rudimentary pseudointerarea, weakly defined median buttress and gently impressed, short dorsal cardinal muscle fields.
**Description.** —Shell ventribiconvex, subcircular to somewhat transversely oval, with very short posterior margin. Ventral valve with maximum width near mid-valve. Ventral valve very widely and low conical, with maximum height close to posterior margin. Ventral pseudointerarea invariably procline, divided by poorly defined, shallow intertrough. Pedicle foramen close to circular, almost entirely outside of larval shell. Dorsal valve gently convex. Dorsal pseudointerarea very short and narrow, orthocline. Median groove poorly defined, broad, shallow.

Ventral interior lacking well defined apical process and apical pits, as well as mantle canals. Dorsal median septum very low and short, not extending to mid-valve. Median buttress poorly defined, low. Dorsal cardinal muscle fields poorly defined and short.

**Discussion.** *Eohadrotreta haydeni* sp. nov. differs from both the type species and *Eohadrotreta zhujiahensis* Li and Holmer, 2004, in having a very poorly developed dorsal median septum and pseudointerarea as well a very poorly defined median buttress and short dorsal cardinal muscle scars.

Genus HADROTRETA Rowell, 1966

*Type species.* Original designation by Rowell (1966) *Acrotreta primaea* Walcott, 1902, from the Early-Middle Cambrian, Pioche Shale, Nevada, USA.

*Hadrotreta timchristiorum* sp. nov.

Figure 23
Derivation of name. After Drs. Timothy Paulsen and Christie Demosthenous who together collected the type material.

Holotype. WIMF/A/3867 ventral valve (Fig. 23H) from the Parahio Formation, sample PI-13 at 74.11 m above the base of the Purni 3 section, Zanskar Valley, India.

Paratypes. Total 121 ventral and 326 dorsal valves, including WIMF/A/3868 (Fig. 23J), WIMF/A/3869 (Fig. 23L, Q), WIMF/A/3870 (Fig. 23J), WIMF/A/3871 (Fig. 23N), WIMF/A/3872 (Fig. 23O), WIMF/A/3873 (Fig. 23U), WIMF/A/3874 (Fig. 23V), WIMF/A/3875-3879, locality and horizon as for holotype.

Other material. 13 ventral and 11 dorsal valves, including WIMF/A/3862 (Fig. 23A, B), WIMF/A/3863 (Fig. 23C), WIMF/A/3864 (Fig. 23D), WIMF/A/3865 (Fig. 23E, G), WIMF/A/3866 (Fig. 23F), from the Parahio Formation, Paramecephalus defossus Biozone, sample PO-25, at 776 m above the base of the Parahio Valley section; 444 ventral and 30 dorsal valves, including WIMF/A/3880 (Fig. 23I), WIMF/A/3881 (Fig. 23K, R), WIMF/A/3882 (Fig. 23S), WIMF/A/3883 (Fig. 23T), Oryctocephalus saltleri Biozone, sample PO-32, at 835.66 m above the base of the Parahio Valley section.

Diagnosis. Ventral valve with slightly hypercline to almost procline pseudointerarea with narrow and shallow intertrough and pedicle foramen touching the boundary of the larval
shell. Dorsal cardinal muscle fields gently impressed, about 25-30% as long as the valve. Faint dorsal median septum extending anterior to mid-valve.

Description. Shell ventribiconvex, transversely oval, with maximum width at mid-length. Posterior margin short, rounded. Ventral valve widely conical, with maximum height in the umbonal area. Ventral pseudointerarea slightly hypercline to almost procline, divided by the shallow and narrow intertrough. Pedicle foramen slightly elongate, suboval, touching a boundary of the larval shell, about 50 $\mu$m long. Dorsal valve gently convex with a short and narrow orthocline to slightly anacline pseudointerarea, about two-fifths as wide as the valve, with narrow propareas. Median groove broad, shallow. Larval shell about 170 $\mu$m covered by hemispherical pits about 1.5-1.8 $\mu$m in diameter. Postlarval shell with faint concentric fila.

Ventral interior with a high, broadly triangular apical process occluding posteriorly the umbonal area and perforated by the conical internal pedicle tube with large circular internal foramen. Deep apical pits situated on both sides of the apical process laterally to the internal foramen. Lateral sides of the apical process bordered by strongly impressed, straight, and widely diverging baculate *vascula lateralia*. Ventral cardinal muscle scars strongly impressed. Dorsal valve interior with gently impressed cardinal muscle fields about 25-30% as long as the valve. Dorsal median septum generally poorly developed and low, extending anterior to mid-valve. Median buttress low, weakly defined. Low, ridge-like central muscle scars present in a centre of the valve on both sides of the median ridge in the largest specimens.
Remarks. Hadrotreta timchristiorum sp. nov. is most similar to the type species H. primaea (Walcott). Both species have an apical process that is flanked by strongly impressed, straight, and widely diverging baculate vasa lateralia and perforated posteriorly by a large internal foramen, as well as a poorly developed and low dorsal median septum. Hadrotreta timchristiorum differs from the type species mainly in having a narrow and shallow ventral intertrough, as well as a shorter and less developed dorsal pseudointerarea, and smaller and shorter dorsal cardinal muscle fields.

Genus LINNARSSONIA Walcott, 1885

Type species. Original designation by Walcott (1885, p. 115); Obolella transversa Hartt in Dawson, 1868; middle Cambrian of New Brunswick, Canada.

Linnarssonia parahioensis (Reed, 1910)

Figure 24

1910 Acrotreta parahioensis Reed; p. 54, pl. 6, figs 18-22.

Lectotype (selected here). GSI 9910a (=CMCIP 71550) (Fig. 21M; illustrated by Reed, 1910, pl. 6, figs 21), Parahio Valley, Parahio Formation, Hayden’s (1904) level 4, Kaotaia prachina Zone, at 580.2 m above the base of the Parahio Valley section.
Paratypes. Four dorsal valves, GSI 9910b-e (=CMCIP 71551 - 71554) (Fig. 24K-L); occurrence and horizon as for lectotype.

Other material. 21 ventral and seven dorsal valves, including WIMF/A/3884 (Fig. 24A, H), WIMF/A/3885 (Fig. 24B, C, E, F), WIMF/A/3886 (Fig. 24D, G), WIMF/A/3887 (24I, J), from Parahio Formation, *Paramecephalus defossus* Biozone, sample PO-21, Hayden’s (1904) level 6, Parahio Valley, Parahio Formation, at 765.14 m above the base of Parahio Valley section.

Description. Shell ventribiconvex, transversely oval, with maximum width at mid-length. Posterior margin short, rounded. Ventral valve widely conical, with maximum height in the umbonal area. Ventral pseudointerarea almost procline, gently curved backwards at the umbonal region, divided by a broad, shallow intertrough. Pedicle foramen, slightly elongate, suboval, about 45 µm long and 35 µm wide, crossing the boundary of the larval shell. Dorsal valve gently convex with a very weak sulcus originating in the umbonal area. Dorsal pseudointerarea short, almost orthocline, slightly less than half sagittal valve width, mainly occupied by the shallow median groove. Larval shell about 220-230 µm wide, with micro-ornament of hemispherical pits varying in size from 1.4 to 2.0 µm in diameter. Postlarval shell ornamented by fine concentric fila.

Ventral interior with a high, boss-like apical process anterior to the internal foramen flanked by a pair of strongly impressed, widely divergent *vascula lateralia* bordered anteriorly by a rim. Dorsal interior with a subtriangular median buttress and gently impressed elongate, suboval cardinal muscle fields about two fifths as long as the valve. Dorsal median
septum ridge-like, about 90% as long as the valve with the highest point slightly behind its anterior termination.

Remarks. Discrimination of the generic identity of the shells described and illustrated by (Reed 1910) as *Acrotreta parahioensis* represents a challenge. Types (illustrated by Reed, 1910, pl. 6, figs 18-22) came from Hayden’s (1904) level 4, which can be placed in a mid part of the 3rd unzoned interval between the *Kaotaia parchina* and *Paramecephalus defossus* biozones. Types were sampled from argillites and do not exhibit the full range of diagnostic morphological characters required for their precise generic identification and there are no limestone beds in proximity of this level, which may be processed to extract organo-phosphatic shells. Nevertheless, it is certain that these specimens cannot be assigned to *Eohadrotreta haydeni* sp. nov., which occurs in the *Kaotaia parchina* Biozone (sample PO-15), because the acrotetide shells from the ‘Hayden’s (1904) level 4’ have significantly large sizes and possess a strong, ridge-like dorsal median septum which excludes their attribution to *Eohadrotreta*. Exfoliated dorsal valves have some resemblance to *Linnarssonia* and indeed specimens of *Linnarssonia* have been recovered from the limestone bed (sample PO-21) 185 m higher up, at the base of the *Paramecephalus defossus* Biozone and at 765.14 m above the base of Parahio Valley section, corresponding to the Hayden’s (1904) level 6. There is no other occurrences of *Linnarssonia* in the studied section, while there is a good probability that acrotetide specimens from the Hayden’s (1904) level 4 and Hayden’s (1904) level 6 are conspecific; therefore, emended concept of *Linnarssonia parahioensis* (Reed, 1910) is based on the specimens dissolved from the limestone bed.
Linnaresia parahioensis, as here redefined, is similar to Linnaresia captiosa Koneva, 1986 from the *Pernopsis? ultimus* to *Goniagnostus nathorsti* biozones of Malyi Karatau Range, South Kazakhstan, but can be easily distinguished by its procline ventral interarea, a stronger and longer (up to 90% valve length) dorsal median ridge and stronger ventral impressions of *vascula lateralia* accentuated anteriorly by divergent ridges.

Genus PROTOTRETA Bell, 1938

*Type species.* Prototreta trapeza Bell, 1938, from the Cambrian Meagher Limestone Formation (*Bathyuriscus* zone) of Montana, USA.

*Prototreta? sumnaensis* sp. nov.

Figure 25

1980 *Sagittodontus* sp.; Bhatt and Kumar; p. 357, fig. 4.

1980 *Problemocmites* spp.; Bhatt and Kumar; p. 357, figs. 5-7.

*Derivation of name.* After the Sumna river, near the type locality.

*Holotype.* WIMF/A/3888, a pair of conjoined valves (Fig. 25F, G, Parahio Valley, Parahio Formation, sample PO9 at 1242.4 m above the base of the Parahio Valley section.)
Paratypes. Total of several thousand dorsal and ventral valves, including WIMF/A/3889 (Fig. 25A), WIMF/A/3890 (Fig. 25B), WIMF/A/3891 (Fig. 25C), WIMF/A/3892 (Fig. 25D), WIMF/A/3893 (Fig. 25E, I, J), WIMF/A/3894 (Fig. 25H), WIMF/A/3895 (Fig. 25K, M), WIMF/A/3896 (Fig. 25L), WIMF/A/3897 to 3950, WIMF/A/4003-4043, locality and horizon as for the holotype.

Diagnosis. Ventral valve very highly conical with concave anterior slope. Ventral pseudointerarea procline to slightly apsacline with a weakly defined intertrough accentuated only by deflections of growth lines. Dorsal median septum triangular with a single upper rod, occupying more than half of valve length. Dorsal cardinal muscle scars weakly impressed, not exceeding one-quarter valve length.

Description. Shell transversely oval, about 80-85% as long as wide. Ventral valve highly conical, 80% as high as long in large adult specimens, up to 1.62 mm wide, 1.37 mm long, and 1.30 mm high, and around 40% as high as wide in younger specimens under 1 mm wide. Anterior slope of ventral valve concave, with characteristic change in growth at around 0.70 mm valve width, becoming wider conical through later growth. Intertrough weakly defined, mainly by deflections of growth lines in the medial part of the ventral pseudointerarea. Ventral pseudointerarea flattened, most commonly strongly apsacline in large adults, but with variable inclination through ontogeny, procline to catacline. Pedicle foramen close to circular, around 70 µm long and 55-66 µm wide, facing posteriorly, cutting across the margin of the larval shell. Dorsal valve low convex in lateral profile, up to 1.77 mm wide and 1.40 mm long, with shallow median sulcus.
Dorsal pseudointerarea orthocline, wide and short, generally occupying more than half valve width and only 5-7% of length. Dorsal median groove shallow and wide. Dorsal propareas small and anacline. Larval shell of both valves, around 200-220 µm wide, ornamented by hemispherical pits varying in size. Dorsal larval shell with shallow median sulcus, in some valves with two indistinct nodes. Postlarval shell ornamented by fine concentric fila.

Ventral interior with the apical process forming low, broadening ridge bridging posterior and anterior slope and occluding the umbonal part of the valve. Internal pedicle tube subconical with a large internal opening. Ventral *vascula lateralia* straight and long, directly bordering apical process. Apical pits and cardinal scars poorly defined.

Dorsal cardinal muscle fields slightly raised, wide and short, occupying more than half of valve width and less than 25% of length. Dorsal median septum well developed, blade-like, triangular, starting directly anterior of small median buttress and extending for more than 60% of valve length, with single upper rod.

*Discussion.* *Prototreta? sumnaensis* sp. nov. provisionally referred to the genus mainly because it has a pedicle foramen facing posteriorly and crossing the boundary of the larval shell, a ridge-like, apical process broad, penetrated by pedicle tube and a high triangular median septum; however, it differs from most of the species assigned to the genus in having a high, conical ventral valve with weakly defined intertrough, and a simple, blade-like dorsal median septum bearing a single upper rod. Among other species assigned to the genus only *Prototreta gribovensis* Popov, 1985 from the Cambrian Snezhnogorskaya Formation of the Novaya Zemlya archipelago has strongly convex...
ventral valve almost as high as long, a weakly defined intertrough and dorsal medial
septum with the single rode, but unlike the later species, *Prototreta? sumnaensis* has a
procline to only slightly apsacline ventral interarea, a concave (not convex) profile of the
anterior valve slope and small dorsal cardinal muscle fields not exceeding one-quarter
valve length.

*Prototreta millsii* Brock and Percival, 2006, from the Wydjah Formation (Pimpira
Member) of north-western New South Wales also has a concave lateral profile of the
anterior ventral valve slope and an upper septal rod, while *Prototreta? sumnaensis* is
characterized by a high conical ventral valve almost as high as long with a ventral
pseudointerarea strongly apsacline in large adults and a weakly defined intertrough.

The specimen Bhatt and Kumar (1980, fig 4) figured as *Sagittodontus*
(presumably the *nomen nudum* “*Agittodontus*” of Vaidyanadhan and Ramakrishnan,
2008, p. 581) and those figured as *Problemoconites* (Bhatt and Kumar, 1980, fig. 5-7) are
available as specimens GSI19607 to 19610. Although it was not possible to either cast or
photograph these small specimens, their high spired shells are apparently phosphatic and
their fine surficial ridges suggest accretionary growth. Specimens GSI19607 and 19608
both have distinct, circular apical foramen located near the tip of the spire. The shell is
divided into two surfaces one of which slopes steeply and convexly from the foramen
down to the aperture, and other of which is a gentler, slightly concave slope. The shell is
bilaterally symmetrical about the midlines of both surfaces. The steep surface has paired
striae, giving a corrugated appearance with the central portion slightly inflated, as is
evident in Bhatt and Kumar’s (1980). All these features agree closely with *Prototreta?
sumnaensis* and these specimens are here attributed to this species.
Class PATERINATA Williams, Carlson, Brunton, Holmer and Popov, 1996

Order PATERINIDA Rowell, 1965

Superfamily PATERINOIDEA Schuchert, 1893

Family PATERINIDAE Schuchert, 1893

Genus PATERINA Beecher, 1891

*Type species.* By original designation *Obolus labradoricus* Billings, 1861, Lower Cambrian of Labrador, Canada.

*Paterina? suspicosa* Aksarina, 1975

Figure 26F, G, I, P, Q

1975 *Paterina? suspicosa* Aksarina; Repina *et al.*, p. 95, pl. 4, figs 11-17.


*Material.* WIMF/A/3797 (Fig. 26P, Q), ventral valve and WIMF/A/3798 (Fig. 26F, G, I), dorsal valve from the Parahio Formation, sample PO-25 at 776 m above the base of the Parahio Valley section, *Paramecephlus defossus* Zone, Parahio Formation, north side of the Parahio River, Spiti region, Kashmir.
Remarks. A record of the occurrence of *Paterina* in the early to mid-Cambrian of Australasian peri-Gondwana is very poor. Yet only two species formally described, including *Paterina alaica* Imanalieev and Pelman, 1988, from Cambrian olistoliths of the Ulugtau Mountains, Alai Range and Kargaily Formation of North Tien Shan, Kyrgyzstan, and *Paterina? suspiciosa* Aksarina, 1975, from the Cambrian olistoliths of Alai Range. The shells from the Parahio Formation show concentric ornament typical for *Paterina*, but also retain a homeodeltidium, which is otherwise known only in *Paterina? suspiciosa*, but absent in other species of the genus which are characterised by the open delthyrium. Therefore, in spite of a small number of specimens, their taxonomic affiliation is not in doubt, but generic affiliation of *Paterina? suspiciosa* remains questionable (for further discussion see Holmer *et al.* 2001, p. 24).

*Paterina sp.*

Figure 26M, N

*Material.* WIMFA3799, dorsal valve (Fig. 26M, N); sample PO-3 (78.07 m above the base of Parahio Valley section), north side of Parahio River, Spiti region, Kashmir.

Remarks. A single dorsal valve is comparable to *Paterina alaica* Imanalieev and Pelman, 1988, from Cambrian olistoliths of the Ulugtau Mountains, Alai Range, Kyrgyzstan in its gently convex sagittal profile, transverse, subrectangular outline and ornamentation of
fine regular concentric rugellae, but without data on the ventral valve morphology its species attribution cannot be made.

Genus *Wynnia* Walcott, 1908

*Type species.* *Orthis warthi* Waagen, 1891, Cambrian, Khussak Formation (lower *Neobolus* Beds), Khussak, eastern Salt Range, Pakistan.

*Remarks.* The type species of the genus is known from a few internal moulds; however, as it was commented by Holmer and Popov (2006) the specimens preserve distinct traces of organophosphatic shell, which prevent its affiliation to the Rhynchonelliformea. It is likely that valves of *Wynnia warthi* were very weakly mineralised, because the shell matrix in the most of lingulide shells from *Neobolus* Beds is well preserved. It recalls *Aldanotreta* Pelman, 1977 and *Askepasma* Laurie, 1986 among paterinides, in having ventribiconvex shell with an open delthyrium and a broadly unisulcate anterior commissure but differs in having a pair of strongly impressed, subparallel *vascula media* in the ventral valve, a shallow dorsal median sulcus and a faint dorsal median ridge extending well beyond the mid-valve.

*Wynnia warthi* (Waagen, 1891)

*Figures 26A-E, H, L, O*

1891 *Orthis warthi* Waagen; p. 102, pl. 1, figs 12-15; pl. 2, figs 1, 2.
1912 *Wynnia warthi* (Waagen); Walcott, p. 771, pl. 89, figs 4, 4a-f.

1955 *Wynnia warthi* (Waagen); Schindewolf, p. 334, pl. 15, figs 8-10.

*Lectotype*. GSI 4122 (=CMCIP 71555), internal mould of ventral valve (Fig. 26A), Khussak Formation (upper Annelid Sandstone), Chél Hill, eastern Salt Range, Pakistan.

*Paratypes*. GSI 4125 (Fig. 26O), dorsal view of internal mould of juvenile specimen, GSI 4124 (=CMCIP 71556) (Fig. 26B) and 4125 (=CMCIP 71557) (Fig. 26C), ventral internal moulds, Khussak Formation (upper Annelid Sandstone), Chél Hill, eastern Salt Range, Pakistan.

*Other material*. TU Br 1080/109, TU Br 1080/110 (Fig. 26D, E, H, L), TU Br 1080/111, internal moulds, lower Cambrian, Khussak Formation (upper Annelid Sandstone, Khussak, Salt Range, Pakistan.

*Description*. Shell ventribiconvex, subcircular in outline, with a narrow, straight, hinge line and a gently unisulcate to almost rectimarginate anterior commissure. Ventral valve lateral profile moderately convex, more strongly curved at the umbonal area with maximum height at about one-fourth to one-fifth valve length from the umbo. Ventral interarea high, gently curved, apsacline with a broad, triangular, open delthyrium. Dorsal valve gently convex with a slightly swollen umbonal area and a vestigial interarea. Shallow dorsal median sulcus originating at the umbo and gradually fading anterior to mid-length. Surface ornament not observed.
Ventral interior with a small visceral area situated posteromedially, bearing subtriangular track of the adductor muscles flanked laterally by weakly impressed oblique muscles. Ventral mantle canal system saccate with a pair of strongly impressed vascula media subparallel in the posterior half of the valve and slightly divergent anterior to mid-length and weakly impressed vascula arcuata separated from vascula media at mid-valve and gradually curved towards posterior valve margin. Dorsal interior with a large, weakly impressed visceral field extending slightly anterior to mid-valve and bisected medially by a faint median ridge, and bearing large, subtriangular radially arranged muscle tracks of the anterior and posterior adductors. Dorsal mantle canals undiscernible.

The stratigraphic occurrence of this species needs to be clarified. Waagen (1891, p. 103) claimed it occurs in the “upper region of the Neobolus beds along with Conocephalites warthi” at Chél Hill (near Khussak). That trilobite glabella has been compared to Yuehsienszella szechuanensis (see Jell and Hughes, 1997, p. 28), but is very poorly preserved, and offers little stratigraphic constraint. Despite being reported from the Neobolus beds, Wynnia warthi has not been reported to co-occur with Neobolus. Schindewolf (1955, p. 80) recorded it from the Neobolus shales of the “lower gallery” of Middlemiss (1891), and Walcott (1905, p. 252) placed it below beds from which Neobolus warthi has been collected, and from the “Upper Annelid Standstone”. Accordingly, we consider it be a little older, but given the uncertainty in its occurrence, do not use it as a named biostratigraphic level.
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Appendix

Fossil localities

Salt Range

Walcott (1912) listed five localities, numbered as 15r and 357a-357d, and we relate material described by others to these localities.

Locality 15r. This number was given to the specimens sampled from dark argillaceous shales (*Redlichia noetlingi* Biozone) of the Khussak Formation (Noetling, 1894) at Kussak (also transliterated as Khussak, or Kusak) and donated by Noetling in 1902 to the USNM. Brachiopods include *Botsfordia granulata* (Redlich), *Eoobolus fuchsi* (Redlich), *Eoobolus wanniecki* (Redlich). Schindewolf’s (1995) collections of these three taxa also included material from this locality which is at N 32°42’34", E 73°3'56". The overlying Jutana Formation (formerly known as the Magnesian Sandstone) also contains a fossiliferous shale horizon that bears *Botsfordia granulata* (Redlich) and *Eoobolus fuchsi* (see Schindewolf, 1955, p. 18).

Locality 357a. This fossil locality is situated at Jutana (also transliterated as Jatana), at N 32°43’13", E 73°9'25". Brachiopods *Neobolus warthi* Waagen and *Schizopholis rugosa* Waagen (listed as *Discinolepis granulata* Waagen) were sampled purplish-colored, fine-grained, micaceous sandstone in the lower part of *Neobolus* beds of the Khussak Formation (Noetling, 1894).

Locality 357b. This fossil locality is situated at Chêl Hill, which is close to Kussak. Only *Neobolus warthi* Waagen is reported from this locality. It was sampled from purplish-
colored, fine-grained, micaceous sandstones of Neobolus beds or upper Annelid Sandstone of the Khussak Formation (Noetling, 1894).

Locality 357c. This locality is situated near the fresh-water springs in a gorge above the salt mines at Kiura (also transliterated as Khewra), N 32°40'15", E 73°0'9"E. Brachiopods Neobolus warthi Waagen and Schizopholis rugosa Waagen (including lectotype selected by Walcott) were sampled from purplish-colored, fine-grained, micaceous sandstones in the power part of Neobolus beds of the Khussak Formation (Noetling, 1894).

Locality 357d. These are several, probably isolated, localities situated between Chél Hill and Kiura. Only Wynnia warthi (Waagen) is reported. It was sampled from concretionary shales, the lower part of Neobolus beds Khussak Formation (Noetling, 1894). The lectotype of Wynnia warthi (Waagen) was sampled from one of these localities in the vicinity of Chél Hill.

Mussoorie Syncline, Garhwal Himalaya

Near Dhaulagiri. MG-1. This is a road side exposure of black shale of Member B of upper Tal Group (Palaeolenus Zone), from a 10 cm thick layer within a black shale up to 3 m thick, situated about 1.5 km from Dhaulagiri towards Maldeota. Here brachiopods Eoobolus? sp. were collected in 1994 by N.C.H.

Loarkha section. This is an exposure of the Member B of the upper Tal Group (Palaeolenus Zone) along the Maldeota-Dhanulti road at 1.6 km south-east of Loarkha. According to Tripathi et al. (1984, p. 222-223, fig. 2), here brachiopods were sampled
from four fossiliferous horizons (samples KT/262-264 and 266) within a shale unit at the lowermost part of the Pulchatti Quartzite Member. Restudy of the specimens illustrated by Tripathi et al. (1984, pl. 1) does not confirm a presence of *Lingulella, Magnicanalis* and *Obolella*. All specimens from that locality belong to a single lingulide species tentatively identified as *Eoobolus?* sp. This is probably close to the Gopi Chandka Mahal locality (GKM11) (N 30° 20.634’, E 078° 09.659’, 1650 m altitude) located on the roadside from Maldeota to Gopi Chandka Mahal, Mussoorie Syncline.

*Marora Section*. This is an exposure of Member B of the upper Tal Group (*Palaeolenus* Zone) situated on the Maldeota-Kaddukhal-Dhanulti road about 100 m downstream over the Song river at Marora. According to Tripathi et al. (1986, p. 585-586, fig. 2) here brachiopods occur in two fossiliferous horizons (samples SM/36 and SM/37) in the shale unit about 26 m thick. Restudy of the specimens illustrated by Tripathi et al. (1986, fig. 3) does not confirm a presence of *Lingulella, Magnicanalis* and *Obolella*. All specimens from that locality belong to a single lingulide species tentatively identified as *Eoobolus?* sp.

*Garhwal Synform, Ganga Uttar Pradesh*

*Ganga River downstream of Kauriyala*. The section of the Tal Group in the area described by Kumar et al. (1983). This publication contains a report on the occurrence of *Diandongia* cf. *D. pista* Rong, 1974 in the lower Tal Group ‘Calcareaous Member’ (*Drepanuroides* Zone). Restudy of the specimen (GSI 19831), illustrated by Kumar et al. (1983, p. 106, pl. 1, figs 1, 2), puts this taxonomic affiliation in doubt, because it does not
preserve diagnostic features that would permit its taxonomic discrimination within Linguloidea.

_Tethyan Himalaya_

_Pohru Valley, Kashmir._ Notiobolus? kashmiricus was collected from the middle Cambrian Nutunus Formation, about 2.8 km WNW of Wadapur, in the Pohru Valley of north western Kashmir, India, and is thought to be close to N 34°25’, E 74°10’ (Reed, 1934; Jell and Hughes, 1997, p. 10). It was Reed’s locality E (K26/512, 513, and 525). The brachiopod occurs with the trilobites Tonkinella breviceps and Hundwarella memor, and has been correlated with the upper part of the Parahio Formation in Zanskar and Spiti (Jell and Hughes, 1997). A poorly preserved brachiopod illustrated by Kobayashi (1934, fig. 7) was also collected close by and co-occurred with _T. breviceps_.

_Purni Section, Zanskar._ This section, which exposes three formations of Cambrian rock (Myrow et al., 2006a), has yielded brachiopods from only the Parahio Formation, which was deposited in deltaic conditions. PI4 with _Acrothele?_ sp. was collected from the lowest prominent, red coloured dolomite bed in the Parahio Formation in the Purni section (that extends north towards Phuktal Gompa). It is at N 33° 14.261’, E 077° 09.674’, 4086 m altitude, and is at 578.47 m in the Purni section (in Purni section 2 of Myrow et al., 2006a). PI9 with _Acrothele?_ sp. was a sample of green-weathering black shale from the Parahio Formation immediately above a 1 m thick dolomite towards the top of the Purni 3 section, lower than the Sudanomocarina sinindica trilobite zone, but likely higher than the PI13 collection. It was collected near the track to Phuktal Gompa at N 33° 15.562’, E 077°
10.087', 3852 m altitude. PI13 contains a rich, monospecific assemblage collected from a prominent dolomite bed low in the Parahio Formation at 71.14 m the Purni 3 section and contains abundant *Hadrotreta timchristiorum* sp. nov. It was collected at N 33° 13.762’, E 077° 09.581’, 4326 m altitude, and is stratigraphically lower than the *Sudanomocarina sinindica* trilobite zone. PI14 was collected in situ from the *Sudanomocarina sinindica* trilobite zone along with a rich trilobite fauna (Peng et al. 2009). It is at N 33° 15.204’, E 077° 10.321’, 3949 m altitude, and is at 500.32 m in the Purni section. PI18 was collected from talus at N 33° 15.266’, E 077° 10.206’, 3944 m altitude, at about 501 m in the Purni 3 section of the Parahio Formation, in the *Sudanomocarina sinindica* trilobite zone.

*Parahio valley, Spiti.* This section, which was Hayden’s (1904) original section, yielded multiple brachiopod collections made at different stratigraphic levels. A detailed description of the section, outline of biostratigraphy and faunal logs of trilobite and small shelly fossil occurrence can be found in Myrow et al. (2006b), Peng *et al.* (2009) and Gilbert et al. (in review).

PO1 is from loose debris below the base of the Parahio Formation section, and contain shell accumulations of *Eoobolus wanniecki* (Redlich). The material was collected along the path at N 32° 02.072’, E 077° 55.649’. It likely originated from rocks stratigraphically above the trace fossil locality exposed at the Khemangar riverbank (see Hughes et al., 2013).

Sample PO3 is at 78.07 m in the section is near the top of Cambrian Stage 4. *Haydenaspis parvatya* Biozone (N 32° 02.700’, E 077° 54.532’ at 3918 m altitude). The
brachiopod assemblage from the sample includes Aksarinaia? sp., Schizopholis napuru (Kruse), Eohadrotreta haydeni sp. nov. and Paterina sp.

Sample PO15 is at 439.44 m in the section. It corresponds to the lower part of Cambrian Stage 5, Kaotaia prachina Biozone (N 32° 02.718’, E 077° 54.750’ at 4104 m altitude). The brachiopod assemblage from the sample includes Acrothele vertex Reed, Eohadrotreta haydeni sp. nov. and Oepikites? haimantensis (Reed).

A collection was also made at 580.2 m in the section, from Hayden’s level 4 and contains only Linnarssonia parahioensis (Reed).

Sample PO21 is from the limestone bed at 765.14 m in the section. It corresponds to the Cambrian Stage 5, Paramecephalus defossus Biozone, Hayden/Reed Level 6 collection inferred to be collected in shales at this level (N 32° 02.393’, E 077° 55.595’ at 4494 m altitude). The brachiopod assemblage from the sample includes Acrothele vertex Reed, Aphelotreta khemangarensis sp. nov., Linnarssonia parahioensis (Reed) and Oepikites? haimantensis (Reed).

Sample PO25 is at 776 m in the section, it is at the same locality as PO21, just a few meters higher in the section. It corresponds to the Cambrian Stage 5, Paramecephalus defossus Zone, which is Hayden/Reed Level 6. The brachiopod assemblage from the sample includes Hadrotreta timchristiorum sp. nov. Paterina? suspicosa Aksarina and Acrothele? praetans (Reed).

Sample PO32 is at 835.66 m, Cambrian Stage 5, Oryctocephalus salteri Biozone (N 32° 02.690’, E 077° 55.099’ at 4448 m altitude). Middle Taijianian of South China, late early or early Late Templetonian. The brachiopod assemblage from the sample includes Acrothele vertex Reed and Hadrotreta timchristiorum sp. nov.
Sample PO31, is at 836.36 m, Cambrian Stage 5, *Oryctocephalus salteri* Biozone, at the same location as PO32. PO 31 is Hayden level 9. The brachiopod assemblage from the sample includes *Acrothele vertex* Reed and *Amictocracens teres* Henderson and MacKinnon. Sample PO13, collected from the south side of the Parahio River at N 32° 01.921’, E 077° 56.944’ at 3642 m altitude, which also contains *Acrothele vertex* Reed is considered to be correlative with PO31.

Sample PV917.47 is from small block of limestone at 917.47 m in the section. It corresponds to the Cambrian Stage 5. It contains numerous shell fragments which belong to *Acrothele vertex* Reed and *Oepikites? haimantensis* (Reed).

Sample PO9 from limestone bed at 1242.4 m in the Parahio Formation section and was collected at N 32° 01.593’, E 077° 57.135’ at 3915 m altitude) it corresponds to the Cambrian Stage 5 and represents a highest fossiliferous level in the sequence. The brachiopod assemblage from the sample includes *Acrothele vertex* Reed, *Oepikites? haimantensis* (Reed), *Amictocracens? brocki* sp. nov. and *Prototreta? sumnaensis* sp. nov.

*Other Himalayan localities bearing Cambrian brachiopods.* Although brachiopods have been mentioned to occur in the upper part of the Martoli Formation of the Gori Valley, Kumaon Tethyan Himalaya (Jamwal and Kacker, 1989) none have been described. The location and systematics of late Cambrian *Billingsella cf. tonkiniana* from Bhutan was provided by Hughes et al. (2010). There shell beds of phosphatic brachiopods also occur in the underlying Maneting Formation (Tangri and Pande, 1995), but material N.C.H. collected was preserved too poorly to permit identification.
APPENDIX 2

Cambrian Stage 4, ‘Botsfordia-Schizopholis faunas’

A1. Gondwana; Antarctica, King George Island (South Shetland Islands), glacial erratics in the Early Miocene Cape Melville Formation (Holmer et al. 1996); *Eoobolus*, *Schizopholis*, *Vandalotretia*.


A4. Laurentia, North-East Greenland, Bastion and Ella Island formations (Skovsted and Holmer 2005); *Botsfordia*, *Eoobolus*, *Micromitra*, *Vandalotretia*.

A5. South China, Shaanxi Province, Guojiaba and Xiannüdong formations (Li and Holmer 2004); *Eohadrotretia*, *Eoobolus*, *Kyrshabaktella*, *Palaeobolus*, *Lingulellotreta*.


A7. Australasian segment of Gondwana; South Australia, Parara and Ramsey limestone formations (Ushatinskaya and Holmer 2001); *Eoobolus*, *Kyrshabaktella*, *Schizopholis*, *Vandalotretia*.

A8. Sub-Himalaya; *Botsfordia*, *Eoobolus*, *Neoobolus*, *Schizopholis*, *Wynnia*.

Transitional ‘Eothele faunas’

B1. Laurentia, Canada, Mackenzie Mountains, Dyeran (Bonnia-Olenellus zone), Laurentia (Voronova et al. 1988); Palaeoschmidtites, Linnarssonia, Eothele, Micromitra, Paterina.’


B3. Australasian segment of Gondwana; western New South Wales, Coonigan Formation (Roberts and Jell 1990), Eothele, Hadrotreta, Kleithriatreta, Dictyonina, Micromitra, Eoobolus (=Palaeoschmidtites), Oepikites (?) (=Lingulella), Westonia.

B4. Australasian segment of Gondwana; north-western New South Wales, Wydjah Formation (Pimpira Member) (Brock and Percival 2006); Dictyonina, Eothele, Eoobolus, Micromitra, Prototreta.


B6. Laurentia, late Dyeran – early Delamaran, Nevada, Pioche Shale (Rowell 1980), and Harkless Formation (Skovsted and Holmer 2006); Dictyonina, Eothele, Hadrotreta.

B7. Laurentia, Nevada, Harkless Formation (Skovsted and Holmer 2006); Eothele, Kyrshabaktella, Hadrotreta.

Cambrian Stage 5, ‘Acrothele faunas’
C1. Karatau-Naryn microplate; Malyi Karatau Range, *Pernopsis? ultimus* and *Pychagnostus intermedius* biozones (Holmer et al. 2001); *Aksarinaia, Akmolina?*, *Canalilatus, Kotylotreta, Kyrshabaktella, Linnarssonia, Prototreta, Schizopholis, Stilpnotreta*.

C2. North Tien-Shan microplate, Kargaily Formation (Holmer et al. 2001); *Anabolotreta?*, *Canalilatus, Canthylotreta, Kleithriatreta, Kotylotreta, Kyrshabaktella, Neotreta, Paterina*.


C4. Novaya Zemlya; Southern Island, Astafiev Formation (Popov 1985); *Hadrotreta, Acrothyra, Acrothele*.

C5. Laurentia; Utah, Pioche Shale (Rowell 1980); *Acrothele, Acrothyra, Aphelotreta, Micromittra*.

C6. Avalonia; New Brunswick (Walcott, 1912); *Acrothele, Acrothyra, Botsfordia, Eoobolus, Palaeobolus*.

C7. Western Mediterranean peri-Gondwana; Spain, Láncara Formation (Wotte and Mergl 2007), Murero Formation (Liñán and Mergl 2001); *Acrothele, Dictyonina, Genetreta, Iberotreta, Luhotreta, Micromittra*.

C8. Baltica, Sweden, Forsemölla Limestone Bed and erratic boulders (Streng 1999, Streng et al. 2008), and Sablinka Formation (Gertovo Member) (Khazanovich et al. 1984); *Acrothele, Canalilatus, Eoobolus, Monophtalma, Kotylotreta, Linnarssonia, Obolus, Oepikites, Vandalotreta*. 


C11. Spiti, Tethyan Himalaya; Parahio Formation, Unnamed Cambrian Stage 5; *Acrothele, Amictocracens, Aphelotreta, Eohadrotreta, Hadrotreta, Linnarssonia, Oepikites?, Paterina, Prototreta.*

FIG. 1. Lithotectonic belts of the Himalaya and the positions of the six outcrop regions discussed herein.

FIG. 2. Locations of Cambrian fossil localities discussed herein in the western Himalaya.
GK Mahal = Gopi Chandka Mahal.

FIG. 3. Composite stratigraphic section of the Cambrian rocks of the Parahio Formation in the Parahio Valley with brachiopod taxa occurrence shown, local brachiopod biozonation scheme outlined and related to existing trilobite biozonation (Peng et al., 2009). 4 and 5 refer to the un-named, informal stages of the Cambrian System. Here we represent the boundary between them at the estimated position of Oryctocephalus indicus. Sh indicates shale, st indicates silt, vfs and fs indicate very fine sandstone and fine sandstone respectively, and carb indicates carbonate.

FIG. 4. Chart showing heights in measured sections of collections in the Parahio Formation, and their relationship to the Hayden (1904)/Reed (1910) levels. Some collections that are mentioned in the text whose precise heights are not well constrained are omitted.

Note that trilobite and brachiopod zones additional to those shown in Fig. 3 are proposed based on the Salt Range and Zanskar successions.

**FIG. 6.** A, B, Results of the pair-group cluster analysis for presence-absence data (Raup- Crick similarity) for the Cambrian linguliform genera (Cambrian Stages 4 and 5) from 26 localities (for details see the Appendix 2); and C, palaeogeographical reconstruction for the Cambrian Stage 4 showing geographical distribution of the localities used in cluster analysis. Relative position of major Early Palaeozoic continents (e.g. Laurentia, Baltica, Gondwana and Siberia) mainly after Cocks and Torsvik (2002) with significant emendations for Australasian peri-Gondwana.

**FIG. 7.** A-J, *Aksarinaia?* sp., Parahio Formation, *Haydenaspis parvatya* Biozone, sample PO-3 (78.07 m above the base of Parahio Valley section), north side of Parahio River, Spiti region, Kashmir; A, B, E, WIMF/A/3751, ventral valve interior, oblique lateral view of interior, posterior part of the shell showing pseudointerarea and pedicle groove; C-D, WIMF/A/3752, dorsal valve interior, pseudointerarea; F-H, WIMF/A/3753, ventral valve exterior, smooth larval shell, enlargement of the anterior shell margin showing smooth surface with occasionally developed faint growth lamellae; H, WIMF/A/3754, dorsal valve exterior; I, WIMF/A/3755, incomplete ventral valve of juvenile specimen showing smooth larval shell. J, WIMF/A/3756, incomplete ventral valve exterior; K, WIMF/A/3757, dorsal valve interior; L, WIMF/A/3758, incomplete dorsal valve exterior; M-T, *Oepikites? haimantensis* (Reed, 1910), Parahio Formation, north side of Parahio
River, Spiti region, Kashmir; M, N, WIMF/A/3759, dorsal valve interior, oblique lateral view of interior; O, P, WIMF/A/3760, exterior of ventral valve fragment, enlarged shell surface; all from sample PO-9 (1242.4 m above the base of Parahio Valley section); Q, WIMF/A/3761, incomplete ventral valve exterior; R, WIMF/A/3764, incomplete dorsal valve interior; S, WIMF/A/3762, incomplete ventral valve interior, all specimens from sample PO-15 (439.44 m above the base of Parahio Valley section), *Kaotaia parchina* Biozone; T, WIMF/A/3766, ventral view of a pair of conjoined valves, sample at 917.47 m above the base of Parahio Valley section.

**FIG. 8.** A, B, *Notiobolus? kashmiricus* (Reed, 1934), Nutunus Formation, 1.75 miles WNW of Wadapur, Kashmir, India; A, GSI 15626 (=CMCIP 71495), partly exfoliated ventral valve exterior; B, GSI 15627 (=CMCIP 71494), lectotype, partly exfoliated ventral valve; scale bars are 1 mm. C-L, *Oepikites? haimantensis* (Reed, 1910); 5-8, 10, Parahio, Parahio Formation; C, WIF/A591, exfoliated dorsal valves; D, WIF/A598, dorsal valve interior; E, WIF/A331, ventral valve exterior; all from sample PO-21 (765.14 m above the base of Parahio Valley section), *Paramecephalus defossus* Biozone, Hayden’s (1904) level 6; F, GSI 9902 (=CMCIP 71499), incomplete dorsal valve interior; G, GSI 9901, dorsal valve exterior; H, GSI 9900 (=CMCIP 71497), dorsal valve exterior; I, GSI 9906, incomplete dorsal valve exterior; J, GSI 9899 (=CMCIP 71496), lectotype, dorsal valve exterior; all from *Paramecephalus defossus* Biozone, Hayden’s (1904) level 6; K, GSI 9908 (=CMCIP 71503) (illustrated by Reed, 1910, pl. 6, fig. 16, 16a as *Lingulepis?* sp.), exfoliated ventral valve exterior, Changnu encamping ground; L, GSI 9903 (=CMCIP 71500), ventral valve exterior (lectotype of *Lingulella spitiensis*);
M-O, *Eoobolus wanniecki* (Redlich, 1899), Parahio Formation, loose sample PO2, from the lower part of Parahio Valley section; M, WIF/A101.1, dorsal valve exterior; N, WIF/A101.2, ventral valve exterior; O, WIF/A101.3, dorsal valve exterior. Scale bars are 1 mm.

**FIG. 9.** A-D, *Eoobolus fuchsi* (Redlich, 1899), Magnesian Sandstone of Khusak; A, USNM 51546a, partly exfoliated ventral valve exterior; B USNM 51546d, exfoliated dorsal valve exterior; C, USNM 51546b, dorsal internal mould of juvenile specimen; D, GSI 7241 (=CMCIP 71505), lectotype, partly exfoliated ventral valve. E, *Eoobolus wanniecki* (Redlich, 1899), Parahio Formation, loose sample PO2, from the lower part of Parahio Valley section; WIF/A101, accumulation of disarticulated valves on the bedding surface. F-H, *Eoobolus?* sp., Sample MG.1, Tal Group; about 1.5 km from Dhaulagiri towards Maldeota, Mussoorie Syncline, Garhwal Himalaya; F, CMCIP 71523, dorsal internal mould, back scatter image; G, CMCIP 71567, ventral internal mould, back scatter image; H, (=CMCIP 71567), exfoliated ventral valve exterior. All scale bars are 1 mm.

**FIG. 10.** A-M. *Eoobolus wanniecki* (Redlich, 1899), Redlichia noetlingi Biozone, Khussak, Salt Range, Pakistan; A, L, GSI 7240a (=CMCIP 71504), lectotype, ventral
valve exterior, enlarged pustulose microornament of postlarval shell; B, USNM 55744a, ventral valve exterior; C, USNM 55744b, ventral valve exterior; D, USNM 51744d, ventral internal mould: E, USNM 51744e, ventral valve interior, F, USNM 51744g, dorsal valve exterior; G, USNM 51744j, dorsal valve interior; H, USNM 55744o, ventral valve exterior; I, USNM 51744h, dorsal valve exterior; J, USNM 51744n, dorsal valve interior; K, USNM 51744m, dorsal internal mould; M, TU Br 1080/33, ventral valve interior; N, TU Br 1080/32, ventral internal mould. O-P, *Eoobolus?* sp., Sample MG.1, Member B, upper Tal Group, about 1.5 km from Dhaulagiri towards Maldeota, Mussoorie Syncline, Garhwal Himalaya; O, CMCIP 71568, dorsal valve exterior, back scatter image; P, CMCIP 71569, ventral internal mould, back scatter image. A-K, N-O, scale bars are 1 mm; L, scale bar is 200 µm.

**FIG. 11.** A-C, E-H, *Eoobolus?* sp., Tal Group; A, GSI 20022 (=CMCIP 71511), ventral valve, sample KT/264, Dhanulti (Tripathi et al. 1984, pl. 1, fig. 15, as *Obolus* sp.); B, GSI 20130 (=CMCIP 71565), ventral valve, sample SM/38, Morora section (Tripathi et al. 1986, fig. 3.8); C, GSI 20010 (=CMCIP 71514), dorsal internal mould, sample KT/264, Dhanulti (Tripathi et al. 1984, pl. 1, fig. 3 as *Obolella* sp.); E, GSI 20009 (=CMCIP 71513), dorsal internal mould, sample KT/266, Dhanulti (Tripathi et al. 1984, fig. 3.2 as *Magnicanalis* sp.); F, GSI 20129 (=CMCIP 71508), ventral external mould, sample SM/37, Morora section (Tripathi et al. 1986, fig. 3.7, as *Lingulella* sp. B); G, GSI 20128 (=CMCIP 71509), dorsal internal mould (SM/37, Tripathi et al. 1986, fig. 3.6, as *Lingulella* sp. A); H, GSI 20019 (=CMCIP 71512), dorsal valve from KT/266 Dhanulti (Tripathi et al. 1984, pl. 1, fig. 12, as *Lingulella cf. haimantensis* Reed). D, Obolidae gen.
et sp. indet. (illustrated by Reed, 1910 as Obolus (Westonia)? sp.), Parahio, Parahio Formation, Oryctocephalus salteri Biozone, Hayden’s (1904) level 9, GSI 9909 (=CMCIP 71570), exfoliated ventral valve exterior. I, Gen. et sp. indet. Obolidea, Tal Group, ‘Calcareous Member’, Ganga River downstream of Kauriyala, GSI 19831 (=CMCIP 71571) (Kumar et al. 1983, pl. 1, figs 1, 2, as Diandongia cf. D. pista Rong, 1974); scale bars are 1 mm. J, Gen. et sp. indet. Obolidea, GSI 20281 (=CMCIP 71572), exfoliated ventral valve (Mathur and Joshi 1989, fig. 8, as Obolopsis sp.); K, Gen. et sp. indet. Obolidea, GSI 20278 (=CMCIP 71573), exfoliated ventral valve (Mathur and Joshi 1989, fig. 5, as Obolella sp.); L, Gen. et sp. indet. Obolidea, GSI 9907 (=CMCIP 71574), Parahio Formation, Hayden’s (1904) level 2 of the Parahio Valley section (Reed 1910, pl. 6, fig. 14 as Lingulella cf. caelata).

**FIG. 12.** Neobolus warthi Waagen, 1885, Cambrian, lower Neobolus beds, Salt Range, Pakistan; A, GSI 3787 (=CMCIP 71535) ventral valve exterior (Waagen 1885, pl. 86 fig. 1 as Davidsonella squama; 1891, pl. 2, fig. 6a, b as Neobolus warthi) from Jutana; B, GSI 3776 (=CMCIP 71529), lectotype, ventral valve exterior (Waagen 1885, pl. 84, fig. 4) from Kiura; C, F, GSI 3777 (=CMCIP 71537), dorsal valve exterior, oblique lateral view (Waagen 1885, pl. 84, fig. 5a, 5b) from Kiura; D, GSI 3786 (=CMCIP 71534), ventral valve interior (Waagen 1885, pl. 85, fig. 6, as Davidsonella linguloides) from Jutana; E, GSI 3783 (=CMCIP 71533), partly exfoliated ventral valve showing submarginal vascula lateralia (Waagen 1885, pl. 85, fig. 3 as Davidsonella linguloides) from Jutana; G, GSI 3785 (=CMCIP 71527), dorsal valve interior (Waagen 1885, pl. 85, fig. 5, as Davidsonella linguloides) from Jutana; H, GSI 3784 (=CMCIP 71540), ventral valve
(Waagen 1885, pl. 85, fig. 4 as Davidsoniella linguloides) from Jutana; I, GSI 3779 (=CMCIP 71538), dorsal valve interior (Waagen 1885, pl. 84, fig. 7) from Kussak; J, TU1080-6, dorsal valve interior (Schindewolf 1955, pl. 14, fig. 3), from Khewra Gorge; K, TUBr 1080-100, dorsal valve exterior (Schindewolf 1955, pl. 14, fig. 7) from Khewra Gorge; L, TUBr 1080-102, ventral valve exterior from Khewra Gorge. Scale bars are 1 mm.

FIG. 13. A, B, Neobolus warthi Waagen, 1885, lower Neobolus beds, Khewra Gorge, Salt Range, Pakistan; back scatter images of TU Br 1080-100, dorsal valve oblique posterior view, umbonal region showing larval shell. C-L, Acrothele vertex Reed, 1910, Parahio Formation, north side of Parahio River, Spiti region, Kashmir; C, WIMF/A/3788, incomplete ventral valve exterior; D, WIMF/A/3787, incomplete ventral valve exterior, sample PO15 at 439.44 m above the base of Parahio Valley section; E, I, WIMF/A/3770, ventral valve exterior, sample PO32 at 836.66 m above the base of Parahio Valley section; F, WIMF/A/3776, incomplete dorsal valve exterior, sample PO-9 at 1242.4 m above the base of Parahio section; G, WIMF/A/3771 oblique view of ventral valve interior, sample PO-32 at 836.66 m above the base of Parahio Valley section; H, WIMF/A/3768, exfoliated ventral valve exterior, sample at 917.47 m above the base of Parahio Valley section; J, WIMF/A/3785. incomplete dorsal valve interior; K, WIMF/A/3784, incomplete ventral valve interior; L, WIMF/A/3782, oblique posterior view of juvenile specimen showing delthyrium; all from sample PO-9 at 1242.4 m above the base of Parahio Valley section. A, scale bar is 1 mm, B-L, scale bars are 200 μm.
**FIG. 14.** A, B, K, *Acrothele vertex* Reed, 1910, Parahio Formation, north side of Parahio River, Spiti region, Kashmir; A, GSI 9912 (=CMCIP 71544), exfoliated ventral valve (Reed 1910, as *Obolella* cf. *crassa* (Hall), pl. 6, figs 23, 24); B, GSI 9917 (=CMCIP 71543), lectotype, ventral valve exterior, Hayden’s (1904) level 9, *Oryctocephalus salteri* Biozone; K, WIF/A595, ventral valve exterior, sample PO-21 (at 765.14 m above the base of Parahio Valley section), *Paramecephalus defossus* Biozone. C, *Acrothele? praetans* Reed, 1910, Parahio Formation, Hayden’s (1904) level 6, *Paramecephalus defossus* Biozone, north side of Parahio River, Spiti region, Kashmir; GSI 9915 (=CMCIP 71541), holotype, ventral valve exterior. D, *Schizopholis napuru* (Kruse, 1990), from Parahio Formation, *Haydenaspis parvata* Biozone, sample PO-3 at 78.07 m above the base of Parahio Valley section, Kashmir; WIF/A1057, ventral valve exterior. E-J, L, *Schizopholis rugosa* Waagen, 1885; Lower *Neobolus* beds, Salt Range, Pakistan; E, TU1060/14, dorsal internal mould from Kussak; F, TU1080/103, ventral valve exterior from Kussak; G, L, GSI 3792 (=CMCIP 71578), ventral valve, enlarged umbonal area, ventral view (Waagen 1885, pl. 86, fig. 6; 1891, pl. 2, fig. 16, as *Discinolepis granulata*) from Jutana; H, TU1080/107, ventral valve exterior from Kussak; I, GSI 3789 (=CMCIP 71579), ventral valve exterior; J, GSI 3790 (=CMCIP 71575), lectotype, ventral valve exterior from Kiura; N, GSI 3791 (=CMCIP 71577), ventral valve exterior (Waagen 1885, pl. 86, fig. 3a, b) from Kiura. O, P, *Botsfordia granulata* (Redlich, 1899), *Redlichia noetlingi* Biozone, indeterminate locality, Eastern Salt Range, Pakistan; O, GSI 7244 (=CMCIP 71547), dorsal valve interior (illustrated by Redlich, 1899, pl. 1, fig. 13, as *Mobergia granulata*), P, GSI 7234 (=CMCIP 71548), dorsal valve. A-F, G-P, Scale bars are 1 mm. G, Scale bar 0.5 mm.
FIG. 15. *Acrothele vertex* Reed, 1910, Parahio Formation, north side of Parahio River, Spiti region, Kashmir; A-H, *Haydenaspis parvatya* Biozone, sample PO-9, at 1242.4 m above the base of Parahio Valley section; I-P, sample PO-31 at 836.36 m above the base of Parahio section; A-C, WIMF/A/3786, ventral valve, enlarged view of pustulose microornament, ventral view, oblique lateral view of exterior; D-F, WIMF/A/3787, ventral valve of juvenile specimen, pitted microornament of larval shell, exterior, umbonal area showing larval shell; G, WIMF/A/3788, incomplete ventral valve exterior; H, WIMF/A/3789, dorsal valve exterior; I, L, WIMFA3793, incomplete ventral valve exterior, umbonal area showing larval shell; J, K, WIMFA3792, incomplete dorsal valve interior, oblique posterior view of interior; M-P, WIMFA3791, juvenile dorsal valve, umbonal area, oblique anterior, oblique lateral and dorsal views.

FIG. 16. A-I, *Botsfordia granulata* (Redlich, 1899); Cambrian, *Redlichia noetlingi* Biozone, Khussak, Salt Range, Pakistan; A, TU Br 1080-50, dorsal valve exterior; B, TU Br 1080-3g, ventral valve exterior; C, TU Br 1060-2, ventral internal mould; D, E, TU Br 1060-3, latex cast of dorsal interior, dorsal internal mould; F, TU Br 1060-3b, ventral internal mould; G-I, GSI 7242 (=CMCIP 71546), lectotype, ventral valve exterior, umbonal area, enlarge shell surface with pustulose microornament. J-L, *Acrothele*? sp., Parahio Formation, Purni, Zanskar valley; J, WIF/A1058, dorsal valve, sample PI18; K, WIF/A1059, dorsal internal mould, sample PI4; L, WIF/A1060, composite mould of dorsal valve, sample PI9. Scale bars are 1 mm. M, *Botsfordia* sp., Member, B upper Tal
Group; J, M, GSI 20124, dorsal internal mould, sample, SM/38A, Morora section
(Tripathi et al. 1986, fig. 3.2, as Magnicanalis sp.). Scale bars are 1 mm.

**FIG. 17.** *Schizopholis napuru* (Kruse, 1990), from Parahio Formation, *Haydenaspis parvatia* Biozone, sample PO-3 at 78.07 m above the base of Parahio Valley section, Kashmir; A, B, E, K WIMF/A/3800, ventral valve, exterior, oblique posterior and lateral view, umbonal area showing larval shell; C, WIMF/A/3801, ventral valve interior, D, G, WIMF/A/3802, ventral valve, lateral and ventral view; F, I, WIMF/A/3803, dorsal valve exterior; H, WIMF/A/3804, dorsal valve interior; J, WIMF/A/3805, dorsal valve exterior. A-J, scale bars are 200 µm; K, scale bar is 50 µm.

**FIG. 18.** *Amictocracens teres* Henderson and MacKinnon, 1981, A-I, Parahio Formation, *Oryctocephalus salteri* Biozone, sample PO-31 at 836.36 m above the base of Parahio Valley section; J, K, Georgina Basin, New South Wales, Australia; A, WIMF/A/3806, ventral valve umbonal region showing pedicle foramen within larval shell, oblique side view and oblique posterior view; B-D, WIMF/A/3807, ventral umbonal region showing larval shell with partly preserved pitted microornament; E, WIMF/A/3808, ventral valve exterior; F, G, WIMF/A/3809, dorsal valve interior, oblique lateral view showing blade-like triangular septum; H, WIMF/A/3810, incomplete dorsal valve exterior; I, WIMF/A/3811, oblique lateral view of ventral valve interior showing apical process; J, SAM L936-03, dorsal valve interior; K, SAM L936-01, pitted ornament of dorsal larval shell.
**FIG. 19.** *Amictocracens? brocki* sp. nov.; from Parahio Formation, sample PO9 at 1242.4 m above the base of Parahio Valley section; A, WIMF/A/4045, dorsal valve exterior; B, C, WIMF/A/3812, holotype, dorsal valve interior, oblique lateral view of interior; D, G, WIMF/A/3813, dorsal valve exterior, pitted ornament of larval shell; E, WIMF/A/3814, oblique lateral view of dorsal valve interior; F, WIMF/A/3815, dorsal valve interior; H, I, WIMF/A/3817, articulated shell, view of dorsal umbonal area showing pitted microornament of larval shell, oblique posterior view; J, WIMF/A/3818, oblique lateral view of juvenile dorsal valve with upper septal rod; K, WIMF/A/3819, oblique lateral view of dorsal interior.


**FIG. 21.** *Aphelotreta khemangarensis* sp. nov., Parahio Formation, *Paramecephalus defossus* Biozone, sample PO-21 at 765.14 m above the base of Parahio Valley section; A-C, F, I, WIMF/A/3826, holotype, articulated shell dorsal view, side view, posterior view, pitted microornament of larval shell; D, E, WIMF/A/3827, dorsal larval shell,

**FIG. 22.** *Eohadrotreta haydeni* sp. nov., Parahio Formation; A-E, G, H, *Kaotaia prachina* Biozone, sample PO15 at 439.44 m above the base of Parahio Valley section, F, I-M, *Haydenaspis parvatia* Biozone, sample PO3 at 78.07 m above the base of Parahio Valley section; A, WIMF/A/3838, dorsal valve exterior; B, C, WIMF/A/3839, dorsal valve exterior, pitted ornament of larval shell; D, WIMF/A/3837, holotype, ventral valve interior; E, WIMF/A/3840, ventral valve exterior; F, I, J, WIMFA3851, ventral valve exterior, oblique lateral, oblique posterior and dorsal views; G, WIMF/A/3841, ventral valve side view; H, WIMF/A/3842, dorsal valve interior; K, WIMF/A/3852, ventral valve interior; L, WIMF/A/3853, dorsal valve exterior; M, WIMF/A/3854, dorsal valve interior. A, B, D-M, scale bars are 100 µm.

**FIG. 23.** *Hadrotreta timchristiorum* sp. nov., Parahio Formation; A-G, *Paramecephalus defossus* Biozone, sample PO-25, at 776 m above the base of Parahio Valley section; H, N-V, *Oryctocephalus salteri* Biozone, sample PO-32, at 835.66 m above the base of Parahio Valley section; A, B, WIMF/A/3862, dorsal valve exterior, oblique lateral view; C, WIMF/A/3863, oblique lateral view of dorsal valve interior; D, WIMF/A/3864, ventral valve exterior; E, WIMF/A/3865, oblique lateral view of ventral valve exterior; F, WIMF/A/3866, ventral valve interior; H, WIMF/A/3867, oblique lateral view of ventral valve interior; I, WIMF/A/3880, oblique posterior view ventral valve umbonal area; J, WIMF/A/3868, ventral
valve interior; K, R, WIMF/A/3881, pitted microornament of larval shell, dorsal umbonal region showing larval shell; L, Q, WIMF/A/3869, ventral valve exterior, oblique posterior view; M, P, WIMF/A/3870, oblique lateral view of dorsal interior, enlarged view of dorsal interarea and cardinal muscle fields; N, WIMF/A/3871, dorsal valve exterior, oblique posterior view; O, WIMF/A/3872, dorsal valve exterior; S, WIMF/A/3882, ventral valve interior; T, WIMF/A/3883, ventral valve side view; U, WIMF/A/3873, dorsal valve interior; V, WIMF/A/3874, dorsal valve interior.

**FIG. 24.** *Linnarssonia parahioensis* (Reed, 1910); Parahio Formation, *Paramecephalus defossus* Biozone, sample PO-21, Hayden’s (1904) level 6, Parahio Valley, Parahio Formation, at 765.14 m above the base of Parahio Valley section. A, H, WIMF/A/3884, ventral valve lateral view, oblique posterior view; B, C, E, F, WIMF/A/3885, oblique side view, umbonal area showing larval shell, oblique posterior view, pitted microornament of larval shell; D, G, WIMF/A/3886, dorsal valve interior, oblique lateral view of interior; I, J, WIMF/A/3887, ventral valve oblique posterior view, side view of interior; K, GSI 9910b (=CMCIP 71551), GSI 9910c (=CMCIP 71552), dorsal valves; L, GSI 9910d (=CMCIP 71553), oblique lateral view of dorsal valve exterior; M, GSI 9910e (=CMCIP 71554), exfoliated dorsal valve showing long median septum; N, GSI 9910a (=CMCIP 71550), lectotype, ventral valve exterior.

**FIG. 25.** Prototreta? *sumnaensis* sp. nov., Parahio Valley, Parahio Formation, sample PO-9 at 1242.4 m above the base of Parahio Valley section; A, WIMF/A/3889, dorsal valve exterior; B, WIMF/A/3890, ventral valve exterior; C, WIMF/A/3891, dorsal valve
interior; D, WIMF/A/3892, ventral valve interior; E, I, J, WIMF/A/3893, ventral valve; oblique posterior view, side view, posterior view of umbonal area showing pedicle foramen; F, G, WIMF/A/3888, holotype, articulated shell oblique lateral view, posterior view of dorsal umbonal area; H, WIMF/A/3894, oblique lateral view of dorsal valve interior showing blade-like triangular median septum with upper rod; K, M, WIMF/A/3895, dorsal valve exterior, oblique posterior view of exterior; L, WIMF/A/3896, ventral valve posterior view showing pedicle foramen crossing boundary of larval shell.

**FIG. 26.** A-E, H, L, O, Wynnia warthi (Waagen, 1891), Cambrian, lower Neobolus Beds, Salt Range, Pakistan; A, GSI 4122 (=CMCIP 71555), internal mould of ventral valve, a.s. - adductor muscle scar, **v.m.** - *vascula media*, **v.a.** - *vascula arcuata*, Chél Hill; B, GSI 4124 (=CMCIP 71556), internal mould of dorsal valve, Chél Hill; C, O, GSI 4125 (=CMCIP 71557), juvenile specimen internal mould ventral and dorsal views, Chél Hill; D, E, H, L, Tu Br 1080/110, internal mould, dorsal, oblique posterior and ventral views, Fort Khussak; scale bars are 1 mm. F, G, I, P, Q, *Paterina? suspicosa* Aksarina, 1975, Parahio Formation, sample PO-25 at 776 m above the base of Parahio Valley section; F,
G, I, WIM/F/A3798, dorsal valve exterior, interior, oblique lateral view; P, Q, WIM/F/A3797, ventral valve interior, exterior; scale bars are 200 µm. J, K, M, N, *Paterina* sp, Parahio Formation, *Haydenaspis parvatya* Biozone, sample PO-3 at 78.07 m above the base of Parahio Valley section, north side of Parahio River, Spiti region, Kashmir; WIMF/A/3799, dorsal valve lateral, oblique posterior and dorsal, views, dorsal umbonal area showing larval shell; F, G, I; scale bars are 200 µm; J, scale bar is 100 µm.
<table>
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<tr>
<th>Stage</th>
<th>Trilobite Zone</th>
<th>Purni section, Zanskar Valley, Ladakh</th>
<th>Parahio section, Parahio Valley, Spiti</th>
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<td>Drumian</td>
<td>Sudanomocarina sinindica Level</td>
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<td>Iranoleesia butes Level</td>
<td>1050m 917.47m PV917 Level 13</td>
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<td>Oryctocephalus indicus Level</td>
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<td>Stage 4</td>
<td>Haydenaspis parvatiya Level</td>
<td>78.07m P03</td>
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**TRILOBITE ZONES**

- **FURONGIAN**
  - Jiangshanian
    - Kaoliuhania granulosa Zone

- **Guzhangian**
  - Proagnostus bulbus Zone
  - Lejopyge acanthra Zone

- **Drumian**
  - Sudanomocarina sinindica Zone
  - T. butes Level
  - Oryctocephalus saltleri Zone
  - Parmecophalus defossus Zone
  - Kaotaia prachina Zone
  - Oryctocephalus indicus Level
  - Haydenaspis parvata Level

- **Stage 5**
  - Hadrotetra timchristiorum Zone
  - Prototreta? sumnaenensis Level

- **Stage 4**
  - Redlichia noettingi Zone
  - Botsfordia granulata Zone

**BRACHIODOP ZONES**

- **Salt Range**
  - Pohru Valley, Kashmir
    - L. parahioensis Zone

- **Zanskar Valley, Ladakh**
  - Acrothele vertex

- **Parahio Valley, Spiti**
  - Notiobolus? kashmiricus

**Krol-Tal Belt**

- **Black Mountain, Bhutan**

**Other Formations**

- **Quartzite Formation**
  - Billingsella cf. tonkiniana

- **Parahio Formation**
  - Eoobolus wanniecki
  - Eoobolus fuchsi

- **Schizopholis Formation**
  - Schizopholis rugosa

- **Botsfordia? sp.**

- **Paterina? sp.**

- **Aksarina? sp.**

- **Ophelotreta? sp.**

- **Eohadrotetra haydeni** new species

- **Amictocracens? brocki** new species

- **L. parahioensis Zone**

- **Khussak Formation**

- **Lolab Formation**

- **Jutana Formation**